

STRUCTURALLY PRESERVED SPHENOPHYTES FROM THE TRIASSIC OF ANTARCTICA: VEGETATIVE REMAINS OF SPACIINODUM, GEN. NOV.¹

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ABSTRACT

Sphenophyte remains of Early-Middle Triassic age are described from silicified peat collected in the Transantarctic Mountains of Antarctica. The new sphenophyte, *Spaciinodum collinsonii* sp. nov., is represented by ribbed, jointed stems with characteristic pith and carinal canals. Stems are relatively small, ranging from 1.8–3.0 mm in diameter, lack secondary tissues, and are characterized by vallicular canals that are restricted to nodal regions. The internodal vascular system consists of 12–18 collateral bundles which alternate between successive internodes. A complete vascular ring is present in the nodal region and is surrounded by a continuous double endodermis. Xylem is endarch and composed of elements ranging from annular to reticulate. The Antarctic sphenophyte is compared with other Gondwana fossil articulates and extant *Equisetum*. Superficial stomata suggest affinities with modern *Equisetum* subgenus *Equisetum*; however, some anatomical differences preclude assignment with living species.

THE MOST SALIENT morphological character that distinguishes members of the Sphenophyta from other vascular cryptogams is the organization of ribbed stems into distinct nodes and internodes. The Sphenophyta is represented in modern floras by the single genus *Equisetum*; however, the antiquity of this group is unequivocal. Extinct sphenophytes have a fossil history which dates back to the Devonian. The division is taxonomically divided into three orders: the Pseudoborniales, the Sphenophyllales, and the Equisetales, with the former two represented only by extinct members (Taylor, 1981).

A substantial amount of information regarding sphenophytes has come from studies of Carboniferous specimens (e.g., Hoskins and Cross, 1943; Eggert, 1962; Taylor, 1967; Good, 1971, 1973; Good and Taylor, 1972; Wilson and Eggert, 1974). The wealth of data that has been accumulated about these plants is the result of their preservation as petrifications. Not until the Tertiary do well preserved petrifications again yield information regarding the anatomical structure of fossil sphenophytes. Brown (1975) described *Equisetum clarnoi* from the Eocene of Oregon and was able to demonstrate affinity with the modern subgenus *Hippochaete* as well as suggest relationship with extant *Equisetum hyemale* var. *affine*.

¹ Received for publication 20 January 1989; revision accepted 24 April 1989.

This research was supported in part by funds from the National Science Foundation (DPP-8611884) and represents Contr. No. 653 from the Byrd Polar Research Center.

Relatively little is known about sphenophytes between the Carboniferous and Tertiary. Although there are a few reports of petrified specimens within that time span (e.g., Gordan-Gray, van Dijk, and Lacey, 1976; Lacey and Lucas, 1981; Watson, 1983), the fossils consist for the most part of fragmentary specimens that reveal only a paucity of information. The majority of data which has amassed on sphenophytes of these ages has been derived from compression-impression fossils; the most common genera are *Neocalamites*, *Schizoneura*, *Phyllothea*, and *Equisetites*. A number of reports have demonstrated the occurrence of these sphenophyte genera from Northern Hemisphere floras (e.g., Halle, 1908; Harris, 1931, 1976; Daugherty and Stagner, 1941; Kon'no, 1962, 1973; Ash, 1985). However, sphenophytes are more common and diverse in the Southern Hemisphere, where they occurred in all of the major Gondwana continents/countries, including India (e.g., Srivastava, 1952; Sadovnikov, 1987), southern Africa (e.g., Gordon-Gray et al., 1976; Anderson and Anderson, 1985), South America (e.g., Frenquelli, 1943, 1944; Menendez, 1958; Jain and Delevoryas, 1967; De Cabrera, 1971; Rohn and Rösler, 1986 a,b), Australia (e.g., Walkom, 1915; Jones and De Jersey, 1947; Gould, 1968; Douglas, 1973; Drinnan and Chambers, 1986), New Zealand (e.g., Arber, 1917) and Antarctica (e.g., Rigby, 1969; Lacey and Lucas, 1981). The present paper describes the first permineralized, equisetalean sphenophyte from the Early-Middle Triassic of Antarctica.

