

ARTHROPOD PREDATION OF CORDAITEAN POLLEN CONES IN PENNSYLVANIAN  
COAL BALLS

A Thesis

by

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## ABSTRACT

Pennsylvanian coal balls are concretions of permineralized peat that contain a rich fossil record of plant-animal interactions. Cordaitean leaf-mat coal balls from the Cliffland and Blackoak coal beds (Kalo Formation, Iowa) commonly contain cordaitean pollen cones with fecal pellets (20 – 200  $\mu\text{m}$  in their widest minimum dimension) filled with macerated pollen (golden in color), or vegetative debris (dark in color). The size of fecal pellets suggests production by ancient collembolans, oribatid mites, or an extinct microarthropod group. Cordaitean leaf-mat peat also contains pollen-filled coprolites (200 – 900  $\mu\text{m}$  in their widest minimum dimension) that are consistent in size with production by insects. Maceration of pollen in fecal pellets and coprolites suggests the producers derived nutrition from pollen consumption, however, pollen-filled fecal pellets and coprolites could result from palynivory or detritivory. We analyzed the distribution of pollen and vegetation-filled fecal pellets and coprolites in two data sets from the Kalo Formation: 192 cordaitean secondary fertile shoots from 84 mounted slides on loan from the Harvard Paleobotanical Herbarium; 111 cordaitean secondary fertile shoots from 26 peels made from 22 coal balls containing cordaitean leaf-mats. In both data sets, pollen-filled fecal pellets occurred in 15 - 20% of all cordaitean cones, and 44 – 53% of mature cones. Only 9 - 14% of all pollen-filled fecal pellets occurred outside of cordaitean secondary fertile shoots, in the peat matrix. In leaf-mat peels, isolated pollen-filled fecal pellets and cordaitean cones with pollen-filled fecal pellets occurred in the same peat layers suggesting that fecal pellets were produced by palynivores in the canopy and shaken out of cones as they fell to the peat surface. Most cordaitean pollen aggregates in cordaitean leaf-mat peat occurred in the form of

pollen-filled coprolites. Pollen cones with undispersed pollen rarely occurred. In both data sets; only 14/303 (5%) of cones had large accumulations of pollen. The scarcity of undispersed cordaitan pollen in cordaitan leaf-mat peat suggests pollen-filled coprolites resulted from palynivory by flying insects in the canopy. The presence of pollen-filled fecal pellets and coprolites in cordaitan cones and leaf-mat peat is among the earliest evidence of probable palynivory.

## DEDICATION

To my wonderful and dearest friend, Baphomet.

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## INTRODUCTION

Since their diversification during the Cretaceous, angiosperms have developed multiple pollination syndromes, anemophily, hydrophily, and entomophily (Proctor et al., 1996). Once thought to be solely wind-pollinated, at least two orders (Cycadales and Gnetales) contain insect-pollinated species (Bino et al., 1984; Norstog and Fawcett, 1989; Kato and Inoue, 1994; Terry et al., 2014; Rydin and Bolinder, 2015). In Cycadales, this zoophilous relationship has been identified to involve Coleoptera and Thysanoptera. Gnetales share this relationship with Diptera and Lepidoptera (Norstog and Nicholls, 1997; Klavins et al., 2005; Rydin and Bolinder, 2015). These unique relationships may have developed as mutualism or commensalism, from pollen predation, as a result of coevolution (Gilbert, 1979; Scott and Taylor, 1983; Stotz et al., 1999; Labandeira, 2000; Tschardt et al., 2004). Pennsylvanian coal balls, which are concretions of peat that preserve direct evidence of arthropod feeding behaviors, might provide evidence of Paleozoic palynivory (Scott and Taylor, 1983), adding to the fossil record of plant-animal interactions provided by fossilized arthropod remains.

## Late Atokan and Desmoinesian Coal Units of Iowa

Pennsylvanian		Moscovian		Iowa Stratigraphy, Selected Coals		Correlation of Iowa Coals to selected Illinois Coals	
				Desmoinesian		Marmaton Group	
Cherokee Group		Swede Hollow Fm.	Marshall				
			Kalo Fm.	Floriss Fm.	Summit	Houchin Creek (No. 4)	
Kilbourn Fm.	Blackoak	Mulky			Colchester (No. 2)		
		Atokan	Bashkirian	Bevier		Dekovan/Greenbush	
Moscovian	Pennsylvanian			Wheeler	Davis/Wiley		
		Desmoinesian	Marmaton Group	Whitebreast		Hermon	
Cherokee Group	Swede Hollow Fm.			Carruthers	Rock Island (No. 1)		
		Kalo Fm.	Floriss Fm.	unnamed			
Kilbourn Fm.	Blackoak			Laddsdale coals			
		Atokan	Bashkirian	Cliffland			
Moscovian	Pennsylvanian						
		Desmoinesian	Marmaton Group				

**Figure 1.** A stratigraphic section for the early to mid-Pennsylvanian coal-bearing systems in Iowa, adapted with permission from Raymond and McCarthy (2009). The age and compositions of coal ball assemblages appear on the right. All coal balls analyzed in this study came from one of two horizons in the Kalo Formation, the Blackoak, or the Cliffland coal.

In modern ecosystems, plant-eating arthropods can feed on living (phytophagy, palynivory) or dead plants (saprophagy: Kevan, 1968). Pollen consumption can occur in two locations, as palynivory or pollen predation, usually in the forest canopy, or on the forest floor as detritivory (Scott and Taylor, 1983). Spore-filled coprolites, relating to plant host interactions, are known from the late Silurian and Devonian (Edwards et al., 1995; Habgood, 2000; Habgood et al., 2003). The Carboniferous record shows a large diversification of these relationships in regards to both spore and pollen-filled coprolites (Baxendale, 1979; Scott and Taylor, 1983; Scott et al., 1992; Cutlip, 1997; Raymond et al., 2001).

Coal balls, which contain permineralized peat from Pennsylvanian swamps, provide a rich record of interactions between terrestrial arthropods and plants in the form of coprolites and damage to plant fossils (Scott and Taylor, 1983; something by Labandeira). Two types of arthropod coprolites occur in coal balls: brown coprolites filled with vegetative debris and golden coprolites filled with spore, pollen, and cuticle (Baxendale, 1979; Scott and Taylor, 1983, Raymond et al., 2001). Raymond et al. (2001) analyzed coprolites in Pennsylvanian coal balls originating from both medullosan and cordaitean peat. In addition to coprolites of all sizes filled with vegetative debris, Raymond et al. (2001) identified two types of pollen-filled coprolites which occurred in coal balls from the Kalo Formation of Iowa: 1, small golden fecal pellets (0.18 – 0.80 mm) containing pollen found in the secondary fertile shoots of compound cordaitean pollen cones; 2, large golden coprolites (1.3 – 5.6 mm) found in *Medullosa* stem peat (Raymond et al., 2001). The authors distinguished fecal pellets as composed solely of pollen or spores due to their light golden color. Large golden coprolites had a reddish-orange color due to the presence of cuticle as well as spores and pollen. Pollen-filled fecal pellets in cordaitean pollen cones may have resulted from palynivory rather than detritivory because these coprolites contain

masticated cordaitean pollen and primarily occur in cordaitean cones (Raymond et al., 2001; Grajeda et al., 2014; Grajeda et al., 2015; Lakeram et al., 2019).

Baxendale (1978) described a diverse assemblage of coprolites from the Middle Pennsylvanian of Kansas and Iowa and the Upper Pennsylvanian of Illinois. A number of coprolites were recorded containing pollen attributed to Cordaites and calamities. Labandeira (1998) identified coprolites consisting of marattialean fern spores of *Convolutispora* and *Apiculatosporites*, medulosan pre-pollen *Monoletes*, and Cordaite pollen attributed to *Florinite* in coprolites from the matrix of coal from Late Pennsylvanian Mattoon Formation (Calhoun Coal). These palynomorphs were found to always be intact in coprolites showing no signs of digestion (Labandeira, 2013).

A magnitude of coprolite types have been identified in Pennsylvanian permineralized peat. Comparisons of the size, morphology and texture of coal-ball coprolites with fecal samples of modern-day arthropods belonging to groups that may have been present in the Pennsylvanian suggest that oribatid mites (Kubiena, 1955; Baxendale, 1979; Scott and Taylor, 1983); collembola (Kuhnelt, 1976; Scott and Taylor, 1983); millipedes (Baxendale, 1979; Scott and Taylor, 1983) and insects belonging to Blattoptera, Megasecoptera, Orthoptera, Palaeodictyoptera, and Protorthoptera (Baxendale, 1979; Scott and Taylor, 1983) could have contributed coprolites to Late Pennsylvanian coal ball peat. Scott and his collaborators (Scott and Taylor, 1983; Scott et al., 1992) described possible arthropod groups that produced coprolites in a lycopsid-dominated coal-ball assemblage from the mid-Pennsylvanian: mites and collembolans may have produced the smallest, most abundant fecal remains, small cylindrical fecal pellets ranging in size from 10 - 100  $\mu\text{m}$ ; millipedes may have produced cylindrical coprolites ranging

in diameter from 200  $\mu\text{m}$  - 7 mm; ancient insects could have contributed large ( $\geq 1$  mm) coprolites.

Habgood (2000) and Habgood et al. (2003) investigated spore-filled coprolites in the Rhynie Chert, an Early Devonian permineralized peat. Because the spores in these coprolites were not masticated, they hypothesized that spore-filled coprolites originated from generalist detritivores, and interpreted spores as indigestible debris that passed intact through the detritivore gut. Labandeira (2013) viewed these spore-filled coprolites as a result of herbivory, which he categorized as palynophagy (the consumption or punching and sucking of whole palynomorphs). Oribatid mites have been found with significant quantities of pollen, along with mycelia inside their guts, and have been observed feeding primarily on dispersed conifer pollen (Grandjean, 1951 in Krantz and Lindquist, 1979). Labandeira (2002) described the types of evidence for identifying arthropod and plant interactions- plant reproductive biology, plant tissue damage by arthropods, dispersed coprolites, arthropod gut contents, and arthropod mouthparts. The definitive evidence for these relations is identifiable plant tissue in the gut cavity of arthropods, whereas mouthpart morphology and reproductive biology are based on an understanding of modern analogs.

In this paper, we investigate the occurrence of pollen-filled fecal pellets in cordaitan secondary fertile shoots and pollen-filled coprolites dispersed in coal balls of cordaitan leaf-mat peat. We expand upon Labandeira's (2002) criteria for identifying arthropod-plant interactions in the fossil record by considering the paleoecological context of spore and pollen-filled fecal pellets and coprolites, including their location in the peat and the availability of spore and pollen sources. If fecal pellets ( $\leq 200$   $\mu\text{m}$ ) filled with cordaitan pollen occur predominantly within the scales of cordaitan secondary fertile shoots, this suggests that they may result from palynivory

in the canopy, however, if fecal pellets filled with cordaitean pollen occur commonly in both cones and the peat matrix, they may result from detritivory on the swamp floor. Likewise, if cordaitean leaf-mat peats contain large amounts of undispersed pollen, large (200 – 900  $\mu\text{m}$ ) coprolites filled with cordaitean pollen could result from detritivory on the swamp floor. However, if large amounts of undispersed pollen seldom occur in coal balls, these coprolites probably signal palynivory by flying insects. We present additional work to identify palynivory or pollen detritivory in modern *Taxodium distichum* secondary fertile shoots (a morphological analog to cordaitean secondary fertile shoots), which might give insight into the taphonomy of ancient cordaitean pollen cones in Appendix 4. Additionally, we present work to recover palynological samples from cellulose acetate peels of coal-ball peat, which might enable palynological comparisons of coal balls and the surrounding coal in Appendix 3. The results of these investigations will contribute to our understanding of the ecological interactions in Pennsylvanian wetlands.



## MATERIALS AND METHODS

The coal balls used in this study contain cordaitean leaf-mat peat and come from three Iowa mines in the Kalo Formation, the Williamson No. 3, the Shuler, or the Urbandale (Fig. 1 and 2), which share a similar diverse cordaitean assemblage (Raymond et al., 2010). The Kalo Formation contains two coal beds. The Shuler and Urbandale mines most likely exploited the youngest Kalo Formation coal, the Cliffland coal bed; the Williamson No. 3 Mine exploited either the older Blackoak coal bed or the Cliffland coal bed.

Kalo Formation coals contain a diverse assemblage of cordaiteans which appears in Iowa and perhaps in some of the coals in the k<sub>8</sub> through l<sub>6</sub> interval of the Donets Basin (Snigirevskaya, 1972; Raymond et al., 2010). Cordaiteans contributed 50-70% of the peat in these deposits; tree ferns and seed ferns contributed most of the rest. Lycopside, usually the most important plant group other mid-to-late Pennsylvanian (Moscovian) peat swamps, seldom contributed more than 5% of the debris in coal balls from the Kalo Formation (Phillips et al., 1985; Raymond, 1988). Most cordaitean secondary fertile shoots occur in cordaitean leaf mats, which comprise from 4% - 10% of coal balls from the Blackoak and Cliffland coal beds (Raymond et al., 2001). Cordaitean leaf mats, which consist of cordaitean leaves, roots, and occasional branches, probably formed near the upper surface of the peat and contain a rich record of plant-arthropod interactions (Raymond et al., 2001).

