Ontogenetic changes in web architecture and growth rate of *Tengella radiata* (Araneae, Tengellidae)

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Abstract.   In some spiders features of the webs of early instars may represent features of the ancestor's web. Some second instar spiderlings (first instar outside of the egg sac) of *Tengella radiata* (Kulczynski 1909) construct a small sheet web without any type of retreat. In subsequent instars, spiderlings construct webs that consist of a sheet with a small retreat that opens near its center. Webs gradually change as spiderlings growth and webs of 7th instar spiders are indistinguishable from those of adult females. Spiders only begin to include cribellate threads in their webs during the 7th instar. The growth of *T. radiata* is slow during the first three instars, but spiders' sizes increase steadily in the subsequent stages. Legs I of adult males are longer than in females, indicating an allometric growth that occurred mainly during the last molt of males.

Keywords: Spiderlings' webs, cribellate silk, cephalothorax and leg growth

Little is known about ontogenetic changes in most spiders' webs, particularly in non-orb weavers (Eberhard 1990). The first webs constructed by newly emerged spiderlings (second instar spiderlings) in several spider families differ from the webs of adults and they tend to represent less derived stages or characters compared to the features of the webs of adult spiders (Nielsen 1931; Eberhard 1977, 1985, 1986, 1990; Robinson & Lubin 1979). Some of these differences might also be related to underdevelopment of silk glands, as is the case in *Uloborus diversus* Marx 1898 (Eberhard 1977). Webs constructed by young spiderlings of this species lack cribellate silk, and radial threads are more numerous than in webs of adult spiders. Another possible difference in young spider-lings' webs may also be related with the type and size of prey that spiderlings can handle (Lubin 1986).

Webs of young cribellate and non-cribellate spiderlings have been studied in Orbiculariae orb-weaving spiders (Eberhard 1977, 1985, 1986). In some of these spiders in which architecture of adult webs depart from a typical orbicular web (Eberhard 1985, 1986), the webs of newly emerged spiderlings are orbicular, indicating that their ancestors probably possessed orbicular webs. A similar pattern is showed by cribellate and non-cribellate non-orb weavers such as the psechrid *Fecenia* sp. (Robinson & Lubin 1979) and some theridiid species (Nielsen 1931; Szlep 1965).

In this study, we focus on the cribellate spider *Tengella radiata* (Kulczynski 1909), a species of Tengellidae that builds funnel webs and is restricted to Costa Rica (Eberhard et al. 1993). Its web is regularly inhabited by some symbiont spiders (e.g., *Philoponella* sp., *Mysmenopsis* spp.) and plokiophilid bugs (e.g, *Lipokophila* spp.) (Eberhard et al. 1993). The structure and production of the cribellate threads of this spider have been described and compared with threads of other cribellate spiders (Eberhard 1988; Eberhard & Pereira 1993). The courtship and copulation have also been reported and compared with those of other spiders in related families (Barrantes 2008), and Santana et al. (1990) investigated the predation rate in the field and estimated the metabolic rate of this spider. Other than this reported work, there have been no published studies on the ontogenetic changes in the funnel, criballete web, or on the growth of this spider.

If there are ontogenetic changes in webs, we expect there to be transitional stages between the first webs and the adult webs. We describe here the architecture of the adult web and changes in the web architecture that occur between the immature stages of *Tengella radiata*. We also describe the number of molts, growth, and feeding behavior of spiderlings for this spider.

METHODS

We observed ($n > 30$) and photographed ($n = 5$) webs of wild mature females of *T. radiata* in San Antonio, Escazú, San José province (= SAE; 10°56′N, 84°08′W) and used this information to describe the adult web. The egg stage period and maternal behavior were described from a female raised from eggs in captivity and maintained in a plastic box (30 × 18 × 11 cm) where she constructed her web.

