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## Structurally preserved sphenophytes from the Triassic of Antarctica: reproductive remains of *Spaciinodum*

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### Abstract

Permineralized cones found organically attached to *Spaciinodum collinsonii* stems are described from the early Middle Triassic silicified flora from the Fremouw Formation of Antarctica, and the species diagnosis is emended to include the reproductive specimens. The apical cones are organized into internodal and leaf-bearing nodal regions. Nodal septations span the central pith and cortex, and thin fimbrials subdivide the internodal areas into smaller chambers. The vascular system consists of 31–33 continuous bundles that do not alternate in position between successive nodes and internodes. Simple sporangia are associated with the cortical chambers and occur in one whorl on the axis. Spores are small, lack elaters, and have no discernible ultrastructure preserved, and they are interpreted to be immature. The Antarctic cones are different in structure from typical cones of modern and fossil members of Equisetales; however, they share similarities with some morphologically aberrant cones of extant *Equisetum* and several Late Paleozoic and Mesozoic compression–impression fossils. *Spaciinodum* is now the most complete anatomically described Mesozoic sphenophyte. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** anatomy; Antarctica; Equisetales; fossils; morphology; *Spaciinodum*; Sphenophyta; Triassic

### 1. Introduction

The Sphenophyta has a rich fossil history that dates to the Devonian; however, the majority of paleobotanical information about the group comes from studies of Carboniferous plants preserved as permineralizations in coal ball floras (Taylor and Taylor, 1993). By comparison, relatively little is known about younger sphenophytes, with most descriptions based on investigations of compression and impression fossils. The morphologically diagnostic ribbed and jointed stems of the group

lend themselves well to these preservational modes, and several taxa have been described.

The most commonly reported sphenophytes in Late Paleozoic (i.e. Permian) and Mesozoic floras include *Equisetites*, *Neocalamites*, *Phyllothea*, and *Schizoneura*. These taxa are known from several Laurasian sites (e.g. Berry, 1912; Daugherty, 1941; Kon'no, 1962; Tralau, 1977; Kimura et al., 1982; Ash, 1985; Kelber and Hansch, 1995; Kelber and van Konijnenburg-van Cittert, 1998); however, they are more common elements among Gondwanan localities (e.g. Jones and de Jersey, 1947; Srivastava, 1952; Archangelsky, 1964; Rigby, 1969; Douglas, 1973; Gordon-Gray et al., 1976; Lacey and Lucas, 1981; Anderson and Anderson,

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1985; Oliveira-Babinski, 1988). In addition, several Mesozoic fossils have been included within the genus *Equisetum* (e.g. Gould, 1968; Harris, 1976, 1979; Watson, 1983; Watson and Batten, 1990).

In addition to gross morphological characters, five of the aforementioned studies have reported limited anatomical information (Gordon-Gray et al., 1976; Lacey and Lucas, 1981; Watson, 1983; Watson and Batten, 1990; Kelber and Hansch, 1995). Unfortunately, however, these specimens are not particularly well-preserved at the structural level and the anatomical data available are fragmentary. In contrast, one Mesozoic sphenophyte is known entirely from permineralized specimens: *Spaciinodum collinsonii* (Osborn and Taylor, 1989). This species occurs in the silicified flora from the Triassic Fremouw Formation of Antarctica and is based on vegetative organs (aerial stems and rhizomes). It is characterized by small, ribbed, jointed stems with diagnostic pith and carinal canals, as well as vallecular canals that are restricted to nodal regions. On the basis of anatomical characters, *S. collinsonii* has been taxonomically allied with modern *Equisetum* subgenus *Equisetum* (Osborn and Taylor, 1989).

The primary objective of this paper is to describe reproductive organs found organically attached to *Spaciinodum collinsonii* stems. In addition, new anatomical data, as well as information from spore fine structure, are compared with those of other fossil sphenophytes and with extant *Equisetum*.

## 2. Material and methods

Fossils of *Spaciinodum collinsonii* were recovered within silicified peat blocks collected from the Fremouw Formation north of Fremouw Peak in the central Transantarctic Mountains (Queen Alexandra Range), Antarctica (Osborn and Taylor, 1989; Taylor et al., 1989). The peat is considered to be early Middle Triassic (Anisian) on the basis of index palynomorphs (Farabee et al., 1990) and vertebrates (Hammer, 1995). Peat blocks were sectioned using lapidary saws, and the individual slabs were serially etched (48% hydrofluoric acid) and peeled (cellulose acetate) using standard techniques. For light microscopy, glass

slides were prepared from cellulose acetate peels and examined/imaged using bright field and differential interference contrast illumination.

