Reproductive Structures of Cretaceous Platanaceae

By ELSE MARIE FRIIS,
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1742

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Abstract

Fossil platanoid reproductive structures are described from Lower and Upper Cretaceous strata of Europe and North America. The Lower Cretaceous fossils were collected from the Patapsco Formation at the West Brothers locality, Maryland, U.S.A. and provide the earliest floral evidence of the Platanaceae. The Upper Cretaceous fossils were collected from the Black Creek Formation at the Neuse River Cut-Off locality, North Carolina, U.S.A. and from near Åsen, Scania, Sweden. Staminate as well as pistillate organs were present in all three of the localities.

Staminate inflorescences are referred to the extinct genus *Platananthus* Manchester. They are globose heads composed of numerous densely packed flowers with a pentamerous androecium surrounded by a prominent perianth. Anthers are elongate, borne on short filaments and have peltate to conical extensions of the connective. Pollen grains are small to very small, tricolpate and reticulate. *Platananthus* is distinguished from modern *Platanus* L. mainly by the pentamerous androecium and the small pollen size. Three distinct species *Platananthus potomacensis* (West Brothers locality), *P. hueberi* (Neuse River locality) and *P. scanicus* (Åsen locality), are established. A fourth type of platanoid staminate organs is described from the Åsen locality based on dispersed stamens.

Pistillate inflorescences are referred to *Platanocarpus* gen.nov. They are globose heads composed of numerous closely packed flowers with an undifferentiated perianth and an apocarpous gynoecium. Carpels have a poorly developed style and are without trichomes. Pistillate flowers from the Lower Cretaceous locality have a distinctly pentamerous gynoecium but the carpel arrangement is less clear in two of the three pistillate inflorescences from the Upper Cretaceous localities. *Platanocarpus* is distinguished from modern *Platanus* mainly by the poorly developed style and the absence of trichomes on the carpels. Three distinct species are recognised, *Platanocarpus marylandensis* (West Brothers locality), *P. carolinensis* (Neuse River locality) and *P.* sp. (Åsen locality). A fourth type of platanoid organ, with a distinctly pentamerous gynoecium is described from the Åsen locality based on a single, charcoalified fragment.

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Contents

This paper is dedicated to Professor
Ove Arbo Høeg
in the year of his 90th birthday.

Introduction

The Platanaceae are a small and well circumscribed family of temperate to tropical trees with an extensive fossil record during the Cretaceous and Tertiary. Today the family contains a single genus, *Platanus* L., with approximately nine species (Ernst, 1963) divided between two sub-genera (Leroy, 1982). Sub-genus *Platanus* includes the familiar plane tree of Europe and the eastern Mediterranean (*P. occidentalis* L.), the sycamore of eastern North America (*P. orientalis* L.) and approximately six other species in the southwestern U.S.A. and Mexico. Sub-genus *Castaneophyllum* Leroy includes only *Platanus kerrii* Gagnepain, an unusual species with unlobed elliptical leaves that is known only from a restricted area of southeastern Asia.

The Platanaceae first appear in the fossil record during the mid-Cretaceous in association with a major radiation of angiosperms in general and of non-magnoliid dicotyledons in particular. Tricolpate or tricolpate-derived pollen diagnostic of the dicotyledonous sub-classes Ranunculidae, Hamamelididae, Caryophylliidae, Dilleniidae, Rosidae and Asteridae is first recorded in low palaeolatitudes (Northern Gondwana; Brenner, 1976) at around the Barremian-Aptian boundary (Hickey & Doyle, 1977; Crane, 1987). By the late Albian and early Cenomanian, at an early stage in the radiation of the higher dicotyledons, leaves and infructescences resembling those of extant *Platanus* are both geographically widespread and locally abundant (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Dilcher, 1979). This platanoid material currently provides some of the earliest unequivocal evidence of the sub-class Hamamelididae. In addition, some forms of these early palmately-lobed platanoid leaves exhibit similar characters of venation and cuticular structure to pinnately-lobed or compound foliage of the *Sapindopsis*-type which have been interpreted as early evidence of the sub-class Rosidae (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Upchurch, 1984). The extent of these foliar similarities raises the possibility that Cretaceous Platanaceae may have played an important role in the initial divergence of the Hamamelididae and Rosidae, and this is further supported by possible similarities in the reproductive structures of platanoid and *Sapindopsis* plants (Crane, Friis & Pedersen 1986; Crane, in press).

In the Late Cretaceous and Tertiary the Platanaceae are represented by a wide variety of leaf morphologies (Crane, in press), but few of the associated reproductive structures have been studied in detail. This has precluded a clear understanding of the extinct diversity in the group and the possible role of the Platanaceae in the early radiation of higher dicotyledons. In this paper we describe eight kinds of Cretaceous platanaceous reproductive structures including four kinds of staminate and four kinds of pistillate organs from two localities in North America and one locality in Europe. The fossil material provides direct evidence of the structure of Cretaceous platanoid flowers and clarifies the range of floral form in this important angiosperm group. It suggests that some early Platanaceae may have been insect pollinated and provides information critical to establishing the relationships of the family to other dicotyledons.

Material and Methods

The fossil material described in this paper was collected from three different Cretaceous localities, one from the Lower Cretaceous (Maryland, USA, p. 7) and two from the Upper Cretaceous (North Carolina, USA, p. 8; Scania, Sweden, p. 8), Tabel I. The material includes both hand specimens and specimens recovered by washing bulk samples over a 125 μm sieve. The material was cleaned by removing adhering mineral matrix with hydrofluoric and hydrochloric acids. After acid treatment the fossils were thoroughly washed in water and dried in air. Specimens selected for scanning electron microscopy were mounted on stubs and coated with about 1000 Å of gold. Specimens were examined with Cambridge S-2 and Jeol JSM 840 scanning electron microscopes.

Specimens for anatomical or ultrastructural examination were embedded in Epon following dehydration in an ethanol-propylene oxide series and sectioned on an LKB Ultratome III ultramicrotome. Anatomical sections are 3 μm thick and were cut with a glass knife. Sections for pollen wall ultrastructure are 500-700 Å thick and were cut with a diamond knife. Ultrastructure sections were post-stained with uranyl acetate and lead citrate and examined using a Jeol JEM-100S transmission electron microscope.

Measurements were taken with micrometers mounted in compound and stereomicroscopes and directly from scanning and transmission electron micrographs. Pollen grains were measured mounted in glycerine with no additional chemical preparation. Pollen grains prepared by standard maceration in concentrated nitric acid and potassium hydroxide or ammonia tended to give slightly larger measurements than unmacerated grains.

Maryland, U.S.A. (Lower Cretaceous)

The plant fossil material from Maryland includes both hand specimens and specimens recovered by sieving from bulk samples of a grey clay collected at the West Brothers locality, Prince Georges County, Maryland (38° 55'N, 76° 55'W). Exposures at this locality are part of the Patapsco Formation (Potomac Group) and the palynoflora suggests a late Albian age, corresponding to Sub-Zone IIB in the palynological zonation established by Brenner (Brenner, 1963; Doyle, 1969; Doyle & Hickey, 1976).

The section at the West Brothers locality comprises about 10 m of predominantly fluvial clays, silts and cross-bedded sands (Hickey, 1984). The plant bearing sediments are lenticular and have been interpreted as the fill of an abandoned channel (Hickey, 1984). Plant fossils are preserved as lignitic compressions and three-dimensionally as charcoal.

TABLE I. Reproductive structures of Cretaceous Platanaceae from Maryland, North Carolina and Scania.

Age	Locality	Staminate organs	Pistillate organs
Santonian-Campanian	Scania	*Platananthus scanicus*	*Platanocarpus* sp.
Santonian-Campanian	Scania	Unassign. dispersed stamens	Unassign. infructescence
Santonian-Campanian	North Carolina	*Platananthus hueberi*	*Platanocarpus carolinensis*
Albian	Maryland	*Platananthus potomacensis*	*Platanocarpus marylandensis*

The pollen flora from the West Brothers locality is dominated by angiosperm pollen (Brenner, 1963; Doyle, 1969; Doyle, Van Campo & Lugardon, 1975; Doyle & Hickey, 1976). The macroflora is dominated by pinnately lobed or compound leaves of the *Sapindopsis* type, but rare platanoid and other leaves have been recorded (Upchurch, 1984; personal communication). The flora obtained by sieving includes fragments of angiosperm and gymnosperm wood, conifer cones, seeds and shoots, and a variety of angiosperm fruits, seeds and other reproductive structures (Crane et al., 1986). The diversity of angiosperm reproductive structures is much higher than that of associated leaves and probably reflects the difference between transported and locally derived elements in the flora. Among the taxa identified are stamens containing pollen of the *Retitricolpites vermimurus* type, a chloranthoid androecium (Friis, Crane & Pedersen, 1986; Crane et al., in press), and the two platanoid species described in detail here, *Platananthus potomacensis* sp. nov. (p. 10) and *Platanocarpus marylandensis* sp. nov. (p. 16). The specimens and preparations from the West Brothers locality used in this study are deposited in the palaeobotanical collections of the Field Museum of Natural History, Chicago, USA (PP).

North Carolina, U.S.A. (Upper Cretaceous)

The plant fossil material from North Carolina was recovered by sieving bulk samples provided by Dr. F. Hueber, National Museum of Natural History, Smithsonian Institution, USA. The samples were collected from the Neuse River Cut-Off, southwest of Goldsboro, Wayne County, North Carolina (35° 21' N, 78° 1'W). The plant bearing unit is part of the non-marine Black Creek Formation considered to be of Santonian or Campanian age (Hazel et al., 1977; F. Hueber, personal communication).

Exposures of the Black Creek Formation in the vicinity of the Neuse River Cut-Off consist predominantly of a variable sequence of presumed fluvial fine sands, silts and clays. Plant material, including leaves, large logs and other macrofossils are common in the sequence, and the samples examined in this study consisted predominantly of allochthonous lignitic plant debris with subordinate sandy layers. The plant fossils are usually lignified, and often more or less compressed with some pyritization. Plant fossil material preserved as charcoal is also present but much less common.

The macroflora from the Black Creek Formation consists of ferns, conifers and a variety of angiosperm leaves including those of palms (Berry, 1914). The flora obtained by sieving from the Neuse River locality includes various megaspores, fern sporangia, conifer twigs, and a diverse assemblage of flowers, fruits and seeds (Friis, 1985a). Among the taxa identified are seeds of *Spirematospermum,* Zingiberaceae (Friis, in press), conifer shoots of *Androvettia* (Hueber, personal communication; Raubeson & Gensel, 1986a) *Brachyphyllum, Moriconia, Sequoia* and *Pinus* (Raubeson & Gensel, 1986b) and the two platanoid species described in detail here, *Platananthus hueberi* sp. nov. (p. 12) and *Platanocarpus carolinensis* sp. nov. (p. 17). The specimens and preparations from the Neuse River locality used in this study are deposited in the palaeobotanical collections of the National Museum of Natural History – Smithsonian Institution, Washington, D.C., USA (USNM).

Scania, Sweden (Upper Cretaceous)

The plant fossil material from southern Sweden was recovered by sieving from bulk samples of unconsolidated sands and clays collected in the Höganäs AB kaolin quarry at Åsen in the Kristianstad Basin, Scania (56°9'N, 14°30'E). These sediments are dated as Upper Santonian or Lower Campanian based on palaeontological and palaeomagnetic evidence (Friis & Skarby, 1981; Mörner, 1983; Skarby, 1986).

The plant bearing sequence at Åsen comprises about 20 m of lacustrine and fluviatile sediments separated into two units by a marked weathering horizon. The predominantly lacustrine lower unit consists of clay gyttja and finely laminated clays, silts and sands. The predominantly fluvial upper unit consists mainly of laminated or cross-bedded sands. Approximately 200 bulk samples have been examined from different parts of the Åsen sequence, and plant fossils preserved both as lignite and as charcoal are abundant throughout. There are, however, significant differences between the fossil floras preserved in the upper and lower units. The platanoid remains described here are exclusively from the lower unit where they typically occur in association with small leaf fragments of ferns, isoetalean megaspores (*Tenellisporites*), abundant twigs and cones of taxodiaceous conifers, flowers, fruits and seeds of *Actinocalyx bohrii* Friis (1985b) and several unidentified angiosperm flowers, fruits and seeds.

The pollen flora from the Åsen sequence has been described by Ross (1949) and Skarby (1964, 1968, 1974, 1978, 1986). In addition to fossils mentioned above the larger plant remains include several kinds of megaspores, pinaceous wood (Nykvist, 1957) several kinds of juglandalean flowers (Friis, 1983), saxifragalean flowers (Friis & Skarby, 1982), hamamelidaceous flowers (Friis, 1985a) and chloranthoid androecia (Friis et al., 1986; Crane et al., in press). The platanoid remains described in detail in this paper comprise two different kinds of staminate fossils, *Platananthus scanicus* sp. nov. (p. 13) and unassigned dispersed stamens (p. 14); and two kind of pistillate heads, *Platanocarpus* sp. and one unassigned infructescence (p. 18).

The specimens and preparations from Scania used in the present study are deposited in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm, Sweden (S).

Systematics

Staminate inflorescences

Platananthus Manchester emend.

Generic diagnosis: Globose staminate inflorescences composed of a spheroidal receptacular core surrounded by numerous closely packed staminate flowers. Each flower consists of five stamens surrounded by prominent tepals. Stamens have elongate anthers on short filaments with peltate to conical extensions of the connectives. Pollen spheroidal to prolate, small to very small, tricolpate reticulate.

Type species: Platananthus synandrus Manchester

Remarks on the genus: This genus was established by Manchester (1986) to accommodate fossil platanaceous staminate inflorescences "differing from *Platanus* in number of stamens, size of anthers, small size of pollen, and a well-developed perianth" (Manchester, 1986, p. 212). We have emended Manchester's combined generic and specific diagnosis slightly so that the genus may serve as a useful repository for other fossil staminate platanoid inflorescences. Only three changes have been made, to remove the dimensions given for inflorescence diameter and pollen size, and to modify the treatment of stamen morphology. The first two changes merely permit more flexibility in using the genus to include specimens with slightly smaller or larger dimensions. The third change concerns the shape of the apical expansion of the connective beyond the pollen sacs. In the absence of a specific diagnosis of *P. synandrus* we regard the conical, elongated connective as one of the diagnostic features of that species and therefore exclude the character from our emended diagnosis of the genus. Our circumscription of *Platananthus* will accommodate fossils in which the apical projection of the connective is shorter than in *P. synandrus* and more like that in the stamens of extant *Platanus*.

Platananthus potomacensis Friis, Crane & Pedersen sp. nov.

Plate 1, figs 1-8; Plate 2, figs 1-6.

Derivation of name: From the Potomac River that runs close to where the material was collected.

Specific diagnosis: Staminate flowers in dense inflorescences. Flower surrounded by elongate, spatulate tepals, about the same length as the pollen sacs. Apical extension of connective peltate and slightly elongate not clearly delimited at the base; typically one third to one fourth the length of the pollen sacs, slightly projecting beyond the tepals. Pollen grains small to very small, prolate and finely reticulate.

Dimensions: Length of stamen without filament: 0.5-0.6 mm; length of pollen sac: 0.35-0.45 mm; length of apical connective: 0.1-0.2 mm; breadth of stamen: 0.15-0.25 mm. Length of pollen: 8.5-12 μm; equatorial diameter of pollen: 5-8 μm.

Holotype: Plate 1, fig. 1 (PP 34569).

Type locality: West Brothers clay pit, Maryland, USA.

Type stratum: Patapsco Formation (Potomac Group).

Age: Early Cretaceous (Late Albian).

Material: Three small fragments of inflorescences and possibly four immature, complete inflorescences. All inflorescences are preserved as lignite. Specimens PP 34569-34575.

Description and remarks on the species: The species is represented by a few inflorescence fragments each comprising several wedge-shaped and closely spaced staminate flowers (Pl. 1, figs 1, 4). The arrangement and shape of the flowers indicate that they were borne in a dense inflorescence, probably a spherical head. The individual flowers have several spatulate tepals surrounding the androecium (Pl. 1, fig. 4). The number and arrangement of the tepals has not been established. The androecium consists of five stamens (Pl. 1, fig. 2). The anthers are 0.5-

0.6 mm long; filaments are evidently very short but have not been observed. The anthers are tetrasporangiate with four elongate pollen sacs (Pl. 1, fig. 6), 0.35-0.45 mm long and 0.15-0.25 mm broad, and with a slightly domed, peltate, apical extension of the connective that projects beyond the tepals (Pl. 1, figs 4-5). The apical extension of the connective is only weakly delimited from the anther thecae. The connective between the pollen sacs is well-developed (Pl. 1, fig. 6). The apical connective extension is 0.1-0.2 mm long and typically one third to one fourth the length of the pollen sacs (ratio length connective/length pollen sac: 0.2-0.4). Dehiscence is apparently valvate with longitudinal slits (Pl. 1, fig. 5) and short transverse slits at the base and apex.

