Palaeontographica, Abt. B	179	Lfg. 5—6	103—137	Stuttgart, November 1981

EARLY ANGIOSPERM REPRODUCTION: *PRISCA REYNOLDSII*, GEN. ET SP. NOV. FROM MID-CRETACEOUS COASTAL DEPOSITS IN KANSAS, U.S.A.

BY

GREG RETALLACK and DAVID L. DILCHER*)

With 7 plates and 9 figures in the text

Abstract

Prisca reynoldsii gen. et sp. nov. is a common angiosperm fructification in the early Cenomanian (mid-Cretaceous) upper Dakota Formation in central Kansas. It is a raceme of distantly-alternate, elongate, apetalous, unisexual multifollicles. On the basis of close association and cuticular similarities, leaves provisionallly referred to *Magnoliaephyllum* are attributed to the same extinct plant.

Prisca reynoldsii can be distinguished from all extinct and living gymnosperms presently known, because it has both carpel-like organs (follicles) and two integuments around its ovules. Although evidently an angiosperm, *Prisca reynoldsii* is a very different plant from any living angiosperm, and from concepts of "primitive" angiosperms, as commonly hypothesized from the comparative morphology of living plants. Some reorganization of the higher taxonomy of angiosperms is to be anticipated as additional extinct kinds of angiosperms are described. For the moment *Prisca reynoldsii* is placed in a new family, the Priscaceae, and its ordinal assignment remains uncertain.

Considering its geological occurrence and functional morphology, the plant producing *Prisca reynoldsii* and *Magnoliaephyllum* was probably a tree or shrub prominent in woodland vegetation of waterlogged peaty soils of interdistributary depressions, in part fringing brackish to freshwater lagoons of a deltaic coastal plain. *Prisca reynoldsii* produced a large number of small seeds, apparently dispersed mainly by wind and water, and was probably wind pollinated. It was thus well adapted as an early successional plant for variety of unstable coastal environments.

Key words: Angiosperm, paleoecology, fossil, fruit, evolution, Kansas, Cretaceous.

Contents

---

*) Address of the authors: Departments of Biology and Geology, Indiana University, Bloomington, Indiana 47405.

0375-0299/81/0179-0103 $ 18.90

Introduction

New finds of structurally-preserved fossil plants from the early Cenomanian (mid-Cretaceous) Dakota Formation of central Kansas, include a variety of fructifications and leaves of early angiosperms (DILCHER, 1979; DILCHER et al., 1976, 1978). From cuticular similarities and association, the various organs and reproduction of specific early angiosperms can be reconstructed. This allows a more meaningful evaluation of the nature and evolution of early angiosperms than is possible from studying their dispersed and mixed remains. The unexpected combinations of morphological features found in these reconstructed ancient plants are proving such that they cannot be placed conveniently within modern angiosperm families or orders. Some of these Cenomanian angiosperms are best placed in new and extinct taxa representing generalized stocks near the base of the spectacular Cretaceous evolutionary radiation of angiosperms.

One such fossil, *Prisca reynoldsii* gen. et sp. nov. is described here. As with prior finds from early Cenomanian rocks in Kansas (DILCHER et al., 1976) this fossil serves to establish what features of angiosperms can be considered ancient. We avoid using the terms "primitive" or "advanced", because their meaning has become extended and unclear. The term "primitive" has been used widely to characterize certain living angiosperms. These are only primitive in the sense that living stone age tribes are sometimes referred to as primitive, compared to the civilized world. They can be considered neither ancestral nor ancient. As with the evolution of our own species, much basic information about the evolution of angiosperms remains to be determined from the fossil record.

A detailed concept of the habitat preferences, pollination biology, fruiting and dispersal of individual Cenomanian plant species can also be established by considering the geological occurrence and functional morphology of these well-preserved fossils. The paleoecology of *Prisca reynoldsii,* as interpreted from such evidence and other considerations, differs from traditional concepts of early angiosperms. Our reconstruction of this mid-Cretaceous angiosperm supports the view of STEBBINS (1974), HICKEY & DOYLE (1977), that early angiosperms were early-successional weed trees.

Towards a definition and higher taxonomy for early angiosperms

The most encouraging effect of the recent upsurge in research on angiosperm origins (HUGHES, 1976; DOYLE, 1978; DILCHER, 1979), is the gathering recognition that the fossil record may furnish critical and important evidence for the origin and diversification of flowering plants as it has for understanding the origins of amphibians, reptiles, mammals, birds and humans. Researchers are despairing less about the lack of fossil evidence for angiosperm origins and concerned more with establishing the level of reproductive organization and possible relationships of an increasing number of extinct plants showing combinations of gymnospermous and angiospermous features (KRASSILOV, 1977a). Within the continuum of extinct plants connecting angiosperms and gymnosperms which will undoubtedly be revealed by future paleobotanical research, some agreement must be reached on how to define an angiosperm. For reasons detailed in the following paragraphs, we propose that early angiosperms be characterized by the joint occurrence of both a carpel and ovules with two integuments.

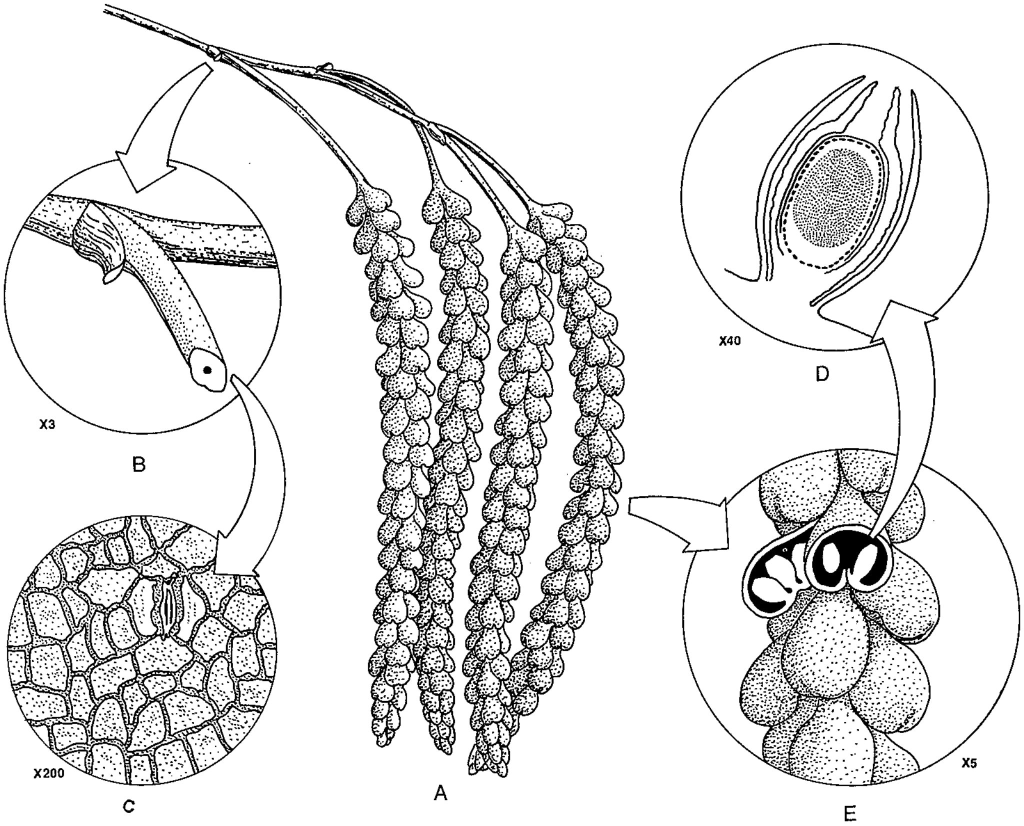
The most traditionally used characteristic of angiosperms is the presence of an enclosing structure which more or less covers or contains the ovules, termed a carpel. The carpel is usually regarded as a completely closed structure which a pollen tube must penetrate to achieve fertilization of an ovule. However, extant angiosperms of several families have incompletely closed carpels for either a part or all of their development (SPORNE, 1975; p. 125). Analogous structures to the carpels of angiosperms are found in a number of unrelated lineages of gymnosperms. These include the large multiovulate cupules of some lyginopterid pteridosperms (for example, *Gnetopsis,* see ANDREWS, 1948), the bivalved "capsules" of Czekanowskiales (HARRIS, 1951; KRASSILOV, 1977a), the "fruits" of Caytoniales (HARRIS, 1940, 1964; KRASSILOV, 1977b), the multiovulate megasporophylls of glossopterids (GOULD & DELEVORYAS, 1977) and the paired "capsules" of the Dirhopalostachyaceae (KRASSILOV, 1975, 1977a). Some of these fertile structures even resemble angiosperm carpels to the extent of showing possible stigmatic differentiation (KRASSILOV, 1977a). Few would claim that all these structures are carpel homologues. Carpel-like structures can no longer be considered an unequivocal hallmark of angiosperms. A unique definition of angiosperms, using the carpel, would have to include the co-occurrence of at least one other feature.

Another angiospermous feature of importance is the double integument of the ovule, which may be retained as two seed coats after fertilization. This feature is not universal in angiosperms, occurring in 67 % of dicotyledonous and 71 % of monocotyledonous families (SPORNE, 1975, p. 160). Embryological studies (MAHESHWARI, 1950) indicate that, in those angiosperms with a single integument, this integument develops from the fusion of two original primordia or by the cessation of growth of one of the two original primordia. Bitegmic and crassinucellate ovules are most widespread in supposedly "primitive" living angiosperms (TAKHTAJAN, 1969, p. 64; STEBBINS, 1974, p. 232). Other features of the integuments of angiosperm ovules indicate that the inner and outer integuments evolved from different types of organs, and so were probably better differentiated in ancestral than some modern angiosperms. These features include the rare presence of stomata on the outer (but not inner) integuments of some angiosperms (MAHESHWARI, 1950, p. 58 and the fossil material described here). Stomata would be maladapted to conditions in the carpel and possibly indicate origin of the outer integument from a photosynthetic organ. There are also strong histological differences between the outer and inner integuments of angiosperm ovules (STEBBINS, 1976). The mismatch of ovule integuments seen in the widespread "zigzag" course of the micropyle in longitudinal sections of so many angiosperm ovules may also be a result of the different origin of the two integuments (STEBBINS, 1974, p. 233, 1976). Thus there is a reasonable case for considering bitegmic ovules an important ancestral feature of angiosperms.

On the other hand there is also some evidence among gymnosperms of analogous structures to the bitegmic ovules of angiosperms. Ovules with more than one integument are seen most unequivocally in the living Gnetales (SPORNE, 1965; CHAMBERLAIN, 1935). The existence of two distinct systems of vascular strands in the integument of cycads and medullosan seed ferns, has been interpreted to suggest that these groups also had a double integument at some stage in their evolution (STOPES, 1904; WALTON, 1953; SPORNE, 1975, p. 154). Although the cutinized "spotted layer" within the integument of the ovule of *Caytonia* is quite different from other seed cuticles (HARRIS, 1958), it could also be interpreted as a remnant of interintegumentary cuticles and thus be an indication of bitegmic or ancestrally bitegmic ovules in the extinct Caytoniales. These various arguments for bitegmic ovules in cycads, medullosans and *Caytonia* merit attention, but considering the inconclusive nature of the evidence, unsupported by other data, remain unconvincing. However, several more definite gymnosperm organs could be and have been homologized with the outer integument of angiosperm ovules by various authors (as discussed by DOYLE, 1978, p. 383). These are the fruit wall (as opposed to ovule integument) of *Caytonia* (DOYLE, 1978, p. 384), the cupules of corystosperm seed fern fructifications (see THOMAS, 1933, 1934) and the megasporophyll of the glossopterid *Lidgettonia* (STEBBINS, 1974, p. 234). The existence and possibility of homologous structures in gymnosperms, indicates that bitegmic ovules cannot be considered an unequivocal hallmark of angiosperms.

Despite these difficulties, carpels and bitegmic ovules are too fundamental to reject as definitive features of angiosperms. We propose that a workable paleontological definition of early angiosperms be based on the joint occurrence of carpels and bitegmic ovules. These organs probably evolved independently and at different rates. This is also likely for other organs or combinations of organs. The appropriateness of this definition is apparent from the exclusion of a number of gymnosperms which may have either carpel-like structures or doubly-integumented ovules. This is in accord with the prevailing view that the angiosperms are a largely monophyletic group (DOYLE, 1978), rather than polyphyletically derived from a variety of unrelated groups of gymnosperms (KRASSILOV, 1977a). The practicality of this definition is apparent from the recognition of both bitegmic ovules and carpel-like structures in the extinct angiosperm fructifications described here and by VACHRAMEEV & KRASSILOV (1979).

There remains a problem that fossil angiosperms, by this definition, often do not fit within the existing taxonomy of flowering plants (as summarized by TAKHTAJAN, 1969; CRONQUIST, 1968). The probability that the ancestral and other groups of early angiosperms are extinct, has also been argued by STEBBINS (1974, pp. 201, 244) on other grounds, such as chromosome numbers, distribution of flavonoids and other characters of living angiosperms and comparison with other major groups of organisms for which a fossil record is available. Thus we anticipate that the hypothetical ancestral complexes at the center of many recent diagrams of angiosperm phylogeny (such as that of STEBBINS, 1974, fig. 11.1) will accomodate several unique and extinct groups of angiosperms as paleobotanical research continues. Considering the fossil record of angiosperm-like fructifications discussed here it now seems unlikely that the ancestral groups of angiosperms will be assignable to any modern order (contrary to TAKHTAJAN, 1969; HICKEY & DOYLE, 1977, fig. 70). This is clearly seen from the remains discussed here which have multifollicular fruits similar to CRONQUIST's (1968) Magnoliidae, but are unisexual and apetalous like the Cercidiphyllaceae of the Hamamelidae (Text-fig. 1). Some reorganization of the higher taxonomy of angiosperms may prove necessary as further extinct fossil fructifications of early angiosperms are discovered and described and their relationships with modern angiosperms elucidated. For the moment, we initiate this revision by proposing a new family, the Priscaceae, of uncertain ordinal affinities, to include the early angiosperm fructification described in the following paragraphs.



Text-Fig. 1. Reconstructed early angiosperm fructification, *Prisca reynoldsii* sp. nov.; A, simple raceme of bracteate, elongate multifollicles (X 1); B, reconstructed bracteate pedicel of the multifollicle attached to the raceme axis (X 3); C, cuticle of pedicel with a brachyparacytic stomate (X 200); D, longitudinal section of seed, showing cuticles of outer integument (smooth outer layers), inner integument (wavy lines), nucellar cuticle (smooth inner layer), megaspore membrane (dashed line), and megaspore contents (stipple) (X 40); E, follicles, cut away to reveal placentation of seeds (X 5).

Systematic paleobotany of a new early angiosperm fructification

Kingdom Plantae

Division Anthophyta

Class Dicotyledonae

Subclass and order incertae sedis

Family Priscaceae fam. nov.

This family is intended for fructifications like *Prisca reynoldsii* and other organs, such as leaves, pollen organs, staminate inflorescences and woods, which appear related to and distinctive of plants with such fructifications. At present, the nature of the family will have to be inferred from the diagnosis of its only genus *Prisca.* A more detailed definition of the family and its higher taxonomy are deferred until further representatives and allied fossils are better understood. Although leaves referred to *Magnoliaephyllum* are attributed to *Prisca reynoldsii,* leaves of this kind are also found in several modern angiosperm families, similarly defined on their reproductive structures. Thus, although the leaves of some Priscaceae are known, they can only be referred to a form-genus for dicotyledonous leaves of uncertain familial status.

Genus *Prisca* gen. nov.

Diagnosis: Lax, fruiting racemes of alternately and distantly-arranged multifollicles; multifollicles elongate, consisting of slender pedicel and receptacle, subtended by small, stem-clasping bracts; bracts with subacute apex and open, reticulate venation; receptacles elongate, flexuous, bearing numerous helically-arranged follicles; follicles with commissure directed adaxially, subcarnose, globular to ellipsoidal when involute, subrectangular with two lateral sinuses and prominent marginal involution when open; seeds numerous, ellipsoidal, orthotropous, bitegmic, smooth, attached by short funicle to involute follicle margin, directed obliquely towards apex and interior of follicle.

Cuticles of pedicel, carpel walls and outer cuticle of outer integument of seed all thick, with straight cell outlines and scattered sunken, brachyparacytic stomata; inner cuticles of seed thin, non-stomatiferous, prominently wrinkled; innermost membrane smooth, featureless.

Type species: *Prisca reynoldsii* sp. nov.

Derivation: The generic name is derived from the Latin adjective *priscus* (old, old-fashioned, ancient) used as a feminine proper name.

Prisca reynoldsii sp. nov.

"Fruit-bearing catkin", Dilcher, 1979, p. 311, figs. 48, 52.

Diagnosis: *Prisca* with slender (1.0—1.2 mm diameter) raceme axis, multifollicles alternate, distantly (13—14 mm apart) spaced, bracteate; bracts up to 5.9 mm long, with subacute apex and with prominent open, reticulate venation; multifollicles elongate, consisting of slender pedicel, 0.8—1.4 mm in diameter and 13.8—43.7 mm long, and an elongate receptacle, 0.4—1.7 mm wide and 50.4—73.4 mm long, bearing 50—90 follicles arranged in a close helix; follicle subcarnose, subglobular to ellipsoidal when infolded 1.8—3.6 mm long, 1.4—3.1 mm wide, subrectangular with prominent involute margin and lateral sinuses when opened out flat, attached by short, pseudostipitate base to receptacle; seeds 2—6, ellipsoidal, 0.6—1.1 mm long, 0.3—0.7 mm wide, bitegmic, orthotropous, attached to involute margin of follicle by short funicle.

Cuticles of pedicel, carpel walls and outer cuticle of outer integument of seed all thick (1—5 μm), with straight, wide (1—8 μm) cuticular flanges delineating epidermal cells and scattered, sunken, brachyparacytic stomata (12—24 μm long by 22—42 μm wide) and rare, scattered, radially arranged cells of possible hair bases; inner cuticles of seed thinner (1—3 μm), prominently wrinkled, defining a prominent conical pollen chamber inside the micropyle; nucellar cuticle thin (1—2 μm) with indistinct cellular outlines; innermost membrane thin (1—3 μm), structureless, enclosing convoluted, translucent, dark organic material.

Holotype: Specimen IU15706—3042 and its counterpart IU15706—3042′; a large fruiting axis with three attached multifollicles (Text-fig. 2a, fig. 1).

Type locality: In the upper bench at the southern end of the northern clay pit (as of 1977—1979), see IU15706 in text-fig. 8), southwest of Hoisington, Kansas; upper Dakota Formation, early Cenomanian (mid-Cretaceous).

Text-Fig. 2. *Prisca reynoldsii* sp. nov.; A, raceme of bracteate multifollicles (holotype, IU15706—3042); B—D, detail of apical to basal nodes (respectively) of holotype, solid lines are natural outlines, dotted lines are broken outlines, dashed lines are ridges of rock on the impression, crossed lines are furrows in the rock of the impression, cross-ruled areas are natural surfaces plunging vertically into the rock matrix (X 5); E, reconstruction of transverse section of pedicel of multifollicle (X 5); F—G, multifollicles with both basal and apical follicles preserved; F, IU15706—3040; G, IU15706—3051; H, exceptionally large multifollicle (IU15706—3047); I, flexuously-bent multifollicle (IU15714—3024); J, multifollicle with long pedicel, IU15706—3044; K, decayed multifollicle, IU15714—3024; L—M, naked receptacle without follicles, part and counterpart; L, IU15703—2586; M, IU15703—2086′. All specimens natural size unless otherwise specified.

Material: *Prisca reynoldsii* is represented by over one hundred specimens in our collections of over 3,000 specimens made prior to the end of 1978 from the uppermost Dakota Formation in central Kansas. These fossils are housed in the Paleobotanical Collection, Department of Geology, Indiana University. Specimen numbers are prefixed by IU and include a five-figure locality number and a four-figure specimen number. The following specimens have been selected as representative from Hoisington (IU15706—3040, 3042 to 3044, 3047 to 3053, 3056 to 3057) and from Linnenbergers' Ranch (specimens IU15703—2585 to 2587, 2589, 2603, 2604, 2606, 2609, 2613 to 2614, 2617 to 2618; IU5714—3024).

Derivation: This species is named in honour of Dr. Howard C. Reynolds, who first found the "discovery site" (Linnenbergers' Ranch, IU15703), which provided the first structurally-preserved megafossil plants from the Dakota Formation of Kansas.

Description

Fruiting axis: The holotype shows clearly the organization of the fruiting axis. Each of the alternately arranged, bracteate fruiting stalks with its helically-arranged follicles is a multifollicle. Thus the entire fruiting shoot preserved is a simple raceme. The central axis of the raceme appears fibrous and is broken up by coal cleat, so was evidently woody. Invoking WALTON's (1936) compression theory, the diameter of the raceme axis averages 1.1 mm (range, = 1.0—1.2 mm, number of measurements, n = 3) in the internodes and 1.7 mm (r = 1.5—1.8 mm, n = 3) at nodes. The raceme axis increases in diameter towards the base of the fruiting shoot and has a zig-zag course, diverging from the pedicels attached at each node. Only two complete internodes are known, one 12.8 mm long and a more basal one 13.6 mm long.

Multifollicles: Each of the pedicels of the multifollicles is subtended basally by the remains of a bract. This clasped the main axis of the raceme for a little more than half its diameter. These bracts have an acute apex and apparently reticulate venation. Bracts are only preserved on the holotype. The most complete is 5.9 mm in length. The poor preservation of this organ and its wide angle of divergence from the fruiting pedicel and from the axis of the raceme, may be due to withering before burial.

Complete pedicels of the multifollicles average 1 mm in diameter (r = 0.8—1.4 mm, n = 13) and 21.3 mm long (r = 13.8—32.8 mm, n = 4). On the holotype raceme, the pedicels increase in length from apex to base; from 13.8 mm, to 14.7 mm, to greater than 20.9 mm, to 23.9 mm. Incomplete longer pedicels (more than 43.7 mm) were found on isolated multifollicles (Text-fig. 2J). This could be an indication that the racemes were originally larger and consisted of more multifollicles than our most complete specimen.

