The role of adhesion in prey capture and predator defence in arthropods

Oliver Betz[a],[*], Gregor Kölsch[b],[1]

[a]*Zoologisches Institut der Universität, Abteilung Evolutionsbiologie der Invertebraten, Auf der Morgenstelle 28, D-72076 Tübingen, Germany*
[b]*Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany*

Abstract

Adhesive devices are used by arthropods not only in terrestrial locomotion but also in prey capture and predator defence. We argue that the physical mechanisms involved in both these contexts must mainly be capillarity and the viscosity of an adhesive secretion, whereas other mechanisms, such as friction or intermolecular forces, are of minor importance. Adhesive prey-capture devices might function as passive devices or might be actively extended toward the prey, sometimes in a very rapid manner. Adhesive mechanisms used for predator defence might involve firm adhesion to the substratum or the discharge of a sticky secretion to immobilize the appendages of the opponent. We review the occurrence of adhesive devices as employed in both functional contexts across the Arthropoda and argue that these mechanisms are of particular importance for slow-moving and relatively clumsy life forms. We discuss three case studies in more detail. (1) *Loricera* larvae (Carabidae) use galeae with an extremely flexible cuticle in combination with an adhesive secretion. (2) Adult *Stenus* species (Staphylinidae) employ two highly flexible paraglossae that are covered by an adhesive emulsion of lipid droplets dispersed in an aqueous proteinaceous liquid. (3) Springtails often adhere to the mouthparts, the antennae, the legs, or other parts of the integument of *Stenus* larvae before being captured with the mandibles.
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1. Introduction

Arthropods make use of adhesive mechanisms in markedly different contexts, such as (1) walking vertically or upside-down on various natural surfaces (Stork, 1980b; Lees and Hardie, 1988), (2) resisting external detachment forces caused by wind gusts (Stork, 1980b) or attacking predators (Eisner and Aneshansley, 2000), (3) attaching to mating partners during copulation, or (4) holding onto the substratum in contexts such as phoresy or parasitism (Gorb, 2001). One additional hitherto neglected functional aspect of adhesive mechanisms involves prey capture. Such mechanisms are not only found in the form of passive devices, such as the well-known spider webs, but also as active systems that have mobile adhesive parts (Gorb, 2001), e.g. the adhesive lower surface of the tarsi of raptorial legs. Predation is widespread among the arthropods, occurring from the Onychophora to the Diptera, and

many arthropods live at the expense of other arthropods (Edwards, 1963). They have often evolved astonishing morphological and physiological specializations to overcome the escape mechanisms of their prey. Conversely, potential prey animals have developed effective defence mechanisms that help to avoid predation. The complex adaptations in predator-prey interactions are often interpreted in terms of an ongoing co-evolution of predator and prey (Dawkins and Krebs, 1979). One crucial factor in such 'arms races' is the capability of the predator to grasp the prey precisely and to retain a firm hold on its integument. In this context, many arthropods have evolved clamp-like structures, as in raptorial legs (Ass, 1973; Gorb, 2001). Other groups have developed specific adhesive organs that have the advantage that they can fix even fast fleeing prey at the moment of contact (Bauer and Christian, 1987), i.e. for a successful predatory strike, it is sufficient to hit the prey with some part of the sticky surface. Hence, organisms with adhesive prey-capture organs may not require particularly advanced sensory and neuromuscular mechanisms that assure the exact control of closing movements, as are necessary in clamp-like raptorial legs or mandibles (Gronenberg and Ehmer, 1995; Just and Gronenberg,

* Corresponding author. Tel.: +49-7071-2972995; fax: +49-7071-295150.
E-mail addresses: oliver.betz@uni-tuebingen.de (O. Betz), gregor.koelsch@uni-hamburg.de (G. Kölsch).
[1] Tel.: +49-7071-2972995; fax: +49-7071-295150.

1999). This might be of special relevance for inert life forms that are physiologically limited with respect to their sensory performance and/or motility. In other predators, immobility does not necessarily result from physiological constraints but is part of their predatory method, since they are ambush-predators or trap-users.

In the context of predator avoidance, adhesive secretions can function in active defence (Dettner, 1999), i.e. they are employed in direct encounters with predators only. Sticky defence agents act mostly mechanically, adhering prey animals tightly to the substratum, so that the predator cannot detach them. Alternatively, they might impair the movements of predators or immobilize their mouthparts or sensilla (Pasteels et al., 1983). In addition, reactive substances of a low molecular weight might be mixed with the sticky secretion and function chemically, i.e. as irritating repellents (Dettner, 1999).

In this survey, we review the use of adhesive mechanisms in both predation and predator defence across the Arthropoda. We restrict our review to real predators, i.e. animals that kill and consume other animals (Gordh and Headrick, 2001); parasites and parasitoids are not considered. We first give a short overview of physical mechanisms of adhesion that play a role in prey capture and predator defence. This includes a discussion on how prey-capture devices might be optimizable in terms of an improved adhesive performance and the manner in which prey integuments should be designed in order to avoid this adhesion. We then survey the patchy distribution of adhesive predatory organs and defence mechanisms across arthropods. We conclude our review with some suggestions for future research topics in this field.

2. Physical mechanisms of adhesion employed in prey capture and predator defence

2.1. General considerations

Many phenomena of adhesion in the living world involve types of stickiness that act like commercially available glue: the glue is applied between two surfaces, sets relatively slowly, and builds up mechanical and chemical bonds with both surfaces. This often involves a process of drying (evaporation of solvent), which also increases the tensile strength of the glue itself (cohesion). Well-known biological examples are the attachment of the byssus threads of mussels or of barnacles to a hard substrate. However, in most cases, these phenomena are not used for active defence or predation, probably because of their slow mode of action. Instead, they are involved in the permanent attachment of sessile organisms (Nachtigall, 1974; Yule and Walker, 1984; Talbot and Demers, 1993). Although more permanent attachment mechanisms might function in predator avoidance, we concentrate, in our review, on more active predatory and defensive adhesive devices.

The physical mechanisms are determined by the requirements imposed upon the morphological structure used for predation or defence. In general, the adhesive mechanism must enable the rapid establishment of a bond during an attack and must be available for speedy deployment, particularly as far as a defensive mechanism is concerned, as it has to be virtually permanently effective. Moreover, it must achieve a compromise between reversibility and strength. On the one hand, the adhesion must be stronger than the impulse exerted by the flight response of the prey (or the attack by a predator, respectively). On the other hand, the overpowered prey usually has to be further handled before ingestion; this is facilitated by an easy release from the adhesive structure, i.e. reversible adhesion must be achieved.

We initially discuss several physical aspects as a basis for subsequently dealing with case studies, where we add further details if appropriate. The reader is referred to the literature (Baier et al., 1968; Kinloch, 1980; Hiemenz, 1986; Eagland, 1988; Israelachvili, 1991; Walker, 1993; Scherge and Gorb, 2001) for more specific descriptions. In general, we have to distinguish between (1) attachment systems encompassing a relatively small contact area and (2) other instances, in which, for example, a secretion is spread over another animal. The case studies below will further illustrate this classification.

2.2. Van der Waals forces

Comparatively weak van der Waals forces arise from the attraction between molecules (Fig. 1a). Although they act over a distance of several nanometres only (Hunter, 1989), the integrated attractive force between two macroscopic bodies can nevertheless be important (Stork, 1980b; Hiemenz, 1986; Israelachvili, 1991), as has been described by Autumn et al. (2002). However, for our considerations, it is important to bear in mind that, on immersion in a liquid, these interaction forces can be considerably shielded (Tadros, 1980; Hiemenz, 1986; Hunter, 1989), depending on the nature of the fluid. The vast majority of adhesive mechanisms that we deal with in our review are based on the effect of a fluid, and hence, the dry adhesion attributable to van der Waals forces is of minor importance.

2.3. Adhesion attributable to capillarity

In those attachment systems, in which the contact zone between both predator and prey is confined to a relatively small area, the relevant force usually occurs perpendicularly to the surface, since some kind of pulling is involved (prey is pulled toward the predator or is detached from the substrate). In these cases, the widespread physical mechanism is the adhesion produced by a thin layer of fluid between the two surfaces involved (Fig. 1b). The surface tension of this fluid spreading on the surfaces leads to lowered pressure within the fluid, which thus holds the two bodies together (Bowden and Tabor, 1950; Israelachvili, 1991). The force of

a) van der Waals forces
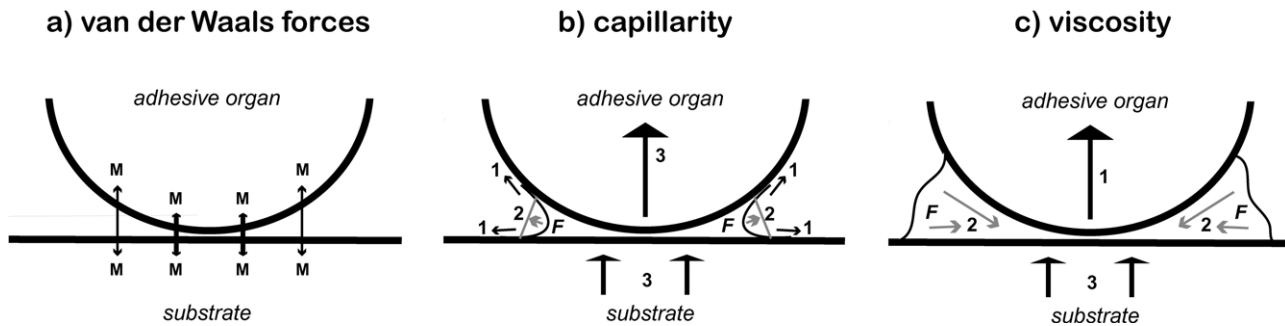
b) capillarity

c) viscosity

Fig. 1. Schematic representation of the three mechanisms of adhesion described in the text. Consecutive processes are indicated by different numbers. (a) Van der Waals forces as based on the interaction between molecules (M). (b) Capillarity: a small amount of adhesive fluid (F) can lead to adhesion because of capillary forces. Once spreading over both the substrates (stage 1), the fluid forms a meniscus. However, this is counteracted by the surface tension of this fluid, which would ideally lead to a planar interface toward the exterior (2, gray arrows and lines). These two concurring processes lead to a decrease in the internal pressure of the liquid, so that the two bodies are pressed toward each other by the higher atmospheric pressure. As the adhesive organ is withdrawn, the substrate (prey) has to follow (3). (c) Viscosity: In the presence of excess fluid (F), the viscosity of the fluid can cause adhesion. When the adhesive organ is withdrawn (1), the emerging gap between the two bodies has to be filled by the fluid (2). If the fluid is too viscous to fill the gap immediately (as indicated by the gray arrows), this gap cannot widen, and the substrate (prey) is drawn instead toward the adhesive organ (3).

adhesion attributable to surface tension can be calculated as

$$F_{surface\ tension} = \frac{(\cos\theta_1 + \cos\theta_2)A\gamma}{d} \qquad (1)$$

where θ_1 and θ_2 are the contact angles of the fluid on the surfaces, A is the area of contact (covered by the fluid), γ is the surface tension of the fluid, and d is the distance between the two surfaces under consideration (Dixon et al., 1990; Alexander, 2003). The formula given above applies to surfaces in general. Other authors use a modification that can be used for modelling the force between a sphere and a flat surface and that can be derived by certain approximations (Bowden and Tabor, 1950; Scherge and Gorb, 2001). One effect of these approximations is that the modified form does not contain the term d. This means that the force becomes essentially independent of the distance between the two bodies. However, the entire model is only appropriate if d is small compared with the dimension of the spherical body.

This mechanism of adhesion resulting from surface tension (also known as capillarity) is fast and universal, since it can be based on the thin layer of water that is almost always present on surfaces due to adsorption from the air (Baier et al., 1968; Scherge and Gorb, 2001). It can be enhanced, however, by small volumes of secretions filling any irregularities on the relevant surfaces (at a microscopic or sub-microscopic scale), thereby increasing the contact area. This depends on a match between the hydrophobic/hydrophilic properties of fluid and surface.

2.4. Adhesion attributable to viscosity

If the amount of secretion is too large in comparison with the space between the contact zones of the two bodies, it will be squeezed out and flow beyond the edges of the bodies, and the effect will resemble that in which the entire system is immersed in excess fluid. As the predator retracts its predatory device, the surfaces of the predatory structure and the prey move apart. The widening slit between them has to be filled with the fluid. If the fluid is viscous and/or the movement is fast, the flow of the fluid will be too slow, and the prey surface will be attracted toward the predator (Fig. 1c). The crucial difference between adhesion caused by viscosity and capillary forces (see above) is the time dependence of the former: viscosity plays a role only in situations in which movements are fast (McFarlane and Tabor, 1950). This is reflected by the term t in the formula for the force resulting from viscosity:

$$F_{viscosity} = \frac{3\pi\eta R^4}{4td^2} \qquad (2)$$

where R is the radius of the contact area, d is the distance between the surfaces, η is the viscosity of the fluid, π is the number pi, and t is the time required for the separation of the surfaces to infinity (the theoretical separation to infinity can be interpreted as the separation when the interaction forces between the bodies are infinitely small, which is the case after the fluid film between them has broken) (McFarlane and Tabor, 1950; Lees and Hardie, 1988).

2.5. Friction and mechanical interlocking

In many instances, the adhesive structure of a predator assists in the firm handling of the prey, even after its initial capture (e.g. adhesive pads on legs). In this case, the forces will act in various directions (struggling prey). Friction and mechanical interlocking on a microscopic scale should then be involved in the mechanism of adhesion. Larger mechanical devices, such as mouthparts and claws, are usually employed for this purpose. Detailed accounts can be found in Nachtigall (1974) and Scherge and Gorb (2001).