The outer epidermis of the anthers consists of slightly elongate cells, arranged in longitudinal rows, while the epidermis of the connective has polygonal and isodiametric cell outlines, about 0.01 mm in diameter. Trichomes and papillae have not been observed on any part of the flower or inflorescences.

Pollen occurs abundantly in the anthers (Pl. 1, fig. 3). The pollen grains are tricolpate and prolate with an inter-semi-angular to circular equatorial outline, 8.5(9.7)12 μm long and 5(6.9)8 μm in equatorial diameter. The colpi are elongate, lenticular, about 3.5-5 μm long with a granular aperture sculpture (Pl. 2, fig. 1). The exine sculpturing is reticulate with isodiametric to elongate lumina. The lumina show considerable variation in size from about 0.1 μm to about 0.6 μm in diameter with a gradual decrease in size towards the apertures (Pl. 2, figs 1-2). Muri are smooth with rounded to triangular profile, about 0.3 μm wide (Pl. 2, fig. 3).

The pollen wall in non-apertural regions is about 0.8 μm thick, tectate and columellate (Pl. 2, figs 4-5). The endexine is thin, about 0.2 μm, but thickens towards the apertures to about 0.7 μm. It is mostly homogenous, but the inner part is finely granular around the apertures (Pl. 2, figs 6-7). The ectexine is about 0.6 μm thick in non-apertural regions with a moderately thick homogenous footlayer, about 0.3 μm. The columellae are simple about 0.1 μm high and the tectum reticulate-perforate, about 0.2 μm thick.

The pollen grains recovered from the anthers of *Platananthus potomacensis* are similar to dispersed pollen of *Tricolpites minutus* (Brenner) Dettmann which is characterized by its very small size (polar axis 9-13 μm) and lumina that become finer toward the colpi margins (Brenner, 1963; Dettmann, 1973; Doyle, Van Campo & Lugardon, 1975). Similar pollen grains have also been recovered in clumps adhering to the surface of the female flowers of *Platanocarpus marylandensis* (Pl. 9, figs 7-8).

Three sessile inflorescences composed of about 50 densely packed flowers have been found associated with *Platananthus potomacensis* (Pl. 1, figs 7-8). Each flower has five central reproductive parts surrounded by spatulate tepals. The inflorescences are about 2 mm in diameter. The individual parts are slightly smaller than those of *P. potomacensis,* but similarities in epidermal structure and general organization strongly suggest that these inflorescences may be immature specimens of *P. potomacensis.* Maceration of individual parts from the inflorescences has, however, failed to yield any pollen and we therefore hesitate to assign this material to the same species. In addition to *P. potomacensis,* two other taxa from the West Brothers locality are known to have inflorescences consisting of flowers with reproductive parts in fives, one is the pistillate *Platanocarpus marylandensis* and the other is an undescribed form possibly related to extant Rosidae (Crane et al., 1986). In these two taxa the flowers are also borne in spherical heads and the possibility that the immature inflorescences represent one of these taxa cannot be excluded.

Platananthus potomacensis is the earliest member of the genus. It is distinguished from all younger species of *Platananthus* by its smaller size and by the weakly defined apical extension of the connective. The pollen grains are also distinguished from those of younger species by their smaller size and the form of the reticulum with lumina decreasing in size toward the apertures (see also Table II).

Platananthus hueberi Friis, Crane & Pedersen sp. nov.
Plate 3, figs 1-7; Plate 4, figs 1-6.

Derivation of name: In honour of Dr. Francis M. Hueber who kindly provided the Neuse River material.

Specific diagnosis: Staminate inflorescences sessile, composed of about 50 closely spaced flowers. Flowers surrounded by membranous tepals, about the same length as the stamens. Apical extension of connective clearly delimited at the base, peltate; less than one fifth the length of the pollen sacs, not projecting beyond the tepals. Papillae arise from the contiguous surfaces of adjacent anthers just below the apical connective. Pollen grains small, prolate and coarsely reticulate.

Dimensions: Diameter of inflorescence: 1.9-3.6 mm. Length of stamen without filament: 0.55-0.9 mm; length of filament: about 0.1 mm; length of pollen sac: 0.45-0.8 mm; length of apical connective: 0.05-0.15 mm; breadth of stamen: 0.2-0.3 mm. Length of pollen: 13-15 μm; equatorial diameter of pollen: 9-12 μm.

Holotype: Plate 3, fig. 1 (USNM 401637).

Type stratum: Black Creek Formation.

Type locality: Neuse River Cut-off, North Carolina, U.S.A.

Age: Late Cretaceous (Santonian or Campanian).

Material: About 25 complete inflorescences and 75 fragments of inflorescences. All inflorescences are preserved as lignite. Specimens USNM 401637-401641.

Description and remarks on the species: The staminate inflorescences are much compressed, circular or slightly elongate in outline, 1.9(3.2)3.6 mm in maximum diameter (Pl. 3; figs 1-2). The inflorescences are all single, but several have remnants of the reproductive axis, about 1.5 mm wide, clearly indicating sessile attachment. The central receptacle is about 0.8 mm, in diameter and bears about 50 closely spaced, wedge-shaped flowers (Pl. 3, fig. 3). Each flower is composed of five stamens surrounded by several membranous tepals (Pl. 3, fig. 4). The tepals are elongate and about the same length as the stamens. Their number and arrangement in the flower is uncertain.

Stamens have not been recovered dispersed and the compression of the inflorescences precludes detailed study of their morphology and structure. They are apparently basifixed, 0.55-0.8 mm long (excluding the filament) and 0.18(0.23)0.3 mm wide, borne on short filaments, about 0.15 mm long. The anthers are tetrasporangiate with two pairs of elongate pollen sacs, 0.45-0.8 mm long, and a peltate apical extension of the connective (Pl. 3, figs 4, 5). The connective is usually distinctly flattened, about 0.05-0.15 mm long, less than one fifth the length of the pollen sac. Dehiscence is apparently by longitudinal slits.

The endothecium is composed of polygonal and isodiametric cells, about 0.02 mm in diameter with thickened inner walls. The outer epidermis of the pollen sacs has elongate cells arranged in longitudinal rows. Groups of papillae arise from the surface of adjacent anthers close to their apex and immediately below the apical extension of the connective (Pl. 3, figs 5-6). The papillae are clavate, about 0.025 mm long, 0.006 mm broad at their base and have a wrinkled surface (Pl. 3, fig. 6). The epidermis of the apical connective has polygonal and isodiametric cells, about 0.01 mm in diameter, also with a wrinkled surface (Pl. 3, fig. 7).

Pollen grains are abundant in the anthers. They are small, tricolpate and prolate with a circular to inter-semi-angular equatorial outline (Pl. 4, figs 1, 3-4), 13(13.6)15 μm long and 9(10.7)12 μm in equatorial diameter (pollen from anthers treated with hydrofluoric and hydrochloric acid, as well as pollen from macerated anthers fall within this size range). The colpi are lenticular, about 7-10 μm long with a granular sculpture (Pl. 4, fig. 1). The exine sculpturing is coarsely reticulate with polygonal to elongate lumina, typically 1-1.5 μm in maximum diameter, and with smooth muri, about 0.3 mm wide, which are triangular in crosssection (Pl. 4, figs 2-6).

The pollen wall is about 1.2 μm thick, in non-apertural regions, tectate and columellate (Pl. 4, fig. 6). The endexine is laminate to granular, extremely thin, about 0.03 μm and thickens towards the apertures to about 0.6 μm (Pl. 9, fig. 5). The ectexine is homogenous composed of a footlayer, about 0.3 μm thick, simple columellae, about 0.3 μm high and a thick reticulate tectum, about 0.5 μm.

Platananthus hueberi is distinguished from other species of *Platananthus* by the presence of papillae on the surface of adjacent anthers below the apical connective and by the coarse exine sculpturing of the pollen. In *P. synandrus* from the Eocene trichomes are also present on the surface of the stamens but these are hair-like and arise from the epidermis of the connective (see p. 22).

Platananthus scanicus Friis, Crane & Pedersen sp. nov.

Plate 5, figs 1-9, Plate 6, figs 1-8.

Derivation of name: From the province of Scania, southern Sweden where the fossils were collected.

Specific diagnosis: Staminate inflorescence pedunculate, composed of about 100 closely spaced flowers. Flowers surrounded by prominent tepals. Tepals elongate and apically expanded, about the same length as the pollen sacs. Apical extension of connective clearly delimited at the base, elongate, triangular in outline; usually half to two thirds the length of the pollen sacs, projecting beyond the tepals. Pollen grains small, prolate to spherical, finely reticulate.

Dimensions: Diameter of inflorescence: 4.9.-5.8 mm. Length of stamen without filament: 1.17-2.8 mm; length of filament: 0.1-0-17 mm; length of pollen sac: 0.62-1.9 mm; length of apical connective: 0.4-1.25 mm; breadth of stamen: 0.35-0.7 mm. Length of pollen: 15-16.5 μm; equatorial diameter of pollen: 13.5-15 μm (pollen treated with HNO_3 and KOH: length: 16-18 μm; equatorial diameter: 15-16.5 μm).

Holotype: Plate 5, fig. 1 (S 100001).

Type locality: Höganäs AB quarry at Åsen, Scania, Sweden.

Type stratum: Lower unit (clay gyttja).

Age: Late Cretaceous (Late Santonian/Early Campanian).

Material: Four complete inflorescences, about 45 fragments of inflorescences and several hundred dispersed stamens. Recovered from the lower unit at Åsen, predominantly in clay gyttja (samples GI32105, GI32107-GI32108, GI32172, GI32189, GI32199). All inflorescences and most of the dispersed stamens are charcoalified. Specimens S 100001-100004, 100008-100021, 100024-100051.

Description and remarks on the species: The staminate inflorescences are much compressed, circular in outline and 4.9-5.8 mm in diameter (Pl. 5, fig. 1). They are all dispersed, but remnants of a stalk, about 1.5 mm wide and up to 2.5 mm long show that the inflorescence is penduculate (Pl. 5, figs 1, 3). The inflorescence is composed of a central receptacle, about 1.5 mm in diameter with numerous closely spaced, wedge-shaped flowers (Pl. 5, fig. 2). The number of flowers per inflorescence has not been established but is estimated to be about one hundred. Each flower has five stamens surrounded by prominent spatulate tepals that are apically expanded (Pl. 5, figs 2-5). There are at least five tepals in each flower, but neither SEM studies of the inflorescence surface nor thin sections through inflorescences have clarified the number and arrangement of perianth parts.

The stamens are basifixed and borne on a short filament that is usually missing in dispersed specimens (Pl. 5, figs 6-8). They are 1.17(1.6)2.8 mm long (without filament), 0.35(0.46)0.7 mm broad and the filament is 0.1-0.17 mm long. The anthers are tetrasporangiate with two thecae, each consisting of a pair of elongate pollen sacs, 0.62(1.02)1.9 mm long and a prominent triangular apical extension of the connective, 0.4(0.74)1.25 mm long. This apical extension projects beyond the tepals for its full length (Pl. 5, fig. 5). The length of the apical connective is typically half to two thirds the length of the pollen sacs (Pl. 5, figs 6–9). Occasionally, the length of the apical connective may exceed that of the pollen sacs (ratio length connective/length pollen sac: 0.4(0.74)1.47. Dehiscence is lateral to ventral by longitudinal slits that open along the middle of the theca between the pollen sacs (Pl. 5, figs 6-7). In one specimen transverse slits have been observed at the base and apex of the pollen sacs (Pl. 5, fig. 6). These may indicate that dehiscence was valvate as described for modern *Platanus* (Endress, 1977).

The theca wall has distinct endothecium of isodiametric and polygonal cells, about 0.025 mm in diameter with thickened anticlinal and inner periclinal walls (Pl. 6, fig. 3). The epidermis of the thecae has narrowly elongated and thin-walled cells, about 0.06 mm long and 0.01 mm wide. These cells are arranged in longitudinal rows and have a wrinkled striate surface (Pl. 6, fig. 1). The epidermis of the apical connective has polygonal and almost isodiametric cells, about 0.04 mm in diameter, also with a wrinkled surface (Pl. 6, fig. 2). Trichomes, papillae or stomata have not been observed on the epidermis of either tepals or stamens.

The anthers contain numerous small pollen grains (Pl. 5, fig. 9, Pl. 6, fig. 4). Pollen is tricolpate, prolate to spherical with circular to inter-semi-angular equatorial outline (Pl. 6, figs 4-5, 7). Grains from anthers cleaned with hydrofluoric acid and hydrochloric acid are 15(15.6)16.5 μm long and 13.5(14.5)15 μm in equatorial diameter, while grains from macerated anthers (treated further with nitric acid and potassium hydroxide) are slightly larger, 16(16.8)18 μm long and 15(16.2)16.5 μm in equatorial diameter. The colpi are lenticular and about 13-14 μm long. The exine sculpturing is finely reticulate except for the aperture sculpture which is granular (Pl. 6, figs 4-6). The reticulum is fine with isodiametric to elongate lumina typically 0.5 μm in maximum diameter. Muri are smooth with rounded or triangular profiles (Pl. 6, figs 7-8), typically 0.2-0.3 μm wide.

The pollen wall is about 1.6 μm thick in nonapertural regions, tectate and columellate (Pl. 6, figs 7-8). The endexine is laminate to granular, extremely thin, about 0.1 μm, and thickens near the apertures to about 0.7 μm (Pl. 6, fig. 8). The footlayer is very thick, about 0.8 μm, and homogenous. The columellae are simple, about 0.2 μm high and the tectum reticulate, about 0.5 μm thick. In some specimens a thin darker staining layer has been observed as a discontinuous cover on the outer surface of the pollen (Pl. 6, fig. 8), which may represent a poorly developed pollenkitt.

Pollen grains resembling those recovered in the anthers of *Platananthus scanicus* were described by Pacltová (1982) from an inflorescence of *Platanus quedlinburgensis* from the Santonian of Quedlinburg, East Germany. These pollen grains are slightly larger (12-14 × 16-19 μm) than those of *Platananthus scanicus*. Staminate as well as pistillate inflorescences from Quedlinburg were later described by Knobloch & Mai (1986) as *Platanus richteri* (see p. 00). Details of their floral structure are unknown (Knobloch & Mai, 1986) but the stamens in the Quedlinburg fossils differ from those of *Platananthus scanicus* in the peltate shape of the connective.

The inflorescences and flowers of *Platananthus scanicus* closely resemble those of the Eocene *P. synandrus* Manchester (1986) in several respects, including size and stamen morphology (see also Table II). They both have very long, triangular apical extensions of the connectives and both have prominent tepals. There is also considerable agreement between the two species in pollen size, exine sculpturing and pollen wall ultrastructure. The inflorescences of *P. scanicus* differ, however, in being pedunculate whereas those of *P. synandrus* are sessile. The flowers of *P. scanicus* also differ from those of *P. synandrus* in having apical connectives which lack hairs and extend beyond the tepals. In *P. synandrus* the five stamens of each flower are shed as a unit, being united by numerous intertwining hairs that arise from the adjacent connectives in a single flower.

Unassigned dispersed stamens
Plate 7, figs 1-7; Plate 8, figs 1-7.

Material: About hundred dispersed stamens. Recovered from the lower unit at Åsen, predominantly in clay gyttja (sample GI 32107-GI 32108, GI 32189, GI 32197 particularly sample GI 32107).

Most of the stamens are preserved as charcoal, while only a few specimens are preserved as lignite. Specimens S 100055-100067.

Description and remarks on the species: All stamens are dispersed and there is no evidence of the structure and organization of the flower or inflorenscence. The stamens are basifixed with a short filament (Pl. 7, figs 1-3). Stamens are 0.62(0.78)1.0 mm long (without filament) and 0.31(0.49)0.65 mm wide. The filament is 0.06(0.15)0.22 mm long. The anthers are apparently tetrasporangiate composed of two thecae each with two elongate pollen sacs, 0.4(0.6)0.8 mm long. The pollen sacs on the dorsal side are usually slightly longer than those on the ventral side (Pl. 7, fig. 3). The apical extension of the connective is flattened and peltate (Pl. 7, figs 1-3), 0.12(0.15)0.2 mm long, typically about one fourth the length of the pollen sacs (ratio length connective/length pollen sac: 0.17(0.26)0.38). Dehiscence is lateral to ventral by longitudinal slits that open between the two pollen sacs. There is no indication of valvate dehiscence.

