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**Comportamiento durante la construcción de la tela en *Oecobius concinnus* (Araneae:
Oecobiidae) apoya una relación cercana con arañas con tela orbicular**

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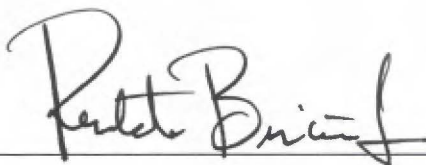
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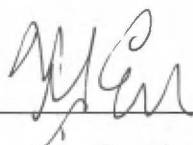
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Resumen. El comportamiento a menudo proporciona información filogenética que puede revelar la historia evolutiva de comportamientos particulares. Recientemente, algunas hipótesis filogenéticas en arañas ubican a Oecobiidae, una familia tradicionalmente vinculada con Hersiliidae, más cerca de Uloboridae. Esta última familia se encuentra dentro del grupo de arañas con tela orbicular, en donde su comportamiento durante la construcción de la tela, ha sido estudiado en detalle. La tela de los oecobiidos ha sido descrita como un refugio conformado por dos capas de seda (la tienda y la alfombra), hilos radiales no pegajosos rodeando el refugio e hilos pegajosos también alrededor del refugio. Sin embargo se desconocen los comportamientos involucrados en la construcción de la tela. El objetivo de este trabajo fue describir los comportamientos durante la construcción de la tela de *Oecobius concinnus* Simon, 1893 (Oecobiidae) y establecer similitudes de los caracteres comportamentales entre los grupos. Si Oecobiidae y Uloboridae están relacionados, espero que *O. concinnus* comparta algunos comportamientos durante la construcción de la tela con Uloboridae y otras arañas con tela orbicular. Para lograr este objetivo, grabé a 60 hembras adultas de *O. concinnus* durante la construcción la tela. A partir de estas grabaciones describí los comportamientos involucrados en la construcción de toda la tela (refugio, hilos radiales e hilos pegajosos). Además determiné algunos patrones en la colocación de los hilos radiales e hilos pegajosos. Encontré 10 comportamientos durante la construcción de la tela que son compartidos entre Oecobiidae y arañas que construyen telas orbiculares. Algunos comportamientos presentes en *O. concinnus* como la secuencia en que construye los componentes de la tela, la colocación de los hilos pegajosos en forma de espiral y la dirección en la que construye la espiral pegajosa, son homologías dentro de las arañas que construyen telas orbiculares. Esta evidencia sugiere la posibilidad de que los comportamientos encontrados en *O. concinnus* sean homólogos con los de arañas de tela orbicular, apoyando las recientes hipótesis filogenéticas de una relación más estrecha entre Oecobiidae y Uloboridae.

Palabras clave: Uloboridae, evolución de telas, comportamiento de peinado, hilo cribelado.

Abstract. The behavior often provides useful phylogenetically informative traits, which could support one particular evolutionary hypothesis over others and enlighten on the evolution of particular behaviors. Recent phylogenetic hypotheses on spider's evolution place Oecobiidae, a family traditionally linked with Hersiliidae, closely related with Uloboridae. Here, we describe the web design and construction behavior in *Oecobius concinnus* Simon, 1893 (Oecobiidae). If Oecobiidae and Uloboridae are related, we expect that *O. concinnus* share some web construction behaviors with Uloboridae and other orb weavers. The web construction sequence, the angle between successive radii, sticky spiral laying orientation, and the combing behavior to produce sticky threads are basically the same than those present in Uloboridae or other orb weavers. This evidence supports a closer relationship of Oecobiidae with Uloboridae, rather than with Hersiliidae as it was previously suggested.

Keywords: Uloboridae, web evolution, combing behavior, cribellate threads

Historically, behavioral traits have often been considered taxonomically uninformative because behaviors are presumably highly variable, and their expression frequently depends on the context, which make traits difficult to homologize (Atz 1970; Wcislo 1989; West-Eberhard 1989; Greene 1999). However, some behavioral traits have proved to be as informative and reliable as morphological and molecular traits (Roe & Simpson 1958; Wenzel 1992; de Queiroz & Wimberger 1993; Agnarsson 2004; Kuntner et al. 2008). For example, in spiders, detailed and precise description of web design and web construction behavior have allowed the use of behavioral traits in taxonomic and phylogenetic studies of different groups (Eberhard 1982; Hormiga et al. 1995; Miller 2007).

In orb webs, building behavior and web design strongly support differences among families (e.g., Araneidae and Tetragnathidae) and subfamilies (e.g. Nephilinae) (Eberhard 1982). Fine behavioral analyses of web construction in uloborids and tetragnathids support monophyly, rather than multiple convergent evolution of orb webs (Eberhard & Barrantes 2015; Eberhard 1972). Similarly, ontogenetic studies of the design of cobwebs (Theridiidae) render some insights that suggest a possible evolutionary path from an orb-web ancestor to a tri-dimensional cobweb (Eberhard et al. 2008a; Barrantes & Eberhard 2010; but see Garrison et al. 2016). Web features were also used as taxonomic and phylogenetic informative characters in other spider groups (Agnarsson 2004; Kuntner et al. 2008; Lopardo et al. 2011; Benjamin & Zschokke 2003; Eberhard et al. 2008b).

Oecobiidae has historically been considered to be related with Hersiliidae, based on prey capture behavior, morphological data and previous molecular data (Coddington & Levi 1991; Hormiga & Griswold 2014; Wheeler et al. 2016; Fernández et al. 2018). Recently, Garrison et al. (2016) placed oecobiids closely related with Uloboridae on the basis of larger

molecular data sets. These phylogenetic hypotheses open a new ground for a more detailed study of web building behavior and web design in oecodiids which could produce further evidence that support the relationship of Oecobiidae with Uloboridae. The lack of information on hersiliids web design and its construction makes difficult to evaluate the relationship between Oecobiidae and Hersiliidae.

The oecobiid's web consists of an oval to circular shelter that includes a tent, and an inner layer (carpet) closer to the ground (Hingston, 1925; Glatz 1967); the spider inhabits the space between the tent and the carpet. The tent is attached at several points to the ground, forming an arched structure between each pair of attachment points that serves the spider to exit and enter to the space covered by the tent. In addition, the web has long radial threads that extend outside of the carpet, and cribellate silk threads surrounding it (Glatz, 1967), both nearly invisible to the naked eye. However, information on web construction and spider's building behavior, which could be important to discern the relationship of Oecobiidae with related spider families is lacking.

We describe here for the first time the web building behavior of *Oecobius concinnus* Simon, 1893, as well as the characteristics of the cribellate and radial threads of the web. We expect that if Oecobiidae is phylogenetically closely related to Uloboridae, the design of the web and the building behavior will share several features with Uloboridae and with other orb weavers.

Materials and Methods

We collected 60 adult female spiders of *O. concinnus* in houses in Turrialba, Cartago province (9°54' N, 83°40' W) and Goicoechea, San José province (9°57' N, 84°3' W) between 2016 and 2018. We placed each spider in a plastic Petri dish (diameter = 8 cm) whose interior had been painted black (Solano et al. in press). We fed spiders with ants (*Crematogaster* sp.) and flies (*Drosophila* sp.) about every three days. We starved each spider for five days prior to recording its web building behavior. We identified the species using the key of Shear (1970), and deposited voucher specimens in the Museo de Zoología of the Universidad de Costa Rica.