2.6. Immobilization by expelled fluid

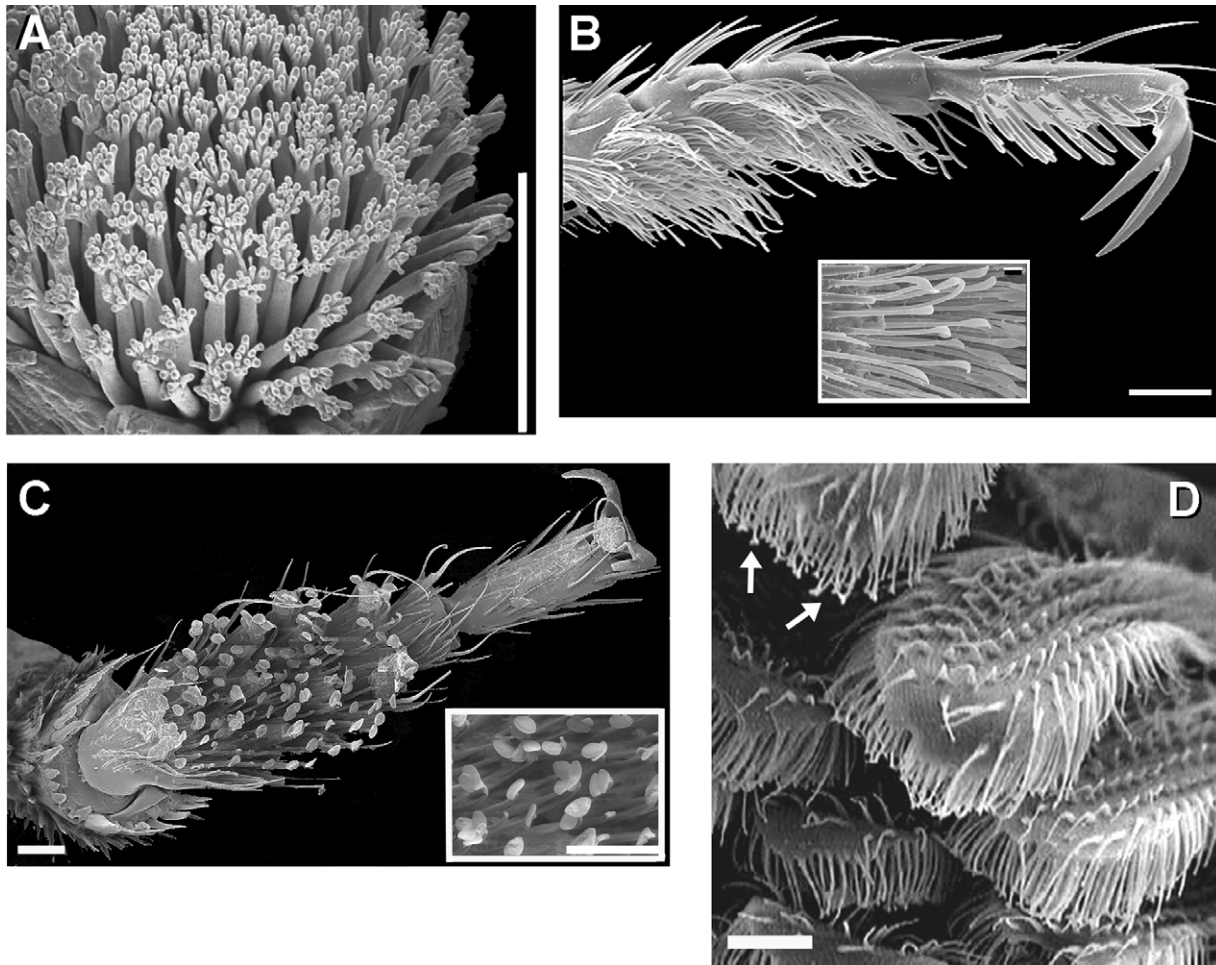When a sticky secretion is used mechanically to

Fig. 2. Examples of 'hairy' adhesion systems as used for prey capture. Similar to adhesive systems used for locomotion, the setae are terminally broadened and/or ramified to increase their surface area. Scanning electron microscopic images. **A** Ventrolateral view of adhesive setae on the paraglossae of *Stenus nitidiusculus* Stephens; scale bar = 20 μm. **B** Lateral view of fore tarsus of *Philonthus lederi* (Eppelsheim); scale bar = 100 μm. Inlet shows spatulate setae in more detail; scale bar = 10 μm. **C** Ventral view of fore tarsus of *Scydmaenus tarsatus* Müller and Kunze; scale bar = 20 μm. Inlet shows spatulate tarsal setae in more detail; scale bar = 10 μm. **D** View of the broadened tarsal setae of the spider *E. arcuata* Clerck (Salticidae), whose surface is differentiated into numerous setules. On the ventral side of the seta, the setules are broadened towards their ends (as indicated by arrows); scale bar = 5 μm. From Kesel et al. (2003).

immobilize prey or an attacking predator, the fluid is applied to a large area of the target. Again, the wetting of the surface is crucial to achieve firm adhesion. However, in this case, a more macroscopic mode of action seems to predominate, i.e. viscous fluid entangles mouthparts and other appendages and interlocks with surface irregularities and cuticular setae or hairs.

3. General design of adhesive prey-capture devices

Many prey-capture devices in arthropods do not involve adhesive mechanisms. They are designed as clamp-like structures, which function in squeezing prey (Ass, 1973; Bauer, 1999; Gorb, 2001). This type of predatory organ is mainly represented in the form of raptorial mandibles, chelicerae, and legs. The last mentioned have convergently evolved within several groups of crustaceans (Stomatopoda,

Amphipoda, Decapoda) and insects (Mantophasmatodea, Mantodea, Ensifera, Heteroptera, Planipennia: Mantispidae, Mecoptera: Bittacidae, some Diptera, and Hymenoptera: Bethylidae (Ass, 1973; Gruner, 1993; Gorb, 1995; Bauer, 1999; Gorb, 2001)). Their function involves the rapid flexure of a distal movable part of the leg against a proximal part. The inner sides of the involved leg segments are usually armed with spines and bristles to enhance the firm hold on captured prey.

In the present review, our focus is on a different type of prey-capture device, which involves adhesion mediated by a secretion. In arthropods, these organs can be located on the legs, the antenna, the mouthparts, or the general body surface. In a few groups, entirely new structures have evolved that cannot be easily homologized with any other known structure (cf. the adhesive head organs in pselaphid larvae described by De Marzo, 1985). Finally, some arachnids have not evolved specific adhesive prey-capture

Fig. 3. Examples for adhesive prey capture mechanisms that involve a sticky secretion that is hurled towards the prey. **A** Peripatid onychophoran (undetermined Columbian species) catching a house cricket, *Achaeta domesticus*. The onychophoran has spit its secretion over the hind legs and cerci of the cricket and moves its head away from the prey (courtesy of C. Brockmann and H. Ruhberg). **B** Bolas spider *Mastophora* sp., swinging a short thread of silk with a small drop of viscous fluid at its end (as indicated by arrow) at a moth flying past. From Eberhard (1977). **C** Adult *Scytodes* sp. (Scytotidae) female (top) moves on to its prey (bottom), a salticid spider. Note spit net over the anterior body and the legs of the prey. From Li et al. (1999).

organs but spit a sticky secretion over the prey to fix it to the substratum and the mouthparts of the predator (Alberti, 1973; Li et al., 1999) (Fig. 3C).

Adhesive prey-capture organs may function as passive devices (similar to lime-twigs), because they might be built as external stationary lime traps (e.g. the webs of orb-weaving spiders), or the organism itself has a sticky coating to which potential prey animals adhere. Alternatively, an adhesive prey-capture apparatus or the adhesive body surface might be actively led toward the prey, sometimes in a very rapid manner (e.g. the protrusible labium of *Stenus* beetles: Fig. 5A). If a sticky secretion is ejected with force (e.g. is spat out of the body), powerful muscular devices are required, for instance, to rapidly compress a secretion reservoir.

As argued above, lateral frictional forces probably contribute only to a minor extent to the total adhesive force in a prey-capture event. Instead, adhesive forces resulting from capillarity and/or viscosity are probably of major importance. Those features of a prey-capture device that are most significant to ensure its adhesive performance can be deduced from the equations for the adhesive forces resulting from either of both these mechanisms (see chapter 2; Kölsch, 2000; Alexander, 2003). Basically, these features

are similar to those that ensure the firm attachment of the tarsi of spiders and insects when they hang upside-down on smooth (plant) surfaces.

3.1. Capillary adhesion

This mechanism functions when two surfaces are separated by a thin liquid film (water or secretion) that does not extend beyond their margins and whose radius clearly exceeds its thickness (McFarlane and Tabor, 1950; Baier et al., 1968). According to Eq. (1) above, adhesion is high, if (1) both the surfaces of the predatory organ and that of the prey are highly wettable by the adhesive (as indicted by low contact angles, θ), (2) the radius A of the liquid drop between the surfaces is large, (3) the surface tension γ of the liquid is large, and (4) the thickness d of the liquid film is low. The first parameter requires the surface energy of the adhesive to remain below that of the integument of the prey (Zisman, 1964). This makes water an inappropriate adhesive in prey-capture devices, because the waxy outer epicuticle of most terrestrial arthropods shows low surface energies making it unwettable by water and reducing transpiration (Holdgate, 1955; Beament, 1960, 1962; Lockey, 1988). Similar to adhesives used for attachment
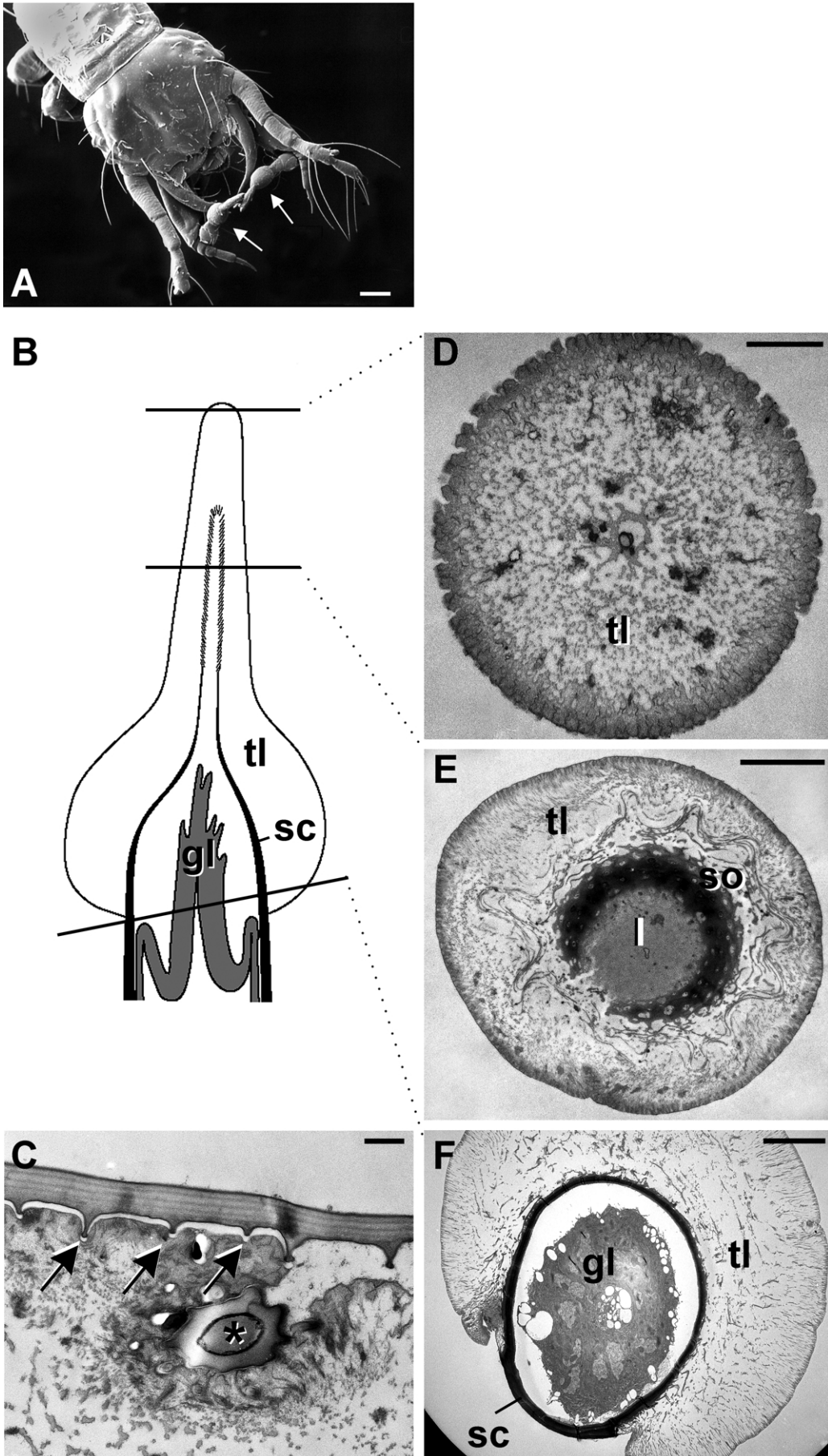
Fig. 4. The adhesive organ (distal part of the galea) of the larva of *Loricera pilicornis* (Col., Carabidae); (A) Scanning electron microscopic image of an L3 larva; (B) Diagrammatic representation; C-F Transmission electron microscopic images of L3 larvae (courtesy of T. Bauer). Note the different scales. **A** Dorsal aspect of head. The arrows point to the bulbiform galeae; scale bar = 100 µm. **B** Longitudinal section, schematically; horizontal and oblique lines indicate the positions of the sections shown in D-F. **C** Part of a scale and a cuticular hair of a collembole on the surface of the transparent layer of the cuticle; the ridges of the scale (arrows) and the hair (asterisk) deeply indent the soft cuticle; scale bar = 0.75 µm. **D** Transverse section through the terminal filum of the galea; scale bar = 1.25 µm. **E** Transverse section through the region with the perforated shaft of solid cuticle, scale bar = 5 µm. **F** Slightly oblique transverse section at the proximal end of the transparent layer; scale bar = 10 µm. gl gland tissue, l lumen in the shaft of solid cuticle, sc solid cuticle, so solid cuticle with openings, tl transparent layer.

to smooth plant surfaces, adhesive secretions used for prey capture should therefore be generally expected to be mixtures of neutral lipids with only low (if any) contents of polar components such as fatty acids, esters, and alcohols. These substances might be capable of spreading on even extremely hydrophobic prey surfaces, provided that the surface polarities of both the adhesive and the substrate match closely (Wu, 1973; Rulison, 2000). However, recent investigations of the chemical composition of the attachment pad secretion of locusts suggest that adhesive secretions are not pure lipoids but form an emulsion consisting of lipid droplets dispersed in an aqueous liquid, which may make the secretion compatible with both hydrophobic and hydrophilic solids (Vötsch et al., 2002). This corresponds well with the ultrastructural findings of Kölsch (2000) regarding the adhesive capture apparatus of *Stenus* beetles. On the surface of the sticky paraglossae of these beetles, a two-phase secretion can be found consisting of a lipoid and a proteinaceous fraction (Fig. 5C). To our knowledge, no efforts have as yet been undertaken to analyse the chemical composition of adhesives used in predatory devices.

