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ANATOMICALLY PRESERVED STAMINATE INFLORESCENCES OF *GYNOPLATANANTHUS OYSTERBAYENSIS* GEN. ET SP. NOV. (PLATANACEAE) AND ASSOCIATED PISTILLATE FRUCTIFICATIONS FROM THE EOCENE OF VANCOUVER ISLAND, BRITISH COLUMBIA

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Anatomically preserved specimens of globose staminate and pistillate inflorescences belonging to Platanaceae have been found in concretions at the Eocene Appian Way fossil locality on Vancouver Island, British Columbia, Canada. The structure of inflorescences and individual flowers, vascular architecture, and pollen morphology were examined. Flowers occur on globose unisexual heads and are supplied at their bases by branching pentagonal vascular traces. Flowers of staminate inflorescences have a well-developed perianth with at least two whorls of tepals. Five stamens with elongate anthers surround a single whorl of five (rarely four) free, nonfunctional carpels that are ovate in longitudinal section and roughly triangular in transverse section. *In situ* tricolpate pollen 16 μm in polar diameter is found in the anthers. This same pollen is found among the persistent styles of larger pistillate fructifications. The pistillate flowers are identical in structure to staminate flowers but have five fully developed carpels, and they lack stamens. Fruits are glabrous achenes up to 8 mm long. Staminate inflorescences compare most closely to those of *Platananthus* sp., but the regular co-occurrence of both stamens and rudimentary carpels in the same flower has not previously been reported in the fossil record, and, thus, these specimens have been placed in a new genus and species, *Gynoplatananthus oysterbayensis*. These platanaceous inflorescences add to our knowledge of the Appian Way flora and provide evidence that rudimentary carpels are an ancient feature within staminate flowers of Platanaceae.

Keywords: Eocene, *Platanus*, *Platananthus*, Platanaceae, Proteales.

Introduction

Known from Early Cretaceous sediments and abundant in the Tertiary, fossils of platanaceous affinity attest to a past diversity that outstrips that known in extant species (Crane 1989; Pigg and Stockey 1991; Kvaček and Manchester 2004). Modern *Platanus* L. species are distinguished by their pedunculate, globose, unisexual inflorescences and alternating palmately lobed leaves (Kubitzki 1993). The one exceptional species, *Platanus kerrii* Gagnepain from Vietnam, has a sessile inflorescence and entire elliptical leaves. One species, *Platanus orientalis* L., is endemic to Mediterranean Europe, while the remaining eight taxa are found in North and Central America, with the highest diversity found in Mexico (Nixon and Poole 2003). Interspecific hybridization is common, and the common London plane tree, *Platanus* × *acerifolia* (Aiton) Willdenow, is grown as an ornamental throughout much of the Northern Hemisphere (Kaul 1997).

Traditionally, the family Platanaceae was placed in the polyphyletic "Amentiferae" (Thorne 1973), and until recently, it was grouped within the Hamamelidales (Cronquist 1981; Schwarzwalder and Dilcher 1991; Takhtajan 1997), based mainly on gross morphological similarities in leaf and inflorescence structure to extant species within the group, specifically, those now placed within the family Altingiaceae (Nixon and Poole 2003). However, recent molecular phylogenetic analyses (Chase et al. 1993; Hoot et al. 1999; Soltis et al. 2003) have placed Platanaceae in the Proteales as sister group to either Proteaceae or Nelumbonaceae. So far, this unexpected and counterintuitive relationship has been supported by embryological studies (Floyd et al. 1999) and leaf cuticular morphology (Carpenter et al. 2005), and both Hoot et al. (1999) and Soltis et al. (2003) have used the fossil record of Platanaceae as evidence for a relationship with Proteaceae.

Crane (1989) and Crabtree (1987) have reviewed the diversity of Cretaceous platanoid leaves, which are a common component of North American floras from that period. The fossil record for the family extends into the Early Cretaceous. Leaf compressions (Hickey and Doyle 1977) and inflorescences (Friis et al. 1988; Crane et al. 1993; Pedersen et al. 1994) of platanaceous affinity are known from the Albian of eastern North America. Three-dimensionally preserved inflorescences from the Late Cretaceous of Sweden (Friis et al. 1988) and North America (Friis et al. 1988; Magallón-Puebla et al. 1997) have shown characters unknown in extant Platanaceae, specifically, elongate tepals and a regular, invariable arrangement of floral parts. These characters are also known in the Cretaceous to Tertiary genera *Platananthus* Manchester and *Macginicarpa* Manchester, the Paleogene genus of pistillate fructifications (Manchester 1986), whereas

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extant *Platanus* have a highly variable merosity and diminutive "petals" (Boothroyd 1930).

This article describes permineralized staminate inflorescences and pistillate fructifications from the Eocene Appian Way locality of Vancouver Island, British Columbia. The platanaceous specimens show floral anatomy and, thus, can be useful in the interpretation of floral evolution within the family. These are the first of many angiosperm fossils that will be described from the locality.

