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Structural Design and Biomechanics of Friction-Based Releasable Attachment Devices in Insects[1]

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SYNOPSIS. Design of attachment devices in insects varies enormously in relation to different functional loads. Many systems, located on different parts of the body, involve surfaces with particular frictional properties. Such systems evolved to attach parts of the body to each other, or to attach an insect to the substratum by providing fast and reversible attachment/detachment. Among these systems, there are some that deal with predefined surfaces, and others, in which one surface remains unpredictable. The first type of system occurs, for example, in wing-locking devices and head-arresting systems and is called probabilistic fasteners. The second type is mainly represented by insect attachment pads of two alternative designs: hairy and smooth. The relationship between surface patterns and/or mechanical properties of materials of contact pairs results in two main working principles of the frictional devices: mechanical interlocking, or maximization of the contact area. We give an overview of the functional design of two main groups of friction-based attachment devices in insects: probabilistic fasteners and attachment pads.

DIVERSITY OF INSECT ATTACHMENT DEVICES

Biological attachment devices are functional systems for temporary or permanent attachment of an organism to the substrate, to another organism, or temporary interconnection of body parts within an organism. Their design varies enormously in relation to different functional loads (Nachtigall, 1974; Betz, 1996; Gorb, 2001; Scherge and Gorb, 2001). Almost all insect species have diverse attachment devices, the morphology of which depends on the biology of the particular species. Since cuticle and its derivatives play a crucial role in the design of attachment devices of insects, these systems are referred to as cuticular attachment systems (Gorb, 2001). There are eight fundamental classes of attachment principles: (1) hooks, (2) lock or snap, (3) clamp, (4) spacer, (5) sucker, (6) expansion anchor, (7) glue, and (8) friction, which can occur in various combinations.

FRICTIONAL AND ANTI-FRICTIONAL SURFACES

Most attachment devices are composed of macroscopical structures and driven by muscular force. However, many systems, located on different parts of the body, involve surfaces with particular frictional properties (Fig. 1). Generally, any movement involving contact between two surfaces or between a surface and a medium deals with the resistance of the surfaces or medium. This resistance is called friction, a phenomenon which has a great influence on the structure of biomechanical systems which arose during evolution. Living creatures possess specialized surfaces enabling the minimization of contact forces (anti-friction systems) or the maximization of them (friction systems) (Fig. 2). The frictional systems evolved to attach parts of the body to each other or to attach an insect to the substratum. Anti-frictional systems are designed to decrease frictional forces within joints. In both cases the resulting task of such a system is to save muscular energy. One always needs friction to generate force for overcoming the drag caused by friction in other parts of the system. Optimization then becomes the exercise of minimizing friction at one end of the system, while maximizing it at the other (Radhakrishnan, 1998). For example, in the case of terrestrial locomotion, for effective propulsive movements, a high friction is necessary for contact of the limbs with the substratum and a lower friction—within the joints of the limbs.

Among various cases of contact pairs in biology, anti-friction systems always have a predefined pair of surfaces, whereas, among friction systems, there are some that deal with predefined surfaces, and others, in which one surface remains unpredictable. The first type of friction system occurs, for example, in wing-locking devices and head-arresting systems and is called *probabilistic fasteners.* The second type is mainly represented by insect *attachment pads* of two alternative designs: hairy and smooth (Scherge and Gorb, 2001). The relationship between surface patterns and/or mechanical properties of materials of contact pairs results in two main working principles of the frictional devices: mechanical interlocking, and maximization of the contact area (Fig. 2). In the present paper, we give an overview on the functional design of two main groups of friction-based attachment de-

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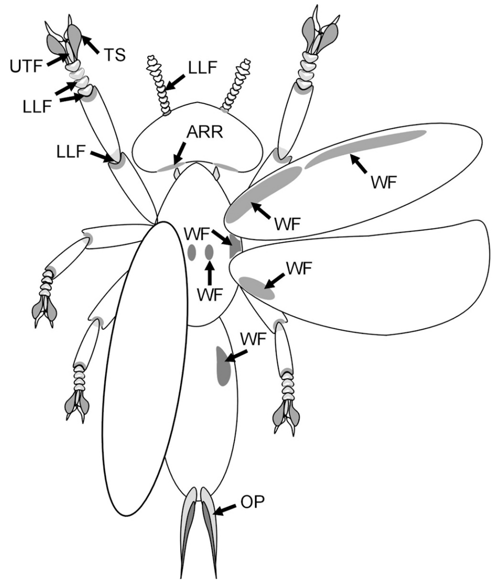

FIG. 1. Diagram showing possible locations of frictional systems. Grey-colored areas are usually covered with cuticular protuberances. ARR, head arresting system; LLF, rough surfaces in antennal and leg joints; OP, ovipositor valves; TS, tarsal attachment pads; UTF, unguitractor plate; WF, wing-attachment devices. From (Gorb, 1998*c*).

vices in insects: probabilistic fasteners and attachment pads.

PROBABILISTIC FASTENERS

Probabilistic fasteners are composed of two functionally corresponding surfaces covered with cuticular micro-outgrowths, such as setae, acanthae or microtrichia (Richards and Richards, 1979). They are called probabilistic (Nachtigall, 1974), because the interlocking takes place without precise positioning of both surfaces. In this case, attachment is based on the use of the surface profile and mechanical properties of materials and is fast and reversible. The single outgrowths, which are called elements, are not hooks as in Velcro fasteners. Probabilistic fasteners with parabolic elements have been described in head arresting systems (Gorb, 1999*a*), intersegmental fixators of leg joints (Gorb, 1996), and wing attachment devices (Schrott, 1986; Gorb, 1998*a*). The most studied examples of the systems are elytra-locking mechanisms in beetles and the head arrester in dragonflies.

Head arrester in dragonflies

The area of head articulation with the neck is very small compared to the head's dimension. It is virtually a single point providing extreme head mobility on the