The second parameter (radius of liquid drop) is directly dependent on the effective contact area of the predatory devices, which mediate the contact with the prey. As in locomotory attachment organs (Hasenfuss, 1999; Jiao et al., 2000; Gorb, 2001), adhesive organs used for prey-capture can be designated as 'hairy' (arrays of tenent setae or trichomes)[2] versus 'smooth' (comparatively large areas of smooth flexible cuticle) systems. In hairy systems (Fig. 2), the total radius of the adhesive liquid film depends on the total number of adhesive hairs and the terminal surface area of each single hair. Selection that gives rise to an extension of the feeding niche toward larger and heavier prey should therefore be paralleled by an increase in either one or both of these parameters. Moreover, the effective contact area of tenent hairs with the substratum might be significantly increased by the high flexibility of their tips, as has been shown for the attachment pads of the blowfly *Calliphora* (Niederegger et al., 2001). The functional advantage of hairy systems lies in the break-up of the sticky surface into a large number of independent elastic elements that compensate for possible surface irregularities of the prey.

Alternatively, the surface of prey-capture organs may not be differentiated into adhesive hairs or trichomes but consist of smooth and flexible cuticle that closely adapts to the profile of the prey surface (Fig. 4A and C), similar to the structure of the attachment pads in orthopterans, lepidopteran larvae, or marsupial feathertail gliders (Hasenfuss, 1999; Rosenberg and Rose, 1999; Gorb and Scherge, 2000; Gorb et al., 2000). The adhesive strength of these organs should be directly dependent on their general surface area. The surface area covered by sticky secretion (in smooth systems) or adhesive single elements (in hairy systems) might be actively enlarged prior to the catch by an increase of the internal hemolymph pressure leading to the discharge of secretion, as found in the adhesive paraglossae of *Stenus* species (Kölsch and Betz, 1998).

The third parameter improving adhesion according to Eq. (1) is the surface tension γ, which should be high. However, practical constraints limit the value of this parameter. If the surface tension of the adhesive fluid is too high, two adverse effects will result. First, the fluid will not spread over the adhesive organ prior to its use but tend to attain the shape of a spherical drop (minimal surface). Second, it will not spread over the surface of the counterpart (i.e. the surface of the prey). This situation might even be exacerbated, since a passive counterstrategy of prey can take the form of the production of surfaces with low surface energies (e.g. by the secretion of hydrophobic waxes). Only if the surface tension of the adhesive fluid is lower than that of the surface of the prey will the fluid readily spread over the prey (cf. Eagland, 1988).

Finally, according to Eq. (1), adhesive strength increases as the thickness d of the secretion film sandwiched between both the surfaces decreases. This can be achieved in both hairy and smooth systems, if (1) only very small amounts of secretion are delivered to the contact areas, and (2) highly flexible cuticle is involved, which assures the close proximity between both solids (Hasenfuss, 1999; Gorb, 2001; Niederegger et al., 2001). Moreover, prey-capture devices may often be accelerated before they hit the prey, so that they transfer a considerable impulse to it. As a result, the secretion film should become considerably thinner, because it is compressed.

3.2. Viscosity

This mechanism may work when the amount of secretion is relatively large, so that it surrounds the area of adhesion.

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[2] Throughout this publication, terms like 'hair' or 'bristle' only refer to the external appearance of these structures and not to their mode of formation or innervation pattern.
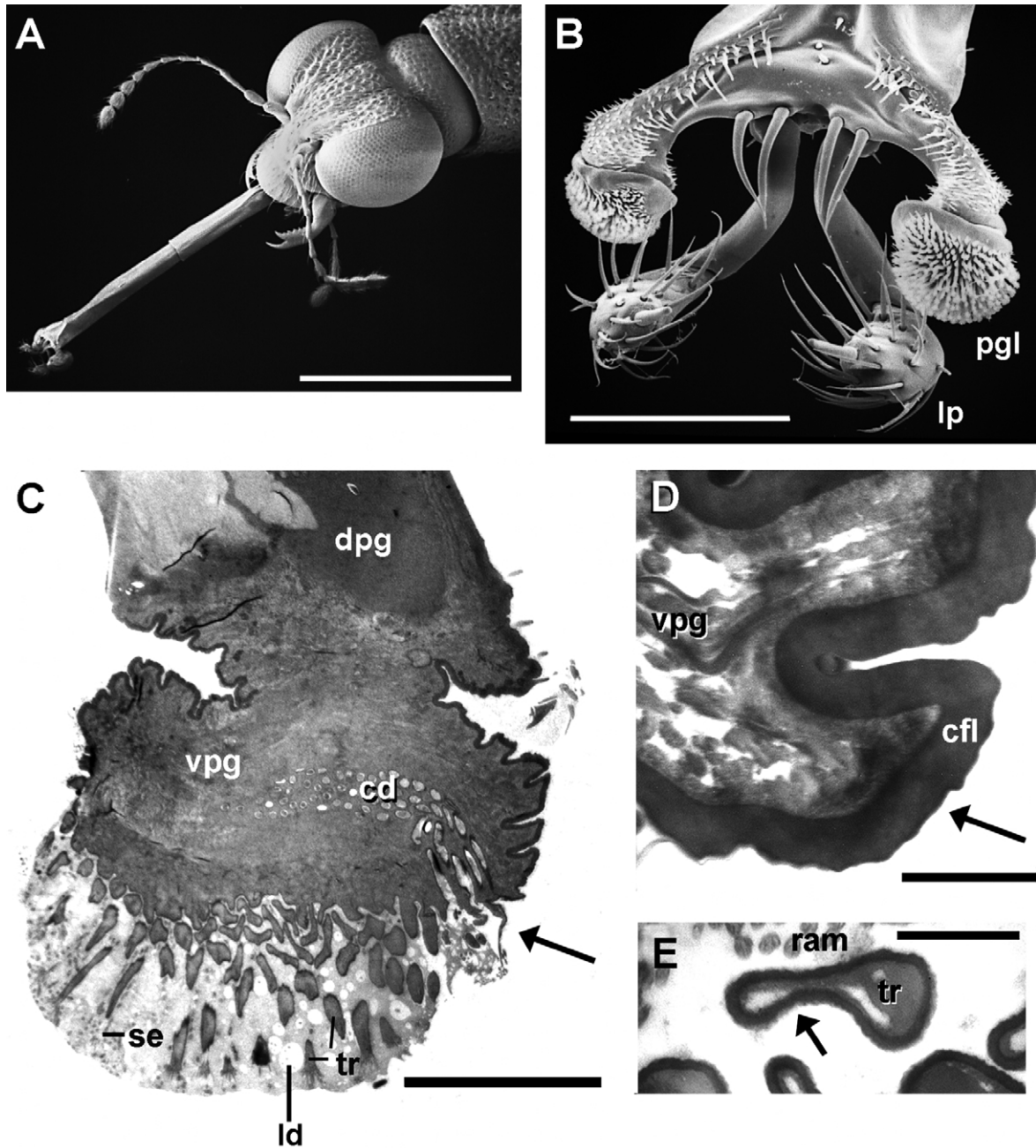
Fig. 5. The adhesive organ of *Stenus* Latreille spp. A-B are scanning electron microscopic images of *S. comma* Leconte. C-E are transmission electron microscopic images of *S. juno* (Paykull). Prior to fixation, pressure was exerted onto the abdomen of a freshly killed beetle, simulating the increase of the hemolymph pressure that is built up by a beetle prior to the strike. The secretion was thus experimentally discharged, and the paraglossa was partially expanded. **A** Head with extended labium; scale bar = 1 mm. **B** Dorso-frontal view of labial tip with paraglossae modified into sticky cushions; scale bar = 100 μm. **C** Transverse section through the sticky cushion formed by the ventral part of a paraglossa; chitinous ductules discharge the adhesive secretion onto the zone of trichomes (arrow); note the deeply folded flank of the paraglossa, suggesting a considerable elasticity of this region; scale bar = 20 μm. **D** The cuticle at the flanks of the ventral part of the paraglossa has a smooth surface (arrow); scale bar = 1 μm. **E** The cuticle of the adhesive trichome has a rough surface (arrow); scale bar = 1 μm. cd cuticular ductules, cfl cuticle of the flank region, dpg dorsal part of the paraglossa, ld lipoid droplet, lp labial palpus, pgl paraglossa, ram terminal ramifications of an adhesive trichome, se proteinaceous secretion, tr adhesive trichome, vpg ventral part of the paraglossa.

If the two surfaces are pulled apart and the viscosity of the secretion is appreciable, the force required to separate them can be very high (McFarlane and Tabor, 1950; Lees and Hardie, 1988). The way in which prey-capture devices, which take advantage of this mechanism, should be designed to achieve reasonable adhesive strength can be

deduced from Eq. (2). As in capillary adhesion, the effective surface area should be high, whereas the thickness of the secretion film should be low. Since both these parameters enter the equation to the fourth and second power, respectively, their influence on total adhesive strength is considerable. In addition to these factors, the viscosity of the

secretion plays an important role. In both pure oily secretions and emulsions of lipoids in an aqueous liquid, viscosity might be considerably enhanced and thus promote adhesion. Preferably, the adhesive fluid should initially have a low viscosity for discharge and spreading over the surface and into surface irregularities. Only after short exposure to air should it polymerise and thus increase its viscosity. This process would be also advantageous in prey-capture events involving the ejection of fluid over the target to hamper the motility of the entangled appendages of the prey by its elasticity, with eventually the fluid drying out completely for mechanical interlocking.

Finally, adhesion resulting from viscosity is directly related to the rate of separation. Consequently, jerky escape movements of captured prey animals might actually prevent their liberation from the viscous secretion. Moreover, in predators such as staphylinids of the genus *Stenus*, prey-capture organs are hurled out of the body (in analogy to the protrusible tongues of lungless salamanders or chameleons) and have to be retracted after prey capture to bring the prey into the range of the mandibles (Weinreich, 1968; Betz, 1996). If this retraction is performed in a rapid manner, adhesive strength will be improved, provided that there was sufficient time for contact formation, which depends on the nature (i.e. the spreading properties) of the fluid and the force of the impact as pointed out above.

Most of the case studies presented below have not involved investigations into whether adhesion is attributable to capillarity or viscosity. In some cases, it might be a combination of both. However, in general, in those cases that involve relatively large amounts of secretion that are externally visible as droplets or coatings, viscosity is most probably the dominating mechanism.

4. Passive counterstrategies of the prey against adhesion

Apart from general strategies such as cryptic behavior and camouflage, prey animals have to develop strategies to evade the hunting strategies of the predators that rely on adhesion. Since the predatory strikes often occur over a distance and by surprise, subsequent escape is the first option. The thrust exerted by a powerful escape mechanism (e.g. the furca of collemboles) might overcome the adhesion and render possible an escape from the adhesive surface of the predator. Escape is further facilitated if the adhesion itself is weak; there are two options of attaining this. First, the effective contact area can be kept small if the prey can prevent the adhesive secretion from spreading over its surface. This can be achieved by coating the surface with substances of low surface energy. However, notwithstanding that arthropod cuticle has to be considered as a low surface energy material, adhesion of (lipophilic) substances may be still possible. The second option for diminishing adhesion to sticky devices of a predator is to 'surrender' part of the body surface. This can be simply achieved by a cover

of hairs or scales that stick to the adhesive organ and that are released when the predator tries to retract its prey capture organ or the prey performs powerful escape movements. Such devices can be found in several arthropod groups such as Collembola, Zygentoma, Archaeognatha, Lepidoptera, Trichoptera, Hemiptera, Psocoptera and (very few) Coleoptera (Eisner, 1970; Nentwig, 1982; Dettner, 1999). Eisner et al. (1964) have demonstrated the adaptive value of scales by testing the adhesive strength of naked versus scaly insect wings in a spider web. Similar experiments have been conducted by Nentwig (1982), who has found a reduction in adhesion to hairy and scaly insects by 15% to 49% compared with the same surfaces after scales or hairs have been removed. In addition, Nentwig (1982) has demonstrated the importance of fatty/waxy layers: removal of fatty layers with organic solvents increases adhesion to the wings of *Decticus* Audinet-Serville (Orthoptera: Tettigoniidae) and *Blaberus* Audinet-Serville (Blattoptera: Blaberidae) by 100%.

Bauer and Pfeiffer (1991) compared the success of *Stenus comma* Leconte (Coleoptera: Staphylinidae) in hunting various species of collemboles. The collemboles differed in their surface structure: the authors used species (1) with setae, (2) with scales, or (3) with no such cover. Attacks with the sticky labium (see below) were significantly less successful in the former two species, since the setae and scales were detached from the prey animal, which in turn could escape.

Likewise, powdery secretions (wax crystals) can prevent adhesion. Some aphids (woolly aphids, Pemphigidae) are covered with long waxy strands (see below). Similar mechanisms can be found in plants that avoid herbivory by producing pubescence or waxy surface secretions (Stork, 1980a; Lee et al., 1986; Eigenbrode and Espelie, 1995; Markstädter et al., 2000; Eigenbrode and Jetter, 2002). Consequently, insect movements on these plant structures can be effectively impeded (Brennan and Weinbaum, 2001; Gorb and Gorb, 2002).

Another factor to be considered is surface roughness. It influences the behavior of a fluid on a surface in a way that depends on the overall physical conditions of liquid and solid. If the fluid tends to spread on the material of which the surface is made, then roughness will further promote wetting. If the fluid does not wet the surface (i.e. the contact angle is larger than 90°), roughness will hamper the spreading to a greater extent (i.e. the apparent contact angle will be larger than the contact angle on a perfectly smooth surface) (Baier et al., 1968; Kinloch, 1980; Eagland, 1988). In other words, if an arthropod has a sculptured lipophilic cuticle, an aqueous secretion will only spread to a limited degree over its surface. Surface roughness does not necessarily refer to structures visible at microscopic magnification. The physical process of adhesion is also influenced by roughness at the electron-microscopic or molecular scale. The relevant properties of a cuticle are determined by its outermost layer. This can be the wax layer

or, commonly, a cement layer, which protects the wax layer (Filshie, 1982). The cement layer can be hydrophilic or hydrophobic and often appears as a 'fuzzy indistinct outline' in ultrathin sections (Locke, 1974).

