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THE CONIFER *FRENELOPSIS RAMOSISSIMA* (CHEIROLEPIDIACEAE) IN THE LOWER CRETACEOUS OF TEXAS: SYSTEMATIC, BIOGEOGRAPHICAL, AND PALEOECOLOGICAL IMPLICATIONS

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Until now, our knowledge of the Lower Cretaceous conifer *Frenelopsis ramosissima* was based exclusively on branches from a few sites in the Potomac Group of eastern Virginia and Maryland. Affinities with the important Mesozoic family Cheirolepidiaceae have been assumed despite the historical absence of diagnostic attached or associated *Classopollis*-producing pollen cones. This plant has been reconstructed as a small, stem-succulent shrub that inhabited diverse, mesic plant communities. Here, we present a reconsideration of *F. ramosissima* based on new fossils from the Jones Ranch sauropod dinosaur quarry site (Twin Mountains Formation) near Glen Rose, Texas, which represents a ca. 2100-km range extension for this conifer. Compelling support for assignment to the Cheirolepidiaceae is provided by the first account of associated pollen cones with *in situ* *Classopollis*-type pollen. Features of associated remains are consistent with this determination, including ovulate cones with persistent bracts, cone scales with a probable epimatium, and wood with mixed pitting on the tracheid radial walls. Our analysis of the new Texas fossils refutes or seriously challenges many widely accepted hypotheses regarding the biogeography, structure, and paleoecology of *F. ramosissima*. For example, this plant can no longer be considered a Potomac Group–endemic taxon. Furthermore, the taphonomy and sedimentology of the Jones Ranch locality indicate a monospecific stand of *F. ramosissima* plants from a semiarid climate rather than a diverse mesic community, as indicated by the Potomac Group occurrences. Finally, associated logs indicate that *F. ramosissima* was a large tree (at least 22.4 m tall, extrapolated from maximum trunk diameter) with abundant wood in the trunk and lower branch orders.

Keywords: *Classopollis*, conifers, Cretaceous, *Frenelopsis*, Glen Rose, Texas, Twin Mountains Formation.

Introduction

The extinct conifer family Cheirolepidiaceae emerged during the Triassic and formed a significant component of the vegetation in many parts of the world by the Lower Jurassic. However, it has become increasingly clear that these conifers were particularly important in the Early Cretaceous, because of an extraordinary radiation of the so-called frenelopsid forms. Evidence for this radiation is mainly based on the numerous species of vegetative shoots (e.g., *Frenelopsis* and *Pseudofrenelopsis*) and their associated or attached *Classopollis*-producing pollen cones described over the past three decades. Interest in these frenelopsid cheirolepidiaceans continues unabated, based on the recent appearance of new species descriptions and paleoecological analyses (Gomez et al. 2002), as well as the first detailed account of an associated ovulate cone (Kvaček 2000).

Despite the recent advances in our understanding of the Cheirolepidiaceae, few whole-plant reconstructions have been forthcoming, and contradictory interpretations of the structure and paleoecology of several species, including some of the most widespread and well-studied forms, remain unre-

solved (Axsmith et al. 2004). Moreover, several published species and reconstructed representatives of the Cheirolepidiaceae, such as the often-cited North American species *Frenelopsis ramosissima*, are actually known from limited and/or ambiguous material.

Before this investigation, *F. ramosissima* was known only from impression/compression fossils of branching systems from a few localities in the Lower Cretaceous Potomac Group of Maryland and Virginia. Nevertheless, this species is listed among “well-authenticated members of the Cheirolepidiaceae” in a comprehensive review of the family (Watson 1988, p. 388). This unqualified determination is remarkable, considering that attached or associated *Classopollis*-producing pollen cones, which in the same review are suggested to be the only synapomorphy and reliable identifying characteristic of the family, were unknown (Watson 1988). Ostensibly, cheirolepidiacean affinities were assumed on the basis of a suite of shoot morphological features, including jointed-appearing stems, leaves with clasping bases and reduced free leaf tips, thick internode cuticles, sunken guard cells, and stomatal pit openings with thickened rims and overhanging papillae (Watson 1977).

Frenelopsis ramosissima has historically been reconstructed as a succulent plant and is, therefore, commonly presented as an exemplar of the angiosperm-like growth habits and

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ecological preferences sometimes attributed to the Cheirolepidiaceae. This conifer has even been compared to herbaceous angiosperm succulents, such as *Salicornia* (Watson 1977). Despite its xeric features, however, *F. ramosissima* was the most common plant at the Fredericksburg, Virginia, locality, where it occurred with abundant angiosperms and ferns indicative of mesic conditions (Fontaine 1889; Upchurch and Doyle 1981).

In this article, we analyze an occurrence of *F. ramosissima* branches and associated plant fossils, including pollen cones, ovulate cones, and wood, from the Jones Ranch sauropod dinosaur locality (Twin Mountains Formation) near Glen Rose, Texas (Winkler et al. 2000). From our report of associated pollen cones with *in situ* *Classopollis*-type pollen, we provide the most compelling evidence to date that *F. ramosissima* was, indeed, a member of the Cheirolepidiaceae. Although the status of *F. ramosissima* as a member of this family has never been seriously questioned since Watson's (1977) determination, our analysis of the new Texas fossils refutes or seriously challenges most of the commonly accepted hypotheses regarding the biogeography, growth habit, and paleoecology of this plant.

Material and Methods

Geological Setting and Age

According to Berry (1910) and Watson (1977), *Frenelopsis ramosissima* was known from several localities in the Potomac Group of Maryland and Virginia, ranging in age from the Barremian through the Aptian. However, Fontaine's (1889) original description and more recent studies of conifer-bearing Potomac Group assemblages by Upchurch and Doyle (1981) give the impression that *F. ramosissima* was known only from the Fredericksburg, Virginia, and Baltimore, Maryland, localities. The only recent report is from the Puddledock locality of Virginia (Srinivisan 1995), but no illustrations or descriptions are provided. If verified, this occurrence would extend the age range of this species into the early or middle Albian. Regardless of the actual number of productive localities and their precise ages, *F. ramosissima* was apparently common only at the Fredericksburg site, which is now inaccessible (Upchurch and Doyle 1981). All of the fossils described here come from the Jones Ranch sauropod dinosaur quarry site in the Lower Cretaceous Twin Mountains Formation of Hood County, Texas (Winkler et al. 2000). Therefore, this occurrence extends the original range of *F. ramosissima* by ca. 2100 km. The Cretaceous section in northern Texas represents several marine transgression-regression episodes, resulting in time-transgressive lithologic units trending from southeast to northwest. The Twin Mountains Formation was deposited in a fluvial environment. However, marine beds of the lower part of the Glen Rose Formation intertongue with the Twin Mountains Formation to the southeast. The Glen Rose Formation preserves marine invertebrates that correlate with known chronostratigraphy, and the base of the formation has been tied to a date marking the Aptian/Albian boundary at 112.2 Ma (Jacobs et al. 1991; Gradstein et al. 1995). The Twin Mountains Formation at the level of the Jones Ranch site is approximately

equivalent to the lower part of the Glen Rose Formation and is most likely between 110 and 112 Ma (Jacobs et al. 1991; Gradstein et al. 1995; Jacobs and Winkler 1998).

