Reports

Eocene Angiosperm Flowers

Abstract. *Collections of well-preserved angiosperm flowers from the Middle Eocene of southeastern North America include a variety of morphological types. The first of these specimens to be studied extensively, a catkin, has yielded a great deal of structural information. Floral morphology, pollen morphology, and the nature of the peltate scales suggest that this catkin is allied with extant genera of the Juglandaceae. This confirms the antiquity of some of the diagnostic floral and pollen features found in extant genera of the Juglandaceae and the importance of structural information available from fossil angiosperm flowers.*

Despite widespread interest in the evolution of floral types and pollination mechanisms, fossilized angiosperm flowers have seldom been the objects of morphological investigations (*1*). Poor quality of preservation has often discouraged and sometimes prevented careful investigations of floral morphology. Regardless of the quality of preservation, sophisticated morphological techniques generally have not been applied to the study of fossil flowers. Consequently, botanists interested in the evolution of floral types and pollination mechanisms have had to rely primarily on comparisons among extant genera for their information (*2*), even though such an approach has inherent weaknesses (*3*). Recent collections of well-preserved angiosperm flowers from Middle Eocene sediments of southeastern North America (*4*) include an interesting variety of morphological types. These offer an opportunity for extensive morphological investigations and, consequently, provide a reliable idea of some of the pollination mechanisms operating during Middle Eocene times.

Flowers exhibiting gross morphological features suggesting both wind and insect pollination mechanisms are present in these collections. There are distinct kinds of catkins, some with well-developed perianth parts (Fig. 1d) and others with the perianth reduced to a cupulate structure (Fig. 1c). Another flower with gross morphological features suggestive of wind pollination has a cupulate perianth and well-exerted stamens (Fig. 1b).

Other types of flowers are radially symmetrical and have well-developed perianth parts (Fig. 1, a and h). Some of these have numerous stamens (Fig. 1a), and the flowers conform with the contemporary notion of an unspecialized insect-pollinated flower (*5*).

Since impressions gained from gross morphological features are not always reliable (*6*), the quality of preservation of these specimens is not only their most outstanding feature, it is also the most important one.

The first of these specimens to be extensively investigated (Fig. 1, d and f) has been adaptable to a variety of investigative techniques and has yielded a surprising amount of structural information. The techniques of degagement (*7*), collodion peels, standard cuticular preparation, and scanning electron microscopy (*8*) have been combined in elucidating the structure of this catkin. Catkins are 6 cm in length and individual flowers are small (3.5 mm in diameter) and spirally arranged on the floral axis (Fig. 1, d and f). Flowers are exclusively pollen-bearing and all parts are uniformly well preserved. Perianth parts are conspicuous and 12 to 15 stamens are borne on the floral axis (Fig. 1d). Anthers, freed from the matrix and cleared, are two-chambered, but have four separate sporangia. The most notable feature of the anthers is that they are often found filled with pollen grains (Fig. 1i). Pollen was studied by teasing cleared, stained anthers apart on a microscope slide and spreading out the pollen before placing the cover slip on the slide. In this way it was possible to compare pollen grains from a single anther for variations in size and exine features. Size was found to be uniform with a maximum variation of 0.9 μm from the mean equatorial diameter of 19.6 μm. Pollen was prepared for scanning electron microscopy by mounting whole cleared anthers on scanning electron microscope stubs and teasing them open, revealing the pollen grains in situ in the anther (Fig. 1g). Pollen grains are usually triporate, although a few tetraporate grains may be present in an anther, with a faintly scabrate exine (Fig. 1g). Many of the pollen grains prepared from whole anthers had a conspicuous fold across one of the poles of the grain. Because similar grains isolated from the matrix surrounding the catkin showed less pronounced folding, it is likely that the folding was accentuated by packing in the anthers. If found dispersed, these grains would most likely be placed in the juglandaceous form genus *Momipites* (*Engelhardia*), within the most primitive coryloides group (*9*).