In order to rear and study numerous spiderlings we collected egg sacs from two mature female from two localities. One was from an adult female in SAE and a second from a female from La Selva Biological Station (= LSBS; 10°26′N, 83°59′W), Organization for Tropical Studies, Heredia province, Costa Rica. Each egg sac was placed on a mass of dry cotton inside a plastic container (13 × 13 × 6 cm) with a little piece of humid cotton at a corner. All containers were maintained indoors at a temperature of 18–20° C. From one egg sac (SAE), 16 spiderlings were separated as they emerged and each one was maintained individually in a plastic container (13 × 13 × 6 cm); some of these spiderlings were placed in a larger container (30 × 15 × 10 cm) when they reached their seventh instar. Webs of some of these 16 individuals were photographed and their shed cuticles measured at each stage (details described below) to describe the ontogenetic changes in the web and the growth of this spider. From a second egg sac (LSBS) we separated three groups of 10 spiderlings and each group was maintained in a container (13 × 13 × 6 cm). Feeding behavior was observed in these groups of spiderlings. (Spiderlings from the second egg sac were released to the wild as they molted the third time as were those remaining spiderlings from the first egg sac). We consider spiderlings that recently emerged from the egg sac as second instar individuals (Foelix 1996).

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The plastic container of each of the 16 spiderlings kept individually had four small rocks, whose base and height varying from 2 to 3 cm. One rolled dry leaf, forming a cone of ca 2 cm with an opening of ca 0.5 cm in diameter, was attached to one of the rocks with masking tape; rocks were all fastened to the bottom of the container. This "rock landscape" was fashioned to offer spiderlings enough supports to construct their webs, and the rolled leaf was offered as a "natural tunnel." Two to four webs constructed by spiderlings from 3rd to 6th instars were lightly coated with cornstarch and then photographed. The longest and widest sides of these, approximately rectangular webs were measured. Spiderlings of the photographed webs were collected and preserved in alcohol to avoid possible effects of cornstarch in the construction of subsequent webs. The web of the second instar spiderlings was sketched using photos and observations under the dissecting microscope; cornstarch adhered to threads of these webs was insufficient to allow good contrast photographs.

We measured the length of tibiae and femora of legs I and IV, and the length and width of the cephalothorax in shed cuticles of the different stages of those 16 spiders maintained individually in containers, three adult males, and three adult females to estimate the spiders' growth between stages (2nd instar to adult stage). Sample sizes were not the same for each stage because some spiderlings were collected and some shed cuticles were destroyed when we withdrew them from the web, and tibiae in all second stage cuticles collapsed and were impossible to measure. To calculate the percentage of growth between subsequent stages, we subtracted the length of a particular structure to the mean of that structure of the previous stage (M_{ps}), then divided this difference between M_{ps},

and multiplied this proportion by 100 (e.g., $[FI_{21} - MFI_1]/MFI_1 * 100$; FI_{21}- femur I from individual 1 of second instar, MFI_1- mean of femur of all individuals of instar 1). We used a digital camera (Nikon, Coolpix 4500) to photograph each femur, tibia, and cephalothorax under a dissecting microscope, and measured them using the software program Image Tool v. 3.0. Four 3rd instar spiderlings were observed under the dissecting microscope to check for the presence of the cribellar plate and calamistrum.

During the 2nd and 3rd instars, spiderlings were offered a *Drosophila* fly every other day, 4th instar spiderlings were offered two *Drosophila* flies every other day, and spiderlings of later instars were offered one blow fly (Calliphoridae) or a moth every three days. All containers had a small piece of wet cotton for the spiderlings to drink. Feeding behavior observations were made on both solitary spiderlings and on those maintained in groups. Additional behavioral observations of adults and spiderlings were obtained from adult spiders raised from eggs in captivity and complemented with the field information from SAE and LSBS. Voucher specimens of spiders from all stages were deposited in the Museo de Zoología of the Universidad de Costa Rica, San José.

