Interdisciplinary Analysis of *Opisthothelae* Silk

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Abstract

Opisthothelae is a suborder of the order of spiders (*Araneae)* and consists of the two infraorders *Mygalomorphae* and *Araneomorphae.* Whereas *Araneomorphae* are "normal" spiders and *Mygalomorphae* include but are not limited to Tarantulas (*Theraphosidae)*. This essay elaborates the different usage of spider silk by *Mygalomorphae* and *Araneomorphae*. In order to understand the specific silk better the physical character and chemical composition of the silk is analysed. This knowledge was then used at the comparison of the two infraorders. Based on literature for the *Araneomorphae* and based on observations of several *Mygalomorphae* which I keep as pets at home I identified differences and equalities. Equalities exist in usage for the production of cocoons, swathing the caught prey and creating sperm webs. Differences occur in the usage of silk as a hunting method and building shelter. Based on my observations of my tarantulas the silk has to differ due to different usage. The difference occurs in physical characteristics and chemical composition of the silk.

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1. Introduction

Spiders have always fascinated me. I got my first tarantula as a pet at the age of seven. After my first tarantula died, I started collecting tarantulas from all over the world and soon I realized that the silk they spun differed between species. Their silks differed in appearance as well as in their physical characteristics, such as extensibility. Chemistry is one of my favourite subjects and I wanted to know more about the chemical structure of tarantula silk. Writing about spider silk enables me to combine my favourite animal with a subject that investigates the features in its basis.

I initially wanted to compare *Nephila* spec. silk and *Monocentropus balfouri (Theraphosidae)* silk on a molecular basis. I hoped to find similarities in the glycine content and transfer the values on the ultimate tensile strength. In a discussion with my supervisor L. Marti he advised that such measurements could not be done in such quality at MNG Zürich, that the results would be meaningful. He recommended contacting a specialist of an institute. Thereupon I contacted various professors at ETH Zürich, who indicated, that ETH Zürich does not have the correspondent measuring instruments for this question. However, I received the contact details of Professor Fritz Vollrath. Unfortunately, the interest in my studies seemed to be limited as I never received an answer on my emails. At that time, I had already invested a lot of time in the studies and I wanted to continue with my elaborations in this field.

The high toughness of spider silk has been known to our ancestors. In earlier days, fishermen already used the web of the spider genus *Nephila* to catch bait fish (Brunetta & Craig, 2012). Nowadays, there is a wide range of potential use in surgery from nerve-repair to wound-dressing and in making implants (Monks, 2016). Deeper investigation into the chemistry of spider silk will allow us to synthesize on the one hand the spider silk itself in laboratories and on the other hand use its properties and perfect it for other uses such as in clothing industry. The structure of spider silk is still widely unknown and this field leaves many opportunities for investigation.

Throughout this assignment I will firstly investigate what contributes to the uniqueness of spider silk. The second part will be a comparison of the characteristics and usage of silk between the two infraorder *Mygalomorphae* and *Araneomorphae*. One of them includes the spider commonly referred as the tarantulas and the other includes the “normal spider”.

2. Basics about Spiders

2.1 History

The origin of the word arachnology arises from the ancient Greek mythology. There was a known and reputable women called Arachne whose art of weaving was much valued by the others. She superciliously believed that her skills in weaving were better than the skills of Athena. One day, Athena came by and challenged Arachne in weaving. Arachne achieved to weave a more imposing tapestry than Athena. Dreading Athena's rage and revenge, Arachne tried to kill herself. Athena interrupted and turned Arachne into a spider, whose life was condemned to weave forever. (Schwab, 1982)

The phylogeny of spiders is inscrutable due the fact that fossils found from the Tertiary period are very similar to the contemporary spiders. However, fossils have been found which are well preserved and date back to 380 million years, in a time where dinosaurs did not exist yet. Fossils found in the time of the Mesozoic era are so rare, that the evolution of spiders in that time is difficult to understand. The oldest fossil of a spider was found in Gilboa, a town in the federal state of New York. The fossil was named *Attercopus fimbriunguis* and palaeontologist found a remarkable fragment in it which looked like a spinneret. It later turned out, that the *Attercopus fimbriunguis* was only a close relative to the spiders. The hairs, which looked similar to spinnerets, were in fact an abdominal plate with excrescent spigots. This relative did spin silk and may have had a common ancestor with today's spider.

2.2 Anatomy

The spider's body is as demonstrated in Figure1 membered in two parts. The anterior section, which holds the eight legs, is called the *prosoma*. The *prosoma* is plated by the *carapax* from above and the *sternum* from below. The posterior part is often unsegmented[1] and called *opisthosoma*. "The *opisthosoma* fulfils chiefly vegetative tasks: digestion, circulation, respiration, excretion, reproduction and silk production." (Foelix, 1996)

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[1] Only species of the suborder *Mesothelae* have a segmented *opisthosoma*

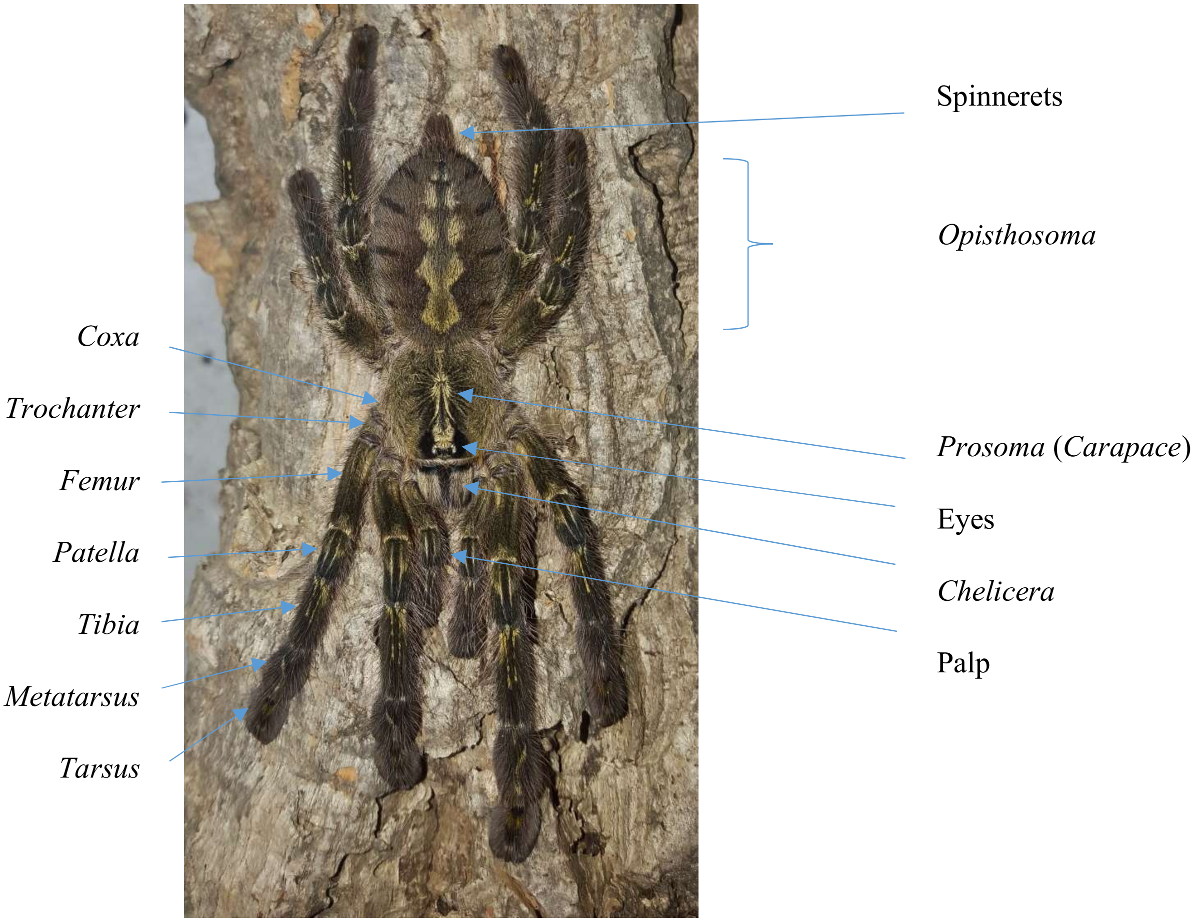


Figure 1. *Poecilotheria rufilata*

Figure 1 shows a *Poecilotheria rufilata.* This tarantula is endemic to South-India, where it is found in the Western Ghats above 1500 metres above mean sea level. It is an endangered species due to habitat loss and pet trade.

On the *prosoma*, there are usually eight eyes, which are arranged asymmetrically in pairs and located on an eye stalk. The importance of the eyesight differs between species. *Phidippus regius* for example do not attempt to seize a prey, which bumps into the spider, when exposed to darkness. The tarantula (*Ephebopus murinus*) illustrated in Figure 2 tends to leave its burrow when the terrarium is exposed to light. This accords to the fact, that most tarantulas are able to perceive a change in brightness and motion.

***Figure 2**. Close up of the eyes of an Ephebopus murinus.*

Every spiders' cuticle is a dull dark (Milius, 2016), however all spiders have a specific colouration. This *Haplopelma lividum* is a tarantula and shows a luminous blue when light is shone on the spider (Figure 3). The light is reflected by nanoscale structures which are embedded on the hair of the tarantula (Milius, 2016). Some *Poecilotheria* species (tarantula) have a bright colour beneath their legs and warn potential predators by holding the legs up high and by making an impression of being bigger.

Figure 3. Colouration of *Haplopelma lividum*.

2.3 Classification

2.3.1 General

Spider is the equivalent name for the order *Araneae.* There are two suborders in the order of *Araneae*: *Mesothelae* and *Opisthothelae*. *Opisthothelae* is divided into two infraorders: *Mygalomorphae* and *Araneomorphae*.

Table 1

<table>
<tr><td colspan="13">Animalia</td></tr>
<tr><td colspan="13">Arthropoda</td></tr>
<tr><td colspan="13">Chelicerata</td></tr>
<tr><td colspan="13">Arachnida</td></tr>
<tr><td colspan="13">Aranea</td></tr>
<tr><td>Mesothelae</td><td colspan="12">Opisthothelae</td></tr>
<tr><td>Liphistiidae</td><td colspan="5">Araneomorphae</td><td colspan="7">Mygalomorphae</td></tr>
<tr><td>Liphistius</td><td colspan="4">Entelegynae</td><td>Haplogynae</td><td colspan="7">Theraphosidae</td></tr>
<tr><td>Liphistius yamasakii</td><td colspan="2">Araneoidae</td><td>Salticidae</td><td>Dictynoidae</td><td>Scytodoidea</td><td>Theraphosinae</td><td>Eumenophorinae</td><td>Ornithoctoninae</td><td colspan="2">Aviculariinae</td><td>Poecilotheriinae</td><td>Psalmopoeinae</td></tr>
<tr><td></td><td>Araneidae</td><td>Nephilidae</td><td>Dendryphantinae</td><td>Cybaeidae</td><td>Sicariidae</td><td>Theraphosa</td><td>Pelinobius</td><td>Haplopelma</td><td>Avicularia</td><td>Ephebopus</td><td>Poecilotheria</td><td>Psalmopeus</td></tr>
<tr><td></td><td>Araneus</td><td>Nephila</td><td>Phidippus</td><td>Argyroneta</td><td>Sicarius</td><td>Theraphosa blondi</td><td>Pelinobius muticus</td><td>Haplopelma lividum</td><td>Avicularia metallica</td><td>Ephebopus murinus</td><td>Poecilotheria rufilata</td><td>Psalmopoeus cambridgei</td></tr>
<tr><td></td><td>Araneus diadematus</td><td>Nephila madagascariensis</td><td>Phidippus regius</td><td>Argyroneta aquatica</td><td>Sicarius terrosus</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Table 1 only shows the taxonomy of all the spiders mentioned in this assignment. There are currently 46386 valid spider *(Araneae)* species listed and classified (World Spider Catalog, 2017). The infraorder *Araneomorphae* includes all the “normal” spiders. If an ordinary person thinks about spiders, the person will imagine aside from Tarantulas a species of the infraorder *Araneomorphae.* This infraorder is called *Araneomorphae* because the species look and behave like a “typical spider”. The *Araneomorphs* illustrated in figure 7, 13 and 25 are “typical spiders”.