Material and Methods

Three pistillate fructifications and four staminate inflorescences were found in rocks collected from the Appian Way fossil locality south of Campbell River on the east coast of Vancouver Island, British Columbia, Canada (49°54′42″N, 125°10′40″W; UTM 10U CA 5531083N 343646E). So far this locality has yielded decapod crustaceans (Schweitzer et al. 2003), polypore fungi (Smith et al. 2004), gleicheniaceous (Mindell et al. 2005) and schizaeaceous (Trivett et al. 2002, 2006) fern remains, taxodiaceous pollen cones (Hernandez-Castillo et al. 2005), and more than 40 taxa of dispersed angiosperm fruits and seeds (Little et al. 2001). Plant remains occur in marine calcareous concretions in a sandy siltstone matrix. Palynological investigations of the locality have dated these shallow marine sediments as late Paleocene to early Eocene (Sweet 1997). Using an assortment of fossil decapods (Schweitzer et al. 2003), mollusks, and shark teeth, Haggart et al. (1997) gave these rocks a middle to late Eocene age. Stratigraphic studies are currently being conducted at the site (J. W. Haggart, personal communication, 2006).

The fossiliferous concretions were cut into slabs, and peels were made using the cellulose acetate peel technique (Joy et al. 1956). Slides were mounted using xylene-soluble Eukitt mounting medium (O. Kindler, Freiburg, Germany). Images were captured using a PowerPhase digital scanning camera (Phase One, A/S, Copenhagen, Denmark), and whole specimens in rock, with a Microlumina digital scanning camera (Leaf Systems, Bedford, MA). Images were processed using Adobe Photoshop 7.0. Pollen was coated with 15 nm of gold using a Nanotek sputter-coater and examined with a JEOL scanning electron microscope (SEM; JEOL 6301F) at 5 kV. All specimens are housed in the University of Alberta Palaeobotanical Collections, Edmonton, Alberta, Canada (UAPC-ALTA).

Systematics

Family—Platanaceae T. Lestib.

*Genus—*Gynoplatananthus *gen. nov. Mindell, Stockey et Beard*

Generic diagnosis. Inflorescences staminate with rudimentary carpels, globose. Flowers numerous, borne on sclerotic, spheroidal receptacular core; floral vascular trace pentagonal; tepal whorls at least two. Stamens five, elongate, spatulate; anthers elongate, connective enlarged apically. Gynoecium nonfunctional, rudimentary carpels five, strongly developed. Pollen tricolpate, semitectate columellate.

*Type Species—*Gynoplatananthus oysterbayensis *Mindell, Stockey et Beard sp. nov. (Figs. 1, 2)*

Specific diagnosis. Inflorescence staminate, diameter 8–9.5 mm with more than 40 flowers, tightly packed. Flowers up to 4.0 mm long, 1.1 mm wide. Tepals spatulate, innermost whorl fused at base. Stamens in single whorl. Rudimentary carpels ovoid to subtriangular, styles lacking. Pollen (14–)16(–18) μm polar diameter, (12)–13–(14) μm equatorial diameter.

Holotype. AW 263 Fbot, Gtop (UAPC-ALTA).

Paratypes. AW 120 A, Btop, AW 103 Gbot, Htop, AW 289 Etop.

Stratigraphic position and age. Oyster Bay Formation, Middle Eocene.

Locality. Appian Way locality, south of Campbell River, British Columbia, Canada (49E 56′00″N, 125E 11′15″W; UTM 10U CA 433331).

Etymology. Generic name, derived from the Latin *gyno*, refers to the gynoecium present in functionally staminate flowers, and *Platananthus*, a fossil genus encompassing five-parted staminate inflorescences with elongate tepals. The specific epithet *oysterbayensis* refers to Oyster Bay, Vancouver Island, the locality from which the specimens were collected.

Description. The four isolated staminate inflorescences occur within the concretions. Inflorescences are commonly abraded with deposits of pyrite found within pollen grains and between floral organs. No peduncles have been observed, so the type of inflorescence attachment (sessile or pedunculate) is unknown. The compound globose inflorescences measure 9.0–9.5 mm in maximum diameter and comprise numerous (at least 40) flowers centrally attached to a sclerotic receptacular core up to 3 mm in diameter (fig. 1*a*, 1*b*). Vascular tissue diverges as a circular to pentagonal bundle that supplies the base of each flower (fig. 1*a*, 1*c*). In transverse section, at the base of every flower, a perianth of at least two whorls of tepals can be seen (fig. 1*b*–1*e*). In longitudinal section, at least one whorl of these tepals is observed to be elongate and strap shaped, up to 4 mm long, extending above the level of the stamens (fig. 1*b*, 1*g*). Stamens occur in a single whorl of five, and most anthers have dehisced. Anthers are elongate and have a very thick connective (fig. 2*a*) that has an apical extension. Pollen both in the anthers and between flowers occurs in large clumps (fig. 2*a*–2*c*). Pollen grains are tricolpate, wider in polar diameter (14–)16(–18) μm than in equatorial diameter (12–)13(–14) μm. Pollen is semitectate, columellate, with a dense reticulate ornamentation, and the exine is 1 μm thick (fig. 2*d*–2*g*). There are five ovoid to subtriangular rudimentary carpels (rarely four) in each flower. These carpels have been followed through completely and lack developed styles, obvious trichomes and ovules, and thus are interpreted as rudimentary (fig. 1*b*–1*e*, 1*g*).

Associated Infructescences

Three platanaceous infructescences derived from pistillate flowers also have been found in Appian Way concretions (fig. 3*a*–3*g*). These infructescences are larger than the staminate heads, measuring up to 20 mm in diameter. Two of these are mature fruiting specimens, and the third has flowers and fruits. Flowers and fruits are clustered around a spheroidal, parenchymatous receptacular core 5–6 mm wide (fig. 3*a*, 3*b*). Vascular traces to the flower originate as a hollow cylinder that changes distally with proximity to the flower, first to a pentagonal trace and then to five individual ovoid strands (fig. 3*b*, 3*c*). Flowers have at least two whorls of tepals (fig. 3*d*, 3*e*). Outside these tepals are numerous thin, filiform appendages that can be seen in both transverse (fig. 3*c*, 3*d*) and longitudinal sections (fig. 3*e*). Tepals are elongate and strap shaped (fig. 3*b*).

