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Web construction behavior of *Deinopis* cf. *cylindracea* (Deinopidae: Araneae) and its comparison to webs of other Deinopidae

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Abstract. Deinopid spiders use highly specialized webs composed of a triangular non-sticky scaffolding (NS scaffolding) containing three radii and a modified orbicular web with a rectangular shape to capture prey. Spiders actively manipulate their webs to capture prey. We describe the web construction behavior of *Deinopis* cf. *cylindracea* and compare it and the shape of the sticky silk spiral (SS spiral) of other deinopid species using images in the literature and on the Internet. The web-building behavior in *D.* cf. *cylindracea* follows the pattern previously described for other species of *Deinopis* MacLeay, 1839. Web construction takes approximately 15 min in *D.* cf. *cylindracea* and has two stages: NS scaffolding construction and SS spiral construction. The final structure of the SS spiral has four closely spaced capture cords, five placed further apart, three near the top of the web, and two cords on the handles, making a total of 12. Other species of *Deinopis* have different numbers of cords. Finally, a novel finding is that the youngest spiders do not make webs with sticky lines, but instead use a simplified web to lunge forward, using only their legs to contact prey. To our knowledge, such behavior has never been described in this or any other group.

Key words: Ogre-faced spider, web-building, sticky-silk spiral, Serra do Japi.

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The construction of webs is a successful foraging innovation among spiders (Blamires et al. 2017), and Brazil alone has arguably the world's greatest web-building spider diversity, containing 112 known families of Araneomorphs (World Spider Catalog 2020). The architecture of the webs varies widely among the species, from the classical orbicular webs (Foelix 2011; Santos & Gonzaga 2017; Eberhard 2020), which can be oriented vertically or horizontally relative to the ground, to sheet webs consisting of a three-dimensional mesh with ascending adhesive lines that support the web and capture prey (Benjamin & Zschokke 2002; Harwood & Obrycki 2005). Although spider webs have the primary function of capturing prey, they can perform other functions, including acting as a sensory system, as a space for mating, and even as a barrier against potential predators (Blamires et al. 2017). Despite their abundance in the environment, little is known about the ecological and structural importance of spider webs in ecosystems.

Spiders belonging to the family Deinopidae are predators with a sit-and-wait strategy that use expansive webs as prey capture tools (Robinson & Robinson 1971; Coddington 1986a, b; Coddington & Sobrevila 1987; Getty & Coyle 1996). The Deinopidae is one of the few spider families that can actively manipulate its web in capture behavior. The highly specialized structure of its web has intrigued researchers and has been the focus of many studies since its discovery (Coddington & Sobrevila 1987). The webs are deemed specialized because analysis of the detailed motor patterns used to construct the web shows that they are derived phylogenetically from the classic orb web, an architecture otherwise found only in the Uloboridae and within the superfamily Araneoidea (Coddington 1986a).

A key feature in the expansive web of *D.* cf. *cylindracea* is the sticky-silk spiral (SS spiral). The silk is produced by cribellar spigots and pulled from the cribellum by rhythmic movements of the calamistrum, a row of hairs situated on the metatarsi of the spider's fourth leg (Clyne 1967; Peters 1992). Using a scanning electron microscope and a light microscope to analyze the sticky-silk threads produced by *Asianopis subrufa* (L Koch, 1878) (formerly *Deinopis subrufa*), Peters (1992) described them as being formed from three main structures: (I): two basal fibers, positioned parallel in the center of the threads; (II) two corrugating fibers, which are next to the basal fibers, but different from them, with a wavy structure; (III) fibrils, which are much less visible than the other fibers and fastened to them with a mixture of rectilinear shapes and irregular tangles. The resulting mesh is stretchable and quickly becomes entangled around the body structures of the prey; moreover, it also adheres to the surfaces of the prey body (Peters 1992; Hawthorn & Opell 2002). The SS spiral is built by the addition of several threads, described as cords by Ackerman (1926); the structure of these cords was illustrated by Ackerman (1926) and Coddington & Sobrevila (1987). Details of the construction of the SS spiral were described by Ackerman (1926) for *Menneus camelus* Pocock, 1902.

The family Deinopidae has 67 species and only three genera: *Asianopis* Lin & Li, 2020, with 33 described species in Asia, Africa, New Guinea, Australia and Mexico; *Menneus* Simon, 1876, with 14 species distributed in Africa, Australia and New Caledonia; and *Deinopis* MacLeay, 1839, present in North and South America and the Caribbean, with 20 described species, nine of which are found in Brazil (World Spider Catalog 2023). The so-called ogre-faced or net-casting spiders of the genus *Deinopis* are distinguished by remarkably large posterior median eyes and an unusual prey capture strategy. When the spiders of the genus *Deinopis* detect some prey below their web using visual signals, they perform a stereotypical predation behavior by launching the web toward the prey and wrapping it with the SS spiral, immobilizing it with the application of more web and feeding (Robinson & Robinson 1971; Coddington 1986a). When the prey is flying, the vibration in the air caused by the flight is perceived by the spider, which performs another stereotypical predation behavior: opening the catching web in the air over its cephalothorax (Robinson & Robinson 1971; Coddington & Sobrevila 1987; Getty & Coyle 1996).

The Deinopidae modified orb web is typical of the entire family (Coddington & Kuntner 2012; Basumatary et al. 2020; Lin et al. 2020). Different web characteristics may eventually be found to distinguish the species (e.g., *A. subrufa*, *D. longipes* FO Pickard-Cambridge, 1902, *D. spinosa* Marx, 1889, and *D. amica* Schiapelli & Gerschman, 1957) or to justify intrageneric groupings. The data required for such analyses have not yet been assembled (Eberhard 1990).

The objective of our work was to describe the web-building behavior of *Deinopis* cf. *cylindracea*. In addition, we determined whether the number of cords in the SS spiral of this species followed a fixed pattern and whether other species of Deinopidae have different numbers of cords in the SS spiral or differences in the architecture of the supporting threads that may characterize genera or species. Our hypothesis is that there are fixed characteristics for the family Deinopidae, while for genera and species, there may be specific characteristics, especially of the SS spiral.