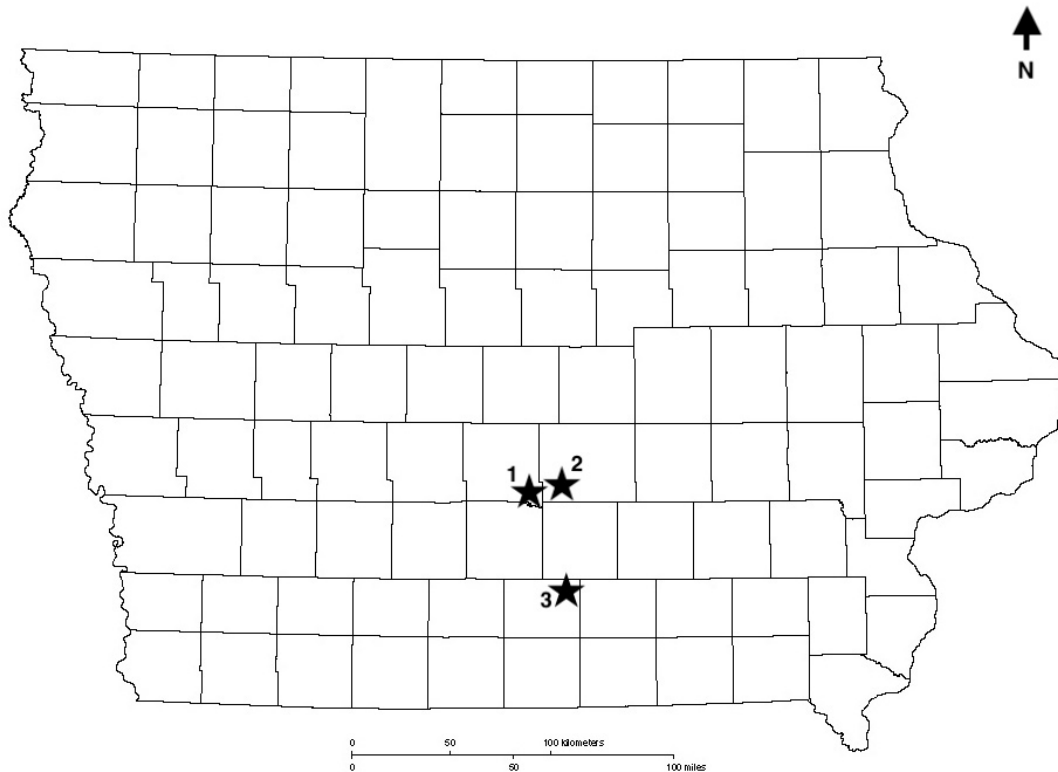
We investigate two samples of cordaitean cones for this study, both from the Thompson-Darrah coal-ball collection on loan to Texas A&M University from the Harvard Paleobotanical Herbarium. The mounted peel data set consists of 192 secondary fertile shoots of compound cordaitean cones mounted on 83 microscope slides (25 x 76 mm<sup>2</sup>). Darrah and his student made

the mounted peels in the 1930's and 1940's using the parlodion peel technique, mounting them on glass slides with Canada balsam (Darrah, 1936). The slides containing these cones were originally selected for a study of the pollen associated with different types of cordaitan cones representing a subset of all mounted peels of cordaitan cones in the Thompson-Darrah coal ball collection. Each mounted peel contains at least one secondary fertile shoot with some slides containing more than one. Cones in the mounted peel data set come from cordaitan leaf mats, based on the presence of layered cordaitan leaves surrounding the cones. The average area of mounted peels is approximately 1.7 cm<sup>2</sup>, and the average height perpendicular to the bedding plane of each is approximately 1 cm. Thus, the mounted peel data set samples approximately 141 cm<sup>2</sup> of the coal-ball surface, and 83 cm of leaf-mat peat measured perpendicular to the bedding plane. The use of mounted peels enables us to identify the content of fecal pellets in cordaitan cones and to assess its taphonomic condition. Additionally, the use of mounted peels enables us to identify the undispersed pollen (if present) in cordaitan cones and the leaf-mat peat immediately surrounding the cones.

The leaf-mat peel data set consists of 111 cordaitan secondary fertile shoots observed in 26 peels made from 22 coal balls that contain cordaitan leaf mats. These peels were made at Texas A&M University using the cellulose acetate peel process (Joy et al., 1956) and sample approximately 635 cm<sup>2</sup> of coal ball surface (average 22 cm<sup>2</sup>, range 12 - 47 cm<sup>2</sup>). The height of each coal ball measured perpendicular to the bedding plane averages 4 cm (range 2.5 - 6.5 cm), and the total sample of leaf-mat peat measured perpendicular to the bedding plane is 97 cm. The use of cones from cordaitan leaf-mat peels expands the number of cordaitan cones in the study and enables us to investigate possible biases in the data set of cones from mounted peels. In addition, because the peels provide a larger sample of leaf-mat peat than mounted peels (635 cm<sup>2</sup>

as opposed to 141 cm<sup>2</sup>) and include leaf-mat peat that is not immediately adjacent to cones, the cordaitan leaf-mat peels enable us to determine the distribution of pollen-filled fecal pellets ( $\leq 200 \mu\text{m}$ ) and pollen-filled coprolites ( $\geq 200 \mu\text{m}$ ) in the peat matrix.

## Location Map of Blackoak and Cliffland Coal Bearing Mines



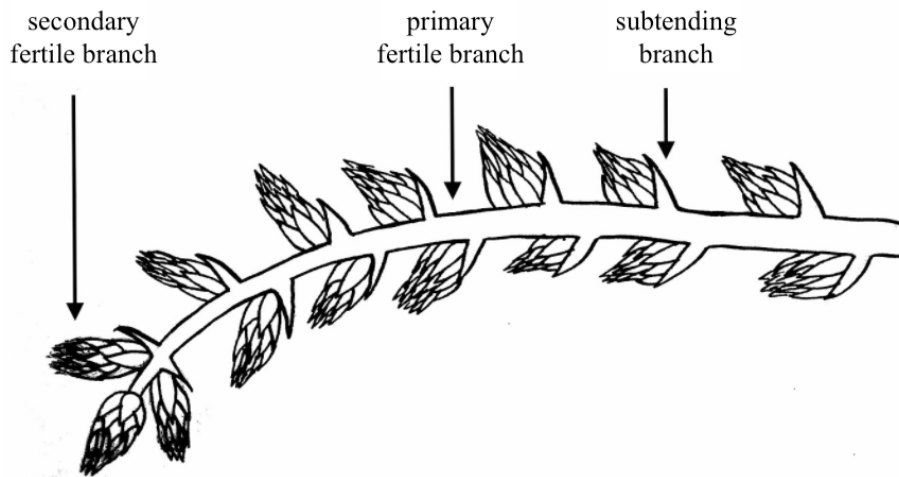
**Figure 2.** Iowa coal mines with permineralized peat from the Kalo Formation; 1, Urbandale Mine, Cliffland coal; 2, Shuler Mine, Cliffland coal; 3, Williamson No. 3 Mine, Blackoak or Cliffland coal, adapted with permission from Raymond et al. (2010).

### **Cordaitean cone morphology**

Cordaitean pollen cones are compound, consisting of a primary fertile shoot or branch that bears secondary fertile shoots in the axis of sterile bracts (Fig. 3). They are similar, but not identical to the compound pollen cones of modern *Taxodium distichum*. Secondary fertile shoots bear both sterile and fertile scales attached helically to the secondary fertile axis. Fertile scales bear 4 - 6 pollen sacs at the tip of the scale or along the margin, which release pollen once sexually mature (Fry, 1956). Cordaiteans and early conifers probably produced both pre-pollen

and pollen (Millay and Taylor, 1976). Pre-pollen, which germinated through the trilete mark, rather than the distal surface, functioned as pollen, but morphologically resembled spores (Florin, 1951; Chaloner, 1970; Millay and Taylor, 1974). Cordaitan pre-pollen is characterized by a trilete aperture; cordaitan pollen lacks a functional trilete aperture and apparently germinated through the distal surface (Millay and Taylor, 1974; 1976). Both had a relatively large saccus (Fig. 6A: Gomankov, 2009). The large saccus would have functioned to increase buoyancy in the air and thereby favored anemophily (pollination by wind: Schwendemann et al., 2007).

## Cordaitian Cone Morphology



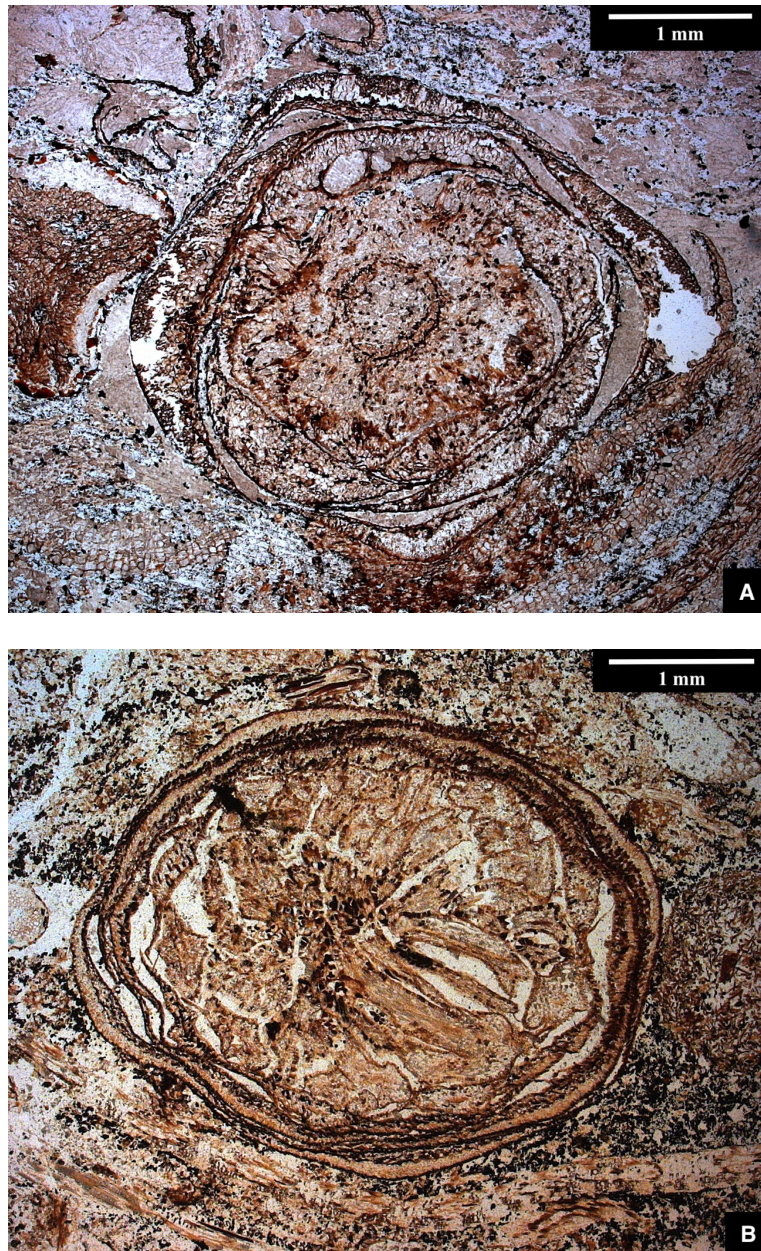
**Figure 3.** A reconstruction of the terminal portion of the male cordaitian secondary fertile shoot.

### Categories of secondary fertile shoots

All of the cordaitian secondary fertile shoots in the sample appear to be basal sections or secondary fertile shoots of pollen cones. As discussed by Fry (1956), coal balls rarely preserve cordaitian seed cones. Secondary fertile shoots are placed in one of the following categories: basal section, immature, mature, or taphonomically degraded (Fig. 4). Basal sections pass through the lower, sclerenchymatous sterile scales of the secondary fertile shoot, or cut across the base of the fertile scales below the pollen sacs and cannot be assigned to gender or developmental category unless they contain pollen grains or pollen aggregates caught between cone scales (Fig. 4A). Immature secondary fertile shoots have developing pollen sacs (Fig. 4B). Sexually mature secondary fertile shoots contain pollen scattered between the secondary fertile

shoot scales, male scales with the broken remnants of pollen sacs, or male scales with pollen sacs that contain pollen (Fig. 4C). We place all cones with pollen-filled fecal pellets in the mature category. Taphonomically degraded secondary fertile shoots have been highly taphonomically altered, making it difficult to determine their original gender and maturity as noted by Costanza (1984: Fig. 4D).

