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Upchurch, Garland R., Jr. and Greg H. Mack
1998, pp. 209-222. <https://doi.org/10.56577/FFC-49.209>

in:
Las Cruces Country II, Mack, G. H.; Austin, G. S.; Barker, J. M.; [eds.], New Mexico Geological Society 49th Annual Fall Field Conference Guidebook, 325 p. <https://doi.org/10.56577/FFC-49>

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LATEST CRETACEOUS LEAF MEGAFLORES FROM THE JOSE CREEK MEMBER, McRAE FORMATION OF NEW MEXICO

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Abstract—The Jose Creek Member of the McRae Formation contains an abundant megaflores of leaf impressions and silicified wood. The megaflores as currently known consists of approximately 40 to 50 species of fern, conifer, cycad, and flowering plant leaves and an unknown number of species of conifer, dicot, and monocot (probably palm) wood. This paper illustrates and informally describes important leaf types belonging to the major plant groups and compares them with leaves from more northerly sites in the Rocky Mountain region. Vegetation of the Jose Creek Member consisted of subtropical to paratropical forest or woodland that grew under low seasonality of temperature and precipitation. This inference is consistent with paleosol data for the Jose Creek Member and paleobotanical analysis of more northerly leaf assemblages. Conifers and cycads have high relative abundance and diversity in the Jose Creek megaflores relative to more northerly assemblages. This may reflect the prevalence of well-drained soils in the Jose Creek Member and favorable preservational environments provided by numerous volcanic ashes.

INTRODUCTION

In New Mexico, plant megafossils of definite latest Cretaceous (Maastrichtian) age have been reported from the Raton and Cutter Sag-Love Ranch Basins (Knowlton, 1917; Lozinsky et al., 1984). Latest Cretaceous leaf floras are best known for the Vermejo and Raton Formations of the Raton basin (Knowlton, 1917), where intensive study of leaf megafossils and dispersed leaf cuticles across the Cretaceous-Tertiary (K-T) boundary indicate rapid extinction at the end of the Cretaceous (Wolfe and Upchurch, 1987a) and important differences in biogeography and ecology between the southern and northern Rocky Mountain regions (Upchurch, 1995). Relatively little is known about coeval leaf megaflores from other basins in New Mexico, despite their relevance to proposed patterns of biogeography and plant extinction across the K-T boundary (e.g., Tschudy and Tschudy, 1986).

This report illustrates and informally describes some latest Cretaceous plant megafossils from the Jose Creek Member of the McRae Formation. These remains represent the most southerly leaf assemblage of latest Cretaceous age currently known from North America and show important differences from more northerly assemblages in terms of floral composition and patterns of relative abundance.

HISTORY OF STUDY

Lozinsky et al. (1984) reported a small assemblage of leaf megafossils from the Jose Creek Member of the McRae Formation as part of a report on dinosaur remains from the overlying Hall Lake Member. These specimens were identified by Coleman Robison and listed in a table but were not illustrated. In 1991, 1992, and 1993, major new collections were made from the Jose Creek Member of the McRae Formation by G. Upchurch, G. Mack, and student co-workers. These localities were discovered by G. Mack during geologic mapping (Mack and Seager, in press) and by G. Upchurch and co-workers during exploration for new localities.

The plant-bearing localities occur east of Elephant Butte Reservoir in the Engle and Elephant Butte Quadrangles on property belonging to the Armendaris Ranch. Most localities are placed within measured sections and can be assigned to an individual lithostratigraphic unit (Mack and Seager, in press). Over 20 leaf

megafossil localities are currently known from the Jose Creek Member along with a comparable number of wood localities, a number that will undoubtedly increase with further exploration.

GEOLOGIC SETTING

The McRae Formation of latest Cretaceous to Paleocene(?) age documents the early depositional history of a Laramide intraforeland basin (Seager et al., 1997). The McRae Formation consists of a lower Jose Creek Member, which is characterized by yellow to olive-brown conglomerates, sandstones, mudstones, and several thin ashfall beds, and an upper Hall Lake Member, which is characterized by purple conglomerates, sandstones, and mudstones with pedogenic carbonate (Buck and Mack, 1995; Seager et al., 1997). The McRae Formation is mainly fluvial in origin and consists of a basal conglomerate, channel sandstones with lateral accretion sets, overbank mudstones, and small tabular to lenticular crevasse-splay sandstones (Seager et al., 1997). The Jose Creek Member has argillic paleosols indicative of subhumid to humid climate, while the overlying Hall Lake Member has calcic paleosols indicative of a change to semiarid climate during the latest Cretaceous and Paleocene(?) (Buck and Mack, 1995).

The over 20 known leaf megafossil localities span the entire thickness of the Jose Creek Member. Facies that preserve leaves include channel sandstone, overbank sandstone, overbank mudstone, and recrystallized volcanic ash. The volcanic ashes preserve leaf assemblages that are tentatively interpreted as fossil leaf litter, based on their occurrence immediately above mudstones and siltstones with pedogenic features. The recrystallized ashes, which occur in the middle and upper parts of the Jose Creek Member, contain the most abundant and best-preserved leaves, many of which are illustrated in this paper. Fossil woods also occur in the middle to upper Jose Creek Member, with over 20 in situ fossil tree stumps preserved in different paleosol horizons.

We tentatively assign a late (but not latest) Maastrichtian age to the Jose Creek Member based on three lines of evidence. First, most conifer species from the Jose Creek Member occur in the Vermejo Formation of the Raton basin, a unit dated as late Maastrichtian, and those not known from the Vermejo Formation occur in the coeval Lance and Medicine Bow Formations. Second, dinosaur fossils described from the lower part of the overlying Hall

Lake Member indicate a Lancian, and possibly late Lancian, age (Lozinsky et al., 1984; Lucas et al., this guidebook), which indicates that the Jose Creek Member is older than latest Maastrichtian. Third, the contact between the uppermost Jose Creek Member and overlying Hall Lake Member is conformable, indicating little or no missing time, while the contact between the lowermost Jose Creek Member and the uppermost Crevasse Canyon Formation (Campanian?) is clearly unconformable, indicating a hiatus. A somewhat older age than late Maastrichtian cannot yet be ruled out, because the stratigraphic ranges of the conifer species are not yet well documented for the earlier Maastrichtian and late Campanian.

METHODS OF FLORAL ANALYSIS

The systematics of Late Cretaceous leaf megafossils is currently in a state of flux, especially for angiosperms (i.e., flowering plants). This is because earlier workers extensively misidentified leaves at the generic, familial, and ordinal levels because they did not understand the systematic distribution of important characters in living plants (see discussions in Wolfe, 1973; Dilcher, 1974; Doyle and Hickey, 1976; Upchurch and Dilcher, 1990). Thus, the generic and familial affinities of many leaf species reported by Lozinsky et al. (1984) are in doubt. Leaves in this study were analyzed using modern methods of foliar architecture combined with extensive surveys of living plants and comparison of Jose Creek species to similar species known with cuticular anatomy and/or associated reproductive structures. Familial, ordinal, and higher-level affinities are emphasized to provide a phylogenetic overview of the flora.

Many previously described species still have incorrect names because of the extensive misidentification of fossil angiosperm leaves at generic and higher taxonomic levels. This creates a problem when referring to a Jose Creek species or when comparing a Jose Creek species to another previously described species. Two approaches have been taken to avoid implying unsubstantiated relationships between fossil species and modern genera and families. First, Jose Creek angiosperm leaves are not given formal names, but instead are discussed as unnamed entities. Formal names will be proposed in future papers. Second, fossil angiosperm leaves from other formations, when used for comparison, are assigned to extinct genera whenever possible, even if more than one biological genus is represented by the extinct genus. When the only available generic name is that of an extant angiosperm, the generic name is placed in quotes.

Important Jose Creek leaf taxa are illustrated photographically and described briefly. This is done to aid geologists during fieldwork and to allow paleobotanists to evaluate the flora prior to publication of a full systematic treatment. Descriptions and illustrations of Jose Creek megafossils are organized in order of phylogenetic advancement, beginning with ferns and ending with flowering plants. Family-level classification of ferns follows Tryon and Tryon (1982). For angiosperms, ongoing molecular systematic studies indicate that the commonly used subclass classification of Cronquist (1981) is in need of revision. To provide some structure at higher taxonomic levels we use the three major groupings of flowering plants proposed by Donoghue and Doyle (1989) and Doyle and Donoghue (1993). These are: (1) paleoherbs plus monocots, (2) woody magnoliids, and (3) eudicots (eu = true). Monocots are treated separately from paleoherbs in this paper. The group known as dicots consists of the paleoherbs, woody magnoliids, and eudicots.

Growth habit (i.e., life form) is reconstructed for the major groups of plants described in this paper. Growth habit is reconstructed on the basis of growth habit in living relatives, leaf physiognomy, e.g., leaf thickness, which is a proxy for evergreen vs.

deciduous foliage (Wolfe and Upchurch, 1987b), and the size of fossil stumps. Inferred growth habit and a preliminary analysis of ring structure in fossil woods are used to reconstruct the seasonality of growth response in the parent vegetation.