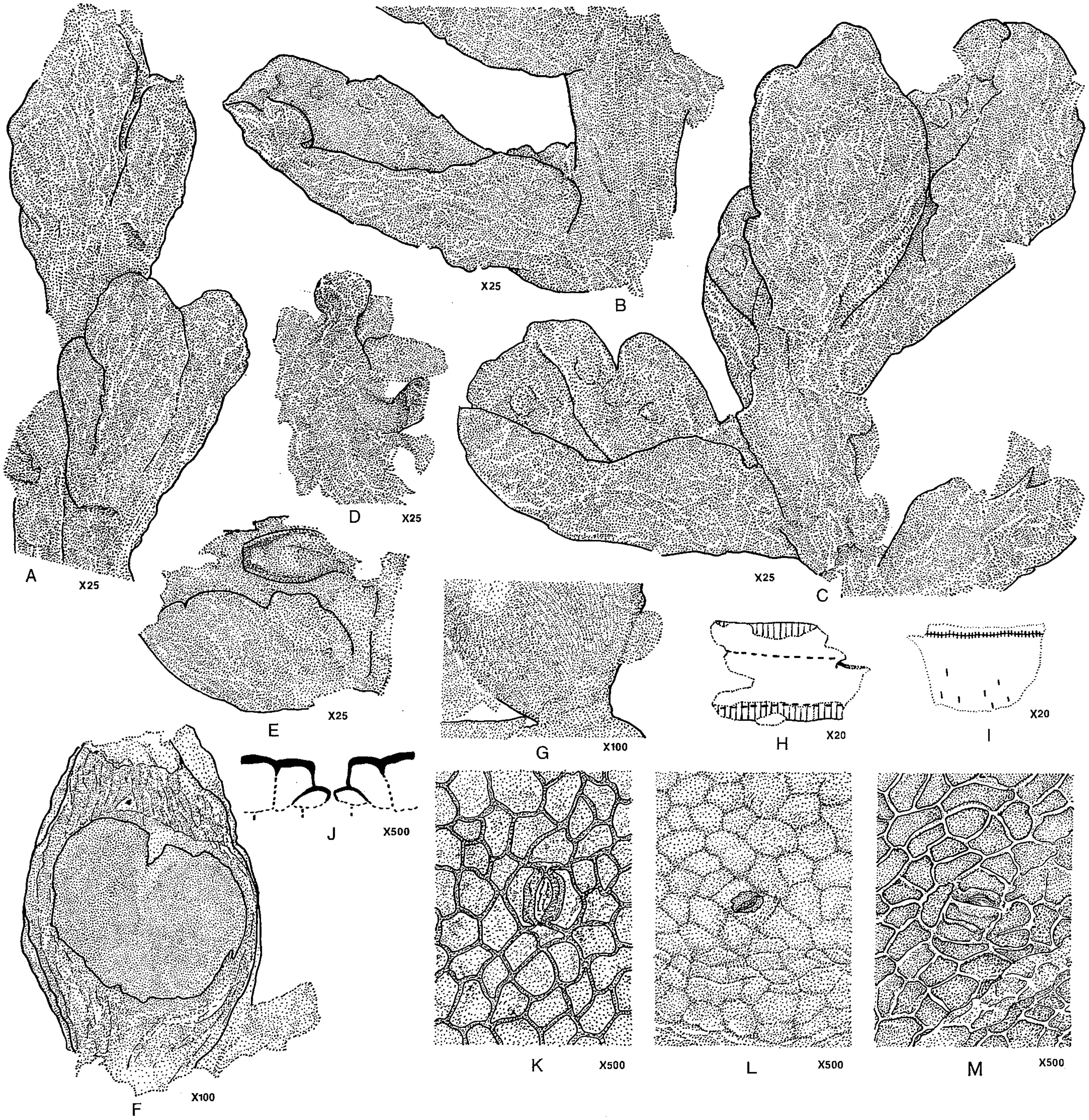
An abscission scar was found at the base of the pedicel in one isolated multifollicle (Figs. 3—4). This is indicated by a basal flaring and basalmost constriction of the pedicel margins and of the central pair of furrows, and also by a moderate development of terminal callus. Evidently some entire multifollicles were shed from the living plant.

The compressed pedicels commonly show two dark, central lines, parallel to the margin. In cuticular preparations, these are a pair of grooves on one side of the pedicel (Text-Fig. 3H, Fig. 34). From the relationships of these at each of the nodes of the holotype (Text-Figs. 2B—2D), they appear to be two grooves defining a broad central rib on the abaxial side of the pedicel (Text-Fig. 2E). The vascular strand appears as a thin carbonized line between these grooves on some specimens (Fig. 4).

The pedicel is covered by a thick (x = 2.9 μm, r = 1—5 μm, n = 11) cuticle, with straight, wide ($\bar{x}$ = 3 μm, r = 1—8 μm, n = 103) cuticular flanges separating the outer portions of the anticlinal walls of the epidermal cells (Fig. 34). The cuticle has scattered, radially-arranged cells of possible hair bases and also some brachyparacytic stomates (Text-Fig. 3K, Fig. 36). The stomates are mostly arranged with their stomatal openings transverse to the axis of the pedicel (Text-Fig. 3I). The entire stomatal complex averages 20 μm long (parallel to the guard cells, r = 18—23 μm, n = 8) and 34 μm wide (r = 30—42 μm, n = 8). Subsidiary cells average 22 μm long (parallel to guard cells, r = 14—36 μm, n = 16) and 8 μm wide (r = 7—11 μm, n = 16). The outer surfaces of the individual cells in the cuticle of the pedicel are moderately bulging. In some areas of the pedicel, particularly around the abaxial grooves (Fig. 34), these bulging outer walls may be folded into irregular, elongate, often-branching ridges. These are restricted to folds in the cuticle, and may be due to pressure during burial and compaction, rather than original features of the plants.

The receptacle of the multifollicle has a width averaging 0.8 mm (r = 0.4—1.7 mm, n = 21) and a length averaging 63.8 mm (r = 50.4—73.4 mm, n = 6). The entire length of the receptacle is covered by closely-spaced, helically arranged follicles. Counts of follicles visible on relatively complete specimens averaged 46 (r = 38—62, n = 6). An estimate of the original number was gained by re-counting each specimen with allowance for follicles indicated by the organotaxy but not visible on the exposed surface of the specimen. This indicated an average number of about 66 follicles per multifollicle (r = 50—90, n = 6).

Follicles: The follicles are ellipsoidal to globular in shape, averaging 2.7 mm long (r = 1.8—3.6. n = 112) by 2 mm wide (r = 1.4—3.1 mm, n = 77). They are of relatively even size and spacing for most of the length of the receptacle except at the apex. There they appear more narrowly elongate, ellipsoidal and smaller than elsewhere on the receptacle, averaging 1.7 mm long (r = 1.0—2.2 mm, n= 6) by 1.0 mm wide (r = 0.5—1.4 mm, n = 5). The follicles are attached to the receptacle by very short bases averaging 0.8 mm wide (r = 0.4—1.2 mm, n = 21).



Text-Fig. 3. *Prisca reynoldsii* sp. nov.; A—C, macerated follicles attached to receptacle (all X 25); A, IU15703—2613, SEM#659; B, IU5703—2606, SEM#813; C, IU15703—2606, SEM#812; D—E, seeds attached to follicle (X 25); D, IU15703—2609, SEM# 811; E, IU15703—2609; F, seed, showing inner cuticle of outer integument (peeled outwards lower right), outer cuticle of inner integument (wrinkled cuticle outlined by inner heavy line), nucellar cuticle (thin line) and megaspore contents (innermost heavy line and dense stipple), drawn from Fig. 29, IU15703—2585 (X 100); G, funicle of seed in outer integument, IU15703—2606 (X 100); H—I, fragments of pedicel cuticle, solid lines are natural folded edges, dotted lines are broken edges, dashed lines are ridges of cuticle (as seen from inside pedicel), crossed lines are depressions in the cuticle (as seen from inside), short bars are stomatal openings, lined area is double thickness of cuticle, IU15703—2585 (X 20); J, reconstruction of transverse section of stomate, with cuticularized (solid lines) and non-cuticularized (dashed lines) cell walls (X 50); K—M, stomates; K, cuticle of pedicel, IU15703—2585 (X 500); L, exterior of outer integument seed cuticle, IU15703—2609, SEM#808 (X 500), M, interior of outer follicle cuticle, IU15703—2609, SEM#811 (X 500).

The cuticles of the follicle are a little more uneven and wrinkled, but otherwise similar to those of the pedicel (Fig. 35). More or less straight cuticular flanges delineate irregular polygonal cells. The outer cuticle of the follicle averages 3 μm thick (r = 2—5 μm, n = 48). The cuticular flange separating the outer portion of the anticlinal walls of the epidermal cells averages 3 μm wide (r = 1—5 μm, n = 61). Maximum dimension of the cells averages 24 μm (r = 13—43 μm, n = 56). The inner cuticle of the follicle is comparable, averaging 2.5 μm thick (r = 1—4 μm, n = 61), the cuticular flanges averaging 3 μm wide (r = 2—5 μm, n = 95) and maximum dimension of the cells averaging 23 μm (r = 10—40 μm, n = 85). Only two stomates were seen in preparations of the follicles (Text-Fig. 3M, Figs. 35, 38). These are similar in shape, size and organization to stomates found on the pedicel and outer integument of the seed of *Prisca reynoldsii* and also to stomates of associated leaves of *Magnoliaephyllum*: length (parallel to guard cells) of stomatal complex 19 and 24 μm; width of stomatal complex 25 and 26 μm; length of subsidiary cells parallel to guard cells averaging 20 μm (r = 19—22 μm, n = 4); width of subsidiary cells all 10 μm. The stomatal opening of these two follicular stomates is poorly defined and both appear to be partly occluded. It is possible that stomates became non-functional with maturation of the fruit, as in some modern angiosperms (ESAU, 1953, p. 593).

The continuity of the cuticle from the follicle to receptacular axis without any evidence of other organs or scars of abscised organs, indicates that *Prisca reynoldsii* is indeed a multifolliculate infructescence, rather than a more complex structure like that of modern Leguminosae, Juglandaceae, Garryaceae, Salicaceae or Chloranthaceae. Although the junction between the follicle and receptacle is irregularly torn in many preparations, the continuity of the cuticle in this area is clearly seen in light microscope (Figs. 32, 33) and scanning electron microscope (Text-Figs. 3A—C, Figs. 18—20, 23).

There are no papillate or pilose surfaces on the follicles which could be interpreted as former stigmatic areas (Figs. 18—23, 39). Scanning electron microscopy of the outside margin of the follicles shows them to be smooth with fine ridging at the very edge (Fig. 39). Much of the inside of the follicle is also smooth (Fig. 39), except for a zone of bulging cell walls near the margin and around funicle bases from which seeds have evidently abscised (Fig. 22). In light microscopic preparations of the follicle, radially arranged cells are occasionally found, but none have attached remnants of hairs, characteristic of hair bases in other fossil cuticles (see THOMAS, 1933). The fructification may have been sparsely hairy during early development, similar to many young plant organs (ESAU, 1953, p. 159). At maturity the follicles of *Prisca reynoldsii* were apparently glabrous.

When living, the follicle was evidently subcarnose, neither excessively fleshy nor woody. The relatively wrinkle-free surface of the follicles is best seen in natural compressions (Fig. 17) and unmacerated transfer preparations (Fig. 15) rather than remains whose internal contents have been removed by oxidative maceration during preparation (Text-Figs. 3A—D, Figs. 18—23). Associated woody twigs and logs have a characteristic fibrous texture and are broken into small cubes (coal cleat), quite unlike the multifollicles of *Prisca reynoldsii.*

Seeds: The seeds are ellipsoidal and orthotropous. Two to six seeds are attached to the inside margin of the follicles, with their micropylar ends directed towards the interior of the follicle (Fig. 27). The total number of seeds in each follicle was calculated from a simple doubling of the number of seeds attached close to each other on follicle remnants and was augmented by observations on compressed specimens (Text-Figs. 5B—C, Figs. 9, 13—14).

The attachment stalk (funicle) of the seed is short and stout (Text-Fig. 3G, Fig. 30). In some scanning electron microscope preparations the funicles are vertically flattened and appear as areas without cellular pattern on the inner cuticular surface of the follicles (compare Text-Fig. 3C and Fig. 18). In one preparation the funicle is laterally folded (Fig. 22). This preparation shows a calloused abscission layer on the broken funicle. Thus, some seeds were probably abscised while the follicle remained attached to the plant.

The seeds are small, averaging only 0.8 mm long (r = 0.6—1.1 mm, n = 6) by 0.5 mm wide (r = 0.3—0.7 mm, n = 6). Their outer surface is smooth. The micropylar end of the seed appears to have been abruptly truncated, although well-preserved in few preparations (Text-Figs. 3E, F, Fig. 29).

The seeds have two distinct integuments which are separated almost to the chalazal end of the seed. The megaspore of the seed is thus enclosed in six cuticular envelopes (Text-Fig. 1D). These are the outer and inner cuticles of the outer integument, the outer and inner cuticles of the inner integument, the nucellar cuticle and a structureless membrane. The outer cuticle of the outer integument is smooth (Text-Fig. 3G, Figs. 25, 30) and thick ($\bar{x}$ = 2.3 μm, r = 1—4 μm, n = 27), with wide cuticular flanges delineating the epidermal cells (x̄ = 3 μm, r = 1—5 μm, n = 72) and irregular polygonal cells (maximum dimension averaging 17 μm, r = 8—39 μm, n = 60). The inner cuticle of the outer integument is similar in thickness (x̄ = 2.4 μm, n = 15), with narrower cuticular flanges (x̄ = 1 μm, r = 1—2 μm, n = 19) and irregular polygonal cells of comparable size (x̄ = 15 μm, r = 9—24 μm, n = 21). A single stomate was found on the outer cuticle of the outer integument of a seed (Text-Fig. 3L, Fig. 37). This is of a similar kind and size to stomates found on the pedicel and follicles of *Prisca reynoldsii* and also in associated fossil leaves referred to *Magnoliaephyllum*. The dimensions of this stomate are: length (parallel to guard cells) of stomatal complex 12 μm; width of stomatal complex 22 μm; length of subsidiary cells, each 13 μm; width of subsidiary cells, each 9 μm. As in modern angiosperms, stomates are rare in seed cuticles. They are found occasionally on the outer integuments of the ovules of modern angiosperms (MAHESHWARI, 1950, p. 58).

The barrel-shaped, smooth outer integument may be contrasted with the slightly-constricted tubular apex and strong longitudinal wrinkling of the inner integument (Text-Fig. 3F, Figs. 26, 29—31). This may indicate that the inner integument was much thicker and more fleshy than the outer integument. The outer cuticle of the inner integument has an average thickness of 1.6 μm (r = 1—3 μm, n = 45), cuticular flanges averaging 2 μm wide (r = 1—3 μm, n = 43) and irregular polygonal cells averaging 14 μm in maximum dimension (r = 9—26 μm, n = 43). The inner cuticle of the inner integument is comparable in thickness(x̄ = 1.5 μm, r = 1—2 μm, n = 17), in width of cell outline (x̄ = 1.2 μm, r = 1—2 μm, n = 34), and in maximum dimensions of the cells (x̄ = 16 μm, r = 10—26 μm, n = 30).

The inner integument is thickest towards the micropylar end of the seed and forms a conical chamber tapering towards a narrow micropylar opening (Fig. 31). The floor of this chamber appears to be raised as a low central dome, but the nucellar cuticle over this dome does not appear to be disrupted. The nucellar cuticle extends very close to the chalazal end of the seed (Figs. 28, 29). It is the most delicate of all the cuticles which have a cellular pattern, averaging only 1.1 μm thick (r = 1—2 μm, n = 14), with cuticular flanges averaging 1 μm wide (r = 1—2 μm, n = 7) and the maximum dimension of polygonal cells averaging 18 μm (r = 9—26 μm, n = 10).

Within the nucellar cuticle is an additional membrane (Figs. 28, 31). This is a dark, structureless, granular layer of moderate thickness (x̄ = 1.6 μm, r = 1—3 μm, n= 14), completely enclosing the inner seed contents.

The innermost membrane commonly encloses convoluted, yellow and gold organic material (Figs. 27—29, 31). This material may have pronounced bilateral symmetry or a deep apical notch (as shown by the innermost heavy line in Text-Fig. 3F, see also Figs. 29, 31).

Comparison

A few described fossil fructifications are similar to *Prisca reynoldsii*, but these are believed to be separate taxa for reasons outlined below.

The most completely known early angiosperm fructification of a similar basic plan to that of *Prisca reynoldsii, is Caspiocarpus paniculiger,* found attached in the axils of leaves referred to *Cissites* sp. cf. *C. parvifolius* (VAKHRAMEEV & KRASSILOV, 1979). This remarkable specimen was found in the middle Albian Kizilschenskaya Suite near Kizil Schen in western Kazakhstan. Its geological age was assessed by associated angiosperm-like leaves, by marine rocks higher in the sequence and by lithological correlation with the marine sequence in the valley of the Emba River to the west (VAKHRAMEEV, 1952). Each axillary fructification consists of three elongate fertile axes, one terminal and two alternate. The fertile axes apparently consist of helically-arranged shorter axes, each shorter axis bearing about ten helically-arranged follicles. It is evidently a more complex fructification than *Prisca.* No other organs or their scars were found which would indicate the nature of the shorter axes of *Caspiocarpus.* The individual follicles of *Caspiocarpus* are similar to those of *Prisca,* although only about one third the size and a little more elongate. Like those of *Prisca,* the seeds of *Caspiocarpus* are bitegmic. According to VAKHRAMEEV & KRASSILOV (1979), the seeds of *Caspiocarpus* are anatropous, although they appear quite symmetrical in the figures and the indicated raphe looks more like an incompletely oxidized portion of the seed. It is also uncertain whether *Caspiocarpus* is a flower or fruit. Only a single leafy shoot with three axillary fructifications has been found. Immature features of the specimen include its thin cutinization, possible herbaceous nature, attachment of relatively complete fructifications, and the weakly cutinized or uncutinized apical seeds compared with the better cutinized and larger basal seeds within the follicle. If immature or near the flowering stage of reproduction, then the fruits of the plant producing *Caspiocarpus* may not have been very different from *Prisca.* Without further data, it is impossible to assess whether its affinities lie with *Prisca* or with modern Ranunculales. Ranunculalean affinities were suggested by VAKHRAMEEV & KRASSILOV (1979) largely on the basis of vegetative features of the fossil shoot.

Several small seed-like fossils have been found in palynological preparations from the Dakota Formation in Minnesota (HALL, 1963). One of these, *Spermatites* sp. (HALL 1963, p. 441, fig. 33) is of comparable size to the seed of *Prisca reynoldsii,* although it has a more conspicuously wrinkled internal cuticle (inner integument?). Even more common in these palynological preparations are bilaterally-symmetrical, homogeneous, brittle bodies, *Microcarpolithes hexagonalis* (HALL, 1963, p. 440, Fig. 34), which are similar to the organic internal bodies in seeds of *Prisca reynoldsii,* although rather more elongate.

Superficially similar to *Prisca,* although a little smaller, is the impression labelled "*Plantae incertae sedis,* an angiospermous infructescence" by SEWARD & CONWAY (1935), from Late Cretaceous (probably Senonian according to KOCH, 1964) rocks in Greenland. This impression fossil is poorly understood.

Affinities

Prisca reynoldsii is best regarded as part of an extinct group of angiosperms characterized by elongate, unisexual multifollicular axes. *Prisca* and *Caspiocarpus* are the only structurally-preserved fossils of this kind known in any detail. Numerous lesser known fructifications also appear to be unisexual and consist of axes bearing helically-arranged follicles. This organization was evidently common in early Cretaceous angiosperms, for example "*Carpolithus*" *geminatus,* "*C.*" *sessilis* and "Capsules sp." of FONTAINE (1889) from the Patuxent Formation at Dutch Gap Canal, Virginia, U.S.A. of late Barremian to Aptian age (DOYLE & HICKEY, 1976); "*Carpolithus*" *ternatus* and "*C.*" *fascicularis* of FONTAINE (1889) from the Arundel Clay at Fredericksburg, Virginia, U.S.A. of early Albian age (DOYLE & HICKEY, 1976): and "*Carpolithes*" *karatcheensis* from the same middle Albian formation as *Caspiocarpus* near Karache Tau in western Kazakhstan, U.S.S.R. (VAKHRAMEEV, 1952; VAKHRAMEEV & KRASSILOV, 1979). Comparable fructifications are also common in Late Cretaceous and early Tertiary floras of the northern hemisphere and have been called reproductive axes by DILCHER (et al., 1976; DILCHER, 1979), "*Carpolithus arcticus*" by HICKEY (1977), *Trochodendrocarpus* (by KRASSILOV, 1973, 1977a), *Jenkinsella* by CHANDLER (1961) and *Cercidiphyllum* by BROWN (1939, 1963), BECKER (1961, 1969, 1973), CHANDRASEKHARAM (1974) and CRANE (1978).

Prisca reynoldsii was evidently a very different plant from any living today particularly in its unique combination of unisexuality and elongate multifollicular reproductive axes. It probably belongs to an extinct group of angiosperms. It is quite unlike previous concepts of ancestral angiosperms or those regarded as living fossils (TAKHTAJAN, 1969). Both *Cercidiphyllum* (Cercidiphyllaceae, Hamamelidales of CRONQUIST, 1968) and *Schisandra* (Schisandraceae, Magnoliales) have unisexual, multifollicle-like fructifications. Both also have such fundamental differences from *Prisca reynoldsii* that they cannot be regarded as closely related.

Cercidiphyllum has unisexual flowers, parietal placentation, follicular fruits and lacks perianth parts. *Cercidiphyllum* differs from *Prisca* in its more elongate follicles, which form a cluster at the end of the pedicel and open extrorsely (Fig. 53). Fossil fructifications identified as *Cercidiphyllum* and (perhaps more appropriately) as *Jenkinsella* are found in rocks as old as Paleocene, at which time the follicles were arranged on more elongate receptacles than in the living species (BROWN, 1939, 1962; CHANDRASEKHARAM, 1974; CRANE, 1978). The living Cercidiphyllaceae includes only two species endemic to China and Japan (LAWRENCE, 1951; SPONGBERG, 1969).

