

## DREWRIA POTOMACENSIS GEN. ET SP. NOV., AN EARLY CRETACEOUS MEMBER OF GNETALES FROM THE POTOMAC GROUP OF VIRGINIA<sup>1</sup>

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### ABSTRACT

*Drewria potomacensis* gen. et sp. nov. from the Lower Cretaceous Potomac Group of Virginia (Zone I, probably Aptian) provides the first definite Mesozoic megafossil record of Gnetales. The stems are slender, display no evidence of secondary growth, and show axillary monopodial branching. Attached leaves are opposite and decussate, borne at swollen nodes, and have clasping sheathing bases. Each leaf is oblong, up to 20 mm long, and has a dense network of longitudinally aligned subepidermal fibers. Leaf venation consists of two, or possibly three pairs of longitudinally parallel veins that form a reticulum at the apex and higher-order crossveins that form apically oriented chevrons. Reproductive structures consist of short, loose spikes that are borne in dichasially arranged groups of three. The dichasia are either terminal or lateral in the axil of a leaf. Reproductive units of the lateral spikes in a dichasium contain seeds, each surrounded by at least one pair of opposite, broadly elliptical or ovate bracts. Characters of *D. potomacensis* that suggest a gnetalean relationship include the opposite bracts surrounding the seeds, the network of subepidermal foliar fibers, and the distinctive leaf venation, which is very similar to that seen in the cotyledons of extant *Welwitschia*. Other features consistent with a gnetalean relationship include opposite and decussate leaves, swollen nodes, and the dichasial arrangement of the reproductive spikes. Masses of polyplicate gnetalean pollen comparable to that of extant *Welwitschia* occur in the same bed as the megafossils. The morphology of *D. potomacensis* indicates that it was an herb or possibly a shrub. The growth habit of *D. potomacensis* and associated plants, combined with the sedimentary occurrence of the fossils, indicate that this species and perhaps related taxa were important components of early successional vegetation during the mid-Cretaceous.

EXTANT SEED PLANTS comprise five major clades: Coniferales, Cycadales, Ginkgoales, Gnetales, and angiosperms. All of these groups, with the exception of Gnetales, have an extensive megafossil record that extends back into the Mesozoic (e.g., Taylor, 1981; Stewart, 1983). The Gnetales, in contrast, lack any well-documented Mesozoic megafossil record and comprise only three extant genera: *Ephedra*,

*Gnetum*, and the monotypic *Welwitschia*. Němejc (1967) suggested that Gnetales were never diverse, but as early as 1908, Arber and Parkin (p. 507) concluded, "Although the Gnetales are unknown to us in the fossil state, we are by no means precluded *ipso facto* from the conclusion that the group may have once flourished more vigorously than at the present day." Arber and Parkin's suggestion has subsequently been corroborated by the recognition of a widespread and diverse group of Mesozoic dispersed pollen comparable to grains of extant *Ephedra* and *Welwitschia* in shape, aperture configuration, surface sculpture, and exine ultrastructure (e.g., Trevisan, 1980), which are especially abundant and diverse in the Early Cretaceous of low paleolatitudes (e.g., Africa, South America) (Brenner, 1976). Only one possible kind of fossil gnetalean pollen (*Equisetosporites chinleanus* Daugherty) has been found within a pollen-bearing organ (*Masculostrobus clathratus* Ash, 1972), but the systematic position of the *M. clathratus* plant is uncertain (Ash, 1972) and pollen wall ultrastructure differs from that of extant Gnetales

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Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Geological Survey.

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(Zavada, 1984). In this report we describe gnetalean megafossils, including stems with attached leaves and reproductive structures, from the Lower Cretaceous Potomac Group of Virginia. These remains, found in association with masses of *Welwitschia*-type pollen, provide the first fully documented report of Mesozoic gnetalean megafossils and have important implications for understanding the ecology and evolution of this enigmatic group of seed plants.

**MATERIALS AND METHODS**—The fossils described in this paper were collected from a 4-cm-thick bed of micaceous gray clay exposed at the northern end of Drewrys Bluff, approximately 9 m above high tide level. This bed is dated palynologically as upper Zone I of Brenner (1963), or probably Aptian (J. A. Doyle, oral communication, 1986) and yields the early angiosperm leaves with cuticles reported by Upchurch (1984a, b). Although fossil vegetative shoots were collected on the outcrop, almost all of the reproductive material was recovered by splitting blocks of matrix in the laboratory and examining them under a dissecting microscope. Organically preserved specimens were coated with Krylon acrylic plastic spray to prevent further fragmentation. Over 100 specimens on approximately 80 pieces of matrix were examined. Leaf cuticles were prepared from one organically-preserved specimen. All specimens are deposited in the University of Michigan Museum of Paleontology (UMMP). Systematic comparisons were made using the published literature (e.g., Pearson, 1929; Martens, 1971; Sporne, 1971), the U.S. Geological Survey reference collections of cleared leaves and modern pollen, and specimens in the herbarium of the Field Museum of Natural History.

Photographic techniques were critical to determining venation and morphological features in many specimens. Organically preserved remains and reddish-brown impressions of vegetative parts were photographed with Kodak Technical Pan 2415 Film developed with HC-110 developer to medium or high contrast levels. Light gray impressions of vegetative parts were photographed either with Polaroid Type 51 high contrast film or Kodak Technical Pan Film 2415 under fluorescent light, which enhanced many details of venation not readily visible to the naked eye. Reproductive structures were photographed with Polaroid Type 55 film. Polarizing filters were used to increase contrast and reduce glare from specimens coated with acrylic plastic.

Cuticles of megafossils were prepared using a combination of standard methods. This in-

cluded removing the cuticle from the rock with a needle, dissolving the acrylic plastic in acetone, demineralizing overnight in HF, macerating in bleach, staining in Safranin O dissolved in a 50:50 mixture of ethanol and toluene, and mounting in Histoclad. A centrifuge was used for the bleaching, staining, and dehydration stages of processing due to the extremely fragmentary nature of the cuticle. Dispersed cuticles and associated masses of pollen, prepared in the course of an earlier study (Upchurch, 1984a, b), also were examined to assess variation in cuticular structure and to determine the possible pollen of the megafossils. Cuticles were photographed with Kodak Technical Pan Film 2415 using a Zeiss Photomicroscope I. Pollen grains were photographed with Kodak Technical Pan Film 2415 on an Olympus Vanox Photomicroscope using Nomarski optics.

**DIAGNOSIS**—*Generic diagnosis*—*Drewria* *gen. nov.*: Stems bearing opposite and decussate leaves. Branching monopodial, branches arising in the axils of leaves. Leaves simple, oblong, margin entire. Leaf venation of two distinct vein orders. First-order venation of two (possibly three) pairs of longitudinal parallel veins; the innermost pair running to the lamina apex and branching to form a reticulum. Second-order venation of crossveins that typically form apically oriented chevrons. Lamina with abundant, longitudinally oriented, subepidermal fibers. Reproductive structures either terminal or in the axil of a leaf, consisting of short, loose spikes borne in dichasial groups of three. Reproductive units of the lateral spikes in a dichasium containing seeds, each surrounded by at least one pair of broadly elliptical to broadly ovate bracts.

*Holotype*: UMMP 65414b (Fig. 22).

*Etymology*: From Drewrys Bluff, Virginia, the type locality.

*Specific diagnosis*: *Drewria potomacensis* sp. nov.—As for genus.

