ULTRASTRUCTURAL AND PALEOBIOCHEMICAL CORRELATIONS AMONG FOSSIL LEAF TISSUES FROM THE ST. MARIES RIVER (CLARKIA) AREA, NORTHERN IDAHO, USA

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ABSTRACT

Miocene angiosperm leaf tissues of Betula, Hydrangea, Platanus, and Quercus, and of Castanea, Persea, and gymnospermous tissues from offshore and onshore lacustrine sediments, respectively, reveal various states of ultrastructural detail in preservation which correlate with their paleobiocchemical profiles. Excellent cytologic preservation of membrane-bound organelles in offshore tissue samples is correlated with relatively mild chlorophyll and fatty acid degradation (chlorins, unsaturated hydrocarbons), while progressive deterioration of ultrastructure seen in onshore specimens is concomitant with extensive chlorophyll degradation and saturation of hydrocarbons. Comparative studies between fossils found in pyroclastic (Succor Creek Flora, Miocene) and lacustrine (Clarkia Flora) environments indicate that the degree of pre- and post-depositional hydration of tissues is a less significant factor in determining preservation than redox potential and secondary metabolites (tannic acids, chlorophyll derivatives). A sequence of organelle degradation in leaf tissues is given, and it is suggested that chloroplasts and cell walls are the most stable cellular constituents, while the endoplasmic reticulum, nuclei, and mitochondria are the most labile.

THE PRESERVATION of fossil tissues may, in principle, be assessed by the analysis of their cytology and biochemistry, which reflect the two major physical manifestations of the fossilization process. Studies of fossil plant tissues indicate that the excellent preservation of subcellular features such as organelles is more widespread than formerly thought (cf. Mamay, 1957; Millay and Eggert, 1974; Niklas, Brown, Santos and Vian, 1978; Oechler, 1977; Taylor and Millay, 1977a, b), while chemical analyses of Tertiary plant remains reveal a broad spectrum of biochemical constituents (cf. Dilcher, Pavlick and Mitchell, 1970; Niklas and Giannasi, 1977a, 1979). While structural and chemical states of preservation are dependent upon the physiochemical factors attending fossilization, the determination of these requisite factors has been limited owing to the small number of reports correlating states of preservation with pre- and post-depositional environments. The present study documents the cytologic and biochemical fidelity observed in selected fossil plant tissues from the Clarkia deposits (Miocene) of northern Idaho. Correlations between ultrastructural features and organic geochemical constituents are drawn and related to the depositional environment associated with each tissue sample, as inferred from their sedimentological context.

The occurrence of plant fossils in the St. Maries River fossil area near the town of Clarkia, northern Idaho has been presented in detail by Smiley, Gray and Huggins (1975) and Smiley and Rember (1979, in press). The vertical sequence of sediments exposed at the type-locality, site P-33 of Smiley et al. (1975), consists of alluvial sands at the base to finely laminated lacustrine clay and volcanic ash in the middle to probable floodplain deposits at the top of the sequence. Fossils from site P-33, which are representative of an "offshore" lacustrine sediment, are frequently observed to have a distinctive red, yellow, or occasionally green coloration. Upon exposure to air and/or light a rapid discoloration reaction occurs, resulting in a "blackening" of leaf tissues. Fossils from site P-40, which are thought to have been preserved in a more shallow "nearshore" or possibly deltaic environment, appear brown in color. Tissues from both sites are hydrated.

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upon excavation. Preliminary field observations and chemical extractions indicated that tissues had to be prepared for study directly in the field. This reduced or wholly eliminated the discoloration of P-33 tissues.

The data from the analyses of the Clarkia deposit fossils will be placed in apposition to those derived from the Succor Creek Flora (Miocene), Oregon. The Succor Creek fossils isolated from volcanic ashfall lenses have cytologic preservation comparable to that observed for Clarkia site P-33, but show evidence of rapid dehydration before post-depositional sediment maturation and consolidation (cf. Giannasi and Niklas, 1977; Niklas and Giannasi, 1977a, b, 1978). Comparisons between the states of preservation found in the Succor Creek and Clarkia deposit fossils will be used to construct a degradation sequence of subcellular features. Such a sequence would provide a basis for interpreting less well preserved ultrastructural components of older plant fossils.