The endothecium is distinct and composed of polygonal and isodiametric cells, about 0.01 mm in diameter, with thickened anticlinal and inner periclinal walls (Pl. 7, fig. 6). The epidermal pattern is very similar to that of *P. scanicus* with elongate cells on the thecae and polygonal-isodiametric cells with a wrinkled outer surface on the apical connective (Pl. 7, figs 4-5). The epidermal cells of the thecae are about 0.06 mm long and 0.02 mm wide, and those of the apical connective are typically 0.03 mm in diameter. Stomata occur scattered on the surface of the connective. They are variously oriented, about 0.025 mm long, paracytic, with one subsidiary cell parallel and contiguous with each guard cell (Pl. 7, fig. 5).

Most of the anthers have dehisced but pollen grains occur frequently on the inner and outer surfaces of the thecae and on the apical connective. Frequently they are adhering together in clumps or are loosely connected by a substance resembling the pollenkitt of some modern insect-pollinated angiosperms (Pl. 7, fig. 7; Pl. 8, fig. 1). In ultrathin sections of the pollen wall this coating appears as a darker staining outer layer, up to 0.4 µm thick. It may form a continuous layer covering the surface of the pollen grain and may also form an infilling of the lumina (Pl. 8, figs 6). Pollen is tricolpate and prolate (Pl. 8, figs 1-2); 12(13.7)15 µm long and 9(9.9)12 µm in equatorial diameter (from anthers cleaned in hydrofluoric and hydrochloric acid). The colpi are lenticular about 10-12 µm long with a granular sculpture (P1. 8, fig. 2). The exine sculpturing is finely reticulate with isodiametric to elongate lumina, typically 0.4 µm in maximum diameter (Pl. 8, fig. 3). In many specimens the muri appear to be contracted and the lumina reduced. This feature may result from the process of charcoalification. The muri are smooth, about 0.4 µm wide, with a rounded or triangular profile (Pl. 8, figs 3-5).

The pollen wall is about 1.1 µm thick in nonapertural regions, tectate and columellate (Pl. 8, figs 4-6). The endexine is laminate, thick, about 0.15 µm, and thickens gradually towards the apertures to about 0.75 µm. The ectexine is homogenous, composed of a moderately thick footlayer, about 0.4 µm, simple columellae, about 0.1 µm high and reticulate tectum, about 0.35 µm thick. A thick pollenkitt-like coating has been observed on the surface of several grains (see above).

The dispersed anthers show general agreement in morphology and epidermal structure with anthers of *Platanus* and *Platananthus* and are tentatively assigned to the Platanaceae. Fossil anthers with a similar flattened and peltate apical connective have been described in platanoid inflorescences from the Santonian of Quedlinburg, East Germany, as *Platanus richteri* by Knobloch & Mai (1986), but these are larger, about 2.8 mm long. The pollen grains found *in situ* in the Quedlinburg material (described by Pacltová, 1982, as *Platanus quedlinburgensis,* see p. 23 and Table II) are also slightly larger.

Generic assignment of this Scania material is precluded by the lack of information on number and arrangement of parts in the flowers that produced the anthers, and by certain unusual features including the presence of stomata on the apical connective and the presence of abundant pollenkitt-like substance at the pollen surface.

Pistillate inflorescences

Platanocarpus Friis, Crane & Pedersen gen. nov.

Derivation of name: From the genus *Platanus* to which this fossil is related and karpos (Greek) fruit.

Generic diagnosis: Globose pistillate inflorescences composed of a spheroidal, central receptacular core surrounded by numerous densely packed pistillate flowers. Each flower with an undifferentiated perianth surrounding an apocarpous gynoecium. Carpels with a ventral slit and poorly developed style. Fruitlets achenes (nutlets). Trichomes not present on the carpels.

Type species: Platanocarpus marylandensis Friis, Crane & Pedersen sp. nov. (p. 16).

Remarks on the genus: This genus is established to accommodate fossil pistillate platanoid inflorescences and infructescences that are distinguished from those of *Platanus* by the lack of trichomes on the carpels and by having a poorly developed style. The latter character also distinguishes this genus from the other extinct platanoid genus based on pistillate organs, *Macginicarpa* Manchester (1986). The genus is deliberately broadly defined by excluding the number of parts per flowers from the diagnosis. This is often extremely difficult to establish in compressed material.

Platanocarpus marylandensis Friis, Crane & Pedersen sp. nov.
Plate 9, figs 1-7; Fig. 2.

Derivation of name: From the State of Maryland, USA, where the fossils were collected.

Specific diagnosis: Pistillate inflorescence sessile on a long axis. Inflorescence composed of about 100 closely spaced flowers. Each flower consists of five carpels surrounded by several layers of linear to spatulate, membranous tepals. Inner tepals about as long as the carpels. Outer tepals typically less than half the length of the carpels. Carpels narrow, obtriangular in outline, with a peltate to pyramidal swelling at the apex.

Dimensions: Diameter of inflorescence: 3-4 mm. Length of flower and carpel: 1.05-1.6 mm; breadth of flower: 0.5-0.8 mm.

Holotype: Plate 9, fig. 1 (PP 34576).

Type locality: West Brothers clay pit, Maryland, USA.

Type stratum: Patapsco Formation (Potomac Group).

Age: Early Cretaceous (Late Albian).

Material: Two fragments of inflorescence axes, four complete inflorescences and about 100 fragments of inflorescences including small groups of detached flowers. All specimens preserved as lignite (PP 34576-34596).

Description and remarks on the species: The pistillate inflorescences are small, globose, about 3-4 mm in diameter, and sessile on a thick reproductive axis, 1.1-1.7 mm broad (Pl. 9, figs 1-2). Only fragments of the axis have been recovered, the largest being about 4 cm long and with two inflorescences (Fig. 1, p. 19). Each inflorescence is composed of a central receptacular core with about 100 densely packed flowers. Individual flowers are wedge-shaped, 1.05(1.49)1.6 mm long and 0.5(0.65)0.8 mm wide (Pl. 9, figs 3-5), with an apocarpous gynoecium surrounded by a number of membranous parts which could include a bract and bracteoles in addition to an undifferentiated perianth. The number and arrangement of the parts is uncertain, but there are possibly as many as three or four layers of helically arranged parts (Pl. 9, figs 3-6). The outer parts are short and broad, about 0.5 mm long (Pl. 9, fig. 6), while the inner parts are typically spatulate to linear and extend almost to the apex of the carpels (Pl. 9, figs 4-5). Clumps of pollen have been observed close to the apex of some of the inner parts (Pl. 9, fig. 7). The possibility that some of these linear inner structures are staminodes cannot be excluded. The outer perianth parts are commonly found attached to the receptacular core in specimens from which the flowers or fruits have been shed (Pl. 9, fig. 2). The carpels are free, narrowly obtriangular in outline and triangular in transverse section. Each carpel leaves a triangular scar on the receptacle (Pl. 9, figs 1-2). The ventral suture is incompletely fused for most of its length and usually rather open apically (Pl. 9, fig. 3). The apices of the carpels are expanded forming a peltate, triangular structure usually with a marked median and dorsal fold (Pl. 9, figs 3-4). There is no distinct style and the stigmatic area is apparently decurrent along the apical part of the ventral slit.

The pollen grains attached to the surface of perianth and carpels are tricolpate and reticulate, about 8-9 µm long and 5-8 µm in equatorial diameter (Pl. 9, fig. 7). They are similar to dispersed pollen grains of *Tricolpites minutus* (Brenner) Dettmann and the pollen grains extracted from *Platananthus potomacensis* (see p. 11).

Platanocarpus marylandensis is distinguished from other known pistillate platanoid inflorescences/infructescences by the more open arrangement of the flowers with the carpels diverging from each other. In the two other species of *Platanocarpus* described here the carpels are more closely packed and the pentamerous arrangement is much less obvious. *P. marylandensis* is also distinguished from the two previously described North American mid-Cretaceous platanoid species (*Platanus primaeva* Lesquereux, *Sparganium aspensis* Brown) by its smaller size.

Platanocarpus carolinensis Friis, Crane & Pedersen sp. nov.
Plate 10, figs 1-8.

Derivation of name: From the State of North Carolina, USA, where the fossils were collected.

Specific diagnosis: Pistillate inflorescence sessile on an axis. Inflorescence composed of about 100 flowers. Each flower apparently consists of five carpels surrounded by short, broad, membranous tepals. Tepals typically about one third the length of the capels. Carpels narrow, obtriangular in outline with slightly pointed apex.

Dimensions: Diameter of inflorescence: 4.3-6.1 mm. Length of flower and carpel: 1.6-2.4 mm; breadth of carpel: 0.35-0.6 mm. Length of seed: 1.5-2.2 mm.

Holotype: Plate 10, fig. 1 (USNM 401642).

Type locality: Neuse River Cut-Off, North Carolina, USA.

Type stratum: Black Creek Formation.

Age: Upper Cretaceous (Santonian or Campanian).

Material: About 250 inflorescences or fragments of inflorescences all preserved as compressed lignite fossils. Specimens USNM 401642-401647.

Description and remarks on the species: The pistillate inflorescences are much compressed, circular in outline, 4.3(5.3)6.1 mm in maximum diameter and sessile on a thick reproductive axis, about 1 mm broad. Only small fragments of the axes have been recovered. The inflorescence is composed of a central receptacular core, 1.6-2.5 mm in diameter with more than 100 closely packed flowers (Pl. 10, figs 1-2, 4). On maceration the inflorescences tend to fall apart in wedge-shaped units apparently representing single flowers, but in unmacerated specimens the individual flowers cannot be distinguished. Each unit (flower) apparently consists of five carpels surrounded by a number of short, broad tepals, about one third the length of the carpels (Pl. 10, figs 3, 5). The tepals are membranous and bear short, simple unicellular trichomes near their margins (Pl. 10, fig. 3). The epidermal cells are more or less equiaxial with straight anticlinal walls (Pl. 10, fig. 3). The carpels are free, narrowly obtriangular and with a slightly pointed apex. Macerated specimens open by a longitudinal split indicating incomplete fusion of the carpel walls. The fruitlets are unilocular with a thin fruit wall. The fruit wall is composed of transversely aligned sclerenchyma overlain by an outer epidermis of tabular, longitudinally elongated cells with straight anticlinal walls aligned in longitudial rows. Epidermal cells about 0.06 × 0.01 mm (Pl. 10, fig. 6). Trichomes have not been observed on the suface of the carpels. The seeds are narrowly ovate, about 1.5-2.2 mm long and 0.57-0.7 mm broad, orthotropous and pendant. The chalaza area is well developed and thick, and the micropyle is pointed (Pl. 10, fig. 8). The seed wall is thin with two distinct cell layers preserved. The cells of the outer layer are polygonal and equiaxial, while those of the inner layer are longitudinally elongate. The cells of both layers have straight anticlinal cell walls (Pl. 10, fig. 8).

Pollen grains have been observed on the surface of several carpels. These are tricolpate, coarsely reticulate (Pl. 10, fig. 7) and are all of one kind. They are identical to the pollen extracted from the staminate inflorescence *Platananthus hueberi* (p. 12).

Platanocarpus carolinensis is distinguished from the three other pistillate organs described in this study principally by the very compact structure of the inflorescences which results from very closely packed carpels.

Platanocarpus sp.
Plate 11, figs 1-7.

Material: Five fragments of inflorescences and about 80 dispersed carpels, recovered from the lower unit at Åsen predominatly in clay gyttja (samples GI 32107, GI 32189, GI 32197). All specimens are compressed and preserved as lignite. Specimens S 100068-100074.

Description and remarks on the species: No complete inflorescences have been recovered, but the shape of the fragments indicate an original spherical form with a diameter of about 7-8 mm. There is no information on attachment to the inflorescence axis. The inflorescence is composed of a central core, about 2.5 mm in diameter, with loosely packed carpels apparently arranged in groups of five and surrounded by a membranous perianth (Pl. 11, figs 1-3). The perianth parts are narrow, linear (Pl. 11, fig. 6), about 0.4 mm long, but are fragmentary and their full length is not preserved. The carpels are 2.0-3.1 mm long and 0.7-1.2 mm broad, narrowly obovate to elliptical in outline and taper gradually into a short apical style (Pl. 11, figs 4-5). The ventral suture is incompletely fused for most of its length (Pl. 11, fig. 4). The fruitlets are unilocular. No seeds have been extracted. The surface of the fruitlets is smooth and distinctly shining in some specimens. Epidermal cells are longitudinally aligned, 0.05-0.1 × 0.01 mm, with straight anticlinal walls (Pl. 11, fig. 6). Trichomes have not been observed on the carpel surface.

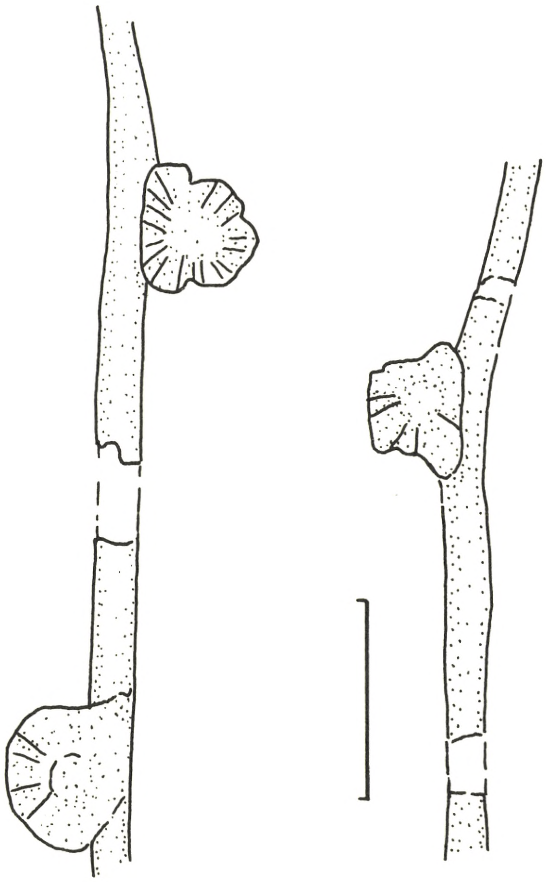
Pollen grains have been observed attached to the surface of the carpels. They are tricolpate, reticulate (Pl. 11, figs 4, 6) and identical to the pollen grains recovered from the stamens of *Platananthus scanicus*.

The pistillate inflorescences exhibit the characters defining the new genus *Platanocarpus* and have been included in this genus. They are distinguished from *P. marylandensis* and *P. carolinensis* by the more ellipsoidal carpel shape and by the very narrow perianth parts. Although these specimens clearly constitute a distinct kind of platanoid inflorescence, the material available is too fragmentary to formally establish a new species.

Unassigned platanoid infructescence
Plate 12, figs 1-7.

Material: 1 charcoalified fragment of a three-dimensionally preserved inflorescence/infructescence. The specimen was recovered from the lower unit at Åsen in clay gyttja (sample GI 32197). Specimen S 100075.

Description and remarks on the species: The pistillate inflorescence/infructescence is globose with an estimated diameter of about 4.5 mm. It is sessile on the reproductive axis (Pl. 12, fig. 1) and composed of a central receptacular core, about 1.5 mm in diameter with about 25 closely spaced flowers. Each flower has a pentamerous, apocarpous gynoecium (Pl. 12, figs 1-2) surrounded by a number of membranous tepals and short trichomes arising between the perianth parts (Pl. 12, fig. 3). The fruitlets are unilocular, with a thin fruit wall composed of transversely aligned sclerenchyma cells overlain by longitudinally aligned epidermal cells (Pl. 12, figs 5, 7). Each fruitlet contains a single seed with a thin seed wall in which three cell layers are visible. The outer layer consists of polygonal and isodiametric cells, about 0.015 mm in diameter,



the middle layer of long narrow, transversely aligned cells, and the inner layer of elongated, longitudinally aligned cells (Pl. 12, fig. 6). The apical part of the seed is rounded, apparently with a thicker wall and probably represents the chalazal area. The basal part of the seed has not been observed, but the shape of the carpels indicates that the seeds were narrowly obovate.

The fragmentary nature of the fossil and the lack of information on the stylar area preclude a firm generic assignment of the fossil, even though the general organization of the inflorescence/infructescence indicates a close relationship to the extinct genera *Platanocarpus* and *Macginicarpa*. However, the specimen is distinguished from the species of *Platanocarpus* and *Macginicarpa* by the smaller number of flowers in the inflorescence and by the presence of trichomes arising from the receptacular core between the perianth parts. Such trichomes are extensively developed in infructescenes of extant genus *Platanus*. The fossil differs from *Platanus* in the pentamerous arrangement of the carpels and the much smaller number of flowers in the infloresence.

Figure 1. Fossil *Platanocarpus marylandensis* Friis, Crane & Pedersen sp. nov. from the Upper Albian of the Patapsco Formation. Fragments of inflorescence axes showing sessile arrangement of inflorescences (a, PP 34593; b, PP 34594). Bar scale = 5 mm.

