Biological adhesion for locomotion: basic principles

B. N. J. PERSSON *

Institut für Festkörperforschung, FZ-Jülich, 52425 Jülich, Germany

Received in final form 8 August 2007

Abstract—Surface roughness is the main reason why macroscopic solids usually do not adhere to each other with any measurable strength; even a root-mean-square roughness amplitude of approx. 1 µm is enough to completely remove the adhesion between normal rubber (with an elastic modulus $E \approx 1$ MPa) and a hard nominally flat substrate. Strong adhesion between solids with rough surfaces is only possible if at least one of the solids is elastically very soft. Biological adhesive systems used by insects, tree frogs and some lizards for locomotion are built from a relatively stiff material (keratin-like protein with $E \approx 1$ GPa). Nevertheless, strong adhesion is possible even to very rough substrate surfaces by using non-compact solid structures consisting of thin fibers, plates and walls. In order to optimize the bonding to rough surfaces while simultaneously avoiding elastic instabilities, e.g., lateral bundling (or clumping) of fibers, Nature uses a hierarchical building principle, where the thickness of the fibers (or walls) decreases as one approaches the outer surface of the attachment pad.

Some lizards and spiders are able to utilize dry adhesion to move on rough vertical surfaces, which is possible due to the very compliant surface layers on their attachment pads. Flies, bugs, grasshoppers and tree frogs have less compliant pad surface layers, and in these cases adhesion to rough surfaces is only possible because the animals inject a wetting liquid in the pad-substrate contact area, which generates a relative long-range attractive interaction due to the formation of capillary bridges.

Keywords: Dry adhesion; wet adhesion; elastically soft; elastic energy; rough surfaces; bundling; peeling; smooth attachment pads; hairy attachment pads; squeeze-out; dewetting transition; viscous adhesion.

1. ORIGIN OF STRONG ADHESION

All natural surfaces and almost all surfaces of engineering interest have surface roughness on many different length scales [1]. Surface roughness has a tremendous influence on the adhesional interaction between solids and is the main reason why macroscopic solids usually do not adhere to each other with any measurable strength [2–6]. The interaction between neutral solids is very short ranged, becoming negligibly small already at separations of the order of a few atomic distances. Thus,
strong interaction is only possible if at least one of the solids is elastically very soft so that the surface can bend and make atomic contact at the interface. In this case there will be a large area of real contact, $A$, between the solids and a small elastic energy, $U_{el}$, will be stored at the interface. During pull-off this stored elastic energy is (partly) given back and may help to break the interfacial bonds. However, if the bonding energy $\Delta \gamma A$, where $\Delta \gamma$ is the change in the (interfacial) free energy (per unit surface area) as two flat surfaces of the two solids are brought together, is much larger than $U_{el}$, the stored elastic energy can be neglected. Thus the first criterion for strong adhesion is that at least one of the solids should be elastically soft so that the area of real contact is large and the stored elastic energy is small.

The second criterion for strong adhesion is that the interaction between the solids should involve “long dissipative bonds”. That is, during pull-off the effective adhesion bonds should elongate a long distance and the elastic energy stored in the bonds at the point where they break should be dissipated in the solids rather than used to break the other interfacial adhesion bonds.

Synthetic adhesives often satisfy both these criteria. Thus, for example, pressure sensitive adhesives, used for Scotch® tapes, consist of thin elastically soft polymer films which form thin filaments (effective bonds) during pull-off, which can be extended a large distance (sometimes up to several millimeters) before they break, and the energy stored in the filament is mainly dissipated in the polymer rather than used to break other polymer filaments [7]. In addition, the effective elastic modulus of pressure sensitive adhesives is very low (often only in the kPa-range) so the relative contact area, $A/A_0$ (where $A$ is the area of real contact and $A_0$ the nominal or apparent contact area), can be very large even for very rough substrates, and the stored elastic energy, $U_{el}$, may be relatively small [8].

Biological adhesive systems used for locomotion cannot be built on the same principles as pressure sensitive adhesives. First, pressure sensitive adhesives are relatively weak materials (almost liquid-like) which would wear rapidly. More importantly, during repeated use on (real) contaminated surfaces, the adhesive would rapidly be covered by small particles (dust, pollen, . . .) and since the particles cannot be (easily) removed, the adhesive would fail after just a few contact cycles. In addition, much of the adhesion strength of pressure sensitive adhesives comes from the formation of long polymer filaments, but for biological applications (at least for insects), such long effective bonds would lead to disaster: the (small) insect would need to lift its legs several millimeters in order to break the bond, which is impossible for legs which may be shorter than a millimeter. Thus, for biological locomotion, the effective adhesive bonds should be long (on an atomic scale) but not too long.

Biological adhesive systems used for locomotion are made from keratin-like materials which are elastically relatively stiff, with an elastic modulus in the GPa-range, i.e., $10^3$ times stiffer than normal (cross-linked) rubber and maybe $10^6$ times stiffer than pressure sensitive adhesives. Thus, the fundamental question is how
Nature has been able to use this material to design an adhesive which satisfies the two adhesion criteria discussed above.

Using the principle of natural selection, Nature has produced adhesive pads in insects, and some lizards and frogs which consist of non-compact material in the form of either foam-like or fiber-like structures [9, 10]; the effective elastic properties of these materials are much lower than of the compact material and the first criterion above can be satisfied, in particular if the material exhibits a hierarchical (fractal-like) construction, with thinner fibers or walls close to the (outer) attachment surface. However, the fibers and walls cannot be made arbitrarily thin as this would result in a weak material and strong wear, or a collapse of the material as a result of the attraction between the (internal) surfaces of the solid. If by a mutation an insect (or lizard) would appear where the attachment system would fail due to this effect, the insect would get quickly eliminated by natural selection: thus one may expect the adhesive system to be highly optimized and close to the limit of what is possible from the point of view of strength and stability.

The effective “long dissipative bonds”, which are required for strong adhesion, arise in different ways for hairy and smooth adhesive pads. For the hairy systems, long thin bent fibers adhere to the (rough) substrate. During pull-off the fibers will straighten out before the bond between the fiber and the substrate is broken. At the point of “snap-off” the elastic energy stored in the straightened fiber will get lost (the fiber will vibrate for a short time and the vibration energy will, e.g., be radiated as sound waves into the surrounding). This will result in effective bonds which are long (compared to the atomic dimension) and dissipative (the stored elastic energy will be mainly dissipated in the solids rather than used to break other fiber adhesion bonds) [11]. For the smooth adhesive pads, the insect (or frog) injects a wetting liquid in the contact region between the toe pad and the substrate. During pull-off from a rough substrate, small liquid capillary bridges will form in many toe pad-asperity contact regions, and the bridges will elongate a long distance (on the atomic scale) before they break because of capillary instabilities. The (surface) energy stored in the stretched capillary bridge will be dissipated in the liquid (because of the liquid viscosity) so again we will have effective “long dissipative bonds” acting between the surfaces.

