ULTRASTRUCTURE OF LOWER CRETACEOUS ANGIOSPERM POLLEN AND THE ORIGIN AND EARLY EVOLUTION OF FLOWERING PLANTS[1]

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ABSTRACT

In the last decade significant new information has been gained about the early evolution of flowering plants through studies of Early Cretaceous angiosperm pollen and the pollen of living primitive flowering plants. Although most recent palynological studies of extant primitive angiosperms have used both scanning and transmission electron microscopy, few ultrastructural studies of early fossil angiosperm pollen grains exist. This paper represents an attempt to remedy this situation. Thirteen different types of Lower Cretaceous angiosperm pollen grains from the Potomac Group of eastern North America and the Fredericksburgian of Oklahoma were examined ultrastructurally, including *Clavatipollenites hughesii*, two aff. *Clavatipollenites* species, *Asteropollis asteroides*, *Stephanocolpites fredericksburgensis*, *Retimonocolpites dividuus*, *R. peroreticulatus*, two aff. *Retimonocolpites* species, *Stellatopollis barghoornii*, and three species of *Liliacidites*. These grains were investigated using a technique that we have developed for working with single fossil pollen grains by which we are able to undertake combined light, scanning electron, and transmission electron microscopy of the same pollen grain. This technique is invaluable for the evolutionary study of small, light-microscopically similar, dispersed fossil pollen grains, such as those that constitute the bulk of the earliest known part of the fossil record of the flowering plants, and provides a much improved means of delimiting Early Cretaceous angiosperm pollen form genera such as *Clavatipollenites, Retimonocolpites,* and *Liliacidites*. Our study also reveals that a close similarity exists between some Early Cretaceous angiosperm pollen and pollen produced by certain living primitive angiosperms. *Clavatipollenites hughesii, Asteropollis asteroides,* and *Stephanocolpites fredericksburgensis* exhibit varying degrees of similarity at the ultrastructural level respectively to pollen of the extant angiosperm genera *Ascarina, Hedyosmum,* and *Chloranthus,* all three of which belong to the modern family Chloranthaceae. Pollen described under the form genus *Liliacidites* possesses many features that are restricted to pollen of living monocotyledons, while *Retimonocolpites* possesses certain monocotyledonous palynological features, but to a lesser extent. Large monosulcate pollen grains with distinctive crotonoid sculpturing described as *Stellatopollis barghoornii* have no counterpart among the pollen of extant angiosperms.

The question of the origin and early evolution of the angiosperms is dealt with in the second part of the paper, and the fossil pollen record of early flowering plants is considered in light of what is known about pollen evolution in living primitive angiosperms. Analysis of the taxonomic distribution of characters of living primitive angiosperms suggests that angiosperm pollen is primitively monosulcate, boat-shaped, large- to medium-sized, psilate or at best only weakly sculptured, noninterstitiate to interstitiate-granular, atectate, and without endexine. This type of pollen is found today only in the otherwise primitive angiosperm families Magnoliaceae, Degeneriaceae, and Annonaceae. It is concluded that *Clavatipollenites* and other currently known types of Early Cretaceous angiosperm pollen grains represent relatively advanced primitive angiosperm pollen that is already too specialized to reveal anything about the earliest evolution (or the origin) of the flowering plants. Finally, what can be deduced about the origin and early evolution of flowering plants from fossil and living primitive angiosperms is considered. The conclusion is drawn that the ancestry of the angiosperms must be sought in the pteridosperms or in a derivative group. A 5-stage model of early angiosperm evolution is proposed, based on the early (Barremian to Middle Cenomanian) fossil pollen record of the flowering plants and the inferred phylogenetic relationships of living primitive angiosperms. From an original, pre-Barremian basal complex of entomophilous flowering plants, whose living descendants include such angiosperms as the Magnoliales, Laurales, and Winterales, we envision evolution of a major line of anemophilous and apetalous angiosperms in the Barremian-Aptian, the descendants of which include advanced magnoliid angiosperms, such as the Chloranthaceae, as well as related primitive hamamelidid angiosperms, such as the Trochodendrales, Cercidiphyllales, and Hamamelidales. The evolution of

wind-pollination so early within the angiosperms may have been connected with the increasing aridity (and possible decline in insect pollinators) that occurred soon after the earliest appearance of *Clavatipollenites*-type pollen in the Barremian of Africa and South America, when major splitting of West Gondwana was taking place. The majority of dicots, including the subclasses Dilleniidae, Rosidae, and Asteridae, appear to be derived from this early group of entomophilous-derived anemophilous angiosperms, and, thus, most of the dicots probably represent flowering plants that have secondarily returned to entomophily.

Palynology has rapidly become an important source of taxonomic and phylogenetic information for angiosperm systematics, and, indeed, few other fields of botanical inquiry provide so much systematic data from so little material (cf. Walker & Doyle, 1975). In the last decade, for example, significant new insight has been gained into the early evolution of flowering plants through investigations of early fossil angiosperm pollen (Brenner, 1967, 1976; Doyle, 1969, 1970, 1973, 1977a, 1977b, 1978a, 1978b; Doyle et al., 1977; Doyle & Hickey, 1976; Doyle et al., 1982; Doyle & Robbins, 1977; Doyle et al., 1975; Hickey & Doyle, 1977; Hughes, 1976, 1977; Hughes et al., 1979; Kemp, 1968; Laing, 1976; Muller, 1970, 1981; Walker et al., 1983), as well as from studies of the pollen of extant primitive flowering plants (Le Thomas, 1980, 1981; Le Thomas & Lugardon, 1974, 1976a, 1976b; Lugardon & Le Thomas, 1974; Praglowski, 1974a, 1974b, 1976, 1979; Walker, 1971a, 1971b, 1971c, 1972a, 1972b, 1974a, 1974b, 1976a, 1976b, 1979; Walker & Doyle, 1975; Walker & Skvarla, 1975; Walker & Walker, 1979, 1980, 1981, 1983).

Although most recent palynological investigations of living primitive angiosperms have used both scanning electron and transmission electron microscopy, few ultrastructural studies of Early Cretaceous angiosperm pollen grains exist (e.g., Davies & Norris, 1976; Doyle et al., 1975; Hughes et al., 1979). Moreover, most workers have employed scanning electron microscopy (SEM) alone, and few (e.g., Doyle et al., 1975) have used transmission electron microscopy (TEM) as well. This is no doubt due to the difficulties inherent in examining dispersed fossil pollen grains with electron microscopy, and by TEM in particular. For this reason we have begun an ultrastructural investigation of Early Cretaceous angiosperm pollen, using a technique that we have developed for working with single fossil pollen grains by which we are able to undertake light, scanning electron, and transmission electron microscopy of the same pollen grain. The purpose of this paper is to discuss the results and evolutionary implications of a preliminary study of Lower Cretaceous angiosperm pollen from the Potomac Group of eastern North America and the Fredericksburgian of Oklahoma, using this technique.

Ultrastructural Study of Lower Cretaceous Angiosperm Pollen

Our initial study of Early Cretaceous angiosperm pollen has centered mainly on the Potomac Group of the Atlantic Coastal Plain of eastern North America. We chose the Potomac Group for a detailed investigation for several reasons. First, much of the important light-microscope-based evolutionary studies of early fossil angiosperm pollen (e.g., Brenner, 1967; Doyle, 1969, 1970, 1977a, 1977b; Doyle & Hickey, 1976; Doyle & Robbins, 1977; Hickey & Doyle, 1977) are based on the pollen of the Potomac Group. Second, Potomac Group pollen is especially well preserved, not only at the light microscope level (cf. Brenner, 1963), but also ultrastructurally. Third, we have been able to acquire numerous Potomac Group rock samples, the most important of which are more than 50 closely spaced core samples from two shallow wells drilled through the Potomac Group near Delaware City, Delaware, which were kindly provided by Dr. Robert R. Jordan, Director of the Delaware Geological Survey (see Doyle & Robbins, 1977, for a detailed light microscope study of angiosperm pollen from these two Delaware wells). In addition to Potomac Group pollen, we have also examined pollen grains isolated from prepared samples taken from the Fredericksburgian (Albian) of Oklahoma. These samples, which were kindly provided by Dr. R. W. Hedlund, are important because they are the same samples from which the type specimens of both *Asteropollis* Hedlund & Norris and *Stephanocolpites fredericksburgensis* Hedlund & Norris were obtained.

The Potomac Group (Table 1) dates from about the Late Barremian-Early Aptian through the Early Cenomanian according to Doyle and Robbins (1977), and consists of four formations—the Patuxent, Arundel Clay, Patapsco, and Elk Neck Beds (or "Maryland Raritan"). The Late

TABLE 1.   Stratigraphy of the Potomac Group, based on Doyle and Robbins (1977). (Boundaries between stages in Ma, after van Eysinga, 1978.)

SERIES	STAGE	SUBSTAGE		FORMATION	ZONE	SUBZONE	
Upper Cretaceous	Cenomanian (100 m.y.)	Lower	upper	Elk Neck Beds	III	Upper	
			lower			Lower	
Lower Cretaceous	Albian (109 m.y.)	Upper	upper	("Maryland Raritan")	II	C	
			lower	Patapsco Formation		B	upper
		Middle	upper				middle
			middle				lower
			lower			A	
		Lower		Arundel Clay	I	Upper	
	Aptian (114 m.y.)	Upper					
		Lower		Patuxent Formation		Lower	
	Barremian (118 m.y.)						

Barremian to Early Cenomanian represents a time span of approximately 18 Ma from about 116–98 Ma, following van Eysinga (1978). The Potomac Group has been divided into three major zones based on pollen and spore types (Brenner, 1963; Doyle, 1970, 1977a; Doyle & Robbins, 1977). Zone I (from ? Upper Barremian through Lower Albian) is characterized by monosulcate angiosperm pollen, Zone II (Middle and Upper Albian) is characterized by tricolpate to tricolporoidate angiosperm pollen, and Zone III (Lower Cenomanian) is characterized by tricolporate angiosperm pollen that is frequently triangular in equatorial outline. Triporate Normapolles enter above Zone III in the Middle Cenomanian. The most detailed palyno-zonation of the Po-

tomac Group is that of Doyle and Robbins (1977), who recognized subzones as well, dividing Zones I and III into lower and upper subzones, and Zone II into subzones IIA, IIB, and IIC. For discussion of the geological setting of the Potomac Group from a paleopalynological perspective the reader is referred to the papers of Brenner (1963), Doyle (1977a), Doyle and Hickey (1976), Doyle and Robbins (1977), Hickey and Doyle (1977), and Wolfe and Pakiser (1971).

We initially have restricted ourselves to examination of monosulcate and monosulcate-derived early fossil angiosperm pollen before we attempt investigation of the more advanced tricolpate and tricolpate-derived pollen types. The pollen grains we have studied fall into six dif-

ferent currently recognized form genera: *Clavatipollenites, Asteropollis, Stephanocolpites, Retimonocolpites, Stellatopollis,* and *Liliacidites.*

MATERIALS

Lower Cretaceous pollen grains examined in this study were obtained from outcrop and core samples (Potomac Group zonation follows Doyle & Robbins, 1977):

(1) Cleaves 27: E. T. Cleaves (1968) sample no. 27, outcrop sample from the undifferentiated Potomac Formation, Maryland; Lower Zone I of the Potomac Group fide Doyle et al. (1975), Barremian-Lower Aptian (ca. 115 Ma old).

(2) Brenner 10: G. J. Brenner (1963) station no. 10, outcrop sample from the Arundel Clay, Maryland; Upper Zone I of the Potomac Group, Upper Aptian-Lower Albian (ca. 110 Ma old).

(3) Cornet Beltway: B. Cornet outcrop sample from Rt. 495 (Beltway), Exit 25, Maryland; Zone IIB of the Potomac Group fide Cornet, Middle-Upper Albian (ca. 105 Ma old).

(4) Hedlund 3916: R. W. Hedlund collection 3916 cited in Hedlund and Norris (1968), outcrop sample from the Fredericksburgian of Oklahoma; correlative with Middle Zone IIB of the Potomac Group fide Doyle and Robbins (1977), upper Middle Albian (ca. 105 Ma old).

(5) D12-515: Tidewater Oil Company well D12 (Delaware Geological Survey no. Dc53-7), near Delaware City, Delaware, core sample from 515 feet (Delaware Geological Survey sample no. 20083); Middle Zone IIB of the Potomac Group fide Doyle and Robbins (1977), upper Middle Albian (ca. 105 Ma old).

(6) D13-535: Tidewater Oil Company well D13 (Delaware Geological Survey no. Ec14-1), near Delaware City, Delaware, core sample from 535 feet (Delaware Geological Survey sample no. 20235); Upper Zone IIB of the Potomac Group fide Doyle and Robbins (1977), lower Upper Albian (ca. 103 Ma old).

"P" numbers in text and figure legends are palynological accession numbers given to each plant collection from which modern pollen was obtained. "FP" numbers represent fossil palynomorph accession numbers given to every individual fossil palynomorph isolated.

METHODS

When we initially began this investigation of early fossil angiosperm pollen our sole interest was in studying the ultrastructure of the pollen grains we examined. However, since most of the literature and almost all the nomenclature of dispersed fossil pollen and spores is based on light microscope studies alone, it was soon apparent that it would also be highly desirable to have photomicrographs of the same pollen grains that we examined with electron microscopy. Moreover, during our palynological studies of extant Myristicaceae (Walker & Walker, 1979), a family whose pollen is similar at the light microscope level to some types of Lower Cretaceous angiosperm pollen grains, we discovered that closely related genera could produce pollen virtually identical with regard to exine sculpturing as seen with the scanning electron microscope that, nevertheless, was always distinguishable by exine structure when examined with the transmission electron microscope (cf. Figs. 1–6). Thus, when investigating dispersed fossil pollen grains for taxonomic and evolutionary (as opposed to stratigraphic) purposes, we felt that it was highly advantageous to be able to undertake combined light, scanning electron, and transmission electron microscopy of the same pollen grain to establish unequivocally that one was actually dealing with pollen produced by one and the same biological entity. To this end we developed a technique that allows us to obtain photomicrographs (PMG), scanning electron micrographs (SEMG), and transmission electron micrographs (TEMG) of the same individual pollen grain. We believe that this technique is a virtual necessity for the evolutionary study of small, light-microscopically similar, dispersed fossil pollen grains such as those that constitute most of the earliest known part of the fossil record of the flowering plants.

Our technique for working with single fossil pollen grains is as follows. Fossil pollen was extracted from Potomac Group outcrop and core samples using a slightly modified version of the sample preparation outlined by Brenner (1963). Rock samples are first crushed in distilled water with a mortar and pestle. The disaggregated material is then centrifuged and ZnCl heavy liquid solution (specific gravity 2) is used to separate organic from inorganic matter by flotation. The float is pipetted off, and a few drops of 10% HCl are added to prevent zinc hydroxide precipitation. The sample is then washed twice with distilled water, and, after centrifugation, HF is added to remove clay particles. After washing and further centrifugation, the sample is oxidized briefly (2–3 minutes) with a 5.25% solution of sodium
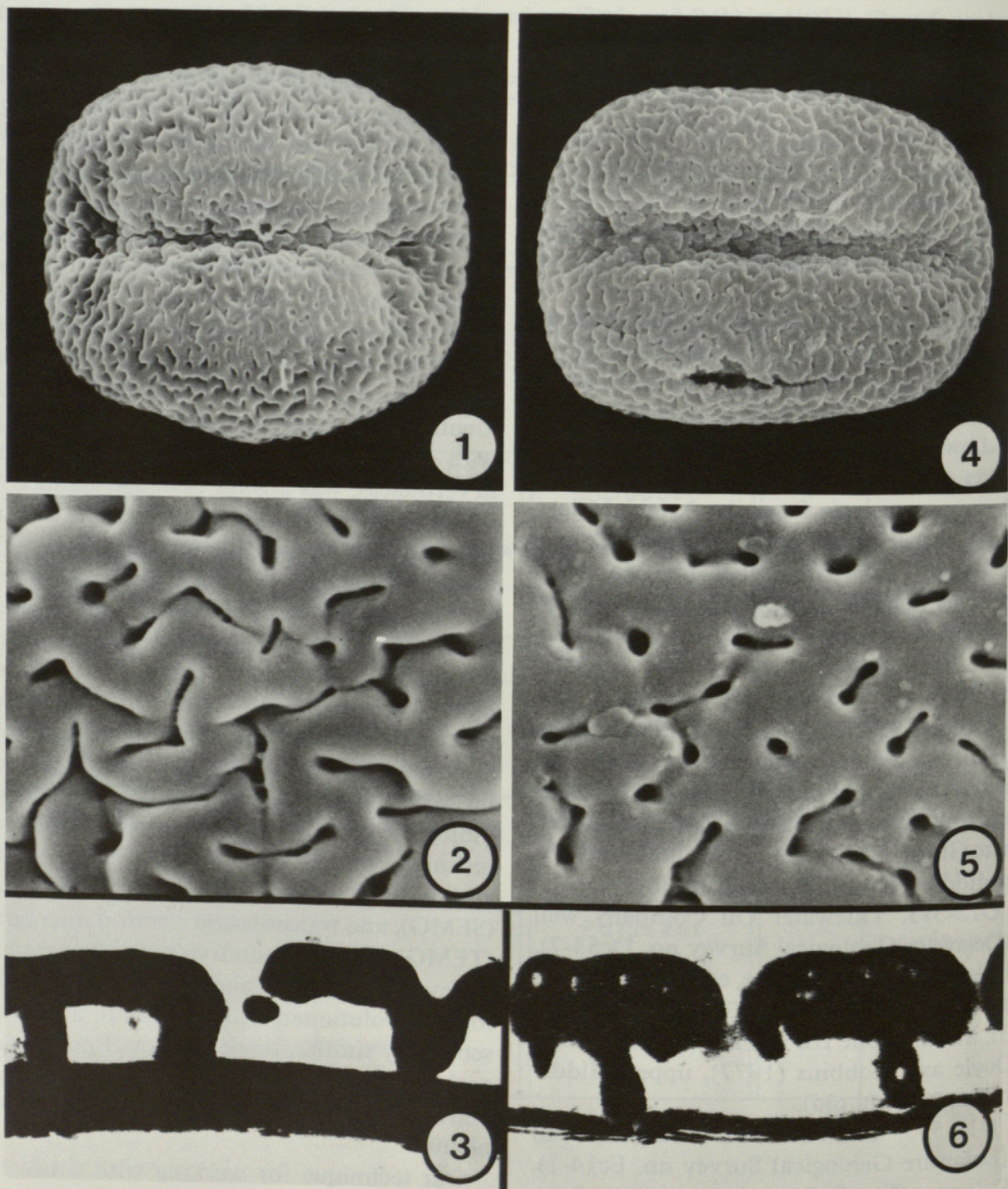
FIGURES 1–6. Myristicaceae. 1–3. *Compsoneura.* 4–6. *Virola.* — 1. Whole grain SEMG, ×2,520. — 2. Exine surface SEMG, ×12,000. — 3. Nonapertural exine section TEMG, ×15,100. — 4. Whole grain SEMG, ×2,360. — 5. Exine surface SEMG, ×16,000. — 6. Nonapertural exine section TEMG, ×18,200. Although pollen grains of some species of *Compsoneura* and *Virola* are virtually identical externally, even in SEMG (cf. Figs. 1 & 4, 2 & 5), pollen of the two closely related genera can be distinguished consistently by features of exine structure evident in TEMG (cf. Figs. 3 & 6). Pollen of *Compsoneura* (Fig. 3) has a relatively thick, non-lamellate nexine, while pollen of *Virola* (Fig. 6) is characterized by a very thin, finely lamellate nexine. In addition, pollen grains of *Virola* (Fig. 6) have conspicuous, spherical, intra-exinous cavities within the sexine that are lacking in the pollen of *Compsoneura* (Fig. 3).

hypochlorite. This is followed by another wash cycle and treatment with 10% NH_4OH for three minutes. Finally, the material is washed again, and the pollen/spore samples are stored in glycerin-water. We found that a shorter period of oxidation than the 20 minutes used by Brenner gave excellent results, and have adopted this modification since we consider it highly desirable for ultrastructural studies to have as gentle a preparatory process as possible.

In order to get single angiosperm pollen grains for study, open glycerin spreads are made on

microscope slides from outcrop and core samples that have had their pollen extracted and prepared as outlined above. These slides are then carefully scanned under low power (160–200×) of a light microscope and individual pollen grains are picked out with an eyelash attached to a wooden applicator stick (or with a micropipette). Single pollen grain slides are prepared, and each grain is given its own "FP" (fossil palynomorph) accession number. Isolation of angiosperm pollen grains from gymnosperm pollen as well as spores may take considerable time since in some Potomac Group samples angiosperm pollen makes up less than 1% of the total pollen grains and spores present.

Each grain is then photographed under a Leitz NPL Fluotar 100× oil immersion objective with a Leitz Dialux 20 brightfield light microscope and a Leitz Vario Orthomat camera, using Kodak High Contrast Copy Film or Kodak Technical Pan Film 2415. Following photomicroscopy, the cover slip is removed from the original slide and the pollen grain is transferred to a clean microscope slide and washed with 70% ethanol several times using a micropipette to remove the glycerin. The washed pollen grain is then placed on an SEM specimen holder and sputter-coated with gold-palladium for about three minutes. After scanning electron micrographs of one side of the grain are taken with a JEOL JSM-35 SEM using Polaroid Type 665 positive/negative film (with 0° tilt and an accelerating voltage of 30 kV), 70% ethanol is used to loosen the grain, and it is turned over with an eyelash under a light microscope. The grain is then re-coated in the sputter coater and its other side is photographed with the SEM.

After scanning electron microscopy has been completed, the grain is treated with dilute aqua regia to remove the heavy metal coating. This is followed by preparation for transmission electron microscopy. First, the grain is placed in agar and fixed in a 1% aqueous solution of OsO_4 for two hours at room temperature. Then, it is washed four times with distilled water and enbloc stained in a saturated aqueous solution of uranyl acetate for two hours at room temperature. After washing four times with distilled water, the grain is dehydrated in an acetone series and embedded in Spurr's low viscosity embedding medium, which is cured in an oven at 70°C for 12 hours. The block containing the single pollen grain is trimmed down to the grain itself (one of the most difficult parts of the entire procedure) and the
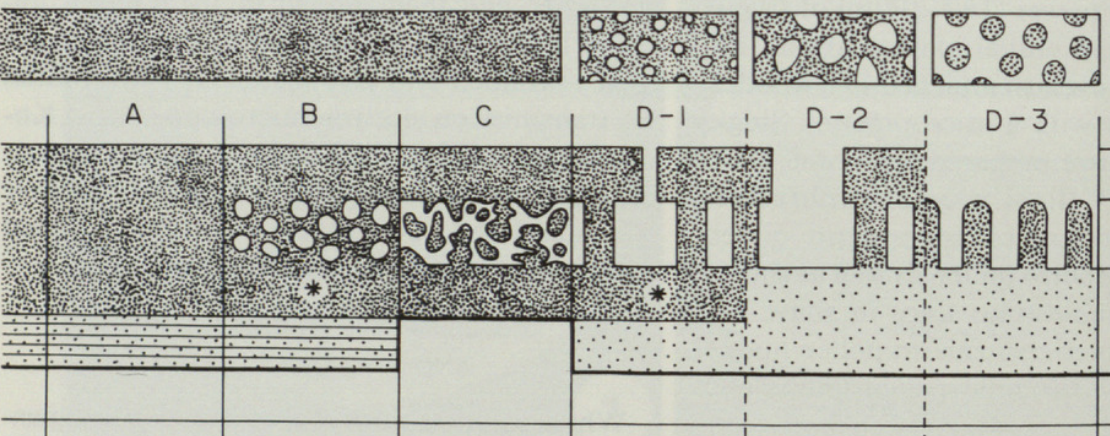
grain is then sectioned with a Reichert ultramicrotome using a Dupont diamond knife. The sections are picked up on formvar-coated, single-slot grids, and then stained in 1% $KMnO_4$ followed by Reynold's lead citrate. The sections are then examined and photographed with a Zeiss 9A transmission electron microscope, using Kodak Electron Image Film 4463. Prints were made on Agfa Brovira paper with Omega Pro-Lab 4 × 5 standard and point-source enlargers equipped with Schneider Componon-S lenses.

POLLEN WALL ARCHITECTURE AND STRATIFICATION

While palynological characters such as aperture type, pollen shape, and pollen size can be readily determined by light or photomicroscopy (LM) alone, scanning electron microscopy (SEM) and transmission electron microscopy (TEM) are required to obtain a thorough understanding of the morphology of the pollen wall itself. Since concepts and terminology dealing with the pollen wall are considerably varied, basic features of pollen wall morphology will be briefly outlined at this point to provide a general background for our ultrastructural study of Lower Cretaceous angiosperm pollen.

As with plant cells in general, the living protoplast of each pollen grain is surrounded by a predominantly cellulosic cell wall layer, which in pollen is known as the intine. Pollen grains, however, have an additional wall layer external to the intine that is known as the exine. The exine, unlike the cellulosic intine, is made-up of sporopollenin, which is a highly chemically and biologically resistant material consisting of carotenoid polymers (Shaw, 1971). The exine represents the taxonomically and evolutionarily most important part of the pollen wall since the intine is generally not preserved in fossil pollen and is usually destroyed as well during the commonly employed preparatory treatment used for modern pollen known as acetolysis. Moreover, the exine is generally a complex layer, both externally (sculpturally) and internally (structurally), whereas the intine with a few notable exceptions is usually simple morphologically. For these reasons the following discussion will be restricted to consideration of the exine alone. Exine morphology will be discussed under the following four headings: nonapertural exine sculpturing, nonapertural exine structure, exine stratification, and aperture ultrastructure. Certain aspects of pollen wall architecture and stratification in gen-

TABLE 2. Composite nonapertural pollen wall section with exine surface views at top, showing basic pollen wall stratification and exine structure (including major exine interstitial and tectal types).

Pollen Wall Strata

- ▨ ektexine } exine
- ▤ endexine }
- ☐ intine
- ∗ foot-layer

Exine Interstitial Types

- A — noninterstitiate (atectate)
- B — cavitate }
- C — granular } interstitiate
- D — columellate }

Exine Tectal Types

- (1) atectate (A)
- (2) tectate
  - (a) tectate—imperforate (B,C)
  - (b) tectate—perforate (D-1)
- (3) semitectate (D-2)
- (4) intectate (D-3)

eral are summarized in Table 2, which will be referred to throughout the following discussion.

Nonapertural exine sculpturing. Nonapertural exine sculpturing refers to all external surface features of the nonapertural exine, and usually is taken to include only features of the outer exine surface, although sometimes the inner surface of the exine may have important sculptural details as well (cf. Van Campo, 1978). Although it can be studied by light microscopy alone, nonapertural exine sculpturing, particularly in small pollen grains, is best observed with scanning electron microscopy (cf. Walker, 1972a). Pollen grains that are (1) psilate (smooth), (2) foveolate (pitted), (3) fossulate (grooved), (4) scabrate (with fine surface features), (5) verrucate (warty), (6) baculate (with rod-like elements), (7) pilate or clavate (with rod-like elements that have swollen heads), and (8) echinate (spiny) include the most commonly encountered types of nonapertural exine sculpturing.

Pollen that is reticulate, i.e., has an open network or reticulum on the surface of its exine (Table 2, D-2), represents another common type of nonapertural exine sculpturing, and, indeed, reticulate sculpturing is characteristic of all Lower Cretaceous angiosperm pollen grains examined in this study. The reticulum in reticulate pollen consists of walls known as muri with spaces between the muri, which are designated as the lumina. In the Lower Cretaceous angiosperm pollen grains examined the muri may be smooth, i.e., psilate (Fig. 89), covered with small spines, i.e., spinulose (Fig. 46), covered with granules, i.e., granulose (Fig. 24), divided into discrete, bead-like subunits, i.e., beaded (Fig. 21), or covered with fine, band-like lines, i.e., banded (Fig. 66). In one pollen type the muri are covered with triangular elements, resulting in a "crotonoid" sculpturing pattern (Fig. 83), named after a similar type of sculpturing found in the pollen of the euphorbiaceous genus *Croton*. Most of the fossil pollen types investigated have an irregular reticulum with a variety of lumina sizes and shapes (Fig. 9), but in a few instances the reticulum is regular with either circular (Figs. 83, 95) or polygonal (Fig. 101) lumina. Sometimes the same pollen grain has both coarsely and finely reticulate areas on its exine surface (Figs. 88–90), and some pollen types exhibit strongly dimorphic lumina with minute lumina interspersed among much larger ones (Figs. 89, 95, 101). Finally, in

a few instances the muri are nodose, i.e., swollen at the points where the underlying columellae meet them (Fig. 34).

Nonapertural exine structure. Nonapertural exine structure refers to all internal morphological features of the nonapertural exine. Although light microscopy can give some idea of exine structure, internal exine features are best observed in scanning electron and transmission electron micrographs of exine sections. In some pollen grains the nonapertural exine is morphologically uniform (Table 2, A). We designate such pollen as noninterstitiate (or atectate). The nonapertural exine of most pollen grains, however, is interstitiate (Table 2, B–D-2), and has an inner structural layer or zone that we have termed the interstitium (Walker & Walker, 1981). There are several exine interstitial types, including cavitate interstitia with a series of structural cavities (Table 2, B), granular interstitia composed of granules (Table 2, C), and columellate interstitia that consist of a series of upright, rod-like structural elements known as columellae (Table 2, D-1, D-2). It is the presence of an interstitium that allows recognition of a basal exine layer, the nexine, and a roof-like layer, the tectum, in the typical pollen grain (cf. Table 2). The interstitium plus the tectum constitutes the so-called sexine. The thickness of the nexine, interstitium, and tectum as a percentage of total nonapertural exine thickness is often a taxonomically important character. For this reason the various exine layers thickness classes used in this paper have been defined in Table 3. If, for example, the nexine constitutes 60% of the total thickness of the nonapertural exine in a particular pollen grain, and the columellae account for 30% while the tectum makes up only 10% of the exine thickness, the pollen grain would be described as having a very thick nexine, an average interstitium, and an extremely to very thin tectum.

