dense onto the surface of fly ash particles during, or soon after, coal combustion, alternative mechanisms, such as the diffusion of certain species to the surface of molten particles, cannot be excluded. It seems probable, however, that the surface predominance of certain elements is a widespread phenomenon in particles derived from high-temperature processes since preliminary studies have established its occurrence for Br, Cl, and Pb in automobile exhaust particulates and for Mn and Zn in fly ash from a municipal incinerator.

These results are of real significance because they show that conventional bulk analyses provide a poor measure of the actual concentrations of many toxic trace elements that are in effective contact with the external environment of a particle. In the case of fly ash, whose matrix consists primarily of an insoluble aluminosilicate glass, it is appropriate to think in terms of an accessible or extractable shell at the particle surface with which body fluids, water, or reactant species can interact. Initial studies indicate that elements extractable from fly ash by water and by dimethyl sulfoxide are derived from within a shell approximately 1000 Å in depth below the external particle surface, and it seems probable that this shell corresponds to the region of surface enhancement discussed here. For the large (75 to 100 μm) particles studied, only a small fraction of the content of a given trace element may be present in the surface layer; however, for a particle with an aerodynamic diameter of 1 μm as much as 80 percent of the trace elemental mass is apparently in this layer (*2*). This point should be recognized in the design of realistic bioassay or inhalation studies involving simulated particles.

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Reproductive and Vegetative Morphology of a Cretaceous Angiosperm

Abstract. *Recent collections from plant-bearing deposits of Cenomanian age in central Kansas have yielded angiosperm axes with helically arranged, seed-bearing, conduplicate carpels. Large leaves associated with these fruits are thought to represent parts of the same kind of plant because the leaves and fruits are the only plant fossils at this locality to have distinctive, morphologically identical, yellow bodies within their carbonaceous remains. These fossils provide a rare opportunity to study the morphology of an ancient angiosperm and illustrate the antiquity of certain features considered primitive by comparative angiosperm morphologists.*

The uncertain nature of the structure of early angiosperms has been the major impediment to understanding the origin and early evolutionary radiation of this important plant group. The earliest evidences of angiospermy in the fossil record are Lower Cretaceous pollen (*1*) and leaf impressions (*2*). Reports of angiosperm reproductive structures of Cretaceous age are not common and, when published, almost never include much morphological or structural detail. As a result, the present concepts of primitive floral features have been determined with little reference to the fossil record.

Deposits of plant-bearing clays have recently been found in the Janssen Clay Member of the Dakota Formation. These clays occur in northeast Russell County, Kansas, and underlie the Rocktown Channel sandstone in that area. Siemers (*3*), in a detailed study of the Cretaceous sediments of Russell County, assigns the Janssen Clay Member to the lowermost Cenomanian and uppermost Albian. Examination of the pollen and spores from the Janssen Clay Member also suggests a lowermost Cenomanian age (*4*).

A diverse assemblage of impressions and well-preserved compressions of angiosperm leaves and reproductive structures, gymnosperm foliage, and ferns has been collected from this clay. The plants are similar to those reported earlier by Lesquereux (*5, 6*) from the Dakota Formation and by Newberry (*7*) from the Amboy Clays of the Raritan Formation of New Jersey. One interesting component of this fossil flora is an angiospermous reproductive axis, which is well enough preserved to allow detailed study of its morphology (*8*).

The reproductive axis is elongate (axes up to 12 cm in length have been discovered; although none were complete) and bears more than 50 helically arranged conduplicate carpels (Fig. 1d). These are elongate, flattened laterally, enlarge gradually from a proximal stalk, and terminate in a narrow rounded tip (Fig. 2). The abaxial surface is rounded, and a suture extends the length of the adaxial surface of the carpel. The adaxial suture is bounded on either side by extensions of the carpel walls, which fold outward about 5 mm, forming an adaxial crest (Fig. 1c). No separate stigmatic surface has been observed, and it is possible that the recurved carpel walls may have served this function.

The carpels are attached to the axes by stalks 1 mm wide and 7 mm long, which have decurrent bases (Fig. 2). A distinctive feature of these stalks is a shallow groove about midway between the carpel and the point of attachment. Since carpels found dispersed in the matrix never have such a groove on their stalks, and the stalks of these dispersed carpels are about 2.5 to 3 mm long, the length that would be expected if they separated at this point, it is assumed that this groove represents a point of abscission. Isolated carpels, open at the adaxial suture and filled with clay, are also found preserved as casts and molds. The fruit is a follicle.

