

The anatomy and ultrastructure of the suctional organ of Solifugae (Arachnida)

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Abstract

Solifugae possess an eversible, adhesive pedipalpal organ (suctional organ) at the tip of the distal tarsus of each pedipalp that is unique among arachnids. When inverted inside the pedipalp, the suctional organ is covered with two cuticular lips, a dorsal upper lip and a ventral lower lip, but it can be protruded rapidly in order to facilitate grasping prey or climbing on bushes or even climbing on smooth surfaces due to its remarkable adhesive properties. In this study, the suctional organs of different species from old world families Galeodidae and Karschiidae and new world families Ammotrechidae and Eremobatidae were investigated by means of light microscopy, scanning and transmission electron microscopy. In all representatives, the suctional organ is formed by an eversible, cuticular pad with a complex internal stabilizing structure. The procuticle of this pad consists of a lattice-like basal plate and numerous stalked structures connected to this basal plate. The shafts of the stalked structures are regularly organized and ramify apically. The surface of the suctional organ is constituted of a very thin epicuticle overlaying the ramifying apices forming ridges and furrows on the ventral side of the suctional organ.

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1. Introduction

Adhesive structures play an important adaptive role in the entire animal kingdom. They are involved in animal–animal interactions such as prey capture, defense, or in movement of the animal. The adhesive setae of Geckos, making geckos exceptional climbers, represent one of the most intensively studied adhesive structures. According to present knowledge, these animals possess one of the most efficient and versatile adhesive structures (e.g., Ruibal and Ernst, 1965; Russel, 1975; Autumn et al., 2000). Within the Arthropoda various types of attachment

devices have also evolved. These devices have extensively been investigated above in all insects and comprise two major categories: (1) hairy attachment systems, consisting of long deformable setae, and (2) smooth attachment pad systems with high flexibility (Beutel and Gorb, 2001). Among others, setal tarsomeres of beetles (Stork, 1980a) and the empodial pulvilli of some Diptera belong to the first category (Beutel and Gorb, 2001), whereas smooth pulvilli of Heteroptera (Ghazi-Bayat and Hasenfuss, 1980), arolia of *Schistocerca gregaria* (Kendall, 1970), euplantulae of Ensifera, Caelifera and Phasmatodea or eversible pretarsal balloon-shaped structures (probably homologous with arolia) of Thysanoptera belong to the second category of adhesive devices (Beutel and Gorb, 2001). These two mechanisms have also evolved in arachnids, but have been far less studied. Claw tufts or scopulae investigated in salticid spiders represent an example of hairy attachment systems (Hill,

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1977; Roscoe and Walker, 1991; Foelix, 1996) and the ventrally located adhesive “suckers” examined in heterozercoid mites and pulvilli of anactinotrichid mites are examples of the second system (Alberti and Coons, 1999; Gerdeman and Alberti, in press). Adhesive setae cover a wide spectrum of morphological complexity from relatively simple structures consisting just of a single seta with a curved tip to more complex systems consisting of setae that split into numerous sub-structures. Even smooth pads show surprisingly distinct surface features (Beutel and Gorb, 2001). The analyses of the mechanisms of adhesive processes involving different physical forces (Stork, 1980b; Dixon et al., 1990; Langer et al., 2004) or secretions (e.g., Hasenfuss, 1977, 1978; Jiao et al., 2000) have been done for insects and recently for spiders as well (Kesel et al., 2003; Gorb et al., 2006; Niederegger and Gorb, 2006).

Heymons (1902) reported on hunting solifuges (Solifugae) using their pedipalpal adhesive pad (Haftlappen) to grasp flying insects. Cloudsley-Thompson (1954) called this adhesive pad at the tip of each pedipalp “suctorial organ”. He observed and Cushing et al. (2005) demonstrated the ability of certain solifuges to climb smooth surfaces, such as glass, with the aid of the suctorial organ. The gross morphology and partly the internal morphology of this organ were investigated by various authors in the past (see e.g., Bernard, 1896; Kaestner, 1933). The first light micrographs were presented by Barrows (1925) and Cushing et al. (2005). The present study aims to reveal the fine structure of this peculiar organ.

2. Materials and methods

2.1. Animals

Juveniles of *Galeodes caspius subfuscus* Birula, 1937 (Galeodidae) were collected in Kazakhstan. *Eusimonia mirabilis* Roewer, 1933 (Karschiidae) was collected near Erfoud, Morocco. An adult male of *Eremobates pallipes* (Say, 1823) (Eremobatidae) was collected in Colorado, USA (38°31'38"N, 104°24'21"W). Different nymphal instars of both species of the family Ammotrechidae, *Oltacola gomezi* Roewer, 1934 and *Oltacola chacoensis* Roewer, 1934 were obtained near San José de las Salinas, in the Salinas Grandes, province of Córdoba, Argentina (64°48'23"S, 30°02' 31"W). Voucher specimens have been deposited in the Zoological Institute & Museum of the Ernst-Moritz-Arndt-University of Greifswald.

2.2. Light microscopy (LM)

The pedipalps were cut off with a pair of microscissors and immediately transferred into fixative solution after the method of Duboscq—Brasil (Romeis, 1989). The specimens were fixed for 3 weeks and afterwards embedded in paraffin. Serial sections of approximately 4 µm were cut with a Leica RM 2125 RT microtome and stained with H–E technique and Azan technique (Romeis, 1989). Sections were studied with a Nikon Eclipse TE300 microscope.

