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Epidermal anatomy of *Glenopteris splendens* Sellards nov. emend., an enigmatic seed plant from the Lower Permian of Kansas (U.S.A.)

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Abstract

Frond morphology and epidermal anatomy of the enigmatic late Early Permian seed plant *Glenopteris splendens* Sellards are described based on material from east central Kansas (Wellington Formation, Sumner Group; Artinskian ICS Stage). The specific diagnosis for *G. splendens* Sellards, 1900 is emended. Frond morphology suggests that *G. splendens* is a member of the seed plant order Peltaspermales. Macroscopical and epidermal features of *G. splendens* are consistent with those extant plants adapted to (seasonal) moisture limitation and elevated soil and ground water salinity. For example, the pachymorphous (succulent) pinnules may help mitigate water stress, because succulent foliage delivers large quantities of storage water, but could also be an adaptation to elevated salinity since storage of large quantities of water increases the salt accumulation capacity of the fronds. Wart- and peg-like cuticular projections may represent an adaptation to (seasonal) moisture limitation because extant xeromorphic plants have similar heavily cutinized anticlinal cell walls. *Glenopteris splendens* fronds are entirely glabrous, which suggests that epidermal outgrowths were not necessary as protective elements against deleterious environmental influences.
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1. Introduction

The late Early Permian of the southwestern and midcontinental United States continues to yield

remarkably diverse impression and compression plant fossils, which have been interpreted as an array of regionally distinct floras (Read and Mamay, 1964; Kerp, 2000). Some components of these floras are well-known from contemporaneous sites in Europe, whereas others have not been documented from elsewhere or remain elusive due to the incompleteness of the fossil record. Among the latter are several forms that appear to have had only very restricted geographical distributions, or may even have been endemic. One of the least understood plant taxa from the late Early Permian of the midcontinental United States is *Glenopteris* Sellards, a genus that is based on a relatively small number of impression foliage remains (pteridophylls) from a single locality in Dickinson County, east central Kansas (Sellards, 1900, 1908). Due to the scarcity of fossils, the biology, ecology, and systematic affinities of *Glenopteris* have remained obscure. Notwithstanding the meager fossil record, *Glenopteris* has been considered significant with regard to paleophytogeography (e.g., Read and Mamay, 1964; Chaloner and Meyen, 1973). In the classic system of upper Paleozoic floral zones and floral provinces in the United States, established by Read and Mamay (1964), *Glenopteris* is used as one of the index taxa for the Permian floral zone 14 (dated as Leonardian), which is comprised of the zone of the older *Gigantopteris* flora in parts of Texas, Oklahoma, and New Mexico, equivalent zone of *Glenopteris* spp. in Kansas, and equivalent zone of the *Supaia* flora in New Mexico and Arizona.

In an old collection, we discovered several specimens of one *Glenopteris* species, *Glenopteris splendens* Sellards, from a second locality in Dickinson County, Kansas. This site was originally discovered and collected by D.C. White in 1909, but appears to have been subsequently overlooked. The fossils collected by White were deposited in the collection of the Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington DC, and apparently were never investigated more fully. What makes these *G. splendens* specimens so significant is that they are not stained impressions like Sellards' material, but rather black compressions with well-preserved cuticles. As a result, we now have a new source of hitherto unavailable data based on epidermal features to interpret this fossil plant. Cuticles provide a wealth of information useful in the

taxonomy of late Paleozoic seed plants, but also important with regard to paleobiological and paleoecological considerations (e.g., Kerp, 1990; Kerp and Barthel, 1993; Krings, 1997). Although cuticular analysis has long since proven to provide a more complete understanding of many ancient seed plants based on biological criteria, it has been largely neglected in studies of late Paleozoic fossils from North America.

Here we describe and illustrate the frond morphology and epidermal anatomy of *Glenopteris splendens* based on the type material and the specimens from the second locality in Dickinson County, Kansas. The specific diagnosis for *G. splendens* Sellards, 1900 is emended based on additional data on macromorphology and epidermal anatomy. In addition, macroscopic and epidermal features are discussed with regard to their paleobiological and paleoecological significance.

2. The genus *Glenopteris* Sellards, 1900

Glenopteris was first described by Sellards in 1900 from a small number of mostly fragmentary specimens collected in Dickinson County, Kansas in 1899. Sellards described 5 species: *Glenopteris splendens*, based on three specimens (Sellards, 1900, pl. XXXVII, 1, pl. XXXVIII, 1, pl. XL), *Glenopteris simplex*, based on "several" specimens (pl. XXXVII, 2, pl. XXXVIII, 2, 3, pl. XXXIX), *Glenopteris lineata*, based on four specimens (pl. XXXVII, 3, pl. XXXVIII, 4, 5), *Glenopteris sterlingii*, based on two specimens (pl. XLI, pl. XLII, 1), and *Glenopteris*? *lobata*, based on a single fragmentary specimen (pl. XXXVII, 4, pl. XLII, 2). The assignment of *G. lobata* to the new genus was questioned because it is the only member of the suite to lack clear auricles at the base of the pinnules; the pinnules also have undulate margins. With the exception of *G. lobata*, the differences between these species are minor, including such characters as size. Given the small number of specimens in the original suite, *G. splendens*, *G. simplex*, *G. lineata*, and *G. sterlingii* could easily be encompassed in the natural range of variation of a single species. Aside from the name *G. splendens*, use of other names probably should be restricted until such time that a large collection of specimens attributable to this genus can be made and gross morphological variation and epidermal anatomy fully analyzed.

3. Geological setting, material, and methods

Glenopteris splendens occurs exclusively in the Wellington Formation of the Sumner Group in east central Kansas (U.S.A.). The Sumner Group is positioned stratigraphically between the Nolans Limestone of the Chase Group and the Harper Sandstone of the Nippewalla Group (Moore et al., 1944, pp. 159/160; Zeller, 1968, pl. 1). It is comprised of (in ascending order) the Wellington Formation, Ninnescah Shale, and Stone Corral Formation, and Artinskian (late Early Permian) in age. The Wellington Formation is a massive unit (up to 215 m thick) composed of marine, brackish, fresh water, and terrestrial deposits, mostly shale, with interspersed layers of salt, limestone, siltstone, and anhydrite. It has been interpreted as a cyclic sequence that represents a coastal plain dotted with small freshwater to brackish lakes that, over time, experienced repeated marine incursions (Dunbar, 1924; Moore et al., 1951; Tasch, 1963, 1964; Moore, 1964). The Wellington Formation has become particularly famous for its exquisite insect fossils (refer to Beckemeyer, 2000 and literature cited therein), and also for *Phasmatocycas kansana* Mamay, an enigmatic seed fern that formed the basis for an influential theory on the evolution of the cycad megasporophyll (Mamay, 1973, 1976; Axsmith et al., 2003). The flora that occurs with *G. splendens* is relatively diverse, and includes sphenophytes (e.g., *Sphenophyllum*), and foliage of marattialean ferns (*Pecopteris*), seed ferns (e.g., *Callipteris*, *Neuropteris*, *Odontopteris*, *Sphenopteris*), and cordaites (White, 1903; Sellards, 1908; Baxter, 1978; Gillespie and Pfefferkorn, 1986).

The type material of *Glenopteris splendens* was collected in 1899 from the head of one of the western tributaries of Turkey Creek, three and one-half miles south of Banner City (now Elmo), Dickinson County, east central Kansas (Sellards, 1900, 1901). The fossils are preserved as brown to rust-brown impressions on a yellowish to gray impure, more or less concretionary limestone matrix, but some carbonaceous material may still be present (e.g., Plate I,5,6). Specimens with well-preserved cuticles were collected by D.C. White in 1909 at a second locality in east central Kansas, i.e. West Holland Creek, three miles south of Carlton, Dickinson County. These fossils are preserved as black compressions in a buff-colored silt-

stone matrix. Unfortunately, the exact locations of both sites have been forgotten. Based on information on the old labels, we have attempted to relocate the sites, but have been unsuccessful to date. Sellards' original material of *G. splendens* is today deposited in the collections of the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas at Lawrence, Kansas, under accession numbers KU 6493, 6495, 6499 (holotype), 6500, 6501, and 6502. White's specimens are from the collections of the United States Geological Survey (USGS locality number 8868) that are today kept in the Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington DC; a few slabs are kept at the Department of Palaeobotany, Swedish Museum of Natural History, Stockholm (accession numbers S127013-S127016). Hand specimens were photographed on low-speed pan- or orthochromatic film (Ilford Pan 50, Macophot Ort 25 ISO); in order to increase contrast, cross-polarization (i.e. polarized light sources together with a polarizing filter over the camera lens, cf. Crabb, 2001) was used.

Cuticles were prepared according to procedures outlined in Kerp (1990), and Kerp and Krings (1999). Plant remains were picked from the rock surface with a preparation needle, and macerated according to a modified procedure using Schulze's reagent (HNO_3 with a few crystals of $KClO_3$) (Krings and Kerp, 1997). Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and subsequently mounted in permanent glycerine-jelly microscope slides. In order to increase contrast, some cuticles were stained with Bismarck Brown according to a procedure detailed in Krings (2000). Permanent cuticle slides are housed in the collections of the Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington DC (USNM numbers 508774-508789) and the Swedish Museum of Natural History, Stockholm, Department of Palaeobotany (numbers S127013/1-S127013/22). Cuticles were photographed on low-speed panchromatic film (Agfapan 25 ASA).