MATERIALS AND METHODS—Sphenophyte remains were recovered within a silicified peat along with a diverse assemblage of permineralized plants and fungi (e.g., Stubblefield, Taylor, and Trappe, 1987; Perovich and Taylor, 1989; Taylor and Taylor, 1989; Osborn, Taylor, and White, 1989). The fossil containing peat was collected from the Fremouw Formation within the Central Transantarctic Mountains in Antarctica (Taylor, Taylor, and Collinson, 1989). The sediments are considered to be Early–Middle Triassic in age based on the stratigraphic positions of the vertebrates *Lystrosaurus* and *Cynognathus* (Barrett, Elliot, and Lindsey, 1986), as well as recent palynological data (Farabee, Taylor, and Taylor, in press). Light microscope slides were prepared from cellulose acetate peels of rock surfaces, which had been etched with 48% hydrofluoric acid, following the techniques of Smoot, Taylor, and Delevoryas (1985). Fossil materials (slides, peels, and slabs) are housed in The Ohio State University Paleobotanical Collection under acquisition nos. 18,623–18,801.

Genus *Spaciinodum* Osborn et Taylor gen. nov.—Diagnosis same as for type species.

Type Species *Spaciinodum collinsonii* Osborn et Taylor sp. nov.

Specific diagnosis—Stems arranged into distinct nodes and internodes, internode lengths ontogenetically variable, 0.1 mm near apices to 3.1 mm distally; stems circular in transverse section with ribs and furrows externally, ranging from 1.8–3.0 mm in diam, prominent pith canal centrally at internodes and complete parenchymatous pith at nodes, cortex parenchymatous with vallecular canals present at nodes, epidermis uniseriate and cuticularized, stomatal apparatus superficial; vascular bundles 12–18 alternating at internodes, forming a complete vascular ring at nodes, bundles collateral with protoxylem lacunae and centrifugal phloem, xylem endarch with annular, annular-helical, helical, and reticulate tracheary elements; double endodermis continuous externally and internally.

Holotype—The Ohio State University Paleobotanical Collection No. 561 B bot β (Fig. 15).

Paratypes—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.

Collection locality—Fremouw Peak, Transantarctic Mountains, Antarctica. Approximately 84°18'S, 164°20'E, Buckley Island quadrangle.

Stratigraphic position—Fremouw Formation, Beacon Supergroup.

Age—Early–Middle Triassic.

Etymology—The generic name *Spaciinodum* refers to the restriction of vallecular canals (L. *spatio*, space of limited extent) to nodal regions (L. *nodo*, node), and the specific epithet *collinsonii* honors James W. Collinson for his assistance with fieldwork in Antarctica.

DESCRIPTION—Stems of *Spaciinodum collinsonii* are organized into characteristic internodes and nodes (Fig. 1). Aerial axes are ribbed and circular in transverse section ranging from 1.8–3.0 mm in diam (Fig. 2). Internodes are characterized by a prominent pith (central) canal and ring of 12–18 vascular bundles which are radially aligned with the external stem ribs (Fig. 2). Cortical tissues are parenchymatous and delimited by a continuous, double endodermis which surrounds the vascular bundles both externally and internally (Fig. 5). Stem surfaces are covered with a uniseriate, cuticularized epidermis (Fig. 3) which also contains stomata embedded within the furrows. Stomata occupy a superficial position (e.g., nonsunken) with the guard cells flanked by two subsidiary cells (Fig. 4).

Vascular bundles are collateral and possess distinct protoxylem lacunae (carinal canals) and centrifugal phloem (Fig. 7). Xylem maturation is endarch (Fig. 6) with the majority of tracheary elements of the annular type (Fig. 14). However, annular-helical and helical tracheids may also be present. At nodes, the vascular bundles form a complete ring and the large central canal is filled with parenchymatous tissue (Fig. 8–10). Discontinuous vascular bundles characterize the vascular transition between adjacent internodes, with the bundles alternating from internode to internode (Fig. 9–12). Anatomical changes with respect to the vasculature and pith are easily detectable in these specimens; however, little of the cortex is preserved in these specimens. Within the nodal vascular ring, tracheids with reticulate secondary wall-thickenings can also be identified (Fig. 13). As bundles emerge from a node into the subsequent internode, carinal canal formation is also observable, due to protoxylem disruption (Fig. 16).

