A NEW PTEROPSID FRUCTIFICATION FROM THE MIDDLE PENNSYLVANIAN OF KANSAS

by GAR W. ROTHWELL

ABSTRACT. Discovery of a well-preserved, fertile frond segment in Middle Pennsylvanian petrifaction material from Kansas provides the basis for description of an annulate pteropsid fructification. Numerous sporangia are attached to the abaxial surface of laminar pinnules in either a solitary fashion or in groups of from two to six. Individual sporangia range up to 240 × 320 μm and are divided into a narrow stalk and a spheroid distal region. Sporangial walls are one cell layer thick. Cells over much of the sporangium exhibit thick walls and represent a massive annulus. Thin-walled sporangial cells occur as a narrow, vertically oriented zone. Spores are radial, 16–20 μm and exhibit a prominent trilete mark. Little or no wall ornamentation is present. Fructifications of this type suggest the presence of leptosporangiate, possibly filicalean, ferns during Pennsylvanian time.

INTERPRETATIONS of fern phylogeny rely heavily upon evidence from Palaeozoic fossil forms. This includes numerous pteropsid fructifications from the Carboniferous of Europe and equivalent strata of North America. Many of these are assignable to the Marattiales or Coenopteridales, while others are of less-certain affinities. Still others may represent progenitors of extant filicaleans. Although relationships to this latter group remain uncertain, the description of several Palaeozoic taxa with abaxially borne, annulate sporangia (e.g. *Oligocarpa*, *Senftenbergia*) increases the probability that leptosporangiate ferns were present during Palaeozoic time. The purpose of this study is to describe an additional late Palaeozoic fructification with these features.

The distinctive suite of characteristics described below demonstrates that this fructification is unlike any previously reported form. It is therefore interpreted as a new genus of Pennsylvanian pteropsid. The generic name *Norwoodia* is proposed in recognition of significant contributions to Palaeozoic palaeobotany by Professor Thomas Norwood Taylor. The specific epithet *angustum* (L. *angustus* = narrow) refers to the sporangial stalk.

The fructification occurs in carbonate petrifaction material collected at the mine dump of the Pittsburg and Midway Coal Company No. 19 Mine, which is located south-west of the town of West Mineral in south-eastern Kansas. The source of these coal balls is the commercially mined, Middle Pennsylvanian Fleming Coal. Material was prepared for microscopic examination by the cellulose acetate peel technique (Joy *et al.* 1956). Morphological features were reconstructed from closely spaced serial sections. Spores were macerated from the matrix with 5% HCl and mounted for light microscopy in Harleco Synthetic Resin. Specimens examined with the scanning electron microscope were allowed to dry from drops of distilled water on specimen stubs and coated with gold.

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SYSTEMATIC DESCRIPTION

Division PTERIDOPHYTA

Genus NORWOODIA gen. nov.

Type species. Norwoodia angustum sp. nov.

Diagnosis. Form genus of pteropsid fructifications consisting of stalked sporangia superficially borne on laminar pinnules; sporangia solitary-soral, maturation simple; sporangial walls one cell layer thick at maturity, consisting of a massive annulus and a narrow, longitudinally oriented, zone of thin-walled cells; spores radial, trilete.

Norwoodia angustum sp. nov.

Plate 45, figs. 1–6; Plate 46, figs. 1–10

Diagnosis. Features of species those of genus; pinnules alternately arranged on terete penultimate frond segment, constricted at base with lobed margins and open dichotomous veination. Sporangia 270–320 μm long, 200–240 μm in maximum diameter, with narrow stalk and spheroid distal region. Spores approximately 250 per sporangium, 16–20 μm in diameter, trilete extending to near equatorial plane with raised commissure and prominent lips; exine thin, homogeneous, psilate.

Holotype. Peels and slides of specimen in University of Alberta coal ball 318D (1) top; nos. 2281–2310 in the Paleobotanical Collection, University of Alberta, Edmonton, Alberta, Canada.

Locality. (West Mineral.) Mine dump of the Pittsburg and Midway Coal Company No. 19 Mine located W. ¼, Sec. 5, T. 33 S., R. 22 E., Columbus Quadrangle, Cherokee County, Kansas, U.S.A.

Stratigraphic position. Fleming Coal, Cabaniss Subgroup, Cherokee Group, Desmoinesian Series, Middle Pennsylvanian (Kansas).

