Phylogenetic diversification of *Equisetum* (Equisetales) as inferred from Lower Cretaceous species of British Columbia, Canada[1]

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Three types of anatomically preserved vegetative shoots with features that characterize crown group *Equisetum* have been discovered in Lower Cretaceous deposits (≈136 Ma) of British Columbia, Canada, suggesting the genus is much older than currently believed. Specimens include two types of aerial shoots described as *E. haukeanum* sp. nov. and *E. vancouverense* sp. nov. and one type of subterranean rhizome. Shoots are 1–2 mm in diameter, jointed, and in cross section have fluted stems with a hollow pith. Distinctive patterns of cortical sclerenchyma and different ridge morphologies characterize each shoot morphotype. Nodes display irregular branching, highly fused leaf sheaths, and a nodal diaphragm. The aerial stem morphospecies have vallecular canals on alternating radii with carinal canals of an equisetostele surrounded by only a few tracheids. No secondary tissues are produced. Bands of surficial stomata flank the furrows of one morphospecies. Rhizomes and aerial shoots are of a similar size, suggesting that the plants were equivalent in stature to the smallest living *Equisetum* species. These fossils augment our understanding of evolutionary transformations that led from Paleozoic Archaeocalamitaceae and Calamitaceae to crown group Equisetaceae, suggesting that the initial diversification of *Equisetum* began far earlier than suggested by molecular-clock-based estimates.

Key words: clade age; Equisetales; *Equisetum*; euphyllophyte phylogeny; fossil; Lower Cretaceous.

Equisetales is one of the most ancient and distinctive clades of living vascular plants, with a rich fossil record from which to infer evolutionary transformations leading to the single living genus, *Equisetum* L. (Boureau, 1964; Good, 1975; Stewart and Rothwell, 1993). The early equisetophytes *Archaeocalamites* Stur and *Calamites* Brongniart are abundantly represented as mold/casts, compressions, and anatomically preserved fossils that range from the Early Mississippian to the Permian (Harris, 1961; Boureau, 1964; Bateman, 1991). Comparisons among extinct and living members of the Equisetales show clear transformational series of both morphology and anatomy documenting a monophyletic group that has developed over an exceptionally long time with relatively few character state changes (Good, 1975; Bateman, 1991). In consideration of this long-term retention of character states and wide geographic and ecological ranges, *Equisetum* has been regarded by some as the most successful living genus of vascular plants (Bierhorst, 1971; Rothwell, 1996).

Equisetophyte systematics has recently attracted substantial attention and has been recognized as being of considerable importance to euphyllophyte phylogeny, but analyses of alternative data matrices have supported dramatically different phylogenetic hypotheses (Rothwell, 1999; Pryer et al., 2001; Rothwell and Nixon, 2006; Smith et al., 2006). The results of morphological analyses that include fossils and a large body of paleobotanical evidence from transformational series both infer that equisetophytes predate all modern fern clades and were derived from trimerophyte-grade ancestors (Stewart and Rothwell, 1993; Rothwell, 1999; Rothwell and Nixon, 2006). By contrast, the results of systematic analyses that include only living plants infer that *Equisetum* nests among clades of living ferns (Pryer et al., 2001; Smith et al., 2006) and suggest that the crown group *Equisetum* did not diversify until the Paleogene (Des Marais et al., 2003).

Over the past two hundred years, studies of the fossil record have developed a wealth of data that contributes important evidence for inferring the evolution of most, but not all, of the features that characterize crown group *Equisetum*. The missing data result largely from fossil *Equisetum* specimens that occur as compressions or impressions, preservational modes where even exquisitely preserved specimens do not show all the details of internal anatomy (e.g., Becker, 1969; McIver and Basinger, 1989). Only a few of the *Equisetum*-like compression fossils that occur throughout the Mesozoic have been classified as the genus *Equisetum* (Boureau, 1964; Harris, 1961). The remaining equisetophyte fossils are assigned to extinct genera, either because they have distinctive apomorphies not found in living *Equisetum* [e.g., *Equicalastrobus* (Daugherty) Grauvogel-Stamm and Ash, 1999; *Cruciaetheca* Cúneo and Escapa, 2006; *Spaciinodum* Osborn et Taylor; Ryberg et al., 2008], or because all of the features diagnostic of modern *Equisetum* have not been documented in the fossils (i.e., *Equisetites* Sternberg; Stewart and Rothwell, 1993). Although the genera *Equisetites* and *Equisetum* are regarded as separate taxonomic entities in the spirit of conservative taxonomic decision-making (Stewart and Rothwell, 1993), in reality there are no diagnostic characters that unequivocally distinguish most species of the two genera (but see Watson and Batten [1990] for a possible exception). Therefore, the generic identities of species assigned to *Equisetites* are often in question, and the stratigraphic ranges inferred for *Equisetites* and *Equisetum* are ambiguous and arguably arbitrary.

The oldest widely recognized fossil species of *Equisetum* is *E. laterale* Gould from the Middle Triassic of Australia (Gould, 1968). The occurrence of *E. laterale* in Triassic deposits supports

an ancient, but incompletely documented fossil record for the genus. However, questions regarding the generic identity of *E. laterale* remain because the distinctive internal anatomy of the genus *Equisetum* is not fully preserved and elaters have not been discovered on spores of that species (Gould, 1968). Permineralized fossils that could provide the remaining characters needed to document the earliest occurrence of *Equisetum* and hypotheses of clade age (i.e., Des Marais et al., 2003) are extremely rare. Only one species of extinct *Equisetum* that displays extensive anatomical preservation of internal tissues has been described previously (i.e., from the Eocene of Oregon; Brown, 1975), and that species is well within the relatively recent age range for diversification of modern *Equisetum* that has been inferred from molecular clock-based estimates (i.e., ~65 MA; Des Marais et al., 2003). A small number of additional species do display some internal anatomical structure [e.g., *Equisetites lyellii* (Mantell) Seward; Watson and Batten, 1990], but those species have not provided all of the anatomical features needed to conclusively identify them as representatives of crown group *Equisetum*.

In the current study, we describe three new morphotypes of anatomically preserved *Equisetum* shoots that have been collected among the wealth of permineralized fossils from Early Cretaceous sediments of Apple Bay on Vancouver Island, British Columbia, Canada (Stockey and Rothwell, 2006). The *Equisetum* fossils consist of two types of aerial shoots and one type of rhizome. The aerial shoots are named *Equisetum haukeanum* Stanich, Rothwell et Stockey sp. nov. and *Equisetum vancouverense* Stanich, Rothwell et Stockey sp. nov., and the rhizomes are described as *Equisetum* sp. All shoots fall within the ranges of variation that characterize living species of *Equisetum*, and one type of aerial shoot has stomatal characters that are characteristic of the subgenus *Equisetum*. The Apple Bay specimens extend the minimum age for the genus *Equisetum*, based on anatomical characters, from the Paleogene (<65 Ma) to the Early Cretaceous (136 Ma). This recalibrates the initial evolutionary diversification of *Equisetum* species with modern morphology and anatomy from the Paleogene to at least the Early Cretaceous, and suggests that crown group *Equisetum* may have evolved as early as the Middle Triassic (~230 Ma; Gould, 1968).

