2021

Diversification of Angiosperms During the Cretaceous Period

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Disclaimer: The following thesis was produced in the Environmental Studies Program as a student senior capstone project.

DIVERSIFICATION OF ANGIOSPERMS DURING THE CRETACEOUS PERIOD

by

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AN UNDERGRADUATE THESIS

Presented to

The Environmental Studies program at the University of Nebraska-Lincoln

In Partial Fulfilment of Requirements

For the Degree of Bachelor of Science

Major: Environmental Studies

With the Emphasis in Biology

Under the Supervision of Dr. David Gosselin and Dr. Christian Elowsky

Lincoln, Nebraska

May 2021

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University of Nebraska, 2021

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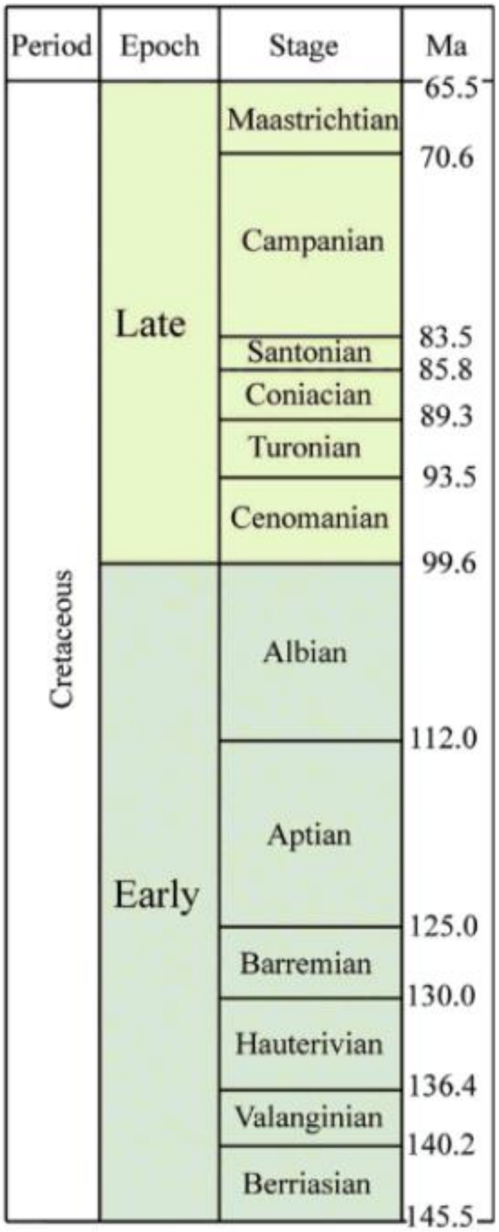
ABSTRACT

The topic of the Angiosperms relatively sudden appearance and diversification is a topic that has puzzled plenty of biologists and is even referred to as an "abominable mystery" by Charles Darwin. Up to date, many hypotheses have been proposed using various forms of data to form them. The available knowledge used to evaluate this topic has changed over the years, which has created some theme shifts. Some of the best supported of these hypotheses are more recent, but this does not make older articles unworthy of being evaluated, as they still often have relevant information. In the past, their appearance was part of the mystery with theories of their origins as abundant as the theories for their success. This study will search for which sort of factors were most likely to have contributed towards angiosperm general success. The objective of this study is to review the evidence supporting the many prevalent theories on causes for the success of angiosperms. To do this, multiple peer-reviewed articles surrounding the topic will be examined, making a note of which ones are backed up by the most complete data and applications towards the history and evolution of the angiosperms. Some of these factors are most commonly theorized to have been environmental, interactions with other species, or the unique adaptations and traits of the plants themselves.

Introduction

The angiosperms, commonly referred to as the flowering plants, make up the majority of land plant life on earth and play crucial roles in terrestrial ecosystems. As the dominant plant taxon, angiosperms are placed second only to insects in terms of species richness. (Oliver, K. R., (2013). Despite their importance, there remains mystery shrouding their existence. An incomplete fossil record does not offer an undisputed answer to their origins, their seemingly rapid diversification, or even their exact age as a taxon. Before angiosperms establishment as the dominant taxon, the gymnosperms and other non-flowering plants were the most common and successful plant phyla on earth. Angiosperms appeared suddenly during a relatively warm period in earth's history, diversified rapidly, and ultimately became a dominant form of plant life.

The Cretaceous period began 145.5 million years ago, where the earliest flowering plant fossils are currently dated back to. The earliest signs of flowering plants in the fossil record are rare and occur as pollen grains dated to the Valenginian, which is described as an age near the beginning of the Cretaceous. The occurrences of flowering plants rapidly increased during the Albian age, which can be described as the middle of the Cretaceous period. It is estimated that about half of the angiosperm or flowering plant orders existing today were present 72-66 Mya during the Maastrichtian, which is the time towards the end of the Cretaceous as Fig.1. shows. During the Maastrichtian, angiosperms represented 70% of terrestrial plant species. Gymnosperms, which appeared 350 million years ago, had comparatively been much less successful. Fossil evidence shows that their dispersal across earth began to dwindle as angiosperms spread, as seen in Fig.2.



Period	Epoch	Stage	Ma
Cretaceous	Late	Maastrichtian	65.5
		Campanian	70.6
		Santonian	83.5
		Coniacian	85.8
		Turonian	89.3
		Cenomanian	93.5
	Early	Albian	99.6
		Aptian	112.0
		Barremian	125.0
		Hauterivian	130.0
		Valanginian	136.4
		Berriasian	140.2
			145.5

Fig.1. Cretaceous timeline. (Friis et al. 2011).

