

## RESEARCH ARTICLE

# Tarantulas cling to smooth vertical surfaces by secreting silk from their feet

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### SUMMARY

Like all spiders, tarantulas (family Theraphosidae) synthesize silk in specialized glands and extrude it from spinnerets on their abdomen. In one species of large tarantula, *Aphonopelma seemanni*, it has been suggested that silk can also be secreted from the tarsi but this claim was later refuted. We provide evidence of silk secretion directly from spigots (nozzles) on the tarsi of three distantly related tarantula species: the Chilean rose, *Grammostola rosea*; the Indian ornamental, *Poecilotheria regalis*; and the Mexican flame knee, *Brachypelma auratum*, suggesting tarsal silk secretion is widespread among tarantulas. We demonstrate that multiple strands of silk are produced as a footprint when the spider begins to slip down a smooth vertical surface. The nozzle-like setae on the tarsi responsible for silk deposition have shanks reinforced by cuticular thickenings, which serve to prevent the shanks' internal collapse while still maintaining their flexibility. This is important as the spigots occur on the ventral surface of the tarsus, projecting beyond the finely divided setae of the dry attachment pads. We also reveal the structure and disposition of the silk-secreting spigots on the abdominal spinnerets of the three tarantula species and find they are very similar to those from the earliest known proto-spider spinneret from the Devonian period, giving another indication that silk secretion in tarantulas is close to the ancestral condition.

Key words: spider, spinneret, adhesion, spigot, tarsus, tarantula.

### INTRODUCTION

Usually, when spiders adhere to smooth vertical surfaces they use pads of finely divided hairs (setae) on the underside of their tarsi (Kesel et al., 2003; Niedregger and Gorb, 2006; Artz et al., 2003; Roscoe and Walker, 1991; Gasparetto et al., 2009); this type of dry adhesion relies on the intra-molecular forces set up between the tips of the hairs and the substrate (Kesel et al., 2003; Niedregger and Gorb, 2006; Artz et al., 2003; Kesel et al., 2004; Roscoe and Walker, 1991; Gasparetto et al., 2009). These pads are known as scopula pads and occur on the tarsi and meta-tarsi of all legs including the pedipalps in female spiders. While the safety factor (maximum adhesive force against body mass) can be as high as 160 for a small, jumping spider (*Evarcha arcuata*) (Niedregger and Gorb, 2006), the safety factor for the much larger, Costa Rican zebra tarantula, *Aphonopelma seemanni*, is much lower, making a fatal fall more likely (Niedregger and Gorb, 2006). Controversy surrounds the report of a novel mechanism demonstrated by the Costa Rican zebra tarantula to increase the odds of it staying attached to a smooth wall. Gorb and colleagues found silk deposits when they passively elevated a tarantula sitting on a flat surface covered with glass microscope slides towards the vertical and concluded that these fibres had been secreted from the tarsi of the tarantula (Gorb et al., 2006). However, Pérez-Miles and colleagues, studying the same species of tarantula, this time free to roam in a glass slide-covered arena, concluded that the silk fibres left behind were drawn from the spinnerets by the legs before being deposited on the substrate (Pérez-Miles et al., 2009). Two lines of evidence supported their view. First, they found urticating hairs, which are commonly rubbed off from the abdomen by the legs as would occur if the legs had been used to pull the silk from the spinnerets. Second, when Pérez-

Miles and colleagues covered the tarantula's spinnerets with a layer of paraffin wax no silk was found on the glass slides (Pérez-Miles et al., 2009).

The tarsus certainly seems an unusual location for silk secretion in a spider, because silk is usually secreted from spinnerets at the end of the abdomen (Coddington and Levi, 1991; Volrath and Knight, 2001; Shultz, 1987; Shear et al., 1989). In fact, a defining feature of all spiders is the production of silk, synthesized by specialist glands inside the opisthsoma (abdomen) and then extruded from the spinnerets on the abdomen. However, tarsal silk secretion would provide strong support for the hypothesis that spider spinnerets are derived from modified limbs (Shultz, 1987; Shear et al., 1989; Damen et al., 2002; Selden et al., 2008), and direct silk secretion from a setae on a limb without any complex storage organ may represent the ancestral condition, with silk production from abdominal spinnerets being the product of much later evolution. The ability of spiders to secrete silk from their feet would show that silk production is controlled by developmental modules able to be expressed in a variety of body parts (Selden et al., 2008).