METHODS

Study site.—The study was conducted in Serra do Japi, Jundiaí-SP, Brazil, in an area of Montane Semidecidual Seasonal Forest. The Serra do Japi comprises a massif of 354 km^2 located within the municipalities of Jundiaí, Itupeva, Cabreúva, Pirapora do Bom Jesus, and Cajamar, approximately in the vicinity of 23°13′ 53.60″S and 46°52′47.01″W (Leitão-Filho 1992; Leitão-Filho & Morellato 1997) with altitudes ranging from 700 m to 1,300 m and a seasonal climate, with hot, humid summers and cold, dry winters (Pinto 1992). While we were studying the population dynamics of *D.* cf. *cylindracea*, we observed the web construction behavior of these spiders on 16 trunks of the native tree *Plinia cauliflora* (Mart.) Kausel 1956 (Myrtaceae), with diameters of 30–60 cm, which represented the sample units. Each trunk was examined for 15 min during the night, between 19:00 h and 00:30 h. These trees were planted about 40 years ago on a 200-m trail through a clearing in the forest near the Ecological Station at Serra do Japi, at a site called Monte Horebe, and all were very similar in height (see da Ponte et al. 2020).

Web construction.—To verify that the construction pattern of the SS spiral was constant in *D.* cf. *cylindracea*, we photographed the SS spiral of individuals from different instars. For our study, we denoted the stages of spider development as "instars." In the case of *D.* cf *cyclindracea*, the first developmental instar would still be inside the eggsac; it molts once inside the eggsac and leaves it as the second instar. Additionally, to facilitate comparison with other studies, we categorized instars 2 and 3 as "spiderlings." From the second instar of development, we recorded steps in web construction for the following age and sex classes: (1) With simplified webs: 2nd instar = 1 and 3rd instar = 1, $n_{\text{total}} = 2$; and (2) with complete webs: 4th instar, $n = 2$; 5th instar, $n = 4$; 6th instar, $n = 11$; subadults – male, $n = 3$, and female, $n = 10$; and adult female, $n = 13$; $n_{\text{total}} = 43$ observations with the net open, so it was possible to count the number of cords. In some photographs, cornstarch had been sprayed on the web to highlight it (Eberhard 1976). Later, some images had the web highlighted by lines added digitally using the Paint Brush software to facilitate the observation and counting of the cords. The terminology used to describe the web structure follows that used by Coddington & Sobrevila (1987), and the threads of the SS spiral are described by the names of the cords used by Akerman (1926).

For other species of Deinopidae, we searched for articles and Internet images in which the species or genus was identified and counted the number of cords in the SS spiral. These records included an additional 10 species (see Table 1). We only used images in which the cords were clearly distinguishable and the net was open. To ascertain the number of cords in each web accurately, two members of the team (JVN and GAVB) each counted the cords four times (See Fig. S1, online at https://doi.org/10.1636/JoA-S-21-076.s1).

Regarding species identification in photography, the genus *Deinopis* MacLeay, 1839 needs to be revised and the characterization of the species must be done through characters of the male and female genitalia. This review is being done by Jonathan A. Coddington. Despite the difficult identification of the species, we consider the *Deinopis* images from the internet morphospecies to be distinct mainly because they are made in very distant regions. However, images of species identified in scientific articles are more reliable since the specimens are deposited in scientific collections. According to Antonio Domingos Brescovit, a renowned taxonomist, it is impossible to identify the species by photo since they are very similar, and the shapes and body colors are convergent. However, we believe that the species observed in the photos are different species to *D. cylindracea* CL Koch, 1846 due to the different number of cords presented by the species studied here. Our main purpose with these comparisons of the number of cords is to stimulate future taxonomic studies that also involve differences in the characteristics of the webs, especially the capture net.

RESULTS

Web construction.—The web of *Deinopis* cf. *cylindracea* has a triangular, non-sticky scaffolding (NS scaffolding) with a square shaped modified orbicular sticky-silk spiral (SS spiral) inside it. While facing a surface, the spider manipulates the four corners of the SS spiral using its first two pairs of legs to grasp the corners.

The web-building process of *D.* cf. *cylindracea* lasts approximately 15 min and has two stages: the construction of the NS scaffolding (3 min) (Figs. 1, 2) and the construction of the SS spiral (12 min). The construction of the web begins with the spider anchoring one end of the main web thread (the Midline – ML) in an upper support position and the other end of this thread on a lower support, usually the soil or, in our study, the base of a *P. cauliflora* trunk (Fig. 1.1). Then, from the upper part of this main thread, the spider constructs one of

Table 1.—Number of cords of SS spiral in different species of Deinopidae.

Deinopidae species	Number of cords	N	Reference or link
Deinopis cf. *cylindracea*	12	41	Our study
D. longipes	14	1	• https://en.wikipedia.org/wiki/Deinopis_longipes#/media/File:Web-casting_Spider_-_Deinopis_longipes,_Caves_Branch_Jungle_Lodge,_Armenia,_Belize.jpg
D. spinosa	18	2	• Stafstrom & Hebets 2016 • https://www.flickr.com/photos/jmays/36205746125
D. amica	14	2	• https://www.flickr.com/photos/28373786@N05/40052045925 • Laborda et al. 2012
Deinopis sp. 1	10	2	• https://www.flickr.com/photos/andreaskay/22489879698 • https://www.flickr.com/photos/andreaskay/22285460174
Deinopis sp. 2	14	1	• https://www.mindenpictures.com/search/preview/ogre-faced-spider-deinopis-sp-do-not-wait-passively-for-an-insect-to-fall/0_00298203.html
Deinopis sp. 3	14	1	• Getty & Coyle 1996, Costa Rica
Menneus camelus	16	3	• Akerman 1926, South Africa
Menneus sp.	20	1	• https://www.flickr.com/photos/rainforests/21757947320
Asianopis subrufa	22	3	• https://www.alamy.com/stock-photo-female-net-casting-spider-deinopis-subrufa-also-known-as-the-ogre-19677962.html • http://www.oceanwideimages.com/species.asp?s=Deinopis+subrufa Stock Photo: 24T5855-39D • Baum 1937
Asianopis wangi	22	1	• Lin et al. 2020, https://doi.org/10.3897/zookeys.911.38761

the two Frame Lines (FL), attaching proximally to the upper main thread (ML) and distally to the lower support, laterally spaced in relation to the midline (Fig. 1.2). After attaching the FL to the lower support, the spider returns on it to the upper ML, rebuilding the frame line with another thread on the way back. About the middle of this return, the spider attaches another thread that connects one end to the middle of the recently constructed frame line and the other end to the middle of the ML; this is the Upper Radius (Ru) (Fig. 1.3). After that, the spider repeats the process on the other side, making the second Frame Line (FL) (Fig. 1.4) and Ru (Fig. 1.5). By the end of this part, we have the right and left FL and Ru.