RESULTS

Adult web.—The adult web of *T. radiata* consists of a large, more or less triangular, horizontal sheet with a dispersed tangle above and beneath it (Fig. 1; Eberhard et al. 1993). It is usually built near a large object such as rock or a tree trunk. At the "interior," most protected section (the apex) of the web the spider constructs a tunnel that varies between 5 and 20 cm long ($n = 20$). The spider rests at the mouth of the tunnel or inside it during the day. At night ($n = 10$) the spider usually
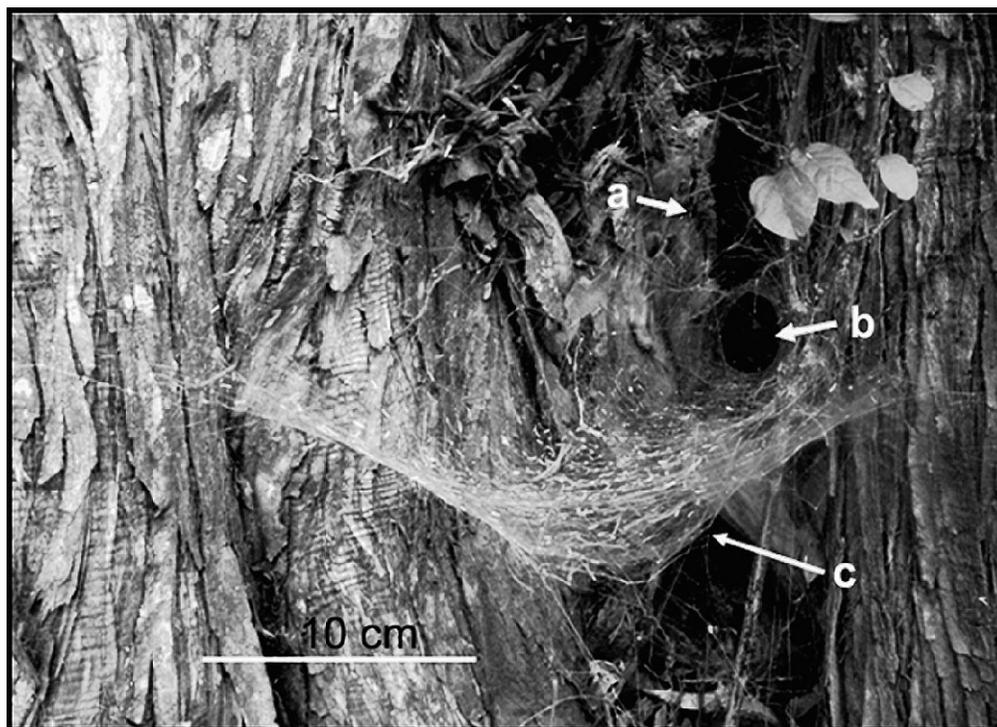

Figure 1.—Frontal view of an adult web of *T. radiata* (without cornstarch): a. Threads of the upper tangle. b. Tunnel at the "interior" section of the sheet. c. Sheet.

rests at the mouth of the tunnel, but is often observed repairing the web or producing adhesive cribellate threads that she lays on the sheet and upper tangle. Newly constructed webs frequently lack cribellate threads, but this silk accumulates on the sheet and upper tangle over time, until the web collapses apparently due to the weigh of debris accumulated on its sheet. Adult males ($n = 3$) did not build webs when placed in a large plastic container. However, they killed and fed on prey that walked nearby. Females ($n = 5$) placed in similar containers built a complete web.

Duration of egg stage and maternal care.—One spider produced two egg sacs in captivity, the first 32 and the second 48 days after copulating. Spiderlings emerged from the first egg sac 58 days later; no spiderlings emerged from the second egg sac. The egg sacs were attached to the roof of the tunnel, as were five egg sacs observed in the field. In captivity, the spider added some small pieces of prey cuticle to the external surface of the egg sacs; egg sacs observed in the field were also covered with detritus. The female spent most of her time (except when capturing prey and feeding) hanging from the tunnel with her legs and palps surrounding the egg sac. Nearly the entire time, she contacted the egg sac with legs II and III (less frequently with legs IV), and her palps. Occasionally, she stood on the bottom of the tunnel, with one of her legs (usually one leg III) raised to contact the egg sac. When the spider produced the second egg sac, she concentrated her care on the second sac. The spider died after living for 18 months and 20 days (from emergence through adulthood).

