The design of the fly adhesive pad: distal tenent setae are adapted to the delivery of an adhesive secretion

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Flies (Brachycera) have adhesive pads called pulvilli at the terminal tarsomere. The pulvilli are covered by tenent setae, sometimes termed tenent hairs, which serve to increase the actual area of attachment to the surface. By using transmission and scanning electron microscopy it is shown that proximal and distal tenent setae have different ultrastructures. The design of distal adhesive setae is adapted for the release of adhesive substances close to the area of contact. It is concluded that secretion injection is precisely targeted under the distal tip of a single seta.

Keywords: cuticle; adhesive setae; leg; attachment; ultrastructure; Diptera

1. INTRODUCTION

'The structure and action of the Fly's foot have been so frequently treated of, and are so generally considered to be fully understood, that it may appear, at the first glance, as if nothing further could be done with so hackneyed a subject.'

Tuffen West (1862), p. 393

Interest in the mechanism of insects walking on smooth surfaces has a long history. The first reports, which described structures responsible for the adherence and provided ideas about possible mechanisms of attachment, are known from the seventeenth century (West 1862; Dewitz 1883, 1884; Dahl 1884, 1885; Rombouts 1884; Simmermacher 1884*a,b*). Different hypotheses, ranging from microsuckers to the action of electrostatic forces, have been proposed (Gillett & Wigglesworth 1932; Maderson 1964). However, most investigators have clearly shown the presence of an adhesive secretion in the contact area between pulvilli (adhesive pads) and substratum (Bauchhenss 1979; Walker *et al.* 1985). In her comprehensive electron microscope study, Bauchhenss (1979) showed that this non-volatile lipid secretion is produced in *Calliphora* flies by large cells located at the base of each pulvillus and stored within a 'spongy' layer of cuticle. The questions of where and how this secretion was released remained unanswered. Bauchhenss (1979) also described a well-developed system of porous channels at the base of the tenent setae located in the basal part of the pulvillus, and hypothesized their role in the release of the secretion onto the surface of the seta bases. However, investigators have usually found the secretion at the spatulate ends of the tenent setae (Walker *et al.* 1985), which means that it may be released in the area located close to the distal tip of such setae. Here, it is shown morphologically and experimentally that tenent setae located in the distal part of the pulvillus are responsible for secretion release very

close to the contact area between the seta tip and substratum. Setae located in the basal part of the pulvillus do not have such a mechanism. The two types of tenent seta design may be adaptations for attachment to a variety of substrata.

2. MATERIAL AND METHODS

Syrphid flies, *Episyrphus balteatus* (de Geer) (Diptera, Syrphidae), were captured in the Schönbuch forest near Tübingen (Southern Germany) and four different procedures were used.

(a) *Scanning electron microscope (SEM) study of pulvilli*

Tarsi fixed in 2.5% glutaraldehyde in phosphate buffer overnight were washed, dehydrated, critical-point dried, mounted on holders, sputter-coated with gold-palladium (10 nm) and examined in a Hitachi S-800 SEM at 20 kV.

(b) *Adherence of the tenent setae to glass*

Coverslips were dehydrated in absolute ethanol and absolute acetone. Tarsi cut off fresh-killed flies were carefully touched to the coverslip using fine forceps. Freshly attached pulvilli were studied in a fluorescent microscope in UV light (DAPI filter), air-dried preparations were studied in SEM.

(c) *Transmission electron microscope (TEM) study of ultrathin sectioned tenent setae*

Whole pulvilli were fixed for 12 h at 4 °C in 2.5% glutaraldehyde (in 0.01 M phosphate buffer at pH 7.3), and postfixed for 1 h in 1% osmium tetroxide in phosphate buffer at 2 °C. After washing, the preparations were stained for 1 h at 4 °C in 0.1% aqueous uranyl acetate solution, washed, dehydrated and embedded in a low-viscosity resin (Spurr 1969). Ultrathin sections were picked up on copper grids coated with a formvar film. Sections were stained with uranyl acetate and lead citrate, and observations were made with a Philips CM10 TEM.