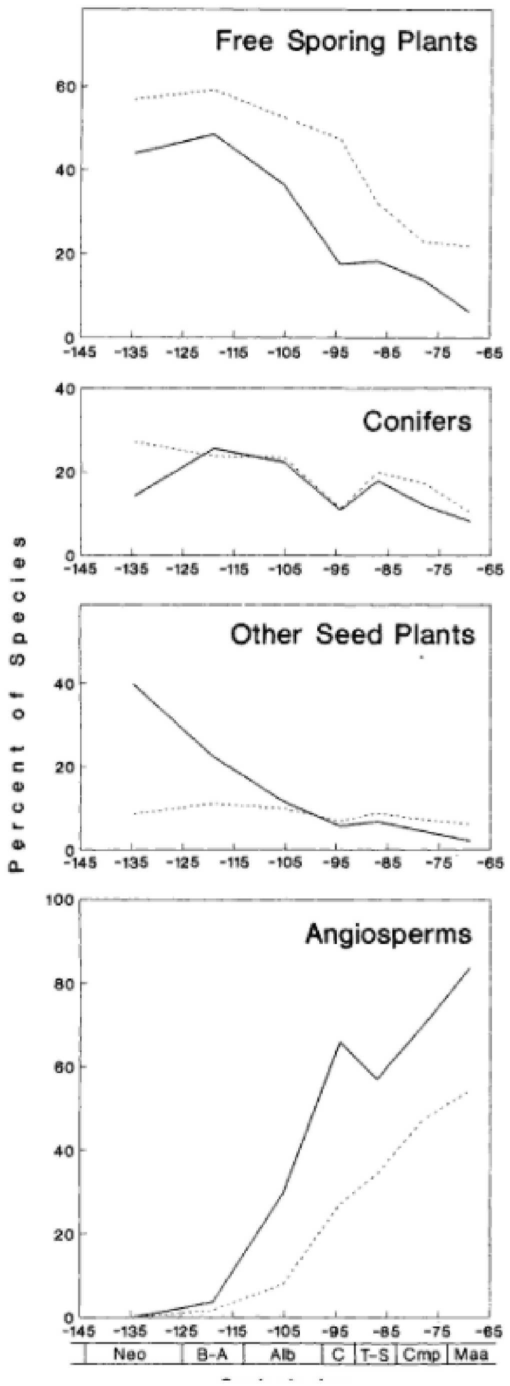


Fig.2. Angiosperm's dispersal rates compared to other plant groups. (Lidgard, S., & Crane, P. 1990).

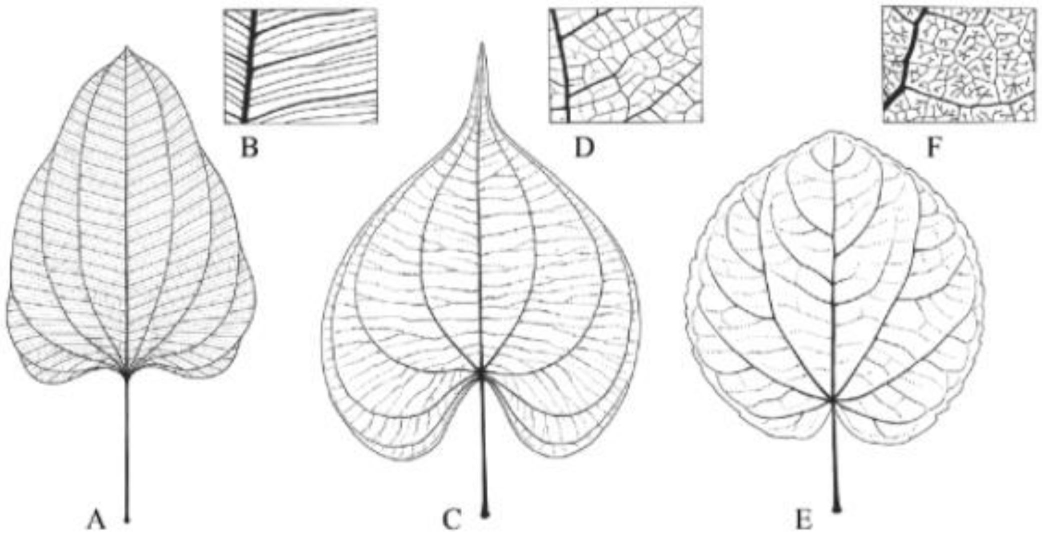


Figure 1.7 Leaves in angiosperms. (A, B) Leaf (A) and detail of venation (B) in *Stemona cochinchinensis* (Stemonaceae, monocot). (C, D) Leaf (C) and detail of venation (D) in *Dioscorea hemsleyi* (Dioscoreaceae, monocot). (E, F) Leaf (E) and detail of venation (F) in *Cercidiphyllum japonicum* (Cercidiphyllaceae, eudicot). Based on herbarium specimens in the Swedish Museum of Natural History.

Fig.3. Leaf venation in angiosperms (Friis, 2011).

Today, there are major differences between gymnosperms and angiosperms. The most noticeable of the differences are that Angiosperms have net leaf venation that is absent in most gymnosperms. Angiosperms can be further divided into subgroups; one of the defining features of these separate groups is once again leaf venation. Monocots have parallel veins, while eudicots have netted venation, as seen in Fig.3. Dicots have venation that is neither parallel nor netted but rather something in-between. Other features include adaptations such as vessels which are structures that comparatively allow more efficient uptake of water and aid in faster growth compared to non-flowering plants. Angiosperms also have distinctive reproduction features such as carpels, flowers, and double fertilization, which set them apart from non-flowering plants.

