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RECONSTRUCTING *EMPORIA LOCKARDII* (VOLTZIALES: EMPORIACEAE) AND INITIAL THOUGHTS ON PALEOZOIC CONIFER ECOLOGY

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A new plant concept for the extinct conifer species *Emporia lockardii* (Mapes & Rothwell) Mapes & Rothwell (Emporiaceae) is developed from fossils collected at the Late Pennsylvanian Hamilton Quarry, Kansas. *Emporia lockardii* has lateral plagiotropic branches with simple and forked leaves, simple pollen cones, and compound ovulate cones. Stems have an endarch eustele with dense wood surrounding a septate pith. Leaves display position-dependent heterophylly with forked leaves on penultimate shoots and simple leaves on ultimate shoots. All leaves are amphistomatic with two stomatal bands and papillate epidermal cells on the adaxial surface and two basal stomatal bands and numerous trichome bases on the abaxial surface. Pollen cones are simple and have helically arranged microsporophylls and adaxial pollen sacs. Prepollen is monolete and monosaccate, and it conforms to the sporae dispersae genus *Potonieisporites* Bharadwaj. Ovulate cones are compound with helically arranged, forked bracts that subtend bilaterally symmetrical, axillary dwarf shoots with one to three narrow megasporophylls interspersed among numerous sterile scales. Ovules are terminal, inverted, and bilaterally symmetrical. This new reconstruction together with additional conifer reconstructions from the Hamilton Quarry locality indicate that the genus *Emporia* has a particularly high species diversity for walchian conifers. These findings support previous hypotheses that propose drier habitats as sites for the first appearances of plants that become dominant during the late Permian and Mesozoic.

Keywords: conifer, Emporiaceae, Pennsylvanian-Permian, Voltziales.

Introduction

The fossil record of early conifers has been extensively documented from the late Paleozoic (Pennsylvanian–Early Permian) of Europe and North America (Galtier et al. 1992; Rothwell et al. 1997). These Euramerican conifer species are commonly referred to as "walchian" conifers (Mapes and Rothwell 1984), which have been classified in several families of the Voltziales (Florin 1938–1945; Visscher et al. 1986; Kerp et al. 1990; Mapes and Rothwell 1991). Most voltzialean species are known as conifer morphotaxa (McNeil et al. 2006) based on isolated and often fragmentary vegetative and/or reproductive organs. Such conifer morphotaxa display broad ranges of morphological, cuticular, and anatomical variation of their vegetative and reproductive organs (Hernandez-Castillo et al. 2001*b*). Such wide ranges of variation create confusion when trying to identify isolated conifer remains, thus leading to questionable species identifications (Hernandez-Castillo et al. 2001*b*). Despite previous attempts by several authors (Florin 1938–1945; Clement-Westerhof 1984; Visscher et al. 1986; Mapes and Rothwell 1991; Meyen 1997), we still lack clear plant concepts for most Paleozoic conifer species. Therefore, a new systematic approach has been proposed that employs a broad spectrum of reliable criteria for the purpose of circumscribing walchian conifers as species of extinct plants (Hernandez-Castillo et al. 2001*a*, 2001*b*, 2003; Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005).

In this study, we employ this approach, already used in the description of newly reconstructed walchian conifers (Hernandez-Castillo et al. 2001*b*; Rothwell and Mapes 2001), to develop a whole plant concept for *Emporia lockardii* (Mapes & Rothwell) Mapes & Rothwell. The reconstruction of *Emporia lockardii* presented here is based on a combination of morphological, cuticular, and anatomical characters that correlate vegetative branches to pollen and ovulate cones. *Emporia lockardii* sensu Hernandez-Castillo, Stockey, Rothwell & Mapes is the third species of extinct conifer plants to be reconstructed from the Hamilton Quarry flora.

This work is part of a broader study that employs this approach to reinvestigate, describe, and reevaluate morphological characters of Euramerican Paleozoic walchian conifers. Our goal is to develop biologically sound species concepts for Paleozoic voltzialean conifer plants which can be used to assess phylogeny as well as biological and ecological facets of these enigmatic and interesting seed plants. In this article, we present a reconstruction for *E. lockardii* and introduce preliminary ideas on the ecology of early Euramerican conifers from information developed for five species of conifer plants (Hernandez-Castillo 2005) from the Hamilton Quarry flora. To date, the Hamilton Quarry, Kansas, is the only Paleozoic fossil locality where all conifers are known as species of plants (Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005), allowing us, for the first time, to characterize

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plant diversity, growth architecture, and adaptations to water-stressed environments for the most ancient walchian conifers. In addition, these data allow us to assess the role of ancient conifers in extra-basinal environments of Euramerica at the end of the Paleozoic.

Material and Methods

Specimens used in this study are preserved as coalified compressions with preserved cuticles and as cellular permineralizations. Some specimens show both modes of preservation. The fossils 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; Bush et al. 1988; French et al. 1988). These beds represent channel deposits in an estuarian environment under tidal influence (French et al. 1988; Fahrer et al. 1990; Fahrer 1991; Feldman et al. 1993). *Emporia lockardii* is represented by 85 specimens. Sixteen are plagiotropic leafy branching systems with penultimate and ultimate shoots attached. Eleven vegetative specimens were used for cuticle preparation and one for anatomy. Fifty-one specimens are pollen cones, and six of these are attached to ultimate leafy shoots; 13 have cuticles preserved, and 16 are anatomically preserved. Eighteen specimens are ovulate cones, and most of them are attached to penultimate shoots with leaves. Eight ovulate cones are new to this study, while the remaining 10 were described by Mapes and Rothwell (1984). Five of the new ovulate cones have cuticles and three are also anatomically preserved.

Specimens were initially revealed on 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 cover slip 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 sheet 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 were captured with a MicroLumina digital scanning camera (Leaf Systems, Bedford, MA) or a PhotoPhase digital scanning camera (Phase One A/S, Frederiksberg, Denmark). Images were processed using Adobe Photoshop. All specimens are housed in the Ohio University Paleobotanical Herbarium (OUPH), Athens, Ohio, as OUPH numbers 3834–3851, 3855–3865, 3867–3912, 3968–

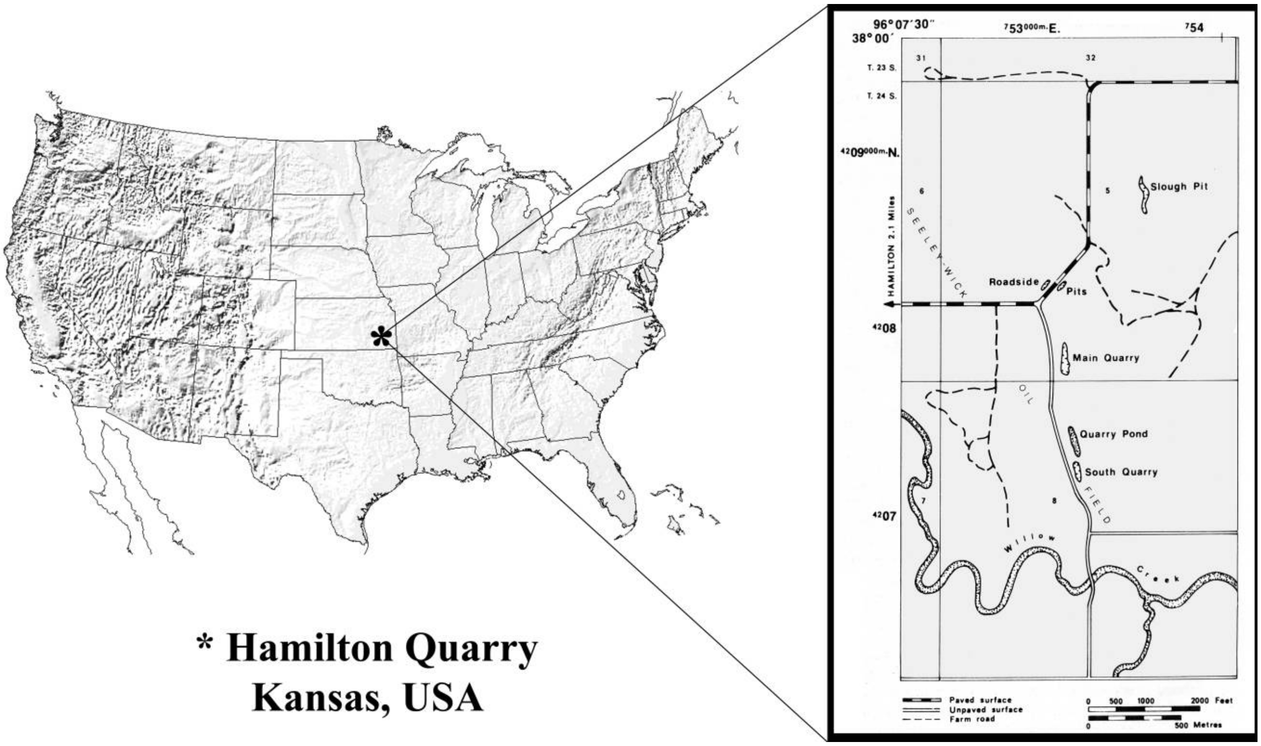

Fig. 1 Map showing location of Hamilton Quarry, Kansas.

4092, 4093–4147, 4160–4218, 4234–4251, 4260–4262, 4267–4268, and 17150–17407.

Systematic Description

Class—Coniferopsida

Order—Voltziales

Family—Emporiaceae Mapes et Rothwell

*Genus—*Emporia *Mapes et Rothwell*

*Species—*Emporia lockardii *(Mapes et Rothwell) Mapes et Rothwell (Figs. 2–9)*

Emporia lockardii *species diagnosis emend.* Leaves with position-dependent heterophylly; tracheids with uni- to biseriate circular bordered pits; vascular rays uni- to biseriate, 1–8 cells high. Pollen cones 0.5–5.3 cm long, 0.5–2.1 cm wide; microsporophylls 0.25–5.0 mm long, 2–3 mm wide; pollen sacs 8–14 per microsporophyll, prepollen monosaccate 87–127 × 64–106 μm. Ovulate cones 4.7–5.1 cm long and 1.2–1.5 cm wide; bracts equal to or slightly longer than dwarf shoots, free from dwarf shoot to base; sterile scales 14–30 per dwarf shoot, 2.1–4.3 mm long, 1.3–1.8 mm wide; sporophylls 1–3 per dwarf shoot.

Holotype. Ovulate cone and subtending penultimate shoot designated by Mapes and Rothwell (1984, p. 72; plate 9, fig. 5; plate 10, figs. 1–3, 5, 6; plate 11, figs. 1, 3, 4, 6; plate 12, fig. 4; plate 13, figs. 1, 3, 5; plate 14, figs. 1–8).