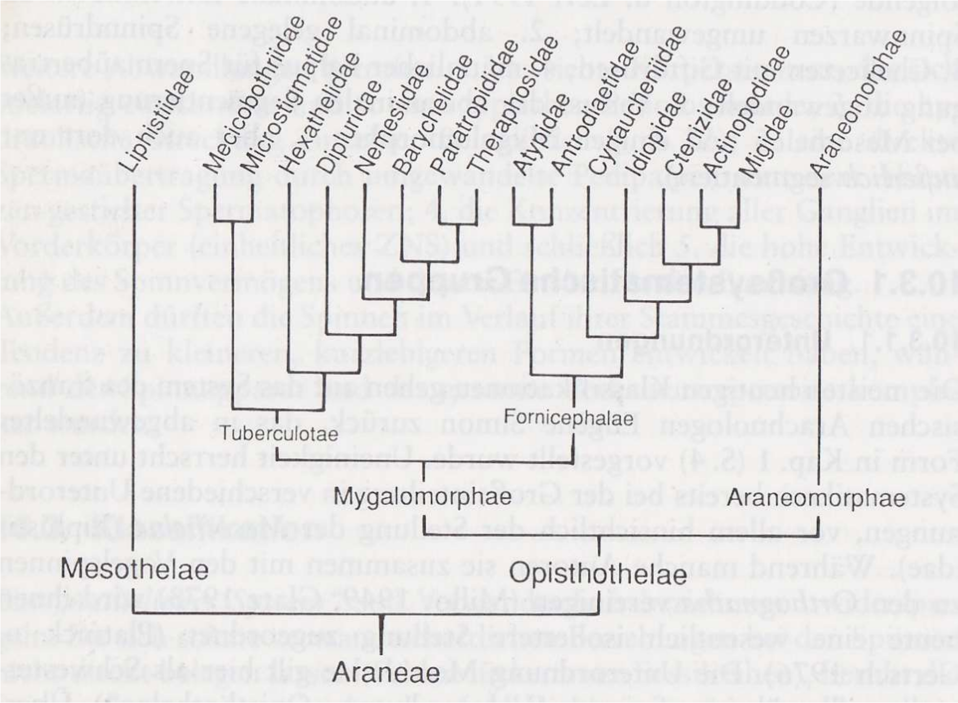


Figure 4. *Araneae* is the most popular order of the class *Arachnida*. Figure 4 shows all the families of the infraorder *Mygalomorphae.* (Foelix, 1996)

The family *Araneomorphae* is the most numerous with an estimated 37,000 species. *Mygalomorphae* is the second largest infraorder with 2,600 species. Species of the suborder *Mesothelae* are only found in Asia, wherefore they are not well-known. The infraorder *Tuberculotae* includes the family *Theraphosidae*, which is commonly referred as the tarantulas. They are typically hairy spiders with thick legs compared to araneomorphs legs. The *opisthosoma* is usually roughly the same size as the *prosoma*. They do not weave any orb webs and hunt their preys by pouncing on them or hiding until the prey nears the tarantula. The size is measured by body length which is usually from the *chelicera* to the spinnerets. Adult female tarantulas’ body length vary between 1.5 cm (*Cyriocosmus spec.)* to 12 cm *(Theraphosa blondi).* All spiders are venomous but none of them lethal for a healthy adult. However, some tarantulas can bite and cause serious harm (*Poecilotheria spec.)*.

2.3.2 *Mesothelae*

Liphistius yamasakii is a species of the infraorder *Liphistiidae* and of the suborder Mesothelae, which is only found in Thailand. They are rarely seen due to subterrestrial way of living. The segmented plates on top of the opisthosoma make them phylogenetically the oldest spiders. Therefore, they are frequently called "living fossils".

Figure 5. Illustration of a *Liphistius yamasakii* (Arachnothec, 2016)

2.3.3. *Opisthothelae*

The suborder *Opisthothelae* is divided into the infraorder *Mygalomorphae* and *Araneomorphae. Mygalomorphae* includes the family *Theraphosidae* which is known as the tarantulas.

2.3.3.1. *Mygalomorphae (example)*

The *Psalmopoeus cambridgei* is a docile tarantula with a body length up to 7 cm . It is endemic to Trinidad and belongs to the subfamily *Psalmopoeinae.* Attempts with their toxin (psalmotoxin) may help researcher understand similar toxin better. There is a potential in stroke prevention for person with high risk (Xiong et al. , 2014) .

Figure 6. Illustration of a *Psalmopoeus cambridgei.*

2.3.3.2. *Araneomorphae (example)*

Phidippius regius are found in eastern North America and West Indies. They prefer habitats which are exposed to a lot of sunlight. The range they can jump is estimated to be up to 50 times their own body length, which varies between 1 mm to 20 mm (Baidya, 2015).

Figure 7. Illustration of a Phidippus *regius*. (Tobler, 2016)

2.4 Spider Silk

There are two classes in the phylum Arthropoda which are able to produce silk: *Insecta* and *Arachnida.* The best known species of the class *Insecta* which produces silk is the silkworm (*Bombyx mori).* Further, spiders (*Araneae)* have developed the capability of producing silk more than species of the class *Insecta* have*.* A silk thread of the spider *Nephila edulis* has a diameter of 5 µm, which is 20 thinner than a human hair (Gilson, 2010). The spider stores the silk as a viscid liquid in a silk gland.

The silk glands of *Araneomorph* have evolved at an unknown point. One specific silk gland has developed 240 million years ago and has made a new habitat accessible for the *Araneomorphs*: the air. It is a specific type of silk that is able to carry the weight of an Araneomorph and withstand even a lot more. The silk, which is only made by *Araneomorphs*, is produced in the *Glandula ampullacea* major and is called *major ampullate* silk. In comparison to the *Mygalomorphs* and *Mesothelaes*, *Araneomorphs* do not need an underground to stand on due to the capability of producing a silk[7] which is able to carry their weight. The silk of the *Mesothelaes* and *Mygalomorphs* cannot carry the weight of the spider, because they do not produce *major ampullate* silk. This is the reason why tarantulas do not build orb webs.

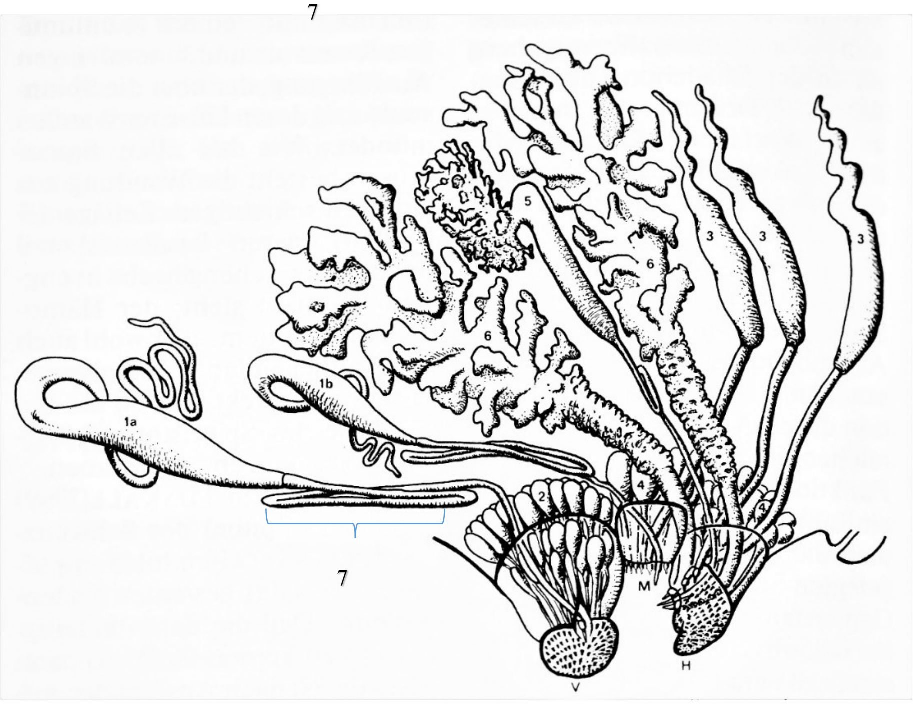


Figure 8. The anatomy of the silk glands of a *Nephila madagascariensis.* (Kullman & Stern, 1981)

As illustrated in figure 10, the silk glands are numbered in the following order:

1. a) *Glandula ampullacea major* b) *Glandula ampullacea minor*
2. *Glandulae piriformes*
3. *Glandulae tubuliformes*
4. *Glandulae aciniformes*
5. *Glandula coronate*
6. *Glandulae aggregatae*
7. Duct with winding

V: anterior spinnerets, M: median spinnerets, H: posterior spinnerets

Major ampullate silk (MA) is a very tough material. The structure is a complex made out of crystalline parts and amorphous parts. Scientist often use the *major ampullate* silk of the genus *Nephila* for research. These so-called golden orb-weavers are found along the equatorial biome.

2.5 Spinnerets and production mechanism

There are between 2 and 8 spinnerets located at the end of the *opisthosoma*. Every type of silk gland usually connects to one spinneret. A well-developed musculature in the inner part of the *opisthosoma* enables the spider to move the spinnerets. The spinnerets may have evolved from other extremities which were not used anymore after leaving the maritime habitat (Kullman & Stern, 1981). The silk threads emerge from the spinnerets, whereupon numerous spigots are found. They are macroscopical structures which form emersion point of a thread. Figure 8 shows a close up view on a spinneret with emerging silk threads.

Figure 9. Spigots of a *Castercantha* spec. secreting *piriformes* silk. (Kunkel, 2000)

The silk glands of a spider are connected to the spigots on the spinnerets. Every silk gland has its own spigots. There are up to two different types of spigots on a spinnerets. The number of silk glands differs, where *Mesothelae* usually have less than *Opisthothelae*. (Mullen, 1969). *Araneus diadematus* has about 800 silk glands (Heimer, 1988). These 800 silk glands can be classified in 7 types of identical glands. Every type of silk gland produces a different kind of silk. This is required due to the various tasks spider silk has to accomplish.

Figure 10. Posterior spinnerets of a *Lasiodora klugi.*

Mygalomorphs, unlike most *Araneomorphs*, have 4 spinnerets while the anterior are strongly reduced (Foelix, 1996). The primary spinnerets (posterior) of a *Lasiodora Klugi* can be moved independently and have probably evolved from a further pair of legs. The silk glands have come from the inner part of the *opisthosoma* trough the ducts and end on the spigots which are found numerous on the spinneret.

2.6 Function of different types of silk and their gland

Depending on their usage, the spider takes different kind of silks. Table 2 shows out of which gland the thread comes from and what for it is used.

Table 2

Silk gland	**Silk function**
Glandulae ampullaceae majors *Glandulae ampullaceae minors*	Drag line, frame thread (ANT and MED)
Glandulae piriformes	Attachment disk (ANT)
Glandulae aciniformes	Egg case (outer wall), swathing silk, sperm web (MED)
Glandulae tubuilformes	Cocoon silk (MED and POST)
Glandulae flagelliformes	Axial thread of sticky spiral (POST)
Glandulae aggregatae	Glue of sticky spiral (POST)

The abbreviations stand for the spinnerets, where the silk emerges.

ANT: anterior spinnerets, MED: median spinnerets, POST: posterior spinnerets

The length of the duct (see figure 8) which connects the silk glands to the spigots depends on the different tasks it has to fulfil, involving a more complex function than just connecting the secretion and passing it through.

There are 3 different functions for the duct:

1. H_2O-resorption: The water content of the secretion decreases from the silk gland to the spigots. (Kullman & Stern, 1981)
2. Transformation of the molecular steric structure: The secretion is structured in α-helical configuration in the silk gland. After passing the duct, the thread features a β-pleated sheet structure. (Kullman & Stern, 1981)
3. Polymerisation: The molecular weight of the fibroin produced by *Nephila madagascariensis* amounts to 30’000 in the silk gland. This is the relative molecular weight and does not have a unit of measurement. However, the finished fibroin in the thread shows a molecular weight of 200’000 to 300’000 (Braunitzer & Wolff, 1955). The polycondensation might be initiated by addition of a promotor between the silk gland and the spigots (Kullman & Stern, 1981).

3. Physical Characteristics of Spider Silk

Different silk glands produce different types of silks. They show diverse physical characteristics and display varying amino acid motifs. This is the consequence of million years of evolution. It is the proper combination of extensibility, tensile strength and viscoelasticity that makes the silk gland unique. Using the example of *Araneus diadematus* silk it is possible to compare the silks with other natural and synthetic products. These products are well analysed and familiar materials, which are used every day.

