ANGIOSPERM ORIGINS AND EVOLUTION BASED ON DISPERSED FOSSIL POLLEN ULTRASTRUCTURE[1]

MICHAEL S. ZAVADA[2]

ABSTRACT

Wall ultrastructure of fossil-dispersed pollen has recently played an important role in increasing our understanding of the origin and early evolution of angiosperms. The criteria currently used to determine the affinities of fossil-dispersed pollen is discussed in relationship to homologies of gymnosperm and angiosperm wall layers based on biochemical, developmental, and morphological data. The bearing of these data on our present interpretation of angiosperm origins and early evolution is discussed along with new data on the wall structure of early Mesozoic dispersed pollen.

The phylogenetic significance of pollen was first recognized by Wodehouse (1928, 1936) long before palynology became a separate botanical subdiscipline. Since Wodehouse's time numerous comparative morphological pollen studies have been initiated with the intent of elucidating taxonomically significant pollen characteristics and the phylogenetic relationships of various plant groups. One of the most intensely studied groups with regard to pollen morphology and phylogeny is the ranalean complex (e.g., Walker, 1974a, 1974b, 1976). The monocots have not received the attention lavished on ranalean taxa, but there have been significant studies of monocot pollen that provide a basis for a preliminary phylogenetic overview (Kuprianova, 1948; Zavada, 1983a). One objective of paleopalynologists is to provide additional data that can either support, refine, or refute these proposed phylogenetic schemes based on studies of extant pollen. Until recently, corroborative fossil evidence has been scanty. However, this situation is being improved by the employment of new techniques that allow a wider range of morphological features to be used in elucidating the taxonomic and phylogenetic relationships of fossil-dispersed pollen [e.g., single pollen grain investigations with scanning electron microscopy (SEM) and transmission electron microscopy (TEM)]. The intent of this paper is to review data on fossil-dispersed pollen and provide new data that bear upon our current understanding of the origin and early evolution of angiosperms. A brief summary of the phylogenetic relationships believed to exist among the primitive dicotyledons and monocotyledons based on comparative palynological studies of extant angiosperms is presented before the fossil evidence is reviewed. This is followed by an examination of the criteria used to distinguish fossil angiosperm pollen from pollen of other major plant groups (e.g., gymnosperms). The establishment of good taxonomic criteria to distinguish pollen of major plant groups is necessary before the phylogenetic implications of the fossil pollen record can be fully appreciated. The value of the dispersed Mesozoic pollen record in clarifying angiosperm origins and evolution is then discussed against the background of these data.

PHYLOGENETIC RELATIONSHIPS OF EXTANT ANGIOSPERM POLLEN

Although there are numerous studies of pollen morphology and wall structure of ranalean taxa, Walker's (1974a, 1974b, 1976) studies are the most comprehensive. He has determined that monosulcate, predominantly atectate or granular walled pollen grains are the most primitive among dicotyledons. This implies that pollen with these features should be encountered in the geologic section prior to derived pollen types; i.e., multiaperturate, tectate-columellate, perforate, or imperforate pollen. Among monocotyledons, monosulcate pollen is also viewed as primitive (Kuprianova, 1948; Walker & Doyle, 1975), however, comparative morphological studies have shown that in monocotyledons the tectate-

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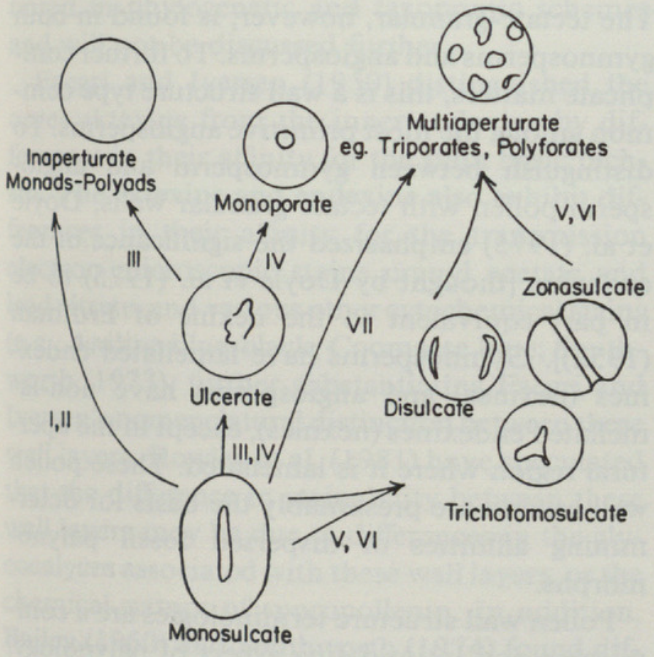
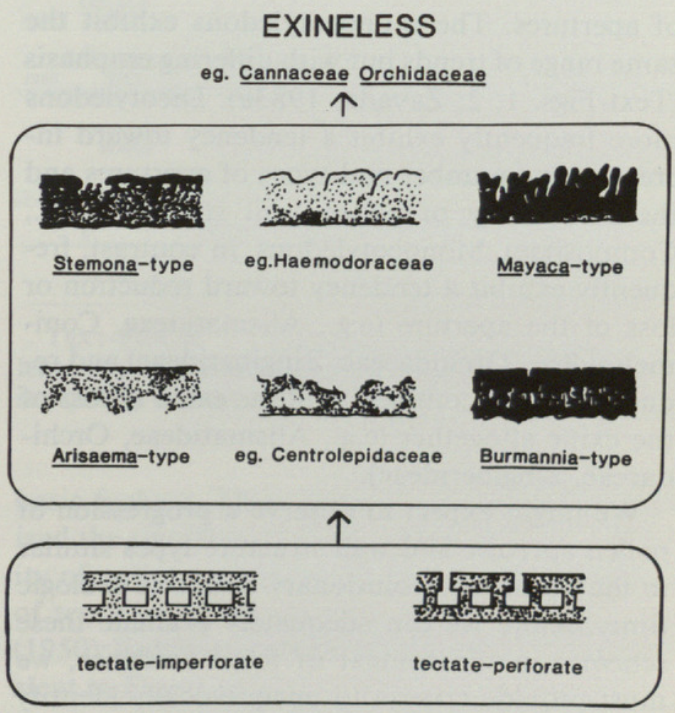
[2] Department of Botany, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210.



TEXT-FIGURE 1. Major evolutionary trends of apertures in monocots.

I. Alismatidean trend, monosulcate → inaperturate.
II. Zingiberidean trend, monosulcate → inaperturate.
III. Orchidacean trend, monosulcate → ulcerate → inaperturate.
IV. Commelinidean trend, monosulcate → ulcerate (irregular colpoid) → monoporate.
V. Arecidean trend, monosulcate → multiaperturate forms.
VI. Liliacean trend, monosulcate → disulcates, trichotomosulcates, zonasulcates → multiaperturate.
VII. Alismatacean trend, monosulcate → multiaperturates (polyforates).



TEXT-FIGURE 2. Major evolutionary trends of wall structure types in the monocots. The primitive tectate-columellate (perforate or imperforate) wall structure type, possibly derived from a Nymphaeacean-like ancestor with atectate or granular walls, gives rise to monocotyledonous atectate or granular walls and finally extreme reduction of the exine, in which it may be completely absent.

columellate, perforate, or imperforate wall structure is primitive (Zavada, 1983a; Text-Figs. 1, 2). The difference between the wall structure of the most primitive dicotyledons and monocotyledons, might be interpreted as contradicting a common origin of the monocotyledons and dicotyledons, and interpreted as supporting a separate origin. If the monocotyledons separated early from a nymphaeacean-like (dicotyledonous) ancestor, as morphological data seem to suggest (Cronquist, 1981), the most primitive monocotyledonous pollen might be presumed to have a granular or atectate wall structure similar to that found in the Nymphaeaceae (Ueno & Kitaguchi, 1961; Ueno, 1962; Rowley, 1967; Roland, 1965, 1968). However, comparative morphological studies of monocotyledon wall structure (Zavada, 1983a) show that the tectate-columellate wall is primitive in extant monocotyledons. It is possible that primitive tectate-columellate monocotyledons are derived from a nymphaeacean-like ancestor with atectate- or granular-walled pollen. Even among ranalean taxa, the shift from the granular or atectate to the tectate-columellate wall appears to be an early evolutionary development. Thus, a shift from the atectate- or granular-walled nymphaeacean-like ancestor to the primitive tectate-columellate type found in monocotyledons parallels the phylogenetic trend in the ranalean taxa, and places the primitive monocotyledons on the same evolutionary level as the derived ranalean taxa with monosulcate, tectate-columellate pollen; a view that seems reasonable in light of the proposed dicotyledonous origin of the monocotyledons.

Comparing evolutionary trends of aperture types and wall structure in dicotyledons and monocotyledons, we find other striking parallels. Walker (1974a, 1974b, 1976) has determined that atectate- or granular-walled pollen among some of the more advanced dicots is secondarily derived from the tectate-columellate wall structure. This is accompanied by reduction or loss of the aperture, or an increase in the number and types

of apertures. The monocotyledons exhibit the same range of trends but with differing emphasis (Text-Figs. 1, 2; Zavada, 1983a). Dicotyledons more frequently exhibit a tendency toward increasing the number and types of apertures and the complexity of pollen wall structure (e.g., Compositae). Monocotyledons, in contrast, frequently exhibit a tendency toward reduction or loss of the aperture (e.g., Alismatideae, Commelinideae, Orchidaceae, Zingiberideae) and reduction in the complexity of the exine or loss of the exine altogether (e.g., Alismatideae, Orchidaceae, Zingiberideae).