MATERIALS AND METHODS

This study is based on seven anatomically preserved shoot fragments that conform to two morphospecies of aerial vegetative shoots and one type of underground rhizome. Specimens occur as cellular permineralizations within iron-rich carbonate concretions that are embedded within carbonaceous sandstones at the Apple Bay locality on the northern end of Vancouver Island (Stockey et al., 2006). The iron-rich concretions crop out at 13 levels (E. H. Gierlowski-Kordesch, Ohio University, personal communication) within a 6-m section of sediments. The locality is on the beach along Quatsino Sound (50°36′21″N, 127° 39′25″W; UTM 9U WG 951068). Strata from which the fossils were collected have been regarded as Lower Cretaceous (Valanginian/Barremian) Longarm Formation equivalents (Jeletzky, 1976; Haggart and Tipper, 1994) and correspond to Jeletzky's (1976) Barremian variegated clastic unit (Sweet, 2000). However, a recent oxygen isotope analysis has narrowed the age to the Valanginian-Hauterivian boundary (D. R. Gröcke, Durham University, personal communication).

Concretions were cut into approximately 1 cm thick wafers, the surfaces of which were examined for plant material. Serial anatomical sections of the *Equisetum* shoots were prepared using the cellulose acetate peel technique (Joy et al., 1956) and mounted on glass slides with Eukitt (O. Kindler GmbH and Co., Freiburg, Germany). Images were captured using a Phase One (Phase One A/S, Frederiksberg, Denmark) digital scanning camera mounted on a Leitz Aristophot bellows camera and a Zeiss WL compound microscope. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

SYSTEMATICS

Subdivision—Euphyllophytina sensu Kenrick and Crane (1997)

Family—Equisetaceae sensu Good (1975)

Genus—*Equisetum* L.

Species—*Equisetum haukeanum* Stanich, Rothwell et Stockey, sp. nov., Figs. 1–9.

Specific diagnosis—Morphospecies of articulated aerial shoot segments consisting of stems with alternating ridges and furrows at surface, with leaf sheaths and diaphragms at nodes, and hollow pith at internodes. Stems, 0.7–1.7 mm in diameter, with five ridges, furrows, carinal canals, vallecular canals, and leaf sheath segments. Ridges convex to flat with triangular hypodermal sclerenchyma bundle; stomata superficial, in bands of two stomata on flanks of furrows. Leaf sheath 3.9–4.5 mm long.

Holotype hic designatus—Permineralized slabs, peels and slides of specimen in P13173 B bot and C top (Figs. 1, 2, 5–9) housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA), Edmonton, Alberta, Canada.

Collecting locality—Apple Bay, northern Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068).

Stratigraphic position and age—Longarm Formation equivalent. Valanginian-Hauterivian boundary, Early Cretaceous.

Etymology—The specific epithet *haukeanum* is proposed in honor of Richard L. Hauke, in recognition of his contributions to our understanding of *Equisetum* taxonomy.

Species—*Equisetum vancouverense* Stanich, Rothwell et Stockey, sp. nov., Figs. 10–14.

Specific diagnosis—Morphospecies of articulated aerial shoot segments consisting of stems with alternating ridges and furrows at surface, with leaf sheaths and diaphragms at nodes and hollow pith at internodes. Stems 1.4–2.0 mm in diameter, with seven ridges, furrows, carinal canals, vallecular canals, and leaf sheath segments. Ridges concave (biangulate); endodermis surrounding individual carinal canals. Leaves with adaxial epidermis of large angular cells.

Holotype hic designatus—Permineralized slabs, peels, and slides of specimen in P13263 C bot and D top (Figs. 10–14) housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA), Edmonton, Alberta, Canada.

Collecting locality—Apple Bay, northern Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068).

Stratigraphic position and age—Longarm Formation equivalent. Valanginian-Hautervian boundary, Early Cretaceous.

Etymology—The specific epithet *vancouverense* refers to the geographic origin of the species on Vancouver Island, British Columbia, Canada.

RESULTS

General features—All three anatomically preserved morphotypes of shoots, including *Equisetum haukeanum* (Figs. 1–9), *E. vancouverense* (Figs. 10–14), and the underground rhizome (Figs. 15–17) display a combination of characters that fall within the range of variation for comparable structures of living *Equisetum* species. Shoot segments consist of one or two nodes and adjacent internodal regions (Figs. 1–3, 10, 11). The fossils are comparable in size to the smallest living species of *Equisetum* (e.g., *E. scirpoides* Michaux, *E. variegatum* Schleicher ex F. Weber & D. Mohr; Hauke, 1963, 1978), ranging 0.7–2.0 mm in diameter. They are characterized by fluted margins (Figs. 3, 10, 11, 15), that in cross sections represent ridges and furrows. At the internodes, all stems have a hollow pith (Figs. 1, 10–12), which is surrounded by a ring of carinal canals that occur on the same radii as the ridges (Figs. 3, 4, 10–12) and a cortex that contains vallecular canals on the same radii as the furrows (Figs. 3, 4, 12). As in living species of *Equisetum*, only a small number of metaxylem tracheids accompany each carinal canal at the internodes (Fig. 4), and the positions of ridges and furrows alternate from internode to internode (Figs. 3, 10, 11). The cortex is bounded by a distinct epidermis (Figs. 3, 10, 12 at arrow), within which cortical sclerenchyma is sporadically preserved (Figs. 2, 6, 13 at upper right, 15).

The fossil stems display nodal diaphragms (Fig. 1) where the pith is parenchymatous (Fig. 13), and the carinal canals close to form solid cauline bundles (Fig. 13) that may be fused into a ring of tracheids (Fig. 2). As is also characteristic of living species of *Equisetum* (Golub and Wetmore, 1948), tracheids of the stele typically have helical or scalariform pitting patterns (Fig. 5, at arrow), but those in the nodal ring display multiseriate pitting (Figs. 5, 16). All the stems branch irregularly (e.g., Figs. 1, 2, 10, 15), with one or two branches diverging from the nodes of aerial shoots and three diverging from one node of the underground rhizome. Not all branches are evident in a single section of most nodes (e.g., Figs. 1, 2, 15). Immediately distal to the level of divergence from the stem stele, the stele of each branch consists of a ring of tracheids that surrounds a parenchymatous pith (Fig. 17).

A prominent leaf sheath, consisting of a ring of leaves connected by thin laminar tissue, occurs at each node (Figs. 3, 10, 11), with the thin commissure extending almost to the apex of each sheath (Figs. 3, 14). Most leaves terminate at the level where they separate from each other (e.g., just distal to the level in Fig. 14). It is unclear whether this is the result of leaf tip abscission or incomplete preservation. In cross sections, each leaf displays a single terete vascular bundle (arrowheads in Figs. 3, 14), that is surrounded by parenchymatous mesophyll. Sclerenchyma also occurs to varying degrees toward the abaxial side of each leaf (Figs. 2, 12 at top, 14).

Aerial shoots are distinguished from underground rhizomes by several features. Whereas the cortical sclerenchyma of aerial stems is restricted to the ridges (Figs. 2, 6, at "s"), underground rhizomes display a continuous cylinder of sclerenchyma (Fig. 15). The leaf sheath of underground rhizomes is typically shorter and less intact than on aerial shoots, and the fossil rhizomes may have a larger number of branches at the nodes (Fig. 15).

