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ESTABLISHING A FOSSIL RECORD FOR THE PERIANTHLESS PIPERALES: *SAURURUS TUCKERAE* SP. NOV. (SAURURACEAE) FROM THE MIDDLE EOCENE PRINCETON CHERT[1]

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Investigations of small permineralized flowers from the Middle Eocene Princeton Chert, British Columbia, Canada have revealed that they represent an extinct species of *Saururus*. Over 100 flowers and one partial inflorescence were studied, and numerous minute perianthless flowers are borne in an indeterminate raceme. Each flower is subtended by a bract, and flowers and bracts are borne at the end of a common stalk. Five stamens are basally adnate to the carpels. Pollen is frequently found in situ in the anthers. Examined under SEM and TEM, pollen grains are minute (6–11 μm), monosulcate, boat-shaped-elliptic, with punctate sculpturing and a granulate aperture membrane. The gynoecium is composed of four basally connate, lobed carpels with recurved styles and a single ovule per carpel. Flower structure and pollen are indicative of Saururaceae (Piperales), and in phylogenetic analyses using morphological characters, the fossils are sister to extant *Saururus*. The fossil flowers are described here as *Saururus tuckerae* sp. nov. These fossil specimens add to the otherwise sparse fossil record of Piperales, represent the oldest fossils of Saururaceae as well as the first North American fossil specimens of this family, and provide the first evidence of sauruaceous pollen in the fossil record.

Key words: Eocene; fossil flowers; magnoliids; Piperales; pollen; Princeton Chert; Saururaceae; *Saururus*.

Piperales today are a diverse, speciose group of early-divergent angiosperms and are important for understanding early angiosperm evolution (Wanke et al., 2007). However, there are few fossils confidently assigned to the order, inhibiting a deeper understanding of evolutionary trends. As circumscribed by APG (2003), Piperales include the families Aristolochiaceae, Hydnoraceae, Lactoridaceae, Piperaceae, and Saururaceae. Saururaceae are a small family consisting of four genera and six extant species: *Anemopsis californica* Hook. et Arnott, *Gymnotheca chinensis* Decaisne, *G. involucrata* Pei, *Houttuynia cordata* Thunb., *Saururus cernuus* L., and *S. chinensis* (Lour.) Baill. (Wu and Kubitzki, 1993). These herbaceous, rhizomatous plants tend to inhabit moist to wet environments (Wu and Kubitzki, 1993; Liang, 1995; Xia and Brach, 1999). Within Saururaceae, two species (*S. cernuus* and *A. californica*) are found in North America and four species (*S. chinensis*, *H. cordata*, *G. chinensis*, and *G. involucrata*) in eastern Asia (Wu and Kubitzki, 1993). The family is likely monophyletic and is sister to Piperaceae in the order Piperales (Tucker and Douglas, 1996; Meng et al., 2002, 2003; Jaramillo et al., 2004; Neinhuis et al., 2005). Flowers of both Piperaceae and Saururaceae are distinct from other piperalean flowers in being small and lacking a perianth. Saururaceous flowers are subtended by a bract and typically have three (*Houttuynia, Anemopsis*) or four (*Saururus, Gymnotheca*) carpels and three (*Anemopsis*) or six (*Houttuynia, Saururus*, and *Gymnotheca*) stamens (Wu and Kubitzki, 1993). However, some variation in the numbers of carpels and stamens within flowers of an infloresence has been described (e.g., Raju, 1961; Tucker, 1975, 1981, 1985; Liang and Tucker, 1989; Liang, 1994).

To date only two fossil species are known for Saururaceae, and there are few confirmed reports of fossil Piperaceae. Fruits and seeds of *Saururus bilobatus* (Nikitin) Mai have been recognized from the Late Eocene to Pliocene of Europe and Siberia (Mai and Walther, 1978; Friis, 1985; Stuchlik et al., 1990; Lesiak, 1994), and seeds of *Houttuynia bavarica* Mai (Mai, 1999) from the Miocene of Germany. These are known from gross morphology and have not been anatomically examined. No fossil vegetative or pollen remains have been firmly placed in the family Saururaceae. However, we recently recognized that fossil flowers from the Middle Eocene Princeton Chert, previously thought to have affinities to Alismatales (Currah and Stockey, 1991; Stockey, 1994, 2001, 2006; Pigg and Stockey, 1996; Smith and Stockey, 2004, 2005), have many similarities to saururaceous flowers. Here, we describe this flower type and demonstrate that while these fossil flowers are similar to certain alismatids, floral and inflorescence structure and anther contents suggest that this flower type is related to Saururaceae (Piperales).

MATERIALS AND METHODS

Fossil material—Fossils were collected from the Princeton Chert outcrop, located on the east bank of the Similkameen River, 8.4 km south of the town of

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Princeton, British Columbia (Boneham, 1968). The outcrop consists of interbedded layers of chert and coal, with occasional ash layers (Stockey, 1983). There are about 49 major chert layers, but these split and anastomose to make approximately 70 individual beds ranging in thickness from 1 to 50 cm (Smith et al., 2006). The Princeton Chert is part of the Princeton Group, Allenby Formation (Boneham, 1968). A Middle Eocene age has been determined based on freshwater fish (Wilson, 1977, 1982), mammals (Russell, 1935; Gazin, 1953) and K-Ar dating (Hills and Baadsgaard, 1967). The ash of Layer #22 is currently dated at 48.7 million yr (H. Baadsgaard, University of Alberta, personal communication, 1999).

Chert blocks were cut into slabs and studied using the cellulose acetate peel technique (Joy et al., 1956) modified for concentrated (48%) hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). Peels were mounted on microscope slides using Eukitt (O. Kindler, GmbH, Freiburg, Germany) xylene-soluble mounting medium. Images were captured with a PowerPhase digital scanning camera (Phase One, A/S, Fredriksberg, Denmark) and a MicroLumina digital scanning camera (Leaf Systems, Bedford, Massachusetts, USA). Photographs were processed with Adobe (San Jose, California, USA) Photoshop CS. Three-dimensional reconstructions were done using photos of serial sections (taken with a Nikon [Tokyo, Japan] Coolpix 5400) and the computer visualization software AMIRA 3.1.1 (TGS Software, San Diego, California, USA).

Electron microscopy—Scanning electron microscopy (SEM) of the fossil pollen was done using the back side of deeply etched peels. Peel sections were mounted on double-sided tape on stubs and covered with 150 Å gold using a Nanotek SEMprep II sputter coater (Prestwich, Manchester, UK). Samples were observed using a JEOL (Tokyo, Japan) 6301F (field emission scanning electron microscope). Extant pollen from herbarium sheets was examined in the same way.

Fossil pollen was prepared for transmission electron microscopy (TEM) by dissolving the acetate matrix in two changes of acetone and demineralizing in concentrated (48%) hydrofluoric acid, with distilled water rinses. Pollen from extant *Saururus* was sampled from herbarium material (*S. cernuus*: ALTA 5509, *E. H. Moss s. n.*, 31 July 1914; *S. chinensis*: LSU 72527, *Liang Hanxing 8709*, 15 June 1987) and fixed in FPA overnight. Fossil and extant pollen was placed in 2% OsO_4 for 2.0–3.5 h, rinsed again in distilled water, and embedded in Spurr's (1969) resin, following an ethanol–propylene oxide dehydration series for fossil material and an ethanol–acetone dehydration series for extant material. Sections were cut at 60–80 nm using a diamond knife, collected on grids, and stained using uranyl actetate and lead citrate. Sections were observed using a Philips/FEI (Hillsboro, Oregon, USA) Morgagni 268 TEM.

Phylogenetics—A morphological cladistic analysis of the Princeton fossils and Piperaceae/Saururaceae was performed, which assumes a priori assignment of the fossil to Piperales. It is beyond the scope of this paper to do a broader analysis including all early-divergent angiosperms, but this should be undertaken in the future. The data matrices of Tucker et al. (1993), Tucker and Douglas (1996), and Meng et al. (2003) were modified, and the fossil data were added to form a new morphological data set, that was then analyzed phylogenetically (Table 1, Appendix 1). Molecular data (e.g., Nickrent et al., 2002; Neinhuis et al., 2005) have recognized Piperaceae/Saururaceae as sister to a clade of Lactoridaceae, Hydnoraceae, and Aristolochiaceae. Analysis of the relationships of the fossil taxon among sauruaceous taxa used *Lactoris* Phil. (Lactoridaceae), *Aristolochia* L., and *Asarum* L. (Aristolochiaceae) as outgroups. The ingroup consisted of *Piper* L., *Peperomia* Ruiz & Pavon, and *Zippelia* Blume for Piperaceae, and *Saururus chinensis, S. cernuus*, *Gymnotheca*, *Anemopsis californica*, and *Houttuynia cordata* for Saururaceae. *Piper* and *Peperomia* were coded as generic placeholders using polymorphic characters. Where inferences about the ancestral states could be made (e.g., stamen and carpel numbers; see Jaramillo and Manos, 2001), these states were used to represent the genus, rather than also including more derived states, and thus some characters are monomorphic. *Anemopsis* and *Houttuynia* are monotypic, and both species of *Saururus* were used. Although *Gymnotheca* has two species, they do not vary in the floral characters coded in the matrix, and so they were treated as one terminal taxon. The only previously known fossils, fruits and seeds of *Saururus bilobatus* and seeds of *Houttuynia bavarica* Mai, were not included because of a lack of scorable characters.

