

A NEW VOLTZIALEAN CONIFER *EMPORIA ROYALII* SP. NOV. (EMPORIACEAE) FROM THE HAMILTON QUARRY, KANSAS

Genaro R. Hernandez-Castillo,^{1,*} Ruth A. Stockey,[†] Gene Mapes,[§] and Gar W. Rothwell[§]

*Instituto de Recursos, Universidad del Mar, Puerto Escondido, Oaxaca 71980, Mexico; †Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; §Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, U.S.A.

A new species of extinct conifer plants, *Emporia royalii* sp. nov. Hernandez-Castillo, Stockey, Mapes et Rothwell (Emporiaceae: Voltziales), is described from the rich fossil biota of the Late Pennsylvanian, Hamilton Quarry, Kansas. This conifer has lateral plagiotropic branches with simple and forked leaves, “age-dependent heterophylly,” simple pollen cones, and compound ovulate cones. Stems have an endarch eustele, dense wood, and secretory cells arranged in nests or plates in the pith. Leaves are amphistomatic with two adaxial stomatal bands and two longitudinal abaxial rows of stomata with numerous trichome bases. Pollen cones are simple and have helically arranged microsporophylls with adaxial pollen sacs. Prepollen is monolete and monosaccate (*Potoneisporites* Bharadwaj). Ovulate cones are compound with bilaterally symmetrical axillary dwarf shoots that bear up to 45 sterile scales and 1–2 sporophylls and occur in the axils of helically arranged bracts with forked tips. Ovules are inverted and winged and resemble those of *Emporia lockardii* and *Emporia cryptica*. *Emporia royalii* is compared to other Euramerican walchian Voltziales, and a summary of the Emporiaceae and evolution of Paleozoic conifers is given. This is the fifth species of extinct conifer plants to be reconstructed from the Hamilton Quarry, making it the only Paleozoic locality in the world with numerous conifers all of which have been characterized as complete or nearly complete plants.

Keywords: conifer, Emporiaceae, evolution, fossil, Paleozoic, systematics, walchian.

Introduction

The Late Pennsylvanian Hamilton Quarry yields an exceptionally well-preserved and rich fauna and an abundant terrestrial flora that is represented by fossil plants that show both external morphology and internal anatomy (Mapes and Rothwell 1988; Rothwell and Mapes 1988, 2001; Fahrer et al. 1990; Fahrer 1991; Feldman et al. 1993). Floristic analyses have documented a conifer-dominated assemblage derived from relatively dry basinal slopes (DiMichele and Aronson 1992; Rothwell et al. 1997). Previous studies of the Hamilton Quarry flora include the most complete description of internal anatomy for Paleozoic conifer plants, the first evidence of inverted ovules among walchian conifers (Mapes and Rothwell 1984), the origin of conifer seed dormancy (Mapes et al. 1989), and the first description of simple pollen cones with adaxial pollen sacs in Paleozoic conifers (Mapes and Rothwell 1998). These well-preserved fossil specimens are the basis for the reconstruction of five species of conifer plants, including four species of the family Emporiaceae (Mapes and Rothwell 1991, 2003; Hernandez-Castillo 2005; Rothwell et al. 2005; Hernandez-Castillo et al. 2009a, 2009b).

The fossil record of the most ancient conifers can be traced back to the Pennsylvanian and early Permian of Europe and North America (Florin 1938–1945; Rothwell 1982; Galtier et al. 1992; Rothwell et al. 1997). Euramerican conifers, also

referred to as “walchian” conifers (Mapes and Rothwell 1984), are classified in several families within the order Voltziales (Florin 1938–1945; Visscher et al. 1986; Kerp et al. 1990; Mapes and Rothwell 1991). The first comprehensive systematic treatment for walchian conifers was proposed by Florin (1927, 1938–1945, 1950, 1951). His work stood more or less unchallenged for many years until more recent authors began to question Florin’s taxonomic treatment and systematic interpretations of the most primitive conifers (Schweitzer 1963, 1996; Rothwell 1982; Clement-Westerhof 1984, 1987, 1988; Mapes and Rothwell 1984, 1991, 1998; Meyen 1984; Winston 1984; Visscher et al. 1986; Kerp et al. 1990; Kerp and Clement-Westerhof 1991; Hernandez-Castillo et al. 2001a, 2001b, 2009a, 2009b; Hernandez-Castillo 2005).

More recently, a complete reevaluation and reexamination of these ancient fossils (Hernandez-Castillo et al. 2001b; Hernandez-Castillo 2005) has led to the development of new and more reliable methodologies and criteria for circumscribing species of walchian conifer plants based on the correlation of numerous vegetative branches to both pollen and ovulate cones. This correlation among individual plant organs relies on interconnections of plant parts and similarities among morphological, cuticular, and anatomical characters of vegetative and fertile organs (Hernandez-Castillo et al. 2001b). In this study, we employ this approach to describe *Emporia royalii* sp. nov. as a species of extinct conifer plants.

Emporia royalii is the fifth conifer reconstructed from the Hamilton Quarry (Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005; Hernandez-Castillo

¹ Author for correspondence; e-mail: genarohc@zicatelamar.mx.

et al. 2009a, 2009b). Four of these conifers belong to the family Emporiaceae (Mapes and Rothwell 1991, 2003; Hernandez-Castillo 2005; Hernandez-Castillo et al. 2009a, 2009b), making it the best-known family of walchian conifers from the Paleozoic worldwide. With the description of *E. royalii* herein, the Hamilton Quarry becomes the only Paleozoic locality in the world with numerous species where all of the conifers have been described as complete plants. The reconstruction provided here is part of broader study to reinvestigate, describe, and reevaluate morphological characters and to reconstruct species of Euramerican Paleozoic walchian conifers so they can be used to resolve systematic relationships among the conifers as a whole.

Material and Methods

Specimens used in this study are preserved as coalified compressions with preserved cuticles and some cellular permineralization. They occur in Late Pennsylvanian laminated carbonate mudstones of the Hartford Limestone, Topeka Limestone Formation, Shawnee Group, located east of Hamilton, Kansas (fig. 1; Mapes and Rothwell 1984; Bridge 1988; Busch et al. 1988; French et al. 1988). These beds represent channel deposits in an estuarine environment under tidal influence (French et al. 1988; Fahrner et al. 1990; Fahrner 1991; Feldman et al. 1993). *Emporia royalii* sp. nov. is represented by 109 specimens. Twenty-eight are plagiotropic leafy branching systems with penultimate and ultimate shoots attached; four have cuticles preserved and two are anatomically preserved.

Seventy are pollen cones, 22 of which are attached to ultimate shoots. Eight have cuticles preserved, and nine are anatomically preserved. Eleven are ovulate cones. Five of them are attached to penultimate shoots with leaves. Three have cuticles, and three are anatomically preserved.

Specimens were initially revealed on the split surfaces of the limestones. Cuticles were macerated from the matrix with dilute (0.5%–1%) HCl, rinsed in distilled water, bleached in Lysol toilet bowl cleaner (Reckitt Benckiser, Toronto), allowed to air dry on microscope slides, and mounted under a coverslip with Eukitt (O. Kindler, Freiburg, Germany). Cuticles for scanning electron microscopy were air-dried on specimen stubs, coated with (100 Å) gold, and examined on JEOL (Japan Electron Optics) 6301 FXV and Phillips XL30 ESEM (FEI, Tokyo) scanning electron microscopes. Some anatomically preserved specimens were prepared with the cellulose acetate peel technique (Joy et al. 1956), and others were cut into wafers and ground thin enough to transmit light. Compressed specimens with some anatomical preservation were etched with 1%–5% HCl and flooded with acetone, and a cellulose acetate peel was placed on the split surface. These surface pulls were removed while the acetate was still plastic enough to be pressed relatively flat under a heavy weight. Light microscopy was conducted using Zeiss Ultraphot IIIB and WL microscopes, and images captured with a MicroLumina digital scanning camera (Leaf Systems, Bedford, MA) or a PhotoPhase digital scanning camera (Phase One, Frederiksberg, Denmark). Images were processed using Adobe Photoshop. All specimens are housed in the Ohio University Paleobotanical Herbarium (OUPH), Athens, Ohio.

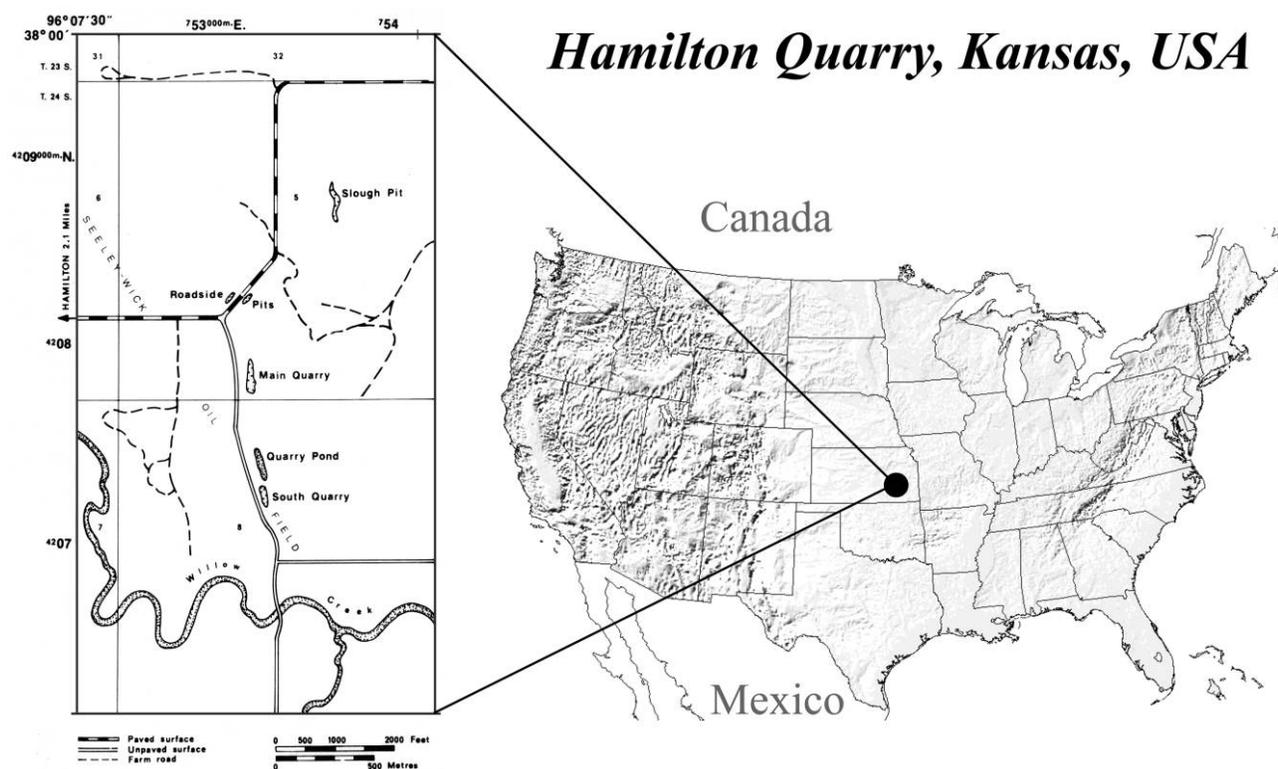


Fig. 1 Map showing location of the Hamilton Quarry locality, Kansas.

Systematics

Class—*Coniferopsida*

Order—*Voltziales*

Family—*Emporiaceae* Mapes et Rothwell

Genus—*Emporia* Mapes et Rothwell

Species—*Emporia royalii* Hernandez-Castillo,
Stockey, Mapes et Rothwell (Figs. 2–14)

Emporia royalii *diagnosis*. Small conifer trees having leaves with age-dependent heterophylly; tracheids with uni- to biseriate circular to semihexagonal bordered pits; vascular rays unibiseriate, 1–2 cells high. Pollen cones up to 3.2 cm long and 1.0 cm wide; microsporophylls stalked with heeled distal lamina; 6–10 adaxial pollen sacs, prepollen monosaccate assignable to the sporae dispersae genus *Potonieisporites* Bharadwaj. Ovulate cones up to 8.2 cm long and 1.6 cm wide; bracts notably longer than dwarf shoots, fused to dwarf shoot at base; sterile scales 20–45 per dwarf shoot. Sporophylls 1–2 per dwarf shoot.

Holotype hic designatus. Specimen OUPH 18285 (fig. 10C); deposited at the Ohio University Paleobotanical Herbarium, Athens, OH.

Paratypes. Lateral branches OUPH 18041, 18003, 18005, 18014, 18015, 18055. Cuticular features of leaves on penultimate shoots OUPH 18026–18034, 18017–18025, 18274–18276, 18322. Cuticular features of ultimate shoots OUPH 18027–18034, 18110–18121. Anatomically preserved stems OUPH 18030–18032. Pollen cones OUPH 18087, 18090, 18109–18121, 18122–18132, 18133. Vegetative leaves of ultimate shoots attached to pollen cones OUPH 18110–18121. Pollen cone macerations OUPH 18122–18132. Anatomically preserved pollen cones OUPH 18194, 18263–18266, 18134–18171. Ovulate cones OUPH 18282, 18347, 18285, 18293–18310, 18311–18312. Ovulate cone macerations OUPH 18315–18379, 18293–18310. Ovulate cone anatomy OUPH 18335–18379.

Type locality. Hamilton Quarry; northwest quarter, secs. 5 and 8, T.24 S., R.12E., Virgil 7.5' quadrangle, Greenwood County, Kansas, U.S.A. (fig. 1).

Lithology and stratigraphy. Hartford Limestone, Topeka Limestone Formation, Shawnee Group.

Age. Late Pennsylvanian (Gzhelian/Virgilian).

Etymology. The specific epithet *royalii* honors Royal Mapes (Ohio University) for his enthusiastic collecting of fossils from this locality and his perennial support of the research.

Description

Branching Systems

Specimens consist of two orders of branching with a penultimate shoot that bears several ultimate shoots (fig. 2). Branch shape ranges from ovoid to deltoid (figs. 2, 3B). The largest plagiotropic branch measures 47 cm long and 9.6 cm wide (fig. 2A). The largest ultimate shoots (~8.6 cm long) occur in the midregion of large branches (fig. 2A). This shoot is plagiotropic, but the ultimate shoots are not located in the same plane, and they are all oriented toward the same side

(fig. 2A). All other branching specimens, however, are plagiotropic (fig. 2B–2D; fig. 3A, 3B). Most lateral branches are broken at the very base or the apex (fig. 2; fig. 3A, 3B). This indicates that some plagiotropic shoots were larger than the specimens available for study. Penultimate shoots are 2.0–4.0 mm wide at the base of the preserved specimens ($n = 14$), and ultimate shoots are 1.0–2.4 mm wide at the base ($n = 16$).

