

Marine and terrestrial palynofloras from transitional Devonian–Mississippian strata, Illinois Basin, U.S.A.

R. Wicander⁽¹⁾ and G. Playford⁽²⁾

(1) Department of Earth and Atmospheric Sciences, Central Michigan University, Mt. Pleasant, Michigan, U.S.A. 48859
reed.wicander@cmich.edu

(2) School of Earth Sciences, The University of Queensland, Brisbane, Australia 4072
g.playford@uq.edu.au

ABSTRACT

Diverse and reasonably well preserved palynofloral assemblages are described from a 12.9 m-thick section of the Upper Devonian Saverton Shale and a 17.0 m-thick section of the Lower Mississippian Hannibal Shale exposed along a bluff at Atlas South, Pike County, Illinois, U.S.A. The microphytoplankton assemblage, consisting of acritarchs and prasinophytes, comprises 17 genera and 38 species, including two new species (*Cymatiosphaera scitula* and *Gorgonisphaeridium savertonense*) and one new combination (*Puteoskortum sprucegrovense*). The miospore assemblage contains 14 species – one new (*Punctatisporites hannibalensis*) and one new combination (*Vallatisporites hystricosus*) – distributed among 13 genera. The overwhelming majority of microphytoplankton and miospore taxa occur in the Saverton Shale. The Saverton microphytoplankton assemblage indicates a latest Devonian (Strunian) age and is most similar in composition to previously described Late Devonian assemblages from North America and China. There is a low to moderate degree of similarity between the Saverton microphytoplankton assemblage and those reported elsewhere in the world. The miospore assemblage further corroborates a latest Devonian age (LN miospore Zone), as signified by its content of *Retispora lepidophyta*, *Verrucosporites nitidus*, *Indotriradites explanatus*, and *Vallatisporites hystricosus*. Based on the significant drop in diversity of the microphytoplankton, the presence of morphologically simple morphotypes, and several taxa, whose range extends into the Early Mississippian, a Kinderhookian date for the Hannibal Shale is reasonable. The Hannibal miospore palynoflora is even more impoverished than the associated microphytoplankton, and its few named taxa are consonant with, albeit not independently corroborative of, an Early Mississippian age. Sedimentologic and paleontologic-palynologic evidence indicates that the Saverton and Hannibal shales were both deposited in a low energy, somewhat offshore, normal marine environment within the Illinois Basin.

Key words: acritarchs, Lower Mississippian, miospores, prasinophytes, Upper Devonian, U.S.A.

Palinofloras marinas y terrestres de los estratos transicionales del Devónico-Misisípico, Cuenca de Illinois, Estados Unidos

RESUMEN

Se describen asociaciones palinológicas diversas y razonablemente bien conservadas de las secciones del Devónico Superior de la Pizarra Saverton, de 12.9 m de espesor, y del Misisípico Inferior de la Pizarra Hannibal, de 17 m. Ambas se encuentran expuestas en Atlas South (Pike County, Illinois, Estados Unidos). Las asociaciones microfítplanctónicas están integradas por acritarcos y prasinofitos. En total, se han identificado 17 géneros y 38 especies, habiéndose descrito dos como nuevas (*Cymatiosphaera scitula* y *Gorgonisphaeridium savertonense*) y una nueva combinación (*Puteoskortum sprucegrovense*). La asociación de miosporas está formada por 13 géneros y 14 especies, de estas una es nueva para la ciencia (*Punctatisporites hannibalensis*) y otra es una nueva combinación (*Vallatisporites hystricosus*). La mayor parte de los taxones que se identifican en este trabajo proceden de la Pizarra Saverton. Aquí, las asociaciones microfítplanctónicas indican una edad Struniense (Devónico Superior) y muestran grandes analogías en su composición con las que se han descrito previamente en el Devónico Superior de Norte América y China. Existe un grado de similitud de bajo a moderado entre estas asociaciones y las registradas en otras partes del mundo. Adicionalmente, las de miosporas corroboran una edad Devónica Superior (LN miospore Zone), como indica su contenido en *Retis-*

pora lepidophyta, Verrucosporites nitidus, Indotriradites explanatus y Vallatisporites hystricosus. Se puede inferir una edad Kinderhookiense para la Pizarra Hannibal basada en la disminución significativa de la diversidad del microfitorplancton, la presencia de morfotipos simples, y por la aparición de varios taxones cuyos rangos estratigráficos se extienden al Misisípico Inferior. La palinoflora de miosporas de la Pizarra Hannibal se halla incluso más empobrecida que la de microfitorplancton y está de acuerdo con una edad Misisípico Inferior, aunque esta no es totalmente segura. Evidencias sedimentológicas y paleontológicas-palinológicas indican que los materiales de las pizarras Saverton y Hannibal fueron depositados en la cuenca de Illinois en un ambiente marino normal de baja energía, algo alejado de la costa.

Palabras clave: acritarcos, Devónico Superior, Estados Unidos, miosporas, Misisípico Inferior, prasinofitos

VERSIÓN ABREVIADA EN CASTELLANO

Introducción

El registro de acritarcos y prasinofitos del Devónico Superior es razonablemente extenso en muchas partes del mundo, incluyendo Norte América (Le Hérissé et al., 2000; Molyneux et al., in press). Considerando la bibliografía de las asociaciones de microfitorplancton de la edad citada, se puede concluir que existieron numerosas especies cosmopolitas y endémicas, y que muchas otras estuvieron limitadas latitudinalmente. Además, desde un punto de vista estratigráfico, un importante conjunto de especies tiene rangos estratigráficos restringidos, por lo que son buenos índices del final del Devónico.

Los resultados publicados sobre las asociaciones de miosporas del Devónico Superior-Misisípico Inferior son mucho más extensos que las contemporáneas de microfitorplancton. Por ejemplo, muchos taxones, como la miospora *Retispora lepidophyta*, combinan rangos estratigráficos cortos con una distribución global o casi global, por lo que tiene una gran importancia estratigráfica y de correlación. Los trabajos de McGregor y Playford (1992), Playford (1993), Playford y McGregor (1993), Clayton (1996) y Streele (2009) confirman el incremento del conocimiento sobre la diversidad y distribución estratigráfica de las floras de miosporas del Devónico Superior-Misisípico inferior en Euroamérica y, en menor grado, en Gondwana.

La abundancia y diversidad de microfitorplancton disminuyó dramáticamente en el límite Devónico/Carbonífero, como indicó Tappan (1968) inicialmente y fue documentado posteriormente por otros autores. Conocido como el "apagón del fitoplancton" (Riegel, 2008), este evento global está sorprendentemente ilustrado en este trabajo debido al contraste cualitativo y cuantitativo de las asociaciones de microfitorplancton del Devónico Superior de la Pizarra Saverton, y los datos para el Misisípico Inferior de la Pizarra Hannibal (Atlas South, Illinois, Estados Unidos) (Fig. 1). Mientras las asociaciones microfitorplanctónicas de la Pizarra Saverton son diversas y abundantes, en las de la Pizarra Hannibal los acritarcos y prasinofitos no se encuentran tan bien representados (Fig. 2).

Metodología

Se recogieron tres muestras del Devónico Superior en la Pizarra Saverton y otras tres del Misisípico Inferior en la Pizarra Hannibal, ambas localizadas en Atlas South, Pike County, Illinois (Fig. 1). En este lugar, los materiales expuestos de la Pizarra Saverton tienen 12.9 m de espesor encontrándose por encima de forma concordante con la Pizarra Grassy Creek y, por debajo, con la Caliza Glen Park. A continuación, la aparentemente concordante Pizarra Hannibal presentan 17 m de espesor y están cubiertas por la Caliza Burlington.

La Pizarra Saverton es arcillosa, físil, y sus colores varían desde gris, a gris verdoso y gris azulado, con niveles arenosos y calcáreos. Por su parte, la Pizarra Hannibal está compuesta por materiales calcáreos y no calcáreos, siltstones y sandstones de grano fino de color gris a gris azulado. Las muestras 1169 ASI-1171 ASI fueron recogidas en los niveles gris verdosos, la 1172 ASI en los siltstones calizos de color negro, ambas en la Pizarra Saverton, mientras que las muestras 1173 ASI y 1174 ASI (en siltstones de color gris a gris verdoso) fueron tomadas en la Pizarra Hannibal.

Se utilizaron las técnicas palinológicas estándar en la preparación de las seis muestras. Estas consistieron en el tratamiento en frío de 25-30 gr de muestra, trituradas a tamaño de gránulo, con HCl al 50%, HF al 40% y HNO₃ concentrado, para la disolución de carbonatos, silicatos y sulfuros, respectivamente. Las soluciones resultantes de cada tratamiento ácido fueron neutralizadas con agua destilada. El residuo orgánico resultante fue filtrado a través de un tamiz de nylon de 20 µm de luz de malla. Se prepararon de forma separada un conjunto de láminas transparentes con las fracciones mayores de 20 µm y las menores de este tamaño.

Se contabilizaron un total de 250 especímenes por lámina (incluyendo acritarcos, ficomas de prasinofitos y miosporas) a partir de las de la fracción de más de 20 µm, con la finalidad de determinar y comparar las abundancias relativas de los diferentes taxones de palinomorfos en las muestras analizadas (Fig. 2). Después de contar los 250, el resto de láminas con fracción mayor de 20 µm fue escaneado para asegurar que todos los taxones se encontraban registrados en cada muestra. La fracción menor de 20 µm fue escaneada para cada muestra para confirmar que todos los taxones habían sido recuperados. Los leiosferidios y los tasmanitidos

no se incluyeron en el conteo de los 250 especímenes por muestra debido a su abundancia ("efecto máscara"), pero su presencia ha sido cualitativamente indicada como rara, común y abundante.

Resultados

La palinoflora del Devónico Superior (Fameniense) de la Pizarra Saverton está integrada por ficomas de prasinofitos, acritarcos, miosporas y escolecodontos (Láms. 1-6). En el conjunto de los prasinofitos (5 géneros) se han identificado 10 especies, dos de ellas indeterminadas, así como una nueva para la ciencia (*Cymatiosphaera scitula*). La asociación de acritarcos (12 géneros) está compuesta de 26 especies, una de ellas con dudas y otra indeterminada. Además, se ha descrito una nueva especie (*Gorgonisphaeridium savertonense*) y una nueva combinación (*Puteoscutum sprucegrovense*). Las miosporas (13 géneros) se dividen en 9 especies, una de ellas con dudas, y tres especies designadas informalmente (sp. A), una nueva especie (*Punctatisporites hannibalensis*) y una nueva combinación (*Vallatisporites hystricosus*).

Por el contrario, las muestras del Misisípico Inferior (Kinderhookiense) de la Pizarra Hannibal están caracterizadas por asociaciones palinológicas pobres que incluyen solo dos taxones de prasinofitos (*Leiosphaeridia spp.* y *Tasmanites spp.*) y siete especies de acritarcos (cinco especies y 2 taxones designados informalmente) distribuidas en 4 géneros. Por su parte, las miosporas están representadas por tres especies ya conocidas y la ya mencionada nueva especie *Punctatisporites hannibalensis*.

En términos cuantitativos, los acritarcos dominan la asociación palinológica de la Pizarra Saverton, constituyendo un 63.2% del total (sin considerar leiosferas ni tasmanítidos), mientras que el de los prasinofitos es del 20.8% y el de miosporas del 16.0% (Fig. 2). Se puede observar un marcado cambio en la composición palinoflorística entre las asociaciones de las pizarras Shaverton y Hannibal. Excluyendo a *Leiosphaeridia spp.* y a *Tasmanites spp.*, los acritarcos representan el 96.7% de los palinomorfos de la Pizarra Hannibal, con unos porcentajes residuales de miosporas del 3.3% (Fig. 2).

Si se comparan las asociaciones de microfitorpláncton de la Pizarra Saverton, con 35 especies, con otras del Devónico Superior, se observa un 67% de coincidencia con las del Struniense de la Pizarra Bedford y la Arenisca Berea de Ohio (Molyneux et al., 1984); un 65% con el Frasnense superior-Fameniense de las pizarras New Albany, Ohio y Bedford de Kentucky (Huysken et al., 1992); y un 52% con el Struniense de la Formación Bakken, sur de Saskatchewan, Canadá (Playford y McGregor, 1993). Aunque existe un gran número de formaciones de edad similar en otras partes del mundo, el mayor grado de similitud se encuentra con el Fameniense de la Formación Hongguleleng de China (Lu-Li chang y Wicander, 1988) en la que se aprecia un 58% de especies coincidentes.

El conjunto de miosporas de la Pizarra Saverton está caracterizado por una preponderancia de especies que han sido registradas en estratos de edad cercanamente similar (Devónico más superior: Struniense) en Norte América y globalmente en otras partes del mundo. De forma usual en las asociaciones de esta edad hay *Retispora lepidophyta*, junto con *Indotriadites explanatus*, *Vallatisporites hystricosus* y *Verrucosisporites nitidus* (Fig. 4). El carácter cosmopolita que reflejan estas asociaciones de miosporas es una manifestación evidente de la composición relativamente uniforme de las floras devónicas en todo el mundo.

La palinoflora de la Pizarra Saverton obtenida en la sección de Atlas South, Illinois, indica una edad Devónico Superior para esta localidad. La asociación microfitorplánctónica es típica del Devónico Superior, con una composición más compatible con las del Fameniense (Fig. 3). Las miosporas, y en concreto *Verrucosisporites nitidus* y *Retispora lepidophyta*, limitan la edad de la Pizarra Saverton a la Zona LN de miosporas de Euramérica y Europa Occidental (Fig. 4).

La palinoflora de la Pizarra Hannibal se encuentra significativamente empobrecida en comparación con la de la Pizarra Saverton. De hecho, la asociación microfitorplánctónica está dominada por unas pocas especies, todas ellas con amplios rangos estratigráficos, y la asociación de miosporas está representada solo por cinco especies. Considerando la significativa caída en la diversidad del microfitorpláncton, la presencia de varios taxones cuyo rango estratigráfico se extiende hasta el Misisípico temprano y los escasos taxones de miosporas, se puede inferir una edad Kinderhookiense para la Pizarra Hannibal.

Conclusiones

Se ha obtenido un conjunto palinoflorístico diverso compuesto por 38 especies de acritarcos y prasinofitos (incluyendo dos especies nuevas y una nueva combinación) y 14 de miosporas (una de las cuales es nueva para la ciencia y otra una nueva combinación) en el Devónico Superior (Struniense; Zona LN de miosporas) de la Pizarra Saverton y el Misisípico Inferior (Kinderhookiense) de la Pizarra Hannibal, en Pike County, suroeste de Illinois, Estados Unidos.

La asociación microfitorplánctónica de la Pizarra Saverton muestra un alto grado de similitud con otras palinofloras del Devónico Superior de Norte América, notablemente con las de las pizarras New Albany Shale, Ohio y Bedford de Kentucky, la Pizarra Bedford y la Arenisca Berea de Ohio, y las de la Formación Bakken del sur de Saskatchewan (Canadá). Además, de una forma global, tiene un elevado número de elementos en común con las del Fameniense de la Formación Hongguleleng de China. La asociación microfitorplánctónica de la Pizarra Hannibal contiene los mismos taxones de morfología simple y largo rango estratigráfico que se encuentran en todo el mundo en sedimentos del Misisípico Inferior, junto con unos pocos taxones que posiblemente se extiendan desde el Devónico hasta el Misisípico Inferior.

Evidencias sedimentológicas y paleontológicas/palinológicas indican que las pizarras Saverton y Hannibal fueron depositadas en un ambiente marino normal de baja energía, algo alejado de la costa dentro de la cuenca de Illinois, que estaba ubicada durante el Devónico Superior-Misisípico Inferior en latitudes cercanas al Ecuador.

Introduction

The published record of Late Devonian acritarchs and prasinophytes now constitutes a reasonably comprehensive coverage for many parts of the world (Le Hérisse *et al.*, 2000; Molyneux *et al.*, 2013). In North America, a number of studies of advantageously preserved, independently age-dated, and stratigraphically constrained microphytoplankton assemblages have been published. These include Staplin (1961), Winslow (1962), Bharadwaj *et al.* (1970), Wicander (1974, 1975), Wicander and Loeblich (1977), Molyneux *et al.* (1984), Wicander and Playford (1985), Turner (1986, 1991), Huysken *et al.* (1992), and Playford and McGregor (1993).

Based on the literature of Late Devonian microphytoplankton assemblages, together with syntheses by Wood (1984), Vanguetaine (1986), Playford (1993), and Vavrdová and Isaacson (1997, 1999, 2000), it is clear that there are numerous cosmopolitan species, many confined largely to lower or higher paleolatitudes, as well as a number of endemic species. Although the stratigraphic range of some of these species commences in the Middle Devonian, even in the Early Devonian, many are restricted to, and hence reliable chronostratigraphic indices for the Late Devonian or portions thereof.

The published accounts of Late Devonian–earliest Mississippian miospore assemblages are much more extensive than those pertaining to coeval microphytoplankton assemblages. Many miospore taxa combine short stratigraphic ranges with global or near-global distribution, thus enhancing their stratigraphic-correlative significance, locally, regionally, and internationally. A pre-eminent and well-publicized example is the widely disseminated latest Devonian species *Retispora lepidophyta* (Kedo, 1957) Playford, 1976 (e.g., Streele, 1986, 2009; Playford, 1993). Among the extensive published literature, studies by Richardson and McGregor (1986), Streele *et al.* (1987), Higgs *et al.* (1988), McGregor and Playford (1992), Clayton (1996), Streele and Loboziak (1996), and Melo and Loboziak (2003) serve to exemplify the accrued knowledge of the diversity and stratigraphic distribution of the Late Devonian–earliest Mississippian miospore floras, particularly in Euramerica and, to a lesser degree, in Gondwana.

As first discussed by Tappan (1968), and by many subsequent authors, organic-walled microphytoplankton abundance, and diversity in particular, decreased dramatically at the Devonian/Carboniferous boundary. This event, known as the “phytoplankton black-out” (Riegel, 2008), is well documented from widely separated regions of the world (e.g., Wicander, 1975;

Molyneux *et al.*, 1984, Vanguetaine, 1986; Le Hérisse *et al.*, 2000; Filipiak, 2005).

The qualitative and quantitative contrast between the Upper Devonian Saverton Shale’s microphytoplankton assemblage, and that recovered from the Lower Mississippian Hannibal Shale, at the Atlas South, Illinois location described and discussed herein, is indeed striking. Whereas the Saverton microphytoplankton assemblage is both diverse and abundant, the immediately succeeding Hannibal assemblage is depauperate in acritarchs and prasinophytes, with only a few morphologically simple taxa represented.

Accordingly, we report here a varied and moderately well preserved assemblage of microphytoplankton and miospores from the Upper Devonian Saverton Shale, and a low-diversity microphytoplankton/miospore suite from the overlying and seemingly conformable, Lower Mississippian Hannibal Shale of Illinois. The palynofloras are compared to those documented previously from coeval strata in North America and elsewhere in the world, and their biostratigraphic and paleogeographic significance is discussed.

This paper was presented orally as a contribution to the CIMP-sponsored Devonian–Carboniferous symposium that honored Professors Geoffrey Clayton and Kenneth T. Higgs during the 45th Annual Meeting of AASP–The Palynological Society, held in Lexington, Kentucky, July 2012. We are pleased to dedicate this paper to these two well-known and respected palynologists, in appreciation of their many contributions to Paleozoic palynologic knowledge.

Stratigraphic synopsis

The Upper Devonian (Famennian) Saverton Shale (Formation) is present in outcrop and subsurface in southern Iowa (Iowa Basin), western and southeastern Illinois as part of the Illinois Basin (formerly known as the Eastern Interior Basin), and northeastern Missouri. It is a grey, greenish- to bluish-grey, fissile, silty shale, that contains both thin sandy beds and calcareous beds, and is well exposed in western Illinois and northeastern Missouri, in and near the Mississippi and Illinois River bluffs (Howe, 1961; Willman *et al.*, 1975). Its thickness varies, reaching a maximum of 36.6 m in western Illinois, whereupon it thins southward and eastward, grading laterally into the Grassy Creek Shale in Indiana and Kentucky. In northeastern Missouri, its maximum thickness is only 4.2 m, and it rapidly thins to the west, south, and east where it also grades laterally into the Grassy Creek Shale.

The sparse invertebrate fauna reportedly includes articulate brachiopods; viz., the spiriferid *Spirifer mar-*

ionensis and the productid *Orbinaria puxidata* (Willman *et al.*, 1975). However, conodonts are generally abundant, especially near the top of the formation, and indicate a Late Devonian (Famennian) age (Collinson *et al.*, 1962). As Collinson *et al.* (1962, p. 14) noted, the conodont fauna from the middle part of the Saverton Shale corresponds to the upper part of the toV and lower part of the toVI goniatite zones of Western Europe, and the conodont assemblage from the upper part of the Saverton Shale suggests a correlation with the uppermost toVI goniatite Zone. However, until the Saverton conodonts are found co-occurring with goniatites, correlation will remain, to some degree, in doubt. Nonetheless, the abundance of certain Devonian forms in the assemblage indicates a Late Devonian age for the Saverton Shale (Scott and Collinson, 1961).