Web construction

We used a Sony HDR-SR11 video camera with a 5+ lens to record the web building behavior of 60 adult female spiders from 08:00 to 18:00 h between 2016 and 2017, employing two techniques. First, we placed the spider in an 8 cm diameter Petri dish previously painted. We initiated recording when the spider started to construct its web and finished when the spider remained still for 30 minutes ($n = 20$). For the second approach, we placed the spider in a smaller black-painted Petri dish (diameter = 5.3 cm), which had approximately 2/3 of its inner floor and wall covered with adhesive plastic ($n = 40$). The adhesive plastic restricted the available building space to 1/3 of the inner surface of the Petri dish, since the spider avoided walking and building webs on this material. The space limitation allowed us to encompass the web construction area in the field of view of the video camera. Each spider was recorded continuously for 8 hours. For both recording procedures, we used low light intensity (400 - 600 lux) for 10 spiders in large Petri dishes and 10 spiders in small, and also infra-red illumination (night shot mode) for 10 spiders in large and 30 in small Petri dishes.

Radial thread patterns

To measure angles between successive radial threads in 20 different webs, we drew a “map” of the radial threads on a clear acetate sheet. We fixed the acetate sheet on a computer screen with transparent adhesive tape, played the video of the web construction in slow motion, drew each attachment point of each radial thread, and then connected the attachment points with straight lines. We measured the smaller angle between each pair of successive radii on the “radial thread map” to determine the average angle at which the spider placed successive radii. We also calculated the coefficient of variation of each angle between each pair of successive radii for all webs (e.g., standard deviation of the angle between radius 3 and 4 for all webs / mean angle between radius 3 and 4 for all webs).

We also examined whether spiders showed any preference for laying radii at a particular direction relative to the last radius laid and for using larger empty (without radii) spaces. To do this, we first measured the angle between each pair of successive radial threads for each of the 20 webs, then calculated the mean and two standard deviations above and below the mean angle, and defined it as the “preferred area” or the area the spider had the highest probability to lay the next radius. It corresponded to the area circumscribed between two radii separated by 58° , and equivalent to 16% of the total available area (Fig 1). This is an arbitrary criterion, but in absence of other spiders’ data we considered that a spider laying the majority of threads within this predicted area, indicates a strong preference. For example, to determine which area would be selected by the spider to lay the 7th radius, we considered the 6th radius as the angle 0° , and then overlaid the area with the highest probability for the spider to lay the 7th radius, and recorded whether the spider laid the radius in or out the predicted area (Fig. 1). When the two radii that limit the largest empty space were not within

the preferred area, we still considered it as the largest empty space if at least 10° of the total angle was inside the preferred area (area between r 05 and r 03 in Fig. 1). We did not measure angles nor areas between the first three radial threads to have more precise information on the spider orientation. We also excluded the webs with less than four radial threads ($n=2$) from the analyses.

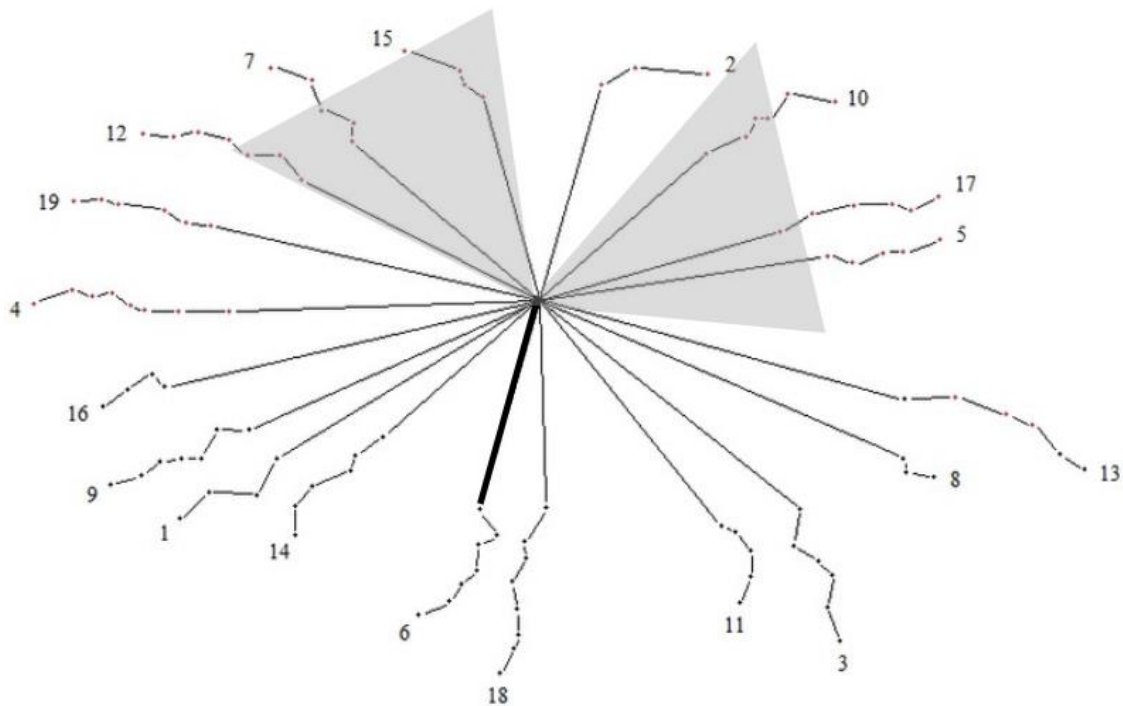


Figure 1. Schematic diagram of radii placement in an *O. concinnus* web. Consecutive numbers the order in which radii were laid. The shaded area indicates the predicted area in which the spider has a greater probability to lay the 7th radius according the angle with the 6th radius.

Description of threads features

We coated the webs with a fine mist of salt solution and/or talcum powder to enhance their contrast and photograph different sections of the web following Solano-Brenes et al. (2018). We also describe the ultrastructure of some web threads using Scanning Electron Microscope (SEM). We collected threads from two tents to see details in SEM using a “U” shape metallic clip with double-sided adhesive tape on the clip arms (4 mm width). We gently placed the clip on the section of the web of interest and cut the threads around the “U” with a hot soldering iron, obtaining a sample of threads between the clip arms without stressing them during their collection. For the radial threads, we used two spider webs built in 5.3 cm Petri dishes. The small size of the dish allowed us to process the entire web in the SEM.

Samples of cribellate and radial threads were placed in a stove at 40°C for 24 hours to dry, and then covered with a 5nm layer of gold at 20 mA for 8 minutes using a sputter coater (EMS 150R S). We photographed them with a Hitachi S-5700N Scanning Electron Microscope (SEM) in the Microscopic Structure Research Center (CIEMic) of the University of Costa Rica.

Data analysis

We tested whether the angle at which the spider place successive radial threads differ from a uniform angle distribution (Ruxton 2017) calculating the circular mean between each successive pair of radii (e.g., mean between 4th and 5th radii of all webs) from “radial thread maps” of all web, with the Rayleigh's R test. We calculated a Rayleigh's test value for each successive pair of radii for all webs, from the pair 1-2, to the pair 24-25, and the general mean angle using the mean of each pair of radii. This statistics test if the spider place successive

radii at any possible direction (uniformly distributed angles) or if the spider has some preference in the direction, relative to the previous laid radius, they place successive radii (e.g., opposite to the previous radius; ca. 180°). The number of radii varied among webs so that the number of angles included in the analyses varied accordingly.

