Anatomically preserved early Cretaceous lycophyte shoots; enriching the paleontological record of Lycopodiales and Selaginellales

GAR W. ROTHWELL[1,2*] and RUTH A. STOCKEY[2]

[1]Department of Environmental and Plant Biology, Porter Hall, Ohio University, Athens, Ohio, 45701 USA;
e-mails: rothwell@ohio.edu; rothwelg@oregonstate.edu, ORCID: 0000-0003-0186-6546

[2]Department of Botany and Plant Pathology, Cordley Hall, Oregon State University, Corvallis, OR 97331
USA; e-mail: stockeyr@oregonstate.edu, ORCID: 0000-0003-4984-9892

ABSTRACT. Anatomically preserved lycophytes of the Lycopodiales and Selaginellales have been discovered among a diverse assemblage of plants and fungi in carbonate marine concretions at the Apple Bay locality along the shore of Holbert Inlet near the northern end of Vancouver Island, British Columbia, Canada. Lycopodialean stems are plectostelic and actinostelic, branch dichotomously, and are similar to both *Lycopodicaulis oellgaardii* and *Lycoxylon* spp. The *Selaginella* specimens represent the first anatomically preserved Selaginellales with excellent internal cellular preservation in the fossil record, and are described as *Selaginella quatsinoense* Rothwell et Stockey sp. nov. Stems have three and five exarch, monarch stelar segments, each of which is surrounded by an aerenchymatous endodermis with trabeculae. The leaf base is indented on the adaxial surface, suggesting the position of a ligule. These fossils document that species with diagnostic internal anatomy of modern Lycopodiales and Selaginellales evolved no later than the Valanginian of the early Cretaceous.

KEYWORDS: Anatomy, Early Cretaceous, *Lycopodicaulis*, Lycopodiales, *Selaginella*, Selaginellales

INTRODUCTION

As one of the two major clades of living vascular plants, lycophytes have a fossil record that extends from the Silurian onward (Thomas, 1992; Kenrick and Crane, 1997; Wikström, 2001; Taylor et al., 2009). Woody, rhizomorphic taxa of the Isoetales (including Lepidodendrales, Pleuromeiales, and Isoetales *sensu* Stewart and Rothwell, 1993) are abundantly represented in Paleozoic, Mesozoic and Cenozoic deposits (Skog and Hill, 1992; Pigg, 1992, 2001; DiMichele et al., 2001, 2022; Taylor et al., 2009). By contrast, herbaceous specimens assignable to the Lycopodiales and Selaginellales are restricted primarily to compression/impression fossils (e.g. Knowlton, 1916; Skog and Hill, 1992; Thomas, 1992; Bateman et al., 2007; Salvi et al., 2008; Cariglino et al., 2023) of highly variable preservational quality. Such lycopodialean taxa can be distinguished from selaginellaleans by the presence of only one type of spore in the strobili (i.e. homosporous life cycle; Zeiller, 1906) and by the absence of a ligule at the base of leaves and sporophylls. Selaginellalean species are heterosporous (i.e. producing both megaspores and microspores) and ligulate (Eames, 1936). While some herbaceous compression/impression lycophyte fossils show these features quite clearly (e.g. Salvi et al., 2008), many either lack fertile parts and/or are not preserved well enough to unequivocally recognize the presence (or absence) of ligules. As a result, they cannot be assigned

* Corresponding author

with confidence either to Lycopodiales or to Selaginellales. One diverse assemblage of fossilized *Selaginella* species with superb preservation has been reported from mid Cretaceous Burmese Amber (Schmidt et al., 2020). Those fossils show exquisite details of external plant form and cellular patterns, but preservation of internal tissues at the cellular level is minimal (see Fig. 2a of Schmidt et al., 2020, 2022; Li et al., 2022).

Although living species of both Lycopodiales and Selaginellales have systematically diagnostic stelar architectures and associated anatomical features (Eames, 1936; Herrera et al., 2022), the paucity of permineralized specimens from the fossil record has left the origin and pattern of evolution for these orders of herbaceous lycophytes far less fully undertsood than for the Isoetales (e.g. Pigg, 1992, 2001; DiMichele et al., 2001, 2022). With the exception of the basal Carboniferous, actinostelic *Hestia eremosa* Bateman, Kenrick et Rothwell (2007) and early Cretaceous stems assignable to *Lycoxylon* Srivastava spp. (Srivastava, 1946; Banerji, 2000) and *Lycopodicaulis oellgaardii* F. Herrera, Testo, A.R. Field, E. Clark, Herend., P.R. Crane et G. Shi (Herrera et al., 2022), lycopodialean fossils with preserved internal anatomy have not been described. Selaginellales are even less commonly encountered as anatomically preserved fossils showing excellent internal cellular structure (Schmidt et al., 2020), the material included in this study being the first well-documented occurrence.