Several different exine tectal types are possible in interstitiate pollen grains. In tectate pollen, i.e., in pollen that has a roof or tectum as part of its exine, the tectum may be solid, resulting in a tectate-imperforate exine (Table 2, B, C), or small holes, i.e., tectal perforations, may be present in the tectum, resulting in tectate-perforate pollen (Table 2, D-1). If the tectal perforations are as large or larger than the remaining solid areas of the tectum that lie between them, the pollen is semitectate (Table 2, D-2). While semitectate pollen is invariably reticulately sculptured as well, tectate-perforate pollen grains may

TABLE 3. Pollen exine layers (nexine, interstitium, and tectum) thickness classes.

Percent of Total Nonapertural Exine Thickness	Thickness Class
>75%	extremely thick
50–75%	very thick
41–49%	moderately thick
25–40%	average
15–24%	moderately thin
10–14%	very thin
<10%	extremely thin

be reticulately sculptured or not. In some pollen the nonapertural exine is represented simply by a solid basal layer and overlying sculptural elements; such pollen may be described as intectate (Table 2, D-3), but this condition is rare.

Exine stratification. Exine stratification refers to chemical differences that may be evident in various layers or strata of the exine. Exine stratification is best observed in exine section transmission electron micrographs as layers of differing electron opaqueness, although basic fuchsin staining and light microscopy can also be used to reveal chemical differences in exine layers, even in fossil pollen grains (cf. Leffingwell et al., 1970). Using the methods outlined above, it is apparent that the exine in many pollen grains consists of two chemically different layers—an outer, generally denser layer designated the ektexine, and an inner, generally less dense layer known as the endexine (cf. Table 2, A, B, D). As a rule, chemically uniform exine appears to be wholly ektexinous and without endexine (Table 2, C). In fossil pollen ektexine-endexine polarity is frequently reversed, with the inner endexine appearing denser than the outer ektexine (cf. Trevisan, 1980).

Endexine may be found throughout the exine or it may occur only as part of the apertures. In gymnosperms, the endexine is generally laminated (Van Campo, 1971) with a series of parallel laminations that are continuous throughout both the apertural and nonapertural regions of the endexine (cf. Table 2, A, B). In angiosperms, on the other hand, endexine is either absent entirely (Table 2, C) or present but non-laminated (Table 2, D) (cf. Doyle et al., 1975). Sometimes, however, the nexine of a wholly ektexinous, non-stratified exine may be lamellate. This, for example, is common in such primitive angiosperm families as the Annonaceae (Le Thomas, 1980,

1981) and Myristicaceae (Fig. 6) (Walker & Walker, 1979, 1980, 1981, 1983). In other instances, the endexine under apertures in angiosperm pollen may be lamellate, but this type of lamellate endexine is generally composed of discontinuous lamellae that apparently are fundamentally different from the truly laminated endexine of gymnosperms. When endexine is present in nonapertural regions of the exine, it most commonly comprises only part of the nexine, i.e., the morphologically defined basal layer of an interstitiate exine, and, when this is the case, the upper ektexinous part of the nexine is termed the foot-layer (Table 2, B, D-1). Rarely, is the nexine wholly endexinous, and a foot-layer absent (Table 2, D-2, D-3).

Aperture ultrastructure. Generally, pollen apertures represent sculpturally (i.e., externally) as well as structurally (internally) distinct areas of the exine. Externally, apertures usually appear as differently sculptured areas of the exine (Figs. 8, 13, 39, 52), while internally they commonly represent disorganized regions of the sexine underlaid by thinner nexine, relative to the nexine in nonapertural regions of the exine (Fig. 85). Sometimes, however, an aperture may be represented internally only by a thinning of the nexine, and by little or no discernible disorganization of the overlying sexine (Fig. 91). In pollen grains with endexine, frequently the endexine is thicker under the apertures (cf. Figs. 48, 49), or as previously indicated, endexine may be restricted to apertural areas and absent entirely in the nonapertural exine (cf. Figs. 16, 17). Although the endexine in angiosperms is usually homogeneous (Fig. 11), sometimes it is heterogeneous and stratified (Figs. 17, 43), and in some instances the foot-layer and endexine may be conspicuously interbedded (Fig. 49).

RESULTS

CLAVATIPOLLENITES COUPER

The most widely discussed type of Early Cretaceous angiosperm pollen consists of medium-sized, slightly boat-shaped to globose, monosulcate pollen grains referred to under the form genus *Clavatipollenites* Couper. Couper's diagnosis of the genus (Couper, 1958) was based on the type species, *Clavatipollenites hughesii* Couper. The holotype of *C. hughesii* comes from the Wealden of England and, according to Kemp (1968), is probably Upper Barremian in age. Couper described *Clavatipollenites* as "mono-

sulcate, sulcus broad and long; grains broadly elliptical to almost spherical in equatorial contour; exine clearly stratified, consisting of an inner unsculptured layer (nexine) arising from which is a sculptured layer (sexine) made up of clavate projections, tending to expand and fuse together at their tips to form a tectate exine."

In 1968, Kemp redescribed *Clavatipollenites hughesii* and published photomicrographs of additional pollen grains of this species, some of which were obtained from the same core sample that originally provided the holotype of *C. hughesii*. Although *Clavatipollenites* as originally described by Couper (1958) and redescribed by Kemp (1968) encompassed only monosulcate pollen, some workers, e.g., Doyle and Robbins (1977), have broadened the circumscription of the genus to include trichotomosulcate pollen grains as well. Pollen of the *Clavatipollenites* type (at least as judged by light microscopy) is geographically widespread in the middle and late Early Cretaceous, occurring according to Doyle (1969) in the Barremian through Albian of West Africa, the Aptian and Albian of Central America, the presumed pre-Albian of southern Argentina, the Albian of Australia, the Aptian and Albian of Portugal, the Barremian through Albian of England, the probable late Barremian through Albian of central Atlantic North America, and the Middle through Late Albian of the Canadian Plains.

Pollen grains from the Potomac Group that would be described as *Clavatipollenites* from light microscope study alone fall into two different groups when examined ultrastructurally. Pollen in the first group is the same we believe as the type species of the genus, *C. hughesii*. The second group contains a diversity of pollen types that at this time we will refer to simply as the aff. (= affinity) *Clavatipollenites* group.

Clavatipollenites hughesii. Preliminary studies suggest that *Clavatipollenites hughesii* Couper, i.e., pollen strictly referable to the type of the genus *Clavatipollenites* from the Wealden of England, also occurs in the Potomac Group, at least in Lower Zone I, which is probably Barremian to Lower Aptian in age. A pollen grain that we consider to belong to *C. hughesii* is shown in Figures 7–11. The photomicrographs (PMG), scanning electron micrographs (SEMG), and transmission electron micrographs (TEMG), as is the case with all Lower Cretaceous angiosperm pollen included in this study, were all obtained from the same pollen grain. For this reason there

can be no doubt whatsoever that all palynological features observed in Figures 7–11 belong to one and the same biological entity, irrespective of whether these characters were observed by means of light (Fig. 7), scanning electron (Figs. 8, 9), or transmission electron (Figs. 10, 11) microscopy. The conspicuous columellae, which have frequently been described as clavae by those working with light microscopy alone, and which are responsible for the name *Clavatipollenites* itself, can be clearly seen at the top right in Figure 7. Scanning electron microscopy, however, shows that *C. hughesii* is not intectate with clavate sculpturing, as originally supposed by Couper (1958) when he described *Clavatipollenites* as "made up of clavate projections, tending to expand and fuse together at their tips to form a tectate exine." It is clear from SEM and TEM examination that *C. hughesii* is tectate-perforate to semitectate (Figs. 9, 10), and not intectate. SEM also reveals that *C. hughesii* is characterized by an irregular reticulum composed of beaded to spinulose muri (Fig. 9). TEM further demonstrates that *C. hughesii* has a moderately to very thick nexine, well-developed columellae, and a distinct tectum (Fig. 10). Moreover, TEM reveals that a thick endexine is present under the aperture of *C. hughesii* (Fig. 11), while in nonapertural regions endexine is absent (Fig. 10).

The aperture of *C. hughesii* is externally verrucate (Fig. 8), while internally it consists of a very thick, apparently homogeneous endexine and a thin, occasionally lamellate foot-layer overlaid by a thick sexine organized into verrucae (Fig. 11). Doyle et al. (1975), however, contended that *C. hughesii* has only low verrucate apertural sculpturing, and that the prominent apertural details observed with light microscopy (cf. Fig. 7) are at least partly internal. This conclusion is based on SEM and TEM study of pollen grains designated as *Clavatipollenites* cf. *hughesii*, which were isolated from the same Potomac Group outcrop sample (Cleaves 27) from which we obtained the pollen grain illustrated in Figures 7–11. Furthermore, they described endexine under the aperture of *C. hughesii* as "endosculptured," and suggested that this internal sculpturing is "responsible for much of the granular appearance of the sulcus membrane as seen with light microscopy." Our whole grain SEMG of *C. hughesii*, in which the aperture is more or less fully expanded, clearly shows that the aperture is conspicuously verrucate (Fig. 8). Moreover, TEMG of this grain (Fig. 11) demonstrate that the endexine under the aperture is not "endosculptured," even though light microscopy of the same grain (Fig. 7) reveals a highly "granular" aperture. We believe that the so-called endosculpturing of the apertural endexine described by Doyle et al. (1975) was probably just a preservational artifact due to selective degradation of part of the endexine, and that the granular appearance of the aperture of *C. hughesii* observed in photomicrographs is due to an externally verrucate surface, and not to any internal sculpturing. In this connection, it is interesting to note that a similar condition, presumably also representing differential preservation with the endexine uniform in some grains and ragged in others, was encountered in *Stephanocolpites fredericksburgensis* (cf. below).

Aff. Clavatipollenites group. We have discovered that many Potomac Group pollen grains that appear to be essentially the same as *C. hughesii* in the light microscope, are actually quite different from *C. hughesii* when examined ultrastructurally. For the present, we have chosen to refer to these pollen types simply as the "aff. *Clavatipollenites* group." Two examples of this type of pollen, which we have designated as aff. *Clavatipollenites* Couper spp. 1 and 2, are shown in Figures 18–22 and Figures 23–26, respectively. Aff. *Clavatipollenites* sp. 1 (Figs. 18–22) is trichotomosulcate, while aff. *Clavatipollenites* sp. 2 (Figs. 23–26) is monosulcate. Both types of pollen are medium-sized and more or less globose, although sometimes aff. *Clavatipollenites* sp. 2 is slightly boat-shaped. In contrast to *C. hughesii*, which has a truly spinulose reticulum, muri of the aff. *Clavatipollenites* group are fundamentally beaded (Figs. 20, 21), although in aff. *Clavatipollenites* sp. 2 it appears that the bead-like subunits of the muri have broken-up into coarse, double-rowed granules (Fig. 24). In addition, pollen of the aff. *Clavatipollenites* group on the whole seems to have somewhat larger tectal perforations than *C. hughesii*, and, therefore, is basically semitectate (Figs. 18, 19, 23) rather than tectate-perforate (Fig. 8). While well-developed columellae are present in both pollen types, the nonapertural nexine is only average in thickness in pollen grains of the aff. *Clavatipollenites* group (Figs. 22, 26), while in *C. hughesii* it is moderately to very thick (Fig. 10). The most distinctive feature of the aff. *Clavatipollenites* group, however, is a lack of endexine, even under the aperture (Figs. 22, 25), which is markedly different from *C. hughesii*, with its well-devel-
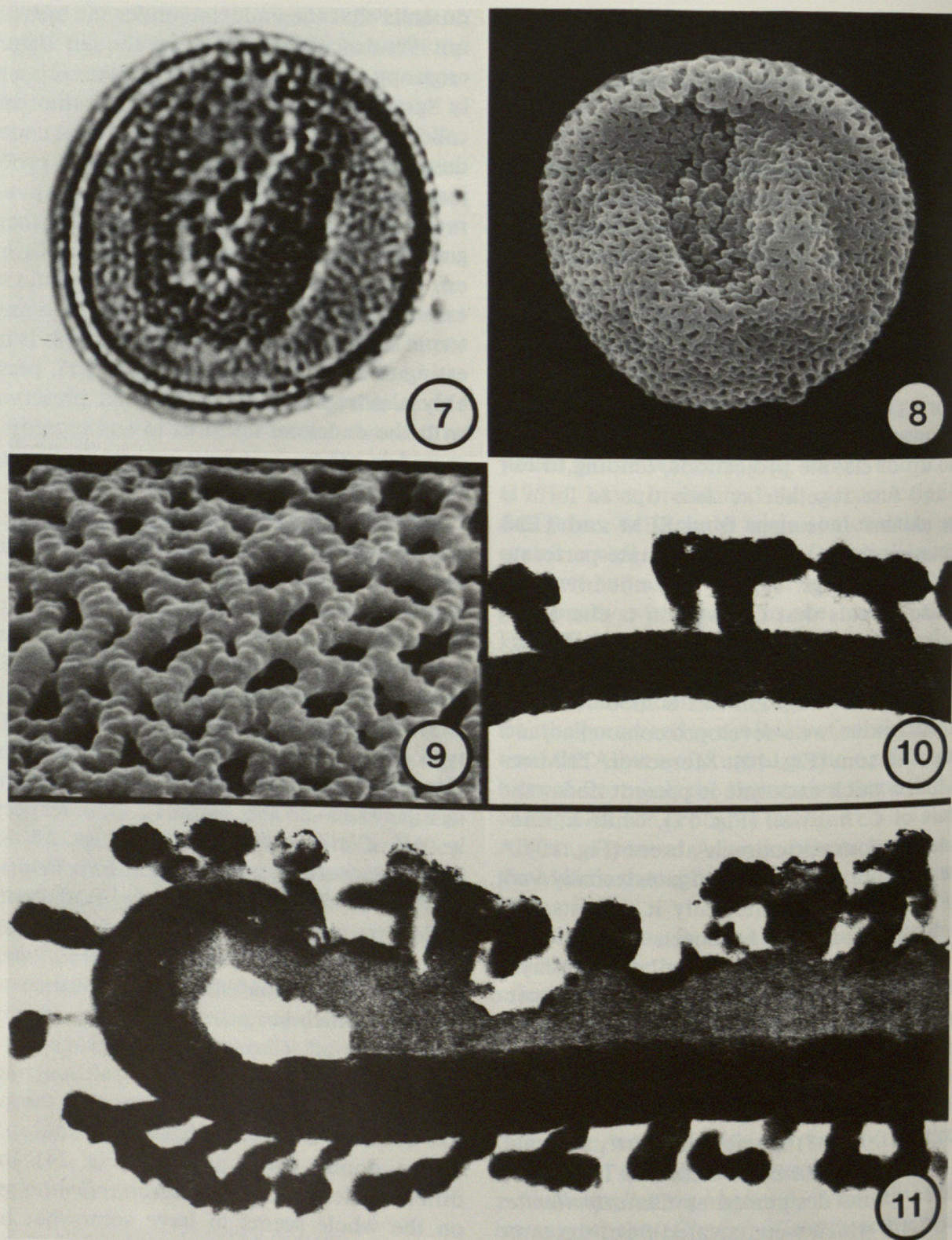
FIGURES 7–11. *Clavatipollenites hughesii* Couper (FP-364; *Cleaves 27*) from Lower Zone I of the Potomac Group, Barremian-Lower Aptian (ca. 115 Ma).—7. Whole grain PMG, ×2,190.—8. Whole grain SEMG, ×2,380.—9. Exine surface SEMG, ×12,000.—10. Nonapertural exine section TEMG, ×17,700.—11. Part of whole grain exine section TEMG, with aperture on top and appressed non-apertural side below, ×18,200.

oped apertural endexine (Fig. 11). In both aff. *Clavatipollenites* sp. 1 and 2, the aperture is evident internally, simply by a thinning of the nexine and disorganization of the overlying sexine.

ASTEROPOLLIS HEDLUND & NORRIS

In 1968, Hedlund and Norris described the genus *Asteropollis* from the Fredericksburgian (Albian) of Oklahoma. They diagnosed the pol-
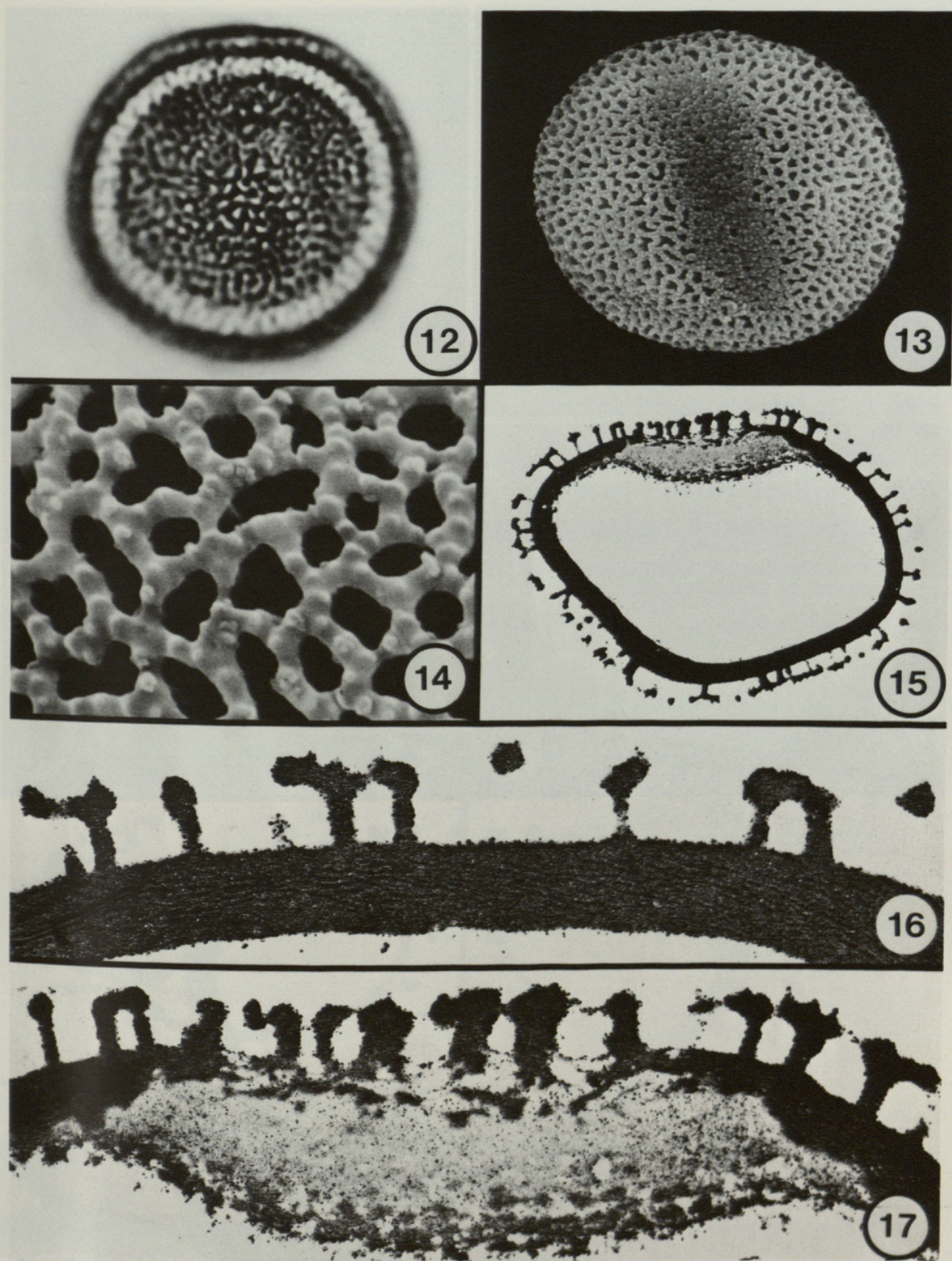
FIGURES 12–17.   *Ascarina diffusa* A. C. Smith of the Chloranthaceae (P-1091; *Kajewski 863,* Arnold Arboretum).—12. Whole grain PMG, ×1,880.—13. Whole grain SEMG, ×2,150.—14. Exine surface SEMG, ×12,000.—15. Whole grain exine section TEMG, with aperture at top, ×2,680.—16. Nonapertural exine section TEMG, ×15,000.—17. Apertural exine section TEMG, ×11,800.

len of their monotypic new genus as "radiosymmetric, oblate, with circular amb; tetra- or pentachotomosulcate; heteropolar." In their description of the type species, *Asteropollis as-* *teroides,* they noted that the pollen has a "sulcus with four or five equally developed branches almost reaching the equator" and that it is columellate and uniformly microreticulate. From a
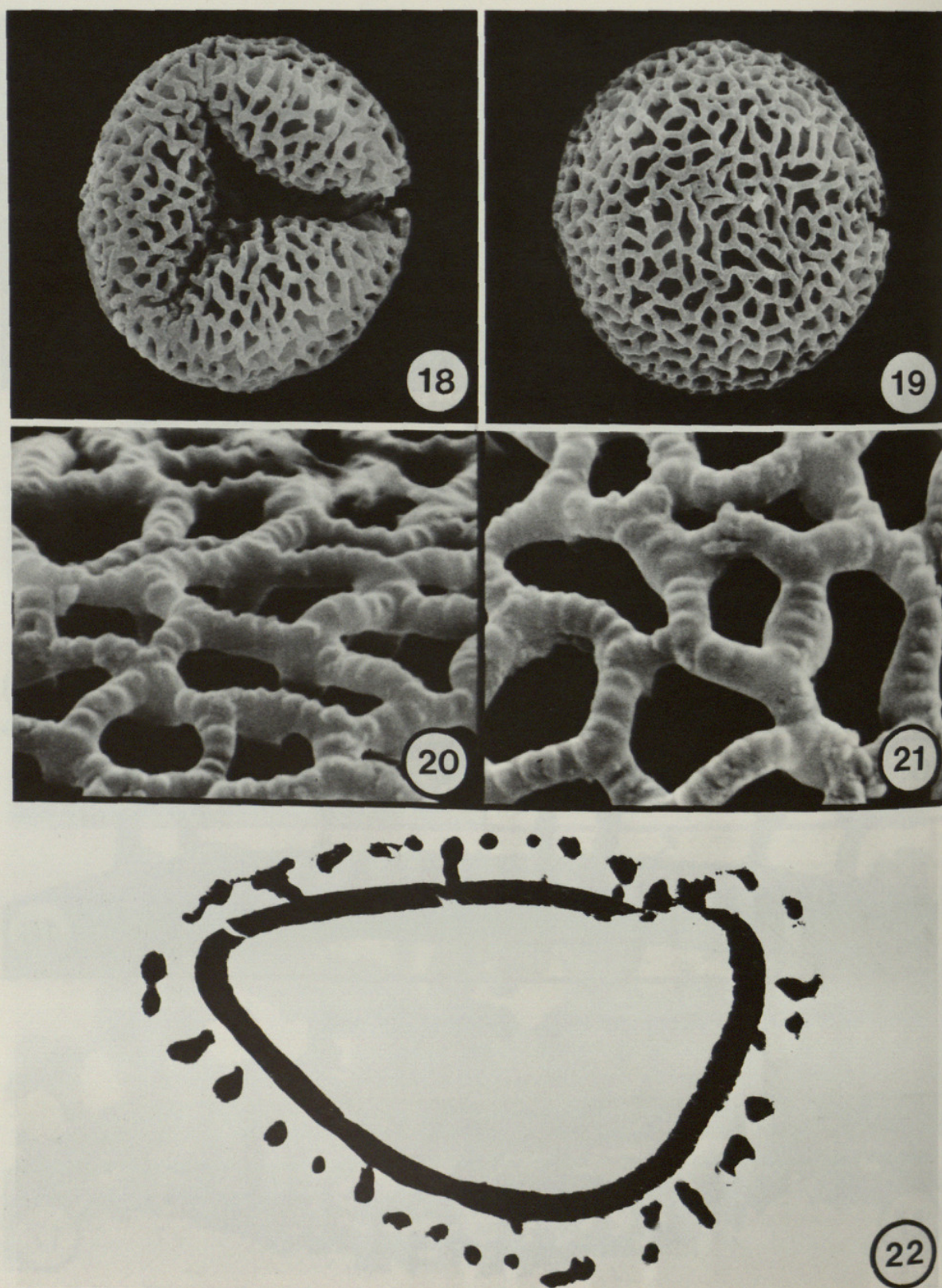
FIGURES 18–22.   Aff. *Clavatipollenites* Couper sp. 1 (FP-43; Cornet Beltway) from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma).—18. Whole grain SEMG, showing apertural side, ×2,000.—19. Whole grain SEMG, showing nonapertural side, ×2,000.—20. Exine surface SEMG on apertural side, ×12,000.—21. Exine surface SEMG on nonapertural side, ×12,000.—22. Whole grain exine section TEMG, with aperture at top right, ×4,820.

survey of 38 grains of *Asteropollis,* Davies and Norris (1976) found that approximately 30% were tetrachotomosulcate, 50% were pentachotomosulcate, and 20% were hexachotomosulcate, the latter condition not having been reported by

Hedlund and Norris (1968) in their original description of the genus. Thus, *Asteropollis* is basically pentachotomosulcate. In addition to the Fredericksburgian, pollen of *Asteropollis* has been found in the Potomac Group of eastern North
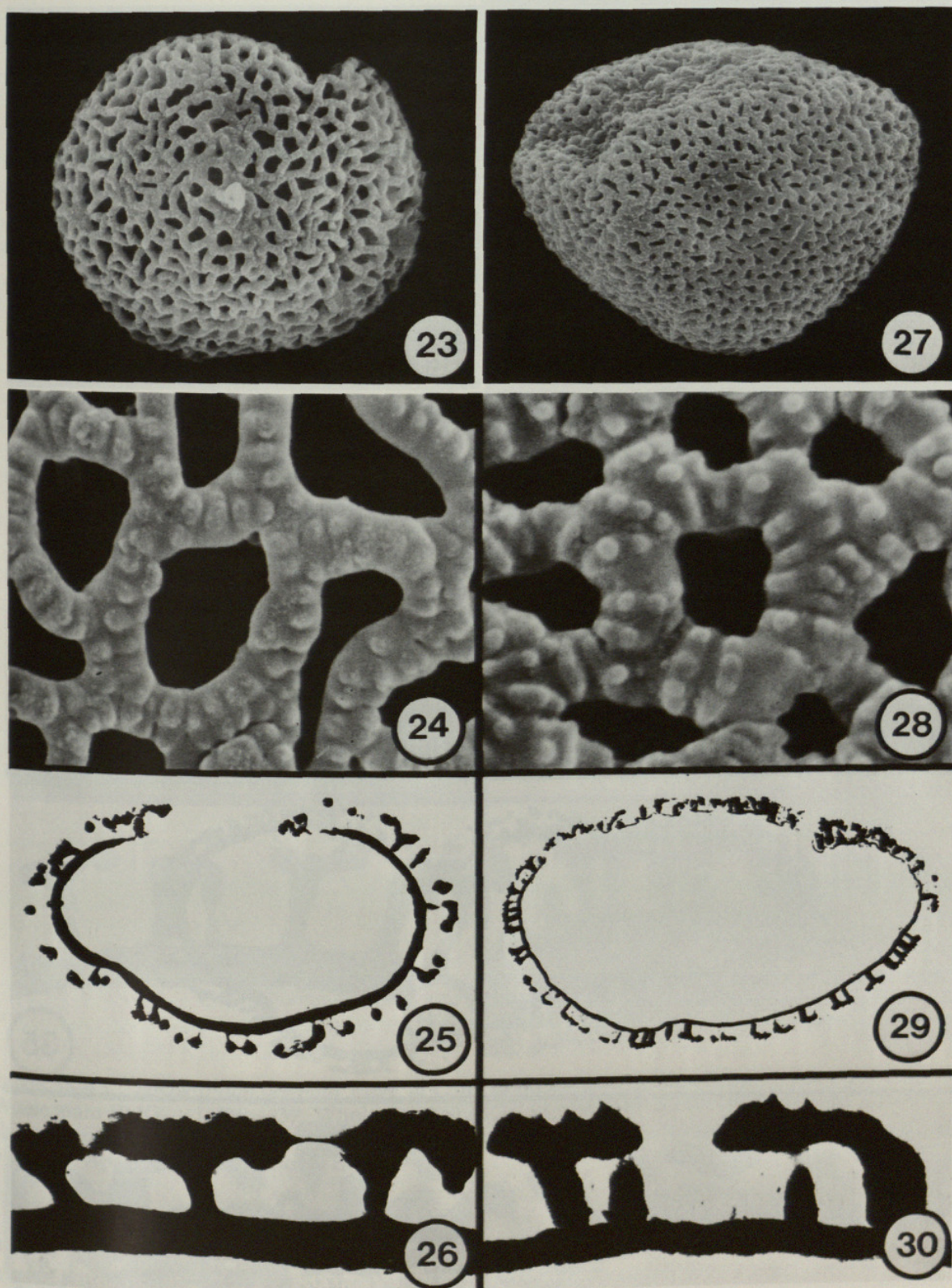
FIGURES 23–30.   Aff. *Clavatipollenites* Couper sp. 2 (FP-41; Cornet Beltway) from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma) (23–26) and *Virola weberbaueri* Markgraf (P-2734; *Tessmann 4339*, Stockholm) of the Myristicaceae (27–30).—23. Whole grain SEMG, ×1,810.—24. Exine surface SEMG, ×12,000.—25. Whole grain exine section TEMG, with aperture at top, ×2,530.—26. Nonapertural exine section TEMG, ×11,200.—27. Whole grain SEMG, ×2,440.—28. Exine surface SEMG, ×24,000.—29. Whole grain exine section TEMG, with aperture at top, ×2,510.—30. Nonapertural exine section TEMG, ×17,900.

America (Doyle & Robbins, 1977), and, according to Dettmann (1973), it also occurs in the Albian of eastern Australia.