To study spore morphology and ultrastructure, sporangial regions of cones were excised from selected cellulose acetate peels. For scanning electron microscopy, the excised portions were dissolved in several acetone rinses in a watch glass, leaving an organic residue that included the in situ spores. The spores were then transferred to an aluminum stub onto which double-sided adhesive tape had been adhered and coated on the edges with colloidal graphite. The stubs were sputter-coated with gold-palladium and examined/imaged using a Jeol JSM-6100 scanning electron microscope at 5 kV. For transmission electron microscopy, the excised peels were transferred onto small pieces of cellulose filter paper, which were then coated on both sides with agar. The spore-containing agar blocks were dehydrated in a series of ethanol and acetone rinses; at least five acetone changes were used to ensure complete removal of the cellulose acetate. The dehydrated agar blocks were gradually infiltrated and embedded in Spurr epoxy resin and then sectioned on an ultramicrotome using a diamond knife. Ultrathin sections (90–100 nm) were collected on 1 × 2 mm slot grids and dried onto Formvar support films (Rowley and Moran, 1975). Grids were stained with 1% potassium permanganate (0–2 min), 1% uranyl acetate (6–10 min), and lead citrate (5–8 min; Venable and Coggeshall, 1965) and then examined/imaged using a Jeol JEM-100SX transmission electron microscope at 80 kV.

## 3. Systematics

Division SPHENOPHYTA  
Order EQUISETALES  
Family EQUISETACEAE

Genus *SPACIINODUM* Osborn et Taylor 1989

Species *Spaciinodum collinsonii* Osborn et Taylor 1989

*Emended diagnosis:* Mature sphenophyte stems with jointed organization, vallecular canals present

only at nodes, and ribbed and furrowed surface; fertile apices organized into distinct nodes and internodes; axis consists of a central pith, a broad cortex divided into chambers by thin, plate-like fimbrials, and 31–33 vascular bundles; vascular bundles transect nodes and internodes independently in same axial position; primary xylem endarch; leaves attached to nodes, fused in a whorl basally and free distally, vascularized by a single trace, rectangular in transverse section, mesophyll unifacial; sporangia simple and associated with cortical chambers; spores spheroidal, average 10 µm in diameter, sporoderm rugulate and 1.0 µm thick.

**Material:** Original descriptions of the vegetative structure of *Spaciinodum collinsonii* are from the following block surfaces: 557 D-top; 561 B-top, B-bot; 580 CSR; 10,019 B1-bot, C1-top; 10,023 B-top; 10,033 A-bot, C-top; 10,048 H-bot, I-bot; 10,189 G2-bot; 10,216 E-bot, F-top; 10,236 E-bot. The reproductive material described in the present paper and the emended diagnosis are based on re-examination of the material noted above and from the following newly studied block surfaces: 10,160 D1-S2, D6a-top, D6a-bot, D6b-bot, D8-top, E2-top, F3; 10,182 A2, C1-top, D1-top; 10,189 I-top; 10,216 D-top; 10,236 B7-bot; 10,771 A, A4a-side, A4b-side, B-top, B-bot. All specimens (slabs, peels, and slides) are deposited in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center of the University of Kansas.

