

RESEARCH ARTICLE

Silk secretion from tarantula feet revisited: alleged spigots are probably chemoreceptors

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Accepted 4 December 2011

SUMMARY

Controversial views have been expressed about whether tarantula feet can secrete fine silk threads that could prevent them from falling off smooth vertical surfaces. Two studies have claimed that ‘ribbed hairs’ on the tarsi of tarantulas produce silk. We examined these ribbed hairs in several tarantula species using light and scanning electron microscopy, and compared them with the silk-producing spigots on the abdominal spinnerets. We found that, morphologically, these ribbed hairs correspond very closely to known chemosensitive hairs in spiders; they have a distinct socket, a bent hair shaft with fine cuticular ridges, an eccentric double lumen within the hair shaft, and a blunt tip with a subterminal pore. Spigots on the spinnerets have a large bulbous base instead of a socket, a long shaft with a scaly surface and a central terminal pore. We never observed any silk threads coming out of these ribbed hairs under the electron microscope. By contrast, silk threads exiting the spigots on the spinnerets were common. Interestingly, ribbed hairs also occur on the spinnerets, often side by side with the silk-producing spigots. Our conclusion is that the ribbed hairs are chemoreceptors, not spigots. Observations of live tarantulas clinging inverted to glass coverslips confirmed that some substance is produced by the ribbed hairs, but it remains unclear whether this secretion is actually silk. In any case, the thousands of adhesive setae on the tarsi of legs and pedipalps almost certainly far outweigh any potential contribution from the sparsely distributed trails secreted by the ribbed hairs.

Key words: spider, tarantula, adhesion, silk, spigot, chemoreceptor.

INTRODUCTION

A few years ago it was reported that tarantulas produce silk threads from their feet, which could presumably prevent these large spiders from falling off smooth vertical surfaces (Gorb et al., 2006). This claim was challenged in a subsequent study by Pérez-Miles et al. (Pérez-Miles et al., 2009), who observed that tarantulas with sealed spinnerets did not produce any silken threads on vertical glass walls. The implication was that silk traces found within the tarantula’s footprints originated from the abdominal spinnerets and not from presumed tarsal silk glands. Recently, however, two publications have appeared that seem to support the original claim by Gorb et al. (Gorb et al., 2006). Rind and colleagues (Rind et al., 2011) gently shook the tarantulas as they clung to a vertical smooth wall. This induced a slight slipping of the tarsi, and fine silk threads were seen to emerge from ribbed ‘spigots’ on the ventral tarsi. Similar threads were described briefly by Peattie et al. (Peattie et al., 2011), but that study focused on unrelated fluid secretions from adhesive pads in diverse arachnids rather than tarsal silk production in tarantulas.

While looking at published scanning electron micrographs of the alleged tarsal spigots (Gorb et al., 2006; Rind et al., 2011), we were struck by their close similarity to known chemoreceptors in spiders (Foelix, 1970; Foelix, 1985; Foelix and Chu-Wang, 1973; Harris and Mill, 1973). We therefore decided to take a closer look at these ‘spigots’ in several tarantula species and to compare their structure with that of the regular silk-producing spigots on the spinnerets. We also made footprints from tarantula tarsi on clean glass slides and compared them with spinneret prints, using light and scanning

electron microscopy. Finally, we wanted to raise some crucial questions: (1) do the observed threads really consist of silk? (2) could these threads possibly serve as a safety line for large and heavy spiders? and (3) do these threads inform our understanding of the evolution of silk? If there is no good evidence for tarsal silk glands, any phylogenetic conclusions as drawn by Gorb et al. (Gorb et al., 2006) and Rind et al. (Rind et al., 2011) regarding the evolution of spinnerets must be reconsidered.

MATERIALS AND METHODS

Molted skins (exuvia) and alcohol-preserved material from the following tarantula species were used in our studies: *Aphonopelma seemanni* (Pickard-Cambridge 1897), *Brachypelma auratum* Schmidt 1992, *Brachypelma smithi* (Pickard-Cambridge 1897), *Grammostola alticeps* (Pocock 1903) and *Poecilotheria regalis* (Pocock 1899). For comparison, we also examined the mesothel spider *Liphistius desultor* Schiödte 1849 with regard to the spinnerets, because *Liphistius* is considered to belong to the phylogenetically oldest spiders. All spiders used in this study were bred in the laboratory.

