THE EVOLUTION OF THE CUTICLE IN EARLY ANGIOSPERM LEAVES FROM THE LOWER CRETACEOUS POTOMAC GROUP (ATLANTIC COASTAL PLAIN, U.S.A.)

by

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CHAPTER I

INTRODUCTION

Within the past two decades there has been a major re-interpretation of the Cretaceous flowering plant record. Formerly it was widely believed that the angiosperms entered the fossil record during the Cretaceous diversified into modern families and genera, after having evolved in upland regions where they left no fossil record (Axelrod, 1952, 1970). More recent studies of Cretaceous flowering plant remains, however, show that during this time there was a steady increase in both the number of morphological types and the number of remains that can confidently be assigned to modern taxa (Doyle, 1969; Muller, 1970; Wolfe et al., 1976; Doyle and Hickey, 1976; Hickey and Doyle, 1977). These results indicate that the Cretaceous was a period of major angiosperm diversification and suggest that further paleobotanical studies can yield new evidence on the course and timing of the group's evolution.

The belief that many of the earliest known flowering plants represented extant families and genera originated during the 19th century from the study of leaf remains. Early paleobotanists, confronted with the tremendous diversity of Cretaceous and Tertiary angiosperm leaf impressions, compared them with the leaves of extant plants,

but without adequate information on the systematic distribution of leaf architectural features in the modern flora. Consequently, studies of Cretaceous angiosperms, such as those by Fontaine (1889), Ward (1905), and Berry (1911) on the Potomac Group, allied the bulk of remains with modern families and genera on the basis of features either now known to occur in numerous unrelated extant groups or presumed to have been present in the fossils. While Ward (1888) and Fontaine (1889) did remark about the "archaic" appearance of the oldest Cretaceous flowering plant leaves, the majority of paleobotanists believed that Early Cretaceous leaf floras were modern in composition (e.g., Berry, 1911; Seward, 1931).

The most widely accepted explanation for this situation was advanced by Axelrod (1952, 1970), who proposed that the flowering plants diversified in tropical uplands during the Triassic and Jurassic, then descended into the lowlands during the mid-Cretaceous in response to increased climatic equability. This theory explained the "sudden" appearance of a modern angiosperm flora during the Cretaceous and was consistent with the sporadic reports of pre-Cretaceous angiosperm remains (e.g., Brown, 1956; Tidwell et al., 1970), which would be expected from a predominantly upland group.

The first major challenge to this view came from studies of Mesozoic palynology. Instead of showing a wide

array of pollen types, Early Cretaceous angiosperm pollen assemblages displayed a low morphological diversity and few forms that could be confidently assigned to extant groups; while younger palynofloras showed a progressive increase in morphological diversity and forms assignable to modern taxa (e.g., Brenner, 1963; Doyle, 1969; Muller 1970). In addition, no undisputed angiosperms were known from the Triassic and Jurassio pollen records (Scott et al., 1960; Hughes, 1961) which, like the record from modern sediments, should include occasional upland elements in addition to lowland forms (Muller, 1959, 1970). These results, coupled with the fact that the Cretaceous pollen sequence showed a close correspondence to evolutionary schemes proposed on the basis of comparative morphology (Doyle, 1969), suggested the absence of any major pre-Cretaceous diversification of angiosperms.

During the same period there was growing dissastisfaction with earlier angiosperm leaf identification (e.g., Mädler, 1950; Kräusel and Weyland, 1950, 1954; Dilcher and Mehrota, 1969; Dilcher and Dolph, 1970; Wolfe, 1973). Detailed studies of Tertiary leaves, using cuticular anatomy and fine venation, showed that a large number of old identifications were incorrect, and that many systematic placements were based on little more than a superficial resemblance to modern forms. Though the number of misidentifications varied with both the researcher and the age of the flora it tended to be quite high:

Dilcher (1973) estimated that 60 to 70 percent of the generic and familial identifications of Eocene leaves from the southeastern United States were incorrect. This problem, along with general questions concerning the theoretical validity of the old identification methods (Wolfe, 1973), made many researchers distrust most conclusions about flowering plant history made on the basis of leaf remains, forcing them either to rely on the dispersed pollen record or else not to speculate at all.

Many of the apparent conflicts between the early angiosperm pollen and megafossil records were resolved by reinvestigations of angiosperm leaf remains from the Cretaceous Potomac Group of the Atlantic Coastal Plain (Doyle and Hickey, 1972, 1976; Hickey and Doyle, 1972, 1977; Wolfe, 1972; Wolfe et al., 1975). An analysis of leaf architecture, combined with the independent dating of megafossil localities by palynology, showed that the oldest leaves consisted of simple, pinnately veined forms with poorly organized venation and a limited range of shape. Later leaves showed a progressively higher diversity of shape, plan of organization, and venational types along with a major trend towards increased vein regularity. When compared with extant dicot leaves, whose architectural features had become better known (Hickey and Wolfe, 1975), the oldest Potomac Group leaves exhibited suites of characters usually restricted to woody Magnoliidae,

while later leaves possessed character combinations found in groups such as Hamamelidae and Rosidae, considered more advanced on the basis of comparative morphology (Cronquist, 1968; Takhtajan, 1969). Since these results showed a general correspondence with interpretations based on dispersed pollen, and since all pre-Cretaceous remains assigned to the flowering plants were shown either to lack diagnostic angiosperms features or else to be stratigraphically misplaced (Scott et al., 1972; Doyle, 1973; Wolfe et al., 1975; Hughes, 1976), it was concluded that the major adaptive radiation of the flowering plants occurred during the Cretaceous, rather than earlier in the Mesozoic.

In an attempt to better understand the relationships of early flowering plants to each other and modern forms, I began a study of Potomac Group angiosperm leaf cuticles, since cuticular anatomy had proven valuable in the systematics of extant angiosperms, Tertiary leaf remains, and Mesozoic gymnosperms (e.g., Harris, 1932, 1964; Kräusel and Weyland, 1950, 1954; Stace, 1965). After preliminary studies demonstrated both a strong correspondence between cuticular anatomy and leaf architecture and the usefulness of cuticle structure in the separation of intergrading leaf complexes, a major study was started in 1978. The investigation analyzed leaves from two major time intervals in the Potomac Group as determined by palynology: Zone I of Brenner, or probable

Aptian, and Subzone II-B of Brenner, or probable middle to late Albian (Hickey and Doyle, 1977; Doyle and Robbins, 1977). In addition, dispersed cuticle was analyzed from Zone I to increase the number of cuticle types known from the oldest part of the sequence. Three major questions were posed in this study: (1) What does cuticular anatomy indicate about the relationships of early angiosperm leaves to each other and modern forms? (2) Does cuticular anatomy show evidence for a Cretaceous angiosperm diversification? and (3) If so, then what does the fossil record say about the relative advancement of different cuticular features seen in the modern flora? In the following pages I will attempt to provide some answers to these and other questions.

CHAPTER II

MATERIALS AND METHODS

Organically preserved leaves from Zone I and Subzone II-B of the Potomac Group were identified on the basis of leaf architecture and then analyzed for their cuticular anatomy. Approximately 50 percent of these preparations were made from non-type specimens in the University of Michigan and U.S. National Museum Paleobotanical Collections. The remaining preparations were made from specimens collected from 1976 to 1979 and deposited in the University of Michigan Paleobotanical Collections. All leaf types with organic preservation were prepared for their cuticles. Every specimen was prepared from groups having four or fewer cuticular remains, while in groups with more numerous cuticular specimens each population was sampled until no new variation was found. The latter method was used to determine how much of the range in structural variation within a leaf complex was present in every population.

Since a relatively small number of structurally preserved specimens (belonging to five different leaf groups) were known from Zone I, dispersed cuticle and tiny leaf frag-

ments were analyzed to obtain a larger sample of cuticle types from this time. Angiosperm leaf beds were sampled from two localities along the James River near Richmond, Virginia: Dutch Gap, dated as lower Zone I (Upchurch and Doyle, (in press) and Drewrys Bluff dated as upper Zone I (Doyle, personal communication). Six additional angiospermous cuticle types from these localities were analyzed in detail, bringing the total number up to about 12; this is approximately the number of different angiospermous leaf types recognized from Zone I on the basis of leaf architecture (Hickey and Doyle, 1977).

Modern reference materials, obtained from the University of Michigan and Harvard University herbaria, were prepared for their leaf cuticles to test ideas on the relationships of certain Potomac Group leaf types to modern groups and to provide one means of weighting the different cuticle features seen in the fossils. A sample of approximately 100 species from relatively primitive modern angiosperm groups was chosen, using the Cronquist and Takhtajan systems of classification as a guide. These systems were used because: (1) they are widely accepted by the botanical community, (2) they show a good correspondence with many features of leaf architecture (Hickey and Wolfe, 1975), and (3) the primitiveness and advancedness of the various groups shows a reasonable correspondence to the order of appearance in the fossil record of many morphological features which characterize them, such

as pollen type (Wolfe et al., 1975; Hickey and Doyle, 1977). Sampling was concentrated at the level of family and order, and was most comprehensive when a modern group showed some similarities to a fossil form.

Preparation Methods

The cuticle of fossil leaf remains was prepared for light microscopy using a combination of standard methods (cf. Dilcher, 1974). After demineralization in HF, each leaf fragment was macerated in a solution of concentrated HNO_3 and $KC10_3$ crystals, followed by a 5 percent NaOH or KOH. The freed cuticle was then stained in safranin O and mounted in glycerine jelly.

Dispersed cuticle was obtained by disaggregating a rock sample in HF or $NaCO_3$, then sieving the slurry through 100-mesh screen. Unoxidized plant fragments, found at Drewrys Bluff, were macerated and stained as above except that a centrifuge was used for processing. The cuticles were mounted in glycerine jelly (for slides) or in glycerine between two paraffin-sealed cover slips. Naturally macerated cuticle, found at Dutch Gap, was mounted in glycerine on paraffin-sealed slides.

Fossil leaf cuticle was also observed with scanning electron microscopy. For external features, leaf fragments were demineralized in HF, rinsed in 3X distilled water, air dried then affixed to SEM stubs covered with dried Duco cement inside a chamber saturated with acetone vapor; this

minimized problems with shrinkage and cracking. Stained cuticle that was left over from light microscope preparations was also used, since test observations made on the cuticle from one leaf revealed no change in structure due to staining. All specimens were coated with gold and observed at 15 kv.

Modern cuticle was prepared for light microscopy by macerating in Jeffrey's solution (1:1 concentrated HNO_3 and 20 percent CrO_3), then staining and mounting as for the fossil materials. Approximately one square centimeter of leaf material, usually from the margin, was macerated for each specimen, since the resulting preparation showed features of the leaf margin as well as the upper and lower epidermis. Cuticle from the midvein region was also prepared when it was available.

CHAPTER III

THE TERMINOLOGY OF CUTICULAR ANATOMY

Since the study of angiosperm leaf cuticles is pursued by relatively few workers, many features of cuticular anatomy and their terminology are unfamiliar to most botanists. Compounding this problem is a lack of agreement over the definition of certain terms, such as those pertaining to stomatal anatomy. As a partial solution to this problem, the present chapter is devoted to the cuticular features seen in Potomac Group dicot leaves and their terminology; this is not a comprehensive treatment of cuticular anatomy in general. The terms have been primarily adopted from Stace (1965) and Dilcher (1974), with those supplied by other workers noted below.

The Nature of the Cuticle

The cuticle is the outermost layer of the epidermis which functions in retarding water loss from the underlying tissue. It is an acellular structure secreted by the epidermal cells which is composed of waxes, cutin (esterfied long-chain carboxylic and hydroxicarboxylic acids), cellulose, and sometimes other substances (Martin and Juniper, 1970). The cuticle forms a continuous sheet

over the epidermis that is almost always thickened at the boundaries of adjacent epidermal cells, producing a series of inwardly projecting ridges called cuticular flanges. These flanges reproduce the outlines of the underlying cells as seen in surface view, but are much narrower than the anticlinal walls of the epidermal cells; when referring to the contours of the cells, the terms flange and wall can be used interchangeably.

The overall thickness of the cuticle, measured from the outer surface to the tips of the flanges, varies both between different species and between different organs of the same plant. It can range from less than one micrometer in thickness (very thin) to over 50 micrometers (very thick). Cuticular thickness is dependent on both genetic and environmental factors, making it a less than reliable taxonomic character by itself even at the level of species; commonly on the same plant it will vary between sun and shade leaves (Stace, 1965). However, when used with other characters that show a strong correlation with environment, cuticle thickness can provide information on the ecology of the parent plants, since it often is proportional to the xeromorphy of the organ (cf. Stace, 1965).

Cuticular Features

Cell Form

Cell form refers to the geometric attributes of the

epidermal cells. In cuticular studies this primarily denotes features seen in surface view, since the cuticle is rarely developed on the inner surface of the epidermis. The major categories of cell form are cell size, cell shape, the number of anticlinal walls, and anticlinal wall pattern.

Cell size is a measure of cell length and width in surface view. It refers to both the absolute size of a cell and its size relative to other epidermal cells.

Cell shape is a measure of cell elongation. Two shapes are recognized: isodiametric, or with length and width approximately equal, and elongate, or with a length to width ratio greater than 1.5. Where the two shapes are found mixed together, cell shape is designated as mixed; tendencies in cell shape may be noted when one type predominates.

The number of anticlinal walls refers to the number of lateral walls visible in a surface view of the cuticle. In Potomac Group angiosperms this number ranges from four to seven.

Anticlinal wall pattern denotes the contour defined by the anticlinal walls of the cell. Three major types are recognized: straight, curved, and undulate (Text-fig. 1, a-c). Undulate walls are further described by three parameters: amplitude, or half the distance from the crest to the trough, wavelength, or the distance

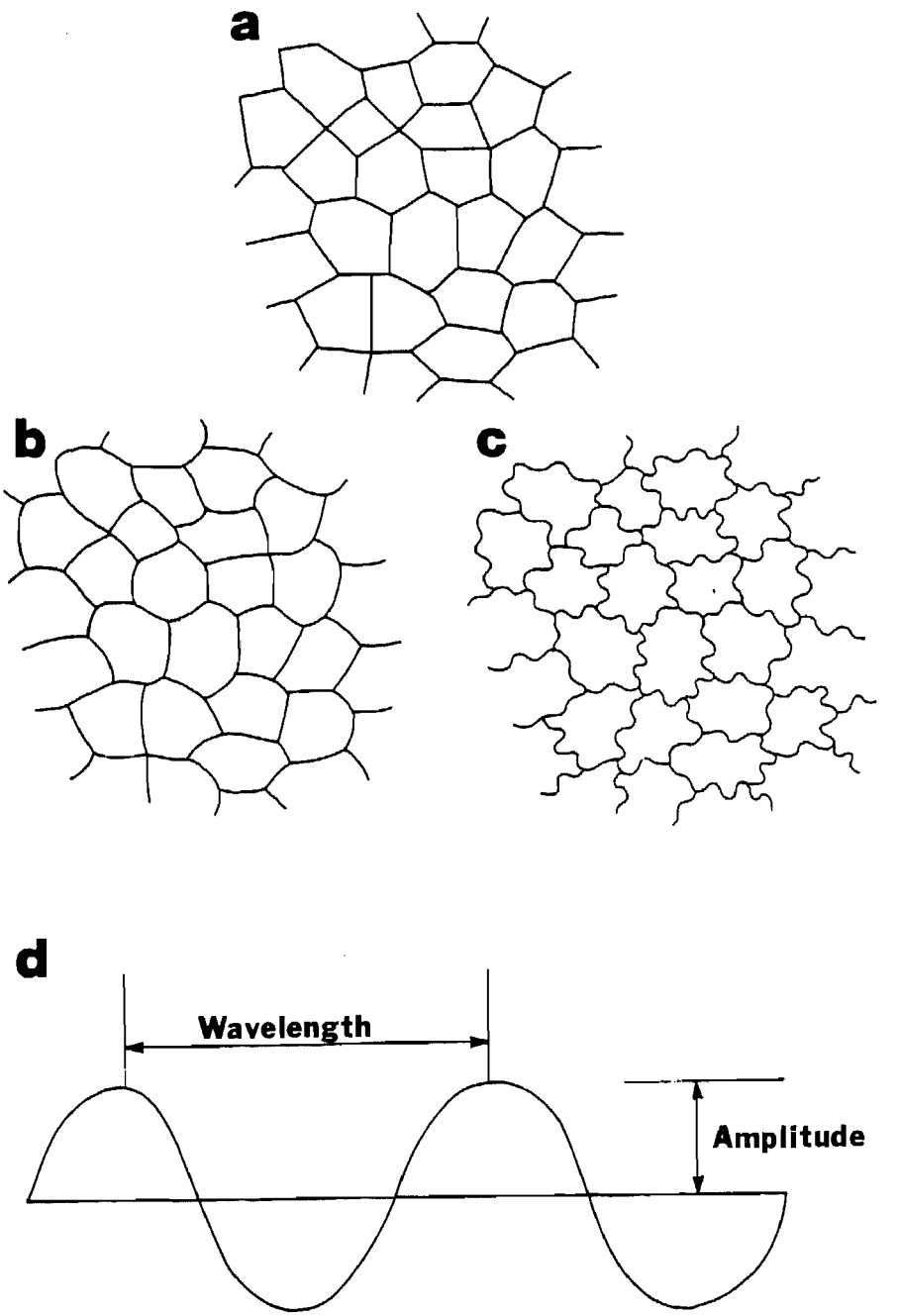
between adjacent crests, and frequency, or the number of wavelengths per side (Text-fig. 1, d). Because the degree of wall undulation typically shows a high amount of variation within a species or even an individual specimen, only maximum amplitude, maximum wavelength, and maximum frequency are measured. Anticlinal wall pattern commonly varies on an individual plant in response to different light intensities, such that shade leaves have more curved or undulate anticlinal walls than sun leaves (Stace, 1965).

Topographic Features

Surface sculpture is the pattern of relief seen on the outer cuticle surface. Three major types are found in Potomac Group angiosperm leaves: psilate, striate, and papillate. Psilate sculpture (Pl. 5, fig. 34) consists of a smooth to minutely lumpy, more or less featureless outer cuticle surface. Striate sculpture is comprised of a variously organized system of ridges, which can show subparallel alignment (Pl. 1, fig. 10), enclose polygonal areas (Pl. 3, fig. 22), or radiate from a particular region (Pl. 3, fig. 20). Papilatte sculpture consists of conical to knob-like projections which can be formed from solid cutin, hollow regions that were occupied by the cell wall and perhaps the cytoplasm (Pl. 4, fig. 27), or some combination of the two (Pl. 4, fig. 29). Commonly there is only one papilla

Text-fig. 1

Anticlinal wall patterns in Potomac Group angiosperms: a = straight; b = curved; c = undulate; d parameters used to describe undulate anticlinal walls.



Text-fig. 1

per cell, which usually is centrally located. A fourth sculptural type, in which the cuticle is folded over on itself (Pl. 2, fig. 13), was observed but not considered a distinct type because it probably represents an artifact of preservation (cf. below).

Internal sculpture is the topographic pattern of the inner cuticle surface. Three types are recognized in Potomac Group angiosperm leaves: smooth, granular, and alveolar. Smooth sculpture (Pl. 1, fig. 9) consists of a smooth, more or less featureless inner cuticle surface. Granular sculpture (Pl. 2, fig. 17) consists of numerous, closely spaced grains of cutin. Alveolar sculpture (Pl. 20, fig. 192) is comprised of numerous internal chambers that open into the inner cuticle surface; this is not to be confused with the alveolar material present on the cuticle surface in such extant groups as Winteraceae (Bailey and Nast, 1944, Bongers, 1973).

Stomatal Apparatus

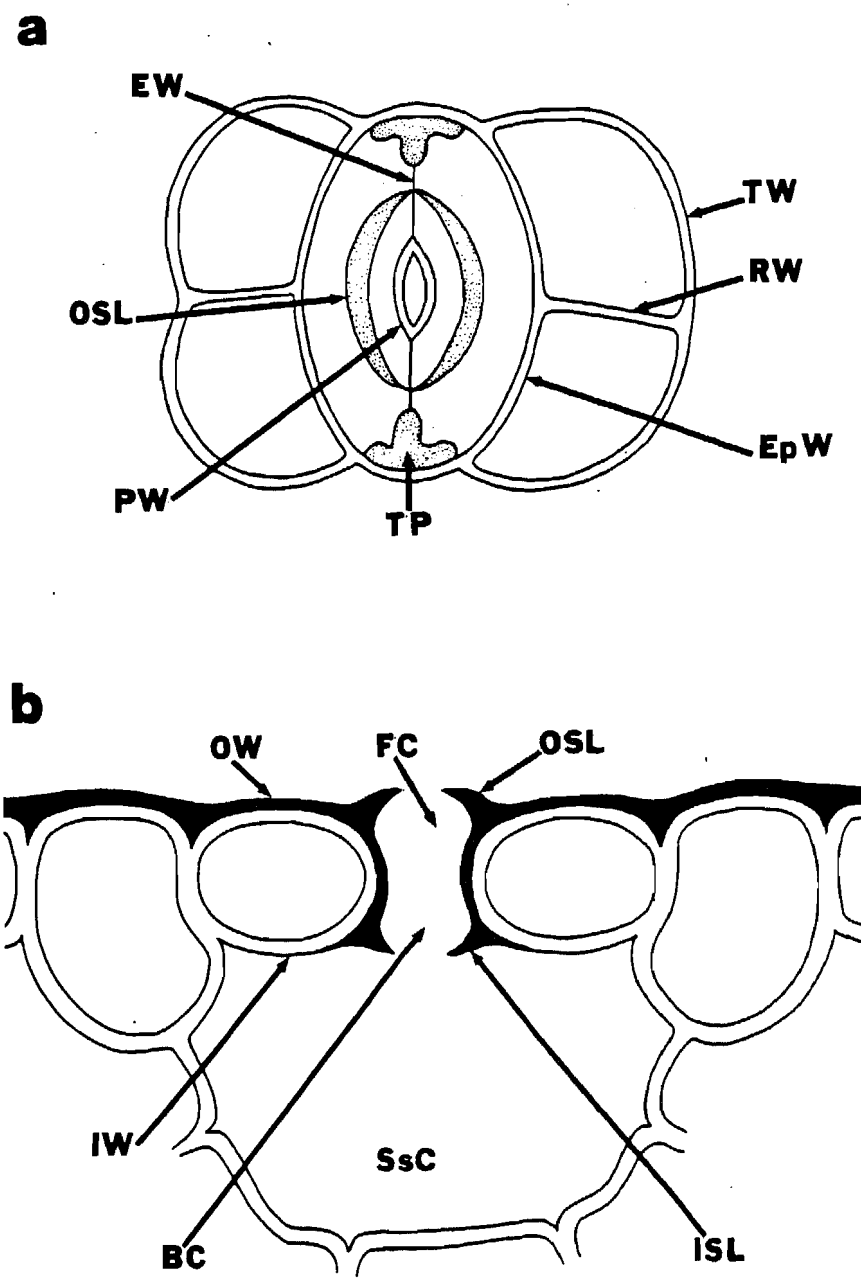
The stomata and their surrounding cells possess numerous characters of systematic importance. Each stoma (plural stomata) consists of one pair of guard cells, which are generally bean-shaped, and a stomatal pore. The stomata may be level with the epidermis, raised

(i.e., underthrust by the adjacent cells), or sunken to various degrees, depending (in part) on the degree of water stress to which the plant is subjected. Adjacent to each stoma are two or more cells called the contact cells (Daghlian, 1979) or neighboring cells, which together with the guard cells are known as the stomatal complex or stomatal apparatus. These cells may resemble the other epidermal cells in all respects, or else be differentiated from them in some way (specialized).

A series of terms has been used to denote the different cell walls of the stomatal complex (Text-fig. 2). In most flowering plants each guard cell possesses two periclinal and four anticlinal walls. The periclinal wall adjacent to the external environment is known as the outer wall, and the one facing the inside of the leaf is called the inner wall. The anticlinal wall which lines the stomatal pore is termed the poral wall, while the one which abuts on the contact cells is termed the epidermal wall. The walls which separate the adjacent guard cells are known as the end walls, and the areas of contact between the end walls and epidermal walls are termed the stomatal poles. The contact cells and other associated, specialized cells have both the outer and inner walls, but only two types

Text-fig. 2

The walls and cuticular thickenings of the stomatal complex. Drawing a is a surface view of the epidermis, b is a cross-sectional view. Legend: BC = back cavity; EW = end wall; EpW = epidermal wall; FC = front cavity; IW = inner wall; ISL = inner stomatal ledge; OSL = outer stomatal ledge; OW = outer wall; PW = poral wall; RW = radial wall; Ssc = substomatal chamber; TP = T-piece; TW = tangential wall.



Text-fig. 2

of anticlinal walls are recognized: (1) the radial walls, which lie along a radius drawn from the stomatal pore, and (2) the tangential walls, which are oriented at right angles to the radial walls.

In most flowering plants and all Potomac Group angiosperms the cuticle is unevenly developed over the stomata (Text-fig. 2). The guard cells commonly lack cuticle on their inner walls, and many times the end walls lack flanges as well. The cuticle of the guard cells is commonly thinner than that of the unspecialized cells, but adjacent to the stomatal pore it can be thickened to form stomatal ledges. Those which occur toward the outside of the stomatal pore are termed outer stomatal ledges and enclose a front cavity, while those adjacent to the mesophyll of the leaf are called inner stomatal ledges and enclose a back cavity. In some cases the outer walls of the guard cells are thickened to form lamellae (Pl. 2, fig. 15), which can be maceration-resistant, as in extant Magnoliales, or else lignified, as in most extant gymnosperms (Baranova, 1972). Finally, the cuticle may be thickened in a T-shaped pattern at the stomatal poles, forming what are known as T-pieces.

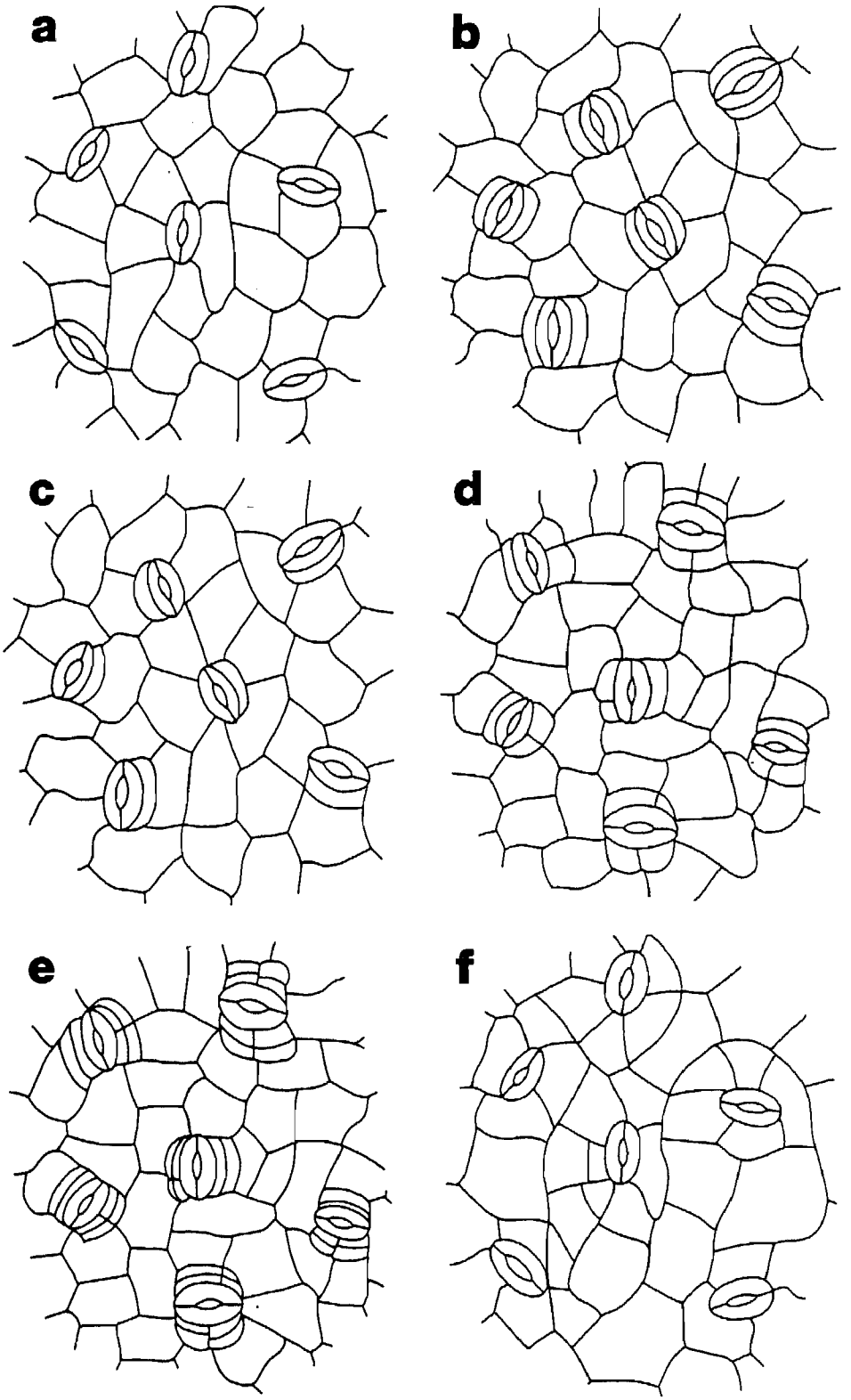
Stomatal shape can be described by several parameters. Stomatal outline is the overall shape of the area enclosed by the epidermal walls of the guard

cells; common shapes include circular (L/W equals 1), elliptic (L/W between 1 and 2), and elongate (L/W greater than 2). The stomatal poles may conform to the general stomatal outline or else deviate from it by being flattened or truncate. In angiosperms the stomatal poles are level with the stomatal pore, but in most gymnosperms the poles are elevated; the latter condition can be observed under SEM or by focusing up and down on an individual stoma with the light microscope.

The arrangement and specialization of the neighboring cells form the basis of stomata classification in flowering plants. While Dilcher (1974) lists over 20 stomatal types for extant angiosperms, only six types are known from Potomac Group dicots. These are defined as follows: (1) anomocytic, or without specialized neighboring cells (Text-fig. 3a), (2) paracytic, or with one lateral subsidiary (or specialized) cell per guard cell, (Text-fig. 3b), (3) hemiparacytic, or with one lateral subsidiary cell per stoma (Text-fig. 3c, (4) laterocytic (Text-fig. 3d), or with three to several lateral, specialized contact cells per stoma (den Hartog and Baas, 1978), (5) complex laterocytic, or laterocytic stomata with more than one order of subsidiary cells (Text-fig. 3e), and (6) cyclocytic, or with a ring of specialized cells (Text-fig. 3f). The epidermis of an individual leaf may possess one stomatal type or have

Text-fig. 3

The six mature stomatal types found in Potomac Group dicotyledons. a = anomocytic; b = paracytic (brachyparacytic); c = hemiparacytic; d = laterocytic; e = complex laterocytic; f = cyclocytic.



Text-fig. 3

several mixed together, depending on the species. The form and degree of cuticle development on the subsidiary cells is also useful in distinguishing leaf groups; the terminology is identical to that for other epidermal cells.

Trichomes and Trichome Bases

The epidermis of many leaves possesses outgrowths known as trichomes (or hairs). Though there appears to be some disagreement on this topic, the cell or cells which constitute the outgrowth are commonly considered the trichome proper, while the area of attachment to the epidermis and the adjacent cells are known as the trichome base. Whereas in extant plants the hairs are almost always available for study, in fossils they are often absent either because of their abscission before leaf fall or because of a lack of cuticle, which renders them more susceptible to decay. As a result angiosperm paleobotanists study the structures of trichome bases to gather information on the systematic affinities of their fossils.

