

A case study on fossil plants (Exceptional preservation of plant fossils)

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Abstract

Whole-plant and incredibly precise anatomical details are the two types of exceptional preservation seen in plant fossils. Transport has a greater influence on whole-plant preservation than anatomical preservation does. Four taphonomic processes have been discussed in this review paper.

Key Words: Fossils, Fossilization, Plant Fossils.

Introduction

The term "exceptional plant preservation" means exactly what it sounds like.

Exceptional fossils are uncommon, and each one is distinctive in its own way. Shells and bones preserved in sediments are typically considered to be fossils.

However, many fossils preserve a great deal more than just these hard, mineralized portions, and we can even uncover fossils of totally soft-bodied species. Plants are configurable life forms that rapidly disarticulate into multiple organs (leaf, plant parts (including the trunks, roots, and root systems). Unlike in animals, disarticulation is a normal process that takes place life cycle of a plant (for instance, deciduous trees) leaf-out seasonally and morbidly) Spicer (1989) Human bodies, which are made up of Polysaccharides (including cellulose, hemicellulose, and lignin) and waxy polymers consisting of the cuticle, have a lower survival rate than animal bodies but are more likely to be preserved because of their smaller carrying capacity. The components of these plants enter the earth's crust in a manner strikingly different from that taken by terrestrial or marine creatures (Spicer & Farnsworth, 2021). There are a lot of marine invertebrates, but nearly none of them are ever kept since they propagate by spreading through the water column like plants do. But, on the other hand, Seeds and pollen are two examples of plant propagules that are particularly well- preserved, with a wide variety of species still present to a large extent all through the Phanerozoic. While it is often clear that groups of animals tend to congregate or flourish near water (e.g., species of calamitaleans and sigillarian lycopsids) during the Carboniferous and Permian; vegetation in the Cenozoic era), this is not always the case when discussing groups of plants As a result, at their core, the processes influence the fossilization of plants and the factors of animal-related ones

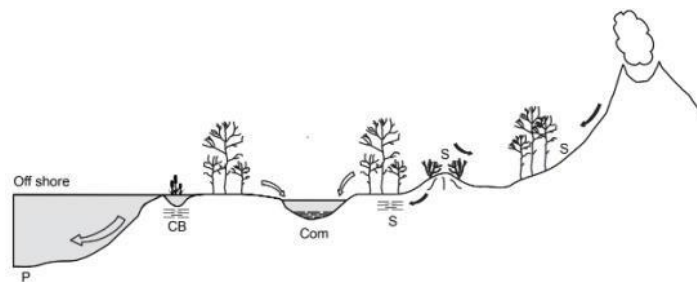


Figure 1: Cutaway view of a made-up landscape illustrating various depositional settings and

The two primary types of plant fossils that have been exceptionally well preserved are as follows: In some rare instances, the fossilized plant has preserved its original structure as well as the original arrangement of its numerous organs, which include everything from stem cells to sperm (Scott and Rex, 1985). It is only when many structures of the same type are found to be identical to how the plant was reconstructed *Archaeopteryx* (Beck, 1960) that these structures are given the same name. If organs are identified separately, they are given their own names (Beck, 1960a, b). Various transit methods, ash falls, and other unusual occurrences all play a role in the discovery of fossils like these (Ferguson, 2005). A second type of extraordinary fossil deposits is characterized by their internal organization and microscopic accuracy (Labandeira, 2021). Despite their rarity, if plants are preserved, paleontologists will have access to information that is truly taxonomically distinct (Smoot, 1984; Smoot and Taylor, 1986). It is pre- and post-burial care that determines how long remains will be preserved, decay, and diagenesis

Reason to look into

an exceptionally preserved plant fossil?

Fossilized remains of land plants have been discovered in the geological record as far back as the middle Ordovician.

Ordovician sea stones from all around the world have yielded an abundance of microfossils, including spores and cuticle fragments (Gensel 2008). According to the studies of a number of different writers, only a small number of these microfossils have been proposed to be taxonomically classified as belonging to the bryophytes (hornworts and liverworts) (e.g., Gray et al., 1985; Wellman et al., 2003).

