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Super-Tough Silk: The Potential of Knots in Evolved Spiders

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Spider silk is renowned for its exceptional mechanical properties, combining low density with high tensile strength and high extensibility and thus very high toughness modulus (*t*., i.e., dissipated energy per unit mass). However, the potential toughness of spider silk can be significantly enhanced if spiders evolved the -currently absent/undiscovered- ability to tie knots in their silk. This advancement will allow for a new level of gigantic toughness (*T*) revealing today "hidden toughness", mimicking human engineering techniques and in particular a related proposal by the author used for realizing the world's toughest fibers. Indeed, knotting can provide additional energy dissipation via friction, enabling spiders to construct webs and traps with unprecedented efficiency. To quantify this scenario, the author calculates the gigantic toughness of 393 real spiders virtually assumed with evolving knot-making behaviors, showing toughness gain ($G = T/t$) of about one or two orders of magnitude. The resulting "super-tough silk" can benefit spiders in their natural habitats and suggests a new perspective on how knotting can serve as a key innovation in spider evolution and in Biology in general.

1. Introduction

Spiders can produce different types of silks for a variety of purposes, such as making webs for capturing preys, sheets for wrapping objects, anchorages for connecting threads to surfaces, nest-building, cocoons for protecting eggs, dragline for safe locomotion, ballooning for rapid movement[1] and even using it as a tool for lifting large masses.[2,3] Spider silks and webs are in general remarkable examples of natural materials and structures that play a crucial role in the spider's survival.[1]

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On the one hand, spider silk has attracted significant attention for material scientists due to its combination of high strength and high deformability and thus very high toughness.[4] On the other hand, the architecture of spider webs provides not only a functional solution for catching preys but also serves as an inspiration for structural engineers.[5] Replicating the remarkable properties of spider silk fibers presents a major challenge to materials scientists,[6] while understanding the web response is equally crucial for engineers.[7]

Research of nearly the last decade, however, suggests that the separate consideration of material properties and structural design is insufficient for understanding spiderweb performance.[8] The material properties of the silk and the structural design of the web are tightly interdependent, creating enhanced functionality through synergistic interactions.[9] These interactions are also evident in spiderweb junctions,[10] where structural features contribute to the web's overall resilience. In particular, at the microscale level in spider silk[4] and at the mesoscale level in spider web junctions[11] and anchorages,[12] the concept of a "hidden length" plays a pivotal role in enhancing the toughness of the material. This hidden length allows for substantial elongation or deformation under relatively high force or stress, resulting in impressive specific energy dissipation and thus material toughness. This hidden length also improves the structural robustness of the web.[9]

In parallel, there has been a growing interest in materials science to develop new materials with high strength and toughness, aiming to surpass the mechanical properties of existing high-performance fibers. Advancements have seen the production of macroscopic carbon nanotube bundles and graphene sheets, though their macroscopic strength remains well below than their theoretical potential (≈100 GPa)[13–15] due to defects that by force statistically increase in number with the size-scale.[16] However, significant progress has been made in improving their toughness. For instance, composite carbon nanotube fibers have been developed with toughness modulus values as high as 570 J g^{-1},[17] or 870 J g^{-1},[18] and even 970 J g^{-1} when combined with graphene.[19] These values far surpass high-tech tough materials like Kevlar, which has a toughness modulus of ≈80 J g^{-1}, or like artificial spider silk today able to reach 110 J g^{-1} (the silk density assumed for computing this number is equal to $\rho = 1300$ kg m^{-3})[6] or even like spider silk itself, with a record toughness of 390 J g^{-1} for the giant riverine orb spider.[20] Also, from spiders fed with nanomaterials, a bionic silk with a toughness modulus up to 588 J g^{-1} (the silk density is again assumed here

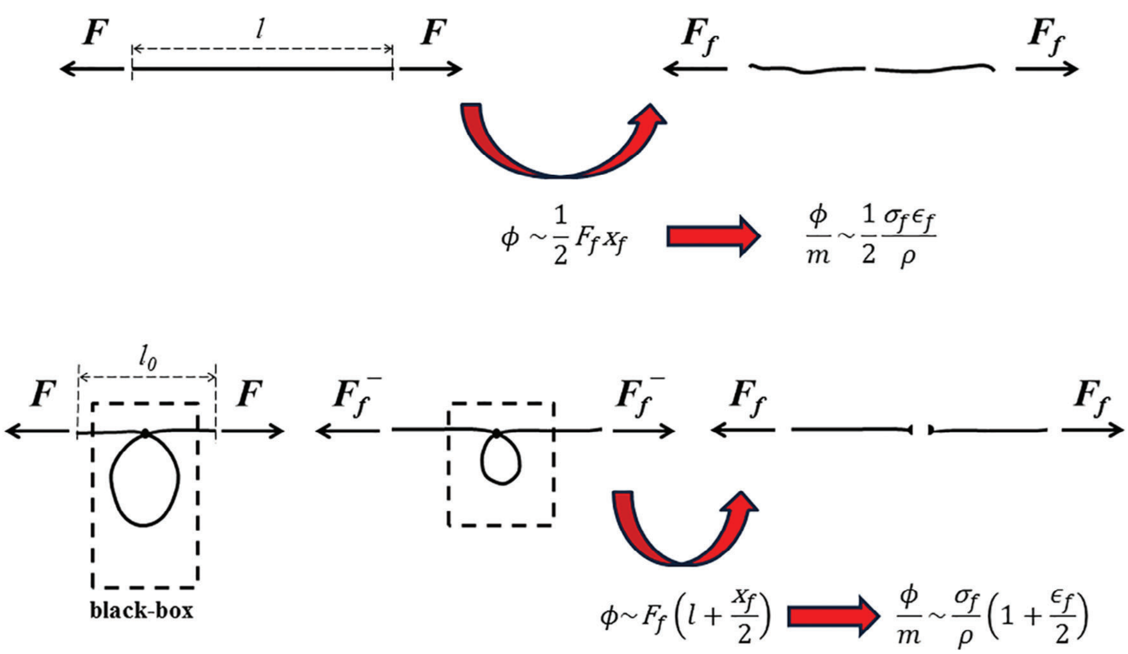

Figure 1. Knots as a key for gigantic toughness. A classical fiber dissipates during fracture its cumulated strain energy (also released in kinetic energy of fragments), thus displays a toughness modulus (dissipated energy per unit mass) of $t = \phi\ /\ m \approx \sigma_f\, \varepsilon_f\ /\ (2\rho)$ (proportional to ultimate stress by ultimate strain divided by density, the constant of proportionality of 1/2 is here reported just as example for linear elastic fibers). In contrast, a fiber with a loop and a knot can dissipate much more energy, thanks to a sliding friction force working for the "hidden length" of the loop. The upper limit of the toughness in this case is constituted by the product of the force F_f^- just below the breaking force F_f and a displacement equal to the entire fiber length l, thus reaching a toughness modulus of $T = \phi/m \approx (\sigma_f\ /\ \rho)(1 + \varepsilon_f\ /\ 2) = t + \Delta t$, where a huge ($1 >> \varepsilon_f$) "hidden toughness" of $\Delta t = \Delta\phi\ /\ m \approx \sigma_f\ /\ \rho$ (i.e., the specific material strength) naturally emerges, independently from the intrinsic material constitutive law.[43]

equal to $\rho = 1300$ kg m^{-3}) has been collected[21] and the proof of this concept has been recently confirmed,[22] suggesting that "bionicomposites"[23,24] (proposed by the author) are in general very promising.

Concerning artificial spider silk, there are two main strategies for their production:[6] one being expression of insoluble spidroins with subsequent solubilization and fiber processing using organic solvents,[25–29] and another being a biomimetic approach involving only aqueous solutions throughout the purification and spinning procedures and in which the molecular mechanisms and triggers for fiber formation are replicated.[30–33] The first approach enables expression of large spidroins that can be spun into fibers with high tensile strength, but the protein yields are far from what is required for industrial production. Using the second approach, mini-spidroins have been developed, that are extremely water-soluble and can be spun into tough fibers using biomimetic spinning set-ups in large quantities and with toughness comparable to that of native spider silk[6] and can also mixed with nanomaterials, e.g. magnetic nanoparticles for added functionalities.[34]

Eventually, recent advancements in analytical modeling[35,36] and physically based machine learning[37,38] applied to spider silk are helping the understanding of their macroscopic mechanical properties starting from their nanoscopic constituents and through its hierarchical architecture as well the design of artificial spider silk. These approaches are completing previous studies performed on spider silk, with molecular dynamics simulations and hierarchical lattice spring models,[39–42] and represent a new powerful design tool especially when coupled.

