

CONQUERING THE TERRESTRIAL ENVIRONMENT:
THE EVOLUTION OF XYLEM ANATOMY IN EARLY TRACHEOPHYTES

By

ELISABETH ANNE BERGMAN

A Thesis Submitted to The Honors College
In Partial Fulfillment of the Bachelors Degree
With Honors in
Biology with an Emphasis in Biomedical Sciences

THE UNIVERSITY OF ARIZONA

D E C E M B E R 2 0 1 7

Approved by:

Dr. Brian Enquist
Department of Ecology and Evolutionary Biology

Acknowledgements

Many thanks go to all of those who made contributions, big and small, to my honors thesis, and more notably, my education. Foremost, I thank Dr. Brian Enquist for accepting me into his lab and serving as my mentor for two years. I appreciate all of the time he put in to meet with me and help me to develop my honors thesis. Additional thanks go to Dr. Sean Michaletz who first introduced me to the work that would eventually become my honors thesis. From the University of Santa Cruz, California, I thank Dr. Jarmila Pittermann who trained me on the techniques for recognizing and measuring the different traits of the xylem anatomy of fossil cross-sections. Finally, I give big thanks to Dr. Alex Brummer for co-mentoring me and always finding time to help me with my coding and analyses in R.

Abstract

Since the first land plants appeared 480-360 million years ago, natural selection has resulted in continued colonization into increasingly drier and harsher environments. The evolution of traits associated with water transport and avoidance of embolisms allowed plants to conquer increasingly more seasonal and drier terrestrial environments. However, it is unclear just how the xylem anatomy of the first Embryophytes differed from extant (living) taxa and if these differences translated to differences in plant functioning. I measured and compared hydraulic traits from stem cross-sections from extant plants and extinct fossil specimens. For 231 stems comprising 115 extant and 116 extinct taxa, measures of xylem conduit diameter/frequency and segment diameter were measured. Comparing these measures of xylem conductive traits indicates that extant plants, for their size, have more and wider conduits leading to a larger total conductive area and higher rates of water conductance. Further, the combination of xylem traits found in extinct paleo plants suggests that they were less efficient at water transport and likely more restricted to less seasonal and more wet environments. Together, these results reveal a unique insight into the functioning of extinct paleo plants and the evolution of xylem form and function.

Introduction

The evolution of the land plants, the Embryophytes, was characterized by adaptations that allowed plants to transition from water to land (Bateman et al. 1998). These adaptations are characterized by traits associated with how plants transport water and avoid embolisms (Oliver et al. 2000, Sperry 2003, Larter et al. 2015). Indeed, one of the central problems plants faced in the transition from water to land was desiccation, or drying out. Selection to avoid desiccation and minimize the hydraulic impediments to transporting water characterize plant taxa that continued to invade and expand further inland into drier regions. The ancestor(s) of terrestrial plants were closely related to present-day aquatic charophytes or the green algae (Lewis and McCourt 2004, Leliaert et al. 2012, Timme et al. 2012). These early land plants were highly dependent on water for survival and reproduction (Komatsu et al. 2013, Niklas 1997). Bryophytes, a group which includes the taxa liverworts, hornworts, and mosses (Renzaglia et al. 2007, Cox et al. 2014), are restricted to marshy environments and cannot live entirely out of water as they have no specialized vascular tissues (Niklas 1997, Proctor 1982). The first and most primitive vascular plants, or tracheophytes, differed from bryophytes in that they had evolved a directed vascular transport network. Their vascular tissue, or xylem, consists of specialized water conducting tubes called tracheids. Furthermore, the evolution of the tracheophytes was characterized by the evolution of traits associated with more specialized hydraulic systems reflected in the size and number of tracheids (Lucas et al. 2013). The evolution of more specialized hydraulic systems allowed plants to more efficiently transport sufficient amounts of water from the roots to the leaves during transpiration, minimizing the risk of hydraulic failure or embolisms in times of drought (Meinzer et al. 2001). As a result, the evolution of specialized xylem traits reflected

selection to increasingly colonize more continental, seasonal, and drier environments (Meinzer et al. 2001). Descendants of the earliest land plants increasingly colonized the driest environments and deserts on the planet (Willis and McElwain 2014) and produced the tallest tracheophytes and the most massive organisms the world has seen (the largest being a redwood measuring at over 115 meters) (Koch et al. 2004).

The evolution of specific conductive traits of xylem anatomy appears to have allowed several lineages of Embryophytes to colonize increasingly more extreme environments and reach new heights (Woodruff et al. 2008, Niklas 1984, Niklas 1997). Several important keys to the evolution of xylem anatomy include adaptations for moisture availability, transpiration rate, and mechanical strength (Carlquist 1975). The trade-off to such adaptations is the increased risk of developing an embolism (Gleason et al. 2016). Water in the xylem is under negative pressure, reflecting the fact that transpiration in the leaves literally pulls the water column in the xylem up through the plant. When the pull on the water column becomes too severe, the water column can break leading to cavitation of the water column and an embolism (Tyree and Sperry 1989). Increasing aridity and seasonality of water availability increases the risk of embolism and hence a risk of hydraulic failure. Specific traits of xylem anatomy evolved in response to natural selection to minimize the physical limitations of water transport in more arid environments. The traits that characterized the xylem of early water transport systems of the earliest tracheophytes likely imposed limit on their growth, productivity, and survival (Brodribb 2009).

The xylem trait most prominent regarding water transport is the first water conducting tube, or conduit, known as the tracheid. The tracheid is essentially a “pipe” for water transport. It is responsible for the transportation of water and nutrients from the roots to the leaves (see **Figure 1A** and **Figure 1B**).