The next step is the construction of the Middle Radii simultaneously to the Anchor Thread (AT). After making the Ru, the spider draws a thread from a point on the ML just below the insertion of the Ru, with the other end being attached to the first Frame Line just below the insertion of the Ru, making a horizontal thread (Fig. 1.6). The spider then displays the same behavior of the FL construction and, on the return to the proximal end of this horizontal thread, while reinforcing it, the spider attaches another thread proximally to the middle of this horizontal thread and distally to the lower support, between the insertion of the ML and the FL, making a vertical thread (Fig. 1.7). This vertical thread makes a "T" shape with the horizontal thread previously made. The spider then returns rebuilding this vertical thread and after reaching the horizontal thread, returns to the ML finishing its rebuilding while releasing its tension. This tension release modifies the shape of the horizontal thread initially made and the distal portion of it aligns with the vertical thread making what we call one of the Anchor Threads (AT), while the proximal portion stays connected to the ML and AT, making one of the Middle Radii (Rm). (Fig. 1.8). The spider then does the same thing on the other side and by the end of this part we have the right and left Rm and AT (Fig. 1.9).

The spider then begins the construction of the Lower Radius (Rl) by attaching one end of a thread to the ML below the insertion of the Rm and the other end to AT, just below the insertion of the Rm (Fig. 1.10). After constructing the same thing on the other side, we have the right and left Rl (Fig. 1.11). After construction of the radii, the spider cuts the ML just below the insertion point of the pair of lower radii (Fig. 1.12). It then connects an auxiliary thread, the right and left non-sticky spiral (NSSr and NSSl), with one end in the middle of the upper radius and the other at the ML, below the point where the FLs are projected (Fig. 1.12). After the construction of the NSSr and NSSl, the NS scaffolding was complete (Fig. 1.13), and the spider then began construction of the SS spiral (SS).

The NS scaffolding is built with a front side (as seen in Fig. 1.13) facing the substrate where the spider will hunt. To start the construction of the SS spiral, the spider attaches itself with one leg of the first pair onto the midline at a point below the insertion of the non-sticky spiral (NSS). The other leg of the first pair holds onto the midline or to one of the upper radii, and it can alternate between these attachment points using the first pair of legs. In this position, it hangs so that the web is between the spider and the substrate, its cephalothorax facing up and its abdomen down, with its venter facing the web. Once it arrives at this position, it pulls the part of the ML that contains the connection with the radii to itself, and the web begins to have a certain depth. The web is pulled back like the elastic of a ready-to-fire slingshot.

The construction of the SS spiral then begins (Fig. 3). While the spider maintains its position with the first pair of legs, the second and third pairs manipulate the median and lower radius. The last pair of legs participates in the processing of the cords of the SS spiral, which will be discussed below. The SS spiral is constructed with a continuous cord attached multiple times to Rl and Rm, forming a rectangle. Two handles then attach this rectangular structure to the Ru. To

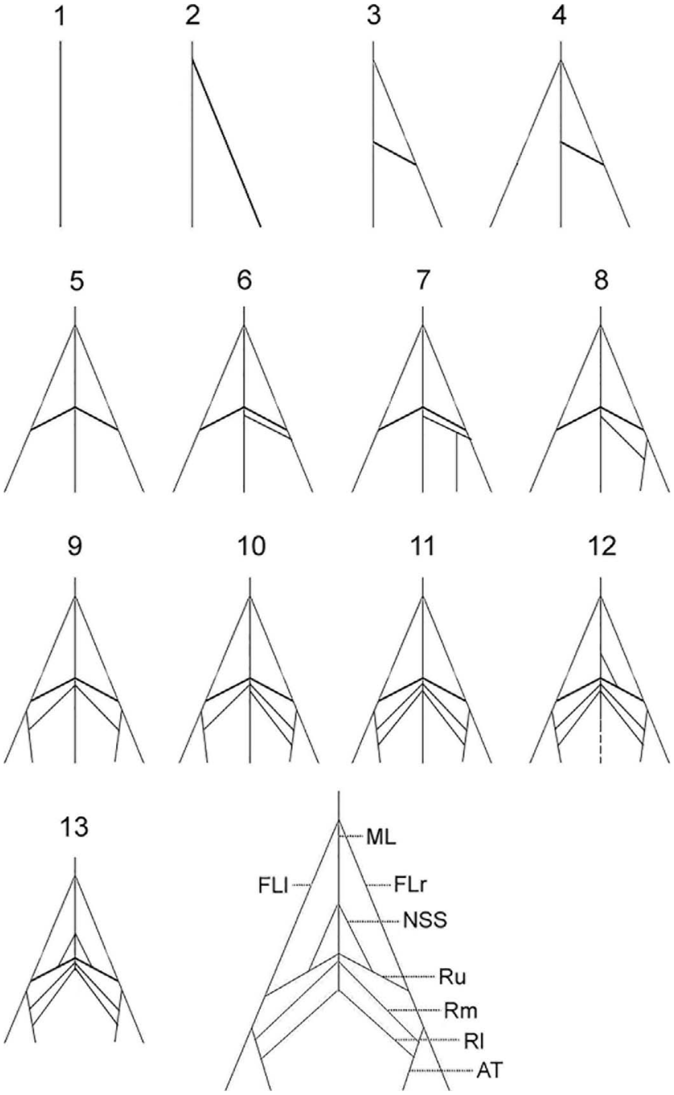

Figure 1.—Scaffolding web construction sequence of *Deinopis* cf. *cylindracea* and its components: Midline (ML), Frame lines (left-FLl; right FLr), Non-sticky spiral (NSS), Upper radius (Ru), Middle radius (Rm), Lower radius (Rl), and Anchor thread (AT).

simplify the descriptions, each thread between the radii is considered a different cord.

The first cord is inserted into the Rm, connecting it to the Rl on the same side (Figs. 3.1, 4.1). The same steps take place on the opposite side of the web (Fig. 4.2). Then, from that point of the lower radius a cord extends that connects it to the median radius just above it. The result is a U-shaped web fixation pattern (Figs. 3.3, 4.3), where the cord is fixed first to the Rm, then to the left side of the Rl, then to the right side of the Rl, and then to the right Rm. The spider then reverses the process, forming a new U-shape above the first one (Fig. 3.4). This procedure is performed a total of four times, with the web gradually being added to in a spaced way above the Rl, but always at the same point in the Rm (Figs. 3.5, 4.4). The same process is repeated five more times, with slightly larger spacing between the insertion points in the Rl (Figs. 4.5, 4.6), and with smaller spacing in the Rm, until a shape close to the final rectangle is reached (Figs. 3.8, 4.7). After nine repetitions (nine cords), the spider constructs two additional cords connecting the web insertion points on the Rm radius (Figs. 3.9, 4.8). As the last step, it builds the final cords, such as the handles binding the rectangular part of the SS spiral to the NS scaffolding at the upper radii, as described next.