2. The Potential of Knots in Toughness

Inspired by the "hidden length" observed in spider silks and web junctions, the author introduced a friction-based system to enhance the toughness of fibers,[43] **Figure 1**. In this approach, a slider –even a simple knot– is incorporated as a frictional element to dissipate energy through a hidden length or loop within the fiber, thereby reshaping the fiber's apparent mechanical constitutive law and revealing what it was termed "hidden toughness". This toughness increment is directly related to the material's specific strength. The resulting constitutive law of the knotted fiber is theoretically nearly perfectly plastic, mimicking the behavior observed in spider silk and elasto-plastic materials in general.

In particular, the energy at break ϕ per unit mass m of a fiber having cross-sectional area A, length l, Young's modulus E, strength σ_f and mass density ρ, can be calculated from the load-displacement curve as $\phi/m = 1/m \int_0^{x_f} F\mathrm{d}x = l_0 A/m \int_0^{\varepsilon_f} \sigma \mathrm{d}\varepsilon = (1 - k_1)/\rho \int_0^{\varepsilon_f} \sigma \mathrm{d}\varepsilon$, where F is the force, x is the displacement, $\sigma = F/A$ is the stress, $\varepsilon = x/l_0$ is the apparent strain, l_0 is the apparent (end-to-end) length of the fiber and $0 \leq k_1 = (l - l_0)/l \leq 1$ is the loop fraction length (thus in principle for large loops $k_1 \rightarrow 1$), whereas the subscript f denotes final/fracture values, see Figure 1.

For a linear elastic fiber, classical thus without an extra-length or loop ($k_1 = 0$), this simply yields a "toughness" (this energy is elastically stored and dissipated in fracture plus kinetic energy of the fragments) $t = \phi/m = \sigma_f\,\varepsilon_f/(2\rho)$, where $\varepsilon_f = \sigma_f/E$; in contrast, for "knotted fibers" the situation changes dramatically and the toughness increases enormously.

When a knot is inserted in a fiber, the fiber strength in general decreases due to the stress concentration imposed by the presence of the knot/localized curvature; the related "knot strength" of the fiber is here denoted by $\sigma_k = k_2\sigma_f$, where accordingly $0 \le k_2 \le 1$. Considering an unfastening knot and/or intrinsically tough fiber, as in the case of spider silk, would result in an upper limit $k_2 \to 1$. During fiber tension, first the strain increases with the fiber sliding through the knot at a mean stress plateau value of $\sigma_p \approx k_3\sigma_k$, where $0 \le k_3 \le 1$ denotes the ratio between plateau stress and fiber knot strength, where in principle in the absence of stick-slips and for sliding force just below the fiber fracture force $k_3 \to 1$. This sliding phase takes place for a displacement $\Delta x \approx l - l_0$, ideally at a force just below the breaking force F_f of the fiber, in order to maximize the dissipated energy; then, the slip-loop further tightens (it could also unfasten, depending on the type of slider/knot topology) and the fiber deforms and finally breaks. Thus, in the stress-strain curve a long plastic-like plateau naturally emerges thanks to the presence of the knot/loop. The increment of the final strain is $\Delta\varepsilon_f \approx \Delta x / l_0 = k_1/(1-k_1)$. Accordingly, the increment in toughness modulus, or previously "hidden toughness", is huge and given by $\Delta t = \Delta\phi / m \approx k_1 k_2 k_3 \sigma_f / \rho$, with the upperbound ($k_{1,2,3} \to 1$) of σ_f / ρ, which is the fibre specific strength.

Also note that since a size-effect is expected on the fracture strength of materials, i.e., $\sigma_f \propto R^{(D-3)/2}$,[16] where R is the structural size and $2 \le D \le 3$ is the dimension of the domain in which the energy dissipation occurs (for brittle fracture $D = 2$ an thus the classical scaling of fracture mechanics $\sigma_f \propto R^{-1/2}$ emerges), we expect a scaling of the toughness increment $\Delta t \propto R^{(D-3)/2}$. Also note that a scaling is expected also in the intrinsic toughness t: the area under the stress-strain curve is the dissipated energy per unit volume, e.g. for a brittle fiber ($D = 2$) it is $\rho t = G_c A/(Al)$ where G_c is the fracture energy of the material, thus $\rho t\,(D = 2) = G_c/l$; accordingly, it should not be surprising that even brittle materials become ductile at the nanoscale ($l \to 0$), whereas vice versa even ductile materials become brittle at the macroscale ($l \to \infty$; also resulting in snap-backs with positive slope in the stress–strain curve and thus kinetic energy release under displacement control, e.g., earthquakes); in general $t \propto R^{D-3}$.[16] Thus smaller is stronger and also tougher (we are here referring to the discussed toughness modulus and not to the fracture toughness or critical stress intensity factor).

This concept has been experimentally validated, with the creation of fibers exhibiting unprecedented toughness. A commercial Endumax fiber, for example, saw its toughness modulus increased from t = 44 J g^{-1} to T = 1400 J g^{-1} through the introduction of knots.[43] The same approach has been applied to carbon fibers and other high-performance fibers[44] as well as silk fibers,[45,46] always yielding significant improvements in toughness. The theoretical limit of this concept is the specific strength of the material, with a huge upper bound max(T) expected to be ≈ 10^5 J g^{-1} for graphene and carbon nanotubes. This concept could work also in compression and bulk materials.[47]

It is the author's opinion that the remarkable ability of knots to increase toughness by one or more orders of magnitude may also provide at least a partial still unknown justification of the evolutionary prevalence of knots in biological systems.[43] Indeed, despite their complexity and the energy costs associated with their formation, knots are observed in many biological structures, including DNA strands and proteins.[43] A very recent review[48] has explored the presence of knots in various soft matter systems, further emphasizing the abundance of this structural feature in Nature. Fibers with loops and knots could become orders of magnitude tougher and in Biology this may result in much higher robustness for the related living systems.

3. The Super-Tough Silk

In spite of this, while humans and weaver birds are capable of intentionally producing knots, spiders are not, whereas other animals –like octopuses, eels, and snakes– may only inadvertently form knots in parts of their bodies. Accordingly, spiders, along with other animals that produce silk and filaments or use fibers, could theoretically gain significant advantages from evolving the ability to intentionally form knots into them, as already demonstrated by weaver birds. In particular, spider silk is already recognized as one of the toughest natural materials known, but if spiders could incorporate knots into their webs, their silk could become significantly tougher, potentially transforming spider webs into even much more resilient and durable structures.

To quantify this scenario, here we analyze the group of 393 spiders recently reported,[49] estimating the potential upperbound of their silk's toughness $T = t + \Delta t$ if they could form knots, with $\Delta t = \sigma_f / \rho$. The calculations, summarized in **Table 1** and **Figure 2**, reveal the potential for dramatic increases in silk toughness if spiders were able to exploit the hidden toughness revealed by the knot-based mechanism. The potential gains in toughness (G) were calculated as the ratio between the hypothetical gigantic toughness (T) that could be achieved through loop and knot formation and the current toughness (t) of the spider silk. The results show that spiders, if able to incorporate loops and knots into their silk, could achieve tremendous increases in material performance. For example, a record of T_{max} = 2740.77 J g^{-1} for Clubionidae, *Clubiona, vigil* (https://spider-silkome.org/organisms/403) emerges as well as of G_{max} = 159 for Salticidae, *Yaginumaella, striatipes*, while t_{max} = 326.92 J g^{-1} is for Araneidae, *Araneus, ishisawai*, see Table 1.

Note that the mechanical data employed for the calculation of the gigantic toughness here are obtained from the Silkome DB project as introduced in ref. [49]. In order to illustrate the range of even higher values of strain at breaking that may be observed in various spider species under different tensile testing conditions it may be worth mentioning the values obtained within the framework of the Spider Silk Standardization Initiative (www.ctb.upm.es/core-facilities/), as presented, for instance, in refs. [50,51]. Slightly different input values would result in sligtly different output results.

4. Conclusion

The advantage of using knots is thus demonstrated to be so compelling for toughness that the author suggests spiders could evolve the ability to tie knots given enough evolution time, see an imaginary picture in **Figure 3** (i).