In oblique section, the nature of a node-

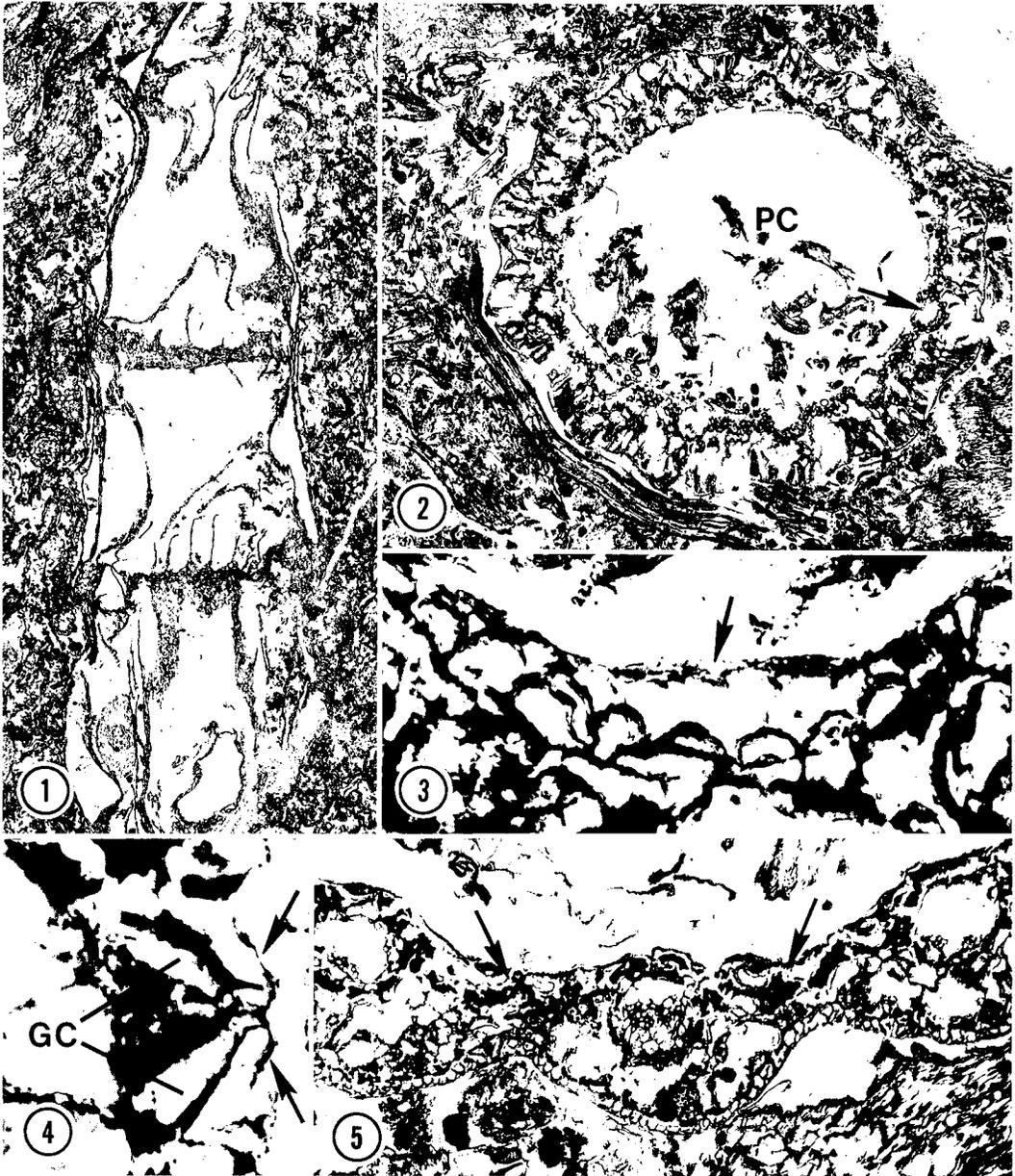