From the Rm insertion point on the left side, the spider connects a cord to an insertion point in the Ru on the same side (Figs. 3.10, 4.9). It then returns a cord to the Rm on the same side, forming the first handle, and another cord connecting the points of both Rm, completing the third closing cord of the rectangle. Finally, it attaches a cord at the point of the Rm to the Ru and makes a final cord to create the reverse path, forming the second handle (Figs. 3.11, 4.10). The creation of these handles concludes the construction of the SS spiral (Fig. 5). Before the spider takes the prey-ready posture, the last stage of construction is the disruption of the midline at the point above where it binds to the upper radius (Fig. 3.12). Before this breakage, the spider positions itself with the cephalothorax down and abdomen upwards, still with its venter facing the web (Fig. 4.10). After the breakage, the spider takes the prey-ready posture, holding the end of the broken thread with the fourth pair of legs (the spider is attached to the midline by a thread called Dragline – DL), holding the upper radius with the third pair of legs, the insertion points of the median radius with the second pair, and the insertion points of the lower radius with the first pair (Fig. 4.11).

Finally, the spider retracts its legs to pull back the entire NS scaffolding, forming a near semi-circular shape, as if the scaffolding were the rubber of a ready-to-fire slingshot. The SS spiral can be retracted (Figs. 2, 4.12) or partially distended, grasped by the first two pairs of legs. When a prey animal approaches and passes under the net, the spider launches itself toward the substrate opening its legs, extending the SS spiral and wrapping it over the prey. Upon contact with the prey, the spider reduces the area of the catching web so that the prey becomes entangled ($n = 22$). Some spiders demonstrated the second stereotypical behavior, which is used to catch flying prey. Here, the spider opens the catching web over its cephalothorax ($n = 9$). This behavior could also be instigated by human observers creating vibrations in the air by clearing their throats.

In *D.* cf. *cylindracea*, construction behavior can be observed in all its phases from the 4th instar ($n = 2$). The final structure of the SS spiral shows a pattern of four closely positioned capture cords, five more widely spaced cords, three cords near the top of the net, and two cords on each of the handles ($n = 43$). This net pattern was recorded in two individuals of 4th instar, four of 5th instar, 11 of 6th instar, 10 subadult females, 13 adult females, and three subadult males. The smallest individuals building the full web had a 4-mm body length. After capturing a prey, the spider holds it close to the chelicerae and makes a new SS spiral, repairing the NS scaffolding if necessary ($n = 52$).

The web construction process of the second instar ($n = 1$) and third instar ($n = 1$) is similar to the initial process of construction by the adult; however, they do not complete the process, leaving a "simplified web" with only one main thread divided into two, with no sticky lines. The individuals position

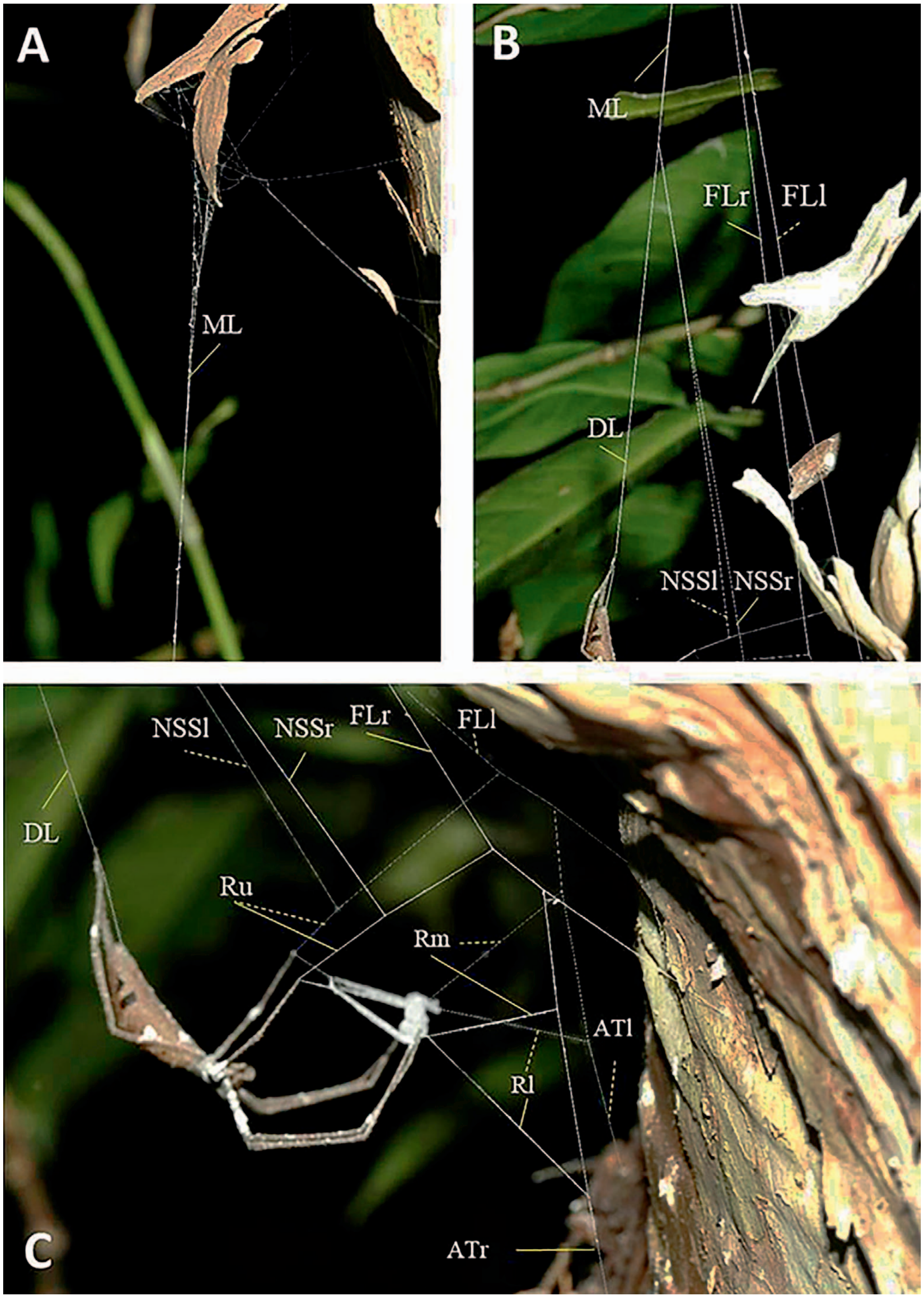

Figure 2.—Side view of the scaffolding web structure of a *D*. cf. *cylindracea* adult female with the nomenclature code for three vertical portions: upper structure (A), middle (B), and inferior (C). Initials: Midline (ML), Frame Line (left – FLl; right – FLr), Dragline (DL), Non-Sticky Spiral (left – NSSl; right – NSSr), Upper Radius (Ru), Middle Radius (Rm), Lower Radius (Rl), Anchor Thread (AT; left – ATl; right – ATr).

themselves with the abdomen facing the main thread, holding it with the two pairs of hind legs. The cephalothorax faces the side where the main thread forks so that the right legs of the first two pairs of legs hold one of the threads, and those on the left hold the other thread of this fork (Fig. 6). The hind legs then pull the main thread, and when a mosquito approaches to land on the web, near the front leg, the spider releases the back legs, launching itself forward and capturing the mosquito with one of the front leg pairs.

