

## DEVELOPMENT AND ECOLOGICAL IMPLICATIONS OF DORMANT BUDS IN THE HIGH-PALEOLALTITUDE TRIASSIC SPHENOPHYTE *SPACIINODUM* (EQUISETACEAE)<sup>1</sup>

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*Spaciinodum collinsonii*, a Triassic sphenophyte from the central Transantarctic Mountains, Antarctica, is reinterpreted based on new material in order to clarify discrepancies from previous work and to detail the development and ecology of the *Spaciinodum* plant. Vegetative stems have alternating nodes and internodes, nodes distinguished by a solid diaphragm of tissue, internodes by the presence of vallecular (cortical) and carinal canals, and a hollow pith. Whorls of branches arise immediately above the nodes, alternating with the leaves of the subjacent nodes. Branches develop in the cortex and are anatomically similar to the stems. While *Spaciinodum* is similar to extant *Equisetum*, it is distinctive in that its large vallecular canals form a complete ring within the cortex and are separated only by thin fimbrials of tissue. The majority of specimens of *Spaciinodum* are now believed to be dormant buds with condensed nodes and internodes, with progressively longer internodal regions more basally. More apical portions of buds have cellular internodes because the areas where the canals will form have not yet ruptured from elongation. The abundance of buds and the absence of elongated stems in the permineralized peat deposit suggest that *Spaciinodum* underwent dormancy during the dark Antarctic winters.

**Key words:** Antarctica; dormancy; Equisetophyte; Triassic; *Spaciinodum*; stem bud.

The Equisetales is thought to be a monophyletic group with unique morphology and includes plants characterized by distinct nodal and internodal regions, whorled leaves and/or branches, and regular longitudinal ribs on the internodal surface. While they have a long fossil record beginning in the Devonian (Taylor and Taylor, 1993), today the group is represented only by the genus *Equisetum*, which has 15 species (Hauke, 1974). Although much is known of the evolution, structure, and ecology of the extinct arborescent equisetaleans comprising the family Calamitaceae, less is known about the fossil record of herbaceous members of Equisetales included in family Equisetaceae. This lack of knowledge is because members of Equisetaceae, with few exceptions (e.g., Brown, 1975; Watson, 1983), are preserved as compression fossils. Of the few permineralized Equisetaceae known, the oldest unequivocal permineralized equisetacean is *Spaciinodum collinsonii*, from the early Middle Triassic Fremouw peat flora of Antarctica (Osborn and Taylor, 1989; Osborn et al., 2000). *Spaciinodum* is a small equisetacean described from vegetative stems and specimens interpreted as reproductive apices with in situ spores. Previously, authors have considered the structure of both the vegetative and reproductive organs of the plant unique among equisetaleans, although certain features (e.g., superficial stomata) have been used to suggest an affinity with *Equisetum* subgenus *Equisetum* (Osborn and Taylor, 1989), one of two subgenera into which *Equisetum* is traditionally divided. Generally, equisetophytes from the Mesozoic are not anatomically preserved. Because *Spaciinodum*

represents the most complete of the Mesozoic equisetophytes (Osborn et al., 2000), it is an important component in understanding the Paleozoic to recent record of the equisetaleans.

Both fossil and extant members of the Equisetales have a global distribution and in general require an environment with a ready supply of water to thrive (Hauke, 1963, 1966; DiMichele et al., 2005). The Triassic landscape of Antarctica has been reconstructed as including a number of braided river systems with meandering streams and broad floodplains (Isbell, 1991). The Middle Triassic world is generally thought to have existed under a greenhouse climate, and the poles did not have permanent ice sheets (Kidder and Worsley, 2004). The diversity of reptiles and amphibians preserved in a lower section of the Upper Fremouw Formation is indicative that the climate in the region was warm, with seldom freezing temperatures (Hammer et al., 1990). The occurrence of a cycad, *Antarcticycas*, in the Fremouw peat may also be indicative of a relatively warm climate without extended periods of frost or snow (Taylor et al., 2000; Hermesen et al., in press), because cycads today are restricted primarily from tropical to warm temperate zones between 30°S and 35°N latitude (Norstog and Nicholls, 1997). Moreover, tree-ring data from the Fremouw peat suggest that the environment was warm and temperate with only rare frosts during the growing season and neither severe cold nor drought (Taylor and Ryberg, 2007). The tree-ring data also clearly indicate that seasonality in the Fremouw peat was dictated by low winter light levels that inhibited photosynthesis (Taylor and Ryberg, 2007; Ryberg and Taylor, 2007). Other evidence of seasonality in the Fremouw peat and surrounding contemporaneous floras includes the presence of leaf mats and abscission layers in the leaf bases of some *Dicroidium* fronds (Meyer-Berthaud et al., 1993; Taylor, 1996; Taylor et al., 2000; Axsmith et al., 2000).

In this paper we describe *Spaciinodum* stem buds, which are another indicator of seasonality in the Fremouw peat flora, and

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also detail the first evidence of branching in this genus. New insights from the anatomy of the buds have allowed us to more accurately interpret the anatomy of the *Spaciinodum* plant and to make inferences about vegetative development of the stem and branches. These new data are used in a discussion of the phylogenetic context of this equisetophyte and the importance of the buds in understanding the ecology of *Spaciinodum* and the Fremouw peat flora.

## MATERIALS AND METHODS

The permineralized peat comes from the Beardmore Glacier area of the central Transantarctic Mountains of Antarctica, north side of Fremouw Peak (84°18'S, 164°20'E). The plants are silicified and dated as early Middle Triassic (Anisian) on the basis of palynology (Farabee et al., 1990). Specimens were prepared using the acetate peel technique (Galtier and Phillips, 1999), after etching in 49% HF for ~1.5–8 min. Pieces of peels were mounted on microscope slides in Eukitt for light microscopy. Fossil specimens prepared for this study include specimen numbers 10771, 11164, 11277, 12741, 13460, 15766, 15771, 15772, 15733, 15998; and slide numbers 22565–23012. Fossil specimens previously prepared include specimen number 10160, and slides 20357 and 15652. Extant specimens examined include a transverse section of an *Equisetum hyemale* stem (from Ripon Microslides Laboratory, Ripon, Wisconsin), two transverse sections of a young *Equisetum* sp. stem apex from the teaching slides of the Paleobotanical Collections, KU Natural History Museum, and Department of Ecology and Evolutionary Biology greenhouse specimens of *E. hyemale*. All specimens are housed in the University of Kansas Natural History Museum, Division of Paleobotany, Lawrence, Kansas collection.

Images were captured using a Leica (Allendale, New Jersey, USA) DC500 camera on either a Leica MZ 16 dissecting microscope or a Leica DM 5000 B compound microscope using Leica DC 500 version 5.2.4 software in conjunction with Photoshop CS2 (Adobe Systems, San Jose, California, USA). Images were processed after capture using Photoshop CS version 8.0. Changes to raw images include resizing using bicubic resampling, rotating, and cropping. Color, contrast, and brightness were not adjusted after capture.