For light microscopy, tarsi from exuvia were dissected and examined in 70% ethanol. For observations with the scanning electron microscope (SEM), tarsi and spinnerets were dehydrated in alcohol series and acetone; after 15 min in hexamethyldisilazane (HMDS) to minimize shrinkage, specimens were air-dried on filter paper. Tarsi and spinnerets were split in half so that external and internal views of the cuticular parts could be obtained in the SEM.

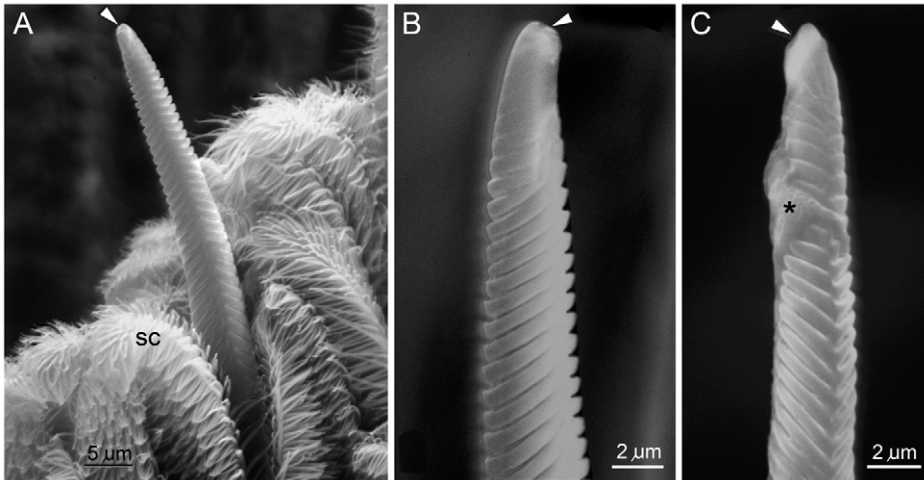


Fig. 1. Ribbed hair on tarsus 1 of *Poecilotheria regalis*. (A) The tip of a ribbed hair extends slightly above the dense pad of adhesive scopula hairs (sc). The terminal pore (arrowhead) is indistinct. (B) The hair tip is blunt, the pore opening (arrowhead) slightly off center. (C) Some kind of secretion (asterisk) is often seen adhering to the hair tip. Note the cuticular ribs forming a herringbone pattern on the hair shaft.

All specimens were glued onto carbon-coated aluminium stubs and then sputtered with gold before examination in a Zeiss DSM-950 SEM. Pictures were taken with a Pentax K20D digital camera at $\times 50$ –5000 magnification.

For the examination of possible silk deposits, tarantulas were held in the hand and the tarsal scopulae (including the distal claw tufts) and the spinnerets were pressed against clean glass slides, which were then inspected using the light microscope (LM) and SEM. About five consecutive footprints from tarsi I–IV were taken from three different tarantula species (*B. auratum*, *G. alticeps* and *P. regalis*), which resulted in about 60 footprints.

For the inspection of any secretion from the ribbed hairs, live specimens of juvenile *Grammostola rosea* (Walckenaer 1837) were confined in a custom-built observation chamber such that, when inverted, they could be induced to cling upside-down to a glass coverslip, through which it was possible to view structures in close (adhesive) contact using interference reflection microscopy (IRM). Images were collected with a 10-bit B/W QICAM camera (QImaging, Surrey, BC, Canada) attached to a Leica DRM HC series microscope (Leica Microsystems, Wetzlar, Germany) using green (546 nm) epi-illumination. Further details of the IRM technique can be found in Peattie et al. (Peattie et al., 2011).

RESULTS

The ‘ribbed spigots’ or ‘nozzle-like setae’ described by Gorb et al. (Gorb et al., 2006) and Rind et al. (Rind et al., 2009) are scattered among the thousands of tarsal adhesive hairs, but can be detected easily because their tips extend slightly above the surrounding adhesive hairs (Fig. 1A). In contrast to the brush-like shape of the

scopula (adhesive) hairs, these hairs are unbranched, with a slightly curved hair shaft and a blunt tip. At higher magnification the hair shaft exhibits regular, cuticular ridges that run obliquely to the longitudinal axis of the hair (Fig. 1B) and which come together at the two midlines of the shaft, thus forming a herringbone pattern (Fig. 1C, Fig. 4C). Close to the hair tip, but slightly off-center, a small pore opening (about 0.5 μm diameter) can be detected. Even under the SEM this pore is usually indistinct because it is often obscured by a dried secretion (Fig. 1C). This pore actually appears clearer in the LM, particularly when using phase contrast (Fig. 2A). The LM also reveals another important feature; namely, a cuticular canal inside the hair shaft (Fig. 2B,C; Fig. 4D). This canal traverses the hair shaft eccentrically and terminates 40–50 μm above the hair base (Fig. 2D). Under the SEM this internal canal could only be seen if the hair shafts had been broken to reveal a cross-section of the hair.

