QUADRIPLATANUS GEORGIANUS GEN. ET SP. NOV.: STAMINATE AND PISTILLATE PLATANACEOUS FLOWERS FROM THE LATE CRETACEOUS (CONIACIAN-SANTONIAN) OF GEORGIA, U.S.A.

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The Platanaceae are one of the basal-most branches of the main evolutionary line of the eudicot clade, and one of the earliest eudicot lineages to be recognized in the macrofossil record. Because of its phylogenetic position, and the documentation of intralineage temporal morphological change provided by an extensive fossil record, the Platanaceae provide crucial information for understanding phylogenetic relationships at the base of the eudicots. Staminate and pistillate inflorescences and flowers from Coniacian-Santonian strata of Georgia, U.S.A., are an important addition to the known fossil record of Platanaceae. Staminate inflorescences are sessile heads, 0.9–2.5 mm in diameter, formed by ca. 40 closely spaced flowers. Staminate flowers have a whorled, tetramerous, unicyclic perianth, and a tetramerous androecium. Each stamen is opposite a perianth member, and all stamens are inserted on a short androecial ring. Anthers are elongate, the connective is abaxially displaced and is expanded at the apex into a protruding, wedge-shaped extension. Four short androecial appendages are placed on the androecial ring and alternate with the stamen bases. Pistillate inflorescences are sessile heads, 1.1–2.4 mm in diameter, formed by ca. 40 flowers. Pistillate flowers have two weakly differentiated perianth cycles: the outer cycle is connate into a tube, and the inner cycle is also connate, but with four free apical lobes. The apocarpous gynoecium has eight carpels, with two carpels opposite each of the free apical lobes of the inner perianth. Carpels are conduplicate, wedge-shaped, and lack a style. Like other Cretaceous platanaceous taxa, the flowers described from the Coniacian-Santonian of Georgia have a well-developed perianth and a fixed floral merosity, but their tetramerous floral plan differs from the pentamerous pattern of previously described Cretaceous and early Tertiary platanaceous flowers.

Introduction

Few families of angiosperms known from the earliest phases of angiosperm evolution have a sequence of extinct forms that provides a connection to Recent species. The best such sequence is currently provided by the family Platanaceae, in which the genus *Platanus* is the single extant representative of an extremely ancient and formerly more diverse lineage (Crane 1989; Drinnan et al. 1994). The Platanaceae are thought to be one of the earliest branches of a major clade that includes about 75% of living angiosperm species, the nonmagnoliid dicotyledons, or eudicots (Crane et al. 1995). The relatively continuous representation of the family in the Cretaceous and Tertiary fossil record has the potential to provide important insights into the basic morphological features of eudicots, possible phylogenetic relationships among major eudicot taxa, as well as information on evolutionary patterns of character change during a crucial and rapid phase of angiosperm evolution.

Reproductive organs of probable platanaceous affinity are known from strata as old as the lower to middle Albian, from the "Bank near Brooke" locality in the Potomac Group of eastern North America (Crane et al. 1993), and similar stamens are known from the even older Torres Vedras locality of Portugal, which is of probable Valanginian to Hauterivian age (Friis et al. 1994). Reproductive remains of platanaceous affinity are subsequently common in Cretaceous strata (see, e.g., Lesquereux 1892; Krassilov 1973; Knobloch and Mai 1986; Friis et al. 1988; Pedersen et al. 1994) and are extensively represented in the Tertiary fossil record

(see, e.g., Bůžek et al. 1967; Kvaček 1970; Manchester 1986; Crane et al. 1988; Pigg and Stockey 1991). Several of these platanaceous reproductive structures have been included as parts of whole-plant reconstructions (see, e.g., Bůžek et al. 1967; Kvaček 1970; Manchester 1986; Crane et al. 1988, 1993; Pigg and Stockey 1991) and contribute significantly to the understanding of the morphological diversity encompassed during the evolutionary history of the group.

The fossil record documents significant variation in leaf form and floral structure among fossil platanoids (see review by Crane 1989; Drinnan et al. 1994). Platanoid leaves include pinnatifid forms (e.g., *Sapindopsis* [Berry 1921; Hickey and Doyle 1977]), palmately lobed forms with numerous lobes (e.g., *Macginitiea angustiloba* [Manchester 1986]), palmately lobed forms with few, mostly three, lobes (e.g., *Araliopsoides* "*Sassafras*" type [Hickey and Doyle 1977] and *Platanus nobilis* type [Wolfe and Wehr 1987; Pigg and Stockey 1991]), leaves with a terminal palmate and two lateral asymmetrical leaflets (*Platanites hebridicus* [Crane et al. 1988]), entire elliptical leaves with pinnate venation (*Platanus neptuni* [Bůžek et al. 1967; Kvaček 1970]), and perhaps pedately compound forms (e.g., *Dewalquea* [Knowlton 1917; Johnson and Gilmore 1921; Rüffle and Knappe 1977]). There also appear to be intergradations in morphology between some of these leaf forms.

In floral features, the most striking variation in the platanoid group involves the degree of development of the perianth, which appears to be linked to the degree of variation in floral merosity (Crane 1989; Drinnan et al. 1994). Variation also occurs in the shape and fine details of stamens and carpels, and in the presence of hairs at the base of carpels—a feature probably related to fruit dispersal.

Today, the Platanaceae are represented by the single genus *Platanus* with six to nine species distributed in southeastern Asia, the Mediterranean region, and North America, with the greatest diversity in Mexico (Cronquist 1981; Kubitzki 1993; Drinnan et al. 1994). *Platanus* is subdivided into two subgenera, distinguished mostly by the shape of leaves, but also by the presence or absence of a peduncle supporting the characteristic globose unisexual inflorescence units (heads). The species included within subgenus *Platanus* have leaves with a palmately lobed lamina and palinactinodromous venation. The heads have a peduncle that can vary within a species from short to relatively long. *Platanus kerrii,* the single species of subgenus *Castaneophyllum,* has elliptical leaves with pinnate venation, and numerous heads that are sessile on the inflorescence axis. In spite of the differences in foliar features and in the placement of the heads, morphological features of flowers, particularly of stamens and carpels, are homogeneous in extant species of the genus.

In this study, we present staminate and pistillate inflorescences and flowers from Upper Cretaceous strata in southeastern North America that display a suite of morphological features previously observed in mid- and late Cretaceous platanaceous reproductive remains, but that also show aspects of floral organization that have not been previously documented in the platanoid lineage. These reproductive remains further document the diversity in floral morphology among Platanaceae.

Material and methods

A new suite of fossiliferous localities on the Coastal Plain of Georgia in southeastern North America has provided numerous three-dimensionally preserved angiosperm reproductive remains, including the platanaceous inflorescences and detached stamens described here. The fossiliferous sediments belong to the lower part of the Eutaw Formation, and crop out along Upatoi Creek on Fort Benning Military Reservation, in central-western Georgia, U.S.A. Upatoi Creek forms the boundary between Chattahoochee County and Muscogee County, and the locality from where the platanaceous reproductive remains were obtained is on the south bank of the creek (Chattahoochee County), at 32°24'30"N and 84°50'W.

The Eutaw Formation was considered to be of pre-Senonian age (latest Cenomanian and Turonian), because of the absence of structurally advanced Normapolles pollen grains in palynological assemblages (Leopold and Pakiser 1964; Christopher 1982). Christopher (1982) suggested possible stratigraphical equivalence between the Eutaw Formation and the Austin Group (Coniacian-Santonian) of Texas. Studies of calcareous nannofossils support this interpretation and indicate an early to middle Santonian age (Christopher 1982).

The mesofossils occur within unconsolidated clays that are interspersed in coarse to fine sand and silt deposits. The mesofossils are preserved as fusainized, three-dimensional remains, allowing the observation of fine details of floral form and structure. Platanaceous pistillate and staminate heads, as well as dispersed stamens similar to those present in staminate flowers, have been found in only one of the fossiliferous samples collected at different sites along Upatoi Creek. The fossils were isolated from the clays by disintegrating bulk samples in water and washing through a series of sieves. Residual lumps of clay were dissolved by immersion in a detergent solution, followed by rinsing with water. Remaining clay matrix and other minerals were removed by sequentially soaking the charcoalified remains in HCl and HF acids, after which the fossils were thoroughly rinsed with water and air-dried. The fossil remains were then sorted using a stereoscopic microscope. Platanoid pistillate and staminate inflorescences as well as dispersed stamens were selected for detailed examination. Specimens were mounted on stubs, coated with gold and observed using a scanning electron microscope (AMRAY 1810). After scanning, several pistillate and staminate inflorescences were dissected, and single flowers were isolated. The staminate and pistillate flowers were recoated with gold, scanned, and after detailed examination, further dissections of the flowers were made. All fossil material is housed in the Paleobotanical Collections at the Field Museum, Chicago (PP45001–PP45077).

Systematics

FAMILY—PLATANACEAE

GENUS—*QUADRIPLATANUS* MAGALLÓN-PUEBLA, HERENDEEN ET CRANE, GEN. NOV.

TYPE SPECIES—*QUADRIPLATANUS GEORGIANUS* MAGALLÓN-PUEBLA, HERENDEEN ET CRANE, SP. NOV.

GENERIC DIAGNOSIS.   Spherical to hemispherical inflorescence units bearing strictly pistillate or staminate flowers. Staminate flowers actinomorphic, formed by a tetramerous perianth and a tetramerous androecium. Perianth unicyclic, with four tepals, each opposite a stamen. Androecium unicyclic, formed by four stamens and four short androecial appendages. Stamens and androecial appendages alternating and originating from a continuous short ring of tissue. Stamens sessile or with a very short filament; anthers basifixed, long, with valvate dehiscence; connective thin and basally narrow, abaxially displaced at the level of the thecae, and forming a pronounced wedge-shaped extension above the thecae. Androecial appendages formed by a short stalk and a broad apex extending toward the center of the flower; may be weakly developed or absent. Pollen grains spherical to prolate, tricolpate; exine ornamentation reticulate. Pistillate flowers tetramerous, actinomorphic, hypogynous with dicyclic perianth and apocarpous gynoecium. Perianth cycles weakly differentiated. Gynoecium with eight free carpels. Carpels wedge-shaped, strongly conduplicate with the adaxial region extending into the center of the flower forming an adaxial edge; ventral suture extending along the length of the adaxial edge and also onto the flat apex of carpel; tissue flanking the suture extending to apex of carpel forming a broad bilobed platform. Each carpel contains one pendulous ovule.

DERIVATION OF GENERIC NAME.   From the Latin prefix *quadri-*, in reference to the tetramerous organiza-

tion of both staminate and pistillate flowers, and *platanus,* in reference to the affinity to Platanaceae.

REMARKS ON THE GENUS. The new genus differs from other genera of fossil and extant Platanaceae in its regular tetramerous floral organization. Previously known fossil platanaceous spheroidal heads bearing staminate flowers with a developed perianth have been assigned to *Platananthus* or to *Hamatia. Platananthus* was erected by Manchester (1986) and emended by Friis et al. (1988) to accommodate extinct platanaceous inflorescences and flowers that differ mostly from extant *Platanus* in having flowers with a well-developed perianth and five stamens. *Hamatia* (Pedersen et al. 1994) includes staminate heads and flowers that are similar in most respects to those of *Platananthus* but differ in stamen morphology, particularly in the presence of an adaxial, downward extension of the connective between the thecae. The staminate inflorescences and flowers of *Quadriplatanus* are similar to those of *Platananthus* in general morphology. The stamens frequently exhibit a downward adaxial prolongation of the connective that is similar to, and sometimes as extensive as, the one present in the stamens of *Hamatia.* However, the staminate flowers of *Quadriplatanus* differ from other known staminate platanaceous flowers in having a tetramerous pattern of organization, which includes four stamens.

Previously known fossil platanaceous heads bearing pistillate flowers with a developed perianth have been accommodated within the genera *Macginicarpa* and *Platanocarpus. Macginicarpa* was erected by Manchester (1986) to include fossil platanaceous pistillate spheroidal heads that differ mostly from extant *Platanus* in having a well-developed perianth, and five carpels. *Platanocarpus* was established by Friis et al. (1988) for fossil platanaceous spheroidal inflorescences that bear pistillate flowers with a well-developed perianth, apocarpous gynoecium, and carpels lacking a differentiated style. The number of carpels in the flowers of *Platanocarpus* was not specified, but all the species assigned to this genus have five carpels. The pistillate flowers of *Quadriplatanus* are similar in general structural features and morphological details to the flowers of *Platanocarpus,* especially regarding the absence of a differentiated style, but differ in having flowers organized on a tetramerous plan. Although most morphological characteristics of staminate and pistillate flowers of *Quadriplatanus* are known in previously described fossil platanaceous taxa, the strong evidence indicating that staminate and pistillate inflorescences were produced by the same plant species, and the tetramerous meristic pattern of staminate and pistillate flowers, provide the basis for establishing a new genus to accommodate these reproductive structures.

