



CHICAGO JOURNALS

A New Fossil Flower and Associated Coprolites: Evidence for Angiosperm-Insect Interactions in the Santonian (Late Cretaceous) of Georgia, U.S.A.

Author(s): Richard Lupia, Patrick S. Herendeen, and Jennifer A. Keller

Source: *International Journal of Plant Sciences*, Vol. 163, No. 4 (July 2002), pp. 675-686

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/340737>

Accessed: 22/04/2014 13:34

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *International Journal of Plant Sciences*.

<http://www.jstor.org>

A NEW FOSSIL FLOWER AND ASSOCIATED COPROLITES: EVIDENCE FOR ANGIOSPERM-INSECT INTERACTIONS IN THE SANTONIAN (LATE CRETACEOUS) OF GEORGIA, U.S.A.

Richard Lupia,¹ Patrick S. Herendeen, and Jennifer A. Keller

Sam Noble Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, 2401 Chautauqua Avenue, Norman, Oklahoma 73072, U.S.A.; Department of Biological Sciences, George Washington University, 2023 G Street, NW, Washington, D.C. 20052, U.S.A.; and Natural Science Division, Southampton College, Southampton, New York 11968, U.S.A.

Plant-insect interactions are readily identifiable in the fossil record when insect activities cause damage to plant tissues, for example, leaf mining, piercing, galls. However, the inference of insect pollination of extinct plants usually must be based on comparative morphology of plants and insects or based on phylogenetic relationships and pollination habits of extant taxa. The presence of insect coprolites can provide additional evidence supporting the inference of plant-insect interactions based on the morphology and composition of the fossilized feces. In this article, we describe *Noferinia fusicarpa* gen. et sp. nov. based on fossil flowers and fruits recovered from the Buffalo Creek Member of the Gaillard Formation (late Santonian, Cretaceous) of central Georgia. The morphology of the flowers—differentiated perianth, basally connate calyx and corolla, inferior ovary, and possible nectiferous pores surrounding the base of the style—is consistent with generalized insect pollination. Associated with *Noferinia* flowers and fruits in the same sediment samples are five morphotypes of coprolites that are similar in shape and composition to the feces produced by modern beetles that feed on pollen and flowers. On the basis of the morphological features exhibited by *Noferinia* and by the coprolites containing its pollen, we suggest that *Noferinia fusicarpa* was insect pollinated.

Keywords: Cretaceous, angiosperm, mesofossil, pollination, coprolites.

Introduction

By the Santonian (ca. 84 Ma), the radiation of angiosperms was well underway both taxonomically and ecologically (Knoll 1986; Lidgard and Crane 1990; Lupia et al. 1999; Nagalingum et al. 2002). One hypothesized factor in this radiation was the evolution of plant-insect relationships leading to specialized pollination syndromes (Grant 1949; Regal 1977; Mulcahy 1979; Burger 1981; Crepet 1984). Although compressed plant remains offer some insight into Cretaceous plant-insect interactions (Dilcher 1979; Basinger and Dilcher 1984; Dilcher and Crane 1984; Crepet and Friis 1987), the recovery of charcoalified and lignitized fossils (mesofossils) has increased dramatically our knowledge of Cretaceous floral form and possible relationships with pollinators (Friis 1984, 1985; Knobloch and Mai 1986; Crepet et al. 1991; Drinnan et al. 1991; Crane et al. 1994, 1995; Crepet and Nixon 1994, 1996, 1998; Crepet 1996; Sims et al. 1998; Herendeen et al. 1999; Friis et al. 2000*b*). Improved sampling of the Cretaceous fossil record of insects affirms the presence of early representatives of numerous clades that today are pollinators (reviews in Labandeira 1997; Grimaldi 1999).

Most of the evidence for insect pollination is based on floral

morphology of fossils and contemporaneous remains of insect pollinators. Fossil insects identifiable to family and preserved with palynomorphs in their gut have been found in Cretaceous sediments (Krassilov and Rasnitsyn 1983; Caldas et al. 1989), but these finds are rare. Coprolites, little studied in mesofossil floras, provide important data for the interpretation of plant-animal interactions in the fossil record (Harris 1957; Hill 1976; Scott 1977; Baxendale 1979; Rex and Galtier 1983; Scott and Taylor 1983; Scott et al. 1992; Labandeira et al. 1994; Edwards et al. 1995; Friis et al. 2000*a*). However, attempts to associate coprolites with the insects that produced them are precluded by the absence of systematic surveys of feces morphology among extant insects. Presence of pollen in coprolites not only indicates pollen feeding, but also can provide evidence of plant-pollinator relationships because pollen-feeding insects often are pollinators of the plants on which they prey (Faegri and van der Pijl 1979). We found only three previous studies of the palynological content of Cretaceous coprolites: coprolites containing monosulcate angiosperm pollen (Friis et al. 2000*a*) and fern spores (Kampmann 1983) and vertebrate (possibly turtle) coprolites containing a diverse palynoflora (Waldman and Hopkins 1970).

In this article, we describe *Noferinia fusicarpa* gen. et sp. nov., with morphological features that indicate generalized adaptations for insect pollination. From the same sediments that preserve these flowers and fruits, we describe five distinct morphotypes of coprolites, two of which contain *Noferinia* pollen

¹ Author for correspondence; e-mail rlupia@ou.edu.

exclusively, that are morphologically similar to feces produced by modern pollen-eating beetles. On the basis of the association and morphology of flowers and coprolites, we postulate that *Noferinia* was insect pollinated, possibly by beetles.

Material and Methods

The fossils were recovered from a carbonaceous clay lens (ca. 20–80 cm thick) that is exposed on the south face of the south pit (“Allon”) of the Atlanta Sand and Supply Company in Gaillard, Crawford County, Georgia (Knoxville Quadrangle; lat. 32°37′47″N, long. 83°59′10″W). These sediments were assigned to the Buffalo Creek Member of the Gaillard Formation by Huddleston and Hetrick (1991). The age of the Buffalo Creek Member is late Santonian (Cretaceous) based on terrestrial palynomorphs (R. A. Christopher, written communication, 1998) that are correlative with assemblages assignable to calcareous nannofossil zone CC17 of Burnett (1996). A preliminary paleoecological assessment based on palynological analyses indicates deposition in a nonmarine lower floodplain environment (R. A. Christopher, written communication, 1998; R. Lupia, unpublished data).

Bulk samples of fossiliferous sediments were collected from the unconsolidated clay and soaked in detergent solution to disaggregate the matrix. Samples were washed through sieves (smallest aperture = 125 μm), and remaining sediments were removed by dissolution in HCl and HF acids. Organic debris, preserved as charcoal or lignitized material, was rinsed in water and allowed to air dry. Samples were sorted and specimens identified under a dissection microscope at $\times 10$ –25 magnification. Specimens for further study were mounted on stubs, coated with gold, and examined and photographed using an AMRAY 1810 and/or LEO 1430VP scanning electron microscope (SEM) at 5–15 kV. Sectioning and maceration of additional specimens of fruits provided no additional morphological information. Two dispersed anthers were macerated, mounted in glycerine jelly, and examined and photographed through a compound microscope (Olympus BX-50 with Nomarski optics).

In addition to charcoaled and lignitized specimens, compression and impression remains were discovered in and below the carbonaceous clay lens (Herendeen et al. 1999). Several dispersed fruits and one infructescence axis were found, prepared, and photographed. The styler end of one dispersed fruit was removed, mounted on a stub, gold coated, and examined with SEM. All fossils are housed in the paleobotanical collections of The Field Museum, Chicago (PP).

Modern feces for comparison were obtained by collecting beetles in northwestern Indiana. Most of the beetles found were pollen eaters (*Chauliognathus*, family Cantharidae; *Diabrotica longicornis* and *Diabrotica ctripennis*, family Phalacridae), but some leaf eaters (family Chrysomelidae) were also present, permitting comparison of more than one coprolite type to feces produced by extant beetles. These insects were found on flowers and inflorescences in the family Compositae, mostly *Helianthus* (sunflowers) and *Solidago* (goldenrod). The feces obtained from these beetles were allowed to dry and mounted on stubs, gold coated, and examined with SEM.

Systematics

Family—Incertae sedis

Genus—*Noferinia* Lupia, Herendeen et Keller gen. nov.