In the current study we introduce and characterize permineralized specimens of both Lycopodiales and Selaginellales from early Cretaceous deposits of Western Canada. The lycopodialean material is assigned to *Lycopodicaulis oellgaardii* (Herrera et al., 2022) because it includes leafy stems with well-preserved stelar architecture, cortical tissues and leaves, but it also bears a striking resemblance to *Lycoxylon* Srivastava spp. (e.g. Srivastava, 1946; Banerji, 2000). Selaginellalean specimens are described as *Selaginella quatsinoense* Rothwell et Stockey sp. nov. These fossil stems resemble living species in several subgenera of *Selaginella*, but do not preserve specifically diagnostic characters needed for assignment to

any. Nevertheless, *S. quatsinoense* does demonstrate that modern appearing internal anatomy, including multi-bundle *Selaginella* stelar architecture were present in the Mesozoic. Recognition of these lycophytes meaningfully enriches the fossil record for herbaceous lycophytes, and demonstrates that species with modern-appearing anatomy evolved no later than the early Cretaceous.

MATERIALS AND METHODS

LOCALITY AND AGE

Deposits containing a diverse assemblage of permineralized plants and fungi, as well as invertebrates and trace fossils are exposed for a few hundred meters along the beach at Apple Bay, located at Holbert Inlet on Quatsino Sound at the northern end of Vancouver Island, British Columbia, Canada (50°36′ 21″N, 127°39′25″W; Gierlowski-Kordesch et al., 2021; Klymiuk et al., 2022). Specimens of Lagerstätten quality are enclosed within calcareous marine concretions imbedded within fine- to medium-grained sandstones and siltstones (Gierlowski-Kordesch et al., 2021). These deposits have been tentatively correlated with the upper Kyuquot Group or the Longarm Formation (Haggart 1991, 1996), and regarded as the Valanginian Stage of the early Cretaceous (Smith et al., 2003; see Gierlowski-Kordesch et al., 2021 for a detailed discussion of stratigraphy and age).

METHODS

Plant fragments are preserved by calcareous cellular permineralizaton within small carbonaceous marine concretions that have been cut into wafers 0.5–1.0 cm thick to expose fossils on the surfaces. Thin sections of each surface were prepared by the classical cellulose acetate peel technique (Joy et al., 1956), and fossils were identified from the peel sections. Specimens were prepared for study as serial sections, mounted on glass microscope slides with the xylene soluble mounting medium Eukitt (O. Kindler, Freiburg, Germany), measured, and photographed with transmitted light. Images were captured with a Better Light digital scanning camera back (Better Light, Placerville, California, USA), and focused through a Leitz Aristophot large-format bellows camera using a Zeiss WL compound microscope. Images were processed using Adobe Photoshop CS5 extended (Adobe Systems Inc., San Jose, California, USA). Concretion wafers, peels, and microscope slides are housed in the Paleobotanical Collections at the University of Alberta (UAPC-ALTA), Edmonton AB, Canada.

SYSTEMATICS

Class LYCOPODIOPSIDA

Order LYCOPODIALES

Family LYCOPODIACEAE
P. Beauv. Mirbel

Subfamily LYCOPODIOIDEAE

Genus *Lycopodicaulis*
F. Herrera, Testo, A.R. Field, E. Clark,
Herend., P.R. Crane et G. Shi 2022

Lycopodicaulis oellgaardii F. Herrera,
Testo, A.R. Field, E. Clark, Herend.,
P.R. Crane et G. Shi 2022

Figs 1, 2

Description. The Apple Bay specimens of *Lycopodicaulis oellgaardii* include stems with closely spaced leaves (Fig. 1A), stems that have a smooth outer margin (Fig. 1B), and stems that have an irregular outer margin of the cortex (Fig. 1D, E). Dichotomous branching of the stems is both isostomous (Fig. 1E) and slightly anisostomous (Fig. 1C). Stems range 0.8–1.7 mm in diameter, with an exarch stele that is plectostelic in the largest stems (Fig. 1A–C; Fig. 2A, B), actinostelic in the smallest stems (Fig. 1E), and of intermediate form in stems of intermediate size (Fig. 1E). The number of protoxylem strands ranges from 6 in the smallest actinosteles (Fig. 1E) to ~30 in the largest plectosteles (Fig. 2B). Protoxylem tracheids are ~7–15 mµ in diameter, while metaxylem tracheids range 25–40 µm.

In the fossil stems, tracheids of the stelar ridges (i.e. actinosteles) or plates (i.e. plectosteles) are separated and/or surrounded by empty space (Figs 1A–E, 2A, B). This is comparable to many specimens of living Lycopodiales (see Herrera et al., 2022), but in the most well-preserved living specimens such areas often are occupied by delicate cells of xylem parenchyma, phloem, and parenchymatous inner cortex (e.g. fig. 3 of Herrera et al., 2022). Two zones of cortex are preserved in most stems (Fig. 1C–E), but in others the zonation is less obvious (Fig. 1A, B). Toward the interior most stems have 3–6 layers of thick-walled cells that range 15–40 µm in diameter, and toward the exterior the cells have conspicuously thinner walls.