*Syntypes*: UMMP 65409-65414a, 65415-65419 (Fig. 1-16, 19-21, 23-27).

*Etymology*: From Potomac Group, the fossil-bearing rock unit.

*Locality*: 37°25'25"N, 77°25'30"W, Chesterfield County, Virginia, south of Richmond on the James River at the north end of Drewrys Bluff, approximately 9 m above high tide level.

*Stratigraphic position*: Potomac Group (undifferentiated), upper Zone I of Brenner (1963), Lower Cretaceous, probably Aptian.

**DESCRIPTION**—Plants consisting of slender branching stems that bear opposite and de-

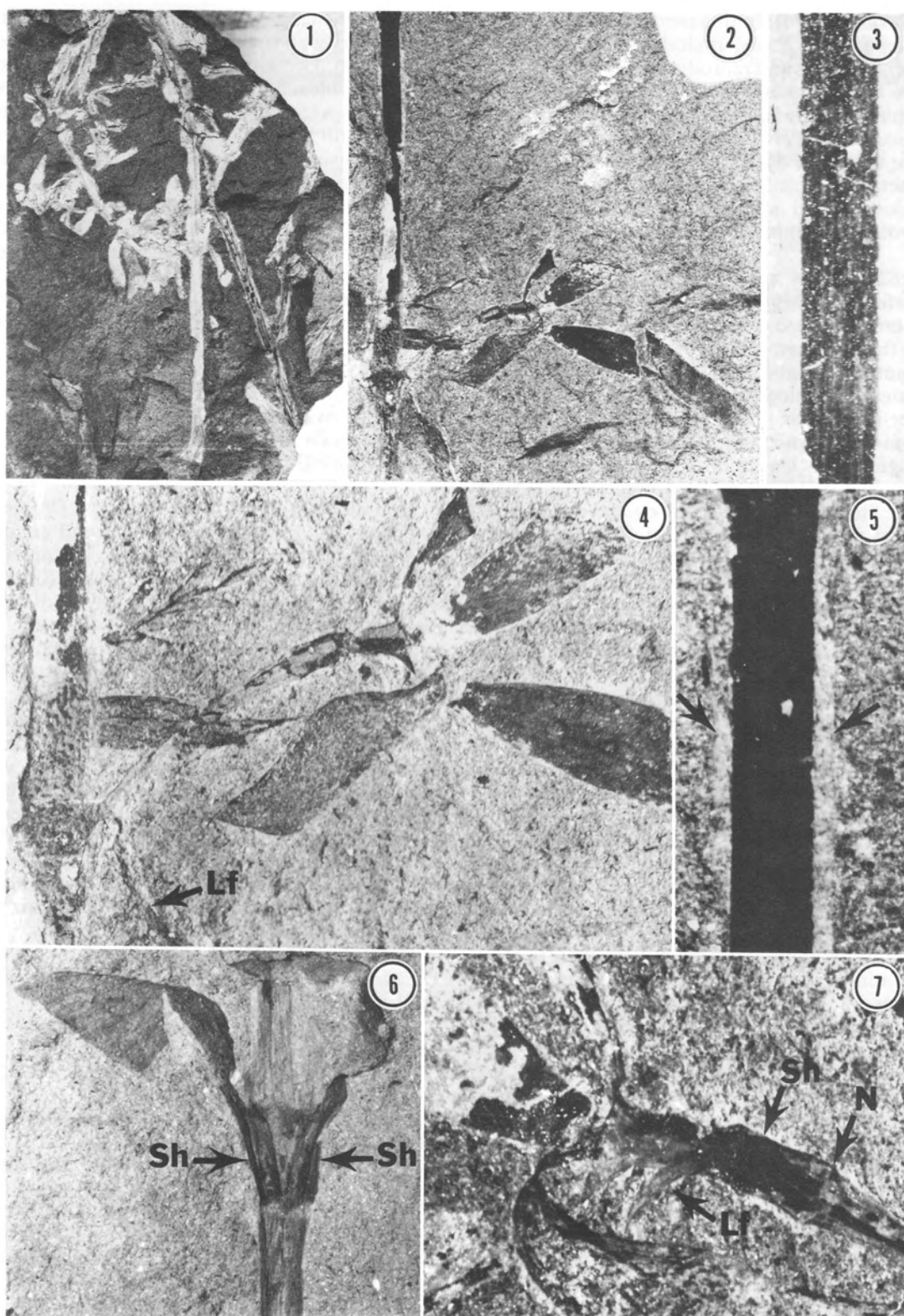


Fig. 1-7. *Drewria potomacensis* gen. et sp. nov. 1. Vegetative specimen showing branching. UMMP 65409,  $\times 1$ . 2. Organically preserved vegetative specimen with axillary branch. Note long internode of main stem. UMMP 65410a',  $\times 2$ . 3. Close-up of stem in Fig. 2, showing central zone with longitudinal bundles. UMMP 65410a',  $\times 10$ . 4. Close-up

cussate leaves. Stems 1–3 mm in diameter, internodes up to 30 mm long, stem diameter constant for most of internode length but gradually increasing at the nodes. Stems showing no evidence of secondary growth, consisting of an inner core and an outer, more readily flattened zone. Inner core up to 1.5 mm in diameter, containing 6–8 longitudinally oriented strands, these strands of similar thickness to the foliar veins. Outer zone up to 0.3 mm wide, typically one-fourth the radius of the stem. Branching monopodial, with pairs of opposite branches arising in the axils of leaves, no evidence of scale leaves associated with the bases of the branches.

Leaves simple, oblong, 10–20 mm long, 2–6 mm wide, midrib absent, apex acute and usually with a sharp tip, base narrow-acute to decurrent, margin entire, texture thin. Bases of opposite leaves clasping the stem to form a short sheath. Venation of two distinct orders. First-order venation consisting of 2 or possibly 3 pairs of parallel longitudinal veins that extend from the base of the leaf, 2 pairs of veins present in the middle part of the lamina, veins about 1 mm apart at the widest part of the lamina. Longitudinal parallel veins forming a reticulum at the leaf apex. Second-order venation consisting of crossveins that typically form apically-oriented chevrons. Leaves with abundant, longitudinally oriented, parallel subepidermal fibers. Fibers much thinner than veins, occasionally branching and anastomosing, tending to obscure the venation. Leaf margin mechanically reinforced (possibly by an additional pair of veins). Foliar cuticle very thin, difficult to prepare, with poorly-developed flanges. Cells in rows, probably elongate, with straight anticlinal walls, about 35–40  $\mu$ m wide. External and internal sculpture smooth under light microscopy. Stomata unknown.

Reproductive structures consisting of short loose spikes in dichasially arranged groups of three. Dichasia either terminal or lateral in the axil of a leaf. Reproductive units of the lateral spikes in a dichasium larger than those of the central spike and bearing seeds. Seeds flattened, narrowly ovate, 1–2.5 mm long, 1–2 mm wide, apex acute, base rounded. Seeds borne between at least one opposite pair of broadly elliptical to broadly ovate inner bracts with rounded apices. Each bract up to 1.5 mm long,

longitudinally striated but showing no obvious venation.