Phylogenetic analyses were conducted using PAUP* version 4.0b10 (Swofford, 2002). Heuristic searches were performed using 1000 random addition replicates with tree-bisection-reconnection (TBR) branch swapping and MULTREES on. Characters were unordered and equally weighted. Analyses were done with or without the fossil taxon. Branch support was estimated using bootstrap analyses (Felsenstein, 1985), with 100 bootstrap replicates and the same search criteria as heuristic searches. Character state reconstructions were done using MacClade 4.08 (Maddison and Maddison, 2005).

Table 1. Morphological data matrix used for phylogenetic analysis of fossil and extant Saururaceae, with other piperalean taxa as outgroups; see Appendix 1 for description of character states.

	Character		
Taxon	1	10	20
Aristolochia	01100?000	2?01001?20	02010
Asarum	00100?051	2?01001120	02010
Lactoris	000000000	0000000000	00000
Piper	11010(01)1(23)0	0(01)10010221	1(02)221
Peperomia	11010(01)110	0011013200	1(02)121
Zippelia	110000100	001?012120	11221
Saururus cernuus	110011100	0110112100	01101
Saururus chinensis	110011100	1010112110	01101
Anemopsis	110100101	2010110220	01011
Gymnotheca	110010101	2110112120	01011
Houttuynia	110100120	1010110220	01011
Fossil *Saururus*	110010140	1010112110	0?101

Sources: Raju, 1961; Tucker, 1975, 1976, 1979, 1980, 1981, 1982, 1985; Xi, 1980; Omori, 1982; Liang, 1992; Kubitzki, 1993; Huber, 1993; Tebbs, 1993; Tucker et al., 1993; Wu and Kubitzki, 1993; Liang and Tucker, 1995; Tucker and Douglas, 1996; Buddell and Thieret, 1997; Bernardello et al., 1999; Lei and Lang, 1999; Tseng et al., 1999; Xia and Brach, 1999; Sampson, 2000; Gonzalez and Rudall, 2001; Jaramillo and Manos, 2001; Kelly, 2001; Mulder, 2003; Jaramillo et al., 2004.

RESULTS

Systematics—*Order*—Piperales Dumort

Family—Saururaceae Martynov

Genus—*Saururus* L.

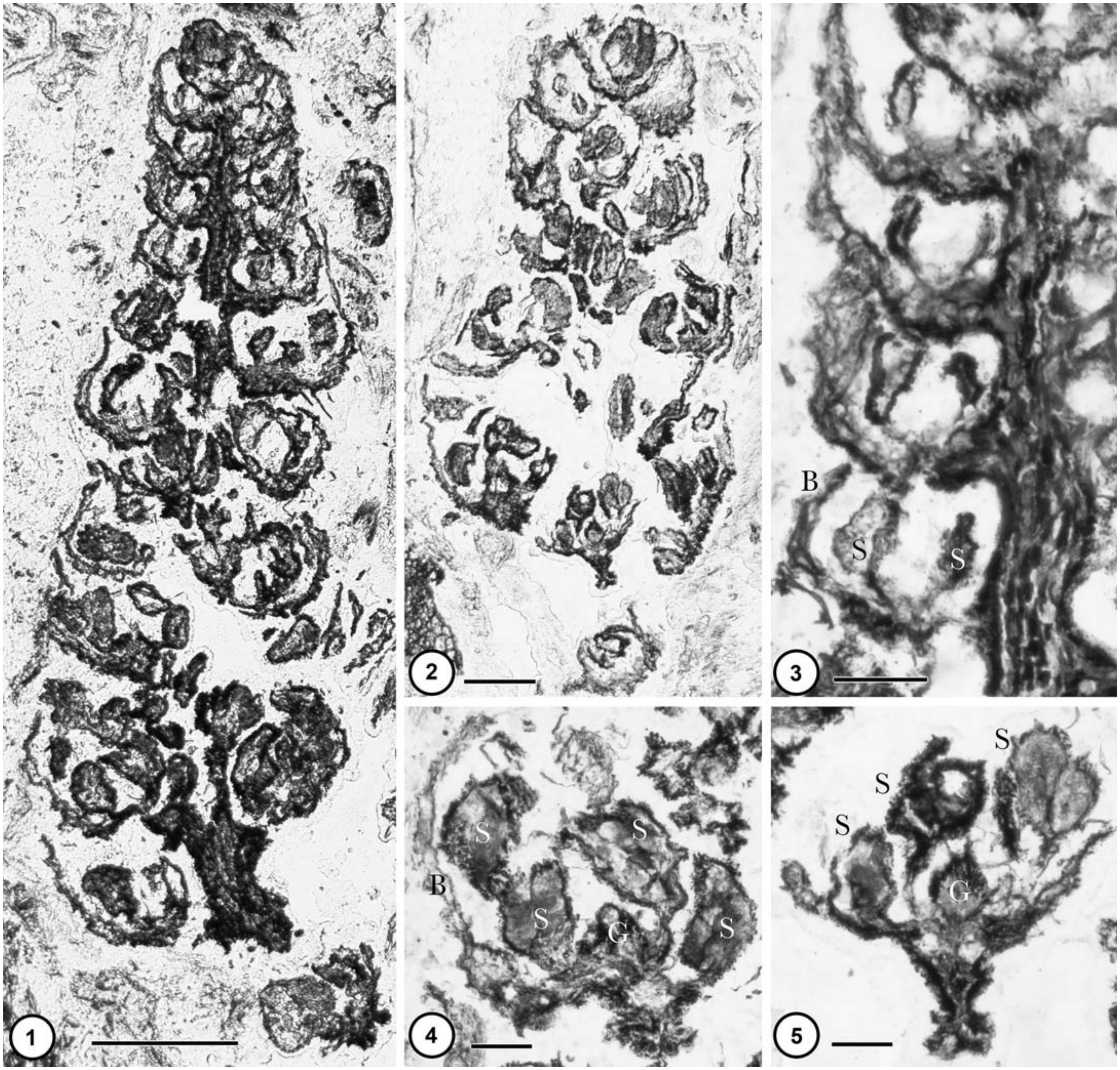
Species—*Saururus tuckerae* S.Y.Smith & Stockey sp. nov.

Specific diagnosis—Inflorescence a raceme, at least 2.9 mm long and 1.0 mm diam. Flowers ca. 0.8 mm diam. Subtending bract, cup-shaped, ovate; flower-bract stalk and pedicel present. Perianth absent. Stamens five, adnate to carpels, up to 0.8 mm long, tetrasporangiate, with latrorse longitudinal dehiscence. Pollen 6–11 μm, monosulcate, boat-shaped-elliptic; sculpturing punctate. Carpels four, basally connate, tapering at apex, up to 1.2 mm long, 0.4 mm wide. Styles one per carpel, recurved. Seeds one per carpel, attached marginally near base.

Holotype—P1631 Bbot a (Figs. 1–5).

Paratypes—P1631 Btop a, Btop b, Btop f, Btop h, Bbot c, Cbot e; P5831 Bbot; P5839 A; P5937 Gbot b; P5991 B (Figs. 8–15, 21, 22, 26, 29–35).

Etymology—The specific epithet "*tuckerae*" is proposed in honor of Dr. Shirley Tucker, University of California-Santa Barbara, for her work on furthering our understanding of floral structure and ontogeny in Saururaceae.



Figs. 1–5. Inflorescence (Holotype P1631 Bbot a) (light micrographs). **1.** Longitudinal section through center of apical part of inflorescence. P1631 Bbot #67a; scale bar = 500 μm. **2.** Tangential section through inflorescence. P1631 Bbot #58a; scale bar = 250 μm. **3.** Enlarged view of apical part of inflorescence showing bracts with one pair of developing stamens. P1631 Bbot #67a; scale bar = 100 μm. **4.** Longitudinal section through one flower near basal part of inflorescence, with cup-shaped bract, large stamens, and small carpels. P1631 Bbot #68a; scale bar = 100 μm. **5.** Longitudinal section through flower showing stalk, gynoecial area, stamens and bract. P1631 Bbot #58a; scale bar = 100 μm. *Abbreviations:* B, bract; G, gynoecium; S, stamen.

Type locality—Princeton Chert, east bank of the Similkameen River, ca. 8.4 km south of Princeton, British Columbia, Canada. Princeton Map Sheet 92 H/7 (1 : 50 000) UTM 10U FK 783724.

