Issues in Evolution
Project - Fall 2016
Evolution of the Orb-Weaving Spiders

Angela Harvey
Braselton, Georgia, USA
Miami University Ohio
Global Field Program

Introduction

Orb weavers are spiders that spin geometric webs consisting of several different types of silk for the frame, the radial lines, and the sticky spiral capture threads (Hormiga & Griswold, 2014). These are the webs that most people think of when they hear the word “spider”. Orb weavers are part of the group of spiders known as Orbiculariae, an informal group containing the superfamilies Deinopoidea and Araneoidea (Brunetta & Craig, 2010; Hormiga & Griswold, 2014). The unique nature of the webs, the behaviors involved, and the chemical composition of the silks produced by these spiders gives an interesting view of their evolution (Tian & Lewis, 2005).

Spiders are classified as arachnids, but spiders are the only arachnids to have abdominal spinnerets, allowing them more control of their silk (see Appendices 1 & 2). Both male and female spiders use silk throughout their lifetimes (Brunetta & Craig, 2010). This is unique in the world of arthropods, making spider silk useful in identifying and tracking spider relationships by studying the molecular proteins of the silk, the purpose of the silk, and the behaviors that accompany those purposes (Dimitrov et al., 2012).

Prehistory

As the aquatic arthropods moved out of the sea onto land more than 450 million years ago, many made their homes underground to avoid predators, help stave off dehydration, and reduce the effects of ultraviolet radiation. Plants were sparse and fairly small in this era, giving little protection. One arthropod that was abundant then, but went extinct 200 million years later, was the trigonotarbid. It had book lungs, which is the same respiratory system used by the more primitive mygalomorph spiders today, such as the tarantula. In this system, oxygen diffuses across flat leaves of tissue into the hemolymph (what spiders use as blood) which carries it to the tissues (Opell, 1998) (see Appendix 1). The trigonotarbid was also similar to extant spiders in shape and number of body parts but lacked the ability to make silk (Garwood et al., 2016). Another fossil specimen from 380 million years ago, named *Attercopus fimbriunguis,* exhibited no spinnerets, but spigots which showed a long fibrous segment that was most likely a silk fiber (Brunetta & Craig, 2010; Garwood et al., 2016).

Although no one seems certain of the spiders' particular ancestor, biologists can trace common ancestry through physical characteristics, behavior, and molecular evidence (Dimitrov et al., 2012). More than likely, the first spiders had chelicerae (pincer-like appendages on the front of the spider's head) tipped with fangs, eight legs, and two basic body parts (see Appendices 1 & 2). The question of venom evolution is more problematic. Fossilized extinct spiders seemed to lack venom glands (Brunetta & Craig, 2010; Garwood et al., 2016; Dimitrov et al., 2012). Tarantulas, funnel-web spiders, and trapdoor spiders developed venom around 250–200 million years ago (Sunagar & Moran, 2015). A study by Foelix and Erb (2010) contends venom glands developed before this, though. The authors found openings, for the passage of venom, in the fangs of primitive spiders in the family Liphistiidae as well as venom glands. This may suggest that the common ancestor of all spiders possessed venom, placing the first appearance of the venom gland before 300 million years ago (Foelix & Erb, 2010).

Spider Families

The two suborders of spider are separated mainly by the placement of the spinnerets, located either in the middle of the abdomen (Mesothelae) or the rear of the abdomen (Opisthothelae). Mesothelae, like the Liphistiidae species, are living fossils (see Appendix 2); they have changed very little from their Paleozoic fossil ancestor of 290 million years ago (Brunetta & Craig, 2010). Behaviorally, they are probably very similar to their ancestors. They are have book lungs, are nocturnal, live in burrows, and move very little. Mesothelae use their silk to line their homes, protect their eggs, and put out radial lines around their burrows to detect prey. These tube-dwelling spiders are segmented on the dorsal side of the abdomen and are found in Southeast Asia and Africa (Brunetta & Craig, 2010; Xin et al., 2015).