SPECIES—*QUADRIPLATANUS GEORGIANUS* MAGALLÓN-PUEBLA, HERENDEEN ET CRANE, SP. NOV. (FIGS. 1–64)

SPECIFIC DIAGNOSIS. Unisexual spherical to hemispherical heads attached helically on inflorescence axis. Staminate flowers obconical. Tepals spatulate with expanded, rounded apices; tepals basally fused, distally valvate to slightly imbricate, but overlapping apically in one of two patterns: with the lateral margins of one tepal internal to all others, the lateral margins of the opposite tepal external to all others, and the two remaining tepals with one margin internal, and the other margin external; or with two opposite tepals internal, and the other two external. Thecae comprising 50%–80% of total length of the stamen, the rest corresponding mostly to the apical extension of the connective. Apical extension of the connective expanded laterally, apically into a short, conical horn, and sometimes adaxially, extending downward between the thecae. Pollen sacs narrow proximally and wider distally; pollen release intermediate between latrorse and introrse. Connective narrow at the base, broadening distally. Center of the flower an undifferentiated mound with eight basal lobes. Pistillate flowers obconical. Outer perianth cycle connate, forming a tube. Inner perianth cycle connate throughout most of its length, but with four free apical lobes; connate portion sometimes folded inwardly, forming longitudinal plications; each free apical lobe is opposite two carpels. Carpels with large glandulose papillae on their lateral flanks and near the apex. Ovule with a longitudinal adaxial flap of tissue.

DERIVATION OF SPECIFIC EPITHET. From the state of Georgia, U.S.A.

HOLOTYPE. PP45014 (figs. 4, 10, 12, 13, 25, 26, 28), housed in the Paleobotanical Collections of the Field Museum, Chicago.

PARATYPES. PP45002 (fig. 2), PP45007 (fig. 1), PP45011 (figs. 5, 7–9, 14), PP45013 (fig. 16), PP45015 (fig. 30), PP45018 (figs. 17, 19), PP45019 (fig. 18), PP45021 (fig. 22), PP45028 (figs. 6, 11, 15, 27, 29), PP45029 (fig. 3), PP45054 (fig. 24), PP45062 (fig. 21), PP45065 (fig. 20), PP45067 (figs. 31, 32), PP45069 (fig. 23).

OTHER MATERIAL. Staminate inflorescences: PP45006, PP45008, PP45012, PP45016, PP45017, PP45020, PP45022, PP45024, PP45032, PP45033, PP45042, PP45043, PP45048–PP45053, PP45055–PP45061, PP45063, PP45064, PP45066, PP45068, PP45070–PP45077. Pistillate inflorescences: PP45001, PP45003–PP45005, PP45009, PP45010, PP45023, PP45025, PP45027, PP45030, PP45031, PP45036, PP45037, PP45040, PP45041, PP45044–PP45047.

TYPE LOCALITY. 32°24'30"N, 84°50'W, on the south bank (Chattahoochee County) of Upatoi Creek, Fort Benning Military Reservation, border between Chattahoochee County and Muscogee County, central-western Georgia, U.S.A.

AGE AND STRATIGRAPHY. Lower part of the Eutaw Formation (Late Cretaceous, Coniacian-Santonian).
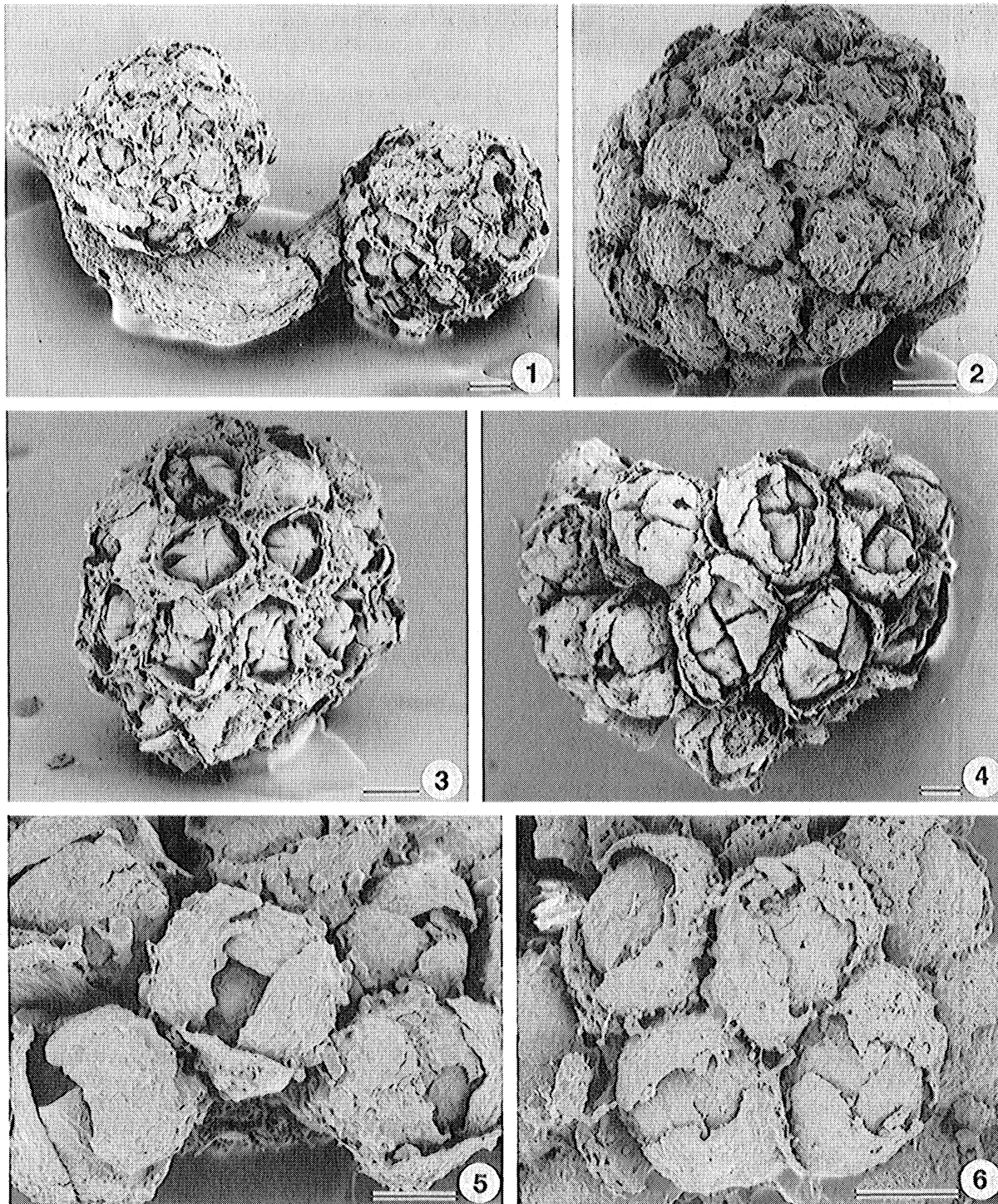
Figs. 1–6 *Quadriplatanus georgianus,* staminate inflorescences and flowers. Fig. 1, Sessile spherical heads spirally attached to inflorescence axis. PP45007. Bar = 200 μm. Fig. 2, Head with flower buds, where tepals cover stamens completely. PP45002. Bar = 200 μm. Fig. 3, Staminate flowers in which apices of tepals have been abraded, showing triangular apices of four stamens. PP45029. Bar = 200 μm. Fig. 4, Incomplete head with partially opened flowers, showing triangular apices of the stamens. PP45014. Bar = 200 μm. Fig. 5, Flowers showing four tepals in which one tepal is innermost, the opposite tepal is outermost, and the two remaining tepals have one margin placed internally, and the other margin externally. PP45011. Bar = 200 μm. Fig. 6, Flowers showing four tepals with expanded apices in an aestivation pattern where an opposite pair of tepals has its margins placed internally, and the two other tepals have their margins placed externally. PP45028. Bar = 200 μm.

DESCRIPTION. *Staminate inflorescences and flowers.* The spherical staminate heads are borne laterally on the inflorescence axis in a spiral pattern (fig. 1). Heads are 0.89–2.55 mm in diameter ($\overline{X}$ = 1.25 mm) and have approximately 40 closely spaced staminate flowers. Staminate flowers are obconical, 0.48–0.74 mm long ($\overline{X}$ = 0.65 mm), and 0.28–0.97 mm in maximum diameter ($\overline{X}$ = 0.52 mm). The flowers are actinomorphic, with whorled phyllotaxis and a tetramerous perianth and androecium (figs. 3–6).

The perianth is unicyclic (figs. 5–8). The tepals are spatulate, tapering basally and rounded apically, with the apex widely expanded laterally (fig. 9). The tepals are basally connate and form a very short tube. Distally, at the level of the anthers, the tepals are valvate or very slightly overlapping (fig. 9). Apically, the expanded apices overlap in two different aestivation patterns. In the most frequent aestivation pattern, the lateral margins of one tepal are placed internally to all other tepals; the opposite tepal has its lateral margins placed externally to all other tepals, and the two remaining ones have one margin outside, and the other one inside (figs. 5, 7, 9). In the less frequent aestivation pattern, the lateral margins of two opposite tepals are internal, and the two other tepals are external (figs. 6, 8). In young flowers, the wide apices of the tepals enclose the stamens almost completely (figs. 5–8). During the early stages of floral development, the tepals are longer than the stamens. Epidermal cells on the abaxial surface of the tepals are rectangular and arranged in longitudinal rows. Near the margins and apex of the tepals, the rectangular cells have undulat-ing walls (fig. 10), and at the apex they become almost isodiametric with pronounced grooves between contiguous cells. Anomocytic stomata are also present near the tepal apices (fig. 11). On the adaxial surface of the tepals, the epidermal cells apparently enclose rectangular to square crystals. These cells are frequently abraded, leaving characteristic superficial angular cavities (fig. 12).

The androecium is formed by four closely spaced stamens, each placed opposite a tepal (figs. 13, 14). Each stamen has a very short filament, long thecae, and a pronounced extension of the connective above the thecae. Detached, mature stamens are 0.86–1.34 mm long ($\overline{X}$ = 1.07 mm), and 0.34–0.63 mm in maximum width ($\overline{X}$ = 0.55 mm) at the level above the anthers. The thecae are 0.71–1.06 mm long ($\overline{X}$ = 0.83 mm) and account for approximately 78% of the length of the stamen, the rest corresponding mostly to the apical extension of the connective. Immature stamens in situ are 0.24–0.51 mm long ($\overline{X}$ = 0.32 mm) and 0.13–0.24 mm in maximum width ($\overline{X}$ = 0.17 mm). The thecae are proportionately much shorter than in mature stamens, being 0.11–0.3 mm long ($\overline{X}$ = 0.17 mm), and corresponding to approximately 51% of the total length of the stamen. The remainder of the length is accounted for mainly by the apical extension of the connective (figs. 14, 15).

Stamens are placed on a very short ring of tissue (fig. 14). The lateral sides of contiguous stamens are in contact throughout their length (fig. 16). Stamens are nearly sessile in early stages of development (figs. 14, 15), but apparently, the filament grows slightly as

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Figs. 7–15 *Quadriplatanus georgianus,* staminate flowers. Fig. 7, Partially opened flower in apical view, showing four free imbricate tepals with the margins of one tepal internal to all others, the margins of the opposite tepal external to all others; the two other tepals have one margin placed internally, and the other externally. PP45011. Bar = 100 μm. Fig. 8, Partially opened flower in apical view, showing four free imbricate tepal lobes with the margins of one pair of opposite tepals placed internally, and the margins of the other two tepals placed externally. PP45011. Bar = 100 μm. Fig. 9, Flower from side view, with tepals slightly overlapping at the level of the anthers, but apically expanded. PP45011. Bar = 100 μm. Fig. 10, Abaxial surface of tepal with elongated epidermal cells forming longitudinal rows, and cells with undulating margins toward the tepal margins. PP45014. Bar = 10 μm. Fig. 11, Abaxial surface of tepal, near the apex, with epidermal cells with undulating walls and deep grooves, and anomocytic stomata. PP45028. Bar = 10 μm. Fig. 12, Adaxial surface of tepal, with abraded epidermal cells that apparently enclose square to rectangular crystals, leaving rows of superficial angular cavities. PP45014. Bar = 10 μm. Fig. 13, Flower from top view showing triangular apices of the four stamens, each opposite a tepal. PP45014. Bar = 100 μm. Fig. 14, Flower in longitudinal section, showing the single perianth cycle, androecium, and an undifferentiated mound at the center of the flower. The flower is at an early developmental stage, and tepals cover the stamens completely. Tepals are opposite the stamens, and the stamens are placed on a short androecial ring (arrows). PP45011. Bar = 100 μm. Fig. 15, Stamen in early developmental stage, dissected from flower, showing elongate thecae and strongly developed apical extension of the connective. PP45028. Bar = 50 μm.