A pollen grain of *Asteropollis* that was isolated

from the same outcrop sample (Hedlund 3916) as the holotype of the genus is shown in Figures 31–37. According to Doyle (1977a), the Fredericksburgian Antlers-"Walnut" sequence of
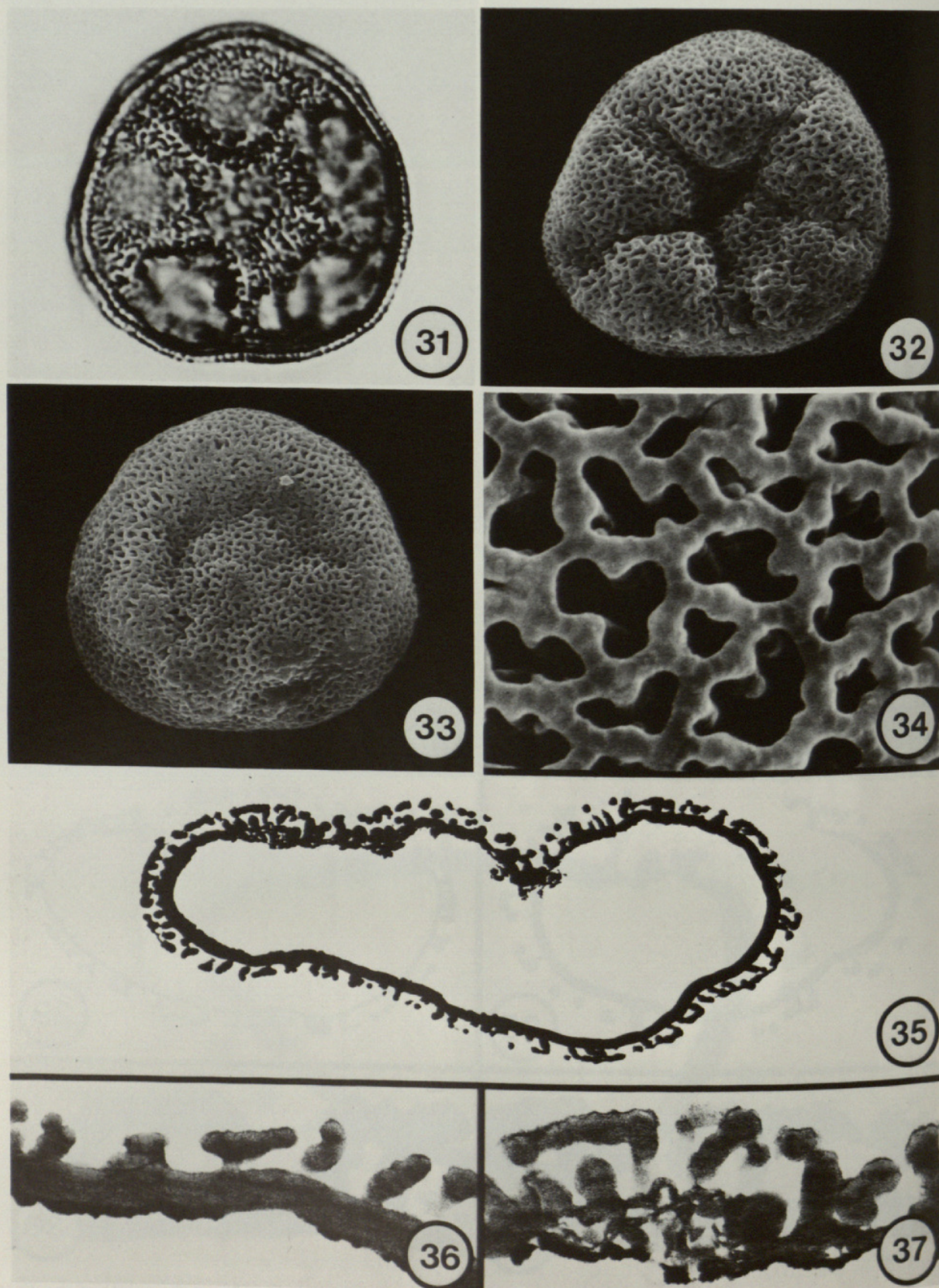
FIGURES 31–37. *Asteropollis asteroides* Hedlund & Norris (FP-338; *Hedlund 3916*) from the Fredericksburgian of Oklahoma, correlative with Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—31. Whole grain PMG, ×1,440.—32. Whole grain SEMG, showing apertural side, ×1,450.—33. Whole grain SEMG, showing nonapertural side, ×1,450.—34. Exine surface SEMG, ×12,000.—35. Whole grain exine section TEMG, with apertural regions on top, ×3,060.—36. Nonapertural exine section TEMG, ×11,100.—37. Apertural exine section TEMG, ×11,100.
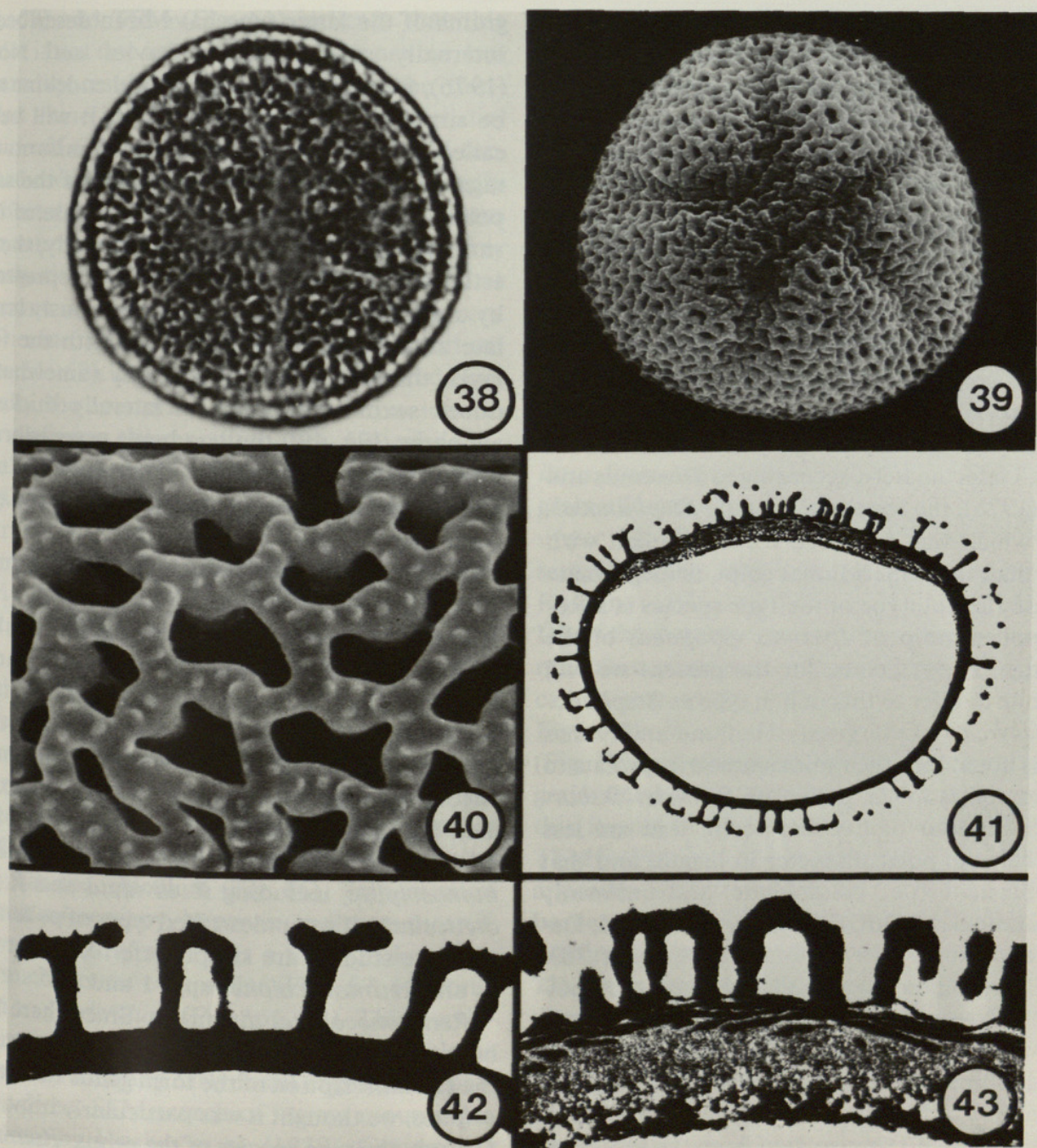
FIGURES 38–43. *Hedyosmum orientale* Merr. & Chun of the Chloranthaceae (P-1102; *Poilane 32871*, Paris).— 38. Whole grain PMG, ×1,480.—39. Whole grain SEMG, ×1,810.—40. Exine surface SEMG, ×12,000.—41. Whole grain exine section TEMG, with aperture at top, ×1,950.—42. Nonapertural exine section TEMG, ×8,360.—43. Apertural exine section TEMG, ×9,350.

Oklahoma that this grain was obtained from is correlated with Middle Zone IIB of the Potomac Group, and, hence, is upper Middle Albian in age. The grain shown in Figures 31–37 is pentachotomosulcate (Figs. 31, 32), although, as previously indicated, *Asteropollis* may also be tetra- or hexachotomosulcate. SEMG of both the apertural (Fig. 32) and nonapertural (Fig. 33) sides confirm that *Asteropollis* has a modified sulcate aperture (being tetra-, penta-, or hexa-chotomosulcate as the case may be) and is not colpate

as suggested by Srivastava (1975). SEM reveals that *Asteropollis* has an irregular reticulum, with weakly beaded to spinulose muri that are conspicuously nodose (Fig. 34). Structurally, *Asteropollis* is tectate-perforate to semitectate (Figs. 32–34). TEM demonstrates that *Asteropollis* has an average to moderately thick nonapertural nexine (Fig. 36), while SEM and TEM together give the impression that columellae in this genus are composed of granule-like subunits (Figs. 34, 36). A thin, somewhat patchy (real or ? artifact) end-

exine is present in both the nonapertural (Fig. 36) and apertural (Fig. 37) exine. The aperture itself is evident internally as a lamellate zone in the nexine that consists of a thin endexine and a somewhat thicker foot-layer overlaid by a disorganized region of sexine (Figs. 35, 37).

STEPHANOCOLPITES FREDERICKSBURGENSIS HEDLUND & NORRIS

From the same outcrop sample of the Fredericksburgian of Oklahoma from which they isolated *Asteropollis,* Hedlund and Norris (1968) described another Early Cretaceous pollen type under the name *Stephanocolpites fredericksburgensis.* Unfortunately, according to Jansonius and Hills (1976), the form genus name *Stephanocolpites,* which was proposed for any pollen with more than three meridional colpi, is illegitimate because the holotype of the type species is a Recent pollen grain of *Lycopus europaeus* of the Labiatae. Nevertheless, for the present we will continue to refer to this pollen type as *Stephanocolpites fredericksburgensis.* Hedlund and Norris (1968) noted that the radiosymmetric, prolate to spheroidal, isopolar pollen of *S. fredericksburgensis* has four or five brevicolpi that are less than half the polar diameter in length, and that it is baculate (i.e., columellate) and uniformly microreticulate. Out of 62 grains examined, Davies and Norris (1976) found that about 70% were tetracolpoidate and 30% were pentacolpoidate. Doyle and Robbins (1977) have reported that *S. fredericksburgensis* also occurs in the Middle-Upper Albian of the Potomac Group.

Material of *S. fredericksburgensis* that we studied (Figs. 44–50) was isolated from the same outcrop sample (Hedlund 3916) that provided the holotype of the species. Figures 44–49 were all obtained from the same grain of *S. fredericksburgensis,* while the whole grain exine section TEMG shown in Figure 50 is from another grain. A pentacolpoidate grain is shown in Figures 44 and 45. SEM reveals that the pollen is irregularly reticulate with spinulose muri (Fig. 46), and that it has small tectal perforations, and consequently is tectate-perforate (Figs. 45, 46). TEM shows that the nonapertural nexine is moderately to very thick and that columellae are present (Fig. 48), and also reveals that well-developed endexine is present throughout the exine, in nonapertural (Fig. 48) as well as apertural (Fig. 49) regions. While some grains of *S. fredericksburgensis* have a relatively uniform endexine (Fig. 48), in others the endexine is ragged (Fig. 50). Although

grains of the latter type have been described as internally sculptured by Davies and Norris (1976), we believe that this ragged endexine may be simply a preservation artifact. It will be recalled that a similar occurrence of uniform and ragged endexine in different grains of the same pollen was also encountered in the case of *Clavatipollenites hughesii.* Ultrastructurally, the apertures of *S. fredericksburgensis* are represented by areas of thick endexine conspicuously lamellate at the top and interbedded with the foot-layer, that in turn are overlaid by somewhat reduced sexine composed of laterally thickened elements (Fig. 49), the last being especially evident in exine section SEMG that show the transitional region between apertural and nonapertural exine (Fig. 47).

RETIMONOCOLPITES PIERCE

The form genus *Retimonocolpites* was described by Pierce (1961) for "reticulate, monocolpate pollen." Several different pollen types have been included in this form genus, and there has been some question about what it should encompass. During the present study we examined four different pollen types that, at the light microscope level at least, are referable to *Retimonocolpites,* including *R. dividuus* and *R. peroreticulatus.* Two undescribed types of pollen that we have studied are simply referred to for now as aff. *Retimonocolpites* spp. 1 and 2.

Retimonocolpites dividuus. Since there have been a number of divergent opinions concerning the circumscription of the form genus *Retimonocolpites,* we thought it was particularly important to study the type species of the genus, *Retimonocolpites dividuus* Pierce. A grain of *R. dividuus* is pictured in Figures 57–62. This particular grain was isolated from the D13-535 core sample of the Potomac Group, which, according to Doyle and Robbins (1977), is Late Zone IIB or early Late Albian in age. The characteristic light microscope appearance of *R. dividuus* is shown at high (Fig. 57) and low (Fig. 58) focus. Frequently the coarse reticulum becomes locally detached from the rest of the grain, and sometimes one even finds completely psilate "nexines" of *R. dividuus* from which the reticulum is entirely detached (cf. Brenner, 1963, under discussion of *Liliacidites dividuus*; Kemp, 1968, under discussion of *Clavatipollenites rotundus*). One of the most distinctive light microscope features of the monosulcate pollen of *R. dividuus* is its conspicuously bordered aperture (Figs. 57, 58). SEM

(Fig. 59) and TEM (Fig. 61) indicate that this border is not due to thickening of the nexine, but apparently results from infolding of the thin-walled exine itself (cf. Kemp, 1968, under discussion of *Clavatipollenites rotundus*). SEM further shows that the pollen, which is decidedly semitectate (Fig. 59), has an irregular reticulum with muri covered by fine bands that are frequently discontinuous (Fig. 60). TEM reveals that the exine is composed of an extremely to very thin nexine, short columellae, and a thick tectum (Figs. 61, 62). Endexine was not observed. Externally, the aperture is represented by a definite interruption in the reticulum (Fig. 59), while internally it is scarcely evident (Figs. 61, 62).

Aff. Retimonocolpites sp. 1. During our ultrastructural study of Potomac Group angiosperm pollen we encountered a pollen type that clearly illustrates the advantage of combined light, SEM, and TEM examination of the same pollen grain. This pollen type, which we have designated aff. *Retimonocolpites* sp. 1, is shown in Figures 63–68. Although this pollen type looks somewhat different from *R. dividuus* at the light microscope level (Fig. 63), scanning electron microscopy (Figs. 64–66) reveals a pollen type that greatly resembles *R. dividuus,* even down to its finely banded reticulum (Fig. 66). Transmission electron microscopy, however, indicates that aff. *Retimonocolpites* sp. 1 has a very thick nexine and much stouter columellae (Figs. 67, 68) compared to *R. dividuus* (Figs. 61, 62). This particular example demonstrates some of the problems inherent in studying early fossil angiosperm pollen by direct SEM search of "strew mounts" as was done by Hughes et al. (1979). Grains that look rather similar in the scanning electron microscope may be vastly different when examined with transmission electron microscopy.

Retimonocolpites peroreticulatus. Another type of Early Cretaceous angiosperm pollen that has been included under the form genus *Retimonocolpites* is represented by pollen grains known as *Retimonocolpites peroreticulatus* (Brenner) Doyle. This species was first described by Brenner (1963) under *Peromonolites,* which is a form genus proposed by Couper (1953) for perinate, monolete spores. Doyle in Doyle et al. (1975) transferred the species to *Retimonocolpites* and gave a number of reasons for considering it an angiosperm pollen grain rather than a fern spore, including the different nature of its detached reticulum from a true perisporium, its non-reniform shape, its apparent true aperture

rather than tetrad scar, and its similarities to certain undoubted angiosperm pollen types, including members of the form genera *Clavatipollenites* and *Retimonocolpites.* Doyle et al. (1975), who examined *R. peroreticulatus* and a possibly related pollen type, *R. reticulatus* (Brenner) Doyle, which is somewhat larger and has a less coarsely developed reticulum, noted that in addition to the Potomac Group, pollen of this general type occurs in the Albian of Oklahoma, western Canada, and Peru, as well as in the Barremian of England and the probable Barremian-Aptian of central Africa.

Although we have also studied *R. peroreticulatus* from the Potomac Group, the particular grain illustrated in Figures 69–73 is from the upper Middle Albian of Oklahoma (Hedlund sample 3916), which according to Doyle and Robbins (1977) is correlative with Middle Zone IIB of the Potomac Group. The coarse, detached reticulum so evident at the light microscope level can be seen in the whole grain PMG shown in Figure 69. Whole grain SEMG of the apertural (Fig. 70) and nonapertural (Fig. 71) sides of the grain show no evidence of any columellae, and this is confirmed by whole grain exine section TEMG (Fig. 73). The grain has a well-developed aperture, which consists of a sharply defined, bordered slit in the reticulum itself (Fig. 70) and a definite thinning of the underlying nexine (Fig. 73). Exine surface SEMG reveal that the reticulum is covered by distinctive recurved spines (Fig. 72). TEMG sections of the whole grain (Fig. 73) show that the smooth central body, i.e., the nexine proper, is moderately to very thick, as is the reticulum itself. The impression is given that the reticulum is directly united with the underlying nexine at only a few points (? possibly only at the aperture), and this may be why the reticulum so frequently appears for all intents to be free of the central body. Although we found no evidence of endexine in the grain of *R. peroreticulatus* shown in Figures 69–73, Doyle et al. (1975) encountered endexine under the aperture of a grain that they considered was probably the related *R. reticulatus.*

Aff. Retimonocolpites sp. 2. A pollen type (Figs. 74–80) that was isolated from an Upper Zone I Potomac Group outcrop sample (Brenner 10) is virtually identical with *R. peroreticulatus* except that it has well-developed columellae (Fig. 77) and a somewhat tighter reticulum (Figs. 75, 76). We have designated this pollen type as aff. *Retimonocolpites* sp. 2. Although aff. *Retimono-*
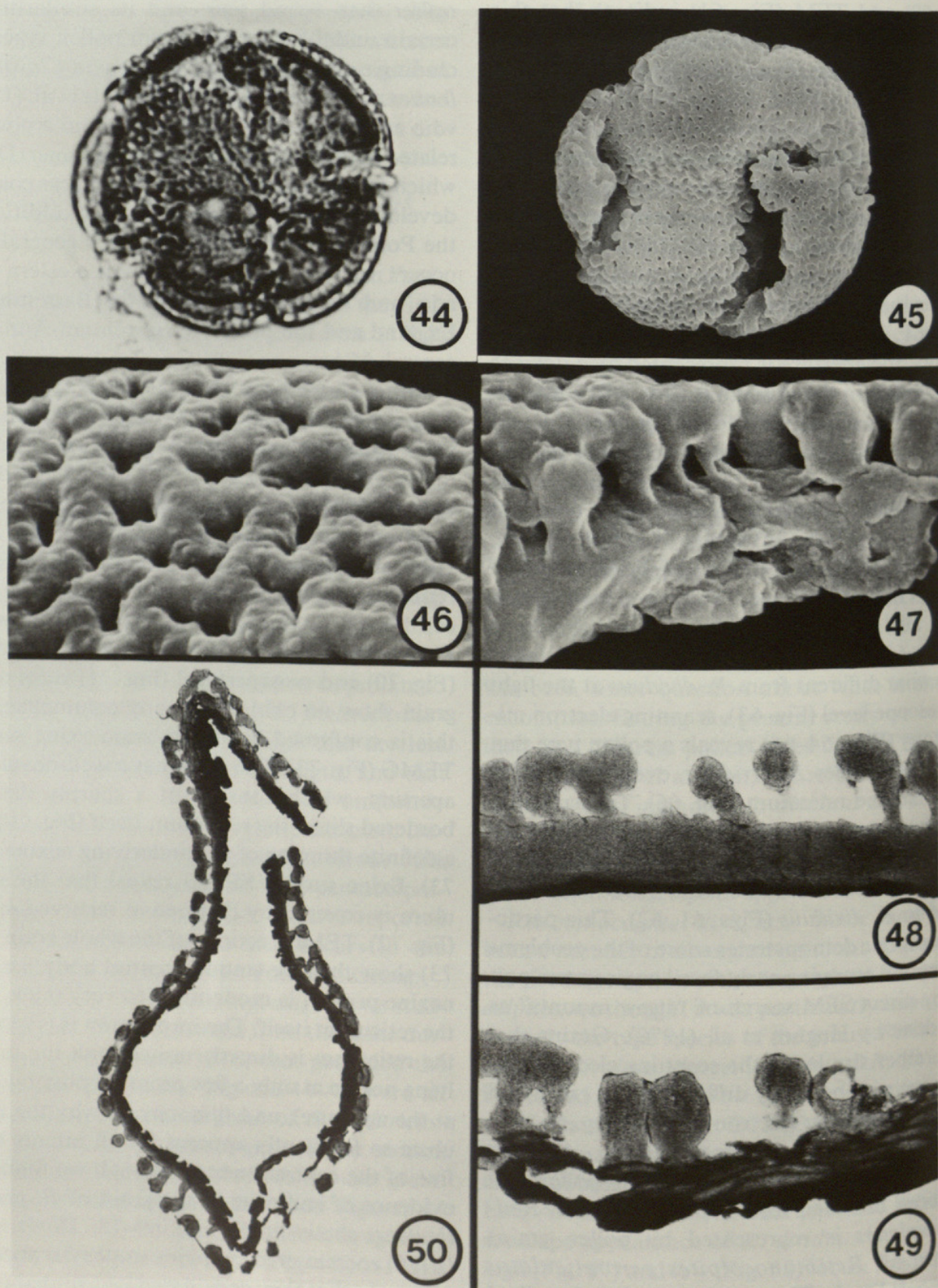
FIGURES 44–50. *Stephanocolpites fredericksburgensis* Hedlund & Norris (44–49, FP-292, 50, FP-306; *Hedlund 3916*) from the Fredericksburgian of Oklahoma, correlative with Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—44. Whole grain PMG, ×1,500.—45. Whole grain SEMG, ×1,540.—46. Exine surface SEMG, ×12,000.—47. Exine section SEMG, showing non-apertural (to the left) and apertural (to the right) exine, ×12,000.—48. Nonapertural exine section TEMG, ×10,800.—49. Apertural exine section TEMG, ×10,700.—50. Whole grain exine section TEMG, ×4,240.
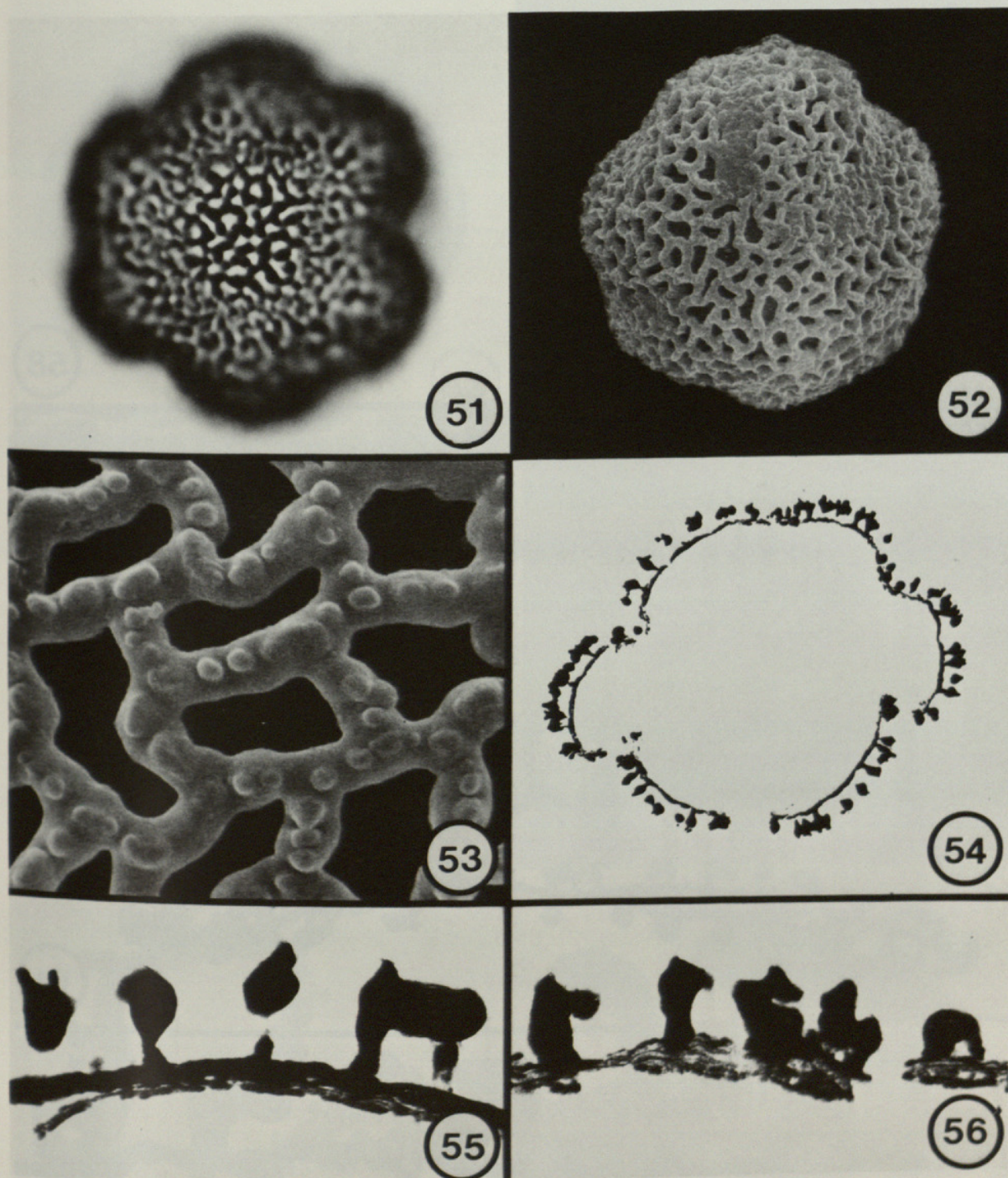
FIGURES 51–56.   *Chloranthus japonicus* Sieb. of the Chloranthaceae (P-2791; *Furuse s.n.,* Stockholm).—51. Whole grain PMG, ×1,770.—52. Whole grain SEMG, ×2,170.—53. Exine surface SEMG, ×12,000.—54. Whole grain exine section TEMG, ×1,700.—55. Nonapertural exine section TEMG, ×10,600.—56. Apertural exine section TEMG, ×10,600.

colpites sp. 2 looks quite different from *R. peroreticulatus* in the light microscope (cf. Figs. 69, 74), SEM and TEM reveal a remarkable resemblance between these two pollen types, including a similar reticulum with distinctive, recurved spines (cf. Figs. 72, 77) and a similarly thick nexine (cf. Figs. 73, 78, 79). Although aff. *Retimonocolpites* sp. 2 has a weakly developed endexine under the apertural (Fig. 80) and nonapertural (Fig. 79) exine, and no endexine was found

in *R. peroreticulatus* shown in Figures 69–73, we suspect that further studies will discover that *R. peroreticulatus* has a thin endexine. The major difference between aff. *Retimonocolpites* sp. 2 and *R. peroreticulatus* is that the former has well-developed columellae (Fig. 77) and the latter has none (Figs. 71, 72). Pollen of the aff. *Retimonocolpites* sp. 2 type, which may actually be a more primitive pollen type that is closely related to *R. peroreticulatus,* is significant, at the least, in that
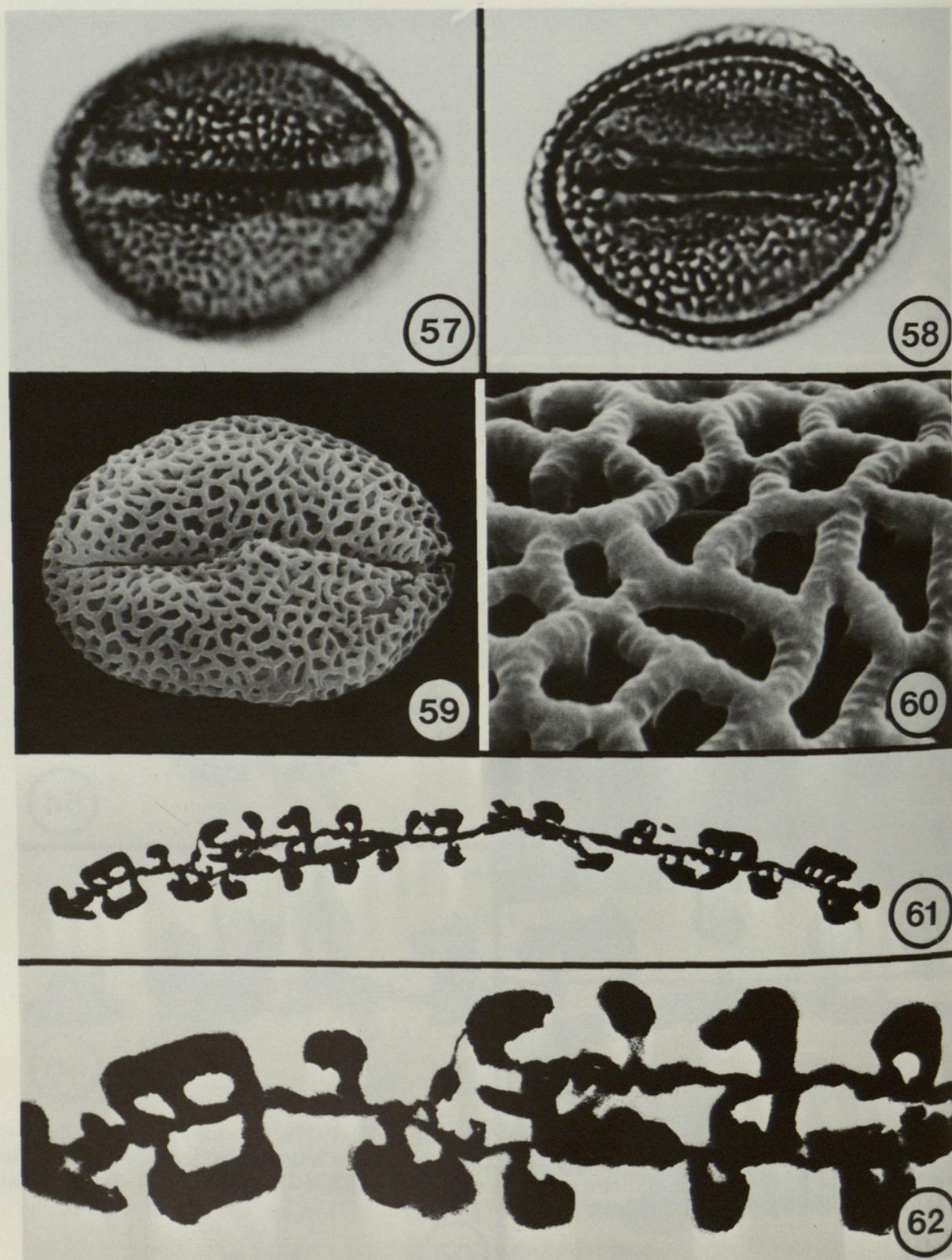
FIGURES 57–62. *Retimonocolpites dividuus* Pierce (FP-372; D13-535) from Upper Zone IIB of the Potomac Group, lower Upper Albian (ca. 103 Ma).—57. Whole grain PMG at high focus, ×1,780.—58. Whole grain PMG at low focus, ×1,780.—59. Whole grain SEMG, ×1,940.—60. Exine surface SEMG, ×12,000.—61. Whole grain exine section TEMG, ×5,900.—62. Part of whole grain exine section TEMG, showing infolded, presumptive apertural region, ×17,200.

it represents a model of a more normal columellate pollen type from which the bizarre, noncolumellate *R. peroreticulatus* could have evolved.