We might expect to observe a progression of pollen aperture and wall structure types similar to the proposed evolutionary trends in geologic time. Before we can adequately evaluate these schemes in the context of fossil evidence, we must provide criteria to unequivocally identify angiosperm pollen in a field of superficially similar non-angiosperm palynomorphs (e.g., monosulcate gymnosperms).

Pollen Wall Homologies and Identification of Fossil-Dispersed Pollen

The monosulcate aperture is generally considered to be most primitive among angiosperm aperture types (Kuprianova, 1948; Walker, 1974a) and appears to be a good character in identifying early angiosperm pollen. However, monosulcate pollen is also common among gymnosperms, and its continuous stratigraphic occurrence since the Permian makes this criterion, in itself, questionable. This has long been recognized by palynologists. However, the presence of the monosulcate aperture in conjunction with pollen wall structure, may provide a basis on which angiosperm pollen can be distinguished from gymnosperm pollen. Van Campo (1971) surveyed pollen wall structure in representative gymnosperm and angiosperm taxa and proposed palynological criteria to distinguish between these groups. Doyle et al. (1975) further discussed these criteria and their application to the interpretation of the fossil record. Van Campo (1971) and Doyle et al. (1975) recognized three basic pollen wall structure types; alveolar and/or endoreticulate, tectate-granular, and tectate-columellate. The alveolar wall structure is known only in gymnosperms and the tectate-columellate wall structure is known predominantly from angiosperms. These appear to be good palynological characters for separating monosulcate pollen of these groups. The tectate-granular, however, is found in both gymnosperms and angiosperms. To further complicate matters, this is a wall structure type common among the most primitive angiosperms. To distinguish between gymnosperm and angiosperm pollen with tectate-granular walls, Doyle et al. (1975) emphasized the significance of the endexine [thought by Doyle et al. (1975) to be in part equivalent to the nexine of Erdtman (1952)]. Gymnosperms have lamellated endexines (nexines) and angiosperms have non-lamellated endexines (nexines), except in the apertural region where it is lamellated. These pollen wall criteria are presumably the basis for determining affinities of dispersed fossil palynomorphs.

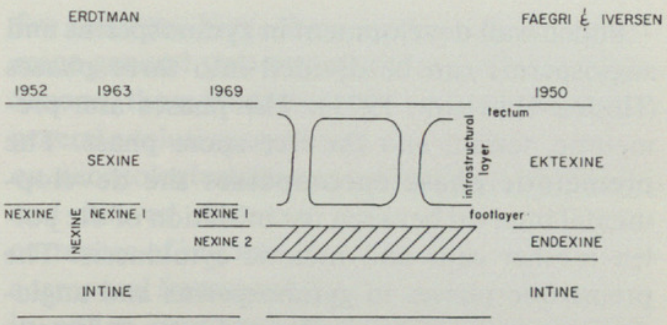
Pollen wall structure terminologies are a complicated and intimidating aspect of palynology. Widely used nomenclatural schemes are, for the most part, based on structural aspects (as opposed to developmental aspects) of the various wall layers, but there has been noticeable disregard in defining the homologies for the various wall layers of the pollen of major plant groups, especially gymnosperms and angiosperms. In addition, many of the terms proposed by various authors to describe pollen wall structure are used interchangeably, implying homologies exist in contradiction to their original definitions [e.g., Faegri's endexine (in part) = Erdtman's nexine]. This has resulted in an ambiguous situation for palynologists who wish to establish taxonomic and phylogenetic relationships among various plant groups based on pollen wall structural data. To help clarify this situation it is necessary to describe in detail the two most widely used terminological systems describing pollen wall structure.

The two most widely used wall structure nomenclatural systems are those of Faegri and Iversen (1950; also Faegri, 1956) and Erdtman (1952, 1963, 1969). Faegri and Iversen (1950) distinguished three major wall layers, the outer sporopolleninous ektexine and endexine, and the inner cellulosic intine. The terms ektexine and endexine were first coined by Erdtman (1943) and correspond to Fritzsche's (1837) exine and intexine, but Erdtman (1952) later abandoned these terms. Erdtman (1952) also identified three primary wall layers, the sporopolleninous sexine and nexine, and the cellulosic intine. The intine, recognized by Faegri and Iversen (1950) and Erdtman (1952), easily corrodes in acetolyzed and fossilized pollen. It has been generally ig-

nored in phylogenetic and taxonomic schemes and will not be discussed further.

Faegri and Iversen (1950) distinguished the outer ektexine from the inner endexine by differences in their affinity for the stain basic fuchsin. The ektexine and endexine also exhibit differences in their affinity for the transmission electron microscopic stains uranyl acetate and lead citrate, and various other cytochemical stains (e.g., Aniline blue-black, Coomasse blue; Southworth, 1973), further substantiating Faegri and Iversen's nomenclatural distinction between these wall layers. Rowley et al. (1981) have speculated that the difference in stainability between these wall layers may be due to differences in the glycocalyces associated with these wall layers, or the chemical nature of sporopollenin. In addition, Bailey (1960) and Southworth (1974) found differences in the solubility of the ektexine and endexine in fresh material treated with hot 2-aminoethanol. The ektexine is readily soluble and the endexine exhibits less solubility. This prompted Southworth (1974) to speculate that there are differences in the chemical nature of the sporopollenin between these two wall layers (cf. with one of the alternative explanations offered by Rowley et al., 1981). Regardless of the reason, Southworth's data further substantiates the terminological distinction of the ektexine and endexine (sensu Faegri & Iversen, 1950). Faegri and Iversen (1950) considered the ektexine to be a three-layered structure, based solely on morphology. The outermost tectum is the sculptured layer of the ektexine. The middle layer or infrastructural layer can be alveolar, endoreticulate, columellate, or consist of spherical or irregularly shaped granules or anastomosing rods. The innermost layer of the ektexine is the footlayer; this layer can be amorphous or lamellated (but not commonly in angiosperms), but is unsculptured.

Erdtman (1952) first identified the sexine and nexine solely by their morphology: the outer sexine referring to the variously sculptured portion of the exine, and the amorphous or lamellated nexine corresponding to the unsculptured portion of the exine. However, in 1963 Erdtman proposed the term nexine 1 for the outer portion of the nexine that is "chemically" and "physically" similar to sexine (thus = to Faegri and Iversen's footlayer) yet "topographically" part of the nexine proper. Later Erdtman (1969) proposed nexine 2 for the inner portion of the nexine that is different from nexine 1 in its response to basic fuchsin. Thus, Erdtman (1969) fully realized the significance of the differential stainability of pollen wall layers and proposed a system of terminology identical to Faegri and Iversen (1950): Erdtman's sexine plus nexine 1 are equivalent to Faegri and Iversen's ektexine, and Erdtman's nexine 2 is equivalent to Faegri and Iversen's endexine (Text-Fig. 3).



TEXT-FIGURE 3. Pollen wall homologies. Equivalent terms in the Erdtman (1969) and Faegri and Iversen (1950) terminological schemes.

There has been a quantum increase in the taxonomic and phylogenetic palynological literature since the inception of these terms, unfortunately without rigorous application of the criteria on which these terms were originally based. Thus, these terms have been confused and their use in suggesting homologies among wall layers in different taxa have been equivocal. This is often reflected in descriptive morphological studies confusing the two different nomenclatural schemes. Some workers have rejected these schemes outright and proposed their own palynological lexicon (e.g., Tsinger & Petrovskaya-Boranova, 1961; Wittmann & Walker, 1965; Reitsma, 1970), further confusing attempts to establish homologies among wall layers in different taxa. It is paramount that before any attempt is made to consider the phylogenetic significance of pollen wall structure, consistent use of terminology be established. Further, wall terminology should accurately reflect structure, histochemistry, and development so that homologies for various wall layers may be established reliably between angiosperms and gymnosperms. Although the developmental aspects of the pollen wall have been generally ignored by descriptive palynologists, the value of developmental data have long been recognized in establishing homologies (e.g., Nageli, 1842; Stebbins, 1974). A sufficient body of literature on pollen wall development has emerged over the past 25 years for providing insight into the homologies between gymnosperm pollen wall layers.

Pollen wall development in gymnosperms and angiosperms can be divided into three phases (Heslop-Harrison, 1971). The phases are: premeiotic, tetrad, and the free spore phase. The premeiotic phase encompasses the developmental interval between the initiation of the pollen mother cells and meiotic cytokinesis. The premeiotic phases in gymnosperms and angiosperms are generally similar and are not directly related to the development of the sporopolleninous exine. Thus, they need not be discussed further in the present context. However, there are significant differences in wall development between angiosperms and gymnosperms during the tetrad and free spore phases.

In cycads and conifers, for example, the sporopolleninous sexine begins development immediately after the four microspores are enclosed in the callose special wall. There is no deposition of a dense staining fibrillar primexine with embedded radially directed elements (procolumellae), as in many angiosperms. A dispersed fibrillar material is deposited between the callose wall and the microspore plasmalemma, at the same time the centripetal development of the sexine is occurring. Audran (1981), Dickinson (1971), Willemse (1971), and Vasil and Aldridge (1970) have interpreted the dispersed fibrillar material as homologous with the primexine of angiosperms. The differences in electron density between the dispersed fibrillar material in cycad and conifers, and the primexine of angiosperms, and that accretion of the sporopolleninous sexine begins immediately, without any recognizable nonsporopolleninous matrix, suggest that the fibrillar material in gymnosperms is not entirely comparable with the primexine of angiosperms.