Compressions and impressions of the carpels often have a partitioned appearance due to a line of depressions in the adaxial two-thirds of the carpel (Figs. 1d and 2). Occasionally, what appear to be small compressed seeds can be observed in these depressions (Fig. 1a). These are small (1.4 by 0.6 mm) and their position suggests that the placentation is submarginal. When carbonaceous material is removed from the area where compressed seeds occur and is cleared, the remains of seed coats can be isolated (Fig. 1b). The size of these agrees with that of the compressed seeds recovered in situ.

No pollen-bearing organs, calyx, or corolla is associated with the carpels or the elongated axes. No complete axis was found, so we cannot speculate on the possible association of these various organs with these axes.

Small (40 to 50 μm in diameter) yellow bodies are commonly distributed over much of the surface of the compressed carpels. Although these bodies may be lost in collecting or preparation, they often leave definite punctate surfaces. Similar yellow bodies are also a common feature in the mesophyll of *Liriophyllum*, one of the leaves found in the same sediments (Fig. 1, e and f), but are not found in any other plant fossils from this locality. The mor-

Fig. 1. (a) Part of a carpel with organic remains and a seed in place in the carpel, indicated by an arrow. A small portion of a compression of a carpel with pits formed from the resinous bodies is in the upper left, K2300′ (× 8.5). (b) Distal end of the seed coats of two seeds removed from a carpel and cleared (× 65). (c) Distal end of a carpel showing the adaxial crest, K2318 (× 2.6). (d) Elongate axis with helically arranged carpels, K2300 (× 1). (e) *Liriophyllum*, deeply bilobed leaf, somewhat distorted in compression, K2272 (× 0.5). (f) Pitted surface of a leaf fragment of *Liriophyllum* showing some features of the fine venation, K2317 (× 11.5). The K numbers refer to the specimen numbers in the Indiana University Paleobotanical Collection.

phologies of these bodies both from the fruits and from the leaves, as observed by light and scanning electron microscopy, appear to be identical. Carbon isotope ratios of these bodies from the fruit and leaf remains are also similar. This suggests that *Liriophyllum* (Fig. 1e) was borne on the same plant that produced the fruits.

Most of the extant families of the Magnoliales, as recognized by Cronquist (*9*) or Takhtajan (*10*), have genera that contain secretory cells in their parenchymatous tissues (*11*). The abundant small yellow bodies in the parenchymatous tissues of the fossil carpels and leaves may be comparable to those found in the Magnoliales. Reproductive features of the fossil are not comparable to those of any extant genus, but there are some general aspects of the fossil that are reminiscent of some extant forms in the Magnoliidae and Hamamelidae (*9*).

Liriophyllum is a large, entire-margined, bilobed leaf with a stout midrib and petiole (Fig. 1e). Secondary veins branch pinnately from the midrib, and the two distal secondary veins form the inner leaf margin of the basal portion of the lateral lobes (*8*). This is an extinct leaf type, which cannot be related to any extant angiosperm family. The most similar fossil species is *Liriophyllum beckwithii* Lesqx. (*6*).

A fragmentary fossil similar to the isolated carpels discussed in the report was described by Lesquereux (*6*) as *Carpites liriophylli?* He considered it a seed and hypothetically assigned his specimen to *Liriophyllum* because it was found associated on the same piece of clay with *Liriophyllum* leaf material. Despite his misinterpretation of the fruiting fragment and unjustified reference to a specific leaf solely because of association, he was correct in relating these plant organs to each other.

In the absence of a usable fossil record of early angiosperm reproductive organs, angiosperm morphologists (*12*) and phylogenists (*9, 13*) have proposed primitive floral types based on the comparative morphology of extant genera. The angiosperm reproductive axes reported here provide a

