

CUTICLE EVOLUTION IN EARLY CRETACEOUS ANGIOSPERMS FROM THE POTOMAC GROUP OF VIRGINIA AND MARYLAND¹

GARLAND R. UPCHURCH, JR.²

ABSTRACT

Studies of angiosperm leaf cuticles from the Lower Cretaceous Potomac Group reinforce previous evidence for a Cretaceous adaptive radiation of the flowering plants and suggest unsuspected trends in the evolution of stomata and trichomes. Early Potomac Group angiosperm leaf cuticles (Zone I of Brenner or Aptian?) show little interspecific structural diversity, particularly in stomatal organization. All species conform to the same highly plastic pattern of variation in subsidiary cell arrangement, in which the stomata on a single leaf conform to several types, including paracytic, hemiparacytic, anomocytic, laterocytic, and weakly cyclocytic. Several species resemble extant Chloranthaceae and Illiciaceae, but none represents a modern family. Later leaves (Subzone II-B of Brenner, or Albion) exhibit greater interspecific structural diversity, particularly in stomatal organization. Three new patterns of variation in subsidiary cell arrangement are present in addition to the older one and each has a subset of the variation present in the older pattern. Cuticular anatomy is consistent with proposed leaf affinities to Platanaceae and Rosidae. The stratigraphic trend in cuticle types supports the concept that the subclass Magnoliidae includes the most primitive living angiosperms. However, it also suggests that the uniformly paracytic stomatal pattern characteristic of Magnoliales, generally considered primitive for the flowering plants, may actually be derived from the variable condition found in Zone I leaves.

Within the past 15 years there has been a major reevaluation of the Cretaceous flowering plant record and the role of fossils in angiosperm phylogeny. Formerly, it was thought that fossils could provide little evidence on the course of angiosperm evolution, since even the earliest known remains were believed to represent modern families and genera (Axelrod, 1952, 1970). This view, based on older studies of leaf remains such as those by Fontaine (1889), Ward (1905), and Berry (1911) for the Potomac Group, has been strongly contradicted by more recent analyses of Cretaceous pollen and leaf architecture (Doyle, 1969; Muller, 1970, 1981; Wolfe et al., 1975; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Hickey, 1978). These newer studies show that practically all of the older leaf identifications are incorrect and that successively younger Cretaceous angiosperm floras show the progressively higher levels of advancement predicted by many modern systems of classification (cf. Cronquist, 1968, 1981; Takhtajan, 1969, 1980; Thorne, 1976). 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 course and timing of flowering plant evolution.

One largely untouched source of data is cuticular anatomy. Despite the fact that cuticles have long provided important characters for the systematic placement of Mesozoic gymnosperms and Tertiary angiosperm leaves (e.g., Harris, 1932, 1964; Kräusel & Weyland, 1950, 1954; Dilcher, 1974), most work on Cretaceous flowering plant leaves has neglected cuticular anatomy and relied solely on leaf architecture (e.g., venation, shape). I began a study of angiosperm leaf cuticles from the Lower Cretaceous Potomac Group of Virginia and Maryland to test previous ideas on early flowering plant evolution. At first, cuticular leaves were known only from the upper part of the Potomac Group (Palynosubzone II-B of Brenner, or probably middle to late Albion), but, later on, organically preserved leaves were collected from the lower part as well (Palynozone I of Brenner, or probably Aptian). This provided

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² Paleontology and Stratigraphy Branch, U.S. Geological Survey, M.S. 919, 25 Denver Federal Center, Denver, Colorado 80225.

the opportunity to compare the stratigraphic changes seen in the systematic affinities and structural diversity of angiosperm leaf cuticles with those observed for leaf architecture and pollen morphology. This report summarizes the results of this investigation and their possible significance for flowering plant evolution: included are a comparison of the diversity of cuticular and leaf architectural features, an assessment of modern affinities based on cuticular anatomy, and two major evolutionary trends suggested by the morphological relationships of cuticular features in conjunction with their stratigraphic distribution.

MATERIALS AND METHODS

All organically preserved leaf types known from Zone I and Subzone II-B were prepared using a combination of standard methods (cf. Dilcher, 1974). For light microscopy, cuticles were demineralized in HF, macerated in Schulze's solution followed by dilute alkali, stained in an aqueous solution of Safranin O, and mounted on slides in glycerine jelly. Preparations for scanning electron microscopy (SEM) varied according to the surface studied. External features were observed on unmacerated, demineralized leaf fragments. Internal features were observed on macerated cuticle that was dried down to SEM stubs coated with Duco cement in a chamber saturated with acetone vapor. All specimens were coated with gold and observed at 15 kV.

Plant debris from Zone I was analyzed to determine how much of the diversity of cuticle types was missing from the one known organically preserved leaf assemblage. Samples were obtained by disaggregating the rock in HF or Na_2CO_3 , then sieving the slurry through 100 mesh screen. Unoxidized plant fragments were prepared as above, using a centrifuge, and mounted in glycerine jelly on slides or in glycerine between pairs of paraffin-sealed cover slips. Naturally macerated cuticle was mounted in glycerine in paraffin-sealed slides pending further study.

Extant angiosperm leaf cuticles were examined to test ideas on the relationships of Potomac Group leaves to modern forms. Taxa were selected for study based on two criteria: 1. their relative primitiveness according to the phylogenetic schemes of Cronquist (1968, 1981), Takhtajan (1969, 1980), and Thorne (1976), and 2. their similarity to Potomac Group angiosperms in leaf venation and pollen morphology.

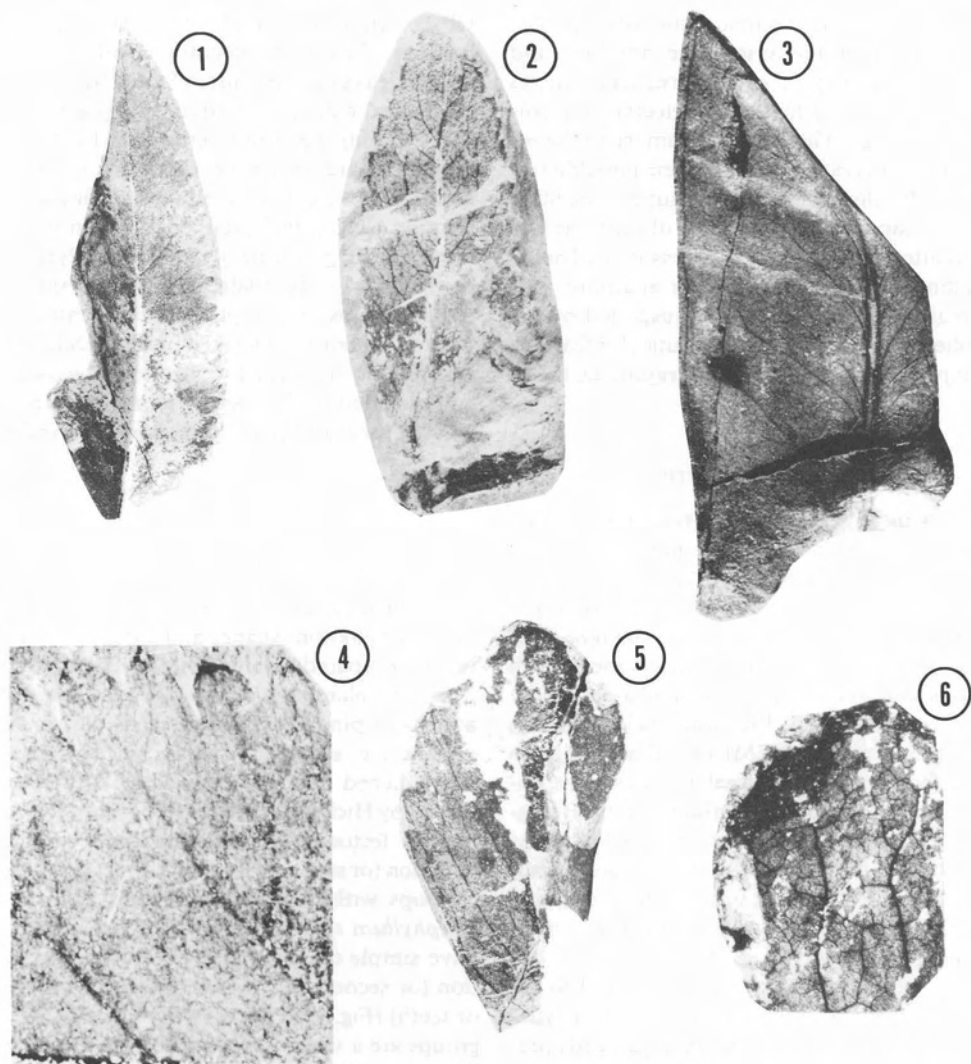
Observations were made on cuticle slides in the Indiana University paleobotanical collections, cleared leaves at the United States National Museum, and cuticles prepared by myself for light and scanning electron microscopy. Light microscope preparations were made from leaf fragments that were macerated in modified Jeffrey's solution (Stace, 1965), stained in Safranin O, then mounted in glycerine jelly or Piccolyte. SEM preparations were made in a manner similar to that for the fossils, except that unmacerated leaves were either boiled or shaken ultrasonically in ethanol for 30 minutes to remove the waxes and adhering debris. All specimens were coated with carbon, then gold/palladium, and observed at 20 kV.

RESULTS

ZONE I ANGIOSPERM LEAVES

Zone I angiosperm leaves exhibit low diversity in their venation, shape, and marginal configuration compared to later Cretaceous and modern flowering plants. All Zone I leaves are simple and have pinnate venation, although in some groups the secondary veins are clustered or strengthened near the base of the leaf (also reported by Hickey & Doyle, 1977). Most leaf types possess festooned brochidodromous secondary venation (or secondaries that form several orders of loops within the margin) (e.g., Fig. 2), but *Vitiphyllum multifidum* and a new serrate form have simple craspedodromous secondary venation (or secondaries that run directly into lobes or teeth) (Fig. 1). The teeth of at least some leaf groups are a variant of the Chloranthoid type of Hickey and Wolfe (1975), with a biconvex shape, a large gland, and a pair of lateral veins that follow the margin and fuse with the gland (Fig. 4). Zone I leaves also show a low systematic diversity compared to later Potomac Group angiosperms: only 12 leaf types are recognized from Zone I, as opposed to over 30 from Subzone II-B (Hickey & Doyle, 1977).

The most distinctive feature of Zone I leaf architecture is the low degree of organization in the vein network. Secondary veins are irregularly spaced, enclose areas of variable size and shape, and often branch decurrently (e.g., Fig. 2). Tertiary and higher order veins are poorly differentiated from the secondaries and have a random course. This "first rank" pattern of venation occurs today in such primitive families as Winteraceae and Canellaceae and is considered primi-



FIGURES 1-6. Organically preserved Zone I leaf types. — 1. Drewrys Bluff Leaf Type #1 (DBLT #1). University of Michigan Museum of Paleontology (UMMP) 64887, $\times 1.5$. — 2. *Celastrorhynchium* sp. with associated stem fragment. UMMP 64892, $\times 1.5$. — 3. *Eucalyptorhynchium oblongifolium*, specimen photographed in infrared light. Note the 2-stranded midrib and the intramarginal vein. UMMP 64859, $\times 1.5$. — 4. DBLT #1, close-up showing simple craspedodromous secondaries and chloranthoid teeth. UMMP 64887, $\times 8$. — 5. Cf. *Celastrorhynchium obovatum*, UMMP 64865, $\times 3$. — 6. Cf. *Ficorhynchium*. UMMP 65101, $\times 3$.

tive for the dicots by Hickey (1971, 1977). Some authors (Wolfe et al., 1975) have suggested that several Zone I leaf types actually may be more primitive than anything extant, because they show even less vein regularity than any modern angiosperm.

All Zone I leaves with cuticle come from a new locality at the north end of Drewrys Bluff, on the James River near Richmond, Virginia. These leaves are dated palynologically as upper Zone I

of Brenner, or probably Aptian (Doyle, pers. comm.), and thus are similar in age to angiosperm leaves reported from the southern end of the exposure (Hickey & Doyle, 1977). Five leaf types are present at this locality, two of which are serrate. The most abundant form is an undescribed species referred to in this paper as Drewrys Bluff Leaf Type #1 (DBLT #1), which has simple craspedodromous secondary venation and Chloranthoid teeth (Figs. 1, 4). The oth-

er serrate leaf type has festooned brochidodromous venation, as in other Potomac Group species of *Celastrophyllum*, but differs in its low number of secondary veins and lack of a distinct petiole (*Celastrophyllum* sp., Fig. 2). Of the three entire-margined forms, *Eucalyptophyllum oblongifolium* has a midrib composed of two fusing vascular strands, numerous irregularly spaced secondary veins that connect with a prominent intramarginal vein, and only three orders of venation (Fig. 3). This suite of features in combination with the leaf's elongate areolation, is unknown in extant flowering plants (Wolfe et al., 1975; Hickey & Doyle, 1977). The other two groups are less unusual. One has an obovate shape, closely spaced, brochidodromous secondary veins, and random reticulate tertiary venation: it resembles the *Celastrophyllum obovatum* complex from Baltimore but differs by its much smaller size (cf. *C. obovatum*, Fig. 5). The other consists of fragments comparable to some specimens of *Ficophyllum* Font. in their reticulate pattern of tertiary and higher order venation (cf. *Ficophyllum*, Fig. 6). Certain characteristic Zone I leaf types, such as pinnately lobate forms (*Vitiphyllum* Font.), elongate obovate leaves (*Rogersia* Font.), and reniform leaves with basally congested secondary veins (*Proteaphyllum reniforme* Font.), are absent. Roughly one-third of the leaf types from Zone I are known with cuticle, since about 12 have been previously recognized for this interval (Hickey & Doyle, 1977).

