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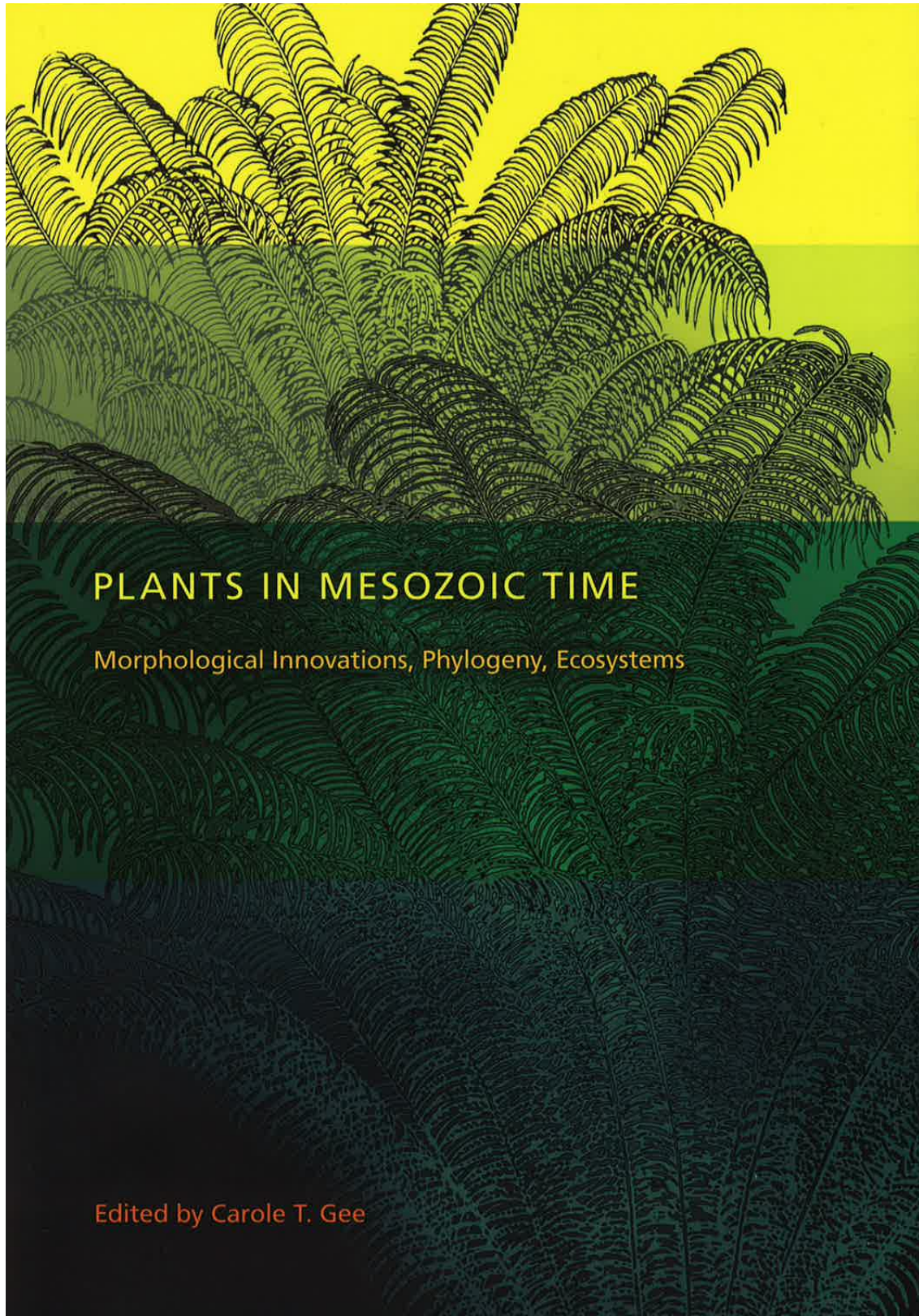
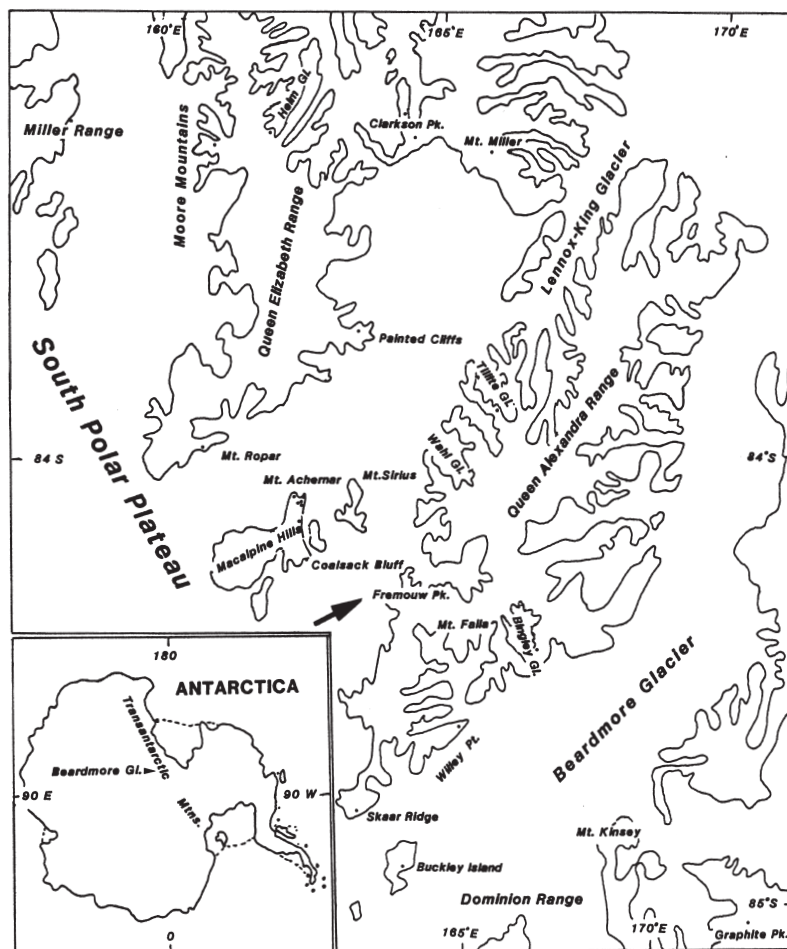


Fig. 2.1. Map showing the location of Fremouw Peak (arrow) within the Queen Alexandra Range of the Transantarctic Mountains. Inset shows the relative position of the collecting site in Antarctica.