2. ADHESION AND FRICTION BETWEEN ELASTIC SOLIDS WITH RANDOMLY ROUGH SURFACES

The breaking of the atomic bonds between two elastic solids during “pull-off” usually occurs by propagating an interfacial crack. For elastic solids, part of the elastic energy stored at the interface because of surface roughness will flow to the crack tip and facilitate the interfacial bond-breaking process, resulting in the small adhesion observed in most situations.

The adhesion between elastic solids with smooth surfaces is determined by the elastic modulus of the solids and by the change in the interfacial energy (per unit
area) $\Delta \gamma$ when two flat surfaces of the solids are brought into contact. A similar description is possible if the solids have small-amplitude and short-wavelength roughness but in this case it is necessary to replace $\Delta \gamma$ with the effective interfacial energy $\gamma_{\text{eff}}$ which depends on the nature of the surface roughness and on the elastic modulus of the solids [4, 5]. If $A_0$ is the nominal contact area and $A$ is the area of real (atomic) contact then $A_0 \gamma_{\text{eff}} = A \Delta \gamma - U_{\text{el}}$, where $U_{\text{el}}$ is the elastic energy stored at the interface as a result of the surface roughness, i.e., $U_{\text{el}}$ is the energy necessary to deform the rubber surface so that it makes atomic contact with the substrate over the area $A$. Negligible adhesion will occur if $\gamma_{\text{eff}} \approx 0$, i.e., if the elastic energy $U_{\text{el}}$ stored at the interface (nearly) equals the interfacial bonding energy $A \Delta \gamma$.

In the theory developed in Refs [4, 5] the interface between two contacting solids is studied as a function of the magnification $\zeta$. The magnification refers to some (arbitrary) length scale which, e.g., could be the lateral size $L$ of the nominal contact area. When the system is studied at the magnification $\zeta$, surface roughness components with wavelength $\lambda < L/\zeta$ cannot be observed and the (apparent) contact area (projected on the $xy$-plane) $A(\zeta)$ between the solids will depend on the magnification $\zeta$. In particular, as we increase the magnification we will observe new surface roughness (see Fig. 1) and the area of (apparent) contact $A(\zeta)$ will, therefore, decrease with increasing magnification. The effective interfacial free energy (per unit surface area) will also change with the magnification with $\gamma_{\text{eff}}(\zeta) \to \Delta \gamma$ as $\zeta \to \zeta_1$, where $\zeta_1$ is the highest magnification corresponding to atomic distances. The pull-off force is determined by the macroscopic interfacial free energy $\gamma_{\text{eff}}(1)$ and if $\gamma_{\text{eff}}(1) = 0$ the pull-off force will vanish, i.e., no adhesion can be detected in a pull-off experiment. Nevertheless, the area of real (atomic) contact $A(\zeta_1)$ will, in general, be enhanced by the adhesional interaction, and since the sliding friction is determined by the area of real contact, the adhesional interaction may strongly increase the friction force in spite of the fact that no adhesion can be detected in a pull-off experiment. This effect has recently been observed for microfiber arrays of stiff polymers [13]. In this case the fiber array system, owing to the high compliance due to fiber buckling and bending [12], exhibits a strongly enhanced contact area and friction as compared to a nominally smooth surface of the same material. Nevertheless, $\gamma_{\text{eff}}(1) = 0$ and the pull-off force vanishes.

Fig. 2 shows as an illustration the calculated [4, 5] relative contact area $A(\zeta)/A_0$ and the (normalized) effective interfacial energy per unit area $\gamma_{\text{eff}}(\zeta)/\Delta \gamma$ as a function of magnification when a rubber block is squeezed against a (rigid) self-affine fractal surface with the root-mean-square roughness $h_0 = 0.5 \mu m$ and the fractal dimension $D_f = 2.2$. In this case the adhesional interaction gives a strong increase in the real contact area (at the highest magnification) and hence also in the friction force, but $\gamma_{\text{eff}}(\zeta) = 0$ for $\zeta < 8$ so the (macroscopic) pull-off force vanishes.
Figure 1. A rubber block (dotted area) in adhesional contact with a hard rough substrate (dashed area). The substrate has roughness on many different length scales and the rubber makes partial contact with the substrate on all length scales. When a contact area is studied at low magnification it appears as if complete contact occurs, but when the magnification is increased it is observed that in reality only partial contact occurs.

Figure 2. (a) The relative contact area $A(\zeta)/A_0$ and (b) the (normalized) effective interfacial energy per unit area $\gamma_{\text{eff}}(\zeta)/\Delta\gamma$ as a function of magnification $\zeta$. The elastic solid has the Young modulus $E = 10$ MPa and the Poisson ratio $\nu = 0.5$. The interfacial energy per unit area $\Delta\gamma = 0.05$ J/m$^2$, and the nominal pressure $\sigma_0 = 0.5$ MPa.
3. ADHESION USING NON-COMPACT SOLIDS

We have shown above that strong adhesion between two solids requires that at least one of them is elastically soft, or that it has a thin coating which is elastically soft. If this is not the case the area of real contact between the solids will be very small, and too much elastic energy will be stored at the interface, which will help to break the adhesional bonds during pull-off. The adhesive pads used for locomotion in many biological systems, e.g., insects, lizards and some tree frogs, are made from materials which are elastically relatively stiff, with an elastic modulus of the order of 1 GPa. Nevertheless, by using non-compact solids Nature has developed adhesive pads which are elastically soft on all relevant length scales, using two different design strategies, namely (a) fiber array structures or (b) foam-like structures. These non-compact solids can be easily deformed to make contact to a substrate with roughness on length scales $\lambda$ much longer than the thickness of the fibers and walls [11, 14, 15]. However real surfaces have roughness on many different length scales, usually all the way down to the atomic length scale. Since the fibers and walls are made from an elastically stiff material, the adhesional interaction is not able to deform the solids to make contact with the substrate at length scales shorter than the thickness of the fibers or walls. For this reason biological adhesive pads are built in a hierarchical way, where for case (a) the thick fibers branch out into many thinner fibers and so on, while for case (b) the wall thickness becomes smaller and smaller the closer one approaches the (outer) surface of the pad [11]. In addition, in case (a) the fibers end with thin plate-like structures, which are smallest and thinnest for lizards (see Fig. 7 below).

4. HAIRY ATTACHMENT PADS

Optimization of adhesive organs via natural selection has resulted in smooth and hairy attachment organs. We consider first the hairy pads and then in Section 5 smooth adhesive pads.

4.1. Fiber condensation and plate self-bonding

During pull-off the toe pad separates from the surface via interfacial crack propagation. If the fibers are curved or bent, during pull-off the fiber straightens out before the fiber-substrate bond is broken. This leads to a large energy per unit area, $\gamma_{\text{eff}}$, to propagate the interfacial crack. Since the pull-off force is (roughly) proportional to $\gamma_{\text{eff}}$ we expect a strong increase in the pull-off force from the “long” (and thin) fiber-mediated bonds between the solids.

