The suctorial organ of the Solifugae (Arachnida, Solifugae)

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Abstract

The ability of members of the arachnid order Solifugae to climb smooth, vertical surfaces and the organs involved in this behavior are investigated. Macroscopic, microscopic, and scanning electron microscopic observations are made of a palpal organ called the suctorial organ. Observations of the behavior but not the microstructure have been made in the past. Histological examination illustrates the internal gross anatomy of this structure and scanning electron microscopy demonstrates the fine structure in adults of four genera: \textit{Eremobates} (Eremobatidae), \textit{Eremochelis} (Eremobatidae), \textit{Eremorhax} (Eremobatidae), \textit{Ammotrechula} (Ammotrichidae), as well as an unidentified late stage immature and third stage instar. The suctorial organ is most likely primarily used for prey capture in the wild.

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1. Introduction

The mostly nocturnal, cursorial Solifugae are among the least studied order of chelicerates. Brownell and Farley (1974) investigated the malleoli but few have researched another interesting organ found at the tip of the palpus. Savory (1964) and Cloudsley-Thompson (1954) called it the suctorial organ while Muma (1951, 1966a,b) and Punzo (1998) denoted it as the palpal organ. We are calling it the suctorial organ since there are other sensory organs found on the palpus. The suctorial organ is barely visible to the naked eye (Fig. 1(A) and (B)).

Lichtenstein (1797) originally described it as olfactory. Dufour (1861) disagreed and suggested that it might serve as a suction device. Various researchers, using different techniques (Bernard, 1893; Heymons, 1902; Barrows, 1925; Hingston, 1925), attributed the previous functions as well as various grasping functions to this organ. Cloudsley-Thompson (1954) and Junqua (1962) suggested that it might be adhesive.

Barrows (1925) dissected the palpi of \textit{Eremobates f"{o}rmicarius} (Koch) (Eremobatidae), \textit{Eremobates constrictus} (Putnam, \textit{nomen dubium}) (Eremobatidae); \textit{Ammotrechella stimpsoni} (Putnam) (Ammotrichidae) and concluded that the structure was the same in each species. He included a detailed description of the covering and tendons as well as macroscopic descriptions of the ‘bubble’. K"{a}stner (1932) illustrated a longitudinal section of the \textit{Haftblase} or ‘sticking or clinging bubble’ of \textit{Galeodes caspius} Birula (Galeodidae). Roewer (1934) included K"{a}stner’s drawing in his discussion of solifugid anatomy. Among all the solifugid systematists only Muma’s regularly figured the everted suctorial organ. Those illustrated in Muma, 1951 publication were \textit{Eremobates similis} Muma (Eremobatidae) (p. 52, Fig. 66); \textit{Therobates morrisi} Muma (Therobatidae) (p. 91, Fig. 163); \textit{Hemerotrecha branchi} Muma (Therobatidae), (p. 113, Fig. 237); all without comment. Those of \textit{Hemerotrecha} are shown with a different structural form. In the Ammotrichidae, Muma illustrates differently shaped suctorial organs for \textit{Ammotrechella sexpicatai} Muma (Ammotrichidae) (p. 128, Fig. 286); \textit{Ammotrecha cobinensis} Muma (Ammotrichidae) (p. 136, Fig. 304); and \textit{Branchia angustus} Muma (Ammotrichidae) (p. 136, Fig. 307). While Roewer (1934) pictured K"{a}stner’s cross sectional drawing he does not illustrate many pedipalps and no suctorial organs. Panouse (1957) illustrates the suctorial organ of \textit{Eusimonia mirabilis} (Karschiidae).
Most observers (Muma, 1966a,b, 1967; Punzo, 1995, 1998) conclude that the palpi, which contain this organ, are used in climbing, mating, grasping food, obtaining moisture, digging burrows, and agonistic behavior. Some of these observations suggest that the suctorial organs may have adhesive qualities. All agree, however, that they impart to the solifugid the ability to climb vertical glass surfaces. The first to record this was Hutton (1843) who lost his entire supply of *Galeodes arabs* C. L. Koch (Galeodidae) when he left them uncovered in a deep-sided glass container. To those who use pitfall traps it is clear that solifugids can and do climb out of pitfalls. Muma (personal communication) lamented the use of dry pitfalls at Mercury Nevada (Muma, 1963) and at the Hanford Site in Idaho (Allred and Muma, 1971). Brookhart and Cushing (2002) did not find any *Hemerotrecha cornuta* (Therobatinae) in pitfall sampling in Colorado with dry traps but found several of this species when using wet pitfalls. Solifugids have been seen climbing trees and walls (Fichter, 1940; Cloudsley-Thompson, 1958; Muma, 1967; Sasha Gromov, personal communication; and Muma and Brookhart, personal observations) but, again, the use of the suctorial organ while climbing these types of surfaces has not been clear. The present study attempts to examine the microstructure and the function of the suctorial organ and to determine if these structures are different in diverse families and genera of Solifugae.