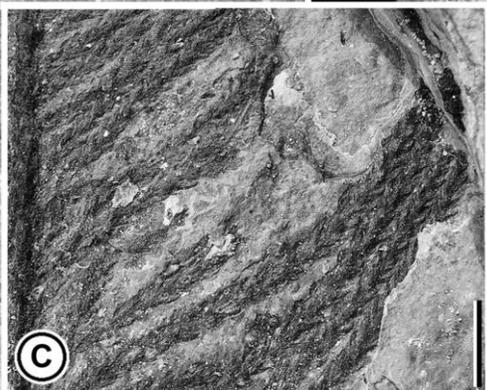
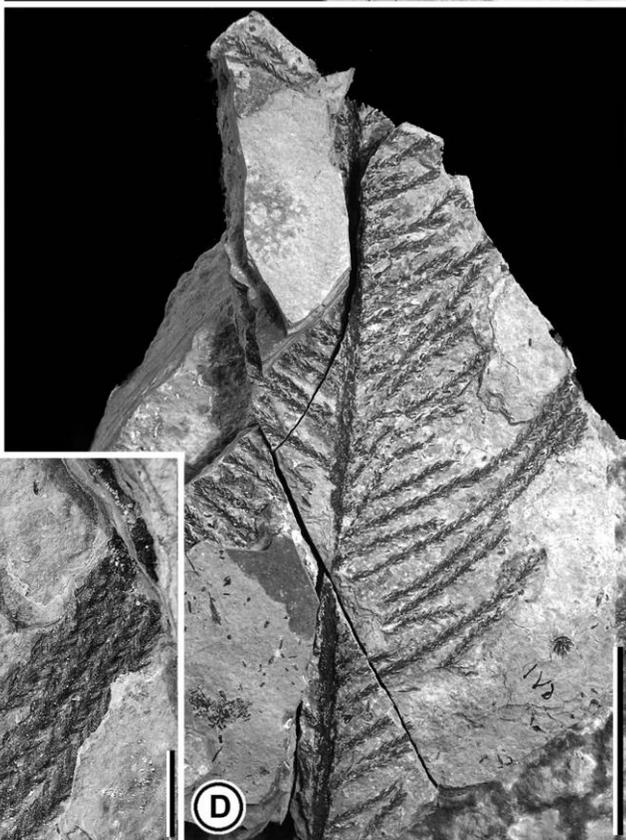
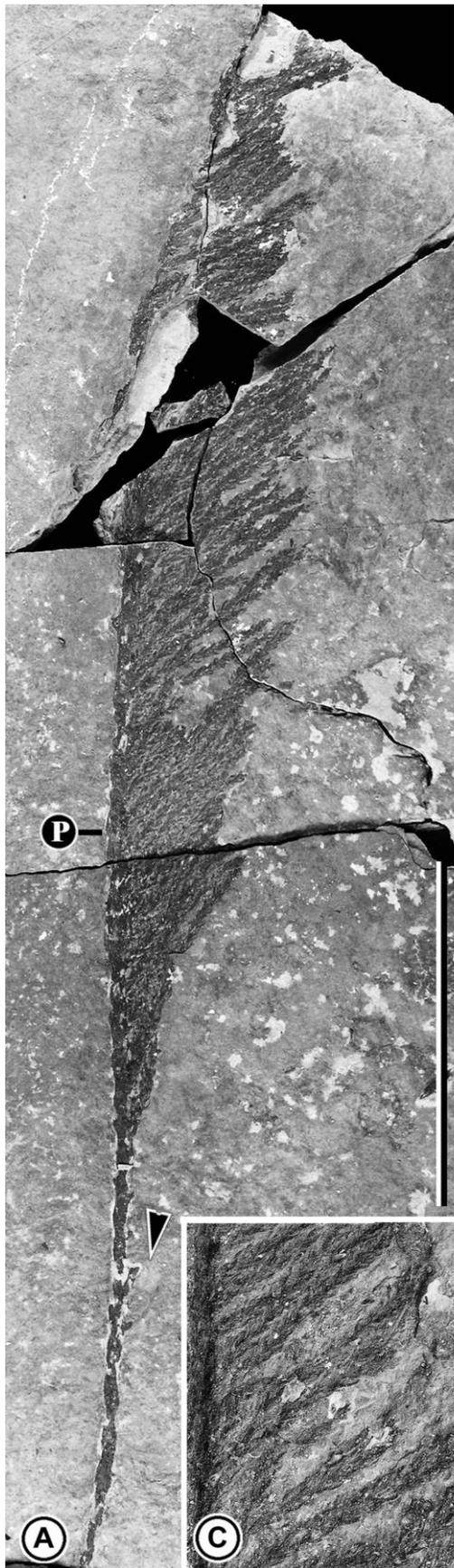
Leaves on Penultimate Shoots

Leaves are helically arranged on penultimate and ultimate shoots (fig. 2; fig. 3A, 3B). Leaves are 1.6–5.3 mm long, and 0.3–1.5 mm wide, simple or forked (table 1; fig. 3C–3F; fig. 4A, 4C; fig. 5A). Only simple leaves are often found on small- and medium-size penultimate branches (fig. 3A, 3B), while forked leaves are found on larger specimens (fig. 2). As explained in the “Discussion,” that distribution of forked leaves reflects a specific facet of growth architecture that we are referring to as “age-dependent heterophylly.” Simple leaves are narrowly triangular with a broad base in face view and S-shaped to slightly S-shaped in side view (fig. 3C–3F, fig. 4A, 4C). Forked leaves are linear below the distal forking and display tips that taper to a point (fig. 5A). In side view, these forked leaves have a shape similar to that of simple leaves on the same shoot order.

Cuticular macerations reveal elongated epidermal cells, stomatal bands, and circular trichome bases (figs. 4B, 5C). There are two adaxial bands of stomata that are 2–6 stomata wide, each having 5–6 subsidiary cells with overarched papillae (table 1; figs. 4A, 5A). Stomata are monocyclic, ellipsoidal, and range from 32 to 42 μm wide and from 42 to 72 μm long (fig. 4B). The length of some stomata may reach 85 μm near the leaf base. Individual stomata may be in contact with adjacent stomata or separated by groups of epidermal cells (figs. 4B, 5C). Bands of stomata are separated by a stomatal-free zone of polygonal to rectangular epidermal cells (figs. 4A, 5A) and elongate epidermal cells that look like undeveloped papillae (fig. 4D). Within this zone there are prominent external cuticular flanges surrounded by a ring of cells (fig. 4D at arrowheads). These cuticular flanges resemble nonfunctional stomata. Epidermal cells with small erect papillae are sometimes interspersed with surficial trichome bases particularly on the leaf margins (fig. 4A, 4C). The abaxial surface is completely covered by surficial trichome bases and has two rows of stomata, but these rows sometimes are multistomatal, forming a narrow stomatal band (fig. 4C, 4E, 4F). Individual stomatal complexes have 6–8 subsidiary cells each with a single overarched papilla (fig. 4F).

Leaves on Ultimate Shoots

Leaves are consistently simple, helically arranged, 1.6–4.5 mm long, and 0.6–1.7 mm wide. They are narrowly triangular to linear in face view (figs. 3D, 5B) and slightly S-shaped to slightly concave in side view, and they display numerous marginal trichomes (fig. 2; fig. 3A, 3B, 3E, 3F). These leaves extend from stems at angles of 24°–57° at the base and 21°–61° at the apex of the leaf. Leaves are amphistomatic with two long adaxial bands of stomata (fig. 5B, 5D). Adaxial stomatal



bands are 2–8 stomata wide and separated by a stomatal-free zone (figs. 5B, 5D). Stomata are monocyclic, ellipsoidal to semicircular, 30–64 μm wide, and 41–84 μm long (average = $55 \times 68 \mu\text{m}$, $n = 27$) and have 6–8 subsidiary cells with erect or overarched papillae (fig. 5D). Stomatal complexes may share subsidiary cells (fig. 5D). Epidermal cells in marginal and stomatal-free zones are elongate, rectangular, papillate, and interspersed with undeveloped papillae. Trichome bases are often short or broken on leaf margins, and they are usually not found among regular epidermal cells (fig. 5B, 5D). The abaxial surfaces of leaves on ultimate shoots have numerous trichome bases and two single rows or narrow bands of stomata as in leaves from penultimate shoots (fig. 4F).

Stem Anatomy

Stems have a parenchymatous pith surrounded by an endarch eustele with secondary xylem, primary cortex, and leaf traces (fig. 6A–6C). The pith is composed of polygonal parenchymatous cells and groups or plates of secretory cells (fig. 6B, 6D). Parenchyma cells are rectangular and adaxially elongated (fig. 6D). Secretory cells with dark contents form horizontal plates in the pith (fig. 6A, 6B, 6D). The primary xylem consists of small diameter tracheids with annular or helical secondary wall thickenings (fig. 6D, at arrow). Secondary xylem has rows of radially aligned tracheids that are hexagonal to circular in shape in cross section, separated by vascular rays (fig. 6A, 6C). In longitudinal section, tracheids show circular to hexagonal, uniseriate, and occasionally biseriate bordered pits on the radial walls (fig. 6E). Vascular rays are uniseriate, 1–2 cells high (fig. 6F). The cortex contains rectangular parenchyma cells and secretory cells with dark contents (fig. 6G). The epidermis is present on some specimens and shows a thick cuticle with numerous, often broken, trichomes (fig. 6G).

Pollen Cones

Pollen cones are simple, terminal, ellipsoidal to obovate, 0.5–3.2 cm long, and 0.2–1.0 cm wide (fig. 7). Cones bear helically arranged microsporophylls, 0.25–4.1 mm long and 2.0–2.6 mm wide (fig. 7A–7E). Microsporophylls have a narrowly triangular distal end and a broad base (fig. 7C, 7E; fig. 8A, 8B, 8F). Mature (fig. 7B, 7C), intermediate (fig. 7A, 7D, 7E), and immature (fig. 7F) pollen cones are all represented among the specimens. Several pollen cones are in organic connection with ultimate shoots that bear leaves (fig. 7A, 7B, 7F), but most are isolated and/or broken (fig. 7C–7E). Leaves on attached shoots are simple and similar to those of penultimate vegetative shoots (table 1). These leaves have two adaxial bands of stomata that are 2–6 stomata wide and separated by a stomatal-free zone. Stomata are ellipsoidal with 6–8 papillate subsidiary cells and may share subsidiary

cells. Leaf margins and stomatal-free zones have rectangular epidermal cells, papillae, and cuticular flanges and lack trichome bases.

Cuticles of Microsporophylls

Microsporophylls display dense marginal trichomes (fig. 8A, 8B, 8F) and have 2–4 long, broad bands of adaxial stomata (fig. 8A, 8B). Two main bands run along the entire distal lamina (fig. 8A), and two short bands are located toward the microsporophyll margin (fig. 8B). Stomata are monocyclic, ellipsoidal, 29–34 μm wide, and 45–58 μm long and have 4–6 subsidiary cells with erect to overarched papillae (fig. 8C). Epidermal cells may be interspersed with individual stomata in these bands (fig. 8C). Stomatal bands are separated by stomatal-free zones with numerous papillate epidermal cells and cuticular flanges (fig. 8D, 8E). Cuticular flanges occur on epidermal cells of the stomatal-free zones (fig. 8D, 8E). The abaxial surface of the microsporophyll is completely covered by circular trichome bases (fig. 8G).

Anatomy of Pollen Cones and Prepollen

Pollen cones have a cone axis (fig. 9A) bearing helically arranged microsporophylls composed of stalk and heeled distal lamina (fig. 9A, 9B). Six to eight adaxial, ellipsoidal pollen sacs are attached to a single area on the stalk (fig. 9A, 9C). The cone axis has a pith and cortex consisting of parenchyma cells. Most parenchyma cells contain dark contents (fig. 9A). Cauline bundles of the cone axis are relatively inconspicuous and terete (fig. 9A, 9D). The sporophyll stalk has a thick epidermis with rectangular cells and parenchyma cells with dark contents (fig. 9D). Internal anatomy of the microsporophyll distal lamina resembles that of vegetative leaves (fig. 9A–9C). Distal lamina is at least four times longer than the microsporophyll's proximal base in mature cones (fig. 9A, 9B). Distal laminae have a thick cuticle that covers an epidermis composed of rectangular cells with dark contents, a two- to five-layered mesophyll, and a single vascular bundle (fig. 9C, 9D). Many cones have only pollen sac bases preserved, but some pollen sacs are full of monosaccate prepollen grains that conform to the sporae dispersae genus *Potomieisporites* Bharadwaj (1964; fig. 9A, 9C). Grains are subcircular to circular with a large saccus that surrounds a central body (fig. 9E). This central body has a proximal monolet suture and parallel folds that are often broken (fig. 9E). Grains are 91–122 μm long by 71–110 μm wide in polar view.

Ovulate Cones

Seed cones are cylindrical to ellipsoidal, 5.0–8.2 cm long, and 1.1–1.6 cm wide (fig. 10), and they bear helically ar-

Fig. 2 *Emporia royalii* sp. nov., lateral branches. A, Penultimate shoot (P) with leaves (arrowhead) and ultimate shoots. OUPH 18041, scale bar = 10 cm. B, Ovoid branch showing penultimate shoot and ultimate shoots with helically arranged leaves on ultimate shoots. OUPH 18003, scale bar = 2 cm. C, Branch showing slightly concave leaves. OUPH 18005, scale bar = 2 cm. D, Deltoid branch with large ultimate shoots. OUPH 18014, scale bar = 5 cm.

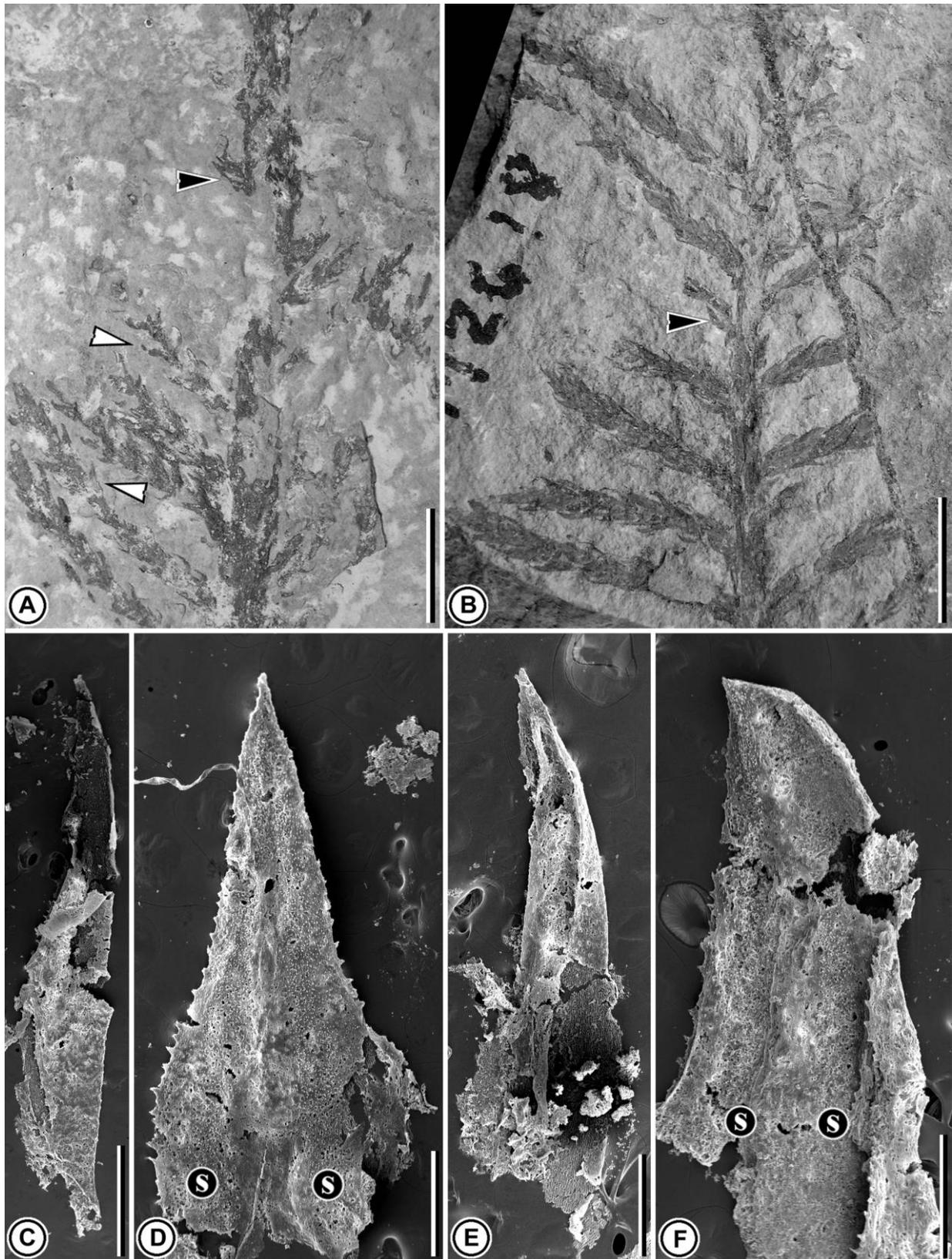


Fig. 3 *Emporia royalii* sp. nov., lateral branches and SEM of leaves. A, Branch showing leaves on penultimate shoots (black arrowhead) and slightly concave to S-shaped leaves on ultimate shoots (white arrowheads). OUPH 18015, scale bar = 1 cm. B, Branch showing leaves on

ranged bracts (figs. 10E, 14A) and axillary ovuliferous dwarf shoots (figs. 10C–10E, 14A). Some ovulate cones are attached to penultimate shoots (fig. 10A). Leaves on these shoots are similar to simple leaves found on vegetative penultimate shoots (table 1). The cones of *Emporia royalii* can be distinguished from other *Emporia*-like seed cones at the locality by their greater length, robust morphology, and subtending bracts that are typically much longer than axillary dwarf shoots (figs. 10A–10D, 11A). Axillary dwarf shoots diverge from the cone axis at $\sim 45^\circ$ (fig. 10E). The number of sterile scales (fig. 10E; fig. 11B, 11D; fig. 12D–12G) ranges from 20 to 45. They are found all around each dwarf shoot, but most of them are located on the abaxial side of the shoot (fig. 10E; fig. 14A, 14B, 14E). Sporophylls are often difficult to identify unless the cone is macerated (fig. 12A).

