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RESEARCH ARTICLE

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Silk structure rather than tensile mechanics explains web performance in the moth-specialized spider, *Cyrtarachne*

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Abstract

Orb webs intercept and retain prey so spiders may subdue them. Orb webs are composed of sticky, compliant spirals of capture silk spun across strong, stiff major ampullate silk threads. Interplay between differences in the mechanical properties of these silks is crucial for prey capture. Most orb webs depend upon insects contacting several radial and capture threads for successful retention. Moths, however, escape quickly from most orb webs due to the sacrificial scales covering their bodies. Cyrtarachne orb webs are unusual as they contain a reduced number of capture threads and moths stick unusually well to single threads. We aimed to determine how the tensile properties of the capture spiral and radial threads spun by Cyrtarachne operate in retention of moth prey. A NanoBionix UTM was used to quantify the material properties of flagelliform and major ampullate threads to test if Cyrtarachne's reduced web architecture is accompanied by improvements in tensile performance of its silk. Silk threads showed tensile properties typical of less-specialized orb-weavers, with the exception of high extensibility in radial threads. Radial thread diameters were 62.5% smaller than flagelliform threads, where commonly the two are roughly similar. We utilized our tensile data to create a finite element model of Cyrtarachne's web to investigate energy dissipation during prey impact. Large cross-sectional area of the flagelliform threads played a key role in enabling single capture threads to withstand prey impact. Rather than extraordinary silk, Cyrtarachne utilizes structural changes in the size and attachment of silk threads to facilitate web function.

KEYWORDS
biomechanics, Cyrtarachne, moth, silk, spider, tensile

1 | INTRODUCTION

Orb webs allow spiders to capture flying insects by first stopping the insects' flight through the deformation of strong and tough radial threads and then adhering to the insects using extensible, glue coated capture threads (Foelix, 2011; Sensenig, Lorentz, Kelly, & Blackledge, 2012). Contact with multiple radial threads is usually required to spread the impact energy of prey across sufficient area to allow sufficient energy dissipation so that threads do not rupture. Dissipation of the flight energy of prey by deformation of radial threads also reduces the work required by the adhesive capture threads to successfully adhere to prey.

Toughness is a common metric for comparing the work done until failure for materials and in the context of web, toughness expresses the amount of energy a silk thread absorbs before breaking (Agnarsson, & Blackledge, 2009; Agnarsson, Boutry, & Blackledge, 2008; Blackledge, Cardullo, & Hayashi, 2005); it is a measure of material strength normalized by the volume of the sample. While toughness is important for comparing energy absorption between materials, ultimately, the volume of material present in the system determines the energy absorbing capability and success rate of prey capture (Sensenig et al., 2012). Silk volume and toughness are interrelated in their determination of maximum prey energy because energy can be absorbed either by a small amount of high toughness material or a large amount of low toughness material (Sensenig, Agnarsson, & Blackledge, 2010; Sensenig et al., 2012). Thus, spider web architecture can be modified to aid in prey retention by increasing the volume of silk to which prey come in contact with through increasing thread thickness or thread length.

Although moths are abundant in many ecosystems, they are unusually difficult prey for orb spiders to capture because the wings and bodies of moths are coated in small scales that flake off, coating the outer surface of the capture spiral's glue droplets and reducing web adhesion (Eisner, Alsop, & Ettershank, 1964; Stowe, 1986). Moth-specialist spiders have evolved several strategies to catch this elusive prey through changes in orb web structure and/or silk properties. In at least two instances, hyper-elongation of vertical orb webs evolved such that moth tumble down an elongate capture surface until their scales are rubbed off and the glue can adhere to an effectively "clean" surface (Stowe, 1986). However, these ladder webs require a substantial investment of time and materials for spiders to spin the large capture surface with its tightly packed capture spiral. Inversely, *Cyrtarachne* is a genus distributed throughout Asia and Oceania that uses a reduced horizontal orb web. These webs consist of very widely spaced capture threads that hang loosely from sparse supporting radii, and which appear to have a specialized glue that sticks especially well to moths (Cartan, & Miyashita, 2000; Shinkai, 2006; Stowe, 1986; Yeargan, 1994; Eberhard, 1980, 1990). Prey usually strike only one or two capture threads yet stick readily to these webs (Miyashita, Sakamaki, & Shinkai, 2001; Stowe, 1986). Capture threads are normally attached to the radial hub using an attachment silk known as piriform silk (Foelix, 2011). Often these capture threads are strongly attached at both ends. Capture threads usually fail before this bond breaks but within *Cyrtarachne* webs, one end of the capture threads contains a "low-shear joint" that breaks upon contact with prey (Foelix, 2011; Stowe, 1986), leaving the other end securely fastened to the radii. Compared to typical orb weavers, *Cyrtarachne* webs contain fewer capture threads covered in a larger volume of aggregate glue. Precisely how the glue sticks to moths is unknown, though proposed hypotheses vary from their utilization of larger droplets than traditional orb-weavers to extraordinary tensile properties (Cartan, 2000).

In typical orb webs, major ampullate silk deforms in the radii to dissipate prey energy, with the capture spiral contributing very little to this process (Sensenig et al., 2012). For all but the smallest prey, at least one radial thread must contact the insect—the majority of prey who strike only capture threads break through the web and are not retained (Sensenig et al., 2012). In *Cyrtarachne* webs, the radii function to support the capture silk but prey typically only contact the capture silk during impact. The wide spacing of the capture threads also means that typically only a single capture thread contacts the moth and individually must dissipate the bulk of the moth's flight energy. Prior analysis of *Cyrtarachne* capture thread tensile properties suggested that it was exceptionally strong, but the silk still seemed to be too weak to dissipate estimated prey energy (Cartan, & Miyashita, 2000). We aim to determine if evolutionary pressure on the relative material properties of the silk spun within *Cyrtarachne*'s reduced web have resulted exceptionally tough capture silk. Here, we test both the capture and radial threads from the web of the species *Cyrtarachne akirai* and compare them to other orb-weaving spiders using an updated and more sensitive testing method calculating the Young's modulus and stress and strain at break. We then compare thread diameters to a model orb-weaver species, *Larinioides cornutus*, and these material properties to previous data on several common orb-weavers.