In all three specimens, there are five carpels per flower. Carpels are ovoid to subtriangular in shape in transverse section (fig. 3*b*, 3*d*). Styles are elongate (up to 4 mm) and persistent with no obvious trichomes (fig. 3*a*, 3*f*). Fruits are achenes measuring up to 8 mm long from base to tip of the persistent style, and they lack dispersal hairs (fig. 3*a*, 3*f*, 3*g*). Fruits have an exocarp one cell thick and a parenchymatous mesocarp four to five cells thick (fig. 3*g*). The endocarp is represented by a single palisade layer of sclerenchyma (fig. 3*g*).

Large amounts of pollen of the same type and dimensions as that found in the anthers of *G. oysterbayensis* are found among the styles of the fructifications along with septate fungal hyphae (fig. 3*h*). Given that this pollen is not observed in association with other fossils in the concretion nor scattered in the surrounding sediment, it is assumed to have landed in the inflorescences prior to burial.

Discussion

Globose flowering heads, free carpels, elongate anthers, apical connective extensions, and tricolpate, semitectate, columellate pollen place these fossils within Platanaceae (Kubitzki 1993; Nixon and Poole 2003). The staminate inflorescences from Appian Way are unlike any extant Platanaceae in their possession of elongate tepals and a consistent arrangement of parts in fives. Extant species typically have a highly reduced perianth and a variable number of stamens (Boothroyd 1930; Nixon and Poole 2003). The small parts in the highly reduced perianth of Platanaceae have over time been interpreted as staminodes (Niedenzu 1910), pistils (Griggs 1909), and bracts (Brouwer 1924). However, work by Boothroyd (1930) showed that these structures are true petals and sepals. The presence of rudimentary carpels has been reported sporadically in some staminate flowers in the inflorescence of *Platanus occidentalis* L., *Platanus acerifolia* (Aiton) Willdenow, *Platanus racemosa* Nutt., and *Platanus orientalis* L.; however, the consistent appearance of rudimentary carpels in a regular arrangement of five is a feature unknown in extant *Platanus* (Boothroyd 1930; Schwarzwalder and Dilcher 1981).

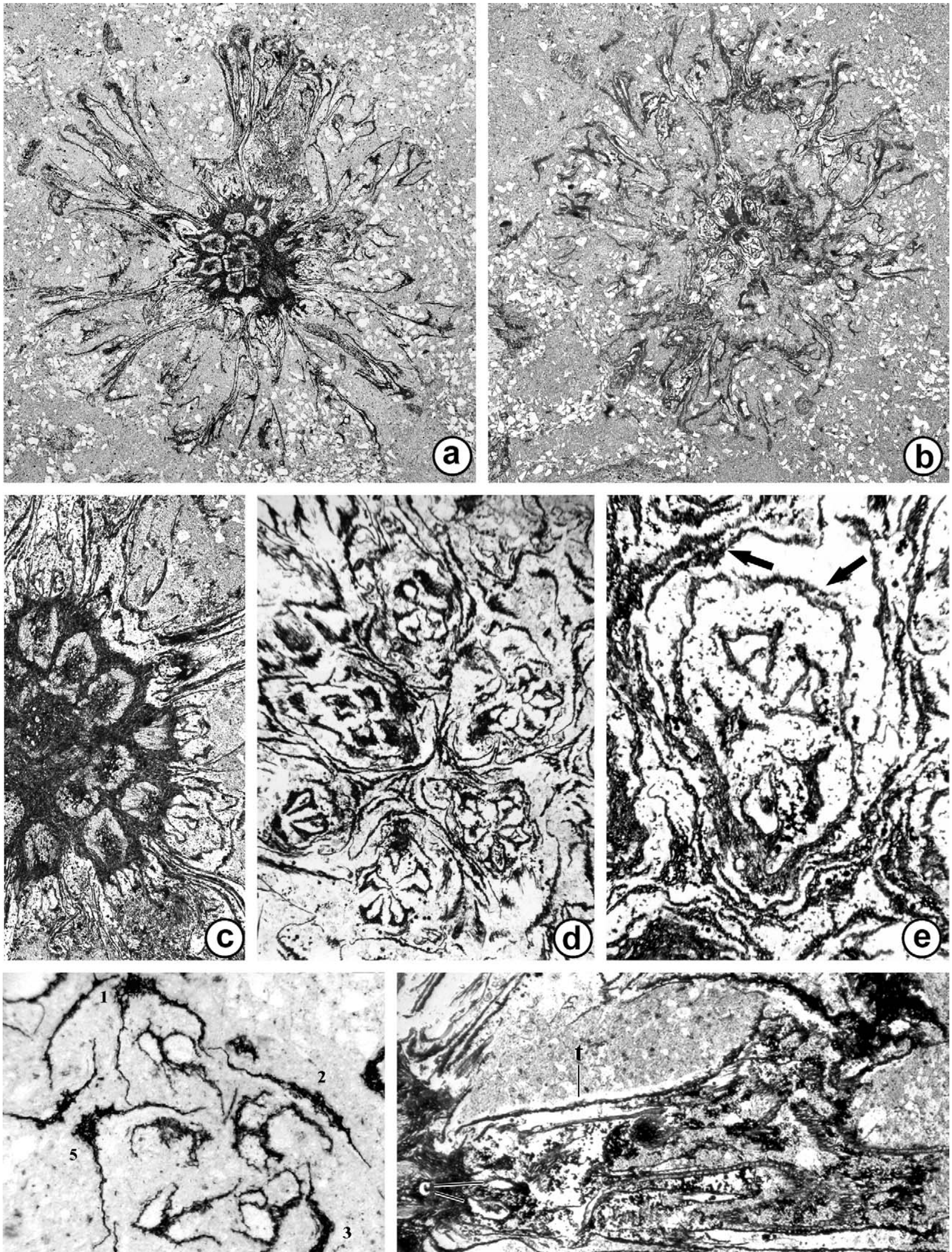
The Appian Way staminate inflorescences show no evidence of peduncle attachment, as they are found isolated in the concretions, and serial sectioning reveals no obvious point of entry for vascular tissues. Since we completely peeled through three specimens, it is unlikely that this part was missing in the saw cut. This leaves two possibilities: attachment was eroded off before or during deposition, or the inflorescences were sessile. The number and arrangement of flowering heads along the peduncle is an important character (Kvaček et al. 2001) in Platanaceae. Though both the stalked and sessile conditions are known within and between species of the subgenus *Platanus*, in subgenus *Castaneophyllum*, globose heads are sessile (Nixon and Poole 2003).