Ontogenetic changes in webs.—During the second instar, 4 of the 16 spiderlings used the tunnels (rolled leaf provided) but did not construct webs, 8 remained under a rock, and 4 constructed a web that consisted of a small, more or less rectangular, sheet (Fig. 2). At first the web consisted only of more or less horizontal threads that extended between rocks or between rocks and the container wall. The horizontal threads were about 1.5 cm above the container floor and other threads connected them to the floor and to the container wall above. These threads were part of the scaffolding that supported the
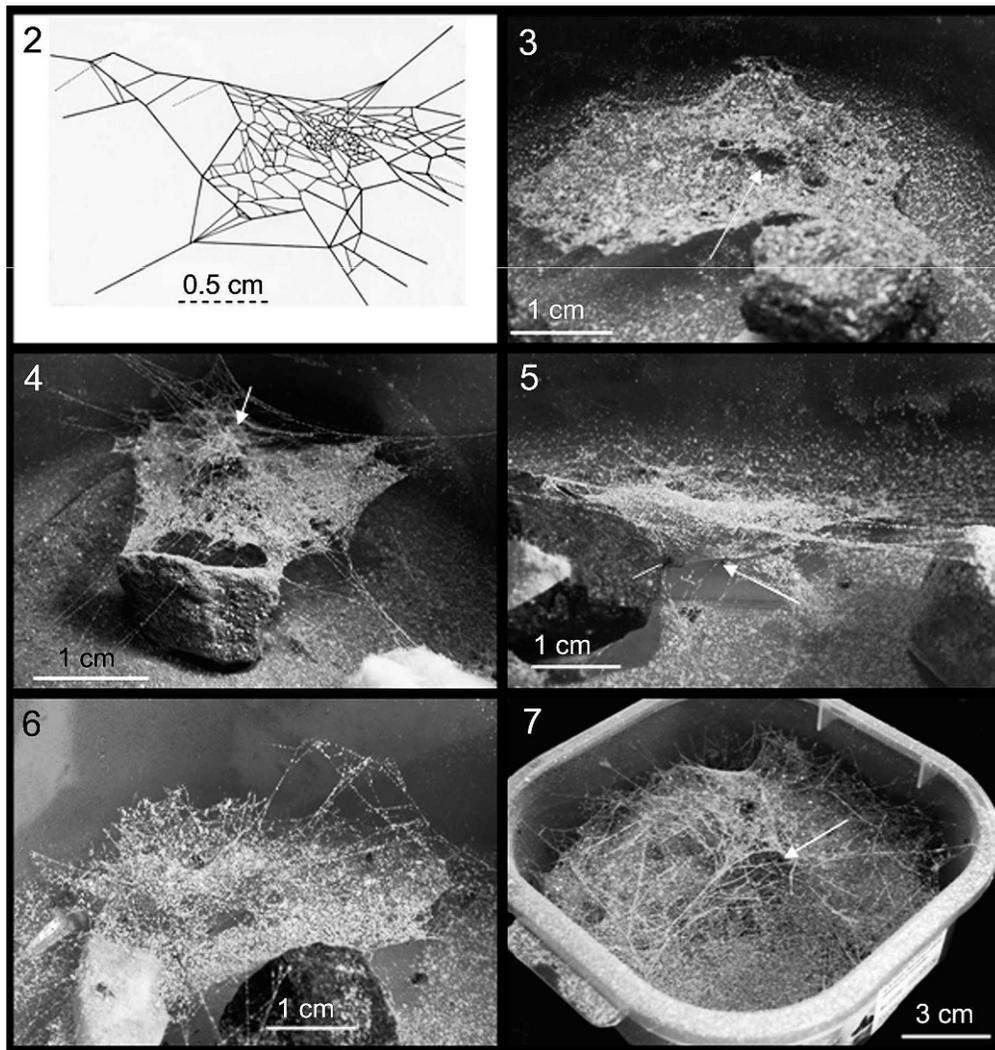
Figures 2–7.—Webs of early stages of *T. radiata* (with cornstarch): 2. Molting web of second stage spiderlings; 3. Type I web of third stage spiderling; 4. Type II web of third stage spiderling; 5. Web of fourth stage spiderling; 6. Web of fifth stage spiderling; 7. Web of seventh stage spiderling. White arrows in Figures 3, 4, 5, and 7 show the tunnel opening. The right tip of the short white line in Figure 5 shows the spiderling inside the retreat.

rest of the web. During the next days the spiderlings constructed a dense sheet of very fine threads. The angle of the sheet varied from nearly horizontal to about 15° (angles were visually estimated). The complete web was constructed over the first 2 to 4 days. When the web was finished, the spiderling remained motionless, near the center, and on top of the sheet until its next molt. These webs all lacked tunnels or any other type of retreat. During this stage, which lasted 11.3 days (SD = 0.4) spiderlings did not feed; they did not react to the presence of prey on their webs.

