

The fossil record of grasses preserved in amber

George Poinar

The Fossil Record of Grasses Preserved in Amber

George Poinar



Tallinn, Estonia

Author

GEORGE POINAR

Department of Integrative Biology

Oregon State University

Corvallis, OR 97331

United States

E-mail: poinarg@science.oregonstate.edu; george4405@gmail.com

ORCID: 0000-0002-3479-6997

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This study briefly discusses the role of extant grasses as food (e.g., wheat, corn, rice) and construction crops (e.g., bamboo, reeds). It then examines fossil grasses based on their presence in amber deposits worldwide. Emphasis is placed on the body fossils of grasses, especially those of the genus *Programinis*, a primitive bamboo dating back to the mid-Cretaceous that suffered from ergot parasitism. It then transitions to the Eocene Baltic amber grass, *Eograminis balticus*, followed by the Miocene *Pharus primuncinatus* that was attached to the pelage of a mammal. Also in Dominican amber were the grasses *Alarista succina* and *Panicum* sp. whose spikelets were being carried by ants. A discussion on grass phytoliths shows their application in identifying various fossil grasses and their potential role as insecticides.

Chapter 1: Introduction

Grasses (Poaceae) represent one of the few mid-Cretaceous plant families still in existence today. These plants can be distinguished by their vegetative organs, which includes primary roots in germinating sprouts, secondary roots produced from nodes, jointed stems (culms), below ground rhizomes or above ground stolons. Grass leaves are normally flat, sessile and narrow. The inflorescences are spikelets with rachilla, glumes, lemmas and flowers with stamens and pistils. Grasses are the widest distributed family of flowering plant in all global habitats from the tropics to the polar regions. The family is ecologically the most dominant and economically, the most important in the world. It provides all the cereal crops, rice, corn, and most of the world's sugar and grazing for domestic and wild animals. As a construction crop, grasses also provide bamboos, canes and reeds. As a soil stabilizer, grasses maintain dunes, fields and all exposed ground areas from the polar regions to the deserts (Heywood, 1993; Hitchcock, 1950; Manske, 2023).

Chapter 2: Extant Grasses (Figures 1–12)

It is impossible to determine the oldest grass lineages present today. There are some aquatic grasses that appear to have primitive traits (Figure 1) and the grasses that grow along the coast under rigid conditions also may be quite ancient (Figures 2, 3). These are in contrast to the recently developed grass strains such as corn (Figures 4, 5) and rice (Figure 6). Dating the first use of grass reeds that were used to construct dwellings is difficult (Figures 7, 8). Most of the grasses used for grazing (Figure 9) and for winter food for cattle (Figure 10) are a mixture of several lineages. In addition, some grasses are used as shelters or even ornaments (Figures 11, 12) and there are some animals that have become nutritionally dependent on various species of bamboo.



Figure 1. Wild grasses in bloom on West Maui Makena Beach in Hawaii.

Perhaps such grasses originated from the far-off **Wallace Line**, a boundary between the Oriental and Australian faunal regions. See further details in “Grasses of the Hawaiian Ranges” (Whitney et al., 1939).



Figure 2. Eventually, certain stalk-forming grasses like *Ammophila arenaria* began stabilizing sand dunes along the Oregon coast.



Figure 3. American dune grass, *Leymus mollis*, followed suite growing along the Oregon coast but not as robust as *Ammophila arenaria*.



Figure 4. Corn (*Zea mays*) field In Nebraska shows one of the most important edible grasses of the world.



Figure 5. Roasting corn (*Zea mays*) in West Africa.



Figure 6. Rice field in Los Banos, the Philippines shows one of the most important edible grasses of the world.



Figure 7. Collecting giant reeds (*Arundo donax*) for home construction in Romania.



Figure 8. Entering a dwelling in Romania made from giant reeds (*Arundo donax*).



Figure 9. Grass with other herbage furnishes pasture to grazing animals.



Figure 10. Putting loose hay (mainly grass) in a barn in Iowa for winter cattle feed.



Figure 11. Pampas grass (*Cortaderia selloana*) in Fort Bragg, California.



Figure 12. *Phyostachys* running bamboo.

Chapter 3: Fossil Grasses (Figures 13–34)

3.1. METHODS AND FIGURES FOR FOSSIL GRASSES FROM AMBER

3.1.1. Mid-Cretaceous Burmese amber *Programinis*

The fossil specimens of *Programinis burmitis* and *Programinis laminatus* were obtained from the Noiye Bum 2001 Summit Site mine, which is located southwest of Maingkhwan in Kachin State (26°20′n, 96°36′e) in Myanmar. Paleontological evidence was used to date this site to the Late Albian of the Early Cretaceous (Cruickshank & Ko, 2003), placing the age at 97 to 110 Mya. A subsequent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Mya or at the Albian/Cenomanian boundary (Shi et al., 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noiye Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar et al., 2007).