MODERN TRAITS IN EARLY MESOZOIC SPHENOPHYTES: THE *EQUISETUM*-LIKE CONES OF *SPACIINODUM COLLINSONII* WITH IN SITU SPORES AND ELATERS FROM THE MIDDLE TRIASSIC OF ANTARCTICA

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Edith L. Taylor, Michael Krings, and Jeffrey M. Osborn

Structurally preserved cones of the early Middle Triassic sphenophyte *Spaciinodum collinsonii* have been discovered within permineralized peat from Fremouw Peak, Antarctica. Cones consist of whorls of peltate sporangiophores bearing approximately 10 sporangia each. Spores have a perispore and four elaters with spatulate ends, making *Spaciinodum* the earliest known Triassic sphenophyte with elater-bearing spores. These equisetalean cones occur alongside the vegetative stems, leaves, and dormant buds of *Spaciinodum collinsonii*. This close association and the absence of other sphenophytes at the locality indicate that the various plant organs comprise a single species. On the basis of information that has recently become available for *Spaciinodum collinsonii*, this taxon can today be regarded as one of the best-understood Mesozoic sphenophytes. The morphology and anatomy of *S. collinsonii* correspond to those of the modern *Equisetum* subgenus *Equisetum*, which suggests that the origin of the extant subgenus *Equisetum* dates as far back as 240 million years ago. Fossil remains previously described as reproductive axes of *Spaciinodum* are reinterpreted as vegetative axes with a fungal infection. The species diagnosis is therefore emended on the basis of the discovery of new reproductive axes that differ significantly from those previously defined.

The Sphenophyta are a phylum of pteridophytes with a rich fossil history dating back to the Devonian, making it one of the most ancient lineages of plants. The group reached its peak diversity during the Late Carboniferous (Pennsylvanian), a time when most sphenophytes were arborescent. Only herbaceous species, however, survived into the Mesozoic (or perhaps not, see Schweitzer et al. 1997) and persist to the present. Much of our understanding concerning the evolutionary history of this

Introduction

group is due to permineralized specimens found in Carboniferous coal balls being correlated with the compression and impression fossils. The ability to characterize the Carboniferous sphenophytes on the basis of their morphology and anatomy has led to increased understanding of their taxonomy and ecology (e.g., DiMichele and Phillips 1994; DiMichele et al. 2005). In contrast, although several Mesozoic sphenophytes have been described, relatively little is known about their phylogenetic relationships, how they evolved from Paleozoic forms, and how they gave rise to the extant representatives of the group (Taylor et al. 2009). This gap in our understanding is largely due to the lack of permineralized sphenophytes from the Mesozoic. To date, only a single anatomically preserved sphenophyte has been described from this era based exclusively on permineralized specimens, *Spaciinodum collinsonii*.

Spaciinodum collinsonii is a permineralized sphenophyte from the lower Middle Triassic of the Fremouw Formation in Antarctica (Osborn and Taylor 1989; Osborn et al. 2000). The species was originally described from aerial stems and rhizomes, and the taxon is characterized by jointed and ribbed stems with diagnostic pith canals, carinal canals, and vallecular canals that are restricted to nodes (Osborn and Taylor 1989). Osborn et al. (2000) later described reproductive remains in organic association with the vegetative stems. The reproductive axes were described by Osborn et al. (2000) as having a vascular system consisting of 31 to 33 collateral vascular bundles that are continuous through successive nodes and internodes. This vascular condition is found in extant *Equisetum* cones (Browne 1912, 1915, 1920, 1933, 1941; Barratt 1920; Page 1972), but not in the vegetative axes (Golub and Wetmore 1948a, 1948b; Bierhorst 1959; Page 1972). Sporangia of *S. collinsonii* were described as occurring in a single whorl attached to the axis in association with cortical chambers, not as occurring on peltate sporangiophores, as in extant *Equisetum* and the majority of Mesozoic sphenophytes. Cell layers of the sporangial wall were unidentifiable as a result of preservation; however, the remains of a tapetal membranelike layer were suggested. Sporangia were reported as containing abundant spores averaging 10 μm in diameter. Spores were described as spheroidal, with rugulate surface ornamentation and a sporoderm averaging 1.0 μm in thickness.

New evidence on the anatomy of dormant buds and vegetative axes of *Spaciinodum* (Ryberg et al. 2008), as well as additional recently discovered reproductive specimens have cast doubt on the interpretation of Osborn et al. (2000). The objective of our study is to describe recently discovered reproductive axes and spores from the Fremouw Peak locality that are comparable to those of extant *Equisetum* and that are associated with the vegetative axes of *Spaciinodum*. Additionally, the taxonomic status of the previously described cone of *S. collinsonii* is discussed.

Cones of *Spaciinodum* are preserved in permineralized peat collected from the Fremouw Peak locality in the Queen Alexandra Range of the Transantarctic Mountains (84°17'41"S, 164°21'48"E; Fig. 2.1; Barrett and Elliot 1973). The peat is dated as early Middle Triassic on the basis of the palynomorph assemblage and vertebrate fossils (Farabee et al. 1990; Hammer et al. 1990). Peat blocks were sectioned and the polished surface etched with 49% hydrofluoric acid (HF) for 1–5 minutes. Cellulose acetate peels (Galtier and Phillips 1999) were made from the prepared surface; some peels were subsequently mounted on slides with Eukitt mounting medium (O. Kindler GmbH, Freiburg, Germany). Slides are housed in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, under accession numbers 23015–23138, 26339, and 26343–26364. Peels and slides of the 13 cones were made from blocks 11277 A, 11277 B_{top}, 11277 B_{side top}, and 11277 B_{side bot}, 10017 C_{bot}, and 10160 D1S2.

Microscopy

For light microscopy, all specimens were photographed with a Leica DC500 digital camera attachment on a Leica DM 5000B compound microscope and a Leica MZ 16 dissecting microscope. Digital images were processed by Adobe Photoshop CS, version 8.0 (1999–2003, Adobe Systems Incorporated). High magnification (>640×) images were taken under oil immersion.

For scanning electron microscopy (SEM), two methods of spore isolation were used. In one method, spores were macerated directly from the slab with 49% HF that had been pipetted within an elevated wax well surrounding *Spaciinodum* sporangia containing spores. The fresh HF was allowed to react with the slab for 2 minutes, after which it was pipetted into a container and diluted with distilled water. The spores were allowed to settle and the supernatant was then pipetted out. After this, fresh distilled water was added to the test tube. These steps were repeated until the solution attained a neutral pH. Subsequently, the mixture was pipetted onto stubs coated with conductive putty. Once the water had evaporated, stubs were sputter-coated with gold and imaged with a Leo 1550 scanning electron microscope at 5 kV. In the second method, spores were recovered from acetate peels by excising a portion of the peel containing sporangia and dissolving the peel with several changes of acetone. Spores were pipetted onto stubs coated with conductive putty, which were then sputter-coated and imaged as described above. SEM stubs are housed in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, under accession numbers AS(1–9) 08.