One may ask: why not make the fibers or walls very thin already at the first stage in the hierarchical structure in which case the solid would be elastically soft on all relevant length scales? The reason why this is impossible has to do with strength and stability. Consider, for example, the fiber array system. In order to be able to
deform or bend the fibers to make contact with a rough substrate (see Fig. 3), the fibers must be much longer than the amplitude of the substrate surface roughness on the length scale of the pad size (or rather, on a length scale where the toe pad skin can be considered as flat and rigid [11]). However, in order to make contact at the shortest length scale the thickness of the fiber may need to be just a few nanometers. Such a system of long thin fibers is unstable against fiber bundling (see Fig. 4, left) or would collapse into a dense mat of closely bonded fibers (fiber condensation) [11]. Also, the tensile strength of the fiber system would be very weak and strong wear would occur. This is the basic reason why the adhesive pads are constructed in a hierarchical manner. In addition, fiber bundling is reduced if the fibers are not smooth but have protrusions [16, 17], and this ‘trick’ is used in Nature, see Fig. 5.

If the terminal plates are too thin or too long, they may self-bond as indicated in Fig. 4, right, or bond to each another (plate-plate bonding). Self-bonding and plate-plate bonding are reduced if the plates are not perfectly flat but slightly corrugated. This may be the reason why the terminal plates in most cases are slightly curved (cup-like) (see also [18]), see Fig. 7. Figure 6 shows a beetle terminal plate adhering
Lizards are the heaviest living objects on this planet that are able to adhere to, e.g., a rough vertical stone wall. Since the surface area of a body increases more slowly than the volume (or mass) with an increase of the linear size of the body, the adhesive system in large living bodies such as lizards must be more effective (per unit attachment area) than in smaller living objects such as flies or beetles. This implies that lizards have the most effective adhesive system in biological evolution for the purpose of locomotion. This is confirmed by electron microscopy studies.
which show that the fibers and plates are much thinner for lizards as compared to flies and bugs, see Fig. 7. This will result in a more compliant surface layer, and larger (relative) area of real contact and less stored elastic energy (per unit area), for the lizards as compared to insects. In addition, while the fibers are mostly unbranched for flies, bugs and beetles, they are always branched for lizards. Thus, for insects the fibers are so thick that no (or negligible) fiber bundling occurs, while for lizards the (terminal) fibers are so thin that bundling would occur if the fibers would be unbranched.

Lizards use dry adhesion, i.e., no liquid is injected in the contact area between the thin plates (which are just a few nanometers thick at the thinnest place) and the rough substrate [20]. On the other hand, flies, bugs and beetles have such large and thick terminal plates that under dry condition only negligible adhesion probably would occur to rough substrates, and for this reason they inject a (wetting) liquid in the contact region between the plates and the substrate [17, 21, 22]. A wetting liquid will be able to fill out the space between the plates and the substrate and form capillary bridges. If $d$ is the thickness of a capillary bridge, a (negative) pressure of the order of $-2\gamma/d$ (where $\gamma$ is the liquid surface tension) will prevail in the liquid bridge and for micrometer (or less) thick liquid films this pressure is typically $\sim-1$ MPa (or more), and will give rise to strong adhesion even if the area of real contact between the solid plates and the substrate is very small, see Fig. 8. Figure 9 shows the contact density of fibers (which is inversely related to the thickness of the fibers) as a function of body mass for different insects and lizards.

The liquid injected by insects seems to be a two-component emulsion comprising a water-soluble fraction and lipid-like nano-droplets [41]; this liquid has been optimized by natural selection to wet most surfaces to which the insect has to adhere.

We mentioned above that the terminal plates are curved (see Fig. 7), and that the physical origin of this may be to avoid self-bonding. Another reason may be that for rough surfaces, and for wet condition, a much stronger capillary bridge may form if the terminal plate is curved downwards at its edges, towards the substrate.
Figure 8. (a) For very rough surfaces, the area of real contact is very small, and the adhesion is negligible. (b) In this case a thin film of a wetting liquid may enhance the effective adhesion by bridging the gap between the surfaces. A (wetting) liquid film with thickness $d$ gives rise to a negative pressure $p \approx -2\gamma/d$ in the region between the two solids.

Figure 9. Relationship between contact density of hairy pads and body mass for animals. Adopted from Ref. [17].

In this case, for a wetting liquid the thickness $d$ of the liquid film at the boundary of the contact region may be much smaller than for a flat plate or a plate with opposite curvature, see Fig. 10. Since the (negative) pressure in the liquid capillary bridge is proportional to $\sim 1/d$, this will give rise to a much larger adhesion than for a flat plate, or a plate with opposite curvature. Close inspection of the electron microscopy images in Fig. 7 reveals that the distal features are often curved as in Fig. 10 to enhance the strength of capillary bridges. In any case, it seems to be clear that natural selection has optimized the shape of the terminal plates to maximize the adhesion. Wet adhesion for smooth adhesive pads will be discussed in Section 5.3 and illustrated with tree frog toe pads.
4.3. Adhesion on humid and flooded surfaces

The reader can easily convince himself (or herself) that a Scotch tape cannot be used when the substrate is wet. Since the surface of a Scotch tape is compact and locally flat it will take very long time to reduce the water film thickness to the nanometer range where the van der Waals interaction may give rise to bonding between the walls.

How is it possible for a lizards to move on a vertical stone wall during heavy rain (flooded surface)? The van der Waals interaction between two surfaces is effectively very short-ranged, and is negligibly small already at a separation of the order of a few nanometers. Thus the first step in building up adhesional contact is that the water must get squeezed out almost completely between the lizards toe pad and the stone wall. This is a very complex problem in elastohydrodynamics [23], but it is clear that the open structure of toe pad fiber array system will facilitate the squeeze-out of the liquid, by allowing the liquid to flow laterally in the space between the fibers (see also Section 5.4). This flow channel becomes very important when the effective water film thickness becomes small enough since for flat surfaces the time $t$ it takes to squeeze the liquid film down to the thickness $d$ diverges as $t \sim d^{-2}$. Complete squeeze-out of the liquid between the thin plates and the solid wall is unlikely to occur, since most stone walls consist of polar oxides which are hydrophilic making a dewetting transition unlikely to occur [24–29]. However, if the liquid layer thickness is $\sim 1$ nm (or less), and if the van der Waals interaction between the solid walls is attractive [31] (which is likely to be the case for the present system involving a keratin-water-stone interface), the interaction may be strong enough to allow the lizard to be able to move on a stone wall also under flooded conditions.
Recently it has been demonstrated experimentally that the pull-off force for a single fiber-plate from a flat glass surface submerged in water is about six times smaller than under dry conditions [30]. That is, the high permittivity of water reduces the van der Waals interaction between the solids [31] and, furthermore, a thin (a few monolayers) layer of water may separate the solids in the contact region giving rise to the small observed adhesional interaction. It is clear that the adhesion force of a whole gecko foot is reduced substantially and this seems to be in agreement with circumstantial evidence from the observation of geckos when running on wet surfaces.