3.1. Fundamentals of extensile deformation

The elastic deformation is defined as the elongation, where the material returns into its initial length without extraneous cause after being disengaged. One physical property is determined by straining a thread and measuring the technical stress. The analysis of the measurement is seen on a stress-strain curve. A Hookean spring shows the simplest graph on a stress-strain curve.

$$\text{Extension} = \frac{current\ length - initial\ length}{initial\ length} = \varepsilon = [-] \qquad \text{Eq. (1)}$$

Diagram 1

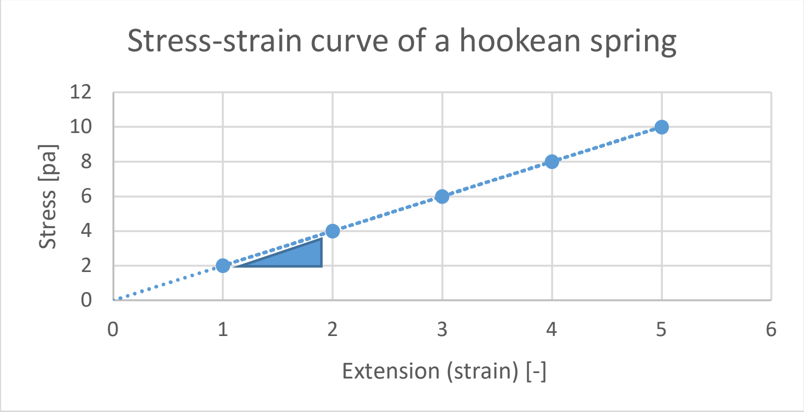


Diagram 1 shows the characteristic of a Hookean spring. The extension increases proportional to the stress added on the thread. The Hooke's law describes the fraction of stress divided by the extension while being constant and is only applicable on the extensile deformation. This is only accurate during elastic deformation. The gradient is defined as the Young's modulus.

$$E = \frac{\sigma}{\varepsilon} = \text{const.} \qquad \text{Eq. (2)}$$

E: Young's modulus [Pa], σ: stress [N/m^2], ε: strain [-]

3.2. Stress-strain curve

Diagram 2 shows a stress-strain curve with the plastic deformation.

3.2.1 Diagrammatic stress strain curve for spider silk

Diagram 2

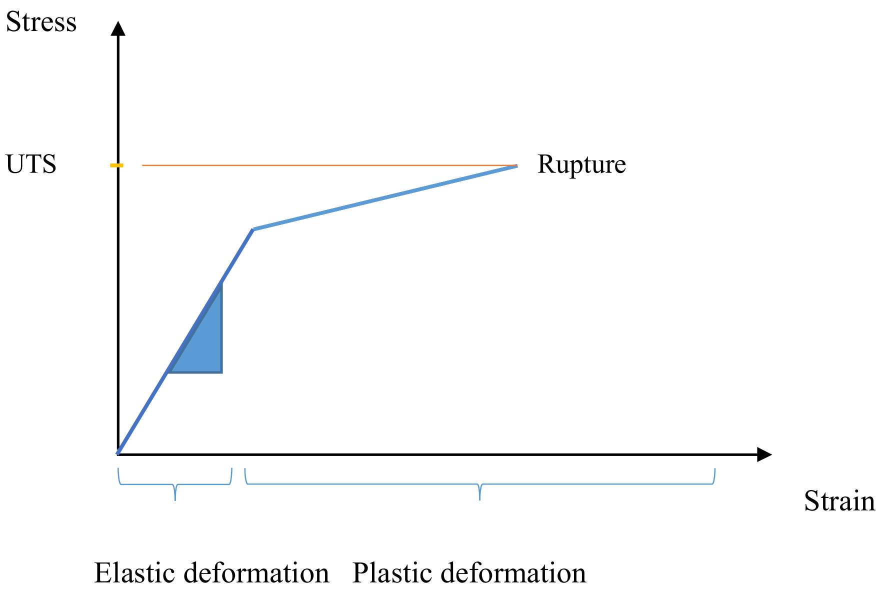


Diagram 2 shows a schematic stress-strain curve of spider silk, whereupon the blue gradient correlates to the Young's modulus. The slope can be divided into two sections: elastic deformation and plastic deformation. As soon as a fibre is stretched over the elastic part, it will not return into its initial state. Further, the gradient in the plastic deformation section rises or flattens in comparison to the Young's modulus. The stress-strain is seldom linear until rupture for a plastic material.

3.2.2. Stress-strain curve applied on *araneus diadematus* silk

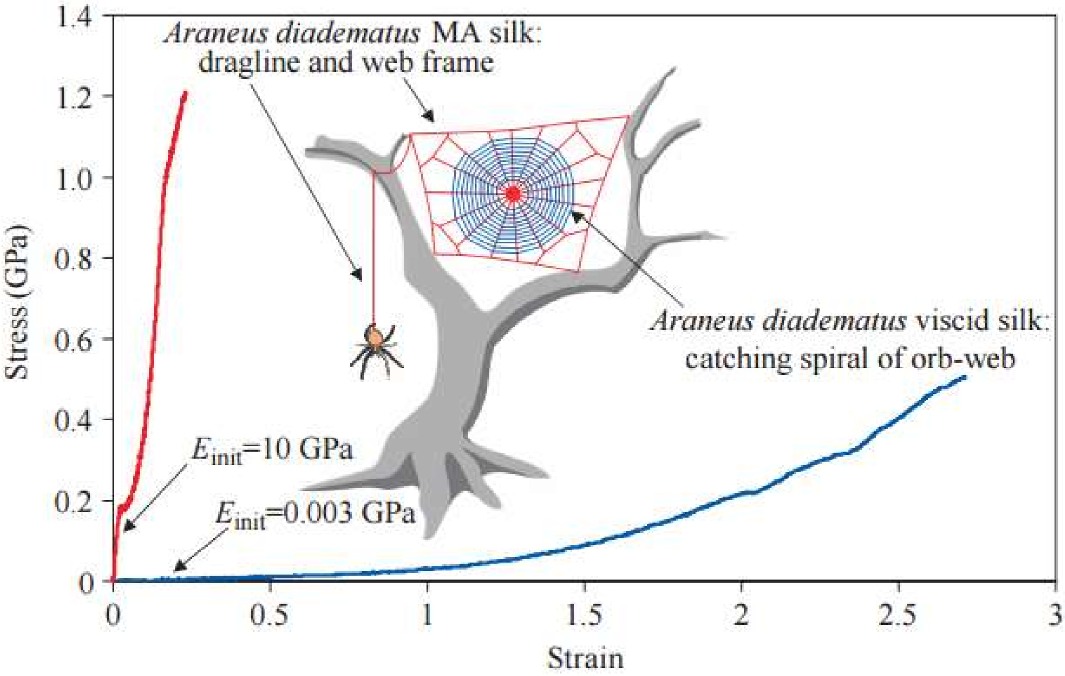


Figure 11. Stress-strain curve of an *Araneus diadematus.* (Gosline, 1986)

The Young-Modulus is the initial slope of the graph. The blue graph correlates to the viscid silk which is coloured blue in the orb web. The red graph correlates to *major ampullate* silk, which is used for drag line and framework of the orb web. The values of the following comparison of Tensile strength, extensibility and Young-Modulus to other natural occurring materials and construction material will refer to this measurement of *Araneus diadematus* silk.

Diagram 3

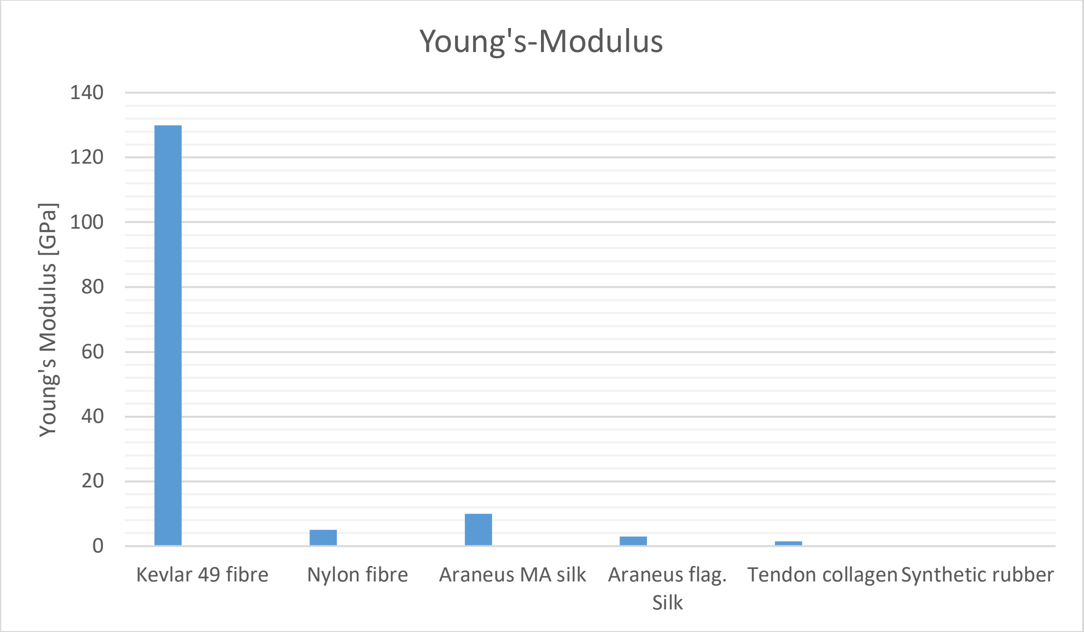


Diagram 3 shows different Young-Modulus (Stiffness/E_{init}) in comparison to *Araneus diadematus* silk. The strain rate of the measurement was not given. The *Araneus diadematus*-value of the Young's modulus is minor by comparison to that of Kevlar. However, materials with great stiffness are for example used in constructions of buildings, where the material should not deform and needs to withstand great static force.

Diagram 4

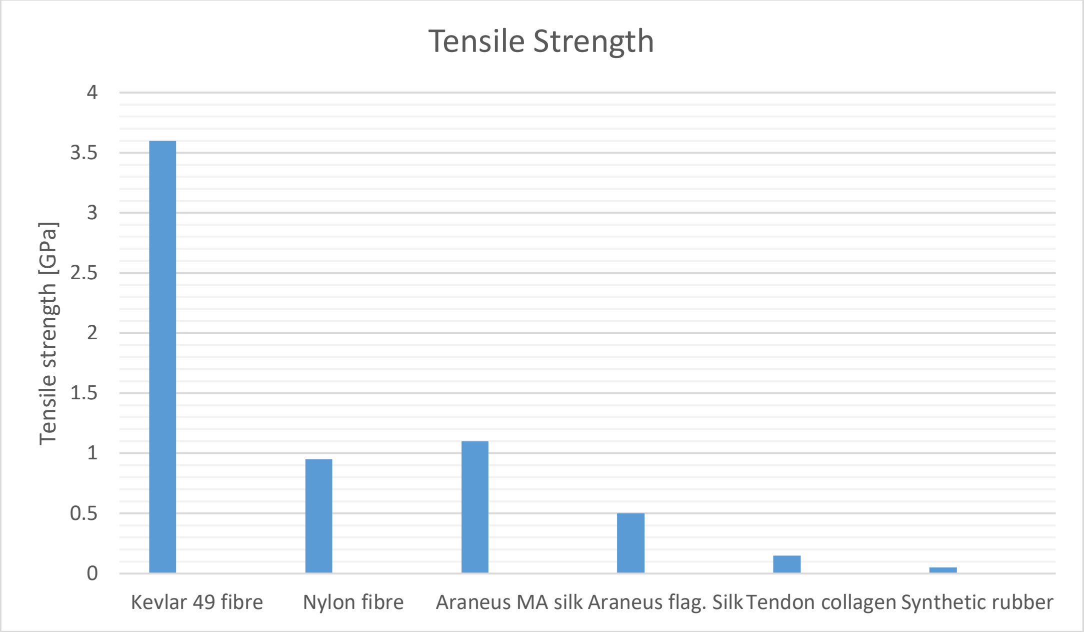
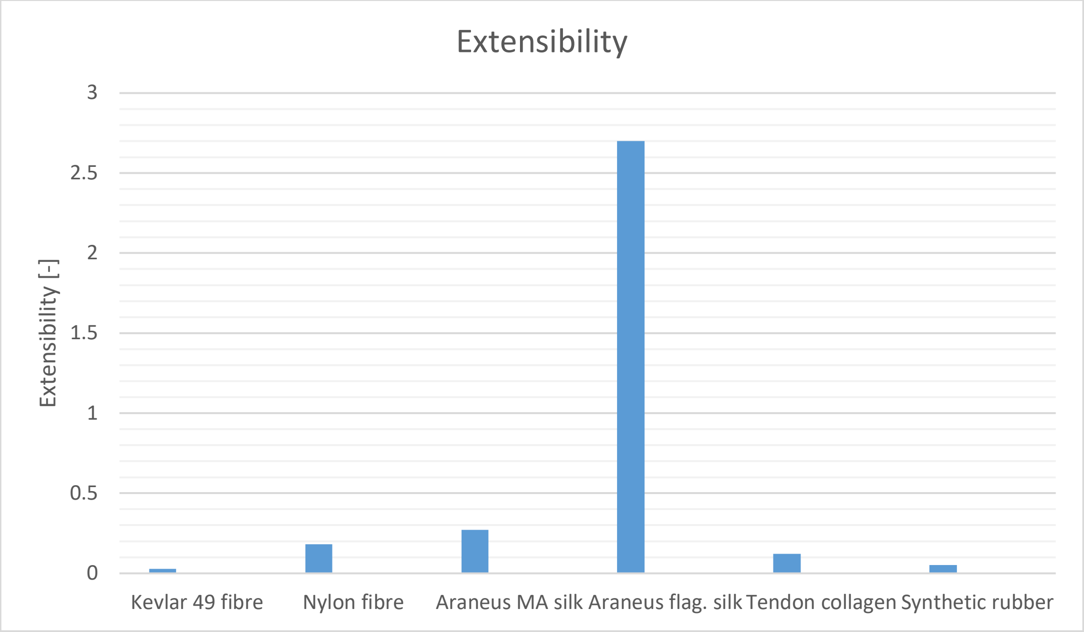


Diagram 4 shows the values of the tensile strength of different natural and synthetic materials from (Gosline, 1986). The strain rate was not stated. *Araneus diadematus major Ampullate* silk is one of the highest tensile naturally occurring polymer (Koch, 2005). Kevlar 49 fibre is nevertheless stronger but the whole structure is made out of a crystalline organisation.