Schisandra has unisexual flowers and fruits with an elongate receptacle. There is a conspicuous zone of scars at the base of the fruiting receptacle, where the perianth was attached, and the fruits are large (5—15 mm long by 4—12 mm in diameter), fleshy, indehiscent and drupe-like (Fig. 52). According to SMITH (1947), the fruiting receptacles of *Schisandra* are mostly solitary or paired. A branched fructification is only found in one species, *Schisandra plena.* A variety of leaf shapes and margin types can be found in the 47 extant species of Schisandraceae recognized by SMITH (1947). The stomatal complexes of the Schisandraceae are paracytic and flanked by distinctive concentric ridges of cutin (JÄHNICHEN, 1976; BAILEY & NAST, 1948). The Cenozoic fossil record of the Schisandraceae indicates that the family had differentiated by the Eocene and was once widespread across Laurasia, ranging from North America and western Europe to the eastern end of the Black Sea, China and

Japan (Jähnichen, 1976; Bones, 1978; Peking Institute, etc., 1978). Living Schisandraceae are confined to southeastern North America and southeast Asia (Smith, 1947).

The likely leaves of *Prisca reynoldsii*

On the basis of close association as common elements of the fossil flora and cuticular similarities, the leaves of the plant producing *Prisca reynoldsii* were probably simple, coriaceous, entire-margined and narrowly ovate to lanceolate, with second-rank festooned-brochidodromous venation (nomenclature after Hickey, 1973, 1977). These fossil leaves are provisionally referred to *Magnoliaephyllum* sp.

Prisca reynoldsii is one of the most common fructifications in our collections of several thousand specimens of fossil plants from the upper Dakota Formation in central Kansas and southern Nebraska. We have over one hundred specimens of *Prisca* from Hoisington (locality IU15706 in Text-Fig 8, see for example Text-Fig. 2A, Fig. 1) and Linnenbergers' Ranch (locality IU15703 inText-Fig. 7, see for example Text-Fig. 5, Figs. 8—15).

Magnoliaephyllum leaves are also common at Hoisington (Fig. 1, lower left center) and on Linnenberger's Ranch (Text-Fig. 4, Figs. 40—47). A variety of other fossil leaves also occur at Hoisington, but are not preserved sufficiently well for cuticular preparation. This locality provides evidence for the association of *Prisca reynoldsii* and *Magnoliaephyllum,* but our collections from Linnenbergers' Ranch also provide anatomical evidence for attributing these organs to the same plant. The epidermal cells and stomates of *Magnoliaephyllum* leaves from Linnenbergers' Ranch, described below, are identical to those of *Prisca reynoldsii,* in both size and shape. *Magnoliaephyllum* leaves appear very coriaceous and have the thickest cuticles of all the leaves at Linnenbergers' Ranch. The cuticle of *Magnoliaephyllum* is hypostomatic, with wide, straight cuticular flanges delineating the epidermal cells and brachyparacytic stomatal subsidiary cells (Text-Figs. 4D—F, Figs. 43—46). The cuticle of the fossil leaves is identical to that of *Prisca reynoldsii* even to the extent of the following measurements, which may be compared with those given in the description of the fossil fructification: width of cuticular flanges in upper cuticle (average, $\bar{x} = 3\ \mu m$, range, $r = 1—5\ \mu m$, number of measurements, $n = 155$), thickness of upper cuticle measured in folds ($\bar{x} = 3\ \mu m$, $r = 1—5\ \mu m$, $n = 86$), width of cuticular flanges on lower cuticle ($\bar{x} = 2\ \mu m$, $r = 1—3\ \mu m$,$n = 139$), thickness of lower cuticle ($\bar{x} = 2\ \mu m$, $r = 1—3\ \mu m$, $n = 113$), length of stomatal complex parallel to guard cells ($\bar{x} = 28\ \mu m$, $r = 11—39\ \mu m$, $n = 96$), width of stomatal complex ($\bar{x} = 36\ \mu m$, $r = 14—48\ \mu m$, $n = 96$), subsidiary cell length parallel to guard cells ($\bar{x} = 27\ \mu m$, $r = 11—56\ \mu m$, $n = 96$) and subsidiary cell width ($\bar{x} = 14\ \mu m$, $r = 5—22\ \mu m$, $n = 96$).

The attribution of *Magnoliaephyllum* leaves and fructifications of *Prisca reynoldsii* to the same extinct plant, is further indicated by the lack of any other likely conspecific leaves at Linnenbergers' Ranch. Other fossil leaves there are either non-angiospermous, or have different cuticular structure, more like that of other associated angiosperm fructifications. Non-angiospermous leaves are rare at Linnenbergers' Ranch. They include sphenopterid fern-like fragments, *Brachyphyllum* — like conifer shoots and parallel-veined bract-like structures. Very rare palmately-lobed angiosperm leaves, with actinodromous venation evidently had a very thin cuticle, which we have not yet been able to prepare. Other rare angiosperm leaves with coarsely dentate margins have distinctive, strongly papillate cuticles with anomocytic stomata. Imparipinnately compound leaves of *Sapindopsis* found at Linnenbergers' Ranch (Dilcher, et al., 1978, Fig. 1B) also have a distinctive cuticle with mixtures of anomocytic, paracytic and laterocytic stomata and hair bases straddling adjacent epidermal cells. Leaves of *Liriophyllum* from here, have been attributed to a different kind of ovulate reproductive axis (Dilcher, et al., 1976, 1978; Dilcher, 1979), because both leaves and fructifications contain small (40—50 μm diameter) resin bodies. Other leaves found at Linnenbergers' Ranch are similar to the likely leaves of *Prisca reynoldsii* in being entire margined and simple, with thick hypostomatic cuticles and brachyparacytic stomata. These leaves differ from those attributed to *Prisca reynoldsii,* in being narrowly ovate to lanceolate, with secondary veins at a more acute angle to the midrib and also in having prominent resin bodies adhering to the cuticle. We have also found an impression fossil at Hoisington (IU15706—3063 and 3063′, part and counterpart) of these narrower leaves attached to a twig with axillary multifollicular axes quite unlike those of *Prisca reynoldsii.*

Magnoliaephyllum is a common fossil leaf in the mid-Cretaceous upper Dakota Formation in Kansas. These are simple entire-margined, coriaceous, narrowly-ovate to lanceolate and have second rank, festooned-brochidodromous venation (Text-Figs. 4A—C, Figs. 40—42). The lamina of the few complete leaves in our collection ranges from 141 x 41 mm to 54 x 26 mm in size. Their apices are attenuate to acute and the base of the lamina is decurrent onto a wide (1.5—2.6 mm) petiole. Several leaves with callosed abscission scars were found. One of these (Text-Fig. 4C, Fig. 41) has a petiole 16.9 mm long, of a leaf with a maximum half-width of 18.3 mm and a likely length in excess of 130 mm. This specimen also shows two light seams in the midrib close to the base of the lamina (Fig. 41), perhaps an indication that the midrib consists of three discrete vascular strands. Another specimen (Text-Fig. 4G, Fig. 47) has two ridges on the adaxial side of the petiole, indicating that it may have had a shallow adaxial sulcus during life (Text-Fig. 4H).

Similar leaf impressions from the ferruginized sandstones of the Dakota Formation in Kansas and Nebraska have been identified by LESQUEREUX as *"Andromeda Parlatorii* HEER" (1892, p. 115, pl. 19, fig. 1, pl. 52, fig. 6), *"Diospyros ? celastroides"* (1892, p. 113, pl. 20, fig. 7), *"Diospyros primaeva"* (1892, p. 109, pl. 20, figs. 1—3), *"Ficus Berthoudi"* (1892, p. 78, pl. 12, fig. 3), *"Ficus inaequalis"* (1892, p. 82, pl. 49, figs. 6—9, pl. 50, figs. 3, 6), *"Ficus praecursor"* (1892, p. 81, pl. 49, fig. 5), *"Magnolia alternans* HEER" (1874, p. 92, pl. 18, fig. 4), some *"Magnolia speciosa* HEER" (1892, p. 202, pl. 60, fig. 3 only), some *"Phaseolites formus"* (1892, p. 147, pl. 55, figs. 5, 12 only), *"Phyllites* species" (1892, p. 216, pl. 59, fig. 7), *"Salix deleta"* (1892, p. 49, pl. 3, fig. 8), and *"Salix Hayei"* (1892, p. 48, pl. 3, fig. 7). The taxonomic variety of these identifications partly reflects the valid observation that similar leaf form and venation are common in a variety of living angiosperms (HICKEY, 1977). Moreover, *Magnoliaephyllum*-like leaves are more common in Cretaceous, than in subsequent, fossil floras (HICKEY, 1978, in press), and were evidently widespread among extinct angiosperms. These Cretaceous leaves are better understood by their associated fructifications, rather than by extensive comparison with leaves of living angiosperms. As has been usual in the study of extinct Mesozoic cycadophytes and pteridosperms, leaves of completely extinct angiosperms should also be referred to form genera. More comprehensive descriptions of *Magnoliaephyllum* and other fossil leves from Linnenbergers' Ranch (localities IU15703, IU15714) are in preparation. We are optimistic that detailed studies of leaf cuticles and associated fructifications will give a more accurate biosystematic concept of these plants than was possible with leaf impressions on ferruginous sandstone, monographed by LESQUEREUX (1874, 1883, 1892). For the moment we refer the likely leaves of *Prisca reynoldsii* to the form genus *Magnoliaephyllum*, used in the broad sense of SEWARD (1926) and SEWARD & CONWAY (1935). The genus *Magnoliastrum* GÖPPERT (1854) has been used in a similar to be a senior is based on a type specimen which appears to have higher rank venation. *Magnoliastrum* appears to be a senior synonym of *Magnoliphyllum* CONWENTZ (1886). The genus *Magnolioides* ETTINGSHAUSEN (1886) has also been confused with these genera, although it is based on a type specimen with markedly non-parallel secondary veins.

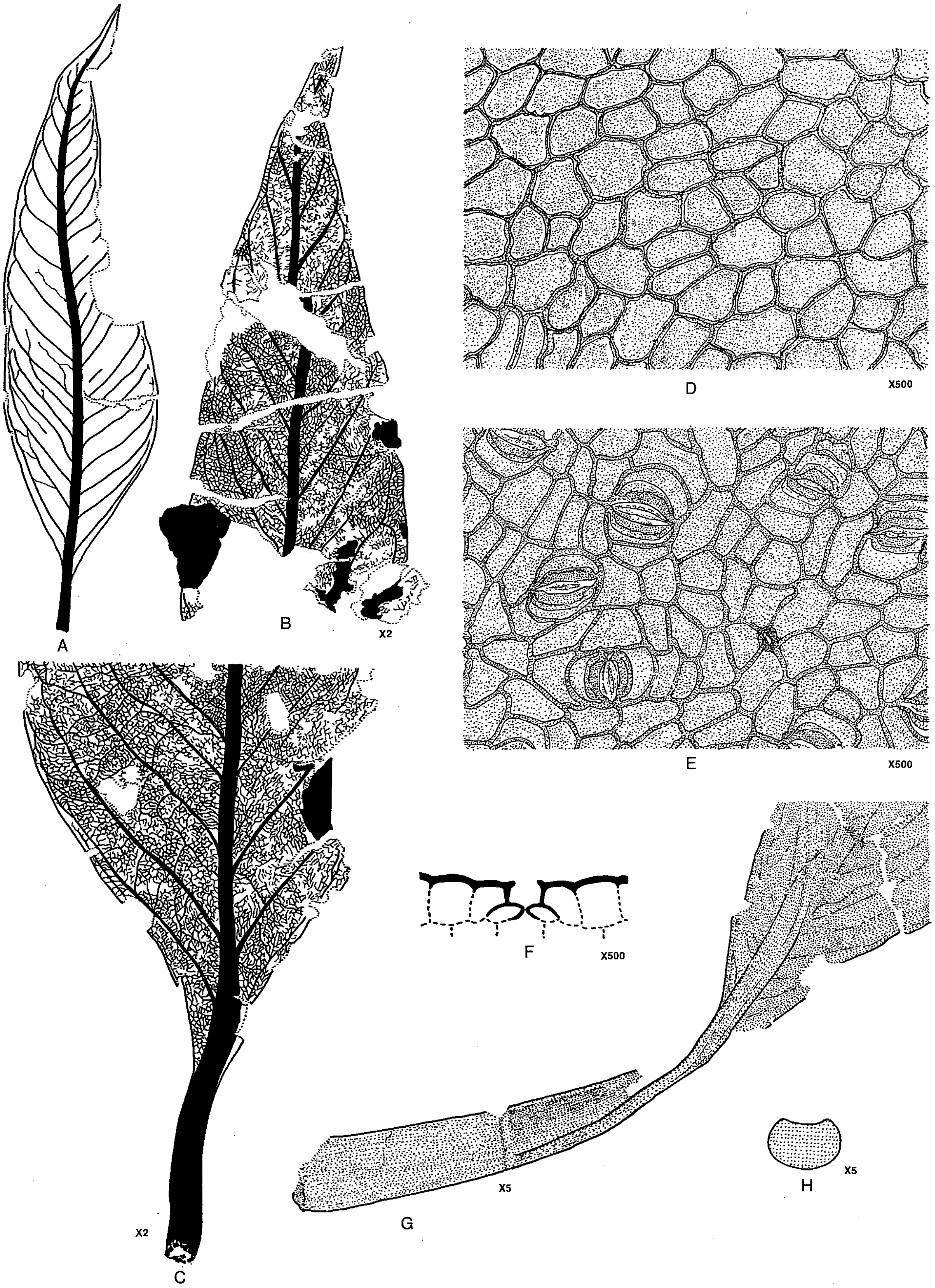
Paleoecology of the *Prisca reynoldsii* plant

Some aspects of the ecology of *Prisca reynoldsii* can be reconstructed from the functional morphology of the fossils and from comparison with living plants. From this kind of evidence, discussed in the following paragraphs, it is likely that the original plant producing these fossils was a tree or shrub. Both seeds and follicles were probably dispersed by wind and water. A few features of its flowering stage can be inferred from the remains at hand. These appear most compatible with pollination largely by wind, perhaps with some non-obligatory insect pollination. With this kind of reproduction, *Prisca reynoldsii* was well-adapted for colonizing disturbed areas, such as clearings, streamsides and shorelines.

Habit

Petioles of the *Magnoliaephyllum* leaves may reach a diameter of 2.5 mm at the abscission scar (Text-Fig. 4C, Fig. 41). They must have been borne on stems of equal or greater diameter, which were thus stouter than the observed axis of *Prisca reynoldsii.* These abscission scars, the thick cuticles of *Magnoliaephyllum* and the woody nature of the axis of *Prisca reynoldsii* (Fig. 2), are evidence that the plant was more likely a woody shrub or tree rather than a herb. This conclusion is also compatible with the geological occurrence of *Prisca reynoldsii,* which is abundant and associated with common fossil logs in a subautochthonous fossil plant accumulation near coal-bearing paleosols containing large fossil roots.

The fructification, *Prisca reynoldsii,* has been reconstructed in a pendent life position (Text-Fig. 1). This is based on the slender nature of the pedicel and main axis supporting long and heavy multifollicles (Text-Fig. 2A, Figs. 1, 2), on the dorsiventral symmetry of the cuticularized pedicels (Text-Figs. 3H, I, Figs. 3, 4, 34), on the



Text-Fig. 4 (Legend see p. 117)

specimens of flexuously-bent receptacles and multifollicles (Text-Figs. 2I, L, M, Fig. 7) and on comparison with modern plants with elongate catkin-like fructifications, such as *Schisandra, Tetracentron* and *Populus.* The complete fructification may have been larger than the size of the most complete apical portion found (Text-Fig. 2A, Fig. 1). This is especially indicated by the occurrence of isolated multifollicles with exceptionally long pedicels (Text-Fig. 2J), as the pedicel length of the multifollicles increases towards the proximal end of our most complete specimen.

The leaves of *Magnoliaephyllum* have clear abscission scars (Text-Fig. 4C, Fig. 41) indicating that they were shed at intervals. This is not to imply that all the leaves were shed seasonally. Leaves may have been shed during irregular periods of deteriorating conditions, seasonally or one at a time. Other early angiosperm fructifications, such as *Caspiocarpus* from the Middle Albian of Kazakhstan (VAKHRAMEEV & KRASSILOV, 1979) and another fructification from the mid-Cretaceous of Kansas (IU15706—3063 and 3063′), are attached in the axils of leafy shoots, so presumably formed while the plant was in full leaf. *Prisca reynoldsii* may have been similar.

Fruit maturation

Several kinds of fossils here attributed to *Prisca reynoldsii* were probably fruits of different maturity, including immature, ripe and partly decayed fruits. All have follicles of similar size and spacing, so none are likely to be flowers or very immature fruits.

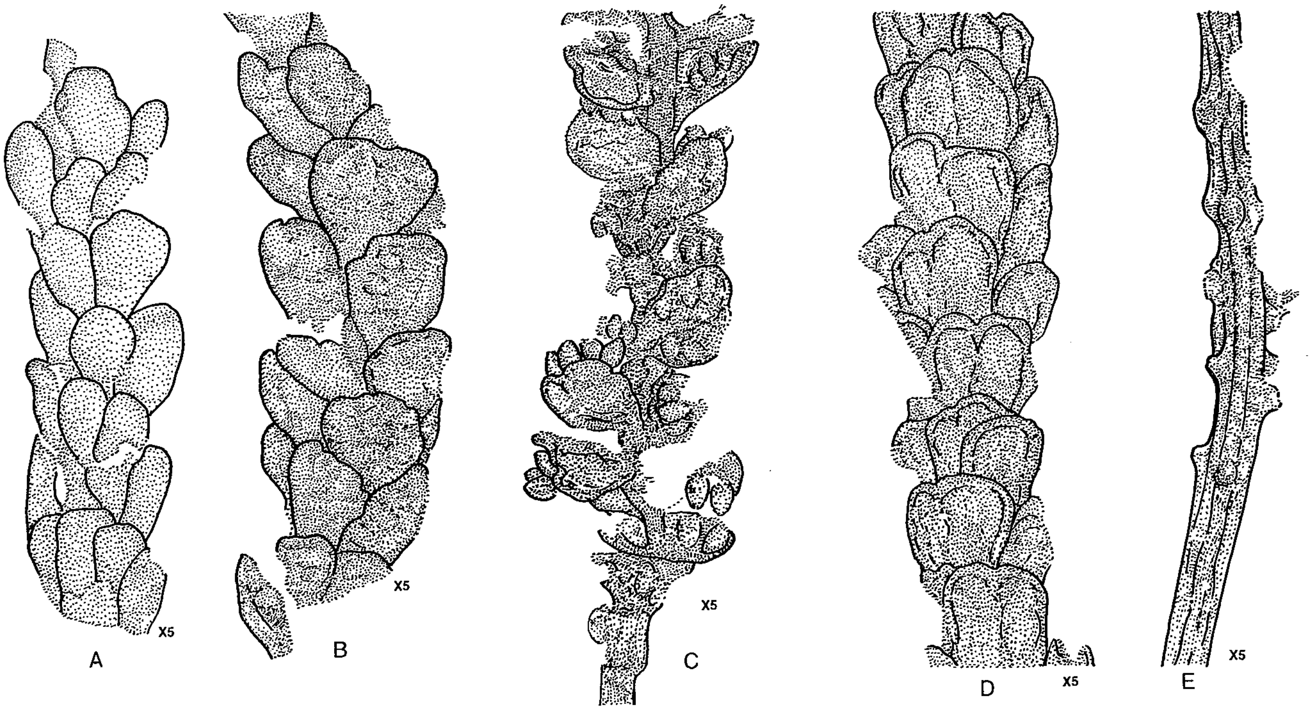
The various remains of *Prisca reynoldsii* can be arranged into likely maturation stages (Text-Fig. 5). Stage 1 (Text-Fig. 5A, Fig. 8) includes elongate multifollicles which have numerous smooth-walled ellipsoidal, involute follicles, whose ovules or seeds, if present, are not cutinized. Stage 2 multifollicles (Text-Fig. 5B, Figs. 9, 17) have more rounded, globular follicles with numerous obvious lumps corresponding to seeds. Several cuticular preparations of seeds were made from remains of this stage. At stage 3 (Text-Fig. 5C, D, Figs. 10, 12—16) the open follicles, with or without attached seeds, reveal their characteristic emarginate apex and lateral lobes (also illustrated in Text-Figs. 3 A, C, Figs. 18—21). Remains of this kind are more numerous in our collections than those of any other stage. Stage 4 (Text-Figs. 2K—M, 5E, Figs. 3, 7) is represented by fruiting axes with follicles disintegrating to various degrees, isolated dehisced follicles and naked receptacles with only thinly-callosed, pseudostipitate bases of the follicles remaining after they have presumably abscised.

Measurements of the spacing of the follicles (or of their bases in stage 4 remains), measured in vertical rows, did not change significantly from stage 1 (average spacing, $\bar{x} = 2.5$ mm, range, $r = 2.2—2.8$ mm, number measured, $n = 9$), to stage 2 ($\bar{x} = 2.3$ mm, $r = 1.1—3.6$ mm, $n = 60$), to stage 3 ($\bar{x} = 2.0$ mm, $r = 0.8—3.7$ mm, $n = 122$) or stage 4 ($\bar{x} = 2.4$ mm, $r = 1.4—3.1$, $n = 22$). Similarly, the compressed follicle width showed little change from stage 1 ($\bar{x} = 2.1$ mm, $r = 1.6—2.5$ mm, $n = 12$), to stage 2 ($\bar{x} = 1.9$ mm, $r = 1.4—2.5$ mm, $n = 50$) or stage 3 ($\bar{x} = 1.9$ mm, $r = 1.6—3.1$ mm, $n = 15$), after which stage fruit width is not adequately preserved. Thus, no elongation of the receptacle or increase in fruit size is apparent in the developmental stages recognized. As additional evidence that stage 1 remains are also fruits, similar ellipsoidal follicles are present at the apices of all the suitably preserved stage 2 and 3 multifollicles (Text-Fig. 2F, Fig. 5).

Flower form and pollination

As all the fossils of *Prisca reynoldsii* appear to be more or less mature fruits, the nature of the flower remains hypothetical, but for the following deductions.