We did not document any adult males of *Deinopis* cf. *cylindracea* with a web, we only saw support threads and a sperm web in additional threads next to the female's web. The

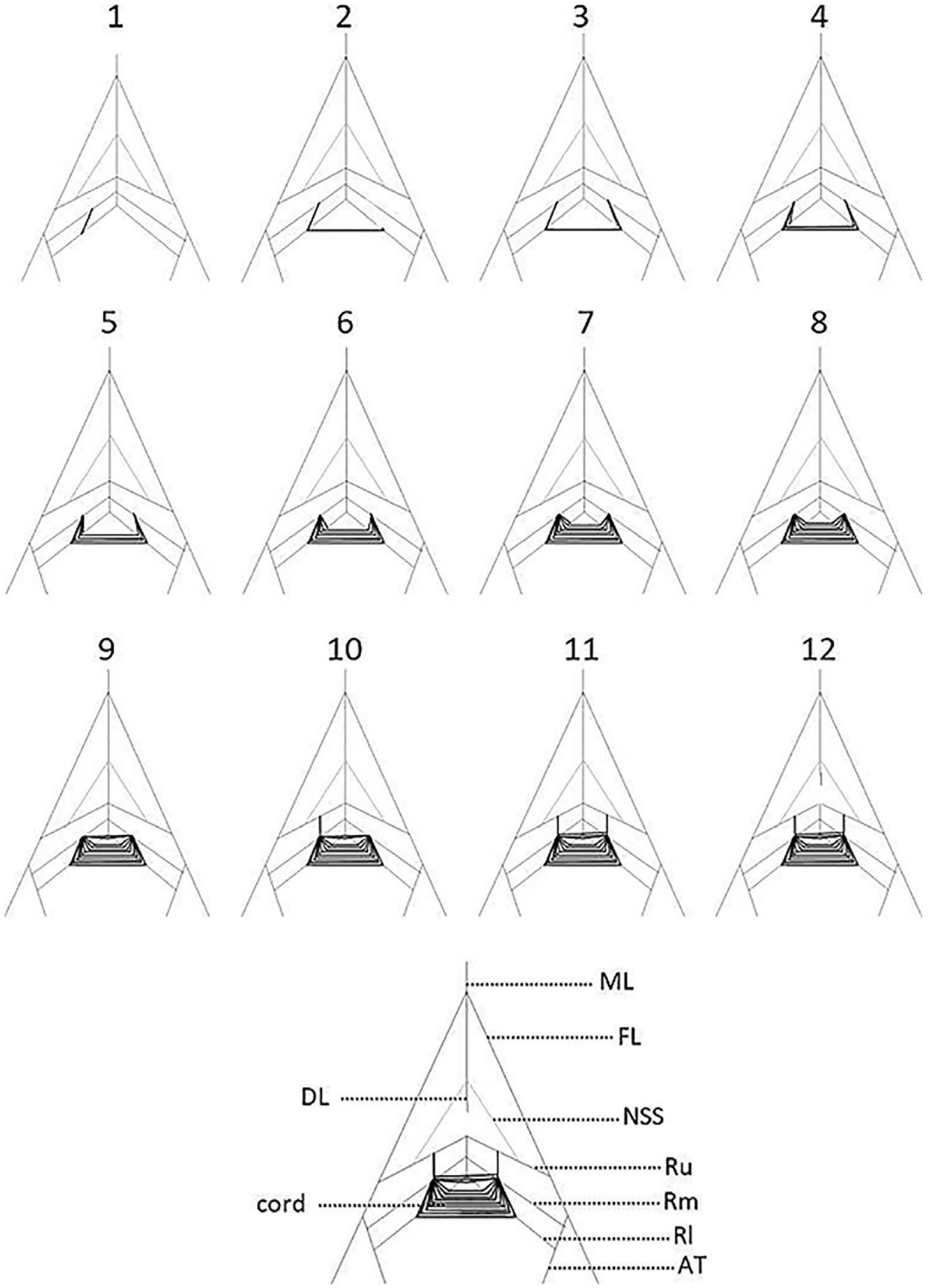

Figure 3.—Sticky-silk spiral construction sequence of *Deinopis* cf. *cylindracea* with nomenclature code: Midline (ML), Frame lines (FL), Non-sticky spiral (NSS), Upper radius (Ru), Middle radius (Rm), Lower radius (Rl), Anchor thread (ATl, ATr), and Dragline (DL).

number of cords of the SS spiral of other Deinopidae differed from the number of cords of *Deinopis* cf. *cylindracea* (Table 1). In *D*. cf. *cylindracea*, the number of cords was 12, with a fixed pattern ($n = 43$), while in other *Deinopis* species, it ranged from 10 to 22; in *Asianopis wangi*, it was 22 and in *Menneus* spp. there were between 16 and 22 cords (Table 1). Among the *Deinopis* species, we found small differences in the fixation points of the NSS, where reinforcements occur in the connection with the upper radius.

We found that NS scaffolding did not seem to differ between the *Deinopis* species, whose webs were observed in photographs from the Internet and articles (Baum 1937; Getty & Coyle 1996; Laborda et al. 2012; Lin et al. 2020).