Second, we hypothesize that the reduced web architecture of *Cyrtarachne* leads to better prey retention potential for individual capture threads. In a vertical web capture thread length is limited by the length of the gap between adjacent radial threads due to the risk entanglement between them. The horizontal orientation of *Cyrtarachne*'s web allows the creation of longer capture threads by hanging them loosely. This increased length leads to an increase in the total work that a single span of capture thread can perform relative to a typical orb web. To test this hypothesis, we created a Finite Element Model using the measured material and structural properties of threads to determine how this unique web dissipates prey energy. We predict that prey energy would be dissipated primarily by the stretching of the individual capture thread contacted by the moth.

2 | MATERIALS AND METHODS

2.1 | Housing of *Cyrtarachne*

Nine mature female *Cyrtarachne akirai* (Tanikawa, Shinkai, & Miyashita, 2014) were collected from tall grass surrounding several rice paddy fields in Chiba prefecture, Japan from June 2015 to September 2015 (35.65635 ° N, 140.2425° E). *Cyrtarachne* were collected in tubes and then immediately shipped to The University of Akron where they were housed in the laboratory for 2 to 3 months.

Spiders were housed in one of three sizes of plastic cages—height × length × width—27 × 17 × 16 cm, 20 × 20 × 20 cm, or 37 × 24 × 21 cm. *Cyrtarachne* require high humidity to induce web spinning (Miyashita, 2017; Baba, Kusahara, Maezono, & Miyashita, 2014), and so cages were designed similarly to those used to house *Pasilobus*, a sister clade that also builds similar webs only at high humidity (Miyashita, Kasada, & Tanikawa, 2017). The floor of each tank was layered with damp towels and filled with approximately 8 cm of water. Tanks were sprayed with water nightly and allowed to dry in the morning. Finally, tanks were wrapped in moist towels during the night to help further maintain adequate humidity. *Cyrtarachne* were fed by placing crickets in their webs if a web was found and the spider had not eaten within the last 7 days.

Spider tanks were checked between the hours of 5 and 8 AM. Fresh webs were most often collected for testing between 8 and 10 AM. Time in captivity prior to making their first web varied between 2–14 days, and spiders typically spun a new web in a position where it could be successfully sampled every 3 days.

In order to directly compare thread properties to a more readily studied orb-weaver, between June and September, eight *Larinioides cornutus* were collected in the early evening from a bridge located in Akron, OH, USA (41.1351682°N, −81.54862730000002°E). Specimens were placed in individual cages and housed at ambient room humidity in the lab of T.B., located in the Auburn Science and Engineering building at the University of Akron, The green house is open to the outside environment and conditions varied based on weather conditions. Cages were sprayed nightly with water to maintain humidity. Crickets were placed in webs every 2–3 days once spiders had begun to eat. Webs were removed the next day to insure the specimens created fresh webs for testing.

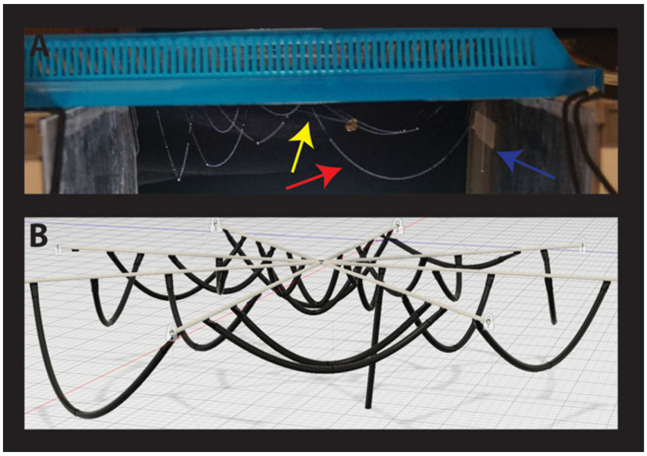

FIGURE 1 Typical web and a finite element model of a web produced by *Cyrtarachne*: (*a*) *Cyrtarachne* utilize a reduced orb web structure which consists of a horizontally oriented orb web with large spacing between long dangling capture threads, red arrow. One end of each of these capture threads contains a "low-shear joint", which breaks upon contact with prey. Sometimes these strands snap prematurely and create a pendulum, blue arrow (often with a large glue at its end). The spider can be seen anchored to the radial thread hub in the center, yellow arrow. The entire web structure is not visible due to partially being attached to the top of the tank. (*b*) Our model consisted of a radial hub made from the intersection of four 100 mm long major ampullate threads. These threads are each connected by long dangling flagelliform threads. Flagelliform threads were 1.5× thicker, 1 mm, than the radial hub threads, 0.66 mm. Due to mesh size limitations thread thickness had to be scaled up. Distinct material properties were applied to the major ampullate and flagelliform threads using our measured values and estimates taken from Vollrath (2001) and Koshi (2013); These values were yield strength, breaking tensile strength, Poisson's ratio, Young's modulus, and density [Color figure can be viewed at wileyonlinelibrary.com]

2.2 | Collection of silk

Once *Cyrtarachne* constructed a web, two adjacent samples of viscid thread were collected from the same span of capture silk. One thread was adhered to paper cards across a 12.58 mm gap for tensile testing while the other was collected onto a glass microscope slide for imaging. Between one and four samples were collected from each web, dependent on the size of the web and whether the spider was disturbed enough that it began to recycle its web during collection. Silk was glued to the cards using polyvinyl acetate, which dries relatively quickly but does not dehydrate the silk strand. For *Larinioides*, capture threads were only collected on paper cards with gaps measuring 12.58 mm.