STELLATOPOLLIS DOYLE

One of the most distinctive types of Early Cretaceous angiosperm pollen is represented by large, monosulcate pollen grains that have a remark-
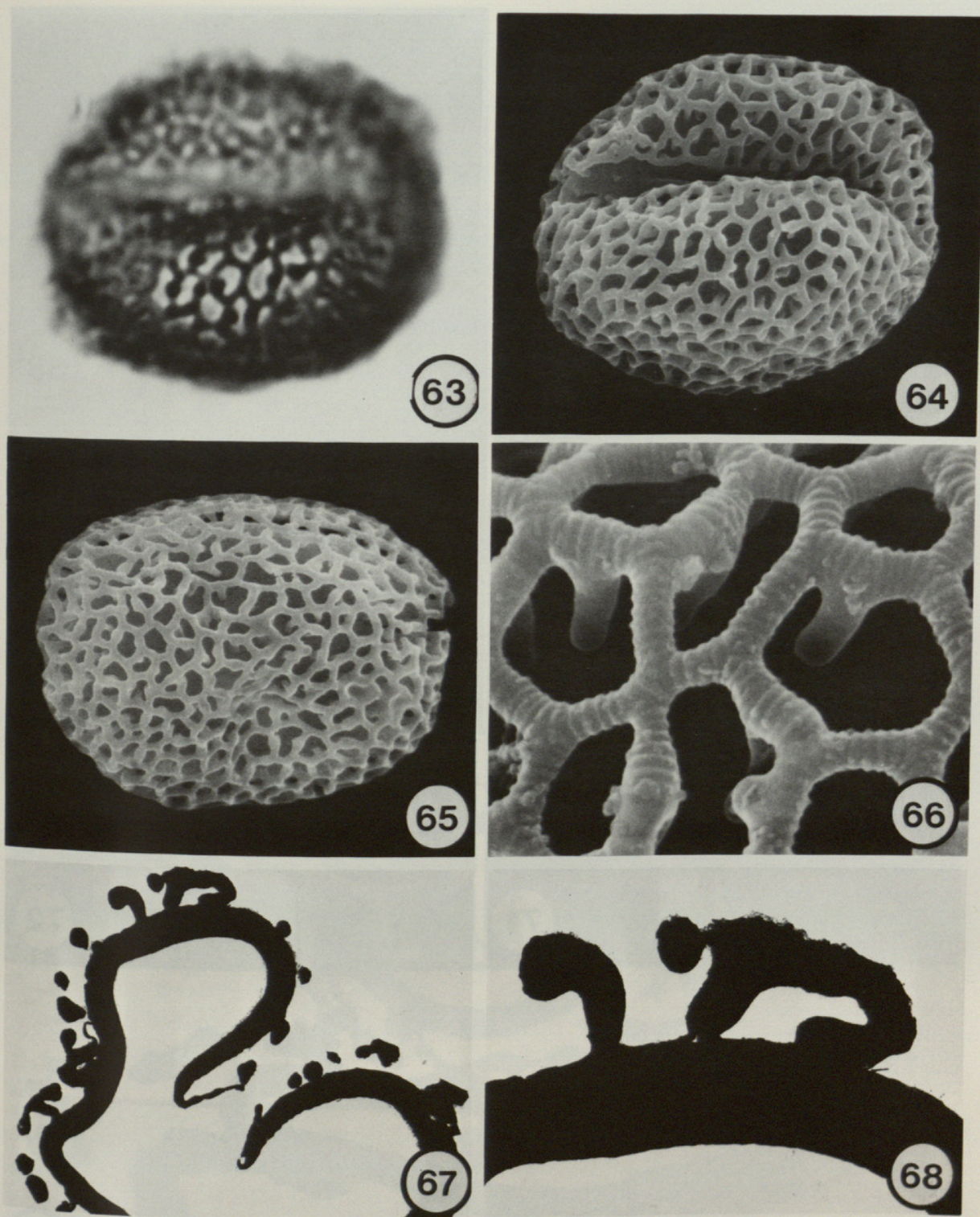
FIGURES 63–68.   Aff. *Retimonocolpites* Pierce sp. 1 (FP-190; Cornet Beltway), from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma).—63. Whole grain PMG, ×2,080.—64. Whole grain SEMG, showing apertural side, ×2,080.—65. Whole grain SEMG, showing nonapertural side, ×2,080.—66. Exine surface SEMG, ×12,000.—67. Whole grain exine section TEMG, showing aperture, ×3,530.—68. Nonapertural exine section TEMG, ×12,200.

ably well-developed "crotonoid" sculpturing. Pollen of this type, with a semitectate-reticulate exine composed of muri bearing triangular to elliptical supratectate elements, has been described by Doyle in Doyle et al. (1975) under the name *Stellatopollis* Doyle. According to Doyle et al. (1975), *Stellatopollis* is known, in addition to the Potomac Group, from the Middle Albian of Oklahoma and Brazil, the Barremian of England, and the presumed Barremian-Aptian of equatorial Africa.

We have studied pollen of the type species of the form genus, *Stellatopollis barghoornii* Doyle, taken from the D12-515 core sample of the Po-
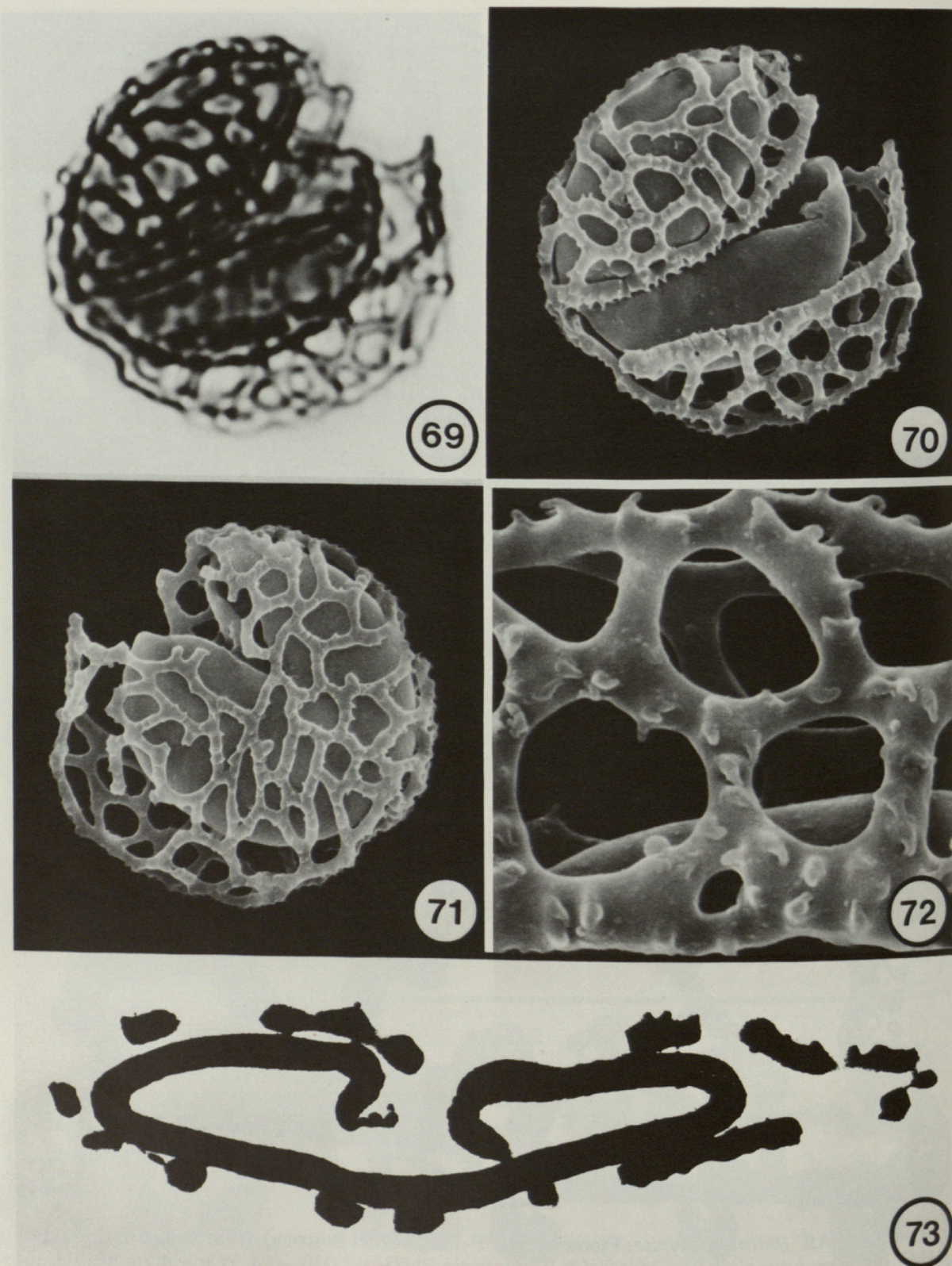
FIGURES 69–73. *Retimonocolpites peroreticulatus* (Brenner) Doyle (FP-341; *Hedlund 3916*), from the Fredericksburgian of Oklahoma, correlative with Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—69. Whole grain PMG, ×2,610.—70. Whole grain SEMG, showing apertural side, ×2,610.—71. Whole grain SEMG, showing nonapertural side, ×2,610.—72. Exine surface SEMG, ×11,500.—73. Whole grain exine section TEMG, with aperture at top middle, ×8,640.

tomac Group (Figs. 81–86), which is the same core sample from which the holotype of the species was obtained. In their ultrastructural investigation of early fossil angiosperm pollen,

Doyle et al. (1975) also examined material of *S. barghoornii* that was isolated from this core sample, and our observations agree with theirs. Whole grains of *S. barghoornii* are so large (to 70
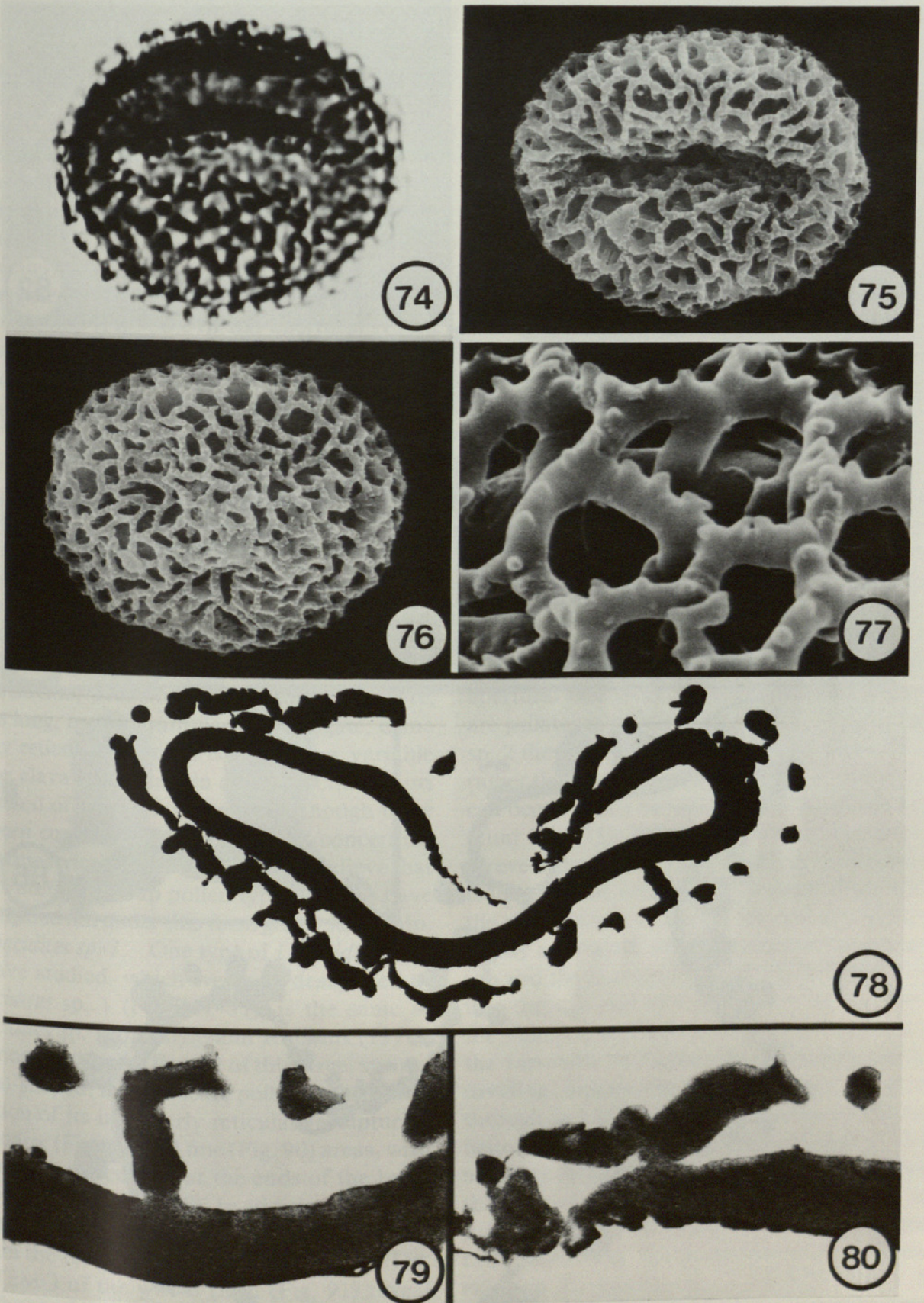
FIGURES 74–80.   Aff. *Retimonocolpites* Pierce sp. 2 (FP-102; *Brenner 10*), from Upper Zone I of the Potomac Group, Upper Aptian-Lower Albian (ca. 110 Ma).—74. Whole grain PMG, ×1,920.—75. Whole grain SEMG, showing apertural side, ×2,040.—76. Whole grain SEMG, showing nonapertural side, ×2,040.—77. Exine surface SEMG, ×11,800.—78. Whole grain exine section TEMG, with aperture at top middle, ×6,430.—79. Nonapertural exine section TEMG, ×18,500.—80. Apertural exine section TEMG, ×18,500.
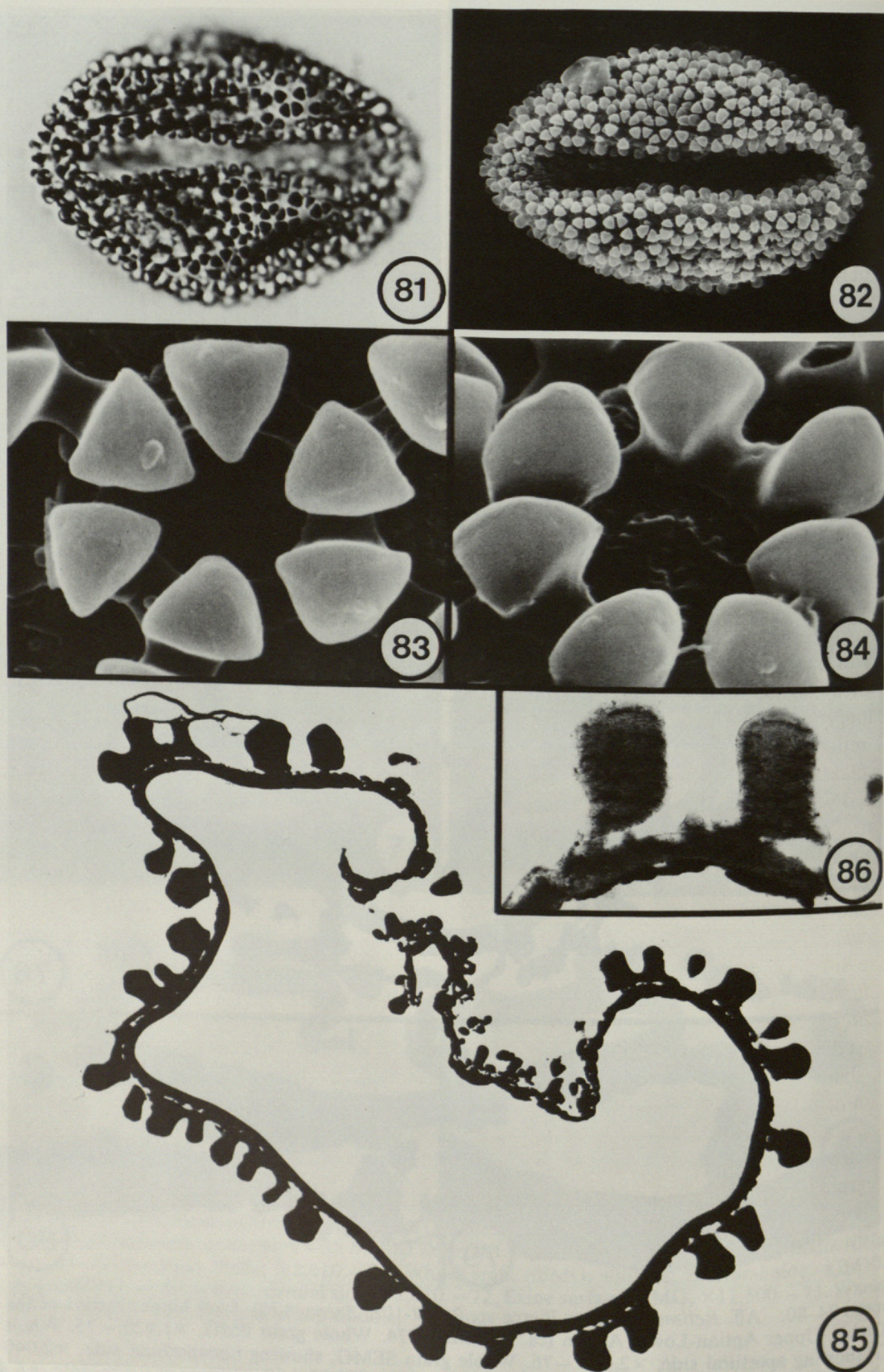
FIGURES 81–86. *Stellatopollis barghoornii* Doyle (FP-377; D12-515), from Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—81. Whole grain PMG, ×1,140.—83–84. Exine surface SEMG, ×12,000.—82. Whole grain SEMG, ×1,030.—85. Whole grain exine section TEMG, with aperture at top center, ×4,300.—86. Nonapertural exine section TEMG, ×11,900.

μm) that the "crotonoid" sculpturing, which appears so beautiful in SEMG (Fig. 82), is clearly evident in PMG as well (Fig. 81). Exine surface SEMG show that the triangular projections that form the "crotonoid" sculpturing pattern are attached to an underlying reticulum that is formed by muri that are distinctly circular (Figs. 83, 84). TEM sections further reveal that short columellae occur below the reticulum itself (Fig. 85). The moderately thin nexine in the nonapertural exine is composed of a thick foot-layer and a relatively thin endexine (Fig. 86). In the apertural region the sexine is highly disorganized (Fig. 85), and, as Doyle et al. (1975) have indicated, endexine probably occurs under the aperture, although we were not able to confirm this with the material we have examined so far.
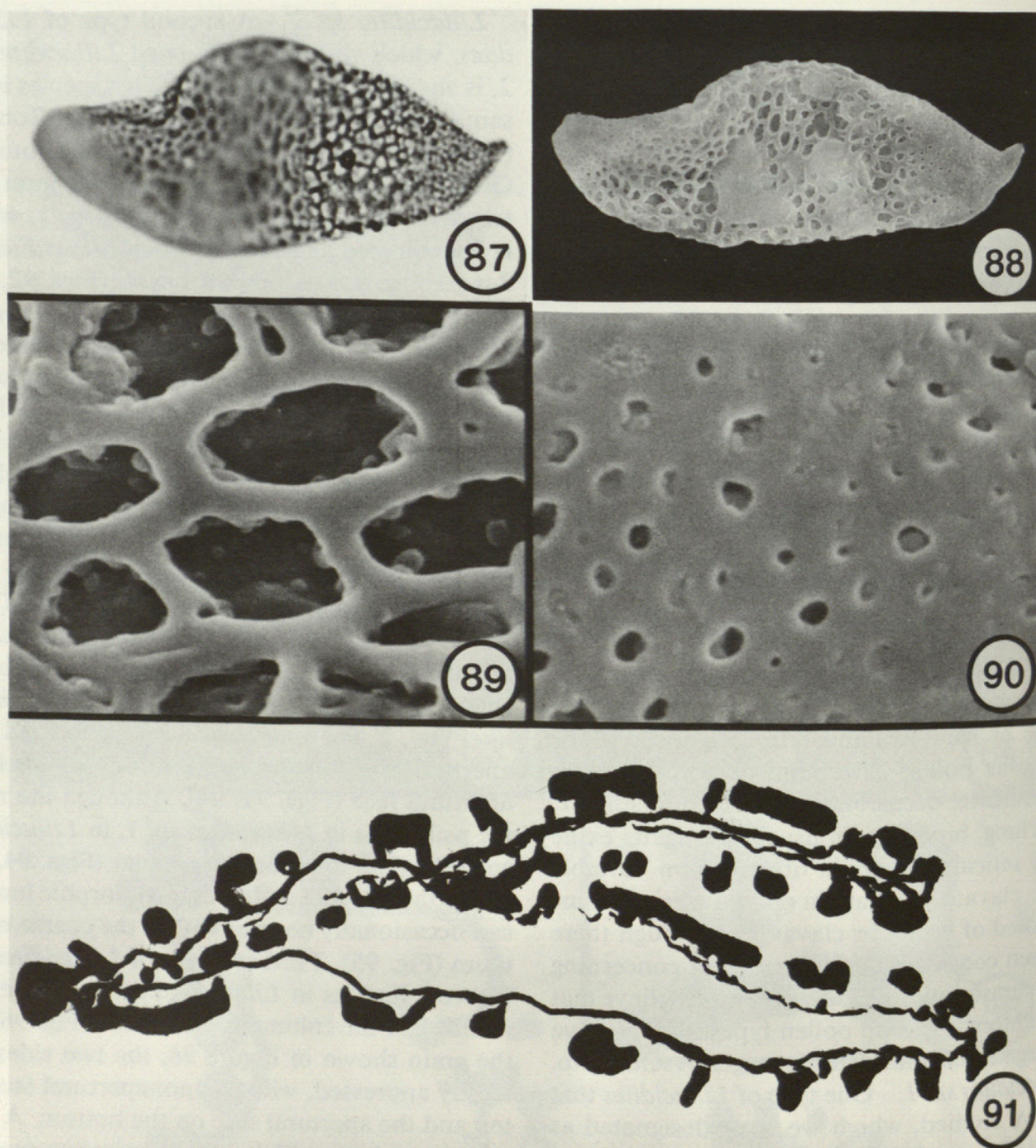
LILIACIDITES COUPER

In 1953, Couper described the form genus *Liliacidites* Couper from the Upper Cretaceous-Eocene of New Zealand. His diagnosis of the genus was pollen "free, anisopolar, bilateral, monosulcate, occasionally trichotomosulcate; sulcus long, broad; grain usually elongate; exine clearly reticulate, lumina of reticulum variable in size; clavate, baculate in optical section (muri composed of baculi or clavae)." Although there has been considerable disagreement concerning the circumscription of *Liliacidites,* we believe that three Potomac Group pollen types that we have investigated fall under this form genus sensu lato.

Liliacidites sp. 1. One type of *Liliacidites* that we have studied, which we have designated as *Liliacidites* sp. 1 (Figs. 87–91), is the same as *Liliacidites* sp. F of Doyle and Robbins (1977). The most distinctive feature of this large, strongly boat-shaped, monosulcate pollen is the differentiation of its irregularly reticulate sculpturing into coarse (Fig. 89) and fine (Fig. 90) areas, with the fine areas occurring at the ends of the boat-shaped grain (Figs. 87, 88). In addition, the muri themselves are psilate, and within the coarse reticulum the lumina are strongly dimorphic (Fig. 89). TEMG of the whole grain (Fig. 91) reveal that the nexine is extremely to very thin, and that it is overlaid by a thick tectum supported by short columellae. Endexine was not observed. The aperture appears to be very broad and consists of a thinner nexine relative to the nonapertural nexine overlaid by a relatively unreduced sexine (the infolded aperture can be seen on the right side in Fig. 91).

Liliacidites sp. 2. A second type of *Liliacidites,* which we have designated *Liliacidites* sp. 2, is shown in Figures 92–97. This species is the same as *Liliacidites* sp. E of Doyle and Robbins (1977) and was obtained from the same Potomac Group core sample (D13-535) as the grain pictured by them. Unlike *Liliacidites* sp. 1, which is boat-shaped and monosulcate, *Liliacidites* sp. 2 is globose and trichotomosulcate (Figs. 92, 93). In the grain shown in Figures 92–97 one arm of the trichotomosulcus is notably smaller than the other two (Fig. 93). This is common in other types of trichotomosulcate pollen (cf. Wilson, 1964), and may be indicative of an evolutionary stage that is intermediate between monosulcate pollen and pollen that has a fully developed, equal-armed, trichotomosulcus. *Liliacidites* sp. 2 is similar to *Liliacidites* sp. 1 in that it also possesses reticulate sculpturing differentiated into coarse and fine areas (Fig. 95), although instead of having the fine reticulum at the ends of a boat-shaped grain, as in *Liliacidites* sp. 1, in *Liliacidites* sp. 2 the fine reticulum is around the aperture (Fig. 93) and in the middle of the non-apertural face (Figs. 92, 94). Although the muri are psilate, as in *Liliacidites* sp. 1, in *Liliacidites* sp. 2 they are more or less circular (Figs. 94, 95) rather than irregular. Strongly dimorphic lumina can occasionally be seen within the coarse reticulum (Fig. 95). TEM sections of *Liliacidites* sp. 2 reveal that, as in *Liliacidites* sp. 1, the nexine is thin and the columellae are short (Fig. 96). In the grain shown in Figure 96, the two sides are tightly appressed, with the nonapertural face on top and the apertural side on the bottom. A section through part of the finely reticulate spot on the nonapertural side of the grain is present at the top right of Figure 96 just below the line dividing Figures 94 and 95, while a section through part of the trichotomosulcus can be seen below and slightly to the right of this. It is interesting to note that the exine is considerably thicker on the nonapertural face because the tectum is thicker on this side. TEMG in the apertural region (Fig. 97) reveal the presence of endexine in *Liliacidites* sp. 2, at least under the aperture itself. Externally, the aperture is apparent as a broad, more or less psilate area (Fig. 93), while internally it appears as a thinner region of the exine that seems to consist largely of endexine.

"Liliacidites" minutus. The third type of Early Cretaceous angiosperm pollen that for the present at least is included under the form genus

FIGURES 87–91. *Liliacidites* Couper sp. 1 (FP-392; D13-535), from Upper Zone IIB of the Potomac Group, lower Upper Albian (ca. 103 Ma).—87. Whole grain PMG, ×1,340.—88. Whole grain SEMG, ×1,340.—89. Exine surface SEMG, showing coarse reticulum, ×12,000.—90. Exine surface SEMG, showing fine reticulum, ×12,000.—91. Whole grain exine section TEMG, with infolded aperture at right, ×8,130.