The other suborder of spiders is the Opisthothelae, which appeared in the Triassic period. These are divided into the Mygalomorphs and the Araneomorphs (see Appendix 2). The Mygalomorphs still retained the book lungs of their ancestors and have chelicerae that are parallel and vertical, while the Araneomorphs have trachea (air tubes), sometimes combined with book lungs, and fangs that face in toward each other, like pincers (Brunetta & Craig, 2010). Mygalomorphs still live mostly on the ground, but they use their webs to build structures above their ground-based burrows to aid in prey detection and capture. By moving up and out, mygalomorphs increased their hunting area, and the sheet webs they lay down help capture prey instead of just detecting it.

Araneomorphs have moved up farther, literally, to take advantage of a more three-dimensional world, seemingly around the same time the plants grew taller and flying insects became more abundant in the early Triassic period (Brunetta & Craig, 2010). Araneomorphs share something their cousins the mygalomorphs lack - major ampullate silk or dragline silk, which is used for structural parts of the web as well as mobility (see Appendix 3). The dragline silk is strong and can support the weight of the spider for dropping, drifting on air currents, or swinging (Brunetta

& Craig, 2010; Tian & Lewis, 2005). Fossil evidence puts the production of major ampullate silk as far back as 240 million years ago, around the same time as the mygalomorphs were constructing their sheet webs. Scientists believe there was a common ancestor sometime before this period (Brunetta & Craig, 2010). Araneomorphs outnumber their relatives by nearly fourteen to one. This diversity is usually attributed to the benefits of major ampullate silk (Brunetta & Craig, 2010).There is no evidence yet for how the silk glands changed to produce this new silk, but it allowed the spiders to climb higher than the ground dwellers and travel longer distances. This silk is much stronger than the silks produced by the mygalomorphs and mesothelae. It can withstand more strain, which gives the frame lines of hanging webs their strength, stretch, and rebound qualities (Brunetta & Craig, 2010; Tian & Lewis, 2005). It also allows the spider better options for evading predators and dispersing to find new territories, since it is strong enough to support the weight of the spider (Brunetta & Craig, 2010). If threatened, the araneomorph can jump great distances with the safety line and spiderlings frequently "balloon", riding air currents after hatching to spread out over a larger area (Brunetta & Craig, 2010).

One Araneomorph considered to be a "link" between the rest of the family and the ancient ancestor they share with the mygalomorphs are the lampshade spiders (family *Hypochilidae*). These spiders evolved early in evolutionary history and are still present today. Lampshade spiders retain their book lungs like the mygalomorphs, and their chelicerae are angled, not vertical or directly opposite each other. The webs also show a combination of characteristics. Lampshade spiders build their webs in protected locations, placing the anchor on a horizontal or slanting surface, then build out a taut structure resembling a lampshade (see Appendix 2). This is constructed from major ampullate silk with sticky cribellate silk that looks something like the structures mygalomorphs build out from their burrows. The web helps to protect the spiders from predators while also aiding the spiders in capturing prey (Brunetta & Craig, 2010).

Spider Silk

Scientists believe that the early spiders only produced one type of silk, but there is no direct evidence of this (Brunetta & Craig, 2010). Most spiders produce at least three to five types of silk, and the orb weavers produce up to seven types (Hormiga & Griswold, 2014). Even the extant species of the spider family that appeared first in the fossil record (Mesothelae) make three types of silk, although they mix and use these silks indiscriminately (Brunetta & Craig, 2010). Orb weavers, on the other hand, use specific silks for specific jobs, such as one for structural web support, one for prey capture, and one for egg sac construction (Hormiga & Griswold, 2014; Elices et al., 2009) (see Appendix 3).