Diagram 5



Araneus diadematus flagelli silk is very extensible. Diagram 5 shows that it can be extended by a factor of 2.7 of its initial length. Whereas, Kevlar is very rigid. The values are from (Gosline, 1986), whereupon this time the strain rates are insignificant due to irrelevance in measuring data. The catching spiral is made out of very extensible silk. The elongation of a thread can be observed by dint of a light optical microscope.

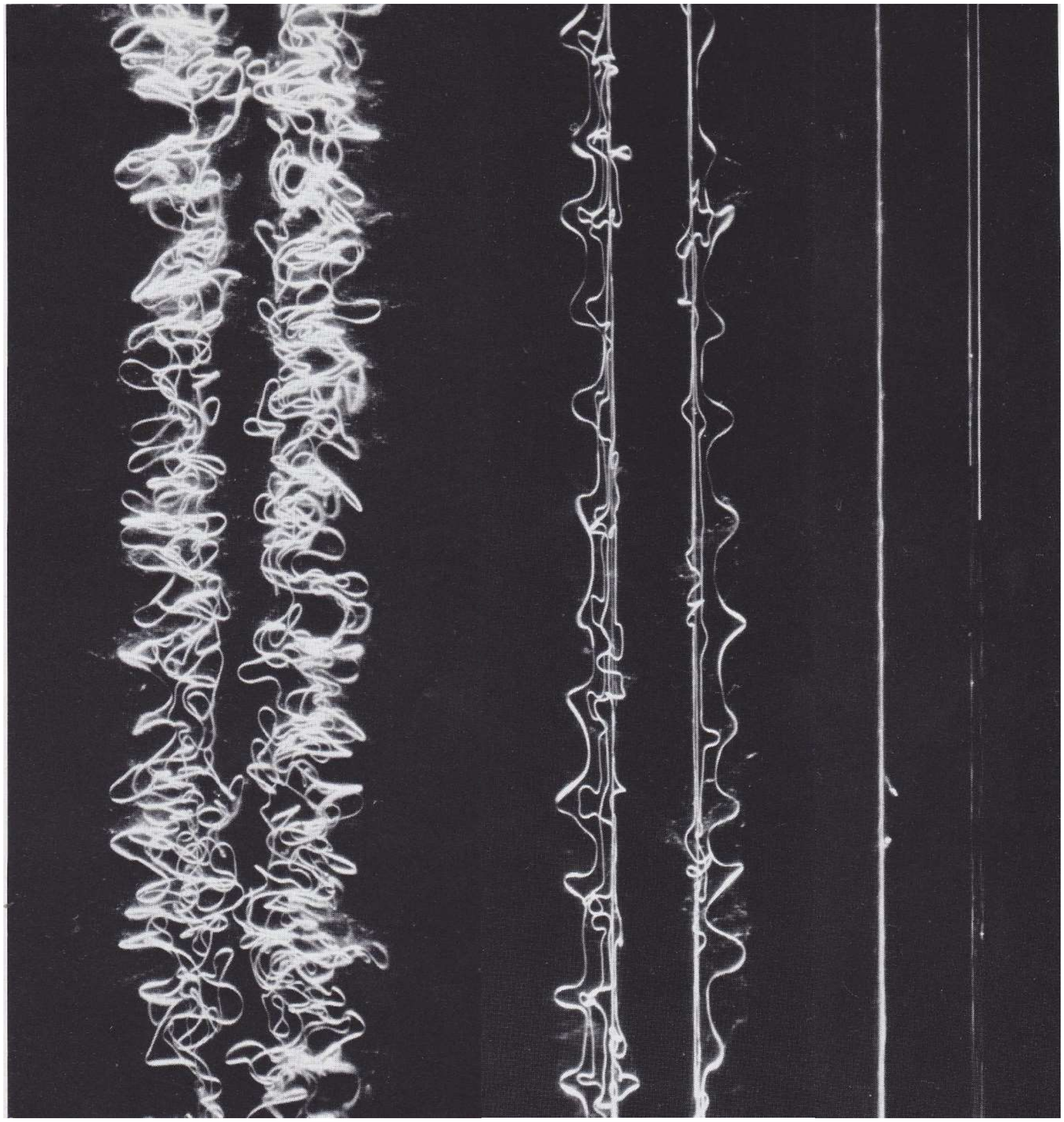


Figure 12.

Figure 12 shows two threads of the social spider Stegodyphus sarasinorum in their initial state, extended by the factor of 5 and 10. Some species are able to produce a thread which is extendable by a factor of 20. Pictures by (Kullman & Stern, 1981)

Diagram 6

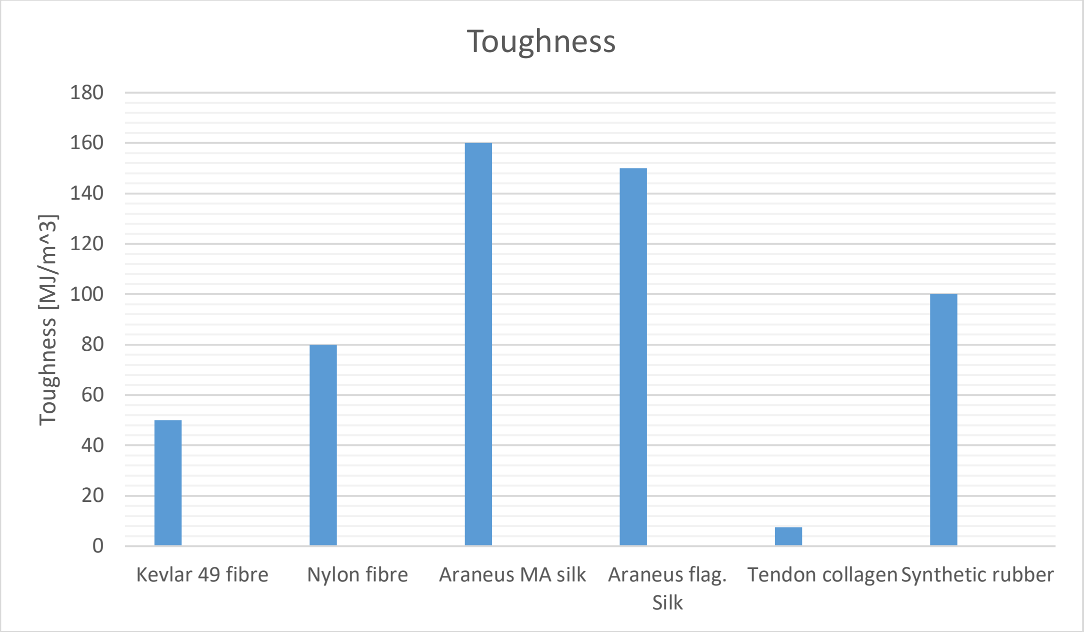


Diagram 6 shows the toughness in $\frac{\mathrm{MJ}}{\mathrm{m}^3}$ of the compared materials. *Araneus diadematus* silks have a similar amount of toughness, although they are very different in extensibility and stiffness. Kevlar however needs 4 times less energy to break. Toughness is the energy required to break a thread while extending it along the length. The derivation of the toughness can be shown with the help of the stress-strain curve of a Hookean spring. It is the area beneath the graph.

$$YM = \frac{stress}{strain}$$

$$F = YM \cdot s$$

$$Work = F \cdot s$$

$$Energy = \int F\, ds$$

$$Energy = \int YM \ \cdot s\, ds$$

Equation 2

$$Energy = \frac{1}{2} YM\, s^2 \ (+\ C)$$

YM: Young’s modulus, s: distance, ds: infinitesimal distance, F: force in [N], stress in [Pa], strain [-], C equals zero

Diagram 7

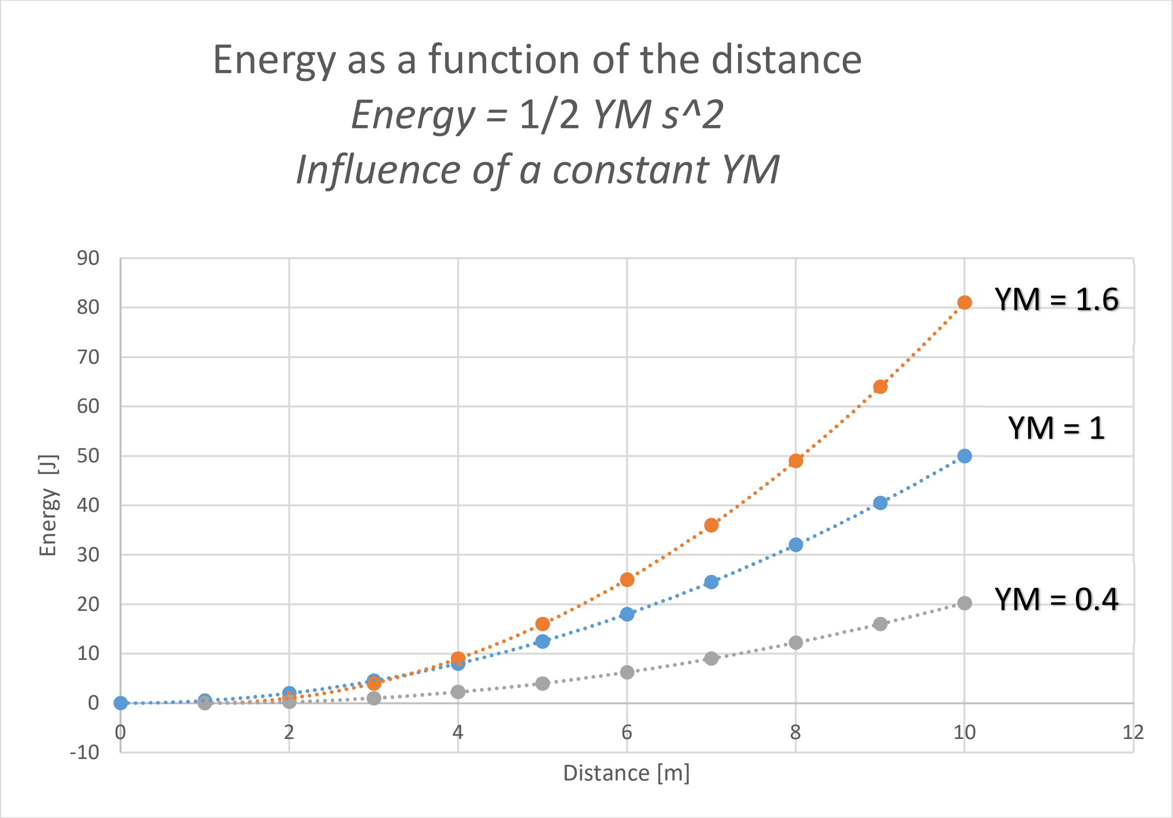


Diagram 7 shows, that a material with greater YM is able to absorb more energy with less extension. These slopes are only conferrable on materials with Hookean properties, wherefore have linear slopes in the stress-strain curve. A greater YM stretches the graph vertically more, while a little YM shrinks the graph. *Araneus major ampullate* silk has twice as much toughness as nylon, which means the graph reaches a higher energy amount before rupture. This comes from greater YM (more gradient) and more extensibility (longer graph in the horizontal direction). The antiderivative of the stress-strain curve is the slope of diagram 7 (Energy as a function of the distance). This is an approximate approach to show the correlation between the YM, extensibility and toughness. The graph of the stress-strain curve of *araneus diadematus* silk is not linear. This has an influence on the derivation considering the initial function. The mathematical function of viscid silk is a function third class (highest exponent = 3) and would result if integrated in a function fourth class (highest exponent = 4). The toughness would proportionally rise more in comparison to a linear initial function.