Phylum Sphenophyta
Order Equisetales Dumortier
Family Equisetaceae Michaux ex DeCandolle
Genus *Spaciinodum* Osborn et T. N. Taylor

SPACIINODUM COLLINSONII OSBORN ET T. N. TAYLOR EMEND.

SCHWENDEMANN ET AL.

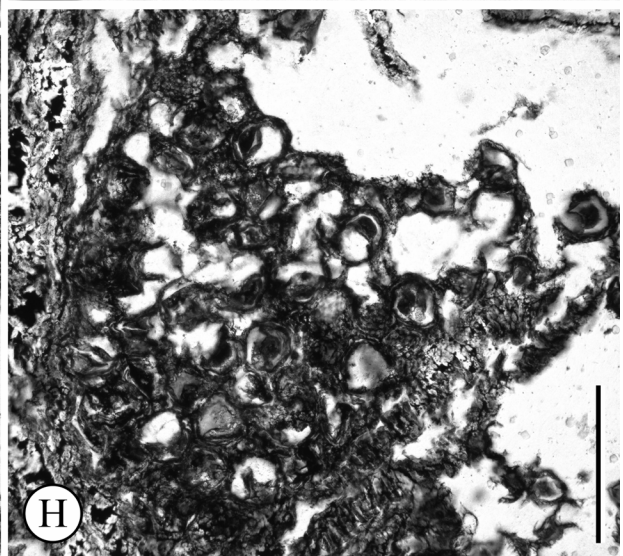
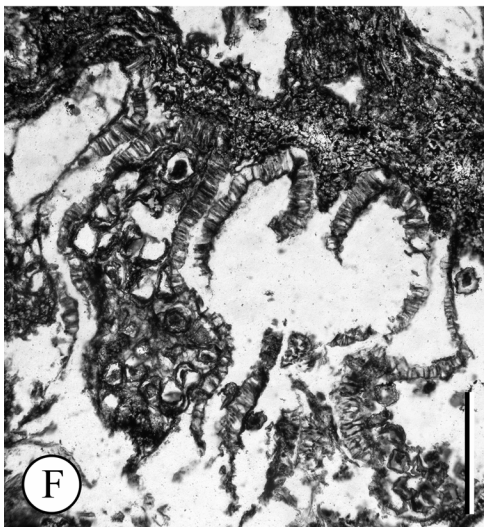
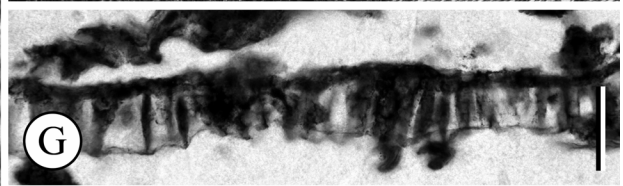
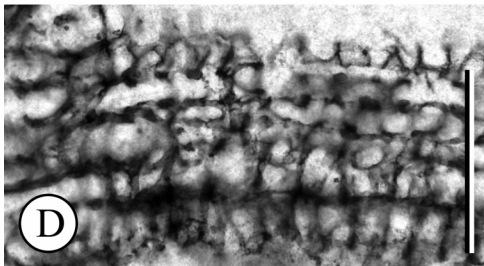
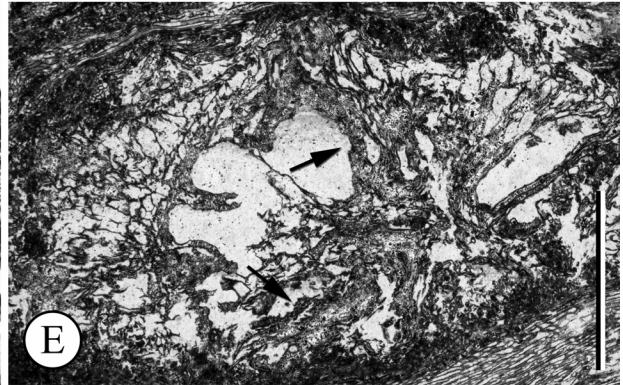
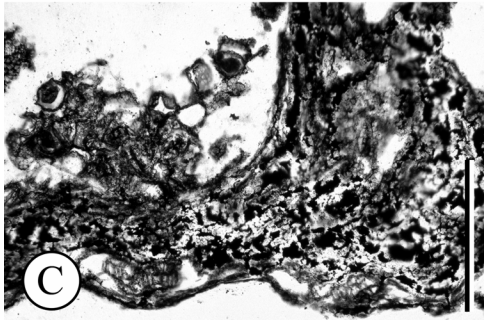
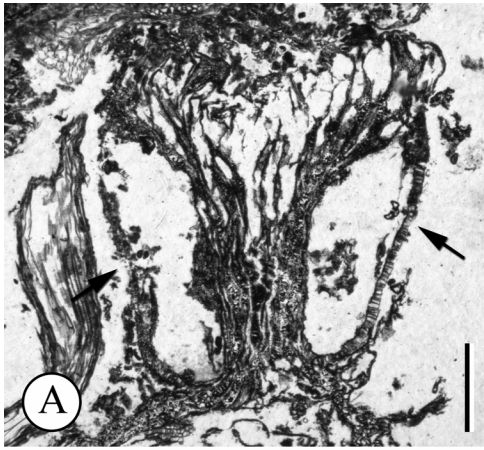
FIGS. 2.2 AND 2.3; PLATES 2 AND 3

Emended diagnosis: Stem with ribbed and furrowed surface and jointed organization representing distinct nodal and internodal regions, in longitudinal section internodal regions completely condensed to partially elongated and becoming progressively taller basally. Nodes characterized by a 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) occurring in a continuous series for 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 filled with cells (although the future 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 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 and enclosing and overarched the apex of the young stem, fused proximally and free and tapering distally, each vascularized by a single bundle with scalariform xylem thickenings, free distal portions rectangular in transverse section, mesophyll unifacial. Branches arising within the cortex of the stem, alternating with the leaves; branches organized internally 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 overarched 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. **Fertile structures** composed of whorls of sporangiophores attached to a central axis and aggregated into a cone, either terminal on the main aerial stem or a lateral branch. Vascular system of 9–12 bundles that occasionally fuse with adjacent bundles; bundles bounded by the endodermis; six sporangiophores in each whorl with approximately 10 sporangia per sporangiophore; sporangiophores alternate at each successive whorl, and sporangia prolate with a sporangial wall 1 cell layer thick and with conspicuous spiral thickenings. **Spores** spheroidal, trilete, averaging 48 µm in diameter, spore wall of a perispore layer attached to spore body at a single point with four elaters terminating in spatulate ends.