### MATERIALS AND METHODS

Experiments were performed on captive-bred tarantulas obtained from local pet shops (Newcastle upon Tyne, UK). To test for physical evidence of tarsal silk secretion, an adult Chilean rose tarantula, *Grammostola rosea* (Walckenaer 1837), was placed in a glass tank that had first been cleaned with detergent and air dried and its internal base layered with 7 pairs of Menzel-Glaser® pre-cleaned 76×26 mm microscope slides. Cleaning was important to prevent dust contamination of the slides. The spider was carefully positioned on the slides at one end of the tank and the positions of

all appendages, including the spinnerets, were recorded. The spider was left to settle and all movements were recorded using a Canon XM2 DV camera with a  $\times 10$  Opteka HD2 macro lens. Slides coming into contact with the spinnerets were excluded from the results. The tank was then tipped so the spider was facing vertically upwards. The camera was repositioned to view the base of the tank and record movement of the legs and pedipalps. In order to induce the legs to slip on the slides, the tank was gently shaken. A tarsal slip was defined as a smooth movement of the tarsus down the microscope slide under the influence of gravity. The tank was then returned to its original orientation and the spider was removed, taking care not to allow the abdominal spinnerets to come into contact with any slides. The glass slides were then removed and inspected under a binocular microscope and photographed. These experiments were repeated successfully eight times with two different female Chilean rose tarantulas. Trials in which the spiders moved and their spinnerets came into contact with more than two slides were not included in the study.

To study their anatomy, both freshly shed cuticle and exoskeletons of recently deceased Chilean rose *G. rosea*, Indian ornamental *Poecilotheria regalis* (Pocock 1899) and Mexican flame knee *Brachypelma auratum*, Schmidt 1992, tarantulas were obtained from captive-bred stock supplied by local pet shops. Some species of tarantula such as the Mexican flame knee tarantula, *B. auratum*, are listed under the Convention on International Trade in Endangered Species (CITES; www.cites.org) index of endangered species and cannot be taken from the wild. For examination under the scanning electron microscope (SEM), material was fixed and dehydrated before being mounted on a stub and coated with gold. Fine structural details of tarsal setae were still present in moulted exoskeletons, viewed after being coated with gold but without prior fixation or dehydration. Being able to use moults increased the amount of material available to us, as moulting occurs throughout the life of a tarantula, which in female tarantulas can be up to 20 years (Coddington and Levi, 1991). Specimens were then viewed using a Cambridge Stereoscan 240 SEM and digital images taken. Moults were also viewed and photographed using a Wild M5a binocular microscope fitted with a digital camera.

## RESULTS

Adults of all three tarantula species were recorded climbing on smooth vertical surfaces. While climbing, the spiders' scopula pads on the tarsi of all eight walking legs were seen to be in contact with the surface (Fig. 1 and Fig. 2A). The tarsal claws (Fig. 1 and inset Fig. 2B) and the scopula tufts around the claws (Fig. 1B, Fig. 2B,C insets) were extended. To test whether silk was secreted by the tarsi of these spiders, we placed a single female Chilean rose tarantula in the bottom of a clean tank whose base was lined with microscope slides (see Materials and methods), raised the tank to the vertical position and shook it slightly. The spider remained attached to the vertical wall (Fig. 2A). We found tarsal silk secretions on the slides in all eight experiments (Fig. 2B,C). We always found traces of silk where we induced a tarsal slip. In one example, we observed the tarantula relocating the tarsi to a more stable position, as evidenced by the new position being maintained while the spider was vertical. Both the first and second right tarsi of the spider slipped and the spider relocated them and regained grip. We found silk traces at all sites where the tarsi of these legs came into contact with the slides and slipped. Multiple silk threads, some up to 2.5 mm in length, were found at the location of the slip on later inspection of the slides under the microscope, with the threads attaching individually to the slide at the position where this sequence of events commenced

