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PALAEOSTACHYA DIRCEI N. SP., AN AUTHIGENICALLY CEMENTED EQUISETALEAN STROBILUS FROM THE MIDDLE PENNSYLVANIAN OF SOUTHERN ILLINOIS[1]

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ABSTRACT

Palaeostachya dircei n. sp. is described from an authigenically cemented specimen collected from the Anna Shale Member occurring above the Herrin (No. 6) Coal Member and below the Brereton Limestone in the Carbondale Formation, Kewanee Group (Middle Pennsylvanian). The strobilus is three-dimensionally disposed within the matrix, allowing the preparation of ground thin sections, as well as selected maceration of the specimen. The imbricate strobilus is preserved for at least 7 cm of its original length and is composed of alternating whorls of sterile bracts and fertile sporangiophores. An articulated axis extends the length of the strobilus and attains a maximum width of 3 mm at the nodal areas. A whorl of 24 sterile bracts arises at each node, with each bract emerging at a 90° angle from the axis. Bracts are free except for a slight adaxial fusion at their point of origin. A slight downward-projecting keel develops at the point where the bract begins ascending at least past the second supra-adjacent node, where it is appressed into an abaxial furrow of the superposed bract. A whorl of sporangiophores originates above the bracts and is equal in number to the bracts. The sporangiophores are obliquely inserted on the axis and possess four superposed and thin-walled sporangia inserted upon a (?) cruciate head. Spores assigned to *Calamospora* have been recovered and range in diameter from 68–115 μm ($\bar{x}$ = 89 μm). The cone appears to be homosporous. *Palaeostachya dircei* n. sp. is compared to the reported permineralized and coalified compression species and appears similar to *P. vera* Seward and *P. gracilis* Renault.

THE DELIMITATION of Carboniferous strobili of the Equisetaceae (sensu Good, 1975) is based primarily upon the relationship between the sporangiophore and the bract. Twelve genera of strobili, based upon coalified compressions and permineralizations, are recognized in the Carboniferous. *Palaeostachya* Weiss (1876) was erected for fructifications which possess an articulated axis with alternating whorls of bracts and sporangiophores, with the origin of the sporangiophore stalk at or slightly above the level of bract attachment, and obliquely inserted. Four sporangia are usually attached to the sporangiophore head and directed towards the cone axis, although three species have been described possessing two sporangia per sporangiophore head. Twenty species of *Palaeostachya* have been established, and a review of the taxa shows that some species are probably assignable to genera in which the bract : sporangiophore relationship is uncertain.

An authigenically cemented *Palaeostachya* was collected from the Anna Shale Member above the Herrin (No. 6) Coal Member west of Carterville, Illinois (SE4 Herrin 15' Quadrangle, S4-T9S-R1E) and is curated in the Southern Illinois University Paleobotanical Collection (SIPC). The Anna Shale Member is placed within the Carbondale Formation, Kewanee Group (Hopkins and Simon, 1975) and is Middle Pennsylvanian in age (Westphalian D/? Cantabrian equivalent). Hibbert and Eggert (1965) have reported the only other equisetalean strobilus collected and described from the Carterville locality, *Paracalamostachys cartervillei*.

Permineralized specimens of equisetalean strobili are easily delimited to a generic and specific level because serial thin sections are easily prepared utilizing the cellulose acetate peel technique (Delevoryas, 1955; Baxter, 1955; Taylor, 1967; Good, 1975). The relationship between the sporangiophore and bract as well as other anatomical and morphological

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features of the fructifications are readily observable. Coalified compressions, on the other hand, are often difficult to assign to a genus due to the fact that the whorls of bracts normally obscure the position of insertion of sporangiophores. In a few rare instances, coalified compressions have been described utilizing thin sections (Selling, 1944; Nemejc, 1950; Kosanke, 1955). Although authigenically cemented specimens of equisetalean strobili have been collected and curated in various institutions, only one specimen has, to date, been described utilizing serial thin sections. Kosanke (1955) erected a new genus of calamitean strobilus, *Mazostachys,* from the Mazon Creek area. The spatial arrangement of the axis, bracts, sporangiophores and sporangia were ascertained by examination of cellulose acetate peels and thin sections.

The *Palaeostachya* strobilus from the Anna Shale Member is the second authigenically cemented equisetalean fructification to be described and reconstructed utilizing serial thin sections and selective maceration. When the specimen was initially examined in the paleobotanical collections of Southern Illinois University (Gastaldo, 1975), only a part of the specimen was curated with the remainder of the Carterville flora. The fructification was partially exposed (Fig. 1) and the concavity had been filled with balsam to prevent loss of preserved material. Attempts at chemical removal of the balsam, in order to discern the nature of the bract : sporangiophore arrangement, met with failure. It became impossible to discern the morphological features of the specimen, and because the exposed portions of the strobilus measured 25 mm in length and 7 mm in width, the specimen was originally assigned to *Paracalamostachys cartervillei* (Gastaldo, 1975, 1977). Subsequently, the counterpart was rediscovered in the collections, but additional morphological features to aid in identification of the specimen were not evident. It was decided that the part and counterpart should be reunited and sectioned in order to ascertain whether additional sporangiophores and bracts were preserved within the matrix. When the formerly exposed portion of the strobilus was cut free from the remainder of the concretion, it was noted that the three dimensionally preserved strobilus continued into the lower portion of the matrix. This allowed a number of techniques to be utilized in the study of the fructification.

METHODS—The upper 3.5 cm of the *Palaeostachya* strobilus was embedded in Bioplastic, and complete infiltration was accomplished utilizing an aspirator. During the operation of the vacuum, a minimum amount of catalyst was added to the partially filled jar. After sealing the jar, the aspirator was run until all the air bubbles were drawn out of the specimen. The specimen was then transferred to an aluminum foil container filled with Bioplastic and catalyst, and allowed to polymerize. Following curing, the specimen was trimmed, oriented and reembedded in order that perpendicular and parallel sections could be prepared. Thin sectioning was accomplished on a Gillings-Bronwell thin-sectioning machine. The sections were measured with an Amers 562M-1 (0.01 mm) micrometer. Line drawings of the serial sections were drawn with the aid of a camera lucida mounted upon a Leitz Labolux microscope. Subsequently each section was ground smooth and permanently mounted on glass slides.

