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Sand transport and burrow construction in sparassid and lycosid spiders

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Abstract. A desert-living spider sparassid (*Cebrennus rechenbergi* Jäger, 2014) and several lycosid spiders (*Evippomma rechenbergi* Bayer, Foelix & Alderweireldt 2017, *Allocosa senex* (Mello-Leitão, 1945), *Geolycosa missouriensis* (Banks, 1895)) were studied with respect to their burrow construction. These spiders face the problem of how to transport dry sand and how to achieve a stable vertical tube. *Cebrennus rechenbergi* and *A. senex* have long bristles on their palps and chelicerae which form a carrying basket (psammophore). Small balls of sand grains are formed at the bottom of a tube and carried to the burrow entrance, where they are dispersed. Psammophores are known in desert ants, but this is the first report in desert spiders. *Evippomma rechenbergi* has no psammophore but carries sand by using a few sticky threads from the spinnerets; it glues the loose sand grains together, grasps the silk/sand bundle and carries it to the outside. Although *C. rechenbergi* and *E. rechenbergi* live in the same environment, they employ different methods to carry sand. *Geolycosa missouriensis* lives in a moister habitat and produces solid sand pellets in which sand grains are caked together (without silk threads); the compact pellets are flung away from the burrow entrance by a rapid extension of the first legs. The spiders stabilize the developing tube inside by repeatedly adding silk rings, while digging down. This wall is very thin, consisting of only a few layers of crisscrossing silk threads. An excavated burrow collapses immediately, indicating that the stability is not due to the silk. Instead, the tight interconnection of neighboring sand grains—as in a vault—yields the necessary solidity to the burrow.

Keywords: Desert spiders, functional morphology, sand digging

Many ground-living spiders dig burrows into the soil, which they line with silk on the inside. This behavior is widespread among different spiders—in the ancient Mesothelae and Mygalomorphae as well as in the more modern Araneomorphae (e.g., in Eresidae, Filistatidae, Lycosidae, Zodariidae). Although there are several descriptions on burrow construction for certain lycosid and sparassid spiders (Gertsch 1949; Henschel 1990, 1997, 1998; Birkhofer & Moldrzyk 2003; Aisenberg & Peretti 2011; Suter et al. 2011), some aspects of the burrowing behavior and tube construction have received less attention. In particular, the question of how the soil material (mostly sand) is transported to the outside of the burrow has rarely been considered. Whereas digging in moist sand and carrying it away hardly poses a problem, it is a real challenge to transport dry sand grains. We here report how spiders living in the same habitat have solved this problem. Another difficulty for spiders living in dry sand is: how can the burrow wall be sufficiently stabilized to provide a solid tube for housing the spider? We have focused on these questions primarily in two desert spiders from Morocco (*Cebrennus rechenbergi* Jäger, 2014, Sparassidae; *Evippomma rechenbergi* Bayer, Foelix & Alderweireldt, 2017, Lycosidae) which build vertical tubes in dry sand dunes (Foelix et al. 2016; Rechenberg, unpublished data). For comparison, we also looked at some other tube-dwelling lycosids from North and South America: *Geolycosa missouriensis* (Banks, 1895) and *Allocosa senex* (Mello-Leitão, 1945). It turned out that the problem of building burrows in dry sand has been solved in different ways by different spiders.

METHODS

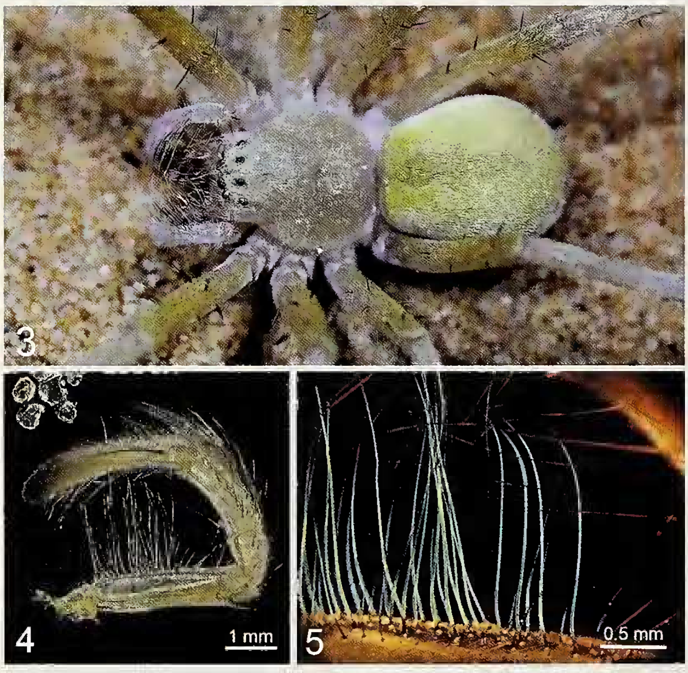
Spiders were observed, photographed and filmed under natural conditions in the field (*C. rechenbergi*: sand dunes of the Erg Chebbi desert in northern Morocco, in 2014; *A. senex*: coastal sand dunes near Salinas, Uruguay, in 2016) and additionally in the laboratory; only in the case of *G. missouriensis* did we rely on previous descriptions in the literature (Emerton 1912; Gertsch 1949; Suter et al. 2011). For morphological studies, alcohol-fixed material and exuvia were examined with light (LM) and scanning electron microscopy (SEM) (Zeiss DSM-950). Specimens were dehydrated in acetone and HMDS (hexa-methyl-di-silazane), air-dried and sputtered with gold before inspection. Small pieces of the burrow walls were inspected from the internal and the external side to understand the interactions between sand grains and silk lines. Isolated deposits of dug-out sand either in the form of sand/silk bundles (*E. rechenbergi*) or compact pellets (*G. missouriensis*) were studied with the SEM. Voucher specimens of *A. senex* were deposited in the collection of sección Entomología, Facultad de Ciencias, Uruguay (FCE Ar from 7776 to 7780), those of *C. rechenbergi* at the Senckenberg Museum Frankfurt, Germany (59794-133).

RESULTS

When spiders are digging vertical tubes into sandy soil, they need to carry away small portions of sand all the time. This is usually done with the pedipalps and chelicerae, but different techniques are used in doing that. We first describe the method of sand transport for the sparassid *C. rechenbergi* and then compare it to the lycosid *E. rechenbergi*, which shares the same habitat in the Moroccan Erg Chebbi dunes (in a northern extension of the Sahara). For comparison, we also report our observations of some additional lycosids, namely *A. senex* from South America (Uruguay), and *G. missouriensis* from North America (Mississippi).

