ARCHAEANTHUS: AN EARLY ANGIOSPERM FROM THE CENOMANIAN OF THE WESTERN INTERIOR OF NORTH AMERICA[1]

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ABSTRACT

Archaeanthus linnenbergeri Dilcher & Crane, gen. et sp. nov., a multifollicular angiosperm fruit, is described from the mid-Cretaceous (uppermost Albian–mid-Cenomanian) Dakota Formation of central Kansas. Clusters of follicles were borne terminally at the apex of a stout branch with helically arranged leaves. Each cluster comprised 100–130 helically arranged follicles on an elongated receptacle. The follicles were stalked with a short, rounded tip and dehisced along a single adaxial suture. Ovules were numerous and borne along either side of the suture; 10–18 seeds matured in each follicle. The receptacle below the gynoecium shows three groups of scars, an upper group of numerous small scars interpreted as those of stamens with six to nine larger scars immediately below, interpreted as those of inner perianth parts. The flower is delimited at the base by three large, narrowly elliptical scars interpreted as those of outer perianth parts. A prominent scar below the base of the flower is thought to mark the position of floral bud-scales. *Archaeanthus* is linked with perianth parts (*Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov. and *Archaepetala obscura* Dilcher & Crane, sp. nov.), bud scales (*Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov.), and leaves (*Liriophyllum kansense* Dilcher & Crane, sp. nov.) on the basis of association evidence and structural agreement in the presence of distinctive resin-bodies. *Liriophyllum populoides* Lesq. is shown to be a separate species. The reconstructed *Archaeanthus* plant is most closely related to Recent Magnoliidae and in some features comes close to the hypothetical angiosperm archetype predicted by magnoliid floral theory; it demonstrates that many of the characters interpreted as primitive from neontological evidence are also ancient. *Archaeanthus* does not predate other kinds of angiosperm reproductive structure in the fossil record but conclusively demonstrates the existence of magnoliid-like plants and flowers early in angiosperm evolution.

Hypotheses of flowering plant phylogeny are inextricably linked to the evolutionary interpretation of angiosperm reproductive organs and thus to concepts of the primitive angiosperm flower. Traditionally such ideas have been based on comparative studies of living plants, and the fossil record has made little contribution. In recent years, however, knowledge of early angiosperm reproductive diversity has increased, and paleobotanical data relevant to these problems have begun to accumulate. In this paper we describe a new species of mid-Cretaceous angiosperm known from multifollicular fruits, perianth parts, bud-scales, and leaves, and discuss its relevance to concepts of floral evolution in flowering plants.

The earliest speculations on the nature of the primitive angiosperm flower developed from the pre-Darwinian classifications of the eighteenth and nineteenth centuries and polarized into two principal hypotheses: either the simple, unisexual and predominantly wind-pollinated flowers of the Amentiferae were primitive (Engler, 1897; Strasburger et al., 1898; Rendle, 1925, 1930; Wettstein, 1935) or the bisexual and predominantly insect-pollinated flowers of the magnoliid (Ranalean) angiosperms most closely approximate to the 'ancestral' flower (Bessey, 1897, 1915;

Arber & Parkin, 1907). Subsequent investigations and interpretations, particularly of anatomical (Bailey, 1944; Eames, 1961; Dickison, 1975) and palynological evidence (Wodehouse, 1935, 1936; Walker 1974a, 1974b, 1976), led to the widespread acceptance of the second hypothesis, that the Magnoliidae are the most primitive living group of flowering plants and exhibit the most primitive floral morphology. This hypothesis is central in most of the putatively 'phylogenetic' classifications of flowering plants that have been proposed in the last 50 years (Hutchinson, 1959; Cronquist, 1968, 1981; Takhtajan, 1969; Stebbins, 1974; Thorne, 1976; Dahlgren, 1980), and although alternative viewpoints have been suggested (Corner, 1949; Melville, 1962, 1963; Meeuse, 1966), none have been widely accepted. Along with the development of the magnoliid hypothesis has come the recognition of 'evolutionary trends' for a wide range of characters. The primitive states in these trends have been combined into a concept of a hypothetical angiosperm morphotype (Takhtajan, 1969).

Until recently, direct paleobotanical evidence relevant to these evolutionary hypotheses has been conspicuously absent. The last two decades, however, have seen considerable advances in angiosperm paleobotany and an increasing awareness of the relevance of fossil material to concepts of flowering plant evolution (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Hughes, 1976; Doyle, 1978; Dilcher, 1979). A major radiation is regarded as having occurred during the Barremian to Cenomanian stages of the mid-Cretaceous, followed by further diversification throughout the Upper Cretaceous and Tertiary. No unequivocal angiosperms have so far been reported from pre-Barremian rocks, although there are many earlier, potentially relevant fossil plants about which we know too little (Doyle, 1978; Hill & Crane, 1982; R. A. Scott et al., 1960). Despite some insight into the timing of angiosperm evolution, the systematic origin of the group remains a mystery that continues to stimulate a variety of speculations (Melville, 1962, 1963; Meeuse, 1966; Retallack & Dilcher, 1981a). Such conjectures inevitably reduce to discussions of homology, particularly of reproductive structures, and have been severely limited by inadequate knowledge of early flowering plants. Few of the mid-Cretaceous angiosperms are known in detail from flowering or fruiting specimens, and even fewer are known from both vegetative and reproductive material. The species described in this paper is currently one of the more completely understood of all early angiosperms. We propose the name *Archaeanthus linnenbergeri* for multifollicular fruits and the vegetative branches on which they are borne. This species is linked with two kinds of perianth parts (*Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov. and *Archaepetala obscura* Dilcher & Crane, sp. nov.), bud-scales (*Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov), and leaves (*Liriophyllum kansense* Dilcher & Crane, sp. nov.) as parts of a single fossil plant on the basis of association and the anatomical similarity that all these organs contain the same distinctive resin-bodies. *Liriophyllum populoides* Lesq. is shown to represent a different species. The reconstructed *Archaeanthus* plant is closely allied to the Magnoliidae sensu lato, and in some features comes close to the hypothetical angiosperm morphotype predicted by magnoliid floral theory.

MATERIAL

With the exception of the specimens of *Liriophyllum populoides,* and one possible specimen of *Archaeanthus linnenbergeri,* from Morrison, Colorado, all of the material described in this paper is from the Dakota Formation at Linnenberger's Ranch near Bunker Hill, Russell County, central Kansas (see Retallack & Dilcher, 1981b, 1981c, for details of this locality). The plant material is preserved as compressions in a brown-gray clay with variable amounts of sand and silt. The specimens typically have good organic preservation. The associated macroflora is dominated by about 15 to 20 kinds of angiosperm leaves, but although the microflora is well preserved, angiosperm pollen accounts for only about 25% of the total palynomorphs. Most of the Linnenberger Ranch material described in this paper comes from a narrow sandy bed, low in the section at the locality; some of this material has been previously described by Dilcher et al. (1976, 1978) and Dilcher (1979). The Linnenberger plant assemblage is interpreted as a flora of local origin, deposited in a fluvial swale on the distal flanks of a levee system (Retallack & Dilcher, 1981b, 1981c).

In central Kansas, the Dakota Formation exhibits considerable lateral sedimentological variation but has been divided into two Members: the Terra Cotta Clay Member below, and the Janssen Clay Member above (Plummer & Romary, 1942). These are not mappable units and

are clearly facies-related (Franks, 1975), but the Terra Cotta Clay Member typically consists of gray to greenish gray clays and shales with abundant lenticular, fine- to coarse-grained sandstone units, whereas the Janssen Clay Member consists of gray to dark gray claystones, siltstones, and shales with lenticular sandstones. Lignites are particularly abundant in the upper parts of the Janssen Clay Member (Schoewe, 1952). The Terra Cotta Clay Member is interpreted as predominantly fluvial and overbank, alluvial plain sediments deposited by streams flowing from the north and east, whereas the Janssen Clay Member represents a greater range of paleoenvironments, some of which, particularly in the higher parts of the section, were associated with the transgressing mid-Cretaceous Graneros Sea (Siemers, 1971; Franks, 1975). The sedimentology, paleontology, and other aspects of Dakota Formation geology are considered more fully by Plummer and Romary (1942, 1947), Siemers (1971), Hattin and Siemers (1978), Bayne et al. (1971), and Retallack and Dilcher (1981b, 1981c). The Linnenberger Ranch material comes from the Janssen Clay Member, relatively high in the Dakota Formation. The classic Dakota Sandstone Flora described by Lesquereux (1868, 1874, 1878, 1883, 1892), Gress (1922), and Newberry (1868) is probably predominantly from the sandstone facies of the same Member.

Toward the south and west, the Dakota Formation overlies the Kiowa Shale (Franks, 1975), which is dated on evidence of marine fauna and palynomorphs as late Albian (R. W. Scott, 1970a, 1970b; Ward, 1981), and in the north and east oversteps onto older Paleozic rocks. In the south and west it interdigitates with, and is overlain by, the Graneros Shale, a shallow-water marine deposit representing the initial transgressive phase of the Greenhorn cyclothem. Sediments from the transitional zone represent a considerable diversity of marginal marine environments. Marine invertebrates securely date the Graneros as Cenomanian (Hattin, 1965; Eicher, 1975) and radiometric determinations of the 'X bentonite' in the upper part of the Graneros (Hattin, 1965, 1967) give an age of about 94.5 Ma (Kauffman, pers. comm.). Palynological investigations (Doyle, pers. comm.; Ravn, 1981) similarly indicate a Cenomanian age probably equivalent to zone III of the palynological zonation established by Brenner (1963), Doyle (1969), Doyle and Robbins (1977), and others for the mid-Cretaceous of the Atlantic Coastal Plain. Zavada (pers.

comm.) has shown that the palynofloras from the upper Dakota Formation and Graneros are similar and contain about 20–35% angiosperm pollen, whereas the upper Kiowa Shale contains less than 5%. On the basis of all the evidence available, it seems likely that the Dakota Formation of central Kansas extends across the Upper and Lower Cretaceous boundary (Zeller, 1968; Kauffman et al., 1976). The fossil plants discussed in this paper from the Janssen Clay Member, therefore, date approximately from the Upper and Lower Cretaceous boundary and are of uppermost Albian or lowermost Cenomanian age.

The specimens of *Liriophyllum populoides* originally described by Lesquereux (1883) and discussed in this paper are from the Dakota Group of Morrison, Colorado, which, on the western edge of the Denver Basin, comprises the Lytle Formation below and the South Platte Formation above (Waage, 1955). The South Platte Formation consists of dark gray to black shales and brown weathering sandstones deposited in a range of marine-influenced estuarine, littoral, and alluvial plain environments (Waage, 1955; Weimer & Land, 1972). The majority of the 'Dakota Sandstone' plants from Morrison described by Lesquereux (1883) and Knowlton (1896, 1920) come from the Kassler Sandstone Member in the upper part of the South Platte Formation (Lee, 1920; Waage, 1955), equivalent to part of the 'J' sandstone (Weimer & Land, 1972) or the lower part of 'genetic unit C' (Weimer, 1970). They are preserved as impressions in a hard, pale gray sandstone. The Kassler Sandstone Member grades laterally into the marine Skull Creek Shales (R. G. Young, 1970) with *Inoceramus comancheanus* (Waage, 1955) and is generally accepted as upper Albian in age (Waage, 1955; McGookey et al., 1970; Kauffman et al., 1976; Berman et al., 1980).

Specific acronyms are used to designate the source of the fossil material studied. IU stands for Indiana University, HU stands for Harvard University, and USNM stands for United States National Museum, which is housed at the Smithsonian Institution.

SYSTEMATICS

In this section we describe six species representing four kinds of organs: multifollicular fruits (*Archaeanthus linnenbergeri*), leaves (*Liriophyllum populoides, L. kansense*), putative perianth parts (*Archaepetala beekeri, A. obscura*), and probable bud-scales (*Kalymmanthus walkeri*).

The measurements in the descriptions are based on all the material cited. Ranges and common dimensions are given in parentheses where available.

Archaeanthus Dilcher & Crane, gen. nov. TYPE: *Archaeanthus linnenbergeri* Dilcher & Crane, sp. nov.

DIAGNOSIS: Reproductive axis a cluster of follicles (a multifollicular fruit) with evidence of having been subtended by other floral organs. Receptacle stout, elongated, consisting of a distal tapering gynoecial zone bearing helically arranged follicles, with a shorter, more or less cylindrical zone below, showing circular and elliptical scars. Base of the flower delimited by three transverse, narrowly elliptic, slit-shaped scars. Follicles ellipsoidal, stalked, with a short, rounded tip and a distinct adaxial suture; containing numerous seeds.

DERIVATION: From *archae*—Greek, meaning beginning or first; *anthos*—Greek, meaning flower.

Archaeanthus linnenbergeri Dilcher & Crane, sp. nov. HOLOTYPE: IU 15703-4152.

DIAGNOSIS: As for the genus.

REFERENCES: '*Magnolia* species,' Lesquereux (1883: 73, pl. 11, fig. 6, brief description and drawing).

'Reproductive axes of *Liriophyllum*,' Dilcher et al. (1976: 854, fig. 1a, b, d, brief description and discussion with photographs and a line drawing).

'Reproductive axis' (*Carpites liriophylli* Lesquereux, 1883), Dilcher (1979: 311, figs. 40, 50, 51, brief discussion with photographs and line drawings. *Carpites liriophylli* is too poorly preserved to evaluate its similarity with our species).

OTHER MATERIAL: IU 15703; 2300, 2317, 2318, 2590, 3022, 3837, 3907, 4105, 4112, 4134–4150, 4152, 4153, 4155–4158, 4163, 4164, 4166–4170, 4198, 4532–4534.

NUMBER OF SPECIMENS EXAMINED: 44.

FIGURES: 1–37, 60a, f–h.

DERIVATION: After Albert and Edward Linnenberger, owners of the central Kansas locality from which this material was collected.

DESCRIPTION: Clusters of follicles (multifollicles) borne terminally and singly at the apex of a substantial vegetative branch 11–16 mm diam. Branch bearing helically arranged leaf scars at intervals of 28–35 mm. Leaf scars broadly elliptic, 1.5–3.3 mm long, 2.5 mm wide, pointed on either side. Surface of axis with occasional short, irregular, longitudinal, and transverse striations. Maximum length of branch preserved, 145 mm. Total length of the longest specimens seen, including branch and receptacle, 215 mm.

Receptacle elongated to 137 mm long (longest specimen incomplete). Gynoecial zone distal with irregular longitudinal ribs, elongating during development; most complete immature specimen 47 mm long, 7 mm wide at the base; longest mature specimen 137 mm long (incomplete), 8–12 mm wide at the base. Gynoecial zone gradually tapering distally and bearing 100–130 follicles. Immature carpels packed into a loose fascicle forming an ellipsoidal head ca. 22 mm diam., 50 mm high. Mature follicles loosely aggregated into an elongated conical head, ca. 70 mm diam. and to 152 mm high. Follicles borne helically leaving elongated, diamond-shaped scars, 1.5–4 mm long, 0.75–1 mm wide on the mature receptacle. Upper part of scars deeply impressed into the axis, becoming shallower in the lower half. Receptacle below the gynoecium short, more or less cylindrical, 7–9 mm long, tapering from 11–15 mm wide proximally to 8–12 mm distally in mature specimens. Receptacle immediately below the gynoecial zone bearing ca. 50–60 transversely elongated, elliptical scars ca. 1 mm broad (interpreted as those of stamens), followed below by 6–9 larger, more or less circular scars ca. 2 mm diam., apparently arranged in pairs (interpreted as those of inner perianth parts). Base of receptacle delimited by three prominent, narrowly elliptical, slit-shaped transverse scars pointed at either end, 2–3 mm high, 11–13 mm wide (interpreted as those of outer perianth parts). Pedicel with a distinct transverse ridge ca. 20–25 mm below the most proximal floral scars. Pedicel gradually broadening toward the ridge.