Figure 1. *Episyrphus balteatus*, pulvilli. (a) Frontal aspect of the pretarsus. (b) Ventral aspect of the left pulvillus. BP, basal part; CL, claw; d, distal direction; DP, distal part; l, lateral direction; PU, pulvillus; TS, tenent setae; v, ventral direction.

(d) SEM study of semithin-sectioned resin-embedded cuticle

Dehydrated cuticle was embedded in a low-viscosity resin (Spurr 1969) and sectioned using a diamond knife (1–2 µm). Sections were picked up on circular coverslips covered with pioloform film, treated with Maxwell's solution (Maxwell 1978) for 2–5 min to remove the resin, washed, dehydrated, and studied in SEM. Measurements of structures were made using analySIS 2.1 image analysis software (Soft-Imaging Software GmbH) from digital images obtained directly from SEM.

3. RESULTS

Pulvilli are structures adapted for attachment to a variety of surfaces. They are ellipsoid in shape and composed mainly of flexible cuticle. The basal part of each pulvillus is hard. The whole pulvillus is connected to the tarsus by an elastic part containing resilin-like cuticle, which can be revealed by UV light in the fluorescence microscope. The area of a pulvillus is $6710 \pm 738 \mu\text{m}^2$ on forelegs, $7450 \pm 538 \mu\text{m}^2$ on middle legs, and $8297 \pm 1057 \mu\text{m}^2$ on hind legs ($n=6$). The dorsal cuticle of each pulvillus is strongly corrugated, and such corrugations are $2.50 \pm 0.70 \mu\text{m}$ wide ($n=31$).

The ventral surface of a pulvillus is covered by the tenent setae (see figure 1). The total number of tenent setae counted on a single pulvillus ranged from 740 for forelegs to 920 for hind legs. There are two types of tenent setae occurring on the ventral side of each pulvillus (figure 2). Setae of the first type occur at the basal part of the pulvillus (see figure 2c). They are spoon-like, $33.88 \pm 4.71 \mu\text{m}$ long ($n=49$) and $0.47 \pm 0.08 \mu\text{m}$ ($n=25$) wide, with a strongly compressed tip region, $0.18 \pm 0.02 \mu\text{m}$ thick (figure 2c). Tip width is $2.04 \pm 0.97 \mu\text{m}$ ($n=35$); tip area is $2.55 \pm 0.44 \mu\text{m}^2$ ($n=37$). Setae of the second type are located at the distal part of the pulvillus (figure 2a). They are characterized by an ellipsoid plate located at the distal tip of each seta. The greatest diameter of this end-plate is $2.17 \pm 0.18 \mu\text{m}$ ($n=42$), area, $3.90 \pm 0.39 \mu\text{m}^2$ ($n=22$). Its dorsal surface has small grooves $0.07 \pm 0.02 \mu\text{m}$ wide ($n=24$) and these grooves run parallel to the longitudinal axis of the hair shaft (figure 3b). The ventral surface also has fine grooves

$0.05 \pm 0.01 \mu\text{m}$ wide ($n=17$), again running parallel to the longitudinal axis of the shaft (figure 2a). The distal part of the seta shaft located just under the plate is thickened ($0.86 \pm 0.09 \mu\text{m}$ diameter, $n=20$). These type 2 seta have been termed tenent hairs or adhesive setae in the literature (Stork & Evans 1976; Walker *et al.* 1985).

Both types of seta are tube-like. Pairs of setae have a common basal part (figure 3a). A seta consists of two sub-units each $0.21 \pm 0.03 \mu\text{m}$ -thick ($n=34$) (figure 3b). In longitudinal and cross-sections the central parts of setae are electron-lucent as viewed in TEM (figure 2b,d). These electron-lucent areas may be interpreted as being composed of lipid-containing substances, most of which are dissolved out during the electron-microscopic preparation when ethanol and propylene oxide are being used. No openings were found in the distal part of type 1 setae. However, for type 2 setae there is transition between the central lumen of the shaft and the outside. This area is located in the postero-distal part of the seta between the seta thickening and distal plate (figure 2b) where large channels $0.1\text{--}0.4 \mu\text{m}$ -wide occur. The distal end of the seta is composed of two types of cuticle with different electron densities (figure 2b). The ventral grooves of seta tips were often covered with amorphous substances as observed in air-dried preparations of pulvilli attached to the coverslip and released after the drying procedure. In such pulvillus preparations, the distal parts of intact tenent setae were often also covered with secretion close to the region of channels. In preparations washed in a variety of solvents, such as ethanol, acetone and propylene oxide, the distal seta surface was almost clean.