Discussion

Associations between dispersed organs

Four kinds of staminate and pistillate organs of platanoid affinity were recovered from the three localities investigated in this study; a single kind of each organ at the two North American localities and two kinds of each organ at the Åsen locality. There is no physical connection between the dispersed organs at any of the localities but there is indirect evidence, particularly at the two localities in North America that some of the pistillate and staminate inflorescences were derived from a single species (Table I).

At the Lower Cretaceous West Brothers locality only one type of staminate organ and one type of pistillate organ have been recognised. Both the staminate *Platananthus potomacensis* and the pistillate *Platanocarpus marylandensis* have pentamerous flowers crowded in dense inflorescences and pollen grains of the *Tricolpites minutus* type were found in both organ. This type of pollen occurs *in situ* in the staminate flowers and abundantly on the surface of the pistillate flowers. Details of hair bases, probable secretory structures and cuticular ornamentation are similar to those reported from palmately-lobed platanoid leaves that are present, although rare, at the West Brothers locality (Upchurch, 1984, personal communication). The possible relationship between the leaves and reproductive structures requires more detailed examination. The other kind of spherical inflorescence with small pentamerous flowers and apocarpous gynoecia recovered from the West Brothers locality (Crane et al., 1986) may be distinguished from the platanoid inflorescences by the presence of abundant tricolporate pollen. The apex of the carpels in this type of inflorescence bears characteristic unicellular hairs which in combination with other cuticle characters suggests a possible relationship to rosid leaves of the *Sapindopsis* type (Upchurch, 1984, personal communication).

At the Upper Cretaceous Neuse River locality the platanoid reproductive structures recognised include only one type of staminate and one type of pistillate organs. The staminate flowers of *Platananthus hueberi* are clearly pentamerous and this may also be true of the pistillate *Platanocarpus carolinensis*. The characteristic tricolpate and coarsely reticulate pollen of *Platananthus hueberi* has also been recovered on the surface of the carpels in *Platanocarpus carolinensis*. There are no leaf fossils closely associated with the Neuse River platanoid material.

Establishing the possible relationships between the different kind of organs is more problematic at the Upper Cretaceous Åsen locality at which two kinds of staminate organs and two kinds of pistillate organs of platanoid affinity were recovered. The more abundant staminate *Platananthus scanicus* and the pistillate *Platanocarpus* sp. are generally preserved as lignite fossils while the two other platanoid organs are mostly preserved as charcoal fossils. Pollen grains similar to those of *Platanocarpus scanicus* have been observed on the surface of the carpels in *Platanocarpus* sp., while pollen grains similar to those of the other staminate type have not been observed associated with pistillate material. Based on the evidence available a connection between *Platananthus scanicus* and *Platanocarpus* sp. seems probable but other possibilities cannot be ruled out. There is no evidence that the charcoalified staminate and pistillate material is conspecific and pollen grains have not been seen on the pistillate organs. Although leaf fragments and small leaves are preserved at the Åsen locality platanoid foliage has not yet been recognised.

Comparison with extant Platanaceae

Although the fossil reproductive organs described here are distinct from all extant Platanaceae their inclusion in the family is supported by a number of shared floral features. The flowers are small, unisexual and aggregated into dense ball-like heads that are either pedunculate or sessile on a long reproductive axis. The perianth is simple and undifferentiated. The flowers are hypogynous with an apocarpous gynoecium. The carpels have only partly fused ventral margins and mature into unilocular nuts with a single seed. The seeds are (hemi-) orthotropous and pendant with an outer epidermis of equiaxial cells and an inner epidermis of narrow, elongated cells (details of seeds in *Platanocarpus* know only for *P. carolinensis*). The stamens have short filaments, and elongated anthers with an apical extension of the connective. The anthers are tetrasporangiate and contain pollen grains which are tricolpate, reticulate with muri which are triangular in cross section. Pollen aperture membranes are granular and the footlayer is relatively thick.

The fossil flowers are mainly distinguished from those of modern *Platanus* in having a more prominent perianth. In the Lower Cretaceous *Platanocarpus marylandensis* this consists of a number of longer inner parts and shorter outer parts, that may indicate partial differentiation into a calyx and corolla. The number of parts in the gynoecium and androecium is fixed (five) in the fossil flowers and the stamens and carpels are apparently radially arranged. The flowers of *Platanus* contain a variable number of stamens (3-5) and carpels (4-9) within each flower. The pollen grains of the fossil flowers are smaller (9-16 μm in length) than those of modern *Platanus* (16-27 μm in length) and the style is not well developed. The fruitlets of *Platanocarpus* are also distinguished from those of *Platanus* in being smooth while those of *Platanus* have abundant trichomes. The following chronological evolutionary trends in the platanoid reproductive organs can be hypothesised based on the limited material currently available: reduction of perianth, loss of fixation in number of stamens and carpels; loss of symmetry in androecium and gynoecium, increase in pollen size and elaboration of style. All of these trends may reflect a change in reproductive biology within the platanoid complex from the Cretaceous through to the Recent.

Modern *Platanus* is wind-pollinated with typical anemophilous characters such as small, simple and unisexual flowers with an inconspicuous perianth, pollen grains in the size range (20-40 μm) characteristic of wind-pollinated angiosperms and long protruding styles (Faegri & van der Pijl, 1979; Whitehead, 1983). Fossil *Platanocarpus* and *Platananthus* also exhibit many of these anemophilous characters. However, the more prominent perianth, the radial arrangement of parts and the very small size of the pollen grains may suggest that wind-pollination was not fully developed in the Cretaceous platanoids, and that insects may have been important pollinators. This is especially pronounced in the Lower Cretaceous platanoids which have a more differentiated perianth, more open flowers and smaller pollen (8.5-12 μm) than in the other Cretaceous platanoids. An insect-pollinated ancestor for modern *Platanus* may also be suggested by the presence of pollenkitt in *Platanus* (Hesse, 1978) and valvate dehiscence of the anthers (Endress, 1977). Both characters are predominant in insect-pollinated Hamamelididae, and only weakly developed in *Platanus* (Endress, 1986, in press).

Comparison with fossil Platanaceae

Although the fossil record of the Platanaceae is extensive our current knowledge of the history of the family is mainly based on leaf remains. Reproductive organs of the Platanaceae are less common in the fossil record and those that are known generally yield very little information on structure and organization of the flower (Table II). This is due primarily to the very dense nature of the inflorescence and the fact that most of the inflorescences are strongly compressed. In general, these reproductive organs have been assigned to the extant genus *Platanus,* although some pistillate organs have also been assigned to the genus *Spar-*

ganium based on superficial resemblances in the shape of the fruitlets and infructescences. One fossil genus, *Tricolpopollianthus* Krassilov, was established on reproductive material from the Upper Cretaceous – Lower Tertiary and three additional genera, *Macginicarpa* Manchester, *Macginistemon* Manchester and *Platananthus* Manchester were established based on reproductive material from the Lower Tertiary.

Staminate inflorescences. The staminate inflorescences are all clearly pentamerous with a distinct perianth, and are assigned here to the extinct genus *Platananthus*. They differ principally from those of extant *Platanus* and the Tertiary *Platanus neptunii* (Ettingshausen) Bůžek, Holý & Kvaček in their smaller size, the fixed number of stamens and smaller pollen (Table II). *Platananthus synandrus* from the Eocene of western North America (Manchester,

TABLE II. Distribution of floral characters in extant and extinct Platanaceae. a. Staminate organs. b. Pistillate organs.

a. Staminate organs	Age	Infl. sessile	Perianth well-devel.	Number of stamens	Trichomes on connect.	Stamens shed in units	Size of pollen
Platanus spp (subg. *Platanus*)	Recent	–	–	3-5	+	–	16-27 µm
Platanus kerrii	Recent	+	–	3-4	+	–	16-18 µm
Platanus neptunii	Oligoc.-Mioc.	–	–	6-7	?	–	20 µm
Platananthus synandrus	Eocene	+	+	5	+	+	11-16 µm
Macginistemon mikanoides	Eocene	?	?	5	+	+	11-16 µm
Platanites hebridicus	Paleocene	–	–	?	?	–	16-22 µm
Tricolpopollianthus burejensis	Maastr.-Dan.	?	?	?	–	?	18 µm
Platananthus hueberi	Santon.-Camp.	+	+	5	(+)	?	13-15 µm
Platananthus scanicus	Santon.-Camp.	–	+	5	–	–	15-16.5 µm
unassign. stamens	Santon.-Camp.	?	?	?	–	–	12-15 µm
Platanus quedlinburgensis	Santonian	?	?	?	–	–	16-19 µm
Platananthus potomacensis	Albian	?	+	5	–	?	8.5-12 µm

b. Pistillate organs	Age	Infl. sessile	Perianth well-devel.	Number of carpels	Trichomes on carpels	Style elongated	Infructescence ≥ 10 mm diam.
Platanus spp (subg. *Platanus*)	Recent	–	–	5-9	+	+	+
Platanus kerrii	Recent	+	–	?	+	+	+
Platanus neptunii	Oligoc.-Mioc.	–	–	4-8	+	+	+
Macginicarpa glabra	Eocene	–	+	5	–	+	+
Platanites hebridicus	Paleocene	?	?	?	?	+	+
Platanocarpus sp.	Santon.-Camp.	?	–	5(?)	–	–	–
unassign. infruct.	Santon.-Camp.	+	–	5	–	?	–
Platanocarpus carolinensis	Santon.-Camp.	+	+	5(?)	–	–	–
Platanus richteri	Santonian	?	?	?	–	?	–
Platanus laevis	Cenomanian	+	?	?	?	+	+
Platanus primaeva	Cenomanian	+	+	5(?)	–	?	–
'Sparganium' aspensis	Albian	+	?	?	?	?	–
Platanocarpus marylandensis	Albian	+	+	5	–	–	–

Information from Brown (1933), Bůžek, Holý & Kvaček (1967), Crane, Manchester & Dilcher (in press), Dilcher (1979), Friis (1985c), Knobloch & Mai (1986), Krassilov (1973), Lesquereux (1892), Manchester (1986), Pacltová (1982), Velenovský (1881, 1889), Zavada & Dilcher (1986).

1986) is distinguished from all of the Cretaceous fossils in having hairs on the connective. These hairs intertwine and unite the five stamens of each flower so that they are shed as a unit. A similar arrangement also occurs in *Macginistemon mikanoides* (Macginitie) Manchester also from the Eocene of western North America (Manchester, 1986). However, this species is known only from isolated groups of stamens and therefore its affinity to *Platanus* cannot be established with certainty (Manchester, 1986). Papillae are developed apically on the inner surfaces of the stamens in the Upper Cretaceous *P. hueberi* and may represent an initial stage in the phylogenetic development of the longer hairs as seen in the two Eocene forms. However, the stamens of *P. hueberi* have never been observed detached from the inflorescence, either in units of fives or individually. In contrast, individual dispersed stamens of *P. scanicus* occur abundantly in some Åsen samples.

Only two types of platanoid staminate inflorescences have been recorded previously from the Cretaceous. *Tricolpopollianthus burejensis* Krassilov was described from the Maastrichtian-Danian of the Amur Basin, Far East of the USSR (Krassilov, 1973). It comprises globular inflorescences of densely crowded flowers. The connective has an apical extension similar to that of *Platananthus* and the pollen grains are also similar being small, tricolpate and reticulate. However, no details are known of the floral structure and according to Krassilov (personal communication, 1986) the preservation of the material precludes the recovery of additional information. Staminate inflorescences of platanoid affinity were also described by Knobloch & Mai (1986) from the Santonian of Quedlinburg, East Germany. The staminate organs were found in association with pistillate organs and both described as *Platanus richteri* Knobloch & Mai, a pistillate specimen being selected as the holotype. However, pollen grains extracted from the staminate organs had previously been described as *Platanus quedlinburgensis* Pacltová (1982), and although no details of the structure of inflorescence and flower were provided the species name obviously applies to the entire structure. Mai (personal communication, 1987) has confirmed the identity between *Platanus quedlinburgensis* and the staminate *P. richteri* and we therefore suggest that the name *P. richteri* should be retained only for the pistillate organs. The staminate inflorescences (*P. quedlinburgensis*) are of comparable size to those of *Platananthus* and the stamens have a peltate apical extension of the connective. Unfortunately there are no details on the number of stamens in each flower and thus the relationship to the other Cretaceous material described in this paper cannot be established with certainty.

Pistillate inflorescences. The three types of pistillate inflorescences/infructescences assigned here to the extinct genus *Platanocarpus* are all considerably smaller than those of modern *Platanus* (Table II). They are also distinguished from *Platanus* by the lack of dispersal hairs on the fruitlets, the poorly defined style, more prominent perianth and the apparently fixed number of carpels. The inflorescences of *Platanocarpus* are also distinguished from those of *Macginicarpa* Manchester (1986) (established for pistillate organs from the Eocene of North America) by their smaller size and by the indistinct style of each fruitlet. However, these two extinct genera are united by the pentamerous arrangement of the gynoecium and the lack of dispersal hairs on the fruitlets. Several other platanoid pistillate inflorescences recorded previously from the Cretaceous (*Platanus primaeva* Lesquereux, *Platanus raynoldsii* Newberry, *Platanus richteri* Knobloch & Mai, *Sparganium aspensis* Brown) are similarly small-sized and may well be more closely related to *Platanocarpus*. The oldest of these, *Sparganium aspensis* from the upper Albian Aspen Shale of Wyoming, North America (Brown, 1933) is poorly preserved and yields no information on carpel number or the nature of perianth. The other North American species, *Platanus primaeva* from the Cenomanian Dakota Sandstone of Kansas (Lesquereux, 1882; Dilcher, 1976) has a pentamerous floral structure, a well-developed perianth and apparently lacks dispersal hairs (Manchester, 1986). However, critical diagnostic features of the carpels such as the delimitation of the style are unclear and *Platanus primaeva* cannot be firmly assigned to *Platanocarpus*. Pistillate infructescences from the Maastrichtian-Danian of the Far East of the USSR described as *Platanus raynoldsii* (Krassilov, 1976) resemble *Platanus primaeva* in the arrangement of infructescences along the axis, but this material yields no information on carpel number, perianth or carpels. The pistillate organ *Platanus raynoldsii* occurs associated with the staminate *Tricolpopollianthus burejensis* (Krassilov, 1976) which is probably also of platanoid affinity.

Platanus richteri described from the Santonian of Quedlinburg, East Germany, is similar to *Platanocarpus* in having obovate carpels with a poorly delimited style, but the number of carpels per flower has not been determined and the nature of the perianth is unclear (Knobloch & Mai, 1986). *Platanus richteri* is distinguished from the three species of *Platanocarpus* and from the other extant and fossil Platanaceae in the presence of numerous shield-shaped trichomes on the perianth.

Platanoid pistillate reproductive organs with larger inflorescences/infructescences are common in the Tertiary, but are rare in the Cretaceous. *Platanus laevis* (Velenovský) Velenovský from the Cenomanian of Czechoslovakia (Velenovský, 1881, 1889) and *Platanus* cf. *laevis* from the Maastrichtian of East Germany (Knobloch & Mai, 1986) have infructescences about 20 mm in diameter and fruitlets with a more distinct style.

Conclusion

The variety of platanoid leaves described from the Cretaceous and Early Tertiary has been used to suggest that the single extant genus represents only a small proportion of the total diversity of the platanaceous clade (Crane, in press; Schwarzwalder & Dilcher, in press). This conclusion is strongly supported by the considerable variation in carpel shape, stamen morphology, perianth form and pollen size among the Cretaceous reproductive structures described in this paper. Nevertheless, despite this diversity all of the Cretaceous flowers in which the arrangement of parts could be observed consistently show either five carpels or stamens in each flower, and this feature evidently persisted in the group at least until the Middle Eocene (Manchester, 1986). The early, and presumed primitive Platanaceae therefore exhibit the same kind of pentamerous floral organization that is widespread and possibly basic in several major groups of extant dicotyledons (sub-classes Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae; Takhtajan, 1980).

A further consistent feature of all Cretaceous platanoid staminate inflorescences so far described is the presence of tricolpate pollen differing from that of the extant genus in size and details of pollen wall structure and sculpture. Stratigraphic evidence and comparative studies of extant plants (Doyle, 1969; Muller, 1970; Walker & Doyle, 1975; Doyle & Hickey, 1976) both indicate that tricolpate pollen is basic among the diverse triaperturate and triaperturate-derived grains that characterize the non-magnoliid dicotyledons (sub-classes Ranunculiidae, Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae; Takhtajan, 1980).