In Iowa and the western Illinois Basin, the Saverton Shale is placed in cycles 10 and 11 of the Iowa T-R cycle scheme (Witzke and Bunker, 1996; Day *et al.*, 2009; Day and Witzke, 2012), which corresponds to the upper IIe and IIf transgressive-regressive relative sea-level curve (Johnson *et al.*, 1985). The upper IIe and IIf T-R cycles include the *trachytera*, *postera*, *expansa*, and *praesulcata* conodont zones (Johnson *et al.*, 1985; Witzke and Bunker, 1996). According to Streel (2009), the upper Famennian through basal Carboniferous interval embraces six conodont zones; viz., the middle *expansa* through *sulcata* zones, which correspond to the Western European LL, LE, and LN miospore interval zones, and the succeeding *Vallatisporites vallatus*–*Retusotriletes incohatus* (VI) assemblage zone, which crosses the Devonian–Carboniferous boundary. Furthermore, the last occurrence of *Retispora lepidophyta* immediately precedes the base of the Carboniferous system as defined by the first occurrence of the *sulcata* conodont zone (Streel, 2009, p. 172). Thus, the LL, LE, and LN miospore interval zones include the upper *expansa* through upper *praesulcata* conodont zones, which correspond to the upper portion of the Saverton Shale (Iowa T-R cycle 11 and T-R cycle IIe): Johnson *et al.* (1985); Witzke and Bunker (1996).

Throughout the Illinois Basin and eastern Missouri, the Saverton Shale is either overlain by, or grades laterally into, the Louisiana Limestone (Howe, 1961; Willman *et al.*, 1975; Heal and Clayton, 2008), a light grey lenticular limestone with shale partings and dolomitic intervals that is up to 12.2 m thick (commonly 3–6 m). The Louisiana Limestone is also considered latest Devonian, based on its conodont fauna (Collinson *et al.*, 1962; Willman *et al.*, 1975).

The Glen Park Limestone (Formation) occurs only in western Illinois, where it unconformably overlies either the Louisiana Limestone or the Saverton Shale,

if the Louisiana Limestone is missing (Willman *et al.*, 1975). Its thickness varies, but does not exceed 7.6 m in outcrop, and its lithology is also variable, consisting of any combination of sandy or silty limestones, silty shales, siltstones, dolomitic siltstones, oolitic limestones, limestones, limestone conglomerates, or sandstones. It is dated as earliest Mississippian (Kinderhookian).

The Hannibal Shale (Formation), comprising grey to blue-green, calcareous and non-calcareous shale, siltstone, and fine-grained sandstone, is exposed throughout northeastern Missouri and western Illinois, and is known also from the subsurface. It conformably overlies the Louisiana Limestone or Glen Park Limestone, and is unconformably succeeded by the Osagean Burlington Limestone at its type locality in Hannibal, Missouri. The Hannibal Shale has a maximum thickness of 30.5 m in Pike County, Missouri and in northern Calhoun County, Illinois, and thins south and southwest toward the Ozark Uplift. To the southeast, the formation grades laterally into the New Albany Formation (Heal and Clayton, 2008). Conodonts are abundant within the Hannibal Shale and indicate a Kinderhookian age, assignable to the lower *S. sandbergi* to lower *S. crenulata* conodont zones (Work *et al.*, 1988; Lane and Brenckle, 2005). Palynological data suggest that the Hannibal Shale, at least at its type location and elsewhere in northeastern Missouri, could be assigned to the Western European VI (*Vallatisporites verrucosus*–*Retusotriletes incohatus*) miospore zone (Heal and Clayton, 2008).

Material and methods

The material basis of this study – three samples of the Upper Devonian Saverton Shale and three of the Lower Mississippian Hannibal Shale – was collected along the bluff at Atlas South, Pike County, Illinois, U.S.A. (Fig. 1). Although neither formation is well exposed here because of a thick vegetative cover, suitable palynologic samples were obtained by digging through the ground cover and regolith.

At this location (Koenig *et al.*, 1961; stop 4 on 2nd day of fieldtrip), the exposed Saverton Shale is 12.9 m thick, and conformably overlies the Grassy Creek Shale, and underlies the 1.1 m-thick Glen Park Limestone, a silty, dolomitic limestone (Fig. 1). The seemingly conformably succeeding Hannibal Shale, 17.0 m thick, is, in turn, overlain (apparently unconformably) by the Burlington Limestone (Fig. 1).

Samples 1169 ASI – 1171 ASI were collected from the greenish-grey Saverton Shale. Sample 1172 ASI, a black carbonaceous siltstone, and samples 1173 ASI

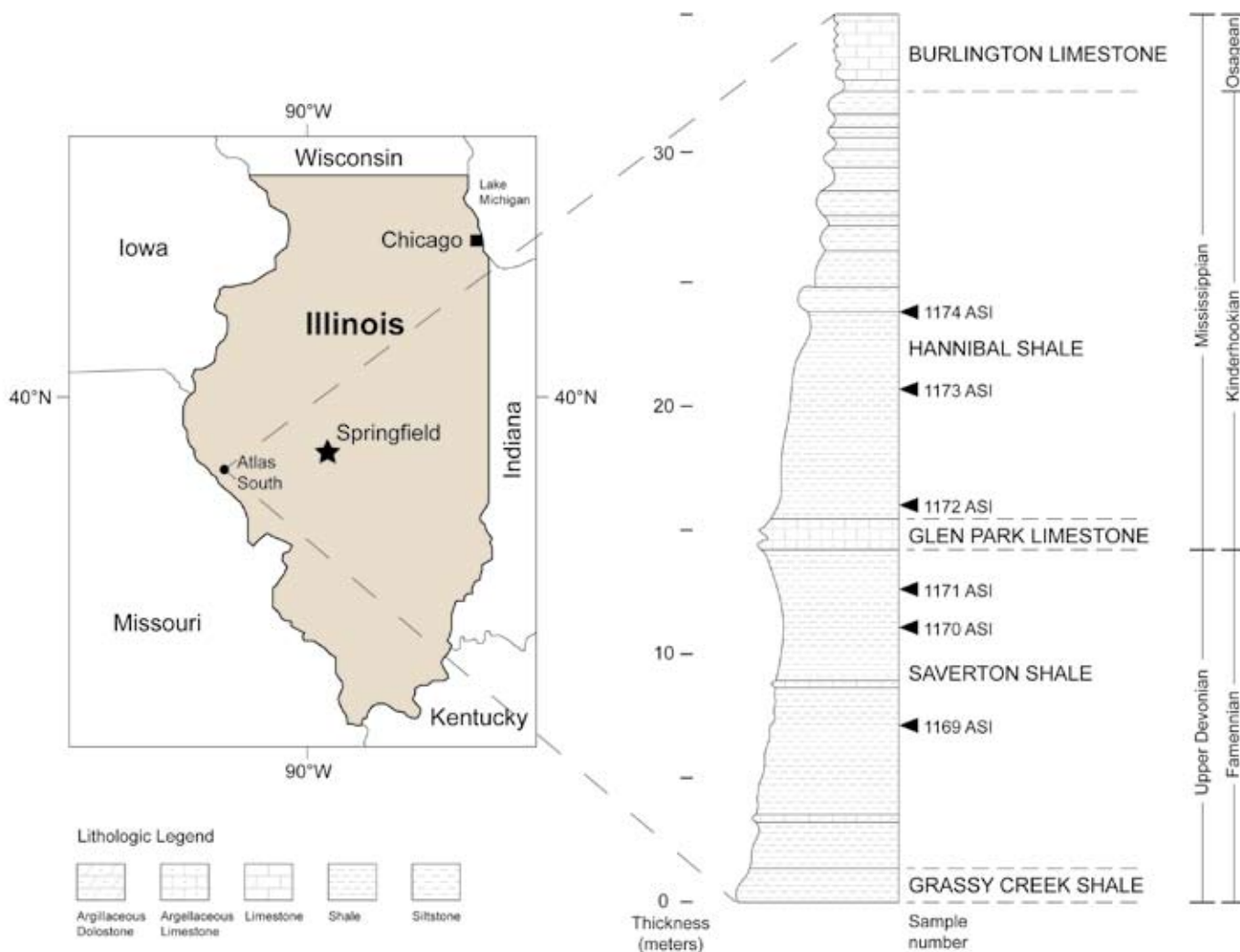


Figure 1. Locality map, Atlas South, Illinois, U.S.A., showing collecting site and stratigraphic section of the Upper Devonian Saverton Shale (Formation) and Lower Mississippian Hannibal Shale (Formation), with lithofacies and sampling levels.

Figura 1. Mapa de localización, Atlas South, Illinois, U.S.A., donde se muestran los sitios de muestreo y las secciones estratigráficas de las formaciones Pizarra Saverton (Devónico Superior) y Pizarra Hannibal (Misísipico Inferior), con niveles de litofacies y muestreo.

and 1174 ASI (both grey to greenish-grey siltstones) came from the overlying Hannibal Shale (Fig. 1).

Standard palynologic techniques were used in the preparation of the six samples. Accordingly, 25-30 g of granule-size sample were treated successively in cold 50% HCl and 40% HF, followed by a brief (~5-minutes) treatment with concentrated HNO₃, for the dissolution of carbonates, silicates, and sulphides, respectively. Samples were neutralized with distilled H₂O between each of the acid treatments. The resultant organic residues were sieved through 20 µm nylon mesh screening, and strew slides (using the same aliquot size of residue per slide) were prepared from the +20 µm and -20 µm fractions.

Eight slides each of the +20 µm organic residue fraction and one slide of the -20 µm fraction were

prepared for the three Saverton Shale samples (1169 ASI – 1171 ASI) and sample 1172 ASI of the Hannibal Shale. Five slides each of the +20 µm organic residue fraction and one slide of the -20 µm fraction were also prepared for samples 1173 ASI and 1174 ASI of the Hannibal Shale. The +20 µm and -20 µm organic residue fractions were mounted on standard microscope slides using Eukitt® as the mounting medium for light microscopy study.

A total of 250 specimens (consisting of acritarchs, prasinophyte phycmata, and miospores) from the +20 µm fraction were counted per sample to determine and compare relative abundances of palynomorph taxa in the six analyzed samples (Fig. 2). After 250 specimens were counted (the number of slides needed to reach 250 specimens ranged from one to three), the remain-

ing +20 µm slides were visually scanned to ensure that all palynomorph taxa preserved in each sample were recorded. An examination of the -20 µm fraction slide for each sample was done as a precautionary measure to ensure that all palynomorph taxa were recovered.

The leiospherids and tasmanitids were not included in the 250-specimen count per sample because of their abundance. Their presence (qualitatively expressed as rare, common, and abundant) is, however, noted in Figure 2.

Light photomicrographs were taken using an Olympus BH2 microscope with Nomarski differential interference contrast illumination, and equipped with an automatic photomicrograph system. Specimens were photographed using Kodak color print 35 mm ISO 400 film and Fuji color print 35 mm ISO 400 film.

All holotypes and other figured specimens are deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A. and are assigned catalogue numbers CM19159 through CM19255. The numbers prefixing the CMNH catalog numbers refer to the particular sample and slide number, and the on-slide location of each specimen is specified via coordinates of a standard England Finder slide. The appendix contains the curatorial information on the figured specimens (Plates 1-6).

Systematic paleontology

The palynomorphs recovered are placed systematically into four broad groups. These are (1) prasinophyte cysts (phycomata), (2) algae *incertae sedis* (acritarchs), (3) miospores (<200 µm in diameter), and (4) scolecodonts (chitinous mouthpart elements of marine annelid worms). The first three groups are documented in the following systematic section, whereas the presence of the scolecodonts is simply noted (Fig. 2). In addition, plant fragments and amorphous organic matter, in varying amounts, are also present in the palynologic residues. Preservation of the palynomorphs ranges from poor to good, with many showing the effects of pyrite degradation and oxidation.

Figure 2. Distribution of prasinophyte, acritarch, and miospore species within the Saverton Shale and Hannibal Shale at Atlas South, Illinois. Percentages of species are based on 250 specimens counted per sample (excluding leiospherids and tasmanitids). For the leiospherids and tasmanitids, the qualitative designations are: abundant (A), common (C), and rare (R).

Figura 2. Distribución de especies de prasinofitos, acritarcos y miosporas dentro de las formaciones Pizarra Shale y Pizarra Hannibal en Atlas South, Illinois. Los porcentajes de especies se basan en 250 especímenes por muestra (excluyendo leiosféridos y tasmanitidos). Para los leiosféridos y tasmanitidos las designaciones cualitativas son: abundante (A), común (C) y rara (R).

Age	Late Devonian			Early Mississippian		
	Formation			Hannibal Shale		
Sample number	1169	1170	1171	1172	1173	1174
	ASI	ASI	ASI	ASI	ASI	ASI
Prasinophyte species						
<i>Cymatiosphaera ambotrocha</i>	1.2	0.8	-	-	-	-
<i>C. antera</i>	0.8	-	-	-	-	-
<i>C. chelina</i>	1.2	1.2	0.4	-	-	-
<i>C. parvicarina</i>	1.6	2.8	0.4	-	-	-
<i>C. perimembrana</i>	1.6	1.6	1.2	-	-	-
<i>C. scitula</i>	2.4	1.6	1.6	-	-	-
<i>Leiosphaeridia</i> spp.	A	A	C	C	C	R
<i>Muraticavea enteichia</i>	4.8	0.8	3.2	-	-	-
<i>Polyedryxium embudum</i>	10.0	5.2	16.8	-	-	-
<i>P. pharaone</i>	0.8	-	0.4	-	-	-
<i>Tasmanites</i> spp.	A	C	C	R	R	R
Acritarch species						
<i>Baltisphaeridium distentum</i>	5.2	8.4	12.0	-	-	-
<i>Barathrisphaeridium chagrinese</i>	0.8	0.8	-	-	-	-
<i>Estiastra culcita</i>	0.8	0.8	-	-	-	-
<i>Gorgonisphaeridium absitum</i>	0.8	2.0	0.4	-	-	-
<i>G. elongatum</i>	2.0	1.2	1.2	-	-	-
<i>G. ohioense</i>	10.0	13.6	10.0	1.2	-	-
<i>G. plerispinosum</i>	1.2	1.6	0.4	-	-	-
<i>G. savertonense</i>	1.6	1.6	2.8	-	-	-
<i>G. winslowiae</i>	0.8	0.4	0.8	-	0.4	-
<i>Lophosphaeridium segregum</i>	0.8	0.4	-	-	-	-
<i>Micrhystridium adductum</i>	1.2	0.4	1.6	-	-	-
<i>M. stellatum</i>	10.4	9.6	14.0	4.0	14.8	14.4
<i>M. sp. cf. M. pentagonale</i>	2.4	4.8	5.2	-	4.8	3.2
<i>M. spp.</i>	3.6	6.4	4.4	90.8	75.6	80.0
<i>Multiplicisphaeridium ramusculosum</i>	0.8	0.8	-	-	-	-
<i>Navifusa bacilla</i>	0.4	0.4	0.4	-	-	-
<i>Puteoscortum polyankistrum</i>	3.2	2.0	0.4	-	-	-
<i>P. sprucegovense</i>	2.0	1.6	0.8	-	-	-
<i>Stellinium comptum</i>	0.8	0.4	0.4	-	-	-
<i>S. micropolygonale</i>	2.0	1.6	1.2	-	-	0.4
<i>Unellium elongatum</i>	1.2	2.4	0.8	-	-	-
<i>U. winslowiae</i>	1.2	0.8	-	-	-	-
<i>Veryhachium arcarium</i>	0.4	0.4	-	-	-	-
<i>V. cymosum</i>	0.8	0.4	0.4	-	-	-
<i>V. europaeum</i>	3.6	2.4	0.8	-	-	-
<i>V. polyaster</i>	0.4	-	-	-	-	-
<i>V. trispinosum</i> "complex"	3.6	4.0	0.4	-	0.4	-
Miospore species						
<i>Punctatisporites hannibalensis</i>	2.8	5.2	3.2	1.6	1.2	1.2
<i>Retusotriletes incohatus</i>	2.8	2.0	1.2	1.2	1.6	0.4
<i>Convruccosporites</i> sp. A	0.4	0.8	0.8	-	-	-
<i>Verrucosporites nitidus</i>	0.4	0.8	0.8	0.4	-	-
<i>V. sp. A</i>	0.8	-	0.8	0.4	0.8	-
<i>Emphanisporites rotatus</i>	0.4	-	0.4	-	-	-
<i>Indotriradites explanatus</i>	0.4	-	0.4	-	-	-
<i>Vallatisporites hystricosus</i>	0.8	1.2	0.4	-	-	-
<i>Ancyrospora</i> sp. cf. <i>A. langii</i>	-	-	0.4	-	-	-
<i>Geminospora</i> sp. A	0.4	-	1.6	-	-	-
<i>Auroraspora macra</i>	1.2	2.4	3.6	0.4	0.4	0.4
<i>Grandispora cornuta</i>	2.0	1.2	0.8	-	-	-
<i>Retispora lepidophyta</i>	0.8	2.8	3.2	-	-	-
<i>Teichertospora torquata</i>	0.4	0.4	-	-	-	-

The prasinophyte phycmata are arranged alphabetically under the Class Prasinophyceae Christensen, 1962. The acritarchs are also arranged alphabetically by genera under the informal *incertae sedis* "group" name Acritarcha (Evitt, 1963), and are treated as form genera and species following the provisions of the International Code of Botanical Nomenclature (ICBN; McNeill *et al.*, 2012). Morphologic terminology for the microphytoplankton follows Williams *et al.* (2000).

The suprageneric, form-classificatory ("Turma") scheme introduced by Potonié and Kremp (1954), and modified by subsequent authors, is utilized for the miospore systematics. Thus, miospore genera and species are, like the acritarchs, treated purely as morphotaxa established under ICBN regulations (McNeill *et al.*, 2012). Descriptive spore-morphological terminology accords with that employed by such authors as Kremp (1965), Smith and Butterworth (1967), Playford and Dettmann (1996), and Traverse (2007).

A complete synonymy is not provided for most species. Instead, the original binomial name (basionym) and any subsequent generic transfers are listed. For those taxa with extensive citations, reference to a complete synonymy is given. In some cases, a description incorporates supplementary morphologic information. Relevant dimensions for all species are specified, as are the number of specimens measured. Where three numerical values are given, the first is the minimum value, the second (in parenthesis) is the arithmetic mean, and the third is the maximum value measured.

Prasinophyte phycmata

Division CHLOROPHYTA Pascher, 1914
Class PRASINOPHYCEAE Christensen, 1962

Genus *Cymatiosphaera* O. Wetzel, 1933 ex Deflandre, 1954

Cymatiosphaera ambotrocha Wicander and Loeblich, 1977
Plate 1, Figs. 1, 2

1977 *Cymatiosphaera ambotrocha* Wicander and Loeblich, pp. 135-136; Pl. 1, Figs. 3-6.

1978 *Cymatiosphaera peifferi* Reaugh, pp. 841-845; Pl. 95, Figs. 1-12; Text-Figs. 2-4.

Dimensions (5 specimens).- Overall diameter 52 (59) 75 μm .

Remarks.- Reaugh (1978) described a new species, *Cymatiosphaera peifferi*, that we consider con-

specific with *C. ambotrocha* Wicander and Loeblich, 1977, based on size, number of fields, and a distinctive granulate eilyma surface. In a 'Note added in press,' Reaugh (1978, p. 844) conceded that the tabulation pattern of *C. ambotrocha* is "similar to that of *C. peifferi*, the latter is slightly smaller and its holotype has a laevigate surface." In the description of *C. peifferi*, Reaugh (1978, p. 841) noted that *C. peifferi* has a laevigate to microgranulate central body. We contend that *C. peifferi* is synonymous with the earlier named *C. ambotrocha*, and that those specimens with a laevigate central body are probably the result of poor preservation due to corrosion and degradation, a condition commonly evident in the Saverton Shale specimens of *C. ambotrocha*.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- Previously reported from the Upper Devonian (Frasnian-Famennian) Antrim Shale, Indiana, U.S.A. (Wicander and Loeblich, 1977), Upper Devonian (Frasnian-Famennian) Chattanooga Shale, Tennessee (Reaugh, 1978), and Lower Mississippian Hannibal Shale (Kinderhookian), northeastern Missouri (not illustrated; Heal and Clayton, 2008). Provisionally reported from the Upper Devonian (upper Frasnian) Lime Creek Formation, Iowa (Wicander and Playford, 1985), Upper Devonian (upper Famennian-Strunian) Iquiri and Itacua formations, Bolivia (Wicander *et al.*, 2011), and Upper Devonian (Famennian) Hongguleleng Formation, China (Lu Li-chang and Wicander, 1988).

