

Ontogenesis of the attachment ability in the bug *Coreus marginatus* (Heteroptera, Insecta)

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Summary

Each tarsus of *Coreus marginatus* L. (Coreidae) bears a pair of smooth flexible pulvilli adapted for attachment to relatively smooth surfaces, such as their host plant *Rumex crispus* L. (Polygonaceae). This account quantifies insect attachment abilities on smooth surfaces at various stages of ontogenesis. Friction (shear) force (FF) of adults and juvenile insects was measured by the use of a computer controlled centrifugal force tester equipped with a fibre optical sensor. Pad area, body size and body mass were determined individually for each experimental insect. Light microscopy revealed no difference in pulvilli area between different leg pairs. Pulvilli area demonstrated a stronger increase with increasing linear dimensions, as predicted by scaling laws. Since friction coefficient (relationship between FF and body weight) (FC) was always higher than 1, it was concluded that adhesion has strongly contributed to the measured friction. The

frictional properties of pulvilli do not change during ontogenesis. Thus, only the growth of pulvilli and, therefore, the increased contact area, contribute to the increasing attachment ability in insects at later larval stages. Due to different scaling of the body mass and area of attachment organs, smaller insects attach relatively more strongly. Both FF and FC were higher in experiments in which higher angular acceleration (AC) was applied. Lateral tenacity determined individually for experimental insects and pooled for all animals and accelerations is 0.097 N m^{-2} . These data led us to suggest that viscosity of the pad secretion and/or visco-elastic properties of the foam-like material of pulvilli play an important role in the attachment ability of insects.

Key words: friction, adhesion, cuticle, pulvilli, attachment, Insecta, *Coreus marginatus*.

Introduction

Many insects bear leg attachment pads that have an excellent ability to adhere to a smooth surface. There are two alternative designs of such systems (Gorb and Beutel, 2001; Beutel and Gorb, 2001). Pads of flies, beetles and earwigs are covered by relatively long deformable setae which, due to the individual bending, increase the number of contact points with the surface. The second type of pads, so-called smooth systems, such as arolia and euplantulae, occurring in cockroaches, bees, grasshoppers and bugs, are soft deformable structures with a relatively smooth surface (Jiao et al., 2000). Pads of this type are composed of a very compliant material, which adapts to the surface profile and can increase the area of real contact (Gorb et al., 2000b). There is also evidence that the non-volatile pad secretion is an essential factor for attachment to smooth substrata with both types of systems (Edwards and Tarkanian, 1970; Dixon et al., 1990; Vötsch et al., 2002).

Attachment forces on smooth surfaces have been previously

measured on the hairy adhesive pads of reduviid bugs (Edwards and Tarkanian, 1970), flies (Walker et al., 1985; Gorb et al., 2001a), beetles (Stork, 1980; Ishii, 1987), and on the smooth pads of cockroaches (Roth and Willis, 1952), aphids (Lees and Hardie, 1988; Dixon et al., 1990), grasshoppers (Jiao et al., 2000; Gorb and Scherge, 2000) and ants (Federle et al., 2000). Until recently, less attention has been paid to the scale effects on attachment systems used in locomotion. Relationships between attachment force and body mass has been studied in the hairy attachment systems of the beetle *Chrysolina polita* (Stork, 1980), arboreal ant species (Federle et al., 2000) and syrphid flies (Gorb et al., 2001a). These results showed that attachment force increases with an increased body mass, but the ratio between the attachment force and body weight decreases.

How attachment ability of an insect develops during ontogenesis is the fundamental question for understanding scaling effects on design and performance of biological

attachment systems. In hemimetabolic insects, the size of attachment structures gradually increases during their larval growth and, therefore, should be optimised according to their mass in each larval instar. Attachment abilities may be tuned in two ways: (1) by changing the size of attachment pads, and (2) by changing the adhesive properties of the pad material and/or secretion. Which is realised in real systems, however, has remained unknown.

This study was undertaken to understand the relationships between the body mass, body size, pad area and attachment performance in a heteropteran insect species during ontogenesis. The approach has two great advantages. It allows us to discover how an animal's adhesive mechanisms keep up with the increases in mass that result from growth, and also can shed light on underlying mechanisms of adhesion. The tarsus of the bug *Coreus marginatus* L. (Coreidae) bears a pair of smooth, flexible pulvilli adapted for attachment to smooth surfaces, such as leaf surfaces of their host plant *Rumex crispus* (Polygonaceae). These bugs were ideal for this study because they can be captured in nature simultaneously at various stages of development and they possess semitransparent, round pulvilli on their tarsi, whose area can be measured from the whole-mount preparations. The friction component of the attachment force of adults and larval insects was measured by using a computer-controlled centrifugal device equipped with a fibre optical sensor (Gorb, 2001; Gorb et al., 2001a). In a separate experiment, the effect of angular acceleration on the frictional force was evaluated. The total area of all pads, body size and weight were determined for each individual insect used in experiments.