Plant fossils are generally only retained as perceptions (no organics are left behind) or compressions (organics are still present) (Collinson, 2011); they portray a slope from remarkably well-preserved to poorly- preserved organic material. Stomata, trichome bases, and the arrangement of epidermal cells are all examples of surface features that can be preserved with or without organic remains.

The degree to which the ultrastructure of the internal anatomy of leaves is preserved varies greatly. The axis and roots, both of which are made of wood, are the parts of a plant that are most frequently found preserved.

Three-dimensional, but fragile tissues (like cellulose-rich, lignin-poor phloem) often don't survive because of faster decay.

Lagerstätten plant fossils are unique in that they preserve internal anatomy and provide more morphological detail than standard compression-impression fossils. For instance, the Rhynie Chert Lagerstätte in the early Devonian contains a diverse In-situ assemblage in which the silicification process has preserved exquisite detail in the anatomy of early plants and other organisms. Authors have found an exceptional fossil deposit at this site.

The exceptional fossil plant is one of many that have revealed previously hidden key turning points in plant evolution.

Furthermore, plants' outward morphology and internal anatomy have been preserved extraordinarily well, enabling the study of the evolution of their vascular systems and plant communities (e.g., Wilson et al., 2009). (Scott and Rex, 1985). Without unusually well-preserved fossils and fossil assemblages, these historical revelations would have been lost.

The functional and ecological information contained within these fossils can only be properly interpreted if the underlying formation processes are known. In this article, we will examine the primary taphonomic routes that result in plant exceptional preservation, with an emphasis on experimental studies of plant preservation

Discussion

TAPHONOMIC PATHWAYS

There are four main issues that need to be considered when analyzing plant fossils: 1)

the preservation of relevant anatomical details; 2) on the basis of taxonomy, and 3) the likelihood of fossilization that may have been presented during the procedure of fossilization; and 4) the extent to which paleo environmental data (for instance, isotopic data in cuticle waxes) are preserved. To become a fossil, a plant part like a leaf must be moved, buried, and deteriorate to some extent, all while being preserved long enough for the nearby sediment to lithify (Rex and Chaloner, 1983; Ferguson, 2005) or for the fibers to be permineralized (e.g., Kenrick and Edwards, fibers to be permineralized (e.g., Kenrick and Edwards, and exposure to oxygen will change the overall product (Yang and Huang, 2003), and the extremely resistant waxy cuticle is assumed to favour this procedure (Collinson, 2011) by offering a comprehensive external layer of protection to the more labile internal tissues of the leaf. Depending on the timescale and environmental factors at play, various taphonomic modes may have an impact on a given archaeological site.

There is variation in the methods used to preserve tissues and organs through various taphonomic processes (Fig. 2). Classically, Schopf (1975) outlined the four preservational methods that are significant in fossil plant preservation: 1) Muriatic (hard part) preservation, 2) organic compression/impression, 3) Authigenic preservation, and 4) Cellular preservation.

In the 1980s, coalification emerged as a viable method for preserving delicate botanicals like flowers (e.g., Friis and Skarby, 1981).

The vast majority of marine shell fossils were preserved in a Muriatic state, proving this to be the case. When the surrounding sediment is rapidly cemented, typically as a concretion, this is an example of authigenic mineralization (Schopf, 1975). The majority of plant fossils are impressions or compressions (Schopf, 1975; Greenwood, 1991), and as a result, they typically only retain the plant's "gross morphological characters" or its "epidermal anatomy" due to the preservation of the cuticle.

Compression-Impression

Plant fossils are multiple relics of their ancestors that were squashed and flattened during the fossilization process, earning them the name "compression fossils." Vegetation and other forms of biological materials are frequently preserved in these fossils. Coal and peat, which both include a wide variety of collected fossil plants, are two typical types of compression fossils (Li et al., 2020).

Impression fossils, even though they share the flat, two-dimensionality of compression fossils these fossils are still not natural remains of the plants they depict. Impression fossils are formed when plant matter presses into delicate, finely grained sediment like clay or silt, leaving behind a fossilized impression. In the event of plant decomposition, the impression left behind can be fossilized (Kopeć et al., 2021).