Ovulate Cone Bracts

Bracts are forked with numerous marginal trichomes (figs. 11A, 12C). They are narrowly triangular to linear with two tips that taper to a point and a broad base (fig. 11A; fig. 12B, 12C). They have cuticles identical to leaves on penultimate vegetative shoots (table 1). The adaxial surface has two bands of stomata, one per forked tip, and each band has 2–6 stomata (fig. 11A). Stomata are ellipsoidal and have 6–7 papillate subsidiary cells with overarching papillae (fig. 11C; fig. 13A, 13B). Leaf margins and stomatal-free zones have rectangular epidermal cells with numerous papillae and few or no trichome bases (fig. 11C; fig. 13A, 13B). The abaxial surface has two narrow bands of stomata and is entirely covered by trichome bases.

Ovulate Cone Sterile Scales

Sterile scales are triangular to narrowly triangular in face view, S-shaped to slightly S-shaped in side view with a mucronate apex (figs. 11B, 12D–12G). They are 1.6–6.6 mm long and 0.5–2.0 mm wide with prominent marginal trichomes (fig. 12D–12G). Scales are amphistomatic with two narrow bands of stomata on adaxial and abaxial surfaces (fig. 12D–12G). Stomatal complexes have 5–7 papillate subsidiary cells (figs. 11D, 13C). Leaf margins and stomatal-free zones have rectangular epidermal cells, few cuticular flanges, numerous papillae, and no trichome bases (fig. 13D). Papillae on epidermal cells may be short and erect, long and hairlike, or short and wide (fig. 13D). The abaxial surface is covered completely with surficial trichome bases (figs. 11D, 13E–13G).

Sporophylls and ovules. Sporophylls are narrow, 2.6–3.9 mm long and 0.8–1.3 mm wide with a subapical V- to U-shaped seed scar (fig. 12A). They are completely covered by trichome bases (fig. 12A). Ovules/seeds are bilateral and flattened (fig. 12H, 12I; fig. 14A, 14B, 14F, 14G), with rounded to subcordate bases (fig. 12H) and a smooth surface that sometimes is cov-

ered with few, often broken, uniseriate trichomes (fig. 12H, 12I).

Ovulate Cone Anatomy

The woody cone axis bears bracts that subtend an axillary dwarf shoot with inverted seeds (fig. 14). The cone axis, as in penultimate shoots, has a large pith with nests or plates of secretory cells with dark contents (fig. 14A–14D) and an endarch eustele (fig. 14A–14C). Cauline bundles of the stele and leaf traces appear as small patches of randomly oriented tracheids at the margin of the pith (fig. 14C). Secondary xylem has radially aligned rows of 4–8 tracheids separated by uniseriate rays (fig. 14C). The bract and dwarf shoot arise as a single unit but separate almost immediately after diverging from the cone axis. Sections reveal that sterile scales extend from all surfaces along the dwarf shoot but are concentrated on the abaxial surface at the apical region of the shoot (fig. 14A, 14E). Axillary dwarf shoots often have 23–45 sterile scales.

Ovule Anatomy

Ovules are bilaterally symmetrical, inverted, ovoid to ellipsoidal, 3.0–6.0 mm long, and 1.0–1.6 mm wide (fig. 14A, 14B, 14F, 14G). The micropylar end faces the cone axis, and each ovule produces two wings (fig. 14A, 14F, 14G). The integument is composed of sarcotesta, sclerotesta, and endotesta (fig. 14F, 14G). The sarcotesta is single-layered, while the sclerotesta is composed of several layers of cells (fig. 14F, 14G). The endotesta is typically single-layered, but up to three layers of cells have been observed (fig. 14F, 14G). There is no evidence of vascular tissue in the integument. The nucellus is one-layered and free from the integument except at the micropylar end (fig. 14G). There is a pollen chamber at the apex of the nucellus that displays a nucellar beak (fig. 14F).

Discussion

Systematic Relationships

Emporia royalii is the last of five species of conifer plants to be reconstructed from the Upper Pennsylvanian Hamilton Quarry locality. This new reconstruction adds another conifer plant for which characters of all the aboveground organs are known (tables 1, 2) and that conforms to the general architecture recently determined for walchian conifers (Lausberg 2002; Hernandez-Castillo et al. 2003). As in most other Paleozoic conifer reconstructions from North American fossils, morphological, cuticular, and anatomical characters are all important for characterizing *Emporia royalii* (table 1; Florin 1938–1945; Kerp et al. 1990; Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001; Hernandez-Castillo 2005, 2009a, 2009b; Rothwell et al. 2005).

penultimate (arrowhead) and ultimate shoots. OUPH 18055, scale bar = 1 cm. C, Side view of slightly S-shaped leaf on penultimate shoot. OUPH 18026, scale bar = 1 mm. D, Triangular leaf of ultimate shoot showing marginal trichomes and adaxial bands of stomata (S). OUPH 18027, scale bar = 0.5 mm. E, Side view of slightly concave leaf from ultimate shoot. OUPH 18027, scale bar = 0.5 mm. F, Side view of leaf from ultimate shoot showing adaxial bands of stomata. OUPH 18027, scale bar = 0.5 mm.

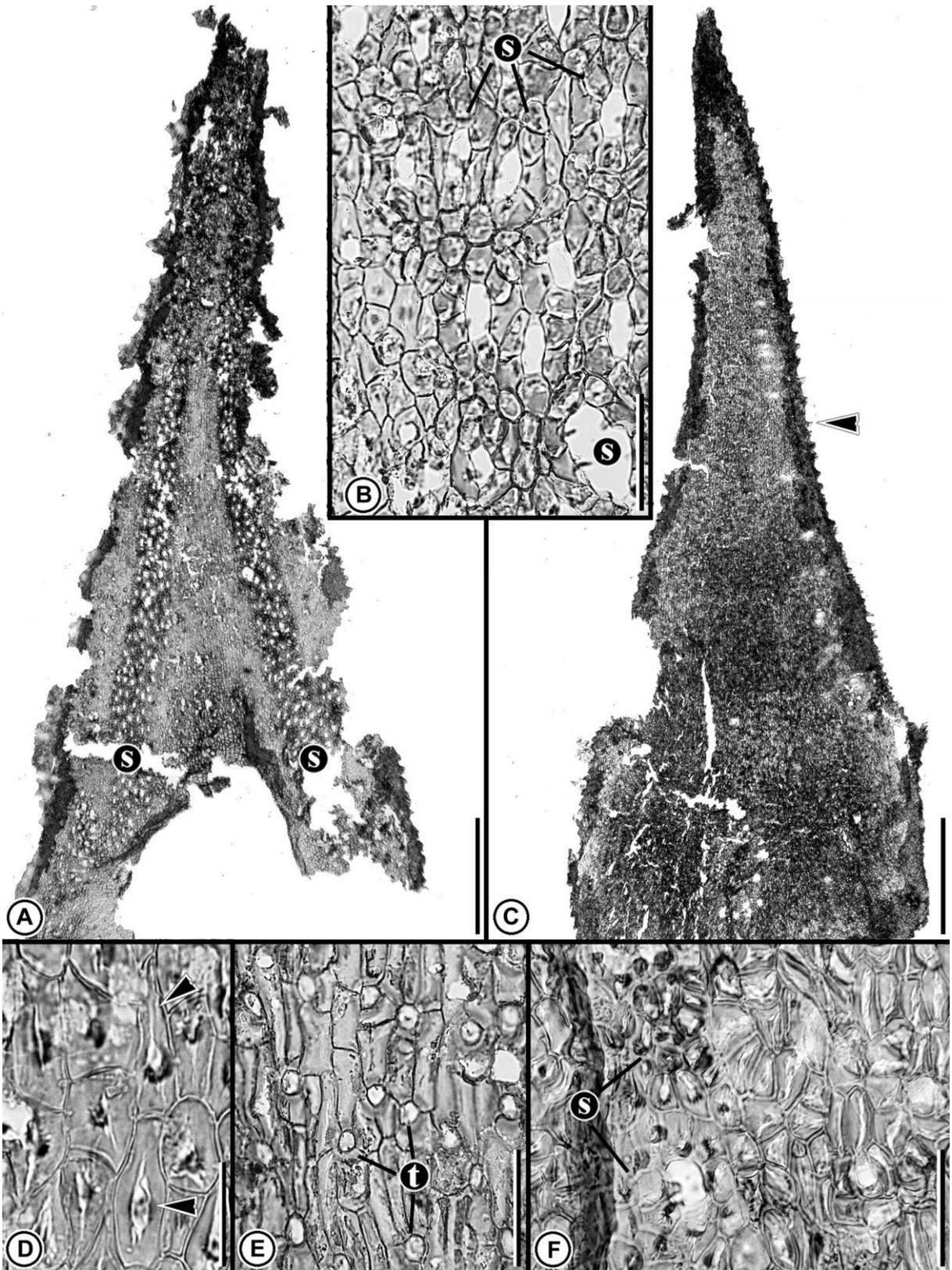


Fig. 4 *Emporia royalii* sp. nov., cuticular macerations of leaves on penultimate shoots. *A*, Leaf from penultimate shoot showing narrowly triangular shape and two adaxial bands of stomata (S) separated by central stomatal-free zone. OUPH 18017, scale bar = 0.5 mm. *B*, Penultimate leaf showing adaxial papillate epidermal cells (left) and stomatal band. OUPH 18017, scale bar = 60 μ m. *C*, Narrowly triangular leaf showing

Paleozoic conifers traditionally have been described and identified from isolated and often fragmentary organs such as vegetative branches, pollen cones, and ovulate cones (i.e., Florin 1938–1945). However, that approach has been abandoned in recent conifer reconstructions because isolated organs do not reflect the broad ranges of variation found within a single conifer fossil plant (Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001; Rothwell et al. 2005; Hernandez-Castillo et al. 2009a, 2009b). Furthermore, isolated organs (morphotaxa) are unreliable for comparing and contrasting whole conifer plants and inadequate for addressing phylogenetic relationships of conifers. Such morphotaxa create taxonomic problems that lead to bias in classifications (Mapes and Rothwell 1991; Hernandez-Castillo et al. 2001b, 2009a; Rothwell et al. 2005).

Comparisons of *E. royalii* to other Paleozoic conifers in this article are made within a whole-plant framework; morphotaxa based on isolated organs are not included. Characters used for taxonomic comparisons in this work employ sets of characters that have been shown to help differentiate among species of fossilized conifer plants (tables 3, 4; Hernandez-Castillo et al. 2001b, 2009a, 2009b). Some nearly complete conifers from Europe and North America, such as *Ortiseia* Clement-Westerhof, *Majonica* Clement-Westerhof, and *Lebowski* Looy, are not included in the discussion because they produce leaves (in all orders of branching) and ovulate cones (with partially fused dwarf shoots) very different from those of early walthians (Clement-Westerhof 1984, 1987; Looy 2007), thus rendering them distinct from walthian conifers at Hamilton Quarry and elsewhere.

Emporia royalii is a relatively small tree with plagiotropic lateral branches that produce terminal pollen cones and ovulate cones. This new species of *Emporia* has a novel combination of characters that includes (1) two orders of lateral branches (penultimate and ultimate shoots); (2) simple and forked needlelike leaves on penultimate shoots and simple leaves on ultimate shoots (=age-dependent heterophylly), where leaves are amphistomatic (two long adaxial/individual abaxial rows of stomata) with numerous adaxial cuticular flanges; (3) simple, terminal pollen cones and microsporophylls with stalk and heeled distal lamina and 6–10 adaxial pollen sacs with monosaccate *Potonieisporites* prepollen grains; (4) compound ovulate cones with forked bracts and ovuliferous dwarf shoots that are fused at the base and free more distally; and (5) dwarf shoots bearing 20–45 sterile scales interspersed with 1–2 sporophylls and one inverted ovule per sporophyll.

Emporia royalii is similar to other Euramerican walthian Voltziales (Rothwell et al. 2005) in several characters, such as plagiotropic lateral branches, leaves on ultimate branches that are simple and amphistomatic, simple pollen cones, and compound terminal ovulate cones with a small number of ovules per dwarf shoot (tables 3, 4; Rothwell et al. 2005;

Hernandez-Castillo et al. 2009a, 2009b). However, this new species has a unique combination of characters that makes it distinct from previously described species of Euramerican conifers (tables 3, 4) and at least seven diagnostic characters support the assignment of *E. royalii* to the Emporiaceae (tables 3–5).

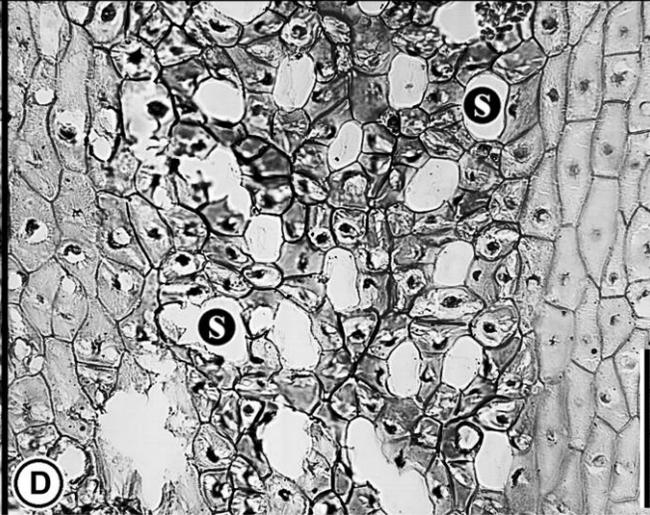
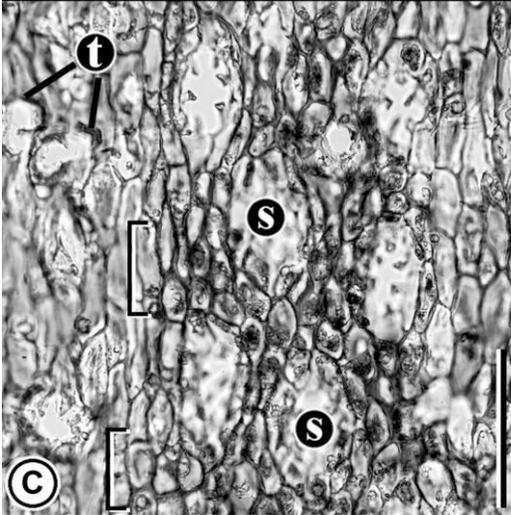
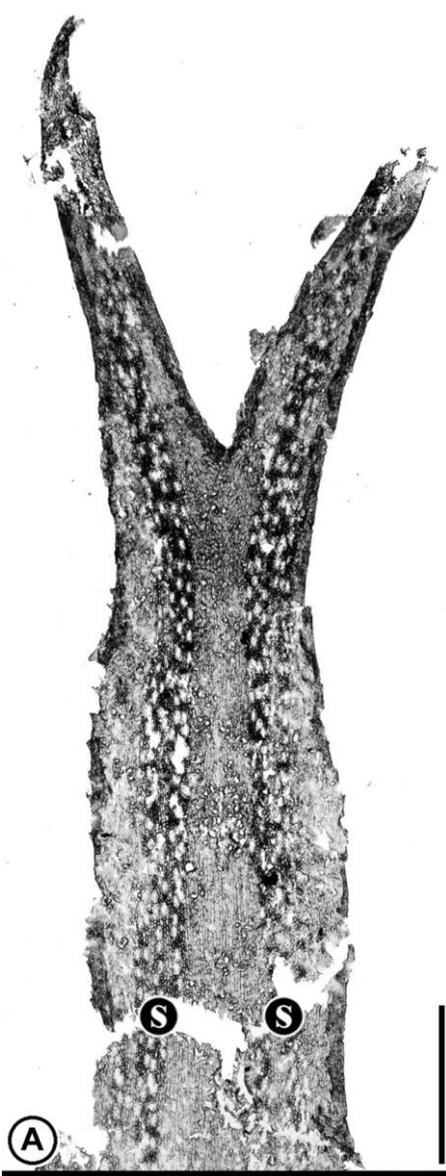
The Emporiaceae is composed of two genera (*Emporia* and *Hanskerpia*) with a total of three previously described species (*Emporia lockardii* [Mapes & Rothwell] Mapes & Rothwell emend. Hernandez-Castillo, Stockey, Rothwell & Mapes; *Emporia cryptica* Hernandez-Castillo, Stockey, Rothwell & Mapes; and *Hanskerpia hamiltonensis* Rothwell, Mapes and Hernandez-Castillo). The character combination displayed by *E. royalii* is most similar to *E. lockardii* and *E. cryptica* (tables 3–5), however, there are several differences among the three species. *Emporia royalii* differs from *E. lockardii* in having cuticular flanges on the adaxial surface of all leaves and leaflike appendages, a smaller number of pollen sacs (6–10 vs. 8–14), distinct attachment of bract and dwarf shoot at the level of divergence (fused at base vs. free throughout), contrasting length of bracts on ovulate cones (much longer vs. equal to longer), a distinct number (20–45 vs. 14–30) and location of sterile scales (mostly abaxial vs. all around) on dwarf shoot, and a smaller number of sporophylls (1–2 vs. 1–3) per dwarf shoot (tables 3–5).