Description. Norwoodia angustum is represented by a single well-preserved frond segment. A terete, penultimate axis bears two ranks of alternately arranged pinnules (text-fig. 1*a*; Pl. 45, fig. 4) that are bent and contorted in such a way as to resemble a loosely arranged cupule-like structure in some sections (Pl. 45, fig. 1). The axis measures 0·3 mm in diameter and contains a single rod of tracheids with scalariform wall thickenings (Pl. 45, fig. 6). A zone of axially elongate, thin-walled cortical parenchyma cells surrounds the bundle (Pl. 45, fig. 4). Cells at the outer margin of the axis are more isodiametric with irregular margins and dark internal contents (Pl. 45, fig. 4). Pinnules are narrowly attached (Pl. 45, fig. 4, arrows at left), but expand

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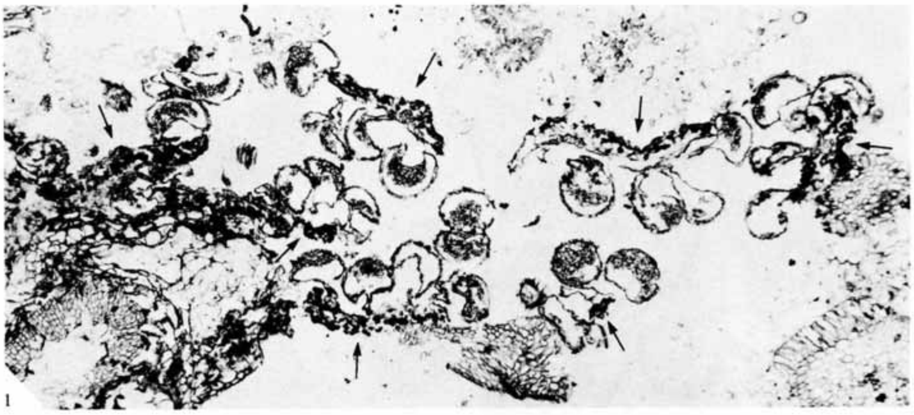
EXPLANATION OF PLATE 45

Figs. 1–6. *Norwoodia angustum* gen. et sp. nov. 1, transverse section of several fertile pinnules (at arrows) arranged such that they resemble a loosely disposed cupule. C.B. 318D top no. 13, ×26. 2, pinnule fragment with sporangia attached in a soral cluster. C.B. 318D top no. 6, ×68. 3, pinnule with sporangia attached along the entire abaxial surface. C.B. 318D top no. 7, ×68. 4, longitudinal section of penultimate pinna showing positions of pinnule attachment (at arrows). Arrows at left indicate pinnules that are sectioned at the point of attachment. C.B. 318D top no. 1, ×50. 5, transverse section near pinnule-lobe tip showing sporangial attachment and anatomical features. C.B. 318D top no. 14, ×210. 6, longitudinal section of vascular bundle showing tracheids with scalariform wall-thickening patterns. C.B. 318D top no. 4, ×340. (p = pinnule, pa = palisade, s = sporangial stalk, v = vascular bundle.)



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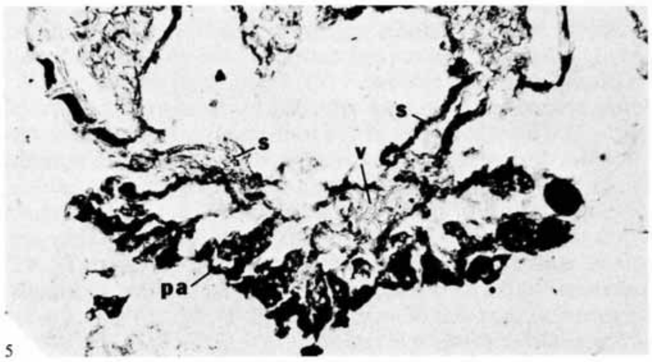