The majority of plant fossils, particularly leaves, have varying degrees of preservation ranging from impression with no organic preservation to specimens with partially or completely organic preservation (compression). A flattened duplicate of the original fossil emerges when a plant organ is buried in mud and allowed to degrade there. This process creates a fossil (Rex and Chaloner, 1983). The impression of the organ is compression fossils as the process of fossilization continues. Compression fossils retain remnants of plant tissue that would have otherwise decomposed and disappeared from the sediment. In the absence of fossilization, these remnants would have been lost. There is a wide variety of properties displayed by these organic compounds.

The original tissues, the context of their deposition, and the circumstances of their burial all play a role in how well they are preserved (Collinson, 2011). On extremely rare occasions, such as certain ultrastructure and subcellular features (such as chloroplasts and mitochondria) of leaves have been preserved.

Nothing happens to the DNA (in this case, the chromosomes). The cuticle and the internal anatomy of other leaves are preserved so well because no other specimens from the same area have been found to date that preserve these details. In addition to their importance in anatomy, compression fossils provide a wealth of geochemical information and can be used as environmental indicators (Yang & Huang, 2003). It has been determined that compression-impression fossils are formed using both external and geochemical processes, and that these methods also serve as a sorting mechanism (Cleal et al., 2021).

When studying compression-impression fossils of leaves, it is important to take into account the inherent biases that result from their physical formation paramount to the process of re-creating ancient ecosystems. Besides providing crucial insights into plant taxonomy, fossil leaves also document important paleoclimatic information.

Chemical Formation: Most plant fossils, especially leaves, are preserved on a spectrum from impressions with no organic preservation to specimens with partial or complete organic preservation (compression). When a plant organ is buried in sediment and allowed to decompose there, a flattened replica of the original fossil forms (Rex and Chaloner, 1983). As the fossilization process continues, the impression of the organ is compression fossils preserve remnants of plant tissue that would otherwise have decayed and disappeared from the sediment. There is a wide variety of properties displayed by these organic compounds.

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DNA (specifically, chromosomes) remains intact. Aside from the cuticle, the internal anatomy of other leaves is completely absent from other specimens collected from the same area which is why the preservation of these detail is so remarkable. Compression fossils, in addition to their anatomical significance, are also a rich source of geochemical data as well as

being used as metrics of past environments (Yang & Huang, 2003). It has been determined that external and geochemical methods play a role in the creation of compression-impression fossils, and that these procedures also act as discrimination in the formation of these fossils.

When studying compression-impression fossils of leaves, it is important to take into account the inherent biases that result from their physical formation paramount to the process of re-creating ancient ecosystems. Besides providing crucial insights into plant taxonomy, fossil leaves also document important paleoclimatic information on former CO₂ levels (Doria et al., 2011). Modifications to the size of the leaf's stomatal density may impact our understanding of ecosystems of the past.

Before recently, it was believed that when a leaf develops in a compression fossil, horizontal movements were minimal and the primary axis of deformation was vertical (Walton, 1936; Schopf, 1975).

It has been demonstrated, however, that during both compaction and dehydration, horizontal changes to the linear dimensions of the leaf may be as significant as vertical ones.

Accordingly, stomatal density is preferable to use the stomatal index, which is the ratio of stomatal density to epidermal cell density, as a proxy for past climate conditions instead. It does not matter if the cuticle contracts or swells to change this proportion.

Silicification

In order to replenish the original skeletal material, silicification entails the concurrent breakdown of calcium carbonate and the deposition of silica. The breakdown of calcium carbonate results in the precipitation of silica. The silica that crystallizes into the organic material that covers the mineral crystallites in the shell aids in this procedure. Aspects of the devolution cycle, such as shell mineralogy, the amount and distribution of organic compounds, and the nature of the surrounding matrix, all influence silicification. All of these elements contribute to the creation of silica. Similar to other forms of fossilization, silicification can lead to taphonomic biases. For instance, silicification is more likely to occur in carbonate formations, with creatures whose calcite shells contain less magnesium, and in environments with lots of residual silica (Wang et al., 2021).

Fossils of silicified plants are among the most valuable for understanding how vascular plants and other photosynthetic organisms have evolved over time.

