Exploring the Environmental Tolerance of Pteridosperms

Nicole Smith

Dr. Thomas Holtz

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Abstract

Introduction & Background

Since their first appearance in the Ordovician, plants have had a relationship with the Earth and their existence will always be intertwined. Changes in the Earth's environment will change plant life. And the opposite is true. Plant changes and evolution will affect the soil, atmosphere, and Earth's environment overall (Dahl and Arens, 2020). Naturally, plants have developed a tolerance for their ever-changing environments. The first plants, mosses, and other non-vascular plants were living in shallow water. These plants soon evolved and found themselves on land. This occurred because of the evolution of the vascular system in plants. This system allowed plants to store water and nutrients and move and grow farther away from water sources. These extinct lineages of early vascular plants started to rise in the Devonian and dominated the land in the Carboniferous. Vascular plants started the forest and jungle building process. Among the first vascular plants was the group Pteridospermatophyta. Often called pteridosperms, "seed ferns", or primitive gymnosperm. These seed ferns lived throughout the Paleozoic and into the Mesozoic. During their time on Earth, pteridosperms had a huge impact on plants coming afterward. Pteridosperms were the first seed-bearing plants. A similar outcome to the vascular system, the seed allowed the plant to store nutrients and protect the embryo. Pteridosperms have been called the backbone of the seed-plant phylogeny (Hilton & Bateman 2006).

Pteridosperms are a paraphyletic group, meaning the taxon consists of a most recent common ancestor and some of its descendants.. This group consists of multiple subgroups or clades. Those are Progymnosperms, Lyginopteridales, Medullosales, Callistophytales, Peltaspermales, and Corystospermales. Pteridosperms were diverse, ecologically heterogeneous, and had a wide range of complex growth morphologies (DiMichele et al. 2006). Some characteristics between clades were the same including their large frond and fern-like foliage, fructification, and their advanced, seed-type reproductive system. The difference in growth morphologies of pteridosperms included scrambling plants, climbing vines and lianas, and trees. The most diversity is seen in the trees, vines, and lianas. Some trees grew self-supporting while others grew in clumps for support, and the vines had different ways of attaching themselves to trees (Krings et al. 2003). These differences in growth habits varied from clade to clade as well as within the clades. The clades of pteridosperms are not related. Each one had a different growth habit and lifestyle.

Lyginopteridales is the earliest known pteridosperm order. Much of our understanding of how and why seeds evolved is based on this group (Cleal & Thomas 2019). They first existed in the Devonian and reached their peak in the Mississippians. The order eventually became extinct before the start of the Permian Period. There is a notable relationship between the decline of Lyginopteridales and the rise of the pteridosperm order Medullosales. Medullosales made their debut in the late Mississippian and flourished in the Pennsylvanian. Sometimes Medullosales grew as a smaller scrambling plant, but mostly as small to medium-sized trees present at heights up to 10 m tall (Taylor et al. 2009). Of all the pteridosperms, Medullosales bore the largest seeds and had the largest foliage diversity. Their large diversity of foliage preserved in rocks during the

Pennsylvanian has been suggested to confirm their growth in humid conditions (Cleal & Thomas 2019). The extinction of Medullosales came during the early Permian. Following along, although not as abundant as Lyginopteridales and Medullosales, was Callistophytales, that first appeared in the mid-Pennsylvanian growing as a shrub with a scrambling vine or lianescent habit. These plants were likely understory elements in the forests. (Rothwell 1981). Out of all the seed ferns, Callistophytales had the most complex reproductive systems, and a short lifespan. Hitting their peak abundance in the late Pennsylvanian and going extinct in the early-mid Permian. The last of the four Paleozoic ferns were Peltaspermales. Living from the Pennsylvanian, growing as both shrubs and small trees with small leaves, all the way to the early Triassic until going extinct. This research will focus on three of the classic Paleozoic pteridosperms that are the most understood and used for classification. Those are Medullosales, Callistophytales, and Peltaspermales.

One similarity between the three Paleozoic pteridosperms is that they all survived worldwide environmental changes. Over the duration of their existence, a series of monumental events took place. The Devonian started out with flourishing biodiversity but ended with mass extinction 375 million years ago. The end of the Devonian extinction was the second major mass extinction and approximately 75% of the world's species died off. Lyginopteridales were not among those species. Both Medullosales and Callistophytales went through extreme temperature changes as both survived the late Paleozoic ice age or the Karoo ice age. This ice age lasted 100 million years from about 360 to 260 million years ago. It was the source of extinction for a large amount of flora and fauna, but not for the pteridosperms. They continued to grow in size and in population. Towards the end of the Permian when Peltaspermales were thriving, the third mass extinction took place. The Permian-Triassic extinction was about 251 million years ago. This is known as Earth's most severe extinction with an estimated loss of 80-96% of species. Once again, pteridosperms were not among those extinct species. All four different pteridosperm clades survived a wide range of environmental changes before going extinct. Over time, pteridosperms numbers declined and finally went extinct as more advanced plants evolved. The relationship pteridosperms had with their environments allowed them to become resilient through major events. Presumably, the response from seed ferns to arge-scale environmental changes would be a change in location and movement towards more suitable climate and growth areas. The exploration of pteridosperms' environmental tolerance has yet to be analyzed despite these plants being such a significant part of the Paleozoic flora, and that is one of the components of the work outlined here.

Objectives of research and broader implications

Research about how plants overall have influenced major climate changes over time has been completed by others. Based on findings he increase of forest trees and dynamic fluxes of atmospheric carbon dioxide and oxygen resulted in a gradual decrease in the Earth's temperature, slowly leading to an ice age. Specifically, the late Paleozoic ice age. Workers have explored through research the substantial difference in plant growth and habits in past environments compared to plants in current environments (Wilson et al. 2017). A particular difference is noted in forests. Most of the research on pteridosperms is qualitative, observing structures and growth habits, leaf types, and how they are classified, as well as their evolutionary connection to later plants. Some researchers believe that the plant adaptation to environmental forcing, the scaling to ecosystems, and biome responses, are too complex. These complexities are intertwined with many biological and environmental conditions making them challenging to quantify (Wilson et al. 2017). This could be the reasoning behind the lack of research on pteridosperm environmental tolerances, as well as the lack of quantitative data focusing on pteridosperms. The origin of most pteridosperms has been discovered through palaeoecological and sedimentological studies that found that they mostly inhabited warm and humid coal-swamp forests (Krings et al. 2003). Where pteridosperms moved during these environmental changes has yet to be explored. Did climate changes and environmental factors affect the distribution of pteridosperm clades? Does each pteridosperm clade have its preferred environment? Does each clade have distinct responses to environmental factors? This study will start exploring answers to these questions mainly using the aid of pteridosperm fossil locations distributed over time in the Paleozoic. The hypothesis is that there is a shift in pteridosperm fossil locations that correspond to a shift in environment type over time. Pteridosperm fossils in the same order will be in the same environments. The null hypothesis is that there is no correlation between the environmental changes and the presence and absence of fossil locations. The results of this research will reveal information about plant evolution as well as pteridosperms group evolution. An understanding of pteridosperms' environmental tolerance can be deduced from the results. Understanding each pteridosperm clade's environmental tolerance poses new questions to explore. Do other plants in the Paleozoic and Mesozoic experience a similar tolerance and correlation? What about plants that are specifically derived from pteridosperms? This research poses many questions to be investigated.