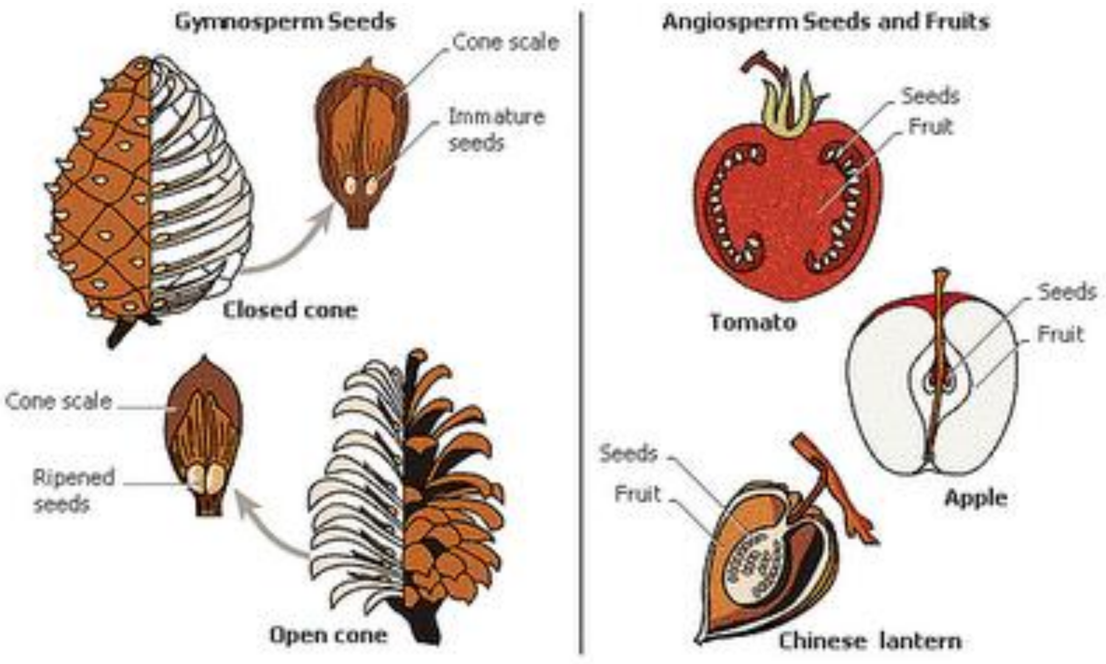
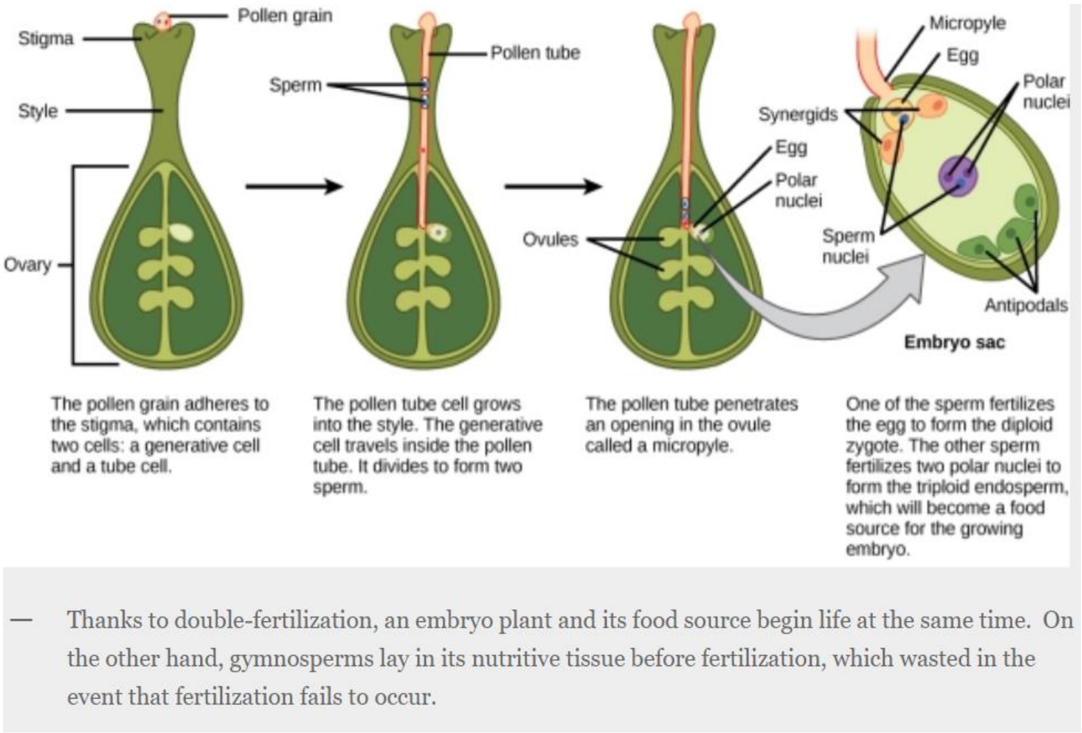


Fig .4. Example of gymnosperm and angiosperm seed holding methods. "(Amborella and the 'Abominable Mystery." 2013)



The pollen grain adheres to the stigma, which contains two cells: a generative cell and a tube cell.

The pollen tube cell grows into the style. The generative cell travels inside the pollen tube. It divides to form two sperm.

The pollen tube penetrates an opening in the ovule called a micropyle.

One of the sperm fertilizes the egg to form the diploid zygote. The other sperm fertilizes two polar nuclei to form the triploid endosperm, which will become a food source for the growing embryo.

> — Thanks to double-fertilization, an embryo plant and its food source begin life at the same time. On the other hand, gymnosperms lay in its nutritive tissue before fertilization, which wasted in the event that fertilization fails to occur.

Fig.5. Example of double-fertilization in angiosperms (Amborella and the 'Abominable Mystery. 2013)

It is worth noting that some distinct members of the gymnosperm order also have a few of the mentioned features which define angiosperms. Fossil records suggest that many similar plants once existed and formed various groups, but most of these groups have since gone extinct, leaving few members remaining. The gnetophytes are one of these groups and have been studied as being a possible answer to the angiosperm’s origins as links between gymnosperms to angiosperms. *Welwitschia* is a member of the gnetophytes and shares similar features with angiosperms, such as insect pollination and vessels.

a, Female. **b**, Close-up of male cone, showing pollen organs and pollination droplet in between them. **c**, Male cones. pd, pollination droplet.

Fig.6. *Welwitschia* cones. (Frohlich, 2007).