Silk is a fibrous protein, similar to other animal protein fibers, such as collagen or keratin. It is used by many different species for many purposes. Arthropod species produce distinct types of silk in a variety of glands. These glands are found in different areas of the body, depending on the species. Each type of silk is comprised of a particular set of proteins, specific to each species (Brunetta & Craig, 2010; Tian & Lewis, 2005). Molecular scientists use the proteins in silk to help determine evolutionary timing. Proteins are built by particular DNA sequences. These pieces of DNA can be identified from fossil evidence and used to trace protein production. When the first appearance of a particular DNA sequence is identified, the first appearance of the protein built by that gene can be ascertained (Brunetta & Craig, 2010).

The structure of the different silks produced by spiders depends on the proteins that make up that silk. Different species have particular structures for their specific types, and major ampullate silk is always recognizable as major ampullate silk compared to other types of silk. Since each protein is dictated by a particular DNA sequence (or several, in some cases), a change in the

DNA produces a change in the proteins being constructed, which makes a different fiber. Minor changes in a sequence can have large effects on the nature of a fiber (Tian & Lewis, 2005). For instance, a minor repeat of three amino acids in a particular sequence can make a silk protein completely change shape and texture. However, while different spider silks show variations in the length and sequence of the middle sections of the proteins, the ends of the proteins are all very similar. This means all spider silk proteins are recognizable as silk proteins and not some other protein. This similarity is too common to be explained by chance, and provides good evidence for a common ancestor for all spider genes dictating silk (Brunetta & Craig, 2010).

By looking at the structure of the major ampullate silk used by araneomorphs, scientists can logically assume that it evolved from older silk proteins and shares ancestry with the mesothelae and mygalomorphs. With this new type of silk came new behaviors. Mesothelae and mygalomorphs use their silk types indiscriminately for various tasks, and the nature of the silks do not seem to differ much. Araneomorphs, on the other hand, use specific silks for specific purposes, such as egg cases, prey wrapping, and web construction (Brunetta & Craig, 2010) (see Appendix 3).

Orb Weaver Debate

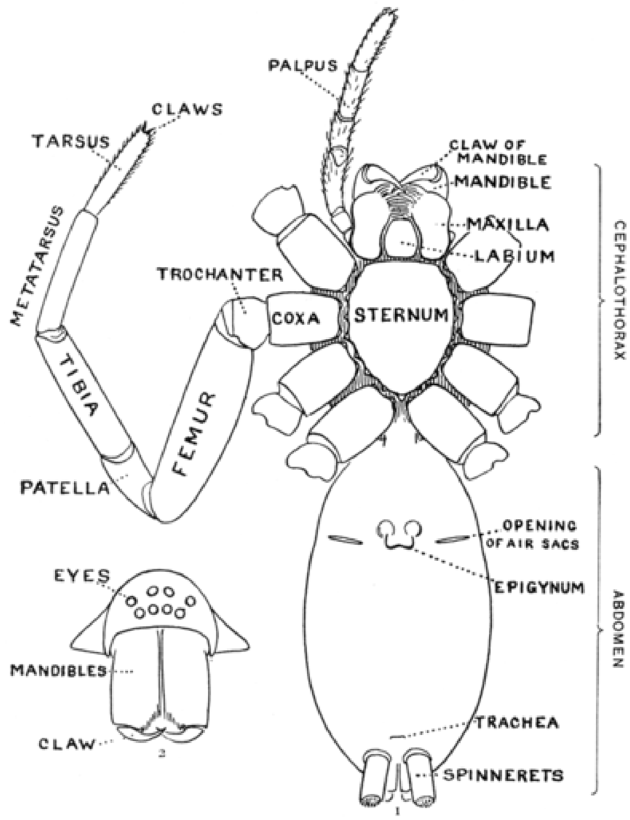
The largest problem in spider evolution comes in determining where and when to place the orb weaver ancestors (Dimitrov et al., 2012; Hormiga & Griswold, 2014) (see Appendix 4). The question is whether the orb web evolved once and then diverged into its various forms, or whether the web forms were separate evolutionary paths. Orb weavers use their varied types of silk to build geometric webs that withstand great stress from the force of the flying insects they are designed to catch (Elices et al., 2009). All araneomorphs have major ampullate silk, but not all of them build hanging geometric webs. In fact, some do not build webs at all, using their silks in a variety of ways to capture prey. Of those that do build geometric webs, either in whole or in part, the families are divided based on the type of silk used. Both Orbiculariae families use major ampullate silk for the structural framework of the web, but the deinopoidae use cribellate silk for the sticky capture spiral while the araneopoidae use a viscous fluid for the sticky spiral (Brunette & Craig, 2010). The fluid is much more sticky and more springy than cribellate fibers (Agnarsson et al., 2009; Opell et al., 2001). Also, most araneopoidae webs are vertical, whereas deinopoidae webs are usually horizontal. Vertical webs have a better chance of catching fast-moving insects and keeping them stuck longer, giving the spider more time to subdue the prey (Opell et al., 2001).