2.3. Transmission electron microscopy (TEM)

The pedipalps were fixed in 2.5% glutaraldehyde buffered in phosphate buffer (pH 7.2, 0.1 M, 1.8% sucrose) overnight at 4 °C. Further fixation processes included treatment with aqueous OsO₄ (2%) for 2 h at 4 °C, rinsing in phosphate buffer, dehydration in ascending ethanol series (60–100%) and final embedding in low-viscosity resin (Spurr, 1969). Ultrathin sections of approximately 50–70 nm were cut with a Diatome diamond knife using a Leica Ultracut microtome. Sections were placed on copper grids, stained with saturated uranyl acetate (in 70% methanol) and lead citrate according to Reynolds (1963) and investigated with a Zeiss EM 10A transmission electron microscope.

2.4. Scanning electron microscopy (SEM)

For scanning electron microscopy the specimens were ultrasonicated, dehydrated in ascending ethanol series (60–100%) and critical point dried in a BAL-TEC CPD 030. Afterwards they were fixed to aluminium stubs with adhesive carbon film and finally sputter coated with gold–palladium (Quorum Technologies SC7620). The scanning electron microscopy was performed with a LEO DSM 940A and images were taken digitally.

2.5. Film material and image processing

Kodak Electron Image Film SO-163 material was used for TEM. Negatives of TEM investigation were scanned with 600 dpi. Light microscopic pictures were taken digitally with a Nikon DXM1200 and directly uploaded using the program Nikon ACT-1.

3. Results

The general anatomy and morphology of the suctorial organ is almost identical in all investigated species.

3.1. External morphology (SEM)

The suctorial organ is located at the tip of the distal tarsus of each pedipalp. When withdrawn into the pedipalp it is covered with a dorsal upper cuticular lip, overlapping a ventral lower one (Fig. 1A). The upper lip is slightly folded in the middle (Fig. 1A) and its margin is provided with minute conically shaped teeth of different sizes, which are oriented in slightly different directions (Fig. 1B). A fold above the insertion region of the cuticular tendon on the lower lip can exhibit slightly different shapes depending on the species. For example, in *G. caspius subfuscus* this fold runs almost horizontally whereas in *E. pallipes* it slightly undulates. When protruded the suctorial organ has a pad-like appearance and a ridged surface (Fig. 1C). Comparative observations revealed only slight differences in shape and size of the suctorial organ between the investigated species. The ventral and the dorsal side of the suctorial organ can clearly be distinguished from each