4.4. Self-cleaning adhesive: origin of resistance towards contamination

Lizards can move on dirty surfaces, e.g., a dirty vertical stone wall. Since the lizard toe pad is able to bond strongly to solid surfaces, one would expect that small solid particles, e.g., stone fragments, dust or pollen, will bond to the pad surface, which will get quickly ‘passivated’. However, this does not seem to occur, and the lizards never clean the toe pads by grooming or liquid secretion, in contrast to flies, bugs and beetles which keep their attachment pads clean by grooming or liquid secretion. In fact, the lizards toe pad retain their stickiness for \( \sim 1/2 \) year (which is the time period between molts) seemingly without being cleaned. It has recently been suggested [32] that small solid particles may bond more strongly to the substrate surface (e.g., a stone wall) than to the toe pad so that after pressing a contaminated toe pad against a clean surface, the particles are removed from the toe pad. This does not seem to me as a plausible explanation since in such a case a Scotch tape contaminated by similar particles should bond strongly to solid surfaces \( \text{via} \) the particles, which is not the case. In fact, if a Scotch tape is squeezed just a couple of times against a dirty surface it will permanently lose its adhesive properties. Thus, one may ask how the lizard is able to keep its attachment pads clean enough to be able to move on dirty solid walls.

This author believes that the explanation for the remarkable self-cleaning properties of the lizard adhesive pads is due to minute lateral movements of the toe pads relative to the substrate which is able to scratch away the particles. It is known that in order to bond strongly to a substrate, the lizard must shear the toe pad in a special direction in order to line-up (or bend) the bonding plates into a position that gives strong bonding to the substrate. It is suggest that motion in the opposite direction, while the toe pad is squeezed against the (rough) substrate, will scratch away solid particles trapped on the toe pad surface, see Fig. 11. A similar picture of self-cleaning has recently been presented by Hui et al. [33].

4.5. Deterioration of adhesive system and fiber wear

Lizards have the most highly optimized adhesive system used for locomotion. Since the adhesion tends to increase when the fibers and plates are made thinner, it is likely that the thicknesses of the lizards fibers and plates are close to the limit of...
what is possible from the point of view of stability and strength, which is consistent with experimental observations. Thus, broken fibers adhering to glass have been observed after shearing the toe pad along the surface [35]. Since the lizard usually does not need to adhere to very smooth surfaces, such as a glass surface, the plate-substrate bonding will in most cases be much weaker than for the glass surface, and the toe pad wear (per unit distance moved) correspondingly much smaller. Nevertheless, it has been shown that for lizards in their natural environment, the toe pad-substrate adhesion rapidly decreases after molt [34, 35], and this is most likely due to fiber wear.

4.6. Attachment and detachment

Experiments have shown that a 25 g heavy lizard may bond so strongly to a flat substrate that a force of the order of \( \sim 10 \) N, or more, may be necessary to pull-off the lizard from the substrate. The bonding to rough substrates may be much weaker but still strong enough for the lizard to move rapidly on the surface. Here two questions are addressed: (a) Why does the lizard keep its legs and arms pointing away from its body with small angle \( \theta \) to the substrate, as illustrated in Fig. 12 for a gecko climbing a bamboo tree? (b) How is it possible for the lizard to rapidly break the toe pad-substrate bond during rapid motion on the substrate?
Both problems are related to interfacial crack propagation (or peeling), and can be understood by a simple analogy with peeling a Scotch tape.

Consider a thin elastic film bonded to a flat substrate as indicated in Fig. 13(a) and (b). If the elastic energy stored in the film does not change during pull-off, the normal component of the pull-off force is given by $F_\perp = F \sin \theta = \Delta \gamma B \sin \theta / (1 - \cos \theta)$ where $\theta$ is the peel angle and $B$ the width of the film. For small peel angle this gives $F_\perp \approx 2 \Delta \gamma B / \theta$ so that the (normal) pull-off force diverges as the peel angle $\theta \to 0$. This is the reason why a very large pull-off force is necessary to remove a rigid block from a flat substrate if a strip of Scotch tape has been glued on the block on the side which is in contact with the substrate; this case corresponds to $\theta = 0$. It is clear that the lizard, by applying muscle force, is able to keep the angle $\theta$ between the arms (and legs) and the substrate very small (as in Fig. 12). This will maximize the pull-off force, which may be important on very rough and contaminated surfaces.

In order to quickly break the toe pad-substrate bond during fast motion on the substrate, the peel angle $\theta$ should be large. In particular, note that $F_\perp \to 0$ as $\theta \to \pi$. Although this limiting case cannot be realized by the lizard, a large peel angle results from the novel way in which the lizard breaks the toe pad–substrate contact by rolling (or peeling) out the toe, from the tip of the toe [36], see Fig. 13(c). It is also likely that at any given time the lizard will only attach a large enough
fraction of the toe pad fibers to the substrate surface, as is necessary to obtain sufficient adhesion.

4.7. Uniqueness of biological adhesive systems for locomotion

In nature two different types of adhesive pads are used for locomotion, involving either smooth or hairy attachment pads. Hairy adhesive organs have evolved independently at least three times in lizards [37], at least three times in insects [38], and occur in three phylogenetically distant groups of spiders [39, 40]. This suggests that hairy pads represent an optimum design for attachment, and it is likely that many living objects on other planets in our universe will make use of similar hairy attachment organs for locomotion.

It is clear that a detailed understanding of the function of biological adhesive systems used for locomotion may result in new improved synthetic adhesives, based on similar principles as in biological adhesive systems. Such systems will have great advantages over adhesives used today, and may make new applications possible such as wall-climbing robots.

5. SMOOTH ATTACHMENT PADS

All animals which use smooth attachment pads inject a wetting liquid in the contact area in order to increase the adhesion. In this section some aspects of wet adhesion for tree frogs are discussed, but the results may also be relevant for other animals using smooth adhesive pads, e.g., grasshoppers [42].

5.1. Toe pad construction

Figure 14 shows the toe pad of a tree frog [43]. Note that the pad surface is covered with an array of hexagonal (epithelial) cells (diameter $D_1 \sim 10 \mu m$) separated by large channels (grooves) (width $W_1 \approx 1 \mu m$, height (or depth) $H_1 \approx 10 \mu m$) that contain the liquid (watery mucus) which provides bonding of the toe pad. Figure 15 shows a magnified view of a few of the hexagonal cells or blocks. The surface of each of these large blocks contains peg-like projections which we will refer to as the small blocks (diameter $D_2 \approx 0.2 \mu m$) surrounded by small channels (see Fig. 16) (width $W_2 \approx 40 \text{ nm}$, height $H_2 \approx 0.2 \mu m$).