The research design of this study was a correlational to study the relationship between pteridosperm clade location and climate types. To approach the research question, data on the presence or absence of pteridosperm fossils for each clade throughout the Paleozoic is key. The important variables in this experiment were the amount of pteridosperm fossil occurrences and the climate types they lived in. To obtain fossil occurrence data the Paleobiology Database (PBDB) will be used. This database is a non-profit, public resource for paleontological data that is organized and operated by palaeobiological researchers. The database provides occurrence and taxonomic data for organisms of all geological ages.(PBDB 2021). Using the PBDB does come with some obstacles. There is the issue that there could be missing data if an area hasn't been explored for pteridosperm or plant fossils. Also, since the PBDB is independently run it is possible that there is more pteridosperm data out there that has not been uploaded onto the PBDB. With the PBDB fossil occurrence data for each of the pteridosperm clades was obtained. To conceptualize the absences of pteridosperm clades other data was necessary. The next data collected was the fossil occurrence for the plant group Embryophyta. The absence of pteridosperms will be decided by the presence of the Embryophyta group. The Embryophyta group represents land plants as a whole and their location data represents all the areas and climates plants were inhabiting during each time period. The Embryophyta group in this experiment acts as a control group. The Embryophyta data was compared against the pteridosperm's clade data. It represents all the possible locations the pteridosperm clades could, have been living in, based on what has been uploaded to the PBDB. The data collected is represented in figures 1 through 5.

Once the occurrence data was collected from the fossil locations for each of the different clades are categorized by climate corresponding to their location on the paleoclimate map. These paleoclimate maps are an important resource for this study. The Phanerozoic Paleoclimate: An Atlas of Lithologic Indicators of Climate (Boucot et al. 2013) is a series of paleoclimate map reconstructions. The maps have five general climate types used to describe the paleoclimates. The five climates are arid, cool, tropical, warm temperature, and cool temperature. These climates were estimated using different index fossils or climate-specific items such a coal samples for the tropical climates and drop stones and glacial till for cool and cold environments. They climate categories used on the maps are a simplified version of the Loppen climate classification. These different climates are independent of the fossil location data and will be used when testing the data. The locations of the fossils will be categorized based on the climate they were found in based on the maps. This research utilizes maps labeled 9-15. The time slices for those maps are Early Carboniferous (Tournaisian-Visean), Early Carboniferous (Serpukhovian), Late Carboniferous (Bashkirian-Moscovian), Late Carboniferous (Kasimovian-Gzhelian), Early Permian (Asselian–Sakmarian), Middle-Late Permian (Artinskian–Lopingian), and Early Triassic. Once the fossil occurrence data was all collected and separated their locations were plotted onto the corresponding paleoclimate map. Plotting the locations gives a visual to see how the locations change over time as well as see if their occurrence values increased or decreased. Figures 6 through 20 are the pteridosperm clade locations plotted on the paleoclimate maps. One of the last steps in the research procedure was to test the data collected.

To test the collected data the PAleontological STatistics software 4.07 (PAST) was used. PAST is a comprehensive statistics package with multiple usages in statistical analysis. PAST will be used in data collection and to run the statistical tests for analysis. Based on the variables, pteridosperm clades, and climate, the test needs to be compatible with nominal data. The chi-squared test of association will be used with PAST for this research. This test is used to see whether the proportions of one variable are different depending on the other variables. In this case, the two variables are the pteridosperm clades and the number of their occurrences, and the different climate types. The chi-squared test is used to calculate the probability of getting the observed data. The probability, p-value, when low, p<0.05, indicates that there is a statistical significance, the observed values are different to the expected values, and you can reject the null hypothesis. With the data set up in data tables the chi-squared test was run comparing the fossil occurrences versus the Embryophyta group in each climate type, figure 21. This allows the results of the test to show if there is any difference, low p value, in the pteridosperm clade locations then what should be expected, the Embryophyta locations and occurrences.

Data

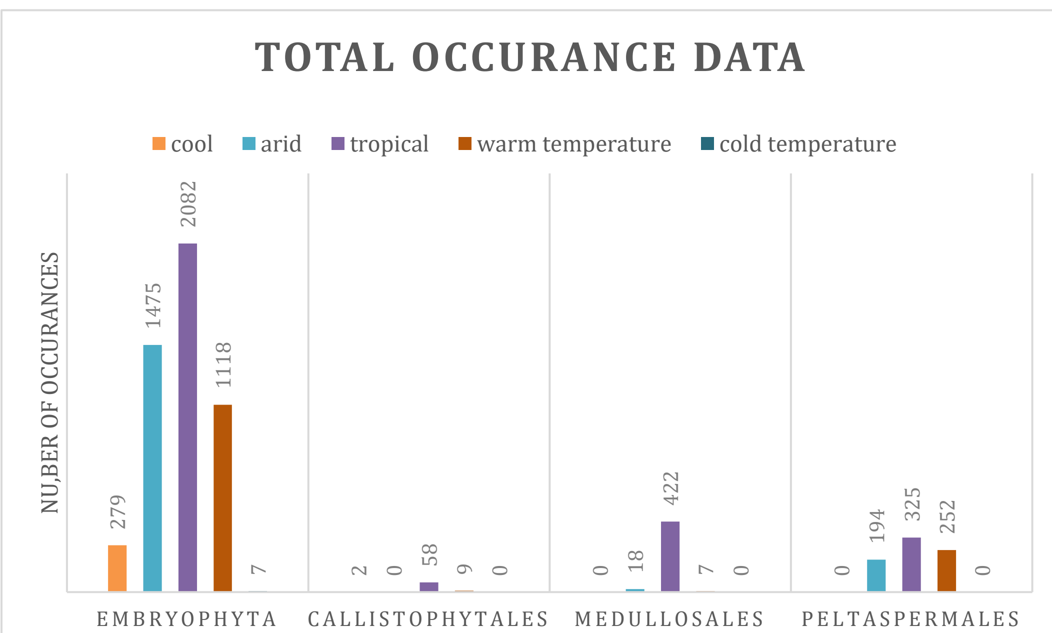

Figure 1. The occurrence data totals for Embryophyta and each of the pteridosperm clades,

Callistophytales, Medullosales, and Peltaspermales. The legend describes each of the climate types that correspond with the maps used. The numbers labeled on each bar represent the number of occurrences in that climate type.

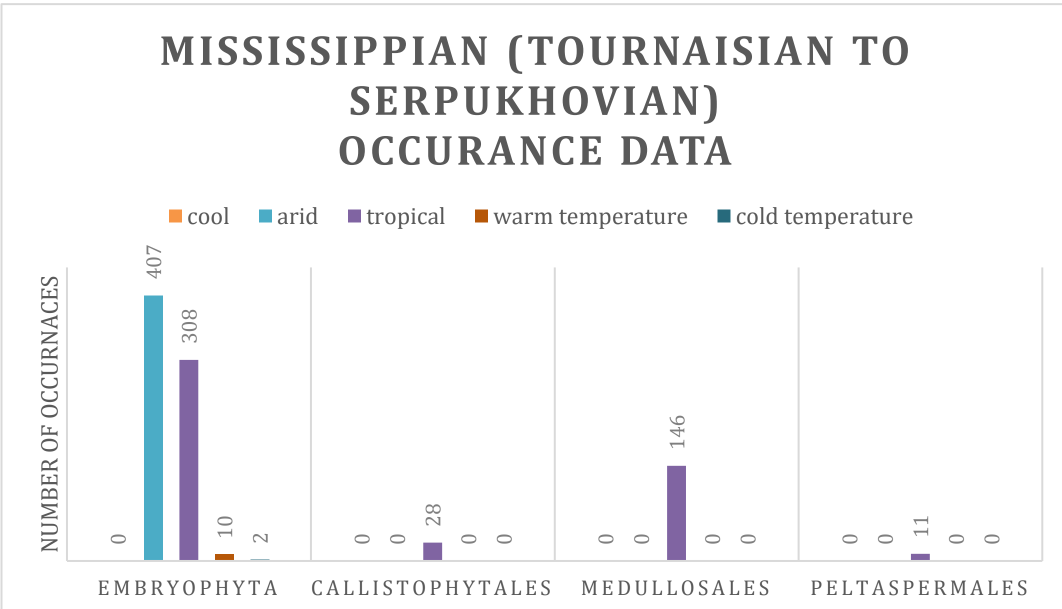

Figure 2. The occurrence data for Embryophyta and each of the pteridosperm clades, Callistophytales, Medullosales, and Peltaspermales during the Mississippian, the early Carboniferous.