4. Systematics

Genus: *Glenopteris* Sellards, 1900
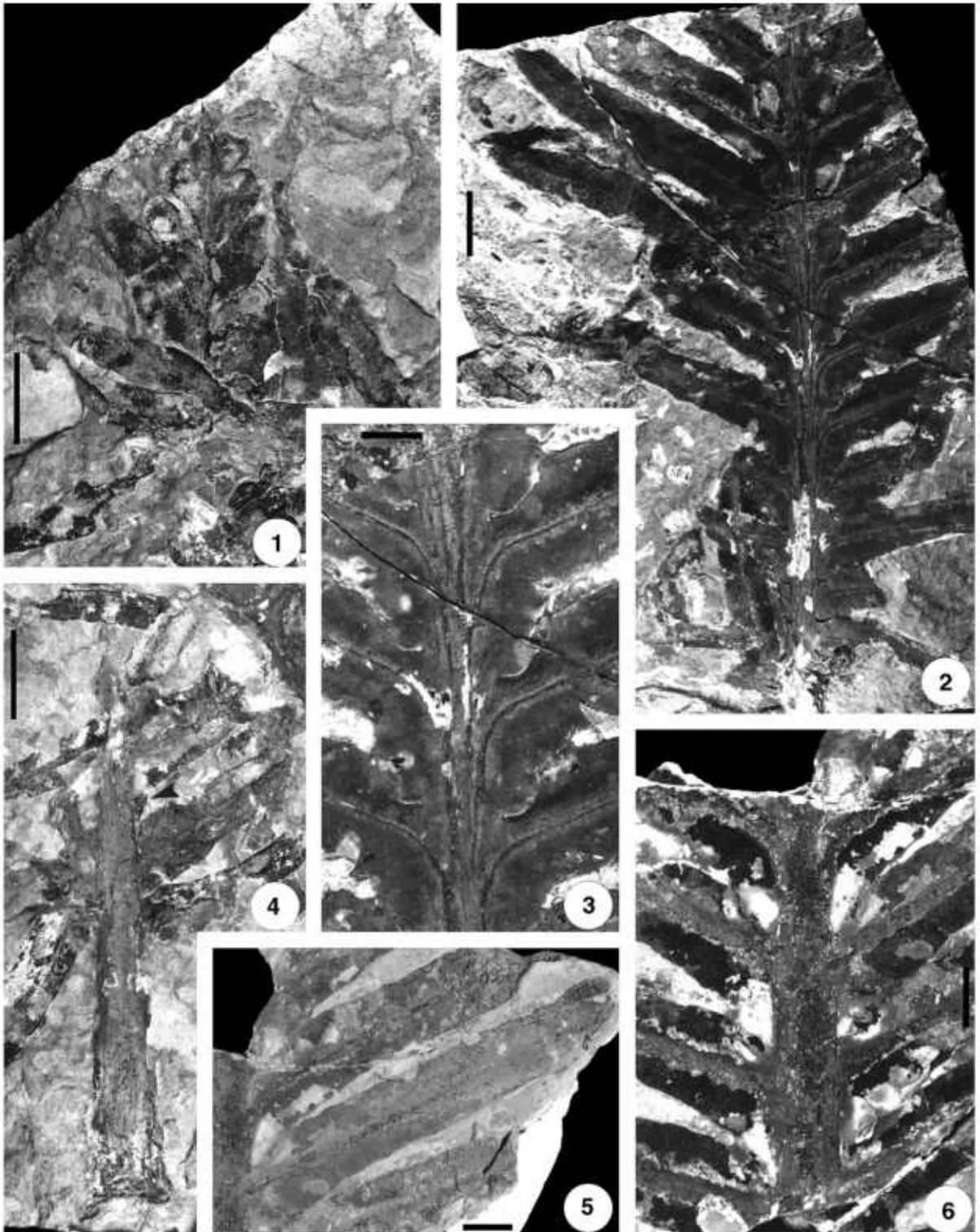
Glenopteris splendens Sellards, 1900, nov. emend. Krings, Klavins, DiMichele, Kerp et Taylor (Fig. 1; Plates I–VII)

References:

1900 *Glenopteris splendens* sp. nov.—Sellards, New genus of ferns, pp. 182–184, pl. XXXVII, fig. 1; pl. XXXVIII, fig. 1; pl. XL (holotype).

1901 *Glenopteris splendens* Sellards—Sellards, Permian plants, p.10, no illustr.

1908 *Glenopteris splendens* Sellards—Sellards, Fossil plants Upper Paleoz. Kansas, pp. 440–442, no illustr.

1964 *Glenopteris splendens* Sellards—Read and Mamay, Upper Paleoz. floral zones, p. 14, pl. 16, 3–4.

Holotype: The specimen figured by Sellards (1900) on plate XL (refigured here in Plate I,2,3), reposited in the collections of the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence KS, U.S.A. (accession number KU 6499).

Emended specific diagnosis: Fronds large, robust, up to 60 cm long, with broad base, pinnate, distal portion pinnatifid, amphistomatic, glabrous; petiole and rachis massive, straight, rigid, roughly marked with longitudinal striae, stomatiferous; rachial epidermis consists of longitudinal rows of penta- to octagonal cells, overlying cuticle with wart- and peg-like projections into the anticlinal cell walls and narrow strings of cuticular material penetrating deeply into the cell corners; stomatal density on rachis low, guard cells slightly sunken, with massive dorsal and circumporal thickenings, subsidiary cells usually 6–8, similar in size and shape to, or smaller than, normal epidermal cells, large idiocuticular warts that project into the
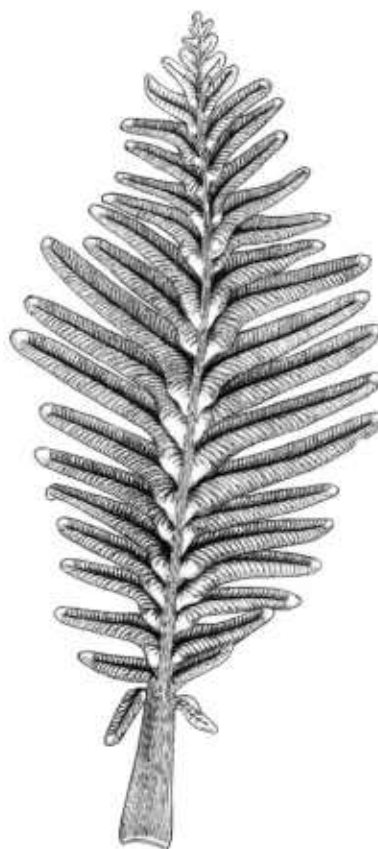

Fig. 1. Reconstruction of a fully differentiated, mature frond of *Glenopteris splendens* (type with densely spaced pinnules) based on the specimens figured on Plate I,1–4. Length of the frond ≈ 50 cm.

anticlinal walls between the lateral subsidiary and guard cells may occur; pinnules pachymorphous, opposite to sub-opposite, oblique to the rachis, loosely to densely spaced, polymorphous, but generally oblong in outline, entire-margined, broadly attached,

Plate I. Type and figured specimens of *Glenopteris splendens* (Sellards, 1900, pl. XXXVII, 1, pl. XXXVIII, 1, pl. XL) from the vicinity of Banner City (Elmo), Dickinson County, east central Kansas (U.S.A.).

1.   Distal portion of an imparipinnate frond with small pinnules; specimen no. KU 6495; scale bar=2.0 cm.
2.   Holotype, displaying the adaxial side viewed from the inner side; specimen no. KU 6499; scale bar=2.5 cm.
3.   Detail of Plate I,2, showing the rachial vascular system and precurring vascular strands that later enter the midveins; scale bar=1.0 cm.
4.   Proximal portion of a frond, showing the broadened base of the petiole and proximal pinnules characterized by reduced auricles [arrow]; specimen no. KU 6495; scale bar=2.0 cm.
5.   Pinnules viewed from the inner side, displaying thick layer of carbonaceous material (remains of the mesophyll); specimen no. KU 6493; scale bar=1.3 cm.
6.   Counterpart (section) of the holotype, displaying the abaxial side of the frond (viewed from the inner side); specimen no. KU 6493; scale bar=1.3 cm.
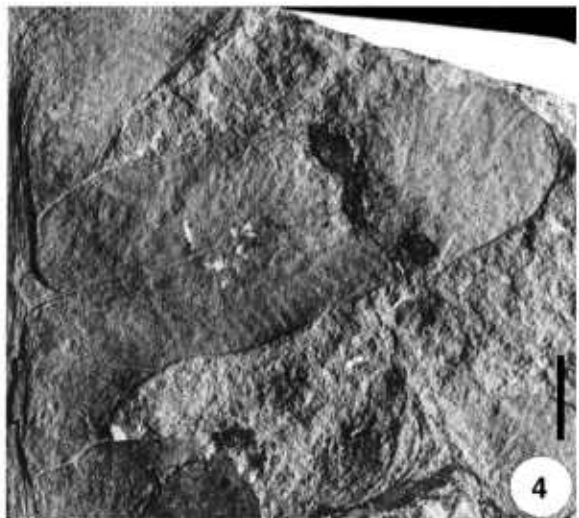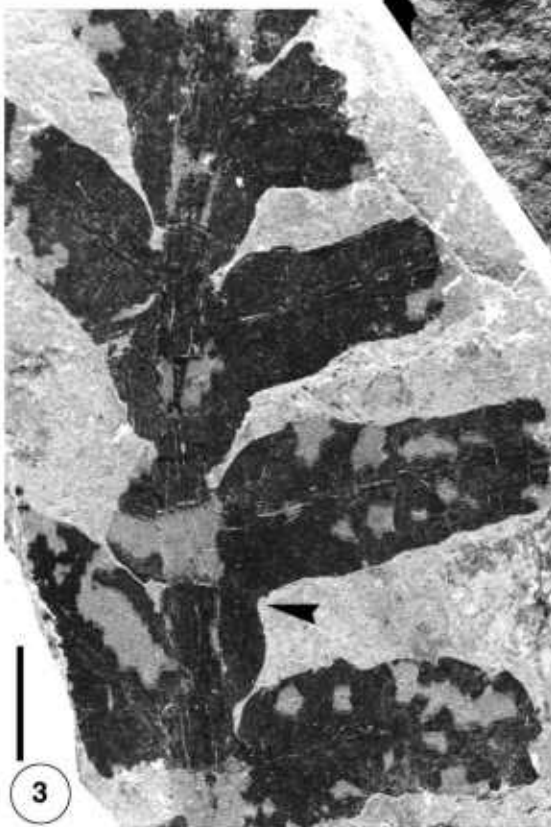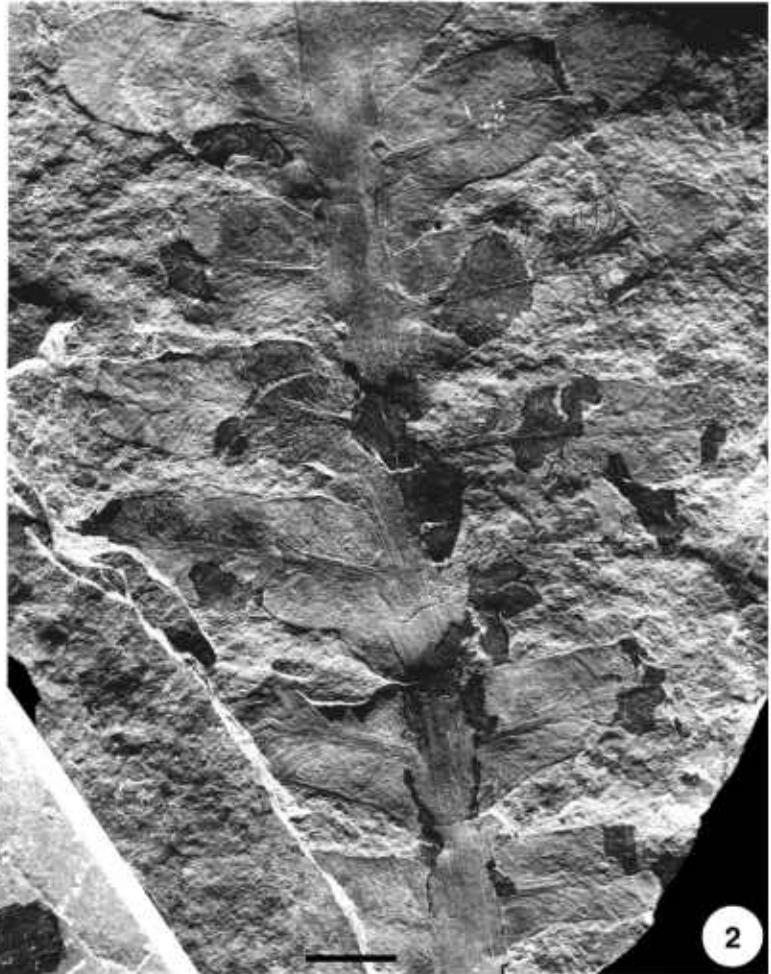
base acroscopically constricted and with a basiscopic auricle; largest pinnules in middle part of blade tongue-shaped, >10 cm long and up to 2.0 cm wide, lateral margins nearly parallel, apices rounded to somewhat tapering, auricles prominent, partly or completely fused with rachis, vascularized by veins arising from rachis and/or basal part of midvein; pinnules in proximal part of blade open or reflexed, narrower in proportion to their length, auricles less distinct; distal pinnules broader in proportion to their length, apices usually rounded, auricles reduced; subterminal two to three pairs of pinnules and terminal pinnule largely fused, auricles absent; pinnule venation conspicuous, but sometimes difficult to discern in adpressions; midvein strong, straight, sunken, abaxially protruding, running up to approximately four-fifths of pinnule length, gradually fading out, giving off lateral veins at acute angles; vascular strand in midvein thin, precurrent, given off by rachial vascular system below the point of midvein insertion; lateral veins arching, simple or forking once to twice in their course to the margin, meeting the margin at almost 90° angles, 12–14 vein endings per cm; pinnule cuticles with wart- and peg-like projections, similar to those of rachis cuticle; epidermal cell pattern of pinnule midvein similar to that of rachis, but with higher stomatal density; stomata monocyclic to incomplete tricyclic, pores typically oriented parallel to midvein, anticlinal walls between subsidiary and guard cells without warts; costal and intercostal fields of adaxial pinnule epidermis differentiated; stomata present in costal and intercostal fields, monocyclic to incomplete tricyclic, guard cells with circum-poral and dorsal thickenings, subsidiary cells up to 15, usually smaller than normal epidermal cells, costal stomatal complexes often with considerable differences in size and shape of polar and lateral subsidiary cells; abaxial cuticle thin, costal and intercostal fields of abaxial epidermis not differentiated, stomata abundant, orientation of stomatal pores random, guard cells with dorsal and circumporal thickenings and narrow radial striae, subsidiary cells variable in size, shape, number (up to 13), and arrangement.