**Materials and Methods**—Fossil plant tissues were collected from Clarkia deposits associated with offshore lacustrine sediments (locality P-33), nearshore sediments (P-40), and lake-border sediments (P-40) (cf. Smiley and Rember, 1979, Fig. 2). Potassium-argon dates were obtained at site P-34 from basalts that intrude the Clarkia deposits (Smiley and Rember, 1979). These intruding rocks are chemically and petrologically similar to basalt flows that overlie the Clarkia beds in the vicinity. The time of this post-depositional volcanic activity appears to have been within 22 and 15.4 million years (m.y.) (Smiley and Rember, 1979), which provides a minimum range for the age of the intruded fossil beds. Smiley and Rember also reported that floral and palaeoclimatic evidence further supports an Early Miocene age (20 or more m.y.) for the Clarkia fossils.

Fossil tissues were collected from freshly exposed strata. Each specimen was handled at a minimum, and reference samples for cuticular, ultrastructural, and biochemical analyses were taken. Tissues were either placed under nitrogen or fixed in the field for transmission electron microscopy by placing them in 2% (v/v) glutaraldehyde, 3% (v/v) tannic acid, and 50 mM cacodylate buffer at pH 7.2. Tissues were then placed in fixative for 45 min at 25 C, then transferred to 4 C for 20 hr. Post-fixation was in 2% OsO4, in 50 mM cacodylate buffer, pH 7.2, for 3 hr at 4 C. For further details, see Niklas et al. (1978). For comparative purposes, tissues stored under nitrogen were fixed in tannic acid; additional tissue samples were also removed from leaf specimens while in the laboratory. The effects of exposure, storage and transport were, therefore, assessed.

Biochemical analyses followed those given by Niklas and Giannasi (1977a), and Giannasi and Niklas (in press). Extraction of tissues with acidified methanol was also performed in the field. In a few cases, the solvent turned either dark brown or occasionally a light green. Organic solvent extractions of leaf material were analyzed on a Perkin-Elmer Sigma 1 gas chromatograph (GC) with a data interchange Sigma 10 system. Details concerning operation systems, columns, and standards are given, where appropriate, along with the data. Voucher specimens of fossils, chemical extractions, and GC printouts are stored in the Plant Science Building, Cornell University, Ithaca, New York.

**Results**—The macroscopic appearance of the angiosperm leaf material examined (Betula, Platanus, Quercus, Persea, and Hydrangea) is shown in Fig. 1–4 and 6–7, respectively, along with indications as to where tissue samples were removed for cuticular (arrows) and ultrastructural (boxed areas) analyses. In addition, an as yet unidentified gymnospermous fossil was studied (Fig. 5). Fossil membranes show a discontinuous distribution of heavy metal during staining, with a distinctive “beading” along the hydrophilic exterior of each half of the bimolecular leaflet (Fig. 8). The ultrastructural and biochemical data for these specimens will be detailed according to individual genera.

**Platanus**—Tissues from a leaf identified as Platanus (C79-P33-5) fixed in tannic acid show a differential preservation of cytologic detail (Fig. 9–11). Ultrastructural evidence for compression of cell walls is seen in Fig. 9, with lumina occluded with electron-dense cytoplasmic remnants. Evidence for an epicuticular (ergastic) covering of the leaf epidermis was found, along with possible epiphytic organisms indicative of an aquatic phase before fossilization. Some cell lumina show incomplete cytologic breakdown where membrane-like structures intergrade with highly degraded material (Fig. 10). In other portions of the specimen, chloroplast-like cytologic details are observable (Fig. 11). Cell wall preservation is also excellent in these areas.