In some occasions the spider moved out the retreat to presumably lay a radius (e.g., r7), but she returned without laying that radius (see results). In these cases, we measured the angle between the last (r 6) and the next radii (r 8) laid after failing to lay the radius r7, and compared this angle with the angle between r6 and r7 of another web in which the spider did not fail to lay the r7. We compared these angles with a paired t-test, expecting that the angles were larger in those webs the spider had failed to lay a radius. We excluded data which were impossible compared with an angle between radii with the same previous radii ($n=4$).

We used a General Linear Model (GLM) with a normal distribution (Christensen 2002) to determine whether the coefficient of variation (CV) of the angle between successive radial threads (as the response variable) was affected by the number of radial threads previously laid in each web (predicted variable). We also tested whether the spider selected the largest empty space available (without radii) within the preferred area (area with highest probability for the spider to lay a radius) to lay the next thread, using a General Linear Mixed Model (Stroup 2012). We used the angle selected as the response variable, the largest angle as the predicted variable, and web identity as random factor to account for measurement of multiple angles in the same web. Then we test if the slope of the model was different of 1 using a t-test. If the spider selected the largest area, the slope will be directly proportional to it. We used the R statistical language for all analyses (R Development Core Team 2008).

Results

The web of *Oecobius concinnus* included a shelter that consisted of a tent that covered a carpet with a central depression, radial threads beyond the edge of the shelter, spiral cribellate threads near the outer ends of the radii, and irregular cribellate threads on the upper surface of the tent itself (Fig. 2). Spiders built the web with the following fixed sequence: the shelter (with the cribellate threads on it), radial threads, and finally the spiral cribellate threads. The radial and the cribellate threads (both on the tent and on the spiral lines) were not placed for all spiders, only 42% ($n = 25$) of the spiders laid cribellate threads or radial threads during the recording time. Detailed descriptions of the components and their construction behavior follow.

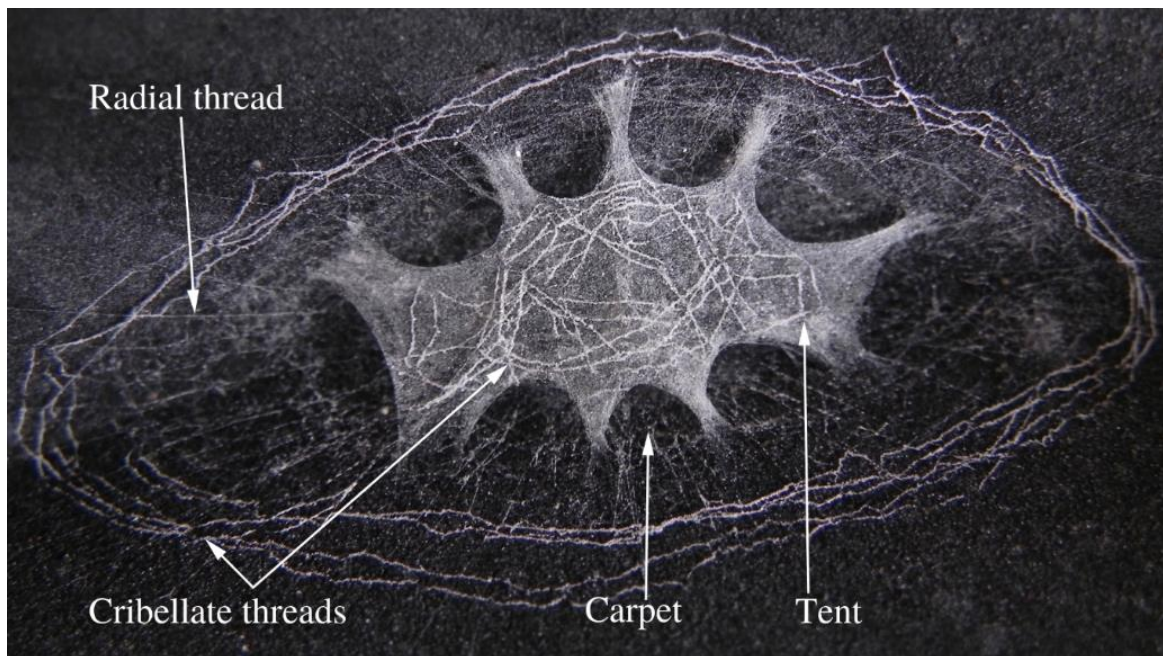


Figure 2. Different sections of *Oecobius concinnus* web

Shelter construction

The carpet is a dense sheet that extends slightly beyond the external border of the tent (Fig. 3), and has a central depression that serve as a retreat for the spider (Fig. 4). The radial threads extend from the edge of the depression to far beyond the carpet (see results of *Radial threads construction*, Fig 4). The external edge of the carpet was lifted a bit above the ground, particularly near the attachments points of the tent to the ground (Fig. 5). When the tent was removed, the external edge of the carpet collapsed.

The tent consisted of a dense sheet that has at least two types of threads with different thickness (Fig. 3). On top of this threads the spider laid cribellate threads (Fig. 2). The tent was attached to the ground at 7 to 10 points, with thick silk pillars that formed an arch structure between contiguous attachment points (Fig. 2, 3, and 5). The tent was not a rigid structure, it collapsed when some pillar were removed.

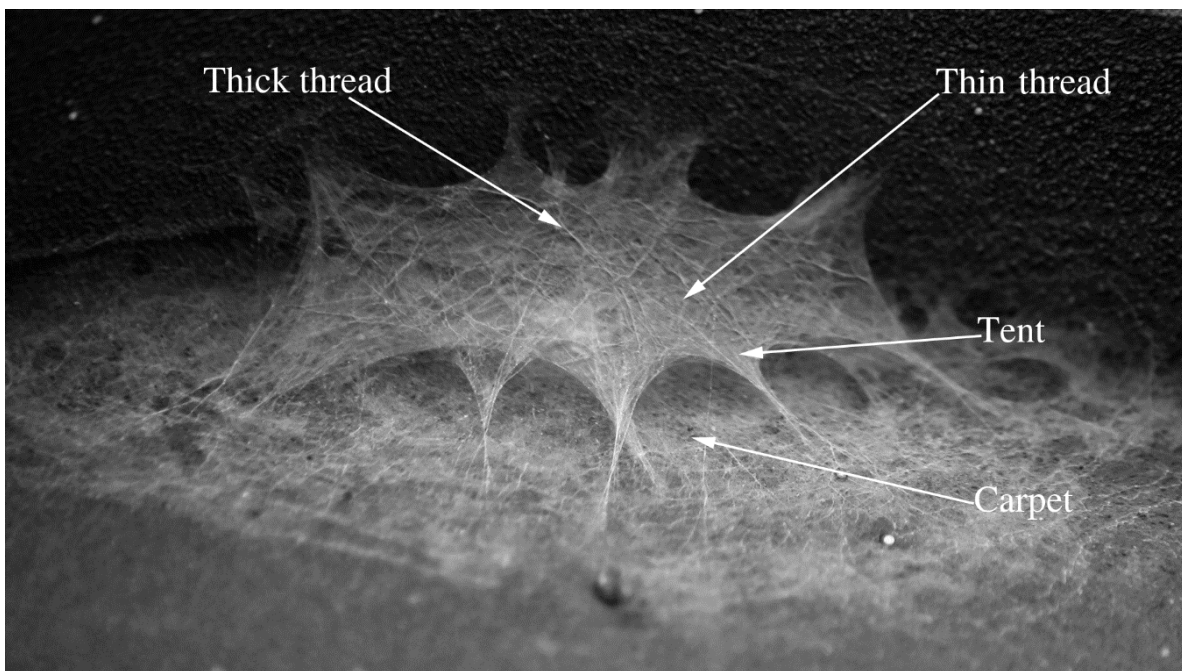


Figure 3. Details of the shelter of *Oecobius concinnus* built at the junction between the floor and the wall of a petri dish.