FIGURES 1–2. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov., IU 15703-4152.—1. Branch bearing the lower part of a receptacle with a cluster of follicles at the apex. Follicles on the extreme left not attached to the receptacle, ×1.—2. Detail of specimen in Figure 1 showing two scars at the base of the receptacle,
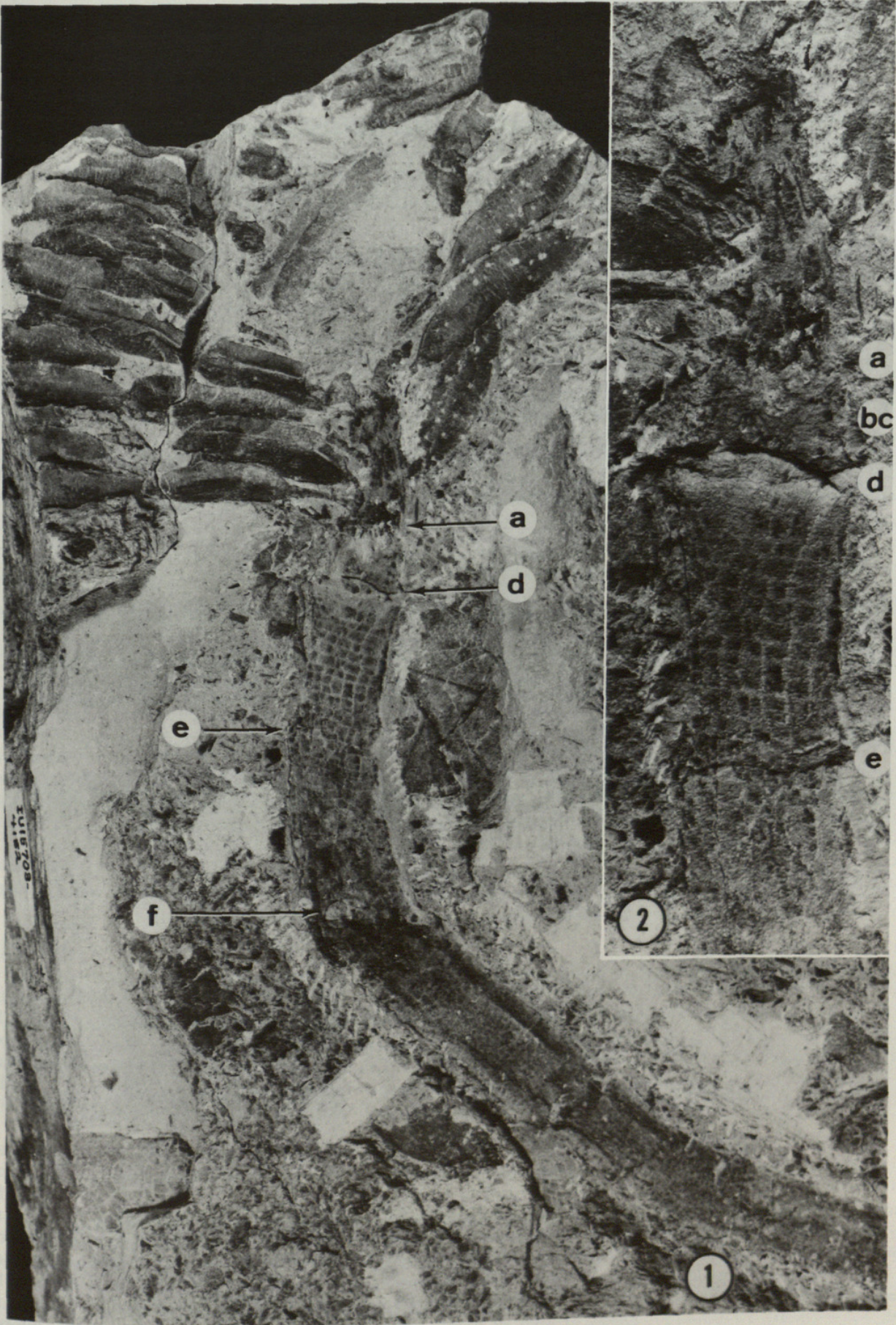
interpreted as part of a whorl of three. Note the zone of the receptacle between these large scars and the base of the gynoecial zone. Compare with Figures 4 and 66, ×2.5. a. Base of gynoecial zone. b, c. Undifferentiated middle zone of the receptacle. d. Scars of outer perianth whorl. e. Pair of scars on pedicel attributed to a calyptra. f. Leaf scar.

Ridge bearing at least 2 narrow, transverse scars about 1 mm high (interpreted as those of bud-scales).

Immature carpels slightly reflexed, ca. 16 mm long, 1 mm wide, with rounded tips. Mature follicles ellipsoidal, more or less straight, occasionally slightly reflexed. Individual follicles 25–35 (–38) mm long, (1–)4–7(–11) mm wide; length of locule (10–)20–29(–31) mm. Follicles contracted proximally into a stalk, 4.5–8 mm long, and distally into a short, rounded apex. Apex sometimes shortly two-lobed; lobes formed by the two adaxial crests at the apex of the follicles. Stalk 1–2 mm wide at its midpoint, broadening proximally to 1.5–4 mm at the point of attachment to the receptacle. Angle of attachment typically 50–80°. Follicles, when shed, breaking away at the base of the stalk.

Mature follicles with a median, longitudinal, adaxial suture along the entire length, flanked on either side by a ridge 1 mm high, forming an adaxial crest. Cuticle of adaxial crest bearing long, simple, unicellular trichomes. Follicles with a single weak abaxial rib extending along the entire length. Locule uninterrupted, but in a few specimens transversely constricted by regular or irregular, ridges and surface undulations into 10–18 weakly delimited oval units (interpreted as indicating positions of seeds), 2–3 mm high, 1–2 mm wide. These units more or less confined to the upper two-thirds of laterally compressed follicles, each unit frequently with a central area of dark organic matter.

Mature follicle wall of at least two distinct layers. Endocarp striated, comprised of transverse, tightly packed fibers, 10–20 μm wide. Fibers frequently separated to form prominent transverse cracks in compressed follicles. Exocarp with no visible cellular detail.

Immature follicles containing numerous (about 100) ovules borne (presumably along either side of the adaxial suture) 1–2 mm below the outer surface of the adaxial crest. Ovules arranged close together and overlapping, elliptical, ca. 2 mm long, ca. 0.75 mm wide; one end pointed and oriented adaxially, the other rounded. Ovules

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FIGURES 3–6. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—3. IU 15703-2300. Composite photograph showing the upper gynoecial zone of a long receptacle bearing numerous helically arranged follicles. Branch on the right of the specimen showing scars of floral organs (see Fig. 4), ×1.—4. Composite photograph showing detail of branch in Figure 3. a. Base of gynoecial zone. b. Upper part of the middle receptacle zone showing small scars interpreted as staminal. c. Lower part of the middle receptacle zone showing larger scars interpreted as those of inner perianth parts. d. Scars of outer perianth whorl. e. Pair of scars on pedicel attributed to a calyptra. Compare Figures 1, 12, and 66, ×2.25.—5. IU 15703-4136. Fragment of a small, presumably aborted receptacle showing closely spaced, linear, helically arranged carpels, ×1.—6. IU 15703-2300. Detail showing several mature follicles attached to the receptacle. Note the ridged receptacle with helically arranged diamond-shaped scars left by the follicle bases, ×2.
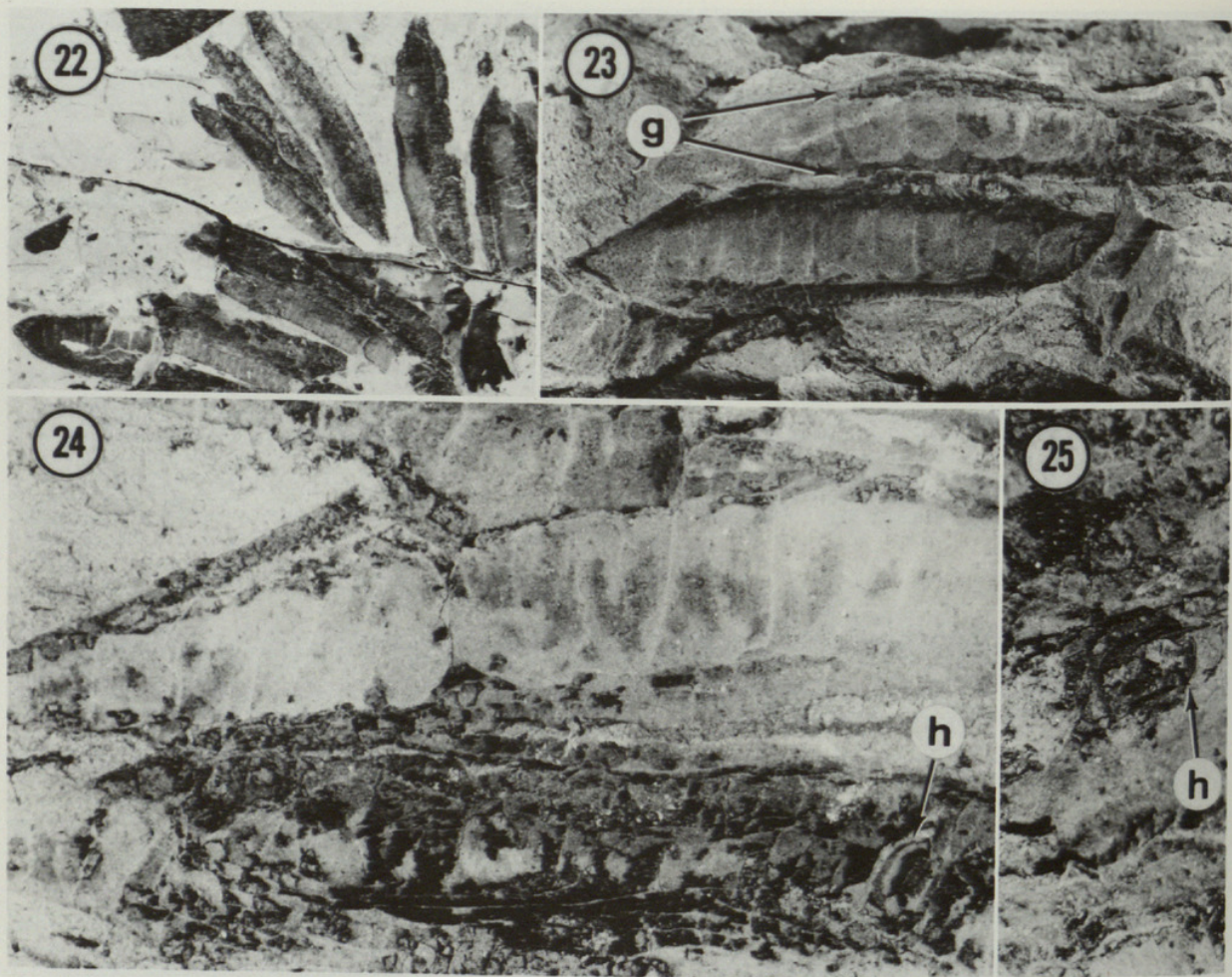
FIGURES 7–12. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—7. IU 15703-4145′. Showing several follicles attached to a long receptacular gynoecial zone, ×1.—8. IU 15703-3022. Showing a mass of compressed follicles associated with a broad, ridged receptacle, ×1.—9. IU 15703-4150. Branch showing the base of a receptacle with attached follicles. Note the clearly defined base (a) of the gynoecial zone, ×1.—10. IU 15703-4532. Gynoecial zone of a small, presumably aborted receptacle showing numerous linear, blunt-tipped carpels (compare Lesquereux, 1883: 73, pl. 11, fig. 6), ×1.—11. Detail of specimen in Figure 10 showing linear, blunt-tipped carpels, ×4.—12. Detail of specimen in Figure 9 showing: a. Base of gynoecial zone. b, c. Undifferentiated middle zone of receptacle. d. Large scar of outer perianth whorl delimiting the base of the flower, ×2.

FIGURES 13–21. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—13. IU 15703-2317. Isolated follicle showing penetration of sediment through the adaxial suture, which has preserved a three-dimensional cast of the locule, ×2.—14. Same specimen as Figure 13 with the locule cast removed to show the abaxial ridge on the follicle surface, ×2.—15. Locule cast of the same specimen as Figure 13 removed from the rock and showing penetration of sediment through the adaxial suture into the follicle, ×2.—16. Locule cast of the same specimen as Figure 13, abaxial view showing longitudinal ridge, ×2.—17. IU 15703-2318. Several follicles. Note the blunt, bilobed tip of the central follicle formed by the apical part of the adaxial crests, ×2.—18. IU 15703-4167. Isolated follicle with distorted stalk and blunt tip. Note penetration of sediment through the adaxial suture, ×2.—19. IU 15703-4157. Detail of apex of dorsi-ventrally compressed follicle showing blunt bilobed tip formed by the adaxial crests. Note median longitudinal groove in the abaxial surface of the follicle, ×4.—20. IU 15703-2318′. Detail of follicle base showing stalk and expanded attachment area, ×4.—21. IU 15703-2317. Detail of Figure 14 showing transverse cracks interpreted as cracks between the endocarp fibers, and small, slit-shaped depressions caused by resin-bodies in the follicle wall. Note the longitudinal ridge in the abaxial follicle surface, ×10.
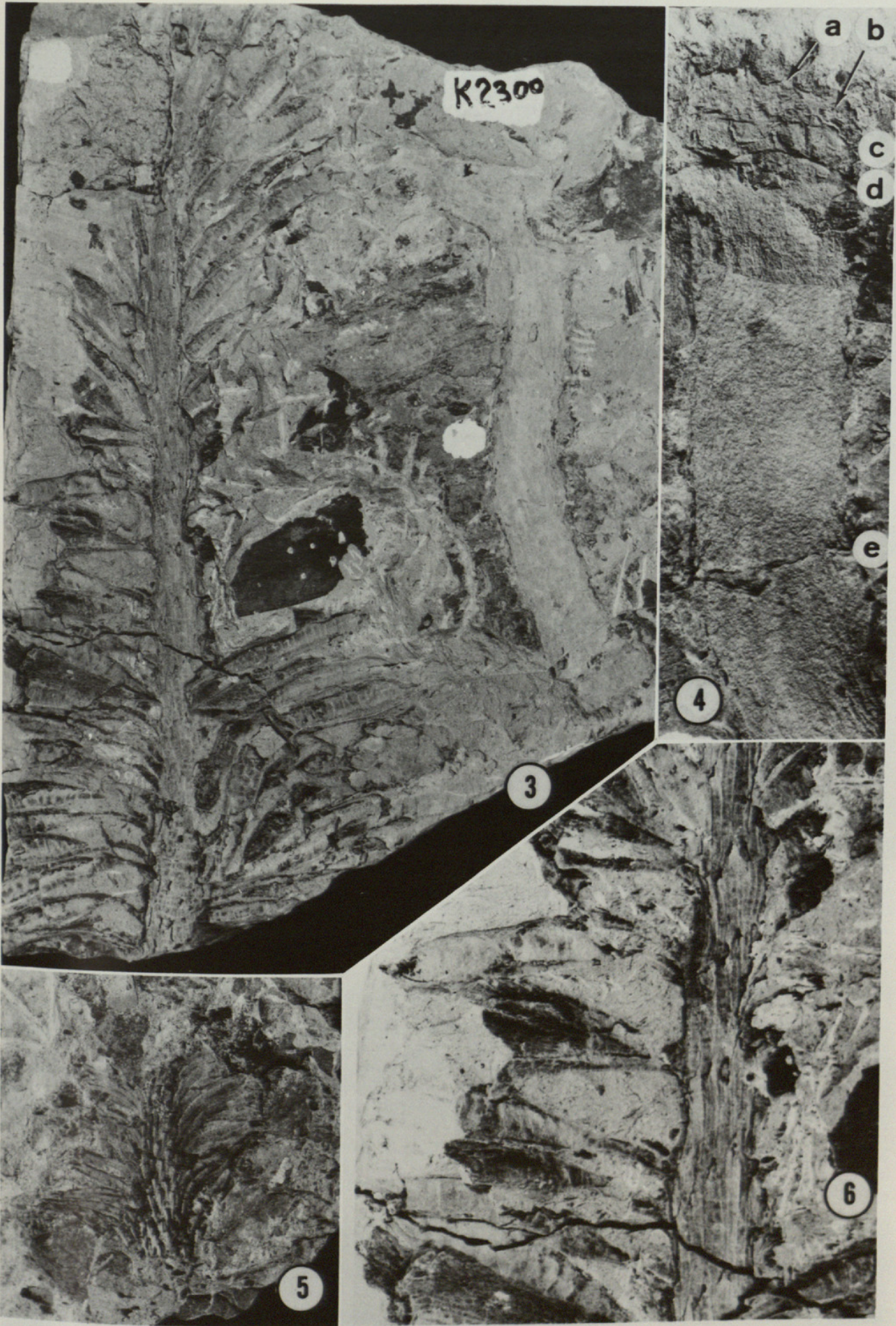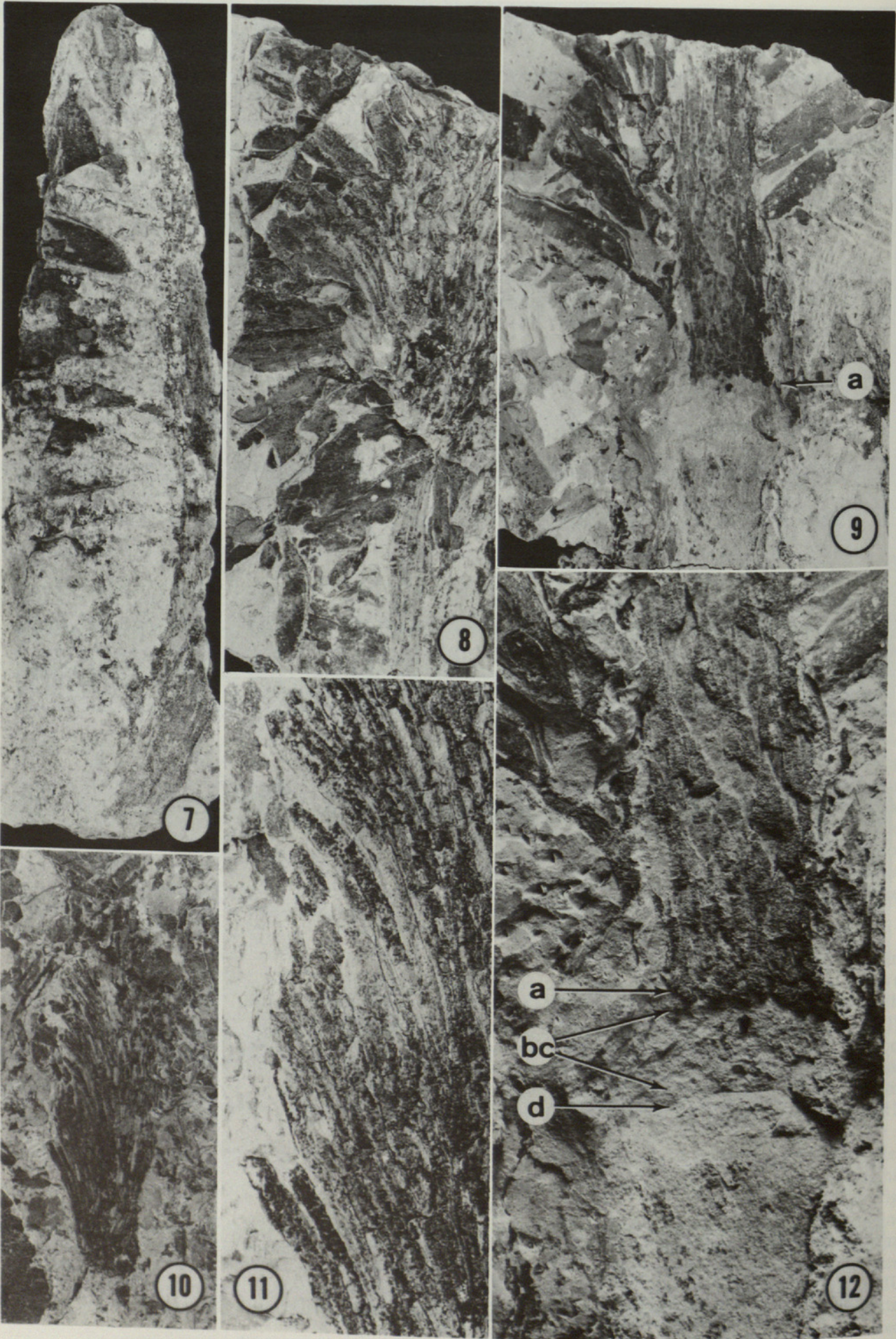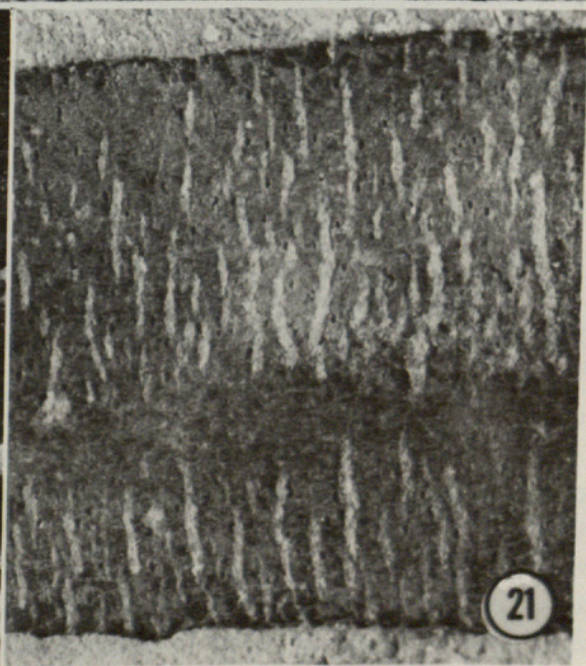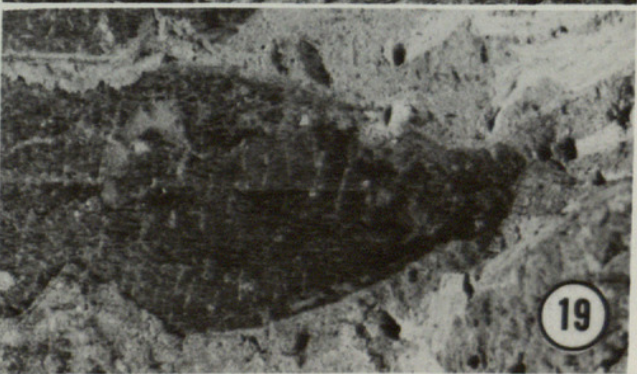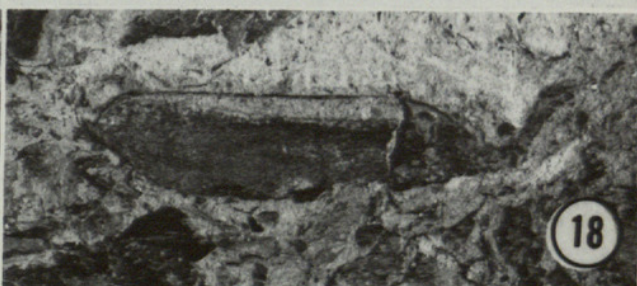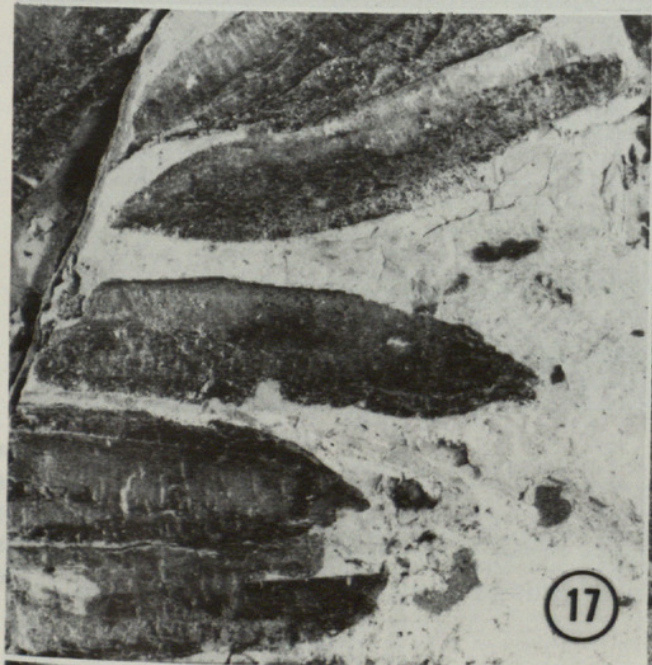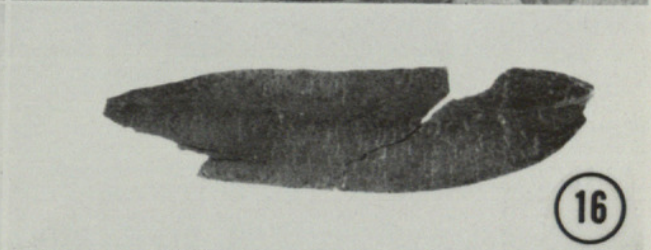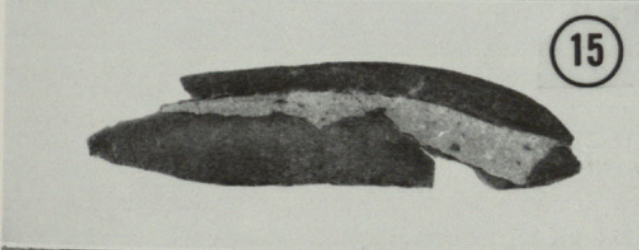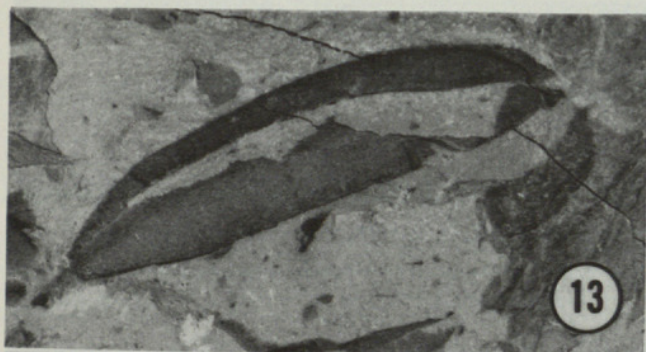
FIGURES 22–25. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—22. IU 15703-2318. Showing several follicles. Note the blunt follicle apices, ×1.—23. IU 15703-2300″. Detail of two laterally compressed follicles showing adaxial crests (g) and oval outlines attributed to the position of seeds. Note the restriction of seed outlines to the upper part of the follicle, ×3.—24. IU 15703-2300′. Detail of two laterally compressed follicles showing irregular outlines of seeds and one possible seed in situ (h), × 6.—25. IU 15703-2300′. Detail of follicle showing possible in situ seed (h), ×10.