Stratigraphy and age—Princeton Group, Allenby Fm.; Middle Eocene

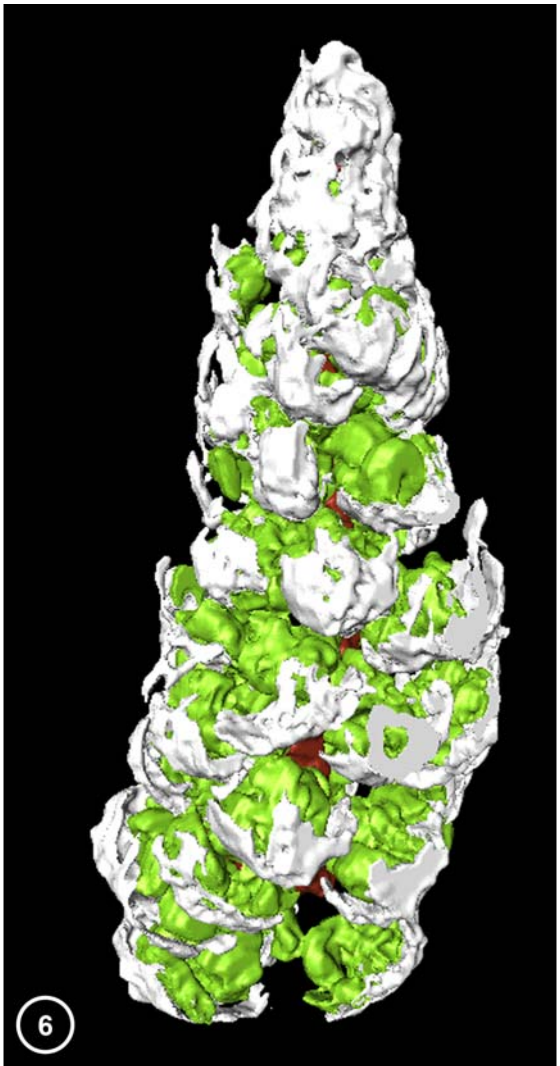
Description—*Inflorescence and floral morphology*—A single specimen representing the apical portion of an inflorescence and several hundred isolated flowers have been found in the chert. The inflorescence is a raceme, the preserved portion 2.9 mm long and ca. 1.0 mm in diameter (Figs. 1, 6). Flowers at the apex are very immature, and their bracts are larger than the androecium and gynoecium (Figs. 1, 3). Those at the base are more mature, with well-developed anthers and poorly developed carpels (Figs. 1, 2, 4, 5). A cup-shaped bract subtends each flower, up to 0.4 mm long, 0.8 mm wide, and 48 µm thick.

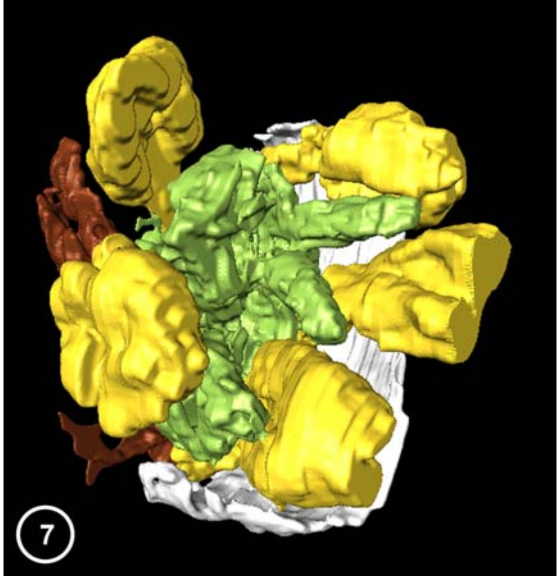
Flowers are minute, up to 1.2 mm long, and 0.8 mm in diameter (Figs. 1–5, 8–11). One vascular strand is found in the flower-bract stalk, which divides into multiple strands in the bract and then into the strands supplying the flower itself. A very short pedicel, up to 96 µm long, is apparent in some specimens, and this separates the carpels and stamens from the bract (Fig. 10). Distally, the bract becomes less enveloping. There is no evidence of a perianth in any of the flowers.

Androecium—There are five stamens per flower, although some cross sections show only four (Figs. 7–9). The small flower size makes reconstruction difficult because much of it may be lost in the saw cut. However, five complete flowers have been reconstructed based on consecutive sections, and all have five stamens: one adaxial median stamen and two pairs of lateral stamens. Stamens are adnate to the base of the carpel and tend to be about the same height as the carpels, at least 0.8 mm long (Figs. 10, 11). Anthers are tetrasporangiate, and most specimens retain pollen inside (Figs. 8, 9, 12). Older dehisced anthers have a longitudinal, latrorse dehiscence pattern (Fig. 13). Thickenings in the endothecium are apparent, especially toward the inside of the anther.

Pollen found within the anthers is minute, about 6–11 µm in diameter, monosulcate, boat-shaped-elliptic, and under light microscopy, appears to be psilate (Fig. 15). Scanning electron microscopy reveals that the pollen grains have punctate (or perforate, both sensu Punt et al., 1994) sculpturing and small granula on the aperture membrane (Figs. 21, 22). Transmission electron microscopy shows that the aperture membrane is thin and the pollen wall is tectate-columellate, up to 380 nm thick (Figs. 26, 27). The tectum measures 75–130 nm thick, and the foot layer is 100–175 nm thick (Fig. 29). There are perforations in the tectum where the puncta occur on the surface (Fig. 29). Columellae are irregularly spaced in section view and 95–115 nm high (Fig. 29).

Pollen of extant Saururaceae—Pollen of *Saururus cernuus* and *S. chinensis* was examined using SEM and TEM. Extant *Saururus* pollen is boat-shaped-elliptic, monosulcate, with granula on the aperture membrane. Grains of *S. cernuus* are 11–13 µm in diameter (Figs. 16, 17) and those of *S. chinensis* 10–12 µm in diameter (Figs. 18, 19). The exine has pronounced punctate sculpturing but lacks supratectal sculpturing (Figs. 16–20, 23). The puncta in extant *Saururus* pollen have raised edges (Figs. 20, 23, 27, 28). In both species, the aperture membrane is thin with poorly developed ectexine and granulate sculpturing (Figs. 24, 25). In *Saururus cernuus*, the ectexine is 450–500 nm thick, the tectum is 95–190 nm thick, and the foot layer is 230–270 nm thick (Figs. 25, 27). Columellae are irregularly spaced, 95–170 nm tall. The infratectal layer is irregular in shape (Fig. 27). A dark layer below the foot layer likely represents endexine (Fig. 27). Ectexine of *S. chinensis* is 360–380 nm thick (Figs. 25, 28). Columellae are irregularly spaced and very short, ca. 20–95 nm





Figs. 6–7. Computer reconstructions based on serial sections through specimens. **6.** Inflorescence showing bracts (white); androecium and gynoecium (green); and inflorescence axis (brown). Reconstructed from Holotype P1631 Bbot a. **7.** Flower showing cup-shaped bract (white), five

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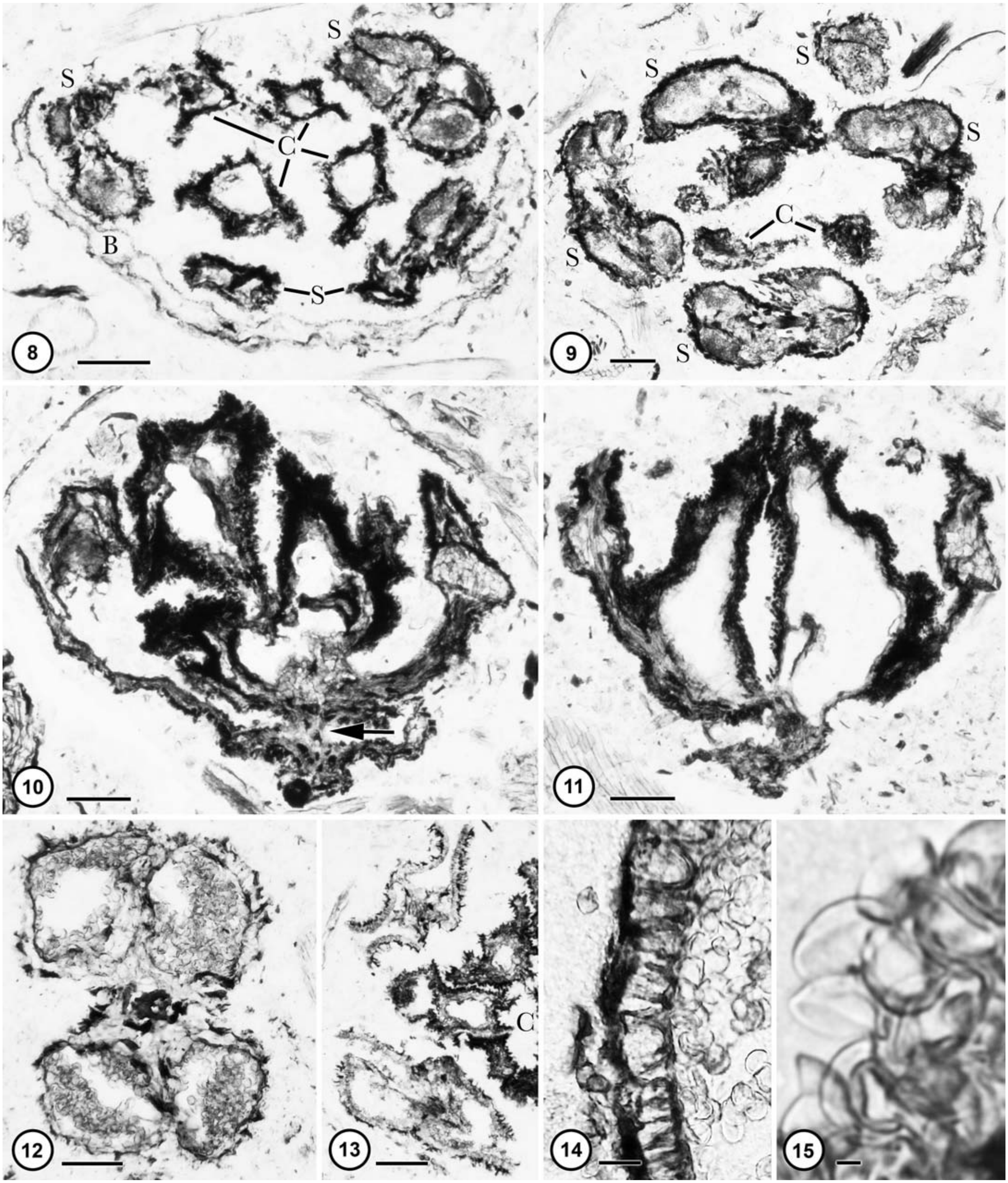
stamens (yellow) about the same height as gynoecium, four carpels (green) with styles reflexing outward, and inflorescence axis (brown). Reconstructed from Paratype P5937 Gbot b.