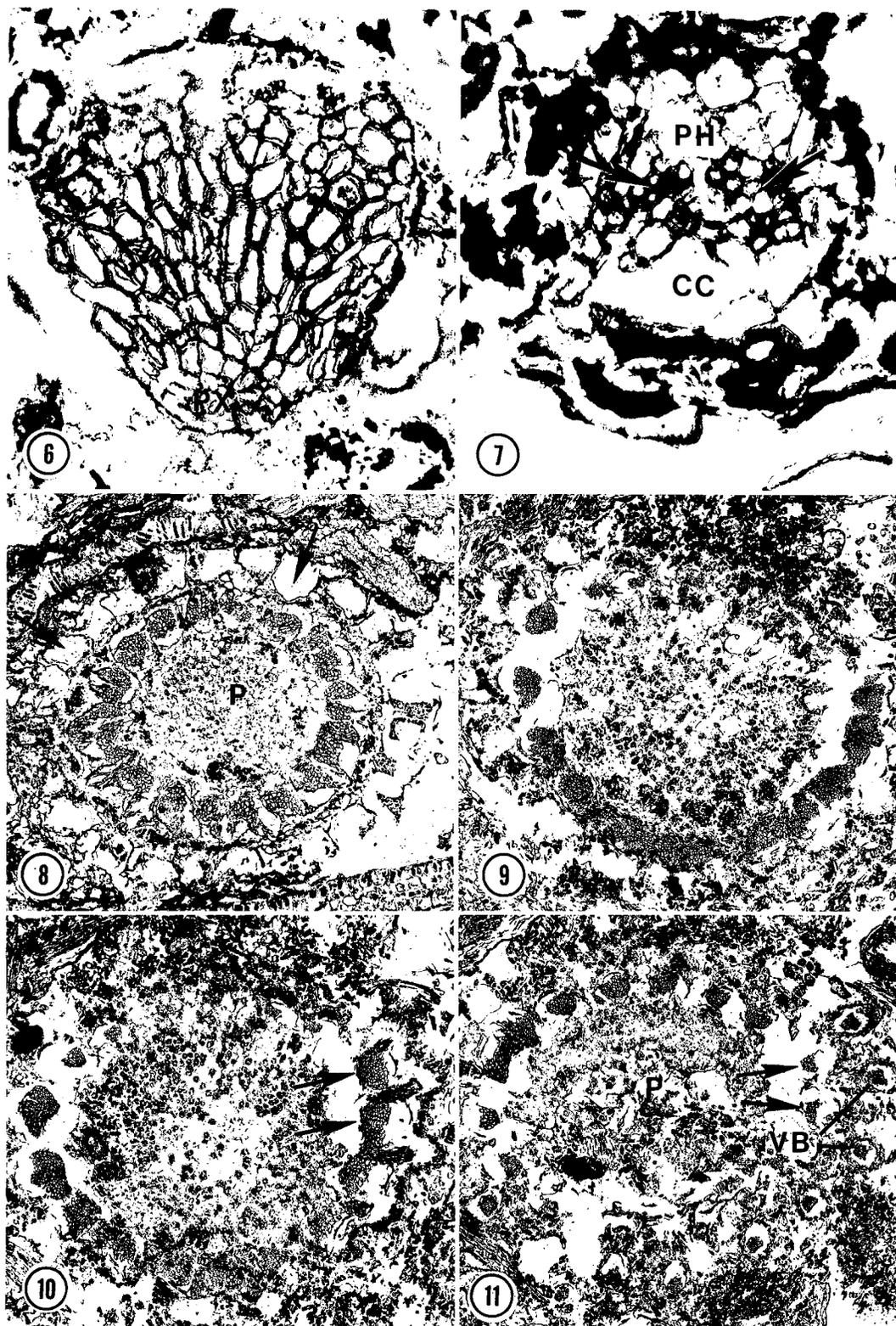
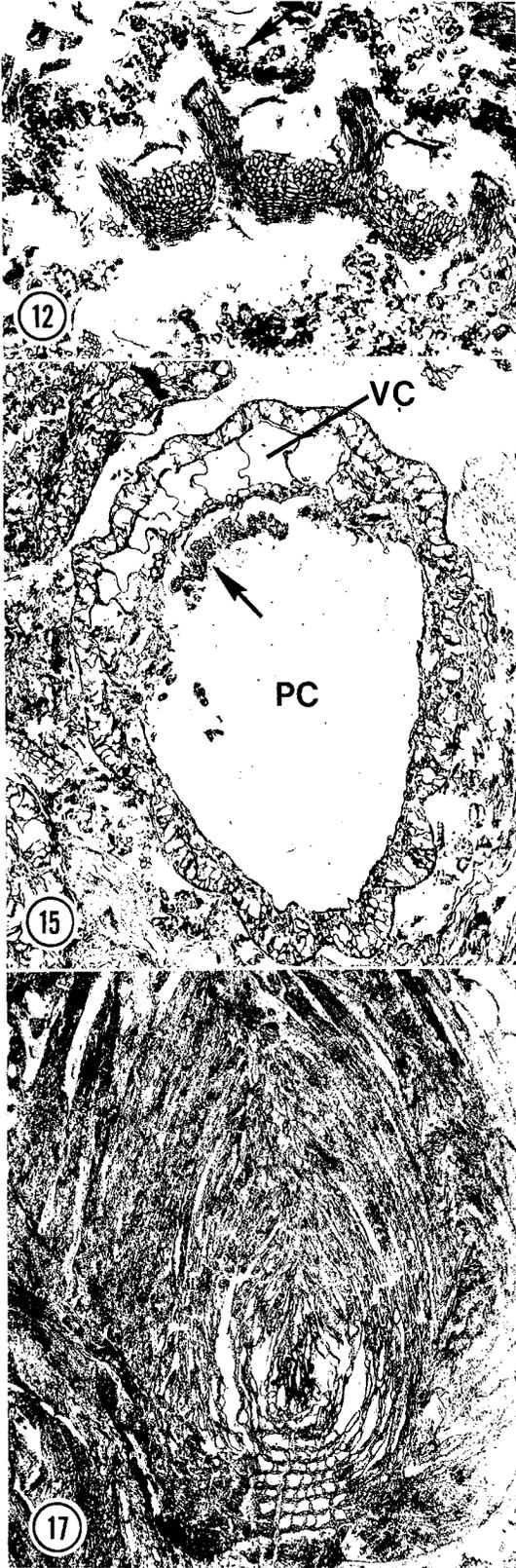