The trichome base is comprised of two regions: (1) the foot, or area of hair attachment, and (2) the base cells, which are adjacent to the foot. The foot may consist of either a pore, into which fits the basal cell(s) of the hair, or one to many foot cells, to

which the hair is attached. The foot cell may resemble the other epidermal cells in all respects, but commonly it is modified in some way. Common modifications of the foot cell include differences in size, shape, number of cell sides, anticlinal wall pattern, cuticle thickness, and relation to the adjacent cells. Often a scar will remain on the foot cell where the trichome was attached. This may consist of a pore (Pl. 3, fig. 24), a round depression in the outer cuticle (Pl. 2, fig. 11), and/or a rim of thickened cuticle demarcating the exterior wall(s) of the basalmost trichome cell(s) (e.g., Pl. 8, figs. 64, 65). The base cells often are unmodified, but in some cases they differ from the other epidermal cells in their size, shape, and/or radial organization.

Trichome structure, which exhibits a high diversity in modern flowering plants, is relatively simple in Potomac Group angiosperms. Trichomes may be unicellular, bicellular, or multicellular, with all the multicellular types being classified as uniseriate (consisting of one row of cells). In the Potomac Group, hair shape is either hemispherical, globose, or elongate, and the hair apex may be rounded or pointed. Hairs are generally oriented away from the leaf surface, but sometimes they are prostrate (lying flat against the leaf surface); care must be taken to be sure that the prostrate

orientation is not the result of compression after fossilization.

Other Types of Specialized Epidermal Cells

In addition to trichomes, other types of specialized cells are found on the epidermis; these either occur singly or in groups. While in extant flowering plants these cells are classified on the basis of their contents and function, in fossil leaf cuticles the contents are almost always absent and function cannot be directly observed. Hence, contents and function must be inferred either by a comparison of the cells with similar types in close modern relatives or through certain diagnostic features of the cuticle. Since several distinct types of structures can possess similar cuticular features (Roselt and Schneider, 1969), a less specific terminology has been adopted. The three major categories of structure recognized in this study are idioblasts, cork warts and wound structures, and secretory structures.

An idioblast is defined as "a specific cell which is clearly distinguished from the other cells of the tissue in which it appears, either by size, structure, or content" (Fahn, 1967). However, the cell is often given a specific title when the contents or function

are known (such as myrosin cell or mucilage cell), and the term idioblast is not used. Because of this usage the term idioblast will be used to denote a specialized cell whose contents and function are unknown.

Cork warts, or cork bodies in the epidermis, commonly produce a round hole in the cuticle that is surrounded by numerous radial files of cells. These structures tend to be taxonomically restricted in extant flowering plants, and hence have systematic value, but unfortunately resemble wound tissue produced in response to insect feeding, mechanical damage, or the eruption of fungal fruiting bodies through the epidermis. Because of their sporadic occurence within individual leaf groups and the occurrence of fungal fruiting bodies on many leaves, all such structures were attributed to wounding.

Secretory structures may be composed of epidermal cells, the epidermis and other tissues, or cells in the mesophyll. In the first two types, the outer cuticle typically is thin relative to the other cells and/or is perforated by one or more pores (Roselt and Schneider, 1969; Martin and Juniper, 1970). Other criteria, such as maceration-resistant contents and resemblances to secretory structures in extant relatives are used whenever possible to corroborate the interpretation. In the case of mesophyll secretory structures, a secretory

function can be inferred by the presence of maceration-resistant contents and their similarity to secretory structures in extant relatives. Secretory structures may further be classified on the basis of cell number, cell form, and their relationships to other cells.

CHAPTER IV

ZONE I ANGIOSPERM LEAVES

Zone I angiosperm leaves exhibit a low diversity in their features of venation, shape, and marginal configuration compared to later Cretaceous and modern flowering plants. In contrast to the six types of primary venation recognized by Hickey (1973) for extant dicots, all Zone I leaves are built on a fundamentally pinnate plan, though some show a tendency for the basal clustering of the secondaries (Doyle and Hickey, 1976). All previously reported leaf types possess festooned brochidodromous secondary venation, and a new serrate form from Drewrys Bluff has simple craspedodromous secondaries. Zone I leaves show a limited number of shapes, ranging from narrowly obovate to reniform, and all have either decurrent or acute bases (Hickey, 1978). The margins of most leaves are entire, but one form (Vitiphyllum Font.) is pinnately lobed and several are serrate; in the latter the teeth are all irregularly spaced, have a convex-convex (A-1) shape, and possess glandular tips (Hickey and Doyle, 1977; personal observations), which contrasts with the wide variety of tooth types found in modern flowering plants (Hickey and Wolfe, 1975). Zone I leaves also display a low taxomonic

diversity compared to those from younger Potomac Group sediments: Hickey and Doyle (1977) recognize over 30 leaf types from Subzone II-B as opposed to only 12 from Zone I. These Zone I leaf groups also show a strong tendency to intergrade with one another, in contrast to the younger leaves.

The most striking characteristic of Zone I leaf venation, found in every group, is the low degree of regularity present in the organization of the veins. The secondary veins show an irregular pattern of spacing and enclose areas of variable size and shape (e.g., Pl. 1, fig. 5). Tertiary veins generally have a more or less random course and often arise at variable angles, while the quaternary and higher order veins are commonly hard to distinguish from the tertiaries. This set of features, which corresponds to Hickey's "first rank" pattern of venation, has been inferred to be primitive for the dicots on the basis of its prevalence in such woody Magnoliid families as Winteraceae and Canellaceae (Hickey, 1971). However, the fact that several fossil leaf types show less venational regularity than any modern mesic angiosperm suggests that some Zone I leaves may be more primitive than anything now extant (Wolfe et al., 1975).

All Zone I leaf remains with cuticle were collected from a 4 cm thick bed of clay exposed at the northern end of Drewrys Bluff. The claybed is found approximately 9 m above high tide level in a 20 m thick

section of gravels, sands, and thin clay units that show numerous erosional contacts and fining-upward sequences, features which Glaser (1969) considered typical of lower Potomac Group sediments and evidence for their fluvial origin. This leaf bed sharply overlies a complex sequence of coarse sands and gravels and is overlain by at least two meters of clays and fine sands that show extensive root burrowing. The pollen flora falls within upper Zone I of Brenner (Doyle, personal communication), consistent with the similarities seen between the angiosperm leaf flora of this bed and those from Fredericksburg and Baltimore, also palynologically dated as upper Zone I (Doyle and Hickey, 1976). Noncuticular angiosperm leaves are known from upper Zone I sediments toward the southern end of Drewrys Bluff (Doyle and Hickey, 1976) and remains of the cheirolepidiaceous conifer Pseudofrenelopsis parceramosa (Font.) Watson occur in a clayball from the northern end of the exposure, near the base of the sequence that has palynologically been dated as lower Zone I (Upchurch and Doyle, in press).

Five distinct dicotyledonous leaf types are recognized from the Drewrys Bluff locality. The most abundant form, represented by more than 20 specimens, is a narrowly lanceolate leaf with numerous serrations, simple crapedodromous secondary venation, and elongate

areolation; it does not closely resemble any previously described species of Early Cretaceous angiosperm leaf (D. B. Leaf Type #1--Pl. 1, figs. 1, 2). The second most abundant type, represented by four specimens, is an elongate leaf assignable to Eucalyptophyllum oblongifolium Font. on the basis of its midvein composed of two discrete vascular strands which fuse apically, numerous irregularly spaced secondary veins, prominent intramarginal vein, and elongate areolation (Pl. 1, fig. 4). This type was previously known only from the Fredericksburg locality of Fontaine (1889). The third type consists of three fragments which possess numerous internal secretory cells and a reticulate pattern of higher order venation suggestive of that found in Ficophyllum Font. (cf. Ficophyllum--Pl. 1, fig. 3). The fourth, which consists of one whole leaf and one large fragment, has the elliptical shape and marginal serrations characteristic of the genus Celastrophyllum but differs from all known Potomac Group species in having both a low number of secondary veins and no distinct petiole (Celastrophyllum--Pl. 1, fig. 5). The fifth form consists of an obovate, entire margined fragment with marginal tears that resemble teeth, closely spaced secondary veins, and tertiary veins which arise at diverse angles but tend to enclose elongate areas oriented parallel to the secondary veins; it is similar to illustrated specimens of the Celastrophyllum obovatum Font. complex from Baltimore but differs in its much smaller size (cf.

Celastrophyllum obovatum Font.--Pl. 1, fig. 6). Certain characteristic Zone I leaf types, such as pinnately lobate forms (Vitiphyllum), elongate obovate leaves with entire margins (Rogersia Font.), and reniforme 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).

Cuticular Descriptions

Whole Leaves

Upper Cuticle (Text-fig. 4)--The upper cuticle of the Drewrys Bluff leaves shows wide variation in its development, ranging from very thin and lacking well-defined flanges in Celastrophyllum (Pl. 1, fig. 7) and cf. Ficophyllum (Pl. 1, fig. 8) to medium or thick and having well-defined flanges in Eucalyptophyllum and D.B. Leaf type #1 (Pl. 1, figs. 9, 10). Each leaf possesses a mixture of isodiametric and elongate cells with four to many walls, which are predominantly straight in Eucalyptophyllum, but curved in D.B. Leaf Type #1. Stomata are found in high frequencies on the upper epidermis in both species of Celastrophyllum (Pl. 1, fig. 7) and in lower frequencies on the upper cuticle of cf. Ficophyllum (Pl. 1, fig. 8). Their occurrence is correlated with a low maximum thickness of both the upper and lower cuticles, suggesting mesic growth

conditions for the parent plants (cf. Salisbury, 1927).

Upper cuticle surface sculpture is relatively simple. Every species except D.B. Leaf Type #1 possesses psilate sculpture, which is associated with subparallel cuticular folds in both species of Celastrophyllum and cf. Ficophyllum (Pl. 1, figs. 7, 8). These folds vary greatly in their width and occur only on thin cuticles, suggesting that they are artifacts of preservation. Striate sculpture is present in D.B. Leaf Type #1 and consists of tightly sinuous subparallel ridges that are one μm wide and traverse cell boundaries (Pl. 1, fig. 10). Internal sculpture is very uniform, being more or less smooth in every species.

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 unmodified base cells which underthrust the foot (Pl. 1, fig. 9). The shape of the foot ranges from isodiametric to elongate and branched, and each possesses four to many straight or curved anticlinal walls. Trichome abscission scars (when present) are centrally positioned, circular, and under 10 μm in diameter, suggesting that the hairs were unseriate (Pl. 2, fig. 11). These hair bases are rare and widely scattered in Leaf Type #1, but are numerous and clustered in Eucalyptophyllum (Pl. 1, fig. 9).

Lower Cuticle (Text-fig. 5)--The lower cuticle is as thick as the upper cuticle in every group except D.B. Leaf Type #1, where it is thinner, (Pl. 2, fig. 14) and cf. Ficophyllum, where it is thicker (Pl. 2, fig. 13). The cells of the lower epidermis are the same size and shape as those on the upper epidermis, but have more curved anticlinal walls in those groups with well-developed flanges. The cells of Eucalyptophyllum (Pl. 2, figs. 12, 17) and cf. Ficophyllum (Pl. 2, 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 (Pl. 2, fig. 14).

Two types of surface sculpture are known from the lower cuticle. Psilate sculpture, with associated cuticular folds (artifacts of preservation?) is found in Celastrophyllum and cf. Ficophyllum (Pl. 2, fig. 13). Complex striate sculpture is present in D.B. Leaf Type #1 and in Eucalyptophyllum. In D.B. 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 (Pl. 2, 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

Text-fig. 4

Features of the upper cuticle, Zone I angiosperms

Text-fig. 4

UPPER CUTICLE, ZONE I ANGIOSPERMS

Leaf Group	Cuticle Thickness	Wall Shape	Stomata	Hair Bases	Surface Sculpture	Internal Sculpture
Drewrys Bluff Leaf Type #1	medium	straight to curved	absent	heavily cutinized small cells (rare)	striate	smooth
Eucalyptophyllum oblongifolium	medium to thick	straight	absent	heavily cutinized small cells, often clustered	psilate	smooth
cf. Ficophyllum	thin, flange barely visible	-------	infrequent	absent	psilate	smooth
Celastrophyllum sp.	thin, flanges absent	-------	frequent	absent	psilate	smooth
cf. Celastrophyllum obovatum	thin, flanges absent	-------	frequent	absent	psilate	smooth
Dispersed Cuticle Type #1	medium, flanges very wide	straight	absent	absent	striate	smooth

are 4 μm wide, tend to enclose areas that are the same shape as the underlying cells, and commonly connect with the smaller striations (Pl. 2, fig. 12; Pl. 3, fig. 22). Internal sculpture is smooth in all leaf groups except Eucalyptophyllum, where it is distinctly granular (Pl. 2, fig. 17).

In contrast to the diversity of form seen in the unspecialized cells, the stomatal apparatus in every leaf group conforms to the same basic plan of construction. While the guard cells may be either level with the rest of the epidermis or else sunken, as in Eucalyptophyllum (Pl. 3, fig. 22), each pair of guard cells lies in one plane, as is typical of modern angiosperms, with the poles at the same level as the stomatal pore; this differs from the predominant condition for gymnosperms, in which the stomatal poles are elevated relative to the pore (Harris, 1932). Outer stomatal ledges (Pl. 2, fig. 15, SL), commonly found in extant flowering plants but rarely encountered in gymnosperms (cf. Florin, 1931; Stace, 1965), are present in every species; in addition, maceration-resistant, lamellar thickenings are found in the outer walls of at least some guard cells in every leaf (Pl. 12, fig. 15, L). These lamellae are identical to those characteristic of extant Illiciales and Magnoliales (Baranova, 1972; personal observations), but are less

Text-fig. 5

Features of the lower cuticle, Zone I angiosperms

Text-fig. 5

LOWER CUTICLE, ZONE I ANGIOSPERMS

Leaf Group	Cuticle Thickness	Wall Shape	T-Pieces	Hair Bases	Secretory Cells	Surface Sculpture	Internal Sculpture
Drewrys Bluff Leaf Type #1	thin, flanges often absent	curved to undulate	absent	small, thickened cells (rare) radiostriate hair bases (rare)	----	striate	smooth
Eucalyptophyllum oblongifolium	medium to thick	straight or curved	absent	volcano hair-bases (rare)	isolated cells on epidermis	striations of two sizes	granular
cf. Ficophyllum	thin	straight or curved	absent	absent	oil cells in mesophyll	psilate	smooth
Celastrophyllum sp.	thin, flanges absent	-----	absent	absent	oil cells in mesophyll	psilate	smooth
cf. Celastrophyllum obovatum	thin, flanges absent	-----	absent	absent	oil cells in mesophyll	psilate	smooth
Dispersed Cuticle Type #1	medium, flanges wide	straight or curved	crossbar well-developed	absent	----	striate	granular
Dispersed Cuticle Type #2	thin	straight	absent	absent	----	psilate, with hollow papillae	smooth
Dispersed Cuticle Type #3	thick	straight to curved	both parts present	small cell with thick outer cuticle & rounded pore	----	striate, with partially solid papillae	granular
Dispersed Cuticle Type #4	thick	straight or curved	absent	small, thickened cells	isolate cells on epidermis	psilate	granular
Dispersed Cuticle Type #5	medium	straight to curved	absent	absent	----	striate, with partially solid papillae	smooth
Dispersed Cuticle Type #6	thin	undulate	present?	radiostriate hair bases (frequent)	---	striate	slightly granular

regularly developed on an individual leaf than in the modern forms.

The most striking feature of the stomatal apparatus in the Drewrys Bluff materials is the high variation found on an individual leaf in both the specialization and arrangement of the cells adjacent to the guard cells, producing stomata that conform to several of the conventionally recognized mature stomatal types. Many stomata might be classified as paracytic, but often they show more irregularity 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 (Pl. 2, figs. 12, 17, P). Many other stomata lack specialized contact cells and conform to the anomocytic type, (e.g., Pl. 2, figs. 14, 16), but in others the contact cells are all somewhat smaller than the unspecialized cells and the stomata might be classified as cyclocytic (Pl. 2, fig. 17, C). Some stomata have three or more specialized lateral contact cells and conform to the laterocytic type (Pl. 2, fig. 17, Lc), but others possess only one specialized lateral contact cell and thus could be classified as hemiparacytic (Pl. 2, fig. 17, H). Compounding matters is the tendency for each of the

above stomatal types to intergrade with one another, making attempts to classify them according to accepted schemes futile. This wide diversity in contact cell arrangement and specialization differs from the condition in most later Potomac Group angiosperm leaves (cf. below) 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 Magnoliid taxa have been reported to possess the same pattern of stomatal variation as Zone I leaves: Austrobaileyaceae (Bailey and Swamy, 1949), Sarcandra of the Chloranthaceae (Swamy, 1953--Pl. 2, fig. 13), and the Schisandraceae (Bailey and Nast, 1948). In addition, illustrations from Baranova (1972) and Bongers (1973) indicate that Liriodendron in the Magnoliaceae and Takhtajania and Drimys winteri in the Winteraceae possess this condition as well.

Two types of trichome bases are known from the lower cuticle. The first, identical to that seen on the upper cuticle, is occasionally found in Leaf Type #1 (Pl. 3, fig. 19). The second, found in very low frequency in both Eucalyptophyllum and D.B. Leaf Type #1 and here termed the "radiostriate" hair base, consists of a small, polygonal, straight-sided foot cell that bears a central trichome abscission scar; the scar consists of a circular region in the center of the cell with striations that

radiate from the periphery (Pl. 3, fig. 20). Structures similar to this hair base are reported to bear abaxial, deciduous ethereal oil cells in modern Illiciales and secretory cells in certain Magnoliaceae (Bailey and Nast, 1948; Baranova, 1962; Jähnichen, 1976), strongly suggesting that these leaves also bore ethereal oil cells or secretory cells on the abaxial epidermis.

In addition to these presumed secretory trichomes numerous inferred secretory cells are present on the lower epidermis of Eucaluptophyllum (Pl. 2, fig. 12, Gl). 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 ethereal oil-bearing cells on the abaxial epidermis of Illiciales and certain Chloranthaceae such as Ascarina polystachya, except that the latter tend to be more rounded and more underthrust by the adjacent cells (cf. Jähnichen, 1976; personal observations). This structural similarity suggests that the secretory cells in the fossil also contained ethereal oils.

The leaves of both Celastrophyllum types and cf. Ficophyllum lack epidermal secretory structures but contain secretory cells in the mesophyll. These cells are spherical, thin walled, average 10 μm in diameter, and often contain dark contents (Pl. 3, fig. 21). They show numerous similarities in size, shape, and appearance

of contents to ethereal oil cells illustrated by Sturm (1971) and Jähnichen 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, together less than 1% as abundant as the gymnosperm fragments in the sample, are similar to the whole leaves in such features as stomatal construction and hair base type. The distinctness of the new cuticle types, as can be seen in Text-figs. 4 and 5, is due to unique character combinations and quantitative differences (e.g., hair base frequency) as well as several characteristics not found in the whole leaves.

Cuticular flanges development is more diverse in the dispersed forms. Generally the unspecialized cells possess the same type of flange as that seen in the whole leaves; that is, the flange tapers smoothly towards the inside of the leaf and narrows to a ridge at its tip (cf. Pl. 2, fig. 17). In Dispersed Cuticle Type #1, however, the flanges are very wide (8 μm), abruptly flatenned to the inside, and often bear a longitudinal

groove in their center (Pl. 3, fig. 23), which may represent the middle lamella of the cell wall (cf. Stace, 1965). The guard cells of the dispersed cuticle types also exhibit a higher diversity than the Drewrys Bluff leaves in that some of them possess T-pieces at the poles. In Dispersed Cuticle Type #1 the walls where the stomatal poles contact the neighboring cells are more strongly thickened than the end walls of the guard cells (Pl. 3, fig. 23). In contrast, both parts of the stomatal poles have strong cuticular thickenings in Dispersed Cuticle Type #3, and the top piece characteristically curves towards the opposite end of the stoma (Pl. 3, fig. 24, arrow).

Surface sculpture also shows greater diversity. Many cuticle types, in contrast to whole leaves, are papillate, with centrally located papillae on the unmodified epidermal cells. These papillae are generally either hollow, as in Dispersed Cuticle Type #2 (Pl. 4 fig. 27), or partially solid, as in Dispersed Cuticle Types #3 and #5 (Pl. 4, figs. 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, more or less isodiametric foot cell and several unmodified, strongly underthrusting base cells (Pl. 3, figs. 25,26). The outer wall of the foot cell is heavily cutized except at

the point of trichome attachment, where there is a pore 12 μm in diameter. 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 are not thickened and the trichome abscission scar consists of a pore.

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; Jansen 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 the same pattern of variation in their stomatal structure. Only three 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) and its elongate areolation is more characteristic of ferns than flowering plants (Hickey and Doyle, 1977). 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 types, abaxial secretory cells, and sunken stomata, are seen in some contemporaneous and younger Potomac Group angiosperm leaves (Upchurch, 1978, 1979 and below). 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 hair bases. This relationship is supported by the structure of the primary vein, which is composed of two discrete vascular bundles that fuse within the lamina (Pl. 1, fig. 4), as is typical of Sarcandra in the Chloranthaceae (Swamy and Baily, 1950). This does not mean that the fossil readily fits into either modern

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. Hence, Eucalyptophyllum probably represents an extinct evolutionary line of at least ordinal rank (cf. Hickey and Doyle, 1977) which has relationships with both modern Chloranthaceae and Illiciales.

Cuticular anatomy suggests similar affinities for D.B. Leaf Type #1, since it possesses a combination of features apparently restricted to Schisandraceae (Illiciales) and Sarcandra (Chloranthaceae): (1) the Zone I pattern of stomatal organization, (2) stomata longer than 30 μm, (3) radiostriate hair bases, and (4) striations both concentric to and radiating from the stomatal pore (Pl. 2, fig. 14; Pl. 3, fig. 18; Pl. 4, figs. 30, 33). This relationship is supported by the tooth structure of these leaves (Pl. 1, fig. 2): the biconvex (A-1) shape, central vein with a glandular tip, and pair of lateral veins which fuse with the central vein are all characteristic of the Chloranthoid tooth type, found today in the Choranthaceae, Illiciales, Trochodendrales and Ranunculales (Hickey and Wolfe, 1975). These similarities with Chloranthaceae and Illiciales do not mean that the fossil should be assigned to either extant group, however, since its simple craspedodromous secondary venation and

elongate areolation are not characteristic of either group (cf. Hickey and Wolfe, 1975; personal observations). Hence, like Eucalyptophyllum, D.B. Leaf Type #1 may belong to a complex of Cretaceous flowering plants that also included the ancestors of modern Illiciales and Chlorentheceae.

Two dispersed cuticle types show a similar pattern of affinities with extant flowering plants. The first, Dispersed Cuticle Type #6 from Dutch Gap (Pl. 4, figs. 31, 32), possesses numerous radiostriate hair bases and rare rounded idioblasts (secretory cells?) on the lower epidermis, suggesting a relationship with the 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 (Pl. 3, figs. 24, 26; Pl. 4, fig. 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 the construction 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 the base cells more strongly underthrust the foot cells. In spite of these marked similarities, however, the fossil differs from all extant members of the order by its slightly shorter stomata which lack lamellae (average 27 μm as opposed to 30 to 70

μm as listed by Bailey and Nast, 1948) and the absence of abaxial glands and radiostriate hair bases (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 were related in some way to Chloranthaceae and Illiciales, but cannot be placed within either modern group.

The results indicate the need for caution in interpreting similarites 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 a, b; 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 of pollen is inferred to be ancestral to the other pollen types within the family (Walker, 1976 b), 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.

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 hair bases bearing glandular hairs. Ethereal oil cells of the type inferred to have been present in the mesophyll of three leaf groups today are characteristic of Magnoliidae (Cronquist, 1968). 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 Sarcandra of the Chloranthaceae. 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 cannot be closely related to any one family within the subclass (Wolfe et al., 1975; Hickey and Doyle, 1977).

The unusually variable stomatal structure seen in Zone I leaves takes on additional phylogenetic interest when viewed in the context of later Potomac Group angiosperm leaves. Subzone II-B leaves differ from Zone I

forms in possessing stomata which generally show a lower variability in neighboring cell arrangement and specialization on an individual leaf, although the total range of stomatal structure in the entire angiosperm element is similar to that found on an individual Zone I leaf. For example, cordate leaves assigned to Populophyllum reniforme Font. possess stomatal complexes that are almost entirely anomocytic (Pl. 5, fig. 34), while those from a new serrate leaf from Red Point all have a ring of neighboring cells with strongly overarching papillae (Pl. 5, fig. 35). Menispermites potomacensis stomata range from anomocytic to paracytic, but never conform to the laterocytic or cyclocytic types (Pl. 21, figs. 204-206), while the "platanoids" (e.g., Pl. 5, fig. 36) and Sapindopsis Font. (Pl. 5, fig. 37) always produce stomata with specialized lateral contact cells. This temporal pattern of stomatal distribution suggests a major evolutionary trend during the Early Cretaceous towards decreased stomatal variation on an individual leaf, with the later stomatal patterns being derived from the Zone I pattern by a decrease in the variability of subsidiary cell arrangement and specialization. If this trend is valid for the dicots as a whole then the uniformly paracytic condition, considered primitive for the flowering plants by Takhtajan (1969), Baranova (1972), and Thorne (1976), is actually derived.

According to this interpretation such Magnoliid taxa as Austrobaileyaceae, Schisandraceae, Sarcandra in the Chloranthaceae, and Takhtajania and Drimys winteri are more primitive in their stomatal structure than most members of the order Magnoliales. Similarly Liriodendron, unique within Magnoliaceae by its possession of the Zone I pattern of stomatal variation, might be interpreted as an early line of evolution which, though specialized in many respects, actually retains the primitive stomatal condition.

This proposed trend of stomatal evolution appears to agree with some previously postulated evolutionary trends in extant Magnoliidae but not with others. On the one hand, there is a general agreement with inferred trends in wood anatomy and leaf architecture. Two of the taxa with the Zone I stomatal pattern, the Winteraceae and Sarcandra in the Chloranthaceae, are vesselless, while most Magnoliiae with vessels possess paracytic or other stomatal types postulated to be derived from the Zone I form (Bailey, 1944; Metcalfe and Chalk, 1950, Swamy, 1953; personal observations). Studies of angiosperm leaf architecture by Hickey (1971) and Hickey and Doyle (1977) have concluded that the large size and tendencies for more rigidly organized venation found in such Magnoliales as Magnoliaceae, Annonaceae, and Myristicaceae are advanced features compared to

those in Zone I angiosperms and the extant Canellaceae and Winteraceae; in the latter family those members with the Zone I stomatal type lack stomatal plugs of alveolar material, a possible advanced feature which sets most of the family apart from other Magnoliales (Baranova, 1972; Bongers, 1973).

On the other hand, the proposed trends in stomatal structure appear to conflict with Walker's (1976b) scheme for pollen evolution in monosulcate Magnoliidae. Extant members of the subclass can be divided into three palynological groups on the basis of grain size, shape, and exine structure, which Walker interprets as grades of evolution. Taxa with his Grade I pollen, such as Degeneriaceae, Magnoliaceae and primitive Annonaceae, generally possess unformly paracytic stomata, while the Zone I stomatal pattern is only found in taxa with his Grade II or Grade III pollen (cf. Walker, 1976b; Praglowski, 1979; Endress and Honegger, 1980). The Potomac Group data conform to this generalization, since Zone I angiospermous monosulcates are assigned to Grade III by Walker (1976b). This conflict might be resolved by postulating that still earlier, pre-Zone I angiosperms had Grade I pollen and uniformly paracytic stomata and that the variable Zone I pattern arose through the breakdown of the paracytic type. However, this hypothesis predicts that angiosperm leaves

with paracytic stomata existed somewhere during Zone I time, and until such leaves are found it must be considered unsupported by fossil evidence. In any case, even if the Zone I stomatal pattern is not primitive for the angiosperms as a whole, it may still be ancestral to the paracytic, laterocytic, and anomocytic stomata found in extant dicots with tricolpate or derived pollen types, since the more primitive members of this group possess an exine structure comparable to that of Grade III monosulcates and since many of the Subzone II-B dicots with cuticle can be related to tricolpate or tricolpate-derived taxa on the basis of leaf architecture (Hickey and Doyle, 1977). Further study of Early Cretaceous leaf cuticles from both lower and middle paleolatitudes, as well as a rigorous analysis of proposed evolutionary trends for their agreement with one another using such cladistic methods as character compatibility (e.g., Meacham, 1980), are needed to resolve the problem of whether or not the observed trend in increased stomatal regularity applies to the angiosperm as a whole.

CHAPTER V

SUBZONE II-B ANGIOSPERMS

Subzone II-B angiosperm leaves show a significantly higher structural diversity than Zone I forms, but still less than that in modern flowering plants. In contrast to just a fundementally pinnate plan of orginization, as in Zone I dicots, Subzone II-B leaves conform to several of Hickey's (1971) primary venation types. For example, Populophyllum Font. (Pl. 20, fig. 188) possesses actinodromous primary venation, with the primaries all radiating from a single point. The "platanoids" are palinactinodromous, with three to many primary veins that all diverge at different points, while Menispermites potomacensis Berry has primaries that arch towards the apex. Secondary venation is more diverse, since in addition to the festooned brochidodromous type so characteristic of Zone I dicots Subzone II-B leaves have simple brochidodromous secondary venation, as in some "platanoids" (cf. Hickey and Doyle, 1977), venation that approaches eucamptodromous, as in some pinnately compound Sapindopsis leaves (Pl. 9, fig. 80), and mixed craspedodromous venation, as in one pinnately compound Sapindopsis leaflet (Pl. 9, fig. 79). Three new classes of leaf shape are present in Subzone II-

B: palmately lobed, as in the "platanoids" (Pl. 15, fig. 138), deeply pinnatifid, as in Sapindopsis variabilis from Brooke (pl. 6, fig. 39), and pinnately compound, as in younger Subzone II-B species of Sapindopsis (e.g. Hickey and Doyle, 1977, fig. 45). Leaf bases are also more diverse, with cordate and peltate types being found in addition to the older ones. Finally, the configuration of the leaf margin exhibits a greater diversity: in addition to the convex-convex (A-1) type of serration found in Zone I, concave-convex (C-1) teeth are found in a few pinnately compound specimens of Sapindopsis from West Brothers (Pl. 9, figs. 79, 82) and straight-convex (B-1) teeth are characteristic of a new serrate leaf from Red Point (Pl. 19, fig. 173).

A key difference between Zone I and Subzone II-B dicot leaves is the strong tendency for the latter to show greater regularity in their vein organization: generally the veins have more regular courses and the vein orders are easier to distinguish from one another. While the "first rank" syndrome of Hickey (1971) is present in many groups, others, such as some pinnately compound Sapindopsis leaves (e.g., Pl. 9, fig. 80), conform to Hickey's "second rank" syndrome, where the secondary veins are regularly spaced and enclose areas of similar size and shape but the tertiary venation is

still poorly organized. Others, such as Platanoid #1 (Pl. 3, fig. 130), have both regular secondary venation and tertiary veins that all have the same orientation, conforming to Hickey's "third rank" syndrome. This greater venational regularity shows a correlation with phylogenic advancement in modern mesic angiosperms, indicating that the higher diversity of Subzone II-B leaves is actually due to an evolutionary diversification and not the immigration of a highly evolved group from elsewhere (Hickey and Doyle, 1977). Further, leaves with a rigidly organized system of quaternary veins, found in such advanced extant groups as Fagaceae, do not appear until the Late Cretaceous (Hickey, 1978), indicating that Early Cretaceous angiosperms still had not attained the level of advancement present in many modern forms.