Several incomplete cones of *Spaciinodum collinsonii* have been found dispersed throughout the silicified peat in various states of decay. All of the 13 specimens identified appear to have undergone microbial degradation, and all cones are typically closely associated with a diverse assemblage of apparently saprotrophic fungi and funguslike organisms. Most abundant in the vicinity of these reproductive structures is *Combresomyces cornifer* (Peronosporomycetes), which is thought to be a saprotroph (Dotzler et al. 2008; Schwendemann et al. 2009). This high degree of fungal degradation could account for the lack of cellular preservation within most of the tissues of *Spaciinodum* cones. However, the overall morphology of the cone axis, as well as the cone axis vasculature, sporangiophores, sporangia, and spores are adequately preserved, and collectively these characters afford the opportunity to provide a detailed description of the structure.

Cone Morphology

The cones consists of whorls of peltate sporangiophores (Fig. 2.2A; Plate 2A), which each originate from the central axis at approximately 90 degrees. The central axis is approximately 1.0 mm in diameter, and the entire cone is approximately 3.0 mm in diameter. A hollow pith (medullary canal) continuing through the nodes and internodes characterizes the axis. In some sections, remains of tissue can be seen associated with the pith (Fig. 2.2B; Plate 2B). The number of sections with this tissue is small, and it is unclear whether the tissue represents the remains of a cellular pith, a nodal diaphragm, or an unrelated structure. Nine to 12 collateral vascular bundles appear throughout the nodes and internodes. More bundles are likely present because the vasculature rarely seems to be preserved for the entirety of the vascular cylinder when viewed in transverse section. Bundles are typically positioned at the base of a sporangiophore located in the same level or at the base of a sporangiophore located at the levels above and below (Fig. 2.2C; Plate 2C). Unlike the stem of *Spaciinodum*, vascular bundles in the cone do not form a complete ring at nodes, but neighboring bundles occasionally fuse, and bundles have also been observed diverging. The periphery of each bundle is tightly appressed to the cortex, with both sides of each bundle bounded by a thin layer that circumscribes the pith cavity (Fig. 2.2C; Plate 2C); this is likely the remains of the endodermis. Tracheids have annular secondary thickenings (Fig. 2.2D; Plate 2D), although a few annular–helical and helical tracheids have also been found. A lack of good preservation obscures the divergence pattern of xylem from the cone axis to the sporangiophores and the branching of xylem to the sporangia within the sporangiophores. In the cones examined, there are typically six sporangiophores per whorl. Most sections, however, show only four or fewer intact sporangiophores, with bases indicating the positions of degraded sporangiophores (Fig. 2.2B; Plate 2B). Sporangiophores alternate in position from node to node. The length of the sporangiophore from



the point where the sporangiophore stalk connects the cone axis to the outermost portion of the sporangiophore head ranges from 0.8 to 1.2 mm in a median longitudinal section. The diameter of the sporangiophore heads ranges from 1.0 to 1.3 mm. Sporangiophore heads are tightly appressed to neighboring heads, making the boundaries of the individual sporangiophores difficult to define in poorly preserved specimens. In some cases, heads from adjacent sporangiophores appear to be fused, creating a structure that encompasses most of the circumference of the cone axis (Fig. 2.2E; Plate 2E). On the basis of the alternation of sporangiophore position from node to node and the possible geometry of this arrangement, the sporangiophore heads are interpreted as hexagonal or rhomboidal in shape.

On the abaxial surface of each sporangiophore head is a single whorl of approximately 10 sporangia. Sporangia are 0.59–0.86 mm long and 0.28–0.40 mm wide. Fragments of sporangia, indicated by the remains of sporangial walls, are found more frequently than intact sporangia attached to the sporangiophore head (Fig. 2.2F; Plate 2F). Sporangia are tightly appressed to the cone axis, pressing against concave indentations on the outer surface of the cone axis. This close association often suggests that sporangial walls are attached to the cone axis. Closer inspection reveals this to not be the case (Fig. 2.2F; Plate 2F). The sporangial wall consists of a single layer of longitudinally elongated cells with spiral thickenings. The thickness of this layer ranges from 26.3 to 58.1 μm , with a mean of 38.2 μm ($n = 23$). No cell layers are found interior to the sporangial wall (Fig. 2.2G; Plate 2G).

Spore Morphology

Within each intact sporangium are numerous spherical, slightly immature spores surrounded by the remnants of the tapetal plasmodium (Fig. 2.2H, Plate 2H). The spore wall is made up of numerous layers, including the spore body proper, a perispore (Fig. 2.3A; Plate 3A) (=middle layer of Uehara and Kurita 1989), and elaters on some spores. The spore body ranges from 19.7 to 47.9 μm in diameter with a mean of 29.3 μm ($n = 38$). The perispore is attached to the spore body proper at a single point, possibly near the aperture, as in spores of extant *Equisetum*. In most peels, there appears to be a significant gap between the spore body and the perispore (Fig. 2.3A; Plate 3A). This may be the actual condition of *Spaciinodum* spores, or alternatively a result of spore body shrinkage during diagenesis associated with fossilization. When measurements of spore diameter include the perispore, the spores range from 29.3 to 64.5 μm with a mean of 48.1 μm ($n = 38$).

There are several structures observed with light microscopy and SEM that represent elaters. Figure 2.3B and Plate 3B show a coiled structure found inside a sporangium. This structure, which is not associated with any spore, consists of coiled bands that measure about 1.5 μm in

Fig. 2.2. Cone of *Spaciinodum collinsonii* from the lower Middle Triassic of Antarctica. (A) Transverse section of cone showing a single peltate sporangiophore with two empty sporangia (arrows); slide no. 23017. Scale bar = 250 μm . (B) Transverse section of cone axis with several intact sporangiophores (arrows), sporangiophore stumps (arrowheads), and tissue (T) in the pith canal; slide no. 23019. Scale bar = 1 mm. (C) Higher magnification of (B) showing vascular bundles and encompassing endodermis at the base of sporangiophores; slide no. 23019. Scale bar = 200 μm . (D) Longitudinal section of cone tracheids showing annular and annular–helical secondary thickenings; slide no. 23020. Scale bar = 50 μm . (E) Transverse section of cone axis with fused sporangiophore heads and unfused sporangiophore stalks (arrows); slide no. 23018. Scale bar = 1 mm. (F) Transverse section of cone axis showing sporangia appressed against concave indentations in the cone axis; slide no. 23068. Scale bar = 200 μm . (G) Longitudinal section through sporangial wall showing the thickening pattern of the wall buttresses; slide no. 23017. Scale bar = 30 μm . (H) Longitudinal section through sporangia displaying spores surrounded by the remains of the tapetal plasmodium; slide no. 23069. Scale bar = 150 μm .