**DISCUSSION—Morphology and anatomy**—At least twelve specimens show attachment between leaves and reproductive structures; these reproductive shoots are identical to associated sterile shoots in size, nonvenational features of foliar morphology, and mode of preservation. The stems of some specimens have a distinct central core and a thinner border (Fig. 2–5), interpreted as a stele and surrounding cortex, respectively. The central core in one organically preserved specimen shows 6–8 thick longitudinal strands (Fig. 3) and longitudinal striations similar in number and size also occur in some stem impressions (Fig. 4). Although the exact number of strands cannot be determined, they are the same thickness as the foliar veins and are therefore interpreted as vascular bundles. One specimen also shows additional, narrower striations on the stem that possibly represent fibers. The outer zone is always the same proportion relative to stem diameter and is interpreted as a decayed parenchymatous cortex; the presence of organic material in the outer zone on one specimen shows that this zone was not produced by drying and shrinkage of the specimens. None of the stems are prominently impressed into the sediment and were evidently easily flattened during preservation. Evidence of extensive wood, therefore, is absent. Although the possibility of secondary growth in some parts of the plant cannot be excluded, the largest stems observed are 3 mm in diameter and appear to be herbaceous.

Branching of the vegetative shoots is opposite, axillary and monopodial (Fig. 1, 2, 4). None of the lateral branches shows evidence of scale leaves at the base (e.g., Fig. 4). In one lateral shoot where the first three nodes are preserved, the distance between the base and the lowest node is much greater than the distance between the first and succeeding nodes (Fig. 4, 7). The leaves of the same shoot show no decrease in size from the lowest to the uppermost node, making it unlikely that the unequal internode length is due to fossilization of an immature shoot. The absence of scale leaves at the base of the lateral shoot and the presence of an elongate region between its base and the lowest node are characteristic of extant

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of axillary branch in Fig. 2, showing subtending leaf (Lf) borne at swollen node. The longitudinal striations on the main stem are interpreted as the impressions of vascular bundles. UMMP 65410a',  $\times 5$ . 5. Close-up of stem in Fig. 2, showing outer zone (arrows) and inner zone. UMMP 65410a',  $\times 10$ . 6. Impression of stem showing opposite leaves with sheathing bases (Sh). UMMP 65411,  $\times 6$ . 7. Counterpart of shoot in Fig. 2, showing first node of axillary shoot. N = node, Sh = sheathing leaf base, Lf = free portion of leaf. UMMP 65410a,  $\times 10$ .

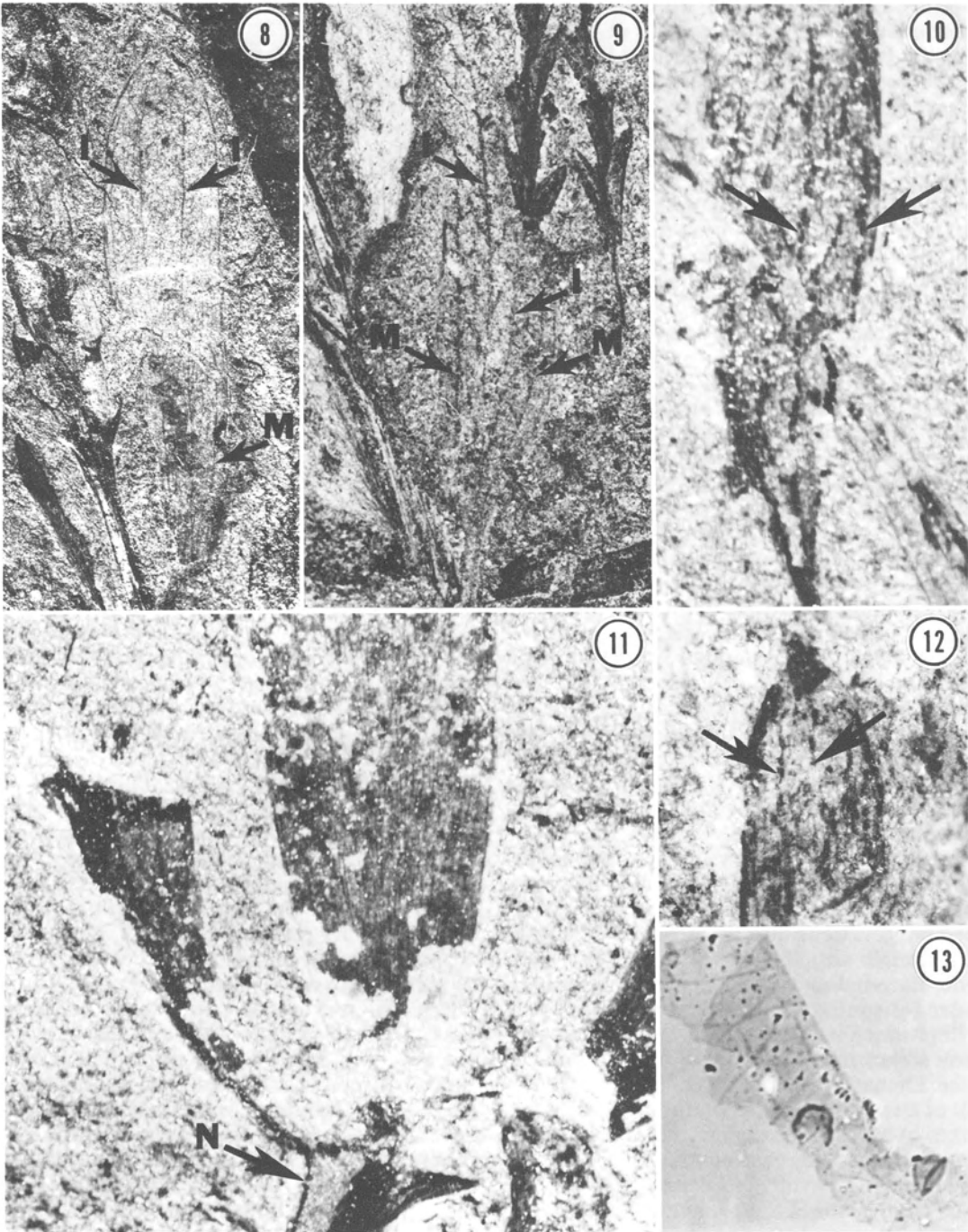


Fig. 8-13. *D. potomacensis* gen. et sp. nov. 8. Nearly complete leaf from vegetative shoot showing longitudinal parallel veins and marginal thickenings. I = inner pair of veins, M = middle pair. UMMP 65410b,  $\times 5$ . 9. Basal portion of leaf showing inner (I) and middle (M) pairs of longitudinal parallel veins and chevron-forming crossveins. UMMP 65410b,  $\times 5$ . 10. Organically preserved leaf fragment showing two longitudinal parallel veins (arrows) and crossveins. UMMP 65410a',  $\times 15$ . 11. Organically preserved leaf showing numerous, thin, longitudinally aligned structures, interpreted as the remains of subepidermal fibers. Note swollen node (N) bearing opposite leaves (arrow). UMMP 65410a',  $\times 15$ . 12. Detail of leaf from reproductive shoot (middle of Fig. 25) showing zig-zag course of longitudinal parallel veins (arrows) at leaf apex. UMMP 68512,  $\times 30$ . 13. Folded cuticle of leaf, photographed under phase contrast, showing cells oriented in rows. UMMP 65410,  $\times 200$ .