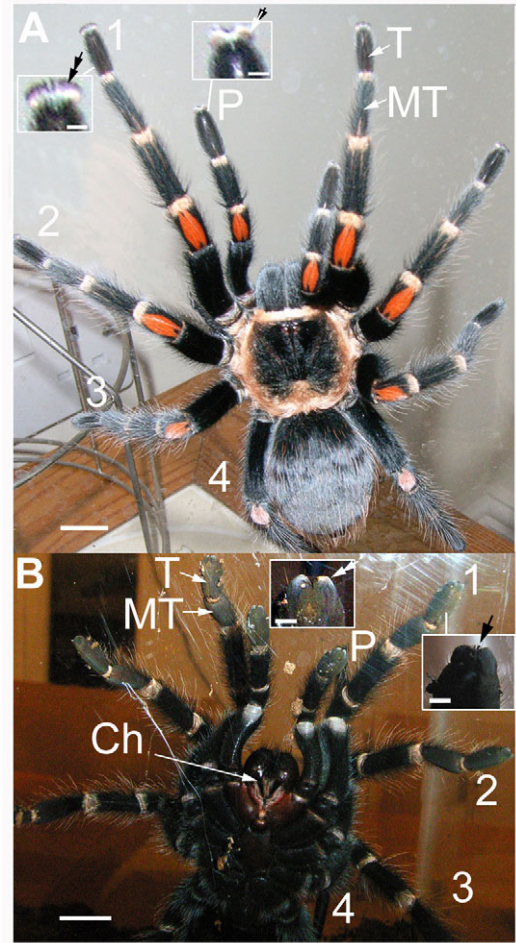


Fig. 1. Mexican flame knee tarantula (*Brachypelma auratum*) climbing a vertical wall. (A) Viewed from above, the tarsi of the walking legs (numbered 1–4) and pedipalps are in contact with the Perspex wall. The setae around the claws are extended (black double-headed arrow). Black/white double-headed arrow, the scopula tufts. Insets show the tarsus and pedipalp. (B) Viewed from outside the tank, lighter shaded areas on the tarsi and pedipalp indicate setae in contact with the wall (inset, white double-headed arrow). Its tarsal claws are extended (inset, black arrow). Ch, chelicerae; MT, meta-tarsal leg segment; P, pedipalp; T, tarsal leg segment. Scale bars: A and B, 10 mm; insets, 1 mm.

(Fig. 2C). We concluded that the silk threads were attached to the initial site and then drawn out throughout the period in which the spider was slipping. We could make out at least 27 individual silk strands over a 1 mm width. For comparison, the total scopula pad (area of densely packed attachment hairs) of the tarsus is around 3 mm across in a walking tarantula, although the area of the pad in direct contact with the wall is about 1 mm across (Fig. 1B and Fig. 2C inset), a similar width to the spread of silk deposits (Fig. 2B,C).

To identify the structures on the ventral surface of the tarsi that secreted the silk, we examined moulted skins from the female Chilean rose tarantulas used above (Fig. 2D). On the leg we saw single strands of silk emerging from the tips of several setae protruding above the scopula pads. The setae were in a regular array, intermingled with the densely packed setae of the scopula pads. One seta is shown with a single strand of silk emerging from its tip in Fig. 2D (lower inset).

A clearer picture of these structures was obtained using a SEM, which revealed that silk-secreting setae were present on the ventral