As a result of their high degree of preservation and abundance in the fossil record (Greenwood, 1991; Knoll, 1985), (Stein, 1982) especially common is silicified wood, which can be found all the way from the Paleozoic to the Holocene. Subcellular preservation of internal anatomy allows for unprecedented insight into everything from cell wall structure to reproductive organ development.

Information about the anatomy of ancient plants provides an overview of plant transformation and historic atmosphere paleoecology using silicified plant fossils requires that the control system relating to silicification can be grasped. Silica can come from many different places setting for deposition (Fig. 1). There is a lot of silica in places like volcanic ash and hydrothermal vent systems, but it's rare to find any in fossil sequences sources consistent

with volcanism and hydrothermal activity (Knoll, 1985). There is a shortage of silica in the oceanic world. Invertebrates like diatoms and radiolarians though spicules from sponges have been suggested as a possible source of silicification (Hesse, 1989), the true origin of the silica used in the skeletons is still.

On land, however, where silica is more easily accessible, plants are typically preserved.

Silica in terrestrial systems can come through diatom or detrital feldspar breakdown in young sediments (Matysová et al., 2010). If there are no other silica sources in a system, dissolved silica from siliciclastic materials can still be an important component.

Plants may be silicified by rocks in groundwater, though this process may take much longer (Knoll, 1985). In most cases, silica supply is not a bottleneck influencer of the silicification of the Earth's surface (Knoll, 1985; Hesse, 1989).

Silica formation could be aided by partial plant decomposition, which would increase the number of hydrogen-bonding sites available.

The decay of organic matter is significant, and with it comes the loss of the Template upon which silicification can take place. Therefore, the duration of silicification depends to some extent on the persistence of organic matter. Depending on the tissues, a quick silicification process that takes days, weeks, or years to complete, would have been responsible for the preservation of plant internal anatomy in deposits where this is the case the natural world (Ballhaus et al., 2012) accelerates past the rate of deterioration.

Coal Balls

A coal ball is a piece of fossilized plant residues that can be found in coal deposits from the Upper Carboniferous Era. Fossils of coal balls have provided scientists with crucial insights into the pre-Coal age forest ecosystem. Carboniferous swamps contained pockets of plant debris that, due to a combination of factors, had become petrified instead of transformed into coal when exposed to trace minerals (Retallack, 2021). These petrifications have already been discovered in the middle of the US, in Britain, in a large region stretching from Berlin to the Eastern Europe, and in Spain, ranging in weight from a few grams to many hundred kilograms.

For Paleozoic paleobotanical studies, concretions (coal balls), typically made of carbonate but occasionally of silica and containing fossilized plant remnants, are an essential source.

oxidized plant material (Scott and Rex, 1985). Although Permian-age coal balls have been found in China, carboniferous age coal balls are more common (e.g., Zhou et al., 2008). Coal balls are found in coal seams as globules of varying sizes and shapes. Since their revelation in 1855, coal balls have provided crucial palaeoecological data for reconstructing the flora of one of the world's most biodiverse regions significant geologic epochs for peat bog formation. Coal balls are made up of mostly calcite, dolomite, ferroan dolomite, and pyrite, with smaller amounts of marcasite, gypsum, quartz, and other minerals.

(DeMaris, 2000) illite, kaolinite, and lepidocrocite. The mineralogy of coal balls is fairly uniform, though the relative amounts of their constituents can vary significantly.

Components are not the same, even between nearby concretions. Calcite is the main component of balls. The lack of detrital minerals is indicative of permineralization occurring in situ. Peat-forming plants, as opposed to those that form coal in brackish water, is where the action is, according to the most recent theory on coal-ball formation. Non-marine muds covered the peat body as it formed levels of deviance. These sludges were originally sourced from freshwater rivers that cut through the peat bog. The Rising sea levels converted rivers into estuaries, which pushed siliciclastic sediment inland(Elrick and Nelson, 2010).

As pCO_2 rose within the peat body due to methanogenesis, the pH dropped and the carbon isotope values became extremely negative; however, when the shale cap was eroded away, CO_2 was released, the pH was raised, and marine water was once again introduced into the peat. The chemical balance quickly shifted in favour of carbonate precipitation as a result. Even though growth rings have been found in certain coal balls with well-preserved anatomy, these coal balls suggest a rapid production process.