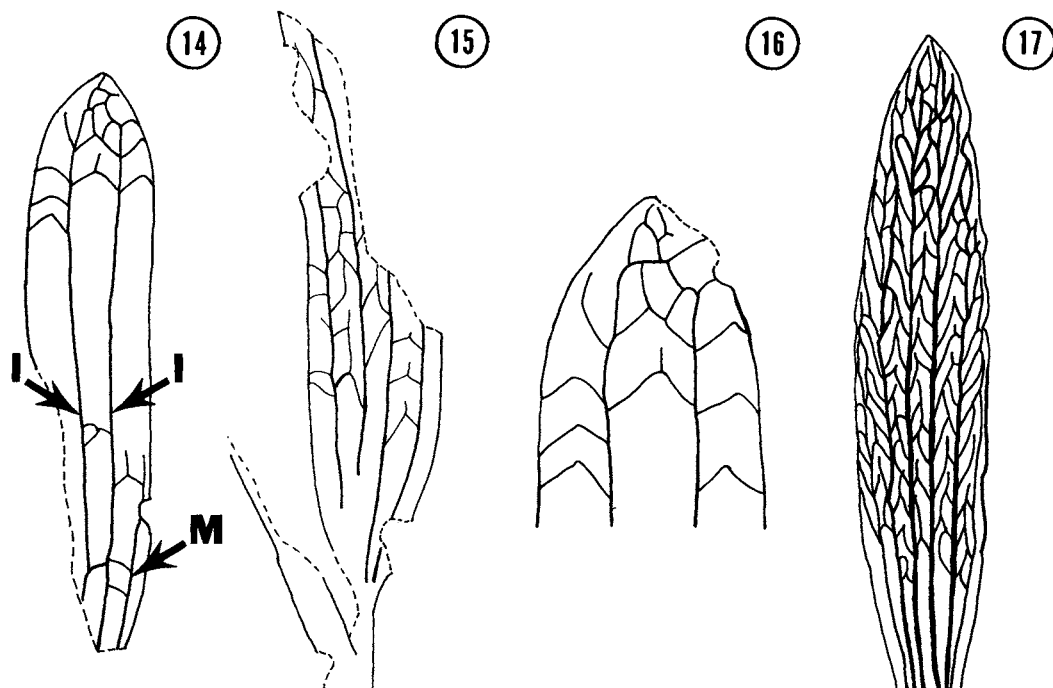


Fig. 14–17. Foliar venation of *D. potomacensis* and *Welwitschia*. 14. Line drawing of *D. potomacensis* leaf in Fig. 8, traced from photograph. Note inner (I) and middle (M) veins. UMMP 65410b,  $\times 5$ . 15. Line drawing of *D. potomacensis* leaf in Fig. 9, traced from photograph. UMMP 65410b,  $\times 5$ . 16. Line drawing of *D. potomacensis* leaf apex in Fig. 8, drawn from photograph with camera lucida. UMMP 65410b,  $\times 15$ . 17. Line drawing of cotyledon of *Welwitschia mirabilis*. Redrawn from Rodin (1953), fig. 7.  $\times 5$ .

plants that lack a period of bud dormancy (Tomlinson and Gill, 1973; Tomlinson, 1978).

Leaf impressions of *D. potomacensis* have little relief in the rock, especially relative to those of associated conifers; thus, the leaves were thin-textured. Preservation varies greatly, but a few leaves from vegetative and reproductive shoots show both the vascular tissue and the subepidermal fibers. In most leaves with good organic preservation, the densely packed fibers obscure the venation (Fig. 11), but in a few the fibers appear to have mostly decayed and the details of venation can be observed (Fig. 8–10, 14–16). None of the leaves has a midvein, and the innermost pair of longitudinal parallel veins runs on either side of the longitudinal plane of symmetry (Fig. 8, 14). The exact number of vein pairs is difficult to determine, but the two inner pairs run at least as far as the middle part of the lamina (Fig. 8, 9, 14, 15). The margin of some specimens appears to be reinforced by an additional pair of longitudinal parallel veins (Fig. 8), but these are thin and cannot be confidently differentiated from marginal bundles of subepidermal fibers, as occur in some extant dicotyledons as well as in *Gnetum* and *Welwitschia*. Excluding the possible pair of marginal veins, only the

innermost pair of veins runs to the apex (Fig. 8, 12, 14). Their more zig-zag course at the tip of the leaf (Fig. 12, 16) suggests that they are giving off lateral branches; simultaneously, they become less distinct and appear to form a reticulum with the crossveins at the leaf apex, rather than running to a point of fusion (Fig. 12, 16).

The foliar cuticle of *D. potomacensis* is very thin and fragments readily upon preparation (Fig. 13). The cuticular flanges are difficult to see under light microscopy even with phase-contrast, but the observed cells are organized into distinct rows. No stomata were observed on either in situ or dispersed cuticle, presumably because only adaxial cuticle was preserved.

Figure 18 shows a reconstruction of the vegetative shoots.

The reproductive structures of *D. potomacensis* consist of three spikes arranged in terminal dichasia (Fig. 19–24, 26, 32). One specimen appears to show a single spike borne in the axil of the leaf on an otherwise vegetative axis (Fig. 25), but is too poorly preserved to exclude the possibility that it is a fragment of a dichasium. Seeds have been observed only on the lateral spikes of dichasia and never on



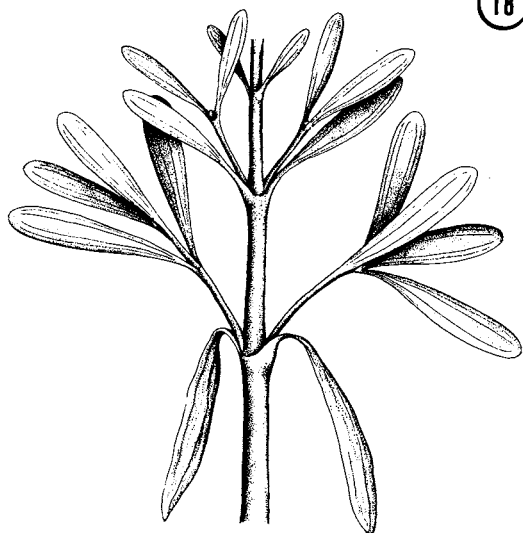


Fig. 18. Reconstruction of vegetative parts of *Drewria potomacensis*, based on specimens in Fig. 1–12.

central spikes. The central spike may have borne pollen-producing reproductive units, but poor preservation precludes more detailed consideration of this possibility.

The lateral spikes are always larger than the central spike of a dichasium (Fig. 19–24), but the number and arrangement of reproductive units in each spike is difficult to determine. In central spikes, the reproductive units appear to be borne in opposite pairs (Fig. 19, 20). These pairs probably are arranged decussately, considering the phyllotaxy of the rest of the plant. If this interpretation is correct, the central spike may have contained about 8–12 reproductive units. Each reproductive unit in the central spike clearly includes a bract, but other details are not preserved.