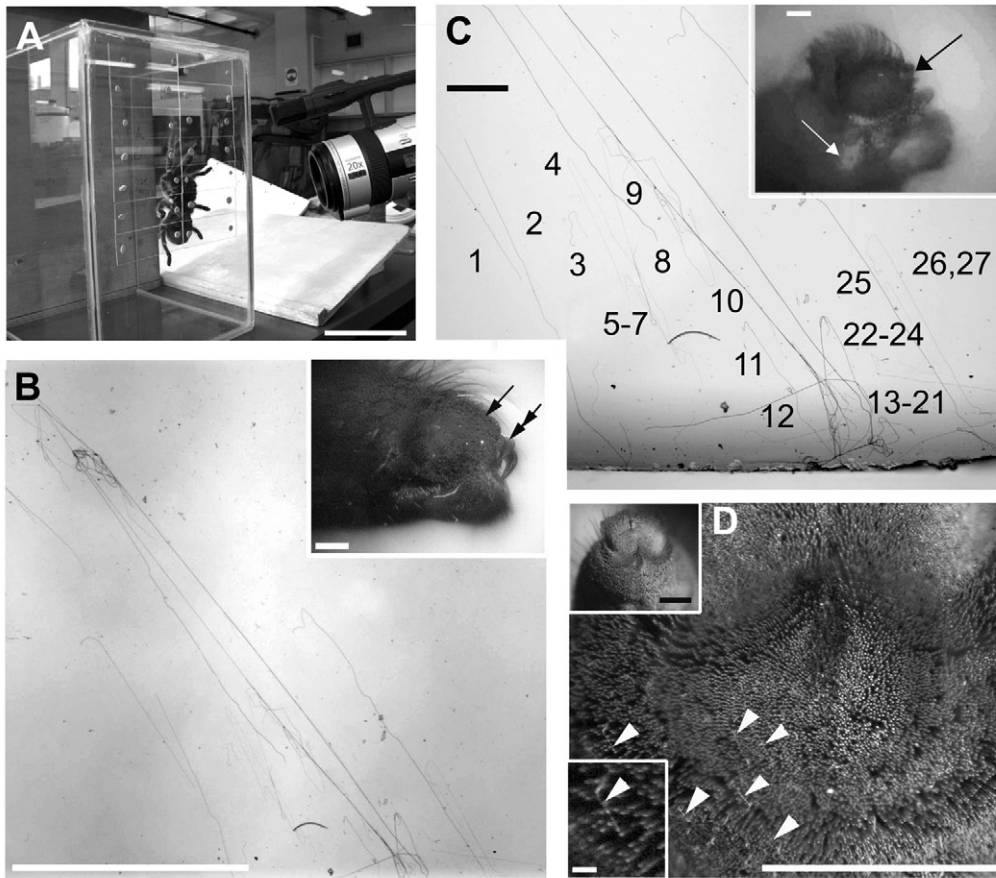


Fig. 2. Chilean rose tarantula (*Grammostola rosea*) secretes silk from its feet. (A) A Chilean rose tarantula on a vertical surface. (B) Silk secretions on a glass slide following a tarsal slip. Inset, scopulae (arrow) and claws (double-headed arrow). (C) The silk deposition area (strands 1–27) matches the tarsal footprint. Inset, tarsal area in contact with glass (lighter area, white arrow). Claw, black arrow. (D) Photomontage of moulted pedipalp. Single silk strands emerge from the tips of setae protruding above the tarsal scopula pads (white arrowheads). Lower inset, a single silk strand (arrowhead). Upper inset, tarsal tip. Scale bars: 1 mm, except A, 100 mm; C, 0.1 mm; D lower inset, 100  $\mu$ m.

tarsi in moults and fresh tarsi from the three tarantula species (Figs 3 and 4). Fig. 3A is a SEM image of a Chilean rose tarsus showing the claw and tarsal scopula pads. The brush-like setae of the scopula pad are punctuated by unbranched setae terminating in tapering tips (Fig. 3B). These are the structures identified in the light microscope as secreting strands of silk (Fig. 2D). We refer to these structures as spigots by analogy to silk-secreting setae on the spiders' spinnerets (Coddington and Levi, 1991). The ribbed spigots, 550–750  $\mu$ m in length, were dispersed through the scopula pad, separated from each other by 50–150  $\mu$ m. Fig. 3B and inset are from an animal that died while shedding its cuticle and the claws are visible inside the partially shed cuticle. At the base of each spigot is a 40  $\mu$ m wide socket embedded in the cuticle; the sockets are evenly distributed over the tarsus (Fig. 3D).

The tarsi of the arboreal Indian ornamental tarantula have an impressive multi-layered array of spigots, the tallest standing 100–200  $\mu$ m above the forest of bent-tipped setae of the scopula pad (Fig. 4A). These tall spigots have regular angled bands of thickening along their projecting parts and terminate in a small, 0.1–0.6  $\mu$ m opening (Fig. 4A inset). The thickened bands on the two sides of the setae are offset relative to one another and only come into alignment at its tip (Fig. 4A). Shorter spigots stand less than 20  $\mu$ m above the scopula pad (Fig. 4C,D) and also have a prominent ribbed structure at their distal ends and terminate in a pore (Fig. 4E,F). A broken spigot base reveals a reinforced central, 1.3  $\mu$ m channel. A third layer of ribbed blunt-tipped spigots terminates level with the scopula pad (Fig. 4G).