**Betula**—Glutaraldehyde-fixed tissues of Betula (C79-P33-20) show excellent chloroplasts with patterns of grana, starch grains, chloroplast envelope membrane (Fig. 12), as well as
Fig. 1–8. Fossil angiosperm leaf tissues from the St. Maries River (Clarkia) area of northern Idaho. Fig. 1–7. Leaf material was removed for cuticular (areas bounded by arrows) and ultrastructural (boxed areas) analysis. 1. Betula. ×1. 2. Platanus. ×0.5. 3. Castanea. ×0.3. 4. Quercus. ×0.3. 5. Gymnosperm. ×10. 1. 7. Three of four bracts of Hydrangea inflorescence. ×3. 8. Transmission electron microscopic detail of typical membrane preservation seen in fossil leaf tissues. Heavy metal deposits in small "beads" along membrane surface showing a discontinuous distribution of unsaturated lipids. ×65,000.
thylakoid membranes (Fig. 13). Despite structural evidence for cellular compression and the absence of cytoplasmic membranes, the cell wall preservation remains excellent (Fig. 12).

**Hydrangea**—Glutaraldehyde-fixed tissues from the bract of *Hydrangea* (C79-P33-2) show well-preserved chloroplasts in negative contrast (Fig. 14), possible mitochondria (Fig. 15), and well-preserved cell wall detail (Fig. 16).

**Castanea and Persea**—Tannic acid-fixed tissues of these two specimens show poor preservation of cytologic details, along with moderate to well-preserved cell wall components. *Castanea* (C79-P40-4) tissue demonstrates extreme degradation of cytologic detail, with granulose spherical bodies occupying cell lumina (Fig. 17). Mesophyll anticlinal walls are frequently fractured and incomplete. *Persea* (C79-P40-6) shows extensive compression of cell walls, while lumina are occluded by a homogenous electron-dense material (Fig. 18).

**Gymnosperm**—Tannic acid-fixed tissues of a gymnosperm (C79-P40-21) demonstrate moderate preservation of chloroplasts (Fig. 19); however, microfibrillar details of the cell walls are frequently encountered (Fig. 20).

**Quercus**—Both glutaraldehyde and tannic acid fixation of oak tissues (C79-P33-22A) show chloroplast and cytoplasmic membrane preservation (Fig. 21–23). Some areas show bacterial contamination that possibly occurred during the fossilization of these tissues (Fig. 24).

The biochemical data obtained from the single specimens illustrated in Fig. 1–7 are summarized as presence-absence of constituents in Table 1. Reliable quantitative data are precluded owing to the limited size of the samples and by the resolution of analytical techniques. The chemical constituents outlined in Table 1 represent what are thought to be critical components of plant tissues that have precedence in the biochemical studies obtained from plant material of comparable or older age (cf. Niklas et al., 1978; Niklas and Giannasi, 1978), and play significant roles in our interpretation of structural fidelity (cellulose, photosynthetic pigments, and lipids).

All specimens reveal the presence of cellulose or of cellulose-like components (Table 1). Mass spectrometry of leaf tissues contain peaks for masses 126 and 144, corresponding to those of levoglucosan and of the cellulose structural unit of molecular weight 162, with two and one molecules of H₂O split off, respectively. Tissues of *Castanea* and *Persea*, however, show infrared absorption spectra characteristic of extreme alteration of cellulosic constituents indicative of oxidized components. These data are similar to those reported for the Succor Creek Flora specimens (cf. Niklas et al., 1978).