Six major leaf architectural types with preserved cuticle are known from Subzone II-B. These are: (1) pinnatifid leaves and similar fragments relatable to Sapindopsis variabilis Font., (2) pinnately compound leaves and numerous isolated leaflets of the type related to Sapindopsis by Hickey and Doyle (1977), (3) palinactinodromous, lobate leaves belonging to the "platanoid" complex, (4) a small, elongate leaf with numerous straight-convex (B-1) serrations, (5) actinodromous leaves with cordate bases belonging to Populophyllum reniforme Font., and (6) several fragments of acrodromous leaves belonging to

Menispermites potomacensis Berry. These forms constitute only a small fraction of the total number of leaf types recognized for Subzone II-B by Hickey and Doyle (1977), but nevertheless represent a large part of the range of morphology seen in the leaves at this time.

Description of Materials

Sapindopsis variabilis Fontaine

Leaves relatable to Sapindopsis variabilis dominate collections from the Bank near Brooke locality in Northern Virginia, dated as middle Subzone II-B by Hickey and Doyle (1977). Most of the organically preserved materials are rather fragmentary, but their similarity to whole leaves in venation and cuticular anatomy clearly indicates that all belong to Sapindopsis. The specimens show some variation in leaf architecture and cuticular anatomy, but cannot be divided into more than one species. Hence, the following description treats the structural diversity in these materials as variation within one taxon.

The leaf is deeply pinnatifid, with a decurrent wing of laminar tissue running along the rachis (Pl. 6, figs. 38, 39). Each lobe has a narrow elliptic shape, acute apex, decurrent base, and an entire margin. The venation of each lobe is brochidodromous, with numerous secondary veins that arise at an acute angle greater than 45° (Pl. 6, fig. 40). Most secondary veins on an individual leaf abruptly arch towards the apex, as

is typical for S. variabilis (Pl. 6, fig. 40). The tertiary venation is reticulate and randomly oriented, with perhaps a slight tendency to be directed towards the midvein (Pl. 6, fig. 41). The quaternary venation is reticulate and randomly oriented.

Upper Cuticle--The upper epidermis of S. variabilis shows moderate cutinization, with most cells having well-defined flanges (Pl. 6, figs. 42-44). The shape of the unspecialized cells ranges from isodiametric to elongate, and each cell may possess from four to six, straight to curved anticlinal walls. In non-veinal regions most cells have a distinctly grouped appearance, such that the epidermis can be subdivided into a series of domains, each consisting of two or more cells packed into a rectangular area, like tiles on a floor (Pl. 6, figs. 42, 43). Commonly the cells of one domain possess a markedly different orientation than the cells of adjacent domains, and occasionally the flanges which demarcate the cells within a domain are thinner than those at the boundary of two adjacent domains. This last feature suggests that each domain orginates from a single protodermal initial, since in modern flowering plants the division of an epidermal cell after growth has ceased it produces a relatively thin cuticular flange between the two daughter cells (Stace, 1965). In contrast, the cells of the veinal areas (Pl. 6, fig. 44) exhibit longitudinal alignment and lack domains. In addition, the region above

the primary vein is the only part of the upper epidermis that bears stomata (Pl. 6, fig. 44).

Surface sculpture on the upper cuticle shows some variation, ranging from smooth to striate, with many specimens having intermediate conditions (Pl. 6, fig. 45). When present, the striations are about one μm wide, subparallel except near trichome bases, and traverse cell boundaries. Internal sculpture is also variable, ranging from smooth in thin cuticles to granular in thicker ones (Pl. 6, figs. 42, 45).

Two types of hair bases are found on the upper cuticle. The first, identical to the first type found in Zone I angiosperms, consists of a heavily cutinized polygonal foot cell which is underthrust by several, often radially oriented base cells (Pl. 6, figs. 43, 47); its frequency ranges from common to rare. The second type, found in very low frequency on only a few specimens, consists of a circular trichome abscission scar that bears radiating striations from its edge (Pl. 7, fig. 48). Since it was only observed on an SEM preparation, its relationship to the underlying cells cannot be adequately determined.

Lower Cuticle--The lower epidermis varies widely in its cutinization, ranging from thin with poorly cutinized anticlinal walls to thick and possessing distinct flanges (Pl. 7, figs. 49, 50). The non-veinal regions are comprised of cells similar to those on the upper epidermis,

except that they lack the strong tendency to appear grouped. Veinal areas are well developed beneath lower order veins and are more clearly defined than corresponding regions on the upper cuticle. The zone beneath the primary vein of each lobe is composed of up to 50 longitudinal files of cells (Pl. 7, fig. 51), and regions beneath the secondary veins consist of several rows of longitudinally oriented cells that tend to be longer than cells from the interveinal regions. Tertiary and higher order veinal areas are not strongly developed, and consist of one to several rows of longitudinally oriented cells each.

Surface sculpture shows some diversity in the Brooke specimens, both within individual leaves and between leaves of the population. Most cells bear striations that average 1.2 μm in width, and many also possess one, central, partially solid papilla each (Pl. 7, figs. 52-54). In non-papillate cells the striations exhibit a tendency for subparallel orientation and are continuous between cells, but in papillate cells they radiate from the papillae and tend to terminate near the anticlinal walls. Some individual leaves completely lack papillae, but most possess a mixture of papillate and non-papillate cells (Pl. 7, figs. 52, 53) and some are even characterized by a predominance of papillae on the lower cuticle (Pl. 7, fig. 54). Internal sculpture shows similar variability, ranging from smooth to somewhat granular (Pl. 7, figs. 55, 56); this variation can be

observed between different cells of the same leaf, suggesting that it may in part be a preservational feature.

The stomatal apparatus consists of a pair of slightly sunken guard cells and two to many variably specialized neighboring cells (Pl. 7, figs. 52, 54, 58). The poles are commonly flattend to truncate, and in some stomata the lateral regions of the epidermal walls are also flattened, producing a jagged, somewhat irregular stomatal outline (Pl. 7, figs. 54, 58). The guard cells are thinly cutinized except adjacent to the stomatal pore, where the cuticle is thickened to form outer and inner stomatal ledges (Pl. 7, figs. 56, ISL; fig. 57, OSL). These ledges enclose front and back cavities of variable shape, but generally they are elongate and somewhat pointed at the poles. In addition, the back cavity is often somewhat smaller than the front cavity.

The arrangement and specialization of the neighboring cells exhibit much diversity on an individual leaf, but unlike the condition in Zone I angiosperms the lateral contact cells are almost always specialized. These and adjacent modified cells form the subsidiary cells, which are distinguishable by their smaller size, radial compression, different anticlinal wall pattern, and thinner cuticles (Pl. 7, figs. 54-56, 58; Pl. 8, fig. 59). The subsidiaries commonly bear striations which radiate from the stomata, and in strongly papillate leaves (e.g., Pl. 7,

fig. 58) they also bear papillae. The stomatal complexes on one leaf generally conform to several of the commonly recognized types. Some are paracytic, with one lateral subsidiary per guard cell (e.g., Pl. 7, fig. 54 upper stoma). A number of stomatal complexes possess three or more lateral contact cells that exhibit at least a small amount of specialization, and hence conform to the simple laterocytic type (e.g., Pl. 7, fig. 54, lower stoma) and in many stomata one or more cells adjacent to these subsidiaries also show modification, producing complex laterocytic stomata (Pl. 7, figs. 55, 58). Some stomata are surrounded by a ring of weakly specialized cells, conforming to the cyclocytic type (Pl. 7, fig. 56), and in others laterocytic stomata are embedded in a ring of weakly specialized cells. In many stomatal types the outer and inner subsidiary cells appear to be derived from the tangential division of protodermal cells near the end of development, since the tangential walls of the subsidiaries are often less cutinized than the radial walls, and in some stomata there is one papilla located over the cuticular flange which separates an outer and an inner subsidiary cell (Pl. 7, fig. 58). The outline formed by the tangential walls of the subsidiary may be smooth, but most often it is jagged, due to the angularity of the subsidiary cells themselves and/or the difference in the radial dimensions of two

adjacent subsidiaries (Pl. 7, figs. 54, 55, 58).

Two types of hair bases are found on the lower cuticle. They are both similar to hair bases from the upper cuticle, but exhibit a wider range of structural variation than their upper epidermal counterparts and tend to intergrade with a type of secretory structure restricted to the lower epidermis.

The first hair base type, found infrequently on some specimens, consists of a polygonal foot cell and several, often radially elongate base cells (Pl. 8, figs. 60-63). Unlike Zone I leaves, the size of the foot is variable, ranging from significantly smaller to much longer than the adjacent cells. The outline of the foot cell ranges from isodiametric to elongate and irregularly branched, as in Zone I forms, but the shape of the lumen is more diverse: in most foot cells it is the same as the overall outline of the cell, but in at least one the anticlinal walls are unevenly cutinized, producing a lumen that appears circular in surface view (Pl. 8, fig. 63). This latter hair base is nearly identical to the type which characterizes Platanoid #2, except that it lacks a pore and the outer cuticle is punctate. The punctate outer cuticle in many foot cells and the total absence of associated trichomes or trichome abscission scars, however, suggests that these structures may be idioblasts rather than hair bases.

The second hair base type, also found in low frequency, consists of a rounded trichome abscission scar and two or more subtending cells (Pl. 8, figs. 64-72). Because of its similarity to the radiostriate hair bases found in Zone I angiosperm leaves this structures is termed the "complex radiostriate" trichome base. The scar ranges from circular to elliptical in shape, and is formed of a ridge of cutin that bears radiating striations. In a few instances the basal cell of the hair possesses one or more cutinized protrusions that are continuous with the scar and oriented parallel to the epidermis, giving the scar a characteristic "plumed" appearance (Pl. 8, fig. 64, Pl.). The placement of the scar and the specialization of the underlying cells show a variability both within individual leaves and between different leaves, producing a series of intergrading morphotypes. In some instances two foot cells with thickened flanges bear the trichome along the zone of contact (Pl. 8, fig. 65), but in others only one of the two cells bears the trichome (Pl. 8, fig. 66) and in some hair bases the trichome may be placed over the junction of one of two specialized cells and an adjacent unspecialized cell (Pl. 8, fig. 67). Sometimes the abscission scar rests on several cells with thick cuticular flanges, which may be as large as the adjacent cells or significantly smaller than them (Pl. 8, figs. 68, 69). In still other cases the scar is subtended by cells that exhibit no substantial modification (Pl. 8, figs. 70-72). Compressed hairs are

occasionally attached to the hair bases, and in every case they are unicellular and hemispherical to elongate, with a punctate cuticle, suggesting a glandular function (Pl. 8, figs. 65, 71). This inferred function is further supported by the fact that in many of the more heavily cutinized trichomes there is a circular to oval zone of weakness in the outer cuticle which allows the central region to act as an operculum (Pl. 8, fig. 66, arrow).

In addition to these trichomes many leaves bear structures which are similar to the abaxial glands present in Zone I leaves. Each consists of a single, circular secretory cell with a thin outer cuticle and several adjacent, unmodified cells that are level with the secretory cell or underthrust it to various degrees (Pl. 8, figs. 73-77). The outer wall of the secretory cell displays substantial variation in its shape on both individual leaves and between different leaves, ranging from flat and level with the rest of the epidermis to cylindrical and strongly protruding. In the latter case the central area sometimes lacks cuticle, suggesting that the structure may represent the basal part of a glandular hair (Pl. 8, fig. 77). Occasionally the outer cuticle of the secretory cell is punctate (Pl. 8, fig. 73), making the differentiation of glands and the previously mentioned secretory trichomes difficult and somewhat arbitrary; however, these variants can generally be

distinguished from the latter by the absence of radiating striations and the only partial underthrusting of the surrounding cells.

Pinnately Compound Sapindopsis

Pinnately compound leaves with organic preservation are known from three localities in Maryland dated as upper Subzone II-B by Doyle and Hickey (1976): (1) West Brothers, near Washington, D.C., (2) Stump Neck, southwest of Washington, D.C., near the Potomac River, and (3) Red Point, at the northern end of Chesapeake Bay. Most of the materials are fragmentary, but their numerous similarities in venation and cuticle structure to whole leaves indicate that they all belong to the same complex. While there is some diversity in leaf architecture and cuticular anatomy both within and between populations, there is no clear-cut way to assign these remains to more than one taxon. Hence, the following descriptions will refer to all the materials, except when a particular characteristic is restricted to only one or two localities.

The leaflets are slightly to strongly asymmetric at the base and range from elliptic to ovate in shape, with L/W from 2 to 5 (Pl. 9, figs. 78-80, 83). When preserved the apex is acute (Pl. 9, fig. 78A) and the base ranges from cuneate to decurrent, with each leaflet possessing a distinct petiolule (Pl. 9, figs. 78B, 83). Contrary to Hickey and Doyle (1977) laminar resin glands

are not present in any of these leaves: examination of leaflets with the SEM indicates that the supposed glands are in fact epidermal eruptions of probable fungal origin (Pl. 9, fig. 84). The leaflets have brochidrodromous to eucamptodromous secondary veins that gently curve towards the apex (Pl. 9, figs. 78-83). Their number ranges from 8 to 16 and both the thickness of the secondaries relative to the primary vein and their spacing are inversely correlated with their number. Intersecondary veins are present and connect with both the secondaries and tertiaries (Pl. 9, fig. 81). The tertiary venation is reticulate and may be directed obliquely tranverse to the secondaries and/or parallel to them. The orientation of the tertiaries, which may vary between different pairs of secondary veins on the same leaf and different leaves of a population, is partially a function of their angle of origin. Tertiary veins always originate at acute angles on the primary veins and on the exmedial (basal) side of the secondaries, but vary widely in their divergence angles on the admedial (apical) side of the secondary veins. Near the margin the tertiaries generally arise at an obtuse angle, but towards the midvein their angle of origin ranges from acute to obtuse. In the first extreme the tertiaries have an ascending appearance, while in the latter they all appear to descend towards the midvein; most leaves possess a mixture of the two conditions (Pl. 9, figs. 80,81). The former situation is more common at West Brothers, while the latter is

characteristic of Red Point materials; Stump Neck leaves are intermediate in this respect. The quaternary and higher order venation is reticulate and not always well preserved. The ultimate venation was not seen.

Upper Cuticle--The upper cuticle of the pinnately compound leaves is generally as thick as in the pinnitafid leaves (Pl. 10, figs. 85-89). The cells of the upper epidermis are slightly smaller than in the Brooke materials, measuring 12-50 by 11-37 μm, but have a similar form and pattern of organization. The non-veinal cells have a mixed shape and four to six, straight or curved anticlinal walls (Pl. 10, figs. 85, 86, 88, 89). In most specimens these cells have a grouped appearance, as in the pinnatifid leaves, but this is difficult to see in a few leaves from West Brothers with predominantly isodiametric cells (Pl. 10, fig. 88). Veinal regions lack the grouped appearance of the cells and are well developed only above the primary vein. The primary veinal zone is comprised of up to 50 or more rows of loosely organized cells (Pl. 10, fig. 87). Stomata are sometimes present in this area and resemble those from the lower epidermis in most structural features. Higher order veinal regions lack stomata and consist of two or more rows of cells each.

The surface of the upper cuticle ranges from smooth to striate, as in the pinnatifid leaves (Pl. 10, figs. 85-87, 90). The striations are less than one μm wide and

resemble striations from the lower cuticle in orientation. Papillate sculpture is rare and only found in some West Brothers specimens: when present, the majority of cells on an epidermis possess papillae. In some leaves the papillae are short and consist of thickened regions in the outer cuticle (Pl. 10, fig. 88), but in others they project more strongly and are completely hollow (Pl. 10, fig. 89). Internal sculpture ranges from smooth to granular, as in the pinnatifid leaves.

The hair bases on the upper cuticle strongly resemble the two types found in the pinnatifid leaves. The first type consists of a thickened, polygonal foot cell and several scarcely modified base cells (Pl. 10, figs. 90, 91). This hair base is identical to its counterpart in pinnatifid Sapindopsis in practically all respects, including the patterns of variation present in foot cell shape, degree of base cell underthrusting, base cell orientation, and hair base distribution. The second type is a variant of the complex radiostriate hair base (Pl. 10, figs. 92-96). As in the Brooke specimens the trichome abscission scar consists of a cutinized rim on the outer cuticle surface, but often the radiating striations are absent and the shape ranges from circular (Pl. 10, figs. 92, 93) or irregularly lobed (Pl. 10, figs. 94, 95) to elongate (Pl. 10, fig. 96). Generally each trichome abscission scar is subtended by two to many base cells that exhibit

some diversity in size. At one extreme the base cells are as large as the unmodified cells (for example, Pl. 10, fig. 93), while at the other they are all significantly smaller (Pl. 10, figs. 94-97); in the latter instance the region occupied by the base cells has a similar size and shape to the trichome abscission scar. This pattern of variation in base cell size is present both on individual leaves and between different leaves in the West Brothers and Stump Neck populations, with specimens from the latter locality generally showing higher degree of base cell modification. Trichomes are attached to a few hair bases, and in all cases they are low-lying structures which are attached to the epidermis by their long axes (Pl. 10, figs. 93-95). These trichomes always possess a thin, punctate cuticle, suggesting a glandular function.

Lower Cuticle--The lower cuticle is usually as thick as the upper cuticle of the same leaf. The non-veinal cells are approximately the same size as those on the upper epidermis, measuring 10-45 by 8-37 μm, and are similar in shape and number of anticlinal walls (Pl. 10, fig. 98). Unlike the cells of the upper epidermis, however, they lack a grouped appearance and, on most leaves, have undulate anticlinal walls, with up to 5 wavelengths/side and a maximum amplitude of 6 μm. Veinal areas, as in pinnatifid Sapindopsis, are most strongly developed on the

lower cuticle. The primary veinal region of each leaflet consists of up to 100 longitudinal files of predominantly four-sided cells (Pl. 11, fig. 99). Secondary veinal regions are relatively thin and consist of up to 10 rows of four to six sided cells, which sometimes are much longer than the adjacent cells, while tertiary and higher order veinal zones are variable in their development and consist of one to several rows of cells each.

Sculptural features in the pinnately compound leaves are also very similar to those in the pinnatifid leaves. Surface sculpture ranges from strongly striate to psilate, with most leaves falling somewhere in the middle (Pl. 11, figs. 100, 101); when present, the striations measure under 1 μm wide, unlike those of the pinnatifid leaves. Papillae are known only from a few West Brothers specimens, where they occur on the majority of cells, and consist of thickenings in the outer cuticle, as on the upper leaf surface. Internal sculpture ranges from smooth in the thinner cuticles (Pl. 11, fig. 104) to somewhat granular in thicker ones (Pl. 11, fig. 102).

The stomatal apparatus is virtually identical to that seen in Sapindopsis variabilis in its essential features. The stomata are level with the epidermis to slightly sunken (Pl. 11, figs. 100, 101) and measure 13-42 by 7-25 um. The stomatal outline is elliptic, as is S. variabilis, but the poles are rounded to flattened and never truncate (Pl. 11, figs. 100, 103-105).

The cuticle of the guard cells is thin except near the stomatal pore, where it is thickened to form outer and inner stomatal ledges (Pl. 11, figs. 101, 102). The shape of the front and back cavities is generally elongate and somewhat pointed at the ends (Pl. 11, figs. 100-105).

The arrangement and specialization of the neighboring cells is essentially the same as that seen in S. variabilis, except that some stomata possess as many as four orders of specialized cells. The lateral contact cells always show some specialization, as evidenced by their similar size, radial compression, distinct anticlinal wall pattern, and cuticular thinning (Pl. 11, figs. 100-105). Often these cells bear striations that radiate from the stomata (Pl. 11, fig. 100), but in contrast to the situation in the pinnatifid leaves papillae are always absent. Polar contact cells and other cells adjacent to the contact cells often show specialization as well, but they tend to lack the thin outer cuticles characteristic of the lateral contact cells. Though some paracytic stomata are encountered (Pl. 11, fig. 103, far left stoma), the majority correspond to some form of laterocytic or cyclocytic. Some stomata are simple laterocytic (e.g., Pl. 11, fig. 100, lower stomata), but many stomata are weakly cyclocytic (Pl. 11, fig. 103, lower two stomata; fig. 105, lower right stoma) and other laterocytic stomata are embedded in a

partial to complete ring of weakly specialized cells (e.g., Pl. 11, fig. 104). While it is possible for all of these subsidiary cell patterns to exist on the same leaf, only two or three are predominant in most leaves. However, these different stomatal types are all considered part of a more general stomatal pattern, since the frequency of the different stomatal types on an individual leaf seems to show continuous variation within a population.

Two types of probable hair bases/hairs occur on the lower cuticle, which are similar to types found on the upper leaf surface. Like S. variabilis, the distinction between these two types and abaxial secretory structures is not hard and fast, and within an entire population it is common to see complete intergradation between these two classes of structures, making their distinction somewhat arbitrary. The first type of hair base consists of a polygonal, somewhat thickened foot cell and several underthrusting base cells that sometimes exhibit radial orientation (Pl. 12, fig. 106). Rare variants include larger, more highly branched polygonal cells with thin outer cuticles (Pl. 12, fig. 107) and rounded cells with very thin outer cuticles (Pl. 12, fig. 108), which closely resemble abaxial glands (cf. below). These "hair bases" (which could, in fact, represent idioblasts in at least some cases, since no attached hairs

have been found) almost always occur singly, but sometimes they are organized into clusters of two or more cells (Pl. 12, figs. 109-111, arrows). The second type of hair base is the "complex radiostriate" hair base, which shows even more structural diversity than in the pinnatifid leaves. The shape of the trichome or its abscission scar in surface view is variable, ranging from circular (Pl. 12, fig. 112), somewhat lobate (Pl. 12, fig. 113), or elliptical (Pl. 12, fig. 114, arrows) to extremely elongate (Pl. 12, figs. 115, 116), and preserved hairs are never taller than they are broad. Radiating striations range from strongly developed to almost completely absent. When the trichome is thinly cutinized the junction of its outer wall and the other epidermal cells is thickly cutinized (e.g., Pl. 12, fig. 115), but when the outer cuticle of the trichome is thick this feature is absent (Pl. 12, figs. 112, 113). Some hairs have circular to oval zones of weakness on their outer surfaces, producing opercula similar to those seen in S. variabilis (e.g. Pl. 12, fig. 113, OP). The presence of thin cuticles and/or opercula on many of these hairs suggests that at least some had a glandular function. Others have one or more heavily cutinized lateral protrusions that are wider than the striations (Pl. 12, figs. 115-117, arrows), again typical of S.

variabilis. Subtending cells show a comparable diversity in number, arrangement, and specialization. A few hairs are attached to the center of one epidermal cell: this cell is generally unmodified, but in one Red Point hair base it is smaller than the adjacent cells and has straight anticlinal walls, as in Zone I forms (Pl. 12, fig. 112). Most hairs are subtended by two or more epidermal cells which show the same variable pattern of specialization as on the upper cuticle (Pl. 12, figs. 113-116), and in a few rare instances the trichome abscission scar is elevated above the surface of the epidermis by one or two polygonal, straight walled, thinly cutinized cells (Pl. 12, figs. 118, 119). The hairs and hair bases generally occur singly, but in one specimen from Stump Neck they are also found in clusters (Pl. 12, fig. 120).

Abaxial structures with an inferred secretory function are present in many leaves. Each consists of one (rarely two) round, specialized cell(s) and several adjacent, scarcely modified cells (Pl. 13, figs. 121-125). The specialized cells have a thin outer cuticle and occasionally possess maceration-resistant contents, suggesting a secretory function (Pl. 13, fig. 123). As in the pinnatifid leaves the three-dimensional shape of the secretory cells exhibits much variation, even on an individual leaf. Some secretory cells are flat and tabular in shape (Pl. 13, figs. 122-124), but others are hemispherical or bulbous

and some are even cylindrical (Pl. 13, figs. 121, 125). Cylindrical cells often lack cuticle in their central regions, suggesting that they represent the bases of glandular hairs or stalked glands (Pl. 13, fig. 121). A few secretory cells possess opercula on their outer walls, recalling some hairs attached to "complex radiostriate" hair bases (Pl. 13, fig. 126). Each secretory cell also exhibits much variation in its position relative to the adjacent cells, as in the pinnatifid leaves. In some cases it is level with the adjacent cells (Pl. 13, figs. 121-123), but in others it is partially or completely underthrust by them (Pl. 13, figs. 124, 125). These subtending cells show little modification except for occasional radial elongation.

Finally one prostrate hair was found attached to a poorly specialized cell in one West Brothers specimen (Pl. 13, fig. 127). Little can be said about its structure since the apical regions are lacking.

The Platanoids

A number of organically preserved leaf fragments assignable to the platanoid complex occur in collections from Stump Neck. These materials possess at least one of the following fetures which are characteristic of the platanoids and their inferred relatives in the Potomac Group (cf. Hickey and Doyle, 1977): (1) palinactinodromous primary venation, (2) trilobate shape, and (3) percurrent tertiary venation, often with stitched intertertiary veins. Though only ten different leaf cuticles were studied in detail, three distinct groups can be recognized on the basis of hair base structure, presence or absence of glands, gland type, and cell size. It is difficult to determine how strongly leaf architecture correlates with cuticular anatomy, since the preservation of the materials is fragmentary, but several distinctive features of venation and margin were seen in only one or two cuticle groups. Hence, the following descriptions of leaf architecture should be considered tentative, pending the study of more complete materials.

Platanoid Type #1

Each of the four specimens from this cuticle group lacks an apex, base, and evidence of lobation. The margin is absent from the apical regions of the leaf, but it is entire near the base (Pl. 13, figs. 128, 129).

The primary venation is palinactinodromous; that is, with a central primary vein and two lateral primaries that diverge from it at slightly different points (Pl. 13, fig. 128). The lateral primaries originate well above the leaf base and each produces at least two thinner basal branches that curve away from the base to connect with the supradjacent branch (Pl. 13, fig. 129). The secondary veins are thick relative to the primaries and arise at an acute angle; the one connection observed between two adjacent secondary veins is brochidodromous. The tertiary veins are precurrent, generally branched, have a convex or sinuous shape, and arise at acute or right angles, (Pl. 13, fig. 130, T). The quaternary venation is reticulate, and as in many species of extant Platanus, there are stitched intertertiaries, at least between the primary veins (Pl. 13, fig. 130, IT). The fifth and higher orders of venation are difficult to see on the specimens.

Upper Cuticle--The upper cuticle of Platanoid Type #1 has a strong tendency to disintegrate upon maceration. When it is preserved it has a medium thickness and well-defined flanges and the cells measure 27-60 by 15-45 μm. The cells of non-veinal regions have mixed shape and four to six, curved to rarely undulate anticlinal walls, with up to one wavelength per side an an amplitude not exceeding 2.5 μm (Pl. 14, fig. 131). These cells exhibit

a tendency to appear grouped, though never as much as in most Sapindopsis specimens. The region above the primary vein was preserved in one preparation and consists of numerous rows of longitudinally aligned, elongate cells with usually four straight or curved walls each (Pl. 14, fig. 132). As in Sapindopsis, stomata are found only in this region; their structure differs from lower epidermal stomata in that the subsidiary cells always lack papillae.

Surface sculpture on the upper cuticle is psilate under light microscopy (Pl. 14, figs. 131-132). Internal sculpture is more difficult to interpret, since many areas of the cuticle appear to be partially degraded; it is tentatively considered to be smooth.

Only one hair base was found on the upper cuticle. This consists of an oval trichome abscission scar that is formed of a ridge of cutin and rests over several unmodified epidermal cells (Pl. 14, fig. 131, arrow). This hair base is identical to some variants of the complex radiostriate hair base that are found on the upper epidermis of Sapindopsis, but lacks the radiating striations that are often associated with the abscission scar.

Lower Cuticle--In contrast to the upper cuticle, the lower cuticle of Plantanoid #1 survives maceration intact. It has a medium thickness, with most cells possessing well-developed flanges, and the cells measure 21-54 by 15-30

μm. The cells of non-veinal regions resemble their counterparts on the upper epidermis in shape and number of cell sides, but differ by their curved to strongly undulate lateral walls, which have up to 4½ wavelengths per side and a maximum amplitude of 5 μm (Pl. 14, figs. 133, 134). Veinal areas exhibit greater differentiation from non-veinal zones than on the upper epidermis, and have cells with four to six, straight and slightly undulate anticlinal walls. The area beneath the primary vein consists of more than 30 longitudinal files of cells, which are more heavily cutinized than the non-veinal cells (Pl. 14, figs. 135, 136). Secondary veinal regions were not observed, but those primary tertiary and higher-order veins consist of up to 8 rows of longitudinally aligned, elongate cells that tend to be longer than the adjacent non-veinal cells.

The surface of non-veinal regions is psilate, many cells also bear one hollow, centrally-positioned papilla each (Pl. 14, figs. 133, 134). Veinal regions range from psilate to weakly striate and always lack papillae (Pl. 14, figs. 135, 136). Internal sculpture in both regions is smooth to granular.

The stomatal apparatus is very similar to that found in the pinnatifid members of Sapindopsis, consisting

of a pair of slightly sunken guard cells and contact cells which always show specialization lateral to the guard cells (Pl. 14, figs. 133, 134). The stomata range from 15-30 by 8-23 μm and are generally elliptic to elongate, with truncate poles. The guard cells are more thinly cutinized than the adjacent cells, but have prominent outer stomatal ledges that enclose more or less elongate, somewhat rounded front cavities.

Subsidiary cells can be distinguished from other cells by their generally thicker (rather than thinner) cuticles, straight or uniformly curved anticlinal walls, smaller size, and tendencies for radial compression. They show the same pattern of topographic variability as the unspecialized cells, ranging from flat to frequently papillate, and their arrangement follows the same pattern of variation as in Sapindopsis. The lateral contact cells always exhibit some specialization, while the adjacent cells may be unspecialized or modified to various degrees. Many stomatal complexes are brachyparacytic, and these have two, three, or four subsidiary cells per stoma (Pl. 14, fig. 133, upper left stoma). Simple and complex laterocytic stomata are also quite common, and the latter have a maximum of two complete orders of subsidiary cells (Pl. 14, figs. 133, 134). The extra order of subsidiary cells is commonly produced by the secondary division of the contact cells. Often one or more of the polar contact cells are also specialized, but rarely is there a complete

ring of specialized cells around a stoma.

Complex radiostriate hair bases are found on the lower cuticle. Each consists of a circular to elliptical trichome abscission scar that is subtended by one or more cells, which may be unspecialized (Pl. 14, fig. 133) or somewhat smaller than adjacent cells (Pl. 14, fig. 136, arrow). As in Sapindopsis many scars bear one or more elongate, heavily cutinized lateral protrusions, which are much wider than any associated striations and confluent with the outer cuticle surface (Pl. 14, figs. 133, 136, arrows). In regions beneath the primary veins striations are attached to the scar (Pl. 14, fig. 136), but these are absent in non-veinal areas (Pl. 14, fig. 133). Preserved hairs are sometimes attached to the hair bases. As in Sapindopsis. they are never taller than they are broad.