Figs. 8–15. General flower structure and stamens (light micrographs). **8.** Cross section through flower at distal level showing subtending bract, four stamens, and four carpels. Paratype P5839 A #0; scale bar = 100 μm. **9.** Cross section through flower showing five stamens and four carpels. Paratype P5937 Gbot #41b; scale bar = 100 μm. **10.** Oblique longitudinal section through flower showing bract, pedicel (at arrow), three (of four) carpels, and portions of two stamens, one of which is clearly attached to carpel base. Note thick filament. Paratype P1631 Btop #27h; scale bar = 100 μm.

(Fig. 28), the tectum is 190–290 nm thick, and the foot layer is 75–170 nm thick (Fig. 28). A dark-staining layer below the foot layer likely represents endexine (Fig. 28).

Gynoecium—Each fossil flower has four carpels, which are basally connate (Fig. 30). Carpels are wider at the base (up to 0.4 mm in diam), taper near the top (ca. 0.1 mm in diam), and are up to 1.2 mm long (Figs. 30–33). Each carpel has two lateral lobes that are apparent in cross section (Figs. 8, 30, 31). Cells of the carpel wall are generally small (Figs. 30–34), but the innermost layer is composed of large, thin-walled cells (Figs. 30, 34, 35). There is one recurved style per carpel (Figs. 32, 33), and the stigmatic surface appears to be papillate (Fig. 33, arrow). Each carpel is uniloculate with a single ovule (Figs. 30, 33, 34). Ovule attachment is marginal, toward the base of the carpel, and helically thickened tracheary elements are preserved in the funiculus of some specimens (Figs. 34, 35). There is no evidence of embryos or other internal tissues. Fungal hyphae are occasionally found inside the ovule or along the cell walls of the carpel. Spherical fungal structures up to 100 μm in diameter also occur in the outermost layers of the carpels in some specimens. No meiospores or conidia were found in these structures, and their exact nature is unclear.

Phylogenetic analyses—Phylogenetic analyses of morphological data were done using only extant taxa or with the fossil taxon *S. tuckerae* included. Both analyses resulted in a single most parsimonious tree of 51 steps (extant only; CI = 0.667, RI = 0.673) or 52 steps (with fossil taxon; CI = 0.673, RI = 0.707) (Fig. 36). *Lactoris* is sister to (*Aristolochia* + *Asarum*). Both Piperaceae and Saururaceae are found to be monophyletic. *Zippelia* is found to be the sister group of all other Piperaceae. Within Saururaceae, (*Saururus* + *Gymnotheca*) is sister to (*Anemopsis* + *Houttuynia*). When the fossil is included in analyses, it is sister to extant *Saururus*.

Character evolution was examined in MacClade (Maddison and Maddison, 2005) for the single most parsimonious tree with the fossil included (Fig. 36; Appendix 2). Piperaceae are supported by three synapomorphies: presence of a sessile stigma (character 20), one ovule per gynoecium (character 22), and basal placentation (character 23). Saururaceae are supported by having boat-shaped pollen (character 14). A clade of *Anemopsis* + *Houttuynia* is supported by two characters showing homoplasy: the presence of sessile flowers (character 4) and three carpels (character 17). The presence of a flower-bract stalk (character 5) and four carpels (character 16; this is homoplasious) support the *Gymnotheca*-*Saururus* clade. The *Saururus* clade is supported by three characters: basally connate carpels (character 18), 1–2 ovules per carpel (character 22), and marginal placentation (character 23). Only the first is nonhomoplasious. The clade formed by extant *Saururus* is supported by the presence of trichomes on the bract (character 6).

DISCUSSION—*Affinities of the fossil flowers*—These fossil flowers have previously been thought to represent an undescribed alismatid taxon (Currah and Stockey, 1991; Stockey, 1994, 2001, 2006; Pigg and Stockey, 1996; Smith and Stockey, 2004, 2005). Morphologically, the fossil flowers resemble some families of Alismatales (particularly Aponogetonaceae, Juncaginaceae, and Potamogetonaceae) and Piperales (Saururaceae), all of which have minute flowers borne on spikes (or racemes). Alismatid flowers, however, generally have tepals, trimerous flowers, and free carpels and stamens (Dahlgren et al., 1985), unlike the fossil flowers described here. The zygomorphic flowers of Aponogetonaceae typically have two tepals; six stamens with longitudinal, extrorse dehiscence; and three free carpels, each with 2–12 ovules and a short style; but some species are variable in numbers of parts (Dahlgren et al., 1985; van Bruggen, 1998). Flowers of Potamogetonaceae are actinomorphic, usually with four tepals (adnate to the androecium), four stamens with longitudinal extrorse dehiscence, and four free carpels with a short style and single ovule (Haynes et al., 1998b). The genus *Maundia* F. Muell. (Juncaginaceae) has four weakly connate carpels; but *Maundia* flowers have no bract, 2–4 tepals, up to eight stamens, and carpels without a style (Haynes et al., 1998a).

Flower structure of the fossils is most similar to that seen in Saururaceae. Typical saururaceous flowers are minute, are borne on a spike or raceme, have a bract and no perianth, three or six stamens and three or four carpels (Liang and Tucker, 1990; Wu and Kubitzki, 1993; Igersheim and Endress, 1998). *Saururus* and *Gymnotheca* flowers have a stalk bearing both bract and flower—the "flower-bract stalk" (sensu Liang and Tucker, 1990). Stamens have a strong degree of adnation to carpels, except in *Saururus cernuus,* where stamens are free. In all species of Saururaceae, carpels are connate at least at the base, except *S. cernuus*, which is apocarpous (Liang and Tucker, 1990; Igersheim and Endress, 1998). Mature fossil flowers have a flower-bract stalk, a bract, no perianth, and five stamens basally adnate to a four-carpellate, basally connate gynoecium.

While variations on the typical floral plan might allow the inclusion of the fossil in Aponogetonaceae, Potamogetonaceae, Juncaginaceae, or Saururaceae, pollen morphology is more diagnostic of Saururaceae. Pollen of Aponogetonaceae is 21–45 μm in diameter, ellipsoidal, monosulcate, with per-reticulate exine sculpturing and supratectectal spinules (Erdtman, 1952; Thanikaimoni, 1985; van Bruggen, 1998). In Potamogetonaceae, pollen is inaperturate, ellipsoid to spheroidal, 20–30 μm in diameter, with homobrochate exine sculpturing (Haynes et al., 1998b; Erdtman, 1952). Pollen grains in *Maundia* (Juncaginaceae) are globose, inaperturate, 27–30 μm in diameter (Erdtman, 1952; Hope, 2006). Thus, pollen grains in these alismatids are at least twice as large as the fossil pollen grains, with reticulate (rather than punctate in the fossil pollen) sculpturing. Pollen of Potamogetonaceae and Juncaginaceae is inaperturate, whereas the fossil pollen is monosulcate.