Materials and methods

Animals and force measurements

Living males and females of the bug *Coreus marginatus* L. were captured in the field near Tübingen, Southern Germany and immediately used in experiments. Prior to the force measurements, the leathery forewings of adults were carefully glued together with a small droplet of melted wax. Force measurements were performed using a centrifugal force tester (Gorb et al., 2001a) (Fig. 1). The insect was placed on the horizontal polished Plexiglas surface of the drum at a rotating speed of 50 rev min^{-1} (0.833 rev s^{-1}). Roughness of the drum surface was determined by the use of the white-light interferometer Zygo New View 5000 (Middlefield, CT, USA), objective $\times 50$, zoom $\times 0.4$, window size $360 \mu\text{m} \times 270 \mu\text{m}$ ($R_a=6.6 \text{ nm}$, $s.d.=1.3$; $R_z=38.2 \text{ nm}$, $s.d.=11.3$; root mean square= 8.1 nm , $s.d.=1.6$, $N=6$).

The position of the insect on the drum was monitored by using a combination of the focused light beam and the fibre-optical sensor. The drum speed was continuously increased until the insect lost its hold on the surface under centrifugal force. The rotational speed at contact loss, position of the insect on the drum (radius of rotation), and the insect mass (determined by weighing on a micro-balance, Mettler Toledo

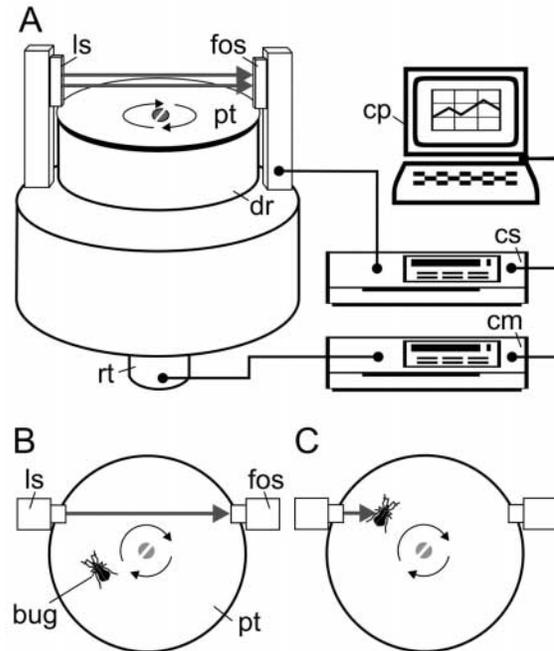


Fig. 1. Computer controlled centrifugal device equipped with a fibre-optical sensor. (A) Scheme of the device. (B,C) Position of the focused light source (ls, sender) and fibre-optical sensor (fos, receiver) relative to the drum centre with an insect rotating on the horizontal drum surface, viewed from above. cm, motor control; cp, computer; cs, sensor control; dr, drum; pt, Plexiglas plate; rt, rotor of the motor.

AG 204 Delta Range, Greifensee, Switzerland) were used to calculate the maximum frictional component of the attachment force. Ten repetitions were done with each individual bug. In order to test the effect of acceleration on the attachment force, two measurements were successively carried out in a separate experiment with each individual bug at accelerations of 1.21 and 12.10 rev s^{-2} .

Microscopy

After the force measurements, pads were fixed in 70% ethanol overnight, cut off, dehydrated in an ascending row of ethanol, and whole mounted in Depex (Serva, Heidelberg, Germany). Pad areas of the whole-mounted pulvilli were measured from digital pictures taken with a Sony 3CCD videocamera mounted on a Zeiss Axioplan light microscope and using AnalySIS (Münster, Germany) software. Measurements were made individually for all 40 insects (480 pulvilli, 12 pulvilli per insect) and studied separately for the fore-, mid- and hindlegs.

For scanning electron microscopy, the tarsi were carefully cut off and fixed in a 2.5% solution of glutaraldehyde in phosphate buffer (pH 7.3). After dehydration in the series of ethanol solutions, the samples were critical point dried, coated with gold-palladium, and observed in a Hitachi-S800 (Tokyo, Japan) scanning electron microscope (SEM) at 20 kV.