with a single cutinized membrane, showing distinct cell outlines, delimited by very finely undulating anticlinal flanges. Pointed end heavily cutinized toward the tip, cell outlines more or less square, ca. 10 μm in both dimensions. Blunt end with a distinct, regular, oval to circular perforation, ca. 80 μm diam. Cell outlines in the median part of the membrane and near to the perforation elongated, 20–30 μm long, 5–10 μm wide.

Carpels, receptacle, and branches all contain numerous, yellow-brown lustrous, resin-bodies, (60–)70–100(–120) μm diam.

DISCUSSION: *Archaeanthus linnenbergeri* is known from 44 specimens, all preserved as compressions in a sandy, silty, brown-gray clay. Many have appreciable organic material remaining and have yielded anatomical details.

Three specimens (Figs. 1–4, 9, 12) show the manner in which the clusters of follicles (mul-

tifollicles) and, hence, flowers were borne singly at the apex of a stout, presumably woody axis. They suggest that the multifollicles may not have been shed at maturity. The three helically arranged scars on the vegetative branch (Fig. 1) are the correct size and shape to correspond to inflated, petiole bases, such as those of small *Liriophyllum* leaves. The upper scar is substantially larger than the lower two and presumably bore a larger leaf.

Two specimens (Figs. 10, 11, and IU 15703-4533) are immature, presumably aborted, gynoecial portions of the receptacle and are very similar to the '*Magnolia*' receptacle figured by Lesquereux (1883: 73, pl. 11, fig. 6). These specimens show that the gynoecium was elongated early in development and elongated further, perhaps passing through a stage represented by IU 15703-4136 (Fig. 5) as the fruits and seeds matured. The organization of the receptacle at maturity
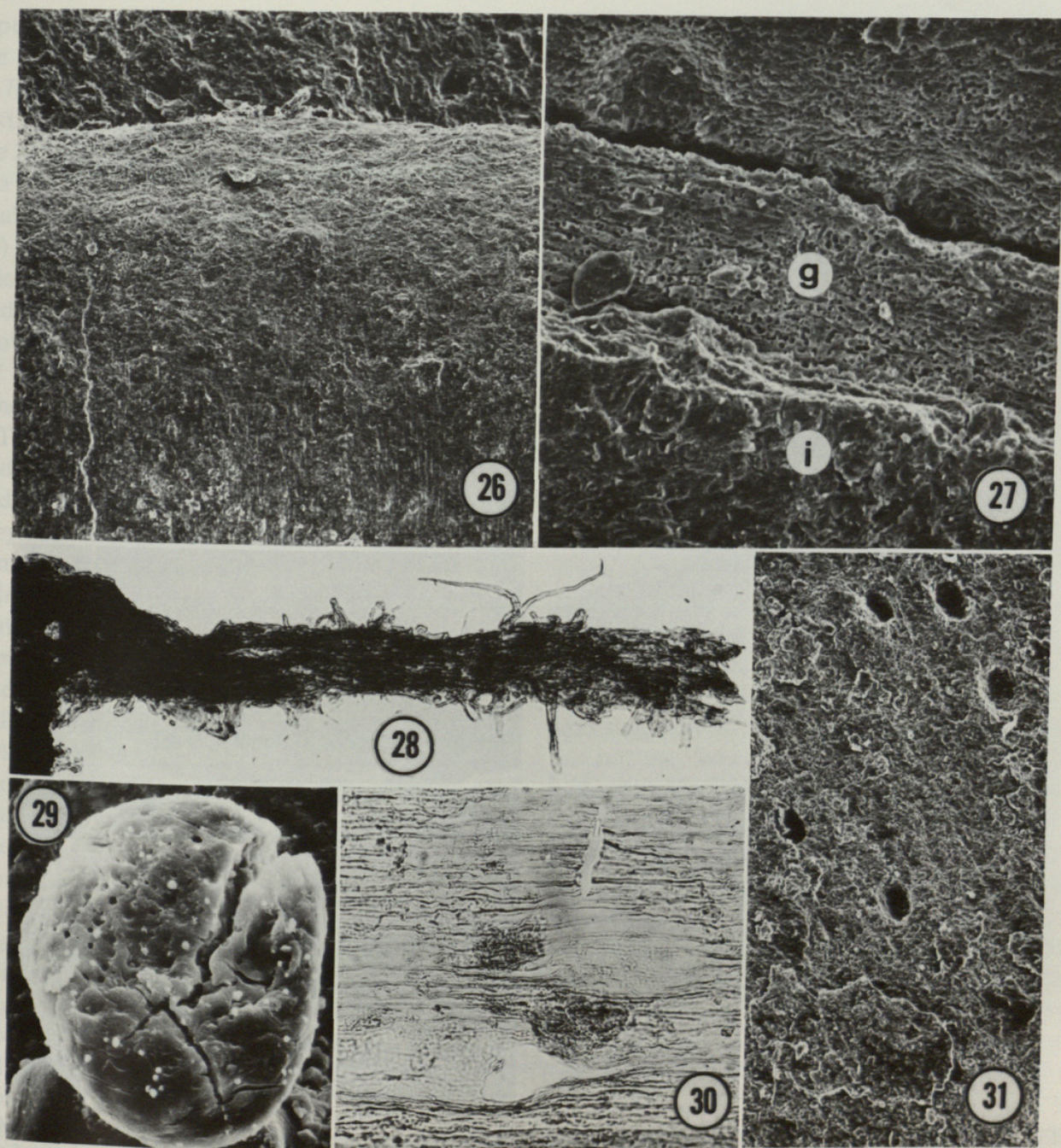
FIGURES 26–31. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—26. IU 15703-2300. Scanning electron micrograph showing impressions of fibers on the surface of a locule cast, ×50.—27. IU 15703-2300. Scanning electron micrograph showing impression of adaxial crest (g) and follicle wall (i). Note the difference in texture between the two areas and the two hemispherical depressions caused by resin-bodies, ×125.—28. IU 15703-2300. Light micrograph of cuticle isolated from an adaxial flange showing numerous simple trichomes, ×50.—29. IU 15703-2300. Scanning electron micrograph of a resin-body isolated from a follicle, ×450.—30. IU 15703-4105. Cuticle of locule surface showing elongated cell outlines and the distortions caused by resin-bodies, ×300.—31. IU 15703-4105. Scanning electron micrograph of surface of locule cast showing hemispherical depressions caused by resin-bodies, ×50.

is clear in the three specimens (Figs. 1–4, 9, 12) that have the base of the receptacle preserved, although none of our specimens show the complete length of the mature gynoecium with attached follicles. The most information can be seen on the axis with the lower part of a receptacle preserved on IU 15703-2300 (Figs. 3, 4). This axis has no attached follicles but is identified

with *A. linnenbergeri* by the numerous resin-bodies which it contains. It may be the lower part of the well-preserved gynoecium with attached follicles to which it is adjacent. By comparison with IU 15703-4150 (Figs. 9, 12), we interpret the four semicircular marks at the broken upper edge of this specimen (Fig. 4) to be the base of the gynoecial zone. Immediately be-
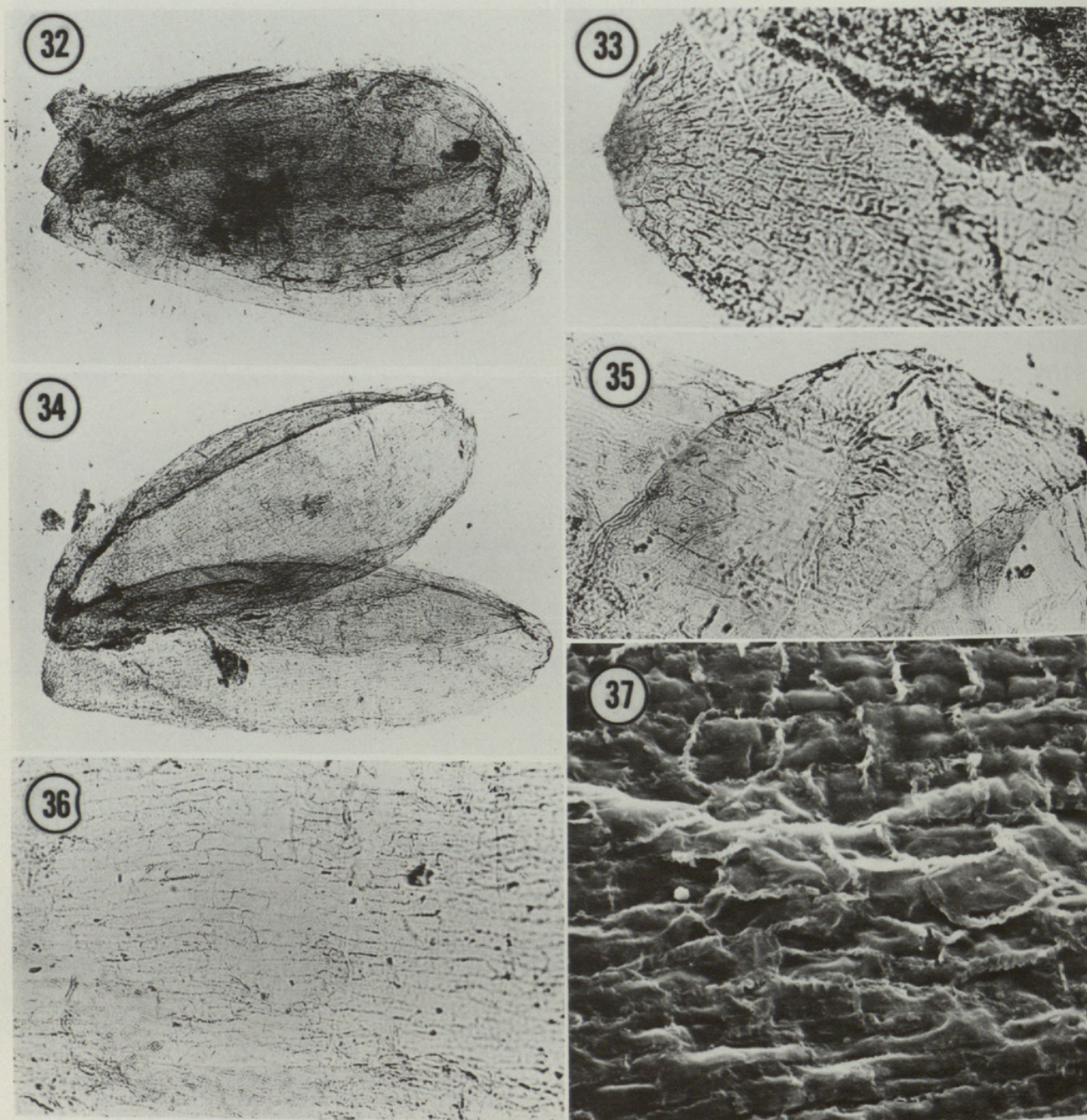
FIGURES 32–37. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—32. IU 15703-4105. Membranes macerated from follicle fragment interpreted as the nucellar or inner integumentary membrane of seeds or aborted ovules. Note the closely overlapping membranes, the strongly cutinized pointed tips interpreted as the micropylar ends, and the rounded bases with a circular perforation interpreted as the chalazal ends, ×30.— 33. IU 15703-4105. Detail of micropylar end of ovule membrane showing cutinized tip and more or less isodiametric cell outlines, ×200.—34. IU 15703-4105. Two ovule membranes, ×30.—35. IU 15703-4105. Detail of circular chalazal perforation, ×200.—36. IU 15703-4105. Detail of cells from central portion of ovule membrane showing finely undulating cell outlines, ×200.—37. Scanning electron micrograph of ovule membrane showing finely undulating cell outlines, ×500.

low these marks are laterally elongated elliptical scars; about 12 are clearly visible, and we estimate that this zone of the receptacle probably contained 50–60 such scars. We interpret them as indicating the former position of stamens. Below this point on the receptacle is another zone of larger scars in which two pairs are clearly visible. We estimate that in life there may have been

6–9 such scars around the receptacle and interpret them as indicating the former position of inner perianth parts. At the base of the flower there is an elliptical mark similar to the scars seen at the base of the flower in Figures 2 and 12. These are particularly distinct in IU 15703-4152 (Fig. 2) and suggest that there was a whorl of three narrowly elliptical scars around the re-

ceptacle base. These scars are similar to that at the base of *Archaepetala beekeri* (Fig. 38). IU 15703-4152 (Fig. 2) and 2300 (Fig. 4) show a distinct ridge on the pedicel 20–25 mm below the base of the flower. In both specimens there is a suggestion that the ridge bore two scars. By analogy with extant *Liriodendron tulipifera* (Fig. 63) and *Magnolia tripetala* (Figs. 61, 66), we interpret the ridge as the position of calyptra-like bud-scales. Below this ridge, IU 15703-4152 shows no branching or evidence of other flowers; IU 15703-2300 (Fig. 3), however, shows a large concave scar which we interpret as a branch point.