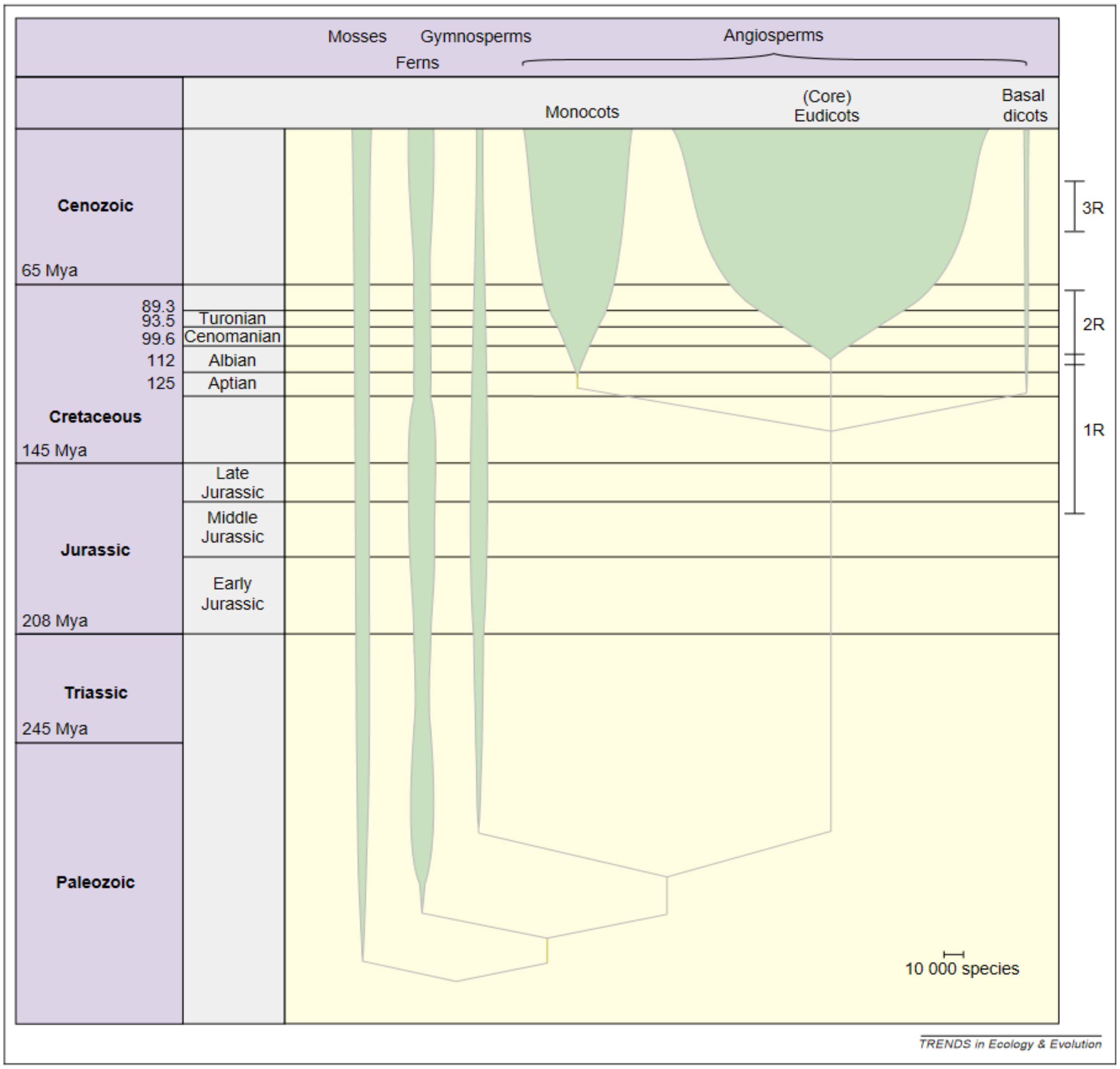


Fig.7. History of plant group occurrences based on fossil evidence. (De Bodt, et al. 2005).

Fossils give a glimpse to the past and can reveal the spread of a species across the planet or exhibit the increasing biological complexity in both plants and animals since the beginning of life on earth. Fig.7. is based on fossil data and displays the occurrence of angiosperms compared to gymnosperms, ferns, and mosses. The chart displays the subdivision of angiosperms into monocots, eudicots, and dicots, as mentioned earlier. The gymnosperms and other flowering plants are shown as much less diverse despite having existed for a comparatively much longer time. A glimpse into the past can also be utilized in revealing what the future could bring. In terms of plants, understanding what their past environment was like in relation to their success can give us clues to what will happen when the earth returns or strays from these same conditions.

Fossil findings hold many answers but are often missing important pieces. The ability to infer the presence of the angiosperm crown-group from incomplete fossil evidence is fundamental to discussions of the age of angiosperms as the fossil record mainly comprises only fragments of extinct plants. (Herendeen, et al. 2017). A dependency on fossil records can create difficulties in piecing together the evolutionary history of plants the same way it does for animals, and some defining features are left unpreserved. Morphological features of flowers or pollen grains are most likely to be left intact, whereas other parts are very unlikely to be preserved (Herendeen, et al. 2017). Even if something is preserved, it may remain undiscovered or incorrectly identified. Along with incomplete knowledge on morphological evolution, the incomplete and various states of preservation quality have led to difficulties in assessment and the existence of many fossils of uncertain taxonomic placement or '*incertae sedis*', (Silvestro et al. 2015). Furthermore, as mentioned previously, some gymnosperms share similar morphological or reproductive features as angiosperms. This allows a high possibility of early fossils being categorized incorrectly.

Fig.8. Example of an angiosperm fossil (Friis, et al. 2011).

Fig.9. Example of an angiosperm fossil (Friis, et al. 2011).

There are many factors influencing the study of angiosperms during the Cretaceous aside from incomplete fossil records. Multiple aspects of pre-historic life are suspected to have influenced angiosperms, selective pressures, and ecological interactions that we may not be able to determine the presence or lack of this leaves some of the ecophysiology and environmental interactions that energized the early angiosperm radiation remain unresolved. Diagnosing the selective pressures and habitat contexts responsible for the evolution of fundamental angiosperm features, such as flowers, rapid growth, xylem vessels, and net-veined leaves, becomes difficult (Feild et al. 2007). The study of plants and angiosperms, in general, is important for multiple reasons. Some of them are based on human benefits. Nature is a master craftsman of molecules, creating almost inexhaustible array of molecular entities (Veeresham, C. 2012.) Plants have played a large role in human health, history, and culture in terms of their medicinal uses. For thousands of years, plants were directly utilized to serve as remedies for varying ailments and diseases and still are in many parts of the world. The contribution of plants to disease treatment and prevention is still enormous despite our ability to create synthetic drugs. Today, about 11% of the 252 drugs considered as basic and essential by the WHO were exclusive of flowering plant origin, and at least 70,000 plant species have been screened for their medicinal use (Veeresham, C. 2012.) An estimated 390,900 described plant species, with about 90% of them being angiosperms, highlights the idea that there is an unknown number of cures or uses that are contained within plant species. Almost all agricultural crops are angiosperms, major parts of our diet such as wheat, corn, rice, and all other fruits come from angiosperms. These plant species could continue diversifying or rapidly go extinct depending on earths conditions.

Outside of human uses, angiosperms play large roles in nearly every other aspect of life on earth as they provide many ecological services. Clearly, they have gained an adaptational advantage which allowed their rapid spread and success. Understanding what factor led to this success is crucial to understanding what will happen when that same factor changes. A deeper understanding may also allow us to better address climate changes and even reverse the damage that has already been made. Major environmental changes such as global temperature change or C02 level changes are directly linked to angiosperms, as are the lives of various animal species that have coevolved with angiosperms and depend on them. Any environmental changes can bring unknown and possibly detrimental results. This makes the topic very much worth understanding. While the issues of climate change and the mystery of angiosperms have been around for a little over 100 years, they are both gaining more attention as they become more important, and new methods and tools are being developed to help address them.

Materials and Methods

The following systematic steps were used to assess the literature:

1. Search for relevant literature based on keywords.
2. Describing the selected papers and identifying their conclusions.
3. Reject papers.
4. Further analysis of remaining papers
5. Provide summaries of each theme.
6. Highlight strengths and weaknesses within the themes and literature.