The spider always started the shelter with the carpet construction. It first laid threads on the floor and the wall of the Petri dish, mainly at the junction between them; it was impossible to observe if the spider lay either individual threads or a band of threads. The spider laid the threads moving its abdomen laterally between its legs IV, attaching the threads to the floor when the abdomen was nearest to each leg. The spider laid the threads while walking without any apparent pattern. The spider did not use any leg to attach threads; it attached the threads with a quick touch of the spinnerets on the ground.

After constructing the carpet for 15 to 180 seconds, the spider began the tent construction by laying some threads between the floor and the wall of the Petri dish which served as a scaffolding to support other tent threads. To lay the scaffolding threads, the spider first attached the thread directly to the ground with its spinnerets and then walked with its abdomen raised above the ground to the next attachment point.

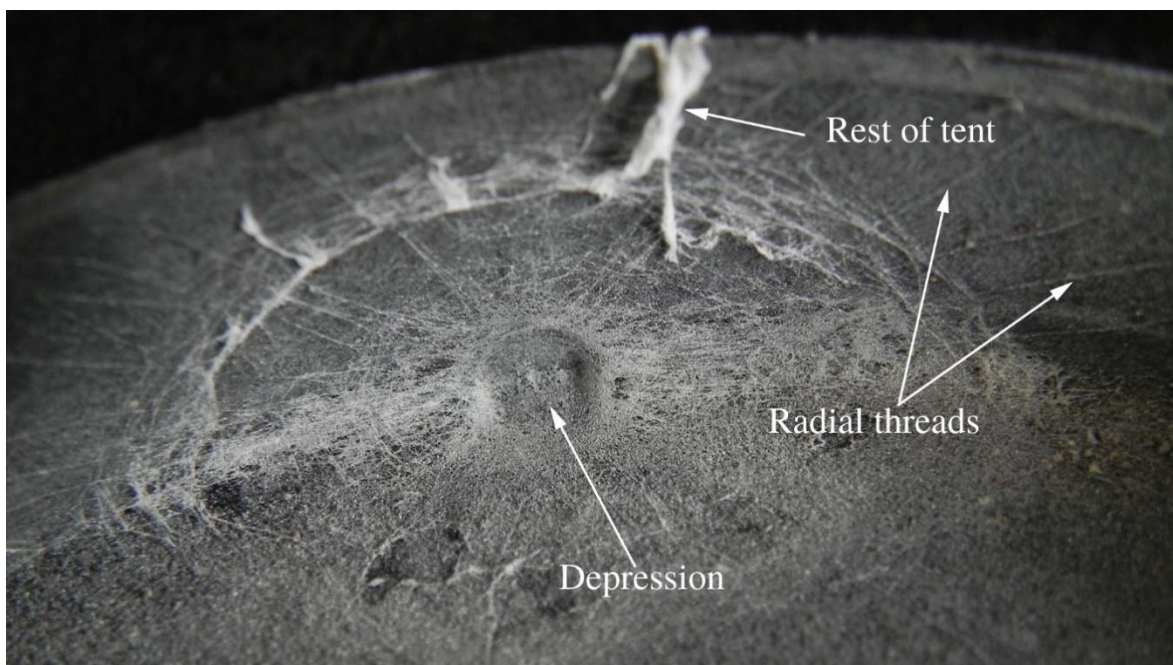


Figure 4. *Oecobius concinnus* carpet after removing the tent

After constructing the scaffolding, the spider began filling spaces with fine threads while walking on either the scaffolding threads or hanging upside down from the scaffolding threads. The spider laid the fine threads by swinging its abdomen from side to side and touching its spinnerets to other lines. The thicker threads on finished tents were likely the scaffolding threads and the thinner were the "fill in" threads (Fig. 3). During tent construction, the spider never used its legs to hold the thread it was attaching or the threads to which it was attaching.

When the tent was nearly finished, the spider laid threads on the floor from the inner of the shelter to the outer of it. First went out in straight lines and returned back by the lateral exits, and then in spiral pattern from the center of the shelter to outward. These extensions of the carpet were attached to the piers of the tent, lifting the external edge of the carpet from the floor (Fig. 5). The spider spent a mean of 7.0 min (SD = 12.0 min, $n = 19$) constructing the shelter. In the nine cases in which the spider laid cribellate threads on the tent. She began either on the external side of the tent ($n = 2$) or inside ($n = 7$) while walking upside down. The cribellate threads on the tent did not follow any apparent pattern. The spider spent 1.8 min (SD = 0.9 min) placing cribellate threads on the tent.