Diversity of Platanaceae is best understood in the fossil record, where most species occur (Crane 1989; Kvaček et al. 2001; Maslova 2003; Kvaček and Manchester 2004). Leaf compression/impressions are common throughout the Cretaceous and Tertiary and have been assigned numerous generic names (Crabtree 1987; Crane 1989; Manchester 1999; Kvaček and Manchester 2004). Inflorescences are usually assigned to morphotaxa (Friis et al. 1988; Pedersen et al. 1994; Magallón-Puebla et al. 1997; Maslova 2002; Maslova and Krassilov 2002), but in exceptional cases, these parts have been hypothesized to represent whole plants (Manchester 1986; Pigg and Stockey 1991).

Inflorescences of Platanaceae are common in the fossil record, but few are well enough preserved to deduce floral structure and anatomical details. Staminate inflorescences assigned to the genus *Platananthus* Manchester are characterized by an arrangement of parts in fives, well-developed tepals, and an apically extended connective that unites the stamens into groups (Manchester 1986). The earliest *Platananthus* comes from the Early Cretaceous of North America. Friis et al. (1988) describe *Platananthus potomacensis* Friis, Crane et Pedersen, from the Late Albian of Maryland, as having a five-parted androecium and elongate tepals, but, unlike the platanoids described in this article, these specimens lack rudimentary carpels and possess smaller pollen (8.5–12 μm polar diameter). The inflorescence of *Platananthus hueberi* Friis, Crane & Pedersen 1988 from the Late Cretaceous of North Carolina is much smaller in diameter (1.9–3.6 mm) than those from Appian Way.

Hamatia elkneckensis Pedersen, Friis and Crane 1994 is an anomalous lignitic compression from the latest Albian of Maryland. While the flowers of this species are seemingly five parted and have a well-developed perianth, the inflorescence is significantly smaller (3–4 mm) than those described from Appian Way. Pollen from *Hamatia* is distinguished from that of all other extant and fossil species, including pollen described here, in being tricolporate, as opposed to the typical tricolpate condition (Pedersen et al. 1994).

Quadriplatanus georgianus Magallón-Puebla, Herendeen & Crane 1997 is represented by both staminate and pistillate inflorescences linked by similarity in structure. Stamens are in groups of four surrounded by two whorls of perianth composed of elongate tepals (Magallón-Puebla et al. 1997). At the center of the staminate flowers, between the stamens, is a central, undifferentiated mass that is interpreted as similar to carpel bases in the pistillate flowers (Magallón-Puebla et al. 1997). This structure seems similar to the Appian Way inflorescences, but our flowers have parts arranged in fives, not fours. This arrangement of four stamens is also known in another late Cretaceous species, *Sarbaya radiata* Krassilov et Shilin (Krassilov and Shilin 1995). These staminate inflorescences from Kazakhstan lack a well-developed perianth and are estimated to have only 24 flowers per head. A tetramerous arrangement has also been observed in *Archaranthus krassilovii* Maslova et Kodrul (Maslova and Kodrul 2003), a fossil from the Cretaceous-Paleocene boundary of the Amur region in eastern Russia. While the perianth in this species is more developed than in *Sarbaya*, only 15 flowers are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estimated per head. The Appian Way staminate inflorescences have at least 40.

Staminate inflorescences of *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, a widespread taxon from the Neogene of Europe (Kvaček and Manchester 2004), have been reported with what have been described as five to eight short, central protrusions of tissue within a whorl of six or seven stamens (Friis 1985). Specimens from the Miocene of Denmark (Friis 1985) show that the central protrusions are "probable reduced carpels," a conclusion with which we are inclined to agree. Staminate inflorescences of *P. neptuni*, unlike those at Appian Way, have a small ellipsoidal receptacular stalk, variable arrangement of parts, and larger pollen (20 μm polar diameter).