New specimens studied. Lateral branches OUPH numbers 17150, 17152, 17154, 17162, 17167, 17271 (figs. 2, 3*A*–3*C*). Branches showing leaves on penultimate and ultimate shoots with cuticles 17166 (fig. 3*D*, 3*F*), 17371 (fig. 3*E*), 17206, 17207 (fig. 4), 17171 (fig. 5*A*, 5*C*), 17271 (fig. 5*B*), 17208 (fig. 5*D*, 5*E*). Compressed pollen cones 17214, 17215, 17215A, 17217, 17253, 17255, 17314, (fig. 6). Vegetative leaves on ultimate shoots attached to pollen cones 17314. Pollen cone macerations and pollen 17217–17219 (fig. 7). Anatomically preserved pollen cones 17221 (fig. 8*A*, 8*B*), 17228, 17229 (fig. 8*C*, 8*D*), and 17217 (fig. 8*E*). Ovulate cones 17371 (fig. 9*A*), 17376 (fig. 9*B*). Cuticular macerations of ovulate cone 17371 (fig. 9*C*–9*H*).

Collecting 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).

Stratigraphic occurrence and age. Hartford Limestone, Topeka Limestone Formation, Shawnee Group, Upper Pennsylvanian (Lower Virgilian).

Synonymy. Lebachia lockardii G. Mapes et G. W. Rothwell (1984, p. 72; plate 9, fig. 5; plate 10, figs. 1–3, 5, 6; plate 11, figs. 1, 3–6; plate 12, fig. 4; plate 13, figs. 1, 3, 5; plate 14, figs. 1–8). OUPH numbers 3834–3851, 3855–3865, 3867–3912, 3968–4092, 4093–4147, 4160–4218, 4234–4251, 4260–4262, 4267–4268.

Emporia lockardii (G. Mapes et G. W. Rothwell) G. Mapes et G. W. Rothwell comb. nov. (1991, p. 183).

Emporia lockardii (G. Mapes et G. W. Rothwell) G. Mapes et G. W. Rothwell (2003, p. 327).

Description

Plant Architecture

Vegetative specimens consist of two orders of branching with penultimate shoots that bear several ultimate shoots with helically arranged leaves (figs. 2, 3*A*–3*C*). Most branches are plagiotropic (figs. 2, 3*A*–3*C*), but a few show slightly irregular branching (fig. 3*A*), most likely due either to reiterative growth following damage or to taphonomic factors during preservation. Main axes resembling orthotropic stems (e.g., *Tylodendron* Weiss) like those of several other walchians have yet to be found. Branch shape ranges from ovoid to deltoid (fig. 2*B*, 2*C*; fig. 3*A*, 3*B*). The largest plagiotropic branch is 18 cm long and 7.5 cm wide (fig. 2*C*). The longest ultimate shoot (3.75 cm long) occurs in the midregion of the branch (fig. 2*C*) and the shortest (1 cm) on a small deltoid lateral branch (fig. 3*B*). Most lateral branches are broken at the very base or apex (fig. 2; fig. 3*A*, 3*B*), indicating that some plagiotropic shoots were larger than the specimens shown here. Penultimate shoots taper from 4.0 to 1.0 mm wide from the base to the apex.

Leaves on Penultimate Shoots

Leaves are helically arranged, simple or forked when found on large branches or at the base of ovulate cones (figs. 2, 3*A*–3*E*). They are 8–10 mm long and 1.0–2.1 mm wide. In face view, leaves on penultimate shoots range from narrowly triangular (figs. 2*C*, 3*C*) to linear (figs. 3*D*, 4*B*), and in side view they range from slightly concave (figs. 2*C*, 3*A*) to slightly S shaped (fig. 3*B*). Leaves on penultimate shoots extend from the stem at angles of 26°–83° at the base and 28°–69° at the tip (table 1; figs. 2*C*, 3*A*–3*C*).

Leaves are amphistomatic (fig. 4), with two long adaxial bands of stomata that contain 2–5 stomata separated by a stomatal-free zone (fig. 4*A*, 4*B*), and abaxial stomata in short and narrow basal bands or rows at the very base of the leaf. Stomata are monocyclic, semicircular to ellipsoidal and have 6–8 subsidiary cells with small, erect papillae (fig. 4*D*). Stomata are separated by groups of epidermal cells that extend along and across the stomatal band (fig. 4*B*, 4*D* [at brackets]). The stomatal-free zone is composed of polygonal to rectangular epidermal cells (fig. 4*B*). Epidermal cells on marginal zones of the leaf and in stomatal-free zones display few or no papillae, and the margin of the leaf has short trichomes (fig. 4*C*). Ordinary epidermal cells with few to no trichome bases are distributed across the remaining abaxial surface (table 1).

Leaves on Ultimate Shoots

Leaves on ultimate shoots are helically arranged, simple, 1.7–5.0 mm long, and 0.4–1.1 mm wide (table 1; figs. 2, 3*A*–3*C*, 5*A*). Leaves on ultimate shoots vary from narrow subtriangular to linear in face view (fig. 5*A*), and are gently concave to slightly S shaped in side view (fig. 2*A*; fig. 3*A*–3*C*, 3*F*). Leaves extend from the base of the shoot at 26°–63° (fig. 2*B*, 2*C*; fig. 3*A*, 3*B*) and at 28°–69° near the apex (table 1; fig. 2*B*, 2*C*; fig. 3*A*, 3*B*). Leaves are amphistomatic with two long bands of adaxial stomata adaxially (fig. 5*A*, 5*C*)

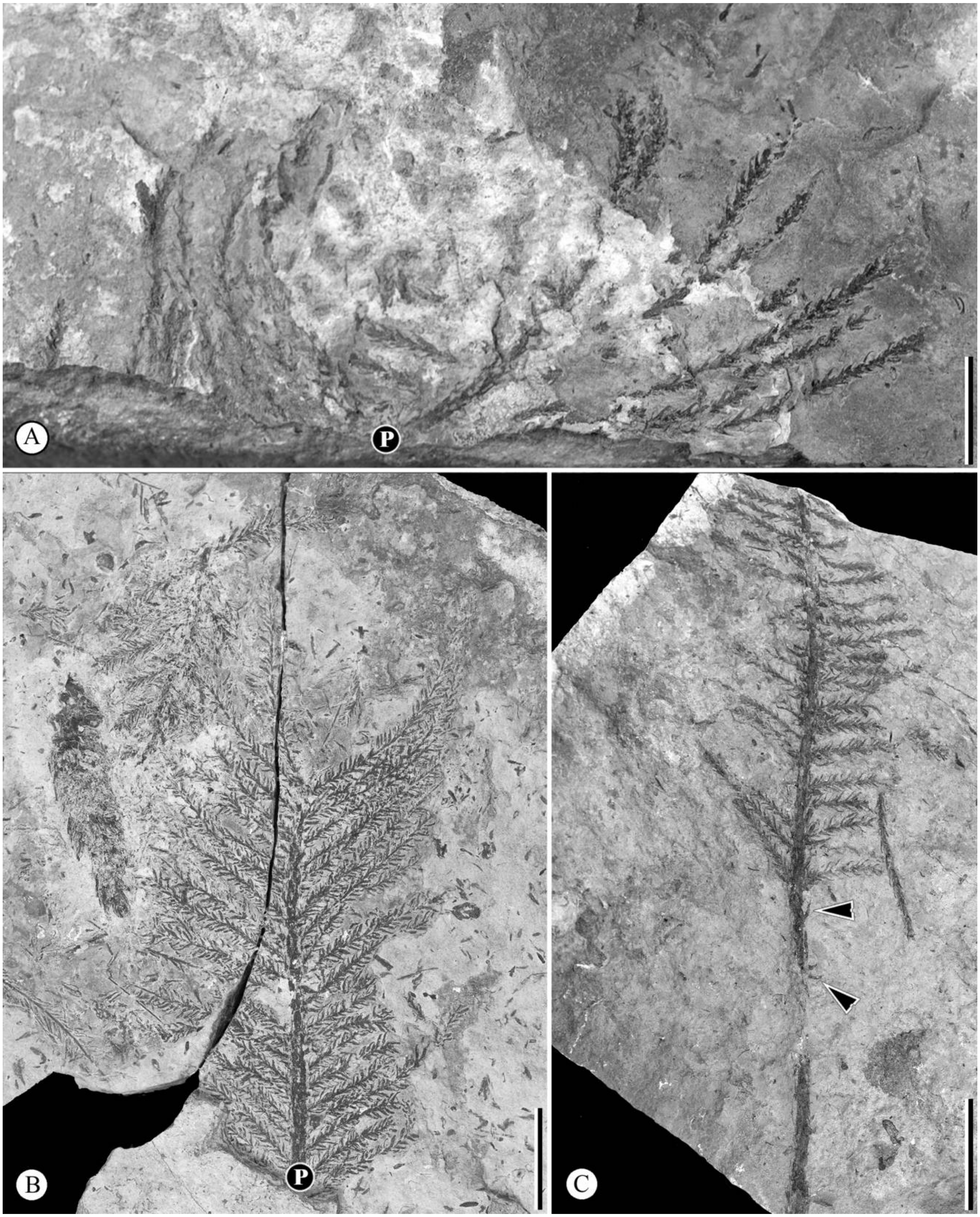

Fig. 2 *Emporia lockardii* lateral branches. *A*, Penultimate shoot (*p*) with several attached ultimate shoots with helically arranged leaves. OUPH 17150. Bar = 1 cm. *B*, Branch showing general ovoid shape, penultimate shoot (*p*), and over 36 ultimate shoots with slightly concave to slightly S-shaped leaves. Note portion of apical branch and isolated ovulate cone (upper left). OUPH 17151. Bar = 2 cm. *C*, Branch showing leaves on penultimate shoots (arrowheads) and several incomplete ultimate shoots with leaves. Note absence of ultimate shoots at base of branch. OUPH 17152. Bar = 2.5 cm.