Equisetum haukeanum—Aerial shoots of *E. haukeanum* are identified by five convex ridges, each having a sclerenchyma strand that is triangular in cross section (Figs. 2, 6). Likewise, there are five carinal canals, five vallecular canals, and five leaves that make up each stem segment (Figs. 3, 4). Stems measure 1.2–1.6 mm in diameter at the nodes and 0.7–0.9 mm in the internodes. Leaf sheaths are 3.8–4.5 mm long, with leaves that are lens-shaped and connected by a thin commissure in cross sections (Fig. 3). Individual leaves are 0.4–0.6 mm wide and 0.1–0.5 mm thick with a single terete leaf trace (Fig. 3, at arrow points) and a triangular sclerenchyma bundle on the abaxial surface (Fig. 2, at "s"). Sclerenchyma is developed at the base of the sheath but is absent at more distal levels. (cf., Figs. 2 and 3).

Only one complete internode is preserved, measuring 5.7 mm long. Two branches are produced at each of the adjacent nodes. Branches are smaller than the stems upon which they are produced, measuring approximately 0.6 mm wide. All the branches are preserved for only a short distance beyond the cortex of the stem upon which they are borne (e.g., Fig. 2, at right). At the nodes the stem stele forms a cylinder of tracheids 0.2–0.5 mm in diameter (Fig. 2). Tracheids measure 7–18 μm in diameter and display multiseriate pitting (Fig. 5, at right). The stem cortex is not preserved within the epidermis at some levels (Fig. 3). Elsewhere it consists of isodiametric, thin-walled cells, 13–37 μm in diameter, toward the inside (Fig. 1, at top center), and wedge-shaped bundles of elongated sclerenchyma fibers 13–28 μm in diameter at the periphery (Figs. 1, 2, 6).

In cross sections of stem internodes, the carinal canals measure 25–34 μm in diameter and are flanked by two to five metaxylem tracheids (Fig. 4, at arrow points) that measure 5–9 μm in diameter and have scalariform secondary wall thickenings (Fig. 5, at arrow). Epidermal cells are oval in cross section (Fig. 3), slightly elongated in face views (Fig. 7), and have smooth margins. Stomatal complexes occur at the internodes in bands two stomata wide that are located on the flanks of the furrows (Figs. 6, 7). Stomatal complexes are surficial rather than sunken (Figs. 6, 9). As is characteristic of living species of *Equisetum*, stomatal complexes of *E. haukeanum* consist of two prominent subsidiary cells that are overlain by the guard cells (Figs. 7–9) (Hauke, 1957). Complexes are oval in surface view, measuring 45–52 μm long and 28–39 μm wide.

Equisetum vancouverense—Stems of *E. vancouverense* are slightly larger than those of *E. haukeanum*, measuring 1.4–2.0 mm in diameter. They have seven carinal canals 56–102 μm in diameter (Figs. 10–12), tangentially elongated vallecular canals, and angular ridges at the stem periphery (Fig. 10). In contrast with *E. haukeanum*, which has convex ridges, each ridge of *E. vancouverense* is biangulate and concave at the center (Figs. 10, 11). At the internodes, the stem cortex is incompletely preserved, but just above the nodes there are vallecular canals adjacent to the stem furrows (Fig. 12). At these levels, the cortex is parenchymatous adjacent to the vallecular canals, and the periphery of the stem is marked by a distinct epidermis (Fig. 12, at arrow). Cortical parenchyma cells measure 13–33 μm in diameter. At the nodes, the vallecular canals close, and the cauline bundles consist of larger numbers of tracheids (Fig. 13). Also at these levels, the pith is parenchymatous, forming a nodal diaphragm, and the cellular cortex is continuous with the stele (Fig. 13). Toward the inside of the cortex, the cells are parenchymatous, and toward the periphery they consist of sclerenchyma fibers, 8–28 μm in diameter (Fig. 13 at upper right). Also near the nodes of *E. vancouverense*, there is a distinct endodermis that surrounds each stem bundle (Fig. 13, at E).
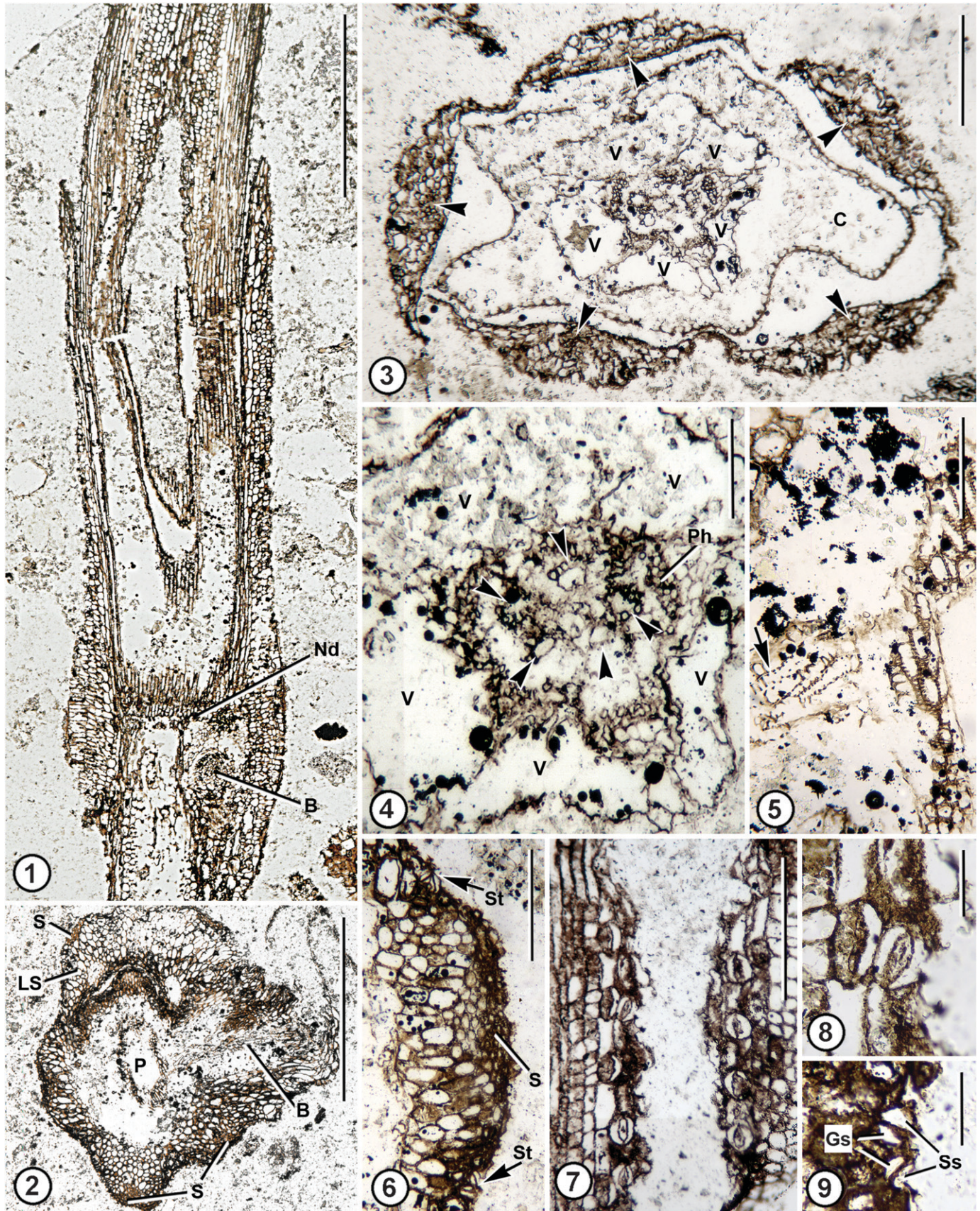
In cross sections, the leaf sheath of *E. vancouverense* consists of a ring of angular leaves that are connected by commisures two to five cell layers thick (Figs. 10–12, at arrows). Near the nodes, the leaves have a slightly convex abaxial surface (Fig. 10), whereas more distally they are abaxially flattened or slightly concave (Fig. 11). There is a distinct adaxial epidermis of angular cells that are larger than the mesophyll cells toward the base of the leaf sheath (Figs. 11, 12) and smaller toward the leaf tips (Fig. 14). Near the nodes, the epidermal cells measure 10–43 μm in diameter. Sclerenchyma occurs as a thin layer within the epidermis around the periphery of the leaf sheath (Figs. 10–12). At the most distal levels, leaves separate from each other (Fig. 14) then terminate. They have a terete vascular bundle (Fig. 14, at arrow heads), parenchymatous mesophyll cells 15–37 μm in diameter, and an abaxial band of sclerenchyma (Fig. 14, at "S").

