

CUTICULAR ANATOMY OF ANGIOSPERM LEAVES FROM THE LOWER CRETACEOUS POTOMAC GROUP.

I. ZONE I LEAVES¹

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ABSTRACT

Angiosperm leaf cuticles from the oldest part of the Potomac Group reinforce previous paleobotanical evidence for a Cretaceous flowering plant diversification. Dated palynologically as Zone I of Brenner (Aptian?), these remains show a low structural diversity compared to later Potomac Group and modern angiosperms. All cuticle types conform to a single plan of stomatal construction that is unusual in its extraordinary plasticity: both the number of subsidiary cells and their arrangement vary greatly on a single epidermis, such that the stomata might be classified as paracytic, anomocytic, laterocytic, and intermediate. Such stomatal diversity is uncommon in extant angiosperms but is known from a few Magnoliidae. Many species possess secretory cells comparable to the oil cells of modern Magnoliidae, and a few show the bases of probable uniseriate hairs. None of the cuticle types can be assigned to a single modern family, but several show similarities with Chloranthaceae and Illiciaceae. These results support the concept that subclass Magnoliidae includes some of the most primitive living angiosperms.

WITHIN THE PAST 15 YEARS there has been a major re-evaluation of the Cretaceous flowering plant record and the role of fossils in angiosperm phylogeny. Formerly, most botanists believed that fossils could provide little direct evidence on angiosperm evolution, since even the earliest remains were almost always related to modern families and genera (Axelrod, 1952, 1970). This view has been contradicted by more recent studies of early angiosperm pollen and leaves, which show that most of the older identifications are incorrect and that Cretaceous flowering plants exhibit a progressive stratigraphic increase in both structural diversity and the percentage of forms relatable to extant taxa (Doyle, 1969, 1973; Muller, 1970, 1981; Wolfe, Doyle and Page, 1975; Doyle and Hickey, 1976; Hickey and Doyle, 1977). These results indicate that the Cretaceous was a period of major angiosperm diversification and that paleobotanical studies should continue to yield new evidence on the group's early evolution.

One largely untouched source of evidence is cuticular anatomy. While systematic studies of both Mesozoic gymnosperms and Tertiary angiosperm leaves have long relied on cuticle structure as an important complement to external morphology (e.g., Harris, 1932, 1964; Kräusel and Weyland, 1950; Dilcher, 1974), most studies of Early Cretaceous flowering plant leaves have neglected the cuticle and dealt only with features such as venation and shape. As a consequence, I began a study of angiosperm leaf cuticles from the Lower Cretaceous Potomac Group of Virginia and Maryland, the most intensively studied sequence of early flowering plant remains in North America (Brenner, 1963; Doyle, 1969, 1973; Wolfe et al., 1975; Doyle and Hickey, 1976; Hickey and Doyle, 1977). While at first cuticular remains were only known from the upper part of the Potomac Group (Subzone II-B of Brenner, probably middle to late Albian; Mersky, 1973; Upchurch, 1979), more recently a locality with numerous organically preserved leaves was discovered from the lower part (Upchurch, 1978). This site, located on the James River south of Richmond, Virginia, at Drewry's Bluff, yields a pollen flora assignable to upper Zone I of Brenner (Aptian?), similar to one described by Doyle and Hickey (1976) from a comparable elevation at the south end of the exposure (Doyle, pers. commun.). The anatomical features of these leaves and their possible evolutionary implications are described below; a systematic treatment involving both leaf architecture and cuticular anatomy will be the

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subject of future publications. Comparisons will be made with contemporaneous dispersed cuticle, later Potomac Group dicots, and extant angiosperms.

MATERIALS AND METHODS—Angiosperm leaves were collected from a 4-cm-thick bed of gray clay exposed at the northern end of Drewrys Bluff approximately 9 m above high tide level. Every fragment with angiospermous venation was saved for laboratory analysis, and cuticular specimens were coated with acrylic plastic to minimize fragmentation upon drying. Larger specimens were identified on the basis of leaf architecture, using the classifications of Fontaine (1889), Ward (1905), and Berry (1911) in addition to the informal morphological groupings of Doyle and Hickey (1976) and Hickey and Doyle (1977). Small fragments were identified on the basis of fine venational and cuticular similarities to larger specimens. Leaf architectural terminology follows Hickey (1973), while cuticular terminology follows Stace (1965), Dilcher (1974), and den Hartog and Baas (1978).