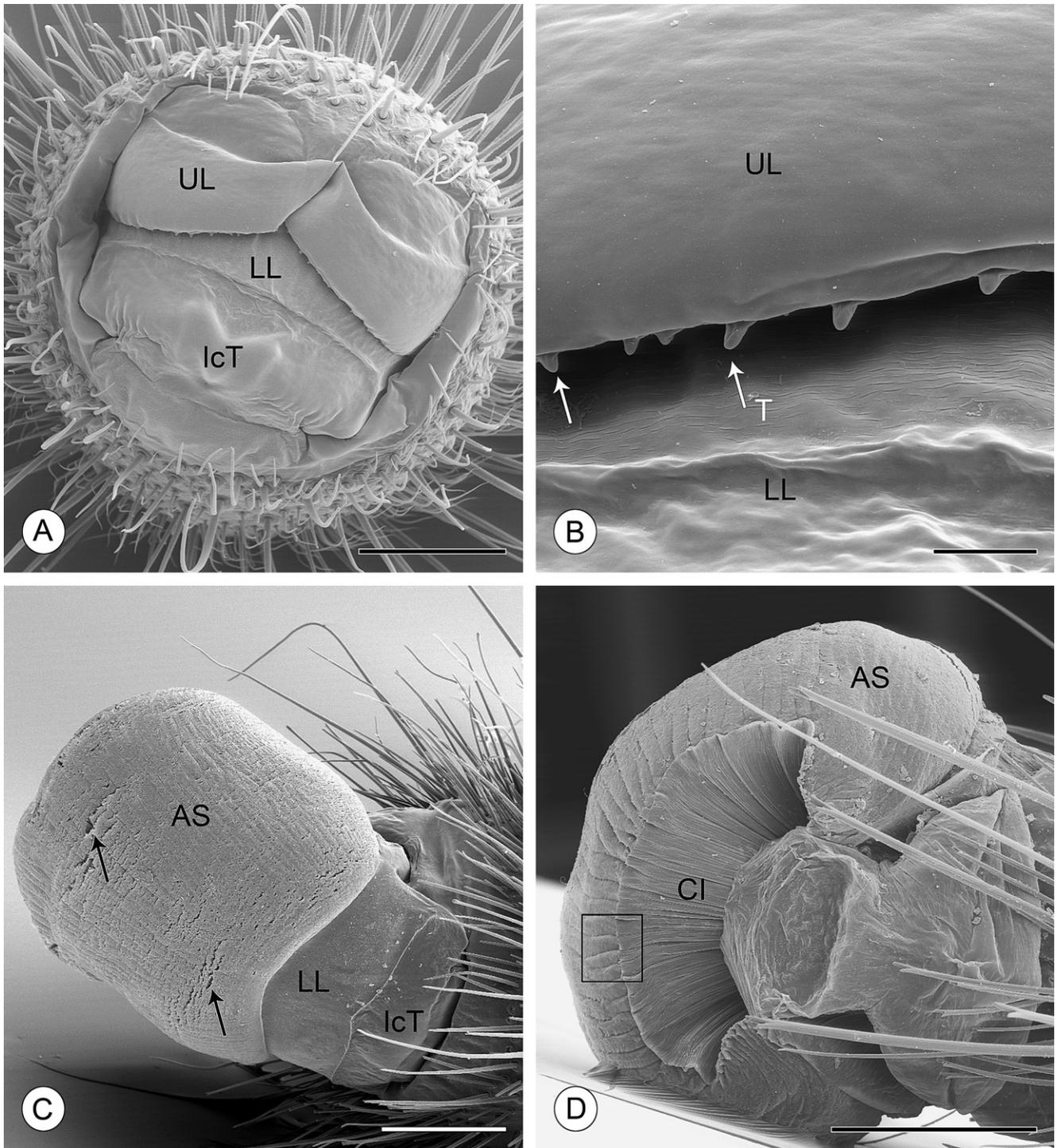
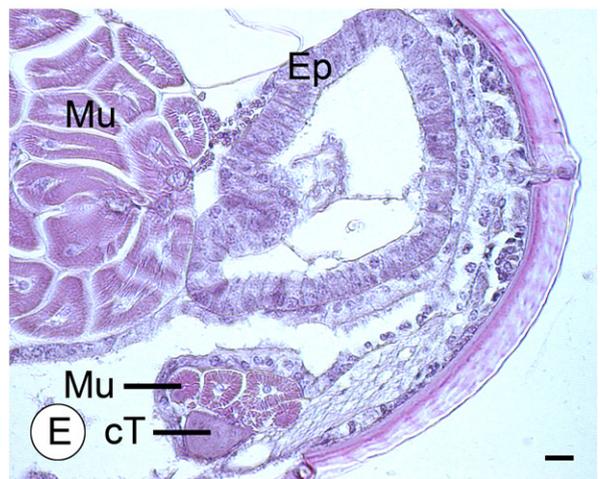
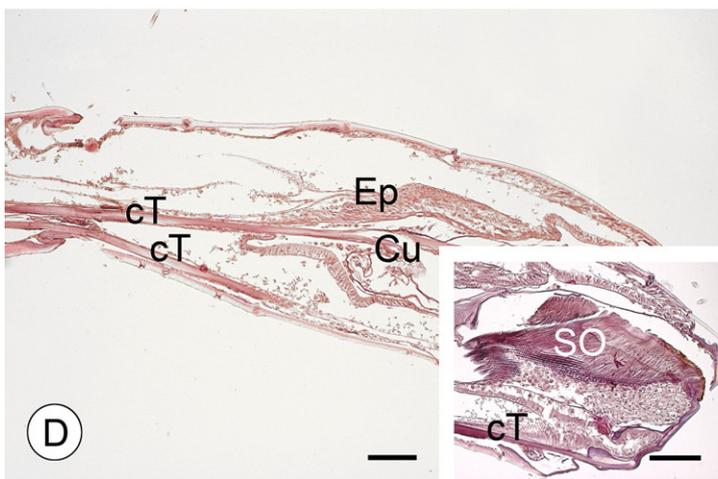
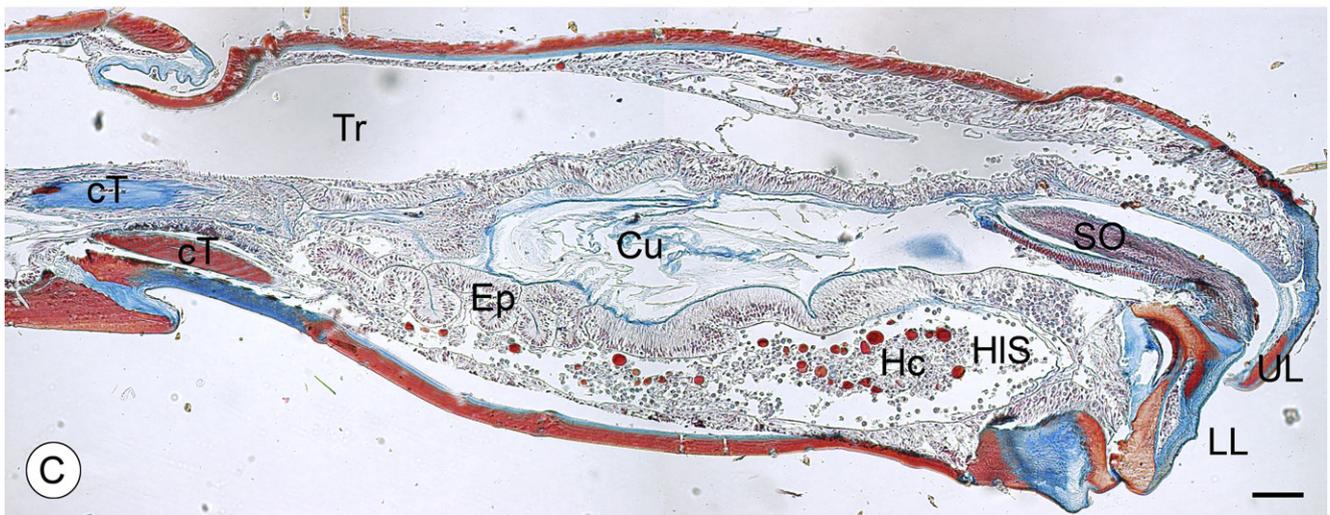
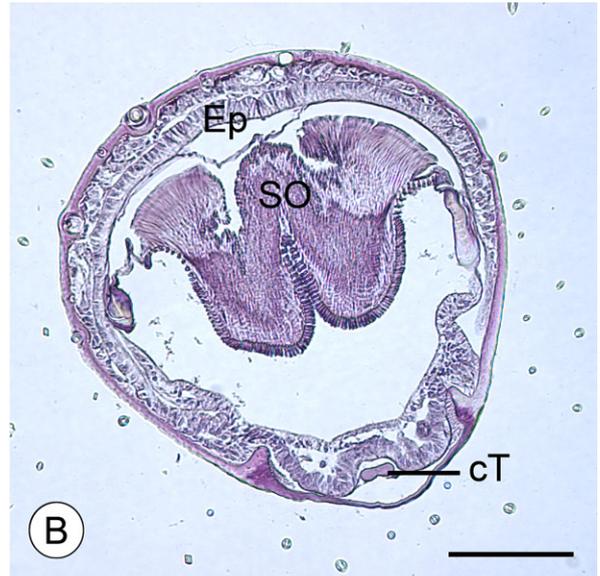
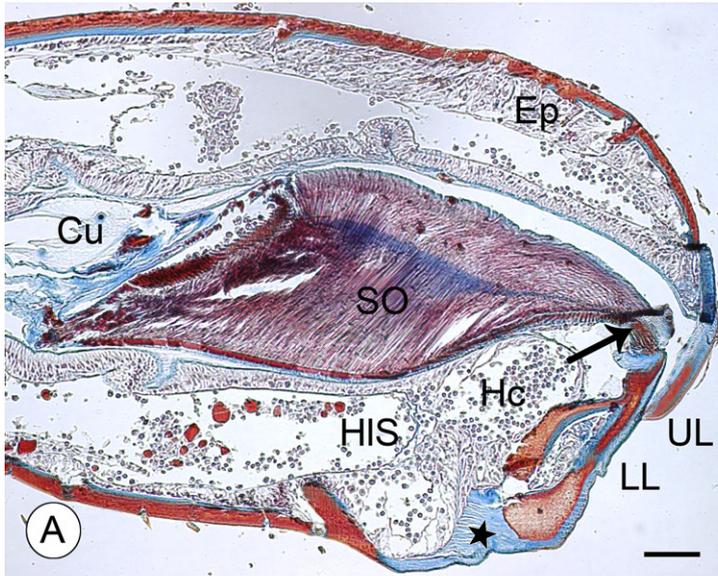