3.1.2. Eocene Baltic amber *Eograminis*

The fossil specimen of *Eograminis balticus* originated from the Samland Peninsula in the Kalinin District of the Russian Federation. Currently, mining operations are underway in the vicinity of the Samland Peninsula and at the Yantarny Amber Quarry near Kaliningrad. There exists a divergence of opinions regarding the true age of Baltic amber. A range of ages have been proposed with some sources suggesting an age between 34 and 38 Myr (Sadowski et al., 2017).

3.1.3. Miocene-Oligocene Dominican amber *Pharus primuncinatus* and *Alarista succina*

The Dominican amber fossil grasses *Alarista succina* whose spikelet was being carried by an ant, and *Pharus primuncinatus*, which was attached to the pelage of a mammal, are notable inclusions in amber. These specimens originated from La Toca mine in the northern mountain range (Cordillera Septentrional) of the Dominican Republic between Puerto Plata and Santiago (Poinar, 1991; Donnelly, 1988). Amber from mines in this region was produced by *Hymenaea protera* Poinar (1991) (Fabaceae). The dating of Dominican amber is a subject of debate, with the youngest proposed age of 20-15 mya based on foraminifera (Iturralde-Vincent & MacPhee 1996) and the oldest of 45-30 mya based on coccoliths (Cepek in Schlee 1990). These dates are based on microfossils found in the strata containing the amber that is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al., 1994).

3.1.3.1. *Programinis burmitis* Poinar and *Programinis laminatus* Poinar

The physical fossils of *Programinis burmitis* (Figure 13) and *Programinis laminatus* (Figure 14) represent the oldest known members of the Poaceae. Both of these fossils were preserved together in the same amber piece so it is likely that they represent a single specimen.

The spikelet of *P. burmitis* with its two basal sterile glumes, a series of lemmas and paleas, remains of stamens and a gynoecium, aligns *P. burmitis* with the Poaceae (Poinar, 2004). Additionally, the numerous stomata (Figure 14) with well-defined sausage-shaped guard cells and rows of

epidermis with long and short cells align *P. laminatus* with the Poaceae. Furthermore, silica bodies shaped as rondals and elongated quadrates in short cell epidermal leaf cells of *P. laminatus* were noted (Poinar, 2004, 2011) (Figure 15).

The earlier study on fossil grasses by Crepet & Feldman (1991) is now outdated since additional fossils have been described since it was published.

The Mid-Cretaceous *Programinis* fossils provide undisputed evidence of true grasses. In their concise overview of the origin of grasses, Saarinen et al. (2020) seemingly disregarded the botanical evidence presented by Poinar (2004: 2011), including an earlier study on the anatomy of the flowers of orchard grass (*Dactylis glomerata*) (Poinar, 1961) conducted under the supervision of Dr. Beirorst at Cornell University.

Conversely, in their study on the nuclear phylogeny of the Poaceae, Huang et al. (2022) employed molecular clock analysis estimating the crown age of Poaceae to be around 101 million years old. This is approximately equivalent to the age of the Burmese amber grass specimens *Programinis burmitis* and *P. laminatus* (Poinar, 2002).

3.1.3.2. Mid-Cretaceous *Programinis* species

Silica bodies are commonly found in grass leaves and occur in the leaves of *Programinus laminatus* (Figure 15). See following section on phytoliths.

Further evidence of grass in mid-Cretaceous Burmese amber is provided by a fossil infected with the ergot fungus, *Palaeoclaviceps parasiticus* (Poinar et al., 2015) (Figures 16,17).

The fungus is characterized by an erect black sclerotium with flattened hyphal outgrowths and adjacent conidia. The ergot fungus's host was identified as a grass,

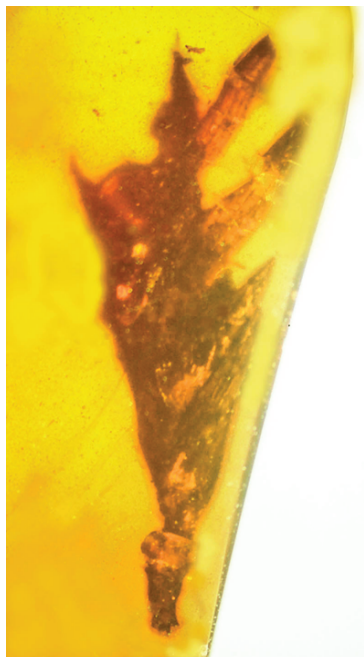


Figure 13. *Programinis burmitis* spiklet.