Upon completion of the sexine, development of the nexine (footlayer) begins by accumulation of sporopollenin on unit-like membranes. These sheets of sporopollenin are successively appressed to one another but retain their lamellated appearance, even at maturity, in both apertural regions and nonapertural regions. After formation of the nexine, the callose special wall is destroyed and the microspores are free in the sporangium. In most gymnosperms no additional sporopolleninous wall layers form during the free spore phase (however, see Rohr, 1977). The *entire* sporopolleninous wall, sexine, and nexine are completed during the tetrad phase (Audran, 1981; Zavada, 1983b).

In angiosperms the tetrad phase is also marked by the sequestering of the four microspores by callose. Prior to the appearance of the sporopolleninous wall, a distinctive fibrillar wall not found in gymnosperms (see above), the primexine, is formed. Embedded in the primexine shortly after it becomes distinct are nonsporopolleninous radially directed probacules (procolumellae). Subsequently, the probacules become more electron dense as sporopollenin accumulates (Heslop-Harrison, 1971; Zavada, 1984). The tectum is then formed by the lateral accumulation of sporopollenin at the distal ends of the bacules. Finally, the footlayer (nexine 1) develops on unit-like membranes (as in gymnosperms) and at times appears lamellated in apertural and nonapertural regions at maturity (e.g., Magnoliaceae, Praglowski, 1974; Annonaceae, Le Thomas, 1981). Next the bases of the bacules become fused to the footlayer (nexine 1). Upon completion of the footlayer (nexine 1), the callose wall is destroyed and the pollen grains are free in the anther locule. During the free spore phase and in contrast to most gymnosperms, an additional sporopolleninous wall layer can develop—the endexine. Along with the footlayer, the endexine has been considered equivalent to the nexine in gymnosperms (Doyle et al., 1975). Endexine appears to have two modes of deposition in angiosperms. In one instance, endexine is the result of the accumulation of unit-like membranes with sporopollenin, similar to footlayer (nexine 1) formation. This imparts a lamellated appearance to this wall layer in apertural and, occasionally, in nonapertural endexine at maturity (e.g., Compositae, Horner & Pearson, 1978; *Ricinus, Saintpaulia,* Larson et al., 1962). The second mode of endexine formation is by the accumulation of sporopolleninous granules in nonapertural regions. Endexine formed in this manner appears homogeneous at maturity in nonapertural regions. However, apertural endexine in the same pollen is formed on unit-like membranes and has a lamellated appearance at maturity. Granular nonapertural endexine is known from a number of taxa (e.g., *Zea,* Skvarla & Larson, 1966; *Helloborus,* Echlin & Godwin, 1969; *Passiflora,* Larson, 1966; *Austrobaileya,* Zavada, 1984).

Another significant aspect of endexine formation is that, in some taxa, endexine is interbedded with intine. When these taxa are treated with acetolysis solution, the intine corrodes and fragments the endexine. This gives the false

impression that endexine is scanty or absent in acetolyzed material (e.g., *Austrobaileya,* Zavada, 1984).

Although the mode of deposition of the various wall layers in angiosperms may vary, the timing of their development is consistent among the angiosperms thus far studied.

Criteria currently used to distinguish fossil gymnosperm from the most primitive angiosperm pollen (e.g., tectate-granular) depend on characteristics of the nexine of gymnosperms and the endexine of angiosperms (Doyle et al., 1975). The use of nexine and endexine synonymously implies that these wall layers are homologous. However, evidence presented above, including the chemical difference between nexine of gymnosperms (which is composed entirely of nexine 1 or footlayer) and the endexine of angiosperms, born out by their differential stainability with various cytochemical and TEM stains, by differential solubility in 2-aminoethanol, and by the different mode of deposition of the endexine in some angiosperms, suggests the nexine of gymnosperms and endexine of angiosperms are not homologous wall layers. Thus, the criteria currently used to distinguish dispersed angiosperm pollen from dispersed gymnosperm pollen, which imply the nexine and endexine are homologous, must be rejected (e.g., Doyle et al., 1975). This does not preclude the use of other pollen characteristics in identifying dispersed fossil angiosperm pollen. The columellate infrastructure is known only from extant angiosperms (cf. Van Campo, 1971). The endexine of angiosperms lamellated or homogeneous has what appears to be a developmentally and cytochemically equivalent wall layer in *Ginkgo biloba* (Rohr, 1977). In addition, the columellate infrastructure and endexine are relatively advanced features among angiosperms (Walker, 1976) and are not likely to be found in primitive fossil angiosperm pollen. To make this situation worse, wall structure characteristics of primitive angiosperms are indistinguishable from those of many gymnosperms (e.g., the granular type occurs in both gymnosperms and angiosperms). Thus, there are no reliable taxonomic features that can be used to distinguish primitive angiosperm pollen and gymnosperm pollen, and it will be difficult to elucidate the origin of the angiospermous condition on palynological data alone.

Despite these difficulties, studies of fossil pollen wall structure can still be enlightening in a few respects. First, these studies can help determine general patterns of pollen wall evolution. Second, these studies can be used to corroborate general evolutionary trends of wall structure based on neontological data, i.e., to identify primitive and derived character states. Further, first occurrences of key wall structure types can provide a temporal framework for the evolutionary trends in pollen proposed on neontological grounds. Third, studies of dispersed pollen correlated with pollen found in fossil fructifications might reveal the affinities of the dispersed pollen. Once a dispersed pollen grain can be associated with a megafossil, the morphological features of the pollen and the megafossil can then be used to evaluate their relationship to angiosperms.

In the following sections new data is presented on fossil pollen wall structure for a number of saccate and non-saccate dispersed pollen. The significance of these data to early angiosperm evolution and origins will be discussed in conjunction with data from other studies on fossil pollen wall structure.

Materials and Methods

Pollen was recovered from sediment by treatment with HCl, HF, Schulze's solution, and KOH. After each treatment the residue was washed with distilled water until neutral (pH 7). After the final washing the residue was centrifuged in the heavy liquid $ZnCl_2$, sp. gr. 2, and the supranatant was collected, dehydrated in an alcohol series and embedded in polystyrene after Frangioni and Borgioli (1979). The suspension was smeared on a microscope slide and allowed to harden, then photographed. Pollen grains were then cut out of the hardened plastic and re-embedded in polystyrene in Beem^R capsules for transmission electron microscopy (TEM). Sectioning was done on an LKB-1 ultramicrotome and pollen was stained for 15 minutes in both uranyl acetate and lead citrate. Sections were viewed with a Philips EM-300. Pollen was prepared for scanning electron microscopy (SEM) by dissolution of the polystyrene embedded pollen in toluene until the pollen was free of all embedding material, or the pollen residue prior to embedding in polystyrene was mounted directly on SEM stubs, coated with gold-palladium, and viewed with a Coates and Welter field emission electron microscope.

The identification of pollen wall layers and determination of pollen wall homologies, as mentioned, is based on staining properties with

various cytochemical and TEM stains, solubility in 2-aminoethanol, development, and morphology in extant pollen. Although it is difficult to study developmental aspects of fossil-dispersed pollen, few of the pertinent biochemical tests have been used in attempts to interpret wall structure in fossil pollen. Thus, identification of wall layers in fossil pollen depends primarily on morphology and staining properties with TEM stains. Interpretation of fossil pollen wall structure based on staining properties with TEM stains must be viewed with some reservation because their reaction to the stains are known to differ from extant pollen. Rowley et al. (1981) have proposed that staining is effectuated by the labile exine moiety (glycocalyx) and not by the relatively inert and decay-resistant sporopolleninous wall fraction. Thus, the depositional microenvironment and diagenetic processes associated with fossilization can have profound effects on the staining properties of fossil pollen walls. Southworth (1974) found that fresh pollen is readily soluble in 2-aminoethanol, but that pollen taken from old herbarium material exhibits less solubility. This suggests that even recent material undergoes biochemical changes that affect the physical and chemical properties of the exine. Stanley (1966) has demonstrated that fossil pollen from various geologic stages can exhibit differential staining with the nonspecific stain Safranin-O, further suggesting that fossilization affects the physical and biochemical aspects of the exine. Until the microenvironmental and diagenetic factors influencing staining can be more fully understood, interpretations based on these criteria are tentative.

POLLEN WALL STRUCTURE OF DISPERSED FOSSIL POLLEN

PRAECOLPATITES SINUOSUS, PERMIAN

This form genus was recovered from Permian sediments of the Olive River Basin, Cape York Peninsula, Queensland, Australia. Foster and Price (1982) examined this taxon using light, scanning electron, and transmission electron microscopy. Pollen is elongate, probably multiaperturate (2–4 sulcate) and exine sculpturing is verrucate-granulate. The pollen wall is 2–3 μm thick and is considered to have two primary layers, an inner laminated layer (possibly footlayer, intexine of Foster & Price, 1982) and an outer structured layer (exoexine of Foster & Price, 1982). The inner part of the outer layer is composed of a granular infrastructure, which is overlain by a tectum that is occasionally perforated with small channels. Foster and Price (1982) considered the wall structure of this taxon to be similar to the granular wall structure types found in extant ranalean taxa (e.g., Magnoliaceae).