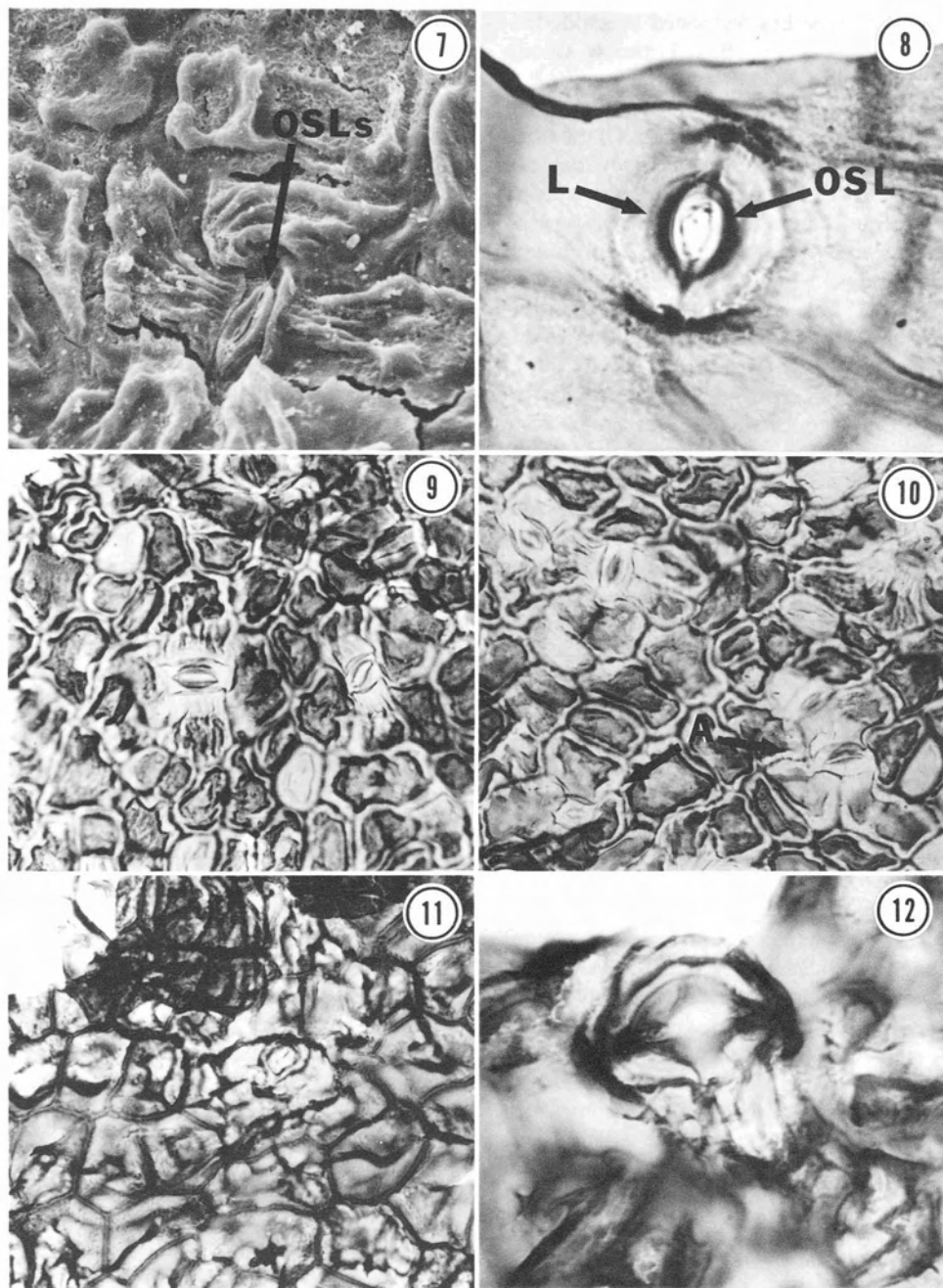
Dispersed angiosperm cuticle is known from two Zone I localities on the James River: 1, the Drewrys Bluff angiosperm leaf bed, palynologically dated as upper Zone I, and 2, Dutch Gap Canal, palynologically dated as lower Zone I (Hickey & Doyle, 1977; Upchurch & Doyle, 1981). At least six cuticle types not known from whole leaves are present in these assemblages. This brings the total number of cuticle types up to 11, which suggests that much of the systematic diversity of Zone I leaves may be represented in the cuticles sampled for this study.

Zone I angiosperms show a limited range of cuticular variation compared to Subzone II-B and modern flower plants. As a rule these leaves are least variable in traits that often have high systematic value in extant angiosperms, while they are most variable in traits that tend to have little systematic significance (cf. Metcalfe & Chalk, 1950; Stace, 1965; Van Staveren & Baas, 1973; Jansen & Baas, 1973). In particular, Zone I leaf cuticles are relatively uniform in plan of stomatal

construction, hair base structure, and types of secretory cells. More variation is present in patterns of cuticular sculpture, particularly on the outer cuticle surface. Traits such as cuticle thickness and cell contour are highly variable and of little value except in the identification of species; hence they are not discussed in the following paragraphs.

The stomatal complex shows a typically angiospermous plan of construction. In the guard cells of all species the stomatal poles are level with the stomatal pore, rather than raised, as in most gymnosperms (Harris, 1932). The stomata of most forms are level with the epidermis, but are distinctly sunken in *Eucalyptophyllum* (Fig. 7). The guard cells often bear cuticular ridges on their outer walls, or outer stomatal ledges (Fig. 7, OSL), and in many groups there are lamellar thickenings (Fig. 8, L), which are typical of primitive extant Magnoliidae (Baranova, 1972; Upchurch, unpubl. data). These lamellar thickenings are commonly associated with outer stomatal ledges, or else tend to intergrade with them. In addition, Dispersed Cuticles #1 and #3 bear strongly developed, T-shaped thickenings at the stomatal poles, or T-pieces (Figs. 8, 12). Such thickenings are present in diverse angiosperms, including the primitive family Illiciaceae (Bailey & Nast, 1948).

The arrangement of the subsidiary cells in all investigated species of Zone I angiosperms exhibits unusually high variation compared to that in extant flowering plants. Most extant angiosperm leaves possess stomata that fit into one or two standard types, defined by the presence or absence of subsidiary (or specialized) cells and their arrangement relative to the guard cells. In contrast, the stomata on a single Zone I angiosperm leaf fit into several of the conventionally recognized types as well as intermediates. This situation makes it necessary to analyze stomatal structure in a new way. In brief, a population of about 50 to 100 stomata is examined for ten features that contribute to the variation in stomatal structure for at least one species of Zone I angiosperm leaf. The range of variation in each is then recorded and the data are displayed in tabular form to facilitate comparisons between species (e.g., Tables 1–4). The ten major components of stomatal variation fall into three major categories: 1. the number and position of the contact cells (or those cells abutting on the guard cells), 2. the position of specialized contact cells, and 3. the position of specialized non-contact



FIGURES 7-12. Zone I angiosperm leaf cuticles.—7. *Eucalyptophyllum*, scanning electron micrograph of outer surface, lower cuticle. Note sunken stoma and two types of striations. UMMP 64862, $\times 1,000$.—8. Dispersed Cuticle #1, stoma showing lamellar thickenings, outer stomatal ledges, and T-pieces. UMMP 65125-G153, $\times 800$.—9. *Eucalyptophyllum*, paracytic stomata. UMMP 64862, $\times 400$.—10. *Eucalyptophyllum*, anomocytic and other stomatal types. UMMP 64862, $\times 400$.—11. Dispersed Cuticle #3, paracytic stoma. Also note partially solid papillae with radiating striations. UMMP 65126-56, $\times 400$.—12. Same, close-up of another stoma showing concentric striations and T-pieces. UMMP 65126-56, $\times 1,000$.

TABLE 1. Stomatal features of selected Zone I angiosperms.

	<i>Eucalyptophyllum</i>	cf. <i>Ficophyllum</i>	Dispersed Cuticle #1	Dispersed Cuticle #3
Number of contact cells	4-6	4-5	4-5	4-7
Number of lateral contact cells (LCCs)	2-4	2-3	2-3	2-4
Stomata with specialized LCCs?	sometimes	sometimes	sometimes	always
LCC specialization pattern within stoma	one or both guard cells	one or both guard cells	one or both guard cells	one or both guard cells
LCC specialization pattern along length of guard cells	either full or partial length	either full or partial length	mostly full length	either full or partial length
Number of polar contact cells (PCCs)	2-3	2	2-3	2-3
Stomata with specialized PCCs?	sometimes	sometimes	sometimes	sometimes
PCC specialization pattern	one or both poles	one or both poles	one or both poles	one or both poles
Other specialized cells?	sometimes	never	sometimes	sometimes
Position of other specialized cells	variable	—	mostly lateral	lateral
Number of variable features	10	7	10	8
Stomatal types*	P, Lc, C, and intermediates (common); H and A (rare)	P, H, A, and intermediates (common); weakly C (rare)	P, Lc, and H, all intergrading with A	P (common); H and transitional between Lc and C (rare)

* Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic; A = anomocytic.

cells. The stomata of Zone I angiosperms are variable for at least seven of these features, with *Eucalyptophyllum* showing variation in all ten. Some of these features are variable in a number of extant angiosperms; these include the total number of contact cells, the presence or absence of specialized polar contact cells, and the presence or absence of specialized non-contact cells. Three, however, rarely vary within extant species; these are all components of lateral contact cell (or LCC) specialization. First, modified LCCs are found in many stomata, yet in others on the same leaf they are lacking entirely (e.g., Fig. 10); the exception is Dispersed Cuticle #3, which always has at least one modified LCC per stoma (Figs. 11, 12). Second, when a stomatal complex possesses modified LCCs, they may occur along both guard cells (e.g., Fig. 13, P, Lc) or else just one

of them (Fig. 13, H). Finally, when a guard cell is flanked by one or more specialized LCCs, they often extend only part of the length of the stoma, rather than the full length (e.g., Fig. 14, arrow). This variation produces stomata that could be classified as anomocytic (Fig. 10, A), hemiparacytic (Fig. 13, H), paracytic (Figs. 9, 11, 13, P), laterocytic (Fig. 13, Lc), weakly cyclocytic (Fig. 13, C), and intermediates. This extreme plasticity in subsidiary cell organization, which is rare in extant flowering plants, produces stomata with a low degree of regularity, analogous to that present in the venation of these and other Zone I leaves.

A survey of extant primitive dicots reveals few groups with stomatal variation approaching that seen in Zone I. Most Magnoliales are paracytic (Baranova, 1972; Bongers, 1973; Koster & Baas,

TABLE 2. Stomatal features of selected Magnoliales.

Family	Winteraceae	Myristicaceae	Magnoliaceae	
Genus	<i>Drimys</i> (Old World)	<i>Knema</i>	<i>Manglietia</i>	<i>Liriodendron</i>
Number of contact cells	4–6	4, rarely 5	3–5	4–5
Number of lateral contact cells (LCCs)	2, rarely 3	2	2, very rarely 3	2–3
Stomata with specialized LCCs?	always	always	always	always
Both guard cells of stoma with specialized LCCs?	always	always	always	always
LCCs specialized full length of adjacent guard cell?	always	always	always	always
Number of polar contact cells (PCCs)	2–4	2, rarely 3	1–2	2–3
Stomata with specialized PCCs?	never	never	never	never
PCCs specialized at both poles?	—	—	—	—
Other specialized cells?	sometimes	sometimes	sometimes	sometimes
Position of other specialized cells	lateral	lateral	lateral	lateral
Number of variable features	~3	~3	~3	4
Stomatal types ^a	P, rarely Lc	P, rarely Lc or subdivided P	P, rarely Lc	P and Lc

^a Key: P = paracytic; Lc = laterocytic.

TABLE 3. Stomatal features of selected Magnoliales.

Family	Canellaceae		Winteraceae	
Genus	<i>Pleodendron</i>	<i>Warburgia</i>	<i>Drimys</i> (New World)	<i>Takhtajania</i>
Number of contact cells	4–6	6–9	4–5(–6–7)	4–5
Number of lateral contact cells (LCCs)	2–3(–4)	3–5	2–4	2–3
One or more specialized LCCs in each stoma	always	always	always	sometimes
LCCs specialized for both GCs?	always	always	always	sometimes
LCCs specialized full length GC?	usually, not always	always	often, not always	sometimes (polar contact cell overlaps GC side)
Number of polar contact cells	2–3	3–4	2–3	2
PCCs specialized in each stoma?	rarely	sometimes	never	never
PCCs specialized at both poles?	sometimes	sometimes	—	—
Other specialized cells?	sometimes	always one or more	sometimes	never
Specialization pattern	lateral	lateral, sometimes polar also	lateral	—
Number of variable features	7	6	5	(4–)5
Stomatal types ^a	P, Lc, C	Lc, C	P, Lc	A, P
Remarks			LCCs strongly compressed	4 stomata in photo

^a Key: P = paracytic; Lc = laterocytic; C = cyclocytic; A = anomocytic.

TABLE 4. Stomatal features of selected Laurales and Illiciales.