Climatic inferences are based on inferred life forms in the fossil plants and the geographic distribution of their living counterparts, which can be predicted on the basis of 8 macroclimatic variables (Box, 1981). The range of possible climates in the Jose Creek Member is defined by the range of overlap in the climatic tolerances of extant life forms inferred to have been present in the fossil assemblage. This method provides estimates of minimum cold-month mean temperature, maximum mean annual range of temperature, and minimum and maximum annual precipitation. Climatic estimates obtained by this method are less precise than those obtained by foliar physiognomic methods such as percent entire-margined species (Wolfe and Upchurch, 1987b) and CLAMP (Wolfe, 1993); however, we think that they are more robust to small sample size. Foliar physiognomic methods such as CLAMP require at least 20–30 species of dicot leaves to obtain a reliable climatic estimate.

PRESERVATION AND OCCURRENCE

Jose Creek leaves consist mostly of impressions, which preserve venation and shape but no tissue structure. Remnant carbon is present on some leaves but does not appear to preserve cuticle. Jose Creek woods consist of abundant silicified twigs, logs, and in situ stumps that preserve much of their tissue structure, sometimes exquisitely. Woods can preserve remnant carbon of the cell wall or show complete replacement of the cell wall by silica.

Plant megafossils occur in channel and overbank facies. Leaf impressions occur in channel sandstones, crevasse-splay sandstones, and fine-grained siliceous beds that represent recrystallized volcanic ashes. The best preserved specimens are found in the volcanic ashes, which commonly preserve unfragmented leaves that show little or no evidence of extensive transport. Volcanic ash beds overlie paleosol horizons, which are characterized by peds, blocky fracture, and horizon development (Buck and Mack, 1995). Some paleosol horizons preserve silicified tree stumps in growth position, commonly at different stratigraphic horizons than leaves. Most silicified wood occurs as float, but at least 20 stumps are found in growth position and are clearly rooted in a paleosol horizon.

DESCRIPTION OF PLANT REMAINS

The currently known Jose Creek megafloora comprises at least 40 leaf species and a yet-to-be-determined number of wood species. This contrasts with the 14 leaf species listed by Lozinsky et al. (1984), which were based on small collections. Total species richness for leaves is undoubtedly much higher than 40 species because many leaf species are rare, and new species are discovered with each collecting season. The leaf megafloora to date consists of ferns (7 species), conifers (7 species), cycads (2 species), monocots (5 species), and woody magnoliids plus eudicots (20–30 species). The wood flora consists of an undetermined number of conifers, dicots, and monocots of shrub to tree habit (probably palms).

Ferns (Division Pterophyta)

Ferns occur as leaf impressions in recrystallized tuffs and in crevasse-splay sandstones that overly paleosols. All known fern leaves are without reproductive structures, but many can be closely compared to the leaves of one or more extant families. All Jose Creek ferns represent leptosporangiate ferns, the dominant ferns of

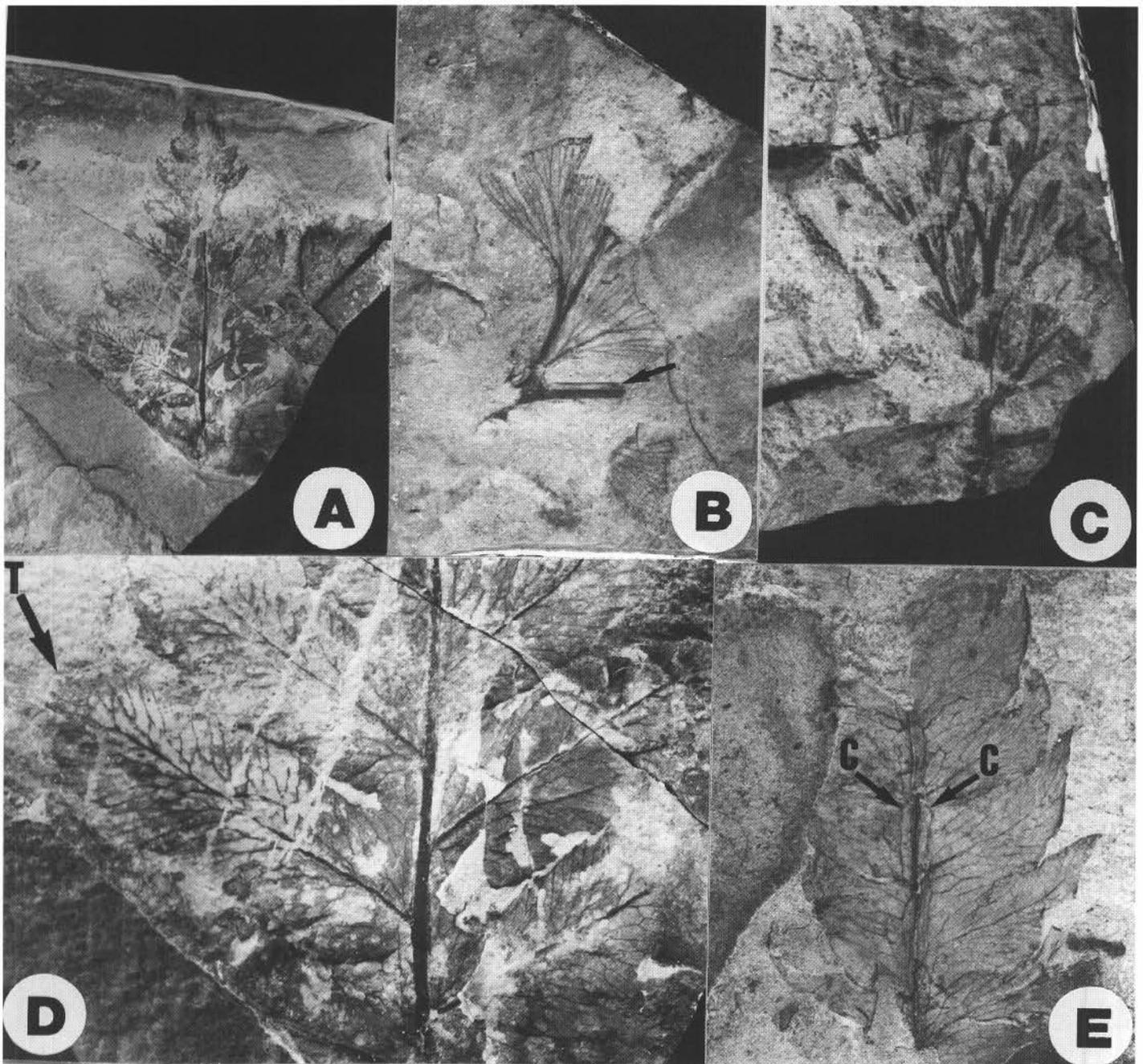


FIGURE 1. Ferns from the Jose Creek Member, McRae Formation. **A**, *Woodwardia*, apical part of leaf, x1. **B**, Leaf fragment with winged rachis (arrow) and pinnules with dichotomous (forking) venation, x3. **C**, Fragment of a flabellate leaf showing very narrow pinnules with 1–2 veins each. This pattern is very characteristic of leaves of certain Schizaeaceae, x3. **D**, *Woodwardia*, same specimen as in 1A, showing teeth (T) and details of venation, x3. **E**, *Woodwardia*, fragment of another leaf showing costal areoles (C) along midvein of pinna and reticulate venation with no freely ending veinlets, x2.

the Mesozoic and Cenozoic (Niklas et al., 1985).

Woodwardia (or chain fern), an extant genus of Blechnaceae known from Campanian and younger rocks of the Western Interior (Brown, 1962; Hickey, 1977; Crabtree, 1987), occurs at some localities (Figs. 1A, 1D, 1E). *Woodwardia* is distinguished from other fern leaves by the presence of a toothed margin, sickle-shaped pinnules, veins that anastomose near the midvein to form a chain of costal areoles, veins outside the costal areoles that run to the margin, and the absence of freely ending veinlets (cf. Tryon and Tryon, 1982). Today *Woodwardia* ranges from Central America to southern Canada but is absent from the Western Interior (Tryon and Tryon, 1982).

Generic and familial affinities of other Jose Creek fern leaves are more problematic because they either do not exactly match a

living genus or have features that occur in two or more families. One distinctive species in this category (Fig. 1C) is characterized by highly divided leaves with a weak rachis and narrow flabellate pinnules that have only 1–2 veins each. These features are most suggestive of Schizaeaceae, (e.g., see illustrations of *Schizaea* in Tryon and Tryon, 1982, and Gifford and Foster, 1989), but occur in species from other families such as Dennstaedtiaceae. A second distinctive species consists of highly fragmented leaves with a winged rachis, wedge-shaped pinnules, and a midvein that divides repeatedly to form an open network of dichotomizing veins (Fig. 1B). These features occur in some species of *Anemia* (Schizaeaceae) and *Lindsaea* (Dennstaedtiaceae) (cf. Tryon and Tryon, 1982; Duncan and Isaac, 1986).