Emporia royalii differs from *E. cryptica* in the distribution of leaf types on penultimate shoots (simple and forked vs. simple only), kind of heterophylly (age dependent vs. no heterophylly; see explanation below), type of stomata (monocyclic vs. monodicyclic), presence of cuticular accessories (cuticular flanges vs. none), number of pollen sacs per microsporophyll (6–10 vs. 4–8), length of bracts on ovulate cones (much longer vs. equal), number of sterile scales (20–45 vs. 20–25), and number of sporophylls (1–2 vs. 2) per dwarf shoot (tables 3–5).

Heterophylly among Conifers

The occurrence of different leaf morphologies at different positions on plants is a well-known phenomenon termed heterophylly. Heterophylly is more often recognized among flowering plants than conifers, but it has been identified in both living and extinct conifers for many years. For example, species of *Pinus* produce only long-shoot leaves on the stems of seedlings, but fascicles of short-shoot leaves characterize more mature shoots. Many species of the taxodiaceous Cupressaceae produce cupressoid (i.e., scalelike) leaves at the beginning of a growth season and taxodioid (i.e., needlelike) leaves toward the end of the growing season. Araucarian species tend to have “juvenile” leaves on seedlings and saplings, and (either one or a succession of) more “mature” leaf types on the more distal branches of reproductively mature trees (de Laubenfels 1972; Veillon 1978). Most conifers also pro-

abaxial surface and marginal trichomes (arrowhead). OUPH 18018, scale bar = 0.5 mm. D, Adaxial stomatal-free zone showing elongated epidermal cells and fused papillae on cuticular flanges (arrowheads). OUPH 18017, scale bar = 10 μ m. E, Penultimate leaf showing abaxial trichome bases (*t*) and elongated epidermal cells. OUPH 18019, scale bar = 40 μ m. F, Abaxial narrow stomatal band showing stomatal complexes with subsidiary cells and overarching papillae. OUPH 18018, scale bar = 40 μ m.



duce bud scales of a distinct morphology, but they are absent from the shoot tips of some conifers, particularly those with a more-or-less continuous pattern of growth (namely, syllepsis; Tomlinson 1983), including some living species of *Araucaria* and many extinct Paleozoic conifers (de Laubenfels 1972; Rothwell 1982; Stockey 1982).

Heterophylly has been recognized among walchian conifers for many years, some species producing both forked leaves and simple leaves (i.e., several species assigned to the illegitimate genus *Lebachia* sensu Florin [1927, 1938–1945]) and other species (e.g., *Ernestiodendron* spp. and *E. cryptica*) producing only simple leaves (Florin 1938–1945; Hernandez-Castillo et al. 2009b). More recently, different patterns of heterophylly have been recognized among walchian conifers. The leaves on ultimate branches of all walchian species are simple, reflecting a determinant growth pattern for the ultimate branches. Forked leaves occur in characteristic positions that differ from species to species, revealing differing patterns of growth exist among walchian conifers. In *Barthelia furcata*, forked leaves occur on penultimate and more proximal branches, but only leaves above a threshold size are forked (Rothwell and Mapes 2001). That pattern has been termed “size-dependent heterophylly” (Rothwell and Mapes 2001). In other species (e.g., *E. lockardii* and *H. hamiltonensis*), leaves on penultimate branches are forked regardless of size. That pattern has been termed “position-related heterophylly” (Rothwell et al. 2005). By contrast, *E. cryptica* lacks heterophylly, having simple leaves throughout the branching system (Hernandez-Castillo et al. 2009b). *Emporia royalii* displays a fourth pattern wherein some leaves on penultimate branches are forked regardless of their size, but forked leaves occur only on the largest branches. That pattern is associated with the phenomenon that successive branches on the stem of many living and extinct conifers are increasingly large and that forked leaves are produced on a branch only after it has exceeded a threshold size. In this article, we have termed that distribution of forked leaves “age-dependent heterophylly” because forked leaves occur on only those penultimate branches of *E. royalii* that are large enough to have been produced on trees of a minimum age.

Emporiaceae and the Evolution of Paleozoic Conifers

Among Paleozoic conifers, the Emporiaceae is the only family where all the members are characterized and understood as species of extinct plants (Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005; Hernandez-Castillo et al. 2009a, 2009b). Data derived from these reconstructions suggests that information about a combination of morphological, cuticular, and anatomical characters improves our chances of identifying and assessing inter-/intraspecies

variation and evolution among fossil conifers. Likewise, a fuller understanding of intraspecific variations among all of these characters, for a larger number of species of conifer plants also, will be most helpful for more fully understanding specific diversity and evolution of ancient conifers. The most important characters for this purpose appear to include growth architecture, cuticular diversity, pollen cone organization, and ovulate or seed cone organization.

The Emporiaceae consists of walchian conifers of small stature with lateral plagiotropic branches that display either age-dependent heterophylly (*E. royalii*) or position-dependent heterophylly (*E. lockardii* and *H. hamiltonensis*) or lack heterophylly (*E. cryptica*). Age-dependent heterophylly in *E. royalii* seems more complex than the position-dependent heterophylly displayed by *E. lockardii*. The differences between these two types of heterophylly are due to the presence of simple leaves on small-diameter penultimate shoots (from small- to medium-sized lateral branches) and forked leaves on large-diameter lateral branches (usually at the base of ovulate cones), suggesting a possible correlation with the size of branches (age dependency), where successively older branches are progressively larger. Although we do not have enough specimens to test this hypothesis in full, it is clear that early walchians were experimenting with different structural designs within a basic tree architectural model (Hernandez-Castillo et al. 2003, 2009a; G. R. Hernandez-Castillo, personal observation, 2003, 2008).

Growth architecture of *E. royalii* and previously described species of Emporiaceae, Thuydiaceae, and Utrechtiaceae conforms to Massart’s architectural model (Lausberg 2002; Hernandez-Castillo et al. 2003, 2009a, 2009b). *Emporia royalii* differs from other walchian plant species in having large lateral branches with ultimate shoots that are all oriented in the same direction (dihedral arrangement; Veillon 1978). Dihedral branches in *E. royalii* resemble branches of *Araucaria heterophylla* (Salisb.) Franco or *Araucaria bernieri* Buchholz (Veillon 1978; G. R. Hernandez-Castillo, personal observation, 2003, 2008). This type of branch is commonly found in the middle and apical regions of mature *A. heterophylla* trees and other species in the same genus that also conform to Massart’s model of tree architecture (Veillon 1978; G. R. Hernandez-Castillo, personal observation). This reveals that typical growth architectural features of living individuals of *A. heterophylla* (Massart’s model; heterophylly and dihedral arrangement) were already present in mature trees of the Emporiaceae and other Euramerican walchian conifers (i.e., Thuydiaceae and some Utrechtiaceae). Conifer diversity at Hamilton Quarry confirms the presence of distinct structural designs in early conifers, similar to those found in living representatives of the Araucariaceae and other conifer families (Florin 1951; de Laubenfels 1972; Veillon 1978; Grosfeld

Fig. 5 *Emporia royalii* sp. nov., cuticular macerations of leaves on penultimate and ultimate shoots. A, Adaxial surface of forked leaf on penultimate shoot showing two broad bands of stomata (S) separated by stomatal-free zone. OUPH 18322, scale bar = 0.5 mm. B, Adaxial surface of leaf of ultimate shoot showing subtriangular shape, two bands of stomata and stomatal-free zone. OUPH 18017, scale bar = 0.3 mm. C, Adaxial surface of leaf on penultimate shoot showing elongated epidermal cells (brackets) separating stomata and circular trichome bases (t). OUPH 18322, scale bar = 70 μ m. D, Adaxial surface of leaf on ultimate shoot showing stomatal band and papillate epidermal cells on both sides of the band. OUPH 18017, scale bar = 40 μ m.

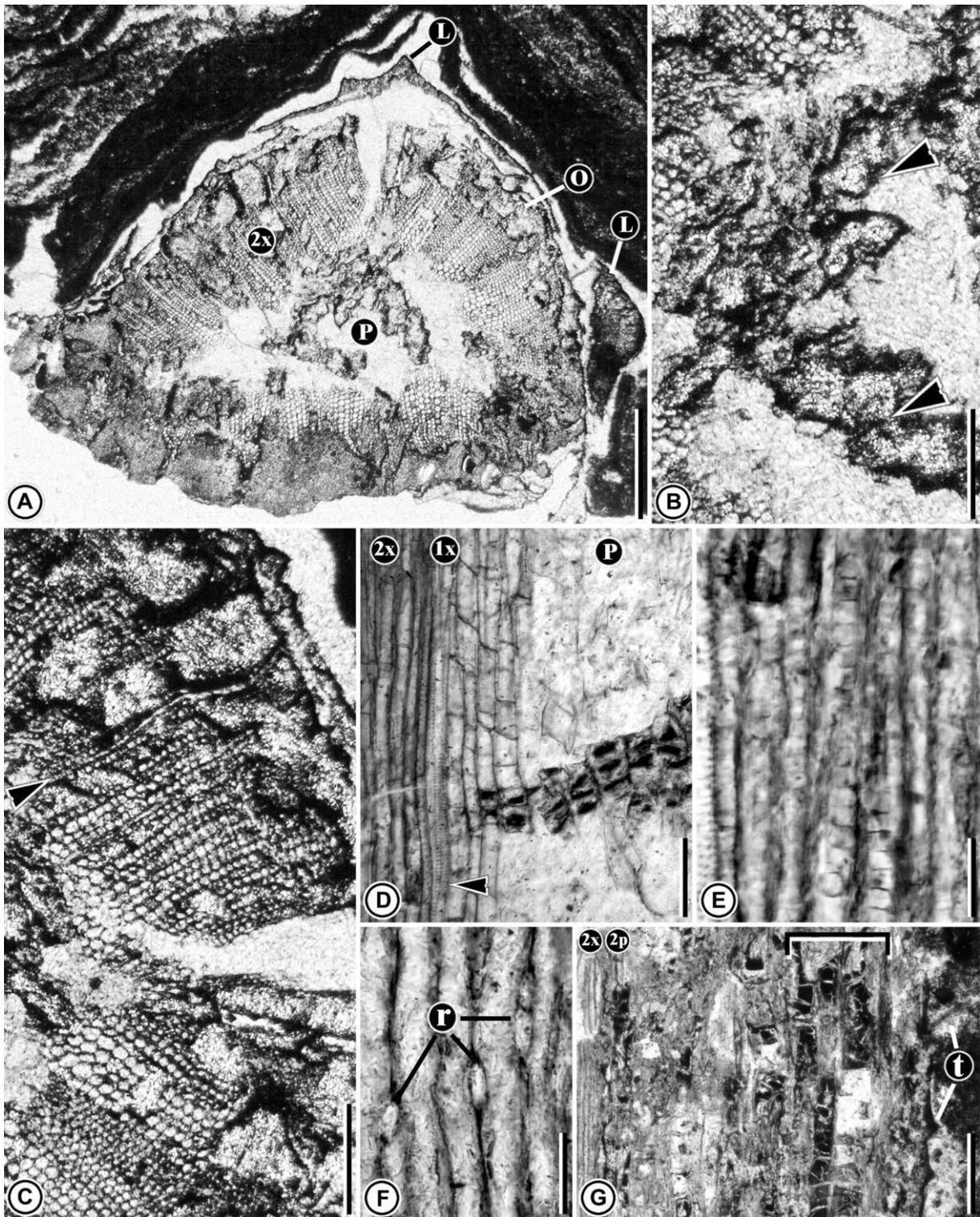


Fig. 6 *Emporia royalii* sp. nov., anatomy of penultimate axis. **A**, Cross section showing pith (*P* with secretory cells), secondary xylem (*2x*), outer cortex (*O*), and leaves (*L*). OUPH 18030, scale bar = 0.3 mm. **B**, Pith showing secretory cells (arrowheads). OUPH 18030, scale bar = 0.5 mm. **C**, Cross section of secondary xylem showing tracheids and rays (arrowhead). OUPH 18030, scale bar = 0.1 mm. **D**, Radial section showing secondary xylem (*2x*), primary xylem (*1x*) with helical thickenings on secondary walls (arrowhead), and pith with secretory cells. OUPH 18031, scale bar = 54 μ m. **E**, Radial section showing metaxylem (on left) and secondary xylem tracheids with circular bordered pits (on right). OUPH 18032, scale bar = 17 μ m. **F**, Tangential section showing uniseriate rays (*r*). OUPH 18032, scale bar = 15 μ m. **G**, Longitudinal section showing secondary xylem, secondary phloem area (*2p*), outer cortex with parenchyma cells and secretory cells (bracket), and epidermis with trichomes (*t*). OUPH 18032, scale bar = 64 μ m.

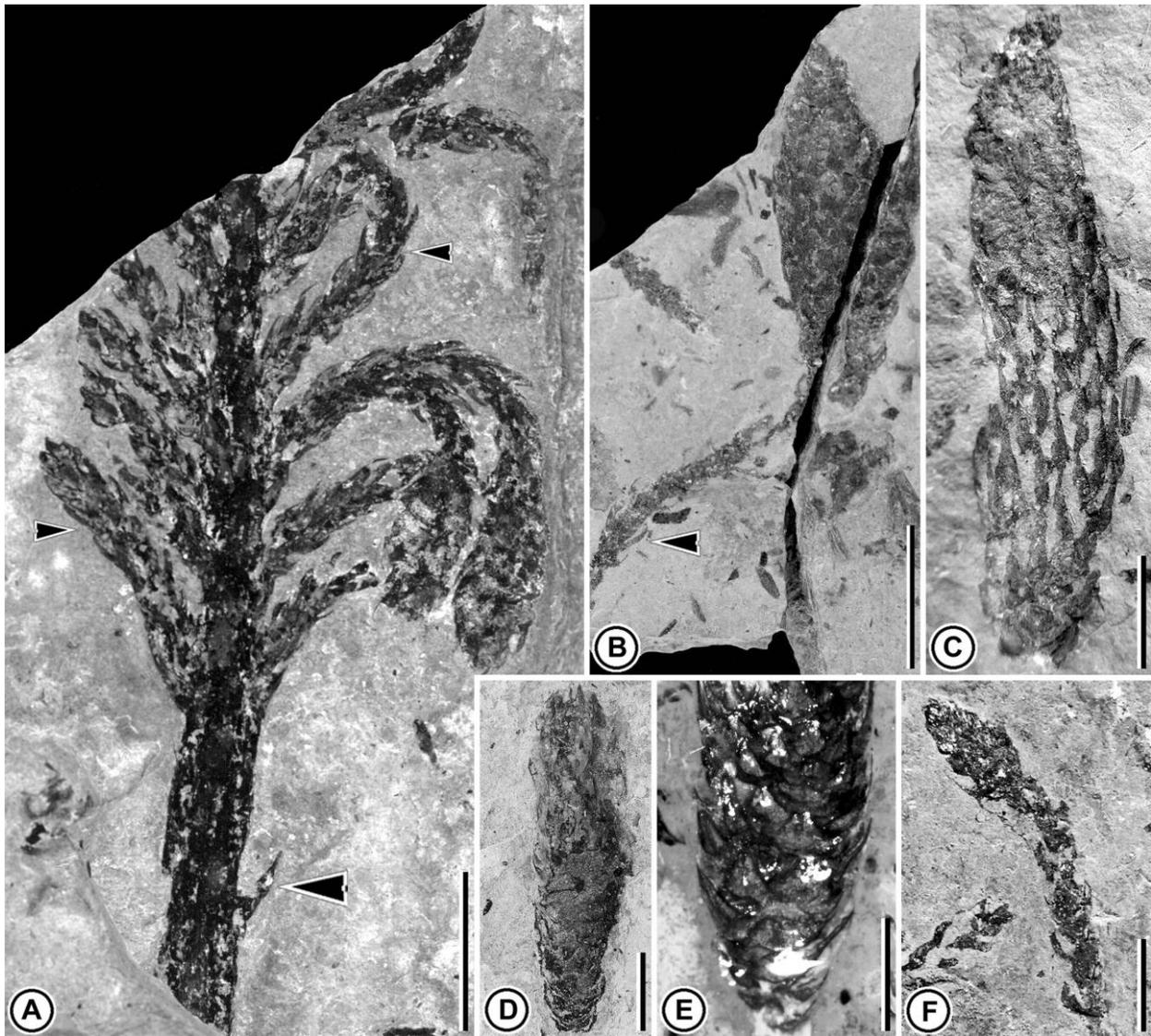


Fig. 7 *Emporia cryptica* sp. nov., pollen cones. **A**, Lateral branch showing ultimate shoots with terminal simple pollen cones. Note leaves on penultimate (large arrowhead) and ultimate shoots (small arrowheads). OUPH 18087, scale bar = 1 cm. **B**, Ellipsoidal cone attached to ultimate shoot (arrowhead). OUPH 18090, scale bar = 1 cm. **C**, Mature ellipsoidal cone with helically arranged microsporophylls. OUPH 18109, scale bar = 5 mm. **D**, Intermediate cone. OUPH 18110, scale bar = 5 mm. **E**, Intermediate pollen cone base showing microsporophylls and vegetative leaves at base. OUPH 18122, scale bar = 3 mm. **F**, Immature cone attached to ultimate shoot. OUPH 18133, scale bar = 5 mm.

et al. 1999; Hernandez-Castillo et al. 2003; G. R. Hernandez-Castillo, personal observation, 2008). Further work in Emporiaceae tree architecture may help in understanding growth architectural patterns in other Paleozoic walchian conifers from Euramerica.