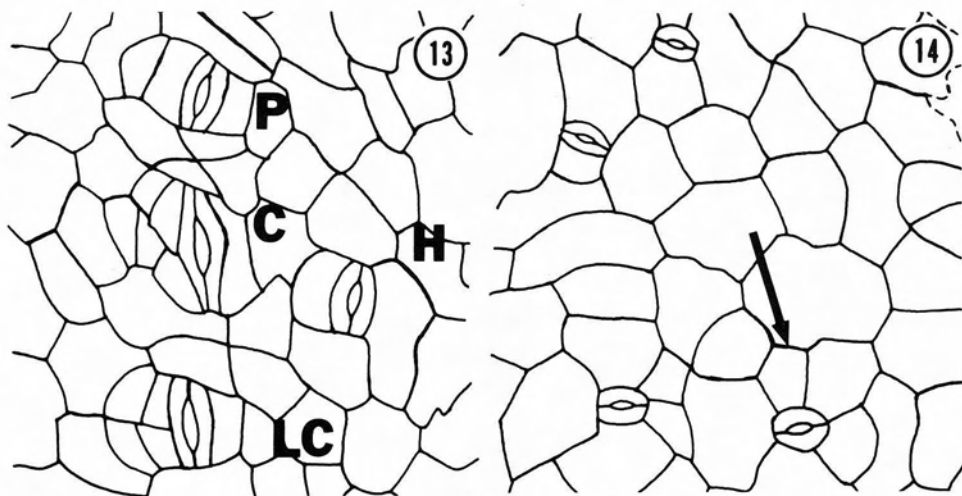
Family	Amborellaceae	Chloranthaceae		Austro-baileyaceae	Schisan-draceae
Genus	<i>Amborella</i>	<i>Chloranthus</i>	<i>Sarcandra</i>	<i>Austro-baileya</i>	<i>Schisandra</i>
Number of contact cells	4–6	4–5	4–6	4–6	4–6
Number of lateral contact cells (LCCs)	2–3	2–3	2–4	2–4	2–4
Stomata with specialized LCCs?	always	always	always	always	always
Both guard cells of stoma with specialized LCCs?	sometimes	sometimes	always	sometimes	always
LCCs specialized full length of adjacent guard cell?	always for one guard cell, other one variable	sometimes	always	sometimes	sometimes
Number of polar contact cells (PCCs)	2–3	2–3	2–3	2–4	2–4
Stomata with specialized PCCs?	sometimes	occasionally	sometimes	never	never
PCCs specialized at both poles?	sometimes	usually	always	—	—
Other specialized cells?	sometimes	sometimes	sometimes	sometimes	sometimes
Position of other specialized cells	mostly lateral	lateral	mostly lateral	lateral	lateral
Number of variable features	~8	8	5	6	5
Stomatal types*	P (common); Lc, H, C, and intermediates (uncommon)	P, Lc (common); H, C, and intermediates between Lc and C (rare)	P, Lc, C	P, Lc (common); H (uncommon)	P, Lc

* Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic.

1981; Roth, 1981) and those that are not show greater regularity than Zone I forms in the arrangement and specialization of their contact cells (Tables 2, 3). Greater variation is present in some Laurales (including Chloranthaceae) and Illiciales, but few taxa approach the extreme condition found in Zone I. The closest approaches are seen in the vesselless family Amborellaceae (Figs. 15, 16) and at least one species of Chloranthaceae (*Chloranthus serratus*), which are identical to Dispersed Cuticle #3 in almost all of their stomatal features (Table 4). Austrobaileyaceae (Figs. 17, 18) and certain Schisandraceae resemble Zone I forms in most respects, but differ by having

uniformly unmodified polar contact cells (Table 4). Finally, the vesselless genus *Sarcandra* (Chloranthaceae) resembles Zone I angiosperms in its number of lateral contact cells and the patterns of specialization in polar and non-contact cells, but differs by having a much more uniform pattern of lateral contact cell modification (Table 4). These similarities suggest that many Laurales and Illiciales are closer to Zone I angiosperms in their level of stomatal advancement than most, if not all, extant Magnoliales.

Only two types of possible hair bases are known from Zone I angiosperms, in contrast to the diverse array found in Tertiary and extant flow-



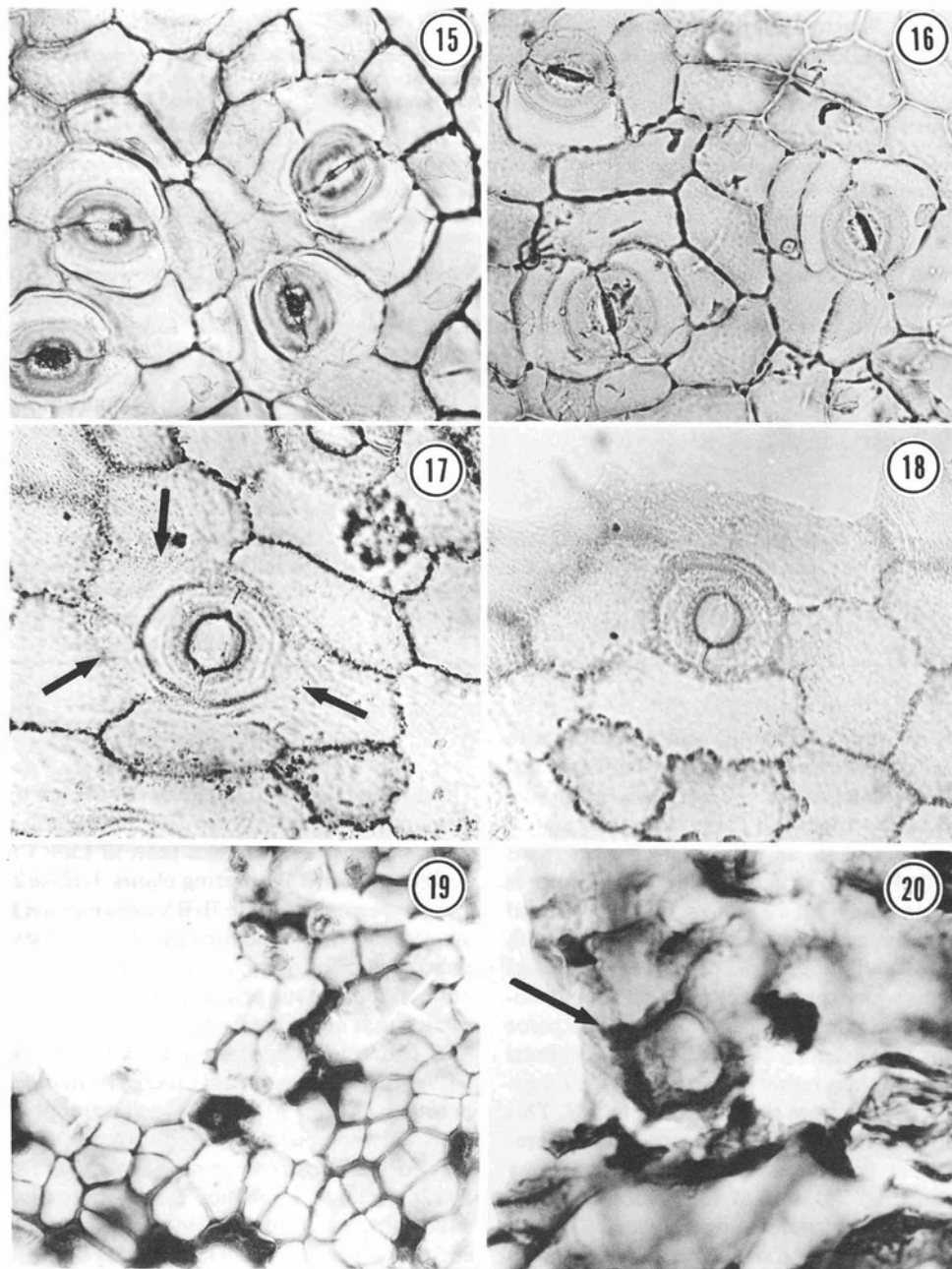
FIGURES 13, 14. Drawings of Zone I angiosperm stomata.—13. *Eucalyptophyllum*, paracytic (P), hemiparacytic (H), laterocytic (Lc), and weakly cyclocytic (C) stomata. UMMP 64892, $\times 750$.—14. Cf. *Ficophyllum*, hemiparacytic and unclassifiable stomata. Note how the lateral contact cells in one stoma are modified for only part of the length of the adjacent guard cell (arrow). UMMP 65107, $\times 250$.

ering plants (cf. Roselt & Schneider, 1969; Dilcher, 1974). Unlike many angiosperm hair bases, which show complex plans of construction, both Zone I types are simple, consisting of a single foot cell (to which the hair was attached) and several unmodified base cells. The first type, found in *Eucalyptophyllum* and DBLT #1, consists of a small, thickened, polygonal foot cell and several base cells that underthrust it (Fig. 19). No attached hairs or distinct abscission scars are known, raising the possibility that the "foot cells" are actually idioblasts, but circular depressions occur on the outer walls of some cells. Similar "foot cells" are found in a variety of extant angiosperm families, including Chloranthaceae, Illiciaceae, and Dilleniaceae (Upchurch, unpubl. data). The second type of hair base, found only in Dispersed Cuticle #3, is similar to the first in its size, shape, and degree of base cell underthrusting. It differs in having a thickened cuticle only on the outer wall of the foot cell and in having a trichome abscission scar, which consists of a pore (Fig. 20). Similar hair bases are found in an Eocene species of Schisandraceae (*Schisandra europaea*, cf. Jähniichen, 1976), but these differ from the Potomac Group type in having a more circular pore and strongly specialized base cells.

Secretory cells are present on the lower epidermis and in the mesophyll of many Zone I

leaves and these strongly resemble the oil cells found in extant primitive angiosperms (Table 5). Two major types occur on the lower epidermis. The first, found in *Eucalyptophyllum* and two dispersed cuticle groups (Fig. 21), has a round to somewhat angular outline and a thin, smooth outer cuticle. Similar epidermal oil cells are found today in several groups of Magnoliidae, including Calycanthaceae and Illiciaceae (cf. Jähniichen, 1976; Upchurch, unpubl. data). The second type of secretory cell, found in *Eucalyptophyllum*, DBLT #1, and Dispersed Cuticle #6, and here termed the radiostriate type (Fig. 22), has an angular outline and striations that radiate from its periphery. Similar oil cells are present on the lower epidermis of a few Magnoliales, many Laurales (Fig. 23), both families of Illiciales, and Saururaceae of the Piperales (Bailey & Nast, 1948; Upchurch, unpubl. data). Finally, mesophyll secretory cells are present in cf. *Ficophyllum* and both species of *Celastrorphyllum* (Fig. 24). These cells are round, about 10 μm in diameter, and contain dark substances. They resemble the mesophyll oil cells of diverse modern Magnoliidae in their size, shape, and appearance of macerated contents (cf. Jähniichen, 1976; Upchurch, unpubl. data).

Several types of cuticle sculpture are found in Zone I angiosperms. Surface sculpture conforms to three of the four major types listed by Dilcher



FIGURES 15–20. Cuticles of extant and Zone I angiosperms.—15. *Amborella trichopoda*, lower cuticle, stomata showing variation in the pattern of lateral contact cell (LCC) specialization along the length of each guard cell. Gray Herbarium, R. F. Thorne #28348, $\times 400$.—16. *Amborella trichopoda*, lower cuticle, stomata showing variation in the number of guard cells with specialized LCCs. Gray Herbarium, R. F. Thorne #28348, $\times 400$.—17. *Austrobaileya* sp., laterocytic stoma. The subsidiary cells (arrows) typically have thinly cuticized tangential walls. Arnold Arboretum, L. J. Bass #18160, $\times 400$.—18. *Austrobaileya* sp., anomocytic (?) stoma. Arnold Arboretum, L. J. Bass #18160, $\times 400$.—19. *Eucalyptophyllum*, upper cuticle showing probable hair bases. UMMP 64860, $\times 400$.—20. Dispersed Cuticle #3, hair base (arrow). UMMP 65126–56, $\times 1,000$.

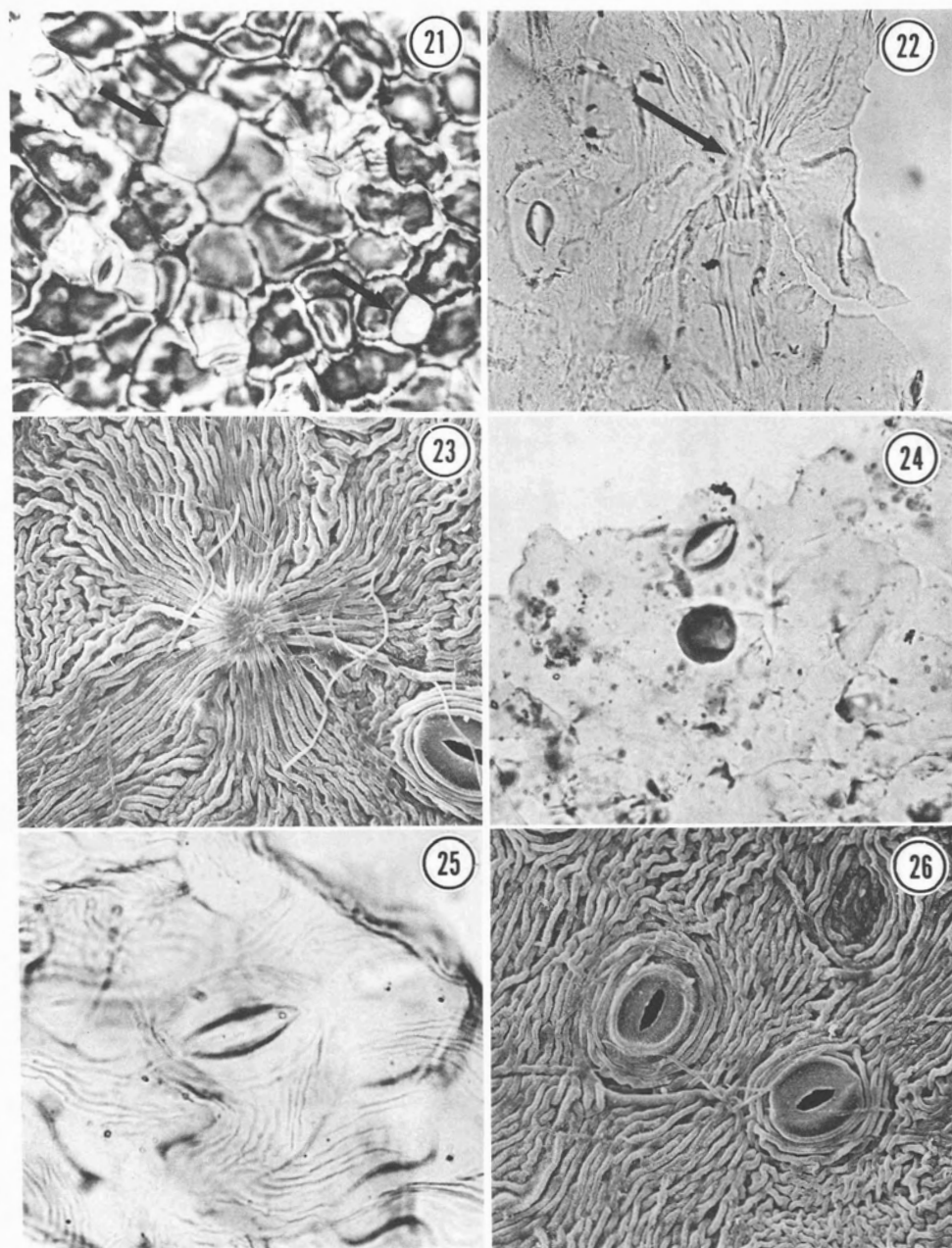
TABLE 5. Secretory cell types of Zone I angiosperms.