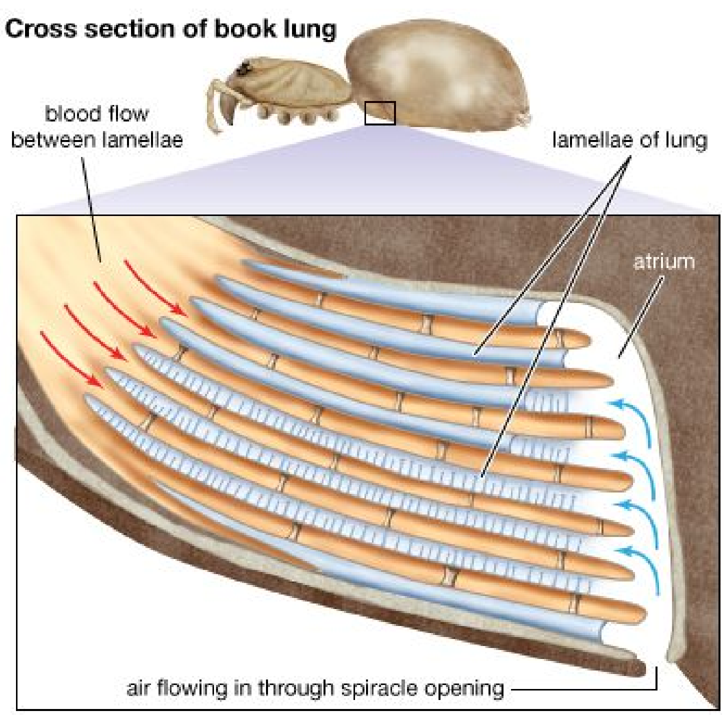
Most scientists believe that the two groups share a common ancestor, that the abilities associated with building an orb web evolved once and then diverged into the variations we see today (Dimitrov et al., 2012; Hormiga & Griswold, 2014; Brunette & Craig, 2010; Blackledge et al, 2009)). But there is some argument that the two types of orb webs evolved convergently in separate lines (Bond, et al., 2014; Brunette & Craig, 2010). Most of those studies supporting a single origin are based on web structure and web-building behavior (Hormiga & Griswold, 2014; Dimitrov et al., 2012). New evidence in the molecular sciences has failed to resolve the argument, since some support the single origin theory, and others support the convergent evolution theory (Hormiga & Griswold, 2014; Dimitrov et al., 2012). To help muddy the waters, the other araneomorphs that are not technically in the Orbicularae are occasionally placed outside of the two superfamilies of orb weavers, and sometimes placed within or between the superfamilies (see Appendix 4). These theories are usually derived from the hypothesis that these spiders share a common ancestor with the orb weavers, but lost the weaving characteristics (Blackledge et al, 2009; Hormiga & Griswold, 2014; Brunette & Craig, 2010).