Diagram 8

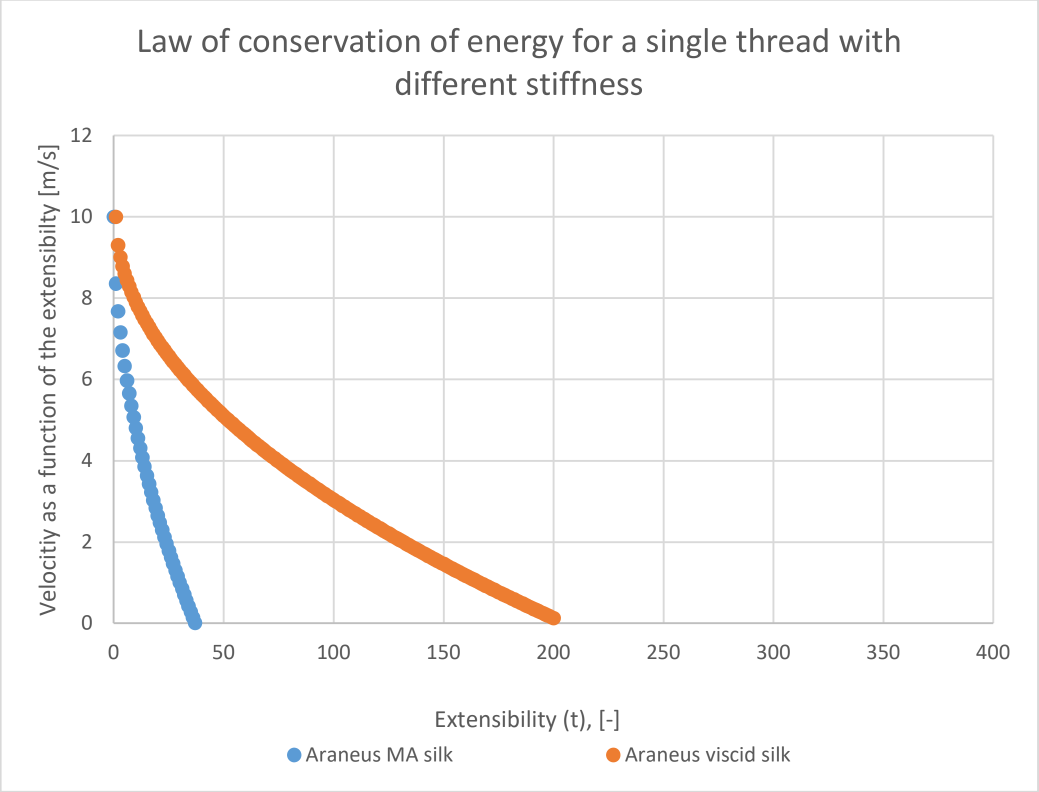


Diagram 8 shows how different type of silks slow down a prey which is flying into a single thread. The kinetic energy of the prey cannot exceed 160 MJ for a thread with the volume of $1m^3$. This is only valid for a linear stress-strain curve. A thread with greater YM can absorb more energy (slowing down the prey) with less extension (blue), while a very extensible thread (orange) can absorb the same energy during a longer period of extension. As soon as a thread can absorb enough energy to slow down the prey in the range of extensibility, it will not snap. Strain-rate properties are not considered in this chart.

Figure 13. *Araneus diadematus* feeding on a caught prey, which is entangled in silk produced by the *Glandulae aciniformes.* (Horton, 2016)

3.2.3. Stress strain curve *Nephila* spec. silk

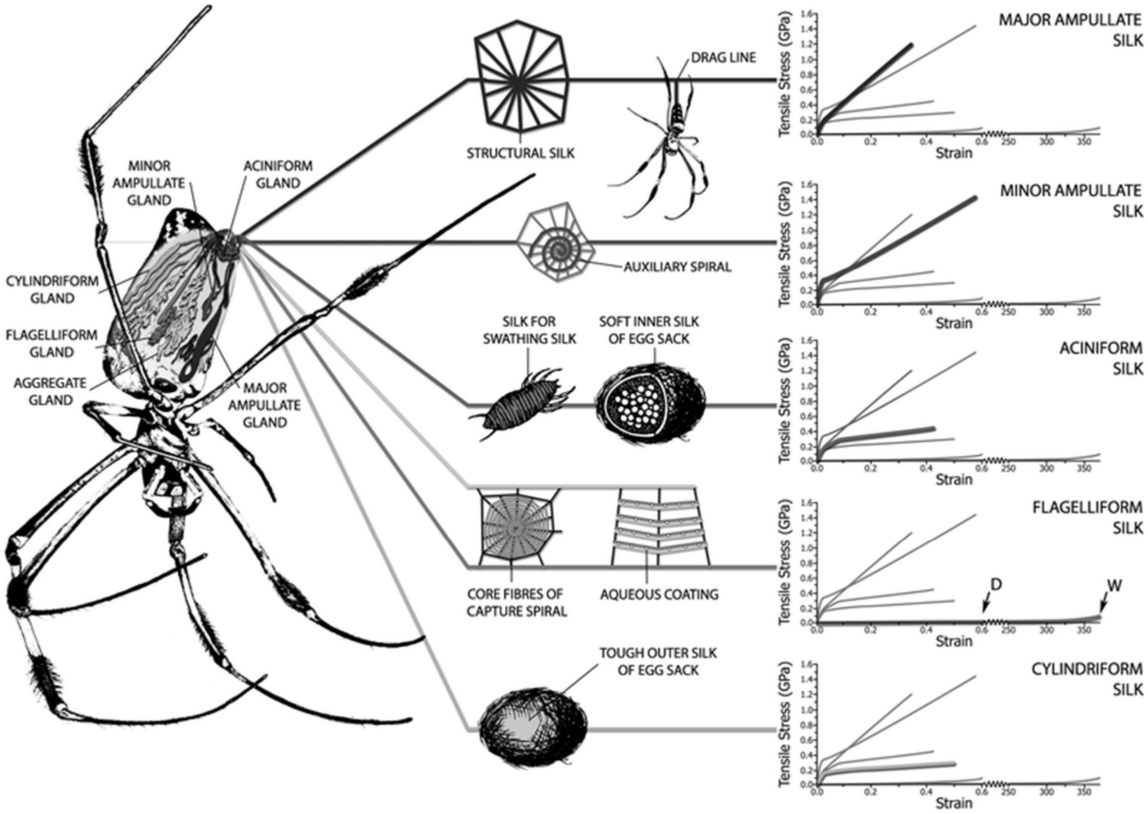


Figure 14. Stress-strain curve of a *Nephila spec.*

The graph shows five different stress-strain curves for the silk glands of a *Nephila* spec, while the graphs are very similar to the ones of *araneus diadematus*. *Major ampullate* silk differs from species to species, but it is possible to identify MA silk from other silks of the spider with help of amino acid motifs. (Vollrath & Porter, 2006)

3.4. Strain-rate-dependant property

On the basis of *araneus diadematus major ampullate* silk, it is possible to measure a strain-rate-dependent material property.

Table 3

Strain rate $[\frac{1}{s}]$	0.0005	0.002	0.024	20-50
E_{init} [GPa]	9.8	8.9	20.5	25-40
Tensile strength [GPa]	0.65	0.72	1.12	2.0-4.0
Extensibility [%]	24	24	27	20-50
Thoughness $[\frac{MJ}{m^3}]$	91	106	158	500-1000

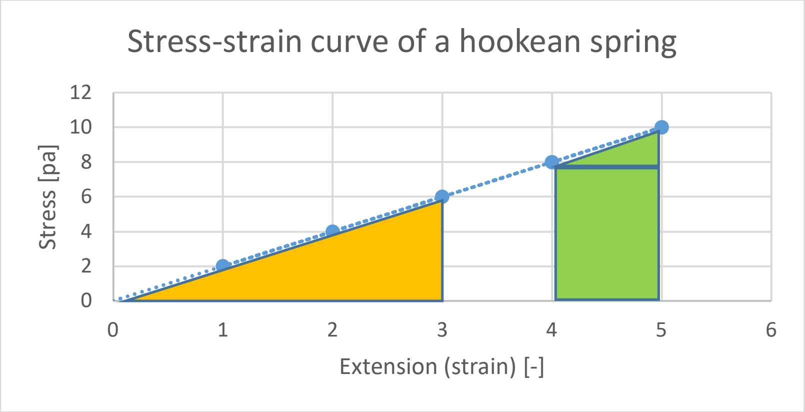
From (Gosline, 1986)

Gosline et al. and Denny were able to measure a non-Newtonian fluid property in silk. This makes silk an even stronger material. The higher a strain rate was, the more force it could withstand. This is a very useful property when a prey flies into the net or when a spider suddenly falls of a branch. What makes *araneus diadematus* silk so strong is the proper combination of extensibility, tensile strength and high amount of hysteresis. The absorbed energy is split into hysteresis and elastic deformation. Hysteresis occurs due to high intermolecular friction. 65% of the energy will be transformed into heat (Denny, 1976). The viscid *flagelli* silk holds the prey back and compensates the remaining energy which would result as a rebound.

3.5. Pre-stress of a web

An important architectural feature for creating a web is the pre-stress of a thread (Craig, 2003). Different pre-stress influence the range of extensibility. This can be shown using the example of the Hookean spring.

Diagram 9



The orange and green surface in diagram 9 correlate to the energy used for the extension. The proof for the equality of the green and orange area is in the appendix[2]. Structural ability is reached by varying the pretensile force on a thread while constructing the orb web (R. Zaera, 2014). The pretensile force has direct influence on the extension of the thread in a web. The more pretensile force is applied on, the less the thread will extend in comparison to the same thread without pretensile force, while the amount of energy applied on the thread staying constant.

The stiffness of spider silk is not constant wherefore the proportionality cannot be translated. However, the comparison is appropriate for the theory of different pretensile forces. The benefit of pre-stressing a thread is due to less extension. MA silk for the frame does not have to absorb the full impact of a prey. The main task is to hold the web in place and maintain structural ability. The pre-stress affects a higher stiffness but less absorbable energy. In contrast, viscid silk has to fulfil a different task in the orb web.

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[2] Evidence for equality of the surface (Hookean spring) - Appendix

Figure 15. Orb web of an araneus diadematus. (Joyfulgypsy, 2016)

The gap between the viscid silk is visible and marked with a yellow double headed arrow in figure 15. The appearance of the gap between the viscid silk threads is based on evolution. The less material an orb web requires, the less silk the spider has to produce, which results in an energetically favourable process. The disadvantage of the energetic saving is a gap between the viscid silks. The density of the viscid silk threads per area decreases, which will lead to more energy a single thread has to absorb if a prey hits the net. Owing to less pre-stress, the thread can absorb to full potential of energy with the help of full extension. The main task of viscid silk beside adhesion is to not snap and to spread the energy on the surrounding threads. This is possible due to great extensibility of viscid silk and lack of pretensile force.

4. Chemical composition of spider silk

4.1. Primary structure of *Araneus diadematus* silk

Table 4

Glycine	35.13%
Alanine	23.4%
l-Leucine	1.76%
Proline	3.68%
l-Tyrosine	8.2%
α-Glutamic acid	11.7%
Diamino carboxylic acid	5.24%
Ammonia	1.16%
Fatty acids	0.66%

(Kullman & Stern, 1981)

Silk is defined as a fibrous protein made up of repetitive sequences of amino acids (Craig, 2003) and phosphate (Koch, 2005). These sequences are found particularly in the large core domain of a thread (Römer & Scheibel, 2008). Table 14 shows the composition of *Araneus diadematus* silk. There are three different amino acids which mainly make up the primary structure. What makes them unique is that their side chain makes them the simplest amino acid possible. Glycine (H), Alanine (CH_3) and Serine (CH_2OH) make up to 50-65 % of the amino acids found in spider silk (Koch, 2005).