Text-Fig. 4. *Magnoliaephyllum* sp., the likely leaf of *Prisca reynoldsii* sp. nov.; A, leaf outline with midrib and secondary venation, IU15703—2262 (X 1); B, leaf apex, with imperfectly preserved details of areolation, IU15703—2666 (X 2); C, leaf base, petiole and abscission scar, IU15703—2263 (X 2); D, upper cuticle, IU15703—2631 (X 500); E, lower cuticle, IU15703—2631 (X 500); F, reconstructed transverse section of stomate, showing cuticularized (solid lines) and non-cuticularized (dashed lines) cell walls (X 500); G, leaf base and petiole showing part of abscission scar and adaxial ridges, IU15703—3085 (X 5); H, reconstructed transverse section of petiole (X 5). Text-Figs. 5B and 5C drawn from photographs of collodion peels of macerated and cleared leaves mounted in glass with Harleco Synthetic Resin. Text-Figs. 5D and 5E drawn from light microscope preparations of macerated, separated and cleared cuticles.



Text-Fig. 5. *Prisca reynoldsii* sp. nov., specimens of multifollicles interpreted as a maturation sequence; A, stage 1, ellipsoidal, inrolled follicles with no apparent seeds (IU15703—2604); B, stage 2, globular inrolled follicles with seeds (IU15703—2613); C, stage 3, open follicles with attached seeds (IU15703—2585); D, stage 3, open follicles without seeds (IU15703—2618); E, stage 4, naked receptacle of multifollicle without follicles (IU15703—2586). Text-Figs. 5C and 5E show the smooth pedicel below the basalmost follicles. All drawings five times natural size.

As in apparently all living angiosperms, and comparable organs of gymnosperms, the flowers were probably smaller than the preserved multifollicles. Perhaps the flowers were only one half to one quarter the size of the multifollicle as in modern *Magnolia* (Millais, 1927), or perhaps as small as one tenth the size, as in *Schisandra* (Smith, 1947). A ten-fold increase in size from flower to fruit is the greatest amount of growth in angiosperm reproductive organs that we have found recorded in the literature. Well-differentiated fleshy fruits of sweet cherry *(Prunus avium)* increase tenfold in size compared to the carpels during flowering (Tukey, 1933). Palms, including the cocount *(Cocos nucifera)* increase up to sevenfold in size (Corner, 1966). The pod of garden pea *(Pisum sativum)* is only five times the length of the gynoecium of the flower (Flinn, 1974).

The fruits of *Prisca reynoldsii* are covered by cuticle. They are neither waxy, woody or corky. Thus, some evidence of flower parts such as nectaries, petals, sepals or anthers, would be expected in the form of scars if they were present. These are clearly seen in fossil magnoliacean fructifications from the Eocene Arkoses de Ravel in France (Marty, 1915, fig. 4) and from the Miocene Clarkia Beds of Idaho (personal observations of collections discussed by Smiley, Gray & Huggins, 1975). Petal and anther scars are also prominent in modern magnolialean fructifications (Figs. 51, 52). As these are absent in *Prisca reynoldsii,* its flower was also most likely apetalate and unisexual.

In summary, it seems likely that even the flowers of *Prisca reynoldsii* had elongate receptacles, and so were neither perfectly actinomorphic nor zygomorphic. They were probably also unisexual and apetalate, a syndrome of features found in modern wind-pollinated flowers (as discussed by Faegri and van der Pijl, 1966; Whitehead, 1969). It is also possible that they were generalists, pollinated both by wind and a variety of insects, like living *Calluna* and *Salix* (Faegri & Van der Pijl, 1966, p. 119). Only specialized insect pollination seems unlikely.

Dispersal

The propagules of *Prisca reynoldsii* appear to have been either whole follicles or seeds. This is evidenced by specimens of seedless dehisced multifollicles (Text-Fig. 5D, Fig. 10), and naked receptacles from which all the follicles have evidently abscised (Text-Fig. 5E, Fig. 11).

It seems unlikely that animals played any significant role in the dispersal of these propagules. The follicles and seeds of *Prisca reynoldsii* lack any of the specialized modifications found in plant propagules transported by clinging to animals (epizoochory as discussed by VAN DER PIJL, 1972). Considering the poorly fleshed nature of the follicles and the apparent lack of any protective stone or analogous structure in seed or follicle, the fruits and seeds were not adapted for ingestion by animals. The diffuse shape of the fructification would have been a poor visual attractant to animals which might disperse the seeds.

Prisca reynoldsii has none of the specialized spines or spring mechanisms found in various types of self dispersal by either the mother plant or by the propagule itself (autochory of VAN DER PIJL, 1972).

The seeds of *Prisca reynoldsii* may have been shaken from the follicles by swaying of the lax fructification in the wind (a "wind ballist" of VAN DER PIJL, 1972). The fructification of *Prisca reynoldsii* was evidently prominent, as it was large, lax and could easily have hung free of the *Magnoliaephyllum* leaves. It would have been even more prominent if the plant was leafless when in fruit. The wing-like nature of the open follicle of *Prisca reynoldsii* is not as well developed as in many modern propagules dispersed by the wind, but may have been a crude functional analogue. When not opened out completely, the abscised open follicle could also have acted as a small float to disperse seeds over standing bodies of water. The small seeds themselves could probably float or be blown considerable distances. Thus, the propagules of *Prisca reynoldsii* were probably dispersed in several very generalized ways, mainly by wind and water.

Reproductive ecology

The apparent wind pollination, large numbers of small seeds, wind and water dispersal and lack of any evident interdependence on specific animal pollinators or dispersers, suggested for *Prisca reynoldsii,* is also a syndrome found today largely in weeds and other early successional plants (RORISON, 1973; HEINRICH, 1976). Thus *Prisca* had an evident potential for colonizing clearings, open woodland, fluvial or deltaic levees and crevasse splays, and shorelines. In contrast to many such modern plants, *Prisca reynoldsii* was evidently a woody shrub or tree. Larger woody plants of a similar early successional nature, include the river colonizing species of *Platanus* (MOORE, 1972) and *Casuarina* (BEADLE, CAROLIN & EVANS, 1972).

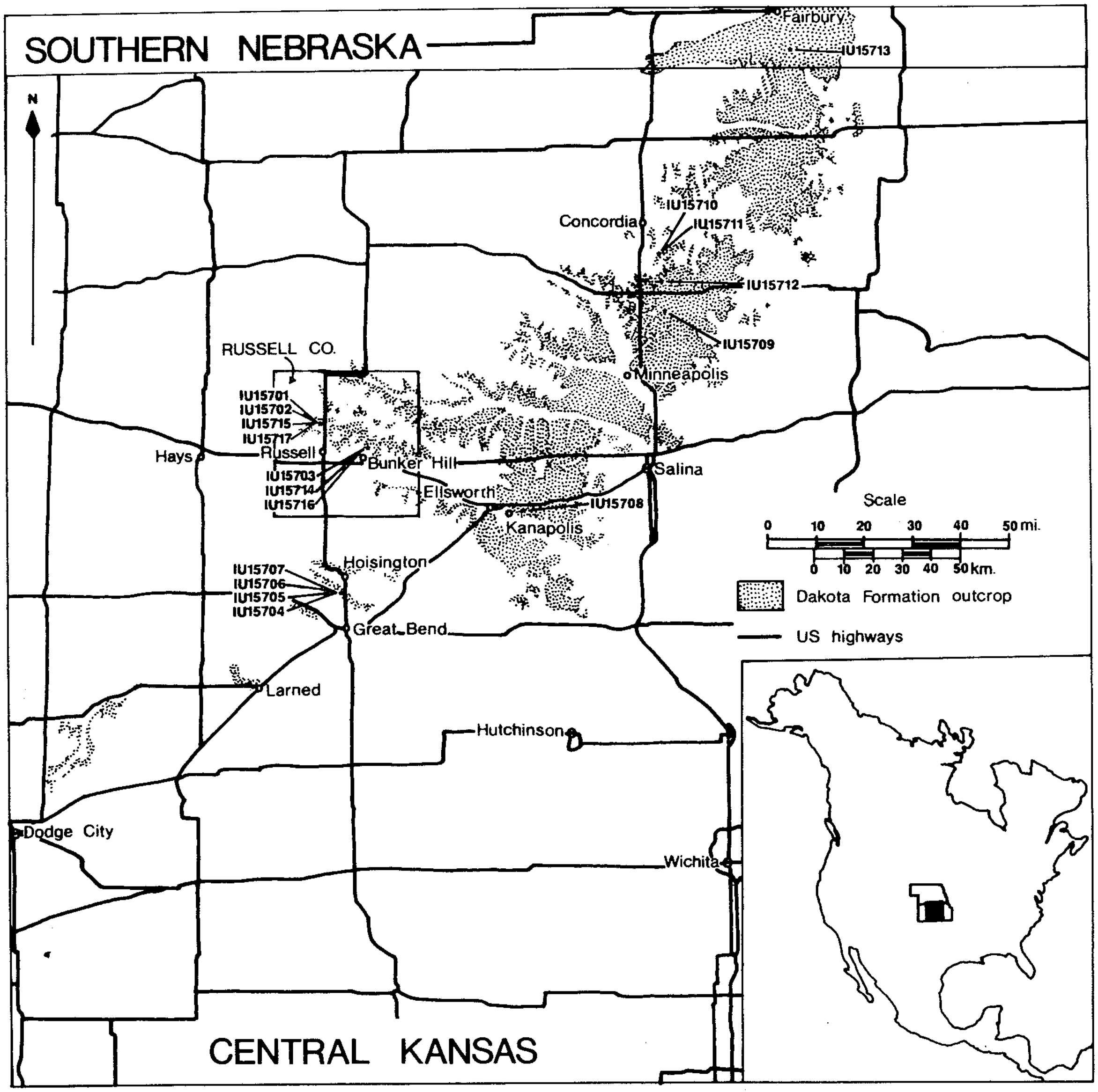
Mid-Cretaceous paleoenvironments and vegetation in Kansas

Although much can be learned by a biological interpretation of *Prisca reynoldsii,* its habitat and importance in mid-Cretaceous vegetation in Kansas are also understood by considering the geological occurrence of the plant fossils. From this evidence, we envisage *Prisca reynoldsii* as a woody shrub or tree of coastal swamp woodlands in interdistributary depressions bordering lagoons and sheltered interdistributary bays of a deltaic coastal plain.

The following account is comprehensive, including our current understanding of all the sedimentary environments, fossil soils and fossil plant associations of the upper Dakota Formation in Kansas and Nebraska. We present evidence for reconstructing coastal mid-Cretaceous environments and ecosystems, both in areas where *Prisca* grew as well as where it did not.

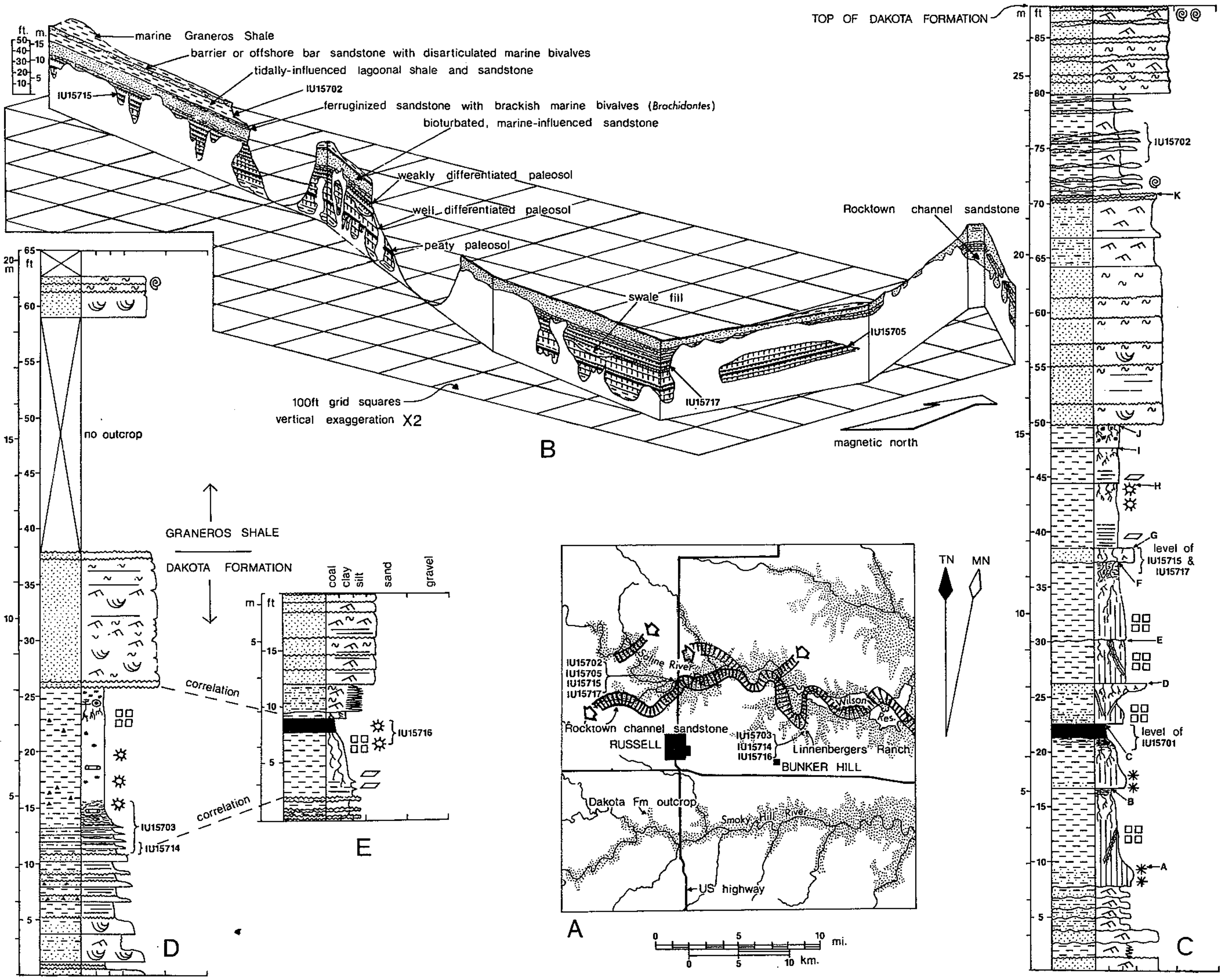
Stratigraphy

The Dakota Formation in central Kansas was deposited between roughly 92 and 94 million years ago (OBRADOVICH & COBBAN, 1975) as a complex lagoonal and deltaic coastal plain overlying the late Albian Kiowa shale and interfingering with and overlain by the early Cenomanian marine Graneros Shale (HATTIN, et al., 1978). All the localities where *Prisca reynoldsii* and *Magnoliaephyllum* sp. have been found in the uppermost Dakota Formation (localities IU15703, IU15706, IU15714 in Text-Fig. 6) were coastal lagoon, interdistributary bay or distributary margin deposits transitional into the overlying marine shale.



Text-Fig. 6. Dakota Formation outcrop (stipple), U.S. highways (heavy lines) and Indiana University, Geology Department, localities for megafossil plants (prefixed IU-) in central Kansas and southern Nebraska.

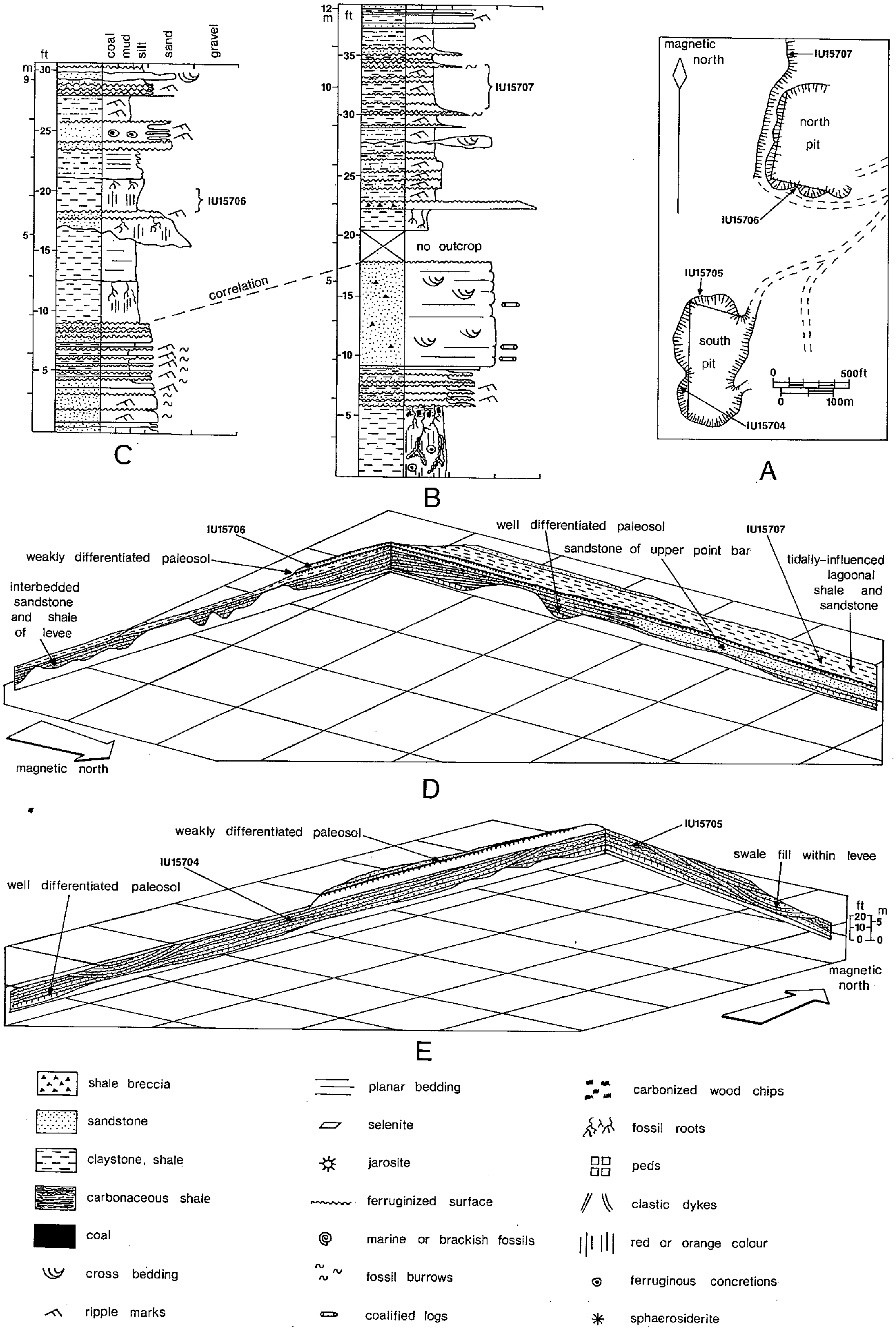
Several different kinds of sediments and fossil soils commonly found in the upper Dakota Formation in Kansas are well-exposed in the extensive bluffs along the northern bank of the Saline River, just west of U.S. highway 281, north of Russell (Text-Figs. 7A—C, Fig. 50, also photographs published by Rubey & Bass, 1925, Fig. 7, Schoewe, 1952, pl. 2A and Merriam, 1963, pl. 8B) and in clay pits south of Hoisington (Text-Fig. 8). These include marine shale, marine sandstone, lagoonal tidally-influenced shale, ferruginized and bioturbated marine-influenced sandstone, channel sandstone, interbedded sandstone and shale of former levees and a variety of fossil soils. There are at least four kinds of fossil soils (paleosols) in the upper Dakota Formation; 1, weakly-differentiated clayey paleosols; 2, coal-bearing paleosols; 3, weakly-differentiated sandy paleosols, and 4, well-differentiated reddish paleosols. Here, as in other terrestrial deposits (Retallack, 1977b), the nature of the paleosols and their relation to sedimentary environments and collections of megafossil plants are an excellent guide to the variety of coastal environments and vegetation in Kansas during mid-Cretaceous time.



Text-Fig. 7. Megafossil plant localities and sedimentology of the upper Dakota Formation in Russell County, Kansas; A, map of Russell County, showing Dakota Formation outcrop (stipple), Rocktown channel sandstone (vertical banding) and its paleocurrents (open arrows), adapted from HATTIN, et al. (1978); B, schematic drawing of the exposures in bluffs along the north bank of the Saline River, just west of U.S. highway 281, north of Russell; C, columnar section at locality IU15702 along the Saline River, showing also equivalent stratigraphic levels of nearby plant fossil localities; D, columnar section at locality's IU15703 and IU15714, east of Linnenbergers' Ranch-house, near Bunker Hill; E, columnar section at locality IU15716, west of Linnenbergers' Ranch-house, near Bunker Hill.

Marine sandstone and shale

The Graneros Shale is a grey montmorillonitic shale, which crops out poorly on hillsides above the bluff-forming sandstones of the upper Dakota Formation and contains a sparse fossil fauna of marine molluscs (HATTIN, 1965; Hattin, et al., 1978). North of Russell (Text-Fig. 7B) the outcrop of the lower Graneros Shale is dark grey, littered with numerous selenite crystals and commonly stained with yellow jarosite blooms. Immediately underlying the Graneros Shale is an orange-brown ferruginized sandstone, with numerous interbeds, 5—10 cm thick of strongly-ferruginized orange-red sandstone. Much of this sandstone is strongly bioturbated and, in places, there are ripple marks and accumulations of disarticulated marine bivalves. This sandstone is best interpreted as a barrier or offshore bar (in the sense of SHEPARD, 1952). There are no obviously intertidal sediments seaward (up section) of this sandstone north of Russell, so it is unlikely to have been a chenier (as described by REINECK & SINGH, 1973).



Text-Fig. 8 (Legend see p. 123)

Similar sandstones, probably also formed as barrier or offshore bars, are present at the top of the Dakota Formation near Hoisington (Text-Fig. 8D), although the outcrop is poor at these localities.

Tidally-influenced lagoonal shales

At several localities in the upper Dakota Formation in Kansas abundant fossil plants, including *Magnoliaephyllum* and *Prisca reynoldsii,* are found in tidally-influenced lagoonal shales.