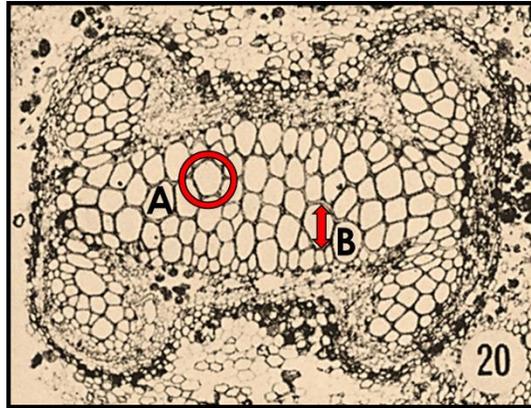


Figure 1A. Example of a fossil cross-section from which measurements were taken.

A represents a whole conduit while **B** represents the diameter of a single conduit. Image from Stewart and Rothwell (1993).

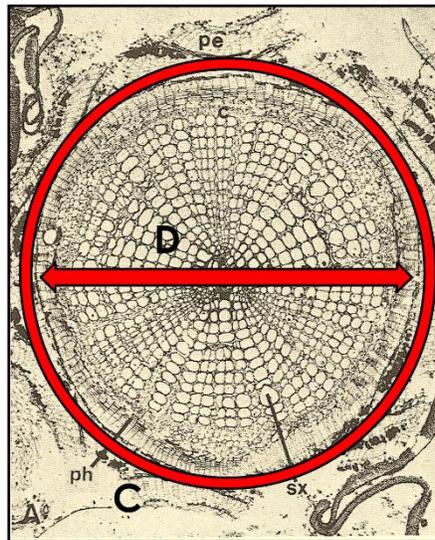


Figure 1B. Example of a fossil cross-section from which measurements were taken.

C represents the segment of the plant from which the cross-section was obtained while **D** represents the diameter of this segment. Image from Stewart and Rothwell (1993).

Water transport in tracheophytes is governed by the size (radius) and number of tracheids per unit area. These traits are relatively straightforward to measure and assess within both fossil

and extant plants. All vascular plants, or tracheophytes, are characterized with these pipe-like cells (Langdale 2008). Together, these hydraulic traits characterize the rate of flow of water and nutrients (Burgess et al. 2001). Tracheophytes include the lycophytes, pteridophytes, gymnosperms, and angiosperms. See the phylogeny in **Figure 2** for the major taxonomic groups of plants mentioned above, their synapomorphies, and the estimated time at which these groups emerged.

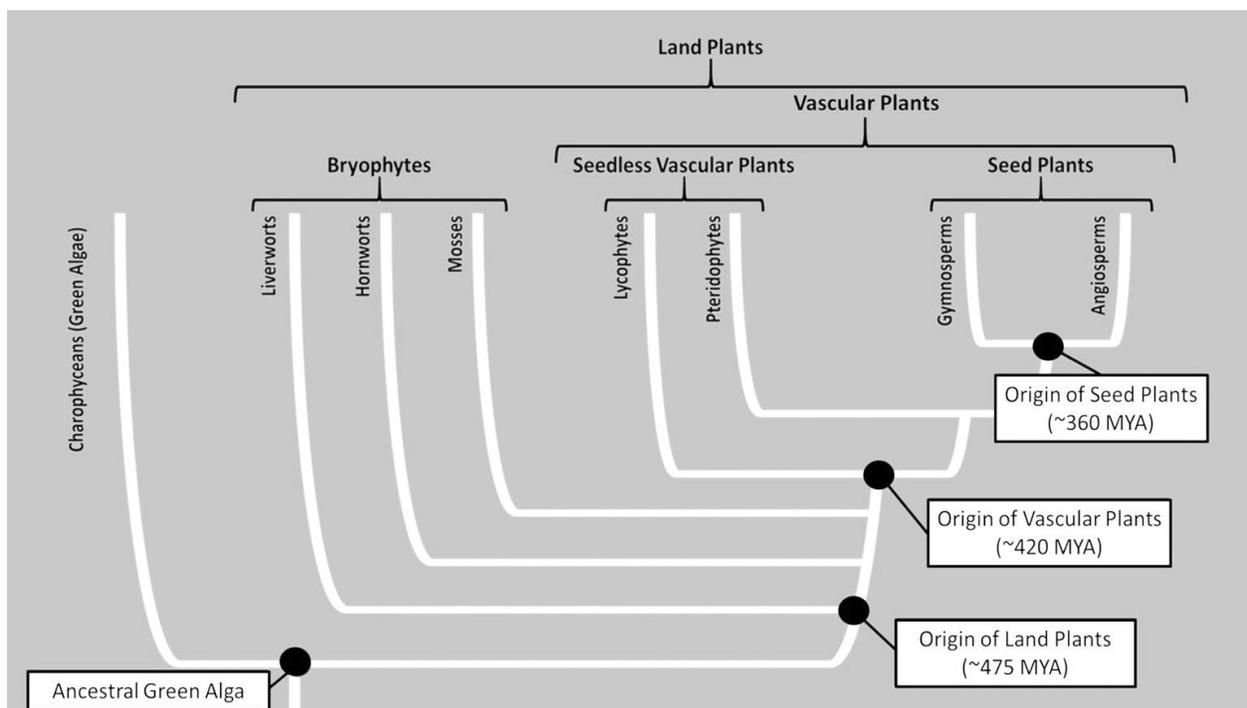


Figure 2. Phylogeny depicting the major taxonomic groups of plants as they evolved from primitive green algae to the modern vascular plants we see today.

Here I assess if the water conducting ability of some of the first tracheophytes differed from the water conducting ability of several extant taxa. On the one hand, with the evolution of xylem the ability of selection to increase hydraulic efficiency and further increase rates of xylem conductivity may have been limited by other factors. For example, biomechanical limitations

due to selection for increasing plant height may have also limited the ability for selection to further increase water transport abilities and minimize risk of embolisms (Niklas 1992, Niklas 2000). On the other hand, continued selection to minimize hydrodynamic constraints of long-distance transport (Enquist 2003) would have resulted in continued selection for more efficient and hydraulically safe xylem (Brodribb 2009). I assessed the hypothesis that continued selection to transport water more efficiently has resulted in clear functional differences in water transport abilities between extinct and extant taxa. To test this hypothesis, I measured the size and frequency of tracheids in the xylem of extant and extinct taxa.