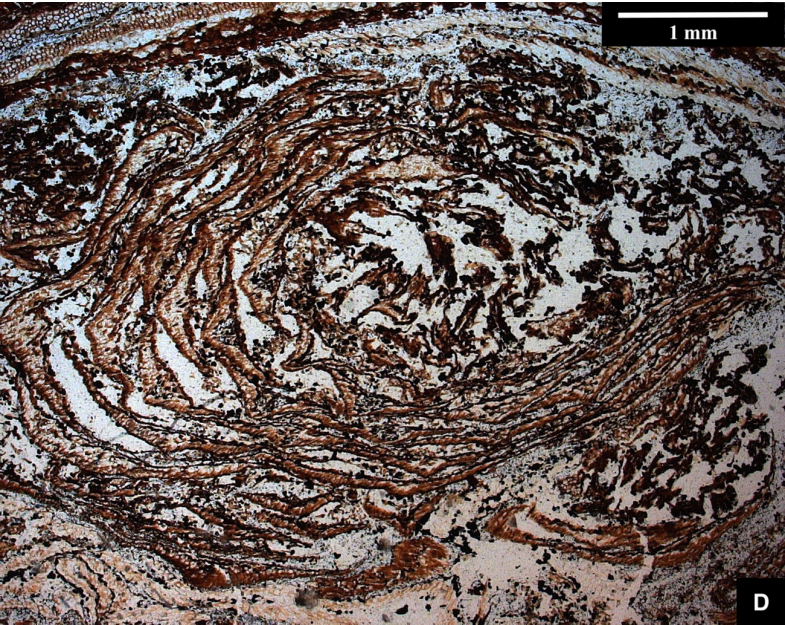
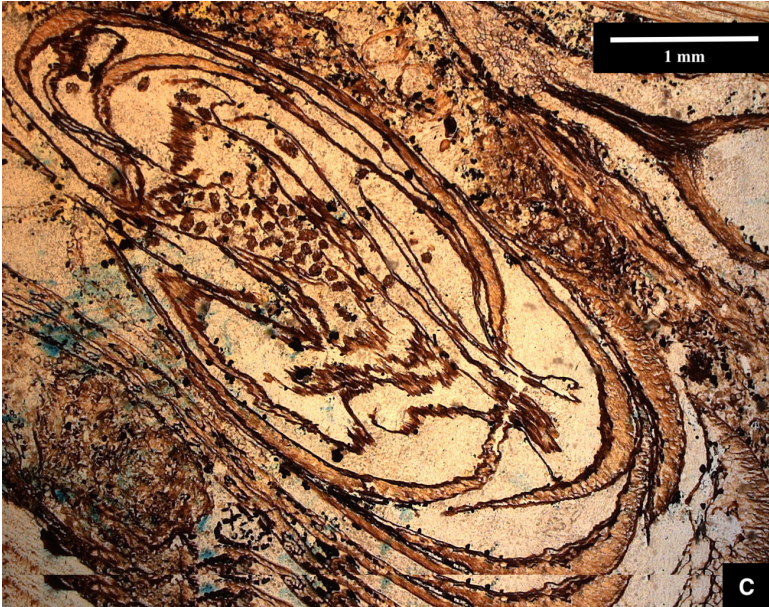
## Cordaitean Secondary Fertile Shoot Categories



**Figure 4.** Cone types identified by maturity level- A, basal section (Plate 26; Lakeram, 2019); B, immature (Plate 82; Lakeram, 2019); C, mature (Plate 04; Lakeram, 2019); D, taphonomically degraded (Plate 34; Lakeram).



Figure 4 Continued.



## **Mounted peels analysis**

We analyze mounted peels with a Zeiss Axioplan 2 Imaging microscope. In each peel, we record the number and size (largest minimum dimension) of vegetative and pollen-filled fecal pellets in each secondary fertile shoot, their spatial distribution, the condition of pollen grains in pollen-filled fecal pellets, and if possible, their identity. Additionally, we tally the number of cordaitean secondary fertile shoots, place them in fertile shoot categories (basal, immature, mature, taphonomically degraded), and record the presence of pollen. Scale bars and measurements are assigned using the Zeiss AxioCam software. Additionally, we visually scan the peat matrix surrounding secondary fertile shoots in the slides for evidence of fecal masses. Using an attached AxioCam HRc digital camera, images of each secondary fertile shoot were taken in order to create a photo library, which is housed in the TAMU Library's OAKTrust Digital Repository (Lakeram, 2019).

## **Cordaitean leaf-mat peels analysis**

We analyze leaf-mat peels with a Nikon SMZ1500 or Zeiss stereomicroscope, using a 1 cm square grid to isolate portions of a peel to accurately define its total contents (Phillips and DiMichele, 1981). In each leaf-mat peel, we tally the number of cordaitean secondary fertile shoots, place them in fertile shoot categories (basal, immature, mature, taphonomically degraded), and record the presence of pollen, and the size and color of fecal pellets between the cone scales or adjacent to the cone. Some secondary fertile shoots occur in more than one peel, either in peels taken from adjacent pieces of the coal ball or in multiple peels of one coal-ball face. In this case, we make observations concerning the presence or absence of pollen and fecal

masses in all available peels, but record the number of fecal masses in a single peel. Finally, we visually scan the entire peel and recorded the location of pollen-filled fecal pellets and coprolites in the leaf mat, as well as the presence and taxonomic affiliation (tree fern, sphenopsid, ‘fern’) of sporangia containing spores.

## **Statistical Methods**

The secondary fertile shoots in mounted peels from the Thompson-Darrah coal ball collection, may not represent an unbiased sample of cordaitan secondary fertile shoots. Typically, museum specimens and specimens chosen for mounted slides are larger, better preserved, or extraordinary in some way (Phillips et al., 1985). In addition, the subset of Thompson-Darrah slides used in this study was chosen originally because they contained large amounts of pollen. We use two methods to evaluate the statistical significance of differences between the mounted peel and leaf-mat peel data sets. We use Newcombe (1998) to determine the 95% confidence interval of the proportion of coprolites and cones in each category of the smaller, leaf-mat peel data set (see also Lowry, 1998-2020). We use the Mann Whitney U test in SPSS (IBM Corp., 2017) to test for significant differences between the number of pollen and vegetation-filled fecal pellets in cones from each data set. A non-parametric test was chosen due to datasets displaying a non-normal distribution based on the results of a Q-Q plot (Rosner, 2015). The relationships tested are as follows: 1, pollen-filled fecal pellets in cones from mounted peels and leaf-mat peels; 2, vegetative-filled fecal pellets in cones from mounted peels and leaf-mat peels.

## RESULTS

### Secondary fertile shoot categories

The 83 slides of mounted peels contain 192 secondary fertile shoots. Of these, 44% are mature and the remaining split approximately equally among the basal, immature and taphonomically degraded categories (Table 1). The 26 leaf-mat peels contain 111 secondary fertile shoots. Of these, 46% are mature, 25% are basal sections and the remaining are split approximately equally between immature and taphonomically degraded (Table 1). The proportions of immature, mature, taphonomically degraded, and basal sections in the larger mounted peel data set fall within the 95% confidence interval of proportions in the smaller, leaf-mat peel dataset (Newcombe, 1998, Lowry, 1999). Thus, both data sets have similar percentages of mature, immature, and degraded secondary fertile shoots, as well as similar percentages of basal sections. (Table 1).

**Table 1.** The number of secondary fertile shoots in each category from mounted peels and leaf-mat peels. The 95% confidence intervals are for the smaller, leaf-mat peel data set.

#### Secondary Fertile Shoot Categories

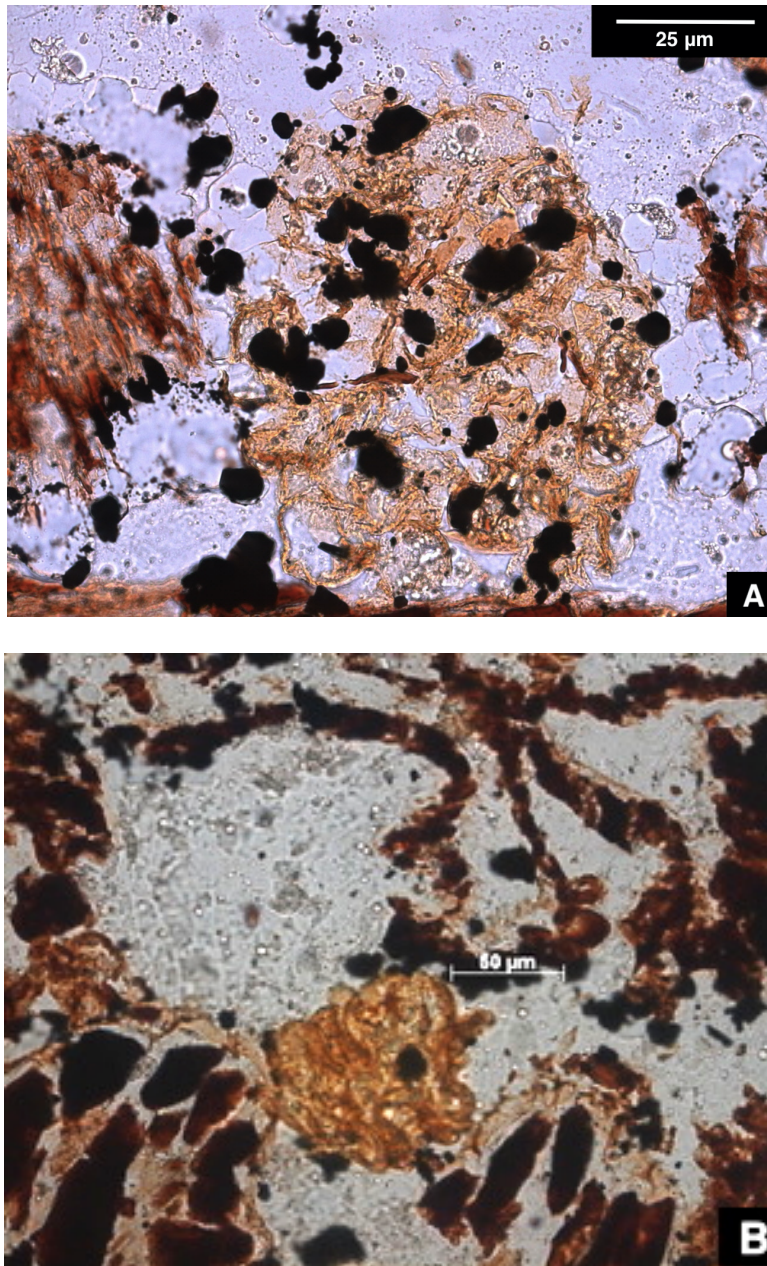
Data Set	Immature	Mature	Degraded	Basal	Total
Mounted peels	21%	44%	17%	18%	192
Leaf-mat peels	14%	49%	12%	25%	111
95% Confidence Interval <sup>a</sup> (leaf-mat peel)	9 - 22%	40 - 59%	6 - 18%	18 - 34%	

<sup>a</sup>Newcombe (1998); Lowry (1998-2020)

## Coprolite types

Four types of fecal masses occur in cordaitan secondary fertile shoots and the leaf-mat peat: 1, small pollen-filled fecal pellets (golden in color), circular to ovoid in cross-sectional shape, ranging in size from 20 - 200  $\mu\text{m}$  (fig 5A). Only a small percentage have identifiable palynomorphs; however when identifiable, they consist of fragmented *Florinites* and perhaps, *Cordaitina*; 2, small vegetation-filled fecal pellets (brown in color), circular to ovoid in cross-sectional shape, ranging in size from 20 - 200  $\mu\text{m}$ , composed of macerated vegetative debris (fig 5C). These occur in both cordaitan secondary fertile shoots and the peat matrix. However, we do not count vegetation-filled fecal pellets in the peat matrix of coal balls other than to note their presence and general abundance; 3, large palynomorph-filled coprolites (golden in color) elongated in cross-sectional shape, ranging in size from >200 - 900  $\mu\text{m}$  (fig 5B). Of the 60 palynomorph-filled coprolites in the mounted and leaf-mat peels, 65% consist of fragmented *Florinites* pollen and occasional entire grains; 8% consist of macerated palynomorphs with recognizable *Florinites* pollen or pollen fragments near the edge; 27% consist of macerated palynomorphs (Table 2). 4, vegetative-filled coprolites (dark in color), ovoid in cross-sectional shape, ranging in size from >200 - 4500  $\mu\text{m}$  (fig 5D).

## The Types of Coprolites Found in Cordaitean Secondary Fertile Shoots and Leaf-mat Peat



**Figure 5.** Coprolite types identified by composition and size- A, pollen-filled fecal pellets in a cordaitean secondary fertile shoot (Plate 27A; Lakeram); B, a pollen-filled fecal pellet in a cordaitean secondary fertile shoot showing partially intact grains of *Florinites*; C, a large pollen-filled coprolite from the cordaitean leaf-mat peat (Plate 71; Lakeram); D, a vegetative-filled coprolite from the cordaitean leaf-mat peat (Plate 15; Lakeram); E, a large vegetative-filled coprolite from the cordaitean leaf-mat peat (Plate 83; Lakeram).

Figure 5 Continued.