In cross section, leaves preserved at the margin of stems are lenticular in shape (Fig. 1A, at right; Fig. 2C), with a conspicuous epidermis and mesophyll of less completely preserved parenchyma cells. Serial sections through intervals where leaves diverge reveal no evidence of ligules, confirming that the stems are eligulate. Discontinuities in the leaf epidermis that are flanked by conspicuously smaller guard cells represent the positions of stomata (Fig. 2C, at arrow), as they also do in leaves of living lycopodialean species (Fig. 2D, at arrow). Also, by comparison to living species of Lycopodiales (Fig. 2D, small leaf traces of the fossil can be identified by faint cells at the center of the leaf, where tracheids of the terete bundle otherwise are incompletely preserved (Fig. 2C, at vb).

Class LYCOPODIOPSIDA

Order SELAGINELLALES

Family SELAGINELLACEAE
Wilk ex Wilk et Lang

Genus *Selaginella* Pal. Beauv.

Selaginella quatsinoense
Rothwell et Stockey **sp. nov.**

Figs 3, 4

Combined generic and specific diagnosis. Plants with small herbaceous, leafy stems having 3–5 exarch, monarch xylem bundles, each surrounded by aerenchymatous endodermis with trabeculae. Cortex parenchymatous, grading to multiseriate hypodermis of thicker walled cells; uniseriate epidermis with anomocytic stomata. Leaves linear with single trace and ligule pit at base.

Holotype. Stem in cross section in P13,307 C bot and 13,307 D top (Figs 3A, C–F, 4A, B).

Repository. Paleobotanical Collections, University of Alberta, Edmonton, Alberta, Canada (UAPC-ALTA).

Type Locality. Beach at Apple Bay, Quatsino Sound, Holberg Inlet, Vancouver Island, British Columbia, Canada (50°36′21″N latitude, 127°39′25″W longitude).