North of the Saline River, just north of Russell (locality IU15702 in Text-Fig. 7) tidal influence is evidenced by the opposed cross-stratification of sandy ripple marks within a shale unit. These sandy ripple marks may be separated by discontinuous clay skins (flaser bedding) or completely isolated within the shale (linsel bedding). Some bedding planes in the upper portion of this shale unit are littered with moderately-oxidized fossil angiosperm leaves and irregular areas of finely comminuted plant debris. The fossil plant remains are diverse and fragmentary, including both conifer shoots and angiosperm leaves. *Magnoliaephyllum,* like that here attributed to *Prisca reynoldsii,* has been identified among these remains, both from its venation and cuticle (specimen IU15702—3174). A fish scale and four species of arenaceous foraminifera have been found in this same shale unit only 100 m (300 ft) south of the bluffs shown in Text-Fig. 7B, in road cuttings east of U.S. highway 281 (Hattin, 1965, locality 8). These indicate brackish water conditions during deposition (Hattin, 1965). Fossil mussels *(Brachidontes arlingtonanus)* have been found near the base of the shale unit in these same bluffs (Siemers, 1971, loc. 15). There are several living species of *Brachidontes,* all of which are found in nearshore or lagoonal water of brackish and fluctuating salinity (see Siemers, 1976; Scott & Taylor, 1977). Thus the shale unit including fossil plant locality IU15702 was evidently deposited in a brackish coastal lagoon.

In the clay pits south of Hoisington (Text-Fig. 8, Fig. 48), similar tidally influenced shales have been excavated in the upper level of the workings (as of October 1978). In addition to flaser and linsel beds with opposed cross sets, this shale unit also contains a variety of fossil burrows and trails, ferruginized horizons and an horizon of isolated, internally cross-bedded, sandstone megaripples, each about 20 cm high. Fossil plants are poorly preserved in this shale unit near the northern margin of the workings (locality IU15707). In laterally equivalent shale 200 m to the south, both *Magnoliaephyllum* and *Prisca reynoldsii* are common in a diverse assemblage of transported conifer shoots and other angiosperm remains, preserved as impressions in a light brownish-grey shale (locality IU15706). This shale forms the C horizon of a weakly-differentiated fossil soil, with sparsely scattered carbonized roots, ferric mottles and persistent relict bedding (Text-Fig. 8C). These fossils were probably an accumulation of plant debris near a lagoonal shoreline intermittently and sparsely vegetated as water level fluctuated.

As in modern lagoonal systems, salinity probably varied dramatically in time as well as in space, from fully marine salinities usual near openings to the sea to completely freshwater common in the innermost reaches of lagoons (Phleger, 1969). This is especially apparent from the paleoecology of invertebrate fossils of the upper Dakota Formation (Hattin, 1967; Siemers, 1976; Hattin, et al., 1978). Low diversity assemblages of bivalves *(Brachidontes* and *Ostrea)* and serpulid worm tubes, probably lived in brackish water, typical of the inland portions of coastal lagoons. Other fossil assemblages from these lagoonal deposits include brackish elements *(Brachidontes, Crassostrea)* and also a variety of typically marine bivalves (such as *Breviarca, Cymbophora, Geltina, Laternula, Parmicorbula, Tellina* and *Volsella*) which indicate normal marine salinities common in the outer (seaward) parts of lagoons. The transitional marine to non-marine nature of these lagoonal shales is also indicated by their clays, including mixtures of montmorillonite as in overlying marine shale, illite as in adjacent fluvial clays and kaolinite as in underlying fossil soils (Siemers, 1971). The plant remains fossilized in these lagoonal deposits were probably transported varying distances from where the plants lived. Some fossil fructifications and larger leaves are remarkably complete, others are fragmentary and plant chaff is common. Almost every taxon of fossil plant ever found in the Dakota Formation is

---

Text-Fig. 8. Megafossil plant localities and sedimentology of the upper Dakota Formation in claypits southwest of Hoisington, Kansas; A, plan of workings during October 1978, showing high walls (ticked lines) and survey lines of schematic drawings of exposures (Text-Figs. 8D, E); B, columnar section at locality IU15707; C, columnar section at locality IU15706; D, schematic drawing of exposure in north pit; E, schematic drawing of exposure in south pit; D, E, drawn with no vertical exaggeration on a grid of one hundred foot squares.

represented in these diverse lagoonal assemblages, which were probably mixed from several former plant communities. Although conifer shoots are common, angiosperm leaves are more abundant. Angiosperms were evidently prominent in lagoon margin vegetation.

Sandstones of a tide-dominated delta

Marine-influenced sandstones of the upper Dakota Formation in Russell County (Text-Fig. 7) are the key to understanding which of the current models of coastal sedimentation (as outlined by Reineck & Singh, 1973; Reading, 1978), with its distinctive suite of depositional subenvironments, best explains the formation of these mid-Cretaceous coastal sediments. Marine-influenced sandstones form a prominent marker horizon, which can be mapped throughout Russell County (Hattin, et al., 1978, Fig. 4). These planar-bedded sandstones also have low angle cross bedding and ripple drift cross lamination. Paleocurrents within these sandstones are typically bimodal or polymodal. Tidal influence is most pronounced in more shale-rich portions of the sandstone, where flaser bedding may be clearly defined and show opposed cross-sets. Most of the sandstone is more or less bioturbated. Trace fossils include *Planolites, Skolithus, Arenicolites* and *Chondrites.* Some beds of this sandstone, 20—30 cm thick, may be so extensively bioturbated as to appear massive and structureless in the field. The sandstones also contain disarticulated shells of brackish water bivalves, largely *Brachidontes* and *Corbicula,* in places mixed with freshwater bivalves such as ?*Unio* and *Trigonarca,* and in other places with the locally abundant marine brachiopod *Lingula* (Seimers, 1976; Hattin, et al., 1978). The underlying Rocktown channel sandstone and several other channel-like sandstones can also be mapped through much of Russell County (Text-Fig. 7A). These lack fossils and their trough cross beds mainly dip westward (Seimers, 1976). While interpretation of the Rocktown channel sandstone as the deposit of a westerly flowing freshwater stream is relatively secure (Seimers, 1976; Karl, 1976), the paleoenvironment of the overlying marine-influenced sandstones is less certain, but critical for understanding details of mid-Cretaceous coastal geomorphology.

The marine-influenced sandstones of Russell County were probably deposited in the wide shoaling mouth of the distributary of a tide-dominated delta, such as the modern Klang Langat (Coleman, et al., 1970), Ganges-Brahmaputra and Mekong Deltas (Morgan, 1970). The phrase "tide-dominated delta" is used here rather than estuary to indicate that these sediments were part of a depositional landscape and sequence, rather than lying on an erosional surface. This interpretation is most compatible with the geological succession, the evidence for tidal sedimentation, the brackish adapted fossil fauna and the close association of the marine-influenced sandstones with underlying channel sandstones in Russell County. Marine-influenced sandstones thicken westward at the expense of the channel sandstone and contain marine fossils only at localities where the channel sandstones are also present (Siemers, 1971, 1976; Hattin, et al., 1978). The Longford Member of the Kiowa Formation (underlying the Dakota Formation in Kansas) has also been interpreted as deposited on an estuarine coast (Franks, 1980). Such tide-dominated sedimentation was probably widespread on the stable, low-relief coasts of the eastern margin of Cretaceous seaways in the interior of North America.

There are other plausible paleoenvironmental explanations for the marine-influenced sandstone, but all are less likely. If formed in an inlet delta at the mouth of a coastal lagoon, like modern examples discussed by Phleger (1969), Oertel (1973) and Elliot (1978b), they would not show the observed relationships to the channel sandstones, as coastal streams debouch into any part of a lagoon. Nor were the marine-influenced sandstones of Kansas deposited on a complex barrier, chenier or beach ridge plain, like the modern Nayarit coast (Curray, et al., 1969). Neither dune cross-bedding, coal, fossil roots nor fully marine shell fragments were seen in these Kansas rocks. For the same reasons, these sandstones are unlikely to have been deposited in a delta strongly influenced by the action of sea waves, such as the modern Grijalva Delta (Elliott, 1978a). Among the subenvironments of digitate deltas, like the modern Mississippi Delta (Shepard, 1956; Coleman & Gagliano, 1965; Frazier, Ozanik & Elsik, 1978), the marine-influenced sandstones of Kansas are most like modern deposits of subaqueous levees, mouth bars and distal bars of distributaries. However, each distributary of such a delta progrades over marine sediments, a relationship never seen in Kansas. Fossil molluscan faunas more like those in other fully-marine Cenomanian rocks in Kansas would also be expected in the distal portion of a digitate marine delta, rather than the brackish and mixed, low-diversity fauna found in the marine-influenced sandstones of Russell County.

Clayey mangal paleosols of distributary margins

Weakly-differentiated clayey paleosols are found mainly in the uppermost Dakota Formation and evidently formed along distributary and lagoon margins. Many of these were probably marine-influenced. One of these paleosols contains brackish-adapted bivalves in life position. Judging from the fossil roots and leaf litter preserved with these paleosols, they were vegetated largely by shrubby angiosperms, mainly with leaves similar to *"Acerites multiformis"* of LESQUEREUX (1892).

These paleosols are found north of Russell (as at 13.5, 14.5 and 15 m in Text-Figs. 7C and G—J in Fig. 50), at Linnenbergers' Ranch (8 m in Text-Fig. 7D and 3 m in Text-Fig. 7E) and near Hoisington (4.5 and 5.5 m in Text-Fig. 8C and 6.5 m in Text-Fig. 8B). These show little evidence of soil formation beyond the presence of carbonaceous roots, moderate accumulation of surficial organic matter and mild leaching. This poor development could be due to the short time available for their formation before covering by later deposits, or to waterlogging or to both these factors. Some of these paleosols contain abundant carbonized wood chips in their upper layers. Similar wood chips have been interpreted as fossil charcoal (for example by HICKEY & DOYLE, 1977, Fig. 69). This is quite possible, as fires do occur periodically even in swampy depositional environments (STAUB & COHEN, 1979). In older rocks, however, there seems no reliable method of distinguishing charcoal from unburnt wood chips coalified during diagenesis, from resorted chips of ancient wood weathered out of sediments, or from older lignite or coal (SCHOPF, 1975). In Kansas, carbonized wood chips occur in paleosols whose carbonized roots indicate that the plants were no larger than shrubs. Whatever their ultimate origin, the carbonized wood chips were most likely transported from elsewhere. It is likely that these paleosols formed on shorelines or intermittently exposed bars which accumulated wood chips, charcoal and other flotsam from deltaic distributaries.

Euhedral clear crystals of gypsum (selenite) up to 7 cm long, are found concordant with relatively undisturbed bedding (specimen IU15713—3304) in the lower portions of these weakly-differentiated paleosols. These may indicate either marine influence of these former soils during the Cretaceous or be due to to modern weathering. The latter interpretation gains much support from the apparent absence of gypsum in drill holes into the subsurface Dakota Formation in Kansas (as reported by LANDES, 1930; LANDES & KEROHER, 1938, 1939; SWINEFORD & WILLIAMS, 1945; MERRIAM, et al., 1959; MACK, 1962). In the marine Graneros Shale, also littered with selenite at some outcrops, the amount of gypsum cementation and replacement of sandstone and fossil seashells decrease with depth of excavation (HATTIN, 1965). The paleosols containing gypsum in their lower horizons all have carbonaceous uppermost horizons, with prominent jarosite blooms. The jarosite is most likely a weathering product of iron sulphide minerals (TEODOROVICH, 1961; BATTEY, 1972), such as pyrite and marcasite, which have been found in outcrops, and drill cores and cuttings of the Dakota Formation in Kansas (by RUBEY & BASS, 1925; SWINEFORD & WILLIAMS, 1945; SWINEFORD, 1947; SCHOEWE, 1952; SEIMERS, 1971). The selenite may thus have precipitated from surface and ground water acidified by the weathering of iron sulphides, a common origin for gypsum (EARDLEY & STRINGHAM, 1952; MURRAY, 1964; BLATT, MIDDLETON & MURRAY, 1972). The source of calcium in such a reaction may be overlying limestones or caliches, as the shale matrix of all the selenite seen within paleosols failed to react with dilute hydrochloric acid and is presumably non-calcareous. Considering the other possible ways in which gypsum may form (as discussed by DEER, HOWIE & ZUSSMAN, 1962; TEODOROVICH, 1971), selenite in the upper Dakota Formation is unlikely to have been an alteration product of anhydrite, because of its elongate habit. Gypsum crystals may also form as an evaporite on the surface or within the upper few meters of modern intertidal and supratidal mudflats (MASSON, 1955; MILLER, 1975; COOK & MAYO, 1977). This alternative must be discounted for selenite in the Dakota Formation until there is conclusive evidence of the mid-Cretaceous age of these crystals.

Nevertheless, some marine influence of these clayey paleosols would be expected considering their weak differentiation and high stratigraphic position. They are overlain by marine influenced sandstone and are along strike from a distributary of a tide-dominated delta and tidally-influenced lagoonal shales. The abundance of pyrite in the uppermost carbonaceous horizon of these paleosols is comparable with that found in marine-influenced coals (see MACKOWSKY, 1975; CARRUCCIO & GEIDEL, 1979). More conclusively, several articulated mussels *(Brachidontes)* have been found in the upper portion of a weakly differentiated clayey paleosol exposed in a quarry into the upper Dakota Formation 9.6 km south of Fairbury, Nebraska (locality IU15713). Most of the *Brachidontes* collected here by Dr. R. PABIAN (University of Nebraska State Museum specimens 17091—17099) are small, compared to those usually found in the upper Dakota Formation (see HATTIN, et al., 1978). All were less than about 15 mm long (larger ones are incomplete) and one only 8.9 mm long had both valves attached and open. One specimen of *Brachidontes* recently found during preparation of our fossil plant collections from this locality by Dr. J. F. BASINGER (Fig. 54) is of normal size (25.5 mm long) and preserved articulated and closed, with the plane of commissure vertical in life position, on a surface including an angiosperm flower petal and penetrated by numerous carbonaceous roots. This epibyssate, brackish water bivalve evidently lived for some time in mudflats immediately adjacent to or within a stand of woody, marine-influenced vegetation.

The leaf litter of these weakly-differentiated paleosols is commonly preserved in their uppermost horizons. These plant remains may be naturally macerated, rolled, broken or crumpled across several irregular bedding planes and are associated with carbonaceous roots and carbonized wood chips. They were evidently not oxidized to any extent, as they are very weakly, if at all, ferruginized and cuticles are preserved on many leaves. At the Nebraska locality (IU15713), where the mussels *(Brachidontes)* were found, the most common remains are angiosperm leaves similar to *"Acerites multiformis"* (of LESQUEREUX, 1892) and radially-symmetrical perfect flowers. A limited diversity of other angiosperm leaves is also present, but fern and conifer fragments are rare. Other leaf litter localities in weakly-differentiated paleosols north of the Saline River, north of Russell (IU15715, IU15717 in Text-Fig. 7B) were not so obviously marine-influenced but also have low diversity assemblages largely of angiosperm leaves. Only a single impression of a poorly preserved angiosperm leaf has yet been found at locality IU15715. Angiosperm leaves from locality IU15717, include palmately-lobed leaves with actinodromous venation, *Liriodendron*-like leaves and entire-margined leaflets of *Sapindopsis* (identified on the basis of cuticles similar to those of that genus at Linnenbergers' Ranch localities IU15703, IU15714 and also reported by UPCHURCH, 1979). Fragments of fern-like and cycadeoid-like leaves and a portion of a follicle (like those described by DILCHER, et al., 1976) are rare at locality IU15717. Work in progress will characterize these fossil plant assemblages in more detail. The remains collected to date are largely angiospermous and low in diversity. They were evidently produced by shrubby vegetation growing on muddy, waterlogged, frequently-flooded and tidally-influenced distributary margins.

Coal-bearing paleosols of interdistributary swamps

There are many paleosols in the upper Dakota Formation with thick coaly organic horizons. These contain large carbonaceous fossil roots, indicating that they formed under swamp woodland vegetation. Some of these paleosols may have been marine influenced, others freshwater. They probably formed in interdistributary depressions in part fringing coastal lagoons and sheltered bays. Recognizable megafossil plants are seldom preserved in the coals. From plant debris associated with such paleosols and in nearby localities and from the palynology of the coal, these swamp woodlands evidently had ferny understories but the trees were largely angiosperms with leaves of *Magnoliaephyllum, Sapindopsis* and *Liriophyllum.*

Coal was mined from an area extending up to 500 m west southwest of Linnenbergers' Ranch-house (Text-Fig. 7) as recently as 1927, but most of the old adits are now covered by slumps (SCHOEWE, 1952; A. LINNENBERGER, pers. comm. 1979). Our excavations of the coal (Text-Fig. 7E) revealed that this was part of a fossil soil, as both coal and underclay contain large carbonaceous fossil roots. Indeterminate angiosperm fragments were found in the underclay of this paleosol. The coal has yielded largely angiosperm pollen and common fern spores, with rare gymnosperm pollen (preparations and identifications courtesy of M. ZAVADA). It is likely that this was the soil which supported the well-preserved fossil pants collected in the creek bend 250 m east of Linnenbergers' Ranch-house (localities IU15703, IU15714 of Text-Fig. 7D, Fig. 49), for the following reasons. Lithological correlation indicates that the fluvial swale at the fossil plant locality was probably accumulating shale and plant debris at the same time as the peaty soil was developing nearby. Both the fossil plant locality and the peaty soil developed on the distal flanks of a levee system. Both were later covered by clay, which was briefly vegetated and then overlain by marine-influenced sandstone. The fossil plant assemblage appears to have accumulated close to where the plants lived. This is indicated by the low taxonomic diversity in our large collections from Linnenbergers' Ranch, by the excellent preservation of the organic material of the plants and by the range of sizes and shapes of plant organs present. These include leaves, fructifications and woody axes, which would react quite differently and be sorted during prolonged transport by wind and water. The megafossil assemblage is broadly similar in composition to the palynology of the coal, although ferns are under-represented as megafossils. This is probably because the ferns were understory plants, known from studies of modern deposition to be poorly represented in depositional sites adjacent to woodlands (Roth & Dilcher, 1978). Conifer and fern fragments are much less common than angiosperms at Linnenbergers' Ranch. *Magnoliaephyllum* is one of the most common fossil leaves and *Prisca reynoldsii* is one of the most common fructifications. *Sapindopsis* and *Liriophyllum* are also common, the latter noticeably more prominent in the sandy basal portion of the deposit (IU15714). Finally there are few other likely paleoenvironments or paleosols at the same stratigraphic level nearby which would have provided these plants. The fossil plant localities are flanked to the south and west by the coal-bearing paleosol and to the north by the Rocktown channel sandstone and associated levee deposits (Text-Fig. 7A). As indicated in other parts of our discussion, both freshwater and marine-influenced streamsides in Kansas supported different kinds of angiospermous vegetation.

The coal at Linnenbergers' Ranch evidently accumulated in interdistributary lowlands. The coal and parts of the underclay are stained with jarosite, presumably a weathering product of iron sulphide minerals and possibly indicating some marine influence. These swamp woodlands probably also fringed coastal lagoons, as *Magnoliaephyllum*, *Sapindopsis* and *Liriophyllum* are abundant in some lagoonal deposits (particularly the Hoisington locality IU15706, Text-Fig. 8, Fig. 48).

Another coal-bearing paleosol, exposed north of the Saline-River, north of Russell (Text-Figs. 7A, B, Fig. 50C), differs from other coal-bearing paleosols in the upper Dakota Formation in its clay-rich organic horizon without abundant jarosite staining, and in its distinct B horizon, iron-stained reddish-brown and with abundant sphaerosiderite. The organic horizon of this paleosol contains indeterminate fragments of angiosperms, carbonized wood chips and large carbonaceous roots, indicating that it formed under an angiosperm-dominated woodland. Although evidently swampy at times, the water table must also have intermittently retreated to at least a meter below the surface to form the B horizon. This particular paleosol is well below any indication of marine influence, so may have formed completely in freshwater.

An angiosperm-fern community of one of these Cenomanian coastal swamps has been remarkably well preserved by a thin ash in coal of the upper Dakota Formation in central easternmost Utah (Rushforth, 1971). This thin (up to 26 cm) ash contains largely fossil fern fronds of *Matonidium, Astralopteris* and *Gleichenia,* as well as their likely rhizomes towards the base of the ash. The upper 5 cm of impure (carbonaceous and silty) ash contains a greater diversity of fern and angiosperm leaves, including some fragments similar to *Magnoliaephyllum* described here from Kansas (Rushforth's "*Ficus daphnogenoides*"). Rushforth interpreted this diverse upper florule as a record of the early successional colonization of the ash. However, it seems unlikely that such a thin ash fall would completely cover or kill existing vegetation, particularly those plants taller than ground ferns. There are large amounts of silicified wood nearby (Rushforth, 1971, p. 8), and trees were also important to the accumulation of coal. This was confirmed during a recent field trip to examine in more detail the thickness changes and abrupt truncations of the ash illustrated by Rushforth (1971, Figs. 3B, 4A). In extensive cuttings beside the road 8 km northwest of Westwater Ranger Station, the fossiliferous ash is now exposed for 45 m. In places (between 10—15 m and 24—25 m from the northern end) the ash is locally eroded away in a shallow scour filled with carbonaceous siltstone and redeposited ash. There are also three conspicuous cradle knolls (sites of former trees, as discussed by Retallack, 1977a) at distances of 6—8 m, 26—27 m and 30—31 m from the northern end. These are areas of little or no ash, partly plugged from below by contorted carbonaceous siltstone, in some cases with carbonized fossil roots up to 2 cm in diameter. The ash thins to nothing and arches upwards around the cradle knolls. The presence of carbonaceous roots, thinning of the ash, size and irregular conical shape and lack of a central conduit, distinguish these cradle knolls from floor rolls (see Williamson, 1967, p. 193), mud lumps (see Morgan, Coleman & Gagliano, 1968) and mud volcanoes (see Reineck & Singh, 1973, p. 48). From these considerations, it seems more likely that the diverse upper florule was contributed by swamp trees or shrubs, which formed a canopy over the ferny understory. This fortuitous ash fall in central eastern Utah is good evidence for the structure of Cenomanian coastal swamp woodlands.

Palynofloras dominated by angiosperm pollen and fern spores, with rare microplankton and conifer pollen, are widespread in coals of the upper Dakota Formation and rock units of equivalent age throughout the North American interior (see PIERCE, 1961; HEDLUND, 1966; AGASIE, 1969; MAY & TRAVERSE, 1973; ROMANS, 1975). As with coastal peats forming today in the Mississippi Delta (FRASIER, OSANIK & ELSIK, 1978), these coaly paleosols probably formed in a variety of environments and in water of changing salinity.