The pollen of the fossil taxon is a key feature for placing it

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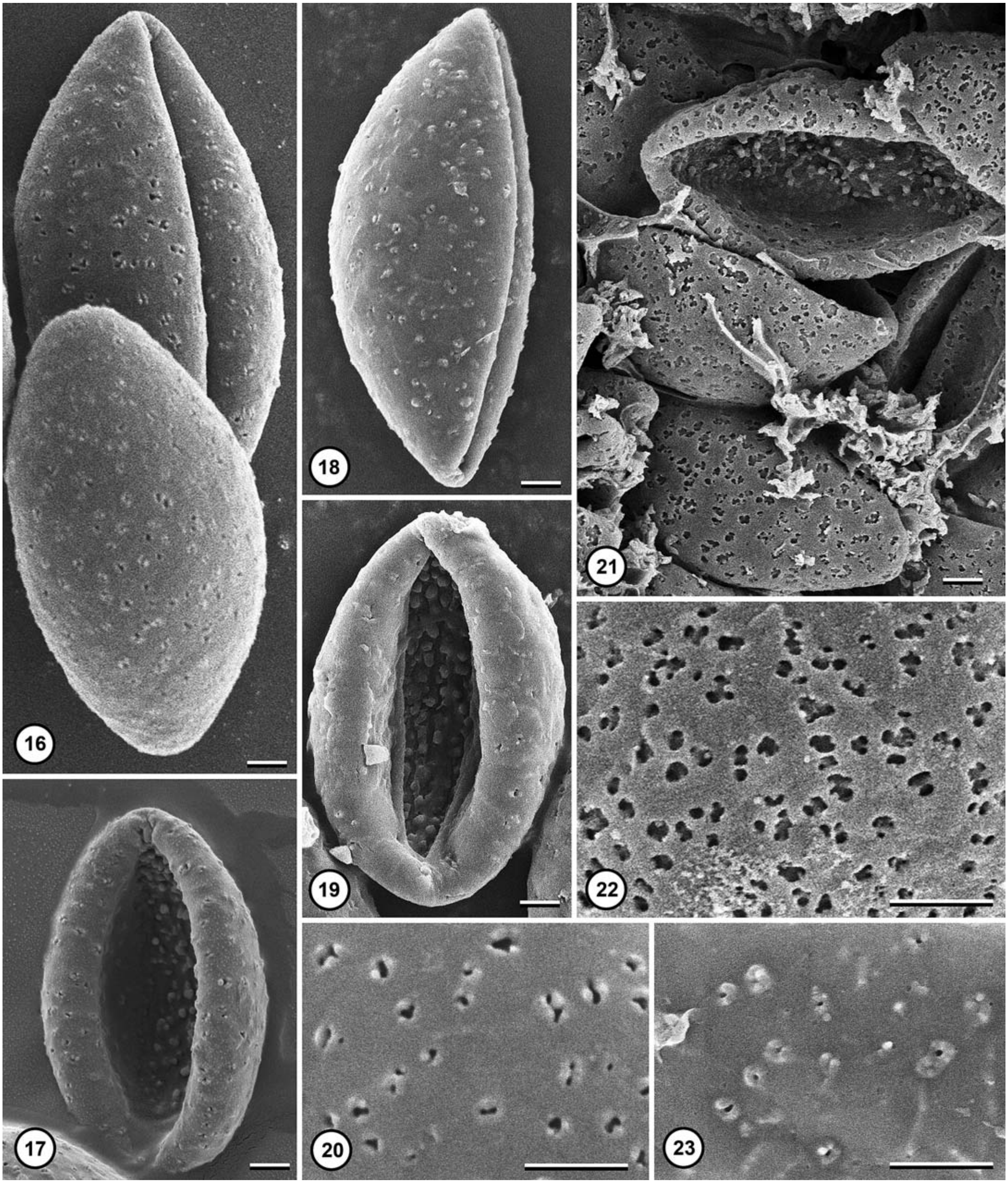
11. Longitudinal section showing two carpels, each with connate stamen. Paratype P1631 Cbot #69e; scale bar = 100 μm. **12.** Cross section through tetrathecal anther showing central vascular strand and enclosed pollen grains. Paratype P5937 Gbot #18b; scale bar = 100 μm. **13.** Two stamens showing latrorse dehiscence by longitudinal slits. Paratype P5831 Bbot #3; scale bar = 100 μm. **14.** Anther wall showing endothecium with well-developed secondary thickenings, and small pollen grains. Paratype P1631 Btop #19a; scale bar = 10 μm. **15.** Boat-shaped-elliptic pollen grains. Paratype P5937 Gbot #18b; scale bar = 2 μm. *Abbreviations:* B, bract; C, carpel; S, stamen.



Figs. 16–23. Scanning electron microscopy of *Saururus* pollen. **16.** *Saururus cernuus*, boat-shaped-elliptic pollen grains. ALTA 5509, stub A. **17.** *Saururus cernuus*, sulcus region with well-developed granula. ALTA 5509, stub A. **18.** *Saururus chinensis*, boat-shaped pollen grain viewed from side. LSU 72527, stub D. **19.** Pollen grain of *S. chinensis*, view of granula in sulcus region. LSU 72527, stub D. **20.** *Saururus cernuus* pollen showing small punctae with raised edges. ALTA 5509, stub A. **21.** *Saururus tuckerae* sp. nov. pollen grains. Note small size, granula in sulcus region. Paratype P5991 B.

within Saururaceae. Saururaceous pollen is characterized as minute (mostly <15 μm), boat-shaped-elliptic to globose, monosulcate with granula on the aperture membrane, and punctate sculpturing (Erdtman, 1952; Walker, 1976; Xi, 1980; Takahashi, 1986; Grayum, 1992; Liang, 1992; Pontieri and Sage, 1999; Sampson, 2000). The fossil pollen has the same features as pollen of Saururaceae. Although the fossil grains were originally thought to be fungal spores (Currah and Stockey, 1991; LePage et al., 1994), it is now clear that size, shape, and structure of the fossil pollen are clearly characteristic of Saururaceae.

Within Saururaceae, flowers of *Saururus* in particular are similar to the fossil flowers. *Saururus* flowers are developed on a racemose inflorescence. Flowers of *Saururus* have a flower-bract stalk, which is longer in *S. chinensis* than in *S. cernuus* (Liang and Tucker, 1990) and diverges at a low angle from the inflorescence axis, and flowers are pedicellate. Flowers of *Saururus chinensis* have basally fused carpels (Raju, 1961; Tucker, 1976; Liang and Tucker, 1990), like those in the fossil taxon, but *S. cernuus* is apocarpous. In *Saururus* flowers, there are six stamens initiated in pairs (Tucker, 1975). In *S. cernuus*, the stamens have long filaments, are distinct from the gynoecium, and overtop the carpels at maturity (Raju, 1961; Liang and Tucker, 1990). In *S. chinensis*, stamens are fused partway up the gynoecium, and filaments are shorter and thicker than in *S. cernuus* (Raju, 1961; Liang and Tucker, 1990). Stamen features of the fossil flowers are most similar to those of *S. chinensis*. The flowers of *Saururus* are reported to be protogynous, with the stigma being receptive prior to anthesis, as are many magnoliids (Thien et al., 1994, 2000). It is difficult to determine exactly whether the fossil is protogynous or protandrous (with the stamens maturing before carpels are receptive). However, the fossil flowers are similar to those of extant *Saururus* in having pre-anthesis stage anthers overtopping the carpels and, after dehiscence, carpels that are somewhat taller than stamens. Extant *Saururus* is self-incompatible (Pontieri and Sage, 1999), so it is possible that the stigmas are receptive before the stamens dehisce, without reducing the chances of outcrossing.

There are several differences between the fossil flowers and those of extant *Saururus*. The fossil flowers are smaller in size, about 0.8 mm in diameter compared to 1.4 mm diameter in *S. chinensis* and 1.7 mm diameter in *S. cernuus* (Liang and Tucker, 1990). Flowers of extant *Saururus* have trichomes on the bracts and inflorescence axis, but no trichomes are seen in the fossil material. Bracts are more ovate and cup-shaped in the fossil than the narrower, elongate bracts seen in extant *Saururus* (Liang and Tucker, 1990). Stamens are five in the fossil and typically six in extant *Saururus*. The fossil taxon also differs from extant *Saururus* in certain features of the pollen grain: grains of *S. cernuus* and *S. chinensis* are typically larger than those of the fossil, have fewer and smaller puncta than the fossil, and the puncta have raised edges not seen in the fossil. In addition, TEM shows that the pollen wall of the fossil specimens has a more open and regularly spaced columellate layer than in extant *Saururus*. *Saururus cernuus* has a thicker ectexine than in the fossil grains. Thus, these fossil flowers clearly fit in Saururaceae and are most similar to *Saururus*. However, the differences in flower size, presence/absence of trichomes, number of stamens, and pollen features between the fossil specimens and extant *Saururus* species warrant the description of a new species, *Saururus tuckerae* sp. nov.

Phylogenetics—In recent molecular analyses, Piperales are usually found to be sister to Canellales (= Winterales), in a clade with Laurales and Magnoliales: the magnoliid clade (Qiu et al., 1999, 2000, 2005; Graham and Olmstead, 2000; Nickrent et al., 2002; Zanis et al., 2002; APG, 2003; Borsch et al., 2003; Hilu et al., 2003; Soltis and Soltis, 2004; Graham et al., 2006). Based on molecular data, Saururaceae are consistently accepted as a monophyletic group within the Piperales, which as circumscribed by APG (2003) consist of Aristolochiaceae, Hydnoraceae, Lactoridaceae, Piperaceae, and Saururaceae. Although relationships within the order are still somewhat uncertain (APG, 2003), Saururaceae and Piperaceae are always found as sister groups. Nuclear and mitochondrial data support inclusion of Hydnoraceae in this order, but delineating the relationships between Hydnoraceae, Lactoridaceae, and Aristolochiaceae requires further study (Gonzalez and Rudall, 2001; Nickrent et al., 2002; APG, 2003).

Several previous studies have examined relationships within Saururaceae. Morphological data were used by Tucker et al. (1993), who analyzed the data in different ways. Their results found three recurrent hypotheses of relationships in Saururaceae: (1) *Saururus* sister to the rest of Saururaceae and Piperaceae (Saururaceae not monophyletic); (2) *Saururus* sister to the rest of Saururaceae, and *Gymnotheca* sister to *Anemopsis* + *Houttuynia*; (3) *Saururus* + *Gymnotheca* sister to *Anemopsis* + *Houttuynia*. The second topology is supported by morphological analyses (Tucker and Douglas, 1996) and either *atpB* or 18S data (Jaramillo et al., 2004). A fourth topology has resulted from analyses using nuclear genes, with *Anemopsis* basal (Meng et al., 2001, 2003). Meng et al. (2003) further resolved the tree to *Saururus* + *Gymnotheca* sister to *Houttuynia*. This topology was not seen in morphological analyses or other analyses with molecular data.