Stratigraphic Horizon and Age. Calcareous marine concretions within fine- to medium-grained sandstones and siltstones of
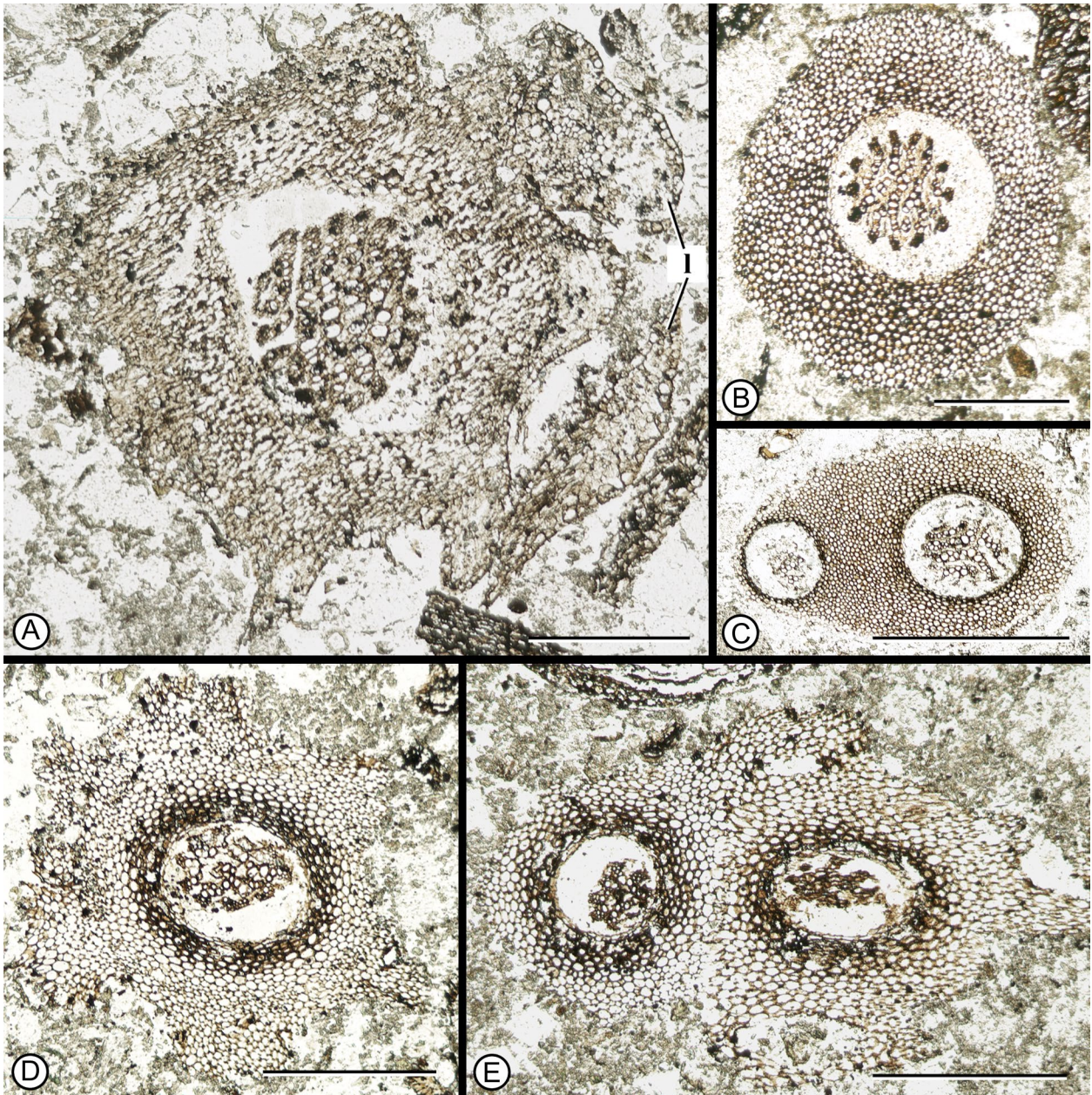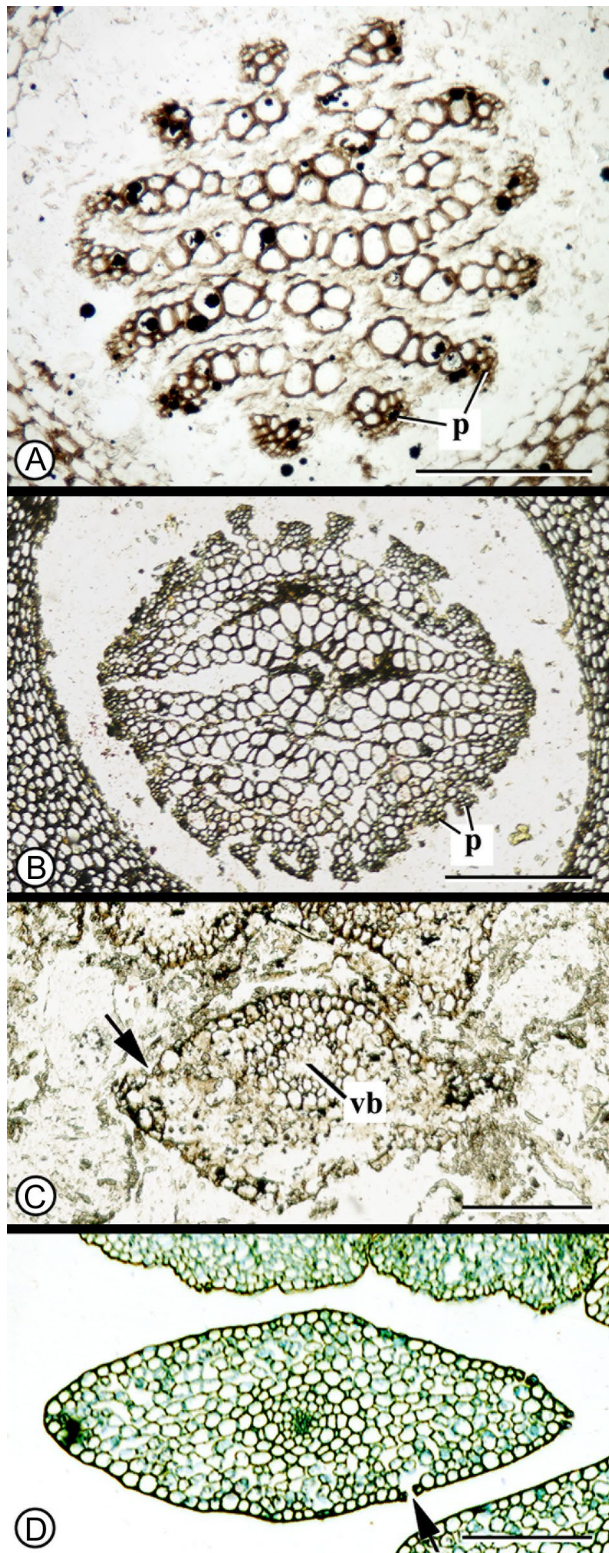
Figure 1. *Lycopodicaulis oellgaardii* from the Upper Cretaceous of western Canada. **A**. Cross section of plectostelic stem with adjacent leaves (l), UAPC-ALTA P13,303 D top No. 49 ×55; **B**. Cross section of plectostelic stem with smooth outer margin, UAPC-ALTA P13,307 C Top No. 27 ×45; **C**. Anisotomously branching actinotelic stem with smooth outer margin, UAPC-ALTA P13,307 A No. 22 ×33; **D**. Actinostelic stem with highly irregular margin of outer cortex, UAPC-ALTA P13,307 B bot. No. 30 ×60; **E**. Isostomously branching actinostelic stem with irregular outer margin of cortex, UAPC-ALTA P13,307 C Top No. 28 ×64. Scale bars = 500 µm in A, B, D, E; 1 mm in C

the Upper Kyuquot Group, Longarm Formation equivalent, early Cretaceous (Valanginian).

Etymology. The specific epithet *quatsinoense* refers to the location of the collecting locality in Quatsino Sound, Vancouver Island, British Columbia, Canada.

Description. Three specimens of *Selaginella quatsinoense* have been discovered at Apple Bay. One (the holotype) is exposed in cross section (Figs 3A, C–F, 4A, B), while the other two are oriented in oblique views (Fig. 3B, G).