Type Species—*Noferinia fusicarpa* Lupia, Herendeen et Keller sp. nov.

Generic diagnosis. Flowers epigynous, perfect, and borne on pedicels in dense, subspherical inflorescences. Flowers subtended by two bracteoles. Perianth in two distinct whorls with synsepalous calyx and sympetalous corolla. Androecium of multiple tetrasporangiate stamens, inserting separately from the corolla tube (exact number unknown). Ovary inferior, syncarpous, trilobular. Styles united basally with three (rarely four) free distal lobes. Ovary walls distinctly ribbed and covered by thick trichomes. Numerous pores around the base of the style. Pollen tricolporate or tetracolporate, reticulate, and tectate.

Etymology. Anagram of “inferno” for an August spent in a clay pit in Georgia.

Species—*Noferinia fusicarpa* Lupia, Herendeen et Keller sp. nov.

Specific diagnosis. As for the genus with the following additions: flowers ca. 2.0–2.9 mm long ($\bar{X} = 2.45$ mm, $n = 2$) and 0.46–0.61 mm wide ($\bar{X} = 0.54$ mm, $n = 2$); fruits ca. 4.0–7.9 mm long ($\bar{X} = 5.6$ mm, $n = 30$) and 0.30–1.2 mm wide ($\bar{X} = 0.78$ mm, $n = 30$) as mesofossils; fruits up to ca. 17 mm long and ca. 2.6 mm wide as compressions; pollen homobrochate to heterobrochate, with lumina decreasing in diameter toward colpi forming distinct margins. Equatorial diameter 25–32 μm wide ($\bar{X} = 28.5$ μm , $n = 27$) in polar view and 25–30 μm ($\bar{X} = 27.5$ μm , $n = 20$) in equatorial view. Polar diameter 24–30 μm ($\bar{X} = 26.4$ μm , $n = 20$).

Etymology. From “fusos” (spindle) and “carpos” (fruit) for the shape of the fruit.

Holotype. PP45197 (figs. 1D, 2B).

Paratype. PP45194 (fig. 1A).

Other material. PP44599 (fig. 2D, 2H); PP45151 (fig. 3C); PP45193 (fig. 1B, 1C; fig. 2A); PP45195 (fig. 1E); PP45196 (fig. 2I); PP45961 (fig. 1F); PP45962 (fig. 2C); PP45963 (fig. 2E); PP45964 (fig. 2F); PP45965 (fig. 2G); PP45966 (fig. 3A, 3B, 3E); PP45967 (fig. 3D); PP45968 (fig. 3F); PP45969 (fig. 4A–4D); and over 2200 additional uncataloged specimens, primarily lignitized fruits lacking floral parts.

Type locality. South pit of Atlanta Sand and Supply Company, Gaillard, Crawford County, Georgia (Knoxville quadrangle; lat. 32°37′47″N, long. 83°59′10″W).

Age and stratigraphy. Buffalo Creek Member of the Gaillard Formation (late Santonian, Late Cretaceous).

Description and Remarks

Although ca. 2000 specimens of *Noferinia* have been recovered, most of these are complete or fragmentary fruits that lack floral parts, which apparently had abscised from the distal end of the maturing inferior ovary. Thus, critical details of the perianth and androecium remain unknown despite our attempts to elucidate floral morphology from the relatively few

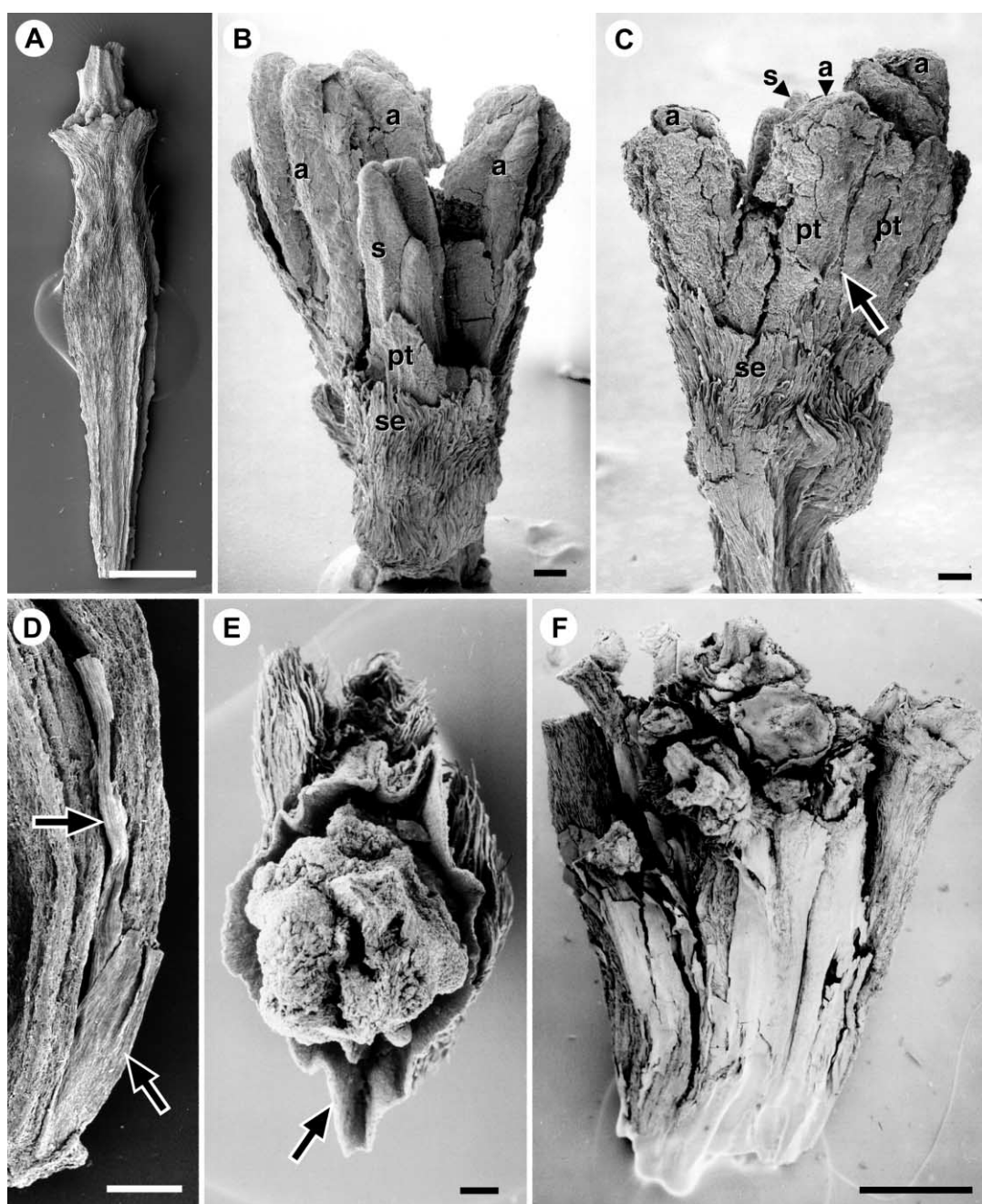


Fig. 1 *Noferinia fusicarpa* gen. et sp. nov. **A**, Lateral view of mature fruit showing style base and dense trichomes covering ovary wall (PP45194). Scale bar = 1 mm. **B**, Lateral view of apex of flower showing base of calyx (*se*) and broken petal (*pt*), three anthers (*a*) with long pollen sacs, and three-lobed style (*s*) (PP45193). Scale bar = 100 μ m. **C**, Reverse of specimen in **B** showing base of synsepalous calyx (*se*), which bears trichomes, and smooth petals (*pt*). Note that the petals, overlapping at the arrow, reach the top of the anthers (*a*) (PP45193). Scale bar = 100 μ m. **D**, Base of fruit surrounded by two prophylls (arrows) (PP45197, holotype). Scale bar = 250 μ m. **E**, Apical view of fruit apex showing the fusion of petals (at least at their bases) forming sympetalous corolla (arrow) (PP45195). Scale bar = 100 μ m. **F**, Lateral view of partial inflorescence containing 10 mature fruits, most of which lack perianth, androecia, and stylar lobes (PP45961). Scale bar = 1 mm.

informative specimens. Dispersed flowers, styles, anthers, and fruits can be tied together on the basis of the presence of the distinctive (within the Allon assemblage) reticulate tricolporate pollen type that covers stigmatic surfaces of *Noferinia* flowers and fruits and is found within *Noferinia* anthers.