In summary, the main morphological features of these ribbed hairs are: (1) a bent hair shaft (slight S-shape), (2) a rather thin hair wall (1–2 μm) that makes these hairs quite transparent under the LM, (3) a herringbone pattern of cuticular ridges along the hair shaft, (4) a small subterminal pore, and (5) a small cuticular tube traversing the distal hair shaft eccentrically and ending shortly before reaching the hair base. All five are diagnostic features of chemosensitive hairs in spiders (Foelix, 1970; Foelix and Chu-Wang, 1973; Harris and Mill, 1973). Therefore, it seems more compelling to interpret this type of hair as a sensory sensillum (contact chemoreceptor) rather than as a silk spigot. This will be treated in more depth in the Discussion.

If the ribbed hairs on tarantula feet could function as spigots, then a detailed comparison with the regular silk-producing spigots

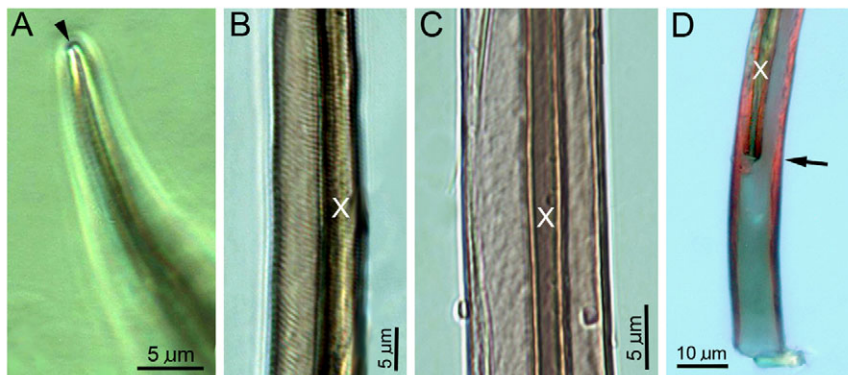


Fig. 2. Ribbed hair from the tarsal scopula, as seen under the light microscope (*P. regalis*, exuvium). (A) The tiny terminal pore (0.5 μm ; arrowhead) can be detected with phase contrast microscopy. (B) A fine striation of the hair shaft becomes apparent at high magnification. Note the double lumen (X) inside the hair shaft. (C) The double lumen is due to a small cuticular tube (X) traversing the hair shaft. (D) This cuticular tube (X) is restricted to the distal part of the hair shaft; its termination (arrow) ~ 40 –50 μm above the hair base is clearly visible under polarized light. Photos by Bruno Erb.