Results

Morphology of the attachment organs

Each pretarsus contains a pair of attachment pads called pulvilli, which are rounded cuticular structures connected to the lateral parts of the claws (Fig. 2A). They are probably homologous to the hairy pulvilli of flies (Bauchhenss and Renner, 1977; Bauchhenss, 1979a). However, in contrast to the fly's pads, their ventral surfaces are exceptionally smooth (Fig. 2B,C). Sometimes a pattern of microfolds can be detected on the ventral surface. This is probably a result of the drying procedure. The ventral side of the pulvillus is hemispherical. The dorsal surface contains grooves running radially from the base of the pulvillus. These grooves have been interpreted by previous authors as a fluid transporting system for the adhesive secretion (Hasenfuss, 1977a; Ghasi-Bayat and Hasenfuss, 1980a–c). Another possible function of such pleated surfaces may be an increase of the contact area during contact formation: the dorsal surface may unfold and aid in spreading the ventral part over the surface.

The material structure of the cuticle on the ventral side of

pulvilli is different from that on the dorsal side. On the ventral side, it resembles the rod-like branching architecture, as described for other attachment pads of the smooth type in the grasshopper *Tettigonia viridissima* (Gorb, 2001; Gorb et al., 2000b), locust *Schistocerca gregaria*, plecopterans (Beutel and Gorb, 2001), hymenopterans (Federle et al., 2001; Baur and Gorb, 2001), and cicada *Cercopis vulnerata* (Scherge and Gorb, 2001). A detailed study of the material ultrastructure of the heteropteran smooth pulvilli is currently in progress.

Relationships between insect dimensions, body mass and contact surface

The relationship between the linear dimensions of the insect (head width) and its body mass is given in Fig. 3. Adult bugs have a mass of 79.9 ± 13.8 mg (mean \pm s.d., $N=14$). Taking into account that an insect has six legs and 12 pulvilli, we can consider that in an adult insect, standing on the horizontal drum surface, the average normal force of $66.6 \mu\text{N}$ acts on a single pulvillus. In a walking insect that keeps three legs in the stance phase and the other three legs in the swing phase, this force is

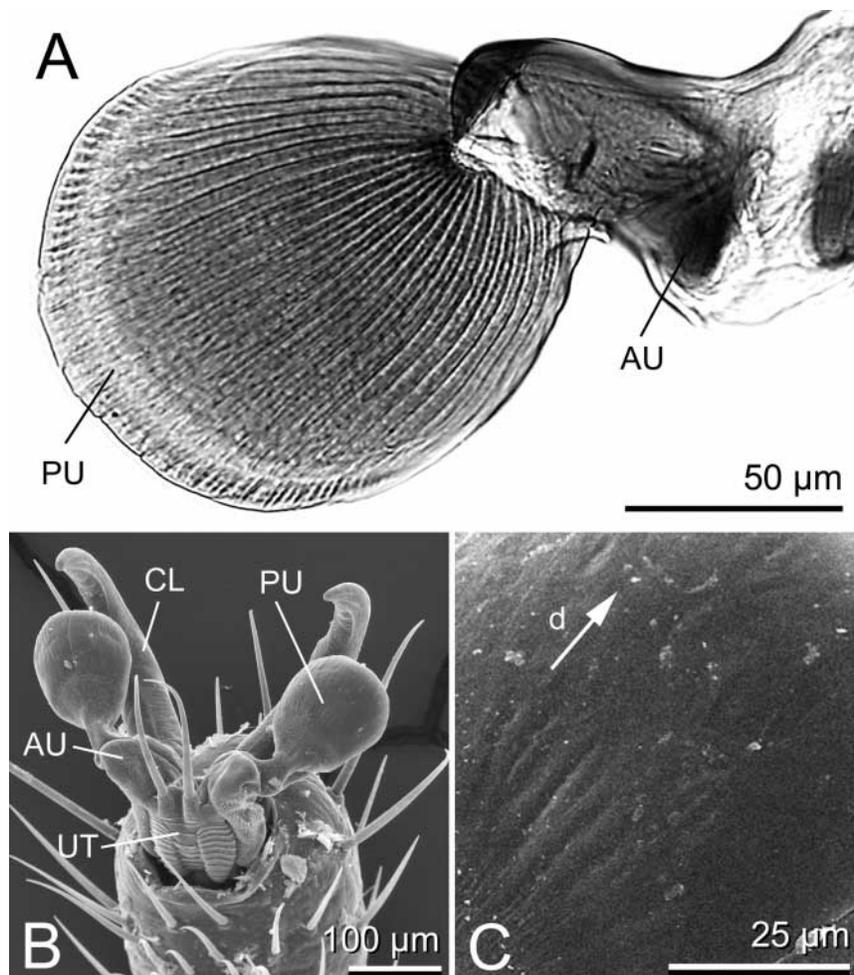


Fig. 2. Pulvilli of adult *Coreus marginatus*. (A) Single pulvillus, light microscopy, phase contrast. Each tarsus bears two pulvilli (PU). (B) Ventro-lateral aspect of the pretarsus with pulvilli, SEM. (C) Detail of the pulvillus surface, SEM. AU, auxiliary sclerite; CL, claw; d, distal direction; UT, unguitactor plate.