The third-stage spiderlings (n = 16) constructed two types of webs. The most common type (13 out of 16) was a small (range = 3–4 × 2–2.5 cm) dense, more or less horizontal sheet with a resting place (retreat) that was constructed nearly perpendicularly under the sheet (type I) (Fig. 3). This retreat was a small bag of loose silk with the exit near the center of the sheet (Fig. 3). The other web (type II) was also a flat sheet, but with the bag-like retreat constructed on the sheet forming a small roof, with a relatively dense tangle above the sheet (Fig. 4). Threads of the tangle served as support for the much finer threads of the sheet and retreat. All spiderlings in this stage captured *Drosophila* flies dropped on the sheet.

The webs of fourth-stage spiderlings were in general larger (range = 5–6 × 3–3.5 cm) than those of the previous stage. Spiderlings expanded the sheet and retreat of the web constructed in the previous stage, and constructed a tunnel under the sheet. The closed end of the tunnel nearly reached one border of the sheet (Fig. 5), and spiderlings rested deep inside the tunnel (Fig. 5). The general shape of these webs was similar to webs of the previous instar and type I and II webs were still distinguishable. Webs of fifth and sixth stages were similar in the general features but larger compared to webs of the previous stage (Fig. 6).

Seventh-stage juveniles constructed a much denser tangle above the level of the sheet. In this stage the tunnel of two webs (n = 9) was constructed on the sheet for most of its length, with its opening near the center of the sheet. The furthest end of the tunnel curved down and under the sheet, similar to a type II design (Fig. 7). The other seven webs were similar to the adult webs, with the opening of the tunnel at one extreme of the sheet. This was the first stage in which cribellate threads were observed on the sheet and upper tangle of the web (Fig. 8), though the cribellar plate and calamistrum were already present in 3rd instar spiderlings. The web of older stages (in larger containers) was indistinguishable from webs of adult spiders.

Spiderling feeding behavior.—Third and fourth instar spiderlings attacked by rushing onto the sheet to the prey and biting it. If prey was small, relative to the spiderling size, the spiderling fed on the prey without releasing it. If prey was large, it was released by the spiderling as soon as the prey's struggling stopped, returning to feed on it a few seconds later. One fourth instar spiderling (in a group of 10) wrapped the prey after biting it. The spiderling released the prey as it stopped struggling and nearly immediately began to wrap it. During wrapping, the spiderling turned in place while attaching wrapping lines to the substrate (the sheet). The wrapping movements were similar to those described for adult spiders (Barrantes & Eberhard 2007). Another spiderling approached a large blow fly (larger than a house fly) slowly. The spiderling backed away as the fly struggled and then cut
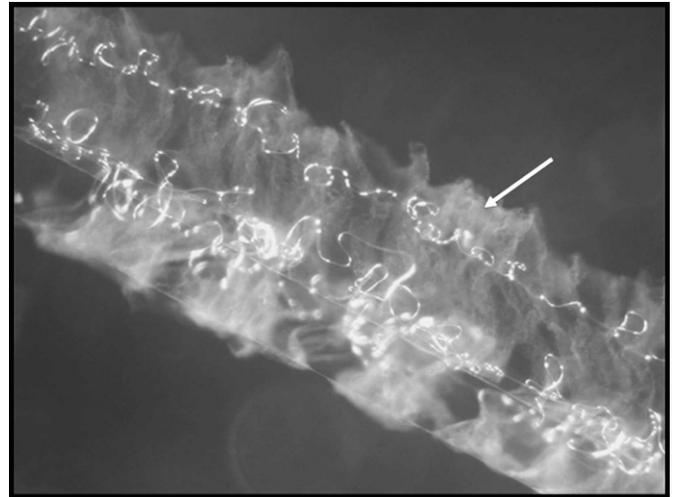