Stamens in *Platananthus synandrus* Manchester, a species known from the Eocene Clarno Nut Beds of Oregon, probably dispersed their stamens in groups held together by intertwining trichomes of the connective extension (Manchester 1986). The fossils from Appian Way show no evidence of this type of dispersal and instead suggest that the anthers dehisced singly within the flower, as evidenced by the presence of withered pollen sacs within the perianth. All species of *Platananthus* have been described as having a well-developed perianth and smaller pollen than *Gynoplatananthus*, but stamens are often found in dispersed groups held together by the intertwining of the apical connective extension (see tables in Manchester 1986; Pigg and Stockey 1991). The Appian Way staminate inflorescences show evidence of dehisced stamens and suggest that pollen dispersed directly from the head. In combination with its prominent tepals, this could be evidence of insect pollination within the family in the Eocene, a condition that has been hypothesized as being present in Cretaceous species (Friis et al. 1988; Crane 1989).

Given these above differences, we have placed the Appian Way staminate platanoids in a new genus and species, *Gynoplatananthus oysterbayensis*, which is similar in most respects to species of *Platananthus* but differs in the presence of rudimentary carpels in every flower. This feature has not been reported in any genus of fossil or extant Platanaceae and cannot be accommodated by any existing diagnoses.

Infructescences

Morphologically, the infructescences from Appian Way are also unlike any extant Platanaceae. While there are similarities in size and fruit structure, no living species has either elongate tepals or a consistent arrangement of parts in fives. As is the case for staminate inflorescences, these features are more common in the fossil record (Manchester 1986; Friis et al. 1988; Pigg and Stockey 1991; Pedersen et al. 1994).

The infructescences from Appian Way contain flowers at different stages of development, so it is possible to deduce floral morphology, fruiting features, and anatomy from the some infructescences. Size differences between Appian Way infructescences and other fossil pistillate inflorescences may in some part be due to completeness of preservation or development, as a fruiting specimen is going to be larger than fossils of the flowering stage. They are otherwise ideal for comparison to both fruiting and flowering pistillate inflorescences.

Platanocarpus Friis, Crane & Pedersen 1988, a Cretaceous genus known from both Europe and North America, has pistillate inflorescences that are similar to those of Appian Way, having a pentamerous construction and hairless achenes. *Platanocarpus* is much smaller in size (3–4 mm in diameter) and has a poorly developed style (Friis et al. 1988) compared with the elongate and persistent styles known from the flowers and fruits at Appian Way.

The exceptionally preserved, fusainized pistillate inflorescences of *Q. georgianus* from the Late Cretaceous of Georgia (USA) have elongate tepals in numerous whorls (Magallón-Puebla et al. 1997). The inflorescences are significantly smaller (1.1–2.4 mm) than those known from Appian Way. Furthermore, individual flowers of *Q. georgianus* have a tetramerous arrangement of basally connate parts, as opposed to the pentamerous arrangement in the Appian Way infructescences.

The Paleogene fossils assigned to the genus *Macginicarpa* Manchester (1986) compare most strikingly with the pistillate fructifications from Appian Way. The five-parted arrangement, numerous elongate tepals, mixed fruit maturation, hairless achenes, elongate persistent styles, and fruit anatomy of permineralized *Macginicarpa glabra* Manchester (1986, 1994) from the Middle Eocene Clarno Nut Beds of Oregon are very similar to the pistillate remains described in this article. While the two differ nominally in size, the only significant difference is the presence of thin, elongate, and planated appendages present at the base of each flower in the Appian Way fossils.

The hairless achenes of the infructescences from Appian Way are noteworthy. The absence of hairs is not due to preservation, as many other fine structures, such as fungal hyphae, have been observed. Hairless achenes are present in numerous fossil species of Platanaceae (Lesquereux 1892; Manchester 1986, 1994; Friis et al. 1988). This character merits further consideration, given that modern members of the family have wind-dispersed achenes with a dense basal tuft of trichomes to aid in dispersal (Tiffney 1986). The Appian Way locality has been interpreted as a shallow marine environment because of the presence of decapods (Schweitzer et al. 2003). The presence of entire infructescences suggests

Fig. 1 *Gynoplatananthus oysterbayensis* Mindell, Stockey et Beard gen. et sp. nov. Holotype. *a*, Transverse section of staminate inflorescence; sclerotic receptacular core with pentagonal floral traces. AW 263 Fbot 50, ×8.5. *b*, Tangential section through inflorescence showing individual flowers. AW 263 Fbot 6, ×8.5. *c*, Transverse section of inflorescence showing pentagonal floral vascular traces. Note carpels in longitudinal section lacking styles. AW 263 Fbot 60, ×21. *d*, Oblique section through cluster of flowers showing regular arrangement of five subtriangular carpels and two-whorled perianth. AW 120 Btop 44, ×28. *e*, Transverse section through base of flower showing five carpels, inner fused whorl of tepals, and outer free whorl of tepals (arrows). AW 120 Btop 42, ×100. *f*, Transverse section through distal region of flower showing five dehisced stamens and five prominent thick tepals (*1–5*). AW 120 Btop 147, ×24. *g*, Longitudinal section through single flower showing carpels (*c*) at base and tepals (*t*) surrounding anthers. AW 120 Btop 1, ×30.