Intergrading with these attached hairs are large protruding cells with an inferred secretory function (Pl. 14, figs. 134, Gl, 137). Each cell has a thick, sometimes punctate outer cuticle and cylindrical to bulbous shape. The cuticle is continuous over the the bulbous cells (Pl. 14, figs. 133, 134, Gl), but often absent from the apex of cylindrical cells (Pl. 14, fig. 137). Each secretory cell is positioned at the junction of two or more unmodified cells, which underthrust it to various degrees (Pl. 14, figs. 133, 134, Gl). These secretory

cells resemble those from Sapindopsis in their positioning, both on the leaf surface and relative to the other cells. They also closely resemble the more strongly protruding secretory cells of Sapindopsis in their shape and general appearance.

Platanoid Type #2

Each of the three leaf fragments from this group lacks an apex. The lobation, base, and margin are absent from two of the specimens, but the third possesses two narrow lobes separated by a rounded sinus, a probable cuneate base, and an entire margin (Pl. 15, fig. 138). The primary venation appears to be palinactinodromous in all specimens, but differs from the other cuticular platanoids in several respects. First, in the one leaf with a preserved base the lateral primaries diverge from the base of the lamina (Pl. 15, fig. 139). Second, the lateral primaries form an angle of 45° or less in all of the leaves, and show a tendency to curve away from the mid-vein (Pl. 15, figs. 138, 141). Third, the most basal branch of each lateral primary may vary considerably in its size, ranging from nearly as thick as the source vein (Pl. 15, fig. 140) to much thinner (Pl. 15, fig. 141). The secondary veins are thin compared to those of the other planatoids, arise at acute angles, and curve towards the apex (Pl.

15, fig. 141, 2°). Their connections with other secondaries were not visible in the materials. The tertiary and higher order veins are either not preserved or else difficult to see in the specimens.

Upper Cuticle--In contrast to the condition in Platanoid #1, the upper cuticle of Platanoid #2 is strongly resistant to maceration. It has a medium thickness and prominent cuticular flanges (Pl. 15, fig. 142). The cells are significanlty smaller than in the other platanoids, measuring 9-30 by 6-21 μm, and have a mixed shape. In non-veinal regions the cells are predominantly isodiametric and have four to six straight anticlinal walls (Pl. 16, fig. 142). Veinal areas are strongly developed over the primary veins and weakly developed above the others. The primary veinal region consists of over 50 longitudinal files of four-sided cells with straight anticlinal walls (Pl. 15, fig. 144). Higher order veinal zones consist of one to several cell rows each.

The sculptural features of the upper cuticle are similar to those of Platanoid #1. Surface sculpture is psilate under both light and scanning electron microscopy in the non-veinal zones (Pl. 15, figs. 142, 143) and ranges from psilate to weakly striate in the veinal areas (Pl. 15, fig. 145). Internal sculpture is smooth to somewhat granular (Pl. 15, fig. 142).

Infrequent hairs occur on both the venal and non-veinal areas. They are unicellular, elongate and measure 3-7 μm in diameter (Pl. 15, figs. 143, 145). Different lengths of hair are preserved in macerated cuticles, suggesting that the cutinization of the hairs is variable. Each hair, attached to the epidermis by a peg base, fits into a pore of variable diameter. The adjacent cells show little modification except for heavy cutinization near the pore (Pl. 15, fig. 142, TB): this cutinization has an irregular pattern and is variable in its development on an individual leaf.

Lower-Cuticle--The lower cuticle is almost as thick as the upper cuticle from the same leaf, and most cells possess discernable flanges (Pl. 16, figs. 146-150). Non-veinal cells measure 8-24 by 5-12 μm, have a mixed shape, and possess at least four straight to gently curved anticlinal walls (Pl. 16, fig. 146). Veinal cells are predominantly four-sided and organized into rows. The cells beneath the primary veins are much larger than the other cells and are organized into numerous well-defined rows (Pl. 16, fig. 147). Cells beneath the secondary and higher order veins, in contrast, are no larger than adjacent cells and organized into fewer than 9 rows.

The sculptural features of the lower cuticle resemble those in Platanoid #1. The surface sculpture

of non-veinal cells is psilate, and many of these cells also possess one central, hollow papilla each (Pl. 16, fig. 149, arrow). Veinal cells, in contrast, lack papillae. The primary veinal region ranges from psilate to weakly striate; when present, the striations are 1 μm wide and oriented parallel to the veins (Pl. 16, figs. 147, 151). Secondary and higher order venal areas are psilate. Internal sculpture is smooth to faintly granular under SEM (Pl. 16, fig. 150).

The stomatal apparatus consists of a pair of thinly cutinized guard cells and three or more weakly specialized contact cells (Pl. 16, figs. 146, 150). The guard cells are level with the epidermis but often are embedded in the lateral contact cells (Pl. 16, fig. 146, arrow). The stomata measure 15-33 by 10-18 μm and have a broadly elliptic shape and rounded poles. As in the other platanoids, the guard cells possess outer and inner stomatal ledges, which enclose elongate front and back cavities (Pl. 16, figs. 146, 150, ISL).

The subsidiary cells are not strongly specialized, but can be distinguished from unmodified cells by their thinner cuticles, smoothly curved tangential walls, radial compression, and the absence of associated glands (Pl. 16, figs. 146, 150). Their pattern of arrangement is the same as in Sapindopsis and the other platanoids: they are always present lateral to each guard cell and commonly

are located at one or both stomatal poles. Hence the most frequent arrangement of subsidiary cells is laterocytic (Pl. 16, figs. 146, arrow, 150) but cyclocytic and types transitional between laterocytic and cyclocytic are also known. In contrast to the other platanoids brachyparacytic stomata are rare.

Two types of hair bases are found on the lower cuticle. The first consists of a small, thickened, polygonal foot cell and several adjacent, unmodified base cells (Pl. 16, fig. 148, TB); this is identical to the type found in all other Subzone II-B angiosperms. The second type is identical to the one found on the upper cuticle, but is more uniform in its construction. The pore shows less variation in width and has a circular or elliptical shape (Pl. 16, fig. 152, arrows). Many hair bases have irregularly thickened cuticle on the base cells, as on the upper epidermis, but in some the thickening is vaguely ring-shaped. Hairs are present beneath the primary vein and in non-veinal areas; and as on the upper cuticle they are variably cutinized and appear to be unicellular. (Pl. 16, fig. 151, H).

Abaxial cells with an inferred secretory function occur in high frequency on non-venal regions. Commonly they are absent from the cuticle and leave characteristic round white areas (Pl. 16, fig. 146, arrows; fig. 150, arrows), but when preserved they are hemispherical and have

a thin, minutely punctate outer cuticle (Pl. 16, fig. 154, Gl). Each secretory cell has a peg base which fits into a round to irregularly polygonal pore formed by the margins of the adjacent cells (Pl. 16, fig. 150, Gl). These secretory structures differ from those in Platanoid #1 by their smaller size and hemispherical rather than cylindrical or bulbous shape. They resemble some glands from Sapindopsis in most essential features but lack the characteristic structural diversity.

In addition to these structures secretory cells occur in the mesophyll at least one specimen (Pl. 16, fig. 153). These cells are subspherical, possess dark contents, and measure 24-27 µm in diameter. Macerated oil cells in modern angiosperms, such as those illustrated by Jähnichen (1976) for Illiciales, have contents with a similar appearance to those found in the fossil secretory cells.

Platanoid Type #3

Three specimens belong to this cuticle group, but only two are large enough to provide reliable information on leaf architecture. One possesses an obtuse apex and a lobed margin with rounded sinuses, but lacks the basal regions (Pl. 17, fig. 155). The other has the base and primary venation partially preserved, but lacks the apical regions (Pl. 17, fig. 156, 158). This specimen has a probable decurrent base and a petiole over 2 cm

long. It cannot be determined whether or not the primary venation is palinactinodromous, since only two of the primary veins are preserved. The angle between the lateral and central primary veins is approximately 30°, which is within the range measured for Platanoid #1. The lateral primary gives rise to basal branches at acute angles, but their termination cannot be seen. The secondary veins are thick relative to the primary and arise at an acute angle (Pl. 16, fig. 155). In the apical regions the secondaries are brochidodromous, but basally the secondaries may run directly into the lobes. The tertiary veins are percurrent, generally unbranched, and originate at acute to nearly right angles (Pl. 16, fig. 157, T). The quaternary venation is reticulate, and one possible stitched intertertiary vein was observed (Pl. 16, fig. 157, IT?). The fifth and higher order venation is reticulate.

Upper Cuticle--The upper cuticle of Platanoid #3 tends to fragment upon maceration. It was preserved in one preparation, and this forms the basis of the description.

The upper cuticle is of medium thickness to thin and all cells have discernable flanges (Pl. 17, figs. 159, 161). The cells measure 20-50 by 10-18 μm and have a mixed shape, and four to six, straight or curved anticlinal walls. Non-veinal cells show no one preferred orientation and have a vaguely grouped appearance (Pl. 17, figs. 159, 161). Veinal cells, in contrast, are organized into poorly

defined rows. The areas above the primary veins of 25 or more rows of cells that show longitudinal alignment (Pl. 17, figs. 160, 162). Secondary and higher-order regions have progressively fewer rows of longitudinally aligned cells.

Surface sculpture appears smooth under light microscopy, but numerous fine pits are visible under SEM (Pl. 17, fig. 160). Internal sculpture is more difficult to determine, since the cuticle tends to disintegrate upon maceration, but it appears to be granular (Pl. 17, figs. 159, 161).

Trichome bases are restricted to veinal regions on the upper cuticle. In each base the trichome is placed above the junction of two or more cells, which usually underthrust the hair completely (Pl. 17, figs. 160, 162, TB). The basal cell of the trichome is well cutinized and always preserved in macerated cuticles. It measures about 20 μm in diameter at its widest region and has the shape of a cylinder or flat-topped cone. Adjacent to each hair there is a narrow, usually weakly developed, ring-shaped zone of thickened cuticle on the base cells. The base cells are generally as large as the adjacent cells, but in a few hair bases they are significantly smaller. Among Potomac Group leaves these trichome bases most closely resemble the type present in Platanoid #1, from which they differ in the more regular positioning of the hair relative to the base cells and the more

regular cutinization of the hair.

Lower Cuticle--The lower cuticle shows greater resistance to maceration than the upper cuticle. It has well-developed flanges and ranges from medium to thin)Pl. 18, figs. 163, 164). The cells have a mixed shape and measure 15-30 by 12-30 um. The non-veinal cells have curved to undulate anticlinal walls, with up to 10 wavelengths/side and a maximum amplitude of 4 um (Pl. 18, fig. 164). Veinal cells have generally straight walls and lack undulations entirely. The region beneath the primary vein consists of more than 50 rows of cells which are always elongate except adjacent to some hairs (Pl. 18, figs. 165, 168). Secondary and higher-order veinal areas were not found in the preparations.

Surface sculpture is similar to the other platanoids. Non-veinal regions are psilate (Pl. 18, fig. 166). In contrast, veinal regions possess numerous, poorly developed striations that run parallel to the vein axis as is typical of the other platanoids (Pl. 18, fig. 169). Internal sculpture in both regions is granular under light microscopy and SEM (Pl. 18, figs. 163, 164, 172).

The stomatal apparatus is nearly identical to pinnatifid Sapindopsis and the other platanoids in its plan of construction. Each pair of guard cells is slightly sunken (Pl. 18, fig. 166) and measures 15-23 by 8-12

μm. The stomata have an elliptical shape and flattened to truncate poles (Pl. 18, figs. 163, 164). The guard cells are thinly cutinized except near the stomatal pore, where they possess well developed outer stomatal ledges. The shape of the front cavity ranges from elliptical to elongate, and the ends are always somewhat pointed (Pl. 18, fig. 163).

The subsidiary cells of Platanoid #3 are not strongly specialized, but can be distinguished from the other cells by their straight or uniformly curved anticlinal walls, smaller size, and tendencies for radial compression. In almost every stomatal complex the lateral contact cells exhibit some specialization, while the adjacent cells may be unspecialized or modified to various degrees. Many stomatal complexes are brachyparacytic (Pl. 18, fig. 164, P), and these may have up to four subsidiary cells per stoma. Simple and complex laterocytic stomata are also quite common (Pl. 18, fig. 163; fig. 164, Lc) and the latter may have a maximum of two complete orders of subsidiary cells. The extra order of subsidiary cells is commonly produced by the secondary division of one or more lateral contact cells along a tangential plane (Pl. 18, fig. 164, Lc). In some stomata one or more of the polar contact cells are also specialized, but rarely is there a complete ring of specialized cells around a stoma; thus, these stomata

are usually transitional between laterocytic and cyclocytic types (Pl. 18, fig. 164, T).

The hair bases from the lower cuticle strongly resemble those of the upper cuticle. Hair bases from veinal regions resemble those from the upper epidermis in all respects except that the range of variation in base cell size is greater: at one extreme the base cells are as large as the adjacent cells (Pl. 18, fig. 167), while at the other each hair is subtended by numerous base cells which are minute compared to the other ones (Pl. 18, fig. 168, arrows). This latter case resembles the situation found in some veinal hair bases from Platanoid #1, except that the positioning of the hair is much less variable, such that the junction of two cells or two cell rows always passes underneath the center of each hair (Pl. 18, fig. 168, arrows). Non-veinal hair bases are more distinct than those on the upper cuticle around the hair-base cell junction and the base cells tend to be radially elongate (Pl. 18, figs. 170, 172).

New Serrate, Red Point

One leaf fragment belonging to a new serrate leaf type was collected in 1972 from Red Point (Pl. 19, fig. 173). This fossil measures 5 cm long by 1.5 cm wide and represents the basal portion of a simple leaf. The margin is serrate, with numerous straight-convex (B-1) teeth, and the base is decurrent. The primary vein is

straight and the secondary and higher order venation is obscure.

Upper Cuticle--The upper cuticle fragments readily upon maceration. Only one small piece was found in the preparation and this forms the basis for the description.

The upper cuticle is thin and possesses well developed cuticular flanges (Pl. 19, fig. 174). The cells measure 32-50 by 17-32 μm and have an elongate shape. They possess four to six, straight or curved anticlinal walls and show no one preferred orientation, though adjacent cells exhibit a tendency for alignment. The one preserved piece of cuticle appears to have come from a non-veinal region.

Surface sculpture on the upper cuticle is generally smooth. Internal sculpture appears smooth under light microscopy.

Lower Cuticle-In contrast, the lower cuticle is strongly resistant to maceration (Pl. 19, fig. 175). Unlike the situation in all other Potomac Group angiosperms every wall of the epidermal cells possesses a cuticle. The cuticle is moderately developed over the outer and anticlinal walls, but it is thin over the inner walls and can only be recognized in light microscopy by its wrinkled appearance (Pl. 17, fig. 176, IC). The cells measure 20-38 by 18-28 um in surface view and have a mixed shape. Non-veinal cells generally have six or seven anticlinal walls

and a random orientation (Pl. 19, fig. 175). Veinal regions are found only beneath the primary and secondary veins. The primary veinal zone consists of mostly elongate, four-sided cells with straight anticlinal walls that are organized into at least 15 clear rows (Pl. 19, fig. 177). Secondary veinal regions are no more than 4 cells wide and consist of cells that are weakly organized into rows (Pl. 19, fig. 178). These cells resemble those from non-veinal regions in most respects, but differ in their pattern of surface sculpture.

Surface sculpture consists of striations and papillae. In non-veinal regions each cell possesses one large, hollow, central papilla and numerous fine striations that radiate from its summit (Pl. 19, figs. 175, 179). In contrast, the veinal areas are predominantly non-papillate and possess striations that exhibit subparallel orientation (Pl. 19, figs. 177; 178). The primary veinal region possesses a few papillate cells. These papillae are lower than those from the non-veinal cells and often consist of a region of thickened cuticle in the center of each cell. Striations are present on the papillate cells, but exhibit subparallel orientation like those on the other veinal cells. Internal sculpture is uniform in all regions, appearing smooth under light microscopy.

The stomatal complex belongs to a distinctive type found in no other Potomac Group angiosperm leaf. Each stoma is level with the epidermis and surrounded by numerous cells with strongly overarching papillae (Pl. 19, figs. 175, 179, 180, 182). The stomata range from 20 to 38 μm long by 18 to 28 μm wide, and like other Potomac Group angiosperms have thinly cutinized guard cell walls except near the stomatal pore. Unlike the guard cells in these other angiosperms, however, the guard cells possess maceration-resistant lamellae but lack stomatal ledges entirely. The lamellae are thick, crescent-shaped, and always preserved in the outer guard cell walls (Pl. 19, fig. 180). Many stomata also possess a pair of identical lamellae on their inner walls, which may be laterally displaced due to compression after fossilization (Pl. 19, fig. 181).

The contact cells resemble non-veinal cells in their size, shape, and pattern of surface sculpture, but may be somewhat smaller in many stomata (Pl. 19, fig. 182). Their most distinctive feature is the possession of papillae that always strongly overarch the guard cells (Pl. 19, figs. 175, 179). This stomatal type is tentatively classified as weakly cyclocytic, since the contact cells all exhibit the same degree of specialization relative to the adjacent cells.

Rare hair bases are present on both the veinal

and non-veinal regions. These are identical to the type found in most major leaf groups, which consists of a small, thickened foot cell and several scarcely modified base cells (Pl. 19, figs. 182, 183). The foot cell is polygonal and ranges from isodiametric to branched. In rare instances the basal portion of a hair is attached to the foot cell (Pl. 19, fig. 184). The base cells vary in their degree of underthrusting, as in other Potomac Group angiosperms. The distribution of these hair bases is sporadic, with many areas possessing clusters of two or more (Pl. 19, fig. 182) and others lacking them entirely (Pl. 19, fig. 175).

Populophyllum reniforme Fontaine

Many leaves assignable to Populophyllum reniforme Fontaine are known from the Bank near Brooke locality. A number of specimens show good organic preservation, and 8 of them were chosen for cuticular study. The majority of remains are in a fragmentary state, but their strong similarities to whole leaves in venation, marginal configuration, and cuticular anatomy indicate that they all belong to the same taxon. The leaves have an orbiculate shape and range from 3.2 to over 6 cm long by 3.6 to 7 cm wide. The margin is entire or weakly crenulate (Pl. 20, fig. 185, arrow) and the base varies from shallow to deeply cordate (Pl. 20 figs. 186-188). The primary venation is actinodromous, with seven

primary veins that originate from the same point at the leaf base (Pl. 20, fig. 188). The course of the primaries is straight at the base, but often becomes sinuous or slightly zig zag towards the margin. The central primary vein extends to the apex and gives off four or fewer pairs of secondary veins at acute angles. The lateral primaries and the secondary veins bifurcate and anastomose repeatedly to form two or more sets of intramarginal loops (Pl. 20, fig. 189). The tertiary and quaternary veins are difficult to distinguish from one another and are organized in a reticulate pattern (Pl. 20, fig. 189). Fifth and higher order veins appear to be random.

Upper Cuticle--The upper cuticle of Populophyllum is thin and difficult to prepare, but possesses well-defined flanges (Pl. 20, figs. 190, 191). Non-veinal cells have a mixed shape and are large compared to those from other Subzone II-B angiosperm leaves, measuring 26-80 by 24-42 μm. The cells possess from four to many, straight to undulate anticlinal walls; the degree of wall curvature tends to vary between specimens and undulate walls have a maximum frequency of 2½ wavelengths per side and maximum amplitude of 4 μm. Not uncommonly, the cells have a grouped appearance (Pl. 29, fig. 190), but this grouping is not as strong as that seen in some specimens of Sapindopsis. Veinal cells are

generally elongate, have a wall pattern similar to non-veinal cells, and are organized into two or more rows of longitudinally oriented cells, which generally lack a grouped appearance (Pl. 20, fig. 191).

Surface sculpture on the upper cuticle is extremely simple, being predominantly smooth. Internal sculpture, in contrast, is rather complex (Pl. 20, fig. 192). The central area of each cell has a smooth to minutely pitted inner cuticle, but the region adjacent to the flanges possesses a complex system of chambers that open only into the inner cuticle surface (alveolar sculpture). In light microscopy the chambers (or alveoli) appear as dots, but under SEM they can be seen to have a more irregular shape and anastomose among themselves. This consistent pattern of internal sculpture sets Populophyllum apart from all other Subzone II-B angiosperm leaf cuticles examined in this study.

Hair bases are present on the upper cuticle. Each consists of a small, thickened, polygonal foot cell and several under thrusting base cells which, as in Sapindopsis, range from unmodified to radially oriented (Pl. 20, fig. 193).

Stomata are found on the upper epidermis of one specimen. They are always much less frequent than on the lower epidermis and are identical to lower epidermal stomata in their size and structure.

Lower Cuticle--The lower cuticle is generally thinner than the upper cuticle, with most cells possessing discernable flanges (Pl. 20, fig. 194). The cells of the non-veinal regions closely resemble those from the upper epidermis in most respects, including size, shape, number of walls, wall contour, and in having a slight tendency to appear grouped. Veinal areas on the lower epidermis also exhibit little differentiation from the upper epidermal veinal regions, and consist of two to many rows of longitudinally aligned cells (Pl. 21, fig. 195). Surface sculpture, internal sculpture, and the structure and frequency of hair bases are all similar to those of the upper cuticle.

The stomata are small relative to the neighboring cells (Pl. 20, fig. 194). The stomata measure 29-45 by 20-30 μm, have an elliptical shape, and often are flattened at the poles (Pl. 21, fig. 198). The guard cell walls are more thinly cutinized than those of unspecialized cells, except adjacent to the stomatal pore, where they form outer and inner stomatal ledges (Pl. 21, fig. 196). As in other Subzone II-B angiosperms the front and back cavities have an elongate, somewhat variable shape. The guard cells are level with the other epidermal cells, but often are embedded in the contact cells (e.g., Pl. 21, fig. 196, arrows), producing the false impression of paracytic stomata (Pl. 21, fig. 198).

The neighboring cells of the stomatal complex show a marked similarity to unspecialized cells in their cuticle thickness, form, and sculptural patterns, being distinguishable only by their position and, in many cases, somewhat smaller size (Pl. 21, figs. 197, 198). Most stomatal complexes are anomocytic, but some possess small contact cells which appear to be derived from the oblique division of a subsidiary cell initial, producing stomata that might be classified as weakly monocyclic (Pl. 21, fig. 197, lower right stoma). This feature of the stomatal complex has only been observed in Populophyllum and serves to distinguish it from the other angiosperm groups examined in this study.

Another characteristic feature of Populophyllum is the presence of an irregularly shaped cuticle layer beneath the stomata (Pl. 21, fig. 198). The exact morphological nature of this layer remains in doubt, but it is tentatively interpreted either as a partially cutinized substomatal chamber or as a cutinized hypodermis that has been torn away from the cuticle in areas between the stomata.

Menispermites potomacensis Berry

Several organically preserved specimens were collected from Stump Neck that possess a combination of leaf architectural features restricted to Menispermites potomacensis Berry. Of these remains only one leaf fragment yielded preparable cuticle. This fragment measures 4.5 cm long by 5 cm wide and represents the basal portion

of a simple leaf (Pl. 21, fig. 199). The base is decurrent and flares outwards on one side to form a shallow lobe. The margin is poorly preserved but appears to be shallowly lobate, as is typical of M. potomacensis. The primary venation is acrodromous, with a central primary vein and 3 pairs of lateral primaries that are of equal thickness. These lateral primaries flare out from near the leaf base and branch near the margin to form at least one order of brochidodromous loops. No secondary veins were observed. The tertiary and higher order venation is obscure and difficult to interpret.

Upper Cuticle--The upper cuticle is thin and lacks well-developed flanges, making the cell outlines difficult to see without photographic enhancement. Non-veinal cells are isodiametric, measure 18-38 by 15-30 μm, and have four or more straight anticlinal walls (Pl. 21, fig. 200). Veinal areas were found only above the primary veins, perhaps due to the high fragmentation that occurred during maceration. These regions consist of 10 or more longitudinal files of elongate cells with four, straight or curved anticlinal walls (Pl. 21, fig. 201). The cells of the primary veinal areas are almost always smaller than non-veinal cells.

Surface sculpture is psilate in both the veinal and non-veinal regions. Internal sculpture is more difficult to ascertain, since the cuticle has a somewhat degraded appearance; it is tentatively interpreted as smooth.

Lower Cuticle--The lower epidermis is as thinly cutinized as the upper epidermis. Non-veinal cells are significantly smaller than those of the upper cuticle and measure 18-25 by 15-18 μm (Pl. 21, fig. 202). They are further differentiated from upper epidermal cells by their mixed shape and their undulate anticlinal walls, which have up to three wavelenghts/side and a maximum amplitude of two um. Veinal areas show greater development on the lower epidermis, and consist of longitudinal files of four to five sided, elongate cells. The region beneath the primary vein is over 25 cells wide (Pl. 21, fig. 203), and two higher order veinal areas were observed that are six and nine cells wide respectively.

Surface sculpture on both the veinal and non-veinal regions is psilate, as on the upper cuticle. Internal sculpture is difficult to interpret, since the lower cuticle also appears somewhat degraded.

Stomata are confined to non-veinal areas and the boundaries of veinal and non-veinal regions. Each stomatal complex consists of one guard cell pair and three to five variously specialized contact cells (Pl. 21, figs. 202, 204-206). The stomata are level with the epidermis and are the smallest of any Potomac Group angiosperm, measuring 12-18 by 5-15 μm. The guard cells have relatively well-cutinized epidermal walls and prominent outer stomatal ledges, which enclose minute fron cavities.

(Pl. 21, figs. 204-206). The stomata are mostly elliptical in outline, rarely circular or elongate, and have rounded to flattened poles.

Each stomatal complex possesses three to five contact cells with various degrees of specialization. In many stomata the contact cells exhibit no appreciable modification (Pl. 21, fig. 205), and the stomatal apparatus conforms to the anomocytic type as defined by Metcalfe and Chalk (1950). The majority of stomata, however, either possess one specialized cell lateral to the stoma (Pl. 21, fig. 206, arrow), conforming to the hemiparacytic type, or else possess one specialized cell adjacent to each guard cell (Pl. 21, fig. 204, arrows), conforming to the brachyparacytic type. Menispermites potomacensis appears to lack the laterocytic and weakly cyclocytic stomata that would also be found on a Zone I leaf, but the poor preservation of the cuticle makes this conclusion tentative.

One hair base is known from the lower cuticle. This consists of a small, thickened, polygonal foot cell which is underthrust by the adjacent, unmodified base cells (Pl. 21, fig. 203, TB). It is identical to the type found in all other Subzone II-B leaf groups.

Diversity of Structural Features

When compared with the 12 angiospermous cuticle types from Zone I, the 8 types known from Subzone II-B show many new features in addition to some found in the earlier

leaves. These younger leaves also exhibit a higher overall structural diversity, which is still low compared to that of Tertiary and extant angiosperms. This increased diversity is particularly prominent in the construction of the stomatal apparatus, trichome bases, and abaxial glands, which are features that tend to show low variability at the generic level in extant flowering plants (Stace, 1965). The new features found in Subzone II-B angiosperm cuticles can also be related to structures found in earlier or contemporaneous leaves, suggesting their relatively recent evolutionary origin.

Two distinct patterns of guard cell thickenings are present in Subzone II-B leaves, as opposed to one type in Zone I. Zone I guard cells possess both outer stomatal ledges and maceration-resistant lamellae, at least in the whole leaves (Pl. 2, fig. 15). Subzone II-B stomata, in contrast, possess either outer stomatal ledges or maceration-resistant lamellae, but never both. Maceration-resistant lamellae occur only in the new serrate leaf from Red Point (Pl. 19, figs. 180, 181), while all other leaf groups have outer stomatal ledges (e.g., Pl. 11, fig. 100). The former pattern of guard cell thickenings is typical of many extant Winteraceae and Magnoliaceae (Baranova, 1972; Bongers, 1973), while the latter is found in many non-magnoliid dicots, which almost always lack maceration-resistant lamellae in their guard cells (Baranova, 1972; personal observations).

Four major patterns of neighboring cell arrangement and specialization are present in the stomata of Subzone II-B angiosperms, as opposed to only one in Zone I. Each plan of organization is also less variable than the Zone I condition in contact cell arrangement and/or specialization. The first, found in Menispermites potomacensis, has a lower variability in the arrangement of specialized contact cells. Some stomata lack specialized contact cells, conforming to the anomocytic type, but others on the same leaf possess one or more lateral specialized cell each, conforming to the hemiparacytic and paracytic types (Pl. 21, figs. 204-206). Conspicuously absent are the laterocytic and weakly cyclocytic stomata that would also be present on a leaf from Zone I. The new serrate leaf from Red Point posses the second major stomatal pattern, which exhibits a low diversity in both neighboring cell arrangement and specialization. Each stomatal complex has a ring of 6 or more subsidiary cells that are differentiated from the adjacent cells by their slightly smaller size and papillae which always overarch the guard cells (Pl. 19, figs. 175, 179). The classification of these stomata as either anomocytic or cyclocytic is somewhat arbitrary, but in any case they have a uniform plan of construction. The third stomatal type, found in Populophyllum reniforme, more or less conforms to the anomocytic type as defined by Metcalfe and Clarke (1950). In this leaf group the contact cells form a ring around each stoma

and exhibit little modification except for some radial elongation and an occasional cell that is smaller than the others (Pl. 20, fig. 194; Pl. 21, fig. 197). The fourth and most widespread plan of stomatal organization is found in Sapindopsis and the "platanoids". In these stomata the lateral contact cells are almost always specialized, but show some variation on an individual leaf in their number and arrangement (Pl. 5, figs. 36, 37). The polar contact cells and other cells associated with the stomata may also exhibit modification, but vary considerably in both their arrangement and degree of specialization. This variation is responsible for the diversity seen on an individual leaf in mature stomatal types, which can possess up to four orders of specialized cells in some specimens of pinnately compound Sapindopsis. Despite the diversity of stomatal types produced by this plan, however, the lateral contact cells are always specialized, unlike the situation in Zone I stomata. When compared to extant flowering plants, Subzone II-B leaves still exhibit a low diversity in the total number of even conventionally recognized stomatal types: conspicuously absent are such types as diacytic, parallelocytic, anisocytic, and helicocytic, which characterize many groups of extant dicots (Metcalfe and Chalk, 1950; Stace, 1965; Payne, 1970).

The trichome bases of Subzone II-B leaves also possess four distinct plans of organization, as opposed to three in Zone I forms. The most systematically widespread

hair base, found in every major leaf complex, consists of a small, thickened, polygonal foot cells and several underthrusting base cells (e.g., Pl. 18, figs. 90, 91). This type is identical to one of the Zone I forms except that the base cells often show radial orientation.

The second hair base type, termed the complex radiostriate base, is found in Sapindopsis and Platanoid #1. Like the radiostriate hair base from Zone I many representatives of this type have a trichome abscission scar with radiating striations (e.g., Pl. 12, fig. 112). However, it is more variable than the Zone I form and exhibits several important differences. First the scar often lacks radiating striations and can have a variable shape, ranging from circular to elongate. Second, the basal portion of some trichomes possesses strongly cutinized outgrowths oriented parallel to the epidermal surface, giving the abcission scar a characteristic "plumed" appearance. Finally, the base cells show a wide range of variation in their specialization and placement relative to the abscission scar. The third hair base type, restricted to Platanoid #2, consists of a circular to oval pore and several base cells that underthrust it (Pl. 16, fig. 152). The base cells show a variable pattern of cuticular thickening in their outer walls adjacent to the pore: many hair bases have irregularly shaped thickening while others have a poorly defined ring of thickened cuticle.