However, there is growing support for the third topology [(*Saururus* + *Gymnotheca*), (*Anemopsis* + *Houttuynia*)]. Molecular analyses, using data from the plastid *rbcL*, *atpB*, *matK*, *trnL-trnF* regions and mitochondrial *matR* and nuclear 18S genes, tend to support this topology (Meng et al., 2002, 2003; Jaramillo et al., 2004; Neinhuis et al., 2005; Wanke et al., 2007), although (as one might expect) relationships vary when one genus is excluded (e.g., Nickrent et al., 2002; Qiu et al., 2005). The morphological and combined molecular–morphological analyses by Meng et al. (2003) also resulted in a single tree with this topology. Furthermore, the analyses using morphological data from our study, both with and without the fossil taxon included, resulted in a single most parsimonious tree with this topology. The fossil taxon, *S. tuckerae*, is always found in a clade with extant *Saururus*, supporting the placement of the fossil within this genus. For confidently resolving relationships between saururaceous taxa, we need to include *G. involucrata* and *G. chinensis* in addition to the more commonly used taxa *Anemopsis*, *Houttuynia*, and *Saururus* in future phylogenetic studies.

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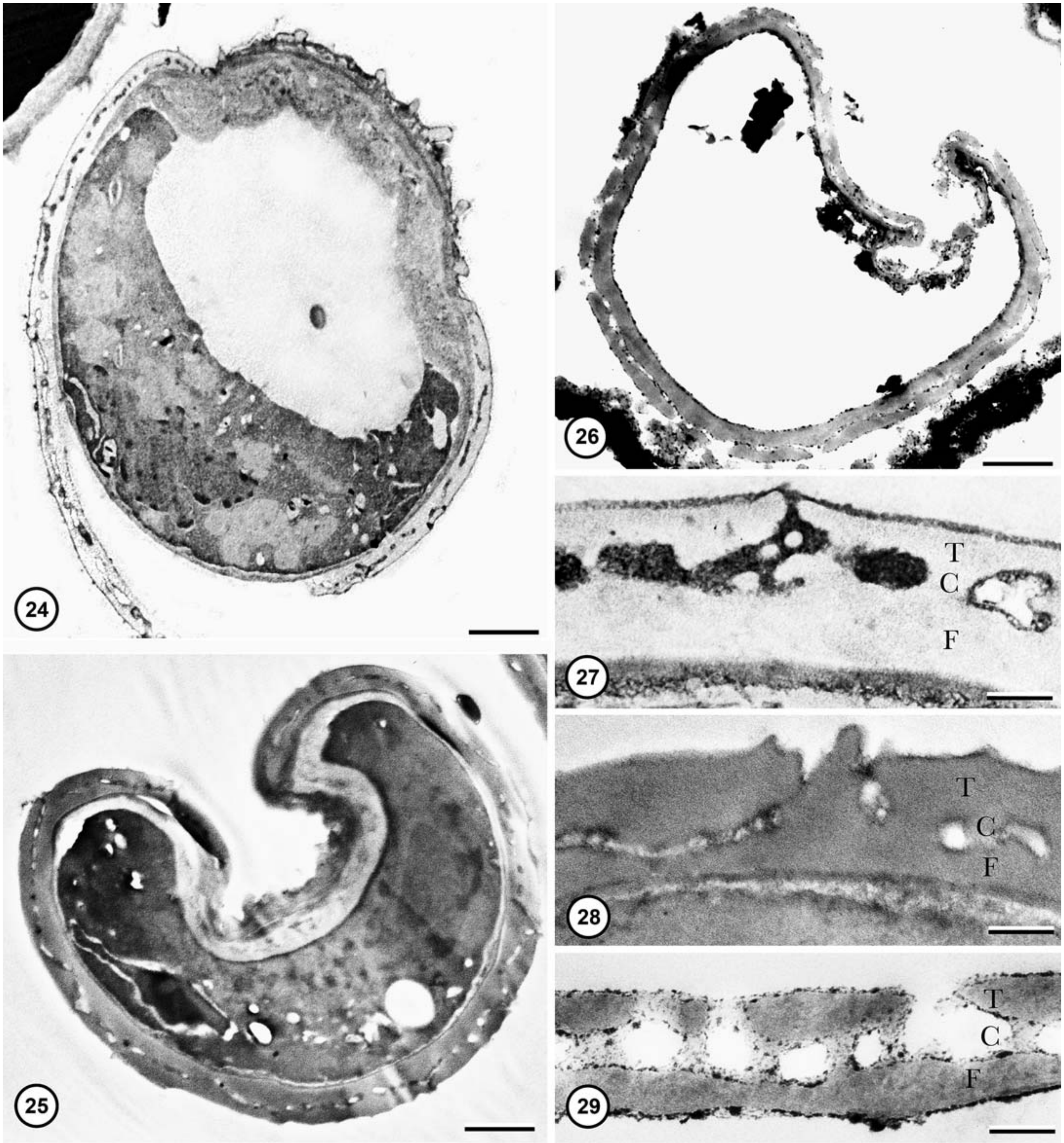
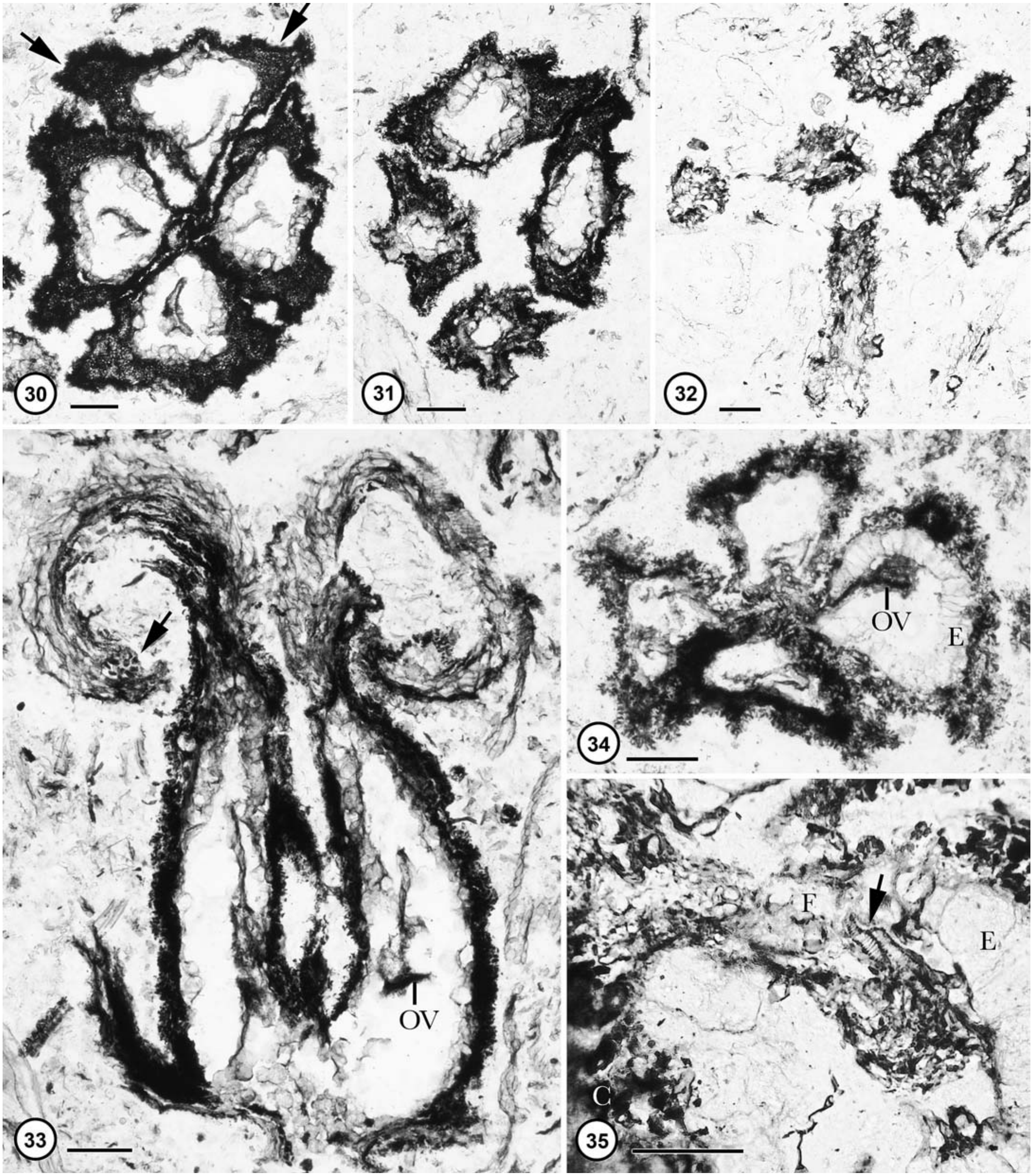
22. *Saururus tuckerae* sp. nov. pollen showing many punctae. Paratype P5991 B. **23.** *Saururus chinensis* pollen, showing punctae with raised edges. LSU 72527, stub D. All scale bars = 1 μm.