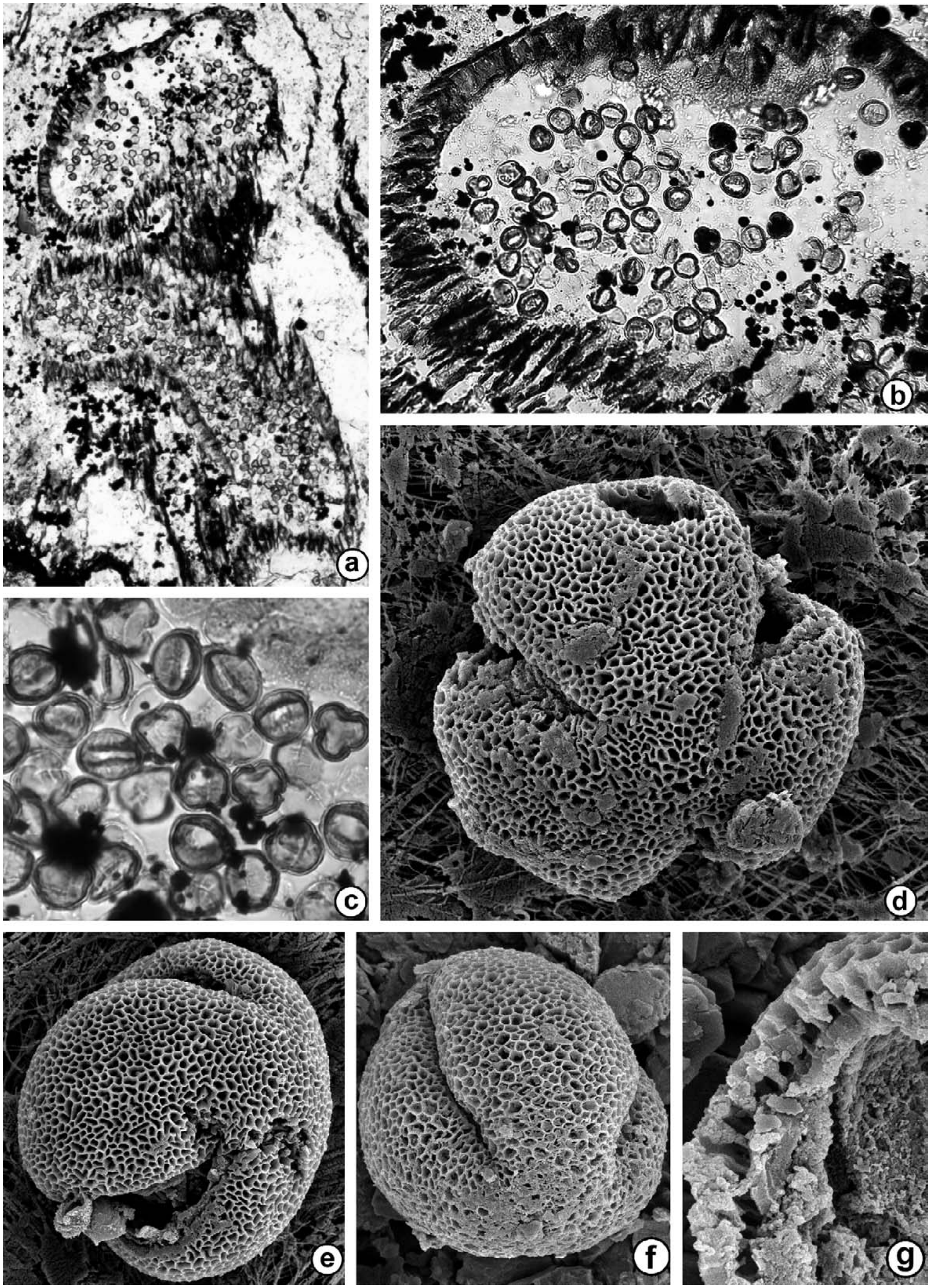

Fig. 2 *Gynoplatananthus oysterbayensis* Mindell, Stockey et Beard gen. et sp. nov. *a*, Transverse section through apical portion of stamen, showing thick connective, anthers, and *in situ* pollen. AW 120 Btop 59, ×110. *b*, Single pollen sac with *in situ* pollen. AW 120 Btop 59, ×240. *c, In situ* tricolpate pollen grains. AW 120 Btop 1, ×612. *d*, SEM showing polar view of reticulate, tricolpate pollen. AW 120 Btop 4, ×5285. *e*, SEM showing near equatorial view of reticulate, tricolpate pollen. AW 120 Btop 4, ×3667. *f*, SEM showing near polar view of pollen. AW 120 Btop 4, ×4500. *g*, SEM micrograph of tectate-columellate pollen wall. AW 120 Btop 4, ×12,000.