As new techniques and technologies continue to appear, molecular evidence may continue to accumulate, which may offer resolution to the argument. However, the debate seems to be generated by different viewpoints on what denotes a family connection - structure, function, or behavior. Hopefully, further studies will shed more light on how these characteristics integrate in a single species to help determine the evolutionary relationships in the orb-weaving spiders.

Appendix 1

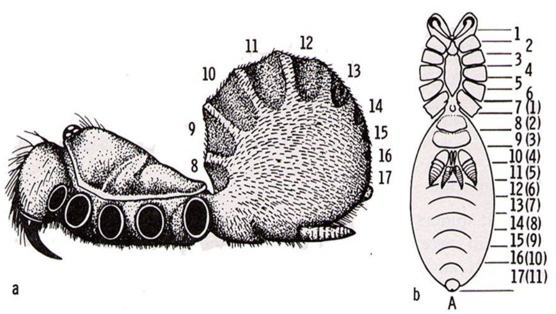
Basic spider anatomy



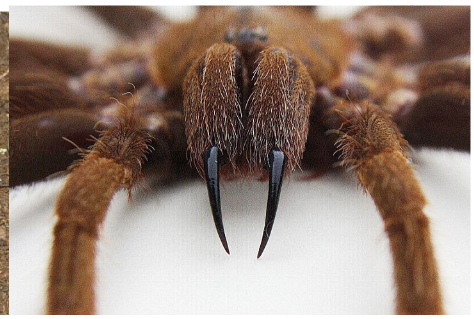


<u>Appendix 2</u>