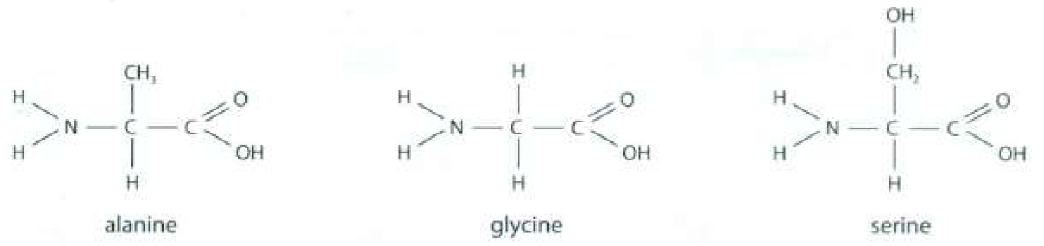
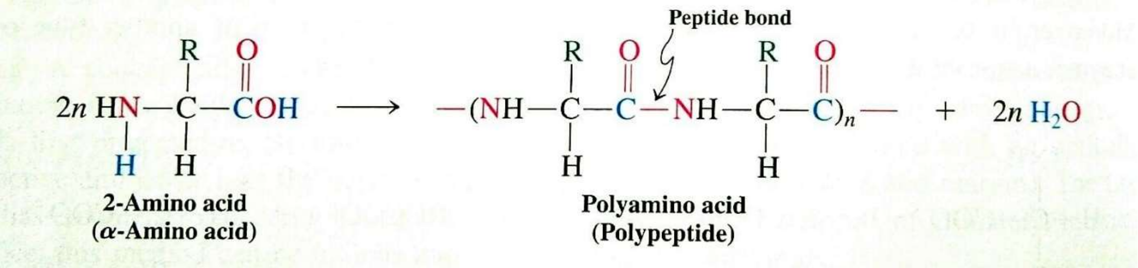


Figure 16. The three simplest amino acid dominate the primary structure of spider silk. (E.L., 2014)

4.2. Amino acids

An amino acid consists of a central carbon atom called $C_{\alpha.}$ It binds 2 functional groups, an amine and a carboxylic acid. The third substitute is a Hydrogen. The fourth substitute is a variable side chain, which defines the amino acid. The simplest amino acid is Glycine with a hydrogen as side chain. A polypeptide is formed by several proteinogenic amino acids with elimination of water as seen in figure 17.



$$2n\,HN{-}C(R)(H){-}COH(=O) \longrightarrow {-}(NH{-}C(R)(H){-}C(=O){-}NH{-}C(R)(H){-}C(=O))_n{-} + 2n\,H_2O$$

Figure 17. The amine group and carboxylic group interact, whereat water is eliminated. (Vollhardt & Schore, 2009)

4.3. Structural set-up on the molecular basis

X-ray crystallography facilitates the determination of the molecular structure of a substance. Studies with X-ray diffraction have shown that silk contains crystalline domains (Gosline, 1986). Simple model conception of the structural set-up have a β-pleated sheet as crystalline and α-helix as amorphous domain (Vollrath, 1992). With regard to material properties, the crystalline part contributes tensile strength to the thread and the amorphous domain creates the extensibility.

More elaborate models are based on cDNA analysis and sequenced genes of spiders (Hayashi, Shipley, & Lewis, 1999). The fibrous protein has recurring amino acid patterns throughout the thread. The short peptide patterns can be subdivided into four categories (Koch, 2005): GPG(X)$_n$/GPGQQ, (GA)$_n$/A$_n$, GGX, and Spacer. G stands for glycine, P for proline, Q for glutamine, A for alanine, and X can be either alanine, serine, valine, or tyrosine. The patterns form a determined steric structure in the thread. GPGXX/GPGQQ pattern shapes into a helix, whereas the pattern (GA)$_n$/A$_n$ transforms into a β-pleated sheet, and the GGX is said to be creating a helix with three amino acid residues (van Beek, Hess, Vollrath, & Meier, 2002). The steric structure of Spacers is not clearly determined yet (Adrianos, et al., 2013). Table 15 shows the repetitive sequence and the correlating steric structure.

Table 5

GPG(X)$_n$/GPGQQ	(GA)$_n$/A$_n$	GGX	Spacer
➢ helix	➢ β-pleated sheet	➢ helix	➢ unknown

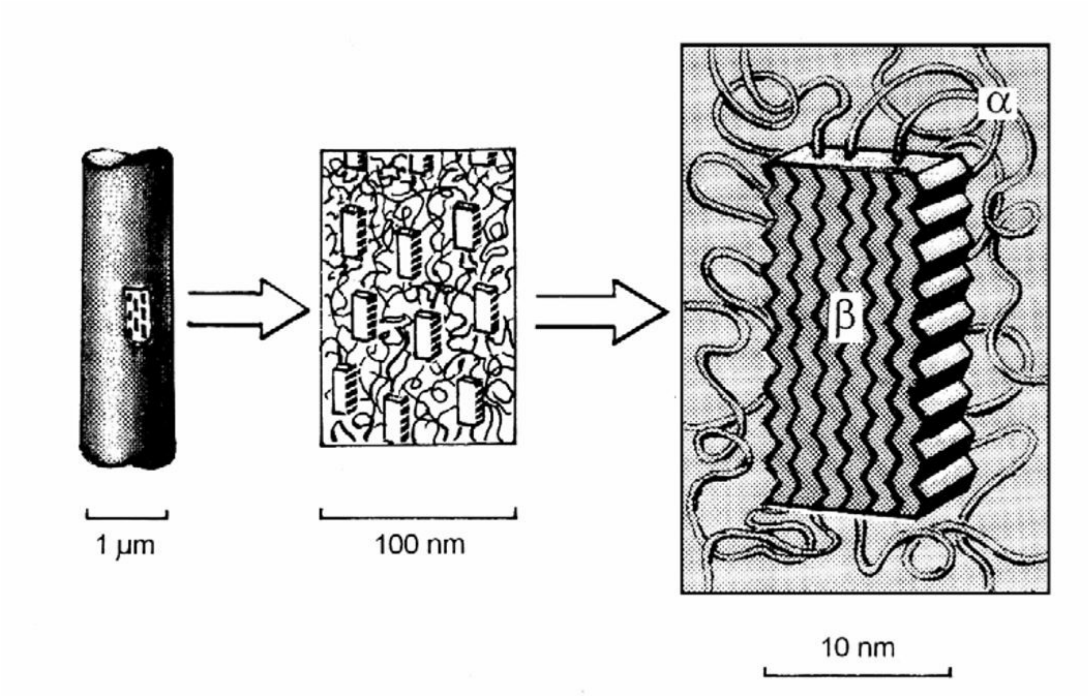


Figure 18. Simple model of a thread. (Foelix, 1996)

Figure 19 shows a simple model, which describes, that spider silk is made out of crystalline (beta-plated sheet) and amorphous (alpha-helix) regions. The chains will make interactions with themselves. This results in different kinds of the steric structure. If the primary structure has a lot of repetitive motifs, the chain can form more bonds with itself. This causes the chain to get more stabilized and the material to be tougher. The fibrous proteins are arranged in multiple domains, which can be α-helical structures, different β-forms and amorphous domains.

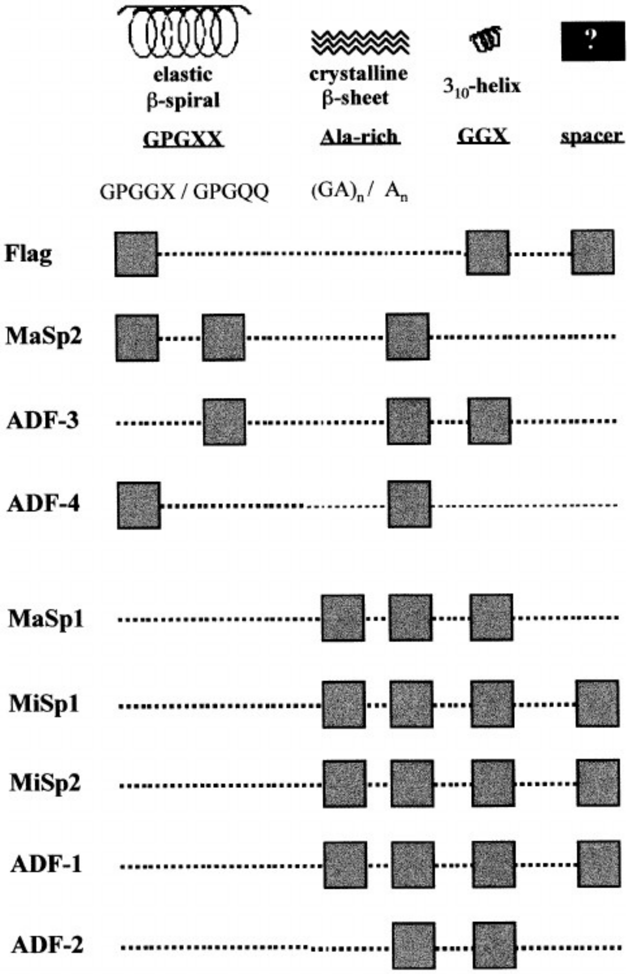


Figure 19. Amino acid motifs in *Araneus spec.* silk. (Hayashi, Shipley, & Lewis, 1999)

The chart in figure 18 shows determined regularity in the silk thread of an *araneus* spec. However, the steric structure of the spacer is still not known.

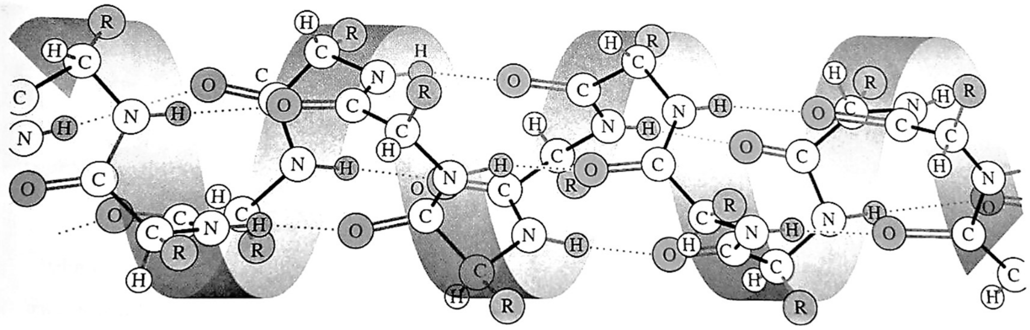


Figure 20. Right handed alpha helix. (Vollhardt & Schore, 2009)

The secondary structure of an alpha-helix is held together by hydrogen bonds between the oxygen of the carboxylic acid and the hydrogen of the amine group. These hydrogen bonds are illustrated in figure 20 as dotted lines. The amine group to which the carboxylic group binds is four amino acid further away. A full turn usually involves 3.6 amino acids. As tertiary structure, the amino acid side chains extending outwards interact. They stabilize the helix by H-bonds. Another steric structure found in *Araneus* spec. silk is the beta-pleated sheet, which contributes to toughness. The beta-pleated sheet is a secondary structure commonly found in fibroins of spider and insects (Craig, 2003). The beta strands (primary structure) make hydrogen bonds with other chains (beta strands) and not within the chain (Stryer, 1995). The alignment of the strands can be in parallel (figure 22) or antiparallel (figure 21) direction. Due to the side chain of the amino acids, the third structure looks like a pleat, wherefore it is called a beta-pleated sheet.