If the sculpturing of the body surface is of an adequate scale (not too small), it will prevent the attachment of an adhesive that polymerizes or dries rapidly: the fluid hardens before it can seep into the indentations, crevices, and other irregularities of the surface (Onychophora, see below). Wagner et al. (1996) have investigated the surfaces of insect wings. Micro-sculpturing by hairs, scales, and a cloth-like layer on the wings significantly decrease surface wetting by water and allow the self-cleaning of the wings (known as the lotus effect). This is the case in orders with wings too large to be cleaned by legs (Odonata, Planipennia, Lepidoptera, Ephemeroptera).

5. Types of adhesive predator–defence mechanisms

Adhesiveness is not only used for prey-capture but also in a converse way, i.e. for predator avoidance. Our literature survey has revealed two basic mechanisms: predation might be avoided by (1) firm temporary or permanent adhesion to the substratum, so that the prey is not detachable by the predator, or (2) exudation of a sticky secretion, which immobilizes the appendages or the sensilla of the opponent (Fig. 7). In the latter case, repellents or toxins may be added to the secretions, although they mainly work mechanically rather than chemically. Chemically, these adhesives are highly diverse: they might be proteinaceous, terpene resins, mixtures of long-chain hydrocarbons and mucopolysaccharides, or waxes (Pasteels et al., 1983). Adhesive defence secretions are thought to protect mainly otherwise unprotected, clumsy, or soft-bodied animals that are unable to perform rapid escape movements. The secretion is effective against small arthropod predators (e.g. ants) (Eisner, 1972) or parasitoids (Edwards, 1966), whereas vertebrates are much less affected (Pasteels et al., 1983). In most cases, the physical mechanisms behind these defence mechanisms have not been unravelled in detail. However, as temporary firm adhesion to a relatively smooth substrate involves the employment of tarsal hairs mediated by an adhesive secretion[3] (Attygalle et al., 2000; Eisner and Aneshansley, 2000), we might expect a combination of capillary, viscous, friction, and, at close contacts, molecular forces (Wigglesworth, 1987; Jiao et al., 2000; Gorb and Scherge, 2000; Scherge and Gorb, 2001). If more permanent adhesion to the surface is required, such as in barnacles (Yule and Walker, 1984), real glues or cements are the major mechanism of adhesion, i.e. both surfaces are held together by the frictional forces mediated by the polymerized adhesive (Gorb, 2001). The effect of sticky secretions, which are

exuded to entangle attacking predators, can be mainly attributed to the viscosity of the secretion. However, in some cases (e.g. in Onychophora), the secretion is reported to harden quickly on exposure to air, so that its mode of action is comparable to that of commercial glue. Indeed, predators exposed to such secretions become partially or entirely immobilized (Roth and Eisner, 1962; Eisner, 1972).

6. Distribution of adhesive devices for prey capture and predator defence across the arthropods

In this section, we summarize the distribution of adhesive structures as used in predation and predator defence across the Arthropoda (cf. Tables 1–2). Apart from numerous original articles, we considered general (textbook) reviews on predation and defence in arthropods or subgroups thereof (Roth and Eisner, 1962; Edwards, 1963; Simon, 1964; Eisner and Meinwald, 1966; Eisner, 1972; Nachtigall, 1974; Hermann and Blum, 1981; Pasteels et al., 1983; Blum, 1981; Bauer, 1999; Dettner, 1999). Moreover, we have consulted textbooks on the systematic zoology of the various groups of arthropods (Grassé, 1949, 1951; Gruner, 1993; Dathe, 2003). In most cases, we give only brief synopses of the published reports and otherwise refer to the literature. If not explicitly mentioned, the following accounts refer to the adult stages. Although spider webs (and similar woven sticky traps) represent a major step in the evolution of adhesive prey-capture devices, we discuss them only briefly, because detailed reviews on this subject are available in the literature (Rudall and Kenchington, 1971; Eberhard, 1990; Foelix, 1996; Craig, 1997; Opell, 1997). In the cases of predatory adhesive organs of *Loricera* larvae (Carabidae, Coleoptera) and *Stenus* species, we also include our own original research.

6.1. Onychophora

Onychophorans (velvet worms) possess large paired slime glands with orifices on the oral papillae. The glands produce a sticky secretion that the animals use for immobilizing prey and for defence (Alexander, 1957, and references cited therein; Eisner, 1970) (Fig. 3A). Alexander (1957) states that the secretion is not toxic, since her experiments give only marginal indications of a paralysing effect on centipedes. The secretion is an aqueous solution of proteins and free amino acids. On contact with air, disulfide bonds are presumably formed, and the fluid attains its sticky and elastic properties (Röper, 1977). No data are available on the formation of chemical bonds with the surface to which the secretion is applied. Alternatively, the secretion might only entangle hairs, setae, and other protrusions on the surface. It also adheres to the cuticle of the onychophorans themselves but can be removed by movements of the flexible integument (Ruhberg and Storch, 1977; Ruhberg, pers. comm.). The cuticle of velvet worms may therefore

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[3] Mechanical interlocking to surface irregularities is not considered in this review.

represent a low energy surface (see above), and the apparent adhesion is only based on mechanical interlocking between the secretion and the highly sculptured integument. This view is supported by the clean appearance of the onychophorans, no matter how damp and dirty their habitat is. After a short while (minutes) in air, the secretion dries and becomes brittle. Scanning electron microscopic (SEM) images of the irregular network of slime, which has been spat off (Ruhberg and Storch, 1977), show drop-like aggregations of secretion that lie along the main threads of the network, and that resemble the droplets of adhesive fluid along a thread of silk of an orb-weaving spider (Eisner et al., 1964). This indicates that one portion of the secretion is relatively more fluid than the rest. The secretion contains molecules of two different size classes (Röper, 1977), which might be correlated with the secretory activity of two histologically distinct parts (Ruhberg and Storch, 1977) of the glands.

6.2. Chelicerata

6.2.1. Araneidae

Bolas spiders (tribus Mastophoreae) produce a short thread of silk with a small drop ('ball') of viscous fluid and curled thread material at its end, which may be swung against prey flying past the perch (Fig. 3B). Both thread and fluid secretion are drawn from the spinnerets of the spider. The secretion that makes up the outer part of the ball is slightly more fluid than the inner part. This might improve its flow between the scales and other surface structures of prey such as moths (Yeargan, 1994). The adhesive mechanism is highly effective, since failure of a strike is usually attributable to the spider missing the target and hardly ever to subsequent escape of the hit prey (Eberhard, 1980). The sticky structure also sometimes accidentally sticks to the cuticle of the spider (Eberhard, 1980). The spiders may attract prey by pheromones (Eberhard, 1977; Haynes et al., 2002) to increase the number of possible strikes and thereby the overall efficiency of the hunting strategy, which is equivalent to the success rate of orb-web spiders.

6.2.2. Scytodidae

Spitting spiders use an adhesive secretion ejected from their chelicerae to glue their prey to the ground by a zigzag pattern of threads (Dabelow, 1958; Li et al., 1999) (Fig. 3C). The immobilization sometimes requires repeated spitting and involves paralysis, especially of small prey, by a poison contained in the secretion. The secretion rapidly vitrifies, and the spider has to clean its own mouthparts and legs of remains from the secretion (which implies immunity of the spider against its own poison). The secretion is occasionally discharged for defence, as reviewed by Blum (1981). McAlister (1960) has observed this defensive behavior in the laboratory in encounters of spiders with scorpions. He concludes that a primarily offensive behavioural trait has subsequently been used for defence.

6.2.3. Wandering (i.e., not orb-weaving) spiders in various families

These spiders have distal pads of hairs on their legs that enable them to climb smooth vertical surfaces and to jump (Dewitz, 1883; Rovner, 1978; Roscoe and Walker, 1991) (Fig. 2D). The brush-like arrangement of the hairs on the legs of spiders (termed scopulae) and their absence in orb-weavers have led to the hypothesis that, in addition to providing traction and firm attachment during jump and landing, they play a role in prey capture (Rovner, 1978). This has been confirmed by Rovner (1980) in experiments with wolf spiders (Lycosidae), in which the adhesive hairs had been removed; shaved spiders had less success in overpowering struggling prey. This can be related to a decreased ability to hold on to the prey surface. In a detailed analysis of the predatory behavior, Melchers (1967) has observed that *Cupiennius salei* Keyserling (Ctenidae) catches prey by touching it only with the tips of their tarsi, i.e. where the scopulae are located. Recently, Kesel et al. (2003) quantified the adhesive performance of the attachment pads (Fig. 2D) of the jumping spider *Evarcha arcuata* (Salticidae). The adhesion in this case does not involve a secretion and is attributed to van der Waals forces (at least in the experimental system using dead spiders).

6.2.4. Acari, Bdellidae

Snout mites possess glands from which an adhesive is secreted through the mouth at the tip of the gnathosoma. A detailed account of the histology of the complex of glands and the relation to the secretion used for weaving the nest is presented by Alberti (1973) (cf. also Evans, 1992). The mites attach the highly elastic secretion to both the prey and the ground, sometimes repeatedly, and wait until the movements of the prey cease. According to the same author, this takes place within seconds, which is important because the secretion rapidly loses its elasticity and stickiness. However, there is no evidence for any immobilizing or paralysing substance in the fluid adding to the purely mechanical effect of the secretion. Only the subsequent manipulations by the mite (biting and addition of a saliva probably containing enzymes) kill the prey (Alberti, in litt.)

Other arachnids. Eisner et al. (1978a) have reviewed the chemical defence of opilionids, whip scorpions (Uropygi), and pseudoscorpions. They do not mention any defensive mechanism that involves or relies on the stickiness of the secretion.

6.3. Crustacea

Not many phenomena among crustaceans fall within the scope of this review. The attachment of barnacles mentioned above can be interpreted as a passive prospective measure against predation, but other aspects could be of

major importance (prevention of drift). Fast and reversible attachment caused by adhesion under water cannot be based on the physical principles outlined above (particularly the surface tension of an adhesive fluid), and van der Waals forces are weakened by the presence of water (Hiemenz, 1986). According to Talbot and Demers (1993), terrestrial crustaceans (isopods, brachyuran crabs) occasionally possess defensive glands that provide deterring chemicals.

6.3.1. Isopoda

Pasteels et al. (1983) refer to an unpublished observation by C. De Vroy, according to which isopods can produce an entangling secretion against predators. This is substantiated by an earlier publication of Gorvett (1952), in which he describes the 'extremely sticky and viscous' secretion of uropod glands in isopods; this can be drawn into long threads that remain flexible when dried. These glands discharge their product earlier than the lateral glands and may be the first-line defence against spiders, the main predators. When exposed to the secretion, the chelicerae and pharynx of the spiders might become entangled and clogged, respectively (Gorvett, 1956). A similar effect can be observed toward ants, which, under certain circumstances, can act as aggressors (Gorvett and Taylor, 1959).

6.3.2. Decapoda—Alpheidae

An indirect adhesive mechanism can be found in snapping shrimps (Alpheidae), which produce a snapping sound and a jet of water by swiftly closing the chela of the first thoracopod. When this chela is opened, two cuticular disks on the propus and dactyl are pressed against each other. The adductor muscle has to build up considerable tension in order to close the chela, which finally happens with great force (Ritzmann, 1974). Although detailed analyses of the mechanics are lacking, adhesion between the cuticular disks attributable to the viscosity of the water surrounding them can be invoked as the responsible mechanism. The animals use the water jet for intraspecific communication, including the defence of a territory, and for catching small prey (Herberholz and Schmitz, 1998; Herberholz and Schmitz, 1999; Versluis et al., 2000).

6.4. Chilopoda

In addition to various glands for chemical defence (Minelli, 1978), centipedes can discharge a sticky secretion from glands associated with their last pair of legs (Lithobiomorpha) or situated on sternites along the body (Geophilomorpha) (there are different views concerning the exact place of origin, Minelli, 1978). The fluid entangles aggressive ants and lycosid spiders (Verhoff, 1925) or carabid beetles (Minelli, 1978). Members of the family Lithobiidae spin long gluey threads to immobilize large prey (Verhoff, 1925; Attems, 1926/1930). The fact that these agile predators, which possess poison glands in their

mouthparts (forcipules), use this strategy illustrates the outstanding benefit arising from adhesive silk.

6.5. Progoneata

6.5.1. Symphyla

Symphyla have silk glands associated with their terminal spinnerets. The silk can be used for escape by being attached as a thread to the ground after which the animal can rope down into crevices in the soil, or it can obstruct a narrow passageway to hinder chasing predators (Verhoff 1934; Eisenbeis and Wichard, 1985). The former strategy resembles the flight behavior of orb-weaving spiders. It cannot be said whether the primary purpose of this silk was nest building or defence. However, as Craig (1997) points out, a new use for 'old' silk might have been a major driving force in evolution.

6.5.2. Diplopoda

Diplopods are well known for the defensive secretion that is produced by segmental dermal glands and expelled upon disturbance (Tichy, 1974; Eisner et al., 1978b). In addition to chemical defence, the stickiness of the secretion might play a role (Blum, 1981), although the physical properties of the viscous fluid may simply warrant effective application to the attacking animal. The secretion of *Glomeris* Latreille (Glomeridae) largely consists of proteins and alkaloids. The latter seem to have no effect on attacking ants, which in turn are affected by the stickiness (the secretion can be drawn out into a thread, Eisner and Meinwald, 1966). Schildknecht et al. (1967) conclude that the chemically acting part of the secretion is against birds or mammals, whereas the mechanically acting fraction (resulting from the viscosity of the fluid) is efficient against arthropod enemies.

6.6. Insecta

6.6.1. Protura

These tiny apterygote insects have a pair of voluminous glands in their abdomen with openings on the eighth segment. The secretion is acid and neither soluble in water nor in alcohol, but in alkali, and contains proteins (Denis, 1949). Dettner (1999) reports that proturans lift their abdomen against predators to apply a sticky secretion.

6.6.2. Collembola

Most collembola have a furca, which is used as a jumping organ to hurl themselves out of the reach of predators. However, many representatives of the family Onychiuridae have lost their furca in correlation with their euedaphic mode of living. They are not defenceless, however, because they have evolved specific secretory glands (pseudocella) that can be found all over their integument (Konček, 1924; Mayer, 1957; Usher and Balogun, 1966; Rusek and Weyda, 1981). When stimulated, these organs secrete a viscous

liquid (reflex bleeding) (Fig. 7A), which glues together the mouthparts and antennae of small predators such as predatory mites (Mayer, 1957; Karg, 1994) and chilopods (Simon, 1964). In addition to their mechanical action, these droplets obviously contain deterrents and toxins, which may paralyse the opponent (Karg, 1994).