Location	Description	Systematic Distribution, Zone I	Systematic Distribution, Modern Flora	
1. Lower epidermis	round-subangular in surface view, outer cuticle smooth	<i>Eucalyptophyllum</i> Dispersed Cuticle #5 Dispersed Cuticle #6	Laurales:	Calycanthaceae Chloranthaceae
			Illiciales:	Illiciaceae Schisandraceae
2. Lower epidermis	strongly angular in surface view, outer cuticle with radiating striations	<i>Eucalyptophyllum</i> DBLT #1 Dispersed Cuticle #6	Magnoliales:	Annonaceae? Eupomatiaceae
			Laurales:	Austrobaileyaceae Chloranthaceae Gomortegaceae Monimiaceae Trimeniaceae
			Illiciales:	Illiciaceae Schisandraceae
			Piperales:	Saururaceae
3. Mesophyll	spherical, with thin walls and dark contents	<i>Celastrophyllum</i> sp. cf. <i>C. obovatum</i> cf. <i>Ficophyllum</i>	Magnoliales:	all families
			Laurales:	most families
			Illiciales:	both families
			Piperales:	both families
			Aristolochiales:	single family

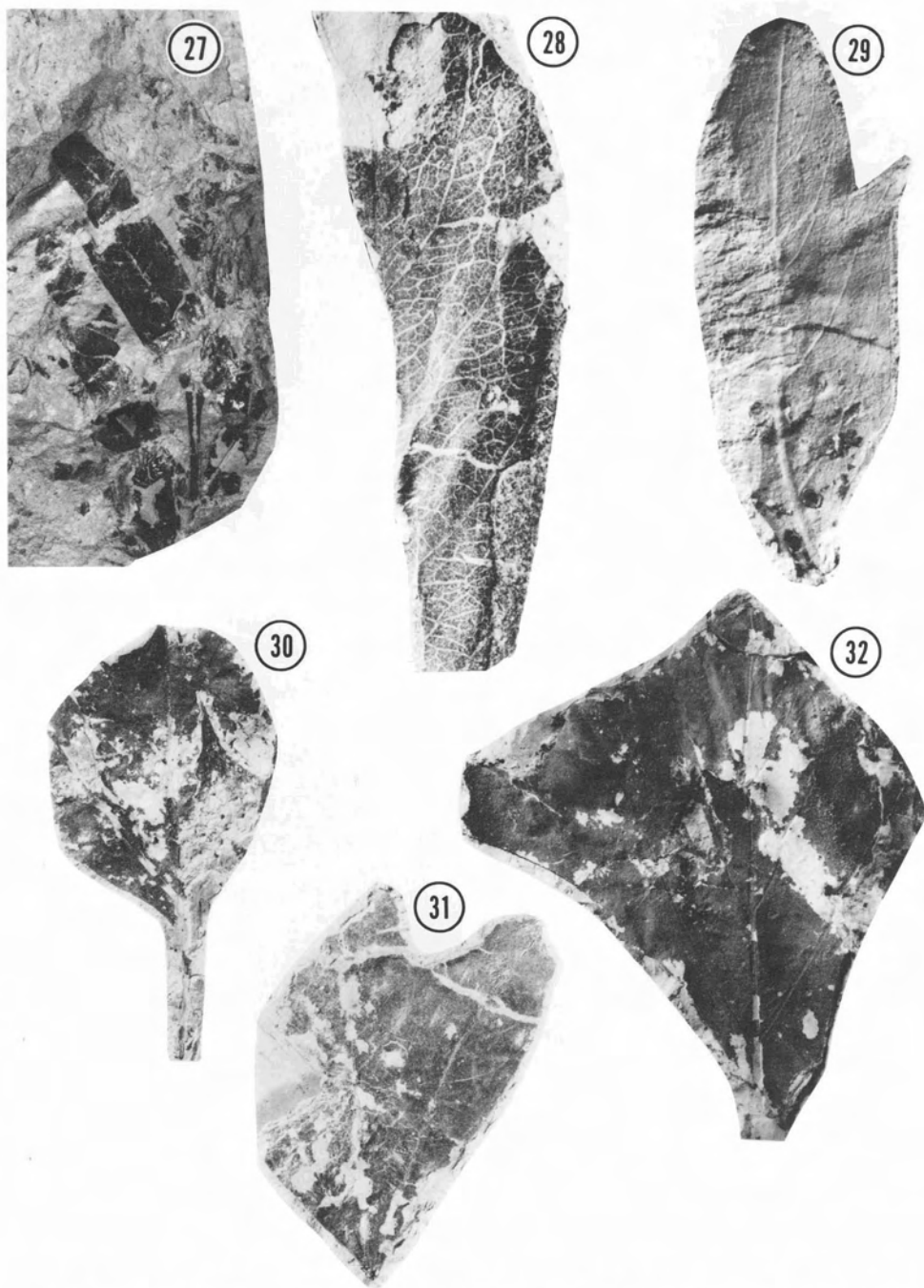
(1974). Psilate (or smooth) sculpture occurs in several different cuticle types. Papillate (or knobbed) sculpture is present in several dispersed cuticle types and commonly the papillae are partially solid, as in Dispersed Cuticle #3 (Fig. 11). Finally, striate (or ridged) sculpture is present in many Zone I groups; this is organized into two distinct patterns. The first, found in both DBLT #1 and Dispersed Cuticle #3, consists of striations which traverse cell boundaries and display two orientations near the stomata: some striations are oriented concentric to the stomatal pore while others either have a random arrangement or radiate from the stomata (Fig. 25). This condition is characteristic of many extant primitive dicot groups, including Illiciales, many Laurales (Fig. 26), and at least some Piperales (Saururaceae, Upchurch, unpubl. data). The second, found only in *Eucalyptophyllum*, consists of two distinct size-classes of striations that display markedly different behavior: the smaller ones traverse cell boundaries and radiate from the stomata, while the larger ones are confined to one cell each and enclose polygonal areas that mimic the shape of the underlying cell (Fig. 7). To date this pattern has not been observed in any extant group of angiosperms, but individual elements occur in scattered families, including Chloranthaceae (Upchurch, unpubl. data).

SUBZONE II-B ANGIOSPERM LEAVES

Subzone II-B angiosperm leaves show a much greater diversity of leaf architectural features than Zone I forms, but still less than in Late Cretaceous and modern flowering plants. Unlike Zone I angiosperms, Subzone II-B leaves include both simple and compound forms and possess several new types of primary venation. *Populophyllum* has actinodromous primary venation, with primaries that all radiate from a single point (Fig. 35). The "platanoids" are palinactinodromous, with primary veins that all diverge from different points (e.g., Fig. 31), and *Menispermites potomacensis* is acrodromous, with lateral primaries that curve towards the apex (Hickey & Doyle, 1977). Secondary venation is also more diverse, with both festooned brochidodromous and several new types present. At least some of the "platanoids" possess simple brochidodromous secondary venation, with secondary veins that form only one order of loops (cf. Hickey & Doyle, 1977; Upchurch, unpubl. data). Some *Sapindopsis* leaflets have eucamptodromous secondary venation, with secondaries that gradually thin towards the apex and do not join with the supraadjacent secondary veins (Fig. 28), while others possess mixed craspedodromous secondary venation, with a mixture of craspedodromous



FIGURES 21–26. Cuticles of extant and Zone I angiosperms.—21. *Eucalyptophyllum*, epidermal secretory cells (arrows). UMMP 64862, $\times 400$.—22. Dispersed Cuticle #6, radiostriate secretory cell (arrow). UMMP 65123A, $\times 400$.—23. *Austrobaileya* sp., scanning electron micrograph of radiostriate secretory cell. Arnold Arboretum, L. J. Bass #18160, $\times 400$.—24. Cf. *Celastrorhynchum obovatum*, mesophyll secretory cell. UMMP 64865, $\times 600$.—25. DBLT #1, anomocytic stoma with concentric and radiating striations. UMMP 64884-G157, $\times 600$.—26. *Austrobaileya* sp., scanning electron micrograph of stomata showing concentric striations. Arnold Arboretum, L. J. Bass #18160, $\times 400$.



FIGURES 27–32. Organically preserved Subzone II-B leaf types.—27. *Sapindopsis variabilis*, pinnatifid leaf. UMMP 65110, $\times 1$.—28. Leaflet of pinnately compound *Sapindopsis* showing eucamptodromous secondary venation. UMMP 65111, $\times 2$.—29. Toothed leaflet of pinnately compound *Sapindopsis* showing mixed craspedodromous secondary venation. UMMP 65112, $\times 2$.—30. Platanoid #3, basal portion of leaf. UMMP 65103, $\times 1$.—31. Platanoid #2. UMMP 65105, $\times 1$.—32. Platanoid #3, apical portion of leaf. UMMP 65104, $\times 1$.

and camptodromous secondary veins (Fig. 29). Finally, there are more tooth types present in Subzone II-B than in Zone I: in addition to convex-convex (A-1) teeth there are concave-convex (C-1) teeth with features of the Rosoid tooth type of Hickey and Wolfe (1975) in some pinnately compound specimens of *Sapindopsis* (Fig. 29) and straight-convex (B-1) teeth in a new serrate leaf from the Red Point locality of Hickey and Doyle (1977).

A key difference between Zone I and Subzone II-B dicotyledonous leaves is the strong tendency in the latter for greater vein regularity: generally the veins have a more regular course and the different vein orders are easier to distinguish from one another. While the older "first rank" syndrome is retained in many leaf groups, some, such as many pinnately compound *Sapindopsis*, are "second rank," with secondary veins that are regularly spaced and enclose areas of similar size and shape. Others, such as Platanoid #3, have regularly organized secondary and tertiary venation and hence conform to Hickey's "third rank" syndrome. This greater venational regularity suggests that many Subzone II-B leaves are more advanced than their Zone I counterparts. However, the fact that leaves with "fourth rank" venation, with an organized system of areoles, do not appear until the Late Cretaceous indicates that Subzone II-B angiosperms still do not have the level of advancement of many Late Cretaceous and modern flowering plants (Hickey, 1978).

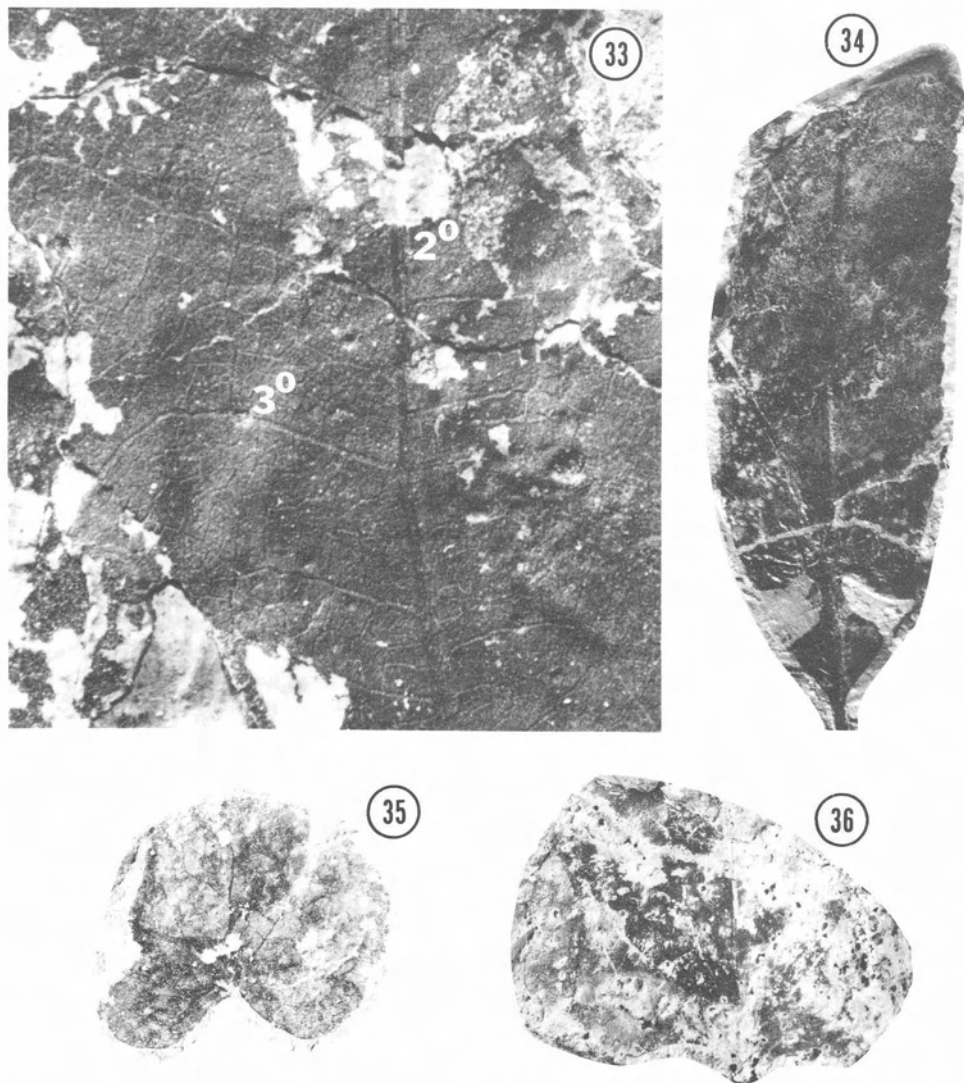
Cuticular angiosperm leaves are known from four of the major leaf localities of Hickey and Doyle (1977). One, the Bank near Brooke locality in northern Virginia, falls in the lower or middle part of Subzone II-B. The other three, all found in Maryland, are assigned to the upper part of Subzone II-B: (1) West Brothers, near Washington, D.C., (2) Stump Neck, southeast of Washington, D.C. near the Potomac River, and (3) Red Point, at the head of the Chesapeake Bay. Only eight of the over 30 leaf types recognized for this interval are known with cuticle, but these belong to six major leaf groups that represent a large part of the range in morphology present. They are: (1) pinnatifid leaves and similar fragments belonging to *Sapindopsis variabilis* Font. (Fig. 27), (2) pinnately compound leaves and isolated leaflets of the type related to *Sapindopsis* by Hickey and Doyle (1977) (Figs. 28, 29), (3) three types of palinactinodromous, trilobate leaves and similar fragments belonging to the

"platanoid" complex (Figs. 30–33), (4) actinodromous cordate leaves belonging to *Populophyllum reniforme* Font. (Fig. 35), (5) a leaf with a lobate base referable to *Menispermites potomacensis* Berry (Fig. 36), and (6) a new species of small, elongate leaf with numerous straight-convex (B-1) serrations (Fig. 34). These forms represent a large part of the range in morphology seen in Subzone II-B leaves, even though they constitute only a small fraction of the species (cf. Hickey & Doyle, 1977).