Cyrtarachne rarely made webs on consecutive nights, and often did not make webs for several days after being fed, limiting the total amount of webs we were able to study. Therefore, all samples were pooled within treatments and *N*-values represent individual threads rather than webs.

2.3 | Microscopy and scanning electron microscopy of tensile diameters

Diameters of *Cyrtarachne* capture threads were measured to calculate cross-sectional area for tensile properties such as toughness and stress. *Cyrtarachne akirai* threads were placed on microscope slides and imaged at 100× magnification on a Leica dmlb2 optical microscope. Pictures were taken using an Olympus q color 5 camera (Blackledge et al., 2005). Thread diameter was then measured using Image-Pro (Agnarsson, Dhinojwala, Sahni, & Blackledge, 2009). Each capture thread consisted of two flagelliform threads. In addition, thread diameters were compared between radial (N = 14) and capture threads (N = 20) within each web (if both were able to be collected). The thickness of flagelliform and major ampullate strands present in the webs were averaged for each spider and these values were graphed against previous measurements of commonly studied orb-weaver species from Sensenig et al., 2010. Mean thickness of each capture thread was calculated and paired t-tests were conducted to determine the difference in ratio of radial and capture thread diameters spun by the same spider.

A subsection of major ampullate and flagelliform thread samples that were collected from the same web were sputter-coated in gold for 1 min and these thread diameters were measured and compared using scanning electron microscopy (SEM) between 188× and 22,588× magnification. Sputter coating added approximately 0.015 μm of thickness to test samples, which should not bias thread thickness measurements (Quorum Technologies, 2002). SEM photos were used to confirm relative thickness ratios observed between capture and radial threads measured through optical methods but were not analyzed statistically.

2.4 | *Cyrtarachne* species tensile material properties comparison

Tensile tests were conducted at the University of Akron, OH using a Nano Bionix® tensile tester (MTS Systems Corp., Oak Ridge, TN, USA). Tensile tests were conducted at 88–90 RH for radial strands (N = 24) and capture threads (N = 31) collected from 15 different webs. This humidity was chosen due to *Cyrtarachne akirai*'s preference for environmental conditions over 80% relative humidity (Baba et al., 2014). To create this high humidity environment, three humidifiers were run within a closed room, in conjunction with an environmental chamber on the tensile tester. Room humidity was measured consistently by a Traceable Hygrometer—VWR, Model 33500–098. Tensile test samples were immediately placed into the grips of the tensile machine after being collected from the web and the silk was then allowed to acclimate to room humidity, ~2 min. Force as a function of time was measured by the Nanobionix UTM machine until the thread snapped. Strain values were calculated using the known gauge length of 12.6 mm (Blackledge, & Hayashi, 2006a). Tests were conducted at 0.015% strain/s, 0.19 mm/s. This value was chosen since it was close to the 0.16 mm/s used by previous studies (Koski, Akhenblit, McKiernan, & Yarger, 2013). Engineering and true values for stress and toughness were calculated from these force measurements. Engineering and true strain values were calculated as the percentage of displacement beyond the known starting gauge length. Properties were calculated assuming constant volume. Means and standard errors were calculated for each tensile property pooling all samples. Average tensile characteristics were compared to more commonly studied orb-weaving spider species to determine if *Cyrtarachne*'s properties were truly extraordinary.