Fig. 1. Scanning electron microscopic images of the pedipalp and the suction organ of different species of solifuges. (A) Tip of the pedipalp of a juvenile *Galeodes caspius subfuscus*. The suction organ is inverted and covered with an upper and a lower cuticular lip. The insertion site of the cuticular tendon is clearly visible. Scale bar = 300 μm . (B) Margin of the cuticular upper lip provided with small conical teeth of different sizes pointing in slightly different directions (indicated by arrows). Scale bar = 30 μm . (C) Ventral side of an everted suction organ of a male *Eremobates pallipes* representing the adhesive surface (arrows indicate cracks – drying artefacts of the epicuticle). Scale bar = 300 μm . (D) Dorsal side of an everted suction organ of a juvenile *Oltacola gomezi*. The characteristic conical invagination of the dorsal side is clearly visible. Area indicated by a square shows the folded epicuticle of the dorsal side (shown in Fig. 4A in higher magnification). Scale bar = 300 μm . Abbreviations: AS = adhesive surface, CI = conical invagination, IcT = insertion of cuticular tendon, LL = lower lip, T = tooth, UL = upper lip.

other (Fig. 1C, D). The everted suction organ itself represents a fragile cuticular pad with a conspicuous ventral surface structure consisting of perpendicular orientated ridges and furrows (Figs. 1C, 4A). The ventral side represents the adhesive

surface (Figs. 1C, 4A), whereas a conspicuous infold can be observed on the dorsal side of the suction organ (Fig. 1D). In the very distal part of the suction organ the epicuticle of the dorsal side is highly folded (Figs. 1D, 4A, B).



3.2. Histology of the suctorial organ (LM)

The cuticle of the pedipalp and the lips exhibit different degrees of sclerotization. The dorsal margin of the upper lip is less sclerotized than the insertion region of the teeth (Fig. 2A, C) and the lower lip is weakly sclerotized only at its ventral margin (Fig. 2A). Both flexible regions with weak sclerotization function as articulations when opening the lips. Inside the pedipalp, the withdrawn suctorial organ appears w-shaped when folded in cross-section (Fig. 2B).

The suctorial organ is underlain by an epithelium consisting of relatively high, prismatic cells secreting the thin fragile cuticle (Fig. 2A, C). This epithelium and its overlying cuticle considerably extend into the proximal part of the pedipalp, where the cuticle forms a tendon (Fig. 2C, D), which is connected to a muscle strand. The muscle cells have centrally located nuclei (Fig. 2E). A second cuticular tendon, which also reaches into the metatarsus of the pedipalp, is directly attached to the lower lip (Figs. 2D insert, 3A, B). This tendon is also connected to a muscle strand in the proximal part of the pedipalp (Fig. 2E). A large hemolymph space is present underneath the epithelium in which numerous individual hemocytes can be observed (Fig. 2A, C). Several tracheae of different diameters extend into the entire pedipalp. The basal lattice, from which the shafts of the suctorial organ arise, can be considered to be a direct prolongation of the lower lip (Figs. 2A, C, D insert, 3A, B).

3.3. Fine structure of the pad (SEM, TEM)

In all representatives, the internal organization of the pedipalpal pad is almost identical. Extremely tiny, thread-like procuticular structures (approximately 0.5 μm in diameter) are located just under the fragile epicuticle of the suctorial organ (Figs. 4C insert, 5). These thread-like structures are the ramifying apices of thicker shafts (Figs. 4C, 5). The more or less equal width of these ramifying apices (e.g., approximately 30 μm in *O. gomezi*) and the arrangement in rows causes the ridges and furrows of the surface as described above. Apices of vicinal shafts are connected to each other via the thin, thread-like structures (Fig. 4C). In contrast to the outbranching apical part, the shafts appear more roundish and solid in cross-section (about 2 μm in diameter) and are of different lengths depending on their position inside the pad. In a protruded pad ventrally

located shafts are shorter than dorsally located ones. A less electron dense substance could be observed between the shafts (Fig. 4D). All these shafts are fixed on a basal lattice-like cuticle plate, which is highly flexible (Fig. 4E). Relatively thick longitudinal and fibrous transverse bars form a regular meshwork constituting this basal lattice (Figs. 4F, 5).