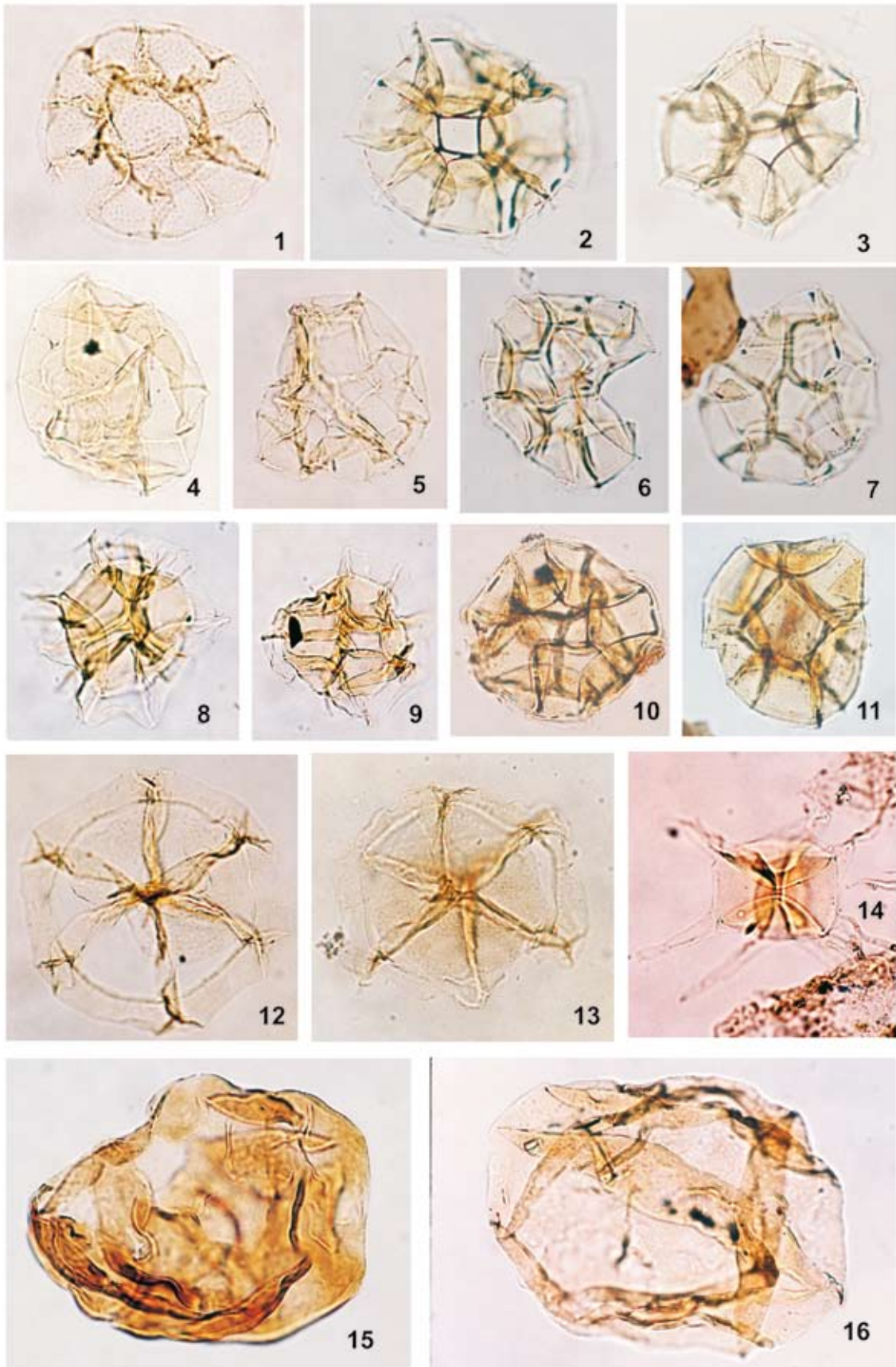
Cymatiosphaera antera Wicander and Loeblich, 1977
Plate 1, Fig. 3

1977 *Cymatiosphaera antera* Wicander and Loeblich, p. 136; Pl. 1, Figs. 7, 10-12.

Dimensions (1 specimen).- Overall diameter 53 μm .

Remarks.- In a 'Note added in press,' Reaugh (1978, pp. 844-845) compared *Cymatiosphaera antera* Wicander and Loeblich, 1977 to *C. ambotrocha* Wicander and Loeblich, 1977, and considered that two of the three illustrated specimens of Loeblich and Wicander (1977, Pl. 1, Figs. 7, 11) should be assigned to *C. ambotrocha*. We do not agree with that assessment. Reaugh (1978) further noted, and we concur, that because the holotype of *C. antera* (Loeblich and Wicander, 1977, Pl.

Plate 1. 1, 2, *Cymatiosphaera ambotrocha* Wicander and Loeblich, 1977. 1, x750; 2, x550. 3, *Cymatiosphaera antera* Wicander and Loeblich, 1977, x680. 4, 5, *Cymatiosphaera chelina* Wicander and Loeblich, 1977. 4, x620; 5, x470. 6, 7, *Cymatiosphaera parvicarina* Wicander, 1974, x550. 8, 9, *Cymatiosphaera perimembrana* Staplin, 1961. 8, x450; 9, x430. 10, 11, *Muraticavea enteichia* Wicander, 1974. 10, x400; 11, x360. 12, 13, *Cymatiosphaera scitula* Wicander and Playford sp. nov., x620. 12, holotype. 14, *Polyedryxium pharaone* Deunff, 1961, x630. 15, 16, *Leiosphaeridia* spp. 15, x720; 16, x280.



1, Figs. 10, 12) does not accord with the tabulation pattern of *C. peifferi* or *C. ambotrocha*, they are probably not conspecific.

Occurrence.- Saverton Shale, sample 1169 ASI.

Distribution.- Previously reported from the Upper Devonian (Frasnian–Famennian) Antrim Shale, Indiana (Wicander and Loeblich, 1977).

Cymatiosphaera chelina Wicander and Loeblich, 1977
Plate 1, Figs. 4, 5

1977 *Cymatiosphaera chelina* Wicander and Loeblich, p. 137; Pl. 2, Figs. 5, 6.

Dimensions (5 specimens).- Overall diameter 45 (58) 65 µm.

Remarks.- Specimens of *Cymatiosphaera chelina* Wicander and Loeblich, 1977 from the Saverton Shale are, on average, nearly twice as large as those reported by Wicander and Loeblich (1977) in their original description of this species from the Upper Devonian Antrim Shale, Indiana. However, the Saverton Shale specimens are only slightly larger than those described and illustrated from the Upper Devonian Lime Creek Formation, Iowa (Wicander and Playford, 1985), and the specimen illustrated by Heal and Clayton (2008, p. 35; Pl. 1, Fig. 9) from the Lower Mississippian Hannibal Shale, northeastern Missouri. Despite preservational factors, the reticulocristate nature of the eilyma wall can still be discerned under high-power oil immersion, and the netlike nature of the diaphanous, laevigate, low, narrow ridges is clearly evident.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Prior records from the Upper Devonian (Frasnian–Famennian) Antrim Shale, Indiana (Wicander and Loeblich, 1977), Upper Devonian (upper Frasnian) Lime Creek Formation, Iowa (Wicander and Playford, 1985), and Lower Mississippian (Kinderhookian) Hannibal Shale, northeastern Missouri (Heal and Clayton, 2008).

Cymatiosphaera parvicarina Wicander, 1974
Plate 1, Figs. 6, 7

1974 *Cymatiosphaera parvicarina* Wicander, p. 13; Pl. 7, Figs. 10-12.

Dimensions (11 specimens).- Overall diameter 43 (61) 75 µm.

Remarks.- The present specimens are, on average, somewhat larger than those reported elsewhere.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Known hitherto from the Upper Devonian (upper Famennian) Chagrin Shale, Ohio (Wicander, 1974), Upper Devonian (Frasnian–Famennian) Antrim Shale, Indiana (Wicander and Loeblich, 1977), and Upper Devonian (Famennian) Hongguleleng Formation, China (Lu Li-chang and Wicander, 1988); and provisionally from the Upper Devonian (upper Frasnian) Lime Creek Formation, Iowa (Wicander and Playford, 1985) and Lower Mississippian (Kinderhookian) Hannibal Shale, northeastern Missouri (unillustrated; Heal and Clayton, 2008).

Cymatiosphaera perimembrana Staplin, 1961
Plate 1, Figs. 8, 9

1961 *Cymatiosphaera perimembrana* Staplin, p. 417; Pl. 49, Figs. 16, 17.

1977 *Cymatiosphaera platoloma* Wicander and Loeblich, p. 140; Pl. 3, Figs. 3, 4.

For further synonymy see Hashemi and Playford (1998, p. 130).

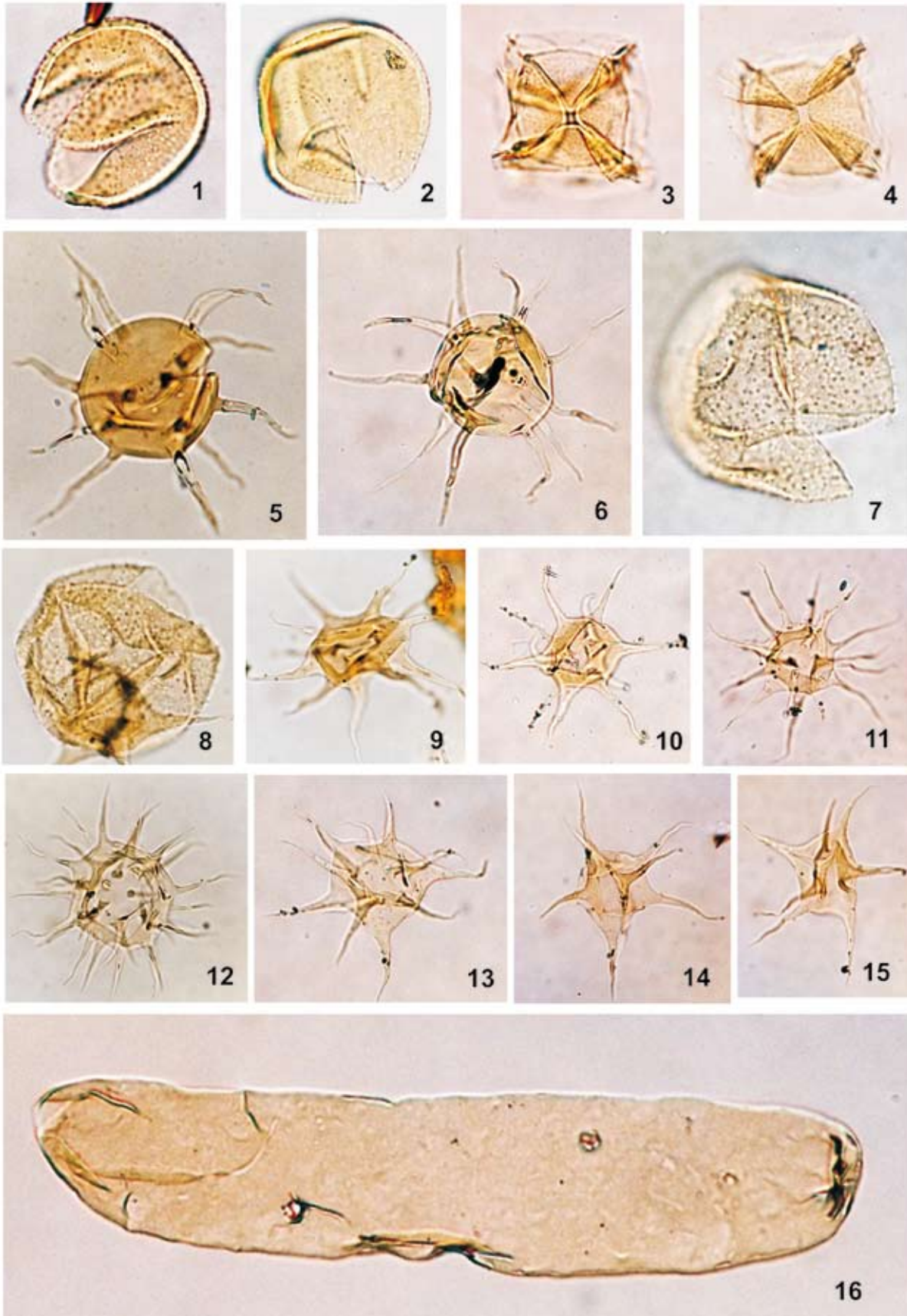
Dimensions (13 specimens).- Overall diameter 60 (68) 80 µm.

Remarks.- Specimens of *Cymatiosphaera perimembrana* Staplin, 1961 from the Saverton Shale are mostly much larger than those reported previously. However, our specimens clearly fit the expanded and detailed description of *C. perimembrana* by Hashemi and Playford (1998, p. 130), as well as matching their illustrated specimens (Pl. 1, Figs. 5-7).

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Widely distributed in Frasnian–Famennian strata from North America, Europe, the Middle East, and China; Frasnian of Australia; uppermost Devonian-possibly basal Mississippian of the Middle East; and ?Middle–Upper Devonian of South America (see Wicander and Playford, 1985; Lu-Li chang and Wicander, 1988; Playford and McGregor, 1993; Hashemi and Playford, 1998; Pereira *et al.*, 2008).

Plate 2. 1, 2, *Tasmanites* spp., x700. 3, 4, *Polyedryxium embudum* Cramer, 1964. 3, x560; 4, x500. 5, 6, *Baltisphaeridium distentum* Playford, 1977. 5, x690; 6, x560. 7, 8, *Lophosphaeridium segregum* Playford, 1981. 7, x1000; 8, x750. 9, 10, *Micrhystridium adductum* Wicander, 1974. 9, x700; 10, x560. 11, 12, *Micrhystridium stellatum* Deflandre, 1945. 11, x610; 12, x600. 13-15, *Micrhystridium* sp. cf. *M. pentagonale* Stockmans and Willièrè, 1963. 13, x640; 14, x550; 15, x560. 16, *Navifusa bacilla* (Deunff, 1955) Playford, 1977, x720.



Cymatiosphaera scitula Wicander and Playford sp. nov.
Plate 1, Figs. 12, 13

Diagnosis.- Vesicle circular to subcircular in outline; surface divided into six distinct, triangular fields (lacunae), delineated by thin, ± wrinkled, diaphanous, laevigate muri (3-10 µm high) emanating from vesicle center to periphery, where they distally bifurcate; lacunae floors faintly granulate, grana evenly spaced, equidimensional, up to 1 µm in height and basal diameter. No excystment structure observed.

Dimensions (11 specimens).- Overall diameter 35 (45) 60 µm.

Holotype.- Sample 1171 ASI, slide 6, England Finder V25/4; Pl. 1, Fig. 12. Vesicle circular in outline, 53 µm in diameter; eilyma divided into six triangular fields with partially granulate lacunae by diaphanous, laevigate muri, 3-4 µm high, radiating from vesicle center to peripheral bifurcation; no excystment structure present.

Type locality.- Illinois, Atlas South section, Saverton Shale, 5.8 m above Grassy Creek Shale.

Name derivation.- Latin, *scitulus*, elegant, neat.

Remarks.- Lacunae floors are frequently corroded, such that only a laevigate or partially granulate surface remains. *Cymatiosphaera scitula* sp. nov. somewhat resembles *C. turbinata* Wicander and Loeblich, 1977 (p. 141; Pl. 3, Figs. 5-7) in appearance, but the characteristic six triangular lacunae, prescribed by distally bifurcating muri, distinguish it from *C. turbinata* and other species of *Cymatiosphaera*.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Genus *Leiosphaeridia* Eisenack, 1958

Leiosphaeridia spp.
Plate 1, Figs. 15, 16

Dimensions (7 specimens).- Overall diameter 63-228 µm.

Remarks.- Numerous specimens of *Leiosphaeridia* Eisenack, 1958 are present throughout the Saverton Shale and Hannibal Shale. Because of their simple, laevigate, spherical morphology and wide size range, we are not speciating them, but simply noting their occurrence as part of the palynoflora. We are, howev-

er, illustrating examples of the two forms most commonly encountered.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI, 1174 ASI.

Distribution.- Widely reported globally from the Proterozoic to Recent.

Genus *Muraticavea* Wicander, 1974

Muraticavea enteichia Wicander, 1974
Plate 1, Figs. 10, 11

1974 *Muraticavea enteichia* Wicander, p. 14; Pl. 15, Figs. 1-3.

Dimensions (14 specimens).- Overall diameter 70 (88) 100 µm.

Remarks.- *Muraticavea* Wicander, 1974 was originally described as having a reticulocrystate surface divided into several fields formed by folding of the vesicle wall, thus producing high ridges. The lack of ridges protruding from the vesicle periphery distinguishes this genus from *Cymatiosphaera* O. Wetzel, 1933 ex Deflandre, 1954 (Wicander, 1974, p. 14).

Numerous specimens recovered from all three Saverton Shale samples display the reticulocrystate surface, number and distribution of fields, and size range of *Muraticavea enteichia* Wicander, 1974. Furthermore, many of the specimens also feature what appears to be a diaphanous ridge extending beyond the vesicle, but which is, in fact, an optical view through the folded vesicle eilyma.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Reported previously from the Upper Devonian (upper Famennian) Chagrin Shale, Ohio (Wicander, 1974).

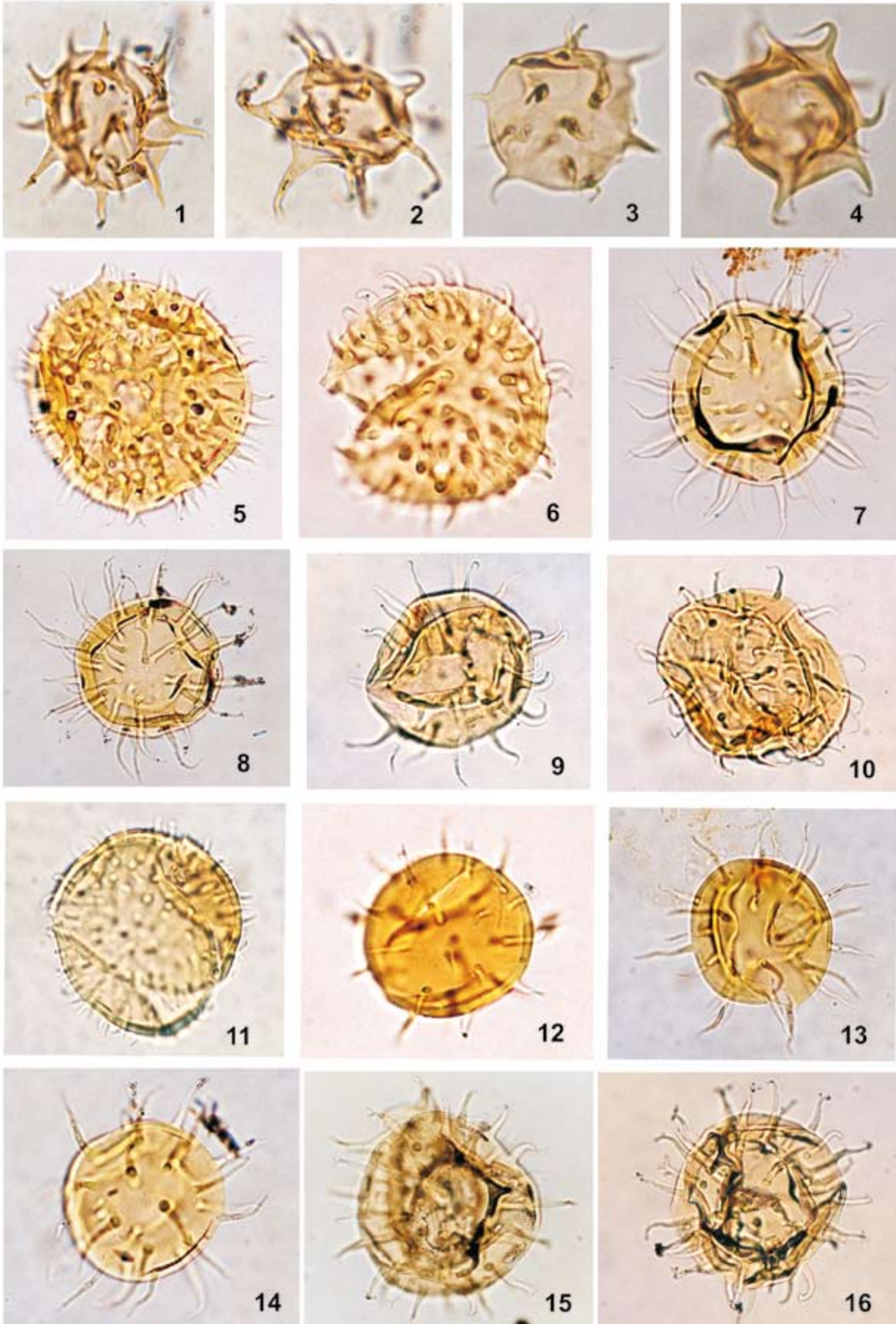
Genus *Polyedryxium* Deunff, 1954 ex Deunff, 1961

Polyedryxium embudum Cramer, 1964
Plate 2, Figs. 3, 4

1964 *Polyedryxium embudum* Cramer, pp. 318-319; Fig. 32(5).

1966 *Polyedryxium nudatum* Deunff, pp. 91-92; Pl. 13, Fig. 150.