thickness; however, at the edge of the structure (Fig. 2.3B; Plate 3B), the coil appears to flatten. This flattened area measures 4.4 μm at the widest point and may represent the spatulate end of an elater. Another coiled structure was found with bands 9.1 μm thick and associated with a spore (Fig. 2.3C; Plate 3C). In the region of the arrow in Figure 2.3C and Plate 3C, the bands appear to form a spatulate end. Information based on transmitted light microscopy can be correlated with data obtained through SEM of spores macerated directly from *Spaciinodum* sporangia. Figure 2.3D and Plate 3D show a highly fractured spore with apparent elaters surrounding the spore body. The thinner strands measure 8.3 μm thick, while the thicker portions that are more spatulate are approximately 12.5 μm thick. Figure 2.3E and Plate 3E show at least three possible elaters originating from a common point on a fractured spore body. Thinner strands are about 3.1 μm thick with the spatulate end approximately 12.5 μm thick. One additional specimen bearing elaters was observed (Fig. 2.3F; Plate 3F). In this specimen, the elaters are thinner and apparently coiled. The strands measure approximately 2.9 μm in thickness and are terminated by two larger spatulate ends measuring approximately 10.3 μm in thickness. Only a single spore with an unequivocal trilete suture was observed (Fig. 2.3G; Plate 3G); however, many spores have apparent trilete sutures that could also be interpreted as folds of the spore wall. It is highly probable that the haplotypic mark is obscured by the perispore in most specimens.

Discussion

Although no organic connection between the vegetative axes of *Spaciinodum collinsonii* and the cones described here have been observed, it appears that this cone type was borne on vegetative axes of *Spaciinodum collinsonii*. To date, only a single species of sphenophyte has been discovered in the permineralized peat at Fremouw Peak (Osborn and Taylor 1989; Ryberg et al. 2008), and numerous specimens of these vegetative shoots occur throughout all of the blocks where the cones have been found. Additionally, the diameter of the cones described here (3.0 mm) is consistent with the described diameter of vegetative *Spaciinodum* axes (1.8–3.0 mm; Osborn and Taylor 1989). This is especially significant given the unusually small size of *Spaciinodum* vegetative axes (Osborn and Taylor 1989). Moreover, the vegetative and reproductive axes share several anatomical features in common, such as a similar number of vascular bundles, vascular bundles surrounded by a double endodermis, and the presence of annular tracheids that grade into helical tracheids (Osborn and Taylor 1989; Ryberg et al. 2008).

On the basis of information available, it appears that the overall organization and structure of the cone of *Spaciinodum* is nearly indistinguishable from that of extant *Equisetum*. This is not entirely unexpected because the vegetative remains of *Spaciinodum* share many features with extant *Equisetum*, particularly species within the subgenus *Equisetum* (Osborn and Taylor 1989; Ryberg et al. 2008). The apparent alliance of

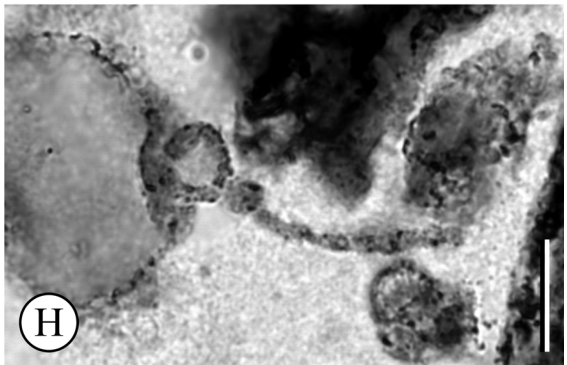
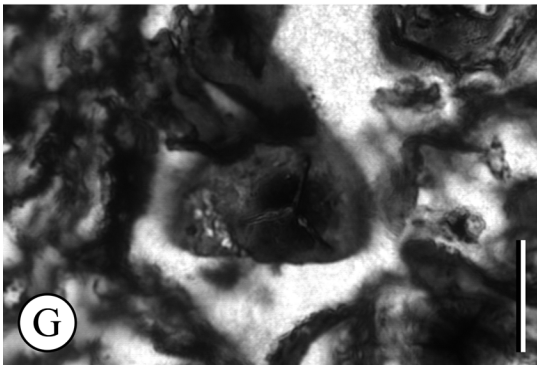
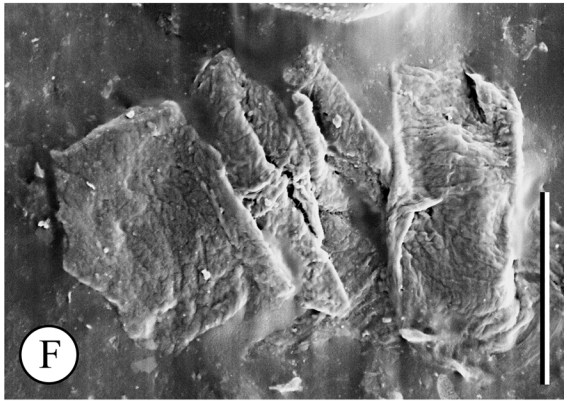
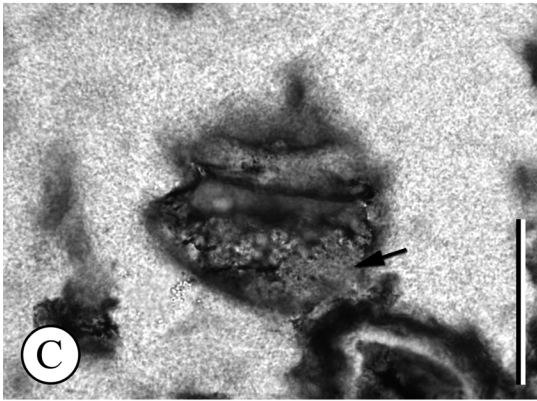
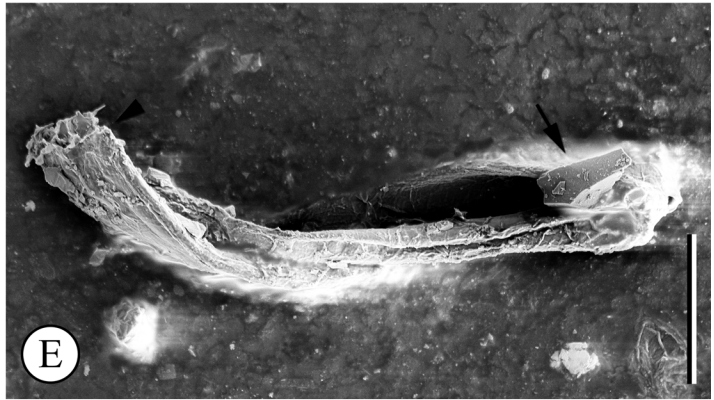
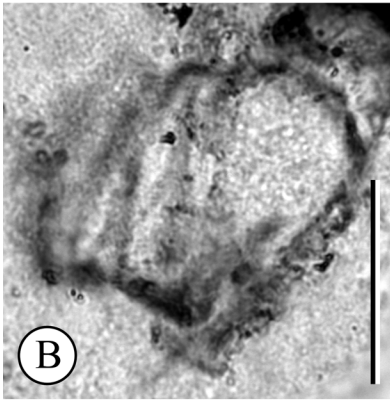
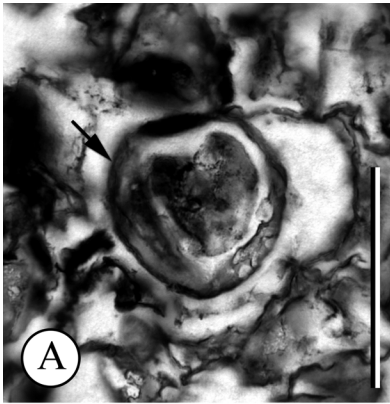
Spaciinodum with subgenus *Equisetum* is of particular interest because subgenus *Hippochaete* was originally thought to have originated in Gondwana, whereas subgenus *Equisetum* was thought to have evolved in Laurasia. These biogeographic hypotheses are based on distributions of extant taxa and the assumption that large stem size and bisexual gametophytes were ancestral in *Equisetum* (Schaffner 1930; Hauke 1963, 1978). Recent molecular phylogenies, however, are at odds with these assumptions, and the molecular studies report that these character states are derived in extant *Equisetum* (Des Marais et al. 2003; Guillon 2004, 2007). The presence of *Spaciinodum*, a relatively small sphenophyte, in Gondwana during the Triassic adds some fossil support to these recent phylogenies.