Sandy paleosols of coastal streamsides

Based upon an interpretation of excellent exposures of the channel and levee deposits of a river in the clay pits near Hoisington, coastal streamsides in Kansas during the mid-Cretaceous appear to have been vegetated largely by shrubby angiosperms, characterized by leaves of *Araliopsoides cretacea.* Streamside swales and ponds also supported a variety of aquatic angiosperms. This interpretation is in agreement with the reconstruction of vegetation in the early and mid-Cretaceous Potomac Group and Raritan Formation of the eastern United States by HICKEY & DOYLE (1977).

Underlying the lagoonal deposits in the clay pits near Hoisington is a unit of finely interbedded sandstone and shale (Text-Fig. 8B—E). This unit is cross-bedded at a very low angle, dipping to the south and includes several low-angle scour-and-fill structures. This is typical for epsilon cross-bedding (as defined by ALLEN, 1963), usually found in deposits of levees, distal scroll bars of meandering streams and deltaic distributaries (examples are discussed by RETALLACK, 1977b, in press). Similar cross-bedding may also form in the point bars of estuarine channels within intertidal mudflats (ALLEN, 1970), but such an origin is unlikely for the deposit at Hoisington, which interfingers laterally with massive, trough cross-bedded sandstone, containing abundant fossil logs (Text-Fig. 8D). The trough cross-bedded sandstone is similar to sands found today in point bars, scroll bars and in-channel bars of meandering streams (described by FRAZIER & OSANIK, 1961; HARMS & FAHNESTOCK, 1965; McGOWEN & GARNER, 1970). This freshwater stream deposit may have been the distributary of a delta building out into the sea or a lagoon elsewhere, but no prodelta sediments are preserved in the clay pits near Hoisington, where the channel truncates a pre-existing well-differentiated paleosol. Thus at Hoisington this was apparently a freshwater reach of a coastal stream.

The epsilon cross-bed (levee deposit) near Hoisington contains fossil plants at two localities (IU15704, IU15705 in Text-Fig. 8E). A bed of strongly ferruginized purple-red sandstone (IU15705 in Text-Fig. 8) contains largely narrow, entire leaves and numerous palmately-lobed leaves of *Araliopsoides.* A similar depositional environment is likely for the large number of leaves collected from surficial, bedding plane exposures of ferruginized sandstones in Kansas, made famous by the widely-distributed collections of CHARLES STERNBERG and the pioneering monographs of LEO LESQUEREUX (1874, 1883, 1892). The regional flora of these sandstones is very diverse, but relatively few species were found at any one locality, perhaps an indication that the leaves preserved at each locality were derived from plants growing nearby (LESQUEREUX, 1892, p. 21). Peltate angiosperm leaves are common in unoxidized shale partings of the epsilon cross-bedded unit near Hoisington (locality IU15704 in Text-Fig. 8). These are similar to fossil leaves interpreted as aquatic by HICKEY & DOYLE (1977, p. 81) and probably grew in swales and ponds of the levee and scroll-bar complex of streams. Considering the small and scattered fossil roots in these epsilon crossbeds, it is likely that the mid-Cretaceous vegetation of streamsides and swales in Kansas, regionally dominated by *Araliopsoides cretacea,* was composed largely of shrubby and aquatic angiosperms.

Shales of freshwater lakes

Shales of freshwater lakes in the middle Dakota Formation contain yet another distinctive assemblage of fossil plants. The abundance of *Sequoia*-like conifer shoots, attests to the prominence of conifers in vegetation away from the coast. *Platanus*-like leaves are also abundant, and probably colonized lake margins or nearby streamsides.

Lacustrine shales are exposed for a distance of about a mile in gullies and in a small quarry on Braun's Ranch, southeast of the intersection of highways 81 and 24, Kansas (locality IU15709 on Text-Fig. 6). Unlike lagoonal shales of the upper Dakota Formation, there is no indication of tidal influence or marine fauna in these shales. Angiosperm leaves and conifer shoots are well-preserved in the even shale partings along with fructifications and insects. No rocks were seen to overlie the shales here. They are probably somewhere in the middle of the Dakota Formation, as they are in the middle of the outcrop area of this westerly dipping formation. Underlying the shales are sandstones with carbonized wood chips and low-angle cross-bedding. As in weakly-differentiated clayey paleosols, the carbonized wood chips may indicate that this was a shoreline. The cross-bedding is similar to that of modern beaches (ELLIOTT, 1978b). These sandstones were probably a lakeside beach. They overlie a well-differentiated reddish paleosol, like those discussed in the next section, probably formed in a largely-dry floorplain.

The most abundant fossil plants in the shales are *Sequoia*-like conifer shoots and *Platanus*-like leaves. *Platanus*-like fructifications (similar to those figured by DILCHER, 1979, Figs. 41, 42) and a few other kinds of angiosperm leaves and fructifications are also found. These remains were probably mixed from a variety of lake margin communities. Several features of the *Platanus*-like remains indicate that these grew in the immediate vicinity of the lake. The *Platanus*-like leaves are well preserved and complete, some with petioles complete to the abscission scar and attached stipules, others are delicate juvenile leaves with marginal glands. The *Platanus*-like fructifications are also unusually common and complete, some with numerous globular heads attached to long axes. Other delicate angiosperm leaves and branching fertile shoots are also well preserved. Some of these angiosperm remains are similar to those found in ferruginized sandstones of Kansas. Like those fossil impressions in sandstone, already discussed, the angiosperms preserved in the shale on Braun's Ranch may have been early successional plants of sandy streamside or lake margin soils. Although conifer shoots are also abundant in the lacustrine shales, they are less well preserved than angiosperm remains and cones are rare. Although some conifers may have vegetated the lake margins and overtopped early successional angiosperms, much of the conifer material may have come from further away from the site of deposition.

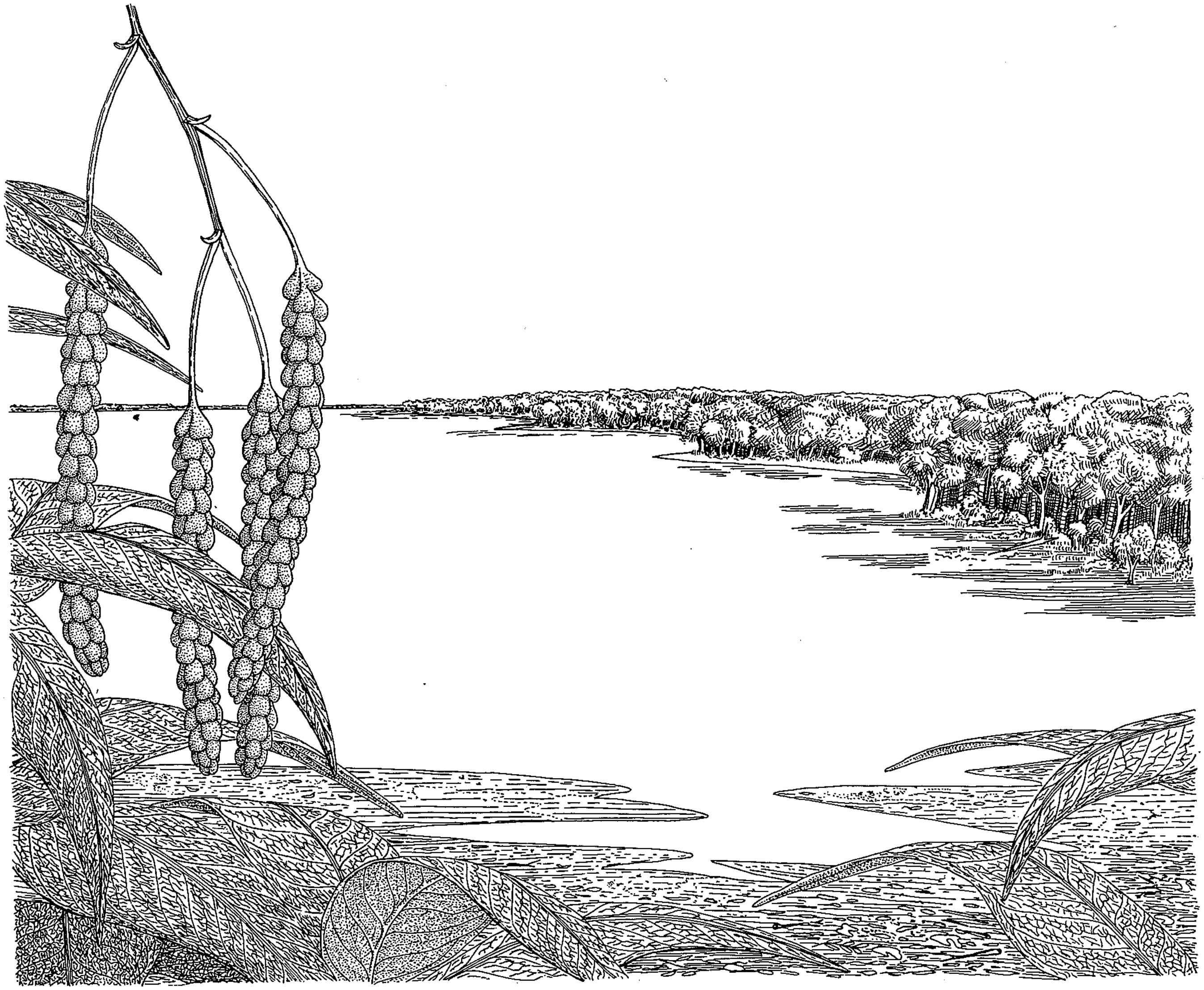
Well-differentiated reddish paleosols of largely-dry floodplains

No fossil plants other than root traces are preserved or associated with the thick well-differentiated reddish paleosols of the Dakota Formation, although they were evidently forested soils of floodplains. As conifer remains are abundant in mixed plant debris of coastal lagoons and in the regional pollen rain, they were probably prominent in these floodplain forests. The most common megafossil remains of these conifers in the Dakota Formation are *Sequoia*-like leafy shoots. This is in agreement with a number of other studies (by BURGESS, 1971; HICKEY & DOYLE, 1977; HICKEY, in press) indicating conifer dominance of inland and floodplain vegetation of North America during the Cretaceous.

Well-differentiated paleosols become increasingly more common lower in the Dakota Formation. These were examined in detail north of Russell (as at 5, 8, 9 and 11.5 m in Text-Fig, 7C) and Hoisington (5 m in Text-Fig. 8B). They have conspicuous reddish brown and mottled B horizons, usually passing upwards into a paler A_2 horizon and then a more or less carbonaceous A_1 horizon. These paleosols may have large fossil roots extending from the surface, distinct clastic dykes (cutans of soil terminology, see BUOL, HOLE & MC CRACKEN, 1973), recognizable soil aggregates (peds), ferric concretions and sphaerosiderite. All these features are more ferruginized within the B horizon. This reddish-brown color has not been produced by surficial weathering, as it has also been found in deep drill holes into the Dakota Formation in Kansas (see LANDES, 1930; LANDES & KEROHER, 1938, 1939; SWINEFORD & WILLIAMS, 1945; MACK, 1962). The clays of these well-differentiated paleosols are mainly kaolinite. X-ray diffractograms of this clay (by SEIMERS, 1971) show low and diffuse peaks characteristic of soils (see RETALLACK, 1977a). Thin sections of these clays also show the characteristic microscopic textures of soils (sepic plasmic fabric of BREWER, 1964; Kansas examples discussed and figured in other terms by SEIMERS, 1971 and FRANKS, 1966). The well-differentiated paleosols are always found below the uppermost Dakota Formation, removed from any independent indications of marine influence. They were probably formed by forest vegetation on low-lying sites where water table was almost permanently one to two metres below the surface (comparable paleosols are discussed by RETALLACK, 1977b and FRANKS, 1980).

Unfortunately, we have not yet been able to find megafossils or pollen in direct association with these well-differentiated fossil soils in Kansas. Conifers, so conspicuous in lagoonal and lacustrine shales in Kansas, do not appear to have grown in other kinds of paleosols already discussed and may have been prominent in the vegetation of these inland floodplain paleosols. The most common and widespread conifer remains are *Sequoia*-like shoots, abundant in mixed plant assemblages of coastal lagoons (IU15706 near Hoisington, in Text-Fig. 8) and of freshwater lakes (IU15709 on Braun's Ranch). A less-likely conifer of these well-differentiated paleosols, was *Brachyphyllum.* This was evidently a minor component of angiospermous swamp woodlands, as it is found sporadically at Linnenbergers' Ranch (IU15703 in Text-Fig. 7), is rare in lagoonal deposits near Hoisington and has not yet been found in inland lake deposits on Braun's Ranch. Well-differentiated paleosols immediately underlie the stream deposit near Hoisington (Text-Fig. 8) and the lakeside beach deposit on Braun's Ranch, and may indicate conditions on the adjacent largely-dry soils of the floodplains.

Conifer dominance of inland vegetation is supported by many palynological studies on the Dakota Formation and rock units of equivalent age in North America (by PIERCE, 1961; HEDLUND, 1966; AGASIE, 1969; MAY & TRAVERSE, 1973; ROMANS, 1975). These studies indicate widespread dominance of assemblages from autochthonous coals by fern spores and angiosperm pollen, but conifer pollen dominates the regional palynoflora of interbedded shale and siltstone. On more general grounds HICKEY & DOYLE (1977) indicate that conifer dominance in floodplains and "backswamps" was maintained at least until the Cenomanian. Other studies (BURGESS, 1971; HICKEY, in press) indicate that conifer dominance persisted, even in coastal areas, well into the late Cretaceous.



Text-Fig. 9. Reconstruction of *Prisca reynoldsii* sp. nov. and *Magnoliaephyllum* sp. in a swamp woodland fringing a coastal lagoon during the early Cenomanian in what is now central Kansas.

A reconstruction of the *Prisca reynoldsii* plant and its habitat

Our reconstruction of *Prisca reynoldsii* and its likely leaves, *Magnoliaephyllum* (Text-Fig. 9), is based on all the foregoing considerations of its structure, paleoecology, and geological occurrence. It was a woody shrub or tree. It grew near sites of deposition such as the margin of a coastal lagoon, but it also grew further inland as a prominent plant of swamp woodlands in interdistributary depressions. With its apparent wind or generalist pollination and numerous small seeds, dispersed by wind and water, it may have been an early successional plant.

Prisca reynoldsii does not appear to have grown in other parts of the mid-Cretaceous coastal plain in Kansas. Within this varied landscape, shrubby angiospermous mangal, characterized by *"Acerites multiformis"*, evidently colonized distributary margins of tide-dominated deltas. Shrubby angiosperms, such as *Araliopsoides cretacea*, and aquatic angiosperms, vegetated levees and swales of freshwater coastal streamsides. Angiosperms with *Platanus*-like leaves were common around freshwater lakes. The largely-dry soils of the floodplains were forested mainly by conifers.

The paleoecology and geological occurrence of *Prisca reynoldsii* and other angiosperms in the Dakota Formation, supports the general conclusion that angiosperms were most abundant in unstable depositional environments, such as coastal swamps, lagoon margins and streamsides. Many were probably early successional plants.

Another notable feature of angiosperms in the Dakota Formation is their abundance and diversity in coastal and near-marine environments. The mid-Cretaceous migration of pioneering early angiosperms in coastal regions may explain many aspects of their spectacular global dispersal and adaptive radiation at a time of dramatic sea level fluctuation (RETALLACK & DILCHER, 1981).

Acknowledgements

The authors greatly appreciate helpful discussions and correspondence with W. L. CREPET (Univ. Connecticut, Storrs), J. A. DOYLE and G. L. STEBBINS (Univ. California, Davis), L. J. HICKEY and E. G. KAUFFMAN (U.S. National Museum, Washington, D.C.), G. J. GASTONY and D. E. HATTIN (Indiana Univ., Bloomington), W. D. TIDWELL (Brigham Young Univ., Provo, Utah), T. DELEVORYAS (Univ. Texas, Austin), and W. A. COBBAN (U.S. Geol. Surv., Denver, Colorado). Few of these workers would agree with all the interpretations presented here, for which we assume complete responsibility. L. J. HICKEY generously showed us localities in the Potomac Group and loaned us material. We thank KARL LONGSTRETH (Indiana Univ., Bloomington) for help with the preliminary sorting of our collections and work on the vegetative remains from Linnenbergers' Ranch. Help during fieldwork and collecting was provided by KARL LONGSTRETH, CHARLES BEEKER, CAROLYN DIEFFENBACH, TOM HAULTER (Indiana Univ., Bloomingtn), W. L. CREPET (Univ. Connecticut, Storrs), BRUCE SERLIN (Univ. Texas, Austin), F. W. POTTER, Jr., H. C. REYNOLDS and MYRL WALKER (Fort Hays State Univ., Hays, Kansas). J. F. BASINGER (Indiana Univ., Bloomington) provided preliminary information on the cuticles of similar plants in the upper Dakota Formation in Nebraska. M. ZAVADA (Univ. Connecticut, Storrs) provided preliminary information on the palynology of coals in the Dakota Formation. This research was funded by National Science Foundation grants BMS 75-02268, DEB 77-04846 and DEB 79-10720 to D. L. DILCHER.

References

AGASIE, J. M. (1969): Late Cretaceous palynomorphs from northeastern Arizona. — Micropalaeontology **15**: 13—30.

ALLEN, J. R. L. (1963): The classification of cross-stratified units, with notes on their origin. — Sedimentology **2**: 93—114.

—,— (1970): Physical processes of sedimentation. — Allen & Unwin, London, 248 pp.

ANDREWS, H. N. (1948): Some evolutionary trends in the pteridosperms. — Ann. Miss. Bot. Gard. **110**: 13—31.

BAILEY I. W. & NAST C. G . (1948): Morphology and relationships of *Illicium, Schisandra* and *Kadsura.* 1. stem and leaf. — J. Arnold Arboretum **29**: 77—89.

BATTEY, M. H. (1972): Mineralogy for students. — Oliver & Boyd, London: 323 p.

BEADLE, N. C. W., EVANS, O. D. & CAROLIN, R. C. (1972): Flora of the Sydney region. — A. H. & A. W. Reed, Wellington: 724 p.

BECKER, H. F. (1961): Oligocene plants from the upper Ruby River Basin, southwestern Montana. — Mem. geol. Soc. Amer. **82**: 127 pp.

—,— (1969): Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. — Palaeontographica **B 127**: 1—142.

—,— (1973): The York Ranch flora of the upper Ruby River Basin, southwestern Montana. — Palaeontographica **B 143**: 18—93.

BLATT, H., MIDDLETON, G. & MURRAY, R. (1972): Origin of sedimentary rocks. — Prentice-Hall, Englewood Cliffs, New Jersey: 634 pp.

BONES, T. J. (1978): Atlas of fossil fruits and seeds from north central Oregon. — Occasional Pap. Nat. Sci. Oregon Mus. Sci. Ind. **1**: 4 pp.

Brewer, R. W. (1964): Fabric and mineral analysis of soils. Wiley, New York: 470 pp.

Brown, R. W. (1939): Fossil leaves, fruits and seeds of *Cercidiphyllum*. — J. Paleont. **13**: 485—499.

—,— (1962): Paleocene flora of the Rocky Mountains and Great Plains. — Prof. Pap. U.S. geol. Surv. **375**: 119 pp.

Buol, S. W., Hole, F. D. & McCracken, R. J. (1973): Soil genesis and classification. — Iowa State University Press, Ames: 360 pp.

Burgess, J. D. (1971): Palynological interpretation of Frontier environments in central Wyoming. — Geoscience & Man **3**: 69—81.

Carruccio, F. T. & Geidel, G. (1979): Using the paleoenvironment of strata to characterize mine drainage quality. — In: Ferm, C. & Horne, J. C. (Eds.): Carboniferous depositional environments in the Appalachian region: collected papers and field guide. — Department of Geology, University of South Carolina, Columbia: 587—596.

Chamberlain, C. J. (1935): Gymnosperms, structure and evolution. — Univ. Chicago Press, 484 pp.

Chandler, M. E. J. (1961): The lower Tertiary floras of southern England. 1. Palaeocene floras. London Clay flora (Supplement). — British Museum Nat. Hist., London. 354 pp.

Chandrasekharam, A. (1974): Megafossil flora from the Genesee locality, Alberta, Canada. — *Palaeontographica* **B 147**: 1—41.

Coleman, J. M. & Gagliano, S. M. (1965): Sedimentary structures: Mississippi River deltaic plain. — In: Middleton, G. V. (Ed.): Primary sedimentary structures and their hydrodynamic interpretation. — Spec. Publ. Soc. Paleont. Miner. Tulsa **12**: 133—148.

Coleman, J. M. & Smith, W. G. (1970): Sedimentation in a Malaysian high tide tropical delta. — In: Morgan, J. P. (Ed.): Deltaic sedimentation, modern and ancient. — Spec. Publ. Soc. Econ. Paleont. Miner. Tulsa **15**: 185—197.

Conwentz, H. (1886): Die Flora des Bernsteins-Band. 2. Die Angiospermen des Bernsteins. — Engelmann, Danzig, Poland: 140 pp.

Cook, P. J. & Mayo, W. (1977): Sedimentology and Holocene history of a tropical estuary (Broad Sound, Queensland). — Bull. Bur. Miner. Resour. Geol. Geophys. Canberra **170**: 206 pp.

Corner, E. J. H. (1966): The natural history of palms. — University of California Press, Berkeley & Los Angeles: 393 pp.

Crane, P. R. (1978): Angiosperm leaves from the lower Tertiary of southern England. — Cour. Forsch. — Inst. Senckenberg **30**: 126—132.

Cronquist, A. (1968): The evolution and classification of flowering plants. — Haughton Mifflin, Boston: 396 pp.

Curray, J. R., Emmel, F. J. & Crampton, P. J. S. (1969): Holocene history of a strand plain, lagoonal coast, Nayarit, Mexico. — In: Castañares, A. A. & Phleger, F. B. (Eds.): Coastal lagoons: a symposium. — Universidad Nacional Autónoma de México: 63—100.

Deer, W. A., Howie, R. A. & Zussman, M. A. (1962): Rock forming minerals. Vol. 5. Non-silicates. — Longmans, London: 371 pp.

Dilcher, D. L. (1979): Early angiosperm reproduction: an introductory report. — In: Taylor, T. N., Dilcher, D. L. & Delevoryas, T. (Eds.): Plant reproduction in the fossil record. — Rev. Palaeobot. Palynol. **27**: 291—328.

Dilcher, D. L., Crepet, W. L., Beeker, C. D. & Reynolds, H. C. (1976): Reproductive and vegetative morphology of a Cretaceous angiosperm. — Science **191**: 854—856.