## SYSTEMATICS

### *Division Equisetophyta*

### *Order Equisetales*

### *Family Equisetaceae*

### *Genus Spaciinodum*

*Type species*—*Spaciinodum collinsonii* Osborn & Taylor, 1989 *emend*—

*Emended diagnosis*—**Stem** with ribbed and furrowed surface and jointed organization representing distinct nodal and internodal regions. In longitudinal section, internodal regions are shorter apically and longer basally. Nodes characterized by solid pith, absence of vallecular (cortical) and carinal (protoxylem) canals, and large vascular bundles that form a nearly continuous ring, internodal regions characterized by vallecular canals separated by uniseriate cellular partitions (fimbrials) around the circumference of the cortex. Position of vascular bundles offset in successive internodes, bundles collateral, xylem endarch. Internodal anatomy differing with degree of maturation of the internode; relatively immature internodes with vallecular canals contain cells, canal boundaries and uniseriate fimbrials are clearly visible, carinal canals absent. More mature (elongate) internodes characterized by open vallecular and carinal canals; most mature internodes also with large pith canal. Sclerenchyma and distinct stem ribs rarely observed, possibly only developing at the periphery of the cortex in very mature stems or rarely preserved. **Leaves** occurring in whorls at nodes,

enclosing and overarching the apex of the young stem; fused proximally, distally free and tapering, vascularized by a single bundle with scalariform xylem thickenings; free distal portions rectangular in transverse section, mesophyll unifacial. **Branches** arising within the cortex, alternating with the leaves; branches internally organized much like larger stems, vascular bundles collateral, inner cortex with developing vallecular canals, outer cortex cellular; branch-borne leaves given off at the nodes and overarching the apices of the branch primordia. **Stomata** superficial. **Buds** consist of a telescoped stem with jointed organization, stem apex overarched by leaves. Bud attached to additional tissue basally that may represent a root or rhizome.

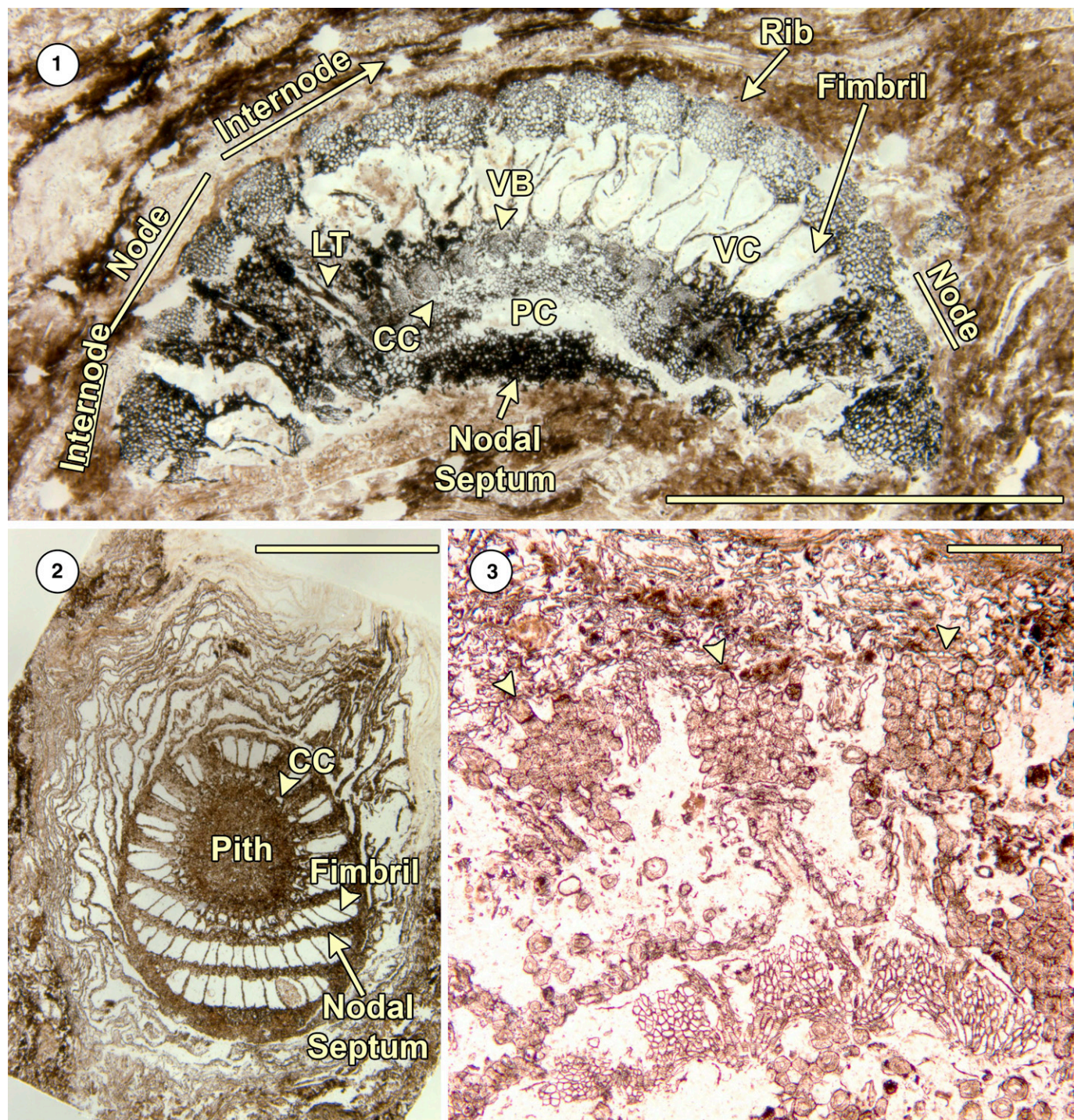
## RESULTS

*Stem anatomy*—Examination of new and well-preserved specimens of *Spaciinodum* has allowed us to formulate a new interpretation of the probable organization of the mature stem, i.e., a stem with fully elongated internodes. In internodal regions, the stem is often characterized by a large open pith (central or pith canal) surrounded by a ring of many small vascular bundles (Fig. 1); in stems that are not fully elongated, the pith is solid in internodal regions (Fig. 2). Vascular bundles are collateral with an associated carinal canal—an open canal in the position of the protoxylem (Figs. 1, 16). External to the vasculature is a continuous ring of large vallecular canals in the cortex of the stem (Figs. 1, 4; see also Osborn et al., 2000, plate 1, fig. 4); partitions between adjacent vallecular canals are formed by thin uniseriate fimbrials (Figs. 1, 2, 4). External to these canals is a thick layer of cortical tissue that forms the external ribs of the stem (Figs. 1, 4). This tissue may be sclerenchymatous, as evidenced by a specimen that has thick-walled cells that may be sclerified (Fig. 3). In the nodal region, vallecular canals are absent, and the solid pith forms a solid diaphragm of tissue across the stem (Figs. 1, 2, 21). Vascular bundles in the stem are offset between successive nodes, such that the leaf traces given off at a node alternate with superjacent internodal bundles (Fig. 1).

*Branching*—Several specimens have evidence of branching, including developing whorls of branches in buds. The branches (4–6) arise in the cortex of the stem (Figs. 4, 5) and alternate with the leaves of the subjacent node. Branches observed in buds depart the stem at a right angle and then curve upward within the leaves of subjacent nodes. Anatomy of the branch is similar to that of the stem. The cortex consists of an outer cellular region and an inner hollow ring that is transected by rows of cells, which form the vallecular canals (Figs. 7, 8). A lining in the internal portion of the cortex is the remnant of the vasculature that has separated from the cortex (Fig. 8, arrowhead). The mass of cells in the center of the branch is pith tissue with occasional xylem tracheids around the margin (Figs. 7, 8). In an oblique transverse section, the node/internode arrangement can be seen, with masses of cells aligned in distinct rows and columns (Fig. 9). Branch-borne leaves are attached at right angles to the nodes; the leaves have broad bases, and each tapers toward its apex (Fig. 9). Branch leaves in buds completely enclose the branch and are themselves enclosed in leaves from subjacent nodes of the stem (Fig. 18).