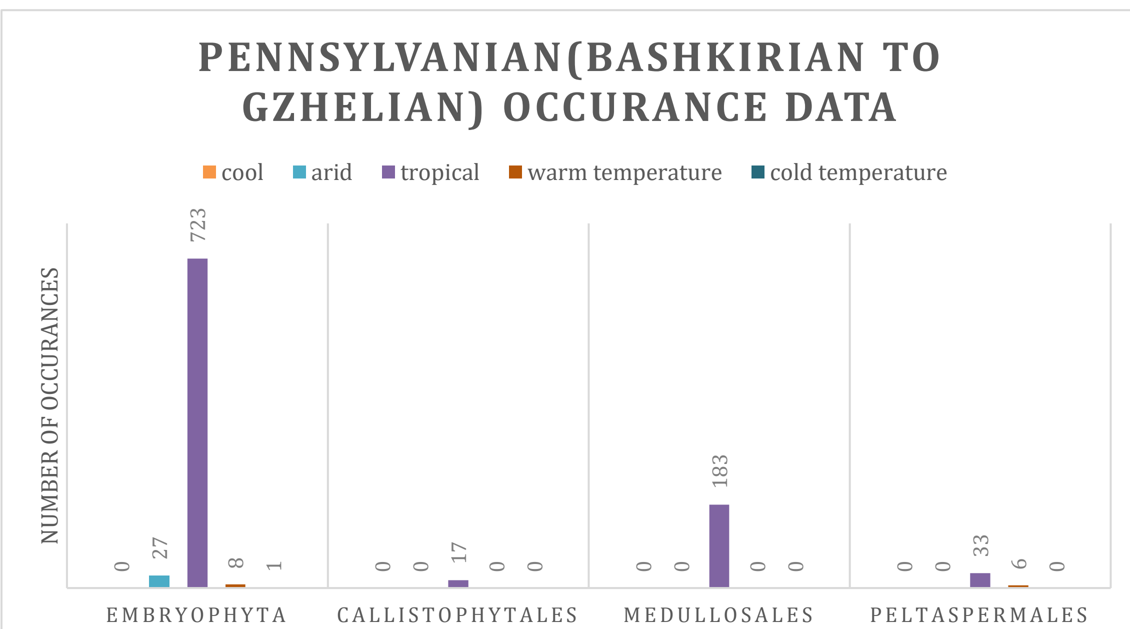

Figure 3. The occurrence data for Embryophyta and each of the pteridosperm clades, Callistophytales, Medullosales, and Peltaspermales during the Pennsylvanian, the late Carboniferous.

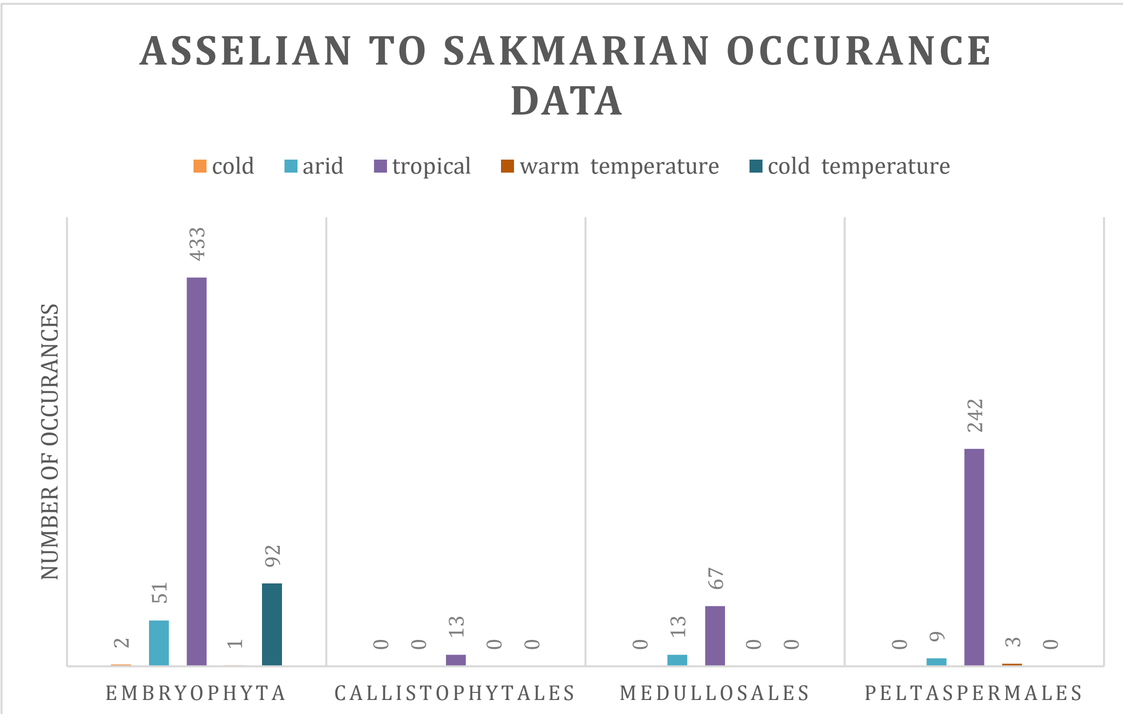

Figure 4. The occurrence data for Embryophyta and each of the pteridosperm clades, Callistophytales, Medullosales, and Peltaspermales during Asselian through the Sakmarian, the early Permian.