Progressive maceration of a selected area of the lower strobilus, utilizing concentrated hydrofluoric acid, was accomplished to expose the longitudinal configuration of the specimen. An auspicious fracture along the bedding plane of the nodule exposed the outer surface of the strobilus. Selling (1944) remarks that a cleavage plane established on the exterior of the cone may be due to compression of the cone by its own weight during the fossilization process. The more compressed side may result in the demarcation of a more distinct cleavage plane. This would seem to account for the breakage of the lower portion of the specimen, but not for the originally exposed surface. A confinement constructed of Silflo, a low viscosity dental impression medium, was built around a 2-cm section of the fructification and lined in paraffin. The reaction between the acid and matrix was allowed to proceed for 4 hr. At the end of this period of time, the HF was removed and stored for palynological preparation. In addition, bract fragments released from the matrix were removed and stored separately. The specimen was washed to neutrality and the confinement was removed. The softened matrix was degáged from around the preserved structures prior to photography. Macrophotography was accomplished using a Mamiya RB-67 camera and Plus-X film. Following the 16th maceration, the specimen was covered with Harleco Synthetic Resin and a coverslip. In this way, the specimen is readily observable, oxidation of the fossil material is retarded, and the mounting medium can be easily removed for future examination if necessary.

The recovered maceration residue was consolidated through centrifugation, treated with

dilute HCl, Schultze's solution, and KOH in standard palynological procedure. Samples were processed from the upper and lower portions of the strobilus in order to ascertain if the fructification was homosporous or heterosporous.

DIAGNOSIS—*Palaeostachya* **dircei** sp. nov.

1977 *Paracalamostachys cartervillei* Hibbert and Eggert; Gastaldo, p. 137, fig. 25.

Authigenically preserved equisetalean strobilus composed of an articulated axis with alternating whorls of bracts and sporangiophores. Strobilus fragment 7 cm in length and about 11 mm in diameter, inclusive of bracts (8 mm in diameter exclusive of bracts but inclusive of sporangiophores); incomplete, lacking extreme distal and proximal portions. Axis diameter 4 mm at nodes, slightly less in internodal regions; with ribs alternating from node to node; internodal length averaging 3 mm; cross section of axis containing 12 areas thought to represent primary xylem surrounding a pith-like region. Whorls of sterile bracts originating at each node; approximately 24 bracts per whorl; slightly fused on the adaxial surface at the point of origin; alternating in position from one node to the next; giving the cone an imbricated appearance. Each bract extending 3 mm horizontally from the point of origin, developing a small downward-projecting keel, then ascending vertically at least 9 mm, tapering to an acuminate point; averaging 0.5 mm in diameter near the point of origin and enlarging to approximately 1 mm at the keel; remaining free for the majority of its length and ascending at least to the base of the third superior internode; bracts with an abaxial groove associated with the development of the keel. Cross-sectional appearance of bract changing in shape from almost papillionoid near the keel to slightly cruciate to an elliptical-terete nature in the distal portion. Sporangiophores obliquely inserted (45°–60°) upon the axis, originating alternately with the bracts of the subadjacent whorl; up to 1 mm above the bract whorl, approximately 24 per whorl; 0.5 mm in diameter and extending obliquely 2 mm to a probably cruciate head upon which are attached four sporangia; sporangiophores alternate with bracts of the same whorl; heads of sporangiophores in transverse section of the strobilus appear to be decurved with a depressed center; sporangia are thin walled, superposed, ovate-elongate in shape, about 2 mm in length, 1 mm in diameter and appearing terete in cross section near the axis. Strobilus homosporous; spores assignable to *Calamospora,* ranging in diameter from 68–115 μm, averaging 89 μm.

HOLOTYPE—Specimen SIPC 663.184 consisting of three portions of a single concretion (663. 184a, b, c) and 56 slide preparations labeled SIPC 663.184.1-663.184.56. Southern Illinois University Paleobotanical Collection, Carbondale, Illinois 62901.

LOCALITY—Anna Shale Member, S-13 Mine, Carterville, Illinois (Herrin 15′ Quadrangle SE4-T9S-R1E).

AGE—Middle Pennsylvanian, Carbondale Formation, Kewanee Group.

DESCRIPTION—*Axis*—*Palaeostachya dircei* n. sp. is an isolated equisetalean strobilus lacking the distal and proximal portions. The strobilus is composed of an articulated axis with alternating whorls of bracts and sporangiophores bearing sporangia. The preserved portion is greater than 7 cm in length and superficially appears imbricated due to the overlapping of subadjacent bract whorls. The