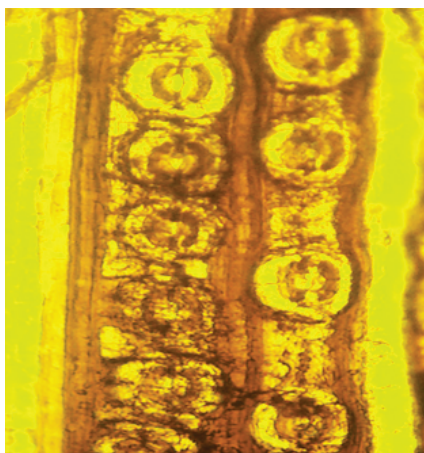


Figure 14. *Programinis laminatus* with two rows of stomata.

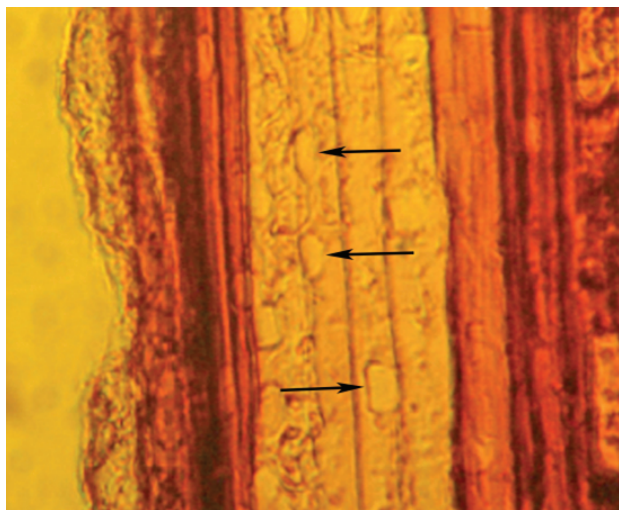


Figure 15. Silica bodies (arrows) in leaf cells of *Programinis laminatus*.

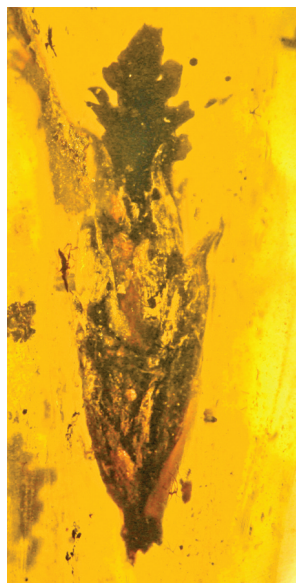


Figure 16. Ergot infecting a mid-Cretaceous grass.

as determined by the pair of sterile glumes that subtend the florets and reniform guard cells flanked by low dome-shaped subsidiary cells. *Ammophila arenaria* and *Lolium perenne*, two contemporary grasses, have been observed to be susceptible to ergot (Figures 18,19).

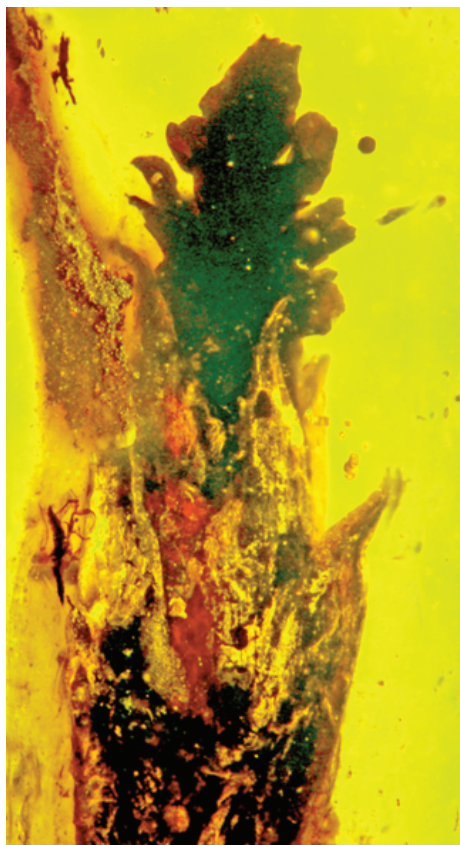


Figure 17. Detail of fungus portion of ergot.