MARSUPIPOLLENITES TRIRADIATUS, PERMIAN

This form genus is from the Blair Athol Basin of central Queensland, Australia. It was studied in detail using light, scanning electron, and transmission electron microscopy by Foster and Price (1982). Pollen is spherical to slightly elongate and has a distal sulcus and a proximal triradiate scar. Exine sculpturing is verrucate to granulate. The pollen wall is composed of two primary layers and an inner unsculptured layer (intexine of Foster & Price, 1982) and an outer layer that has a granular infrastructure and a tectum occasionally perforated by small channels (Foster & Price, 1982). The wall structure of this taxon also shows striking similarities to the granular infrastructure of some ranalean taxa.

MONOSULCITES SPP., UPPER PALEOZOIC-TERTIARY

This widespread Mesozoic form genus is monosulcate, ovoid to boat-shaped, and exine sculpturing is psilate. Trevisan (1980) investigated the wall structure of one form from the Lower Cretaceous of Italy, and, in the present study, one form was investigated from the Yorkshire Jurassic. Both are identical in every respect. Pollen wall structure consists of two layers, an inner continuous lamellated footlayer (Layer A of Trevisan) and an outer massive layer. The inner portion of the outer massive layer consists of closely packed, somewhat homogeneous granules. This imparts a spongy appearance to the inner portion of the outer massive layer. The outer portion of this wall layer appears homogeneous and may comprise the tectum. The outer massive layer thins in the region of the sulcus, however, the basal layer (footlayer) remains of constant thickness throughout. Trevisan (1980) noted a thin electron dense marginal layer of the exine, also present in my material. This is not considered a distinctive layer, but an artifact of preservation (see discussion on *Eucommidiites*). Taylor (1973) investigated pollen from the Cretaceous taxon *Cycadeiodea dacotensis*, which is similar in many respects to the dispersed pollen investigated in this study and by Trevisan (1980).

CLASSOPOLLIS SPP., TRIASSIC-LOWER CRETACEOUS

This form genus has been associated with a few gymnosperm fructifications and probably represents a diverse group of plants (e.g., *Cheirolepis muensteri,* Harris, 1957; *Pseudofrenelopsis,* Alvin et al., 1978). Pollen has a distal aperture in addition to a proximal triradiate suture and frequently occurs in tetrads. Pollen wall structure has been investigated by Pettitt and Chaloner (1964); they offered two interpretations of the complex wall structure. One interpretation viewed the pollen wall consisting of an outer tectum, a columellate infrastructure with the columellae fused to a thick three-layered footlayer. The outermost portion of the footlayer is a thick homogeneous layer. The middle of the footlayer consists of large, irregular shaped, inwardly directed columns which rest on a thick lamellated inner layer. The alternative interpretation considered the innermost lamellated layer—the footlayer, in toto, the large irregular shaped columns—the columellate infrastructure and the outermost layer—tectum. The tectum is now considered the complex three-layered structure consisting of an inner homogeneous layer fused to a supratectal layer (also see Taylor & Alvin, 1984). Regardless of what interpretation is favored, the wall structure of this taxon is unique among fossil and extant gymnosperms. It represents a gymnosperm pollen type with a columellate infrastructure, a characteristic thought only to occur in angiosperms.

EUCOMMIIDITES SPP., TRIASSIC-LOWER CRETACEOUS

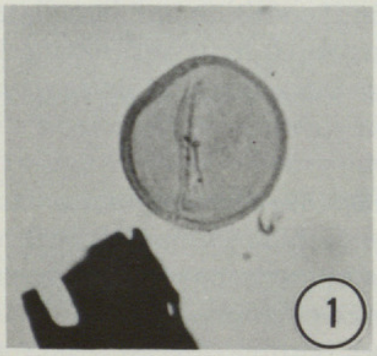
This form genus occurs abundantly in Lower Mesozoic sediments. Pollen is elliptical to broadly oval and has three apertures. One aperture is a conspicuous, broad, sulcus-like aperture and the two other apertures are thin and fold-like (Figs. 1, 2). They are evenly distributed on the pollen grain, all with their long axes parallel to the long axes of the pollen grain. Pollen has been studied using TEM (Doyle et al., 1975; Trevisan, 1980; present study Figs. 1–3). Three forms are recognized based on pollen wall structure.

A Jurassic form investigated in the present study and a Lower Cretaceous form investigated by Trevisan (1980, *Eucommiidites* sp., Fig. 1) have a three-layered wall. The innermost layer (layer A of Trevisan) is unsculptured, often lamellated, and doesn't thin in the apertural region (Figs. 2, 3). Based on its position and lamellated nature it can be considered footlayer (nexine 1). The middle layer or infrastructural layer (layer B_1 of Trevisan) consists of irregular shaped columellae, often interspersed with irregularly shaped granules (Fig. 3). The columellae and granules are fused to a thick tectum (layer B_2 of Trevisan), which is homogeneous in the lower portion and comprised of compacted supratectal granules in the outer portion (Fig. 3). Trevisan considered the outer layer of granules a distinct (layer C) layer due to its differential stainability with SEM and TEM stains. She divided this C layer into a three-layered structure consisting of C_1, C_2, and C_3. Erdtman (1963) proposed the term stegine for the outer margin of the exine that stains differently from the more central region. This phenomenon may not be indicative of true biochemical differences in the exine. It may be due to differential chemical extraction of the more labile moiety (glycocalyx) of the exine during fossilization or affected by preparation of the sediment to recover fossil-dispersed pollen (cf. Rowley et al., 1981). This differential marginal staining is common in many of the fossil taxa investigated (see below), and probably doesn't represent a distinctive biochemical layer.

Trevisan (1980) described a second form of *Eucommiidites* (*E.* sp. 2). She considered its wall to consist of three layers, an A layer similar in all respects to the A layer of *E.* sp. 1 and appears to represent footlayer (nexine 1). The middle B layer is further divided into B_1, B_2, and B_3. Layers B_1 and B_2 represent a granular infrastructural layer and B_3 a homogeneous layer comprising the tectum. The outer C layer is distinguished once again on its differential staining from the inner portion of the tectum, and is a similar situation to that observed in the C layer of *E.* sp. 1.

Doyle et al. (1975) described a third form of *Eucommiidites* from the Lower Cretaceous. Its wall consists of three layers. An inner lamellated layer, which Doyle et al. (1975) term endexine, probably represents footlayer (nexine 1), in light of its position, staining characteristics and presumed gymnospermous origin. The infrastructural layer is comprised of spherical granules that are overlain by a homogeneous tectum that is traversed by small perforations.

The three taxa of *Eucommiidites* all have three-layered exines, a lamellated footlayer [nexine 1, A layer of Trevisan, endexine of Doyle et al. (1975)], an infrastructural layer consisting of spherical granules (Doyle et al., 1975), or a ho-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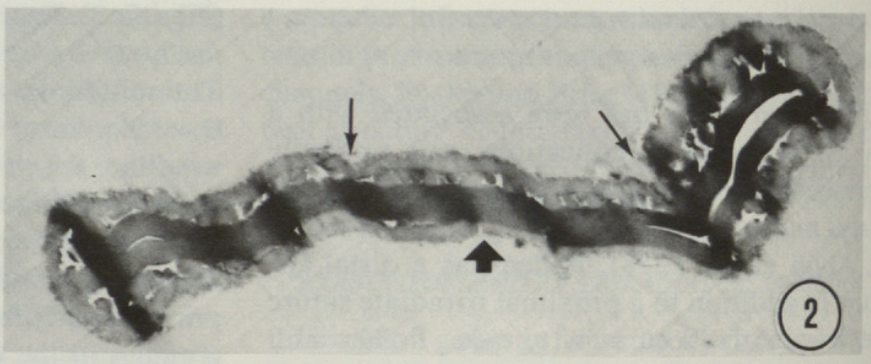
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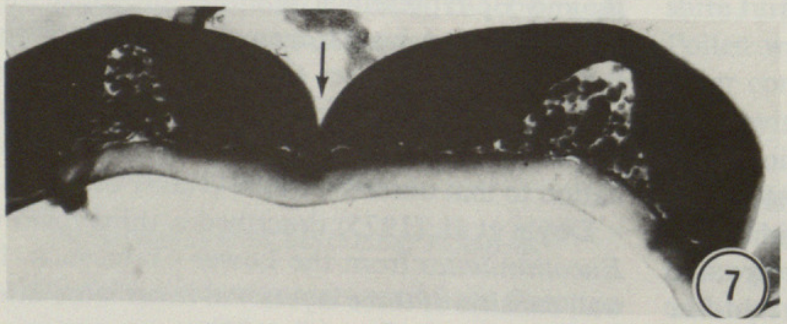
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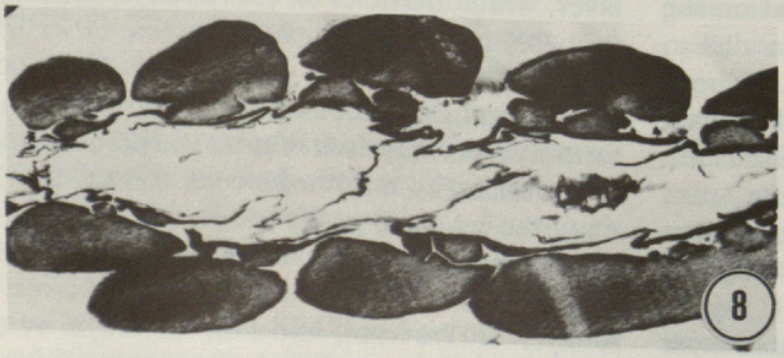
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mogeneous to granular layer (Trevisan, 1980, *E.* sp. 2) or a columellate to granular infrastructure (Trevisan, 1980, *E.* sp. 1, form investigated in the present study), and a tectum that may or may not have supratectal ornaments and can be minutely perforate.