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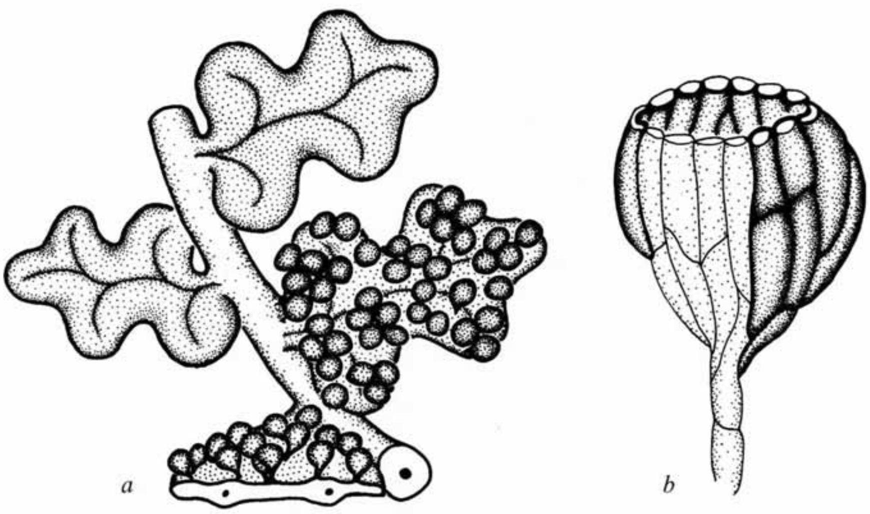
ROTHWELL, *Norwoodia angustum* gen. et sp. nov.



TEXT-FIG. 1. *Norwoodia angustum* gen. et sp. nov. 1*a*, reconstruction of small frond segment showing general features of pinnules, pinnule arrangement, and sporangial attachment from an abaxial view. Sporangia included on basal pinnules only. 1*b*, cut-away reconstruction of a single sporangium.

rapidly and are laminar in more distal regions (Pl. 45, fig. 3). Examination of serial sections indicates that the pinnules have lobed margins. A single vascular bundle enters the base of each pinnule (Pl. 45, fig. 4, at arrows) and dichotomizes to supply a strand to each lobe (Pl. 45, fig. 5). Individual strands consist of six to nine tracheids with scalariform wall thickenings (Pl. 45, fig. 6). A single layer of palisade parenchyma with internal contents like those at the outer margin of the penultimate pinna (Pl. 45, figs. 3, 5) delimits the abaxial margin of most pinnules. Cells toward the abaxial surface are thin-walled and periclinally elongated (Pl. 45, fig. 3). Toward the tips of the lobes this latter zone is reduced or absent (Pl. 45, fig. 5). Larger, more thick-walled cells occur between the vascular bundle and the palisade in some sections. A few cells are occasionally present at the adaxial margin of the palisade and may represent remnants of a poorly preserved epidermis (Pl. 46, fig. 1, at arrow).

Numerous small, closely spaced sporangia are attached to the abaxial surface of each pinnule (Pl. 45, figs. 1–3). They are not restricted to the marginal areas or to the proximity of vascular bundles, but appear to be distributed over the entire pinnule surface (text-fig. 1*a*; Pl. 45, figs. 1, 3). Some sporangia occur in a solitary fashion (Pl. 45, fig. 3), while others form sori of from two to six (Pl. 45, fig. 2). Individual sporangia are 270–320 μm long and 200–240 μm in maximum diameter. They are differentiated into a narrow stalk (Pl. 45, fig. 5) and spheroid distal region (Pl. 45, fig. 3; Pl. 46, fig. 1). Sporangial stalks are up to 100 μm long and in some sporangia appear to consist of a single cell at the point of attachment (Pl. 45, fig. 5; Pl. 46, fig. 1). There is no evidence of a specialized receptacle region.

Sporangial walls are one cell layer thick, with no evidence of what may have been a tapetum (Pl. 46, figs. 1–3). In section view most of the sporangial cells exhibit thickened walls (Pl. 46, figs. 1, 3). This is especially true of the inner and lateral cell walls (Pl. 46, fig. 1, at right). Dark internal contents are present in many of these cells (Pl. 45, fig. 5; Pl. 46, figs. 2, 3). In surface view, cells of this type are longitudinally elongated (Pl. 46, fig. 4) except at the sporangial tip where they are more isodiametric (Pl. 46, fig. 5). These cells are interpreted as representing a massive annulus. In longitudinal sections of some sporangia the annulus extends from the base of the sporangium to a point slightly beyond the apex (Pl. 46, fig. 2). In others it extends completely over the distal end of the sporangium (Pl. 46, fig. 1). In transverse sections cells of the annulus make up about three-quarters of the wall surface (Pl. 46, fig. 3). By comparison of sporangia seen in these views it is concluded that the annulus extends over the entire sporangium except in a narrow, longitudinally oriented zone on one side (text-fig. 1*b*). This latter zone is made up of poorly preserved, thin-walled cells that presumably function as a stomium. All sporangia appear to be preserved at comparable stages of development, suggesting that maturation is of the simultaneous or simple type.