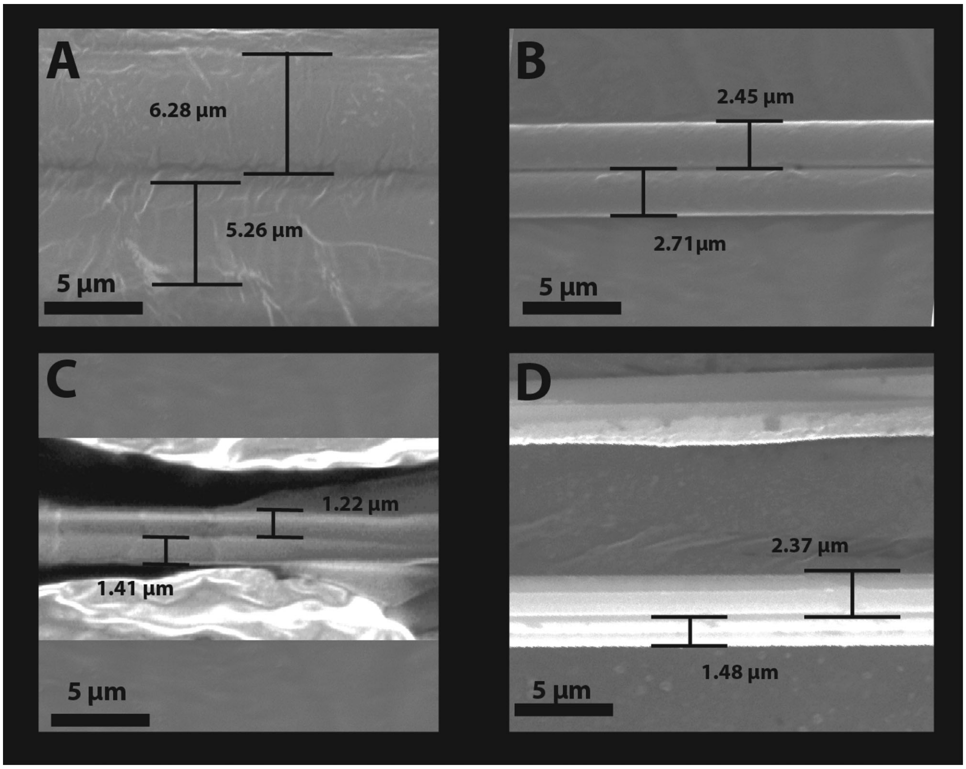

FIGURE 2 Major ampullate and flagelliform thread diameter comparison. (*a*) Scanning Electron Microscopy of *Cyrtarachne akirai* capture silk at 5647×. (*b*) Scanning Electron Microscopy of *Cyrtarachne akirai* radial silk *at* 11,294× from the same web as shown in (a). (*c*) Scanning Electron Microscopy of *Larinioides cornutus* capture silk at 22,588×. (*d*) Scanning Electron Microscopy of *Larinioides cornutus* radial silk at 5647×. *Cyrtarachne* spins capture threads which are thicker than their associated major ampullate threads. This relationship is the inverse of typical orb-weaver species, such as *Larinioides*, which spin thicker major ampullate threads in their webs to act as the primary source of prey energy absorption. This might be due to *Cyrtarachne*'s unique web structure which relies on capture threads as its primary method of prey energy dissipation

For all radial thread ($N = 24$) tensile tests the Young's modulus was calculated for the linear portion of the stress–strain curve. For capture thread tests ($N = 31$), which showed very little yield, the modulus was calculated by determining the slope of the curve between the beginning of the test and 0.4 mm of extension where the stress was still close to zero.

2.5 | Finite element analysis (FEA) of *Cyrtarachne* web structure

The horizontal reduced orb-web structure of *Cyrtarachne* relies on the collision between prey and a single capture thread. The energy of incident prey must be dissipated by that single capture thread and its connecting radial thread. This differs from the typical orb-web structure which relies on the collision of prey with radial threads to absorb prey energy and subsequent capture threads to retain prey (Sensenig et al., 2012). To analyze the propagation of energy and view the areas of high stress within the *Cyrtarachne* capture web, a finite element model (FEM) was created using Fusion 360 (Autodesk Fusion 360, 2018).

The model consisted of eight 50 mm long major ampullate threads that were joined in the center to create the hub of the web. Radial threads supported 2–4 capture threads, which arced below the plane of the web hub. For simplicity, we assumed that the piriform silk connections between capture threads and radii were rigid. Capture thread diameter was set to 1.5× the size of the radial threads, which was taken from our measurement of real webs. The outer ends of each radii were considered rigidly connected the substrate, the web would be built on and were unable to move. A *Cyrtarachne* web and our model are shown in Figure 1. These dimensions are similar to the averages measured in Cartan and Miyashita (2000) of a web with a diameter of 13 cm with 2–3 capture threads strung between radial threads.

We plugged the measured values for Young's modulus, breaking true stress, and yield stress measured from our tensile tests into the model. These values were used internally by the Fusion 360 system to calculate the ultimate toughness of the threads. Unfortunately, Fusion 360 is only currently capable of modeling linear material properties, which limits our model due to spider silk naturally behaving as a viscoelastic solid. This linear modeling over-estimates the toughness by increasing the work done by threads prior to fracture. Thread density and Poisson's ratio were set to 1.3 g/cm^3 and 0.49, respectively (Koski et al., 2013; Vollrath, 2001). For simplicity, piriform silk properties were listed as the same as capture threads.

Due to limitations in processing power the threads were not able to be properly meshed at life size thread diameters, major ampullate = 6 μm and flagelliform = 10 μm. To ease simulation computations silk threads were modeled as a single large strand. Because a single thread of diameter 10 μm would have greater cross-sectional area than two 5 μm threads so applied forces were doubled. Thread model cross sectional area was increased by basing on a major ampullate diameter of

TABLE 1 List of tensile properties of *Cyrtarachne akirai* major ampullate and flagelliform silk: Tensile properties measured through strain to break with calculated standard errors. Unit less strain values are expressed as the ratio of initial length to thread length at fracture (L_0/L_f) in mm

Silk Type	Major Ampullate (*N* = 24)	Flagelliform (*N* = 31)
Average Single Fiber Diameter (μm)	3.78 ± 1.28	6.13 ± 2.15
Young's Modulus (GPA)	2.65 ± 0.31	0.007 ± 0.004 (N = 19)
Toughness (MJ/m^3)	184.29 ± 20.78	177.62 ± 36.59
Engineering Strain (at break) (mm/mm)	0.89 ± 0.06	6.43 ± 0.52
True Strain (at break) In (mm/mm)	0.62 ± 0.03	1.92 ± 0.07
Engineering Stress (at break) (MPa)	504.05 ± 49.09	111.81 ± 25.05
True Stress (at break) (MPa)	948.35 ± 97.11	853.1 ± 235.5

0.6 mm and a flagelliform fiber diameter of 1 mm. Applied forces were then scaled by multiply them by the percentage increase, 2500×, in volume between our natural and model silk threads. This was known as our thick thread condition. We sought to determine the influence of thread diameter on energy propagation and created a model where capture threads were smaller than radial threads using the common 1.43: 1 ratio, Major Ampullate = 6 μm and Flagelliform = 4.20 μm (Sensenig et al., 2010).