The plant fossils at the Jones Ranch site co-occur with the bones of at least three individual sauropod dinosaurs referred to as *Pleurocoelus* sp. but which may be a new taxon (P. Rose, personal communication, 2004). Recently, remains of smaller vertebrates have been found, including crocodile and theropod dinosaur teeth.

Specimen Collection and Preparation

Crews from the Fort Worth Museum of Science and History and Southern Methodist University exposed several silicified logs in the field during initial excavation of the sauropod bones. Fifteen of the most complete log specimens were measured and their positions mapped (Winkler et al. 2000). Shoots, cones, and fusain occur together in hard, well-cemented sandstone among the silicified logs. Some specimens were recognized in the field, but additional material was uncovered in the laboratory during preparation of the dinosaur bones. All of this material is difficult to prepare because of the hardness of the matrix and the lack of distinct bedding. Some preparation with needles and power tools was attempted, but most specimens were observed directly on the fractured rock matrix surfaces.

Some cuticle fragments requiring no preparation occur on the terminal shoots, but the preservation is generally poor. Better-preserved shoot cuticles were obtained by removing pieces of carbonaceous material from the fossil surface with needles and treating them in dilute (ca. 5%) commercial bleach until the cuticles could be separated and their major features recognized. The macerated cuticles were then mounted on slides in glycerin jelly for light microscopic examination. Other cuticle specimens were mounted on aluminum stubs and sputter-coated with gold/palladium for scanning electron microscope (SEM) study with a Phillips XL20 or a Leo 1450 VPSE scanning microscope at 25.0 kV.

In situ masses of *Classopollis*-type pollen, orbicules, and tapetal membrane fragments were isolated by macerating a ca. 2 mm area of the fractured internal surface of a pollen cone in 5% HCl. The dissolved matrix was pipetted into a 15-mL test tube, washed twice with distilled H₂O (using centrifugation between treatments), and left to stand in 48% HF until the mineral fraction had dissolved. The remaining residue was centrifuged, washed repeatedly with distilled water, and transferred into a vial. Some of the concentrated organic residue was mounted in glycerin on slides for light microscopy. Additional residue was applied to aluminum stubs, dried, and sputter-coated with gold/palladium for SEM examination.

The ovulate cones were studied directly from the fractured matrix surfaces. Some bract-scale cuticles were obtained by probing into the molds with tweezers. The retrieved cuticular fragments were treated in dilute commercial bleach, and some were mounted in glycerin jelly on slides. Others were mounted on aluminum stubs for SEM study. Although these cuticles are poorly preserved and ambiguous, we consider their description and illustration essential because of the extreme rarity of frenelopsid ovulate reproductive structures of any kind.

A silicified log portion was prepared for anatomical study by cutting longitudinal, radial, and tangential standard thin sections. The preservation of the silicified wood is poor, but some regions of the trunk section revealed anatomical details. Associated fusain fragments were removed from the matrix with needles and cleaned in concentrated HF. Fresh sections were produced by splitting them with a razor blade; however, because of the brittle nature of the fusain, the only good sections obtained were radial, because the wood has a natural tendency to split along the radial face of the rays. Some of the best sections were attached to SEM stubs and sputter-coated with gold/palladium for SEM observation.

Nomenclatural Considerations

The branches from the Jones Ranch locality are here assigned to the shoot morphospecies *F. ramosissima* on the basis of gross morphological and cuticular features. In accordance with the International Code of Botanical Nomenclature provisions mandating that all fossil plant names be considered morphotaxa for nomenclatural purposes, the name *F. ramosissima* refers strictly to vegetative shoots. The term "*F. ramosissima* plant" is used here merely as a convenience for discussing the hypothetical reconstructed plant, but no formal taxonomic status is implied.

Although we suggest new interpretations of the reconstructed plant, the shoot features fall within the range of the type material, making an emended specific diagnosis unnecessary. Additional fossils that, on the basis of exclusive association and features consistent with cheirolepidiaceus affinities, we regard as probably produced by the *F. ramosissima* plant are treated in the "Description" section below but are not formally named. For example, only one kind of pollen cone with *in situ* *Classopollis* pollen occurs at the Jones Ranch locality, and it is most likely from the *F. ramosissima* plant. Although it is customary to name pollen cones associated with cheirolepidiaceus foliage as species of the form genus *Classostrobus* (Alvin et al. 1994), we refrain from doing so here because pollen cone cuticles are lacking, and only gross morphological features common to most cheirolepidiaceus pollen cones can be discerned. This is particularly problematic in terms of specific delimitation, because most of the comparative diagnostic features of *Classostrobus* are based on details of the microsporophyll head outer (i.e., abaxial) surface (Axsmith et al. 2004).

The larger cones at the Jones Ranch site are probably ovulate cones, a speculation based on their size and the persistent rhomboidal structures that we interpret as bracts. We also describe fragmentary cuticles, some of which may be cone scale remains. Nevertheless, these remains are still too poorly understood to justify assigning them to new or established ovulate cone morphotaxa.

The fusainized and silicified woods from Jones Ranch are poorly preserved, but features common to other woods attributed to the Cheirolepidiaceae are discernible on a few specimens. These features, in addition to exclusive association evidence, convincingly link this wood to the other remains at the locality as parts of a single plant species. We provide a description of this material but refrain from assigning any of it to new or established wood morphotaxa because of poor preservation, in addition to long-unresolved

problems regarding the consistent application of Mesozoic wood morphotaxon names throughout the literature.

Systematics

Order—Coniferales

Family—Cheirolepidiaceae Takhtajan

Genus—Frenelopsis Schenk

Species—Frenelopsis ramosissima (Fontaine) Watson

Material. All described and figured specimens are deposited in the paleontological collections of Southern Methodist University in Dallas, Texas. All specimen numbers bear the prefix SMUPL. Vegetative shoots examined include specimens 57, 58, 313, 318, 319, 320–324, 326, and 327. Associated fossils attributed to the same plant were also examined and include pollen cone specimens 52–55, 281, 305–309, 312, 315–317, and 329; ovulate cone specimens 56, 279, 285, 310, 311, 314, 325, 328, and 330; thin sections from silicified wood, specimen 157, and fusain fragments extracted from the matrix surrounding, specimen 285.

Locality. Jones Ranch dinosaur quarry site, Hood County, Texas.

Stratigraphy. Twin Mountains Formation.

Age. Lower Cretaceous (ca. Aptian/Albian boundary).