Figure 8.—Cribellate threads (white arrow) from webs of seventh stage spiderlings.

some sheet threads and walked, hanging under the sheet to the prey and bit one of the fly's legs through the sheet. Neither wrapping nor attacks from under the sheet were observed in any fifth instar individuals. Older juvenile spiders (sixth or older instars) always moved on the upper surface of the sheet, and often wrapped large prey (e.g., moths and large flies), with movements similar to those of adult spiders (Barrantes & Eberhard 2007). Large prey were carried inside the tunnel by 7th stage, subadult, and adult spiders, and their carcasses were left inside the tunnel.

Additional behavioral observations.—Early instar spiders did not molt at any consistent site in the web (n > 50). However, older stages (7th to pre-adult) molted inside the tunnel but they carried the shed skin to the farthest extreme of the web (n = 9).

Number of molts and growth.—The males had eight molts (n = 4) and the females nine (n = 4) to attain their adult stages. The mean time from emergence from the egg to the eighth molt was 186.7 days (± 10.5), when males molted to the adult stage. Females lasted 42 days (± 7) more to their next and last molt (Fig. 9).

The general pattern of growth of the cephalothorax (width and length) and legs I and IV (tibia and femur) were similar. In the three first stages these structures grew very little, but during the following stages the size of the cephalothorax and legs increased steadily (Figs. 10–12). In fact, the growth of all morphological features was proportionally much larger between the third and the fourth stage, than between other subsequent stages (Table 1). It is also evident that the length of the cephalothorax increased faster than its width (Fig. 10), indicating an allometric growth of the length relative to the width of the cephalothorax. In addition, legs of adult males were also notably longer than those of adult females, despite the additional molt of females.