The two different xylem traits, tracheid size and number, can be linked to the water conducting ability of the plant by using the Hagen-Poiseuille equation. This equation relates the hydraulics of fluid flow to the dimensions of a pipe. Assuming simple Newtonian flow of a fluid, we can link how certain characteristics of a plant and its conduit system (the radius and length of the conduit) then influence fluid flow rate. The Hagen-Poiseuille equation states

$$\Delta P = (8\eta l / \pi r^4) Q \quad (1)$$

where $\Delta P = RQ$. Here, the Hagen-Poiseuille equation is written two different ways, both relating flow pressure to characteristics of the hydraulic system of a plant. The variables involved are Q (fluid flow rate), ΔP (change in pressure along the pipe), r (radius of the conduit/pipe), η (fluid viscosity), l (the length of the tubing), and R (the resistance to fluid flow). The simplified version of this equation, for our purposes, is given here: **Resistance** $\propto (1/r^4)$. This version of the Hagen-Poiseuille equation illustrates the relationship between the radius of a conduit and the resistance of a fluid.

From the latter equation, we see that as the radius of a pipe increases, the resistance drastically decreases to the 4th power. To more efficiently transport water from the roots to the

tips, a bigger radius is needed to reduce the resistance met by the flow of water. In this study, we test the hypothesis that tracheophytes evolved to more efficiently transport water and have done so by evolutionary changes in the xylem anatomy that assist with making this process easier.

Methods

In order to determine the evolutionary changes that tracheophytes underwent to conquer the terrestrial environment, a list of hydraulic traits was compiled and gathered for an extant and extinct dataset. These datasets were also used to determine how extant and extinct tracheophytes differ with regards to xylem anatomy. Due to their commonality and occurrence across both the extant and extinct datasets, the central xylem traits focused on were conduit diameter/frequency and segment diameter. The extant dataset consisted of data from 115 extant specimens that was provided by Dr. Jarmila Pittermann at the University of Santa Cruz, California. These measurements were collected from live specimens. The extinct dataset consists of fossil cross-sections that I gathered from literature searches. Over 116 fossil cross-sections from 22 different papers were collected from these literature searches, most of which came from the Devonian period (419-359 million years ago). While the raw data for the extant dataset was already provided to me, no such dataset existed for extinct species prior to my analysis of fossil cross-sections.

An important aspect to consider is how the two datasets compare. The extant dataset consists of only three species – one fern and two lycopods. The extinct dataset, on the other hand, consists of nearly 40 different species (perhaps more as some of the species' names were unlisted within the literature). While the extant dataset consists of tracheophytes that are currently living, the extinct dataset has plants ranging from the late Devonian period to the late Carboniferous period (about 358.9-298.9 million years ago, a range of nearly 60 million years). While we generally know where in the plant the extant cross-sections were obtained, rarely is there any information about where in the plant the fossil cross-sections came from. This is

important to acknowledge because it is entirely possible that by comparing the extant and extinct datasets, we are comparing cross-sections from different places in the total plant architecture (e.g., closer to the base, closer to the tips, somewhere in the middle). Additionally, many of the fossil cross-sections did not have any information as to where they were obtained. The results would be more consistent if we were to compare tracheophytes of different ages in the same climates/regions. It makes sense to compare very old extinct tracheophytes to moderately old extinct tracheophytes. This is done in order to determine how the anatomy has evolved over time (thus making it important to have a range of ages for the extinct dataset). There are several abiotic and biotic factors that could factor into the evolution of these extant tracheophytes, but it is nearly impossible for us to assume the exact environment of these plants millions and billions of years ago.

The fossil cross-sections were analyzed with the image-processing program ImageJ/Fiji. These measurements were compiled in a dataset as well, and then the two datasets were compared using the computer programming language R. Using code written in R, many plots were produced that allowed for the comparison of the extant and extinct datasets; this code also allowed for the extensive analysis of both datasets. Boxplots were generated and include the mean values along with the p-values for each comparison. For each trait, two-sided t-tests of the extinct species versus the extant species were performed in order to determine if significantly different mean values occurred. This would indicate a change in hydraulic traits and vascular form. These boxplots can be seen in **Figure 3**.

Results and Analysis

All of the analyses performed in R are reported for each comparison in the following table (**Table 1**). It was found that the mean conduit diameter was significantly greater for the extant taxa than the extinct taxa. Additionally, there was a significant difference in the mean number of conduits, with more conduits for the extant taxa.

	P-Value	DF	Extinct 95% CI Lower Limit of Mean	Extinct 95% CI Upper Limit of Mean	Extant 95% CI Lower Limit of Mean	Extant 95% CI Upper Limit of Mean	Extinct Mean	Extant Mean
Mean Conduit Diameter (μm)	2.20×10^{-16}	86	0.05	0.07	12.87	16.64	0.06	14.76
Mean Segment Diameter (mm)	0.36	107	0.96	2.48	1.92	2.92	1.72	2.42
Mean Number of Conduits	2.20×10^{-16}	112	29.07	35.65	125.93	200.01	32.36	162.97

Table 1. The P-value, the degrees of freedom for the combined extant and extinct datasets, the lower and upper limits for the 95% confidence interval of the means for each dataset, and the sample estimates of the mean for each trait measured (mean conduit diameter, mean segment diameter, and mean number of conduits). The P-value comes from performing a two-sample t-test comparing the extinct and extant datasets.