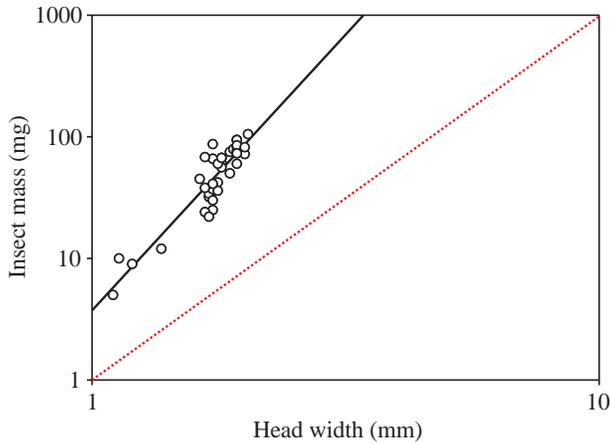


Fig. 3. Mass of individual insects, used for force measurements, versus the head width ($N=40$). Data fit: $a=0.571$, $b=4.538$, $r^2=0.837$, ANOVA: $F=367.9$, $P<0.001$. Red dotted line shows predicted slope for the regression line.

doubled ($\sim 133.2 \mu\text{N}$). In the experimental situation, at a certain rotational speed of the centrifuge ($\sim 200 \text{ rev min}^{-1}$), the insect usually stopped walking and stood on the surface with all six legs.

The pulvillus area increases exponentially with the head width (Fig. 4A) and linearly with the body mass (Fig. 4B). However, there was not an exact correlation between the pulvillus area and body mass, because the mass may fluctuate depending on the physiological state of the insect (hungry, additional mass of eggs in females, etc.) and is not always exactly related to the insect size. Data on the pulvillus area vs. body size are less dispersed.

Friction force dependence on the body mass

Absolute values of measured friction force increased with an increasing body mass (Fig. 5A,B). The friction coefficient (relationship between friction force and body weight) was always higher than 1. It ranged, for averaged data, from 5 to 40 and for maximum data from 7 to 70 under different experimental conditions. These values also show how much of its own weight the insect can hold in the situation of walking on the wall or resist in the shear direction on the horizontal surface.

The frictional coefficient decreased slightly with increasing body mass (Fig. 5C,D). This means that relatively (larger) heavier animals generate relatively lower force. Taking into account that higher load and pressure (Fig. 4C) must positively contribute to measured friction, such an opposite effect can only be explained by adhesion, which plays a considerably greater role in smaller objects than in larger ones (Kendall, 2001), and may promote friction to a relatively higher extent in smaller insects.

Effect of angular acceleration on the friction force

Absolute values of friction force, as well as frictional coefficients, were higher in experiments in which higher