The presence of tetrapyrrole pigments extracted from tissue specimens is given in Table 1. Several homologous series of porphyrins are demonstrable in specimens having well-preserved cytologic details. In particular, *Betula*, *Platanus*, and to a lesser extent, *Hydrangea* have significant amounts of these constituents. Both deoxophyloerythritolpyrrosporphorin (DPEP)
Fig. 9–17. Ultrastructural preservation (TEM) of fossil leaf material from Clarkia localities. Fig. 9–11. Tannic acid-fixed material of *Platanus*, site P-33 (Fig. 2). 9. Compression-distortion of cell walls and partial coalification of cytoplasm. ×6,800. 10. Detail of Fig. 9. Membrane introgression into coalified material (seen right). ×75,000. 11.
### TABLE 2. Degradation sequence of organelles and distribution of occurrence in fossil leaf tissues

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a From Niklas et al., 1978, and unpublished data.

b heter. = chromatin-like material visible in the nucleus.

c In order of increasing probability of occurrence.

and etioporphyrin (EP) were detected in the *Castanea* and *Persea* specimens, and are thought to be the end products of chlorophyll degradation. Mass spectra of *Castanea* and *Persea* acetone-methanol extracts show m/e peaks at 476 (DPEP) or m/e 478 (EP). All specimens other than *Castanea, Persea* and the gymnosperm tissue have pheophytin a (major mass spectral peaks are 278, 459, 461, 516, 592, 870). The m/e 592 peak represents a loss of 278 from pheophytin a (mass 870), which is probably phytadiene. The 278 peak is of variable height and dependent upon the source temperature. The 516 peak is thought to be the result of the loss of the 10-carboxymethyl group producing the ketene (mass 516). A major red absorption at 668 nm suggests that metallochlorins are not present as significant components of the extractions. Phytadienes were not detected in all of the tissue specimens collected.

A wide range of paraffinic components is found in all the tissues examined (Table 1). The carbon preference index (CPI; cf. Niklas et al., 1978) is variable and indicative of diagenesis. *Castanea* and *Persea* (CPI = 5.4 and 5.0, respectively) show extreme alteration of their fatty acid components. In general, all other specimens have straight chain saturated fatty acids (C_{12} to C_{34}), monosaturated with even carbon numbers in the C_{16}-C_{24} range, and some branched chain (iso, anteiso, 10-methyldecanoic) acids. Other than *Castanea* and *Persea, Quercus* tissues, which show evidence of microbial contamination, show the most significant reconstruction of the fatty acid distribution.

Qualitative correlations between ultrastructural and biochemical states of preservation are possible provided that cytologic and organic chemical components may be ranked in order of the potential for preservation under geologic conditions. On the basis of various studies detailing the age and the condition of physical preservation (cf. Knoll and Barghoorn, 1975; Millay and Eggert, 1974; Niklas et al., 1978; Taylor and Millay, 1977a, b), we have listed some major cytologic components in the order of the observed probability of preservation (Table 2). Cell walls, chloroplasts, and starch grains appear to be the most commonly found structures in both the Succor Creek fossils and the Clarkia specimens. Evidence for endoplasmic reticulum (ER) and nuclei was not seen in any specimen from Clarkia, and found only occasionally in the Succor Creek material.