Figs. 16–24 *Quadriplatanus georgianus,* stamens. Fig. 16, Flower with tepals removed, showing stamens from abaxial side. Lateral sides of adjacent stamens are in contact throughout their length, and apical extensions of connectives converge at the center of the flower. PP45013. Bar = 100 μm. Fig. 17, Dispersed stamen in adaxial view with short filament, long anthers, and apical extension of connective. The apical extension of the connective is distally flattened, overhangs slightly the anthers, and has a moderate downward adaxial prolongation between the thecae. PP45018. Bar = 100 μm. Fig. 18, Dispersed, incomplete stamen in adaxial view. Pollen sacs are narrow near the base, and wider apically, dehiscence is valvate, and pollen release is intermediate between introrse and latrorse. PP45019. Bar = 100 μm. Fig. 19, Dispersed stamen, seen from below, showing the thin, abaxially displaced connective. PP45018. Bar = 100 μm. Fig. 20, Dispersed stamen in abaxial view. The connective is narrow at the base, broadens apically, and above the thecae it expands laterally and distally, forming the protruding apical extension. PP45065. Bar = 100 μm. Fig. 21, Dispersed stamen in partial lateral view. The apical extension of the connective forms a short, conical, horn-like prolongation that is displaced adaxially. Glandulose papillae occur on the surface of thecae (arrows). PP45062. Bar = 100 μm. Fig. 22, Dispersed stamen in adaxial view. The apical extension of the connective shows the apical, horn-like extension (arrow) and forms a downward prolongation with a rounded tip between the thecae. PP45021. Bar = 100 μm. Fig. 23, Dispersed stamen in adaxial view. The apical extension of the connective forms a long, thin downward prolongation between the thecae. PP45069. Bar = 100 μm. Fig. 24, Dispersed stamen in lateral view, with massive downward adaxial prolongation of the apical extension of the connective. PP45054. Bar = 100 μm.
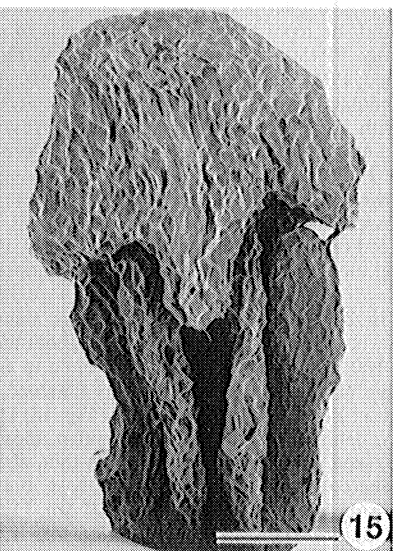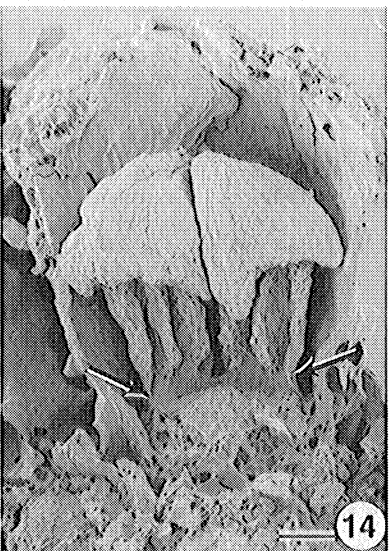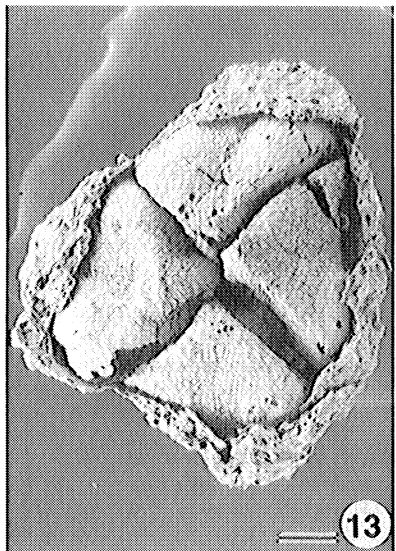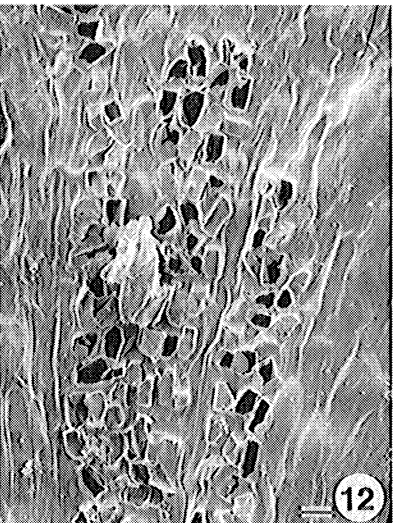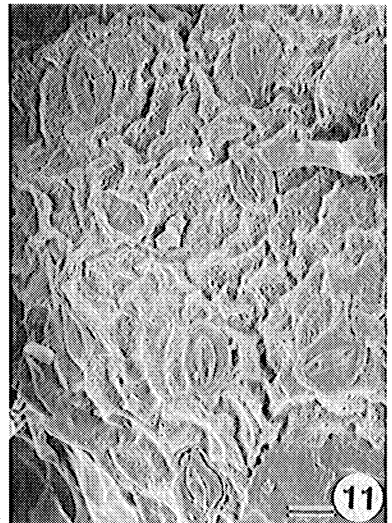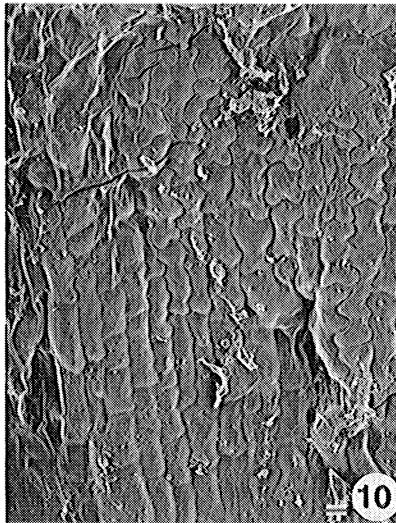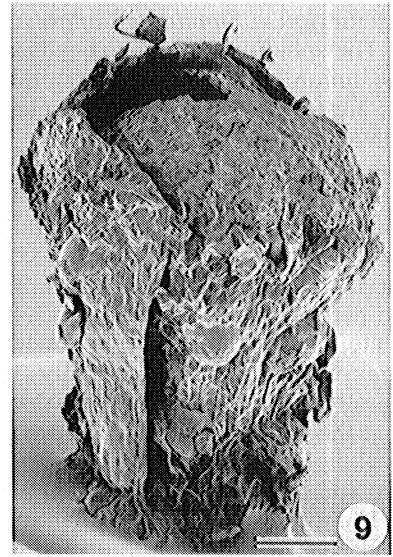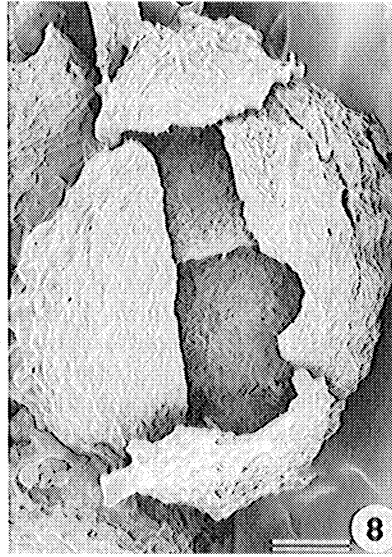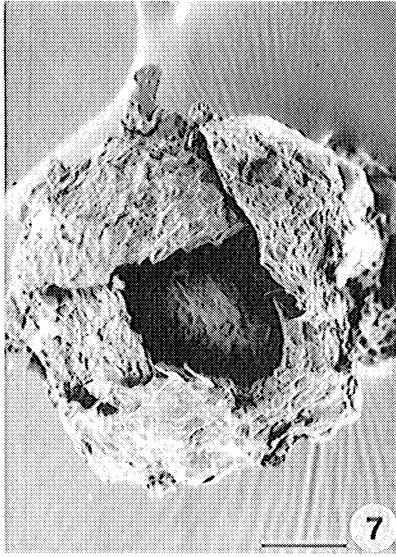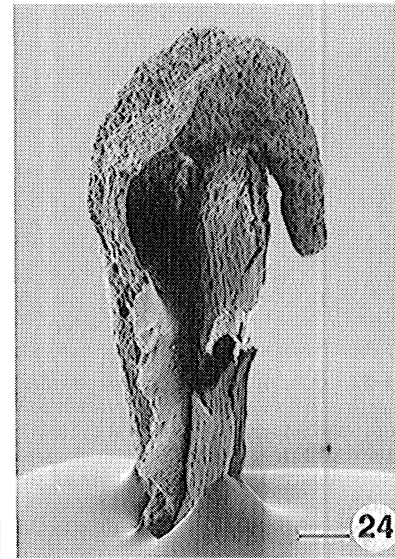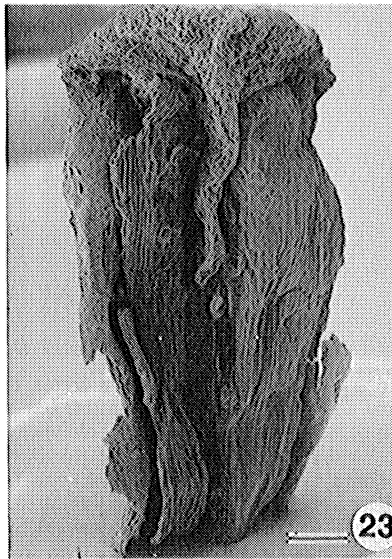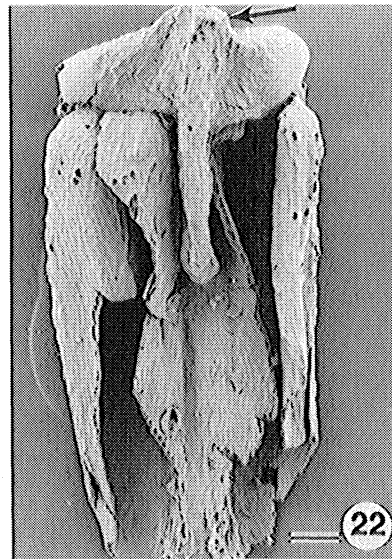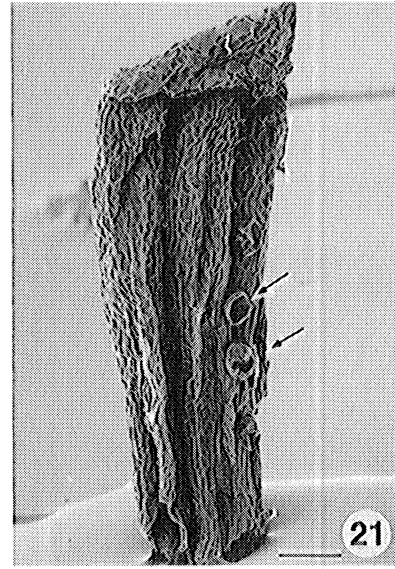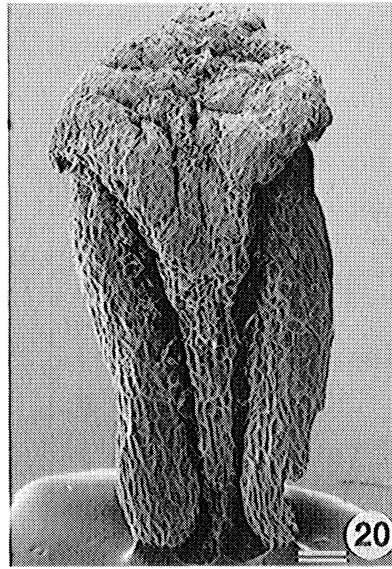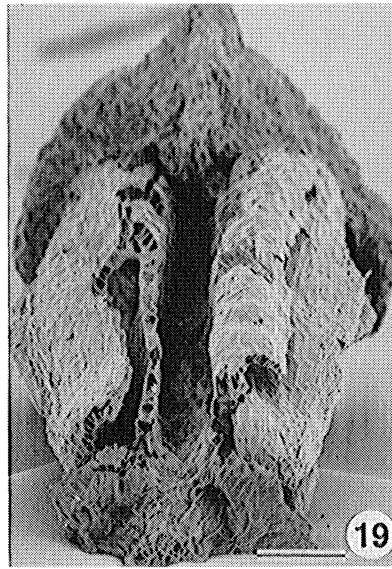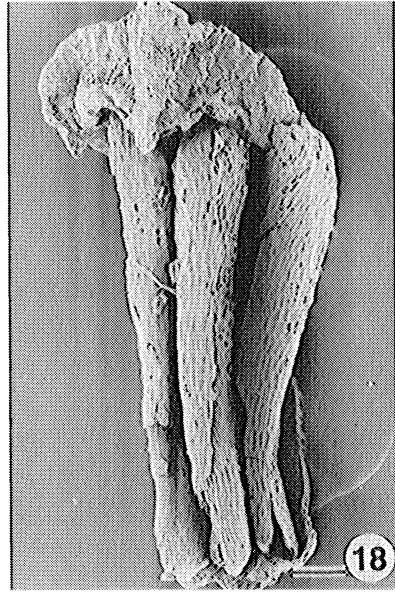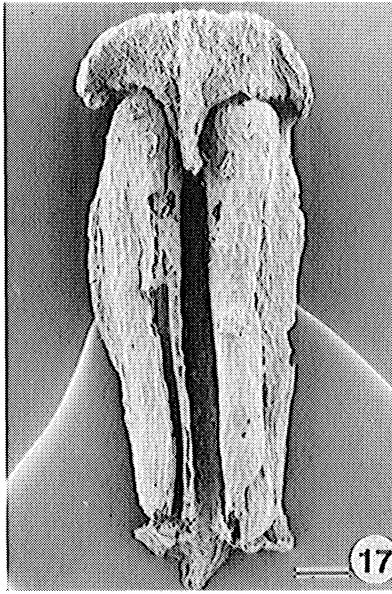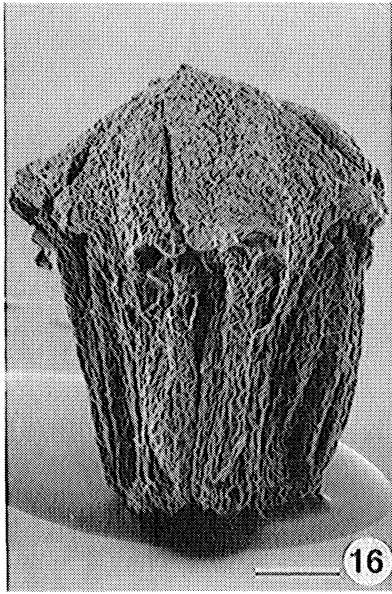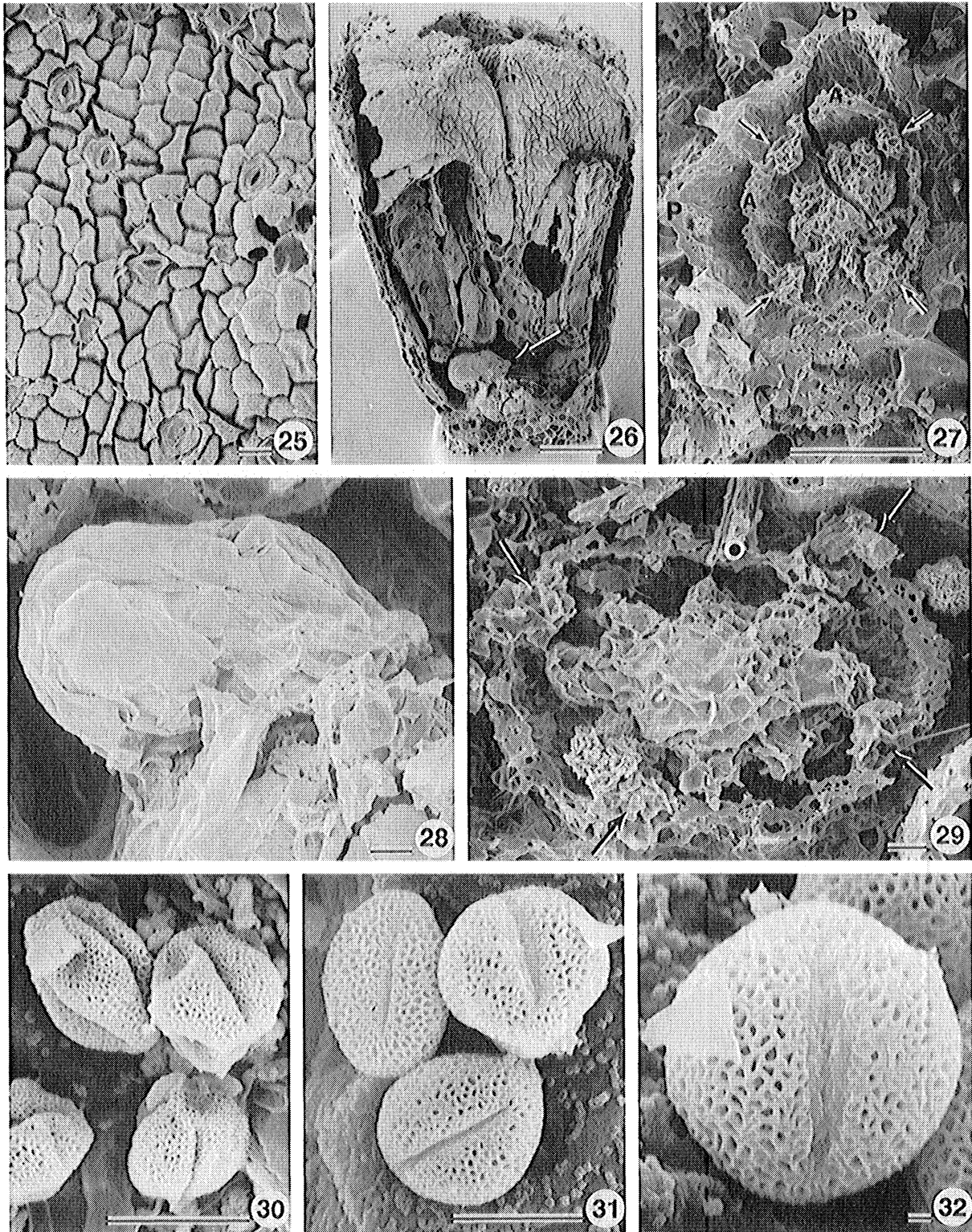
Figs. 25–32 *Quadriplatanus georgianus,* dissected staminate flowers and pollen grains. Fig. 25, Epidermal cells on the apical extension of the connective, with deep grooves between cells, and anomocytic stomata. PP45014. Bar = 10 μm. Fig. 26, Flower in longitudinal section, showing the perianth cycle, androecial cycle with stamens, and one of the androecial appendages (arrow). The androecial appendage is placed on the androecial ring, alternating with stamens, and underneath the thecae. PP45014. Bar = 100 μm. Fig. 27, Dissected flower with tepals and stamens removed, showing the base of the perianth cycle (*P*) and androecial cycle (*A*). The androecial cycle has four flaps of tissue corresponding to androecial appendages (arrows) alternating with filament bases. PP45028. Bar = 100 μm. Fig. 28, Magnification of fig. 26 showing androecial appendage with rounded to flattened fleshy apex, extending toward center of the flower. PP45014. Bar = 10 μm. Fig. 29, Dissected flower with tepals and stamens removed, showing androecial cycle with small flaps (arrows) and the filament of one stamen (dot). The center of the flower is an undifferentiated mound of tissue with eight basal lobes. PP45028. Bar = 10 μm. Fig. 30, Pollen grains