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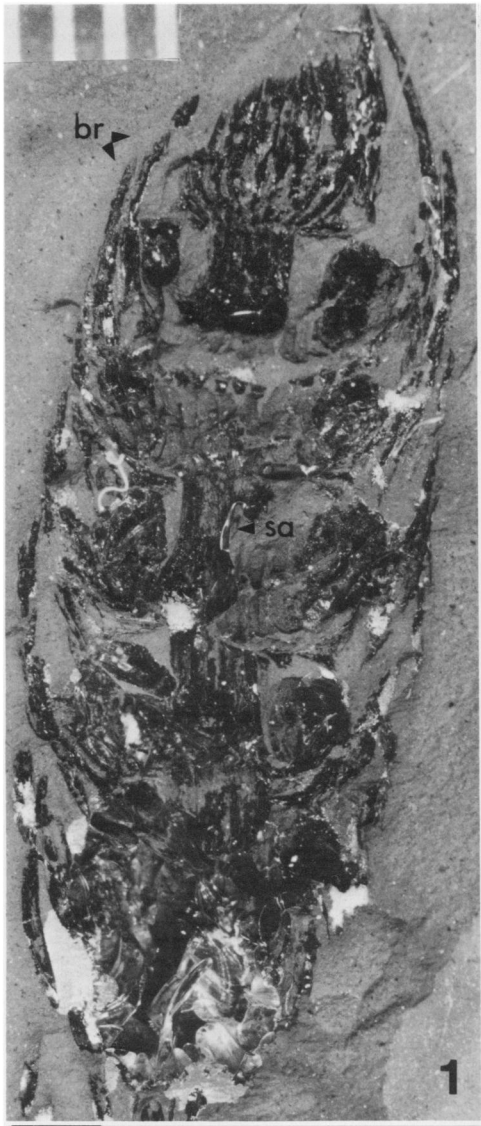
Fig. 1–4. *Palaeostachya dircei* n. sp. **1.** Specimen SIPC 663.184a, distal portion of holotype as originally exposed upon fracture of authigenically cemented concretion. Photograph prior to sectioning showing articulated strobilar axis (sa) which appears ribbed within the internodal region. Whorls of bracts (br) originate at the nodal areas and ascend past the base of the second supra-adjacent bract whorl. Scale in mm. **2.** Specimen SIPC 663.184c, photographed during selected maceration revealing the disposition of the bracts (br) in relation to the strobilus axis (sa), the vertical height to which the bracts ascend, the position of the sporangiophore stalks (sph) at the point of origin and the oblique nature of the sporangial units (sp). Scale same as Fig. 1. **3.** Slide 663.184.1. Transverse ground thin section of 663.184a and b, showing the strobilar axis (sa) composed of 12 areas (the 12th area missing) in which primary xylem occurred. A whorl of bracts (br) surrounds a whorl of sporangiophore heads (sph). Proximal to the sporangiophores are sections of sporangia (sp). **4.** Slide 663.184.14. Section of cone at the level where bract 3 (br 3) begins its ascent. Bract 1 (br 1) arose two nodal areas below br 3. These two bracts are superposed, and the distal portion of br 1 was appressed within the abaxial furrow (abf) of br 3 prior to dispersal of the spores. Bract 2 originated in an alternate position one nodal area subadjacent to br 3. The bracts change morphology during their ascent from a papillionid configuration (br 3), to a cruciate configuration (br 2), to an elliptical to terete shape (br 1).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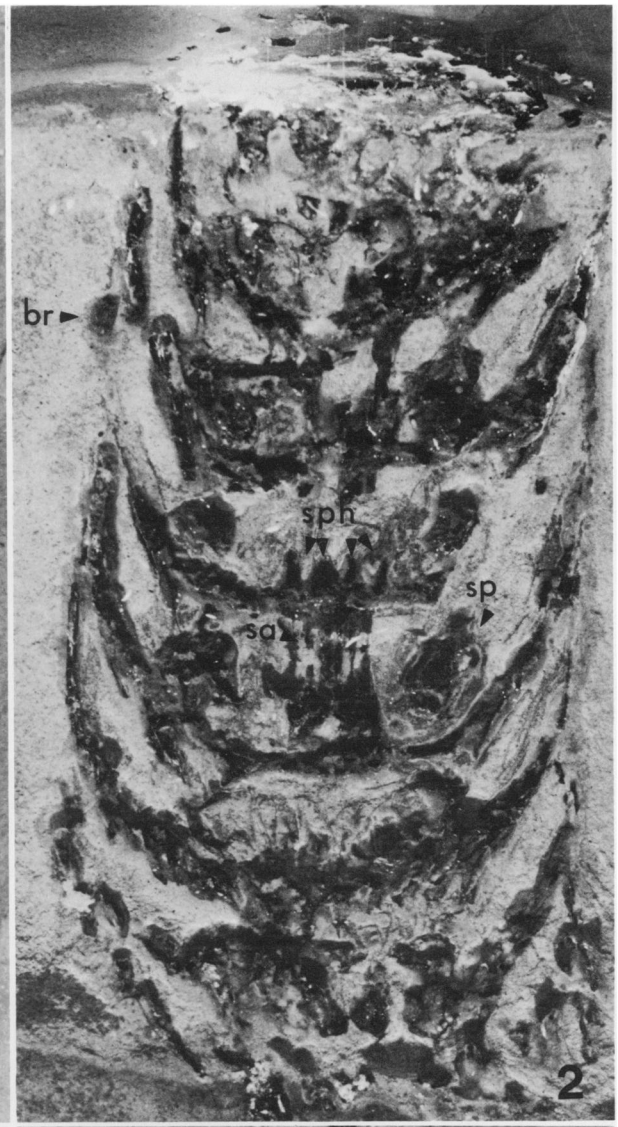
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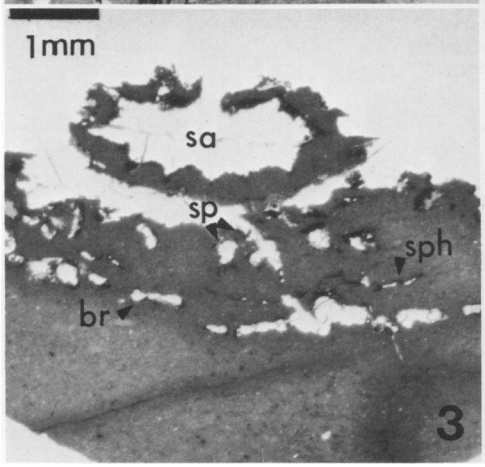
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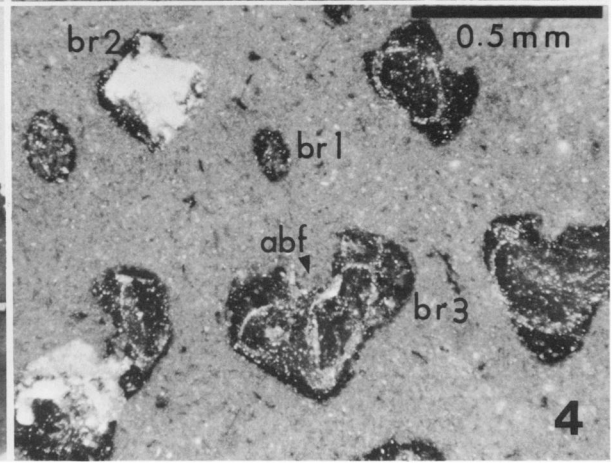
br2
0.5mm
br1
abf
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4

strobilus was transversely compressed during preservation, giving it an elliptical shape in transverse section, but was most likely cylindrical and measured about 11 mm in diameter. The articulated axis (Fig. 1, 2) is approximately 4 mm in diameter at the nodal areas and slightly less in the internodal regions. The ribbed internodal areas average 3 mm in length, and there is an alternation of ribs from one node to the next. In transverse section (Fig. 3) the preserved axis is seen to be composed of at least 11, more likely 12, areas which represent the position of the primary xylem. A small area of the axis is missing in transverse section which is the probable position of the twelfth protoxylem area.

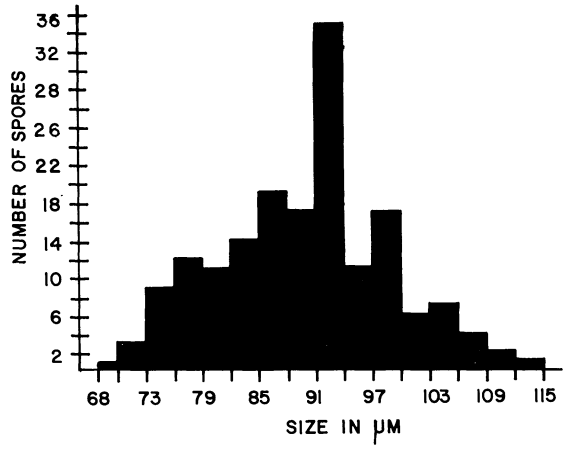

Fig. 5. Histogram of liberated *Calamospora* spores from *Palaeostachya dircei* n. sp.; 169 spores were measured and macerated spores from the distal and proximal portion of the strobilus ranged in size from 68–115 μm, averaging 89 μm.