Hairs are infrequently preserved in macerated

cuticles and are in all cases uniseriate. These hairs appear to be variably cutinized, since in some hair bases none of the trichome is preserved, yet in others large parts of the hair remain intact (Pl. 15, fig. 153; Pl. 16, fig. 152). The fourth type is restricted to Platanoid #3 (Pl. 18, figs. 167-172). As in the complex radiostriate hair base there is a ring of thickened cuticle near the base of the hair and (in veinal regions) the tendency for base cells to be smaller than other cells. However, the hair consists of at least two cells, the basal which is always well-cutinized and has the shape of a truncate cone. Its positioning relative to the base cells is also much more regular: the hair is almost always positioned directly over the junction of two or more cells. Compared to Zone I forms the trichomes and trichome bases of Subzone II-B are more diverse, but relative to Tertiary and extant dicots they still show a low complexity and structural diversity. Conspicuously absent are such types as cutinized peltate scales, multiseriate hairs, and hair bases with a uniform pattern of strong base cell specialization, which are found in many groups of fossil and modern angiosperms (Metcalfe and Chalk, 1950; Stace, 1965; Litke, 1966; Baranova, 1972; Dilcher, 1974).

Two major types of abaxial secretory structures are present in Subzone II-B leaves, as opposed to only one in Zone I leaves. Unlike the glands in Zone I, Sub-Zone II-B secretory structures intergrade with certain hair base types, such as the complex radiostriate hair base. The first type, found in both types of Sapindopsis, consists of a round secretory cell with a thin outer cuticle and several associated cells that underthrust the secretory cell to various degrees (Pl. 13, figs. 121-125). Unlike comparable structures from Zone I, the secretory cells in Sapindopsis show a wide array of three dimensional shapes, ranging from tubular and level with the epidermis to bulbous or cylindrical and strongly protruding. The second type of abaxial secretory structure is found in Platanoids #1 and #2. As in Sapindopsis and Zone I leaves, these glands have a single rounded secretory cell with a thin outer cuticle. Unlike the secretory cells of the other leaf groups, however, they always have protruding outer walls and the base cells always underthrust the secretory cell (Pl. 14, figs. 134, GL, 137; Pl. 10, figs. 150, 154, Gl). Compared to Zone I leaves Subzone II-B angiosperms possess a larger number of secretory structures, but compared to modern forms their diversity and structural complexity are still low. Conspicuously absent is the diverse array of multi-cellular secretory structures found in many groups of extant dicots (Metcalfe and Chalk, 1950).

Affinities of Subzone II-B Dicot Leaves

In addition to showing that Subzone II-B dicot leaves possess a higher structural diversity than their Zone I counterparts, cuticular anatomy also provides evidence on the affinitites of several different leaf groups with each other. First, cuticular anatomy is highly consistent with the idea that the pinnately compound leaves of upper Subzone II-B are derived from the complex of pinnatifid leaves present in middle Subzone II-B (Doyle and Hickey, 1976); since the two groups are virtually identical in their cuticular features. In both groups the stomata are slightly sunken and the patterns of subsidiary cell arrangement and specialization are practically identical, including the tendency for the lateral contact cells to have thinner cuticle than any of the other associated cells. The same two classes of trichomes/trichome bases are present in both leaf types, and on the lower cuticle they intergrade with inferred secretory structures. The secretory structures are similar in both leaf groups and exhibit the same pattern of variation in a population ranging from level with the leaf surface to strongly protruding and underthrust by the adjacent cells. Surface sculpture in both groups is striate and the striations tend to have a subparallel orientation in non-papillate leaves, except where they radiate from the stomata. The

differences between the two groups tend to be a matter of degree rather than kind: the stomatal poles tend to be more flattened in the pinnatifid leaves, the size of striations and degree of anticlinal wall undulation on the lower epidermis differ between the two groups, and the maximum number of orders of specialized cells associated with the stomata is higher in the pinnately compound leaves.

Cuticular anatomy is also consistent with the idea of a relationship between these groups of pinnatifid and pinnately compound leaves (hereafter referred to as Sapindopsis) and members of the platanoid complex (Hickey and Doyle, 1977). Close affinities have been inferred on the basis of tendency for the terminal leaflets of Sapindopsis to resemble platanoid leaves and on the association of the two leaf groups with the same inflorescence type. Cuticular anatomy reveals a pattern of overlapping character distributions in many features that ties the platanoids together with Sapindopsis, particularly the pinnatifid members of the group. Both complexes share the same pattern of subsidiary cell arrangement and specialization found in no other Subzone II-B dicots, and in addition Platanoids #1 and #3 possess elliptic, somewhat sunken stomata with flattened to truncate poles, like pinnatifid Sapindopsis. Complex radiostriate hair bases are found in Sapindopsis and Platanoid #1. In addition, the characteristic ring-

shaped cuticular thickening at the base of the hair and the tendency for the base cells in veinal regions to be smaller than the adjacent cells relate this hair base to the type found in Platanoid #3. Interestingly, Platanoids #1 and #3 are more similar to each other in features of their leaf architecture than they are to any other Subzone II-B group. Platanoids #1 and #2 possess isolated secretory cells restricted to the lower epidermis, which in Platanoid #1 show a strong tendency to intergrade with complex radiostriate hair bases, as in Sapindopsis. These secretory cells are less variable in their shape and positioning relative to other cells than those in Sapindopsis and tend to resemble the more strongly protruding ones in the latter group. Finally, the characteristic hair base found in Platanoid #2, with its circular pore and irregularly thickened outer cuticle, strongly resembles a variant of one hair base type present in pinnatifid Sapindopsis.

The other three leaf groups possess cuticular features that are either found in no other leaf group or else are so widespread systematically as to be of little use in evaluating relationships. Populophyllum reniforme has a type of trichome base found in every major Subzone II-B leaf complex and several features unique to itself, which include predominantly anomocytic stomata, large epidermal cells, and a distinctive pattern of internal sculpture. Menispermites potomacensis, referred to the complex of actinodromous leaves which

includes Populophyllum (Hickey and Doyle, 1977), stands apart from Populophyllum and other leaf groups by its small cells, minute stomata, and a pattern of subsidiary cell arrangement that ranges from anomocytic to hemiparacytic and paracytic. Finally, the new serrate leaf from Red Point is unique in possessing maceration-resistant lamellae in its guard cells while lacking stomatal ledges entirely, in its ring of subsidiary cells which all bear strongly overarching papillae, and in the cutinization of the inner walls of the epidermal cells. The isolation of each of these leaf groups from all others in features of cuticular anatomy suggests that they may all be distantly related to each other and to members of the Sapindopsis - Platanoid group.

Cuticular anatomy also provides new evidence on the affinities of some Subzone II-B dicots to modern forms. First, the numerous similarities seen between Platanoid #3 and extant Platanaceae strongly support Hickey and Doyle's (1977) suggestion that the Potomac Group platanoids are related to the Hamamelidales. Platanoid #3 closely resembles modern Platanus in its stomatal pattern and the details of its hair base construction, features which together set the latter apart from related families such as Hamamelidaceae and Myrothamnaceae. The stomata conform to the general Sapindopsis - Platanoid pattern, in which the lateral contact cells always exhibit some specialization, but the other adjacent cells range from unspecialized to distinctly modified (Pl. 22, fig. 209). Each

hairbase consists of a single foot cell that is positioned over the junction of two or more base cells (Pl. 18, figs. 167-172; Pl. 22, figs. 207, 208). Each foot cell has the shape of a truncate cone, with its widest portion at the surface of the epidermis, and at the junction of the foot and underlying base cells there is often a ring of thickened cuticle (Pl. 18, fig. 170, arrow; Pl. 22, fig. 207, arrow). The base cells show some variation in the veinal areas, ranging from as large as the adjacent cells to distinctly smaller (Pl. 18, fig. 168, arrow; Pl. 22, figs. 207, 208). These similarities, along with the overlapping character distributions that relate Platanoid #3 to the other platanoids support the concept that the Potomac Group platanoids are representatives of the complex that gave rise to the modern Platanaceae. This does not mean that all the features of the modern family had evolved by Subzone II-B: Platanoid #3 differs from all extant Platanaceae by its smaller stomata (15-23 microns long as opposed to an average of over 40 microns), strongly flattened stomatal poles, lateral contact cells with well-defined flanges along the tangential walls, and lack of striations on the non-veinal cells.

Cuticular anatomy is also consistent with the proposed relationship of Sapindopsis and the extant subclass Rosidae (Hickey and Doyle, 1977), but knowledge of cuticle structure in extant dicots is not yet extensive enough for this to be considered certain. Sapindopsis shows many

similarities to the extant Cunoniaceae and Sapindaceae in stomatal anatomy and hair base construction. The stomata of both families possess lateral contact cells that are commonly smaller than the adjacent cells and that show pronounced cuticular thinning adjacent to the guard cells (Pl. 22, figs. 210, 213). The cells adjacent to the lateral contact cells are often small as well, producing stomata with up to two orders of specialized cells. Hair base construction in Sapindaceae is different from Sapindopsis, but certain Cunoniaceae strongly resemble the latter group, particularly Weimannia crenata. The abaxial hair bases of W. crenata conform to the same patterns of construction as Sapindopsis, including the same patterns of variation in foot cell shape and size (compare Pl. 22, fig. 211 with Pl. 8, fig. 62 and Pl. 22, fig. 212 with Pl. 12, fig. 108).

The other groups of Subzone II-B dicots cannot be confidently related to extant angiosperms on the basis of cuticle structure. Further systematic studies of extant dicot leaf cuticles will be undertaken to better determine their relationship to modern forms.

Cuticular Evolution in Early Angiosperms

A comparison of Subzone II-B angiosperm leaves with Zone I forms suggests several evolutionary trends in the leaf cuticles. These trends have been inferred by using the order of appearance in the fossil record to determine the polarity of a morphocline. This method was chosen for three reasons. First, it is independent of the presumed

modern affinities of the fossil forms and can be used to test hypotheses on the relative advancement of modern taxa. Second, this method can be used to determine whether or not the informal leaf groups used by Doyle and Hickey (1976) and Hickey and Doyle (1977) are polyphyletic since it is independent of the proposed classification. Third, since polarity is determined independently of other characters, it avoids the pitfalls of character correlation, where an advanced character can easily be misinterpreted as primitive because it occurs in a primitive group. The use of stratigraphic data makes the assumption that the fossil record is good enough to provide the correct sequence of character state changes within a group, but does not assume that the record will provide the ancestors of all taxa. This means that: (1) there is no factor, such as a facies shift or climatic change, that biases the time of occurence of an organism in the fossil records and (2) the odds of fossilization for the different groups of organisms are roughly equal. The first assumption appears to be supported by published accounts (e.g., Glasser, 1969) and unpublished observations of Potomac Group sedimentology, which imply the persistence of fluvial conditions from Zone I through Subzone II-B in the outcrop belt. The second assumption may be less valid, since Zone I angiosperm leaves are rare compared to Subzone II-B types. However, this problem is at least partially offset by the intensive search for

angiospermous dispersed cuticle from Zone I, since 12 cuticle types are known from this time as opposed to only 8 in Subzone II-B.

The only characters used in this analysis were those considered to be morphologically equivalent; that is, homologous in the sense of Remane (1952) and Kaplan (1977). Two characters were considered equivalent if they met at least one of three criteria: (1) equivalent position in a common ground plan; (2) special qualities, or (3) connection through intermediate structures. Equivalent position refers to the position on the leaf surface, which in this study was either on both sides of the leaf or restricted to the abaxial epidermis. Since two or more phenetically distinct structural types could be considered equivalent on the basis of position, the subcriterion of overall resemblance was also used, with structures in Zone I angiosperm leaves serving as points of organization. Special qualities refers to properties of a structure that are independent of position; for a cuticular example, a functional stoma in flowering plants always consists of two guard cells, no matter what its position. Connection through intermediate structures refers to the connection of two unlike structures by one or more intermediate forms, which can be found on the same organ (in this case the leaf), within members of a population or cuticle group, or between different leaf/cuticle groups. This method proved the most valuable of the three for establishing

structural equivalencies.

Proposed Evolutionary Trends

1. (a) Outer stomatal ledges present on guard cells
   (b) Outer stomatal ledges absent.

All Zone I angiosperm leaves possess outer stomatal ledges, which in many groups are associated with maceration-resistant lamellae. Subzone II-B angiosperms all possess outer stomatal ledges, except for a new serrate form from Red Point, which has well-developed lamellae but lacks stomatal ledges entirely. The later occurrence of the ledgeless condition and its restriction to one leaf group are both consistent with the concept that it represents an advancement within the dicots. However, the fact that this group is known from only one specimen suggests that the trait may have arisen much earlier. Dispersed cuticle studies should be undertaken to determine more accurately the first time of appearance for this character.

2. (a) Guard cell lamellae present (b) Guard cell lamellae absent.

The majority of dicot leaves in Zone I possess maceration-resistant lamellae while they are absent among Subzone II-B forms except for the new Serrate at Red Point. The decreased percentage of taxa with guard cell lamellae in Subzone II-B is consistent with the trend proposed by Baranova (1972) on the basis of comparative anatomy in extant Magnoliidae.

3. (a) Zone I pattern of stomatal variation (b) The four Subzone II-B patterns of variation in neighboring cell arrangement and specialization.

As discussed in Chapter IV Subzone II-B angiosperm stomata differ from their Zone I counterparts by having a lower variation in neighboring cell arrangement and specialization, yet the range in conventionally recognized stomatal types in the angiosperm element is similar to that seen on a Zone I leaf. As a result each of the four Subzone II-B patterns seen in this study is inferred to be independently derived from Zone I pattern by a decrease in stomatal variation on an individual leaf.

4. (a) Radiostriate hair base (b) Complex radiostriate hair base (c) Platanoid #3 type of hair base.

Zone I leaves possess three types of hair bases. Two are similar to each other in that each possesses a foot cell that is strongly cutinized on at least one wall. The radiostriate hair base lacks the heavily cutinized foot and has radiating striations from the base of the hair, unlike the others. It is most similar to the complex radiostriate hair base, found in Sapindopsis and Platanoid #1. The complex radiostriate hair base shows a higher variation in the structure of the scar, its positioning relative to the base cells, and the number and specialization of the base cells. While many of these hair bases bear little resemblance to the radiostriate type, they are connected by a series of intermediate structures to forms that strongly resemble the radiostriate type. The Platanoid

#3 type is likewise dissimilar to most complex radiostriate hair bases, but some of the latter approach it in the features of hair positioning, base cell modification, and shape of the cuticular thickening at the trichome base cell junction. The radiostriate type is the oldest, while the most divergent (and the inferred intermediate) are first seen in younger sediments.

5. (a) Abaxial secretory structures flat with epidermis
   (b) Abaxial secretory structures ranging from flat to protruding.
   (c) Abaxial secretory structures always protruding from epidermal surface.

Potomac Group angiosperm leaves possess a wide range of variation in the structure of their abaxial secretory cells. In Zone I they are all flat with the surface of the epidermis, while in Subzone II-B they span the full range of variation. In Sapindopsis this diversity can be seen within a population or even on an individual leaf. In contrast, the secretory cells in Platanoid #1 and #2 always protrude from the surface of the epidermis. One end of the series is found in Zone I, the other (and the intermediate state) are first seen in Subzone II-B.

6. (a) Highly distinct abaxial hair bases and secretory structures. (b) Intergradation of these two structural types.

In Zone I leaves all hair bases and abaxial secretory structures are distinct. In contrast, they show complete intergradation even on the same leaf in Sapindopsis and Platanoid #1, found in Subzone II-B. This suggests a trend

less differentiation between these two structural types, at least in this subgroup of Potomac Group angiosperm leaves.

7. (a) Internal sculpture smooth to granular. (b) Internal sculpture alveolar.

All Zone I leaves have smooth to granular internal sculpture, as is typical of extant flowering plants. This holds true for every Subzone II-B leaf type except Populophyllum reniforme, which has an extensive system of chambers that open to the inner cuticle surface near the flanges. These chambers appear as light areas under light microscopy, making this pattern detectable without the SEM. The later appearance of this trait, as well as its confinement to one leaf type, supports the idea that it represents an advancement.

Systematic Distribution of Advanced Features

The systematic distribution of these postulated advanced features in Subzone II-B dicot leaves strongly corroborates the phenetic relationships inferred on the basis of overlap in cuticular features. First, the pinnatifid and pinnately compound leaves referred to Sapindopsis by Hickey and Doyle (1977), which are virtually identical in all aspects of their cuticular structure, possess advanced features for five of the seven character groups; the loss of lamellae in the guard cells, the Sapindopsis stomatal pattern, complex radiostriate hair bases, abaxial secretory structures that range from level with the epidermis

to strongly protruding, and the intergradation of these secretory cells with hair bases and their associated hairs. These advancements or still more derived conditions are all found in the "platanoids" but are absent from the other three leaf groups, with the exception of the loss of lamellae, found in Menispermites potomocensis and Populophyllum reniforme. This possession of numerous advanced features by Sapindopsis and the platanoids strongly supports the relationship inferred by Hickey and Doyle (1977) for the two groups. If Sapindopsis is indeed an early member of subclass Rosidae and the platanoids do indeed represent the Platanaceous alliance, then cuticular anatomy supports the concept that extant Platanaceae and subclass Rosidae are more closely related than has generally been thought (Hickey and Doyle, 1977). Further studies on the distribution of cuticular features in modern angiosperms, coupled with studies of the reproductive structures associated with both the fossil leaf groups, are needed to test this hypothesis.

The distant relationships to other leaf groups inferred for Menispermite potomacensis, Populophyllum reniforme, and the new serrate from Red Point are supported by the general restriction of advanced features to only one leaf type. The new serrate from Red Point possesses the advanced features of no stomatal ledges and its characteristic stomatal type, which are shared with no

other leaf group. The stomatal type of Menispermites potomacensis is inferred to be derived separately of the other contemporaneous stomatal types. Populophyllum reniforme has its own uniquely derived stomatal type and the advanced feature of alveolar internal sculpture. The latter two groups do share the trait of no stomatal lamellae, but this is also found in the Sapindopsis-platanoid complex as well. This may mean that the new serrate from Red Point is more distantly related to the other leaf groups than they are to each other; however, the fact that the loss of lamellae can be inferred to have taken place more than once in the Magnoliaceae (cf. Baranova, 1972) suggests that other characters are needed before this hypothesis can be accepted.

Conclusions

In conclusion, the study of leaf cuticles provides new evidence for Cretaceous angiosperm evolution. The low diversity of cuticular features seen in Zone I, along with the progressive increase in diversity seen in later Cretaceous and Tertiary Cuticles, indicates that the flowering plants were undergoing a steady diversification throughout this time and that the angiosperms had yet to approach even a significant fraction of their overall diversity by the end of the Early Cretaceous. The fact that the order of appearance of cuticular features shows a general correspondence with the relative/primitiveness or

advances of modern counterparts inferred on the basis of comparative morphology provides additional evidence for the general validity of modern systems of angiosperm classification. This correspondence, along with the fact that the Potomac Group record has supplied leaf remains with features intermediate between those of some modern groups, indicates that future studies of fossil flowering plan remains should provide additional solutions to our understanding of angiosperm phylogeny.

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PLATE DESCRIPTIONS

Plate 1

Zone I angiosperm leaves

Fig. 1. D.B. Leaf Type #1, showing numerous convex-convex (A-1) serrations and simple craspedodromous secondary venation. x1.5.

Fig. 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). x25.

Fig. 3. cf. Ficophyllum, transfer of leaf fragment showing reticulate higher order veins. The two thick veins running from left to right are interpreted to be secondaries. x3.

Fig. 4. Eucalyptophyllum oblongifolium, specimen photographed in infra-red light which shows a two-stranded primary vein, irregularly space secondaries, and an intramarginal vein (arrow). x2.

Fig. 5. Celastrophyllum sp. Note stem fragment associated with the leaf base. x1.5.

Fig. 6. cf. Celastrophyllum obovatum, obovate leaf fragment with marginal tears showing secondary and tertiary venation. x3.

Fig. 7. Celastrophyllum sp., upper cuticle showing stomata and subparallel folds. x160.

Fig. 8. cf. Ficophyllum, upper cuticle with faint flanges, occasional folds, and one stoma (top of frame). x160.

Fig. 9. Eucalyptophyllum, upper cuticle showing prominent flanges, numerous hair bases, and psilate sculptural features. x400.

Fig. 10. D.B. Leaf Type #1, upper cuticle showing prominent flanges and numerous fine striations that traverse cell boundaries. x250.

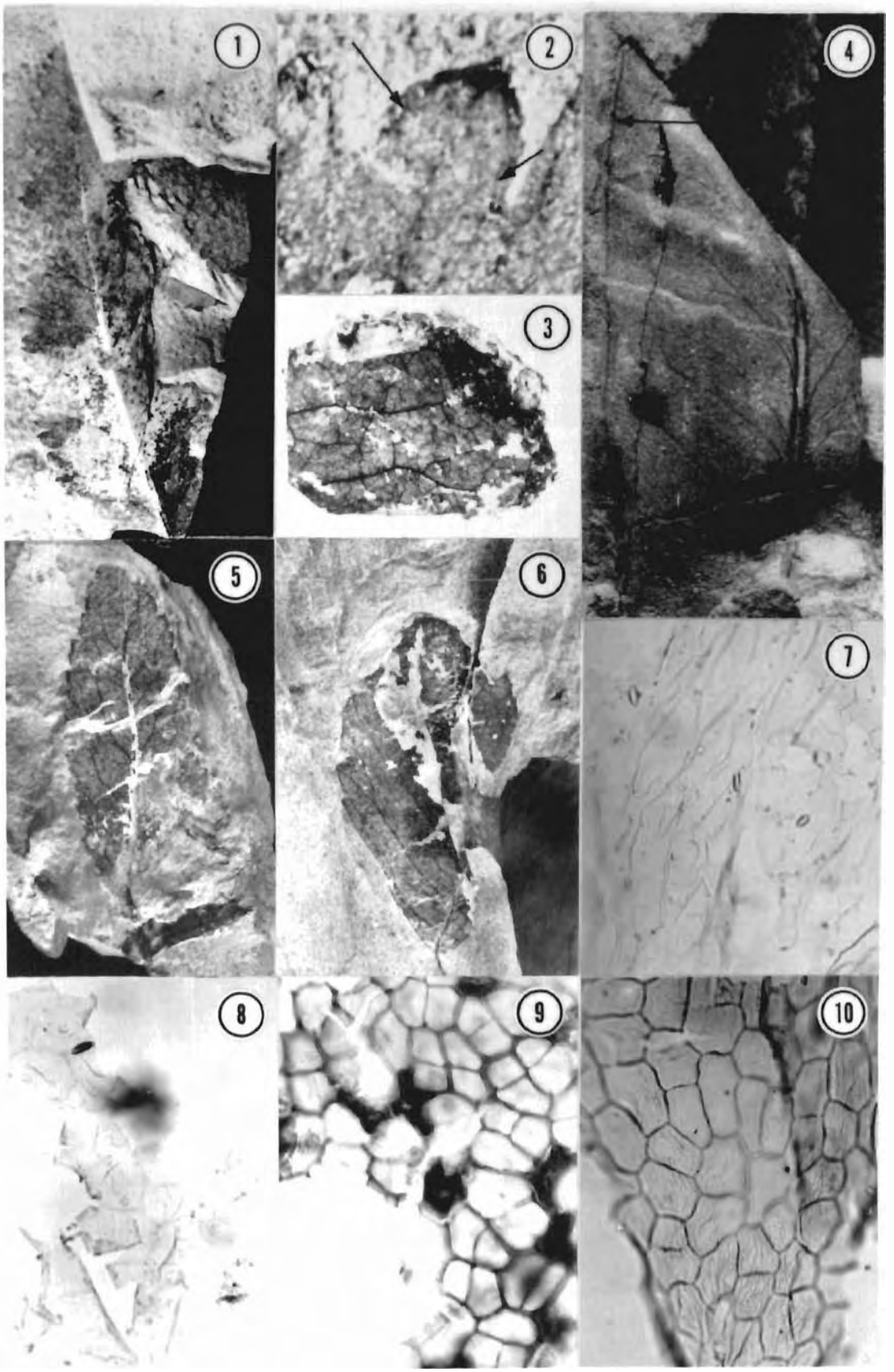

Plate 1

Plate 2

Zone I angiosperm cuticles

Fig. 11. Eucalyptophyllum, SEM of outer surface of upper cuticle showing trichome abscission scars. x1000.

Fig. 12. Eucalyptophyllum, lower cuticle with paracytic (P) and laterocytic (Lc) stomata and glandular cells (G). x400.

Fig. 13. cf. Ficophyllum, general shot of lower cuticle showing subparallel folds and variable stomatal complexes. x160.

Fig. 14. D.B. Leaf Type #1, anomocytic stoma showing characteristic pattern of striations on the stomatal complex.

Fig. 15. cf. Ficophyllum, stoma showing lamellar thickenings (L) and outer stomatal ledges (SL) on guard cells. x1000.

Fig. 16. cf. Ficophyllum, stoma unclassifiable as any one convential type showing a high range of variation in contact cell size. x750.

Fig. 17. Eucalyptophyllum, SEM of inner surface of lower cuticle showing granular sculpture and four conventionally recognized stomata types: paracytic (P), cyclocytic (C), hemiparacytic (H), and laterocytic (Lc). x1000.

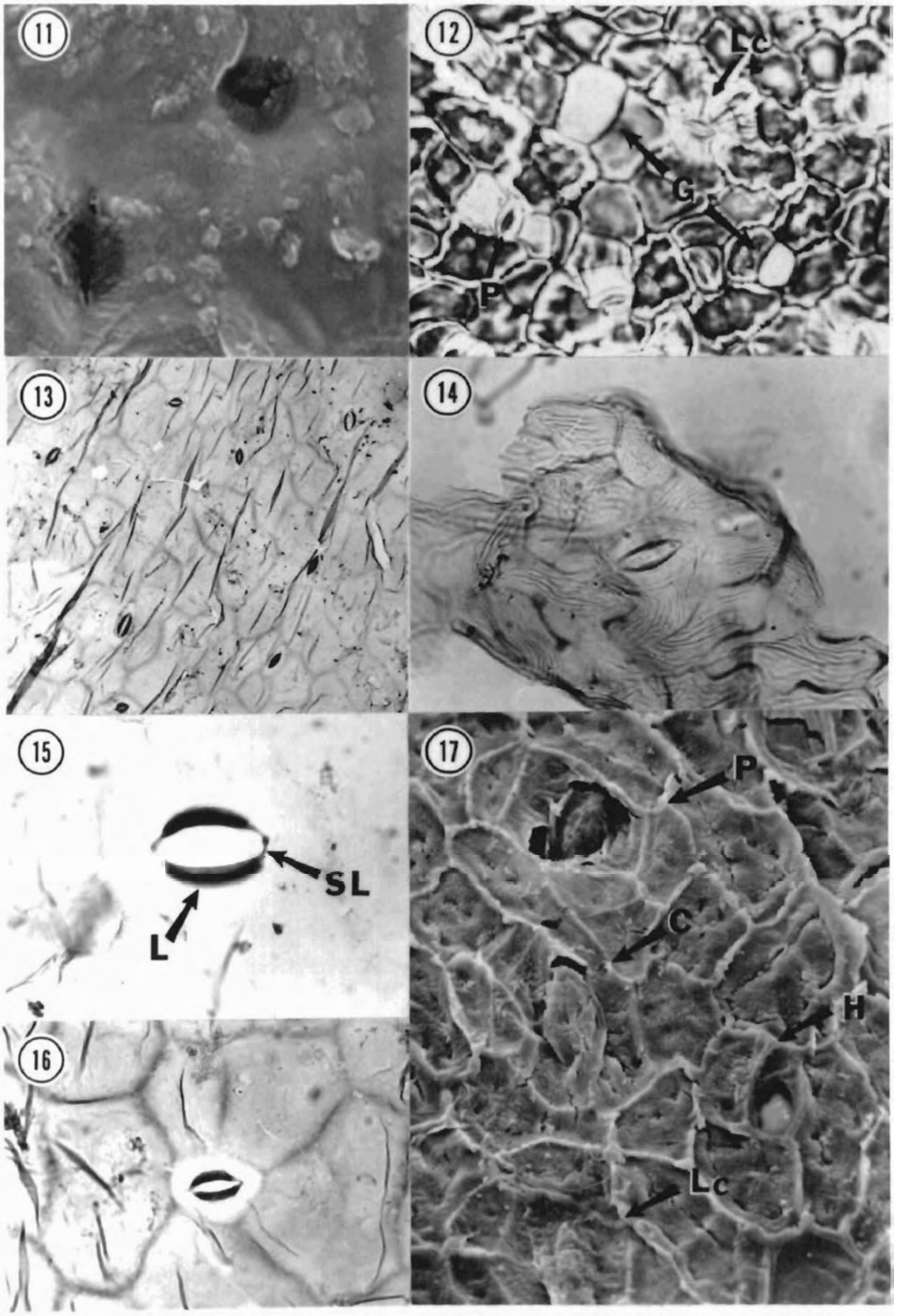

Plate 2

Plate 3

Extant and Zone I angiosperm leaf cuticles

Fig. 18. Sarcandra glaba (Chloranthaceae), partially macerated lower cuticle showing the Zone I pattern of variation in contact cell arrangement and specialization. x200.

Fig. 19. D.B. Leaf Type #1, elongate and branched hair base from lower cuticle. x400.

Fig. 20. Eucalyptophyllum, radiostriate hair base from lower cuticle (arrow). x400.

Fig. 21. cf. Celastrophyllum obovatum, secretory cell associated with the cuticle (arrow). x400.

Fig. 22. Eucalyptophyllum, SEM of outer surface of lower cuticle showing sunken stomata with outer stomatal ledges and two sizes of striations. x1000.

Fig. 23. dispersed Cuticle Type #1 from Dutch Gap, stomatal complex with T-pieces. Note also the characteristic grooves in the broad cuticular flanges. x400.

Fig. 24-26. Dispersed Cuticle Type #3 from Drewrys Bluff.

Fig. 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. x1000.

Fig. 25. Hair base showing thickened outer cuticle with pore (arrow). x1000.

Fig. 26. Same hair base showing strongly underthrusting base cells (arrow). x1000.