Plate 3. 1-4, *Micrhystridium* spp. 1, x850; 2, 3, x860; 4, x950. 5, 6, *Gorgonisphaeridium absitum* Wicander, 1974. 5, x680; 6, x600. 7, 8, *Gorgonisphaeridium elongatum* Wicander, 1974. 7, x440; 8, x420. 9, 10, *Gorgonisphaeridium ohioense* (Winslow, 1962) Wicander, 1974. 9, x420; 10, x500. 11, *Gorgonisphaeridium plerispinosum* Wicander, 1974, x850. 12-14, *Gorgonisphaeridium savertonense* Wicander and Playford sp. nov. 12, holotype, x840; 13, x660; 14, x810. 15, 16, *Gorgonisphaeridium winslowiae* Staplin, Jansonius, and Pocock, 1965. 15, x420; 16, x410.



Dimensions (15 specimens).- Sides of vesicle 33 (38) 45 µm in length; membranous ridge 2.5 (6) 10 µm in height; overall diameter 43 (50) 58 µm.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- *Polyedryxium embudum* Cramer, 1964 has a stratigraphic range of Pragian–Famennian, and has been reported from North America, South America, Europe, the Middle East, China, and Australia (see Lu Li-chang and Wicander, 1988; Ottone, 1996; and Ghavidel-syooki, 1994 for occurrences in the aforementioned regions).

Polyedryxium pharaone Deunff, 1961
Plate 1, Fig. 14

1961 *Polyedryxium pharaonis* Deunff, p. 217.
For extensive synonymy, see Wicander and Wood (1981, pp. 28-29).

Dimensions (3 specimens).- Vesicle side length 29, 34, 45 µm; process length 25-28 µm; process width 5-13 µm.

Occurrence.- Saverton Shale, samples 1169 ASI, 1171 ASI.

Remarks.- Although rare, and usually poorly preserved, the specimens here recorded are unequivocally *Polyedryxium pharaone* Deunff, 1961.

Distribution.- Widely disseminated in North America, South America, North Africa, the Middle East, Europe, and China, with a stratigraphic range of Pragian–Famennian (Playford and McGregor, 1993; Hashemi and Playford, 1998).

Genus *Tasmanites* Newton, 1875

Tasmanites spp.
Plate 2, Figs. 1, 2

Dimensions (10 specimens).- Overall diameter 36-92 µm.

Remarks.- *Tasmanites* spp. occur abundantly in the Saverton Shale and Hannibal Shale samples as simple, thick-walled, punctate specimens.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI, 1174 ASI.

Distribution.- This genus is globally dispersed, ranging from Proterozoic through Holocene.

Acritarchs

Group ACRITARCHA Evitt, 1963

Genus *Baltisphaeridium* Eisenack, 1958 ex Eisenack, 1959 emend. Eisenack, 1969

Baltisphaeridium distentum Playford, 1977
Plate 2, Figs. 5, 6

1977 *Baltisphaeridium distentum* Playford, pp. 12-13; Pl. 1, Figs. 13, 14; Pl. 2, Figs. 1-5; Text-Fig. 4.

1993 *Baltisphaerosum* sp. A of Playford and McGregor, pp. 12-13; Pl. 3, Figs. 3, 4.

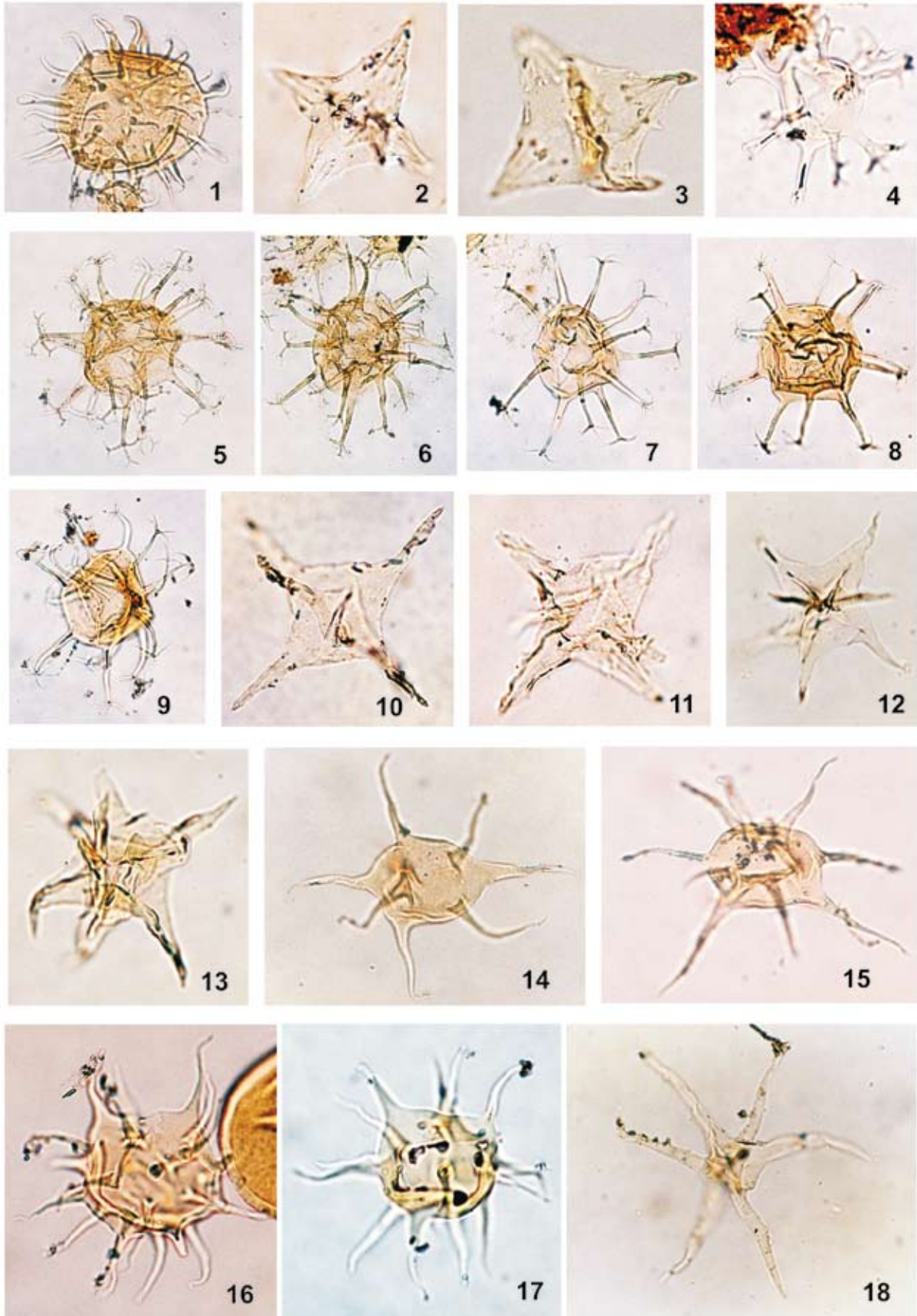
1996 *Baltisphaerosum distentum* (Playford, 1977) Ottone, pp. 121-122; Pl. 4, Fig. 8.

For further synonymy see Ottone (1996, p. 121).

Dimensions (37 specimens).- Vesicle diameter 30 (35) 48 µm; eilyma thickness 1-2 µm; process length 18 (27) 40 µm; process basal width 2 (3.5) 5 µm; process basal plug 1-2 µm; 8 (13) 21 processes.

Remarks.- Specimens of this species show a wide range of preservation. Many display extensive corrosion and degradation, particularly in the processes where they seemingly are partially to wholly infilled, thus appearing solid. However, in moderately- to well-preserved specimens, it is obvious they are hollow with a thickened basal plug that prevents free communication with the vesicle interior. The eilyma is laevigate to slightly scabrate under light microscopy, with the process surfaces laevigate, conforming to the original description by Playford (1977). The only difference between the Saverton Shale specimens and those described and illustrated previously is that they have a mostly larger vesicle. However, the present specimens have the same vesicle diameter and process length size range as *Baltisphaerosum* sp. A of Playford and McGregor (1993) from the Upper Devonian (Famennian) Bakken Formation of eastern Canada.

Plate 4. 1, *Barathrisphaeridium chagrinese* Wicander, 1974, x330. 2, 3, *Estiastra culcita* Wicander, 1974, x550; 3, x710. 4, *Multiplicisphaeridium ramusculosum* (Deflandre, 1945) Lister, 1970, x750. 5, 6, *Puteosortum polyankistrum* Wicander and Loeblich, 1977, x370; 6, x360. 7-9, *Puteosortum sprucegrovense* (Staplin, 1961) Wicander and Playford comb. nov. 7, x470; 8, x400; 9, x420. 10, 11, *Stellinium comptum* Wicander and Loeblich, 1977, x580; 11, x680. 12, 13, *Stellinium micropolygonale* (Stockmans and Willièrè, 1960) Playford, 1977, x450; 13, x670. 14, 15, *Unellium elongatum* Wicander, 1974, x610; 15, x600. 16, 17, *Unellium winslowiae* Rauscher, 1969, x850; 17, x1000. 18, *Veryhachium polyaster* Staplin, 1961, x670.



Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Previously reported from the Pragian–Strunian of North America (Playford, 1977; Wicander and Wood, 1981; Wicander and Wright, 1983; Wood and Clendening, 1985; Wood, 1986; Playford and McGregor, 1993) and Givetian–Strunian of South America (Barreda, 1986; Ottone, 1996; Wicander *et al.*, 2011).

Genus *Barathrisphaeridium* Wicander, 1974

Barathrisphaeridium chagrinese Wicander, 1974
Plate 4, Fig. 1

1974 *Barathrisphaeridium chagrinese* Wicander, p. 17; Pl. 5, Figs. 3, 4.

Dimensions (2 specimens).- Vesicle diameter 45, 73 μm ; eilyma thickness 1.5-2.0 μm ; process length 8-22 μm ; process basal width 1.5-3.5 μm ; foveolae diameter 1.0-1.5 μm ; 34-46 processes.

Remarks.- The presence of a distinctively foveolate eilyma easily differentiates this genus from the morphologically similar *Gorgonisphaeridium* Staplin, Jansonius, and Pocock, 1965, even when specimens are poorly preserved.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- Known from the Upper Devonian of Ohio, thus: Chagrín Shale (upper Famennian), Cleveland Shale (Strunian), and Bedford Shale (Strunian) (Wicander, 1974).

Genus *Estiastra* Eisenack, 1959

Estiastra culcita Wicander, 1974
Plate 4, Figs. 2, 3

1974 *Estiastra culcita* Wicander, p. 23; Pl. 10, Figs. 7-9.

Dimensions (4 specimens).- Vesicle diameter 23, 26, 27 μm ; process length 10 (14) 23 μm ; process basal width 5 (9) 13 μm ; overall diameter from process tip to process tip 48, 48, 48, 60 μm ; 6-10 processes.

Remarks.- These specimens, although slightly larger overall, fit the circumscription of *Estiastra culcita*

Wicander, 1974. Because of preservational factors, the grana of the eilyma and of the processes are not always distinct, and the distal tips of the processes frequently display minor longitudinal folding.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- The only previous record is from the Upper Devonian (upper Famennian) Chagrín Shale, Ohio (Wicander, 1974).

Genus *Gorgonisphaeridium* Staplin, Jansonius, and Pocock, 1965

Gorgonisphaeridium absitum Wicander, 1974
Plate 3, Figs. 5, 6

1974 *Gorgonisphaeridium absitum* Wicander, p. 25; Pl. 11, Figs. 10-12.

Dimensions (5 specimens).- Vesicle diameter 53 (56) 58 μm ; eilyma thickness 1.5-2.0 μm ; process length 5.0 (7.5) 10 μm ; process basal width 2.0-2.5 μm ; 62 (68) 72 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Widely reported from Upper Devonian (Frasnian–Famennian) strata in North America, Europe, and China (Lu-Li chang and Wicander, 1988).

Gorgonisphaeridium elongatum Wicander, 1974
Plate 3, Figs. 7, 8

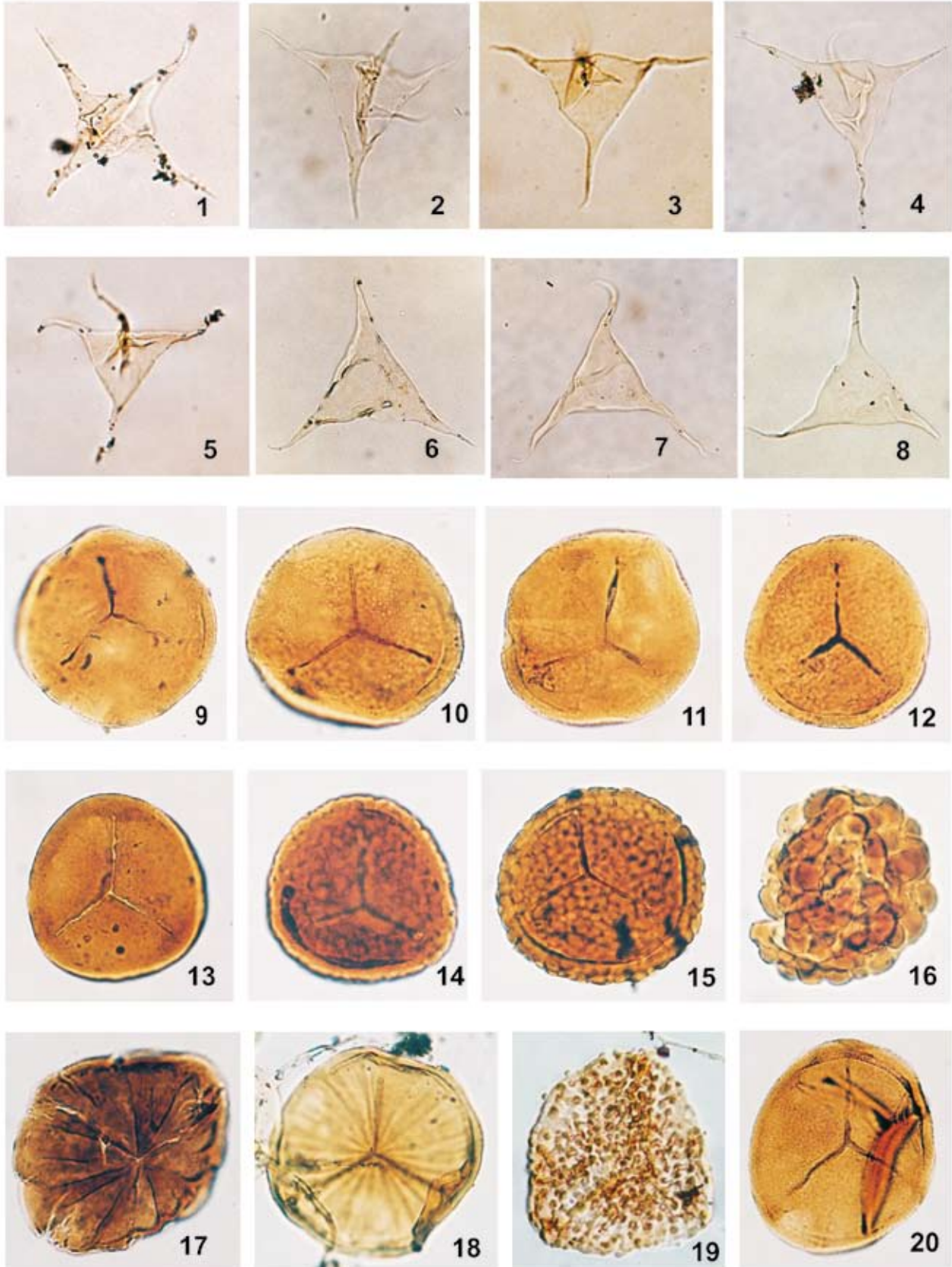
1974 *Gorgonisphaeridium elongatum* Wicander, p. 25; Pl. 12, Figs. 1-3.

Dimensions (13 specimens).- Vesicle diameter 53 (59) 68 μm ; eilyma thickness 2.0 μm ; process length 18 (24) 30 μm ; process basal width 2.5 μm ; 28 (36) 46 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Known hitherto from the Upper Devonian (Frasnian–Famennian) of North America (Wicander, 1974; Wicander and Loeblich, 1977), and provisionally from the Upper Devonian (Famennian) of China (Lu-Li chang and Wicander, 1988).

Plate 5. 1, *Veryhachium arcarium* Wicander and Loeblich, 1977, x620. 2, 3, *Veryhachium cymosum* Wicander and Loeblich, 1977. 2, x660; 3, x600. 4, 5, *Veryhachium europaeum* Stockmans and Willièrè, 1960, x500. 6-8, *Veryhachium trispinosum* (Eisenack, 1938) Stockmans and Willièrè, 1962 "complex." 6, x440; 7, x550; 8, x590. 9-12, *Punctatisporites hannibalensis* Wicander and Playford sp. nov., median foci. 9, x580; 10, x550; 11, x600; 12, holotype, x500. 13, *Retusotriletes incohatus* Sullivan, 1964, proximal focus, x500. 14, 15, *Verrucosisporites* sp. A. 14, median focus, x600; 15, proximal focus, x650. 16, *Verrucosisporites nitidus* Playford, 1964, distal focus, x650. 17, 18, *Emphanisporites rotatus* McGregor, 1961 emend. McGregor, 1973, median foci. 17, x800; 18, x680. 19, *Convrrucosisporites* sp. A, distal focus, x550. 20, *Geminospora* sp. A, near-proximal focus; x500.



Gorgonisphaeridium ohioense (Winslow, 1962)

Wicander, 1974

Plate 3, Figs. 9, 10

1962 *Hystriosphæridium ohioensis* Winslow, p. 77; Pl. 19, Fig. 1; Pl. 22, Fig. 9.

1974 *Gorgonisphaeridium ohioense* (Winslow) Wicander, p. 26; Pl. 12, Figs. 7-9.

Dimensions (24 specimens).- Vesicle diameter 53 (63) 68 µm; eilyma thickness 2.0-2.5 µm; process length 10 (13) 20 µm; process basal width 2.0-2.5 µm; 40 (52) 62 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, sample 1172 ASI.

Distribution.- Cosmopolitan in Upper Devonian (upper Frasnian–Strunian) and possibly Tournaisian strata (see Playford, 1993, p. 146; Playford and McGregor, 1993, p. 14; González *et al.*, 2005, p. 66).

Gorgonisphaeridium plerispinosum Wicander, 1974

Plate 3, Fig. 11

1974 *Gorgonisphaeridium plerispinosum* Wicander, p. 26; Pl. 12, Figs. 10-12.

Dimensions (10 specimens).- Vesicle diameter 33 (42) 48 µm; eilyma thickness 1.0-1.5 µm; process length 2.0-2.5 µm; process basal width 1.0-1.5 µm; >100 processes.

Remarks.- These specimens display simple, distal process tips, consistent with previously reported occurrences, except those of Wicander and Loeblich (1977, p. 145, Pl. 6, Fig. 14), which have uncommonly "slightly bifurcated" processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Widely dispersed in the Upper Devonian (Frasnian–Famennian) of North America, North Africa, Europe, the Middle East, and China (Hashemi and Playford, 1998; González *et al.*, 2005; Pereira *et al.*, 2008).

Gorgonisphaeridium savertonense Wicander and

Playford sp. nov.

Plate 3, Figs. 12-14

Diagnosis.- Vesicle originally spherical, outline circular to subcircular. Eilyma 1.0-1.5 µm thick, laevigate

to scabrate (under high-power oil immersion). Processes numerous, distinct from vesicle, and evenly distributed over vesicle surface; processes solid, homomorphic, laevigate, tapering from a circular base to simple, acuminate distal tip. Excystment by splitting of eilyma.

Dimensions (12 specimens).- Vesicle diameter 28 (35) 41 µm; process length 10 (13) 22 µm; process basal width 1.0 (2) 2.5 µm; 17 (21) 29 processes.

Holotype.- Sample 1169 ASI, slide 7, England Finder H33/4; Pl. 3, Fig. 12. Vesicle circular in outline, 32 µm in diameter; eilyma ca. 1.5 µm thick, laevigate; 29 distinct, evenly distributed, solid, laevigate processes, 1.0-1.5 µm in basal diameter, 7-9 µm long, tapering to acuminate distal tip; excystment by splitting of eilyma.

Type locality.- Illinois, Atlas South section, Saverton Shale, 5.8 m above Grassy Creek Shale.

Name derivation.- After the Saverton Shale.