4. Discussion

Bernard (1896), Barrows (1925), Kaestner (1933), and Cushing et al. (2005) already revealed some aspects of the complex anatomy of the suctorial organ. Our study confirms these former results, but shows in more detail the fine structure of the entire organization of the suctorial organ. Although different types of smooth attachment pads have evolved in insects, the described ones exhibit a similar inner structure of fibrous (e.g., thin filamentous in the hymenopteran *Apis mellifera*) or foam-like type (e.g., in *Cercopis vulnerata* Auchenorrhyncha) (Beutel and Gorb, 2001; Schargott et al., 2006). Comparisons with other adhesive devices show that the internal structure of the solifugid pedipalpal adhesive pad with its characteristic filaments most resembles the inner structure of the arolia of *S. gregaria* (Caelifera), of euplantulae of *Tettigonia viridissima* (Ensifera) (Kendall, 1970; Beutel and Gorb, 2001), or of the ventral suckers of heterozeticonid mites (Acari) (Gerdeman and Alberti, in press). Slifer (1950) and Henning (1974) reported very thoroughly on the morphology of the arolia of *Melanoplus differentialis* and of the euplantulae of *T. viridissima* (Saltatoria). Both, the arolia and the euplantulae consist of endocuticular, elongated rods that branch as they approach the surface; an organization that is almost identical to the suctorial organ of solifuges. Hence this organization of smooth adhesive pads evolved convergently in different groups of arthropods. Barrows (1925) hypothesized that the suctorial organ of solifuges is serially homologous to the pretarsus and arolium of the legs, with the empodium enlarged and claws modified.

The large hemolymph space in the distal part of the pedipalp probably contributes greatly to the eversion process, thus confirming the hypothesis of Bernard (1896), Kaestner (1933), Roewer (1934) and Cushing et al. (2005). Rising hemolymph pressure presumably lowers the ventral lip and this would protrude the suctorial organ. Additionally the ventrally located tendon attached to the lower lip probably pulls the

Fig. 2. Light microscopic overview of the suctorial organ. (A) Longitudinal section of the tip of the tarsus of the pedipalp of *Galeodes caspius subfuscus*. The inverted suctorial organ covered with the upper lip. The asterisk indicates the flexible margin of the lower lip, which works as movable joint (blue stained cuticle with Azan technique shows less sclerotization). The basal plate, to which the shafts are attached, clearly extends from the lower lip (as indicated by black arrow). Numerous hemocytes float in the hemolymph space. Scale bar = 100 μm . (B) Transverse section through the tip of the tarsus of the pedipalp of *Ottacola chacoensis*. The suctorial organ is folded when withdrawn inside the pedipalp. Scale bar = 100 μm . (C) Oblique longitudinal section through the tarsus and partly through the metatarsus of the pedipalp of *Galeodes caspius subfuscus*. The high prismatic cells of the epithelium underlying the suctorial organ secrete a thin cuticle that forms the cuticular tendon (stained blue) in the proximal part of the tarsus. Scale bar = 100 μm . (D) Longitudinal section through the tarsus and partly through the metatarsus of the pedipalp of *Ottacola gomezi*. Clearly visible are the two cuticular tendons extending into the metatarsus of the pedipalp. Scale bar = 100 μm . Insert: The ventral cuticular tendon is connected to the lower lip pulling it back, when the suctorial organ is protruded. Scale bar = 100 μm . (E) Cross-section through the proximal part of the pedipalp showing median muscle strand close to the epithelium and a ventrally located muscle strand adjacent to the cuticular tendon. The muscle cells possess centrally located nuclei. Scale bar = 10 μm . Abbreviations: cT = cuticular tendon, Cu = cuticle, Ep = epithelium, Hc = hemocytes, HIS = hemolymph space, LL = lower lip, Mu = muscle strand, SO = suctorial organ, Tr = trachea, UL = upper lip.