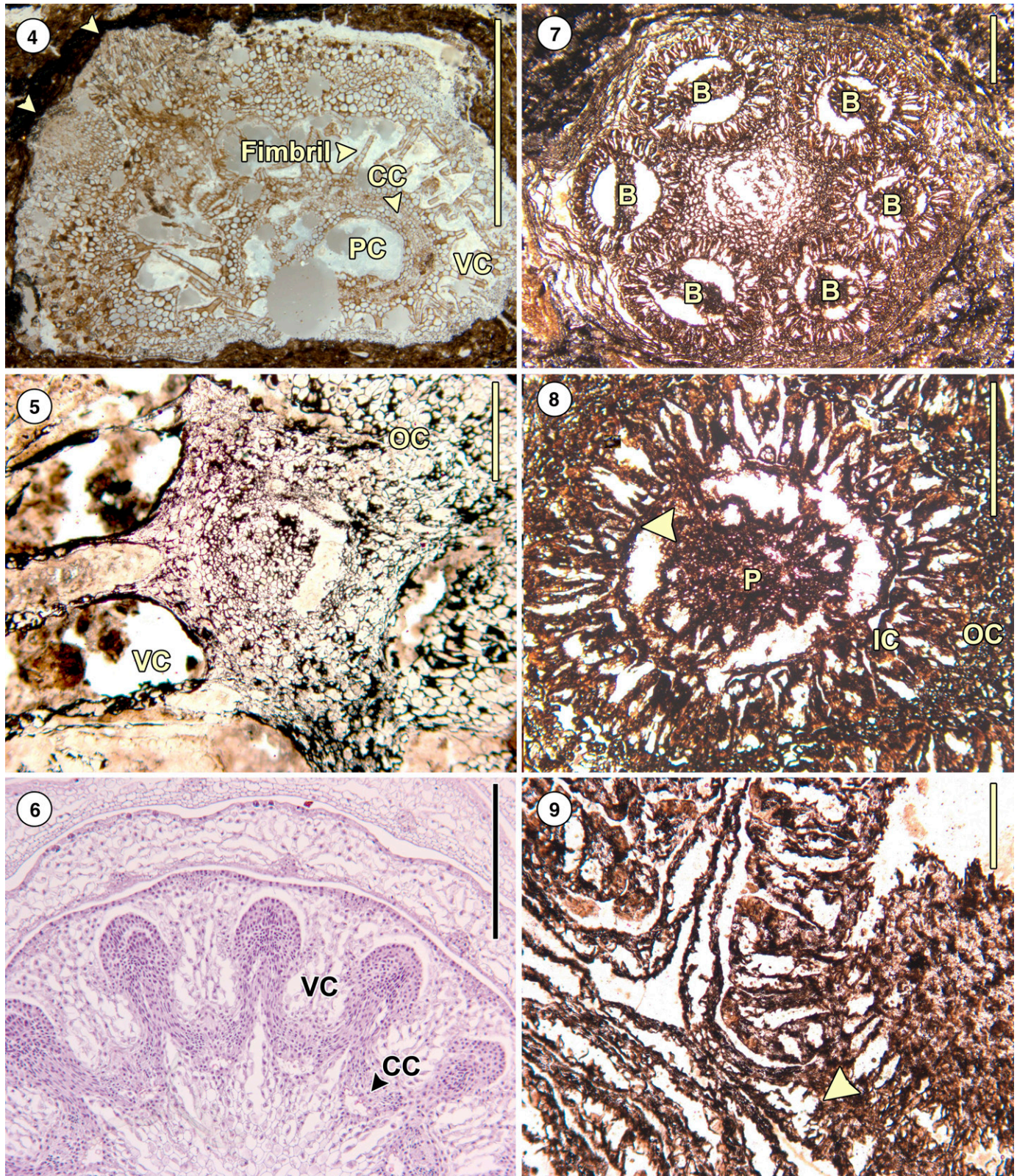
*Buds*—The majority of *Spaciinodum* specimens previously described as isolated apices may in fact be shoot buds. These





Figs. 1–3. *Spaciindoum collinsonii*. **1.** Oblique transverse section showing organization of both nodal and internodal regions in a mature stem. Nodal regions display a solid pith (Nodal Septum), a solid cortex with no vallecular canals, and leaf traces (LT) traversing the cortex. Internodal regions display prominent vallecular canals (VC) in the cortex separated by uniseriate, thin-walled fimbrils (Fimbril). A prominent pith canal (PC) is also present. Collateral vascular bundles (VB) with associated carinal canals (CC) occur in the internodal region. Slide no. 22573, bar = 1 mm. **2.** Oblique section of a stem, covering eight nodes. Internodal regions are traversed by thin fimbrils that mark the boundaries of the vallecular canals in the cortex. In this section, the pith is solid in both internodal and nodal regions, perhaps indicating that cellular tearing has not yet occurred in that region. Carinal canals (CC) are present. Slide no. 20357, bar = 2 mm. **3.** Transverse section of poorly preserved stem clearly showing cortical sclerenchyma (arrowheads). Slide no. 26339, bar = 300  $\mu$ m





Figs. 4–9. Transverse sections of branching stems and branches of *Spaciinodum collinsonii* and *Equisetum* sp. **4.** Transverse section of stem showing emerging branch (arrowheads), open pith (PC), vallecular canals (VC), and carinal canals (CC). Slide no. 22595, bar = 2 mm. **5.** Transverse section showing detail of branch primordium in cortex with vallecular canals (VC). Note air space around developing branch bud. The vallecular canal (VC) is toward the center of the stem and the outer cortex (OC) is toward the outside of the stem. Slide no. 22886, bar = 0.5 mm. **6.** Transverse section of *Equisetum* sp. stem showing branch primordia, developing vallecular canals (VC) and carinal canals (CC). Note air spaces around developing branch buds, similar to Fig. 5.



buds contain condensed, multinodal (up to 14 nodes) shoots (Figs. 19, 20). Comparison of more condensed with more elongated buds suggest that they undergo elongation from the base toward the apex, i.e., acropetally (Figs. 19, 20). Some buds have a flattened basal region, which appears to be the actual boundary of a structure, and some appear to be attached to more tissue basally (Figs. 19, 21). In internodal regions with immature tissue, developing buds lack open vallicular canals—although the positions of the canals are clearly delimited by large parenchymatous cells divided by uniseriate rows of cells that will become the fimbrials (Figs. 10, 11, 19)—the pith is solid, and carinal canals are lacking (Figs. 10, 14, 15).

## DISCUSSION

**Reinterpretation of vegetative and reproductive stems of *Spaciinodum***—Although in most respects, the description of the organization of the stem of *Spaciinodum* given here corresponds to its original (Osborn and Taylor, 1989) and previously emended (Osborn et al., 2000) descriptions, it differs in one major respect: in past papers, the vallicular canals have been described as occurring only in the nodal regions of vegetative stems, and in the internodal but not the nodal regions of fertile apices. Reexamination of previously published and newly prepared material clearly indicates, however, that (1) the vallicular canals of *Spaciinodum* consistently occur in the internodal regions of the stem only; and (2) there is little evidence that the previously described fertile apex is indeed an equisetacean reproductive structure rather than a sterile stem bud.