Figs. 24–29. Transmission electron microscopy of *Saururus* pollen. **24.** Entire grain of *S. cernuus*, showing aperture membrane with granula (top right). ALTA 5509. **25.** Entire grain of *S. chinensis* showing sunken granulate aperture membrane. LSU 72527. **26.** Entire grain of *S. tuckerae* sp. nov. with thin, sunken aperture membrane. P5991 B. **27.** Pollen wall of *S. cernuus* with punctate tectum (T), irregular columellar layer (C), and thick foot layer (F). ALTA 5509. **28.** Pollen wall of *S. chinensis* with punctate tectum (T; note raised edge of puncta), irregular columellar layer (C), and foot layer (F). LSU 72527. **29.** Pollen wall of *S. tuckerae* sp. nov. with punctate tectum (T), well-formed columellar layer (C), and thick foot layer (F). P5991 B. Scale bars: Figs. 29, 30, 31 = 1 μm; Figs. 32, 33, 34 = 200 nm.



Figs. 30–35. Structure of gynoecium. **30.** Basal section showing four connate carpels. Note lobes on carpels (arrows) and ovule in each locule. Paratype P1631 Btop #27b; scale bar = 100 μm. **31.** More distal section showing free carpels. Lobes are more prominent. Paratype P1631 Btop #38b; scale bar = 100 μm. **32.** Distalmost section showing two styles, recurved outwards. Paratype P1631 Btop #44b; scale bar = 100 μm. **33.** Longitudinal section through two basally fused carpels, with recurved styles; papillae indicated by arrow. Paratype P1631 Btop #104f; scale bar = 100 μm. **34.** Basal cross section through four carpels; single ovule visible in carpel at right. Paratype P1631 Bbot #43c; scale bar = 100 μm. **35.** Enlarged view of funiculus showing vascular tissue (arrow). Paratype P1631 Bbot #42c; scale bar = 50 μm. *Abbreviations:* C, carpel; E, endocarp; F, funiculus; OV, ovule.

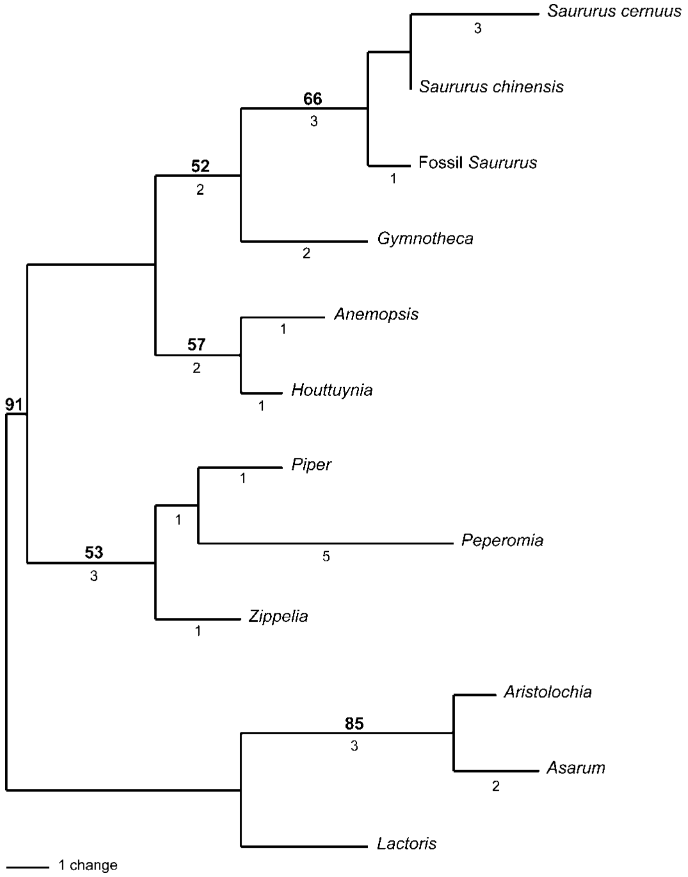


Fig. 36. The single most parsimonious tree found with the fossil taxon included, resulting from heuristic search including 11 extant taxa and fossil species of *Saururus* (length = 52, CI = 0.673, RI = 0.707). Analysis of only extant taxa results in a single most parsimonious tree of the same topology (length = 51, CI = 0.667, RI = 0.673). Numbers in bold above branches represent bootstrap values. Branch lengths calculated with ACCTRAN optimization (shown in parentheses above branches). The number of unambiguous character changes for a given branch are shown below branches (see Appendix 2 for details of unambiguous character changes).

Variability of flower structure—Although Saururaceae are often described as having three or six stamens and three or four carpels, flowers with other numbers of parts have been documented. In their investigation of *Gymnotheca,* Liang and Tucker (1989) noted the presence of abnormal flowers; some had five or seven stamens rather than six, or three carpels instead of the usual four. Further investigations by Liang (1994) found that *Gymnotheca* flowers had anywhere from 4–8 stamens on three- or four-carpellate flowers. Liang (1994) examined 381 flowers and found only 79% had the "typical state" of four carpels and six stamens; nearly 11% had four carpels and seven stamens, while 6% had four carpels and five stamens, as seen in the fossil flowers. In *Anemopsis,* flowers usually have six stamens and three carpels. Abnormal *Anemopsis* flowers include those with five stamens, two carpels, or unisexual staminate flowers (Tucker, 1985). In *Houttuynia*, flowers at the apex of the inflorescence are unisexual and reduced (Raju, 1961; Tucker, 1981). *Saururus* flowers are also reported to have variable numbers of parts, from five to eight stamens and three or four carpels (Raju, 1961; Tucker, 1975). Tucker (1975) noted that these flowers tend to be those found closest to the apex of the inflorescence. Although abnormal stamen numbers occur on the same inflorescence as typical flowers in extant taxa, with the limited data currently available for the fossils, we cannot say if this is the same in *S. tuckerae*. While the fossil taxon at first seems to have an unusual stamen number compared to other Saururaceae, as determined from the five complete flowers studied, five stamens are known from abnormal extant saururaceous flowers.

Ontogenetic sequences of stamen development in Piperaceae and Saururaceae are well understood; these are summarized in Jaramillo et al. (2004), and for Saururaceae in Liang (1994) and Hufford (1997). All Piperaceae as well as *Anemopsis* and *Houttuynia* start with the initiation of two lateral stamen primordia. In contrast, the first-initiated primordia in *Saururus* are two median stamen primordia (Tucker, 1975; Liang, 1994; Jaramillo et al., 2004). *Gymnotheca* initially has one adaxial median stamen primordium (Liang and Tucker, 1989; Liang, 1994; Jaramillo et al., 2004). The development of stamen primordia in *Gymnotheca*, however, then becomes similar to that in *Anemopsis*, *Houttuynia*, *Piper,* and *Zippelia* (Jaramillo et al., 2004). The sequence of stamen initiation in the fossil flowers is not clear. However, a five-staminate condition could be arrived at by arresting development in earlier stages; *Anemopsis*, *Gymnotheca*, and *Zippelia* all go through a stage with five stamen primordia, and therefore it is not a developmentally difficult state at which to arrive; thus the fossil taxon would show a derived stamen character state.

Pseudanthia—Inflorescences of Saururaceae have been described as pseudanthia because the showy basal bracts in *Anemopsis*, *Gymnotheca involucrata*, and *Houttuynia* give the whole inflorescence the appearance of a flower (Classen-Bockhoff, 1990; Liang and Tucker, 1990). Raju (1961) first proposed that individual flowers of Saururaceae represent pseudanthia, with each small flower representing a reduced inflorescence. This scenario has been suggested for many taxa, including those in the monocot families Triuridaceae, Aponogetonaceae, Potamogetonaceae, Scheuchzeriaceae, and Juncaginaceae (Burger, 1977; Posluszny et al., 1986; Rudall, 2003). Raju's (1961) evidence for pseudanthial saururaceous flowers, such as spirally arranged floral organs and lack of stamens on the last-formed carpel, has been refuted by the work of Tucker (1976), Omori (1982), and Liang and Tucker (1990). Tucker (1976) and Liang and Tucker (1990) provide other lines of argument against the saururaceous flower being a pseudanthium. For example, *Saururus* flowers are bilateral, not radial, as are most inflorescences (Tucker, 1976). The properties of the floral apex differ from the inflorescence apex as well; the floral apex produces dorsiventrally organized organs, while the inflorescence apex produces laterally organized organs and can produce atypical flowers or peloria (e.g., in *Houttuynia* and *Anemopsis*) (Liang and Tucker, 1990). In addition, no branched inflorescences have been observed in Saururaceae (Tucker, 1976); although floral parts show plasticity, the inflorescence structure does not, as one might expect if the flowers were actually reduced inflorescences.