Platananthus potomacensis and *Platanocarpus marylandensis* are currently the oldest fossils in which pentamerous floral organization has been demonstrated, and *P. potomacensis* is the earliest angiosperm reproductive structure from which triaperturate pollen has been described *in situ*. The very early appearance of these features in the platanaceous clade, combined with foliar, and possible reproductive, similarities to mid-Cretaceous Rosidae (Hickey & Wolfe, 1975; Doyle & Hickey 1976; Upchurch, 1984; Crane et al., 1986) and Fagales (Crane, in press), supports the view that the Platanaceae played a significant role in the initial diversification of non-magnoliid dicotyledons. Additional information on the reproductive structures of Cretaceous Platanaceae and related plants will be critical for further clarifying the major features of the early angiosperm radiation.

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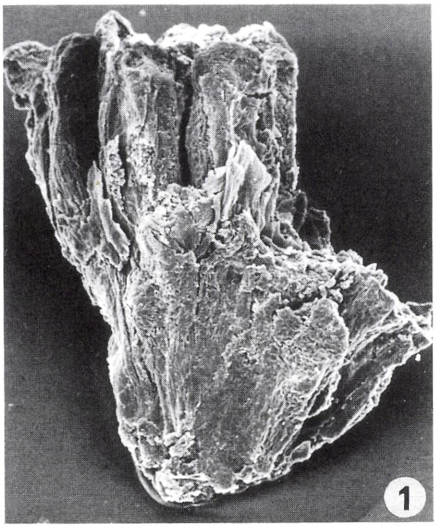
Plates 1-12

PLATE 1

Fossil *Platananthus potomacensis* Friis, Crane & Pedersen sp. nov. from the Upper Albian of the Patapsco Formation (Potomac Group), Maryland, U.S.A.

1. Holotype. Group of staminate flowers in lateral view (PP 34569, x 65).
2. Holotype. Staminate flowers in figure 1 in apical view showing five stamens in a flower; one stamen broken showing pollen grains (PP 34569, x 110).
3. Holotype. Lateral view of a broken pollen sac showing pollen *in situ* (PP 34569, x 625).
4. Lateral view of single staminate flower showing stamens and intact tepals (PP 34570, x 75).
5. Lateral view of single staminate flower showing line of anther dehiscence (arrow) and apical expansion of the connectives (PP 34570, x 90).
6 Transverse section through a single stamen showing four pollen sacs and thick connective (PP 34571, x 200).
7. Inflorescence with numerous, possibly immature staminate flowers (PP 34572, x 43).
8. Detail of inflorescence showing two flowers with reproductive parts in fives and well-developed tepals (PP 34572, x 145).

Figs. 1-5, 7, 8 SEM, fig. 6 transmitted light micrograph.
st = stamens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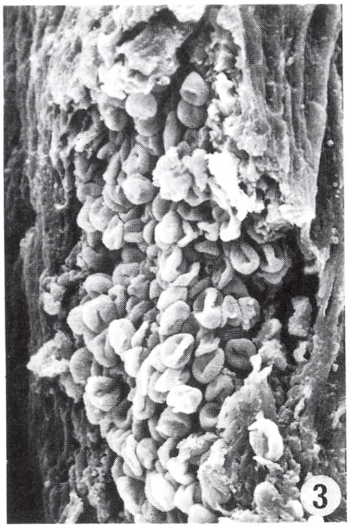
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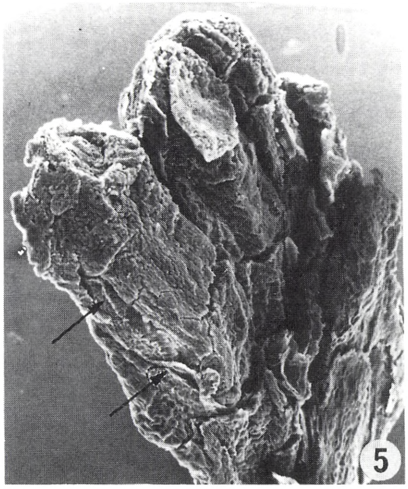
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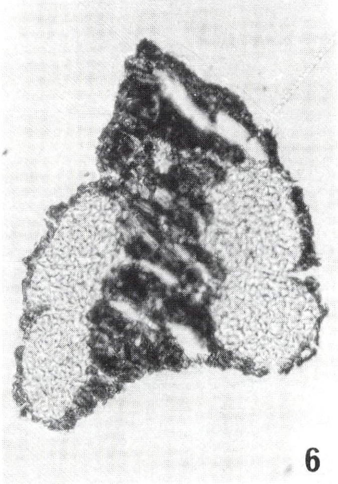
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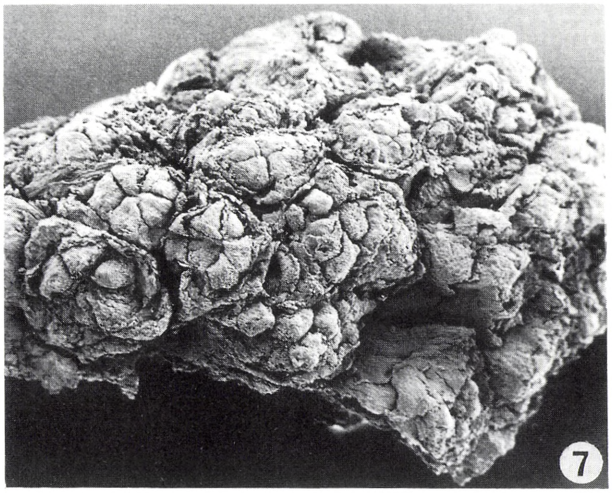
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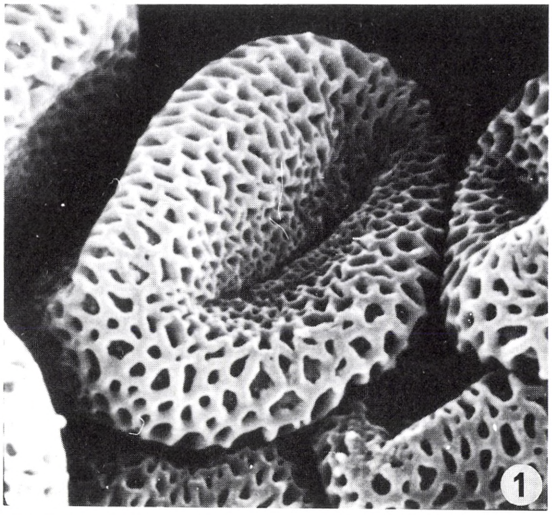
PLATE 2

Fossil *Platananthus potomacensis* Friis, Crane & Pedersen sp. nov. from the Upper Albian of the Patapsco Formation (Potomac Group), Maryland, U.S.A.

1. Pollen grain from the stamen in Plate 1, figure 6, showing colpus and reticulate exine structure (PP 34571, x 6800).
2. Detail of exine surface (PP 34571, x 20000).
3. Ultrathin section through several pollen grains (PP 34571, x 5300).
4. Ultrathin section through the equator of a single pollen grain (PP 34571, x 7800).
5. Detail of pollen wall in apertural region (PP 34571, x 34300).
6. Detail of pollen wall in non-apertural region (PP 34571, x 34300).

Figs. 1-2 SEM, figs 3-6 TEM.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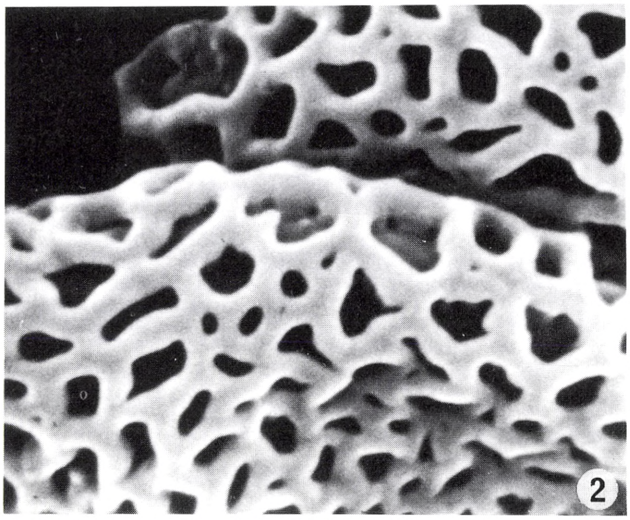
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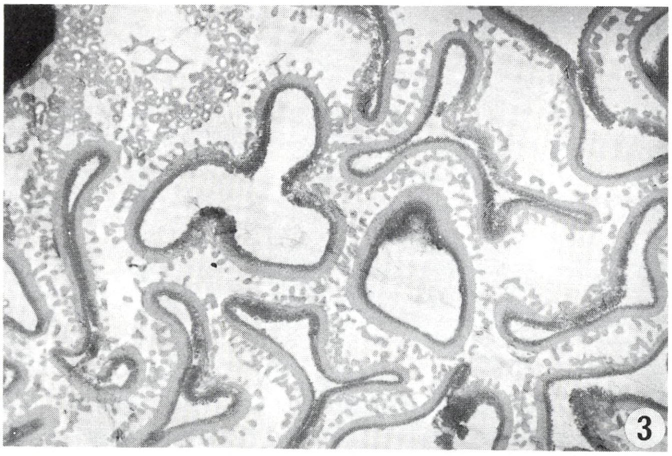
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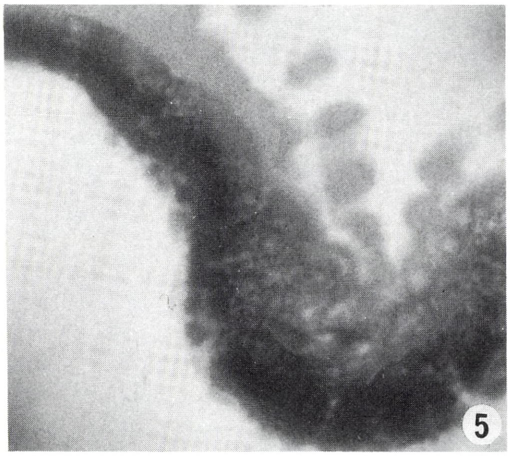
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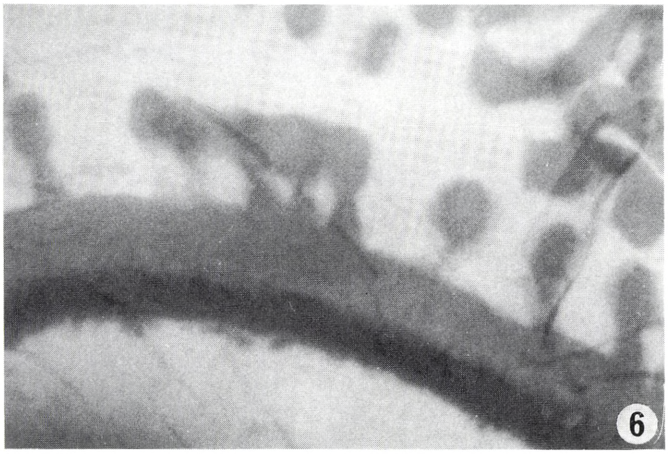
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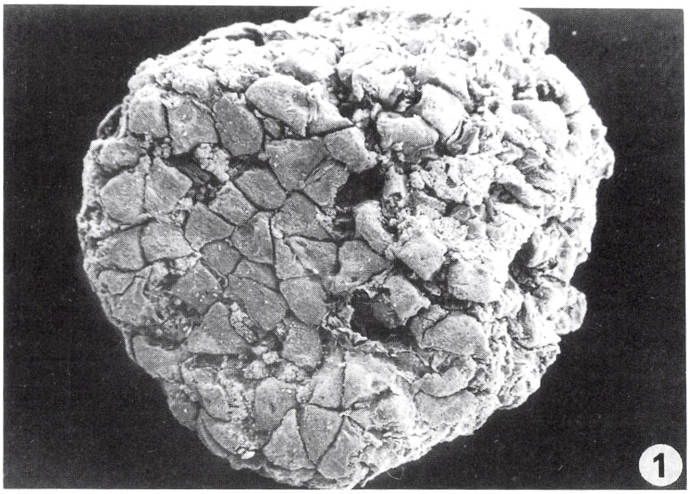
PLATE 3

Fossil *Platananthus hueberi* Friis, Crane & Pedersen sp. nov. from the Santonian-Campanian of the Black Creek Formation, North Carolina, U.S.A.

1. Holotype. Complete inflorescence with numerous staminate flowers (USNM 401637, x 20).
2. Inflorescence sessile on a short portion of the inflorescence axis (USNM 401639, x 20).
3. Lateral view of several staminate flowers (USNM 401638, x 50).
4. Detail of inflorescence showing staminate flowers, each with five stamens and well-developed tepals (USNM 401639, x 75).
5. Holotype. Detail of a single staminate flower showing five stamens and papillae on the outer surface of the anthers (arrow) (USNM 401637, x 100).
6. Holotype. Detail of papillae (USNM 401637, x 1000).
7. Holotype. Surface detail of apical expansion of connective (USNM 401637, x 1500).

All figures SEM
P = papillae, st = stamens, t = tepals.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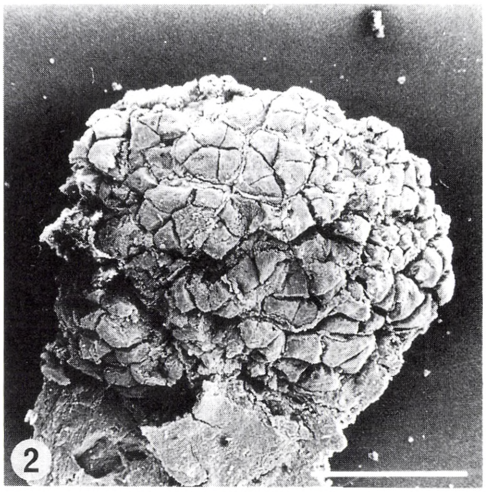
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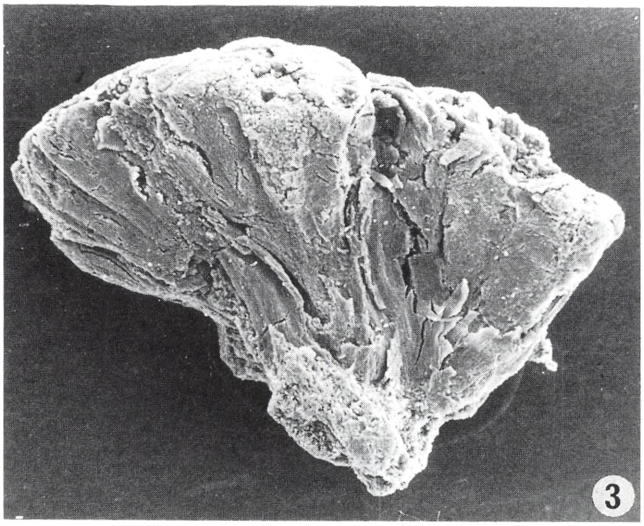
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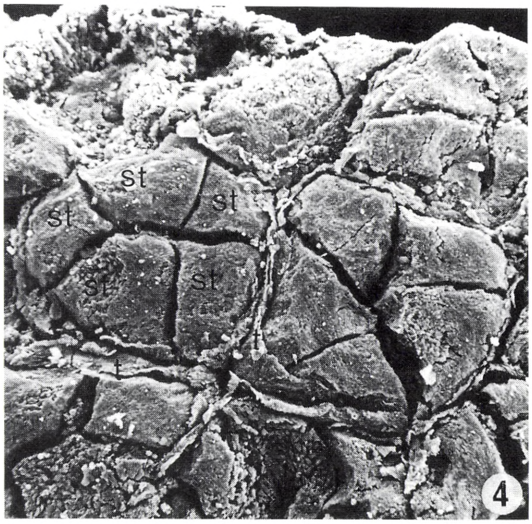
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st
st
st
st
t
4


5


p
6

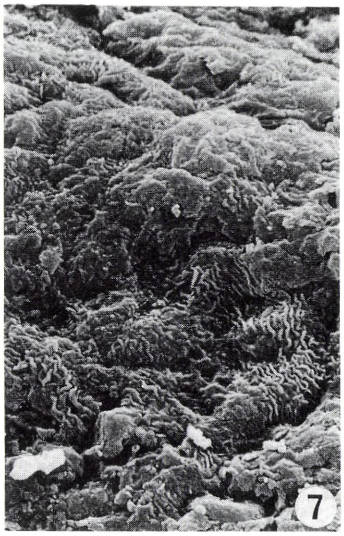
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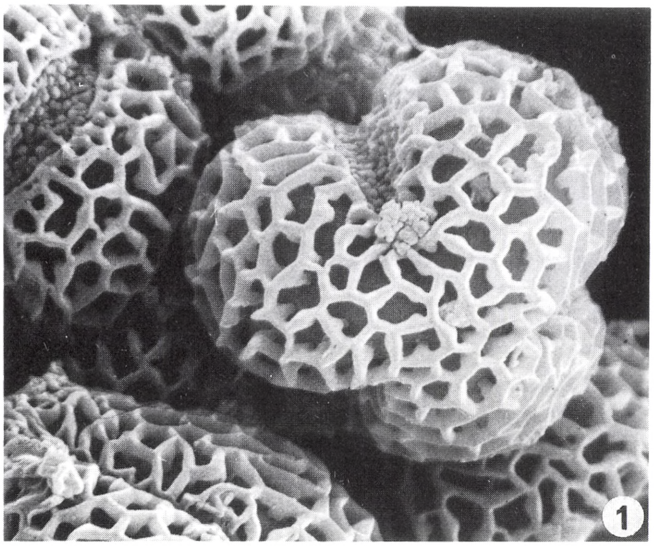
PLATE 4

Fossil *Platananthus hueberi* Friis, Crane & Pedersen sp. nov. from the Santonian-Campanian of the Black Creek Formation, North Carolina, U.S.A.