There is no evidence that the vascular and nodal–internodal anatomy of the specimen that is considered to be a reproductive apex by Osborn et al. (2000) differs from the anatomy of other stems of *Spaciinodum*. Particularly, we reinterpret all stems of *Spaciinodum* as having vallicular canals in the internodal but not nodal regions. These canals in the internodal region are most obvious in longitudinal section, where nodal septa traverse both the pith and cortex of the stem, whereas each internodal region has an open cortex and sometimes an open pith (Fig. 20; see also Osborn and Taylor, 1989, fig. 17 and Osborn et al., 2000, plate 1, figs. 1–3, 5). Thin cortical fimbrials that form partitions between adjacent vallicular canals in internodal regions can also be observed in transverse (Figs. 1, 4; see also Osborn and Taylor, 1989, figs. 8, 15 and Osborn et al., 2000, plate 1, fig. 4), longitudinal (Fig. 20; see also Osborn and Taylor, 1989, fig. 17 and Osborn et al., 2000, plate 1, figs. 2, 3), and oblique sections (Fig. 2). Previously, oblique transverse sections such as the one in Fig. 2 were interpreted as oblique through a single node, at least in the region of the pith (Osborn et al., 2000). However, this section clearly shows multiple nodal diaphragms traversing the cortex, suggesting that the section in fact cuts across multiple nodal and internodal regions. That the pith is solid throughout both nodal and internodal regions (possibly indicating that the stem is not fully

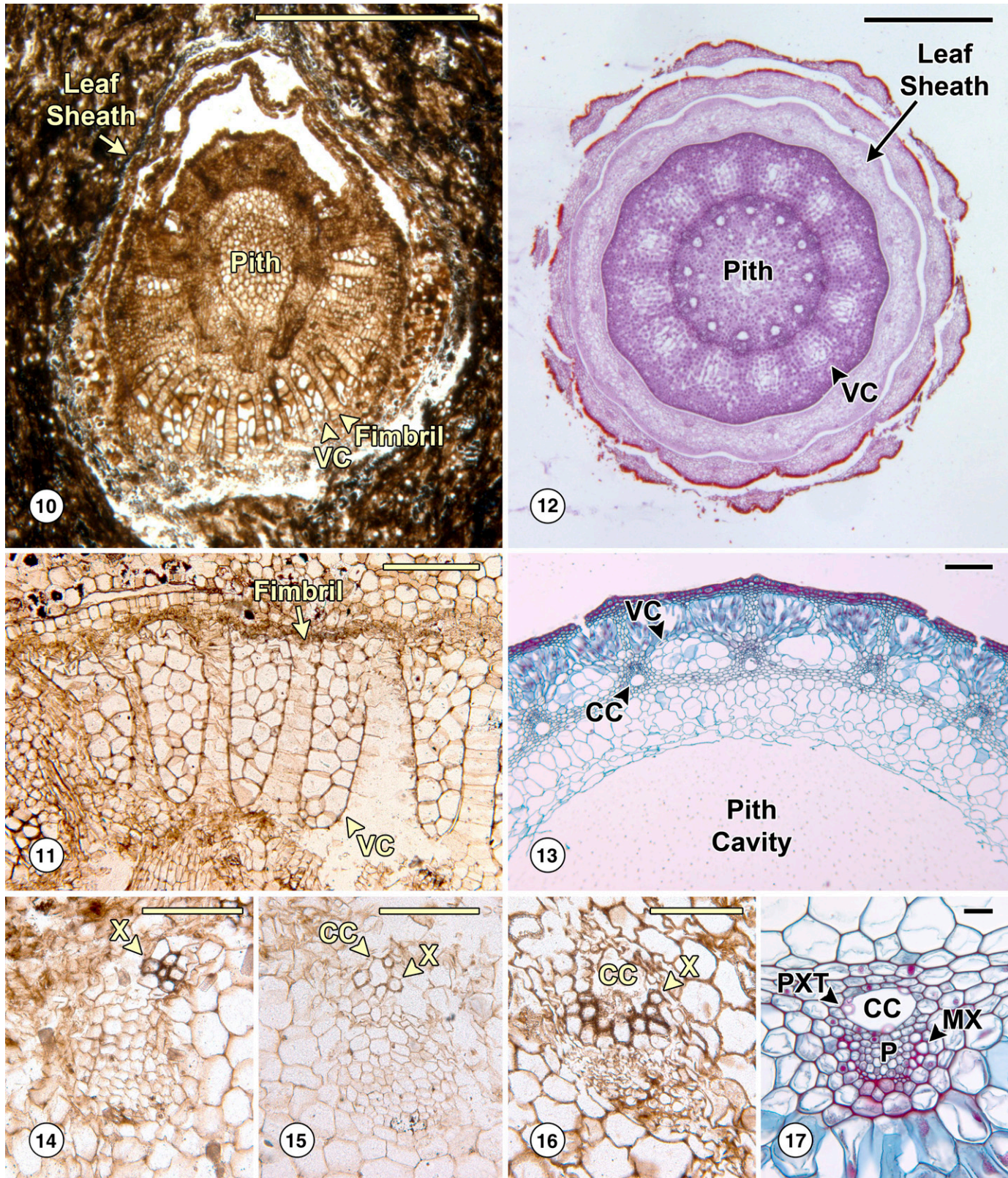
elongated) may have made interpretation of the section more difficult, although other, similar sections also show nodal diaphragms traversing the pith with open internodal regions (see Osborn et al., 2000, plate II, fig. 3).

Osborn et al. (2000) identified a single specimen of *Spaciinodum*, including the specimen shown here in Fig. 20, as a fertile apex of *Spaciinodum*. The primary reason for this was the identification of spore-filled sporangia at the base of one of these fertile apices (see Osborn et al., 2000, plate 1, figs. 3, 5, and plate 3, figs. 1–4). The sporangia described from the “fertile apex” do not resemble equisetacean sporangia. According to Osborn et al. (2000), the sporangia are associated with the cortical chambers, rather than being born externally on sporangio-phores as in extant *Equisetum* (Foster and Gifford, 1959). No reproductive spores are found within the stem of any other extant or fossil equisetaleans, casting doubt as to whether the spores belong to *Spaciinodum*. The “spores” macerated from the base of this specimen are also somewhat small for equisetacean spores, as pointed out by Osborn et al. (2000). The “sporangia” may simply be cortical chambers filled with fungal spores. Thus, we consider it unlikely that this apex is the fertile structure of the *Spaciinodum* plant.

**Stem development of *Spaciinodum*: Anatomy of aerial stem buds**—Many of the specimens newly figured in this paper are thought to represent aerial stem buds, and their anatomy reflects various stages of development. These specimens are considered buds since the longest internodal length (0.6 mm) is shorter than that found in elongated internodes (3.1 mm). Understanding the development of the *Spaciinodum* stem is facilitated by the unique way in which the stem of *Equisetum* develops, as detailed by Golub and Wetmore (1948a, b) for *E. arvense*. In extant *E. arvense*, an intercalary meristem that originates from the lower three to four layers of the leaf sheath primordium gives rise to the extravascular tissues, particularly those of the epidermis and cortex. As the epidermis and outer cortex (hypodermis) differentiate, one or more layers of cells of the outer cortex elongate and become fibrous. These cell layers may increase through periclinal division, especially under the ribs, and form the periphery of the cortex. While the inner cortical cells also elongate and expand radially, they do not maintain pace with expansion of the internode in length and width. Schizogamous intercellular spaces begin to develop between the cells of the inner cortex, eventually forming the vallicular canals (Figs. 12, 13). The intercalary meristem contributes no cells to the pith in the internodal region after the fourth or fifth internode, and the hollow pith forms by mechanical tearing of the cell walls (Figs. 12, 13). Carinal canals are also formed by rupturing of cells and separating of the tissues. Internodal protoxylem elements mature between the fourth to seventh internodes, and neither new protoxylem nor protophloem is produced by the intercalary meristem. As the internodes elongate following maturation of the xylem elements, they eventually tear; several xylem elements sometimes remain at the peripheries of the canals (Figs. 13, 17).