6.6.3. Blattoptera

Among the diverse epidermal glands of cockroaches, there are at least two sets that produce a defensive secretion (Roth and Stahl, 1956; Plattner et al., 1972; Brossut and Sreng, 1980). The gland tissues are located dorsally in abdominal segments V to X and on the cerci. Predators are mechanically impeded by the viscous secretion, which forms long threads that usually break on the side of the cockroach and stick to the predator. This demonstrates its excellent adhesive properties. The secretion consists of 90% proteins (dry mass) and is not toxic, since cockroaches occasionally eat their exuvia smeared with the secretion (Roth and Stahl, 1956). Adult males, which are the only fully winged stages, lack these glands, the secretions of which would probably interfere with the membranous wings (Plattner et al., 1972); the males presumably do not depend on this defensive mechanism because of their ability to fly.

6.6.4. Isoptera

Termites possess not only a wide variety of chemical defences, but also secretions that are effective glues (Blum, 1981; Pasteels et al., 1983; Prestwich, 1984). Soldiers of several families use a secretory product that usually stems from a specialised frontal gland to entangle the body appendages of their opponents (usually ants) (Cook, 1900; Ernst, 1959; Eisner, 1970; Eisner et al., 1976). Prestwich (1984) has described the types of cranial glands involved. The termites sometimes shake their head during discharge in order to spread the fluid over the aggressor, and they clean their own head from the remains of the discharged glue (Ernst, 1959; Eisner et al., 1976). Eisner et al. (1976) and Blum (1981) have also obtained evidence that toxic or irritating chemicals play a role in addition to the observed mechanical impediment (further references in Deligne et al., 1981). In other cases, the secretion is initially fluid and becomes gum-like soon after discharge, a process that is described as tanning, i.e. the formation of chemical binding between the proteins (Deligne et al., 1981). This is in accordance with the point made above regarding the advantage of such secretions being fluid for expulsion and spreading, and becoming sticky only immediately afterwards. An extreme case of defence is the so-called 'autothysis' (cf. Section 6.6.10.5) of workers of termites that lack the soldier caste (Apicotermitinae): individuals sacrifice themselves by violent rupture of their body wall following extreme muscle contractions, a feat that leads to the spreading of 'odiferous slime' from cephalic glands that are enlarged into the abdomen (Prestwich, 1984). The same

behavior can be found in soldiers of some other subfamilies (e.g. Amitermitinae: Deligne et al., 1981).

6.6.5. Saltatoria

The elaborate tarsal pads of Tettigonia viridissima Linné and probably other Ensifera are not only used for climbing plants, but also for grasping prey with the fore- and midlegs, which is further assisted by the spines on tibia and femur. The animals actively wet the tarsi with saliva on a regular basis (Henning, 1974).

There are descriptions of both Ensifera and Caelifera that discharge hemolymph as a defensive fluid. Although chemical defence often plays a role (Eisner, 1972), in many cases the deterrent effect is at least supported by the viscosity of the fluid. The orifices for the discharge of hemolymph are located on the abdomen, thorax, or legs. They can be frequently found in flightless or slowly moving species (Hesse and Doflein, 1943).

6.6.6. Auchenorrhyncha

Cicadina. The flightless larvae of the genus Flata Fabricius and related genera protect themselves by laniferous threads, which entangle the mouthparts of their opponents (Hesse and Doflein, 1943). The larvae of cuckoo-spit insects (Cercopidae) exude a fluid through the anus; this fluid is mixed with a secretion from the abdominal glands. Air bubbles are introduced through a special valve on the abdomen to create spittle, a frothy substance that protects the larva from enemies and desiccation.

6.6.7. Sternorrhyncha

Aleyrodoidea. These specialized phloem-sap suckers have immobile second to fourth larval instars that are glued to the surface by marginal wax palisades (Zahradnik, 1972; Gill, 1990; Byrne and Bellows, 1991). In this way, they protect themselves from unfavourable weather conditions and predators.

Aphidina. The secretion discharged from the cornicles of aphids contains not only alarm pheromones, but also waxes (triglycerides mixed with aliphatic sesquiterpenes) that block the mouthparts of assailants (Hesse and Doflein, 1943; Blum, 1981; Strümpel, 2003). These waxes are secreted as drops within an aqueous fluid. On contact with a surface, they crystallize spontaneously. Dixon (1958) coined the term 'waxing' for this behavior of aphids toward coccinellid larvae and provided experimental evidence that the waxy nature of the secretion promotes the escape of aphids that are attacked. The melting points of the waxes investigated by Edwards (1966) were above normal ambient temperatures (37.5, 42 and 48 °C, respectively), which means that, in the fluid state, they are supercooled and solidify after contact with a seeding crystal. Because of this delayed crystallization, the waxes can literally form a cast around the mouthparts of a predator and impede any further movement.

Wooly aphids (Pemphigidae) are covered by waxy

exudates that would smear the mouth of predators (also vertebrates; Hesse and Doflein, 1943).

Coccina. In this group of plant-sap sucking insects, the females and their offspring are sessile and protect themselves by layers of wax, silk, lacquer, and other (proteinaceous) secretion (Schmutterer, 1972; Miller and Kosztarab, 1979; Foldi, 1990; Strümpel, 2003). As in the Aleyrodoidea, these layers might also affix the animals to the plant surface and protect them from adverse weather conditions and predators. In the Pseudococcidae, an anterior and posterior pair of openings (ostioles) pour out a sticky secretion to entangle the mouthparts of assailants (Jacobs and Renner, 1988). In addition, these mealybugs often produce waxy secretions in the form of powder or threads, which are employed in a similar fashion.

6.6.8. Heteroptera

Reduviidae. The reduviid bug *Zelus leucogrammus* (Perty) has, on its legs, a sticky secretion that is produced by epidermal glands and kept in place on the cuticle by a dense arrangement of hairs (trichomes). The hairs themselves have a brush-like surface to maximize their retention potential. The fluid is hygroscopic and water soluble. Insect prey (flies) is not poisoned by the secretion but is mechanically immobilized by the large amount of fluid applied by the bug (Barth, 1953).

Other assassin bugs employ ventral adhesive pads at the distal end of their tibia to hold struggling prey (Miller, 1942; Edwards, 1960, 1962). This is the same structure that enables *Rhodnius prolixus* Stål to climb vertical surfaces (Gillet and Wigglesworth, 1932). Homology is assumed because of morphological and positional similarity (these so-called *fossulae spongiosae* occur only on the pro- and mesotibia). Miller (1942) summarizes the discussion on the *fossula spongiosa* up to his time and attributes a primarily predatory function to it. The Apiomerinae have taken this structure to the extreme: the adults are able to catch their prey from the air, because their legs are covered by 'a sticky resinous matter', hence the name resin bugs (Miller, 1942; Weber and Weidner, 1974). Furthermore, the female bugs collect sticky fluid from gland hairs of plants (genus *Heterotheca*) and spread it over their eggs after oviposition. Hatching larvae obtain the sticky secretion for their leg traps from this slime (Eisner, 1988). In the subfamily Harpactorinae, a sticky fluid on their legs stems from glandular setae; however, Miller (1942) does not explicitly state that it is used for predation.

Tingidae. Larvae of lace bugs possess numerous cuticular trichomes, which bear drops of a defensive secretion that has a primarily mechanical effect on the biting and chewing mouthparts of their predators. Fluid-feeding predatory insects (chrysopid larvae) are less effectively deterred (Scholze, 1992; Dettner, 1999).

6.6.9. Coleoptera

In Coleoptera, adhesive prey-capture devices are known in carabids, staphylinids, and scydmaenids. In some representatives of these groups, we find highly advanced prey-capture devices, which have been the subject of intense research. Two of them (the maxilla of *Loricera* and the labium of *Stenus*) will be discussed in more detail below. Adhesive mechanisms used for defence are found within several families in the form of sticky secretions or slimy excrements.

6.6.9.1. Carabidae. Bauer and Kredler (1988) have investigated the larva of *Loricera pilicornis* F., which possesses adhesive mouthparts for catching collemboles. The galea is distally transformed into a bulb with a terminal filum (Fig. 4A). The outer layer of the cuticle is transparent and sponge-like. Gland cells inside the galea produce a secretion that probably is discharged to the surface through small pores. In dehydrated larvae, the soft cuticle collapses. The beetle larvae clean the galeae regularly by drawing them through notches on the mandibles. Fig. 4D–F show transverse sections through the galea at three different levels. In the proximal region of the bulb, sponge-like material is derived from the solid cuticle, from which loose fibres and thin layers delaminate (Fig. 4F). The solid cuticle extends as a shaft further distally and into the terminal filum, where it becomes perforated (Fig. 4E). Only longitudinal sections (not shown) demonstrate that the holes seen here are in fact oblique slits penetrating the cuticle. Furthermore, the cuticular shaft is not fully closed but, instead, is open on one side in the apical region. The structure of the material in the lumen of the shaft resembles that of the adhesive secretion that can occasionally be found as a thin layer on the surface of the galea. The thin distal part of the terminal filum does not contain solid cuticle (Fig. 4D). The secretion probably seeps through the holes in the cuticular shaft into the spongy cuticle and from there onto the surface. However, the pores that can be seen on the outer surface of the galea in SEM images (Bauer and Kredler, 1988) might actually be deep indentations occurring where the cuticular fibres of the spongy cuticle insert at the inside of the surface layer. The insufficient resolution of light microscopy has led Bauer and Kredler (1988) to postulate an orifice for the discharge of fluid at the proximal end of the bulb, between the solid and sponge-like cuticle. However, transmission electron microscopy has revealed that this pore does not exist. Instead, there are several small sensilla at the position in question, which might be mistaken for a pore when sectioned tangentially.

The softness of the sponge-like cuticle is shown in Fig. 4C. It shows a scale and presumably a cuticular hair of a springtail that is sticking to the outer surface of the cuticle. The cuticle is deeply indented by the ridges on the scale and by the larger hair. This is in accordance with the principles outlined above stating that intimate contact between two adhering surfaces is advantageous for attachment ('system with one adaptable surface' according to Scherge and Gorb, 2001). Although there is no adhesive secretion visible on the

cuticle, the particles still adhere to its surface. However, it cannot be ruled out that the particles are remains of a past predatory strike and that the previously active fluid has dried to invisibility in the meantime.

6.6.9.2. Staphylinidae. *Pselaphinae*. In most taxa, the larvae have a pair of specific organs (eversible glands?) that can be rapidly protruded out of the head by hemolymph pressure like the finger of a glove (De Marzo, 1985, 1986, 1987, 1988). In the genera *Pselaphus* Herbst and *Batrisodes* Reitter their structure and function have been more intensely studied (De Marzo, 1985, 1988): these sac-like membranous organs appear to arise from the articular membrane connecting the antenna with the head capsule. They function in capturing prey such as springtails, which stick to their terminal part, which is differentiated into a number of hair-like trichomes. Specific head glands produce a sticky secretion, which is led via cuticular ductules toward the base of the protrusible organs. From here, it is transported to the exterior surface. After a successful attack, the protruded organ is retracted by large muscles, so that the prey can finally be seized with the mandibles. Apart from this particular autapomorphy, the entire dorsal body surface of *Batrisodes* larvae is covered by an adhesive film (De Marzo, 1984, 1985), which may form sticky secretion droplets at the tip of the body setae.

Oxytelinae. The reduction of the elytra in staphylinids is paralleled by the development of abdominal exocrine defensive glands, which produce an astonishing variety of defensive secretions (Dettner, 1993). Whereas most of these substances contain toxins and function in topical irritancy, the oxyteline *Deleaster dichrous* (Grav.) produces an iridodial-containing adhesive, which serves as a mechanical defence as demonstrated toward ants and drosophilids (Dettner et al., 1985; Dettner, 1993).

Steninae

General description of adult prey-capture apparatus. The genus *Stenus* Latreille, 1796 is one of the largest beetle genera, comprising more than 2100 species widely distributed throughout the world (Puthz, 1971; Herman, 2001). The adults are optically oriented predators of springtails and other arthropods. They have a unique protrusible labium (Fig. 5A), which is one of the most specialized prey-capture structures among insects. Its general structure and function have been elucidated in several studies (Schmitz, 1943; Weinreich, 1968; Bauer and Pfeiffer, 1991; Betz, 1996; 1998a,b; Kölsch and Betz, 1998; Kölsch, 2000). The elongated prementum carries, on its apex, a pair of paraglossae, which are modified into membranous sticky cushions (Figs. 2A and 5B). Within the prementum, bundles of ductules, which transport an adhesive secretion produced by special secretory glands in the head, lead to the sticky cushions. When not in use, the labium is withdrawn back into the head, where it is wrapped by a connecting membranous tube. In order to capture prey, the beetles rapidly protrude their prementum from this resting position within just 3–5 ms. The prey adheres to the sticky cushions and is seized by the mandibles after immediate retraction of the prementum. The rapid protrusion of the labium is made possible by a catapult mechanism, which involves the antagonistic action of increased hemolymph pressure on the one hand and the contraction of large retractor muscles on the other.

Structure and function of the adhesive paraglossae. Internally, the sticky cushions at the apex of the labium are made up of a complex reticulum of endocuticular fibers (Betz, 1996; Kölsch and Betz, 1998). Together with the mesocuticular nature of their outer wall, this makes these structures highly flexible and elastic, so that they can closely adapt themselves to the shape and surface irregularities of the prey. Moreover, according to their loose arrangement, the sticky cushions can be expanded immediately prior to the strike by the increased hemolymph pressure. Furthermore, the special arrangement of these fibers probably helps to reduce the mechanical stretching stress during the rapid retraction of the labium after prey capture (Kölsch and Betz, 1998). On their external surface, the sticky cushions are differentiated into a large number of adhesive trichomes (Figs. 2A and 5B). Each trichome branches out terminally, which dramatically increases the total number of adhesive contacts (Fig. 2A). The number of both trichomes and terminal branches is species-specific and may range from one to several thousands (Bauer and Pfeiffer, 1991; Betz, 1996). It has been established experimentally that larger surface areas of the paraglossae and more adhesive setae and adhesive contacts lead to improved adhesion and consequently increased capture success (Betz, 1996). Moreover, larger and heavier springtails detach more easily from the adhesive cushions than do small ones (Betz, 1996; 1998a,b). Hence, the external structures of the sticky cushions must have been subject to great selective forces that have been effective in the direction of their functional improvement. Indeed, a comparison of different subgroups consisting of closely related species has revealed that, in each subgroup, species with large relative numbers of adhesive contacts occur side by side with species with low relative numbers of adhesive contacts on their sticky paraglossae (Betz, 1996). These results suggest that the general type of the sticky cushion, once established within the genus, has independently been functionally advanced in different phylogenetic lines in the same direction. In several species, such an improvement of the adhesive strength of the sticky cushions might have led to an enlargement of the feeding niche toward large and, at the same time, fast fleeing prey (Betz, 1998a). This provides an advantage especially for relatively clumsy species, which are physiologically constrained in terms of their reaction ability and agility. Indeed, in several very agile and reactive *Stenus* species, an expansion of the feeding niche has not taken place by morphological improvement of the sticky cushions, but rather by a behavioural shift. These species capture large

springtails predominantly by the rapid and precise grip of their mandibles (Bauer and Pfeiffer, 1991; Betz, 1998a,b).