Only four individual pollen grains of this form genus have been studied with TEM thus far. These studies have revealed that three distinctive taxa exist based on pollen wall ultrastructure, suggesting that this form genus (sensu lato) was quite diverse during the Mesozoic. Although the granular infrastructure is most common, there is a tendency toward the columellate infrastructure in *E.* sp. 1 of Trevisan and the form investigated in the present study (which are considered here to be the same taxon).

EPHEDRIPITES SPP., TRIASSIC-RECENT

This form genus, as Mchedlishvili and Shakmoundes (1973) have pointed out, does not form a natural group. Trevisan (1980) sectioned two species from the Lower Cretaceous and in the present study one species from the Triassic Chinle Formation was investigated (*Equisetoporites chinleana*).

The pollen is oval to elliptical approximately 25–60 μm long, monosulcate to inaperturate (or possibly multiaperturate) with conspicuous longitudinal ridges. It is superficially similar to pollen of the extant taxon *Ephedra* (however, compare Figs. 8, 9 with Fig. 5 of *Gnetum* and Fig. 7 of *Ephedra*). Trevisan (1980) sectioned a monosulcate form and distinguished two major wall layers; an inner continuous lamellated layer (layer A) and an outer complex layer that comprises the ridges and grooves. The inner A layer, based on its position in relationship to the outer wall layers and lamellated nature, probably is footlayer (nexine 1). The outer layer, the infrastructural layer, and tectum is further subdivided into layers B_1, B_2, B_3, C, and D by Trevisan (1980). Layer B_1 is a thin, continuous layer that underlies the B_2 layer, which is composed of fragmented and anastomosing units. The B_2 layer is similar to the granular infrastructural layer in extant *Ephedra* (Fig. 7) and *Gnetum* (Figs. 5, 6). Layer B_3 is homogeneous and thins in the regions of the grooves (as does the tectum in extant *Ephedra* pollen). The outer margin of the tectum stains differently than the inner portion, in a similar manner to that observed in other fossil taxa (see above) and is distinguished as layer C by Trevisan (1980). On the surface of the exine are scattered "globulets" 0.01–0.09 μm in diameter, which Trevisan terms the discontinuous D layer. The globulets are possibly the remains of a tapetal deposit.

The Triassic Chinle form genus *Equisetoporites chinleana* (Daugherty, 1941) also falls within the morphological circumscription of *Ephedripites* and has been reported as tectate-columellate by Cornet (1979). Pollen of this type has been found associated with the gymnospermous taxon *Masculostrobus clathratus* (Ash, 1972). My investigation of this taxon has shown the pollen to lack a conspicuous aperture (however, see below; Figs. 4, 8). The wall is a three-layered structure consisting of a thin, lamellated footlayer (Fig. 8), which is fused to short stout columellae (Figs. 8, 9) (their stout appearance may be a result of compression). The columellae are overlain by a thick homogeneous tectum, which forms the conspicuous ridges (Fig. 8). Both

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FIGURES 1–9. 1–3. *Eucommiidites* sp.—1. Yorkshire Jurassic, ×400.—2. Transmission electron micrograph of the same grain pictured in Figure 1. Note the three apertures (arrows) and the three-layered exine, ×4,040.—3. Transmission electron micrograph of the same grain pictured in Figure 1, showing three-layered exine; the inner dark staining footlayer (nexine 1), infrastructural layer with columellate-like structures and interspersed granules, and the homogeneous tectum with a supratectal granule layer. This grain is similar in all respects to the *Eucommiidites* sp. 1 of Trevisan, 1980, ×12,975.—4. *Equisetoporites chinleana,* Triassic Chinle Fm., ×400. 5–7. Pollen of the Gnetales.—5. Transmission electron micrograph of *Gnetum* showing thick footlayer (nexine 1), fine granular layer beneath the homogeneous tectum comprising a spine, ×32,200.—6. Scanning electron micrograph of *Gnetum* showing sulcus and echinate sculpturing, ×1,200.—7. Transmission electron micrograph of the polyplicate pollen of *Ephedra californica,* showing inner footlayer (lightly staining), granular infrastructural layer and thick tectum. Note tectum is continuous in the groove (arrow), ×21,000. 8–9. *Equisetoporites chinleana.*—8. Transmission electron micrograph of the same grain pictured in Figure 4, showing thin lamellated footlayer (nexine 1), stout columellae, and thick outer tectum. Note tectum is discontinuous in the grooves (compare with Fig. 7), and that the wall structure is remarkably different from the Gnetaceous taxa in Figures 5 and 7, ×11,600.—9. Transmission electron micrograph of the same grain pictured in Figure 4, tangential section of the pollen wall showing the columellate structures underlying the tectum (arrow), ×14,200.

the tectum and columellae are absent in the region of the grooves (Figs. 8, 9). The grooves might constitute structurally weak areas of the pollen wall and might have functioned as apertures (thus this form would be multiaperturate; Fig. 8). The tectate-columellate structure in this Triassic form genus represents the earliest occurrence of this wall structure type in the fossil record, a wall structure type thought to be restricted to angiosperms.

BISACCATE POLLEN WITH GRANULAR INFRASTRUCTURE, TRIASSIC-CAMPANIAN

In all extant plant groups bisaccate pollen has alveolar (more precisely endoreticulate) wall structure. Many of the Paleozoic saccate gymnosperms thus far investigated also have endoreticulate wall structures (e.g., see Millay & Taylor, 1974). Thus Mesozoic saccate pollen, although little studied, is generally considered a morphologically homogeneous group. However, my continuing studies of Triassic, Jurassic, and Cretaceous saccate pollen have confirmed the existence of the granular infrastructure among pollen of this type.

In all the forms investigated, the corpus is circular to elliptical with a distally located sulcus flanked by two relatively small sacs (Figs. 10–17). Pollen ranges from about 30 μm to greater than 50 μm in size (including sacs). The sacs may appear fully functional, as in many of the Triassic and Lower Jurassic forms (Figs. 10, 11), or may be small, apparently highly reduced, vestigial structures (Figs. 12–17). Pollen with the small, highly reduced sacs often appears to be morphologically similar (except for the sacs) to monosulcate, non-saccate pollen of the genus *Verrumonocolpites* (compare Figs. 18, 21, 22 with Figs. 12–17, 19, 20). The pollen wall in all of the taxa investigated is a three-layered structure (Figs. 23–30, including the non-saccate genus *Verrumonocolpites*). The inner layer is homogeneous or lamellated (Figs. 23–30) and, based on its position and similar staining properties to the outer wall layers, represents footlayer (nexine 1). The infrastructural layer consists of spherical to irregularly shaped granules or anastomosing rods (Figs. 23–30), and in some of the Cretaceous forms approaches the columellate condition (Figs. 24, 25). The outer layer, tectum, is thick and may (Figs. 25, 27) or may not be perforated (Figs. 29, 31). Exine sculpturing is usually scabrate (Figs. 19–22, 26, 29, 31). The sacs in many cases result from a separation of the footlayer and intrastructural layer, identical to sac formation in extant endoreticulate (alveolar) walled gymnosperm pollen (Figs. 27, 28). However, in some forms, i.e., *Punctamultivesiculites inchoatus* (Figs. 15, 30) and *Granabivesiculites inchoatus* (Figs. 13, 24), the sacci result from a build up of exinal material.

Pollen wall structure of these saccate gymnosperms is similar in many respects to granular wall structure of extant ranalean taxa.