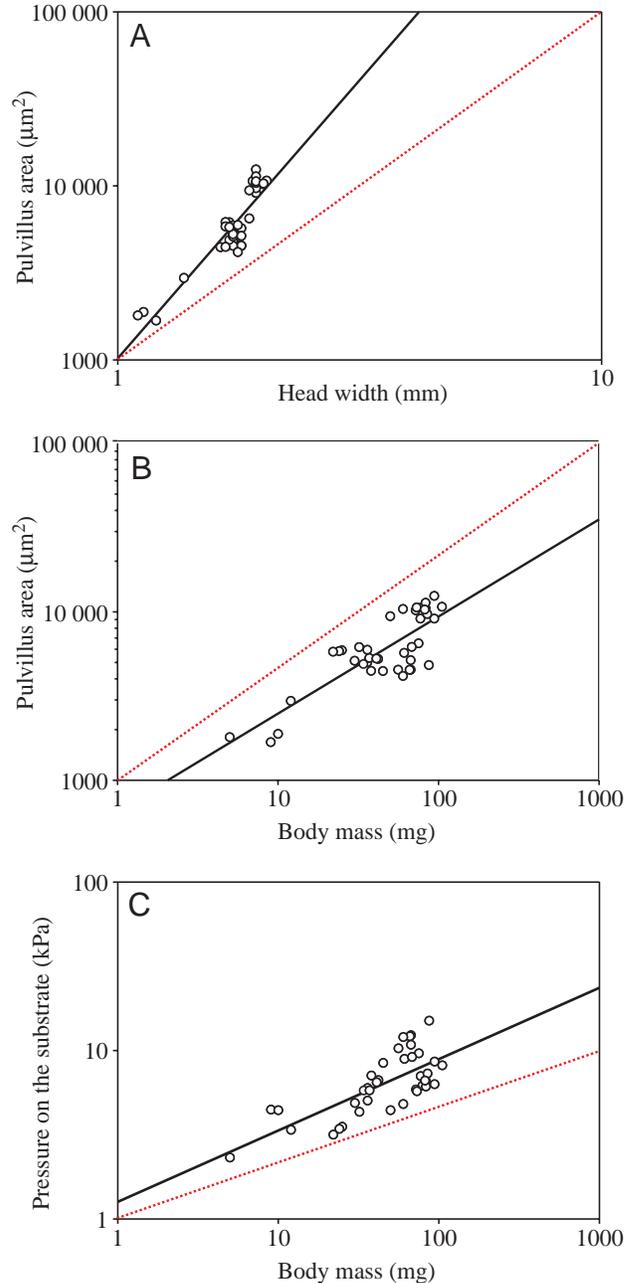


Fig. 4. Dependence of the area of a single pulvillus on the head width (A) and body mass (B) ($N=40$) and dependence of the pressure on the substrate on the body mass (C). Each point represents the average pulvillus area ($N=12$) of an individual insect. In all, 480 pulvilli were measured. (A) Data fit: $a=3.009$, $b=3.197$, $r^2=0.83$, ANOVA: $F=360.0$, $P<0.001$. (B) Data fit: $a=2.820$, $b=0.576$, $r^2=0.67$, ANOVA: $F=150.2$, $P<0.001$. (C) Data fit: $a=0.101$, $b=0.424$, $r^2=0.52$, ANOVA: $F=81.1$, $P<0.001$. Red dotted lines show predicted slopes for regression lines.

angular acceleration was applied (Fig. 5). There is a statistically significant difference between friction measured at different accelerations ($P=0.003$; two-way ANOVA for individuals and accelerations). However, the difference

between forces measured at accelerations differing by one order of magnitude, was in the range of 25–50%. The characteristics of all relationships mentioned in the previous section did not depend on the acceleration applied to experimental animals.

The difference between forces measured at different accelerations is slightly increased with an increasing body mass (Fig. 6A). The difference between frictional coefficient obtained at a higher acceleration and that measured at a lower acceleration slightly decreased with an increasing body mass (Fig. 6B).

Lateral tenacity

Measured force was higher in animals with higher overall area of pulvilli (Fig. 7), indicating that adhesion contributed to the friction force measured. The graphs of the friction force *versus* contact area provide information about the lateral tenacity of the pulvilli material (Fig. 7). Lateral tenacity is determined as friction force divided by the overall area of all pulvilli. This variable was individually measured for experimental insects and pooled for all animals and

accelerations giving $0.097 \pm 0.50 \text{ N m}^{-2}$ (mean \pm s.d., $N=77$). Lateral tenacity was not different for animals with a different pulvilli area [$H=0.640$, d.f.=2, $P=0.726$, Kruskal–Wallis one-way analysis of variance (ANOVA) on Ranks] (Fig. 8). Lateral tenacity was lower for low acceleration experiments ($0.085 \pm 0.39 \text{ N m}^{-2}$, $N=39$) than for high acceleration experiments ($0.109 \pm 0.57 \text{ N m}^{-2}$, $N=39$). The values are significantly different ($P=0.005$, Mann–Whitney rank sum test). Thus, the attachment properties of pulvilli are strongly dependent on the velocity.

Discussion

Since the friction coefficient was always higher than 1, indicating adhesion-mediated friction, an effect well known for elastically soft rubber in contact with relative smooth substrates (Persson, 1998). In other words, we sheared adhesive contact between attachment organs and the drum surface. Similar data have been previously obtained for the hairy attachment system of five species of syrphid flies (Gorb et al., 2001a). The coefficient ranged, for averaged data, from