Physical mechanism behind the adhesive action. The physical mechanism behind the adhesive action of the paraglossae and the nature of the secretion have been investigated by Kölsch (2000). According to his ultrastructural findings, the secretion consists of two immiscible phases, i.e. lipoid droplets are found within a larger proteinaceous fraction (ld and se in Fig. 5C). As suggested for the pad secretion of locusts (Vötsch et al., 2002), such an emulsion could be advantageous for the effective spreading of the secretion over various types of surfaces (hydrophilic and lipophilic). Interestingly, the wetting behavior across the area of the sticky cushions is not uniform. The secretion has to spread all over its distal surface from a very restricted zone at the outer margin of the paraglossae (arrow in Fig. 5C). Indeed, the empty space between the shafts of the adhesive trichomes is well filled with the secretion (se in Fig. 5C). Since the major fraction of the secretion is a probably watery proteinaceous liquid, it is assumed that the surface layer of the cuticle (cement layer) in this area is hydrophilic. Wetting might be further facilitated, because the cement layer in this region is roughened (Fig. 5E). On the other hand, the secretion does not spread over the lateral sides of the sticky cushions proximally adjacent to the zone of adhesive trichomes (Fig. 5C). This makes functional sense, since this part does not come into direct contact with the prey. Non-wetting by the hydrophilic secretion might be achieved by the cement layer of this region being lipophilic and, at the same time, very smooth (Fig. 5D). On account of the large amount of secretion involved (se in Fig. 5C), viscosity is the likely process of adhesion involved in this prey-capture mechanism (Kölsch, 2000). Since *Stenus* beetles hurl their body forward during the strike, the labium length is larger than the remaining distance that must be bridged by the labium (Betz, 1996; 1998a,b). This means that the labium transfers a definite impact pressure to the prey, enhancing adhesion resulting from the reduction of the thickness of the liquid film between the surfaces (Eq. (2)).

Larval stages. In the larval stages of *Stenus* species, adhesive mechanisms can also be involved in prey-capture (Larsen, 1959, 1963). According to observations in our own laboratory and on several species, springtails often adhere to the mouthparts, the antennae, the legs, or other parts of the integument before they are taken off with the legs and/or captured with the mandibles (Fig. 6A). Accordingly, the entire body surface of *Stenus* larvae often has a shiny appearance and, as in pselaphine larvae mentioned above, sometimes secretion droplets can be found at the apex of the body setae (Fig. 6B). Although fast fleeing prey such as springtails might be captured without any involvement of adhesive mechanisms (namely, by a rapid grasp with the mandibles after mechanosensitive recognition of the prey with fine hair sensilla on the body surface), adhesion certainly contributes to the high capture success of these larvae that we observed toward *Heteromurus nitidus*

Templeton springtails. Under laboratory conditions, in *S. pubescens* Stephens and *S. comma* Leconte, the capture success attains 70–90%. The origin of the adhesive secretion in *Stenus* larvae has not as yet been investigated. Potential candidates are glands possibly associated with the paired openings found dorsally on the head, the meso- and metathorax, and the abdominal tergites I-IX. Prominent subantennal glands are also present in the larvae of other 'higher staphylinids' such as Paederinae and Staphylininae (Beutel and Molenda, 1997) and might be generally involved in prey capture.

Euaesthetinae. The members of this subfamily are closely related to the genus *Stenus* dealt with in the previous paragraph. Interestingly, at least two genera within this subfamily have evolved a labial adhesion-capture apparatus analogous or even homologous to that of *Stenus* (Leschen and Newton, 2003): the genus *Tyrannomastax* from Madagascar (Orousset, 1988) and an undescribed genus from Australia, which might actually belong to the Steninae (A. Newton and O. Betz, unpublished observations). More detailed studies on the form and function of this structure are not as yet available.

Staphylininae. Representatives of the subgenus *Onychophilonthus*, such as *Philonthus marginatus* (Stroem) or *P. lederi* (Eppelsheim), are characterized by their forelimbs, which are modified into raptorial legs (Neresheimer and Wagner, 1924; Betz and Mumm, 2001) (Fig. 2B). Both sexes have especially widened fore tarsi. With these legs, the beetles are capable of striking even prey with a particularly fast escape mechanism such as springtails. The actual strike takes the form of a rapid depression of the unfolding forelegs toward the prey. Contact with the prey is mediated by a large number of adhesive hairs at the underside of the tarsus. During the subsequent withdrawal of the forelegs the last tarsomere is almost perpendicularly deflected, securing the prey at the front like a hook.

Ultrastructurally, the pro-tarsomeres I–III are supported by an active glandular epithelium, which probably produces an adhesive secretion that is released via numerous tarsal setae at the underside of the tarsi. In this way, the beetles are capable of fixing the prey at the very moment of contact.

Capture success under laboratory conditions toward *Heteromurus nitidulus* springtails amounts to 25%. The specific structure of the perpendicularly bendable tarsomere V with its strong bristle sensilla and long claws appears to be restricted to the subgenus *Onychophilonthus*. However, asexually widened tarsi obviously form the ancestral pattern not only for the subtribe Philonthina (Smetana, 1995), but for all Staphylininae plus Paederinae (Newton, personal communication). It is uncertain whether these tarsi involved in the predaceous function of the foreleg in *Onychophilonthus*, and forming the general pattern within the whole subfamily, are also used in this functional context in all these other taxa. However, their wide distribution, plus the ancestral (often specialized) predaceous pattern in the Staphylininae and Paederinae (Lawrence and Newton,
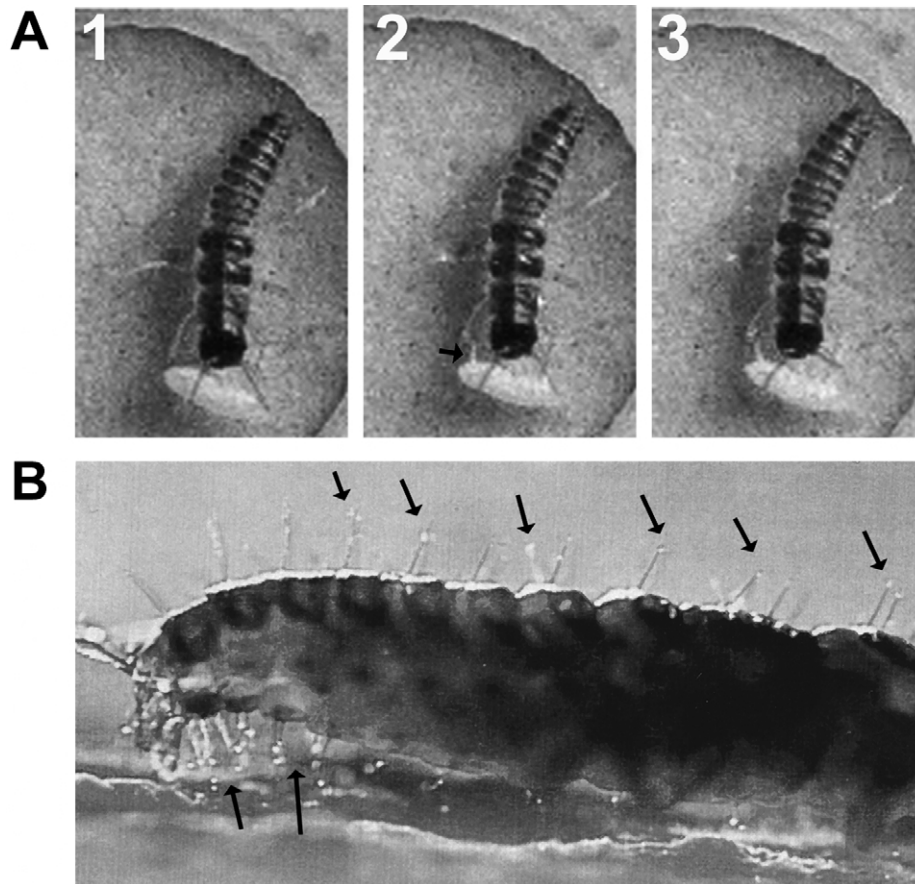
Fig. 6. **A** An L3 larva of *Stenus fossulatus* Erichson with a springtail adhering to the right antenna. Although the springtail releases its furcal escape mechanism (arrow in picture 2 points to the unfolding furca), it remains captured by the adhesive antenna. Images from a high-speed film; time course of the depicted sequence [milliseconds that lapsed from the start (= picture 1)]: (1): 0; (2): 18; (3): 28. Length of larva amounts to 3.5 mm. **B** Lateral view of the abdomen of the L3 instar of *Stenus pubescens*. Arrows point to adhesive droplets at the ends of the macrosetae. The terminal part of the abdomen is left.

1982), suggest that this character may form an ancestral adaptation for prey capture and/or subsequent handling (Newton, personal communication), leaving the subgenus *Onychophilonthus* merely as a particularly derived taxon.

For example, the use of especially widened tarsi in prey capture seems likely for the genus *Pinophilus* Gravenhorst. Members of this genus have been observed walking on their middle and hind legs only, while keeping their forelimbs in a potential 'pre-capture position' away from the ground (Holcomb, 1978).

Another example are *Nordus fungicola* (Sharp) specimens that rapidly extend their forelegs during prey capture and capture and manipulate drosophilids with their enlarged protarsi (Chatzimanolis, 2003). Other staphylinines and paederines may use their widened fore tarsi for holding captured prey during the feeding process, as we have observed in the genera *Acylophorus* Nordmann and *Bisnius* Stephens.

6.6.9.3. Scydmaenidae. Because of their hard and often smooth cuticle and the lack of arthrodial membranes in the idiosoma, mites are not easy to catch. Scydmaenids show two different adaptations for catching them (Schmid, 1988). (1) The beetles have four suction cups at the tip of the labium (prementum), which are used for holding a mite and lifting it from the ground. The suction cups look relatively delicate and soft in SEM images, and to our knowledge, there are neither data on the mechanism of attachment (e.g. on the potential role of an adhesive secretion) nor on the histology of the structure (existence and potential role of muscles on the inner side of the cuticle of the suction cup that might help to build up a vacuum). The hydrophobic and sculptured surface (cuticle and an additional layer, the cerotegument) of certain mites is an effective counter strategy against this adhesive device (although this feature may have arisen because of other selective pressures, such as the need to conserve water). (2) The distal two thirds of the tibia of the first leg of the beetles are covered with setae that have spatulate tips (Schmid, 1988). Sometimes, this pad extends to the proximal parts of the tarsus (Fig. 2C). This structure might play a role in the mating of the beetles, since it is only found in males. However, it can (secondarily?) be used for the firm handling of preyed upon mites. The beetles have to turn the mites around in order to access the softer parts on the ventral side, where they can cut into the cuticle with the mandibles along the genital or anal plate of the mite (O'Keefe, 2001).

6.6.9.4. Coccinellidae. Coccinellid adults exudate hemolymph droplets from the tibio-femoral articulation membrane of their legs (reflex bleeding), when molested by potential opponents such as ants (Happ and Eisner, 1961; Roth and Eisner, 1962). This secretion not only works chemically (because of its content of toxic alkaloids) but also mechanically, since it hardens on exposure to air. The appendages of ants exposed to the viscous secretion of the coccinellid *Epilachna varivestis* Mulsant become stuck to one another, so that they are immobilized (Happ and Eisner, 1961). Coccinellid larvae are similarly protected by glands on the abdomen (Vandenberg, 2002). Moreover, the larvae of many species produce coatings of waxy threads, which have been found, in many species, to be markedly sticky (e.g. in the genera *Scymnus* Kugelann, *Cryptolaemus* Mulsant, and *Hyperaspis* Redtenbacher) and very likely are employed to entangle the mouthparts of ants and other predatory arthropods (Pope, 1979).

6.6.9.5. Meloidae. Similar to coccinellids, meloids discharge hemolymph droplets (reflex bleeding) when assaulted. Whereas this secretion contains cantharidin that functions as a repellent (Carrel et al., 1993; Dettner, 1999), it might also mechanically smear the appendages of arthropod predators.

6.6.9.6. Chrysomelidae. The cassidine *Hemisphaerota cyanea* (Say, 1824) prevents predation by activating a tarsal adhesion mechanism. Adhesion is mediated by an oil which contains a mixture of hydrocarbons, and which is found on the surface of around 60,000 tenent setae at the bottom side of the tarsi (Eisner, 1972; Attygalle et al., 2000; Eisner and Aneshansley, 2000). When assaulted by a predator (e.g. an ant), the beetles press their tarsi down flatly, which dramatically increases their adhesion with the surface. In this way, they can withstand lateral and vertical pulling forces (as exerted by the attacking predator) of many times their body mass.

As described above for coccinellids, some chrysomelids (e.g. *Timarcha* Latreille) also show reflex bleeding from the tibio-femoral articulation of their legs (Hesse and Doflein, 1943) (Fig. 7B).

It might be a borderline case to include the larvae of most Criocerinae, the cassidoid Hispinae, and the genus *Blepharida* Chevrolat (Alticini) in this review, but they place fecal material on their dorsum for defence (Riley et al., 2002). As long as this material is fluid or viscous, it might not only function in camouflage but also in entangling predators.

6.6.9.7. Curculionidae. Like the chrysomelid groups mentioned above, larvae of the tribe Cionini are reported to be dorsally covered by a slimy mass of excremental material (Crowson, 1981).

6.6.10. Hymenoptera

6.6.10.1. Tenthredinidae. The larvae of *Caliroa* Costa species are covered by a slimy secretion, which helps to repel predators (Brauns, 1991; Dathe, 2003). Larvae of the genus *Siobla* Cameron spray adhesive hemolymph from lateral openings when assaulted (Brauns, 1991). Since no chemically active ingredients have been found in this substance, it probably functions solely mechanically (Dettner, 1999).