Jose Creek ferns probably represent herbaceous plants that

formed part of the ground cover. This inference is based on their possible modern relationships, the small size of preserved leaves, and evidence for thin-leaf texture in some species. As has been noted by various authors (e.g., Vakhrameev, 1991), the leaves of herbs are generally not shed but instead decay on the parent plant. The preservation of herbaceous fern leaves in association with paleosols, therefore, implies that ferns represent locally derived elements of vegetation.

Conifers (Division Coniferophyta)

Conifers occur abundantly throughout the Jose Creek Member. Conifer woods occur in many paleosol horizons as in situ stumps, in some sandstones as allochthonous logs, and most commonly as float. Conifer leaves occur at every leaf locality and can form up to half of the collected specimens. At least seven distinct species are present. This number is high relative to other latest Cretaceous leaf assemblages from North America (cf. Upchurch and Wolfe, 1993) and is equaled only by the megafloora of the Vermejo Formation (Knowlton, 1917) and the Big Cedar Ridge assemblage of the Meeteetse Formation (Wing et al., 1993). Five species of Jose Creek conifer leaves are reported from the Vermejo Formation of northern New Mexico and Southern Colorado (Knowlton, 1917); the remaining two occur in other assemblages of late Maastrichtian age.

Jose Creek conifer leaves represent an admixture of species with "modern" structural features and species with archaic structural features of Mesozoic aspect. Three extant conifer families are represented by Jose Creek megafossils. Taxodiaceae (bald cypress family) is the most abundant extant family in ash-bed assemblages. The most common species is "*Sequoia*" *obovata* (Fig. 2B, Sq), a taxon whose position within Taxodiaceae is not well understood. *S. obovata* typically occurs as isolated branchlets or branched shoots showing only a single season's growth, in contrast to Tertiary remains of *Sequoia*. Two additional species, *Geinitzia reichenbachii* (Fig. 2A) and *G. formosa*, have leaves that resemble those of Taxodiaceae such as *Cryptomeria*, but they cannot be assigned to the family because their leaves also resemble those of Araucariaceae such as *Araucaria*, section Eutacta. Araucariaceae, a family widely reported from the Late Cretaceous pollen record, are represented by shoots with elongate leaves assignable to *Araucarites longifolius* (Figs. 2C, 2D) and by isolated seed-cone scales (not illustrated). Pinaceae are represented by large isolated needles similar to those of extant *Pinus* and the extinct pinaceous genera *Prepinus* and *Aachenia* (Fig. 2B, P). Today, Taxodiaceae and Pinaceae occur in North America, while Araucariaceae are restricted to the Southern Hemisphere and Southeast Asia (e.g., Maberly, 1988).

Conifer species with extinct morphologies give the Jose Creek flora an archaic look relative to Paleocene assemblages. One conspicuous taxon in this category is *Brachyphyllum*, (Figs. 3A, 3B), a taxon characterized by shoots with pseudoplanate branching and thick, spirally arranged, scale-shaped leaves. *Brachyphyllum* leaves characterize many species of the extinct family Cheirolepidiaceae but also characterize some Mesozoic species of Araucariaceae (e.g., Harris, 1979; Watson, 1988; Raubeson and Gensel, 1991). A second conspicuous taxon with extinct morphology is *Androvettia* (Fig. 3C). *Androvettia* is characterized by flattened photosynthetic stems with planate branching and minute, oppositely arranged scale leaves that occur on both the margins of the photosynthetic stems and on the upper and lower stem surfaces (Hollick and Jeffrey, 1909; Berry, 1910; Hueber and Watson, 1988; Raubeson and Gensel, 1991). Cuticular anatomy indicates that *Androvettia* probably represents the extinct family Cheirolepidiaceae, which produced highly distinctive pollen assigned by palynologists to the genus *Classopollis* (alias *Corollina*) (Watson, 1988 and references therein). Additional

Jose Creek specimens have flattened photosynthetic stems like *Androvettia* but differ in having narrower, more elliptic stems and a strong tendency to produce alternate branches (Figs. 3D, 3E). Poorly preserved specimens from the Vermejo Formation described as *Widdringtonia? complanata* by Knowlton (1917, pl. 32, figs. 4, 5) may represent this species.

Physiognomically, Jose Creek conifers represent highly branched trees of medium to large size. The tree inference is based on the predominance of the tree habit in living conifers and the occurrence of fossil conifer stumps that measure as much as 1.5 m in diameter above the roots (see below). Most conifers appear to represent evergreen trees. This inference is based on: (1) thick leaf texture in many taxa, such as *Brachyphyllum*, *Geinitzia*, and *Araucarites*, (2) the presence of photosynthetic stems (*Androvettia*), which usually persist on the parent plant for years, and (3) evergreen tree habit in extant genera that are closely related to Jose Creek conifers. The one possibly deciduous species of Jose Creek conifer is "*Sequoia*" *obovata*, which often occurs as isolated shoots with attached leaves that represent a single season's growth. This invites comparison with deciduous extant genera of Taxodiaceae such as *Taxodium* (bald cypress) and *Glyptostrobus*, which occur in climates with mild winters but have leaves that are shed on deciduous lateral shoots (e.g., Krüssman, 1960).

Conifer woods

Conifer woods are less understood taxonomically but provide important information on growth patterns and climate. Conifer stumps can measure up to 1.5 m in diameter above the buttress roots, which indicates the tree habit. Growth rings in all Jose Creek conifer woods are indistinct, and most cells within a growth ring consist of large-diameter tracheids that represent early wood. Early wood is produced during the favorable part of the growing season (e.g., Creber, 1977). Some fossil wood specimens display discontinuous growth rings, which disappear when followed laterally or vertically. Today indistinct and discontinuous growth rings characterize evergreen conifers of tropical to subtropical climates, where tree growth and ring structure are controlled by fluctuations in precipitation and internal hormonal levels, rather than temperature (e.g., Ash and Creber, 1993 and references therein). Strongly developed annual rings characterize evergreen and deciduous conifers of temperate and cooler climates, where growth is controlled most strongly by the annual cycle of temperature (e.g., Creber, 1977).

Cycads (Division Cycadophyta)

Cycads occur at many plant localities in the Jose Creek Member. Variation in the size of leaflets and the shape of leaflet bases indicates that at least two species are present. The common occurrence of cycads in the Jose Creek megafloora contrasts with the typical condition for Late Cretaceous megaflooras from the southern Western Interior and Atlantic and Gulf coastal plains, where few or no cycad specimens and a maximum of one cycad species are present (Upchurch and Wolfe, 1993). Cycads occur in channel sandstones and recrystallized volcanic ashes, where they typically preserve as detached leaflets of compound leaves and as isolated scale leaves.

At least three whole leaves with attached leaflets are known from recrystallized volcanic ashes (e.g., Figs. 4A, 4C). These leaves and similar detached leaflets are most closely related to extant *Ceratozamia*, *Microcycas*, and *Zamia*. This relationship is based on the occurrence in the fossils of a distinct abscission layer on the leaflets and the absence of a decurrent wing of laminar tissue on the rachis. This evolutionary advancement unites extant *Ceratozamia*, *Microcycas*, and *Zamia* into a monophyletic group (Crane, 1988; Stevenson, 1990). Similar leaflets from other formations have been