None of the sporangia have dehisced, but spores occupy only about one-half of each sporangial cavity. They are usually closely packed together toward one side of the sporangium (Pl. 45, fig. 1; Pl. 46, fig. 1) and appear to have been subjected to a hypertonic salt concentration prior to fossilization. Thirty to fifty spores can be seen in a single sporangial section (Pl. 46, figs. 1, 3) suggesting a spore production of about 250 per sporangium. Individual spores are radial and trilete, and are highly folded and collapsed (Pl. 46, figs. 6–8). Consequently, accurate observations of spore size and shape could not be made. Measurements of macerated spores range from 16 to 20 μm. Many spores are folded along the trilete, suggesting that their original shape was triangular (Pl. 46, figs. 6–8); possibly with concave interradial sides. Rays of the trilete are prominent and extend nearly to the equatorial plane. The commissure is conspicuously raised and typically closed (Pl. 46, fig. 8). The lips are also raised, and up to 2 μm wide on each side of the commissure (Pl. 46, figs. 7–8). Spore walls are thin (0·3–0·5 μm) and psilate (Pl. 46, fig. 9). Examination of broken walls in section view indicate that they are solid and homogeneous (Pl. 46, fig. 10). Spores of this type are possibly referable to dispersed spore genus *Granulatisporites* (Ibrahim) Schopf, *et al.* (1944), which is of frequent occurrence throughout Middle Pennsylvanian sediments of North America (Peppers 1970; Schopf *et al.* 1944). Spores of the *Granulatisporites* type are known from previously described Carboniferous fern fructifications (i.e. *Boweria*, *Renaultia*, Knox 1938) and possibly represent a natural group of pteropsid origin (Schopf *et al.* 1944). Other *sporae-dispersae* genera to which *Norwoodia* spores may possibly be assigned are *Leotriletes* (Naumova) Potonié and Kremp (1954), *Punctatisporites* (Ibrahim) Potonié and Kremp (1954), or *Triquitrites* (Wilson and Coe) Schopf *et al.* (1944). Species of these genera typically range from slightly larger to much larger than the spores of *Norwoodia*, and usually also have more ornamented exines (e.g. Peppers 1964, 1970). At the present time it is not known whether this is entirely due to taxonomic dissimilarity or whether ontogenetic variation may also be a factor. Specimens assignable to *Calamospora* Schopf *et al.* (1944) are also somewhat similar to *Norwoodia* spores. They are sometimes as small and typically have smooth, folded exines, but are characterized by a much less extensive trilete and are typically associated with sphenopsid fructifications.

DISCUSSION

In many respects *Norwoodia* resembles several previously described Palaeozoic pteropsids. Among these *Oligocarpa* Goeppert (1841), *Senftenbergia* Corda (1845), *Renaultia* Stur (1883), *Boweria* Kidston (1911), *Tedelia* Eggert and Taylor (1966), and *Sermaya* Eggert and Delevoryas (1967) also have independent annulate sporangia that are borne on the abaxial surface of lobed, possibly sphenopterid, pinnules. However, none of these exhibit an annulus similar to that of *Norwoodia*. In *Senftenbergia* and *Tedelia* the annulus is terminal, while that of *Oligocarpa* is horizontal-oblique. In *Boweria* and *Sermaya* cells of the annulus are described as extending over the apex of the sporangium and down each side for a short distance. That of *Renaultia* is apparently rudimentary. Thick-walled cells extend over almost the entire *Norwoodia* sporangium and comprise the most massive annulus thus far discovered in either fossil or extant material. If the phylogenetic reduction in annulus size proposed among representatives of the Schizeaceae (Radforth 1938, 1939) can be considered as characteristic of fern evolution in other families, then the extensive annulus of *Norwoodia* must be considered extremely primitive.

The sporangial stalk of *Norwoodia* is also of interest. In Palaeozoic taxa superficially borne sporangia are typically sessile or have only poorly differentiated stalks. The sporangia of *Norwoodia* are distinctly stalked and possibly attached by a single cell; features associated with relatively advanced filicalean families. *Oligocarpa* is an additional Palaeozoic genus with stalked sporangia (Abbott 1954). Unfortunately specimens of this genus are typically preserved as compressions so that a more precise comparison to the sporangial stalks of *Norwoodia* cannot be made.