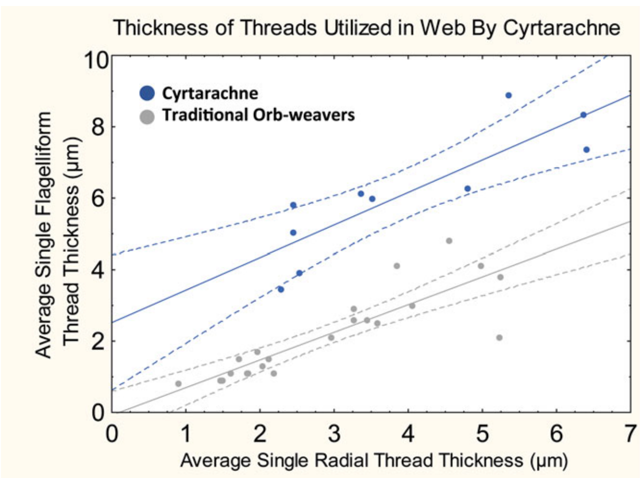

FIGURE 3 Diameter of major ampullate and flagelliform threads present in *Cyrtarachne* web: Average single radial threads versus single capture thread strand thickness for *Cyrtarachne*, blue, average shown with error bars, compared to thread thickness of common orb-weavers species with trend line; gray, previously measured in Sensenig et al. (2010). Single strand capture thread diameters used in *Cyrtarachne* webs are 1.61× larger than that of radial threads spun ($P = < 0.001$). *Cyrtarachne* falls outside of the 95% confidence interval, shown in light gray, around the trend line ratio of other species in capture diameter relative to radial threads. Radii are ~1.4× thicker as calculated from Sensenig et al. (2010) [Color figure can be viewed at wileyonlinelibrary.com]

In a horizontal *Cyrtarachne* web in the field, a captured moth falls downward and does not become tangled in additional threads, leaving them typically tethered by a single capture thread. Cartan and Miyashita (2000) calculated that the kinetic energy of flying moth prey during tests for *Cyrtarachne* was between 7 and 54 μJ with an average of 23.7 μJ. Due to limitations in the FEA software, we were unable to apply impulse forces upon our model and instead applied remote static forces. To determine our loading conditions, we used the weight of a large wax-moth, *Achroia grisella*, 27.2 mg, and multiplied by our volume increase to calculate the scaled kinetic energy of our prey (Jang, & Greenfield, 1998). To convert prey kinetic energy into a force, we calculated how much force would be necessary to stop the prey energy over the length of 5 mm. In nature, *Cyrtarachne* threads will typically stop prey momentum over several centimeters, which we believe makes our 5 mm stopping distance representative of a ceiling of possible force exerted by this prey's momentum. This decision biases our model against our capture threads, which normally extend as much as 5–10× their length without breaking, as it should apply higher than natural forces. Our calculations resulted in incident forces of 17.46, 55.94, and 113.24 N. These values were applied along a single long capture thread that hung perpendicular to the horizontal plane of the web and then to one of the radial threads. In a horizontal web, as the moth attempts to drop it may do so by removing its forward momentum, accidentally making it easier to retain them. The loose structure of the spanning threads may "trick" the moths into slowing their flight enough that the overall momentum transferred to silk is minimized. In this case the amount of energy which needs to be dissipated is substantially less, making our load forces 2.67 N. This was again applied to both types of threads. Stress, strain, and overall safety factor (breaking stress-strain/applied stress-strain) experienced by the web was calculated using Fusion 360′s static load software. This was done to determine energy propagation, and stress–strain distribution in this unique web structure relative to that of a typical orb-web structure.

3 | RESULTS

3.1 | Major ampullate and flagelliform thread diameter

Single flagelliform threads ($N = 22$) were 1.6× thicker than single major ampullate threads spun within *Cyrtarachne*'s web ($N = 18$, *t*-test $P \leq 0.001$). This is unusual as most spider webs rely on thicker, stiffer radial threads to absorb prey impact energy. For example, Figure 2 shows the SEM images comparing diameter between major ampullate and flagelliform threads from the webs of *Cyrtarachne akirai* and that of a typical orb-weaver, *Larinioides cornutus*. *Cyrtarachne*'s utilization of thicker capture threads than radial threads is unique as shown by Figure 3. This figure shows the radial versus capture thread thickness of optically measured thread bundle diameter for 22 orb-weaving spider species previously measured by Sensenig et al. (2010). The ratio of radial to capture thread is shown as 1.43 ± 0.34.