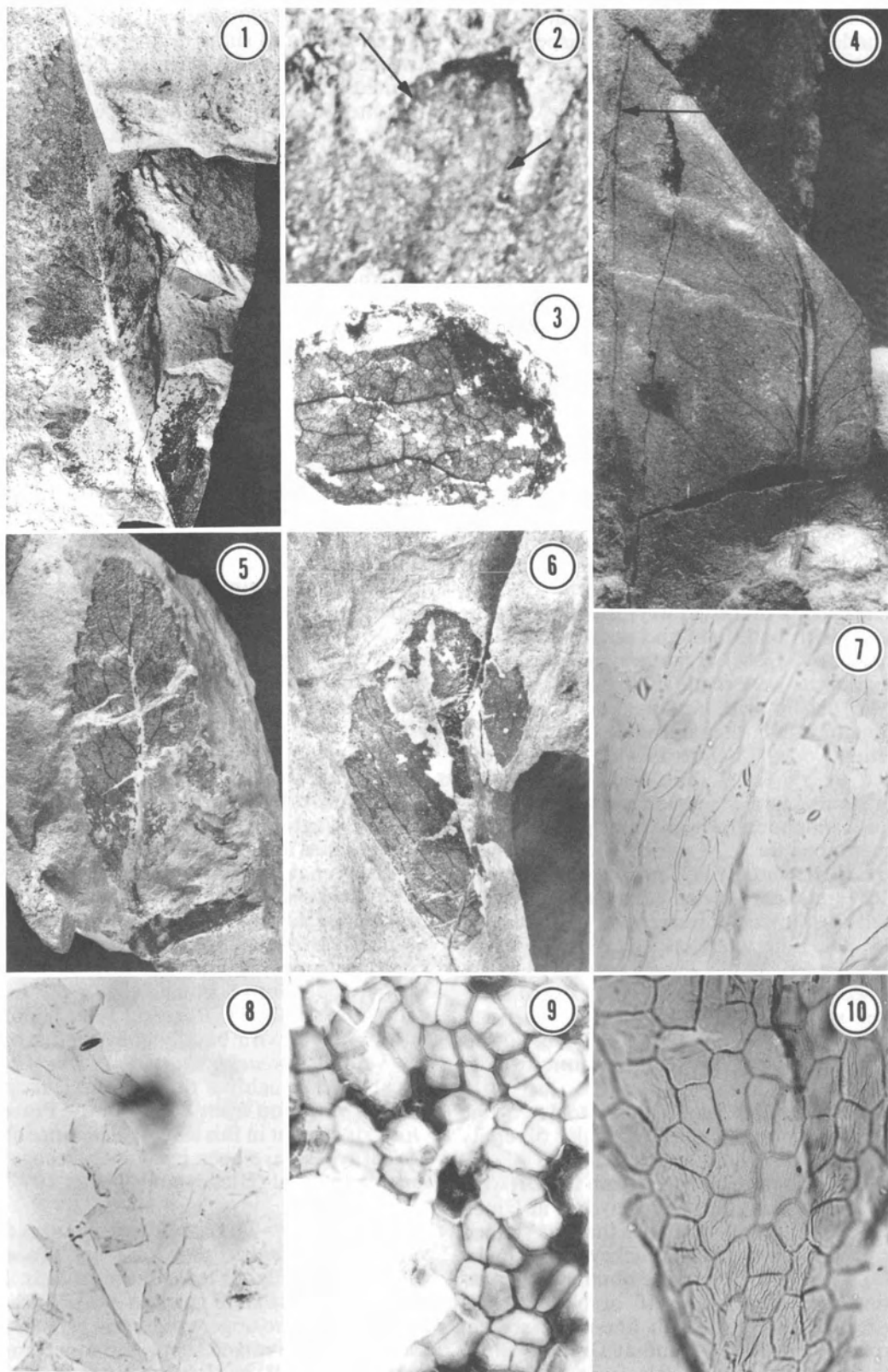
The cuticles of the Drewrys Bluff leaves were studied with both light and scanning electron microscopy (SEM). Light microscope (LM) preparations were made by first removing the acrylic plastic with acetone, demineralizing overnight in HF, then macerating in Schulze's solution (conc. HNO_3 and KClO_3 crystals) followed by 5% KOH. The freed cuticles were then stained in a 1% aqueous solution of Saffranin O and mounted in glycerine jelly on slides. Preparations for SEM varied with the surface studied. The outer cuticle surface was observed on leaf fragments which were cleaned in HF, rinsed in $3\times$ distilled water, then glued to SEM stubs. The inner cuticle surface was observed on macerated cuticle which was rinsed in $3\times$ distilled water, then dried down to SEM stubs coated with Duco Cement in a chamber saturated with acetone vapors. All preparations were coated with gold for three minutes and observed at 15 kv.

Dispersed cuticle was analyzed to determine what proportion of Zone I cuticular diversity was present in whole leaves. Samples of dispersed cuticle were prepared from the Drewrys Bluff angiosperm bed and a clay bed at Dutch Gap Canal of lower Zone I age that has yielded rare angiosperm leaves (Hickey and Doyle, 1977). Plant fragments were obtained by macerating the sediment in HF or Na_2CO_3 and sieving the slurry through fine-mesh screen. Unoxidized remains, found at Drewrys Bluff, were treated like materials from the whole leaves except that a centrifuge was used for

processing; the cuticles were then mounted in glycerine jelly on slides or in glycerine between two paraffin-sealed cover slips. Naturally macerated cuticle, found at Dutch Gap, was mounted in glycerine on slides pending further study. No dispersed cuticle was observed with SEM due to the small number of specimens available.

RESULTS—Over 30 specimens belonging to five distinct dicotyledonous leaf types are known from the Drewrys Bluff locality. At least 20 represent a new elongate leaf type that has numerous glandular teeth, simple craspedodromous secondary venation, and elongate areolation (D.B. Leaf Type #1—Fig. 1, 2). This form does not closely resemble any previously described species of Early Cretaceous angiosperm leaf. The others can be related to previously described genera and species. Four specimens are assignable to *Eucalyptophyllum oblongifolium* Font. on the basis of their oblong shape, numerous irregularly spaced secondary veins, and prominent intramarginal vein (Fig. 4). Three leaf fragments show a random reticulate pattern of tertiary and higher order venation similar to that found in *Ficophyllum* Font. (cf. *Ficophyllum*—Fig. 3). Two specimens have the elliptical shape and marginal serrations characteristic of the genus *Celastrophyllum*, but differ from all known Potomac Group species in having a low number of secondary vein pairs and in lacking a distinct petiole (*Celastrophyllum* sp.—Fig. 5). Finally, one obovate fragment has the closely spaced secondary veins and random reticulate pattern of tertiary venation characteristic of the *Celastrophyllum obovatum* Font. complex from Baltimore, but differs by its much smaller size (cf. *C. obovatum*—Fig. 6). Certain characteristic Zone I leaf types, such as pinnately lobate forms (*Vitiphyllum* Font.), elongate obovate leaves with entire margins (*Rogersia* Font.), and reniform leaves with basally congested secondary veins (*Proteaephyllum reniforme* Font.), are absent. Roughly a third of the leaf architectural variation from Zone I in the Potomac Group is present in this assemblage, since about 12 leaf types have been previously recognized for this interval (Hickey and Doyle, 1977).

Upper cuticle—The upper cuticle ranges from very thin in *Celastrophyllum* (Fig. 7) and cf. *Ficophyllum* (Fig. 8) to medium in D.B. Leaf Type #1 (Fig. 10) and thick in *Eucalyptophyllum* (Fig. 9). The upper epidermal cells in each leaf type have a mixed shape and four to many anticlinal walls, which are predominantly straight in all groups except D.B. Leaf Type



#1, where they are curved. Stomata occur on the upper cuticles of *Celastrorphyllum* (Fig. 7) and cf. *Ficophyllum* (Fig. 8). Their occurrence is correlated with a thin upper cuticle.