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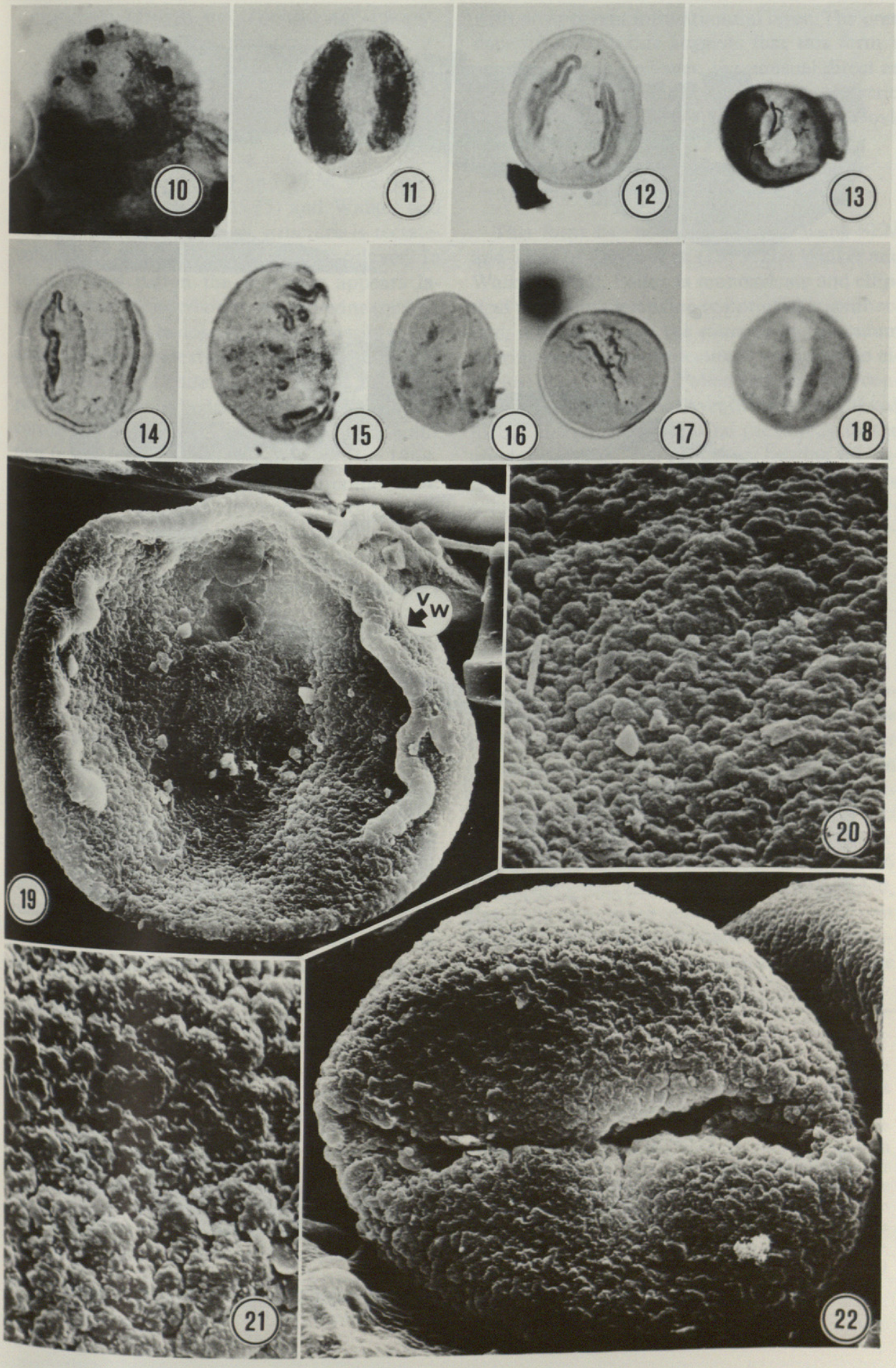
FIGURES 10–22. Fossil saccate pollen.—10. Bisaccate grain from the Triassic Chinle Fm. (transmission electron micrograph of the same grain is pictured in Fig. 23), ×400.—11. Bisaccate grain from the Yorkshire Jurassic, showing relatively small sacci (similar to *Bacubivesiculites inchoatus* of the Cenomanian Dakota Fm., Minnesota, Fig. 12), ×400.—12. *Bacubivesiculites inchoatus,* Cenomanian Dakota Fm., Minnesota, showing small sacci flanking the sulcus, ×400.—13. *Granabivesiculites inchoatus,* Cenomanian Dakota Fm., Minnesota, showing small, vestigial-like sacci (transmission electron micrographs of the same grain are pictured in Figs. 24 and 25), ×400.—14. *Granabivesiculites* sp., Cenomanian Dakota Fm., Minnesota, showing vestigial-like sacci flanking the sulcus (transmission electron micrographs of the same grain are pictured in Figs. 26 and 27, scanning electron micrographs of a similar grain are Figs. 19 and 20), ×400.—15. *Punctamultivesiculites inchoatus,* Cenomanian Dakota Fm., Minnesota, showing small pustule-like sacci (transmission electron micrographs of the same grain are pictured in Figs. 29 and 30), ×400.—16. Vestigial saccate pollen from the Albian Kowa Fm., Kansas (transmission electron micrograph of the same grain is pictured in Fig. 28), ×400.—17. *Clavabivesiculites pannosus,* Cenomanian Dakota Fm. of Minnesota, showing very rudimentary sacci flanking the sulcus, ×400.—18. *Verrumonocolpites conspicuus,* Cenomanian Dakota Fm., Minnesota, showing sulcus (transmission electron micrograph of the same grain is pictured in Fig. 31). This species is similar to many of the saccate forms, but lacks sacci, ×400.—19. *Granabivesiculites* sp., Cenomanian Dakota Fm. of Minnesota, scanning electron micrograph showing vestigial sacci (VW) and sulcus. Similar to the grain pictured in Figure 14, ×1,650.—20. *Granabivesiculites* sp., same grain as in Figure 19, scanning electron micrography showing details of exine sculpturing which is similar to the exine sculpturing of *Verrumonocolpites conspicuus* (Fig. 21), ×9,000.—21. *Verrumonocolpites conspicuus,* Cenomanian Dakota Fm. of Minnesota, scanning electron micrograph showing details of exine sculpturing, compare with Figure 20 of *Granabivesiculites* sp., ×9,460.—22. *V. conspicuus,* same grain as in Figure 21, scanning electron micrograph showing sulcus and exine sculpturing, ×1,800.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CLAVATIPOLLENITES SPP., LOWER CRETACEOUS (BARREMIAN-CENOMANIAN)

This form genus appears to encompass a diverse array of taxa (Walker & Walker, 1984). Pollen is monosulcate to ulceroid, and ovoid to spherical. Exine sculpturing is reticulate. Pollen wall structure using SEM and TEM was investigated by Doyle et al. (1975) and Walker and Walker (1984). Pollen wall structure is tectate-columellate with a homogeneous footlayer. In the apertural region the footlayer appears lamellated and is underlain by an endexine (nexine 2) that exhibits endosculpturing. Possibly, the endosculptured endexine is due to corrosion during fossilization. Endexines of extant taxa, especially when interbedded with intine, exhibit corrosion upon treatment with acetolysis solution (e.g., *Helleborus,* Echlin & Godwin, 1969; *Austrobaileya,* Zavada, 1984). The columellate infrastructure and especially endexine (nexine 2) are features of angiosperm pollen grains. *Clavatipollenites* shares many character states with pollen of the Chloranthaceae (Kuprianova, 1981; Walker & Walker, 1984).

RETIMONOCOLPITES PERORETICULATUS, LOWER CRETACEOUS (APTIAN)

This widespread and diverse form was investigated using TEM and SEM by Doyle et al. (1975) and Walker and Walker (1984). Pollen appears monosulcate and elliptical in outline; exine sculpturing is an open reticulum. Pollen wall structure consists of a thick homogeneous inner layer, footlayer, which is underlain in the apertural region by a thin endexine (nexine 2). The sculptured outer layer of the wall forming the reticulum is attached directly to the footlayer with no apparent infrastructural layer. The presence of an endexine suggests that this form is angiospermous, however, the unusual direct attachment of the wall layer comprising the reticulum is unknown in extant angiosperms (Doyle et al., 1975; Walker & Walker, 1984).

STELLATOPOLLIS SPP., ALBIAN-CENOMANIAN

This form has been investigated using SEM and TEM by Doyle et al. (1975) and Walker and Walker (1984). Pollen is monosulcate and elliptical to subcircular; exine sculpturing is semitectate, reticulate, with the muri of the reticulum bearing supratectal projections, triangular to elliptical in surface view. Pollen wall structure consists of a thick inner footlayer (nexine 1), believed to be underlain by endexine (nexine 2) in the apertural region. The reticulum bearing the supratectal triangular to elliptical processes has a columellate infrastructure. The presence of endexine (nexine 2) and the columellate infrastructure suggests that this form is angiospermous.

LILIACIDITES SPP. (MONOCOTYLEDONOUS POLLEN TYPES), APTIAN/ALBIAN-UPPER CRETACEOUS

Forms similar to those investigated in the present study from the Cenomanian of Kansas were studied by Doyle (1973) and Walker and Walker (1984) using SEM and TEM, respectively. Pollen is predominantly monosulcate, but serial sections of single pollen grains investigated in this study have shown them to be inaperturate (Figs. 33–35). Pollen is elliptical, large, averaging 36 μm along its long axis, and is invariably folded, giving the impression that an aperture is present (Fig. 32). The exine is reticulate, and the reticulum becomes finer toward opposite ends of the