One branch diverges from the stem at each node of the available *E. vancouverense* stems (Fig. 10, at top), and branches at adjacent nodes diverge from opposite sides of the stem. Branches measure 0.5–0.9 mm in diameter. Each branch extends outward through the leaf sheath of the stem (Fig. 10) and displays parenchymatous pith and cortex at the branch base (Fig. 10). More distal levels of the branches are not preserved.

Underground rhizome—Two specimens of underground rhizomes have been recovered. These are 0.9–1.3 mm in diameter, and both show fluted margins that represent ridges and furrows in cross sections (e.g., Fig. 15). However, as in many living species of *Equisetum* (e.g., *E. laevigatum* A. Braun.; Fig. 18), the fluting is somewhat less pronounced than in the aerial stems (e.g., Figs. 3, 11). Also, as is characteristic of underground rhizomes in living species of *Equisetum* (e.g., Fig. 18), sclerotic cortex is more-or-less evenly distributed around the periphery of the underground rhizomes (c.f., Figs. 15, 18). The zone of outer sclerenchymatous cortex is 65–135 μm thick in the fossil rhizomes, and consists of fibers that are 9–34 μm in diameter. Neither rhizome has internal stelar tissues preserved, and in one specimen, the internal cavity is filled with debris (Fig. 15). If the internal anatomy of the fossil rhizomes was as aerenchymatous as, and constructed of delicate tissues similar to those of, the rhizomes of living *E. laevigatum* (Fig. 18), the absence of cells in the interior of the fossils would be easily explained.

Both fossil rhizomes show some evidence of a leaf sheath at the nodes (Fig. 15, at LS), and both branch. One specimen shows three branches, whereas the other has only one. Branch diameters range from 0.6 to 1.0 mm, and steles within the branch bases consist of a cylinder of tracheids that surrounds a parenchymatous pith (Fig. 17). Tracheids in this region are 11–20 μm in diameter and show multiseriate pitting (Fig. 16). Because all branches are broken near the points of attachment, we were unable to determine whether they represent underground rhizomes, tubers, or aerial shoots.

DISCUSSION

All three Lower Cretaceous morphotypes of *Equisetum* shoots that occur together at the Apple Bay locality have well-defined nodes and internodes, whorled appendages, elongated internodes with distinct ridges and furrows at the periphery, leaf sheaths at the nodes, hollow pith at internodes, and ridges and furrows that alternate from node to node. Leaf sheaths are tightly pressed to the stem, and there is little or no evidence of free leaf tips. The stem stele of the aerial shoots consists of a ring of carinal canals at the internodes, and there are few metaxylem tracheids (two to five) at the periphery of each carinal canal. No secondary tissues are produced. At the nodes, the carinal canals close, and the cauline bundles anastomose to form a ring of tracheids within a nodal diaphragm. Leaf traces are formed by apical extension of bundles from the subtending internode. Branches arise on radii that alternate with the positions of leaf traces and are at the base of a carinal canal in the internode above. Among both living and fossil plants, this combination of features is diagnostic for vegetative shoots of the genus *Equisetum* (Table 1; Eames, 1936; Hauke, 1963, 1978; Bierhorst, 1971; Des Marais et al., 2003).

Growth form and plant architecture—Fossils described in this paper include both underground rhizomes and vegetative aerial shoots. We do not know which, if either (or both), of the *E. haukeanum* and/or *E. vancouverense* specimens belong(s) to the underground rhizomes from the same locality. Because aerial shoots of living *Equisetum*, fossil Calamitaceae and extinct Equisetaceae (where known) all arise from underground rhizomes, it is reasonable to assume that the aerial *Equisetum* shoots from Apple Bay do as well. If correct, then the plants that produced *E. haukeanum* and *E. vancouverense* are similar to living species of *Equisetum* in overall growth form. Aerial shoots of these fossil morphospecies range from 0.7 to 2.0 mm in diameter, which is comparable to the smallest living species of *Equisetum* (Hauke, 1963, 1978). Although there is a theoretical possibility that the fossilized aerial shoots could represent ultimate branches of a larger plant, that alternative is unlikely