Cuticular remains of the perianth parts show that the epidermal cells were small (50 by 50 μm) and irregularly polygonal in surface view. Large peltate scales (240 μm in diameter), similar to those of extant genera of the Juglandaceae, were sparsely distributed on the adaxial surfaces of the perianth parts (Fig. 1e). Scales are unstalked and, because they separate easily from the epidermal cuticle, the collodion peel technique was necessary to obtain them in attachment to the cuticle of the perianth parts.

Although these catkins do not fit into any extant genus, the nature of the pollen, the peltate scales, and the floral

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morphology (*10*) indicate that they are closely allied to genera of the extant Juglandaceae, particularly *Engelhardia*. These catkins confirm the antiquity of some of the diagnostic floral and pollen features found in extant genera of the Juglandaceae. They also demonstrate the amount of structural information available in fossil angiosperm flowers from these localities.

The question of whether fossilized isolated plant parts provide a reliable index to the level of evolution attained by the rest of the plant has been of key importance in considerations of angiosperm evolution. If pollen, for example, evolved at a different rate from the rest of the plant, then the evolutionary picture provided by palynological studies would be misleading. This catkin provides a rare opportunity to compare a suite of diagnostic features in organic connection: floral morphology, trichomes, epidermal features of flower parts, and pollen. Comparison between the pollen and rest of the floral features indicates an encouragingly high degree of conformity in the level of evolution.

Detailed structural knowledge of a variety of types of fossil flowers from different times (*11*) would be an important consideration in schemes of evolution of floral structures and pollination mechanisms. The potential availability of such knowledge is demonstrated by the catkin illustrated in Fig. 1, d–g and i.

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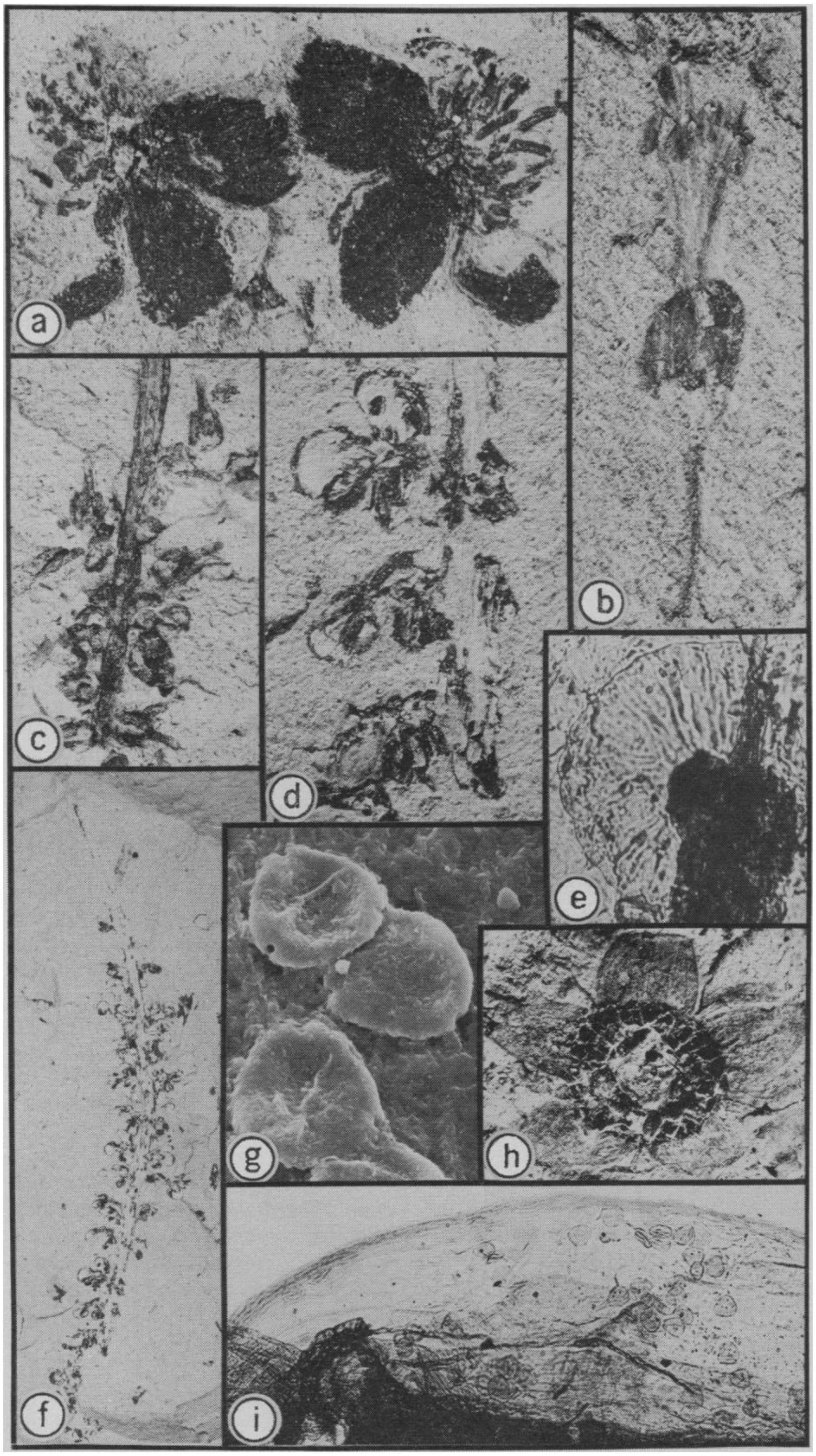