None of the lateral spikes is complete, and the arrangement of the reproductive units is unclear. Although the bracts are larger, the lateral spikes probably contained about the same number of reproductive units as the central spikes. Several specimens show that each reproductive unit consists of a seed surrounded by at least one pair of opposite bracts and that these bracts are apparently lateral with respect to the plane of flattening of the seed (Fig. 22

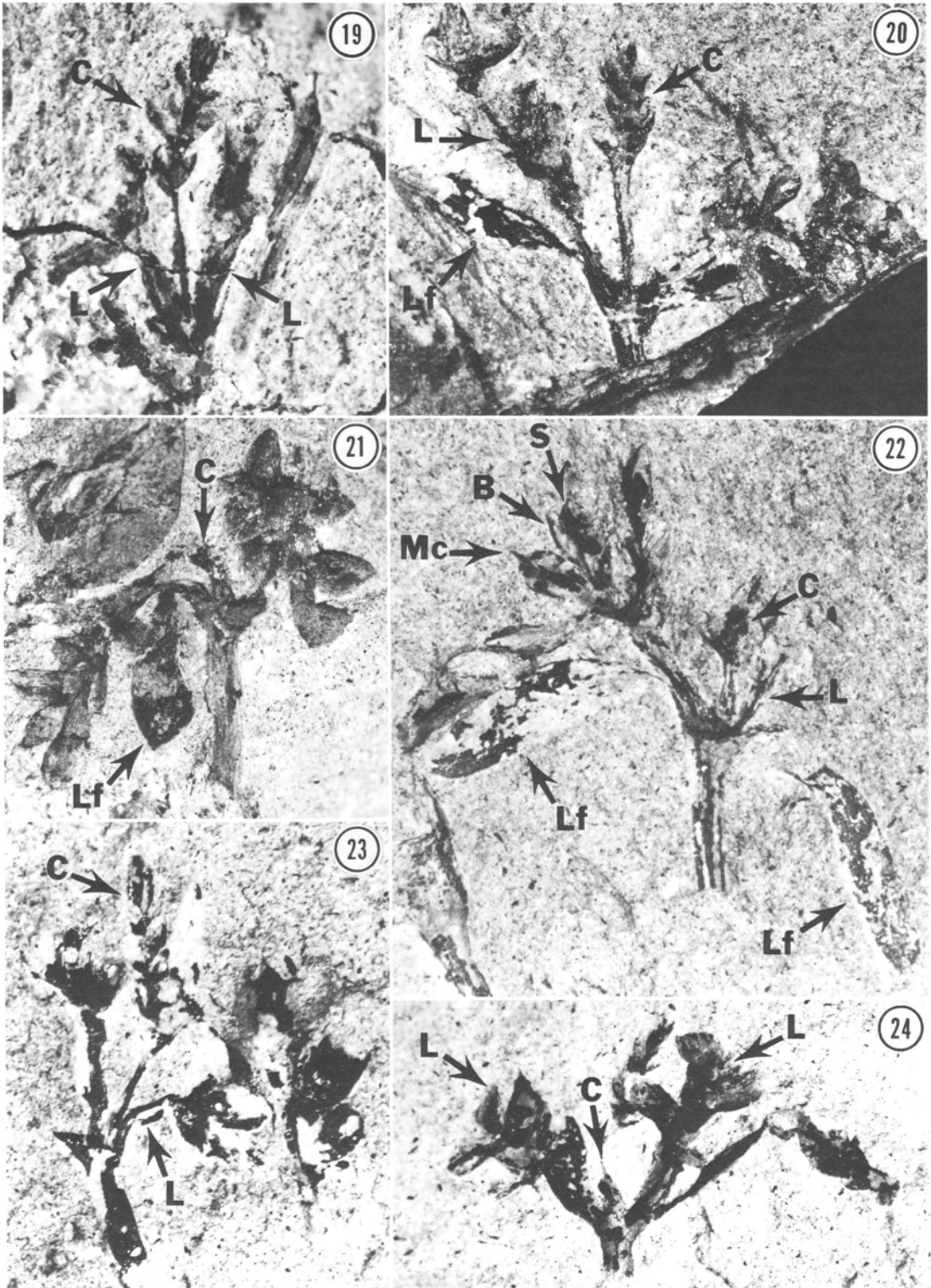
B; 27, middle arrows). However, in some specimens additional bracts are associated with each reproductive unit, and typically these bracts are positioned in an anterior-posterior plane with respect to the flattening of the seed (Fig. 27, bottom arrow). The interpretation of these anterior-posterior bracts is unclear. Some may represent a primary bract subtending a reproductive unit while others could represent tertiary bracts. Each ovulate reproductive unit therefore consists of at least three, and perhaps five “bracts” surrounding a single seed. These would be interpreted most straightforwardly, respectively, as a primary bract plus a pair of lateral secondary bracteoles, or as a primary bract with two pairs of opposite and decussate secondary and tertiary bracteoles.

Seeds of *D. potomacensis* were sufficiently hard to resist compression during fossilization, and occasional specimens preserve the seed outline as a cavity in the matrix. The seed is bilaterally symmetrical, and some seeds appear to have a prominent ridge down the center of both flattened surfaces (Fig. 22, Mc). Whether the ridge is a feature of the seed or the keel of a pair of anterior-posterior bracts is uncertain. A single specimen (Fig. 22, Mc) shows a projection 0.25 mm long from the apex of a seed that probably is an elongated micropyle.

Figure 32 shows a reconstruction of the reproductive structures.

*Comparison with other fossil material*—*Drewria potomacensis* cannot be assigned to any previously described genus of fossil plant but shares significant similarities with four fossil taxa. One isolated leaf of *Conospermites hakeaefolius* Ettingshausen described from the mid-Cretaceous (Cenomanian) of Czechoslovakia (Vidovle locality) by Velenovský and Vlníklá (1926, pl. 3, fig. 5, left-hand specimen) has venation almost identical to that of *D. potomacensis*. The lamina of the specimen is larger (up to 2 cm wide) than that of *D. potomacensis* and has a more rounded apex and more gradually tapering base. However, there are two prominent veins that arise at the base of the leaf, and these run parallel toward the apex where they become less distinct and form a reticulum. The longitudinal veins are linked by crossveins that frequently form apically ori-

Fig. 19–24. Reproductive structures of *D. potomacensis* gen. et sp. nov. 19. Dichasium showing central spike with bracts and two poorly preserved lateral spikes. UMMP 65413,  $\times 13$ . 20. Dichasium showing subtending leaves, central spike, one well-preserved lateral spike, and one poorly preserved lateral spike. UMMP 65414a,  $\times 9$ . 21. Dichasium showing the remains of two leaves, poorly preserved central spike, and two lateral spikes. UMMP 65415,  $\times 16$ . 22. Holotype showing stem with a swollen node bearing a pair of opposite leaves and the terminal dichasium. Dichasium



consisting of one poorly preserved lateral spike, one poorly preserved central spike, and one well preserved lateral spike showing a seed with subtending bracts and a seed with elongate micropyle. UMMP 65414b',  $\times 9$ . **23**. Dichasium showing central spike and lateral spikes. Note the larger size of the lateral spikes. UMMP 65416,  $\times 9$ . **24**. Dichasium with central spike and two lateral spikes with larger bracts. UMMP 65417,  $\times 7$ . B = bract, C = central spike, L = lateral spike, Lf = leaf, Mc = micropyle, S = seed.