stamens reach maturity (fig. 17). Anthers are bithecal and tetrasporangiate. Pollen sacs are narrow near the base, and wider distally (fig. 18). Each theca dehisces through a longitudinal slit with proximal and distal transverse prolongations, to form valves (fig. 18). Because of the basal narrowing of the pollen sacs, the transverse prolongations of the dehiscence line are more extensive at the distal end of the thecae than at its proximal end, and the valves are wider distally than proximally (fig. 18). Pollen release is intermediate between latrorse and introrse (fig. 18).

The connective is displaced toward the abaxial side of the anther (fig. 19). It is narrow near the base but broadens gradually distally (fig. 20). Above the thecae, it expands strongly laterally, distally, and adaxially, forming a massive apical extension (figs. 14–18, 20–24). The apical extension of the connective is wedge-shaped (fig. 21) and triangular when viewed from above (fig. 13). It slightly overhangs the thecae laterally (fig. 17, 20), and abaxially it has a shallow median longitudinal groove, forming two slight abaxial lobes (figs. 13, 20). In lateral view, the apical extension of the connective increases in height radially toward the center of the flower, forming a slightly prominent adaxial horn-like conical crest (fig. 21). In several stamens, the apical extension of the connective grows downward adaxially between the thecae, forming a narrow prolongation (figs. 22–24), sometimes with a rounded, drop-like tip (fig. 22). Epidermal cells on the pollen sacs are longitudinally elongate, arranged in longitudinal rows. Epidermal cells on the apical expansion of the connective are polygonal, approximately isodiametric, with deep grooves between contiguous cells. Anomocytic stomata are present on the apical extension of the connective (fig. 25). Large papillae may occur along the adaxial surface of the thecae (fig. 21).

In some flowers there are four androecial appendages in addition to the stamens. The androecial appendages are small, relatively undifferentiated structures placed on the ring of tissue that bears the stamens (figs. 26, 27). These structures alternate with stamen bases and are situated beneath the thecae of adjacent stamens (fig. 26). In young flowers, the androecial appendages appear as small undifferentiated flaps on the androecial ring (fig. 27). In more developed flowers, the androecial appendages have a narrow base, and a laterally and radially expanded fleshy apex that is oriented toward the center of the flower (fig. 28). Although it is uncertain whether these structures represent staminodes, their placement in the same whorl as the stamens, and their origin from the same ring of tissue, indicates that they are androecial in nature. The

center of the flower is occupied by a shallow, undifferentiated mound of tissue with eight weakly differentiated basal lobes (fig. 29).

Pollen grains found inside the dispersed anthers are tricolpate and prolate to nearly spherical (figs. 30, 31). They are small, 11–16.9 μm in polar length ($\overline{X} = 12.7$ μm), and 7.7–16.5 μm in equatorial diameter ($\overline{X} = 10$ μm). Exine ornamentation is uniformly reticulate, with stout muri (figs. 31, 32). The colpi extend nearly from pole to pole, are lenticular, and the aperture membrane is slightly granulose (fig. 32).
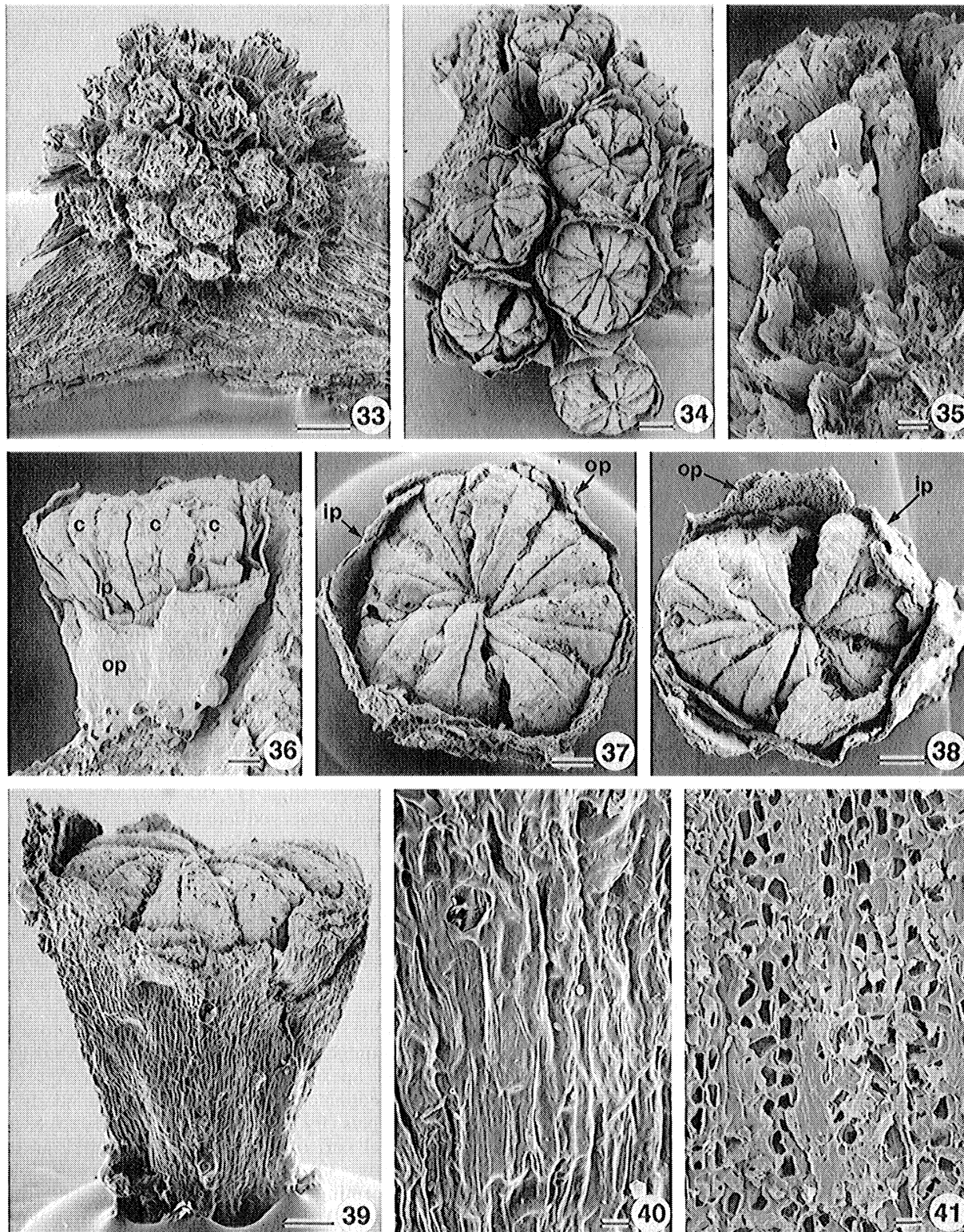
Pistillate inflorescences and flowers. The sessile pistillate spherical to hemispherical heads are borne laterally on the inflorescence axis (figs. 33, 34). Some heads appear to be subtended by a bract. Heads are 1.14–2.39 mm in maximum diameter ($\overline{X} = 1.89$ mm). There are approximately 40 closely spaced flowers in each head, and thin, linear bract-like structures between contiguous flowers (fig. 35). The pistillate flowers are 0.82–0.97 mm long ($\overline{X} = 0.89$ mm), and 0.47–0.94 mm in maximum diameter ($\overline{X} = 0.67$ mm). The flowers are obconical (fig. 36), hypogynous and actinomorphic (fig. 37), although because of mutual pressure in the head, some flowers have a somewhat elliptical outline when viewed from above (fig. 38). The floral organs are arranged in whorls, with a basic tetramerous pattern of organization. Flowers have two cycles of perianth and an apocarpous gynoecium (figs. 36–38).

The two perianth cycles are weakly differentiated (figs. 39, 42, 46, 47, 49, 50). The members of the outer perianth cycle are at least as long as the carpels in mature flowers (figs. 39, 45–47); they are connate through their preserved length, but their apices are not preserved in the available material. The outer perianth tube tightly encloses the inner floral cycles (figs. 39, 46, 47). The abaxial epidermal cells are rectangular and arranged in longitudinal rows (fig. 40). The adaxial epidermal cells are square to rectangular and apparently each contains a square to rectangular crystal. The cells are frequently abraded, leaving characteristic cavities (fig. 41).