Literature search:

For this literature review, 24 papers written on the topic of angiosperms appearance and diversification during the Cretaceous period have been selected to ensure the likely representation of the most research done on the topic. The literature selected can be based on varying methods, including fossils, molecular, or assessments of past research. The first step was to search for literature. This was done by identifying relevant keywords. To find these keywords I searched “Angiosperm’s diversification during Cretaceous” and various other rewordings of the topic. I took note of the re-occurring themes and used them to search for more relevant papers. The keywords I ended up with included:

- Angiosperms/flowering plants
- Cretaceous
- Evolution
- Diversification
- Interactions
- Innovation/adaptations
- Paleobotany
- Phylogeny

Once I had collected a wide variety of papers on the topic, I searched through the abstract to ensure that they contained information and ideas on angiosperm that met the selection requirements.

Literature selection:

To ensure that the literature I selected was most likely to represent reasonable ideas and research, I set selection requirements. Papers that do not meet the requirements are rejected; these requirements included that:

- The paper must be peer-reviewed.

- The paper must come to some sort of conclusion or theory as an answer to the question of the success/spread, evolution, or rapid diversification of angiosperms during the Cretaceous.

- The paper must be within context.

Literature analysis:

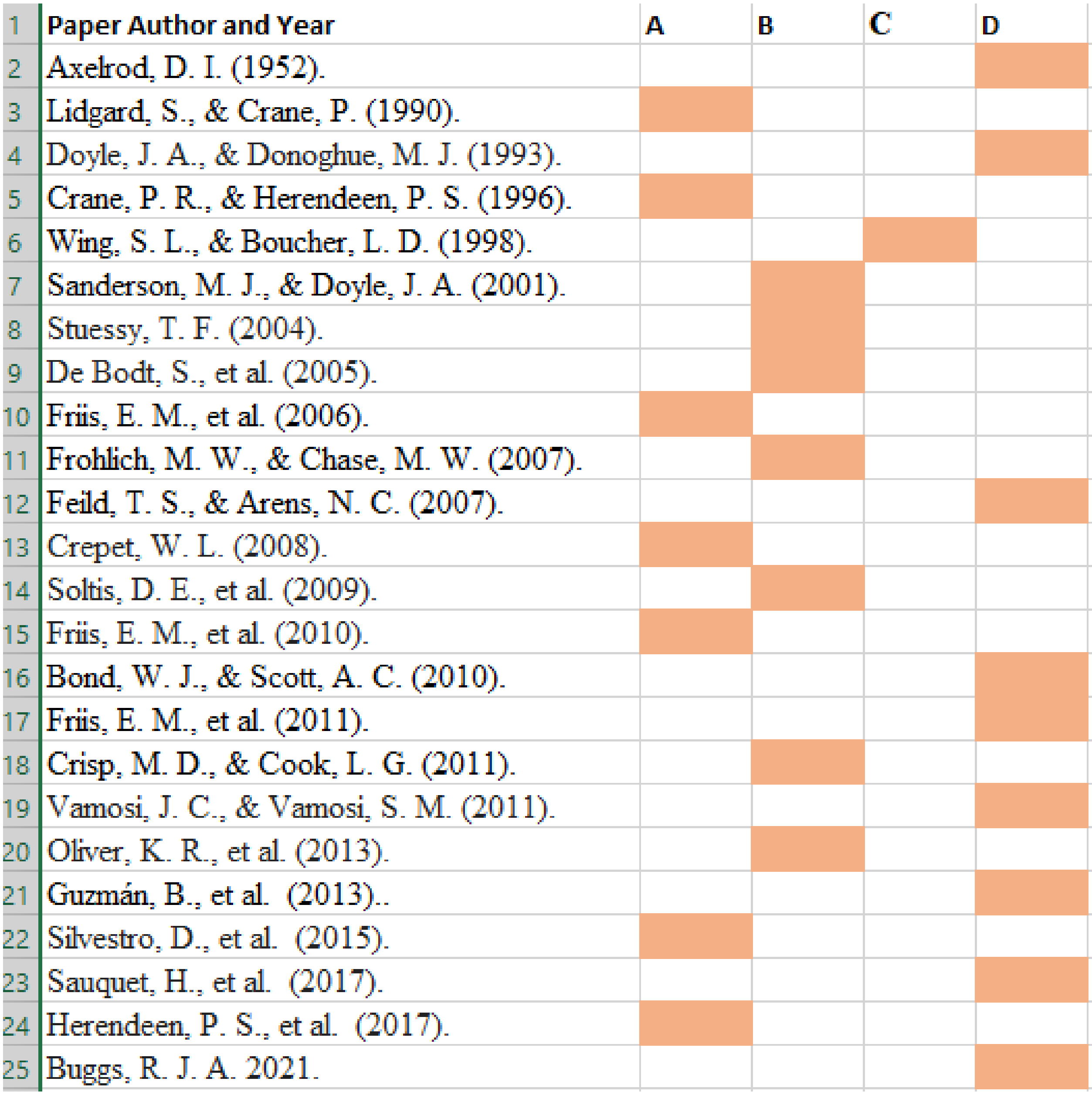
I will take a sample of papers from both current findings and from past findings in relation to the evolutionary history of angiosperms during the Cretaceous. I will define past as papers written before the year (1990), and I will define current as papers written after that, then look for trends in methodology and results based on the year of publication. While looking for trends, I will take note of themes, and once themes are identified, I will find strengths as well as weak points within each theme, such as:

- Is the information outdated or not?
- Is the paper conclusive?
- Whether or not methodology is reliable
- Theories that are still backed by modern findings/discoveries.

Results

A considerable amount of research has been done on the topic of angiosperm evolution during the time of the Cretaceous. There is no shortage of possibilities to be explored in relation to the topic. The research will be centered around what can be grouped into categories. These categories are based on the reviewed papers' most common methods used. Category A is for papers that utilize Fossil data and nothing else. Group B is for papers that utilize DNA evidence alone or paired with fossil data. Group C is for papers that utilize inferred data such as paleoecology or geology, alone or paired with fossil data. Group D is for papers that utilize a combination of the groups.