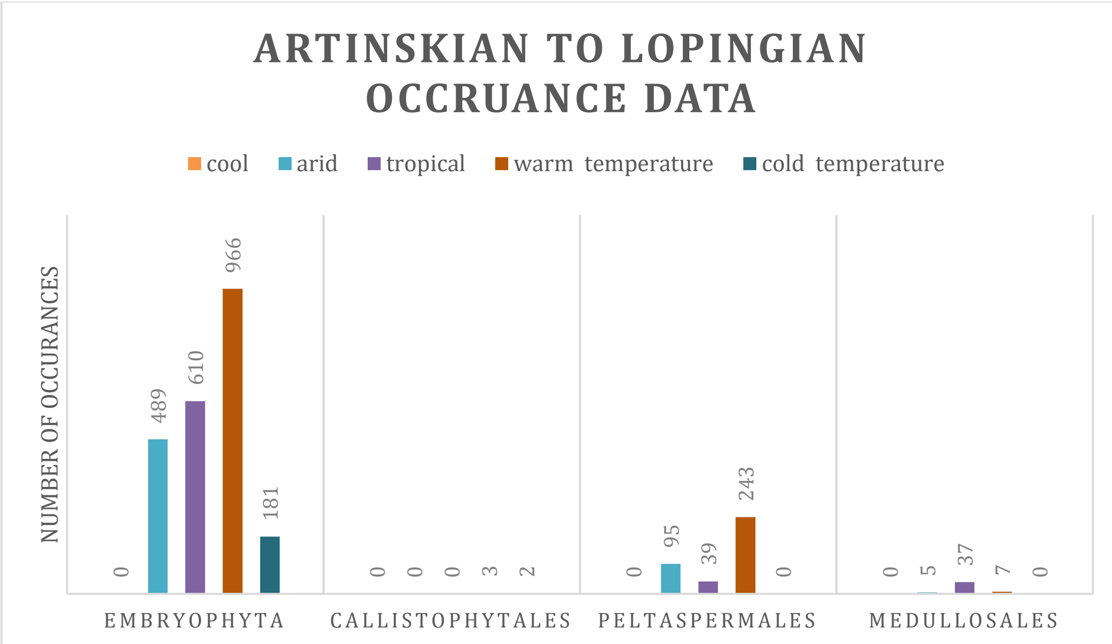

Figure 5. The occurrence data for Embryophyta and each of the pteridosperm clades, Callistophytales, Medullosales, and Peltaspermales during the Artinskian through the Lopingian, the late Permian.

Callistophytales location mapped out on paleoclimate maps from first to last occurrence in PBDB

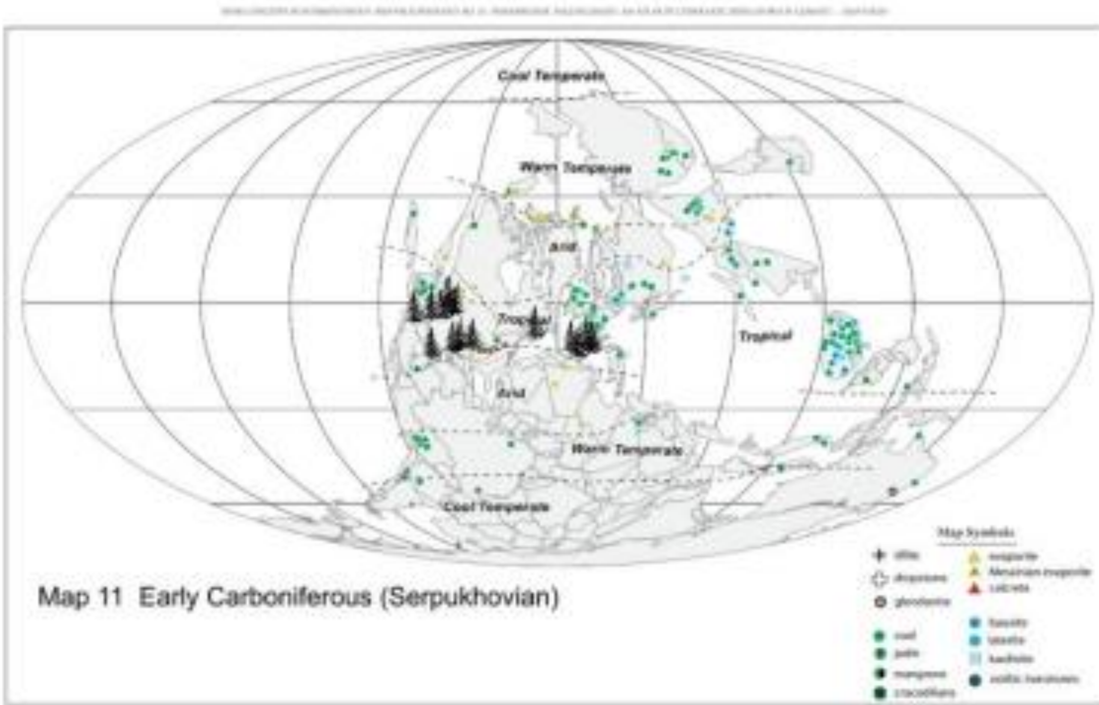

Figure 6. The locations for Callistophytales are plotted, the black fern leaves, on the paleoclimate map for the early Carboniferous.

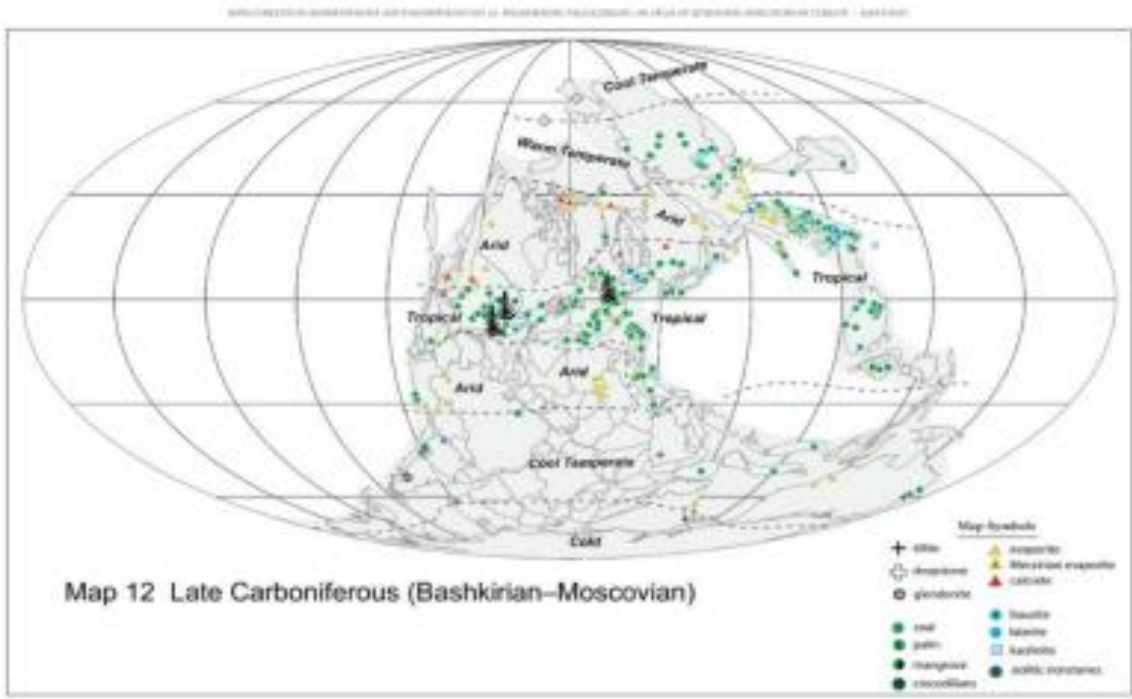

Figure 7. The locations for Callistophytales are plotted, the black fern leaves, on the paleoclimate map for the late Carboniferous.