Bracts—Whorls composed of 24 bracts arise at each nodal region and alternate from one node to the next. The bracts extend 3 mm horizontally from their point of origin and enlarge into a slightly downward-projecting keel (Fig. 6). This keel does not seem to overlap the subadjacent sporangia as in other taxa. In a transverse section of the strobilus at a level where three individual whorls of bracts overlap (Fig. 4), the largest bracts appear almost papillinoid in shape at the level where the bracts begin their vertical ascent. An abaxial furrow is present on the bracts, and develops at the point where the keel originates. The smaller, cruciate-shaped bracts, alternate in position to the largest bracts, arise from the whorl immediately below, while the smaller, elliptical-shaped bracts, superposed in position to the largest bracts, originate from two whorls below. The bracts average 0.5 mm in diameter for the majority of their length, broadening to 1.0 mm with the development of the keel, and then taper to less than 0.5 mm near the apex. The bracts of this specimen appear to curve slightly in their course and taper to an acuminate tip. The apparent change in shape from the papillinoid configuration near the keel to the elliptical character at the tapered apex is a consistent feature of all bracts. During maturation of the strobilus the abaxial furrow apparently accommodated the apex of the superposed bract originating two whorls below. This allows the cone to remain undisturbed until maturation and subsequent dispersal of the spores.

The development of the keel appears to coincide with the curvature of the apex of the sporangiophore, but the keel does not project downward to enclose the sporangiophore. This may be due to the imbricated nature of the bracts, and the unnecessary protection offered by a downward-projecting collar with this arrangement. The bracts are slightly fused (Fig. 7) on their adaxial surfaces at the point of origin, but are free from each other the remainder of their length. Bracts removed from the macerations (Fig. 8) have been examined for cuticular remnants, but no cuticle is preserved.

Sporangiophores—Sporangiophore whorls alternate with inferior whorls of sterile bracts. The sporangiophores originate between the bracts, and are obliquely inserted on the axis at angles varying from 45° and 60° (Fig. 6). The sporangiophores appear to arise within the

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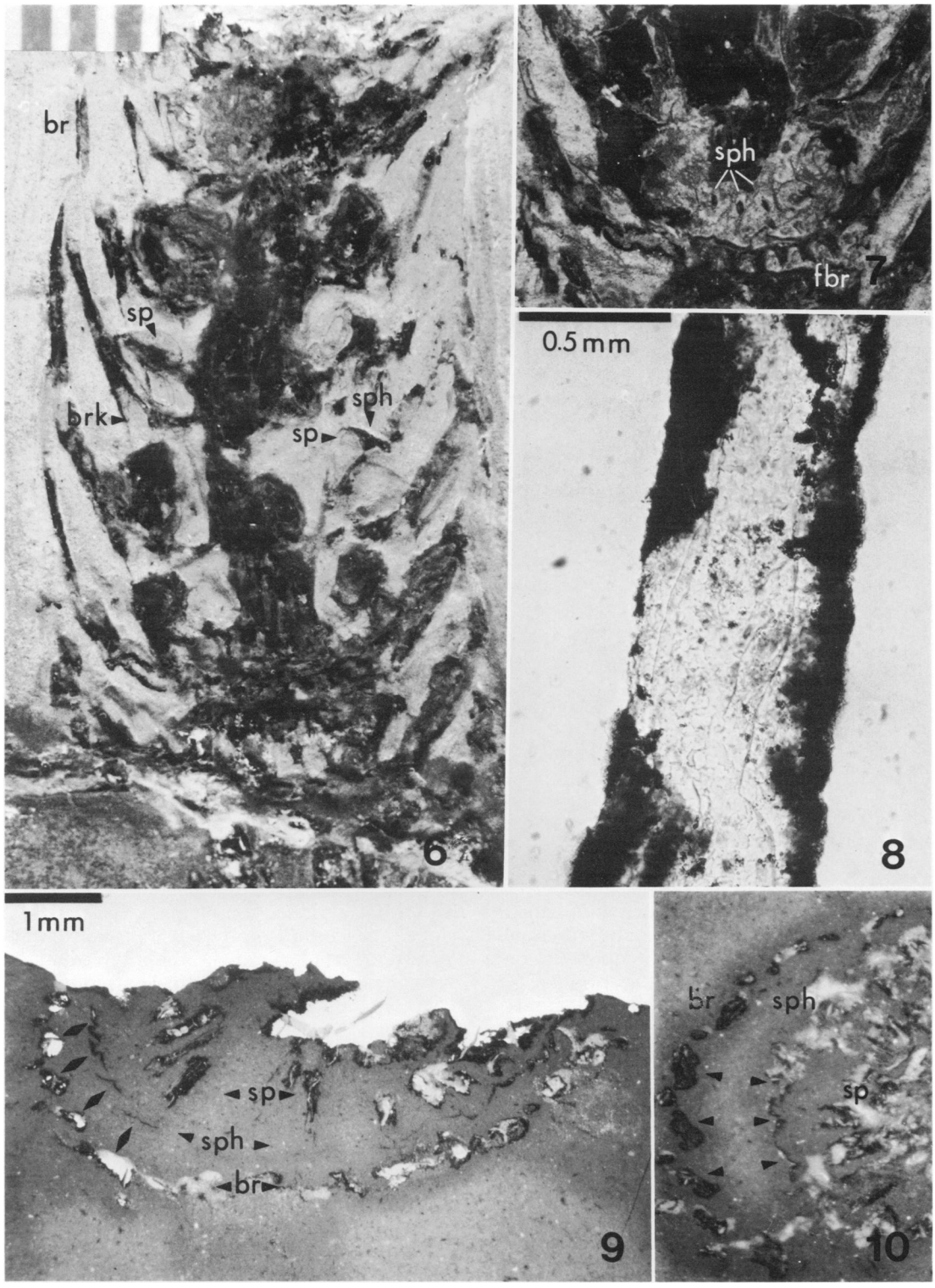
Fig. 6–10. *Palaeostachya dircei* n. sp. **6.** Specimen 663.184c. Longitudinally exposed section revealing the configuration of the bracts (br) and the development of a slightly downward-projecting keel (brk). Sporangiophores (sph) are inserted obliquely on the strobilar axis, and the sporangiophores possess thin-walled sporangia (sp) attached to the sporangiophore head and directed towards the axis. Scale in mm. **7.** The bracts are seen to be slightly fused on the adaxial surface (fbr) near their point of origin. It can also be observed that the sporangiophores (sph) are located between bracts, and, hence, not axillary in position. The bract : sporangiophore relationship (1:1) can be discerned. If additional information concerning the disposition of the sporangiophore in relation to the bract had not been obtained, the configuration displayed by the sporangiophore could lead one to classify this specimen within *Calamostachys*. Sporangiophore (sph). **8.** Slide 663.184.26. Bract liberated by maceration displaying the absence of a preserved cuticle.