External sculpture on the upper cuticle is smooth in every species except D.B. Leaf Type #1, where it is striate (Fig. 10). These striations are 1 μm wide, tightly sinuous, and traverse cell boundaries. Larger cuticular ridges are present in *Celastrorphyllum* and cf. *Ficophyllum*, but these are interpreted as artifacts of preservation because the cuticle appears to be folded over upon itself. Internal sculpture is smooth in every species under light microscopy.

Hair bases are known from the upper cuticles of *Eucalyptophyllum* and D.B. Leaf Type #1. Each hair base is formed by a small, thickened foot cell and several scarcely modified base cells which underthrust the foot (Fig. 9). Foot cell shape ranges from isodiametric to elongate and branched, with each cell having at least four straight or curved anticlinal walls. Trichome abscission scars (when present) are centrally positioned, circular, and under 10 μm in diam, suggesting that the hairs were uniseriate (Fig. 11). These hair bases are rare and widely scattered in D.B. Leaf Type #1, but are numerous in *Eucalyptophyllum* (Fig. 9).

Lower cuticle—The lower cuticle is as thick as the upper cuticle in every species except cf. *Ficophyllum*, where it is thicker (Fig. 13), and D.B. Leaf Type #1, where it tends to be thinner (Fig. 14). The cells of the lower epidermis are the same size and shape as those on the upper epidermis but have more curved anticlinal walls. The cells of *Eucalyptophyllum* (Fig. 12, 17) and cf. *Ficophyllum* (Fig. 13) have a mixture of straight and curved walls, while the cells of D.B. Leaf Type #1 have a mixture of curved and sinuous walls (Fig. 14).

Two types of surface sculpture are known from the lower cuticle. Smooth sculpture, with associated cuticular folds (artifacts of preservation?), is found in *Celastrorphyllum* and cf.

Ficophyllum (Fig. 13). Complex striate sculpture is present in D.B. Leaf Type #1 and in *Eucalyptophyllum*. In D.B. Leaf Type #1 there are striations on the guard cells concentric to the stomatal pore, other striations that radiate from the periphery of the guard cells, and subparallel striations in non-stomatal regions (Fig. 14). In *Eucalyptophyllum* there are two distinct size classes of striations: the smaller ones are 1 μm wide in surface view and tend to radiate from the stomata, while larger ones are 4 μm wide, tend to enclose areas that are the same shape as the underlying cells, and commonly connect with the smaller striations (Fig. 12, 22). Internal sculpture is smooth in all leaf groups except *Eucalyptophyllum*, where it is distinctly granular (Fig. 17).

The stomatal apparatus in every leaf group conforms to the same basic plan of construction. Each pair of guard cells lies in one plane, with the poles at the same level as the stomatal pore; in contrast, the poles are raised in most gymnosperms (Harris, 1932). The guard cells are generally level with the epidermis, but are distinctly sunken in *Eucalyptophyllum* (Fig. 22). These guard cells often bear cuticular ridges on their outer walls, or outer stomatal ledges (Fig. 14, SL), and in many groups there are lamellar thickenings (Fig. 14, L), which either are associated with the stomatal ledges or tend to intergrade with them. Such lamellae are common in extant Magnoliidae, particularly in primitive orders such as Magnoliales (Baranova, 1972; Upchurch, pers. observ.).

The arrangement of the subsidiary cells in all Drewrys Bluff leaf groups shows extraordinary variation, producing stomata that conform to several of the conventionally recognized types. Many stomata might be classified as paracytic, but these show less regularity than is typical for paracytic stomata in extant angiosperms: one of the two subsidiary cells in an individual stoma often does not extend the full length of the adjacent guard cell, and the polar contact cells may be smaller than the nearby unspecialized cells (Fig. 12, 17, P). Many

Fig. 1-10. 1. D.B. Leaf Type #1—note numerous convex-convex (A-1) serrations and simple craspedodromous secondary venation. $\times 1.5$. 2. D.B. Leaf Type #1—close-up of tooth from same specimen showing the glandular tip, medial vein, and two lateral veins that fuse with the medial vein (arrows). $\times 25$. 3. Cf. *Ficophyllum*—transfer of leaf fragment showing reticulate higher order veins. The two thick veins running from left to right are interpreted as secondaries. $\times 3$. 4. *Eucalyptophyllum oblongifolium*—specimen photographed in infra-red light. Note the two-stranded primary vein, irregularly spaced secondaries, and an intramarginal vein (arrow). $\times 2$. 5. *Celastrorphyllum* sp. $\times 1.5$. 6. Cf. *Celastrorphyllum obovatum*—obovate leaf fragment showing secondary and tertiary venation. $\times 3$. 7. *Celastrorphyllum* sp.—upper cuticle showing stomata and subparallel folds. $\times 160$. 8. Cf. *Ficophyllum*—upper cuticle with faint flanges, occasional folds, and one stoma (top of frame). $\times 160$. 9. *Eucalyptophyllum*—upper cuticle showing prominent flanges, numerous hair bases, and psilate sculptural features. $\times 400$. 10. D.B. Leaf Type #1—upper cuticle showing prominent flanges and numerous fine striations that traverse cell boundaries. $\times 250$.