2. Materials and methods

2.1. Behavior

A male *Eremobates pallipes* (Say) (Eremobatidae) collected under ‘buffalo chips’ from Daniels Park, Douglas County, Colorado (39°28′N, 104°92′W) was placed on a brick wall near a porch light and his climbing habits were observed. Additional males collected from the same site were placed in various glass and plastic terraria and a glass Petri dish for observations and photographed using a Nikon FM 2 camera with a 55 mm macro lens and a 4× magnifier (Fig. 1). We also observed and photographed everted suctorial organs from living specimens whose palpi were held in place with forceps using a Nikon FM 2 body mounted to the phototube of an Olympus SZH stereo microscope. A female *Eremobates durangonus* Roewer (Eremobatidae) was placed on a vertically oriented wooden board and the climbing behavior photographed using a Sony digital video (DV) camera, Model VX-1000, shooting NTSC at 30 frames (60 fields) per second. Individual frames were isolated and output to CD using Adobe Premiere Pro, v 1.5 video edit software. The filming was then repeated with the female climbing the vertical clear plastic surface of a terrarium.

2.2. Internal anatomy and histology

The palpus of an adult *Eremobates palpisetulosus* Fichter (Eremobatidae) with the suctorial organ nearly fully everted was dissected in order to examine the tendons and muscles involved in eversion and inversion of the organ. A drawing was made of this dissected palpus and was compared to scanning electron micrographs (SEMs) of the everted organ.

Palpi of *Hemerotrecha fruitana* Muma (Eremobatidae) preserved in 3% gluteraldehyde were prepared for serial sectioning by dehydrating the tissue through graded ethanol (50–100%) and then into xylene and then heated paraffin under negative pressure. The paraffin tissue was cooled on ice immediately before cutting. Tissue sections were cut at 5 μm. The tissue sections were stained with hematoxylin and eosin and coverslipped for microscopic examination. Digital photographs were taken using a Nikon E400 microscope and a Nikon Coolpix 995, 3.34 megapixel digital camera.

![Fig. 1. *Eremobates pallipes* male climbing up the side of a glass aquarium. (A) Ventral view of male with suctorial organ of right palp attached to glass surface (arrow). (B) Close-up of same structure (arrow).](image-url)
2.3. Scanning electron microscopy (SEM)

Solifugids captured in ethylene glycol pitfall traps and preserved in 75% ethyl alcohol were examined for everted and partly everted suctorial organs. The palps of *Eremochelis bilobatus* (Muma) (subfamily Therobatinae, family Eremobatidae), *Eremorhax puebloensis* Brookhart (subfamily Eremobatinae, family Eremobatidae), and *Ammotrechula peninsulana* (Banks) (subfamily Ammotrechinae, family Ammotrechidae) were sonicated in 70% ethanol, air dried, and mounted on stubs using carbonized glue. The samples were sputter coated with gold to avoid charging under the electron beam. SEM observations were performed using a FEI Quanta microscope operating at 30 kV.

A series of *E. palpisetulosus* specimens were examined and several were chosen showing varying degrees of suctorial organ eversion. SEM observations were made of a palpus from a specimen showing no eversion, of the palpus of another specimen just opening to expose the organ, of a specimen showing a partly everted suctorial organ, and of a palpus with the organ fully everted.

3. Results

3.1. Behavior

The suggestion that the palpi, including the suctorial organ, are used in climbing on rough surfaces such as branches, wood, or rough walls, was not supported by our observations. The palpi were held in front of the solifugid and did not contact the surface while the animal was...
Fig. 3. An adult female *Eremobates durangonus* climbing up the smooth wall of a terrarium. (A)–(H) Still frames of the climbing sequence. The suctorial organs of the palps are almost exclusively used for climbing smooth surfaces. Note the appearance of the suctorial organ and the relative constancy of leg positions I, II, III, and IV between sequences.
climbing (Fig. 2(A)–(F)). The first pair of legs also does not seem to be involved in climbing. This can be seen in Fig. 2 as the position of the first pair of legs does not change from one frame of the sequence to the next (Fig. 2(A)–(F)). Only leg pairs II, III and IV are involved in climbing on rough surfaces. Only when coming in contact with glass or glasslike material such as the smooth plastic wall of a terrarium does the suctorial organ evert and attach itself to the surface. A small edge of white is visible to the naked eye when the suctorial organ everts upon contact with smooth transparent surfaces (Fig. 3(A)–(H)). The solifugid begins climbing using alternating palps. Note the relative constancy of the positions of leg pairs I, II, III, and IV between sequences in Fig. 3. While climbing a smooth surface, the legs are involved only in providing a counterbalance to the animal as the suctorial organs and palps pull the animal upwards. The legs and tarsal claws do not appear to be involved at all in pulling the animal upwards.