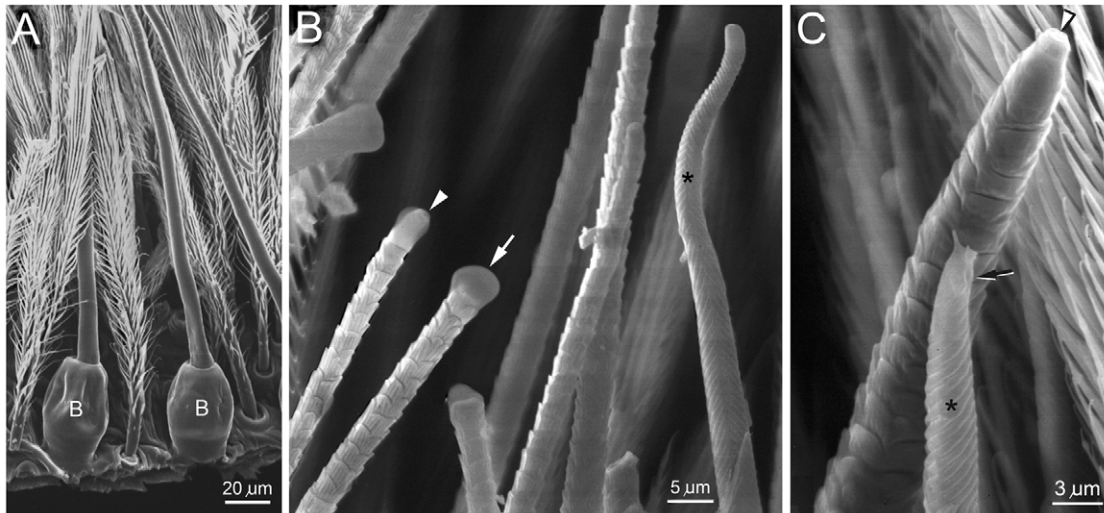


Fig. 3. Spigots from the spinnerets of *P. regalis* (A,B) and *Brachypelma auratum* (C). (A) Two spigots with their typical bulbous base (labelled B) surrounded by (mechanosensitive?) hairs. (B) Several spigot shafts next to a ribbed hair (asterisk). Note the terminal pore (arrowhead) and tiny silk balls (arrow) on some spigot tips. (C) Close-up of a spigot with a central terminal pore (arrowhead) and of an adjacent ribbed hair (asterisk) with a subterminal pore (arrow).

on the spinnerets is warranted. After looking at the abdominal spigots of several tarantula species with the SEM, we found the following features to be characteristic. (1) Each spigot starts with a bulbous part at its base (Fig. 3A), but not with a socket as in sensory (ribbed) hairs. (2) The spigot shaft has a typical scaly appearance (Fig. 3B, Fig. 4A,B) but never a fishbone pattern of cuticular ridges (Fig. 4C). (3) The pore opening (1–2 µm diameter) always lies at the very end of the spigot, in the center and not subterminal (Fig. 3B,C).

The main criterion for a silk spigot is certainly that some secreted silk should emerge from its terminal pore. This is often seen on spinnerets from exuvia in the form of small silk balls adhering to the spigot tips (Fig. 3B), and in alcohol material as drawn out silk threads (Fig. 4A, Fig. 5A,B). When examining abdominal spigots from the inside, a silk canal was often present in the center of the spigot base (Fig. 5C, Fig. 8C inset). By contrast, we never observed any silk threads with the SEM when looking at the tarsal ribbed hairs – either on the outside (hair tip) or on the inside of tarsal scopulae.

We tried to obtain footprints – and also spinneret prints – from several tarantula species (*B. auratum*, *G. alticeps* and *P. regalis*) by gently pressing clean glass slides against the tarsal scopulae and the abdomen of spiders that were held in the hand. Whereas the paired spinnerets gave off a copious amount of hundreds of silk threads that produced a visible, symmetrical pattern on the slide (Fig. 6C), the footprints yielded nothing visible to the naked eye. Even under the LM, only a few short strands of silk were found; they were subsequently also inspected under the SEM (Fig. 6A,B). It is likely that these few silk threads had actually come from the spinnerets and had been transferred secondarily to the legs before we took the footprints.

During IRM observations of live spiders, we were able to induce secretion of threads similar to those observed by Gorb et al. (Gorb et al., 2006) and Rind et al. (Rind et al., 2011). Thin trails were clearly seen emanating from ribbed hairs (and no other hairs) during the IRM observations (Fig. 7A). Video of the strands in the process of being secreted can be seen in the supplementary material of Peattie