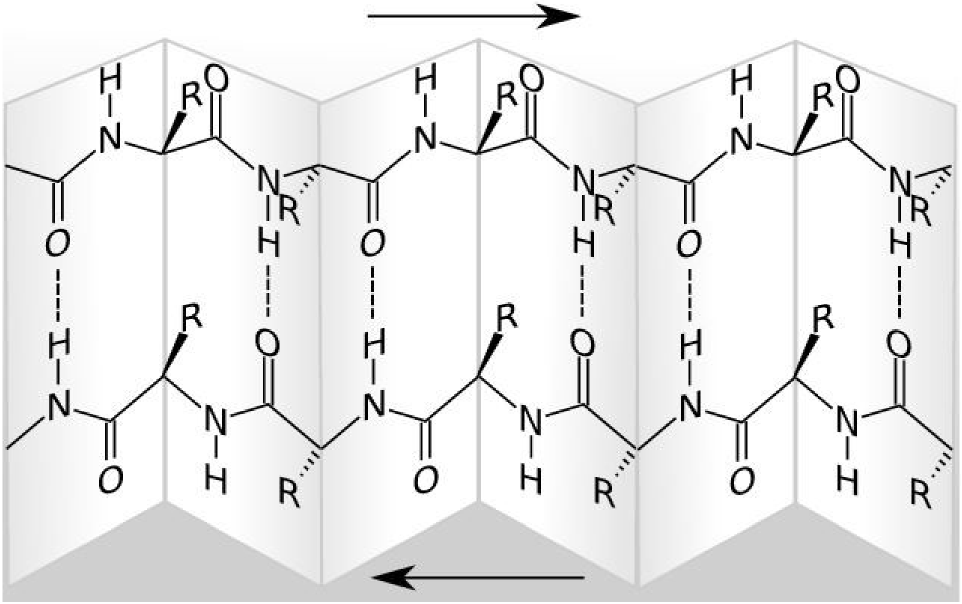


Figure 21. Schematic model of an antiparallel orientated beta-pleated sheet. (Roland.chem, 2012)

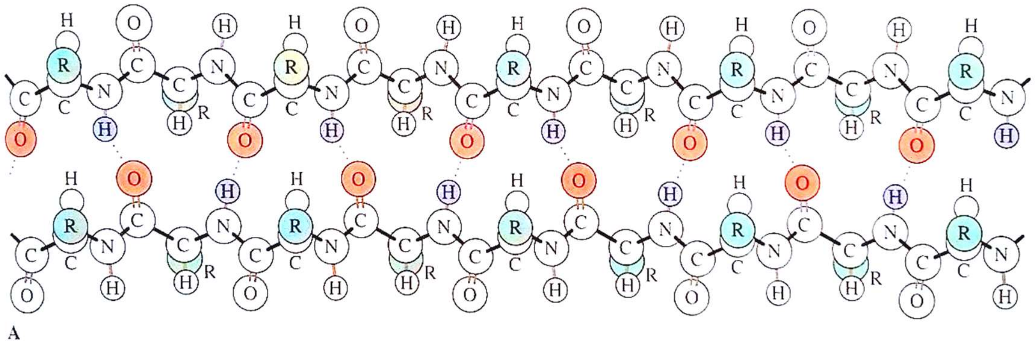


Figure 22. Parallel orientated beta-pleated sheet which is held together by the dotted lines (H-bonds). (Vollhardt & Schore, 2009)

Figure 23. *Poecilotheria subfusca*

5. Comparison between Araneomorphous silk and Mygalomorphous silk use

5.1 Araneomorphae usage of silk (Nephila spec.)

Araneomorphs have up to 7 types of silk glands and whereupon every silk gland type produces one type of silk which is only used for a single task.

5.1.1 Hunting and shelter

If the task to draw a spider web is given to a child, it will presumably draw a vertical orb web (Figure 23). The vertical orb web is the result of million years of evolution and well known as the characteristic web of a spider. The *Araneomorphs* are capable of producing *major ampullate* silk, which is used to create an orb web. All spiders are predators i.e. they feed on other animals. Every spider has a specific hunting method which is determined by its taxonomy. There are several different hunting strategies like using a web or attacking a prey unpredictably from behind and injecting poison in it. The most familiar is using the orb web. The spider waits for a prey to fly onto the web and launches into it as soon as it entangles itself. The orb web is a masterwork of nature. Millions of years have passed until this type of web had evolved. The orb web is able to cover a great surface with a very small quantity of silk. At the same time, the orb web only needs a few points of attachment to be held in position. The web can be orientated into any direction (vertical, horizontal, diagonal). The threads pointing radially away from the centre form the framework of the net. They do not have the ability to stick and are used by the spiders to move on the web. The radial threads conduct vibrations, which signal the spider where approximately the prey is located.

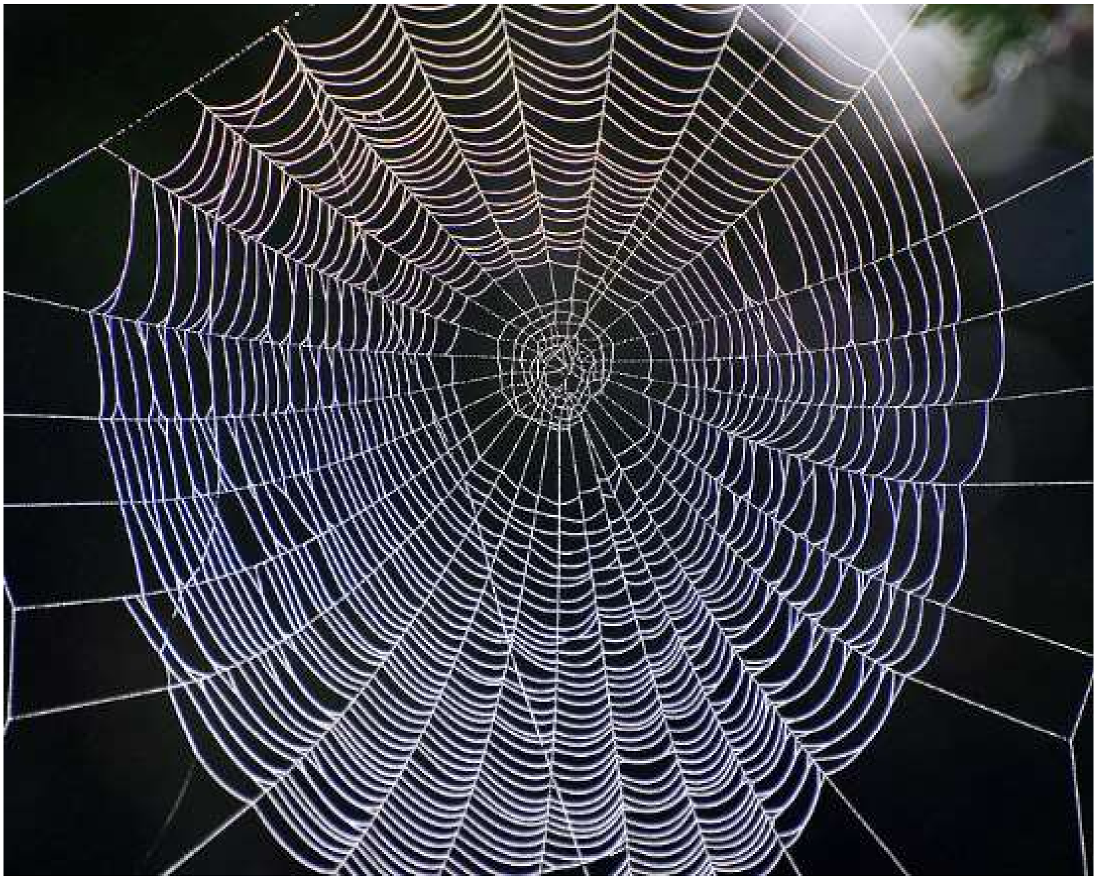


Figure 24. This orb web was built by an *Araneus diadematus* and consist primary out of amino acids. (Clare, 2012)

5.1.2 Egg case

The egg case protects the eggs from the environment and is made out of silk. Eggs need higher humidity for development which is contributed by the egg case. The outer layer of the case is made out of a very tough material which provides as a mechanical barrier against egg parasites (Hieber, 1985). The silk used for the egg case is produced in different silk glands.

5.1.3 Protein storage and food conservation

An orb-weaver creates its web every day, irrespective whether the web is damaged or not. Creating a new web requires a high demand of protein (see table 14), which cannot be covered when the spider did not catch a prey during the precedent day. For this reason, the spider ingests the old web which will be digested in the sucking stomach and absorbed by the glandular epithelium. If the web is labelled radioactively with [^{3}H]alanine before it gets ingested, the web created after 30 minutes shows 80-90 % of the initial radioactivity (Foelix, 1996). From this it follows that the recycling of the old web is very fast and done with high effectiveness. Hardly any body proteins are used for this synthesis (Foelix, 1996).

If a spider catches more food than required it will swath the caught prey with silk and store it in the web. This is a typical comportment of species of the infraorder *Araneomorphae.* They do not eat them immediately but as soon as they catch less prey they will devour the conserved prey from the “storage”. The silk preserves the prey with help of its antimicrobial property which prevents the caught prey from decay.

5.1.4 Sperm web

A mature male has to transfer its sperm from the tubular testes which is located at the *opisthosoma* to the palpal bulbs which are adnate to the palps. The sperm is deposited on a sperm web, whereof the palpal bulbs will absorb the sperm.

5.1.5 Silk used as a gill

Spiders are spread all over the world and found in all climes except in Antarctica (Brunetta & Craig, 2012) due to great adaptiveness. The Six-eyed sand spider (*Sicarius terrosus, table 1)* for example are found in very dry places such as the Atacama Desert. However, there is a spider living its entire life under water called the Diving bell spider (*Argyroneta aquatica, table 1).* This species builds diving bell webs to store air, which was collected at the surface of the water with its *opisthosoma*. The diving bell (see figure 24) is used for moulting and during the digestive process of the caught prey. The digestive fluid is useless under water, therefor the spider moves the prey into the diving bell and intersperses it with fluid inside of the diving bell. The diving bell is made out of different sheets of silk and a hydrophilic polymer. The bell is a semi-permeable membrane. Water cannot penetrate the bell, whereas gas exchange is possible via diffusion. The partial pressure of nitrogen and oxygen is roughly equivalent. The amount of oxygen in the diving bell decreases as the spider requires oxygen for the metabolism. The concentration of dissolved oxygen in the water relatively rises and starts diffusing into the bell. Carbon dioxide released by the spider is water-soluble and diffuses out of the bell. The concentration of nitrogen increases relatively to the concentration in water, which results in diffusion of nitrogen out of the bell. The diving bell shrinks and the spider needs to go to the surface and collect air around its *opisthosoma*.

The size of the diving bell depends on the size and age of the spider. Females tend to stay more often inside the diving bell, whereas males go out of the diving bell for hunting, using an air bubble around the abdomen.

Figure 25. *Argyroneta aquatica* inside the diving bell. Same spider leaving the diving gill with air around its *opisthosoma*. (Baehr & Baehr, 1987)

5.1.6 Ballooning

Young spiders are called spiderlings and have the ability to balloon. This is the phenomena spiderlings use to travel great distance through the air, which is reasonable for the dispersion of the spiders. They climb up a high point and float out threads of *major ampullate* silk. The wind will eventually "catch" the thread and lift the spider up. If the pull is high enough, the spiderling lets go and flies with the current for long distance. There are reports from sailors, who witnessed entangled spiderlings in the ship's sails 1600 Km away from the coast (Hormiga, 2002). Some spiderlings were collected in air samples 4900 metres above sea level (van Dyk, 2016). However, the possibility that a spider balloons lessens with the increase in weight. Spiderlings weighing more than 1 mg are unlikely to transpose with ballooning (Suter, 1999). Charles Darwin witnessed tiny spiders ballooning 100 Km off the coast of Argentina during his voyage aboard the Beagle (Darwin, 1839).

Figure 26. The spider of the genus *Xysticus* has a floated out *major ampullate* silk. The current of the wind is at that moment not strong enough, wherefore the spider is still waiting for the ideal pull. (Antje, 2007)

5.1.7 Orientation and safety

As soon as an *Araneomorph* is outside of its shelter or orb web, it will usually leave a thread behind while moving. This thread is attached regularly on the ground or on other objects in order that the *Araneomorph* has a safety thread. This thread catches the spider when it gets blown away by wind or if the spider has to flee from a potential predator. It will then drop itself to a certain depth and catch itself with the safety thread. This phenomena can be observed while handling an *Araneomorph* with shaking hands.

The same thread contributes to the orientation of the spider, when it returns to the initial place. Mature males and adult females have certain pheromones added onto the thread so that finding each other for reproduction is simplified.

5.2 Mygalomorphous usage of silk

Mygalomorphous silk usage observed on my own tarantulas

5.2.1. Hunting

The webs made by tarantulas do not have the function of catching the prey. The threads which point out radially from the burrow are trip lines, which give a signal to the tarantula when a potential prey is near the burrow. These threads do not have the ability to adhere to the prey and is only an aid for the spider.

5.2.2 Shelter

Tarantula species can be subdivided by preferred habitat. The species *Haplopelma minax spec. big black* is an old world (Asia and Africa) tarantula found in Northern Thailand, which lives buried in deep tunnels. The burrow entrance (see figure 26) has radially arranged trip lines, which help the tarantula to notice passing prey. The hydrophobic silk prevents moisture and water from entering the burrow of the tarantula from the surrounding soil. While burrowing, the tarantula carries the soil to the entrance and makes heaps, which are stabilized with silk. It is possible, that it prevents dirt from falling into the tunnel and water entering the burrow.

Figure 27. *Haplopelma minax spec. big black* at dawn guarding its burrow and waiting for prey.