Table 1. 393 spiders (family, genus, species; see ref. [49]) are compared in terms of current mechanical properties of their silk (d = diameter; E = Young's modulus; σ_f = strength; ε_f = strain at break; t = toughness modulus, i.e., dissipated energy per unit mass) and predicted gigantic toughness T of knotted silk reachable when/if spiders will become able to realize (in a proper way, with loops) knots and related toughness gain $G = T/t$ (the silk density is assumed here equal to $\rho = 1300$ kg m^{-3}). Spiders are listed as emerging from the calculation in descending order of T, with first/second/third place values of T, t, and G reported in **bold**/***bold&italic***/*italic*, respectively. Concerning Statistical Analysis (including standard deviations, here omitted for brevity) please refer to the full data reported in ref. [49]

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ε_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Clubionidae	*Clubiona*	*Vigil*	0.48	20.3	3.33	12.7	179.23	**2740.77**	15.292
Araneidae	*Plebs*	*Sachalinensis*	0.72	30.4	3.06	24.1	***323.85***	***2677.69***	8.268
Araneidae	*Nephilingis*	*Livida*	3.37	16.9	2.97	21.4	*300.00*	*2584.62*	8.615
Deinopidae	*Deinopis*	sp.	0.49	31.2	2.98	12.9	156.15	2448.46	15.680
Araneidae	*Araneus*	*Ishisawai*	1.39	17.5	2.62	31	**326.92**	2342.31	7.165
Araneidae	*Metazygia*	*Zilloides*	0.36	19	2.52	23.6	238.46	2176.92	9.129
Araneidae	*Argiope*	*Keyserlingi*	0.43	31.7	2.45	22.4	283.08	2167.69	7.658
Thomisidae	*Phrynarachne*	*katoi*	0.43	33.5	2.64	8.9	87.69	2118.46	24.158
Araneidae	*Larinia*	*argiopiformis*	0.56	9.92	2.45	27.2	220.00	2104.62	9.566
Araneidae	*Poltys*	*columnaris*	3.6	19.1	2.4	20.9	224.62	2070.77	9.219
Thomisidae	*Stephanopis*	*cambridgei*	0.4	25.1	2.49	14.5	129.23	2044.62	15.821
Pisauridae	*Hygropoda*	sp.	0.38	8.64	2.5	15.1	110.00	2033.08	18.483
Segestriidae	*Ariadna*	*lateralis*	0.54	37	2.46	8.6	116.92	2009.23	17.184
Araneidae	*Cyclosa*	*japonica*	0.54	17.3	2.42	12.3	110.00	1971.54	17.923
Agelenidae	*Agelena*	*labyrinthica*	0.32	18.6	2.31	21.7	178.46	1955.38	10.957
Theridiidae	*Parasteatoda*	*tepidariorum*	0.71	10.9	2.23	27.1	235.38	1950.77	8.288
Araneidae	*Araneus*	*marmoreus*	2.34	21.9	2.37	15	123.08	1946.15	15.813
Araneidae	*Argiope*	*amoena*	2.08	15.6	2.2	23.7	220.00	1912.31	8.692
Thomisidae	*Xysticus*	sp.	0.45	13.7	2.34	13	103.85	1903.85	18.333
Araneidae	*Trichonephila*	*clavata*	2.26	15.7	2.22	21.5	189.23	1896.92	10.024
Tetragnathidae	*Leucauge*	*dromedaria*	0.52	17.3	2.3	13.3	123.85	1893.08	15.286
Araneidae	*Nuctenea*	*umbratica*	0.43	28.6	2.21	15.5	166.15	1866.15	11.231
Araneidae	–	sp.	0.55	14.5	2.27	13	96.15	1842.31	19.160
Theridiidae	*Parasteatoda*	*angulithorax*	0.58	6.59	2.18	20.8	147.69	1824.62	12.354
Uloboridae	*Octonoba*	*varians*	0.76	16.8	2.12	20.2	192.31	1823.08	9.480
Araneidae	*Plebs*	*sachalinensis*	0.41	8.11	2.12	19.8	165.38	1796.15	10.860
Araneidae	*Gea*	*spinipes*	0.48	13	2.17	13.7	98.46	1767.69	17.953
Theridiidae	*Cryptachaea*	*gigantipes*	0.41	14	2.04	19.7	186.92	1756.15	9.395
Theridiidae	*Yunohamella*	*yunohamensis*	0.37	13.1	2.13	11.2	86.15	1724.62	20.018
Araneidae	*Araneus*	sp.	0.35	4.61	1.97	31.3	205.38	1720.77	8.378
Araneidae	*Acusilas*	*coccineus*	0.57	13.1	2.06	16.6	120.00	1704.62	14.205
Mimetidae	*Mimetus*	*testaceus*	0.44	13.6	2.06	15.8	110.77	1695.38	15.306
Araneidae	*Eriophora*	*transmarina*	1.43	13.7	1.93	25.6	210.00	1694.62	8.070
Theridiidae	*Latrodectus*	*hasselti*	1.37	15.1	1.99	17.9	163.08	1693.85	10.387
Araneidae	*Nephilingis*	*livida*	3.96	13.1	1.9	23.7	192.31	1653.85	8.600
Sparassidae	*Heteropoda*	sp.	0.36	26.8	1.88	27.1	205.38	1651.54	8.041
Araneidae	*Arachnura*	*melanura*	0.46	10.1	1.91	21.9	156.92	1626.15	10.363
Araneidae	*Herennia*	sp.	1.47	12.3	1.84	26.4	201.54	1616.92	8.023
Salticidae	*Carrhotus*	*xanthogramma*	0.49	16.9	1.91	24.1	144.62	1613.85	11.160
Tetragnathidae	*Leucauge*	*tessellata*	0.42	15.1	1.91	13.2	128.46	1597.69	12.437
Araneidae	*Cyclosa*	*ginnaga*	0.33	16.4	1.87	18.7	133.85	1572.31	11.747
Theridiidae	*Rhomphaea*	*labiata*	0.43	13.3	1.84	19	140.77	1556.15	11.055
Psechridae	*Psechrus*	sp.	0.52	9.19	1.86	16.8	123.85	1554.62	12.553
Theridiidae	*Parasteatoda*	*culicivora*	0.57	16.6	1.84	17.9	139.23	1554.62	11.166
Theridiidae	*Meotipa*	sp.	0.45	10.2	1.81	19.8	161.54	1553.85	9.619
Araneidae	*Trichonephila*	*inaurata*	3.92	14.6	1.73	27.2	219.23	1550.00	7.070

(*Continued*)

Table 1. (Continued)