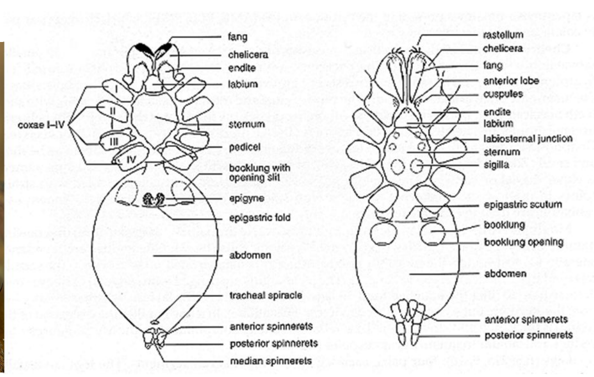
Mesothelae

Mygalomorph

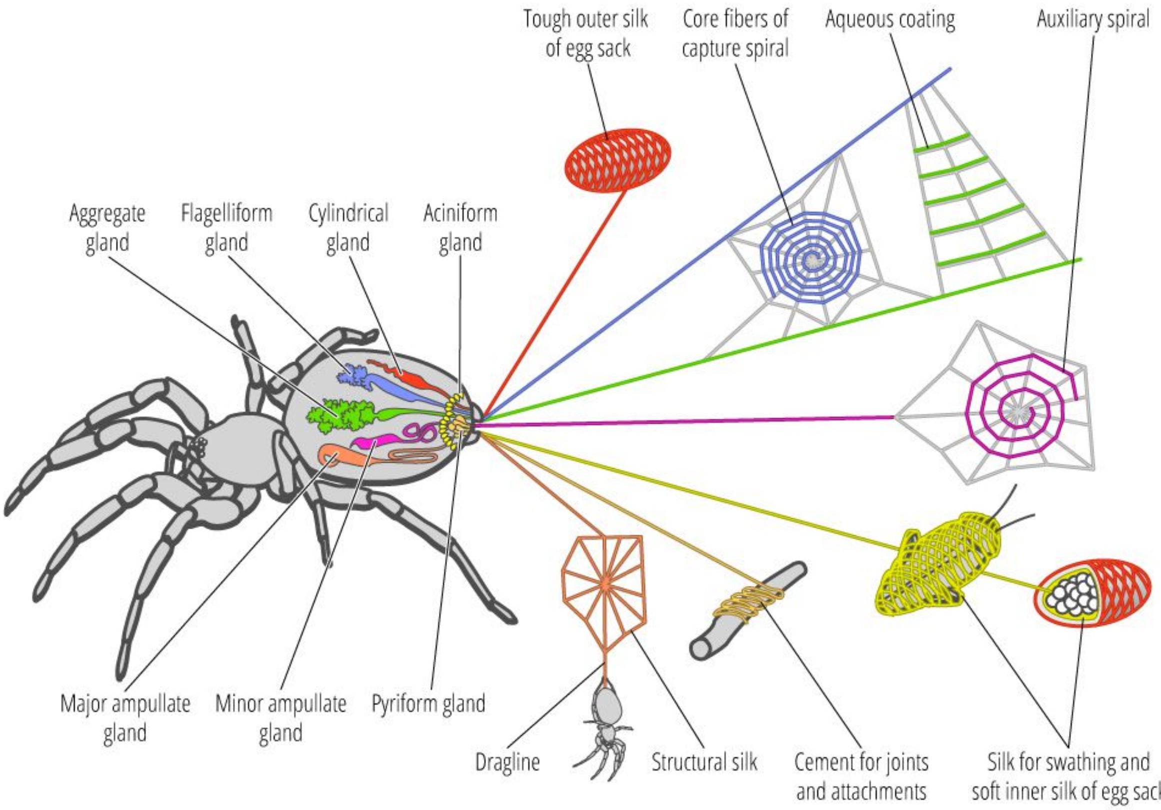



Araneomorph

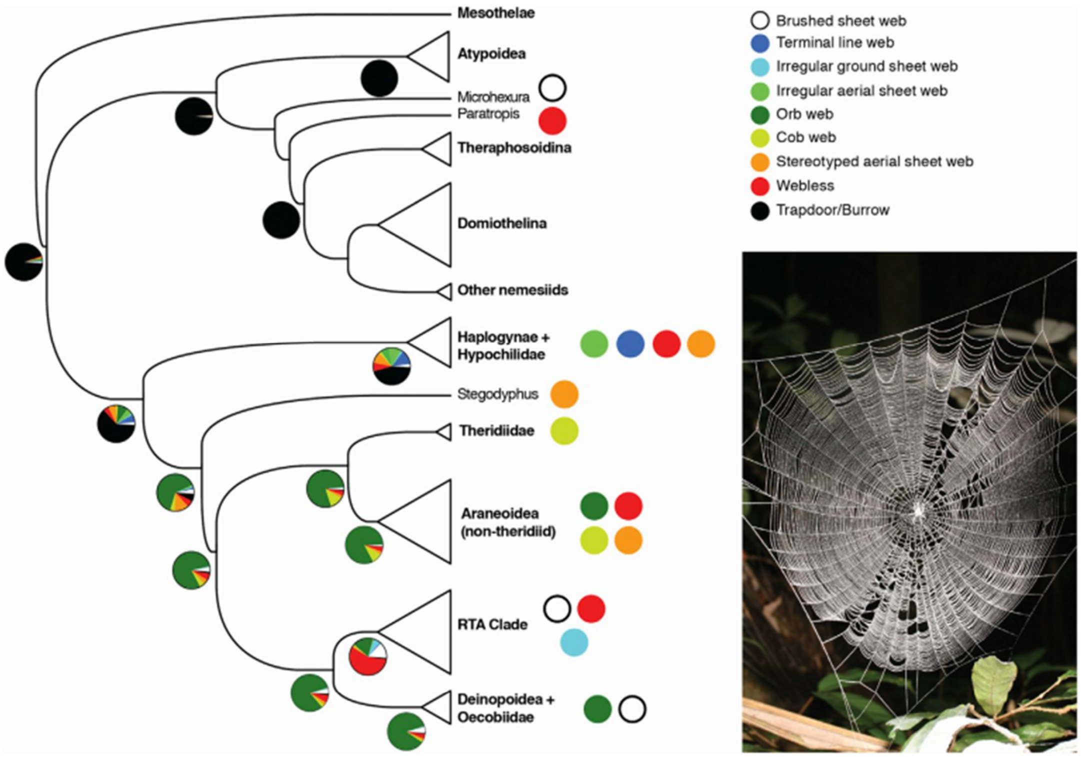
Lampshade spider web

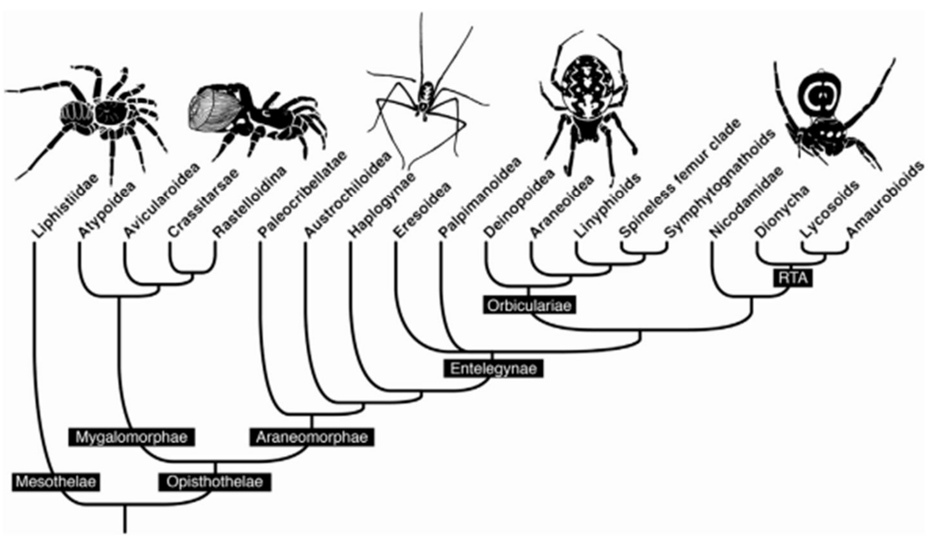
<u>Appendix 3</u>
Silks and usage



Appendix 4

Two ancestries of the spider lineage - notice the different placement of the Deinopoidea





References

Agnarsson, I. & Blackledge, T. (2009). Can a spider web be too sticky? Tensile mechanics constrains the evolution of capture spiral stickiness in orb-weaving spiders. *Journal of Zoology, 278,* 134-140. doi: 10.1111/j.1469.7998.2009.00558.x

Blackledge, T., Scharff, N., Coddington, J., Szuts, T., Wenzel, J., Hayashi, C., & Agnarsson, I. (2009). Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of the National Academy of Science, 106*(13), 5229-5234.
doi: 10.1073/pnas.0901377106

Bond, J., Garrison, N., Hamilton, C., Godwin, R., Hedin, M. & Agnarsson, I. (2014). Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Current Biology, 24*, 1765-1771. http://dx.doi.org/10.1016/j.cub.2014.06.034.

Brunetta, L. & Craig, C. (2010). *Spider Silk: Evolution and 400 Million Years of Spinning, Waiting, Snagging, and Mating.* New Haven, Connecticut, and London, England; Yale University Press.