The holotype has a maximum diameter of 1.0–1.1 mm and three stelar segments that are separated by cortical parenchyma (Fig. 1A). One of the other stems also has three stelar segments, while the third stem has five (Fig. 3B). Each stelar segment consists of an exarch monarch xylem bundle surrounded by a hollow space (Figs 3A, C, 4A). In a few sections fragments of trabeculae are preserved attached to the cortex, and extend toward the xylem bundle (Fig. 3F, at arrow). Each trabecula is uniseriate, and consists of cells that are ~15 µm in diameter.

Figure 2. *Lycopodicaulis oellgaardii* from the Upper Cretaceous of western Canada, and *Lycopodium clavatum*. **A**. Exarch plectostele with protoxylem strands (p) at periphery of stele. UAPC-ALTA P13,307 C top No. 29 ×140; **B**. Exarch plectostele with numerous protoxylem strands (p) and sclerotic inner cortex. UAPC-ALTA P13,158 A No. 5a ×45; **C**. Cross section of leaf with prominent epidermis showing stomata (arrow) and incompletely preserved tracheids of leaf trace (vb). UAPC-ALTA 13,303 D top No. 49 ×100; **D**. Cross section of *Lycopodium clavatum* leaf with prominent epidermis showing stomata (arrow) and terete leaf trace. ×103. Scale bars = 200 µm in A, C, D; 500 µm in B

The cortex is largely parenchymatous, consisting of thin-walled cells that range 15–60 µm in diameter. As also is characteristic of living species of *Selaginella*, cells of the innermost layer of cortex surrounding each stelar segment are distinctive. Such cells have somewhat thicker walls than the remainder of the cortex, and show slightly darker lumina (Figs 3A–C, 4A). The hypodermis consists of several layers of somewhat smaller cells than the rest of the cortex. Such cells are 12–40 µm in diameter, with more prominent and slightly thicker walls (Fig. 3A, C, E). The outer margin of the stems is irregular and appears to have suffered pre-preservational abrasion (Fig. 3D, E), but in one area adjacent to a diverging leaf there is a uniseriate epidermis of closely spaced rectangular cells (Fig. 4A, at arrowhead).

One leaf base is preserved as part of the holotype (Fig. 4B). That base is consistent with a linear leaf, but is abraded on the abaxial surface (Fig. 4B) and truncated somewhat distal to divergence from the stem. In the series of sections immediately proximal to the incipient leaf base, a terete leaf trace diverges from the adjacent stelar segment and extends toward the leaf (Fig. 4A, at lt). Progressing distally, the leaf trace enters the leaf base (Fig. 4B), and then the leaf base separates from the stem (Fig. 4B). The preserved segment consists primarily of cells comparable to those of the stem hypodermis, and also has short segments of adaxial epidermis (Fig. 4B, at arrowheads).

There is a conspicuous indentation at the center of the adaxial surface of the leaf base (Fig. 4B, at gp?). This feature (Fig. 4B) corresponds to the position of the glossopodium of the ligule in living *Selaginella*, which otherwise is not preserved. A small segment of adaxial leaf surface is represented by closely spaced rectangular epidermal cells (Fig. 4A, at lower right, Fig. 4B, at arrowhead). Epidermal cell walls are darker at the periphery of the leaf, suggesting the presence of a thin cuticle (Fig. 4B, at arrowhead).