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Chloroplast-like cytologic detail. ×63,000. Fig. 12–13. Glutaraldehyde-fixed *Betula*, site P-33 (Fig. 1). 12. Chloroplasts, starch grains, and osmophilic dense cytoplasm. ×5,000. 13. Detail of stroma/grama seen in Fig. 12 showing "negative" staining typical of many specimens. Fig. 14–16. Glutaraldehyde-fixed tissue of *Hydrangea* bracts, site P-33 (Fig. 7). "Negative-stained" appearance of chloroplast. ×24,000. 15. Possible mitochondrion showing highly distorted internal structure and incomplete outer membrane. ×77,700. 16. Multilaminate cell wall. ×23,400. 17. Tannic acid-fixed *Castanea* tissue, site P-40 (Fig. 3) showing complete ultrastructural degradation of electron-dense cytoplasm. Cell wall preservation (top) is moderate to good. ×4,000.
Fig. 18–24. Ultrastructural details (TEM) of fossil leaf specimens from Clarkia localities. 18. Extensive coalification of cytoplasm and cell wall deformation due to compression failure in *Persea*, site P-40 (Fig. 6). Longitudinal fracturing of cell constituents is probably an artifact of sectioning ("shattering"). ×23,000. Fig. 19–20. Gymnosperm fossil from site P-40 (Fig. 5). 19. Chloroplast-like structures are rarely preserved and are oppressed to cell wall. ×63,000. 20. Microfibrillar detail of cell wall. ×13,000. Fig. 21–24. Details of *Quercus* leaf, site P-33 (Fig. 4). 21. Tannic acid fixation showing tracheid element with secondary wall thickenings and surrounding mesophyll. ×15,300. 22. Glutaraldehyde fixation of cell walls and chloroplasts in mesophyll. ×5,800. 23. Chloroplast, starch grain and cell wall revealed by glutaraldehyde fixation. ×15,800. 24. Tannic acid-fixed mesophyll cell showing fossil bacteria occluding cell lumen. Bacteria cells are seen as spheroidal, granular bodies (b) and show evidence of increased diagenesis from the inside to the outside of each cell mass. ×13,300.
Mitochondria appear with intermediate frequency, and are less common in the Clarkia tissue specimens. Phaeophorbidate and pheophytin are always associated with all tissues having well-preserved chloroplasts. The chlorophyll derivatives DPEP and EP are found in all tissues that have preserved membranes. Cellulose is always found in tissues with preserved starch; however, not all tissue specimens with cellulose have starch grains preserved.

The degree to which cytologic features are preserved correlates directly with the fidelity of organic chemical profiles. *Castanea* and *Persea* show extreme chemical diagenesis, as indicated by the presence of DPEP, EP, and altered CPI’s. Ultrastructurally their tissues appear electron-opaque and lack cytologic detail. Extracts of these tissues reveal the bulk of non-cellulosic material to be a melanoidin complex composed of polymerized proteinaceous and polysaccharide constituents. Steroids are completely lacking. The chemical profiles of these two specimens are indicative of thermal diagenesis, since even the cellulosic fraction of the cell walls appears thermally altered. *Platanus, Quercus,* and *Betula* demonstrate profiles similar to contemporary dried tissues, and conversely have the greatest ultrastructural fidelity.

**Discussion—Ultrastructural and organic geochemical analyses of plant tissues from the Clarkia fossil area of northern Idaho confirm the presence of typical plant organelles and of organic profiles consistent with that of relatively unaltered plant biochemistry. On the basis of comparisons among preserved cytologic features, the Clarkia fossil tissues appear less well preserved than tissues of comparable age (Miocene) from the Succor Creek Flora (Niklas et al., 1978). The radical difference in the depositional environments associated with the Clarkia and Succor Creek areas provides some basis for interpreting these differences, and suggests that the degree to which tissues are hydrated during the preliminary phases of fossilization may play less of a role in determining chemophysical profiles than does the presence of specific organic compounds or the redox potential of the depositional environment. Preliminary data are also useful in inferring at least a partial sequence of ultrastructural deterioration during the fossilization of plant tissues, where chloroplasts and cell wall materials are more stable than the ER, nucleus, and mitochondria.