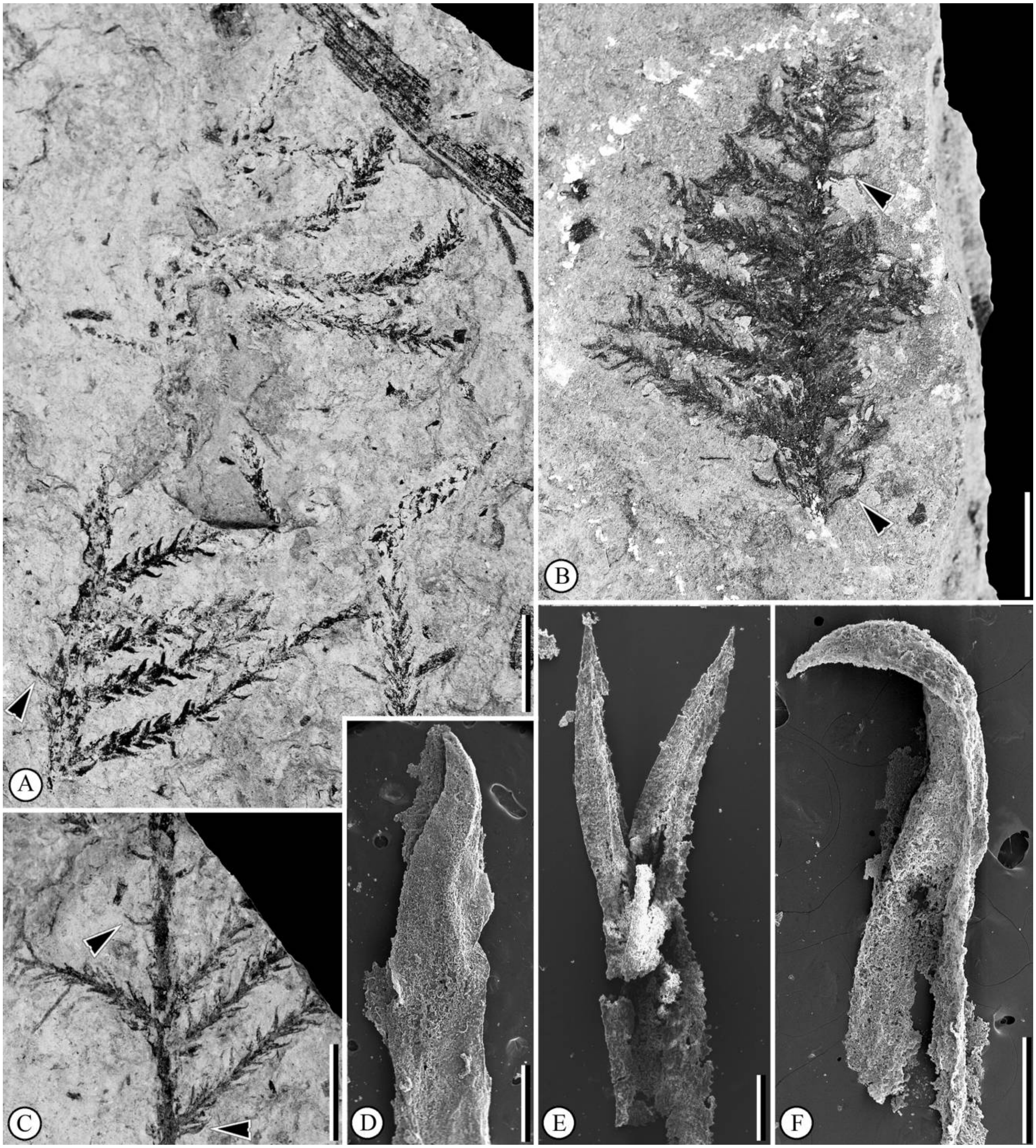

Fig. 3 *Emporia lockardii* lateral branches and SEM of leaves. *A*, Leaves on penultimate shoots (arrowhead) and ultimate shoots. OUPH 17154. Bar = 1 cm. *B*, Branch apex showing deltoid shape and leaves on penultimate shoot (arrowheads). OUPH 17271. Bar = 1 cm. *C*, Branch showing leaves on penultimate shoot (arrowheads) and ultimate shoots. OUPH 17167. Bar = 1 cm. *D*, Leaf from penultimate shoot showing abaxial surface, linear shape, and slightly curved apex. OUPH 17166. Bar = 1 mm. *E*, Forked leaf from penultimate shoot showing adaxial surface. OUPH 17371. Bar = 0.5 mm. *F*, Side view of slightly concave leaf on ultimate shoot with highly incurved apex. OUPH 17166. Bar = 0.5 mm.

and more restricted stomatal areas on the abaxial surface (fig. 5*D*–5*E*). Adaxial stomatal bands are 2–5 stomata wide, extend from the apex to the very base of the leaf, and are separated by a stomatal-free zone (fig. 5*A*, 5*B*). Leaf margins and stomatal-free zones have rectangular epidermal cells that are elongated longitudinally with few or no papillae (fig. 5*A*, 5*B*). Stomatal complexes are separated by groups of ordinary epidermal cells; some stomata may be in contact with each

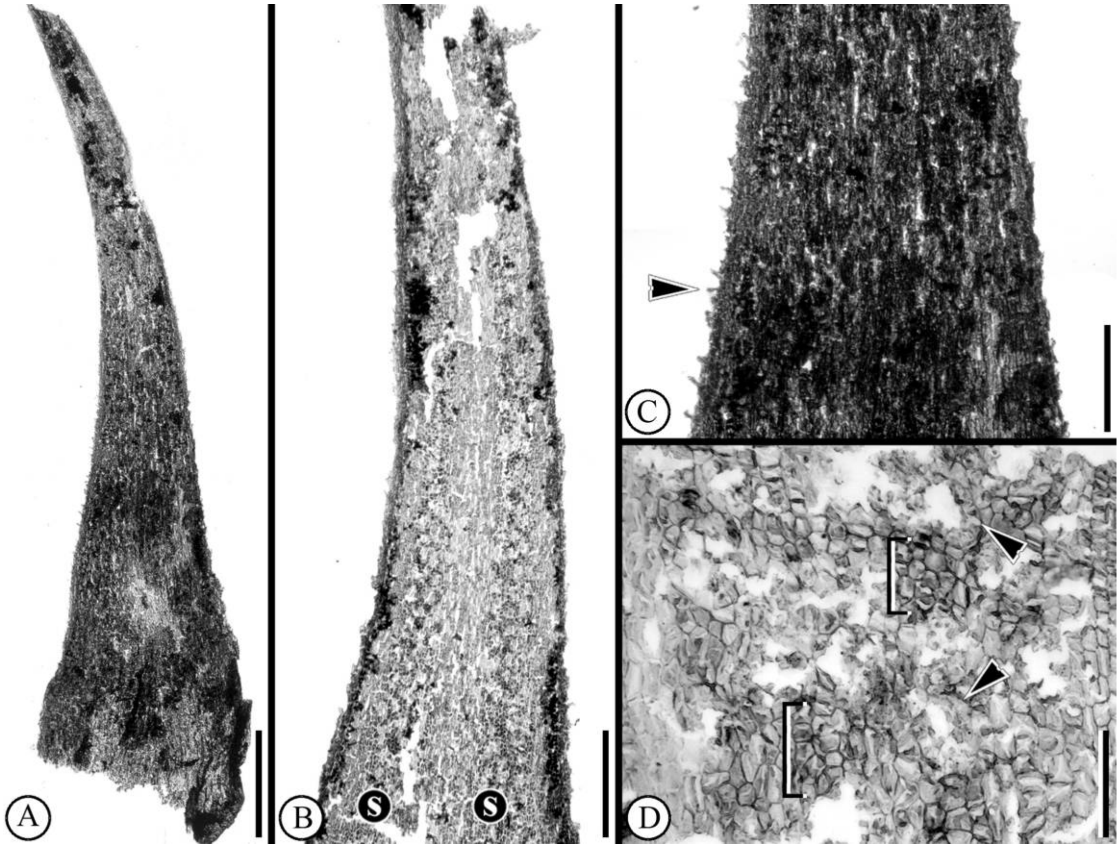

Fig. 4 *Emporia lockardii* cuticular macerations of leaves on penultimate shoots. *A*, Adaxial surface showing narrowly triangular shape. OUPH 17206. Bar = 0.5 mm. *B*, Adaxial surface showing two stomatal bands (*s*), central stomatal-free zone. OUPH 17207. Bar = 1 mm. *C*, Adaxial surface showing marginal trichomes (arrowhead). OUPH 17207. Bar = 0.5 mm. *D*, Adaxial stomatal band showing several stomatal complexes (arrowheads) and numerous epidermal cells separating them (brackets). OUPH 17206. Bar = 0.1 mm.

other, but subsidiary cells usually are not shared (fig. 5*B*, 5*C*). Stomata are monocyclic, ellipsoidal, 58×46 μm, and have 5–9 papillate subsidiary cells (fig. 5*B*, 5*C*). Papillae are thin, small, and usually overarching (fig. 5*C*). Stomatal bands on the abaxial surface are short and narrow (fig. 5*D*, 5*E*), often located at the leaf base, and are 2–4 stomata wide. However, several leaves have rows of stomata that extend along the entire abaxial surface of the leaf (fig. 5*D*). These abaxial rows are commonly found in the central part of the leaf, but they may be located near the margins as well. Scattered abaxial stomata also may be found near the base of the leaf. Ordinary epidermal cells across the entire abaxial surface display trichome bases (table 1; fig. 5*D*, 5*E*).

Internal Anatomy of Stems and Leaves

Stem anatomy is comparable to that of the seed cone axis, described earlier by Mapes and Rothwell (1984). Stems have a prominent parenchymatous pith with sclerotic nests surrounded by an endarch eustele with abundant secondary xylem, vascular cambium, and a narrow zone of phloem. Primary tracheids are characterized by helical wall thickenings, while secondary tracheids have uniseriate to biseriate circular bordered pits. Rays are primarily uniseriate and 1–8 cells high. The primary cortex is parenchymatous with abundant longitudinally oriented resin rodlets, a narrow zone of bark, and thick cuticle.

Leaves in cross section range from widely rhomboidal to narrowly transversely rhombic (pl. 10, fig. 6 of Mapes and Rothwell 1984). Leaves are covered by a thick cuticle on top of a single layer of epidermal cells. The epidermis is composed of thin-walled rectangular cells that surround a 1–3-cell layered hypodermis. Mesophyll is composed of thin-walled parenchyma cells. The vascular bundle seems to have a bundle sheath (endodermis) surrounding it. This bundle sheath is not well preserved but it appears to be composed of large thick-walled polyhedral cells often with dark contents.