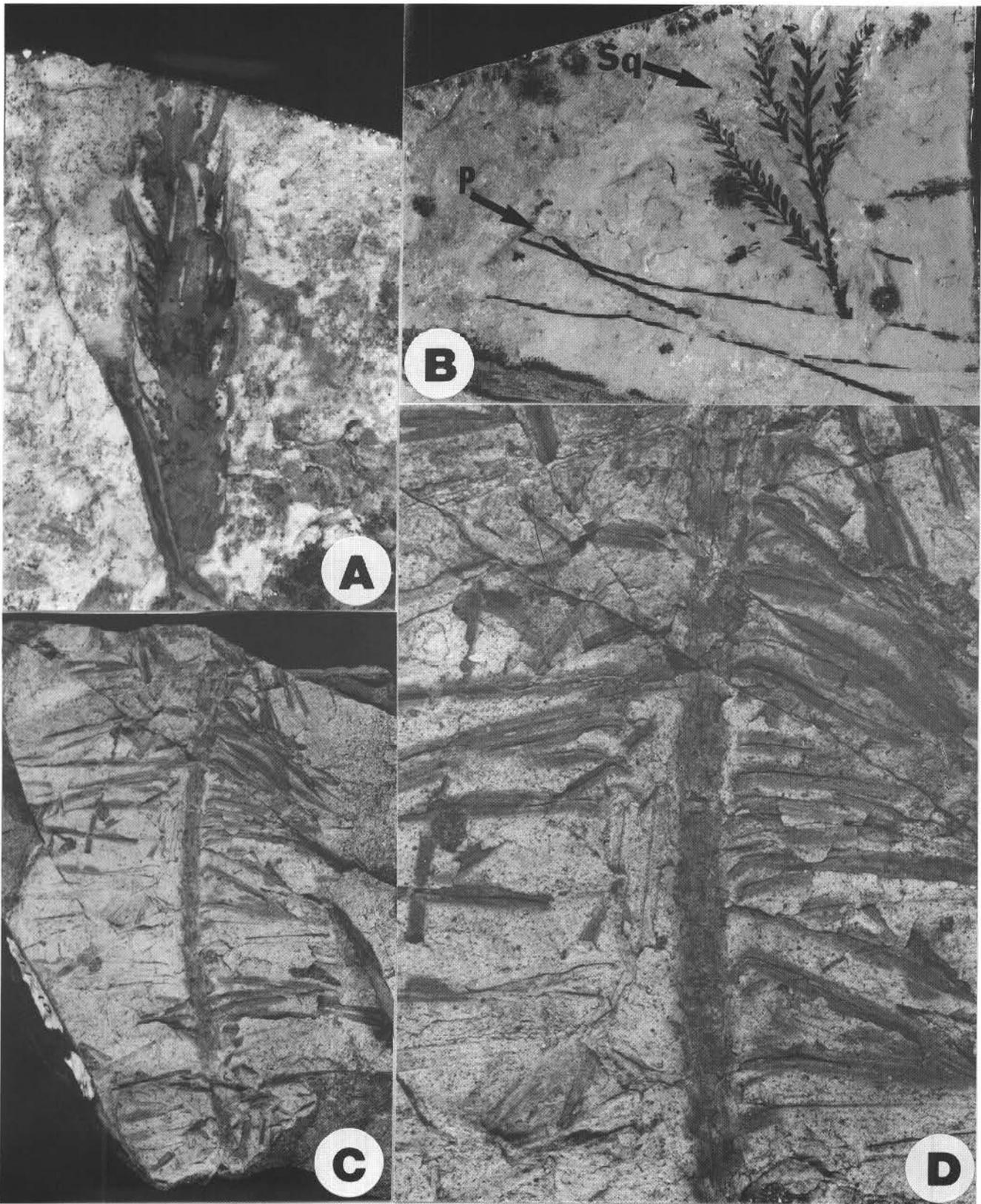


FIGURE 2. Conifers of extant families from the Jose Creek Member, McRae Formation. **A**, *Geinitzia reichenbachii*, shoot fragment resembling Taxodiaceae or Araucariaceae, x2. **B**, Leaves of Pinaceae (P) and a shoot of "*Sequoia*" *obovata* (Sq), x1. **C**, *Araucarites longifolius*, shoot of probable Araucariaceae, x1. **D**, *Araucarites longifolius*, same specimen as 2C showing attachment of leaves and the presence of a distinct midvein on each leaf, x3.

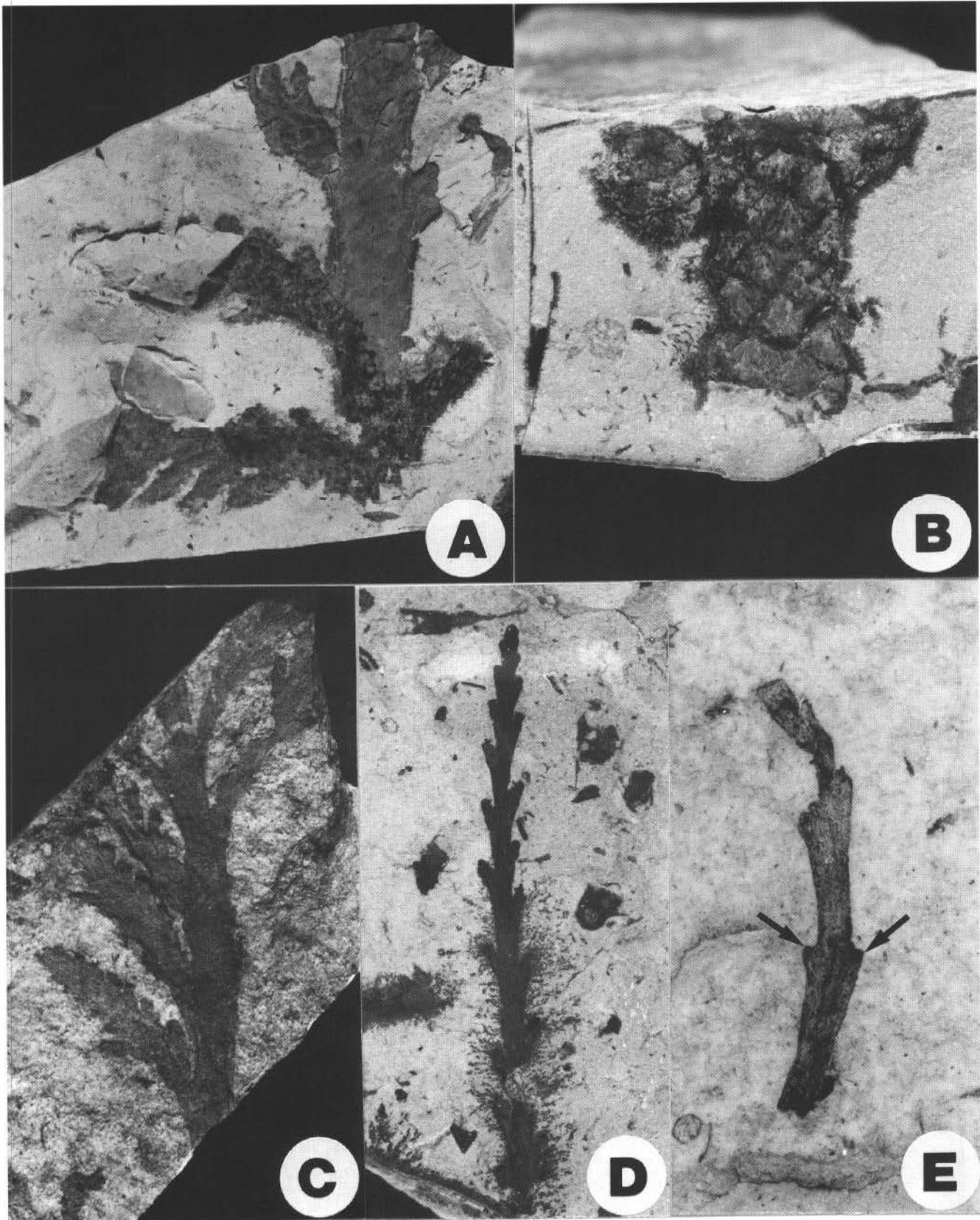


FIGURE 3. Conifers with extinct structural features from the Jose Creek Member, McRae Formation. **A**, *Brachyphyllum* sp., specimen showing three orders of branching, x1. **B**, *Brachyphyllum* sp., second specimen showing thick scale-shaped leaves, x2. **C**, *Androvetitia*, specimen showing flattened stems with three orders of branching. The smallest branches are closely spaced as in the type species, x2.5. **D**, aff. *Androvetitia*, specimen with flattened stems showing alternate branching. The name is preceded by an aff. because opposite branching is characteristic of *Androvetitia*, x2. **E**, aff. *Androvetitia*, flattened branch of another specimen showing highly reduced leaves (arrows), x3.