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Figs. 1–9.   *Equisetum haukeanum* Stanich, Rothwell et Stockey sp. nov. **1.** Nodal region of aerial stem (holotype) in longitudinal section showing leaf sheath, nodal diaphragm (ND), branch base (B), and hollow pith. P13173 C side #35. ×33. Scale bar = 1 mm. **2.** Cross section of holotype in nodal region showing divergence of branch (B) and separation of leaf sheath (LS). Note hollow pith (P) surrounded by ring of stelar tracheids, and sclerenchyma (S) at ridges of stem and leaf sheath. P13173 B_1 bot #9 ×33. Scale bar = 1 mm. **3.** Cross section of paratype at internode showing stem surrounded by leaf sheath. Five vallecular canals (V) alternate with ridges on stem. Cortex (C) largely degraded, epidermis well preserved. Note rounded abaxial surface of leaves with terete vascular bundles (at arrowheads). P13173 B_2 bot #3. ×80. Scale bar = 0.25 mm. **4.** Enlargement of stem in Fig. 3 showing vallecular canals (V) and the positions of four carinal canals (arrow points) flanked by metaxylem tracheids on alternating radii. Note that phloem (Ph) is preserved at the periphery of some carinal canals. P13173 B_2 bot #7. ×180. Scale bar = 1 mm. **5.** Tracheids of stele in nodal region of holotype, showing pitted metaxylem tracheids at right and helical protoxylem (arrow). P13173 B_1 bot #9. ×185. Scale bar = 0.1 mm. **6.** Cross section of stem cortex and epidermis of holotype, with ridge at center and flanks of furrows at top and bottom. Arrows identify stomatal complexes (St). Note sclerenchyma bundle (S) at periphery of cortex on ridge. P13173 C top #244. ×100. Scale bar = 0.2 mm. **7.** Tangential section at stem surface of holotype showing internode with furrow at center. Biseriate bands of stomata located on flanks of furrow. Note longitudinally aligned rows of cortical parenchyma cells beneath epidermis (at sides of photo). P13173 C side #29. ×105. Scale bar = 0.25 mm. **8.** Enlargement of two stomata in band at left of Fig. 7, showing subsidiary cells of stomatal complexes. P13173 C side #29. ×240. Scale bar = 50 μm. **9.** Cross section of stem cortex of holotype on margin of furrow showing stomatal complex. Note subsidiary cells (Ss) overlie guard cells (Gs). P13173 C Top #242. ×260. Scale bar = 50 μm.
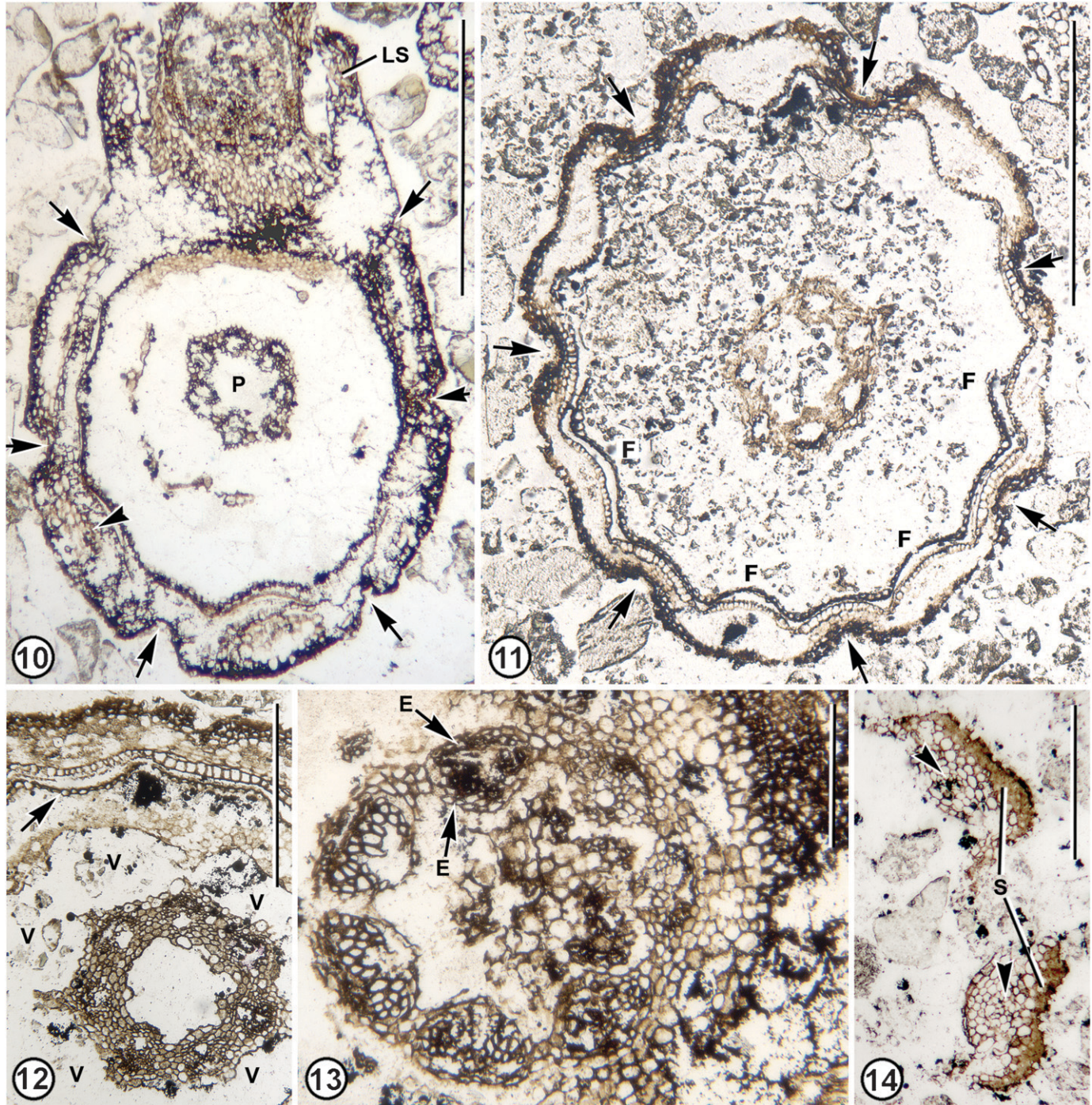
Figs. 10–14.   *Equisetum vancouverense* Stanich, Rothwell et Stockey sp. nov. (holotype) **10.** Cross section immediately below nodal diaphragm showing features of stem with hollow pith (P). Note branch extending from within leaf sheath (LS) at top, and position of leaf trace (at arrowhead). Arrows identify radii of stem ridges and thin tissue connecting leaves to form sheath. P13263 D top #1. ×45. Scale bar = 1 mm. **11.** Cross section above node, at level where leaf sheath is continuous, showing hollow pith, carinal canals, scalloped appearance of stem surface, and angular leaf sheath segments. Arrows identify radii of stem ridges and thin tissue connecting leaves to form sheath that alternate with positions of furrows (at "F"). P13263 C bot #60. ×46. Scale bar = 1 mm. **12**. Enlargement of stem at base of internode showing hollow pith, ring of carinal canals embedded in ground tissue, vallecular canals (V), and parenchymatous cortex with distinct epidermis (arrow). Leaf sheath shows sclerenchyma at periphery of ridges and prominent inner epidermis of angular cells. P13263 C bot #20. ×60. Scale bar = 0.5 mm. **13**. Enlargement of stem at level of nodal diaphragm, with parenchymatous pith and inner cortex, and sclerenchymatous outer cortex (at upper right). Note vascular bundles have no carinal canals at this level, and each partly or completely (arrow) surrounded by endodermis (E). P13263 D top #4. ×93. Scale bar = 0.25 mm. **14**. Cross section of leaf sheath segments at level where individual leaves are almost separated from each other. Each leaf displays concave outer surface, terete trace (arrowheads), and external sclerenchyma (S). Note angular cells of adaxial epidermis. P13263 C bot #150. ×50. Scale bar = 0.5 mm.
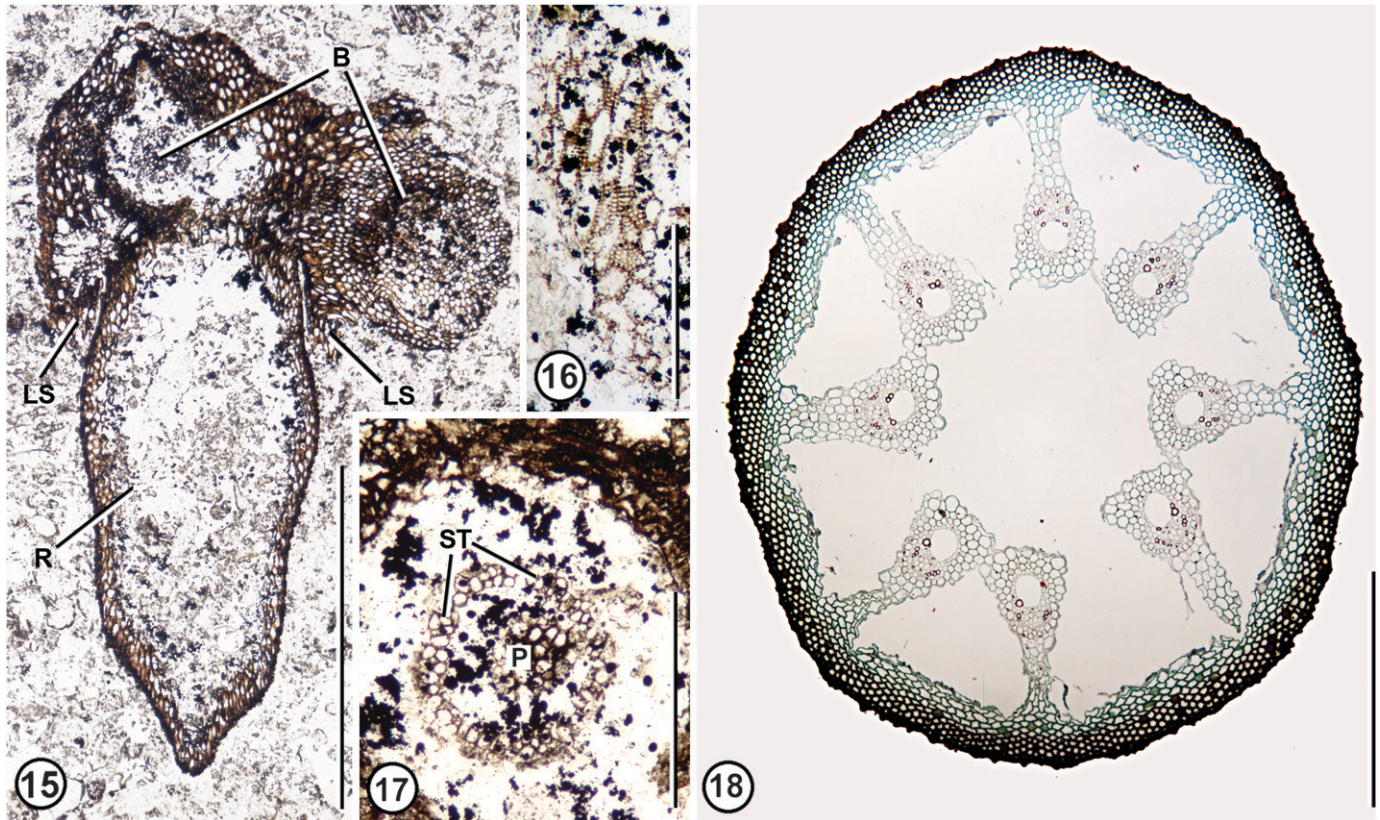
Figs. 15–18.   *Equisetum* sp. **15.** Oblique cross section of underground rhizome (R) at node showing divergence of two branches (B) at top and remnants of leaf sheath (LS). *Note:* stem and branches have more uniformly distributed cortical sclerenchyma than aerial stems. P13349 F top #14. ×29. Scale bar = 1 mm. **16.** Metaxylem tracheids at base of branch in upper left of Fig. 15, showing multiseriate, alternate pitting. P13349 F top #3. ×115. Scale bar = 0.2 mm. **17.** Cross section of stele (ST) in base of branch at upper left of Fig. 15. Stele consists of ring of tracheids surrounding parenchymatous pith (P) at this level. P13349 F top #14. ×100. Scale bar = 0.25 mm. **18.** Rhizome of living *E. laevigatum* showing less fluted exterior, as well as more continuous and more evenly thickened hypodermal sclerenchyma than aerial stems. Aerenchymatous pith and vallecular canals more extensively developed (and interconnected) in rhizome of this species than most other species. ×32.