The residual secretion remaining on the coverslips after detachment of tenent setae can be seen easily in the light microscope under phase contrast or in the fluorescence microscope. The SEM study of preparations of pulvilli attached to coverslips shows that lipid substances are not spread over the whole area of contact between the pulvillus and the substratum, but as discrete droplets just under the distal end-plate of the type 2 setae. Furthermore, the surfaces of seta bases remained clear after attachment; setae were very seldom glued to each other, and space between setae was usually not covered by the secretion. Such observations allow the conclusion that the

Figure 2. *Episyrphus balteatus*, two types of setae located in the distal (*a, b*: type 2) and proximal (*c, d*: type 1) parts of the pulvillus. Both seta types are tube-like and contain lipid substances. Type 1 setae (*c, d*) are compressed distally, but do not have any specialized structures at their tips. Type 2 setae (*a, b*) have grooves at the ventral surface of their end-plates and openings under the plate where secretions are released (black arrows). (*a, c*) Scanning electron micrographs; (*b, d*) transmission electron micrographs. DL, electron-dense layer; LU, lumen; PL, end-plate.

adhesive lipid-containing substances are targeted directly to the contact area between the distal plate of a single tenent seta and substratum (see figure 3).

4. DISCUSSION

There is a variety of insect attachment systems employing principles of friction and adhesion. Such systems serve mainly mechanical functions (Stork 1981; Schrott 1986; Gorb 1989, 1990*a, b*, 1991, 1993, 1996, 1997*b*). Generally, both these principles are based on the highest possible number of contact points between two surfaces (Bowden 1957). Adhesive pads of insects may be designed in a very different way, but their surfaces are usually adapted to fit the microtopography of surfaces so that the pulvillus is in contact with the maximum number of attachment points (Blackwall 1930; Slifer 1950; Kendall 1970; Edwards & Tarkanian 1970; Arnold 1974; Hennig 1974; Bauchhenss & Renner 1977; Bauchhenss 1979; Stork 1980*a, b*, 1983*a, b*; Röder 1984; Kennedy 1986; Pelletier & Smilowitz 1987; Wigglesworth 1987; Lees & Hardie 1988). All these systems are supplemented by adhesive secretions, the source and exit paths of which remain mainly

unknown. In ladybird beetles, these adhesive secretions consist of hydrocarbons and true waxes (Kosaki & Yamaoka 1996). The corrugations of the dorsal surface of the adhesive pads of flies and bugs have been interpreted previously as fluid-transporting structures (Ghasi-Bayat 1979; Ghasi-Bayat & Hasenfuss 1980*a, b*, 1981; Hasenfuss 1977, 1978). However, the present study shows that in flies the fluid is transported within the seta shaft and released at the terminal part of the seta.

The setae occurring on the ventral surface of the fly pulvillus are small cuticular protuberances, each derived from one epidermal cell (Whitten 1969). It is shown here that two setae have a common junction at their basis. This fact allows the suggestion that the single epidermal cell may produce two setae. Tenent setae bearing an end-plate have been described previously in flies (Walker *et al.* 1985) and beetles (Stork 1980*b*, 1983*b*, 1987).

There are several theories explaining how the fly holds on to a smooth surface. Walker *et al.* (1985) summarized them as follows: (i) the purely mechanical hold of setae; (ii) setae acting as suckers; (iii) electrostatic forces between setae and substratum (Maderson 1964); and (iv) the seizure theory of Gillett & Wigglesworth (1932).