The flowers are epigynous, bisexual, and apparently actinomorphic (fig. 1A, 1B; fig. 2B). The sepals are basally connate (fig. 1A–1C). The number of lobes is unknown. The sepals bear coarse trichomes abaxially (fig. 1C, 1E). The petals are smooth (fig. 1C, 1E) and also are basally connate (fig. 1E);

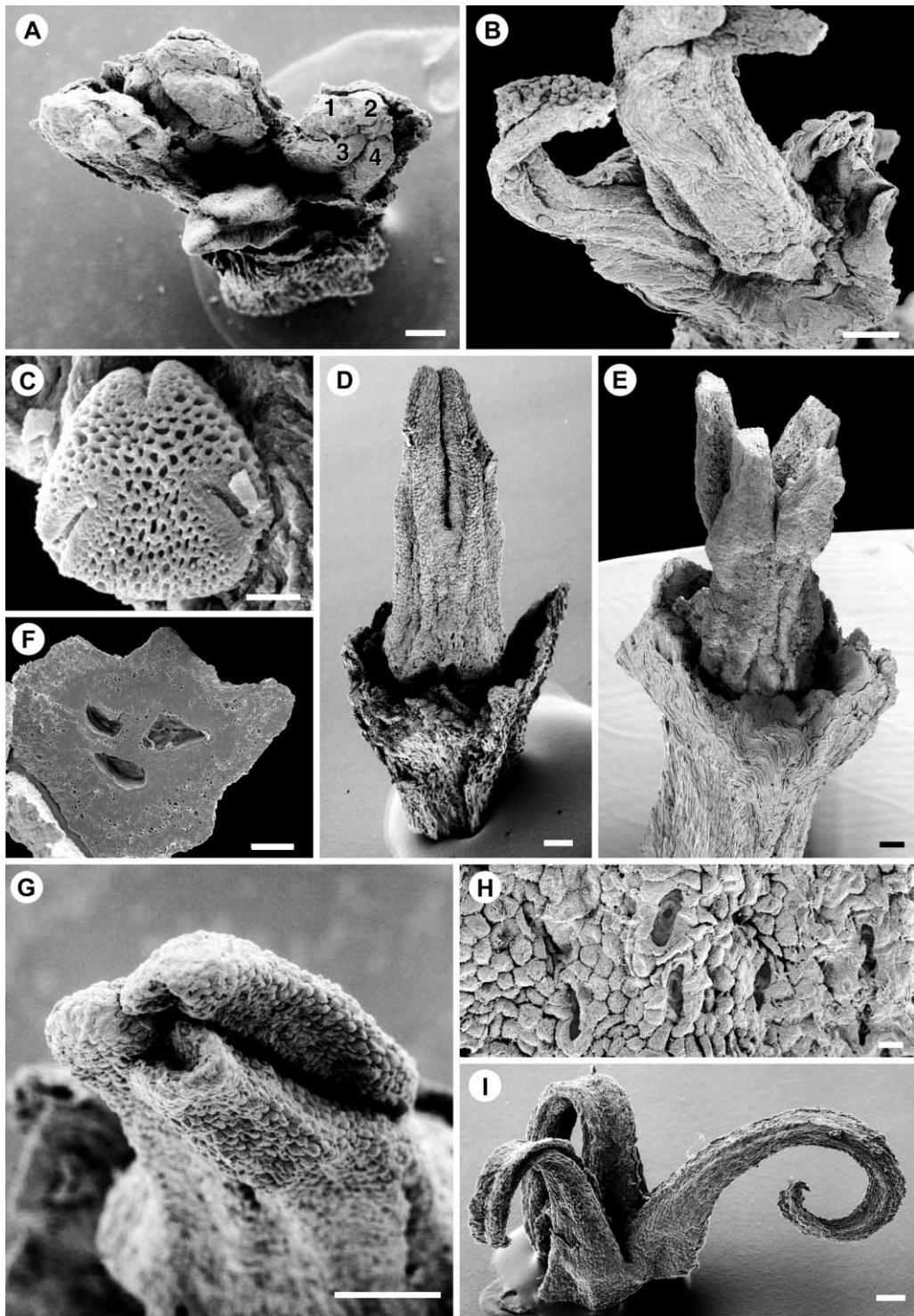


Fig. 2 *Noferinia fusicarpa* gen. et sp. nov. *A*, Apical view of flower illustrating three tetrasporangiate anthers, with pollen sacs numbered (PP45193). Scale bar = 100 μm . *B*, Close-up of style illustrating the insertion of one filament at the base of the style. Note that the filament is broad and slightly enroled or grooved adaxially and that one of the style lobes is markedly shorter than the other two (PP45197, holotype). Scale bar = 100 μm . *C*, Tricolporate pollen grain found at the base of a style. Identical grains are found in anthers (PP45962). Scale bar = 2.5 μm . *D*, Lateral view of floral apex showing single style with two lobes (third lobe hidden from view) and ring of nectary-like stomata around the base of the style (PP44599). Scale bar = 100 μm . *E*, Rare floral morphotype bearing four stylar lobes (PP45963). Scale bar = 100 μm . *F*, Cross section of fruit from near base illustrating three locules (PP45964). Scale bar = 50 μm . *G*, Close-up of apex of style lobes showing adaxial fluting (PP45965). Scale bar = 100 μm . *H*, Close-up of specimen in *D* showing nectary-like stomata (PP44599). Scale bar = 10 μm . *I*, Dispersed distal portion of styles. Note recurved shape and inequality of length of lobes (PP45196). Scale bar = 100 μm .