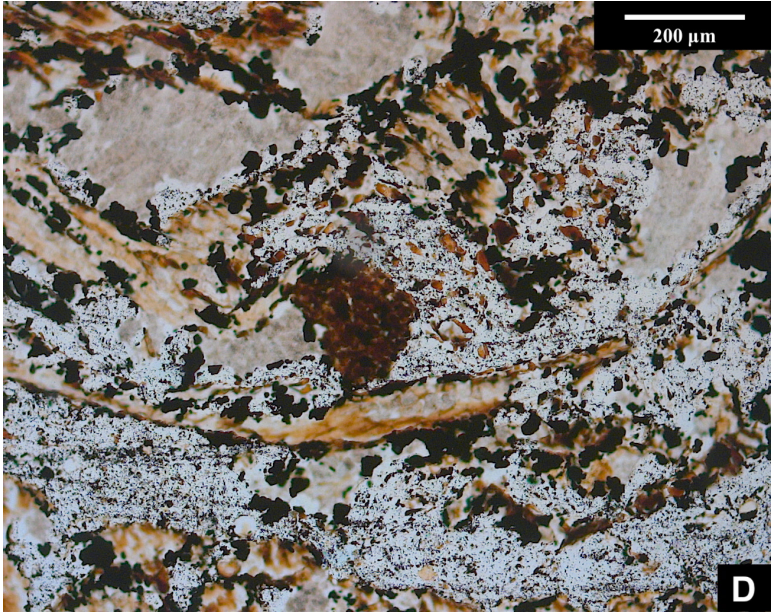
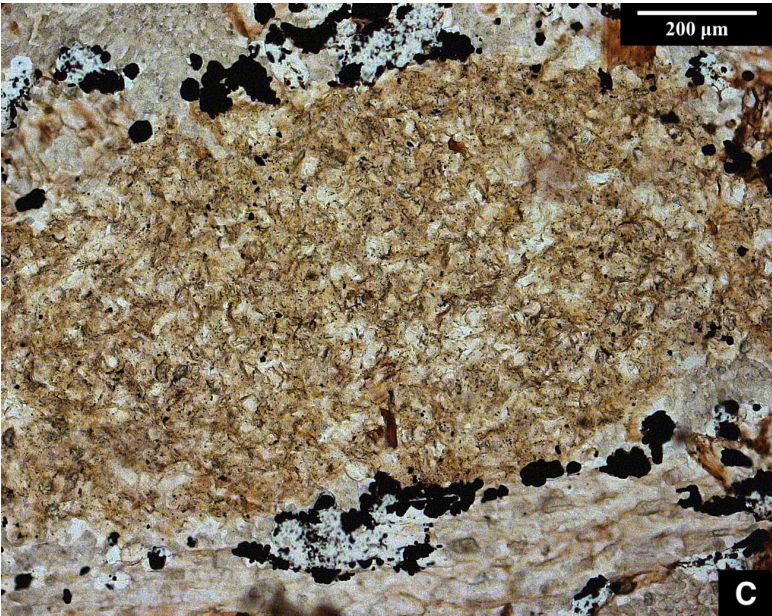
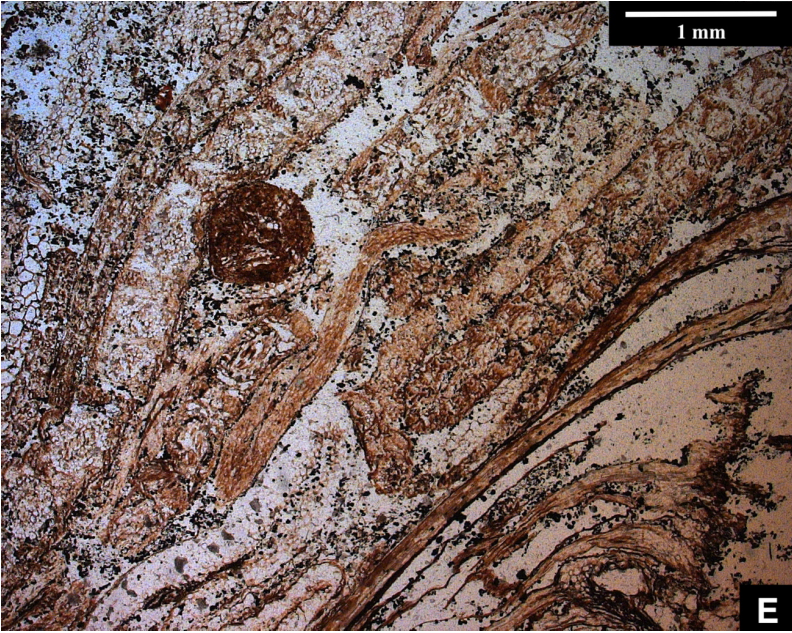


Figure 5 Continued.





**Table 2.** The condition and identity of palynomorphs in palynomorph-filled coprolites (>200 – 900  $\mu\text{m}$ ) from the mounted and leaf-mat peels.

**Palynomorph Condition and Identity**

Data Set	<i>Florinites</i> pollen and saccus fragments	Macerated palynomorphs rare <i>Florinites</i> pollen and saccus fragments	Macerated palynomorphs	Total
Mounted peels	39 (65%)	2 (3%)	15 (25%)	56
Leaf-mat peels	NA	2 (3%)	1 (2%)	4

## **Fecal pellet distribution in cordaitean secondary fertile shoots**

Overall, 20 - 30% of the secondary fertile shoots in each data set contain fecal pellets ( $\leq 200 \mu\text{m}$ ) of some type (Table 3). A slightly higher percentage of secondary fertile shoots from leaf-mat peels contain fecal pellets (30%) than from the mounted peel data set (22%); however, the 95% confidence limit of the percentage from the smaller data set (leaf-mat peel) overlaps that of the larger (mounted peel) data set, and the difference is not statistically significant (Table 3). Mature secondary fertile shoots are more likely to have fecal pellets than other cone categories: approximately half of the mature secondary fertile shoots in both data sets have fecal pellets (48% in the mounted peels; 57% in the leaf-mat peels: Table 3). Further, in both populations, nearly half of mature cones contained pollen-filled fecal pellets (44% in the mounted peels; 50% in the leaf-mat peels: Table 3). Although both populations have similar percentages of mature cones with pollen-filled fecal pellets, significantly more mature secondary fertile shoots in leaf-mat peels have vegetation-filled fecal pellets than in mounted peels (33% in leaf mat peels; 8% in mounted peels: Table 3). The 95% confidence interval of the smaller, leaf-mat percentage is 22 - 47%, suggesting that this difference is statistically significant (Newcombe, 1998; Lowry, 1998 - 2020). In both data sets, basal sections and immature secondary fertile shoots occasionally contained vegetation-filled fecal pellets, from 3% to 10% of all specimens in these categories (Table 3).

Fecal pellet count data reflect similar trends, in both data sets, most fecal pellets occur in mature secondary fertile shoots (96% in mounted peels; 97% in leaf-mat peels: Table 4), and most of these fecal pellets are pollen-filled (84% in mounted peels; 60% in leaf-mat peels; Table 4). Similarly, the 95% confidence limits around proportions in the smaller (leaf-mat peel) data

set, indicate that mature secondary fertile shoots from leaf-mat peels have significantly more vegetative fecal pellets, and significantly fewer pollen-filled fecal pellets than those from the mounted peel data set (Table 4). To further test the relationship between both data sets, we also investigated differences in the number of pollen-filled and vegetation-filled fecal pellets using the Mann Whitney U test. In total, 451 pollen-filled fecal pellets and 122 vegetative-filled fecal pellets occurred in cordaitan secondary fertile shoots in the combined data sets (Table 4). A large proportion of secondary fertile shoots did not contain fecal pellets, which resulted in the dataset displaying a non-normal distribution based on the results of a Q-Q plot (Rosner, 2015). Results of a Mann Whitney U test, which is the appropriate test to evaluate differences in the mean of non-normal variables between two populations, indicate that the average number of vegetative-filled fecal pellets per cordaitan secondary fertile shoot did not differ significantly between the two data sets, however, the average number of pollen-filled fecal pellets in secondary fertile shoots did (Table 5).

Most of the 135 mature secondary fertile shoots in the combined data sets contain relatively small amounts of undispersed pollen; only 14 contain copious amounts of undispersed pollen in pollen sacs, or in the center of the cone surrounded by pollen-sac remnants. Among all mature pollen cones, 47% contain pollen-filled fecal pellets; among mature pollen cones with copious amounts of undispersed pollen, only 14% contain pollen-filled fecal pellets, which is significantly lower than 47% (Table 6).

**Table 3.** Cordaitan secondary fertile shoots containing fecal pellets. Pollen and vegetation-filled fecal pellets are abbreviated respectively as p-f and v-f. Bold percentages are statistically significantly different.

**Secondary Fertile Shoots Containing Fecal Pellets**

Data set	Immature		Mature				Total	Degraded	Basal	All
	v-f	p-f	v-f	both	w/p-f	w/v-f		v-f	v-f	
Mounted peels	10%	37%	<b>1%</b>	<b>7%</b>	44%	<b>8%</b>	<b>45%</b>		3%	22%
Leaf-mat peels	6%	24%	<b>13%</b>	<b>26%</b>	50%	<b>33%</b>	<b>57%</b>	NA	NA	30%

95% Confidence Interval<sup>a</sup> (leaf-mat peel) (1-28%) (15-37%) (6-24%) (16-39%) (37 - 63%) (22 - 47%) (44 - 70%) (21 - 38%)

<sup>a</sup>Newcombe, 1998; Lowry, 1998-2020

**Table 4.** The distribution of small fecal pellets in cordaitan secondary fertile shoots. Percent values in rows reflect the percentage out of all cones with fecal pellets in that data set. Pollen and vegetative-filled fecal pellets are abbreviated respectively as p-f and v-f. Bold percentages are statistically significantly different.

**The Distribution of Fecal Pellets in Cordaitan Secondary Fertile Shoots**

Data set	Immature		Mature			Degraded	Basal	Total		All
	v-f	p-f	v-f only	v-f w/p-f	total	v-f	v-f	p-f	v-f.	
Mounted peels	4%	<b>84%</b>	<1%	<b>11%</b>	96%		<1%	<b>84%</b>	<b>16%</b>	452
Leaf- mat peels	3%	<b>60%</b>	<b>6%</b>	<b>31%</b>	97%			<b>60%</b>	<b>40%</b>	122
95% Confidence Interval <sup>a</sup> (leaf-mat peel)	(1 - 7%)	(51 - 68%)	(3 - 12%)	(24 - 40%)	(82 - 99%)			(51 - 68%)	(47 - 65%)	

<sup>a</sup>Newcombe, 1998; Lowry, 1998-2020

**Table 5.** The results of a Mann-Whitney U test analyzing the relationship of fecal pellet distribution in cordaitean secondary fertile shoots in the mounted and leaf-mat peels data set.

**The Statistical Relationship between the Mounted and Leaf-mat Peels Data Set**

Scale	Group	N	Mean	P-value
p-f in all cones	Mounted peels	378	1.97	0.289
	Leaf-mat peels	73	0.56	
v-f in all cones	Mounted Peels	54	.281	0.012
	Leaf-mat Peels	46	0.42	

**Table 6.** The percentage of all mature pollen cones and mature cones with abundant undispersed pollen that have pollen-filled fecal pellets. Pollen-filled fecal pellets are abbreviated as p-f.

**Frequency of Pollen-filled Fecal Pellets in Cones with Large Amounts of Undispersed Pollen**

Data Set	Total	Number with p-f fecal pellets (percent)	95% confidence interval <sup>a</sup>
All mature cones	135	64 (47%)	39 - 56%
Mature cones with abundant pollen	14	2 (14%)	4 - 40%

<sup>a</sup>Newcombe, 1998; Lowry, 1998-2020

## **Pollen-filled fecal pellets in cordaitan secondary fertile shoots and the peat matrix**

A small number of pollen-filled fecal pellets occur outside the cone scales of cordaitan secondary fertile shoots, in the peat matrix (14% in the mounted peels; 12% in the leaf-mat peels: Table 7). Because exterior cone scales may not appear in all sections of a secondary fertile shoot, we considered all fecal pellets touching the exterior of the outermost visible cone scale, or no further from the outermost visible cone scale than the average distance between other cone scales for that shoot as being within a secondary fertile shoot. A single pollen-filled coprolite with a cavity containing three pollen-filled fecal pellets, interpreted as coprophagy (Raymond et al., 2001) occurs in the matrix of a leaf-mat peel (3%).

## **The size distribution of pollen-filled fecal pellets and coprolites**

Pollen-filled fecal pellets in cones and the peat surrounding them range in size from 20-200  $\mu\text{m}$  in their largest minimum dimension. However, most pollen-filled fecal pellets in both mounted and leaf-mat peels fall between 40 - 120  $\mu\text{m}$  (Fig. 6A and B). The small number of pollen-filled fecal pellets in the 180 – 200  $\mu\text{m}$  size class may be pollen-filled coprolites small enough to become trapped by the cone scales, and fall to the swamp floor with the cone. In addition to pollen-filled fecal pellets, cordaitan-leaf mat peat also contains larger pollen-filled coprolites, 200 - 900  $\mu\text{m}$  in their largest minimum dimension. The histogram of pollen-filled coprolites size classes indicates peaks in the 300–399  $\mu\text{m}$  size category and in the 800–899  $\mu\text{m}$  size category (Fig. 6C).

**Table 7.** The distribution of pollen-filled fecal pellets in cordaitan secondary fertile shoots and the peat matrix. Pollen-filled fecal pellets are abbreviated as p-f.

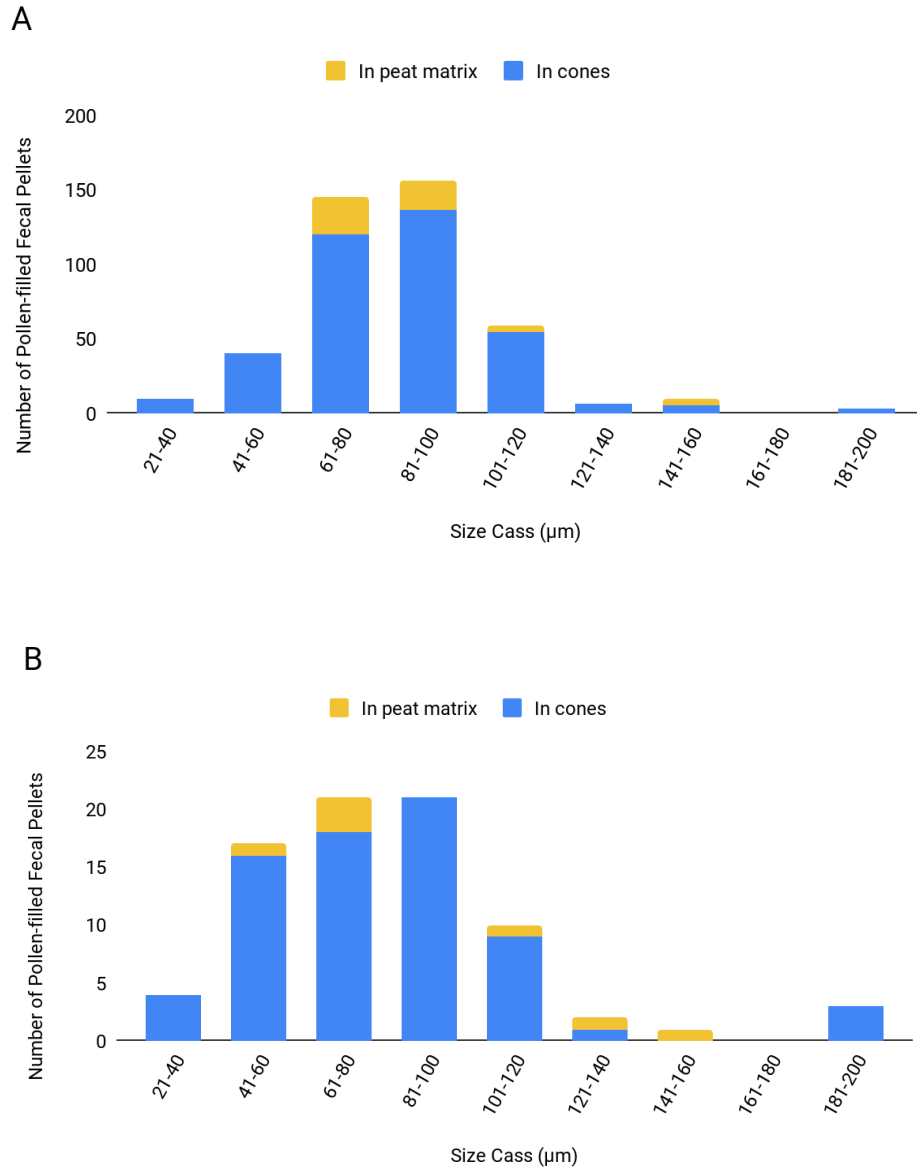
**The Distribution of Fecal Pellets in Cordaitan Cones and the Matrix**