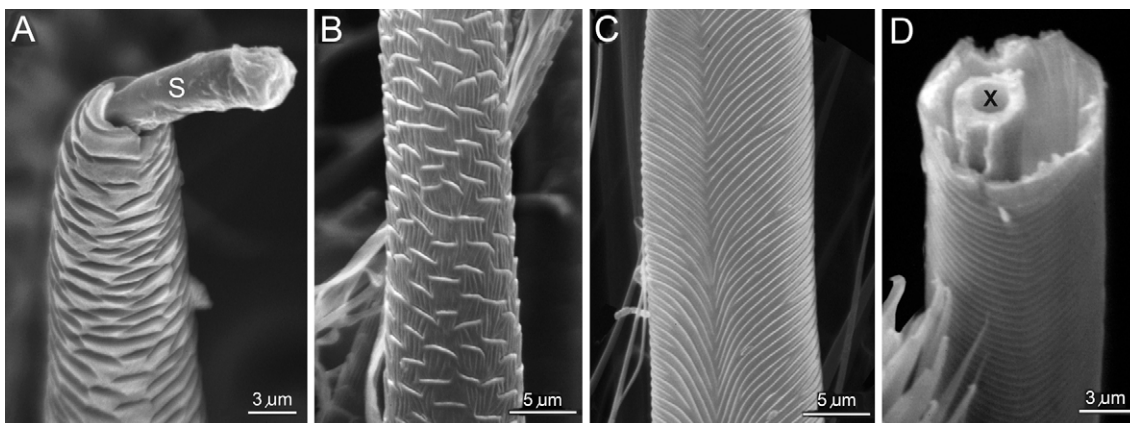


Fig. 4. Comparison of a spigot (A,B) and a ribbed hair (C,D). (A) A relatively thick silk thread (S) emerges from the terminal pore. The structure of the spigot shaft is reminiscent of a pine cone. (B) Close-up of a spigot shaft showing many small scales with longitudinal ridges. (C) The hair shaft of the ribbed hairs shows fine, often branching ridges that meet in the midline (herringbone pattern). (D) Broken hair shaft of a ribbed hair showing the eccentric cuticular tube (X) that is typical of chemosensory hairs (see Fig. 2B–D).

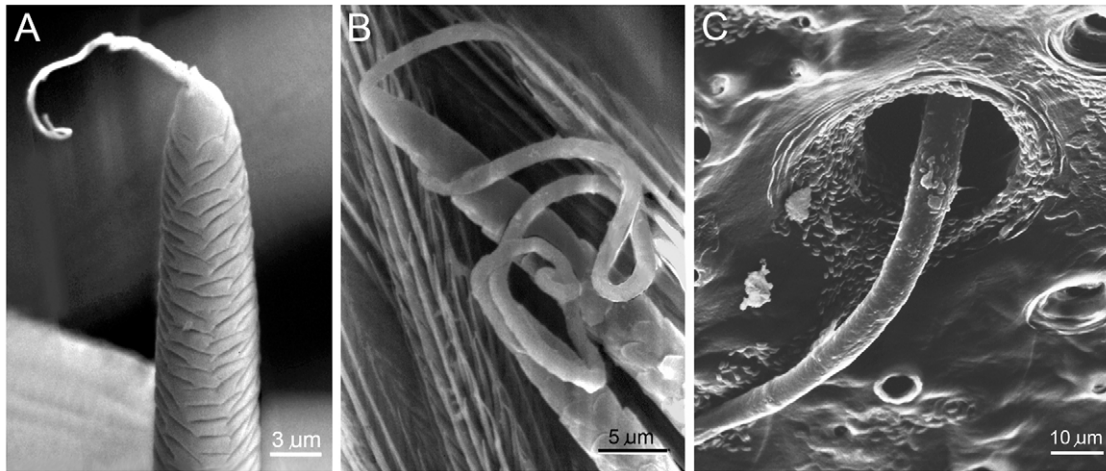


Fig. 5. Spigots associated with silk threads. (A) Often, a short silk thread is seen exiting from the terminal pore. (B) More rarely, longer silk threads are found emerging from the spigot tip. (C) Even on the inside of a spinneret (exuvium), a silk canal is often present underneath a spigot.

et al. (Peattie et al., 2011), available freely online. The secreted strands emerged only as the foot slid across the glass. Their length matched the length of the sliding motion; unlike abdominal silk, the strands broke immediately when the foot was lifted from the glass. There was no continuity between the anchored threads and the animal after it lost its purchase on the glass. While the trails sometimes resembled threads, at other times they resembled droplets (Fig. 7B). It should be noted that these droplets were quite distinct from the more general fluid secretions associated with adhesive footpads of arachnids (Peattie et al., 2011).

DISCUSSION

After our re-examination of tarantula feet, we challenge three claims that have been made by Gorb et al. (Gorb et al., 2006) and more recently by Rind et al. (Rind et al., 2011): (1) special ‘nozzle-like setae’ on the tarsi produce silk threads; (2) these threads provide additional adhesion to the substrate, thus preventing ‘catastrophic falls’; and (3) extant tarantulas represent a

phylogenetically ancient condition, with silk-producing spigots occurring on all extremities.

In our morphological studies we found strong evidence that the alleged tarsal spigots are actually chemosensory hairs rather than secretory devices. The typical features of spider chemosensitive hairs (bent hair shaft with regular ridges; blunt hair tip with a subterminal pore; cuticular canal with sensory fibers inside) are well known from studies of many spider species (Foelix, 1970; Foelix and Chu-Wang, 1973; Harris and Mill, 1973; Barth, 2002), and practically all of these traits are present in the ribbed hairs. Despite this close resemblance, neither of the previous publications (Gorb et al., 2006; Rind et al., 2011) considered the possibility that ribbed hairs were chemoreceptors. The occurrence of this hair type within scopula pads had been described for several araneomorph spiders but also for theraphosids, and sensory innervation has been proven with transmission electron microscopy (TEM) (Foelix, 1970; Foelix and Chu-Wang, 1973; Foelix et al., 2010). Admittedly, this has not been shown for the