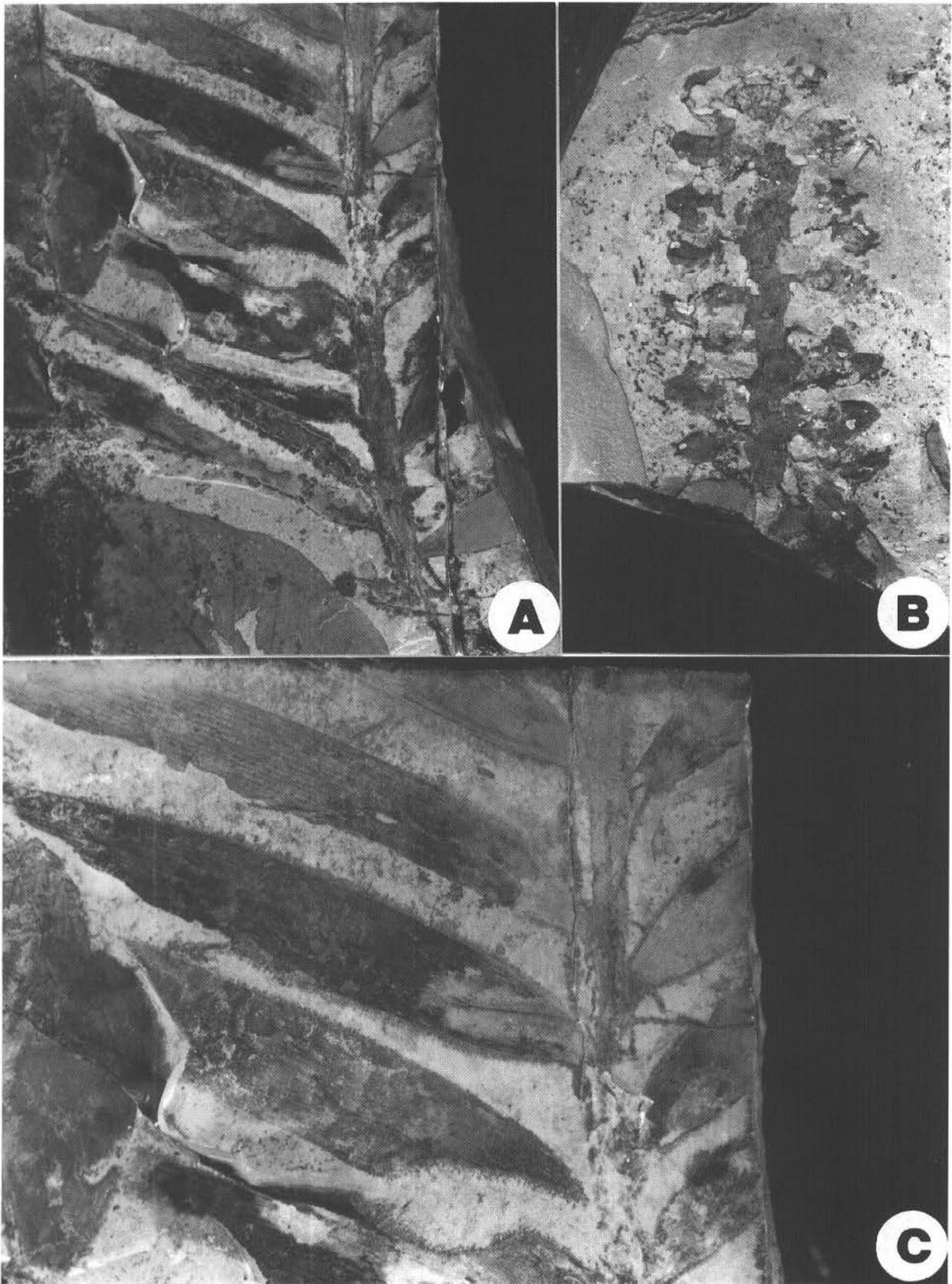


FIGURE 4. Cycads from the Jose Creek Member, McRae Formation. **A**, Leaf of *Zamioidae* showing pinnately compound organization and elongate leaflets, x1. **B**, Cone of *Zamioidae*, x2. **C**, Same leaf as Fig. 4A, close-up of rachis showing the narrowing of leaflets near the point of attachment and the absence of a decurrent wing of tissue along the rachis. In living cycads this indicates the abscission of leaflets, x2.

assigned to *Zamia* (e.g., Brown, 1939a). Cycad cones (Fig. 4B) occur at one locality in association with pinnately compound cycad leaves, isolated leaflets, and scale leaves. Each cone is elongate and bears spirally arranged structures interpreted as sporophylls. These sporophylls expand to a peltate head, as in the above three genera. *Ceratozamia*, *Microcycas*, and *Zamia* collectively range from Mexico and the southeastern U.S. to Central America and the islands of the Caribbean (Stevenson et al., 1990).

Jose Creek cycads represent evergreens, based on the thick texture of leaflets and scale leaves. In terms of growth habit they probably represent rosette trees, rosette shrubs, or ground herbs, based on the range of growth habits found in *Ceratozamia*, *Microcycas*, and *Zamia* (Stevenson, 1990). Jose Creek cycads indicate mild winters, because extant evergreen cycads are sensitive to freezing temperatures (Box, 1981; Editors of Sunset Magazine, 1988). Deciduous and possibly cold-tolerant cycads, such as the extinct genus *Nilssonia*, are absent from the Jose Creek flora, although they are present in cooler assemblages to the north (Upchurch and Wolfe, 1993).

Flowering plants (Division Anthophyta)

Anthophyta comprise the angiosperms (or flowering plants), the extant seed plant order Gnetales, and the extinct seed plant orders Bennettitales and Pentoxylales (e.g., Doyle and Donoghue, 1992). Jose Creek anthophytes consist solely of flowering plants, as is the case for other Maastrichtian megaflores from the Western Interior (Upchurch and Wolfe, 1993). Recent phylogenetic analyses of angiosperms indicate that extant flowering plants comprise three distinct groupings: (1) paleoherbs plus monocots; (2) woody magnoliids, which belong to the primitive subclass Magnoliidae; and (3) eudicots, which belong to every dicot subclass except Magnoliidae (Donoghue and Doyle, 1989; Doyle and Donoghue, 1993). Eudicots form a distinct monophyletic group and represent the majority of angiosperm species; whether or not the other two are monophyletic or paraphyletic is unclear. All three groups of angiosperms are present in the Jose Creek megaflores.

Monocots

Monocots are common and belong to taxa of subtropical to tropical aspect. Palms (family Arecaceae) are a common component of some assemblages and include costapalmate leaves assignable to *Sabalites montana* (Fig. 5A) and petrified stem material up to 20 cm in diameter. Probable screw pines (family Pandanaceae) are represented by a new small-leaved species of *Pandanites* (not illustrated). *Pandanites* leaves are characterized by minutely spinose margins and three longitudinal folds, the middle of which occurs over the midvein (Dorf, 1942). Gingers (family Zingiberaceae) are represented by leaves assignable to *Zingiberopsis magnifolia* (Fig. 5B), the oldest and most primitive species of *Zingiberopsis* (Hickey and Peterson, 1978). Jose Creek specimens of *Zingiberopsis* can form up to one-third of the collected remains at a single site in recrystallized volcanic ashes but are absent from other facies. This indicates that the rarity of *Zingiberopsis* in coeval Western Interior assemblages could also result from taphonomic bias.

Other Jose Creek monocots are distinct morphologically but have systematic affinities that are not yet well understood. One common species in this category has broad strap-shaped leaves with a midrib composed of clustered parallel veins (Fig. 5C). Cross veins are prominent and traverse the thinner parallel veins. This condition differs from that of Zingiberaceae and related families (order Zingiberales), where the leaves have cross veins that connect only with adjacent parallel veins.

Jose Creek monocots represent different growth habits but rein-

force evidence from cycads for above-freezing cold-month mean temperatures. Palms represent rosette trees or rosette shrubs, based on growth habit in extant palms and the presence of palm trunks up to 0.2 m in diameter (see below). *Zingiberopsis* probably represents a rhizomatous herb based on its common occurrence in paleosol-associated facies and growth habit in extant Zingiberaceae. Both palms and gingers are restricted to climates where mean winter temperatures are above freezing (e.g., Box, 1981; Editors of Sunset Magazine, 1988).

Woody Magnoliidae

Woody Magnoliidae are diverse and belong to taxa known from other Late Cretaceous localities in the Western Interior. Laurales are the most abundant and diverse group of woody Magnoliidae and comprise a mixture of mid-Cretaceous holdover taxa and taxa of Tertiary aspect. The mid-Cretaceous holdovers are characterized by: (1) palmate venation where a pair of lateral primary veins is free from the midvein into the petiole, and (2) poorly organized high-order venation that often forms highly branched freely ending veinlets. Jose Creek species in this group include "*Cinnamomum*" *linifolium* (Fig. 6C), a taxon characterized by a highly elongate unlobed leaves; *Pabiania* (Figs. 6A, 6B), a genus characterized by less elongate three- to five-lobed leaves; and the "*Ficus*" *praetriner* is complex (Figs. 5D, 6D), a group characterized by unlobed to shallowly lobed leaves. These mid-Cretaceous holdover taxa have features of higher-order venation and cuticular anatomy that are more primitive than those in extant Lauraceae, despite similarities in lower-order venation (Upchurch and Dilcher, 1990). *Pabiania* has one of its highest stratigraphic occurrences in the Jose Creek flora. Other Jose Creek taxa of mid-Cretaceous aspect become extinct at or above the Cretaceous-Tertiary boundary in the Raton and Denver Basins (e.g., Wolfe and Upchurch, 1987a; Kauffman et al., 1990).

Laurales of Tertiary aspect differ from mid-Cretaceous holdovers in having pinnate venation and strongly reticulate tertiary and quaternary venation; in addition, at least one species is characterized by a thick vein that runs along the leaf margin (Fig. 6E). Laurales of Tertiary aspect are more evolutionarily advanced in their venation than the mid-Cretaceous holdovers and have a suite of characters restricted to extant Lauraceae (cf. Upchurch and Dilcher, 1990). Lauraceous features include: (1) secondary veins that are looped and widely spaced, (2) brochidodromous looping of the secondary veins that is angular and can occur near the midrib, (3) tertiary veins that are widely spaced, transversely oriented, and reticulate, (4) strongly reticulate quaternary and higher-order venation that encloses areoles of regular size and shape, and (5) marginal venation that consists of a strongly thickened vein that runs along the margin (i.e., a strong fimbrial vein). Systematic relationships between extant genera and Laurales of Tertiary aspect are not yet elucidated.