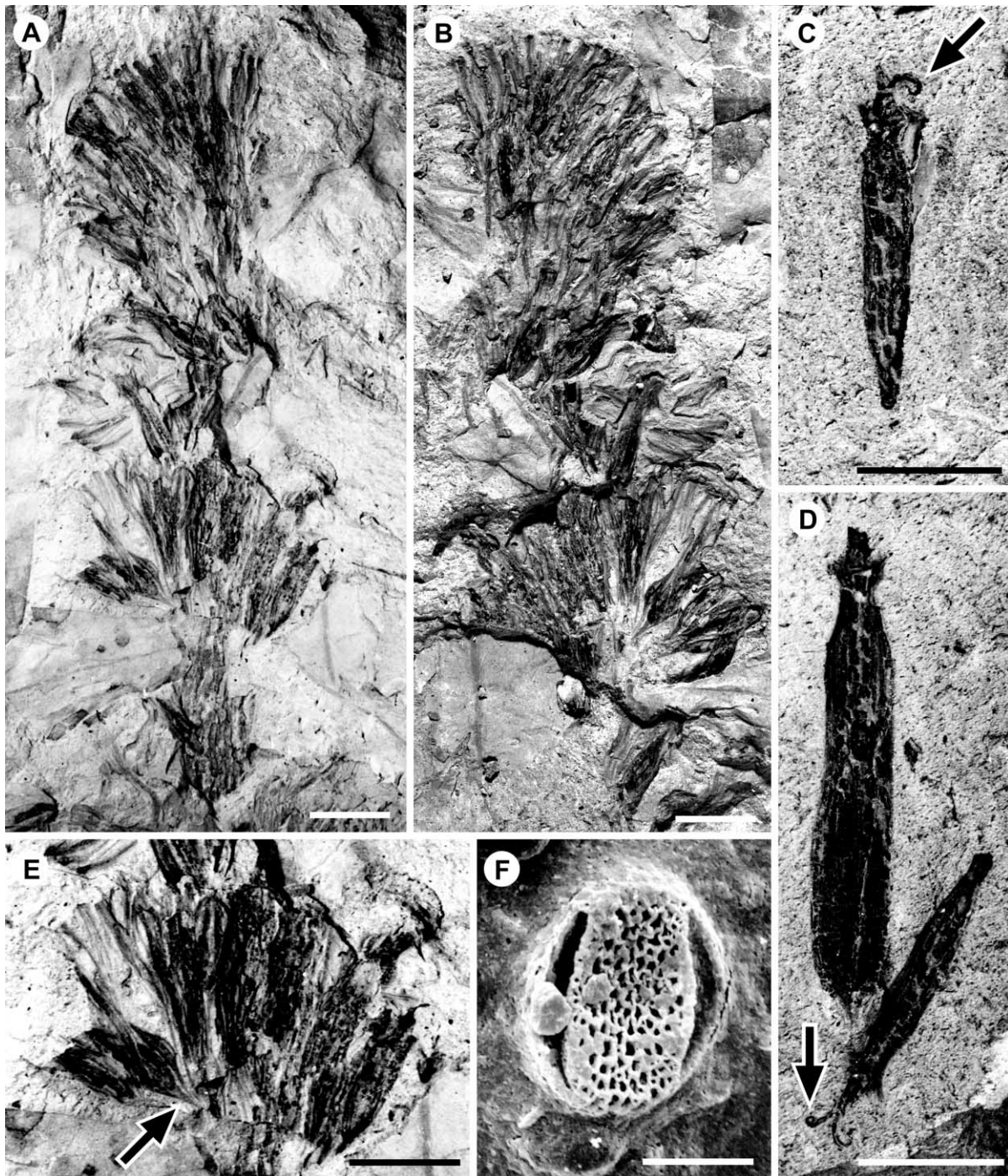


Fig. 3 Compression material of *Noferinia fuscicarpa* gen. et sp. nov. *A*, Two, possibly three, subspherical inflorescences of mature fruits lacking perianth, androecia, and styles. The top inflorescence bears at least 25 fruits (PP45966). Scale bar = 10 mm. *B*, Counterpart of specimen in *A* (PP45966). Scale bar = 10 mm. *C*, Isolated dispersed fruit showing remnant of style with recurved stylar lobe (arrow) (PP45145). Scale bar = 5 mm. *D*, Two isolated dispersed fruits. Note that top specimen is longer and thicker than bottom specimen, which still retains two recurved stylar lobes (arrow) (PP45967). Scale bar = 5 mm. *E*, Close-up of specimen in *A* showing base of one fruit with attached pedicel (arrow) (PP45966). Scale bar = 10 mm. *F*, Electron micrograph of dispersed pollen grain exposed in the impression of a style in sediment block (PP45968). Scale bar = 10 μ m.

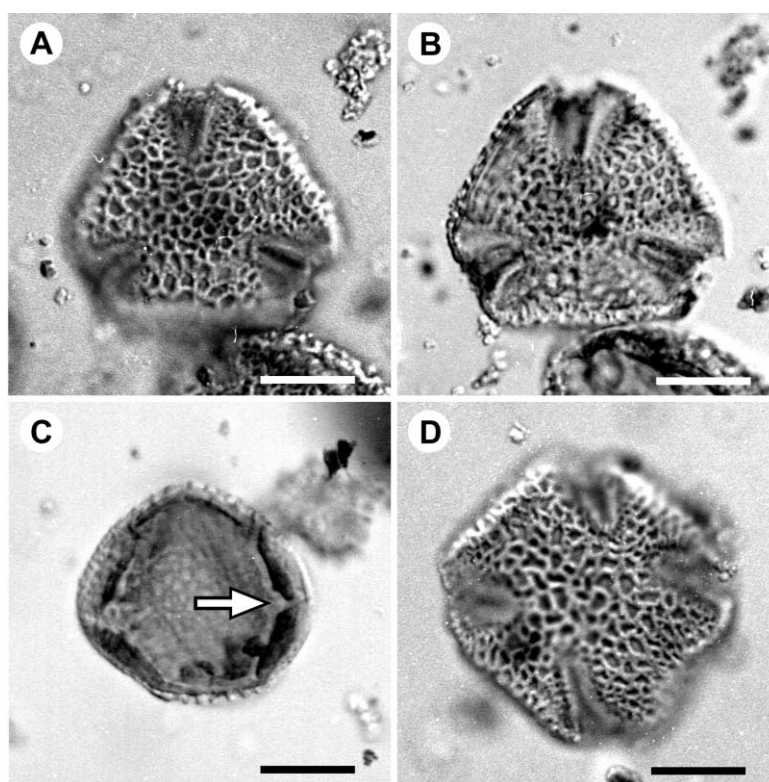


Fig. 4 Pollen isolated from dispersed anther (PP45969). *A*, High focus of tricolporate grain in polar view showing reticulate exine sculpture. Note decreasing lumina size near colpi. *B*, Midfocus of same grain as in *A* showing distinct margins surrounding colpi. *C*, Midfocus of tricolporate grain in equatorial view showing simple pore (arrow). *D*, Polar view of rare tetracolporate grain showing heterobrochate reticulum at pole. All scale bars = 10 μm .

the extent of fusion and presence of distal free lobes is unknown. Individual flowers are pedicellate (fig. 3*A*, 3*B*, 3*E*) and are subtended by two prophylls sheathing the base (fig. 1*D*). Dense, subspherical inflorescences consisting of 10–30 flowers apparently are arranged in series along an axis (fig. 1*F*; fig. 3*A*, 3*B*).

The androecium consists of free stamens with tetrasporangiate anthers inserted at the base of the style, free of the petals (fig. 2*A*, 2*B*). No specimen is preserved with more than three anthers in place. The anthers contain numerous reticulate, tectate, tricolporate (rarely tetracolporate) pollen grains (figs. 2*C*, 3*F*, 4*A*–4*D*). The reticulum varies among grains in a single anther from homobrochate (fig. 2*C*) to heterobrochate (fig. 4*D*). The lumen, generally less than 1 μm in diameter, decrease in size toward the colpi forming distinct margins (fig. 2*C*; fig. 4*A*, 4*B*). The pore is simple (fig. 4*C*).

The gynoecium is tricarpellate, syncarpous, with a trilocular, inferior ovary (figs. 1*A*, 2*F*). The carpel wall bears longitudinal ribs and is covered by dense trichomes (fig. 1*A*). The styles are fused basally with three free lobes apically (fig. 2*D*, 2*F*). Very rare specimens with four free lobes, presumably tetracarpellate, have been found (fig. 2*E*). The free lobes are fluted adaxially and are recurved strongly at maturity (fig. 2*F*, 2*I*; fig. 3*C*, 3*D*). One of the three lobes is usually shorter than the other two (fig. 2*B*, 2*I*). The free lobes are shed typically as a unit (fig. 2*I*) and often are not found attached to mature fruits (fig.

1*A*, 1*F*; fig. 3*D*). A ring of possible nectariferous pores is located at the base of the style above the point of filament insertion (fig. 2*D*, 2*H*). Ovule number and placentation are unknown.

Systematic Affinities

Noferinia fusicarpa is assignable to the eudicot clade (*sensu* Doyle and Hotton 1991) within angiosperms (Hoot et al. 1999) on the basis of its tricolporate pollen. The combination of characters exhibited by *Noferinia* and the absence of several important characters (e.g., ovule number and placentation) preclude confident assignment to a lower taxonomic group. Nevertheless, a search of “*The Families of Flowering Plants*” (Watson and Dallwitz 1993) using characters from pollen aperture and gynoecium structure (pollen triaperturate, apertures colporate, ovary with three locules, ovary inferior, style present, style partly joined, three style lobes) yielded seven families (Bruniaceae, Cornaceae s.l., Hydrangeaceae, Philadelphaceae, Theaceae, Daphniphyllaceae, Rubiaceae), most of which are relatively basal members of the asterid clade (*sensu* APG 1998). Of these families, Cornaceae s.l. is comparable to *Noferinia* in many respects, but too many morphological details are lacking in the fossil to make a meaningful comparison at this time. However, we note that *Noferinia* and several undescribed fossil fruits from the Upatoi Creek locality (Magallón-Puebla et al.