Features of the cone are relatively conserved throughout the extant species, whereas morphology and anatomy of the stem are variable and are therefore the primary characters traditionally used to differentiate extant species (Hauke 1963, 1978). Reproductive characters that may have taxonomic significance—such as position of the cone or cones on the plant, whether or not the axis of the cone is extended above the uppermost whorl of sporangiophores, and whether stems of the species are dimorphic or monomorphic—are inapplicable in this study because the *Spaciinodum* cone specimens are incomplete. The incompleteness of the specimens is not surprising because of the rapid decomposition seen in extant *Equisetum* (Marsh et al. 2000) and the abundance of decomposers in the same peat blocks in which *Spaciinodum* occurs. Marsh et al. (2000) have also demonstrated that relative to its biomass, extant *Equisetum* absorbs a disproportionate amount of phosphorus, potassium, and calcium by extending its rooting system into the C soil horizon. If these characteristics were shared by *Spaciinodum*, a significant amount of otherwise trapped nutrients could have been rapidly recycled within the plant community and would have allowed *Spaciinodum* to play a significant role in the structuring of ancient plant communities.

Cone Morphology in Comparison to Other Mesozoic Sphenophytes

To date, *Spaciinodum collinsonii* represents the only Mesozoic sphenophyte known only from permineralized remains. Comparisons with Mesozoic compression specimens are difficult because of the few characters that are comparable between the two types of preservation. However, numerous compressed sphenophyte cones have been described from the Mesozoic, and a comparison between them could help to correlate the morphological features of the compressions with the anatomy of *Spaciinodum*.

Equisetites fertilis from the Upper Triassic of Argentina (Frenguelli 1944) is not comparable; although it is considered to have reproductive structures, they are not aggregated into cones as in *Spaciinodum*. Several additional cones can also be dismissed on the basis of the size of the specimens. The *Spaciinodum* cone is fairly small, measuring approximately



3.0 mm in diameter. Cones such as *Equisetites arenaceus*, *Equisetites mougeotii*, *Equisetites quindecimdentata*, *Neocalamostachys takahashii*, *Equisetostachys suecicus*, *Equisetum muensteri*, and *Equisetum columnare* all have cones that measure at least 20 mm in diameter, and their cones bear sporangiophores of a size considerably larger than those of *Spaciinodum* (Halle 1908; Menéndez 1958; Kon'no 1962, 1972; Boureau 1964; Barnard 1967; Harris 1978; Kelber and van Konijnenburg-van Cittert 1998; Kustatscher et al. 2007). The cone axes of *Equisetites nagatensis* and *Equisetites naitoi* are less substantial, but still measure over 10 mm (Kon'no 1962).

Although some *Spaciinodum* specimens contain remains of the tapetal plasmodium (Fig. 2.2H; Plate 2H), which indicates that the cone was not fully mature, the sporangial wall in all specimens is only a single layer thick, indicating that the cone was close to maturity at the time of fossilization (Bierhorst 1971). It is possible, however, that the cone fragments described here may have comprised the uppermost or lowermost portions of the cone and therefore represent the narrowest parts of the cone. Although possible, it appears unlikely that each of the 13 cones discovered to date represents only these portions of *Spaciinodum* cones.

Several Mesozoic sphenophyte compressions bearing cones have been found with cone sizes that are more comparable to *Spaciinodum* (≤ 10 mm). Of these, *Equisetum boureaui* (Upper Triassic of Cambodia) differs from *Spaciinodum* in that it has only four sporangia per sporangiophore (Vozenin-Serra and Laroche 1976). In the Upper Triassic *Equisetostachys verticillata*, the length of the sporangia (up to 1.5 mm) and the sporangiophore stalk (up to 3 mm) extend beyond the size range of *Spaciinodum* (Grauvogel-Stamm 1978). Unlike *Spaciinodum*, *Equisetostachys nathorstii* has at least 16 sporangiophores per whorl (Halle 1908), and *Equisetites woodsii* has been described as bearing 50 to 60 sporangia per sporangiophore (Jones and de Jersey 1947). Disarticulated sporangiophores of *Equisetites lyellii* have been described by Watson (1983) and Watson and Batten (1990); these specimens differ most obviously from *Spaciinodum* in having rounded sporangia, as opposed to the elongated shape of a prolate spheroid. Additionally, *E. lyellii* has circular sporangiophore heads with 24 surface ribs radiating from its surface (Watson and Batten 1990). No surface ribs were detected in *Spaciinodum*, and the heads of the sporangiophores are thought to be hexagonal. *Spaciinodum* differs from *Equisetites pusillus* from the Aptian of Patagonia in having sporangiophores that are helically arranged on the cone axis (Villar de Seoane 2005). *Neocalamostachys pedunculatus* has fertile whorls composed of 20 sporangiophores, with sporangiophore stalks twice as long as those found in *Spaciinodum* (Kon'no 1962, 1972; Boureau 1964). Similarly, the sporangiophore stalks of *Equisetites asaensis* are nearly four times as long as those of the cone described here (Kon'no 1962). *Equisetites bracteosus* is an interesting cone from the Upper Triassic of Japan with several whorls of sporangiophores that are occasionally interrupted by a single whorl of leaves (Kon'no 1962), but no leaf whorls are