When placed in a horizontally oriented glass Petri dish and observed under a dissecting microscope, the suctorial organ is not seen, but when the dish is oriented in a perpendicular position and gently agitated, the suctorial organ is everted and the solifugid begins to climb. After this strenuous activity, the suctorial organ can be seen to evert slightly and pulsate irregularly. This may be caused by pulsating hemolymph. When lightly pinched with forceps, the suctorial organ is seen to evert. No macroscopic or microscopic evidence of an adhesive material was observed. Thus, there is no evidence that the suctorial organ is glandular in nature. Examination of 45 solifugid third instars reveal several with everted suctorial organs. Thus, the organs are present during every stage of development.

3.2. Internal anatomy and histology

The suctorial organ is inverted inside the palpus when not in use (Fig. 4(A)). It is tightly folded (Fig. 4(A)–(C)) and appears to be anchored on each side by a tendon (arrows in Fig. 4(A) and T in Fig. 4(D)) attached to muscles encircling the suctorial organ internally (M in Fig. 4(D)). A dissection through the E. palpisetulosus palp with a partially everted suctorial organ reveals the tendons attached to the organ laterally and, themselves, attached to two muscle bands encircling the organ. Two longitudinal muscle bands project from the base of the organ down through the palp (T in Fig. 4(D) point to the tendons and LO indicates the longitudinal muscle bands). A central muscle band is attached to the inner cuticle of the ‘lip’ that covers the suctorial organ when it is inverted inside the palp (MM in Fig. 4(D)). In the everted state shown in the drawing (Fig. 4(D)), this medial band is shown attached to the inner cuticle of the palp because the muscle has already drawn the lip downward, exposing the suctorial organ. Two cuticular plates we refer to as lips cover the suctorial organ when not in use (Fig. 5).

3.3. SEM

Unlike the scopula of some spiders (Foelix, 1996), the feet of a Gecko (Autumn et al., 2000, 2002) or the arolium of some insects (Haas and Gorb, 2004), there are no stalked cups on the surface of the suctorial organ providing a surface area for adhesive forces, but rather the surface consists of a series of ridges with shelves oriented perpendicular to the ridges (Figs. 6(B), (D) and (F) and 7(D)). As with other adhesive structures found in arthropods, the suctorial organ provides a large surface area for adhesion. No pores are present on the surface of the suctorial organ suggesting that no adhesive material is secreted by the organ.

Fig. 6 compares the structure of the suctorial organ from two species in the family Eremobatidae: Eremochelis bilobates and Eremorhax pueblosensis and one species from the family Ammotrechidae, Ammotrechula penisularana. The surface structure of Eremobates palpisetulosus (subfamily Eremobatinae, family Eremobatidae) is shown in Fig. 7(D). In all these species, the surface structure is similar (Figs 6(B), (D) and (E) and 7(D)).

Fig. 7 shows the gradual opening of the cuticular lips of the palpal tip exposing the suctorial organ. As the dorsal lip is pulled down, the suctorial organ is exposed (Fig. 7(B)). In the everted suctorial organ, the accordion-like folded ridges of the organ are clearly seen (Fig. 7(C) and (D)). Lateral tendons attached to muscle bands encircling the suctorial organ (Fig. 4(D)) may be involved in unfolding the organ. An increase in hemolymph pressure may complete the eversion process. This is supported by the pulsation of the suctorial organ observed with live solifugids after climbing up a smooth surface (see above in Section 3.1).

4. Discussion

4.1. Behavior

Since solifugids are typically nocturnal, cursorial inhabitants of deserts and other xeric habitats, often running across the desert floor, it is difficult to discern the adaptive function of the suctorial organ. Bolwig (1952), Muma (1966a,b, 1967) and Punzo (1997, 1998) and personal observation of ‘searching behavior’ involves the palpi which are either held out in front of the solifugid or seen tapping the ground. This appears to be consistent with usual invertebrate strategies of ‘zig zagging’ until an object is contacted at which point the animal then backs up and reorients itself until it can pass the object. Climbing is generally not required in the habitats in which solifugids are found. Muma (1966b) states ‘Barriers that require the palpi in climbing do not seem to exist in nature.’ Our observations suggest that the palpi are rarely, if ever, used for climbing in the habitats in which these animals are found and support
the hypothesis that the palpi function partly as tactile organs.