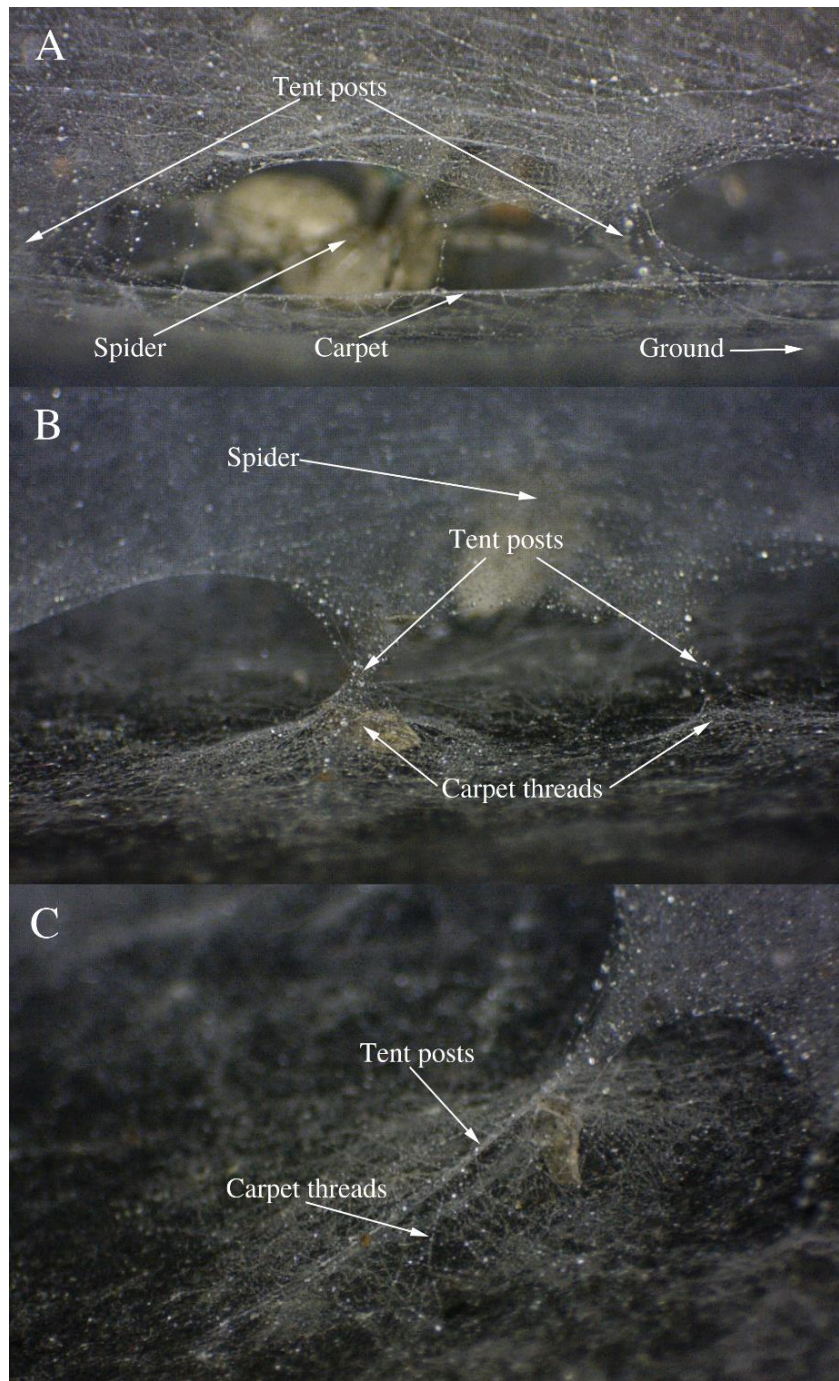


Figure 5. *Oecobius concinnus* shelter with the carpet slightly elevated above the ground. A) It shows a section of the carpet raised above the ground and the distance between the carpet and the ground. B) It shows threads of the carpet attached to the fixation points of the tent. C) Carpet threads on the fixation points of the carpet, elevating the carpet from the ground.

Radial threads construction

The non-adhesive radial lines included a central line with several secondary, short lateral lines (Fig. 6). The spider laid both the radial and the lateral lines in the way out of the shelter. As the spider laid the radial line and short lateral, nearly perpendicular lines that connect the radial line to the ground (Fig. 7). The spider began each radial line at the edge of the central depression of the carpet, and ended it beyond (between 1.6 cm and 3.5 cm, $n=68$) the external edge of the shelter; here the spider usually attached the line to some elevated irregularity of the ground. The spider generally alternated the side at which the lateral lines connect the central line to the ground (Fig. 6). The spider constructed straight radial threads without lateral lines when the substrate lacked elevated irregularities on the ground (e.g., piece of glass). The spider placed between 3 and 39 radial threads during 8.58 min (SD= 13.97, $n = 20$).

The spider began each radial thread by placing her spinnerets directly on the carpet several times while it moved laterally along the edge of the depression. Then, the spider walked out the shelter approximately twice her body length before stopping at approximately regular intervals (*ca.* less than one body length). She moved her abdomen laterally back and forth, while contacting the ground with her spinnerets during the stops. The stops were did only in the way out, never on the way back to the shelter. The spider generally changed slightly the direction after each stop resulting in a zigzag pattern of the radial line. Probably the stops and the movement of the abdomen were to produce the lateral lines, however it was not possible to observe the movement of the spinnerets nor the contact of them on the ground while producing these lateral lines. When the spider made the last attachment of a radial line, she generally returned directly to the shelter walking along the radial thread (94% of times,

$n = 322$); the spider did not lay any thread when she returning to the shelter. Inside the shelter, the spider contacted the carpet with the spinnerets, as making some attachments to before resting in the retreat (carpet depression).



Figure 6. Radial threads with its central line (yellow arrows) and some lateral lines (white arrows).

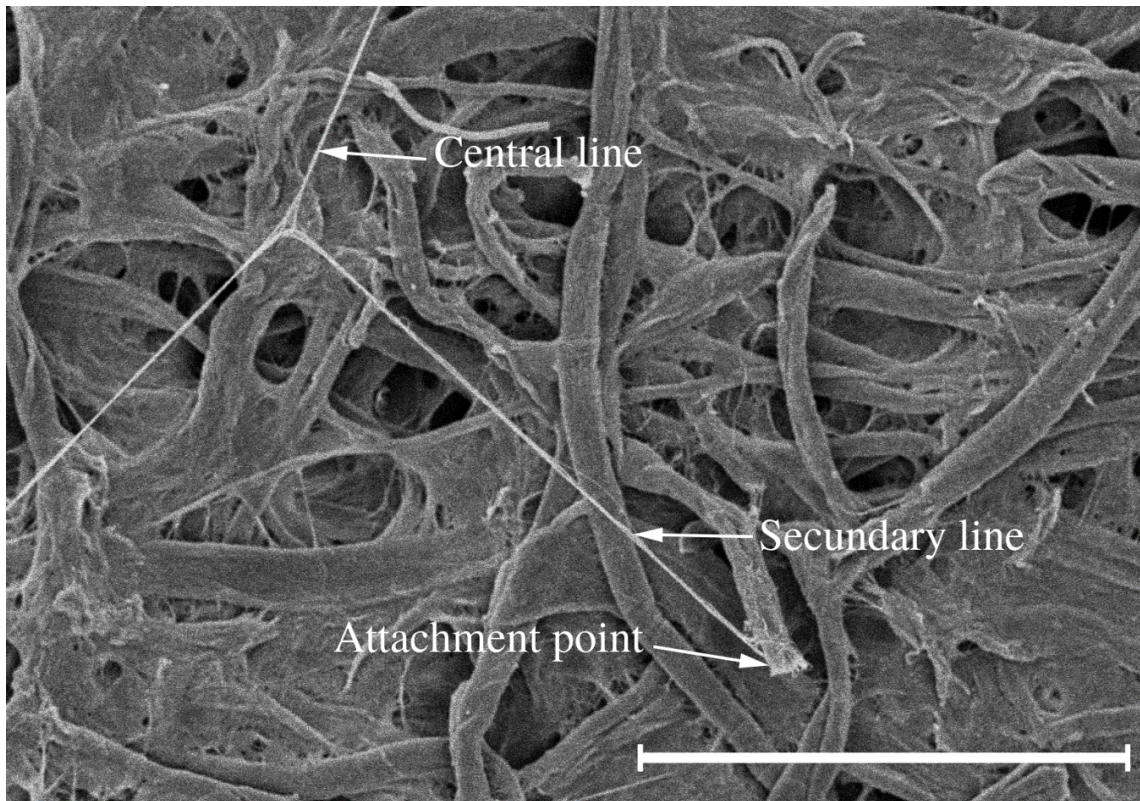


Figure 7. Scanning Electron Microscope image of a radial thread on filter paper. Scale = 200 μm .

Patterns in radial thread placement

The mean angle between successive radii was 124 degrees with a range between 103 and 145 degrees (Table 1). The coefficient of variation between successive radii increased with the number of radii previously laid; though the significance of this pattern is unclear (Slope = 0.007, $t = 2.24$, $df = 22$, $p = 0.036$; Fig. 8). The slope between the largest empty space available and the selected area by the spider was different to 1 ($t = -5.31$, $df = 261$, $p < 0.001$; Fig. 9). It means the spider did not use the largest empty space available in the preferred zone to lay radial threads.

Spiral cribellate threads and combing behavior

After the spider had placed all radial threads, she began laying cribellate threads in circular pattern around the shelter ($n=7$). The spider usually spiraled inward, moving closer to the shelter with each spiral turn; though in a few places a spiral thread was laid on top of a previous one (Fig. 1). The spider did not build the entire spiral continuously, instead she laid two or three turns of cribellate threads and then went inside the shelter. She can added some additional turns during the next six days. The added threads were laid by the spider out of the recording period, so that we did not observe if the spider follow the same outer-inner placement pattern nor if the spider laid some turns on top of those already laid.