Fig. 2.3. Spores of *Spaciinodum collinsonii* from the lower Middle Triassic of Antarctica. (A) Spore with perispore (arrow) surrounding the spore body proper; slide no. 23021. Scale bar = 50 μ m. (B) Helically coiled elaters detached from spore and found within *Spaciinodum* cone; slide no. 23111. Scale bar = 20 μ m. (C) Spore showing coiled elaters tightly appressed to the spore. Arrow marks the position of spatulate end; slide no. 23070. Scale bar = 30 μ m. (D) Spore surrounded by elaters terminating in spatulate ends (arrow); SEM no. AS1 08. Scale bar = 60 μ m. (E) Elaters with spatulate ends (arrowhead) attached to a spore at a single point (arrow); SEM no. AS5 08. Scale bar = 25 μ m. (F) Coiled elaters detached from spore with spatulate ends at top and bottom of image; SEM no. AS2 08. Scale bar = 15 μ m. (G) Spore without perispore showing a prominent trilete suture; slide no. 23021. Scale bar = 20 μ m. (H) Spore with germinating hypha from "sporangia" described by Osborn et al. (2000); slide no. 15651. Scale bar = 10 μ m.

known to occur in the cone of *Spaciinodum*. *Equicalastrobus chinleana* and *Equisetites aequicaliginosus* are Triassic sphenophytes that have the general structure of an equisetalean cone, but with an additional lanceolate, leaflike structure attached to the center of the sporangiophore head that is not found in *Spaciinodum* (Grauvogel-Stamm and Ash 1999; Weber 2005). *Equisetites laterale* has a comparable cone width to that of *Spaciinodum*, but the preservation of *E. laterale* inhibits any further comparison (Gould 1968).

The inability to correlate structurally preserved remains of *Spaciinodum* with equisetalean compressions says more about the diversity of equisetalean cones during the Mesozoic than it does about the preservation quality of the specimens. Equisetaleans, although prevalent throughout most of the Paleozoic, apparently did not reach a cosmopolitan distribution until the Late Permian and the Triassic (Escapa and Cúneo 2005; Cúneo and Escapa 2006). The array of equisetalean fossils found during the Mesozoic suggests an increase in the diversity of herbaceous equisetalean plants, perhaps the largest diversity of the group since the decline of the arborescent habit within the group. Discovery of additional structurally preserved cones from the Mesozoic would facilitate a more accurate quantification of equisetalean diversity at this important geological time and help elucidate the evolutionary history of one of the most ancient plant lineages.

Spores, Elaters, and Comparisons to Other Elater-Bearing Spores

Spores of *Spaciinodum collinsonii* are comparable to those of modern *Equisetum* as well as to those of the Mesozoic sphenophytes. Spores of extant *Equisetum* generally range from 35 to 65 μm in diameter (Hauke 1963, 1978; Duckett 1970), whereas spore diameter in Mesozoic taxa ranges from 28 to 68 μm (e.g., Halle 1908; Barnard 1967; Gould 1968; Vozenin-Serra and Laroche 1976; Grauvogel-Stamm 1978; Harris 1978; Watson 1983; Watson and Batten 1990; Kelber and van Konijnenburg-van Cittert 1998; Villar de Seoane 2005); the majority of these taxa have spore diameters from 40 to 50 μm . The range of diameters and the mean diameter of *Spaciinodum* spores fits well within the ranges reported for related spores.

The seemingly large range of spore diameters in *Spaciinodum* may reflect natural variation in spore size, but it also may reflect immaturity of some spores. Although a few spores were found with attached elaters (Fig. 2.3C–E; Plate 3C–E), most have shown no evidence of elaters. There are several reasons why elaters may have not been reported in more in situ spores. One is that the spores were still immature and the elaters had not yet been deposited on most spores. Evidence for this exists in the form of a preserved structure interpreted as the remains of the tapetal plasmodium (Fig. 2.2H; Plate 2H). In extant *Equisetum*, the tapetal plasmodium is responsible for the deposition of the spore wall layers, including the elaters,

which are deposited after the perispore (Lugardon 1969; Uehara and Kurita 1989; Uehara and Murakami 1995). The continued presence of the tapetal plasmodium in the fossil after the deposition of the perispore (Fig. 2.2F, H; Plate 2F, H) indicates that the elaters were in the process of being deposited when fossilization occurred. Another scenario involves the elaters being lost during the fossilization process. Elaters are delicate structures (Halle 1908; Kedves et al. 1991) and may not have survived fossilization. Although the darkened nature of the preserved tissue indicates that the material may have been exposed to heat during fossilization, the preservation of the tapetal plasmodium implies that the first scenario is perhaps more accurate. Another possibility is that the structures that are interpreted here as elaters are not actually elaters, but some form of detritus or contamination with an elater-like appearance.

The similarity in both morphology and size of the elaters discussed in this chapter with those of extant *Equisetum* support the belief that the *Spaciinodum* structures are elaters. The width of elaters in extant *Equisetum* is approximately 2.5 μm (Uehara and Kurita 1989), and these widths can range up to 5 μm (Lugardon 1969), similar to several of the elater-like structures we describe (Fig. 2.3B–F; Plate 3B–F). The widths of elaters in Figures 2.3B, 2.3E, and 2.3F (see also Plate 3B, E, F) are comparable to those of extant *Equisetum*, whereas those in Figures 2.3C and 2.3D (Plate 3C, D) appear to be much wider. The elater-like structures in Figures 2.3C and 2.3D (Plate 3C, D) are within the natural variation of *Spaciinodum* elater width, but with such a small sample size, it is difficult to determine whether this is actually the case. It is possible that the structures in Figure 2.3C and Plate 3C are actually parts of a ripped perispore that give the impression of being elaters. In Figure 2.3D and Plate 3D, the elater-like structures are also considerably larger than those of extant *Equisetum*, but they do not appear to be the remains of a torn perispore. This structure could represent contamination or a natural variation in elater width.

Other similarities with spores of *Equisetum* are the spatulate ends of the elaters. In Figure 2.3E and Plate 3E, the elaters are attached to a common point on the spore. This position of attachment is also found in spores of *Equisetum* (Lugardon 1969; Uehara and Kurita 1989) and *Elaterrites triferens* (Wilson 1943; Kurmann and Taylor 1984). Spores of extant *Equisetum* have four narrow elaters, which are spirally coiled around the spore and terminate in spatulate ends, while each of the three broad elaters of *Elaterrites triferens* are circinately coiled against themselves, and those coils rest against the spore and terminate in a blunt tip (Wilson 1943; Kurmann and Taylor 1984). The evolution of elater number from three to four likely occurred as a result of more efficient packing. Of the few *Spaciinodum* spores found with attached elaters, the largest number of elaters found on any specimen is three. With such a small sample of elater-bearing spores, it is difficult to determine whether this is the actual number of elaters borne by spores of *Spaciinodum*. The narrow width and spatulate ends of its elaters indicate that *Spaciinodum* spores had

four elaters; a calculation of surface area by using the available images of *Spaciinodum* elaters indicates that four elaters would be required to cover the surface area of typical *Spaciinodum* spore. Additional specimens will have to be discovered to answer these questions unequivocally.