5. Description

5.1. Frond morphology

The specimens (including the type material, cf. Sellards, 1900, pl. XXXVII, fig. 1, pl. XXXVIII, fig. 1, pl. XL [holotype], most original specimens refigured here in Plate I,1–6) consist of frond fragments up to 25 cm long; the holotype (Plate I,2) represents the largest specimen discovered to date. Based on the material, we estimate that fully differentiated fronds of *Glenopteris splendens* were up to 60 cm long (Fig. 1). The petiole (Plate I,4) is approximately 6–8 cm long, with a broadened base up to 2 cm wide. The pinnate to pinnatifid blade is broadly elliptical, with its widest spread reaching well over 20 cm. The rachis is massive and straight, basally up to 1.5 cm wide, but the width decreases considerably toward the tip. Petiole and rachis are roughly marked with longitudinal striae. The rachidal vascular system is composed of two major parallel strands that occasionally anastomse (Plate I,3). Pinnules appear to have been pachymorphous (succulent), which is implied by the fact that the carbonaceous material, present in many specimens, is sometimes >1.5 mm thick and obscures the laminar venation (cf. Plate I,5,6 and Plate II,3). The pinnules are oppositely to sub-oppositely positioned (Plate I,2,6 and Plate II,2,3), polymorphous (size and shape strongly depend on the position in the frond), generally oblong in outline, with rounded to somewhat tapering apices (Plate I,2,4,5 and Plate II,1–4). The largest pinnules occur in the middle portion of the blade where they are elongate tongue-shaped, entire-mar-

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Plate II. Specimens of *Glenopteris splendens* with well-preserved cuticles, collected by D.C. White in 1909 in the vicinity of Carlton, Dickinson County, east central Kansas (U.S.A.).

1. Individual pinnule (detail of Plate II,2), displaying the venation; specimen no. S127013; scale bar=0.33 cm.
2. Frond portion. Note the massive rachis; specimen no. S127013; scale bar=1.0 cm.
3. Distal frond portion (type with loosely spaced pinnules). Arrow indicates shallow constriction of the auricle at the base of the pinnule; specimen no. S127014; scale bar=0.9 cm.
4. Detail of Plate II,2, showing a single pinnule with barely recognizable venation, scale bar=0.5 cm.
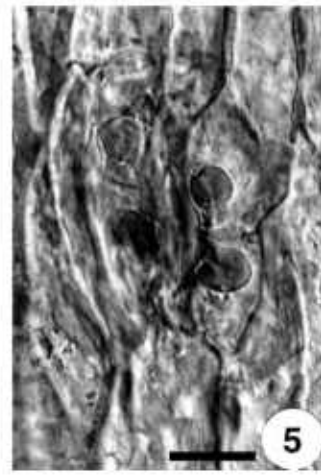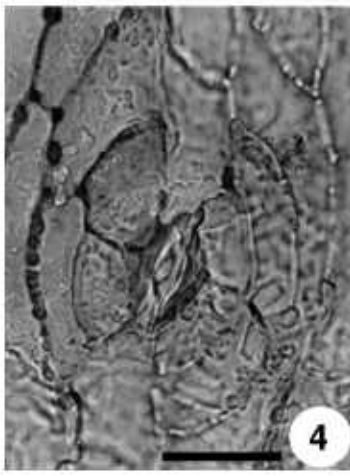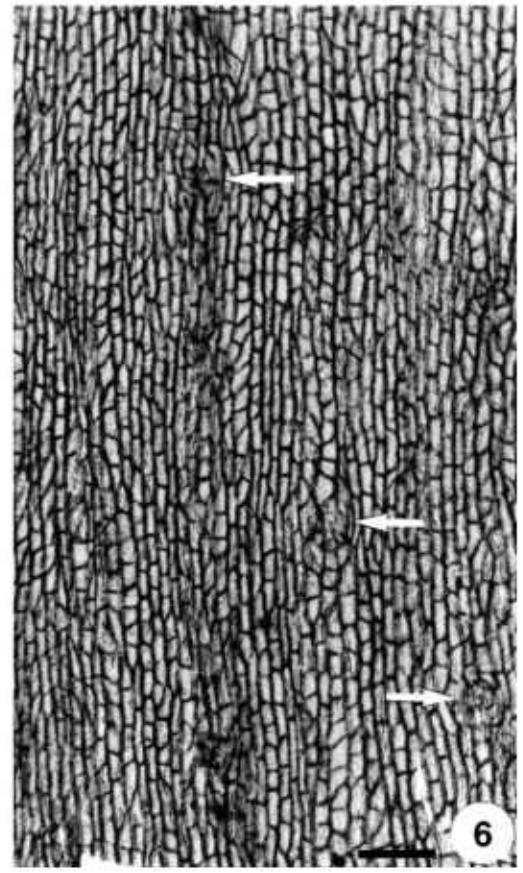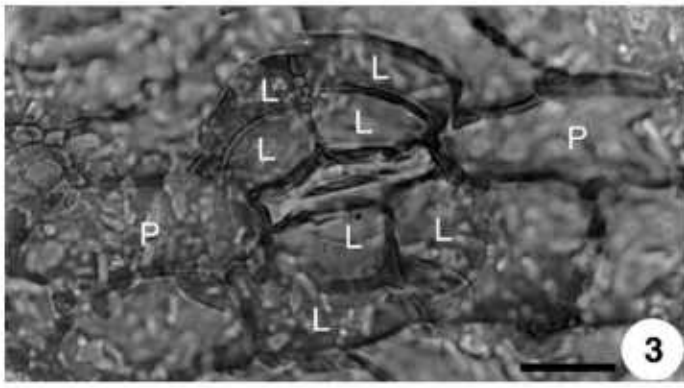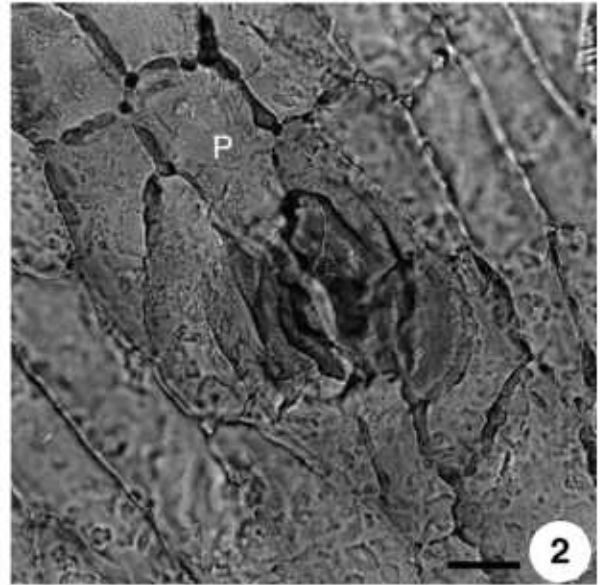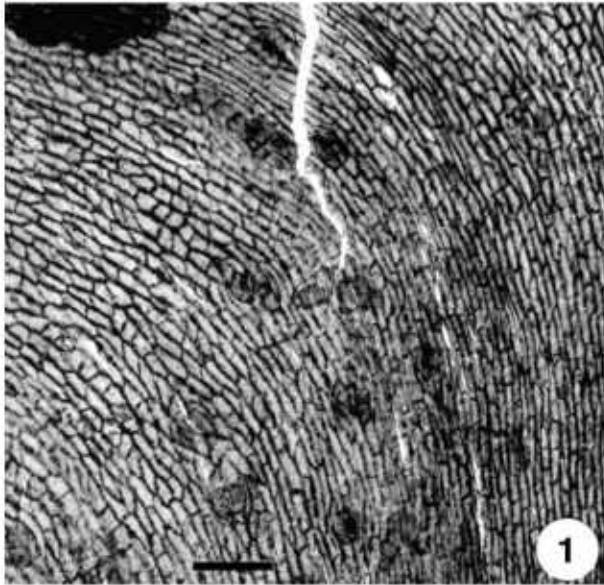
gined, with straight, nearly parallel margins, and may reach 12 (or more) cm long and up to 2 cm wide. They are broadly attached, acroscopically constricted, and possess a prominent basiscopic auricle. The auricles are up to 1.8 cm long and 0.8 cm high, and partly or completely fused with the rachis; some display a shallow constriction at the base of the pinnule (Plate II,3 [arrow]). In the proximal portion of the blade, the pinnules are shorter, up to 6 cm long, and between <1 and 1.4 cm wide, open or reflexed, narrower in proportion to their length, and possess only relatively small auricles (Plate I,4 [arrow]). Toward the frond apex, the pinnules gradually decrease in size, are broader in proportion to their length, and have less distinct auricles. The subterminal two to three pairs of pinnules and the terminal pinnule are between 0.5 and 1.5 cm long and 0.6 to 1 cm wide, often largely fused, and do not possess auricles (Plate I,1; Read and Mamay, 1964, pl. 16, 4). With regard to pinnule spacing, two basic blade types can be distinguished. In some specimens (including the holotype), the pinnules are relatively closely spaced, with the auricles overlapping the subjacent pinnules (e.g., Plate I,2 and Plate II,2,4; Fig. 1), whereas in others the pinnules are loosely spaced with the auricles hardly reaching the pinnules positioned below (e.g., Plate II,3; Read and Mamay, 1964, pl. 16, 3). In specimens of the latter type, the pinnules sometimes appear to be interconnected by narrow laminar wings, less than 0.1 cm wide, on each side of the axis (Plate II,3). The pinnule venation is conspicuous, but sometimes difficult to discern in adpressions (e.g., Plate II,4). A prominent, adaxially sunken and abaxially protruding midvein (proximally up to 4 mm wide) extends up to four-fifths of the pinnule length (Plate I,2,5 and Plate II,1,2,4) but then gradually fades out. It produces lateral veins at acute angles that are much thinner than the midvein (0.1–0.5 mm wide) and thus often barely discernible in adpressions. Most of the veins dichotomize once or twice in their course to the margin (Plate II,1); between 12 and 14 veins per centimeter meet the lateral margins at almost 90° angles. The pinnule auricles are vascularized by a few delicate, curved veins that arise from the rachis and/or basal part of the midvein, and usually branch once in their course to the margin. The vascular strand in the midvein is relatively thin, only up to 0.5 mm wide. It is given off by the rachial vascular system below the point of insertion of the midvein and runs up to 2 cm through the outer tissues of the rachis before entering the pinnule (Plate I,3).