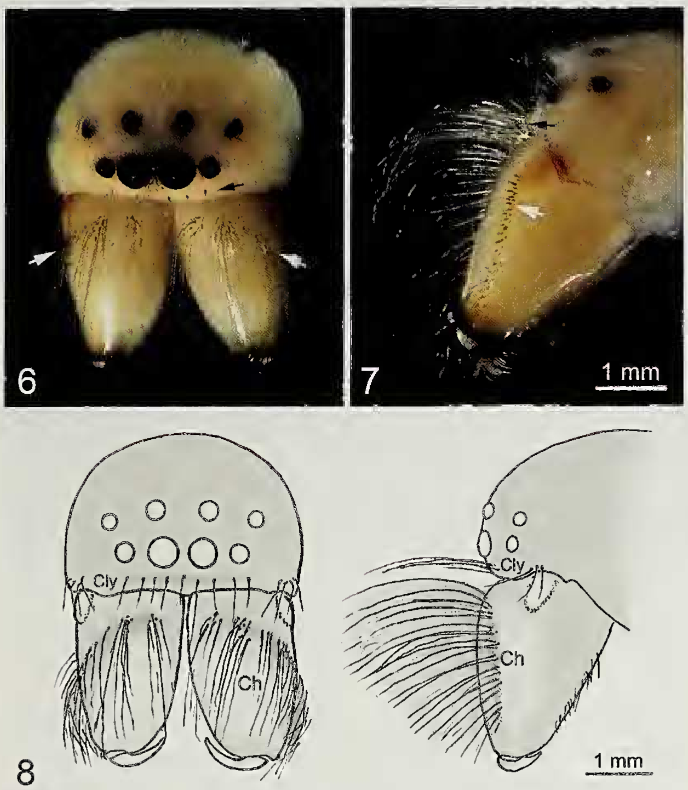
Figures 1–2.—Sand transport in the sparassid *C. rechenbergi*. 1. Spider just coming out of its burrow, carrying a load of sand. 2. Dispersing the dry sand load close to the burrow entrance. Note that the seemingly compact ball of sand disintegrates into single sand grains.

Sand transport in the sparassid *Cebrennus rechenbergi*.—*C. rechenbergi* (body length 2 cm) is a recently discovered desert spider that is renowned for a rapid wheeling locomotion that is used when disturbed or threatened (Rast et al. 2015; Rechenberg, unpublished data). When this spider has found a suitable spot for its burrow in a sand dune, it will turn around several times and then push together small amounts of sand with the pedipalps. A little heap of sand is thus formed that needs to be carried away (Figs. 1, 2). However, this poses a problem because the sand is absolutely dry and the sand grains do not stick together. How can the spider turn the loose sand grains into a "ball" that will not fall apart during transport? A closer look at the pedipalps and chelicerae suggests an answer: long, curved bristles extending 2 mm from the dorsal and ventral sides of the pedipalps and from the frontal side of the chelicerae form a basket-like structure (Fig. 3). In particular, a bristle row on the femur of the palp overlaps a ventral bristle row of the tibia (Figs. 4, 5), thus forming a fine meshwork that is narrow enough to hold tightly the relatively large sand grains (0.3–0.6 mm). Often these long bristles also bear thousands of small surface rugosities along the hair shaft (Foelix et al. 2015), which probably enhance friction with the sand grains and thus ensure a better grip (Duncan et al. 2007). The long bristles on the pedipalps represent the lower and the lateral walls of a carrying basket, but there are similar bristles on the chelicerae and the clypeus forming an additional, inner basket (Figs. 6–8). The few bristles on the clypeus stick out horizontally (Figs. 7, 8) and can be considered as the "roof" of the carrying basket. The many long bristles on the chelicerae are arranged in three clusters of 5, 10 and 30 bristles respectively; together they form an arc that begins medially and continues downward to the lower lateral margins of the basal segments of the chelicerae (Figs. 6, 8). The spider scoops up the loose sand at the bottom of a developing tube with its pedipalps, then turns around and carries the sand load to the entrance and flicks it away. Video recordings show clearly how the "ball" of sand disintegrates immediately into single sand grains (Fig. 2), which proves that the sand grains are completely dry. The diameter of such a sand "ball" measures about 6 mm; its volume can thus be calculated as 0.1 ml. Since the average burrow of *C. rechenbergi* (2 cm diameter, 25 cm depth, see Fig. 23) has a volume of about 80 ml, this means that the spider has to make 800 runs for the construction of a single tube. This is accomplished at night and is completed in less than two hours.



Figures 3–5.—Pedipalps of *C. rechenbergi*. 3. Dorsal view of a female spider showing long white bristles on chelicerae and palps, which together form a carrying basket (Photo: Bastian Rast). 4. Isolated palp with long bristles on femur and tibia. A few sand grains are pictured on the upper left for size comparison. 5. Femoral bristles (blue) overlap with tibial bristles (red) forming a narrow mesh work (Polarized light microscopy).

Sand transport in the lycosid *Evippomma rechenbergi*.—Although the exact taxonomic position of this wolf spider (Fig. 9) is still under study, the genus *Evippomma* Roewer, 1959 seems fairly certain, as indicated by the typical white scales covering most of the body (Alderweireldt 1992; Figs. 10,



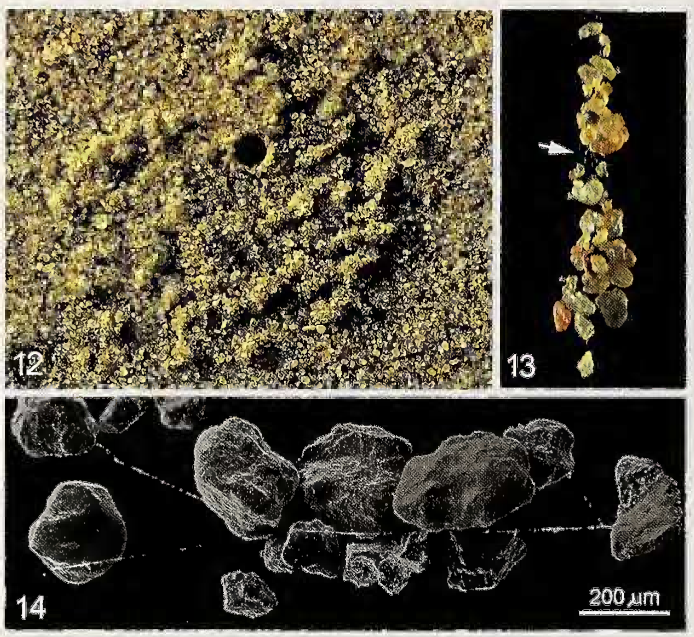
Figures 6–8.—Carrying basket on chelicerae and clypeus. 6. Frontal view of carapace and chelicerae. A single row of bristles is seen on the clypeus (black arrow), while several groups of long bristles form an arc on the anterior side of the chelicerae (white arrows). 7. As Fig. 6, but lateral view. 8. Summarizing drawing of figures 6 and 7. Cly, clypeus; ch, chelicerae.