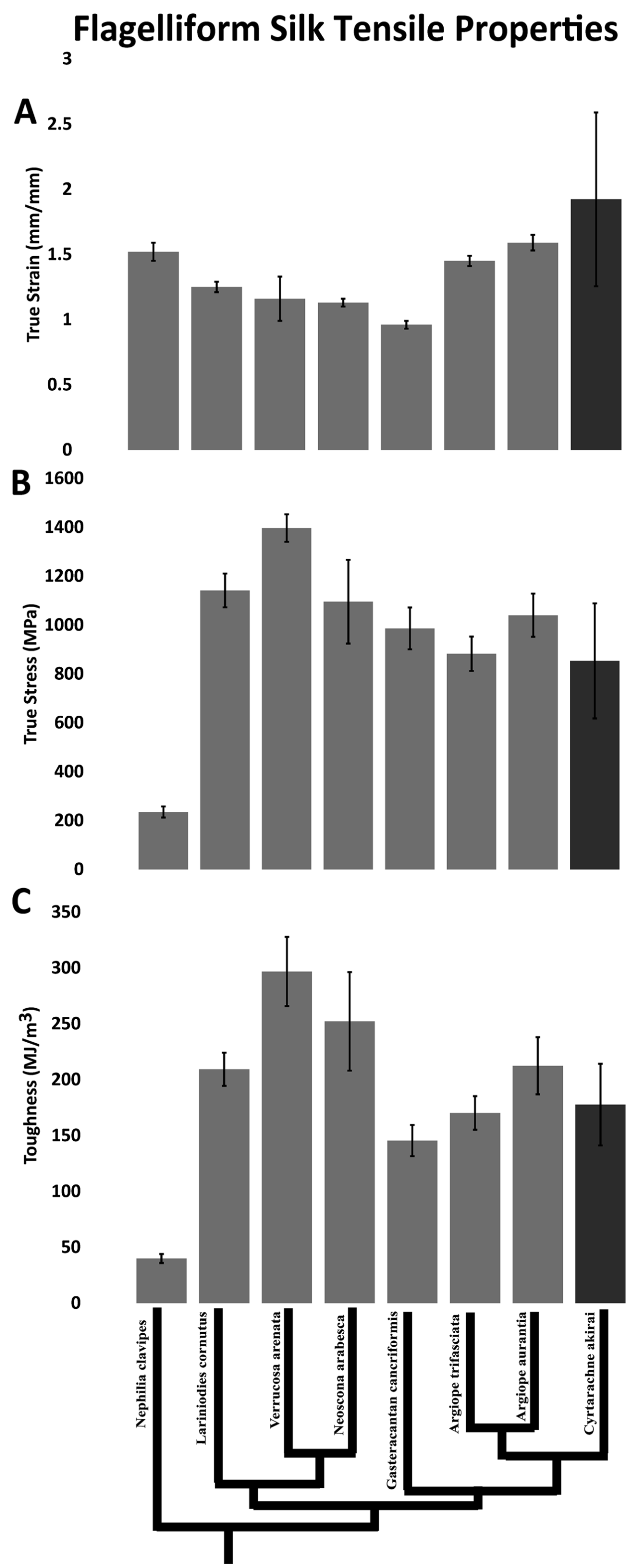

FIGURE 4 Graphs comparing flagelliform thread tensile properties between several species of orb-weaving spiders: The red tinted graphs correspond to *Cyrtarachne* test conditions, red, 90% RH with other species are shown as blue. At the bottom of each figure is a corresponding phylogenetic tree used to display the relatedness of these spider clades (Scharff & Coddington, 1997). This phylogeny was used as it contains all compared species. Graph (a) displays the average true strain for various spider species' capture thread. Silk produced by *Cyrtarachne* are proportionally as extensible as many other thick threads. Graph (b) shows the average True stress for various spider species' capture thread. Silk produced by *Cyrtarachne* has true strain is on the high end for spider species but not unusual than other commonly tested species. Graph (c) displays the average toughness for various spider species capture thread. Silk produced by *Cyrtarachne* are proportionately as tough as other measured silks. Values for other spider species taken from Agnarsson et al. (2009) and Swanson (2007) at room humidity

3.2 | Tensile strength of major ampullate threads and flagelliform threads

Tensile properties of both radial and capture threads are shown in Table 1. Average tensile diameters are of single fibers and refer to average diameter among all tensile tests conducted of that type. Overall thread toughness was found to be the same for major ampullate and flagelliform threads. Interestingly, radial threads were found to be highly extensible for their type, straining 2× or ~0.3 ln (mm/mm) more than other tested major ampullate threads. Capture threads are highly extensible as well, but they were not unusual compared to other species. Figure 4 shows how *Cyrtarachne* flagelliform thread's average true strain, true stress, and toughness values compared to more common orb-weaver species. Figure 5 compares the average true strain and toughness of *Cyrtarachne* major ampullate to other orb-weaver species.

3.3 | Finite Element Analysis (FEA) of *Cyrtarachne* web structure

Applying force to a single radial thread caused high levels of strain and stress to be propagated along all radial threads, leading to hub failure. This condition was true for all loading conditions. Bending of the incident radial thread led to high levels of radial displacement with little transfer of energy to capture threads. Safety factors dropped below 1, meaning structural failure would most likely have occurred.

Energy propagation through a naturally proportioned capture thread, thick, applied a more spread out stress among all radial threads with very little propagation to surrounding capture threads or displacement of the web hub until the highest two test conditions. This seems to imply that preys captured in a web cause little damage to the overall structure even if they thrash or escape. The web structure was stable at the two lowest energy conditions, though areas of high stress did occur at the impact site. The highest areas of strain and stress were located at piriform junctions between the capture and radial threads.

When forces were applied to the model with thinner capture threads the capture thread failed once the prey had any kinetic energy. Ultimately, energy propagation was the same for force applied to capture threads. Thick capture threads required higher forces before failure occurred. Figure 6 shows the energy propagation within a typical orb-web structure when force is incident upon the thin and thick capture threads, and radial threads for our two lowest test conditions. Supporting Information Figure 1 shows the energy propagation of all webs at all test conditions.