1. Holotype. Pollen grains showing colpi and reticulate exine structure (USNM 401637, x 5000).
2. Detail of exine surface (USNM 401637, x 20000).
3. Ultrathin section through several pollen grains (USNM 401640, x 4500).
4. Ultrathin section through the equator of a single pollen grain (USNM 401640, x 6800).
5. Detail of pollen wall in apertural region (USNM 401640, x 23000).
6. Detail of pollen wall in non-apertural region (USNM 401640, x 26000).

Figs 1-2 SEM, figs 3-6 TEM.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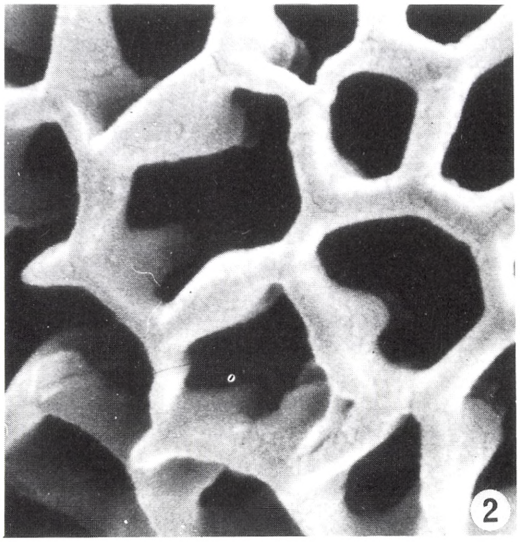
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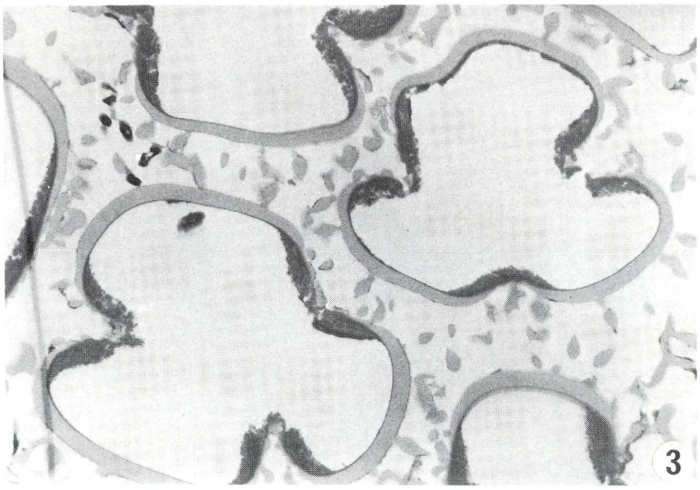
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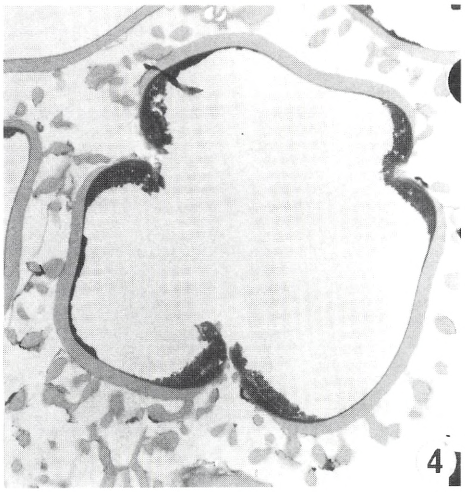
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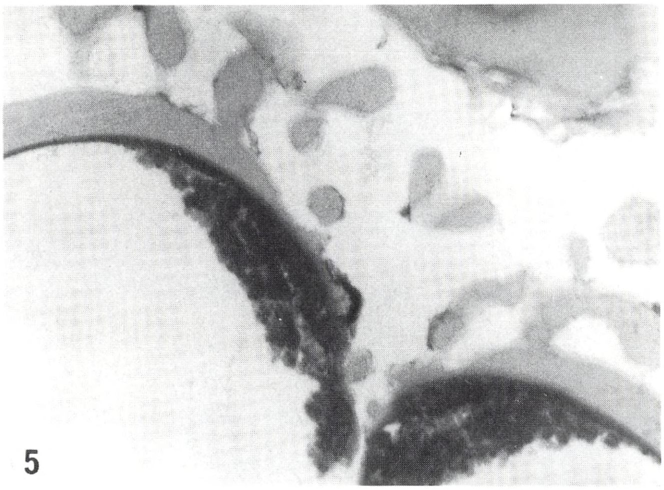
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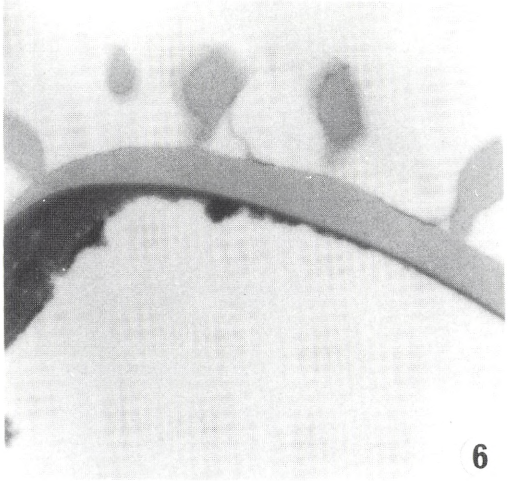
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PLATE 5

Fossil *Platananthus scanicus* Friis, Crane & Pedersen sp. nov. from the Santonian-Campanian of Scania, Sweden.

1. Holotype. Complete inflorescence with numerous staminate flowers and short portion of the peduncle (S 100001, x 10).
2. Fragment of inflorescence showing several staminate flowers with well-developed tepals (S 100002, x 20).
3. Fragment of inflorescence with portion of peduncle (S 100003, x 10).
4. Detail of inflorescence showing expanded apex of tepals (S 100002, x 60).
5. Details of the apex of a single flower showing tepals and stamens with elongated apical extension of the connective (S 100004, x 35).
6. Single stamen showing anthers with valvate lines of dehiscence (arrows) and an elongated apical extension of the connective, (S 100008 x 30).
7. Single stamen with dehisced anther (S 100016, x 30).
8. Single stamen (S 100014, x 30).
9. Longitudinal section through a single stamen showing pollen sac and elongated apical extension of the connective (S 100027 x 35).

Fig. 1 reflected light micrograph, figs 2-8 SEM, fig. 9 transmitted light micrograph.

c = connective, st = stamens, t = tepals.

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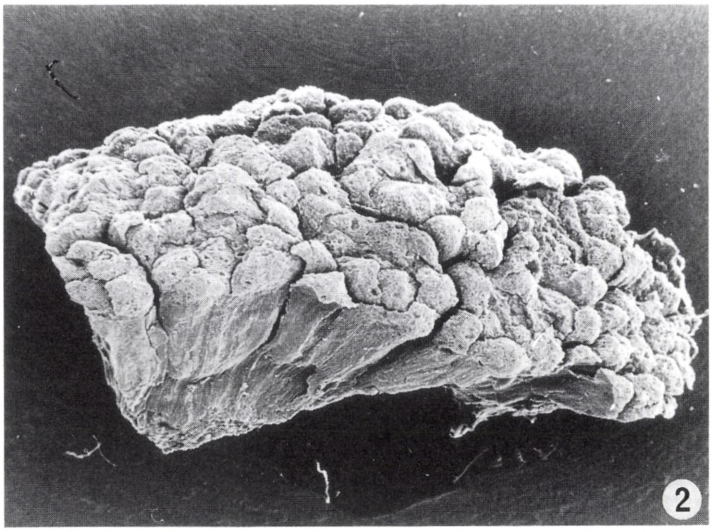

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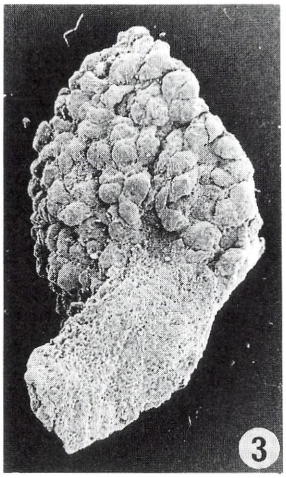

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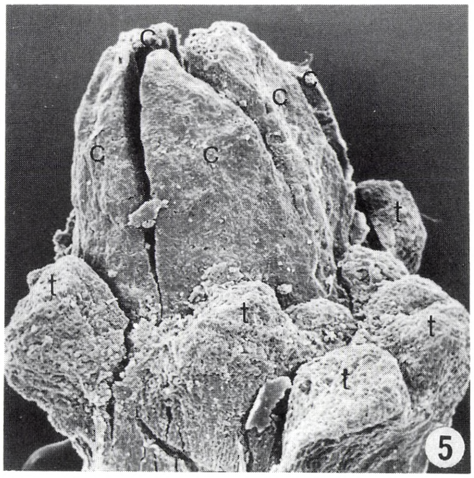

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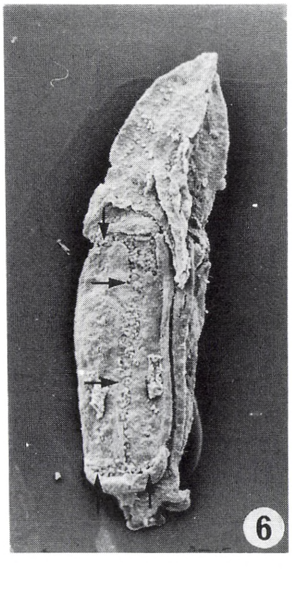

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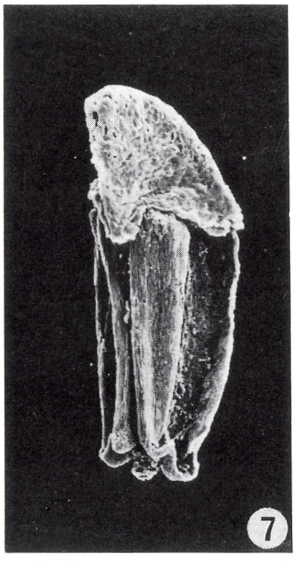

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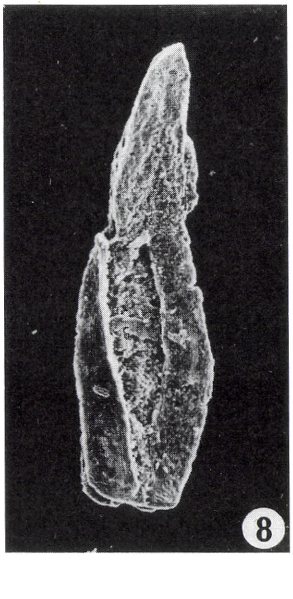

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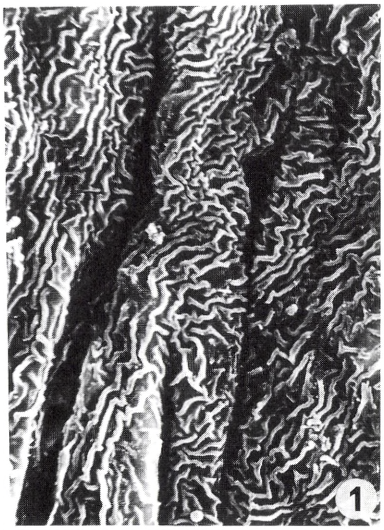
PLATE 6

Fossil *Platananthus scanicus* Friis, Crane & Pedersen sp. nov. from the Santonian-Campanian of Scania, Sweden.

1. Surface detail of theca (S 100016, x 1500).
2. Surface detail of apical extension of connective (S 100016, x 1500).
3. Fracture through anther wall showing endothecial cells (S 100019, x 2000).
4. Pollen grains from the stamen in Plate 5, figure 6 (S 100008, x 1500).
5. Single pollen grain from the stamen in Plate 5, figure 6 showing colpi and reticulate exine structure (S 100008, x 4000).
6. Detail of exine surface (S 100008, x 20000).
7. Ultrathin section through several pollen grains (S 100027, x 4500).
8. Detail of pollen wall (S 100027, x 36000).

Figs 1-6 SEM, figs 7-8 TEM.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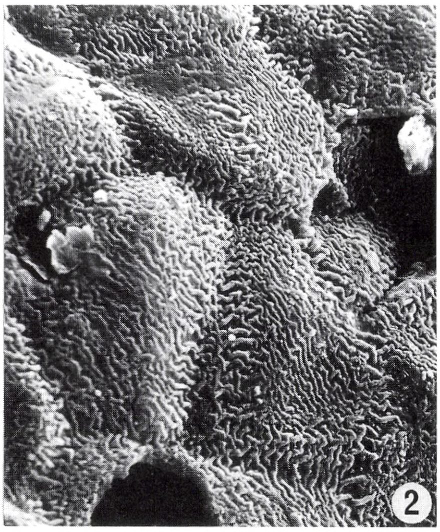
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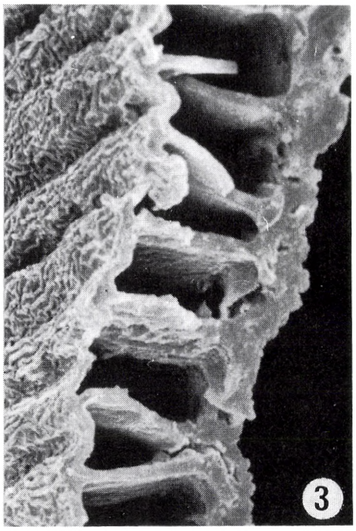
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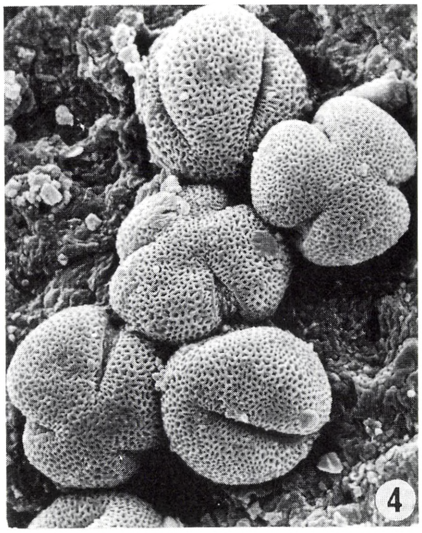
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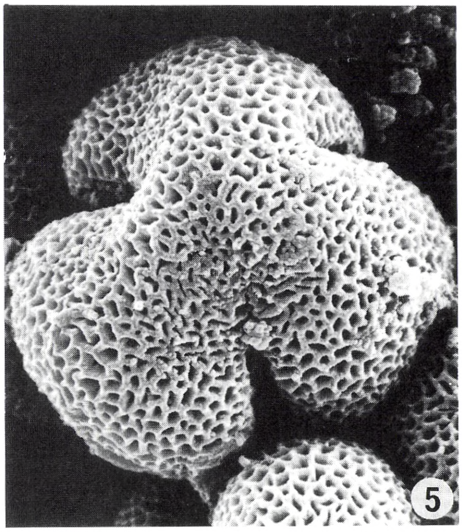
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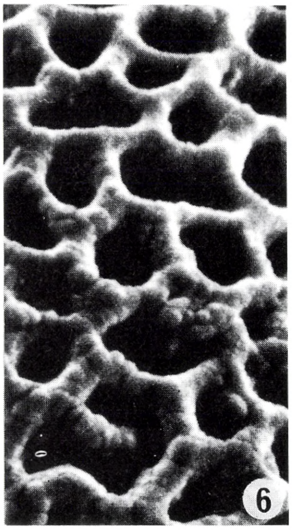
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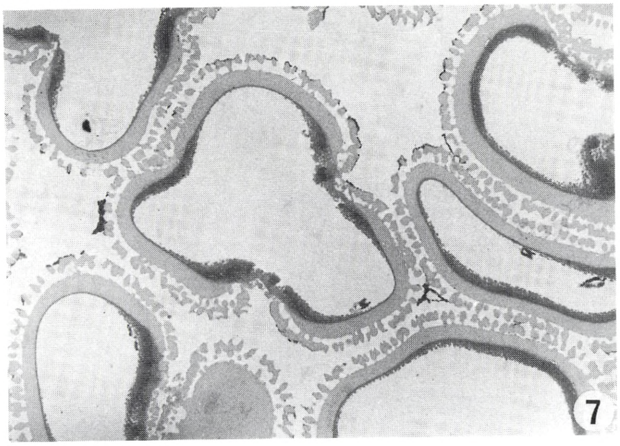
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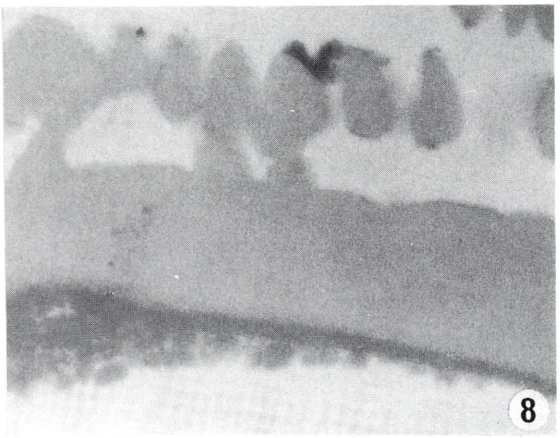
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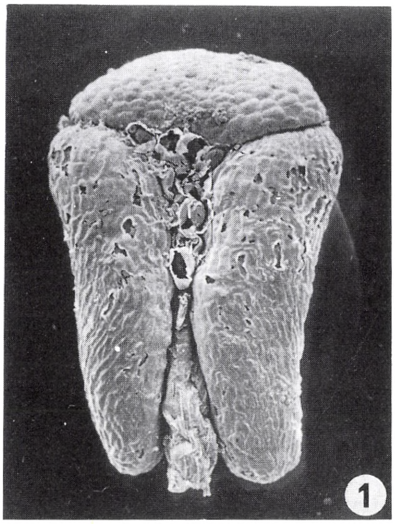
PLATE 7

Fossil unassigned dispersed platanaceous stamens from the Santonian-Campanian of Scania, Sweden.