A single coal ball may have experienced precipitation from multiple sites of nucleation, which eventually coalesced into a spherical coal ball.

It looks like coal balls formed where the grey muds was removed as a result of marine transgression's continuing impact. It's worth noting that DeMaris (2000) found that coal balls only form beneath marine, typically black shale roof rocks in the coal beds he examined. Coal sulfur is typically lower than under marine conditions in areas where grey shale was thick and remained intact. There are no rocks on the roof or coal spheres.

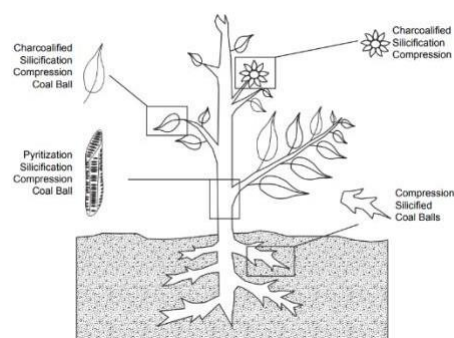


Figure 2: Major Plant organs

Conclusion

As we've seen, there are clear biases in each type of preservation method. With the exception of compression floras, the

The dependence on particular depositional environments, rather than obvious taxonomic differences, is the source of the major bias of each taphonomic pathway.

The ideal setting for the preservation of plants in pyrite, as determined by fossil observations and taphonomic experiments, is a typical marine environment.

Since the specifics of each taphonomic pathway depend on their respective environments, the relative abundance and distribution of various fossilized plants found in rock strata. Most coal balls are found in peats that date back to the Carboniferous and the lower Permian, making this period of time the most significant for peat formation in the entire Phanerozoic (Scott and Rex, 1985).

Similar to how plants seldom migrate into marine environments, the total number of local areas and pyritized plant fossils illustrate this uncommon occurrence.

The creation of silicified plant fossils is not influenced by the silica quantity; rather, it is influenced by how long the organic template was preserved.

References

BECK, C. B. (1960). The connection between *Archaeopteris* and *Callixylon*. *Science*, 131:1524– 1525.

BECK, C. B. (1960). The identity of *Archaeopteris* and *Callixylon*. *Brittonia*, 12:351–368.

BALLHAUS, C., C. T. GEE, C. BOCKRATH, K. GREEF, T. MANSFELDT, AND D. RHEDE. (2012).

The silicification of trees in volcanic ash—an experimental study. *Geochimica et Cosmochimica Acta*, 84:62–74.

COLLINSON, M. E. (2011). Molecular taphonomy of plant organic skeletons, p. 223–247. In P. A. Allison and D. J. Bottjer (eds.), *Taphonomy: Process and Bias through Time*. Topics in Geobiology 32, Springer, New York

Cleal, C., Pardoe, H. S., Berry, C. M., Cascales-Miñana, B., Davis, B. A., Diez, J.B., ... & Uhl, D. (2021). Palaeobotanical experiences of plant diversity in deep time.1: How well can we identify past plant diversity in the fossil record?. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 576,110481

DETTMANN, M. E., H. T. CLIFFORD, AND M. PETERS. (2009). *Lovellea wantonness* gen. et sp. nov.—Early Cretaceous (late Albian), anatomically preserved, angiospermous flowers and fruits from the Winton Formation, western Queensland, Australia. *Cretaceous Research*, 30:339–355

DORIA, G., D. L. ROYER, P. A. WOLFE, A. FOX, J. A. WESTGATE, AND D. J. BEERLING. (2011). Declining atmospheric CO₂ during the late Middle Eocene climate transition. *American Journal of Science*, 311:63–75

FERGUSON, D. K. (2005). Plant taphonomy: ruminations on the past, the present, and the future. *PALAIOS*, 20:418–428

GENSEL, P. G. (2008). The earliest landplants. *Annual Review of Ecology, Evolution, and Systematics*, 39:459–477

GREENWOOD, D. R. (1991). The taphonomy of plant macrofossils, p. 141–169. In S. K. Donovan (ed.), *The Processes of Fossilization*. Columbia University Press, New York

GRAY, J., W. G. CHALONER, AND T. S. WESTOLL. (1985). The microfossil record of early land plants: a *dvance in understanding of early terrestrialization, 1970–1984 [and Discussion]*. *Philosophical Transactions of the Royal Society of London B-Biological Sciences*, 309:167–195..