5.2. Epidermal anatomy

Cuticles were obtained from all parts of the frond, i.e. petiole/rachis (Plate III, Plate I,5,6) and adaxial (Plate III,2–4, Plate IV,1–8, Plate V,1–6 and Plate VI,1–6) and abaxial (Plate VII,1–11) pinnule surfaces. Fronds of *Glenopteris splendens* are amphistomatic and glabrous.

5.2.1. Rachis
The epidermis of the adaxial rachis surface (i.e. the portion between the points of insertion of the pinnules) displays a regular cell pattern, consisting of elongate, penta- to heptagonal cells, up to 160 μm long and 45 μm wide, which are arranged in longitudinal rows of up to 20 individual cells (Plate III,1 [right side of image], 6). Stomata are occasionally present in the adaxial epidermis of the rachis (Plate III,6 [arrows]). The abaxial epidermal cell pattern of the rachis is very similar to that of the adaxial side, but the individual epidermal cells may be longer, up to

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Plate III. Epidermal anatomy of *Glenopteris splendens* Sellards. Rachis and adaxial surface of the pinnule midvein: cell pattern and stomatal complexes.

1.   Epidermal cell pattern of the transition from rachis [right side] to pinnule midvein [left side of image]; slide no. S127013/15; scale bar=150 μm.
2.   Stomatal complex from the midvein costal field; slide no. USNM 508775; scale bar=20 μm.
3.   Stomatal complex with nine subsidiary cells from the midvein costal field. Note the differences in size and shape of the polar [P] and lateral [L] subsidiary cells; slide no. USNM 508788; scale bar=30 μm.
4.   Stomatal complex with eight subsidiary cells from the midvein costal field; slide no. USNM 508785; scale bar=50 μm.
5.   Rachial stomatal complex with six subsidiary cells, viewed from the inner side. Note that idiocuticular warts project into/between the anticlinal walls between the lateral subsidiary and guard cells; slide no. S127013/12; scale bar=20 μm.
6.   Epidermal cell pattern of the rachis and adaxial midvein costal field. Arrows indicate stomata; slide no. S127013/15; scale bar=150 μm.
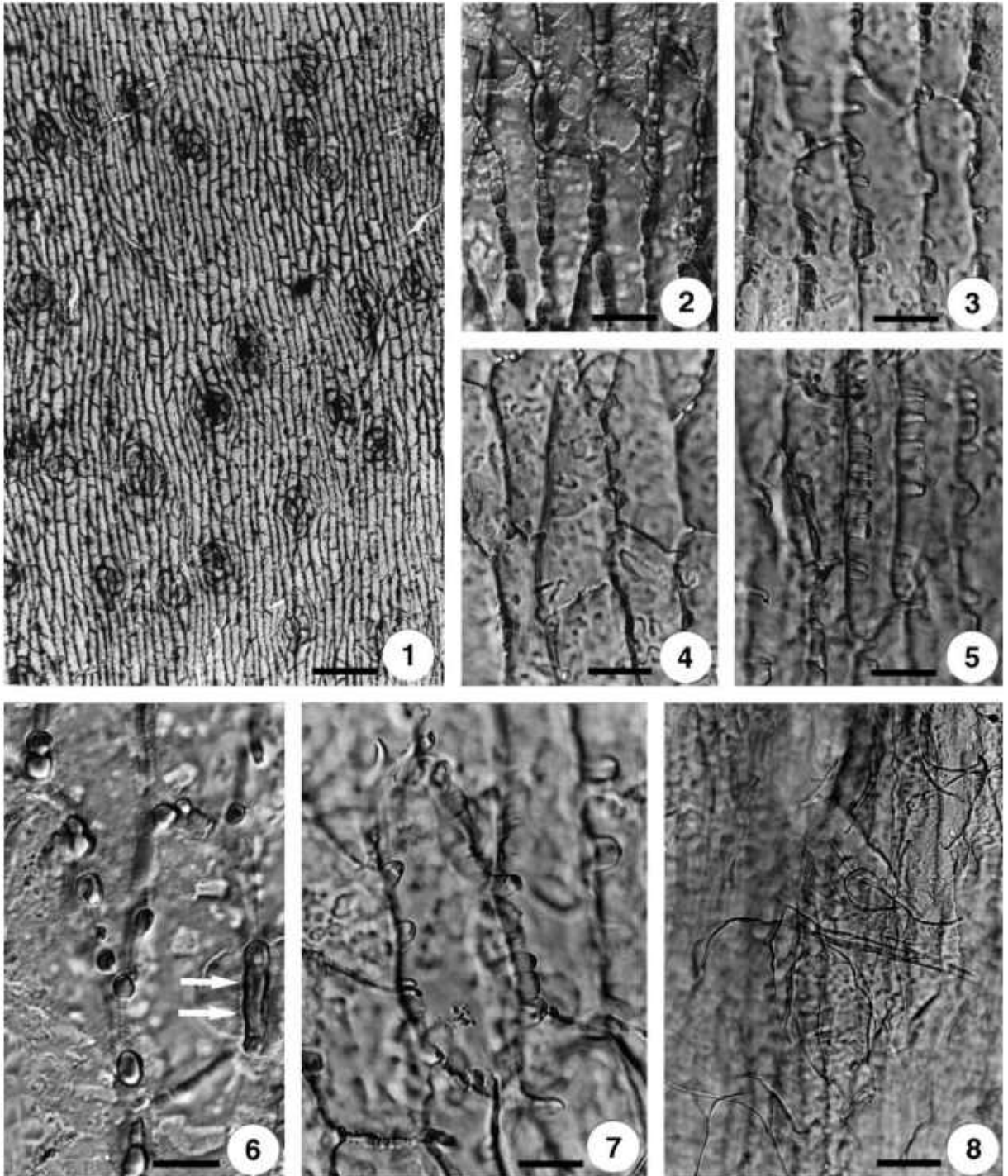
180 μm long and between 20 and 40 μm wide. Stomatal complexes, similar to those seen in the adaxial side, are sometimes present. Each rachial stomatal complex (Plate III,5) consists of a pair of slightly sunken guard cells with heavily cutinized dorsal walls, surrounded by 6–10 (usually 6–8) subsidiary cells of which one or two shorter cells are positioned at each lateral side, and two to three longer cells are located at each of the polar positions; in some, large idiocuticular warts, up to 10 μm in diameter, project into/between the anticlinal walls between the lateral subsidiary cells and the guard cells. The anticlinal walls of all epidermal cells display intramembranous cutinizations/cuticularizations (sensu Barthlott and Ehler, 1977) in the form of wart- and peg-like projections that will be detailed within the description of the adaxial pinnule cuticle.