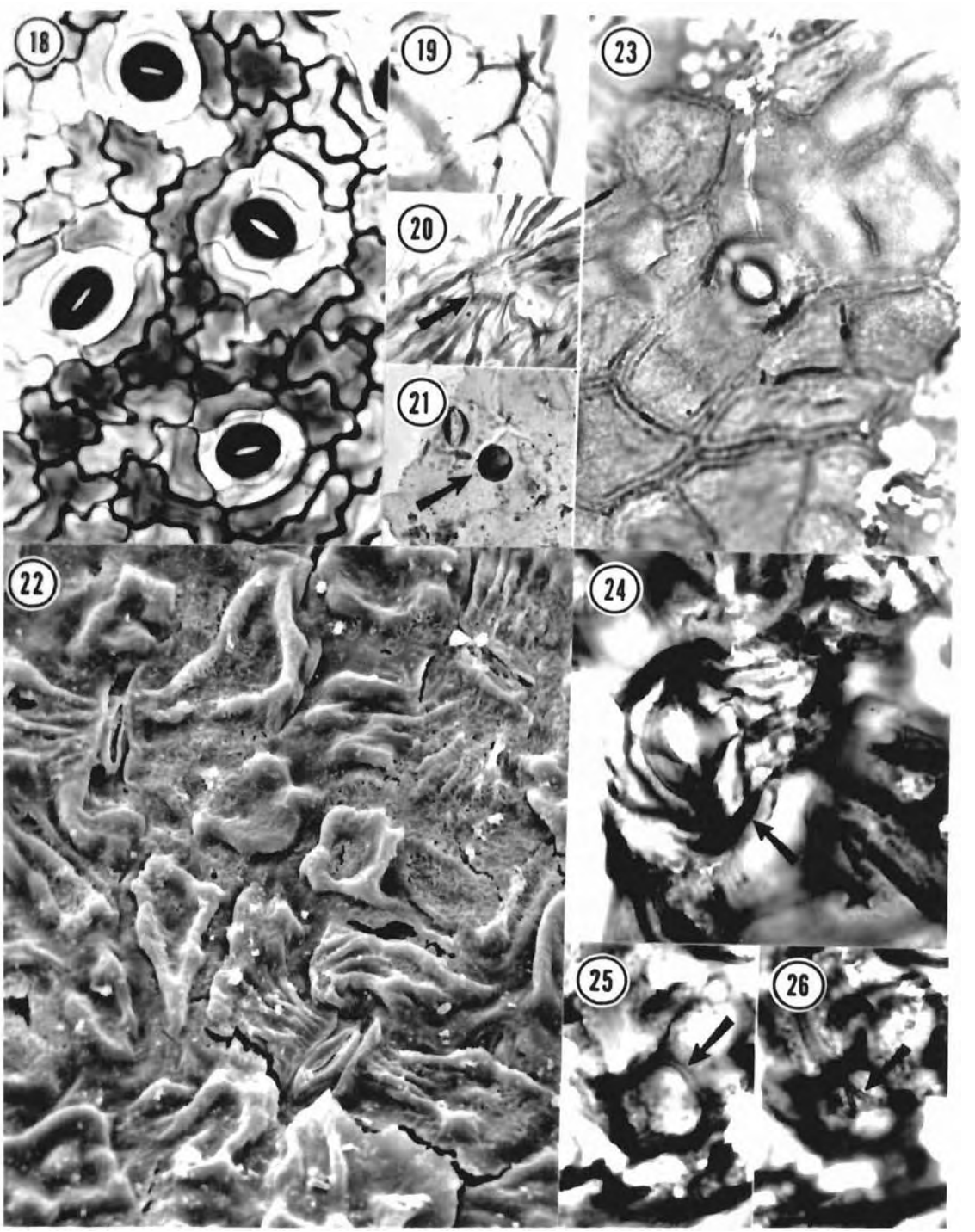

Plate 3

Plate 4

Lower cuticles of Sarcandra (Chloranthaceae) and Zone I angiosperms.

Fig. 27. Dispersed Cuticle Type #2 from Dutch Gap, showing two stomata and a hollow papilla (arrow). x400.

Fig. 28. Dispersed Cuticle Type #3 from Drewrys Bluff, general shot showing straight-walled, polygonal cells with partially solid papillae and radiating striations. x200.

Fig. 29. Dispersed Cuticle Type #5 from Dutch Gap, longitudinally aligned cells with striations and partially solid papillae. x160.

Fig. 30. Sarcandra glabra, fully macerated lower cuticle showing lamellar thickenings in the guard cells and pattern of striations similar to D.B. Leaf Type #1. x400.

Fig. 31. dispersed Cuticle Type #6 from Dutch Gap showing numerous radiostriate hair bases (arrows). x200.

Fig. 32. Dispersed Cuticle Type #6 rounded idioblast secretory cell (arrow). x400.

Fig. 33. Sarcandra glabra, radiostriate hair base from lower cuticle. x1000.

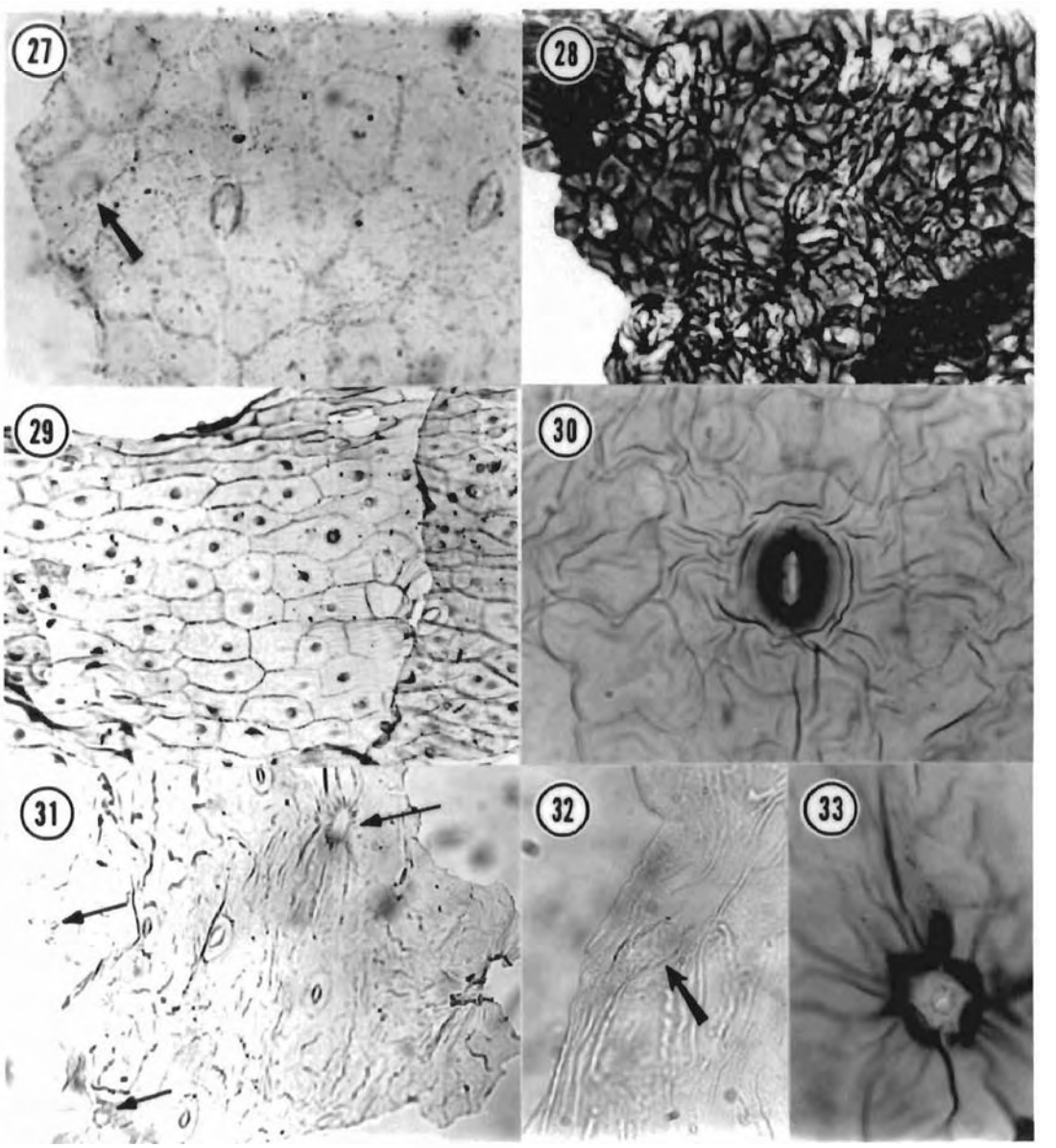

Plate 4

Plate 5

Stomata of Subzone II-B angiosperms.

Fig. 34. Populophyllum reniforme, anomocytic stomata. x250.

Fig. 35. New Serrate from Red Point, two stomatal complexes which each have a ring of contact cells with strongly overarching papillae (st). x400.

Fig. 36. Platanoid #1, complex laterocytic stomata. x400.

Fig. 37. Pinnately compound Sapindopsis, stomata which conform to the laterocytic type. Note the tendency for the stomatal complex to be surrounded by a ring of cells that are smaller than the adjacent cells. x400.

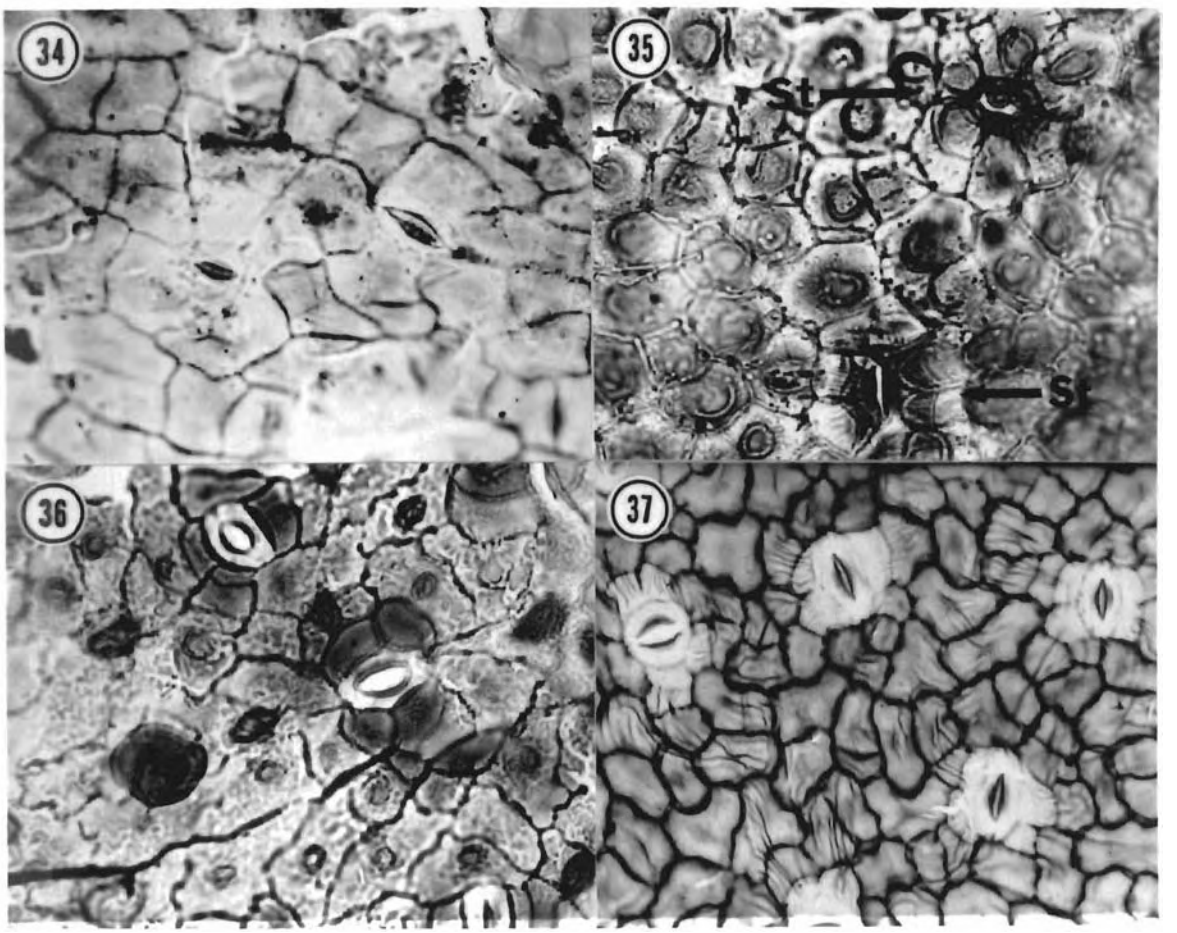

Plate 5

Plate 6

Sapindopsis variabilis

Fig. 38. Specimen with 3 terminal lobes. x1.

Fig. 39. Specimen with lateral lobes and wing of laminar tissue along the rachis. x1.

Fig. 40. Close up of upper left lobe in fig. 40, showing brochidodromous arches that abruptly curve towards the apex. x3.

Fig. 41. Same lobe as fig. 40, showing random reticulate tertiary and quaternary venation (upper right). x5.

Fig. 42. SEM of upper cuticle, showing domains of cells and weakly granular internal structure. x360.

Fig. 43. Upper cuticle, showing strongly grouped appearance of cells and high frequency hair bases. x136.

Fig. 44. Region above primary vein (upper half of photo) showing weakly aligned cells and stomata (light round regions(. x136.

Fig. 45. Upper cuticle, showing widely spaced striations and granular internal sculpture. x425.

Fig. 46. Hair base from upper cuticle, showing slightly punctate outer cuticle of foot cell. x340.

Fig. 47. SEM of hair base, upper cuticle. x340.

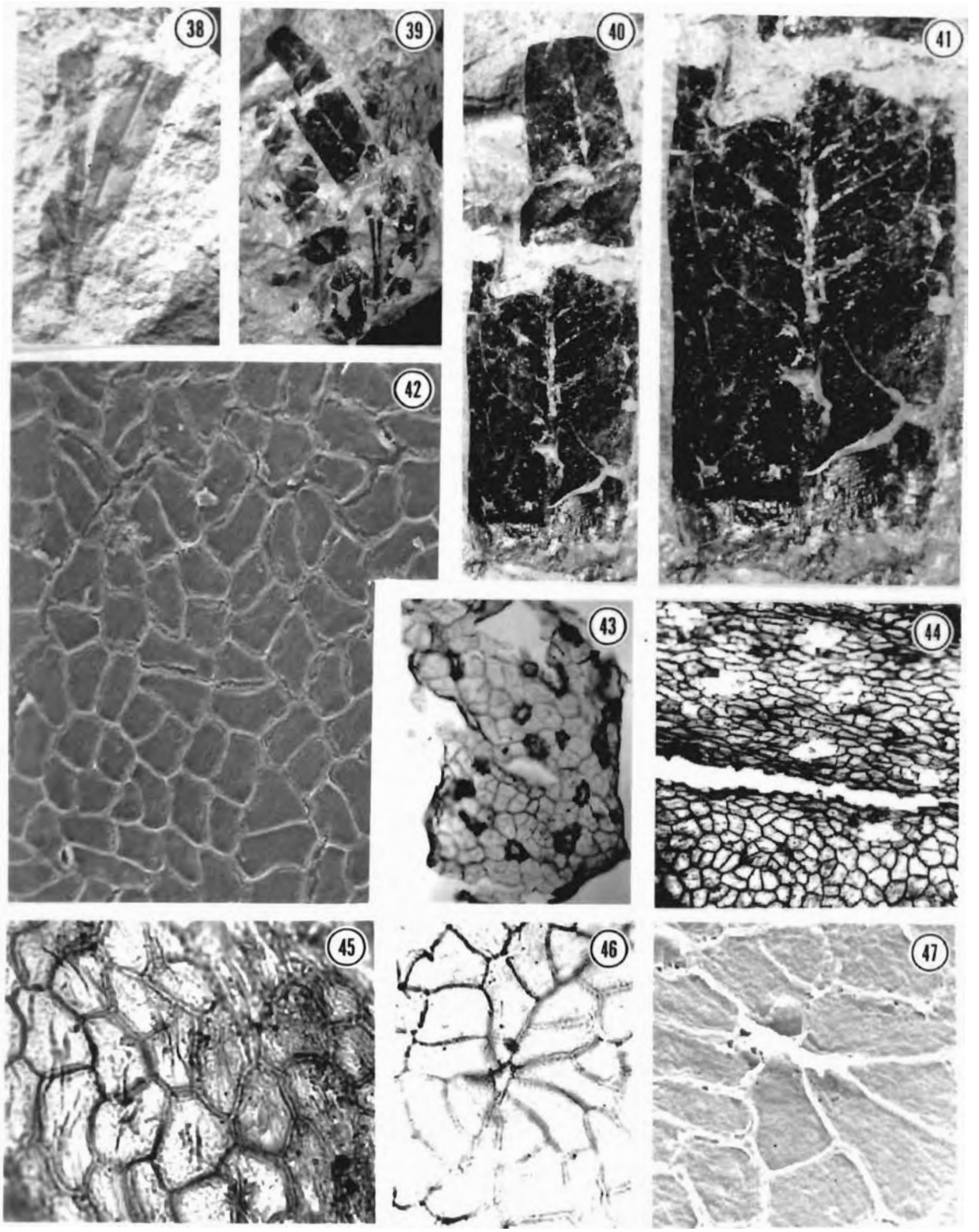

Plate 6

Plate 7

Sapindopsis variabilis

Fig. 48. SEM of probable complex radiostriate hair base from upper cuticle (arrow). x1200.

Fig. 49. SEM of inner surface of a thin lower cuticle. x850.

Fig. 50. SEM of inner surface of a thick lower cuticle. x340.

Fig. 51. Region beneath a primary vein, lower cuticle. x136.

Fig. 52. Lower cuticle, showing prominent striations, a mixture of papillate and non-papillate cells, and one stomatal complex with the characteristic cuticular thinning over the lateral contact cells. x340.

Fig. 53. SEM of lower cuticle, showing characteristic striation patterns of papillate and non-papillate cells. x340.

Fig. 54. Lower cuticle of a predominantly papillate epidermis, showing a paracytic (top) and laterocytic (bottom) stomata, each surrounded by a partial ring of weakly modified cells. x340.

Fig. 55. SEM of lower cuticle showing slightly granular cuticle and strongly specialized lateral cells (arrows). x850.

Fig. 56. SEM of another lower cuticle showing a more or less psilate internal sculpture pattern and a weakly cyclocytic stoma with prominent inner stomatal ledges (ISL). x1000.

Fig. 57. SEM of outer surface of the lower cuticle, showing a slightly sunken stoma with outer stomatal ledges (OSL). x1530.

Fig. 58. Stoma from a predominantly papillate cuticle, showing angular stomatal outline and papillae

on the subsidiary cells. The lower right pair of subsidiary cells is separated by a thinly cutinized tangential, which passes beneath a papilla. x850.

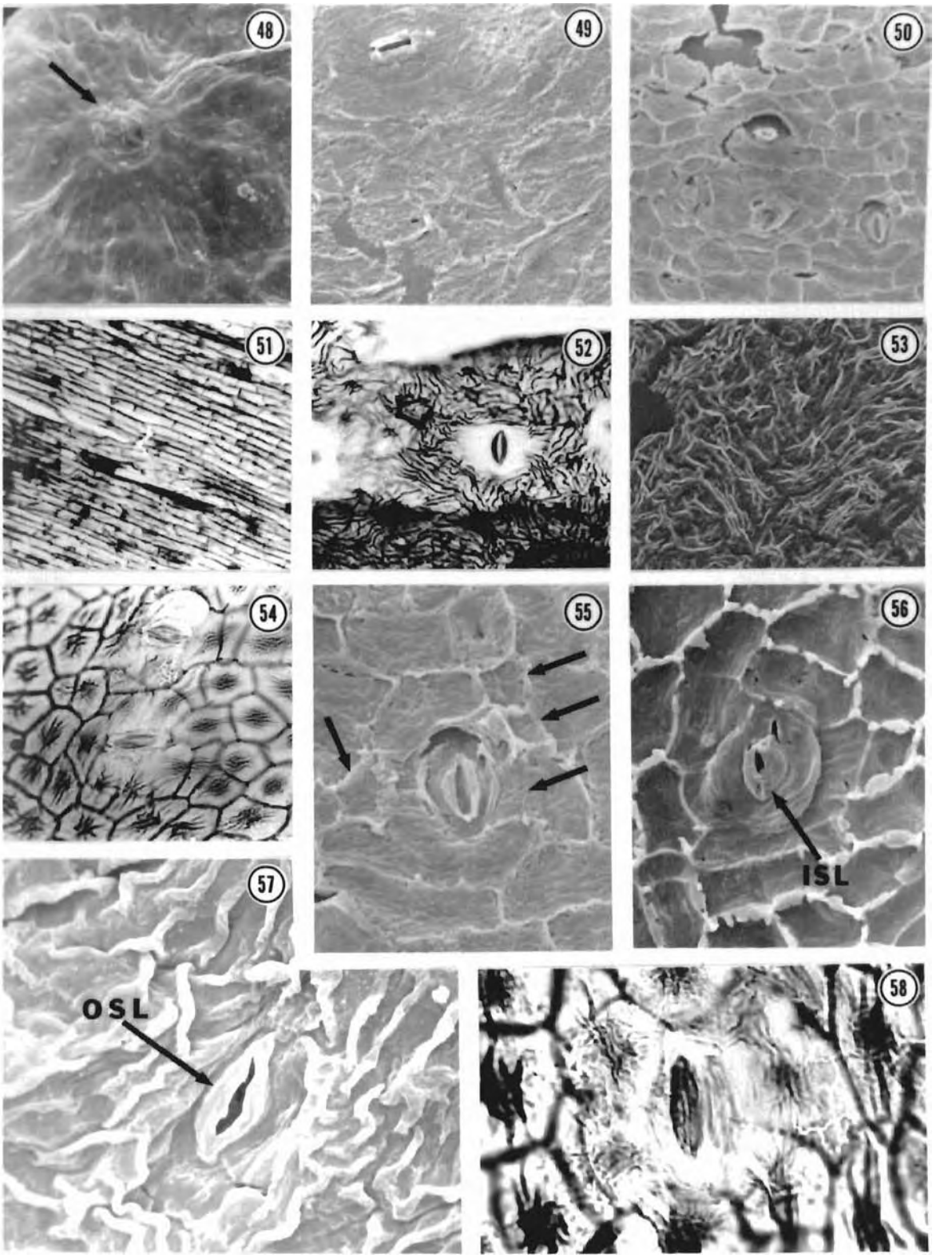

Plate 7

Plate 8

Sapindopsis variabilis, lower cuticle

Fig. 59. Complex laterocytic stoma showing marked cuticular thinning over the lateral contact cells. x340.

Fig. 60. Polygonal hair base with thickly cutinized anticlinal walls (arrow). x340.

Fig. 61. SEM of inner cuticle surface showing a hair base with radially elongate base cells. x850.

Fig. 62. Hair base with an elongate, polygonal foot cell. x340.

Fig. 63. Hair base on a venal region with a circular lumen. This form is very similar to the type that characterizes Platanoid #2. x850.

Fig. 64. Hair base with heavily cutinized lateral protrusions (Pl) that give it a "plumed" appearance. x340.

Fig. 65. Hair base with two base cells that have thick cuticular flanges. The hair is positioned over their junction and has a punctate outer cuticle. Note the zone of weakness where the hair is attached to the base cells (arrow). x850.

Fig. 66. Hair base with two base cells and a hair attached to only one of them. Note the development of an operculum on the outer cuticle of the hair (arrow). x850.

Fig. 67. Hair base with two modified base cells and a trichome abscision scar placed over one base cell and the adjacent unmodified cells (arrow). x340.

Fig. 68. Hair attached to three base cells with thick flanges and an adjacent, unmodified cell (arrow). x340.

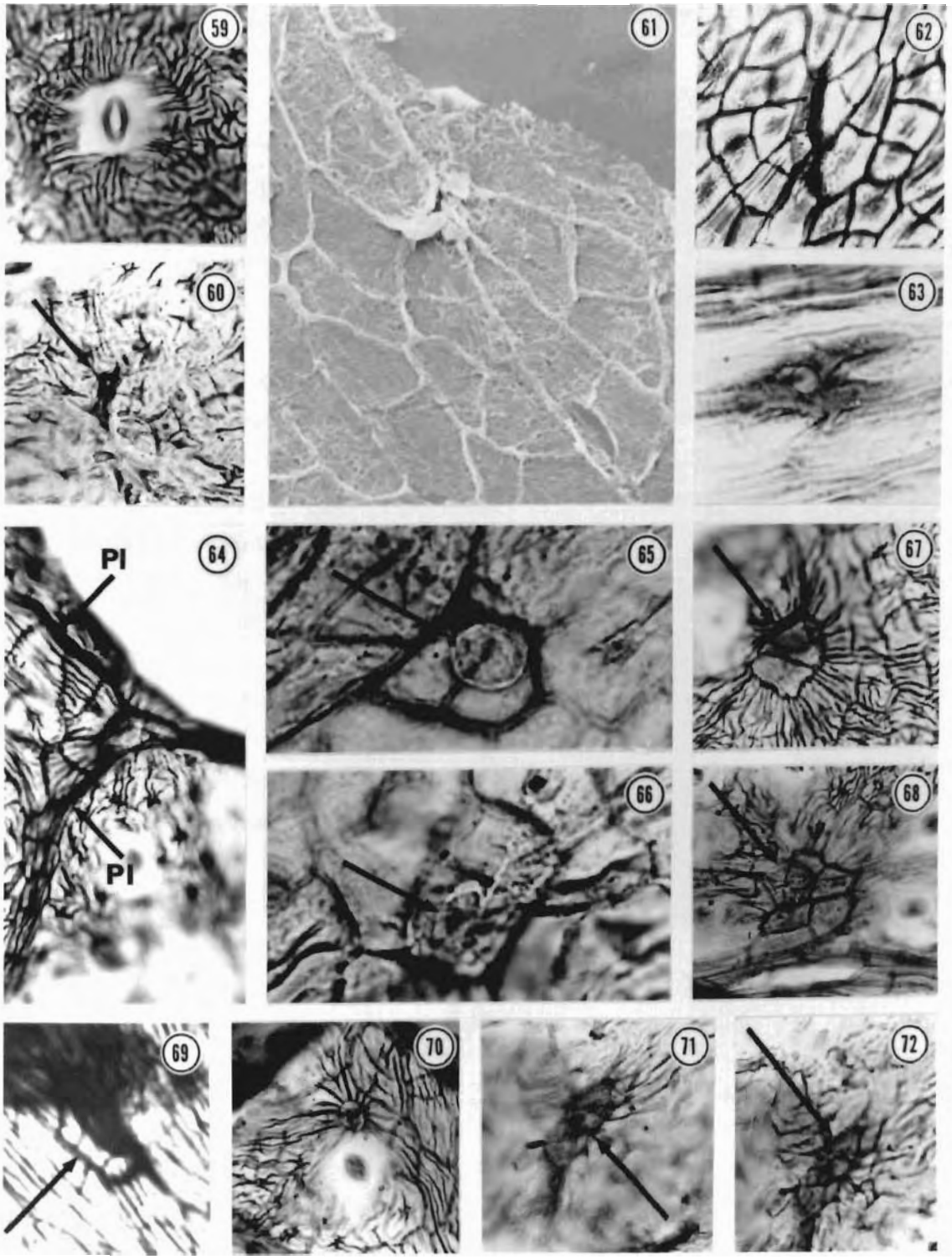

Plate 8

Plate 9

Figs. 73-77. Abaxial secretory structures, Sapindopsis variabilis.

Fig. 73. Secretory cell with thick rim and punctate outer cuticle (arrow). x340.

Fig. 74. Same cell as fig. 73 (arrow) showing partial underthrusting of adjacent cells. x340.

Fig. 75. SEM of outer cuticle surface showing round abaxial secretory structure (Gland) that is partially underthrust by the adjacent cells. x850.

Fig. 76. Cylindrical secretory cell lacking cuticle in central region (arrow).

Fig. 77. Same cell as in fig. 76 (arrow), showing complete underthrusting of subtending cell. x340.

Figs. 78-84. Pinnately compound Sapindopsis leaves from West Brothers.

Fig. 78. Two adjacent leaflets, one with an acute apex (A) and with a decurrent, asymetric base (B). x1.

Fig. 79. Leaflet with one large, concave-convex (C-1) tooth and mixed craspedodromous secondary venation.

Fig. 80. Leaflet with eucamptodromous secondary veins and tertiaries obliquely oriented toward mid-vein. x2.

Fig. 81. Close-up of leaflet in fig. 78 B, showing festooned brochidodromous secondary venation, intersecondary veins, variable angle of tertiary vein origin, and randomly oriented higher order veins. x5.

Fig. 82. CLose-up of leaflet in fig. 79, showing details of tooth (arrow). x5.

Fig. 83. Obovate leaflet with widely spaced secondary veins. x1.

Fig. 84. SEM of upper leaf surface showing eruptions of probable fungal origin. x 255.

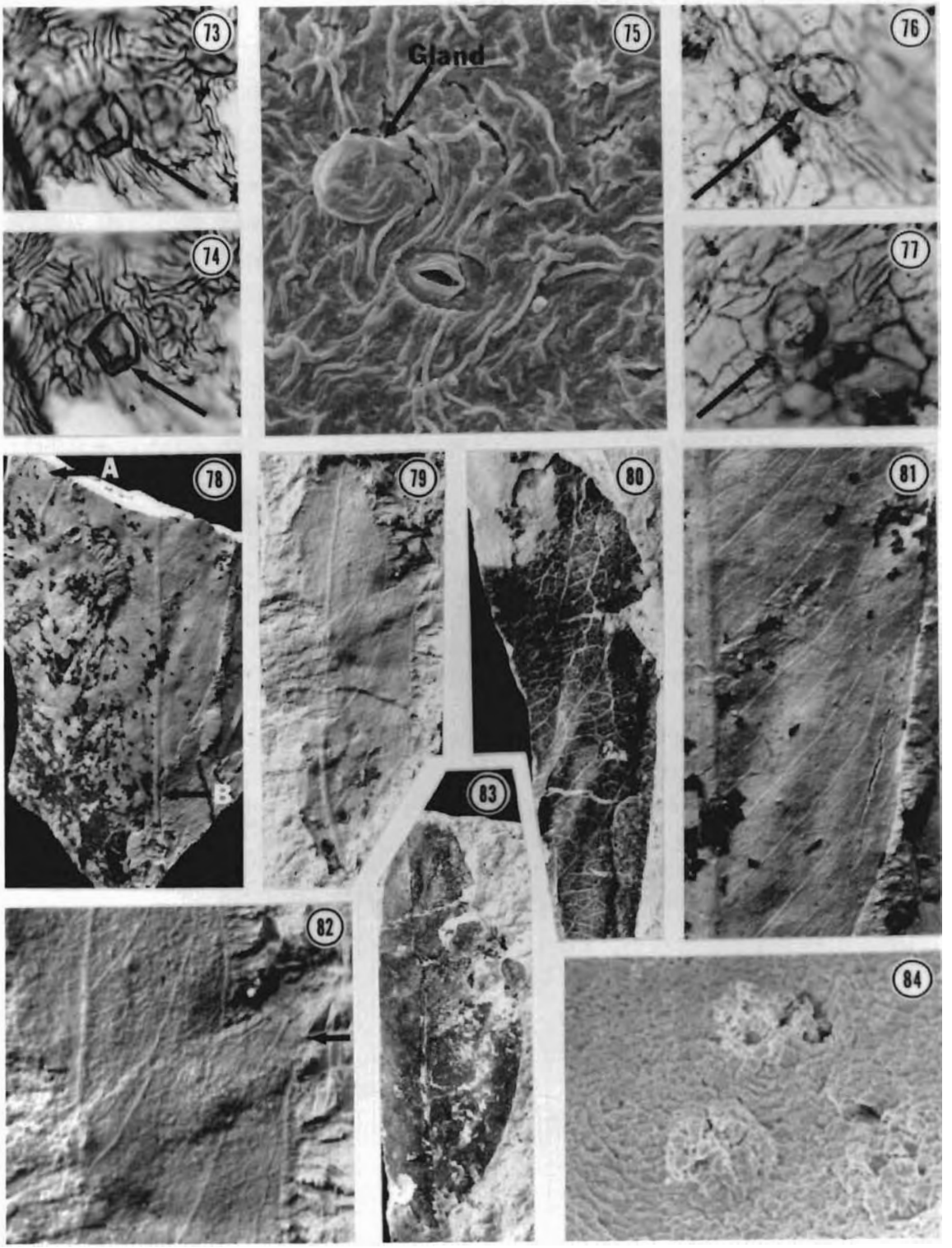

Plate 9

Plate 10

Pinnately compound Sapindopsis, cuticle

Figs. 85-97. Upper Cuticle.

Fig. 85. Striate cuticle with grouped cells. x136.

Fig. 86. Psilate cuticle with less strongly grouped cells and the base cells from a complex radiostriate hair base (arrow). 136x.