Dilcher, D. L., Potter, F. & Reynolds, H. C. (1978): Preliminary account of middle Cretaceous angiosperm remains from the interior of North America. — Cour. Forsch.-Inst. Senckenberg **30**: 9—15.

Doyle, J. A. (1978): Origin of angiosperms. — Ann. Rev. Ecol. Syst. **9**: 365—392.

Doyle, J. A. & Hickey, L. J. (1976): Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. — In: Beck, C. B. (Ed.): Origin and early evolution of angiosperms. — Columbia Univ. Press, New York: 139—206.

Eardley, A. J. & Stringham, B. (1952): Selenite crystals in the clays of the Great Salt Lakes. — J. Sedim. Petrol. **22**: 234—238.

Elliott, T. (1978a): Deltas. — In: Reading, H. G. (Ed.): Sedimentary environments and facies. — Elsevier, New York: 97—142.

—,— (1978b): Clastic shorelines. — Ibid.: 143—177.

Esau, K. (1953): Plant anatomy. — Wiley, New York: 735 pp.

Ettingshausen, C. (1886): Die fossile Flora von Sagor im Krain. — Denkschr. Kgl. Akad. Wiss. Wien **50**: 1—56.

Faegri, K. & Van der Pijl, L. (1966): The principles of pollination biology. — Pergamon, Oxford: 291 pp.

Flinn, A. M. (1974): Regulation of leaflet photosynthesis by developing fruit in the pea. — Physiol. Plant. **31**: 275—278.

Fontaine, W. M. (1889): The Potomac or younger Mesozoic flora. — Monogr. U.S. geol. Surv. **15**: 377 pp.

Franks, P. C. (1966): Petrology and stratigraphy of the Kiowa and Dakota Formations (basal Cretaceous) north-central Kansas. — Unpub. PhD. thesis Dept. Geology, Univ. Kansas, Lawrence.

—,— (1980): Models of marine transgression-example from Lower Cretaceous fluvial and paralic deposits, north-central Kansas. — Geology **8**: 56—81.

Frazier, D. E. & Ozanik, A. (1961): Point bar deposits, old river locksite, Louisiana. — Trans. Gulf. Coast Ass. Geol. Soc. **11**: 121—187.

Frazier, D. E., Ozanik, A. & Elsik, W. C. (1978): Environments of peat accumulation-coastal Louisiana. — In: Kaiser, W. R. (Ed.): Proceedings of the Gulf Coast Conference: Geology, utilization and environmental aspects, 1976. — Rept. Invest. Bur. Econ. Geol. Univ. Texas Austin **90**: 5—20.

Göppert, H. R. (1854): Die Tertiärflora auf der Insel Java. — Martini and Grüttefien, Elberfeld (Germany): 162 pp.

Gould, R. E. & Delevoryas, T. (1977): The biology of *Glossopteris*; evidence from petrified seed- and pollen-bearing organs. — Alcheringa **1**: 387—399.

Hall, J. W. (1963): Megaspores and other fossils in the Dakota Formation (Cenomanian) of Iowa. — Pollen et Spores **5**: 425—443.

Harms, J. C. & Fahnestock, R. K. (1965): Stratification, bedforms and flow phenomena (with an example from the Rio Grande). — In: Middleton, B. V. (Ed.): Primary sedimentary structures and their hydrodynamic interpretation. — Spec. Publ. Soc. Econ. Paleont. Miner. Tulsa **12**: 84—115.

Harris, T. M. (1940): *Caytonia.* — Ann. Bot. **4**: 713—734.

—,— (1951): The fructification of *Czekanowskia* and its allies. — Phil. Trans. R. Soc. Lond. **B 235**: 483—508.

—,— (1958): The seed of *Caytonia.* — Palaeobotanist **7**: 93—106.

—,— (1964): The Yorkshire Jurassic flora. II. Caytoniales, Cycadales and pteridosperms. — British Museum Nat. Hist., London: 191 pp.

Hattin, D. E. (1965): Stratigraphy of the Graneros Shale (Upper Cretaceous) in central Kansas. — Bull. Geol. Surv. Kansas **178**: 83 pp.

—,— (1967): Stratigraphic and paleoecologic significance of macroinvertebrate fossils in the Dakota Formation (upper Cretaceous) of Kansas. — In: Teichert, C. & Yochelson, E. L. (Eds.): Essays in paleontology and stratigraphy, Raymond C. Moore commemorative volume. — Spec. Publ. Dept. Geol. Univ. Kansas **2**: 570—589.

Hattin, D. E., Seimers C. T. & Stewart, G. F. (1978): Guidebook. Upper Cretaceous stratigraphy and depositional environments of western Kansas. — Guidebook Series. Geol. Surv. Kansas **3**: 102 pp.

Hedlund, R. W. (1966): Palynology of the Red Branch Member of the Woodbine Formation (Cenomanian), Bryan County, Oklahoma. — Bull. Geol. Surv. Oklahoma **112**: 69 pp.

Heinrich, B. (1976): Flowering phenologies: bog, woodland and disturbed habitats. — Ecology **57**: 890—899.

Hickey, L. J. (1973): Classification of the architecture of dicotyledonous leaves. — Amer. J. Bot. **60**: 17—33.

—,— (1977): Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. — Mem. geol. Soc. Amer. **150**: 183 pp.

—,— (1978): Origin of the major features of angiospermous leaf architecture in the fossil record. — Cour. Forsch.-Inst. Senckenberg **30**: 27—34.

—,— (in press): Changes in the angiosperm flora across the Cretaceous-Tertiary boundary. — In: Berggren, W. A. & Van Couvering, J. (Eds.): The new uniformitarianism. — Princeton Univ. Press, New Jersey.

Hickey, L. T. & Doyle, J. A. (1977): Early Cretaceous fossil evidence for angiosperm evolution. — Bot. Rev. **43**: 3—104.

Hughes, N. F. (1976): Palaeobiology of angiosperm origins. — Cambridge Univ. Press: 242 pp.

Jähnichen, H. (1976): Schisandraceae und Illiciaceae als holarktische und subtropische Florenelemente im mitteleuropäischen Alttertiär. — Paläont. Abh. Zentr. Geol. Inst. **26**: 151—197.

Karl, H. A. (1976): Depositional history of Dakota Formation (Cretaceous) sandstones, southeastern Nebraska. — J. Sedim. Petrol. **46**: 124—131.

Koch, B. E. (1964): Review of fossil floras and non-marine deposits of west Greenland. — Bull. geol. Soc. Amer. **75**: 535—548.

Krassilov, V. A. (1973): Mesozoic plants and the problem of angiosperm ancestry. — Lethaia **6**: 163—178.

—,— (1975): Dirhopalostachyaceae — a new family of proangiosperms and its bearing on the problem of angiosperm ancestry. — Palaeontographica **B 153**: 100—110.

—,— (1977a): The origin of angiosperms. — Bot. Rev. **43**: 143—176.

—,— (1977b): Contributions to the knowledge of the Caytoniales. — Rev. Palaeobot. Palynol. **24**: 155—178.

Landes, K. K. (1930): The geology of Mitchell and Osborne Counties, Kansas. — Bull. Geol. Surv. Kansas **16**: 1—55.

Landes, K. K. & Keroher, R. P. (1938): Oil and gas resources of Rush County, Kansas. — Miner. Resour. Circ. Geol. Surv. Kansas **4**: 1—31.

—,—, —,— (1939): Geology and oil resources of Logan, Gove and Trego Counties, Kansas. — Miner. Resour. Circ. Geol. Surv. Kansas **11**: 1—45.

Lawrence, G. H. M. (1951): Taxonomy of vascular plants. — Macmillan, New York: 823 pp.

Lesquereux, L. (1874): Contributions to the fossil flora of the western interior. Part 1. The Cretaceous flora. — Rept. U.S. Geol. Surv. **6**: 136 pp.

—,— (1883): The fossil flora of the western territories. Part III. The Cretaceous and Tertiary floras. — Rept. U.S. Geol. Surv. **8**: 283 pp.

—,— (1892): The flora of the Dakota Group. — Monogr. U.S. Geol. Surv. **17**: 256 pp.

Mack, L. E. (1962): Geology and groundwater resources of Ottawa County, Kansas. — Bull. Geol. Surv. Kansas **154**: 1—145.

Mackowsky, M.-Th. (1975): Comparative petrography of Gondwana and northern hemisphere coals related to their origin. — In: Campbell, K. S. W. (Ed.): Gondwana geology. — Australian National University Press, Canberra: 195—220.

Maheshwari, P. (1950): An introduction to the embryology of angiosperms. — McGraw Hill, New York, 453 pp.

Marty, P. (1915): *Magnolia* fossile des Arkoses de Ravel (Puy-de-Dôme). — Bull. Soc. Geol. France **15**: 242—259.

Masson, P. H. (1955): An occurrence of gypsum in southwest Texas. — J. Sedim. Petrol. **25**: 72—77.

May, F. E. & Traverse, A. (1973): Palynology of the Dakota Sandstone (middle Cretaceous), near Bryce Canyon National Park, southern Utah. — Geoscience and Man **7**: 57—64.

McGowen, J. H. & Garner, L. E. (1970): Physiographic features and stratification types of coarse-grained point bars: modern and ancient examples. — Sedimentology **14**: 77—111.

Merriam, D. F. (1963): The geologic history of Kansas. — Bull. Geol. Surv. Kansas **162**: 317 pp.

Merriam, D. F., Atkinson, W. R., Franks, P. C., Plummer, N. & Preston, F. W. (1959): Description of a Dakota (Cretaceous) core from Cheyenne County, Kansas. — Bull. Geol. Surv. Kansas **134**: 5—104.

Millais, J. G. (1927): Magnolias. — Longmans, Green and Co., London: 251 pp.

Miller, J. A. (1975): Facies characteristics of Laguna Madre wind-tidal flats. — In: Ginsburg, R. M. (Ed.): Tidal deposits. — Springer New York: 67—73.

Moore, D. M. (1972): Trees of Arkansas. — Arkansas Forestry Commision, Little Rock: 142 pp.

Morgan, J. P. (1970): Depositional processes and products in the deltaic environment. — In: Morgan, J. P. (Ed.): Deltaic sedimentation, ancient and modern. — Spec. Publ. Soc. Econ. Miner. Paleont. Tulsa **15**: 31—47.

Morgan, J. P., Coleman, J. M. & Gagliano, S. M. (1968): Mudlumps: Diapiric structures in Mississippi Delta sediments. — In: Braunstein, J. & O'Brien, G. D. (Eds.): Diapirism and diapirs, a symposium. — Mem. Am. Assoc. Petrol. Geol. **8**: 145—161.

Murray, R. C. (1964): Origin and diagenesis of gypsum and anhydrite. — J. Sedim. Petrol. **34**: 512—523.

Obradovich, J. D. & Cobban, W. A. (1975): A time scale for the late Cretaceous of the western interior of North America. — In: Caldwell, W. G. E. (Ed.): The Cretaceous System in the western interior of North America. — Spec. Pap. Geol. Assoc. Canada **13**: 31—54.

Oertel, G. F. (1973): A sedimentary framework of the substrates adjacent to Georgia tidal inlets. — In: Frey, R. W. (Ed.): The Neogene of the Georgia coast. — Dept. Geol., Univ. Georgia, Athens: 59—66.

Peking Institute Botany & Nanking Institute Geology and Palaeontology (1978): Fossil plants of China. III. Cenozoic plants of China (in Chinese). — Science Press, Peking, 232 pp.

Phleger, F. B. (1969): Some general features of coastal lagoons. — In: Castañares, A. A. & Phleger, F. B. (Eds.): Coastal lagoons: a symposium. — Universidad Nacional Autónoma de Mexico, Mexico City: 5—26.

Pierce, R. L. (1961): Lower Upper Cretaceous plant microfossils from Minnesota. — Bull. Geol. Surv. Minnesota **42**: 1—82.

Reading, H. G. (Ed.) (1978): Sedimentary environments and facies. — Elsevier, New York: 557 pp.

Reineck, H.-E. & Singh, I. B. (1973): Depositional sedimentary environments. — Springer, Berlin: 439 pp.

Retallack, G. J. (1977a): Triassic palaeosols in the upper Narrabeen Group of New South Wales. Part I. Features of the palaeosols. — J. Geol. Soc. Aust. **23**: 383—399.

—,— (1977b): Triassic palaeosols in the upper Narrabeen Group of New South Wales. Part II. Classification and reconstruction. — J. Geol. Soc. Aust. **24**: 19—35.

—,— (in press): Two new approaches for reconstructing fossil vegetation: with examples from the Triassic of eastern Australia. — In: Gray, J. & Boucot, A. J. (Eds.): Communities of the past. — Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Retallack, G. J. & Dilcher, D. L. (1981): A coastal hypothesis for the dispersal and rise to dominance of flowering plants. — In: Niklas, K. J. (Ed.): Paleobotany, paleoecology and evolution. — Praeger, New York: 27—77.

Romans, R. C. (1975): Palynology of some upper Cretaceous coals of Black Mesa, Arizona. — Pollen et Spores **17**: 273—329.

Rorison, I. H. (1973): Seed ecology-present and future. — In: Heydecker, W. (Ed.): Seed ecology. — Pennsylvania State University Press, University Park: 497—519.

Roth, J. L. & Dilcher, D. L. (1978): Some considerations in leaf size and leaf margin analysis of fossil leaves. — Cour. Forsch.-Inst. Senckenberg **30**: 165—171.

Rubey, W. W. & Bass, N. W. (1925): The geology of Russell County, Kansas. — Bull. Geol. Surv. Kansas **10**: 1—86.

Rushforth, S. R. (1971): A flora from the Dakota Sandstone (Cenomanian), near Westwater, Grand County, Utah. — Sci. Bull. Brigham Young Univ. Biol. Ser. **14**: 44 p.

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

Schopf, J. M. (1975): Modes of fossil preservation. — Rev. Palaeobot. Palynol. **20**: 27—53.

Scott, R. W. & Taylor, A. M. (1977): Early Cretaceous environments and paleocommunities in the southern western interior. — Mountain Geologist **14**: 155—173.

Seward, A. C. (1926): The Cretaceous plant-bearing rocks of western Greenland. — Phil. Trans. R. Soc. Lond. **B 215**: 57—174.

Seward, A. C. & Conway, V. (1935): Additional Cretaceous plants from western Greenland. — K. svenska VetenskAkad. Handl. **15**: 14 pp.

Shepard, F. P. (1952): Revised nomenclature for depositional coastal features. — Bull. Am. Assoc. Petrol. Geol. **36**: 1902—1912.

—,— (1956): Marginal sediments of the Mississippi Delta. — Bull. Am. Ass. Petrol. Geol. **40**: 2537—2623.

Siemers, C. T. (1971): Stratigraphy, paleoecology and environmental analysis of upper part of Dakota Formation (Cretaceous), central Kansas. — Unpub. PhD. thesis, Dept. Geol., Indiana Univ., Bloomington, Indiana.

—,— (1976): Sedimentology of the Rocktown channel sandstone, upper part of the Dakota Formation (Cretaceous), central Kansas. — J. Sedim. Petrol. **46**: 97—123.

Smiley, C. J., Gray, J. & Huggins, L. M. (1975): Preservation of Miocene fossils in unoxidized lake deposits, Clarkia, Idaho. J. Paleont. **49**: 833—844.

Smith, A. C. (1947): The families Illiciaceae and Schisandraceae. — Sargentia **7**: 1—224.

Spongberg, S. A. (1969): Cercidiphyllaceae hardy in temperate North America. — J. Arnold Arb. **60**: 367—376.

Sporne, K. R. (1965): The morphology of gymnosperms. — Hutchinson, London: 216 pp.

—,— (1975): The morphology of angiosperms. — Hutchinson, London: 207 pp.

STAUB, J. R. & COHEN, A. D. (1979): The Snuggedy Swamp of South Carolina: a back barrier estuarine coal-forming environment. — J. Sedim. Petrol. **49**: 133—144.

STEBBINS, G. L. (1974): Flowering plants: evolution above the species level. — Belknap Press, Harvard Univ., Cambridge, Massachusetts: 399 pp.

—,— (1976): Seeds, seedlings and the origin of angiosperms. — In: BECK, C. B. (Ed.): Origin and early evolution of angiosperms. — Columbia Univ. Press, New York: 300—311.

STOPES, M. C. (1904): Beiträge zur Kenntnis der Fortpflanzungsorgane der Cycadeen. — Flora **93**: 435—482.

SWINEFORD, A. (1947): Cemented sandstones of the Dakota and Kiowa Formations in Kansas. — Bull. Geol. Surv. Kansas **70**: 53—104.

SWINEFORD, A. & WILLIAMS, H. L. (1945): The Cheyenne Sandstone and adjacent formations of a part of Russell County, Kansas. — Bull. Geol. Surv. Kansas **60**: 101—168.

TAKHTAJAN, A. (1969): Flowering plants: origin and dispersal. — Oliver and Boyd, Edinburgh: 310 pp.

TEODOROVICH, G. I. (1961): Authigenic minerals in sedimentary rocks. — Translated from Russian by Consultants Bureau, New York: 120 pp.

THOMAS, H. H. (1933): On some pteridospermous plants from the Mesozoic rocks of South Africa. — Phil. Trans. R. Soc. Lond., B **222**: 193—265.

—,— (1934): The nature and origin of the stigma. — New Phytol. **33**: 173—198.

TUKEY, H. B. (1933): Embryo abortion in early ripening varieties of *Prunus avium*. — Bot. Gaz. **94**: 433—468.

UPCHURCH, G. R. (1979): The cuticular anatomy of *Sapindopsis* from the Lower Cretaceous Potomac Group of Virginia and Maryland. — Misc. Ser. Bot. Soc. Am. **157**: 39.

VAKHRAMEEV, V. A. (1952): Regionalinay stratigrafii SSSR. Tom 1. Stratigrafii i iskopaemay flora Meloviix otlozhenii zapdnogo Kazakhstana (Regional stratigraphy of the U.S.S.R. Vol. 1 Stratigraphy and fossil flora of the Cretaceous deposits of western Kazakhstan). — Nauka, Moscow: 340 pp.

VAKHRAMEEV, V. A. & KRASSILOV, V. A. (1979): Reproduktinie organi tsvetkoviikh iz aliba kazakhstana (Reproductive organs of a shoot of a flowering plant from the Albian of Kazakhstan). — Paleont. Zh. for **1979**: 121—128.

VAN DER PIJL, L. (1972): Principles of dispersal in higher plants. — Springer, Berlin: 161 pp.

WALTON, J. (1936): On the factors which influence the external form of fossil plants; with descriptions of some species of the Palaeozoic equisetalean genus *Annularia* STERNBERG. — Phil. Trans. R. Soc. Lond. B **226**: 219—237.

—,— (1953): The evolution of the ovule in pteridosperms. — Advanc. Sci. **10**: 223—230.

WHITEHEAD, D. R. (1969): Wind pollination in the angiosperms: evolutionary and environmental considerations. — Evolution **23**: 28—35.

WILLIAMSON, I. A. (1967): Coal mining geology. — Oxford University Press, Oxford: 266 pp.

Explanation of plates

Plate 1

Figs. 1—7. *Prisca reynoldsii* sp. nov. angiospermous fructification.
1. Raceme of elongate multifollicles, holotype IU15706—3042 (X 1).
2. Raceme axis, showing bracteate pedicel bases of multifollicles, holotype IU15706—3042 (X 5).
3. Isolated, fragmentary multifollicle with long pedicel, IU15714—3024 (X 1).
4. Base of pedicel, showing two abaxial furrows (arrows) and partly-rounded base, possibly from abscission, IU15714—3024 (X 5).
5. Multifollicle showing pedicel and small apical follicles, IU15706—3056 (X 1).
6. Portion of well-preserved multifollicle compression, IU15703—2589 (X 1).
7. Pedicel and naked receptacle of multifollicle, after dehiscence of follicles, IU15703—2586 (X 1).

Plate 2

Figs. 8—17. *Prisca reynoldsii* sp. nov., angiospermous fructification.
8. Immature multifollicle, with little development of seeds, IU15703—2604 (X 5).
9. Mature multifollicle with numerous well-developed seeds in closed follicle, IU15703—2613 (X 5).
10. Multifollicle with open seedless follicles, IU15703—2618 (X 5).
11. Pedicel and naked receptacle, IU15703—2586 (X 5).
12. Counterpart of specimen of Fig. 10, open seedless follicles IU15703—2618′ (X 5).
13. Multifollicle with open, seed-bearing follicles, base of basal follicle indicated by arrow, IU15703—2585 (X 5).
14. Counterpart of specimen of Fig. 13, base of basal follicle indicated by arrow, IU15703—2585′ (X 5).
15. Walton transfer preparation of multifolicle, IU15703—2617 (X 5).
16. Portion of open seedless multifollicle, IU15706—3049 (X 5).
17. Portion of multifollicle with seed-bearing, closed follicles, IU15703—2589 (X 5).

Plate 3

Figs. 18—23. *Prisca reynoldsii* sp. nov., scanning electron micrographs of follicles.
- 18—20. Dehisced seedless follicles attached to receptacles without subtending scars or appendages (X 25).
  - 18. IU15703—2606, SEM#812.
  - 19. IU15703—2613, SEM#659.
  - 20. IU15703—2606, SEM#813.
- 21. Isolated follicle, showing marginal fold, IU15703—2613, SEM#660 (X 25).
- 22. Detail of follicle apex, showing funicle of abscised seed and surrounding weakly papillate cuticle, IU15703—2613, SEM#660 (X 25).
- 23. Detail of follicle base and attachment to receptacle, without subtending scars or appendages, IU15703—2613, SEM# 660 (X 25).

Plate 4

Figs. 24—31. *Prisca reynoldsii* sp. nov., seeds.
- 24. Seeds attached to remnants of multifollicle and with micropyle sunken back onto megaspore, IU15703—2609, SEM# 811 (X 50).
- 25. Longitudinally fractured seed showing smooth outer cuticle of outer integument on left hand side and several internal layers, IU15703—2609, SEM#807 (X 100).
- 26. Attached seed showing wrinkled outer cuticle of inner integument (left), smooth outer cuticle of outer integument (right) and pollen chamber (upper sunken area), IU15703—2609, SEM#811 (X 125).