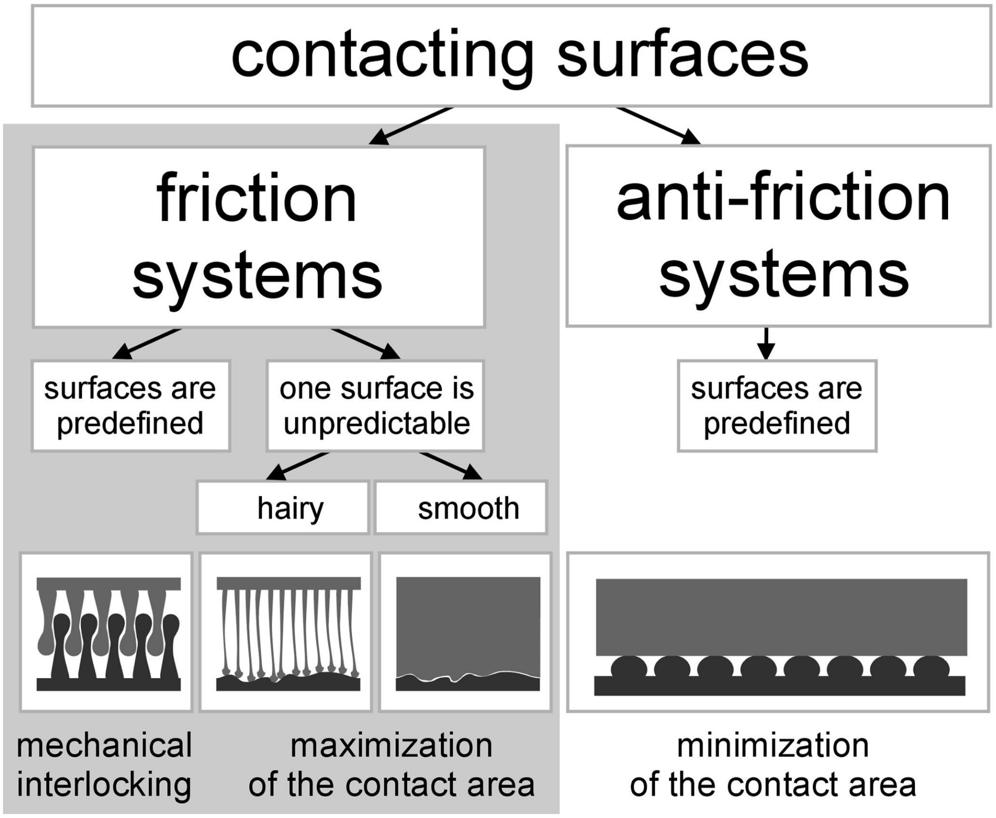

FIG. 2. Functional significance and working principles of contacting surfaces in biological objects. Living creatures possess specialized surfaces enabling the minimization of contact forces (anti-friction systems) or maximization of them (friction systems). Among such systems, there are some composed of two co-opted (predefined) surfaces, whereas in others one surface remains unpredictable. The relationship between surface patterns and/or mechanical properties of the material of contact pairs results in three main working principles: (1) mechanical interlocking, (2) maximization of the contact area, and (3) minimization of the contact area.

roll, pitch, and yaw planes. Such mobility of the head compensates for the absence of a specialized gravity organ. The head is analogous to a statolith, the movements of which are monitored by fields of hair sensilla located on the head, neck, and prothorax. The head-neck articulation has little mechanical strength but the head, however, must at times be rigid with the rest of the body, for example, during copulation, while feeding, to prevent disturbances caused by large mandibular muscles, and to stabilize gaze while perching or holding prey in flight. The arrester serves to immobilize the head during feeding or when the dragonfly is in tandem flight. It involves adjusting organs of two body segments—the head and neck, with fields of outgrowths on the rear surface of the head and on the neck (Fig. 3C, D). Different modifications of outgrowth shape, occurring in functionally corresponding fields, have been previously described (Gorb, 1998*b*).

Elytra locking mechanism in beetles

Insects, such as Hymenoptera, Heteroptera, Coleoptera (Samuelson, 1994, 1996), Dermaptera, some Diptera, and some Lepidoptera have convergently developed an ability to attach their wings to the body when resting. Independent of the general design, these systems have a major similarity: co-opted fields of cuticular outgrowths are present on two separate parts of the body. Such outgrowths differ in the shape, density, and directionality (Fig. 3A, B) (Gorb, 1999*b*). The complete wing-locking system in beetles contains five surfaces covered by outgrowths on the body and eight surfaces on the wings (Gorb, 1998*a*). Each of these specialized surfaces prevents movement of the closed wings in some preferred direction. The locations of surfaces and directionality of outgrowths make wings stable against shifting in any direction, when they are fixed to the body. Elytra provide complete cover for the delicate hind wings and abdomen. When elytra are interlocked with thorax and abdomen, the body forms a stable unit. Elytra protect the flight-wings from becoming wet, dirty or damaged. Elytral coverage also minimizes loss of water. As previously suggested (Hammond, 1989), these strengthening and protective functions provided the selection pressure that resulted in successive changes of fore wing design and interlocking mechanisms.

Behavior of probabilistic fasteners

Force measurements on an artificial system (Fig. 3E) show that the attachment force is strongly dependent on the load force (Fig. 3F–G). At small loads, the increase of attachment was very slow, whereas rapid increase of attachment was detected at higher loads. At very high loads, a saturation of the attachment force was revealed. A simple explanation of the attachment principle is as follows: with an increasing load, elements of both surfaces slide into gaps of the corresponding part. This results in an increase of lateral loading forces acting on elements. High lateral forces lead to an increase of friction between single sliding elements.

The main feature of such a system is the existence of a critical compressive force needed to ‘‘interlock’’ the frictional fastener. After overcoming this critical value, the attachment force increases with the loading force. The attachment force has the same order of magnitude as the loading force needed to achieve interlocking. The attachment force is, however, always lower than the loading force and is of the same order of magnitude as the elastic force needed to deflect the fastener elastically in the horizontal direction to a distance equal to the diameter of the element tips. This feature can be used as an experimental test of the frictional nature of a fastener.

A theoretical model of probabilistic fasteners with parabolic elements shows that dependence of the attachment force on the loading force is sensitive to the shape of the element (Gorb and Popov, 2002). For example, in the case of cone-shaped elements, the attachment force is linearly proportional to the loading force and no critical interlocking force exists. The stronger the convexity of the basic curve of the rotating body of the element, the higher the critical interlocking force.

In biological systems, the density of surface irregularities may vary depending on the body size. However, the existing model does not consider the element density of counterparts. One might expect that the density would correlate with the number of contact points between elements, which must have a direct effect on the mechanical interaction between the surfaces. It has been previously shown that the density of irregularities correlates to the length, width, and especially the distance between single elements so that, in biological frictional systems, the longest and the widest protuberances are usually sparsely distributed within the field (Gorb, 1998*a*). However, there is only a weak correlation between length and width of outgrowths. Interplay of these parameters may result in different behavior of element assemblages and remains unknown.

ATTACHMENT PADS

Two design principles of attachment pads

Diversity of attachment structures, used in terrestrial locomotion, is generally based on only two mechanisms: hairy surfaces or relatively smooth flexible pads. We suggest that a fibrous composite material, such as hexapod cuticle (Neville, 1975), is preadaptative and may provide only limited options for design of attachment systems. The main similarity of both mechanisms is that the structured pad surface or particular properties of pad materials guarantee a maximum real contact with diverse substrata profiles. It is remarkable that these highly-specialized structures are not restricted to one particular area of the leg (Fig. 4A–J). They may be located on different parts, such as claws, derivatives of the pretarsus, tarsal apex, tar-