5.2.2. Adaxial pinnule surface

The adaxial pinnule cuticle displays a clear differentiation of the epidermis into costal and intercostal fields, whereas this feature is missing in cuticles from the abaxial side. In the adaxial pinnule cuticle, a well-developed, up to 0.4 cm wide, costal field occurs over the midvein that possesses an epidermal cell pattern similar to that seen in the adaxial rachis surface; however, individual cells may be longer and narrower. The epidermal cells in the center of the midvein costal field are elongate, up to 190 μm long and 45 μm wide (Plate III,1 [left side of image], Plate IV,1, and Plate V,1 [left side of image]), but, toward the sides, cells become gradually wider (Plate V,1 [right side of image]). Numerous wart- and peg-like projections into/between the anticlinal cell walls are irregularly distributed on the inner surface of the cuticle, along the cuticular expressions of the anticlinal cell walls. The warts (Plate IV,2,6) are spherical to slightly elongate, up to 12 μm long and 6–8 μm wide, whereas pegs (Plate IV,3,5,7) are cylindrical to platelet-like, up to 10 μm high and 2–10 μm wide. Transitional forms

between warts and pegs are common. If closely spaced, the warts occasionally fuse to form short chains (Plate IV,6 [arrows]); pegs, however, rarely display this feature. Narrow strings of cuticular material (Plate IV,8) project downward from the cuticular expressions of the cell corners, indicating that these spots were cutinized deeply into the epidermis. The epidermal expression of the midvein gradually becomes reduced in the distal portion of the pinnule (Plate V,3 [right side of image; left side shows adjacent intercostal field]); epidermal cells in the distal portion of the midvein are comparatively short. The lateral adaxial pinnule surface shows a diverging epidermal cell pattern from the midvein region (Plates V and VI). Individual cells of the lateral costal fields (Plate V,5 and Plate VI,1) are regularly arranged in longitudinal rows, penta- to octagonal, 40–200 μm long and 15–50 μm wide; near the pinnule margins they may be even longer. Around the pinnule base, epidermal cells are more isodiametric. In the intercostal fields, the epidermal cells are irregularly arranged. The individual cells (Plate V,2,3 [left side of image; right side shows epidermal expression of midvein tip], 4 [left side of image; right side shows adjacent lateral vein]) are more or less isodiametric or slightly elongate, usually penta- to octagonal, and measure between 50 and 130 μm long and 20–65 μm wide. Integrated in the costal and intercostal fields of the adaxial pinnule epidermis are stomata (stomatal density: 5–35 stomata/mm^2). The stomatal pores are regularly oriented parallel to the direction of the longitudinal cell rows in the costal (e.g., Plates IV,1 and V,1 [arrows]), but randomly oriented in the intercostal fields (e.g., Plate V,2). Stomatal complexes are variable in morphology, monocyclic, incomplete dicyclic, or dicyclic, but occasionally even incomplete tricyclic. The guard cells are slightly sunken, up to 65(−75) μm long and 20(−22) μm wide, and possess dorsal and circum-poral thickenings; they are surrounded by 6–13 (occasionally up to 15) subsidiary

Plate IV. Epidermal anatomy of *Glenopteris splendens* Sellards. Adaxial surface of the pinnule midvein and special cutinization/cuticularization features of the rachis and pinnules.

1.   Epidermal cell pattern of the midvein costal field (central portion); slide no. USNM 508788; scale bar=150 μm.
2–7. Wart- and peg-like projections into/between the anticlinal cell walls, irregularly distributed on the inner surface of the cuticle, along the cuticular expressions of the anticlinal cell walls. Arrows in Fig. 6 indicate fusion of several closely spaced warts; slides no. S127013/22 (Fig. 2), USNM 508788 (Figs. 3, 4, 7) and USNM 508775 (Fig. 6); scale bars=35 μm (Figs. 2–5) and 20 μm (Figs. 6, 7).
8.   Strings of cuticular material projecting downward from the cuticular expressions of cell corners; slide no. S127013/2; scale bar=20 μm.
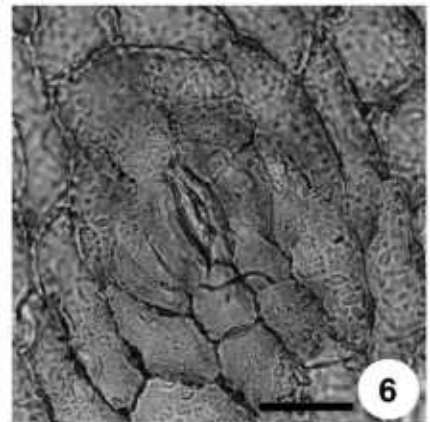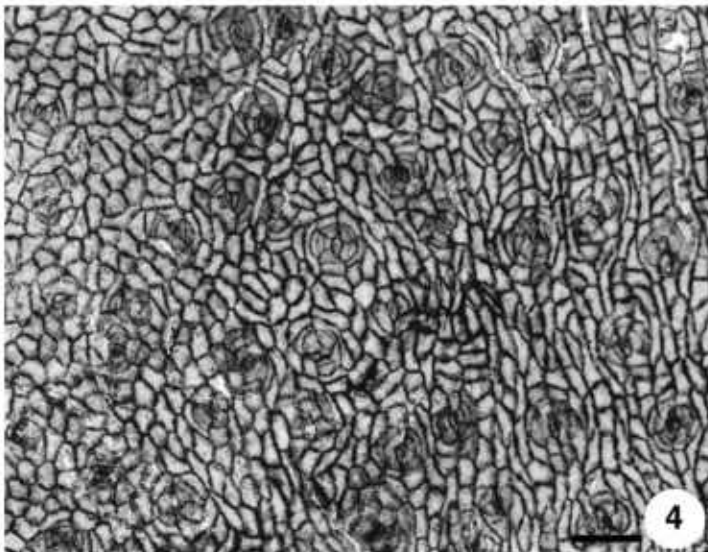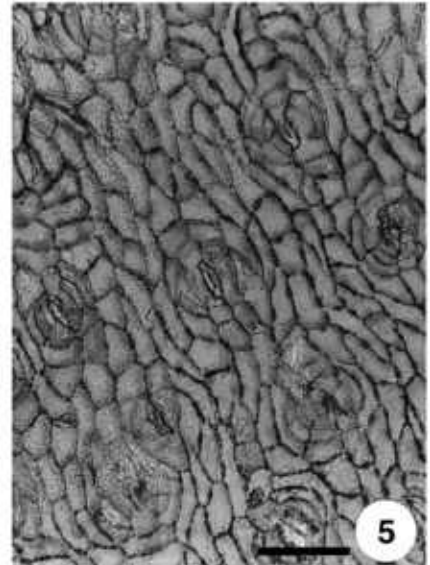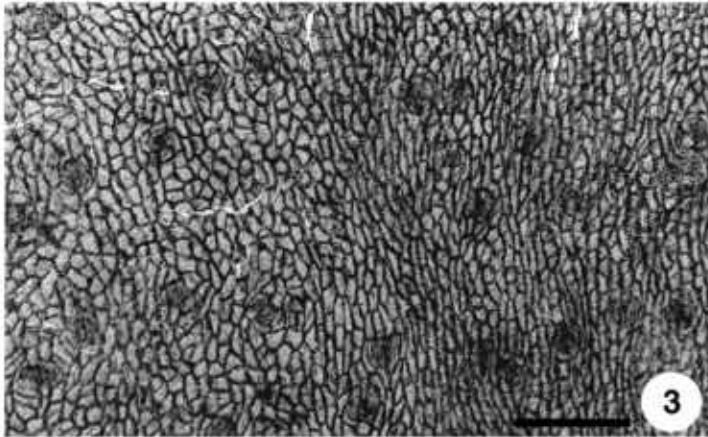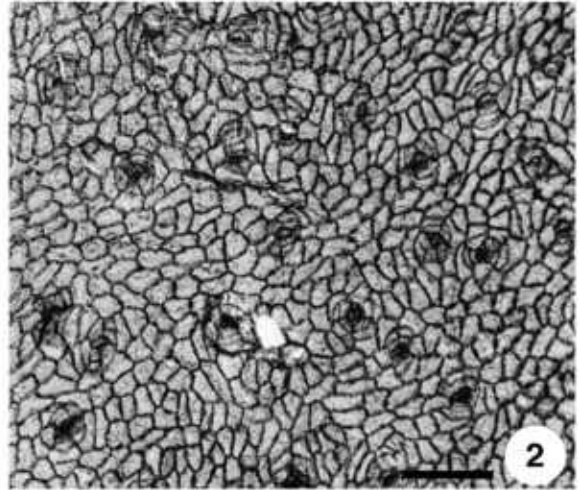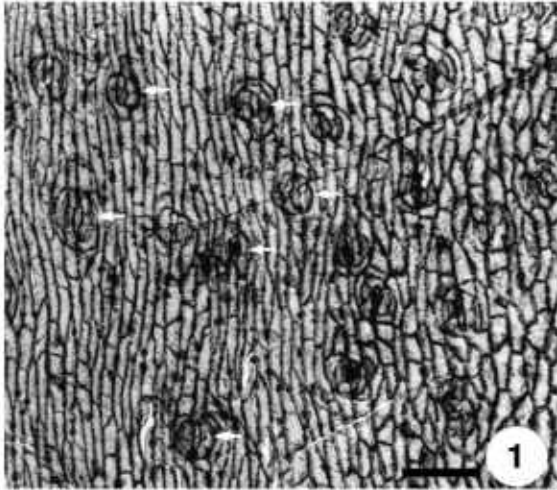
cells, which overarch the peripheral regions of the guard cells (cf. Plate VI,5 [arrows indicate peripheral borders of guard cells]). The subsidiary cells are usually (slightly) smaller than the normal epidermal cells, up to 70 μm long and 6–35 μm wide, but some do not differ in size and shape from normal epidermal cells. Many stomatal complexes that occur in the midvein region and lateral costal fields (Plate III,2–4, Plate V,6, and Plate VI,2,4,5) display a clear difference in size and shape between the polar (Plate III,3 [P]) and lateral (Plate III,3 [L]) subsidiary cells; stomatal complexes in the intercostal fields (Plates V,4 and VI,3,6) do not normally display this feature (compare Plate III,3,4 and Plate VI,2 and 6 with Plate VI,3,6). In an intermediary costal type of stomatal complex, only one of the subsidiary cells in polar position is differently shaped (Plate III,2 [P]).