- Fossil evidence only. Group A
- DNA evidence. Group B
- Inferred data from other sources. Group C
- Multiple datasets. Group D



1	Paper Author and Year	A	B	C	D
2	Axelrod, D. I. (1952).				🟧
3	Lidgard, S., & Crane, P. (1990).	🟧			
4	Doyle, J. A., & Donoghue, M. J. (1993).				🟧
5	Crane, P. R., & Herendeen, P. S. (1996).	🟧			
6	Wing, S. L., & Boucher, L. D. (1998).			🟧	
7	Sanderson, M. J., & Doyle, J. A. (2001).		🟧		
8	Stuessy, T. F. (2004).		🟧		
9	De Bodt, S., et al. (2005).		🟧		
10	Friis, E. M., et al. (2006).	🟧			
11	Frohlich, M. W., & Chase, M. W. (2007).		🟧		
12	Feild, T. S., & Arens, N. C. (2007).				🟧
13	Crepet, W. L. (2008).	🟧			
14	Soltis, D. E., et al. (2009).		🟧		
15	Friis, E. M., et al. (2010).	🟧			
16	Bond, W. J., & Scott, A. C. (2010).				🟧
17	Friis, E. M., et al. (2011).				🟧
18	Crisp, M. D., & Cook, L. G. (2011).		🟧		
19	Vamosi, J. C., & Vamosi, S. M. (2011).				🟧
20	Oliver, K. R., et al. (2013).		🟧		
21	Guzmán, B., et al. (2013)..				🟧
22	Silvestro, D., et al. (2015).	🟧			
23	Sauquet, H., et al. (2017).				🟧
24	Herendeen, P. S., et al. (2017).	🟧			
25	Buggs, R. J. A. 2021.				🟧

Fig.10. Selected papers organized with author and year, grouped into themes.

Sampled papers were grouped into categories based on the data and methods. Reviews of functional morphology and ecological roles such as Flowers and Pollen—Inferences on Reproduction, Seeds and Fruits—Inferences on Dispersal and Establishment, Wood—Inferences on Size and Growth Rate and Leaves—Inferences on Growth Form and Phenology, (Wing et al. 1998) as well as molecular phylogenetic and DNA sequenced data are common in current studies. The sole reliance of fossils is rare and is likely more common in papers at dates later than what was sampled. Research on intrinsic traits has brought researchers to have varying but similar conclusions.

Some of these conclusions ultimately point towards angiosperms possession of genes that promote diversity, such as the occurrence of polyploidy which is the multiplication of a genome. Polyploidy is considered a significant evolutionary force for angiosperms as it affects gene expression and creates morphological variation. (Soltis et al., 2009).

Another notable genomic occurrence is transposable elements which are present in most angiosperms. Transposable elements (TEs) are fragments of DNA that can insert into new chromosomal locations and make duplicate copies of themselves. Evidence is accumulating that suggests plant genomes are remarkably dynamic, largely due to the activity of TEs. (Feschotte, C., Jiang, N., & Wessler, S. R. 2002). Thanks to these innovations, it was likely that angiosperms could quickly adapt to new environments and create the great amount of diversity which they are known for. This was probably beneficial and likely played a role in gymnosperms experiencing extinction events while angiosperms spread rapidly. Along with TE’s or polyploidy, it is suspected that many ancestral angiosperms were likely “weedy” plants whose growth habits, such as quick growth and short life cycles, allowing for a rapid succession of areas that would take gymnosperms and other lower plants much longer.

Aside from the growth and reproductive capabilities of angiosperms, some theories have been made based on the climate during the Cretaceous, which has been studied as a possible influencer of angiosperm success. These papers were based on geological and fossil data. It is thought that the high levels of CO_2 caused by volcanic activity during the time may have played a large role as it warmed the environment and created environments which were less suited for gymnosperms but allowed for angiosperms to overtake large areas of land. Other common theories include interactions with animals such as browsing patterns of Cretaceous herbivores or insects whose co-evolution with angiosperms have influenced flowering characteristics.

Despite the theories for angiosperm’s rapid evolution, it is not uncommon for research to point to the idea that angiosperms existed before the Cretaceous. The oldest article selected was written in 1952, A Theory of Angiosperm Evolution, presents a theory that was mostly unsupported at the time-but similar suggestions have appeared since then. The Upland theory being an unpopular one is mostly unique in its interpretation of fossil and geological data. This theory suggests that angiosperms existed at dates earlier than what fossil records reveal and that the reason for the lack of evidence for their existence at earlier dates is due to them inhabiting upland regions away from deposition sites, thus preventing their fossilization and later their discovery. The main idea of this theory is that pro-angiosperms were undergoing quantum evolution and existed in the Permo-Triassic time. (Axelrod, D. I. (1952).

Fig.11. below shows the proposed dates for the appearances of land plants beginning at psilopsida, which are also known as psilotophytes, along with lycopsida, which are known as Lycophytes. These two groups are some of the first plants with vasculature and true roots, which allows more efficient uptake of water and nutrients, all groups are further split into subgroups.

The last plants to appear are the Gymnospermae which are gymnosperms, and finally, the Angiospermae which are angiosperms. A thin line extends from this group to show the period where they may possibly have appeared, the Permian rather than the Cretaceous.