Further evidence of grass in mid-Cretaceous Burmese amber is a fossil infected with the ergot fungus, *Palaeoclaviceps parasiticus* (Poinar et al., 2015) (Figures 16,17). The

fungus is characterized by an erect black sclerotium with adjacent conidia. The host of the ergot was determined to be a grass, based on the pair of sterile glumes subtending the florets and reniform guard cells flanked by low dome-shaped subsidiary cells.

Many of today's grasses, such as *Ammophila arenaria* and *Lolium perenne* are also infected by ergot sclerotia (Figures 18,19). Some of these ergots are very poisonous and during periods of famine in the Middle Ages, the only bread available (black grain bread) was made from ergot-infected grain. Eating this bread caused a disease known as ergotism, which could result in gangrenous limbs and death (Poinar et al., 2015).



Figure 18. Ergot-infected dune grass floret.



Figure 19. Ergot-infected rye grass florets.

3.1.4. *Eograminis balticus* (Poinar & Soreng, 2021) from Baltic amber and present-day descendant

Another striking discovery was the first grass to be found in Baltic amber (Poinar & Soreng, 2021). This was a complete spikelet of *Eograminis balticus* that was perfectly preserved (Figure 20). The fossil spikelet had some properties of species of the extant genus *Molinia* (Figure 21). Details of the lemma were also available (Figure 22) as well as preserved associated organisms such as an orthopteroid feeding on the floral tissues (Figure 23) (see extant grass-feeding grasshopper) (Figure 24) and an *Alternaria*-like fungal spore attached to the lemma (Figure 25).

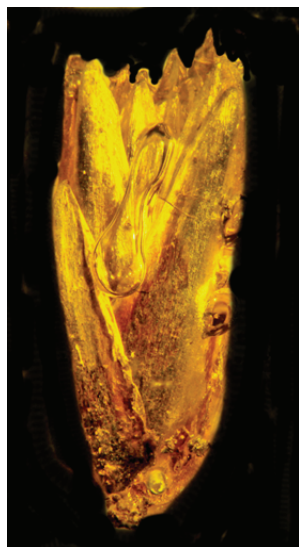


Figure 20. *Eograminis balticus* spikelet.



Figure 21. Extant *Molinia caerulea* spikelet.

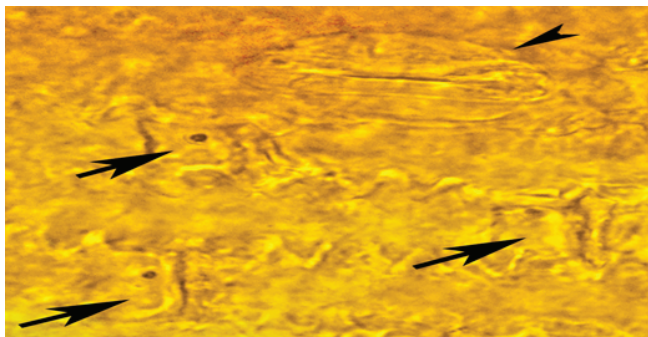


Figure 22. A lemma of *Eograminis balticus* showing stomata (arrowhead) and short cells (arrows).

3.1.4.1. Other creatures associated with *Eograminis balticus*

Associated with *Eograminis balticus* was an orthopterid that appears to have been feeding on the grass when it was covered with resin (Figure 23). Today, it is possible to find grasshoppers feeding on a number of different grasses (Figure 24).



Figure 23. Orthopteroid feeding on *Eograminis balticus*.



Figure 24. Pygmy grasshopper feeding on extant beach grass.

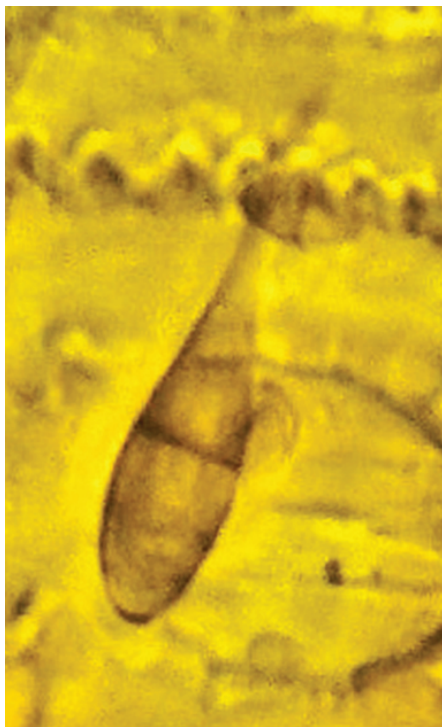


Figure 25. Fossil fungal spore on lemma of *Eograminis balticus*.