Angiosperm leaf tissues from isolated pyroclastic deposits of the Succor Creek Flora (cf. Graham, 1966; Giannasi and Niklas, 1977; Niklas and Giannasi, 1977a, b, 1978; Niklas et al., 1978) are relatively rare and have chloroplasts with stroma/grana arrangements, starch grains, infrequent nuclei and mitochondria, and excellent microfibrillar cell wall preservation. Definitive bimolecular leaflet staining of the membranes was, however, lacking, as were discernable Golgi bodies, ER, and vacuolar membranes. Bereft of other comparisons, this preservation was tentatively ascribed to a rapid burial of the tissues in a desiccating inorganic matrix, followed by mild post-depositional sediment maturation. It was further speculated that cell wall fracturing incurred by compaction further facilitated dehydration, while the necrotic release in tissues of tannic acids, polyphenols, and aldehyde-rich compounds may have acted as a biofictive of cytologic detail. In contradistinction to the Succor Creek material, the St. Maries River (Clarkia) fossil area is richly fossiliferous, and provides an opportunity for a more detailed study of the chemophysical phenomena of fossilization. Fossils are preserved in finely laminated, lacustrine or deltaic deposits associated with the neogene Clarkia Lake (Smiley and Rember, 1979, in press). Sedimentological data indicate that a variety of depositional microenvironments occurred when the Clarkia lake was formed by the basaltic damming of the proto-St. Maries River valley (Smiley and Rember, 1979). The type-locality (site P-33 of Smiley et al., 1975) is thought to represent an offshore environment and contains fossils in oxidized clay and volcanic ash (unit numbers 2 to base of 5; Smiley et al., 1975). Site P-40 is interpreted to be lake-border or possibly deltaic sediments which was later intruded by a dike sill complex. Fossils found near the basalt intrusions appear blackened or are mere impressions. Fossils found at progressively greater distances from basalt intrusions are less altered in appearance and show macroscopic preservation similar to that of fossils of site P-33.

Tissues from the Clarkia area contain geochemical constituents that serve as independent indicators of paleoenvironmental conditions, and provide correlations indicating the potential for the preservation of specific cytologic details. Pristine to phytane ratios (Pr/Ph) and chlorin geochemical profiles are particularly sensitive to redox potentials, and provide useful biochemical correlations with chloroplast ultrastructure. Lipid compositions (in particular, unsaturated fatty acids) and cellulose-hemicellulose are good indicators of geo thermal and microbial degradation. Similarly, they provide a biochemical link with the ultrastructural integrity of membranes and cell walls, respectively. Pr/Ph ratios determined for
the Clarkia P-33 tissue samples are equal to or less than unity (Table 1), and are interpreted as indicative of anoxic paleoenvironmental conditions. The $C_4$ isoprenoid skeleton of phytyl in has a greater potential for preservation under anoxic conditions than does the $C_19$ skeleton of pristane. The ephephytins $a$ and dihydrophephytin, both byproducts of chlorophyll degradation, yield dihydrophephytol upon hydrolysis. However, oxidation of dihydrophytolen produces phytic acid, which converts to phytyl. Similarly, P-33 specimens are relatively rich in biolipids, carotenoids and chlorins, which is consistent with an anoxic interpretation. In addition to a high organic carbon content (14.2% dry weight), the associated inorganic sediments of site P-33 have a high percent of HCl-extractable sugars and amino acids. The chlorin content of these tissues and the presence of ephephytin $a$ indicate that chlorophyll degradation is incomplete. These data are interpreted as indicative of mild geophysical gradients during sediment maturation. Tissues from site P-40 (Castanea and Persea), which are thought to have been preserved in lake margin or deltaic environments, have Pr/Ph ratios of unity and show chlorophyll byproducts reflecting severe oxidative degradation (DPEP and EP). These compounds and the Pr/Ph ratios indicate an oxic or alternating oxic-anoxic environment of deposition. A lake-border or deltaic environment could have been associated with episodic oxic-anoxic phases, which in turn may have been responsible for the altered chlorophyll profiles in tissues and the low organic carbon content of the associated inorganic sediments (0.78% dry weight). While thermal diagenesis is also capable of yielding the same geochemical profiles as are reported for site P-40, the presence of native cellulose, albeit altered to some extent, indicates that the thermal gradient was relatively mild, since cellulose is a sensitive indicator of high temperatures (Madorsky, 1964). The observations made on ultrastructure parallel closely the biochemical profiles of the P-33 and P-40 tissue samples. Chlorin-rich tissues (Platanus, Betula and Quercus) have well-preserved chloroplasts, while tissues showing severe chlorophyll degradation have virtually no ultrastructural detail (Castanea and Persea).