Ultimate Shoots with Attached Pollen Cones

Numerous pollen cones have been found at the locality (figs. 6, 8*A*–8*C*). Several cones are attached to ultimate leafy shoots (fig. 6*A*, 6*B*, 6*F*), but most are isolated and/or broken (fig. 6*C*, 6*D*). Leaves on subtending ultimate shoots have been used to correlate pollen cones with vegetative branches. Such leaves are 3–5 mm long and 1.6–2.2 mm wide. As with ultimate leaves on vegetative branches, leaf shape ranges from narrowly triangular to slightly elliptical (table 1). Leaves have two bands of adaxial stomata separated by a stomatal-free zone and epidermal cells with few or no papillae. Stoma-

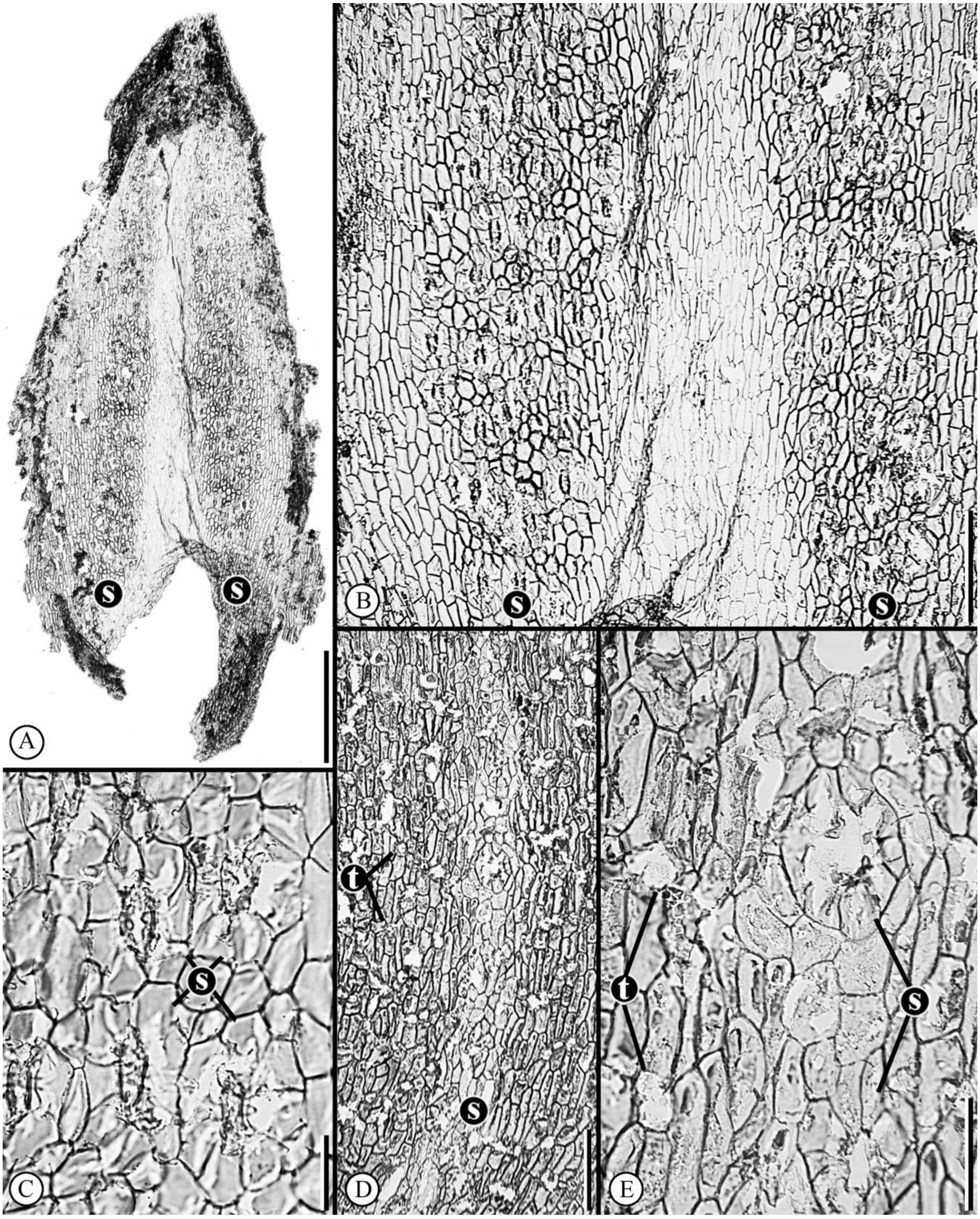

Fig. 5 *Emporia lockardii* cuticular macerations of leaves on ultimate shoots. *A*, Adaxial surface showing subtriangular shape, two broad bands of stomata (*s*) separated by stomatal-free zone. OUPH 17171. Bar = 1 mm. *B*, Adaxial surface showing (left to right) elongated epidermal cells with small papillae, stomatal band (*s*), and elongated epidermal cells of central stomatal-free zone. OUPH 17171. Bar = 0.5 mm. *C*, Adaxial stomatal complexes (*s*) showing seven to eight subsidiary cells with erect to overarching papillae, that are separated by groups of epidermal

tal bands contain 2–5 stomata per band with 5–7 papillate subsidiary cells. Stomata within these bands are separated from each other by groups of ordinary polygonal epidermal cells.

Pollen Cone Morphology

Pollen cones are simple, terminal, cylindrical to ellipsoidal (table 2), 0.5–5.3 cm long, and 0.5–2.1 cm wide (fig. 6). Cones bear helically arranged microsporophylls, 0.25–5.0 mm long and 2–3 mm wide with a narrowly triangular distal lamina (fig. 6*A*, 6*C*, 6*D*) and broad base (fig. 6*C*, 6*D*). Both mature (fig. 6*A*–6*E*) and immature (fig. 6*F*, 6*G*) pollen cones are present in the collection. Microsporophylls have 2–4 bands of adaxial stomata (fig. 7*A*). Two main bands extend along the entire distal lamina, and two short bands are usually found at the base of the lamina (fig. 7*A*, 7*B*). The main stomatal bands are separated by a stomatal-free zone (fig. 7*A*–7*C*). Stomata are monocyclic, 20 × 25 μm with 4–5 papillate subsidiary cells (fig. 7*C*). The microsporophyll is covered by epidermal cells with erect papillae (fig. 7*B*, 7*C*). The abaxial surface is entirely covered by trichome bases (fig. 7*D*–7*F*). Trichome bases are circular and often broken showing a raised basal area and elongated epidermal cells surrounding the trichome base (fig. 7*E*, 7*F*). Microsporophylls have marginal trichomes (fig. 7*G*).

Pollen Cone Anatomy and Prepollen

Most mature cones have dehisced pollen sacs, while the microsporangia of young cones are intact (fig. 8*A*, 8*B*). Longitudinal sections show a cone axis bearing peltate microsporophylls with a distal lamina that is at least three times larger than the heel (fig. 8*A*). Pollen sacs are adaxial, ellipsoidal, and attached to a single area on the shank (fig. 8*A*–8*C*). Eight to 14 pollen sacs have been found per microsporophyll (fig. 8*A*, 8*B*). Most mature pollen sacs are empty but some contain prepollen grains that are semicircular with a single saccus surrounding a central body with a bent monolete suture and parallel folds (fig. 8*D*). Grains are 87–127 μm long, 64–106 wide μm and conform to *Potonieisporites* (Bharadwaj 1964). Grains here closely resemble those described as *Potonieisporites neglectus* Potonié and Lele by Taggart and Ghavidel-Syooki in 1988 (fig. 8*D*, 8*E*).

Ovulate Cone Morphology and Anatomy

Ovulate cones have been correlated with vegetative branches by features of the subtending vegetative leaves and internal anatomy. Seed cones of *Emporia lockardii* have been thoroughly described previously (Mapes and Rothwell 1984). However, two additional cones were macerated in this study that show a previously unknown variability in size and shape of sterile scales and sporophylls. This added variability is included in both the diagnosis and tables (fig. 9; table 1). Compound ovulate cones are 4.7–5.1 cm long, 1.2–1.5 cm wide, and cylindrical to ellipsoidal in shape (fig. 9*A*, 9*B*). Some are attached terminally to penultimate shoots that also bear leaves (fig. 9*A*), thus allowing for identification of ovulate cones and vegetative branches as a common species. The cone axis bears helically arranged, forked bracts with axillary dwarf shoots that each bear 1–3 sporophylls and 14–30 sterile scales. Sterile scales range in shape from lanceolate (fig. 9*C*) to ellipsoidal (fig. 9*D*) to widely ovate (fig. 9*E*). Most sterile scales have short marginal trichomes (fig. 9*C*–9*E*) and are 2.1–4.3 mm long and 1.3–1.8 mm wide. The epidermis of sterile scales is similar to that of leaves on ultimate shoots with two large adaxial bands of stomata separated by a stomatal–free zone (fig. 9*C*). Individual stomata have 6–7 unipapillate subsidiary cells with a single erect or overarching papilla (fig. 9*F*). The abaxial surface is completely covered by trichome bases (fig. 9*G*). Sporophylls are linear with a broad apex and upturned tip and their surface is completely covered by trichome bases (fig. 9*H*).

Discussion

Emporia lockardii conforms to the general architecture recently established for walchian conifers (Lausberg 2002; Hernandez-Castillo et al. 2003; Rothwell et al. 2005). In contrast to most modern conifers and the popular concept of Paleozoic conifers, initial walchian conifer plants were diminutive trees with determinate growth (Hernandez-Castillo et al. 2003). They produced plagiotropic lateral branches on orthotropic stems and displayed terminal ovulate and pollen cones. *Emporia lockardii* (=*Lebachia lockardii*; Mapes and Rothwell 1984) was originally established for the first walchian conifer to be represented by both the morphology and anatomy of ovulate cones (Mapes and Rothwell 1984). In this study, we have reconstructed *E. lockardii* plant using features of morphology, cuticles, and internal anatomy of all types of vegetative and reproductive shoots. Over 40 characters have been used to describe, compare, and contrast this species to some of the most well-known species of walchian, angaran, and voltzialean conifers (tables 1–4).

From all these characters (tables 1–4), the following combination distinguishes *E. lockardii* from other species of Paleozoic conifers: (1) plagiotropic lateral branches with simple and forked leaves on penultimate shoots and simple leaves on ultimate branches; (2) leaves of all orders amphistomatic with two adaxial bands of monocyclic stomata and abaxial narrow stomatal bands or single rows of monocyclic stomata; (3) stems showing ground tissues with resin rodlets composed of short secretory parenchyma cells; (4) simple, terminal pollen cones bearing peltate microsporophylls with 8–14 adaxial pollen sacs, and monosaccate, *Potonieisporites* prepollen grains; (5) compound, terminal ovulate cones bearing forked bracts with bilateral axillary dwarf shoots with 1-3 sporophylls interspersed among 14–30 sterile scales.