9. Slide 663.184.4. Transverse section demonstrating the 1:1 bract : sporangiophore relationship (diamonds). A partial whorl of sporangiophore heads (sph) is proximal to the bract whorl (br). The sporangiophore heads appear decurved with a depressed center. Sporangia (sp) are preserved within the whorl of sporangiophores. **10.** Slide 663.184.13. Transverse section demonstrating the 1:1 ratio (arrowheads) between sporangiophores (sph) and bracts (br). Sporangia (sp) are preserved proximal to the sporangiophore heads.

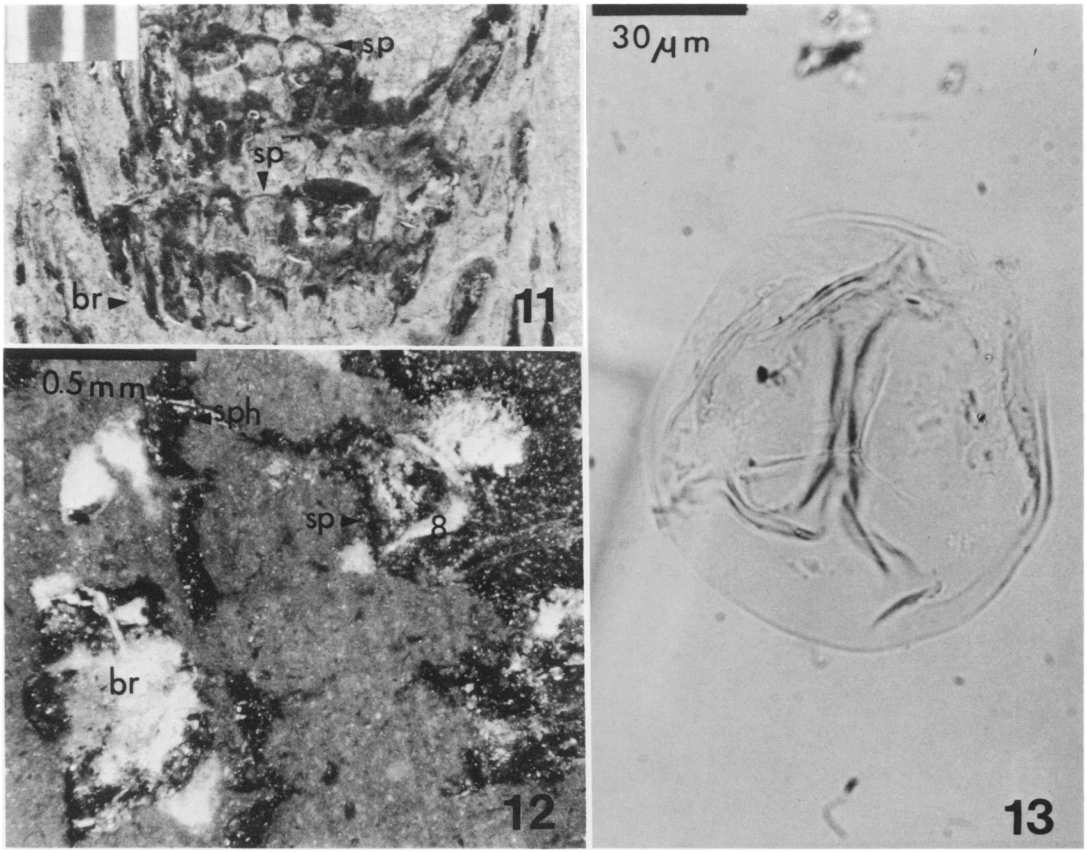


Fig. 11–13. *Palaeostachya dircei* n. sp. **11.** Specimen 663.184c demonstrates the superposed arrangment of sporangia (sp) between adjacent whorls of bracts (br). The sporangia appear terete in oblique section near the axis. Scale in mm. **12.** Slide 663.183.14. The sporangiophore heads (sph) are proximal to the whorl of bracts (br); the sporangiophore heads are decurved with a depressed center, and the arms of the sporangiophore are separated. This gives the impression that the sporangiophore head was cruciate. Sporangia (sp) are preserved proximal to the sporangiophore heads. **13.** *Calamospora* sp. liberated from sporangia of *Palaeostachya dircei* n. sp.

lower third of the internodal region, up to 1 mm above the level of the bract. The number of sporangiophores per whorl equals the number of bracts per whorl (Fig. 9, 10). The sporangiophores are 0.5 mm in diameter and extend 2 mm to a (?) cruciate head. In transverse section (Fig. 9, 10, 12) the sporangiophore head appears 'birdlike,' or decurved with a depressed center, and the arms separate from their point of attachment to the sporangiophore stalk. This separation of arms from a central point of origin suggests that there was an absence of tissue between the arms, and therefore it is suggested that the sporangiophore head is not peltate in appearance, but rather cruciate. Four sporangia are attached to each sporangiophore and are superposed (Fig. 11). The sporangia are thin walled, elongate-ovoid in shape, measuring up to 2 mm in length and 1 mm in width, and apparently terete in oblique transverse section near the cone axis (Fig. 11). In ground thin section (Fig. 9), the sporangia appear to be elongate because of their oblique insertion. The sporangia are attached to the sporangiophores at their apical extremities, but the actual degree of fusion of the two units is unknown.

Spores—Spores recovered from macerations of the fructifications are assigned to the dispersed spore genus *Calamospora* (Fig. 13) and range in diameter from 68–115 μm and average 89 μm (Fig. 5). Palynological preparations were made from the preserved upper and lower portions of the strobilus, and the spores recovered from each section were identical. Therefore, it is believed that the fructification was homosporous. A summary of the characteristics of *Palaeostachya dircei* is given in Table 1, and a reconstruction of the fructification is presented in Fig. 14.