#### 4. Description

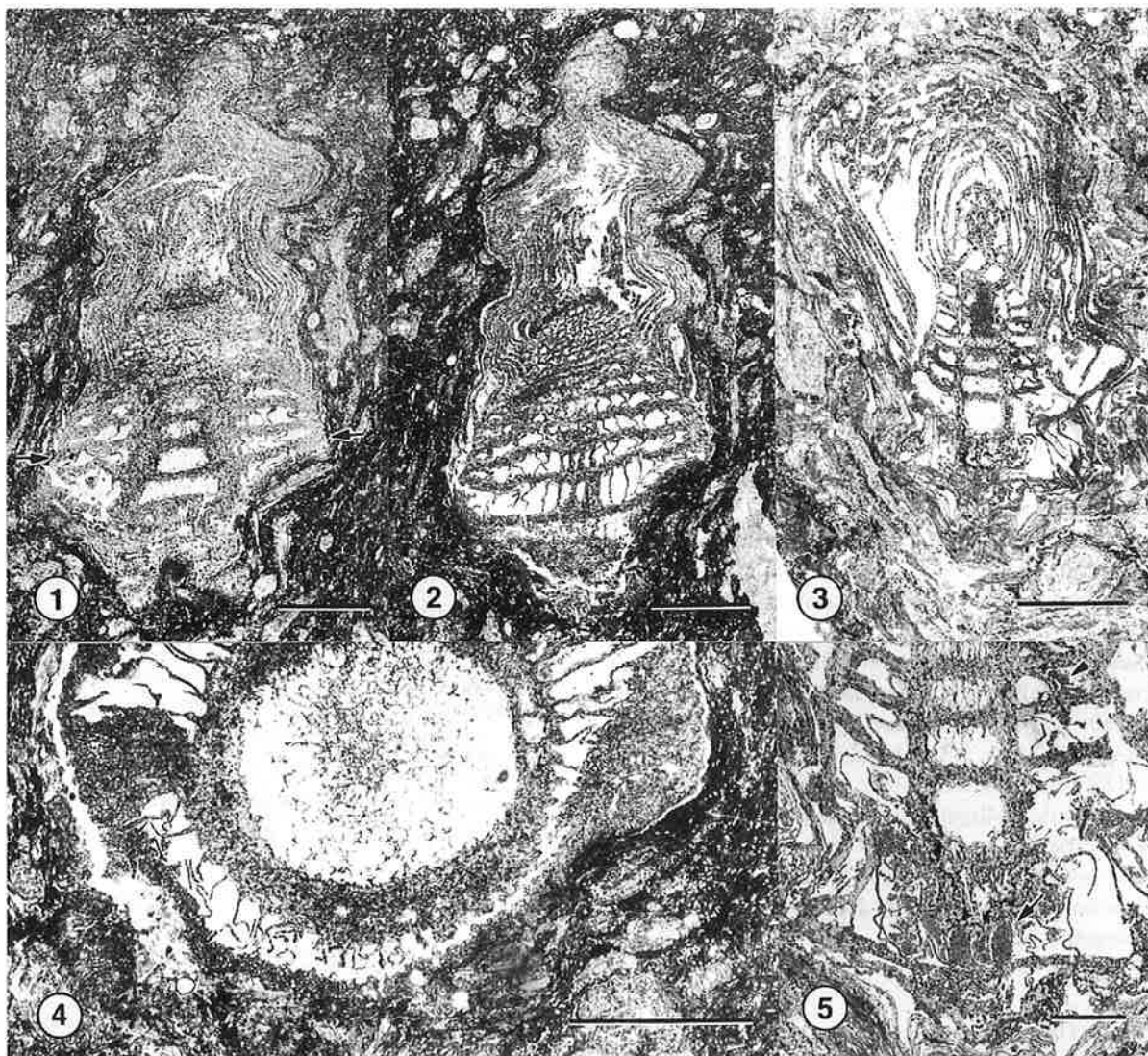
The reproductive specimens of *Spaciinodum collinsonii* consist of fertile apices organized into distinct nodes and internodes, with numerous leaves originating from the nodal regions (Plate I, 1–3). The apical axis consists of a central pith and a relatively broad cortex, with the nodal septations spanning both (Plate I, 1–3, 5). The nodal septations are generally uniform in thickness, averaging 0.25 mm (Plate I, 1–3, 5); however, septations near the apex are slightly thinner (Plate I, 2). Internode lengths vary along the length of the axis, becoming shorter near the apex where the nodal

septations are more closely spaced (Plate I, 1, 2). Thin, plate-like fimbrials also span the internodal cortex and separate the internodal regions into several chambers (Plate I, 1–5; Plate II, 2, 3).

The vascular system consists of 31 to 33 collateral vascular bundles that independently transect both the nodal and internodal regions (Plate II, 2–4). The primary xylem is endarch (Plate II, 4, 5) and composed of annular and scalariform tracheids. Distinct carinal canals are not present in the bundles near the apex; however, extraxylary cavities are located in positions where the primary phloem is not well-preserved (Plate II, 4). The central pith is hollow at the internodes (Plate II, 3) and completely filled with parenchymatous tissue at the nodes (Plate II, 2). Single leaf traces emerge from the nodal vascular bundles and horizontally cross the cortical region of the parenchymatous nodal septation to vascularize the leaves (Plate II, 5). The leaf bases are attached to the axis in a fused whorl at the nodes and then each leaf separates distally to extend above the apex (Plate I, 1–3; Plate II, 1–3). Individual leaves are rectangular in transverse section (Plate II, 1, 6) and become pointed toward the distal tips (Plate II, 1). Each leaf is vascularized by a single bundle, and although the mesophyll is not particularly well-preserved, it appears to be unifacial (Plate II, 6).