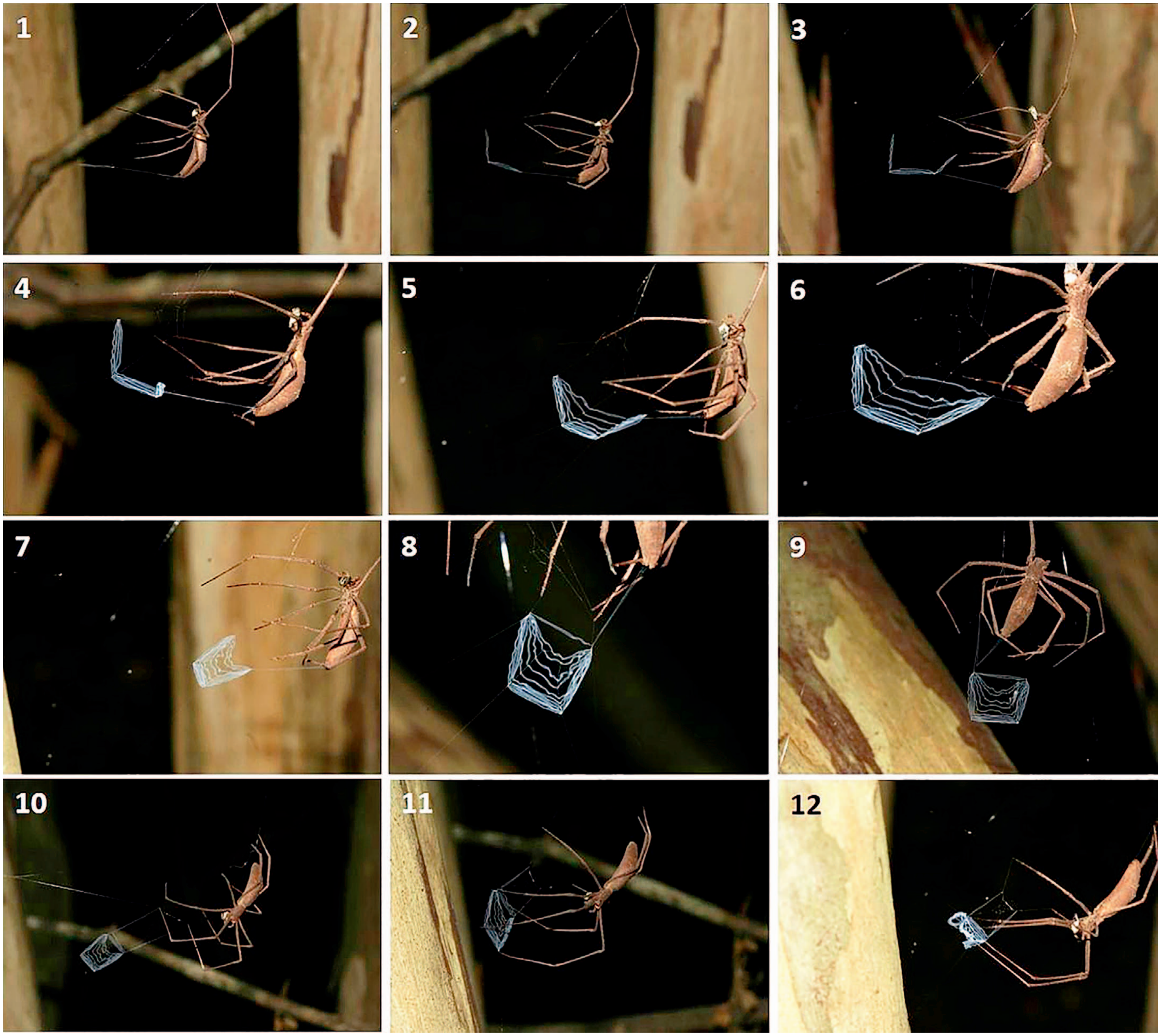

Figure 4.—Sticky-silk spiral (SS) construction sequence of an adult female of *Deinopis* cf. *cylindracea* comprising the construction a basic U-shape (1–3) repeated four times (4), and then five more times (4–6), with two final cords forming the square shape (7–8), finishing with two vertical handles (9–10), and assuming the prey-ready posture (11–12).

DISCUSSION

Orb web spiders have a monophyletic origin. Their web architecture evolved only once, and the Deinopidae family is a basal group (Coddington 1986b; Blackledge et al. 2009; Garrison et al. 2016; Coddington et al. 2019). The abandonment of costly cribellate capture thread was associated with the origin of the Araneoidea and an increase in the diversity of modern orb-weaving spiders (Blackledge et al. 2009).

Ogre-faced spiders (Deinopidae) are known to produce cribellate capture threads and have a unique prey-capture method (Blamires et al. 2017). All known deinopid webs are bilaterally symmetric, modified orbs (Coddington 1986a) with three radii on each side where the SS spiral is made. This web pattern and the SS spiral launch behavior to capture prey are unique to the Deinopidae (e.g., Ackerman 1926; Robinson & Robinson 1971; Coddington & Sobrevila 1987; Blamires et al. 2017).

The web of *D*. cf. *cylindracea* has the typical structure of deinopid webs and is built following all steps reported for *Deinopis* sp. (Coddington 1986a) and *A*. *subrufa* (Clyne 1967). Clyne (1967) recorded that this construction pattern was presented by individuals of *Asianopis subrufa* above 4 mm, and this was also observed in our study. According to Baum (1937), spiderlings and third instars did not build a web under laboratory conditions. Furthermore, the spiderlings did not feed when they were offered a fruit fly (*Drosophila*). Baum saw

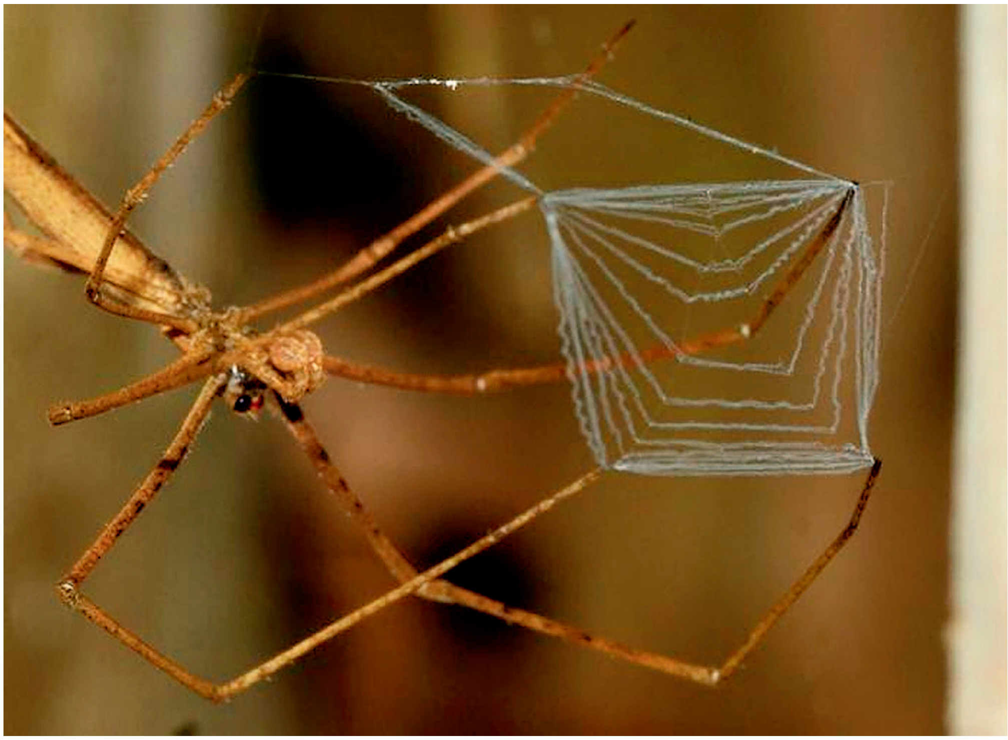

Figure 5.—Complete sticky-silk spiral with a detail of the cord pattern built by a *Deinopis* cf. *cylindracea* subadult male.