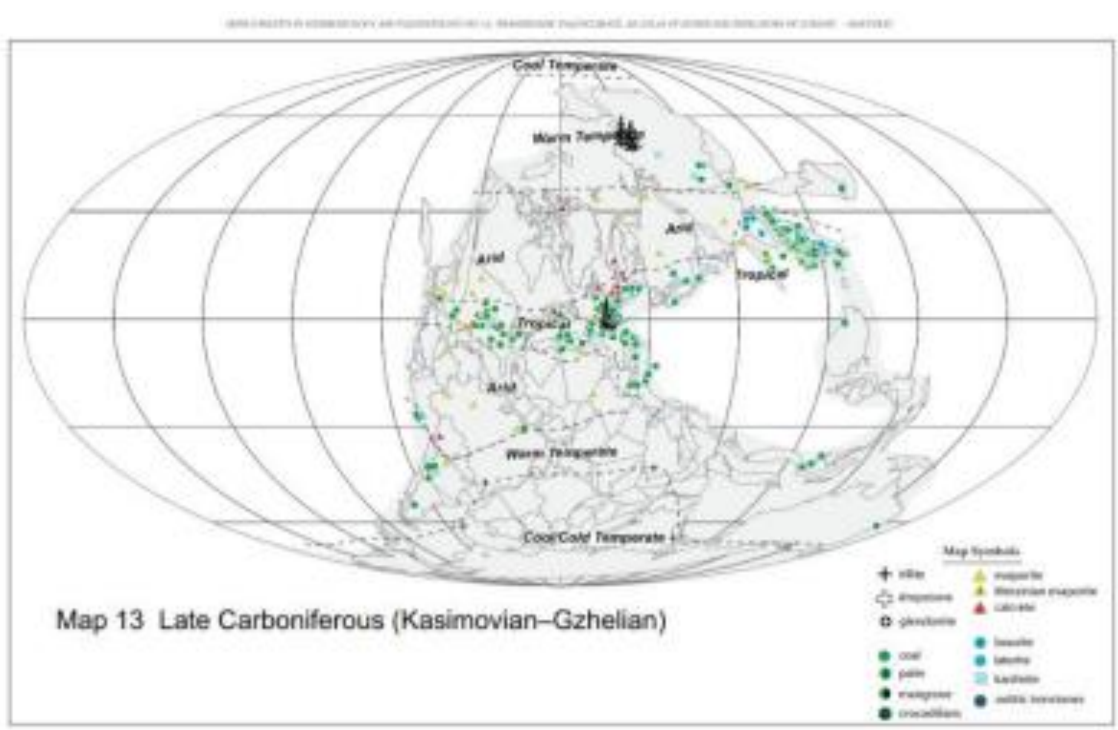

Figure 8. The locations for Callistophytales are plotted, the black fern leaves, on the paleoclimate map for the late Carboniferous.

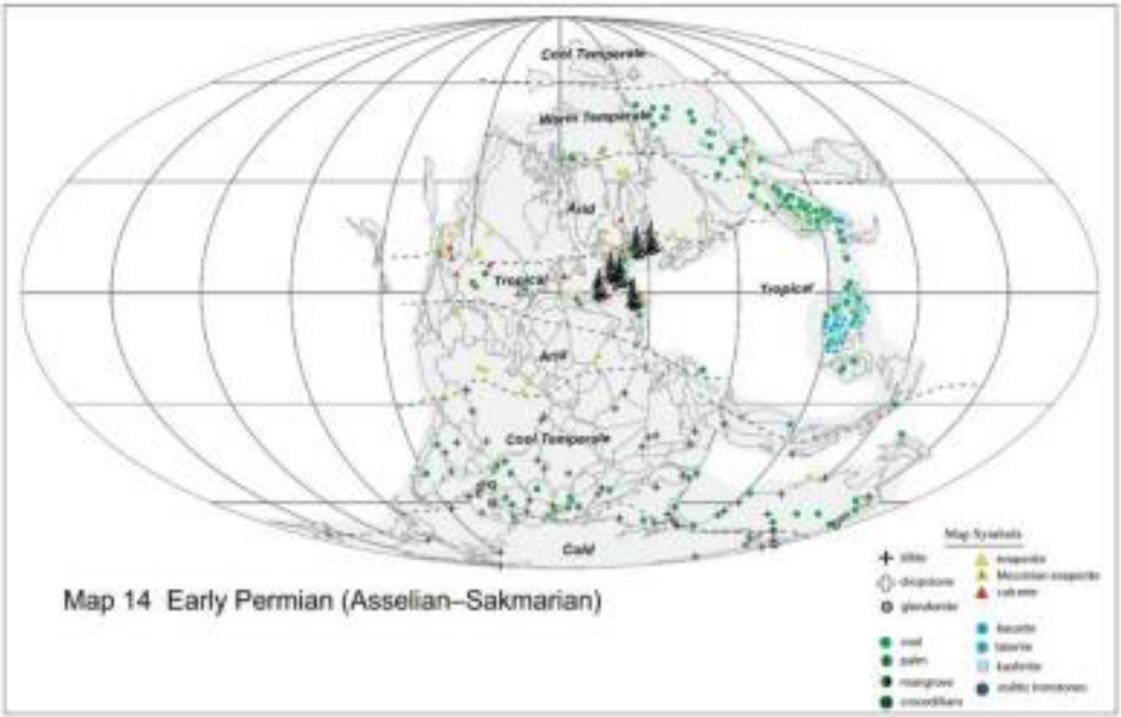

Figure 9. The locations for Callistophytales are plotted, the black fern leaves, on the paleoclimate map for the early Permian.

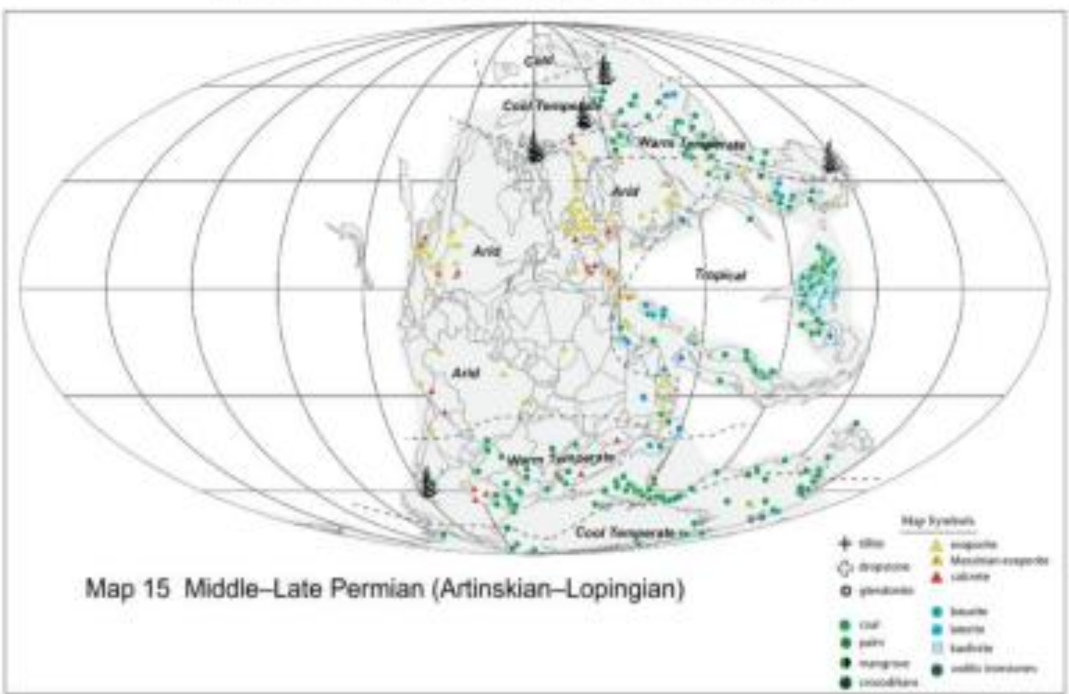

Figure 10. The locations for Callistophytales are plotted, the black fern leaves, on the paleoclimate map for the middle to late Permian.