Elaters are thought to function in both mechanical ejection from the interior of the sporangia and in dispersal away from the sporangia. Intertwining elaters of neighboring spores create a spore mass, which is able to disperse farther than would be the case with individual spores. This phenomenon can be explained by the increase in surface area accompanied by a proportionally smaller increase in mass (Niklas 1992; Vogel 1994; Schwendemann et al. 2007). Spore masses also allow gametophytes to develop in close association with each other, making fertilization more likely. This functional aspect of elaters may carry extra significance for *Spaciinodum* because of its occurrence at a high paleolatitude. The Fremouw Peak flora was located at 70–75°S latitude (Kidder and Worsely 2004), greatly limiting the amount of photosynthetic active radiation (PAR) available for photosynthesis in species living underneath the canopy of larger plants. The amount of PAR available is known to affect the sex ratios in gametophyte populations of extant *Equisetum* (Guillon and Fievet 2003). Guillon and Fievet (2003) demonstrated that fewer female gametophytes develop at lower PAR than at higher PAR, and that the gametophyte fitness of both sexes is reduced at lower levels of PAR. Less fit gametophytes with fewer females to fertilize could have deleterious effects on *Spaciinodum* populations if the individual gametophytes were dispersed at significant distances from one another. These effects could also have been avoided if *Spaciinodum* grew in an unshaded habitat where the PAR was not further reduced by a canopy. The occurrence of *Spaciinodum* alongside the broad-leaved conifer *Notophytum kraeuselii* (Meyer-Berthaud and Taylor 1991; Axsmith et al. 1998) indicates that this was not the case and underscores the importance of elaters in this paleoecosystem.

The presence of a trilete mark sets the spores of *Spaciinodum* apart from those of extant *Equisetum* (Lugardon 1969; Uehara and Kurita 1989) and from several other Mesozoic spheophytes (Halle 1908; Barnard 1967; Gould 1968; Vozenin-Serra and Laroche 1976; Grauvogel-Stamm 1978; Harris 1978; Watson 1983; Watson and Batten 1990; Kelber and van Konijnenburg-van Cittert 1998; Villar de Seoane 2005). Extant *Equisetum* was long thought to be inaperturate, but subsequent studies that used electron microscopy indicated a small circular preformed aperture on the proximal surface of the spore too small to see with light microscopy (Lugardon 1969; Uehara and Kurita 1989). A few Mesozoic spheophytes have been identified as trilete (e.g., *Equisetites arenaceus*: Kelber and van Konijnenburg-van Cittert 1998; *Equisetostachys nathorstii*: Halle 1908; *Equisetostachys verticillata*: Grauvogel-Stamm 1978), but most have been described as alete. The situation with alete Mesozoic taxa is likely similar to that of extant *Equisetum*, in which their small aperture size resulted in them not being identified. Spores of *Spaciinodum* may represent a

transitional state between spores with elaters and germination through a trilete mark and spores with elaters and a specialized circular aperture. Evidence for this is confounded by the presence in younger strata of spores lacking elaters and described as alete. It is quite possible that these geologically younger spores once bore elaters that were destroyed during fossilization or preparation.

Status of Previously Described Reproductive Structures

Osborn et al. (2000) originally described reproductive remains of *Spaciinodum* mainly on the basis of two features: the anatomy of the axis and the presence of spores found in a single whorl of the axis. Recent work on *Spaciinodum collinsonii* dormant buds by Ryberg et al. (2008) has resulted in a reinterpretation of the axes described by Osborn et al. (2000). Ryberg et al. (2008) have concluded that the axis is actually a dormant bud and that the anatomy of the axis is similar to that of vegetative axes. In fact, Osborn et al. (2000: 233) did not completely rule out the possibility that the specimens were not reproductive: “Another interpretation of the new *Spaciinodum* fossils is that they are not fertile apices, but vegetative apices that are infected by fungal spores produced either by a saprophytic or a parasitic organism.” As noted by Osborn et al. (2000), the fungus *Paleofibulus* (Osborn et al. 1989) is present in the “reproductive” specimens of *Spaciinodum collinsonii*, but the spores found in the *Spaciinodum* axis are much smaller than those of *Paleofibulus* or any other Antarctic fossil fungus described up to that time. However, the spores described by Osborn et al. (2000) do fit the size range and general morphology of zoospore cysts of a peronosporomycete. Moreover, peronosporomycete oogonia have recently been discovered in silicified peat from Fremouw Peak (Schwendemann et al. 2009) and are also present in close association with the “reproductive” axes figured in Osborn et al. (2000). Reexamination of the spores and associated axes described in Osborn et al. (2000) was undertaken for this current study. A small number of “spores” in the “sporangia” of the *Spaciinodum* axis have been found with a germinating hypha (Fig. 2.3H; Plate 3H), leading to the conclusion that the previously described reproductive axis is most likely a dormant bud harboring spores of a funguslike organism.

A great diversity of equisetalean cones can be found throughout Mesozoic sediments. The new Triassic sphenophyte cone described in this chapter adds more depth to the evolutionary history of this group. *Spaciinodum collinsonii* is an equisetalean plant displaying affinities with *Equisetum* subgenus *Equisetum*, suggesting an origin of this subgenus by the Triassic. Spores of *S. collinsonii* bear elaters of the equisetalean type, marking the first appearance of these structures in the fossil record. Reexamination of material previously described as the reproductive axes of *S. collinsonii*

Conclusions

has led to the conclusion that those axes were most likely dormant buds of *S. collinsonii* harboring spores of a peronosporomycete.

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**Paleontology
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"It has been some time since there was a volume dedicated to Mesozoic plants. . . . This book will have merit as a reference for years to come."

*Kirk R. Johnson,
Denver Museum of Nature and Science*



Plants in Mesozoic Time showcases the latest research of broad botanical and paleontological interest from the world's experts on Mesozoic plant life. Each chapter covers a special aspect of a particular plant group—ranging from horsetails to ginkgophytes, from cycads to conifers—and relates it to key innovations in structure, phylogenetic relationships, Mesozoic vegetation, or to animals such as plant-eating dinosaurs. The book's geographic scope ranges from Antarctica and Argentina to the western interior of North America, with studies on the reconstruction of the Late Jurassic vegetation of the Morrison Formation and on fossil angiosperm lianas from Late Cretaceous deposits in Utah and New Mexico.

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