Conclusions—Saururaceae have an interesting distribution, with four species native to eastern Asia (*Gymnotheca chinensis*, *G. involucrata*, *Houttuynia cordata*, and *Saururus chinensis*), one to western North America (*Anemopsis* *californica*), and one to eastern North America (*S. cernuus*). These plants prefer moist or wetland habitats (Wu and Kubitzki, 1993; Xia and Brach, 1999), a characteristic likely shared by the fossil plant described here. The presence of *Saururus* at Princeton provides yet another piece of evidence that the Princeton Chert preserved a wetland environment as shown by Cevallos-Ferriz et al. (1991). *Saururus tuckerae* is always found associated with *Decodon allenbyensis* Cevallos-Ferriz and Stockey (1988). Layer #43 of the Princeton Chert likely preserves a marginal area of a small lake or pond, with *Decodon* and *Saururus* growing along the edge of and out into the water. Today, *Decodon* and *Saururus* do occasionally co-occur in swampy areas of the southeastern United States (Bennett, 2001; J. Richard Abbott, University of Florida, Gainesville, personal communication, 2006), and these environments might represent a close modern analog to the Middle Eocene floral assemblage of the Princeton Chert.

The fossil record of Saururaceae, like Piperales in general, is sparse. There is no palynological record of Saururaceae (see Muller, 1981), and Song et al. (2004) suggest piperaceous pollen is neglected because it is geologically insignificant and the grains are minute in size. The same could be said for saururaceous pollen. If more fossil pollen records like the one presented here were found for these two groups, we could better understand the past geographic distribution and stratigraphic occurrence of this magnoliid group. The only previously described fossil Saururaceae are seeds of *Houttuynia bavarica* Mai, from the Lower Miocene of Germany (Mai, 1999), and fruits and seeds of *Saururus bilobatus* (Nikitin ex Dorofeev) Mai, from the Upper Eocene to Pliocene of Europe and Siberia (Mai and Walther, 1978; Friis, 1985; Stuchlik et al., 1990; Lesiak, 1994). Thus, the inflorescence and flowers of *S. tuckerae* represent the oldest macrofossils, the only recognized fossil pollen, and the first North American record for Saururaceae.

Early Cretaceous fruits and associated pollen described as *Appomattoxia ancistrophora* Friis, Pedersen and Crane (1995) have been suggested to have affinities to Piperaceae, Saururaceae, Chloranthaceae, or *Circaeaster* (Circaeasteraceae, Ranunculales). Although it is similar in having a thick nexine and sculptured sulcus, *Appomattoxia* pollen is quite distinct from that of Saururaceae in having a continuous (not perforate) tectum, a granular to columellate infratectum, and verrucate to finely echinate (rather than smooth) tectal sculpturing (Friis et al., 1995). Until we better understand relationships among extant magnoliids or find floral and vegetative material of *Appomattoxia*, relationships of this fossil will remain elusive (Friis et al., 1995).

Another fossil that has been compared closely to Saururaceae, as well as to Piperaceae, Chloranthaceae, Disocoreaceae, and Smilacaceae, comes from the Aptian of Australia (Taylor and Hickey, 1990). It is known from leaves with attached lateral pistillate inflorescences (Taylor and Hickey, 1990). While the fossil resembles Saururaceae (among other families) in leaf characters and in having small apetalate flowers subtended by a bract and arranged in a spike, the presence of bracteoles (like Chloranthaceae) and single-carpeled flowers with truncate stigmas are very dissimilar (Taylor and Hickey, 1990).

The occurrence of fossil *Saururus* in western North America, in combination with the fossil fruit record of Europe, shows that ancestral *Saururus* (and perhaps all Saururaceae) were once widespread. The cooling climate of the middle Paleogene may explain why Saururaceae became extinct from Europe and other areas, while it survived in southeast Asia and eastern North America where the climate remained relatively humid and subtropical (Liang, 1995). Developing better search patterns and, especially, looking for minute pollen grains with the characteristic structure of Saururaceae, will help provide unequivocal evidence of the former distribution and evolutionary history for Saururaceae. The Princeton fossils show that Saururaceae, and thus Piperales, were well developed by the Middle Eocene. Specimens of *Saururus tuckerae* sp. nov. represent the first fossil saururaceous flowers, the first fossil pollen record, and the first North American fossil species for the family and thus will help to elucidate the evolutionary of Saururaceae and Piperales in general.

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APPENDIX 1. Characters used in phylogenetic analysis of fossil and extant Saururaceae.

1. Inflorescence type: 0, solitary flower; 1, raceme or spike
2. Floral symmetry: 0, radial; 1, dorsiventral or zygomorphic
   Flowers in Saururaceae have been described as radial, but developmental studies have shown these flowers are zygomorphic (see Liang and Tucker, 1990).
3. Flowers: 0, minute, inconspicuous; 1, showy
4. Presence of pedicel/peduncle: 0, pedicellate or pedunculate; 1, sessile
   Solitary flowers will have a peduncle. Note that flowers in *Piper* are coded as sessile, but can be pedicellate in subsection *Arctottonia* (Jaramillo and Manos, 2001).
5. Flower-bract stalk: 0, floral-bract stalk absent; 1, floral-bract stalk present
   In *Saururus* and *Gymnotheca* an elongated stalk bears the flower and bract (see Liang and Tucker, 1990).
6. Trichomes on bract: 0, absent; 1, present
7. Perianth: 0, present; 1, absent
8. Number of stamens: 0, six; 1, two; 2, three; 3, four; 4, five; 5, twelve
   Stamens may develop in whorls or in pairs in different taxa, but for the purpose of this analysis, the total number of stamens was used regardless of how they are borne. Note that here *Piper* is coded as having three or four stamens, but there are sections with two or six stamens (Jaramillo and Manos, 2001).
9. Stamen connation: 0, stamens free; 1, stamens connate
10. Stamen adnation to carpels: 0, free; 1, fused at base of carpel; 2, fused more than half carpel height
11. Length of filaments: 0, less than or equal to gynoecium height; 1, taller than gynoecium
12. Anther dehiscence: 0, extrorse; 1, latrorse
13. Pollen aperture type: 0, monosulcate; 1, inaperturate
    Note that the monosulcate type pollen can include occasionally trichotomosulcate grains, for example, *Houttuynia* (Liang, 1992).
14. Pollen shape: 0, globose; 1, boat-shaped-elliptic
    Pollen of Saururaceae is coded here as boat-shaped-elliptic because it is not as globose as the pollen of Piperaceae. However, in a larger context (e.g., Doyle, 2005), both Saururaceae and Piperaceae may be interpreted as having globose pollen because that of Saururaceae is somewhat intermediate in shape.
15. Average pollen size: 0, greater than 20 μm; 1, less than 20 μm
16. Carpel number: 0, three; 1, six; 2, four; 3, one
    Most species of *Piper* have a tricarpellate gynoecium, but in section *Ottonia*, flowers have four carpels (Jaramillo and Manos, 2001).
17. Median sagittal carpels: 0, one carpel (abaxial) in median sagittal plane; 1, adaxial and abaxial carpels present in median sagittal plane; 2, one carpel (adaxial) in median sagittal plane
18. Carpel fusion: 0, apocarpous; 1, syncarpous only at base; 2, syncarpous most of carpel length
19. Styles and stigmas: 0, style and stigma numbers equal to carpel number; 1, style and stigma numbers less than carpel number
20. Style presence: 0, style present (zonal growth between ovary and stigma); 1, sessile stigma (no zonal growth)
21. Stigma shape: 0, capitate or tufted; 1, stigmatic stylar cleft; 2, divided stigma
22. Ovule number: 0, three or more per carpel; 1, one or two per carpel; 2, one ovule per gynoecium
    In Piperaceae, carpels are fused, and a single ovule is produced per gynoecium (Igersheim and Endress, 1998).
23. Placentation: 0, marginal; 1, parietal; 2, basal
24. Ovule orientation: 0, anatropous; 1, orthotropous

Appendix 2. Unambiguous character changes on single most parsimonious tree recovered.

Branch	Character (from : to)	Homoplasious
Asarum	8 (0 : 5)	no
	9 (0 : 1)	yes
(*Aristolochia*, *Asarum*)	3 (0 : 1)	no
	13 (0 : 1)	yes
	16 (0 : 1)	no
Lactoris	17 (1 : 0)	no
	18 (1 : 0)	yes
	23 (1 : 0)	yes
Piper	19 (0 : 1)	no
Peperomia	4 (0 : 1)	yes
	13 (0 : 1)	yes
	16 (0 : 3)	no
	18 (2 : 0)	yes
	22 (2 : 1)	yes
(*Piper*, *Peperomia*)	17 (1 : 2)	yes
Zippelia	16 (0 : 2)	yes
Piperaceae	20 (0 : 1)	no
	22 (0 : 2)	no
	23 (1 : 2)	no
Saururus cernuus	10 (1 : 0)	yes
	11 (0 : 1)	yes
	18 (1 : 0)	yes
(*S. cernuus, S. chinensis*)	6 (0 : 1)	no
Fossil *Saururus*	8 (0 : 4)	no
Fossil + extant *Saururus*	18 (2 : 1)	no
	22 (0 : 1)	yes
	23 (1 : 0)	yes
Gymnotheca	9 (0 : 1)	yes
	11 (0 : 1)	yes
(*Gymnotheca*, *Saururus*)	5 (0 : 1)	no
	16 (0 : 2)	yes
Anemopsis	9 (0 : 1)	yes
Houttuynia	8 (0 : 2)	no
(*Anemopsis*, *Houttuynia*)	4 (0 : 1)	yes
	17 (1 : 2)	yes
Saururaceae	14 (0 : 1)	no