The two specimens of aborted receptacles show that the immature carpels were long, narrow, and had rounded tips (Figs. 10, 11). As they ripened, they increased both in length and width to become ellipsoidal at maturity.

Individual follicles are occasionally found separated from the receptacle, and there may have been a tendency for them to be shed at maturity. They broke away at the very base of each fruit stalk (Fig. 20) to leave clear scars on the receptacle (Fig. 6). A few carpels show one or several transverse cracks on their stalk, corresponding to the groove reported by Dilcher et al. (1976). They are not, however, consistent or significant morphological features, and there is no evidence for any structures subtending the individual carpels in this region or at the base of the stalk. We therefore reject any interpretation of *A. linnenbergeri* as a raceme of unifollicular flowers (Krassilov, 1977).

The follicles clearly dehisced along an adaxial suture, and the locule of many is filled with sediment (Figs. 13–16, 18). There is a prominent adaxial ridge on most of the better preserved follicles (Figs. 23, 24), and some carpel apices clearly show that this adaxial flange continued over the apex, wrapping around the end and giving a bilobed appearance to the carpel tips (Figs. 17, 19). SEM examinations of sediment with impressions of the flange show that it had a different texture to the outer follicle wall (Fig. 27). Cuticle preparations show that both flanges were furnished with long, simple hairs, perhaps related to the stigmatic surface in younger carpels (Fig. 28).

We have obtained only a thin cuticle from the inner surface of the endocarp (Fig. 30), but there are clearly at least two layers in the follicle wall. An inner layer of transverse fibers is indicated by the fine transverse striations seen on the internal locule casts of some specimens (Fig. 26) as well as the transverse cracks (Fig. 21), which we interpret as splits between the fibers. The cuticle of the inner follicle surface shows elongated cells with obvious distortions made by resin-bodies compressed into it (Fig. 30). Many of the resin-bodies are more or less spherical (Figs. 29, 31); others are elongated and seem themselves to have been distorted by the endocarp fibers (Figs. 21, 30). Where organic material or impressions of the outer carpel surface are preserved, they show no obvious cellular detail.

A few specimens of *A. linnenbergeri* show 10–18 more or less oval areas along the length of the follicles (Figs. 3, 23). These are always restricted to the adaxial two-thirds, or half, of laterally compressed follicles and may appear as depressions or raised areas, depending on how the fracture plane passed through the compression, and the extent to which the locule was filled with sediment. We interpret these areas as bulges and constrictions in the follicle wall caused by seeds, and suggest that about ten to 18 seeds matured in each pod. Some of the seed outlines are slightly pointed toward the adaxial margin, perhaps indicating attachment. Seed outlines are seen in relatively few specimens, and where present vary considerably in the regularity with which they are developed; in some follicles they are very regular, but in others the outlines are more confused and overlap, perhaps indicating more than one row of seeds compressed on top of each other. Only two follicles (Figs. 24, 25) show what may be seeds in situ, but they add nothing to our knowledge of their morphology. We have not been able to confidently recognize dispersed seeds in our collections.

The membranes that we have isolated from the carpels are small (Figs. 32–37), and crowded together (Fig. 32). They are variable in size; some may correspond to the seed outlines discussed above while others may be the remains of aborted ovules. Each membrane is a single structure that we suggest is probably the outer cuticle of the nucellus, or possibly the remains of the inner integument, which is extremely thin in extant *Magnolia* (Earle, 1938). Macerations of aborted ovules from *Magnolia tripetala* have yielded similar internal membranes from around the nucellus (Fig. 68). There is no megaspore membrane (Harris, 1954; Hill & Crane, 1982). We are not certain whether the ovules were anatropous or orthotropous. None of our specimens

show a raphe, but neither do the membranes from the anatropous ovules of *M. tripetala*. As far as we can tell, the ovules were oriented with the chalazal scar directed away from the suture and were therefore probably anatropous.

The ovules were attached below the base of the adaxial flanges and, like the seed outlines, are restricted to the upper half of the follicle. The ovules were numerous and borne overlapping (Fig. 32), presumably on either side of the suture. We estimate that each carpel probably contained about 100 ovules, but none of the locule casts show any indication of placental scars.

Archaepetala Dilcher & Crane, gen. nov. TYPE: *Archaepetala beekeri* Dilcher & Crane, sp. nov.

DIAGNOSIS: Simple, laminar, entire-margined, isolated, fossil petal-like structures.

DERIVATION: From *archae*—Greek, meaning beginning or first; *petalos*—Greek, meaning broad, flat, outspread.

DISCUSSION: This genus is established as a broad form-genus for accommodating isolated, fossil petal-like structures with the above morphology.

Archaepetala beekeri Dilcher & Crane, sp. nov.
HOLOTYPE: IU 15703-3179.

DIAGNOSIS: Lamina elliptical, length-to-width ratio approximately 2:1. Base with a prominent attachment area, apex rounded. Lamina with a broad rib running from the base to the apex.
OTHER MATERIAL: IU 15703-3882.
NUMBER OF SPECIMENS EXAMINED: 2.
FIGURES: 38, 41, 44, 60d.
DERIVATION: After Mr. Charles Beeker, who helped collect much of the material from Linnenberger Ranch.
DESCRIPTION: Lamina simple, elliptical, 70–80 mm long, ca. 40 mm wide (maximum); length-to-width ratio approximately 2:1. Margin entire. Base with a prominent scar that is rounded above,

straight below, and pointed at either end; 14 mm wide, 5 mm high. Apex rounded. Lamina with a broad midrib of numerous fine striations running from the attachment area at the base to the apex (further details of venation not seen). Midrib the same width as the attachment area proximally, narrowing distally, 4–6 mm wide in the central part of the lamina. Surface of lamina wrinkled with fine, irregular areolae ca. 0.3–0.8 mm diam. and with numerous spherical resinbodies (60–)80–100(–110) μm diam.

DISCUSSION: *Archaepetala beekeri* is known from only two specimens (Figs. 38, 41), but both are almost complete. They show evidence of having been at least partially rigid with some three-dimensional curvature in life. The surface texture imparted by the wrinkles and irregular small areolae is distinctive and like that seen in *Kalymmanthus walkeri*, making fragmentary specimens difficult to separate. We are uncertain as to the cause of these areolae, but they could result from clusters of harder cells, such as sclerenchyma, in the lamina.

The shape and size of the attachment area on *A. beekeri* is very similar to the three scars that occur at the base of the receptacle in *Archaeanthus linnenbergeri*. For this and other reasons discussed later (see Reconstruction of the *Archaeanthus* Plant), we suggest that *A. beekeri* are the outer perianth parts of *Archaeanthus* flowers. The irregular wrinkled surface is similar to that of certain dried *Magnolia* perianth parts.

Archaepetala obscura Dilcher & Crane, sp. nov.
HOLOTYPE: IU 15703-2266.

DIAGNOSIS: Lamina obovate, length-to-width ratio approximately 1.5:1; ca. 18 evenly spaced, more or less parallel veins diverging slightly from the base.
NUMBER OF SPECIMENS EXAMINED: 1.
FIGURES: 40, 45, 60c.
DERIVATION: From *obscurus*—Latin, meaning

FIGURES 38–46. Other organs attributed to the *Archaeanthus linnenbergeri* plant.—38. *Archaepetala beekeri* Dilcher & Crane, gen. et. sp. nov., IU 15703-3179. Showing broad midrib and attachment point at the base, ×1.—39. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-2747. Showing bilobed apex and narrow midrib, ×1.—40. *Archaepetala obscura* Dilcher & Crane, sp. nov., IU 15703-2266. Showing poorly defined, straight, veins diverging toward the apex, ×1.—41. *Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov., IU 15703-3822. Poorly preserved specimen showing broad midrib, ×1.—42. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-4115. Showing bilobed apex, broad midrib, and concave point of attachment, ×1.—43. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-4114. Showing bilobed
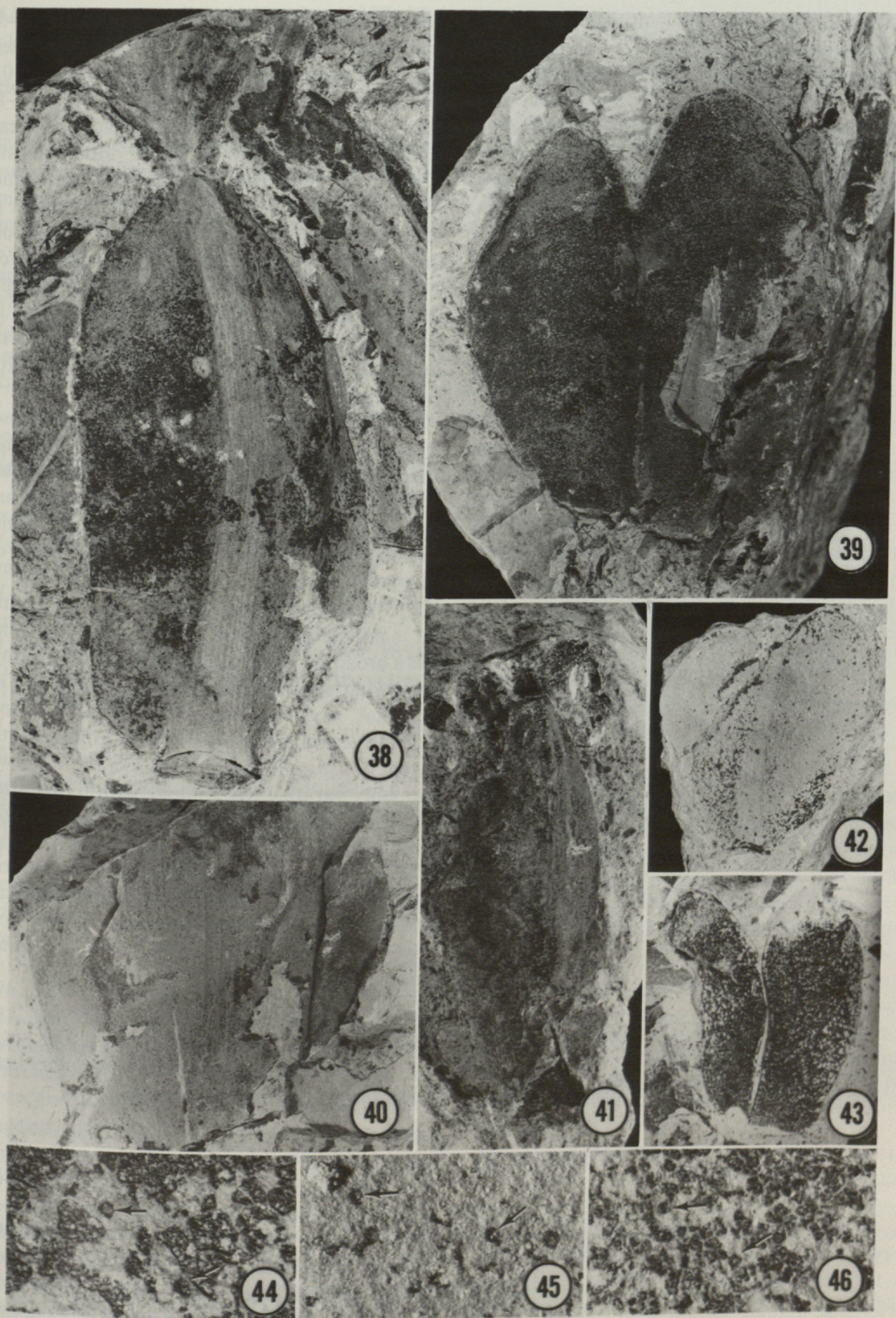
apex and the split along the line of the midrib, ×1.5.—44. *Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov., IU 15703-3179. Detail showing resin-bodies (arrows), ×15.—45. *Archaepetala obscura* Dilcher & Crane, sp. nov., IU 15703-2266. Detail showing resin-bodies (arrows), ×15.—46. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-2747. Detail showing resin-bodies (arrows), ×15.

indistinct, and referring to the unknown apex and base of the holotype.

DESCRIPTION: Lamina simple, obovate, estimated lamina length 80 mm, ca. 50 mm wide (maximum); length-to-width ratio approximately 1.5:1. Margin entire (base and apex unknown). Lamina with ca. 9 prominent, more or less parallel veins diverging slightly from the base. A single, more weakly developed vein present in each space between the more prominent veins. Prominent veins linked by a reticulum in the distal part of the lamina. Texture of lamina smooth; the substance of the lamina thin and containing numerous spherical resin-bodies, (80–)90–100(–130) μm diam.

DISCUSSION: *Archaepetala obscura* is known from only a single fragmentary but distinctive specimen (Fig. 40), which was folded prior to compression. The shape and venation of *A. obscura* is very petal-like, but we cannot be certain of its botanical nature. However, we suggest that it may have formed an inner perianth immediately above the three large scars that, in our view, bore the *A. beekeri* parts.

Kalymmanthus Dilcher & Crane, gen. nov. TYPE: *Kalymmanthus walkeri* Dilcher & Crane, sp. nov.

DIAGNOSIS: Lamina broadly elliptical to broadly ovate, bilobed. Length-to-width ratio approximately 1.2:1. Base straight or slightly concave, lacking an obvious attachment area. Apices of lobes broadly rounded. Lamina with a rib running from the base of the sinus.

DERIVATION: From *kalymma*—Greek, meaning a covering or hood; *anthos*—Greek, meaning flower.

DISCUSSION: This genus is established as a broad form-genus for accommodating isolated, fossil bud-scale, stipule, or calyptra-like structures.

Kalymmanthus walkeri Dilcher & Crane, sp. nov.
HOLOTYPE: IU 15703-2747.
DIAGNOSIS: As for the genus.
OTHER MATERIAL: IU 15703-4114, IU 15703-4115.
NUMBER OF SPECIMENS EXAMINED: 3.
FIGURES: 39, 42, 43, 46, 60e.
DERIVATION: After Mr. Merle Walker, who aided in the discovery of the Linnenberger Ranch locality and has given us considerable assistance during our collecting in central Kansas.
DESCRIPTION: Lamina broadly elliptical to broadly ovate, bilobed; 26–65 mm long, 21–50 mm wide. Length-to-width ratio approximately 1.2:1. Margin entire with a prominent lip 0.5 mm wide. Base straight or slightly concave 6–15 mm wide, lacking an obvious attachment scar. Apices of lobes broadly rounded; lobes typically 0.3–0.2 of the lamina length, but sometimes splitting beyond the original sinus to the base of the lamina. Lamina with a midrib running from the base to the sinus, midrib either narrow, ca. 1 mm wide, or slightly broader and tapering distally. Surface of lamina wrinkled with fine, irregular areolae ca. 0.3–0.8 mm diam., and with numerous resin-bodies typically (60–)80–100 (–110) μm diam.

DISCUSSION: *Kalymmanthus walkeri* is known from three specimens (Figs. 39, 42, 43). Other specimens with the distinctive areolate surface texture do occur at the Linnenberger locality, and although they cannot be confidently distinguished from fragments of *A. beekeri*, some do show a marginal lip, like that in *K. walkeri*. In IU 15703-4115 (Fig. 42), however, this marginal lip is not clearly visible, and the same specimen has a broad rib running from the base to the sinus somewhat similar to that in *A. beekeri*. We interpret *K. walkeri* as bud-scales, probably of both vegetative and flowering shoots. At maturity, the extent of the split along the line of the sinus was probably variable. By analogy with living *Magnolia*, the bud-scales may be of stipular origin, although none of our specimens show any sign of a leaf lamina attached to an extended midrib. Our specimens are unlike the putative bud-scale described and figured by MacNeal (1958) from the Cenomanian Woodbine Sand flora of Denton County, Texas.