because the underground rhizomes at Apple Bay fall within the same size range as the aerial shoots. Therefore, one or both of the plants that produced *E. haukeanum* and *E. vancouverense* were almost certainly as small as the most diminutive of living *Equisetum* species (Hauke, 1963, 1978).

A combination of branching patterns and maximum stem diameters of the *Equisetum* fossils are informative of plant architecture. Many living species of *Equisetum* subgenus *Equisetum* have vegetative shoots that branch profusely at each node to produce symmetrical shoot systems with an overall conical shape (e.g., *E. arvense* L., *E. telemateia* Ehrh.). Other species, particularly in *Equisetum* subgenus *Hippochaete*, have aerial shoots that either are unbranched (e.g., *E. variegatum* Schleicher ex F. Webber & D. Moore) or are only sparsely branched (e.g., *E. scirpoides* Michaux). Such species typically produce only one or two branches at those nodes where branches do occur. If the one or two branches preserved at each node of the fossils are characteristic of the plants by which they were produced, both morphospecies of aerial shoots represent species that were sparsely and irregularly branched.

Interspecific relationships of* Equisetum *species—Classical studies have divided living species of *Equisetum* into two subgenera, *Equisetum* L. (*E. pretense* L., *E. telemateia* Ehrhart, *E. fluviatile* L., *E. arvense* L., *E. diffusum* D. Don, *E. sylvaticum* L., and *E. palustre* Ehrhart) and *Hippochaete* Milde (*E. scirpoides* Michaux, *E. variegatum* Schleicher ex F. Weber, *E. giganteum* L., *E. laevigatum* A. Braun, *E. myriochaetum* Cham. et Schldtl., *E. ramosissimum* Desfontaines, and *E. hyemale* L.). Depending upon the source of data evaluated and the methods of systematic analysis employed, a 15th species, *E. bogotense* Kunth, resolves as sister to the remaining living species (Des Marais et al., 2003), as basal within subfamily *Hippochaete* (Des Marais et al., 2003; Guillon, 2007), or else is placed within the subfamily *Equisetum* (Page, 1972a). Finer resolution of species relationships has been difficult to achieve from morphological characters (Hauke, 1963, 1978; Page, 1972a), but analyses of nucleotide sequences have provided greater, if not uniformly consistent, patterns of resolution (Des Marais et al., 2003; Guillon, 2007).

Taxonomic placement of *E. haukeanum* and *E. vancouverense* among living species is difficult to assess because fertile structures of the fossils have yet to be discovered and because there is a dearth of known informative morphological characters for inferring relationships within the genus *Equisetum* (Hauke, 1963, 1978, 1993; Des Marais et al., 2003). Stomatal position and branching pattern are among the very small number of morphological characters that appear to be informative for that purpose (Page, 1972a; Hauke, 1993), and those have been employed primarily for placing species in one of the two

TABLE 1. Characters of equisetophytes through time. Characters that are concordant with or fall within range of variation of living *Equisetum* spp. are in boldface type.