Cuticular characters have been assessed for many Paleozoic conifers; however, the Emporiaceae, Bartheliaceae, and Thucydiaceae are the only families of reconstructed Paleozoic conifers for which the entire range of cuticular characters for leaves and leaflike organs has been fully analyzed for several species of extinct plants. Cuticular features of these species show two trends within early conifer plants. The first trend includes plants with vegetative and reproductive branches

bearing leaves with the same or similar cuticular features, such as stomatal structure and distribution, number of stomata per band, and number of subsidiary cells per stomatal complex. Examples of this trend can be found in members of the Emporiaceae and Bartheliaceae (table 1; Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005; Hernandez-Castillo et al. 2009a, 2009b). The second trend includes taxa with leaves on vegetative branches that have different cuticular patterns than leaves and leaflike appendages on reproductive branches within the same plant. This trend has been observed in the family Thucydiaceae, where bracts and sterile scales have different stomatal distribution than vegetative leaves on penultimate and ultimate shoots

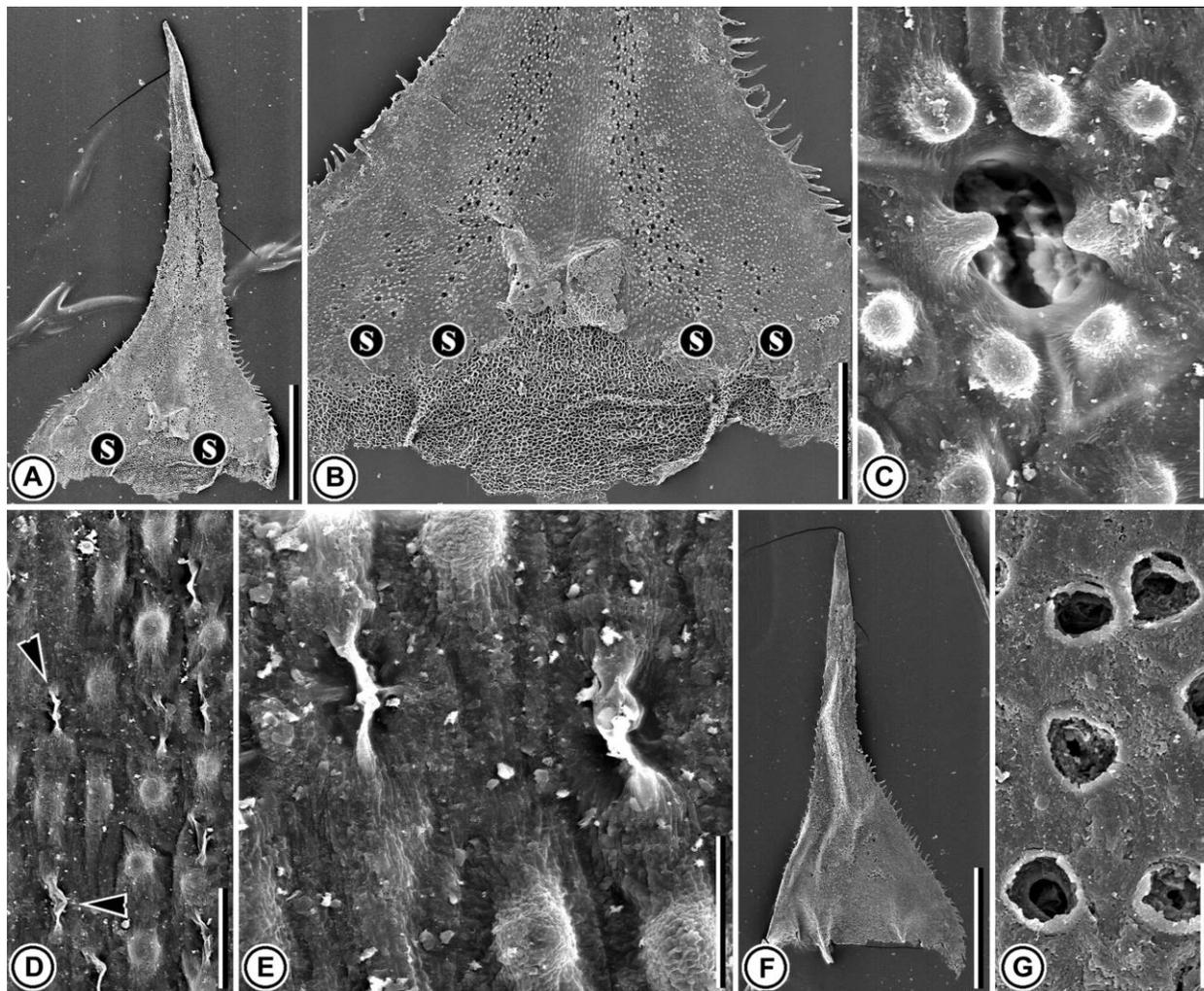


Fig. 8 *Emporia royalii* sp. nov., SEM microsporophylls. All specimens macerated from OUPH 18122. A, Narrowly triangular microsporophyll showing adaxial stomatal bands (S). Scale bar = 1 mm. B, Microsporophyll with two long and two short bands of stomata. Scale bar = 400 μ m. C, Stomatal complex showing six subsidiary cells with erect and overarching papillae. Scale bar = 10 μ m. D, Epidermal cells with normal papillae and cuticular flanges (arrowheads). Scale bar = 20 μ m. E, Close-up of adaxial cuticular flanges. Scale bar = 10 μ m. F, Narrowly triangular microsporophyll showing abaxial surface. Scale bar = 1 mm. G, Abaxial trichome bases. Scale bar = 20 μ m.

(Hernandez-Castillo et al. 2001b). Therefore, cuticles from isolated and/or fragmentary branches, where no organic connections and/or only a small number of specimens are known (e.g., Florin 1938–1945), are not necessarily diagnostic for accurately identifying species of walchian conifer plants.

Pollen cones in the Emporiaceae are simple and terminal on ultimate shoots. Cones have an axis bearing series of helically arranged microsporophylls with adaxial pollen sacs attached to the surface of the stalk (Mapes and Rothwell 1998; Hernandez-Castillo 2005; Rothwell et al. 2005). These cones resemble some Mesozoic conifer pollen cones such as *Darneya* Grauvogel-Stamm and *Kobalostrobus* Serlin, Delevoyas & Weber, where numerous pollen sacs are found on the adaxial surface or around the sporophyll stalk, respectively (Grauvogel-Stamm 1978; Serlin et al. 1981; Grauvogel-Stamm and Galtier 1998). However, such cones differ from those of living conifers in which the pollen sacs are uniformly

attached to the abaxial surface of the sporophylls. (Florin 1951; Mapes and Rothwell 1998; Hernandez-Castillo et al. 2001a). Thus, where known, adaxial pollen sacs characterize Euramerican Paleozoic walchian conifers, regardless of the microsporophyll's nature (leaflike or stalked with a heeled distal lamina). Number of pollen sacs per microsporophyll is also important for differentiating species in Emporiaceae and other walchian conifers (table 5). Therefore, number, position, and type of microsporophylls are crucial to assessing pollen cone diversity and evolution in conifers. The evolution of conifer pollen cones can be derived from understanding key characters and character states such as (a) pollen cone organization (compound, simple), (b) microsporophyll type (leaflike, stalked with heeled distal lamina), (c) pollen sac position (adaxial, abaxial), and (d) microgametophyte development and germination (prepollen, true pollen). However, pollen cone characters are often missing for Paleozoic spe-

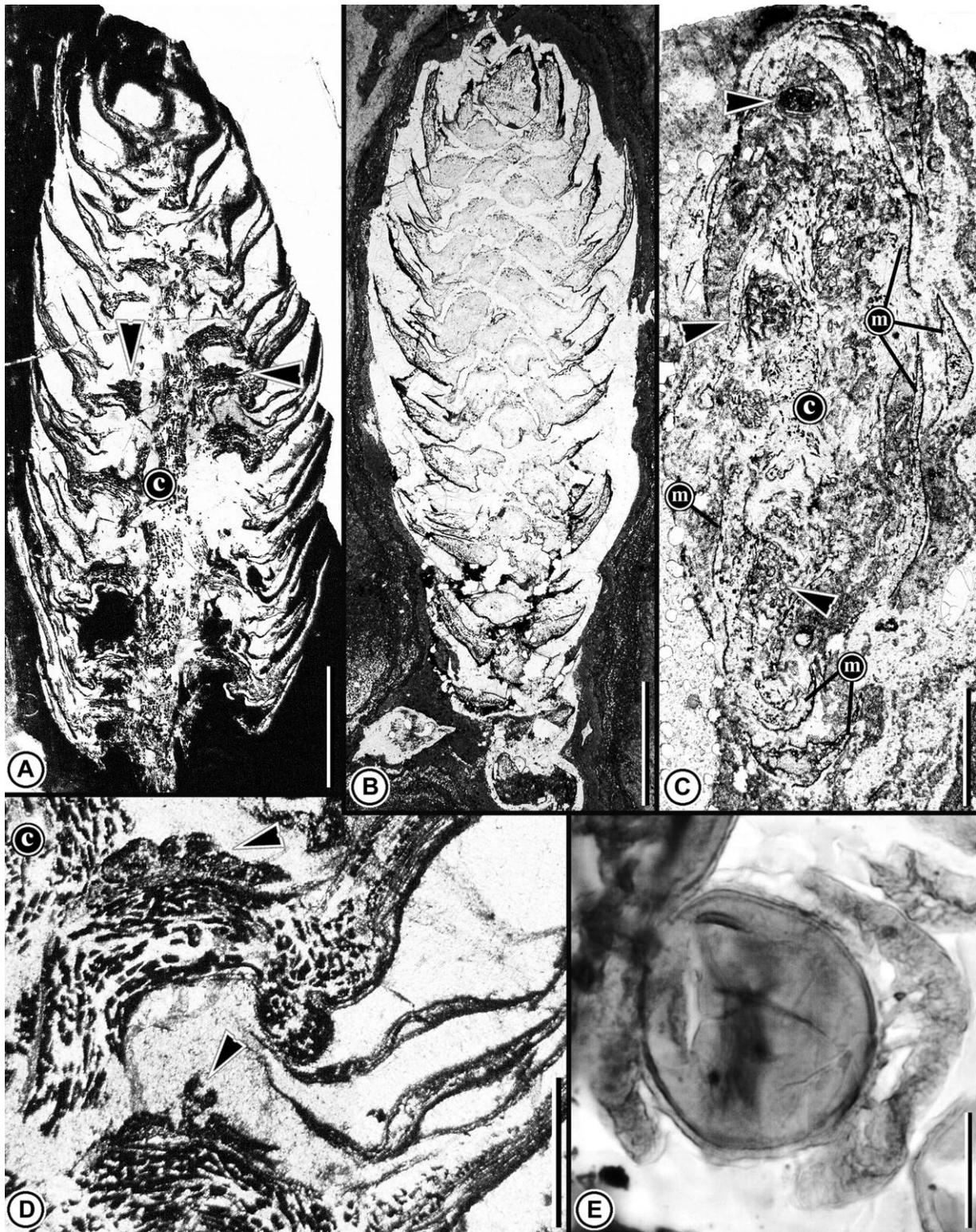


Fig. 9 *Emporia royalii* sp. nov., anatomy of pollen cones. **A**, Longitudinal section showing cone axis (*c*), microsporophylls with pollen sac bases (arrowheads). OUPH 18194, scale bar = 5 mm. **B**, Pollen cone showing cross sections (center) and longitudinal sections (margins) of microsporophylls. Note overall microsporophyll morphology. OUPH 18263, scale bar = 10 mm. **C**, Cross section showing cone axis (*c*), microsporophylls (*m*), and pollen sacs with enclosed prepollen (arrowheads). OUPH 18135, scale bar = 2.5 mm. **D**, Radial section showing microsporophylls with adaxial pollen sac bases on stalks (arrowheads). OUPH 18263, scale bar = 1.25 mm. **E**, Monosaccate *Potonieisporites* prepollen grains in pollen sac. OUPH 18142, scale bar = 40 μ m.

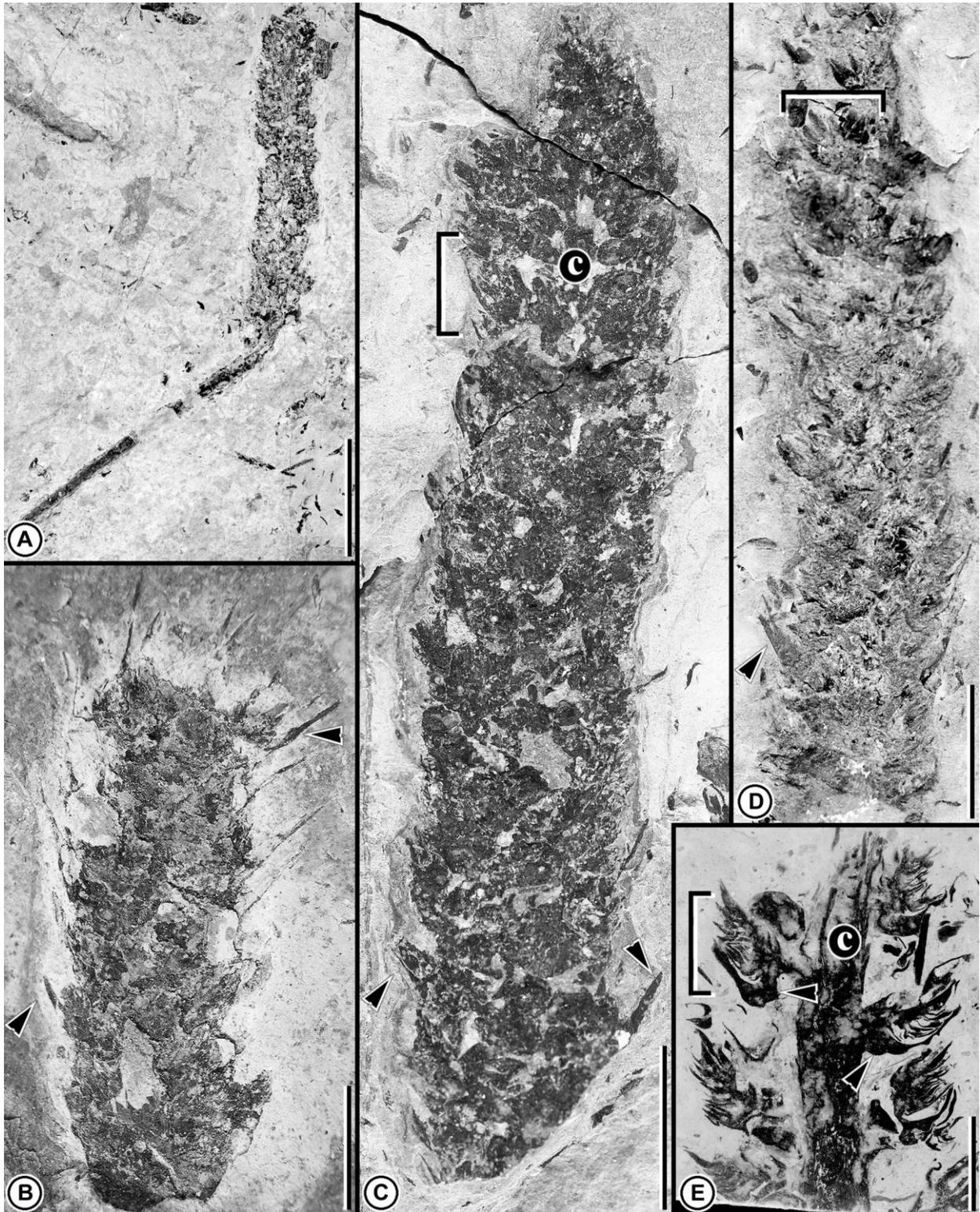


Fig. 10 *Emporia royalii* sp. nov., ovulate cones. *A*, Cone attached to penultimate shoot. OUPH 18282, scale bar = 3 cm. *B*, Cone showing bract tips (arrowheads). OUPH 18347, scale bar = 1 cm. *C*, Cone showing axis (*c*), bracts (arrowheads), and axillary dwarf shoots (bracket). Holotype, OUPH 18285, scale bar = 1 cm. *D*, Cone showing bract (arrowhead) and sterile scales in face view (bracket). OUPH 18293, scale bar = 1 cm. *E*, Longitudinal section showing axis, bracts (arrowheads), and axillary dwarf shoot (bracket). OUPH 18311, scale bar = 5 mm.