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ϵ_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Araneidae	*Nephila*	*pilipes*	2.75	7	1.72	41.8	224.62	1547.69	6.890
Cheiracanthiidae	*Cheiracanthium*	*japonicum*	0.36	10.1	1.89	17.9	90.00	1543.85	17.154
Tetragnathidae	*Orsinome*	sp.	0.69	7.96	1.76	24.7	173.08	1526.92	8.822
Araneidae	*Argiope*	*aemula*	1.89	6.5	1.74	32.7	188.46	1526.92	8.102
Araneidae	*Araneus*	*ventricosus*	3.05	9.86	1.75	28.4	171.54	1517.69	8.848
Araneidae	*Larinioides*	*cornutus*	2.84	15.4	1.82	15.3	106.92	1506.92	14.094
Araneidae	*Araneus*	sp.	0.43	5.86	1.79	20.3	120.77	1497.69	12.401
Theridiidae	*Rhomphaea*	*labiata*	0.57	11	1.7	18	128.46	1436.15	11.180
Araneidae	*Cyrtophora*	sp.	1.73	16.1	1.68	17.6	138.46	1430.77	10.333
Araneidae	*Araneus*	sp.	0.58	6.57	1.66	27.4	149.23	1426.15	9.557
Theridiidae	*Episinus*	*nubilus*	0.33	6.31	1.7	18.9	100.77	1408.46	13.977
Araneidae	–	sp.	1.47	11.1	1.64	21.5	135.38	1396.92	10.318
Zoropsidae	*Zoropsis*	*spinimana*	0.47	22.8	1.65	16.5	126.15	1395.38	11.061
Tetragnathidae	*Orsinome*	sp.	0.47	6.4	1.66	20.5	118.46	1395.38	11.779
Araneidae	*Backobourkia*	*brouni*	0.64	5.77	1.6	25.6	163.08	1393.85	8.547
Araneidae	*Nephilingis*	*livida*	3.86	8.78	1.63	22.5	139.23	1393.08	10.006
Theridiidae	*Parasteatoda*	*tepidariorum*	1.67	17.3	1.65	15.9	122.31	1391.54	11.377
Araneidae	*Eriovixia*	*poonaensis*	0.47	12.8	1.56	27.6	185.38	1385.38	7.473
Araneidae	*Argiope*	*keyserlingi*	0.66	11.6	1.59	19.9	155.38	1378.46	8.871
Araneidae	*Singa*	*perpolita*	0.38	3.41	1.63	24.4	119.23	1373.08	11.516
Araneidae	*Cyrtophora*	sp.	1.2	9.28	1.47	35.6	233.08	1363.85	5.851
Araneidae	*Cyrtophora*	sp.	2.49	14	1.63	16.5	109.23	1363.08	12.479
Araneidae	*Neoscona*	sp.	1.28	24.1	1.68	8.7	66.92	1359.23	20.310
Araneidae	*Caerostris*	sp.	1.06	9.81	1.56	21	140.00	1340.00	9.571
Araneidae	*Plebs*	sp.	0.41	8.65	1.6	18.9	109.23	1340.00	12.268
Arkyidae	*Arkys*	sp.	0.55	9.59	1.51	25.4	173.85	1335.38	7.681
Araneidae	*Zygiella*	*dispar*	0.36	10.4	1.63	13.2	78.46	1332.31	16.980
Araneidae	*Argiope*	sp.	2.05	7.16	1.52	31.4	163.08	1332.31	8.170
Theridiidae	*Parasteatoda*	*tepidariorum*	0.54	9.67	1.6	15	92.31	1323.08	14.333
Araneidae	–	sp.	2.25	12.9	1.57	17.7	110.77	1318.46	11.903
Theridiidae	*Parasteatoda*	*tepidariorum*	0.87	10.6	1.5	25.5	159.23	1313.08	8.246
Araneidae	*Poltys*	*illepidus*	2.2	7.14	1.5	25.9	158.46	1312.31	8.282
Araneidae	*Cyrtophora*	sp.	1.92	16.1	1.54	16.9	126.92	1311.54	10.333
Theridiidae	*Argyrodes*	*kumadai*	0.46	10.3	1.52	23.6	142.31	1311.54	9.216
Clubionidae	*Clubiona*	*riparia*	0.68	25.3	1.64	6.6	47.69	1309.23	27.452
Araneidae	*Trichonephila*	*clavipes*	0.8	10.4	1.56	17.1	100.77	1300.77	12.908
Araneidae	*Caerostris*	*darwini*	3.44	11.7	1.46	25.2	176.15	1299.23	7.376
Araneidae	*Cyrtarachne*	*nagasakiensis*	0.33	9.52	1.53	19.2	120.77	1297.69	10.745
Araneidae	*Nephilingis*	*livida*	3.51	9.93	1.55	15.7	100.77	1293.08	12.832
Araneidae	*Gea*	*spinipes*	0.51	4.66	1.54	21.9	108.46	1293.08	11.922
Araneidae	*Trichonephila*	*clavata*	3.03	11.8	1.51	19.2	130.00	1291.54	9.935
Araneidae	*Argiope*	*aemula*	4.55	11.7	1.48	22.7	137.69	1276.15	9.268
Uloboridae	*Hyptiotes*	*affinis*	0.86	9.71	1.45	27.4	150.00	1265.38	8.436
Thomisidae	*Oxytate*	*striatipes*	0.94	15.3	1.43	21.4	148.46	1248.46	8.409
Tetragnathidae	*Tetragnatha*	*montana*	0.4	5.92	1.51	16.2	80.00	1241.54	15.519
Araneidae	*Cyclosa*	*argenteoalba*	0.6	15.9	1.46	17.9	109.23	1232.31	11.282
Oxyopidae	*Peucetia*	*viridans*	1.15	9.24	1.47	15.9	98.46	1229.23	12.484
Araneidae	*Parawixia*	*dehaani*	3.14	5.8	1.34	40	193.85	1224.62	6.317
Theridiidae	*Argyrodes*	*miniaceus*	0.38	8.62	1.51	12.3	59.23	1220.77	20.610
Araneidae	*Araneus*	sp.	1.02	10.2	1.35	28.7	177.69	1216.15	6.844

(*Continued*)

Table 1. (Continued)

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ε_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Araneidae	*Trichonephila*	*plumipes*	0.46	12.1	1.44	18.1	104.62	1212.31	11.588
Araneidae	*Eriophora*	*pustulosa*	0.57	15.3	1.41	18.1	126.92	1211.54	9.545
Tetragnathidae	*Leucauge*	sp.	0.4	5.41	1.47	21.7	80.77	1211.54	15.000
Araneidae	*Hypsosinga*	*pygmaea*	0.45	10.9	1.45	18.2	90.77	1206.15	13.288
Theridiidae	*Takayus*	*latifolius*	0.47	14.9	1.45	14.8	89.23	1204.62	13.500
Thomisidae	*Tmarus*	*rimosus*	0.38	8.76	1.46	14.2	77.69	1200.77	15.455
Pimoidae	*Weintrauboa*	*contortipes*	0.85	10.3	1.39	20.3	126.92	1196.15	9.424
Araneidae	*Mecynogea*	*lemniscata*	0.75	7.76	1.4	17.6	116.92	1193.85	10.211
Tetragnathidae	*Metellina*	*merianae*	0.64	11.6	1.43	16.8	93.08	1193.08	12.818
Theridiidae	*Parasteatoda*	*tepidariorum*	1.32	9.12	1.35	24.8	150.77	1189.23	7.888
Araneidae	*Neoscona*	*nautica*	1.18	9.4	1.34	29.2	156.15	1186.92	7.601
Theridiidae	*Parasteatoda*	*tepidariorum*	0.61	8.9	1.38	21	121.54	1183.08	9.734
Araneidae	*Gasteracantha*	sp.	1.78	10.2	1.3	26.3	171.54	1171.54	6.830
Araneidae	*Trichonephila*	*inaurata*	6.69	11.1	1.35	21.1	127.69	1166.15	9.133
Araneidae	*Cyclosa*	*octotuberculata*	0.97	8.85	1.34	19.4	126.92	1157.69	9.121
Pisauridae	*Pisaura*	*lama*	0.35	7.08	1.37	18.7	99.23	1153.08	11.620
Salticidae	*Plexippus*	*paykulli*	0.48	7.7	1.43	7.8	49.23	1149.23	23.344
Araneidae	*Poltys*	*illepidus*	1.06	6.97	1.36	19.8	100.77	1146.92	11.382
Theridiidae	*Yunohamella*	*yunohamensis*	0.57	9.54	1.37	14.6	90.00	1143.85	12.709
Araneidae	*Neoscona*	sp.	1.08	9.24	1.36	20.4	96.92	1143.08	11.794
Araneidae	*Cyclosa*	*omonaga*	0.62	5.35	1.33	27.1	117.69	1140.77	9.693
Araneidae	*Caerostris*	*extrusa*	1.45	8.91	1.31	23.5	132.31	1140.00	8.616
Araneidae	*Argiope*	sp.	2.78	5.85	1.32	24.8	123.08	1138.46	9.250
Araneidae	*Araneus*	*seminiger*	1.63	9.5	1.31	25.1	126.92	1134.62	8.939
Araneidae	*Argiope*	sp.	1.79	6.75	1.32	26.3	116.15	1131.54	9.742
Araneidae	*Caerostris*	*darwini*	4.13	10.6	1.21	35.3	197.69	1128.46	5.708
Tetragnathidae	*Tetragnatha*	*nitens*	0.81	13.7	1.35	16.5	87.69	1126.15	12.842
Linyphiidae	*Turinyphia*	*yunohamensis*	0.75	9.35	1.28	18.9	139.23	1123.85	8.072
Cheiracanthiidae	*Cheiracanthium*	*lascivum*	0.37	11.1	1.34	15.4	90.00	1120.77	12.453
Araneidae	*Caerostris*	*darwini*	3.31	8.73	1.17	42.8	218.46	1118.46	5.120
Sparassidae	*Thelcticopis*	*severa*	2.59	7.93	1.32	21.5	99.23	1114.62	11.233
Tetragnathidae	*Tetragnatha*	sp.	0.79	4.89	1.3	23.8	113.85	1113.85	9.784
Mimetidae	*Mimetus*	sp.	0.9	6.77	1.32	18.7	95.38	1110.77	11.645
Tetragnathidae	*Metellina*	*merianae*	0.54	8.74	1.35	14.5	71.54	1110.00	15.516
Pholcidae	*Pholcus*	*phalangioides*	0.78	9.1	1.28	21.9	116.92	1101.54	9.421
Araneidae	*Araneus*	*ventricosus*	3.51	6.31	1.24	31.9	145.38	1099.23	7.561
Deinopidae	*Deinopis*	sp.	0.38	8.66	1.32	17.7	80.77	1096.15	13.571
Theridiidae	*Parasteatoda*	sp.	0.69	3.34	1.3	21.7	88.46	1088.46	12.304
Oxyopidae	*Oxyopes*	*macilentus*	0.87	13	1.31	14.2	78.46	1086.15	13.843
Araneidae	*Eriophora*	*pustulosa*	0.82	7.61	1.27	23.5	108.46	1085.38	10.007
Theridiidae	*Enoplognatha*	*ovata*	0.46	8.05	1.32	13.6	64.62	1080.00	16.714
Araneidae	*Cyclosa*	*alba*	0.6	2.38	1.25	29.2	117.69	1079.23	9.170
Tetragnathidae	*Metleucauge*	*yunohamensis*	0.54	12.9	1.25	20.2	106.92	1068.46	9.993
Araneidae	*Herennia*	*multipuncta*	2.14	12.1	1.27	15.4	90.00	1066.92	11.855
Araneidae	*Metepeira*	*labyrinthea*	0.7	4.04	1.26	20.3	96.92	1066.15	11.000
Araneidae	*Cyrtophora*	*ikomosanensis*	2.07	16.6	1.18	25	152.31	1060.00	6.960
Zoropsidae	*Zoropsis*	*spinimana*	0.45	10.8	1.22	22.6	120.77	1059.23	8.771
Araneidae	*Neoscona*	*mellotteei*	1.94	11.3	1.26	17.2	86.15	1055.38	12.250
Theridiidae	*Argyrodes*	*flavescens*	0.65	2.44	1.23	30.9	107.69	1053.85	9.786
Araneidae	*Gasteracantha*	*kuhli*	1.52	6.59	1.21	24.5	122.31	1053.08	8.610