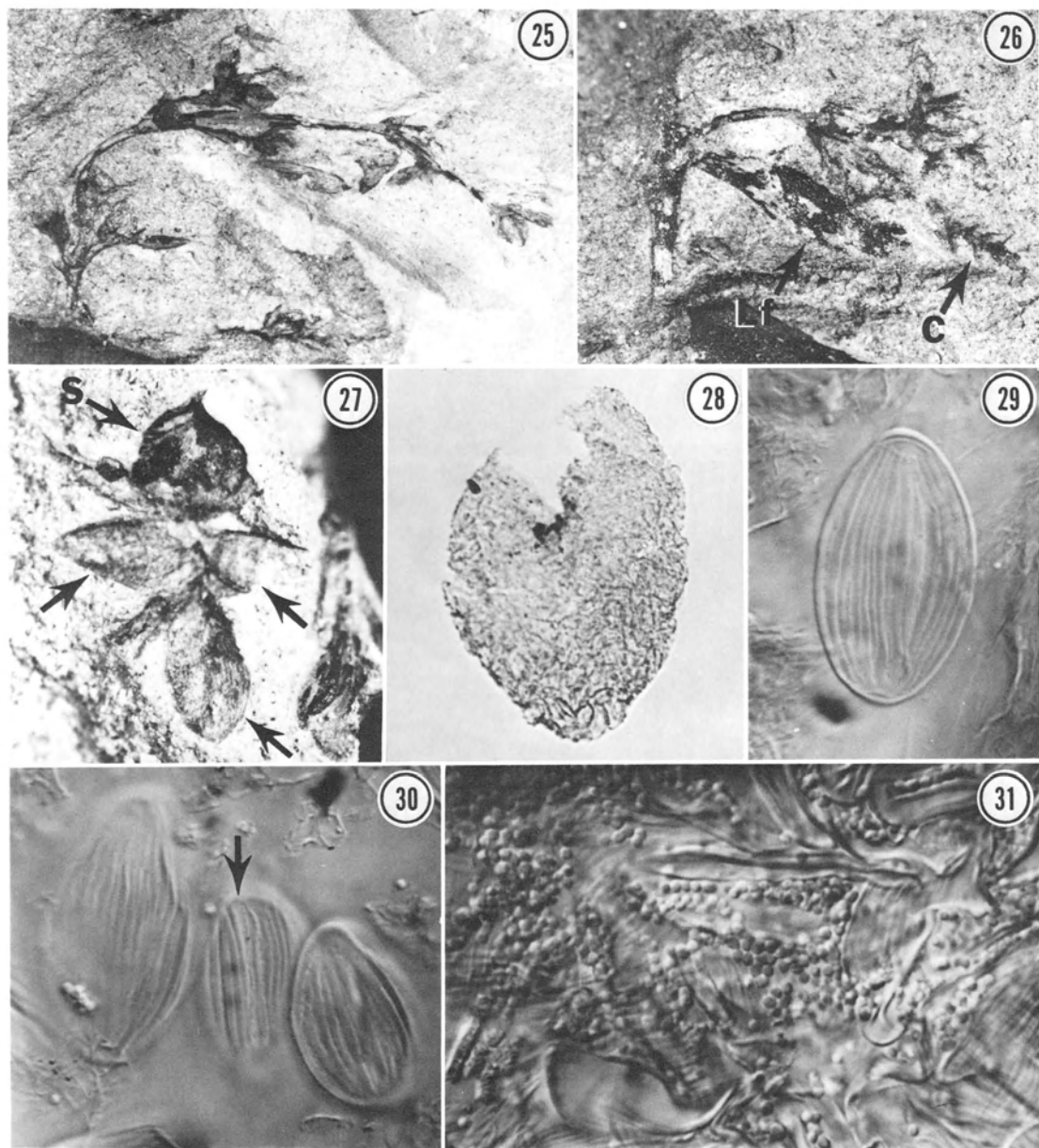


Fig. 25–31. *D. potomacensis* gen. et sp. nov. and associated pollen. 25. Axis showing leaves and poorly preserved dichasia or axillary spikes. UMMP 65418,  $\times 5$ . 26. Shoot showing leaf subtending a dichasium. Lateral spikes of dichasia poorly preserved. Note central spike. UMMP 65419,  $\times 7$ . 27. Reproductive unit from a lateral spike showing seed, probable primary bract (bottom arrow), and pair of opposite bracteoles (middle arrows). UMMP 65419,  $\times 7$ . 28. Pollen mass associated with *D. potomacensis*. UMMP 65420,  $\times 200$ . 29. Close-up of pollen grain, showing numerous longitudinal ridges. Note thin cuticle near pollen grain. UMMP 65421,  $\times 1,250$ . 30. Pollen grain showing weak sulcus (arrow). UMMP 65421,  $\times 1,250$ . 31. Ubisch bodies associated with pollen grains. UMMP 65421,  $\times 1,250$ . Legend: as in Fig. 19–24.

ented chevrons. Other specimens assigned to *C. hakeaefolius* differ from *D. potomacensis* either in being pinnately lobed (Knobloch 1978, fig. 18, 21) or in having a distinct midrib (Velenovský, 1884, fig. 11–13; Velenovský and

Vinklâf, pl. 3, fig. 5, right-hand specimen) or in having pinnate venation (type material, Ettingshausen, 1867, pl. 3, fig. 4, 12).

*Decheyllia gormanii* Ash from the Upper Triassic Chinle Formation of northeastern Ar-

izona was described as a peculiar conifer of uncertain relationship (Ash, 1972) but shares several similarities with *D. potomacensis*. The leaves of *Decheyllia* are attached in opposite and decussate pairs, and the linear vegetative leaves are flattened into a single plane. The linear vegetative leaves have a thickened midrib, while the wider sporophylls lack a midrib and have venation composed of two broad longitudinal "ribs" and two narrow marginal "strands." (A pair of longitudinal strands is illustrated for the midrib of linear vegetative leaves, along with a pair of marginal strands [Ash, 1972, Text-fig. 6A–C]; however, venation on the type specimens is difficult to interpret.) Despite these similarities to *D. potomacensis*, crossveins appear to be absent in *Decheyllia*, and other features of vegetative and reproductive morphology differ from those of *D. potomacensis*. It is of interest, however, that the pollen organs associated with *Decheyllia* (*Masculostrobus clathratus* Ash) contain pollen grains of *Equisetosporites chinleanus* Daugherty (Ash, 1972). The longitudinal striations of these grains are similar to those in pollen in extant *Ephedra* (Scott, 1960), but the details of pollen wall ultrastructure are different (Zavada, 1984).

The single specimen of *Cyperacites* sp. described by Krassilov (1982) from the Lower Cretaceous (Valanginian-Barremian) Manlaj locality, Mongolia, consists of a stem with a terminal dichasial arrangement of three reproductive "spikes" arising from a swollen node. Each spike apparently consists of bracts ("glumes") and long bristles. Although additional information is not available, the size of plant, the swollen node, and the dichasial arrangement of three spikes are very similar to what is seen in *D. potomacensis*.

*Eoanthus zherikhinii* Krassilov, an ovulate reproductive structure from the Lower Cretaceous of the Lake Baikal area (Krassilov, 1986), resembles *D. potomacensis* in several respects. In *E. zherikhinii*, each ovule has an elongate micropyle and is associated with a flattened, presumably foliar structure (compared with an opened follicle by Krassilov); additionally, polylicate gnetalean pollen is found in the micropyles of the ovules. However, *E. zherikhinii* differs from *D. potomacensis* in having a whorled arrangement of ovules and transverse ridges on the structures subtending the ovules. In addition, the type of gnetalean pollen found in the micropyles of *E. zherikhinii* differs from that found in association with *D. potomacensis* (cf. below) in having fewer and wider plications that are spirally arranged.



Fig. 32. Reconstruction of dichasium of *D. potomacensis*.