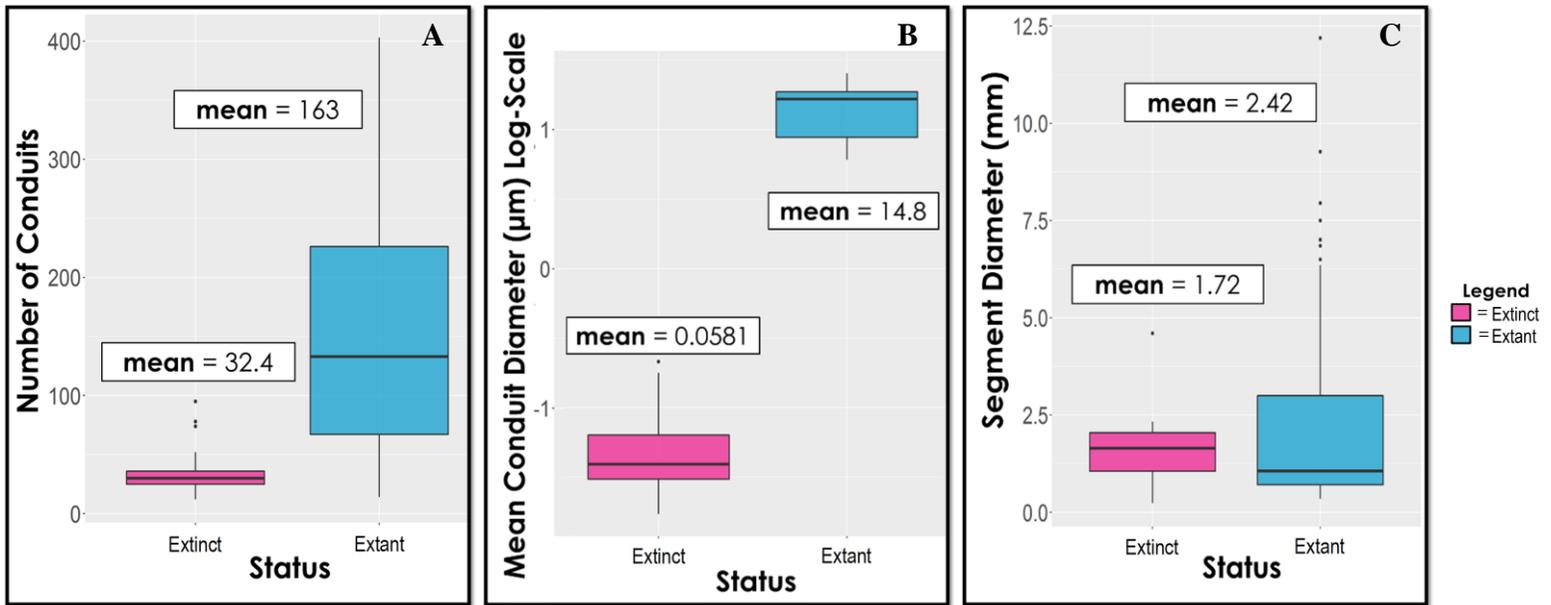


Figure 3. **A.** Comparison between the extinct and extant datasets for number of conduits. The average number of conduits is 32.4 and 163 conduits for the extinct and extant datasets, respectively. **B.** Comparison between the extinct and extant datasets for mean conduit diameter reported in micrometers (μm). This plot has been log-transformed to be seen more clearly. The average mean conduit diameter is 0.0581 μm and 14.8 μm for the extinct and extant datasets, respectively. **C.** Comparison between the extinct and extant datasets for segment diameter reported in millimeters (mm). The average segment diameter is 1.72 mm and 2.42 mm for the extinct and extant datasets, respectively.

Several important observations can be drawn from **Figure 3A** and **Figure 3B**. From **Figure 3A**, the frequency of conduits has significantly increased as we move from the extinct tracheophytes to the extant tracheophytes. The mean number of conduits in a cross-section for a given tracheophyte is 32.4 conduits for the extinct dataset and 163 for the extant dataset. A two-sample t-test was performed within R, giving a p-value of 2.20×10^{-16} for this relationship. This

indicates that there is a significance difference between the mean of the extinct dataset and the mean of the extant dataset.

From **Figure 3B**, there is a significant difference between the mean conduit diameter in the extinct and extant datasets. As we move from the extinct tracheophytes to the extant tracheophytes, the mean conduit diameter has increased from a mean of 0.0581 μm to 14.8 μm . A two-sample t-test was performed giving a p-value of 2.20×10^{-16} for this relationship, again indicating a significant difference between the means.

In **Figure 3C**, no relationship is indicated. While the p-value of 0.36 implies no significant difference in segment diameter, a relationship can still be concluded with regards to the conductive area of the tracheophyte rather than its segment diameter. This non-significant relationship between extinct and extant segment diameters controls for variation between the two datasets. Had there been a significant difference, the data would have had to be normalized. These results allow for the findings of **Figure 3A** and **Figure 3B** to be compared with respect to cross-sections with the same segment diameter.

Discussion

My analyses support the hypothesis that selection has resulted in increasingly more efficient water transport systems. Extant plant taxa differed in xylem anatomy (Figure 3; Table 1). Results indicate that there has been an increase in both conduit frequency and conduit size. While the above plots indicate that the frequency and size of conduits has increased as tracheophytes have evolved, we cannot conclude any certain relationships with regards to segment diameter, other than it allows for control of segment diameter variation. Recalling the general feature of the Hagen-Poiseuille relation that greater radius means easier conductance, it is favorable for the conduits of a plant to have a larger radius in order to significantly decrease the resistance the plant experiences when transporting water from its roots to its leaves (Tyree and Sperry 1988). With the relationships that **Figure 3A** and **Figure 3B** have indicated, conduit size and frequency have both increased as tracheophytes have evolved. Since both relate to the hydraulic efficiency of plants, it must be that the conductive area has also increased with regards to these plants. Therefore, we cannot conclude that segment diameter has increased, but rather, the conductive area has increased. This conclusion can be better understood by thinking about how closely packed the conduits are. As the number of conduits increases, the segment diameter does not necessarily increase as well. Rather, the conduits pack closer together and there is more conductive area, even if the segment cross-section area remains the same.