Fig. 1-5. *Spaciinodum collinsonii*. 1. Longitudinal section through two nodes and three internodes (one complete). 561 B top 5 α . $\times 12$. 2. Transverse section through internode showing pith canal (PC), individual collateral vascular bundles (arrow), and characteristic ribbed external morphology. 10,023 B top 19 δ . $\times 33$. 3. Transverse section through an internode showing portion of uniseriate epidermis and associated cuticle (arrow) which has separated from furrow. 580 CSR 12 γ . $\times 700$. 4. Transverse section through epidermis showing superficial stoma; note guard cells (GC) and subsidiary cells even with epidermis (arrows). 580 CSR 3 γ . $\times 780$. 5. Transverse section of internode showing parenchymatous cortex, collateral vascular bundles, and continuous double endodermis (arrows). 580 CSR 3 γ . $\times 110$.

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 Fig. 6-11. *Spaciinodum collinsonii*. 6. Transverse section through vascular bundle at node-internode transition region; note position of protoxylem (PX) and endarch xylem maturation. 561 B bot 8 γ . $\times 275$. 7. Transverse section through vascular bundle bounded by continuous double endodermis at an internode; note carinal canal (CC), lateral metaxylem (arrows), and phloem (PH). 580 CSR 3 γ . $\times 440$. 8. Transverse section through node showing complete parenchymatous pith (P), ring of vascular tissue, and portions of cortical vallicular canals (arrows). 557 D top 14 γ . $\times 27$. 9. Oblique transverse section through node showing portion of complete vascular ring at bottom. 561 B bot 21 γ .