Table 1
Observed Sizes, Shapes, and Contents (Sample of *n* Specimens) of Each Category of Fossil Coprolites and Modern Fecal Material

Type	<i>n</i>	Length (mm)		Diameter (mm)		Shape	Content
		Mean	Min/max	Mean	Min/max		
Fossil coprolites:							
I	3	1.2	0.88/1.5	0.58	0.47/0.77	Spiral	Pollen (1 type)
II	10	1.1	0.57/1.5	0.46	0.24/0.65	Oblong	Pollen (1 type)
III	2	1.2	1.1/1.3	0.47	0.36/0.58	Oblong	Pollen (≥ 2 types)
IV	3	1.3	0.83/2.1	0.72	0.61/0.87	Oblong	Pollen and plant fragments
V	5	1.1	0.75/2.0	0.58	0.44/0.75	Oblong	Plant fragments
Modern fecal material:							
I	5	0.61	0.42/0.72	0.28	0.23/0.34	Spiral	Pollen (1 type)
II	3	0.63	0.42/0.94	0.40	0.19/0.71	Oblong	Pollen (1 type)
III	1	0.42	...	0.41	...	Round	Pollen (≥ 2 types)
IV	8	0.91	0.62/1.3	0.43	0.19/0.67	Round to sinuous	Pollen and plant fragments
V	2	1.0	0.75/1.3	0.60	0.37/0.83	Oblong	Plant fragments
VI	2	0.89	0.67/1.1	0.53	0.44/0.62	Spiral	Plant fragments

1997) are comparable to fruits of the extinct genus *Amersinia*, which was described from the Paleocene of North America and eastern Asia and assigned to the order Cornales (Manchester et al. 1999). Like *Noferinia*, fruits of *Amersinia* are spindle shaped, trilobular, and derived from an inferior ovary. When compared to other known Cretaceous mesofossils, *Noferinia* is found to be larger than many other published mesofossils (up to 7.9 mm long as a mesofossil and up to 17 mm long as a compression). Fruits of *Amersinia* are 6.5–12 mm long and 4–7 mm wide, whereas fruits of *Noferinia* are roughly comparable in size but have a greater length : width ratio (4.0–17 mm long and 0.3–2.6 mm wide).

Fossil Coprolites from Allon

Coprolite specimens recovered from the Allon locality are divided into five types on the basis of shape and content (table 1). Type I specimens are spiral, 0.88–1.5 mm long, and contain only one pollen type (fig. 5A–5D). Type II specimens are oblong, 0.57–1.5 mm long, and contain only one pollen type (fig. 5E, 5F). In coprolite Types I and II, the pollen grains are well preserved with little or no damage (i.e., evidence of mastication) to most of the grains. Type III specimens are oblong, 1.1–1.3 mm long, and contain two or more pollen types (fig. 6A–6D). Pollen grains in these coprolites often are fragmented (fig. 6D). Type IV specimens are oblong, 0.83–2.1 mm long, and contain whole pollen grains, pollen fragments, and fragmentary plant tissues (fig. 6E, 6F). Type V specimens are oblong, 0.75–2.0 mm long, and contain only fragmentary plant tissues (fig. 6G, 6H). *Noferinia* pollen has been observed in all fossil coprolite types except Type V, which contains only plant tissue.

Modern beetle feces obtained for comparison can be separated into six distinct types: Modern Type I (fig. 5G, 5H), Modern Type II (fig. 5I, 5J), Modern Type III (fig. 7A, 7B), Modern Type IV (fig. 7C, 7D), Modern Type V (fig. 7E, 7F), and Modern Type VI (fig. 7G, 7H) (table 1). These types broadly conform to the descriptions for the fossil specimens in shape and content, but the modern feces studied are smaller and less often composed of pure pollen. Many feces contain indeterminate, large (40–50 μm), smooth, saclike inclusions

(see fig. 5G). Modern Type III is based on only one specimen that is round rather than oblong; the depauperate sample is due possibly to the restricted taxonomic sampling of both insects and plants in our modern sample. Modern Type VI specimens, not observed among the fossil coprolite assemblage, are spiral, 0.67–1.1 mm long, and contain only fragmentary plant tissues. Note that modern feces in figures 5I, 5J, and 7C–7H show a possible peritrophic membrane covering the fecal contents. The remnant of possibly the same structure is observed on some of the fossil coprolites as a smooth film obscuring grains and plant material (fig. 6C, 6E).

Discussion

Noferinia fusicarpa possesses several features that are associated closely with insect pollination. Grant (1950) proposed that epigynous flowers, which *Noferinia* possesses, are characteristic of insect pollination because reproduction is increased by interposing floral tissues between potential visitors (e.g., pollinivores) and the ovules. The features that are most suggestive of insect pollination are the differentiated perianth, sympetalous corolla, and pores at the base of the style. Sympetalous corollas are associated with insect pollination (Crepet 1996) and have been used to infer evolution toward advanced pollination syndromes involving faithful insect pollinators (Friis 1985; Crepet 1996). The presence of pores at the base of the style, if they produced nectar or a fragrant odor (Endress 1994), is strongly suggestive of insect pollination (Faegri and van der Pijl 1979). In particular, the presence of the pores surrounded by the connate remnants of the corolla forming a shallow “dish” is consistent with beetle pollination, although not diagnostic of it.

Noferinia fusicarpa gen. et sp. nov. possesses three characters that are common among plants that are wind pollinated: production of very large numbers of pollen grains, intermediate-sized pollen grains (observed 24–30 μm), and radial symmetry. However, none of these features is associated exclusively with wind pollination, while many characters that are tied more closely to wind pollination are absent. Insect-pollinated plants that employ pollen as the reward for visitation often produce copious amounts of pollen (Faegri