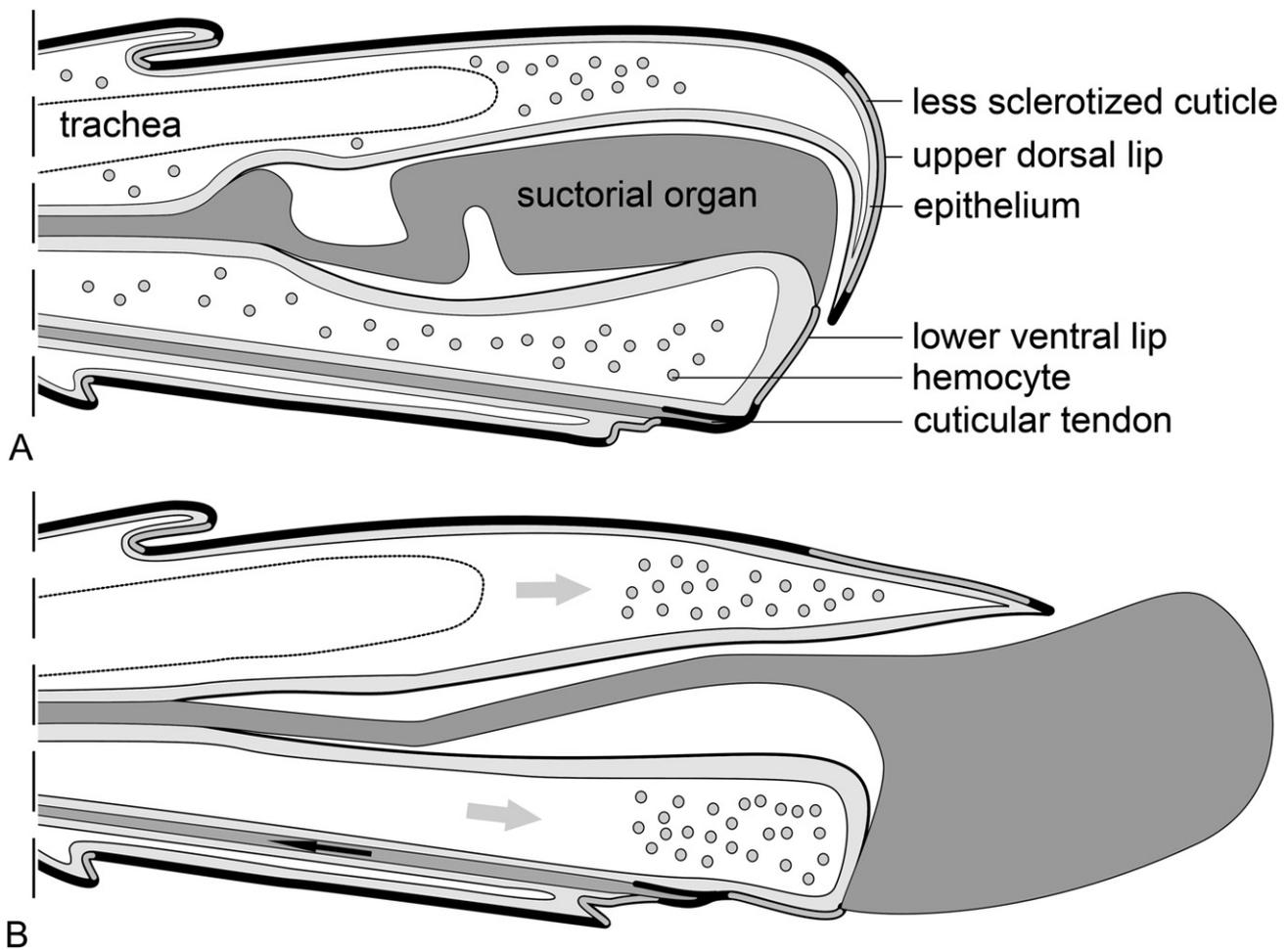


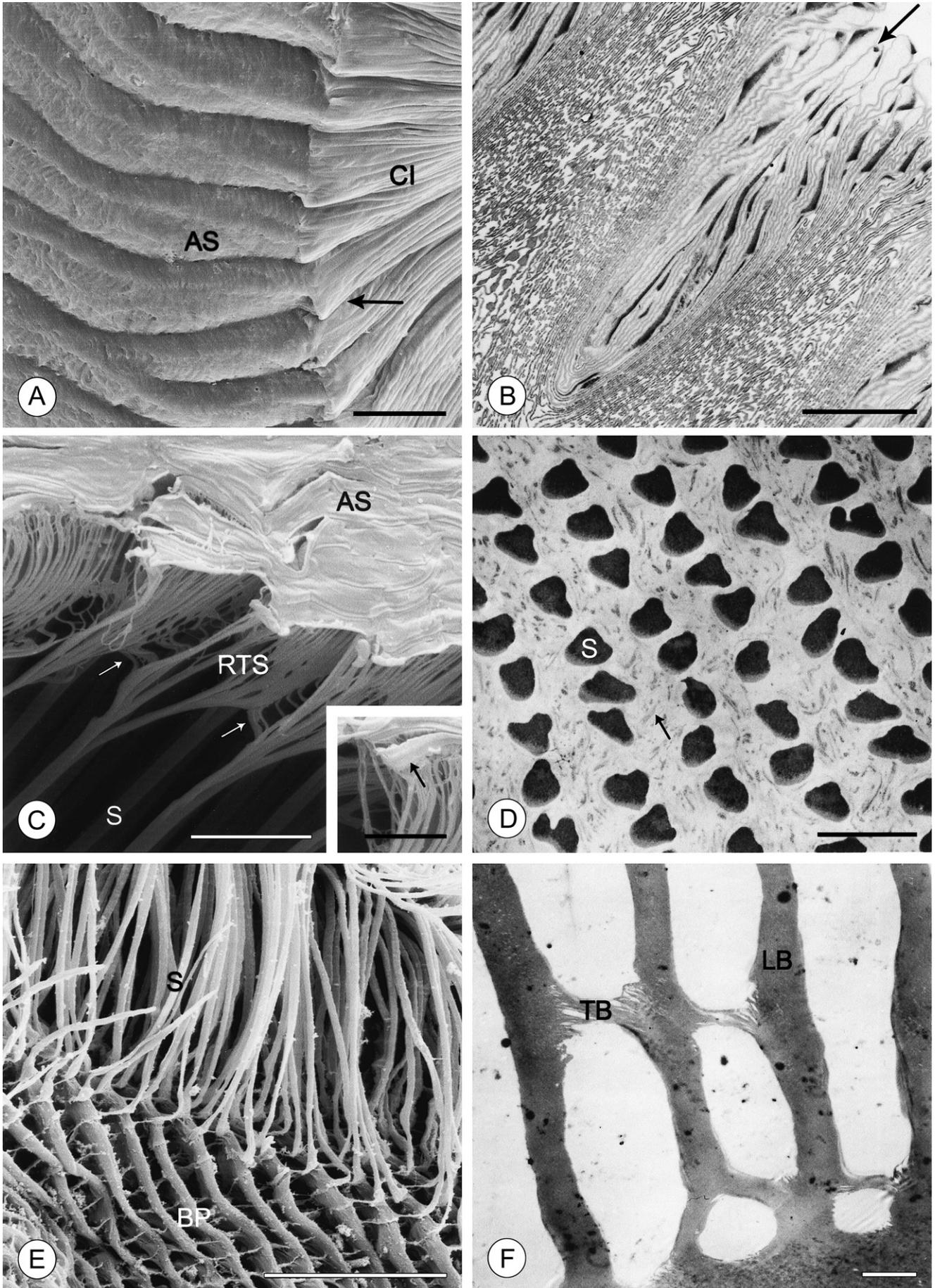
Fig. 3. Schematic drawings of the suctorial organ. (A) Tarsus of the pedipalp with inverted suctorial organ. (B) Tarsus of the pedipalp with everted suctorial organ. The ventrally located tendon slightly pulls back (indicated by black arrow) the lower lip thus facilitating the eversion process of the suctorial organ elicited by the rising hemolymph pressure (indicated by grey arrow) in the ventral region underneath the suctorial organ. The upper lip is probably opened by both rising hemolymph pressure (indicated by grey arrow) and by the protrusion of the suctorial organ.