Subzone II-B angiosperm leaves show greater diversity in their cuticular structure than Zone I forms, particularly in stomatal organization. Three new patterns of variation in subsidiary cell arrangement are present in addition to the older one, but all of the stomatal types in each new pattern occur as variants in the Zone I pattern. New types of secretory structures (and their homologous hair bases) also are found and these show numerous similarities to Zone I types, suggesting their derivation from them. The systematic distribution of new cuticular features shows a strong correspondence with many of the leaf architectural groups recognized by Hickey and Doyle (1977); as a result they are described by group rather than by character.

The fewest new stomatal features are found in *Populophyllum reniforme* Font., a cordate, actinodromous leaf from the Bank near Brooke (Fig. 35). The guard cells differ from those in many Zone I forms by possessing outer stomatal ledges but lacking lamellar thickenings entirely (Figs. 37, 38). In addition, the guard cells often appear to be embedded in the adjacent cells, unlike earlier forms (Fig. 38). But despite these new features *Populophyllum* retains the pattern of contact cell arrangement and specialization found in Zone I, having up to ten variable features in some specimens (Table 6). This pattern most closely resembles that of cf. *Ficophyllum* in its low percentage of paracytic stomata, but differs by its specialized non-contact cells.

More new stomatal features occur in the new serrate leaf from Red Point, which has a characteristically papillate lower epidermis (Figs. 39, 40). The guard cells possess lamellar thickenings identical to those found in Zone I, but lack stomatal ledges entirely (Fig. 40). The number of contact cells is higher than in any Zone I form (Table 6) and the pattern of contact cell specialization is more regular, with each contact cell having a papilla that overarches the adjacent guard cell (Fig. 39). This stomatal pattern has



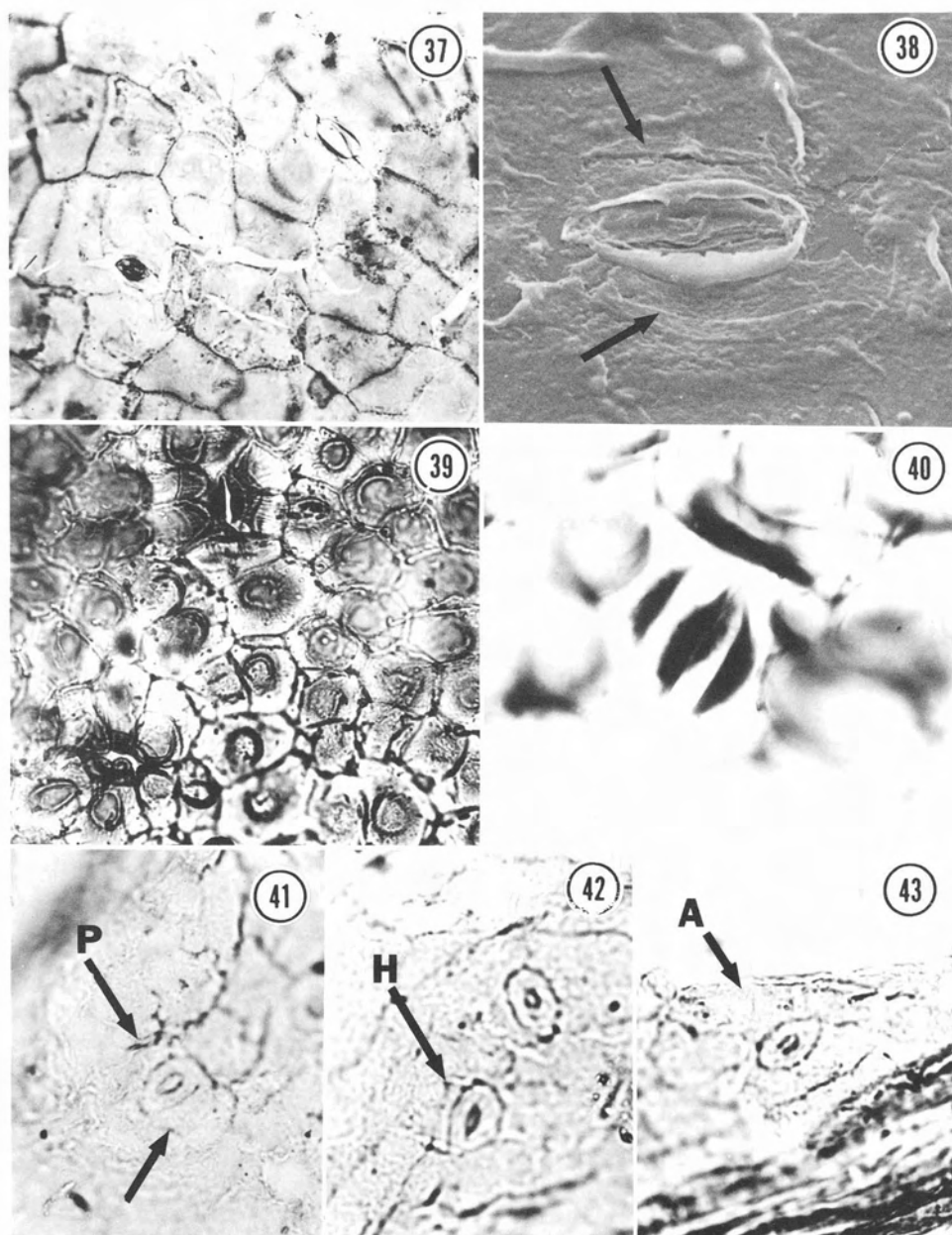
FIGURES 33–36. Organically preserved Subzone II-B leaf types.—33. *Platanoid* #3, close-up of venation showing tertiary (3°) and higher order venation. UMMP 65104, $\times 5$.—34. New Serrate, Red Point. USNM 222856, $\times 2$.—35. *Populophyllum reniforme*. UMMP 65108, $\times 1$.—36. *Menispermities potomacensis*. UMMP 65102, $\times 1$.

only five variable features, as opposed to seven to ten in Zone I forms (Table 6), and is best classified as weakly cyclocytic.

The second new stomatal pattern occurs in *Menispermities potomacensis* Berry from Stump Neck (Figs. 41–43). The guard cells in this species are smaller than those in all other Potomac Group angiosperms (8–15 μm long), but, as in most other Subzone II-B forms, they lack lamellar thickenings. The contact cells show some variation in arrangement and specialization, but less than that

seen in Zone I (Table 6). Specialized LCCs never number more than one per guard cell and always extend the full length of the stoma. PCCs are always unspecialized and number two, while modified non-contact cells are always lateral. This pattern possesses only five variable features and has stomata that conform to three major types: paracytic (Fig. 41, P), hemiparacytic (Fig. 42, H), and anomocytic (Fig. 43, A).

The largest number of new cuticular features is shared by two groups of Subzone II-B leaves



FIGURES 37-43. Cuticles of Subzone II-B angiosperms.—37. *Populophyllum reniforme*, stomata. UMMP 65109, $\times 250$.—38. *Populophyllum reniforme*, scanning electron micrograph of stoma showing outer stomatal ledges and embedded guard cells (arrows). UMMP 65109, $\times 2,000$.—39. New Serrate, Red Point, stomata. Note how the papillae overarch the guard cells. USNM 222856, $\times 400$.—40. New Serrate, Red Point, close-up of stoma showing outer and inner lamellar thickenings. USNM 222856, $\times 1,000$. 41-43. *Menispermites potomacensis*. UMMP 65102.—41. Paracytic stoma, $\times 600$.—42. Hemiparacytic stoma, $\times 600$.—43. Anomocytic stoma, $\times 600$.

that have been related to one another on the basis of leaf architecture: pinnatifid and pinnately compound leaves assigned to *Sapindopsis* (Figs. 27-29) and trilobate, palinactinodromous leaves

of the "platanoid" complex (Figs. 30-33). In both groups the guard cells lack lamellar thickenings and tend to be slightly sunken (Fig. 44). The contact cells also show greater regularity in ar-

TABLE 6. Comparison of Zone I and Subzone II-B stomatal patterns.

Taxon	Zone I Pattern	<i>Populophyllum</i>	New Serrate	<i>Menispermities</i>	<i>Sapindopsis</i> /Platanoids
Number of contact cells	4-5(-7)	4-7	6-7	4-5	4-6(-8)
Number of lateral contact cells (LCCs)	2-3, 2-4	2-5	3-5	2-3	2-4(-5)
Specialized LCCs in every stoma?	sometimes/always	sometimes	always	sometimes	always
LCCs specialized length of stoma?	sometimes	sometimes	always	always	almost always
Number of polar contact cells	2, 2-3	2-3	1-3	2	2-3
PCCs specialized in each stoma?	sometimes	sometimes	always	never	sometimes
PCCs specialized at both poles?	sometimes	sometimes	always	—	sometimes
Other specialized cells?	sometimes/never	sometimes	sometimes	sometimes	sometimes
Position	variable	variable	variable	lateral	lateral
Number of variable features	7-10	10	5	5	6(-7)
Stomatal types ^a	—	A (common); P, H, and weakly C (rare)	weakly C	P, H, and A	P, Lc, and weakly C

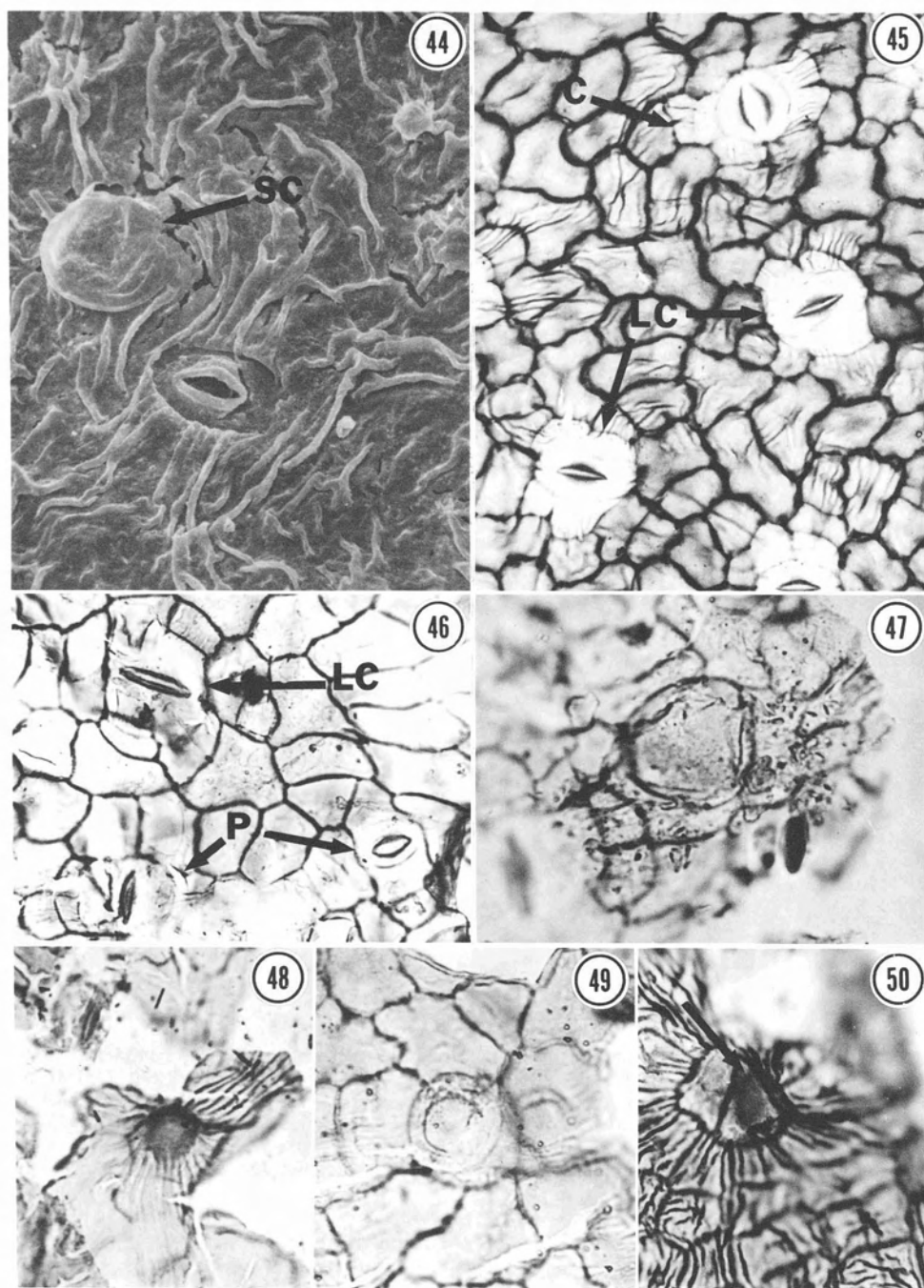
^a Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic; A = anomocytic.

range and specialization than in Zone I forms, but less than in *Menispermities* and the new serrate (Table 6). Specialized LCCs occur next to every guard cell on a leaf and they almost always extend the full length of the stoma (Figs. 45, 46). PCCs and other associated cells, in contrast, show the same variation as in Zone I. This pattern has six to seven variable features and produces stomata that conform to three major types: paracytic (Fig. 46, P), laterocytic (Figs. 45, 46, Lc), and weakly cyclocytic (Fig. 45, C).