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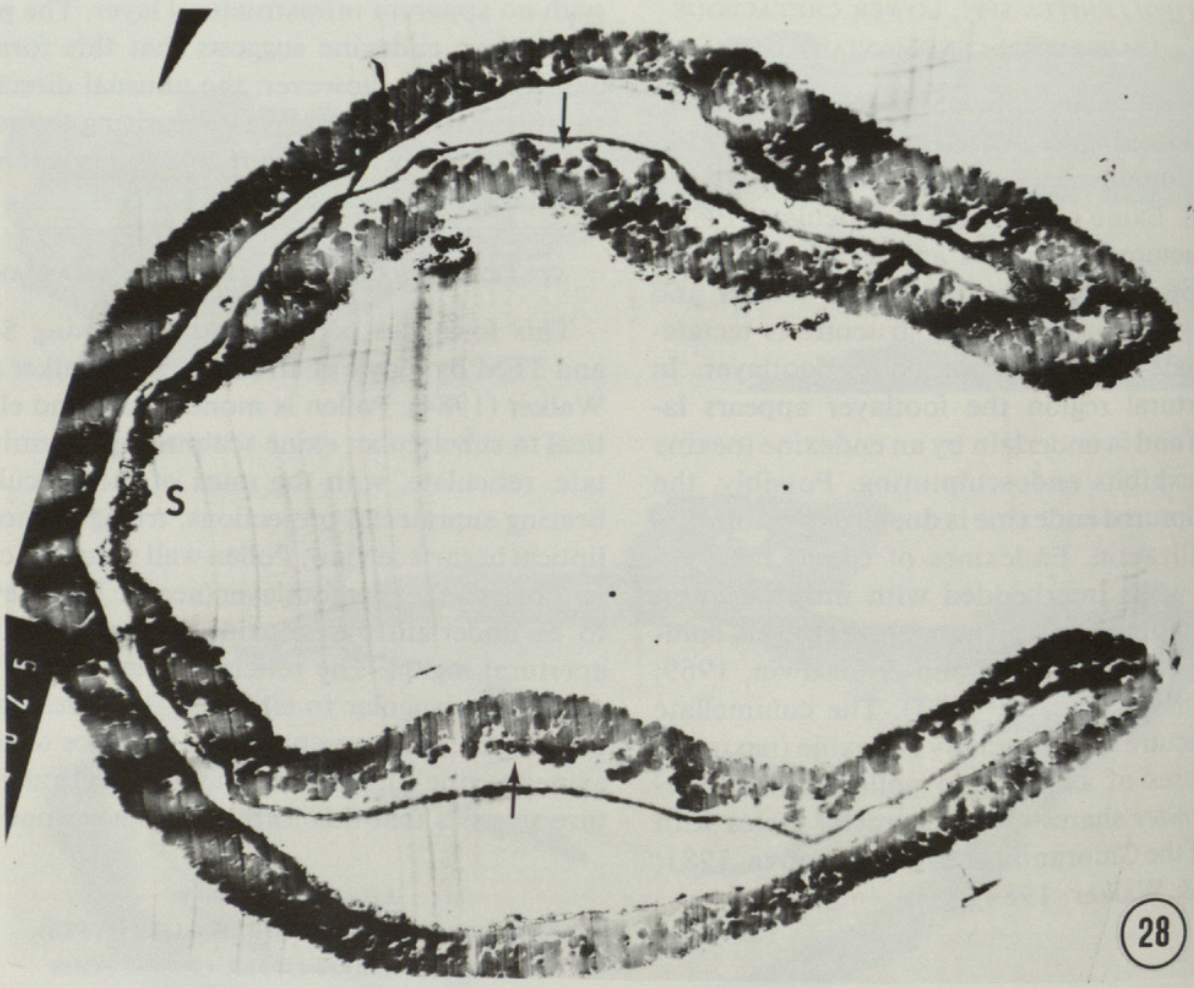
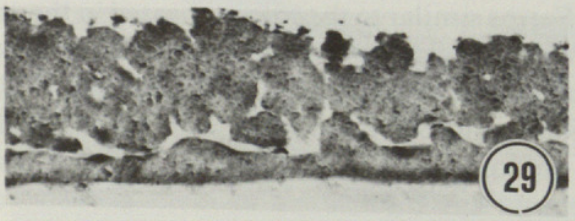
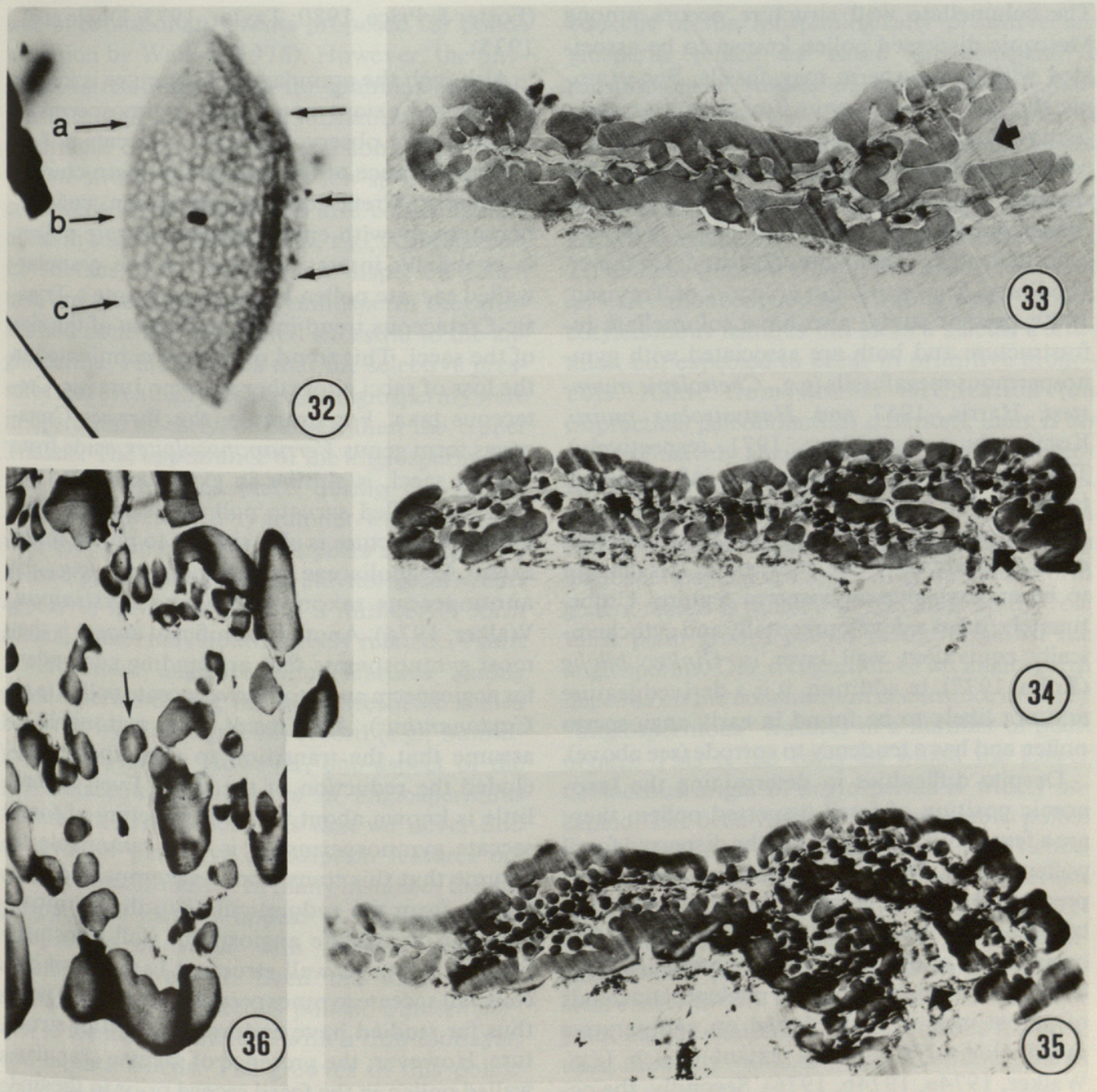
FIGURES 23–27. Transmission electron micrograph of fossil saccate pollen.—23. Bisaccate grain from the Triassic Chinle Fm. (same grain pictured in Fig. 10). Transmission electron micrograph of the corpus showing thin footlayer (nexine 1), granular infrastructure and thin tectum, ×11,600.—24. *Granabivesiculites inchoatus,* same grain pictured in Figure 13, transmission electron micrograph showing thin non-lamellated footlayer (nexine 1), granular infrastructural layer and thick occasionally perforate tectum. Note the sacci do not result from a simple separation of the footlayer and the outer wall layers, ×6,060.—25. *G. inchoatus,* same grain pictured in Figures 13 and 24. Transmission electron micrograph showing details of the wall structure, note that some elements in the granular infrastructural layer appear columellate, ×24,150.—26. *Granabivesiculites* sp., same grain pictured in Figures 14 and 27. Transmission electron micrograph showing pollen wall structure in the nonapertural region, ×24,150.—27. *Granabivesiculites* sp., same grain pictured in Figures 14 and 26. Transmission electron micrograph showing a sac (arrow) which results from a separation of the footlayer (nexine 1) and the outer portion of the wall, and flanks the sulcus (S), ×12,500.





FIGURES 28–31. Transmission electron micrograph of fossil saccate pollen.—28. Transmission electron micrograph of vestigial saccate pollen grain (same grain pictured in Fig. 16), showing sulcus, separation of the footlayer (nexine 1), and outer wall layers (arrows) resulting in the sac and the granular infrastructure, ×7,000.—29. *Punctamultivesiculites inchoatus,* same grain pictured in Figure 15, transmission electron micrograph showing details of the wall structure; a thin inner non-lamellated footlayer (nexine 1), granular infrastructure, and outer tectum with supratectal scabrae, ×14,200.—30. *P. inchoatus,* same grain pictured in Figures 15 and 29, transmission electron micrograph showing wall structure of the pustule-like sacci, note it is not a simple separation of the footlayer and the outer layers of the exine, but is constructed of exinal material, ×11,600.—31. *Verrumonocolpites conspicuus,* same grain is pictured in Figure 18, transmission electron micrograph showing wall structure; thick footlayer (nexine 1), which is underlain by a thin, ragged lamellated layer (possibly endexine), granular infrastructural layer and thick tectum, ×29,000.



FIGURES 32–35. 32. Monocotyledonoid pollen grain from the Cenomanian Dakota Fm. of Kansas. Note the reticulum becomes finer toward the polar areas and appears to be monosulcate, ×400.—33–35. Transmission electron micrograph of serial sections of the same grain in Figure 32. The wall structure consists of a very thin footlayer, a columellate layer, and a relatively thick tectum. Note that in the area where there is presumably a sulcus (arrows) there is no modification of the exine, thus is inaperturate, ×3,600.—36. Transmission electron micrograph of the same grain pictured in Figure 32. Tangential section showing that the tectum is underlain by isolated islands of sporopollenin (arrows), columellae, ×10,600.

pollen grain (Fig. 32), a characteristic of some monocotyledonous pollen. Pollen wall structure consists of a columellate infrastructure and a tectum (Figs. 33–36). The columellae are not fused to the thin footlayer, a feature observed in some alismatidean taxa. This form exhibits many monocotyledonous features, however, the lack of a sulcus makes the combination of features observed in this taxon unique among primitive monocotyledons.