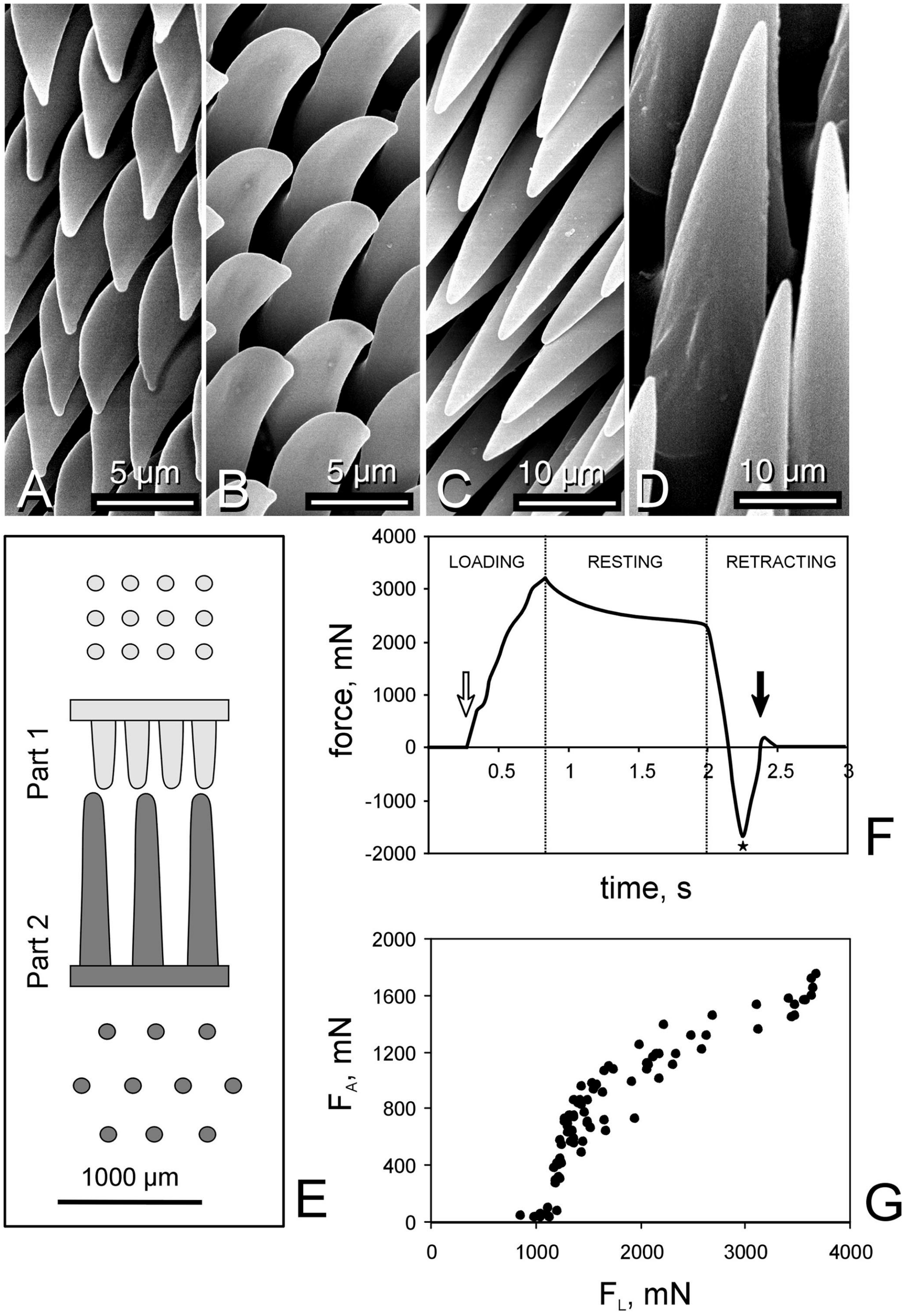

FIG. 3. Probabilistic fasteners in biological attachment devices. A–D. Diversity of the shape of protuberances from two different functional systems (SEM micrographs). A–B. Thoracic (A) and elytral (B) counterparts of the elytra-to-body locking device in the tenebrionid beetle *Tenebrio molitor*. C–D. Neck (C) and head (D) counterparts of the head arresting system in the cordulegastrid dragonfly *Anotogaster sieboldii*. E–G. Results of the force measurements on the dry artificial fastener system. E. The model system used in the force measurements; circles above and below the scheme indicate distribution of single elements on each counterpart. F. An example of the force-time curve consisting of three main parts: loading, resting and retracting. White arrow indicates contact initiation; black arrow indicates contact breakage; asterisk indicates the beginning of element sliding. G. Dependence of the attachment force (F_A) on the load force (F_L). (From Gorb and Popov 2002).

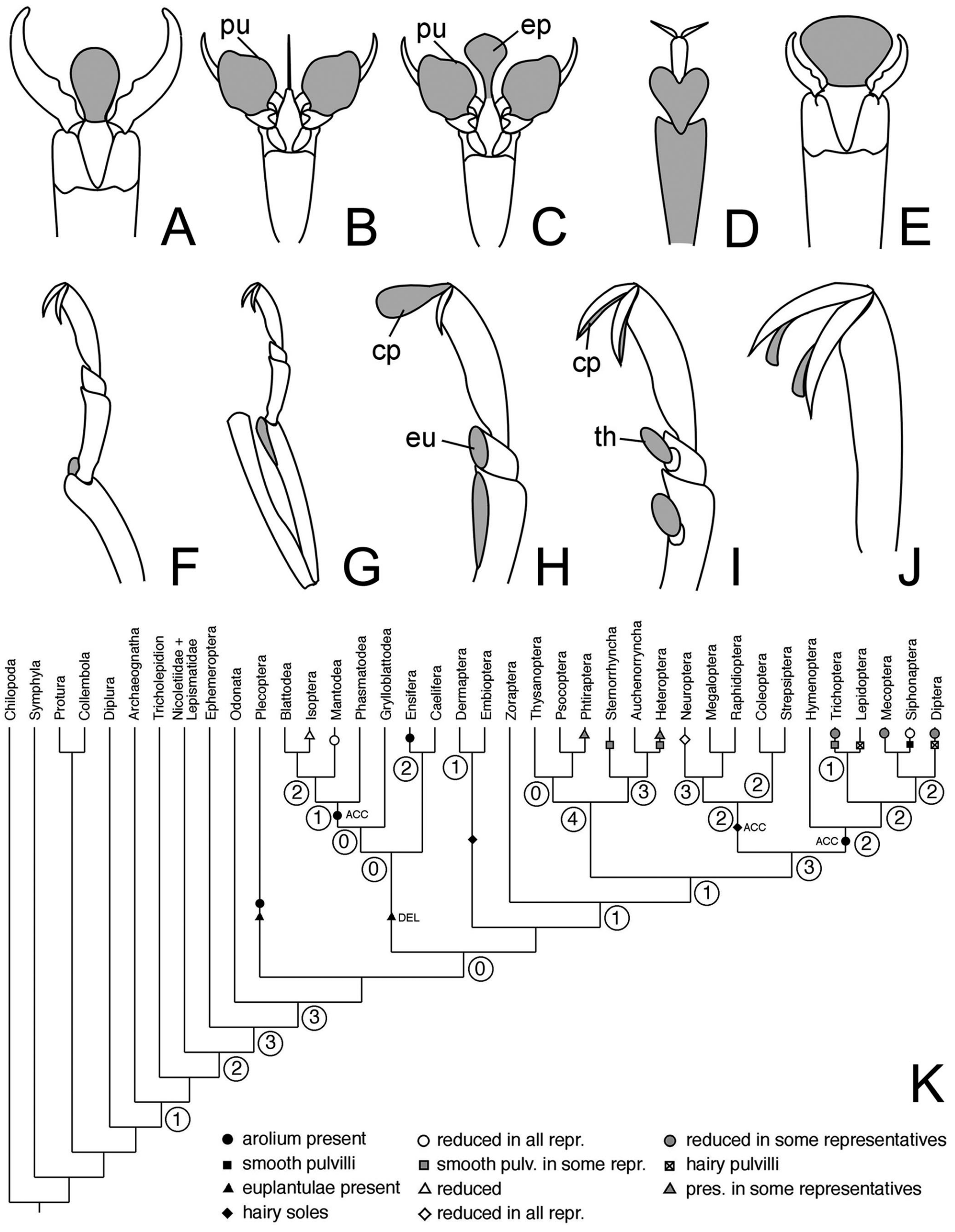

FIG. 4. Diversity of leg attachment devices (grey-colored areas) in hexapods. A. Arolium (smooth). B. Pulvilli (smooth or hairy). C. Empodial pulvillus (ep) (hairy). D. Hairy adhesive soles of tarsomeres. E. Eversible pretarsal bladder (smooth). F. Eversible structure between tibia and tarsus (smooth). G. Fossula spongiosa (hairy). H. Euplantulae (eu) and claw pad (cp) (both smooth). I. Tarsal thorns transformed into adhesive structures (th), claw pad (cp) (both smooth). J. Adhesive claw setae. K. Selected tree of 24 minimal length trees, adhesive pad characters are mapped on cladogram; numbers left of branches are branch support values for selected clades. ACC (character transformation accelerated) and DEL (character transformation delayed) are alternative options to the character state optimisation in PAUP. From (Beutel and Gorb, 2001).