**Systematics**—The habit of *Drewria potomacensis*, combined with the morphology of the reproductive organs and leaves, excludes a close relationship to any known group of living or fossil seed plants except Gnetales and angiosperms. Within flowering plants, a close relationship to the monocotyledons is excluded by the organization of the foliar venation, especially the absence of a midvein and the thinning and branching of the longitudinal veins at the leaf apex to form a reticulum. In both extant monocotyledons that have few pairs of longitudinal parallel veins and in putative fossil relatives such as the Early Cretaceous *Aca-ciaephyllum*, each leaf has a midvein and longitudinal veins that persist to the leaf apex, where they fuse (Doyle, 1973). Additionally, almost all extant monocotyledons have alternate, rather than opposite, phyllotaxy. The group of extant dicotyledons most similar to *D. potomacensis* is the Chloranthaceae. This family and closely related extinct forms are of particular interest because of their well-documented Early Cretaceous fossil record based on pollen, leaves, and reproductive structures (Upchurch, Hickey, and Niklas, 1983; Walker and Walker, 1984; Upchurch, 1984a, b; Friis, Crane, and Pedersen, 1986). Similarities shared by *D. potomacensis*, Chloranthaceae, and Gnetales include opposite and decussate leaves borne at swollen nodes, dichasially arranged spike-like inflorescences, and reproductive structures surrounded by pairs of bracts. However, leaves of extant Chloranthaceae are toothed, possess a midrib with pinnately arranged secondary veins, and lack a network of subepidermal fibers. In contrast, the leaves of both *Gnetum* and *Welwitschia* lack teeth and have a dense network of subepidermal fibers, and the venation of *Drewria* leaves is strikingly similar to that of the cotyledons of *Welwitschia* (Takeda, 1913; Rodin, 1953; Fig. 17). These cotyledons are supplied by two vascular bun-

dles that dichotomize at the base of the lamina to produce a pair of inner bundles, a pair of lateral bundles and a pair of marginal bundles that run longitudinally on either side of the midline. Toward the apex of the cotyledon, the six longitudinal veins become less distinct and form a reticulum (Rodin, 1953, 1958a). Secondary crossveins form apically oriented chevrons between the longitudinal veins, as in the mature foliage of *Welwitschia* (Rodin, 1958b). As far as we are aware, this distinctive pattern of venation is unique to *Welwitschia* and *Drewria*, and in combination with previously cited features provides strong evidence for a close relationship between the fossil and extant Gnetales.

Recent cladistic analyses of seed plants resolve the Gnetales as a monophyletic group in which *Gnetum* and *Welwitschia* are more closely related than either is to *Ephedra* (Hill and Crane, 1982; Crane, 1985; Doyle and Donoghue, 1986). Coulter and Chamberlain (1917) reached a similar conclusion. Hypothesized synapomorphies of *Gnetum* and *Welwitschia* include the presence of reticulate venation composed of two or more vein orders, syndetocheilic stomata, a well-developed system of hypodermal fibers, tetrasporic megagametophyte development, absence of archegonia, exclusively cellular embryogenesis, and the presence of a "feeder" in the embryo (see Crane [1985] and literature cited therein). Of these features, only two are preserved in *Drewria*. The presence of reticulate venation with more than one vein order and a well-developed system of hypodermal fibers suggests that *Drewria* is more closely related to *Gnetum* and *Welwitschia* than to *Ephedra*. However, the validity of this hypothesis is largely dependent on the arrangement of outgroups accepted for the Gnetales. Cladistic analyses of seed plants suggest that the most appropriate outgroups are angiosperms, Bennettitales, or *Pentoxylon*, in one or another arrangement (Crane, 1985; Doyle and Donoghue, 1986). Subepidermal fibers are known in some Bennettitales, and the combination of subepidermal fibers and reticulate venation composed of two or more vein orders is present in certain extant angiosperms. Thus, the possibility exists that these features have been lost in the small simple leaves of *Ephedra*. In the absence of a clearer understanding of the relationships of the Gnetales to other seed plants, the phylogenetic position of *Drewria* within the group cannot be confidently established.

Indirect evidence supporting the assignment of *Drewria* to Gnetales is derived from pollen associated with the megafossils. In addition to

individual "ephedroid" pollen grains, preparations of dispersed cuticles from the same bed as the megafossils yielded three large clumps of polyplicate pollen similar to that of extant *Ephedra* (Steeves and Barghoorn, 1959) and *Welwitschia* (Wodehouse, 1935; Erdtman, 1965). These clumps are all of similar size and ovoid shape (Fig. 28) and are interpreted as pollen sacs. One clump is enclosed by a cuticle (Fig. 29) and shows numerous Ubisch bodies associated with the pollen grains (Fig. 31). Individual pollen grains are boat-shaped, ellipsoidal, 18–32  $\mu\text{m}$  long, 8–18  $\mu\text{m}$  in diameter, with a L/W ratio ranging from 1.7–2.9 (Fig. 29, 30). Some grains in each clump are weakly monosulcate, with a long narrow sulcus (Fig. 30). Many other grains show no sulcus under light microscopy, but some of these are folded longitudinally along an apparent line of weakness. The surface of each grain has over 20 ridges (plications) parallel to the long axis of the grain, each less than 0.5  $\mu\text{m}$  wide. The exine is 0.5–1.0  $\mu\text{m}$  thick and appears homogeneous under light microscopy. These pollen grains do not belong to any species described from the Potomac Group by Brenner (1963), but clearly relate to other types of Early Cretaceous pollen allied with extant Gnetales by Trevisan (1980). Among extant Gnetales they are most similar to the pollen of *Welwitschia* in having a sulcus and a large number of narrow longitudinal ridges. Although there is no direct evidence that these grains were produced by *Drewria*, the presence of gnetalean pollen clumps in the megafossil-bearing bed supports our interpretation that gnetalean plants were present in the local flora.

*Paleoecology*—The functional morphology of *D. potomacensis*, coupled with its floristic and sedimentary associations, indicate that it was an herbaceous or shrubby, early successional plant of mesic environments. The stems of *D. potomacensis* appear to have a well-developed cortex and show no evidence of extensive secondary tissues. These features indicate that the plant was either herbaceous or, like many suffrutescent shrubs, had young shoots that lacked secondary growth. The foliage is thin-textured, with a thinner cuticle than almost all other gymnosperms seen at Drewrys Bluff and other Potomac Group localities. This indicates that the plant probably grew under conditions of relatively low moisture stress, perhaps resulting from its low stature (cf. Salisbury, 1927) and streamside habit (cf. below). Like extant *Gnetum* and many extant tropical angiosperms (Tomlinson and Gill, 1973; Tomlinson, 1978), *D. potomacensis* ap-

pears to have lacked a period of bud dormancy. Such an interpretation is consistent with recent paleobotanical analyses of Early Cretaceous climates, which infer relatively mesic conditions for the Potomac Group (Brenner, 1976; Vakhrameev, 1978).