DISCUSSION

It has already been demonstrated that, based on neontological data, the only exclusive angiosperm pollen feature is the columellate infrastructure. Wall structure of fossil-dispersed pollen, however, indicates that the clear demarcation in pollen wall structure between extant gymnosperms and angiosperms based on this criterion doesn't exist among the Mesozoic taxa.

The columellate wall structure occurs among Mesozoic dispersed pollen known to be associated with gymnosperm megafossils. For example, the Triassic form genus *Equisetoporites chinleana* clearly exhibits the angiospermous columellate infrastructure. This pollen type is associated with the gymnosperm fructification *Masculostrobus clathratus* (Ash, 1972). Two other form genera, *Classopollis* (Pettitt & Chaloner, 1964) and *Eucommiidites* (*E.* sp. 1 of Trevisan, 1980; present study) also have columellate infrastructure and both are associated with gymnospermous megafossils (e.g., *Cheirolepis muensteri,* Harris, 1957 and *Hastystrobus muirii,* Konijnenburg-van Cittert, 1971, respectively). Thus, the use of the columellate infrastructure to determine taxonomic affinities of fossil-dispersed pollen breaks down when the dimension of time is involved. Endexine (nexine 2) is thought to be an exclusive angiosperm feature. Unfortunately, it has a developmentally and cytochemically equivalent wall layer in *Ginkgo biloba* (Rohn, 1977), in addition, it is a derived feature and not likely to be found in early angiosperm pollen and has a tendency to corrode (see above).

Despite difficulties in determining the taxonomic position of fossil-dispersed pollen, there are a few significant aspects of the dispersed fossil pollen record. First, the temporal occurrences of presumably primitive pollen wall characteristics based on neontological studies, precede the first occurrences of derived wall characteristics. This lends support to the proposed phylogenetic trends of pollen wall structure based on comparative morphological studies of extant pollen (e.g., Walker, 1974a, 1974b, 1976). Secondly, the occurrences of angiosperm wall structural and apertural features prior to the alleged Lower Cretaceous origin of the angiosperms, suggests the selective pressures important to the derivation of angiospermous pollen features may also have acted on earlier Mesozoic gymnosperms.

Comparative morphological studies of extant pollen have shown the granular or atectate wall structure to be most primitive (Walker, 1976). The first occurrence of this wall structural type is in the Permian and is exemplified by the form genera *Praecolpatites* and *Marsupipollenites* (Foster & Price, 1982) and the early Mesozoic genera *Monosulcites* and *Eucommiidites* (*E.* sp. 2 of Trevisan, 1980; Doyle et al., 1975). All these genera are presumably gymnosperms or have been associated with gymnosperm fructifications (Foster & Price, 1980; Taylor, 1973; Doyle et al., 1975).

Although the granular wall structure is known from some extant nonsaccate gymnosperms, it has not been observed in extant saccate pollen. The appearance of the granular wall structure in Triassic to Cretaceous saccate pollen, contemporaneously with endoreticulate saccate pollen, is especially interesting. Among the granular-walled saccate pollen types we also note a Triassic-Cretaceous trend in the reduction of the size of the sacci. This trend may have culminated in the loss of sacci altogether in some Jurassic/Cretaceous taxa. For example, the Jurassic/Cretaceous form genus *Verrumonocolpites,* aside from lacking sacci, is similar in every respect to the granular walled saccate pollen. Its morphology and wall structure is also similar to pollen in the extant Magnoliaceae and Annonaceae (e.g., the annonaceous taxon *Miscogyne ellistianum,* Walker, 1976). Another significant aspect is that most gymnosperms that are leading contenders for angiosperm ancestors have saccate pollen (e.g., *Caytonanthus*). As a result, it is reasonable to assume that the transition to angiospermy included the reduction of the sacci. Even though little is known about the wall structure of fossil saccate gymnosperms, it is also reasonable to assume that this transition is accompanied by a change from the endoreticulate to the primitive granular or atectate angiosperm wall structure. Such a change in wall structure is assumed because all saccate gymnosperms (extant and fossil) thus far studied have endoreticulate wall structure. However, the presence of saccate granular-walled pollen in the fossil record prior to the first unequivocal angiosperm pollen makes the saccate-nonsaccate transition conceptually more palatable. Thus, by the Permo-Triassic, the granular infrastructure is well established in a number of morphologically diverse, dispersed pollen genera that persisted through the Jurassic and Lower Cretaceous.

The next major palynological event is the Upper Triassic appearance of the columellate infrastructure in the form genera *Equisetoporites* and *Classopollis* (Chaloner, 1976). The appearance of the columellate structure post-dates the first appearance of the granular types. Although the taxonomic relationship of these taxa to the earlier occurring granular-walled dispersed pollen is unknown, the latter temporal occurrence of the columellate infrastructure parallels the progres-

sion of evolutionary events proposed for pollen evolution by Walker (1976). However, the phylogenetic relationships of the granular and columellate wall structure is substantiated by the occurrence of the granular and somewhat columellate structures found in a few species of *Eucommiidites* (such structures also coincidentally occur in some extant families, e.g., Annonaceae, Le Thomas, 1981). All of these dispersed pollen taxa are associated with gymnosperm megafossils and none are considered ancestral to the angiosperms. This suggests that the selective pressures that eventually resulted in angiospermy were in operation as early, or earlier, than the Upper Triassic. The appearance of the angiosperm-like wall structure takes place during the Upper Permian (represented by granular-walled pollen), then the columellate type appears subsequently in the Upper Triassic. These palynological events appear to have occurred in a number of form genera, which may not be closely related. A shift toward more angiospermous features among gymnosperms during the early Mesozoic is also born out by the megafossil record (e.g., *Sanmiguelia, Caytonia*). However, one aspect of the pre-Cretaceous occurrences of angiospermous features in gymnosperms is that we never find an array of primitive angiosperm features occurring concomitantly. In many instances the angiospermous features appear to be isolated developments or occur with features that are considered advanced. Even the most angiosperm-like pre-Cretaceous pollen, *Equisetoporites,* is tectate-columellate with a thin footlayer, and lacks a sulcus. The grooves in this pollen could be interpreted as apertures, in which case it would be called multiaperturate, but in either case these characteristics are thought to be indicative of the more advanced columellate angiosperm pollen and would not be expected to occur in the first tectate-columellate fossil pollen. The pre-Cretaceous taxon *Classopollis* also exhibits a columellate infrastructure but has an unusual apertural arrangement and other exinal elaborations not known in extant angiosperm pollen. It is not until we encounter the Lower Cretaceous forms, i.e., *Retimonocolpites, Clavatipollenites,* and *Liliacidites,* that we see the greatest number of coincident angiosperm features occurring in combinations expected of angiosperm pollen. But, even among these earliest angiosperm pollen grains, there are notable differences between their morphology and our concept of the morphologically primitive angiosperm pollen as based on comparative morphological studies of extant pollen. *Retimonocolpites peroreticulatus,* for example, is similar to many reticulate, monosulcate angiosperm pollen types but lacks a columellate infrastructure, a combination of characteristics unknown in extant angiosperms (Doyle et al., 1975). *Liliacidites* (present study), thought to represent an early monocotyledon, exhibits some monocotyledonous features but lacks a sulcus, a situation not expected to occur in primitive monocots. Aside from double fertilization (an impractical paleobotanical criterion), there is no one exclusively angiosperm morphological feature, and the scattered occurrences of pre-Cretaceous angiosperm features (and in some cases features that are presumably advanced among angiosperms) in a few apparently unrelated form genera makes is difficult to speculate on the role these plant groups played in the origin of the angiosperms. Our recognition of an angiosperm depends on the concomitant occurrence of many "angiospermous" features in a number of plant organs. This is the basis on which the Lower Cretaceous origin of angiosperms is widely accepted. The occurrence of angiospermous pollen and leaves, and their subsequent persistence, tends to support the Lower Cretaceous origin (Doyle & Hickey, 1976). The acceptance of pre-Cretaceous occurrences of plant organs with angiospermous features (e.g., *Sanmiguelia, Equisetoporites*) awaits their association with other plant organs exhibiting angiospermous features, thus, mutually validating their identification as an angiosperm.

The broad definition of angiospermy that is currently adhered to involves characteristics of different plant organs that undoubtedly were subject to a diverse array of selective pressures. These selective pressures, however, were not necessarily contemporaneous in effect, or interrelated. Thus the simultaneous (in terms of geologic time) acquisition of the wide range of features we use to define angiospermy seems unlikely. It is more likely that angiospermy was achieved by the cumulative acquisition of angiospermous features over an extended period of time (cf. Faegri, 1980), culminating in a combination of characteristics we currently use to define angiospermy. As Stebbins (1981) has suggested, the initial radiation and continuing success of angiosperms is due to the cumulative effect of a number of indepen-

dently derived advantageous angiosperm features that involve pollination biology; seed development, morphology and dispersal; vegetative anatomy and morphology; and biochemistry. Thus, our reluctance to seriously consider pre-Cretaceous plants with angiosperm features, as angiosperms, seems more related to our broad definition of angiospermy and in some respects to our deep-seated hypothetical notions that have prevailed in past years, than to major inadequacies of the fossil record. Undoubtedly, further palynological investigations of dispersed pollen will lead us to the most likely angiosperm ancestor(s) and possibly into pre-Cretaceous sediments, but our own definition of angiospermy seems to relegate the further elucidation of angiosperm origins to a concerted effort by paleobotanists and palynologists.

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