Liriophyllum Lesq. (1878) emend. Dilcher & Crane. TYPE: *Liriophyllum populoides* Lesq. (designated by Berry, 1902a: 55).

EMENDED GENERIC DIAGNOSIS: Leaf petiolate, bilobed, deeply divided for at least half its length. Venation pinnate. Midrib stout extending to the base of the sinus and forking into two prominent veins, distinct from the secondary veins below, which form the leaf margin typically for about 0.3–0.16 of the lobe length. Above this point the lamina arches away from the vein into the sinus and broadens distally to form each lobe.

SPECIES EXCLUDED FROM THE GENUS: *Liriophyllum obcordatum* Lesq. (1883: 77).

Liriophyllum obcordatum Lesq. (1892: 210, pl. 28, fig. 7).

Liriophyllum sachalinense Krysht. (1937: 85, pl. 12, figs. 4–6).

Liriophyllum populoides Lesq. emend. Dilcher & Crane. HOLOTYPE: USNM 2079.

EMENDED DIAGNOSIS: Petiole with a proximal, laminar, alate appendage in its lower part. Appendage attached along its full length, entire margined, rounded and tapering above.

SYNONYM: *Liriophyllum beckwithii* Lesq.

REFERENCES: *Liriophyllum beckwithii* Lesq. (1878: 482–483, brief description).

Liriophyllum populoides Lesq. (1878: 482–483, brief description).

Liriophyllum beckwithii Lesq. (1883: 75, pl. 10, fig. 1, generic diagnosis, specific diagnosis, discussion, and line drawing).

Liriophyllum populoides Lesq. (1883: 76, pl. 11, figs. 1–2, specific diagnosis, description, and line drawings).

Liriophyllum beckwithii Lesq. (1892: 210, mention only).

Liriophyllum populoides Lesq. (1892: 211, mention only).

Liriophyllum populoides Lesq. (Hollick, 1894: 470–471, pl. 221, brief description, discussion, and line drawing).

Liriophyllum populoides Lesq. (Holm, 1895: 316, brief discussion of affinities).

Liriophyllum populoides Lesq. (Hollick, 1896: 249, pl. 269, fig. 2, brief discussion and line drawing).

Liriophyllum Lesq. (Berry, 1902a: 47–56, brief discussion and comparison with putative fossil *Liriodendron*, p. 55, takes *Liriophyllum populoides* as the type species of the genus).

OTHER MATERIAL: Morrison, Colorado, USNM 2076, 2078 (two leaves), 2080, 2135, 2142; HU 2881, 2882, 2883, 2884, 2885, 2888, 2892, 2897.

NUMBER OF SPECIMENS EXAMINED: 15.

FIGURES: 47–50.

DESCRIPTION: Leaves petiolate. Outline of lamina square to broadly ovate, 90–185 mm long, 85–240 mm wide, broadest in the lower quarter of the lamina. Lamina bilobed, deeply divided for at least half its length. Midrib stout 1–2 mm wide, 23–36 mm long, extending to the base of the sinus and forking at an angle of 45–70° into two prominent veins that form the leaf margin in the lower part of the sinus. Veins contiguous with the sinus margin for 8–25 mm, typically about 0.25–0.16 of the lobe length. Above this the lamina arches away from the veins into the sinus and broadens distally to form each lobe. Each fork of the midrib enters the distal part of

the lobe, branching several times, and gradually becoming finer. Apex of each lobe rounded, lateral margins more or less straight, slightly convex or prominently concave, and forming two distinct lobes on either side of the midrib. Leaf base obtuse or acute, straight or decurrent where it joins the petiole.

Secondary venation pinnate, camptodromous; 2–3 secondary veins on either side of the midrib, alternately arranged, more or less decurrent. Angle of divergence of secondary veins 40–50°. Secondary veins branching well within the margin. (Details of finer venation not preserved.) Extreme base of lamina with two basal veins of secondary or intermediate secondary-tertiary order. Petiole to 27 mm long (longest specimen incomplete) with a proximal, laminar, alate appendage in its lower part. Appendage 13 mm wide, including the petiole, attached along its entire length; entire margined, rounded and tapering above.

Liriophyllum kansense Dilcher & Crane, sp. nov. HOLOTYPE: IU 15703-2272.

SPECIFIC DIAGNOSIS: Petiole simple, lacking a proximal, laminar, alate appendage.

REFERENCES: *Liriophyllum beckwithii* Lesq. Dilcher et al. (1976: 854–856, fig. 1e, f, description, discussion, and photograph).

Liriophyllum Lesq. Dilcher et al. (1978: 11, brief mention and line drawing).

Liriophyllum sp. Retallack and Dilcher (1981c: 39, figs. 2–14, brief mention and photograph).

OTHER MATERIAL: Linnenberger's Ranch IU 15703; 2267, 2271–2277, 2309, 2456, 2463–2466, 2469–2471, 2473, 2475–2477, 2479, 2480, 2482, 2484, 2485, 2487, 2488, 2492, 2493, 2679, 2948, 3443, 3813, 3816–3818, 3823, 3826, 3827, 3836, 3839, 3859, 3885, 3886, 3890, 3894, 3895, 3992, 4028, 4029, 4051, 4120.

NUMBER OF SPECIMENS EXAMINED: Fort Harker, Kansas, USNM 2718. Fifty-four and numerous other fragments.

FIGURES: 51–59, 60b.

DESCRIPTION: Leaves petiolate. Outline of lamina square to very broadly ovate, (60–)100(–140) mm long, (64–)120(–186) mm wide, typically broadest in the lower quarter of the lamina. Lamina bilobed, deeply divided for at least half its length. Midrib stout 1–3 mm wide (10–)20–30 (–44) mm long extending to the base of the sinus and forking at an angle of (40–)60–70(–80)° into two prominent veins that form the leaf margin in the lower part of the sinus. Veins forming the sinus margin for (15–)25(–48) mm, typically
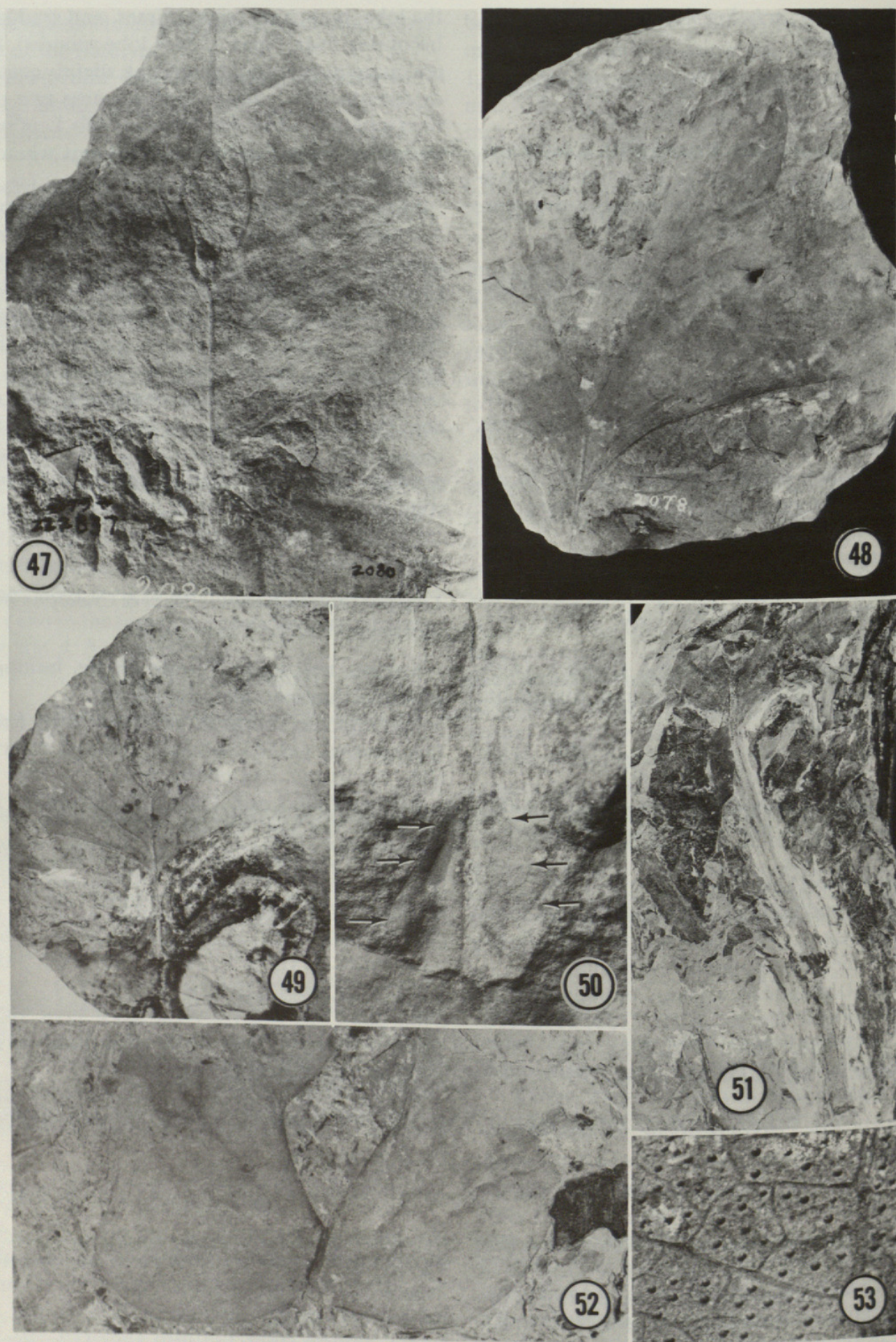
FIGURES 47–53. 47. *Liriophyllum populoides* Lesq., USNM 2080. Figured by Lesquereux (1883, pl. 11, fig. 2). Note also the structure at the bottom right, *Carpites liriophylli* Lesquereux (1883, pl. 11, fig. 5), which may be an isolated *Archaeanthus* follicle, ×0.75.—48. *L. populoides* Lesq., USNM 2078. Figured by Lesquereux (1883, pl. 10, fig. 1). Note the two lobes in the right side of the lamina, ×0.3.—49. *L. populoides* Lesq., USNM 2078. Specimen on the reverse of block in Figure 48, not figured by Lesquereux. Note the long petiole, ×0.5.—

about 0.3–0.25 of the lobe length. Above this the lamina arches away from the veins into the sinus and broadens distally to form each lobe. Each fork of the midrib enters the distal part of the lobe, branching 4 or 5 times and gradually becoming finer. Apex of each lobe broadly rounded, lateral margins more or less straight, occasionally concave or slightly convex. Leaf base shallowly cordate, acute or obtuse, straight, or more typically decurrent, where it joins the petiole.

Secondary venation pinnate, camptodromous; (2–)4(–5) secondary veins on either side of the midrib, alternately arranged, frequently more or less decurrent. Angle of divergence of secondary veins gradually decreasing apically, up to 90° at the base, ca. 30° distally. Secondary veins branching and becoming finer well within the margin to form weak, camptodromous loops, typically of tertiary order. Extreme base of lamina with 2 basal veins of secondary or intermediate secondary/tertiary order. Angle of divergence of tertiary venation variable, but tertiary veins frequently more or less decurrent where they join the secondaries and the midrib. Toward the margin, tertiary, quaternary, and quinternary veins forming polygonal areolae, frequently more or less elongated toward the center of the leaf; areolae often more regular, pentagonal and orthogonal toward the margin. Areolae open; vein endings simple and compound. Pattern of venation equivalent to leaf rank 2 or 3 (Hickey, 1977). Petiole to 100 mm long, 2–4 mm wide, simple, with no alate appendage, swollen to 6 mm at the base with a terminal crescentic abscission scar. Leaf mesophyll containing spherical, yellow-brown resin-bodies (50–)80–100(–110) μm diam.

DISCUSSION: All of the specimens of *Liriophyllum populoides* are from the Kassler Sandstone of the South Platte Formation near Morrison, Colorado. Lesquereux (1878, 1883) recognized three species in the Kassler Sandstone collection. *Liriophyllum beckwithii* and *L. populoides* have a very distinctive morphology and venation and are synonymized as variants of one species. *Liriophyllum obcordatum* does not show

these diagnostic features, particularly the bifurcation of the midrib, and we have excluded it from the genus (Berry, 1902a). We also exclude *Liriophyllum sachalinense* Kryshtofovich (1937), which subsequently has been referred to *Bauhinia* by Vakhrameev (1966), Takhtajan (1974), and Tanai (1979). Lesquereux did not designate a type species for *Liriophyllum,* and although Andrews (1966) cites the first named species *L. beckwithii,* we follow Berry (1902a) in taking *L. populoides* as the type. The specimens of *L. populoides* from the Kassler Sandstone (Figs. 47–50) are poorly preserved but are clearly very similar to the *Liriophyllum* leaves from Kansas. The only significant feature in which they differ is the presence of an alate appendage attached to the proximal part of the petiole in *L. populoides.* Hollick (1894, 1896) was the first to call attention to this feature, but it is also shown by a *Liriophyllum populoides* leaf (Figs. 49, 50) on the same block as one of the specimens figured by Lesquereux (1883). The other specimens in Lesquereux's original collection have too little of the petiole preserved to show whether the appendage was present. None of the *Liriophyllum kansense* specimens, some of which have the complete petiole preserved (Fig. 51), shows any sign of an alate petiolar appendage. Although the two species do show a suggestion of other subtle differences, for example, the pronounced lateral lobes of USNM 2078 (Fig. 48) and variations in the prominence of the forks of the midrib, we have too little *L. populoides* material from Colorado to evaluate the patterns of variation in these characters more carefully. The difference in petiole is our primary reason for formally recognizing two distinct species. The alate petiolar appendage of *L. populoides* has been interpreted by Hollick (1894, 1896) as an early stage in the formation of the prominent stipules of *Liriodendron.* In view of the features of the *Archaeanthus* with which these leaves are now known to be associated (see Reconstruction of the *Archaeanthus* Plant), such a hypothesis seems more plausible. We do not pursue this point further here but merely point out that we have no good evi-