The inner perianth cycle is formed by four tepals that are connate for most of their length, but that are free at the apex and form rounded lobes (figs. 42, 49, 50). The connate portion of the tepals is nearly as tall as the carpels (fig. 42), and the free lobes cover at least the abaxial part of the apex of the carpels in mature flowers (fig. 38). The inner perianth cycle folds inwardly, forming longitudinal tube-like folds (figs. 42, 43, 49, 50). There are apparently four longitudinal folds per flower, placed regularly at approximately 90°

Figs. 33–41 *Quadriplatanus georgianus,* pistillate inflorescences and flowers. Fig. 33, Sessile spherical head attached to inflorescence axis, with heavily abraded flowers. PP45023. Bar = 200 µm. Fig. 34, Incomplete head with closely spaced pistillate flowers. PP45037. Bar = 200 µm. Fig. 35, Head with broken flowers, showing bracts (arrow) among flower bases. PP45037. Bar = 100 µm. Fig. 36, Flower in lateral view, with perianth partially broken, showing an outer cycle (*op*), an inner cycle (*ip*), and abaxial sides of carpels (*c*). PP45037. Bar = 100 µm. Fig. 37, Flower in apical view, circular in outline, showing apical portions of the outer perianth cycle (*op*), and apical portions of inner perianth cycle (*ip*), which are at least as tall as the carpels. PP45037 [flower d]. Bar = 100 µm. Fig. 38, Flower in apical view, elliptical in outline, with outer perianth cycle (*op*), and lobes of inner perianth cycle (*ip*) covering the abaxial portion of carpels. PP45037 [flower a]. Bar = 100 µm. Fig. 39, Flower in lateral view, showing outer perianth cycle completely connate into a conical tube. PP45037 [flower d]. Bar = 100 µm. Fig. 40, Abaxial surface of outer perianth cycle, with elongated epidermal cells in longitudinal rows. PP45037 [flower d]. Bar = 10 µm. Fig. 41, Adaxial surface of tepal, with abraded epidermal cells that apparently enclose square to rectangular crystals, leaving superficial angular cavities. PP45037 [flower d]. Bar = 10 µm.

from one another. The epidermal cells on the abaxial and adaxial surfaces of the tepals of the inner perianth cycle are rectangular, organized in longitudinal rows, and their transverse walls are not strongly marked. The tips of the tepals are somewhat thickened and fleshy (fig. 44). Figures 45–50 show the sequential dissection of a flower, and the placement and differences between the outer and inner perianth cycles.

The apocarpous gynoecium is formed by eight tightly packed carpels (figs. 34, 37, 38, 51). In rare samples, fewer than eight carpels (i.e., seven, and apparently six in one badly preserved flower) are present (figs. 45, 48). Two carpels are opposite each lobe of the inner perianth (figs. 48, 51). The carpels are wedge-shaped (figs. 52, 53) and triangular in top view (fig. 51), 0.38–0.56 mm long ($\overline{X}$ = 0.46 mm), 0.21–0.22 mm in radial length ($\overline{X}$ = 0.22 mm), and 0.28–0.3 mm in maximum tangential width ($\overline{X}$ = 0.29 mm). The carpel base is narrow and free from that of contiguous carpels (figs. 52, 54). Carpels become wider distally and are expanded toward the center of the flower, forming an adaxial edge (fig. 53).

The carpels are conduplicate (fig. 54). The ventral suture extends from near the base to the apex of the carpel (fig. 54) and continues along the flat apex to form a distinct radial groove (figs. 51, 55). The ventral suture is flanked by a differentiated band of protruding tissue (fig. 54). On the adaxial edge of the carpel, near the base, this band of tissue is narrow, but distally it becomes gradually broader, and on the apex of the carpel it expands greatly to form a broad platform on each side of the suture that extends to the abaxial surface (fig. 54). The apex of each carpel has a dome-like, bilobed appearance (figs. 52, 53, 55). Epidermal cells on the apical platform are polygonal and approximately isodiametric, with deep grooves between contiguous cells (fig. 56). Frequently, these cells are covered by a thick cuticle that has small, randomly arranged folds that obscure individual cell outlines (fig. 56). The abaxial side of each carpel has a longitudinal median narrow groove that extends from near the base to the apex, forming two lateral, slightly protruding lobes (fig. 57). On the sides of the carpel and on the radial walls of the apical platform, very large papillose, concave structures are present (fig. 58). These structures seem to cause contiguous carpels to adhere together (fig. 53). In dissected flowers, each carpel leaves a distinct triangular scar where it was attached to the floral receptacle (fig. 59). The bases of the carpels surround a central, undifferentiated mound of tissue that occupies the center of the flower (fig. 59). The center of pistillate flowers from which carpels have been dissected resembles the center of staminate flowers, in having a central mound of tissue with eight basal lobes that indicate the points of carpel attachment (figs. 29, 59).

In only one specimen was it possible to perform a dissection of the gynoecium where contiguous carpels were opened more or less longitudinally to reveal the ovules (fig. 60). There is one ovule in each carpel, and

placentation is apical (figs. 61, 62). The abaxial side of the ovule is elliptical (fig. 61). The end of the ovule opposite the attachment point is rounded, and in the few specimens that have been examined, a micropyle has not been observed (fig. 61). The adaxial side of the ovule has a longitudinal median narrow flap of tissue that may correspond to a narrow wing, or a ventral raphe (figs. 62, 63). The external seed wall is formed by rectangular to nearly square cells that form longitudinal rows (fig. 61).

Pollen grains similar to those found inside dispersed anthers of the staminate flowers have been found on the pistillate flowers. The pollen grains occur on the perianth, especially between the outer and inner cycles, and on the apical dome of the carpels, usually near the sutural groove (fig. 64). On several flowers of one head, the carpels were completely covered by masses of pollen grains.

Discussion

ASSOCIATION OF STAMINATE AND PISTILLATE INFLORESCENCES AND FLOWERS

Several lines of evidence indicate that the staminate and pistillate heads and flowers are dispersed parts of a single plant species. (1) Although the fossiliferous localities along Upatoi Creek are very rich in fossil angiosperm reproductive remains, the staminate and pistillate heads and flowers, as well as detached stamens, are present at only one collecting site, where they occur together. (2) The staminate and pistillate reproductive organs are the only fossils in the Upatoi Creek samples that exhibit morphological features similar to those of previously known platanaceous plants. (3) The staminate and pistillate flowers share a tetramerous or tetramerous-derived meristic plan. (4) Pollen grains identical to those found inside anthers of the staminate flowers occur frequently on the perianth and carpels of pistillate flowers (fig. 64), and this type of pollen has not been found on any other types of flowers or fruits from the Upatoi Creek sites. (5) The epidermal cells and histological pattern on the abaxial and adaxial surfaces of the tepals of the staminate flowers are similar to those on the outer perianth cycle of the pistillate flower, particularly in the presence of cells that enclose rectangular crystals on the adaxial surface of the tepals (cf. figs. 10, 40; 12, 41).

INTERPRETATION OF FLORAL MORPHOLOGICAL FEATURES

Most of the organs of staminate and pistillate flowers are sufficiently well preserved to allow straightforward interpretation of floral features. However, floral merosity and features of the ovules require additional comment.

TETRAMEROUS MEROSITY. The staminate and pistillate flowers of *Quadriplatanus georgianus* are organized according to a tetramerous plan. In the staminate flowers, the tetramerous arrangement is clearly manifested in the perianth, which is formed by four tepals
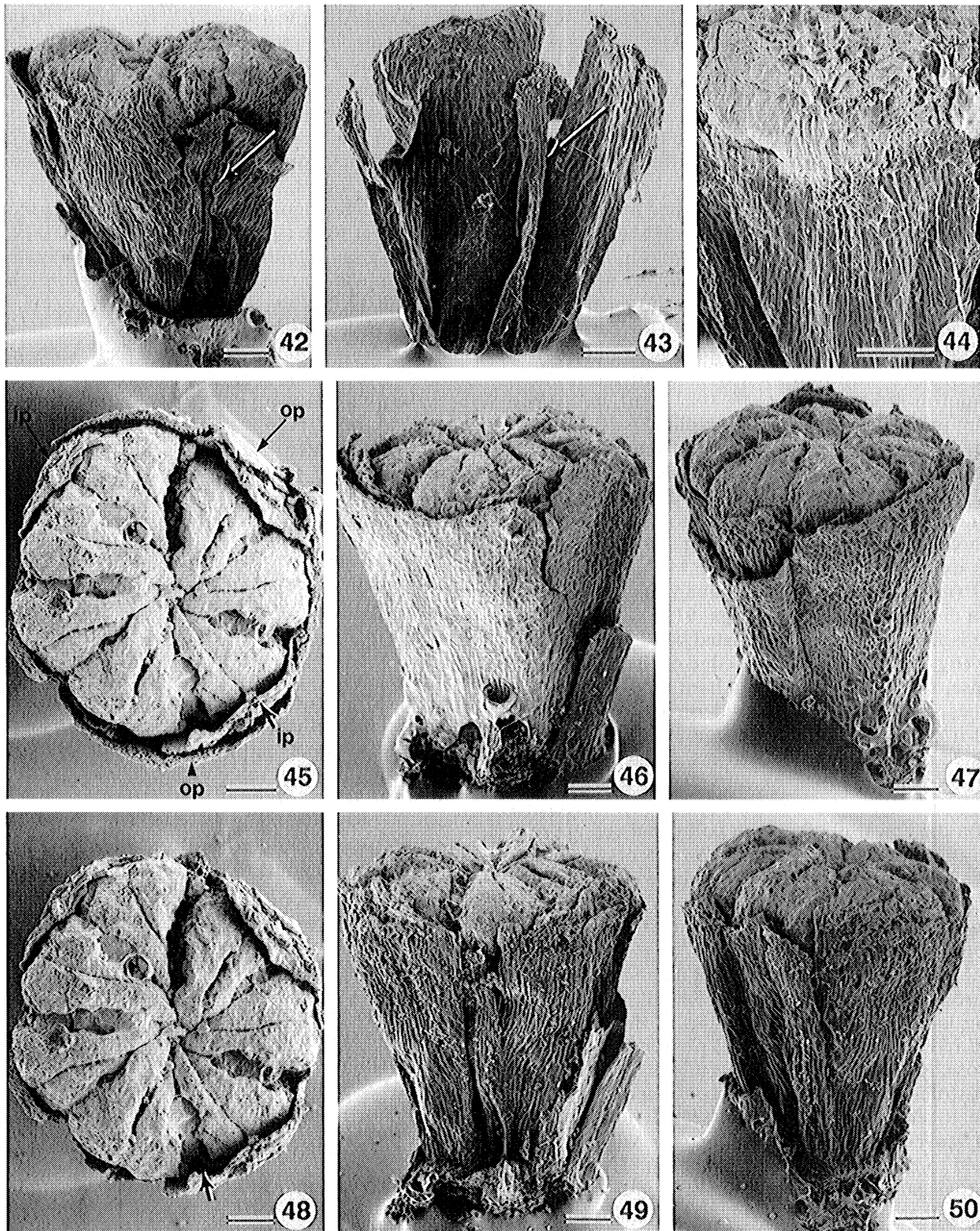
Figs. 42–50 *Quadriplatanus georgianus,* pistillate flowers. Fig. 42, Dissected flower in lateral view, with the outer perianth cycle removed. Members of the inner perianth cycle are basally connate, but apically free, forming rounded lobes. The inner perianth cycle folds inwardly, forming longitudinal plications (arrow). PP45037 [flower b]. Bar = 100 μm. Fig. 43, Inner perianth cycle removed from a flower, from adaxial view. Perianth members are basally connate, and apically free, forming rounded to square lobes. The connate portions fold inwardly, forming longitudinal plications (arrow). Epidermal cells on adaxial surface are elongate, with weakly marked transverse walls. PP45037. Bar = 100 μm. Fig. 44, Inner perianth cycle from abaxial side, showing elongated epidermal cells with weak transverse walls, and fleshy apex of perianth lobe. PP45037 [flower d]. Bar = 100 μm. Figs. 45–50, Sequential dissection of a pistillate flower to show floral organization. Fig. 45, Flower with seven carpels, from top view. The outer perianth cycle (*op*) and inner perianth cycle (*ip*) are almost as tall as the carpels. PP45037 [flower c]. Bar = 100 μm. Fig. 46, Lateral view of flower, showing outer perianth cycle connate into a conical tube and base of broken bract. PP45037 [flower c]. Bar = 100 μm. Fig. 47, Lateral view of flower, opposite side from fig. 46, showing outer perianth

that are free from one another throughout most of their length. The presence of four well-developed stamens also indicates a tetramerous organization in the androecium. However, the discovery in some staminate flowers of four additional appendages originating from the same ring of tissue as the stamens (figs. 26, 27) indicates the androecium is either tetramerous, formed only by four stamens, or octamerous, formed by four stamens and four additional appendages that alternate with the stamens. Stamens are opposite the tepals, while the four small androecial appendages alternate with the tepals (fig. 68A–C).