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cells. OUPH 17171. Bar = 0.1 mm. *D*, Abaxial surface showing numerous trichome bases (*t*) and narrow stomatal row (*s*). OUPH 17208. Bar = 0.5 mm. *E*, Abaxial surface showing trichome bases (*t*) with elongated epidermal cells, and stomata (*s*) with eight to nine subsidiary cells and overarching papillae. OUPH 17208. Bar = 0.1 mm.

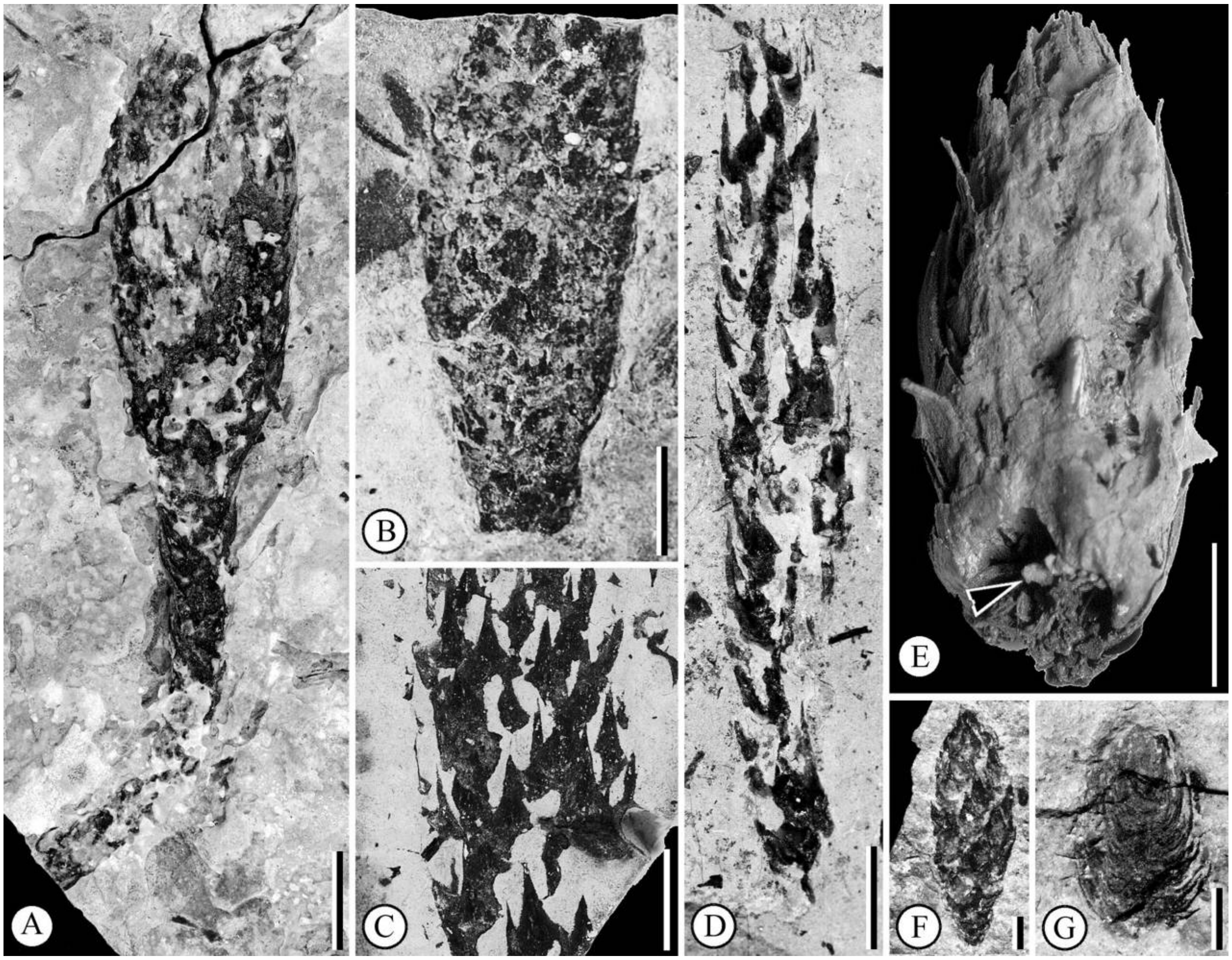

Fig. 6 *Emporia lockardii* pollen cones. *A*, Mature ellipsoidal cone attached to ultimate shoot with slightly-concave leaves. OUPH 17214. Bar = 5 mm. *B*, Mature cone with ultimate shoot attached at base. OUPH 17215. Bar = 5 mm. *C*, Mature cone with widely spaced microsporophylls. OUPH 17215A. Bar = 5 mm. *D*, Mature cone showing large microsporophylls. OUPH 17217. Bar = 5 mm. *E*, Macerated immature cone showing microsporophylls and adaxial pollen sacs on microsporophyll shank (arrowhead). OUPH 17253. Bar = 2 mm. *F*, Immature cone showing ellipsoidal shape, helically arranged microsporophylls, and ultimate shoot at base. OUPH 17255. Bar = 2 mm. *G*, Immature cone. OUPH 17314. Bar = 2 mm.

Systematic Relationships of Emporia lockardii

Emporia lockardii is most comparable to the European walchian conifers *Utrechtia floriniformis* Rothwell et Mapes and *Otovicia hypnoides* Kerp, Poort, Swinkels et Verwer (tables 3, 4). *Utrechtia floriniformis* differs from *E. lockardii* by having only forked leaves on penultimate shoots, two bands of adaxial stomata on ultimate shoot leaves, and one ovule borne on each terminal "fertile scale" (table 4). These characters contrast with simple to forked leaves on penultimate shoots, varying abaxial stomatal distributions, and variable number of sporophylls interspersed with sterile scales in *E. lockardii* (tables 3, 4). *Otovicia hypnoides* differs from *E. lockardii* by having only forked leaves on penultimate shoots, falcate leaves, and primarily adaxial stomata with scattered abaxial stomata (table 3). The structural similarities of *E. lockardii* to *O. hypnoides* and *U. floriniformis* support the most recent phylogenetic hypothesis based on concepts of the most completely known voltzialean conifer plant species (Rothwell et al. 2005), where *O. hypnoides* + *U. floriniformis* are sister to *Emporia* spp. within the "Lebachioid clade." Additional taxa within this Lebachioid clade include *Hanskerpia hamiltonensis* Rothwell, Mapes et Hernandez-Castillo and *Barthelia furcata* Rothwell et Mapes that subtend the *Emporia* spp.+ (*O. hypnoides* + *U. floriniformis*) clade at successive nodes on the tree (fig. 10 of Rothwell et al. 2005).

While the character combinations of *E. lockardii* are unique among walchian conifer plants, many of the same individual characters also occur in other walchian species (tables 3, 4) and contrast with early Permian broad-leaved Voltzian conifers (Looy 2007). Since walchian conifers traditionally have been described as morphotaxa based on isolated organs such as vegetative branches, pollen cones, or ovulate cones, which are usually fragmentary (e.g., Florin 1938–1945), many of the discussions in the literature are restricted to organ-by-organ comparisons. These discussions never reach an understanding of the whole plant concept and prevent us from attaining a complete understanding of these

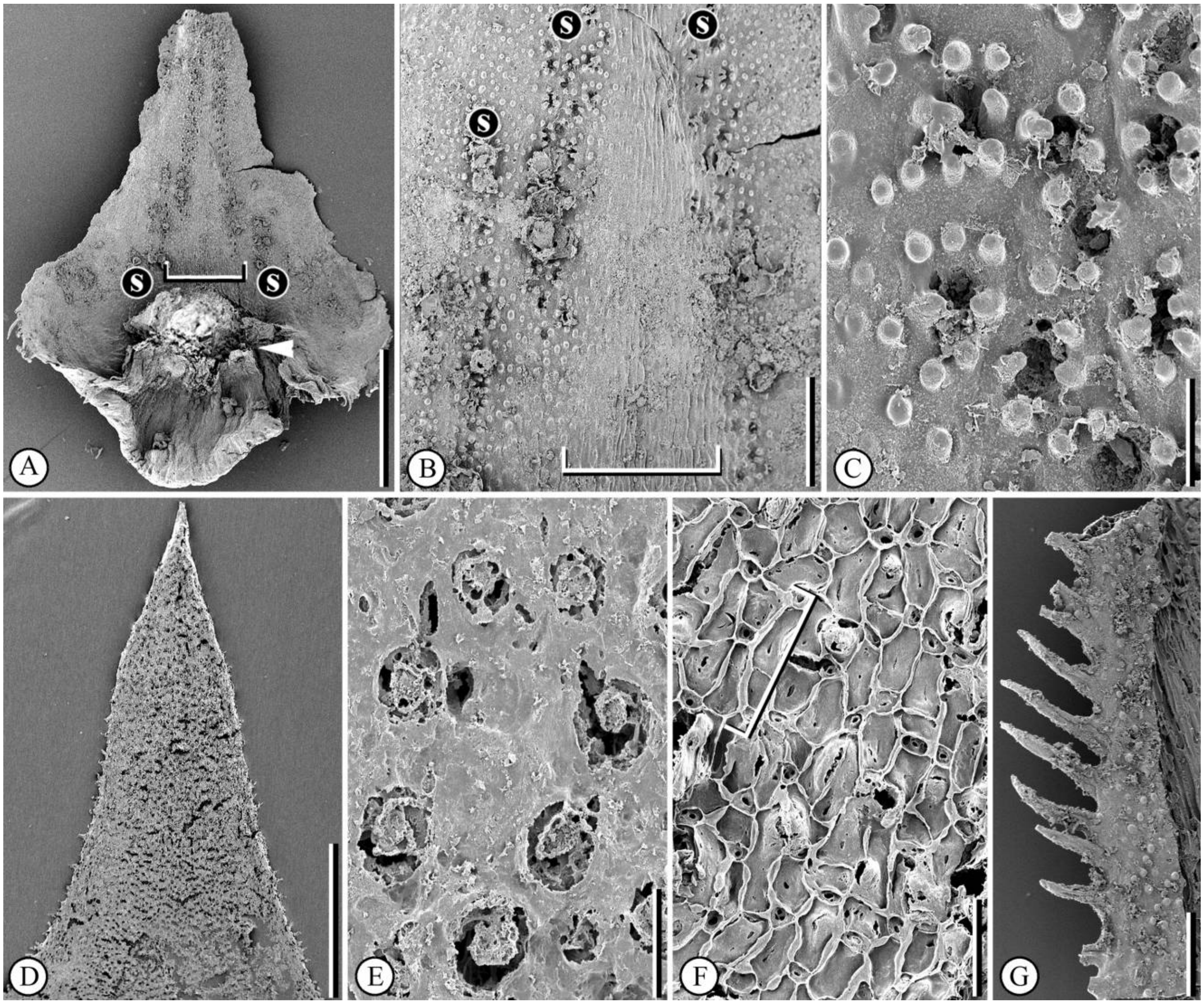

Fig. 7 *Emporia lockardii* SEM of microsporophylls and *Potonieisporites* prepollen grains. Specimens macerated from OUPH 17217 (adaxial) and OUPH 17218 (abaxial). *A*, Adaxial surface showing triangular shape, two major bands of stomata (*s*) separated by stomatal-free zone (bracket), and remnants of shank (arrowhead). Bar = 1000 μm. *B*, Three adaxial bands of stomata with papillate subsidiary cells (*s*), papillate epidermal cells, and elongated epidermal cells in stomatal-free zone (bracket). Bar = 200 μm. *C*, Adaxial stomatal band showing circular to slightly ellipsoidal stomatal complexes with erect to overarching papillae. Bar = 20 μm. *D*, Abaxial surface entirely covered by trichome bases. Bar = 1000 μm. *E*, Abaxial trichome bases. Bar = 40 μm. *F*, Internal view of abaxial surface with trichome bases and elongated epidermal cells (bracket). Bar = 40 μm. *G*, Marginal trichomes. OUPH 17219. Bar = 100 μm.