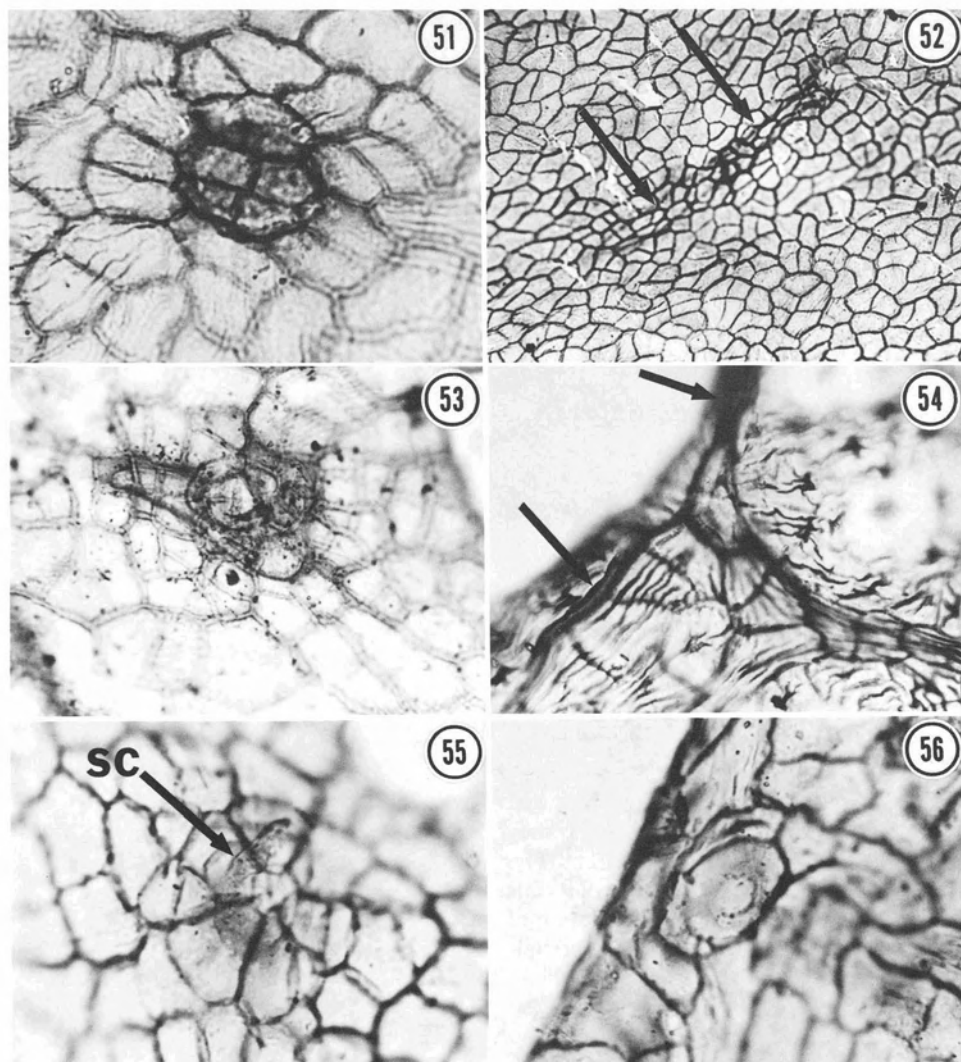
This same group of leaves also possesses four new patterns of secretory/hair base construction, all of which appear to be homologous. The first (and most variable) is found in both pinnatifid and pinnately compound species of *Sapindopsis* (Table 7). In this pattern there are some secretory cells that strongly resemble their counterparts in Zone I (e.g., Figs. 47, 48), but these intergrade with other types of secretory cells and even rare hair bases on the same leaf. Secretory cells (or SCs) range from level with the epidermis, as in Zone I, to raised, and in the latter case each SC is commonly asymmetrically positioned over the junction of two or more subtending cells (Fig. 50). These subtending cells are unspecialized ad-

jacent to some SCs (Fig. 51) but modified adjacent to others (Fig. 50). SC shape in surface view is often angular or circular, as in Zone I (Figs. 47, 48) but many times it is broadly to narrowly elliptical (Fig. 52) to lobate (Fig. 53) and in some cases one or more heavily cutinized lateral protrusions also are present (Fig. 54). The outer wall of the SC is commonly level with the leaf surface, but sometimes it is strongly protruding (Fig. 55); this latter condition is found only on the lower epidermis. Finally, many secretory cells possess radiating striations and/or a ring of thickened cuticle (e.g., Figs. 51, 56), but this is sometimes missing (e.g., Figs. 47, 55). Hair bases strongly resemble certain types of protruding secretory cells that lack striations, but differ from them in having an apical hair abscission scar (Fig. 49).

The three other plans of secretory cell/hair base construction, found in the "platanoid" complex, represent portions of the spectrum of variation present in *Sapindopsis*. The largest amount of variation is present in Platanoid #1 (Table 7), whose secretory cells differ from those in *Sapindopsis* in only three respects. First, the SCs are always raised, rather than level with the epidermis in some cases (Fig. 57). Second, the SCs are



FIGURES 44–50. *Sapindopsis*, lower cuticle.—44. Scanning electron micrograph showing slightly sunken stoma and round, slightly underthrust secretory cell. UMMP 65113-G72, $\times 1,000$.—45. Stomatal complexes. UMMP 65120, $\times 500$.—46. Stomatal complexes. UMMP 65116, $\times 500$.—47. Epidermal secretory cell of the round, flat Zone I type. UMMP 65117, $\times 600$.—48. Epidermal secretory cell similar to the radiostriate type of Zone I. UMMP 65118, $\times 600$.—49. Hair base which resembles protruding secretory cells. The flat top is interpreted as a hair abscission scar. UMMP 65119, $\times 600$.—50. Radiostriate epidermal secretory cell that is irregularly positioned over two subtending cells. UMMP 65114-G77, $\times 400$.



FIGURES 51-56. Secretory cells, *Sapindopsis*.—51. Round radiostriate secretory cell completely subtended by several cells. UMMP 65121, $\times 600$.—52. Attachment scar of an elongate secretory cell. UMMP 65112, $\times 400$.—53. Irregularly lobate secretory cell subtended by numerous small epidermal cells. UMMP 65115, $\times 400$.—54. Radiostriate secretory cell with heavily cuticized protrusions (arrows). UMMP 65114-G77, $\times 400$.—55. Torn bulbous secretory cell of the type found in some Rosidae. UMMP 65115-G98, $\times 600$.—56. Secretory cell with a diffuse ring of thickened cuticle that defines a possible operculum. UMMP 65117, $\times 600$.

always circular to elliptical, rather than angular in some cases. Finally, the subtending cells are never modified in non-veinal regions (Fig. 58), but often are smaller than the adjacent cells in veinal regions (Fig. 59).

The other two plans of secretory cell/hair base construction represent different subsets of the variation present in Platanoid #1 (Table 7). In Platanoid #2, there are only secretory cells. These are raised above the epidermis and are always

symmetrically positioned over the junctions of at least two cells (Figs. 61, 62). Also present in this species are mesophyll secretory cells (Fig. 60). In Platanoid #3, there are only hair bases. These are similar to the hair bases of Platanoid #1, except that the foot cells always are symmetrically positioned over the junctions of two or more cells, and the base of the foot cell often has a ring of thickened cuticle (Figs. 63, 64). In addition, the base cells show a pattern of size

TABLE 7. Secretory cells and homologous epidermal structures of Zone I and Subzone II-B angiosperms.

Taxon	Zone I Angiosperms	<i>Sapindopsis</i>	Platanoid #1	Platanoid #2	Platanoid #3
Type of epidermal structure	Secretory cells (SCs) only	SCs and rare hair bases	SCs and rare hair bases	SCs only	Hair bases only
Position relative to epidermis	level	level-raised	raised	raised	raised
Specialization of adjacent/un- derlying cells, veinal re- gions	—	variable	variable	—	variable
Specialization of adjacent/un- derlying cells, non-veinal regions	none	variable	none	none	none
Shape of SC or foot cell, sur- face view	polygonal or rounded	polygonal to circular and elliptical	circular to elliptical	circular	circular
Lateral protrusions from SC or foot cell?	none	sometimes	sometimes	none	none
SC or foot cell shape, outer wall	flat	flat to protrud- ing	protruding	protruding	protruding
Cuticular sculpture	smooth or striate	smooth to striate	smooth to striate	smooth	smooth
Ring of thickened cuticle?	present in one species	sometimes	sometimes	never	sometimes

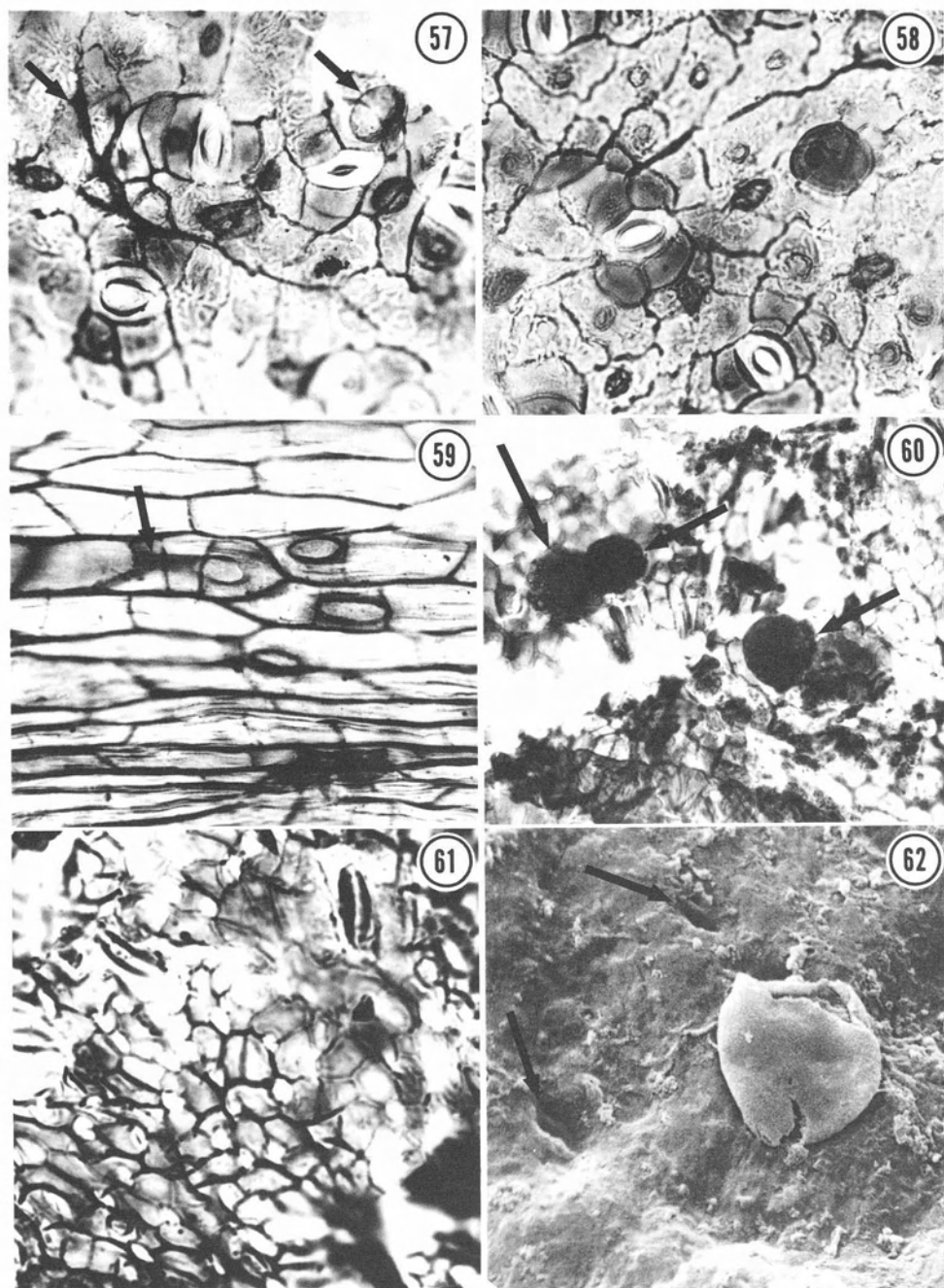
variation that is identical to that for the cells that subtend the secretory cells in Platanoid #1: they are scarcely modified in non-veinal regions (Fig. 63), but are often smaller than the adjacent cells underneath major veins (Fig. 64). This suite of characters is identical to that found in the hair bases of all extant Platanaceae (Figs. 65, 66).