Physiognomic analysis of Jose Creek Laurales is not yet complete. At least some species represent woody broad-leaved evergreens, based on extant affinities and physiognomy inferred for related fossils from the Raton and Denver Basins (Wolfe and Upchurch, 1987b).

Eudicots

Jose Creek eudicot leaves are comparable to those in a variety of extant families. Some species represent primitive members of the eudicots that have palmately veined leaves with serrate margins. These leaves have three or more primary veins that radiate from the base of the blade and strongly convex teeth on the margin that conform to the chloranthoid or modified chloranthoid types of

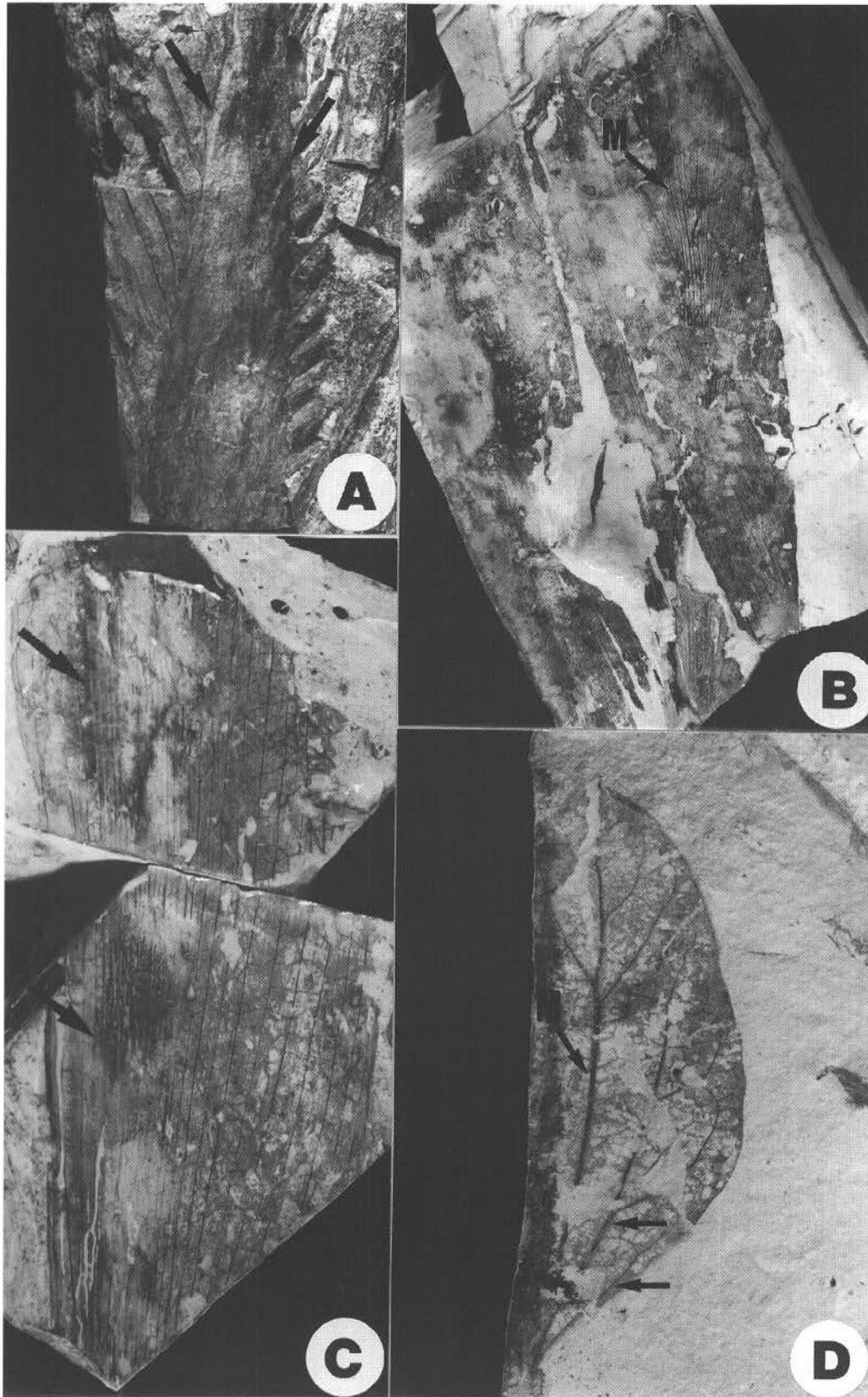


FIGURE 5. Monocots and a woody magnoliid dicot from the Jose Creek Member, McRae Formation. **A**, *Sabalites montana*, fragment of a specimen showing strongly developed and elongate costa (arrows), x1. **B**, *Zingiberopsis magnifolia*, specimen showing multi-stranded midvein (M) and numerous parallel veins that arise from the midvein at a narrow acute angle, x1. **C**, New species of monocot showing a midrib composed of closely spaced vascular strands (arrows) and cross-veins that traverse thin parallel veins, x1. **D**, Member of "*Ficus*" *praetriner* is group showing midvein (M) and two lateral primary veins that are decurrent into the petiole (arrows), x2.

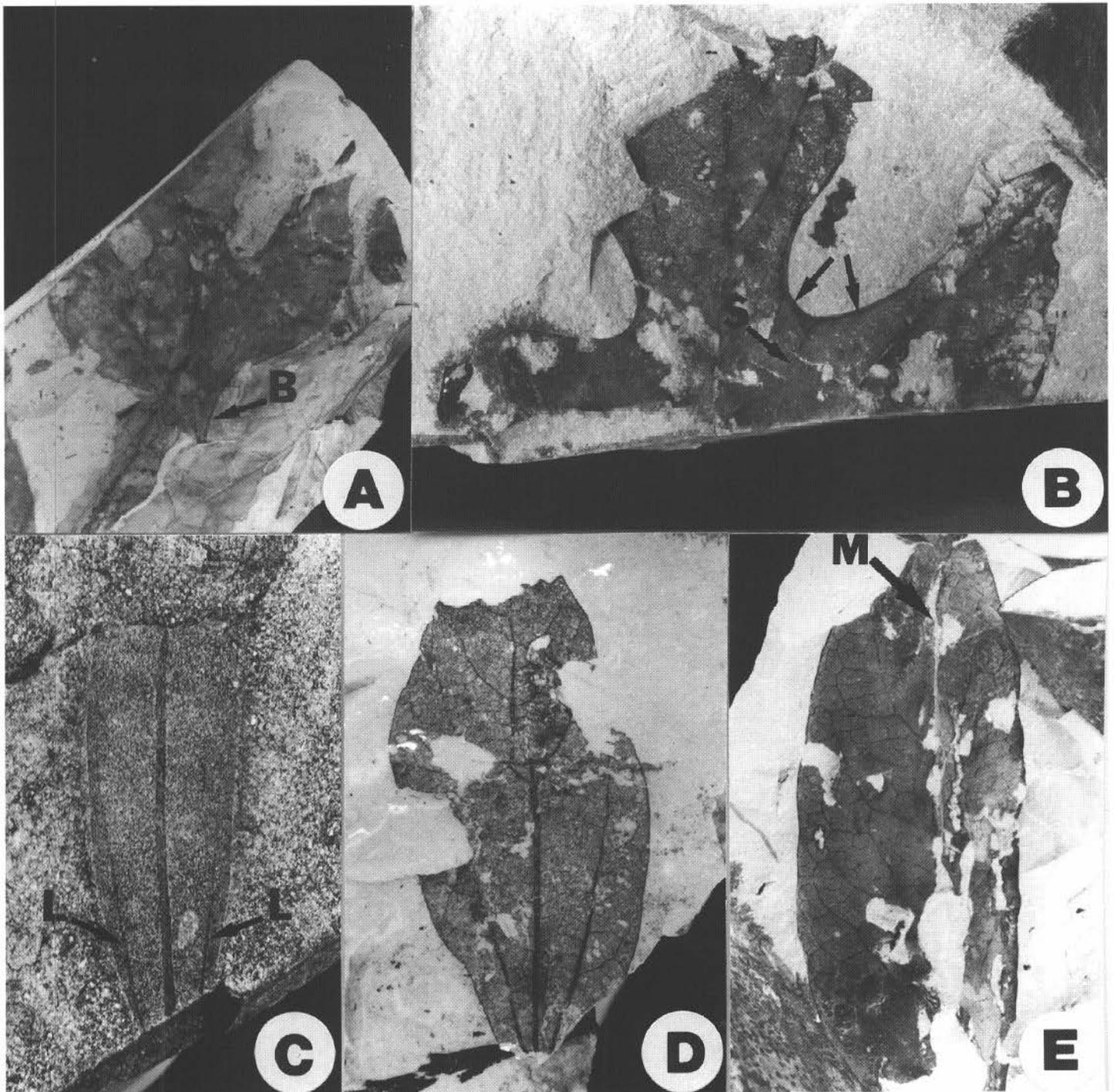


FIGURE 6. Laurales from the Jose Creek Member, McRae Formation. **A**, *Pabiania* sp., specimen showing characteristic three-lobed organization and basilateral primary veins (B), x1. **B**, *Pabiania* sp., close-up of another specimen showing characteristic pattern of sinus bracing in which a special vein (S) runs to the margin and bifurcates to form a marginal vein (arrows), x2. **C**, "*Cinnamomum*" *linifolium*, specimen showing characteristically elongate shape and a thin pair of lateral primary veins that run nearly parallel to the midvein (L), x2. **D**, "*Ficus*" *praetriner* is group, specimen showing stronger lateral primary veins that run into the apical half of leaf and weakly percurrent tertiary venation, x2. **E**, Pinnate Lauraceae, folded leaf showing midvein (M), looped and apically curved secondary veins, and strong vein running along the left margin, x2.