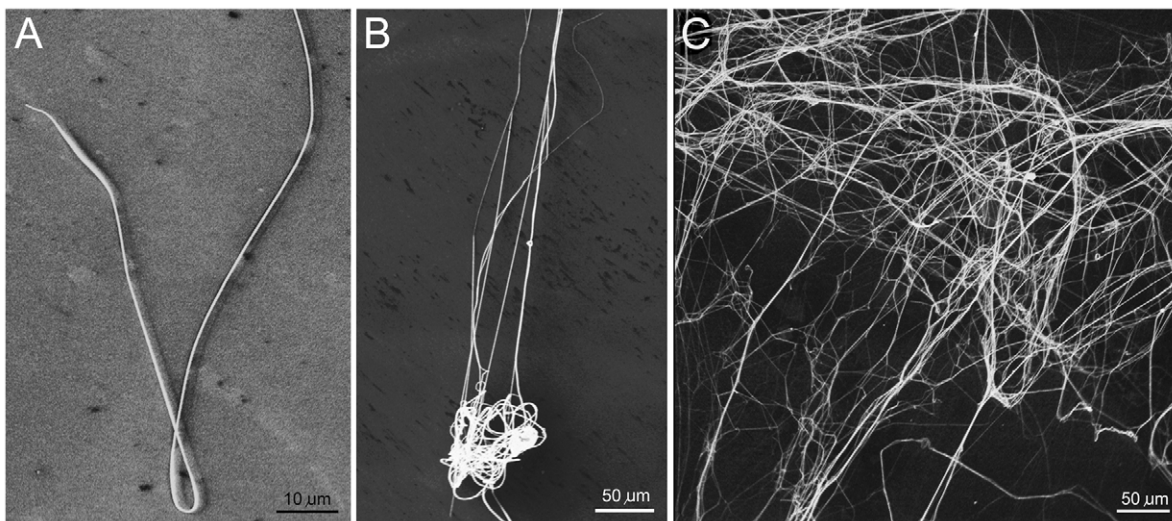


Fig. 6. Silk threads from tarsal footprints (A,B) and from spinneret prints (C) for comparison. (A,B) A few short pieces of thread were found in a footprint of a *Grammostola alticeps* on a glass slide. (C) Thousands of silk threads were deposited in an orderly fashion when a glass slide was pressed briefly against the spinnerets of a *P. regalis*.

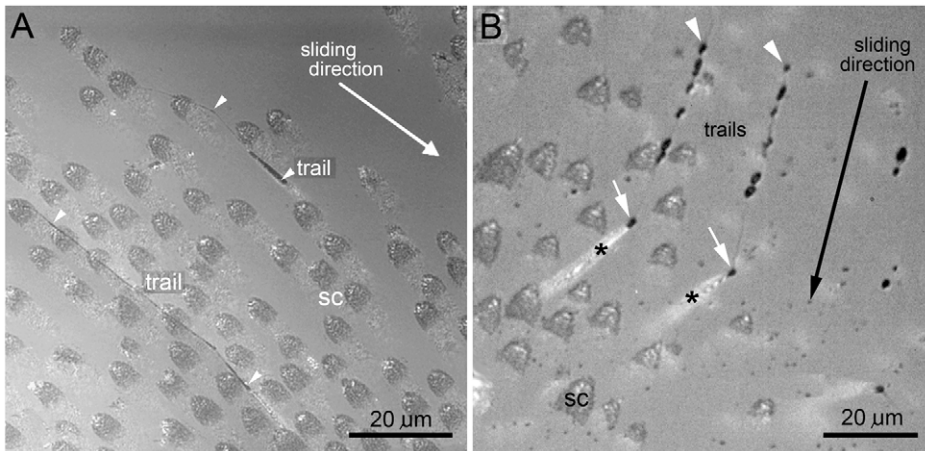


Fig. 7. Interference reflection microscopy (IRM) images of a *Grammostola rosea* tarsus sliding across glass. (A) Thread-like trails (arrowheads) are left behind by ribbed hairs (asterisks in B). (B) Trails were not always thread-like, but sometimes appeared as a series of droplets. SC, adhesive scopula hairs.

tarantula hairs in this study (because we did not have access to a TEM lab), but for final proof of the sensory nature of these hairs, thin sections and TEM still need to be done. Also, electrophysiological studies of those 'ribbed hairs' are warranted to demonstrate their chemosensory properties. We want to point out, however, that such studies have been performed on the corresponding chemosensitive hairs of other spiders (Harris and Mill, 1977; Vallet et al., 1998; Tichy et al., 2001).