11). This spider species has now been described in a paper in the same issue of this journal (Bayer et al. 2017).

The medium-sized *E. rechenbergi* (1.5 cm body length; Fig. 9) lives in the same habitat as *C. rechenbergi* and also digs vertical burrows in the dry sand dunes. Therefore, we expected to find the same method of carrying sand as in *C. rechenbergi*. However, the pedipalps of *E. rechenbergi* do not have any long, curved bristles that could serve as a carrying basket. How then can *E. rechenbergi* solve the problem of transporting dry sand? When inspecting the immediate surrounding of its burrow entrance, small, indistinct heaps of sand become evident (Fig. 12). Carefully picking up such heaps with forceps reveals that individual sand grains are connected by fine silk threads (Fig. 13). A direct observation of the initial phases of the burrow construction shows how those silk threads come about: the spider stands above the loose sand and dabs its spinnerets briefly onto the sand grains. Then, after turning around, the front legs grab a sand/silk bundle which is quickly transported upwards and deposited around the burrow entrance. It is quite remarkable that only a few thin silk threads are needed to hold the sand grains together (Fig. 14). The connecting strands are strong enough that even large bundles can be carried away, which is often seen in immature spiders.

Sand transport in the lycosid *Allocosa senex*.—*Allocosa senex* is a medium-sized wolf spider (1–2 cm body length; Fig. 15) that builds vertical tubes in coastal sand dunes of South America (Aisenberg et al. 2007). Although humidity is very high in this environment, the top sand layer is usually quite dry due to the exposure to the blazing sun. Male spiders are larger than females and build deeper burrows (Aisenberg & Peretti 2011; De Simone et al. 2015). The cast of a male's

Figures 9–11.—The tube-dwelling lycosid spider *Evippomma rechenbergi*. 9. Female spider sitting in the sand of the Erg Chebbi desert in Morocco. 10. Portrait of *Evippomma rechenbergi*. Most of the body is covered with white scales. 11. Single scale under high magnification (oil immersion). Note the internal cuticular mesh work.

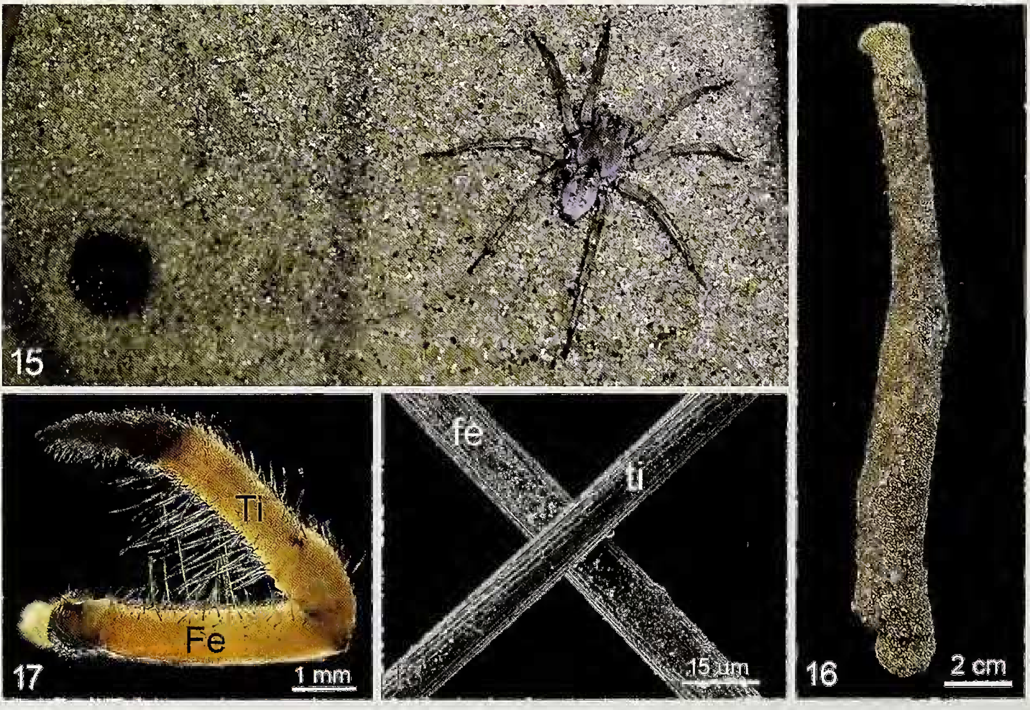


Figures 12–14.—Deposits of dug-out sand grains in *Evippomma rechenbergi*. 12. Burrow entrance with many bundles of sand and silk mixtures. 13. The silk threads become visible (arrow) when those bundles are lifted with forceps. 14. The SEM reveals how few silk lines are used to bind the dry sand grains together.