DISCUSSION

The architecture of the webs of *T. radiata* changes as spiders mature. The first web constructed by 2nd instar spiderlings, which have recently emerged from the egg sac, apparently serves as a molting place, since spiderlings in this stage did not capture prey. In nature and in captivity the second instar spiderlings construct a communal molting web inside the
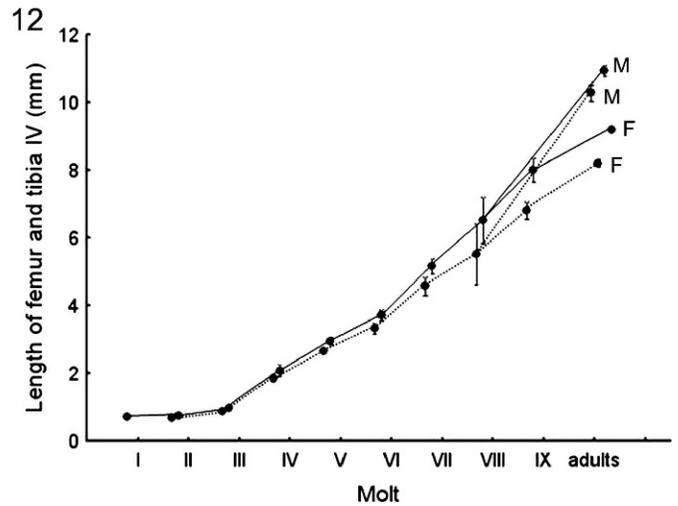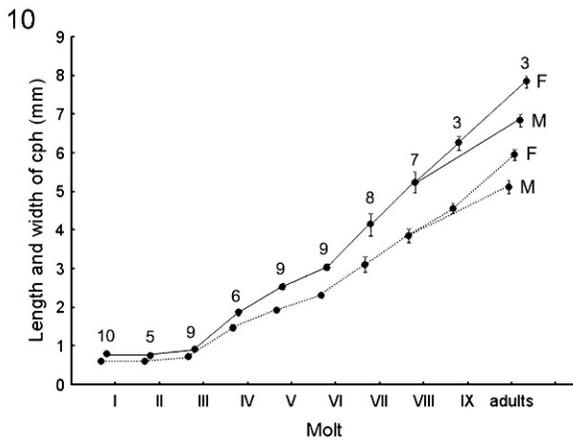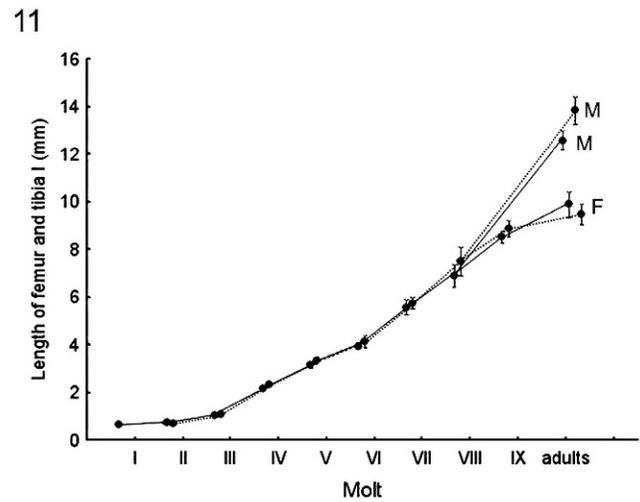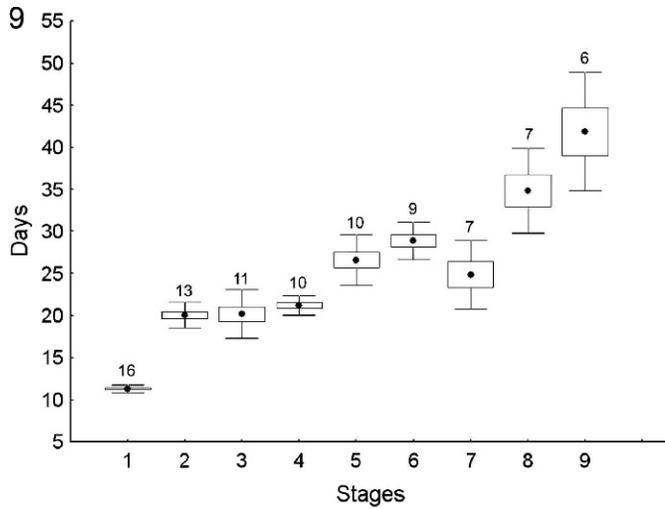
Figures 9–12.—Inter-molt time and growth of *T. radiata*: 9. Intermolt time (mean, standard error and standard deviation) from the first to the ninth stage out of the egg sac; sample size above each stage mean; 10. Mean and standard deviation of the length (solid line) and width (dotted line) of cephalothorax (cph); sample size above each mean, F and M indicate the values for adult females and adult males respectively; 11. Mean and standard deviation of the length of femur (solid line) and tibia (dotted line) of leg I; 12. Mean and standard deviation of the length of femur (solid line) and tibia (dotted line) of leg IV.

tunnel of their mother's web, and only begin to abandon the tunnel and the web after they molt to the third instar (GB unpublished data).

Both of the two types of webs constructed by third through sixth instar spiderlings had retreats that opened near the center of the sheet (Figs. 3–7). If, as in other groups, the webs of early instars represent less derived characters than those of the adult web (Eberhard 1986, 1990), the ancestral web of *Tengella* might have been a sheet with a tunnel retreat extending below its center. However, comparative data of closely related species (Coddington 2005) are required to test this hypothesis.

The lack of cribellate threads on the sheet of juvenile spiders (2nd to 6th instar) may either represent an ancestral condition, an undeveloped condition of the cribellum

Table 1.—Percentage of growth of the width and length of the cephalothorax (cph) and the femur (F) and tibia (T) of legs I and IV between successive stages (first row). Sample size in parentheses beside or under the stage codes.