Perhaps one reason we may not see trends where they are expected (e.g., an increase in segment diameter) is due to possible bias in the fossil record. Whenever working with fossil cross-sections of plants, there is always the factor of compressional distortion and decortication (removal of the outermost layers) that may affect the values of certain measurements (Niklas

1984). This would have resulted in unexpected variation in segment diameter. In addition to this, the fossil record itself is limited and finding intermediate forms is difficult (Kenrick and Crane 1997, Wellman et al. 2003, Clarke et al. 2011). Despite any uncontrollable sources of error, the data are sufficient in concluding how certain aspects of xylem anatomy – in particular, conduits – have evolved to allow for plants to conquer the terrestrial environment.

Conclusions and Further Work

Looking at fossil cross-sections of extinct tracheophytes and comparing them with extant tracheophytes is a method that has not before been used. With this approach, we can see how plants have evolved not only to first overcome desiccation to colonize the land (Wodniok et al. 2011), but to move into more extreme environments as niches became more specialized and difficult to find (Chapin et al. 1987). This is evident by the difference in water conducting ability for the extinct and extant tracheophyte taxa tested, with the extant taxa having evolved to transport water more efficiently. What can be concluded from this study is that as tracheophytes evolved, they developed increased conduit size and frequency for a given segment diameter, thereby assisting in the process of making water transport easier. And while it cannot be concluded that segment diameter increased as we move from the extinct tracheophytes to the extant tracheophytes, it can be said that total conductive area has increased as tracheophytes have evolved to become larger to support the increasing need for efficient water transport in plants (Sperry et al. 2006, Tyree et al. 1994).

Several more interesting questions can be addressed with this research. One idea would be to test if the xylem of these extinct tracheophytes follow the predicted packing rules as presented in the Savage et al. 2010 paper, suggesting that plants have evolved to optimize the distribution of resources via changes in the vascular system. It would be meaningful to confirm whether tracheophytes have evolved according to this scaling principle (Savage et al. 2010).

Collecting more data (i.e., more fossil cross-sections) would be beneficial for several reasons, the first being that it would contribute more phylogenetic data that could allow for more comparisons across groups (e.g., ferns) (Swenson 2011, Graham and Fine 2008). This would

also allow for the control of intraspecific variation. By carefully selecting extinct tracheophyte cross-sections, being sure to collect those that are like each other with regards to local climate, temperature, and precipitation, we would essentially be controlling for these traits to reduce variation within the dataset that is associated with these traits.

The importance of this work is that it relates to the current issue of climate change that the world is presently facing. This study looked at how tracheophytes have evolved from some of the earliest tracheophytes to those that are living today, with selection for xylem anatomy allowing the most efficient transport of water (Pittermann 2010). Now, what if we could determine what tracheophytes will look like in the future? This research could possibly be taken further to predict future plant form and function, establishing what plants may be more likely to survive the increasing atmospheric temperatures in terms of their xylem anatomy (McDowell et al. 2008).

References

1. Andrews, H. N., Read, C. B., & Mamay, S. H. (1971). A Devonian Lycopod Stem with Well-Preserved Cortical Tissues. *Palaeontology*, *14*(1), 1-9.
2. Banks, H. P., & Davis, M. R. (1969). *Crenaticaulis*, a New Genus of Devonian Plants Allied to *Zosterophyllum*, and Its Bearing on the Classification of Early Land Plants. *American Journal of Botany*, *56*(4), 436-449.
3. Bateman, R. M., Crane, P. R., DiMichele, W. A., Kenrick, P. R., Rowe, N. P., Speck, T., & Stein, W. E. (1998). Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annual Review of Ecology and Systematics*, *29*(1), 263-292.
4. Beck, C. B. (1953). A New Root Species of *Callixylon*. *American Journal of Botany*, *40*(4), 226–233.
5. Beck, C. B. (1957). *Tetraxylopteris schmidtii* Gen. Et sp. Nov., A Probable Pteridosperm Precursor from the Devonian of New York. *American Journal of Botany*, *44*(4), 350-367.
6. Bonamo, P. M. (1977). *Rellimia thomsonii* (Progymnospermopsida) from the Middle Devonian of New York State. *American Journal of Botany*, *64*(10), 1272–1285.
7. Brodribb, T. J. (2009). Xylem hydraulic physiology: the functional backbone of terrestrial plant productivity. *Plant Science*, *177*(4), 245-251.
8. Burgess, S. S., Adams, M. A., Turner, N. C., White, D. A., & Ong, C. K. (2001). Tree roots: conduits for deep recharge of soil water. *Oecologia*, *126*(2), 158-165.

9. Carlquist, S. J. (1975). *Ecological strategies of xylem evolution*. University of California Press.
10. Carluccio, L. M., Hueber, F. M., & Banks, H. P. (1966). *Archaeopteris macilenta*, Anatomy and Morphology of Its Frond. *American Journal of Botany*, 53(7), 719–730.
11. Chapin, F. S., Bloom, A. J., Field, C. B., & Waring, R. H. (1987). Plant responses to multiple environmental factors. *Bioscience*, 37(1), 49-57.
12. Clarke, J. T., Warnock, R., & Donoghue, P. C. (2011). Establishing a time-scale for plant evolution. *New Phytologist*, 192(1), 266-301.
13. Cox, C. J., Li, B., Foster, P. G., Embley, T. M., & Civián, P. (2014). Conflicting phylogenies for early land plants are caused by composition biases among synonymous substitutions. *Systematic Biology*, 63(2), 272-279.
14. Dannenhoffer, J. M., & Bonamo, P. M. (1989). *Rellimia thomsonii* from the Givetian of New York: Secondary Growth in Three Orders of Branching. *American Journal of Botany*, 76(9), 1312–1325.
15. Delevoryas, T. (1957). Anatomy of *Sigillaria approximata*. *American Journal of Botany*, 44(8), 654-660.
16. Edwards, D. (1970). Further Observations on the Lower Devonian Plant, *Goslingia breconensis* Heard. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 258(821), 225–243.
17. Eggert, D. A., & Gaunt, D. D. (1973). Phloem of *Sphenophyllum*. *American Journal of Botany*, 60(8), 755–770.