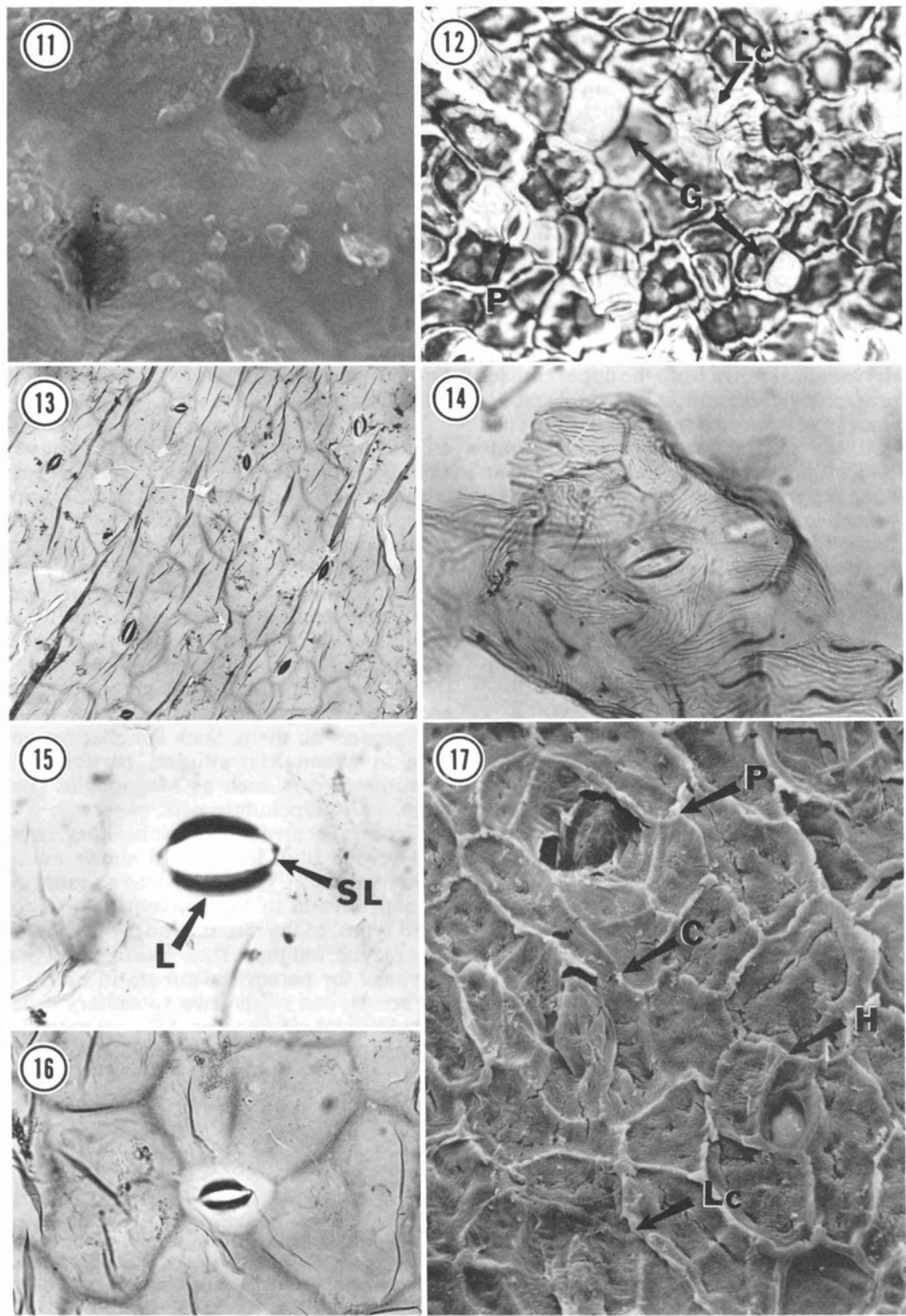


Fig. 11-17. 11. *Eucalyptophyllum*—SEM of outer surface of upper cuticle showing trichome abscission scars. $\times 1,000$. 12. *Eucalyptophyllum*—lower cuticle with paracytic (P) and laterocytic (Lc) stomata and glandular cells (G). $\times 400$. 13. Cf. *Ficophyllum*—general shot of lower cuticle showing subparallel folds and variable stomatal complexes. $\times 160$. 14. D.B. Leaf Type #1—anomocytic stoma showing characteristic pattern of striations on the stomatal complex. 15. Cf.

other stomata lack subsidiary cells and conform to the anomocytic type (e.g., Fig. 14, 16?), but in others there is a ring of weakly specialized cells and hence the stomata might be classified as cyclocytic (Fig. 17, C). Some stomata have three or more lateral subsidiary cells and conform to the laterocytic type (Fig. 17, Lc), but others possess only one lateral subsidiary cell and thus could be classified as hemiparacytic (Fig. 17, H). Compounding matters is the tendency for all of the above stomatal types to intergrade, making attempts to classify them according to accepted schemes futile. This wide diversity in subsidiary cell arrangement differs from the condition in most later Potomac Group angiosperm leaves (Upchurch, in press) and in the bulk of extant Magnoliales described by Baranova (1972), which are almost always uniformly paracytic. In contrast to these groups, however, certain other Magnoliidae appear to have a pattern of variation in subsidiary cell arrangement similar to that in Zone I leaves: Amborellaceae (Fig. 18), Schisandraceae, Austrobaileyaaceae, and some Chloranthaceae (Upchurch, in press).

Three types of secretory cells are present on the lower epidermis or in the mesophyll of the Drewrys Bluff leaves. The first, termed the "radiostriate" secretory cell, occurs in very low frequencies on the lower epidermis of *Eucalyptophyllum* and DBLT #1 (Fig. 20). (This has only been observed in Dispersed Cuticle referable to these species.) It consists of a small, polygonal cell with straight to concave anticlinal walls and striations that radiate from near its margin. Similar cells are present in Illiciales (Bailey and Nast, 1948; Jähnichen, 1976), certain Laurales (including Austrobailleyaceae), and Magnoliales (Upchurch, in press). The second type of secretory cell is found on the lower epidermis of *Eucalyptophyllum* (Fig. 12, G). Each secretory cell is rounded, has a thin outer cuticle, and is level with the adjacent cells or else partially underthrust by them. These secretory cells are similar in appearance to the oil-bearing cells on the abaxial epidermis of Illiciales except that they tend to be less rounded and less underthrust by the adjacent cells than those in the modern forms (cf. Jähnichen, 1976; Upchurch, pers. observ.). The third type is found in the mesophyll of *Celastrorhynchium* and cf. *Ficophyllum* (Fig. 21). These cells are

spherical, thin-walled, average 10 μm in diam, and often contain dark contents (Fig. 21). They show numerous similarities in size, shape, and appearance of contents to oil cells illustrated by Stürm (1971) and Jähnichen (1976) from preparations of extant and Tertiary angiosperm leaf cuticles.