×21. 10. Serial section into Fig. 9 showing alternate position of vascular bundle emergence into successive internode; note position of vascular bundles from former internode (arrows). 561 B bot 17γ. ×21. 11. Serial section into Fig. 10 showing alternate position of successive vascular bundles (VB); note position of former vascular bundles (arrows) as this section is emerging into an internode and disruption of pith (P). 561 B bot 4γ. ×21.



internode transition, with individual vascular bundles at the internode and a complete vascular ring at the node, is easily observed (Fig. 15). Furthermore, the occurrence of vallicular canals, which are restricted to nodal regions, is apparent (Fig. 15). Some portions of the vallicular canals can also be seen in transverse sections through other nodes (Fig. 8), although the preservation of these canals as well as cortical tissue is not optimal in this section.

In addition to sections through relatively mature stems of *S. collinsonii*, longitudinal sections through several apices have been discovered in the peat. The apex possesses a large number of leaves emerging from apical nodes (Fig. 17). Internode lengths in the apex as narrow as 0.1 mm, are substantially smaller than those in more mature axes (cf. Fig. 17, 1), because of the constricted nature of these nodal septa. Collateral bundles can also be detected in transverse section within apical nodes (Fig. 18), as they emerge to vascularize leaves.

DISCUSSION—*Spaciinodum collinsonii* clearly exhibits anatomically diagnostic features of Sphenophyta, the most prominent of which are ribbed, jointed stems. It is well known that the shoot system of sphenophytes consists of an aerial stem and a subterranean rhizome, which often functions as a perennial organ in extant *Equisetum*. Some of the specimens of *Spaciinodum collinsonii* definitely are the remains of aerial stems, particularly those represented by internodal transverse sections (Fig. 2–5, 15). This interpretation is based primarily upon the presence of a cuticularized epidermis and stomata in some sections, although it is possible that the basipetal portion of a rhizome (e.g., transition area between rhizome and aerial stem) could be cuticularized if it occupied a relatively soft, soil medium. On the other hand, the nodal sections of *S. collinsonii* (Fig. 8–12) cannot be unequivocally identified as either aerial or rhizomatous because these specimens lack well preserved cortical tissues. However,

in the event that these sections also represent aerial axes, one would expect the presence of peripheral rings of leaves in transverse section external to the axes, because all sphenophytes, extant and extinct, possess whorled leaves at their nodes. Taking this into account, along with the fact that the longitudinal section through three internodes and two nodes (Fig. 1) also lacks leaves at the nodes, is suggestive of a rhizomatous nature of some axes.

The presence of a fused whorl of nodal leaves has been traditionally used as a distinguishing character for the genus *Equisetites*. Moreover, this genus is primarily known from casts and compression-impression fossils, which lend themselves well to leaf preservation. Such emphasis has been placed on these leaves because of their importance in differentiating an equisetean stem from a distal portion of a calamitean branch (Taylor, 1981). Even though mature nodal leaves have not been demonstrated in *S. collinsonii*, we believe that its taxonomic affinities lie with the Equisetaceae rather than the Calamitaceae (sensu Boureau, 1964). This conclusion is predominantly based upon the small size of *Spaciinodum collinsonii* axes and the absence of any secondary tissues within the specimens. Furthermore, no secondary calamitean tissues have been noted in the Triassic peat, in which *S. collinsonii* is preserved. The equisetalean affinities of *S. collinsonii* are further strengthened by the absence of cortical vallicular canals in calamitean plants (Taylor, 1981); *S. collinsonii* has clearly been shown to possess these air chambers.