The megaf flora at Drewrys Bluff consists of *D. potomacensis*, ferns, angiosperms, conifers, and cycadophytes. Fern fronds, angiosperm leaves, and remains of *D. potomacensis* are the commonest fossils. Most species of ferns are known from at least one specimen in which one or two orders of frond branching are preserved, and the fragmentary nature of many specimens appears to be due to the tendency of the matrix to break irregularly, rather than along well-defined bedding planes. The common occurrence of angiosperm megafossils contrasts markedly with the absence of angiosperms from most Zone I Potomac Group localities (cf. Fontaine, 1889; Doyle and Hickey, 1976). Three of the five angiosperm species reported by Upchurch (1984a, b) are known from at least one complete leaf, and two of these are known either attached or closely associated with cutinized stems that show little evidence of secondary growth (Upchurch, Hickey, and Niklas, 1983; Upchurch, 1984a, fig. 5). Conifers and cycadophytes are rare and fragmentary, in contrast to their abundant and relatively complete preservation at many other Zone I megafossil localities. Taken together, these data imply that 1) *D. potomacensis*, ferns, and angiosperms were the major elements of an herbaceous to shrubby local vegetation, and 2) conifers and cycadophytes were either rare local elements or transported to the site of deposition from a more distant source.

Sedimentological interpretations of the Drewrys Bluff locality indicate that the plant-bearing bed is the basal unit of an abandoned channel fill. The rocks exposed at the locality show a wide range of grain sizes and are, in ascending stratigraphic order, a >1-m-thick basal conglomerate; a 4-cm-thick megafossil-bearing gray claystone; a 15-cm-thick, fine-grained, massive, argillaceous sandstone; and a >2-m-thick, extensively root-bioturbated, gray sandy mudstone. Based on sections exposed 5–15 m to the north and south of the megafossil locality, the conglomerate is laterally persistent, but the overlying units are replaced laterally by trough-crossbedded sandstone with gravel lag. (The lateral contacts between lithological units could not be observed due to soil cover.) The conglomeratic sandstone is massive and poorly sorted, indicating rapid deposition of bed-load material under turbulent, high-energy conditions. The

overlying, plant-bearing gray clay has a sharp basal contact and little coarse material except for mica, indicating an abrupt decrease in the energy of the depositional environment. The gray color, absence of bedding, preservation of some megafossils at an oblique angle to the dip of the bed, and almost complete absence of bioturbation suggest relatively rapid deposition in a poorly aerated environment, probably during floods. The overlying argillaceous sandstone records a brief resumption of bed-load deposition, but finer grain size indicates much lower-energy conditions than for the conglomeratic sandstone. The thick, gray, sandy mudstone at the top of the sequence represents a return to the deposition of predominantly suspended sediment in a poorly aerated environment. Extensive bioturbation and presence of numerous carbonized roots indicate that this unit formed a substrate for plant growth and probably represents shallower water conditions than the fossiliferous gray clay. Features especially indicative of an abandoned channel fill deposit are the abrupt decrease in the energy of the depositional environment seen at the conglomeratic sandstone/claystone contact, the lateral discontinuity of the fossiliferous gray claystone and overlying units, and the development of a rooted mudstone horizon in the upper part of the sequence (cf. Allen, 1965). This is consistent with other evidence for the fluvial (i.e., stream) origin of Potomac Group sediments in this region and other parts of the outcrop belt (Glaser, 1969). The occurrence of abundant fern, angiosperm and *Drewria* remains in a stream channel environment, at an abrupt shift from high-energy to low-energy depositional conditions, indicates that these plants were early successional colonizers of disturbed habitats, an ecology inferred for early angiosperms as a whole by Doyle and Hickey (1976) and Hickey and Doyle (1977).

These conclusions on the probable growth-habit and habitat of *Drewria potomacensis* are of considerable interest in light of recent discussions on the ecology of Cretaceous Gnetales. Brenner (1976) and Vakhrameev (1970) hypothesize that Cretaceous Gnetales were primarily adapted to hot and dry climates and had an ecology similar to that of *Classopollis*-producing conifers (Cheirolepidiaceae). Both authors compare the pollen of Cretaceous Gnetales to extant *Ephedra*, which lives in dry climates, and assume comparable ecology for the fossil plants that produced this pollen. In addition, they note that gnetalean pollen is most abundant at low paleolatitudes and correlated on a regional scale with possible indicators of aridity such as low percentages of fern spores

and high percentages of *Classopollis*. Doyle, Jardine, and Doerenkamp (1982), in contrast, hypothesize that Cretaceous Gnetales were adapted to warm, but not necessarily dry, climates and had an ecology more similar to that of angiosperms than that of *Classopollis*-producers. They argue that palynological diversity in Cretaceous Gnetales is too great to justify ecological interpretations based on the climatic tolerances of two relictual extant genera, *Ephedra* and *Welwitschia*, especially in a world where angiosperms had yet to become dominant. In addition, Doyle et al. (1982) note that in the Lower Cretaceous Cocobeach sequence of central Africa, located at a paleolatitude of 15° S (Smith, Hurley, and Briden, 1981), the percentages of gnetalean pollen and *Classopollis* show an inverse relationship typical of ecological segregation. The highest percentages of *Classopollis* are found in the middle Aptian, during an interval of basinal flooding by marine waters and salt deposition, suggesting adaptation to dry upland habitats and possibly saline conditions. In contrast, the highest percentages of Gnetales are found in an earlier interval of fluvial-deltaic deposition and are coincident with the highest percentages of angiosperms, suggesting ecological co-occurrence and adaptation to floodplain habitats. The data from our study provide direct support for the view that Gnetales and early angiosperms had similar ecological tolerances, probably arising from fundamental similarities in their reproductive biology (Crane, 1987) and vegetative morphology. Both in terms of branching and leaf morphology *D. potomacensis* is more mesomorphic than any extant Gnetales, and this indicates that these extant genera provide insufficient basis from which to generalize about the ecology of fossil Gnetales.

*Fossil history of the Gnetales*—Despite the abundance and diversity of gnetalean pollen in southern Laurasia and especially northern Gondwana during the Early Cretaceous (Brenner, 1976; Doyle et al., 1982), gnetalean megafossils have not been described prior to this study. Two hypotheses have been advanced to account for the apparent scarcity of gnetalean megafossils. Arber and Parkin (1908) and Seward (1919) emphasized the possibility of confusing *Gnetum*-like foliage with that of dicotyledons, while extrapolations based on extant *Ephedra* and *Welwitschia* led Wilson (1959) to suggest that the group had a low fossilization potential because of restriction to arid environments. *Drewria* demonstrates that not all Mesozoic Gnetales were restricted to such habitats and indicates a further possible bias against

the preservation of gnetalean megafossils. The vegetative organs of herbs have a low fossilization potential relative to those of trees (e.g., Spicer, 1980); therefore, if an herbaceous to shrubby growth habit was widespread in extinct Gnetales it may partially explain the discrepancy between their extensive microfossil, but sparse megafossil, record.

Notwithstanding these possible biases of representation and recognition, the gnetalean megafossil record seems certain to be expanded by the discovery of new material and perhaps by the reinterpretation of previously described Mesozoic fossils. In addition to previously mentioned taxa, described forms that share some similarities with extant Gnetales include *Cyperacites potomacensis* Berry and *Casuarina covilli* Ward from the Potomac Group (Ward, 1895; Berry, 1911), *Montsechia vidali* (Zeiller) Teixeira from the Early Cretaceous (Berriasian) of Spain (Blanc-Louvel and Barale, 1983), *Hexagonocaulon minutum* Lacey and Lucas (1981) from the Triassic of the South Shetland Islands, and *Gurvanella dictyoptera* Krassilov and the "Potamogeton-like spike" from the Early Cretaceous of Mongolia (Krassilov, 1982). Careful reevaluation of these and other problematic Mesozoic megafossils may considerably enhance our knowledge of the early diversity of Gnetales, and this will be crucial to further clarifying how Gnetales are related to other groups of seed plants.

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