Sporangia have been identified in one obliquely sectioned specimen and occur in a whorl near the base of the axis (Plate I, 3, 5; Plate III, 1, 2). The sporangia are simple, occur singly, and appear to be associated with the cortical chambers (Plate III, 1, 2). Numerous spores fill the chambers; however, the cell layers of the sporangial walls are not identifiable because the basal regions of this axis are distorted. Several sporangia do have a thick, tapetal membrane-like layer that surrounds the spores and is located to the inside of the fimbrials (Plate III, 2). The spores are spheroidal and small, averaging 10 µm in diameter. The sporoderm has a rugulate surface ornamentation (Plate III, 3) and averages 1.0 µm in thickness (Plate III, 4). Infrastructural data are not available because of considerable diagenetic alteration. In addition to these sporangia, the internodal chambers in sev-

## PLATE I

*Spaciinodum collinsonii*

1. Longitudinal section of apex showing internodal and leaf-bearing nodal regions. Arrows indicate position where the transverse section depicted in 4 is derived. 10,771 A #15. Scale bar: 2 mm.
2. Tangential longitudinal section through the outer cortex of the same specimen shown in 1. Note the thin cortical fimbrials and shorter internodal lengths near the apex. 10,771 A #2. Scale bar: 2 mm.
3. Oblique longitudinal section of a fertile apex. Note the whorls of leaves that appear in transverse section above the apex. 10,160 D1-S2 #6. Scale bar: 3 mm.
4. Transverse section through an internodal region of the same specimen shown in 1. Note that the central pith and broad cortex (which is traversed by thin fimbrials) show some infilling of parenchymatous tissue. The tissue is present in this section because it has glanced the contiguous nodal septation. 10,771 A4a-side #5. Scale bar: 2 mm.
5. Longitudinal section through the same fertile apex shown in 3. Note the basal whorl of sporangia (arrow) and a more apical whorl of dense, organic material (arrowhead). 10,160 D1-S2 #7. Scale bar: 1 mm.

eral, more apical whorls contain dense aggregations of organic material (Plate I, 5).

## 5. Discussion

The segmented organization of *Spaciinodum collinsonii* apices, along with short internode lengths, chambered cortical regions, and whorls of fused leaf bases at the nodes render the apical anatomy fairly complex in this Triassic sphenophyte. Apices differ from previously described stem axes of *S. collinsonii* in several anatomical characters. One of the most prominent differences is the organization of the vasculature. In the apices, vascular bundles traverse both the nodal and internodal regions independently. The bundles do not alternate in position through successive internodes or fuse to form a continuous vascular ring at the nodes as the bundles do in mature regions of the stems (Osborn and Taylor, 1989). Apices further differ from older stems in having a broad cortex that is divided into internodal chambers by thin fimbrials. In contrast, in older sections of stems the cortex is narrower and the septations are only present in nodes where they contribute to the large, nodal vallecular canals that characterize the species (Osborn and Taylor, 1989).

It is clear that the structural organization of the *Spaciinodum* apices described in the present paper does not resemble that of typical equisetalean cones. Most cones of modern *Equisetum* are terminal in position and consist of a central axis that bears successive whorls of peltate sporangiophores, with the lowermost whorl subtended by a collar-like, vegetative annulus (e.g. Barratt, 1920; Hauke, 1963, 1978; Page, 1972). Furthermore, several compression–impression sphenophytes described from Mesozoic sediments have been found with reproductive organs, and most of these consist of cones that exhibit the fundamental equisetalean morphology seen in extant *Equisetum*. For example, cones and/or disarticulated sporangiophores have been described for the following taxa: *Echinostachys* (e.g. Grauvogel-Stamm, 1978), *Equicalastrobus* (Grauvogel-Stamm and Ash, 1999), *Equisetites* (e.g. Compter, 1911; Harris, 1931; Jones and de Jersey, 1947; Menendez, 1958;