(*Continued*)

Table 1. (Continued)

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ϵ_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Araneidae	*Caerostris*	*darwini*	3.47	8.21	1.15	30.5	166.92	1051.54	6.300
Araneidae	*Araneus*	*pentagrammicus*	1.89	8.52	1.21	23.4	117.69	1048.46	8.908
Tetragnathidae	*Leucauge*	*argyra*	1.37	11.9	1.19	26.3	131.54	1046.92	7.959
Araneidae	*Nephila*	*pilipes*	3.25	12.2	1.14	30.2	170.00	1046.92	6.158
Araneidae	*Araniella*	*yaginumai*	1.2	11.6	1.2	24.5	123.85	1046.92	8.453
Araneidae	*Araneus*	*variegatus*	1.79	4.85	1.2	27.3	118.46	1041.54	8.792
Araneidae	*Araneus*	*pentagrammicus*	1.45	8.9	1.21	24.3	110.77	1041.54	9.403
Araneidae	*Larinioides*	*cornutus*	1.74	10.7	1.25	15.2	78.46	1040.00	13.255
Zoropsidae	*Zoropsis*	*spinimana*	1.49	14.7	1.21	18.4	107.69	1038.46	9.643
Desidae	*Badumna*	*insignis*	0.7	13.1	1.28	10.7	53.85	1038.46	19.286
Araneidae	*Araneus*	*bicentenarius*	5.37	7.93	1.23	18.4	86.15	1032.31	11.982
Araneidae	*Cyclosa*	*octotuberculata*	1.16	8.37	1.16	28	140.00	1032.31	7.374
Pisauridae	*Dolomedes*	sp.	1.4	14.1	1.27	9.2	53.08	1030.00	19.406
Uloboridae	*Zosis*	*geniculata*	0.48	6.5	1.23	17	76.92	1023.08	13.300
Araneidae	*Caerostris*	*darwini*	4.31	8.46	0.97	65.3	276.15	1022.31	3.702
Tetragnathidae	*Tylorida*	*ventralis*	0.6	7.47	1.24	13.5	62.31	1016.15	16.309
Araneidae	*Argiope*	sp.	2.44	10.7	1.21	14.8	76.15	1006.92	13.222
Oxyopidae	*Peucetia*	sp.	2.8	11.5	1.17	19.9	105.38	1005.38	9.540
Araneidae	*Nephila*	*pilipes*	0.98	9.38	1.17	19.7	103.85	1003.85	9.667
Araneidae	*Neoscona*	sp.	0.69	5.42	1.2	23.4	79.23	1002.31	12.650
Araneidae	*Argiope*	*bruennichi*	2.47	4.4	1.15	30.7	114.62	999.23	8.718
Uloboridae	*Octonoba*	*grandiconcava*	0.44	2.16	1.21	23.3	64.62	995.38	15.405
Thomisidae	*Thomisus*	*labefactus*	1.33	14.9	1.18	14.2	86.15	993.85	11.536
Araneidae	*Araneus*	*mitificus*	0.68	9.01	1.05	34.3	183.85	991.54	5.393
Uloboridae	*Miagrammopes*	sp.	0.8	3.36	1.1	26.3	144.62	990.77	6.851
Araneidae	*Plebs*	*eburnus*	0.37	7.93	1.17	17.4	86.15	986.15	11.446
Araneidae	*Neoscona*	*mellotteei*	2.72	10.5	1.18	22.3	77.69	985.38	12.683
Araneidae	*Eriovixia*	*sakiedaorum*	0.54	6.53	1.16	18.9	90.77	983.08	10.831
Pisauridae	*Hygropoda*	sp.	0.44	6.13	1.23	10.1	36.15	982.31	27.170
Araneidae	*Cyclosa*	*omonaga*	0.46	14.6	1.14	21.4	103.08	980.00	9.507
Araneidae	*Neoscona*	*punctigera*	2.18	9.01	1.14	20.2	102.31	979.23	9.571
Tetragnathidae	*Mesida*	sp.	0.48	3.14	1.18	19.1	70.00	977.69	13.967
Tetragnathidae	*Zhinu*	*reticuloides*	1.19	8.23	1.13	19.8	106.92	976.15	9.129
Tetragnathidae	*Zhinu*	*reticuloides*	0.7	9.45	1.1	22.3	123.85	970.00	7.832
Linyphiidae	*Neriene*	sp.	0.73	11.7	1.13	57.1	100.77	970.00	9.626
Araneidae	*Cyrtarachne*	*nagasakiensis*	1.52	8.54	1.09	30.5	129.23	967.69	7.488
Araneidae	*Thelacantha*	*brevispina*	1.03	16.4	1.09	22.4	125.38	963.85	7.687
Araneidae	*Cyrtarachne*	*akirai*	4.54	11.2	1.12	19.3	102.31	963.85	9.421
Araneidae	*Micrathena*	*sagittata*	1.67	9.54	1.1	24.5	117.69	963.85	8.190
Theridiidae	*Steatoda*	sp.	0.49	6.31	1.11	28.3	107.69	961.54	8.929
Tetragnathidae	*Orsinome*	sp.	0.47	13.6	1.15	16.8	76.92	961.54	12.500
Araneidae	*Neoscona*	*punctigera*	1.85	4.25	1.08	32.7	124.62	955.38	7.667
Salticidae	*Myrmarachne*	*japonica*	1.03	19.5	1.17	8.3	53.08	953.08	17.957
Araneidae	*Araneus*	*uyemurai*	2.75	9.75	1.05	26.8	143.85	951.54	6.615
Theridiidae	*Platnickina*	*sterninotata*	0.63	10.7	1.14	11.3	72.31	949.23	13.128
Araneidae	*Nephilengys*	*malabarensis*	1.57	12.3	1.12	17.6	83.85	945.38	11.275
Araneidae	*Nephilengys*	*malabarensis*	4.96	13.2	1.12	15.4	83.08	944.62	11.370
Araneidae	–	sp.	0.94	6.89	1.09	25	102.31	940.77	9.195
Tetragnathidae	*Leucauge*	*celebesiana*	1.33	7.05	1.15	15	55.38	940.00	16.972
Lycosidae	*Trochosa*	*ruricola*	0.41	6.2	1.14	15.1	62.31	939.23	15.074

(*Continued*)

Table 1. (Continued)