fossil conifers as extinct species of plants that can be used in phylogenetic analyses (Clement-Westerhof 1984, 1987; Mapes and Rothwell 1984; Winston 1984; Kerp and Clement-Westerhof 1991; Broutin and Kerp 1994; Kerp et al. 1996; Meyen 1997; Lausberg and Kerp 2000). However, they are extremely useful for other types of studies (i.e., paleofloristics, taphonomy, stratigraphy, etc.) and serve as the bases for paleoecological analyses that have changed our views on past vegetation types and their spatiotemporal complexity (DiMichele and Aronson 1992; DiMichele et al. 2008).

Consequently, most current familial and generic concepts and diagnoses of Paleozoic conifers are cryptic and lack sets of diagnostic characters needed to accurately identify specimens as belonging to them. Previous Carboniferous conifer plant reconstructions from the 7–11 mine in Ohio (Hernandez-Castillo et al. 2001*b*), Hamilton Quarry in Kansas (Rothwell and Mapes 2001; Rothwell et al. 2005), additional reconstructions of new species of *Emporia* from Hamilton Quarry (Hernandez-Castillo 2005; Hernandez-Castillo et al. 2009*a*, 2009*b*), and this new *E. lockardii* reconstruction will allow us to thoroughly reevaluate the most diagnostic characters for defining families and genera of Paleozoic conifers in the near future.

Conifer Diversity at the Hamilton Quarry and Elsewhere

The Hamilton Quarry yields an exceptional number of well-preserved conifer plant species. These conifers are represented by three genera: *Barthelia* Rothwell & Mapes (Bartheliaceae Rothwell & Mapes), *Emporia* Mapes & Rothwell, and *Han-*

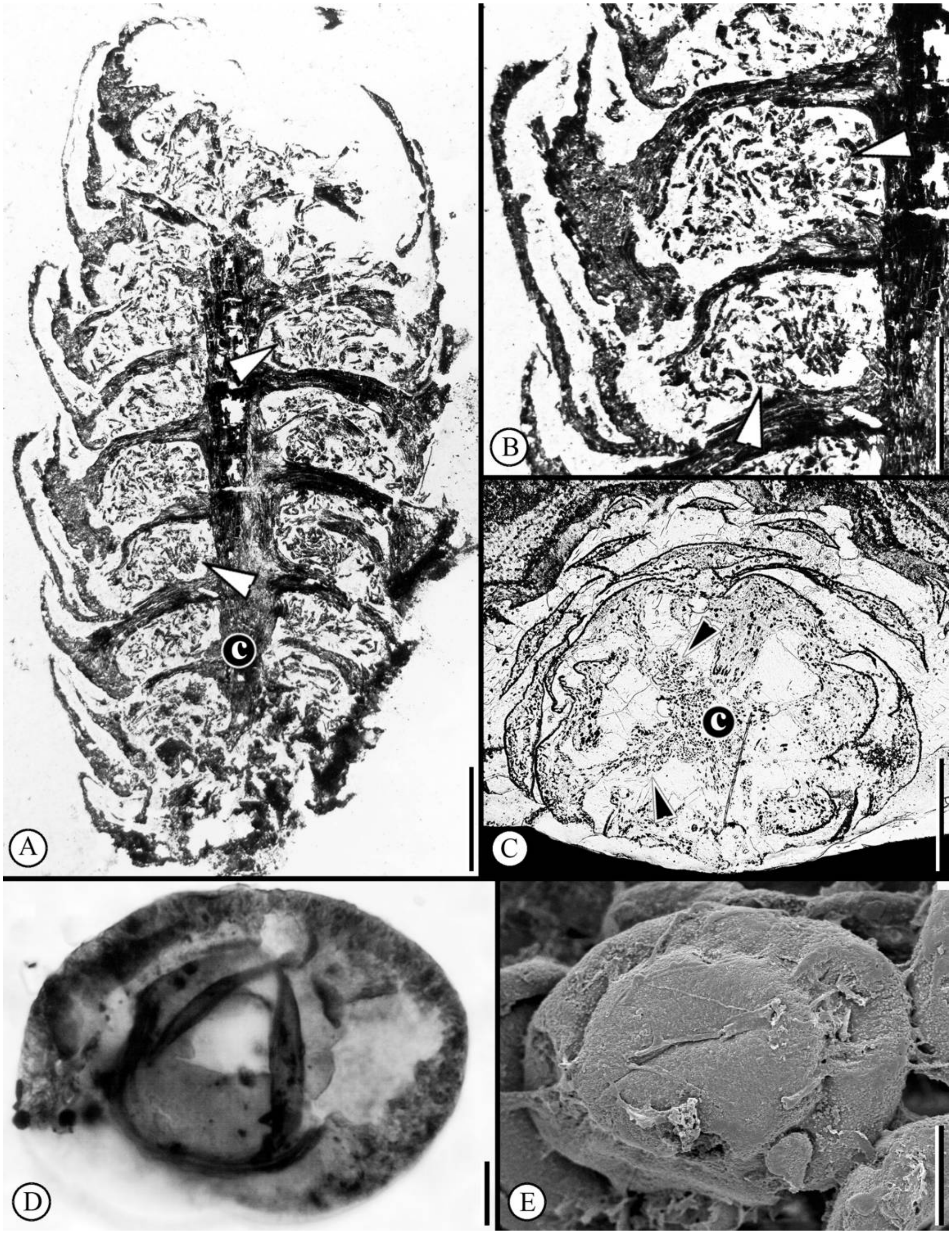

Fig. 8 *Emporia lockardii* anatomy of pollen cones and *Potonieisporites* prepollen grains. *A*, Radial section of ellipsoidal cone showing cone axis (*c*), peltate microsporophylls with attached adaxial pollen sacs (arrowheads). OUPH 17221. Bar = 1 mm. *B*, Radial section showing microsporophylls with attached adaxial pollen sacs (arrowheads). OUPH 17221. Bar = 1 mm. *C*, Cross section showing cone axis (*c*), helically arranged microsporophylls, and adaxial pollen sacs (arrowheads). OUPH 17228. Bar = 1 mm. *D*, Distal view of *Potonieisporites* prepollen. OUPH 17229. Bar = 0.02 mm. *E*, SEM of *Potonieisporites* prepollen showing saccus and central body with monolete suture. OUPH 17217. Bar = 0.02 mm.

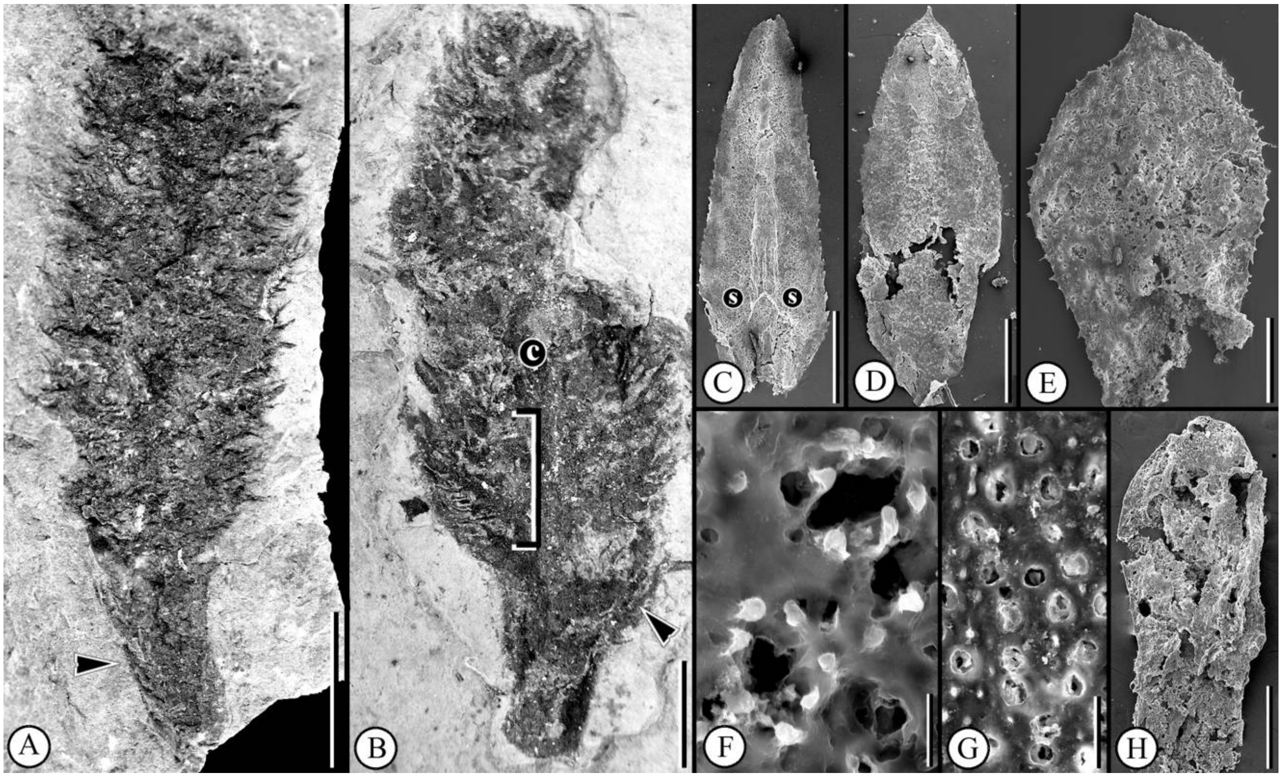

Fig. 9 *Emporia lockardii* ovulate cones and SEM of sterile scales and megasporophylls (specimens macerated from OUPH 17371). *A*, Mature cone on penultimate shoot with leaves at base (arrowhead). OUPH 17370. Bar = 1 cm. *B*, Incomplete cone showing cone axis (*c*), bract (arrowhead), and axillary dwarf shoot (bracket). OUPH 17376. Bar = 0.5 cm. *C*, Adaxial surface showing lanceolate shape, marginal trichomes, and two broad bands of stomata (*s*). Bar = 1 mm. *D*, Abaxial surface showing ellipsoidal shape and trichome bases. Bar = 1 mm. *E*, Abaxial surface showing widely obovate shape and trichome bases. Bar = 0.5 mm. *F*, Sterile scale showing adaxial stomatal complexes with overarching papillae. Bar = 0.02 mm. *G*, Sterile scale showing abaxial surface with several trichome bases. Bar = 0.05 mm. *H*, Adaxial surface of megasporophyll. Bar = 0.5 mm.