18. Enquist, B. J. (2003). Cope's Rule and the evolution of long-distance transport in vascular plants: allometric scaling, biomass partitioning and optimization. *Plant, Cell & Environment*, 26(1), 151-161.
19. Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., ... & Cochard, H. (2016). Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*, 209(1), 123-136.
20. Graham, C. H., & Fine, P. V. (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology letters*, 11(12), 1265-1277.
21. Grierson, J. D. (1976). *Leclercqia complexa* (Lycopsida, Middle Devonian): Its Anatomy, and the Interpretation of Pyrite Petrifications. *American Journal of Botany*, 63(9), 1184–1202.
22. Hartman, C. M. (1981). The Effect of Pyrite on the Tracheid Structure of *Drepanophycus spinaeformis*, a Long-Ranging Devonian Lycopod. *Review of Palaeobotany and Palynology*, 32, 239-255.
23. Kenrick, P., & Crane, P. R. (1997). The origin and early evolution of plants on land. *Nature*, 389(6646), 33-39.
24. Koch, G. W., Sillett, S. C., Jennings, G. M., & Davis, S. D. (2004). The limits to tree height. *Nature*, 428(6985), 851-854.
25. Komatsu, K., Suzuki, N., Kuwamura, M., Nishikawa, Y., Nakatani, M., Ohtawa, H., ... & Hayashi, T. (2013). Group A PP2Cs evolved in land plants as key regulators of intrinsic desiccation tolerance. *Nature communications*, 4.

26. Langdale, J. A. (2008). Evolution of developmental mechanisms in plants. *Current opinion in genetics & development*, 18(4), 368-373.
27. Larter, M., Brodribb, T. J., Pfautsch, S., Burlett, R., Cochard, H., & Delzon, S. (2015). Extreme aridity pushes trees to their physical limits. *Plant physiology*, 168(3), 804-807.
28. Leliaert, F., Smith, D. R., Moreau, H., Herron, M. D., Verbruggen, H., Delwiche, C. F., & De Clerck, O. (2012). Phylogeny and molecular evolution of the green algae. *Critical Reviews in Plant Sciences*, 31(1), 1-46.
29. Lewis, L. A., & McCourt, R. M. (2004). Green algae and the origin of land plants. *American journal of botany*, 91(10), 1535-1556.
30. Lucas, W. J., Groover, A., Lichtenberger, R., Furuta, K., Yadav, S. R., Helariutta, Y., ... & Patrick, J. W. (2013). The plant vascular system: evolution, development and functions. *Journal of integrative plant biology*, 55(4), 294-388.
31. Mathews, S. (2009). Phylogenetic relationships among seed plants: persistent questions and the limits of molecular data. *American Journal of Botany*, 96(1), 228-236.
32. Matten, L. C. (1973). The Cairo Flora (Givetian) from Eastern New York. I. Reimannia, Terete Axes, and Cairoa lamanekii Gen. Et Sp. N. *American Journal of Botany*, 60(7), 619-630.
33. Matten, L. C., & Banks, H. P. (1969). Stenokoleos bifidus sp. n. in the Upper Devonian of New York State. *American Journal of Botany*, 56(8), 880-891.

34. McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... & Yopez, E. A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New phytologist*, *178*(4), 719-739.
35. Meinzer, F. C., Clearwater, M. J., & Goldstein, G. (2001). Water transport in trees: current perspectives, new insights and some controversies. *Environmental and experimental botany*, *45*(3), 239-262.
36. Niklas, K. J. (1984). Size-related changes in the primary xylem anatomy of some early tracheophytes. *Paleobiology*, *10*(4), 487-506.
37. Niklas, K. J. (1992). *Plant biomechanics: an engineering approach to plant form and function*. University of Chicago press.
38. Niklas, K. J. (1997). *The evolutionary biology of plants*. University of Chicago Press.
39. Niklas, K. J. (2000). The evolution of plant body plans—a biomechanical perspective. *Annals of Botany*, *85*(4), 411-438.
40. Oliver, M. J., Tuba, Z., & Mishler, B. D. (2000). The evolution of vegetative desiccation tolerance in land plants. *Plant Ecology*, *151*(1), 85-100.
41. Phillips, T. L. (1974). Evolution of Vegetative Morphology in Coenopterid Ferns. *Annals of the Missouri Botanical Garden*, *61*(2), 427-461.
42. Pittermann, J. (2010). The evolution of water transport in plants: an integrated approach. *Geobiology*, *8*(2), 112-139.
43. Proctor, M. C. F. (1982). Physiological ecology: water relations, light and temperature responses, carbon balance. In *Bryophyte ecology* (pp. 333-381). Springer, Dordrecht.

44. Pryer, K. M., Schneider, H., Smith, A. R., Cranfill, R., Wolf, P. G., Hunt, J. S., & Sipes, S. D. (2001). Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature*, *409*(6820), 618-622.
45. Renzaglia, K. S., Schuette, S., Duff, R. J., Ligrone, R., Shaw, A. J., Mishler, B. D., & Duckett, J. G. (2007). Bryophyte phylogeny: advancing the molecular and morphological frontiers. *The bryologist*, *110*(2), 179-213.
46. Savage, V. M., Bentley, L. P., Enquist, B. J., Sperry, J. S., Smith, D. D., Reich, P. B., & von Allmen, E. I. (2010). Hydraulic Trade-Offs and Space Filling Enable Better Predictions of Vascular Structure and Function in Plants. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(52), 22722–22727.
47. Scheckler, S. E. (1975). A Fertile Axis of *Triloboxylon ashlandicum*, a Progymnosperm from the Upper Devonian of New York. *American Journal of Botany*, *62*(9), 923–934.
48. Scheckler, S. E., & Banks, H. P. (1971). Anatomy and Relationships of some Devonian Progymnosperms from New York. *American Journal of Botany*, *58*(8), 737–751.
49. Serbet, R., & Rothwell, G. W. (1992). Characterizing the Most Primitive Seed Ferns. I. A Reconstruction of *Elkinsia polymorpha*. *International Journal of Plant Sciences*, *153*(4), 602–621.
50. Skog, A. J. E., & Banks, H. P. (1973). *Ibyka Amphikoma*, Gen. et sp. n., a New Protoarticulate Precursor From the Late Middle Devonian of New York State. *American Journal of Botany*, *60*(4), 366–380.