second-instar individuals feeding in the forest, but he was unable to explain how this happened because he did not record second-instar spiders building or using webs. In our study, we observed twice the second and third instars feeding on flying prey using the simplified web construction, which represents a stark contrast to the closest relatives of the deinopids. With our results, we resolve an old mystery originally described by Baum: "how *Deinopis* spiderlings are able to feed and grow without making prey capture webs" (Eberhard pers. communication).

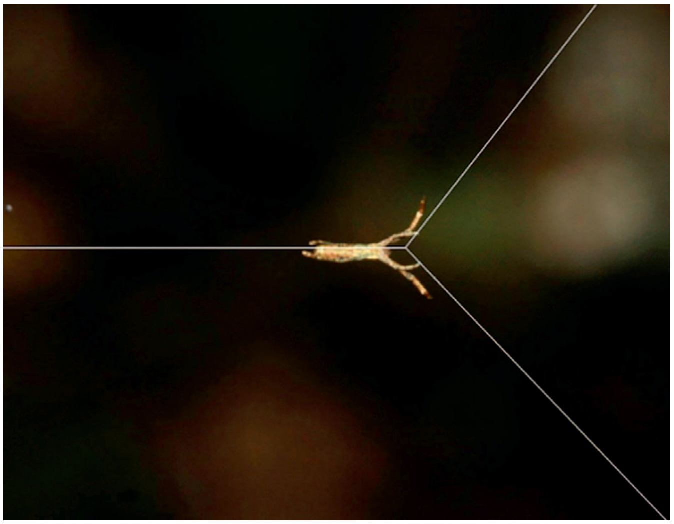

Figure 6.—Second instar *Deinopis* cf. *cylindracea* with its web (threads highlighted by software).

After the 3rd instar ecdysis, some individuals with a long silk thread fed on *Drosophila*. After 47 days, after the 4th instar ecdysis, these spiders began to build webs with SS spirals (Baum 1937). Our data indicate similar behavior for *D.* cf. *cylindracea*. Regarding the orientation of the SS spiral, our study found that vertical and smooth surfaces were more suitable for web construction (see also da Ponte et al. 2020). This result differs from those of previous studies, in which horizontal surfaces were most frequently chosen (Austin & Blest 1979).

Deinopis cf. *cylindracea* also presented the two stereotypical predation behaviors described for *D. spinosa* (Coddington & Sobrevila 1987). Both *D.* cf. *cylindracea* and *D. spinosa* have the ability to capture both flying and wandering prey; however, the fact that their diet has virtually no flying prey reinforces the specialization of their diet in wandering prey (da Ponte et al. in press).

As reported for other species in the genus *Deinopis*, the males of *D.* cf. *cylindracea* do not build a web, and it is likely that they do not feed during adult life (Clyne 1967; Robinson & Robinson 1971; Austin & Blest 1979).

The study by Austin & Blest (1979) describes the web construction of *A. subrufa* and *Menneus unifasciatus* (*nomina dubia*, see Coddington et al. 2012), with the first species placing its web to face horizontal surfaces (ground), while *M. unifasciatus* places its web to face vertical surfaces, in this case, vegetation. The two species differ in their diets, which is why they differ in their webs. An illustration in Austin & Blest (1979) shows a partial web of *A. subrufa* that is similar to the web of *Deinopis* as described in more detail by Coddington & Sobrevilla (1987). With regard to the web of *D.* cf. *cylindracea*, there is no reinforcement in the upper radius where the support handles of the SS spiral are fastened. In other *Deinopis*, this may differ, but the details are still unknown. The web of *Menneus unifasciatus* has frame lines and a midline where the spider hangs. The lower and median radii are attached to the vegetation, and the upper radius is subdivided into two small parts where the handles of the SS spiral are located, while its end is connected to the apex of the frame line (Getty & Coyle 1996). The web of *M. camelus* is similar to that described for *M. unifasciatus*, where the radii are attached to the vegetation and to the apex of the frame line (see fig. 3c. in Coddington et al. 2012 and figs. 1, 2 in Akerman 1926).

The SS spiral in the web of *D.* cf. *cylindracea* has a fixed number of 12 cords from the fourth instar to the adult stage (except for adult males who do not build a web). The number of cords in SS spirals of other *Deinopis* species ranged from 12 to 14 but seemed to be a distinct pattern in each species. Unfortunately, we have only indications from replicates of examples where we can determine the number of cords for each species; it is possible that the number of cords may vary among species. For the genus *Menneus*, the number of cords may be fixed in each species, and the number of cords in the SS spiral may differ. Regarding *Asianopis*, we found one image for *A. wangi* and three for *A. subrufa*, whose nets have 22 cords. There is no record or description of the NS scaffolding for *A. wangi*. It would be interesting to know more about the number of cords in the SS spiral and whether this number is fixed for each species. It would also be important to know if the number of cords in the SS spiral is related to the type and size of the target prey. However, we must keep in mind that our claims of a "fixed" pattern in other species of Deinopidae are based on a rather small sample size obtained from different manuscripts and internet images, so it is necessary to expand the sampling and counting of cords in a larger number of species and individuals of Deinopidae species to confirm our result proposed here. Additionally, although the *Deinopis* images used in our study are from the internet and there may be errors in the nomenclature of Deinopidae species, we believe that they are distinct morphospecies and that the "number of cords" character is important to separate species or a group of species. Future work should examine our hypothesis that cord number constitutes a taxonomic character.

We believe that the basic archetype of the NS scaffolding, the SS spiral, and the three radii characterize the web of spiders of the family Deinopidae. Moreover, the arrangement of the radii and where they connect appears to characterize the genus, and specific characteristics such as the number of cords and the presence of reinforcements at the junction of the handles of the net with the upper radius can characterize the species.