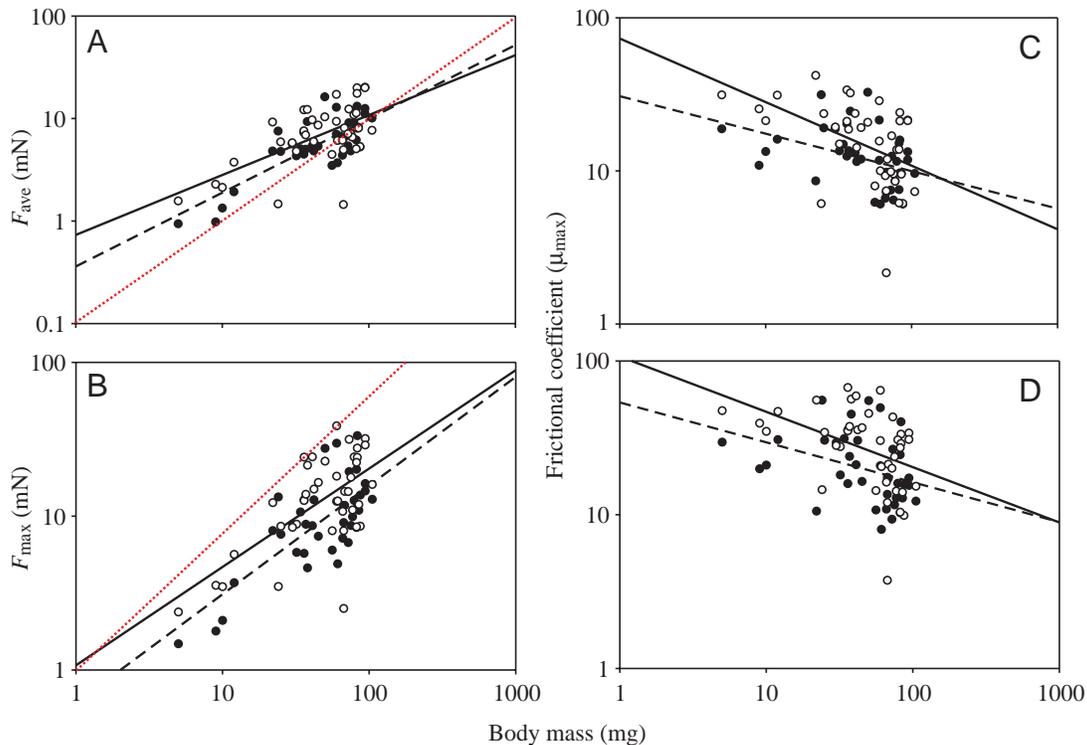


Fig. 5. Dependence of the friction force (F_{friction}) (A,B) and frictional coefficient ($\mu = F_{\text{friction}}/F_{\text{normal}}$) (C,D) on the body mass for individual insects ($N=40$). (A,C) Average values for individual experimental insects. (B,D) Maximum values for individual experimental insects. Data are fitted with the linear regression and the fitted results were compared to the original data using one-way ANOVA. Solid lines and open circles, results of experiments at high acceleration (HAC, 12.1 rev s^{-2}); broken lines and black circles, results of experiments at low acceleration (LAC, 1.21 rev s^{-2}). (A) Average friction (LAC fit data: $a=-0.446$, $b=0.720$, $r^2=0.63$, ANOVA: $F=64.9$, $P<0.001$; HAC data fit: $a=-0.135$, $b=0.585$, $r^2=0.37$, ANOVA: $F=22.0$, $P<0.001$). (B) Maximum friction (LAC data fit: $a=-0.215$, $b=0.707$, $r^2=0.55$, ANOVA: $F=46.4$, $P<0.001$; HAC data fit: $a=0.030$, $b=0.640$, $r^2=0.41$, ANOVA: $F=25.6$, $P<0.001$). (C) Average frictional coefficient (LAC data fit: $a=2.488$, $b=-0.245$, $r^2=0.16$, ANOVA: $F=7.3$, $P=0.010$; HAC data fit: $a=2.864$, $b=-0.415$, $r^2=0.23$, ANOVA: $F=11.1$, $P=0.002$). (D) Maximum frictional coefficient (LAC data fit: $a=2.730$, $b=-0.259$, $r^2=0.129$, ANOVA: $F=5.7$, $P=0.022$; HAC data fit: $a=3.029$, $b=-0.360$, $r^2=0.18$, ANOVA: $F=8.1$, $P=0.007$). Red dotted lines show predicted slopes for regression lines.

5 to 40 and for maximum data from 7 to 70 under different experimental conditions. These values also show how much of its own weight the insect can hold in the ‘walking on the wall’ situation.

Ontogenesis of the attachment ability

The simple physical principle that smaller objects adhere relatively stronger than larger objects (Kendall, 2001) is found in the attachment system of *C. marginatus*. Interestingly, in a living system, this has an important biological significance. Small (juvenile) animals are flightless and stronger attachment ability might be essential for them to stay attached to the host plant.

The frictional properties of the bug pulvilli do not change during ontogenesis. Thus, pulvilli growth and the consequent increased contact area contribute to the increasing attachment ability in insects at later larval stages. We expected an increase of the lateral tenacity in older instars, since the pressure in the contact area increases in larger insects because of different scaling laws for the mass and surface area (Fig. 4C). However, the lateral tenacity was similar in all instars, which could be