1. Single stamen in probable abaxial view showing short filament, thecae and peltate apical extension of the connective (S 100055, x 60).
2. Single stamen in probable adaxial view (S 100058, x 60).
3. Single stamen in probable adaxial view (S 100056, x 60).
4. Surface detail of theca (S 100056, x 700).
5. Surface detail of apical extension of the connective showing open stomata and several pollen grains (S 100057, x 700).
6. Fracture through anther wall showing endothecial cells (S 100057, x 1500).
7. Cluster of pollen grains adhering to the surface of the stamen in figure 2 (S 100058, x 1500).

All figures SEM.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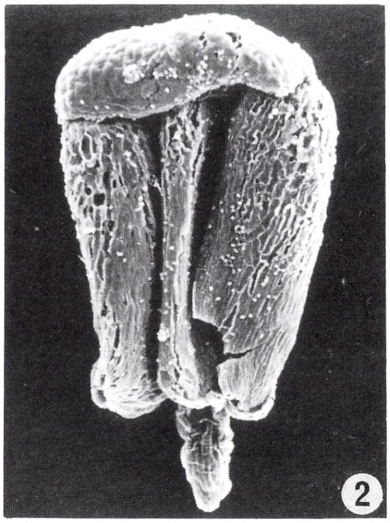
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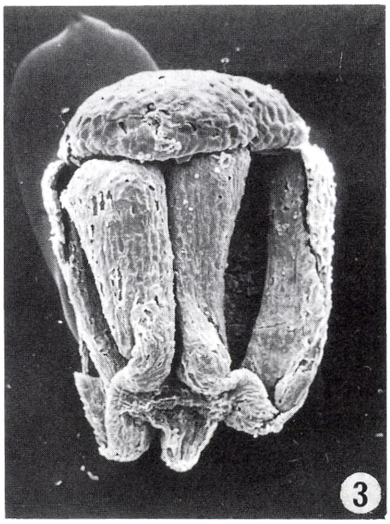
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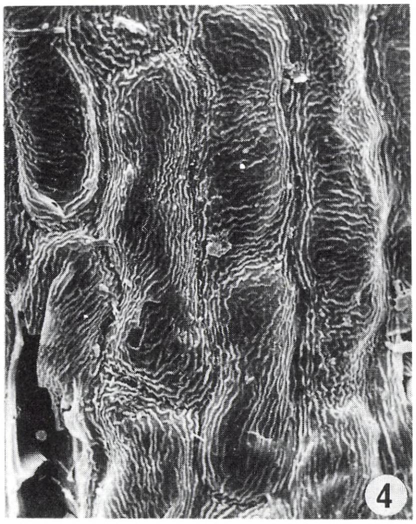
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7

PLATE 8

Fossil unassigned dispersed platanaceous stamens from the Santonian-Campanian of Scania, Sweden.

1. Pollen grains with adhering material resembling pollenkitt (S 100056, x 3500).
2. Single pollen grain showing colpi and reticulate exine structure (S 100057, x 5000).
3. Detail of exine surface (S 100057, x 20000).
4. Ultrathin section through the equator of a single pollen grain (S 100060, x 10000).
5. Ultrathin section close to the pole of a single pollen grain (S 100060, x 12000).
6. Detail of pollen wall in apertural region (S 100060, x 36000).
7. Detail of pollen wall (S 100060, x 36000).

Figs 1-3 SEM, figs 4-7 TEM.


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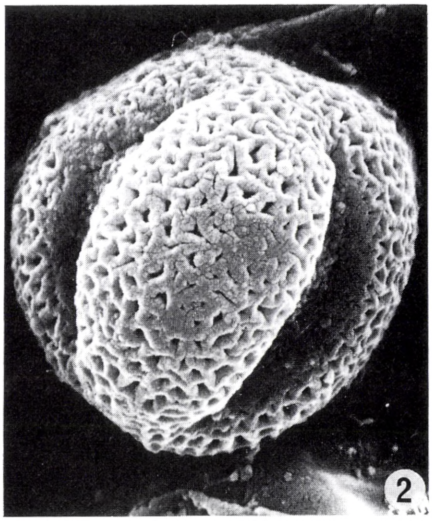
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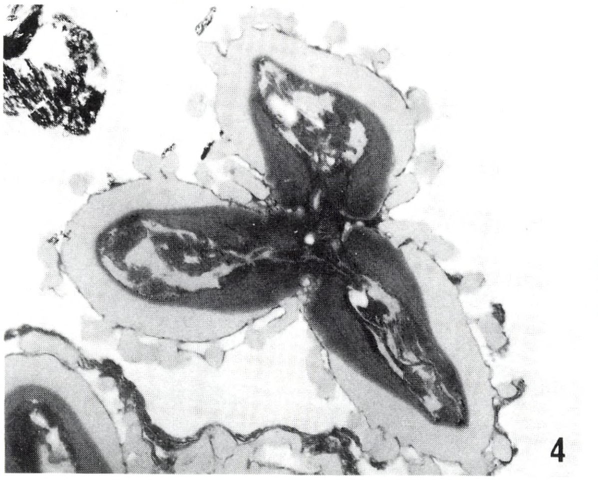
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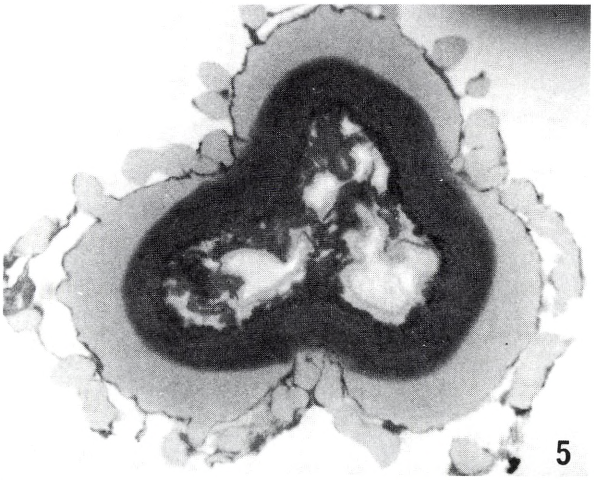
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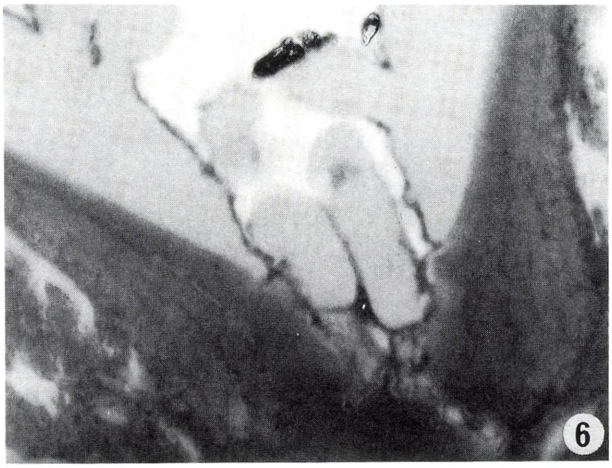
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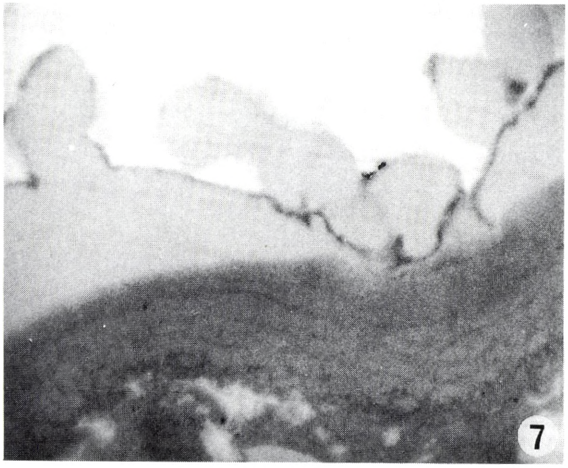
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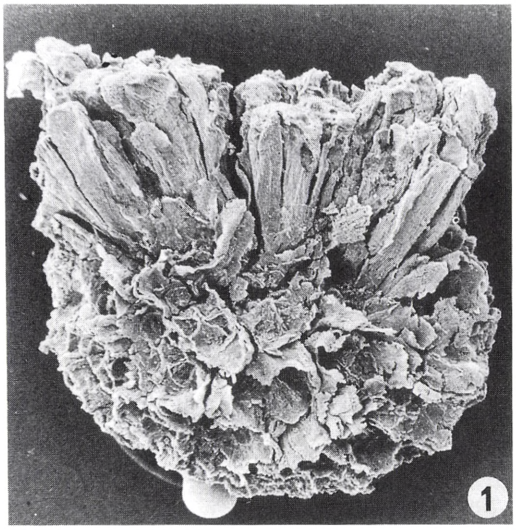
PLATE 9

Fossil *Platanocarpus marylandensis* Friis, Crane & Pedersen sp. nov. from the Upper Albian of the Patapsco Formation (Potomac Group), Maryland, U.S.A.

1. Holotype. Inflorescence showing scars and remains of floral organs and attached pistillate flowers (PP 34576, x 20).
2. Inflorescence showing scars and remains of floral organs and a short portion of the inflorescence axis (PP 34577, x 20).
3. Single pistillate flower showing five carpels with incompletely fused ventral suture (PP 34578, x 90).
4. Single pistillate flower with five carpels and well-developed tepals (PP 34580, x 57).
5. Single pistillate flower with five carpels and well-developed tepals (PP 34581, x 57).
6. Basal part of pistillate flower showing several layers of perianth parts (PP 34595, x 105).
7. Group of pollen grains attached to the surface of perianth of pistillate flower (PP 34585, x 2400).

All figures SEM.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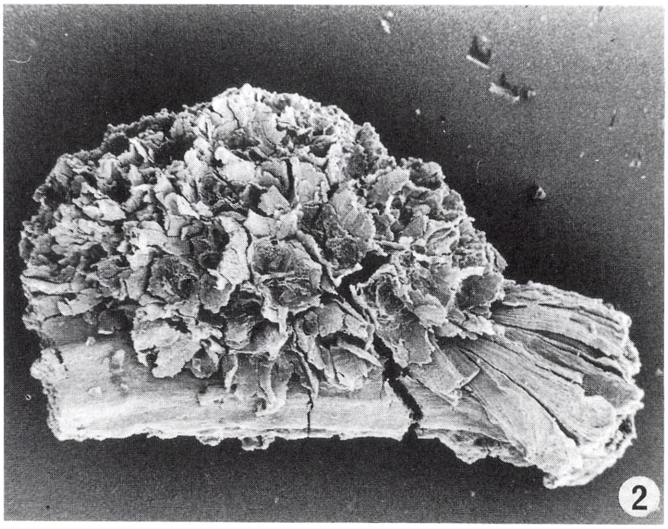
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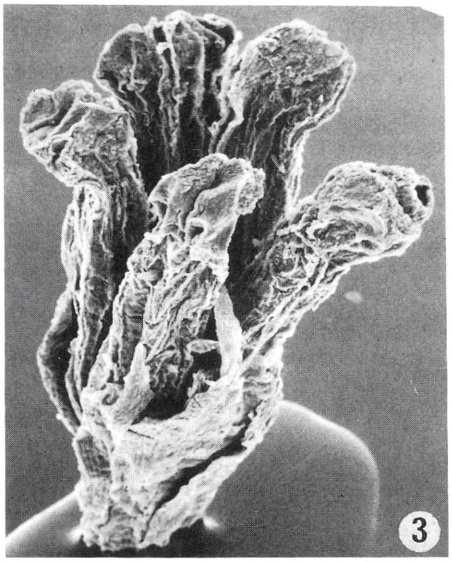
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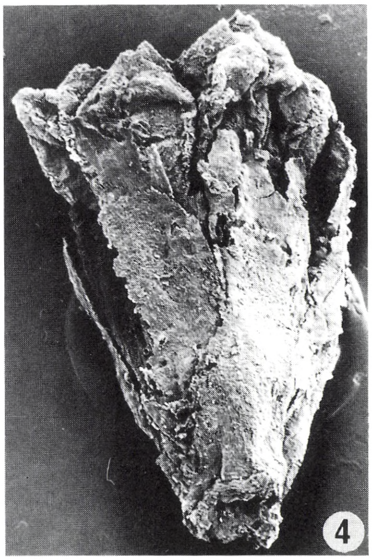
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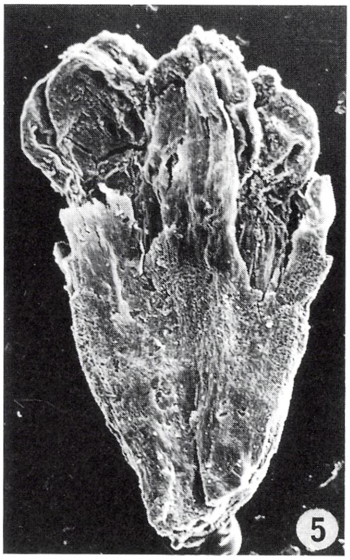
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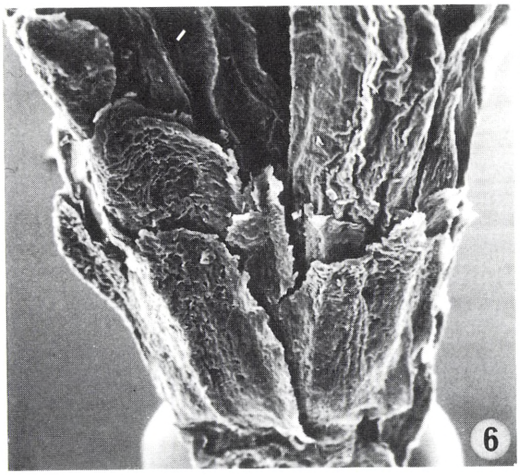
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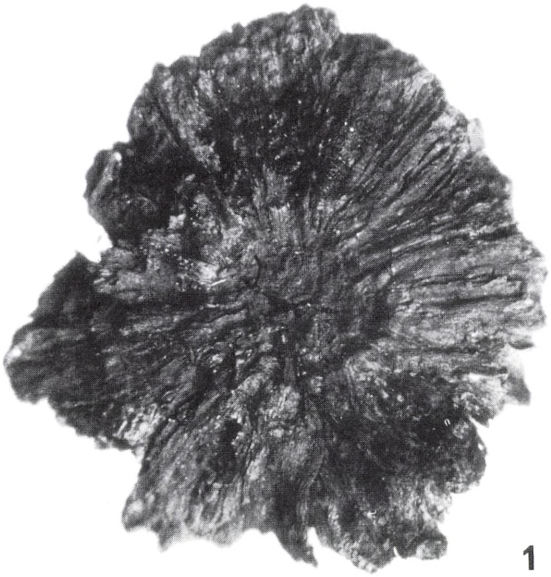
PLATE 10

Fossil *Platanocarpus carolinensis* Friis, Crane & Pedersen sp. nov. from the Santonian-Campanian of the Black Creek Formation, North Carolina, U.S.A.