In contrast to the tarsi, the spinnerets of the Indian ornamental and a Chilean rose tarantula were found to have silk-secreting spigots in rows on the ventral midline intermingled with other setae

(Fig. 5A–D). The spigots have prominent, 50–70  $\mu$ m unornamented rounded bases (Fig. 5A,C). The short, 250  $\mu$ m cuticular shank of the spigot emerges from the base of the spigot and is ornamented with small cuticular scales. The shank terminates in a small, 1–2  $\mu$ m pore, which can be open or occluded with globules of silk (Fig. 5D,E).

## DISCUSSION

One of the main objections raised to the secretion of silk from the tarsus is a functional one: the silk-secreting nozzles would have to be below the surface of the scopula pad for the spider to adhere to the substrate and then how could the silk be attached to the substrate (Pérez-Miles et al., 2009)? In all of the six tarantulas of the three species we examined in this study, we found spigots projecting beyond the finely divided attachment setae making up the bulk of the scopula pads on the underside of the tarsi. We also observed silk secretions coming from the spigots and found tarsal silk secreted by Chilean rose tarantulas as they struggled to hold on to a vertical surface. The three species of tarantula we studied were large, with adult body masses of 15–50 g and came from diverse habitats: the Indian ornamental was arboreal, the Chilean rose and the Mexican flame knee were ground-dwellers. We therefore conclude that tarsal silk secretion is a feature shared by large tarantulas and is used in addition to the dry attachment system to prevent falls when climbing on smooth surfaces.

Why do tarantulas use silk when a dry attachment system gives a safety factor (adhesive force/body mass) of 160 in the 15 mg jumping spider *E. arcuata* (Kesel et al., 2003)? The safety factor is dependent on the mass of the spider; in the Costa Rican zebra tarantula (17.9 g) and the hunting spider *Cupiennius salei* (3.3 g) the adhesive forces generated by the tarsal and meta-tarsal pads on a