HESSE, R. (1989). Silica diagenesis: origin of inorganic and replacement cherts. *Earth-Science Reviews*, 26:253–284.

- Labandeira, C.C. (2021). Ecology and evolution of gall-inducing arthropods: The pattern from the terrestrial fossil record. *Frontiers in Ecology and Evolution*, 9, p.632449
- Li, G., Chen, L., Pang, K., Zhou, G., Han, C., Yang, L., ... & Yang, F. (2020). An assemblage of macroscopic and diversified carbonaceous compression fossils from the Tonian Shiwangzhuang Formation in western Shandong, North China. *Precambrian Research*, 346, 105801.
- Retallack, G. (2021). Modern analogs reveal the origin of Carboniferous coal balls. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 564, p.110185.
- REX, G., AND W. CHALONER. (1983).
The experimental formation of plant compression fossils. *Palaeontology*, 26:231–252.
- Spicer, R. A. (1989). The formation and interpretation of plant fossil assemblages. In *Advances in botanical research* (Vol. 16, pp. 95-191). Academic Press
- Scott, A. C., & Rex, G. (1985). The formation and significance of Carboniferous coal balls. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 311(1148), 123-137.
- SCHOPF, J. M. (1975). Modes of fossil preservation. *Review of Palaeobotany and Palynology*, 20:27– 53.
- SMOOT, E. L., AND T. N. TAYLOR.
(1986) . Structurally preserved fossil plants from Antarctica: II. A Permian moss from the Transantarctic Mountains. *American Journal of Botany*, 72:1683–1691.
- WELLMAN, C. H., P. L. OSTERLOFF, AND U. MOHIUDDIN. (2003).
Fragments of the earliest land plants. *Nature*, 425:282–285.
- WILSON, J. P., A. H. KNOLL, N. M. HOLBROOK, AND C. R. MARSHALL.
(2009) . Modeling fluid flow in Medullosa, an anatomically unusual Carboniferous seed plant. *Paleobiology*, 34:472–493.
- KNOLL, A. H. (1985). Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. *Philosophical Transactions of the Royal Society of London B-Biological Sciences*, 311:111–122
- Spicer, R. A., & Farnsworth, A. (2021). Progress and challenges in understanding Asian palaeogeography and monsoon evolution from the perspective of the plant fossil record. *Journal of Palaeosciences*, 70, 213-236
- STEIN, C. (1982). Silica recrystallization in petrified wood. *Journal of Sedimentary Research*, 52:1277– 1282.
- Kopeć, K., Soszyńska-Maj, A., Kania- Kłosok, I., Coram, R. A., & Krzemiński, W. (2021). Morphology of the oldest fossil subfamily of Limoniidae (Diptera, Archtipulinae) in the light of exceptionally preserved Mesozoic material. *Scientific Reports*, 11(1), 1-11.
- KENRICK, P., AND D. EDWARDS.
(1987) . The anatomy of Lower Devonian *Gosslingia breconensis* Heard based on pyritized axes, with some comments on the permineralization process. *Botanical Journal of the Linnean Society*, 97:95–123
- WALTON, J. (1936). On the factors which influence the external form of fossil plants, with descriptions of the foliage of some species of the Palaeozoic equisetalean genus *Annularia* Sternberg. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 226:219– 237.
- Wang, T., Feng, Q., & Huang, Y. (2021). Fossil evidence provides new insights into the origin of the Mesoproterozoic ministromatolites. *Precambrian Research*, 366, 106426.
- 23) YANG, H., AND Y. HUANG. (2003).

24) Preservation of lipid hydrogen isotope ratios in Miocene lacustrine sediments and plant fossils at Clarkia, northern Idaho, USA. *Organic Geochemistry*, 34:413–423.