Although Rind et al. (Rind et al., 2011) also examined the spigots on the spinnerets, they apparently did not notice that the exact same ribbed hairs they found on the tarsi also occur on the spinnerets (see Fig. 3B,C). This is not really surprising because chemosensitive hairs are present on all extremities, including the spinnerets and the mouth parts (Foelix, 2011). Conversely, the typical silk-producing spigots are only found on the spinnerets, never on the legs.

One decisive argument for a silk spigot would be a thread coming out of a terminal pore. This is indeed commonly seen on the spigots of the spinnerets (Fig. 4A, Fig. 5A,B) (Felgenhauer, 1999; Griswold et al., 2005) but not on the alleged spigots (ribbed hairs) on the tarsus. In the publication of Rind et al. (Rind et al., 2011) there is only one picture (see their fig. 2D) in which threads

are supposedly exuded from ribbed hairs, but unfortunately the magnification is too low for this to be convincing. No SEM image exists to date showing a silk thread being secreted from the tip of this hair type, although several SEM images of abdominal spigots clearly show silk secretion [see fig. 5E in Rind et al. (Rind et al., 2011); Figs 3–5 in this paper]. Histological sections of tarantula feet also failed to provide any evidence of tarsal silk glands (Pérez-Miles et al., 2009).

When we compared footprints from tarantulas with spinneret prints, we found thousands of silk threads from the spinnerets on glass slides but only very few from the tarsi (Fig. 6). Whether these tarsal threads really came from the tarsus or were originally secreted by the abdominal spigots is not yet clear. Experiments by Pérez-Miles et al. (Pérez-Miles et al., 2009; Pérez-Miles and Ortiz-Villatoro, 2012) strongly indicate that such pieces of thread do not arise from the tarsus, as tarantulas with sealed spinnerets do not leave any silk threads on glass slides.

Using IRM, however, we were able to confirm the presence of fine threads within tarantula footprints, and we noted that the secretions were directly correlated with ribbed hairs; that is, the trails did not appear to originate from the tips of any other hair