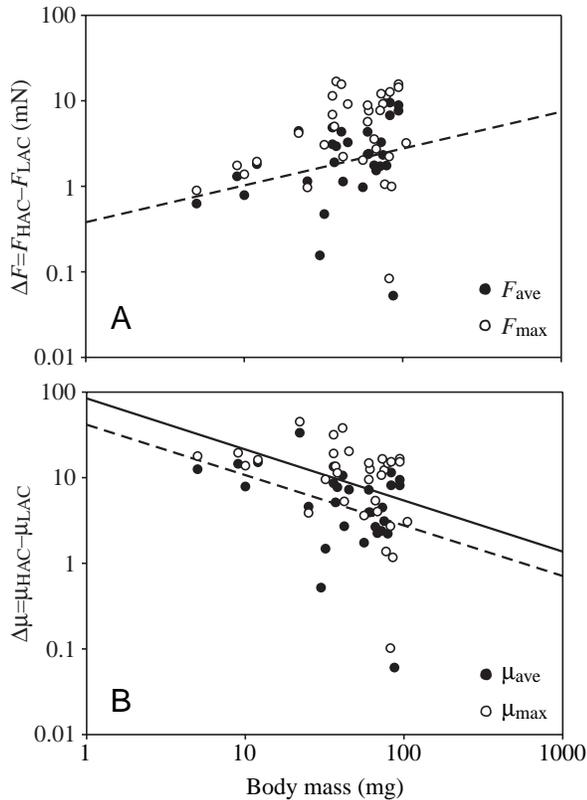


Fig. 6. Differences between data obtained for individual insects ($N=40$) at low and high accelerations ($LAC=1.21 \text{ rev s}^{-2}$; $HAC=12.1 \text{ rev s}^{-2}$, respectively). (A) Friction force (fit for average data: $a=-0.420$, $b=0.430$, $r^2=0.08$; fit for maximum values: $a=-0.104$, $b=0.425$, $r^2=0.08$). (B) Friction coefficient (fit for average data: $a=2.619$, $b=-0.589$, $r^2=0.14$; fit for maximum values: $a=2.926$, $b=-0.597$, $r^2=0.14$). Black circles and broken lines, average data; white circles and solid lines, maximum values for individual insects.

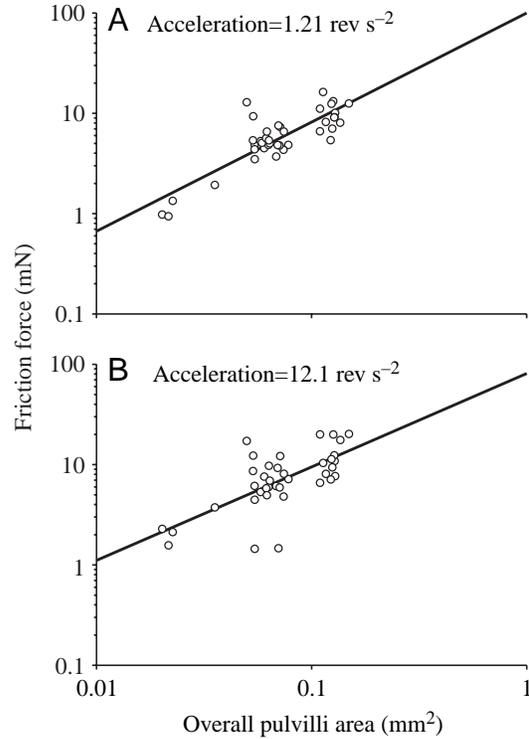


Fig. 7. Dependence of the friction force on the pulvilli area for low (A) and high (B) acceleration ($LAC=1.21 \text{ rev s}^{-2}$; $HAC=12.1 \text{ rev s}^{-2}$, respectively). (A) Data fit: $a=2.000$, $b=1.088$, $r^2=0.70$, ANOVA: $F=88.2$, $P<0.001$. (B) Data fit: $a=1.908$, $b=0.932$, $r^2=0.47$, ANOVA: $F=31.4$, $P<0.001$. $N=40$.

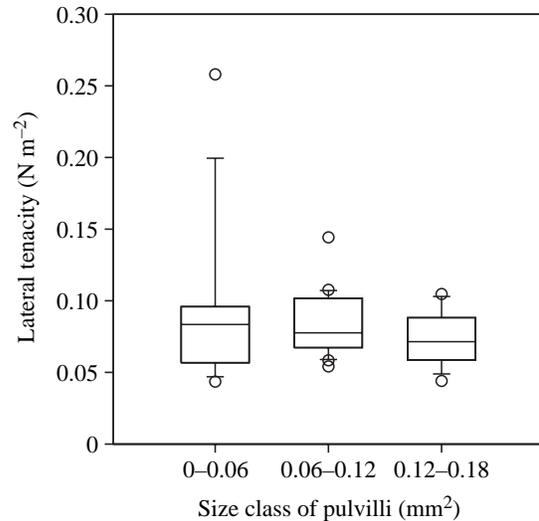


Fig. 8. Lateral tenacity (friction force/total contact area of 12 pulvilli) calculated for insects of various size. Three groups of insects with different average areas of pulvilli are considered. The first group consists of juvenile insects, the third group consists of adults, the second group is mixed. There is no significant difference in the lateral tenacity between the groups ($H=0.64$, $d.f.=2$, $P=0.726$, Kruskal–Wallis one-way ANOVA on Ranks).

explained by (1) pulvilli having possibly stiffer material properties in older (heavier) animals and, therefore, a smaller real contact area of the pulvilli with the substrate at the same pressure and/or (2) different amounts, composition and properties of the pad secretion. These hypotheses, however, need further experimental evidence.