5.2.3. Abaxial pinnule surface

The cuticle of the abaxial pinnule surface (Plate VII,1–11) is thinner than that produced on the adaxial side. Most of the abaxial epidermis lacks a differentiation into costal and intercostal fields; only the epidermal anatomy along the midvein is different, being comparable to that of the abaxial rachis surface. The abaxial epidermal cells (apart from those that occur in the epidermal expression of the midvein) are randomly oriented, usually more or less isodiametric, and up to 65 μm in diameter (Plate VII,1); however, elongate cells also occur that are up to 95 μm long and 35 μm wide. Wart- and peg-like projections similar to these seen in the rachial and adaxial pinnule cuticles are present in the abaxial pinnule cuticle, but are less prominent. Integrated in the abaxial epidermis are numerous stomatal complexes. Stomatal density of the abaxial pinnule epidermis is considerably higher than that of the respective adaxial side, between 40 and >80 stomata/mm^2. The stomatal complexes (Plate VII,2–11) consist of a pair of slightly sunken guard cells (each between 30 and 50 μm long and 8–15 μm wide) with characteristically cutinized polar regions (Plate VII,11 [arrow]), and usually between 7 and 10 subsidiary cells, which overarch the lateral and polar peripheral portions of the guard cells. The guard cells are thickened in the central portion of the dorsal wall (Plate VII,3,8 [arrows]) and around the pores (Plate VII,2,6–10); moreover, the central portion of the dorsal wall bears narrow radial striae (Plate VII,10 [arrows]). Arrangement of subsidiary cells displays two distinct patterns. Simple stomatal complexes possess a single ring of up to 8, more or less equally shaped subsidiary cells (Plate VII,4), whereas a second, more complex type is dicyclic or incomplete tricyclic, with up to 13 subsidiary cells, of which the two in near-polar position (Plate VII,5 [P]) may be slightly larger than those located laterally (Plate VII,5 [L]).

6. Discussion

The description of the cuticles of *Glenopteris splendens* from Kansas provides the first account of the epidermal anatomy of one of the obscure and incompletely understood seed plants that appear in the southwestern and midcontinental United States during the late Early Permian. Frond morphology permits a comparison of *G. splendens* with other, superficially similar taxa, and the epidermal anatomy, along with macroscopical features, provides a basis for a refined concept relating to the paleobiology/ecology of this here-to-fore enigmatic plant.

Plate V. Epidermal anatomy of *Glenopteris splendens* Sellards. Adaxial pinnule surface: midvein, costal and intercostal fields, stomatal complexes.

1. Epidermal cell pattern of the central [left side] and lateral [right side of image] portion of the midvein costal field. Arrows indicate stomata; slide no. S127013/5; scale bar=150 μm.
2. Intercostal field with numerous randomly distributed stomata; slide no. USNM 508782; scale bar=210 μm.
3. Epidermal expression of the midvein tip [right side] and adjacent intercostal field [left side of image]; slide no. S127013/5; scale bar=300 μm.
4. Lateral costal [right side] and adjacent intercostal [left side of image] field with numerous stomata. Note the differences in orientation of the pores in costal and intercostal stomata; slide no. USNM 508781; scale bar=150 μm.
5. Section of a lateral costal field. Note the orientation of stomatal pores; slide no. USNM 508781; scale bar=150 μm.
6. Detail of Plate V,5, showing a stomatal complex with one enlarged polar subsidiary cell; scale bar=75 μm.
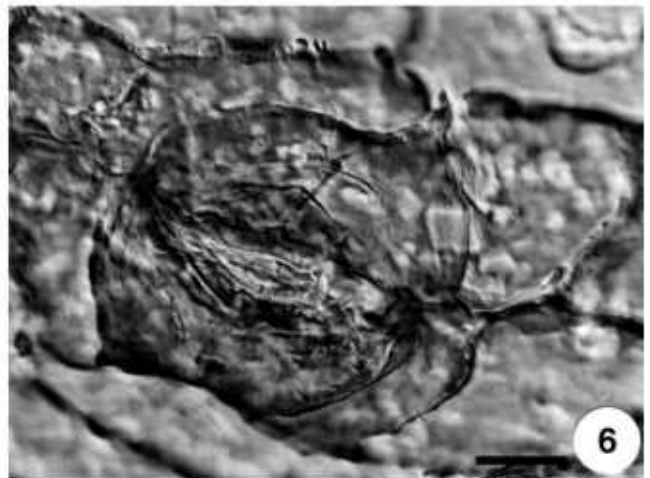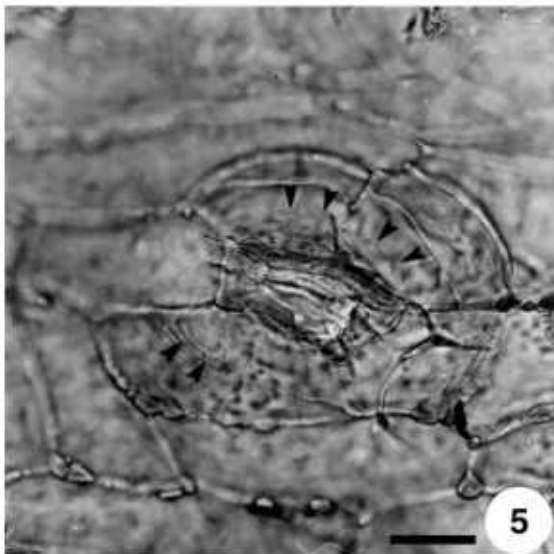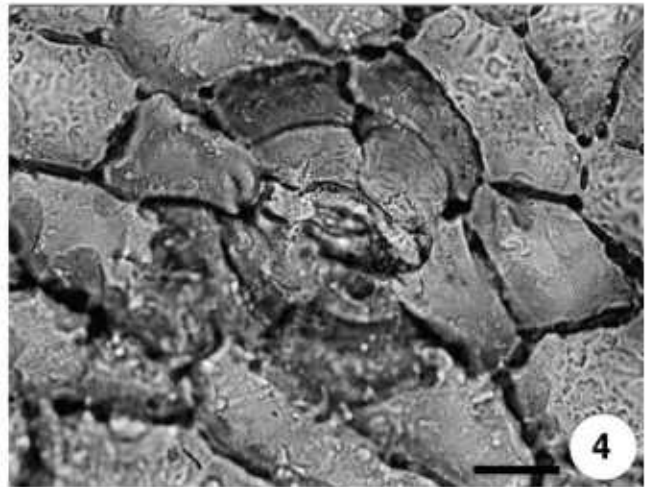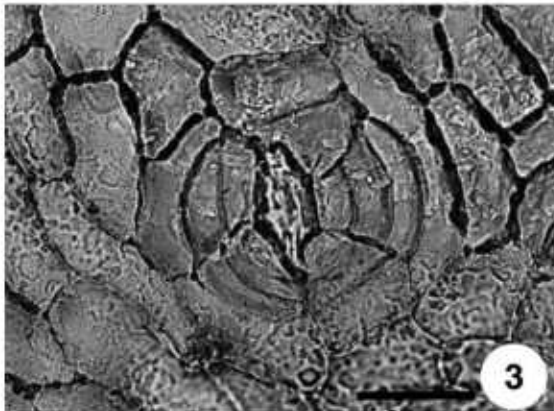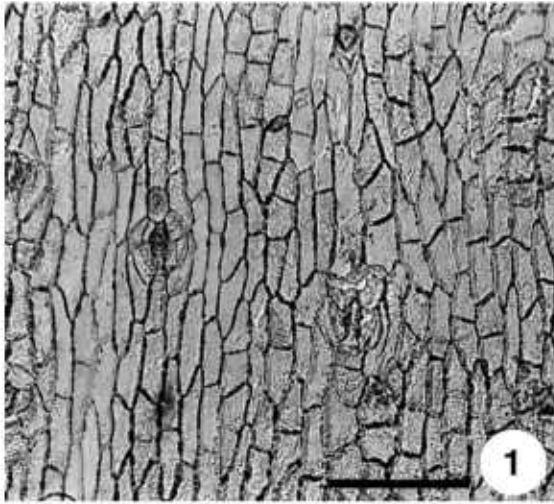
6.1. Comparisons

Glenopteris is similar in gross morphology (Plates I and II; Fig. 1) to a number of other taxa described from the Permian (Naugolnykh, 1999). This group includes most (but not all) species of *Supaia* White (1929), *Protoblechnum wongii* Halle (1927), species of *Compsopteris* Zalessky emend. Naugolnykh (1999) and of *Brongniartites* Zalessky (1927), which appears to be an invalid name (Naugolnykh, 1999). Naugolnykh (1999), in a review of these genera, adds several additional Late Permian taxa from Russia and argues that the entire group are members of the Peltaspermales and derived from callipterid ancestors. Indeed, several of these taxa and others, which differ in frond architecture but display other morphological traits linking them to the group (as, for example, *Comia*, the callipterid complex, and the North American "gigantopterids"), are consistently associated with the peltaspermalean reproductive structures *Autunia* Krasser (*Sandrewia* Mamay) (e.g., Mamay et al., 1996; DiMichele et al., submitted for publication).

Based on frond morphology alone, it is difficult to differentiate specimens of *Supaia*, *Glenopteris*, *Protoblechnum* sensu Halle, and *Compsopteris* especially if specimens are fragmentary, due to the similarities of pinnule shape and venation. Branching of the rachis helps to alleviate this problem. Fronds of most *Supaia* species are forked into two equal rachides, above a petiolar segment. However, for *Supaia merriami* White, a form from the Hermit Shale in Arizona that closely resembles or is even indistinguishable from *Glenopteris splendens* with regard to pinnule morphology and arrangement (compare White, 1929, pl. 19 with Plate I,2), forking has never been documented, but only assumed based on the fact that the pinnules on one (i.e. the supposed external) side of the rachis are longer than those of the other (i.e. the supposed internal) side (White, 1929, p. 156). This feature, however, is not exclusively found in bipartite fronds, but may also occur in monopartite (unforked) fronds where one side is exposed to full sunlight, while the other is shaded by other fronds (e.g., in plants possessing densely spaced, spirally arranged fronds) (Kerp, 1988, p. 340). *Protoblechnum wongii* also appears to be forked, a characteristic proposed tentatively, but not well documented, by Halle (1927) in his original description of *P. wongii*. White (1929) recognized the similarities between *Supaia* and *Protoblechnum*, but argued, based on examination of Chinese specimens, that the two genera could be separated on the basis of the absence of forked fronds in *Protoblechnum*, a characteristic clearly demonstrated much later (Sze, 1955; Sun et al., 1999). Forking in *Protoblechnum* sensu Halle, unfortunately, blurs its distinction from *Supaia*. Even the use of the name *Protoblechnum* is problematic because the original attribution by Lesquereux (1879/80) concerns North American material of Pennsylvanian age, perhaps the earliest appearance of the Peltaspermales. The shapes of the pinnule bases in *P. wongii* are similar to those of *G. splendens* in being flared on occasion. Naugolnykh (1999) argues that *Compsopteris* is a uniquely *Angaran* genus and that attributions of non-Russian specimens to this genus are in error, such specimens likely belonging to *Supaia* or *Glenopteris*, both of which were first described from the Lower Permian of the western United States. Unfortunately, *G. splendens* is to date the only representative of the above listed suite of enigmatic plant taxa from the Permian of the southwestern and midcontinental United States for which the epidermal anatomy has been described, and hence cuticular and epidermal features cannot, at present, be utilized to decipher the

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Plate VI. Epidermal anatomy of *Glenopteris splendens* Sellards. Adaxial pinnule surface: costal and intercostals fields, stomatal complexes.