Fig. 87. Region above primary vein showing the weak organization of cells into rows and stomata (St). x136.

Fig. 88. Cells with short, solid papillae. x340.

Fig. 89. Cells with taller, hollow papillae. x340.

Fig. 90. Clusters of hair bases, x136.

Fig. 91. Close-up of hair base, showing thickened foot cell. x340.

Figs. 92-97. Complex ratiostriate hair bases.

Fig. 92. Upper focus hair showing punctate cuticle. x340.

Fig. 93. Lower focus of hair in fig. 92 showing thickened cuticle at base and radiating striations. x340.

Fig. 94. Upper focus of an irregularly lobate hair. x340.

Fig. 95. Lower focus of hair in fig. 94, showing small subtending cells. x340.

Fig. 96. Elongate trichome abscission scar with small subtending cells (arrow). x136.

Fig. 97. Close-up of small subtending cells in a hair base. x340.

Fig. 98. Lower Cuticle. x136.

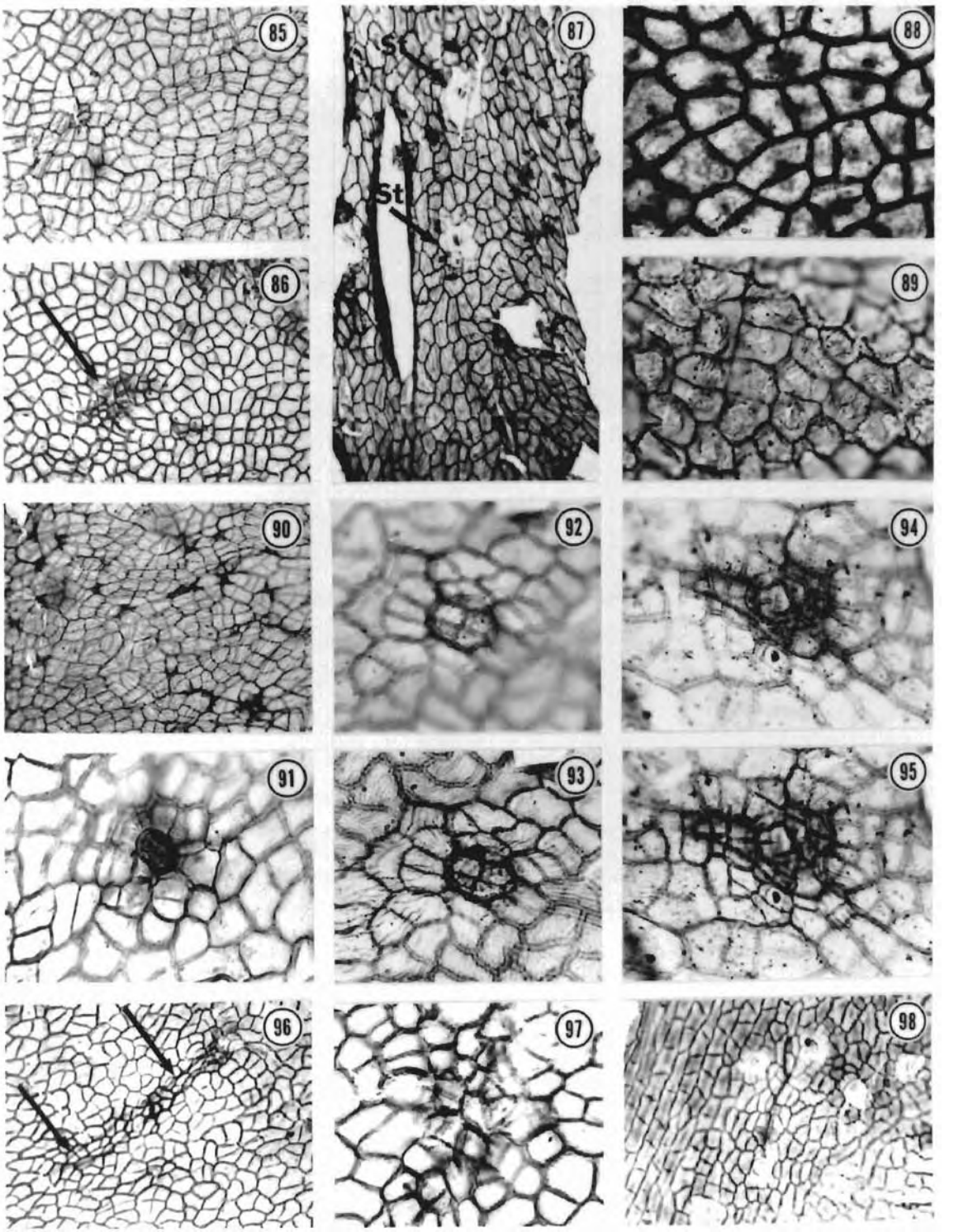

Plate 10

Plate 11

Pinnately compound Sapindopsis, lower cuticle

Fig. 99. Cells beneath primary vein. x136.

Fig. 100. Laterocytic stomata showing characteristic cuticular thinning over the subsidiary cells. x510.

Fig. 101. SEM of outer cuticle surface showing slightly sunken stoma (sl). x340.

Fig. 102. SEM of inner cuticle surface showing granular internal sculpture and a stomatal complex with well-developed inner stomatal ledges (ISL). x1530.

Fig. 103. Stomata conforming to three conventionally recognized types: paracytic (stoma at far left), weakly cyclocytic (lower two stomata, center), and complex laterocytic (upper two stomata, center). x510.

Fig. 104. Laterocytic stoma with strongly specialized subsidiaries that is embedded in a partial ring of weakly modified cells. x510.

Fig. 105. Laterocytic (left) and cyclocytic (right) stomata with subsidiary cells that are poorly differentiated from the surrounding cells. x510.

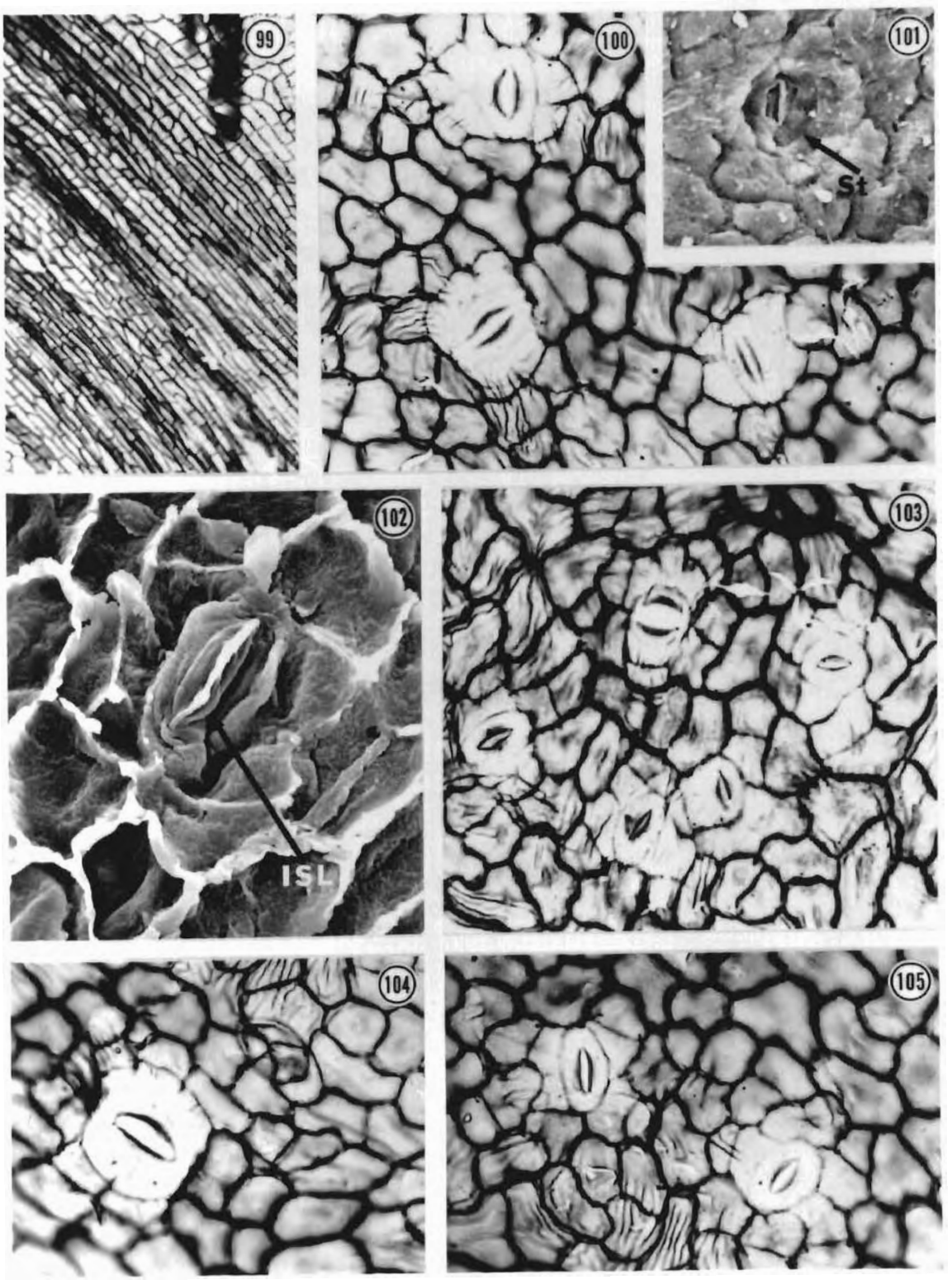

Plate 11

Plate 12

Pinnately compound Sapindopsis hairs and hair bases from the lower cuticle

Fig. 106. Hair base with radially oriented base cells (arrow). x340.

Fig. 107. Hair base (?) with large, polygonal, branched foot cell. x340.

Fig. 108. Rounded hair base (?) that strongly resembles an abaxial secretory cell. x340.

Fig. 109-111. Cluster of hair bases (arrows).

Fig. 109. Upper focus. x340.

Fig. 110. Middle focus. x340.

Fig. 111. Lower focus. x340.

Fig. 112-120. Complex radiostriate hair bases.

Fig. 112. Heavily cutinized hair with radiating striations attached to a small, polygonal cell with straight anticlinal walls (arrow). x340.

Fig. 113. Heavily cutinized hair with operculum (op). x340.

Fig. 114. Hairs on a region beneath the primary vein (arrows). Note their variable positioning relative to the underlying cells. x340.

Fig. 115. Hair with three strongly cutinized lateral protrusions (arrows). x340.

Fig. 116. Hair base with one lateral protrusion (arrow). x340.

Fig. 117. Hair base with a tapered lateral protrusion (arrow). x850.

Fig. 118-119. Hair base with polygonal, straight-walled cells between the abscission scar and rest of epidermis.

Fig. 118. Upper focus showing scar and radiating striations. x850.

Fig. 119. Lower focus showing subtending cells. x850.

Fig. 120. Cluster of round, dome-shaped hairs. x340.

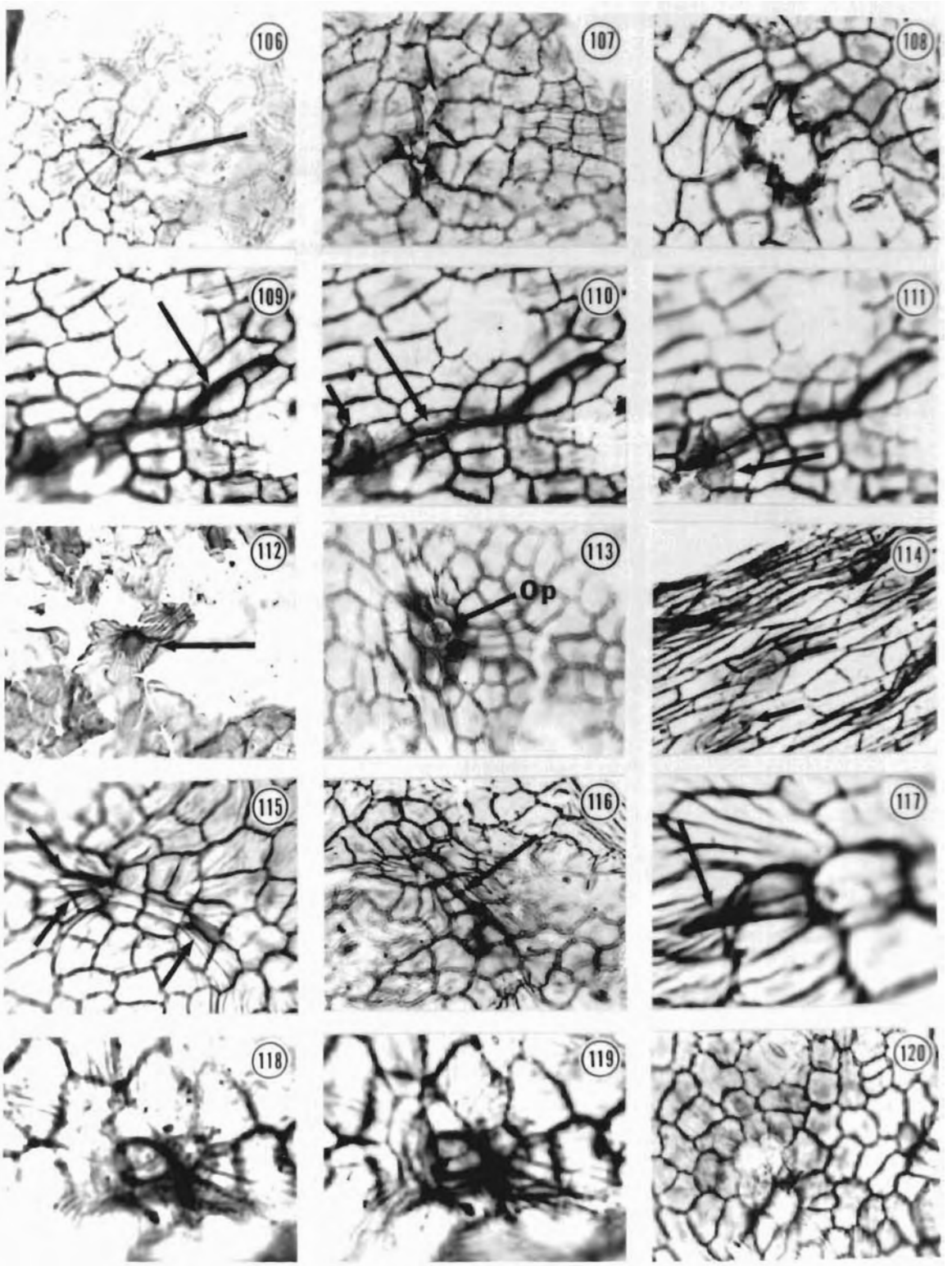

Plate 12

Plate 13

Figs. 121-
127. Pinnately compound Sapindopsis lower cuticle

Fig. 121. Strongly protruding secretory cell level that is not underthrust by the other epidermal cells. x850.

Fig. 122. Two-celled secretory structure level with the adjacent cells. x340.

Fig. 123. Secretory cell with maceration-resistant contents (arrow). x340.

Fig. 124. Secretory cell completely underthrust by the epidermal cells (arrow). The small light dots inside the cell represent contents that survived maceration. x510.

Fig. 125. SEM of secretory cell which lacks cuticle in the central region (Gland). x850.

Fig. 126. Secretory cell with operculum (arrow). x340.

Fig. 127. Prostrate hair attached to unmodified epidermal cell. x850.

Figs. 128-
130. Leaves of Platanoid #1.

Fig. 128. Basal portion of leaf with palinactinodromous primary venation. x1.

Fig. 129. Basal portion of a lateral lobe. x1.

Fig. 130. Close-up of leaf in fig. 128 showing tertiary veins (T), stitched intertertiaries (IT), and faint quaternary venation. x5.

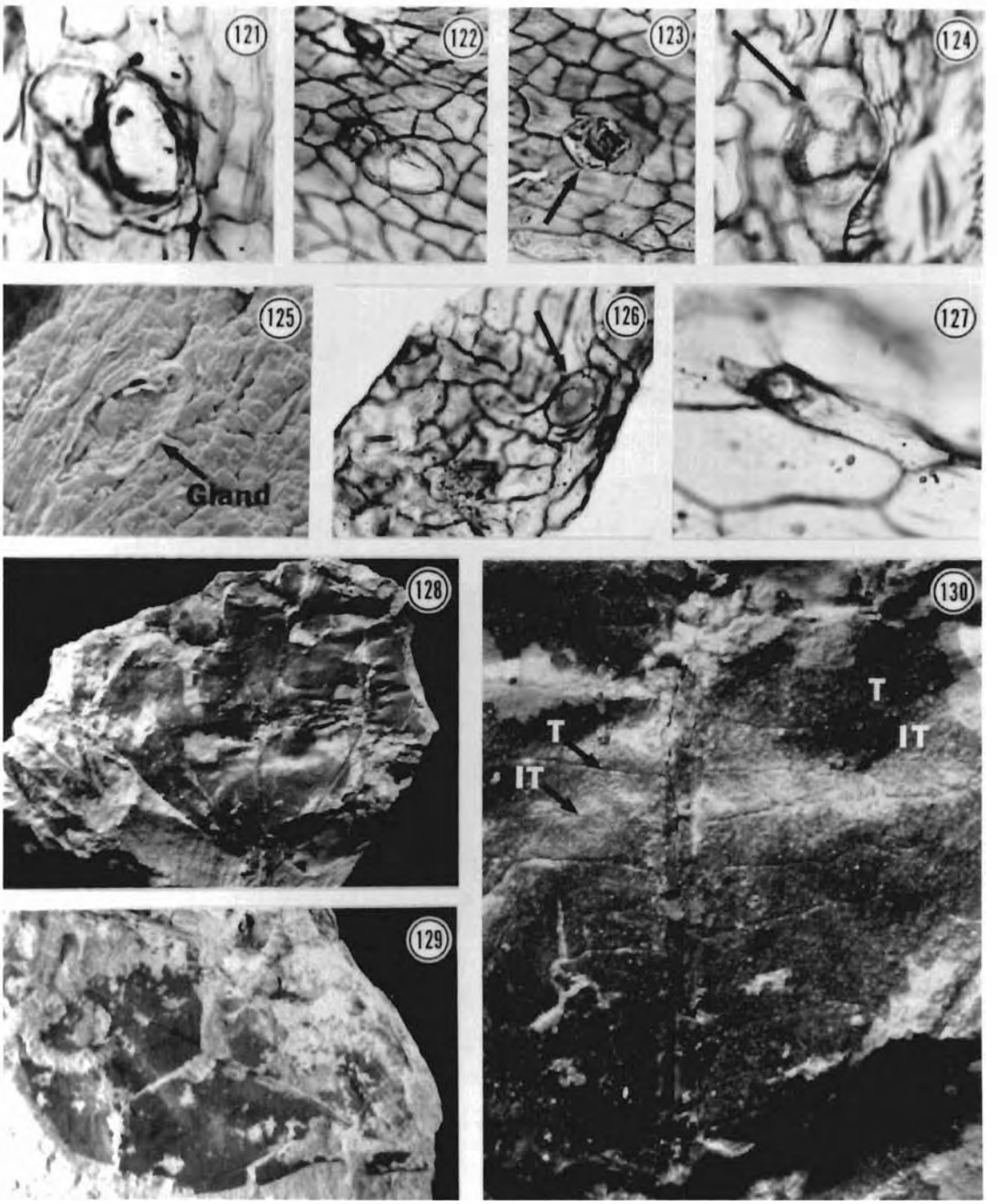

Plate 13

Plate 14

Platanoid #1, cuticle.

Fig. 131. Upper cuticle of non-veinal region with a hair base that resembles the complex radiostriate type. x340.

Fig. 132. Upper cuticle above primary vein showing longitudinally aligned cells and stomata (st). x136.

Fig. 133. Lower cuticle with stomata, complex radiostriate hair bases, and secretory cells. Stomatal types include paracytic (upper left and upper right) and complex laterocytic (upper center and lower left). One complex radiostriate hair base (arrow) bears lateral protrusions. x340.

Fig. 134. Lower cuticle with secretory cell (G1). Most cells have a central hollow papilla and undulate clinical walls. x340.

Fig. 135. Region beneath primary vein showing numerous hair bases. x136.

Fig. 136. Region beneath primary vein showing striations and positioning of hair bases relative to the sutbtending cells. One hair base (arrow) has a lateral protrusion and base cells that are smaller than the adjacent cells. x340.

Fig. 137. Close-up of a cylindrical secretory cell that lacks cuticle in its central region. x850.

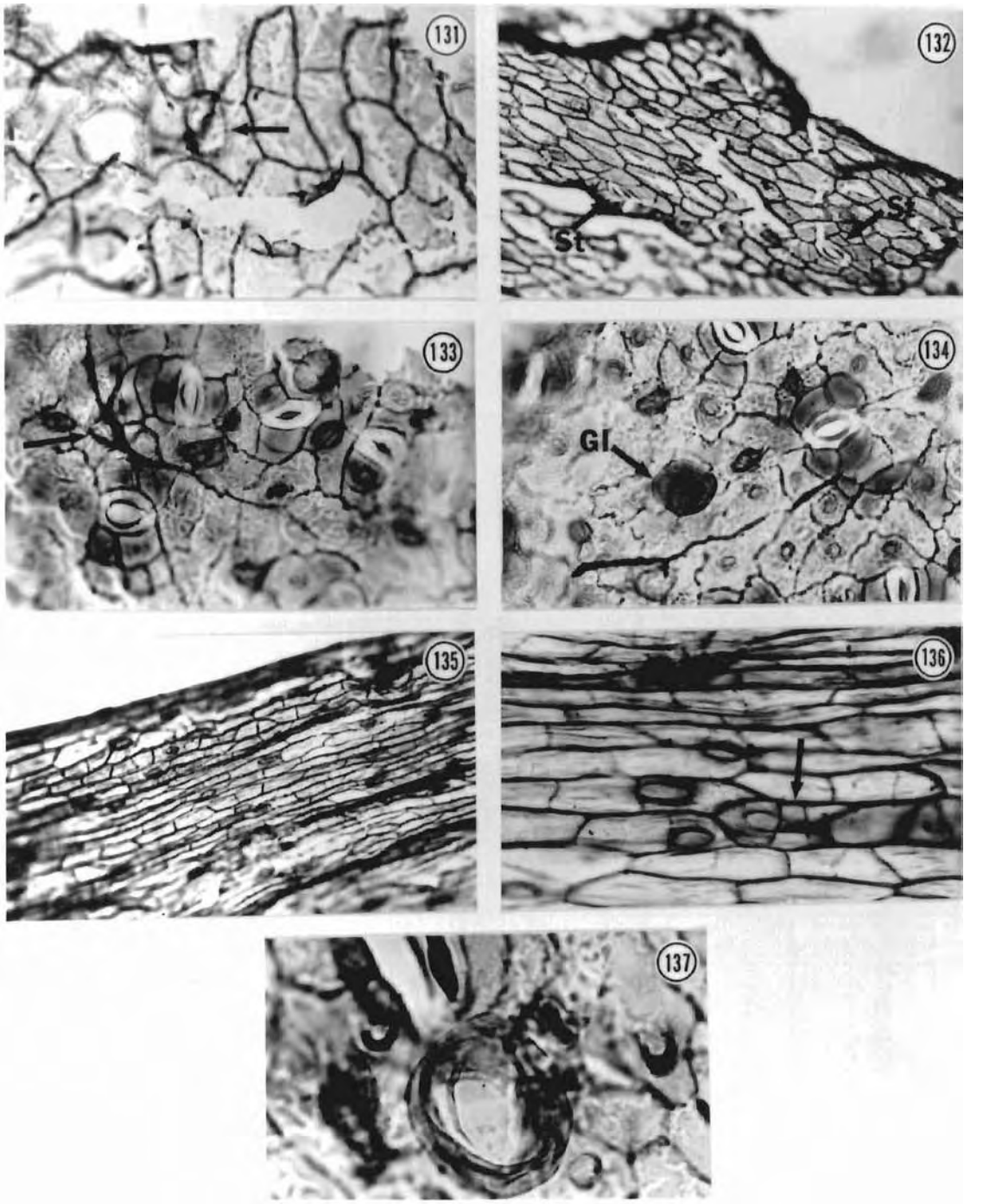

Plate 14

Plate 15

Platanoid #2, leaf fragments and upper cuticle

Fig. 138. Lobate fragment showing rounded sinus and exmedially curving lateral primary vein. x1.

Fig. 139. Close-up of fig. 138 showing lateral primary veins that originate at the base of the leaf (arrows). x3.

Fig. 140. Leaf fragment with a thick basal branch of the lateral primary vein (arrow). x3.

Fig. 141. Leaf fragment showing thin, apically curving secondary vein (2°). x2.

Fig. 142. Upper cuticle of non-veinal region with trichome base (TB). x340.

Fig. 143. SEM of upper cuticle from a non-veinal region showing psilate surface sculpture and basal portion of a hair (H). 1700.

Fig. 144. Region above a primary vein, upper cuticle. 136x.

Fig. 145. Region above a primary vein showing weakly striate surface sculpture and two attached hairs. (H). x1700.

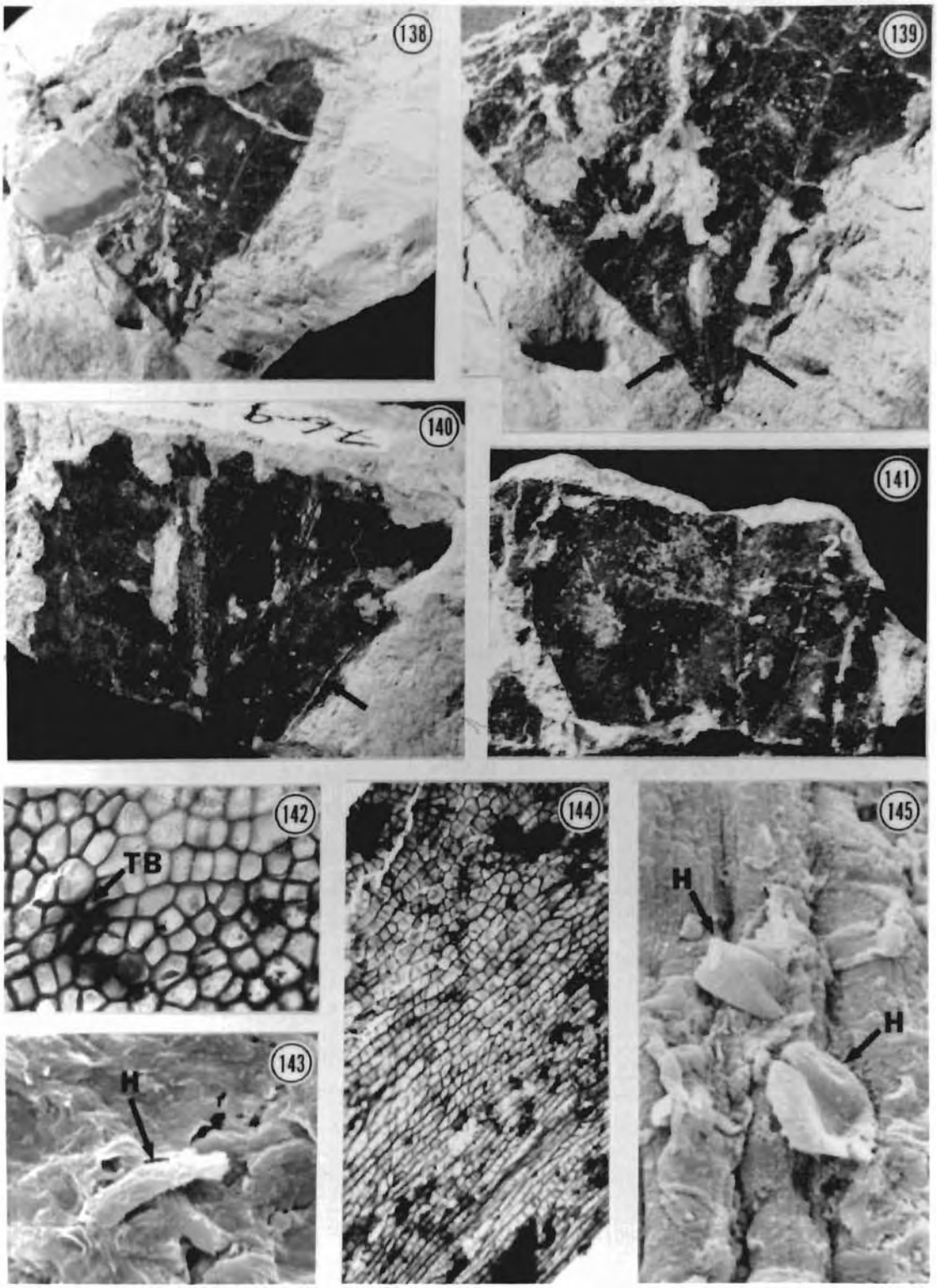

Plate 15

Plate 16

Platanoid #2, lower cuticle

Fig. 146. General shot showing laterocytic stoma embedded in the subsidiary cells (arrow) and numerous light regions marking the point of secretory cell attachment. x510.

Fig. 147. Cells beneath primary vein showing weakly striate surface sculpture. x340.

Fig. 148. Trichome base on veinal area (TB). x340.

Fig. 149. Close-up of non-veinal cells showing prominent papillae (arrow). x850.

Fig. 150. SEM of stomatal complex and associated cells. The guard cells bear inner stomatal ledges (ISL). The subsidiaries have faint cuticular flanges and are arranged in a complex laterocytic pattern. Numerous secretory cells (Gl) are positioned between two or more unspecialized cells. x1700.

Fig. 151. Cells beneath primary vein with an attached hair (H). x1700.

Fig. 152. Hair bases beneath primary vein showing pores and base cells with irregular cuticular thickenings (arrow). x340.

Fig. 153. Mesophyll secretory cells (arrows). x340.

Fig. 154. Non-veinal region showing psilate surface sculpture, secretory cells (Gl), and regions where the secretory cells were abscised (arrows). x3400.