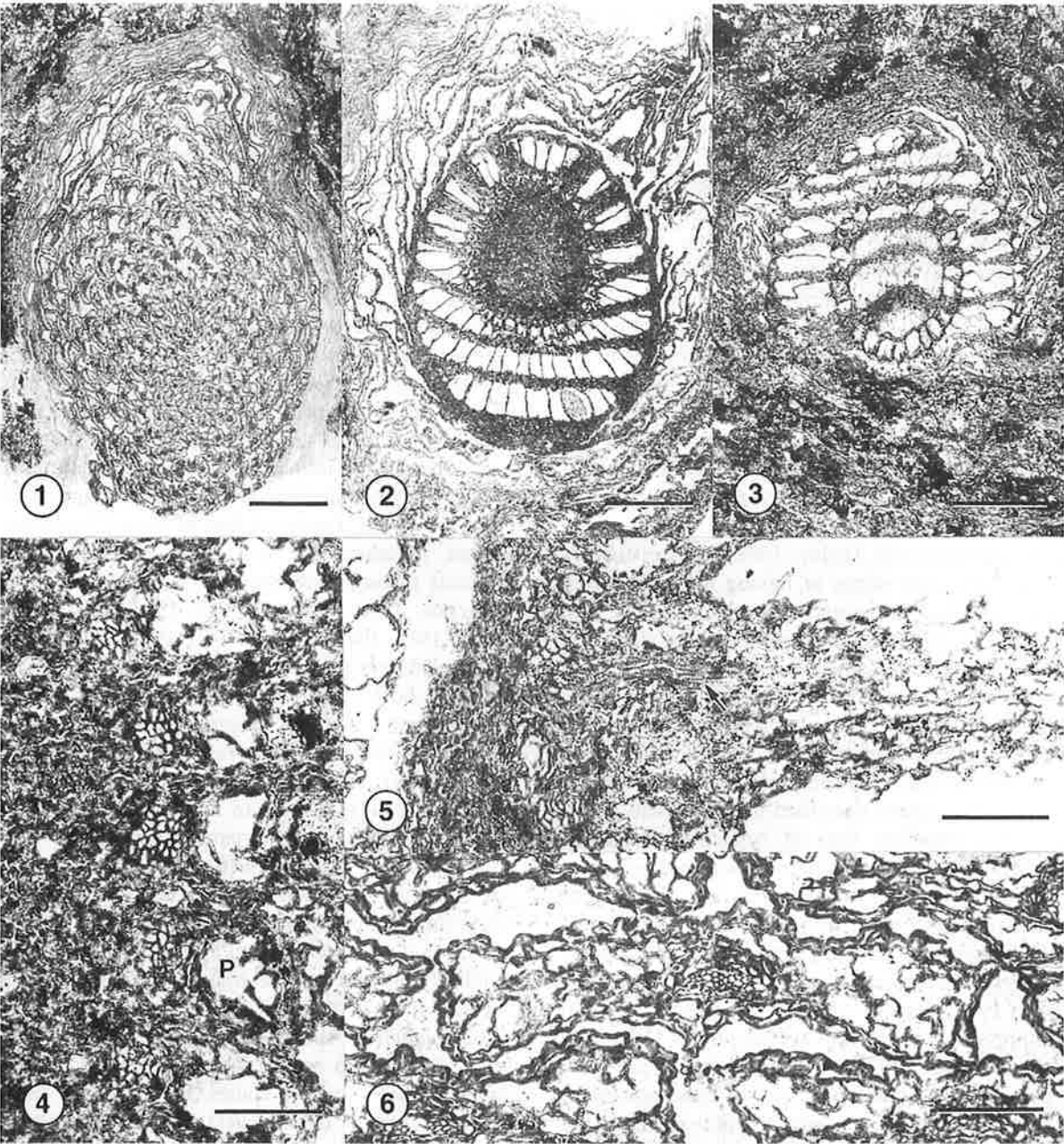
Kon'no, 1962; Watson, 1983; Watson and Batten, 1990; Kelber and Hansch, 1995; Kelber and van Konijnenburg-van Cittert, 1998), *Equisetostachys* (e.g. Halle, 1908; Grauvogel-Stamm, 1978), *Equisetum* (e.g. Gould, 1968), *Neocalamites* (e.g. Anderson and Anderson, 1985), *Phyllothea* (e.g. Mamay and Read, 1956; Anderson and Anderson, 1985), and *Schizoneura* (e.g. Anderson and Anderson, 1985; Ash, 1985). The reproductive morphology of many of these taxa has recently been reviewed by Kelber and van Konijnenburg-van Cittert (1998) in a comprehensive study of *Equisetites arenaceus* (Jaeger) Schenk from the Upper Triassic of Germany.