The presence of an *Alternaria*-like fungal spore attached to the lemma of the Baltic amber *Eograminis balticus* (Figure 25) suggests the potential for fungal infection of this fossil grass.

3.1.5. Miocene -Oligocene Dominican amber *Pharus primuncinatus*

One especially interesting fossil in Dominican Republic amber was a spikelet belonging to the grass genus *Pharus*, which was associated with mammalian hair (Poinar & Columbus, 1992) (Figures 26, 27).

This species is characterized by its diminutive curved floret, relatively short glumes and the uncinat portion of the floret extending downwards to the middle or slightly below the middle of the lemma. The closest extant relative may be the Mesoamerican *Pharus mezii*. Notably, this specimen represents the earliest documented instance of a fossil grass that can be definitely assigned to an extant genus, the earliest record of a member of the basal subfamily Pharoideae and the only known fossil *Pharus* spikelet. The manner by which the spikelet arrived in amber was by its attachment to a mammal (epizoochory) (Poinar & Columbus, 2012). One of the uncinat mammal hairs associated to the spikelet is still attached to the lemma. An analysis of the hairs associated with *Pharus primuncinatus* indicates their origin from a carnivorous mammal, possibly a jaguar. The hypothesis is that the carrier probably tried to dislodge the hairs by rubbing up against a resinous *Hymenaea protera* tree, thus leaving some hairs attached to a resin deposit (Poinar & Judziewicz, 2005). The presence of a fungus gnat (Diptera: Mycetophilidae) in debris at the base of the spikelet (Figure 26) suggests the potential for its breeding in this environment.

The manner by which the spikelet arrived in amber was by its attachment to a mammal (epizoochory) (Poinar & Columbus, 1992). One of the uncinatate mammal hairs associated to the spikelet is still attached to the lemma (Figures 26, 27). An analysis of the hairs associated with *Pharus primuncinatus* show them to be from a carnivorous mammal, possibly a jaguar. The carrier probably tried to remove the hairs by rubbing up against a resinous *Hymenaea protera* tree, thus leaving some hairs attached to a resin deposit (Poinar & Judziewicz, 2005).



Figure 26. *Pharus primuncinatus* surrounded by the hairs of a carnivore and a fungus gnat.

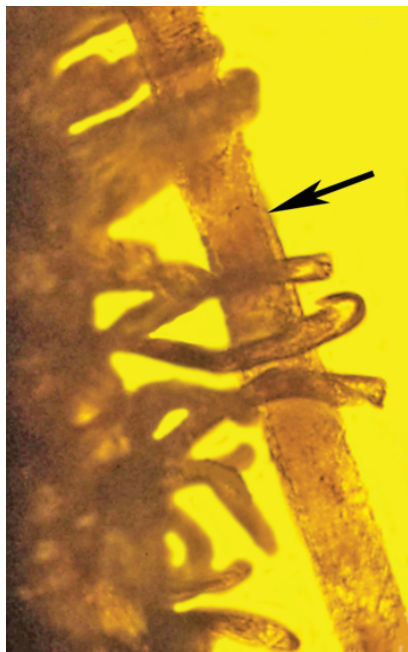


Figure 27. The hooks of *Pharus primuncinatus* clasp the hair (arrow) of a carnivore.

Chapter 4: Ants and Grasses

Ants are generally regarded as carnivores however certain ant groups have adopted a vegetarian diet, particularly those inhabiting warm, arid parts of the country. Competition for protein is intense and what are known as harvester ants collect seeds for protein, particularly from many grasses (Figures 28-31). Many of these harvesting ants also have tendencies to consume plant juices that serve as nectar or extra-floral nectaries, as well as exudations from the bodies of aphids and other Homoptera (Wheeler, 1910).

Carnivory in ants requires a strong pair of mandibles to penetrate the chitinized exoskeleton of prey. These robust mandibles can be used to open the coatings of many plant seeds, especially those of grasses. Harvester ants store their collected seeds in nests in the ground but these nests are often inundated during storms. The ants will then take grass seeds wetted by the rain out of the nest and dry them in the sun. Species of the genus *Messor* construct nests containing “granaries”, which are essentially chambers inter-connected by galleries distributed over an area up to 6 feet in diameter. Worker ants collect seeds from growing plants as well as the ground and remove and discard the seed coats outside the nest. Some ant species carry grass seeds beneath their bodies by holding it firmly in their mandibles against a notch under their heads.