DISCUSSION—Hibbert and Eggert (1965) report the first equisetalean fructification from the Carterville locality, *Paracalamostachys cartervillei*. The strobili of *P. cartervillei* varied from 11–17 mm in length, 4–4.5 mm in width, and the sporangiophore : bract relationship is unknown. The holotype material of *Paracalamostachys cartervillei* is reported to be curated in the Southern Illinois University Paleobotanical Collections, but it is not. Attempts at locating the type material in order to reassess the strobilus have failed, and the holotype is, at present, lost. Thus comparison of the only two described equisetalean strobili from the Carterville site is not possible.

A survey of *Palaeostachya* Weiss has revealed that 22 species have been recognized, 20 of which will be compared with *P. dircei*. Two species, *Palaeostachya alabamensis* White and *P. domherri* Zalessky are excluded from this survey. *Palaeostachya alabamensis* White (1900) is listed only as a floral component of the Pottsville, and the species is neither described nor illustrated. *Palaeostachya domherri* Zalessky (1907), on the other hand, was placed into synonymy with *P. paucibracteata* von Sandberger by Jongmans (1911), and will be treated as such.

In order to compare and contrast the taxa within *Palaeostachya* with *P. dircei,* characteristics used in the original diagnoses and subsequent descriptions of the species have been compiled (Table 1). A revision of the genus is not attempted herein, because the holotypes of each taxon have not been reevaluated. The majority of diagnoses, descriptions and illustrations of taxa are incomplete, and examination of the type material is necessary to establish missing characteristics and intertaxa relationships.

Palaeostachya dircei can be distinguished from the majority of species of *Palaeostachya* by its bract : sporangiophore ratio. Three taxa, *Palaeostachya schimperiana* Weiss (1876), *P. vera* Seward (1898), and *P. gracilis* Renault (1876) are reported to possess a 1:1 bract : sporangiophore ratio.

Palaeostachya dircei can be distinguished from *P. schimperiana* by a number of characters. The overall size and nature of the strobili are extremely different. *Palaeostachya dircei* is a relatively small cone with a maximum diameter of 11 mm, while *P. schimperiana* may attain 40 mm in diameter. The internodes are almost twice the length in *P. schimperiana* as they are in *P. dircei,* while the same is true of the axial diameter. *Palaeostachya dircei* possesses 24 bracts which alternate from whorl to whorl, while *P. schimperiana* is reported to have 16–18 superposed bracts. The bracts of *P. dircei* are free for almost their entire length with a slight fusion of the adaxial surface near the point of origin, while those of *P. schimperiana* are united for the greatest part of their length. There is a prominent downward-projecting basal collar present in *P. schimperiana*. This feature is absent in *P. dircei,* and the bract size differs in both taxa. *Palaeostachya dircei* has small, linear lanceolate bracts which are 1 mm in

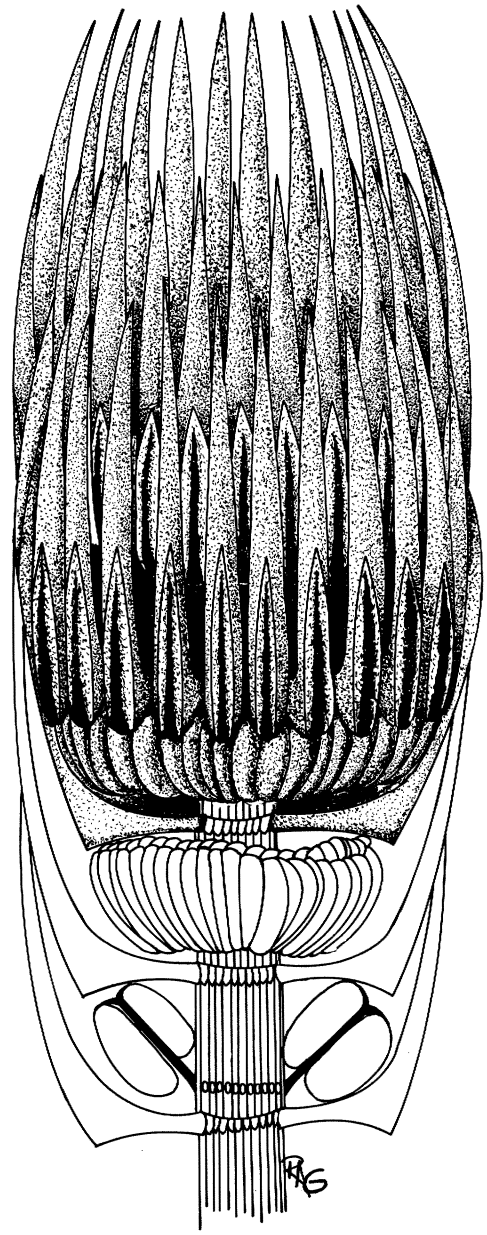


Fig. 14. Reconstruction of *Palaeostachya dircei* n. sp.

TABLE 1. *Comparison of* Palaeostachya dircei *with recognized species of* Palaeostachya

Characters	*P. dircei* n. sp.	*P. acicularis* Matthew, 1906	*P. andrewsii* Baxter, 1955	*P. aperta* (Lesq.) Abbott, 1968	*P. cylindrica* Nemejc, 1951	*P. decacnema* Delevoryas, 1955	*P. distachya* Sternberg, 1911
Cone length/width (mm)	>70/11	>30/9	>22/15	>100/24	85/8	>6.5/4.0–8.5	>200/15–18
Axis width/ribbing	4 at node/alternate	1.5/?	5/?	?/nonalternating	1.5/?	1–3/?	3.5–5.0/?
Internode length	$\bar{x}$ = 3	3	4.7	4.0–4.5	3.5	3.0–3.6	
Bract no.	approx. 24 per whorl		18–30; alternating			14–24; superposed	24–40
Length/width	3H; 9V/0.5 (1 at keel)	5/?	H6; V11/?	H6; V10–15/?		H?; V5/?	H?; V14–16/?
Height	2 internodes	0.5 internodes	2.5 internodes	2 internodes	1 internode	1.5 internodes	3–4 internodes
Fusion	near point of origin		basal & vertical*	basal & vertical*		basal disk	
Sporangiophore no.	approx. 24 per whorl		12–20	6–8		6–13	
Angle	oblique 45°	oblique	oblique	oblique	oblique	oblique	oblique
Attachment	axillary to slightly above*	axillary	axillary	axillary	axillary	approx. axillary	axillary
Head	cruciate		peltate	cruciate		expanded	
Length/width	2/0.5			7/?		2/?	
Sporangia no.	4	2(?)	4	2		4	
Shape	ovate-elongate			ovoid		pear-shaped	
Length/width	2/1		3.0–3.5/1.2–1.5	5/1.5		2/1	
Spore avg (μm)	68–115; $\bar{x}$ = 89		55–105/270–320	60–80		35–54	80–100
Remarks	* within lower third of internode		* bracts fused into disk or cup. heterosporous	* bracts fused into collar		no superposition of bracts and sporangiophores	