skerpia Rothwell, Mapes & Hernandez-Castillo (Emporiaceae Mapes & Rothwell). With the exception of *H. hamiltonensis* (which lacks pollen cones), each of these species is known from a reconstruction that is based on all of the above ground organs (Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005). *Barthelia* was originally considered to be a coniferophyte s.l. rather than a conifer s.s. on basis of several ovulate fertile zone characters (Rothwell and Mapes 2001). However, further character reevaluation and inclusion in phylogenetic analyses demonstrated that *Barthelia* should be regarded as a walchian conifer genus (Rothwell et al. 2005). Both *Barthelia* and *Hanskerpia* are monotypic, while *Emporia* is now known to comprise three distinct species (Hernandez-Castillo 2005). Recognizing this rich diversity of conifer taxa as whole plants at Hamilton Quarry is very informative because it reinforces previous observations of high conifer species diversity based on conifer morphotaxa and previously reconstructed species of conifer plants (i.e., Florin 1938–1945; Rothwell 1982; Broutin and Gisbert 1985; El Wartiti et al. 1986; Mapes and Rothwell 1988; Broutin et al. 1990, 1998; Kerp et al. 1990; Lausberg and Kerp 2000; Hernandez-Castillo et al. 2001*a*, 2001*b*; Rothwell and Mapes 2001; Hernandez-Castillo 2005; Rothwell et al. 2005; Looy 2007). Localities such as Hamilton Quarry provide evidence for the initial diversity (Pennsylvanian) of walchian conifers, while younger localities (early to late Permian) serve as evidence for the diversification of walchian and voltzialean conifers (Clement-Westerhof 1987; Kerp et al. 1990; Schweitzer 1996; Looy 2007).

The Pennsylvanian-Permian Vegetational Turnover in Euramerica and Ecology of Early Conifers

The Carboniferous-Permian boundary is characterized by a vegetational transition at most sites in Euramerica that is the result of a turnover in floral composition in both late Paleozoic basins and in extra-basinal habitats (Kerp 2000; DiMichele 2007). Traditionally, basinal regions were dominated by "wetland" floras composed of many water-dependent lineages of plants (i.e., lycophytes, sphenophytes, lyginopterid and medullosan seed ferns, etc.) and extra-basinal or "upland" regions dominated by "dryland" floras represented mainly by seed plants, marattiaceous ferns, and a few lycophytes (Rothwell and Mapes 1988; Lyons and Darrah 1989; Broutin et al. 1990; DiMichele and Aronson 1992).

However, recent work on different localities throughout the world indicates that the traditional "wet" and "dry" contrast of floral composition is erroneous. This new evidence implies

Table 1

Comparison of Morphological and Cuticular Characters of Leaves on Vegetative and Fertile Organs of *Emporia lockardii*

					Stomata			Papillae			
Organs/characters	Shape (FV)	Shape (SV)	Length (mm)	Width (mm)	Structure	Distribution (adaxial/abaxial)	No. stomata/band	Subsidiary cell number	Subsidiary cells	Epidermal cells	Trichome bases (adaxial/abaxial)
Leaves on penultimate shoots	Nt, Li, Fr	Sc, sSs	5–10	1.0–2.1	Monocyclic	Two long bands/ two basal short, narrow bands or individual rows	2–5	6–8	Erect	Few or none	Few, none/ abundant
Leaves on ultimate shoots	Nt, Li	Sc, sSs	1.7–5.0	.4–1.1	Monocyclic	Two long bands/two narrow bands or individual rows	2–5 (8)	5–9	Overarching	Few to abundant	Few, none/ abundant
Leaves on branches attached to pollen cones	Nt, Sl, Li	Sc, sSs	3–5	1.6–2.2	Monocyclic	Two long bands/two individual rows	2–5	5–7	Overarching	Few or none	Few, none/ abundant
Microsporophylls	Tr	Sc	.25–5.0	2–3	Monocyclic	Two long bands/few scattered or none	2–4	4–5	Overarching	Abundant	None/abundant
Leaves on branches attached to ovulate cones	Nt, Li, Fr	Sc, sSs	7–10	1–2.1	Monocyclic	Two long bands/two short, narrow bands or ind. rows	2–5	6–8	Erect	Few or none	Few, none/ abundant
Bracts of ovulate cones	Nt, Li, Fr	Sc, sSs	8–21	2–3	Monocyclic	Two long bands/two short, narrow bands or individual rows	2–5	6–8	Erect	Few or none	Few, none/ abundant
Sterile scales of ovulate cones	El, La, Wo	Sc, sSs	2.1–4.3	1.3–1.8	Monocyclic	Two long bands/two narrow bands or individual rows	2–5	6–7	Erect, overarching	Few or none	Few, none/ abundant

Note. FV = leaves in face view; SV = leaves in side view. Leaf shape abbreviations: El = elliptical, Fr = forked tip, Li = linear, La = lanceolate, Nt = narrowly triangular, Sc = slightly concave, Sl = slightly lanceolate, sSs = slightly S-shaped, Tr = triangular, Wo = widely oblong.

Table 2

Whole-Plant Characters of *Emporia lockardii*

Growth architecture/vegetative branches	Stem anatomy	Pollen cones	Ovulate cones	Seeds
Stem: orthotropic	Stele type: endarch stele	Cone type: simple	Cone type: compound	Sterile scale number: 14–30
Branch type: plagiotropic	Pith organization: resin rodlets or sclerotic nests in ground tissues	Cone position: terminal	Cone position: terminal	Sterile scale organization: interspersed among sporophylls
Leaf morphology: simple	Primary xylem: tracheids with helical to scalariform wall thickenings	Order of attached branch: ultimate shoot	Order of attached branch: penultimate shoot	Sterile scale location: adaxial and apical
Heterophylly: position dependent	Wood: pycnoxylic	Leaves on attached branch: same as vegetative ultimate leaves	Leaves on attached branch: forked and similar to leaves on penultimate shoots	Sporophyll number: 1–3
Leaf distribution: penultimate shoots with simple and forked leaves	Secondary xylem: tracheids, uniseriate to biseriate, circular bordered pits	Microsporophyll type: simple	Bract type: forked	Sporophyll organization: free from sterile scales
Leaf distribution: ultimate shoots with simple leaves	Wood rays: uniseriate to biseriate, 1–8 cells high	Microsporophyll shape: peltate	Bract length: equal to slightly larger than axillary dwarf shoot	Seed type: winged
Leaf stomatal distribution: amphistomatic, two adaxial bands and abaxial short, narrow bands or individual rows	Bark: sparse	Microsporophyll stomatal distribution: two to four bands of adaxial stomata and abaxial trichome bases	Bracts stomatal distribution: amphistomatic, two bands of adaxial stomata and two abaxial short, narrow bands or individual rows	Seed shape and symmetry: ellipsoidal, bilateral
		Pollen sac position and number: adaxial on stalk, eight to 14	Bract attachment to dwarf shoot: free from bract	Seed ornamentation: pilose
		Prepollen grains: monosaccate, *Potonieisporites* Bharadwaj	Dwarf shoot symmetry: bilateral, dorsiventral	Seed anatomy: three-layered integument, simple pollen chamber, and nucellar beak

Table 3

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

Taxa/characters	Stem	Lateral branches	Penultimate leaves	Ultimate leaves	Heterophylly[a]	Stomatal distribution (vegetative leaves)	Stomatal pattern (adx/abx)	Pollen cone	Pollen cone attached branch/ leaves	Microsporophylls (type, shape, stomatal distribution)	Pollen sacs	Source
Emporia lockardii	Orthotropic?	Plagiotropic	Simple and forked	Simple	Position dependent	Amphistomatic, monocyclic	2 bands/2 short, narrow bands or individual rows	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, peltate, 2–4 narrow bands/absent	Adaxial, 8–14	Mapes and Rothwell 1984, 1991
Hanskerpia hamiltonensis	Orthotropic?	Plagiotropic	*Forked*	Simple	Position dependent	Amphistomatic, monocyclic	**Parallel rows/ parallel rows**	?, ?	?, ?	?, ?, ?	?,?	Rothwell et al. 2005
Thucydia mahoningensis	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. 2001*b*
Utrechtia floriniformis	Orthotropic?	Plagiotropic	*Forked*	Simple	Position dependent	Amphistomatic, monocyclic	2 bands/*2 bands*	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, peltate, ?	Adaxial, ?	Mapes and Rothwell 1991
Walchia garnettensis	?	Plagiotropic	Simple	Simple	**Absent**	Amphistomatic, monocyclic	2 long bands/ **few scattered**	Simple, terminal	?, ?	Simple, ?, 1–2 narrow bands/ **2 narrow bands forming rows later**	?, ?	Emended by Winston (1984)
Otovicia hypnoides	?	Plagiotropic	*Forked*	Simple	Position dependent	**Primarily adaxial, mono-inc** dicyclic	2 bands/**scattered**	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, peltate, 2 long bands/ **few stomata groups**	Adaxial, ?	Kerp et al. 1990
Ernestiodendron filiciforme	?	Plagiotropic	Simple	Simple	**Absent**	Amphistomatic, **mono-inc** dicyclic	**Parallel rows/ parallel rows**	Simple, terminal	Ultimate, simple as veg. ult. leaves	Simple, peltate, ?	?, ?	Florin 1938–1945
Barthelia furcata	?	**Irregular**	*Forked*	**Simple and forked**	**Size dependent**	**Adaxial,** monocyclic	2 bands/**absent**	Simple, terminal	**?, forked as veg. leaves**	**Forked, leafy,** 2 long bands with rows/ absent	Adaxial, ?	Rothwell and Mapes 2001

Note. Characters that differ from those of *Emporia lockardii* are recorded in boldface type; overlapping characters are recorded in italics. adx = adaxial surface, abx = abaxial surface; veg. = vegetative, ult. = ultimate; mono-inc = monocyclic to incompletely dicyclic stomata.