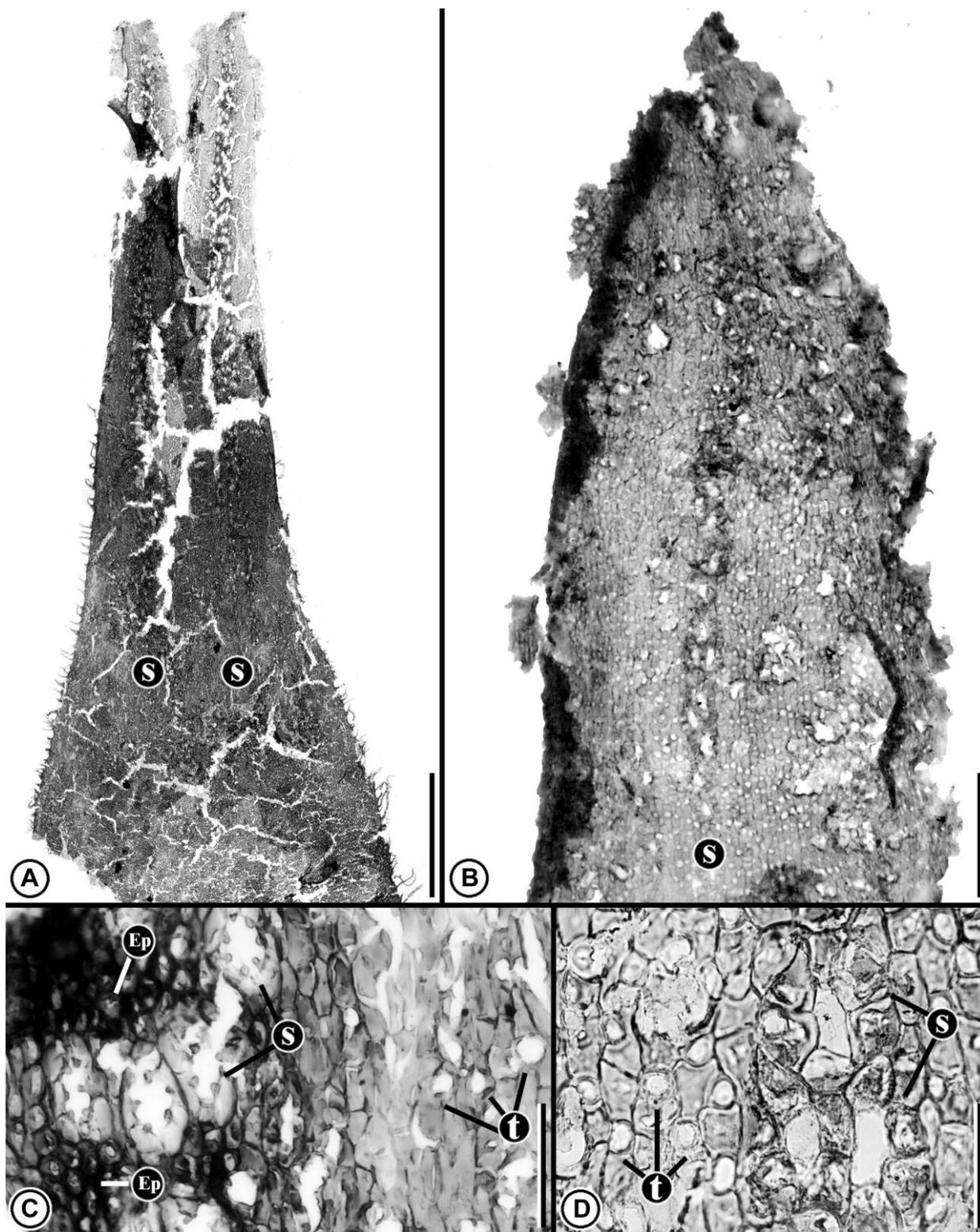


Fig. 11 *Emporia royalii* sp. nov., cuticular macerations of bracts (A, C) and sterile scales (B, D) from ovulate cones. A, Adaxial surface of forked bract showing two stomatal bands (S). OUPH 18315, scale bar = 1 mm. B, Abaxial surface of sterile scale showing narrow band of stomata. OUPH 18293, scale bar = 200 μ m. C, Adaxial surface of bract showing band of stomata, thick-walled cells between stomata (Ep), and trichome bases (t). OUPH 18315, scale bar = 600 μ m. D, Sterile scale abaxial surface showing trichome bases (t), and narrow stomatal band. OUPH 18293, scale bar = 45 μ m.

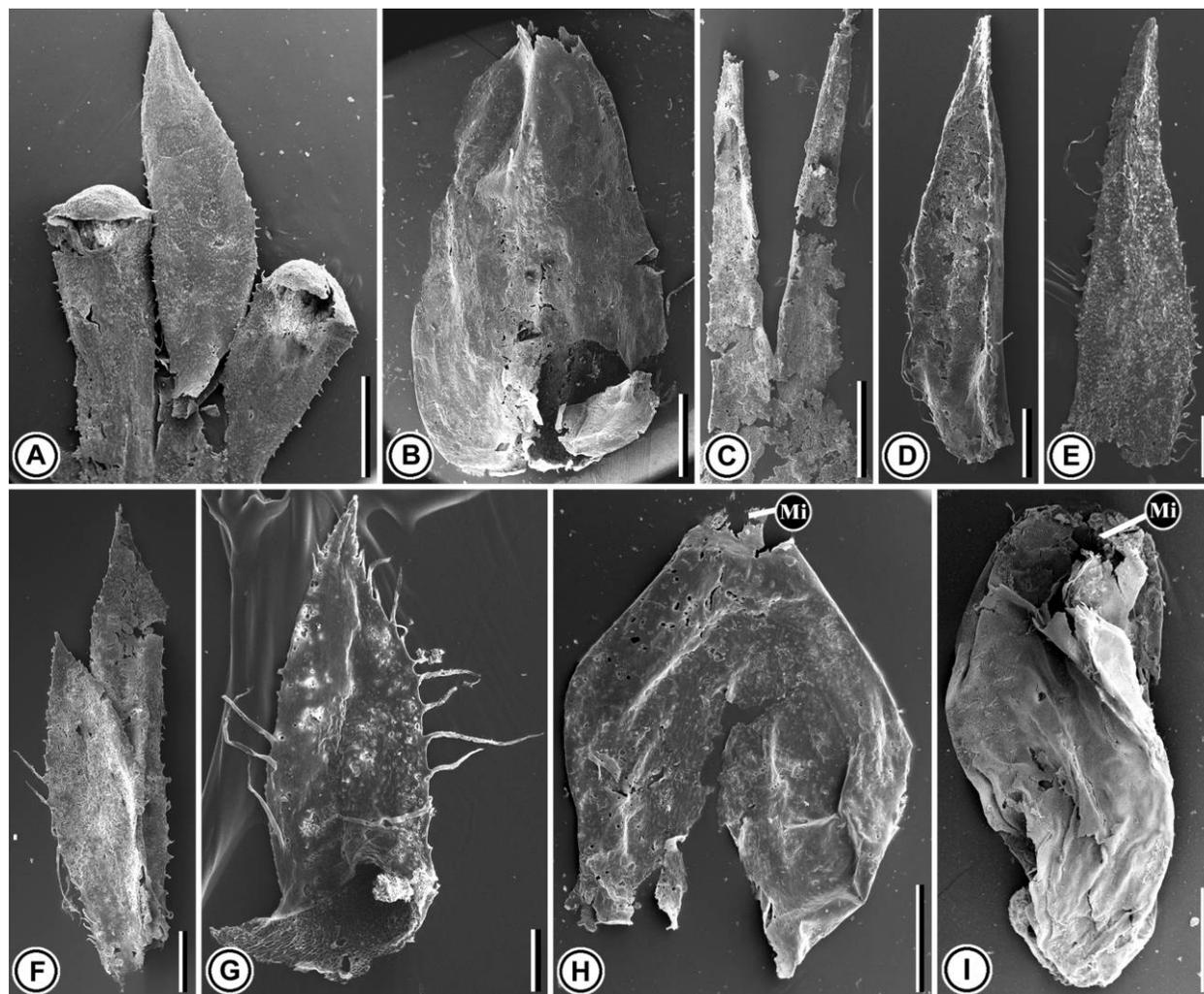


Fig. 12 *Emporia royalii* sp. nov., SEM of sporophylls (A), bracts (B, C), sterile scales (A, D–G), and seeds (H, I) from ovulate cones. All specimens macerated from OUPH 18293. A, Abaxial surface showing two sporophylls with seed scars and sterile scale. Scale bar = 1 mm. B, Abaxial surface of basal region of inflated bract. Scale bar = 1 mm. C, Adaxial surface of apical region of forked bract. Scale bar = 1 mm. D, Triangular sterile scale with marginal trichomes. Scale bar = 0.5 mm. E, Abaxial surface showing narrowly triangular shape and marginal trichomes. Scale bar = 1 mm. F, Abaxial surface showing two linear sterile scales with marginal trichomes. Scale bar = 1 mm. G, Abaxial surface showing trichome bases and marginal trichomes. Scale bar = 0.2 mm. H, Seed showing micropyle (Mi) and smooth surface. Scale bar = 1 mm. I, Seed showing micropyle. Scale bar = 0.5 mm.

cies, and more attention needs to be paid to this character in future conifer descriptions.

Prepollen grains of Emporiaceae are monosaccate and correspond to the sporae dispersae genus *Potoniaesporites* Bharadwaj (1964). Taggart and Ghavidel-Syooki (1988) described three prepollen types (*Potoniaesporites neglectus* Potonié et Lele, *Potoniaesporites granulatus* Bose et Kar, and an unknown species) from the Hamilton Quarry locality, but these cannot be accurately correlated to pollen cones of individual species due to their rather similar morphology and size (Hernandez-Castillo 2005). Variation among these grains is equivalent to variation surveyed by Bharadwaj (1964), and grains from the pollen sacs of several species need to be analyzed in more detail to understand intra-/interspecies variation before that feature can be used to differentiate Paleozoic conifer species.

Ovulate or seed cones in the family Emporiaceae are compound and bear distinct forked bracts subtending bilaterally symmetrical axillary dwarf shoots. Such dwarf shoots produce numerous sterile scales and a small number of interspersed sporophylls. However, ovulate cone organization in *Hanskerpia* and other walchian conifers (Hernandez-Castillo et al. 2001b, 2009a, 2009b; Rothwell et al. 2005) shows that Euramerican Paleozoic conifers had a broad diversity of ovulate cones (table 4; Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001). Furthermore, some of these reproductive structures were not even cones but fertile zones with the same organization (cone axis, bract, and axillary dwarf shoots) of traditional walchian conifer ovulate cones (Schweitzer 1996; Hernandez-Castillo et al. 2001b).

Species of the Emporiaceae currently provide the most complete evidence for the reproductive biology of Paleo-

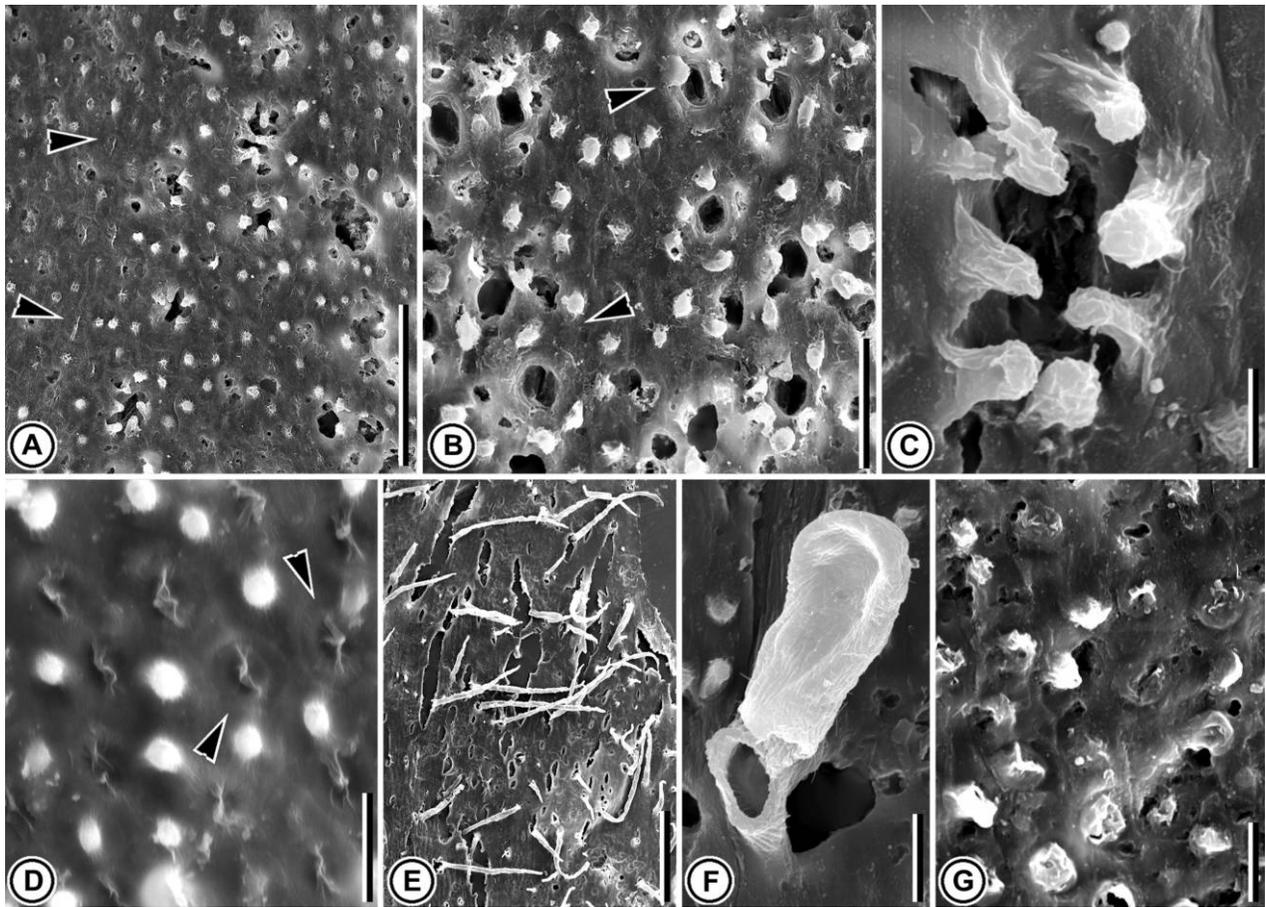


Fig. 13 *Emporia royalii* sp. nov., SEM of cuticular features of bracts (A, B) and sterile scales (C–G). All specimens macerated from OUPH 18293. A, Adaxial narrow band of stomata, cuticular flanges (arrowheads), and papillae. Scale bar = 100 μm . B, Adaxial stomatal band showing stomata (arrowheads) with erect to overarching papillae. Scale bar = 50 μm . C, Adaxial surface showing stomatal complex with overarching papillae on subsidiary cells. Scale bar = 10 μm . D, Adaxial surface showing erect papillae and cuticular flanges (arrowheads). Scale = 500 μm . E, Abaxial surface showing long trichomes. Scale bar = 100 μm . F, Sterile scale showing short broad trichome. Scale bar = 20 μm . G, Sterile scale showing small abaxial trichome bases. Scale bar = 10 μm .

zoic conifers. Different species of the family have exquisitely preserved ovules and seeds that allow us to describe and compare features of the integument, pollen chamber, nucellar beak, megagametophytes, and embryos. Furthermore, the presence of well-preserved polycotyledonary embryos serve as the oldest evidence for seed dormancy in conifers (Mapes et al. 1989; Hernandez-Castillo et al. 2009b). Similarly, the large prepollen grain size versus small micropyle size suggests a pollination-drop mechanism in Paleozoic conifers (Mapes and Rothwell 1984; Kerp et al. 1990; Hernandez-Castillo et al. 2009a, 2009b). This pollination mechanism is similar to that of conifers with saccate pollen and a pollination-drop mechanism (Owens and Blake 1983; Owens et al. 1987; Runions et al. 1999; Tomlinson and Takaso 2002). Thus, suggesting a similar reproductive biology to that of living conifers, with the most important difference being microgametophyte development and pollen germination (distal vs. proximal; Mapes and Rothwell 1984; Kerp et al. 1990; Hernandez-Castillo et al. 2009b).