Figure 3. *Episyrphus balteatus*, SEM-micrograph of the pulvillus attached to a coverslip (dorsal aspect). Distal end-plates are adhered to the glass. Two setae are joined at a common base. PR, pair of tenent setae with a joint basis; SB, two subunits coming off a single basis. Arrow indicates direction of pulling force by leg.

Experiments on chrysomelid beetles allowed Stork (1983a) to reject the named theories, and to conclude that cohesive forces plus surface tension of adhesive secretion plus molecular adhesion are involved in the mechanism of attachment of adhesive pads of the 'fly-like type'. Lipid vesicles have been found in the cells of the pulvilli (Bauchhenss 1979) and lipid-containing substances have been found when fly pads were applied to a surface

(Walker *et al.* 1985). This secretion seems to be critical for successful attachment to smooth surfaces. Indeed, flies lose the ability to walk on smooth inclines after walking for 15–30 min on a silica gel substrate (S. N. Gorb, unpublished data); similar results have been obtained for aphids (Dixon *et al.* 1990). It has been shown that the tarsal secretion in *Calliphora erythrocephala* is produced by cells within the pulvillus and stored within a 'spongy' layer of cuticle (Bauchhenss 1979). Bauchhenss (1979) hypothesized that the secretion is released through well-developed porous channels by the pressure exerted by the weight of the fly. Such porous channels occur in the cuticle underlying setae and on bases of setae located at the basal part of the pulvillus. The loss of secretion could be minimized by the return of secretion back into the cuticle when the fly detaches itself, owing to the capillarity of such a system.

Walker *et al.* (1985) doubted this hypothesis, but did not propose any ideas about secretion release. However, they observed in their SEM preparations that fluid secretion covers the spatulate ends of the tenent setae. In the present paper, the opening allowing fluid-secretion release from the tenent seta is shown. Results of experiments together with data from the TEM study suggest that the secretion is released close to the contact area between the distal seta end-plate and the substratum. A similar adhesive setae design also occurs in some muscid and calliphorid flies, such as *Calliphora erythrocephala* (see figure 4), *Lucilia caesar*, and *Musca domestica*.

The position of setae on the substratum is always the same when a fly holds on to an inclined surface (figure 5). It seems that the end of the tenent seta, together with the seta orientation, is adapted to release secretion when a pulling force is directed along the substratum surface to the proximal part of the pulvillus (figure 3b). When force is directed in the opposite direction, both types of setae can detach from the substratum and some part of the released secretion can be returned back into the channels of tenent setae.

The fact that tenent setae are adapted to release secretion distally does not exclude the idea that the porous-channel system is involved in secretion release. Porous channels are well-known structures, serving mainly a

Figure 4. *Calliphora erythrocephala*, right pulvillus. (a) Ventral aspect of the pulvillus; (b) tenent setae. BP, basal part; d, distal direction; DP, distal part; l, lateral direction; PL, end-plate. White arrowheads indicate opening locations at the ends of setae where secretions are released.

Figure 5. Scheme of position of type 1 (a) and type 2 (b) setae on the substratum. Dotted area indicates lipid-containing secretion. Black arrows indicate the route of secretion release. White arrow indicates direction of pulling force by leg.

transporting function (Locke 1961; Neville 1975). Some frictional devices such as microtrichia of the head-arresting system of dragonflies are supplemented with adhesive secretions, which are transported to the cuticle surface via porous channels (Gorb 1997a). In the case of fly pulvillus, the porous channels occur at the bases of type 1 setae, and presumably serve as an additional path for secretion release.

An interesting point is the origin of the distal openings. There are two hypotheses that can be suggested. The first is that the distal opening is a sort of porous channel penetrating the cuticle of the tip of each seta. In this case, the space within the tenent seta is part of the inside of the body of the fly (channel hypothesis). Evidence for this is that the lumen is directly connected with inner layers of cuticle of the pulvillus in the deepest portion of the seta (S. N. Gorb, personal observation). An alternative hypothesis is that the distal opening is an invagination. In this case, the lumen within the tenent seta is 'outer space' (invagination hypothesis). Possible evidence for this is the presence of an electron-dense layer covering the walls of the lumen. This layer may be interpreted as epicuticle. Each of these hypotheses needs more evidence.

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