Comparison of *Spaciinodum collinsonii* to other Gondwana fossil sphenophytes is difficult because of differing modes of preservation. Some general similarities, however, can be addressed, foremost of which is resemblance in size. The relatively small diameter of *S. collinsonii* axes most closely resembles the transverse dimensions of *Equisetites minuta* (Lacey and Lucas, 1981) from the early Mesozoic of New Zealand (= *Phyllothea minuta* Arber,

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Fig. 12–18. *Spaciinodum collinsonii*. 12. Higher magnification of Fig. 10 showing alternate position of vascular traces into successive internode and new forming endodermis (arrow). 561 B bot 17γ. ×42. 13. Oblique transverse section through node showing portion of vascular ring with tracheids possessing reticulate secondary wall thickenings. 561 B bot 4γ. ×224. 14. Longitudinal section through node showing tracheids with annular secondary wall thickenings. 561 B bot 3δ. ×440. 15. Oblique transverse section through node-internode transition showing portion of nodal vascular ring at top (arrow) and individual internodal vascular bundles at bottom; note pith canal (PC) and cortical vallicular canals (VC) which are restricted to the node. 561 B bot 3β. ×27. 16. Transverse section through vascular bundle at node-internode transition showing disruption of protoxylem and carinal canal formation (arrow). Pith canal is at top of the figure. 561 B bot 20γ. ×224. 17. Oblique longitudinal section through apex showing multiple leaves emerging from constricted apical nodes. 10,189 G2 bot 16α. ×9. 18. Transverse section through apical node showing collateral vascular bundle emerging into leaf; note absence of phloem (PH) due to preservation. 10,189 G2 bot 6α. ×325.

1917) and *Equisetites* sp. collected from Triassic sediments of Livingston Island, Antarctica (Lacey and Lucas, 1981). Comparison between *S. collinsonii* and the extant species of *Equisetum* is perhaps more revealing, because the anatomical structure of stems is characteristic enough to taxonomically delineate species (Bierhorst, 1971).

Modern *Equisetum* is subdivided into two subgenera, subgenus *Equisetum* and subgenus *Hippochaete* (Hauke, 1963, 1978, 1983). A number of characters distinguish between these two subgenera, although the nature of the stomatal apparatus as revealed in structurally preserved specimens of *Spaciinodum collinsonii* suggests affinities with subgenus *Equisetum*. *Spaciinodum collinsonii* possesses superficial stomata (Fig. 4), similar to those of *Equisetum* subgenus *Equisetum*, whereas members of subgenus *Hippochaete* bear sunken stomata within an outer chamber. What is perhaps more interesting is the fact that the anatomical structure of *S. collinsonii* does not conform to the anatomy of any extant species of *Equisetum*. It differs from all living species in lacking cortical collenchyma and, most importantly, valvular canals only occur in nodal regions.

Hauke (1983) recognizes 15 extant species and several hybrids of *Equisetum* with the genus being most widespread in the Northern Hemisphere. It is notably absent from New Zealand, Australia, and Antarctica. Phylogenetic relationships between species of *Equisetum* have been suggested with respect to biogeography by Schaffner (1930), and subsequently modified by Hauke (1963, 1978). Interestingly, subgenus *Hippochaete* is more abundant in modern Southern Hemisphere floras and has been suggested to have had a Gondwanic origin (Hauke, 1963), whereas subgenus *Equisetum* occurs more frequently above the equator and was proposed to have originated in Laurasia (Hauke, 1978). If our interpretation of the relationship of *Spaciinodum collinsonii* with *Equisetum* subgenus *Equisetum* is correct, then it appears this subgenus also occurred relatively early in the Southern Hemisphere. Furthermore, the anatomical structure and morphology of *S. collinsonii* suggest it was a somewhat advanced equisetalean plant, in that it was small in size, possessed a double common endodermis, and no cortical collenchyma.

A sizeable database exists on Gondwana equisetalean compression-impression specimens. The discovery of structurally preserved specimens now affords the opportunity to evaluate the anatomical nature of some of these sphenophytic plants. Specimens of *Spaciino-*

dum collinsonii represent the most complete anatomically preserved Triassic sphenophytes known to date, which augments information regarding the distribution and possible origins of contemporary *Equisetum*.

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