Similar to *C. marginatus*, lateral tenacity in syrphid flies also does not depend on the body mass. Frictional and adhesive properties of pads are precisely adapted to the animal mass. This seems to be an important feature of locomotory attachment devices. The attachment forces of an animal should be tuned to an optimum between the ability to hold onto the wall and ceiling, and simultaneously to walk without high energy expenditure when the contact breaks. Too high attachment is not desirable, because it could hamper locomotion. Some animals with smooth attachment devices can actively change the contact area of pads when carrying loads, as is done by some ants (Federle and Endlein, 2004). Hymenopterans and probably other insect groups with a retractable arolium are also able to passively control the contact area. However, nothing is known about such an ability in *C. marginatus*.

Interestingly, the value for lateral tenacity determined for *C. marginatus* is within the same range as previously measured for six species of syrphid flies (Gorb et al., 2001a), which may reflect the similarity of mechanical properties of the surface in different types of insect attachment pads. Division of a large contact area into many single contacts makes the surface less stiff than the bulk material (Persson, 2003). Since flies possess a hairy type of pulvilli, the material of their setae should be stiffer than in that of *C. marginatus* pulvillus in order to end up with the same mechanical properties of the surface. This prediction should be experimentally tested.

The present set of experiments shows stable functioning of the attachment system during ontogenesis. However, variables such as time after the last moulting were not determined here. One has to take into account that freshly moulted animals may have other attachment abilities because of different material properties of pads in particular (Ridgel et al., 2003) and the cuticle in general (Hepburn, 1985).

Acceleration-dependent attachment

Since the attachment properties of pulvilli are strongly dependent on velocity, the viscosity of the secretion and visco-elastic properties of foam-like material of the pulvilli may be important variables contributing to time-dependent processes in the contact area during attachment and detachment processes. For smooth systems, such as ant arolium or grasshopper euplantulae, visco-elastic properties of the pad material have been previously suggested (Brainerd, 1994; Gorb et al., 2000b).

Fluid secretions have previously been reported in hairy adhesive pads (Edwards and Tarkanian, 1970; Bauchhenss and Renner, 1977; Bauchhenss, 1979a,b; Walker et al., 1985; Ishii, 1987) and in smooth pads (Roth and Willis, 1952; Lees and Hardie, 1988; Dixon et al., 1990). The smooth pulvilli of various Heteroptera also produce fluid secretions in the contact

area (Hasenfuss, 1977a,b, 1978; Ghasi-Bayat and Hasenfuss, 1980a–c). It is generally accepted that the pad secretion of diverse insects contains non-volatile, lipid-like substances (Hasenfuss, 1977a; Bauchhenss, 1979a; Ishii, 1987; Lees and Hardie, 1988; Kosaki and Yamaoka, 1996). However, latest studies on secretion in flies (Gorb, 2001), locusts (Vötsch et al., 2002) and ants (Federle et al., 2002) suggest that the pad secretion is biphasic, probably delivered in the contact area as a kind of micro-emulsion. The most elaborate chemical study of insect pad secretion has been published for the locust. It demonstrated that the water-soluble fraction of the fluid contains amino acids and carbohydrates. It is obvious that such a biphasic fluid is rather viscous (Stadler et al., 2001), the flow of each phase being constrained by the presence of another fluid that is not mixed with the first one. The visco-elastic role of the pad material in attachment has not been previously studied. As a general rule, visco-elasticity should result in higher adhesion in the case of slow contact formation and fast contact breaking.

An alternative explanation of the experimental results showing dependence of attachment force on angular acceleration is the presence of active control over attachment ability. Since, in the present experimental situation, high acceleration conditions automatically mean a shorter time under external force for an insect, the results obtained are time dependent: insects can withstand a higher external force for a relatively shorter time. Even if *C. marginatus* does not possess active control over the pulvilli area, the muscle system is involved in tarsus control and generally in posture control. Since the insect will become tired under external force after a certain time prior to detachment, low acceleration conditions rather than high acceleration conditions would automatically result in lower detachment force. In other words insects can withstand higher external force if it is applied for a relatively short time. In a real situation, it might be important for resisting strong but short wind pulses.

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