	I to II (5)	II to III (9)	III to IV (6)	IV to V (9)	V to VI (9)	VI to VII (8)	VII to VIII (7)	VIII to IX (6)	VIII to ♂ (3)	IX to ♀ (3)
Cph W	0.6 ± 9.9	19.9 ± 1.9	104.4 ± 11.7	30.7 ± 2.9	19.8 ± 4.3	35.3 ± 8.7	23.9 ± 5.8	18.6 ± 3.5	32.9 ± 4.7	30.5 ± 3.3
Cph L	0.1 ± 0.2	21.6 ± 3.3	106.4 ± 9.2	35.6 ± 4.4	20.1 ± 3.7	36.6 ± 9.7	26.5 ± 6.4	19.3 ± 3.4	30.5 ± 3.2	25.3 ± 2.6
FI	21.4 ± 5.2	41.0 ± 3.9	104.4 ± 14.6	46.5 ± 5.5	22.4 ± 9.8	42.0 ± 8.4	23.8 ± 8.7	23.7 ± 3.7	82.4 ± 5.9	15.8 ± 6.5
TbI		56.6 ± 5,6	114.5 ± 8.0	41.8 ± 7.3	24.4 ± 8.1	38.9 ± 5.9	30.6 ± 10.8	18.5 ± 4.5	84.8 ± 7.7	18.3 ± 7.1
FIV	5.9 ± 3.3	32.3 ± 4.0	110.9 ± 17.2	42.0 ± 5.0	26.2 ± 5.5	38.7 ± 6.0	26.3 ± 13,3	22.8 ± 5.3	67.8 ± 2.6	14.2 ± 1.4
TbIV		29.6 ± 5.5	109.5 ± 13.3	44.0 ± 4.2	25.1 ± 5.5	37.5 ± 8.3	26.3 ± 11.1	23.1 ± 4.7	86.3 ± 4.3	20.2 ± 2.0

apparatus, or both. The presence of the cribellum and calamistrum in third instar spiderlings but the lack of criballate silk on their webs, indicate that these structures may not be functional in the early stages of *T. radiata*, as occur in some uloborids (Eberhard 1977; Opell 1982), or that the high demand of energy involved in drawing the cribellar fibrils (Eberhard 1988) prevent young spiderlings from using this type of silk.

The lack of cribellate silk in early stages and newly constructed webs of adult *T. radiata* did not prevent spiders from using their webs to capture prey, though cribellate silk possibly restrain and reduce movements of prey on the web. Spiderlings at early stages showed attack and wrapping behaviors similar to those of adult spiders (Barrantes & Eberhard 2007). The wrapping behavior of spiderlings only differed from that of adults in that spiderlings did not hold the prey while wrapping it as adults do (Barrantes & Eberhard 2007). In addition, one spiderling attacked a large prey from under the sheet. This attack is apparently restricted to early spiderling stages, as it has not been observed in either large juveniles or adult spiders. The low frequency of occurrence of this behavior is unclear since attacking a large prey from under the sheet provides some protection to the spiderling as the sheet restrains the struggling prey and reduces the force of its movements (Robinson 1975; Lubin 1980).

In general the growth of *T. radiata* is slow, as expected from its apparently extremely low metabolic rate (Santana et al. 1990). Growth was very slow during the earliest stages (Figs. 10–12), but the relative increment in cephalothorax and leg size was more than 100% between the third and fourth stage. After the fourth stage, the cephalothorax and legs increased steadily with each subsequent molt, though the intermolt period tended to increase with each stage. This possibly indicates the need for more energy and time for growth and development of internal organs as spiders mature. Length of legs I and IV is nearly the same until the fourth instar. However, in the following stages, increments in the length of leg I are larger than in leg IV, possibly reflecting the different functions of these legs in young and adult spiders. For example, the tactile function of legs I likely favor their longer length (Foelix 1996).

The comparatively longer legs of adult males result from the allometric growth that occurred mainly during the last molt of males, as happens in wolf spiders (Framenau 2005). Though experimental evidence is lacking, field observations (e.g., males observed near or on females' webs) indicate that adult males abandon their webs to find receptive females, so that longer legs may result in greater step size to bridge gaps. If a more efficient search for females lead to a higher reproductive success in males, it is likely that longer legs in males evolved, at least partially, through indirect male-male sexual competition (Anderson 1994; Framenau 2005). Additionally, natural selection might have also favored longer legs in males, if such a trait allows them to run faster to escape from predators and from females during courtship, and provides them a greater sensory range (Gertsch 1949; Framenau 2005). Accordingly, the larger size of adult females' cephalothorax correlates with their larger body which is related to their capacity to produce large numbers of eggs (Gertsch 1949).

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