For pistillate flowers, interpretation of floral merosity is less clear. In the perianth, merosity can be inferred only from the inner perianth cycle in which the four free apical lobes document an origin from four original elements. The outer perianth cycle is fused entirely into a tube, with no histological indication of possible borders between contiguous perianth members, and hence provides no information about the original number of organs in this cycle. The gynoecium is formed by eight carpels arranged in a pattern where two carpels are opposite each lobe of the inner perianth cycle. The arrangement of the eight carpels may indicate an originally tetramerous arrangement for the gynoecium. It is possible that the eight carpels were derived evolutionarily from the duplication of

four original carpel primordia, leading to the development of two carpels in the sector of the flower that was formerly occupied by only one (fig. 68D, E). This is different from the possible octamerous condition of the androecium in the staminate flowers, in which the small androecial appendages alternate with the tepals, indicating that the former originated from primordia on the androecial cycle additional to the stamen primordia.

OVULES. Ovules have been observed only in four contiguous carpels that were dissected in an approximately oblique tangential plane. While the occurrence of a single apically attached ovule in each locule was demonstrated, other details of the ovule are not clear. The end of the ovule opposite its attachment point is rounded, and a micropyle is not apparent (fig. 61). The adaxial side of the ovule has a median longitudinal narrow flap of tissue (fig. 62). The size and type of preservation of the fossil remains have not permitted further dissection of the ovules that may clarify the nature of this flap of tissue, but it could represent a narrow wing, or an adaxial raphe.

The absence of a micropyle in the region of the ovule opposite its attachment point indicates that the ovule is not orthotropous. If the longitudinal flap of tissue on the adaxial side of the ovule is a raphe, this


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cycle connate into a conical tube, with its apical portion broken off, and showing apical portion of inner perianth cycle. PP45037 [flower c]. Bar = 100 μm. Fig. 48, Flower with outer perianth cycle removed, showing each lobe of inner perianth cycle opposite two carpels, but opposite a single carpel, where apparently a carpel is missing (arrow). PP45037 [flower c]. Bar = 100 μm. Fig. 49, Dissected flower in lateral view, in the same angle as fig. 46, with outer perianth cycle removed. Inner perianth cycle forming longitudinal folds, and showing free apices. PP45037 [flower c]. Bar = 100 μm. Fig. 50, Dissected flower in lateral view, in the same angle as fig. 47, and opposite side of fig. 49, the outer perianth cycle removed. Inner perianth cycle forming longitudinal folds, and showing free apices. PP45037 [flower c]. Bar = 100 μm.

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Figs. 51–59 *Quadriplatanus georgianus,* pistillate flowers, carpels, and dissected flowers. Fig. 51, Flower from apical view, showing eight apically triangular carpels. Each lobe of inner perianth is opposite two carpels (arrows). PP45037. Bar = 100 μm. Fig. 52, Carpel dissected from a flower, in lateral view, showing narrow base, and broad apex. PP45037. Bar = 100 μm. Fig. 53, Laterally coherent carpels removed from a flower. The adaxial portion of each carpel is extended centripetally forming an adaxial edge that converges with those of other carpels on the center of the flower. Glandulose papillae are present on the lateral sides of the carpels. PP45037 [flower b]. Bar = 100 μm. Fig. 54, Carpel in adaxial view, showing ventral suture extending from near the base to the apex, along the adaxial edge. A distinct band of tissue flanks the ventral suture, broadening from approximately the middle of the carpel, and extending laterally on the apex of the carpel. PP45037. Bar = 100 μm. Fig. 55, Carpel from apical view, showing prolongation of ventral suture on the apex of the carpel, forming a radial groove, flanked by the band of distinct tissue that expands laterally, forming a broad, flat apical platform. PP45037. Bar = 100 μm. Fig. 56, Cells on the apex of the carpel, approximately isodiametric, with deep grooves between contiguous cells, and covered by a thick cuticle with superficial wrinkles that obscures individual cell outlines. PP45037 [flower d]. Bar = 10 μm. Fig. 57, Carpels in abaxial view, each with a longitudinal median shallow groove, forming two lobes. PP45037 [flower b]. Bar = 100 μm. Fig. 58, Carpel in lateral view, showing large glandulose papillae on upper portion of lateral sides. PP45037. Bar = 100 μm. Fig. 59, Dissected flower with perianth members and carpels removed, showing base of outer perianth cycle (*op*), base of inner perianth cycle (*ip*), and eight scars of carpels surrounding an undifferentiated mound of tissue at the center of the flower. PP45044. Bar = 100 μm.

Figs. 60–67 Figs. 60–64, *Quadriplatanus georgianus,* dissected carpels and seeds. Fig. 60, Dissected carpels in oblique section, showing one ovule in one of the carpels (arrow). PP45037 [flower c]. Bar = 100 μm. Fig. 61, Higher magnification of fig. 60 showing ovule from abaxial-lateral view, with attachment to the apex of the locule, and rounded lower portion. PP45037 [flower c]. Bar = 50 μm. Fig. 62, Ovule from adaxial side, showing longitudinal flap of tissue. PP45037 [flower c]. Bar = 50 μm. Fig. 63, Ovule from adaxial-lateral view, showing longitudinal flap of tissue. PP45037 [flower c]. Bar = 50 μm. Fig. 64, Apex of carpel showing radial groove and pollen grains similar to those of staminate flowers of *Q. georgianus.* PP45037 [flower c]. Bar = 10 μm. Figs. 65–67, *Platanus* sp., subgen. *Platanus* (Recent), dissected staminate flowers. Fig. 65, Stamen with androecial appendages surrounding its filament (arrows). Bar = 500 μm. Fig. 66, Filament of stamen and androecial appendages, originating from a basally continuous tissue. Bar = 100 μm. Fig. 67. Base of filament, with distal portion of the stamen broken off, showing association with androecial appendages. Bar = 100 μm.
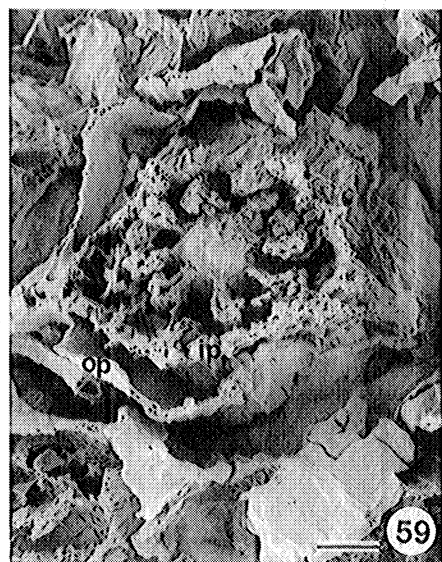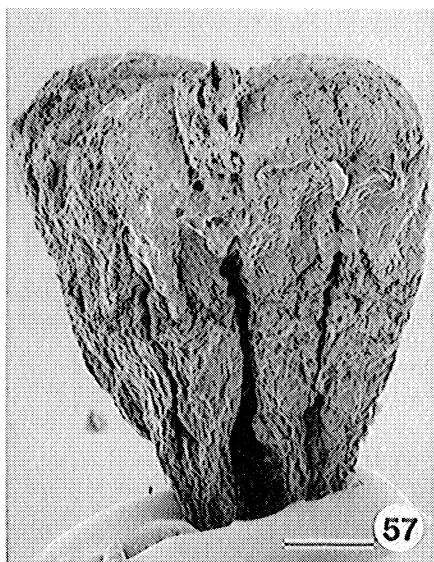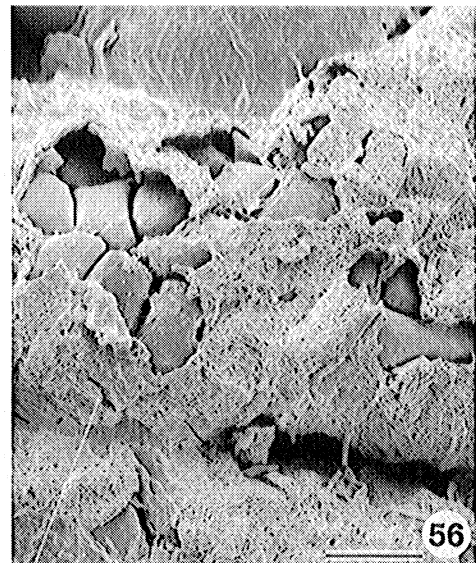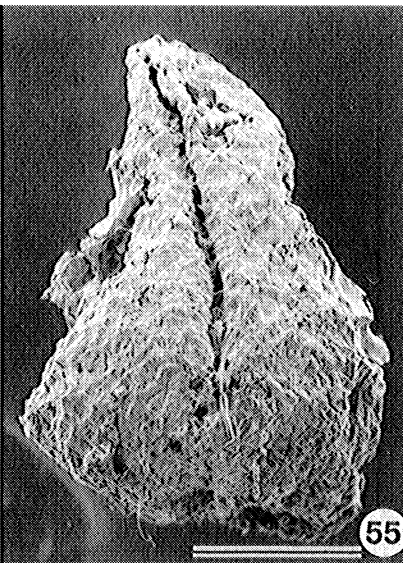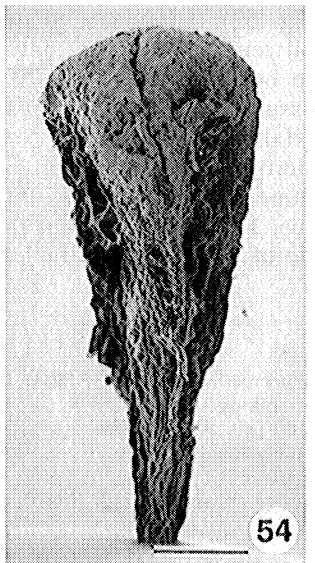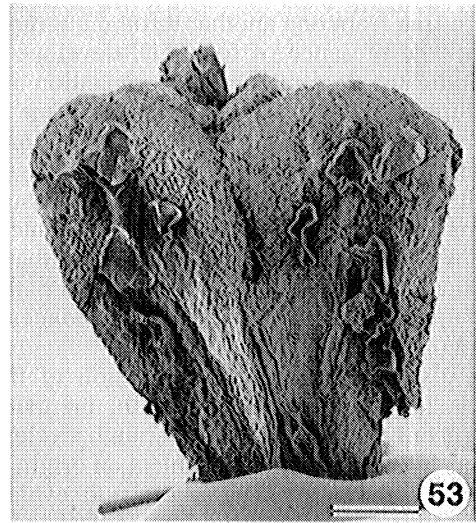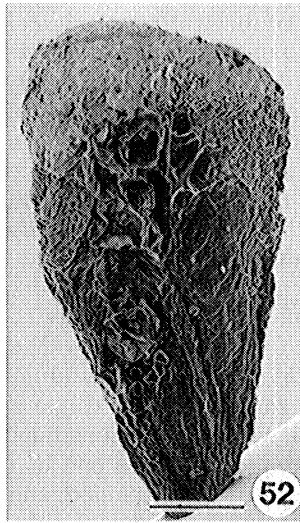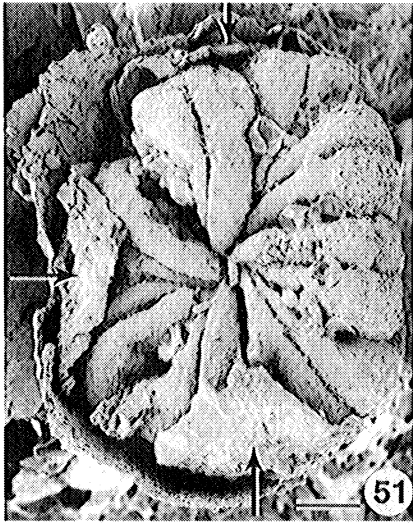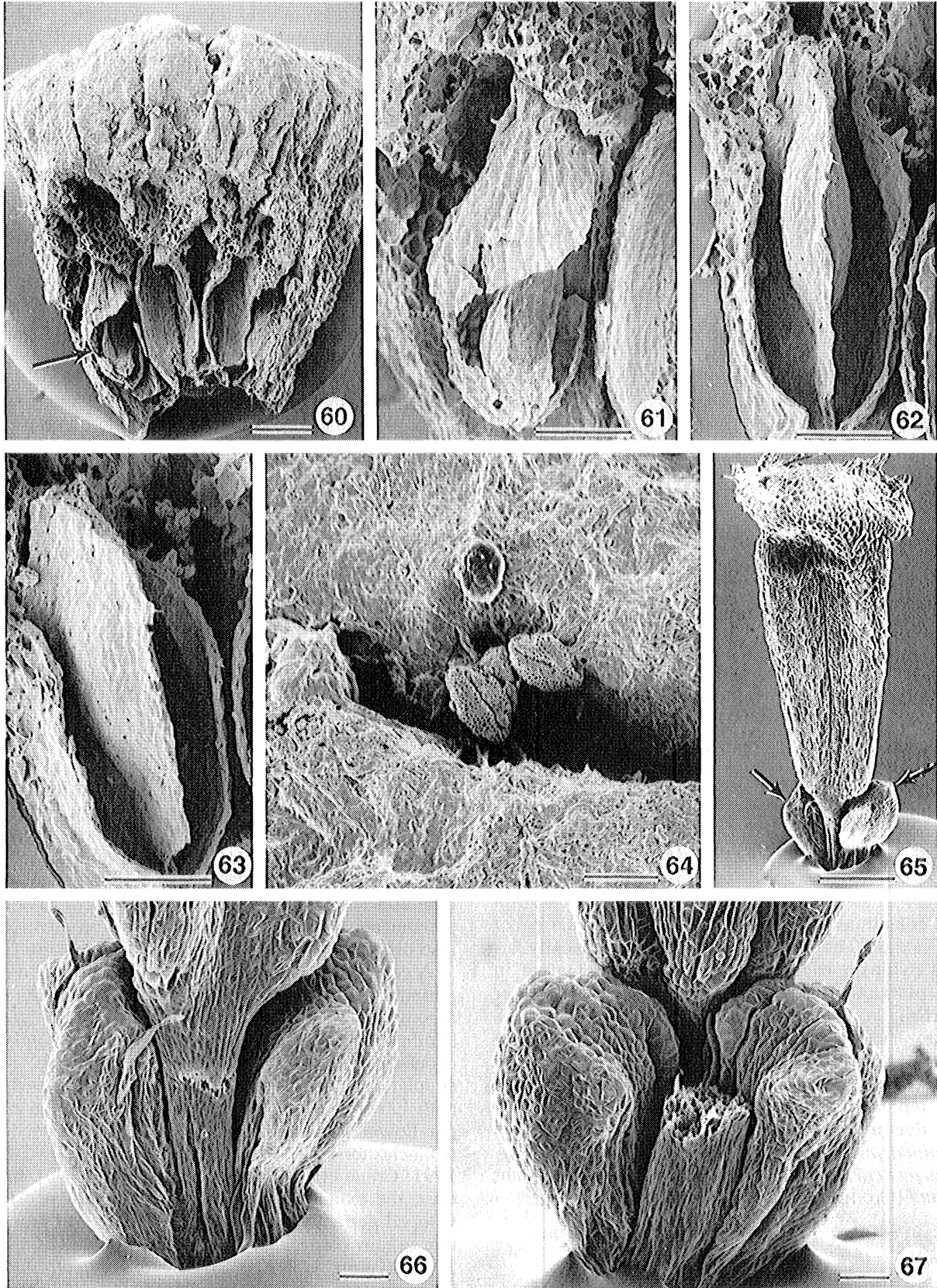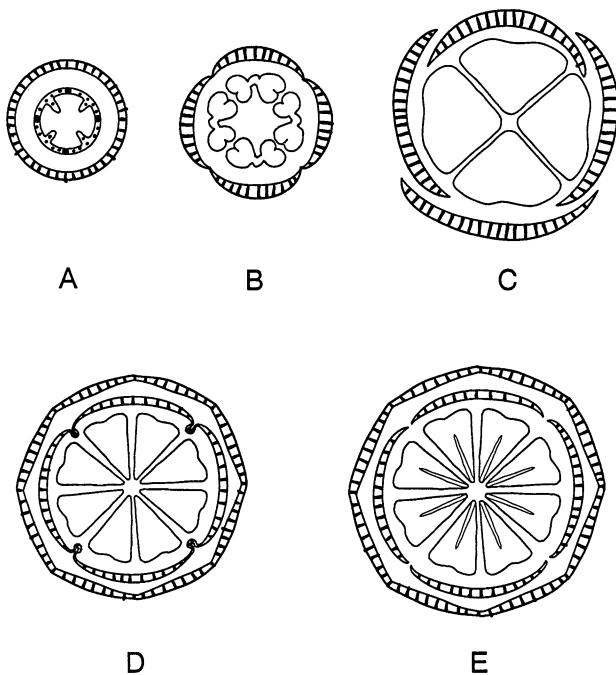
Fig. 68 Floral diagrams of *Quadriplatanus georgianus*. *A–C*, Floral diagram of staminate flowers. *A*, Cross section at the base of the flower, showing cycle of perianth forming a connate short ring, the androecial cycle showing the bases of filaments (black) and the androecial appendages alternating with filaments. *B*, Cross section at the level of anthers, showing cycle of perianth with four valvate tepals, and four stamens, each opposite a tepal. *C*, Cross section at apex of the flower, showing perianth cycle of four tepals with expanded, overlapping apices, and the apical extension of the connective of the four stamens. The apices of tepals are imbricate, with the margins of one tepal internal, the margins of the opposite tepal external, and the two remaining tepals with one margin internal and the other external. *D, E*, Floral diagram of pistillate flowers. *D*, Cross section at mid-level, showing the connate outer perianth cycle, the inner perianth cycle with plications, and eight carpels. *E*, Cross section near the apex of the flower, showing connate outer perianth cycle, inner perianth cycle with four free apical lobes, each opposite two carpels, and eight carpels.