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ε_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Araneidae	*Parawixia*	*dehaani*	2.66	5.98	1.12	26.9	76.15	937.69	12.313
Araneidae	*Nephilengys*	*malabarensis*	5.58	6.3	1.04	28.9	137.69	937.69	6.810
Araneidae	*Thelacantha*	*brevispina*	1.08	8.62	1.08	28	106.15	936.92	8.826
Araneidae	*Trichonephila*	*clavata*	2.68	9.05	1.12	16.9	70.77	932.31	13.174
Pisauridae	*Dolomedes*	*yawatai*	0.82	10.7	1.08	20	101.54	932.31	9.182
Pisauridae	–	sp.	0.65	3.53	1.13	18.5	61.54	930.77	15.125
Araneidae	*Gasteracantha*	*kuhli*	2.38	6.16	1.01	36.2	150.00	926.92	6.179
Araneidae	*Neoscona*	*mellotteei*	1.75	7.54	1.04	27.2	120.77	920.77	7.624
Araneidae	*Cryptaranea*	sp.	2.13	8.73	1.09	18.7	81.54	920.00	11.283
Araneidae	*Eriophora*	sp.	0.42	5.76	1.04	24	118.46	918.46	7.753
Tetragnathidae	*Tylorida*	*ventralis*	0.71	8.39	1.07	23.1	95.38	918.46	9.629
Tetragnathidae	*Metellina*	*merianae*	0.79	12.4	1.13	9.8	48.46	917.69	18.937
Pisauridae	*Dolomedes*	sp.	1.1	12.1	1.09	15.9	77.69	916.15	11.792
Araneidae	*Argiope*	amoena	4.56	9.61	1.09	16.4	74.62	913.08	12.237
Theridiidae	*Parasteatoda*	sp.	0.74	6.34	1.04	26.8	110.00	910.00	8.273
Araneidae	*Micrathena*	*sagittata*	0.95	15.5	1.04	20.8	108.46	908.46	8.376
Araneidae	*Gasteracantha*	*cancriformis*	2.56	8.62	1.03	26.9	113.08	905.38	8.007
Araneidae	*Acrosomoides*	sp.	2.23	9.02	1.02	26.1	112.31	896.92	7.986
Araneidae	*Araneus*	*diadematus*	1.39	6	1.08	17.8	63.08	893.85	14.171
Araneidae	*Cyclosa*	*bifida*	0.75	2.49	1.06	25.8	76.15	891.54	11.707
Araneidae	*Araneus*	*amabilis*	2.7	6.85	1.03	25.3	97.69	890.00	9.110
Theridiidae	*Chrysso*	sp.	0.72	5.51	1.05	18.4	81.54	889.23	10.906
Araneidae	*Araneus*	*seminiger*	7.95	6.85	0.98	32.9	134.62	888.46	6.600
Araneidae	*Neoscona*	*scylloides*	0.45	4.92	1	28.4	114.62	883.85	7.711
Araneidae	*Cyrtophora*	*unicolor*	1.69	6.07	1.06	16.5	68.46	883.85	12.910
Araneidae	*Neoscona*	*scylla*	1.28	6.48	1.01	26.7	106.92	883.85	8.266
Araneidae	*Gibbaranea*	*abscissa*	1.08	7.36	0.99	24.4	106.15	867.69	8.174
Araneidae	*Cyrtophora*	*unicolor*	2.08	7.13	1	23.2	96.92	866.15	8.937
Araneidae	*Araneus*	*macacus*	2.44	6.41	1.04	17.9	64.62	864.62	13.381
Tetragnathidae	*Tetragnatha*	sp.	0.66	4.16	1.03	18.6	70.00	862.31	12.319
Thomisidae	*Phrynarachne*	*ceylonica*	0.28	12	1.05	10.7	50.77	858.46	16.909
Philodromidae	*Philodromus*	*subaureolus*	0.48	4.56	1.04	14.4	55.38	855.38	15.444
Araneidae	*Araneus*	*pinguis*	2.54	4.2	0.99	53.2	93.08	854.62	9.182
Tetragnathidae	*Metleucauge*	*yunohamensis*	1.12	9.3	0.97	19.4	107.69	853.85	7.929
Araneidae	*Poltys*	*columnaris*	2.16	7.88	0.97	23.4	105.38	851.54	8.080
Theridiidae	–	sp.	0.81	8.94	1	18	81.54	850.77	10.434
Araneidae	*Argiope*	*ocula*	4.46	7.2	1.01	19.7	73.85	850.77	11.521
Araneidae	*Argiope*	*bruennichi*	2.09	8.16	1.02	18.7	66.15	850.77	12.860
Araneidae	*Argiope*	sp.	4.26	9.51	1.02	16.3	63.08	847.69	13.439
Araneidae	*Neoscona*	sp.	2.07	6.84	0.97	30.8	100.00	846.15	8.462
Araneidae	*Larinia*	*argiopiformis*	1.3	10.1	1.03	12.2	46.92	839.23	17.885
Theridiidae	*Nihonhimea*	*japonica*	0.59	4.64	1	20.2	69.23	838.46	12.111
Theridiidae	*Latrodectus*	*geometricus*	2.49	9.77	0.97	19.6	90.77	836.92	9.220
Araneidae	*Mecynogea*	*lemniscata*	0.69	7.63	1.01	11.2	59.23	836.15	14.117
Araneidae	*Thelacantha*	*brevispina*	1.61	7.1	0.99	20.5	71.54	833.08	11.645
Pisauridae	*Dolomedes*	*saganus*	0.8	10.5	1.04	8.7	32.31	832.31	25.762
Araneidae	*Yaginumia*	*sia*	0.87	10.1	0.97	16.7	81.54	827.69	10.151
Araneidae	*Yaginumia*	*sia*	1.19	8.79	0.96	19.7	89.23	827.69	9.276
Araneidae	*Poecilopachys*	*australasia*	1.49	7.89	0.95	23.7	94.62	825.38	8.724
Araneidae	*Nephila*	*pilipes*	1.95	5.59	0.98	19.5	68.46	822.31	12.011

(Continued)

Table 1. (Continued)

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ε_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Araneidae	*Cyclosa*	sp.	0.37	8.38	1	10.8	41.54	810.77	19.519
Desidae	*Badumna*	sp.	0.79	7.37	0.97	16.4	63.85	810.00	12.687
Viridasiidae	*Vulsor*	sp.	1.25	10.5	0.96	14.5	68.46	806.92	11.787
Araneidae	*Araneus*	*amabilis*	1.72	6.17	0.92	25.7	98.46	806.15	8.188
Araneidae	*Cyrtarachne*	*akirai*	3.21	12.1	0.94	17.3	80.00	803.08	10.038
Araneidae	*Cyclosa*	*laticauda*	1.96	8.02	0.94	21.9	79.23	802.31	10.126
Araneidae	*Argiope*	sp.	1.14	6.67	0.86	36	140.00	801.54	5.725
Araneidae	*Argiope*	*minuta*	2.34	8.29	0.93	20.3	81.54	796.92	9.774
Tetragnathidae	*Leucauge*	*subblanda*	0.59	6.25	0.96	14.7	58.46	796.92	13.632
Tetragnathidae	*Tetragnatha*	*ceylonica*	0.93	8.43	0.91	21.7	96.92	796.92	8.222
Araneidae	*Zygiella*	*hiramatsui*	0.57	2.34	0.92	29.8	85.38	793.08	9.288
Araneidae	*Parawixia*	*dehaani*	3.33	8	0.94	18.3	69.23	792.31	11.444
Araneidae	*Araneus*	*mitificus*	1.97	7.19	0.87	32	121.54	790.77	6.506
Tetragnathidae	*Orsinome*	sp.	1	7.64	0.94	18.2	66.15	789.23	11.930
Pisauridae	*Pisaura*	*bicornis*	0.68	3.23	0.97	17.9	42.31	788.46	18.636
Tetragnathidae	*Metleucauge*	*kompirensis*	1.24	5.65	0.94	16.5	60.00	783.08	13.051
Theridiidae	*Enoplognatha*	*margarita*	0.43	14.2	0.98	7	28.46	782.31	27.486
Araneidae	*Eustala*	*anastera*	1.19	8.17	0.91	18	81.54	781.54	9.585
Pholcidae	*Holocnemus*	*pluchei*	0.43	7.62	0.92	18.3	64.62	772.31	11.952
Theridiidae	*Nihonhimea*	*japonica*	0.88	8.82	0.89	21	87.69	772.31	8.807
Araneidae	*Neoscona*	*mellotteei*	1.23	5.21	0.87	27.4	103.08	772.31	7.493
Agelenidae	*Agelenopsis*	sp.	1	6.72	0.95	10.8	40.77	771.54	18.925
Oxyopidae	*Oxyopes*	sp.	0.46	2.98	0.93	18.7	55.38	770.77	13.917
Araneidae	*Argiope*	*aetheroides*	2.87	7.06	0.89	24.3	86.15	770.77	8.946
Araneidae	*Gasteracantha*	*diadesmia*	2.42	5.85	0.89	26.5	83.85	768.46	9.165
Araneidae	*Araneus*	sp.	1.74	6.64	0.87	26.8	99.23	768.46	7.744
Araneidae	*Plebs*	*astridae*	1.18	8.58	0.92	16.4	57.69	765.38	13.267
Araneidae	*Argiope*	*bruennichi*	4.19	10.1	0.93	11.9	46.15	761.54	16.500
Araneidae	*Thelacantha*	*brevispina*	3	4.5	0.83	35.5	120.77	759.23	6.287
Araneidae	*Gasteracantha*	sp.	3.46	4.5	0.83	31.8	116.15	754.62	6.497
Tetragnathidae	*Leucauge*	sp.	2.06	9.3	0.82	34.4	119.23	750.00	6.290
Thomisidae	*Oxytate*	*hoshizuna*	0.57	10.6	0.9	10.8	53.85	746.15	13.857
Tetragnathidae	*Tetragnatha*	*makiharai*	0.68	5.01	0.91	13.2	44.62	744.62	16.690
Thomisidae	*Oxytate*	*striatipes*	1.3	10.9	0.86	17.6	77.69	739.23	9.515
Tetragnathidae	*Metellina*	*mengei*	0.56	3.39	0.88	17.9	56.15	733.08	13.055
Uloboridae	*Octonoba*	*yesoensis*	0.75	3.57	0.85	43.2	74.62	728.46	9.763
Tetragnathidae	*Tetragnatha*	*praedonia*	1.25	8.61	0.87	16.6	59.23	728.46	12.299
Araneidae	*Trichonephila*	*plumipes*	1.25	7.81	0.81	28.2	103.85	726.92	7.000
Tetragnathidae	*Zhinu*	*reticuloides*	0.89	10.2	0.88	13.4	49.23	726.15	14.750
Theridiidae	*Parasteatoda*	sp.	2.25	10.4	0.81	8.9	100.77	723.85	7.183
Salticidae	*Pancorius*	*submontanus*	0.64	15.8	0.91	5.4	21.54	721.54	33.500
Theridiidae	*Parasteatoda*	*tepidariorum*	2.43	9.46	0.79	18.8	110.77	718.46	6.486
Araneidae	*Argiope*	*amoena*	4.94	8.31	0.87	15.2	47.69	716.92	15.032
Pisauridae	*Dolomedes*	*pegasus*	2.58	13.4	0.85	15.4	58.46	712.31	12.184
Tetragnathidae	*Zhinu*	*reticuloides*	0.92	10	0.86	16.2	49.23	710.77	14.438
Salticidae	*Portia*	*fimbriata*	0.8	4.5	0.85	16.4	46.92	700.77	14.934
Tetragnathidae	*Tetragnatha*	sp.	1.11	6.48	0.84	17.1	53.08	699.23	13.174
Theridiidae	*Parasteatoda*	*ryukyu*	0.89	8.1	0.81	20.8	73.08	696.15	9.526
Dictynidae	*Dictyna*	*felis*	0.67	9.06	0.84	13	47.69	693.85	14.548
Salticidae	*Plexippoides*	*doenitzi*	1.18	8.41	0.77	25.2	101.54	693.85	6.833