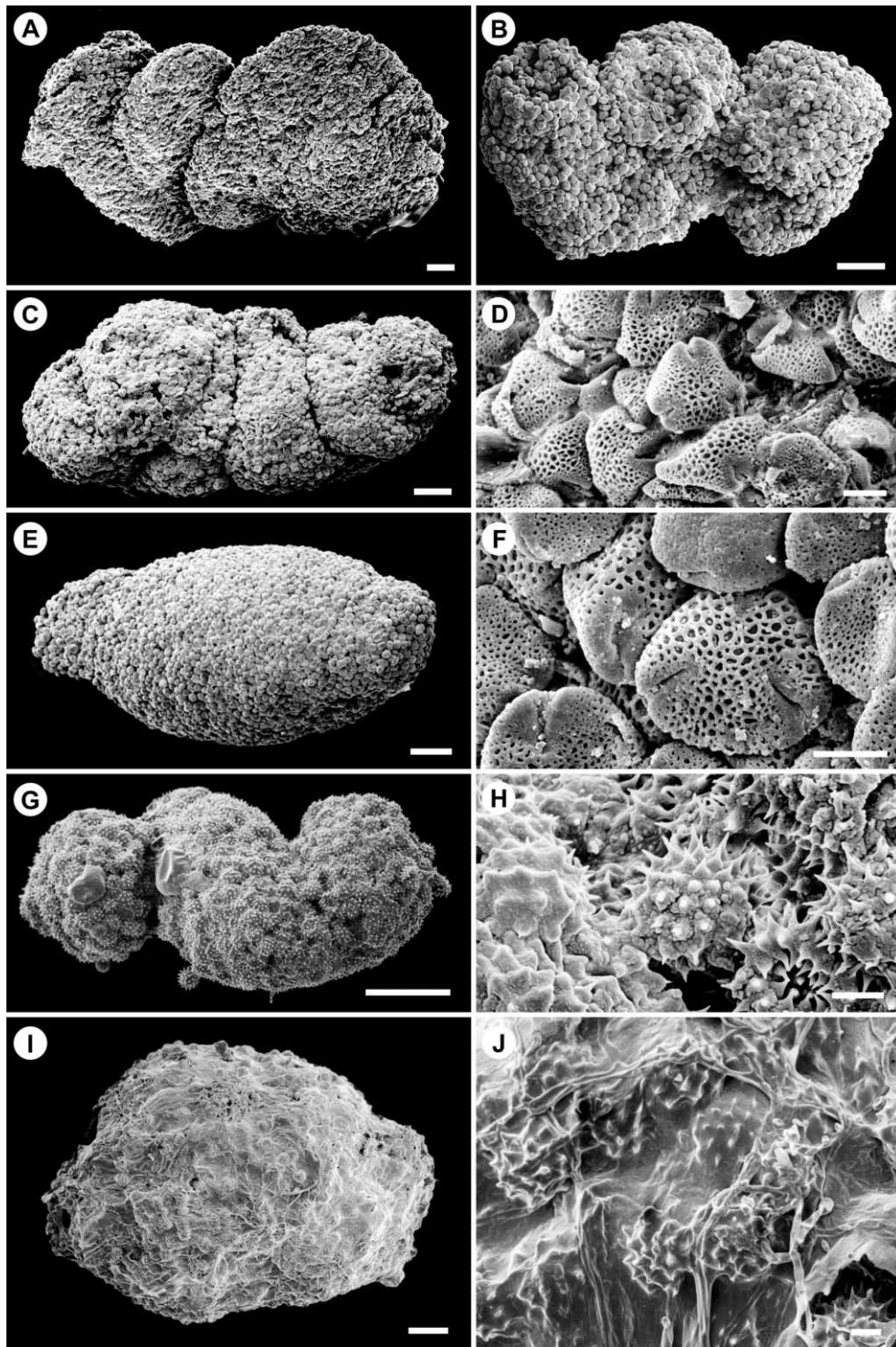


Fig. 5 Fossil coprolites from the Allon locality (A–F) and modern beetle feces (G–J). A–C, Type I coprolites: spiral, containing only one type of pollen. A, Type I coprolites containing *Noferinia* pollen exclusively (PP446225). Scale bar = 100 μm . B, PP44627. Scale bar = 100 μm . C, PP44623. Scale bar = 100 μm . D, Close-up of pollen in A showing good preservation and lack of damage to most grains (PP44655). Scale bar = 10 μm . E, Type II coprolite: oblong, containing only one type of pollen. In all recovered specimens, *Noferinia* pollen was the exclusive component (PP44642). Scale bar = 100 μm . F, Close-up of pollen in E. Note lack of damage to grains (PP44642). Scale bar = 10 μm . G, Modern beetle feces similar to Type I (A–D) showing spiral morphology and containing only one type of pollen. Scale bar = 100 μm . H, Close-up of pollen in G showing no apparent damage to grains. Scale bar = 10 μm . I, Modern beetle feces similar to Type II (E, F) showing only one type of pollen. Note presence of peritrophic membrane surrounding entire bolus. Scale bar = 100 μm . J, Close-up of pollen in I showing peritrophic membrane. Scale bar = 10 μm .

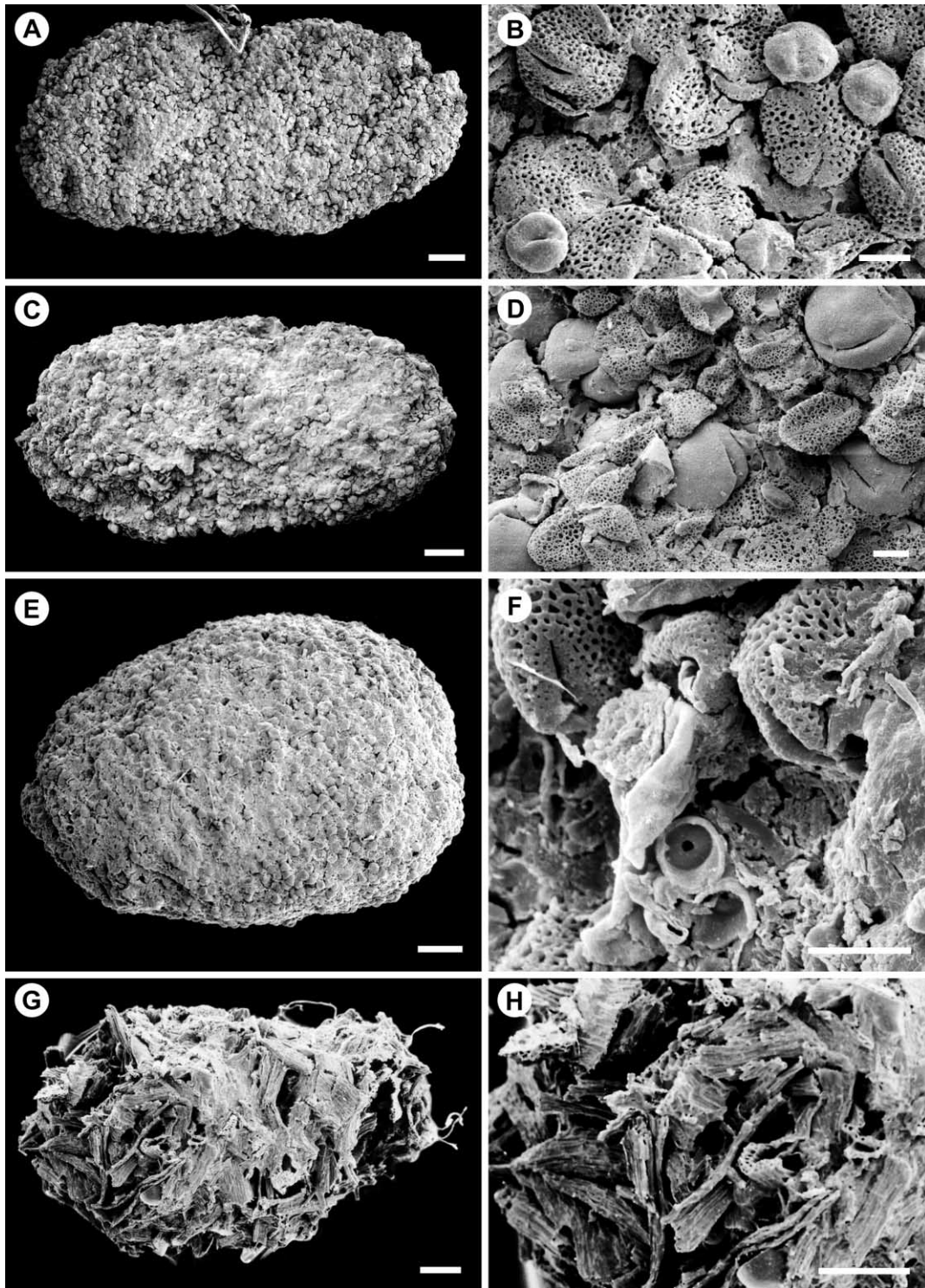


Fig. 6 Fossil coprolites from the Allon locality. *A–D*, Type III coprolites: oblong, containing at least two different pollen types. *A*, Type III coprolite containing *Noferinia* pollen and second, much smaller type of tricolp(or?)ate pollen (PP44633). Scale bar = 100 μm . *B*, Close-up of pollen in *A* showing little damage to most grains (PP44630). Scale bar = 10 μm . *C*, Type III coprolite containing tricolporate and monosulcate pollen (PP44630). Scale bar = 100 μm . *D*, Close-up of pollen in *C* showing damage to many grains, primarily to monosulcate grains (PP44630). Scale bar = 10 μm . *E*, Type IV coprolite: oblong, containing pollen, usually damaged, and fragmentary plant tissues (PP44640). Scale bar = 100 μm . *F*, Close-up of coprolite contents of *E* illustrating *Noferinia* pollen and fragmented tissues (PP44640). Scale bar = 10 μm . *G*, Type V coprolite: oblong, containing only fragmentary plant tissues (PP44642). Scale bar = 100 μm . *H*, Close-up of fragmented plant tissues in *G* (PP44642). Scale bar = 100 μm .