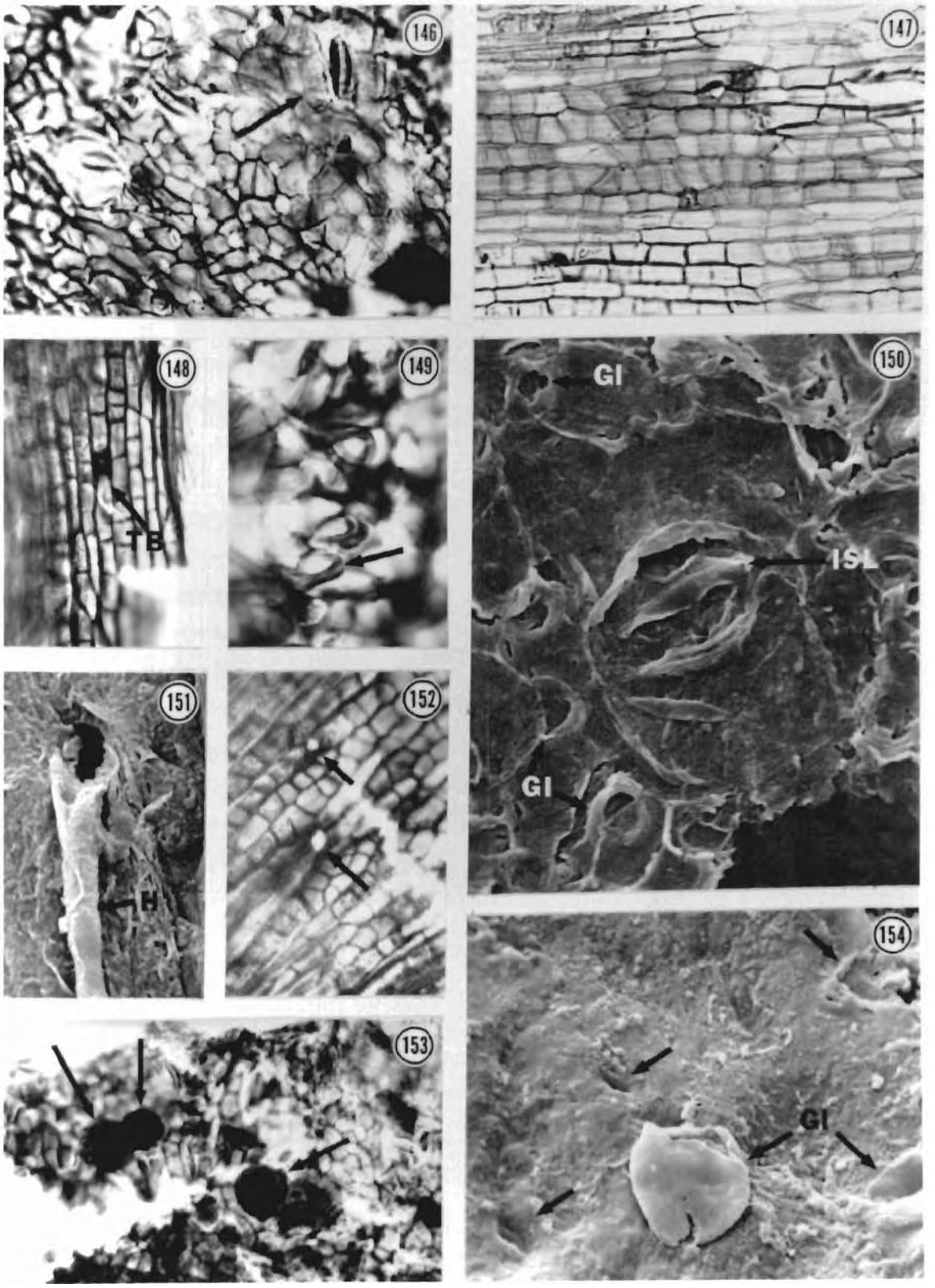

Plate 16

Plate 17

Platanoid #3, leaf fragments and upper cuticle

Fig. 155. Leaf fragment with secondary veins and lobate margin. x1.

Fig. 156. Leaf fragment with preserved base and petiole. x1.

Fig. 157. Close-up of fig. 155 showing percurrent tertiary veins (T), possible stitched intertertiary (IT?) and reticulate quaternary and higher order venation. x5.

Fig. 158. Close-up of fig. 156 showing base and petiole. x2.

Fig. 159. Upper cuticle of non-veinal region. x340.

Fig. 160. SEM of outer cuticle over primary vein, upper cuticle, showing longitudinally aligned cells, trichome bases (TB), and wound structure (arrow). x850.

Fig. 161. SEM of inner cuticle surface, upper epidermis, showing faintly granular internal sculpture. x340.

Fig. 162. Veinal region on upper cuticle with hair base (TB). x150.

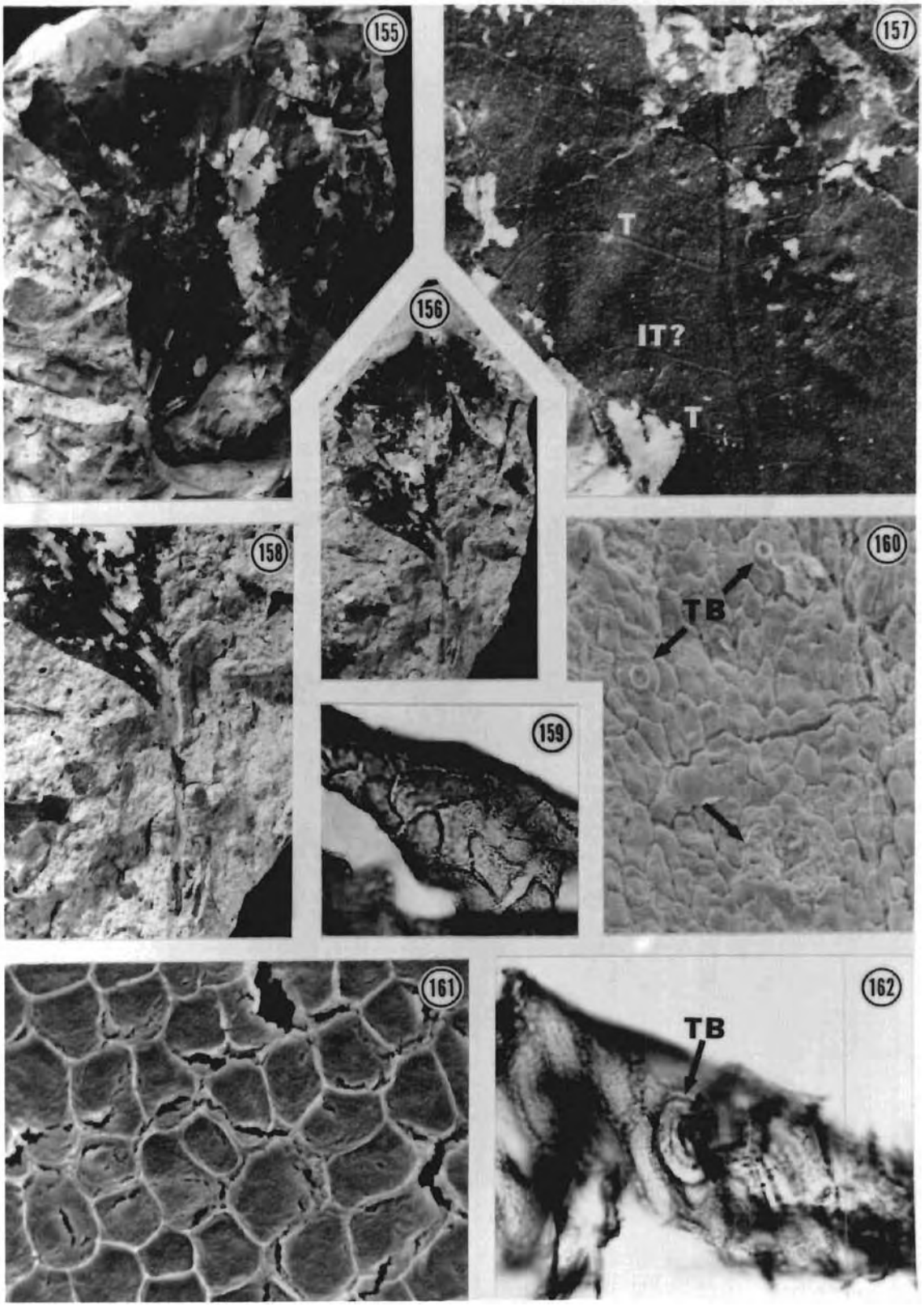

Plate 17

Plate 18

Platanoid #3, lower cuticle

Fig. 163. General shot of non-veinal region. x340.

Fig. 164. SEM of inenr cuticle surface showing granular sculpture and the following stomatal types: paracytic (P), laterocytic (LC) and transitional between laterocytic and cyclocytic (T). x850.

Fig. 165. General shot, region beneath primary vein. x340.

Fig. 166. Outer cuticle surface, non-veinal region, showing psilate sculpture and slightly sunken stoma with outer stomatal ledges (OSL). x1700.

Fig. 167. Close-up of hair bases on veinal cells, showing scarcely modified base cells and a poorly defined ring of thickened cuticle (arrow). x510.

Fig. 168. Hair bases under primary vein (arrows). showing base cells that are small relative to other veinal cells and the placement of the foot cell over the junction of two or more cells. x340.

Fig. 169. SEM of region beneath primary vein showing striate sculpture and several hair bases. x340.

Fig. 170. Hair base on non-veinabl region with a prominent ring of thickened cuticle (arrow). x340.

Fig. 171. SEM of outer cuticle surface, non-veinal region, showing partially collapsed hair base. x1700.

Fig. 172. SEM of inner cuticle surface showing granular sculpture and hair base. x850.

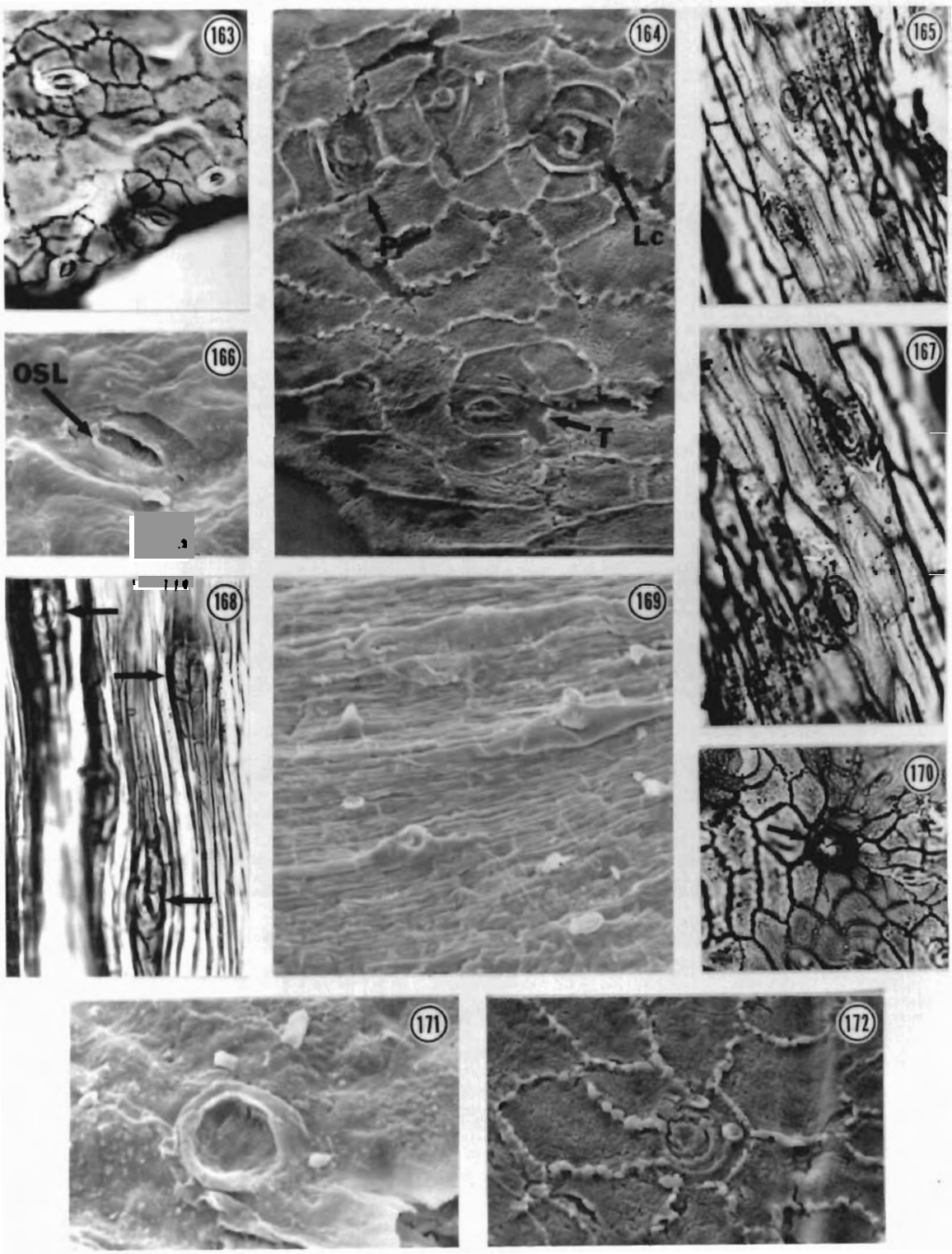

Plate 18

Plate 19

New Serrate, Red Point

Fig. 173 Fragment of an elongate leaf with a decurrent base and numerous straight-convex (B-1) serrations. x2.

Fig. 174. Upper Cuticle. x340.

Fig. 175. General shot of lower cuticle with two stomata (St). x340.

Fig. 176. Close-up of lower cuticle showing cuticle on the inner epidermal surface (IC). x850.

Fig. 177. Region beneath primary vein showing rows of cells, parallel striations, and trichome base (TB). x212.

Fig. 178. Cells beneath secondary vein showing the low papillae on veinal cells. x212.

Fig. 179. Close-up of stoma showing striate subsidiary cells with overarching papillae. x850.

Fig. 180. Lower focus of fig. 179, showing maceration-resistant lamellae in the guard cells and two underthrusting subsidiary cells (arrow). x850.

Fig. 181. Close-up of stoma showing laterally displaced outer and inner lamellae. x850.

Fig. 182. Cluster of hair bases on lower cuticle. x340.

Fig. 183. Close-up of hair base, lower focus. x850.

Fig. 184. Close-up of hair base, upper focus, showing base of attached hair (arrow). x850.

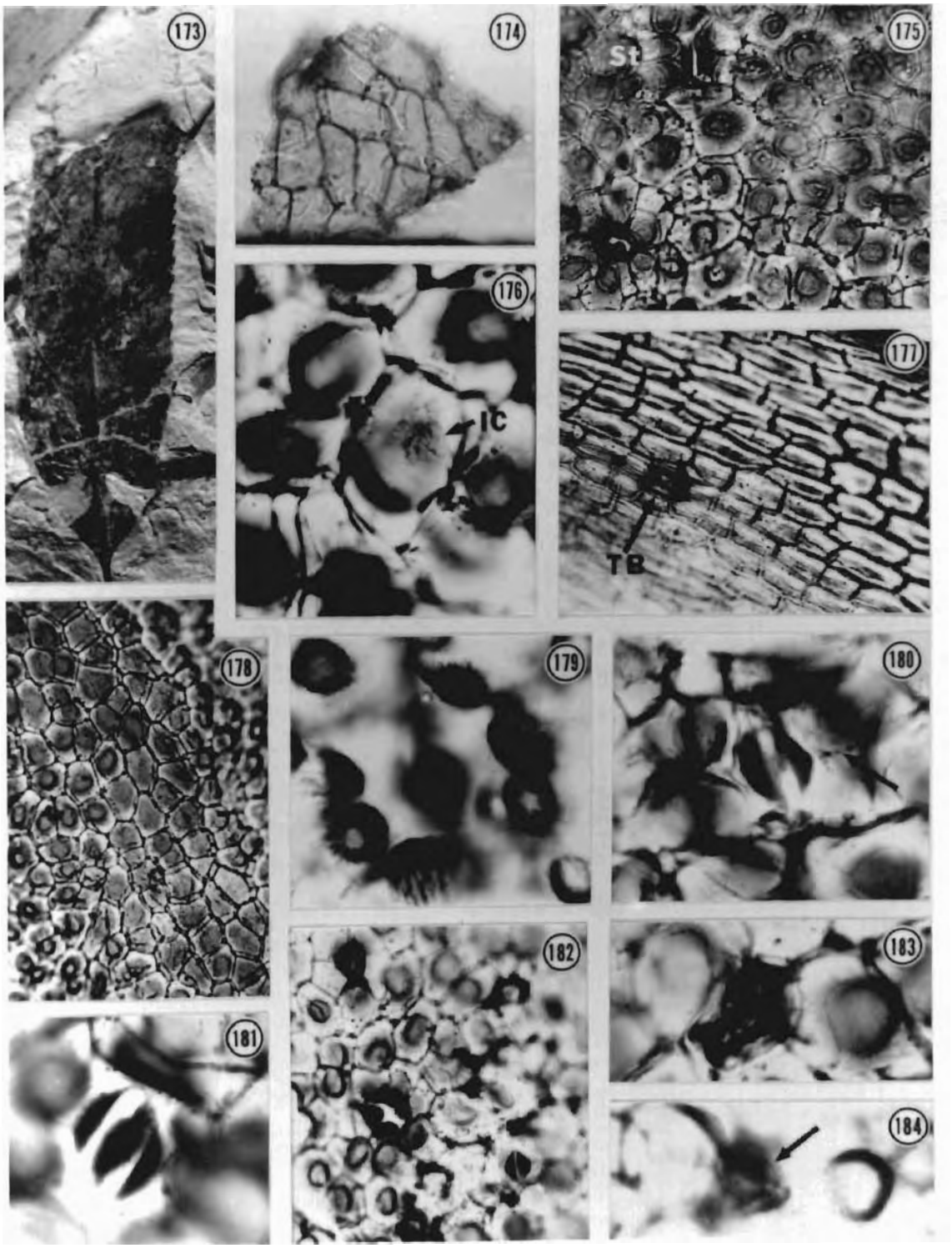

Plate 19

Plate 20

Populophyllum reniforme

Fig. 185. Leaf fragment with crenulate margin (arrow). x1.

Fig. 186. Leaf with shallowly cordate base. x1.

Fig. 187. Leaf fragment with a more deeply cordate base. x1.

Fig. 188. Close-up of fig. 186 showing actinodromous primary venation. x2.

Fig. 189. Leaf fragment photographed with infra-red light showing intra-marginal loops and random reticulate tertiary and quaternary venation. x2.

Fig. 190. Non-veinal region, upper cuticle. x 2.

Fig. 191. Veinal region, upper cuticle. x136.

Fig. 192. SEM of inner cuticle surface, which is minutely pitted except adjacent to the flanges, where there are numerous chambers that open into the inner cuticle surface. x850.

Fig. 193. Hair base with radially elongate base cells, upper cuticle. x340.

Fig. 194. Stomata on lower cuticle showing anomocytic pattern of neighboring cell arrangement. x212.

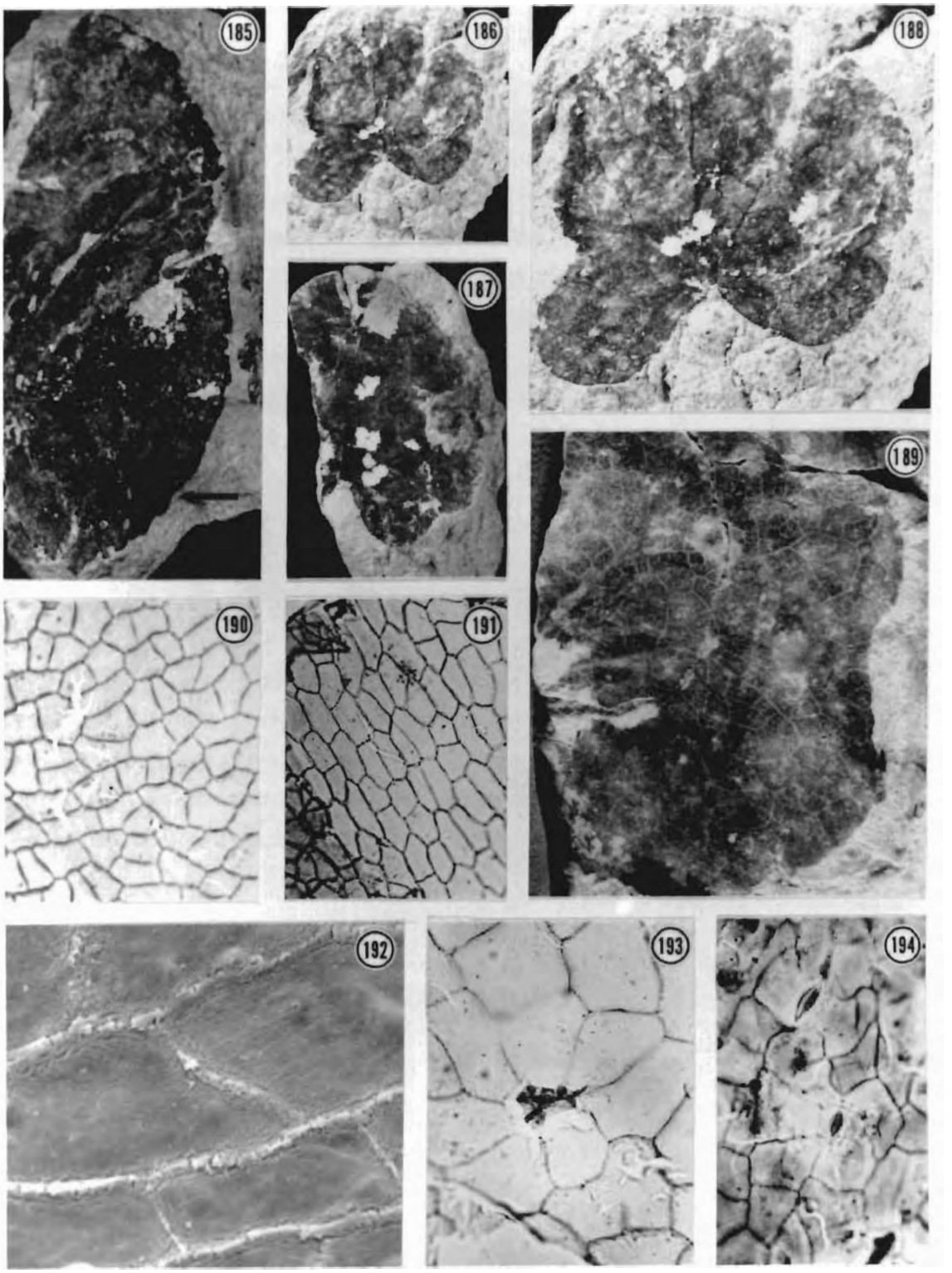

Plate 20

Plate 21

Figs. 195-198. Lower Cuticle of Populophyllum reniforme.

Fig. 195. Veinal region, lower cuticle.

Fig. 196. Guard cells with outer stomatal ledges. The stomata is embedded in the lateral contact cells (arrows). x1700.

Fig. 197. Two stomata. The lower right stoma has contact cells of very different sizes which give the stomatal complex an irregular appearance similar to some Zone I stomata. x212.

Fig. 198. Close-up of stoma showing an irregularly shaped piece of cuticle beneath it. x340.

Figs. 199-206. Menispermites potomacensis

Fig. 199. Leaf fragment. x1.

Fig. 200. Upper cuticle of non-veinal area showing polygonal cells with straight walls. x340.

Fig. 201. Upper cuticle showing cells with undulate anticlinal walls. x136.

Fig. 202. Lower cuticle showing cells with undulate anticlinal walls. x136.

Fig. 203. Lower cuticle showing cells beneath primary vein and trichome base (TB). x136.

Fig. 204. Paracytic stomatal complex with two subsidiary cells (arrows). x510.

Fig. 205. Anomocytic stoma. x510.

Fig. 206. Anomocytic stoma (left) and hemiparacytic stoma with a narrow subsidiary cell (arrow). x510.

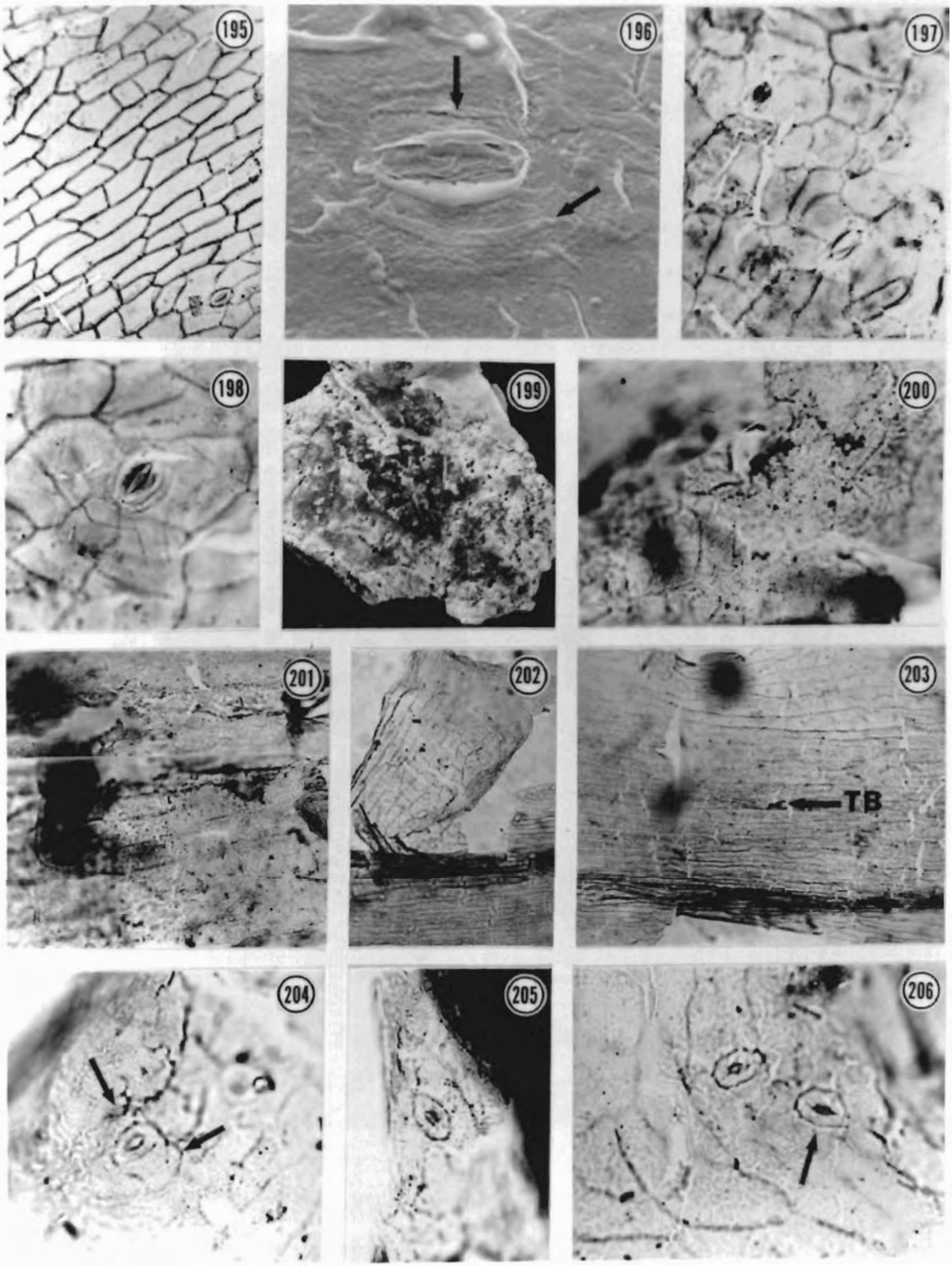

Plate 21

Plate 22

Cuticles of extant angiosperm leaves.

Fig. 207. Platanus chiapensis (Platanaceae), upper cuticle showing hair bases from veinal regions. Note how the hairs are always positioned over the junction of four cells, the base cells are smaller than the other cells, and the cuticle is thickened around the base of each hair in the shape of a ring (arrow). 136.

Fig. 208. P. chiapensis, lower cuticle of same specimen showing veinal hair bases with weakly specialized base cells. Again, note the regularity in the positioning of the hairs above the base cells. x136.

Fig. 209. Platanus sp., two stomatal complexes from the lower cuticle that conform to the complex laterocytic type. Note how the tangential walls of many subsidiary cells are poorly cutinized (arrows). In poorly cutinized leaves the stomata appear anomocytic. x340.

Figs. 210-212. Weinmannia crenata (Cunoniaceae), lower cuticle.

Fig. 210. Stomata showing Sapindopsis pattern of subsidiary cell arrangement and specilization. x510.

Fig. 211. Hair base from same cuticle as fig. 210, showing an elongate foot cell with thickened anticlinal walls and base cells with radial orientation. x340.

Fig. 212. Another hair base from the same cuticle as fig. 210 where the foot cell has a more isodiametric shape. x340.

Fig. 213. Allophyllus apetala (Sapindaceae), stomata showing the Sapindopsis pattern of subsidiary cell arrangement and specialization. x510.

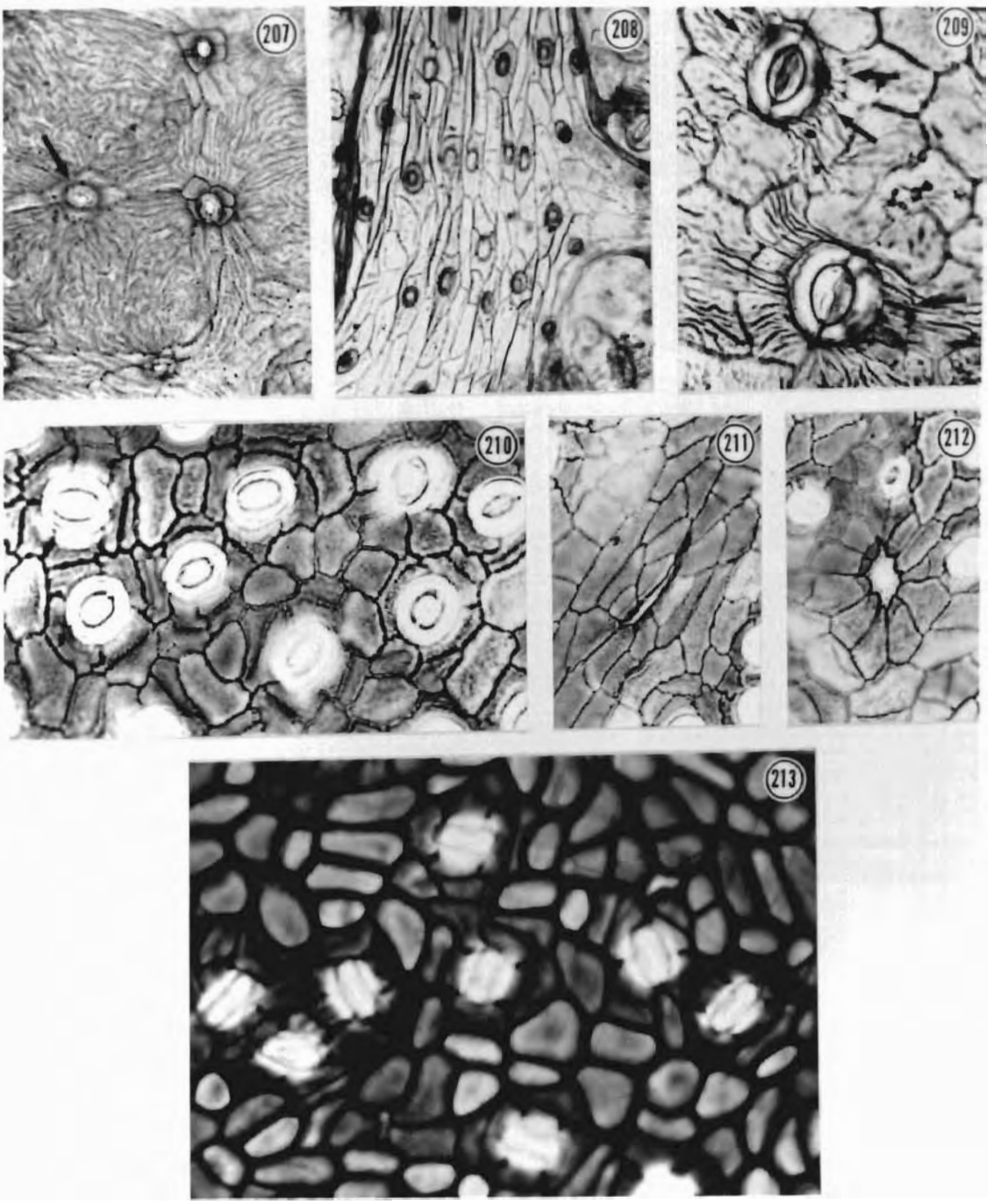

Plate 22