Hickey and Wolfe (1975) and Wolfe (1989). This combination of features today occurs in Trochodendrales and Cercidiphyllales, which can be distinguished from each other by details of tooth structure and patterns of higher order venation. Two Jose Creek species have features today found in Trochodendrales and Cercidiphyllales.

The more abundant species (Figs. 7A, 7B) has broad elliptic leaves with crenate margins, palmate venation, secondary veins

that diverge at a higher angle than the lateral primary veins, reticulate tertiary venation, and teeth that are similar to the chloranthoid type of Hickey and Wolfe (1975). The teeth have an apical indentation at the gland, a feature that distinguishes extant *Cercidiphyllum* from Trochodendrales. The fossil species probably belongs to a new genus because it differs from extant *Cercidiphyllum* and extinct Cercidiphyllales such as *Joffrea* in having a doubly serrate margin, simple craspedodromous secondary

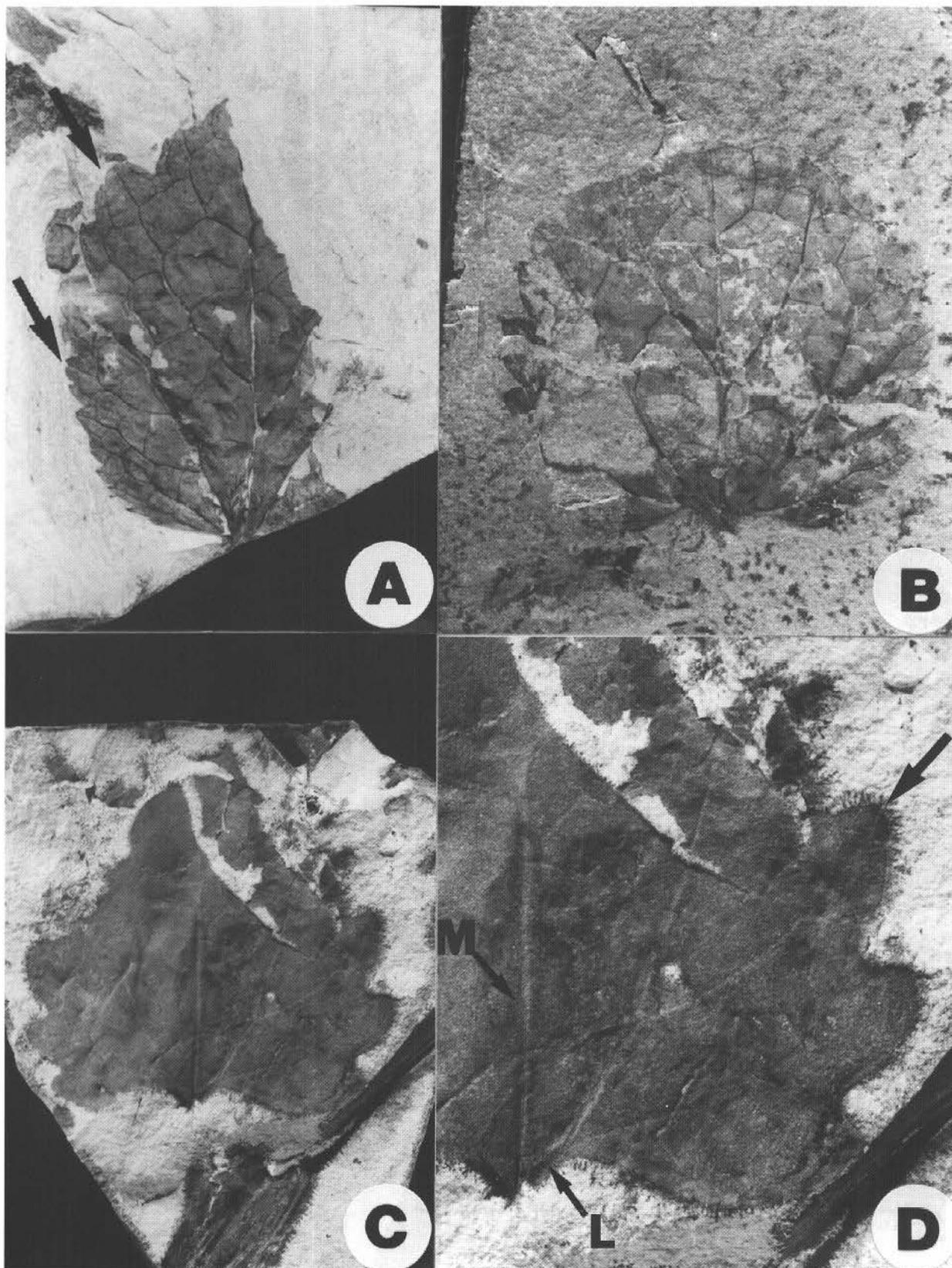


FIGURE 7. Primitive eudicots from the Jose Creek Member, McRae Formation. **A**, Undescribed species with possible affinities to *Cercidiphyllaceae* showing palmate (actinodromous) primary venation, craspedodromous secondary venation, and chloranthoid teeth with an apical indentation (arrow), x2. **B**, Second specimen of same species showing shape and secondary venation, x2. **C**, Leaf with shape, margin, and primary venation characteristic of *Marmarthia trivialis*, x1. **D**, *Marmarthia trivialis*, specimen from 7C showing midvein (M), lateral primary vein (L), and a large convex tooth entered by a branch of the lateral primary vein (arrow), x2.