Betz and Kölsch (2004) speak to the role of adhesion in prey capture but do not include references to solifugids. Young solifugids frequently use termites as a food source as well as other tiny invertebrates (Muma, 1966b). An eversible structure at the tip of the palp that can hold onto smooth surfaces would enable the young solifugid to probe termite tunnels and adhere to the relatively smooth exoskeleton of the prey. Such a structure would also

Fig. 4. The anatomy of the suctorial organ. (A) A cross-section through an inverted suctorial organ. Arrows point to tendons attaching the suctorial organ to the cuticle. SO indicates the accordion-like folds of the inverted suctorial organ. (B) A partially everted suctorial organ of an immature Eremobates sp. Scale bar 400 μm. Note the folds of the suctorial organ, SO. (C) The partly everted suctorial organ of a third instar unidentified solifugid. Scale bar 200 μm. (D) Drawing of a dissected palp with a partly everted suctorial organ. T indicates tendons; M indicates muscle bands encircling the suctorial organ; MM indicates median muscle band; LO are longitudinal muscle bands attached to the underside of the organ (see text for explanation).
facilitate prey capture in adult solifugids. Sergio Henriques (personal communication) has observed *Gluvia dorsalis* (Latreille) (Daesiidae) grasping small insects with the tip of the palpi. How this structure and behavior have evolved into use as a climbing mechanism remains to be investigated. However, analogous structures on the tarsi of spider legs that are involved in both climbing smooth surfaces and in prey capture have been investigated. These structures, called claw tufts and scopula are tufts of hair; each hair split into thousands of cuticular extensions (Foelix, 1996). Kesel et al. (2003) demonstrated that van der Waal’s forces alone can explain the adhesive properties of the spider’s claw tufts and can provide the adhesive forces necessary to support a spider’s body as it climbs up a smooth vertical surface. Rovner (1980) demonstrated that the scopula, in addition to allowing the spider to crawl up smooth surfaces, also facilitate prey capture. We hypothesize that the suctorial organ functions in a manner similar to the scopula and claw tufts of spiders in both facilitating prey capture and in allowing the animal to climb up a smooth surface. Kesel et al. (2003) points out that ‘a soft material is required to conform to the substrate surface texture’ in order for a strong enough bond to form between the adhesive structure and the contact surface via van der Waal’s forces. Although the role of van der Waal’s forces was not investigated in the present study, we suggest that these forces and the pliable nature of the suctorial organ may be sufficient to explain the ability of solifugids to use the suctorial organs and palps exclusively in climbing up a smooth surface. The internal musculature, particularly the longitudinal muscle bands attached to the inner distal surface of the suctorial organ (Fig. 4(D)), upon contraction, may provide sufficient counter force to break the bonds formed between the organ and the smooth surface.

4.2. Internal anatomy and histology

The histological section of the suctorial organ indicate that these organs are inverted and folded into the tip of the palp when not in use and are anchored to the cuticle by two lateral tendons. The opening through which the organ emerges is closed by two cuticular plates we refer to as lips. Upon contraction of a median muscle band attached to the inner surface of the dorsal lip, the lip opens revealing the folded suctorial organ. Contraction of muscle bands surrounding the suctorial organ may act to effectively unfold the organ. We hypothesize that hemolymph pressure completes the eversion process. Inversion may be accomplished by contraction of the two longitudinal muscle bands attached to the distal inner surface of the suctorial organ.

4.3. SEM

While Muma’s (1951) drawings indicate a structural difference among several species, our SEM material demonstrates a consistent pattern among the various families and genera of Solifugae. The difference in surface structure among these genera and between these families may reflect phylogenetic differences or may simply reflect differences in the degree of eversion of the organ or differences due to surface anomalies or degradations of the organ caused by poor initial preservation of the specimen. Our observations indicate that the suctorial organ most likely evolved as an organ involved in prey capture and is not typically used for climbing in the habitats in which solifugids are most commonly found.

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Fig. 6. Everted suctorial organs of three species from two different families of Solifugae and close-ups of the surface structures. (A) *Eremochelis bilobates* (Eremobatidae). (B) Close-up of the surface structure of *E. bilobates*. (C) *Eremorhax puebloensis* (Eremobatidae). (D) Close-up of the surface structure of *E. puebloensis*. (E) *Ammotrechula peninsulana* (Ammotrechidae). (F) Close-up of *A. peninsulana*. Scale bars for A, D, and E = 100 μm; scale bars for B, E, and F = 10 μm.
References