Dispersed cuticle—In addition to providing cuticle fragments comparable with *Eucalyptophyllum* and D.B. Leaf Type #1, the study of plant debris yielded six new cuticle types with angiospermous features. These six new types are similar to the cuticles of whole leaves in their stomatal structure and secretory cells, but differ in having more diverse cuticular flanges, surface sculpture, and hair bases.²

Cuticular flange development is more diverse in the dispersed forms. The cuticular flanges of most dispersed cuticle types, as in whole leaves, taper smoothly toward the inside of the leaf and form a system of sharp ridges (cf. Fig. 17). In contrast, the cuticular flanges of the unspecialized cells in Dispersed Cuticle #1 are very wide (8 μm), abruptly flattened to the inside, and often bear a longitudinal groove in their center (Fig. 23), which may represent the middle lamella of the cell wall (cf. Stace, 1965). In addition, T-shaped thickenings (or T-pieces) are found in the stomata of two dispersed cuticle groups. In Dispersed Cuticle #1, the end walls of the guard cells are less strongly cutinized than the stomatal poles (Fig. 23). In contrast, both the end walls of the guard cells and the stomatal poles are strongly cutinized in Dispersed Cuticle #3 and the top piece characteristically curves toward the opposite end of the stoma (Fig. 24, arrow).

Papillate surface sculpture is found in several dispersed cuticle groups in addition to the types found in whole leaves. Papillae always are located in the center of each cell and are either hollow, as in Dispersed Cuticle #2 (Fig. 27), or partially solid, as in Dispersed Cuticles #3 and #5 (Fig. 28, 29). When striations are also present, they radiate from the papillae.

One new hair base type is found in Dispersed Cuticle Type #3. This consists of a polygonal,

² Charts showing the systematic distribution of cuticular features in both whole leaves and dispersed cuticle are available from the author upon request.

Ficophyllum—stoma showing lamellar thickenings (L) and outer stomatal ledges (SL) on guard cells. $\times 1,000$. 16. Cf. *Ficophyllum*—stoma unclassifiable as any one conventional type that shows a high range of variation in neighboring cell size. $\times 750$. 17. *Eucalyptophyllum*—SEM of inner surface of lower cuticle showing granular sculpture and four conventionally recognized stomatal types: paracytic (P), cyclocytic (C), hemiparacytic (H), and laterocytic (Lc). $\times 1,000$.

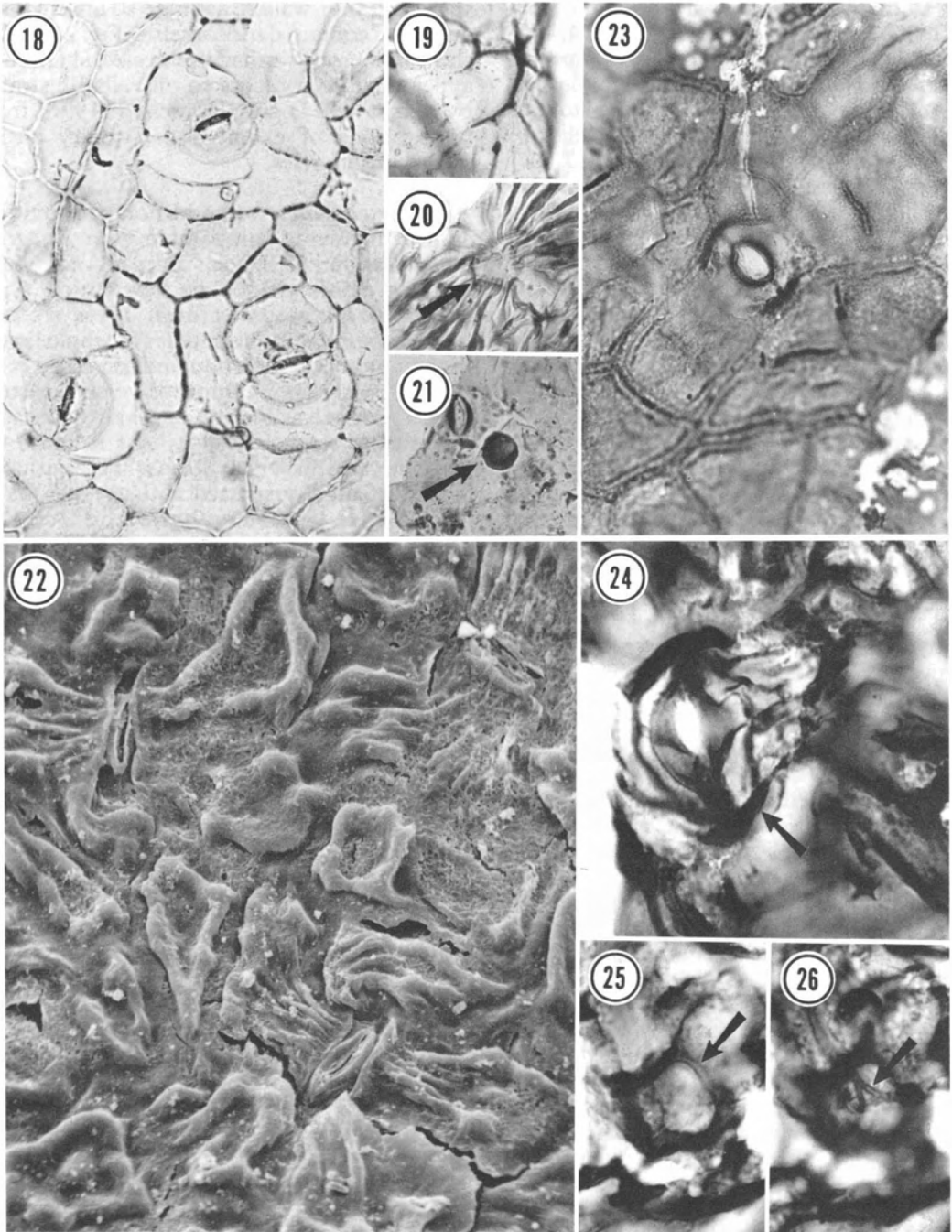


Fig. 18–26. 18. *Amborella trichopoda* (Amborellaceae)—lower cuticle showing the Zone I pattern of variation in subsidiary cell arrangement. $\times 400$. 19. D.B. Leaf Type #1—elongate, branched hair base from lower cuticle. $\times 400$. 20. *Eucalyptophyllum*—radiostriate secretory cell from lower cuticle (arrow). $\times 400$. 21. Cf. *Celastrophyllum obovatum*—mesophyll secretory cell associated with the cuticle (arrow). $\times 400$. 22. *Eucalyptophyllum*—SEM of outer surface of lower cuticle showing sunken stomata with outer stomatal ledges and two sizes of striations. $\times 1,000$. 23. Dispersed Cuticle Type #1 from Dutch Gap—stomatal complex with T-pieces. Note also the characteristic grooves in the broad cuticular flanges. $\times 400$. 24–26. Dispersed Cuticle Type #3 from Drewrys Bluff. 24. Close-up of stoma showing striation pattern similar to D.B. Leaf Type #1 and strongly developed T-pieces. Arrow points to top part (“crossbar”) of T-piece. $\times 1,000$. 25. Hair base showing thickened outer cuticle of base cell with pore (arrow). $\times 1,000$. 26. Same hair base showing strongly underthrusting base cells (arrow). $\times 1,000$.