Slide no. 23010, bar = 0.5 mm. 7. Slightly oblique transverse section through branches above the apex of the stem. The whorled arrangement of branches (B) is apparent. Leaves between the branches are those from higher nodes on the stem and leaves outside of the branches are those from nodes below the point of branch development. Slide no. 22968, bar = 2 mm. 8. Slightly oblique cross section of a single branch. The center of the branch consists of pith tissue (P), while the outer portion consists of the inner (IC) and outer (OC) cortex. The arrowhead points to the lining that is the remnant of vascular tissue. Slide no. 22968, bar = 0.5 mm. 9. Oblique transverse section of a branch showing the emergence of a leaf at a node (arrowhead). The leaf subsequently curves upward to enclose the branch. Slide no. 22988, bar = 0.2 mm.





Figs. 10–17. Transverse sections of immature stems of *Spaciindoum collinosonii* (10, 11, 14–16) and *Equisetum* (12, 13, 17). **10.** Transverse section of stem showing a solid pith, uniseriate cortical fimbrils, cell-filled vallicular canals (VC), and external leaves. Slide no. 22605, Scale = 1 mm. **11.** Detail of immature vallicular canals (VC) filled with cells and separated by uniseriate fimbrils. Slide no. 22654, bar = 200  $\mu$ m. **12.** *Equisetum* sp., showing pith with central canal beginning to open, opening vallicular canals (VC), and leaf sheaths. Slide no. 23011, bar = 1 mm. **13.** Detail of cell-filled vallicular canals (VC) in *E. hyemale*, also showing vascular bundles with open carinal canals (CC) and open pith. Slide no. 23012, Scale = 200  $\mu$ m.



Sections of nonelongated *Spaciinodum* stems show that they have a solid pith in transverse section (Fig. 10) and clearly delimited vallecular canals (Figs. 10, 11). These developing canals are quite similar to those in *Equisetum hyemale* (Fig. 13) and those described from for *E. kansanum* by Browne (1939); the boundaries of the future vallecular canals are clearly visible in the condensed internodes of the stem, although the canals are filled with large parenchymatous cells. The development of the canals appears different from what are interpreted as vallecular canals forming in the cortex of a young *Equisetum* sp. apex (Fig. 12). Some longitudinal sections of *Spaciinodum* have a pith that is at least partially solid in apical regions, but more open basally, suggesting that the development of the pith canal proceeded acropetally. Such acropetal development reflects typical development of *Equisetum* aerial stem buds, which mature from base to apex (Hauke, 1985). Open vallecular canals are visible in regions of the same bud where the pith canal is not fully developed, suggesting that they opened before the pith canal (Fig. 20). The opening of vallecular canals before pith canals is corroborated by other oblique and transverse sections, which have open vallecular canals and a cellular pith (Fig. 2). Transverse and oblique sections additionally suggest that the carinal canals also opened before the pith canal. Perhaps they opened near the same level as that at which the vallecular canals opened, because open carinal and vallecular canals have been observed to co-occur in sections with cellular material in the pith (Fig. 2), and sections with closed vallecular canals show little or no development of the carinal canals (Figs. 10, 19). Although rupturing of cells to form the carinal canals in longitudinal sections of *Spaciinodum* has not been observed, some transverse sections show immature vascular bundles lacking canals (Fig. 14), perhaps showing the early stages of canal formation (Fig. 15), and fully developed bundles with well-developed carinal canals (Fig. 16).

Other specimens of *Spaciinodum* show evidence of branching, including developing whorls of branches that have been initiated within dormant buds. In extant *Equisetum*, branches are interpreted as originating exogenously at the top of the node (Hauke, 1987), although according to Sharma (1990), branches develop deep in the cortex (Fig. 6). The specimens of *Spaciinodum* that show evidence of branching suggest that the branches differentiate in the cortex (Figs. 4, 5). As they emerge, branches in *Equisetum* are protected by a small air space (Sharma et al., 1986), visible in a branching specimen of *Equisetum* (Fig. 6), and in one specimen of *Spaciinodum* (Fig. 5). Although branches in *Equisetum* are generally considered to be associated with nodal regions, it is notable that the nascent branches in *Spaciinodum* occur at the same level with vallecular and carinal canals, two features that are generally considered as an indication that the region is internodal (Figs. 4, 5). The breakdown of cells, perhaps indicating the initial stages of development of vallecular canals, can also be seen in the transverse section of *Equisetum*, and carinal canals are clearly present as well (Fig. 6). Duval-Jouve (1864, plate 6, figs. 22–23) also illustrated *E. arvense* with vallecular and carinal canals in

the same sections as the branches, suggesting that the co-occurrence of branches with open canals characteristic of internodal anatomy may be typical of *Equisetum* and may not represent a feature unique to *Spaciinodum*. Unfortunately, vascular connection of the branches to the main stem in *Spaciinodum* has not been observed.

Two *Spaciinodum* aerial stem buds contain more fully developed branch primordia, arising from at least two nodes, thus providing the first definitive evidence that *Spaciinodum* was a sphenophyte that bore secondary branches. These branches, four observed at one node in one specimen and six at one node and at least one branch at a higher node in another specimen, alternate with the leaves (Fig. 7), as in extant *Equisetum*. The branches depart the bud at right angles and then curve upward within the leaves of subjacent nodes. The production of branches at multiple nodes suggests that *Spaciinodum* is a branching sphenophyte and that this branching is not a wound response as seen in some extant *Equisetum* (Hauke, 1963). The internal structure of the branches is similar to that of the larger stems (Figs. 7–9). Because the anatomy of the branches is not preserved in great detail, the degree of branching in *Spaciinodum* cannot be determined. However, all branches were found enclosed within buds, indicating that the buds themselves are most likely not secondary branches with a different morphology from a primary stem.