6.6.10.2. Diprionidae and Pergidae. In some groups, the larvae store ethereal oils from their host plant (e.g. *Pinus*, *Eucalyptus*) in special evaginations of the foregut. On assault, the larvae regurgitate the sequestered sticky substances toward the attacker (Eisner, 1972). According to their content of mono- and sesquiterpenes, these secretions have a repellent function (Gullan and Cranston, 1994; Dettner, 1999).

6.6.10.3. Cimbicidae. Like *Siobla* (Tenthredinidae), cimbicid larvae spray hemolymph droplets on assault (Hesse and Doflein, 1943; Brauns, 1991; Dathe, 2003) (Fig. 7C).

6.6.10.4. Vespidae. Members of the subfamily Stenogastrinae (e.g. *Parischnogaster* Schulthess spp.) use the secretion from the Dufour's gland to construct sticky defensive barriers (known as 'ant guards') that protect the immature brood from predation by ants (Hermann and Blum, 1981; Turillazzi and Pardi, 1982). The barriers are placed by the females on the nest substratum just above the brood cells (Fig. 7D). They are composed of long-chain saturated and unsaturated hydrocarbons and alcohols (Sledge et al., 2000).

6.6.10.5. Formicidae. Similar to the staphylinid *Deleaster*, members of the dolichoderine genus *Tapinoma* Foerster produce a secretion, composed of ketones, quinones, and iridodial, in their abdominal glands. Iridodial polymerizes on contact with air, adheres to the predator, and diminishes the evaporation of the toxic components mixed with it (Trave and Pavan, 1956; Pavan and Trave, 1958; Roth and Eisner, 1962; Dettner, 1999). The metapleural gland of various ants (e.g. *Crematogaster inflata* Smith) contains a sticky defence secretion that is released as a repellent (Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990). Similar to the extreme defence mechanism described above for some termites, workers of the *Camponotus saundersi* Emery group sacrifice themselves by bursting the abdomen by muscle contraction to release large quantities of sticky secretion from the mandibular glands that are hypertrophied and enlarged into the abdomen (Maschwitz and Maschwitz, 1974; Hermann and Blum, 1981; Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990) (Fig. 7E). This behavior has been termed
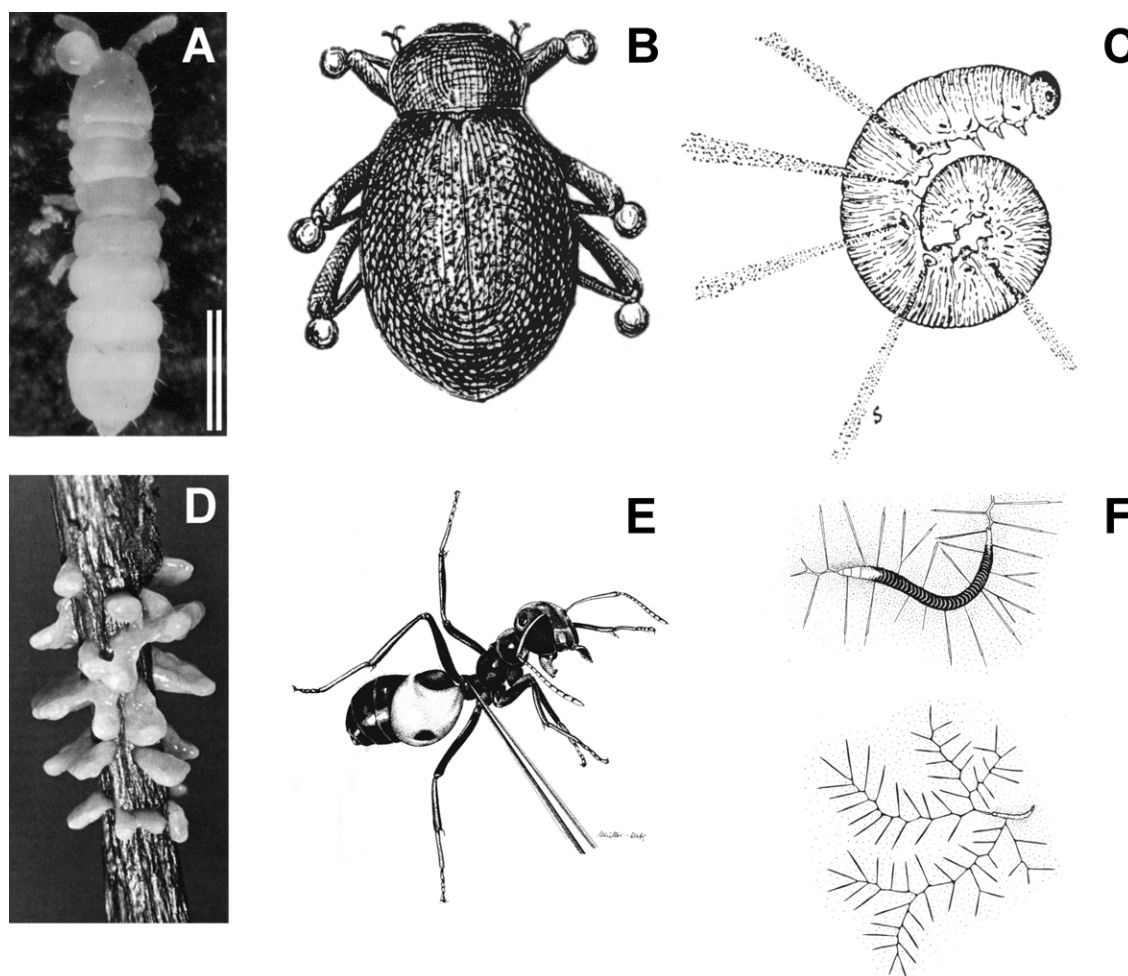
Fig. 7. Examples for adhesive defence mechanisms that involve the exudation of a sticky secretion. **A** Springtail of the genus *Onychiurus* releasing a secretion droplet from a pseudocellus. From Dettner (1999). **B** The chrysomelid *Timarcha* showing reflex bleeding from the tibio-femoral articulation of the legs. From Hesse and Doflein (1943). **C** Cimbicid larva (*Cimbex* sp.) spraying hemolymph droplets. From Hesse and Doflein (1943). **D** Sticky 'ant guards' produced by *Parischnogaster jacobsoni* von Schulthess. From Turillazzi (1991). **E** If a worker of *Camponotus saundersi* is seized with a pair of forceps, it contracts its abdominal wall violently, finally bursting open to release secretion from its hypertrophied mandibular glands. From Buschinger and Maschwitz (1984). **F** Larva of the mycetophilid *Platyura fultoni* Fisher produces sticky threads, in which it ambushes prey on the ground. The frontal and terminal parts of the larvae are luminescent. From Séguy (1951).

'autothysis' (cf. Section 6.6.4) and functions to immobilize attacking ants.

6.6.10.6. Sphecidae. Some species (e.g. *Passaloecus* Shuckard spp.) form protective adhesive rings of resin around their nest entrance. They can also close their nest with resin plugs. Indeed, dead ants can be found captured in the resin (Hermann and Blum, 1981).

6.6.10.7. Apidae. Whereas some bees forcefully eject liquid faeces to defend their nests (Janzen, 1966), others may cover an assailant with honey (*Bombus* Latreille and some Trigonini) or resin (trigonines) (Drory, 1872; Stephen et al., 1969; Hermann and Blum, 1981; Roubik, 1989). Brief descriptions of such behavior in stingless bees are given by Kerr and Lello (1962), Michener (1974), and Nates and Cepeda (1983). In some bees, waxes mixed with vegetable gums and resins are employed as entrance blockages, often

arranged in a ring-like fashion around the nest entrance (Maidl, 1934; Hermann and Blum, 1981).

6.6.11. Diptera

6.6.11.1. Mycetophilidae. The larvae of several species (e.g. of the genus *Phronia* Winnertz) mask their surface with a slimy coating, which gives them the appearance of tiny slugs (Hesse and Doflein, 1943; Brauns, 1991; Ziegler, 2003). In the bioluminescent mycetophilid fungus gnats (Keroplatinae), the larvae produce webs (in analogy to many spiders) that function in prey capture (Herring, 1978; Sivinski, 1998; Bauer, 1999; Dettner, 1999). The Malpighian tubules of the larvae of the cave-dwelling *Arachnocampa luminosa* (Skuse) are modified into luminous organs. These produce strands of sticky mucus and silk that are used to produce webs and long hanging 'fishing lines'. These illuminated traps attract flying insects, which

are captured in the adhesive threads. In a similar way, the larvae of the genus *Platyura* Meigen lay sticky threads in which they ambush prey on the ground (Fig. 7F). At the same time, these larvae are protected by this retreat, which might also be provided with poisonous substances such as oxalic acid (Buston, 1933; Mansbridge, 1933; Sivinski, 1998; Bauer, 1999).

6.6.11.2. Therevidae, Asilidae, Empididae. The predaceous members of these families are reported to capture their prey in flight with their (predatory) legs. The well-developed adhesive pulvilli of these flies might be employed in prey capture, although, to our knowledge, no detailed studies have been undertaken to verify this.

6.6.11.3. Syrphidae. Syrphid larvae feeding on aphids are known to defend themselves against aggressive ants by releasing a droplet of viscous fluid from the mouth, which is brought into contact with the assailant (Eisner, 1972). It is not known whether this fluid contains additional repellents.

6.6.12. Lepidoptera

To our knowledge, there are no adhesive mechanisms to be considered in the Lepidoptera. Because of the biology of butterflies, only a defensive strategy, notably among larvae, seems probable. However, it is not clear whether, in the rare cases of the reflex bleeding of caterpillars (e. g. among Lymantriidae; Hesse and Doflein, 1943), the physical properties of the fluid play a role.

7. Conclusion and future prospects

Predation and predator defence are among the most important interactions between living organisms. Because of the strong selective pressures emanating from such relationships, predators have often evolved highly specialized and efficient methods of capturing prey. In answer, potential prey animals have developed elaborate defensive adaptations (*sensu* Edmunds, 1974) against their opponents. According to their universal presence, it is small wonder that the physics of adhesion is employed by small animals such as arthropods in these contexts. These mechanisms have the advantage that predators can catch their prey merely by contacting it and sticking to it, so that the evolution of highly derived sensory and/or neuromuscular equipment is not required. In the context of defence, stickiness is advantageous especially for slow-moving arthropods (Pasteels et al., 1983). Moreover, adhesive defences are universally effective as long as the predator is in the size range of the prey. In solely chemically acting defence secretions, some predators might easily evolve mechanisms of countering the efficiency of these substances (selection of specialists according to Remmert, 1989). This might not be easily attainable in adhesively acting defence secretions, because their main mode of action is physical.

Thus, they might be equally effective toward both specialist and generalist predators. Another advantage of sticky secretions might lie in the possibility that an animal can use it in both predation and defence (as observed in onychophorans or spitting spiders). This is in contrast to chemically acting defence mechanisms of arthropods, which are usually not used in offence (Roth and Eisner, 1962).

Although adhesive mechanisms can be highly efficient in both predation and defence, our literature survey has revealed a patchy distribution among the arthropods (cf. Appendices A and B). However, to date, probably only a very small fraction of such instances has been discovered. This is probably especially true for tiny inconspicuous animals (e.g. in soil biota), whose biology has not as yet been sufficiently studied, e.g. only around 2% of the 56,000 species of staphyliniform beetles have been described as larvae (Newton, 1990). On the other hand, the production of adhesive mechanisms might be expensive in terms of energy requirement, because such viscous substances have to be produced and discharged in relatively large quantities to be effective. Since they might easily polymerize or dry on exposure to air, they have to be permanently supplied by specialized glands, unless they are sequestered from externally ingested resins. Hence, concurrent mechanisms such as chemical or other mechanical defence devices (e.g. armoured integuments) might have evolved to protect otherwise vulnerable clumsy life forms. Another functional problem connected with the employment of adhesives in both predation and defence is the risk of self-contamination. Adhesive body surfaces might impede movement in highly mobile phenotypes, whereas this should be of minor importance for sluggish life forms. In any case, adhesive surfaces might require special mechanisms to avoid the spreading of the sticky secretions over functionally important body parts (e.g. mouthparts). Whereas this can be achieved by the production of surfaces non-wettable by the secretion (as suggested for the *Stenus* labium), it might entail extensive self-grooming in other groups.

Several areas in this field deserve further exploration. In addition to complementing our basic knowledge on the occurrence of adhesive mechanisms in the context of predation, future studies should focus on the influence of the specific surface properties of both the predatory device and the prey in terms of overall structure, roughness, and chemistry. This would enhance our understanding of the physical mechanisms behind the interlocking of predator and prey. These investigations should thus include (1) analyses of the chemical composition of the involved adhesive secretions, (2) anatomical studies on the specific ultrastructure of the predatory devices, (3) the determination of roughness, surface energy, and surface polarity of both the involved surfaces, and (4) direct measurements of the adhesive strength between both these surfaces. In this respect, such studies will greatly benefit from the extensive scientific and methodological progress recently attained in

Table 1

Survey of the occurrence of adhesive mechanisms as employed in predation across the Arthropoda. Hyphens indicate that data on this subject are not available