someres, or tibia. Phylogenetic analysis of the pad characters, processed together with characters of other organ systems, shows that different lineages of insects have convergently developed one of these two types (Beutel and Gorb, 2001; Gorb and Beutel, 2001) (Fig. 4K).

Construction and properties of attachment pads may correlate with the preferred substrata, normally used by particular insect species. Insect attachment pads probably evolved to facilitate walking on plant surfaces. Plant surfaces have a wide range of textures: they may be smooth, hairy, and covered with waxes or with moist secretions. As with any integument, plant cuticle is a functional organ reflecting the response of ultrastructure and chemistry of the plant surface to a variety of environmental pressures. During the long period of co-evolution between flowering plants and hexapods, plants have not only developed structures attracting pollinators, but also a wide variety of structural and chemical attributes of their surfaces related to defense against herbivores (Stork, 1980*b*; Eigenbrode *et al.*, 1999; Eigenbrode, 2002). The co-evolution of plant surfaces and insect pads results from a competition between insect attachment systems and plant anti-attachment surfaces. However, the exact mechanism of most anti-adhesive plant surfaces remains largely unknown.

Pad secretion

The pad secretion of diverse insects contains a non-volatile, lipid-like substance that can be observed in footprints stained with Sudan Black. The chemical composition of the secretion was mainly studied in beetles. It has been shown by the use of thin-layer chromatography that in lady-bird beetles (Coccinellidae) the chloroform-soluble part of the pad secretion consists mainly of hydro-carbons, fatty acids, and alcohols (Ishii, 1987). Gas chromatography has revealed that pad adhesive secretions consist of hydro-carbons and true waxes (Kosaki and Yamaoka, 1996), which correspond well to the composition of the cuticle coverage. It was noted that the contact surface of the tarsi of the beetle *Hemisphaerota cyanea* (Chrysomelidae, Cassidinae) is water-repellent (Eisner and Aneshansley, 2000). Observations on the smooth pads of the grasshopper *Tettigonia viridissima* show that footprints, embedded in water, form oily droplets (Jiao *et al.*, 2000*a*). Chemical extracts of *H. cyanea* tarsi, or of glass surfaces to which they had clung, yielded mixtures of saturated and unsaturated linear hydrocarbons of C_{20} to C_{28} chain length, with (Z)-9-pentacosene as the principal component. The results led previous authors to presume that the fluid is an oily substance (Attygalle *et al.*, 2000).

Measurements, made with the use of the Atomic Force Microscope, demonstrated a low contact angle of the secretory droplets on hydrophilic substrata: height-to-diameter ratio of the droplets was about 1/50 (Stadler *et al.*, 2001). After several hours, droplets evaporated by up to 15%. The residues remain on the surface for a long time. These results indicate the presence of water or other solvents in the secretion. The water-soluble fraction of the fluid contains amino acids and a considerable amount of saccharides (Voetsch *et al.*, 2002). Pad secretion increases capillary and viscous forces in the contact area and presumably serves as a kind of coupling agent between otherwise incompatible materials. Viscosity of the adhesive liquid dominates in horizontal pulls, whereas other forces (capillary or intermolecular forces) are more significant in the vertical direction (Federle and Full, 2002).

HAIRY PADS

Despite numerous studies of the anatomy and function of the hairy attachment system, there is still a lack of agreed solutions concerning the attachment mechanism of flies and beetles walking on smooth surfaces. Different hypotheses have been proposed to explain the mechanism of attachment. Theories of a sticking fluid, microsuckers, and the action of electrostatic forces have been discussed (Gillett and Wigglesworth, 1932; Edwards and Tarkanian, 1970). Based on experiments with beetles, the named theories have been rejected and it has been concluded that cohesive forces of the pad secretion, surface tension and molecular adhesion are involved in the mechanism of attachment (Stork, 1983*a, c*).

Cuticle protuberances

Hairy systems always contain cuticle protuberances on their surfaces. Interestingly, protuberances on the hairy pads of Coleoptera, Dermaptera, and Diptera belong to different types of cuticular outgrowths. Representatives of the first two lineages have socketed setae on their pads (Stork and Evans, 1976; Stork, 1980*c*). Setae range in length from a few micrometers to several millimeters. Dipteran protuberances are acanthae, single sclerotised protuberances originating from a single cell (Richards and Richards, 1969). Acanthae range in length from a few micrometers to, at most, 0.5 mm. The key morphological characteristic of acanthae is a lack of a socket and a sensory cell (Richards, 1965). Both types of structures can be covered with additional, minute outgrowths referred to as microtrichia. Fimbriate setae were found in the beetle *Priacma serrata*, a representative of the basal suborder Archostemata (Gorb and Beutel, 2001).

Material behavior

Most tenent setae bear discs or widened compressions called *terminal elements* or *spatulae* on their tips (Fig. 5D, E). The area of single terminal element varies even in closely related species and is oppositely correlated with the density of hairs (Gorb *et al.*, 2001). To enable strong attachment between pad material and diverse substrata, a high proximity between contacting surfaces is required. One mechanism, which can provide an intimate contact of solids, is a high flexibility of at least one of both materials. It has been previously presumed that setae are composed of flexible cuticle, and are able to replicate the surface profile (Bauchhenss, 1979; Stork, 1983*a*). The results of freeze-substitution experiments show that the area of the setal tips becomes larger when the pulvillus is in contact with the surface (Niederegger *et al.*, 2002). This deformation is best seen in the middle of the attachment pad, whereas setae are often not in contact on the sides (Fig. 5G). Since single setae are adapted to deform under load and fit the microtexture of various surfaces, a contact with the maximum number of attachment points would be possible on various substrate profiles. This presumably results in an increase of real contact area between surfaces.