Although the *Spaciinodum* apices described here do not exhibit a typical equisetalean cone morphology, several lines of evidence indicate that the specimens are immature reproductive organs. First, the vasculature in the fertile apices of *Spaciinodum* is similar to that of extant *Equisetum* cones, in which the vascular bundles are continuous through successive internodes and nodes (Barratt, 1920; Browne, 1912, 1915, 1920, 1921, 1923, 1933, 1941; Hauke, 1963; Page, 1972). This pattern differs from the vasculature of vegetative axes in both *Spaciinodum* (Osborn and Taylor, 1989) and modern *Equisetum* (Golub and Wetmore, 1948a,b; Bierhorst, 1959; Hauke, 1963; Page, 1972), where the axial bundles alternate in position from internode to internode. Despite the differences in vascular organization, Page (1972) has suggested that the fertile and vegetative axes of *Equisetum* are serially homologous. The new data on vascular anatomy of *Spaciinodum* provide additional support for the Page (1972) hypothesis.

The diameter of the apices described here is broader than that of mature stem axes of *Spaciinodum* (Osborn and Taylor, 1989). This character is also concordant with a reproductive interpretation for the apices. For example, when the apex shifts from vegetative to reproductive growth in modern *Equisetum*, the apical dome increases in size due to a positional shift in mitotic activity (Hauke, 1985).

The immaturity of the fertile *Spaciinodum* apex is further supported by the size and structure of the spores. Spores are uniformly small, averaging 10 µm in diameter. Mature (and fresh) spores of

PLATE II





modern species of *Equisetum* average 35 to 65  $\mu\text{m}$  in diameter (e.g. Hauke, 1963, 1978; Duckett, 1970), as do most dispersed Mesozoic spores attributed to Equisetales (e.g. Batten, 1968; Watson and Batten, 1990; Kelber and van Konijnenburg-van Cittert, 1998). Furthermore, *Spaciinodum* spores lack discernible elaters. This is also consistent with the hypothesis that the spores are young, as elaters do not form until relatively late during sporoderm ontogeny in extant *Equisetum* (Lehmann et al., 1984; Uehara and Kurita, 1989). A haptotypic mark is also not obvious on the *Spaciinodum* spores. This may be reflective either of immaturity of the spores and/or the relative obscurity of the equisetalean germinal area. Spores of modern *Equisetum* have historically been regarded as alete or inaperturate based on morphological studies. However, a unique plug-like structure (obturator) is now known to develop below a thin area of the proximal exospore following tetrad dissociation (Uehara and Kurita, 1989; Tryon and Lugardon, 1991).

In addition to immaturity, the small spores of the *Spaciinodum* apex may also be indicative of hybridity. In modern *Equisetum*, several interspecific hybrids produce relatively small spores (Duckett, 1970) that are in the size range of the *Spaciinodum* spores.

The nature of the *Spaciinodum* sporangia is also different from that of the typical equisetalean cone. A single whorl of sporangia is present in a basal position of the axis. These sporangia contain well-defined, albeit young, spores. However, additional whorls in a more apical position contain dense,