Systematic unit	Observed taxon	Developmental stage	Ecology	Involved body structure/behavior	Details of secretion	Literature source
Onychophora	*Peripatopsis moseleyi*	Juvenile, adult	Predator of arthropods	Paired slime glands with openings on oral papillae/slime expelled onto prey	Proteins and amino acids, which denature in air	Alexander, 1957; Röper, 1977; Ruhberg and Storch, 1977
Chelicerata						
Araneidae	bolas spiders (*Mastophora* spp. and several other genera worldwide)	Adult	Specialised predator of flying insects (moths)	Thread of silk with liquid droplet, which may be swung selectively against prey	Sticky silk globule (mainly proteinaceous?)	Eberhard, 1977; Eberhard, 1980; Yeargan, 1994; Foelix, 1996
Scytotidae	*Scytodes* spp.	Adult	Predator of arthropods	Secretion ejected from chelicerae	Also contains poison	McAlister, 1960; Blum, 1981
Wandering spiders	*Cupiennius salei* (Ctenidae); *Lycosa* spp. (Lycosidae); Salticidae	Adult	Predator of arthropods	Pads of hairs (scopulae) at tips of legs	–	Melchers, 1967; Rovner, 1978, 1980; Roscoe and Walker, 1991
Acari						
Bdellidae	9 species in 4 subfamilies	–	Predator of arthropods	Glands with opening at tip of gnathosoma/prey is tied to substrate	–	Alberti, 1973
Crustacea						
Decapoda	Alpheidae	Adult	Mainly predaceous; marine in coral reefs	Indirect role of adhesion in snapping mechanism of claw/production of a jet of water and a clicking sound	Water	Ritzmann, 1974
Chilopoda	Lithobiidae	Juvenile, adult	Predator	Openings of glands on last pair of legs	Can be drawn out into sticky threads	Verhoeff, 1925; Attems, 1926/1930
Insecta						
Saltatoria	*Tettigonia viridissima*	Adult	Predator	Tarsal pads/holding of prey	Pads are regularly wetted with saliva	Henning, 1974
Heteroptera						
Reduviidae	*Zelus leucogrammus*, Apiomerinae, Harpactorinae, and others	Larva, adult	Predator	Legs covered by secretion produced in epidermal glands; fossula spongiosa on tibiae	Water soluble, hygroscopic; Apiomerinae collect additional fluid from plants	Miller, 1942; Barth, 1953; Edwards, 1960, 1962; Weber and Weidner, 1974; Eisner, 1988
Coleoptera						
Carabidae	*Loricera pilicornis*	Larva	Predator	Galea (bulb-shaped, soft cuticle) with internal gland	–	Bauer and Kredler, 1988
Staphylinidae—Pselaphinae	*Pselaphus* spp.	Larva	Predator, e.g. of springtails	Eversible organs (head glands?) close to antennal insertion	–	De Marzo, 1984, 1985, 1987, 1988
	Batrisodes spp.	Larva	Predator, e.g. of springtails	Dorsal body surface/'tail-stroke'	–	De Marzo, 1984, 1985
Staphylinidae—Steninae	*Stenus* spp.	Adult	Predator, e.g. of springtails	Paraglossae of elongated labium/labium is hurled out from the body	Emulsion of lipoid droplets within proteinaceous fraction	Schmitz, 1943; Weinreich, 1968; Bauer and Pfeiffer, 1991; Betz, 1996, 1998a,b; Kölsch and Betz, 1998; Kölsch, 2000 Larsen, 1959, 1963; present study
	Stenus spp.	Larva	Predator, e.g. of springtails	Prey sticks to mouthparts, antennae, legs, general integument	–	
Staphylinidae - Euaesthetinae	*Tyrannomastax* spp., Gen. sp.	Adult	Predator?	Paraglossae of elongated labium	–	Orousset, 1988; Leschen and Newton, 2003; Newton and Betz, unpublished observations
Staphylinidae—Staphylininae	*Philonthus marginatus*, *Pinophilus* spp., *Nordus fungicola*	Adult	Predator, e.g. of springtails or flies	Fore tarsi/fast strike of the fore legs	–	Neresheimer and Wagner, 1924; Holcomb, 1978; Betz and Mumm, 2001; Chatzimanolis, 2003
Scydmaenidae	*Scydmaenus* sp.	Adult	Predator of mites	Suction cups at tip of labium; fore legs (tibia, tarsus) with setal pads	–	Schmid, 1988
Diptera						
Mycetophilidae	Keroplatinae; *Arachnocampa luminosa*; *Platyura* sp.	Larva	Predator of various flying insects	Luminescent sticky threads produced by Malpighian tubules	–	Buston, 1933; Mansbridge, 1933; Herring, 1978; Sivinski, 1998; Bauer, 1999; Dettner, 1999
Therevidae	Various predaceous genera	Adult	Predator of various flying insects	Strike with tarsi of the legs?	–	–
Asilidae	Various predaceous genera	Adult	Predator of various flying insects	Strike with tarsi of the legs?	–	–
Empididae	Various predaceous genera	Adult	Predator of various flying insects	Strike with tarsi of the legs?	–	–

Table 2
Survey of the occurrence of adhesive mechanisms as employed in defence across the Arthropoda. Hyphens indicate that data on this subject are not available

Systematic unit	Observed taxon	Developmental stage	Ecology	Involved body structure/behavior	Details of secretion	Literature source
Onychophora	*Peripatopsis moseleyi*	Juvenile, adult	Predator of arthropods	Paired slime glands with openings on oral papillae/slime expelled onto predator	Proteins and amino acids that denature in air	Alexander, 1957; Röper, 1977; Ruhberg and Storch, 1977
Chelicerata Scytotidae	*Scytodes* spp.	Adult	Predator of arthropods	Secretion ejected from chelicerae	Also contains poison	McAlister, 1960; Blum, 1981
Crustacea Isopoda	*Porcellio scaber, Oniscus asellus, Armadillidium vulgare, Philoscia muscorum, Platyarthrus hoffmannsegii*	Juvenile, adult	Detritivore	Secretion from uropod glands/can be drawn into threads	–	Gorvett, 1956; Gorvett and Taylor, 1959
Decapoda	Alpheidae	Adult	Mainly predaceous; marine in coral reefs	Indirect role of adhesion in snapping mechanism of claw	No secretion involved	Ritzmann, 1974
Chilopoda	Lithobiomorpha, Geophilomorpha	Juvenile, adult	Predator	Glands on last pair of legs or along the body	Sticky, entangling fluid	Verhoeff, 1925; Minelli, 1978
Progoneata Symphyla		Juvenile, adult	Detritivore (herbivore)	Gland associated with spinnerets/thread for escape into crevices	–	Verhoeff, 1934; Eisenbeis and Wichard, 1985
Diplopoda	Glomeridae (and other families)	Juvenile, adult	Detritivore	Lateral glands on segments producing a deterring but also sticky secretion	Proteins and alkaloids (in *Glomeris*)	Eisner and Meinwald, 1966; Schildknecht et al.,1967; Blum, 1981
Insecta Protura		Juvenile?, adult	Euedaphic, fungivore	Voluminous abdominal glands	Proteinaceous, acid, soluble in alkali	Denis, 1949
Collembola	Onychiuridae	Adult	Euedaphic detritivore and fungivore	Secretory glands (pseudocella) on the body surface/reflex bleeding	Viscous secretion includes deterrents and toxins	Konček, 1924; Mayer, 1957; Usher and Balogun, 1966; Rusek and Weyda, 1981
Blattoptera	*Blatta orientalis*	Larva, adult	Omnivore	Abdominal glands in several segments, not in adult males	Sticky, not toxic; 90% protein	Roth and Stahl, 1956; Plattner et al., 1972; Brossut and Sreng, 1980
Isoptera	Several subfamilies	Adult	Social insects, fungivore	Cephalic glands/excretion is discharged; autothysis (in Apicotermitinae)	Sticky fluid with additional toxic effects	Cook, 1900; Ernst, 1959; Eisner, 1970; Eisner et al., 1976; Blum, 1981; Deligne et al., 1981; Pasteels et al., 1983; Prestwich, 1984
Saltatoria	Many Ensifera and Caelifera	Larva, adult	Herbivore (Caelifera, Ensifera), carnivore (Ensifera)	Defensive glands on various parts of the body, depending on the species	Deterring hemolymph with probable additional mechanical effect	Hesse and Doflein, 1943; Eisner, 1972
Auchenorrhyncha Cicadina	*Flata* spp. and related genera	Larva	Plant-sap sucker	Body surface	Entangling laniferous threads	Hesse and Doflein, 1943
	Cercopidae	Larva	Plant-sap sucker	Fluid exuded through anus; mixed with secretion from abdominal glands	Air bubbles introduced into fluid, which contains proteins and/or mucopolysaccarides	Jacobs and Renner, 1988
Sternorrhyncha Aleyrodoidea	*Trialeurodes* spp. and other genera	Larval instars II-IV	Phloem-sap sucker	Wax palisades discharged from glands at body margin	Waxes	Zahradnik, 1972; Gill, 1990; Byrne and Bellows, 1991
Aphidina	Most representatives of Aphidoidea	Larva, adult	Plant-sap sucker	Discharged from abdominal cornicles; secretion solidifies after contact with predator	Triglycerides and aliphatic sequiterpenes, exudate contains alarm pheromones	Hesse and Doflein, 1943; Blum, 1981; Strümpel, 2003
	Pemphigidae	Larva, adult	Gallforming plant-sap sucker, secondary host: plant roots	Body surface	Waxes	Hesse and Doflein, 1943
Coccina	Pseudococcidae and representatives of most other families	Adult females and their offspring	Plant-sap sucker	Body surface, anterior and posterior openings (osteoles)	Waxes, silk, lacquer, proeinaceous secretion	Schmutterer, 1972; Miller and Kosztarab, 1979; Jacobs and Renner, 1988; Foldi, 1990; Strümpel, 2003
Coleopitera Staphylinidae—Oxytelinae	*Deleaster dichrous*	Adult	Predator?	Abdominal defensive glands; secretion solidifies after contact with predator	Monomeric adhesive containing iridodial	Dettner et al., 1985; Dettner, 1993
Coccinellidae	Representatives of most genera, e.g. *Epilachna* spp.	Larva, adult	Predator, herbivore, fungivore or pollenivore	Tibio-femoral articulation membrane (adult); abdominal glands (larva)/reflex bleeding	Hemolymph mixed with alkaloids	Happ and Eisner, 1961; Roth and Eisner, 1962; Vandenberg, 2002
	Representatives of Scymnini, Ortaliini, Hyperaspini, Coccidulini, Noviini, Cryptognathini, Azyini, Telsimiini	Larva	Predator	Body surface (wax covering)	Waxes	Pope, 1979
Meloidae	Many species	Adult	Herbivore	Leg articulation membranes/reflex bleeding	Hemolymph mixed with cantharidin	Carrel et al., 1993; Dettner, 1999

Table 2 (continued)

Systematic unit	Observed taxon	Developmental stage	Ecology	Involved body structure/behavior	Details of secretion	Literature source
Chrysomelidae	*Hemisphaerota cyanea*	Adult	Herbivore	Fore, middle, and hind tarsi/successful opposition of pulling force exerted by a predator	Oil consisting of C_{22} to C_{29} *n*-alkanes and *n*-alkenes	Eisner, 1972; Attygalle et al., 2000; Eisner and Aneshansley, 2000
	Timarcha spp. and other genera	Adult	Herbivore	Mouth, tibio-femoral articulation membrane/reflex bleeding	Hemolymph	Hesse and Doflein, 1943
	Criocerinae, Hispinae, *Blepharida* spp. (Alticini)	Larva	Herbivore	Fecal material placed on dorsum	Fecal material	Riley et al., 2002
Curculionidae	Cionini	Larva	Herbivore	Fecal material placed on dorsum	Fecal material	Crowson, 1981
Hymenoptera						
Tenthredinidae	*Caliroa* spp.	Larva	Herbivore	Dorsal body surface	Slimy secretion	Brauns, 1991; Dathe, 2003
	Siobla spp.	Larva	Herbivore	Abdominal defensive glands/spray adhesive hemolymph	Hemolymph	Brauns, 1991
Diprionidae	*Neodiprion sertifer*	Larva	Herbivore	Evagination of foregut/regurgitation of sticky substances	Sequestered ethereal oils and resins containing mono- and sesquiterpenes	Eisner, 1972
Pergidae	*Perga* spp.	Larva	Herbivore	Evagination of foregut/regurgitation of sticky substances	Sequestered ethereal oils and resins containing mono- and sesquiterpenes	Gullan and Cranston, 1994; Dettner, 1999
Cimbicidae	*Cimbex* spp.	Larva	Herbivore	Abdominal defensive glands/spray adhesive hemolymph	Hemolymph	Hesse and Doflein, 1943; Brauns, 1991; Dathe, 2003
Vespidae	Stenogastrinae	Adult	Predator	Secretion from Dufour's gland/building of 'ant guards'	Long-chain saturated and unsaturated hydrocarbons and alcohols	Hermann and Blum, 1981; Turillazzi and Pardi, 1982; Sledge et al., 2000
Formicidae	*Tapinoma* spp.	Adult	Predator, honey dew feeder	Abdominal glands/secretion solidifies after contact with predator	Ketones, quinones, and iridodial	Trave and Pavan, 1956; Pavan and Trave, 1958; Roth and Eisner, 1962; Dettner, 1999
	Crematogaster inflata and other species and genera	Adult	Predator, honey dew feeder	Metapleural gland	Sticky defence secretion	Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990
	Camponotus saundersi	Adult	Predator, honey dew feeder	Hypertrophied mandibular glands/autothysis	Large quantities of sticky secretion	Maschwitz and Maschwitz, 1974; Hermann and Blum, 1981; Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990
Sphecidae	*Passaloecus* spp. and other genera	Adult	Predator	Adhesive rings around nest entrance	Resin	Hermann and Blum, 1981
Apidae	*Xylocopa* spp., *Bombus* spp., some Trigonini, some Meliponinae	Adult	Nectar and pollen feeder	Ejection of liquids via the anus	Liquid faeces, honey, or resin	Drory, 1872; Kerr and Lello, 1962; Stephen et al., 1969; Michener, 1974; Hermann and Blum, 1981; Nates and Cepeda, 1983; Roubik, 1989
	Lestrimelitta lima, Trigona canifrons	Adult	Nectar and pollen feeder	Adhesive blockages or rings around nest entrance	Waxes mixed with vegetable gums	Maidl, 1934; Hermann and Blum, 1981
Diptera						
Mycetophilidae	*Phronia* spp.	Larva	Fungivore	Slimy coating on dorsum	–	Hesse and Doflein, 1943; Brauns, 1991; Ziegler, 2003
Syrphidae	Many aphidivorous species	Larva	Predator	Discharge of salivary gland secretion from the mouth	Proteinaceous?	Eisner, 1972
Lepidoptera						
Lamyntriidae	*Leucoma salicis*	Larva	Herbivore	Prothorax/reflex bleeding	Hemolymph	Hesse and Doflein, 1943

the analysis of attachment systems employed in insect locomotion (Scherge and Gorb, 2001). Chemical analyses together with electron microscopic studies of the adhesive should also elucidate the functional role and taxonomic distribution of two-phase secretions consisting of a lipoid and a proteinaceous fraction. In contrast to adhesive defence mechanisms, predatory devices often have to be employed in a highly specific manner connected with complex behavioural patterns. Detailed analyses of the predatory strike (in terms of its kinematics and mechanics) should therefore improve our understanding of the extent to which behavioural mechanisms interact with adhesive organs, so that the organs can attain optimal adhesive strength.

In the vast majority of case studies described in this review, the specific physical and chemical mechanisms involved are unknown. Comparative functional analyses as suggested above would widen our knowledge of these mechanisms and contribute to our understanding of animal construction in general.

Appendix A

Table 1

Appendix B

Table 2

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