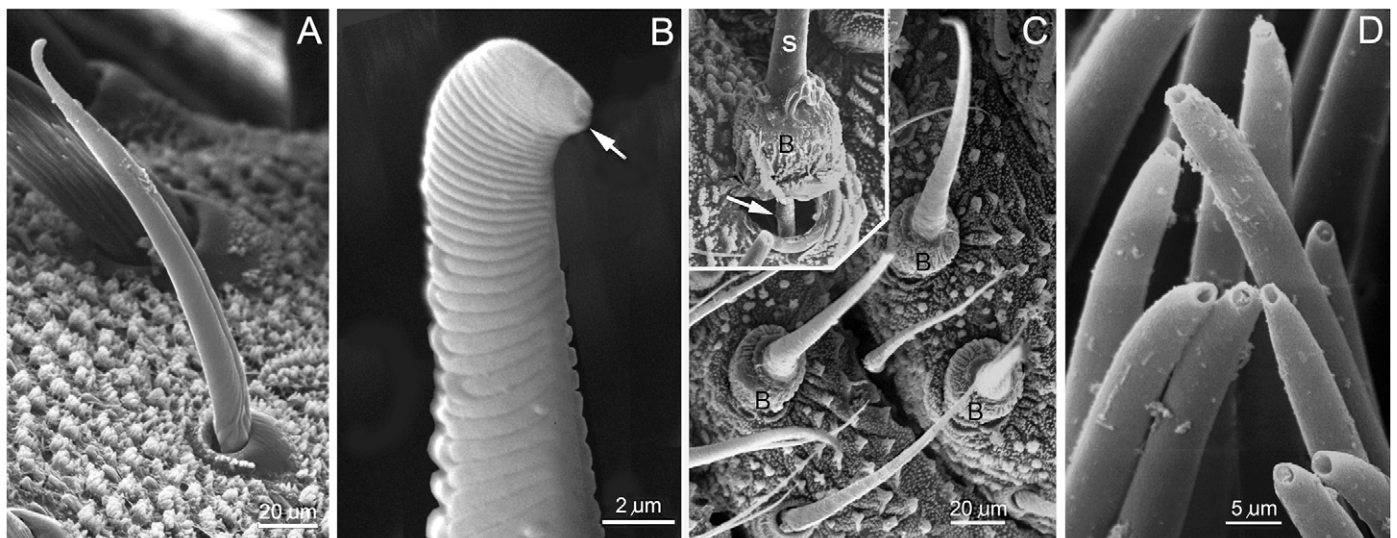


Fig. 8. A chemosensitive hair on the tarsus of a *Liphistius desultor* shows the typical bent hair shaft arising from a distinct socket (A) and also a blunt tip with an indistinct pore (arrow) and fine cuticular ridges (B). (C) Spigots on the spinnerets of *Liphistius* have the same bulbous base (B) as in tarantulas (see Fig. 3A). Inset: a partly broken spigot base (labelled B) reveals how the spigot shaft (s) continues as a silk canal (arrow) to the inside of the spinneret. (D) Spigot tips from the spinnerets showing a smooth shaft and a distinct terminal pore of 1–2 μm diameter.

types on the tarsus (Fig. 7A). Yet, in the light of the morphological evidence presented above, and because the trails did not always appear to be solid (Fig. 7B), it seems reasonable to question whether the secretion is actually silk. The sparsely distributed, thin trails we observed were easily distinguished from the copious, macroscopic and sticky silk secreted from the tarantula's abdominal spinnerets (Fig. 6C).

It is known that chemosensory hairs are filled with a proteinaceous fluid ('receptor lymph') that surrounds the dendrites of the sensory cells up to the pore opening (Foelix and Chu-Wang, 1973; Ozaki et al., 1995; Stürckow, 1967), and globules adhering to the tip of chemosensitive hairs have been described for insects (Slifer et al., 1959) and spiders (Foelix, 1970). As a distally directed flow of this fluid has been shown in the taste hairs of flies (Hodgson, 1968), it could well be that some receptor lymph oozes out when the hair tip is touching the ground and leaves a trail when sliding.

Because it is unlikely that these threads consist of silk and because these threads are very thin and are present in small numbers, we object to the assertion that tarantulas 'cling to smooth surfaces by secreting silk from their feet' (Rind et al., 2011). Adhesive setae outnumber the ribbed hairs by approximately 50:1, and the attachment forces of adhesive setae are well established, for spiders and other unrelated animals (Peattie et al., 2011), reinforcing the supposition that they are adaptive for climbing smooth surfaces. No data exist for the attachment forces of these threads, which are apparently limited to theraphosid tarantulas. The species tested so far are mostly ground-dwelling, further complicating adaptational inferences related to their attachment structures.

Considering the lack of conclusive evidence for tarsal silk secretion in tarantulas, any phylogenetic considerations should be met with skepticism. It is tempting to assume that the occurrence of silk-producing spigots on all extremities is the ancient condition and that spigots were more recently restricted to the abdominal spinnerets. However, we would then expect a higher likelihood of observing the 'primitive' condition in the more basal spiders of the suborder Mesothelae (e.g. in *Liphistius*) than in the mygalomorph tarantulas. This is not the case: *Liphistius* has the same 'ribbed spigots' (chemoreceptors) on all extremities (Fig. 8A,B), but has no tarsal scopulae (adhesive hairs) and cannot scale smooth surfaces (Foelix and Erb, 2010). A putatively adhesive tarsal silk secretion would not impart any adaptive value to this ground-living spider. Finally, the abdominal spigots in *Liphistius* also have a bulbous base (Fig. 8C), just like the oldest known fossil spigots from the arachnid *Attercopus* (Shear et al., 1989; Selden et al., 2008). The assumption that the tarsal 'ribbed spigots' in tarantula feet – which lack a bulbous base – would represent an evolutionary precursor of the abdominal silk-producing spigots (Rind et al., 2011) is therefore unfounded.

In conclusion, independent lines of morphological, biomechanical and phylogenetic argument contradict the claim that tarantulas secrete weight-bearing silk from plesiomorphic spigots on their tarsi. Such a hypothesis, if validated, would have significant implications

for our understanding of the evolution of silk, and as such it demands well-founded evidence.

ACKNOWLEDGEMENTS

We thank Benno Wullschleger for providing several of his tarantulas and for his help in some experiments; Jan de Vries for technical support with the scanning electron microscope and Bruno Erb for taking photographs with the light microscope; Fernando Pérez-Miles for stimulating discussions; and Jerome Rovner for critically reading our manuscript. The Neue Kantonsschule Aarau generously let us use their electron microscope facilities.

FUNDING

A.M.P. was supported by a Royal Society International Postdoctoral Fellowship.

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