Liliacidites is apparently the same as pollen described by Brenner (1963) as *Clavatipollenites minutus* Brenner and pictured in Doyle and Robbins (1977). Although this pollen type is probably best treated as a distinct genus, for the time being we will refer to it as "*Liliacidites*" *minutus*. "*Liliacidites*" *minutus* (Figs. 98–102) is characterized by its small size (generally about 15 μm long) and psilate reticulum (Figs. 99–101). The relatively coarse reticulum of "*L*." *minutus*, which is clearly evident even in PMG (Fig. 98),

gives this pollen an appearance that is considerably different from that of *Clavatipollenites*. Moreover, "*L*." *minutus* resembles *Liliacidites* spp. 1 and 2 in having a psilate reticulum with dimorphic lumina (Fig. 101), although it differs from them in that its reticulum is frequently strongly polygonal. TEM sections (Fig. 102) reveal that "*L*." *minutus* has a moderately thick nexine, however, that is different from the thin nexine of *Liliacidites* spp. 1 and 2. This thick nexine is overlaid by short columellae and a thick
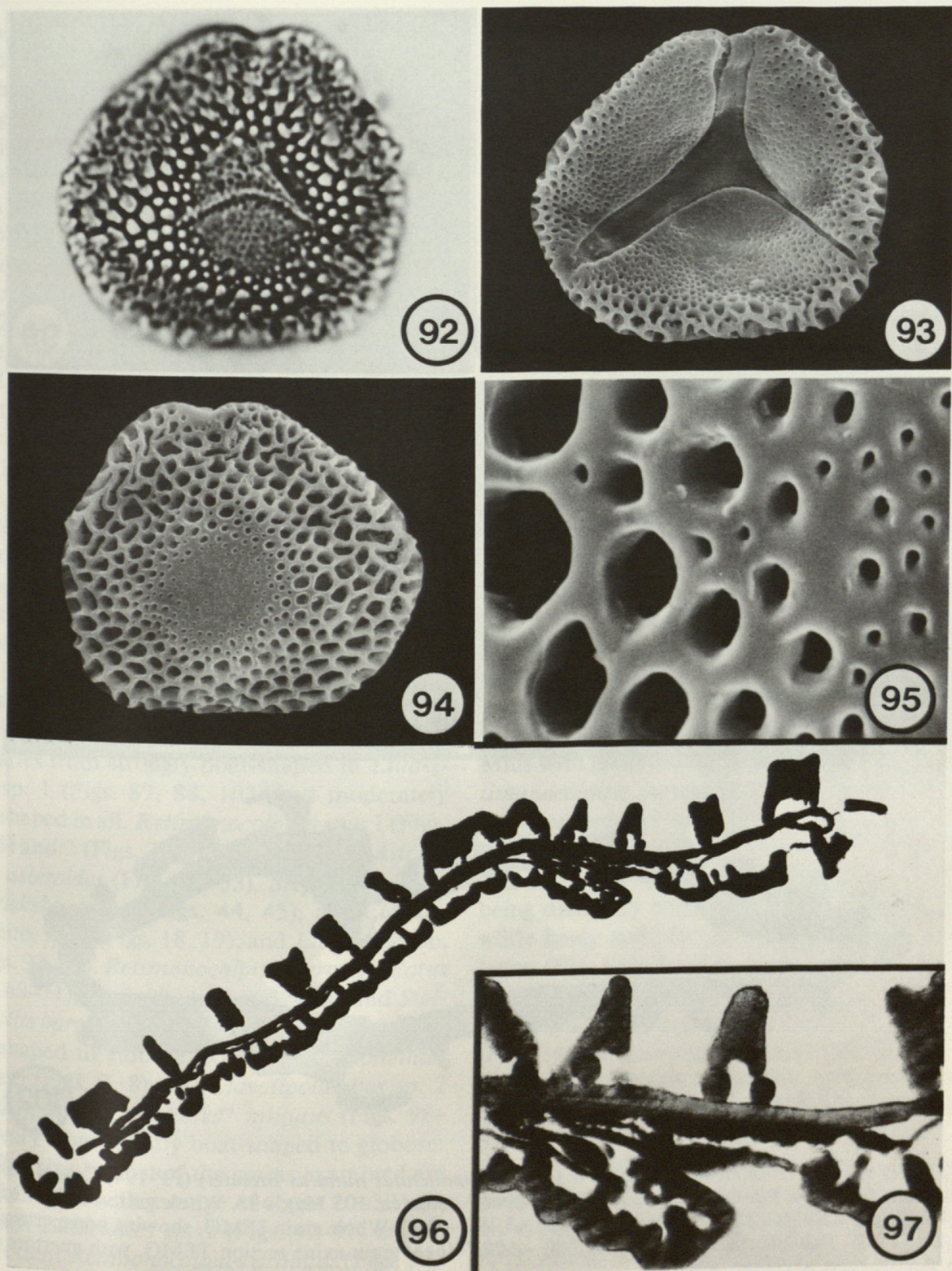
FIGURES 92–97. *Liliacidites* Couper sp. 2 (FP-366; D13-535), from Upper Zone IIB of the Potomac Group, lower Upper Albian (ca. 103 Ma).—92. Whole grain PMG, ×1,350.—93. Whole grain SEMG, showing apertural side, ×1,620.—94. Whole grain SEMG, showing nonapertural side, ×1,620.—95. Exine surface SEMG, ×12,000.—96. Whole grain exine section TEMG, with aperture at bottom right, ×5,680.—97. Apertural exine section TEMG, with apertural region at bottom and appressed non-apertural side above, ×14,300.
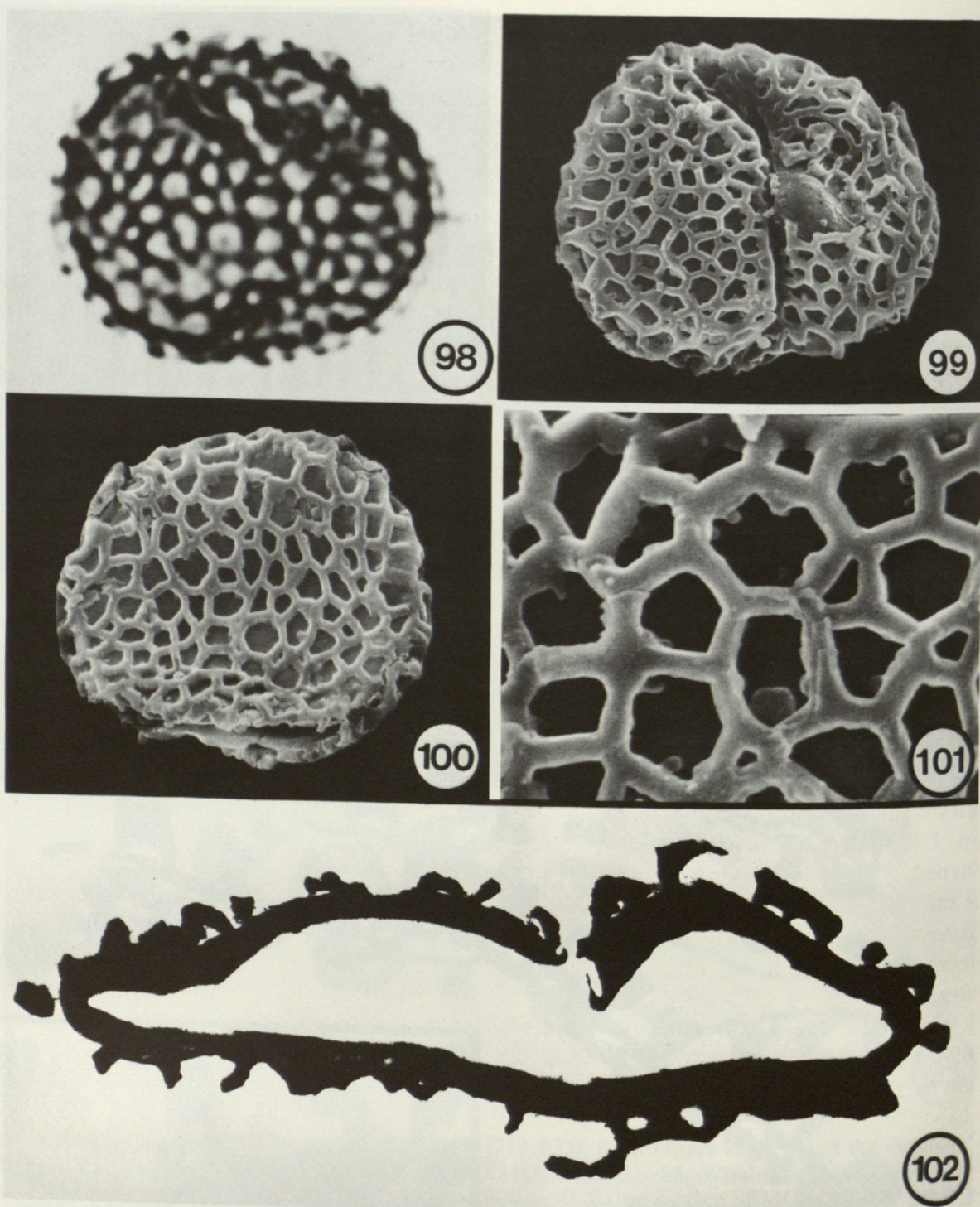
FIGURES 98–102. "*Liliacidites*" *minutus* (= *Clavatipollenites minutus* Brenner) (FP-194; Cornet Beltway), from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma).—98. Whole grain PMG, ×2,800.—99. Whole grain SEMG, showing apertural side, ×3,100.—100. Whole grain SEMG, showing nonapertural side, ×3,100.—101. Exine surface SEMG, ×12,000.—102. Whole grain exine section TEMG, with aperture at top and slightly right of center, ×9,270.

tectum. Endexine was not observed. Although "*Liliacidites*" *minutus* does not agree with typical *Liliacidites* pollen, such as *Liliacidites* spp. 1 and 2, in all respects, this pollen type appears to have a greater overall similarity with *Liliacidites* than with *Clavatipollenites*, and for this reason we have chosen to include it under our discussion of the pollen of *Liliacidites*.

MAJOR FEATURES OF LOWER CRETACEOUS ANGIOSPERM POLLEN

The major features of the 13 types of Lower Cretaceous angiosperm pollen grains that we have investigated with combined light, scanning electron, and transmission electron microscopy are summarized in Table 4. Characters of these Early

Cretaceous pollen grains are considered under the following seven headings: aperture type, pollen shape, pollen size, nonapertural exine sculpturing, nonapertural exine structure, exine stratification, and aperture ultrastructure.

Aperture type. The majority of pollen grain types included in this study (nine out of 13) have a monosulcate aperture, e.g., *Clavatipollenites hughesii* (Figs. 7, 8), *Retimonocolpites peroreticulatus* (Fig. 70), *Stellatopollis barghoornii* (Figs. 81, 82), and "*Liliacidites*" *minutus* (Fig. 99). Two pollen types, aff. *Clavatipollenites* sp. 1 (Fig. 18) and *Liliacidites* sp. 2 (Fig. 93) have trichotomosulcate apertures, while pollen grains of *Asteropollis asteroides* are basically pentachotomosulcate (Figs. 31, 32), although sometimes they may be tetra- or hexachotomosulcate. *Stephanocolpites fredericksburgensis* is the only type of pollen included in our investigation that has several equatorial apertures instead of a single polar aperture. According to Davies and Norris (1976), *S. fredericksburgensis* is basically tetracolpoidate, less commonly pentacolpoidate as pictured in Figures 44 and 45.

Pollen shape. Shape of the pollen grains studied varies from strongly boat-shaped in *Liliacidites* sp. 1 (Figs. 87, 88, 103) and moderately boat-shaped in aff. *Retimonocolpites* spp. 1 (Figs. 63–65) and 2 (Figs. 74–76) to globose in *Asteropollis asteroides* (Figs. 31–33), *Stephanocolpites fredericksburgensis* (Figs. 44, 45), aff. *Clavatipollenites* sp. 1 (Figs. 18, 19), and *Liliacidites* sp. 2 (Figs. 92–94). *Retimonocolpites peroreticulatus* (Figs. 69–71), *R. dividuus* (Figs. 57–59), and *Stellatopollis barghoornii* (Figs. 81, 82) all vary from boat-shaped to globose, while *Clavatipollenites hughesii* (Figs. 7, 8), aff. *Clavatipollenites* sp. 2 (Fig. 23), and "*Liliacidites*" *minutus* (Figs. 98–100) vary from slightly boat-shaped to globose.

Pollen size. Most of the grains examined are medium-sized with a range of about 20–30 μm, although *Liliacidites* sp. 2 (Figs. 92–97) and to some extent *Retimonocolpites dividuus* (Figs. 57–62) average a little above this size range. *Retimonocolpites peroreticulatus* (Figs. 69–73), which is usually somewhat below 20 μm, is basically small- to medium-sized. Pollen of *Liliacidites* sp. 1 (Figs. 87–91) and *Stellatopollis barghoornii* (Figs. 81–86) is mostly large (usually over 50 μm), while pollen grains of "*Liliacidites*" *minutus* (Figs. 98–102) are small (usually around 15 μm).

Nonapertural exine sculpturing. Most of the pollen types studied are irregularly reticulate, e.g.,

Clavatipollenites hughesii (Fig. 9), *Asteropollis asteroides* (Fig. 34), *Stephanocolpites fredericksburgensis* (Fig. 46), although *Stellatopollis barghoornii* is regularly reticulate with circular muri (Figs. 82–84) and *Liliacidites* sp. 2 is more or less regularly reticulate with muri that are almost circular (Figs. 94, 95). "*Liliacidites*" *minutus*, which is irregularly to more or less regularly reticulate (Figs. 99, 100), is distinctive in that its muri are mostly decidedly polygonal (Fig. 101). *Liliacidites* spp. 1 and 2 are characterized by differentiation of their reticulate sculpturing into coarse and fine areas (Figs. 89, 90, 95). In *Liliacidites* sp. 1 the finer reticulum is at the ends of the boat-shaped pollen (Figs. 87, 88, 103), while in *Liliacidites* sp. 2 the area around the aperture (Fig. 93) and the middle of the nonapertural side of the grain (Fig. 94) are both surrounded by a finer reticulum.

The nature of the muri or walls of the reticulum varies considerably. In *Clavatipollenites hughesii,* the muri are beaded to spinulose (Fig. 9), while they are weakly beaded to spinulose in *Asteropollis asteroides* (Fig. 34), and spinulose in *Stephanocolpites fredericksburgensis* (Fig. 46). Muri with recurved spines are found in both *Retimonocolpites peroreticulatus* (Fig. 72) and aff. *Retimonocolpites* sp. 2 (Fig. 77). Banded muri occur in aff. *Retimonocolpites* sp. 1 (Figs. 63–68) and in *Retimonocolpites dividuus* (Figs. 57–62), being distinctly banded in the former (Fig. 66) while finely and discontinuously banded in the latter (Fig. 60). Beaded muri characterize aff. *Clavatipollenites* sp. 1 (Figs. 20, 21), while aff. *Clavatipollenites* sp. 2 has beaded-granulose muri (Fig. 24). *Stellatopollis barghoornii* has muri covered by psilate, triangular supratectal elements, which form a "crotonoid" sculpturing pattern (Figs. 83, 84). In all three species of *Liliacidites* the muri are psilate and the lumina are generally strongly dimorphic, with small lumina mixed in with much larger ones (Figs. 89, 95, 101). Nodose muri with node-like, swollen areas at points where columellae and muri meet occur in *Asteropollis asteroides* (Fig. 34) and aff. *Retimonocolpites* sp. 1 (Figs. 63–66).

Nonapertural exine structure. Most of the pollen types investigated are semitectate, except *Stephanocolpites fredericksburgensis*, which is tectate-perforate (Figs. 45, 46), and *Clavatipollenites hughesii* (Figs. 8, 9) and *Asteropollis asteroides* (Figs. 32–34), which are tectate-perforate to semitectate. The coarse and finely reticulate *Liliacidites* spp. 1 and 2 are basically

TABLE 4. Major features of Lower Cretaceous angiosperm pollen.

Pollen Type	Aperture Type, Pollen Shape, and Pollen Size	Nonapertural Exine Sculpturing
(1) *Clavatipollenites hughesii*	Monosulcate; slightly boat-shaped to globose; medium-sized	Irregularly reticulate, muri beaded to spinulose
(2) *Asteropollis asteroides*	(4–)5(–6)-chotomosulcate; globose; medium-sized	Irregularly reticulate, muri weakly beaded to spinulose, nodose
(3) *Stephanocolpites fredericksburgensis*	4(–5)-colpoidate; globose; medium-sized	Irregularly reticulate, muri spinulose
(4) *Retimonocolpites peroreticulatus*	Monosulcate; boat-shaped to globose; small- to medium-sized	Irregularly reticulate, muri with recurved spines, reticulum ± free from nexine
(5) aff. *Retimonocolpites* sp. 2	Monosulcate; boat-shaped; medium-sized	Irregularly reticulate, muri with recurved spines
(6) aff. *Retimonocolpites* sp. 1	Monosulcate; boat-shaped; medium-sized	Irregularly reticulate, muri distinctly banded, nodose
(7) aff. *Clavatipollenites* sp. 1	Trichotomosulcate; globose; medium-sized	Irregularly reticulate, muri beaded
(8) aff. *Clavatipollenites* sp. 2	Monosulcate; slightly boat-shaped to globose; medium-sized	Irregularly reticulate, muri beaded-granulose
(9) *Stellatopollis barghoornii*	Monosulcate; boat-shaped to ± globose; large	Regularly reticulate, muri circular, with psilate, triangular supratectal elements, i.e., "crotonoid"
(10) *Liliacidites* sp. 1	Monosulcate; strongly boat-shaped; large	Irregularly coarsely and finely reticulate, muri psilate, lumina within coarse reticulum strongly dimorphic
(11) *Liliacidites* sp. 2	Trichotomosulcate; globose; a little above medium-sized	± regularly coarsely and finely reticulate, muri psilate, ± circular, lumina within coarse reticulum occasionally strongly dimorphic
(12) "*Liliacidites*" *minutus*	Monosulcate; slightly boat-shaped to globose; small	Irregularly to ± regularly reticulate, muri psilate, mostly decidedly polygonal, lumina dimorphic
(13) *Retimonocolpites dividuus*	Monosulcate; boat-shaped to globose; ± medium-sized	Irregularly reticulate, muri finely and discontinuously banded

TABLE 4. (Continued).

Nonapertural Exine Structure	Exine Stratification	Aperture Ultrastructure
(1) Tectate-perforate to semitectate; nexine moderately to very thick, columellae well-developed	Thick endexine under aperture only	Aperture externally verrucate, internally with a very thick, apparently homogeneous endexine and a thin, occasionally lamellate foot-layer overlaid by a thick sexine organized into verrucae
(2) Tectate-perforate to semitectate; nexine average to moderately thick, columellae seemingly composed of granules	Thin endexine throughout	Aperture evident internally as a lamellate nexine consisting of a thin endexine and a somewhat thicker foot-layer overlaid by a disorganized sexine
(3) Tectate-perforate; nexine moderately to very thick, columellae present	Well-developed endexine throughout, conspicuously interbedded with foot-layer under aperture	Apertures internally with a thick endexine conspicuously lamellate at top and interbedded with foot-layer, sexine somewhat reduced, composed of laterally thickened elements
(4) Semitectate; nexine moderately to very thick, columellae absent	Thin endexine possibly present	Aperture represented externally by a definite, distinctly bordered slit in the reticulum, evident internally by a definite thinning of the nexine
(5) Semitectate; nexine average to moderately thick, well-developed columellae present	Thin endexine throughout	Aperture evident internally by a definite thinning of the nexine and a disorganization of the sexine
(6) Semitectate; nexine moderately thick, well-developed columellae present	Endexine not observed	Aperture appearing externally as an interruption in the reticulum, evident internally by a marked thinning of the nexine
(7) Semitectate; nexine average, well-developed columellae present	Endexine not observed	Aperture evident internally by a thinning of the nexine and a disorganization of the sexine
(8) Semitectate; nexine average, well-developed columellae present	Endexine not observed	Aperture evident internally by a thinning of the nexine and a disorganization of the sexine
(9) Semitectate; nexine moderately thin, columellae very short, tectum and overlying elements thick	Thin endexine probably throughout	Aperture probably appearing externally as a differently organized, non-"crotonoid" region of the exine, evident internally by a thinning of the nexine, which becomes lamellate, and a marked disorganization and reduction of the sexine
(10) Semitectate to tectate-perforate at ends of grain; nexine extremely to very thin, columellae short, tectum thick	Endexine not observed	Aperture evident internally as a broad, infolded region of the exine with a thinner nexine but apparently unreduced sexine

TABLE 4. (Continued).

Nonapertural Exine Structure	Exine Stratification	Aperture Ultrastructure
(11) Semitectate to tectate-perforate around aperture and in middle of non-apertural side; nexine very to moderately thin, columellae short, tectum thick (especially on non-apertural side)	Well-developed endexine, at least under aperture	Aperture appearing externally as a broad, ± psilate area, evident internally as a thinner region of the exine that appears to consist largely of endexine
(12) Semitectate; nexine moderately thick, columellae short, tectum thick	Endexine not observed	Aperture appearing externally as an interruption in the reticulum, evident internally by a thinning of the nexine
(13) Semitectate; nexine extremely to very thin, columellae short, tectum thick	Endexine not observed	Aperture represented externally by a definite interruption in the reticulum that in the light microscope appears characteristically folded on either side, scarcely evident internally, "border" observed in PMG presumably due to infolding of the exine

semitectate, with tectate-perforate areas at the ends of the boat-shaped pollen of *Liliacidites* sp. 1 (Figs. 87, 88, 90) and around the aperture and in the middle of the nonapertural side of *Liliacidites* sp. 2 (Figs. 93, 94).

Nexine thickness in the nonapertural exine (cf. Table 3) ranges from very thick to extremely thin. *Clavatipollenites hughesii* (Fig. 10), *Stephanocolpites fredericksburgensis* (Fig. 48), and *Retimonocolpites peroreticulatus* (Fig. 73) have a moderately to very thick nexine, aff. *Retimonocolpites* sp. 1 (Fig. 68) and "*Liliacidites*" *minutus* (Fig. 102) have a moderately thick nexine, and *Asteropollis asteroides* (Fig. 36) and aff. *Retimonocolpites* sp. 2 (Fig. 78) have an average to moderately thick nexine. An average nexine characterizes the pollen of aff. *Clavatipollenites* spp. 1 and 2 (Figs. 22, 26). By contrast, the nexine is moderately thin in *Stellatopollis barghoornii* (Figs. 85, 86), very to moderately thin in *Liliacidites* sp. 2 (Fig. 96), and extremely to very thin in *Retimonocolpites dividuus* (Figs. 61, 62) and *Liliacidites* sp. 1 (Fig. 91).

Most of the pollen types have well-developed columellae, although the columellae are short (and the tectum is thick) in *Stellatopollis barghoornii* (Figs. 85, 86), *Retimonocolpites dividuus* (Figs. 61, 62), and in all species of *Liliacidites* (Figs. 91, 96, 102). *Liliacidites* sp. 2 is noteworthy in that the tectum is considerably thicker on the nonapertural side of the pollen grain (Fig. 96). *Retimonocolpites peroreticulatus* is unusual in that columellae are absent and the reticulum is more or less free from the underlying nexine (Figs. 69–73). The columellae are seemingly composed of granules in *Asteropollis asteroides* (Figs. 34, 36).

Exine stratification. Endexine was not observed in the pollen of aff. *Clavatipollenites* spp. 1 (Fig. 22) and 2 (Figs. 25, 26), aff. *Retimonocolpites* sp. 1 (Figs. 67, 68), *Retimonocolpites dividuus* (Figs. 61, 62), *Liliacidites* sp. 1 (Fig. 91), and "*Liliacidites*" *minutus* (Fig. 102). A thin endexine is possibly present in *Retimonocolpites peroreticulatus,* although it cannot be seen in the TEMG shown in Figure 73. Thick endexine only under the aperture occurs in *Clavatipollenites hughesii* (Fig. 11) and well-developed endexine, at least under the aperture, was found in *Liliacidites* sp. 2 (Fig. 97). A thin endexine throughout the grain (in both apertural and nonapertural regions) characterizes *Asteropollis asteroides* (Figs. 36, 37) and aff. *Retimonocolpites* sp. 2 (Figs. 79, 80), and is probably present in *Stellatopollis*

barghoornii as well (cf. Fig. 86, in which definite endexine can be seen in sections of the nonapertural exine). In *Stephanocolpites fredericksburgensis,* a well-developed endexine is present throughout the grain (Figs. 48, 50), and the endexine is conspicuously interbedded with the footlayer under the aperture (Fig. 49).

Aperture ultrastructure. Considerable variation exists in the pollen grains examined with regard to aperture ultrastructure, with reference both to external sculpturing and internal structure. Externally apertures may appear either as differentially sculptured areas of the exine or as definite interruptions in the reticulum itself. In *Clavatipollenites hughesii* the aperture is conspicuously verrucate (Fig. 8), while in *Liliacidites* sp. 2 the aperture appears as a broad, more or less psilate area (Fig. 93). The aperture is marked by an interruption in the reticulum itself in aff. *Retimonocolpites* sp. 1 (Fig. 64), "*Liliacidites*" *minutus* (Fig. 99), and *Retimonocolpites dividuus* (Fig. 59), while in *Retimonocolpites peroreticulatus* the aperture is represented externally by a definite, distinctly bordered slit in the reticulum (Fig. 70). The aperture probably appears externally as a differently organized, non-"crotonoid" region of the exine in *Stellatopollis barghoornii* (cf. Fig. 85).

Apertures are just as varied internally or structurally. In many instances the aperture is marked by a thinning of the nexine and a disorganization of the sexine relative to the nonapertural exine, e.g., aff. *Clavatipollenites* sp. 1 (Fig. 22) and *Stellatopollis barghoornii* (Fig. 85). If endexine is present in the pollen grain, it may be restricted to the aperture, as in *Clavatipollenites hughesii,* which has a particularly thick apertural endexine (Fig. 11), and in *Liliacidites* sp. 2 (Fig. 97), or it may be thicker under the aperture, as in *Stephanocolpites fredericksburgensis* (cf. Figs. 48, 49). In *Asteropollis asteroides* (cf. Figs. 36, 37) and in aff. *Retimonocolpites* sp. 2 (cf. Figs. 79, 80) endexine is apparently about equally developed in apertural and nonapertural areas. The nexine under the aperture is lamellate in *Asteropollis asteroides* (Fig. 37) and *Stellatopollis barghoornii* (Fig. 85), while in *Clavatipollenites hughesii* occasionally the foot-layer appears lamellate (Fig. 11). In *Stephanocolpites fredericksburgensis* the apertural endexine is conspicuously lamellate at the top and interbedded with the foot-layer (Fig. 49). In some pollen types the apertural sexine is relatively unreduced but differently organized as compared with the nonapertural sexine, e.g., the apertural sexine is organized into verrucae in *Clavatipollenites hughesii* (Figs. 8, 11) and into laterally thickened elements in *Stephanocolpites fredericksburgensis* (Figs. 47, 49). The broad aperture in *Liliacidites* sp. 1, which we have not observed expanded, and which can be seen infolded on the right side of the grain pictured in Figure 91, consists of an extremely to very thin nexine overlaid by a conspicuously well-developed and little reduced sexine. By contrast, the aperture of *Liliacidites* sp. 2 shows considerable reduction of its sexine (Figs. 93, 96, 97). The bordered aperture that is so conspicuous in PMG of *Retimonocolpites dividuus* (Figs. 57, 58) is scarcely evident in TEMG (Figs. 61, 62), and is apparently the result of infolding of the thin-walled exine itself.

DELIMITATION OF LOWER CRETACEOUS ANGIOSPERM POLLEN

Asteropollis, Stephanocolpites fredericksburgensis, and *Stellatopollis,* even at the light microscope level, are reasonably distinct taxa of Lower Cretaceous angiosperm pollen because of their characteristic apertures (4–6-chotomosulcate in *Asteropollis,* 4–5-colpoidate in *S. fredericksburgensis*) and sculpturing (monosulcate and "crotonoid" in *Stellatopollis*). In contrast, delimitation of *Clavatipollenites, Retimonocolpites,* and *Liliacidites* based on light microscope studies alone has proved to be extremely difficult. This is evident by the fact that the type species of the genus *Retimonocolpites, R. dividuus,* has been formally transferred to *Liliacidites* by Brenner (1963), as *Liliacidites dividuus* (Pierce) Brenner, while pollen that appears to be identical with *R. dividuus* has been described by Kemp (1968) as *Clavatipollenites rotundus* Kemp. Some authors, by contrast, have at times referred to pollen of the *Liliacidites* type under the name *Retimonocolpites* (cf. Doyle, 1973).

As might be expected, our same grain combined light and electron microscope study of Lower Cretaceous angiosperm pollen grains has revealed a number of differences that can be used to delimit *Clavatipollenites, Retimonocolpites,* and *Liliacidites. Clavatipollenites,* at least in the restricted sense of *C. hughesii,* has a beaded to spinulose reticulum that is tectate-perforate to semitectate (Fig. 9), a thick nexine (Fig. 10), well-developed columellae (Fig. 10), and a thick plug of endexine under the aperture (Fig. 11), while *Retimonocolpites,* at least in the sense of its type

TABLE 5. Systematic affinities of Lower Cretaceous angiosperm pollen.

I. CHLORANTHACEOUS POLLEN TYPES

    (1) *Clavatipollenites hughesii* (chloranthaceous, extremely similar to *Ascarina*)

    (2) *Asteropollis asteroides* (chloranthaceous, with a large number of similarities to *Hedyosmum*)

    (3) *Stephanocolpites fredericksburgensis* (chloranthaceous, with certain similarities to *Chloranthus*)

II. MYRISTICACEOUS-LIKE POLLEN TYPES

    (1) aff. *Clavatipollenites* sp. 2 (similar to some myristicaceous pollen)

    (2) aff. *Clavatipollenites* sp. 1 (certain similarities to myristicaceous pollen)

III. MONOCOTYLEDONOUS POLLEN TYPES

    (1) *Liliacidites* sp. 1 (monocotyledonous)

    (2) *Liliacidites* sp. 2 (monocotyledonous)

    (3) "*Liliacidites*" *minutus* (possibly monocotyledonous)

    (4) *Retimonocolpites dividuus* (probably monocotyledonous)

IV. POLLEN TYPES OF UNCERTAIN OR UNKNOWN AFFINITY

    (1) *Retimonocolpites peroreticulatus*

    (2) aff. *Retimonocolpites* sp. 2

    (3) aff. *Retimonocolpites* sp. 1

    (4) *Stellatopollis barghoornii*

species, *R. dividuus,* differs considerably in its banded, semitectate reticulum (Fig. 60), thin nexine (Fig. 61), short columellae (Fig. 61), and apparent lack of endexine (Fig. 62). Some authors, e.g., Doyle et al. (1975), have suggested restricting *Liliacidites* to monosulcate pollen grains that exhibit a differentiation into coarsely and finely reticulate areas such as observed in *Liliacidites* spp. 1 (Figs. 87, 88, 103) and 2 (Figs. 93, 94). However, unless one wishes to create a separate genus for "*Liliacidites*" *minutus* (Figs. 98–102), which is probably warranted, the most important features of *Liliacidites* as presently delimited would appear to be its psilate, semitectate reticulum and strongly dimorphic lumina (cf. Figs. 89, 95, 101).