lower, less sclerotized margin backwards, which supports the eversion process caused by the rising hemolymph pressure. The less sclerotized and thus flexible margins of both lips work as movable joints. In contrast to Cushing et al. (2005) no muscles attached to the upper lip could be observed. Thus, it seems more likely that the upper lip is passively opened as a consequence of the protruding suctorial organ. The observed large muscle strand connected to the cuticular

tendon of the suctorial organ probably withdraws the suctorial organ inside the pedipalp upon contraction.

All efficient adhesive pads are able to highly adapt to any kind of surface topography they are apposed to. Gorb et al. (2000) demonstrated that the deformation of the euplantulae of *T. viridissima* replicated the surface to micrometer roughness and that the pad material itself showed both elastic and viscous behavior under loads. Gorb and Scherge (2000) suggested that

Fig. 4. Scanning and transmission electron microscopic images of the surface and the internal organization of the suctorial organ. (A) SEM micrograph of the surface structure of the suctorial organ of *Ottacola gomezi*. Clearly visible are the furrows and ridges of the ventral, adhesive surface (compare Fig. 1D). Arrow indicates infolded epicuticle. Scale bar = 30 μm . (B) TEM micrograph of a transverse section through the apical, dorsal part of the suctorial organ of *Eusimonia mirabilis* (infold also indicated by arrow in Fig. 4A). The furrows (indicated by arrow) are infoldings of the dorsal epicuticular surface. Scale bar = 3 μm . (C) SEM micrograph of a detail of the internal organization of the suctorial organ of *Galeodes caspius subfuscus*. Internal procuticular shafts ramify towards the adhesive surface. The vicinal apices are connected to each other (indicated by white arrows). Scale bar = 10 μm . Insert: The tips of the delicate thread-like apices are covered with a very thin epicuticle (indicated by black arrow). Scale bar = 5 μm . (D) TEM micrograph of a transverse section through the internal shafts of the suctorial organ of *Galeodes caspius subfuscus*. All shafts consist of solid procuticular material and are very regularly arranged. A less electron dense substance can be observed between the shafts (indicated by black arrow). Scale bar = 3 μm . (E) *Galeodes caspius subfuscus*. SEM micrograph – the shafts are fixed on a basal plate. This plate has a lattice-like structure and is very flexible. Scale bar = 30 μm . (F) TEM micrograph – relatively thick longitudinal bars are connected to each other via thin, fibrous transverse bars forming the basal plate. Scale bar = 3 μm . Abbreviations: AS = adhesive surface, BP = basal plate, CI = conical invagination, LB = longitudinal bar, RTS = ramifying tips of the shafts, S = shaft, TB = transverse bar.