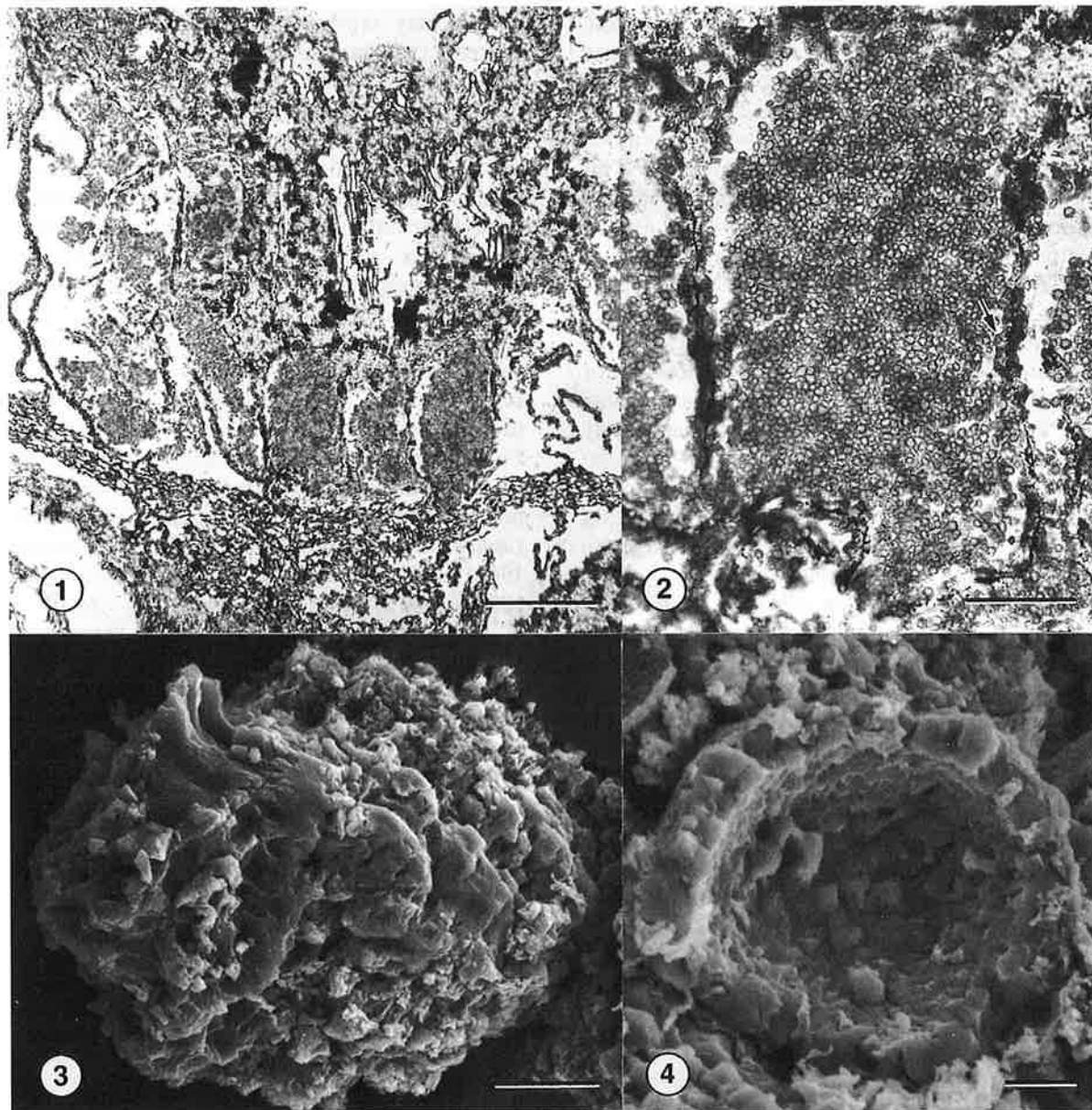
organic material. The organic material in these whorls may represent even younger sporangial contents (i.e. sporogenous tissue or spore mother cells) that are poorly preserved. If this interpretation is correct, the fertile apices of *Spaciinodum* have acropetal sporangial maturation. Although this is ontogenetically different from cones of modern *Equisetum arvense*, which are reported to have basipetal sporangial development (Uehara and Kurita, 1989), an array of aberrant cone morphologies is known in *Equisetum* (e.g. Schaffner, 1933; Tschudy, 1939; Page, 1972). Little is known about the development of such abnormal cones [see Page (1972)]; however, several of these forms could be considered morphological models for the *Spaciinodum* apices described here. Furthermore, a number of Permian and Triassic fossil sphenophytes have been described with morphologically aberrant cones (e.g. *Equisetinostachys*, *Gamophyllites*, and *Koretophyllites*; Boureau, 1964) similar to those found in modern *Equisetum* (Page, 1972). Another intriguing fossil is *Notocalamites*, described from the Permian of Brazil (Rigby, 1970; Oliveira-Babinski, 1988). *Notocalamites* is characterized by a stem tip bearing apical, vegetative leaves and basal whorls of simple sporangia that are not separated by bracts or any other vegetative appendages. Direct comparisons of *Spaciinodum* apices with *Notocalamites* and other aberrant fossil cones are not possible because of differences in preservation type. However, these compression–impression fossils do convincingly indicate that equisetalean sphenophytes displayed a range of reproductive morphol-