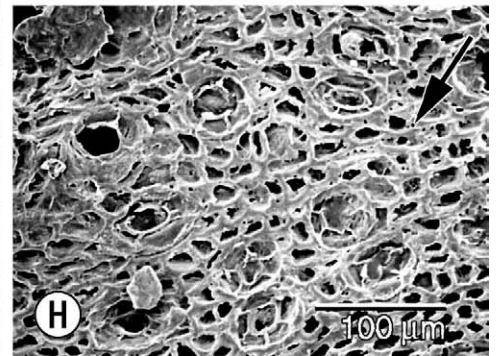
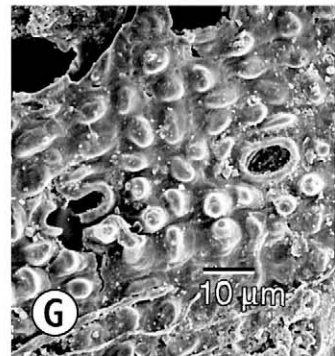
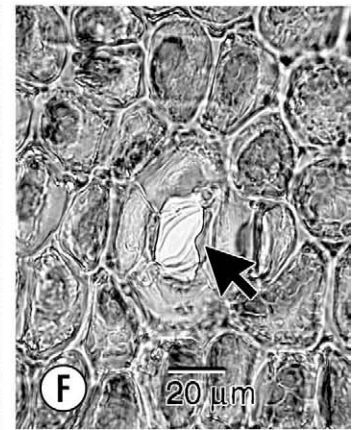
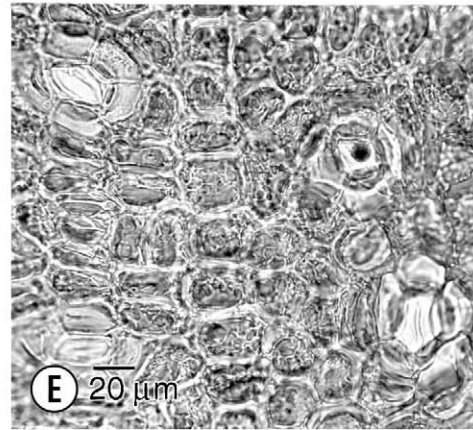
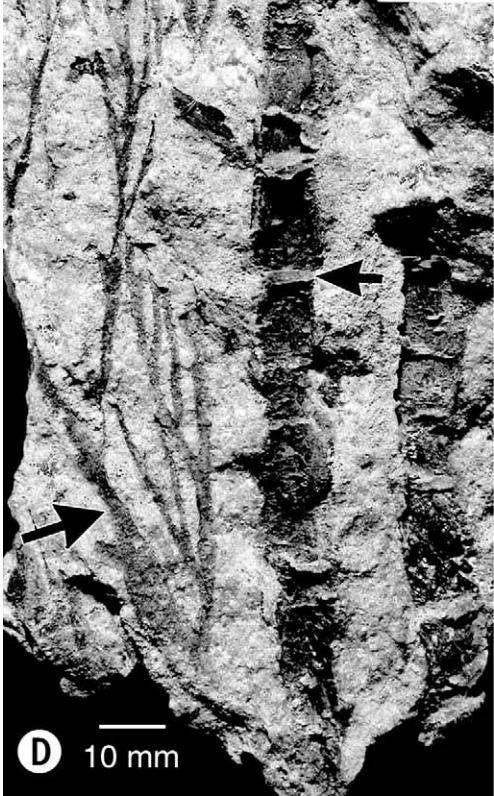
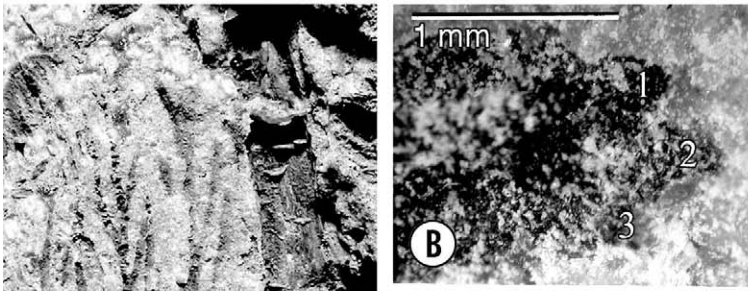
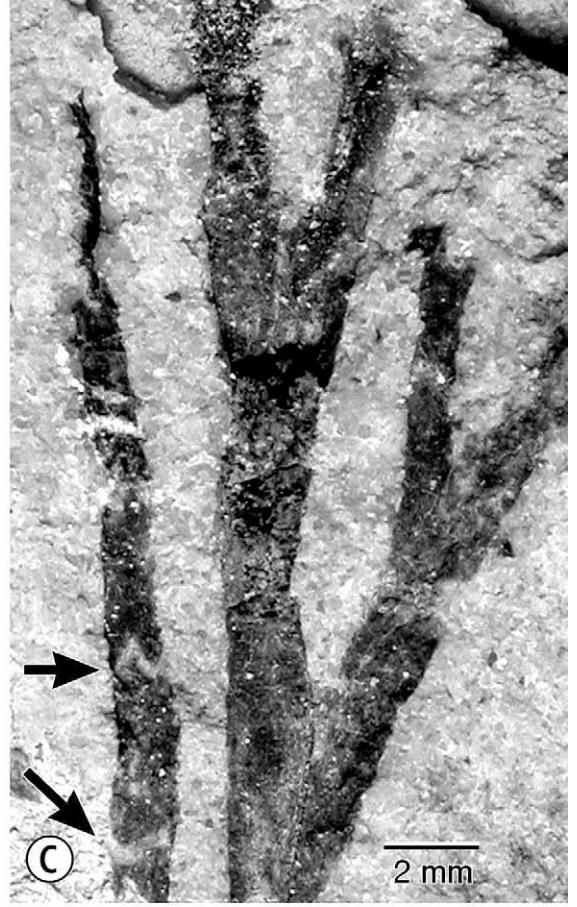
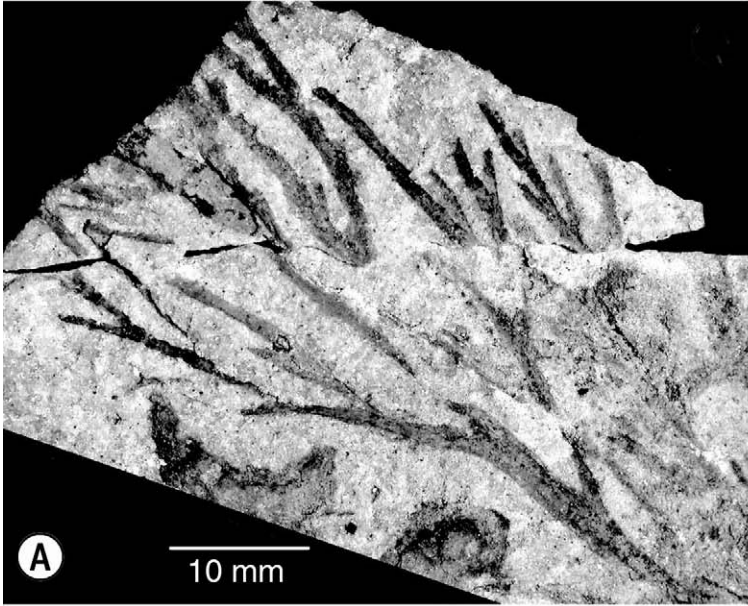
Description

Branches

Vegetative branches attributed to the morphotaxon *Frenelopsis ramosissima* are common at the Jones Ranch locality (fig. 1A–1D). The most extensive articulated system collected to date was more than 12.5 cm long and displayed four branch orders over this length. The lowest branch orders of such articulated systems average 6.0 mm in diameter. Second-order and antepenultimate branches are typically 2.5 and 1.5 mm wide, respectively. The penultimate and ultimate orders are both ca. 1.0 mm in diameter (fig. 1C). Despite the abundance and relatively close spacing of the higher-order branches on a given shoot system, at least by frenelopsid standards, the branches almost never overlap. This indicates that in life the branches were flattened out in a single plane like those of many extant cupressaceous conifers (e.g., *Chamaecyparis* and *Thuja*).