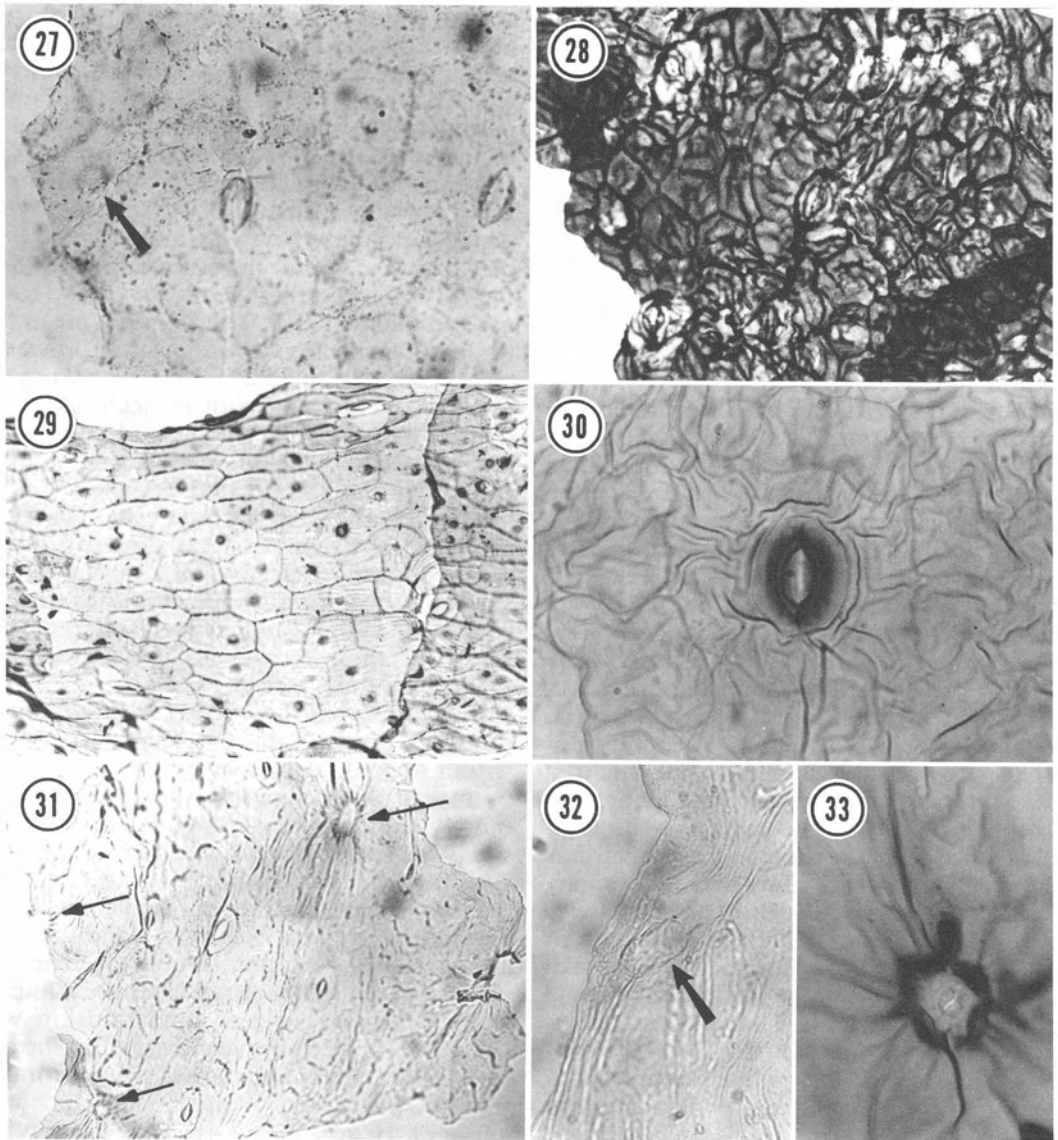


Fig. 27-33. 27. Dispersed Cuticle Type #2 from Dutch Gap—two stomata and a hollow papilla (arrow). $\times 400$. 28. Dispersed Cuticle Type #3 from Drewrys Bluff—general shot showing straight-walled, polygonal cells with partially solid papillae and radiating striations. $\times 200$. 29. Dispersed Cuticle Type #5 from Dutch Gap—longitudinally aligned cells with striations and partially solid papillae. $\times 160$. 30. *Sarcandra glabra*—lower cuticle showing lamellar thickenings in the guard cells and pattern of striations similar to D.B. Leaf Type #1. $\times 400$. 31. Dispersed Cuticle Type #6 from Dutch Gap—note radiostriate secretory cells (arrows). $\times 200$. 32. Dispersed Cuticle Type #6—rounded idioblast (arrow). $\times 400$. 33. *Sarcandra glabra*—radiostriate secretory cell from lower cuticle. $\times 1,000$.

more or less isodiametric foot cell and several unmodified, strongly underthrusting base cells (Fig. 25, 26, arrows). The outer wall of the foot cell is heavily cutinized except at the point of trichome attachment, where there is a pore 12 μm in diam. This hair base is most similar to the type found on the upper cuticle of *Eucalyptophyllum*, but differs in that the lateral walls

of the foot cell are not thickened and the trichome abscission scar consists of a pore rather than a depression.