## PLATE II

### *Spaciinodum collinsonii*.

1. Oblique section through the apical region of an axis showing several whorls of leaves. 10,160 D6a-bot #2. Scale bar: 1.5 mm.
2. Oblique section through a more basal position of the same axis shown in 1. Note the external whorls of leaves, solid pith within the nodal region, and the radially oriented cortical fimbrials. 10,160 D6-bot #5. Scale bar: 1.5 mm.
3. Oblique section through an axis that has glanced the central pith in an internodal region. Note also the external whorls of leaves, cortical fimbrials, and continuous nature of the nodal septations. 10,216 D-top #8. Scale bar: 1.5 mm.
4. Transverse section through a central cylinder at a nodal region. Note the parenchymatous tissue at left, five independent vascular bundles with endarch primary xylem, and extraxylary cavities where the primary phloem (P) is not well-preserved. 10,160 D6a-top #7. Scale bar: 0.5 mm.
5. Oblique section through a nodal septation showing leaf trace (arrow) emerging from an axial vascular bundle. 10,160 D6b-bot #27. Scale bar: 0.5 mm.
6. Transverse section of a leaf showing single vascular bundle and unifacial mesophyll. 10,160 D6a-bot #2. Scale bar: 0.5 mm.

## PLATE III

*Spaciinodum collinsonii*.

1. Longitudinal section through the basal whorl of simple sporangia shown in Plate I, 5. Note that three sporangia are intact and the remaining portions of the whorl are preservationally distorted. 10,160 D1-S2 #7. Scale bar: 1.0 mm.
2. Detail of one sporangium shown in 1. Note the simple organization, numerous spores, and presence of a resistant layer (arrow) lining the sporangium. 10,160 D1-S2 #7. Scale bar: 0.25 mm.
3. Detail of spore surface showing rugulate ornamentation. 10,160 D1-S2. Scale bar: 3.0  $\mu$ m.
4. Fractured spore showing overall preservation and sporoderm thickness. 10,160 D1-S2. Scale bar: 1.0  $\mu$ m.



ogies during the Late Paleozoic and Mesozoic. Whether the fossils described in the present paper are indicative of the typical reproductive condition of *Spaciinodum*, or are themselves aberrant forms, will require the recovery of additional, more mature fertile specimens.

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. Although this hypothesis cannot be entirely ruled out, it is unlikely for several reasons. First, the spores are restricted in their position on the *Spaciinodum* axis, occurring in one well-defined whorl. If the spores were produced by a fungus, it would be expected that spores, along with fungal hyphae, would be found in other regions of the sphenophyte apex and in the surrounding plant material as well, which is not the case. Secondly, several fossil fungi have been described from the silicified peat in which the sphenophyte specimens occur, including *Palaeofibulus* (Osborn et al., 1989), a saprophytic basidiomycete found on *Spaciinodum* and present in several apices reported in this paper. The spores of *Palaeofibulus*, as well as those of other Antarctic fossil fungi described to date, are larger and morphologically different from the spores found in the *Spaciinodum* apices described here.

An important biological question about the evolution of the Sphenophyta through geologic time concerns the nature of the elaters. Carboniferous members of the Calamitaceae produced spores with three elaters (e.g. Good and Taylor, 1975; Kurmann and Taylor, 1984), whereas spores of modern *Equisetum* have four elaters (e.g. Uehara and Kurita, 1989; Tryon and Lugardon, 1991). In addition to number, calamitean elaters also differ in being attached to the distal pole in comparison with the proximal attachment of those of *Equisetum* (Uehara and Kurita, 1989; Uehara and Murakami, 1995). Only one Mesozoic sphenophyte has been described with attached elaters; however, these elater-bearing spores were only illustrated in a line drawing (Harris, 1976) and are therefore difficult to verify. Unfortunately, due to the immaturity of the spores, the new Antarctic *Spaciinodum* fossils do not

directly resolve the query concerning the phylogenetic shift in number and position of elaters within Sphenophyta. Moreover, it may be that the Antarctic sphenophyte is representative of an extinct, elater-less group within Equisetaceae that was prevalent in the Mesozoic (Watson and Batten, 1990). If this is the case, then additional mature specimens of *Spaciinodum* with in situ spores would not be expected to bear elaters. Nevertheless, *Spaciinodum* now represents the most complete structurally preserved sphenophyte of Mesozoic age known.

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