We will assume that the (mucus) liquid wets the surface of the toe pad. The free energy of the system is minimized when the liquid is localized to the channels, and if there is more liquid than can be contained in the channels it will also form a thin film on the (outer) surface of the toe pad. However, since the evaporation rate will be much faster from this area it is possible that under normal circumstances only the channels are filled with liquid. The liquid is secreted from glands that open into the channels between the blocks. Measurements have shown that the liquid viscosity $\eta \approx 0.0014 \text{ Pa s}$ (i.e. about 40% larger than for water) [43] and the surface tension $\gamma \approx 0.07 \text{ J/m}^2$. 
Figure 14. Tree frog toe pad. The diameter of the toe pad is of order $\sim 1$ mm. Note the hexagonal array of cells or blocks, separated by grooves or channels. The diameter of one hexagonal block is of order $\sim 10\, \mu$m. Adapted from [43].

Figure 15. Magnified view of tree frog toe pad. The diameter of one hexagonal cell (or block) is of order $\sim 10\, \mu$m. Adapted from [43].

5.2. Toe pad function

The channels between the blocks (see Figs 15 and 16) may have at least three functions:
(A) The bending elasticity of the toe pad on distances larger than the size of the blocks will be reduced by the channels; this will increase the toe pad-substrate contact area and adhesion.

(B) The liquid stored in the channels will act as a liquid reservoir which will facilitate fast adhesion to rough substrate surfaces. In Section 5.3 this point is discussed, which may be crucial for strong and fast adhesion to rough surfaces.

(C) The channels will facilitate the squeeze-out of liquid between the toe pad and the substrate, e.g., during rain. During fast pull-off the channels between the cells at the outer boundary of the toe pad may close, resulting in a suction-cup type of effective “adhesion” on flooded surfaces, see Section 5.5.

We now consider (qualitatively) the liquid flow at the interface upon forming and breaking the pad-substrate contact. When the frog toe pad comes in contact with a substrate surface, liquid is pulled out from the channels because of capillary suction, see Fig. 17. If the separation $h$ between the solid walls at the toe pad-substrate interface is smaller than the width $W$ of the channels, the pressure in the film between the toe pad and the substrate will be lower than in the grooves, resulting in the flow of liquid into the space between the toe pad and the substrate. Since all the grooves are connected laterally, liquid will flow laterally within the network of grooves in such a way as to conserve the volume of liquid. For substrates with large enough surface roughness, there will be regions between the surfaces where the height $h(x, y) > W$, and when the liquid reaches such region the flow will stop, see Fig. 18. During pull-off the liquid (or part of it) may be pulled back into the grooves by capillary forces. That is, when the separation $h$ becomes larger than the width $W$ of the grooves, the free energy for the system is reduced if the liquid
Figure 17. When the frog toe pad comes in contact with a substrate surface liquid is pulled out from the channels because of capillary suction. If the separation $h$ between the solid walls at the toe pad-substrate interface is smaller than the width $W$ of the channels, the pressure in the film between the toe pad and the substrate will be lower than in the grooves, resulting in the flow of liquid into the space between the toe pad and the substrate. Since all the grooves are connected laterally, liquid will flow laterally within the network of grooves in such a way as to conserve the volume of liquid.

Figure 18. For substrates with large enough surface roughness, there will be regions between the surfaces where the height $h(x, y) > W$, and when the liquid reaches such region the flow will stop.

is transferred back to the grooves, see Fig. 19, where the liquid flow direction is indicated by the vertical arrows. This “conservation” of liquid may be important during fast movement where the frog toe pads could become dry if the liquid would remain trapped on the substrate surface.

5.3. Wet adhesion

Let us first consider the case of flat surfaces with a network of channels as illustrated in Fig. 20. If the width $W$ of the channel is larger than the spacing $h$ between the solid walls (as in Fig. 20) the local liquid pressure in the film between the flat surfaces will be lower than in the channel, and liquid will rapidly be sucked out from the channel. If the liquid completely wet the surfaces the pressure of the liquid in the thin interfacial film will be of order $p_1 \approx -\gamma/r$, where the radius of curvature $r = h/2$. Similarly, the pressure of the liquid in the channel will be $p_0 \approx -\gamma/r^*$, where $r^* = W/2$. The pressure difference $p_1 - p_0 < 0$ will result in liquid flow
Figure 19. During separation of toe pad from the substrate, liquid will flow back into the channels or grooves when the separation between the solid walls is larger than the width of the channels, i.e., $h > W$. The liquid flow direction is indicated by the vertical arrows.

Figure 20. Model problem with liquid flow between smooth flat surfaces (see text for details).

From the channel into the space between the parallel surfaces. We can estimate the flow velocity $v$ in the thin liquid film between the solid walls using the equation

$$ -\nabla p + \mu \nabla^2 v = 0, $$

which in the present case, if $W \gg h$, takes the form

$$ 2\gamma(h^{-1} - W^{-1})/L \approx \mu 12\tilde{v}/h^2, \quad (1) $$

where $\tilde{v}$ is the liquid velocity averaged over the thickness $h$ of the film. Here we have used that the liquid velocity must vanish on the surfaces $z = 0$ and $z = h$, i.e., $v(z) = 6\tilde{v}z(h - z)/h^2$. If $W \gg h$ we obtain from (1):

$$ \tilde{v} = \gamma h/6\mu L. \quad (2) $$

Next, since $v = \dot{L}$ we obtain from (2):

$$ L \ddot{L} = \gamma h/6\mu $$
or, if \( L(0) = 0 \),
\[
L^2(t) = \gamma h t / 3\mu. \tag{3}
\]
Thus, the time \( t_0 \) for the liquid film to extend the distance \( L_0 \) is given by
\[
t_0 = \frac{3\mu L_0^2}{\gamma h}. \tag{4}
\]

We are interested in the contact between a toe pad with a network of channels, and a rough surface. If the root-mean-square roughness of the substrate surface over the lateral size of a big block (which is of order 10 \( \mu m \) ) is denoted by \( h_0 \), then the ‘natural’ separation between the surfaces at the interface is likely to be of order \( h_0 \). If \( h_0 \approx 0.1 \mu m \) and if \( L_0 \) is chosen to be of order of the size of the big blocks (approx. 10 \( \mu m \) ) we obtain for water (\( \gamma \approx 0.07 \) N/m and \( \mu \approx 0.001 \) Pa s) \( t_0 \approx 4 \times 10^{-5} \) s.