Although for the present we prefer to keep the 13 taxa of Lower Cretaceous angiosperm pollen grains that we have investigated in six form genera delimited largely on the basis of light microscopy, we believe that the majority of these 13 taxa probably represent good genera in a biological sense. For example, *Retimonocolpites peroreticulatus* is certainly sufficiently distinct from *R. dividuus* to warrant its recognition as a separate genus. However, until more examples of Lower Cretaceous angiosperm pollen grains have been investigated ultrastructurally, especially using same grain combined light, scanning electron, and transmission electron microscopy, we believe that for now it is prudent simply to

refer to the pollen grains that we have studied under established form genera such as *Clavatipollenites, Retimonocolpites,* and *Liliacidites.*

SYSTEMATIC AFFINITIES OF LOWER CRETACEOUS ANGIOSPERM POLLEN

The Lower Cretaceous angiosperm pollen that we have examined can be placed into four different groups based on systematic affinity. One group of pollen grains is clearly related to the primitive dicotyledon family Chloranthaceae, while a second group exhibits certain resemblances at least to pollen of the family Myristicaceae. A third group consists of pollen grains with features that are characteristic of monocotyledon pollen. Finally, there is a fourth group of pollen types that are of uncertain or unknown systematic affinity. Table 5 summarizes the possible systematic affinities of the Lower Cretaceous angiosperm pollen included in this study.

CHLORANTHACEOUS POLLEN TYPES

A number of workers, including Couper (1960), Kuprianova (1967, 1981), Kemp (1968), Doyle (1969), and Muller (1981), have noted certain resemblances between some Early Cretaceous angiosperm pollen types and pollen of the extant primitive dicot family Chloranthaceae. Since these suggested relationships have virtually all been based on light microscope comparisons

TABLE 6. Major features of pollen of the family Chloranthaceae.

Pollen Feature	Ascarina[a]	Hedyosmum[b]	Chloranthus[c]
Aperture Type, Pollen Shape, and Pollen Size	Monosulcate; slightly boat-shaped to globose; medium-sized	5(–6)-chotomosulcate; globose; ± medium-sized	(4–5–)6-colpoidate; globose; medium-sized
Nonapertural Exine Sculpturing	Irregularly reticulate, muri beaded to spinulose	Irregularly reticulate, muri conspicuously spinulose, nodose	Irregularly reticulate, muri bluntly spinulose to ± granulose
Nonapertural Exine Structure	Tectate-perforate to semitectate; nexine moderately to very thick, columellae well-developed	Tectate-perforate to semitectate; nexine average, columellae well-developed	Semitectate; nexine moderately thin to average; columellae present
Exine Stratification	Thick endexine under aperture only	Thick endexine under aperture only; foot-layer under aperture conspicuously coarsely lamellate	Endexine throughout, finely lamellate, especially under aperture
Aperture Ultrastructure	Aperture externally finely verrucate, internally with a very thick, somewhat heterogeneously stratified endexine and a disorganized foot-layer overlaid by a thick sexine organized into verrucae	Aperture represented externally as more tightly organized regions of the reticulum, evident internally as a very thick, somewhat heterogeneously stratified endexine and a conspicuously lamellate foot-layer overlaid by a thick, hardly reduced sexine that is scarcely disorganized relative to the non-apertural sexine	Apertures represented externally as solid, ± scabrate areas in the reticulum, evident internally by development of a finely lamellate endexine, extreme thinning of the foot-layer, and reduction and disorganization of the sexine

[a] Ultrastructure based on *Ascarina diffusa* A. C. Smith.
[b] Ultrastructure based on *Hedyosmum orientale* Merr. & Chun.
[c] Ultrastructure based on *Chloranthus japonicus* Sieb.

alone, we decided to examine pollen of the Chloranthaceae with SEM and TEM to see if there were ultrastructural similarities as well.

The Chloranthaceae is a very small family of five genera and approximately 70 species. The largest genus, *Hedyosmum*, with some 40 species, is restricted to the American tropics except for one species, *H. orientale*, which is found only in southeast Asia. *Ascarina*, with 11 species (Smith, 1976), is basically Australasian, while the monotypic *Ascarinopsis* is endemic to Madagascar. *Chloranthus* (15 species) and *Sarcandra* (three species) are Indomalaysian. Major features of pollen of the three main genera of Chloranthaceae (*Ascarina, Hedyosmum,* and *Chloranthus*) are summarized in Table 6. Three taxa of Lower Cretaceous angiosperm pollen grains, *Clavatipollenites, Asteropollis,* and *Stephanocolpites fredericksburgensis,* exhibit various degrees of similarity to particular genera of Chloranthaceae.

Clavatipollenites and Ascarina. Many people have noted a similarity between *Clavatipollenites* and pollen produced specifically by the chloranthaceous genus *Ascarina*. From light microscopy alone it is apparent that pollen grains of both *Clavatipollenites* (Figs. 7–11) and *Ascarina* (Figs. 12–17) are monosulcate, slightly boat-shaped to globose, and medium-sized. Moreover, both types of pollen have well-developed columellae, which in optical section appear more as sculptural clavae (cf. Figs. 7, 12) than as internal structural elements. SEM and TEM examination, however, reveals an even more remarkable similarity between *Ascarina* and *Clavatipollenites* in the strict sense of *C. hughesii. Clavatipollenites hughesii* and *Ascarina* are identical in all the following ultrastructural features; an irregular reticulum with beaded to spinulose muri (cf. Figs. 9, 14), a tectate-perforate to semitectate exine (cf. Figs. 8, 9, 13, 14), a moderately to very thick nona-

pertural nexine with well-developed columellae and a thin tectum (cf. Figs. 10, 16), thick endexine present under the aperture only (cf. Figs. 11, 15, 17), and a somewhat verrucate aperture composed of tightly organized sexinous elements (cf. Figs. 8, 11, 13, 17). Thus, in ultrastructural as well as light microscope observable characters, *Clavatipollenites hughesii* is for all intents identical to the pollen of *Ascarina*. Pollen of the two genera differs only in minor details, and not in any substantive morphological features. We agree with Muller (1981) that *Clavatipollenites* has little in common with pollen of *Austrobaileya,* which was suggested by Endress and Honegger (1980).

Asteropollis and Hedyosmum. Since the distinctive, fundamentally pentachotomosulcate aperture of *Asteropollis* (Figs. 31–37) is particularly suggestive of the aperture in the pollen of the extant chloranthaceous genus *Hedyosmum,* we thought that it would be interesting to examine pollen of *Hedyosmum* (Figs. 38–43) ultrastructurally. Although *Hedyosmum* pollen appears to be basically pentachotomosulcate (Fig. 39), sometimes, just like *Asteropollis,* it exhibits variation in the number of apertural arms present (cf. Fig. 38, which shows a PMG of a pollen grain of *Hedyosmum* that has a six-armed aperture). In addition, in both genera the pollen is globose and medium-sized. Ultrastructurally, *Asteropollis* exhibits a number of similarities to *Hedyosmum* pollen, including an irregular, nodose reticulum with somewhat spinulose muri (cf. Figs. 34, 40), a tectate-perforate to semitectate exine (cf. Figs. 32–34, 39, 40), a nonapertural nexine that is more or less average in thickness (cf. Figs. 36, 42), and a conspicuously lamellate apertural foot-layer (cf. Figs. 37, 43). Although both *Asteropollis* and *Hedyosmum* have a spinulose reticulum, the spinules are better developed in *Hedyosmum* (at least in the species shown in Fig. 40). Also, columellae are not as well-developed in *Asteropollis* (Fig. 36) as they are in *Hedyosmum* (Fig. 42). Finally, *Hedyosmum* (again at least in the species examined) has endexine only under the aperture (Figs. 41–43), while in *Asteropollis* traces of endexine are evident in both the apertural (Fig. 37) and nonapertural (Fig. 36) exine. Thus, while not agreeing in every morphological feature, *Asteropollis,* nevertheless, does exhibit a number of ultrastructural resemblances to pollen of *Hedyosmum,* in addition to its strikingly similar aperture type.

Stephanocolpites fredericksburgensis and Chloranthus. *Stephanocolpites fredericksbur-gensis* has been compared to the pollen of the genus *Chloranthus* because both pollen types are polycolpoidate. In light of this we decided to study pollen of *Chloranthus japonicus* with SEM and TEM in order to determine how *S. fredericksburgensis* (Figs. 44–50) compares ultrastructurally with the pollen of *Chloranthus* (Figs. 51–56). *Chloranthus* pollen appears to be mostly 6-aperturate (Figs. 51, 52), although sometimes it is 4–5-aperturate as well. Davies and Norris (1976) found that *S. fredericksburgensis* was most commonly 4-aperturate. The pollen of *Chloranthus japonicus* is semitectate (Figs. 52, 53) rather than tectate-perforate, as in *S. fredericksburgensis* (Figs. 45, 46), and the spinules on its reticulum are much coarser (cf. Figs. 46, 53). Moreover, the nonapertural nexine is moderately thin to average in *C. japonicus* (Figs. 54, 55), while it is moderately to very thick in *S. fredericksburgensis* (Fig. 48). *Chloranthus japonicus,* just as *S. fredericksburgensis,* has endexine throughout the grain, under both the apertural (cf. Figs. 49, 56) and nonapertural (cf. Figs. 48, 55) regions. Although *S. fredericksburgensis* resembles pollen of *Chloranthus* in its aperture type, its ultrastructure is somewhat different (at least as judged by *C. japonicus*). Moreover, *S. fredericksburgensis* exhibits some general chloranthaceous attributes, including a spinulose reticulum (Fig. 46), a thick nonapertural nexine (Fig. 48), which is reminiscent of *Ascarina* (Fig. 16) and *Clavatipollenites hughesii* (Fig. 10), and a conspicuously lamellate apertural foot-layer (Fig. 49), which is similar to the foot-layer that occurs in the apertural region of the pollen of *Hedyosmum* (Fig. 43). The definite presence of endexine in the pollen of *S. fredericksburgensis* may also be taken to support the idea of a general chloranthaceous relationship. Thus, while *Stephanocolpites fredericksburgensis* shows some resemblance to the pollen of *Chloranthus,* it has a number of features that can only be described as generalized chloranthaceous palynological attributes.

MYRISTICACEOUS-LIKE POLLEN TYPES

Unlike *Clavatipollenites hughesii,* which, as we have seen, strikingly resembles pollen of the Chloranthaceae, particularly of the genus *Ascarina,* pollen grains of what we have termed the aff. *Clavatipollenites* group exhibit more similarity to pollen of the primitive dicot family Myristicaceae (cf. Walker & Walker, 1979, 1980, 1981, 1983) than to the Chloranthaceae. Both

aff. *Clavatipollenites* spp. 1 (Figs. 18–22) and 2 (Figs. 23–26) appear more myristicaceous than chloranthaceous in their beaded (Figs. 21, 24) rather than spinulose reticulum, average (Figs. 22, 26) rather than thick nonapertural nexine, and apparent total lack of endexine (Figs. 22, 25, 26). Aff. *Clavatipollenites* sp. 2 (Figs. 23–26), for example, is very similar to pollen of *Virola weberbaueri* Markgraf (Figs. 27–30) of the Myristicaceae, both having the same distinctive type of beaded-granulose reticulum with granules in rows (cf. Figs. 24, 28). We have designated pollen of the aff. *Clavatipollenites* group as "myristicaceous-like" instead of "myristicaceous" to emphasize our belief that this type of early angiosperm pollen was not necessarily produced by members of the family Myristicaceae as such. The reason for suggesting this is that myristicaceous pollen is not as ultrastructurally distinctive as chloranthaceous pollen, and, moreover, the Myristicaceae, unlike the Chloranthaceae, produces exceedingly small amounts of pollen, so that it is rather unlikely that myristicaceous pollen grains would occur in such relative abundance as does pollen of the aff. *Clavatipollenites* group in Lower Cretaceous rocks.

MONOCOTYLEDONOUS POLLEN TYPES

Several types of Lower Cretaceous angiosperm pollen grains that we have examined have features characteristic of monocot pollen. While none of these fossil pollen grains can be compared directly with the pollen of any particular extant monocotyledon, they do seem to represent monocotyledonous rather than dicotyledonous pollen types. In Figures 103–110 various Lower Cretaceous angiosperm pollen grains (Figs. 103–106) are compared with similar pollen produced by different living monocots (Figs. 107–110). Monocotyledonous features observed in these Lower Cretaceous angiosperm pollen grains include (1) reticulate sculpturing differentiated into coarse and fine areas (cf. Figs. 103, 107); (2) psilate muri (cf. Figs. 104, 105, 108, 109); (3) dimorphic lumina (cf. Figs. 104, 105, 108, 109); (4) "frilled" muri due to lateral extension of underlying columellae (cf. Figs. 104, 108); (5) more or less regular, decidedly polygonal lumina (cf. Figs. 105, 109); (6) a thin pollen wall in general, especially relative to pollen grain size, combined with a very thin nonapertural nexine in particular relative to the rest of the exine (cf. Figs. 106, 110); and (7) a total lack of endexine (cf. Figs. 106, 110).

Differentiation of reticulate sculpturing into coarse and fine areas, as stressed by Doyle (1973), appears to be a characteristic monocotyledonous pollen feature. We have never encountered this character in any monosulcate dicot pollen, and, moreover, it is very common in monocots as a whole, occurring often in the pollen of families such as the Liliaceae, Amaryllidaceae, Bromeliaceae, Butomaceae, and Araceae among others. Psilate muri, "frilled" muri, and dimorphic lumina are also rather frequently encountered in the pollen of monocots, as is a thin exine with a very thin nonapertural nexine. While not particularly common in monocot pollen as a whole, polygonal reticula do occur in some monocotyledonous pollen grains, and, moreover, are rarely encountered in monosulcate dicot pollen. Finally, a total lack of endexine seems to be characteristic of monocot pollen in general, and is certainly true of various primitive monocot pollen types that we have studied (Walker & Walker, unpubl. data).

Two fossil pollen types that we have investigated (*Liliacidites* spp. 1 and 2) appear to be definitely monocotyledonous, while two other types are probably (*Retimonocolpites dividuus*) or possibly ("*Liliacidites*" *minutus*) monocotyledonous.

Liliacidites spp. 1 and 2. *Liliacidites* sp. 1 (Figs. 87–91) has the following monocotyledonous features: (1) reticulate sculpturing differentiated into coarse (Fig. 89) and fine (Fig. 90) areas, with the finer reticulum at the ends of the strongly boat-shaped grain (Figs. 87, 88); (2) psilate and "frilled" muri (Fig. 89); (3) lumina that are strongly dimorphic within the coarse reticulum (Fig. 89); (4) a thin exine with a particularly thin nonapertural nexine (Fig. 91); and (5) no endexine (Fig. 91). The trichotomosulcate *Liliacidites* sp. 2 (Figs. 92–97) also has many monocotyledonous features, including a coarse and fine reticulum, which in this instance is finer around the aperture (Fig. 93) and in the center of the nonapertural side (Fig. 94). In *Liliacidites* sp. 2 the muri are also psilate (Figs. 94, 95), but they are not "frilled" as in *Liliacidites* sp. 1. Furthermore, *Liliacidites* sp. 2 also has dimorphic lumina within its coarse reticulum (Fig. 95) and a thin exine with a very thin nonapertural nexine (Fig. 96). Surprisingly, however, endexine appears to be present in *Liliacidites* sp. 2, at least under the aperture (Fig. 97).

Retimonocolpites dividuus. Another Lower Cretaceous angiosperm pollen type, *Retimono-*
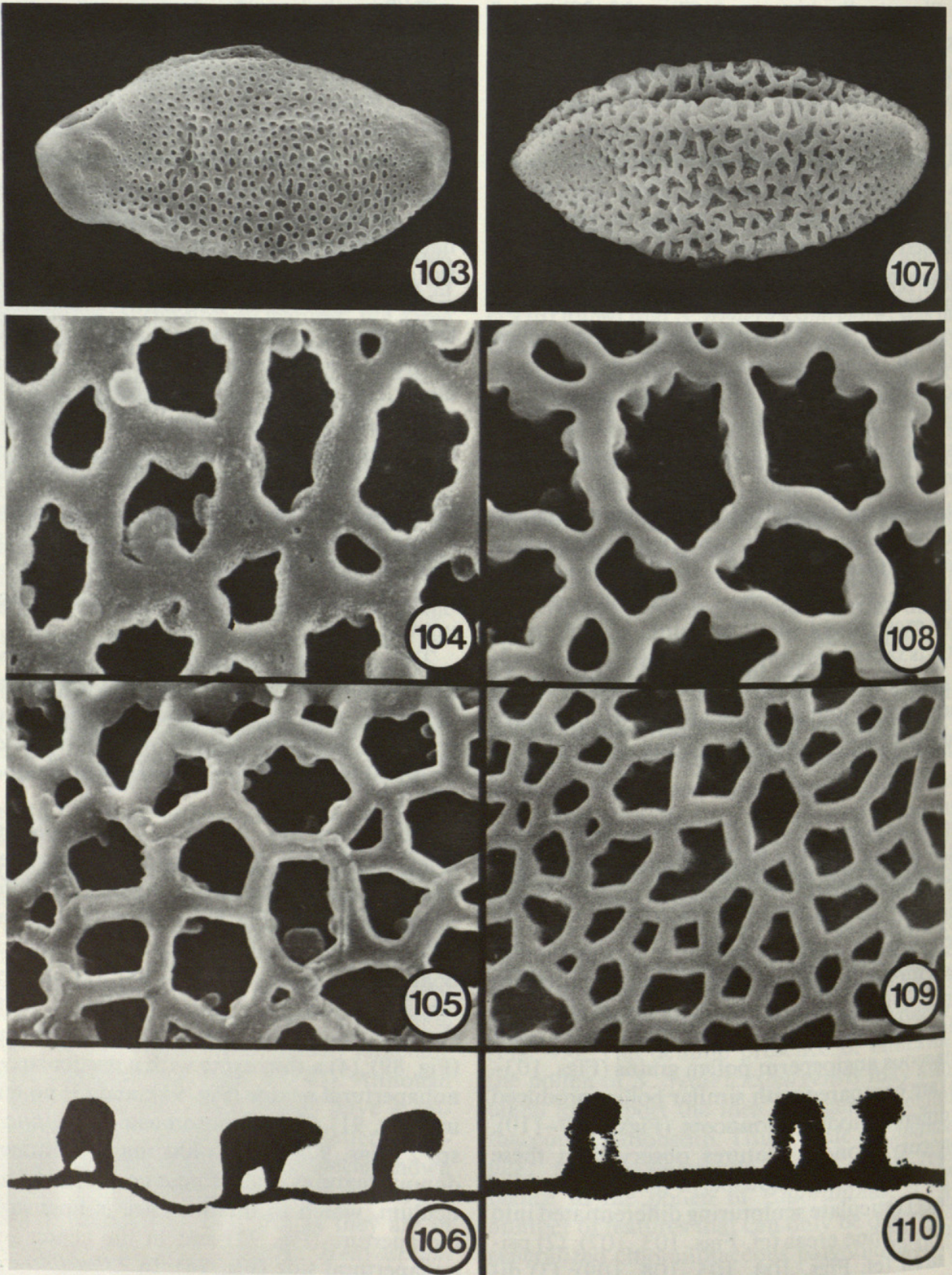
FIGURES 103–110. *Liliacidites* Couper from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 103–105 Ma) (103–106) and extant monocot pollen (107–110).—103. Whole grain SEMG of *Liliacidites* Couper sp. 1 (FP-388; D13-535), ×1,390.—104. Exine surface SEMG of *Liliacidites* Couper sp. 1 (FP-368; D13-535), ×12,000.—105. Exine surface SEMG of "*Liliacidites*" *minutus* (= *Clavatipollenites minutus* Brenner) (FP-194; Cornet Beltway), ×12,000.—106. Nonapertural exine section TEMG of *Liliacidites* Couper sp. 1 (FP-392; D13-535), ×16,500.—107. Whole grain SEMG of *Hemerocallis* of the Liliaceae (P-1538), ×675.—108. Exine surface SEMG of *Butomus* of the Butomaceae (P-3117), ×12,000.—109. Exine surface SEMG of *Xerophyllum* of the Liliaceae (P-3819), ×12,000.—110. Nonapertural exine section TEMG of *Hechtia* of the Bromeliaceae (P-3114), ×16,500.

colpites dividuus (Figs. 57–62), probably has monocotyledonous affinities as well, although it lacks some of the monocot pollen features previously enumerated. The chief argument for a probable monocotyledonous relationship of *Retimonocolpites dividuus* is its extremely to very thin nonapertural nexine combined with short columellae, a thick tectum, and an apparent lack of endexine, all of which give it a striking resemblance to the pollen of *Liliacidites* spp. 1 and 2 (cf. Figs. 61, 62 of *R. dividuus* with Figs. 91, 96 of *Liliacidites* spp. 1 and 2). Moreover, Doyle and Robbins (1977) have reported a Potomac Group pollen type ("*Retimonocolpites* sp. A") that looks just like *R. dividuus* except that it has a finely reticulate patch of sculpturing on its nonapertural side reminiscent of *Liliacidites* sp. 2 (Figs. 92, 94). Thus, *Retimonocolpites dividuus* is probably a monocotyledonous rather than a dicotyledonous pollen type, even though it clearly represents a genus that is distinct from *Liliacidites* itself.

"*Liliacidites*" *minutus.* While possibly monocotyledonous, "*Liliacidites*" *minutus* (Figs. 98–102) has fewer monocotyledonous features than *Liliacidites* spp. 1 and 2 and *Retimonocolpites dividuus.* Its chief monocotyledonous features are its psilate muri and dimorphic lumina (Figs. 99–101). The reticulum of "*L.*" *minutus,* however, is not differentiated into coarse and fine areas, as in *Liliacidites* spp. 1 and 2, and, moreover, the reticulum is decidedly polygonal in outline. Although no endexine was observed, the moderately thick nonapertural nexine of "*L.*" *minutus* (Fig. 102) is very different from the nonapertural nexine of *Liliacidites* spp. 1 and 2 (Figs. 91, 96) and *Retimonocolpites dividuus* (Figs. 61, 62). Another feature, however, that links the three species together is their colorless, transparent exine that does not take up stains such as safranin or basic fuchsin long after other pollen and spore types have become heavily stained.

POLLEN TYPES OF UNCERTAIN OR UNKNOWN AFFINITY

Four Lower Cretaceous angiosperm pollen types that we have studied (*Retimonocolpites peroreticulatus,* aff. *Retimonocolpites* sp. 2, aff. *Retimonocolpites* sp. 1, and *Stellatopollis barghoornii*) have no close counterparts among the pollen of living primitive angiosperms. *Retimonocolpites peroreticulatus* (Figs. 69–73) is especially difficult to place with its loose, non-col-umellate, spine-covered reticulum, although its thick nexine and spinose reticulum suggest a possible chloranthaceous affinity. If it is, indeed, related to *R. peroreticulatus,* aff. *Retimonocolpites* sp. 2 (Figs. 74–80) may have a similar affinity. Aff. *Retimonocolpites* sp. 1 (Figs. 63–68) may also be part of this same complex. Its moderately thick nonapertural nexine (Figs. 67, 68) is similar to that of *R. peroreticulatus* (Fig. 73) and aff. *Retimonocolpites* sp. 2 (Fig. 78), although its banded reticulum (Fig. 66) is somewhat reminiscent of *Retimonocolpites dividuus* (Fig. 60). Finally, *Stellatopollis barghoornii* (Figs. 81–86) is particularly difficult to place, and could have either dicotyledonous or monocotyledonous affinities.

PRIMITIVE ANGIOSPERM POLLEN AND THE ORIGIN AND EARLY EVOLUTION OF FLOWERING PLANTS

Scanning electron and transmission electron microscopy, particularly when used together to examine the same fossil pollen grain, reveal a whole new dimension in the morphology of Early Cretaceous angiosperm pollen. The evolutionary implications of what we have learned in this ultrastructural study of Lower Cretaceous angiosperm pollen will now be discussed. First, we will review major evolutionary trends in the pollen of living primitive angiosperms. Then, we will evaluate the fossil pollen record of early flowering plants in light of what is known about pollen evolution in living primitive angiosperms in order to obtain a better understanding of the evolution of early fossil angiosperm pollen. Finally, we will discuss a model for the early evolution of flowering plants based on a synthesis of our knowledge of both extant and fossil primitive angiosperm pollen.

POLLEN EVOLUTION IN LIVING PRIMITIVE ANGIOSPERMS

Since the trends in pollen evolution in living primitive angiosperms that we recognize are based on the putative phylogenetic relationships of primitive angiosperms, we shall first discuss our concept of evolutionary relationships among the families of primitive angiosperms themselves before reviewing the major evolutionary trends in the pollen of living primitive angiosperms. The putative phylogenetic relationships of the 26 families that we delimit as the subclass Magnoliidae are shown in Figure 111. These families
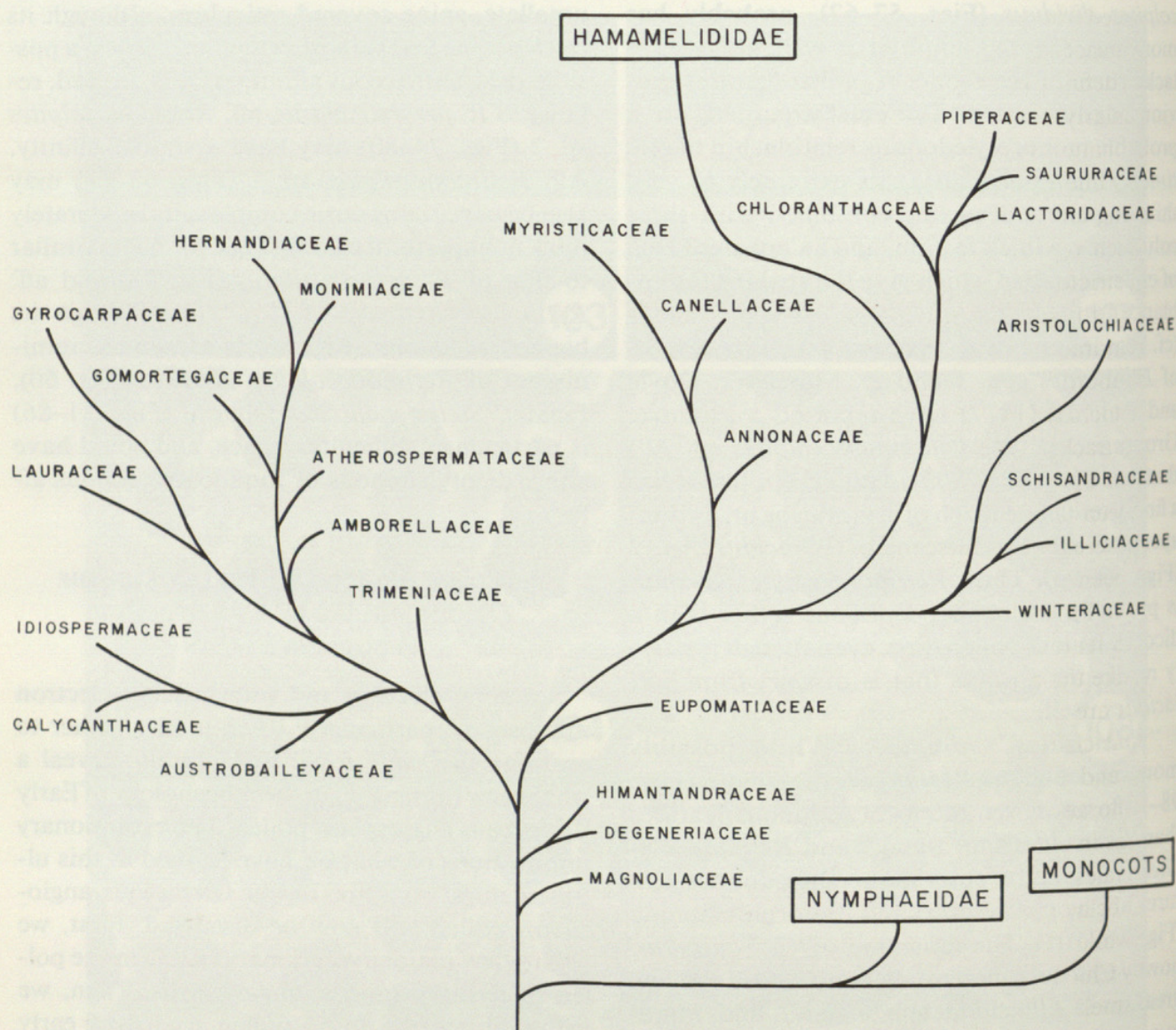
FIGURE 111. Putative phylogenetic relationships of the families of primitive angiosperms (subclass Magnoliidae).

of dicotyledonous angiosperms, which are classified in Table 7, have been designated in whole or part by various taxonomists as the Ranales, Polycarpicae, Apocarpicae, Monochlamydeae, Magnoliales, Magnoliiflorae, Magnoliidae, Magnolianae, or Annoniflorae, and are generally regarded by the majority of modern phylogenists as the most primitive group of living flowering plants (cf. Cronquist, 1968, 1981; Dahlgren, 1975, 1980; Hutchinson, 1973; Takhtajan, 1969, 1973, 1980; Thorne, 1974, 1976). As a group these families possess many features that are usually considered to be primitive angiosperm characters—vesselless wood, monosulcate pollen, laminar, 3-trace stamens, apocarpous gynoecia, unsealed carpels, and free, spirally arranged floral parts indefinite in number. In fact, it appears that

no other living flowering plants have any characters more primitive than those possessed by at least some members of the subclass Magnoliidae.