Taxon	Stratigraphic range	Max. stem diameter (mm)	Dichotomizing leaves	Leaf sheath fusion (%)	Leaf tip orientation	Spore type	Elaters	Cone bracts alternate with sporangiophores	Carinal canal position at successive internodes	Secondary xylem
Archaeocalamites Stur	L. Miss.–M. Permian.	48	present	0	spreading	trilete	absent	**no**	continuous	present
Calamites Suckow	L. Miss.–M. Permian.	>600	**absent**	0	spreading	trilete	3	yes	**alternating**	present
Neocalamites Halle	L. Permian–Jurassic	76	**absent**	0	spreading	unknown	?	**no**	**alternating**	?
Equisetites Sternberg spp.	M. Triassic–L. Cretaceous	90	**absent**	7.3–100 [a]	**appressed**	trilete-alete	?	usually **no**	**alternating**	?
Equisetites lyellii (Mantell) Sweard [b]	L. Cretaceous	**20**	**absent**	**>90**	**appressed**	**alete**	absent	**No?**	**alternating**	**absent**
Equisetum laterale [c]	M.–L. Triassic	**15**	**absent**	25–50	spreading	**alete**	absent	**no**	**alternating**	probably **absent**?
Equisetum columnare [d]	M. Jurassic	50	**absent**	80–90	spreading	**alete**	4?	**no**	**alternating**	?
E. haukeanum, *E. vancouverense*	L. Cretaceous	**2**	**absent**	90%	**appressed**	?	?	?	**alternating**	**absent**
Living *Equisetum* L. spp. [e]	Recent	**25**	**absent**	**60–90**	**appressed**	**alete**	**4**	usually **no**	**alternating**	**absent**

[a] Highest percentages probably reflect abscised leaf tips.
[b] Data from Watson and Batten (1990)
[c] Data from Gould (1968)
[d] Data from Harris (1978)
[e] Data from Hauke (1963, 1978)

subgenera (Hauke, 1990). Those characters can be recognized from anatomically preserved vegetative shoots.

Stomata are surficial and usually scattered or in bands two or more wide in subgenus *Equisetum* (i.e., horsetails), while those of *Hippochaete* (i.e., scouring rushes) are distinctly sunken below the ordinary epidermal cells and are usually arranged in single lines (Hauke, 1990). Aerial shoots of subgenus *Equisetum* branch in regular whorls or are unbranched, while those of subgenus *Hippochaete* are either irregularly branched or unbranched. A third feature, position of endodermis (i.e., common exterior ring in subgenus *Equisetum* and as double common or individual endodermis in subgenus *Hippochaete*; Hauke, 1990) is not fully consistent within the subgenera (Hauke, 1963, 1978). Page (1972a) has identified additional anatomical and fine-structure characters (with scanning electron microscopy) that appear to be of systematic value (e.g., Table 2), but such characters have not yet been employed in phylogenetic analyses.

Equisetum haukeanum and *E. vancouverense* share with subgenus *Hippochaete* an irregular pattern of branching (Table 2). Endodermal positioning in *E. vancouverense* aligns more closely to subgenus *Hippochaete*, while stomatal features of *E. haukeanum* conform more closely to those of subgenus *Equisetum*, but the data are inconclusive and the systematic reliability of these characters remains untested. Nevertheless, the combination of morphological characters displayed by *E. haukeanum* and *E. vancouverense* suggests that these species combine characters of the two subgenera (Table 2). These novel combinations of characters with respect to living species of *Equisetum* may reflect a Mesozoic species richness that has since been reduced by extinction.

***Evolution and phylogeny of* Equisetum**—There is a long and rich fossil record of equisetophytes that extends from the uppermost Devonian to the Recent and that documents excellent transformational series of morphologies and anatomy from which to infer the evolution of plant organs (i.e., leaves and sporangiophores), of stelar architecture, and of the features that

characterize crown group *Equisetum* (Boureau, 1964; Stewart and Rothwell, 1993; Taylor et al., 2008). Fossils contributing to the transformational series are assignable to several families sensu Boureau (1964), including Archaeocalamitaceae (Upper Devonian to the Lower Permian), Calamitaceae (Late Mississippian to Permian), and Equisetaceae (most common from the Triassic to the Recent; Stewart and Rothwell, 1993; Taylor et al., 2008). Other authors (e.g., Good, 1975) have chosen to place most of the same species in the single order Equisetales or even in the single family Equisetaceae. The latter classification emphasizes close relationships among many equisetophytes and allows us to focus on the relatively small number of structural changes that have led to evolution of the genus *Equisetum* (Table 1).

Only a few structural characters differentiate the Mississippian to Permian *Archaeocalamites* from the Late Mississippian to mid-Permian *Calamites*, from the Lower Permian to Jurassic *Neocalamites* Halle, from the mid-Triassic to Lower Cretaceous *Equisetites* Sternberg, and from modern-appearing *Equisetum* that ranges from the mid-Triassic to the Recent (Table 1). There is a general progression of changes in the characters of these plants through time that includes (1) a overall reduction in plant size, (2) the loss of leaf dichotomies, (3) progressive fusion of leaves forming a sheath, (4) change from spreading leaves or leaf tips to leaves/leaf tips that are pressed against the stem, (5) change from trilete to alete spores, (6) change from no spore elaters or three elaters to four elaters, (7) changes in the presence/absence of bracts within cones, (8) change from ridges and furrows that are aligned (or opposite) from internode to internode, to ridges and furrows that alternate from internode to internode, and (9) the change from woody to herbaceous (i.e., the loss of secondary vascular tissue) growth leading to crown group *Equisetum* (Table 1; Stewart and Rothwell, 1993; Taylor et al., 2008).

If a minimum age for each of the pertinent characters of crown group *Equisetum* can be determined from available fossils (Table 1) and if the most ancient date at which all of the

TABLE 2. Systematically informative morphological characters of *Equisetum* subgenera and Apple Bay aerial shoots. Data for living species from Hauke (1963, 1978, 1990) and Page (1972a).

Character	*Equisetum*	*Hippochaete*	*E. haukeanum*	*E. vancouverense*
Branching in regular whorls	+			
Branching irregular		+	+	+
Stomata surficial	+		+	?
Stomata sunken		+		?
Common external (only) endodermis	+		?	
Common internal and external endodermis (or surrounding each cauline bundle) [a]		+	?	+
Ornamentation of stomatal cell areas as mamillae [b]	+			?
Ornamentation of stomatal cell areas massive [b]		+	+?	?

[a] Common internal/external endodermis intergrades with endodermis that surrounds each bundle in stems of living *Equisetum* species. Therefore, that variation is scored as a single character state.