Medullosales location mapped out on paleoclimate maps from first to last occurrence in PBDB

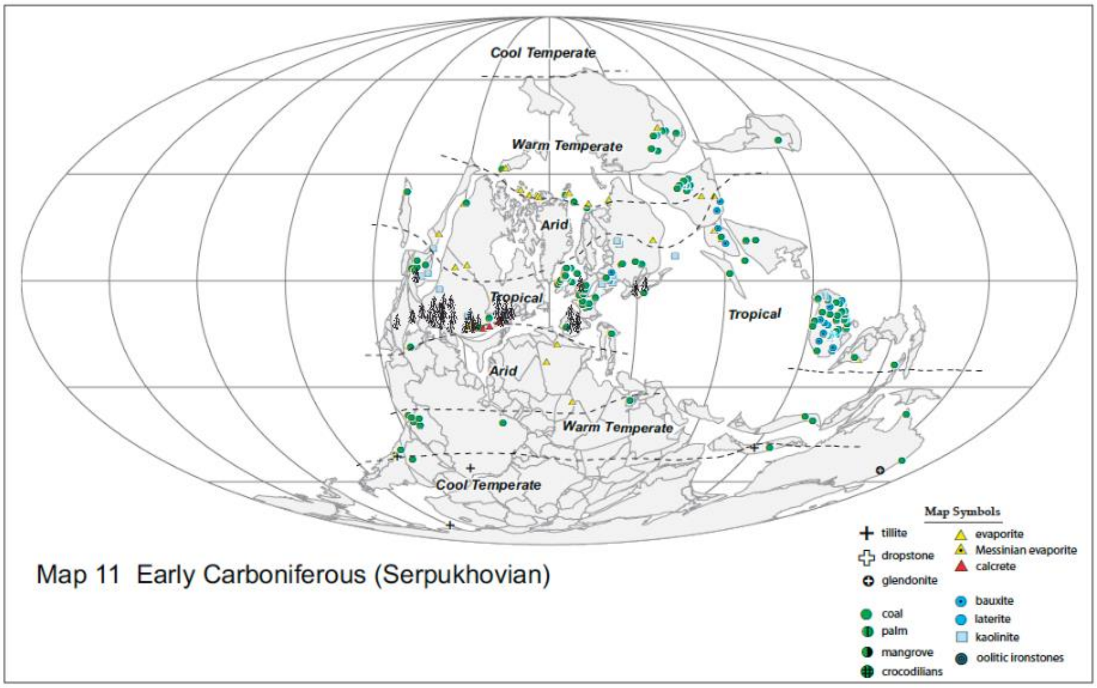

Figure 11. The locations for Medullosales are plotted, the black fern leaves, on the paleoclimate map for the early Carboniferous

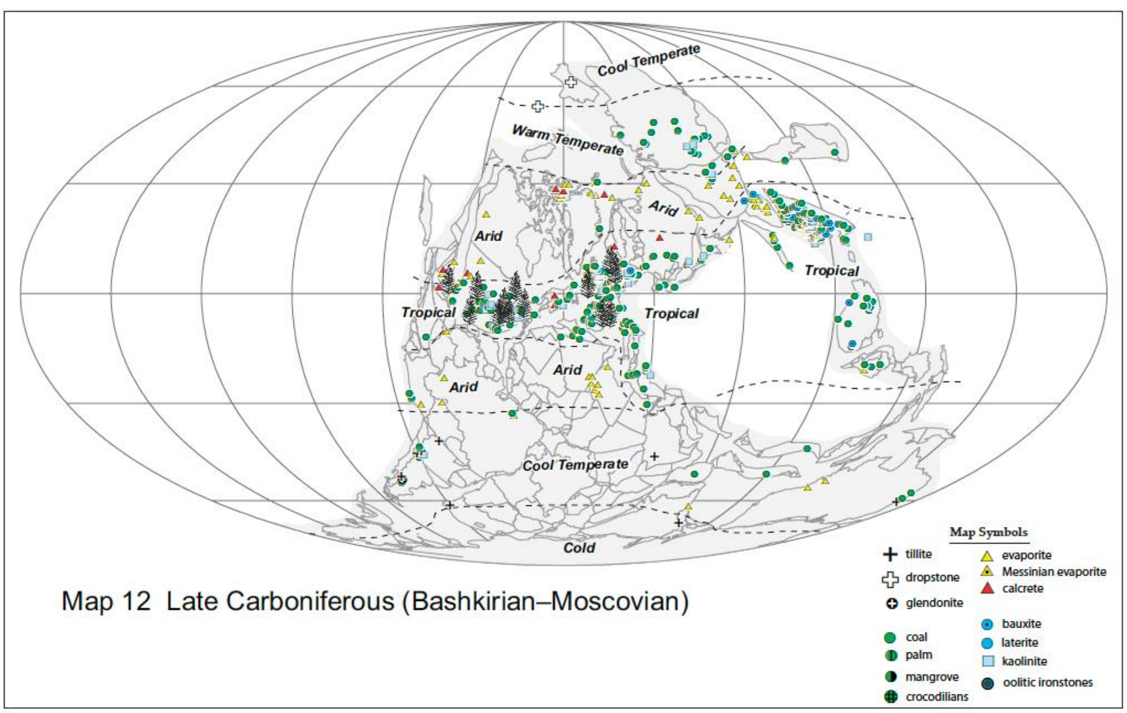

Figure 12. The locations for Medullosales are plotted, the black fern leaves, on the paleoclimate map for the late Carboniferous

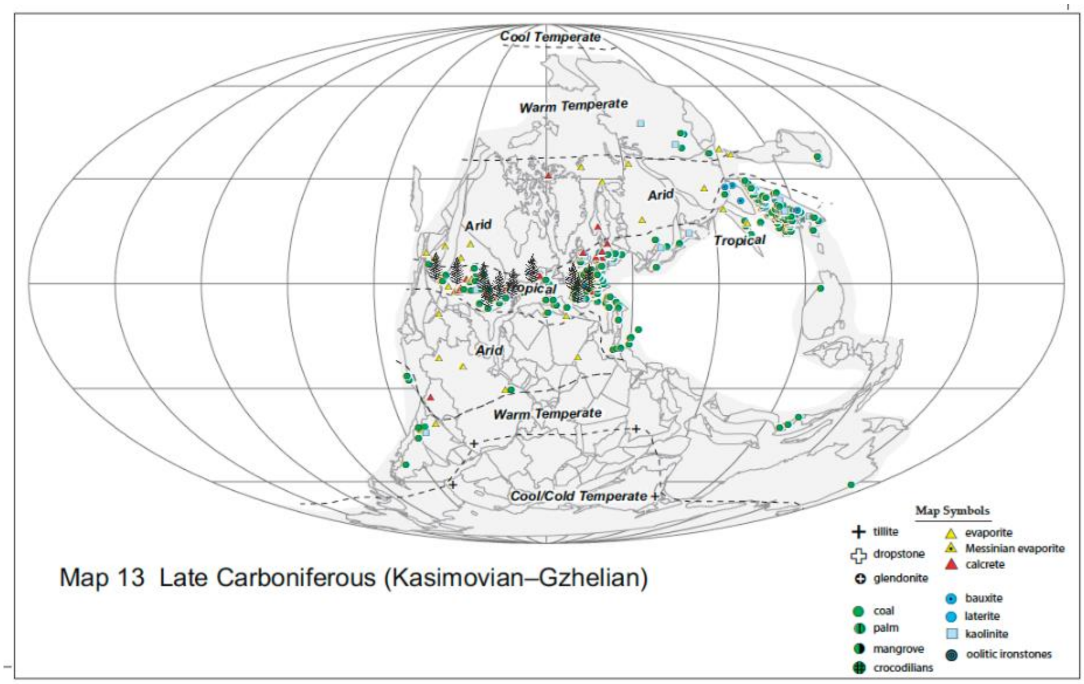

Figure 13. The locations for Medullosales are plotted, the black fern leaves, on the paleoclimate map for the late Carboniferous