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50. *L. populoides* Lesq. Same specimen as Figure 49 showing alate appendage attached to petiole (arrows), ×1.—51. *L. kansense* Dilcher & Crane, sp. nov., IU 15703-4029. Complete petiole showing expanded base and absence of alate appendage, ×0.5.—52. *L. kansense* Dilcher & Crane, sp. nov., IU 15703-2464′. Showing dichotomy of midrib and the veins forming the sinus margins, ×1.—53. *L. kansense* Dilcher & Crane, sp. nov., IU 15703-2317. Detail of leaf fragment from the same block as Figures 13–16 showing ultimate venation and hemispherical depressions caused by resin-bodies, ×15.
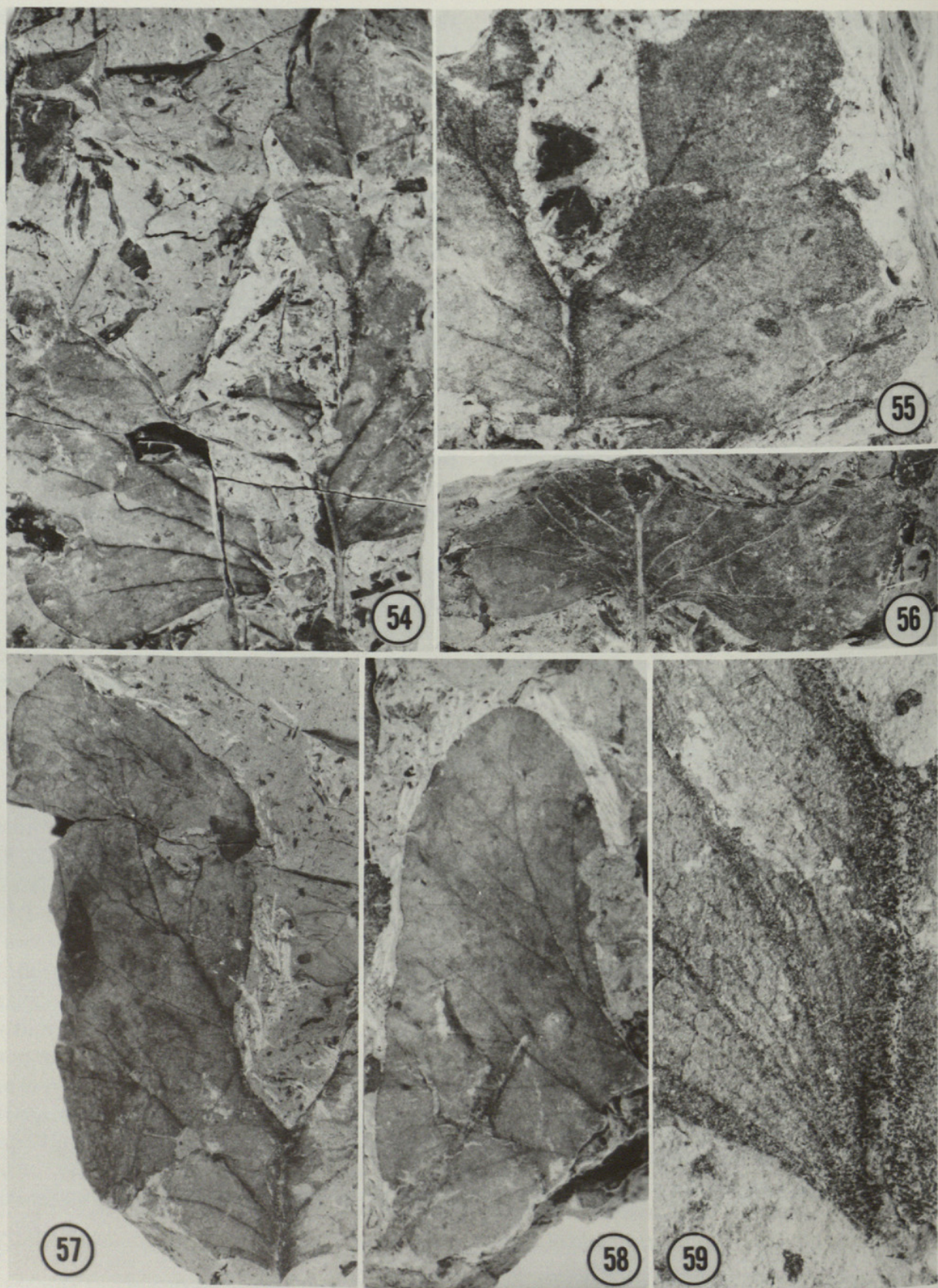
Figures 54–59.   *Liriophyllum kansense* Dilcher & Crane, sp. nov.—54. IU 15703-2272. Large leaf showing characteristic venation, ×0.5.—55. IU 15703-2463. Leaf fragment showing major venation, ×1.—56. IU 15703-2477. Fragment of large leaf base. Note the cordate leaf lobes bond the lamina decurrent down the petiole, ×0.5.—57. IU 15703-2469. Leaf lobe with well-preserved venation, ×1.—58. IU 15703-2479. Leaf lobe, ×1.—59. IU 15703-2472. Detail of midrib and fine venation, ×4.5.
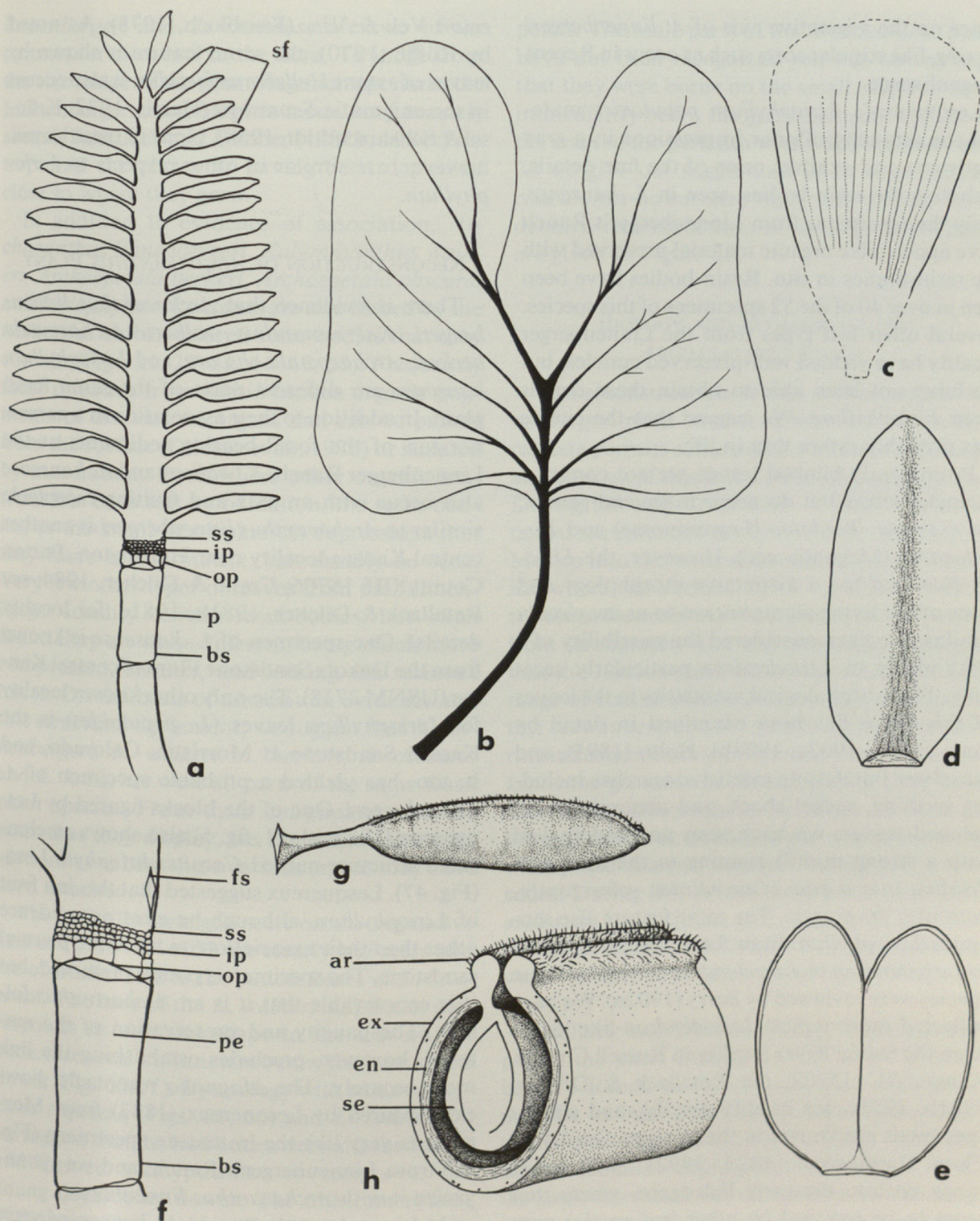
FIGURE 60.   Reconstructions of parts of the *Archaeanthus linnenbergeri* plant.—a. *Archaeanthus linnenbergeri*, diagram showing the organization of the multifollicle.—b. *Liriophyllum kansense* leaf showing major venation.—c. *Archaepetala obscura*, inner perianth part.—d. *Archaepetala beekeri*, outer perianth part.—e. *Kalymmanthus walkeri*, bud-scale.—f. *Archaeanthus linnenbergeri*, diagram of the base of the multifollicle.—g. *Archaeanthus linnenbergeri*, reconstruction of a single follicle.—h. *Archaeanthus linnenbergeri*, section through a follicle. sf, stalked follicles; ss, staminal scars; ip, inner perianth scars; op, outer perianth scars; pe, pedicel; bs, bud-scale scars; ar, adaxial ridge; ex, exocarp containing resin-bodies; en, endocarp of transverse fibers; se, anatropous seed borne adaxially.

dence on the vegetative axis of *A. linnenbergeri* for ring-like stipular scars such as occur in Recent Magnoliaceae.

Lesquereux's *Liriophyllum populoides* material consists only of poor impressions in a gray sandstone and exhibits none of the fine details, including the resin-bodies, seen in *L. kansense*. Only the specimens from Linnenberger's Ranch have appreciable organic material preserved with the resin-bodies in situ. Resin-bodies have been seen in over 40 of the 52 specimens of this species. Several other leaf types from the Linnenberger locality have yielded well-preserved cuticles, but we have not been able to obtain these details from *Liriophyllum*. We suggest that the cuticle was probably rather thin in life.

Prominently bilobed leaves are not common in angiosperms but do occur in several genera; for example, *Bauhinia* (Leguminosae) and *Liriodendron* (Magnoliaceae). However, the *Liriophyllum* leaf has a distinctive morphology and none of the living plants known to us are closely similar. We have considered the possibility of a relationship to *Liriodendron* particularly carefully. The morphological variability in the leaves of this genus has been examined in detail by Berry (1901, 1902a, 1902b), Holm (1895), and ourselves, but despite extensive searches including seedling, sucker-shoot, and abnormally developed leaves, we have seen no modern leaf with a strong midrib running to the apex and *dividing into a pair of prominent veins contiguous with the margin.* The same feature also separates *Liriophyllum* from fossil species assigned to *Liriodendron* or *Liriodendropsis* Newb. These species were reviewed by Berry (1902a). We have collected more typical *Liriodendron*-like leaves from the Saline River locality in Russell County, Kansas (IU 15702; see Retallack & Dilcher, 1981b, 1981c, for locality details), and similar specimens are known in the 'Dakota Sandstone Flora' (Lesquereux, 1883, 1892). Such leaves range up into the early Paleogene, where they seem to be replaced by other leaf species even more similar to extant *Liriodendron*. Curiously, only one *Liriophyllum* leaf is known from the 'Dakota Sandstone Flora' of Kansas and Nebraska.

The distinct inequilateral development of the lamina exhibited by *Liriophyllum* also occurs in several other mid-Cretaceous leaves such as *Fontainea grandiflora* (Newberry, 1895: 96, pl. 45), *Halyserites reichii* Sternb., *Halyserites elegans* (Vel.) Knobloch, and *Diplophyllum creta-*

ceum Vel. & Vin. (Knobloch, 1978). As noted by Rüffle (1970), the same feature is shown by leaves of extant *Helleborus foetidus*; it also occurs in the enigmatic *Scoresbya* (Harris, 1932; Kräusel & Schaarschmidt, 1968). None of these leaves, however, are similar in other respects to *Liriophyllum*.

Reconstruction of *Archaeanthus* Plant

There is evidence that *Archaeanthus linnenbergeri*, *Kalymmanthus walkeri*, *Archaepetala beekeri*, *Archaepetala obscura*, and *Liriophyllum kansense* are different parts of the same fossil plant. In addition to their association in a narrow horizon of the fossil-bearing sediments at the Linnenberger Ranch, *K. walkeri* and *L. kansense* also occur with an axis and fruiting receptacle similar to *Archaeanthus linnenbergeri* at another central Kansas locality near Hoisington, Barton County (IU 15706; Crane & Dilcher, 1984; see Retallack & Dilcher, 1981b, 1981c, for locality details). One specimen of *L. kansense* is known from the Dakota Sandstone Flora of central Kansas (USNM 2718). The only other known locality for *Liriophyllum* leaves (*L. populoides*) is the Kassler Sandstone at Morrison, Colorado, and it, too, has yielded a probable specimen of *A. linnenbergeri*. One of the blocks figured by Lesquereux (1883, pl. 11, fig. 5) also shows an elongated structure named *Carpites liriophylli* Lesq. (Fig. 47). Lesquereux suggested that this is a fruit of *Liriophyllum*, although he cites no evidence other than their association on the same piece of sandstone. The specimen is poorly preserved, but it is conceivable that it is an *Archaeanthus* follicle. The paucity and preservation of the material, however, precludes establishing the link more securely. The *Magnolia* receptacle, however, figured by Lesquereux (1883) from Morrison is very like the immature specimens (Fig. 10) from Linnenberger's Ranch, and we synonymize it with *Archaeanthus linnenbergeri*.

At Linnenberger's Ranch, *L. kansense* leaves and *A. linnenbergeri* are particularly abundant in a silty, gray clay, with occasional sand stringers, that is ca. 30 cm thick and occurs 3 m below the base of the sandstones which cap the section. In this distinct horizon immediately below the major plant bearing clays, these two species are the commonest plant fossils and occur matted together on the same bedding plane. Considering the Linnenberger flora as a whole, the taxonomic diversity of the plant assemblage is low, and *A.*

linnenbergeri and *L. kansense* are two of the commoner elements in the flora. To judge from the size range of the plant fragments present, the Linnenberger assemblage is mixed and scarcely sorted; Retallack and Dilcher (1981b, 1981c) interpreted the plants as having been deposited close to where they grew.

In addition to evidence of association, *Archaeanthus linnenbergeri, Kalymmanthus walkeri, Archaepetala beekeri, Archaepetala obscura,* and *Liriophyllum kansense* are also linked by the numerous amber-colored resin-bodies that they contain (Figs. 21, 29–31, 44–46, 53). Frequently these protrude from within broken organic fragments of the various organs and can be picked from the surface (Dilcher et al., 1976) or isolated by maceration. Even where other organic material has been lost by oxidation, the resin-bodies, or the small hemispherical depressions that they leave in the matrix, can usually be seen. Very few other types of leaves from the Linnenberger locality contain resin-bodies, but when found they are quite different, being much more compressed, smaller, and lacking the resinous luster. On the basis of association evidence and this structural agreement, we suggest that *A. linnenbergeri, K. walkeri, A. beekeri, A. obscura,* and *L. kansense* were all parts of the same fossil plant species. From their morphology and the scars that they display, we can make some suggestions as to how these various organs may have been attached.

The helically arranged scars on the vegetative axis of IU 15703-4152 are clearly leaf scars and are of similar size to the petiole bases of *L. kansense.* The base of the *K. walkeri* bud-scales corresponds in size and shape to the scar on the pedicel several millimeters below the base of the flower (Fig. 60a, f). By analogy with extant *Magnolia tripetala* (Figs. 61, 66) and *Liriodendron,* we suggest that the bud-scales were attached there and formed a calyptra-like covering over the young developing flower. The attachment area at the base of *A. beekeri* (Fig. 38) corresponds in size and shape to one of the three large scars that delimit the base of the flower (Figs. 2, 4, 12). We suggest that *A. beekeri* was attached in this position and formed an outer perianth of three robust, narrowly elliptical sepals. We interpret *A. obscura* to have been less robust than *A. beekeri* and to have been attached to the more or less circular scars immediately above the three large basal flower scars. The inner perianth probably consisted of relatively few, either six or nine,

petals. The male parts of the *Archaeanthus* plant have not been recognized yet, but we envisage that they were borne on the small elliptical scars immediately below the gynoecial zone, and above the scars of the perianth whorl. In Figures 69 and 70 we give our suggestions as to what the *Archaeanthus* flower may have looked like; more detailed reconstructions of the individual parts are given in Figure 60.

BIOLOGY AND ECOLOGY OF THE *ARCHAEANTHUS* PLANT

The reconstruction of the *Archaeanthus linnenbergeri* plant combined with sedimentological data permits some conclusions on the biology and ecology of this mid-Cretaceous angiosperm. During the mid-Cretaceous, a major epicontinental sea extended northward from the Gulf of Mexico into the western interior of North America where, at various times, it linked with a southward extension of the Arctic Sea. Evidence from stratigraphy and sedimentology indicates that the Kansas plant beds were deposited in a range of coastal plain environments adjacent to this seaway and under variable amounts of marine influence. Both the Morrison, Colorado, and Linnenberger material dates approximately from the Albian–Cenomanian boundary: a time of lowered sea-level, bracketed above and below by widespread marine, eustatic transgressive episodes. During this period, both areas were situated at an approximate paleolatitude of 36–37°N (Smith & Briden, 1977) and were experiencing warm-temperate or sub-tropical climates (Kauffman, 1977).

Retallack and Dilcher (1981b, 1981c) interpreted the plant bearing sediments at Linnenberger's Ranch as shales associated with levee deposits in inter-distributary depressions vegetated by swamp woodland. To judge from the almost exclusive angiosperm macrofossil flora, the local vegetation was dominated by flowering plants; although in the palynoflora, angiosperm pollen comprises less than 25% of the total palynomorph assemblage (Dilcher & Zavada, unpubl. data).

Despite the large collections available and the geological proximity of shale and sand facies in the Dakota Formation, only one *Liriophyllum kansense* leaf is known from the classic Dakota Sandstone Flora, which represents a number of localities in and around Ellsworth County, Kansas. Equally many of the characteristic plants of

that flora (for example, *Betulites* and the *Platanus-Sassafras* complex) either do not occur or are not common at Linnenberger's Ranch or Hoisington. They are found, however, at other shale localities. Although the fossils known from any locality are an incomplete representation of the living vegetation, where local differences exist (such as those in the Dakota Formation), they may reflect specific associations of plant species in particular environments.

The pollination and dispersal biology of the *Archaeanthus* plant was probably relatively unspecialized. The size of the floral and vegetative organs and the dimensions of the axes that supported them suggests that the plant was woody in life. From the size and features of the leaves, and from the petiole bases, we conclude it was probably a deciduous tree or shrub. The apparently bisexual flowers, and hence the fruits, were borne terminally on leafy, woody axes, probably prominently, beyond or near the margin of the leafy crown. Such a position combined with the large perianth parts indicated by the basal floral scars, and the size of *Archaepetala beekeri* and *A. obscura,* suggests that the flower was probably visually conspicuous and insect-pollinated. Coleoptera, Thysanoptera, and incurvariid Lepidoptera have been recorded as pollinators that feed on pollen in recent 'primitive' angiosperms (Thien, 1974, 1980), and all have a fossil record extending back into the Cretaceous (Thien, 1974, 1980; Whalley, 1978). Following pollination, we suggest that the stamens and perianth parts were shed and that the receptacle elongated as the follicles and seeds matured. Dispersal was probably unspecialized, involving both shedding of the numerous small seeds through the open adaxial suture, and occasional shedding of the complete follicles in a manner analogous to extant *Liriodendron.*

COMPARISON WITH RECENT PLANTS

Vegetative morphology. Similarity in leaf architecture between *Liriophyllum* and certain extant angiosperms has been mentioned already, but we know of no closely comparable Recent leaf. *Asarum* (Aristolochiaceae) shows a similar pattern of venation in which the major veins form the margin of the leaf for some distance before entering the lamina; but in *Asarum* it is the base rather than the apex of the leaf that is involved. Judging from the one axis of *Archaeanthus* in which leaf scars are preserved, the phyllotaxy was helical; a widespread condition generally regarded as primitive in flowering plants.

We interpret the resin-bodies preserved throughout the *A. linnenbergeri* plant as the diagenetically altered contents of oil cells. Ethereal oil cells are particularly common in Recent Magnoliidae, especially Magnoliales, Laurales, Piperales, Aristolochiaceae, and Illiciales (Cronquist, 1981), and are frequently preserved in younger fossil material confidently referable to these groups; for example, Tertiary lauraceous leaves.

We assume that the vegetative axes of *Archaeanthus* were woody, but we regrettably have no knowledge of the secondary xylem, which would be of considerable interest.

Floral organization. The basic organization of the *Archaeanthus* flower consists of numerous, helically arranged, separate carpels borne on a stout, elongated receptacle probably with numerous helically arranged stamens below; these are followed in turn below by two kinds of perianth parts arranged in apparent whorls. This combination of features occurs most commonly in the Magnoliidae, but also occurs in a few families of the Ranunculidae and Dilleniidae, such as the Ranunculaceae, Paeoniaceae, and the Dilleniaceae, which are often regarded as primitive.