Remarks.- Although some specimens superficially resemble *Gorgonisphaeridium ohioense* (see above), *G. savertonense* sp. nov. has a smaller ratio of average vesicle diameter to process length (2.7 vs. 4.8) and fewer processes than *G. ohioense*. Furthermore, *G. savertonense* has a slightly larger ratio of average vesicle diameter to process length (2.7 vs. 2.5) and fewer processes, on average, than *Gorgonisphaeridium elongatum*.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Gorgonisphaeridium winslowiae Staplin, Jansonius

and Pocock, 1965

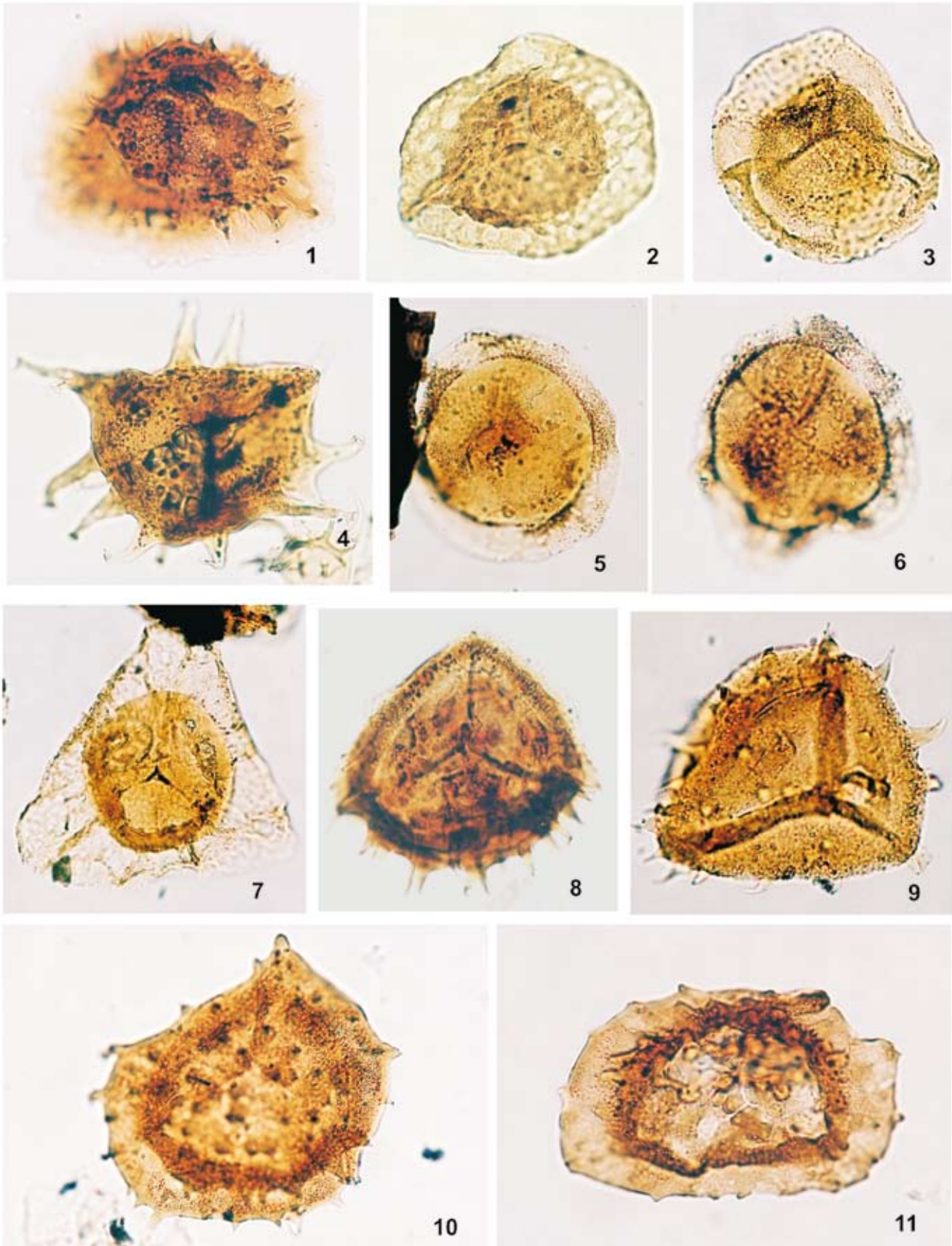
Plate 3, Figs. 15, 16

1965 *Gorgonisphaeridium winslowii* Staplin, Jansonius and Pocock, p. 193; Pl. 19, Figs. 11, 18-20; Text-Fig. 4.

Dimensions (7 specimens).- Vesicle diameter 58 (66) 75 µm; eilyma thickness 2 µm; process length 10 (14) 20 µm; process basal width 2 µm; 35-38 processes.

Remarks.- Playford and McGregor (1993, pp. 15-16; Text-Fig. 5) provided an expanded diagnosis that takes into account the heteromorphic distal termini of the processes, which are predominantly furcate, ranging

Plate 6. 1, *Vallatisporites hystricosus* (Winslow, 1962) Wicander and Playford comb. nov., distal focus, x750. 2, 3, *Retispora lepidophyta* (Kedo, 1957) Playford, 1976. 2, median focus, x720; 3, near-proximal focus, x750. 4, *Ancyrospora* sp. cf. *A. langii* (Taugourdeau-Lanz, 1960) Allen, 1965, proximal-equatorial aspect, x650. 5, 6, *Auroraspora macra* Sullivan, 1968, median foci, x800. 7, *Teichertospora torquata* (Higgs, 1975) emend. McGregor and Playford, 1990, proximal-median focus, x520. 8, 9, *Grandispora cornuta* Higgs, 1975 emend. Higgs, Prestianni, Streel, and Thorez, 2013, median foci. 8, x750; 9, x950. 10, 11, *Indotriradites explanatus* (Luber in Luber and Waltz, 1941) Playford, 1991, median foci. 10, x760; 11, x920.



from bifurcate to multifurcate, but also occasionally simple, tapering to a pointed to rounded distal tip.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hanibal Shale, sample 1173 ASI.

Distribution.- Famennian and possibly Mississippian of North America, North Africa, and Europe [Playford and McGregor, 1993; Heal and Clayton, 2008 (un-illustrated)].

Genus *Lophosphaeridium* Timofeev, 1959
ex Downie, 1963

Lophosphaeridium segregum Playford, 1981
Plate 2, Figs. 7, 8

1981 *Lophosphaeridium segregum* Playford in Playford and Dring, pp. 44-45; Pl. 11, Figs. 17-19; Pl. 12, Fig. 17; Text-Fig. 8.

Dimensions (3 specimens).- Vesicle diameter 40, 43, 45 μm ; process length and basal width $\leq 1 \mu\text{m}$.

Remarks.- The Saverton Shale specimens are larger than those originally diagnosed (Playford and Dring, 1981), but are the same size as those reported by Wicander and Playford (1985).

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- From the Upper Devonian (Frasnian) of Europe, Iowa, and Australia (Le Hérissé and Deunff, 1988; Wicander and Playford, 1985; Playford and Dring, 1981), and Upper Devonian (Frasnian-Famennian) of the Middle East (Ghavidel-syooki and Owens, 2007).

Genus *Micrhystridium* Deflandre, 1937

Micrhystridium adductum Wicander, 1974
Plate 2, Figs. 9, 10

1974 *Micrhystridium adductum* Wicander, p. 27; Pl. 13, Figs. 7-9.

Dimensions (3 specimens).- Vesicle diameter 15, 18, 25 μm ; process length 15 (20) 23 μm ; process basal width 2.0-2.5 μm ; 9 (11) 12 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Upper Devonian (upper Famennian), Ohio (Wicander, 1974), and Upper Devonian (Frasnian-Famennian), Indiana (Wicander and Loeblich, 1977).

Micrhystridium stellatum Deflandre, 1945
Plate 2, Figs. 11, 12

1945 *Micrhystridium stellatum* Deflandre, p. 65; Pl. 3, Figs. 16-19.

Dimensions (16 specimens).- Vesicle diameter 18 (24) 28 μm ; process length 13 (16) 23 μm ; process basal width 2.0-2.5 μm ; 14 (19) 28 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI, 1174 ASI.

Distribution.- This morphologically simple and generalized form category, as recognized here and by numerous previous authors, is cosmopolitan in distribution, and stratigraphically long-ranging (Ordovician-Mesozoic).

Micrhystridium sp. cf. *M. pentagonale* Stockmans and Willièrè, 1963
Plate 2, Figs. 13-15

cf. 1963 *Micrhystridium pentagonale* Stockmans and Willièrè, pp. 470-471; Pl. 3, Fig. 18; Text-Fig. 32.

Dimensions (7 specimens).- Vesicle diameter 15 (19) 23 μm ; process length 13 (16) 20 μm ; process basal width 2.5 μm ; 8-12 processes, 5 processes co-planar, 3-7 not in same plane.

Remarks.- The Saverton Shale specimens accord with those discussed and illustrated by Playford and Dring (1981) and Hashemi and Playford (1998) as *Micrhystridium* sp. cf. *M. pentagonale* Stockmans and Willièrè, 1963. We are placing our specimens in this provisional assignment because the original diagnosis of *M. pentagonale* by Stockmans and Willièrè (1963) was very brief, and their illustrated specimens were poorly preserved.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1173 ASI, 1174 ASI.

Distribution.- Prior reports from the Upper Devonian (Frasnian) of Australia and Iran (Playford and Dring, 1981; Hashemi and Playford, 1998).

Micrhystridium spp.
Plate 3, Figs. 1-4

Dimensions (10 specimens).- Vesicle diameter 18 (22) 25 μm ; process length 5 (12) 15 μm ; process basal width ca. 2.0-2.5 μm ; 12 (17) 21 processes.

Remarks.- Those specimens, not readily attributable to named species of *Micrhystridium* Deflandre, 1937, are consequently placed here in open nomenclature.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI, 1174 ASI.

Genus *Multiplicisphaeridium* Staplin, 1961 emend. Staplin, Jansonius, and Pocock, 1965

Multiplicisphaeridium ramusculosum (Deflandre, 1945) Lister, 1970
Plate 4, Fig. 4

1945 *Hystrichosphaeridium ramusculosum* Deflandre, p. 63; Pl. 1, Figs. 8-16; Text-Figs. 38, 39.

1961 *Multiplicisphaeridium ramispinosum* Staplin, p. 411; Pl. 48, Fig. 24; Text-Fig. 9g-h.

1970 *Multiplicisphaeridium ramusculosum* (Deflandre, 1945) Lister, pp. 92-93; Pl. 11, Figs. 8, 11-14; Text-Fig. 25a.

1974 *Multiplicisphaeridium anastomosis* Wicander, p. 29; Pl. 14, Figs. 7-9.

For additional synonymy see Wicander and Wood (1981, pp. 50-51) and Hashemi and Playford (1998, pp. 159-160).

Dimensions (4 specimens).- Vesicle diameter 18, 20, 23, 28 μm ; 13 (16) 20 μm ; process basal width 2.5 (3.5) 5.0 μm ; 7-11 processes.

Remarks.-We follow Lu Li-chang and Wicander (1988, p. 125) in adopting a broad interpretation of *Multiplicisphaeridium ramusculosum* (Deflandre, 1945) Lister, 1970 to include the type species *M. ramispinosum* Staplin, 1961 and *M. anastomosis* Wicander, 1974, as well as subsequent attributions to these two species. For additional synonymy and discussion of the possible differences between *M. ramusculosum* and *M. ramispinosum*, see Martin (1981, pp. 22-24; 1982, p. 4) and Colbath (1990, p. 125).

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- *Multiplicisphaeridium ramusculosum*, as here recognized, is a cosmopolitan species that ranges from Upper Ordovician through Upper Devonian.

Genus *Navifusa* Combaz, Lange and Pansart, 1967

Navifusa bacilla (Deunff, 1955) Playford, 1977
Plate 2, Fig. 16

1955 *Leiofusa bacillum* Deunff, p. 148; Pl. 4, Fig. 2.

1977 *Navifusa bacillum* (Deunff) Playford, pp. 29-30; Pl. 12, Figs. 1-9.

For further synonymy, see Fatka and Brocke (2008).

Dimensions (2 specimens).- Vesicle length 138, 185 μm ; vesicle width 33, 40 μm .

Remarks.- The Saverton Shale specimens have a laevigate to slightly scabrate eilyma, with no evidence of grana.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- A cosmopolitan Devonian (Emsian-Famennian) species (Le Herisse *et al.*, 2000).

Genus *Puteoscortum* Wicander and Loeblich, 1977

1977 *Puteoscortum* Wicander and Loeblich, p. 148.

1981 *Craterisphaeridium* Deunff, p. 67.

Remarks.- *Craterisphaeridium* Deunff, 1981 is clearly congeneric with *Puteoscortum* Wicander and Loeblich, 1977, both featuring foveo-reticulate eilyma, together with hollow processes that freely communicate with the vesicle interior, are enlarged basally, and furcate distally into solid branches. A translation of Deunff's (1981, p. 67) original diagnosis by Turner (1986, p. 602) specified that "the surfaces of the processes bear a series of ring-like ridges from base to top." As noted by Turner (1986), the specimens of *Craterisphaeridium sprucegrovense* (Staplin, 1961) Turner, 1986 lack the ring-like ridges, as do several specimens of the type species of *Craterisphaeridium*.

We do not consider the presence of ring-like ridges on the processes to be a sufficient criterion to separate *Craterisphaeridium* from *Puteoscortum*; hence the latter is accorded priority over the former.

Puteoscortum polyankistrum Wicander and Loeblich, 1977
Plate 4, Figs. 5, 6

1977 *Puteoscortum polyankistrum* Wicander and Loeblich, pp. 148-149; Pl. 8, Figs. 1-4.

Dimensions (15 specimens).- Vesicle diameter 38 (45) 58 μm ; process length 13 (19) 24 μm ; process basal width 2.5 (3.5) 5.0 μm ; 10 (15) 21 processes.

Remarks.- The Saverton Shale specimens are clearly conspecific with *Puteoscortum polyankistrum* Wicander and Loeblich, 1977, and distinct from *P. sprucegrovense* (Staplin, 1961) Wicander and Playford comb. nov. (see below) in displaying multi-order distal branching.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Reported from the Upper Devonian (Frasnian-Famennian) Antrim Shale of Indiana (Wicander and Loeblich, 1977), and uppermost Devonian

(Strunian) Berea Sandstone of Ohio (Molyneux *et al.*, 1984).

Puteoscortum sprucegroense (Staplin, 1961)
Wicander and Playford comb. nov.
Plate 4, Figs. 7-9

1961 *Multiplicisphaeridium? sprucegroense* Staplin, p. 411; Pl. 48, Fig. 22; Pl. 49, Fig. 6; Text-Fig. 9j.

1986 *Craterisphaeridium sprucegroense* (Staplin, 1961) Turner, pp. 602, 606; Pl. 1, Figs. 1-6; Pl. 2, Figs. 1-4.

For further synonymy and discussion, see Turner (1986).

Dimensions (8 specimens).- Vesicle diameter 30 (37) 43 μm ; process length 17 (21) 25 μm ; process basal width 2.5-3.0 μm ; 12 (14) 18 processes.

Remarks.- Turner (1986) transferred *Multiplicisphaeridium? sprucegroense* Staplin, 1961 to *Craterisphaeridium* on the basis of its foveolate vesicle surface (eilyma). He reillustrated Staplin's (1961) specimens and provided excellent SEM and light photomicrographs of topotype material. Turner (1986) thereby demonstrated the foveolate nature of the eilyma; the hollow processes that open into, and freely communicate with the vesicle interior; and the distal branching of the processes into "long, slender, tapering, flexible, solid filaments whose points of origin all lie in a single plane," and are 3 (5) 6 in number.

Turner (1986) further discussed the seeming confusion between (a) the single-order distal branching that produces tapering, flexible, solid branches, that arise in a single plane, and is found only in *Puteoscortum sprucegroense* comb. nov.; and (b) other species with the same eilyma sculpture (foveolate), but display multi-order distal branching, such as *P. williereiae* Martin, 1981.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Previously reported from the Upper Devonian (Frasnian-Famennian) of Europe (Deunff, 1981; Martin, 1981, 1982, 1985; Vanguetaine *et al.*, 1983; Le Hérisse and Deunff, 1988), and China (Lu Lichang and Wicander, 1988).

Genus *Stellinium* Jardiné, Combaz, Magloire,
Peniguel, and Vachey, 1972

Stellinium comptum Wicander and Loeblich, 1977
Plate 4, Figs. 10, 11

1977 *Stellinium comptum* Wicander and Loeblich, pp. 151-152; Pl. 9, Figs. 1-6.

Dimensions (3 specimens).- Vesicle diameter 23, 24, 25 μm ; process length 13 (16) 23 μm ; process basal width 5-7 μm ; 6-7 processes.

Remarks.- Although Colbath (1990, p. 131) raised the possibility of *Stellinium comptum* Wicander and Loeblich, 1977 and *S. micropolygonale* (Stockmans and Willièrè, 1960) Playford, 1977 being synonymous, these two species are easily separated on the basis of vesicle shape (quadrate vs. polyhedral outline) and number and arrangement of the processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Widely reported from the Givetian-Famennian, and possibly lowermost Mississippian of North America; Givetian-Frasnian, South America; Frasnian-Famennian, Middle East; Frasnian-Tournaisian, Europe; and Frasnian-Famennian, China (Playford and McGregor, 1993; Hashemi and Playford, 1998; Pereira *et al.*, 2008).

Stellinium micropolygonale (Stockmans and Willièrè, 1960) Playford, 1977
Plate 4, Figs. 12, 13

1960 *Micrhystridium micropolygonale* Stockmans and Willièrè, p. 4; Pl. 1, Fig. 12.

1961 *Veryhachium octoaster* Staplin, pp. 413-414; Pl. 49, Figs. 3, 4.

1962 *Veryhachium vandenbergheni* Stockmans and Willièrè, pp. 86-87; Pl. 2, Figs. 11, 13; Figs. 5a, b. [1962b]

1977 *Stellinium micropolygonale* (Stockmans and Willièrè) Playford, p. 36; Pl. 18, Figs. 7-9.

For further synonymy see Wicander and Wood (1981, pp. 57-58).

Dimensions (12 specimens).- Vesicle diameter 20 (25) 28 μm ; process length 15 (20) 25 μm ; process basal width 5 (6) 8 μm ; overall diameter from process tip to process tip 50 (62) 75 μm ; 8 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, sample 1174 ASI.

Distribution.- Common and widely distributed in the northern and southern hemispheres with a stratigraphic range of Pragian-Famennian, and possibly lowermost Mississippian (Wicander and Wood, 1981; Playford and McGregor, 1993; González *et al.*, 2005).

Genus *Unellium* Rauscher, 1969

Unellium elongatum Wicander, 1974
Plate 4, Figs. 14, 15

1974 *Unellium elongatum* Wicander, p. 35; Pl. 18, Figs. 10-12.

Dimensions (8 specimens).- Vesicle diameter 20 (23) 25 µm x 23 (27) 30 µm; length of major processes 20 (27) 30 µm; basal width of major processes 2 (3.8) 5 µm; length of minor processes 18 (25) 28 µm; basal width of minor processes 2 (2.5) 3 µm; 2 major processes, 5 (7) 9 minor processes.

Remarks.- The specimens from the Saverton Shale are comparable in size to those diagnosed by Wicander (1974). The only discernible difference is that the present specimens have fewer minor processes (5-9 vs. 11-16).

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Prior reports are from the Upper Devonian (upper Famennian–Strunian) of Ohio (Wicander, 1974; Molyneux *et al.*, 1984).

Unellium winslowiae Rauscher, 1969
Plate 4, Figs. 16, 17

1969 *Unellium winslowae* Rauscher, p. 36; Figs. 7-13.
1977 *Unellium cornutum* Wicander and Loeblich, pp. 153-154; Pl. 8, Figs. 5-12.

Dimensions (5 specimens).- Vesicle diameter 16 (20) 25 µm x 19 (23) 27 µm; length of major processes 9 (13) 18 µm; basal width of major processes 2 (3) 4 µm; length of minor processes 7 (12) 15 µm; basal width of minor processes 1-2 µm; 2 major processes, 9 (17) 24 minor processes.

Remarks.- We concur with Lu Li-chang and Wicander (1988, p. 129) and Playford and McGregor (1993, p. 19) in regarding *Unellium cornutum* Wicander and Loeblich, 1977 as conspecific with *U. winslowiae* Rauscher, 1969.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- Upper Devonian (Frasnian–Strunian) of North America; ?Middle Devonian–Upper Devonian (Famennian) of Europe; Frasnian of Australia; and Upper Devonian (Famennian) of China (Lu Li-chang and Wicander, 1988; Playford and McGregor, 1993).

Genus *Veryhachium* Deunff, 1954 ex Downie,
1959 emend. Sarjeant and Stancliffe, 1994

Veryhachium arcarium Wicander and Loeblich, 1977
Plate 5, Fig. 1

1977 *Veryhachium arcarium* Wicander and Loeblich, p. 154; Pl. 10, Figs. 1, 2.

Dimensions (2 specimens).- Vesicle diameter 13, 15 µm; process length 20-23 µm; process basal width 3-4 µm; 6 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI.

Distribution.- Upper Devonian (Frasnian–Famennian) of Indiana (Wicander and Loeblich, 1977); Upper Devonian (upper Frasnian) of Iowa (Wicander and Playford, 1985); and Upper Devonian (Famennian) of China (Lu Li-chang and Wicander, 1988).

Veryhachium cymosum Wicander and Loeblich, 1977
Plate 5, Figs. 2, 3

1977 *Veryhachium cymosum* Wicander and Loeblich, p. 155; Pl. 10, Figs. 5-10.

Dimensions (2 specimens).- Vesicle diameter 18, 20 µm; process length 15-18 µm; supplementary process length 10-18 µm; 2 supplementary processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Upper Devonian (Frasnian) of Indiana and Iowa (Wicander and Loeblich, 1977; Wicander and Playford, 1985).