(*Continued*)

Table 1. (Continued)

Family	Genus	Species	d [μm]	E [GPa]	σ_f [GPa]	ε_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Agelenidae	*Agelena*	*silvatica*	0.83	14.1	0.81	17.8	69.23	692.31	10.000
Pisauridae	*Dolomedes*	*raptor*	0.72	6.74	0.82	16.4	61.54	692.31	11.250
Araneidae	*Cyclosa*	*mulmeinensis*	0.64	3.41	0.81	24.5	67.69	690.77	10.205
Uloboridae	*Octonoba*	*yesoensis*	0.7	5.98	0.83	16.4	52.31	690.77	13.206
Araneidae	*Neoscona*	*scylloides*	2.85	3.21	0.77	35.4	96.92	689.23	7.111
Araneidae	*Neoscona*	*theisi*	1.07	13	0.79	20.3	81.54	689.23	8.453
Cheiracanthiidae	*Cheiracanthium*	*japonicum*	0.48	14.2	0.82	14.3	54.62	685.38	12.549
Theridiidae	*Chrysso*	*scintillans*	1.1	6.2	0.78	34.7	83.85	683.85	8.156
Theridiidae	*Enoplognatha*	*abrupta*	1.37	10	0.81	14.2	56.92	680.00	11.946
Araneidae	*Cyrtophora*	*exanthematica*	3.19	7.1	0.81	17	56.92	680.00	11.946
Araneidae	*Neoscona*	*subpullata*	1.16	6.31	0.8	18.6	63.85	679.23	10.639
Theridiidae	*Ariamnes*	*cylindrogaster*	1.26	7.05	0.79	20.6	71.54	679.23	9.495
Theridiidae	*Spheropistha*	*melanosoma*	0.62	4.54	0.8	19.2	62.31	677.69	10.877
Araneidae	*Neoscona*	sp.	0.8	2.9	0.82	19.1	46.15	676.92	14.667
Theridiidae	*Rhomphaea*	sp.	0.54	1.9	0.77	31.1	80.00	672.31	8.404
Sparassidae	*Heteropoda*	*venatoria*	1.84	7.57	0.75	27.2	92.31	669.23	7.250
Oxyopidae	*Oxyopes*	*sertatus*	1.77	5.58	0.78	19	68.46	668.46	9.764
Lycosidae	*Piratula*	*iriomotensis*	2.43	7.89	0.74	26.7	96.92	666.15	6.873
Sparassidae	*Sinopoda*	*forcipata*	3.71	8.47	0.74	24.6	96.15	665.38	6.920
Araneidae	*Cyrtarachne*	*bufo*	1.23	10.3	0.73	25.9	93.08	654.62	7.033
Araneidae	*Neoscona*	*subpullata*	0.73	11.1	0.78	13.1	53.85	653.85	12.143
Philodromidae	*Tibellus*	*oblongus*	1.14	5.91	0.8	11.5	37.69	653.08	17.327
Araneidae	*Neoscona*	*scylla*	1.83	3.99	0.75	25.5	75.38	652.31	8.653
Araneidae	*Larinioides*	*cornutus*	1.64	6.42	0.75	20.9	74.62	651.54	8.732
Araneidae	*Cyrtophora*	*unicolor*	0.64	4.42	0.76	18.5	65.38	650.00	9.941
Pisauridae	*Dolomedes*	*orion*	2.42	11.6	0.76	16.1	63.85	648.46	10.157
Salticidae	*Sibianor*	*pullus*	0.4	6.65	0.77	13.5	50.77	643.08	12.667
Araneidae	*Neoscona*	*theisi*	1.19	6.68	0.76	16	58.46	643.08	11.000
Araneidae	*Neoscona*	*adianta*	1.36	4.31	0.71	28.2	96.92	643.08	6.635
Araneidae	*Zygiella*	*x-notata*	0.57	5.87	0.75	14.7	60.77	637.69	10.494
Theridiidae	*Nesticodes*	*rufipes*	0.38	3.26	0.76	19.8	52.31	636.92	12.176
Araneidae	*Araneus*	sp.	0.96	4.29	0.74	20.3	56.92	626.15	11.000
Salticidae	*Portia*	sp.	1.2	10.8	0.77	8.8	31.54	623.85	19.780
Salticidae	*Yaginumanis*	*sexdentatus*	1.33	9.07	0.7	21	82.31	620.77	7.542
Salticidae	*Yaginumaella*	*striatipes*	2.08	1.29	0.79	28.2	3.85	611.54	**159.000**
Araneidae	*Gasteracantha*	sp.	2.33	4.11	0.72	19	48.46	602.31	12.429
Pisauridae	*Dolomedes*	*silvicola*	0.87	6.19	0.73	13.1	38.46	600.00	15.600
Araneidae	*Araneus*	*diadematus*	1.27	9.16	0.68	21.2	75.38	598.46	7.939
Theridiidae	*Argyrodes*	*bonadea*	0.65	1.65	0.71	25.6	51.54	597.69	11.597
Uloboridae	*Uloborus*	sp.	0.64	5.73	0.68	19.6	63.08	586.15	9.293
Araneidae	*Cyrtophora*	*moluccensis*	2.18	10.9	0.66	21.8	76.92	584.62	7.600
Salticidae	*Burmattus*	*pococki*	0.56	9.44	0.73	5.9	16.15	577.69	35.762
Salticidae	*Phintelloides*	*versicolor*	0.69	8.74	0.72	7.7	23.85	577.69	24.226
Araneidae	*Neoscona*	*nautica*	2.09	6.33	0.7	13.1	38.46	576.92	15.000
Tetragnathidae	*Tetragnatha*	*praedonia*	0.87	6.36	0.67	21.3	60.77	576.15	9.481
Salticidae	*Menemerus*	*fulvus*	0.67	7.85	0.72	6.7	22.31	576.15	25.828
Araneidae	*Araneus*	*ventricosus*	4.68	6.72	0.62	28.9	99.23	576.15	5.806
Araneidae	–	sp.	0.45	3.07	0.71	13.2	27.69	573.85	20.722
Araneidae	*Gasteracantha*	*kuhli*	2	3.23	0.64	30.9	78.46	570.77	7.275
Pholcidae	*Pholcus*	*opilionoides*	0.57	8.93	0.68	14.4	45.38	568.46	12.525

(*Continued*)

Table 1. (Continued)