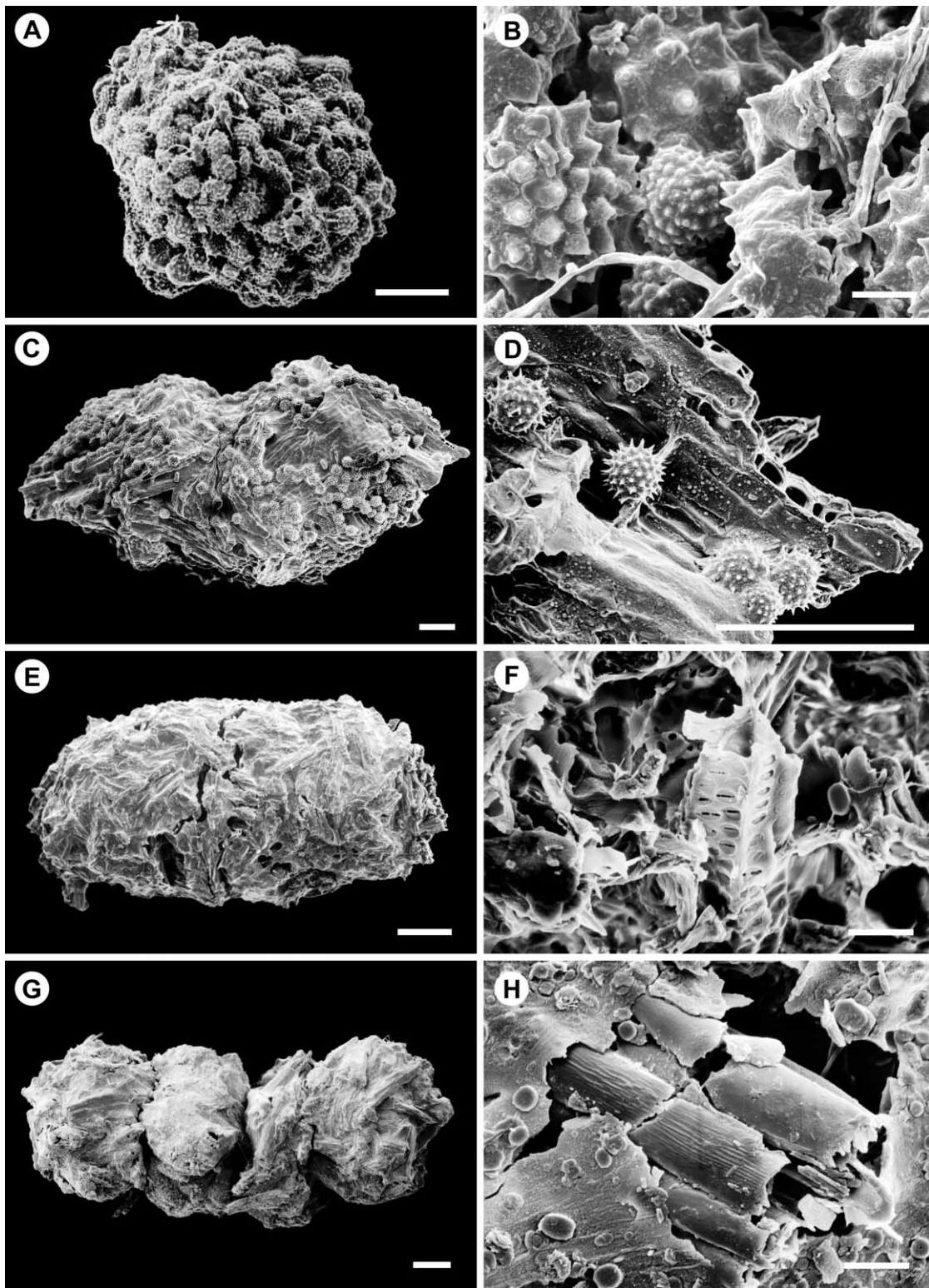


Fig. 7 Modern beetle feces. *A*, Fecal type similar to Type III coprolites in figs. 6A–6D. Scale bar = 100 μm . *B*, Close-up of pollen in *A* showing two (or three) types of Asteraceae pollen. Scale bar = 10 μm . *C*, Fecal type similar to Type IV coprolites in figs. 6E and 6F containing pollen and fragmented plant tissues. Scale bar = 100 μm . *D*, Close-up of pollen and plant tissue fragments. Note that, as in Type IV coprolites, the pollen is not necessarily damaged. Scale bar = 100 μm . *E*, Fecal type similar to Type V coprolites in figs. 6G and 6H containing only fragmented plant tissues. Note the peritrophic membrane covering the bolus. Scale bar = 100 μm . *F*, Close-up of plant tissues in *E*. Scale bar = 10 μm . *G*, Fecal type not observed in the fossil assemblage; spiral, containing only fragmented plant tissues. Scale bar = 100 μm . *H*, Close-up of plant material in *G*. Scale bar = 10 μm .

and van der Pijl 1979). Wind-pollinated plants typically have pollen grains that are 20–40 μm in diameter (Whitehead 1969), and *Noferinia* falls within that range, but many insect-pollinated plants also have intermediate-sized grains (e.g., Leguminosae, Rosaceae). Zygomorphy is correlated strongly with advanced insect-pollination mechanisms (Faegri and van der Pijl 1979; Crepet 1996), but the opposite state, radial symmetry, is plesiomorphic and not diagnostic of wind pollination. Although the perianth of *Noferinia* is preserved incompletely (figs. 1C, 2A), it is adequate to show that the petals are large and extend to the top of, and perhaps around, the stamens (fig. 1C). By contrast, perianth parts are absent or reduced in most obligately wind-pollinated plants (Whitehead 1969; Faegri and van der Pijl 1979). Finally, *Noferinia* does not have unornamented and/or brevicolporate/porate pollen grains, which often are found in obligately wind-pollinated plants (Whitehead 1969; Hesse 1981).

If insect pollination did occur and pollen was the main reward, then we would expect those insects to have produced feces containing indigestible exines of *Noferinia* pollen. Examination of the acid-resistant residue collected during the search for mesofossils yielded numerous small clusters containing pollen and/or plant tissue. On the basis of the similarity in shape and content to feces produced by the modern pollinivorous and phytophagous coleoptera that we surveyed, we interpret the specimens described here as insect coprolites. However, the modern material surveyed for comparison represents a very limited sample (beetles only), and we have found no other sources of published data on comparative feces morphology in phytophagous insects. Therefore, it is impossible to reach definitive conclusions about the source of the coprolites, although the similarity to beetle feces is striking.

When eaten by an insect with nonmasticating mandibles, pollen germinates in the gut allowing the contents to be digested and the exine excreted (Crowson 1981). This is most probably true for Types I and II coprolites in which the pollen is in excellent condition (fig. 5A–5F). It is worth noting that, on the basis of the description and illustrations, the coprolites described by Friis et al. (2000a), which contain exclusively or almost exclusively the acolumellate monosulcate pollen of *Penistemon*, agree in shape, composition, and size with Type II coprolites illustrated here. Type III coprolites show evidence of mixed feeding and variable preservation (fig. 6A–6D) with some pollen grains showing evidence of damage (fig. 6D) that might be the result of mastication. Types IV and V coprolites

contain highly fragmented (masticated) plant tissues (fig. 6E–6H). Beetles are referred to as “mess and soil” pollinators (Faegri and van der Pijl 1979), and the consumption of some plant material does not preclude a role in pollination for producers of Type IV coprolites. The producers of Type V coprolites appear to have been strictly herbivorous on nonpollen tissues and probably would not have served as pollinators. We hypothesize that the insects producing Types I and II coprolites were pollinators of *Noferinia*, with the producers of Types III and IV being incidental, or accidental, pollinators judging by their more generalized feeding habits. The presence of coprolites composed entirely of *Noferinia* pollen, that those coprolites are morphologically similar to feces from extant pollen-feeding insects and that *Noferinia* possesses several features consistent with insect pollination, argues strongly for a relationship between *Noferinia* and pollen-feeding insects for the purpose of pollination.

Mesofossils have dramatically improved our ability to document the evolution of insect-pollination syndromes during the Cretaceous angiosperm radiation. However, insect coprolites preserved in the same mesofossil assemblages that yield flowers and fruits offer additional evidence in support of biological interactions proposed on the basis of morphology alone. Further investigations of coprolites found in association with fossil floras, combined with systematic surveys of the morphology of feces from extant insects, may significantly improve our understanding of the angiosperm radiation and the role that specific clades of insects played in it.

Acknowledgments

We gratefully acknowledge D. Herendeen, J. Kobylinska, S. Magallón-Puebla, L. Panko, H. Sims, and A. Wilcek for assisting in collecting, preparing, and photographing specimens. We would like to thank M. Thayer for identifying the modern beetles that produced fecal material for comparison. We also thank S. J. Ashe, O. Pellmyr, and L. Thien for comments and suggestions concerning the fossil coprolite material. L. Amati, A. Douglas, E. M. Friis, and an anonymous reviewer generously contributed comments on and criticisms of this manuscript. This work was supported in part by National Science Foundation grants DEB-9616443 and EAR-9614672 to P. R. Crane and P. Herendeen.