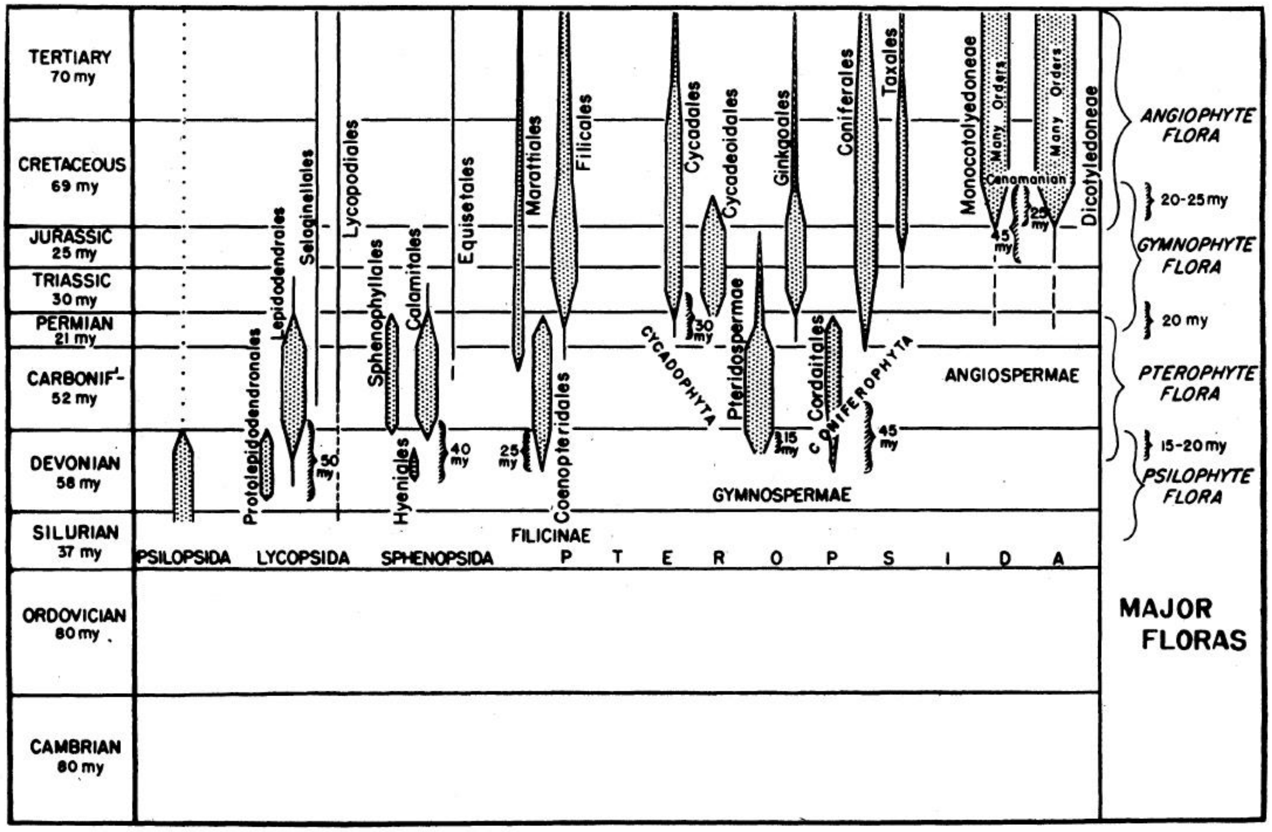


FIG. 12. Showing approximate time (in millions of years) for (*a*) replacement of World Floras (right column), and for (*b*) phyla of vascular plants to rise to dominance following first appearance in record.

Fig.11. Timeline of angiosperm appearance in the Permian-Triassic rather than Cretaceous. (Axelrod, D. I. (1952).

This theory suggests that angiosperms evolved slowly from seed ferns in the Jurassic, beginning first with the carpel, followed later by double fertilization, and lastly by the appearance of flowers. These three fundamental transitions may have taken more than 100 million years to complete.

Discussion

Very few articles sampled claim to know the origins of angiosperms despite the varying sources of data available. This would require more knowledge on how angiosperms are related to other seed plants, such as homologies among the reproductive structures of different plant groups. Currently, there is no clear consensus on the pattern of relationships among the varying groups of seed plants. Phylogenetic analyses of DNA sequence data from extant groups yield inconclusive results (Burleigh and Mathews, 2004) (Friis, E. M., et al. 2006). With this being known, it is understandable why the origins of angiosperms have remained more of a mystery while multiple and varying ideas on the cause of their success are available.

After reviewing the themes within the various papers, additional themes were identified: an intrinsic or extrinsic trait. Both categories have equally researched and promising ideas. Most research focuses on a combination of the two. As mentioned earlier, angiosperms have many defining traits that gymnosperms typically lack such as vessels, ovaries, flowers, and double fertilization. These can be referred to as intrinsic traits. There are also traits within an angiosperms environment that could offer an advantage such as CO_2 levels, global temperatures, damp or dry soil, and even animals. These can be defined as extrinsic traits.

Each article sampled offers an interpretation of available data to determine possible reasons for the success and spread of the flowering plants. Some of these interpretations were unique, while others were common and often repeated in other papers. Understandably, the sources, as well as the quality/and or quantity of available data to form these theories, have changed over time. New discoveries, observations, and techniques have been developed, which enable theories that are likely closer to the truth. For example, most papers written before 1990 rely heavily on fossil data alone which has presented many setbacks. Technology has offered help with organizing and analyzing data quickly, and more efficiently. A new program called PyRate is capable of handling fossil occurrence data and dealing with the inherent incompleteness of the fossil record. (Silvestro et al., 2014). Also, the study of DNA and genes has presented new sets of theories.

Trait	Mechanism	Putative correlated traits
Intrinsic traits		
Zygomorphy; biotic pollination	More specialized pollination leads to increased divergence	Hermaphroditism
Fleshy fruits; biotic dispersal	Increased dispersal results in reduced extinction or reductions in gene flow	Tropical environments, woody growth form
Herbaceousness	Fast life history/shorter generation time results in higher fixation rates in disparate populations	Dry fruit, temperate environments; geographical extent
Polyploidy	Sudden drop in gene flow with polyploidization events; increased temperature tolerance	Temperate environments, perenniality; geographical extent
Defense traits (latex canals)	Reduced herbivory leads to decreases in extinction	Tropical environments
Hermaphroditism, self-incompatibility	Less stochastic pollen receipt and seed dispersal; evolution of self-recognition leads to greater speciation rates	Temperate environments, herbaceousness, zygomorphy
Extrinsic traits		
Tropics	Older, more stable environments; Higher speciation rates with increased energy	Available area, time, smaller geographical extent, zygomorphy, self-incompatibility
Available area	Increased opportunities for allopatric speciation	Tropical environments
Geographic extent of constituent species	Reduced extinction rates	Tropical environments, herbaceousness
Time	Speciation occurs at a constant rate such that older lineages have more species	Tropical environments, geographic extent

Fig. 12. Common intrinsic and extrinsic traits, (Vamosi, et al. 2011).