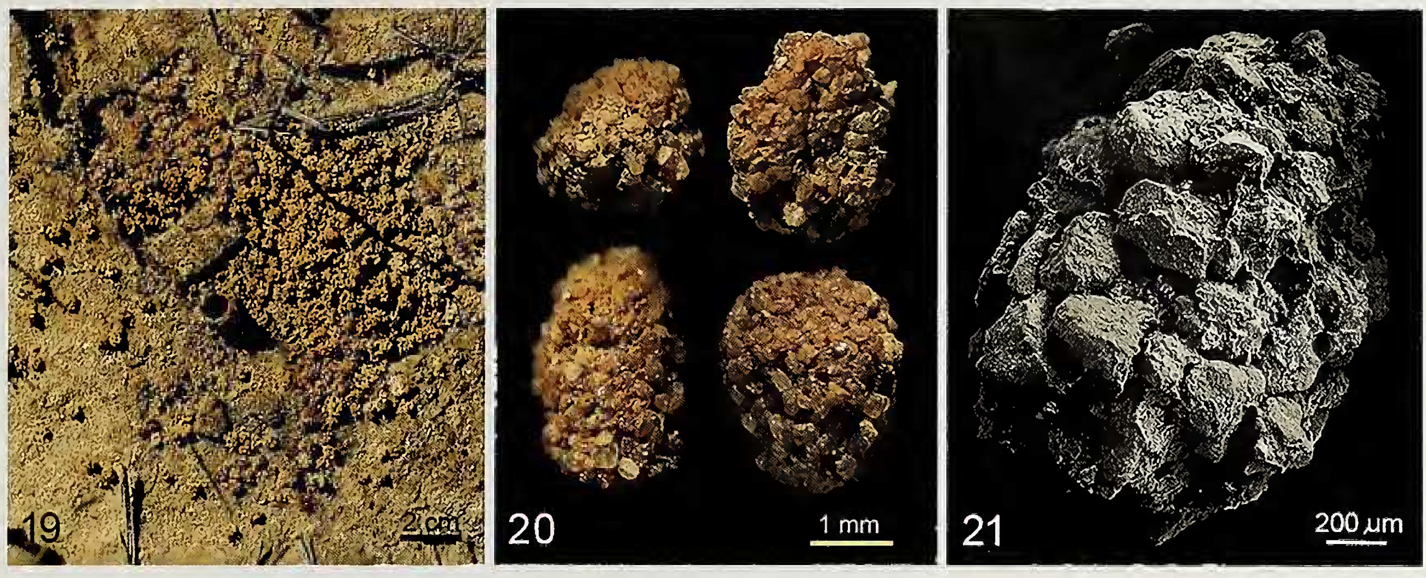
burrow shows a length of approximately 20 cm and a diameter of 1 cm at the entrance, but almost 2 cm at the bottom (Albin et al. 2015; Fig. 16). This may be of advantage when the spider needs to turn inside its tube, for instance while digging and transporting sand or during mating, which takes place inside the male's burrow (Aisenberg et al. 2007). The morphology of the pedipalps is very similar to that described for *C. rechenbergi*, i.e., there are also long bristles (2 mm) on the femur and tibia, which overlap at almost right angles, thus forming a good meshwork for a carrying basket (Figs. 17, 18). There are also a few long bristles present on the basal segments of the chelicerae, but they are not arranged in an arc as in *C. rechenbergi* and thus cannot function as an inner carrying basket. The clypeus does not bear any long bristles.

Video recordings of the beginning of a tube's construction show strong scratching movements of the front legs and then a scooping up of the loose sand with the pedipalps. At least in the initial stages, the spider moves up backward, then swings laterally and drops the sand held between the pedipalps very close to the entrance. There are no heaps of sand deposited as in *E. rechenbergi* and only occasionally are sand grains found interconnected by silk. In these rare cases, silk lines were probably added later outside the burrow entrance, but not initially for the transport of sand grains.

Sand transport in the lycosid *Geolycosa missouriensis*.—This medium-sized wolf spider (body length 1.5–2.2 cm) also builds vertical tubes in sandy or loamy soil, usually with a short elevated burrow entrance ("turret"; Fig. 19). In contrast to the tube-dwelling lycosids described above, *G. missouriensis* is not dealing with strictly dry sand. The surface of those sand grains is often covered with small (clay?) particles which under moist conditions probably cause sand grains to stick together. At least, this is evident in the solid pellets which *G. missouriensis* produces during burrow construction (Fig. 20). Under higher magnification, most sand grains appear to be caked together



Figures 15–18.—The tube-dwelling wolf spider *A. senex*. 15. Female spider close to a male's burrow (Photo: Marcelo Casacuberta). 16. Cast of a burrow, after filling the tube with bee's wax. Note the larger diameter of the tube at the bottom. 17. Isolated pedipalp of a male spider showing long bristles on femur (Fe) and tibia (Ti), forming a carrying basket. 18. Overlapping femoral (fe) and tibial (ti) bristles on the palp. The contact zone shows some abrasion of the femoral bristle.



Figures 19–21.—Solid sand pellets made by the wolf spider *G. missouriensis*. 19. Burrow entrance, slightly raised into a turret, surrounded by hundreds of discarded pellets (Photo: Gail Stratton). 20. Four sand pellets collected around the burrow entrance. 21. SEM-picture of a pellet, showing that sand grains are caked together but lack connecting silk threads.

by some material filling the interspaces (Fig. 21). More important, no silk threads are seen connecting the sand grains. Because we did not have access to live *G. missouriensis* spiders, we do not know exactly how these solid pellets are formed, whether it is the moisture within the tube that causes the sand grains to turn into a compact bolus, or whether the spider adds some secretion from its mouth parts. A close inspection of the pedipalps and chelicerae reveals many short hairs and bristles; however, these are not arranged as a distinct carrying basket as in *C. rechenbergi*. Still, the hairy pedipalps apparently serve well to hold a compact pellet securely, so it can be transported to the burrow entrance. Interestingly, as video-footage by Suter et al. (2011) shows, these pellets are not simply dropped at the entrance, but are either silked into the turret or flicked far away. This is accomplished by a rapid extension (1 m/s) of the first legs that causes the pellets to fly in a long arc over a distance of 10–50 cm (Fig. 22; Suter et al. 2011).