Fig. 1. (a) Two attached, radially symmetrical flowers, specimen number L1356 in the Indiana University Paleobotany Collection (× 6). (b) Flower with reduced perianth and exerted stamens, P2202 (× 7). (c) Catkin with small flowers with reduced perianths, NW2200 (× 3). (d, e, f, g, i) All of the same catkin, NW2204. (d) Higher-magnification view of the catkin in (f) showing the perianth parts and the stamens of the exclusively pollen-bearing flowers (× 7). (e) Peltate scale attached to perianth cuticle (× 170). (f) Catkin having flowers with well-developed perianths (× 1.6). (g) Scanning electron micrograph of pollen in the anther, showing occasional folding and faintly scabrate nature of the exine, SEM286 (× 1250). (i) Part of an anther showing the triporate pollen grains within (× 150). (h) Single radially symmetrical flower, M2203 (× 8).

References and Notes

1. H. Goeppert and A. Menge, *Die Flora des Bernsteins* (1883), vol. 1; H. Conwentz, *ibid.* (1886), vol. 2; V. Krassilov, *Palaeontology* **16**, 41 (1973).
→ H. Baker and P. Hurd, *Annu. Rev. Entomol.* **13**, 385 (1968).
3. S. Carlquist, *Phytomorphology* **19**, 332 (1969).
4. D. Dilcher, *Palaeobotanist* **20**, 7 (1971).
5. At the time this manuscript was being prepared, pollen was also isolated from the stamens of the flowers that are illustrated in Fig. 1a.
6. D. Dilcher, *Science* **164**, 299 (1969).
7. S. Leclercq, *Senckenb. Lethaea* **41**, 483 (1960).
8. D. Dilcher, *Bot. Rev.*, in press.
→ D. Wodehouse, *Bull. Torrey Bot. Club.* **60**, 479 (1933); D. Whitehead, *J. Arnold Arbor. Harv. Univ.* **46**, 369 (1965); D. Nichols, *Geosci. Man* **7**, 103 (1971).
10. A separate manuscript deals specifically with the morphology of the flowers of the catkin illustrated in Fig. 1, d and f (W. L. Crepet. D. L. Dilcher, F. W. Potter, in preparation).
11. This report represents the first results of our morphologically oriented studies of a variety of angiosperm flowers of both Eocene and Cretaceous age.
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