Terminal elements are well known not only for insects, but also for hairy attachment pads of other animals, such as spiders (Foelix, 1982) and geckos (Stork, 1983*b*; Autumn *et al.*, 2000). In the latter two animal groups, terminal elements are branches of the

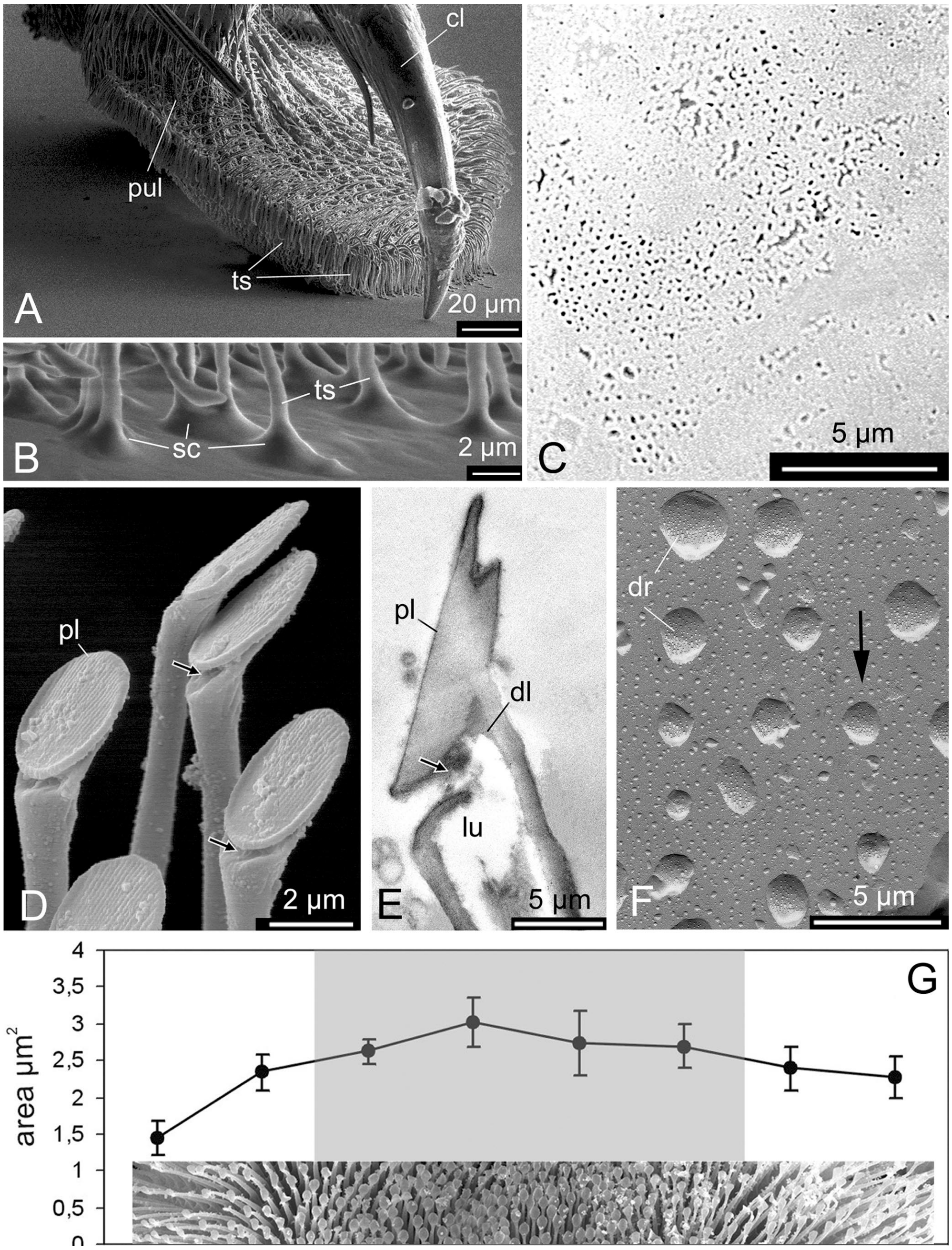

FIG. 5. Hairy attachment pads. A. Pulvillus of the syrphid fly *Eristalis pertinax* in contact with the glass surface. B. Tips of tenent setae surrounded by secretion. C. Footprints on a glass surface. D–E. SEM (D) and TEM (E) micrographs of tenent setae in the syrphid fly *Episyrphus balteatus*. F. Carbon-platinum replica of the frozen footprints of the fly *Calliphora vicina* in TEM. Black arrow indicates direction of coating. G. The area of the setal tips in the fly *C. vicina*. Setae are deformed when in contact with the surface. The grey area indicates the region of the setae that is in contact with the substrate. cl, claw; dl, dense layer; dr, droplets; lu, lumen; pl, end plate; pul, pulvillus; sc, secretion; ts, tenent setae. (From Gorb, 2001; Niederegger *et al.* 2002).

basal elements. The size of terminal elements decreases and the density strongly increases with an increased body weight (Scherge and Gorb, 2001). Presumably, animals cannot increase the area of attachment devices proportionally to the body weight because of different scaling of the mass and surface. This scaling effect shows other mechanisms to increase attachment abilities by increasing the number of single contacting points and real contact area in heavier animals.

Fluid transport

In *Calliphora* flies, the non-volatile lipid secretion is produced by large cells, located at the base of each pad, and stored within a ‘‘spongy’’ layer of cuticle (Bauchhenss, 1979). A well-developed system of pore canals has also been described at the base of the tenent setae, located on the basal part of the pad. It has been hypothesized that the canals are responsible for the

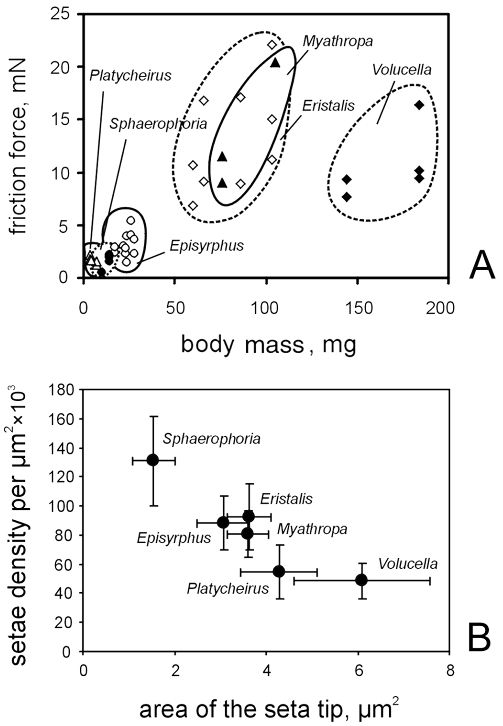

FIG. 6. Scale effects on friction force and pad structure in closely related insect species with the hairy type of attachment pads. A. Friction force versus body mass in six species of syrphid flies. B. Dependence of the setal density on the area of the setal tip. From (Gorb *et al.,* 2001).