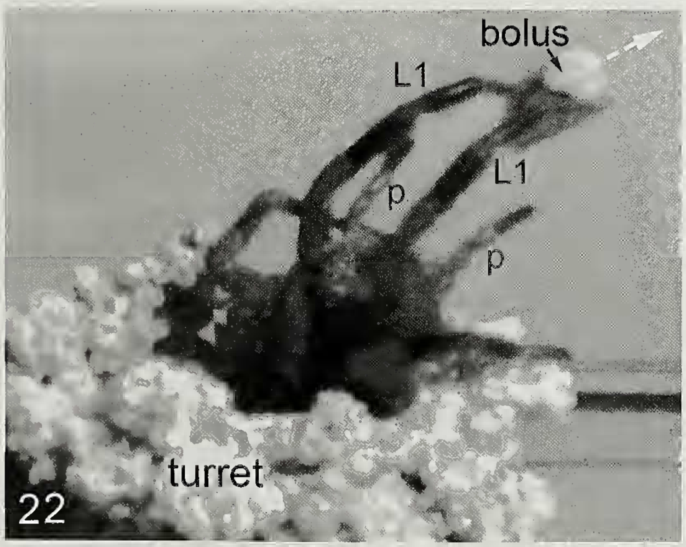
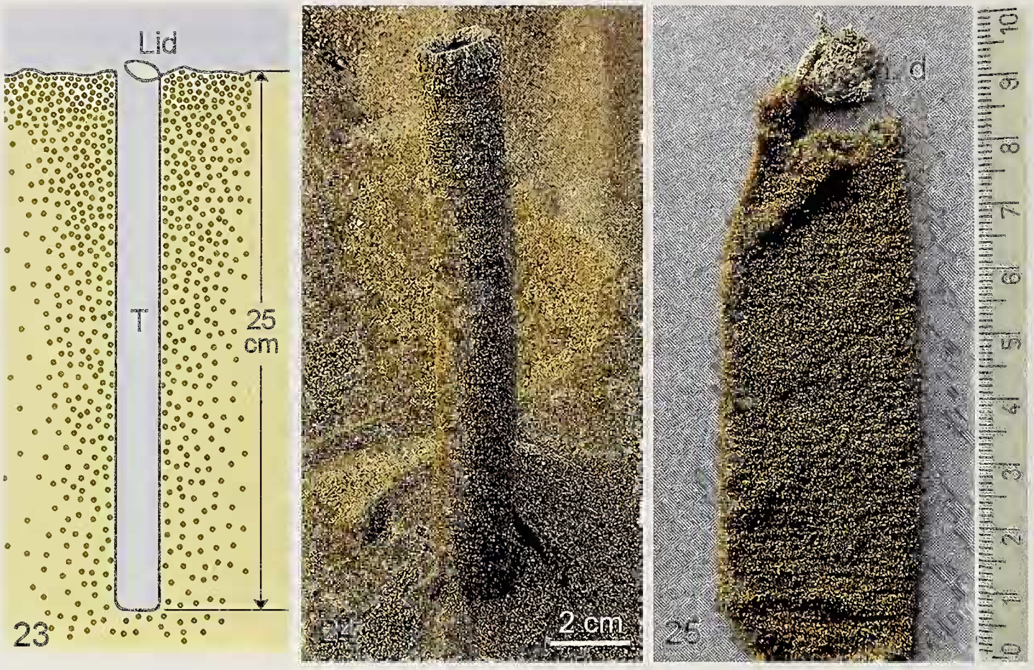


Figure 22.—Single frame from a video-film showing a *G. missouriensis* at the tube entrance (turret) throwing away a sand bolus with the front legs (L1), while the palps (p) have already released their lateral hold (Courtesy of R. Suter).

Vertical burrows and their construction.—Carrying sand away is, of course, only a part in the construction process of a burrow. In the following section, we describe how such a tube is actually built and how it can be turned into a relatively stable structure that will withstand the lateral pressure from the surrounding sand. Because digging a new tube usually takes place at night and mostly below the surface, direct observations are difficult. Only the initial phases can be followed under natural conditions, later phases of the tube construction can sometimes be studied in a terrarium, if the spider happens to dig along a glass wall. We will present a general picture of tube construction based on our observations on *C. rechenbergi* but also point out differences in other tube-dwelling spiders, if known.

Any spider trying to dig a vertical tube into dry sand faces the problem that even the first shallow excavation will not be a cylinder, but inevitably a funnel, due to the loose and sliding sand grains. In order to stop the trickling of sand grains *C. rechenbergi* soon applies a ring of silk threads at the top (the later tube entrance). This ring measures about 2 cm in diameter and reaches only 1–2 mm down. The spider then scoops up a load of dry sand from the bottom of that funnel with its pedipalps and carries it quickly to the outside. After 5 to 6 of such runs, another silken ring will be added below the first one. This pattern of alternating sand transport and silk ring construction will then be repeated for about two hours until the tube has extended to a depth of 20–25 cm (Fig. 23). The consecutive addition of silk rings is still visible in a finished burrow as a fine horizontal striation of the tube wall (Figs. 24, 25). In *C. rechenbergi*, the tube always goes straight down and does not change in diameter; in contrast, in *A. senex*



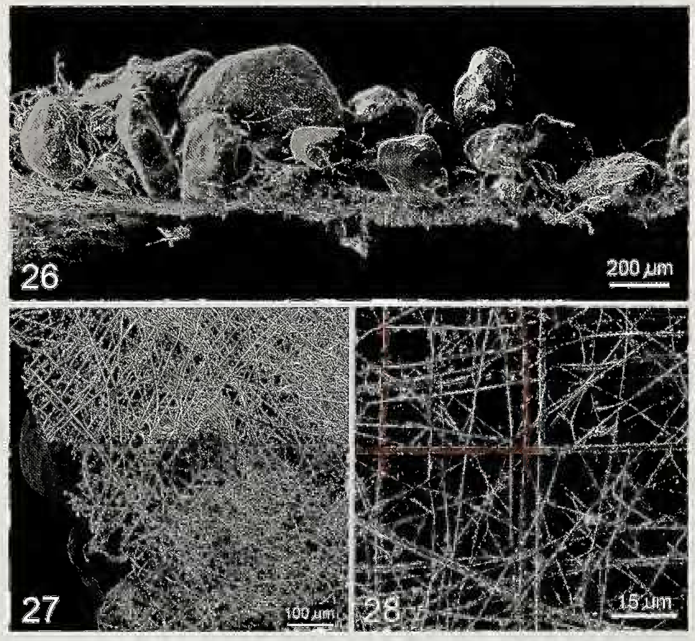
Figures 23–25.—Vertical burrow of the sparassid *C. rechenbergi*. 23. Diagram of the tube (T), which extends about 25 cm into dry sand and is covered by a thin lid. 24. This vertical burrow had been filled with dry sand, before the surrounding sand was carefully removed. This procedure was chosen to provide mechanical stability for the tube. 25. If a tube is excavated normally, as here, it will collapse immediately. Note the horizontal striation of the tube wall, which results from successively adding small silk rings during tube construction.

and *G. missouriensis* the tube may bulge toward the bottom (Fig. 16; Suter et al. 2011; Albin et al. 2015).