In most magnoliid families the floral receptacle is rather short, but in the Magnoliaceae and some Annonaceae it is frequently elongated, and elongates further during the maturation of the fruits, as we suggest for *A. linnenbergeri* (Figs. 61, 62). Numerous helically arranged stamens occur more widely in flowering plants than helically arranged carpels, but both are nevertheless very common in the Magnoliidae. The lack of a more detailed understanding of the staminate parts of *Archaeanthus* is currently the most conspicuous gap in our knowledge of the plant. Trimerous perianth parts are widespread (for example, in the monocotyledons, Burger, 1977), but they also occur in the Magnoliidae. In the Lactoridaceae (Magnoliales) there are only three tepals, and in *Degeneria,* three sepals. Again, in the Annonaceae and Magnoliaceae, a trimerous arrangement of perianth parts is common.

A calyptra similar to that envisaged for *A. linnenbergeri* occurs in many Magnoliidae. In *Drimys* and *Tasmannia* (Winteraceae) the sepals are connate into a deciduous calyptra. In *Liriodendron* and *Magnolia* the large, frequently lobed, bud-scales enclosing the developing flower are interpreted as stipular in origin (Howard, 1948).
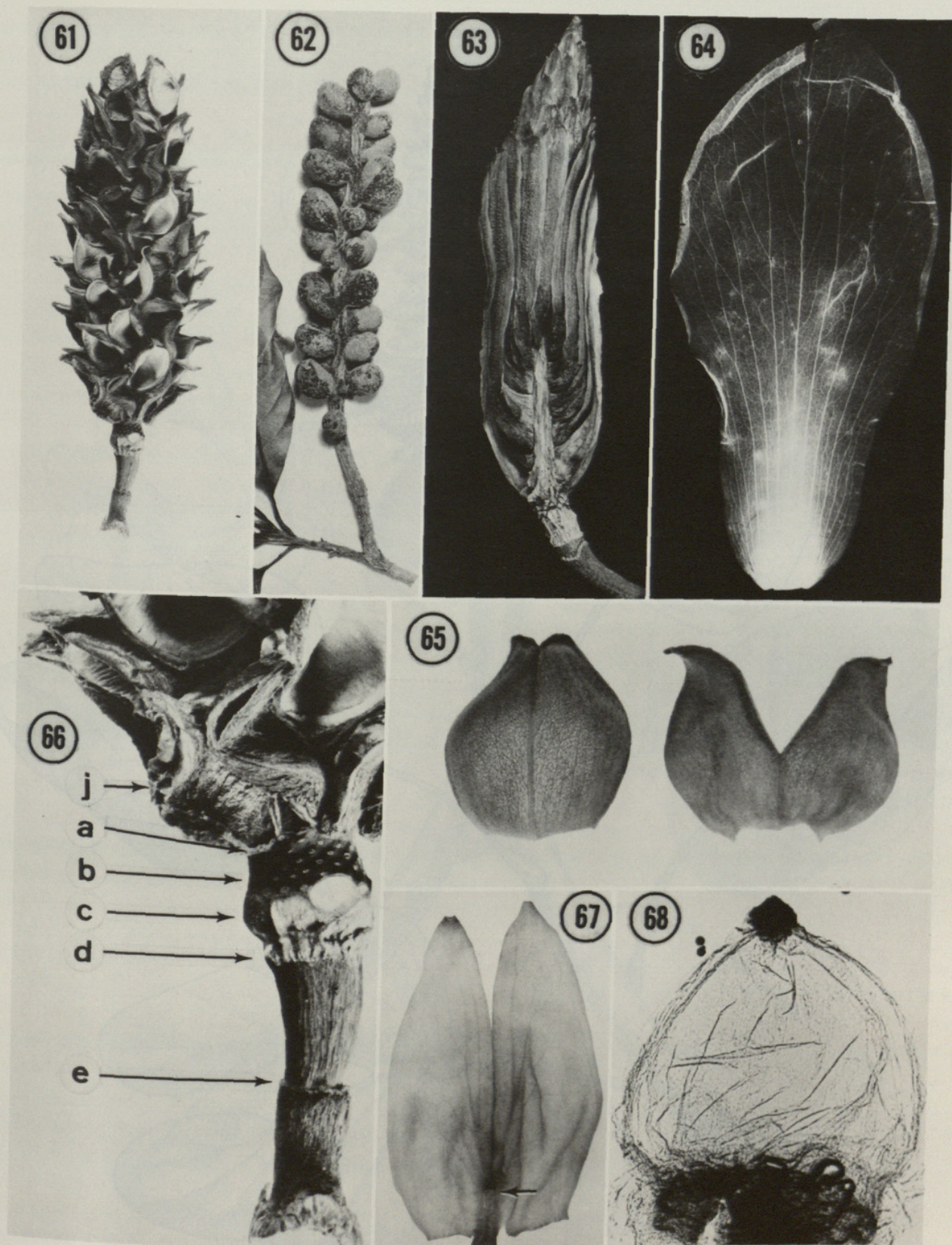
FIGURES 61–68. Extant Magnoliaceae.—61. *Magnolia tripetala* L. Fruiting receptacle (multifollicle) showing closely spaced follicles dehiscing abaxially, ×0.5.—62. *Michellia champaca* L. Luzon, Phillipines, collected by E. D. Merrill, Missouri Bot. Gard. 865046, fruiting receptacle (multifollicle). Note spacing of follicles along the receptacle, ×0.5.—63. *Liriodendron tulipifera* L. Fruiting receptacle (multifollicle) with several samaroid follicles removed to reveal ridged receptacle. Note staminal and perianth scars; the bud-scale scars are just below the base of the flower, ×1.—64. *Magnolia tripetala* L. Cleared petal showing details of venation. Compare with Figure 40, ×1.—65. *Magnolia grandiflora* L. Bud-scales for comparison with Figures 39, 42, and 43. Note the narrow rib and the splitting, ×0.75.—66. *Magnolia tripetala* L. Base of fruiting receptacle (multifollicle) showing follicles (j), the base of the gynoecial zone (a), scars of stamens (b), scars of inner (c) and outer perianth (d) parts, and the position of the bud-scales (e), ×4.—67. *Magnolia tripetala* L. Stipular bud-scale. Note the attachment point left by the leaf lamina (arrow), ×0.5.—68. *Magnolia tripetala* L. Nucellar or inner integumentary membrane isolated from an aborted ovule in an immature multifollicle. Compare Figures 32 and 34, ×30.

FIGURE 69. *Archaeanthus linnenbergeri.* Reconstruction of leafy twig bearing a multifollicular axis.

Both *Magnolia tripetala* (Figs. 61, 66) and *Liriodendron tulipifera* (Fig. 63) show calyptra scars below the base of the flower.

Follicles and seeds. The follicles of *Archaeanthus* are assumed to have developed from conduplicate carpels with two stigmatic crests along the adaxial surface. Although this kind of carpel is basic in the Magnoliidae, adaxial dehiscence is much less common. In most Magnoliaceae, dehiscence is abaxial but in *Kmeria* the follicle splits adaxially and apically, as it does in *A. linnenbergeri.* Adaxial dehiscence also oc-

FIGURE 70. *Archaeanthus linnenbergeri.* Reconstruction of leafy twig and flower.

curs in *Illicium,* as well as in a few Ranunculidae and Hamamelidae.

Prominently stalked follicles like those in *Archaeanthus* occur in many Annonaceae such as *Anaxagorea, Guatteria, Unonopsis, Xylopia* (Fries, 1930, 1931, 1934, 1937, 1939), as well as *Austrobaileya, Drimys* (Winteraceae), and *De-*

generia. In the Magnoliaceae the carpels are generally tightly fused to the receptacle (Fig. 61) and often more or less concrescent. Several of the annonaceous genera cited above have follicles that break away from the receptacle at the base of the stalk at maturity, but the closest analogy to the dispersed fruits observed in *Archaeanthus*

is in *Liriodendron*, in which the two-seeded, indehiscent follicle acts as the unit of dispersal and separates from the receptacle leaving narrow diamond-shaped scars (Fig. 63). Both the shape of the follicle bases and the scars are similar to those in *A. linnenbergeri*.

The number of seeds borne in the *A. linnenbergeri* follicles is higher than in most Recent Magnoliaceae. Multi-seeded follicles do, however, occur in *Degeneria*, some Annonaceae, and a few other groups of Magnoliidae.

Conclusions. *Archaeanthus* is clearly most similar to extant Magnoliidae and shares some features with supposedly primitive members of the Hamamelidae and Dilleniidae. A summary of the similarities with a range of families is given in Table 1. All of the characters of the fossil with the possible exception of the unusual form and venation of *Liriophyllum* occur in the Magnoliidae, but no living species comes close to the combination of features that *Archaeanthus* displays. Within the Magnoliidae it seems most closely related to the Magnoliales sensu Cronquist (1981), viz. Annonaceae, Austrobaileyaceae, Canellaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Lactoridaceae, Magnoliaceae, Myristicaceae, and Winteraceae. However, we do not believe that *Archaeanthus* usefully can be assigned to any extant family; *Archaeanthus* is a unique and extinct genus of fossil angiosperms.

EVOLUTIONARY SIGNIFICANCE

The occurrence of *Archaeanthus* and the floral structure it exhibits, as early in flowering plant evolution as the mid-Cretaceous, is of considerable relevance to concepts of flowering plant evolution. The late Albian to mid-Cenomanian age established for *Archaeanthus* places it approximately 10 to 15 Ma after the first generally accepted angiosperm fossils appear in the fossil record (Hughes et al., 1979). *Archaeanthus* is one of the most completely known of all early angiosperms, and in the characters that it exhibits it comes close to the hypothetical angiosperm archetype developed by adherents of classical magnoliid floral theory over the last 80 years. This archetype, although admittedly hypothetical, has been most explicitly elaborated by Takhtajan (1969) and is summarized in Table 2. The reasoning behind the magnoliid theory is largely based upon neontological data, and a range of

approaches have been utilized in formulating the concepts of primitive and advanced characters (Sporne, 1956). In view of this historical decoupling of paleontological and neontological data, the correspondence that exists between the hypothetical archetype and *Archaeanthus* is significant. The details of this similarity are summarized in Table 2, from which it is clear that *Archaeanthus* displays many characters generally regarded as 'primitive' or generalized among Recent plants. There are, however, differences: for example, *Archaeanthus* was probably deciduous rather than evergreen, had small rather than large seeds, and had a lobed rather than a simple leaf; but probably *Archaeanthus* combines more 'primitive' features than any living plant. In terms of magnoliid theory it demonstrates that many of these generalized characters are also ancient. It would be easy to interpret *Archaeanthus* as an ancestor to a range of extant plant groups, but we can see little value in such a naive exercise. Its real significance is in conclusively establishing that the basic magnoliid flower was one of the earliest kinds of floral organization to be developed during the mid-Cretaceous radiation of flowering plants.

Taken in the broader context of mid-Cretaceous fossil flowers, *Archaeanthus* fits well into a pattern that is rapidly becoming established. Other magnoliid flowers similar to *Archaeanthus* occur in the Dakota Sandstone Flora, the Janssen Clay of Hoisington, Kansas (Crane & Dilcher, 1984), the Amboy Clays of New Jersey, and the Crowsnest Formation of southern Alberta (Crane & Dilcher, 1984). None of this material occurs earlier than sub-zone IIC or possibly sub-zone IIB of the palynological zonation established for the mid-Cretaceous of the Atlantic coastal plain (Brenner, 1963; Doyle, 1969; Doyle & Robbins, 1977). However, there is evidence of similar floral morphology as early as zone I. The floral axis figured by Fontaine (1889, pl. 137, fig. 4) and Dilcher (1979, fig. 28) is a cluster of follicles borne on the swollen apex of a simple axis. Other than the swelling at the apex and faint indications of a few scars, no differentiation into receptacle and pedicel is clear. The specimen does, however, show that clusters of follicles are among the earliest of all angiosperm fossil fruit types. Slightly later, Vakhrameev and Krassilov (1979) described *Caspiocarpus paniculiger* from the middle Albian of Kazakhstan, which is thought to be equivalent to zone IIB in the Atlantic coastal

Table 1. Comparison of the *Archaeanthus linnenbergeri* plant with selected Recent families of Magnoliidae, Ranunculidae, and Hamamelidae. Data for extant families from D. A. Young (1981). + indicates that at least some members of the extant family display the character indicated.

Characters of Fossil Plant	Magnoliidae											Ranunculidae		Hamamelidae			Dilleniidae	
	Austrobaileyaceae	Magnoliaceae	Winteraceae	Degeneriaceae	Himantandraceae	Annonaceae	Myristicaceae	Canellaceae	Eupomatiaceae	Amborellaceae	Monimiaceae	Illiciaceae	Schizandraceae	Tetracentraceae	Trochodendraceae	Cercidiphyllaceae	Dilleniaceae	Paeoniaceae
1 Flowers Bisexual	+	+	+	+	+	+	0	+	+	0	0	+	0	+	+	0	+	+
2 Receptacle Flat or Convex	+	+	+	+	+	+	+	+	+	0	0	+	+	0	+	+	+	+
3 Perianth Parts Spirally Arranged	0	+	+	0	0	0	0	0	0	+	0	+	+	0	0	0	+	+
4 Perianth Well-Differentiated into Sepals and Petals	0	0	0	+	+	+	+	+	+	0	0	0	0	0	0	0	+	+
5 Stamens Numerous	+	+	+	+	+	+	+	0	+	+	+	+	+	0	+	+	+	+
6 Carpels free	+	0	+	+	0	+	+	0	0	+	+	+	+	0	0	+	+	+
7 Carpel Dehiscence Adaxial	+	0	0	0	0	+	0	0	0	0	0	+	0	+	+	0	+	+
8 Carpels More Than Five	+	+	0	0	+	+	0	0	+	+	+	+	+	0	+	+	+	0
9 Ovules More Than Two Per Carpel	+	+	+	+	0	+	0	+	+	0	0	+	0	+	+	+	+	0
10 Style Absent, Stigma Sessile	0	+	+	+	0	+	+	+	+	+	+	0	+	+	+	+	0	+
11 Leaves Simple	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12 Phyllotaxy Helical	0	+	+	+	+	+	+	+	+	+	0	+	+	+	+	+	+	0
13 Reproductive Shoot Well-Defined	+	+	+	+	+	+	+	+	+	0	0	+	+	+	+	+	0	+
14 Flowers Solitary on a Leafy Cyme	+	+	+	+	+	0	+	+	+	0	+	+	+	0	0	0	+	+

TABLE 2. Comparison of the *Archaeanthus linnenbergeri* plant with the angiosperm morphotype elaborated by Takhtajan (1969). + indicates agreement. − indicates disagreement. ? indicates character unknown in *A. linnenbergeri*. ( ) indicates uncertainty but possible agreement.

Vegetative	Reproductive
+ Woody	(+) Flowers Entomophilous
− Evergreen	+ Radially Symmetrical
+ Leaves Simple	(+) Bisexual
+ Leaf Margin Entire	+ Flowers Terminal on Leafy Branches
+ Leaves Pinnately Veined	+ Receptacle Elongated
? Leaves Glabrous	− Perianth Parts Numerous
? Stomata Paracytic	− Perianth Parts Passing Gradually into Foliage Leaves
? Multilacunar Nodes with a Median Double Trace	(+) Stamens Numerous
	? Stamens Laminar
? Vessels Absent	? Microsporangia Long and Narrow
? Tracheids with Scalariform Pits	? Pollen Monosulcate
? Wood Parenchyma Absent or Diffuse Apotracheal	+ Carpels Numerous−Helically Arranged
	+ Carpels Large
? Rays Multiseriate with High Uniseriate Wings	+ Carpels Stalked
? Phloem Companion Cells Absent	+ Carpels Conduplicate−Suture Adaxial
	(+) Carpels Incompletely Closed
	+ Fruits Multifollicles
	+ Ovules Numerous
	(+) Ovules Anatropous
	? Ovules Bitegmic
	(+) Ovules Borne Between Median and Lateral Carpel Veins
	− Seeds Large
	? Endosperm Abundant
	? Embryo Small and Undifferentiated

plain zonation. This, too, shows follicles, but they are apparently borne in a unisexual, panicle-like cluster.

From these records alone it is clear that follicles were a very early innovation in flowering plant evolution and that the origin of the conduplicate carpel remains an important issue in angiosperm phylogeny. Contemporaneous with these species, however, are other kinds of floral organs that are very different. A well-preserved pentamerous flower is known from the Janssen Clay Member of southern Nebraska and also occurs at the Linnenberger Ranch locality (Basinger & Dilcher, 1984; Dilcher & Basinger, unpubl. data). Each flower had five loosely fused carpels with abaxial dehiscence. Leaves and reproductive structures very similar to those of extant *Platanus* are common in the Dakota Formation (Dilcher, 1979) and also occur as early as subzone IIB (Krassilov, 1977; G. Upchurch, pers. comm.; Dilcher & Schwartzwalder, unpubl. data). Other mid-Cretaceous angiosperm reproductive structures may also have been unisexual (Dilch-

er, 1979; Retallack & Dilcher, 1981b). Such plants clearly demonstrate that on present evidence the magnoliid floral organization seen in *Archaeanthus* does not predate other very different kinds of flowers, including apparently unisexual forms, in the fossil record. *Archaeanthus* does, however, add significantly to our knowledge of early angiosperm reproductive diversity and demonstrates the existence of a well-differentiated, relatively sophisticated floral organization during the mid-Cretaceous. *Archaeanthus* demonstrates conclusively that magnoliid flowers are among the earliest known, and that magnoliid-like plants were an early development in angiosperm evolution.

LITERATURE CITED

ANDREWS, H. N. 1966. Index of generic names of fossil plants, 1820–1965. Bull. U.S. Geol. Surv. 1300: 1–354.
ARBER, E. A. N. & J. PARKIN. 1907. On the origin of angiosperms. J. Linn. Soc., Bot. 38: 29–80.
BAILEY, I. W. 1944. The development of vessels in

angiosperms and its significance in morphological research. Amer. J. Bot. 31: 421–428.