Dimitrov, D., Lopardo, L., Giribet, G., Arnedo, M., Alvarez-Padilla, F., & Hormiga, G. (2012). Tangled in a sparse spider web: single origin of orb weavers and their spinning work unravelled by denser taxonomic sampling. *Proceedings of the Royal Society B, 279*, 1341-1350. doi: 10.1098/rspb.2011.2011

Elices, M., Plaza, G., Arnedo, M., Perez-Rigueiro, J., Torres, F., & Guinea, G. (2009). Mechanical behavior of silk during the evolution of orb-web spinning spiders. *Biomacromolecules, 10,*1904-1910. doi: 10.1021/bm900312c

Foelix, R. & Erb, B. (2010). Mesothelae have venom glands. *Journal of Arachnology, 38,* 596-598. doi: 10.1636/B10-30.1

Garwood, R., Dunlop, J., Selden, P., Spencer, A., Atwood, R., Vo, N., & Drakopoulos, M. (2016). Almost a spider: a 305-million-year-old fossil arachnid and spider origins. *Proceedings of the Royal Society B, 283*, 20160125. http://dx.doi.org/10.1098/rspb.2016.0125

Hormiga, G. & Griswold, C. (2014). Systematics, phylogeny, and evolution of orb-weaving spiders. *Annual Review of Entomology, 59,* 487-512. doi: 10.1146/annurev-ento-011613-162046

Opell, B. (1998) The respiratory complementarity of spider book lung and tracheal systems. *Journal of Morphology, 236,* 57-64.

Opell, B., Tran, A., & Karinshak, S. (2011). Adhesive compatibility of cribellar and viscous prey capture threads and its implication for the evolution of orb-weaving spiders. *Journal of Experimental Zoology, 315,* 376-384. doi: 10.1002/jez.684

Opell, B. & Bond, J. (2001). Changes in the mechanical properties of capture threads and the evolution of modern orb-weaving spiders. *Evolutionary Ecology Research,3,* 367-581.
http://www.jstor.org.proxy.lib.miamioh.edu/

Penney, D., Dunlop, J., & Marusik, Y. (2012). Summary statistics for fossil spider species taxonomy. *Zookeys, 192,* 1-13. doi: 10.3897/zookeys.192.3093

Sunagar, K. & Moran,Y. (2015). The Rise and Fall of an Evolutionary Innovation: Contrasting Strategies of Venom Evolution in Ancient and Young Animals. *PLoS Genetics, 11*(10), 1-20. DOI: 10.1371/journal.pgen.1005596

Tian, M. & Lewis, R. (2005). Molecular characterization and evolutionary study of spider tubuliform (eggcase) silk protein. *Biochemistry, 44,* 8006-8012. doi: 10.1021/bi050366u

Xin, X., Liu, F., Chen, J., Ono, H., Li, D., Kuntner, M. (2015). A genus-level taxonomic review of primitively segmented spiders (Mesothelae, Liphistiidae). *Zookeys, 488*, 121-151. https://doi.org/10.3897/zookeys.488.8726

Photos

Anatomy-By James Henry Emerton - Scanned from The common spiders of the United States (1902), Public Domain, https://commons.wikimedia.org/w/index.php?curid=7499247
Book lung- Encyclopaedia Britannica, https://media1.britannica.com/eb-media/14/55014-004-B80B2BEF.jpg
Tube dwelling spider - http://arachnos.eu/media/k2/items/cache/af2ef6a0e2c9c528b09655df79f3b312_XL.jpg
Mesothelae - https://classconnection.s3.amazonaws.com/940/flashcards/330940/png/mesothelae1366866613031.png
Mygalomorph- http://dailymacro.yakohl.com/pic/erdtigerspinne_732012.jpg
Araneomorph - https://i1.wp.com/fc08.deviantart.net/fs70/f/2012/083/a/9/wolf_spider_fangs_by_nicksmacro-d4trsrf.jpg?zoom=2
Comparison araneomorph/mygalomorph - http://www.biodiversityexplorer.org/arachnids/spiders/images/anat2a.gif
Silks - http://www.spiber.se/assets/upload/images/Final_Spindel%20med%207%20typer%20av%20tra%CC%8Ad.jpg
Lampshade spider - https://hikinginthesmokies.files.wordpress.com/2012/08/spider-web-lampshade-hypochilus-sp-deep-creek-trail-august-04-2012.jpg
Clade Photos - Bond et al (2014) page 1766 & page 1768