Because of poor preservation in a grainy matrix, nodes with preserved leaves are rare. However, a few specimens of young terminal shoots showing the jointed nodes with three small, whorled, triangular leaves have been found (fig. 1B, 1C). No trichomes can be seen on the leaf tips, but this is probably due to lack of preservation.

The articulated ultimate branching systems are closely associated with single branches up to 1.0 cm wide and more than 20.0 cm long, representing lower-order branches of uncertain level. Some specimens have calcite infillings at the nodes, which occur at intervals of ca. 1.5–2.0 cm. Parts of some of the larger stems (up to at least 4.0 cm in diameter) are preserved as three-dimensional casts partially infilled with calcite (fig. 1D).



Small patches of internode cuticle occur on a few penultimate and antepenultimate branches. Recovered internode cuticles are ca. 15.0 μm thick, as measured over normal epidermal cells, with the stomata arranged in well to poorly organized rows ca. 60.0 μm apart. Individual stomatal complexes average 57.0 μm in diameter and consist of a stomatal pit typically surrounded by five subsidiary cells, but complexes with four or six subsidiary cells occur occasionally. The subsidiary cells of a given complex are thickened (up to 10.5 μm wide) along the edge adjacent to the stomatal pit and collectively form a raised rim (fig. 1G). Under the light microscope, this thickening appears as a prominent dark ring surrounding the stomatal pit (fig. 1E, 1F). The rim is usually smooth, but it can sometimes be lobed or weakly papillate (fig. 1F). No papillae occur within the throat of the stomatal pit.

The ordinary epidermal cells occur in well to weakly defined rows between the stomatal rows (fig. 1E). Cells within the stomatal rows are more randomly arranged (fig. 1E, 1H). The range of maximum dimension of ordinary epidermal cells is 16.0–42.0 μm , with anticlinal wall thicknesses of ca. 5.0 μm . The surfaces of individual epidermal cells often possess a single rounded or somewhat elongated papilla, averaging 6.5 μm wide and 6.6 μm high (fig. 1G). Remnants of a well-cutinized hypodermis with small pits are sometimes visible in SEM (fig. 1H).

Associated Pollen Cones

The pollen cones are preserved in three dimensions, with little evidence of flattening (fig. 2A–2C). They are round to ovoid and up to 1.1 cm in diameter. The pollen cone axis is ca. 1.0 mm wide, with spirally arranged microsporophyll stalks up to 1.8 mm long attached along the entire length (fig. 2D). The expanded microsporophyll heads are peltate with acute apices and are up to 3.3 mm long and 4.0 mm wide at the widest point (fig. 2C, 2D). No cuticles have been found adhering to the microsporophyll heads of any specimens so far.

As a result of preservational limitations, the number and position of the pollen sacs could not be discerned, but macerations have produced *in situ* pollen, orbicules, and tapetal membrane fragments. Pollen grains are of the *Classopollis* type and occur in clumps (fig. 2F, 2G). Measurements were made from 25 pollen grains from a single cone. Individual pollen grains average 22.7 μm in diameter. The proximal triradiate thinning is ca. 1.5 μm in diameter, with laesurae extending out up to 1.5 μm from the corners (fig. 2I). Exinal threads protruding from this thinning are often visible on specimens separated from their sister grains (fig. 2I). The distal cryptopore averages 3.9 μm in diameter (fig. 2G). The equatorial region

features a prominent rimula ca. 2.7 μm wide and a weakly thickened equatorial belt up to 5.3 μm wide with five internal striations (fig. 2H). The exine is 1.6 μm thick, with outer sculpturing most similar to the “mixed” (i.e., combined rugose-verrucose) type (*sensu* Reyre 1970; text fig. 1) (fig. 2J, 2K). The internal sculpturing could not be discerned. Orbicules are common on the tapetal membrane and pollen grain surfaces (fig. 2J). They average 1.6 μm in diameter and have an outer sculpturing identical to that of the pollen grains.

Associated Ovulate Cones

The larger associated strobili interpreted here as ovulate cones are up to at least 4.0 cm long (no complete specimens are known) and 2.4 cm in diameter. They are often preserved with little flattening (fig. 3A, 3C, 3D) and split either longitudinally through the central axis (fig. 3B) or along the outer surface, revealing a layer of rhomboidal, lateral appendages interpreted here as bracts (fig. 3C, 3D). One specimen is split in such a way that both the external surface and the cone interior are visible in different areas of the cone (fig. 3C). The lateral appendages (probable bract-scale complexes) oriented perpendicular to the matrix surface are represented by molds extending into the rock. These cavities sometimes contain cuticular fragments of the decayed bract-scale complexes.

The structures interpreted as bracts are large, rhomboidal, and spirally arranged on the cone axis. The largest specimen observed is ca. 1.4 cm long and expands from an 8.5-mm-wide base to 1.75 cm wide near the midpoint. The bracts are imbricate, forming, with their thick structure (ca. 3.0 mm thick at the base thinning to 0.6 mm distally), an essentially continuous outer surface to the cones (fig. 3A, 3C, 3D). The individual bracts narrow distally to a somewhat rounded apex.

One fragment may represent at least part of an ovulate cone scale, but it must be stressed that this determination is tentative. This structure is small (ca. 2.2 mm long and 4.0 mm wide) and roughly semicircular in outline (fig. 3E). The small size relative to the subtending bracts may be a serious objection to the interpretation of this structure as a scale, but it may be immature and/or fragmentary. There is no indication of distal lobing. The cells of the scale surface are isodiametric and average 16.0 μm in diameter. Each cell surface has rounded or sometimes pointed papillae covering nearly the entire cell diameter. This arrangement collectively imparts a cobblestone-like appearance to the scale surface (fig. 3F). Near the central flap (epimatium?), the papillae grade into prominent, elongate trichomes up to 100.0 μm tall (fig. 3I).

A central flaplike structure 0.5 mm wide, which is interpreted here as a possible cheirolepidiaceus epimatium, emerges from the scale surface near the distal margin and

Fig. 1 *Frenelopsis ramosissima* branches and cuticles. Hood County, Texas. All specimen numbers begin with the prefix SMUPL. A, Articulated terminal branching system; no. 313. B, Nodal area detail with three free leaf tips (numbered); no. 319. C, Detail of terminal branches, showing nodes with triangular free leaf tips (arrows indicate two adjacent nodes); no. 324. D, Articulated terminal branching system (left arrow) and two lower-order branches (on each end of right arrow). Right arrow indicates a mineral-infilled node; no. 57. E, Light microscopy (LM) view of internode cuticle outside surface with four stomatal complexes; no. 319. F, LM detail of stomatal apparatus from internode cuticle with shallow papilla (arrow) on stomatal pit rim; no. 319. G, Scanning electron microscopy (SEM) of internode cuticle outer surface, showing raised rims surrounding stomatal openings. Also note papillae; no. 325. H, SEM of internode cuticle inner surface, showing stomatal complexes and pitted hypodermal cuticle. Arrow indicates a single pit; no. 325.