Data Set	p-f fecal pellets in cones	p-f fecal pellets in peat matrix	p-f fecal pellets in pollen-filled coprolites (coprophagy)	Total
Mounted Peels	86%	14%	NA	438
Leaf-mat Peels	85%	12%	3%	86
95% confidence interval <sup>a</sup>	(76 - 91%)	(6 - 20%)	(1 - 10%)	

<sup>a</sup>Newcombe, 1998; Lowry, 1998-2020

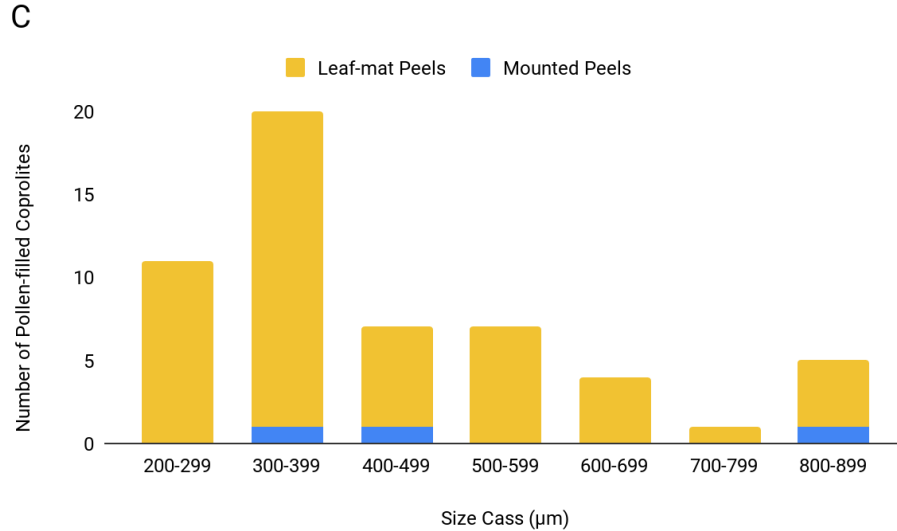


## The Size Distribution of Pollen-filled Fecal Pellets and Coprolites



**Figure 6.** A) A stacked histogram of the distribution in size of pollen-filled fecal pellets in cordaitean secondary fertile shoots and the peat matrix for the mounted peels. B) A stacked histogram of the distribution in size of pollen-filled fecal pellets in cordaitean secondary fertile shoots and the peat matrix for the leaf-mat peels. C) A stacked histogram of the distribution in size of pollen-filled coprolite from the cordaitean leaf-mat peat for the mounted and leaf-mat peels.

Figure 6 Continued.



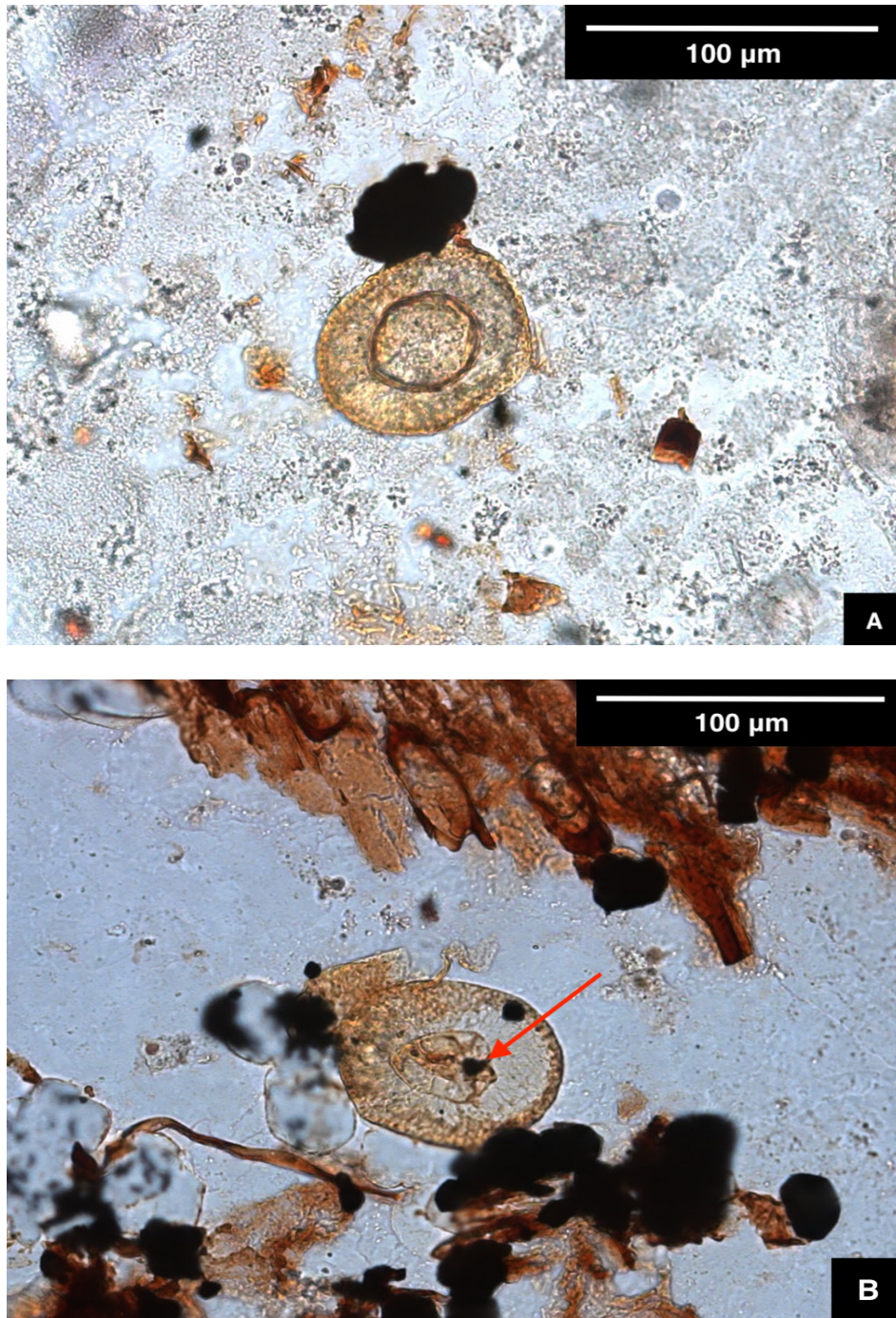
### Pollen types in Cordaitean leaf-mat matrix

The mounted peel data set captures 303 slices of 192 secondary fertile shoots. Of these 303 slices, 39% (119/303) contained pollen, most attributed to the genus *Florinites* the North American cordaitean pollen grain associated with *Cordaianthus concinus* and *Cordaianthus shuleri* secondary fertile shoots (Fig. 6A: Fry, 1956; Costanza, 1984; Rothwell, 1993). In general *Florinites* pollen has a broadly spherical corpus and is monosaccate (Ravn, 1986). Grains of *Florinites* measure 60 - 70 µm in diameter (n=5); the exterior of the saccus is psilate whereas the interior is reticulate (Fig 7A: Schopf et al., 1944). The corpus may have a trilete mark, often viewed as vestigial (Schopf et al., 1944; Smith and Butterworth, 1967), and in coal balls, is sometimes pyritized. The total saccus width is about  $\frac{1}{3}$  to  $\frac{1}{2}$  of the overall maximum diameter. Some grains of *Florinites* in secondary fertile shoots investigated for this study bear a ruptured trilete mark, in which the pollen wall appeared to be peeled back and folded over (fig. 6B).

*Florinites* is often found dispersed in cordaitean secondary fertile shoots and pollen-filled fecal pellets and coprolites.

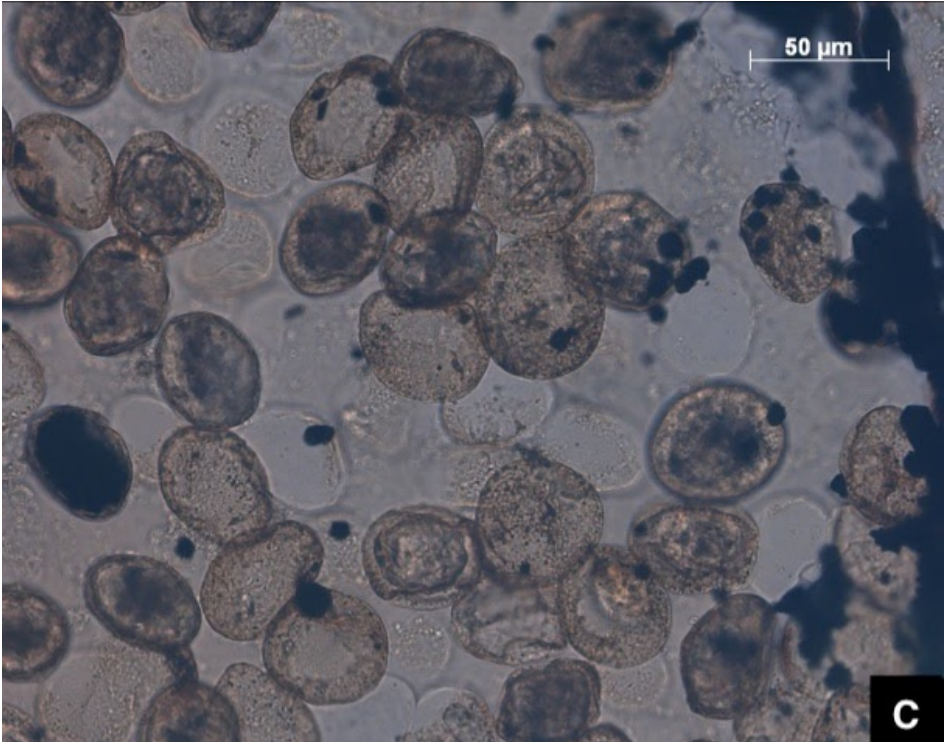
A small percentage of pollen grains found in the study sample possibly belong to *Cordaitina* but appear to differ from *Cordaitina sp.* identified by Ravn (1986) from the Kilbourn and Cliffland coal beds in size (fig. 6C). In general, *Cordaitina* is a monosaccate grain that is relatively elliptical in shape and is inaperturate (Samoilovich, 1953; Hart, 1965). Grains of *Cordaitina* in coal balls measure  $\approx 54 \mu\text{m}$  in length and  $\approx 42 \mu\text{m}$  in width ( $n=5$ ;  $W/L = 0.777$ ) and appear to have a psilate surface texture. The saccus width of *Cordaitina* is  $\frac{1}{4}$  of the overall maximum diameter. A small proportion of *Cordaitina* grains in coal balls appear to have their saccus folding inward due to taphonomic. This can be identified by the exine creating a dark line which is overlapped by the folded saccus. *Cordaitina* is primarily found in cordaitean secondary fertile shoots and seldom occurs in the cordaitean leaf-mat peat.

## Pollen Types Identified



**Figure 7.** A) A grain of *Florinites* measuring 60 - 70 µm in diameter with a reticulate surface texture B) A single pollen grain of *Florinites* displaying a ruptured trilete mark, indicated by the arrow. C) Pollen grains of a *Cordaitina* measuring 80 - 90 µm in diameter with a psilate surface texture.

Figure 7 Continued.