We conclude that the spreading of the liquid at the interface will occur very fast and after a short time the liquid film will cover the most of the interface. For rigid solids this will result in the maximal adhesion force of order \(-p_0A_0\), where \( p_0 \) is the (negative) pressure in the film and \( A_0 \) the nominal area of the contact region. If liquid still occurs in the large channels, \( p_0 = -2\gamma/W \approx 0.1 \) MPa. This stress is much larger than the stress which is obtained if the weight of a tree frog is divided by the total toe pad area \([44]\): \( p \approx 0.001 \) MPa. Thus the capillary stress \( p_0 \) is typically \( \sim 100 \) times larger than the \( p \). However, the bond between the toe pad and the substrate is not broken uniformly over the contact area during pull-off but rather \textit{via} crack propagation (or peeling) from the periphery towards the center (see below).

Let us now discuss the friction force between the toe pad of a frog and the substrate. Since the total force acting on the frog must vanish (as long as the frog does not move), the attractive capillary force \(-p_0A_0\) (plus the contribution from the weight of the frog) must be balanced by a repulsive force acting in the area of real (atomic) contact between the frog toe pad and the substrate. Since the regions where the solids are separated by more than just a few nanometers of (water-like) liquid will contribute with a negligible friction force during lateral sliding, the friction force will arise almost entirely from the area of atomic contact. Experiments have shown that when a toe pad is in contact with a smooth glass surface, the area of atomic contact (where the surfaces are separated by at most \( \sim 1 \) nm) is of order 10\% of the nominal contact area \([43]\). For the same system experiments have shown that the nominal frictional shear stress is of order \( \sim 10^3 \) Pa (which is just large enough for the tree frog to move on a vertical surface), so that the frictional shear stress in the area of atomic contact must be of order \( \sim 10^4 \) Pa. This shear stress is small compared to the shear stress which acts in most dry sliding contacts (where, however, the normal stress in the contact areas is much higher (typically of order 1 GPa for glassy polymers) than in the present case), which for (glassy) polymer materials may be of order \( 10^7 \) Pa. However, the shear stress is similar to what has been observed for boundary lubricated surfaces in water. Thus, in Ref. \([45, 47]\) it
was observed that the shear stress was of order $\sim 10^4$ Pa for mica surfaces covered by organic grafted molecules and sliding in water.

The separation of a toe pad from a substrate occurs by crack propagation (or peeling) from the periphery of the contact area. Because of stress concentration at the crack tip, this gives a much smaller pull-off force than the force $-p_0 A_0$ which would result if the bonds at the interface would break simultaneously during pull-off. If the toe pad can be approximated as a homogeneous spherical cup the pull-off force $F$ would be given by the JKR expression [46, 47]

$$F = \frac{3\pi}{2} R \gamma_{\text{eff}},$$

(5)

where $\gamma_{\text{eff}}$ is the effective interfacial energy, which can be estimated as follows. Assume that the (average) separation between the solids at the interface $h \ll W$. During separation, at the crack edge the liquid film thickness is equal to $W$ (see Fig. 21). Thus, the work (per unit area) necessary to separate the surfaces must be $\gamma_{\text{eff}} \approx (W - h) p_0 \approx W p_0 = W 2 \gamma / W = 2 \gamma$. Here we have assumed that the separation speed is so low (at least until the onset of the snap-off instability) that the liquid can flow into the grooves in such a way that the film thickness always takes its equilibrium value $W$ at the crack edge. Assuming that the radius of curvature of the toe pad is $R \approx 1$ cm and using the surface tension of water ($\gamma \approx 0.07$ N/m) we obtain the pull-off force for one pad $F \approx 0.006$ N. The mass of a tree frog is typically $m \sim 0.01$ kg corresponding to the gravitational force 0.1 N. Thus, if all the fingers are attached to the substrate, the theoretical pull-off force $\sim 0.1$ N may be similar than the weight of the frog.

Experiments have shown that the toe pad material of grasshoppers is highly viscoelastic (like rubber), and the same may be true for the tree frog toe pads. Depending on the pull-off velocity, viscoelasticity of the pad material can result in a strong enhancement of $\gamma_{\text{eff}}$. For a (homogeneous) viscoelastic solid [48, 49]

$$\gamma_{\text{eff}} \approx \gamma_0 (1 + f(T, v)),$$

(6)

where $f(T, v)$ is due to viscoelastic deformation close to the crack tip, with $f \to 0$ as the crack tip velocity $v \to 0$. For rubber-like materials the enhancement factor $f$ could be as large as $10^3$ or $10^4$. Recent experiment have shown that there may be

Figure 21. During pull-off an opening crack propagates (velocity $v$) at the pad-substrate interface (see text for details).
a similar enhancement factor for the toe pad of grasshoppers and most likely for smooth adhesive pads in general. Thus, experiments by Goodwyn et al. [42] found $\gamma_{\text{eff}} \approx 10 \text{ J/m}^2$ for the toe pads of two different types of grasshoppers, and since one expect $\gamma \approx 0.07 \text{ J/m}^2$ due to capillary bridges, one obtains $f \approx 140$ at the crack tip velocities probed in the experiments by Goodwyn et al. This would result in a strongly enhanced pull-off force which would allow the tree frog to adhere to even very rough surfaces inclined at any angle relative to the earth gravitational force.

The toe pad bulk viscoelasticity, which may result in a strong increase in $\gamma_{\text{eff}}$, may also be importance for sliding friction on rough substrates, and may result in very large sliding friction as observed for rubber materials. Thus, during sliding the substrate asperities generate pulsating deformations of the pad material and if the pad material behaves as viscoelastic at the perturbing frequencies, a very large friction may result as observed for rubber sliding on rough substrates [1, 50]. We note that this is the case even if the pad and the substrate are separated by a very thin viscous liquid film, assuming that the film thickness is smaller than the size of the (relevant) substrate asperities. This effect has, in fact, been observed in a recent experiment for rubber lubricated by different organic oils and sliding on a rough substrate [51].

5.4. Squeeze-out

Tree frogs can adhere and move on rough (hard) vertical surfaces during heavy rain where the surfaces are flooded with water. This cannot be explained by the capillary bridge picture since no capillary bridges can form on a flooded surface. We will discuss how the adhesion may be generated for flooded surfaces. Here we first consider the liquid squeeze-out, which is a prerequisite for non-negligible adhesion and friction.