The ants remove the husks at the nest sites, then store the edible kernels in granaries within the nests. They also remove the radicles, elaiosomes and funicules (fleshy structures attached to the outside of the seed that support germination). When the radicles with their associated elaiosomes and funicules are removed, the chances of germination is greatly reduced (Wheeler, 1910). Soldiers and

large workers that function as seed crushers will feed the ant larvae bits of crushed seeds.

An interesting account of large sand ants in India was made by Herodotus (1942). These desert ants remove large piles of sand as they construct their underground burrows. Neighboring Indian tribes are reported to collect, boil and eat seeds the size of millet grains. Whether the ants also harvest similar seeds is not known.

So, a typical pattern of seed eating ants is to bring the seeds back to the nest, remove the husks and store the edible kernels in the granaries. The chaff and seed-pods are carried out and dumped on the kitchen middens (refuse heap). One researcher observed that a species of harvester ant (*Pogonomyrmex*) in Texas will actually sow grass seeds and subsequently cultivate plants of ant rice (*Aristida stricta* and *A. oligantha*) in addition to harvesting and storing them in its granaries (Wheeler, 1910). Over the years, some vertebrates, such as the bamboo lemur, bamboo sloth and bamboo giant panda have become dependent on grasses for survival.

4.1. MIOCENE DOMINICAN AMBER *ALARISTA SUCCINA*

How *Alarista succina* arrived in the amber is unknown. A worker ant, *Dolichoderus caribbaea* (Wilson), adjacent to the spikelet (Figures 28, 29) raises the possibility that the ant was carrying the floret back to its nest since extant species of *Dolichoderus* are known to carry seeds (Wheeler, 1910).

Other genera of ants have been observed associated with seeds in Dominican amber. A worker harvester ant, *Pogonomyrmex* sp. apparently was carrying a *Panicum* sp. grass spikelet that was released when the ant encountered the resin (Figures 30, 31).

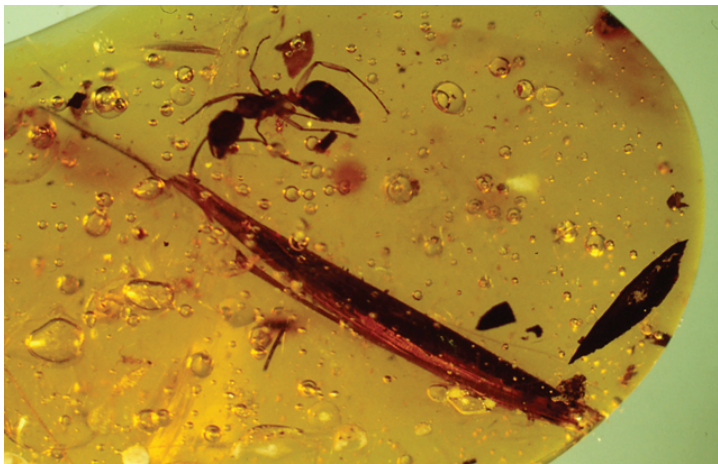


Figure 28. *Alarista succina* being carried by a *Dolichoderus* sp. ant in Dominican amber.



Figure 29. *Dolichoderus* sp. ant that was carrying *Alarista succina* in Dominican amber.

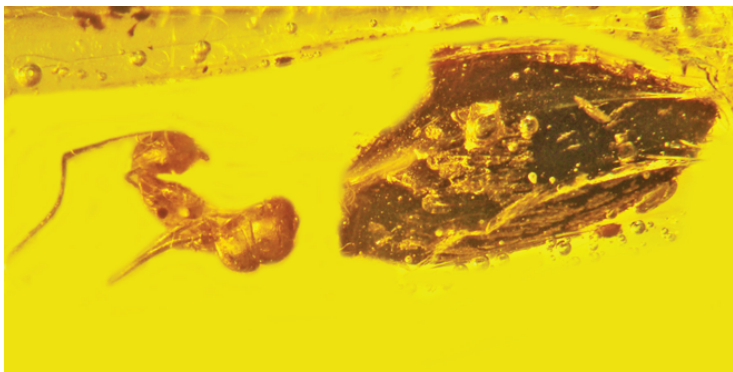


Figure 30. Worker harvester ant, *Pogonomyrmex* sp. that was carrying a *Panicum* sp. grass spikelet in Dominican amber.