The small, undehisced sporangia and folded pinnules of *Norwoodia* are reminiscent of quite immature pteropsid fructifications. Thin-walled, unornamented spores are also suggestive of an early maturation stage. One must therefore question whether a more mature specimen would exhibit similar features, or perhaps be recognized as an additional specimen of a previously described taxon. As indicated above, the

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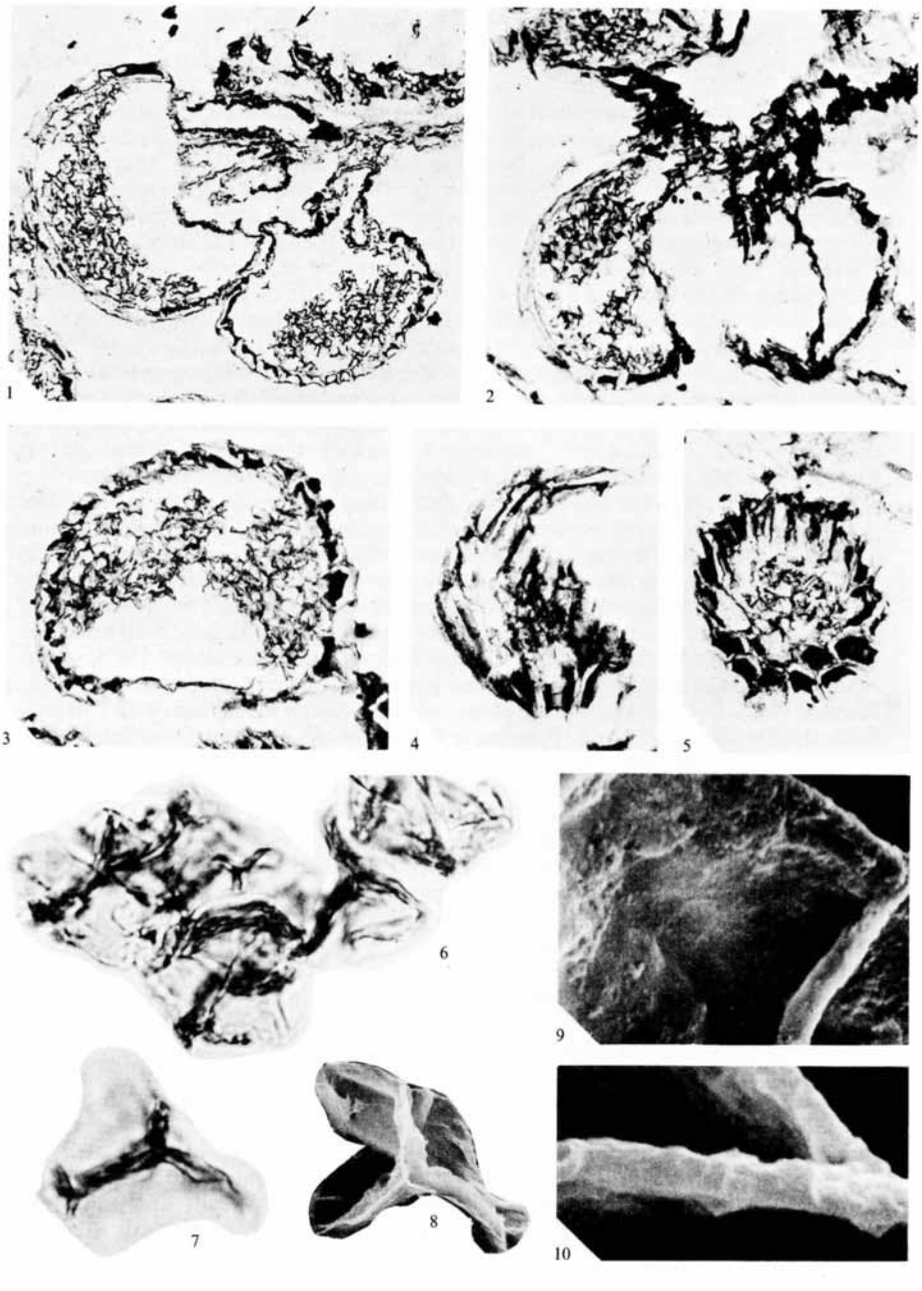
EXPLANATION OF PLATE 46