DISCUSSION

### ANATOMICALLY PRESERVED LYCOPODIALEAN FOSSILS

Herbacous protostelic stems similar to those of living lycopodialeans are uncommon in the fossil record. With the possible exception of the lowermost Mississippian age
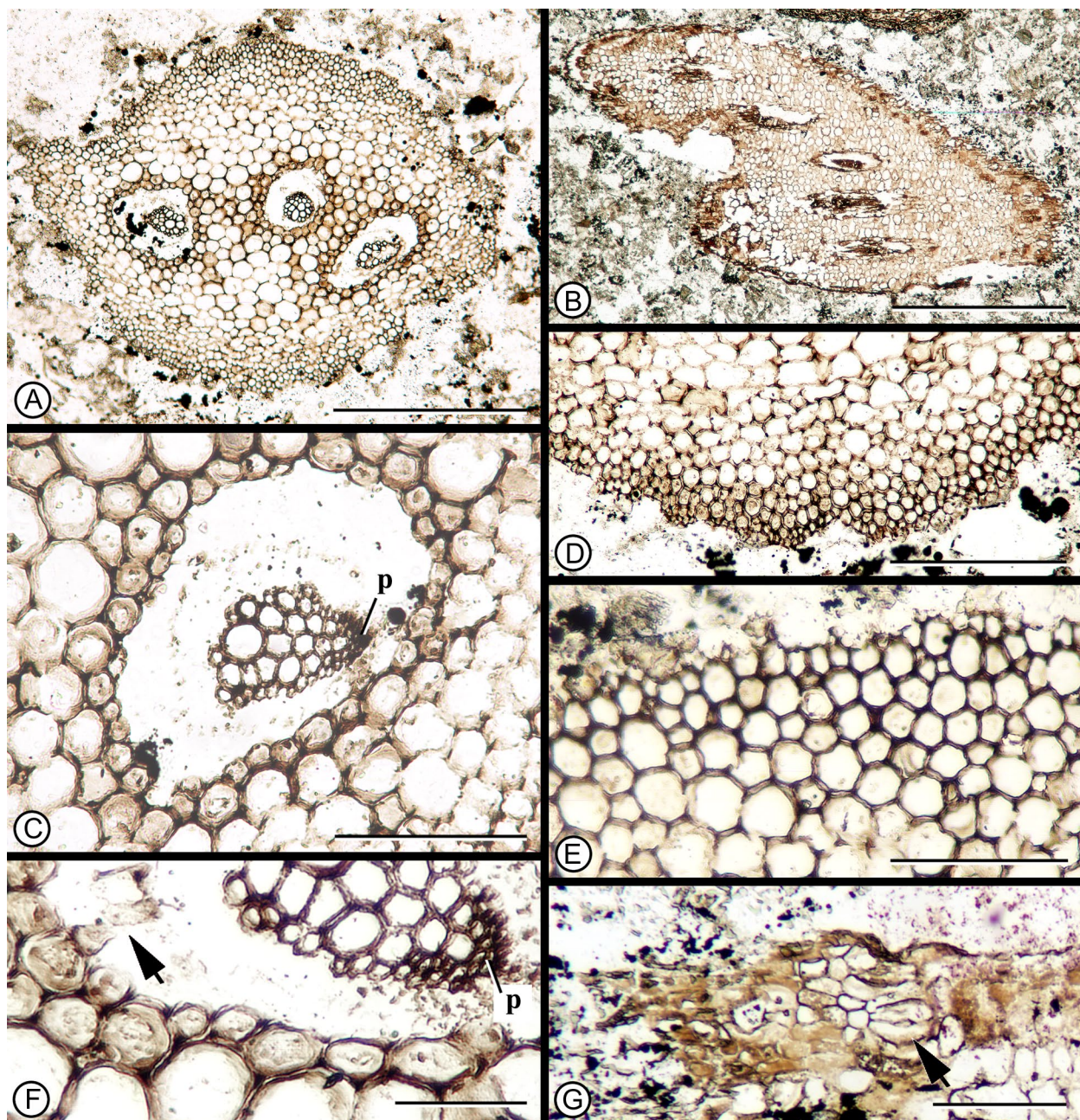
Figure 3. *Selaginella quatsinoense* sp. nov. from the Upper Cretaceous of western Canada. **A**. Cross section of stem with three stelar segments (Holotype), UAPC-ALTA P13,307 C bot No. 7 ×70; **B**. Oblique section of stem with five stelar segments, UAPC-ALTA P13,039 E top No. 5 ×30; **C**. Stelar segment of holotype showing monarch, exarch bundle surrounded by aerenchymatous endodermis and cortex (Holotype), UAPC-ALTA P13,307 D top No. 21a ×33; **D**. Cortex of holotype with parenchymatous inner zone, sclerenchymatous outer zone and eroded exterior, UAPC-ALTA P13,307 D top No. 6 ×150; **E**. Enlargement of outer margin of cortex with possible areas of preserved epidermis (Holotype), UAPC-ALTA P13,307 C bot No, 2 ×310; **F**. Stelar segment with monarch xylem bundle of holotype showing, aerenchmatous endodermis, and fragment of trabecula (arrowhead), UAPC-ALTA P13,307 D top No. 24 ×480; **G**. Oblique surface view of stem epidermis with a single stomatal complex, UAPC-ALTA P13,309 E top No. 1 ×150. Scale bars = 500 μm in A, 1 mm in B, 100 μm in C, E, G, 200 μm in D, 50 μm in F