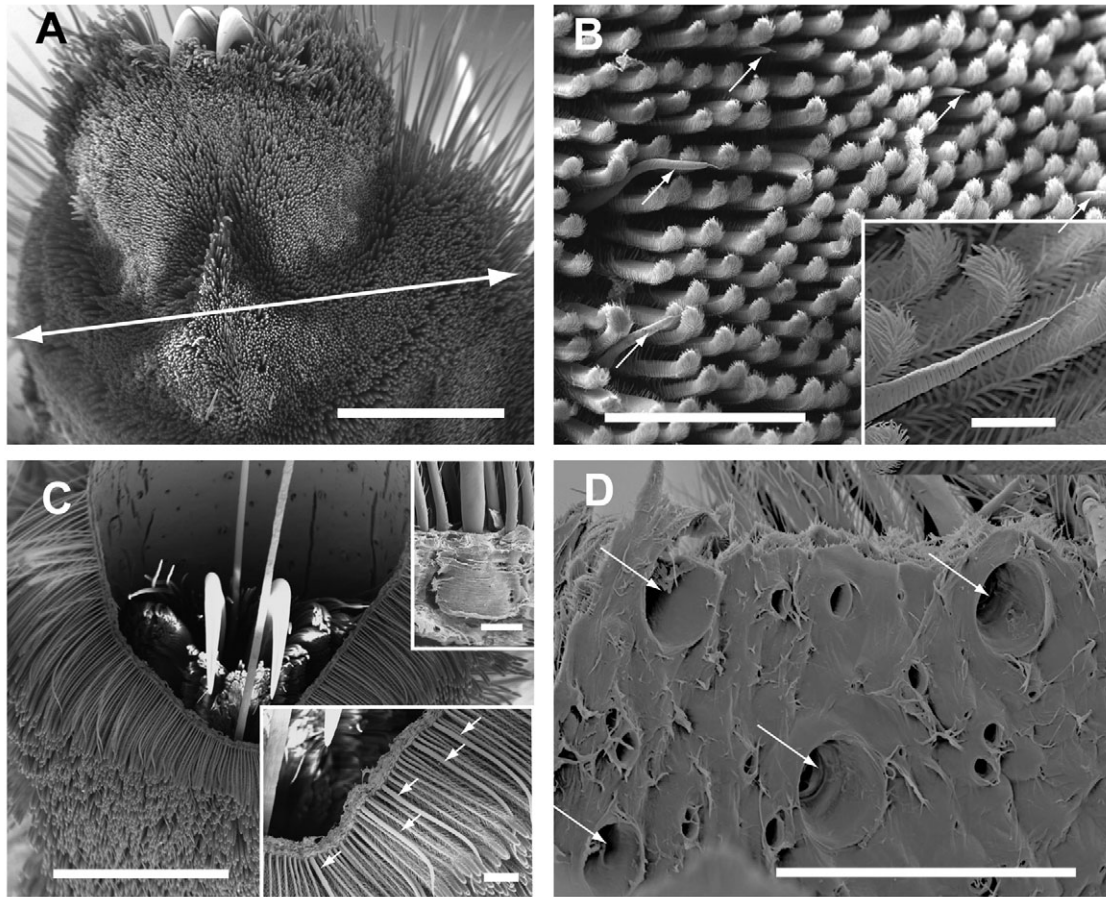


Fig. 3. Scanning electron microscope images (SEMs) showing spigot-like setae on the tarsi of both Chilean Rose (*G. rosea*) and Mexican flame knee (*B. auratum*) tarantulas. (A) Scopula pads on the ventral side of the Chilean rose tarsus (left leg number 2). (B) The bent brushes of the dry attachment setae, interspersed with taller, un-branched spigot-like setae (arrow). (C) View into a partially moulted Chilean rose tarsus at the level indicated in by the arrow in A. Lower inset, regular arrangement of spigot-like setae (arrows). Upper inset, spigot socket within cuticle. (D) Internal view of spigot insertions (arrows) onto the cuticle of an immature Mexican flame knee tarsal moult. Scale bars: A and C, 1 mm; B and D, 100  $\mu$ m; insets, 20  $\mu$ m.

smooth glass surface were equal in magnitude but the tarantula had a 5 times greater body mass, reducing the safety factor for the tarantula to around 1 (Niedregger and Gorb, 2006). In practice, we found that the dry attachment forces of the scopula pads do not always suffice in heavier tarantulas and silk is secreted when the tarantula slips on a vertical smooth surface.

The tarantulas we examined had several lengths of tarsal spigots that projected beyond the finely divided setae of the scopula pads, and the spigot bases were inset into the tarsal cuticle so that only the slim spigot shank interrupted the setae of the scopula pads. The shank itself is adapted so it will not be crushed when the spider walks or collapse during silk extrusion and it can bear the tension of the silken tether anchoring the tarantula tarsus to the glass. The linked, angled annular thickenings, offset across the width of the shank are similar to the reinforcements seen in pressure vessels (Karam, 2005; Wigglesworth, 1965; Rach, 1990) and suggest the spigot's role as a silk delivery and anchoring device. Can we explain why no tarsal silk deposits were found by Pérez-Miles and colleagues (Pérez-Miles et al., 2009) when they blocked the spinnerets of the zebra tarantula and allowed it to roam in a shallow tank? First, we calculate that the tank may have had a wall height that allowed the animal to partially support its weight on the ground so there was no need for silk secretion. Second, no attempts were reported to dislodge the spider from the vertical surface and make it slip (Pérez-

Miles et al., 2009). We think these factors could explain why no evidence of tarsal silk secretion was found and suggest the importance of a slip in causing silk to be secreted from the tarsi of large tarantulas.

Our evidence of secreted tarsal silk suggests a pathway for the evolution of spider silks. The earliest known silk-secreting animal was the spider *Attercopus* from the Devonian period (Selden et al., 2008), which secreted sheets of silk not from spinnerets but from spigots arranged along the edges of an abdominal plate on body segments 4 and 5. The spinnerets themselves originated later from biramous appendages on the same segments (Damen et al., 2002; Selden et al., 2008). In adult spiders the silk-secreting spigots on the spinnerets do not resemble generalized mechanosensory setae but have large bases important for the transition of the stored liquid silk protein to a long silk fibre. Liquid silks are stored in glands in the abdomen (Vollrath and Knight, 2001). We found that tarsal silk-secreting spigots more closely resemble mechanosensory setae (Foelix, 1970); they lack external silk-storage organs (Vollrath and Knight, 2001) and could represent a missing link to their ancestral condition. Interestingly, the first functional spigot on the *Antrodiaetus unicolor* spiderling's spinneret also lacks a bulbous base (Bond, 1994) but may still be connected to external silk-storage organs. Alternatively, because the tarantula family Theraphosidae is a diverse group and includes many of the largest known spiders