Consider the squeeze-out of liquid from the space between two solid bodies. Assume first rigid solids with perfectly flat surfaces without draining channels. Since in the present applications the pressure is low, we can assume an incompressible liquid so that

$$\nabla \cdot \mathbf{v} \approx 0,$$  \hspace{1cm} (7)

$$-\nabla p + \mu \nabla^2 \mathbf{v} \approx 0.$$  \hspace{1cm} (8)

Assume that $h(t)$ is the separation between the surfaces at time $t$. We will use simple (dimensional) arguments to obtain an approximate form of $h(t)$. Assume that the nominal contact region is circular with the diameter $D_0$. Assume that $h(t)$ changes by the amount $\Delta h < 0$ during the time interval $\Delta t$. Liquid mass conservation gives

$$-D_0^2 \Delta h \approx D_0 h \nu \Delta t$$

or

$$\dot{h} \approx -h \nu / D_0,$$  \hspace{1cm} (9)
where \( v \) stands for the radial component of the liquid velocity averaged over the thickness \( 0 < z < h \) of the liquid film. Since the flow velocity vanishes on the surfaces \( z = 0 \) and \( z = h \) the strongest spatial variation in \( \mathbf{v}(x, t) \) will be derived from the variation of \( \mathbf{v} \) with \( z \) so that, from dimensional arguments, \( \nabla^2 \mathbf{v} \sim v/h^2 \). Thus, (8) gives \( p/D_0 \approx \mu v/h^2 \), where \( p = F_N/\pi D_0^2 \) is the squeezing pressure. Combining this with (9) gives

\[
\dot{h} \approx -\frac{\alpha p}{\mu D_0^2} h^3, 
\]  
(10)

where \( \alpha \) is a number of order unity. An accurate calculation gives \( \alpha = 4/3\pi \). If the external load \( F_N \) is constant it is easy to integrate (10) to obtain

\[
\frac{1}{h^2(t)} - \frac{1}{h^2(0)} \approx \frac{\alpha pt}{\mu D_0^2}. 
\]  
(11)

Next let us assume that the substrate surface has vertical draining channels as in Fig. 20. Let us first consider the situation where \( h \) is so small (but not too small — see below) that nearly all the squeeze-out of the liquid occurs via the channels. Consider first the flow in one channel. We assume that the height \( H_1 \) of the channel is much larger than its width \( W_1 \), see Fig. 20. In this case we expect the strongest spatial variation of \( \mathbf{v}(x, t) \) to be derived from the variation of \( \mathbf{v} \) with \( y \) so that, from dimensional arguments, \( \nabla^2 \mathbf{v} \sim v/W_1^2 \), where \( v \) is the flow velocity in the channel, averaged over the channel cross-sectional area \( H_1 W_1 \). Thus, (8) takes the form

\[
p/D_0 \approx \mu v/W_1^2. 
\]  
(12)

Let us now assume a network of channels on the surface forming a square (or hexagonal) lattice with the ‘lattice constant’ \( D_1 \). Liquid mass conservation gives

\[
-\dot{h}D_0^2 \approx NvH_1 W_1, 
\]

where \( N \approx D_0/D_1 \) is the number of channels crossing the outer boundary of the nominal contact area. Thus we obtain

\[
\dot{h} \approx -v \frac{H_1 W_1}{D_0 D_1}. 
\]  
(13)

From (12) and (13) we obtain

\[
\dot{h} \approx -\frac{p W_1^3 H_1}{\mu D_0^2 D_1} = -\frac{\alpha p}{\mu D_0^2} h_0^3, 
\]  
(14)

where

\[
h_0 = \left( \beta \frac{W_1^3 H_1}{D_1} \right)^{1/3}. 
\]  
(15)

and the dimensionless number \( \beta \) is of order unity. We can interpolate smoothly between the limits (10) and (14) using

\[
\dot{h} \approx -\frac{\alpha p}{\mu D_0^2} (h + h_0)^3. 
\]  
(16)
Thus, the draining channels will effectively increase the separation between the surfaces with the distance \( h_0 \), and hence facilitate the squeeze-out. Equation (16) is only valid until the film thickness \( h \) reaches some lower critical value \( h_1 \) which can be determined as follows. For \( h > h_1 \) (but \( h < h_0 \)) the ‘bottleneck’ for squeeze-out is the viscous resistance to liquid flow in the channels. For \( h < h_1 \) the ‘bottleneck’ for squeeze-out is instead the viscous squeeze-out (transfer) of the liquid from the block-substrate \( D_1 \times D_1 \) interface area to the channels. To study this quantitatively, let us consider the squeeze-out of the liquid film from a basic unit (area \( \sim D_1^2 \)) to the surrounding draining channels. If the film is very thin the squeeze-out is very slow and the liquid pressure in the draining channels will be similar to the external (atmospheric) pressure. In this case the squeeze-out of the thin liquid film into the draining channels will be mathematically identical to the squeeze-out of the liquid between smooth surfaces studied above [equation (10)], but with \( D_0 \) replaced by \( D_1 \). Thus, for a very thin liquid film we have

\[
\dot{h} \approx -\frac{\alpha p}{\mu D_1^2} h^3.
\]  

(17)

We can determine \( h_1 \) by the condition that the squeeze rates (14) and (17) are equal:

\[
\frac{h_1^3}{D_1^2} \approx \frac{h_0^3}{D_0^2}
\]

or

\[
h_1 = h_0 \left( \frac{D_1}{D_0} \right)^{2/3} = \left( \frac{\beta W_1^3 H_1 D_1}{D_0^2} \right)^{1/3}.
\]

(18)

From the analysis above it is clear that if the squeeze-pressure \( p \) (or the force \( F_N \)) is constant the liquid film thickness will first decrease with time as \( \sim t^{-1/2} \) until \( h(t) \) reaches \( \sim h_0 \) which takes the time

\[
t_0 \approx \frac{\mu D_0^2}{\alpha h_0^2}.
\]

(19)

From here on the squeeze-out will occur mainly via the draining channels, and \( h(t) \) will decrease linearly with time until \( h(t) \approx h_1 \). If \( h_1 < h_0 \) the time \( t_1 \) it takes to decrease \( h(t) \) from \( h_0 \) to \( h_1 \) will be [from (14)] of order \( t_1 \approx t_0 \) so the total squeeze-out time to reach \( h = h_1 \) will be of order \( 2t_0 \). If the basic \( D_1 \times D_1 \) units have perfectly flat surfaces, for \( t > 2t_0 \) the squeeze-out will again follow the \( t^{-1/2} \) time dependence. However, the squeeze-out will occur faster if the \( D_1 \times D_1 \) surface units have draining channels with appropriate width \( W_2 \), depth \( H_2 \) and density. It is clear that for maximum squeeze-out speed the system has a hierarchical distribution of draining channels where a basic unit surrounded by ‘large’ draining channels has a network of much smaller draining channels and so on. The theory above can be used to estimate the squeeze-out time for such complex hierarchical systems. We also note that, to some extent, the channels can be replaced by surface roughness. However, in this case the squeeze-out channels will not have a uniform
size but will exhibit strong fluctuations leading to the possibility of trapped liquid (liquid islands), in particular when the elastic deformation of the solids is taken into account. Such trapped or “sealed off” water islands have recently been suggested to be the origin of why tires on wet roads at low car velocities exhibit $\sim 20–30\%$ lower friction than for dry road surfaces (the trapped water effectively smoothens the road surface profile resulting in less asperity-induced viscoelastic deformation of the rubber).