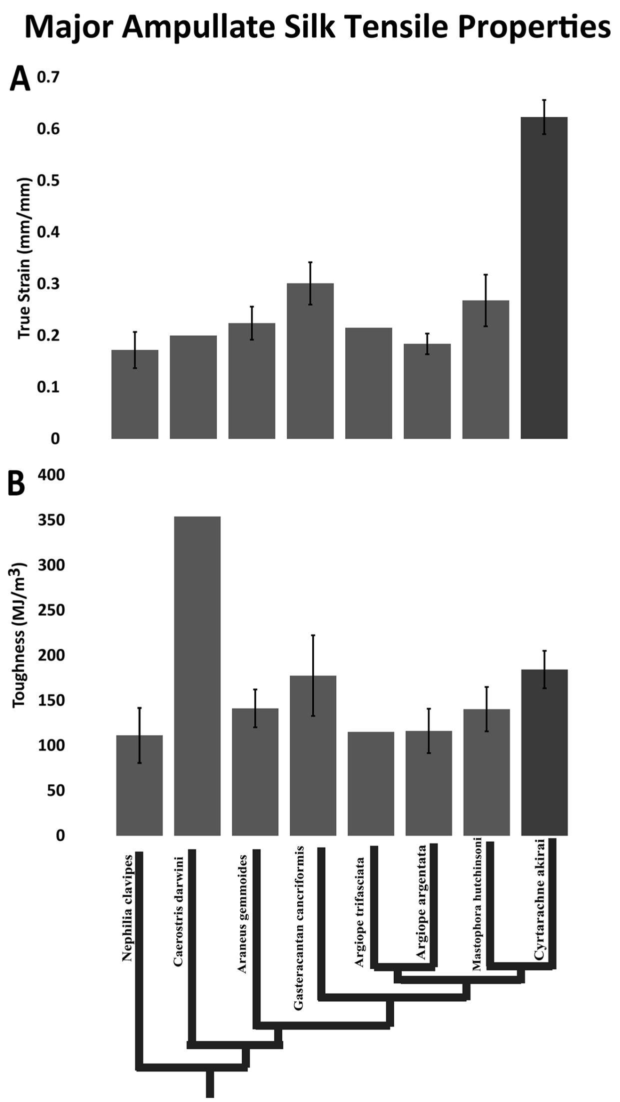

FIGURE 5 Graphs comparing major ampullate thread tensile properties between several species of orb-weaving spiders: The red tinted graphs correspond to *Cyrtarachne* test conditions, red, 90% RH with other species are shown as blue. At the bottom of each figure is a corresponding phylogenetic tree used to display the relatedness of these spider clades (Scharff & Coddington, 1997). This phylogeny was used as it contains all compared species. Graph (a) displays the average true strain for various spider species' capture thread. Major ampullate silk s produced by *Cyrtarachne* is more extensible than other recorded silks. Silk produced by *Cyrtarachne* has true strain that is higher than other commonly tested species. Graph (b) displays the average toughness for various spider species capture thread. Silk produced by *Cyrtarachne* are proportionately as tough as other measured silks. Values for other spider species taken from Swanson et al. (2006) and Agnarsson et al. (2008) and except for *Caerostris darwini* (Agnarsson, Kuntner, & Blackledge, 2010)

4 | DISCUSSION

We aimed to test the tensile properties of the major ampullate and flagelliform silk utilized by the moth specialist genus *Cyrtarachne* to determine if its web retains its prey by using extraordinary tensile properties, leading to enhanced prey stopping potential. Specifically, we tested the hypothesis that utilization of isolated capture threads would result in viscid threads with exceptionally higher toughness than typical orb-weaver capture silk to absorb prey collision energy, which is generally absorbed by collision with the webs radial threads. We discovered that the capture threads used by *Cyrtarachne* are not proportionately different from the capture threads utilized by other studied orb-weavers. We also discovered that the webs of *Cyrtarachne akirai* utilize major ampullate threads that are smaller than their flagelliform counterparts, the opposite of traditional orb webs from which they are derived. In our model, contact with a radial thread led to extensive damage. In contrast, contact with a capture thread at the highest prey energy led to only minimal damage. The web of *Cyrtarachne* seems well equipped to absorb the energy of even large prey.

Overall, *Cyrtarachne* radial threads and capture threads show proportionally average tensile properties compared to other species. Strangely however, radial threads were found to be highly extensible compared to other major ampullate threads. This might be because *Cyrtarachne* only spins webs at 90% RH. Major ampullate silk undergoes super-contraction at high humidity, which may tighten *Cyrtarachne* capture threads in their webs, allowing them to extend further due to increased radial silk density per length (Blackledge et al., 2009; Work, 1985). From a structural perspective, this would allow the frame to strain further when pulled upon by contact with a capture thread, and lower overall stress on the remainder of the web during prey retention. Although capture threads of *Cyrtarachne akirai* showed average strain at break, their maximum strain was high among spiders and showed extensions up to 10 times its initial length (Agnarsson, 2009). This is not unheard of since it has been documented that capture threads can often stretch anywhere between two and 10 times their original length depending on test humidity and pulling speed (Blackledge, & Hayashi, 2006b, Opell, 2000). Due to their higher average environmental humidity, tests for *Cyrtarachne* were conducted at 90% RH whereas others were conducted at 60% RH. This biases our threads to both higher strains and Young's modulus and implies that elongation for *Cyrtarachne* at the same humidity as the other tests species would be lower, further supporting that threads are mediocre (Agnarsson, 2009; Agnarsson et al., 2009; Swanson, Blackledge, & Hayashi, 2007).

The method of prey retention thus is not the particular mechanical properties of the silk produced by *Cyrtarachne* but primarily the overall structure of its web. *Cyrtarachne* utilizes thicker capture threads made of two flagelliform fibers that are both thicker than those spun by spiders of similar size and these threads are thicker than their radial threads (Cartan, & Miyashita, 2000). In a typical web, the spider relies on the radial threads to absorb large prey but due to the widely spaced nature of the capture threads *Cyrtarachne* retains prey with contact with only a single capture thread. This leads to less overall stress being placed on tough radial threads, lowering evolutionary pressure on them and allowing them to function while being thinner. This however makes it so that *Cyrtarachne*'s individual capture threads have to undergo higher stresses compared to common orb-weaver species (Miyashita et al., 2001). We found this increase in stress is offset by longer and looser capture threads spun by *Cyrtarachne* as it creates its web. This is the key to understanding how they are capable of absorbing the energy of prey fall without snapping. This structure enhancing