The presence of tanniferous compounds in most of the P-33 tissues is of particular interest. Some tissues fixed in glutaraldehyde (Quercus, Fig. 23) appear to have a "negative staining" in their chloroplasts which is similar to tissues fixed in tannic acid. Tannins occur naturally in many plant tissues and bind strongly to proteins and polysaccharides. Similarly, by complex formation, tannins may inactivate, to varying degrees, enzymatic processes. The ultrastructural appearance of some tissues and the presence of unusually high concentrations of tannins are interpreted as evidence that these tissues may have undergone either auto-fixation through the necrotic release of cytoplasmically compartmentalized tannins, or were infiltrated gradually by water supercharged with tanniferous products. Peaty or swamp conditions generate high tannic acid concentrations, which inhibit microbial activity. Condensed tannins liberated by the leaching of wood by water, as well as aldehyde-rich lignin degradation byproducts, may have been responsible for the preservation of some tissue samples.

Comparisons between the ultrastructure of the Clarkia and the Succor Creek tissue samples indicate that among all the organelle types, chloroplasts are the most frequently preserved. Golgi bodies, ER, and vacuolar membranes have not been observed in any of our tissue samples, while nuclei and mitochondria are rare. Two possible reasons for this are: a) the chloroplast is the largest double membrane-bound organelle in the typical plant cell and is also the most easily identifiable in terms of its internal structure of stroma/grana, and b) the presence of specific compounds comprising the bulk of an organelle type may provide for a differential susceptibility to deterioration through mechanical or chemical factors. Minor structural alterations of a single membrane-bound structure, such as Golgi bodies, tonoplasts, or the ER, would result in the loss of any clearly definable ultrastructural analog. Numerous cells in fossil specimens have compact highly fragmented membranes which may be remnants, albeit unrecognizable ones, of single membrane organelles. Similarly, nuclei and mitochondria, while double membrane-bound, have little internal structure (heterochromatin and cristae are polymorphic and identifiable only within context). Minor damage to these organelle types would result in amorphous, unidentifiable structures. Chloroplasts, by virtue of their size and internal complexity, are the most easily identifiable organelles. Their numerical abundance in our tissue samples may reflect little more than our inability to resolve other, altered structures. In apposition to this, the high concentrations of organic acids and aldehyde-rich compounds formed from the preliminary breakdown of chlorophyll may result in the rapid internal fixation of chloroplast ultrastructure. Other organelles such as nuclei and mitochondria have organic compounds equally as labile as chlorophyll, but are less likely to generate degradation byproducts capable of auto-fixation.
Regardless of the mechanism(s) responsible for the apparent differential preservation of cytologic details, a degradation sequence is clearly evident—cell walls and chloroplasts are more stable than any other cellular component.

The implications of the preliminary sequence of organelle degradation (cf. Table 2) to the interpretation of other older plant fossils are still speculative. Using electron microscopy, Oehler (1977) reported the inclusion of intracellular bodies in the Late Precambrian alga Glenobotrydion aenigmatis which resembled starch-enclosed pyrenoids and remnants of chloroplasts. Using similar techniques, Taylor and Millay (1977a) have demonstrated the presence of granular and vesiculate subcellular material within the Pennsylvanian age spore of Biscalitheca musata (Zygopteridaceae). Provided that the data from Tertiary angiosperm and gymnosperm leaf tissues are examples of an organelle degradation sequence, the subcellular inclusions reported in many fossil plant tissues are most probably the cytologic remnants of plastids and plastid metabolic byproducts (lipids, protein, starch).

The excellent preservation of the Clarkia specimens indicates that rapid dehydration of tissues is not a requisite to ultrastructural fidelity. Unlike the Succor Creek material, the Clarkia fossils were probably deposited and preserved under hydrated conditions. Thus other factors, such as the presence of naturally occurring secondary metabolites within or around the tissues and the redox potential of the depositional environment may be more significant determinant factors. It is hoped that the continued analyses of biochemical, ultrastructural and sedimentological correlations in the Clarkia area, as well as other fossil localities, may yield information on the chemophysical factors attending fossilization.

LITERATURE CITED