## DISCUSSION

### **Coprolites and coprolite producers**

Golden coprolites from the Kalo Formation fall into two size categories, fecal pellets ( $\leq 200 \mu\text{m}$  in their largest minimum dimension), which occur primarily in cordaitean secondary fertile shoots and larger coprolites ( $>200 - 900 \mu\text{m}$  in their largest minimum dimension), which occur scattered among other plant debris in cordaitean leaf-root peat (Table 3; Figure 6A and B). Because 85% or more of the golden fecal pellets occur associated with cordaitean pollen cones, and because the only identifiable palynomorphs in them belong to *Florinites* or *Cordaitina*, we assume that the small golden fecal pellets in our data set are pollen-filled (Fig. 5A, 5B). Based on their morphology and size, pollen-filled fecal pellets  $>200 \mu\text{m}$  found in cordaitean secondary fertile shoots resemble those of collembolans and oribatid mites; although they could derive from an extinct microarthropod group (Scott and Taylor, 1983; Cutlip, 1997; Raymond et al., 2001; Lakeram et al., 2019). Previous workers used a smaller size range for fecal pellets attributed to oribatid mites and collembolans. Habgood et al. (2003) used  $<100 \mu\text{m}$ . Scott and Taylor (1983) used  $<150 \mu\text{m}$  (generally  $30 - 60 \mu\text{m}$ ) for coprolites attributed to mites and collembolans. Fecal pellets in coal balls, which Labandeira et al. (1998) attributed to mites, ranged from  $47 - 107 \mu\text{m}$ . Mite coprolites are ovoid in shape and up to  $150 \mu\text{m}$  in diameter (Labandeira et al. 1998); Scott and Taylor, 1983) imaged fecal pellets that measured  $150 \mu\text{m}$  in length inside the gut of modern oribatid mites. Collembola fecal pellets range in size from  $30 - 180 \mu\text{m}$  in diameter and often show clear evidence of the material that was consumed by the producer (Christiansen, 1964; Labandeira et al., 1998). We use  $\leq 200 \mu\text{m}$  as a cut-off because some of the pollen-filled fecal pellets preserved within the cone scales of secondary fertile shoots in our data are  $200 \mu\text{m}$  in

diameter. However, most pollen-filled fecal pellets from secondary fertile shoots were  $\leq 160 \mu\text{m}$  in diameter (Figs. 6A, 6B). The small number of pollen-filled fecal pellets in the 180 – 200  $\mu\text{m}$  size class may have been produced by the same organisms that produced pollen-filled coprolites in the peat matrix.

Most of the cordaitan leaf-root coal balls investigated in this study also contain larger golden coprolites, from  $>200 - 900 \mu\text{m}$  in their largest minimum dimension (fig 6C). Cordaitan pollen and pollen fragments, occurring in 65% of the population, are the only recognizable palynomorph in these coprolites (Table 2). Thus, we assume that all golden coprolites encountered in cordaitan leaf-mat peat are pollen-filled. Baxendale (1979) reported large coprolites filled with cordaitan pollen from the Calhoun Coal (Berryville locality, Late Pennsylvanian) and either the Mineral or Fleming Coal (West Mineral locality, Late Pennsylvanian). Labandeira (2013) also reported large coprolites filled with cordaitan pollen from the Calhoun Coal. Large coprolites filled with cordaitan pollen from this locality figured by Baxendale (1977) and Labandeira (2013) were respectively approximately  $440 \mu\text{m}$  and  $370 \mu\text{m}$  in diameter. Scott (1977) recovered 12 large (up to  $1000 \mu\text{m}$  in the largest minimum diameter) coprolites from a Pennsylvanian (Duckmantian) shale in Great Britain, one filled with cordaitan pollen, but did not report the size of the pollen-filled coprolite. Raymond et al. (2001) reported larger pollen-filled coprolites (1.3–5.6 mm) from medullosan stem peat, but not cordaitan leaf-mat peat, perhaps due to the small amount of cordaitan leaf-root peat used in that study. Raymond et al. (2001) based their conclusions on three leaf-mat coal balls, with a combined surface area of  $171 \text{ cm}^2$ . The surface area of leaf-mat coal balls used for this study is  $776 \text{ cm}^2$  ( $141 \text{ cm}^2$  in the mounted peels,  $635 \text{ cm}^2$  in the leaf mat peels). Based on size and morphology, the producers of larger pollen-filled coprolites could be millipedes or insects,

including the Megasecoptera and Palaeodictyoptera, as well as Pennsylvanian grylloblatids orthopteroids and roachoids (Baxendale, 1979; Scott and Taylor, 1983). Many groups formerly placed in Protorthoptera are now considered grylloblatids (Grimaldi and Engel, 2005).

### **Identifying Palynivory in the Fossil Record**

Pollen of modern-day plants contains high levels of proteins, amino acids, starch, lipids, and vitamins, making them a valuable and nutritious food source (Haslett, 1989; Beckman and Hurd, 2003; Lundgren and Wiedenmann, 2004; Vandekerkhove and De Clercq, 2010; Di Pasquale et al., 2013). Pre-pollen, although possibly different in nutritional content from modern pollen, also could have provided a rich food source to palynivores. The criteria for identifying palynivory in the fossil record include- entomophilous plant reproductive features; insect damage to plant reproductive tissues; matrix dispersed coprolites; insect gut contents, and insect mouthpart and ovipositor structure (Labandeira, 1998a; Labandeira, 2002; Labandeira, 2003). Labandeira (2003, 2013) assumed that all spore or pollen-filled coprolites result from palynivory (consumption of spores or pollen prior to dispersal). However, permineralized peat deposits often contain concentrated masses of pollen and spores in the peat matrix, which could serve as a concentrated source of spores and pollen for detritivory. In the Early Devonian Rhynie Chert, concentrations of spores occur in sporangia as well as in the peat matrix (Gensel and Andrews, 1984; Habgood et al., 2003). Permineralized peat assemblages in coal balls contain masses of spores and pollen in sporangia, cones, and other reproductive organs, and also in spore and pollen-filled coprolites. Thus, we consider both the location of pollen-filled fecal pellets and coprolites, and the location of pollen concentrations within the peat in our assessment of cordaitan palynivory in Pennsylvanian swamp communities.



Fecal pellets from coal balls filled with macerated pollen could result from either detritivory or palynivory. Cordaitean pollen cones commonly contain small amounts of undispersed pollen, which might have been sufficient to sustain small detritivores, such as oribatid mites and collembolans. In modern ecosystems, oribatid mites and collembolan consume dispersed pollen from the surface of rocks and soil (Grandjean, 1951 in Krantz and Lindquist, 1979; Gisin, 1948; Christiansen, 1964). Three species of alpine oribatid mites (*Saxicolestes auratus* Grandjean, *Litholestes altitudinus* Gr. and *Zetorchestes flabrarius* Gr) live underneath rocks and eat dispersed conifer pollen that falls onto the rock surface; Grandjean reported significant quantities of pollen along with a small proportion of fungal mycelia in the digestive tracts of these three species (Grandjean, 1951 in Krantz and Lindquist, 1979).

Two lines of evidence suggest that these fecal pellets derive from palynivory in the canopy, rather than detritivory in the peat. The first is the association between pollen-filled fecal pellets and cordaitean pollen cones. Most pollen-filled fecal pellets occur within the cone scales of cordaitean pollen secondary fertile shoots (86% in the mounted peels; 85% in the leaf-mat peels: Table 7). In leaf-mat peels, where we can document the distribution of pollen-filled fecal pellets throughout the coal ball, nearly all of the pollen-filled fecal pellets that are not in cordaitean cones occur close to cordaitean cones in the same bedding plane, consistent with the hypothesis that these fecal pellets originated in cordaitean cones in the canopy and were shaken loose as the cones fell to the peat surface. Exceptions are the pollen-filled fecal pellets that result from coprophagy (the consumption of coprolites by other organisms) in cavities within large pollen-filled coprolites. The second is the scarcity of fecal pellets in cones with large concentrations of cordaitean pollen. While many cordaitean cones contain small amounts of undispersed pollen, anthers with pollen sacs full of undispersed pollen rarely occur. In the

combined data sets, 10% of mature secondary fertile shoots have pollen sacs filled with undispersed pollen or large masses of pollen surrounded by pollen-sac remnants (Table 6). Of these, 14% have pollen-filled fecal pellets, significantly fewer than the percentage of all mature cones with pollen-filled fecal pellets in either data set (Table 6). This pattern of fecal pellets occurring in cones with relatively little remaining pollen is consistent with pollen consumption by palynivores in the canopy. Cones with large amounts of undispersed pollen that fell to the peat surface would be sheltered from further attack. If detritivores produced pollen-filled fecal pellets in the peat, we would not expect cones with large amounts of undispersed pollen to be sheltered from attack. In addition to secondary fertile shoots with large amounts of undispersed pollen, the largest concentrated source of cordaitan pollen in the cordaitan leaf-mat peat was pollen-filled coprolites, yet coprophagy of these coprolites appears to have been rare. Of the 60 pollen-filled coprolites in both data sets, only 3% experienced coprophagy (Table 7). Both the distribution of pollen-filled fecal pellets in cordaitan leaf-mat peat and the low occurrence of coprophagy in pollen-filled coprolites suggest that palynivores rather than detritivores produced the pollen-filled fecal pellets in cordaitan cones.

Over 40% of mature cordaitan pollen cones in both datasets have pollen-filled fecal pellets, indicating that cordaitan pollen was a valuable resource to its microarthropod consumers. This percentage is higher than the percent herbivory observed on foliage species in the Late Pennsylvanian Williamson Drive flora of Texas, although, in two species from that assemblage, *Pseudomariopteris cordata-ovata*, and *Annularia carinata*, over 30% of specimens showed signs of herbivory (Xu et al., 2018). Both the specificity of attack (consumers primarily ate cordaitan pollen) and high frequency of attack argue for herbivory rather than detritivory as the cause. The physiological adaptations for consuming and processing material attained by

herbivory are much more intricate allowing for more specialization among herbivores than detritivores (Brues, 1924; Labandeira, 1998). Many modern herbivores have evolved specializations to target specific plant tissue, which can typically be identified in their excrement. In contrast, detritivores usually show a large diversity in the consumed material from their excrement, with microarthropod detritivores showing a strong preference for fungi, which are higher in Nitrogen than most plant tissue (Seastedt, 1984; Lussenhop, 1992).

Cones in both datasets also show signs of detritivory in the form of vegetation-filled fecal pellets, although some vegetation-filled fecal pellets in cones that co-occur with pollen-filled fecal pellets may result from palynivorous microarthropods chewing through vegetative tissues to access pollen. Relatively few mature secondary fertile shoots from mounted peels had vegetation-filled coprolites (1% had only vegetation-filled coprolites; 6% had both pollen-filled and vegetation-filled coprolites: Table 4). More mature secondary fertile shoots in leaf-mat peels had vegetation-filled coprolites (13% had only vegetation-filled coprolites; 26% had both; Table 3). This difference is statistically significant. Likewise, mature secondary fertile shoots from mounted peels had a significantly lower percentage of vegetation-filled fecal pellets (12%) than mature secondary fertile shoots from leaf mat peels (37%: Table 3). We attribute these differences to a bias for cones with large amounts of pollen in the mounted peel data set, which was originally chosen for a study of cordaitan pollen associated with different cordaitan cone morphologies. The frequency of vegetation-filled fecal pellets in cordaitan cones from leaf-mat peels most likely indicates the percentage of detritivory more accurately than the mounted peel data. However, the abundance of pyrite and overall poor preservation of some leaf-mat coal balls increases the difficulty of discerning small pollen-filled fecal pellets, which could contribute to a bias for low numbers of pollen-filled fecal pellets. All mature secondary fertile shoots in peat

could have been attacked by generalized microarthropod detritivores. Nonetheless, pollen-filled fecal pellets in these cordaitean secondary fertile shoots likely resulted from palynivory rather than detritivory.

Although the ecology of modern arboreal collembolans and oribatids remains poorly known, Arctic collembolans eat pollen from *Lesquerella arctica* (Arctic bladderpod) a low-growing herbaceous plant (Kevan and McKevan, 1970; Kevan, 1972). The detritivorous oribatid mites observed by Grandjean (1951) eat dispersed conifer pollen and fungi. No modern oribatid mite has been observed eating pollen from cones or flowers. However, in mangrove swamps, oribatids eat fungi on canopy leaves (Neely, pers. comm 2020), and oribatid palynivores may be discovered as we learn more about arboreal microarthropods.

Because large, concentrated sources of undispersed cordaitean pollen rarely occur in cordaitean leaf mat peats, we attribute large fecal pellets filled with cordaitean pollen ( $>200\ \mu\text{m}$ ) to palynivory by relatively large flying insects, raiding mature secondary fertile shoots in the canopy. As previously discussed, the mounted peels, 16% of mature secondary fertile shoots have large masses of undispersed pollen in pollen sacs or surrounded by pollen-sac remnants. However, only one occurs in well-preserved secondary fertile shoots from leaf-mat peels, and this data set, which represents an unbiased sample of mature secondary fertile shoots, may indicate the amount of cordaitean pollen available to large detritivores more accurately than the mounted peel dataset (Table 5). As these insects consumed pollen, they would excrete digested material, which fell to the swamp floor to become incorporated in the peat matrix (Scott and Taylor, 1983). Although no Pennsylvanian insects with pollen-filled guts have been discovered, a number of Early Permian insects from the Chekarda locality in the Urals have pollen in their

guts, including three grylloblattids, two species related to psocids and a paleomantid (Krassilov et al., 2007). One species assigned to the grylloblattids, *Tillyardembia antennaeplana* G. Zalessky had two pollen-masses in its gut, approximately 400 mm and 280 mm in diameter both composed of *Cladatina* pollen (Afonin, 2000). The size of these pollen-masses is similar to the size of pollen-filled coprolites from cordaitan leaf-mat peats. Afonin (2000) identified the pollen in them (*Cladatina*) with pollen from the Permian gymnosperm pollen cone, *Kungurodendron*, which has been placed in the conifers (Afonin, 2000; Wachtler, 2017). Labandeira (1997) observed that, due to the difficulty of locating large concentrations of wind-blown pollen in the environment outside of pollen organs, Chekarda insects with wind-blown pollen in their gut were probably palynivores. The size distribution of pollen-filled coprolites peaked at 200–399  $\mu\text{m}$  with a smaller peak at 800–899  $\mu\text{m}$ , which may indicate two different groups of producers (Figure 6C). In leaf-mat coal balls, pollen-filled coprolites are the most common concentrated source of cordaitan pollen or pollen remnants.