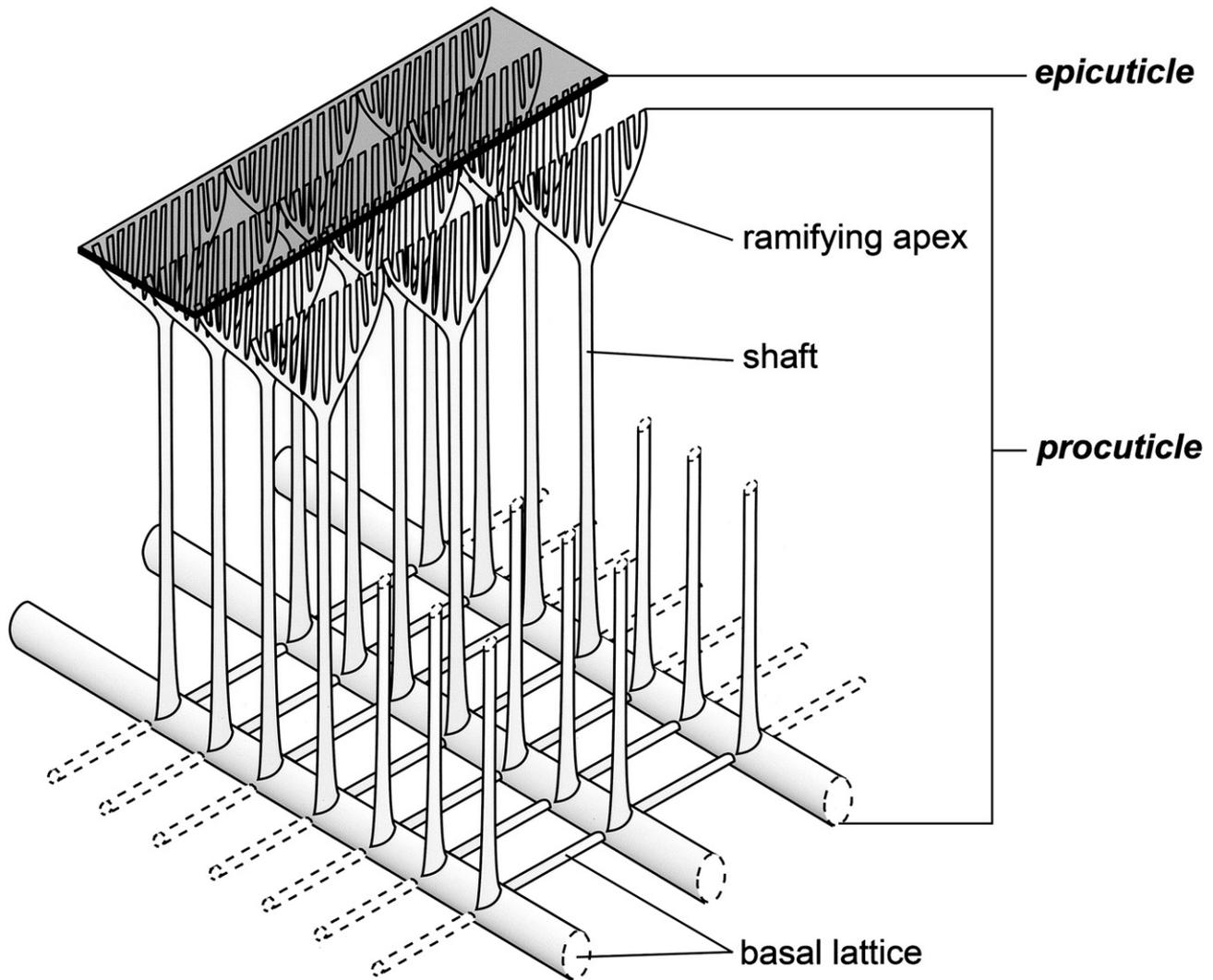


Fig. 5. Schematic drawing of the internal organization of the adhesive pad. Stabilizing procuticular shafts, which are connected to a lattice-like basal plate, ramify in the apical region covered with a fragile, delicate epicuticle.

the specific construction of the adhesive pad of *T. viridissima* assures an optimal contact to the substrate. We therefore assume that the suctorial organ might exhibit similar mechanical properties like that one of *T. viridissima*. The internal procuticular shafts of the suctorial organ of Solifugae, which ramify apically, contribute to a certain degree to the stability of the adhesive pad whereas the delicate epicuticle provides a good adaptation to micro-scale surfaces. Possible mechanisms of adhesion are capillarity, viscosity and van-der-Waals-forces (Betz and Kölsch, 2004). Capillarity and viscosity are dependant upon a liquid. Huber et al. (2005) discovered that the adhesion force of the spatulate setae of the gecko increases significantly with higher humidity and for hydrophilic substrates thus suggesting an involvement of capillarity in adhesion processes. The adhesive mechanism involving pad secretion in insects is known in Heteroptera (e.g., Ghazi-Bayat and Hasenfuss, 1980), Diptera (e.g., Hasenfuss, 1977, 1978), Ensifera (e.g., Jiao et al., 2000) and Coleoptera (e.g., Betz, 2003). One of the first studies on the chemical composition of the pad secretion of the beetle *Epilachna*

vigintioctomaculta showed the lipid nature of the secretion (Ishii, 1987). Later studies revealed that the compositions, depending on the investigated animal, involves different kinds of components, such as, e.g., hydrocarbons, fatty acids, carbohydrates and alcohols (Kosaki and Yamaoka, 1996; Attygalle et al., 2000; Vötsch et al., 2002). Very recently it was discovered that even *Aphonopelma seemanni* (Theraphosidae, Araneae) produce a silk-like secretion as a third attachment system apart from their small distal claws and the spatulate setae (Gorb et al., 2006). Although it is considered that adhesive secretion is an important factor in any kind of attachment systems (Beutel and Gorb, 2001), we hypothesize that the latter two forces described above seem to be subordinate in Solifugae, since no glands could be observed in the pedipalps of solifuges thus far. Therefore, the forces involved in adhesion of the euplantulae of *T. viridissima* cannot be fully compared to the forces involved in suctorial organ adhesion of solifuges, although the two adhesive pads are morphologically very similar. However, capillarity and viscosity cannot entirely be excluded either,

since liquid could also originate from the prey itself or from other external environmental sources. Hence, the origin of the less electron dense substance observed between the shafts and the physical mechanism of adhesion remain to be investigated. Adhesion caused by van-der-Waals-forces is described for hairy attachment systems, like the spatulate setae of the Tokay gecko (Autumn et al., 2002) and the scopulae of certain spiders (Kesel et al., 2003). Cushing et al. (2005) hypothesized that the adhesion of the suction organ of solifuges might be mainly attributed to van-der-Waals-forces. The exact adhesion force or mechanism of the suction organ is not fully understood yet. Nevertheless, the suction organ represents a very efficiently working adhesive device, which is predominantly used to capture prey (Cloudsley-Thompson, 1954, own observations).

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