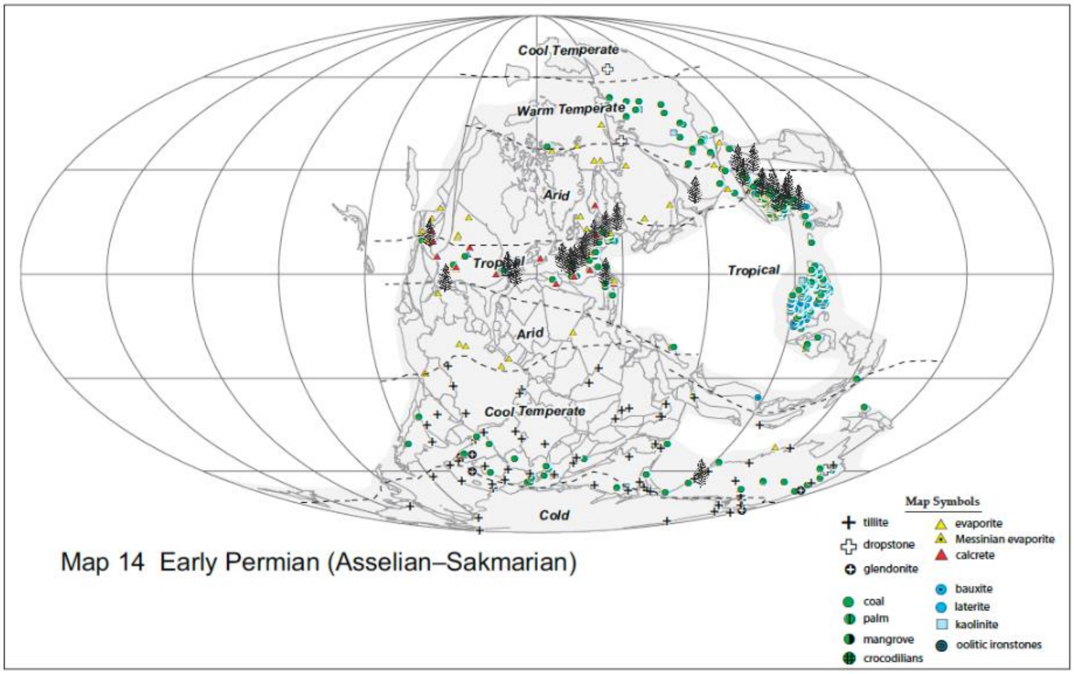

Figure 14. The locations for Medullosales are plotted, the black fern leaves, on the paleoclimate map for the early Permian

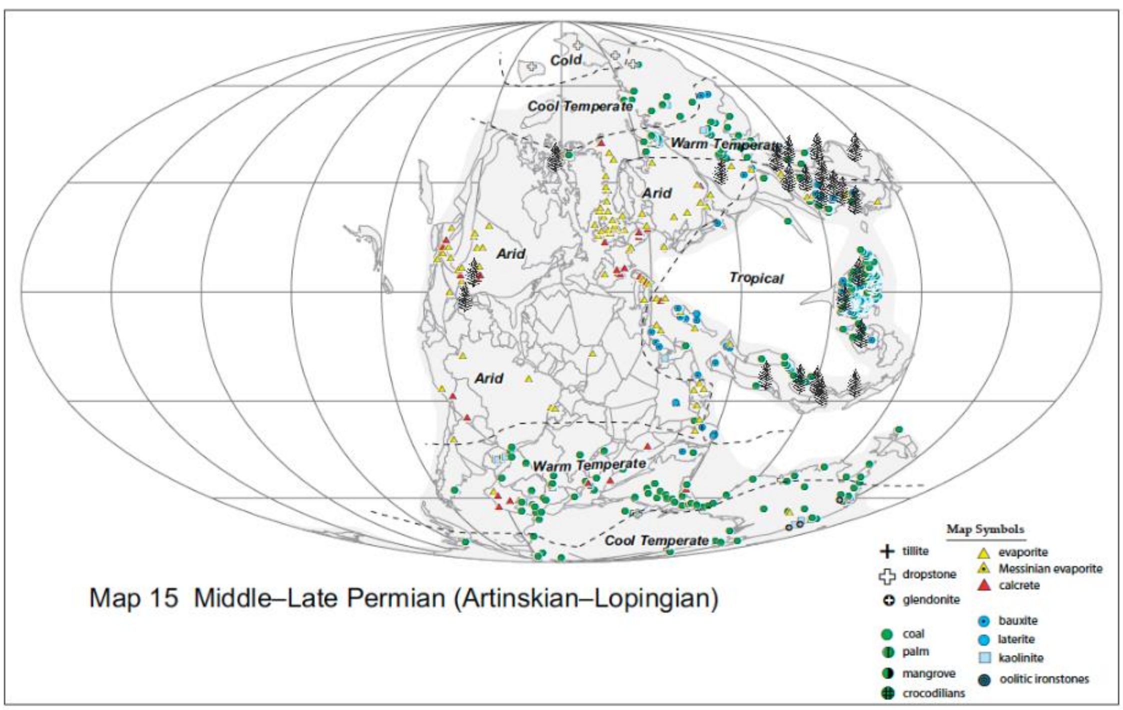

Figure 15. The locations for Medullosales are plotted, the black fern leaves, on the paleoclimate map for the middle to late Permian

Peltaspermales location mapped out on paleoclimate maps from first to last occurrence in PBDB

Figure 16. The locations for Peltaspermales are plotted, the black fern leaves, on the paleoclimate map for the

Figure 17. The locations for Peltaspermales are plotted, the black fern leaves, on the paleoclimate map for the

Figure 18. The locations for Peltaspermales are plotted, the black fern leaves, on the paleoclimate map for the

Figure 19. The locations for Peltaspermales are plotted, the black fern leaves, on the paleoclimate map for the