DISCUSSION—When compared with extant dicot leaves, Zone I angiosperms exhibit a low diversity in cuticular structure. As a rule, these leaves show more diversity in traits commonly

found to have little systematic importance in modern flowering plants than in those which generally have high systematic value (cf. Metcalfe and Chalk, 1950; Stace, 1965; VanStaveren and Baas, 1973). Examples of the former include surface sculpture, internal sculpture, and anticlinal wall pattern. Except for thin areas in the cuticle, all the major types of surface sculpture listed by Dilcher (1974) are present in the Zone I leaves. Internal sculpture shows the range of form listed by Dilcher (1974) and anticlinal wall pattern ranges from straight to strongly undulate, as in extant flowering plants. In contrast, the plan of stomatal organization, structure of the hairs/hair bases, and construction of the secretory cells show a relatively narrow range of diversity. Although individual stomata might be assigned to several of the conventional types recognized in modern angiosperms, all Zone I angiosperms show a similar pattern of variation in their stomatal structure. Only two kinds of trichome bases are present, as opposed to many in modern flowering plants, and in each the foot cell is the only part exhibiting substantial modification, unlike many modern and later fossil types (cf. Roselt and Schneider, 1969). Trichomes appear to have been exclusively uniseriate and were poorly cutinized and/or shed before leaf fall; conspicuously absent are the well-cutinized peltate scales, prostrate hairs, and various multiseriate trichomes characteristic of many extant dicots. Finally, all glands are unicellular and poorly differentiated from the adjacent cells, which contrasts with the well-defined, multicellular secretory organs found in many modern flowering plants. Thus, cuticular anatomy supports the concept that Zone I angiosperms had attained only a fraction of the systematic diversity present in modern angiosperms (Hickey and Doyle, 1977) and the idea that many complex epidermal structures in modern flowering plants arose later in angiosperm evolution.

While the cuticle of the Drewrys Bluff leaves does not permit assignments to extant families or orders, it does suggest more distant relationships between two leaf types and modern taxa. The affinities of *Eucalyptophyllum* have always been problematic, since its combination of venational features is unknown in extant angiosperms (Wolfe et al., 1975). However, cuticular anatomy clearly indicates angiospermous affinities: the plan of stomatal construction is shared with other Zone I angiosperms and other cuticular features, such as hair base type, abaxial secretory cells, and sunken stomata, are seen in some contemporaneous and younger Potomac Group angio-

sperm leaves (Upchurch, 1978, 1979, and above). In addition, *Eucalyptophyllum* possesses three features today found together in Chloranthaceae and Illiciales: 1) the Zone I pattern of stomatal organization; 2) abaxial secretory cells; and 3) radiostriate oil cells. A relationship with Chloranthaceae is also suggested by the structure of the primary vein, which is composed of two major vascular bundles that fuse within the lamina (Fig. 4), as is typical of the vesselless genus *Sarcandra* (Swamy and Bailey, 1950). This does not mean that the fossil readily fits into either taxon, however, since it appears to differ from both in its elongate sunken stomata with truncate poles, reticulate pattern of striations, and possibly its less rounded abaxial glands, as well as in its distinctive leaf architecture.

The cuticular anatomy of Drewrys Bluff Leaf Type #1 shows its strongest similarities with extant Chloranthaceae. The combination of stomata longer than 30 μm , striations that run concentric to the stomatal pore, and radiostriate epidermal secretory cells is restricted today to some Laurales (sensu Takhtajan, 1969) and Illiciales. The hair bases of D.B. Leaf Type #1 occur in diverse modern angiosperms, but within Magnoliidae have only been observed by myself in Illiciaceae and Chloranthaceae. Finally, the Zone I pattern of variation in subsidiary cell arrangement is known only in certain Chloranthaceae, Amborellaceae (Fig. 18), Schisandraceae, and Austrobaileyaceae. These features, along with biconvex glandular teeth and elongate areolation (found together only in certain Chloranthaceae; Upchurch, unpublished), strongly suggest a relationship with Chloranthaceae; however, simple craspedodromous secondary venation is absent from the family (Hickey and Wolfe, 1975; Upchurch, unpubl.). Hence, D.B. Leaf Type #1 may belong to a group that includes the ancestor of extant Chloranthaceae, but represents an extinct taxon within the alliance.

Two dispersed cuticle types show a similar pattern of affinities with extant flowering plants. The first, Dispersed Cuticle Type #6 from Dutch Gap (Fig. 31, 32), possesses numerous radiostriate secretory cells and rare rounded idioblasts (secretory cells?) as in Chloranthaceae and Illiciales; however, its structure is too generalized to permit a more definite systematic assignment. The second, Dispersed Cuticle Type #3 from Drewrys Bluff (Fig. 24, 26, 28), resembles modern Illiciales in its pattern of stomatal striations, T-pieces, and cuticular thinning over the subsidiary cells, and is similar to members of the Schisandraceae in many features of its stomatal complex. It also has a

hair base similar to one illustrated by Jähnichen (1976) for the Eocene species *Schisandra europaea*, except that its base cells more strongly underthrust the foot cell. In spite of these marked similarities, however, the fossil differs from all extant members of the order by its slightly shorter stomata (27 μm vs. 30 to 70 μm as listed by Bailey and Nast, 1948) and its lack of abaxial, rounded or radiostriate secretory cells (which could, however, be a function of the minute size of the one known specimen). This pattern of character distribution in dispersed cuticle supports the picture derived from whole leaves that a number of Zone I angiosperm leaves are related in some way to Chloranthaceae and Illiciales, but cannot be placed within either modern group.