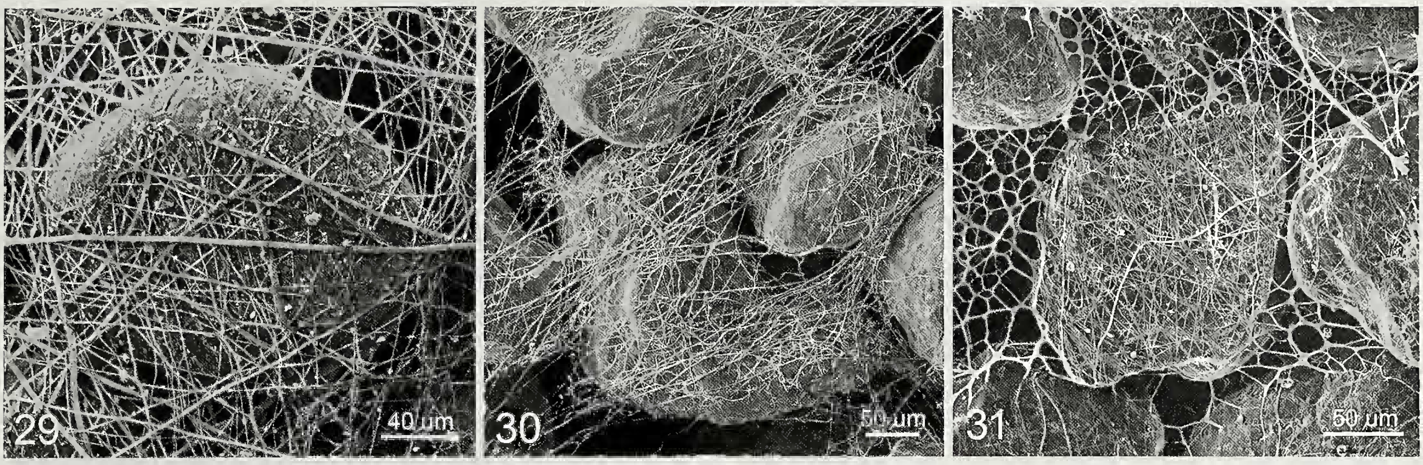
After the vertical tube is completed, *C. rechenbergi* returns to the entrance and begins the construction of a lid (Fig. 23). While the spider faces down into the tube entrance, its hind legs are stretched outside radially and then bent to pull sand grains toward the spinnerets. Long spigots apply many fine threads to weave a small blanket that is studded on top with 1–2 layers of sand grains (Fig. 26). Eventually a circular platelet (a bit less than 2 cm diameter) is formed that is hinged to the rim of the tube opening. This lid closes the burrow effectively, mostly to prevent sand from being blown into the tube, but also to keep enemies like hunting wasps outside (Stanley et al. 2013).

Under the SEM, the outside of the burrow wall shows mostly plain sand grains and only very few silk threads, whereas the inside exhibits many silk lines covering the surface of the sand grains (Figs. 27, 29–31). This silk lining is extremely thin (a few µm) and each underlying sand grain can still be discerned (Fig. 27). The individual silk fibers are also of rather small diameter, ranging from 0.3–3 µm. The thicker threads are often the result of several thinner threads fusing with each other, but that may not always be the case. In *C. rechenbergi*, it is easy to differentiate thinner and thicker threads (Figs. 28, 29), whereas the tube wall in *E. rechenbergi* consists only of thin fibers (Fig. 30). This may explain why the burrow wall is more frail in *E. rechenbergi* than it is in *C. rechenbergi*. It is difficult to say whether the structure of the tube wall has a specific pattern of silk lines or not. The basic design consists of diagonally crisscrossing silk fibers that are overlain by a large meshwork of thick fibers and a less conspicuous meshwork of thin fibers (Fig. 28). When two fibers cross each other, it seems that they are fused at the points of contact (Foelix et al. 2016), probably due to some sticky substance coating the surface of those threads.

When observing *C. rechenbergi* individuals directly while they are weaving near the tube entrances, all six spinnerets



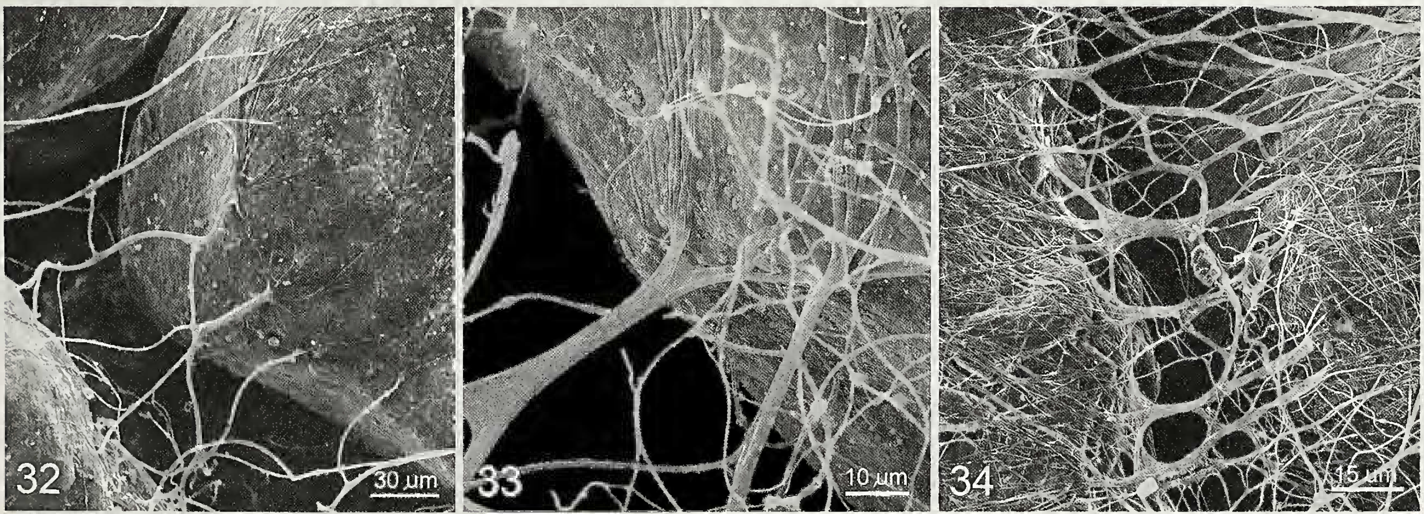
Figures 26–28.—Structure of the burrow wall in *C. rechenbergi*. 26. Cross section of the lid in lateral view. Note that only 1-2 layers of sand grains are attached to the thin silk mat. 27. Inside of the burrow wall showing fine silk threads crossing several sand grains. 28. A high magnification of the silk lining reveals a mesh of thick fibers (marked in red) overlying a fine mesh of thin fibers (in blue).