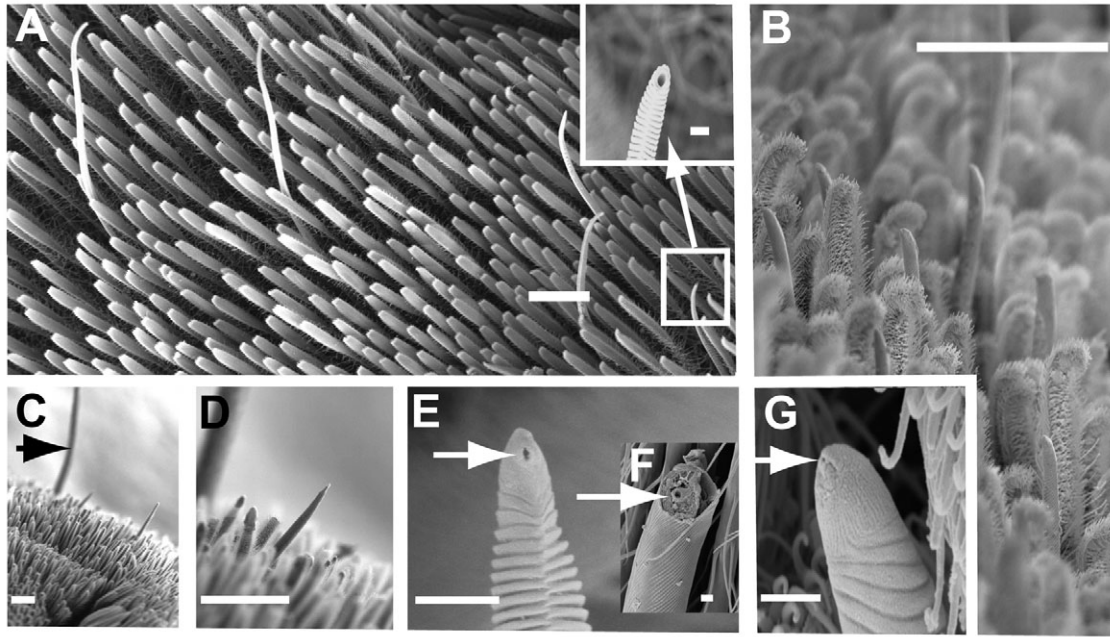


Fig. 4. SEMs showing spigot-like open-pored setae from the tarsi of Indian ornamental tarantulas (*Poecilotheria regalis*). The spigots project beyond the numerous bent-tipped brushes of the dry attachment system. (A) Long spigots on the ventral tarsal claw scopula pad. Inset, detail of the spigot tip with 1 µm diameter opening. (B) Shorter spigots interspersed with setae of the dry attachment system. (C,D) Multi-layered arrangement of spigots. A longer spigot is indicated by the arrow. (E) Tip of a spigot with a pore. (F) A central channel is visible in the spigot base. (G) Blunt-tipped spigot with a small pore (arrow). Scale bars: A–D, 50 µm; insets, 20 µm.

(Coddington and Levi, 1991), tarsal silk may have evolved independently several times within the group to enable tarantula species to climb without slipping. The presence of tarsal silk secretion in the three phylogenetically disparate (Pérez-Miles et al., 1996) tarantula genera examined, plus the Costa Rican zebra

tarantula, argues against such a piecemeal process. Both the different suggestions for the origin of tarsal silk secretion are consistent with the homology of legs and spinnerets as arthropod appendages (Shultz, 1987; Shear et al., 1989; Damen et al., 2002; Selden et al., 2008). As not all tarantulas are large, some being less than 1 mm