Hestia eremosa Bateman, Kenrick et Rothwell (Bateman et al., 2007) and early Cretaceous specimens from India (Banerji, 2000) and Mongolia (Herrera et al., 2022), fossils with stelar anatomy similar to that of living Lycopodiales have not been discovered previously (Bateman et al., 2007). The most ancient possible anatomically preserved lycopodialean, *Hestia eremosa*, is based on three exarch actinostelic stems up to 4.7 mm in diameter that have diverging leaf traces and cortex. In contrast to *L. oellgaardii* which has ~six narrow ribs in smaller actinostelic stems and larger stems that are plectostelic, all stems of *H. eremosa* are actinostelic and have seven to ten ribs that fork and expand in width toward the periphery of the stele. The latter features do not characterize either the Mongolian or
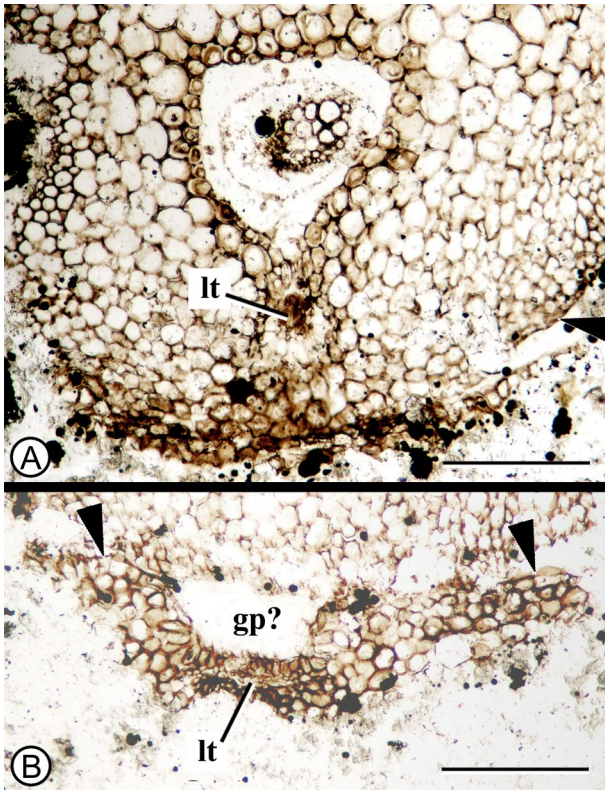
Figure 4. *Selaginella quatsinoense* sp. nov. from the Upper Cretaceous of western Canada. **A**. Cross section of Holotype showing terete leaf trace (lt) diverging toward leaf base (at bottom). UAPC-ALTA P13,307 D top No. 3a ×216; **B**. Cross section slightly more distal than Fig. 4.1 showing the base of diverging leaf with centrally located leaf trace (lt) and adaxial indentation (gp?) that marks the position of the ligule glossopodium. UAPC-ALTA P13,307 D top No 14a ×220. Scale bars = 100 μm

Vancouver Island *Lycopodicaulis* stems, the Indian stems of *Lycoxylon*, or living species of Lycopodiales (e.g. Herrera et al., 2022). Whereas the leaf traces of *Lycoxylon* spp. and *Lycopodicaulis oellgaardii* are terete, those of *H. eremosa* are tangentially expanded (Bateman et al., 2007). Specimens of *H. eremosa* with preserved outer cortex and leaf bases have not been discovered. Therefore, it is unknown whether *H. eremosa* is ligulate like isoetalean and selaginellalean lycophytes or eligulate like lycopodialean species.

By contrast to the Devonian/Mississippian lycopodalean specimens of *H. eremosa* from Oxroad Bay (Bateman and Scott, 1990), specimens of *Lycoxylon* spp. from India and *Lycopodicaulis oellgaardii* from Mongolia and Vancouver Island all occur in early Cretaceous deposits. Small stems of *L. oellgaardii*, those from Vancouver Island, and *Lycoxylon* spp. are all actinostelic like *H. eremosa*, but those approaching 1 mm in diameter from all three Lower Cretaceous sources are

plectostelic (Table 1), a stelar configuration not known to occur in *H. eremosa* (Bateman et al., 2007). Stems of *H. eremosa*, *Lycoxylon* spp. and *L. oellgaardii* all have sclerenchymatous inner cortex surrounding the stele. More peripheral tissues of *L. oellgaardii* stems from both Mongolia and western Canada consist of thinner walled parenchyma cells. Some specimens have a relatively smooth outer margin as do internodal regions of living lycopodialean stems with long internodes. Others show the divergence of relatively closely-spaced leaves, and a few specimens from Apple Bay have an irregular outer margin of the stem. The possible presence of ligules is not known for *Lycoxylon* spp., but ligules are clearly absent from leafy stems of *L. oellgaardii* derived from Mongolia and Vancouver Island.

Because of the absence of outer cortical features, leaves, and ligules, those characters remain unknown for the Indian specimens. Such stems resemble both *L. oellgaardii* and living species of several genera assignable to Lycopodiaceae, subgenus Lycopodioideae that cannot be distinguished from one another by stelar characters alone. As a result, Herrera et al. (2022) treat *Lycoxylon* as a morphotaxon for lycopodiacean stems with actinostelic-plectostelic stelar architecture. By contrast, Herrera et al. (2022) regard *L. oellgaardii* to be the vegetative leafy shoots of extinct lycopodiaceans that share stelar features with *Lycoxylon* spp., and that also have the parenchymatous outer cortex and eligulate leaves that characterize upright stems of many living lycopodiacean species that live in terrestrial habitats. We follow this conservative approach to recognizing genera of extinct Lycopodiales, and find no characters to distinguish the Vancouver Island lycopodiacean specimens from those described by Herrera et al. (2022) as *Lycopodicaulis oellgaardii*.