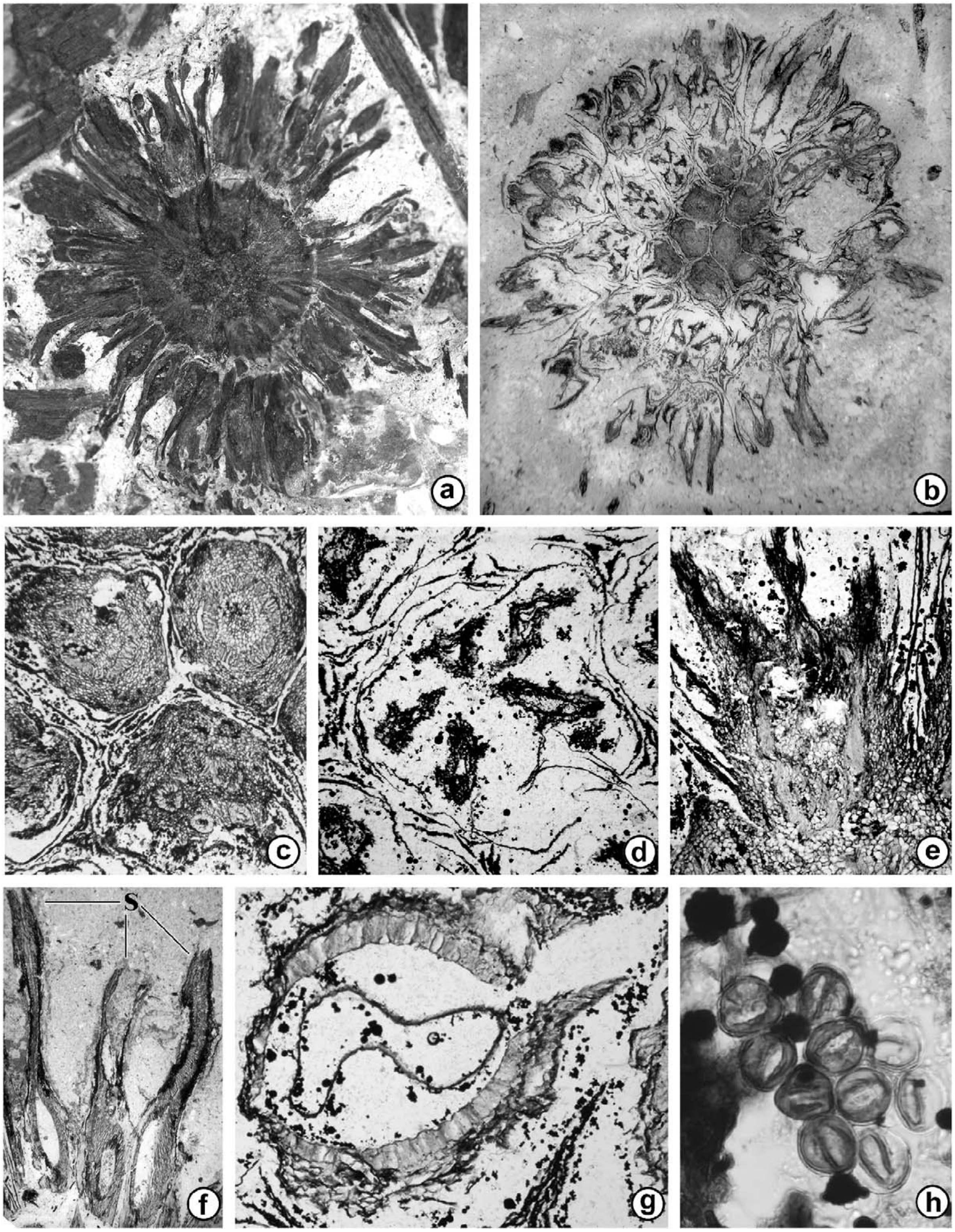

Fig. 3 Associated pistillate infructescences. *a*, Permineralized fructification exposed on surface of rock. AW 699 B, ×5. *b*, Transverse section through pistillate fructification showing five-carpelled flowers. AW 142 Ltop 76, ×5.3. *c*, Transverse section through base of flowers showing parenchymatous receptacle, pentagonal floral trace (top) and circular carpel traces (bottom right). AW 142 Ltop 76, ×30. *d*, Transverse section through flower showing five carpels and two whorls of thin tepals. AW 142 Ltop 83, ×68. *e,* Longitudinal section through base of flower showing numerous whorls of basal appendages. AW 142 Ltop 18, ×32. *f,* Longitudinal section of mature achenes showing persistent styles (*S*). AW 699 B 2, ×7.5. *g,* Transverse section through base of mature fruit with palisade-like endocarp surrounded by remnant mesocarp. Note seed remnant inside. AW 142 Ltop 8, ×45. *h,* Tricolpate pollen found between styles of pistillate flowers. AW 142 Ltop 5, ×568.

the plants were growing in a riparian environment, like most extant members of the family (Nixon and Poole 2003), and that the infructescences floated downstream to the shallow marine environment into which they were finally deposited. Given the lack of dispersal hairs, it is plausible that the fruits of this species, like those of *Macginicarpa*, were dispersed by water (Manchester 1986).

Relationship between Staminate and Pistillate Flowers

A relationship between the staminate and pistillate platanoids at Appian Way is supported by similarities in vascular and floral structure and the presence of the same pollen type in both flowers. Both pistillate and staminate flowers are supplied by pentagonal vascular traces that subsequently divide into five major ellipsoidal traces. Both types of flowers have their parts in fives and elongate, strap-shaped tepals. The carpels, when immature in the pistillate flowers, are the same shape as the rudimentary carpels in the staminate flowers. The only difference between the two types of flowers is that the pistillate flowers lack stamens, while their gynoecium is fully developed, with an elongate style and ovules. The presence of pollen of the same dimensions and shape as that found in the anthers of *G. oysterbayensis* proximal to the styles in the pistillate flowers supports the idea that these two inflorescence types are probably of the same species, though further evidence in the form of attached vegetative parts linking the two is needed to confirm this relationship.

In the fossil record of Platanaceae, *G. oysterbayensis* has the clearest record of rudimentary carpels, as evidenced by the absence of a style or stigmatic surface. While some Cretaceous species are known to have short styles (Friis et al. 1988) or even to lack styles (Magallón-Puebla et al. 1997), these species have elongate carpels and specialized apical platforms. They are clearly functional, as evidenced by the presence of ovules and seeds. The rudimentary carpels of *G. oysterbayensis* have been followed through successive peels and lack any evidence of styles, stigmatic surfaces, apical platforms, trichomes, or any other structure conducive to pollen trapping.