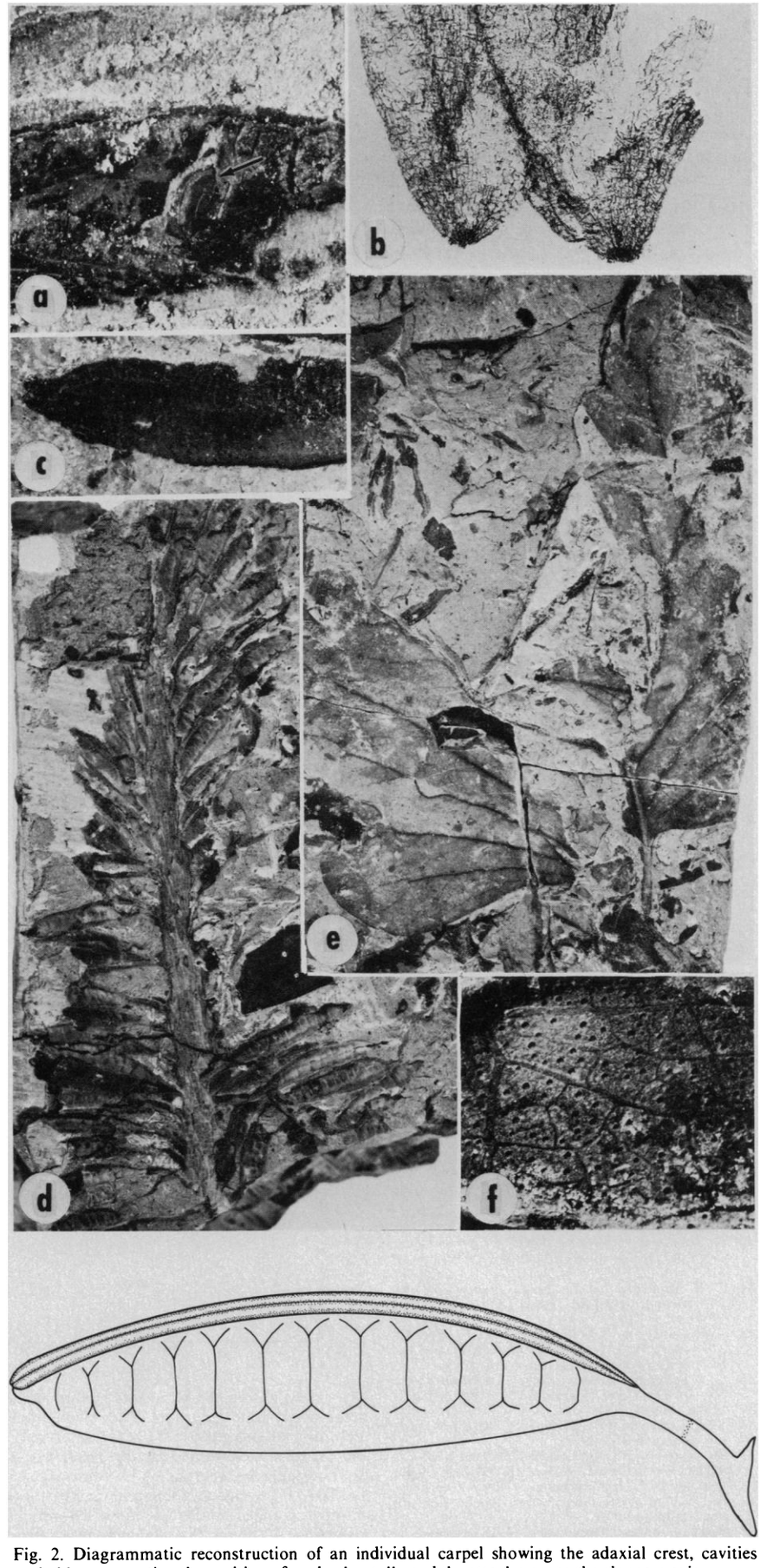

Fig. 2. Diagrammatic reconstruction of an individual carpel showing the adaxial crest, cavities probably representing the position of seeds, the stalk, and the attachment to the elongate axis.

rare opportunity to compare some of these hypotheses to the actual fossil record. The important morphological features of this fossil reproductive axis—(i) numerous helically arranged carpels on an elongated axis, (ii) multiseeded carpels, (iii) seeds borne near the adaxial side of the carpels, (iv) an adaxial suture extending the length of the carpel, (v) conduplicate carpel, and (vi) extension of the carpel walls folding out from the adaxial suture to form an adaxial crest—have been considered primitive by comparative angiosperm morphologists (*12*). The existence of these features in an angiosperm at the beginning of the Upper Cretaceous confirms their antiquity and further supports the consideration of these features as primitive. The presence of other angiosperm reproductive remains from the Cenomanian and earlier sediments (*14*), however, suggests that angiosperm reproductive structures had already diversified morphologically by the early Upper Cretaceous. Most of these other remains have not yet been subjected to investigations aimed at elucidating their detailed morphology. This report establishes that many characters considered primitive in the angiosperm flower by comparative morphologists were actually present during the early history of the angiosperms.