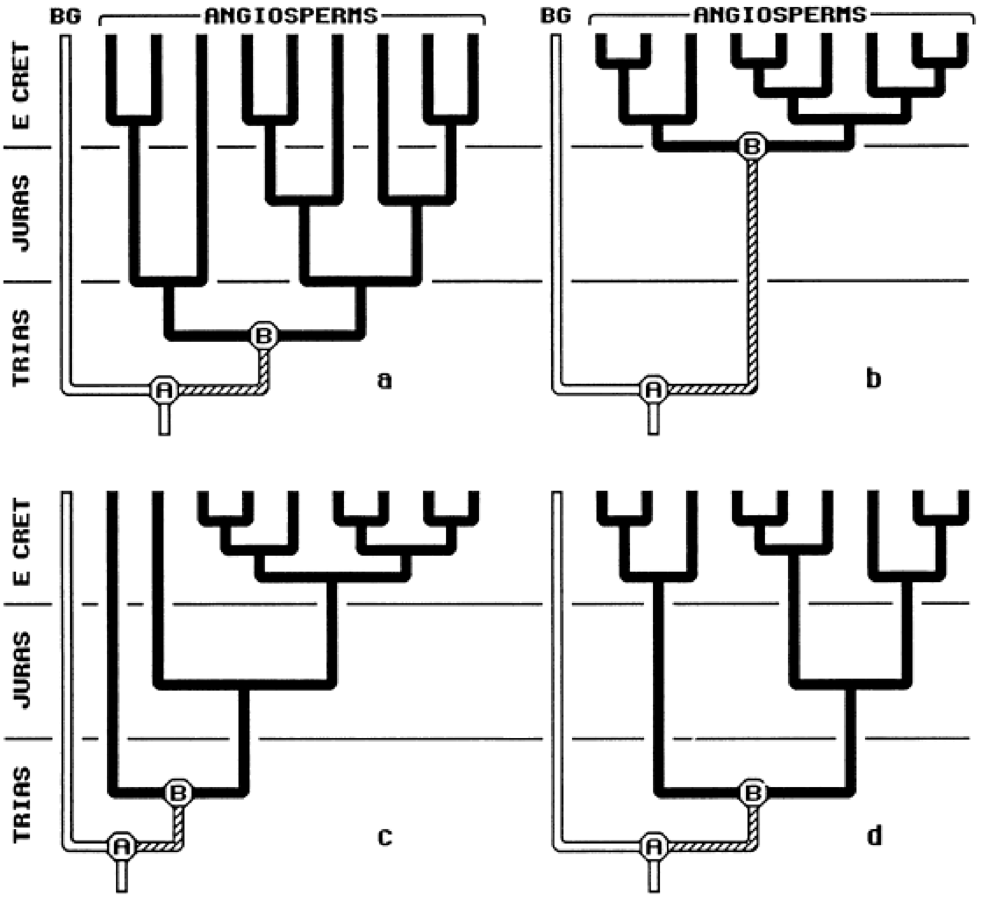


FIGURE 11. Four scenarios for the timing of angiosperm diversification. Scenario a corresponds to the view that angiosperms (the crown-group) originated and radiated extensively before the Cretaceous; b, that angiosperms originated not long before their observed radiation; c and d, that angiosperms originated in the Triassic but radiated in the Cretaceous, with magnolialian and paleoherb rootings, respectively. In c, pre-Cretaceous diversification might have been inhibited by intrinsic factors; in d, by extrinsic factors. BG, Bennettitales, *Pentoxylon*, and Gnetales.

Fig.13. Examples of alternatively proposed timelines for angiosperm occurrence.

The pro-angiosperms occupied regions where preservation was unlikely to happen. (Axelrod, D. I. (1952). This is one of few articles which suggest that angiosperms existed before the Cretaceous, which goes against the most widely accepted view. The time of angiosperms appearance is widely agreed upon but is sometimes questioned. The occurrence happening earlier would simplify the topic regarding their rapid spread across the earth. Today, no pre-Cretaceous fossils are known that unambiguously represent angiosperms (Herendeen et al., 2017; Corio et al., 2019;

Bateman, 2020; Buggs, R. J. A. 2021). Some pre-Cretaceous fossils have been found that share similar traits to angiosperms, but as discussed earlier, a few gymnosperms exist today that share similar traits to angiosperms, and it is likely that others existed before and during the Cretaceous.

Many papers written after 1990 have more knowledge to form theories, and an overarching commonality is a suggestion that angiosperms' success was mostly due to their own adaptations rather than environmental or interactions with other species. Multiple papers support theories of this type, and large amounts of data have been accumulated to help support it. Research done on intrinsic traits can be easier to be accepted as fact, partially because the evidence is visible. We have angiosperms fossils, and we have angiosperms available to study today. The study of fossils along with modern angiosperms has allowed the construction of phylogenetic trees, which are used to determine the relationship between species and their divergences, but it also is used to determine their relative ages. Although the angiosperms today are not the same as those which existed 350Mya, plenty of safe inferences can be made. While their intrinsic traits may not have been the only reason for their success during the Cretaceous, they seem to be the most likely.

Insects have been often said to have contributed largely to angiosperms success but there are also claims against it, such as the idea that insect populations decreased during the Cretaceous which makes it seem unlikely that they played as large a role as commonly thought. Along with this, some scientists will point out that angiosperms who do not use insects as pollinators or seed dispersers, such as grass that used wind, have been extremely successful. It is still difficult to dismiss the role of animals because of the clear influence over angiosperm evolution they have had, such as flowers and fruits which attract them.

Almost all past and current research on the origins of angiosperms is based on fossil records but with varying degrees of dependence. What was surprisingly common in the sampled articles was the recurring theme of molecular data to aid in research done with fossils or other data. Recently, DNA technology has provided varying but insightful results. rcbL analysis is an example of the various forms of molecular research done to help uncover angiosperm history. rcbL is used as a molecular clock and is used to determine the relative age of an organism. This has been extracted from a variety of existing plants to help create phylogenetic trees. Often molecular research has yielded results that conflict with inferences made from fossil data, including the age of angiosperms. The figure below is a phylogenetic tree created from rcbL analysis.

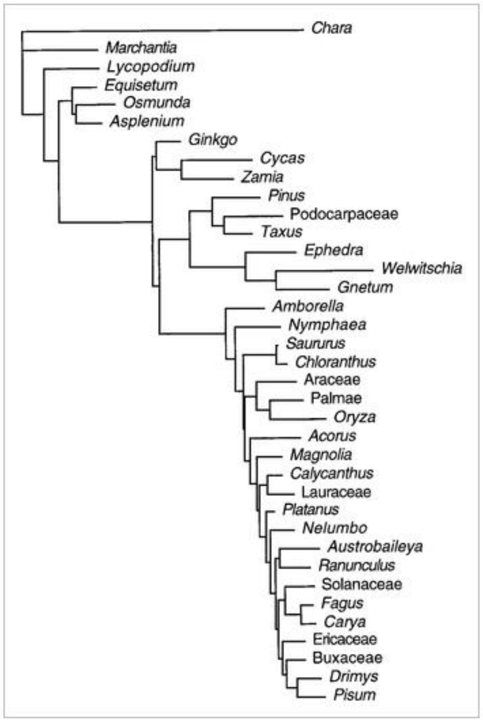


Fig.14. A phylogenetic tree made from molecular data. Sanderson, M.J. and Doyle, J.A. (2001).

While the technology is promising, it still has limitations. These limitations include the state of preservation that the tissue must be in to allow extraction of DNA. Multiple types of tissue preservation have proven to yield results, but those being preserved by desiccation or freezing are the most likely to hold recoverable DNA (Kistler L. 2012). Another limitation is the sample's age, which does not allow the likely extraction of Cretaceous samples. However, the literature supports preserved tissue as far back as the Holocene has successfully been extracted. Molecular research on angiosperms has helped piece together the history of angiosperms from the Cretaceous to the current period. DNA and other genetic studies may be the next step in uncovering unknowns from the past, which will ultimately help us predict the future of angiosperms.

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