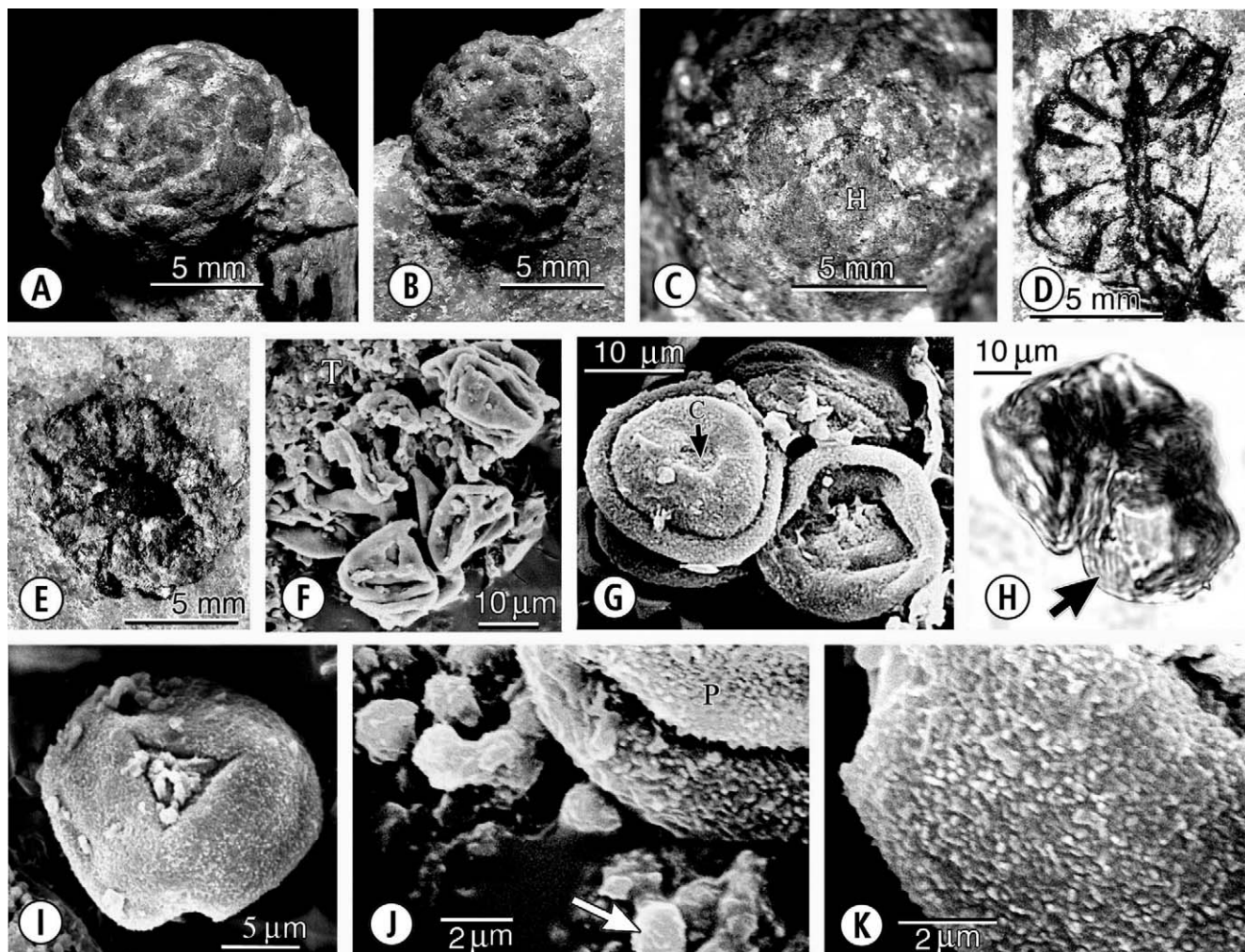


Fig. 2 Pollen cones and *in situ* *Classopollis*-type pollen associated with *Frenelopsis ramosissima*. Hood County, Texas. *A*, Three-dimensional pollen cone in surface view; no. 312. *B*, Pollen cone with microsporophyll heads broken away; no. 306. *C*, Light microscopy (LM) detail of pollen cone surface, showing imbricate microsporophyll heads (*H*); no. 312. *D*, Pollen cone split through axis longitudinally, showing peltate microsporophylls; no. 281. *E*, Pollen cone in oblique, transverse section. This cone was the source of the *in situ* pollen grains detailed in *F*–*K*; no. 305. *F*, Scanning electron microscopy (SEM) of *in situ* pollen grains, orbicules, and tapetal membrane fragments (*T* = tapetum); no. 305. *G*, SEM detail of pollen grains. Specimen on left displays prominent distal cryptopore (*C*) and rimula. *H*, Pollen tetrad viewed in LM focused on internal striations (arrow); no. 305. *I*, Pollen grain proximal-surface SEM, showing triradiate thinning and protruding exinal threads; no. 305. *J*, Pollen grain (*P*) margin SEM, showing complex outer sculpturing, rimula, and associated orbicules (arrow) attached to tapetal membrane; no. 305. *K*, SEM detail of subequatorial region of grain in *I*, showing external sculpturing; no. 305.

extends at least 2.0 mm toward the base (fig. 3*E*, 3*G*). It is open at the bottom and sides. The outer surface consists of longitudinal rows of nonpapillate, elongate cells of dimensions that are uncertain because of poor preservation. The cells of the inner surface of the flap are generally elongate (up to 50.0 μm long and 12.0 μm wide), with diagonal end walls, and often occur as lateral groupings of probable sister cells (fig. 3*G*, 3*H*).

A few other indeterminate cuticle fragments have been recovered from the bract-scale complex cavities. One of these consists of elongate cells associated with a layer of indistinct crossing cells (fig. 3*J*). Another poorly preserved fragment shows randomly arranged isodiametric cells and stomatal complexes with thickened rims somewhat similar to those of

the *F. ramosissima* internode cuticles (fig. 3*K*). No ovules or cuticles definitely attributable to ovules have been identified.

Associated Wood

Wood at Jones Ranch is represented by large silicified logs and small pieces of fusain (fig. 4). The anatomical features of both kinds are not well preserved. Nevertheless, some features could be discerned, indicating that these woods probably represent the same species. The shared spiral-fracturing pattern of the tracheid walls is particularly similar (fig. 4*F*, 4*G*).