would constitute further evidence that the ovule is not orthotropous. The presence of a single, apically attached ovule in each locule is a constant feature in fossil platanaceous pistillate flowers (Manchester 1986; Friis et al. 1988; Crane et al. 1993), as well as in extant species of *Platanus* (Boothroyd 1930; Cronquist 1981; Kubitzki 1993). Nevertheless, the presence in *Q. georgianus* of ovules that are not orthotropous would represent an important departure from the condition documented in other fossil platanaceous taxa (*Platanocarpus brookensis* [Crane et al. 1993]; *Platanocarpus caroliniensis* [Friis et al. 1988]) and extant *Platanus* (Cronquist 1981; Kubitzki 1993).

STRUCTURAL COMPARISON OF STAMINATE AND PISTILLATE FLOWERS

The staminate and pistillate flowers of *Q. georgianus* are both comprised of three floral cycles. The staminate flowers have one perianth cycle and one androecial cycle, and the center of the flower is occupied

by an undifferentiated mound of tissue with eight slightly protuberant lobes at its base (fig. 29), which are similar to carpel bases in the pistillate flowers. The pistillate flowers have two perianth cycles and a central apocarpous gynoecium. Dissections of pistillate flowers in which the perianth cycles were sequentially removed (figs. 45–50, 59) show that there is no additional floral cycle between the inner perianth cycle and the gynoecium that could correspond to an androecium.

Histological evidence indicates a possible structural homology between the single perianth cycle of the staminate flowers and the outer perianth cycle of the pistillate flowers. In both flowers, the adaxial side of perianth members bears distinctive epidermal cells that enclose rectangular to square crystals. These cells are frequently abraded, which leaves characteristic angular cavities on the surface (figs. 12, 41). If this interpretation of homology is correct, then the pistillate flowers have an "extra" perianth cycle between the "original" perianth and the gynoecium. This "extra" cycle is positionally homologous to the androecial cycle in the staminate flowers.

PHYLOGENETIC AFFINITY AND COMPARISON OF *QUADRIPLATANUS GEORGIANUS* WITH CRETACEOUS PLATANACEOUS TAXA

Most of the morphological features described for staminate and pistillate inflorescences and flowers of *Q. georgianus*, including general floral structure and fine details of reproductive organs, have been observed in previously described fossils assigned to Platanaceae from the Cretaceous and Tertiary (tables 1, 2). A universal feature within Platanaceae is the presence of unisexual flowers grouped in strictly staminate or pistillate compact spherical to hemispherical heads. Features such as the degree of development of the perianth and fine characteristics of reproductive organs exhibit some variation, but nevertheless there appears to be a common suite of characters exhibited by Cretaceous platanaceous flowers and inflorescences, which are also displayed by the new material from Upatoi Creek.

A correlation between degree of development of the perianth and fixation of floral merosity has been noted among diverse angiosperm taxa (Endress 1990), and a similar correlation has been observed among platanaceous flowers (Crane 1989; Drinnan et al. 1994). Fossil platanaceous flowers with a well-developed perianth have a constant number of reproductive organs per flower and exhibit a fixed pentamerous merosity (Manchester 1986; Friis et al. 1988; Pigg and Stockey 1991; Crane et al. 1993; Pedersen et al. 1994). In contrast, the extant species, which all have a poorly developed perianth, have a variable number of reproductive organs (especially carpels) per flower (Boothroyd 1930; Kubitzki 1993). The staminate and pistillate flowers of *Q. georgianus*, like other Cretaceous platanoids, have a well-developed perianth and a fixed number of reproductive organs per flower. However, the staminate flowers of *Q. georgianus* differ from pre-

Table 1

MORPHOLOGICAL FEATURES OF CRETACEOUS AND EARLY TERTIARY STAMINATE PLATANACEOUS REPRODUCTIVE STRUCTURES WITH FLOWERS HAVING WELL-DEVELOPED PERIANTH

Taxon	Age	Locality	Heads	Perianth	Number of stamens	Filament	Connective	Apical extension of connective
Aquia brookensis (1) (Crane et al. 1993)	Early to middle Albian	"Bank near Brooke", Virginia, U.S.A.	Globose, attachment to axis unknown	Well developed	Unknown	Long	Massive, between thecae	Weakly developed, conical
Platananthus potomacensis (2) (Friis et al. 1988)	Late Albian	West Brothers, Maryland, U.S.A	Globose, sessile	Well developed	5	Short (inferred)	Thick, central between thecae	Strongly developed, wedge-shaped
Hamatia elkneckensis (3) (Pedersen et al. 1994)	Late Albian	Bull Mountain, Maryland, U.S.A.	Globose, sessile	Well developed	5	Short	Thin, abaxially displaced	Strongly developed, wedge-shaped, sometimes extending downward on the adaxial side
Staminate heads and flowers (Crepet et al. 1992; Crepet and Nixon 1996)	Turonian	Crossman pit, New Jersey, U.S.A.	Globose, attachment to axis unknown	Well developed, one cycle of tepals, each opposite a stamen	4	Short	Thin, abaxially displaced	Strongly developed, wedge-shaped
Quadriplatanus georgianus gen. et sp. nov. (4)	Coniacian-Santonian	Upatoi Creek, Georgia, U.S.A.	Globose, sessile	Well developed, one cycle of tepals, each opposite a stamen	4	Short, or anthers sessile in early developmental stages	Thin, abaxially displaced	Strongly developed, wedge-shaped, sometimes extending downward on the adaxial side
Platananthus hueberi (5) (Friis et al. 1988)	Santonian-Campanian	Neuse River, North Carolina, U.S.A.	Globose, sessile	Well developed	5	Short	Unknown	Strongly developed, wedge-shaped
Platananthus scanicus (6) (Friis et al. 1988)	Santonian-Campanian	Höganäs, Scania, Sweden	Globose, pedunculate	Well developed	5	Short	Thin, abaxially displaced	Strongly developed, wedge-shaped, sometimes extending downward on the adaxial side
Platanites hebridicus (7) (Crane et al. 1988; Boulter and Kvaček 1989)	Paleocene	Ardtun, Mull, Scotland	Globose, pedunculate	Reduced	Unknown	Short	Unknown	Moderate broad conical extension
Platananthus speirsae (8) (Pigg and Stockey 1991)	Paleocene	Joffre Bridge, Alberta, Canada	Globose, pedunculate	Obscured by preservation	5 (inferred)	Short	Unknown	Moderate broad conical extension
Platananthus synandrus (9) (Manchester 1986)	Eocene	Clarno Formation, Oregon, U.S.A.	Globose, sessile	Well developed	5	Short	Unknown	Moderate broad conical extension

Note. Numbers in parentheses indicate the corresponding pistillate reproductive structure in table 2.

Table 2

MORPHOLOGICAL FEATURES OF CRETACEOUS AND EARLY TERTIARY PISTILLATE PLATANACEOUS REPRODUCTIVE STRUCTURES WITH FLOWERS HAVING WELL-DEVELOPED PERIANTH

Taxon	Age	Locality	Head	Perianth	Number of carpels	Carpels	Apex	Adaxial side/ ventral suture
Platanocarpus brookensis (1) (Crane et al. 1993)	Early to middle Albian	"Bank near Brooke," Virginia, U.S.A.	Globose, sessile	Well developed, at least two cycles	5	Obtriangular, basal hairs absent	Apical platform, style not differentiated	Ventral suture flanked by protruding tissue reaching the apex
Platananthus marylandensis (2) (Friis et al. 1988)	Late Albian	West Brothers, Maryland, U.S.A.	Globose, sessile	Well developed	5	Obtriangular, basal hairs absent	Apical platform, style not differentiated	Ventral suture flanked by protruding tissue reaching the apex
Platanocarpus elkneckensis (3) (Pedersen et al. 1994)	Late Albian	Bull Mountain, Maryland, U.S.A.	Globose, sessile	Well developed, at least two cycles; outermost cycle connate into a tube	5	Obtriangular, basal hairs absent	Apical platform strongly developed, style not differentiated	Ventral suture flanked by protruding tissue reaching the apex
Quadriplatanus georgianus gen. et sp. nov. (4)	Coniacian-Santonian	Upatoi Creek, Georgia, U.S.A.	Globose, sessile	Well developed, two cycles: outer cycle connate into a tube, inner cycle with free tips of four elements	4	Obtriangular, basal hairs absent	Apical platform, style not differentiated	Ventral suture flanked by protruding tissue extending on apex
Platanocarpus caroliniensis (5) (Friis et al. 1988)	Santonian-Campanian	Neuse River, North Carolina, U.S.A.	Globose, sessile	Well developed	5	Obtriangular, basal hairs absent	Slightly pointed, style not differentiated	Details unknown
Platanocarpus sp. (6) (Friis et al. 1988)	Santonian-Campanian	Höganäs, Scania, Sweden	Globose (inferred), attachment to axis unknown	Well developed	5	Obtriangular, basal hairs absent	Slightly pointed, style not differentiated	Ventral suture extending on adaxial side of pointed apex
Platanites hebridicus (7) (Crane et al. 1988; Boulter and Kvaček 1989)	Paleocene	Ardtun, Mull, Scotland	Globose, attachment to axis unknown	Reduced	Unknown	Unknown	Differentiated style, elongated, curved	Details unknown
Macginicarpa manchesteri (8) (Pigg and Stockey 1991)	Paleocene	Joffre Bridge, Alberta, Canada	Globose, pedunculate	Obscured by preservation	5 (inferred)	Basally elliptical to obovate, hairs absent	Differentiated style, elongated, slightly curved	Extending on style
Macginicarpa glabra (9) (Manchester 1986)	Eocene	Clarno formation, Oregon, U.S.A.	Globose, sessile, or pedunculate	Well developed	5	Basally elliptical to obovate, hairs absent	Differentiated style, elongated, slightly curved	Extending on style
Platanus hirticarpa (Manchester 1994)	Eocene	Clarno Formation, Oregon, U.S.A.	Globose, attachment to axis unknown	Reduced	4 (or more?)	Achenes obovate to obtriangular, with basal hairs	Differentiated style, elongate	Extending on style
Tanyoplatanus cranei (Manchester 1994)	Eocene	Clarno Formation, Oregon, U.S.A.	Cylindrical	Well developed	3–4	Basally ovate to obovate, with basal hairs	Differentiated style, elongated	Extending on style

Note. Numbers in parentheses indicate the corresponding staminate reproductive structure in table 1.

viously described platanaceous staminate flowers in having a tetramerous plan in both the perianth and the androecium (table 1). The pistillate flowers of *Q. georgianus* differ from previously described platanaceous pistillate flowers in having eight carpels, which may be a manifestation of an originally tetramerous pattern (table 2).