The species *Grammostola porteri* is a terrestrial tarantula, which is endemic of Chile. They do not burrow and are bad climbers. The silk is usually not visible, unless the ground is moisturized, then the tiny droplets are visible, which developed due to the hydrophobic property of the silk. The "carpet" these tarantulas spin around their shelter, helps them to find nearby preys, and prevent the soil from sticking onto the legs of the tarantulas. Terrestrial tarantulas are often nocturnal outside of their burrow renewing the carpet. Tarantulas living in captivity tend to renew the "carpet" less frequently, since the silk doesn't get destroyed during the day.

Avicularia means mygalomorphous in Latin, and was introduced in 1758 by Carl von Linné to the spider taxonomy. The species *Avicularia metallica* is an arboreal living tarantula. They hunt at night and do not use any silk, therefore they wait until the prey approaches and then pounce on it. Some arboreal species, for example the genus *Poecilotheria,* do not use any silk for shelter, except during heat-waves, drought or heavy rain. Also during the moulting process, arboreal living species use silk to close the shelter from any kind of predator. Even small animals like house crickets (*Acheta domesticus)* can be a threat, due to the delicate vulnerability of a moulting tarantula.

Figure 28. *Poecilotheria vittata*

5.2.3. Egg case

All female spiders wrap their eggs into silk, in order to provide optimal conditions for development. The silk has antimicrobial property (Wright & Goodacre, 2012) and keeps humidity at a constant level. The egg case is made out of two different types of silk while the inner layer being a soft material and the outer layer being hard material.

Figure 29. Egg case made by a *Haploplema vonwirthi*. (Dominic.al97, 2016)

Figure 27 shows tarantulas in the stadium in which is called EWL (eggs with legs). They are not able to move independently and do not spin any silk. The egg case was cut open for a better control of the development stadium and for later separation. If this is done too late – after development into the second instar -, the offspring will be spread all over the burrow or even in the enclosure. They might escape through the essential ventilation grid. *Poecilotheria ornata* for example have cannibalism beginning at the second instar. The separation leads to more offspring and better control during feeding.

5.2.4 Sperm web

Male tarantulas can build up to several sperm webs where the sperm is applied on and taken from by the palpal bulbs. The web shows distinctive holes which may originate from the removal of the sperm by the palpal bulbs out of the web.

Figure 30. *Chilobrachys sp. Kaeng Krachan* mature male drinking from the web. The hydrophobic characteristic is made visible by the reflecting property of water.

6. Discussion

The separation in the order of the Opisthothelae into *Mygalomorphae* and *Araneomorphae* dates back to the Middle Triassic (Craig, 2003). While *Araneomorphae* have a better developed silk production, the usage are nevertheless very similar. *Mygalomorphae* lack of *major ampullate* silk which limits the possibility of silk usage definitely. This lack rules out the possibility of creating orb webs, ballooning and having a safety thread. This has influence on the hunting method and shelter choice. Pouncing on prey is not only observed in the infraorder *Mygalomorphae* but also in the infraorder *Araneomorphae.* The jumping spider illustrated in figure 7 follows the same hunting method as the tarantulas' tough without trip lines. In addition, burrowing is a typical comportment of, which requires silk to stabilize the shelter. The silk of a *Mygalomorphae* species has less toughness and they use it lavish. I have never observed a tarantula recycling its old web but rather forming it into a ball of silk and throwing it away from its shelter. The safety thread of a tarantula is rather a stream of protein than a dense thread. The force which is required to pull out a thread arises from different movements. While *Araneomorphae* are able to pull out a thread by using their legs, *Mygalomorphae* adhere the thread to a point and move on with the *opisthosoma* whereupon the movement of the *opisthosoma* is the force. In contrast to the ballooning, some *Mygalomorphae* species are able to jump small distances while spreading out their legs for more air resistance.

On the other hand there are many similarities even though *Mygalomorphae* species have a less developed silk producing mechanism. The egg case is two layered in both infraorders and they both create sperm webs. It is difficult to state, whether the chemical composition is similar, due to absence of measurements for the *Mygalomorphae*. Above all the silk produced by both infraorders has a white to grey colour and they both are biodegradable. Some tarantula breeders put a part of the used sperm web into the enclosure of the female to determine, whether she is willing for reproduction. The pheromones are certainly applicable on the threads of both infraorders.

Table 6

	araneomorphous	**mygalomorphous**
Usage	Hunting (webs), egg case, shelter, mating (spermweb), safety thread, ballooning, gill, orientation, storage, conservation, messenger	Hunting (trip lines), egg case, shelter, sating (spermweb), messenger
Recycling	Yes	No
Spinnerets	Anterior, median, posterior	Posterior, anterior strongly reduced
Presence of *major ampullate* silk	Yes	No
Initial force for the spinning process	Pulling out the silk with legs	Need an anchor point and pull it out while moving the body
Silk protein trail behind spider	*Major ampullate* silk	Glue, stream of protein (Brunetta & Craig, 2012)

7. Conclusion

The phylogenetical development in the order *Araneae* is essential for the understanding of the problem. This assignment is matter of the separation in the order of the Opisthothelae into *Mygalomorphae* and *Araneomorphae* during the Middle Triassic. *Major ampullate* Silk made the great difference between *Mygalomorphae* and *Araneomorphae* and is the result of 240 million years of evolution. This complex polymer, which is still not fully understood yet, has physical properties which outperform many contemporary materials in ultimate tensile strength, extensibility and toughness. These properties are result of the primary structure of the polymer. Spider silk is mainly consisting of amino acids, which are cohered by peptide bonds. The sequence of the amino acids form a steric structure which is divided into amorphous regions (alpha-helix), crystalline regions (beta-pleated sheet) and a spacer, whose steric structure is not determined yet.

Appendix

Evidence for equality of the surface (Hookean spring)

Initial function for the stress-strain curve of the spring: $f(x) = 2x$

The area under the graph equals the absorbed energy: $\int 2x\,dx$

The orange area is defined between 0 and 3: $\int_0^3 2x\,dx = 9$

The limits of the green area are 4 and 5: $\int_4^5 2x\,dx = 9$

Q.E.D.

Calculation of function for viscid silk

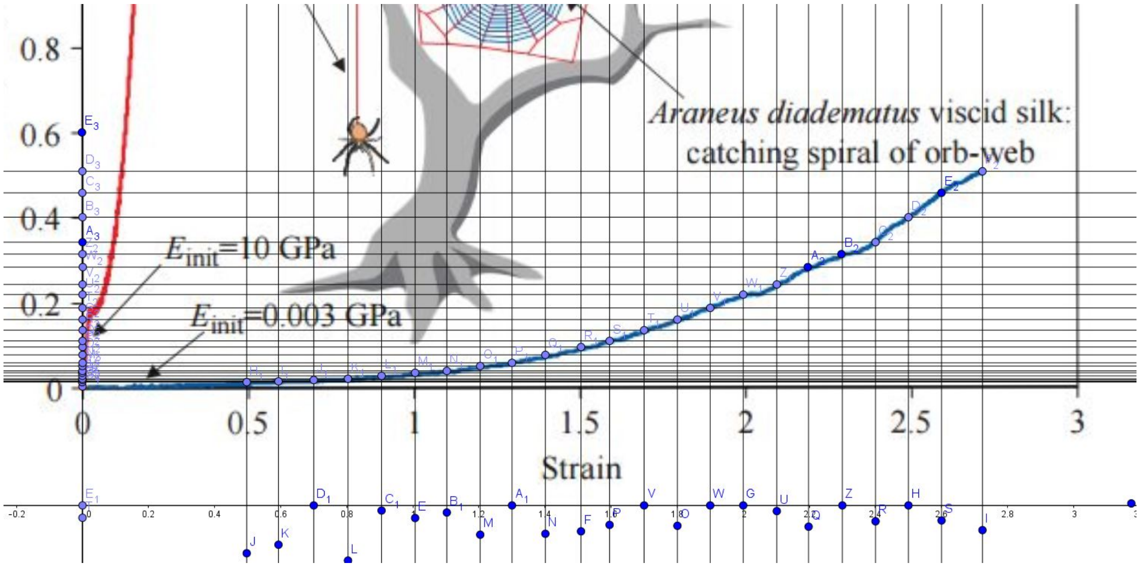
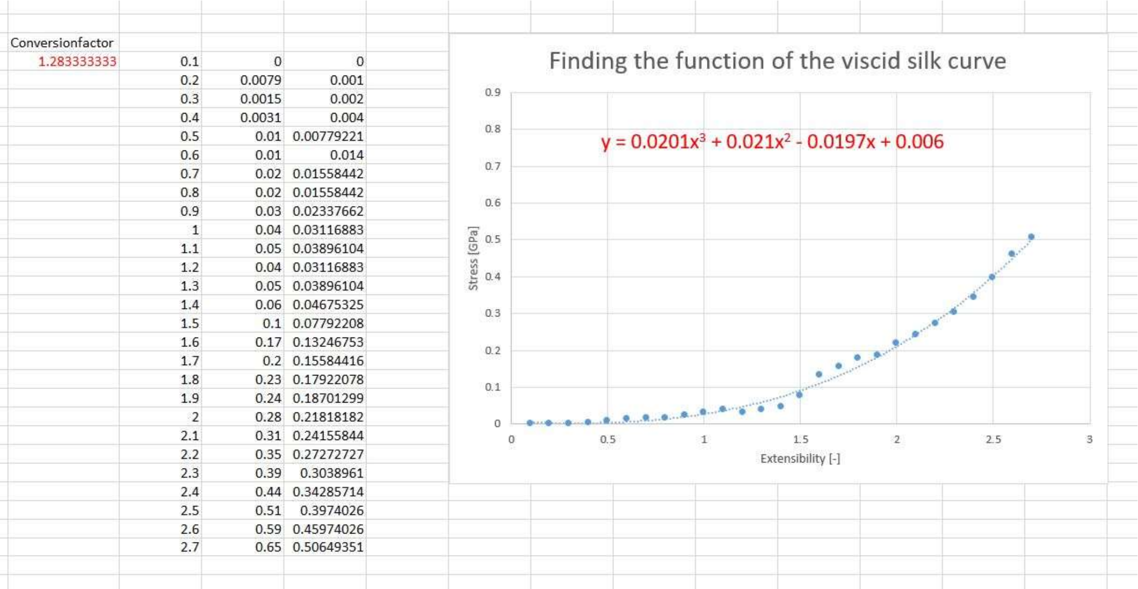


Figure 31. The function of the graph was charted with GeoGebra and calculated with a trend line on Microsoft Excel.



Conversionfactor			
1.283333333	0.1	0	0
	0.2	0.0079	0.001
	0.3	0.0015	0.002
	0.4	0.0031	0.004
	0.5	0.01	0.00779221
	0.6	0.01	0.014
	0.7	0.02	0.01558442
	0.8	0.02	0.01558442
	0.9	0.03	0.02337662
	1	0.04	0.03116883
	1.1	0.05	0.03896104
	1.2	0.04	0.03116883
	1.3	0.05	0.03896104
	1.4	0.06	0.04675325
	1.5	0.1	0.07792208
	1.6	0.17	0.13246753
	1.7	0.2	0.15584416
	1.8	0.23	0.17922078
	1.9	0.24	0.18701299
	2	0.28	0.21818182
	2.1	0.31	0.24155844
	2.2	0.35	0.27272727
	2.3	0.39	0.3038961
	2.4	0.44	0.34285714
	2.5	0.51	0.3974026
	2.6	0.59	0.45974026
	2.7	0.65	0.50649351

Figure 32. The values below 0.5 can be elided due to inaccuracy and are insignificant.

$$\text{Toughness} = \int_{significant\ stress}^{rupture} stress - strain\ curve\ ds$$

$$= \int_{0.5}^{2.7} (0.0201x^3 + 0.021x^2 - 0.0197x + 0.006)\,dx$$

$$= \frac{0.0201 \cdot 2.7^4}{4} + \frac{0.021 \cdot 2.7^3}{3} - \frac{0.0197 \cdot 2.7^2}{2} + \frac{0.006 \cdot 2.7}{1} - \frac{0.0201 \cdot 0.5^4}{4} - \frac{0.021 \cdot 0.5^3}{3} + \frac{0.0197 \cdot 0.5^2}{2} - \frac{0.006 \cdot 0.5}{1}$$

$$= 0.347 \cdot 10^9 \frac{J}{m^3}$$

$$= 35 \cdot 10 \frac{MJ}{m^3}$$

It can be inferred that the measurement of the stress-strain curve for the viscid silk was conducted with a higher strain rate than the measurement for the toughness. The result depends on various parameters such as:

- measuring error of the stress-strain curve
- inaccuracy of the analysis on GeoGebra
- indisposition of the trend line
- distortion of the diagram

Two significant digits are arguable since GeoGebra measured with 2 digits.

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