Conclusions

Emporia royalii displays an additional novel combination of characters among walchian conifer species and now may be added to the growing list of reconstructions that establish extinct plant species concepts for conifers from Paleozoic localities (Hernandez-Castillo et al. 2001b, 2009a, 2009b; Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005). As a result, we have a better understanding of Paleozoic conifer growth architecture, ranges of variation within mature vegetative and fertile organs (leaves, pollen cones, and ovulate cones), developmental variations, and reproductive biology for these important paleofloristic elements. This information provides a sound basis for modifying and improving systematics and for inferring the evolution of Paleozoic conifers. *Emporia royalii* is the fifth and final conifer plant to be reconstructed from the Hamilton Quarry (Rothwell and Mapes 2001; Rothwell et al. 2005; Hernandez-Castillo et al. 2009a, 2009b). The Hamilton Quarry has the largest number of Paleozoic conifers ever reconstructed from

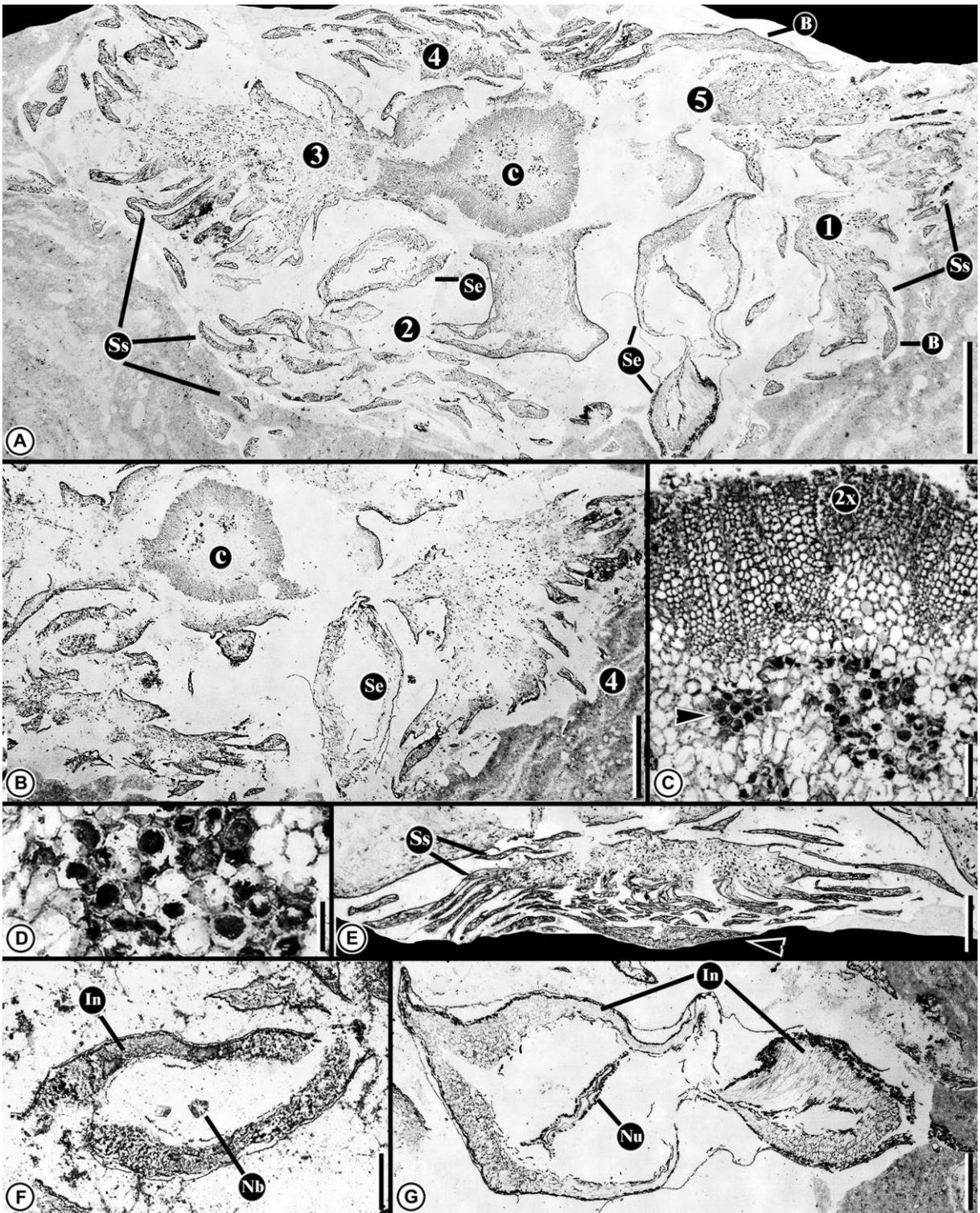


Fig. 14 *Emporia royalii* sp. nov., ovulate cone anatomy. A. Cross section showing cone axis (C), bracts (B), axillary dwarf shoots (numbers) with sterile scales (Ss), and seeds (Se). OUPH 18347, scale bar = 4 mm. B. Cross section showing cone axis (C) and axillary dwarf shoot with seed. OUPH 18375, scale bar = 2 mm. C. Cone axis showing pith with secretory cells (arrowhead), primary bundles, and secondary xylem (2x). OUPH 18355, scale bar = 0.3 mm. D. Cross section of pith with secretory cells. OUPH 18376, scale bar = 0.15 mm. E. Cross section of axillary dwarf shoot showing subtending bract (arrowhead) and several sterile scales. OUPH 18369, scale bar = 1.3 mm. F. Seed showing integuments (In) and nucellar beak (Nb) of pollen chamber. OUPH 18355, scale bar = 0.8 mm. G. Seeds showing integuments and collapsed nucellus (Nu). OUPH 18365, scale bar = 1 mm.

Table 1
Comparison of Morphological and Cuticular Characters of Leaves on Vegetative and Fertile Organs of *Emporia royaltii* sp. nov

Organs/characters	Morphology				Stomata			Papillae			
	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Structure	Distribution (adaxial/abaxial)	No. stomata per band	Subsidiary cell no.	Subsidiary cells	Epidermal cells	Trichome bases (adaxial/abaxial)
Leaves on penultimate shoots	Nt, Li, Fr	Ss, Sss	1.6-5.3	.3-1.5	Monocyclic, 2 long bands/2 narrow bands Cu fla	2 long bands/2 individual rows	2-6	5-6	Overarching	Abundant	None, few/abundant
Leaves on ultimate shoots	Nt, Li	Sss, Sc	1.6-4.5	.6-1.7	Monocyclic, 2 long bands/2 narrow bands Cu fla	2 long bands/2 individual rows	2-8	6-8	Erect, overarching	Abundant	None/abundant
Leaves on branches with attached to pollen cones	Nt, Li	Sss, Sc	1.2-2.5	.3-1.4	Monocyclic, 2 long bands/2 narrow bands Cu fla	2 long bands/2 individual rows	2-6	6-8	Overarching	Abundant	None/abundant
Microsporophylls	Nt	Sc	.25-4.1	2.0-2.6	Monocyclic, 2-4 bands/none or few scattered Cu fla	2-4 bands/none or few scattered	2-4	4-6	Erect, overarching	Abundant	None/abundant
Leaves on branches with attached to ovulate cones	Nt, Li, Fr	Ss, Sss	1.7-5.0	.4-1.4	Monocyclic, 2 long bands/2 narrow bands Cu fla	2 long bands/2 individual rows	2-6	5-6	Overarching	Abundant	None, few/abundant
Bracts of ovulate cones	Nt, Li, Fr	Li, Sc	1.6-2.1	2.1-4.0	Monocyclic, 2 long bands/2 narrow bands Cu fla	2 long bands/2 individual rows	2-6	6-7	Overarching	Abundant	None/abundant
Sterile scales of ovulate cones	Tr, Nt	Ss, Sss	1.6-6.6	.5-2.0	Monocyclic, 2 long bands/2 narrow bands Cu fla	2 long bands/2 individual rows	1-2	5-7	Erect	Abundant	None/abundant

Note. Fr = forked tip, Li = linear, Nt = narrowly triangular, Sc = slightly concave, Ss = S-shaped, Sss = slightly S-shaped, Tr = triangular, Cu fla = cuticular flanges.

Table 2
***Emporia royalii* sp. nov. Whole-Plant Characters**

Growth architecture/vegetative branches	Stem anatomy	Pollen cones	Ovulate cones	Sterile scales and seeds
Stem: orthotropic	Stele type: endarch strele	Cone type: simple	Cone type: compound	Sterile scale number: 20–45
Branch type: plagiotropic	Pith organization: secretory cells forming nests or plates	Cone position: terminal	Cone position: terminal	Sterile scale organization: interspersed among sporophylls
Leaf morphology: simple and forked	Primary xylem: tracheids with helically to scalariform wall thickenings	Order of attached branch: ultimate shoot	Order of attached branch: penultimate shoots	Sterile scale location: all around, mostly abaxial
Heterophylly: age dependent	Wood: picroxylic	Leaves on attached branch: same as vegetative ultimate leaves	Leaves on attach branch: forked, similar to leaves on penultimate shoots	Sporophyll number: 1–2
Leaf distribution: penultimate shoots with simple and forked leaves	Secondary xylem: tracheids uni- to biseriata circular to slightly hexagonal bordered pits	Microsporophyll type: simple	Bract type: forked	Sporophyll organization: free from sterile scales
Leaf distribution: ultimate shoots with simple leaves	Wood rays: uni- to biseriata, 1–2 cells high	Microsporophyll shape: stalked with a heeled distal lamina	Bract length: much longer than axillary dwarf shoot	Seed position and type: terminal, inverted
Stomatal complexes: monocyclic	Bark: scarce	Microsporophyll stomatal distribution: 2–4 adaxial narrow bands/abaxial trichome bases	Bracts stomatal distribution: amphistomatic, 2 long bands/ 2 individual rows to narrow bands	Seed shape and symmetry: ellipsoidal, bilateral
Leaf stomatal distribution: amphistomatic, 2 long adaxial bands and 2 abaxial rows to narrow bands		Pollen sacs position and number: adaxial on stalk, 6–10	Bract attachment to dwarf shoot: fused at base	Seed ornamentation: smooth
Cuticular features: cuticular flanges on stomatal-free zones		Prepollen grains: monosaccate, <i>Potamoisporites</i> Bharadwaj	Dwarf shoot symmetry: bilateral, dorsiventral	Seed anatomy: 3-layered integument, simple pollen chamber, and nucellar beak

Table 3

Comparison of Growth Architecture, Leaf, and Pollen Cone Characters of *Emporia royalii* sp. nov. and Other Paleozoic Conifers

Taxa-distribution/ characters	Stem	Lateral branches	Penultimate leaves	Ultimate leaves	Heterophylly ^a	Stomatal distribution (vegetative leaves)	Stomatal pattern (adaxial/abaxial)	Pollen cone	Pollen cone attached branch/ leaves	Microsporophylls (type, shape, stomatal distribution)	Pollen sacs	Sources
<i>Emporia royalii</i> , U.S.A.	Orthotropic	Plagiotropic	Simple and forked	Simple	Age dependent	Amphistomatic, monocyclic	2 long bands/2 narrow bands or individual rows	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, stalked-heel, 2 2-4 narrow bands/ absent	Adaxial, 6-10	
<i>Emporia cryptica</i> , U.S.A.	Orthotropic	Plagiotropic	Simple	Simple	Absent	Amphistomatic, monocyclic, dicyclic	2 bands/2 narrow bands	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, stalked-heel, 2 narrow bands/absent	Adaxial, 4-8	Hernandez-Castillo 2005; Hernandez- Castillo et al. 2009b
<i>Emporia lockardii</i> , U.S.A.	Orthotropic?	Plagiotropic	Simple and forked	Simple	Position dependent	Amphistomatic, monocyclic	2 bands/2 short, narrow bands, individual rows	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, stalked-heel, 2-4 narrow bands/ absent	Adaxial, 8-14	Mapes and Rothwell 1984, 1991; Hernandez-Castillo et al. 2009a
<i>Hanskerpia hamiltonensis</i> , U.S.A.	Orthotropic?	Plagiotropic	Forked	Simple	Position dependent	Amphistomatic, monocyclic	Parallel rows/ parallel rows	? , ?	? , ?	? , ? , ?	? , ?	Rothwell et al. 2005
<i>Thuexia mahoningensis</i> , U.S.A.	Orthotropic	Plagiotropic	Simple	Simple	Absent	Adaxial, monocyclic	2 bands/absent	Compound, terminal	Ultimate, simple as veg. ult. leaves	No microsporophylls present	Terminal, 3-4	Hernandez-Castillo et al. 2001b
<i>Utrecthia floriformis</i> , G	Orthotropic?	Plagiotropic	Forked	Simple	Position dependent	Amphistomatic, monocyclic	2 bands/2 bands	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, stalked-heel, ?	Adaxial, ?	Mapes and Rothwell 1991.
<i>Walchia garnettensis</i> , U.S.A.	?	Plagiotropic	Simple	Simple	Absent	Amphistomatic, monocyclic	2 long bands/ few scattered	Simple, terminal	? , ?	Simple, ? , 1-2 narrow bands/2 narrow bands forming rows distally	? , ?	Winston (1984) reconstruction needed
<i>Otoevia hypnoides</i> , G ?	?	Plagiotropic	Forked	Simple	Position dependent	Primarily adaxial, mono-inc. dicyclic	2 bands/scattered	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, stalked-heel, 2 long bands/ few stomata groups	Adaxial, ?	Kerp et al. 1990
<i>Ernstiodendron fliciforme</i> , G, F	?	Plagiotropic	Simple	Simple	Absent	Amphistomatic, mono-inc. dicyclic	Parallel rows/ parallel rows	Simple, Terminal	Ultimate, simple as veg. ult. leaves	Simple, stalked-heel, ?	? , ?	Florin 1938-1945
<i>Barbelia furcata</i> , U.S.A.	?	Irregular	Forked	Simple and forked	Size dependent	Adaxial, monocyclic	2 bands/absent	Simple, terminal	Ultimate, forked as some veg. leaves	Forked, leafy, 2 long bands with rows/absent	Adaxial, ?	Rothwell and Mapes 2001

Note. Characters that differ from those of *E. royalii* are underlined, and overlapping characters are recorded in italics. Stalked-heel = microsporophyll composed of a stalk and a heeled distal lamina; veg. ult. = vegetative ultimate; mono-inc. dicyclic = monocyclic to incompletely dicyclic. Geographic locations of best specimens known, F = France, G = Germany, U.S.A. = United States.

^a Heterophylly = where two distinctive types of leaves are known; see types in Hernandez-Castillo et al. 2001b.