The morphological characteristics of tepals and stamens of staminate flowers of *Q. georgianus* are similar to those of other Cretaceous platanoids (Friis et al. 1988; Crane et al. 1993; Pedersen et al. 1994). A well-developed perianth has been documented in all Cretaceous platanaceous taxa in which floral features are well preserved (Friis et al. 1988; Crane et al. 1993; Pedersen et al. 1994), and also in some Tertiary fossils (Manchester 1986; Pigg and Stockey 1991), but in most cases, the exact number of tepals and their arrangement has not been determined.

Stamens with a short filament, long thecae corresponding to ca. 50% or more of the length of the stamen, and a peltate-to-wedge-shaped extension of the connective above the level of the thecae are present in all Cretaceous platanoids described so far, with the exception of *Platananthus brookensis* (Crane et al. 1993). In particular, the stamens of *Platananthus scanicus* (Friis et al. 1988) and *Hamatia elkneckensis* (Pedersen et al. 1994) share a number of distinctive features with staminate flowers of *Q. georgianus*. The thecae are narrow proximally and wider distally, dehisce through valves, and pollen release is intermediate between latrorse and introrse. The connective is abaxially displaced, and, at least in *H. elkneckensis,* it is narrow near the base of the stamen. In both genera, the apical extension of the connective overhangs the anthers laterally. In *P. scanicus,* there is an adaxial upward prolongation that forms a short horn-like cone, and in some stamens, an additional adaxial downward prolongation, forming a long and thin hook between the thecae. This last feature is strongly developed in *H. elkneckensis.*

Pollen grains corresponding to all known fossil and living platanaceous taxa are of the same general type as those described for *Q. georgianus.* However, the pollen morphology (tricolpate apertures, reticulate exine ornamentation) is generalized and lacks prominent distinctive features. The most evident structural differences between the stamens of Cretaceous platanaceous flowers and those of extant *Platanus* are the more weakly developed apical extension of the connective, and stomia that are branched only distally and therefore have thecae that exhibit partial valvate dehiscence (Hufford and Endress 1989; Hufford 1996) in extant *Platanus.*

The tepals of pistillate flowers of *Q. georgianus* are similar to those of previously described three-dimensionally preserved Cretaceous platanaceous taxa (Friis et al. 1988; Crane et al. 1993; Pedersen et al. 1994). Although in these fossils the number and exact arrangement of tepals is not clear, at least *Platanocarpus brookensis* (Crane et al. 1993), *P. marylandensis* (Friis

et al. 1988), and *P. elkneckensis* (Pedersen et al. 1994) have two perianth cycles.

Carpels of *Q. georgianus* display several distinctive features previously documented from well-preserved Cretaceous pistillate platanaceous flowers. The carpels are conduplicate and obtriangular in shape and extend into the center of the flower to form an adaxial edge. The carpel apex is flat, and a differentiated style is lacking. The ventral suture extends along the adaxial edge and also onto the carpel apex and is flanked by a differentiated tissue that expands on the apex to form a broad bilobed platform (cf. Friis et al. 1988; Crane et al. 1993; Pedersen et al. 1994). The apical platform of the carpels of *P. marylandensis* (Friis et al. 1988) and *P. elkneckensis* (Pedersen et al. 1994) is especially similar to that in *Q. georgianus,* although in *P. elkneckensis* the apical platform is more strongly developed and distinctly bilobed on its abaxial side. This is less marked in *Q. georgianus.* The carpels of extant *Platanus* species differ structurally from those of Cretaceous platanoids in having a distinct style and lacking the strong centripetal expansion into the center of the flower.

The staminate inflorescences and flowers of *Q. georgianus* exhibit a striking morphological and structural similarity to fossils previously described from Turonian-age strata of the Raritan Formation of New Jersey (Crepet et al. 1992; Crepet and Nixon 1996). The fossils from the Raritan Formation are heads bearing closely packed staminate flowers. The flowers are composed of a well-developed, unicyclic perianth and an androecium. There is no evidence of a gynoecium or pistillodia. The perianth is formed by four basally connate and apically free tepals. The androecium is formed by four well-developed stamens, each opposite a tepal. The stamens have a very short filament, or the anthers are sessile. The anthers are long and are thought to open through valves (Crepet et al. 1992). The connective is abaxially displaced. Above the level of the anthers, the connective expands laterally, upwardly, and adaxially, to form a massive wedge-like extension that is triangular in top view and forms a short, conical, horn-like projection on its adaxial portion. The four stamens originate from a short, continuous ring of tissue, which also bears the bases of four additional small structures that alternate with the bases of stamens. These four additional structures are composed of a narrow base or stalk, and a centripetally expanded sagittate apex shaped like the apical extension of the stamen connective. Because of the similarity of the expanded apex with the apical extension of the connective of stamens, these structures were interpreted as staminodes (Crepet et al. 1992; Crepet and Nixon 1996). Associated pollen grains are slightly prolate, tricolpate with long colpi, and have reticulate exine ornamentation pattern. Pollen size is close to that of the average reported for pollen grains of *Q. georgianus.* Because the filament tube is extremely thin, the relative position of stamen bases and staminode bases on the common ring of tissue was difficult to

interpret, but it was suggested that the bases of the staminodes are placed slightly more externally than the bases of stamens on the common androecial ring (Crepet et al. 1992). These structures are morphologically and positionally equivalent to the androecial appendages described for the staminate flowers of *Q. georgianus,* and both resemble and occupy a similar position to the androecial appendages ("staminodes" or "fleshy masses"; Boothroyd 1930) that are found associated with stamen bases in extant species of *Platanus* (figs. 65–67). The features described for the staminate inflorescences and flowers from the Turonian Raritan Formation of New Jersey correspond well to the characters of *Q. georgianus.*

Fossils that were interpreted to represent the pistillate counterparts of the well-preserved staminate flowers from the Raritan Formation are capitate heads of sessile flowers similar to the staminate heads. The pistillate flowers were thought to be composed of a four-lobed sepal cup and a partially inferior, syncarpous, bilocular gynoecium. The available inflorescences and flowers are abraded, and better-preserved material is needed to confirm presence of a syncarpous, bilocular gynoecium in the putative pistillate flowers.

Differences between the staminate flowers of *Q. georgianus* and the staminate flowers from the Raritan Formation are few. The androecial appendages that alternate with the stamens are routinely observed in flowers from the Raritan Formation, and these structures converge at the center of the flowers. In contrast, in *Q. georgianus* the equivalent structures are more weakly developed and have not been consistently observed in all flowers. Some other features cannot be compared because of lack of information. Features that are not known in the flowers of the Raritan Formation are the presence of a basally narrow connective (the abaxial surface of stamens is not figured), and the presence of an adaxial downward prolongation of the apical extension of the connective (only one stamen in the appropriate orientation is figured). A more detailed comparison between *Q. georgianus* and the staminate inflorescences and flowers from the Raritan Formation is needed for a more detailed assessment of similarities and differences between these fossils. Structural comparisons between the pistillate flowers of the Raritan Formation and the pistillate flowers of *Q. georgianus* are not possible because the specimens from the Raritan Formation are abraded.

The fossils from the Raritan Formation were considered to exhibit a mosaic of characters found in modern Platanaceae and Hamamelidaceae (Crepet et al. 1992). Features cited as indicating an affinity to Platanaceae are: (1) the form and unisexual nature of the heads, (2) reticulate-tricolpate pollen grains obtained from in situ stamens, (3) the close packing of the stamens in the fossil flowers, and (4) the broad triangular apical extension of the connective. Features suggested to indicate an affinity with Hamamelidaceae are: (1) the presence of a well-developed sepal cup, (2) the presence of a staminal tube, (3) the interpretation of

the staminodes (i.e., androecial appendages) as having nectariferous functions, (4) the interpretation of the staminodes as morphological intermediates between stamens and petals, and (5) the interpretation of the presence of a syncarpous bicarpellate gynoecium in the pistillate flowers.

Because of the structural and morphological similarity between the staminate heads and flowers from the Raritan Formation and those of *Q. georgianus,* we have carefully considered the possibility of a relationship to the Hamamelidaceae in assessing the phylogenetic affinity of the new fossils from Georgia. We have compared the features suggesting hamamelidaceous affinity with equivalent features in fossil and extant Hamamelidaceae and Platanaceae. (1) The perianth cycle of staminate flowers of *Q. georgianus* exhibits a basic similarity in form and degree of connation with previously described Cretaceous platanaceous staminate flowers (e.g., *Platananthus potomacensis* [Friis et al. 1988]). In extant *Platanus,* the sepals are reduced and inconspicuous. Within extant Hamamelidaceae, the sepals are much shorter than other floral organs, particularly stamens, at anthesis. The well-developed perianth of *Q. georgianus* is unlike that of extant members of both Hamamelidaceae and Platanaceae, but it is similar to that of Cretaceous fossils assigned to Platanaceae. (2) The presence of a staminal tube in previously described fossil platanoids is not known. However, there is a strong similarity between the short androecial ring in the staminate flowers of *Q. georgianus* and the lateral fusion between stamens and staminodes (or "fleshy masses") observed in extant *Platanus* (fig. 66). A staminal tube is rarely formed in Hamamelidaceae. The bases of the filaments of *Embolanthera* and *Dicoryphe* are fused with the bases of the petals. Only in *Mytilaria* is there fusion among the bases of stamens, staminodes, and petals (Endress 1993). However, the condition in *Mytilaria* is different from the one in *Q. georgianus,* because in the former genus, three different floral whorls are involved. (3) There is no conclusive evidence indicating that nectar was produced by any of the floral organs of Cretaceous platanoids, including *Q. georgianus,* and nectar production is not known for extant *Platanus.* However, in most genera of Hamamelidaceae, the nectariferous functions are performed by a number of scales fused into a shallow ring placed between the androecium and the gynoecium. In *Hamamelis,* the staminodes, which are additional to and opposite the petals, are nectariferous, and only in *Disanthus* are there nectariferous functions associated with the base of petals (Endress 1989, 1993). (4) There is positional equivalence and morphological similarity between the androecial appendages of the fossil flowers and the staminodes, or fleshy masses, associated with the stamens in extant *Platanus* (figs. 65–67). (5) If it could be established more clearly, the syncarpous, bicarpellate, and partially inferior gynoecium in the fossils from the Raritan Formation would be the most compelling feature that would support possible affinity

of these fossils to Hamamelidaceae. However, the pistillate flowers of *Q. georgianus* are clearly hypogynous, and the apocarpous gynoecium is composed of eight carpels.

The flowers of *Q. georgianus* exhibit structural organization equivalent to that of fossil and extant Platanaceae, as well as fine detailed morphological features similar to those of Upper Cretaceous Platanaceae. The interpretation of the structures that alternate with the stamens as androecial derivatives, and the apocarpous gynoecium in *Quadriplatanus,* are both features that would be highly unusual in the Hamamelidaceae. The comparison of features of staminate and pistillate flowers of *Q. georgianus* with Hamamelidaceae and previously known fossils assigned to Platanaceae supports a phylogenetic affinity of these new fossils within Platanaceae.

Conclusions

Many taxa belonging to the evolutionary lineage of modern *Platanus* are known in the fossil record, and they document considerable morphological variety in vegetative and floral features within the constraints of common structural themes. The staminate and pistillate inflorescences and flowers of *Q. georgianus* conform to this pattern in displaying features of floral organization and details of stamens and carpels that had been previously observed in other Cretaceous platanaceous taxa. However, they also extend the known pattern by displaying a tetramerous or tetramerous-derived floral meristic arrangement, in contrast to the previously observed pentamerous plan.

Because of its phylogenetic position, and the documentation of intralineage temporal morphological change provided by an extensive fossil record, Platanaceae can provide crucial information for understanding phylogenetic relationships and character homology at the base of the eudicots. However, a major comparative synthesis that includes fossil and living platanoids, as well as closely related groups of plants, is needed to fully understand phylogenetic relationships among these taxa, and to recognize evolutionary lineages within Platanaceae.

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