Despite the fact that organically preserved leaves from Zone I cannot be assigned to modern families or orders, many of their structural features provide additional evidence for theories which postulate the subclass Magnoliidae (though not necessarily Magnoliales!) as the most primitive living angiosperm group. Maceration-resistant guard cell lamellae, found in many Zone I angiosperms, are today restricted to Magnoliidae (Baranova, 1972) as are radiostriate epidermal secretory cells of the type found in the fossils. Oil cells of the type inferred to have been present in the mesophyll of three leaf groups today are characteristic of Magnoliidae (Cronquist, 1968, 1981). Finally, the variable arrangement and specialization of the neighboring cells in Zone I stomata are present in several woody Magnoliid groups, including Austrobaileyaceae, Schisandraceae, and certain Chloranthaceae, but appear to be absent from more advanced groups such as Hamamelidales, Sapindales, and Dilleniales (Upchurch, in press). Leaf architectural studies provide a compatible picture of early Potomac Group angiosperms: Zone I leaves possess numerous Magnoliid features such as festooned brochidodromous secondary venation and "first rank" organization, but do not fit into any one family within the subclass (Wolfe et al., 1975; Hickey and Doyle, 1977). Hence, foliar analysis clearly indicates that Zone I angiosperms represent an early stage in the evolutionary history of the flowering plants. Earlier stages will be elucidated through the combined study of Zone I and older remains.

LITERATURE CITED

- AXELROD, D. I. 1952. A theory of angiosperm evolution. *Evolution* 5: 29–60.
- . 1970. Mesozoic paleogeography and early angiosperm history. *Bot. Rev.* 36: 277–319.
- BAILEY, I. W., AND C. G. NAST. 1948. Morphology and relationships of *Illicium*, *Schisandra*, and *Kadsura*, I. Stem and leaf. *J. Arnold Arbor. Harv. Univ.* 29: 77–89.
- BARANOVA, M. A. 1972. Systematic anatomy of the leaf epidermis in the Magnoliaceae and some related families. *Taxon* 21: 447–469.
- BERRY, E. W. 1911. Systematic paleontology, Lower Cretaceous: Fossil plants. In W. B. Clark [ed.], *Lower Cretaceous*, pp. 214–508. Maryland Geological Survey, Baltimore.
- BRENNER, G. J. 1963. The spores and pollen of the Potomac Group of Maryland. Maryland Dept. Geol., Mines and Water Resources Bull. 27.
- CRONQUIST, A. 1968. The evolution and classification of flowering plants. Houghton Mifflin Co., Boston.
- . 1981. An integrated system of classification of the flowering plants. Columbia University Press, New York.
- DEN HARTOG, R. M., AND P. BAAS. 1978. Epidermal characters of the Celastraceae sensu lato. *Acta Bot. Neerl.* 27: 355–388.
- DILCHER, D. L. 1974. Approaches to the identification of angiosperm leaf remains. *Bot. Rev.* 40: 1–157.
- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. *J. Arnold Arbor. Harv. Univ.* 50: 1–35.
- . 1973. Fossil evidence on early evolution of the monocotyledons. *Q. Rev. Biol.* 48: 399–413.
- , AND L. J. HICKEY. 1976. Pollen and leaves from the Mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In C. B. Beck [ed.], *Origin and early evolution of angiosperms*, pp. 139–206. Columbia University Press, New York.
- FONTAINE, W. 1889. The Potomac or Younger Mesozoic Flora. U.S. Geol. Surv. Monogr. 15. Washington, D. C.
- HARRIS, T. M. 1932. The fossil flora of Scoresby Sound, East Greenland. *Medd. Groenl.* 85: 1–112.
- . 1964. The Yorkshire Jurassic Flora. II. Caytoniales, Cycadales, and Pteridosperms. Trustees of the British Museum (Natural History), London.
- HICKEY, L. J. 1973. Classification of the architecture of dicotyledonous leaves. *Amer. J. Bot.* 60: 17–33.
- , AND J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.* 43: 3–104.
- , AND J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Mo. Bot. Gard.* 62: 538–589.
- JÄHNICHEN, H. 1976. Eozäne Floren des Geiseltales. *Paläontologische Abhandlungen, Abt. B. Heft* 26: 151–197.
- KRÄUSEL, R., AND H. WEYLAND. 1950. Kritische Untersuchungen zur Kuticular-analyse tertiärer Blätter II. *Palaeontographica, Abt. B* 96: 106–163.
- MERSKEY, M. L. 1973. Lower Cretaceous (Potomac Group) angiosperm cuticles. *Amer. J. Bot.* 60(suppl.): 17–18.
- METCALFE, C. R., AND L. CHALK. 1950. *Anatomy of the dicotyledons*. Clarendon Press, Oxford.
- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev.* 45: 417–450.
- . 1981. Fossil pollen records of extant angiosperms. *Bot. Rev.* 47: 1–46.
- ROSELT, G., AND W. SCHNEIDER. 1969. Cuticulae dispersae, ihre Merkmale, Nomenklatur, und Klassifikation. *Paläont. Abh. B* 3: 1–128.

- STACE, C. A. 1965. Cuticular studies as an aid to plant taxonomy. *Bull. Brit. Mus. (Bot.)* 4 (1).
- STÜRM, M. 1971. Die Eozäne Flora von Messel bei Darmstadt 1. Lauraceae. *Palaeontographica, Abt. B* 134: 1-60.
- SWAMY, B. G. L., AND I. W. BAILEY. 1950. *Sarcandra*, a vesselless genus of the Chloranthaceae. *J. Arnold Arbor. Harv. Univ.* 31: 117-129.
- TAKHTAJAN, A. 1969. Flowering plants: origin and dispersal. (Transl. by C. Jeffry.) Smithsonian Institution Press, Washington, D.C.
- UPCHURCH, G. R. 1978. A preliminary report of an investigation of the cuticular structure of the oldest structurally preserved angiosperm leaves. *Bot. Soc. Amer. Misc. Ser.* 156: 78 (abstr.).
- . 1979. The cuticular anatomy of *Sapindopsis* from the Lower Cretaceous Potomac Group of Virginia and Maryland. *Bot. Soc. Amer. Misc. Ser.* 157: 39 (abstr.).
- . In press. Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland. *Ann. Mo. Bot. Gard.*
- VANSTAVEREN, M. G. C., AND P. BAAS. 1973. Epidermal characters of the Malesian Icacinaceae. *Acta Bot. Neerl.* 22: 329-359.
- WARD, L. F. 1905. Status of the Mesozoic Floras of the United States. *U.S. Geol. Surv. Monogr.* 48, Washington, D.C.
- WOLFE, J. A., J. A. DOYLE, AND V. M. PAGE. 1975. The bases of angiosperm phylogeny: Paleobotany. *Ann. M. Bot. Gard.* 62: 801-824.