TABLE 1. *Continued*

Characters	*P. elongata* (Presl) Weiss, 1876	*P. ettingshausii* Kidston, 1903	*P. feistmantelii* Nemejc, 1951	*P. gracilis* Renault, 1876	*P. gracillima* Weiss, 1884	*P. minuta* Kidston, 1914	*P. ovalis* (Lesq.) Abbott, 1968
Cone length/width (mm)	70/8	40–80/8–10	70–80/10–17	?/8–9	>80–110/?	15/2.5	>70/10–17
Axis width/ribbing				2.5/?		?/nonalternating	
Internode length	3–4	3.0–3.5	3.5	2	3–4.5	1–1.25	3
Bract no.	8			20			6–10
Length/width	H?; V6–7/?	1H; 5V/?	?H; 10V/?	1.5H; 4–5V/?	?H; 6.5V/1		?H; 5–10V/1–1.5
Height	1 internode	1.5–2 internodes	>2 internodes	2 internodes	1 internode	1.5 internodes	1 internode
Fusion				basal			
Sporangiophore no.	8	6(?)		20(?)			8(?)
Angle	oblique	oblique	oblique	oblique	oblique	oblique	oblique
Attachment	axillary	axillary	axillary	axillary or above	axillary	axillary	axillary
Head				discoid			
Length/width	3–4/0.25						5/?
Sporangia no.	4	4		4			4
Shape	ovate	oval		ovoid	oval-elliptical		ovoid
Length/width	3/1.25	2.7–3.1/?		0.7/0.3		3.5–4.5/2.0–2.5	
Spore avg (μm)				70–100 ($\bar{x}$ = 80)			
Remarks						superposed bracts and sporangiophores	

TABLE 1. *Continued*

Characters	*P. paucibracteata* von Sandberger, 1866	*P. pendunculata* Williamson, 1884	*P. raconicensis* Nemejc, 1951	*P. schimperiana* Weiss, 1876	*P. superba* (Weiss) Jong. & Kukuk, 1913	*P. trabeculata* Abbott, 1968	*P. vera* Seward, 1898
Cone length/width (mm)	>30/?	25–70/?	>95/?	?/10	>52/20	30/5–8	?/11
Axis width/ribbing					?/nonalternating	1/?	3/?
Internode length	2	2–4	6–7	5–6	4	2.0–2.5	
Bract no.		12–16		16(?)	12(?)	10	16–20
Length/width	2H; 2–5V/?	?H; 5–8V/?	?H; 20V/1.5		5H; 13V/?	?H; 5V/?	
Height	1.5 internodes	1 internode		2 internodes	3 internodes	0.5 internode	1 internode
Fusion		none		basal collar			basal disk
Sporangiophore no.		6–8		16(?)			16–20
Angle	oblique	oblique	oblique(?)	oblique	oblique	oblique	oblique
Attachment	axillary	axillary or above*	axillary(?)	axillary	axillary	axillary	axillary
Head				quadrilobate		cruciate	peltate
Length/width		2/?		5–6(?)		2/0.33	?/0.75
Sporangia no.	2	4			several	4	4
Shape		oval			pear shaped	ovate	
Length/width					3.4/2.4	1.5–2/1.0–1.5	
Spore avg (μm)						27–37	$\bar{x}$ = 80
Remarks		* 0.25–0.75 mm above	superposed bracts				

maximum diameter (at the keel), attain a length of at least 9 mm, and ascend to at least the base of the second superior whorl. The bracts of *P. schimperiana* are 2.5 mm in diameter and are reported to attain 20 mm in length. This would allow the bracts to reach at least three internodal regions. It is evident from the comparison of these two taxa that they each represent distinct entities.

Palaeostachya vera Seward (1898) is exclusively known from the Westphalian A of England and Holland. The strobilus measures 11 mm in diameter with an axial diameter of 3 mm. The bract : sporangiophore ratio has been reported by various authors as 1:1 (Hickling, 1907; Good, 1975), 2:1 (Williamson and Scott, 1894), and greater than 2:1 (Seward, 1898). Based upon published illustrations, Good (1975) believes that the assessment of Hickling (1907) is probably correct, but neither author had examined the type material to arrive at this conclusion. The bracts are reported to be free for almost their entire length with a slight fusion near the point of origin. The bracts extend only as far as the next internode and possess lateral laminar wings derived from additional abaxial tissue. The spores are reported to average 80 μm in diameter.

Even though the overall dimensions and characteristics of *P. vera* approach *P. dircei,* these two taxa are considered distinct. The bracts of *P. vera* and *P. dircei* are similar in being free from one another for almost their entire length and possessing a slight fusion near their point of origin, but differ in the extent to which they ascend in height. The bracts of *P. vera* reach only to the base of the superior whorl, whereas the bracts of *P. dircei* reach past the base of the second superior whorl. The whorls of bracts in *P. dircei* alternate from one node to the next, whereas the disposition of bracts in *P. vera* has not been established. The bract : sporangiophore ratio, although reported as 1:1 in *P. vera,* is questionable and should be reinvestigated in order to definitely ascertain the relationship of these units. The few specimens attributable to *P. vera* are restricted to the Westphalian A of England and Holland, and are not known above this horizon or outside this geographic area. It is believed, at present, that these two taxa should remain separate until the holotype and described specimens of *P. vera* have been reexamined.