Veryhachium europaeum Stockmans and Willièrè, 1960
Plate 5, Figs. 4, 5

1960 *Veryhachium europaeum* Stockmans and Willièrè, p. 3; Pl. 2, Fig. 25.

1962 *Veryhachium legrandi* Stockmans and Willièrè, p. 54; Pl. 1, Figs. 3, 4; Text-Figs. 11a, b. [1962a]

Dimensions (6 specimens).- Vesicle diameter 15 (20) 25 µm; process length 13 (19) 25 µm; process basal width 2.5-3.0 µm; supplementary process length 13 (18) 25 µm; supplementary process basal width 2.5-3.0 µm; 3 major processes, 1-2 supplementary processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Cosmopolitan species, ranging from Silurian through Devonian (Lu Li-chang and Wicander, 1988).

Veryhachium polyaster Staplin, 1961
Plate 4, Fig. 18

1961 *Veryhachium polyaster* Staplin, p. 413; Pl. 49, Fig. 20.

1961 *Veryhachium polyaster* var. *hexaster* Staplin, p. 413; Pl. 49, Fig. 19.

Dimensions (1 specimen).- Vesicle diameter 13 µm; process length 25-28 µm; process basal width 3-5 µm; 6 processes.

Occurrence.- Saverton Shale, sample 1169 ASI.

Distribution.- Cosmopolitan species in Pragian through Famennian strata (Playford and McGregor, 1993; Ottone, 1996). Unillustrated record by Heal and Clayton (2008) from the Hannibal Shale.

Veryhachium trispinosum (Eisenack, 1938)
Stockmans and Willièrè, 1962 "complex"
Plate 5, Figs. 6-8

1938 *Hystrichosphaeridium trispinosum* Eisenack, p. 14, 16; Text-Figs. 2, 3.

1962 *Veryhachium trispinosum* (Eisenack) Stockmans and Willièrè, pp. 46-47; Pl. II, Figs. 25, 26; Text-Fig. 1. [1962a]

For a complete synonymy and discussion of this informal taxonomic grouping ("complex"), see Wicander and Wood (1981) and Servais *et al.* (2007).

Dimensions (12 specimens).- Vesicle diameter 15 (22) 35 µm; process length 13 (23) 38 µm; process basal width 2.0-2.5 µm; 3 processes.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI, 1174 ASI.

Distribution.- Globally distributed in Ordovician through Permian strata (Wicander and Wood, 1981).

Miospores

Anteturma PROXIMEGERMINANTES R. Potonié, 1970
Turma TRILETES Reinsch, 1881 emend. Dettmann, 1963
Suprasubturma ACAVATITRILETES Dettmann, 1963
Subturma AZONOTRILETES Lubert, 1935 emend.
Dettmann, 1963

Infraturma LAEVIGATI Bennie and Kidston, 1886
emend. R. Potonié, 1956

Genus *Punctatisporites* Ibrahim, 1933 emend.
R. Potonié and Kremp, 1954

Punctatisporites hannibalensis Wicander and Playford sp. nov.
Plate 5, Figs. 9-12

1962 *Punctatisporites* sp. A of Winslow, pp. 60-61; Pl. 17, Figs. 13, 15.

Diagnosis.- Spores radial, trilete, with circular to convexly subtriangular amb. Laesurae distinct, simple, ± straight, length two-thirds to three-quarters of amb radius. Exine 3.5-4.5 µm thick, laevigate to scabrate.

Dimensions (16 specimens).- Equatorial diameter 42 (51) 61 µm.

Holotype.- Sample 1172 ASI, slide 7, England Finder Q31/2; Pl. 5, Fig. 12. Amb subcircular, diameter 60 µm; laesurae distinct, three-quarters of spore radius in length; exine faintly scabrate, 3.7 µm thick.

Type locality.- Illinois, Atlas South section, Hannibal Shale, 1.5 m above Glen Park Limestone.

Name derivation.- After the Hannibal Shale.

Remarks.- The specimens are prone to corrosion, resulting in a fine, "peppery" surficial appearance. They are clearly consonant with the three specimens described by Winslow (1962) as *Punctatisporites* sp. A. Although a number of morphologically similar species of the genus have been described from North American Upper Devonian–Mississippian successions, the present specimens could not positively be attributed to any one of them and are therefore instituted here as *Punctatisporites hannibalensis* sp. nov. For instance, among the species described by Hacquebard (1957) from the Lower Mississippian of Nova Scotia, Canada, *P. planus* is thinner walled than *P. hannibalensis* and its amb is invariably circular-subcircular; *P. solidus* features laesurate lips; and *P. viriosus* is larger and thinner walled with a circular-subcircular amb.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI.

Distribution.- Uppermost Devonian (Strunian)–lowermost Mississippian (Kinderhookian) of Ohio: Cleveland Shale (also known as the upper member of Ohio Shale), Bedford Shale, and Sunbury Shale (Winslow, 1962).

Infraturma RETUSOTRILETI Streeel, *in* Becker, Bless, Streeel and Thorez, 1974

Genus *Retusotriletes* Naumova, 1953 emend. Streeel, 1964

Retusotriletes incohatus Sullivan, 1964
Plate 5, Fig. 13

1964 *Retusotriletes incohatus* Sullivan, pp. 1251-1252; Pl. 1, Figs. 5-7.

1974 *Aneurospora incohata* (Sullivan) Streeel, *in* Becker, Bless, Streeel, and Thorez, p. 24; Pl. 14, Fig. 4.

Dimensions (10 specimens).- Equatorial diameter 41 (51) 67 µm.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, samples 1172 ASI, 1173 ASI, 1174 ASI.

Distribution.- Commonly reported, particularly from the northern hemisphere, in uppermost Devonian through Lower Mississippian deposits, including the Hannibal Shale (Heal and Clayton, 2008).

Infraturma APICULATI Bennie and Kidston, 1886
emend. R. Potonié, 1956

Subinfraturma VERRUCATI Dybová and Jachowicz,
1957

Genus *Converrucosporites* R. Potonié and Kremp,
1954

Converrucosporites sp. A
Plate 5, Fig. 19

Description.- Spores radial, trilete. Amb subtriangular with rounded apices and convex to ± straight sides. Laesurae ± straight, almost attaining equator, flanked by indistinct, narrow, membranous lips. Exine ca. 2 µm thick; distal surface sculptured conspicuously with both discrete and basally coalescent verrucae having subcircular-rounded polygonal bases 1.5-2.5 µm in diameter; verrucae 1.5 µm high, with obtuse to almost flat apices, distribution somewhat irregular, relatively sparse in equatorial region. Proximal exine essentially laevigate.

Dimensions (2 specimens).- Equatorial diameter, excluding sculpture, 57, 61 µm.

Remarks.- This form closely resembles *Punctatisporites? logani*, as described by Winslow (1962, p. 61; Pl. 18, Figs. 17-19), but differs in sculptural detail insofar as the verrucae evidently lack the "terminal distal apiculi" specified by Winslow.

Occurrence.- Saverton Shale, samples 1169 ASI, 1171 ASI.

Genus *Verrucosporites* Ibrahim, 1933 emend. Smith and Butterworth, 1967

Verrucosporites nitidus Playford, 1964
Plate 5, Fig. 16

1964 *Verrucosporites nitidus* Playford, pp. 13-14; Pl. III, Figs. 3-6.

non 2002 *Verrucosporites nitidus*; Jäger, Pl. 1, Fig. 18. [no description]

For additional synonymy, discussion, and typification, see Turnau *et al.* (1994).

Dimensions (3 specimens).- Equatorial diameter 48, 52, 67 µm (including sculpture).

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, sample 1172 ASI.

Distribution.- Numerous authors have reported this species worldwide, from successions ranging through the Upper Devonian–Mississippian interval, including the Hannibal Shale (Heal and Clayton, 2008).

Verrucosporites sp. A
Plate 5, Figs. 14, 15

Description.- Spores radial, trilete. Amb circular to very broadly rounded subtriangular. Laesurae distinct, simple, straight, length 0.7-0.8 of spore radius. Exine 3.5-4.8 µm thick; densely sculptured distally and proximo-equatorially with very low, closely packed verrucae, both discrete and basally coalescent; height of verrucae <1.2 µm, bases subcircular or irregularly rounded, 1.5-4.5 µm in diameter. Contact faces laevigate-scabrate or with sparse, minute verrucae and grana.

Dimensions (3 specimens).- Equatorial diameter 48, 51, 61 µm (including sculpture).

Remarks.-The thick exine, bearing low, dense, pavement-like sculpture – the verrucate elements of which are defined by a very fine negative reticulum – distinguishes this form from other members of the genus, including *Verrucosporites nitidus* Playford, 1964.

Occurrence.- Saverton Shale, samples 1169 ASI, 1171 ASI.

Infraturma MURORNATI R. Potonié and Kremp, 1954

Genus *Emphanisporites* McGregor, 1961

Emphanisporites rotatus McGregor, 1961 emend.
McGregor, 1973
Plate 5, Figs. 17, 18

For synonymy see McGregor (1973, pp. 46-47) and Balme (1988a, p. 131).

Dimensions (2 specimens).- Equatorial diameter 44, 48 µm.

Remarks.- The two figured specimens (both from the Saverton Shale, sample 1171 ASI) exhibit, respectively, relatively robust and more subdued radial ribbing; i.e., within the infraspecific sculptural variation that is exemplified by, *inter alia*, Balme's (1988a, Pl. 6, Figs. 6-9) photomicrographs.

Occurrence.- Saverton Shale, samples 1169 ASI, 1171 ASI.

Distribution.- Known extensively from strata spanning most of the Devonian (Balme, 1988a, p. 132).

Suprasubturma LAMINATRILETES Smith and Butterworth, 1967

Subturma ZONOLAMINATRILETES Smith and Butterworth, 1967

Infraturma CINGULICAVATI Smith and Butterworth, 1967

Genus *Indotriradites* Tiwari, 1964 emend. Foster, 1979

Indotriradites explanatus (Luber in Luber and Waltz, 1941) Playford, 1991
Plate 6, Figs. 10, 11

1941 *Zonotriletes explanatus* Luber in Luber and Waltz, p. 10; Pl. 1, Fig. 4.

1991 *Indotriradites explanatus* (Luber) Playford, pp. 103-104; Pl. 3, Figs. 17, 18.

2005 *Kraeuselisporites explanatus* (Luber in Luber and Waltz, 1941) Azcuy and di Pasquo, p. 173.

For additional synonymy see Higgs *et al.* (1988, p. 79), Playford (1991, p. 103), and Playford and McGregor (1993, p. 32).

Dimensions (6 specimens).- Overall equatorial diameter 57 (69) 80 μm ; diameter of exoexinal cavity (polar view) 45 (51) 62 μm .

Remarks.- The few specimens encountered are readily identifiable with *Indotriradites explanatus* (Luber in Luber and Waltz, 1941) Playford, 1991, exhibiting the following main diagnostic features: cavate, zonate exine; darker inner part of zona of cuesta-like appearance; wider outer part of zona may in part be radially strutted or striated; exoexine sculpture essentially distal and consisting mostly of coni and short spinae, with some verrucae and pila; and intexine only slightly separated from exoexine. Higgs *et al.* (1988) and Playford (1991) provide more detail.

Occurrence.- Saverton Shale, samples 1169 ASI, 1171 ASI.

Distribution.- A near-cosmopolitan species reported by numerous authors from strata collectively ranging from uppermost Devonian (Strunian) through Mississippian (upper Tournaisian or lower Visean): Playford (1991, 1993).

Genus *Vallatisporites* Hacquebard, 1957

Vallatisporites hystricosus (Winslow, 1962) Wicander and Playford comb. nov.
Plate 6, Fig. 1

1962 *Cirratriradites hystricosus* Winslow, pp. 41-42; Pl. 18, Fig. 5.

1962 *Cirratriradites* sp. A of Winslow, p. 42; Pl. 18, Figs. 1, 2.

Dimensions (8 specimens).- Overall equatorial diameter 58 (63) 72 μm ; spore cavity diameter, in polar view, 40 (47) 52 μm .

Remarks.- The specimens accord well with those described by Winslow (1962, as per above synonymy) and with many of those reported by previous authors as either *Vallatisporites hystricosus* (Winslow, 1962) Byvsheva, 1985 or *V. pusillites* (Kedo, 1957) Dolby and Neves, 1970. The former epithet is here adopted, because the species was more definitively circumscribed and illustrated, although it is recognized that the latter, as described originally (Kedo, 1957), is, at least in part, synonymous with Winslow's (1962) species. Despite the binomial combination *Vallatisporites hystricosus* being commonly attributed to Byvsheva (1985) – e.g., by Higgs *et al.* (2002, p. 155), Melo and Loboziak (2003, p. 185), and many others – Byvsheva (1985, p. 136) failed to comply with the dictates of the International Code of Botanical Nomenclature (ICBN; McNeill *et al.*, 2012, Article 41.1) that are requisite for establishing a new combination. Byvsheva merely cited "*Vallatisporites* (al. *Cirratriradites*) *hystricosus* (Winslow)" as an incidental mention in a paragraph concerned with "*Vallatisporites pusillites* (Kedo) Dolby et Neves emend. Byvsheva". Hence, the binomial combination *Vallatisporites hystricosus* is here formalized.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Commonly recorded from latest Devonian successions of Euramerica and Western Gondwana.

Suprasubturma PSEUDOSACCITRILETES
Richardson, 1965

Infraturma MONOPSEUDOSACCITI Smith and Butterworth, 1967

Genus *Ancyrospora* Richardson, 1960 emend.
Richardson, 1965

Ancyrospora sp. cf. *A. langii* (Taugourdeau-Lantz, 1960) Allen, 1965
Plate 6, Fig. 4

cf. 1960 *Archaeotriletes langii* Taugourdeau-Lantz, p. 145; Pl. 3, Figs. 33, 34, 39.

cf. 1965 *Ancyrospora langii* (Taugourdeau-Lantz) Allen, p. 743; Pl. 106, Figs. 5-7.

Dimensions (1 specimen).- Equatorial diameter 62 μm (excluding sculptural projections); diameter of intexine 51 μm .

Remarks.- Morphology of the single specimen, though not well preserved, approaches that of *Ancyrospora langii* (Taugourdeau-Lantz, 1960) Allen, 1965, differing chiefly in its more sparsely distributed ancyrate projections. *Ancyrospora simplex* Guennel, 1963 (p. 257; Fig. 13) reputedly features, at least predominantly, simple (non-ancyrate) spinae.

Occurrence.- Saverton Shale, sample 1171 ASI.

Distribution.- *Ancyrospora langii* (*sensu stricto*) has been widely identified in upper Middle through Upper Devonian rocks.

Genus *Geminospora* Balme, 1962

Geminospora sp. A
Plate 5, Fig. 20

Description.- Spores radial, trilete, with subcircular to very broadly rounded subtriangular amb. Cavate exine with laevigate intexine, <1 µm thick, occupying bulk of exoexinal cavity, commonly in close proximity to exoexine, the latter 2.0-3.8 µm thick and bearing very fine, dense, granulate, predominantly distal sculpture. Laesurae distinct, straight, extending *ca.* three-quarters of distance to equatorial margin, associated with narrow, undulant, elevated lips 1-2 µm high.

Dimensions (7 specimens).- Overall equatorial diameter 46 (55) 63 µm; diameter of intexine 36 (42) 52 µm.

Remarks.- The above specimens appear to be separable from previously described members of the genus, but the relatively few encountered are insufficient for designation as a new species. They differ, for instance, from the well-known type species *Geminospora lemurata* Balme, 1962 emend. Playford, 1983 (pp. 316-318; Figs. 1-9) mainly in having a finer, microgranulate exoexinal sculpture, no distinct contact faces, and differently lipped laesurate margins.

Occurrence.- Saverton Shale, samples 1169 ASI, 1171 ASI.

Genus *Auroraspora* Hoffmeister, Staplin and Malloy, 1955

Auroraspora macra Sullivan, 1968
Plate 6, Figs. 5, 6

1968 *Auroraspora macra* Sullivan, pp. 124-125; Pl. 27, Figs. 6-10.

Dimensions (21 specimens).- Overall equatorial diameter 37 (51) 67 µm; diameter of intexinal body, in polar view, 27 (37) 50 µm.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI; Hannibal Shale, sample 1172 ASI.

Distribution.- Widely disseminated in strata of latest Devonian through Mississippian age (e.g., Higgs *et al.*, 1988, 2002; Playford, 1991; Pérez Loinaze, 2008; González *et al.*, 2011; Melo and Playford, 2012), including the Hannibal Shale (Heal and Clayton, 2008).

Genus *Grandispora* Hoffmeister, Staplin, and Malloy, 1955

Grandispora cornuta Higgs, 1975 emend. Higgs, Prestianni, Streel and Thorez, 2013
Plate 6, Figs. 8, 9

1975 *Grandispora cornuta* Higgs, pp. 398-399; Pl. 4, Figs. 4-6.

2013 *Grandispora cornuta* Higgs, 1975 emend. Higgs, Prestianni, Streel, and Thorez, p. 86; Pl. 1, Figs. A-F; Pl. 3, Figs. K, N.

For further synonymy see Higgs *et al.* (2013, p. 86).

Description.- Spores radial, trilete. Amb subtriangular with rounded to ± pointed apices and convex to near-straight sides. Laesurae distinct, straight to slightly sinuous, almost attaining equatorial margin; lips membranous, conspicuous or somewhat subdued, variable in height and width. Exoexine 1.5-3.0 µm thick; sculptured distally and equatorially with coarse spinae and galeae, length 7.5-15.0 µm, bases 2.5-4.5 µm in diameter and 2-6 µm apart, elements ± uniform in size and spacing on a given specimen. Exoexine laevigate to scabrate proximally and elsewhere between spinae/galeae. Intexine ± clearly defined, laevigate, outline mostly conformable with amb, locally folded peripherally.

Dimensions (5 specimens).- Equatorial diameter 45 (54) 65 µm; diameter of intexinal body (polar view) 35 (42) 52 µm.

Comparison and remarks.- Higgs *et al.* (2013) distinguished *Grandispora cornuta* Higgs 1975 (as per their emendation) from *G. tamariae* Loboziak in Higgs *et al.*, 2000 (p. 223; Pl. VI, Figs. 5, 6, 8), the latter bearing consistently smaller apiculate sculptural elements that are normally <6 µm long; i.e., do not attain the minimum spine length (8 µm) prescribed for *G. cornuta* (see Higgs *et al.*, 2013, Fig. 4). The small cohort of coarsely sculptured specimens described above is

clearly attributable to *G. cornuta*; no specimens identifiable as *G. tamariae* were encountered.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Initially described from the LL through PC miospore Zones (late Famennian through mid Tournaisian) of Ireland (Higgs, 1975; Higgs *et al.*, 1988). Subsequently reported from correlative rocks elsewhere (González *et al.*, 2005). In eastern Belgium, Maziane *et al.* (1999) specified that the introduction of *Grandispora cornuta* (and of two other miospore species) marks the base of the Western European VCo miospore Opper Zone (Famennian Fa2c; = immediately pre-Strunian). Subsequently, however, based on their study of the upper Famennian Condruz Group in eastern Belgium, Higgs *et al.* (2013) particularized the incoming of this species, as emended, to define the base of their newly proposed *Grandispora cornuta* (Cor) miospore Interval Zone (= upper subdivision of the VCo Zone, tentatively correlated with the Middle *expansa* conodont Zone: Higgs *et al.*, 2013, Fig. 10).

Genus *Retispora* Staplin, 1960

Retispora lepidophyta (Kedo, 1957) Playford, 1976
Plate 6, Figs. 2, 3

For synonymy see Playford (1976, p. 45) and Byvsheva (1985, p. 140).

Dimensions (28 specimens).- Overall equatorial diameter 50 (60) 75 µm; diameter of intexinal body (polar view) 29 (36) 46 µm.

Remarks.- Although generally not well preserved, the present specimens are readily identifiable with *Retispora lepidophyta* (Kedo, 1957) Playford, 1976, with their distinct, laevigate intexine enveloped by exoexine that is reticulate to foveolate distally and is essentially laevigate proximally. Morphological details – fully enunciated in prior publications (e.g., Playford, 1976, 1991; Van der Zwan, 1980) – need no reiteration here.

Occurrence.- Saverton Shale, samples 1169 ASI, 1170 ASI, 1171 ASI.

Distribution.- Exceptionally widespread – virtually global – distribution and stratigraphic confinement to the latest Devonian (Famennian: Fa2d–Strunian), as documented by numerous authors. Thus, *Retispora lepidophyta* is regarded as a pre-eminent palynostratigraphic index species, its last appear-

ance marking, or approximating very closely to, the Devonian–Mississippian boundary. The durable morphology and *in-situ* abundance of the species signal its susceptibility to recycling; consequently, post-Devonian occurrences are mostly, and reasonably, ascribed to that process (see discussions in Playford and McGregor, 1993, pp. 46-47; Playford, 1993, p. 150).

Genus *Teichertospora* Balme, 1988

Teichertospora torquata (Higgs, 1975) emend.
McGregor and Playford, 1990
Plate 6, Fig. 7

1975 *Auroraspora torquata* Higgs, p. 398; Pl. 4, Figs. 1-3.