As delimited by us (Table 7), the subclass Magnoliidae consists of 26 families grouped into three infraclasses (the Magnoliiflorae, Aristolochiiflorae, and Piperiflorae), five superorders, and nine orders. Our concept of the evolutionary relationships of the families of primitive angiosperms (the subclass Magnoliidae) may be summarized as follows. The order Magnoliales is the central and most primitive order in the subclass. It is divisible into two groups. One, the suborder Magnoliineae, contains the exceedingly primitive families Magnoliaceae, Degeneriaceae, Himantandraceae, and Eupomatiaceae. The other, the suborder Annonineae, consists of the more

advanced families Annonaceae, Canellaceae, and Myristicaceae. The superorder Lauranae, which shows definite connections with the Magnoliales, particularly through its most primitive family Austrobaileyaceae, represents a terminal evolutionary line that has given rise to no other groups of living angiosperms. The family Winteraceae has been removed from the order Magnoliales sensu stricto and made the type of an order Winterales, to which the families Illiciaceae and Schisandraceae have also been added, although in a suborder of their own. Finally, the family Aristolochiaceae has been made the type of its own infraclass, the Aristolochiiflorae, while the families Chloranthaceae and Lactoridaceae have both been taken out of the order Laurales sensu lato, where they have frequently been placed, and have been included with the families Saururaceae and Piperaceae in the infraclass Piperiflorae, each in its own monotypic order.

Unlike the terminal Lauranae, the Winterales (which are phenetically closest to the Magnoliales but cladistically closer to the Aristolochiiflorae and Piperiflorae), Aristolochiiflorae, and Piperiflorae exhibit definite connections with families in other subclasses of dicotyledons. The Winterales and Aristolochiiflorae have ties with the subclasses Ranunculidae and Caryophyllidae, while the Piperiflorae, and especially the family Chloranthaceae, are linked to the subclass Hamamelididae, and through it to the bulk of the dicots, including the subclasses Dilleniidae, Rosidae, and Asteridae (cf. Walker, 1976b, fig. 4). In fact, the Piperiflorae appears to be the sister-group of the subclass Hamamelididae. Characters of the family Chloranthaceae that indicate a relationship with the subclass Hamamelididae include apetaly, anemophily, frequent catkin-like inflorescences, and often unisexual flowers. Moreover, the two most primitive families in the Hamamelididae, the Trochodendraceae and Tetracentraceae, are both primitively vesselless just like the chloranthaceous genus *Sarcandra,* and they both have the same distinctive tooth type on their leaf margins as does the Chloranthaceae (the so-called Chloranthoid tooth of Hickey & Wolfe, 1975). Finally, there are striking similarities between the pollen of chloranthaceous genera such as *Ascarina* and *Hedyosmum* and pollen of primitive hamamelidid families such as the Trochodendraceae, Cercidiphyllaceae, and Eupteleaceae, including similar reticulate sculpturing with the same type of spinulose muri, well-de-

TABLE 7. Classification of the families of primitive angiosperms (subclass Magnoliidae).

Subclass Magnoliidae
Infraclass 1. Magnoliiflorae
  Superorder 1. Magnolianae
    Order 1. Magnoliales
      Suborder 1. Magnoliineae
        1. Magnoliaceae
        2. Degeneriaceae
        3. Himantandraceae
        4. Eupomatiaceae
      Suborder 2. Annonineae
        5. Annonaceae
        6. Canellaceae
        7. Myristicaceae
    Order 2. Winterales
      Suborder 1. Winterineae
        8. Winteraceae
      Suborder 2. Illiciineae
        9. Illiciaceae
        10. Schisandraceae
  Superorder 2. Lauranae
    Order 1. Austrobaileyales
      Suborder 1. Austrobaileyineae
        11. Austrobaileyaceae
      Suborder 2. Calycanthineae
        12. Calycanthaceae
        13. Idiospermaceae
    Order 2. Trimeniales
        14. Trimeniaceae
    Order 3. Laurales
      Suborder 1. Monimiineae
        15. Amborellaceae
        16. Atherospermataceae
        17. Monimiaceae
        18. Gomortegaceae
        19. Hernandiaceae
      Suborder 2. Laurineae
        20. Lauraceae
        21. Gyrocarpaceae
Infraclass 2. Aristolochiiflorae
  Order 1. Aristolochiales
        22. Aristolochiaceae
Infraclass 3. Piperiflorae
  Superorder 1. Chloranthanae
    Order 1. Chloranthales
        23. Chloranthaceae
  Superorder 2. Piperanae
    Order 1. Lactoridales
        24. Lactoridaceae
    Order. 2. Piperales
        25. Saururaceae
        26. Piperaceae

veloped columellae, and the presence of endexine (cf. Walker, 1976b).

The putative phylogeny of primitive angiosperms outlined above is based on an analysis of the taxonomic distribution of characters both within and without the subclass Magnoliidae, i.e., on both in-group and out-group analysis. Taxonomic characters from many fields, including floral morphology, vegetative morphology, vegetative anatomy, palynology, and cytology, were examined, and using the principle of reciprocal illumination (Hennig, 1966), the putative phylogeny of the Magnoliidae shown in Figure 111 was established. We intend to discuss the basis for our classification and phylogeny of primitive angiosperm families at a later date. Based on our proposed phylogeny, which, again, we would like to emphasize is based on character analysis from many different fields, we shall now consider the taxonomic distribution of individual palynological characters in order to determine the most probable direction or polarity of major evolutionary trends in the pollen of living primitive angiosperms. Our discussion will be organized under seven different categories of pollen characters, including aperture type, pollen shape, pollen size, nonapertural exine sculpturing, exine interstitial type, exine tectal type, and exine stratification.

Aperture type. Although some other miscellaneous aperture types characterize a few primitive angiosperms (cf. Walker, 1974b, 1976a; Sampson, 1975), most members of the subclass Magnoliidae have pollen with one of the following aperture types: (1) monosulcate pollen (with a single, furrow-like aperture), (2) zonasulculate pollen (with a ring-like aperture), (3) ulcerate pollen (with a pore-like aperture), (4) inaperturate pollen (without any apertures), (5) disulculate pollen (with two furrow-like apertures), (6) tricolpate pollen (with three furrow-like apertures), or (7) polycolpate pollen (with more than three furrow-like apertures).

Monosulcate pollen occurs in some or all members of every family of the Magnoliales except the Eupomatiaceae, which has zonasulculate pollen grains. Monosulcate pollen is the only type in the families Magnoliaceae, Degeneriaceae, and Himantandraceae, and is also clearly the basic type in the Canellaceae and Myristicaceae as well, although occasionally pollen in the Canellaceae may be trichotomosulcate (with a three-armed aperture), and sometimes pollen of the Myristicaceae is ulcerate. Although the Annonaceae, the largest family of primitive angiosperms with some 130 genera and 2,300 species, has a few other aperture types, most of its pollen is either monosulcate or inaperturate. Detailed character analysis within the family indicates that monosulcate pollen is the primitive type (Walker, 1971b; Le Thomas, 1980, 1981). Outside the Magnoliales, monosulcate pollen is found in the Austrobaileyaceae in the Lauranae, rarely in the Aristolochiiflorae (in the primitive genus *Saruma*), and in at least some members of every family of the Piperiflorae. In contrast to the Magnoliales, most members of the Lauranae have inaperturate pollen, although the Calycanthineae is characterized by disulculate pollen and the Austrobaileyaceae, as previously mentioned, has monosulcate pollen. An ulcerate aperture type is a constant feature of the Winteraceae. Tricolpate pollen occurs in the Illiciaceae and in a few Schisandraceae, while polycolpate pollen is found in many Schisandraceae and in some Aristolochiaceae and Chloranthaceae.

The overwhelming presence of monosulcate pollen in the primitive order Magnoliales, along with its occurrence in such primitive elements as the Austrobaileyaceae in the Lauranae and *Saruma* in the Aristolochiiflorae, strongly suggests that monosulcate pollen represents the primitive aperture type for the Magnoliidae. Outgroup comparison further confirms this in as much as monosulcate pollen is clearly the primitive type in monocotyledonous angiosperms and gymnosperms as well.

Pollen shape. With regard to shape, pollen grains in general are either boat-shaped or globose (globe-shaped). In the Magnoliidae boat-shaped pollen grains are characteristic only of the Magnoliaceae, Degeneriaceae, and many Annonaceae. Pollen may be weakly boat-shaped in some Myristicaceae, as well as in a few Chloranthaceae and in some Piperales; elsewhere in the Magnoliidae pollen grains are basically globose. The restriction of boat-shaped pollen entirely to the order Magnoliales, as well as its presence in primitive monocots, such as the Liliaceae, Butomaceae, Araceae, and Palmae, and in many types of gymnosperms strongly suggest that boat-shaped pollen grains represent a primitive feature of angiosperm pollen.

Pollen size. With regard to overall size, pollen grains may be categorized as minute (<10 μm), small (10–24 μm), medium-sized (25–49 μm), large (50–99 μm), very large (100–199 μm), or gigantic (200 μm or larger). Large or large-to

medium-sized pollen characterizes a number of primitive families within the Magnoliidae, including the Magnoliaceae and Degeneriaceae within the Magnoliineae, the Annonaceae within the Annonineae, and the Austrobaileyaceae and Calycanthaceae within the Lauranae. On the other hand, the somewhat more advanced Winterales have medium-sized pollen, the highly advanced Chloranthaceae and Myristicaceae have medium-sized to small pollen, and the exceedingly advanced Piperales have minute pollen. Thus, character distribution suggests that the most primitive angiosperm pollen was large or large-to medium-sized.

Nonapertural exine sculpturing. Many of the most primitive members of the subclass Magnoliidae have pollen grains that are remarkably psilate, even when examined with scanning electron microscopy. Psilate pollen of this extreme type occurs in at least some members of virtually every family of the order Magnoliales. Other exine sculpturing types, represented by verrucate or echinate pollen, for example, occur sporadically in several families of the Magnoliidae, including advanced members of the Annonaceae and Myristicaceae. Reticulate pollen, by contrast, is rare within the Magnoliales, occurring only in a few Annonaceae and in some Myristicaceae. On the other hand, reticulate pollen is basically the only pollen type in the Winterales and in the Chloranthaceae. The strong concentration of psilate or at most foveolate (pitted) to fossulate (grooved) pollen in the primitive order Magnoliales, and the occurrence of other sculpturing types in more advanced members of the Magnoliidae suggests that angiosperm pollen was primitively psilate, or at most only weakly sculptured, e.g., foveolate, fossulate, or scabrate.

Exine interstitial type. Noninterstitiate to interstitiate-granular pollen characterizes many members of the primitive order Magnoliales. For example, the Degeneriaceae and Eupomatiaceae have noninterstitiate pollen grains, while most members of the Magnoliaceae have pollen with a granular interstitium. Within the family Annonaceae many primitive genera have a granular interstitium, while a few are almost noninterstitiate. Both the Canellaceae and Myristicaceae have some primitive members with interstitiate-granular pollen. Pollen with well-developed columellae, by contrast, characterizes advanced members of the Annonaceae, Canellaceae, and Myristicaceae, as well as most members of the more advanced orders Winterales and Chlo-

ranthales. Thus, the taxonomic distribution of exine interstitial types strongly suggests that columellate pollen is advanced within the Magnoliidae, and that primitive angiosperm pollen is noninterstitiate to interstitiate-granular.

Pollen of living primitive angiosperms, however, exhibits several different types of granular interstitia, e.g., in the Magnoliaceae the granular interstitium occurs more or less in the middle of the exine, in the Annonaceae the interstitium develops in the lowermost part of the exine, and in the Myristicaceae the interstitium is found as a series of granules that in their most primitive evolutionary state appear to be pendent from the inner face of the incipient tectum, and not at all or only weakly attached to the basal nexine. Thus, the morphological diversity of interstitial types within the Magnoliidae indicates that noninterstitiate pollen probably represents the basic primitive type from which the various kinds of interstitiate-granular pollen grains have been derived. Columellate pollen, in turn, has apparently evolved independently a number of times from granular pollen types.

Exine tectal type. Atectate to tectate-imperforate pollen characterizes many members of the order Magnoliales, including most Magnoliaceae, the Degeneriaceae, the Himantandraceae, the Eupomatiaceae, many primitive Annonaceae, and some primitive Canellaceae and Myristicaceae. By contrast, pollen grains in advanced members of the Annonaceae, Canellaceae, and Myristicaceae are tectate-perforate. Finally, pollen in the order Winterales is almost always semitectate, while in the family Chloranthaceae pollen varies from tectate-perforate to semitectate. The heavy concentration of atectate to tectate-imperforate pollen grains in primitive members of the highly primitive order Magnoliales suggests that atectate to tectate-imperforate pollen represents the primitive exine tectal type in the Magnoliidae, and, hence, probably in the angiosperms as a whole.

Exine stratification. Except for the Canellaceae, which may have pollen with endexine under the aperture, pollen of the order Magnoliales is totally without endexine, and consequently has a wholly ektexinous exine. By contrast, at least some endexine is present throughout the pollen of many Lauranae, well-developed endexine occurs throughout the pollen of the Winterales, and endexine is present either only in the apertural region or throughout the pollen in the Chloranthaceae. Thus, the taxonomic distribution of

endexine within the Magnoliidae, along with the fact that endexine appears to be absent in almost all monocots, strongly suggests that endexine is primitively absent in angiosperms. Furthermore, one gets the impression that endexine in the Magnoliidae initially evolved in the apertural areas (e.g., as in the Canellaceae and in primitive Chloranthaceae such as *Ascarina*) and subsequently developed in nonapertural regions as well (e.g., as in the Winterales and in advanced Chloranthaceae such as *Chloranthus*).

The presence of a distinctive, laminated type of endexine in both extant and fossil gymnosperms (cf. Doyle et al., 1975) suggests either that angiosperms arose from some group of gymnosperms that had not yet evolved endexine or that endexine was secondarily lost in the group of gymnosperms that gave rise to the flowering plants. In any case, clearly the endexine present in gymnosperm and angiosperm pollen is not homologous.

Nature of primitive angiosperm pollen. Major evolutionary trends in the pollen of living primitive angiosperms of the subclass Magnoliidae, many of which have been previously discussed by the senior author in past contributions (Walker, 1974a, 1974b, 1976a, 1976b; Walker & Skvarla, 1975), are summarized in Table 8.

Analysis of the taxonomic distribution of palynological and non-palynological characters within living primitive angiosperms strongly suggests that primitive angiosperm pollen is monosulcate, boat-shaped, large- to medium-sized, psilate (or at best only weakly sculptured), noninterstitiate (or at best only weakly granular), basically atectate, and without endexine. This type of pollen is found today only in the otherwise primitive angiosperm families Magnoliaceae, Degeneriaceae, and Annonaceae. At a somewhat higher level is the pollen of the families Canellaceae and Myristicaceae, which, although monosulcate and sometimes psilate, is at best only weakly boat-shaped, and at the same time is medium-sized to small. Moreover, pollen of these two advanced magnolialean families is never noninterstitiate as in some of the more primitive Magnoliales, and in the Canellaceae at least endexine is present, although only under the pollen aperture itself.

Pollen of the family Winteraceae, by contrast, is uniformly advanced in being ulcerate, globose, medium-sized, reticulate, in permanent tetrads, interstitiate-columellate, semitectate, and in having well-developed endexine throughout. All

of these features (along with certain other non-palynological attributes, such as complicated, basically cymose inflorescences, medium-sized to small flowers, a perianth that is differentiated into a distinct calyx and corolla, 1-trace (rather than 3-trace) stamens, basically whorled carpels, a short receptacle, baccate fruits, and estipulate leaves) emphasize the taxonomic distinctness and relative advancement of the Winteraceae compared to the order Magnoliales sensu stricto. In a similar fashion, pollen of the family Chloranthaceae is also quite advanced. For example, it may be polychotomosulcate (*Hedyosmum*), polycolpoidate (*Chloranthus*), or inaperturate (*Sarcandra*). Furthermore, chloranthaceous pollen is at best only weakly boat-shaped, being more commonly globose, while at the same time it is medium-sized to small, has reticulate sculpturing and well-developed columellae, is tectate-perforate to semitectate, and has well-developed endexine either only under the aperture or throughout the grain.

FOSSIL POLLEN RECORD OF EARLY FLOWERING PLANTS

The major characteristics of the Lower Cretaceous angiosperm pollen grains that we have examined ultrastructurally are summarized in Table 9. A comparison of Table 8, which lists the major evolutionary trends evident in the pollen of living primitive angiosperms of the subclass Magnoliidae, with Table 9 reveals that in almost every respect these early fossil pollen grains represent advanced rather than primitive angiosperm pollen types. Lower Cretaceous angiosperm pollen grains, for example, are rarely strongly boat-shaped (notable exceptions being the clearly specialized *Stellatopollis barghoornii* and the monocotyledonous *Liliacidites* sp. 1); instead, they are mostly weakly boat-shaped to globose or even wholly globose. Again, except for the two species named above, most monosulcate Lower Cretaceous angiosperm pollen is medium-sized to small, rather than large- to medium-sized, as in the most primitive members of the subclass Magnoliidae. Without exception all early fossil angiosperm pollen that we have examined is reticulately sculptured, and none is psilate or otherwise weakly sculptured. All except the obviously specialized *Retimonocolpites peroreticulatus* have columellae, and none have a truly granular interstitium. Moreover, none of the monosulcate pollen grains investigated are tectate-imperforate; instead, they are tectate-per-

TABLE 8. Major evolutionary trends in the pollen of living primitive angiosperms of the subclass Magnoliidae.

Character	Primitive State(s)	Advanced State(s)
Aperture Type	Monosulcate	Other aperture types, including trichotomosulcate, ulcerate, and inaperturate
Pollen Shape	Boat-shaped	Globose
Pollen Size	Large- to medium-sized	Medium-sized to small or very large
Nonapertural Exine Sculpturing	Psilate, foveolate, fossulate, or scabrate	Other sculpturing types, including verrucate, echinate, and reticulate
Exine Interstitial Type	Noninterstitiate to interstitiate-granular	Interstitiate-columellate
Exine Tectal Type	Atectate to tectate-imperforate	Tectate-perforate to semitectate
Exine Stratification	Endexine absent	Endexine present only under aperture to present throughout grain

forate to more commonly semitectate. Finally, many of the fossil angiosperm grains examined have a well-developed endexine that in some cases is present not only under the aperture but throughout the nonapertural exine as well.

Detailed examination of monosulcate Lower Cretaceous angiosperm pollen independent of any consideration of palynological trends observed in extant primitive angiosperms also indicates that the earliest currently known angiosperm pollen grains represent advanced rather than primitive types of monosulcate angiosperm pollen. Our present study, for example, has shown that Lower Cretaceous angiosperm pollen grains that may appear at the light microscope level as "several partially intergrading morphologic complexes assignable to the form genera *Clavatipollenites* Couper (1958), *Retimonocolpites* Pierce (1961), and *Liliacidites* Couper (1953)" (cf. Doyle & Hickey, 1976) are in reality not an inter-related evolutionary series but a mixed collection of distinctive pollen types that are easily discernible when observed at the ultrastructural level. Moreover, some of these Early Cretaceous angiosperm pollen grains, including one of the oldest known, *Clavatipollenites hughesii,* are clearly related to the magnoliid dicot family Chloranthaceae, which is one of the most advanced families of the subclass Magnoliidae.

The reason that the more primitive "magnoliaceous" types of angiosperm pollen grains have not yet been discovered in Barremian-Albian or even older rocks is probably the result of a number of factors. First, as Muller (1970) suggested, the *Magnolia*-type of pollen may fossilize badly or not at all. Second, *Magnolia*-type pollen may

be present in the Lower Cretaceous but in such low amounts that it has not been discovered yet. This was, for example, true of the highly distinctive pollen of the primitive angiosperm family Winteraceae, which was only recently discovered in the Lower Cretaceous of Israel (Walker et al., 1983). Furthermore, Muller (1963) has shown that only 39% of the genera and 58% of the families of angiosperms known to be in Sarawak could be detected in a palynological examination of a peat swamp near Marudi, Sarawak. Moreover, even easily recognizable columellate angiosperm pollen types, such as *Clavatipollenites hughesii,* sometimes comprise less than 1% of the total pollen grains and spores present in a particular Lower Cretaceous rock sample. Third, and most importantly, *Magnolia*-type angiosperm pollen would have either a granular interstitium or none at all (i.e., it would be noninterstitiate), and, hence, it would be virtually impossible to distinguish it at the light microscope level from similar psilate, boat-shaped, monosulcate pollen produced by a variety of gymnosperms.

Finally, while the marked absence of tricolpate angiosperm pollen from pre-Aptian rocks throughout the world (Doyle et al., 1977), the stratigraphically controlled sequence of tricolpate–tricolporoidate–tricolporate–triporate pollen types observed in the Potomac Group (Doyle & Robbins, 1977), and the marked poleward migration of tricolpate and tricolpate-derived angiosperm pollen types (cf. Hickey & Doyle, 1977, fig. 64) all strongly suggest a true evolutionary origin and progression, it must be stressed that this is an evolutionary origin and progression of

TABLE 9. Major characteristics of Lower Cretaceous angiosperm pollen.

Character	Character State(s)
Aperture Types	Mostly monosulcate, sometimes trichotomosulcate, polychotomosulcate, or polycolpoidate
Pollen Shapes	Boat-shaped to frequently globose
Pollen Sizes	Mostly medium-sized to small, occasionally large
Nonapertural Exine Sculpturing	Variously reticulate
Exine Interstitial Types	Interstitiate-columellate[a]
Exine Tectal Types	Tectate-perforate to more commonly semitectate
Exine Stratification	Endexine not observed or commonly with endexine, either only under aperture or throughout grain

[a] Columellae absent in *Retimonocolpites peroreticulatus*.

tricolpate and tricolpate-derived pollen-bearing angiosperms, and as such has nothing to do with the evolution of the more primitive monosulcate pollen-bearing flowering plants, i.e., virtually all of the magnoliid dicots, the nymphaealean dicots, and the monocotyledons. That an earlier stage of monosulcate pollen-bearing angiosperms is yet to be discovered is indicated by the fact that closely comparable monosulcate angiosperm pollen grains representing the earliest known types of angiosperm pollen occur in pre-Aptian palynofloras (presumably Barremian in age) of such widely separated areas as the Lower Cocobeach System of equatorial Africa, the Upper Wealden of Europe, and the basal Potomac Group of eastern North America (Doyle et al., 1977).

ORIGIN AND EARLY EVOLUTION OF FLOWERING PLANTS

In the following section we shall develop a model for the early evolution of flowering plants, based on a synthesis of what is known about early angiosperms from studies of both living primitive angiosperms and of the early fossil record of flowering plants. First, however, the question of the origin of the angiosperms will be discussed.

ORIGIN OF THE ANGIOSPERMS

Probably more papers have been written on the subject of the origin of the angiosperms than on any other major aspect of angiosperm evolution. In the past many authors have stressed the supposedly rapid rise of the flowering plants. But, as Hickey and Doyle have shown, this idea was based on gross misidentification of early fossil angiosperm leaves (Doyle & Hickey, 1976; Hickey & Doyle, 1977). Furthermore, Doyle (1969), Doyle and Hickey (1976), and Hickey and Doyle (1977) have provided convincing paleopalynological, as well as fossil leaf evidence, for the progressive evolution of tricolpate and tricolpate-derived pollen-producing flowering plants starting in the Aptian. Unfortunately, as we have stressed in the previous section of this paper, there is no comparable evolutionary series known for the more primitive monosulcate pollen-producing angiosperms, and in fact no *Magnolia*-type fossil pollen has yet been found in the Lower Cretaceous for reasons that we have discussed. Thus, until fossil evidence is discovered that relates to the earliest stage of angiosperm evolution, we are forced to rely solely on extrapolation backwards from living primitive angiosperms that do produce monosulcate pollen, i.e., the subclass Magnoliidae, and on extrapolation upwards from gymnosperms that exhibit various angiospermous features, to provide more insight about the origin of the flowering plants.

With Beck's (1960a, 1960b) discovery of the organic connection between *Archaeopteris* and *Callixylon* and the subsequent recognition of a previously unknown group of vascular plants, the progymnosperms, which combined pteridophytic reproduction with gymnospermous anatomy, a new chapter was opened in our understanding of gymnosperm evolution. Consideration of what is now known about the progymnosperms as well as about living and fossil gymnosperms suggests the following scenario about gymnosperm evolution.

The gymnosperms themselves appear to be diphyletic, and it seems evident (cf. Bierhorst, 1971) that the seed arose independently in the two different lines of gymnospermous seed-plants, both of which, the coniferophyte line and the cycadophyte line, were already recognized, although on a somewhat different basis, in Chamberlain's (1935) classic work on gymnosperms.

The two lines of gymnosperms may be delimited as follows. The coniferophyte line is char-

acterized by simple leaves that are frequently small by reduction, dense pycnoxylic wood with generally low, uniseriate rays, cauline (i.e., stem-related) reproductive organs (microsporangia and ovules) that are usually in cone-like, compound strobili, and bilateral seeds with a two-parted integument that are basically unitegmic and never cupulate. By contrast, members of the cycadophyte line of gymnosperms have basically compound leaves (although leaves may be secondarily simple in certain advanced representatives), loose manoxylic wood with generally high multiseriate rays (as well as uniseriate rays), phylline (i.e., leaf-related) reproductive organs that are basically non-strobilate except in certain advanced members (and then the strobili are always simple and never compound), and radiosymmetric seeds with a multi-parted integument that are basically cupulate and often, in more advanced members, bitegmic due to cupule reduction. The coniferophyte line consists of basically tall, often much branched, monopodial trees, while the cycadophyte line, at least in its most primitive representatives, is represented by fundamentally weakly to unbranched, slender trees and shrubs. Microsporangia are frequently synangiate in the cycadophyte line, and not so in the coniferophyte line, while saccate or winged pollen is common in the coniferophyte line, and less so in the cycadophyte line. Finally, the coniferophyte line appears to be derived from the archaeopterid progymnosperms, while the cycadophyte line seems to be connected to the aneurophyte progymnosperms. Members of the coniferophyte line include the ginkgophytes, the cordaites and conifers, and the gnetophytes. The cycadophyte line contains the pteridosperms or seed-ferns (including lyginopteran, callistophytalean, and medullosan pteridosperms, as well as the peltasperms, corystosperms, and caytonialean pteridosperms), the glossopterids, the cycads, and the cycadeoids.

With reference to the origin of the angiosperms, there seems little doubt that the flowering plants were derived from the cycadophytic rather than the coniferophytic line of gymnosperms. Angiosperm features that suggest this include manoxylic wood, phylline reproductive organs that are in simple rather than compound strobili, bitegmic ovules, and microsporangia that are more or less synangiate. Moreover, many advanced groups of cycadophytic gymnosperms exhibit angiospermous characteristics, including simple leaves in the glossopterids and some cy-

cadeoids (e.g., *Williamsoniella*), tetrasporangiate pollen-producing organs in the caytonialean pteridosperms, megasporophyll-infolded ovules in the glossopterids, and bisexual strobili in certain cycadeoids, e.g., *Williamsoniella* and *Cycadeoidea*. Thus, there is no great mystery concerning the origin of the angiosperms, as has often been invoked by writers in the past. The angiosperms are no more isolated than many other groups of vascular plants. In fact, there are a number of problematic Mesozoic gymnosperms, such as the Czekanowskiales and Vojnovskyales, whose relationships are much more conjectural than those of the angiosperms.

Some of the best prospects for resolving the remaining uncertainty concerning angiosperm origins lie in expanded studies of Mesozoic cycadophytic gymnosperms in general, particularly with ultrastructural examination of in situ pollen grains from known pollen-producing organs of groups such as the peltasperms and other pteridosperms, as well as in continued ultrastructural investigation of Lower Cretaceous monosulcate angiosperm pollen, especially from Barremian and even older rocks. For now, however, the most that can be reasonably concluded is that the ancestry of the angiosperms must be sought in the pteridosperms sensu lato or in some as yet unknown derivative of this group of cycadophytic gymnosperms.