As an application, consider the tree frog toe pad. In this case $D_0 \approx 1\,\text{mm}$, $D_1 \approx 10\,\mu\text{m}$, $H_1 \approx 5\,\mu\text{m}$ and $W_1 \approx 1\,\mu\text{m}$. Thus, $h_0 \approx 1\,\mu\text{m}$ and $h_1 \approx 50\,\text{nm}$. Using the measured viscosity (similar to that of water) $\mu = 0.0014\,\text{Pa}\,\text{s}$ and $p = 10^4\,\text{Pa}$ (typical frog toe squeezing stress) we obtain the squeeze-out time $2t_0 \approx 0.1\,\text{s}$.

5.5. Adhesion on flooded surfaces

It has been observed that tree frogs are able to adhere and move on vertical solid walls also during heavy rain where the substrate surface is flooded by water [44]. The reason for this is non-trivial because under flooded conditions it appears that no capillary bridges can form and one would, therefore, expect that only a negligible force will be required to separate the surfaces, at least during slow separation. Here this remarkable problem is analyzed and some explanations are suggested.

5.5.1. Long-range interactions between solids in liquids. Solid surfaces in water sometimes interact with long-range forces derived from ion adsorption on their surfaces [24]. Such forces can be both attractive (if the charges of the adsorbed ions on the two surfaces have opposite sign) or repulsive [24]. However, it is very unlikely that such forces are of any relevance for attachment systems in animals because animals must be able to adhere to many different types of surfaces (such as stone or leaf) with very different properties, and it is highly unlikely that these surfaces, if at all charged, would have the same sign of the charges (and opposite to that of the animal toe pad surface).

The long-range van der Waals interaction will also act between solids separated by a thin water layer. While the van der Waals interaction always is attractive between solids in vacuum, it can be either attractive or repulsive in a liquid [31]. However, it is highly unlikely that this interaction is important for animals which secrete a liquid because if it would be important in water, it would (usually) be even more important when no liquid separates the surfaces, and the animal would not need to secrete any liquid at all. Thus, it is highly unlikely that any long-range interaction is of important for animal locomotion on water covered surfaces.

5.5.2. Dewetting transition. Complete liquid removal from the region between closely spaced solids has been studied both experimentally and theoretically for several years [25–29]. A liquid film confined between two elastic solids with flat surfaces is thermodynamically unstable if

$$\gamma_{1L} + \gamma_{2L} - \gamma_{12} > 0,$$  \hspace{1cm} (20)
where $\gamma_{1L}$ and $\gamma_{2L}$ are the solid–liquid interfacial energies and $\gamma_{12}$ the solid–solid interfacial energy. In this case squeeze-out of the liquid may start by the formation (due to a thermal fluctuation) of a small dry patch, which then spreads laterally until the whole liquid film is expelled. However, for water this relation is unlikely to be obeyed for all surfaces to which the animal must be able to adhere. Thus stones, for example, are likely to have polar surfaces which are wetted by water, and it is unlikely that (20) will be obeyed for these substrates. In addition, if the liquid would be removed by a dewetting transition, then the contact region would be dry but we already know that the adhesion for the dry contact most likely is negligible (it is for this reason that the tree frog injects a wetting liquid into the contact area).

5.5.3. Viscous ‘adhesion’. When two closely spaced surfaces are separated rapidly in a liquid, strong effective adhesion may occur between the solids. The origin of this effect is the viscosity of the liquid: because of the viscosity, if the separation between the surfaces is very small it will take long time for the liquid to flow into the ‘empty space’ generated during the separation between the solids. This can result in a large negative pressure and even cavity formation between the surfaces of the solids [23, 52, 53]. This ‘viscous adhesion’ is a dynamical effect and disappears if the surfaces are separated very slowly. For rigid flat walls the magnitude of the attraction can be estimated from (10): when $\dot{h} > 0$ (separation) (10) gives $p < 0$ i.e., an effective attraction prevails between the solid surfaces during separation. A large pull-off force is only observed if the separation $h$ between the solids is very small (or the pull-off speed very high). That is, before strong adhesion is possible the liquid must be nearly completely removed (squeezed-out) from the region between the surfaces. An accurate analysis of this problem requires in general that one include the elastic deformation of the solids when determining the pull-off force.

In Section 5.4 we showed that the squeeze-out was facilitated by a network of draining channels on the the surface of the adhesive pad. Here we note that while these channels are ‘open’ during squeeze-out they may be closed during pull-off, at least close to the boundary of the contact region. The reason for this is that during pull-off there is lower pressure inside the contact area than outside, and there will be lateral (radial) forces acting tending to compress the contact area laterally, and this may close the space between the hexagonal units. This will slow down the flow of liquid into the region between the surfaces, which may strongly increase the pull-off force.

5.6. Detachment

The tree frog toe pads are detached from surfaces by peeling, the pads being removed from the rear forwards during forward locomotion up a vertical surface [54]. When the frog is induced to walk backwards down, peeling occurs from the front of the pad rearwards. Experiments have shown that during forward locomotion up a
vertical slope the detachment forces are much smaller than during backward walking down the slope. That peeling occurs automatically during forward locomotion is supported by the observation that frogs on a rotating vertical surface adjust their orientation back towards the vertical whenever their deviation from the vertical reaches \( \sim 85^\circ \). During forward locomotion peeling occurs as a natural consequence of the way in which the toes are lifted off surfaces from the rear forwards, while during backward locomotion it is an active process involving the distal tendons of the toes.

6. SUMMARY AND CONCLUSION

All natural surfaces have surface roughness on many different length scales. Natural selection has optimized the toe pads of many animals for maximum adhesion to natural surfaces. It is believed that the construction of the toe pads is mainly the result of two principles:

(a) Maximum adhesion requires using non-compact solids built from thin fibers and plates (or walls).
(b) The fibers and plates (or walls) cannot be too thin as this would result in collapse of the structures, e.g., fiber condensation.

Tree frogs and most insects use wet adhesion to adhere and move on many different surfaces, e.g., glass windows, stone walls, or plant leaves. Here we have discussed the origin of adhesion and friction for the tree frog but the results may be relevant for other animals using smooth adhesive pads, e.g., grasshoppers. In fact, the similarity between the adhesive pads of tree frogs and grasshoppers is very great, indicating highly optimized (by natural selection) and unique adhesive systems.

Considerable theoretical work has been devoted to adhesion to perfectly smooth substrates. For bioadhesion this special case is uninteresting since natural surfaces have always roughness, and it is only when this fact is taken into account that one can understand why natural selection has generated the adhesive structures observed in animals which rely on sticky toe pads for locomotion.

Acknowledgements

Tha author thanks K. Autumn, W. Federle and S. Gorb for useful communications. Also the Editors are thanked for drawing my attention to Ref. [33].

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