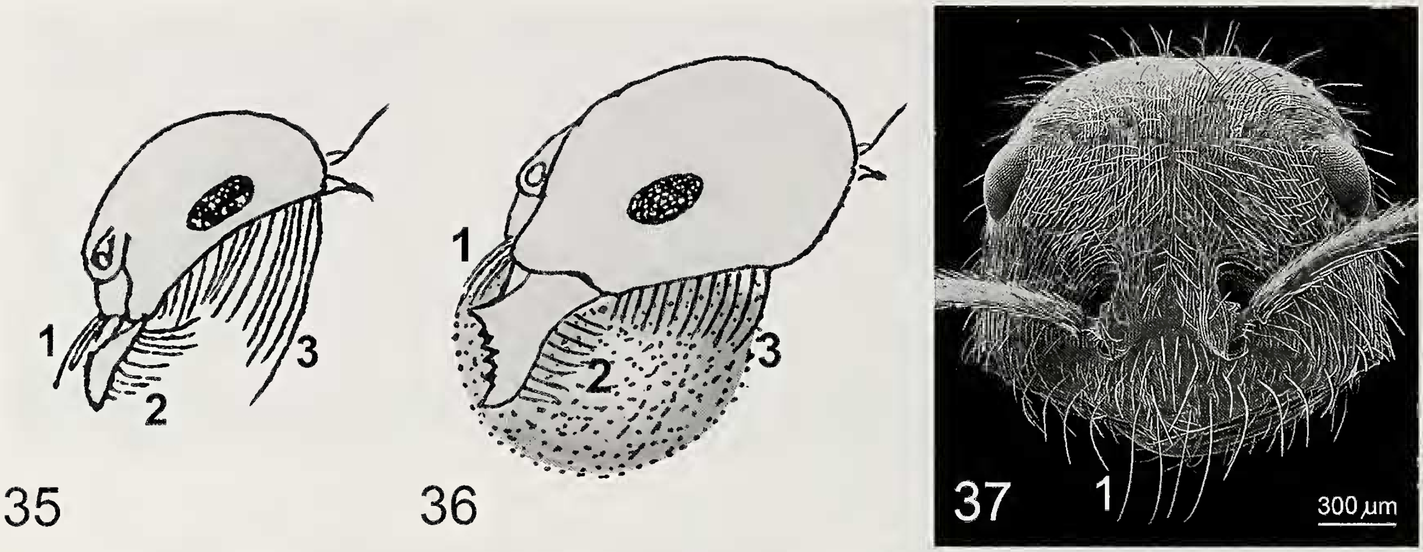
Figures 29–31.—Structure of the inner burrow wall in different spiders. 29. Tube wall of *C. rechenbergi*: thick and thin silk lines crisscross a single sand grain. 30. Tube wall of *Evippomma rechenbergi*: Mostly thin silk lines cover adjacent sand grains. 31. Tube wall of *A. senex*: The coarser webbing in the interspaces between sand grains is probably caused by moisture, which causes the threads to clump together.

seem to be in action. It was not possible, however, to determine which spinnerets or spigots produce which kinds of threads. Using video footage, it is clearly seen that the spinnerets are spread apart and pushed into the loose sand grains; and many fine silk threads seem to be squeezed out actively. It is at this moment that neighboring sand grains become interconnected. Since most spigots are rather long (500 µm), they can easily reach in between sand grains and thus make lateral connections (Figs. 32–34). Typically, many thin silk lines cover the surface of a sand grain but then combine into a thicker "cable" that crosses the gap to the adjacent sand grain (Fig. 33). We assume that these lateral connections are most important for providing a certain stability to the tube. It must be stressed though, that the silken burrows are very delicate, flimsy structures. The tube is most "solid" in *C. rechenbergi* (although it collapses immediately when excavated), and more frail in *E. rechenbergi*, and even more so in *A. senex*. So the question remains how any of these silken tubes can be stable enough to withstand the lateral pressure from the surrounding sand, and how a spider can climb up and down such a delicate tube wall.

Some experiments with Moroccan desert sand probably provide the right answer: an aluminum rod (15 mm diameter) was covered with thin (10 µm) household foil and then gently pushed vertically into the dry sand to a depth of 20 cm. When this rod was carefully pulled out, the remaining foil soon became compressed due to the lateral pressure of the surrounding sand. In a second experiment, a diluted solution of wallpaper glue was thinly brushed onto the outer surface of the foil before the rod was pushed into the soil. After several hours the glue had hardened and when the rod was now withdrawn, the tube (foil) was perfectly stable. Even when the surrounding sand was removed, the foil tube stood free as a vertical cylinder (compare Fig. 24), only covered by a single layer of sand grains on its surface. This means that the mechanical stability of the tube is not due to the foil but to the interconnected sand grains around the tube (similar to the stones in a vault). By analogy, we conclude that the silk tube



Figures 32–34.—Silk fibers connecting neighboring sand grains arise from very fine threads on the surface of a sand grain, which then coalesce into thicker fiber bundles. 32. Tube wall of *C. rechenbergi*. 33. Same as in Fig. 25, but in higher magnification (Photo: A. C. Joel). 34. Tube wall of *A. senex*.



Figures 35–37.—Sand carrying baskets (psammophores) in African desert ants. 35. The harvester ant *Messor caviceps* (Forel, 1902) bears long bristles on the clypeus (1), mandibles (2) and inferior side of its head (3), which together form a basket. 36. *Messor arenarius* (Fabricius, 1787), carrying a pellet of moist sand (after Santschi 1909). 37. Portrait of the Namibian desert ant *Ocymyrmex robustior* (Stitz, 1923) showing the clypeal bristles (1) of its psammophore. Figures 35 and 36 modified after Santschi (1909).

of sand-dwelling spiders likewise owes its stability to the continuously connected sand grains on the outside of the tube, but not to the silk tube itself.

DISCUSSION

Our study of how sand-dwelling spiders can transport sand during burrow construction has yielded several interesting results: (1) Some species (*C. rechenbergi*, *A. senex*) developed long curved bristles on the pedipalps and chelicerae which together act as a carrying basket for dry sand. (2) Another species (*E. rechenbergi*) lacks such a basket but uses silk threads to connect sand grains before transporting the resulting sand/silk bundles. (3) Still another species (*G. missouriensis*) produces solid sand pellets, probably caked together by moisture, that are flung away from the burrow entrance (Emerton 1912; Suter et al. 2011). Thus, different methods apparently evolved in different spiders, even in exactly the same habitat (Erg Chebbi dunes, Morocco) and even within the same family (Lycosidae). It is remarkable, that on one hand the same method of sand transport (i.e., connecting sand grains with silk lines) evolved independently in sparassids and lycosids and, on the other hand, three kinds of sand transport developed within the lycosids.