DISCUSSION

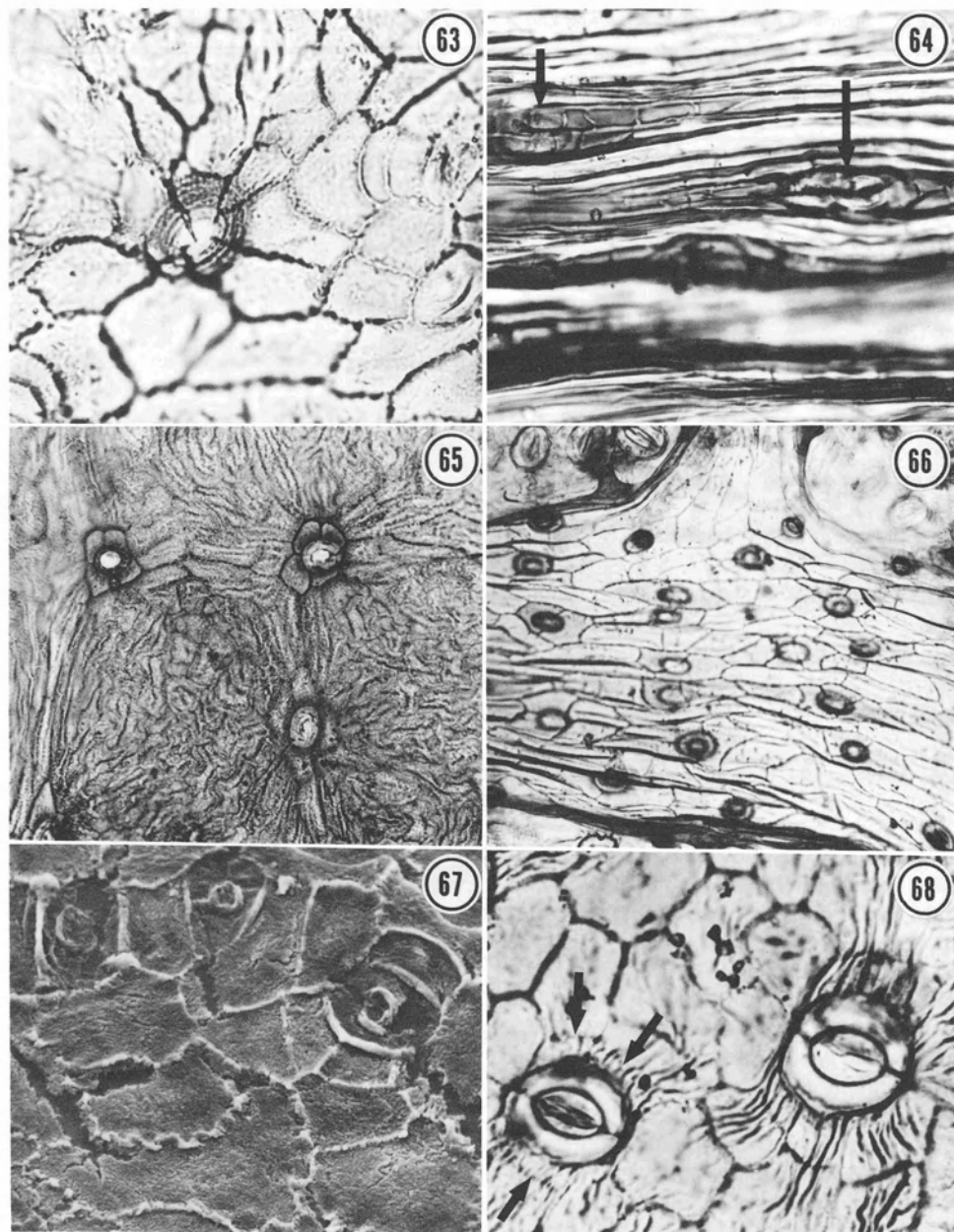
The stratigraphic distribution of cuticle types supplements previous evidence from palynology and leaf architecture on the direction and timing of early flowering plant evolution. First, cuticular anatomy strongly supports the concept of a Cretaceous (rather than pre-Cretaceous) angiosperm adaptive radiation. Zone I flowering plants show a limited range of structural diversity compared to later Potomac Group forms, and these in turn are less diverse than Tertiary and modern angiosperms. The guard cells of all Zone I species bear outer stomatal ledges, which are often associated with maceration-resistant lamellae; in contrast, Subzone II-B forms bear either outer stomatal ledges or lamellar thickenings, but never both. The stomata of Zone I angiosperms all conform to a similar pattern of variation in sub-

sidary cell specialization, which is characterized by a large number of stomatal types. In contrast, the stomata of Subzone II-B angiosperms conform to both the Zone I pattern and three new ones, each of which possesses one or more of the stomatal types found in the earlier leaves. Finally, the epidermal secretory cells of Zone I leaves conform to two basic types, while those of Subzone II-B leaves (along with their homologous hair bases) conform to many different types that fall into four major patterns of organization. This increase in structural diversity through time is similar to that seen for leaf architecture and pollen morphology: Subzone II-B angiosperms are structurally diverse compared to Zone I forms but have features that can be derived from the earlier types.

The similarities seen between Potomac Group angiosperm leaf cuticles and those of modern groups also provide evidence for classical theories of flowering plant evolution, which postulate subclass Magnoliidae (but not necessarily the order Magnoliales!) as the most primitive living group. A survey of many primitive and intermediate level angiosperm families (Tables 2–4, 8) suggests that Zone I forms, when comparable to extant families and orders, most closely re-



FIGURES 57-62. *Platanoids*, lower cuticle.—57. *Platanoid* #1, epidermal secretory cells (arrows) and diverse stomatal types. UMMP 65106, $\times 400$.—58. *Platanoid* #1, strongly protruding secretory cell and numerous papillate cells. UMMP 65106, $\times 400$.—59. *Platanoid* #1, secretory cells beneath a primary vein showing irregular placement relative to the subtending cells. Also note the heavily cutinized protrusion on one secretory cell (arrow) and the tendency for the subtending cells to be smaller than the others. UMMP 65106, $\times 400$.—60. *Platanoid* #2, mesophyll secretory cells. UMMP 64105, $\times 400$.—61. *Platanoid* #2, laterocytic stoma and numerous attachment spots for epidermal secretory cells (light areas). UMMP 64105, $\times 600$.—62. *Platanoid* #2, scanning electron micrograph of collapsed secretory cell and the attachment scars for two others (arrows). UMMP 64105, $\times 4,000$.



FIGURES 63-68. Platanoid #3 and extant Platanaceae.—63. Platanoid #3, hair base, non-veinal region, showing symmetrical positioning of the hair over the base cells. Note the flat top of the foot cell and the ring of thickened at its base. UMMP 65103, $\times 600$.—64. Platanoid #3, hair bases beneath a primary vein (arrows). Note the tendency for the base cells to be smaller than the others. UMMP 65104, $\times 400$.—65. *Platanus chiapensis*, upper cuticle, hair bases over small veins. Note the ring of thickened cuticle at the base of each foot cell and the smaller size of the base cells. Michigan, D. E. Breedlove #9796, $\times 160$.—66. *Platanus chiapensis*, hair bases beneath major vein showing the symmetrical positioning of the foot cells over the junctions of two or more base cells. Michigan, D. E. Breedlove #9796, $\times 160$.—67. Platanoid #3, scanning electron micrograph of laterocytic and weakly paracytic stomata. UMMP 65103, $\times 1,000$.—68. *Platanus* sp., laterocytic stomata. Note the thinly cutinized tangential walls of the subsidiary cells (arrows), $\times 400$.

TABLE 8. Stomatal patterns of *Sapindopsis* and selected Rosidae.

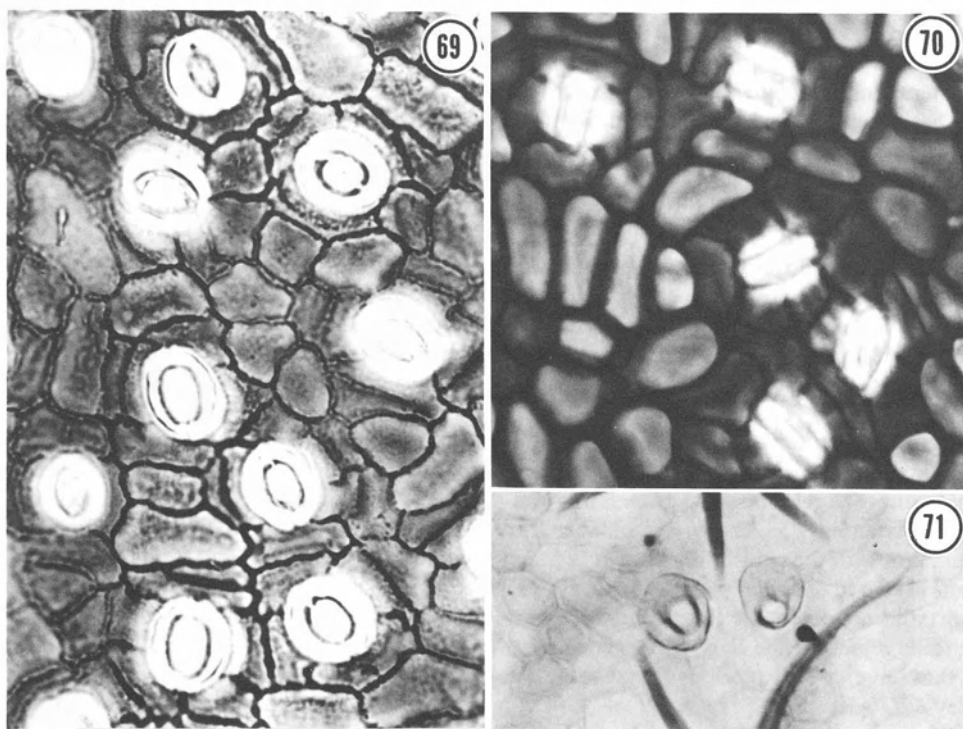
Taxon	<i>Sapindopsis</i>	Sapindaceae <i>Allophylus</i>	Cunoniaceae <i>Weinmannia</i>	Rhamnaceae Extant Members	Rosaceae <i>Quillaja</i>
Number of contact cells	4–8	4–6(–7)	4–5	4–6	5–6(–7)
Number of lateral contact cells (LCCs)	2–5	2–4(–5)	2–4	2–3, 2–4	3–5
Specialized LCCs in every stoma?	always	always	always	always	always
Specialized LCCs for each GC?	always	always	always	always	always
LCCs specialized length of stoma?	almost always	almost always	almost always	always	always
Number of polar contact cells	2–3	2–3	2–3	2–3	2–3
PCCs specialized in each stoma?	sometimes	sometimes	sometimes	sometimes	sometimes
PCCs specialized at both poles?	sometimes	sometimes	sometimes	sometimes	never
Other specialized cells?	sometimes	sometimes	sometimes	never	sometimes
Position	lateral	lateral	lateral	—	lateral
Number of variable features	6(–7)	6(–7)	7	5	5
Stomatal types ^a	P, Lc, and weakly C	P, Lc, and weakly C	P, Lc, and weakly C	P, Lc, and weakly C	Lc and transitional to C

^a Key: P = paracytic; Lc = laterocytic; C = cyclocytic.

semble Laurales (including Chloranthaceae) and Illiciales, but cannot be assigned to a single family. Two leaf groups and one dispersed cuticle type deserve special mention. The first, Drewrys Bluff Leaf Type #1 (Figs. 1, 4, 25), is similar to Chloranthaceae. The combination of stomata longer than 30 μm , striations that run concentric to the stomatal pore, and radiostriate epidermal secretory cells is found only in some Laurales and Illiciales. The “hair bases” of DBLT #1 today occur in many angiosperm families, but in Magnoliidae have been observed only in Illiciaceae and Chloranthaceae. Finally, the Zone I pattern of variation in subsidiary cell arrangement is known only from Amborellaceae and certain Chloranthaceae, while other Chloranthaceae and Schisandraceae differ in only two to three features (Tables 1, 4). These similarities, along with the Chloranthoid teeth, strongly suggest affinities with the family Chloranthaceae; however, simple craspedodromous secondary venation is absent from the family (Hickey & Wolfe, 1975; Upchurch, unpubl. data). Hence, DBLT #1 may belong to a group that includes the ancestor of modern Chloranthaceae but represents an extinct taxon within the alliance.

The second leaf group, *Eucalyptophyllum oblongifolium* (Figs. 3, 7, 9, 10, 19), most closely resembles Chloranthaceae and Illiciales but has a number of features unknown from either group. This taxon has always been difficult to place systematically because its combination of venational features is unknown in extant angiosperms (Wolfe et al., 1975; Hickey & Doyle, 1977). Cuticular anatomy, however, clearly indicates angiospermous affinities because *Eucalyptophyllum* possesses the same stomatal features, “hair base” type, and epidermal secretory cell types as other Zone I and certain extant flowering plants. In fact, this combination of features today is restricted to Chloranthaceae, and Illiciales differ only in their less variable stomatal complexes. In spite of these similarities, however, the fossil differs from both modern taxa in its elongate sunken stomata, truncate stomatal poles, pattern of striations, and distinctive leaf architecture. Hence, *Eucalyptophyllum* probably represents an extinct group of at least ordinal rank (cf. Hickey & Doyle, 1977) that is related in some way to Chloranthaceae and Illiciales.

The third group, Dispersed Cuticle #3 (Figs. 11, 12, 21), most strongly resembles extant Illici-



FIGURES 69–71. Lower cuticles, extant Rosidae. —69. *Weinmannia crenata* (Cunoniaceae), stomata showing *Sapindopsis* pattern of variation in subsidiary cell arrangement. Michigan, B. A. Krukoff #11053, $\times 600$. —70. *Allophylus apitata* (Sapindaceae), stomata showing *Sapindopsis* pattern of variation in subsidiary cell arrangement. Indiana University Cuticle Slide #308, Yale, Wright #1604, $\times 600$. —71. *Flindersia schottiana* (Rutaceae), abaxial secretory cells. Compare these with the one in Figure 55. National Cleared Leaf Collection #5958, $\times 600$.

ales. The striation pattern around the stomatal complex is typical of that found in Illiciaceae and Laurales (Fig. 26), whereas the pronounced T-shaped thickenings at the poles are characteristic of Illiciaceae (Bailey & Nast, 1948). The variable pattern of contact cell arrangement and specialization differs from the paracytic condition in Illiciaceae, but it does resemble the pattern found in Schisandraceae in most respects (cf. Tables 1, 4). In addition, the one known hair base is similar to the type found in *Schisandra europaea*, an Eocene member of the order. Despite these similarities, however, the fossil has smaller stomata than modern Illiciaceae (27 μm long versus 30–70 μm) and appears to lack both the lamellar guard cell thickenings and epidermal oil cells characteristic of the order. Hence, Dispersed Cuticle #3 may be related to Illiciaceae but represents an extinct taxon within the alliance.