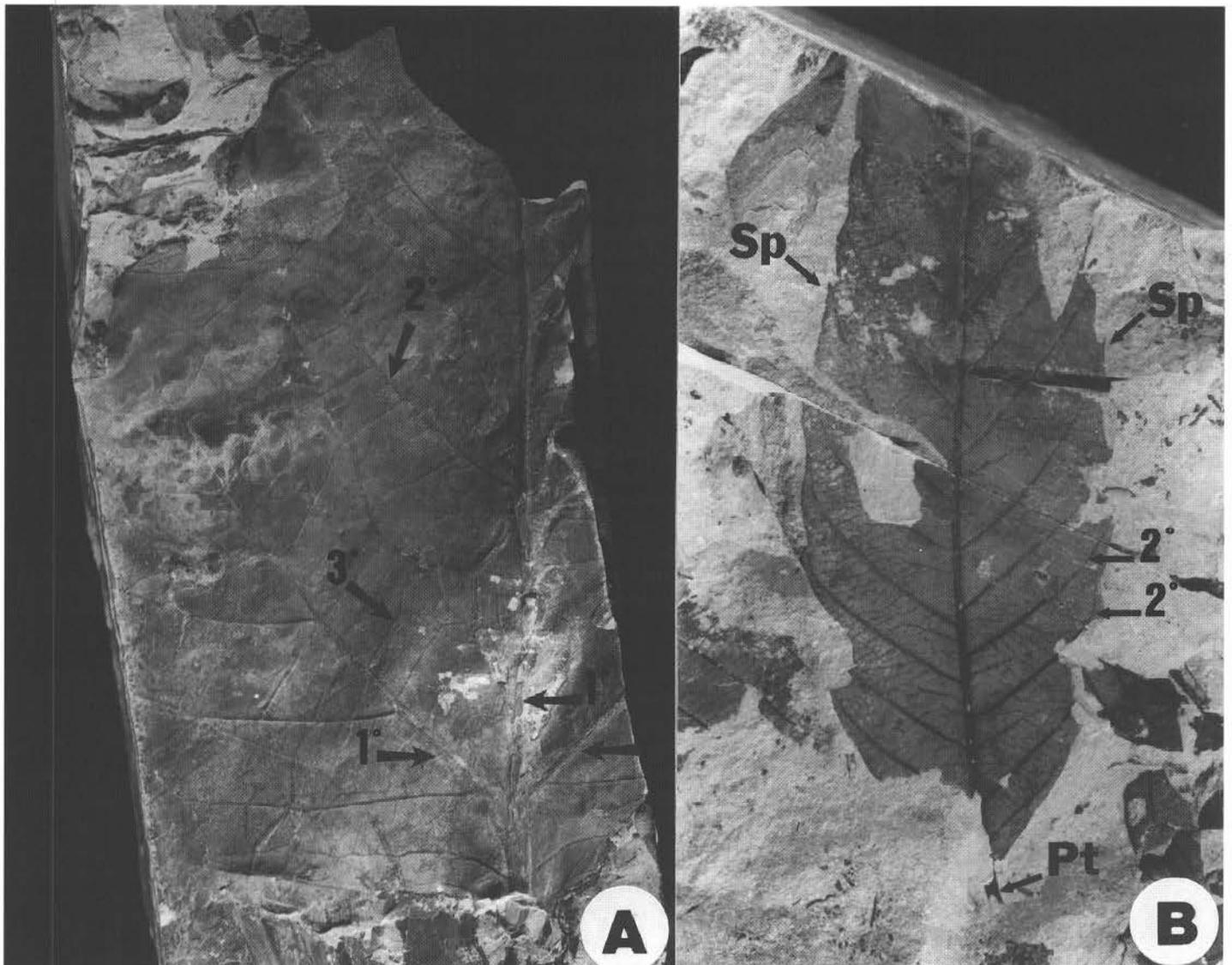


FIGURE 8. Eudicots from the Jose Creek Member, McRae Formation. **A**, *Platanus raynoldsii/guiellemae*. Note three primary veins (1° and lowermost arrow), secondary veins (2°), and percurrent tertiary veins that fork in the axil of the lateral primary veins (3°), x1. **B**, Leaf tentatively assigned to *Dryophyllum subfalcatum*. Note the petiole (Pt), spinose teeth (Sp), and apically curved (eucamptodromous) secondary veins (2°), x2.

venation (that is, secondary veins that run directly to the teeth), tertiary venation that is nearly as thick as the primary and secondary venation, chloranthoid teeth with a distinct pair of accessory veins, and a fimbrial vein that fuses with the glands of the teeth. *Trochodendroides nebrascensis* is one of the more similar described fossil species; however, it differs from the Jose Creek taxon in having a more strongly doubly serrate margin and much weaker and more numerous tertiary veins. Cercidiphyllales are a common group in the Late Cretaceous and early Tertiary of North America, especially from the northern Rocky Mountain region, and are recognized on the basis of leaves, woods, and reproductive structures (e.g., Brown, 1939b; Crane and Stockey, 1985; Crane, 1989).

A second Jose Creek species is tentatively assigned to the eudicots. This species is referable to *Marmarthia trivialis* on the basis of its ovate shape, pattern of lobation, and apically arching lateral primary veins that form the basal margin of the leaf and run directly into large rounded teeth (Figs. 7C, 7D). Secondary and higher-order venation is poorly preserved, possibly indicating thick texture. The systematic position of *Marmarthia trivialis* is somewhat problematic. Johnson (1996) refers this species to Laurales because of similarities to other fossil Laurales in its pattern of primary

venation and moderately well-organized intercostal venation. However, large convex teeth are anomalous within Laurales and are more at home within primitive palmately-veined members of the eudicots. Examination of cuticular anatomy and associated reproductive structures may resolve this systematic ambiguity.

Some palmately veined leaves are related to sycamores (Platanaceae), another primitive family within the eudicots. A few Jose Creek leaves are referable to the *Platanus guiellemae/P. raynoldsii* group (e.g., Fig. 8A), which is characterized by three shallow lobes, three primary veins that diverge at different points and produce external branches, strong percurrent tertiary veins that are widely spaced and fork between the primary veins, and higher-order venation that forms 4- to 5-sided polygons of regular size and shape. Additional Jose Creek leaves probably relate to Platanaceae but may belong to extinct genera. These include "*Vitis*" *stantonii* (not pictured), a toothed species characterized by a more pronounced midvein and less pronounced lateral primary veins. Jose Creek Platanaceae occur in channel and overbank deposits. Today Platanaceae are deciduous trees that live at the margin of streams, ponds, and lakes.

Remaining groups of eudicots, while distinct at the species level,

are not yet well understood taxonomically. One common species in this category is assignable to *Dryophyllum subfalcatum* (Fig. 8B), a taxon that is commonly assigned to the oak family (Fagaceae) (Dorf, 1942). The Jose Creek specimens are characterized by an elliptic to ovate shape, a margin that often bears small spinose teeth, pinnate venation, intersecondary veins, thin percurrent tertiary venation that is oriented obliquely to the midrib, and "aparallel" tertiary veins near the teeth (that is, tertiary veins that are thicker than other tertiary veins and oriented at a different angle).

Dicot woods

Dicot woods are poorly understood taxonomically but provide important information on vegetation and climate. Dicot stumps measure up to 0.4 m in diameter above the roots, which indicates that some dicots comprised trees of small to medium stature. No species of dicot woods displays growth rings, which indicates the absence of seasonal growth rhythms. These physiognomic features are congruent with those reported for other Late Cretaceous dicot woods from the Southern Western Interior and Atlantic/Gulf Coastal plains (Wolfe and Upchurch, 1987b) and reinforce evidence for evergreen vegetation that grew under low seasonality of temperature and precipitation. The absence of growth rings in dicot woods cannot be explained solely by an absence of temperature seasonality and use of ground water by trees during the dry season. This is because at least one species preserves a trunk that has no taproot and large lateral roots that are confined to the top-most 30 cm of soil. Ground water is estimated to have been 1–2 m below the soil surface in this and other paleosols of the Jose Creek Member (Buck et al., 1992; Buck and Mack, 1995).

VEGETATION, CLIMATE, AND REGIONAL ECOLOGY

Jose Creek megaflores assemblages preserve diverse life forms. Trees and shrubs are represented by conifers, cycads, magnoliids, eudicots, and possibly monocots (e.g., certain palms). This inference is based on growth form in extant relatives and the occurrence of conifer, dicot, and monocot stems at least 0.2 m in diameter. Herbs are represented by ferns and by monocot groups such as gingers (family Zingiberaceae), which produce aerial leaves or shoots that arise from horizontal underground stems (or rhizomes). In terms of specific life forms Jose Creek assemblages document the presence of: (1) broad-leaved evergreen trees (e.g., many Magnoliidae); (2) broad-leaved deciduous trees (e.g., Platanaceae); (3) rosette trees and shrubs (e.g., palms and cycads); (4) evergreen needle-leaved trees (conifers); and (5) broad-leaved herbs with probable evergreen foliage (e.g., Zingiberaceae). Today this combination of life forms occurs only in evergreen vegetation that grows under mean winter conditions that are above freezing (Wolfe, 1979; Box, 1981). Previous analysis of leaf margin, leaf shape, and leaf size indicates that these conditions were prevalent over much of North America during the Late Cretaceous (Wolfe and Upchurch, 1987b; Upchurch and Wolfe, 1987; Wolfe, 1990).

Jose Creek conifer and dicot woods reinforce previous interpretations of hydrology for the southern Western Interior and Mississippi Embayment, and in particular subhumid conditions with little seasonality of precipitation (Wolfe and Upchurch, 1987b). In situ stumps measure up to 1.5 m in diameter and include the following indicators of year-round water: (1) palms, which require abundant precipitation or a readily available source of ground water, (2) dicots with no annual rings, and (3) conifers with weakly developed and sometimes discontinuous growth rings. This inference is consistent with evidence from Jose Creek paleosols for

subhumid to humid conditions with no pronounced drought (Buck et al., 1992; Buck and Mack, 1995).

A noteworthy feature of Jose Creek leaf assemblages is the co-occurrence at every locality of needle-leaved trees (conifers) and broad-leaved trees (flowering plants). This contrasts with Raton- and Denver-basin leaf assemblages, where conifers are absent or rare. Two factors may explain these differences. First, the Jose Creek member has a much greater abundance of well-drained soils than most megafossil-bearing formations from the southern Western Interior, which would favor conifers due to edaphically drier conditions (cf. Retallack and Dilcher, 1981). This inference is based on the near absence of carbonaceous beds and gley paleosols in the McRae Formation (Buck and Mack, 1995) and is consistent with deposition of the McRae Formation in a Laramide intraforeland basin (Seager et al., 1997). Second, abundant input of volcanic ash into the upper part of the Jose Creek Member enhanced preservation of vegetation from well-drained floodplains, which rarely preserves in non-volcanic sequences. Ash-preserved megaflores assemblages from the mid-Maastrichtian of the Northern Western Interior show similar enhanced abundance of conifers, plus ferns (Wing et al., 1993), supporting this taphonomic interpretation.

ACKNOWLEDGMENTS

We thank Richard Sanders for assistance with fieldwork and curation; Barton Jacques, Ed Koehler, George Mapus, Tony Rodriguez, and Amy, Michael, and Lauren Upchurch for assistance with fieldwork; and Andrea Wakefield for providing preliminary data on relative abundance. Research was supported, in part, by National Science Foundation Grant BSR-9024820 to G. R. Upchurch, Jr., and an American Chemical Society-Petroleum Research Fund Grant to G. H. Mack.

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