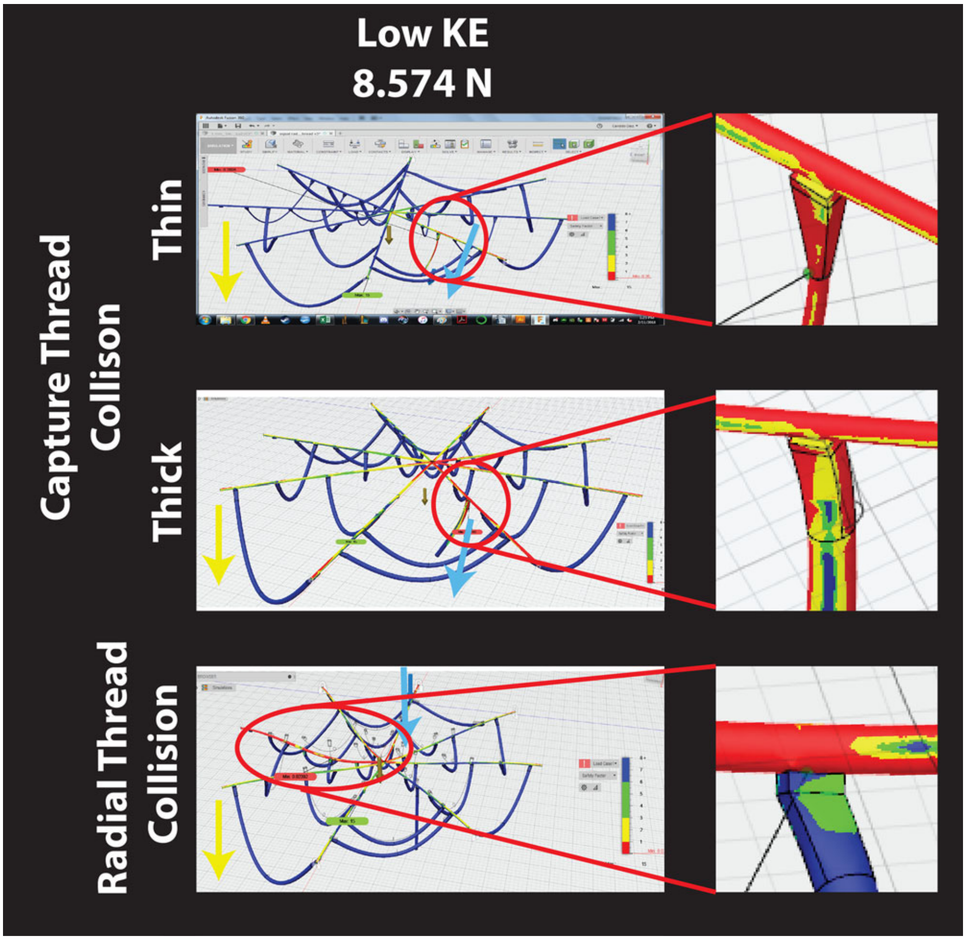

FIGURE 6 Finite element analysis of energy propagation through a *Cyrtarachne*: Each panel shows the safety factor of our model after force application. The yellow arrow signifies the direction of gravity. The blue arrow shows the remote force applied to the web. Red signifies areas of low safety factor, <1, which would indicate web failure. Dark blue are areas of high safety factor and structurally sound under the applied forces. The top row shows the reaction of our thin capture threads under the low KE force condition. The second row shows the same forced applied of our naturally proportioned thread model. At low KE our thin thread completely fails, which can be shown by a hole in the thread after the failed faces have been removed. Our thick capture threads begin to experience low safety factor regions but once you remove the failed faces it can be seen that a connection and solid radial thread still exist. This we interpret as a structurally sound web remaining. The bottom row shows low KE conditions when applied to a radial strand. Comparing the response of our model for the same magnitude of force applied to radial for capture threads show far more extensive damage caused by collision with a radial thread. Energy propagates significantly further and affects over all web structure. It also fails at all energy conditions [Color figure can be viewed at wileyonlinelibrary.com]

form extends prey capture time, lowers impulse forces, and ultimately provides more volume of flagelliform thread. This allows prey to fall for several centimeters before the thread begins to stretch and energy is absorbed.

Within our model, when forces were applied to the radial threads the web hub failed and energy was propagated into the nearby capture threads. When forces were applied to the capture threads, however, stress was more evenly spread out along the radial threads, leading to overall lower levels of strain and stress. Under these conditions, it seems *Cyrtarachne*'s web is strengthened for lower energy impacts. Smaller prey's energy is easily dissipated utilizing a single thread, but our model also hints that *Cyrtarachne* may rely on multiple strand collisions to retain larger prey. It is important to note that our model is biased against capture threads by forcing them to absorb force over a shorter fall distance than would typically be found in nature. Thinning of the capture thread diameter to coincide with typical orb-weaver major ampullate to flagelliform proportions lead to failure at much lower forces. We believe this shows the increase in capture thread diameter relative to radial thread diameter is important in prey capture as it allows single flagelliform threads to perform more work prior to tensile failure. The culmination of web structure and prey behavior aids in explaining why *Cyrtarachne* is capable of stopping prey with overall average toughness flagelliform silk.

In this web structure, capture threads act as tethers transferring forward momentum into angular momentum and lowering the relative tension incident on the glue droplets compared to a full speed collision. Collision and flight energy might be further decreased by prey self-deceleration. Thus capture threads would only need to absorb the free fall energy of the insect. These factors might explain why evolutionary pressure was not placed on tough threads. By relying on prey to slow their own motion, *Cyrtarachne* webs may take longer to stop prey but in turn lower the momentum and thus impulse force placed on the cuticle of the prey. Striking of radial threads may only be necessary in web structures where prey have a higher momentum and a substantially higher impulse force is placed on the web since typical orb webs aim to absorb prey energy as fast as 100 ms (Sensenig et al., 2012). Lowering this force would lower the burden of energy absorption placed on these individual capture threads.

It is important to remember that this unique web structure not only relies on a single thread but on the incorporation of large glue droplets. The aggregate glue placed on capture threads is responsible for its stickiness and often aids in hydrating viscid silk (Blackledge, 2006b; Vollrath, 1989). Given our discovery of *Cyrtarachne*'s average capture threads, it is necessary to study its aggregate glue as it is vital to understanding how *Cyrtarachne* retains prey. Its decrease in reliance on capture threads is offset by its greater dependence on aggregate glue adhesion. From our tests it seems that *Cyrtarachne* have not adapted their flagelliform thread properties specifically, but may have other adaptations that aid in the capturing of moths, most specifically their web structure and the adhesive properties of their aggregate glue. If we wish to understand how *Cyrtarachne* is capable of retaining their 'contaminated' prey to aid in our own synthetic systems, it seem apparent that we will need to assess the material properties of the aggregate glue present in webs.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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