1988 *Teichertospora cuvierica* Balme, pp. 165-166; Pl. 1, Figs. 1-6; Text-Fig. 2. [1988b]

1990 *Teichertospora torquata* (Higgs) emend. McGregor and Playford, p. 12; Pl. 1, Figs. 1-7; Pl. 2, Figs. 1-9.

Dimensions (1 specimen).- Overall equatorial diameter 96 µm; diameter of intexine (polar view) 52 µm.

Remarks and occurrence.- The single specimen exhibits the triangular amb and circular inner body (intexine) that characterize *Teichertospora torquata* (Higgs, 1975) emend. McGregor and Playford, 1990. However, the endoreticulation of the exoexine – well described and well illustrated by Foster and Balme (1994) – is only vaguely evident in this imperfectly preserved specimen from the Saverton Shale (sample 1170 ASI).

Distribution.- Reported widely from Upper Devonian (Frasnian–Famennian) strata, as documented by González *et al.* (2005, p. 37).

Composition and comparison with other Late Devonian and Early Mississippian palynofloras

General features

The Upper Devonian (Famennian) Saverton Shale palynoflora consists of prasinophyte phycmata, acritarchs, miospores, and scolecodonts. The prasinophytes, distributed among five genera, comprise eight previously named species, one new species (*Cymatiosphaera scitula*), and two "spp." designations. The acritarch assemblage (12 genera) is composed of 24 established species, one new species (*Gorgonisphaeridium savertonense*), one new combination (*Puteo-*

scortum sprucegrovense), one "cf." and one "spp." designation. The miospore palynoflora (13 genera) contains eight recognized species, one new species (*Punctatisporites hannibalensis*), one new combination (*Vallatisporites hystricosus*), one "cf." designation, and three informally named species (sp. A).

In contrast, the samples from the Lower Mississippian (Kinderhookian) Hannibal Shale feature a much-reduced palynomorph assemblage including only two prasinophyte taxa (*Leiosphaeridia* spp. and *Tasmanites* spp.), five recognized acritarch species, one "cf." designation, and one "spp." assignment, all of which are distributed among four genera. The Hannibal's scant miospore representation comprises just three established species, together with the aforementioned *Punctatisporites hannibalensis* sp. nov.; these belong to four genera and all have also been identified in the subjacent Saverton Shale samples. Both scolecodonts and amorphous organic matter are present in varying amounts in both formations.

The prasinophyte taxa *Leiosphaeridia* spp. and *Tasmanites* spp. occur consistently in the studied samples of both the Saverton Shale and Hannibal Shale (Fig. 2). Because of their abundance and lack of speciation, we are only noting their occurrence in Figure 2.

In quantitative terms, the acritarchs dominate the Saverton palynomorph assemblage (prasinophytes, acritarchs, and miospores), comprising, on average, for the three analyzed samples (1169ASI – 1171 ASI), 63.2% of the total assemblage (not counting the leiospherids and tasmanitids), whereas the prasinophytes average 20.8%, and the miospores 16.0% (Fig. 2). As previously mentioned, there is a significant reduction in both diversity and abundance for the three studied samples (1172 ASI – 1174 ASI) of the Hannibal Shale. Except for *Leiosphaeridia* spp. and *Tasmanites* spp., which were not counted because of their abundance, no other prasinophytes were encountered in the Hannibal Shale samples. Thus, excluding *Leiosphaeridia* spp. and *Tasmanites* spp., the acritarchs comprise, on average, 96.7% of the Hannibal's palynomorph assemblage, with the miospores accounting for the remaining 3.3% (Fig. 2).

Excluding *Leiosphaeridia* spp. and *Tasmanites* spp., the Saverton Shale prasinophytes are distributed among three genera (*Cymatiosphaera*, *Muraticavea*, and *Polyedryxium*) with *Polyedryxium embudum* making up, on average, 51.3% of the prasinophyte assemblage, followed by *Muraticavea enteichia* at 14.1%, and the other seven species fairly evenly divided among the remaining 34.6% (Fig. 2).

Within the Saverton Shale acritarch assemblage, there are six species assigned to *Gorgonisphaeridium*, five species of *Veryhachium*, four species of

Micrhystridium, two species each of *Puteoskortum*, *Stellinium*, and *Unellium*, and one species each of the remaining six genera. The two most abundant species are *Micrhystridium stellatum* (17.9% average) and *Gorgonisphaeridium ohioense* (17.7% average), followed by *Baltisphaeridium distentum* (13.5%), *Micrhystridium* spp. (7.6%), and *M. cf. M. pentagonale* (6.5%). The remaining species range from <1.0% to 4.2% of the assemblage, and their abundance is fairly consistent among the three samples (Fig. 2).

Five species comprise 73.3% of the Saverton Shale miospore assemblage. The most abundant species is *Punctatisporites hannibalensis* sp. nov. (23.3% average), followed by *Auroraspora macra* (15.0%), *Retusotriletes incohatus* (12.5%), *Retispora lepidophyta* (14.2%), and *Grandispora cornuta* (8.3%). The remaining nine taxa are generally rare in the three Saverton samples, comprising 1.7-5.0% of the miospore palynoflora (Fig. 2).

There is a marked change in the composition of the palynoflora between the Saverton Shale and the Hannibal Shale assemblages. Excluding *Leiosphaeridia* spp. and *Tasmanites* spp., no other prasinophytes were identified in the three Hannibal samples.

Among the seven recovered acritarch taxa, *Micrhystridium* spp. dominates the Hannibal microphytoplankton assemblage, comprising 94.6% of sample 1172 ASI, 78.8% of sample 1173 ASI, and 81.6% of sample 1174 ASI. *Micrhystridium stellatum* is a distant second, encompassing only 4.2% of the microphytoplankton in sample 1172 ASI, 15.4% of sample 1173 ASI, and 14.7% of sample 1174 ASI, followed by *Micrhystridium* sp. cf. *M. pentagonale* with just 5.0% of sample 1173 ASI and 3.3% of sample 1174 ASI.

The miospores comprise only 4.0%, 4.0%, and 2.0% of the palynoflora of the respective three Hannibal samples (1172 ASI, 1173 ASI, and 1174 ASI). Only one to four specimens of a single taxon occur in any of these samples, thus rendering meaningless any perception of dominance by particular species.

Comparison with other Late Devonian prasinophyte and acritarch assemblages

As indicated in the introduction, there is now a fairly comprehensive published record of Late Devonian microphytoplankton assemblages for many parts of the world (Le Hérisse *et al.*, 2000; Molyneux *et al.*, 2013). Unfortunately, many of the papers lack detailed stratigraphic constraints, the assemblages being dated no more precisely than Late Devonian, i.e., without attribution to Frasnian, Famennian, or Strunian. Nonetheless, we herein compare our microphytoplankton assemblage recovered from the latest Devonian (Strunian)

Saverton Shale to other Late Devonian North American and extra-North American assemblages.

North America

Although a number of papers dealing with well-dated acritarch and prasinophyte occurrences from North America have been published (Molyneux *et al.*, 2013), we limit ourselves here to the assemblages reported by Staplin (1961; Frasnian, Alberta, Canada), Wicander (1974; Famennian–Strunian, Ohio), Wicander and Loeblich (1977; Frasnian–Famennian, Indiana), Molyneux *et al.* (1984; Strunian, Ohio), Wicander and Playford (1985; late Frasnian, Iowa), Huysken *et al.* (1992; late Frasnian–Famennian, Kentucky), and Playford and McGregor (1993; Strunian, southern Saskatchewan, Canada). These assemblages are well preserved, diverse, provide illustrations of the taxa, and are well documented in terms of stratigraphic and paleontologic control.

It should be noted before comparing the Saverton Shale microphytoplankton assemblage with other Late Devonian assemblages, that similarity between the assemblages does not necessarily indicate a close stratigraphic correlation. It could be due, in part, to the presence of stratigraphically long-ranging species that are cosmopolitan in distribution. Conversely, a low similarity, expressed as a percentage of species in common between two sections, could result from dissimilar paleoecologic or paleoenvironmental conditions, or disparate taxonomic and nomenclatural interpretations among different authors.

Seventeen genera and 35 named or “cf.” species (excluding *Leiosphaeridia* spp., *Tasmanites* spp., and *Micrhystridium* spp.) comprise the Saverton microphytoplankton assemblage (Fig. 2). Of the 35 recorded species, 25% also occur in the Frasnian Duvernay and Ireton Members of the Woodbend Formation, and Beaverhill Lake Formation of Alberta, Canada (Staplin, 1961); 19% in the Famennian Chagrin Shale and the Strunian Cleveland Shale and Bedford Shale, Ohio (Wicander, 1974); 31% in the Frasnian–Famennian Antrim Shale, Indiana (Wicander and Loeblich, 1977); 67% in the Strunian Bedford Shale and Berea Sandstone, Ohio (Molyneux *et al.*, 1984); 42% in the upper Frasnian Lime Creek Formation, Iowa (Wicander and Playford, 1985); 65% in the upper Frasnian–Famennian New Albany Shale, Ohio Shale, and Bedford Shale, Kentucky (Huysken *et al.*, 1992); and 52% in the Strunian Bakken Formation, southern Saskatchewan, Canada (Playford and McGregor, 1993): Figure 3.

An apparently low similarity exists between the Saverton microphytoplankton assemblage and that

of the Frasnian Woodbend and Beaverhill Lake formations, i.e., disregarding the numerous species of *Protoleiosphaeridium* and *Leiosphaeridium*. This is accountable by the fact that Staplin (1961) created numerous new species of *Micrhystridium* and *Veryhachium*, all of which are of simple morphology, and many of which we consider to be synonymous. Of the 28 species of acritarchs and prasinophytes, 18 (64%) are assigned to *Micrhystridium* and *Veryhachium*. Of the remaining 10 species, six are common to the two assemblages, and only one (*Puteoscorium sprucegrovense*) is restricted to the Late Devonian and has a global distribution.

A similar situation occurs when comparing similarity of microphytoplankton between the Saverton Shale and the Chagrin Shale, Cleveland Shale, and Bedford Shale of Ohio (Wicander, 1974). These formations are all late Famennian/latest Famennian (Strunian) in age and are in close geographic proximity (Illinois and Ohio), yet seemingly have only 19 percent of species in common. This apparent disparity can be attributed, in large part, to the naming of numerous new species recovered from the Chagrin, Cleveland, and Bedford shales based on minor morphological differences and/or to insufficient numbers of specimens in support of a new taxon. It is beyond the scope of this paper to rectify that situation. However, there are clearly a number of species with restricted stratigraphic ranges (Upper Devonian) and either regional (more than one locality) or global geographic occurrences. These include *Cymatiosphaera parvicarina*, *Gorgonisphaeridium absitum*, *G. elongatum*, *G. ohioense*, *G. plerispinosum*, *Micrhystridium adductum*, and *Unellium elongatum*.

The same situation arises in comparing assemblages from the Saverton Shale and the Antrim Shale of Indiana (Wicander and Loeblich, 1977), although the Antrim Shale is considered somewhat older (Frasnian–Famennian). Just as with the Chagrin, Cleveland, and Bedford shales of Ohio (Wicander, 1974), many of the new species erected from the Antrim Shale will probably turn out to be synonymous. Nevertheless, a number of stratigraphically useful species (Upper Devonian) are shared by these two proximate localities. These include *Cymatiosphaera chelina*, *C. parvicarina*, *Gorgonisphaeridium absitum*, *G. elongatum*, *G. ohioense*, *G. plerispinosum*, *Micrhystridium adductum*, *Puteoscorium polyankistrum*, *Veryhachium arcarium*, and *V. cyomosum*. In addition, the globally widespread and common Givetian–Famennian taxa *Stellinium comptum* and *Unellium winslowiae*, also co-occur.

Many of the species found in the Antrim Shale of Indiana (Wicander and Loeblich, 1977) are also components of the upper Frasnian Lime Creek Formation of Iowa (Wicander and Playford, 1985). These include

Taxa	DEVONIAN				MISSISSIPPIAN
	MIDDLE		UPPER		LOWER
	Eifelian	Givetian	Frasnian	Famennian	Kinderhookian
Prasinophyte species					
<i>Cymatiosphaera ambotrocha</i>					
<i>C. chelina</i>					
<i>C. parvicarina</i>					
<i>C. perimembrana</i>		---			---
<i>Muraticavea enteichia</i>				—	
<i>Polyedryxium embudum</i>	←				
<i>Polyedryxium pharaone</i>	←				
Acritarch species					
<i>Baltisphaeridium distentum</i>	←				
<i>Barathrisphaeridium chagrinese</i>					
<i>Estiastra culcita</i>				—	
<i>Gorgonisphaeridium absitum</i>					
<i>G. elongatum</i>					
<i>G. ohioense</i>					---
<i>G. plerispinosum</i>					---
<i>G. winslowiae</i>				—	---
<i>Lophosphaeridium segregum</i>					
<i>Micrhystridium adductum</i>					
<i>Navifusa bacilla</i>	←				
<i>Puteoscortum polyankistrum</i>					
<i>P. sprucegroense</i>					
<i>Stellinium comptum</i>					---
<i>S. micropolygonale</i>	←				---
<i>Unellium elongatum</i>				—	
<i>U. winslowiae</i>			---		
<i>Veryhachium arcarium</i>					
<i>V. cymosum</i>					

Figure 3. Stratigraphic ranges of selected Saverton Shale prasinophyte and acritarch species. Dashes indicate uncertainty of range limits; arrows denote ranges extending into strata older than the Middle Devonian.

Figure 3. Intervalos estratigráficos de especies seleccionadas de prasinofitos y acritarcos de la Pizarra Saverton. La línea discontinua indica incertidumbre en los límites del intervalo; las flechas indican intervalos que se extienden a estratos más antiguos que el Devónico Medio.

Cymatiosphaera chelina, *C. sp. cf. C. parvicarina*, *Stellinium comptum*, *Unellium winslowiae*, *Veryhachium arcarium*, and *V. cymosum*. Other Late Devonian microphytoplankton species in common between the Saverton Shale and Lime Creek Formation are *Cymatiosphaera ambotrocha* (reported as "cf." from Iowa), *C. perimembrana*, *Lophosphaeridium segregum*, and *Stellinium comptum*.

A high degree of similarity (65% co-occurrence) is evident between the Saverton Shale microphytoplankton assemblage and those of the upper Frasnian–Famennian New Albany Shale, Ohio Shale, and Bedford Shale, Kentucky (Huysken *et al.*, 1992). Among the strati-

graphically restricted and geographically widespread, jointly occurring taxa are *Cymatiosphaera ambotrocha*, *Gorgonisphaeridium absitum*, *G. ohioense*, *G. plerispinosum*, *Veryhachium arcarium*, *V. cymosum*, together with *Stellinium comptum* and *Unellium winslowiae*.

There is also a close correlation between the microphytoplankton assemblages of the Strunian Saverton Shale and the Strunian Bedford Shale and Berea Sandstone of Ohio (Molyneux *et al.*, 1984), and the Strunian Bakken Formation of southern Saskatchewan, Canada (Playford and McGregor, 1993). Among the stratigraphically restricted taxa common to all four formations are *Gorgonisphaeridium ohioense* and

G. winslowiae. Additional stratigraphically restricted taxa that are found in the Saverton Shale and either the Bedford Shale or Berea Sandstone are *Puteoscorium polyankistrum* and *Unellium elongatum*. Lastly, taxa that are common to both the Saverton Shale and Bakken Formation and are confined to the Upper Devonian include *Cymatiosphaeridium perimembrana* and *Gorgonisphaeridium plerispinosum*.

Extra-North America

Molyneux *et al.* (2013) provide a comprehensive inventory of publications dealing with Late Devonian microphytoplankton assemblages that have been reported from outside of North America. Unfortunately, many of the earliest studies described assemblages that were poorly preserved (e.g., Bain and Doubinger, 1965; Stockmans and Willère, 1966, 1967, 1969, 1974). There was also a tendency to name new species, particularly among the morphologically simple forms (e.g., *Michrystidium* and *Veryhachium*), based on one specimen, or at best, on a few poorly preserved and inadequately illustrated specimens, thus making it difficult to compare the degree of similarity among assemblages. Fortunately, a number of well-preserved, diverse, and suitably illustrated Late Devonian microphytoplankton assemblages have been described from South America, Europe, the Middle East, China, and Australia, thus allowing comparison of the Saverton Shale microphytoplankton assemblage to these extra-North American localities.

As noted above, the Saverton microphytoplankton assemblage consists of 35 named or "cf." species, and in our comparisons we exclude species left in open nomenclature as well as *Leiosphaeridia* and *Tasmanites*. Of the 35 recorded species, 37% also occur in the upper Famennian Iquiri Formation and Strunian Itacua Formation of Bolivia (Wicander *et al.*, 2011); 37% in the lower Famennian of the southern margin of the Dinant Basin, Belgium (Martin, 1981); 13% in the upper Frasnian-lower Famennian of the southern margin of the Dinant Basin, Belgian Ardennes (Martin, 1985); 15% in the upper Givetian Blacourt Formation and lower-middle Frasnian Beaulieu and Ferques formations, Boulonnais, France (Le Hérissé and Deunff, 1988); 28% in the upper Famennian-Strunian Iberian Pyrite Group, southwest Spain (González *et al.*, 2005); 29% in the upper Famennian-Strunian Phyllite Quartzite Group and Volcano Sedimentary Complex of the Iberian Pyrite Group, Portugal (Pereira *et al.*, 2008); 23% in the Frasnian-Famennian Geirud Formation, Iran (Ghavidel-syooki, 1994); 20% in the Frasnian Shishtu Formation, east-central Iran (Hashemi and Playford, 1998); 19% in the Frasnian Padeha Formation and Frasnian-upper

Famennian Bahram Formation, central Iran (Ghavidel-syooki, 2001); 27% in the Frasnian-Famennian Padeha Formation and Famennian Khoshyeilagh and Mobarak formations, northeastern Iran (Ghavidel-syooki and Owens, 2007); 58% in the Famennian Hongguleleng Formation, Xinjiang, China (Lu Li-chang and Wicander, 1988); and 16% in the Frasnian Gneudna Formation, Western Australia (Playford, 1981; Playford and Dring, 1981); Figure 3.

In comparing the Strunian Saverton Shale microphytoplankton assemblage to the similarly dated Itacua Formation (Strunian) and slightly older (upper Famennian) Iquiri Formation of Bolivia (Wicander *et al.*, 2011), most of the co-occurring species are stratigraphically long-ranging, and geographically widespread. Only *Cymatiosphaera ambotrocha*, *C. perimembrana*, *Gorgonisphaeridium ohioense*, and *G. winslowiae* are restricted to the Upper Devonian and possibly lowermost Mississippian (*G. ohioense* and *G. winslowiae*).

As indicated previously, there is a low degree of similarity in the composition of the Saverton microphytoplankton assemblage and those reported from Europe (Martin, 1981, 1985; Le Hérissé and Deunff, 1988; González *et al.*, 2005; Pereira *et al.*, 2008). However, the greatest similarities are with assemblages from the lower Famennian of Belgium (Martin, 1981) and the Saverton Shale age-equivalent portion of the Iberian Pyrite Group of Spain and Portugal (González *et al.*, 2005; Pereira *et al.*, 2008), where there are respectively 37%, 28%, and 29% of co-occurring species. The relatively high similarity with the Belgian assemblage is due mainly to the co-occurrence of long-ranging species. Although relatively low in terms of common species, the Iberian Pyrite Group microphytoplankton assemblages contain such typically southern latitude taxa as *Umbellasphaeridium* and numerous forms of *Maranhites*. Nonetheless, several Late Devonian species such as *Cymatiosphaera perimembrana*, *Craterisphaeridium sprucegrovense*, *Gorgonisphaeridium ohioense*, and *G. plerispinosum*, are found in both the Saverton Shale and the Iberian Pyrite Group.

The degree of similarity between the Saverton's microphytoplankton assemblage and those reported from Iran (Ghavidel-syooki, 1994, 2001; Hashemi and Playford, 1998; Ghavidel-syooki and Owens, 2007) is equally as low as those from Europe. The most common co-occurring species include the Late Devonian and globally widespread *Cymatiosphaera perimembrana*, *Gorgonisphaeridium ohioense*, and *G. plerispinosum*, as well as *Stellinium comptum* (Givetian-Famennian).

Not surprisingly, there is also a low degree of similarity between the Saverton microphytoplankton assemblage and that of the Frasnian Gneudna Formation of

Western Australia (Playford, 1981; Playford and Dring, 1981). *Cymatiosphaera perimembrana* is the only Late Devonian species common to these two formations. The other eight co-occurring species all have stratigraphic introductions predating the Late Devonian.

The highest degree of similarity between the Saverton microphytoplankton assemblage and those reported from extra-North American locations is with the Famennian Hongguleleng Formation of China (Lu-Li chang and Wicander, 1988), where there are 58% co-occurring species. The shared Saverton/Hongguleleng species, all of which are restricted to the Late Devonian, include *Cymatiosphaera ambotrocha*, *C. parvicarina*, *C. perimembrana*, *Craterisphaeridium sprucegrovense*, *Gorgonisphaeridium absitum*, *G. elongatum*, *G. ohioense*, *G. plerispinosum*, and *Veryhachium arcarium*.