[a] Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known; see types in Hernandez-Castillo et al. 2001*b*; Hernandez-Castillo 2005.

Table 4

Comparison of Prepollen and Ovulate Cone Characters of *Emporia lockardii* sp. nov. and Other Paleozoic Conifers

Taxa/characters	Prepollen	Compound ovulate organ	Attached branch to Oc/Fz and leaves	Leaves on attached shoot		Bract	Bract and ovuliferous dwarf shoot	Dwarf shoot symmetry	Sterile scale position/ number	Sporophyll position/ number	Ovules/seeds	
				Stomata type	Stomatal distribution						Position, type	Shape, symmetry
Emporia lockardii	*Potonieisporites*, monosaccate	Cone, terminal	Penultimate, forked	Amphistomatic, monocyclic	2 bands/2 short, narrow, individual rows	Forked, equal to larger than dwarf shoot	Separate throughout	Bilateral	All around, 14–30	Interspersed with Ss, 1–3	Terminal, inverted	Ellipsoidal, bilateral
Hanskerpia hamiltonensis	?, ?	**Cone/zone?**	Penultimate, forked	Amphistomatic, monocyclic	**Parallel rows/ parallel rows**	Forked, **much larger than dwarf shoot**	**Fused at base**	Bilateral	All around, **<15?**	Interspersed with Ss, **1–2**	Terminal, inverted	Ellipsoidal, bilateral
Thucydia mahoningensis	*Potonieisporites*, monosaccate	**Fertile zone, intercalary**	Penultimate, **simple**	**Adaxial**, mono-cyclic	Two bands/ **absent**	**Simple, larger than dwarf shoot**	Separate throughout	Bilateral	All around, **10–15**	**Terminal, 3–4**	Terminal, inverted	Ellipsoidal, bilateral
Utrechtia floriniformis	*Potonieisporites*, monosaccate	Cone, terminal	Penultimate, forked	Amphistomatic, monocyclic	2 bands/ **2 bands**	Forked, **larger than dwarf shoot**	Separate throughout	Bilateral	All around?, >10	**Terminal,** ***1***	Terminal, inverted	Ellipsoidal, bilateral
Walchia garnettensis	*Potonieisporites*, monosaccate	Cone, terminal	Penultimate, **simple?**	Amphistomatic, monocyclic	2 bands?/?	Forked; equal to, larger than dwarf shoot	?	Bilateral	?, <*5*?	?, ≥*3*?	?, ?	?, ?
Otovicia hypnoides	*Potonieisporites*, monosaccate	Cone, terminal	Penultimate, **simple?**	**Primarily adaxial, monocyclic**	2 bands/**few groups**	Forked, **larger than dwarf shoot**	Separate throughout	Bilateral	All around?, ***12–18***	Interspersed with Ss, ***2***	Terminal, inverted	Ellipsoidal, bilateral
Ernestiodendron filiciforme	?, ?	Cone, terminal	Penultimate, **simple**	Amphistomatic, **mono-inc** dicyclic	**Parallel rows/ parallel rows**	Forked, **larger than dwarf shoot**	Separate throughout	Bilateral	All around?, **5–10**	**Terminal, 1**	Terminal, inverted	Ellipsoidal, bilateral
Barthelia furcata	*Potonieisporites*, monosaccate	**Fertile zone, intercalary**	Penultimate, forked	**Adaxial**, mono-cyclic	2 bands/**absent**	Forked, **larger than dwarf shoot**	Separate throughout	**Radial**	All around, >10	Interspersed with Ss, **?**	Terminal, inverted?	Ellipsoidal, bilateral

Note. Characters that differ from those of *Emporia lockardii* are recorded in bold face type. Overlapping characters are recorded in italics. References as in table 3. Oc/Fz = ovulate cone/fertile zone; Ss = sterile scales; mono-inc = monocyclic to incompletely dicyclic stomata. Stomatal distribution of both adaxial/abaxial surfaces.

that more than two ("dry" and "wet") vegetation types coexisted simultaneously in Euramerica during the Carboniferous and Permian (DiMichele et al. 2008). These vegetation types or biomes seemed to have depended mostly on climatic and edaphic conditions at different spatiotemporal scales. The Hamilton Quarry contains a conifer-dominated flora that corresponds to one of the four main vegetation types or biomes now recognized during the Paleozoic (DiMichele et al. 2008).

The Pennsylvanian-Permian vegetation turnover is correlated with drying conditions in many Pennsylvanian/Permian basins throughout Euramerica (DiMichele and Aronson 1992; Roscher and Schneider 2006) and Pangea (DiMichele et al. 2008 and citations therein). Although, this growing aridity was global, different basins reflect slightly different patterns of climatic change in Euramerica due to their unique paleoclimatic, paleogeographic and paleotopographic characteristics (Broutin et al. 1998; Roscher and Schneider 2006). Climatic patterns at different spatiotemporal scales suggest that not all regions experienced increasing aridity simultaneously, resulting in some regions within Pangea that remained humid throughout the Permian. The best example of humid climatic regions are the Late Pennsylvanian-Permian floras of North China (Hilton and Cleal 2007). North China Permian floras contain wetland plant communities similar to those of earlier communities (Pennsylvanian) in Euramerica.

Climatic conditions in Pangea have been linked to plate movements, the Variscan Orogeny, and Pennsylvanian glaciations with consequent changes in eustatic water levels and modification of lowland basinal settings (Hilton and Cleal 2007). As in today's environments, many climatic, geographic, topographic, and edaphic factors influenced basinal and extra-basinal regions during the Pennsylvanian-Permian transition. All these factors combined with increasing aridity in many regions of Euramerica probably favored the movement of taxa from extra-basinal environments into the basins as water availability diminished and seasonal dryness intensified during the Permian. Thus, successive pulses of climatic drying allowed extra-basinal floristic elements, such as conifers, to be increasingly represented in basinal floras and into the fossil record during the Early and Late Permian (DiMichele and Aronson 1992; Kerp 2000; Looy 2007).

Many taxa in extra-basinal areas, including conifers, probably inhabited stressed environments with low water availability and/or extreme exposure to sunlight and/or well-drained habitats with humid conditions (DiMichele and Aronson 1992; Kerp et al. 1996; Falcon-Lang 2003; DiMichele et al. 2008). Conifers are certainly one the most important lineages with which this vegetational turnover has been correlated throughout Euramerica (Florin 1938–1945; Lyons and Darrah 1989; Broutin et al. 1990, 1998; Lopez et al. 2005; DiMichele 2007). "Lebachioid" (Rothwell et al. 2005) conifer plant species, including *E. lockardii*, at the Hamilton Quarry provide exceptionally good evidence for this initial rise of conifer diversity in extra-basinal environments of Euramerica.

Plant Architecture and Paleoecology

Tree architecture of the most ancient species suggests that late Pennsylvanian walchian conifer plants were small trees bearing plagiotropic lateral branches covered by small, simple (and/or less often forked) leaves and that produced terminal cones on the same branches (Lausberg 2002; Hernandez-Castillo et al. 2003). The diminutive stature of early walchian conifer trees coupled with abundant wood suggests the relatively slow growth that is characteristic of plants in water-stressed environments (Grime 1977).

This slow growth for walchian conifers contrasts with that of their closest relatives, the Cordaitales (Stewart and Rothwell 1993) and late Permian conifers within the voltzian Voltziales clade (Rothwell et al. 2005). Many cordaitalean species seem to have grown as large trees in comparison to the diminutive trees produced by initial walchian conifers. Cordaitaleans are a complex group that grew mainly in wetlands; however, there is evidence suggesting that some cordaitaleans may have lived in extra-basinal areas, forming gallery forests composed of large trees (Rothwell and Mapes 1988; Simunek 2000; DiMichele et al. 2008). Similarly, some Early and Late Permian conifers may have been larger trees than those of the initial Pennsylvanian conifer radiation. For example, a single walchian conifer branch from the Central Massif in France shows large vegetative shoots and leaves similar to that of mature individuals of living *Araucaria heterophylla* (Salisb.) Franco (G. Hernandez-Castillo, personal observation). The presence of extra-basinal cordaitaleans and Permian conifers suggests the presence of trees larger than those of the initial walchian conifer radiation. These large trees may be responsible for some of the large coniferophyte trunks found in Permian localities that have been traditionally and informally assigned to conifers. However, we do not know which of the coniferophytic plants produced the large trunks.

Additional adaptations of *E. lockardii* and other early conifers to water-stressed environments include very thick leaf cuticles, mostly adaxially located bands of stomata, and numerous epidermal papillae (adaxial) and trichomes (abaxial) covering all leaflike organs of the plant (i.e., microsporophylls, sterile scales, seeds, etc.). These adaptations have been widely used to explain how early conifers may have reduced direct UV incidence on leaves, pollen, and ovulate cones. Such adaptations also can be employed to explain stomatal efficiency by improving gas exchange and preventing water loss from the plant, supporting traditional views that place early conifers in water-stressed environments (Florin 1951; Kerp et al. 1990; Rothwell et al. 1997). However, some of the same characters are sometimes also associated with more mesic habitats (Haworth and McElwain 2007). The large number of adaptations for water-stressed environments displayed by *E. lockardii* reinforces the widely held interpretation that walchian conifers grew in dry or seasonally dry environments, where plant speciation would be expected to occur most frequently (DiMichele and Aronson 1992).

The new whole plant concept of *E. lockardii* developed in the current study reveals distinct ranges of morphological and cuticular variation within a single species of fossil conifer plants and a novel combination of characters for a walchian conifer. This reconstruction and previous conifer reconstructions from the Hamilton Quarry reinforce the notion that isolated organs do not reveal the entire suite of characters required to recognize and characterize a single species of fossil conifer plant. *Emporia lockardii* is the third conifer plant to be reconstructed from the Hamilton Quarry. This species, together with two new species of the genus *Emporia* (Hernandez-Castillo 2005) that are yet to be described, make the Hamilton Quarry the only Paleozoic locality in the world where all conifer remains are now understood as whole plants (Hernandez-Castillo 2005).

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