Renault (1876) described a permineralized specimen from the Autun of France which approaches the configuration of *P. dircei.* According to Renault (1876, 1893, 1896), *Palaeostachya gracilis* attains a total diameter of 8–9 mm. The articulated axis measures 2.5 mm in diameter and the internodal distance is 2 mm. Twenty basally fused bracts occur per whorl, and extend for several internodes enclosing superior whorls. The bracts, though, are reported to attain a vertical height of only 4–5 mm. The bract morphology of *P. gracilis* appears to be quite unusual for a *Palaeostachya.* The bract is figured as arising perpendicularly from the axis and producing a downward-projecting expansion of abaxial tissue near the point of vertical ascension. In the illustrations of Renault (1876, pl. 2, fig. 1, 4, 5), the keel appears to be extremely large. The cross-sectional aspect of the bract, as illustrated, demonstrates a discontinuity in laminar tissue directly above the keel. This distinct separation of tissue in the laminar portion of the bract is illustrated in longitudinal, as well as transverse section. Sporangiophores are obliquely inserted above the bract whorl and are very small in relation to the bract. The longitudinal section of the cone, in which the sporangiophores are figured, is near the apex, and these sporangiophore stalks may not have fully matured prior to preservation. The sporangiophores are reported to attain a total length of 0.7 mm and a width of 0.3 mm. The position of the sporangiophore is variable in insertion, being axillary to supraxillary. The sporangiophores are said to be immediately above and between bracts of the subadjacent bract node. Good (1975) interprets this disposition to represent a 1:1 sporangiophore : bract relationship. Selling (1944) notes that Renault (1882) guessed that the sporangiophores would be found between two sterile bracts in *P. gracilis,* but whether he meant one sporangiophore between each bract (1:1) or between a pair of bracts (1:2) was not clearly expressed. Selling (1944) believes that there are twice as many bracts as sporangiophores, as stated in the description by Renault (1876), and cites the study of Browne (1923) as confirmation of this condition.

Although *Palaeostachya gracilis* and *P. dircei* are morphologically similar, the two taxa should remain at present as separate species. The degree of bract fusion in *P. gracilis* is not exactly known, while *P. dircei* possesses a slight fusion of bracts at the point of origin. Both taxa possess bracts which ascend for at least two internodal regions, but it is not known whether bracts in *P. gracilis* alternate from one node to the next or are superposed. The illustrations of Renault (1876) appear to display the possible superposition of bracts, but it is difficult to discern. The downward-projecting tissue evident in *P. gracilis* is dissimilar to the slightly developed keel encountered in *P. dir-*

cei. The longitudinal aspect of the bracts of these two taxa also differ. The bracts in *P. dircei* are entire, while those of *P. gracilis* possess laminar divisions of the tissue directly above the development of the keel. As noted above, the exact ratio of bracts to sporangiophores is debatable in *P. gracilis,* while *P. dircei* indeed manifests a 1:1 ratio. The size of the sporangiophores of the two taxa is distinctly different, with the former exhibiting a much reduced sporangiophore unit. Spores are not reported from *P. gracilis* and therefore cannot be compared.

One character which appears to be found in both taxa, and not reported in any other, is the variable insertion of sporangiophores. If the figures of Renault (1876) are accurate, *P. gracilis* demonstrates a variable insertion pattern of sporangiophores. These sporangiophores originate both 'axillary,' as in other species such as *P. andrewsii* Baxter, and supraxillary similar to the genus *Calamostachys*. This configuration may be due to the small nature of the sporangiophores and the plane of section, but this can only be verified upon reexamination of the type material. *Palaeostachya dircei,* on the other hand, appears to display sporangiophores inserted at different angles.

Palaeostachya dircei may be synonymous with any one of the following taxa, but cannot be directly compared to them because of the absence of differentiating characteristics in their original diagnoses (Table 1). *Palaeostachya feistmantelii* is described by Nemejc (1951) for a cone 7–8 cm in length and 1.0–1.7 cm in diameter. The internodes average 3.5 mm and whorls of bracts alternate with whorls of sporangiophores. The bracts are reported to attain a vertical height of about 1 cm, or greater than two internodal regions, and are 1 mm in diameter. The sporangiophores are axillary and inserted obliquely. Neither the number of bracts, sporangiophores or sporangia, nor their relationships are known. Spores have not been recovered from the strobilus, and it is thought that without these differentiating characters, the Carterville material cannot be assigned to this taxon even though, on overall dimensions, these taxa appear very similar.

Nemejc (1951) also erects a taxon, *Palaeostachya cylindrica,* for cones described as being 8.5 cm long and 8 mm in diameter, possessing an axis 1.5 mm in thickness, and internodal lengths averaging 3.5 mm. The bracts are figured as attaining at least the next internode in vertical height, and the sporangiophores are reported as being axillary and obliquely inserted. It appears that the only difference between *P. cylindrica* and *P. feistamantelii* is in overall diameter and length of bracts. Again, because of a lack of knowledge about several characters, *P. dircei* cannot be accurately compared to either of these taxa.

Kidston (1903) described *Palaeostachya ettingshausenii,* a Westphalian age strobilus 4–8 cm in length and 6–8 mm in diameter (exclusive of bracts). Internodal distances average 3.0–3.5 mm, and whorls of bracts alternate with whorls of sporangiophores. Bracts are 1 mm in diameter and attain a vertical height of 5 mm and, hence, overlap approximately two internodes. The sporangiophores are inserted obliquely in the axils of the bracts and are reported as possibly numbering six per whorl. Four sporangia are attached to each sporangiophore and are oval in outline. The strobilus is reported to be homosporous with spores ranging in diameter from 70–100 μm ($\bar{x}$ = 80 μm). Even though the species is similar in overall dimension to the material collected from Carterville the amount of information not known is critical, and until reevaluation of the holotype material is completed, these two taxa should remain separate.

CONCLUSIONS—*Palaeostachya dircei* appears to be a valid species delimited from the other reported taxa by possessing a definite 1:1 bract : sporangiophore ratio, basally fused bracts which ascend to at least the base of the second superior whorl, obliquely inserted sporangiophores within the lower third of the internode possessing four sporangia per sporangiophore, and variable angles of divergence of the sporangiophores. The disposition of whorls of bracts is an interesting character displayed by this taxon. The imbricated appearance of the strobilus may have been integral in the reproductive strategy of the fructification. The presence of an abaxial groove on the 'outer' surface of the bract seems to indicate that, prior to maturation of the cone, the superposed whorl of bracts was appressed to this whorl of bracts. The tapered apex of the lower bract was situated within the abaxial groove of the upper bract. Because each whorl of bracts alternates, the cone would have been tightly closed during the period of sporangiophore and sporangial development. Upon maturation and possible elongation of the cone axis, these whorls of bracts probably opened up allowing the aerial dispersal of the spores into the environment. This may explain the differences in bract position exhibited by various specimens. In some taxa, the bracts are reported to be at an angle of about 45° to the axis. This is probably a cone which has matured and is

in the process of spore dispersal. *Palaeostachya dircei,* on the other hand, was preserved prior to the dispersal stage of maturation, and appears imbricated.

Another character which *P. dircei* exhibits is the apparent mechanism for accommodating the large number of sporangia and sporangiophores in a limited diameter. The sporangiophores apparently arise from the cone axis at different angles, primarily at 45° and 60° to the axis. This alternation of sporangiophore angles may solve the spatial problem of spacing 24 sporangiophores, each with four sporangia, around the axis.

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