BASINGER, J. F. & D. L. DILCHER. 1984. Ancient bisexual flowers. Science 224: 511–513.

BAYNE, C. K., P. C. FRANKS & W. IVES. 1971. Geology and groundwater resources of Ellsworth County, central Kansas. Bull. Kansas Univ. Geol. Surv. 201: 1–84.

BERMAN, A. E., D. POLESCHOOK & T. E. DIMELOW. 1980. Jurassic and Cretaceous Systems of Colorado. Pp. 111–128 *in* H. C. Kent & K. W. Porter (editors), Colorado Geology. Rocky Mountain Association of Geologists, Denver, Colorado.

BERRY, E. W. 1901. Notes on *Liriodendron* leaves. Torreya 1: 105–107.

———. 1902a. Notes on the phylogeny of *Liriodendron*. Bot. Gaz. (Crawfordsville) 34: 44–63.

———. 1902b. Additional notes on *Liriodendron* leaves. Torreya 2: 33–37.

BESSEY, C. E. 1897. Phylogeny and taxonomy of the angiosperms. Bot. Gaz. (Crawfordsville) 24: 145–178.

———. 1915. The phylogenetic taxonomy of flowering plants. Ann. Missouri Bot. Gard. 2: 109–164.

BRENNER, G. J. 1963. The spores and pollen of the Potomac Group of Maryland. Bull. Maryland Dept. Geol. Mines Water Resources 27: 1–215.

BURGER, W. C. 1977. The Piperales and the Monocots, alternate hypotheses for the origin of monocotyledonous flowers. Bot. Rev. (Lancaster) 43: 345–393.

CORNER, E. J. H. 1949. The Durian Theory or the Origin of the Modern Tree. Ann. Bot. (London) n.s. 13: 367–414.

CRANE, P. R. & D. L. DILCHER. 1984 [1985]. *Lesqueria*: an early angiosperm fruiting axis from the mid-Cretaceous. Ann. Missouri Bot. Gard. 71: 384–402.

CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin, Boston.

———. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

DAHLGREN, R. M. T. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80: 91–124.

DICKISON, W. C. 1975. The bases of angiosperm phylogeny: vegetative anatomy. Ann. Missouri Bot. Gard. 62: 590–620.

DILCHER, D. L. 1979. Early angiosperm reproduction: an introductory report. Rev. Palaeobot. Palynol. 27: 291–328.

———, F. POTTER & H. C. REYNOLDS. 1978. Preliminary account of Middle Cretaceous angiosperm remains of North America. Courier Forschungsinst. Senckenberg 30: 9–15.

———, W. L. CREPET, C. D. BEEKER & H. C. REYNOLDS. 1976. Reproductive and vegetative morphology of a Cretaceous angiosperm. Science 191: 854–856.

DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. J. Arnold Arbor. 50: 1–35.

———. 1978. Origin of angiosperms. Ann. Rev. Ecol. Syst. 9: 365–392.

——— & L. J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. *In* C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

——— & E. I. ROBBINS. 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic coastal plain and its application to deep wells in the Salisbury embayment. Palynology I: 43–78.

EAMES, A. J. 1961. Morphology of Angiosperms. McGraw Hill, New York.

EARLE, T. T. 1938. Origin of the seed coats in *Magnolia*. Amer. J. Bot. 25: 221–222.

EICHER, D. L. 1975. Foraminifera and biostratigraphy of the Graneros Shale. J. Paleontology 39: 875–909.

ENGLER, A. 1897. Principien der systematischen Anordnung, insbesondere der Angiospermen. *In* A. Engler & K. Prantl, Die Natürlichen Pflanzenfamilien. Nachtrage zum 2 bis 4 Teil. Nachtrag 1, Lieferung 155–156: 5–14. Wilhelm Engelmann, Leipzig.

FONTAINE, W. M. 1889. The Potomac or Younger Mesozoic Flora. Monogr. U.S. Geol. Surv. 15: 1–377.

FRANKS, P. C. 1975. The transgressive-regressive sequence of the Cretaceous Cheyenne, Kiowa, and Dakota Formations of Kansas. *In* W. G. E. Caldwell (editor), The Cretaceous System in the Western Interior of North America. Special Pap., Geol. Assoc. Canada 13: 469–521.

FRIES, R. E. 1930. Revision der Arten einiger Anonaceen-Gattungen. I. Acta Horti Berg. 10: 1–128.

———. 1931. Revision der Arten einiger Anonaceen-Gattungen. II. Acta Horti Berg. 10: 129–341.

———. 1934. Revision der Arten einiger Anonaceen-Gattungen. III. Acta Horti Berg. 12: 1–220.

———. 1937. Revision der Arten einiger Anonaceen-Gattungen. IV. Acta Horti Berg. 12: 221–288.

———. 1939. Revision der Arten einiger Anonaceen-Gattungen. V. Acta Horti Berg. 12: 289–577.

GRESS, E. M. 1922. An annotated list of fossil plants of the Dakota Formation (Cretaceous) in the collections at the Carnegie Museum, including descriptions of three new species. Ann. Carnegie Mus. 13: 274–329.

HARRIS, T. M. 1932. The fossil flora of Scoresby Sound East Greenland Part 2. Description of seed plants *incertae sedis* together with a discussion of certain Cycadophyte cuticles. Meddel. Gronland 85: 1–112.

———. 1954. Mesozoic seed cuticles. Svensk Bot. Tidskr. 48: 281–291.

HATTIN, D. E. 1965. Stratigraphy of the Graneros Shale (Upper Cretaceous) in central Kansas. Bull. Kansas State Geol. 178: 1–83.

———. 1967. Stratigraphic and paleoecological significance of macroinvertebrate fossils in the Dakota Formation (Upper Cretaceous) of Kansas. Pp. 570–589 *in* C. Teichert & E. L. Yochelson (editors), Essays in Paleontology and Stratigraphy. R. C. Moore commemorative volume. Department

of Geology, University of Kansas. Special Publication, 2.

———— & C. T. SIEMERS. 1978. Guidebook, Upper Cretaceous Stratigraphy and Depositional Environments of Western Kansas. Guidebook Series 3: Geological Survey of Kansas.

HICKEY, L. J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. Mem. Geol. Soc. Amer. 150: 1–183.

———— & J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. Bot. Rev. (Lancaster) 43: 3–104.

HILL, C. R. & P. R. CRANE. 1982. Evolutionary cladistics and the origin of angiosperms. In K. A. Joysey & A. E. Friday (editors), Problems of Phylogenetic Reconstruction. Academic Press, London.

HOLLICK, A. 1894. Wing-like appendages on the petioles of Liriophyllum populoides Lesq. and Liriodendron alatum Newb. with a description of the latter. Bull. Torrey Bot. Club 21: 467–471.

————. 1896. Appendages to the petioles of Liriodendron. Bull. Torrey Bot. Club 23: 249–250.

HOLM, T. 1895. On the validity of some fossil species of Liriodendron. Bot. Gaz. (Crawfordsville) 20: 312–316.

HOWARD, R. A. 1948. West Indian Magnoliaceae. Bull. Torrey Bot. Club 75: 335–357.

HUGHES, N. F. 1976. Palaeobiology of Angiosperm Origins. Cambridge Univ. Press, Cambridge.

————, G. E. DREWERY & J. F. LAING. 1979. Barremian earliest angiosperm pollen. Palaeontology 22: 513–535.

HUTCHINSON, J. 1959. The Families of Flowering Plants. Volumes 1 & 2. 2nd edition. Clarendon Press, Oxford.

KAUFFMAN, E. G. 1977. Geological and biological overview: Western Interior Cretaceous Basin. In E. G. Kauffman (editor), Cretaceous, facies, faunas, and palaeoenvironments across the Western Interior Basin. Mountain Geol. 14: 75–99.

————, W. A. COBBAN & D. L. EICHER. 1976. Albian through Lower Coniacian strata, biostratigraphy, and principal events, western interior, United States. Ann. Mus. Hist. Nat. Nice, IV, XXIII: 1–52.

KNOBLOCH, E. 1978. On some primitive angiosperm leaves from the Upper Cretaceous of the Bohemian Massif. Palaeontographica, Abt. B, Paläophytol. 166: 83–98.

KNOWLTON, F. H. 1896. The fossil plants of the Denver Basin. Monogr. U.S. Geol. Surv. 27: 466–473.

————. 1920. A dicotyledonous flora in the type section of the Morrison Formation. Amer. J. Sci. 49: 189–194.

KRASSILOV, V. A. 1977. The origin of angiosperms. Bot. Rev. (Lancaster) 43: 143–176.

KRÄUSEL, R. & F. SCHAARSCHMIDT. 1968. Scoresbya Harris (Dipteridaceae) aus dem Unteren Jura von Sassendorf. Palaeontographica, Abt. B, Paläophytol. 123: 124–131.

KRYSHTOFOVICH, A. N. 1937. Cretaceous flora of Saghalien. Mgach and Polovinka. Trans. Far-East. Branch, Acad. Sci. USSR, Ser. Geol. 2: 1–103 (in Russian).

LEE, W. T. 1920. Type section of the Morrison Formation. Amer. J. Sci. 49: 183–188.

LESQUEREUX, L. 1868. On some Cretaceous fossil plants from Nebraska. Amer. J. Sci. 46: 91–105.

————. 1874. United States Geological Survey of the Territories. Contributions to the fossil flora of the Western Territories. Part I. The Cretaceous Flora. United States Department of the Interior Report of the United States Geological Survey of the Territories 6: 1–136.

————. 1878. Remarks on specimens of Cretaceous and Tertiary plants secured by the survey in 1877; with a list of the species hitherto described. Pp. 481–520 in F. V. Hayden (editor), Tenth Annual Report of the United States Geological and Geographical Survey of the Territories.

————. 1883. United States Geological Survey of the Territories. Contributions to the fossil flora of the Western Territories. Part III. The Cretaceous and Tertiary Floras. Department of the Interior. Report of the United States Geological Survey of the Territories 8: 2–108.

————. 1892. The flora of the Dakota Group. Monogr. U.S. Geol. Surv. 17: 1–400.

McGOOKEY, D. P., J. D. HAUN, L. A. HALE, H. G. GOODELL, D. G. McGUBBIN, R. J. WEIMER & G. R. WULF. 1970. Correlation chart of Cretaceous formations. Mountain Geol. 7: inside back cover.

MACNEAL, D. L. 1958. The flora of the Upper Cretaceous Woodbine Sand in Denton County, Texas. Acad. Nat. Sci. Philadelphia Monogr. 10: 1–152.

MEEUSE, A. D. J. 1966. Fundamentals of Phytomorphology. Ronald Press Co., New York.

MELVILLE, R. 1962. A new theory of the angiosperm flower. I. The gynoecium. Kew Bull. 16: 1–50.

————. 1963. A new theory of the angiosperm flower. II. The androecium. Kew Bull. 17: 1–63.

NEWBERRY, J. S. 1868. Notes on the later extinct floras of North America. Amer. J. Sci. 46: 401–407.

————. 1895. The flora of the Amboy Clays, edited by A. Hollick. Monogr. U.S. Geol. Surv. 26: 1–260.

PLUMMER, N. & J. F. ROMAKY. 1942. Stratigraphy of the pre-Greenhorn Cretaceous beds of Kansas. Bull. Kansas State Geol. Surv. 41: 313–348.

———— & ————. 1947. Kansas clay, Dakota Formation. Bull. State Geol. Surv. Kansas 67: 1–241.

RAVN, R. L. 1981. Preliminary observations on the palynology of the upper Dakota Formation lignites in northwestern Iowa and northeastern Nebraska. Iowa Geol. Surv. Guidebook, Ser. 4: 123–127.

RENDLE, A. B. 1925. The Classification of Flowering Plants. Volume 2. Dicotyledons. Cambridge Univ. Press, Cambridge.

————. 1930. The Classification of Flowering Plants. Volume 1. Gymnosperms and Monocotyledons. 2nd edition. Cambridge Univ. Press, Cambridge.

RETALLACK, G. & D. L. DILCHER. 1981a. Arguments for a glossopterid ancestry of angiosperms. Paleobiology 7: 54–67.

———— & ————. 1981b. Early angiosperm reproduction: Prisca reynoldsii gen. et sp. nov. from mid-Cretaceous coastal deposits, Kansas, USA. Palaeontographica, Abt. B, Paläophytol. 179: 103–137.

———— & ————. 1981c. A coastal hypothesis for the dispersal and rise to dominance of flowering plants. Pp. 27–77 *in* K. J. Niklas (editor), Palaeobotany, Palaeoecology, and Evolution. Volume 2. Praeger, New York.

RÜFFLE, L. 1970. Reliktformen als Lehrbeispiele für Geset-massigkeiten in Evolutionsprozess—ihre Rolle in Garten und in den offentlichen Teilen des Museums für Naturkunde. Wiss. Z. Humboldt-Univ. Berlin, Math.-Naturwiss. Reihe 19: 259–268.

SCHOEWE, W. H. 1952. Coal resources of the Cretaceous System (Dakota Formation) in central Kansas. Bull. Kansas State Geol. Surv. 96: 69–156.

SCOTT, R. A., E. S. BARGHOORN & E. B. LEOPOLD. 1960. How old are the angiosperms? Amer. J. Sci. 258A: 284–299.

SCOTT, R. W. 1970a. Palaeoecology and palaeontology of the Lower Cretaceous Kiowa Formation, Kansas. Univ. Kansas Paleontol. Contr. Pap. 52: 1–94.

————. 1970b. Stratigraphy and sedimentary environments of Lower Cretaceous rocks, southern Western Interior. Bull. Amer. Assoc. Petrol. Geol. 54: 1225–1244.

SIEMERS, C. T. 1971. Stratigraphy, Paleoecology, and Environmental Analysis of Upper Part of Dakota Formation (Cretaceous), Central Kansas. Unpublished Ph.D. thesis. Indiana Univ., Bloomington.

SMITH, A. G. & J. C. BRIDEN. 1977. Mesozoic and Cenozoic Paleocontinental Maps. Cambridge Univ. Press, Cambridge.

SPORNE, K. A. 1956. The phylogenetic classification of angiosperms. Biol. Rev. Biol. Proc. Cambridge Philos. Soc. 31: 1–29.

STEBBINS, G. L. 1974. Flowering Plants, Evolution Above the Species Level. Harvard Univ. Press, Cambridge.

STRASBURGER, E., H. SCHENCK, F. NOLL & A. F. W. SCHIMPER. 1898. A Textbook of Botany (translated by H. C. Porter). Macmillan, London.

TAKHTAJAN, A. 1969. Flowering Plants, Origin and Dispersal. Oliver and Boyd, Edinburgh.

———— (ed.). 1974. Magnoliophyta Fossilia U.R.S.S. Volume 1. Magnoliaceae–Eucommiaceae. Nauka, Leningrad.

TANAI, T. 1979. Late Cretaceous floras from the Kuji District, Northeastern Honshu, Japan. J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol. 19: 75–136.

THIEN, L. B. 1974. Floral biology of *Magnolia.* Amer. J. Bot. 61: 1037–1045.

————. 1980. Patterns of pollination in primitive angiosperms. Biotropica 12: 1–13.

THORNE, R. F. 1976. A phylogenetic classification of the angiosperms. Evol. Biol. 9: 35–106.

VAKHRAMEEV, V. A. 1966. The late Cretaceous floras from the USSR Pacific coast, their stratigraphic range and pecularities of composition. Proc. Acad. Sci. USSR, Ser. Geol. 1966(3): 76–87 (in Russian).

———— & V. A. KRASSILOV. 1979. Reproduktivnye organy tsvetkovykh iz al'ba kazakhstana (reproductive organs of a shoot of a flowering plant from the Albian of Kazakhstan). Paleontol. Zurn. 1979: 121–128.

WAAGE, K. M. 1955. Dakota group in northern Front Range foothills, Colorado. Profess. Pap. U.S. Geol. Surv. 274-B: 15–51.

WALKER, J. W. 1974a. Evolution of exine structure in the pollen of primitive angiosperms. Amer. J. Bot. 61: 891–902.

————. 1974b. Aperture evolution in the pollen of primitive angiosperms. Amer. J. Bot. 61: 1112–1137.

————. 1976. Comparative pollen morphology and phylogeny of the ranalean complex. *In* C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

WARD, J. V. 1981. Cheyenne and Kiowa angiosperm pollen—a new late Albian record from the southern part of the Western Interior [abstract]. American Association of Stratigraphic Palynologists, 14th Annual Meeting, Abstracts.

WEIMER, R. J. 1970. Dakota Group (Cretaceous) Stratigraphy, southern Front Range, South and Middle Parks Colorado. Mountain Geol. 7: 157–184.

———— & C. B. LAND. 1972. Field guide to Dakota Group (Cretaceous) stratigraphy Golden-Morrison Area, Colorado. Mountain Geol. 9: 241–267.

WETTSTEIN, R. 1935. Handbuch der Systematischen Botanik. 4th edition. Franz Denticke, Leipzig and Vienna.

WHALLEY, P. 1978. New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). Ann. Transvaal Mus. 31: 71–86.

WODEHOUSE, R. P. 1935. Pollen Grains. McGraw Hill, New York.

————. 1936. Evolution of pollen grains. Bot. Rev. (Lancaster) 2: 67–84.

YOUNG, D. A. 1981. Are the angiosperms primitively vesselless? Syst. Bot. 6: 313–330.

YOUNG, R. G. 1970. Lower Cretaceous of Wyoming and the Southern Rockies. Mountain Geol. 7: 105–121.

ZELLER, D. E. (editor). 1968. The statigraphic succession in Kansas. Bull. Kansas State Geol. Surv. 189: 1–81.