Figs. 1–10. *Norwoodia angustum* gen. et sp. nov. 1, longitudinal section of two attached sporangia. Note the disposition of the thick-walled annulus cells and possible pinnule epidermis (at arrow). C.B. 318D top no. 8, ×165. 2, longitudinal section of sporangia showing disposition of annulus, from sporangial base to slightly beyond the apex. C.B. 318D top no. 3, ×165. 3, transverse section of sporangium showing disposition of the annulus. 4, surface view of sporangium showing longitudinal orientation of annulus cells. C.B. 318D top no. 10, ×210. 5, transverse section near sporangial tip showing isodiametric annulus cells in surface view. C.B. 318D top no. 11, ×210. 6, aggregation of spores from maceration preparation. C.B. 318D top no. A, ×1500. 7, isolated spore from maceration preparation showing folded, psilate exine and prominent trilete. C.B. 318D top no. C, ×1880. 8, scanning electron microscope (S.E.M.) photograph of spore similar to that in 7. Note the distinctly raised commissure and absence of surface ornamentation, ×2000. 9, S.E.M. close-up of spore wall, ×6500. 10, S.E.M. of broken section of spore wall with solid apparently homogeneous structure, ×15000.

PLATE 46



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massive annulus of *Norwoodia* is much more extensive than that of any other known pteropsid fructification. In light of the thick-walled nature of the annulus cells it is unlikely that any substantial changes in sporangial size or shape would occur with further development. The complete absence of a tapetum in all sporangia also suggests that they are more mature than the above features would indicate. Moreover, in crosiers of fertile pteropsids the pinnules are folded with the sporangia (abaxial surfaces) facing outward, while the sporangia of *Norwoodia* are oriented toward the centre of the aggregation (text-fig. 1). Maturity of the spores is more difficult to determine. It is quite possible that mature spores of this species are small and unornamented. On the other hand, in at least two genera of Palaeozoic pteropsids, *Senftenbergia* (Radforth 1938) and *Tedelia* (Eggert and Taylor 1966) spores from what otherwise appear to be relatively mature sporangia are known to exhibit a wide range of size and exine ornamentation. These differences are interpreted as representing ontogenetic variations; the smallest unornamented spores being the least mature (Eggert and Taylor 1966). While there is at present no evidence of such variation among *Norwoodia* spores, one cannot overlook the possibility that further development may significantly alter both spore size and exine ornamentation.

The features discussed above clearly distinguish *Norwoodia* as an independent genus of Palaeozoic ferns. However, its relationships to other pteropsids are more difficult to interpret. Among extant ferns sporangia with a well-developed annulus are found only among the Filicales, and are traditionally regarded as indicating leptosporangiate development. Similar features in Palaeozoic ferns are unfortunately less diagnostic. For instance, sporangia of this type are known to have been produced by *Botryopteris* (e.g. Phillips 1961), *Sermaya* (Eggert and Delevoryas 1967), *Ankyropteris* (Jennings and Eggert 1972), and possibly *Zygopteris* (e.g. Bertrand 1911; Mamay 1957), but the vegetative anatomy of these clearly allies them with Coenopteridales. On the other hand, Palaeozoic fructifications are sometimes interpreted as possible filicaleans when more proximal structures are unknown (e.g. *Oligocarpa*) or even when vegetative structures conform to those of the Coenopteridales (e.g. *Tedelia*, Eggert and Taylor 1966). While the early sporangial development of these fossil forms remains unknown it is impossible to determine if they are truly leptosporangiate or if they are derived from more than one sporangial initial. The occurrence of this latter development in presumably primitive, extant filicaleans (e.g. *Stromatopteris*, *Osmunda*, Bierhorst 1971) suggests a similar development in the Palaeozoic taxa that have small, annulate sporangia.

At the present time the affinities of *Norwoodia* remain uncertain. The small sporangial size, distinct annulus, single-cell layered wall, and prominent stalk demonstrate the similarity of the superficially borne *Norwoodia* sporangia to those of more recent filicaleans. However, many of these features are also shared by late Palaeozoic coenopterids. If future studies document the origin of the filicaleans from among the Coenopteridales, *Norwoodia* may represent a transitional form or even an early representative of the former. When one considers that there are several, simple, Pennsylvanian ferns for which fertile parts have not yet been assigned (i.e. *Apotropteris minuta* Morgan and Delevoryas, 1954; *Catenopteris simplex* Phillips and Andrews, 1965; *Rabdoxylon americanum* Dennis, 1968) it is likely that unquestionable filicaleans may be discovered in the late Palaeozoic of North America.

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