There are few descriptions of other sand-dwelling spiders in the literature. The sparassids *Cebrennus villosus* (Jézéquel & Junqua, 1966) and *May bruno* Jäger & Krehenwinkel, 2015 seem to use a "sand basket" (Jäger 2000, 2014; Jäger & Krehenwinkel 2015) very similar to that described above for *C. rechenbergi*. The South American wolf spider *A. senex*, which digs vertical tubes in coastal sand dunes (Aisenberg et al. 2007; Aisenberg & Peretti 2011; De Simone et al. 2015), has a "sand basket" like *C. rechenbergi*, yet less developed (cheliceral bristles are reduced). In contrast, the large sparassid species *Cerbalus* Simon, 1897, which also live in tubes in sand deserts, lack such a carrying basket, but carry sand/silk bundles to the outside (Henschel 1998; Rechenberg, unpublished data).

It should be mentioned that very similar "sand baskets" (psammophores) are known from certain sand-digging insects, e.g., in ants (Wheeler 1907; Santschi 1909) and in wasps (Evans & West-Eberhard 1970). Initially, Wheeler had suggested that the long curved bristles on the ant's mouthparts would serve to transport liquid droplets, but then Santschi could prove that they enclosed little sand pellets (Figs. 35–37). In fact, it was Santschi who coined the term *psammophores* for such miniature sand-carrying devices. Whereas Santschi claimed that harvester ants would carry little pellets ("*boulettes*") of moist sand, it was later shown that psammophores work even better when transporting dry sand (Porter & Jorgensen 1990). To our knowledge our study is the first to demonstrate the presence of psammophores in spiders; it seems they are mainly adapted for handling dry sand. A comparison of the psammophore in a spider (Fig. 8) and an ant (Figs. 34, 35) also shows how the long curved bristles occur in similar positions, each group forming one wall of the "sand basket". The interesting point is that such psammophores have evolved independently in insects and in spiders.

After having found a psammophore in *C. rechenbergi*, we expected the same method for carrying dry sand in *E. rechenbergi*, since it lives in the same environment. Surprisingly, however, *E. rechenbergi* does not have any specialized pedipalps ("sand baskets") but uses a completely different technique, namely connecting loose sand with a few silk threads; the resulting sand/silk bundles are then carried to the outside of the burrow. It is amazing how little silk is needed to bind several sand grains together – even under the microscope, it is difficult to detect the few silk lines (Figs. 13, 14). Incidentally, we were not the first to discover this unusual technique: Emerton (1912) gave a detailed description for several species of *Geolycosa*: "*...The digging is done by covering the sand with silk enough to hold the grains together* *and it is then gathered into pellets of convenient size and carried in the mandibles to the mouth of the burrow, where it is thrown outward by the ends of the front feet...*". Unfortunately, after looking at those pellets of *G. missouriensis* with the SEM, we did not find any connecting silk lines (Fig. 21); instead, neighboring sand grains seemed to be caked together by some clay material. For producing rather solid pellets, some moisture seems necessary, but we do not know whether it stems from moisture inside the tube or whether the spider adds some liquid from its mouth parts. Although the latter possibility is a tempting idea, this is not very likely considering that *G. missouriensis* produces over 900 pellets when excavating a single tube (Suter et al. 2011). It remains a bit puzzling though that Emerton described quite correctly the flicking away of the pellets from the burrow entrance (Suter et al. 2011) but claimed that silk threads were holding the sand grains together. Perhaps Emerton studied wolf spiders that were living in a rather dry habitat and eventually those used the same technique as *E. rechenbergi*. The palps of *G. missouriensis* do not have a distinct psammophore, i.e., they lack the long curved bristles. This is understandable because this spider carries the sand as solid pellets rather than loose and dry sand grains.

The construction of the vertical silk tube could only be studied in its initial phases when the spider is still visible close to the surface. Most observations were made on the sparassid *C. rechenbergi* but probably also apply to lycosids. The typical technique starts with a silken ring laid down at the later tube entrance, then carrying out several loads of sand from the bottom of the pit to the surface, followed by another silken ring added at a slightly deeper level. From video-films, we gain the impression that all spinnerets are involved in weaving the silken tube. It is noteworthy that the spigots located terminally on each spinneret can spread like a fan while at the same time squeezing out many fine threads. Most likely this is done by a hydrostatic pressure increase inside the opisthosoma. Due to the considerable length of most spigots (500 μm) they can reach deep between the sand grains and thus make strong lateral connections (Figs. 32–34). Most likely those "bridging threads" are responsible for the mechanical stability of a burrow. The many fine threads making up the inner silken lining must also provide some strength but probably serve more to facilitate the spider's climbing up and down the burrow wall.

It has been pointed out that rather little silk is used for the silken tube (Marshall 1995); and indeed a macroscopic inspection reveals only a very thin silk mat. However, under the SEM even the most delicate silk tubes (Figs. 30, 31) reveal easily a hundred thin threads covering a single sand grain. Whether weaving an entire silken tube is a costly process in terms of energy, is hard to say, because physiological data are lacking. In *C. rechenbergi*, a newly built tube lasts for about one month, before it is replaced; if it is damaged, e.g., due to a sand storm, the spider readily and quickly repairs its tube, or will build a new one. In *G. missouriensis*, it is assumed that the spider stays practically all her life in the same burrow (Wallace 1942) and only maintains and enlarges the tube; the energy expense for silk production thus seems limited.

There are, of course, many other tube-dwelling spiders that have hardly been studied with respect to their tube construction and their method of carrying sand. For example, *Lutica* Marx, 1891 (Zodariidae) living in the coastal sand dunes of California also builds silk-lined tubes (Ramirez 1995), but little is known about its sand transport and tube construction. It would be quite interesting to find out whether it uses the same—or different—methods as *A. senex* inhabiting the sand dunes of the Atlantic coast in South America (Aisenberg & Peretti 2011; De Simone et al. 2015). Even more interesting would be to find out whether environmental factors (e.g., soil humidity) could determine which sand carrying technique is used, or if the same species can employ different methods when faced with different environmental conditions.

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