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SUPPLEMENTAL MATERIALS

Figure S1.— Examples of the number of cords counted for three *Deinopis* species (Deinopidae). Online at https://doi.org/10.1636/JoA-S-21-076.s1

LITERATURE CITED

Akerman C. 1926. On the spider, *Menneus camelus* Pocock, which constructs a moth-catching, expanding snare. *Annals of the Natal Museum* 5:411–422.

Austin AD, Blest AD. 1979. The biology of two Australian species of deinopid spider. *Journal of Zoology* 189:145–156.

Basutamary P, Caleb JTD, C., Das S, Brahma D. [Басуматари П, Калеб ДТ, Дас С, Брахма Д.] 2020. Redescription of the net-casting spider *Asianopis goalparaensis* (Tikader et Malhotra, 1978) comb. n. (Araneae: Deinopidae) from India. *Arthropoda Selecta* 29:325–329.

Baum J. 1937. On the habits of the Australian spider *Dinopis subrufa* L. Koch. *Věstnik Československe Zoologicke Společnosti* 5:28–33.

Benjamin SP, Zschokke S. 2002. Untangling the tangle web: web construction behaviours of the gumfooted spider *Steatoda triangulosa* and comments on phylogenetic implications (Araneae: Theridiidae). *Journal of Insect Behavior* 15:791–809.

Blackledge TA, Nikolaj N, Coddington JA, Szüets T, Wenzel JW, Hayashi CY, et al. 2009. Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of National Academy of Sciences* 106:5229–5234. Doi: 10.1073pnas.0901377106

Blamires SJ, Zhang S, Tso I-M. 2017. Webs: diversity, structure and function. Pp. 137–164. *In* Behaviour and Ecology of Spiders. (Viera C, Gonzaga MO, eds.) Springer, Cham.

Clyne D. 1967. Notes on the construction of the net and sperm-web of a cribellate spider *Dinopis subrufa* (Koch) (Araneida: Dinopidae). *Australian Zoologist* 14:189–197.

Coddington JA. 1986a. Orb webs in "non-orb weaving" ogre-faced spiders (Araneae: Dinopidae): a question of genealogy. *Cladistics* 2:53–67.

Coddington JA. 1986b. The monophyletic origin of the orb web. Pp. 319–363. *In* Spiders-Webs, Behavior, and Evolution. (WA. Shear, ed.). Stanford University Press, Stanford.

Coddington JA, Sobrevila C. 1987. Web manipulation and two stereotyped attack behaviors in the ogre-faced spider *Deinopis spinosus* Marx (Araneae, Deinopidae). *Journal of Arachnology* 15:213–225.

Coddington JA, Agnarrson I, Hamilton CA, Bond JA. 2019. Spiders did not repeatedly gain, but repeatedly lost, foraging webs. Peer J 7:e6703.

Coddington JA, Kuntner M, Opell BD. 2012. Systematics of the spider family Deinopidae with a revision of the genus *Menneus*, *Smithsonian Contributions to Zoology* 636. pp. i–iv, 1–61, 32 figures.

da Ponte RP, Stefani V, Vasconcellos-Neto J. 2020. Natural history of the ogre-faced spider *Deinopis* cf. *cylindracea* (Araneae: Deinopidae): revealing its phenology. *Studies on Neotropical Fauna and Environment* 56:210–219.

Eberhard WG. 1976. Photography of orb webs in the field. *Bulletin of the British Arachnological Society* 3:200–204.

Eberhard WG. 1990. Function and phylogeny of spider webs. *Annual Review of Ecology and Systematic* 21:341–372.

Eberhard W. 2020. Spider Webs. University of Chicago Press.

Foelix RF. 2011. Biology of Spiders. 3rd. Oxford: Oxford University Press.

Garrison NL, Rodriguez J, Agnarsson I, Coddington JA, Griswold

CE, Hamilton CA, et al. 2016. Spider phylogenomics: untangling the Spider Tree of Life. PeerJ 4: e1719; DOI 10.7717/peerj.1719.

Getty RM, Coyle FA. 1996. Observations on prey capture and anti-predator behaviors of ogre-faced spiders (*Deinopis*) in southern Costa Rica (Araneae, Deinopidae). *Journal of Arachnology* 24:93–100.

Harwood JD, Obrycki JJ. 2005. Web-construction behavior of linyphiid spiders (Araneae, Linyphiidae): competition and co-existence within a generalist predator guild. *Journal of Insect Behavior* 18:593–607.

Hawthorn AC, Opell BD. 2002. Evolution of adhesive mechanisms in cribellar spider prey capture thread: evidence for van der Waals and hygroscopic forces. *Biological Journal of the Linnean Society* 77:1–8.

Laborda A, de Oca LM, Useta G, Pérez-Miles F, Simó M. 2012. Araneae, Deinopidae, *Deinopis amica* Schiapelli and Gerschman, 1957: First record for Uruguay and distribution map. *Check List* 8:1301–1302.

Leitão-Filho HF. 1992. A flora arbórea da Serra do Japi. Pp. 40–63. *In* História Natural da Serra do Japi. (Morellato LPC. ed.). Editora da UNICAMP, FAPESP, Campinas.

Leitão-Filho HF, Morellato LPC. 1997. Semideciduous forests of Southeastern Brasil - Serra do Japi. Pp. 381–384. *In* Centres for Plant Diversity: a Guide and Strategy for their Conservation. (Davis SD, Heywood VH, Herrera-MacBryde O, Villa-Lobos J, Hamilton AC. eds.). IUCN, WWF, Washington

Lin Y, Shao L, Hänggi A, Caleb JTD, Koh JKH, Jäger P, et al. 2020. *Asianopis* gen. nov., a new genus of the spider family Deinopidae from Asia. *ZooKeys* 911:67–99.

Peters HM. 1992. On the spinning apparatus and the structure of the capture threads of *Deinopis subrufa* (Araneae, Deinopidae). *Zoomorphology* 112:27–37.

Pinto HS. 1992. Clima da Serra do Japi. Pp. 30–38. *In* História Natural da Serra do Japi. (Morellato LPC. ed.). Editora da UNICAMP, FAPESP, Campinas.

Robinson MH, Robinson B. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). *American Midland Naturalist* 85:85–96.

Santos AJ, Gonzaga MO. 2017. Systematics and natural history of *Uaitemuri*, a new genus of the orb-weaving spider family Uloboridae (Araneae: Deinopoidea) from south-eastern Brazil. *Zoological Journal of Linnean Society* 180:155–174.

Stafstrom JÁ, Hebets EA. 2016. Nocturnal foraging enhanced by enlarged secondary eyes in a net-casting spider. *Biology Letters* 12:20160152.

World Spider Catalog. 2021. World Spider Catalog. Version 21.0 Natural History Museum, Bern. Online at http://wsc.nmbe.ch, accessed on 11 November 2021.

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