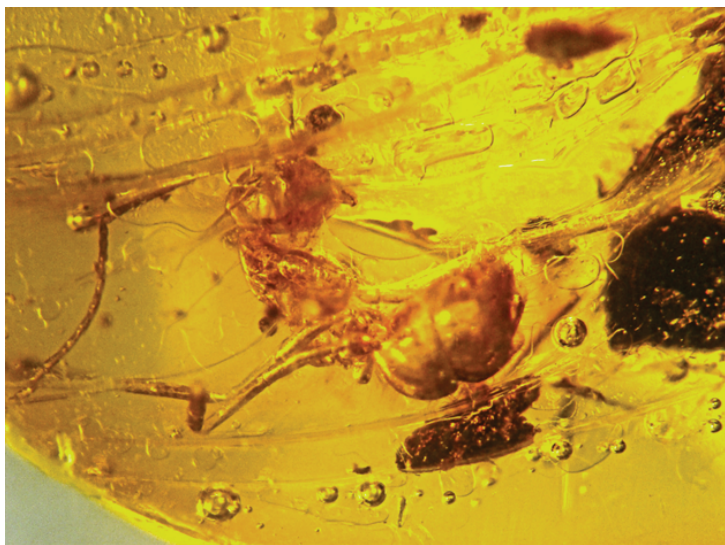
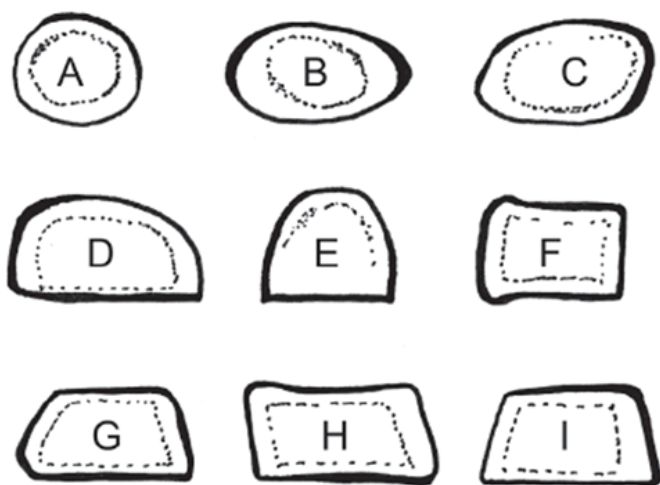


Figure 31. Detail of worker harvester ant, *Pogonomyrmex* sp., that was carrying a *Panicum* sp. grass spikelet in Dominican amber.

Chapter 5: Phytoliths

Phytoliths are rigid microscopic structures made of silica in the tissues of living plants. After plant death, the phytoliths are released into the soil where they can persist for millions of years. The presence of phytoliths in the remains of fossil grasses in amber shows how resilient they can be (Figures 32-50). The function of phytoliths is not known. Some believe they are to protect the plant from herbivores, especially chewing insects and fungi. The hypothesis that phytoliths function as a defensive mechanism in plants could well be plausible.



Planar view of basic types of silica bodies in epidermal leaf cells of *Programinis laminatus*. A = circular (entire) rondel; B = elliptical rondel; C = oblong rondel; D = long rondel; E = short (flat) rondel; F = short rectangle; G = pentagon; H = long rectangle; I = trapezoid. – Bar = 17 μm .

Figure 32. Silica bodies (phytoliths) in *Programinis laminatus*.

Some plant families like Cactaceae have very few phytoliths (uncommon to rare) a trait that is thought to be the result of their reliance on external spines for protection. Ancient plant lineages, like *Amborella* and members of the family Nymphaeaceae also lack phytoliths. The following figures show the presence of phytoliths in leaf cells of *Programinis laminatus*.

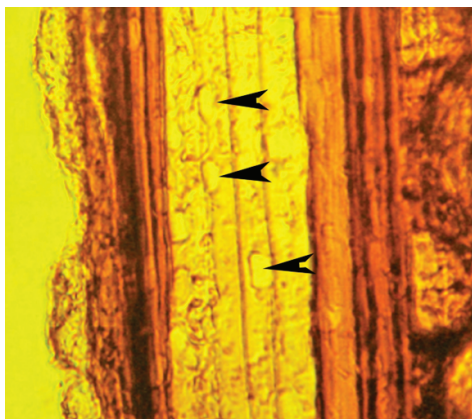


Figure 33. Rondel phytoliths (arrowheads) in leaf of *Programinis laminatus*.

The above examples are the first time phytoliths have been found “in situ” in fossil plants. One important function of phytoliths is to protect plants from herbivores and pathogenic fungi (Marshner, 1995; Piperno, 2006). Phytoliths could well be used as defense measures of plants. However some plant families like Cactaceae have very few phytoliths (uncommon to rare) but don’t need them with external spines as protection. Ancient plant genera and families that lack phytoliths, like *Amborella* and Nymphaeaceae, two of the most basal lineages of flowering plants, could have lost their herbivores and did not need phytoliths, so stopped producing them (Piperno, 2006).