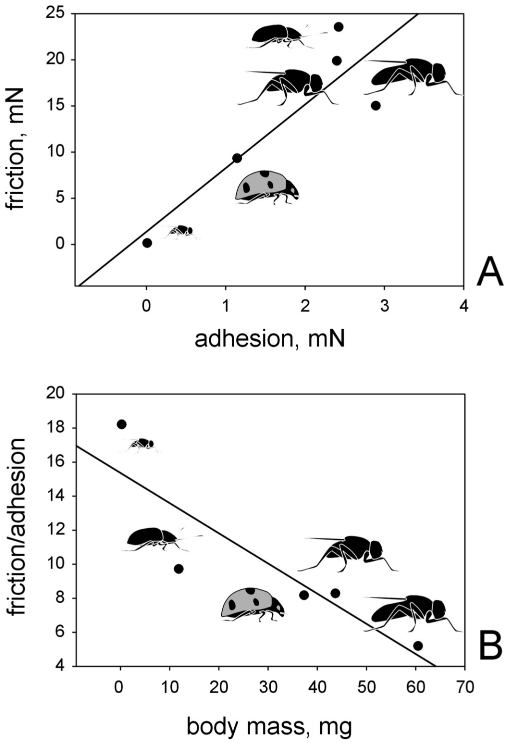

FIG. 7. Interrelationship between friction and adhesion in insects with the hairy type of attachment pads. Results are based on the centrifugal experiments (for methods see Gorb *et al.* [2001]). A. Friction vs adhesion. B. Friction/adhesion vs body mass. Silhouettes indicate insect species. In Figure B from left to right: fly *Drosophila melanogaster* (Drosophilidae), beetle *Gastrophysa viridula* (Chrysomelidae), beetle *Coccinella septempunctata* (Coccinellidae), fly *Calliphora vomitoria* (Calliphoridae) (Walker *et al.*, 1985), fly *Eristalis tenax* (Syrphidae). With the exception of *C. vomitoria*, data were obtained from measurements with a centrifugal device.

release of secretion onto the surface of the setal bases. The loss of secretion could presumably be minimized by its re-absorption back into the cuticle when the fly detaches, due to the high capillarity of the system (Bauchhenss, 1979).

In fly pads attached to cover-slips, lipids are not spread over the whole contact area between pad and substratum, but are discrete droplets just under the setal spatulae (Fig. 5A–C, F). Moreover, the surfaces of a setal base remain clear after attachment. Setae are very seldom glued to each other, and space between them is usually not covered by the secretion. Such observations allowed the conclusion that the secretory substances are targeted directly to the contact area between the distal plate of a single tenent seta and the substratum. Tenent setae, located on the distal part of the pads in the fly *Episyrphus balteatus*, are responsible for secretion release very close to the contact area: the acanthae are hollow inside, and some of them contain pores under the end plate (Gorb, 1998*d*) (Fig. 5D–E). Setal tips on the substratum are always bent distally, when a fly holds onto an inclined surface (Niederegger *et al.*, 2002). It seems that the tip of the tenent seta is adapted to release secretion when a pulling force is directed along the substratum surface to the proximal part of the pad. When force is directed in the opposite direction, setae can detach from the substratum, and openings of tenent setae can probably be closed by such an action. Setae, located on the basal part of the pad, do not have such a mechanism.

Friction and adhesion

Although heavier species demonstrate higher friction force (Fig. 6A), the relationship of mass-to-friction is considerably higher in the smallest species (Gorb *et al.,* 2001). In six closely-related species of syrphid flies studied, the setal tip area increased somewhat and setal density slightly decreased with increased body weight. The interrelationship between surface characteristics is especially well expressed, when both measured parameters are plotted against each other: with an increasing setal tip size, the setal density decreased (Fig. 6B).

Frictional properties of the material of the setal tips in closely-related species do not depend on the body mass. In other words, friction forces, generated by the surface unit of setal tips, are similar in the species studied. This means that adhesive properties of secretion and mechanical properties of the material of setal tips are more or less constant, and that differences in friction force are mainly related to the real contact area generated by the pad. Although the parameters vary

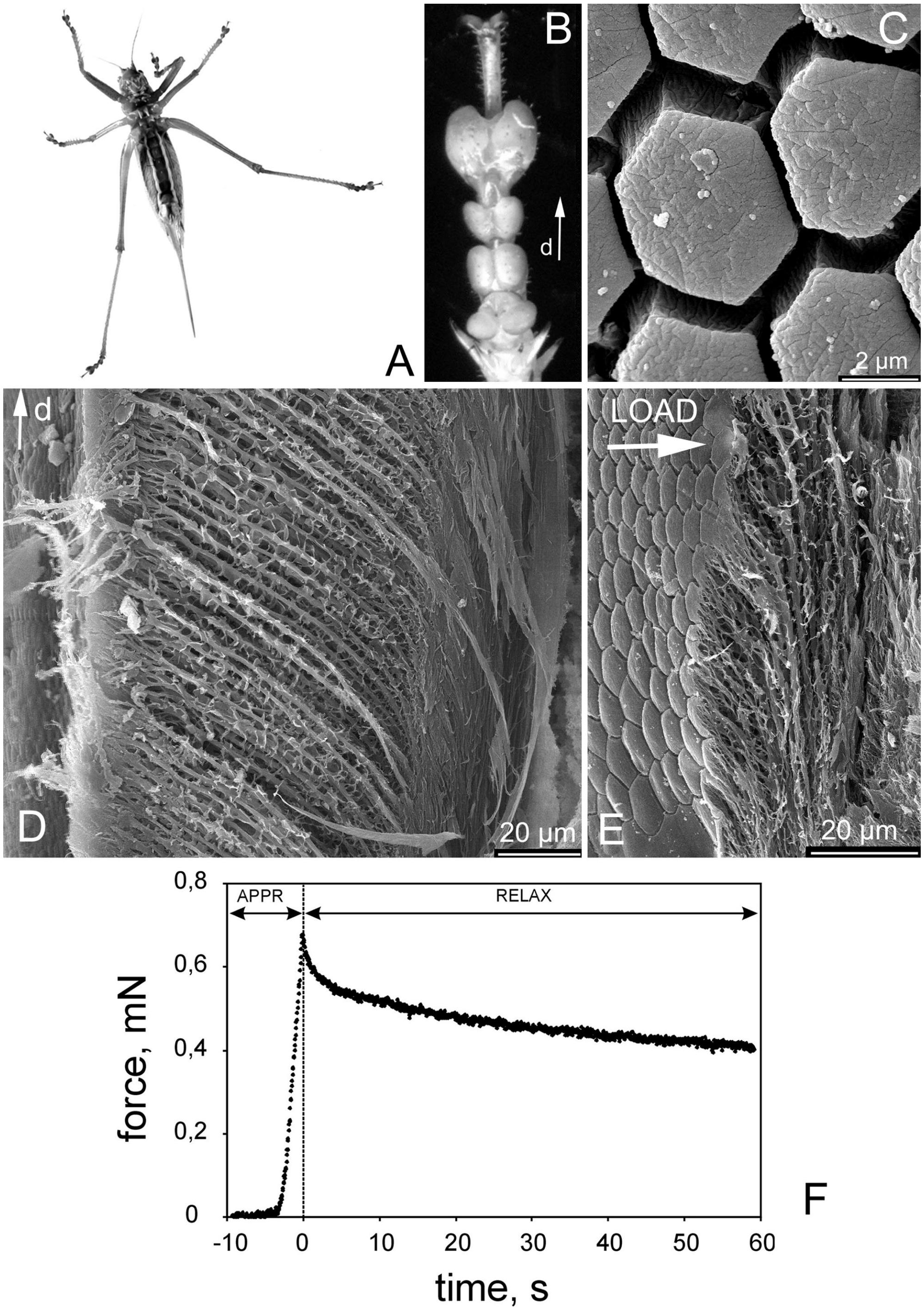

FIG. 8. Ultrastructure and viscoelastic properties of attachment pads of the grasshopper *Tettigonia viridissima* (Orthoptera, Tettigoniidae). A. Animal on a vertical glass surface. B. Tarsus of the third leg with four euplantulae. C. SEM image of the pad surface. D–E. Shock-frozen pad cuticle after substitution and fracture. D. Free pad that has not been in contact with the substratum. Rods are sloped in a distal direction at an angle of about 45°. E. Pad that has been pressed against the substratum. Rods are sloped in a distal direction at an angle of about 5°. F. A typical force curve reflecting mechanical properties of the pad. The curve includes two distinct parts, approaching process (APPR) and remaining period (RELAX). During the approaching process, the pad was rapidly approached to the hard silicon surface to reach an interacting force (applied force). After that the pad was kept in contact with the silicon surface, the interacting force slowly relaxed. d, distal direction. From (Gorb and Scherge, 2000; Gorb *et al.*, 2000).