Table 4
Comparison of Prepollen and Ovulate Cone Characters of *Emporia royalii* sp. nov. and Other Paleozoic Conifers

Taxa/characters	Prepollen	Compound ovulate organ	Attached branch to OCFZ and leaves	Leaves on attached shoot		Bract	Bract and ovuliferous dwarf shoot	Sterile scale position/number	Sporophyll position/number	Ovules/seeds		Sources
				Somata type	Stomatal distribution					Position, type	Shape, symmetry	
<i>Emporia royalii</i>	<i>Potoniaisporites</i> monosaccate	Cone, terminal	Penultimate, forked	Amphistomatic, monocyclic	2 long bands/ 2 individual rows to narrow bands	Forked, much longer than dwarf shoot	Fused at base	All around mostly abaxial, 20–45	Interspersed with SS, 1–2	Terminal, inverted	Ellipsoidal, bilateral	
<i>Emporia cryptica</i>	<i>Potoniaisporites</i> monosaccate	Cone, terminal	Penultimate, simple	Amphistomatic, monocyclic, dicyclic	2 long, broad bands/2 narrow bands	Forked, equal to dwarf shoot	Fused at base	All around mostly abaxial, 20–25	Interspersed with SS, 2	Terminal, inverted	Ellipsoidal, bilateral	Hernandez-Castillo 2005; Hernandez-Castillo et al. 2009b
<i>Emporia lockardii</i>	<i>Potoniaisporites</i> monosaccate	Cone, terminal	Penultimate, forked	Amphistomatic, monocyclic	2 bands/2 short, narrow, individual rows	Forked, equal to longer than dwarf shoot	Separate throughout	All around, 14–30	Interspersed with SS, 1–3	Terminal, inverted	Ellipsoidal, bilateral	Mapes and Rothwell 1984, 1991; Hernandez-Castillo et al. 2009a
<i>Hanskerpia hamiltonensis</i> ? , ?	?	Cone/zone, ?	Penultimate, forked	Amphistomatic, monocyclic	Parallel rows/parallel rows	Forked, much longer than dwarf shoot	Fused at base	All around, <15?	Interspersed with SS, 1–2	Terminal, inverted	Ellipsoidal, bilateral	Rothwell et al. 2005
<i>Thuclia mabonngensis</i>	<i>Potoniaisporites</i> Monosaccate	Fertile zone, intercalary	Penultimate, simple	Adaxial, monocyclic	2 bands/absent	Simple, longer than dwarf shoot	Separate throughout	All around, 10–15	Terminal, 3–4	Terminal, inverted	Ellipsoidal, bilateral	Hernandez-Castillo et al. 2001b
<i>Utrecthia floriformis</i>	<i>Potoniaisporites</i> monosaccate	Cone, terminal	Penultimate, forked	Amphistomatic, monocyclic	2 bands/2 bands	Forked, longer than dwarf shoot	Separate throughout	All around?, >10	Terminal, 1	Terminal, inverted	Ellipsoidal, bilateral	Mapes and Rothwell 1991
<i>Walchia garnettensis</i>	<i>Potoniaisporites</i> monosaccate	Cone, Terminal	Penultimate, simple?	Amphistomatic?, monocyclic	2 bands/?	Forked, equal to longer than dwarf shoot	?	?, <5?	?, ≥3?	?, ?	?, ?	Winston 1984, reconstruction needed
<i>Otoicia hypnoides</i>	<i>Potoniaisporites</i> monosaccate	Cone, terminal	Penultimate, simple?	Primarily adaxial, monocyclic	2 bands/few groups	Forked, longer than dwarf shoot	Separate throughout	All around?, 12–18	Interspersed with SS, 2	Terminal, inverted	Ellipsoidal, bilateral	Kerp et al. 1990
<i>Ernstiodendron fliciforme</i> ? , ?	?	Cone, terminal	Penultimate, simple w ribleaf scar	Amphistomatic, mono-inc. dicyclic	Parallel rows/parallel rows	Forked, longer than dwarf shoot	Separate throughout	All around?, 5–10	Terminal, 1	Terminal, inverted	Ellipsoidal, bilateral	Florin 1938–1945
<i>Barbelia furcata</i>	<i>Potoniaisporites</i> monosaccate	Fertile zone, intercalary	Penultimate, Forked	Adaxial, monocyclic	2 bands/absent	Forked, longer than dwarf shoot	Separate throughout	All around, >10	Interspersed with SS, ?	Terminal, inverted?	Ellipsoidal, bilateral	Rothwell and Mapes 2001

Note. Characters that differ from those of *E. royalii* are underlined, and overlapping characters are recorded in italics. SS = sterile scales; OCFZ = ovulate cone/fertile zone; mono-inc. dicyclic = monocyclic to incompletely dicyclic; stomatal distribution indicates adaxial/abaxial surfaces.

Table 5
Comparison of Diagnostic Characters among *Emporia* Species at Hamilton Quarry, Kansas

Taxa	Leaf and leaflike appendages			Internal anatomy		Pollen cone		Ovulate cone			Sources	
	Growth architecture	Cuticles on adaxial surface	Secretory cells	Secondary xylem (tracheids)	Vascular rays	Pollen sac number	Pollen cone number	Bract type and length	Bract/dwarf shoot attachment	Sterile scale position		Sterile scale number
<i>Emporia royalii</i>	Age dependent	2 long bands of stomata, monocyclic, Cu fla	Sclerotic nests/plates	Uniseriate to biseriate, circular to slightly hexagonal bordered pits	1–2 cells high	6–10	6–10	Forked, much longer than dwarf shoot	Fused at base	All around, mostly abaxial	20–45	1–2
<i>Emporia cryptica</i>	Absent	2 bands of stomata, monocyclic-dicyclic, REC	Sclerotic nests/plates	Multiseriate with hexagonal bordered pits	1–3 cells high	4–8	4–8	Forked, equal to dwarf shoot	Fused at base	All around, mostly abaxial	20–25	2
<i>Emporia lockardii</i>	Position dependent	2 bands of stomata, monocyclic, REC	Resin rodlets or sclerotic nests	Uniseriate to biseriate circular bordered pits	1–8 cells high	8–14	8–14	Forked, equal to slightly longer than dwarf shoot	Free	All around	14–30	1–3

Note. Characters that differ from those of the type species *E. royalii* are underlined; overlapping characters are recorded in italics. Cu fla = cuticular flanges, REC = regular epidermal cells. Pollen cones are attached to branches of ultimate order, while ovulate cones are attached to branches of penultimate order.

a single material source. In that regard, plants from the locality have made a major contribution to the first phylogenetic analysis for species of conifer plants (Rothwell et al. 2005), making the Emporiaceae the best-known family of Paleozoic conifers worldwide.

Acknowledgments

We thank Royal Mapes for his help, enthusiasm, and dedication in collecting material for over 30 years; Zhao-Hua Liu (Ohio University) for rendering some cuticle preparations; George Braybrook, Rakesh Bhatnagar, and Jack Scott

(University of Alberta) for some SEM assistance; Lance Carr (Mountain Range Nursery, Dapto) for his help in surveying and collecting data of *Araucaria heterophylla* trees in Australia; and Jean Galtier (CIRAD, Montpellier) for thoughtful discussions and additional bibliography on European Carboniferous-Permian geology, stratigraphy, and paleobotany. This work was supported in part by Consejo Nacional de Ciencia y Tecnología (CONACyT) grants 050213 and 054521 to G. R. Hernandez-Castillo, National Science Foundation grant EF-0629819 to G. W. Rothwell, G. Mapes, and R. A. Stockey, and Natural Sciences and Engineering Research Council grant A-6908 to R. A. Stockey.

Literature Cited

- Bharadwaj DC 1964 *Potomiesporites* Bhard., ihre Morphologie, Systematik und Stratigraphie. Fortschr Geol Rhein Westfalen 12: 18–27.
- Bridge TE 1988 Geology and stratigraphy of the Hamilton Quarry area. Pages 27–35 in G Mapes, RH Mapes, eds. Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area in southeastern Kansas. Kans Geol Surv Guide Ser 6.
- Busch RM, MA Bogina, MH Clark 1988 Genetic stratigraphy of fossil localities. Pages 59–65 in G Mapes, RH Mapes, eds. Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area in southeastern Kansas. Kans Geol Surv Guide Ser 6.
- Clement-Westerhof JA 1984 Aspects of Permian palaeobotany and palynology. IV. The conifer *Ortiseia* Florin from the Val Gardena Formation of the Dolomites and the Vicentian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Göeppert) Schimper. Rev Palaeobot Palynol 41:51–166.
- 1987 Aspects of Permian palaeobotany and palynology. VII. The Majoniaceae, a new family of Late Permian conifers. Rev Palaeobot Palynol 52:375–402.
- 1988 Morphology and phylogeny of Paleozoic conifers. Pages 298–337 in CB Beck, ed. Origin and evolution of gymnosperms. Columbia University Press, New York.
- de Laubenfels DJ 1972 Flore de la Nouvelle Calédonie et dépendances. Gymnosperms. Vol 4. Muséum National d'Histoire Naturelle, Paris.
- DiMichele WA, RB Aronson 1992 The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. Evolution 46:807–824.
- Fahrer TR 1991 Paleocology and sedimentology of the Late Carboniferous (Pennsylvanian) Hamilton Lagerstätte, Greenwood County, Kansas. MS thesis, Ohio University, Athens.
- Fahrer TR, RH Mapes, G Mapes 1990 Geometry of the Late Carboniferous Hamilton Lagerstätte, Greenwood County, Kansas. Geol Soc Am Abstr Program 22:A6.
- Feldman HR, AW Archer, EP Kvale, CR Cunningham, CG Maples, RR West 1993 A tidal model of Carboniferous Konservat-Lagerstätten Formation. Palaios 8:485–495.
- Florin R 1927 Preliminary descriptions of some Palaeozoic genera of Coniferae. Arkiv Bot 21:1–7.
- 1938–1945 Die Koniferen des Oberkarbons und des unteren Perms. I–VII. Palaeontogr 85B:1–729.
- 1950 Upper Carboniferous and Lower Permian conifers. Bot Rev 16:258–282.
- 1951 Evolution in cordaites and conifers. Acta Hort Berg 15: 285–388.
- French JA, WL Watney, JE Anderson 1988 Stratigraphic and sedimentologic considerations relating to the fossiliferous limestones (Upper Pennsylvanian?) at Hamilton Quarry, Greenwood County, Kansas. Pages 37–58 in G Mapes, RH Mapes, eds. Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area in southeastern Kansas. Kans Geol Surv Guide Ser 6.
- Galtier J, AC Scott, JH Powell, BW Glover, CN Waters 1992 Anatomically preserved conifer-like stems from the Upper Carboniferous of England. Proc R Soc B 247:211–214.
- Grauvogel-Stamm L 1978 La flore du Grès à Voltzia (Buntsandstein Supérieur) des Vosges du Nord (France), morphologie, anatomie, interprétations phylogénique et paléogéographique. Mémoires Sciences Géologiques 50. Institut de Géologie, Université Louis Pasteur, Strasbourg. 225 p.
- Grauvogel-Stamm L, J Galtier 1998 Homologies among coniferophyte cones: further observations. Comptes Rendus de l'Académie des Sciences. Ser II. Sci Terre Planet 326:513–520.
- Grosfeld J, D Barthélémy, C Brion 1999 Architectural variations of *Araucaria araucana* (Molina) K Koch (Araucariaceae) in its natural habitat. Pages 109–122 in MH Kurman, AR Hemsley, eds. The evolution of plant architecture. Royal Botanic Gardens, Kew, 491 pp.
- Hernandez-Castillo GR 2005 Systematics of the most ancient conifers. PhD thesis, University of Alberta.
- Hernandez-Castillo GR, GW Rothwell, G Mapes 2001a Compound pollen cones in Paleozoic conifers. Am J Bot 88:1139–1142.
- 2001b Thuydiaceae fam. nov., with a review and reevaluation of Paleozoic walchian conifers. Int J Plant Sci 162:1155–1185.
- Hernandez-Castillo GR, RA Stockey, GW Rothwell, G Mapes 2003 Growth architecture of *Thucydia mahoningensis*, a model for walchian conifer plants. Int J Plant Sci 164:443–452.
- 2009a Reconstructing *Emporia lockardii* (Emporiaceae) Voltziales, and initial thoughts on Paleozoic conifer ecology. Int J Plant Sci 170:1056–1074.
- 2009b Reconstruction of the Pennsylvanian-age walchian conifer *Emporia cryptica* sp. nov. (Emporiaceae: Voltziales). Rev Palaeobot Palynol, doi:10.1016/j.revpalbo.2009.05.03.
- Joy K, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in palaeobotany. Ann Bot, NS, 20:635–637.
- Kerp H, JA Clement-Westerhof 1991 Aspects of Permian palaeobotany and palynology. XII. The form-genus *Walchiostrobus* Florin reconsidered. Neues Jahrb Geol Palaeontol Abh 183:257–268.
- Kerp JHF, RJ Poort, HAJM Swinkels, R Verwer 1990 Aspects of Permian palaeobotany and palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe Basin (?Late Carboniferous–Early Permian; SW-Germany) with special reference to the reproductive biology of early conifers. Rev Palaeobot Palynol 62: 205–248.
- Lausberg S 2002 Neue Kenntnisse zur saarpfälzischen Rotliegend-Flora unter besonderer Berücksichtigung der Coniferentaxonomie und des Hinterlandes. PhD thesis. Westfälische Wilhelms-Universität.

- Looy CV 2007 Extending the range of derived Late Paleozoic conifers: *Lebouskia* gen. nov. (Majonicaceae). *Int J Plant Sci* 168: 957–972.
- Mapes G, GW Rothwell 1984 Permineralized ovulate cones of *Lebachia* from Late Paleozoic Hamilton Quarry area in southeastern Kansas. *Palaeontology* 27:69–94.
- 1988 Diversity among Hamilton conifers. Pages 225–244 in G Mapes, RH Mapes, eds. *Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area in southeastern Kansas*. *Kans Geol Surv Guide Ser* 6.
- 1991 Structure and relationships of primitive conifers. *Neues Jahrb Geol Palaeontol Abh* 183:269–287.
- 1998 Primitive pollen cone structure in Upper Pennsylvanian (Stephanian) walchian conifers. *J Paleontol* 72:571–576.
- 2003 Validation of the names Emporiaceae, *Emporia* and *Emporia lockardii*. *Taxon* 52:327–328.
- Mapes G, GW Rothwell, MT Hawthorne 1989 The evolution of seed dormancy. *Nature* 337:645–646.
- Meyen SV 1984 Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Bot Rev* 50:1–112.
- Owens JN, MD Blake 1983 Pollen morphology and development of the pollination mechanism in *Tsuga heterophylla* and *T. mertensiana*. *Can J Bot* 61:3041–3048.
- Owens JN, SJ Simpson, GE Caron 1987 The pollination mechanism of Engelmann spruce (*Picea engelmannii*). *Can J Bot* 65:1439–1450.
- Rothwell GW 1982 New interpretations of the earliest conifers. *Rev Palaeobot Palynol* 37:7–28.
- Rothwell GW, G Mapes 1988 Vegetation of a Paleozoic conifer community. Pages 213–223 in G Mapes, RH Mapes, eds. *Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area in southeastern Kansas*. *Kans Geol Surv Guide Ser* 6.
- 2001 *Barthelia furcata* gen. et sp. nov., with a review of Paleozoic coniferophytes and a discussion of coniferophyte systematics. *Int J Plant Sci* 162:637–677.
- Rothwell GW, G Mapes, GR Hernandez-Castillo 2005 Cladistic relationships among the most ancient conifers (Voltziales). *Taxon* 52:733–750.
- Rothwell GW, G Mapes, RH Mapes 1997 Late Paleozoic conifers of North America: structure, diversity, and occurrences. *Rev Palaeobot Palynol* 95:95–113.
- Runions CJ, KH Rensing, T Takaso, JN Owens 1999 Pollination of *Picea orientalis* (Pinaceae): saccus morphology governs pollen buoyancy. *Am J Bot* 86:190–197.
- Schweitzer H 1963 Der weibliche Zapfen von *Pseudovoltzia liebeana* und seine Bedeutung für die Phylogenie der Koniferen. *Palaeontogr* 113B:1–29.
- 1996 *Voltzia hexagona* (Gischoff) Geinitz aus dem Mittleren Perm Westdeutschlands. *Palaeontogr* 239B:1–22.
- Stockey RA 1982 The Araucariaceae: an evolutionary perspective. *Rev Palaeobot Palynol* 37:133–154.
- Serlin BS, T Delevoryas, R Weber 1981 A new conifer pollen cone from the Upper Cretaceous of Coahuila, Mexico. *Rev Palaeobot Palynol* 31:241–248.
- Taggart RE, M Ghavidel-Syooki 1988 Palynology of the conifer macrofossil horizon. Pages 245–252 in G Mapes, RH Mapes, eds. *Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area in southeastern Kansas*. *Kans Geol Surv Guide Ser* 6.
- Tomlinson PB 1983 Tree architecture. *Am Sci* 71:141–149.
- Tomlinson PR, T Takaso 2002 Seed cone structure in conifers in relation to development and pollination: a biological perspective. *Can J Bot* 80:1250–1273.
- Veillon JM 1978 Architecture de espèces Néo-calédoniennes du genre *Araucaria*. *Candollea* 35:609–640.
- Visscher H, JHF Kerp, JA Clement-Westerhof 1986 Aspects of Permian palaeobotany and palynology. VI. Towards a flexible system of naming Palaeozoic conifers. *Acta Bot Neerl* 35:87–99.
- Winston RB 1984 The Upper Pennsylvanian conifer *Walchia garnettensis*; structure and affinities. *Palaeontogr* 194B:97–108.