1. Holotype. Complete inflorescence with numerous pistillate flowers (USNM 401642, x 15).
2. Fragment of inflorescence showing attached pistillate flowers (USNM 401643, x 15).
3. Cuticle of tepals showing attached unicellular hairs (USNM 401645, x 150).
4. Fractured fragment of inflorescence showing attached fruits and occasional seeds (USNM 401644, x 20).
5. Detail of pistillate flowers showing the carpel bases and tepals (USNM 401644, x 70).
6. Detail of carpel surface (USNM 401644, x 500).
7. Pollen grains adhering to carpel surface (USNM 401644, x 3000).
8. Seed cuticle showing chalaza and micropyle (USNM 401646, x 30).

Figs 1-2 reflected light micrographs, figs 3-8 transmitted light micrographs, figs 3-6 SEM.

ch = chalaza, mi = micropyle, t = tepal.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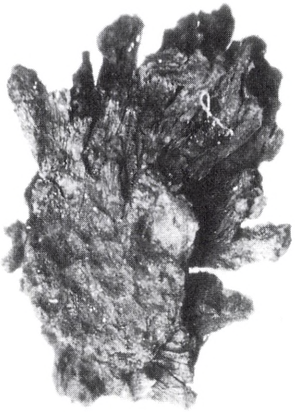
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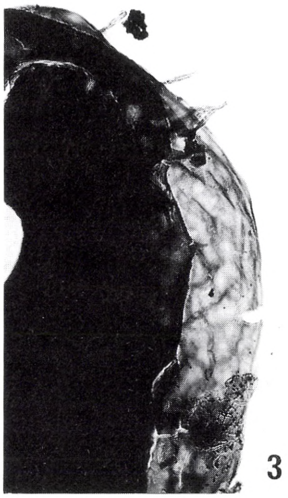
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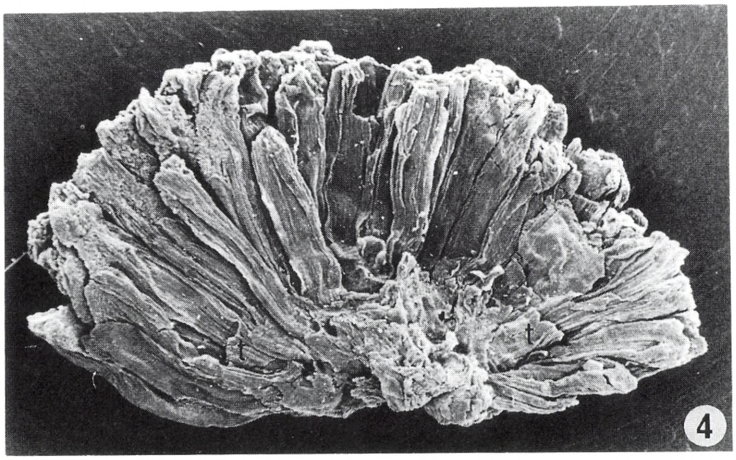

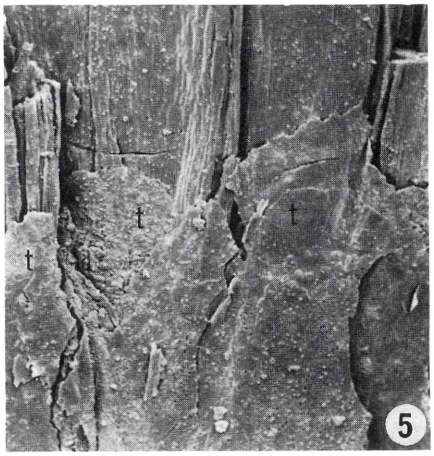

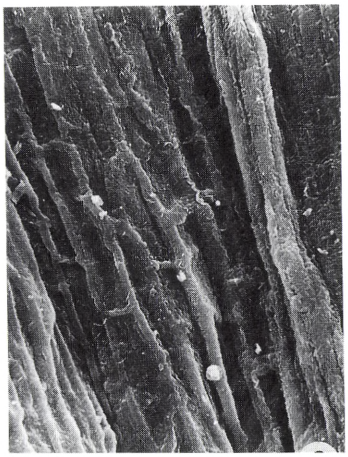

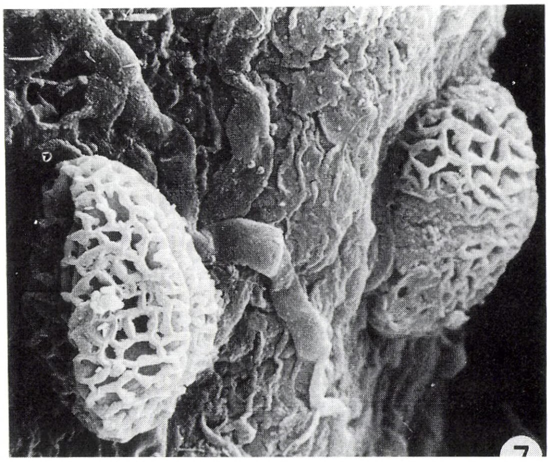
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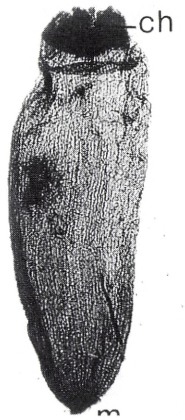

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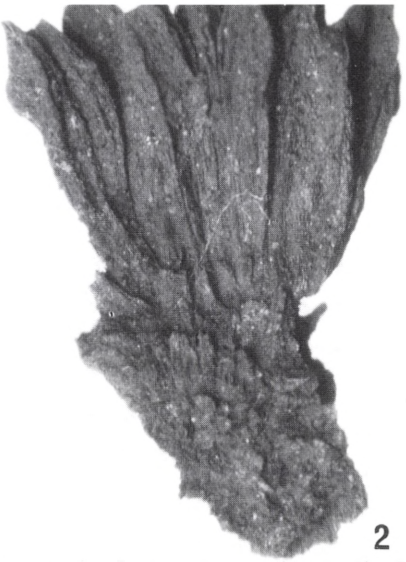
PLATE 11

Fossil *Platanocarpus* sp. from the Santonian-Campanian of Scania, Sweden.

1. Fragment of inflorescence showing numerous carpels (S 100068, x 15).
2. Fragment of inflorescence showing several carpels attached to part of the central spherical receptacle (S 100071, x 15).
3. Fragment of inflorescence showing several carpels (S 100070, x 15).
4. Detail of carpel from figure 3 showing ventral suture (S 100070, x 60).
5. Dispersed fruitlet (S 100069, x 25).
6. Detail of carpel surface (S 100070, x 2000).
7. Pollen grain adhering to carpel surface (S 100070, x 3000).

Figs 1-2 reflected light micrographs, figs 3-7 SEM.

1



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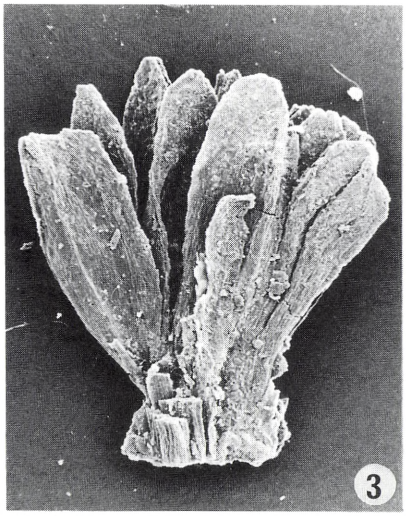

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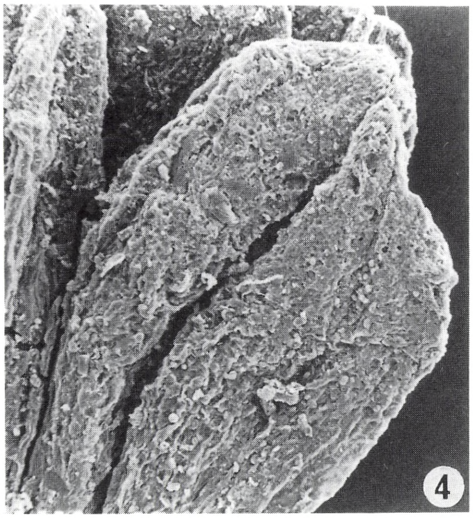

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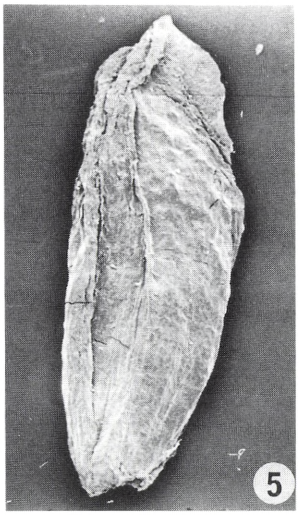

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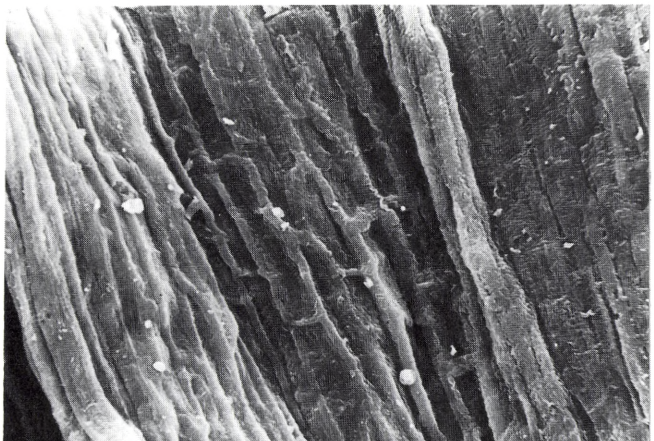

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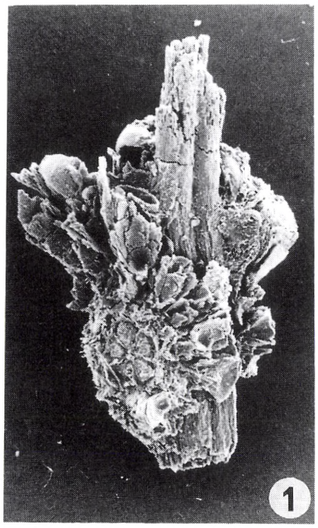
PLATE 12

Fossil unassigned platanaceous pistillate inflorescence from the Santonian-Campanian of Scania, Sweden.

1. Fragment of inflorescence showing scars and remains of floral organs and portion of inflorescence axis (S 100075, x 15).
2. Detail of inflorescence showing scars produced by the five carpels of a single flower (S 100075, x 50).
3. Detail of inflorescence showing attached trichomes (S 100075, x 250).
4. Detail of inflorescence showing fragments of fruitlets and seeds (S 100075, x 75).
5. Detail of inflorescence showing fragment of fruitlet and seeds (S 100075, x 75).
6. Detail of seed wall (S 10075, x 500).
7. Detail of fruit wall (S 100075, x 500).

All figures SEM.
f = fruitlet, s = seed.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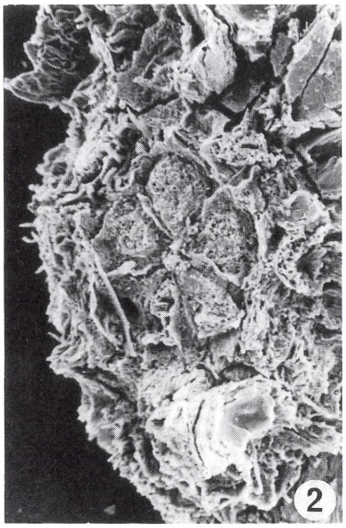
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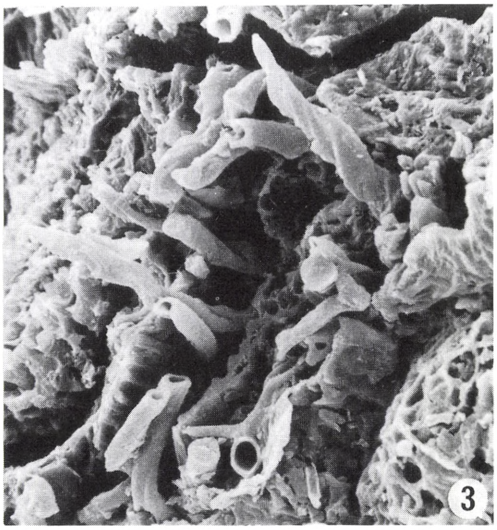
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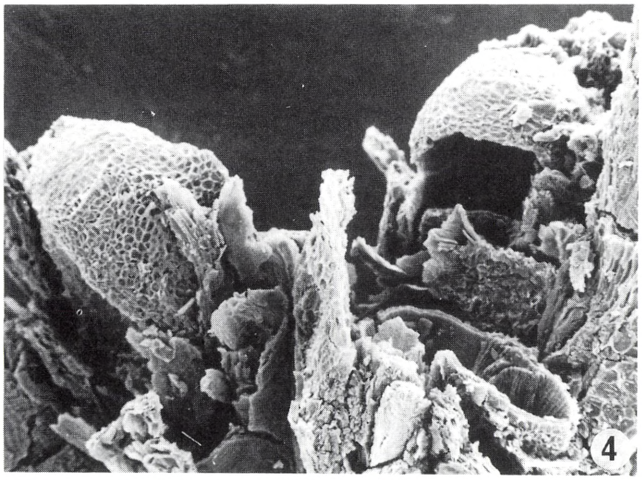
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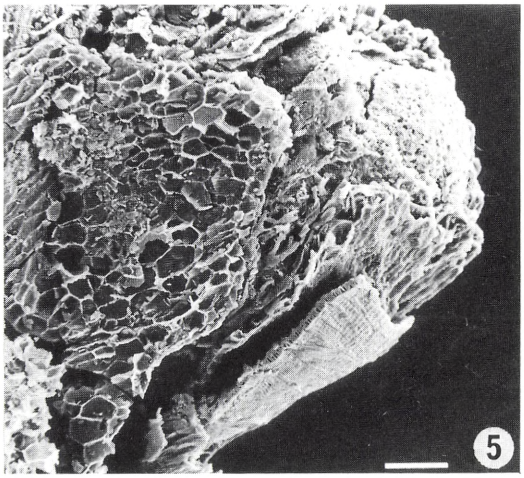
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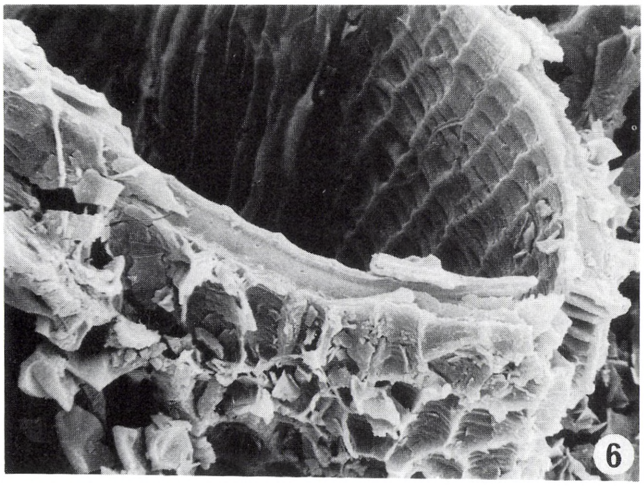
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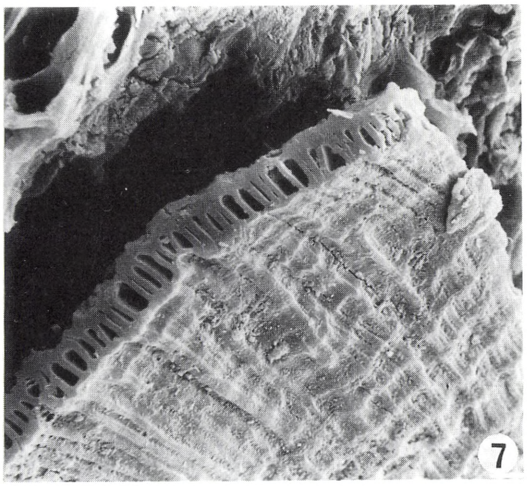
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