In their study of Early Devonian arthropod coprolites from the silicified Rhynie Chert, Habgood (2000) and Habgood et al. (2003) argued that spore-rich fecal pellets resulted from detritivory rather than palynivory. Coprolites in the Rhynie Chert ranged from 200–1000  $\mu\text{m}$  in diameter. Spore and vegetation-filled coprolites formed a continuum in the Rhynie Chert, and the size of coprolites with spores apparently does not differ systematically from the size of coprolites filled with vegetative debris (Habgood et al., 2003). Only 8% of the fecal pellets consisted mainly (>80%) of spores. Additionally, spores in fecal pellets showed the same amount of taphonomic degradation as spores found dispersed in the peat matrix of the Rhynie Chert, suggesting to Habgood et al. (2003) that consumers derived very little nutrition from spores. Palynomorphs can pass through the guts of detritivores without showing significant damage to

the exine (Christiansen, 1964; Scott and Taylor, 1983; Chaloner et al., 1991). Habgood et al. (2003) also noted that the Rhynie Chert contains aggregations of spores in the peat, which could have been the source of spores in coprolites. Finally, spore-filled coprolites in the Rhynie Chert did not occur near sporangia (Habgood et al., 2003). Likewise, Edwards et al. (1995) suggested that spore-filled coprolites from the Late Silurian and Early Devonian shales might result from detritivory. In this scenario, spore-filled coprolites contain the residue that early detritivores were unable to digest (Edwards et al., 1995; Habgood et al., 2003).

Although Habgood et al. (2003) made a strong case for detritivores as the producers of Rhynie Chert coprolites filled with spores and vegetative detritus, Labandeira and collaborators interpreted spore-filled coprolites from the Rhynie Chert and other Late Silurian – Early Devonian shales as evidence for palynivory (Labandeira, 2000; Xu et al., 2018). Coprolites with spores from the Rhynie Chert may have more than one origin and the small percentage of coprolites (about 8%) that consist primarily (>80%) of spores indeed may result from palynivory.

### ***Cordaitina***

The genus *Cordaitina* was originally proposed by Samoilovich (1953) as a radially symmetric monosaccate grain. Hart (1965) amended the definition of *Cordaitina*, as having an exoexine that completely surrounds the body, being attached over the proximal and distal sides and detached near the equator, forming a single saccus. *Cordaitina* is circular to oval in shape with a trilete mark present in some but not all species in the genus (Hart, 1965). Kirkland and Frederikson (1969) noted that the saccus of the three Pennsylvanian *Cordaitina* species from North America has infra-reticulate ornamentation.

Ravn (1986) provisionally identified two potential grains of *Cordaitina*, which he assigned to *Cordaitina? sp.* with question because his grains had a clearly distinct central body and lacked crenulations in the saccus characteristic of most *Cordaitina* species. Like Ravn's (1986) specimens, most *Cordaitina sp.* from secondary fertile shoots in our study sample have a distinct corpus outlined by the exine and lack crenulations in the saccus. Ravn's *Cordaitina* are circular monosaccate grains, 55.8 and 42.2  $\mu\text{m}$  in diameter, in which the width of the saccus extension from the central body is relatively uniform ( $\frac{1}{4}$  to  $\frac{1}{3}$  of the total miospore radius). His specimens have a psilate copus and a saccus with infra-reticulate ornamentation. Although similar in diameter to Ravn's specimens, coal-ball *Cordaitina* differ in shape and ornamentation from the *Cordaitina sp.* of Ravn (1986). Whereas Ravn's specimens are circular, coal-ball *Cordaitina* are elliptical; whereas Ravn's specimens have reticulate ornamentation on the saccus; in coal-ball *Cordaitina*, the saccus appears smooth.

*Cordaitina* species have been recorded primarily from early Mississippian and late Permian strata (Dempsey, 1967; Gupta, 1970). *Cordaitina sp.* from secondary fertile shoots in coal balls also appears distinct from *Cordaitina* species described by Kirkland and Frederiksen (1969) from Pennsylvanian strata in Texas and Oklahoma. It is smaller and less ornamented than all three of the species identified by the authors: *Cordaitina readi*, which has an infra-reticulate texture on the saccus and corpus; *C. coalensis*, which has a saccus with radial folds (these may be the crenulations of Ravn, 1986); and *C. uralensis*, which has infra-reticulate sculpting. Unlike in *Cordaitina* from Texas and Oklahoma, the saccus of *Cordaitina sp.* from coal balls appears smooth. Due to the unique morphology and dimensions of *Cordaitina* grains found in cordaitean leaf-mat coal balls, it is plausible that these grains represent a new species of *Cordaitina sp.* and may have value for distinguishing species of cordaitean cones.

## CONCLUSIONS

Golden fecal-pellets and coprolites in cordaitan leaf-mat peats are filled with cordaitan pollen. While many golden fecal pellets are too macerated for us to identify the contents, those that have identifiable contents contain fragments of cordaitan pollen; none contain other recognizable palynomorphs. Both their content and location (85% or more occur in cordaitan pollen cones) suggest that they consist of cordaitan pollen. Likewise, *Florinites* pollen or pollen fragments occur in 65% of the large golden coprolites (>200 – 900  $\mu\text{m}$  in cordaitan leaf-mat peat, nor do these coprolites contain other recognizable spores or pollen, again suggesting that they consist entirely of cordaitan pollen.

The presence of pollen-filled fecal pellets and coprolites in cordaitan cones and leaf-mat peat is among the earliest evidence of probable palynivory in gymnosperms. The size of small pollen-filled fecal pellets ( $\leq 200$   $\mu\text{m}$  in their widest minimum dimension) in cordaitan cones suggests production by ancient collembolans, oribatid mites, or an extinct microarthropod group. The macerated condition of pollen in these fecal pellets suggests that producers derived nutrition from eating pollen; however, this could apply equally to microarthropod detritivores and palynivores.

Three lines of evidence support the hypothesis that palynivores produced these fecal pellets in the canopy. First, they occur primarily in mature cordaitan pollen cones (86% in the mounted peels; 85% in the leaf-mat peels). Pollen-filled fecal pellets found in the matrix occurred close to cordaitan pollen cones on the same bedding plane. This observation is consistent with the production of small pollen-filled fecal pellets by palynivores in the canopy. Presumably, most fecal pellets deposited in cones by palynivores remained in cones during deposition; pollen-filled fecal pellets in the peat near cones may have shaken loose as



cones fell. Second, mature pollen cones with large aggregations of undispersed pollen in pollen sacs or pollen surrounded by remnants of rupture pollen sacs, have significantly fewer pollen-filled fecal pellets than other mature pollen cones (14% as opposed to 47%). This observation is consistent with the idea most pollen consumption occurred in the canopy and that cones on the swamp floor were sheltered from microarthropod pollen consumers. Third, although other plant groups, notably *Psaronius* tree ferns, calamitean trees and small ferns occur in abundance in Kalo Formation coal-ball assemblages (Raymond, 1988; Raymond et al., 2001), all of the recognizable palynomorphs in small golden fecal-pellets are cordaitean. Notably we found no tree-fern, calamitean or other fern spores in these fecal pellets. The specificity of attack (consumers that appear to target only cordaitean pollen) argues for palynivory rather than detritivory. Insect herbivores are often specialized, whereas most detritivores are generalists (Labandeira 2013).

Large pollen-filled coprolites (>200 – 900  $\mu\text{m}$  in their widest minimum dimension), in the leaf-mat peat also result from palynivory. These coprolites were most likely produced by large flying insects, which fed on cordaitean cones in the canopy, depositing large fecal pellets that fell to the peat surface to become incorporated in the peat matrix. Labandeira (1997) commented that large coprolites composed of wind-blown pollen (like cordaitean pollen) generally indicate palynivory due to the difficulty of finding large concentrations of wind-blown pollen to serve as a source for detritivores. Aside from pollen-filled coprolites, large masses of cordaitean pollen rarely occur in cordaitean leaf-mat peat. Evidence of flying insects containing pollen masses (ranging in size from 300-700  $\mu\text{m}$ ) in their hindgut can be found in the Early Permian Chekarda locality in the Ural Mountains of Russia, (Krassilov and Rasnitsyn, 1997; Krassilov, 1999, Afonin, 2000).

Palynivory appears more common in the Pennsylvanian than in the Late Silurian-Early Devonian. Insects with pollen-filled guts from the Early Permian of Russia, Late Jurassic of Kazakhstan and Early Cretaceous of Transbaikalia suggest that pollen feeding may have continued to be an important ecological strategy during the Mesozoic (Krassilov et al., 2007), although we lack corresponding evidence in the form of pollen-filled coprolites from Late Permian and Mesozoic wetlands due to the scarcity of permineralized peat during this interval. However, the importance of pollen and spore feeding in peat-accumulating wetlands has declined in modern wetlands (Raymond et al., 2001). Although many modern insect groups eat pollen (Roulston and Cane, 2000), pollen-filled coprolites do not commonly occur in modern peat. Whereas most coal-ball assemblages contain abundant spore and pollen-filled coprolites, spore or pollen-filled fecal pellets have not been observed in modern peat from tropical and subtropical marine and freshwater wetlands (Cohen, 1968; Spackman et al., 1976; Cohen and Spackman, 1977; Raymond, 1988; Esterle, 1989; S. H. Neely, pers. comm.). Studies of coprolites in Early Permian coal balls from China and in Devonian through Recent shales containing adpressed leaf floras would reveal more of the Paleozoic – Mesozoic evolutionary history of palynivory. Although *Psaronius* tree-fern sporangia (*Scolecopteris*) in all conditions (i.e. empty, with scattered undispersed spores, or spore-filled) occur commonly in cordaitan leaf-mat peats, golden fecal pellets do not occur in the vicinity of this resource, suggesting that the producers of the golden fecal pellets in cordaitan cones were either specialized detritivores of cordaitan cones (for which there are no modern ecological analogs) or palynivores that targeted cordaitan pollen cones in the canopy.

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APPENDIX 1

COUNT AND CHARACTER MATRIX FOR THE MOUNTED PEELS

Pollen present cone - Yes (1) No (2)

Maturity - Immature (1) Mature (2) Degraded (3) Basal Section (4)

Peel	Cone	Pollen Present Cone	Pollen-filled fecal pellets		Vegetative-filled fecal pellets		Maturity
			In Cone	In Matrix	In Cone	In Matrix	
1		2	0	0	0	0	1
2		1	0	0	0	2	2
3		1	6	1	0	0	2
4		1	41	0	0	0	2
5	A	1	0	0	0	0	2
5	B	1	0	0	0	0	2
6		2	0	0	0	0	1
7		2	0	0	0	0	1
8A	A	1	3	0	0	0	2
8A	B	1	0	0	0	0	2
9	A	1	0	0	0	0	2
9	B	2	0	0	0	0	4
10		2	0	0	0	0	1
11		1	10	0	0	1	2
12		1	2	0	0	1	2
13		1	3	0	0	0	2
14		1	0	0	0	0	3

15		1	0	0	0	1	2
16		1	0	0	0	0	2
17		1	0	0	0	0	2
18		1	13	0	0	0	2
19E		1	1	0	0	0	2
20A	A	1	4	0	17	0	2
20A	B	1	24	0	1	0	2
20C		1	7	0	0	0	2
21	A	2	0	0	0	0	1
21	B	2	0	0	0	0	1
22C	A	2	0	0	16	0	1
22C	B	2	0	0	1	0	4
22A	C	2	1	0	10	0	2
22B	D	2	0	0	0	0	1
22A	E	2	1	1	4	0	2
22C	F	`	0	0	1	0	1
22B	G	1	4	0	3	0	2
23B	A	2	0	0	0	0	1
23B	B	2	0	0	0	0	1
23B	C	2	0	0	0	0	1
25A	A	2	0	0	0	0	1
25A	B	2	0	0	0	0	1
26	A	2	0	0	0	0	1
26	B	2	0	0	0	0	4
27A	A	1	2	0	0	0	2
27A	B	1	0	0	0	0	2
28A	A	2	0	0	0	0	1
28A	B	2	0	0	0	0	1

28A	C	1	1	0	0	0	2
29A	A	1	13	0	0	0	2
29A	B	2	0	0	0	0	1
30	A	2	0	0	0	0	4
30	B	2	0	0	0	0	1
31	A	1	54	0	14	0	2
31	B	2	0	0	0	0	4
32	A	2	0	0	0	0	3
32	B	2	0	0	0	0	3
33	A	1	0	0	0	0	2
33	B	1	0	0	0	0	2
33	C	1	0	0	0	0	2
34		2	0	0	0	0	3
35	A	2	0	0	1	0	1
35	B	2	0	0	0	0	4
36	A	2	0	0	0	0	4
36	B	2	0	0	0	0	1
36	C	2	0	0	0	0	1
37B	A	2	0	1	1	0	1
37B	B	2	0	0	0	0	1
38A		2	4	0	0	0	2
38B	A	2	0	0	5	0	2
39		1	0	0	0	0	2
40		1	0	0	0	0	2
41	A	1	0	0	0	0	2
41	B	1	0	0	0	0	2
41	C	1	0	0	0	0	2
42	A	1	0	0	0	0	2



42	B	1	0	0	0	0	2
42	C	2	0	0	0	0	1
43		2	0	1	0	0	3
44		1	0	0	0	0	2
45	A	1	23	3	0	0	2
45	B	1	18	0	0	0	2
46		1	5	5	0	0	2
47		1	0	0	0	0	2
48		1	0	0	0	0	2
49A	A	2	0	0	0	0	3
49A	B	2	0	0	0	0	3
50	A	2	0	0	0	0	4
50	B	2	0	0	0	0	3
51A		1	4	0	0	0	2
51B		1	3	0	0	0	2
52		2	1	0	0	1	2
53A		1	0	0	0	0	2
54	A	2	0	0	0	0	4
54	B	2	0	0	0	0	4
54	C	2	0	0	0	0	4
54	D	2	0	0	0	0	4
54	E	2	0	0	0	0	1
54	F	2	0	0	0	0	4
55A	A	2	0	0	0	0	3
55A	B	2	0	0	0	0	3
55A	C	2	0	0	0	0	1
55A	D	2	0	0	0	0	1
56	A	2	0	0	0	0	3