Figs. 27—31. Photomicrographs of macerated seeds mounted in glycerine jelly.
- 27. Three attached seeds with and without megaspores (arrows), IU15703—2606 (X 25).
- 28. Megaspore with organic contents enveloped by nucellar membrane and fragments of cuticle of inner integument, IU15703—2585 (X 50).
- 29. Seed with outer integument dissected away from the right hand side, "oo" is outer cuticle of outer integument, "io" is inner cuticle of outer integument, "oi" is outer cuticle of inner integument, megaspore contents are dark, IU15703—2609 (X 100).
- 30. Outer cuticle of outer integument of seed, showing funicle (arrow) attached to cuticle of follicle (below), IU15703—2606 (X 200).
- 31. Apex of seed, "m" is non-cellular membrane, "n" is nucellar cuticle, "mi" is micropyle above pollen chamber, "x" is invagination in dark megaspore contents, IU15703—2609 (X 300).

Plate 5

Figs. 32—39. *Prisca reynoldsii* sp. nov. cuticles.
- 32—36. Light photomicrographs of follicles and cuticles mounted in glycerine jelly.
  - 32. Follicle attached to receptacle, IU15703—2606 (X 30).
  - 33. Follicle attached to receptacle, arrow indicating space for tissue inside cylindrical cuticle of receptacle, IU15703—2606 (X 30).
  - 34. Abaxial cuticle of pedicel, showing two abaxial furrows (arrows), IU15703—2585 (X 90).
  - 35. Follicle outer cuticle, with a partly-occluded paracytic stomate (indicated by arrow), IU15703—2589 (X 500).
  - 36. Pedicel adaxial cuticle with a paracytic stomate (indicated by arrow), IU15703—2585 (X 500).

Figs. 37—39. Scanning electron micrographs of cuticles.
- 37. Outer surface of outer cuticle of outer integument of seed, showing stomatal opening, IU15703—2609, SEM#808 (X 1000).
- 38. Inside surface of outer cuticle of follicle showing paracytic stomate, IU15703—2609, SEM#811 (X 1000).
- 39. Outer surface of follicle margin (wrinkled lower surface) and inner surface of follicle (smooth surface above), IU15703—2606, SEM#812 (X 250).

Plate 6

Figs. 40—47. *Magnoliaephyllum* sp., the likely leaf of *Prisca reynoldsii* sp. nov.
- 40. Leaf compression, IU15703—2262 (X 1).
- 41—42. Light macrophotographs of collodion peels of leaf compressions, treated by oxidative maceration and mounted in Harleco Synthetic Resin (X 2).
  - 41. Leaf base, showing abscission scar (at base of petiole), details of venation and two clear lines probably separating three strands of midrib (arrows), IU15703—2263.
  - 42. Leaf apex, with at least one clear closed arch of secondary venation (arrow) IU15703—2666.
- 43—44. Light photomicrographs of macerated cuticles, stained with Safranin 0 and mounted in Harleco Synthetic Resin, IU15703—2631 (X 500).

43. Thick adaxial (upper) cuticle.
44. Thinner abaxial (lower) cuticle, with numerous paracytic stomates and a hair base (at arrow).
45—46. Scanning electron micrographs of cuticle, IU15703—2314, SEM#568 (X 500).
45. Inside surface of abaxial (lower) cuticle.
46. Outside surface of abaxial (lower) cuticle.
47. Detail of petiole, showing a pair of adaxial ribs (arrows) and portion of basal abscission scar, IU15703—3085 (X 5).

Plate 7

Figs. 48—50. Plant fossil localities in the mid-Cretaceous, upper Dakota Formation in central Kansas, U.S.A.
48. Southern margin of northern claypit, south of Hoisington, showing locality IU15706 (arrow) in shale overlying conspicuous epsilon cross-set of pit wall, viewed from northwest, August 1977.
49. Natural exposure in stream bend, east of Linnenbergers' Ranch-house, northeast of Bunker Hill, showing localities IU15703 (arrow) and IU15714 (near figure to left) and marine-influenced cross-bedded sandstone capping exposure, viewed from northwest, July 1978.
50. Bluffs (20 m high) overlooking the Saline River south of Russell, showing sequence of paleosols underlying locality IU15702 in tidally-influenced shales and siltstone with plant fossils (above K); A, top of massive sphaerosideritic sandstone; B, top of moderately differentiated reddish-brown paleosol; C, top of coal-bearing paleosol; D, top of well-diferentiated reddish-brown paleosol; E, portion of well-differentiated reddish-brown paleosol; F, top of thick, well-differentiated reddish-brown paleosol; G—J, tops of poorly-differentiated paleosols; K, ferruginized top of marine-influenced sandstone.
Figs. 51—53. Dried modern angiosperm fructifications.
51. Multifollicle of *Magnolia tripetala,* showing small stamen scars and larger petal scars at base of large woody dehisced follicles (campus ornamental, Indiana University, Bloomington, Indiana, U.S.A.).
52. Indehiscent fruits (right) and receptacle and pedicel (left) of *Schisandra glabra,* with well-spaced scars of fruits on receptacle and prominent zone of perianth scars (arrow) above pedicel (Field Museum of Natural History Chicago, specimen F1481, from Beaufort, South Carolina).
53. Follicular fructification of *Cercidiphyllum japonicum* (campus ornamental, University of Connecticut, Storrs, Connecticut, U.S.A.).
54. Brackish water bivalve *Brachidontes* in life position from mangal paleosol in upper Dakota Formation, 9.6 km south of Fairbury, Nebraska (IU15713—3033).

Greg Retallack & David L. Dilcher: *Prisca reynoldsii*, gen. et sp. nov.


8


9


10


11


13


12

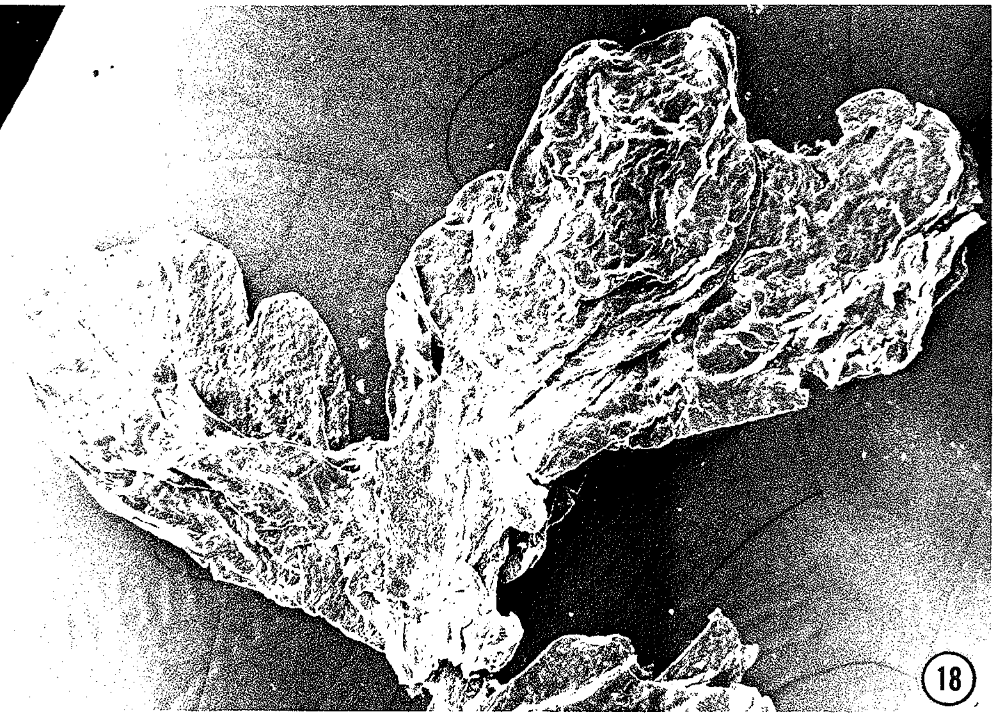

14


15

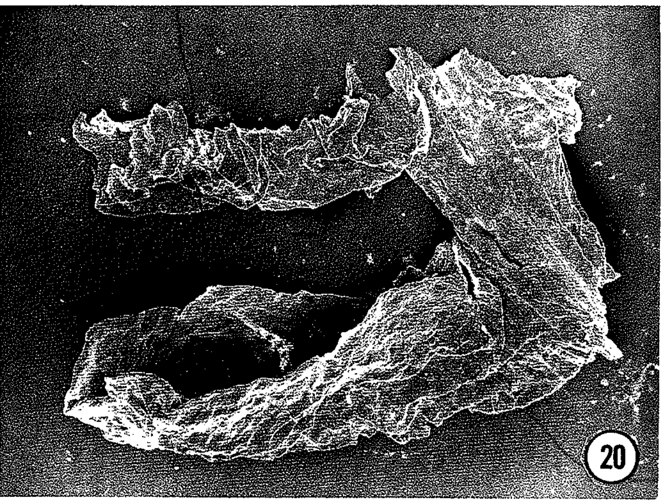

16

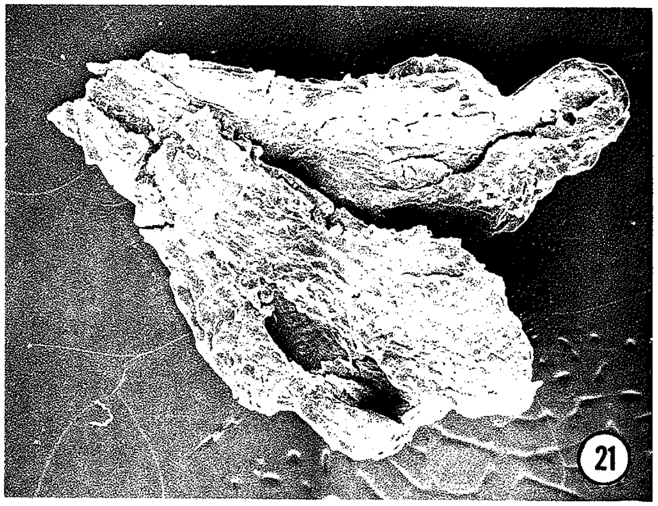

17

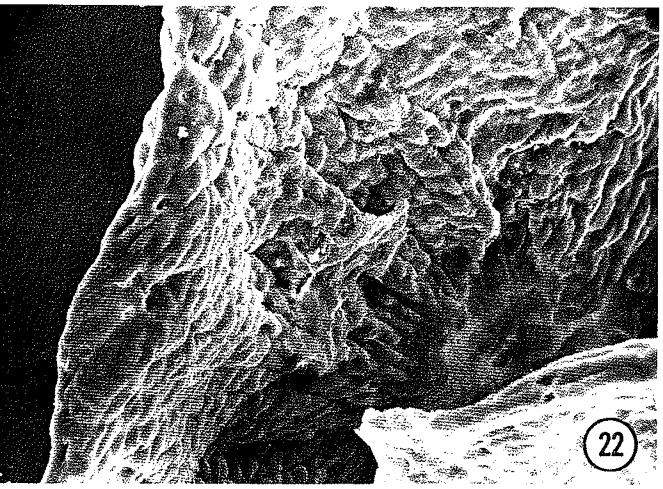
Greg Retallack & David L. Dilcher: *Prisca reynoldsii*, gen. et sp. nov.

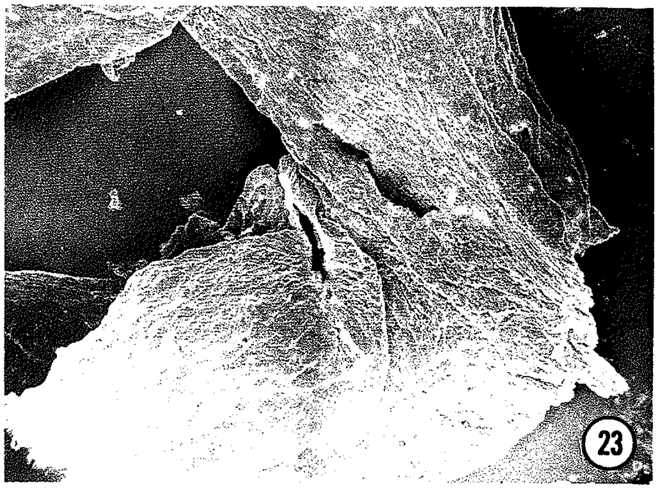

18


19

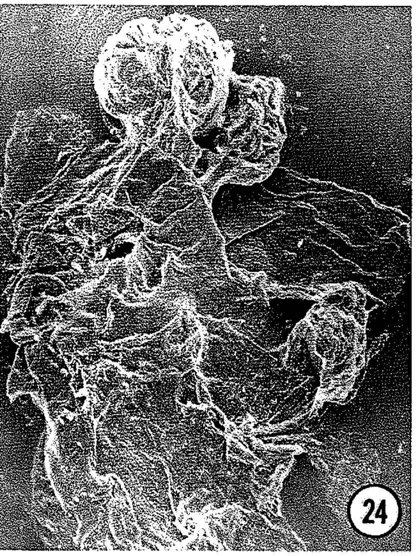

20


21


22

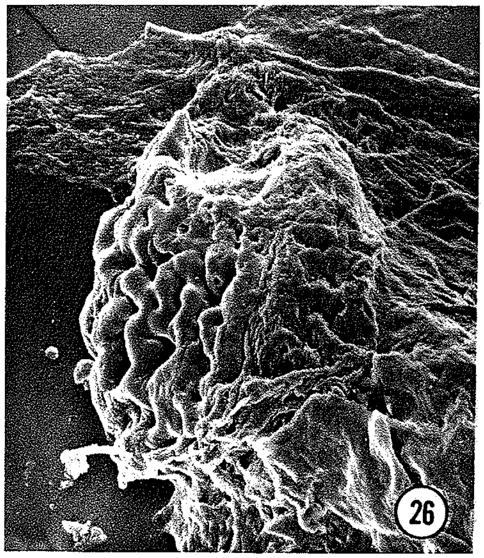

23

Greg Retallack & David L. Dilcher: *Prisca reynoldsii*, gen. et sp. nov.



24

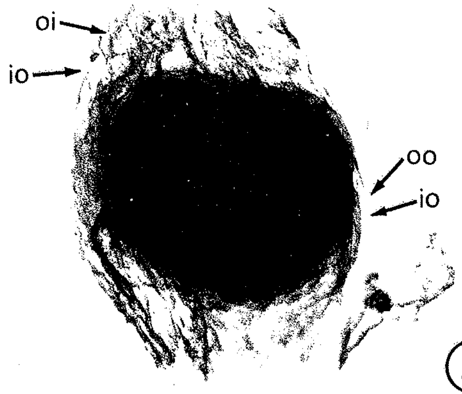
25



26

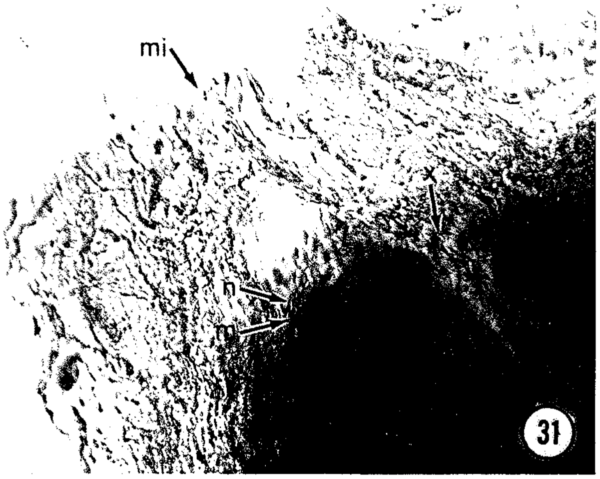
27

28



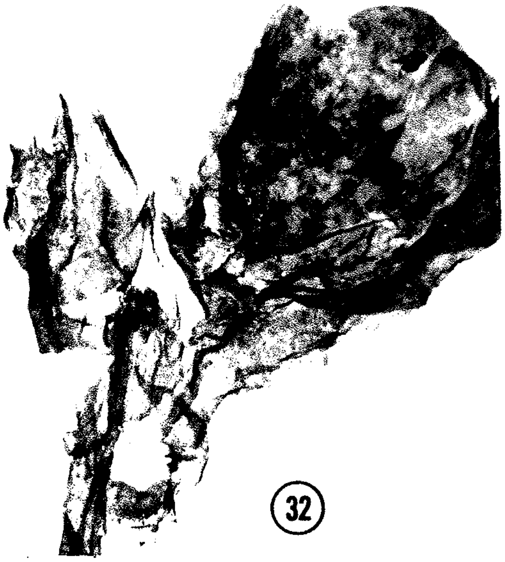
29

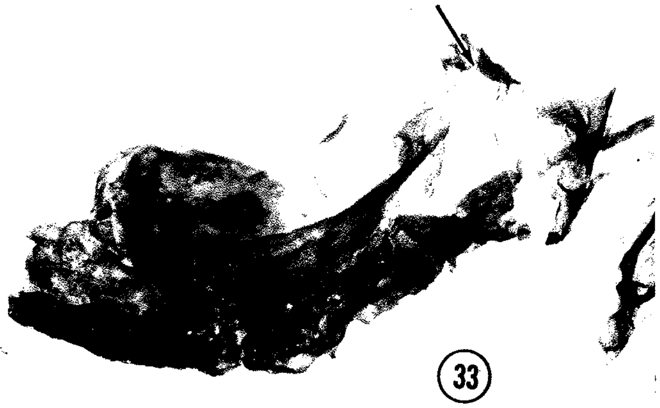
30



31

Greg Retallack & David L. Dilcher: *Prisca reynoldsii,* gen. et sp. nov.


32

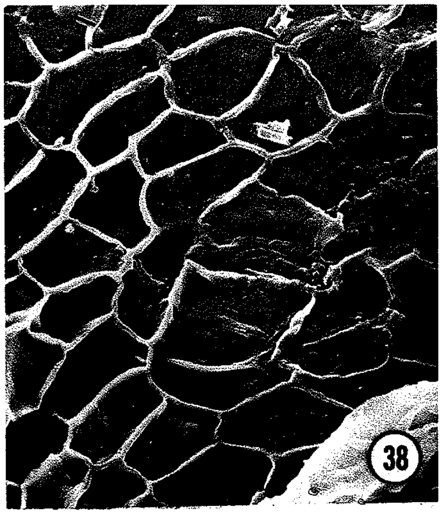

33


34


35


36


37

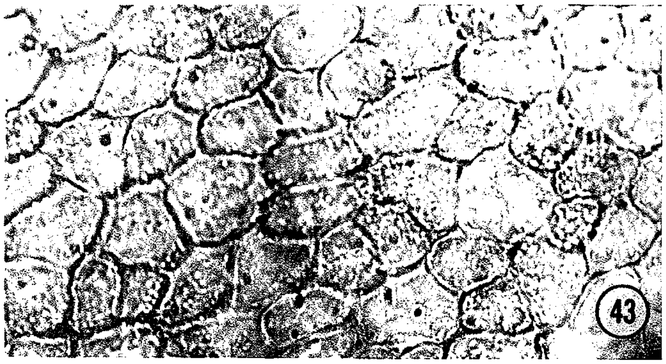

38


39

Greg Retallack & David L. Dilcher: *Prisca reynoldsii,* gen. et sp. nov.

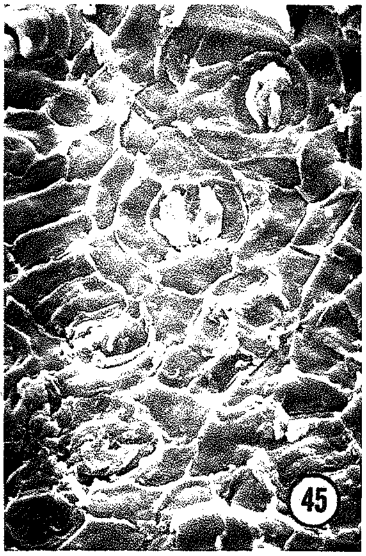

40


42

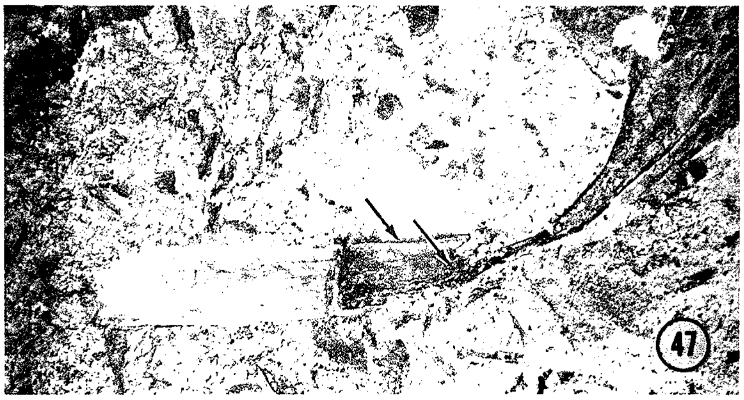

43


44

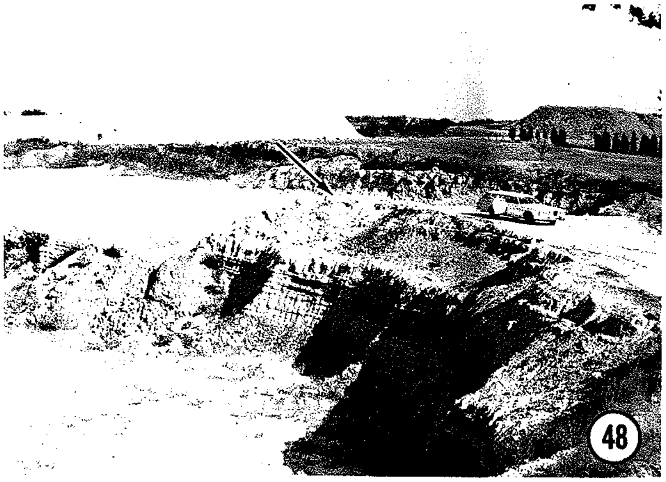

41


45


46


47

Greg Retallack & David L. Dilcher: *Prisca reynoldsii,* gen. et sp. nov.


48

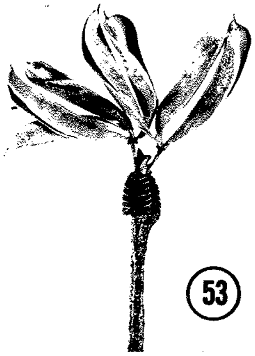

51


49

50


54


52


53

Greg Retallack & David L. Dilcher: *Prisca reynoldsii,* gen. et sp. nov.