These results indicate the need for caution in interpreting similarities between the pollen of Zone I and modern angiosperms. While monosulcate pollen grains assigned to *Clavatipollenites* cf. *hughesii* as described by Doyle et al. (1975)

closely resemble *Ascarina* of the Chloranthaceae (Walker, 1976; Walker & Walker, 1984; Muller, 1981), no angiosperm leaf with preserved cuticle or dispersed cuticle type possesses all of the characters needed to be assigned confidently to extant Chloranthaceae. Since the *Ascarina*-type pollen is inferred to be ancestral to the other pollen types within the family (Walker, 1976), similar pollen could also have been characteristic of the larger Early Cretaceous ancestral complex from which the Chloranthaceae are derived, which may have been much more primitive than the modern family in non-palynological characters.

In contrast to Zone I forms, Subzone II-B angiosperm leaf cuticles are most similar to the subclasses Hamamelididae and Rosidae. The closest resemblances are seen between Platanoid #3 and extant Platanaceae (Hamamelididae). Platanoid #3, like many other Potomac Group platanoids, shares several important venational characters with extant Platanaceae, which include probable palinactinodromous primary venation, closely spaced, percurrent tertiary veins, and orthogonal higher order venation (Figs. 30,

32, 33). Cuticle structure shows an equally strong resemblance. In both groups, contact cell arrangement and specialization conform to the same basic pattern, with the fossil differing in having fewer lateral contact cells that tend to have thicker cuticular flanges along their tangential walls (cf. Figs. 67, 68). Hair base structure is even more similar. In both groups the basal cell of each hair has the shape of a flat-topped cone and is the only cell present in the mature leaf. This cell often possesses a ring of thickened cuticle where it joins the underlying cells, which in veinal areas tend to be smaller than the adjacent cells (Figs. 63–66). These features of both leaf architecture and cuticle structure readily distinguish Platanaceae from other groups and thus strongly suggest a relationship between this family and Platanoid #3. These resemblances, in conjunction with the similarities shown between Platanoid #3 and the other platanoids (cf. above), support the concept that the Potomac Group platanoids represent the Early Cretaceous complex that gave rise to modern Platanaceae (cf. Hickey & Doyle, 1977).

Cuticular anatomy is also consistent with the proposed relationships of *Sapindopsis* and subclass Rosidae (Hickey & Wolfe, 1975; Hickey & Doyle, 1977), but it is not known whether the similarities shared by the two groups are restricted to the subclass. Pinnately compound organization of the *Sapindopsis*-type is almost entirely restricted to Rosidae and inferred derivatives (Hickey & Wolfe, 1975) and admedially oriented tertiary venation of the type present in many *Sapindopsis* leaflets is common within the subclass (Upchurch, unpubl. data). In addition, some West Brothers specimens possess teeth with numerous Rosid features, which include a concave-convex (C-1) shape, symmetrically placed medial vein, and a pair of converging lateral veins, as in the Rosoid tooth type of Hickey and Wolfe (1975) (Fig. 29). The stomatal structure of *Sapindopsis* has many counterparts in extant Rosidae and some of its secretory cells resemble those of a few Rosids. In *Sapindopsis* each guard cell is flanked by at least one specialized lateral contact cell (LCC) and these cells generally extend the full length of the stoma. Polar contact cells (PCC) and other associated cells are variable in their number and patterns of modification. All modified cells are weakly differentiated from the surrounding cells but characteristically have a thinner cuticle, at least adjacent to the guard cells. Many Rosidae

have similar stomatal patterns, except that the region of thin cuticle, when present, is almost always restricted to a distinct zone next to the guard cells. Some Cunoniaceae (Fig. 69) and Sapindaceae (Fig. 70) conform to the basic *Sapindopsis* stomatal pattern, while Rhamnaceae and primitive Rosaceae such as *Quillaja* differ only in lacking specialized non-contact cells (Table 8). Other Rosidae with comparable stomatal patterns include Nyssaceae, Alangiaceae, and certain members of Rutaceae, Cornaceae, Celastraceae, and Anacardiaceae (cf. den Hartog & Baas, 1978; Upchurch, unpubl. data). Implications of secretory cell structure are problematic, since no extant angiosperm has been observed with the variable pattern present in *Sapindopsis*; however, the abaxial unicellular, glandular hairs of *Knightia* (Proteaceae), *Platea* (Icacinaeae), and *Flindersia* (Rutaceae, Fig. 71) are similar in shape and position to some protruding *Sapindopsis* secretory cells (cf. Dilcher & Mehrotra, 1969; van Staveren & Baas, 1973). Other Rosidae, such as Sapindaceae, Anacardiaceae, and certain Juglandaceae, bear multicellular, generally abaxial glands that are either uniseriate or have a uniseriate stalk, suggesting that they may be derived from the protruding type of secretory structure found in *Sapindopsis*. Additional studies of leaf cuticles from extant angiosperms, along with a detailed phylogenetic analysis of possible *Sapindopsis* relatives from the Late Cretaceous (such as *Anacardites* and "*Rhus*" *powelliana*), are needed to test further the idea of a *Sapindopsis*-Rosidae relationship.

The morphological relationships of Potomac Group cuticle types, in conjunction with their stratigraphic distribution, suggest two previously unsuspected evolutionary trends in the epidermis of early flowering plants. First, stratigraphic and morphologic evidence suggests that the Zone I pattern of secretory cell (SC) construction, with its two distinct types of SCs, gave rise to the highly variable *Sapindopsis* pattern through an increase in developmental plasticity; conversely, the related platanoid patterns appear to be derived through the canalization of one part of this variation (Fig. 72). The epidermal secretory structures of Zone I angiosperms are all unicellular and level with the leaf surface. They conform to two distinct types: one is rounded and has a smooth outer cuticle, while the other is angular and bears radiating striations. The *Sapindopsis* pattern produces variants that are identical to Zone I forms, but these intergrade with

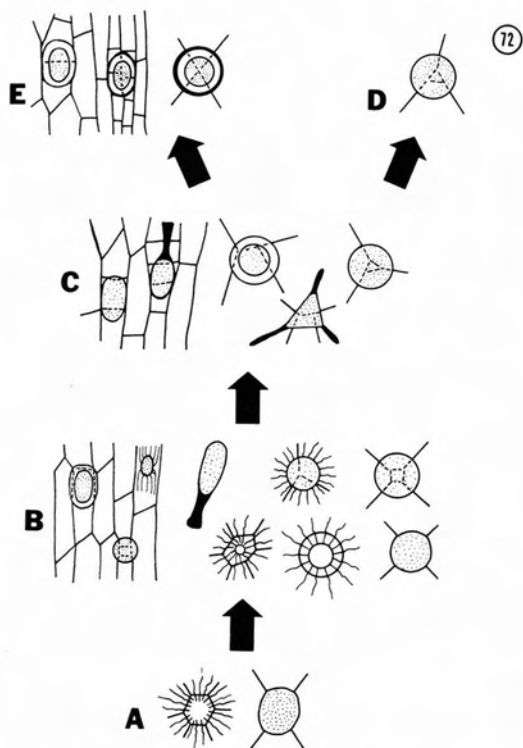


FIGURE 72. Evolution of epidermal secretory cells and homologous hair bases in Potomac Group angiosperm leaves. Legend: A = Zone I secretory cell types. B = *Sapindopsis* pattern of secretory cell and hair base organization. C = Platanoid #1 pattern of secretory cell and hair base organization. D = Platanoid #2 pattern of secretory cell organization. E = Platanoid #3 pattern of hair base organization.

each other, divergent types of secretory cells, and the bases of uniseriate hairs. Some secretory structures are level with the epidermis and have flat outer walls, but most rest at least partially on top of other epidermal cells and have protruding outer walls; in addition, they have a variable pattern of positioning relative to the subtending cells. Hair bases resemble this latter type of SC except that each foot cell bears an apical hair abscission scar. The pattern of variation for secretory cells and hair bases in Platanoid #1 is similar to that for *Sapindopsis* except that the Zone I types of secretory cells appear to be absent. The secretory cells of Platanoid #2 and the hair bases of Platanoid #3 are interpreted as independent fixations of different portions of the variation in Platanoid #1 because they resemble different sets of structures found in the latter group. If indeed these proposed homologies among secretory cell and hair base types are cor-

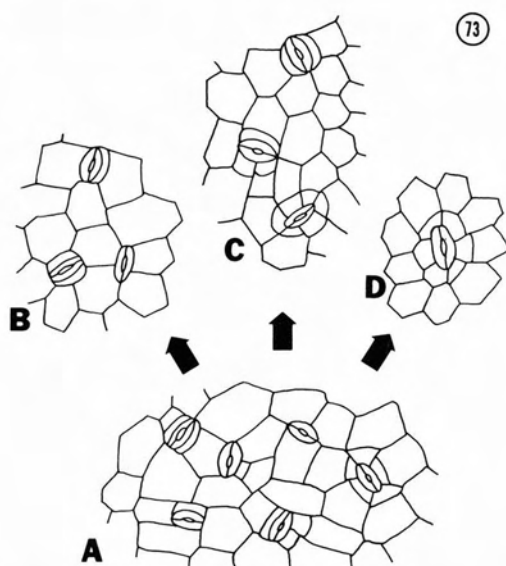


FIGURE 73. Evolution of patterns of variation in subsidiary cell arrangement, Potomac Group angiosperms. Each derived pattern represents one portion of the range of variation present in the ancestral pattern. Legend: A = Zone I pattern. B = *Menispermites potomacensis* pattern. C = *Sapindopsis*/Platanoid pattern. D = New Serrate, Red Point pattern.

rect, then the deciduous hairs of extant Platanaceae are an evolutionary modification of the radiostriate epidermal oil cells present in diverse Magnoliidae. In addition, this proposed series would indicate that the transition between these two structural types was characterized by a stage of extreme developmental plasticity.

The stratigraphic and morphological relationships of the different patterns of variation in stomatal structure also suggest an evolutionary trend towards decreased stomatal variation in early angiosperms, with the later patterns representing independent fixations of a portion of the variation found in Zone I (Fig. 73). The Zone I pattern of variation in subsidiary cell arrangement shows an average of nine out of ten variable features, ranging from seven in cf. *Ficophyllum* to ten in *Eucalyptophyllum*. Stomatal types on a single leaf include paracytic, hemiparacytic, laterocytic, weakly cyclocytic, and (in most groups) anomocytic. Subzone II-B patterns of stomatal variation, in contrast, show an average of only six non-uniform features, with three new, less variable patterns present in addition to the older one. The number of non-uniform features ranges from five in the new serrate from Red Point to

TABLE 9. Stomatal features of Late Cretaceous angiosperms.

Taxon	<i>Araliephyllum polevoi</i>	<i>Debeya tikhonovichii</i>	<i>Araliopsis wellingtoniana</i>	<i>Dewalquea westerhausiana</i>	<i>Dryophyllum cretaceum</i>
Number of contact cells	4-5(-6)	4-6(-7)	5-7	5-8	5-8
Number of lateral contact cells (LCCs)	2(-3)	2-4	2-4	3-4	3-5
Specialized LCCs in every stoma?	always	always	always	always	always
Specialized LCCs for each GC?	sometimes	always	always	always	always
LCCs specialized full length of stoma?	always	always	mostly	always	always
Number of polar contact cells	2-3(-4)	2-3	2-4	3	2-4
PCCs specialized in each stoma?	never	sometimes	sometimes	sometimes	sometimes
PCCs specialized at both poles?	—	sometimes	sometimes	sometimes	sometimes
Other specialized cells?	sometimes	sometimes	sometimes	sometimes	sometimes
Position	lateral	lateral	variable	variable	variable
Number of variable features	5	6	7	6	7
Stomatal types ^a	P, H	Lc, weakly C	Lc, C	Lc, C	Lc, C

^a Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic.

ten in *Populophyllum*, and the stomatal types present in each new pattern represent a subset of those found in Zone I. Judging from the illustrations of Krassilov (1973), Němejc and Kvaček (1975), and Ruffle and Knappe (1977), Late Cretaceous angiosperms show even less stomatal

variation than their Subzone II-B counterparts. The stomata of these angiosperms have an average of 5.5 non-uniform features, ranging from three in *Debeya insignis* to seven in *Araliopsis wellingtoniana* and *Dryophyllum cretaceum* (Tables 9, 10). Usually a leaf possesses no more than

TABLE 10. Stomatal features of Late Cretaceous angiosperms.

Taxon	<i>Proteophyllum laminarium</i>	<i>Grevilleophyllum constans</i>	<i>Cocculophyllum extinctum</i>	<i>Debeya insignis</i>
Number of contact cells	4-6	4-6	4-6	5-6
Number of lateral contact cells (LCCs)	2	2	2-4	3-4
Specialized LCCs in every stoma?	always	always	always	always
Specialized LCCs for each GC?	always	always	sometimes	always
LCCs specialized full length of stoma?	always	always	always	always
Number of polar contact cells	2-4	2-4	2-4	2-3
PCCs specialized in each stoma?	sometimes	never	never	always
PCCs specialized at both poles?	never	—	—	always
Other specialized cells?	sometimes	sometimes	sometimes	always
Position	lateral	lateral	lateral	form ring
Number of variable features	6	3	5	3
Stomatal types ^a	P	P	P, Lc	C

^a Key: P = paracytic; Lc = laterocytic; C = cyclocytic.

two distinct stomatal types, but these belong to the categories found in the Potomac Group. This progressive decrease in stomatal variation, analogous to the contemporaneous trend towards greater vein regularity, suggests that the uniform stomatal patterns characteristic of many extant angiosperms were derived from less uniform patterns through the canalization of the variation in subsidiary cell arrangement. If indeed this trend turns out to be valid for the angiosperms as a whole, then the uniformly paracytic condition of many Magnoliales, considered primitive for the angiosperms by Takhtajan (1969, 1980), Baranova (1972), and Thorne (1976), would be derived. Thus, groups such as Amborellaceae, Austrobaileyaaceae, Schisandraceae, and certain Chloranthaceae would be more primitive in their stomatal structure than Magnoliales. In addition, this would suggest that Magnoliales with relatively low stomatal regularity, such as Canellaceae and the New World and Madagascar groups of Winteraceae, are more primitive in stomatal anatomy than uniformly paracytic groups such as Annonaceae and Myristicaceae. Tests of this hypothesis will come from the study of other Early Cretaceous angiosperm leaf floras from low and middle paleolatitudes along with the detailed cladistic analysis of modern and select fossil flowering plants.

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