Cribellate spirals contacted the radial threads (Fig. 10), but the spider fixed them to the ground rather than to radial threads; we could not determine if piriform attachments were used to fix cribellate threads to the ground. Neither the legs nor the pedipalps seemed to search for the previous spiral loop, so it was unclear what cues the spider use during the placement of cribellate spiral turns. The spider spent 4.26 min ($SD=3.74$) laid 1 or 3 cribellate turns around the tent.

Table 1.

Mean angles and its 95% confidences limits between successive radii, and Rayleigh's R to test the preferred direction. The number between parentheses shows the number of webs used to each pair of angles.

Radial thread pair	Mean	Lower limit	Upper limit	Rayleigh's R	Probability
1-2(20)	119.93	92.9	147	0.79	<0.001
2-3(20)	130.61	105.8	155.5	0.92	<0.001
3-4(19)	129.93	103	156.9	0.86	<0.001
4-5(18)	137.54	109.4	165.7	0.88	<0.001
5-6(17)	139.5	110.7	168.3	0.89	<0.001
6-7(17)	123.82	96.89	150.8	0.89	<0.001
7-8(16)	137.25	104.9	169.6	0.81	<0.001
8-9(16)	135.6	106.1	164	0.9	<0.001
9-10(14)	124.19	91.87	156.5	0.83	<0.001
10-11(13)	112.62	82.09	143.2	0.85	<0.001
11-12(13)	138.19	101.9	174.5	0.81	<0.001
12-13(13)	140.88	107	174.8	0.88	<0.001
13-14(12)	126.39	93.51	159.3	0.89	<0.001
14-15(12)	143.6	105.2	182	0.82	<0.001
15-16(11)	111.34	77.14	145.5	0.83	<0.001
16-17(11)	117.12	60.17	174.1	0.57	0.02
17-18(8)	118.4	60.24	175.8	0.63	0.04
18-19(7)	117.96	73.64	162.3	0.84	0.002
19-20(6)	111.97	65.38	158.6	0.88	0.004
20-21(6)	85.098	28.49	141.7	0.65	0.07
21-22(6)	119.7	75.58	163.8	0.93	0.001
22-23(6)	133.65	85.63	181.7	0.93	0.001
23-24(6)	118.71	54.3	183.1	0.75	0.03
24-25(6)	94.445	50.07	138.8	0.79	0.01
General	123.81	102.9	144.7	288.4	<0.001

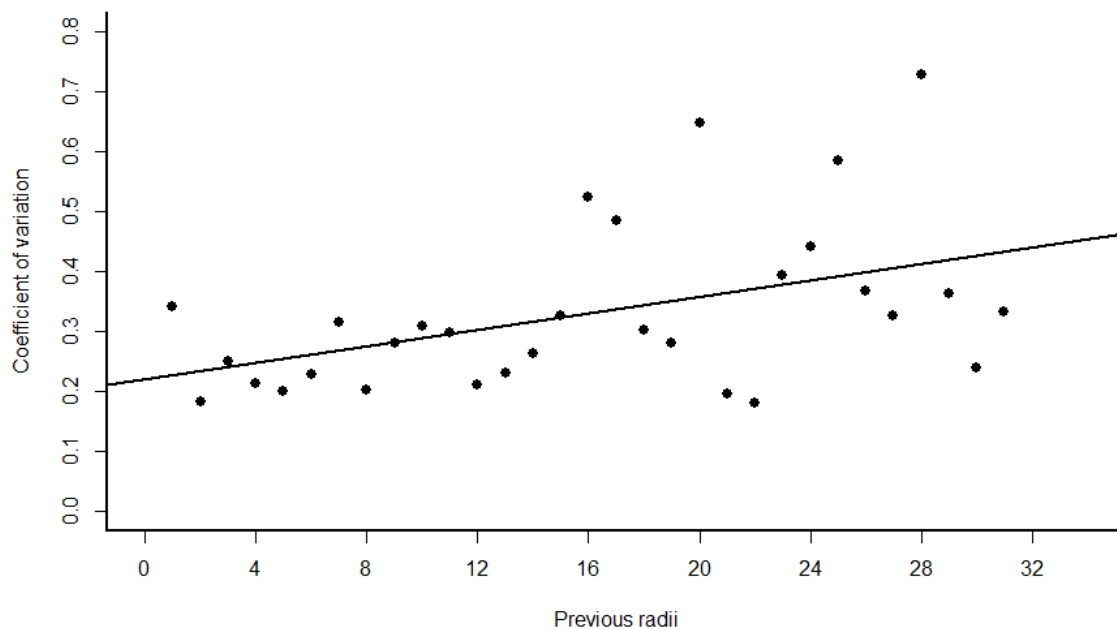


Figure 8. Coefficient of variation between successive angles in oecobiid webs related with the number of radial threads already in place.

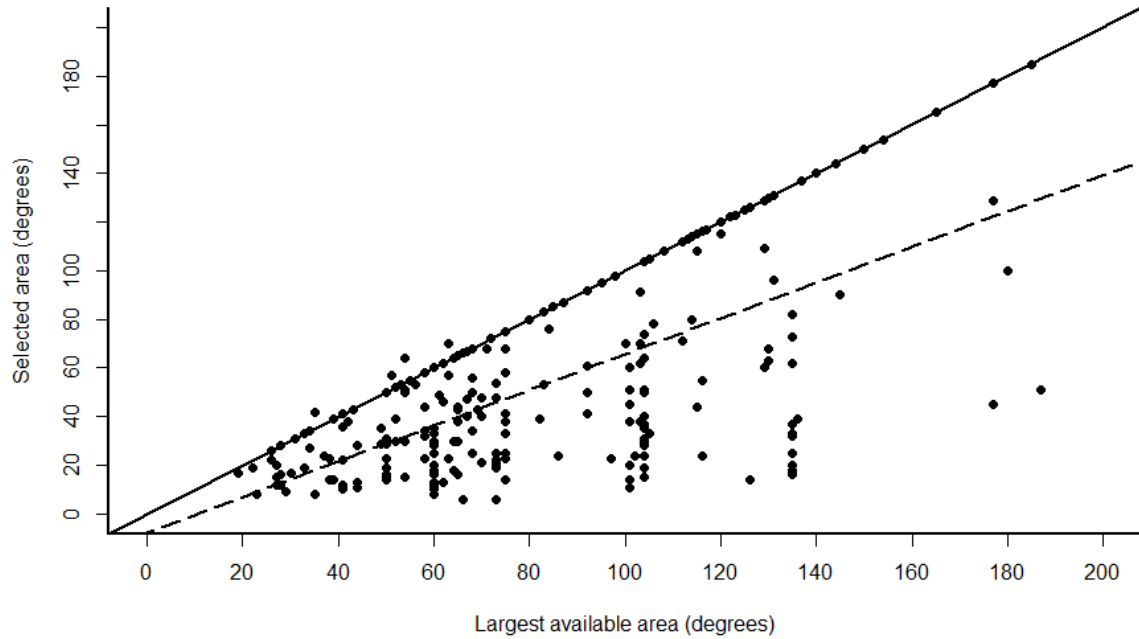


Figure 9. Relation between the largest available area in the most probable zone to put the next radius, and the selected area by the spider laying the next radius. The continuous line is the predicted relationship between the variables if the spider always selects the area to lay the next radius according the largest available area in the preferred zone. The dashed line is the slope of the regression between the two variables.