Apparently herbaceous, heterosporous, ligulate lycophytes with shallowly ribbed actinosteles are common fossils in Pennsylvanian age coal balls collected from both Europe and North America (Phillips, 1980); and stems with a similar stelar structure have been recognized in Mississippian age deposits (Bateman et al., 2007). The Pennsylvanian age specimens, traditionally identified as *Paurodendron fraipontii* (Leclercq) Fry, produce bisporangiate cones at the apices of highly branched shoots (Schlanker and Leisman, 1969). As a result, Schlanker and Leisman (1969) recognized the

Table 1. Comparative features of anatomically preserved Early Cretaceous Lycopodiales

Taxon/Character	*Lycoxylon indicum* (& *Lycoxylon* spp.)	*Lycopodicaulis oellgaardii*	Apple Bay Lycophyte
Geography	Rajmahal Hills, India	Inner Mongolia, China	Vancouver Island, Canada
Age	Early Cretaceous	Early Cretaceous, Barremian–Aptian	Early Cretaceous Valanginian
Organs	smooth stem	smooth and leafy stems, leaves	smooth and leafy stems, leaves
Branching	somewhat unequal dichotomous	somewhat unequal dichotomous	somewhat unequal dichotomous
Axes diameters	1–2 mm	0.9–2.3 mm	0.4–1.1 mm
Stele	plectostele	actino-plectostele	actino-plectostele
Stele diameter	~1.0 mm ?% of stem diameter	~0.4–1.1 mm >1/3 stem diameter	<~0.8 mm 1/3–1/2 stem diameter
Xylem plates	~7	<~6	<~6
Protoxylem strands	~18	6–18	7–26
Cortex	sclerotic inner, ? outer	sclerotic inner, parenchymatous outer	sclerotic inner, parenchymatous outer
Leaf shape (x.s.)	?	lenticular	lenticular
Ligule	?	absent	absent

plant as a species of *Selaginella*, *Selaginella fraipontii* (Leclercq) Schlanker and Leisman. While the bisporangiate cones of this species would seem to confirm that determination, megaspores and microspores of the *P. fraipontii* are unlike any produced by living species of *Selaginella* (Schlanker and Leisman, 1969; Tryon and Lugardon, 1990). Moreover, the plant has a woody base, and it produces a small rhizomorph that is diagnostic of isoetalean lycophytes (Rothwell and Erwin, 1985). Therefore, *Paurodendron fraipontii* is actually a diminutive, highly branched representative of the isoetalean clade (Pigg, 1992, 2001; DiMichele et al., 2022) rather than a selaginellalean (Rothwell and Erwin, 1985).

SELAGINELLALEAN FOSSILS

One of the most ancient plants to show the diagnostic features of *Selaginella* is *S. harrisiana* Townrow from the Permian of New South Wales (Townrow, 1968). Specimens of this species have equally and unequally forking shoots with small, helically arranged leaves and apical fertile zones that yield typical lycopsid trilete spores of two distinct sizes. As reconstructed (Text fig. 5 of Townrow, 1968), plants of *S. harrisiana* have leafy aerial shoots that arise from a naked rhizome, and ligulate leaves. Internal anatomy is not preserved.

Up to the present there have been few reports of selaginellalean plants that display anatomical structure, but recent reports and descriptions of fossils preserved in mid-Cretaceous amber from Myanmar provide excellent

evidence for the epidermal cellular structure for several species of *Selaginella* (Schmidt et al., 2020, 2022; Li et al., 2022). These show detailed evidence for epidermal cellular patterns (e.g. Schmidt et al., 2022), but preserve little internal anatomy at a cellular level (see fig. 2a of Schmidt et al., 2020). Ash (1972) described a species of *Selaginella* from the Triassic of Arizona that is preserved by coalified compression, but that shows evidence of vascular tissue and cell structure in acetate transfer preparations. Preparations show one to three strands of tracheids in the stems (fig. 4B of Ash, 1972) that are interpreted to be stelar segments (= "steles" of Ash, 1972) that may have been similar to the stelar segments of *S. quatsinoense*, but apparently are much smaller than the stelar segments of the latter.

The first apparently anatomically preserved specimen to be described as a species of *Selaginella* is also the most ancient, occurring in a Middle Pennsylvanian age concretion from the Mazon Creek assemblage in Illinois (Darrah, 1938). That specimen consists primarily of a permineralized cone with well-preserved sporangia containing flanged, trilete megaspores identified as *Triletes circumtextus* Zerndt (Darrah, 1938). The paucity of internal anatomical preservation for Darrah's cone (Darrah, 1936) precludes direct comparisons to *S. quatsinoense*.

Selaginella quatsinoense represents the first unequivocal evidence from the fossil record for Selaginellales with excellent internal cellular preservation. Specimens display the diagnostic anatomical stem structure of living species of *Selaginella*, which is represented by a novel

combination of characters not found elsewhere among vascular plants. Pertinent characters allying these leafy herbaceous fossils with living species of Selaginellales (Eames, 1936) are a stem stele that consists of several exarch, monarch cauline xylem strands, an aerenchymatous endodermis traversed by uniseriate trabeculae, microphyllous leaves with a single vascular bundle, and an apparent ligule. Because nearly all fossilized herbaceous lycophytes are preserved by coalified compression/impression (sensu Schopf, 1975) or entombed within amber, timing for the appearance of this diagnostic suite of selaginellalean lycophyte characters in geological time previously has not been assessed. Although the genus *Selaginella* clearly was highly diversified by the mid-Cretaceous (Schmidt et al., 2022), *S. quatsinoense* provides the first direct evidence that modern selaginellalean internal anatomy evolved no later than the early Cretaceous.

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