The silicified wood occurs as log sections (fig. 4*A*) washed in by the flood event that created the Jones Ranch plant and vertebrate assemblage. The largest log specimen excavated in

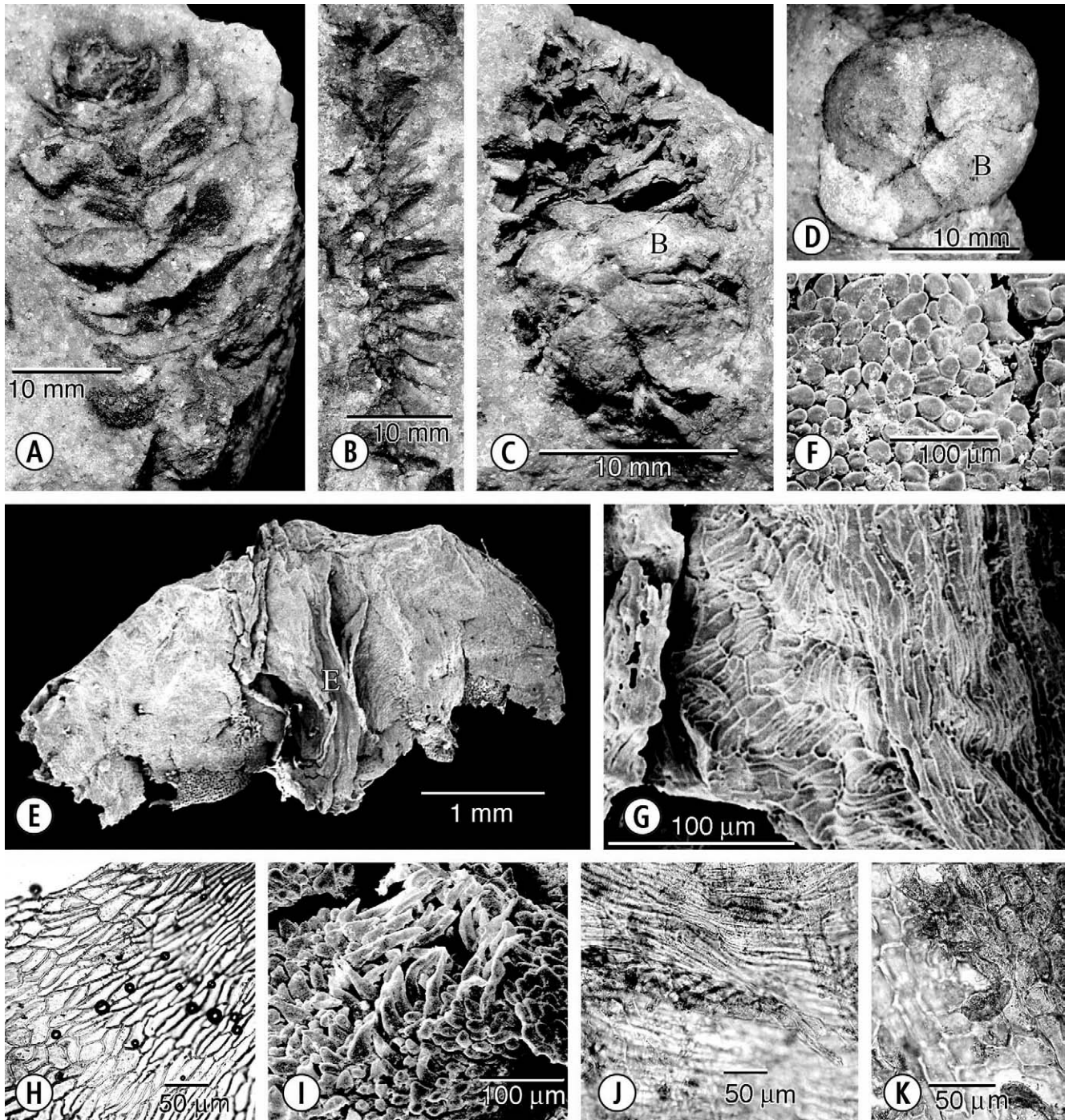


Fig. 3 Ovulate cones and cuticles associated with *Frenelopsis ramosissima*. Hood County, Texas. **A**, Large cone with spirally arranged structures interpreted as thickened bracts; no. 285. **B**, Cone in longitudinal section. Bottommost bract in plan view; no. 325. **C**, Cone preserved in surface view in bottom half, showing outer layer of rhomboidal bracts (**B**); upper portion with cavities representing the bract-scale complexes extending into the matrix; no. 56A. **D**, Cone apex in surface view with large, overlapping bracts (**B**); no. 330. **E**, Scanning electron microscopy (SEM) of cuticle fragment interpreted as a partial cone scale with epimatium (**E**). **F**, Papillate cells of lateral scale surface under SEM; no. 325. **G**, SEM detail of inner cuticle of epimatium with groups of elongate sister cells; no. 325. **H**, Light microscopy (LM) of epimatium inner surface, showing elongate cells in sister groups; no. 56. **I**, SEM of elongate trichomes adjacent to epimatium; no. 325. **J**, LM of bract-scale cuticle fragment with crossing cells of unknown origin; no. 56. **K**, LM of bract-scale cuticle with stomata; no. 56.