[b] See Page (1972a) for explanation of character.

crown group characters are present can be hypothesized as marking a minimum age for *Equisetum*, then the fossil record can provide solid evidence for the origin and early diversification of the genus (Nixon, 2008). Many of the characters that together characterize crown group *Equisetum* (i.e., stem diameter, leaf shape and orientation to the stem, spore type, alternating positions of carinal canals [or ridges and furrows] from internode to internode; Table 1) are relatively well established from known fossils (e.g., Becker, 1969; McIver and Basinger, 1989; Denk, et al., 2005), but a few require additional evidence or interpretation. The well-known change from alternating whorls of sporangiophores and bracts in Paleozoic calamitalean cones to only sporangiophore whorls in living *Equisetum* is not as clear an evolutionary transition as is popularly believed. Cones of *Archaeocalamites*, which predate *Calamites*, are similar to modern *Equisetum* in that they typically produce only sporangiophores (Walton, 1949; Bateman, 1991). Likewise, not all living *Equisetum* plants have terminal cones that consist of only sporangiophores. Well-known *Equisetum* teratologies include alternating sporangiophore and branct whorls, alternating fertile and vegetative zones along the stem, and irregularly occurring bract whorls within cones (e.g., Page, 1972b). Such teratologies and the extinct equisetophytes they resemble are reviewed by Naugolnykh (2004).

The transition from trilete to alete spores is incompletely documented because in situ spores have not been characterized for many extinct Mesozoic equisetophyte species (Kelber and van Konijnenburg-van Cittert, 1998). However, from the specimens that have been described, the transition appears to have occurred during the Triassic (for a detailed discussion, see Kelber and van Konijnenburg-van Cittert, 1998). For example, about 70% of the spores of the Lower/Middle Triassic *Equisetum laterale* are alete (Gould, 1968), whereas spores of the Upper Triassic *Equisetites arenaceus* are either alete or display a small trilete mark (Kelber and van Konijnenburg-van Cittert, 1998). Alete spores characterize most Jurassic and more recent species. Similarly, the presence/absence and number of spore elaters is not known for most fossil equisetophyte species (e.g., Watson and Batten, 1990). Three elaters characterize Paleozoic calamitaleans (Good, 1975; Good and Taylor, 1975). In contrast, elaters are not preserved in Triassic species (but see possible exception for *E. arenaceus*; Kelber and van Konijnenburg-van Cittert, 1998). The first well-documented occurrence of elaters on spores from *Equisetum* sporangia is from the Middle Jurassic *Equisetum columnare* (Harris, 1978; Table 1).

With the discovery of essentially modern *Equisetum* internal anatomy in *E. haukeanum* and *E. vancouverense*, we now have evidence that all of the diagnostic characters of crown group *Equisetum* species had evolved by the Lower Cretaceous (Table 1). Moreover, because there are at least two Early Cretaceous species of *Equisetum* present in the same depositional setting at the Apple Bay locality, and because both fall at the lower end of the size range for living *Equisetum* species, it is highly unlikely that *E. haukeanum* and *E. vancouverense* represent the initial diversification of the genus *Equisetum*.

As is illustrated by the *Equisetum* morphospecies present at the Apple Bay locality, well-dated extinct species provide a strong minimum age determination for the origin and evolutionary radiation of clades (Nixon, 2008) that can be regarded as a test of clade age assessments derived from other methodologies (e.g., Des Marais et al., 2003). There are several levels of rigor with which the available fossil evidence can be employed as tests of clade age-hypotheses. The least rigorous level employs fossils that display features that all are concordant with those of the crown group, but that are only a subset of the synapomorphies that characterize the crown group. The oldest widely recognized evidence of this type for the genus *Equisetum* is represented by *E. laterale* Phillips from the mid-Triassic of Queensland, Australia; Gould, 1968). *Equisetum laterale* is preserved by coalified compression and displays all of the morphological features of living *Equisetum* species. However, the *E. laterale* fossils provide little evidence for the characteristic internal anatomy or spores of the genus. If this species does represent crown-group *Equisetum*, then the genus is at least 230 million years old.

A higher level of rigor requires that minimum clade age be inferred from an assemblage of extinct morphotaxa that together document all of the synapomorphies of living species. Using this criterion, *E. haukeanum* and *E. vancouverense* provide both of the remaining characters (e.g., characteristic internal stem anatomy and small plant size; Table 1) needed to confidently set a minimum clade age for crown group *Equisetum* of Early Cretaceous (i.e., at 136 Ma; Table 1).

The most cautious approach for determining minimum clade ages from the fossil record recognizes the possibility of mosaic character evolution among related species. A minimum age is not acceptable unless all of the diagnostic characters of the crown group are known from a single extinct species. In the case of equisetophytes, there is excellent evidence that Mesozoic diversity was far greater than for the extant flora (Taylor et al., 2008) and therefore that a large percentage of morphotaxa displaying subsets of crown group synapomorphies could possibly represent stem group representatives of the clade. Because

extinct species of fossil plants are infrequently complete enough to document the whole suite of synapomorphies for a crown group, that level of rigor for testing hypotheses can rarely be applied. For the genus *Equisetum*, the fossil record has yet to provide data of this type from a single species.

In this regard, there is one species of fossil equisetophytes that prompts us to proceed with caution. *Equisetites lyellii* (Mantell) Seward is well represented in lowermost Cretaceous sediments (i.e., Berriasian-Valanginian; Watson and Batten, 1990) and is therefore only slightly older than the morphospecies *Equisetum haukeanum* and *E. vancouvenrense* (i.e., Valanginian/Hauterivian boundary). *Equisetites lyellii* is represented by specimens that display excellent evidence for growth architecture, vegetative morphology, reproductive morphology (i.e., peltate sporangiophores), spores, cuticular features, and some internal anatomy of the sporophyte (Table 1). That species displays all the synapomorphies of crown group *Equisetum* except for the absence of spore elaters and a larger number of metaxylem tracheids surrounding carinal canals of the stem than is present in living species (Table 1; Watson and Batten, 1990).

Clearly, clade age for the genus *Equisetum* is difficult to establish with certainty from either questionable molecular clock calculations (i.e., unknown levels of nucleotide substitution rate heterogeneity) based on systematic relationships of contested accuracy (i.e., euphyllophytes; Rothwell and Nixon, 2006) that are inferred from highly restricted taxon sampling (i.e., living species only; Pryer et al., 2001; Des Marais et al., 2003), or from incomplete data for extinct species of *Equisetum* plants. Nevertheless, the fossil record does provide valuable evidence for testing hypotheses of systematics, phylogeny, and clade ages. With the characterization of *E. haukeanum* and *E. vancouverense* from the Lower Cretaceous, we now know that all of the synapomorphies of living *Equisetum* had evolved by at least 136 Ma (Table 1) and therefore that the crown group probably originated during the Mesozoic. Although the mid-Triassic date for potential crown group *Equisetum* (i.e., *E. laterale*) remains to be verified by internal anatomical and spore data (Table 1), that species is only one example of a rich and diverse fossil record (Stewart and Rothwell, 1993; Taylor et al., 2008) that is continuously providing new and more convincing evidence that equisetophytes are derived from among trimerophyte-grade species of the Euphyllophytina (sensu Kenrick and Crane, 1997; Friedman et al., 2004), that stem/leaf organography has evolved independently among several clades of euphyllophytes (Stewart and Rothwell, 1993; Friedman et al., 2004; Tomescu, 2009; Sanders et al., 2009), and that the equisetophyte clade has been distinct since at least the Upper Devonian (Good, 1975; Bateman, 1991; Rothwell, 1999; Taylor et al., 2008).

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