1.   Section of a lateral costal field; slide no. USNM 508777; scale bar=200 μm.
2.   Detail of Plate VI,1, showing a stomatal complex with eight subsidiary cells. Note the difference between polar [P] and lateral [L] subsidiary cells; scale bar=25 μm.
3.   Intercostal stomatal complex with twelve subsidiary cells (detail of Plate V,4); scale bar=50 μm.
4.   Costal stomatal complex with enlarged polar subsidiary cells; slide no. USNM 508777, scale bar=25 μm.
5.   Costal stomatal complex, viewed from the inner side. Arrows indicate peripheral margins of the guard cells; slide no. USNM 508789; scale bar=25 μm.
6.   Intercostal stomatal complex, viewed from the inner side. Note the dorsal thickenings of the guard cells; slide no. USNM 508782; scale bar=20 μm.
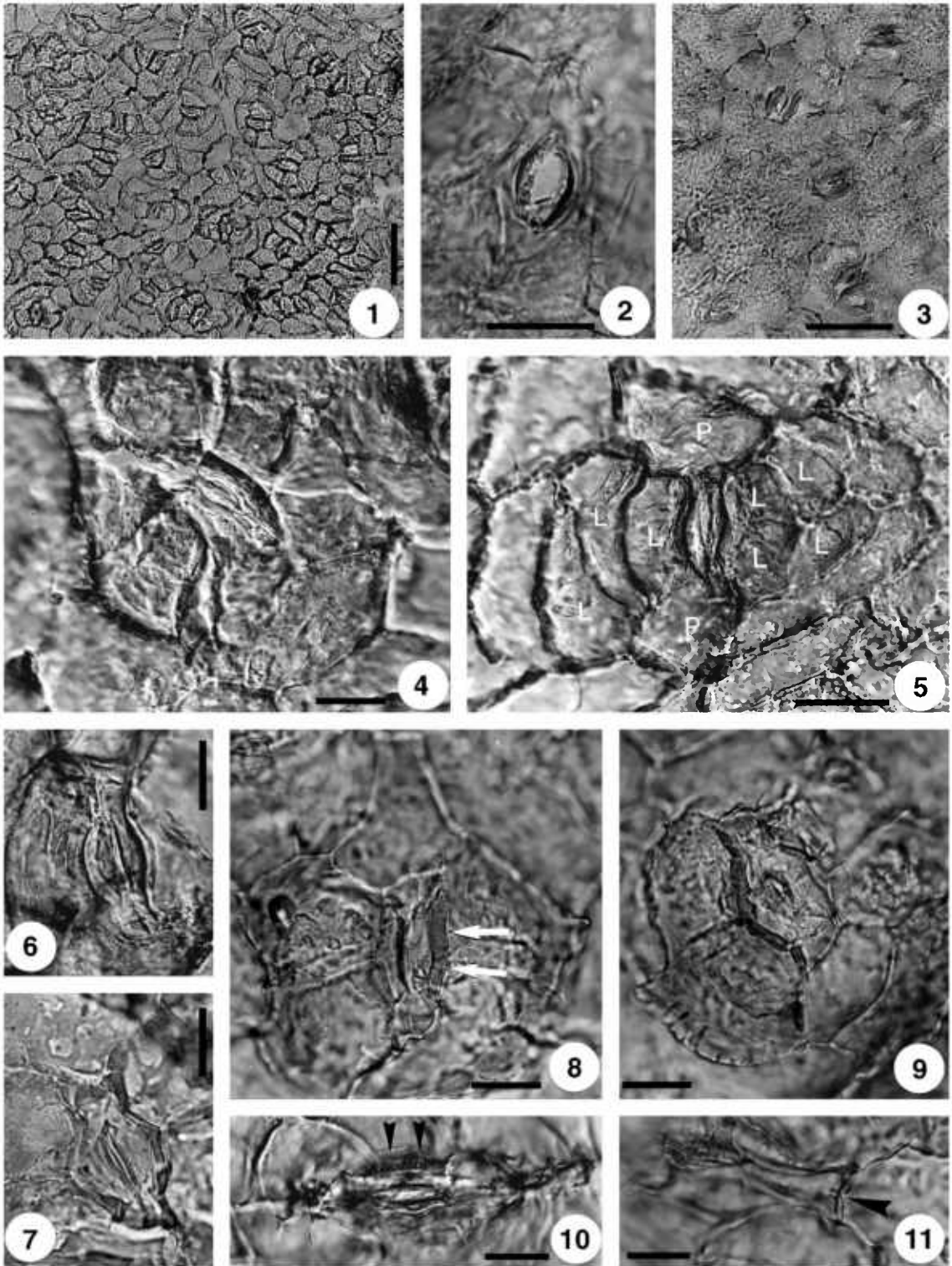
systematic relationships that may have existed between *Supaia*, *Glenopteris*, *Protoblechnum* sensu Halle, and *Compsopteris*.

6.2. Paleobiology and paleoecology

Glenopteris splendens is known only from foliage fossils; because its growth habit cannot be reconstructed, it is difficult to construct hypotheses regarding the paleobiology and paleoecology in detail. Nevertheless, it is possible to relate macromorphological and cuticular/epidermal features of the foliage to habitat conditions, in part based on other fossil plants for which abundant data are available. The depositional environment of *G. splendens* has been interpreted as a coastal plain with small freshwater to brackish lakes that, over time, experienced repeated marine incursions (Dunbar, 1924; Tasch, 1963, 1964; Moore et al., 1944, 1951; Moore, 1964; Swanson and Carlson, 2002). Based on the large size of many *Glenopteris* fossils (e.g., Sellards, 1900, pl. XXXIX–XLII; Read and Mamay, 1964, pl. 16, 3), transport was probably limited, and deposition occurred relatively close to the place of growth. Mamay (personal communication 1988, cited after DiMichele and Hook, 1992, p. 270) suggests that *Glenopteris* thrived in a coastal habitat, because plant-bearing beds are intercalated regionally with marine limestones. It is therefore possible that *G. splendens* was, at least periodically, affected by elevated soil and ground water salinity. DiMichele and Hook (1992, p. 271) hypothesize that late Early Permian floras from the southwestern and midcontinental United States did not receive high rainfall throughout the year because, with more regular rainfall, a much more homoge-

neous flora would have been present since "extrinsic factors would have damped the effects of micro- and macrohabitat differences". Artinskian age paleosols from North–Central Texas indicate seasonal moisture regimes and a general trend toward ever greater moisture limitation through time (Tabor and Montañez, 2004). In addition, the temporal patterns of vegetational change indicate the progressive restriction of "Late Pennsylvanian" floristic elements, those characteristic of extensive peat-lands and wet flood-basins, to increasingly more restricted wet patches, probably in areas close to water bodies or in riparian swampy areas embedded within these moisture limited landscapes (DiMichele et al., in press). In coastal habitats, moisture availability may have been further reduced by intensive solar radiation (high-light environment), sustained wind, and the "physiological drought" effect of elevated salinity (cf. Mothes, 1932). The environmental conditions encountered by *G. splendens* were probably similar to those described for a late Early Permian coastal flora from the Clear Fork Group in the North Robertson Unit of the Robertson Clear Fork oilfield of Gaines County, western Texas (DiMichele et al., 2000).

The fronds of *Glenopteris splendens* display macromorphological features that may be beneficial for a plant that grows under moisture limited conditions. In fronds with closely spaced pinnules (Plate I, 2), the pinnule auricles overlap the subjacent (basipetal) pinnules, which may facilitate the flow of rain water from all areas of the lamina to (or near to) the frond base. If the pinnules were differently arranged (i.e. overlapping the auricles of superjacent (acropetal) pinnules), water would not be directed to the frond

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Plate VII. Epidermal anatomy of *Glenopteris splendens* Sellards. Abaxial pinnule surface: cell pattern and stomatal complexes.

1.   Epidermal cell pattern with numerous randomly distributed stomata; slide no. USNM 508777; scale bar=100 μm.
2.   Stomatal complex viewed from the outer side. The guard cells are slightly sunken, and thus only their central portions bearing circumporal thickenings are visible; slide no. S127013/20; scale bar=25 μm.
3.   Section of the epidermis with several stomata. Note the prominent dorsal thickenings of the guard cells; slide no. USNM 508782; scale bar=75 μm.
4 and 5.   Stomatal complexes. Arrangement of subsidiary cells displays two distinct patterns: simple stomatal complexes (Fig. 4) with a single ring of up to eight, more or less equally shaped subsidiary cells vs. a more complex type (Fig. 5) with up to thirteen subsidiary cells, of which the two in near-polar position [P] may be slightly larger than those located laterally [L]; slides no. S127013/8 (Fig. 4), S127013/20 (Fig. 5); scale bars=20 μm (Fig. 4), 45 μm (Fig. 5).
6–11. Special features of abaxial stomatal complexes. Arrows indicate dorsal thickenings of the guard cells in Fig. 8, radial striae on the dorsal guard cell wall in Fig. 10, and characteristically cutinized polar contact area of the guard cell pair in Fig. 11; slides no. S127013/19 (Figs. 1–9), S127013/20 (Fig. 10), USNM 508788 (Fig. 11); scale bars=20 μm (Figs. 6–10) and 15 μm (Fig. 11).

base, but would rather run off as soon as it reached the rachis. Broad frond/leaf bases, similar to those seen in *G. splendens* fronds (Plate I,4), also are known to occur in many extant ferns and some seed plants (e.g., some members of the Apiaceae) where they often represent various adaptations. In ferns, for example, specialized frond bases (trophopodia) serve as storage sites (Wagner and Johnson, 1983). Some extant plants possess specialized tissues in broadened leaf bases that permit movement of the leaves, e.g., toward or away from the sunlight (von Guttenberg, 1971, pp. 191–203). The vascular strands that enter the pinnules of *G. splendens* from the rachis are conspiciously thin, only up to 0.5 mm, in comparison to the midveins, which are basally up to 4 mm wide (Plate I,2,3,5,6). This suggests that a multilayered bundle sheath was once present around the midvein vascular strand. The sheath was probably parenchymatous, i.e. it did not contain much sclerenchyma, because lignified tissue usually survives fossilization and diagenesis (Krings and Kerp, 1998). While it is intriguing to view the bundle sheath in *G. splendens* as representing a structural component of a major physiological adaptation to life in moisture limited regions (e.g., C_4-metabolism), this hypothesis will require additional material to verify.