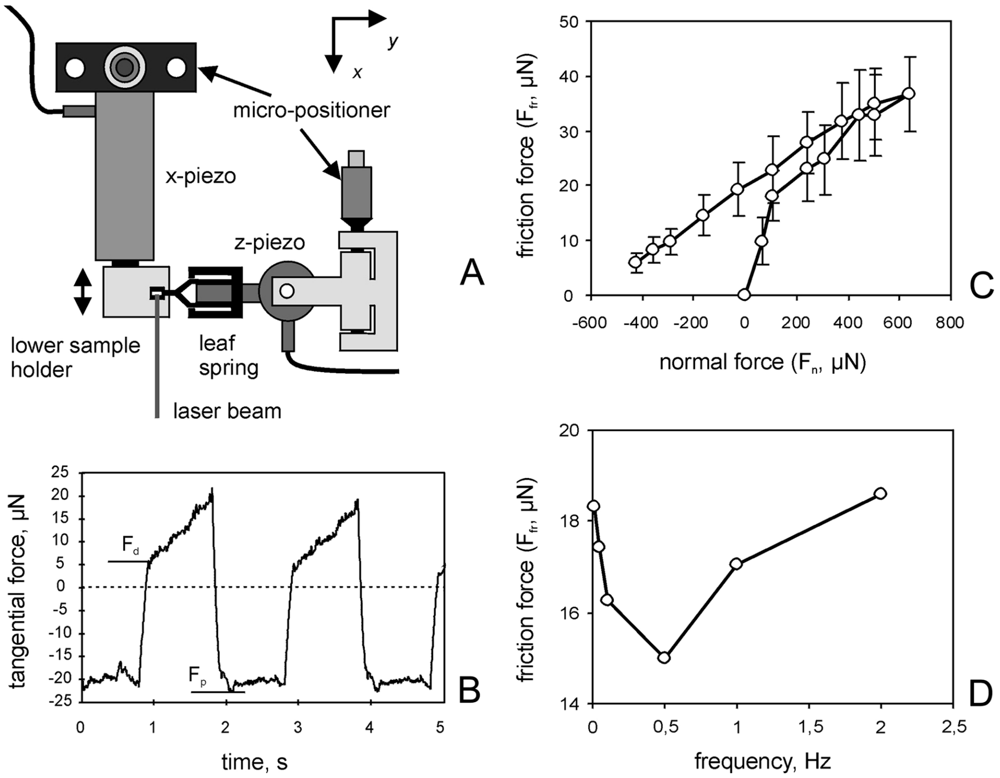

FIG. 9. Friction measurements of the euplantulae of the grasshopper *Tettigonia viridissima*. A. Micro-tester set up. The oscillatory motion is provided by an x-piezo. The pad is attached to the x-piezo. A silicon plate, attached to a glass spring, served as an upper sample. A laser beam, reflected by a mirror, attached to the spring, was used to detect deflection of the spring. In the z-direction, a z-piezo is attached to adjust the normal force. B. Friction behavior of the pad in different directions. F_d, friction force to the distal direction of the pad; F_p, friction force to the proximal direction of the pad. C. Friction force versus normal force at a frequency of 0.5 Hz. The lower part of the curve was obtained with an increasing normal force, the upper part was recorded with a decreasing normal force, after full contact between the pad and silicon surface was reached. D. Friction force versus frequency at a normal force of 87 µN. From (Gorb and Scherge, 2000).

among animals with different dimensions, there is usually a compensation: a smaller area of setal tips is compensated by a higher setal density.

The data of previous authors on beetles show that frictional forces (as when an insect walks on a wall), generated by attachment pads are considerably higher than adhesion forces (as when an insect walks on the ceiling): 22.7 mN (*Chrysolina polita*, Chrysomelidae) (Stork, 1980*a*) and 2.9 mN (*Epilachna vigintioctomaculata*, Coccinellidae) (Ishii, 1987). Our data shows that this difference is scale-dependent and is larger in lighter species (Fig. 7). This fact may be explained by the faster increase of adhesion than friction with the increased size of attachment pads. Assuming that capillary adhesion is the major player in insect hairy pads, adhesion would strongly depend on the perimeter of the solid-fluid interface. In hairy systems, the perimeter tends to increase not only due to the increased body size but also due to the multiplication of contact areas in larger animals. Friction mostly depends on the total area of sold-fluid interface and less on the multiplicity of contact areas.

SMOOTH PADS

Surface sculpture

The surface of smooth systems appears smooth under a light microscope (Fig. 8B). However, it may consist of a pattern of hexagonal structures as in representatives of Orthoptera (Fig. 8C). The hymenopteran and mecopteran arolium may be patterned in lines. A similar pattern exists on the surface of attachment thorns in some species of non-apocritan Hymenoptera (Gorb, 2001). The surface of a tipulid arolium exhibits a complex pattern of microfolds.

Fluid transport

In some specimens, residual secretory substances are present on the arolium surface. Footprints on glass surfaces were previously reported in Blattodea (Roth and Willis, 1952), Orthoptera (Jiao *et al.*, 2000*a*), Sternorrhyncha (Lees and Hardie, 1988). It was also previously noted that the cavity of the adhesive organ is connected with the external surface through fine epicuticular filaments. These presumably are places for the extrusion of the adhesive secretion (Lees and Hardie, 1988).

Material structure

Ultrastructural studies show the cuticle of smooth pads to consist of a friction-active material with a specific inner structure. In orthopterans, tiny threads of 0.1 µm in diameter are located just under the epicuticle of euplantulae (Fig. 8D, E). These filaments are