These rudimentary carpels occur in fives in the center of every staminate flower. An arrangement of five carpels is common in pistillate flowers of extant *Platanus* species (Cronquist 1981) but has been reported only sporadically in staminate inflorescences (Boothroyd 1930; Schwarzwalder and Dilcher 1981). Pistillate flowers of *P. racemosa* have staminodia (Boothroyd 1930; Floyd et al. 1999), while stamens in some pistillate flowers of *P. occidentalis* have been shown to intergrade between a rudimentary condition to fully functional, the latter being part of truly perfect flowers (Schwarzwalder and Dilcher 1981). While inflorescences of *Platanus* are generally unisexual, the co-occurrence of separate male and female flowers on the same globose head is known to occur in *P. racemosa* (Floyd et al. 1999). This same type of arrangement has been observed in both Eocene and Oligocene fossils (S. R. Manchester, personal communication, 2005).

While the idea of an ancestral bisexual condition in Platanaceae has been put forth by Schwarzwalder and Dilcher (1981), fossil species do not provide clear evidence for this. As discussed above, some fossil staminate inflorescences have flowers with central protrusions of tissue between the stamens. Due to their exceptional preservation, Late Cretaceous *Q. georgianus* (Magallón-Puebla et al. 1997) and Miocene *P. neptuni* (Friis 1985) show these protrusions, and in both cases these are interpreted as rudimentary carpels. The presence of rudimentary carpels in *G. oysterbayensis* confirms that this feature is long-lived within the family, arising possibly in the Late Cretaceous (Magallón-Puebla et al. 1997), certainly by the Eocene, and persisting to the present. The occurrence of these features in fusainized and permineralized material suggests the possibility of a preservation bias, as such cryptic characters would be difficult to deduce from compression/impression fossils. The presence of rudimentary carpels in fossil Platanaceae could be far more prevalent than current estimates. If these rudimentary carpels are the result of a reduction from earlier bisexual flowers, we would expect to see evidence of this in the early fossil record for the family.

The fossil inflorescences and infructescences from Appian Way are of interest in debating the validity of hypothesized relationships between Platanaceae, Nelumbonaceae, and Proteaceae within the Proteales as put forth by recent molecular phylogenetic studies (Chase et al. 1993; Hoot et al. 1999; Hilu et al. 2003). The initial grouping of Platanaceae with Nelumbonaceae and Proteaceae in what is currently known as the "Proteales clade" was thought to be a product of the small number of species sampled (Chase et al. 1993). The group has very little morphological or anatomical continuity, but molecular phylogenies have consistently grouped these families together (Hoot et al. 1999; Soltis et al. 2003). As a consequence, there has been an effort to find features in common. Hoot et al. (1999) point to the fossil record to show a relationship between Platanaceae and Proteaceae, suggesting that the Cretaceous *Q. georgianus* points to an ancestral tetramerous arrangement. Using extant taxa in a combined analysis (morphology, *rbc*L, 18S, and *atp*B sequences), Doyle and Endress (2000) generated the same grouping of families (though morphology alone could not resolve the same grouping) and pointed to orthotropous ovules, nuclear endosperm, and large embryos as features uniting Platanaceae and Proteaceae as sister taxa.

Gynoplatananthus oysterbayensis, much like living Platanaceae, has characters that could be employed both to support and to refute the Proteales grouping. Hoot et al. (1999) state that the regular merosity of fossil Platanaceae suggests derivation from a four-parted ancestral condition, as is the case with the perianth and androecium of Proteaceae. Regularly (Magallón-Puebla et al. 1997) and irregularly (Manchester 1994) tetramerous Platanaceae flowers are known from the fossil record. *Gynoplatananthus* falls among the Tertiary constituents of a long line of pentamerous flowers with a deeper stratigraphic range, stretching from the Lower Cretaceous (Friis et al. 1988; Pedersen et al. 1994) through the Paleocene (Pigg and Stockey 1991) to the Eocene (Manchester 1986; Maslova 2003). Extant Proteaceae and Nelumbonaceae both have perfect flowers, while Platanaceae is strictly unisexual. While functionally bisexual flowers have been observed (Schwarzwalder and Dilcher 1981) in extant *Platanus*, and *Gynoplatananthus* does have rudimentary carpels, caution should be taken to avoid extrapolating bisexual ancestors in the absence of a clear Cretaceous fossil example.

In conclusion, staminate and pistillate platanaceous inflorescences from Appian Way, linked by similarities in structure and pollen, are among the best-preserved fossils of Platanaceae. Three-dimensional permineralization has revealed details of anatomy and presence of structures that would not be observable in compressions. The occurrence of rudimentary carpels in staminate flowers of *G. oysterbayensis* suggests that this condition, occasionally reported in extant *Platanus*, has long been held within the family and could represent an intermediate step from an ancestral perfect flower to the present unisexual condition. The recovery and recognition of fossil platanoid flowers containing fully developed stamens and carpels would clarify the validity of this proposed transition. A well-developed perianth and anthers dehiscing within the flower suggest possible insect pollination (Crane 1989), and the hairless achenes of the infructescences suggest water dispersal of fruits, as is observed in both living (Tiffney 1986) and fossil (Manchester 1986) fruits of Platanaceae.

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