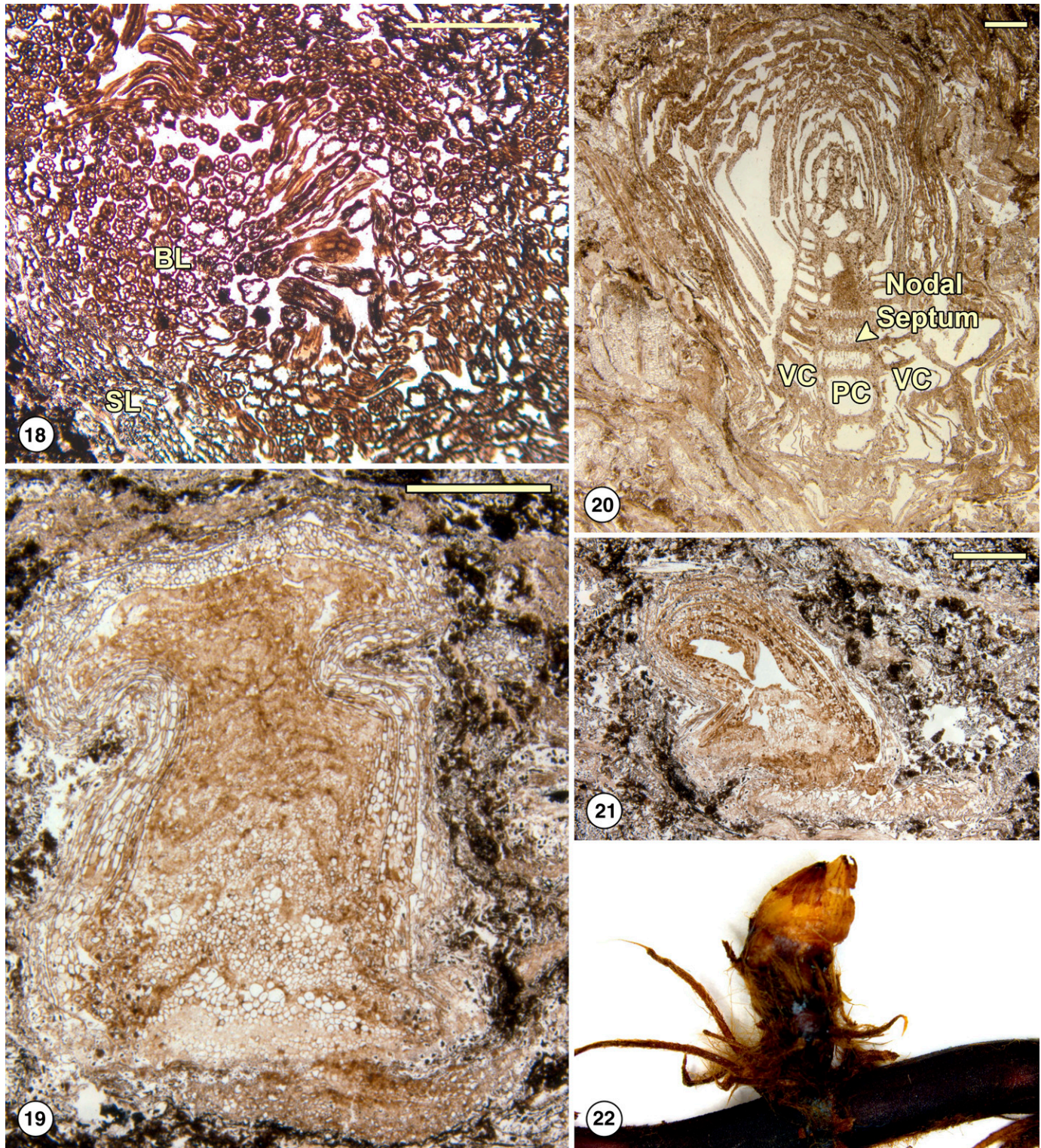
**Subterranean structures in Equisetales: Evidence of seasonality**—Reports of fossilized subterranean portions of equisetaleans consist mostly of roots and tubers. In *Phyllothea* (McLoughlin et al., 2005) and fossil *Equisetum* (e.g., Gould, 1968; Brown, 1975; Watson and Batten, 1990), roots and rootlets have been described from impression specimens, but no other organs are attached to the rhizomes. In *Equisetum*, tubers, which are starch-filled storage organs, are produced when aerial shoots become dormant and photosynthesis ceases (Hauke, 1985; Marshall, 1986). Tubers and roots have been reported from numerous Mesozoic and Cenozoic sediments of the northern hemisphere (e.g., McIver and Basinger, 1989; Watson and Batten, 1990; Skog and Dilcher, 1994; Zhang et al., 2007), but few from the southern hemisphere. The starch content in tubers may make them more likely than aerial branch buds to be preserved, which may explain why they are present in the fossil record while buds are not. Another possibility is that individual impressions of tubers may represent buds with little detail preserved and therefore would look similar to tubers. No previous records of fossil equisetalean buds are known from either the northern or southern hemisphere; therefore, this paper is the first report of fossil equisetalean buds.

In extant *Equisetum*, buds develop on the subterranean portions of the stems (Fig. 22) that constitute the dormant structures of the plants (aerial stems of some species die back in the fall); one or more buds protrude from each node for up to several inches in the soil (Hofmeister, 1862). Fertile and vegetative buds, constituting the initial stems of the next year's growth, are fully developed by the time dormancy sets in, each containing all

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**14.** Immature vascular bundle of *Spaciinodum* with few differentiated xylem elements (X) and no carinal canal. Slide no. 22658, bar = 100  $\mu$ m. **15.** Immature bundle of *Spaciinodum* with few differentiated xylem elements, perhaps surrounding developing carinal canal (CC). Slide no. 22656, bar = 100  $\mu$ m. **16.** Mature bundle of *Spaciinodum* showing open carinal canal (CC) and xylem (X). Slide no. 22761, bar = 100  $\mu$ m. **17.** Mature bundle of *E. hyemale* showing open carinal canal (CC), protoxylem tracheids at periphery of canal (PXT), metaxylem (MX), and phloem (P). Slide no. 23013, bar = 100  $\mu$ m.





Figs. 18–22. *Spaciinodum collinsonii* (18–21) and *Equisetum* sp. (22) stem buds. **18.** Slightly oblique transverse section of the apical-most point in a branch. Branch leaves (BL) completely enclose the branch before elongation. Stem leaves (SL) enclose the branch as well as the branch leaves. Slide no. 22973, bar = 0.5 mm. **19.** Longitudinal section of an immature stem bud showing internodal regions with parenchymatous cellular material in cortical and pith regions. Slide no. 15652, bar = 1 mm. **20.** Longitudinal section of *Spaciinodum* stem bud with progressively longer internodes from the apex toward the base. Distinct vallecular canals (VC) and a pith canal (PC) are observed in basal internodes. A nodal diaphragm (Nodal Septum) indicates the position of the nodes. Slide no. 22667, bar = 1 mm. **21.** Longitudinal section of a stem bud showing leaves and basal attachment to another structure. Slide no. 22820, bar = 1 mm. **22.** Stem bud on the rhizome of an extant *Equisetum*. Actual size.



the components of an aerial axis. All growth contributed by the apical cell is completed in the autumn, and it has been reported that the apical cell is used up in some species once the stem bud has been organized, but before elongation occurs (Hauke, 1985). The following spring, the condensed buds extend by intercalary meristematic growth from the base to the tip of the bud (Hauke, 1985). Buds are rarely seen during the growing season, because most of the resources are allocated to rhizome expansion during that time (Golub and Wetmore, 1948a; Sakamaki and Ino, 2006); suggesting that the presence of numerous buds indicates a dormant period in the life cycle of *Spaciinodum*. By analogy, the discovery of numerous buds in the peat would indicate that they were preserved during a dormant period in the life cycle of *Spaciinodum*. In fact, it is now unclear whether any specimens of *Spaciinodum* heretofore identified and described are fully mature or whether all specimens represent buds that are only partially elongated.

The presence of numerous buds may be an indicator that the growth of *Spaciinodum* was partially dictated by a seasonally changing environment. The Fremouw Peat flora, despite its very high paleolatitude—70–75°S, well within the Antarctic Circle—probably represents a warm temperate environment (Kidder and Worsley, 2004). Tree-ring data from the Fremouw peat clearly indicate that seasonality was dictated by low winter light levels, which inhibited photosynthesis, rather than by temperature or water availability (Taylor and Ryberg, 2007; Ryberg and Taylor, 2007). Leaf mats preserved in contemporaneous compression floras and abscission layers documented in compression fossils and permineralized leaves of *Dicroidium* indicate that taxa assigned to the gymnosperm group *Corytospermales* were seasonally deciduous in response to low winter light levels (Meyer-Berthaud et al., 1993; Taylor, 1996; Axsmith et al., 2000; Taylor et al., 2000). Low light levels have been shown to induce a state of quiescence in extant *Equisetum* (Sakamaki and Ino, 2002), thus suggesting that the presence of aerial stem buds of *Spaciinodum* is another indicator of a seasonal climate in Antarctica. The stems of *Spaciinodum* would have died back during the dark winter and survived underground by means of subterranean rhizomes that contained fully developed dormant buds. Once light levels were adequate for growth, elongation would have commenced and buds would not have been common.