The cribellate threads had multiple fine cribellate fibrils with a disorderly appearance (not sculpted into consistent, complex forms as in many other families - see Opell 2013), and some thicker, convolute threads immerse into the mass of cribellum fibrils (Fig. 11), similar to the reserve warp lines of Kullmann (1975). The width of the dense cloud of cribellate fibers was variable along the thread. The cribellate treads placed on the tent and those of the spiral were similar in appearance.

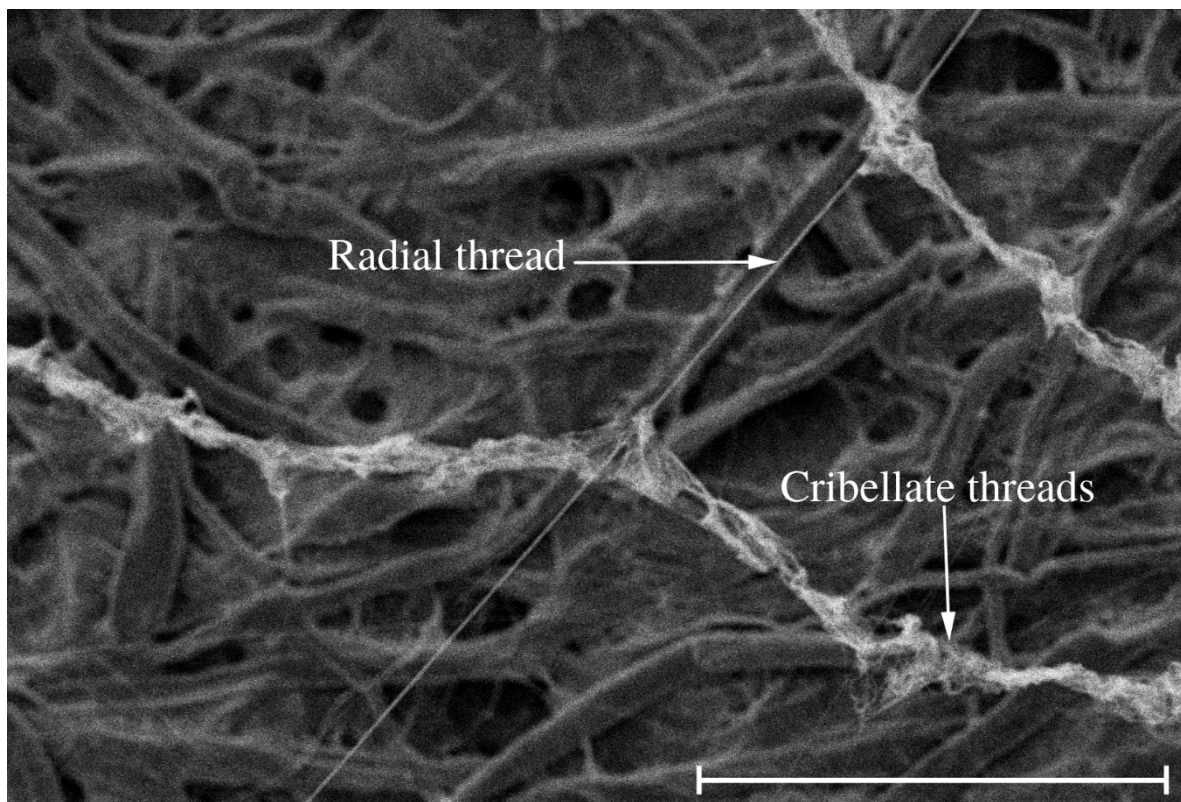


Figure 10. Scanning Electron Microscope image of a section of the cribellate spiral. Scale = 200 μm .

Before combing the cribellate threads, the spider remained quiet for a few seconds. During this time, it was possible to see some abdominal lateral vibration and the posterior lateral spinnerets moving back and forth laterally. To comb the cribellate threads, the spider used one leg IV as the “combing leg” and the other as the “supporting leg” (position 2 in

Eberhard 1988). The tibia and metatarsus of the combing leg crossed underneath the abdomen, and the tarsus of this leg rested on the metatarsus of the supporting leg. The angle between the femur and the tibia of the supporting leg changed of near 90 degrees to more obtuse angles when the legs moved posteriorly, but the angle between the tibia and the metatarsus (110 degrees approximately) did not seem to change with the legs movements. During the combing, the spider moved both legs simultaneously anteriorly and posteriorly as the calamistrum combed out cribellate silk.

The spider could either remain still or walk while combing. After each attachment the spider walked forward a distance as long as nearly its body size. She then stopped for a few seconds to produce additional cribellar threads, spread laterally the posterior lateral spinnerets and then bent the distal extreme of its abdomen, presumably to attach the threads to the ground. During the fixation of cribellate threads, the legs IV did not contact the cribellate threads. After each attachment, the spider commonly shifted her legs IV: the supporting leg became the combing leg and vice versa.

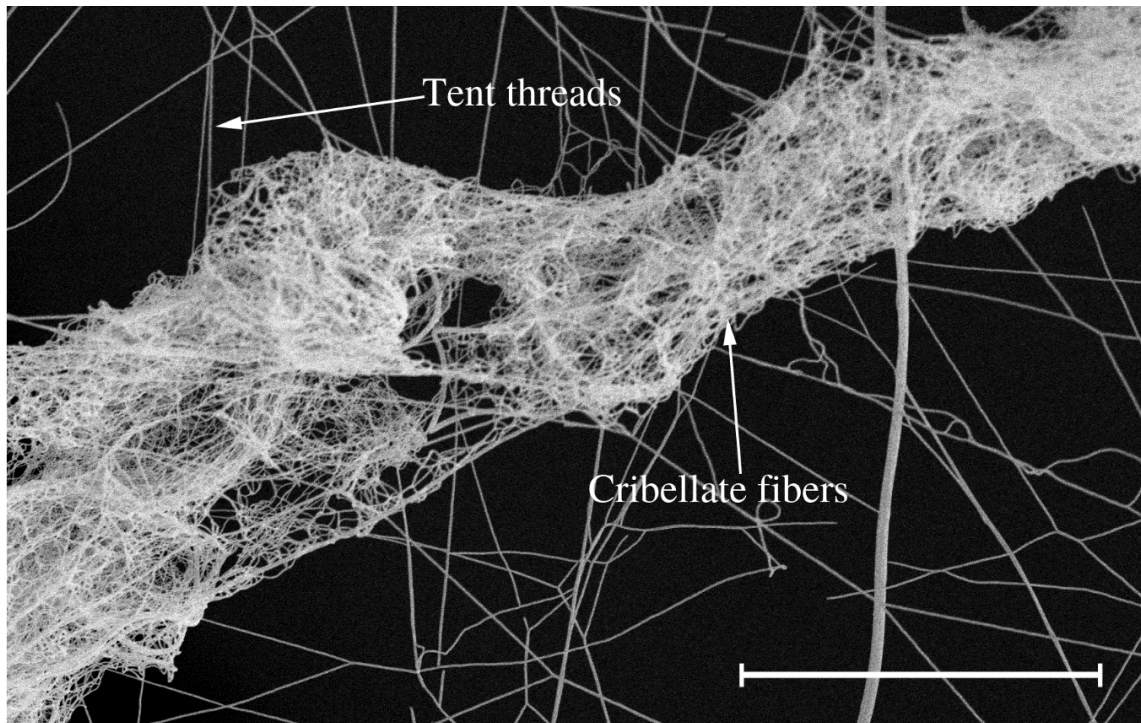


Figure 11. Scanning Electron Microscope image of a cribellate thread laid by the spider on the tent of *Oecobius concinnus*. Scale = 20 μm .