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Glycerol Phosphate Shuttle in Virus-Transformed Cells in Culture

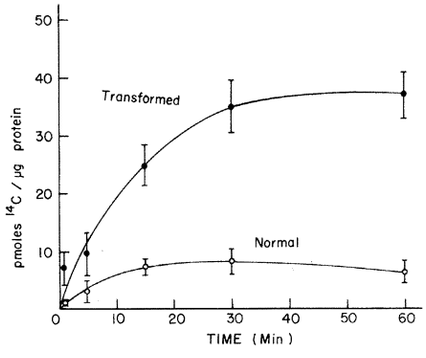
Abstract. *The glycerol phosphate shuttle is shown not only to be present and functional in virus-transformed cells, but its level is higher than in normal cells in culture. The increased aerobic glycolysis that has been demonstrated for these cells after transformation, therefore, is not due to an impairment of hydrogen transfer pathways.*

The mechanism of increased aerobic glycolysis of tumor cells, when it occurs, is as yet not understood. One of the more widely accepted explanations is that the enzymes necessary for generation of nicotinamide adenine dinucleotide (NAD^+) are lacking in malignant cells (*1*). Of the three reduced NAD (NADH) shuttles proposed for transport of electrons to the mitochondria (*2*), the glycerol phosphate (GP) shuttle is the most important. During the catabolism of one molecule of glucose, two molecules of NAD^+ are reduced to NADH when glyceraldehyde 3-phosphate (GAP) is converted to 1,3-diphosphoglycerate (1,3-DPGA). The cytoplasmic NADH is used, in turn, either to convert dihydroxyacetone phosphate (DHAP) to α-GP or to convert pyruvate to lactate. The affinity of glycerol phosphate dehydrogenase (GPDH) (E.C. 1.1.1.8) for NADH is greater than that of lactate dehydrogenase (LDH) (E.C. 1.1.1.27) (*3*). Thus, under aerobic conditions, little lactate is produced by normal cells in vivo. However, many tumor cells were reported to lack, or have drastically reduced levels of, cytoplasmic GPDH (*1, 2*). Boxer and Devlin proposed that LDH could now compete favorably for the cytosolic NADH with a resulting increase in lactic acid production (*2*). The NAD^+ thus produced would allow the continuous degradation of glucose.

The general applicability of this postulate has been questioned occasionally (*4*), although the postulate itself has gained general acceptability (*5*). More recently, in one kind of Ehrlich ascites tumor cells with a high rate of aerobic glycolysis, the shuttle was shown to be absent. However, in another strain with an equally high rate of glycolysis, the shuttle was fully operative (*6*). Ascites tumor cells do not have a normal counterpart in culture. A comparison between normal and malignant cells under comparable environmental conditions has not been reported and was therefore called for.

While normal chick embryo fibroblasts grown in tissue culture do produce an appreciable amount of lactic acid (*7, 8*), Rous sarcoma virus (RSV) –transformed cells have been shown to produce even more lactate (*8, 9*). The increase was demonstrated under steady-state conditions and was in excess of the changes due to growth rates (*8, 9*). An examination of the extent of the GP shuttle in these cells was undertaken to determine whether a decrease in shuttle activity accompanies the increased lactic acid production.

Primary cultures were prepared from 10-day-old chick embryos free of resistance-inducing factor (*10*). The single cells were plated in 100-mm culture dishes at 8×10^6 cells per plate in medium 199 supplemented with tryptose phosphate broth (2 percent) and chick and calf serums (1



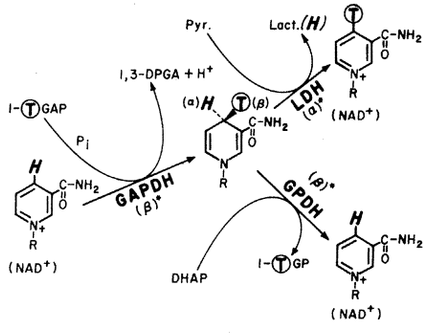


Fig. 1 (left). Glycerol 3-phosphate in normal and transformed cells. Secondary cultures were placed in the steady-state apparatus. After 1 hour of incubation in serum-free medium, medium containing uniformly labeled glucose (536 c/mole; 5.5 m*M*) was added. At intervals, the medium was removed, and the cells were washed rapidly and killed. After scraping and sonication, a portion was applied to filter paper for analysis by two-dimensional chromatography and autoradiography (*9, 13*). GP and DHAP traveled as a single spot under these conditions. The spot was eluted and the eluate was chromatographed on diethylaminoethyl-cellulose paper in a phenol, water, acetic acid (84 : 16 : 1) system for 72 hours; the two components separated under these conditions and the radioactivity was counted (*13*). Fig. 2 (right). Transfer of tritium from the 1-position of GAP to the β position of NADH; $(\alpha)^*$ and $(\beta)^*$ refer to the specificity of the dehydrogenases.