56	B	2	0	0	0	0	3
56	C	2	0	0	0	0	3
56	D	2	0	0	0	0	3
56	E	2	0	0	0	0	4
56	F	2	0	0	0	0	4
56	G	2	0	0	0	0	4
56	H	2	0	0	0	0	4
56	I	2	0	0	0	0	4
56	J	2	0	0	0	0	4
57	A	1	33	0	0	0	2
57	B	1	0	0	0	0	3
57	C	1	0	0	0	0	3
58A	A	1	1	0	0	0	2
58A	B	1	34	0	0	0	2
58A	C	1	0	0	0	0	2
58A	D	1	0	0	0	0	2
58C	E	2	0	0	0	0	3
58A	F	2	0	0	0	0	3
58B	G	2	0	0	0	0	4
59A	A	2	0	0	0	0	4
59B	B	1	0	0	0	0	2
59A	C	2	0	0	0	0	4
59B	D	2	0	0	0	0	2
59A	E	2	0	0	0	0	3
59B	F	1	0	0	0	0	3
59B	G	2	0	0	0	0	3
60A	A	2	0	0	0	0	4
60A	B	1	3	0	0	0	2

60A	C	1	0	0	0	0	2
60A	D	1	0	0	0	0	2
61	A	1	7	0	0	0	2
61	B	2	0	0	0	0	4
62	A	2	0	1	0	0	1
62	B	2	0	0	0	0	4
62	C	2	0	0	0	0	3
63	A	2	0	0	0	0	4
63	B	2	0	0	0	0	4
63	C	2	0	0	0	0	3
63	D	2	0	0	0	0	4
63	E	2	0	0	0	0	4
64	A	1	0	0	0	0	2
64	B	2	0	0	0	0	1
64	C	1	0	0	0	0	2
65	A	1	2	0	0	0	2
65	B	2	0	0	0	0	4
65	C	2	0	0	0	0	1
65	D	2	0	0	0	0	4
66	A	2	0	0	0	0	4
66	B	1	0	0	0	0	3
66	C	2	1	0	0	0	2
67A	A	1	0	0	0	0	2
67B	B	1	0	0	0	0	2
68A	A	2	0	0	0	0	3
68A	B	2	0	0	0	0	3
68B	C	2	0	0	0	0	3
69A	B	1	10	0	0	0	2

69B	A	1	20	0	0	0	2
70	A	2	0	0	0	0	2
70	B	1	11	0	0	0	2
71		1	0	1	0	1	2
72		1	0	0	0	0	2
73B	A	1	0	0	0	0	3
73B	B	2	7	0	0	0	2
74	A	1	0	0	0	0	2
74	B	1	0	0	0	0	2
75		1	1	0	0	0	2
76	A	1	0	0	0	0	2
76	B	2	0	0	0	0	3
77C	A	1	0	0	0	0	2
77A	B	1	0	0	0	0	3
77A	C	2	0	0	0	0	2
77B	D	1	0	0	0	0	2
77A	E	2	0	0	0	0	1
77B	F	2	0	0	0	0	3
78A	A	2	0	0	0	0	1
78A	B	2	0	0	0	0	4
78A	C	2	0	0	0	0	3
78B	D	2	0	0	0	0	4
79	A	2	0	0	0	0	1
79	B	2	0	0	0	0	4
80	A	2	0	0	0	0	1
80	B	1	0	0	0	0	2
81		1	0	0	0	0	2
82		2	0	0	0	0	4

83	A	2	0	0	0	1	1
83	B	1	0	0	0	0	2
83	C	1	0	0	0	0	2
84	A	2	0	0	0	0	1
84	B	2	0	0	0	0	1
84	C	2	0	0	0	0	1
84	D	2	0	0	0	0	1

APPENDIX 2

COUNT AND CHARACTER MATRIX FOR THE LEAF MAT PEELS

Pollen present cone - Yes (1) No (2)

Maturity - Immature (1) Mature (2) Degraded (3) Basal Section (4)

Peel	Cone ID	Pollen in cone	Pollen-filled			Vegetative-filled		Maturity
			In Cone	In Matrix <200 µm	In Matrix >200 µm	In Cone		
1	A	1	1	1	280x600		1	A
1	B	2					1	B
1	C	2					1	C
1	D	2					1	D
1	E	2					1	E
1	F	2					1	F
1	G	1	1			3	1	G
2	A	2		1	300		2	A
2	B	2					2	B
3	A	2		1	340		3	A
3	B	2		1	360		3	B
3	C	1		1	560		3	C
3	D	2	7		60	1	3	D
4	A	2		1	800		4	A
4	B	1					4	B
4	C	2					4	C

5	A	2					5	A
5	B	2					5	B
5	C	1					5	C
5	D	1					5	D
6		2					6	
7	A	2		1	500		7	A
7	B	2		1	500		7	B
8		2		3	280, 340, 400	1	8	
9	A	1		1	400		9	A
9	B	1		1	280		9	B
9	C	2					9	C
9	D	2					9	D
9	E	2					9	E
10	A	2	1	1	500		10	A
10	B	2			820		10	B
11	A	1		1	300		11	A
11	B	2	1	1	300		11	B
11	C	1	2			?	11	C
12		1	6	6	520, 640, 240, 240, 300, 520		12	
13	A	2			160		13	A
13	B	2		1	240		13	B
13	C	2		1	300		13	C
13	D	1		1	540		13	D
13	E	2					13	E
13	F	1					13	F
13	G	2					13	G
13	H	1				4	13	H

14	A	2		1	240		14	A
14	B	2					14	B
14	C	2					14	C
14	D	2					14	D
15	A	2		1	480		15	A
15	B	1	1	1	340		15	B
15	C	2					15	C
16	A	1					16	A
16	B	2					16	B
17	A	1					17	A
17	B	1	4			2	17	B
17	C	2					17	C
18	A	2		1	300		18	A
18	B	2		1	340, 380		18	B
18	C	1		1	440, 460		18	C
18	D	1	1	1	600		18	D
18	E	2		1	640		18	E
19	A	2		2	300, 320		19	A
19	B	1	3	1	700x4000	3	19	B
19	C	2	2				19	C
19	D	2					19	D
19	E	2					19	E
19	F	1					19	F
19	G	1	2			3	19	G
19	H	1	2				19	H
19	I	2	1			2	19	I
19	J	2					19	J
19	K	2	2			1	19	K



20	A	1	10			1	20	A
20	B	1	1				20	B
20	C	2	2				20	C
20	D	1	1			2	20	D
20	E	1					20	E
20	F	1					20	F
20	G	1	2				20	G
20	H	2					20	H
20	I	2					20	I
20	J	2					20	J
20	K	2					20	K
20	L	2					20	L
20	M	2					20	M
20	N	2					20	N
20	O	1	3			5	20	O
21	No cone				140		21	No cone
22		1	2		120, 80, 80		22	
23	A	2		1	220		23	A
23	B	1					23	B
23	C	1			80		23	C
23	D	1		2	300		23	D
23	E	2		2	860		23	E
23	F	1					23	F
23	G	2					23	G
23	H	2					23	H
23	I	1					23	I
24	A	1	2	4	1000, 800, 200, 200	3	24	A

24	B	1					24	B
24	C	1	3			2	24	C
25	A	2		1	270		25	A
25	B	1		1	340		25	B
25	C	2					25	C
25	D	2					25	D
25	E	1	2			2	25	E
26	A	2	1	1	400		26	A
26	B	1	1	1	620	1	26	B
26	C	1		1	740		26	C
26	D	1	1				26	D
26	E	2				3	26	E
26	F	2					26	F
26	G	1	1				26	G

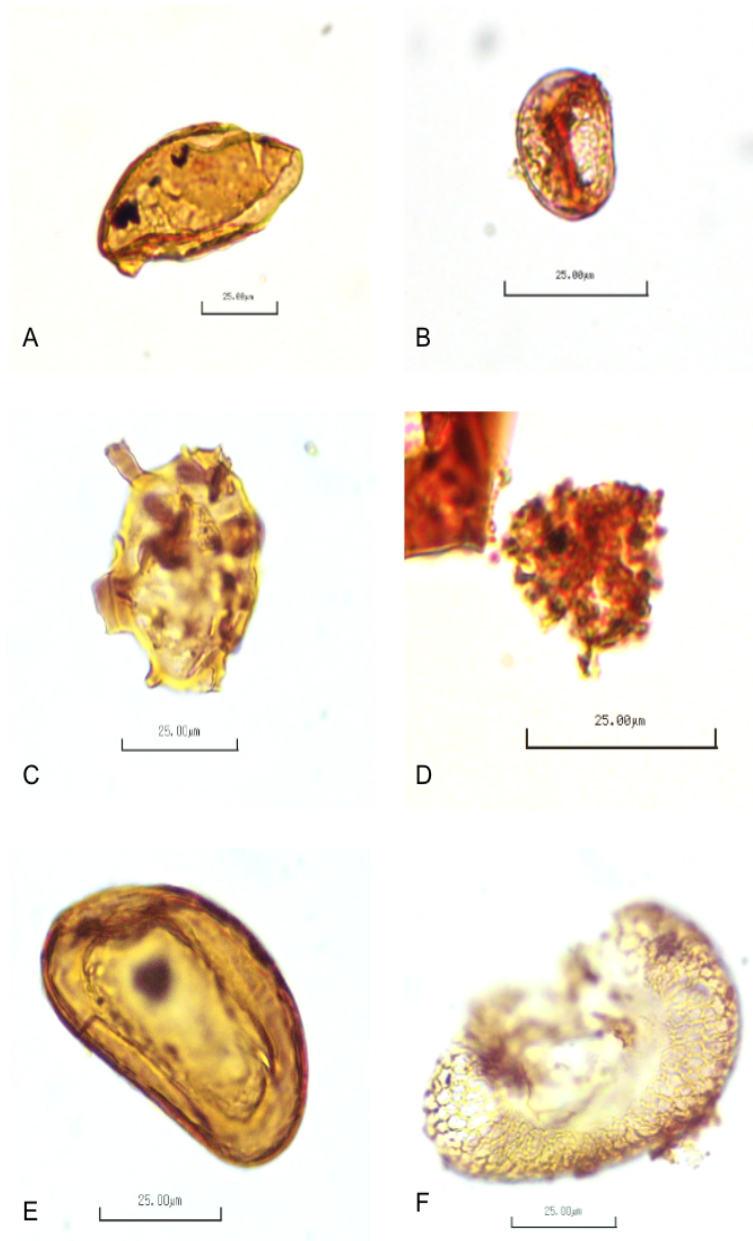
## APPENDIX 3

### POLLEN EXTRACTION FROM PEELS

In order to enhance the optical quality of pollen grains *in situ*, attempts were made to extract pollen grains from acetate peels for identification. Peels of coal balls containing mature cordaitan cones and pollen-filled fecal pellets/coprolites were made using the cellulose acetate peel process (Joy *et al.*, 1956). Using a modified method from Daghlian and Taylor, (1979) three peels were censused to isolate pollen-rich material and coprolites. The censused peels were dissolved hot acetone for 10 min. The solutions washed with several changes of distilled water, tetra-butyl alcohol, and 95% ethanol. In alcohol, samples were stained using red dye and suspended in glycerin. The suspended material was mounted onto glass plates and analyzed under a Zeiss Axioplan 2 Imaging microscope. Measurements and scale bars were assigned using the Zeiss AxioCam software.

Pollen grains  $\geq 25 \mu\text{m}$  from peels collapsed due to the loss of the peat matrix which potentially acts as a structural support mechanism (fig. 9A, E, F). Pollen grains  $\leq 25 \mu\text{m}$  were highly deformed or fragmented (fig. 9 B, C, D). The extraction of palynomorphs from coal ball peels proved not to be a viable method for pollen analysis and identification. Cellulose acetate peels seldom capture the entire *Florinites* grain that was targeted for this procedure; the process of making cellulose acetate peels creates thin sections. Peel preparation mounted onto slides for light microscopy offers a controllable approach to ensure that grains are intact upon removal from a coal ball. Multiple peels from a sequence containing grains could provide detailed images of a grain's morphology and characteristics (Daghlian and Taylor, 1979).

### Pollen Grains Extracted from Peels



**Figure 8.** Pollen grains retrieved from the digestion of coal ball peels- A, unknown. B, unknown. C, *Raistrickia protensa*. D, *Acanthotriletes echinatus*. E, *Florinites* sp. (highly deformed corpus). F, *Vestipora luminata* (fragment).

## APPENDIX 4

### ANALYSIS OF *TAXODIUM* CONES

To explore palynivory in modern conifers, the secondary fertile shoots of *Taxodium distichum*, which have compound pollen secondary fertile shoots morphologically similar to Cordaitales were analyzed and observed for signs of predation and arthropod fecal material. Reproductive secondary fertile shoots were collected from 3 locations in Brazos County, Texas for a duration of once a week for 7 weeks during March - April. *T. distichum* secondary fertile shoots were collected from the soil surface and directly from trees. Cones were analyzed for traces of fecal material or signs of damage from predation (bite marks, burrows, etc.) using a Nikon SMZ1500 Stereomicroscope. Secondary fertile shoots collected from the soil surface was contaminated with inorganic particles making it difficult to identify potential fecal pellets. Cones were sonicated in ethanol for 5 minutes to extract potential fecal pellets, the residue was suspended in glycerin and analyzed under a Zeiss Axioplan 2 Imaging microscope.

No evidence of predation was identified on *T. distichum* secondary fertile shoot collected from trees and the substrate.