Discussion

Web design and its construction behavior have proven to be phylogenetically informative and have often been used to provide support to spider phylogenetic hypotheses (Agnarsson 2004; Eberhard et al. 2008b). This study showed that the design and web construction of *O. concinnus* have several similarities with those of Uloboridae and other orb weavers (Table 2), supporting a close relationship between Uloboridae and Oecobiidae (Garrison et al. 2016).

During the spiral loops placement, *Oecobius* can walk on the substrate without following any particular line. However the collocation of each thread in an aerial web requires previous lines walking along them (Witt & Reed 1965; Coddington 1986; Zschokke 2000b). Despite the fact that construction of *Oecobius* spiders is not limited in the same way as that aerial orb weavers, the web construction of both *O. concinnus* and orb weavers follow the sequence: first the radii colocation and then the adhesive spiral. This sequence is a character shared by any orb weaver (with some variations) and its presence during the web construction in *O. concinnus* cannot be explain by construction constraints (Coddington 1986).

Table 2.

List of behaviors recorded during web construction of *Oecobius concinnus* shared with orb weavers.

Behavior	Orb weavers	Reference	Homology
Radii placement prior to sticky spiral	Yes	Eberhard 1982	Probably yes
Sticky lines in spiral pattern	Yes	Eberhard 1982	Probably yes
Sticky spiral begins at outer edge, working gradually inward	Yes	Eberhard 1982	Probably yes
Radial lines	Yes	Eberhard 1990	Probably not
Successive radii nearly opposite	In Araneidae	Dougdale 1969	Probably not
Alternate “hub” with radii construction	In <i>Nephila</i> and Uloboridae	Eberhard 1982	Probably not
Interruptions during sticky spiral colocation	In Uloboridae	Eberhard 1972	Probably not
Sticky spiral not attach to each radius crossed	In Uloboridae	Eberhard 1972	Probably not

How the spider place the cribellate threads on the web varied among family spiders (Eberhard 1972, 1987, Lopardo & Ramirez 2007). However only in Deinopoidea and Oecobiidae, the cribellate threads are placed in a spiral pattern. On other hand, *O. concinnus* places the sticky spiral turns from the outer to the inner section of the web as any orb weaver (Eberhard 1982). The placement of the sticky lines of the web of *Oecobius* was not constrained in the same way as in aerial orbs, because they did not need radii which attaching their sticky lines, as occurs in an aerial web by building in the air (Witt 1965; Coddington 1986; Zschokke 2000b). Thus similarities in both families (the placement of radii before the sticky lines, the colocation of cribellate threads in spiral pattern and the direction (outer to inner) the spider construct the spiral turns), suggest a common ancestry rather than an independent evolution of these behaviors (Coddington 1986; Wenzel 1992; de Pinna 1991).

The angle between successive radii laid by *O. concinnus* tended to be obtuse, similar to some araneids (Zschokke 2000a; Hingston 1920; Reed 1969; Dugdale 1969; Coddington 1986), but different from *Uloborus diversus* that which constructs successive radii at acute angles (Eberhard 1972). After the construction of each radial thread *O. concinnus* returned to the shelter where it rested facing the opposite direction of the last radius built. It then rotated slightly its body in either direction (clockwise or anti-clockwise), before beginning the construction of the next radius. *O. concinnus* also laid threads to the “hub” between radii collocations. Uloboridae and *Nephila* alternate the hub construction with radii placement (Eberhard 1982), and *O. concinnus* alternate placement of some threads to the carpet with radii construction.

During the collocation of sticky spiral lines, *O. concinnus* did not attach the cribellate threads to the radii. *U. diversus* attaches the cribellate thread to most, but not all radii (table

2, Eberhard 1972). In *U. diversus* skipping some radii is likely associated with the time required to comb the cribellate threads and the distance the spider walk during combing (Eberhard 1972. In aerial webs is necessary to attach the sticky lines to at least some radii to support the sticky lines and maintain the prey retention function of the web (Eberhard 1990). However, *O. concinnus* can attach the spiral threads to any point of the substrate around the shelter without losing the prey retention function nor the capacity of radii to transmit information on prey location, since radii are in contact with the spiral threads.

We also found that *O. concinnus* placed more loops of sticky threads days after laying the first ones. It also happens in and *U. diversus* and *Zosis geniculata*, which sometimes interrupt several times the construction of the sticky spiral and rest during hours to days of the center of the web and then continue with the construction of the sticky spiral (Eberhard 1972; Eberhard & Barrantes 2015). It might be associated with the energetic cost of the combing behavior (Opell 2013) or with environmental disturbances which stop the web construction.

The combing behavior of *O. concinnus* is shared with Uloboridae and Deinopidae (position 2 in Eberhard 1988). However this behavior is poor of information because it is also share with other phylogenetically less related families (Eberhard 1988). *O. concinnus* also does not attach the cribellate threads onto non-sticky lines (Eberhard 1988). This explains why *O. concinnus* did not hold non-sticky lines during the attachment of cribellate threads and the absence of a central line seen in cribellate threads of other spiders (Joel et al. 2015; Joel et al. 2016; Eberhard 1988).

Contrary to orb weavers, *O. concinnus* did not use their legs to cense other threads during the sticky spiral construction. Such difference is likely a consequence of *O. concinnus*

constructing its web on a continuous substrate rather than in the air. Thereby, it has not been a strong selection on this group of spiders to attach some web threads on specific points (e.g., to other threads) or at certain distance from each other to maintain the functionality of the web, as presumably has occurred in most aerial orb webs (Eberhard 1987).

O. concinnus did not follow any known behavior placing the radial thread in orb weavers (Eberhard 1982). The spiders placed the radial thread while went out but when returned to the shelter she did not double it. The behavior in Uloboridae (F4 in Eberhard 1982) involved the utilization of previous radial threads going out to the edge, and then, double the thread when return back the hub.

Several behaviors indicate that *O. concinnus* did not use cue webs in the shelter to lay additional radial threads. First, the spider did not move the legs in a manner appropriate to sense the angles nor distance between radii, prior the placement of a new radius, which could allow the spider to evaluate the magnitude of available zones. Then, there was not selection for larger available areas to place radial threads, and large areas with few radii remained uncovered, while the spider added new radii to areas with less available area. In contrast, some orb weavers sense the space between adjacent radii at the hub, prior the placement of the following radius (Reed 1969; Eberhard in press). However, the knowledge of the cues orb weaver spiders use to select where to place the next radius is insufficient to make robust comparisons between orb weavers and other groups such as Oecobiidae.

The design of the web of *O. concinnus* was similar in some respects to that described for other Oecobius and *Uroctea durandi* (Hingston 1925; Glatz 1967). All webs have

elevated radial threads that began at the carpet and extended farther of the shelter periphery. In *O. concinnus* elevation is achieved by connecting the radial threads to the ground to elevated projections, and *U. durandi* by making silk posts (Eberhard in press). The cribellate threads have not previously been photographed in Oecobiidae. The cribellate threads in other families, as Uloboridae and Filistatidae, have a regular shape, but in *O. concinnus* those threads do not have a consistent shape along their length (Joel et al. 2015; Joel et al. 2016; Hawthorn & Opell 2003; Opell 2013).

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