The absence of well-defined, fertile buds may suggest that *Spaciinodum* was dimorphic. In extant *Equisetum*, the first buds to elongate are those containing cones (Golub and Wetmore, 1948a). Elongation of the internodes occurring at the base of numerous buds of *Spaciinodum* suggests that they were beginning to elongate at the time of deposition, during the Antarctic spring. If the sterile shoots were beginning to elongate, then all the reproductive axes may already have completed elongation, explaining their scarcity in the matrix. Taylor et al. (1989) suggested that the peat blocks were deposited on sandbars downstream of their origin during a flooding event. The condensed buds would have been more protected than elongated stems, roots, and other organs and thus less likely to be destroyed by a flood. The slightly elongated stems in these peat blocks may indicate that a spring flood occurred, depositing the material.

**Relationship of *Equisetum* and *Spaciinodum***—The interpretation presented here, that the vallecular canals of *Spaciinodum* stems occur in internodal regions, indicates that the anatomy of *Spaciinodum* is more similar to that of *Equisetum*

than previously thought. Osborn and Taylor (1989) suggested that *Spaciinodum* may be allied with subgenus *Equisetum* based on its superficial stomata. Our data would appear to support that supposition; stem branching (Figs. 4–7) is a feature found throughout subgenus *Equisetum*, although several species of subgenus *Hippochaete* also branch (Guillon, 2004). Additionally, the presence of numerous sterile stem buds and the lack of reproductive buds may indicate that *Spaciinodum* was dimorphic and produced separate sterile and fertile aerial shoots. The subgenus *Equisetum* contains all four species that produce dimorphic stems (Hauke, 1963; Guillon, 2007); thus, dimorphism in *Spaciinodum* is another character allying it with subgenus *Equisetum*. Recent phylogenetic analyses based on molecular sequence data, however, suggest that subgenus *Equisetum* is probably paraphyletic, with a monophyletic *Hippochaete* clade nested within it (Des Marais et al., 2003; Guillon, 2004, 2007). In these analyses, *E. bogotense*, traditionally placed in subgenus *Equisetum*, either attaches to the tree below the remaining species of *Equisetum* or at the base of (or even within) the *Hippochaete* clade. This unresolved placement of *E. bogotense* suggests that some characteristics of *Equisetum* subgenus *Equisetum*—particularly relevant here, superficial stomata and branching stems—may be plesiomorphic within the genus *Equisetum* (Guillon, 2004). Furthermore, recent analyses have suggested that stem dimorphism and stem branching may be homoplastic characters within *Equisetum* (Des Marais et al., 2003; Guillon, 2007). Thus, based on this new information, characteristics of *Spaciinodum* that are congruent with those of subgenus *Equisetum* are equivocal in providing grouping information with respect to the infrageneric phylogeny of the extant genus as presently understood.

Perhaps *Spaciinodum* as a genus is distinct from *Equisetum*. An obvious difference between the two genera is the frequency and spacing of vallecular canals in the cortex. In *Equisetum*, vallecular canals are the same in number and alternate in position with the vascular bundles, whereas in *Spaciinodum*, the vallecular canals form a continuous ring around the circumference of the cortex, with only thin, uniseriate fimbriae serving as partitions between adjacent canals (Fig. 1; see also Osborn and Taylor, 1989, fig. 8 and Osborn et al., 2000, plate 1, fig. 4). Reproductive remains may help to clarify the amount of similarity or difference between the two genera and provide additional evidence bearing on whether *Spaciinodum* should be recognized as distinct at the generic level or whether it would be better treated as a species within *Equisetum*.

**Conclusions**—This study adds to our growing knowledge of the Equisetales, *Spaciinodum*, and the Triassic Fremouw peat flora of Antarctica. It is now clear that as early as the early Middle Triassic, plants with anatomy, development, and ecology similar to extant *Equisetum* existed. This study documents the first report of aerial stem buds, a dormant structure characteristic of extant *Equisetum*. New structural data provided by these buds indicates that *Spaciinodum* is anatomically distinct from *Equisetum*, although the differences are minor (in the number and arrangement of vallecular canals) and stem development is similar in both taxa. *Spaciinodum* can be placed in Equisetaceae given its herbaceous habit and fused leaf bases (Taylor and Taylor, 1993). However, classification of *Spaciinodum* to family level does little to enhance our understanding of its phylogenetic relationship to other herbaceous and arborescent equisetaleans, nor our understanding of character evolution within the order. Since the vast majority of the diversity



within Equisetales is extinct, a rigorously defined phylogenetic hypothesis including morphological data of extant and fossil taxa is clearly needed. This should help clarify relationships within Equisetales (including the position of *Spaciinodum*) and also help to better polarize characters within the extant genus *Equisetum*. If only extant taxa are considered—as is the case in recent phylogenies of the genus (Des Marais et al., 2003; Guillon, 2004, 2007)—the morphological features of *Equisetum* can be polarized only with reference to the most basally diverging extant *Equisetum* species or monilophyte outgroups from which *Equisetum* is structurally very distinct.

While aerial buds are continually produced in extant *Equisetum*, it is only during the dormant stages when telescoped buds can be found with any frequency. The presence of *Spaciinodum* buds throughout the Fremouw peat matrix suggests that the plant was most likely in a dormant stage during deposition. With the warm climate occurring in Antarctica during this time, frost and cool temperatures that induce dormancy in extant temperate *Equisetum* would not be factors in inducing dormancy in *Spaciinodum*. Light levels at these high latitudes were most likely the cause for dormancy, since low light levels have been shown to induce dormancy in extant *Equisetum* (Sakamaki and Ino, 2002). With this new information on the ecology of *Spaciinodum*, the reconstruction of the Antarctic landscape during the Triassic is becoming more complete. Particularly, the presence of elongating, vegetative buds in the peat may suggest that the deposition of the peat occurred in the spring, when buds would be expected to be numerous and beginning to break their winter dormancy.