Literature Cited

- APG (Angiosperm Phylogeny Group) 1998 An ordinal classification for the families of flowering plants. *Ann Mo Bot Gard* 85:531–553.
- Basinger JF, DL Dilcher 1984 Ancient bisexual flowers. *Science* 224:511–513.
- Baxendale RW 1979 Plant-bearing coprolites from North American coal balls. *Palaeontology* 22:537–548.
- Burger WC 1981 Why are there so many kinds of flowering plants? *BioScience* 31:572, 577–581.
- Burnett JA 1996 Nannofossils and Upper Cretaceous (sub-)stage boundaries—state of the art. *J Nannoplankton Res* 18:23–32.
- Caldas MB, RG Martins-Neto, FP Lima-Filho 1989 *Afropollis* sp. (polém) no trato intestinal de vespa (Hymenoptera: Apoidea: Xyelidae) no Cretáceo da Bacia do Araripe. *Atas II Simposio Nacional de Estudos Tectonicos. Soc Bras Geol Bras* 11:195–196.
- Crane PR, EM Friis, KR Pedersen 1994 Paleobotanical evidence for the early radiation of magnoliid angiosperms. *Plant Syst Evol Suppl* 8:73–91.
- 1995 The origin and early diversification of angiosperms. *Nature* 374:27–33.
- Crepet WL 1984 Advanced (constant) insect pollination mechanisms: pattern of evolution and implications vis-à-vis angiosperm diversity. *Ann Mo Bot Gard* 71:607–630.
- 1996 Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. *Rev Palaeobot Palynol* 90:339–359.

- Crepet WL, EM Friis 1987 The evolution of insect pollination in angiosperms. Pages 181–201 in EM Friis, WG Chaloner, PR Crane, eds. The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge.
- Crepet WL, EM Friis, KC Nixon 1991 Fossil evidence for the evolution of biotic pollination. *Philos Trans R Soc Lond B Biol Sci* 333: 187–195.
- Crepet WL, KC Nixon 1994 Flowers of Turonian Magnoliidae and their implications. *Plant Syst Evol Suppl* 8:73–91.
- 1996 The fossil history of stamens. Pages 25–57 in WG D'Arcy, RC Keating, eds. The anther: form, function, and phylogeny. Cambridge University Press, Cambridge.
- 1998 Fossil Clusiaceae from the Late Cretaceous (Turonian) of New Jersey and implications regarding the history of bee pollination. *Am J Bot* 85:1112–1133.
- Crowson RA 1981 The biology of the Coleoptera. Academic Press, New York.
- Dilcher DL 1979 Early angiosperm reproduction: an introductory report. *Rev Palaeobot Palynol* 27:291–328.
- Dilcher DL, PR Crane 1984 *Archaeanthus*: an early angiosperm from the Cenomanian of the Western Interior of North America. *Ann Mo Bot Gard* 71:351–383.
- Doyle JA, CL Hotton 1991 Diversification of early angiosperm pollen in a cladistic context. Pages 169–195 in S Blackmore, SH Barnes, eds. Pollen and spores. Systematics Association Special Volume 44. Clarendon, Oxford.
- Drinnan AN, PR Crane, EM Friis, KR Pedersen 1991 Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. *Am J Bot* 78: 153–176.
- Edwards D, PA Seldon, JB Richardson, L Axe 1995 Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature* 377:329–331.
- Endress PK 1994 Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.
- Faegri K, L van der Pijl 1979 The principles of pollination ecology. 3d rev. ed. Pergamon, New York.
- Friis EM 1984 Preliminary report of Upper Cretaceous angiosperm reproductive organs from Sweden and their level of organization. *Ann Mo Bot Gard* 71:403–418.
- 1985 *Actinocalyx* gen. nov., sympetalous angiosperm flowers from the Upper Cretaceous of southern Sweden. *Rev Palaeobot Palynol* 45:171–183.
- Friis EM, KR Pedersen, PR Crane 2000a Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen form the Early Cretaceous of Portugal. *Grana* 39:226–239.
- 2000b Reproductive structure and organization of basal angiosperms from the Early Cretaceous (Barremian or Aptian) of western Portugal. *Int J Plant Sci* 161(suppl):S169–S182.
- Grant V 1949 Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3:82–97.
- 1950 The protection of the ovules in flowering plants. *Evolution* 4:179–201.
- Grimaldi D 1999 The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann Mo Bot Gard* 86:373–406.
- Harris TM 1957 The investigation of a fossil plant. *Proc R Inst G B* 36:456–466.
- Herendeen PS, S Magallón-Puebla, R Lupia, PR Crane, J Kobylinska 1999 A preliminary conspectus of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, USA. *Ann Mo Bot Gard* 86:407–471.
- Hesse M 1981 The fine structure of the exine in relation to the stickiness of angiosperm pollen. *Rev Palaeobot Palynol* 35:81–92.
- Hill CR 1976 Coprolites of *Pityophyllum* cuticles from the Middle Jurassic of North Yorkshire. *Bull Br Mus Nat Hist (Geol)* 27: 289–294.
- Hoot SB, S Magallón-Puebla, PR Crane 1999 Phylogeny of basal eudicots based on three molecular data sets: atpB, rbcL, and 18S nuclear ribosomal DNA sequences. *Ann Mo Bot Gard* 86:1–32.
- Huddleston PF, JH Hetrick 1991 The stratigraphic framework of the Fort Valley Plateau and the Central Georgia Kaolin District. *Georgia Geological Society Guidebook* 11(1). Georgia Geological Society, Atlanta.
- Kampmann H 1983 Ein Insekten-Exkrement aus Sporen aus dem unterkretarischen Saurierlager van Nehden (Sauerland, Westfalen). *Palaeontol Z* 57:75–77.
- Knobloch E, DH Mai 1986 Monographie der Früchte und Samen in der Kreide von Mitteleuropa. *Rozpr Ustred Ustavu Geol* 47: 1–219.
- Knoll AH 1986 Patterns of change in plant communities through geological time. Pages 126–141 in J Diamond, TJ Case, eds. Community ecology. Harper & Row, New York.
- Krassilov VA, AP Rasnitsyn 1983 A unique find: pollen in the intestine of Early Cretaceous sawflies. *Paleontol J* 1982:80–95.
- Labandeira CC 1997 Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annu Rev Ecol Syst* 28: 153–193.
- Labandeira CC, DL Dicher, DR Davis, DL Wagner 1994 Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. *Proc Natl Acad Sci USA* 91:12278–12282.
- Lidgard S, PR Crane 1990 Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* 16:77–93.
- Lupia R, S Lidgard, PR Crane 1999 Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation. *Paleobiology* 25:305–340.
- Magallón-Puebla S, PS Herendeen, PR Crane 1997 *Quadriplatanus georgianus* gen. et sp. nov.: staminate and pistillate platanaceous flowers from the Late Cretaceous (Coniacian-Santonian) of Georgia, U.S.A. *Int J Plant Sci* 158:373–394.
- Manchester SR, PR Crane, LB Golovneva 1999 An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and eastern Asia. *Int J Plant Sci* 160: 188–207.
- Mulcahy DL 1979 The rise of angiosperms: a genecological factor. *Science* 206:20–23.
- Nagalingum N, AN Drinnan, R Lupia, S McLoughlin 2002 Fern diversity and abundance in Australia during the Cretaceous. *Rev Palaeobot Palynol* (in press).
- Regal PJ 1977 Ecology and evolution of flowering plant dominance. *Science* 196:622–629.
- Rex G, J Galtier 1983 Sur l'évidence d'interactions animal-végétal dans le Carbonifère inférieur français. *C R Acad Sci Paris Ser II* 303: 1623–1626.
- Scott AC 1977 Coprolites containing plant material from the Carboniferous of Britain. *Palaeontology* 20:59–68.
- Scott AC, J Stephenson, WG Chaloner 1992 Interaction and coevolution of plants and arthropods during the Paleozoic and Mesozoic. *Philos Trans R Soc Lond B Biol Sci* 335:129–165.
- Scott AC, TN Taylor 1983 Plant/animal interactions during the Upper Carboniferous. *Bot Rev* 49:259–307.
- Sims HJ, PS Herendeen, PR Crane 1998 New genus of fossil Fagaceae from the Santonian (Late Cretaceous) of central Georgia, U.S.A. *Int J Plant Sci* 159:391–404.
- Waldman M, WS Hopkins Jr 1970 Coprolites from the Upper Cretaceous of Alberta, Canada, with a description of their microflora. *Can J Earth Sci* 7:1295–1303.
- Watson L, MJ Dalwitz 1993 The families of flowering plants: interactive identification and information retrieval. CSIRO, Melbourne.
- Whitehead DR 1969 Wind pollination in the angiosperms: evolutionary and environmental considerations. *Evolution* 23:28–35.