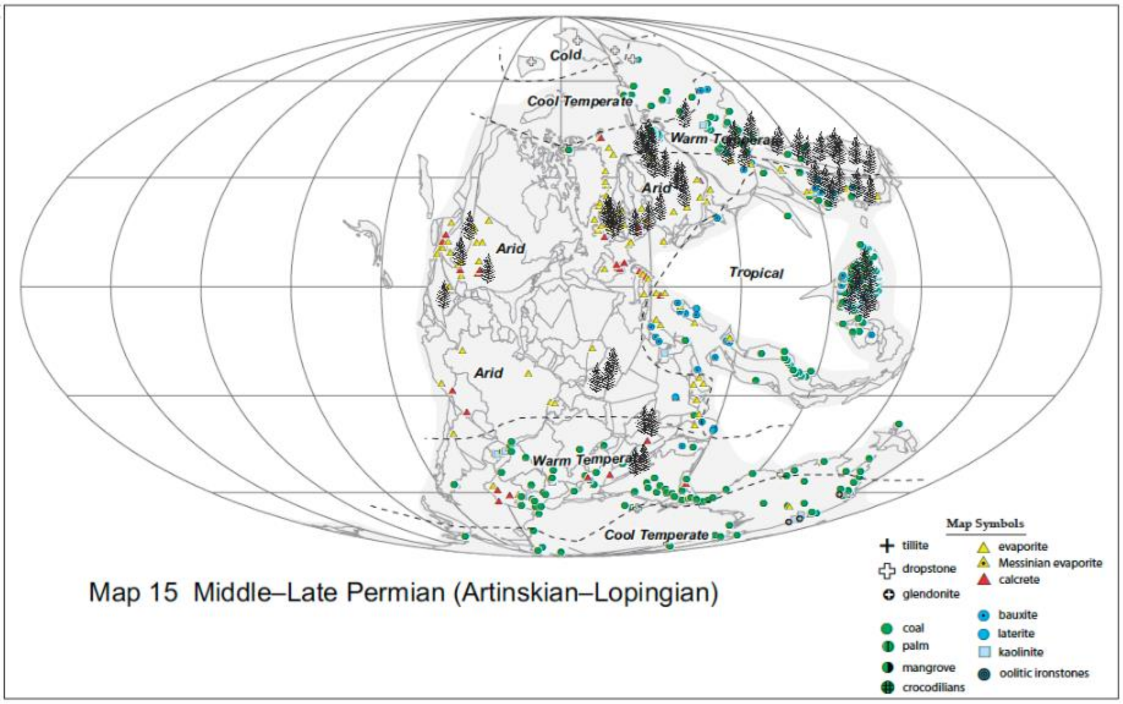

Figure 20. The locations for Peltaspermales are plotted, the black fern leaves, on the paleoclimate map for the middle to late Permian.

Results

As stated, to test the collected data the chi-squared test of association was used. The chi-squared test determines if there is a significant statistical association between two variables. Figure 21 below represents the results of the chi-squared test when testing pteridosperm clades against the Embryophyta group.

	Mississippian	Pennsylvanian	Permian (Asselian - Sakmarian)	Permian (Artinskian - Lopingian)
Callistophytales	Yes p <0.000001	Yes p <0.001	No p> 0.05	Yes p <0.02
Medullosales	Yes p <0.001	Yes p <0.02	Yes p <0.001	Yes p <0.000001
Peltaspermales	Yes p <0.002	Yes p <0.000001	Yes p <0.000001	Yes p <0.000001

Figure 21. The chi-squared results when comparing Embryophyta to clades.

When the chi-squared test is run between the total occurrences, $p < 0.05$ for all clades meaning that there is a statistical correlation between the variables The pattern for pteridosperms and their locations is distinctly different from Embryophyta, and plants overall. Testing the relationship between the pteridosperm clades and Embryophyta for the climate types gives us the result that the locations of the pteridosperm clades in each climate type is statistically different than what would be expected by the Embryophta group, the control group. This statical correlation can be used to infer that there is a relationship between the two variables.

	Mississippian	Pennsylvanian	Permian (Asselian - Sakmarian)	Permian (Artinskian - Lopingian)
Callistophytales vs Medullosales	No p > 0.05	Yes p < 3.11*10^-6	No p > 0.05	Yes p <0.000001
Callistophytales vs Peltaspermales	No p > 0.05	No p > 0.05	No p > 0.05	Yes p <0.000001
Medullosales vs Peltaspermales	No p > 0.05	Yes p <0.000001	Yes p < 7.49*10^-5	Yes p <0.000001

Figure 21. Chi-squared results comparing the clades against each other.

When the chi-squared test is run between the clades the p value results vary. Half of the results came back with no statistical correlations while the other half said yes, there is a statistical correlation. Based on the results the clade with the largest correlation or dependence would be Medullosales. When compared with Callistophytales and Peltaspermales there is almost always a statistical correlation, besides in the Mississippian. The only agreeable test results here are at the end of the Permian, nearing the Permian/Triassic extinction. Based on the results of the chi-squared test between the clades it can be inferred that the locations of Medullosales was dependent on the other clades, Callistophytales and Peltaspermales especially during the Permian. With the knowledge of this relationship statistically creates the opportunity to explore the relationship in an environmental way. The environmental way being comparing the pteridosperm clade locations with what was happening environmentally and with the climate during different times in the Paleozoic. Of the relationship between the clades and the environment was only statical it could be inferred that their change in location and climate is only based in adaptation and ecology. From the data seen in the maps and the results seen by the chi-squared test it seems that their relationship is both environmental and statistical.

Conclusion

The main purpose of this research was to characterize the environmental tolerance of pteridosperm clades. There is much to discuss when analyzing the data involving these extinct seed ferns Do pteridosperm clades share a preferred environment? Yes, it seems they do. All the pteridosperm clades have a preferred environment of tropical or warm temperatures. This preference is also seen in the Embryophyta group. After the tropical and warm environments, the arid climate is the next dominant climate. Then cool and cold climate types. Only one pteridosperm clade was found in cold temperatures and that was Callistophytales at the end of the Permian. The patterns in the data revealed more questions to be answered. Is there a drastic or gradual change in the preferred climate type if there is a preference at all? The change in preferred climate type varied within the pteridosperms. Medullosales and Callistophytales had a slow and minor change in climate type. They both stayed in the tropical climate for most of its existence until the Permian. In the Permian some Medullosales and Callistophytales plants shifted into arid environments. This could be due to the increase in temperatures that caused the Permian-Triassic extinction. It is possible that the tropical climates were getting too warm for Medullosales to thrive in. Peltaspermales on the other hand had a drastic change in climate type. As well as a drastic increase in occurrence data. Along with the main purpose, the main problem looking to be solved was if the environmental changes pteridosperms went through had any effect on their distribution over time, regarding the occurrence and climate type at occurrence locations Based on the results it seems that the Paleozoic ice age did not impact the location or environment that pteridosperm clades were found in. During the Paleozoic ice age, the number of occurrences of the clades did not vary much and neither did their climate locations. All the clades moved to stay in tropical climates. Leading up to the Permian-Triassic extinction the results show a change in the number of occurrences. For Callistophytales and Medullosales their occurrence numbers decreased. And for both the climates their fossils were located in changed slightly. The Peltaspermales clade increased in occurrence and increased in their distribution of climate types. Based on these results it seems that the Permian-Triassic extinction affected Callistophytales and Medullosales the most. This could be for a variety of reasons. As mentioned, the temperature increase in the tropical regions was too much for them to handle. With Peltaspermales developing later than the other two clades it could have been ready to change and adapt to a new location and climate setting because it was younger and newer. It is also possible that Callistophytales and Medullosales decreased in numbers during the Permian due to the increase of other plant species. Callistophytales and Medullosales have a few occurrences in other climate types like arid and cool which could be their attempt to survive in other climates where other plant species were not as dominant. The research done in this study is just the beginning of studying the relationships between pteridosperms and the climates they are found in. Based on the results it can be inferred that some of the environmental changes happening during the Paleozoic played a role in their distribution and the climate they were living in. It seems that the Permian-Triassic extinction had a larger effect on Pteridosperms than the end of the Devonian extinction or the Paleozoic ice age.

Discussion

Learning about pteridosperms' relationship to the environment by proxy helps us learn more about the Earth's past climate, past evolutionary choices, and more about the relationship pteridosperms and all plants have with the Earth. It can also help us determine and hypothesize what could happen in the future as we are reaching similar conditions like the Permian-Triassic extinction where the Earth's temperature is rising. The research that has been done in this study is a good starting point in exploring all these relationships. By disproving the null hypothesis, it creates the opportunity to study these statistical and environmental relationships more. Knowing there is both a statical and an environmental correlation between the pteridosperm clades and the climate types their found in opens the door for more research. Future research could explore what happens to pteridosperms like Peltaspermales after the Permian-Triassic extinction. As well as do other flora in the Paleozoic like Cycads or Lycopods have a similar tolerance and relationships like the pteridosperms do with their environment? As for right now this study has told us that the locations of pteridosperms were mildly affected by the environmental changes happening during the Paleozoic.

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