The pinnules of *Glenopteris splendens* are pachymorphous (succulent), indicated by the thick layer of carbonaceous material that occurs on many specimens (Plate I,5,6). It is likely that this feature mitigates the effects of (intermittent) water stress, because succulent foliage delivers large quantities of storage water (Dickison, 2000). However, because *G. splendens* lived in a coastal habitat, pachymorphy also may have been effective as an adaptation to elevated soil and ground water salinity. Most plants are unable to grow in saline soils since 1) high salinity is associated with a loss of soil water potential, giving rise to symptoms similar to those of water stress, 2) saline soils frequently accumulate toxic levels of specific ions (e.g., K^+, Mg^{2+}, Na^+, Cl^-, HCO_3^-, NO_3^-), and 3) high levels of NaCl may result in ion imbalance (predominantly Ca^{2+}) that leads to deficiency symptoms (Lambers et al., 1998, pp. 277–280). Plants that tolerate elevated salinity (salt-resistant glycophytes) or thrive exclusively in saline environments (halophytes sensu Stocker, 1928) have evolved physiological and structural adaptations effective in the exclusion and/or

excretion of salt (e.g., exclusion of salt from the roots and/or xylem stream, excretion of salt through specialized salt glands, compartmentalization of salt in vacuoles, cf. Waisel, 1972; Larcher, 1994). It is impossible to demonstrate physiological adaptations to elevated or high soil and ground water salinity in *G. splendens* because these processes cannot normally be reconstructed based on adpression fossils. Moreover, *G. splendens* does not display structural adaptations in the form of internal glands or glandular trichomes that may have been effective in the excretion of salt. On the other hand, many extant halophytes exhibit various degrees of succulence (so-called halo-succulence sensu Lerch, 1991, p. 232), because they compensate for the osmotic effect of the elevated salt concentration in the tissues by uptake and storage of water (Waisel, 1972; Dickison, 2000, pp. 306/307). Thus, the pachymorphous nature of the pinnules of *G. splendens* is consistent with the suggestion that this species possessed a mechanism to increase the salt accumulation capacity by uptake and storage of large quantities of water in the foliage. The fact that the pinnules are amphistomatic may be positively correlated with their pachymorphous nature. It has been noted that, in extant plants, amphistomy tends to be more common among plants that possess thick leaves and thrive in xeric habitats (Parkhurst, 1978; Fahn and Cutler, 1992, p. 58). The presence of stomata on both sides of the leaf is interpreted as an adaptation to reduce the internal diffusion distance of CO_2 in thick leaves (e.g., Parkhurst et al., 1988). On the other hand, Mott et al. (1982) state that amphistomy is characteristic for plants living in high-light environments and possessing high photosynthetic capacities, and may represent an adaptation to allow high stomatal conductances, which are necessary to take advantage of high photosynthetic capacities.

The cuticle sensu lato is an important protective element of the leaf surface, buffering against a wide array of harmful environmental factors (Barthlott and Ehler, 1977). However, it is difficult to interpret the protective effectiveness of fossil cuticles because in addition to thickness of the cuticle other characters that are important to consider include the ultrastructural organization (texture), form and spatial arrangement of (epi-)cuticular waxes, and special cutinization/cuticularization features (cf. Lyshede, 1982). Unfortunately, (epi-)cuticular waxes are rarely pre-

served, and paleoecological interpretation of the ultra-structure of fossil cuticles is generally difficult for various reasons. Thus, the significance of fossil cuticles as paleoecological proxy markers is largely restricted to special cutinization/cuticularization features (Kerp, 1990). In this respect, the cuticles of *Glenopteris splendens* are rather undiagnostic. However, they do display wart- and peg-like projections into/between the epidermal anticlinal cell walls (Plate IV,2–7) that may be an adaptation to (seasonal) moisture limitation. In extant plants, heavily cutinized/cuticularized anticlinal cell walls are often associated with a xeromorphic epidermis, and found in plants that live under arid conditions (Frey-Wyssling, 1959; Barthlott and Ehler, 1977). The idiocuticular warts that occur in the rachial stomatal complexes of *G. splendens* (Plate III,5) are larger than the warts and pegs projected into/between the anticlinal walls of normal epidermal cells, and thus presumably possessed a different function. It is known from extant gymnosperms that stomatal morphology changes as stomata age (Napp-Zinn, 1966). Secondary alterations of stomatal complexes also are known to occur in several Late Pennsylvanian pteridosperms, including *Neurodontopteris auriculata* (Krings, 1999), *Odontopteris subcrenulata* (Krings et al., 2000), and *Pseudomariopteris busquetii* (Krings and Kerp, 2000). In these taxa, alterations occur in the form of progressive cutinization/cuticularization on the outside and/or in the stomatal antechamber that eventually result in the closure of the stomatal pore. In *G. splendens*, however, the idiocuticular warts occur inside, in/between the anticlinal cell walls of the lateral subsidiary and guard cells. It remains unclear whether the warts represent primary or secondary features. We interpret the warts as being of secondary origin, because they do not occur in the stomatal complexes of the pinnules. Studies of extant plants have shown that secondary alterations may significantly affect stomatal physiology. In *Equisetum*, for example, progressive lignification of the guard and subsidiary cells eventually leads to loss of function in older stomata (e.g., Riebner, 1926). Jeffree et al. (1971) demonstrate that epicuticular waxes in the form of intermeshed tubes in the stomatal antechambers of *Picea sitchensis* (Böng.) Carr. reduce the rate of transpiration by about two thirds, but reduce the rate of photosynthesis by only about one third, and thus contribute to drought resistance. Such effects

cannot be reconstructed for the warts that occur in the rachial stomatal complexes of *G. splendens*. However, it is possible to envisage that these structures ultimately impaired the opening and closure of the pore by arresting the guard cells, perhaps as an adjustment to physiological changes that concur with the aging of the fronds.

The mature frond of *Glenopteris splendens* is glabrous. Moreover, the absence of trichome bases indicates that young and developing foliage also did not possess trichomes that were later shed from the epidermis. Trichomes are known to be highly effective in altering leaf microenvironment (Uphof, 1962; Werker, 2000). For example, they may decrease light absorptance, which affects leaf temperature, photosynthetic rate, and transpiration (Ehleringer, 1984), form barriers to excessive evapotranspiration (Dell, 1977; Woodman and Fernandez, 1991), prevent irreversible desiccation by absorbing water (Benzing et al., 1985; Brewer et al., 1991; Grammatikopoulos and Manetas, 1994), inhibit infestations of phytopathogenic microorganisms (e.g., Mmbaga et al., 1994; Kortekamp and Zyprian, 1999), and protect the plant from herbivores (Levin, 1973; Johnson, 1975; Duffey, 1986). In this context, trichomes are significant especially as defensive mechanisms against herbivores, in light of the insect fossils known from the Wellington Formation (from Elmo, cf. Beckemeyer, 2000 and literature cited therein). These occurrences demonstrate that a diverse insect fauna existed in the late Early Permian. Moreover, abundant folivory in the late Early Perminan has been documented by Beck and Labandeira (1998) for a gigantopterid-dominated riparian flora from Texas. The absence of trichomes on the foliage of *G. splendens* suggests that, in this species, these structures were not necessary in herbivory abatement; protection was probably accomplished by alternative mechanisms. The relatively thick cuticles of *G. splendens* perhaps provided some protection against small arthropods with piercing–sucking feeding behavior. Another feature of possible effectiveness in protection is the pachymorphous nature of the pinnules with massive bundle sheaths around the vascular strands, which undoubtedly made the vascular tissues less easily accessible, especially for small herbivores with short probosces. On the other hand, if the foliage of *G. splendens* displayed halo-succulence, elevated salt concentration in the tissues also could have pro-

vided protection since the fronds may have become impalatable.

7. Conclusions

The late Early Permian floras of the southwestern and midcontinental United States display regional variations with regard to species composition, proportional abundance, and physiognomy (e.g., DiMichele and Hook, 1992), and also seem to differ in part from the late Early Permian floras from Europe (Kerp, 2000). Read and Mamay (1964) suggest that these differences may be the result of an increasing dissimilarity of local environmental conditions during the Late Pennsylvanian to late Early Permian that gradually subjected the "cosmopolitan coal-forming plant assemblages of the Pennsylvanian . . . to more variable and, in some areas, more rigorous conditions. More demanding physiological requirements were imposed on plant populations and new forms appeared." The majority of late Early Permian plants from North America are preserved as adpressions, with limited information on paleobiology and paleoecology available. However, our re-investigation of *Glenopteris splendens* from Kansas revealed that some of these intriguing fossils yield well-preserved cuticles. The cuticles of *G. splendens* underscore the value of new discoveries (be it in old collections) in more accurately depicting individual components of fossil floras, and demonstrate how new specimens can contribute to a more sharply focused concept of ancient ecosystems. We offer that a thorough analysis of the epidermal anatomy of other late Early Permian plants from North America will provide a wealth of valuable information with regard to a greater understanding of the floral composition and floristic changes that occurred in North America during the Late Pennsylvanian to late Early Permian transition, and how these changes are related to major geological events, and climatic and environmental changes during this significant period of time (cf. Kerp, 1996, 2000). Moreover, it appears that some plant fossils from the classic North American "red beds" display iron-permineralized anatomy (personal communication D.S. Chaney, 2005), which provides an exciting oportunity to include yet another, entirely different data set into the paleobiological and paleoecological analyses.

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