51. Sperry, J. S. (2003). Evolution of water transport and xylem structure. *International Journal of Plant Sciences*, 164(S3), S115-S127.
52. Sperry, J. S., Hacke, U. G., & Pittermann, J. (2006). Size and function in conifer tracheids and angiosperm vessels. *American journal of botany*, 93(10), 1490-1500.
53. Stein, W. E. (1993). Modeling the Evolution of Stellar Architecture in Vascular Plants. *International Journal of Plant Sciences*, 154(2), 229–263.
54. Stein, W. E., & Beck, C. B. (1983). Triloboxylon arnoldii From the Middle Devonian of Western New York. *Contributions from the Museum of Paleontology, the University of Michigan*, 26(12), 257–288.
55. Swenson, N. G. (2011). Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PloS one*, 6(6), e21264.
56. Taylor, E. L. (1988). Secondary Phloem Anatomy in Cordaitan Axes. *American Journal of Botany*, 75(11), 1655–1666.
57. Timme, R. E., Bachvaroff, T. R., & Delwiche, C. F. (2012). Broad phylogenomic sampling and the sister lineage of land plants. *PLoS one*, 7(1), e29696.
58. Tyree, M. T., Davis, S. D., & Cochard, H. (1994). Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA journal*, 15(4), 335-360.
59. Tyree, M. T., & Sperry, J. S. (1988). Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant physiology*, 88(3), 574-580.

60. Tyree, M. T., & Sperry, J. S. (1989). Vulnerability of xylem to cavitation and embolism. *Annual review of plant biology*, 40(1), 19-36.
61. Wellman, C. H., Osterloff, P. L., & Mohiuddin, U. (2003). Fragments of the earliest land plants. *Nature*, 425(6955), 282-285.
62. Willis, K., & McElwain, J. (2014). *The evolution of plants*. Oxford University Press.
63. Wodniok, S., Brinkmann, H., Glöckner, G., Heidel, A. J., Philippe, H., Melkonian, M., & Becker, B. (2011). Origin of land plants: do conjugating green algae hold the key? *BMC Evolutionary Biology*, 11(1), 104.
64. Woodruff, D. R., Meinzer, F. C., & Lachenbruch, B. (2008). Height-related trends in leaf xylem anatomy and shoot hydraulic characteristics in a tall conifer: safety versus efficiency in water transport. *New Phytologist*, 180(1), 90-99.

Appendix I

Status	Taxonomy			Age (MYA)	Mean Conduit Diameter (µm)	Mean Segment Diameter (mm)	Mean Number of Conduits	Location	Citation
	Family	Genus	Species						
Extinct	Lycopodiaceae	Leclerqi	complexa	Middle Devonian	na	1.078451354	1193.548387	Near Blenheim, NY	(Grierson 1976)
Extinct	Archaeopteridaceae	Callixylon	petryi	Upper Devonian?	0.032857926	na	896.5517241	Finger Lakes region of NY	(Beck 1953)
Extinct	Archaeopteridaceae	Callixylon	petryi	Upper Devonian?	0.041766914	na	636.3636364	Finger Lakes region of NY	(Beck 1953)
Extinct	Archaeopteridaceae	Callixylon	petryi	Upper Devonian?	0.036824428	na	810.8108108	Finger Lakes region of NY	(Beck 1953)
Extinct	Archaeopteridaceae	Callixylon	petryi	Upper Devonian?	0.027584308	na	2090.909091	Finger Lakes region of NY	(Beck 1953)
Extinct	Archaeopteridaceae	Callixylon	petryi	Upper Devonian?	0.050562608	na	622.2222222	Finger Lakes region of NY	(Beck 1953)
Extinct	Archaeopteridaceae	Archaeopteris	macilenta	Lower Frasnian	na	na	1290.322581	NY	(Carluccio et al. 1966)
Extinct	Archaeopteridaceae	Archaeopteris	macilenta	Lower Frasnian	na	na	1061.22449	NY	(Carluccio et al. 1966)
Extinct	Archaeopteridaceae	Archaeopteris	macilenta	Lower Frasnian	na	na	1192.307692	NY	(Carluccio et al. 1966)
Extinct	Archaeopteridaceae	Archaeopteris	macilenta	Lower Frasnian	na	na	823.5294118	NY	(Carluccio et al. 1966)
Extinct	Archaeopteridaceae	Archaeopteris	macilenta	Lower Frasnian	0.017133038	na	1666.666667	NY	(Carluccio et al. 1966)
Extinct	Archaeopteridaceae	Archaeopteris	macilenta	Lower Frasnian	na	na	769.2307692	NY	(Carluccio et al. 1966)
Extinct	Drepanophyceae	Drepanophycus	spinaeformis	Probably Late Emsian (Early Devonian)	0.038436591	na	540.5405405	Gaspé Bay, Quebec	(Hartman 1981)
Extinct	na	Metadineuron	ellipticum	Visean (Mississippian)	0.063144106	0.231307554	247.8632479	Scotland	(Phillips 1974)
Extinct	na	Dineuron	pteroides	Visean (Mississippian)	0.068746132	na	292.3076923	France	(Phillips 1974)
Extinct	Botryopteridaceae	Botryopteris	antiqua	Visean (Mississippian)	0.098281687	na	164.4736842	France	(Phillips 1974)
Extinct	na	Metaclepsydropsis	duplex	Visean (Mississippian)	0.178180412	na	104.4776119	Scotland	(Phillips 1974)
Extinct	na	Diplolabis	roemeri	Visean (Mississippian)	0.136249	na	83.69098712	Scotland	(Phillips 1974)
Extinct	na	Etapteris	scottii	na	0.119667194	na	75.37688442	Minearl Coal, Kansas	(Phillips 1974)
Extinct	na	Etapteris	na	na	0.138062702	na	60.13745704	Calhoun Coal, Illinois	(Phillips 1974)
Extinct	na	Etapteris	scottii	Pennsylvanian	na	na	2210.526316	na	(Phillips 1974)
Extinct	Zygopteridaceae	Zygopteris	na	Pennsylvanian	na	na	62.78283005	na	(Phillips 1974)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.027685328	0.978104236	1439.393939	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	na	490.0662252	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	na	192	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.035695138	2.326803116	857.1428571	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	1.800566082	1333.333333	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.033518923	na	1351.351351	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	na	468.0851064	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.030578415	na	1208.333333	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.030652248	na	1468.75	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	1.73462307	970.5882353	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	na	1700	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.035597243	na	857.1428571	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.039171053	na	631.5789474	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.051093197	na	404.040404	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.031338505	na	1103.448276	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.054044864	na	395.8333333	South Mountain, Schoharie County, NY	(Matten & Banks 1969)