Upon plant decay, the phytoliths become incorporated into soil and other sediments where they may remain stable within a wide pH range (pH 3–9) across varied environments with wet, dry, or alternating wet and dry climatic conditions (Piperno, 2006).

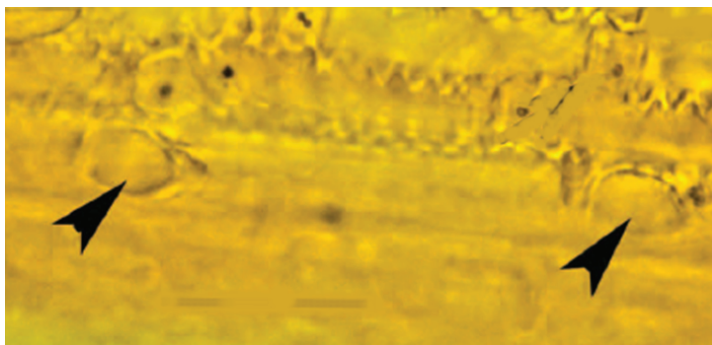


Figure 34. Two phytolith rondels (arrowheads) in the lemma of *Eograminis balticus*

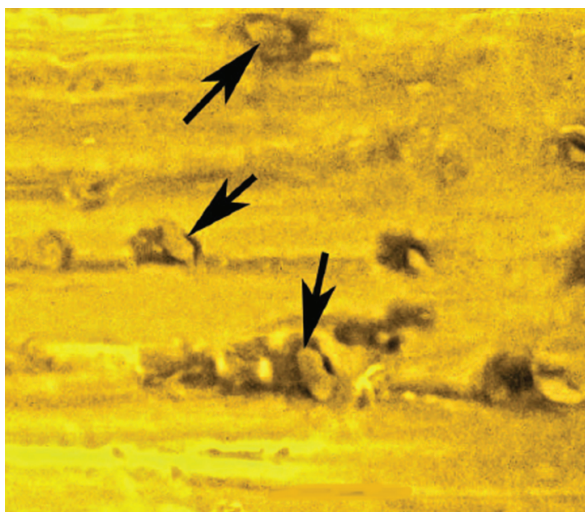


Figure 35. Additional phytolith rondels (arrows) in lemma of *Eograminis balticus*.

Chapter 6: Discussion

The comprehensive observations presented in this study were only made possible due to the preservative qualities of amber. These preservative qualities are, in large part, due to the immediate action of the resin on the organs, tissues and cells of plant remains.

The methodology involved in the preservation of amber inclusions involves four major actions: infiltration, fixation, dehydration and polymerization. As the resin infiltrates over and throughout the entrapped inclusions, it restricts oxygen and releases antimicrobial compounds that destroy decay-causing microorganisms that could decompose the tissues. Fixatives, such as various terpenoids and resin acids play a crucial role in preserving the integrity preserve the organs, tissues and cells of entrapped plant material by natural products in the resin. The process of dehydration is achieved by sugars and terpenes in the resin that replace water within the plant tissues, resulting in a condition similar to the type of physical preservation known as inert dehydration. In brief, the dehydration processes produce an extreme case of mummification, very similar to a natural embalming process. This process preserves details of flowers so they can be studied and compared to present day forms (Poinar, 2022).

After fixation and dehydration, polymerization and cross bonding of the molecules begins as the resin hardens. During this polymerization process, a semi-fossilized material known as copal is produced after several thousand years. Amber is eventually formed when the state of fossilization of the resin reaches a hardness of between 2-3 on the Moh's scale, a refractive index between 1.5 and 1.6, a specific gravity between 1.06 and 1.10, and a melting point between 250-300 degrees °C. (Poinar & Hess, 1985).

Chapter 7: Conclusions

The present work discusses the important uses of extant members of the grass family (Poaceae) for food, shelter, soil binding, etc. then continues with the traits of the known fossil species, including the mid-Cretaceous Burmese amber *Programinis burmitis* and *P. laminatus*, the Eocene Baltic amber *Eograminis balticus* and the Dominican amber.

Pharus primuncinatus and *Alarista succina*. The study also includes associations between ants and grasses as well as insects, fungi and phytoliths associated with the fossil grasses.

Acknowledgments

The author thanks the late Kenton L. Chambers for assistance on the taxonomic placement of various grass genera and Maya Dawson for supplying Figure 1 of the aquatic grass in Maui.

Conflict of Interest

The author claims to have no conflict of interest.

Statement of Data Consent

The author claims to have full consent of all data used in the present manuscript.

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