#### LITERATURE CITED

- AXSMITH, B. J., E. L. TAYLOR, T. N. TAYLOR, AND N. R. CUNEO. 2000. New perspectives on the Mesozoic seed fern order Corystospermales based on attached organs from the Triassic of Antarctica. *American Journal of Botany* 87: 757–768.
- BROWN, J. T. 1975. *Equisetum clarnoi*, a new species based on petrifications from the Eocene of Oregon. *American Journal of Botany* 62: 410–415.
- BROWNE, I. M. P. 1939. Anatomy of the aerial axes of *Equisetum kansanum*. *Botanical Gazette (Chicago, Ill.)* 101: 35–50.
- DES MARAIS, D. L., A. R. SMITH, D. M. BRITTON, AND K. M. PRYER. 2003. Phylogenetic relationships and evolution of extant horsetails, *Equisetum*, based on chloroplast DNA sequence data (*rbcL* and *trnL-F*). *International Journal of Plant Sciences* 164: 737–751.
- DI MICHELE, W. A., R. A. GASTALDO, AND H. W. PFEFFERKORN. 2005. Plant biodiversity partitioning in the Late Carboniferous and Early Permian and its implications for ecosystem assembly. *Proceedings of the California Academy of Sciences* 56 (Supplement I): 32–49.
- DUVAL-JOUE, J. 1864. Histoire naturelle des *Equisetum* de France. J. B. Baillière et Fils, Paris, France.
- FARABEE, M. J., E. L. TAYLOR, AND T. N. TAYLOR. 1990. Correlation of Permian and Triassic palynomorph assemblages from the central Transantarctic Mountains, Antarctica. *Review of Palaeobotany and Palynology* 65: 257–265.
- FOSTER, A. S., AND E. M. GIFFORD. 1959. Comparative morphology of vascular plants, 2nd ed. W. H. Freeman, San Francisco, California, USA.
- GALTIER, J., AND T. L. PHILLIPS. 1999. The acetate peel technique. In T. P. Jones and N. P. Rowe [eds.], *Fossil plants and spores: Modern techniques*, 67–70. Geological Society, London, UK.
- GOLUB, S. J., AND R. H. WETMORE. 1948a. Studies of the development in the vegetative shoot of *Equisetum arvense* L. I. The shoot apex. *American Journal of Botany* 35: 755–767.
- GOLUB, S. J., AND R. H. WETMORE. 1948b. Studies of the development in the vegetative shoot of *Equisetum arvense* L. II. The mature shoot. *American Journal of Botany* 35: 767–781.
- GOULD, R. E. 1968. Morphology of *Equisetum laterale* Phillips, 1829, and *E. bryanii* sp. nov. from the Mesozoic of South-Eastern Queensland. *Australian Journal of Botany* 16: 153–176.
- GUILLON, J.-M. 2004. Phylogeny of horsetails (*Equisetum*) based on the chloroplast *rps4* gene and adjacent noncoding sequences. *Systematic Botany* 29: 251–259.
- GUILLON, J.-M. 2007. Molecular phylogeny of horsetails (*Equisetum*) including chloroplast *atpB* sequences. *Journal of Plant Research* 120: 569–574.
- HAMMER, W. R., J. W. COLLINSON, AND W. J. RYAN. 1990. A new Triassic vertebrate fauna from Antarctica and its depositional setting. *Antarctic Science* 2: 163–167.
- HAUKE, R. L. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*. *Nova Hedwigia* 8: 1–123.
- HAUKE, R. L. 1966. A systematic study of *Equisetum arvense*. *Nova Hedwigia* 13: 81–109.
- HAUKE, R. L. 1974. The taxonomy of *Equisetum*: An overview. *New Botanist* 1: 89–95.
- HAUKE, R. L. 1985. The transition from vegetative to reproductive growth of shoot apices of holoheterophytic species of *Equisetum*: Phenology, morphology, and anatomy. *Canadian Journal of Botany* 63: 2430–2438.
- HAUKE, R. L. 1987. The ochrole of *Equisetum*: A prophyllar sheath. *American Fern Journal* 77: 115–123.
- HERMSEN, E. J., E. L. TAYLOR, AND T. N. TAYLOR. In press. Morphology and ecology of the *Antarcticycas* plant. *Review of Palaeobotany and Palynology*.
- HOFMEISTER, W. 1862. On the germination, development, and fructification of the higher Cryptogamia. Robert Hardwicke, London, UK.
- ISBELL, J. L. 1991. Evidence for a low-gradient alluvial fan from the palaeo-Pacific margin in the Upper Permian Buckley Formation, Beardmore Glacier area, Antarctica. In M. R. A. Thomson, J. A. Crame, and J. W. Thomson [eds.], *Geological evolution of Antarctica*, 215–217. Cambridge University Press, Cambridge, UK.
- KIDDER, D. L., AND T. R. WORSLEY. 2004. Causes and consequences of extreme Permo-Triassic warming to globally equable climate and relation to the Permo-Triassic extinction and recovery. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203: 207–237.
- MARSHALL, G. 1986. Growth and development of field horsetail (*Equisetum arvense* L.). *Weed Science* 34: 271–275.
- MCIVER, E. E., AND J. F. BASINGER. 1989. The morphology and relationships of *Equisetum fluviatoides* sp. nov. from the Paleocene Ravenscrag Formation of Saskatchewan, Canada. *Canadian Journal of Botany* 67: 2937–2943.
- MCLOUGHLIN, S., K. LARSSON, AND S. LINDSTRÖM. 2005. Permian plant macrofossils from Fossilryggen, Vestfjella, Dronning Maud Land. *Antarctic Science* 17: 73–86.
- MEYER-BERTHAUD, B., T. N. TAYLOR, AND E. L. TAYLOR. 1993. Petrified stems bearing *Dicroidium* leaves from the Triassic of Antarctica. *Palaeontology* 36: 337–356.
- NORSTOG, K. J., AND T. J. NICHOLLS. 1997. The biology of the cycads. Cornell University Press, Ithaca, New York, USA.
- OSBORN, J. M., C. J. PHIPPS, T. N. TAYLOR, AND E. L. TAYLOR. 2000. Structurally preserved sphenophytes from the Triassic of Antarctica: Reproductive remains of *Spaciinodum*. *Review of Palaeobotany and Palynology* 111: 225–235.
- OSBORN, J. M., AND T. N. TAYLOR. 1989. Structurally preserved sphenophytes from the Triassic of Antarctica: vegetative remains of *Spaciinodum*, gen. nov. *American Journal of Botany* 76: 1594–1601.
- RYBERG, P. E., AND E. L. TAYLOR. 2007. Silicified wood from the Permian and Triassic of Antarctica: Tree rings from polar paleolatitudes. In *Antarctica: A keystone in a changing world; proceedings of the 10th International Symposium on Antarctic Earth Sciences*, A. K. Cooper, P. J. Barrett, H. Stagg, B. Storey, E. Stump, W. Wise, and the 10th ISAES editorial team [eds.], U.S. Geological Survey Open File Report 2007-1047, Short Research Paper 080. National Academies Press, Washington, D.C., USA. doi: 10.3133/of2007-1047.srp080.
- SAKAMAKI, Y., AND Y. INO. 2002. Influence of shade timing on an *Equisetum arvense* L. population. *Ecological Research* 17: 673–686.



- SAKAMAKI, Y., AND Y. INO. 2006. Tubers and rhizome fragments as propagules: Competence for vegetative reproduction in *Equisetum arvense*. *Journal of Plant Research* 119: 677–683.
- SHARMA, B. D. 1990. The ochreole in *Equisetum ramosissimum* Desf. *Geophytology* 20: 96–97.
- SHARMA, B. D., R. SINGH, AND M. S. VYAS. 1986. Studies on the anatomy of *Equisetum ramosissimum* Desf. *Bionature* 6: 77–82.
- SKOG, J. E., AND D. L. DILCHER. 1994. Lower vascular plants of the Dakota Formation in Kansas and Nebraska, USA. *Review of Palaeobotany and Palynology* 80: 1–18.
- TAYLOR, E. L. 1996. Enigmatic gymnosperms? Structurally preserved Permian and Triassic seed ferns from Antarctica. *Review of Palaeobotany and Palynology* 90: 303–318.
- TAYLOR, E. L., AND P. E. RYBERG. 2007. Tree growth at polar latitudes based on fossil tree ring analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255: 246–264.
- TAYLOR, E. L., T. N. TAYLOR, AND J. W. COLLINSON. 1989. Depositional setting and paleobotany of Permian and Triassic permineralized peat from the central Transantarctic Mountains. *International Journal of Coal Geology* 12: 657–679.
- TAYLOR, E. L., T. N. TAYLOR, AND N. R. CÚNEO. 2000. Permian and Triassic high latitude paleoclimates: Evidence from fossil biotas. In B. T. Huber, K. G. MacLeod, and S. L. Wing [eds.], *Warm climates in earth history*. Cambridge University Press, Cambridge, UK.
- TAYLOR, T. N., AND E. L. TAYLOR. 1993. *The biology and evolution of fossil plants*. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- WATSON, J. 1983. Two Wealden species of *Equisetum* found *in situ*. *Palaeontologica* 28: 265–269.
- WATSON, J., AND D. J. BATTEN. 1990. A revision of the English Wealden Flora, II. Equisetales. *Bulletin British Museum of Natural History (Geology)* 46: 37–60.
- ZHANG, Y. L., D. K. FERGUSON, A. G. ABLAEV, Y. F. WANG, C. S. LI, AND L. XIE. 2007. *Equisetum* CF. *pratense* (Equisetaceae) from the Miocene of Yunnan in southwestern China and its paleoecological implications. *International Journal of Plant Sciences* 168: 351–359.