EARLY EVOLUTION OF THE FLOWERING PLANTS

The early evolution of the flowering plants can be divided into five different major stages (Fig. 112), based on the early (Barremian to Middle Cenomanian) fossil pollen record of the angiosperms and the phylogenetic relationships evident among living primitive angiosperms. Stage 1 is represented by the evolution of angiosperms with primitive monosulcate pollen of the *Magnolia*-type. Since more advanced monosulcate angiosperm pollen of the *Clavatipollenites-Ascarina*-type occurs in the Barremian, it is fair to assume that this initial phase of angiosperm evolution began in the pre-Barremian. Stage 1 was characterized by the evolution of the "Lower Magnoliidae," i.e., by the evolution of dicots whose descendants include such living primitive angiosperms as the Magnoliaceae and Degeneriaceae. That both advanced monosulcate dicotyledonous and monocotyledonous pollen occurs together in the earliest known angiosperm palynofloras of the Barremian suggests that the mon-
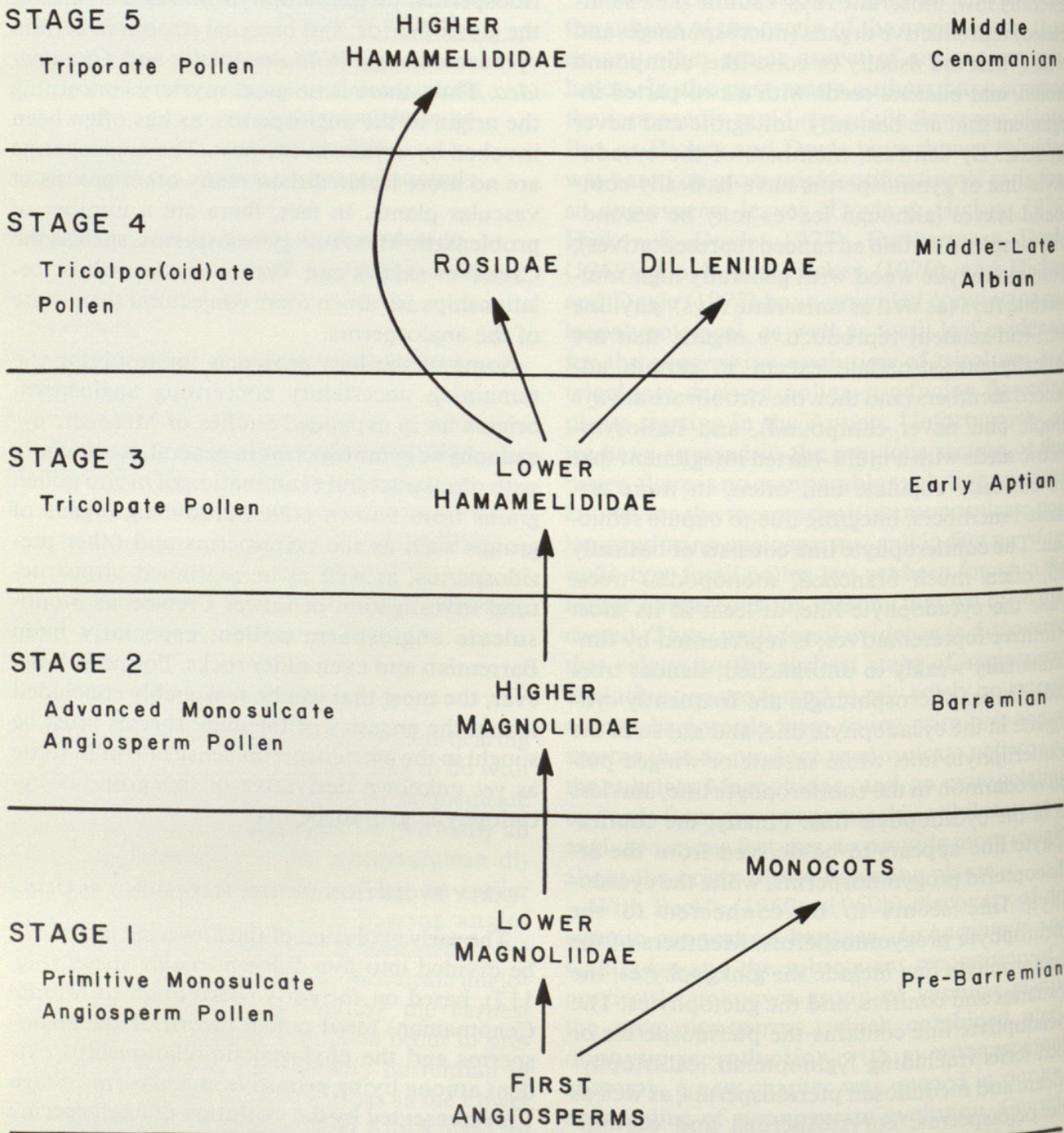
STAGE 5
Triporate Pollen

STAGE 4
Tricolpor(oid)ate Pollen

STAGE 3
Tricolpate Pollen

STAGE 2
Advanced Monosulcate Angiosperm Pollen

STAGE 1
Primitive Monosulcate Angiosperm Pollen

HIGHER HAMAMELIDIDAE — Middle Cenomanian

ROSIDAE   DILLENIIDAE — Middle–Late Albian

LOWER HAMAMELIDIDAE — Early Aptian

HIGHER MAGNOLIIDAE — Barremian

MONOCOTS

LOWER MAGNOLIIDAE — Pre-Barremian

FIRST ANGIOSPERMS

FIGURE 112. Outline of the early evolution of flowering plants based on the early (Barremian–Middle Cenomanian) fossil angiosperm pollen record and putative phylogenetic relationships of major groups of living angiosperms.

ocots had already separated from the dicots by Barremian time.

Stage 2 of early angiosperm evolution, which begins in Africa and South America, as well as in England and eastern North America, in the Barremian (cf. Hickey & Doyle, 1977), is represented by the evolution of flowering plants with advanced monosulcate pollen, and includes both dicotyledonous pollen types, such as *Clavatipollenites,* and monocotyledonous pollen types, such as *Liliacidites.* This stage was characterized by the evolution of the "Higher Magnoliidae," including the evolution of the advanced magnoliid family Chloranthaceae.

The development of tricolpate pollen constitutes Stage 3 and probably is indicative of the

origin of the "Lower Hamamelididae," i.e., the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, and Platanaceae. Stage 3, i.e., the evolution of tricolpate pollen-producing dicots, begins in the Early Aptian of Africa-South America (i.e., West Gondwana), and somewhat later in Europe-North America (i.e., West Laurasia), where tricolpate pollen first appears in the Early Albian (cf. Hickey & Doyle, 1977; Doyle et al., 1977).

The appearance of tricolpor(oid)ate (i.e., tricolporoidate to tricolporate) pollen in the Middle-Late Albian suggests that this may represent the beginning of the differentiation of the subclass Rosidae and possibly Dilleniidae as well, since both are characterized basically by tricolporate pollen. The evolution of tricolpor(oid)ate pollen, and with it the initial differentiation of the Rosidae (and possibly Dilleniidae) constitutes Stage 4 in the early evolution of the flowering plants.

The final phase of early angiosperm evolution, Stage 5, begins in the Middle Cenomanian with the appearance of triporate pollen, especially of the Normapolles type, in Europe and North America. Stage 5 probably represents the initial differentiation of the "Higher Hamamelididae," i.e., the Betulaceae, Casuarinaceae, Myricaceae, and Juglandaceae. That pollen of certain relatively primitive rosid families, such as the Aquifoliaceae, Gunneraceae, and Sapindaceae, occurs earlier in the Turonian-Coniacian, while pollen of such "higher" hamamelidid families as the Fagaceae, Betulaceae, and Myricaceae first appears later in the Santonian (cf. Muller, 1981) also suggests that the initial differentiation of the Rosidae began sometime before that of the "Higher Hamamelididae."

A MODEL FOR THE EARLY ADAPTIVE EVOLUTION OF THE ANGIOSPERMS

The picture of early angiosperm evolution outlined in Fig. 112 suggests the following model of the early adaptive evolution of the flowering plants. As Stebbins (1976) has stressed, the characters that most strongly set the flowering plants apart from gymnosperms are all features of the reproductive rather than vegetative part of the angiosperm life-cycle. Although it will probably never be possible to know with certainty the exact sequence by which the gymnospermous forebearers of the flowering plants acquired their angiospermous features, it is likely that entomophily

was one of the earliest characteristics of the proto-angiosperms since so many basic angiosperm features, such as the perianth, carpel closure, and bisexuality of sporophytic reproductive structures (i.e., flowers), can best be explained as responses to the evolution of insect pollination. Evolution of the perianth in flowering plants in particular provides further evidence in support of the evolutionary scheme outlined in Figure 112. The taxonomic distribution of perianth types among primitive dicots of the Magnoliidae (Fig. 111), as well as throughout the major groups of dicots in general (Fig. 112), provides strong evidence that perianth evolution, which undoubtedly reflects basic changes in angiosperm pollination biology, has gone through at least six different major evolutionary stages (grades), as pictured in Figure 113.

Grade I in the evolution of the angiosperm perianth is represented, we suggest, by flowers whose sterile floral parts consisted simply of floral bracts, i.e., the flowers were composed of leaf-like elements associated with fertile floral parts, the stamens and carpels, but these sterile floral parts could only be distinguished arbitrarily as bracts versus tepals. The primitive magnoliid families Austrobaileyaceae (Endress, 1980) and Trimeniaceae (Money et al., 1950) may possibly be living representatives of this earliest stage in the evolution of the angiosperm perianth.

Grade II is typified by the evolution of a distinct perianth that initially was undifferentiated, and consisted wholly of tepals that were either entirely sepaloid or completely petaloid. With the development of this tepalar perianth into a differentiated perianth that consisted of a distinct calyx of sepals and a distinct corolla of tepalar petals, i.e., petals derived evolutionarily from an undifferentiated tepalar perianth, Grade III was reached. Most of the living primitive angiosperms of the subclass Magnoliidae have a Grade II or III perianth. Undifferentiated tepalar perianths of the Grade II type, for example, occur in some of the Magnoliaceae, most of the Lauranae, the Illiciaceae, and the Schisandraceae, while a Grade III perianth that is differentiated into tepalar petals and distinct sepals characterizes Magnoliidae such as the Degeneriaceae, Annonaceae, Canellaceae, and Winteraceae.

Flowering plants with Grade I–III perianths constitute what we shall term the "basic entomophilous angiosperms." In addition to most members of the Magnoliidae, this group includes the Nymphaeales, most of the monocotyledons,
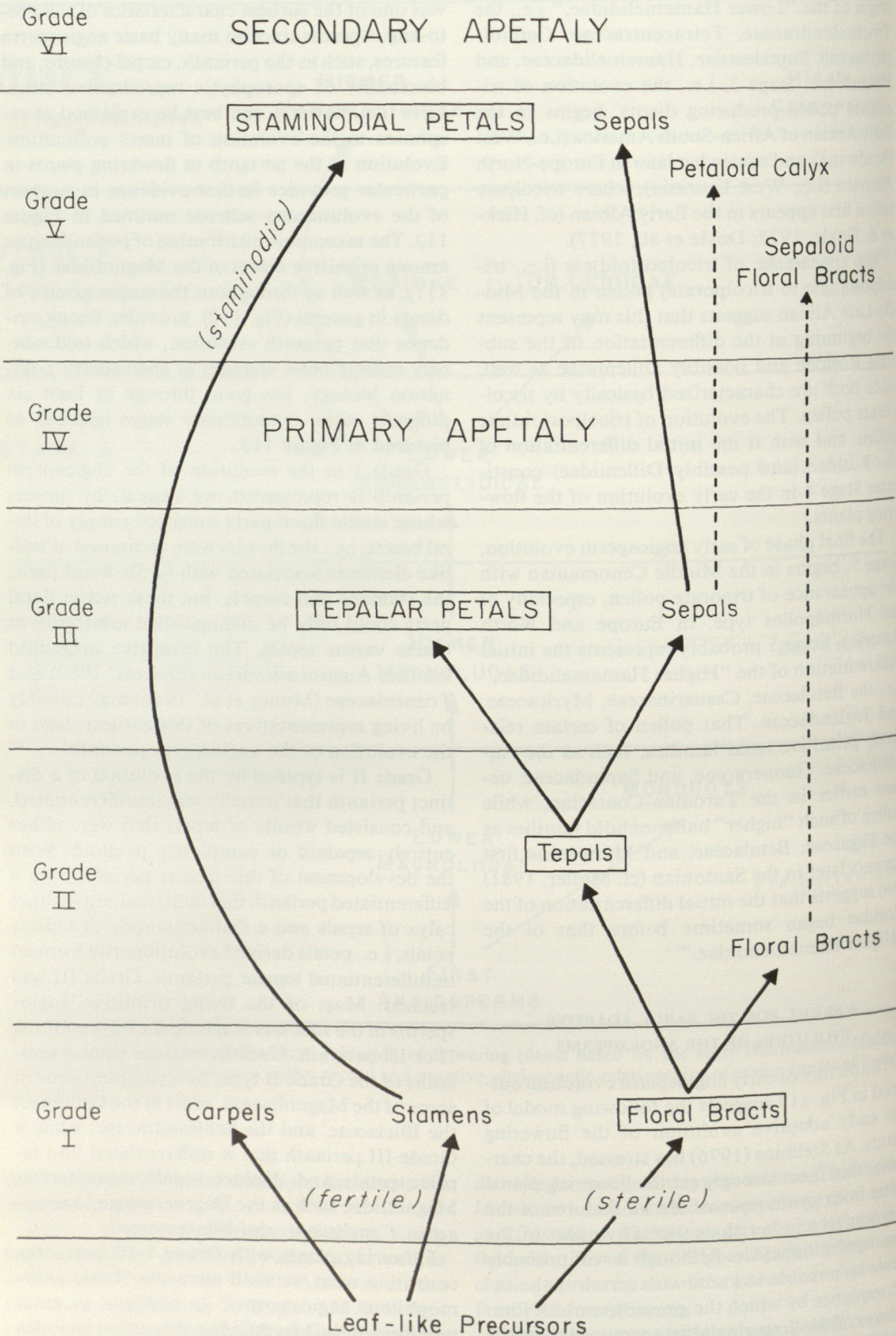
Grade VI

SECONDARY APETALY

Grade V

Grade IV

PRIMARY APETALY

Grade III

Grade II

Grade I

STAMINODIAL PETALS

Sepals

Petaloid Calyx

Sepaloid Floral Bracts

(staminodia)

TEPALAR PETALS

Sepals

Tepals

Floral Bracts

Carpels   Stamens

Floral Bracts

(fertile)

(sterile)

Leaf-like Precursors

FIGURE 113. Evolution of the perianth in flowering plants.

and probably a few members of the dicot sub-classes Ranunculidae and Caryophyllidae, e.g., the Paeoniaceae and Polygonaceae. Following the evolution of "basic entomophily" and the development of tepalar petals in the earliest flowering plants, it appears that the main line of angiosperm evolution (at least in the dicots) lost these original tepalar petals and reverted back to the wind pollination that characterized their gymnospermous ancestors. These early anemophilous-apetalous Grade IV flowering plants, which we designate the "primary anemophilous angiosperms" to distinguish them from later, separately derived anemophilous angiosperms, include advanced Magnoliidae, such as the Chloranthaceae, and almost all the Hamamelididae. The reason for this initial early return to anemophily may well have been tied in with the increasing aridity (and subsequent possible decline in insect pollinators) that apparently occurred soon after the earliest appearance of angiosperm pollen of the *Clavatipollenites*-type in the Barremian (cf. Hickey & Doyle, 1977; Doyle et al., 1977).

Although Dilcher (1979) has suggested that the flowers of such angiosperms as the Trochodendrales, Cercidiphyllales, Eupteleales, Hamamelidales, and Piperales may be primitively anemophilous (as well as primitively unisexual), comparative morphological studies of living primitive angiosperms as a whole, and the resultant phylogeny of the Magnoliidae-Hamamelididae as a group, do not support this contention. The Trochodendrales and Eupteleales, as well as some Hamamelidales and Piperales, all have bisexual rather than unisexual flowers as implied by Dilcher (1979) anyway. In order to accept Dilcher's hypothesis that the angiosperms enumerated above are primitively anemophilous and apetalous, one must be able to demonstrate that they are characterized by a number of other primitive features, and especially that they have some features that are even more primitive than those that occur in entomophilous, perianth-possessing magnoliid angiosperms such as the Magnoliales. Consideration of all the characters of the extant Magnoliidae-Hamamelididae, however, does not provide any evidence for the idea that the Chloranthaceae—"Lower Hamamelididae" represent a separate branch of angiosperms that evolved independent of the "Lower Magnoliidae."

The Chloranthaceae, which, unlike the "Lower Hamamelididae," at least has some members with monosulcate rather than tricolpate pollen, is characterized by a suite of advanced features, including a unicarpellate gynoecium, solitary ovules with apical placentation, drupaceous fruits, and opposite leaves. Moreover, the small scales ("tepals") that are sometimes present at the top of the chloranthaceous ovary seem to indicate that the flowers are fundamentally epigynous, which is hardly a primitive attribute.

The fossil record of angiosperm leaves also suggests that the Chloranthaceae—"Lower Hamamelididae" are advanced rather than primitive angiosperms. As Hickey and Doyle (1977) have shown, most of the earliest fossil angiosperm leaves (as well as those of most living members of the Magnoliidae) are brochidodromous and have entire margins. The leaves of the Chloranthaceae, on the other hand, are basically semi-craspedodromous and have distinctive marginal teeth that have been named Chloranthoid Teeth by Hickey and Wolfe (1975). The Chloranthaceae share these Chloranthoid Teeth with the relatively advanced magnoliid families Illiciaceae and Schisandraceae, the Ranunculidae, and certain "Lower Hamamelididae," such as the Trochodendraceae, Tetracentraceae, and possibly the Cercidiphyllaceae. Reference to Figure 111 shows that our phylogenetic placement of the Chloranthaceae positions it in close proximity to all angiosperms that have Chloranthoid Teeth.

Thus, the preponderance of evidence from both living and fossil primitive angiosperms supports the conclusion that the Chloranthaceae—"Lower Hamamelididae" are secondarily apetalous-anemophilous, and that they are derived from the "Lower Magnoliidae," and not from some separate line of proto-angiosperms.

The early reversion of flowering plants back to wind-pollination in the Barremian–Early Aptian provides some understanding of why pollen of the *Clavatipollenites*-type is so abundant in the Middle Lower Cretaceous. Plants that produced pollen of the *Clavatipollenites*-type were in all probability *the earliest angiosperms that produced pollen with well-developed columellae that at the same time were wind-pollinated* (cf. Walker, 1976b). Although, in general, we agree with Hickey and Doyle (1977) that the "well-developed reticulate exine sculpture of *Clavatipollenites, Retimonocolpites, Liliacidites,* and *Stellatopollis*" provides "strong evidence that the flowering plants which produced them were insect-pollinated," for *Clavatipollenites-Ascarina,*

at least, this is probably not true. Van der Hammen and González (1960), for example, have shown that the chloranthaceous genus *Hedyosmum*, which also has pollen with well-developed reticulate sculpturing, is wind-pollinated; and in addition they have indicated that the genus has a high pollen production, and that its pollen fossilizes well. That reticulate sculpturing is not always an indication of entomophily, and conversely that psilate pollen is not always indicative of anemophily, is also suggested by the fact that members of such primitive angiosperm families as the Magnoliaceae, Degeneriaceae, Eupomatiaceae, and Annonaceae frequently have perfectly psilate pollen grains and yet are entomophilous. Moreover, pollen of *Ascarina lucida,* a common coastal plant, occurs as up to 12% of the total pollen and spores present in coastal Pliocene-Pleistocene sediments of New Zealand (Mildenhall, 1978). As Muller (1981) has indicated, this "throws an interesting light on the lower Cretaceous abundance of *Clavatipollenites.*" Thus, *Clavatipollenites* was not the pollen of the earliest angiosperms, instead, it was probably the pollen of the first anemophilous angiosperms.

Neither comparative morphology of living primitive angiosperms nor the early fossil pollen and leaf record of the flowering plants provides evidence for Stebbins's (1965, 1974) idea that the first angiosperms were weedy shrubs that arose in a semiarid rather than mesic environment, as suggested by Hickey and Doyle (1977). Semixerophytic Magnoliidae are rare, and more importantly they are obviously advanced within the subclass as a whole. Moreover, the Potomac Group pollen and leaf sequence so eloquently correlated by Doyle and Hickey (1976) has nothing to do with the earliest phase of angiosperm evolution since it represents Stages 2 and 3, and not Stage 1, in the early evolution of the flowering plants (cf. Fig. 112).

Hickey and Doyle (1977: 62ff.) admit as much when they say that "it must be realized that they [these data] apply directly to only one subgroup of the angiosperms, the tricolpate dicots, and cannot automatically be extended to the angiosperms as a whole." What the Potomac Group pollen and leaf sequence does provide is data concerning the adaptive radiation of the "Higher Magnoliidae" and the "Lower Hamamelididae," and this of course has nothing to do with either the evolution of the "Lower Magnoliidae" or with the origin of the angiosperms themselves.

Apparently, soon after the origin of the wind-pollinated Chloranthaceae—"Lower Hamamelididae" in the Barremian-Early Aptian, conditions changed so that insect pollination was again favored, and the result was a secondary return to entomophily among the dicotyledonous angiosperms. The majority of the dicotyledons, including the subclass Rosidae (and its derivative the Asteridae) as well as the subclass Dilleniidae, have probably evolved as part of this secondary reversion to entomophily.

Petals evolved again in these "secondary entomophilous angiosperms," but this time they developed from stamens (Fig. 113, Grade V) rather than from tepals, as they had in the original "basic entomophilous angiosperms." Thus, the staminodial petals of the Rosidae-Dilleniidae-Asteridae are apparently not homologous with the more primitive tepalar petals of the "Lower Magnoliidae," Nymphaeales, and monocots. Although most secondarily petaliferous dicots presumably regained their petals through sterilization of stamens, in a few instances petal-like floral parts were formed from petaloid calyces, e.g., *Aristolochia,* and in a few angiosperms, such as *Mirabilis* (Nyctaginaceae), transference of function even went so far that floral bracts assumed the appearance of a calyx, while the calyx itself took over the function of a corolla. Finally, a few advanced members of the Dilleniidae-Rosidae-Asteridae, such as the Salicaceae, the Garryaceae, and *Fraxinus* of the Oleaceae, again became anemophilous-apetalous, representing yet another level (cf. Fig. 113, Grade VI) in the evolution of the angiosperm perianth.

Thus, consideration of neontological as well as paleobotanical evidence suggests that there are no living flowering plants that are primitively anemophilous. Furthermore, it is apparent that a major line of anemophilous angiosperms, including the magnoliid family Chloranthaceae and the related "Lower Hamamelididae," evolved in the Barremian-Early Aptian from more primitive "basic entomophilous angiosperms" of the "Lower Magnoliidae." It was from these "primary anemophilous angiosperms," and from the "Lower Hamamelididae" in particular, that the majority of living dicots, i.e., the subclasses Dilleniidae, Rosidae, and Asteridae, apparently evolved in the Middle-Late Albian. The major stimulus for the adaptive radiation of these higher dicots was probably their secondary return to entomophily concomitant with the evolution of staminodial petals that replaced the original te-

palar petals of their distant entomophilous ancestors in the "Lower Magnoliidae," these original tepalar petals having been lost when certain "Higher Magnoliidae," including the Chloranthaceae, reverted to wind-pollination in the Barremian.

SUMMARY AND CONCLUSIONS

In the last decade significant new information has been gained about the early evolution of flowering plants through studies of Early Cretaceous angiosperm pollen and the pollen of living primitive flowering plants. Although most recent palynological studies of extant primitive angiosperms have used both scanning electron and transmission electron microscopy, few ultrastructural studies of early fossil angiosperm pollen grains exist. This paper represents an attempt to remedy this situation. Thirteen different types of Lower Cretaceous angiosperm pollen grains from the Potomac Group of the Atlantic Coastal Plain of eastern North America and the Fredericksburgian of Oklahoma were investigated ultrastructurally, using a technique that we have developed for studying single dispersed fossil pollen grains by combined light, scanning electron, and transmission electron microscopy. This technique is invaluable for the evolutionary study of small, light-microscopically similar dispersed fossil pollen grains, such as those that constitute the bulk of the earliest known microfossil record of the flowering plants.

After discussion of materials and methods and a brief review of concepts and terminology dealing with pollen wall morphology, results are presented, based on our examination of the following Lower Cretaceous angiosperm pollen types: *Clavatipollenites hughesii,* two aff. *Clavatipollenites* spp., *Asteropollis asteroides, Stephanocolpites fredericksburgensis, Retimonocolpites dividuus, Retimonocolpites peroreticulatus,* two aff. *Retimonocolpites* spp., *Stellatopollis barghoornii,* and three species of *Liliacidites.* Use of same grain combined light, scanning electron, and transmission electron microscopy provides a much improved means of delimiting Early Cretaceous angiosperm pollen form genera such as *Clavatipollenites, Retimonocolpites,* and *Liliacidites. Clavatipollenites,* in the restricted sense of its type species, *C. hughesii,* has a beaded to spinulose reticulum that is tectate-perforate to semitectate, a thick nexine, well-developed columellae, and a thick plug of endexine under the aperture, while *Retimonocolpites,* based on its type species, *R. dividuus,* has a banded, semitectate reticulum, a thin nexine, short columellae, and apparently no endexine. The most important features of *Liliacidites* sensu lato are a psilate, semitectate reticulum and strongly dimorphic lumina, while *Liliacidites* sensu stricto is probably best restricted to pollen that has reticulate sculpturing differentiated into coarse and fine areas. Other features frequently observed in pollen of the *Liliacidites*-type include "frilled" muri due to lateral extension of underlying columellae, a thin pollen wall, especially relative to grain size, a very thin nonapertural nexine relative to the rest of the exine, and a general lack of endexine.

This study further reveals that a close similarity exists between some Early Cretaceous angiosperm pollen types and pollen produced by certain living primitive angiosperms. *Clavatipollenites hughesii, Asteropollis asteroides,* and *Stephanocolpites fredericksburgensis* exhibit varying degrees of similarity at the ultrastructural level respectively to pollen of the extant angiosperm genera *Ascarina, Hedyosmum,* and *Chloranthus,* all three of which belong to the family Chloranthaceae. Pollen described under the form genus *Liliacidites* possesses many features that are presently restricted to the pollen of living monocotyledons. *Retimonocolpites dividuus* probably also has monocotyledonous affinities. Other Lower Cretaceous pollen types, including *Stellatopollis barghoornii* and *Retimonocolpites peroreticulatus,* have no counterparts among the pollen of extant angiosperms.

In the last part of the paper the question of the origin and early evolution of the flowering plants is examined. First, the phylogeny and classification of the families of the primitive angiosperm subclass Magnoliidae is discussed, and the following major taxa are recognized within the Magnoliidae: infraclasses Magnoliiflorae, Aristolochiiflorae, and Piperiflorae; superorders Magnolianae, Lauranae, Aristolochianae, Chloranthanae, and Piperanae; and orders Magnoliales, Winterales, Austrobaileyales, Trimeniales, Laurales, Aristolochiales, Chloranthales, Lactoridales, and Piperales.

Next, major evolutionary trends in the pollen of living primitive angiosperms are considered. Taxonomic distribution of characters of living primitive angiosperms suggests that angiosperm pollen is primitively monosulcate, boat-shaped, large- to medium-sized, psilate, or at best only weakly sculptured, noninterstitiate to possibly

interstitiate-granular, atectate, and without endexine. This type of pollen is found today only in the otherwise primitive angiosperm families Magnoliaceae, Degeneriaceae, and Annonaceae. The fossil pollen record of early flowering plants is then considered in light of what is known about pollen evolution in living primitive angiosperms, and the point is stressed that *Clavatipollenites* and other currently known types of Early Cretaceous angiosperm pollen grains represent relatively advanced primitive (i.e., monosulcate) angiosperm pollen that is already too specialized to be able to reveal anything about the origin (or even the earliest evolution) of the flowering plants.

Finally, what can be deduced about the origin and early evolution of the flowering plants from fossil and living primitive angiosperms is considered. It is concluded that the ancestry of the angiosperms must be sought in the pteridosperms sensu lato, or more probably in some as yet unknown derivative of this group of cycadophytic gymnosperms. Following this, a 5-stage model of early angiosperm evolution is proposed, based on the early (Barremian to Middle Cenomanian) fossil pollen record of the flowering plants and the inferred phylogenetic relationships of living primitive angiosperms and their immediate derivatives.

Stage 1 of this model constitutes the yet undiscovered pre-Barremian evolution of angiosperms with primitive monosulcate pollen of the *Magnolia*-type, and represents the evolution of the "Lower Magnoliidae," i.e., dicotyledonous angiosperms whose descendants include such living primitive flowering plants as the Magnoliaceae and Degeneriaceae. The fact that monocotyledonous pollen and advanced monosulcate dicot pollen occur together in the Barremian suggests that monocots had already separated from dicots by then. Stage 2, which begins in the Barremian, is represented by the evolution of angiosperms with advanced monosulcate pollen, and includes both dicotyledonous pollen types, such as *Clavatipollenites,* and monocotyledonous pollen types, such as *Liliacidites.* This stage is characterized by the evolution of the "Higher Magnoliidae," including the family Chloranthaceae. The development of tricolpate pollen in the Early Aptian of Africa-South America, i.e., West Gondwana, constitutes Stage 3 of early angiosperm evolution, and is probably indicative of the origin of the "Lower Hamamelididae" (i.e., angiosperms whose descendants include such families as the Trochodendraceae, Tetracentra-

ceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, and Platanaceae) from the "Higher Magnoliidae." The evolution of tricolpor(oid)ate pollen in the Middle-Late Albian constitutes Stage 4, which probably represents the beginning of the differentiation of the angiosperm subclasses Rosidae and Dilleniidae from the "Lower Hamamelididae" since both of these dicot subclasses are characterized by tricolporate pollen. The final phase of early angiosperm evolution, Stage 5, begins in the Middle Cenomanian with the first appearance of triporate pollen (especially of the Normapolles type in Europe and North America, i.e., West Laurasia). This stage probably represents the initial differentiation of the "Higher Hamamelididae," whose descendants include such angiosperm families as the Betulaceae, Casuarinaceae, Myricaceae, and Juglandaceae.

The picture of early angiosperm evolution outlined above suggests the following model for the early adaptive evolution of the flowering plants. From an original complex of "basic entomophilous angiosperms" that had "tepalar" petals, and whose living descendants are today included in such orders as the Magnoliales, Laurales, and Winterales, the early evolution is envisioned of a major line of secondarily anemophilous-apetalous angiosperms, whose descendants include advanced magnoliid angiosperms, such as the Chloranthaceae, as well as related "Lower Hamamelididae," such as the Trochodendrales, Cercidiphyllales, and Hamamelidales. The reason for this early reversion back to the wind pollination that characterized the gymnospermous ancestors of the flowering plants may have been connected with the increasing aridity (and possible decline in insect pollinators) that apparently occurred soon after the earliest appearance of angiosperm pollen of the *Clavatipollenites*-type in the Barremian of Africa and South America at the time that major splitting of West Gondwana was taking place. The majority of living dicots, including the subclass Rosidae (and eventually its derivative the Asteridae) and probably the subclass Dilleniidae as well, apparently arose in the Middle-Late Albian from these early anemophilous angiosperms. This marked the beginning of the first major adaptive radiation of tricolpate (as opposed to monosulcate) pollen-producing dicotyledonous angiosperms. The major stimulus for this momentous event in the history of flowering plants may have been the secondary return of the main line of dicotyledonous flowering plants back to entomophily.

This secondary return to entomophily appears to be correlated with the evolution of new "staminodial" petals that replaced the more primitive, "tepalar" petals of the original "basic entomophilous angiosperms," i.e., the "Lower Magnoliidae," these original tepalar petals having been lost at the time when certain "Higher Magnoliidae," such as the Chloranthaceae, changed from entomophily to anemophily.

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