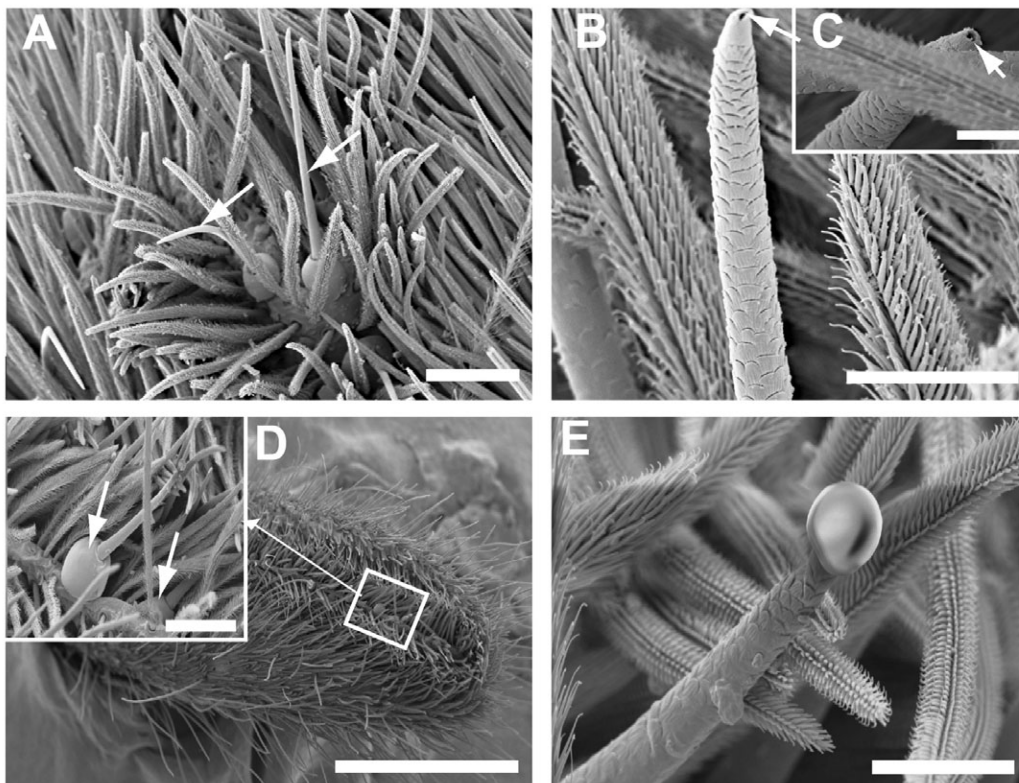


Fig. 5. Silk-secreting spigots on tarantula spinnerets (SEM images). (A) Chilean rose spigots with their enlarged bases are in a mid-ventral position on the spinneret. (B,C) The shank of the Chilean rose spigot has scale-like cuticular ornamentation and terminates in a 1.6 µm pore. (D) Distal segment of the Indian ornamental spinneret showing the arrangement of the spigots along its ventral midline. Inset, detail of an individual spigot. (E) Indian ornamental spigot shank with scale-like ornamentation and a silk droplet at its tip. Scale-bars: A and D inset, 100 µm; B, C and E, 20 µm; D, 1 mm.

in length (Coddington and Levi, 1991), it should be possible to disambiguate the influence of size and primitiveness on tarsal silk secretion by determining whether small representatives of the Theraphosidae family can secrete silk from their tarsi.

The different properties of spider silk for prey capture, mating and egg laying and as a drag-lines are determined by the expression of variants of a spider fibroin gene family (Guerette et al., 1996; Garb et al., 2006; Garb and Hayashi, 2005). Until recently, most analysis of these gene families concentrated on araneomorph spiders, which separated from mygalomorph spiders, such as tarantulas, 240 million years ago (Vollrath and Selden, 2007). Recently, two spidroin (SP) cDNA sequences were characterized from silk glands of the arboreal Amazonian tarantula, *Avicularia* spp. (Bittencourt et al., 2010). The most abundant spidroin gene sequence, *SPI*, was similar to that for araneomorph tubuliform (egg case) silk but the other was a MaSP2-like spidroin gene sequence, most similar to the tough major ampullate (MA) silk of araneomorph spiders, used both for web building and for draglines and thought to be a defining feature of orb web-building spiders. If tarsal silks belong to this same spidroin gene family, as is likely, then comparison of tarsal and spinneret silks could help our understanding of the ancestral function and molecular evolutionary history of spider silk.

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