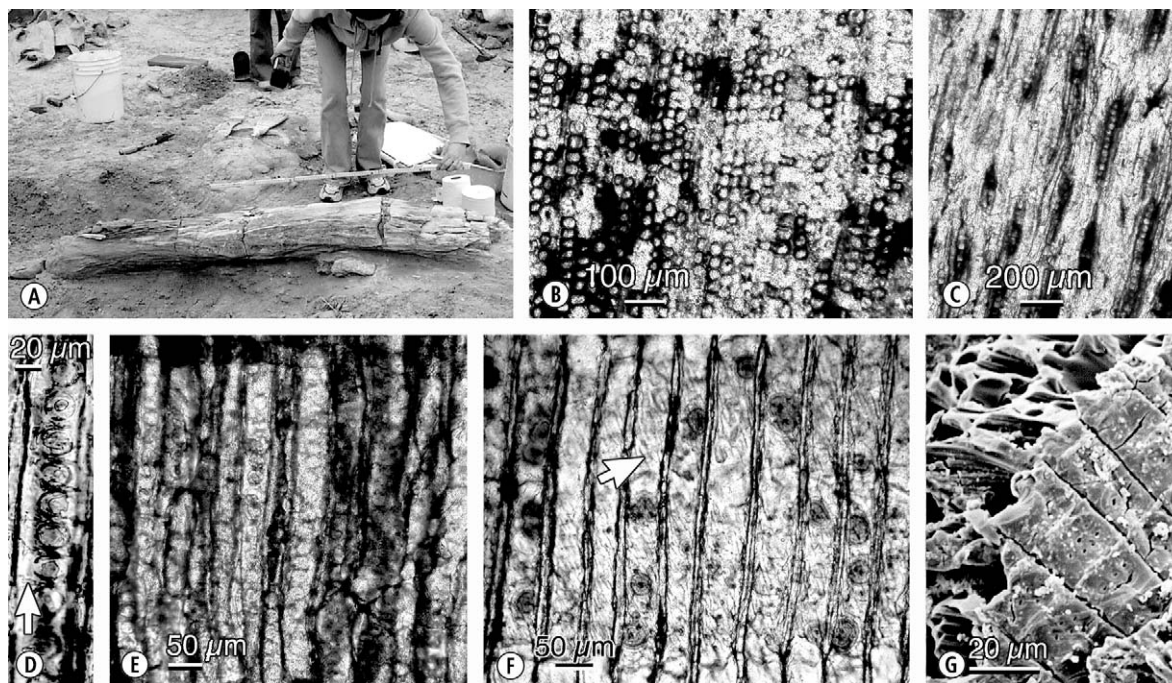


Fig. 4 Silicified (A–F) and fusainized (G) wood associated with *Frenelopsis ramosissima*. Hood County, Texas. A, Partially excavated log in the field. Measuring device is open to 1.2 m; no. 157. B, Light microscopy (LM) of transverse section, showing closely spaced tracheids; no. 157. C, LM of tangential section, showing uniseriate rays; no. 157. D, LM of tracheid with araucaroid radial pitting, with thickenings between the pit margins (arrow); no. 157. E, LM of radial section, showing region dominated by tracheids with araucaroid pitting; no. 157. F, LM of radial section, showing region dominated by abietian pitting. Arrow indicates spiral fracturing of the tracheid wall; no. 157. G, Scanning electron microscopy of oblique transverse section of fusain through tracheids (upper left) and radial section along ray; no. 285. Note spiral fracturing of the tracheid walls like that in E. Also, note crossfield pitting.

the field was 2.85 m long and 33.0 cm in diameter. One specimen bears root bases, proving that at least some of these logs represent main trunks. The anatomy is poorly preserved, as revealed by light microscopic examination of thin sections. The xylem is entirely composed of tracheids and parenchymatous rays (i.e., pinoxylic). No resin ducts were observed. The tracheids are polygonal in transverse section, with lumen diameters averaging $41.0\ \mu\text{m}$ (fig. 4B). No tangential pitting was observed. The rays are mostly uniseriate and range from one to at least 15 cells high (fig. 4C). The crossfield size and pitting could not be discerned because of poor preservation. In radial view, the tracheid pitting appears completely uniseriate, with circular bordered pits ca. $25.0\ \mu\text{m}$ in diameter with round apertures (fig. 4D–4F). On some tracheids, the pits are closely spaced in long rows (araucaroid pitting), with thickened bars between adjacent pits (fig. 4D, 4E). Other tracheids have well-spaced (abietian) pits (fig. 4F). The co-occurrence of these radial pit arrangements probably indicates the so-called mixed, or protopinaceous, structure reported for all woods attributed to the Cheirolepidiaceae to date. The absence of resin ducts is also typical of these wood types.

The fusain occurs as poorly preserved fragments (fig. 4G). The observable features are similar to those of the silicified wood, but only araucaroid pitting has been observed. This does not rule out the presence of mixed pitting, because the sample size is small, and the preservation of pits is poor because of fracturing of the tracheid walls. As in the silicified specimens, the tracheids are polygonal in cross section, but

the lumens are smaller (averaging $24.5\ \mu\text{m}$) in diameter. This is consistent with the hypothesis that the fusain is from the same plant as the silicified wood, because burning typically shrinks tissues. Some of the rays were at least 25 cells tall, with crossfields averaging $18.5\ \mu\text{m}$ wide and $14.7\ \mu\text{m}$ high. Each crossfield bears one to at least six closely spaced pits. The pit apertures are somewhat ovoid but are completely contained within a border ca. $4\ \mu\text{m}$ in diameter (fig. 4G).

Discussion

Structure and Affinities

The vegetative branch specimens described here from the Jones Ranch locality in Texas share many gross morphological features with the Potomac Group type material, including profuse branching, flattening of the ultimate branching systems, and the presence of three whorled leaf tips at the nodes (Watson 1977). The evidence for conspecificity based on these features is particularly convincing in a slab with several shoot specimens from Texas (fig. 1D) that is strikingly similar in structure and arrangement to a figure in the original species description (cf. Fontaine 1889, plate 99, fig. 2).

Most of the epidermal features of the Texas and Potomac Group specimens are similar. These include the arrangement and structure of the stomatal complexes as well as features otherwise unknown among other *Frenelopsis* species, including papillae on the ordinary epidermal cells of the

internodes, a lack of papillae within the stomatal pits, and a distinctive hypodermal cuticle with small pits. However, the cuticle thickness reported here for the Texas material (15 μm) is much less than that of the Potomac Group specimens (38 μm), as reported by Watson (1977). We suspect that this discrepancy is due, in part, to the fact that the Texas cuticles are from young, distal branches. Furthermore, Watson's (1977) measurements appear to be based on maximum thickness, which includes the thickened regions of the subsidiary cells and papillae, whereas we measured the normal epidermal cell cuticles between the papillae. The lack of long trichomes on the Texas internode cuticles is also within the known range of variation for *Frenelopsis ramosissima*. In fact, Berry (1910) and Watson (1977) note that some Potomac Group specimens lack long trichomes. On the basis of this evidence, we submit that the Texas branch specimens fall within the range of variation of the Potomac Group type material of *F. ramosissima* in all major morphological and cuticular features and represent the same species. This is significant from a biogeographical standpoint because it represents a major range extension (ca. 2100 km) of a species previously considered a Potomac Group–endemic taxon.

Although ca. 15 species of *Frenelopsis* have been described, the general lack of whole-plant reconstructions precludes a meaningful discussion of phylogenetic relationships within the genus. In fact, the monophyletic status of the genus itself is still uncertain, especially since the discovery of opposite leaves in *Pseudofrenelopsis* (Srinivisan 1995). Rather than indicating affinities with particular *Frenelopsis* species, many of the features of *F. ramosissima*, including cuticular details in support of the conspecificity of the Texas and Potomac Group material, are unique within the genus. The profuse branching of *F. ramosissima* is a rare characteristic shared with *Frenelopsis kanaviensis* (Barale and Doludenko 1985) and *Frenelopsis ugnaensis*, but there is little else to indicate a particularly close relationship between these taxa. Clearly, more information is needed on all aspects of the biology of these plants to resolve their phylogenetic relationships.

The discovery of *Classopollis*-producing pollen cones at the Jones Ranch locality is significant in providing the most compelling evidence to date that *F. ramosissima* is a member of the Cheirolepidiaceae. However, comparisons with other pollen cone species in the Cheirolepidiaceae are hampered by the lack of microsporophyll head cuticles in the Jones Ranch material. Gross morphological features, including cone size and shape, microsporophyll head size and shape, and pollen size, are often listed on comparative charts of pollen cone features; however, the consistency of these characters is questionable because of highly uneven sample sizes. When large pollen cone samples are available (e.g., *Classostrobus arkansensis*), it becomes apparent that all of these features are highly variable within a particular species (Axsmith et al. 2004). This is problematic because several taxa, including the type species *Classostrobus comptonensis*, are known from only a few specimens, which may seriously underestimate the true range of variation (Alvin et al. 1994). Other potentially useful characteristics, such as pollen sac number and position, are known for too few taxa to be useful at this time (Axsmith et al. 2004).