Family	Genus	Species	d [µm]	E [GPa]	σ_f [GPa]	ϵ_f [%]	t [J g^{-1}]	T [J g^{-1}]	$G = T/t$
Araneidae	*Yaginumia*	*sia*	1.91	5.48	0.65	22.5	66.15	566.15	8.558
Psechridae	*Psechrus*	sp.	2.42	5.96	0.66	18.2	56.15	563.85	10.041
Tetragnathidae	*Leucauge*	*blanda*	1.16	7.58	0.66	17.3	51.54	559.23	10.851
Araneidae	*Trichonephila*	*antipodiana*	6.29	4.71	0.55	49.9	130.77	553.85	4.235
Theridiidae	*Dipoena*	*punctisparsa*	1.16	6.03	0.64	20.3	58.46	550.77	9.421
Araneidae	*Cyrtophora*	*unicolor*	0.72	5.08	0.67	12.2	33.08	548.46	16.581
Araneidae	*Araneus*	*ventricosus*	2.69	2.59	0.6	31	78.46	540.00	6.882
Pisauridae	*Dolomedes*	*sulfureus*	2.86	9.26	0.63	13.9	47.69	532.31	11.161
Araneidae	*Cyclosa*	*confusa*	1.17	5.29	0.64	16.3	38.46	530.77	13.800
Theridiidae	*Chrysso*	*viridiventris*	0.56	2.75	0.65	14.6	27.69	527.69	19.056
Araneidae	*Araneus*	*ishisawai*	2.3	9.6	0.63	12.1	38.46	523.08	13.600
Thomisidae	*Oxytate*	*striatipes*	1.35	10.1	0.64	9.9	30.00	522.31	17.410
Theridiidae	*Parasteatoda*	*ryukyu*	1.26	5.74	0.62	15.2	44.62	521.54	11.690
Araneidae	*Neoscona*	*adianta*	1.9	5.76	0.59	20.7	50.77	504.62	9.939
Tetragnathidae	*Tetragnatha*	*tanigawai*	0.54	2.93	0.62	14.5	26.92	503.85	18.714
Araneidae	*Neoscona*	*mellotteei*	2.76	5.02	0.58	22.4	55.38	501.54	9.056
Salticidae	*Epeus*	*sumatranus*	0.56	8.46	0.63	5.1	12.31	496.92	***40.375***
Clubionidae	*Clubiona*	sp.	1.38	4.69	0.54	30.8	79.23	494.62	6.243
Pisauridae	*Dolomedes*	*sulfureus*	1.28	5.63	0.6	11.9	30.77	492.31	16.000
Araneidae	*Neoscona*	sp.	2.07	4.23	0.59	17	35.38	489.23	13.826
Theridiidae	*Cryptachaea*	*gigantipes*	1.04	3.47	0.57	20.2	49.23	487.69	9.906
Theridiidae	*Chrysso*	*foliata*	1.09	4.07	0.58	17	40.77	486.92	11.943
Araneidae	*Nephilingis*	*livida*	2.63	6.7	0.53	25.3	73.08	480.77	6.579
Agelenidae	*Allagelena*	*opulenta*	1.67	5.14	0.54	20.2	58.46	473.85	8.105
Araneidae	*Thelacantha*	*brevispina*	4.63	3.15	0.52	36.1	69.23	469.23	6.778
Araneidae	*Arachnura*	*melanura*	0.53	6.41	0.55	20.5	44.62	467.69	10.483
Pisauridae	*Hygropoda*	*higenaga*	1.45	6.03	0.55	11.4	25.38	448.46	17.667
Thomisidae	*Bassaniana*	*decorata*	0.77	4.25	0.55	9.6	19.23	442.31	23.000
Araneidae	*Larinia*	*fusiformis*	0.79	2.57	0.54	14.4	26.15	441.54	16.882
Tetragnathidae	*Leucauge*	*celebesiana*	0.89	2.09	0.53	18.4	33.08	440.77	13.326
Araneidae	*Araneus*	*acusisetus*	1.23	3.26	0.5	19.7	40.77	425.38	10.434
Uloboridae	*Hyptiotes*	*affinis*	1.13	2.98	0.49	22.2	39.23	416.15	10.608
Araneidae	*Araneus*	*pinguis*	6.29	5.83	0.49	18.1	35.38	412.31	11.652
Araneidae	*Araneus*	*marmoreus*	2.07	6.99	0.5	8.1	17.69	402.31	22.739
Salticidae	*Telamonia*	*vlijmi*	0.77	5.46	0.49	6.9	10.77	387.69	*36.000*
Thomisidae	*Oxytate*	*hoshizuna*	0.7	2.11	0.46	14.7	21.54	375.38	17.429
Agelenidae	*Allagelena*	*donggukensis*	0.74	2.85	0.44	17.4	28.46	366.92	12.892
Araneidae	*Eustala*	*anastera*	1.25	4.21	0.45	9.9	19.23	365.38	19.000
Cheiracanthiidae	*Cheiracanthium*	sp.	0.61	2.15	0.42	13.1	22.31	345.38	15.483
Araneidae	*Araneus*	*pentagrammicus*	1.09	2.19	0.36	34.5	38.46	315.38	8.200
Hersiliidae	–	sp.	0.49	0.38	0.34	48.9	49.23	310.77	6.313
Salticidae	*Marpissa*	*milleri*	1.08	2.83	0.33	25	26.92	280.77	10.429
Araneidae	*Cyclosa*	*hamulata*	1.18	1.68	0.33	16.7	23.08	276.92	12.000
Salticidae	*Pancorius*	*crassipes*	1.5	4.05	0.31	22.9	36.92	275.38	7.458
Pisauridae	–	sp.	1.31	2.85	0.32	13.4	16.15	262.31	16.238
Thomisidae	*Thomisus*	*kitamurai*	1.45	2.85	0.31	9.8	10.77	249.23	23.143
Araneidae	–	sp.	1.58	1.01	0.17	15.3	11.54	142.31	12.333

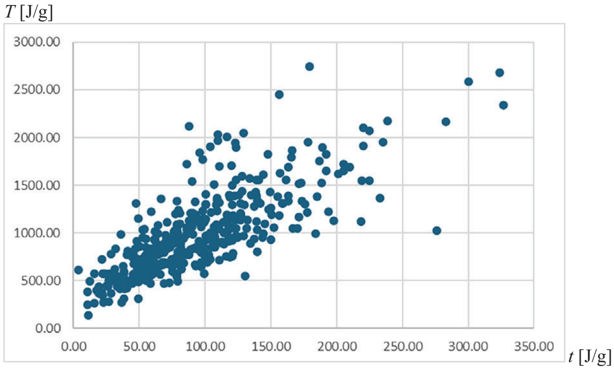

Figure 2. Asbhy's Plot of $y = T$ (gigantic toughness of spiders evolved with knotting abilities) versus $x = t$ (toughness of current spiders, unable to realize knots).

This same advantage of course applies to other animals that produce (or use) silk or silk-like fibers, each adapting the material for various purposes, from building nests and cocoons to anchoring and protection. These best well-known animals include –in addition to spiders– silkworms (e.g., *Bombyx mori*, produce silk cocoons for metamorphosis; the silk from these cocoons is the primary source of silk used in the textile industry), moths and butterflies (some moth and butterfly larvae produce silk to construct cocoons or protective shelters), weaver ants (the larvae of some ant species produce silk, which adult ants use to build nests by binding leaves and branches together), mussels and other bivalve mollusks (may produce byssus, a silk-like thread used to anchor themselves to rocks and prevent dislodging by ocean currents), pine processionary caterpillars (may produce silk threads to create communal nests and pathways, especially during group development), silk mites (some mites produce silk threads for building shelters and moving across vertical surfaces), bees

Figure 3. A futuristic Clubionidae, *Clubiona, vigil* (https://spider-silkome.org/organisms/403) spider, the one emerged with the highest gigantic toughness T, hypothetically doing a spiderweb with loops/knots in the radial threads, in order to increase (by about one order of magnitude, see Table 1) the dissipated specific energy (image adapted by Vincenzo Fazio).

and bumblebees (for certain types of nests, some bee species use silk-like secretions to build small structures within their nests), etc. (ii).

More in general, this new concept could have important consequences in Biology as already discussed by the author in ref. [43]. In particular, proteins separated by a billion years of evolution often display slipknots, also observed in DNA strands, and are conserved in different families and species. This happens even if the folding process resulting in the formation of knots is intrinsically more energetically expensive and topologically difficult than the process of producing unknotted proteins. Thus knotting might seem unlikely to occur during evolution but, in contrast and still surprising,[48] it does regularly occur. Thus, despite the larger energy cost and topological difficulty in the formation of knots, they are somehow advantageous and important to the function of the protein. Biological structures may have evolved with knots in order to easily and dramatically (1-2 folds, as we have here demonstrated for the example of spider silk) increase their robustness. This huge robustness enhancement of the protein could be crucial for resisting against different types of diseases and thus better preserving life (iii).

Conflict of Interest

The author declares no conflict of interest.

Keywords

friction, knot, loop, spider silk, toughness

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