Status	Taxonomy			Age (MYA)	Mean Conduit Diameter (μm)	Mean Segment Diameter (mm)	Mean Number of Conduits	Location	Citation
	Family	Genus	Species						
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.054179422	na	545.4545455	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	na	895.8333333	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	na	2.28537304	na	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleos	bifidus	Lower Mississippian	0.063950916	na	438.5964912	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleus	simplex	Lower Mississippian	0.048831285	na	702.7027027	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Stenokoleus	simplex	Lower Mississippian	0.030488692	na	1095.238095	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	Stenokoleaceae	Reimanniopsis	indianensis	Lower Mississippian	0.023118328	na	2052.631579	South Mountain, Schoharie County, NY	(Matten & Banks 1969)
Extinct	na	Tetrazylopteris	schmidtii	Devonian	0.027363645	na	1129.032258	Cave Mountain, Greene County, NY	(Scheckler & Banks 1971)
Extinct	na	Triloboxylon	ashlandicum	Devonian	0.033712594	na	740	Cave Mountain, Greene County, NY	(Scheckler & Banks 1971)
Extinct	na	Triloboxylon	ashlandicum	Devonian	0.024811343	na	1428.571429	Cave Mountain, Greene County, NY	(Scheckler & Banks 1971)
Extinct	na	Triloboxylon	hallii	Devonian	0.023147597	na	1409.090909	Cave Mountain, Greene County, NY	(Scheckler & Banks 1971)
Extinct	na	Ibyka	amphikoma	Erian (= Givetian)	0.057552626	na	401.8691589	Eastern NY	(Skog & Banks 1973)
Extinct	Trimerophytaceae	Psilophyton	dawsonii	Lower Devonian (Late Emsian)	0.028248123	na	1250	Gaspé, Quebec	(Stein 1993)
Extinct	Trimerophytaceae	Psilophyton	dawsonii	Lower Devonian (Late Emsian)	na	na	1260.869565	Gaspé, Quebec	(Stein 1993)
Extinct	Trimerophytaceae	Psilophyton	dawsonii	Lower Devonian (Late Emsian)	0.021280346	na	1526.315789	Gaspé, Quebec	(Stein 1993)
Extinct	na	Aneurophytales	na	Middle Devonian (Upper Eifelian)	0.041766664	na	641.025641	Millboro Formation Radford, Virginia	(Stein 1993)
Extinct	na	Aneurophytales	na	Middle Devonian (Upper Eifelian)	0.050787488	na	619.047619	Millboro Formation Radford, Virginia	(Stein 1993)
Extinct	na	Arachnoxylon	kopfi	Middle Devonian (Upper Givetian)	na	na	306.9306931	Windom Formation Erie County, NY	(Stein 1993)
Extinct	na	Arachnoxylon	kopfi	Middle Devonian (Upper Eifelian)	na	na	521.7391304	Millboro Formation Radford, Virginia	(Stein 1993)
Extinct	Calamopityaceae	Stenokoleos or Calamopitys	na	Lower Carboniferous	0.059412682	na	290.5982906	na	(Stein 1993)
Extinct	Calamopityaceae	Diichnia	kentuckiensis	na	na	na	149.122807	na	(Stein 1993)
Extinct	na	Triloboxylon	ashlandicum	Upper Devonian (Lower Frasnian)	na	na	465.7534247	Oneonta Formation Greene County, NY	(Stein 1993)
Extinct	na	na	na	Middle Devonian (Upper Eifelian)	na	na	740.7407407	Millboro Formation Radford, Virginia	(Stein 1993)
Extinct	na	Crenaticaulis	verreculosus	Emsian or Eifelian	0.034880111	na	636.3636364	Gaspé Bay, Quebec	(Banks & Davis 1969)
Extinct	na	Crenaticaulis	verreculosus	Emsian or Eifelian	0.017962904	na	2600	Gaspé Bay, Quebec	(Banks & Davis 1969)
Extinct	na	Tetrazylopteris	schmidtii	Upper Devonian	0.031091897	na	560	Eastern NY	(Beck 1957)
Extinct	na	Rellimia	thomsonii	Middle Devonian (Givetian)	0.056293806	na	258.9928058	Eastern NY	(Bonamo 1977)
Extinct	na	Rellimia	thomsonii	Middle Devonian (Givetian)	0.214094644	na	1615.384615	Eastern NY	(Bonamo 1977)
Extinct	na	Gosslingia	breconensis	Siegenian-Emsian	0.036503382	na	794.8717949	South Wales	(Edwards 1970)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	na	1.194467074	na	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	na	1.644523822	na	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	na	1.03751295	na	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	0.026854515	na	1217.391304	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	0.101170118	4.59977845	71.11111111	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	0.116709885	na	64.1025641	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	0.104279519	na	81.55339806	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	0.109688826	na	69.51871658	na	(Eggert & Gaunt 1973)
Extinct	Sphenophyllaceae	Sphenophyllum	plurifoliatum	Middle Pennsylvanian	0.110217837	na	76.92307692	na	(Eggert & Gaunt 1973)