The *in situ* pollen features are also variable within and between species, and at least some of this variation is probably at-

tributable to differences in ontogenic stage. It is sometimes assumed that features such as the size, the number of internal striations, and the outer sculpturing details are of particular systematic significance (Reyre 1970; Gomez et al. 2002), but this has never been tested within an explicitly phylogenetic context. In fact, it has proved exceedingly difficult to distinguish modern conifer species based on such pollen features. With these caveats in mind, we regard the pollen from Jones Ranch as somewhat similar to that of cones associated with *Frenelopsis alata* in possessing a mixed outer sculpturing and five internal striations (but there may be up to nine striations in the *F. alata*-associated grains). However, the pollen associated with the Texas *F. ramosissima* is smaller overall, with smaller proximal and distal polar apertures and a thinner equatorial belt.

The associated ovulate cones are difficult to interpret because of poor preservation, but they may possess features similar to those of other cones attributed to the Cheirolepidiaceae. For example, large, persistent bracts are known in all members of the family. The bract structure and shape is particularly similar to that of *Alvinia bohemica*, which is an ovulate cone associated with *F. alata* branches in the Cenomanian of the Czech Republic (Kvaček 2000). The probable cone scale fragment is also somewhat similar to the scales of *A. bohemica*, but it is much smaller, and there is no indication of distal lobes or a distal, stigma-like pollen reception area. The region of long trichomes lateral to the flap (epimatium?) in the Texas cone scales is somewhat like the surface of the “protostigmatic” area of *Alvinia*, but no pollen has been found with the Texas specimen. The inner cuticle of the structure that we interpret as an epimatium shows elongate groups of lateral sister cells like those of all cheirolepidiaceous epimatia described to date; these cells are particularly like those reported in *A. bohemica* (Kvaček 2000).

The only other possibly unlobed cheirolepidiaceous cone scales described to date are associated with *Frenelopsis oligostomata* shoots from the Upper Cretaceous of France. However, comparisons are hampered by the poor preservation of this material (Pons and Broutin 1978). Better material of the ovulate cones from Jones Ranch will be needed to verify the interpretations presented here.

The presence of probable mixed pitting on the tracheid radial walls of the silicified wood is consistent with cheirolepidiaceous affinities. Also, the crossfield pitting visible on the fusain specimens is of the general “cupressoid” type, which is also common in the Cheirolepidiaceae. The lack of resin canals is another typical feature of cheirolepidiaceous woods. Although these features provide support for the conspecificity and cheirolepidiaceous affinities of the Jones Ranch plant fossils, the wood is too poorly preserved for a detailed comparison with the various “*Protopodocarpoxylo*” and “*Protocupressinoxylon*” wood morphotaxa attributed to the family. The most important aspect of the wood for this investigation, however, is the information it provides regarding the probable growth habit of the *F. ramosissima* plant.

Paleoecology

It is often emphasized that members of the Cheirolepidiaceae, including *F. ramosissima*, exhibited growth habits otherwise unknown among conifers. For example, Fontaine (1889) proposed that *F. ramosissima* was a large shrub or tree

with succulent distal branches on the basis of his observation that the internal strip of carbonaceous material representing the woody tissue of the shoots was much narrower than the enclosing stem impressions and thick epidermal cuticles. This arrangement may show the presence of a wide zone of parenchymatous tissue between the wood and the epidermis that did not survive fossilization. Furthermore, woody tissue of any kind is apparently absent from many of the ultimate shoots.

Watson (1977) explicitly compared *F. ramosissima* with the halophytic, herbaceous angiosperm *Salicornia*. She later offered a drawn reconstruction depicting *F. ramosissima* as a small, stem-succulent, xerophytic shrub (Watson 1988, fig. 9.14). The assertion that this plant was small with little woody tissue throughout is based on the presence of stems in the type collection up to 2.0 cm wide that retained a narrow woody core and an epidermis with evidence of cell divisions to accommodate stem expansion. Fontaine (1889) reported observing even larger stems (up to 5.0 cm wide) with narrow woody cores in the field.

The logs at the Jones Ranch locality show that the *F. ramosissima* plant was not a small shrub but actually a large tree with abundant wood in the main trunk and possibly the lowest branch orders. An estimate of the plant height based on stem diameter was calculated using Niklas's (1994) "woody species" allometric equation [$\log_{10} H = 1.59 + 0.39(\log_{10} D) - 0.18(\log_{10} D)^2$], where H = stem height and D = stem diameter. Substituting the largest diameter measured from a silicified log in the field at Jones Ranch for D (0.34 m) indicates that the *F. ramosissima* plant may have achieved heights of at least 23.4 m. It appears likely, therefore, that in larger axes the zone of secondary xylem eventually increased in diameter relative to the cortex, resulting in a typical pinoxylic conifer stem. Nevertheless, the evidence for succulence in the more distal shoots remains convincing. Such a combination of lower-order branches with abundant pinoxylic woody tissue and distal shoots with weak wood development possibly indicating succulence is, to our knowledge, unknown in other modern or fossil seed plants, except for the cheirolepidiacean *Pseudofrenelopsis parceramosa* described by Alvin (1983).

Unlike many other frenelopsid cheirolepidiaceans, which tend to occur in monospecific or low-diversity assemblages indicative of arid climates and/or saline conditions (e.g., *Pseudofrenelopsis varians*), the *F. ramosissima* specimens from the Potomac Group sites occur within diverse assemblages indicative of mesic environments. In fact, the Fredericksburg and Puddledock sites are among the most diverse of the entire Potomac Group and include abundant nonxeromorphic angiosperms, ferns, and bryophytes (Upchurch and Doyle 1981; Crane et al. 1994). The well-articulated condition of most of the fossils, including large branching systems

of *F. ramosissima* at the Fredericksburg site, indicates that the plants were not simply transported from diverse localities and deposited together. Under this interpretation, the morphological features usually considered evidence of adaptation to saline and/or xeric environments or as nonadaptive phylogenetic holdover features from xeric ancestors (Berry 1910), may have been adaptations to growth on localized rock outcrops or well-drained sandy soils within otherwise mesic settings (Upchurch and Doyle 1981).

The paleoecological setting indicated by the new Jones Ranch, Texas, occurrence differs substantially from that of the Potomac Group assemblages. For example, the Texas assemblage appears to represent a monospecific stand of *F. ramosissima* plants, as opposed to the diverse assemblages occurring at the Potomac Group sites. Furthermore, sedimentological features at Jones Ranch, such as slack-water organic accumulation within channels, clay drapes, mud rip-up clasts, and carbonate nodules, indicate a semiarid climate (Winkler et al. 2000). This climatic interpretation, along with the fact that the coastline of the Texas platform sea was just a few kilometers from the Jones Ranch site during the time of deposition, indicates that *F. ramosissima* could closely approximate one of the classic paleoecological interpretations of the frenelopsids as arid coastal forest-inhabiting xerophytes (Vakhrameev 1970). However, there is no evidence that *F. ramosissima* was a halophyte from the Jones Ranch sedimentology.

Gomez et al. (2002) asserted that the frenelopsids as a group were adapted to a wider range of ecological situations than previously thought and therefore should be considered on an individual species basis. On the basis of the divergent paleoecological settings of the Texas and Potomac Group *F. ramosissima* sites, it may be that some individual species also exhibited great ecological amplitude. Clearly, more research is needed to resolve the issues surrounding the contradictory interpretations of *F. ramosissima* paleoecology.

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