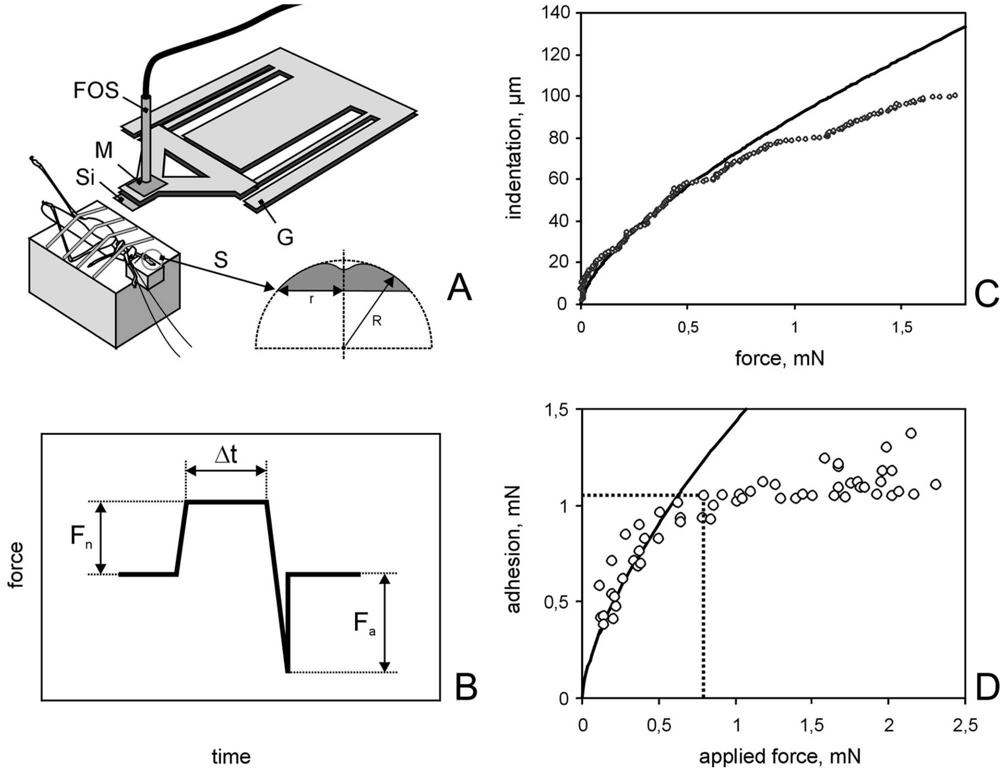

FIG. 10. Adhesion measurements of the euplantulae of the grasshopper *Tettigonia viridissima*. A. Force tester set up. The lower sample (S), the pad of a living insect, is fixed to the platform, and the upper sample (Si), a silicon chip, is attached to the spring. Driven by a motor, the platform moves the lower sample to make contact with, and retract from the upper sample. The deflection of the glass spring (G) is monitored by the fibre-optical sensor (FOS) through the mirror (M). Inset shows a cross section of the pad outlined by a semi-circle. R, radius of pad curvature; r, pad width. B. Diagram of a typical curve of the interacting force recorded versus time. F_n, applied force, F_a, adhesive force, Δt, remaining time. C. The pad indentation versus applied force (dotted line). The solid line is the indentation data, fitted according to the Hertz theory. D. Dependence of adhesion on applied force. At smaller applied forces, the adhesive force increased with increasing applied force, and was saturated at an applied force over 0.8 mN (dotted line). The saturated adhesive force was about 1.1 mN. Based on the assumption that the adhesive force is proportional to the contact area, caused by applied force, the data were fitted in accordance to the Hertz theory. From (Jiao *et al.*, 2000*b*).

branches of thicker threads, of 1 µm diameter, located more deeply in the cuticle (Kendall, 1970; Henning, 1974). It has been shown that these threads can change their shape under loads (Gorb *et al.*, 2000). The arolium of bees contains thinner and longer threads (Baur and Gorb, 2001; Federle *et al.*, 2001), which may provide a higher flexibility of the material. Internal architecture of the arolium of cicadas resembles foam, consisting of fluid-filled cells, surrounded by flexible cuticle. The diameter of the cells increases in deeper layers of the material.

Material behavior

The key property of smooth attachment devices is deformability and the visco-elastic properties of the pad material (Gorb *et al.*, 2000). Profile changes of the surface of the euplantulae of the grasshopper *Tettigonia viridissima* and the orientation of cuticle microfibrils, visualized by means of scanning electron microscopy, followed by freezing-substitution experiments, show that the flexible pad material deforms replicating the substrate profile down to the micrometer roughness. The pad material showed both elastic and viscous behavior under loads. Elastic modulus of the pad is very low (27.2 ± 11.6 kPa). At the beginning of the resting period, the interacting force between the pad and surface showed a rapid decrease followed by a slower decrease. The decrease of the interacting force indicates relaxation of the pad material. This behavior reflects the visco-elastic properties of the pad material (Fig. 8F). Two viscous relaxation processes were found, time constants $\tau_1 = 1.88 \pm 0.616$ sec and $\tau_2 = 41.2 \pm 9.95$ sec. Low stiffness of material studied here aids in surface replication and an increase in the area of real contact between the pad and the underlying substrate.

Frictional properties of smooth pads

Friction of the grasshopper pad surface was obtained by oscillating the sample over a distance of 10 µm along the x-axis (distal-proximal) in both directions (Fig. 9A). The experiments revealed that the static friction during proximal movement was larger and more stable, compared with distal movement (Fig. 9B). The dependence of the friction force on load is given in Figure 9C. The friction behavior of the pad changes with the velocity. Friction force is minimal at the velocity of 10 μm/sec and higher at slower and faster velocities (Fig. 9D). The ultrastructural study shows that the inner architecture of pads provide stability and, simultaneously, extreme flexibility. This allows the pad material to adapt to different substrate roughness, which is unpredictable for mobile insects. Through particular orientation of stiff components in the composite material, the material is optimized for maximal friction in one direction.

Adhesive properties

Adhesive force, measured on the fresh grasshopper pad, increased at smaller applied forces, and remained constant when the applied force exceeded a certain value (Fig. 10) (Jiao *et al.*, 2000*a*). The saturated adhesive force of 0.7 to 1.2 mN was reached at an applied forces of 0.7–1.5 mN (Fig. 10D). The freshly cut sample had the same adhesive force as a living pad. However, the adhesive force decreased to 0 after 70–75 min of the experiment. This effect can be explained by higher evaporation rates of the pad cuticle compared with the regular leg cuticle.

The saturated adhesive force of 1.1 mN was reached at an applied force of 0.8 mN, and the corresponding indentation was found to be about 75 μm (Fig. 10C), which corresponds to the maximum contact of the pad with a silicon surface (thickness of pad *ca.* 100 μm). The contact area did not increase with greater applied force after maximum contact. The attachment force of smooth pads strongly depends on the contact area caused by the mechanical deformation of the pad. This seems to be a general principle involved in the function of smooth attachment pads. However, as previously shown for ants, variation in the attachment force cannot always be explained by different surface area/weight ratios of smaller and larger species (Federle *et al.*, 2000). This suggests additional adaptations to walk on various types of surfaces.

CONCLUSIONS

Since biological surfaces are part of the physical world, most of the friction and adhesion phenomena in these biomechanical systems can be explained by mechanical interlocking and/or area of contact between surfaces, independent of the basic physical forces involved in the particular attachment mechanism. This indicates that the geometry of the surface, load forces, at which the system operates, and mechanical properties of material will play essential roles in the design of the particular system. In addition, chemistry of surfaces, presence and nature of secretory fluids additionally mediate surface forces. In particular, the following questions require attention. (1) What are scaling effects on the structure and attachment forces in probabilistic fasteners and attachment pads? (2) Which is the contribution of basic physical forces (capillary adhesion, Wan der Waals interaction etc.) to overall friction and adhesion in two alternative types of attachment pads? (3) How does the geometry of terminal elements (spatulae) influence attachment in hairy attachment pads? (4) Which are physical properties of secretion? (5) What are evolutionary adaptations of the microstructure of insect attachment pads to attachment on various substrata? Since friction and adhesion are very complex physical phenomena, the biggest challenge in studying them in biological systems is to collect maximum information about gross morphology, ultrastructure, chemistry, and mechanics of surfaces to explain the functional principles of particular attachment systems.

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