Comparison with other Early Mississippian prasinophyte and acritarch assemblages

As noted earlier, there is a very striking decline in both abundance and diversity of the microphytoplankton assemblage between the Upper Devonian (Strunian) Saverton Shale and the seemingly conformably overlying Lower Mississippian (Kinderhookian) Hannibal Shale (Fig. 2). Except for *Leiosphaeridia* and *Tasmanites*, no other prasinophytes were encountered in the three Hannibal samples analyzed. In terms of the acritarchs, only seven species were recovered, with *Micrhystridium* taxa comprising 99.2% of the total microphytoplankton assemblage from the three samples (Fig. 2).

Heal and Clayton (2008) reported the presence of three prasinophyte (excluding *Leiosphaeridia* and *Tasmanites*) and 12 acritarch species from two successions of the Hannibal Shale in northeastern Missouri. Many of these species are stratigraphically long-ranging, and hence of limited stratigraphic value, whereas others (e.g., *Cymatiosphaera ambotrocha*, *C. chelina*, *C. parvicarina* (reported as "cf."), *Gorgonisphaeridium furcillatum*, *Lophosphaeridium segregum*, *Micrhystridium ampillatum*, and *Villosacapsula ceratoides* (reported as "cf.") are reputedly confined to the Late Devonian, or possibly persist into the Early Mississippian (*Gorgonisphaeridium winslowiae* and *Unellium piriforme*).

With the exception of the palynoflora described by Playford and McGregor (1993) from the Bakken Formation of southern Saskatchewan, Canada – in which they indicated tentatively the possibility of an early Tournaisian age for the upper shale member (i.e., if its content of *Retispora lepidophyta* is not due to rework-

ing) – there are no other studies of Mississippian microphytoplankton assemblages from North America.

As noted by Mullins and Servais (2008), 10 studies have described organic-walled microfossils from undifferentiated Famennian–Tournaisian strata, in which the assemblages contain mainly species of *Leiosphaeridia*, or predominantly Late Devonian taxa. A total of 20 studies have been published from Tournaisian strata in a number of locations throughout the world, and this stratigraphic interval has yielded the most diverse assemblages of Mississippian age (Mullins and Servais, 2008). The majority of taxa from these assemblages are referred to species of *Micrhystridium* and *Veryhachium*, along with assignments, albeit of one or a very few species, to *Cymatiosphaera*, *Polyedryxium*, *Baltisphaeridium*, *Solisphaeridium*, *Tornacia*, and *Unellium*.

In comparing the Hannibal Shale assemblage to those listed by Mullins and Servais (2008), the only assemblage with a diversity of taxa other than *Micrhystridium* and *Veryhachium* is that recorded from the purportedly Tournaisian Yali Formation of Nyalam county, Xizang (Tibet), China (Gao Lianda, 1986). This assemblage contains 24 prasinophyte and acritarch species (excluding *Leiosphaeridia* and *Tasmanites*), most of which are typically Late Devonian. The overlying Naxin Formation, originally assigned to the Vissean, and containing a meager microphytoplankton suite, is considered by Mullins and Servais (2008) to also be of Tournaisian age.

Comparison with other Late Devonian–Early Mississippian miospore assemblages

The extensive literature on miospore floras of Frasnian and, particularly, of latest Famennian (Strunian)–earliest Mississippian age derives from investigations of many sedimentary basins in both the northern and southern hemispheres (e.g., Richardson and McGregor, 1986; Streel, 1986, 2009; Streel *et al.*, 1987; Streel and Loboziak, 1996; Avkhimovitch *et al.*, 1988, 1993; McGregor and Playford, 1992; Playford, 1993, 2009; Melo and Loboziak, 2003; Filipiak, 2004; Playford and Melo, 2012; Melo and Playford, 2012). Given below is a brief conspectus of the Saverton and Hannibal miospore assemblages as these relate to coeval assemblages known from within and beyond North America.

The Saverton Shale's miospore suite, however quantitatively and qualitatively depauperate, features a preponderance of species that have been reported – as per above literature and references therein – from strata of closely similar (latest Devonian: Strunian) age in North

America and globally elsewhere. Chief among these is *Retispora lepidophyta*, together with such associates as *Auroraspora macra*, *Emphanisporites rotatus*, *Grandispora cornuta*, *Indotriradites explanatus*, *Retusotriletes incohatus*, *Teichertospora torquata*, *Vallatisporites hystricosus*, and *Verrucosisporites nitidus*. The cosmopolitanism reflected by this miospore assemblage is evidently a manifestation of the relatively uniform composition of Devonian floras, virtually worldwide. Within North America, essentially similar miospore associations are known for instance from Ohio (Cleveland and Bedford shales: Winslow, 1962); Kentucky (Cleveland Member of Ohio Shale, and Bedford Shale: Heal *et al.*, 2009); Nova Scotia (basal Harding Brook Member of lowermost Horton Group: Martel *et al.*, 1993); and Saskatchewan (lower, middle, and possibly upper members of Bakken Formation: Playford and McGregor, 1993); together with other locations and publications cited in Playford and McGregor (1993, Fig. 1).

The miospores recovered from the three samples of the Hannibal Shale are – as in the Saverton Shale samples – quantitatively subordinate to the microphytoplankton content, and their taxonomic representation is even lower than in the Saverton. Thus, only four miospore species proved identifiable; viz., *Auroraspora macra*, *Punctatisporites hannibalensis* sp. nov., *Retusotriletes incohatus*, and *Verrucosisporites nitidus*, all of them occurring also in the Saverton samples. Aside from *P. hannibalensis*, the other three species have been recorded widely, both regionally and globally, from latest Devonian through Mississippian strata, as

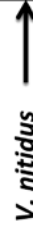
cited individually in the systematic paleontology section. The same three species are components of more abundantly (and more age-definitively) palyniferous samples of Lower Mississippian (Kinderhookian) strata in the neighbouring states of Missouri (Hannibal Shale; Heal and Clayton, 2008) and Kentucky (Sunbury Shale; Heal *et al.*, 2009) and have likewise been reported from coeval deposits elsewhere in North America.

Age and biostratigraphic significance of the palynofloras

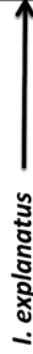
Saverton Shale

The Saverton Shale palynoflora recovered from the Atlas South section, Illinois, signifies a latest Devonian (LN miospore Zone) age for the formation at this locality. As discussed below, the microphytoplankton assemblage is typically Late Devonian, with a composition most compatible with a Famennian placement (Wicander, 1974; Martin, 1981; Molyneux *et al.*, 1984; Lu Li-chang and Wicander, 1988; Playford and McGregor, 1993; González *et al.*, 2005; Pereira *et al.*, 2008; Wicander *et al.*, 2011). The recovered miospores, however, specifically the presence of *Verrucosisporites nitidus* and *Retispora lepidophyta*, constrain the age of the Saverton Shale to the LN miospore Zone of Euramerica and Western Europe (Richardson and McGregor, 1986; Streel *et al.*, 1987; Higgs *et al.*, 1988; Playford and McGregor, 1993; Streel, 2009): Figure 4.


Ser.	Stage	EURAMERICA	WESTERN EUROPE	KEY INDEX SPECIES
LATE DEVONIAN	FAMENNIAN	STRUNIAN	<i>R. lepidophyta</i> - <i>V. nitidus</i>	<i>R. lepidophyta</i> - <i>V. nitidus</i> (LN)
			<i>V. pusillites</i> - <i>R. lepidophyta</i>	<i>R. lepidophyta</i> - <i>I. explanatus</i> (LE)
				<i>R. lepidophyta</i> - <i>K. literatus</i> (LL)
				<i>V. hystricosus</i> (VH)
			<i>R. flexuosa</i> - <i>G. cornuta</i>	<i>D. versabilis</i> - <i>G. cornuta</i> (VCo)




V. nitidus



I. explanatus



R. lepidophyta



V. hystricosus

Figure 4. Stratigraphic ranges of key index miospore species identified in the Saverton Shale samples with reference to Euramerican and Western European biozones.

Figure 4. Rangos estratigráficos de especies índice de miosporas identificadas en las muestras de Pizarra Saverton con referencia a biozonas de Euramerica y Europa Occidental.

Microphytoplankton assemblage

The Saverton microphytoplankton assemblage indicates a Late Devonian (Famennian) age, corroborating the miospore age determination (discussed below). There are numerous acritarch and prasinophyte species that are restricted to the Late Devonian, and specifically the Famennian (Fig. 3). Some taxa are regional in distribution, but a number of them are cosmopolitan. In addition, there are a number of stratigraphically longer ranging species that have a global distribution. It should, however, be pointed out that several common and cosmopolitan Late Devonian microphytoplankton species, discussed below, are absent.

Regional and cosmopolitan microphytoplankton species that are restricted to the Late Devonian, or that also have been reported from the Early Mississippian, and are a common component of the Saverton microphytoplankton assemblage include *Cymatiosphaera ambotrocha*, *C. chelina*, *C. parvicarina*, *C. perimembrana*, *Muraticavea enteichia*, *Barathrisphaeridium chagrinese*, *Estiastra culcita*, *Gorgonisphaeridium absitum*, *G. elongatum*, *G. ohioense*, *G. plerispinosum*, *G. winslowiae*, *Lophosphaeridium segregum*, *Micrhystridium adductum*, *Puteoscortum polyankistrum*, *P. sprucegrovense*, *Unellium elongatum*, *Veryhachium arcarium*, and *V. cymosum* (Fig. 3).

In addition, a number of geographically widespread Devonian species also occur in the Saverton Shale's microphytoplankton assemblage. These include *Polyedryxium embudum*, *P. pharaone*, *Baltisphaeridium distentum*, *Stellinium micropolygonale*, and *Veryhachium polyester*, all of which have a stratigraphic range of Pragian–Famennian. *Navifusa bacilla* (Emasian–Famennian), *Stellinium comptum*, and *Unellium winslowiae* (Givetian–Famennian) are also cosmopolitan species restricted to the Devonian (Fig. 3).

Although the Saverton microphytoplankton assemblage contains numerous stratigraphically restricted and cosmopolitan species, there are a number of Late Devonian global species that have been recorded from other Late Devonian North American assemblages, but are not present in this assemblage. In particular, *Maranhites mosesii* has been recorded from the Bedford Shale of Ohio (Strunian; Molyneux *et al.*, 1984) and the Bakken Formation of Saskatchewan, Canada (Strunian; Playford and McGregor, 1993), and *Maranhites brasiliensis* also from the Bakken Formation (Playford and McGregor, 1993). Wood (1984) recorded his informal "*Maranhites brasiliensis* complex," which also included *M. mosesii* from uppermost Devonian strata of the eastern United States and Ontario, Canada. *Maranhites* is a Devonian taxon that is particularly

common in the Middle and Late Devonian, and typically occurs in the southern hemisphere (González, 2009). The aforementioned occurrences are the only record of it in North America (Wood, 1984; Molyneux *et al.*, 1984; Playford and McGregor, 1993).

The occurrence of *Umbellisphaeridium deflandrei* or *U. saharicum* from North America has been reported by Molyneux *et al.* (1984: *U. saharicum*) from the Strunian Bedford Shale, and from five localities by Wood (1984). However, Wood (1984) considered that the only genuinely *in-situ* specimens of *U. deflandrei/U. saharicum* came from the Famennian Chattanooga Shale, Tennessee (Reaugh, 1978) and from undifferentiated black shale, thought to be the Cleveland Shale of northern Ohio. Those from the other three localities (Bedford Shale) remain suspect and could well be judged remanié, because they occur only where reworked Lower–Middle Silurian acritarchs are present (Wood, 1984). Vavrdová and Isaacson (1999) discussed the presence of *Umbellasphaeridium saharicum* as defining a high-latitude microplankton community during the Late Devonian, with the exception of its occurrence in North America.

Daillyidium pentaster is another species known widely from the northern and southern hemispheres with a range of Givetian–upper Famennian, and most characteristically the Upper Devonian (Hashemi and Playford, 1998). This ubiquitous species has been reported from a number of Upper Devonian localities in North America, several in close geographic proximity to Illinois (Reaugh, 1978; Wicander and Wood, 1981; Wicander and Playford, 1985).

It is unclear why *Daillyidium pentaster*, *Umbellisphaeridium deflandrei/U. saharicum*, or *Maranhites brasiliensis/M. mosesii* are absent in this otherwise diverse Saverton assemblage. It could possibly be related to paleoenvironmental conditions at this location, or more likely, paleoceanic currents that did not disperse the more typically southern latitude species this far north during deposition of the Saverton Shale.

Based on the microphytoplankton assemblage and the known stratigraphic ranges of the various species, a Late Devonian age is indicated for the Saverton Shale. Although many of the Late Devonian taxa range into the Frasnian, the total assemblage is a characteristic Famennian one.

Miospore assemblage

Representation of miospores in the Saverton Shale samples, albeit scant, provides independent and definitive information concerning the formation's precise age. The association of the species listed previously is clearly demonstrative of a latest Devonian (Strunian:

likely LN miospore Zone) age; most importantly, the evidently *in-situ* occurrence in the three Saverton samples of *Retispora lepidophyta*, in conjunction with *Vallatisporites hystricosus* (three samples), *Verrucosisporites nitidus* (three samples), and *Indotriradites explanatus* (two samples): Figure 4. In particular, the joint presence of *R. lepidophyta* and *V. hystricosus* implies correlation with part of the New Albany Shale (Three Lick Bed through Bedford Shale) of northeastern Kentucky, as reported by Heal *et al.* (2009, p. 43; Fig. 40). It should be noted, however, that subsequent work by Clayton *et al.* (2012) has shown that the Three Lick Bed in Kentucky is considerably older (VH miospore Zone) than previously reported (Heal *et al.*, 2009). It is now thought likely that the single 'LN' sample obtained for the Heal *et al.* (2009) study may have been contaminated by debris from the stratigraphically higher Bedford Shale (Clayton, pers. comm.).

Hannibal Shale

As mentioned in previous sections, the Hannibal Shale palynoflora is significantly impoverished compared to that from the Saverton Shale. In fact, the microphytoplankton assemblage is dominated by only a few species, all of which are stratigraphically long-ranging. The miospore assemblage is also depauperate with only five species recovered.

Microphytoplankton assemblage

Only nine microphytoplankton species are recorded from the Hannibal Shale (Fig. 2). Among the acritarchs, *Gorgonisphaeridium ohioense* and *G. winslowiae* are present, but are represented by only a few specimens. Both of these species are typically Famennian, with several references to their possible continuation into the lowermost Mississippian (Playford and McGregor, 1993). Except for an occurrence in one sample, the only other Devonian-restricted taxon is *Stellinium micropolygonale*. The other four acritarch species are stratigraphically long-ranging and cosmopolitan in distribution.

Heal and Clayton (2008) reported a similar, but, overall, more diverse assemblage (dominated by acanthomorphic acritarchs) from two sections of the Hannibal Shale in northeastern Missouri, not far from our locality. Interestingly, Heal and Clayton (2008) identified, in addition to *Leiosphaeridia* sp. and *Tasmanites* sp. (both of which are present in our samples), three other prasinophyte species (*Cymatiosphaera ambo-trocha*, *C. chelina*, and *C. cf. C. parvicarina*) that are lacking from our Atlas South, Illinois location. Furthermore, the only co-occurring acritarch species from the

western Illinois and northeastern Missouri locations are *Gorgonisphaeridium winslowiae*, *Micrhystridium stellatum*, *Stellinium micropolygonale*, and *Veryhachium trispinosum* "complex."

None of the microphytoplankton taxa is known to be restricted to the Kinderhookian. However, a Kinderhookian dating seems reasonable, based on the few species recovered that possibly extend into the lowermost Mississippian, as well as the dramatic drop in diversity, and the abundant occurrence of morphologically simple forms, i.e., *Micrhystridium stellatum* and *M. spp.*

Miospore assemblage

The Hannibal Shale samples are, as previously noted, even less palyniferous in terms of miospore qualitative/quantitative composition than those collected from the underlying Saverton Shale (Fig. 2). Moreover, the very few named Hannibal miospore species – *Auroraspora macra*, *Punctatisporites hannibalensis* sp. nov., *Retusotriletes incohatus*, and *Verrucosisporites nitidus* – although generally indicative of the Late Devonian–Mississippian interval, are not individually or collectively precisely age-prescriptive.

However, given the apparently conformable Saverton/Hannibal relationship at the collecting site, and the admittedly negative evidence of the conspicuous absence of *Retispora lepidophyta* and *Vallatisporites hystricosus* in the Hannibal samples, it is reasonable to infer that the latter are of immediately post-Devonian (Kinderhookian; Hastarian) age, an inference supported by the findings of Heal and Clayton (2008). Their Hannibal Shale samples (from northeastern Missouri) yielded a somewhat more varied miospore assemblage (but still characterized as of "low taxonomic diversity"), lacking *R. lepidophyta* and *Vallatisporites hystricosus* and dated as early Kinderhookian, with a stated resemblance to the Western European *Vallatisporites verrucosus*–*Retusotriletes incohatus* (VI) miospore Zone.

Paleoenvironmental and paleobiogeographic synthesis

Paleoenvironmental interpretation

Sedimentologic and paleontologic-palynologic evidence indicates that the Saverton and Hannibal shales were both deposited in a low energy, somewhat offshore, normal marine environment within the Illinois Basin. As discussed earlier, the Saverton Shale is a grey, greenish- to bluish-grey, fissile, silty shale,

with both thin sandy beds and calcareous beds, that grades upwards to calcareous siltstone. The Hannibal Shale comprises grey to blue-green, calcareous and non-calcareous shale, siltstone, and fine-grained sandstone.

Other than the brachiopods *Spirifer marionensis* and *Orbinaria puxidata*, few megafossils have been reported from the Saverton Shale (Willman *et al.*, 1975). Among the microfossils, fish teeth have been noted, and conodonts are abundant, especially in the siltstones at the top of the formation (Scott and Collinson, 1961; Collinson *et al.*, 1962, 1967; Willman *et al.*, 1975).

Like the Saverton Shale, fossils are sparse in the Hannibal Shale, with brachiopods (e.g., *Chonopectus*) and bivalves comprising the major megafaunal constituents (Howe, 1961; Willman *et al.*, 1975). In addition, the ichnofossils *Taonurus caudagalli* and *Scalartuba missouriensis* are common features of the Hannibal Shale, the former producing "rooster-tail" markings, and the latter forming irregular tubular features, thought to be worm borings (Howe, 1961; Willman *et al.*, 1975). The Hannibal's microfossil assemblage consists of a number of arenaceous foraminifera (Conkin *et al.*, 1965), as well as conodonts (Collinson, 1961; Collinson *et al.*, 1962; Thompson, 1986). Heal and Clayton (2008) described the acritarch, prasinophyte, and miospore assemblages from two sections in Missouri, one of which was the type section.

An appreciable number of studies have demonstrated that qualitative changes in microphytoplankton morphotypes, diversity and abundance fluctuations, and changes in the ratio of marine microphytoplankton to terrestrial spores and pollen, can be used to determine shoreline proximity (e.g., Sarmiento, 1957; Upshaw, 1964; Gray and Boucot, 1972; Jacobson, 1979; Dorning, 1981; Al-Ameri, 1983; Wicander and Playford, 1985; Wicander and Wood, 1997; Vecoli, 2000; Li *et al.*, 2004; Stricanne *et al.*, 2004; Vecoli and Le Hérissé, 2004).

The diversity (38 species, none predominant), abundance, and morphological aspects of the Saverton Shale microphytoplankton assemblage, commonly associated with significant amounts of amorphous organic matter, are indicative of a normal marine, somewhat offshore shelf environment. Furthermore, the microphytoplankton percentage of the microphytoplankton/miospore assemblage is 87% for sample 1169 ASI, 83% for sample 1170 ASI, and 82% for sample 1171, for an average of 84% for the three samples, indicating a definite offshore environment.

The presence of a large proportion of acanthomorphic acritarchs and prasinophytes, together with scolecodonts and amorphous organic matter, confirms a low energy, normal marine depositional environment

for the overlying Hannibal Shale. The microphytoplankton percentage of the microphytoplankton/miospore assemblage is 96% for samples 1172 ASI and 1173 ASI, and 98% for sample 1174 ASI, for an average of 97% for the three samples. Palynofacies analysis of samples from the two Hannibal Shale successions from Missouri indicates a shelf-to-basin environment consistent with their position west of the Borden Delta front (Heal and Clayton, 2008). This interpretation is in agreement with the microphytoplankton morphotype and diversity results, and the microphytoplankton/miospore ratio for the Hannibal Shale palynoflora at Atlas South, Illinois.

Based on their lithology, stratigraphy, sparse megafauna, but more abundant microfauna, a low energy, somewhat offshore, normal marine depositional environment can be inferred for the Saverton and Hannibal shales. Palynologic evidence corroborates this interpretation.

Paleobiogeographic implications

During the Late Devonian, Gondwana comprised a continental mass that stretched from *ca.* 20° north of the equator, to the southern polar region. Laurentia and Baltica were in such close proximity to each other as to effectively form a single continental landmass (Laurasia) that stretched from *ca.* 30° north to *ca.* 30° south of the equator. Siberia, Kazakhstan, and North China occupied the mid to high latitudes between *ca.* 30° and 60° north of the equator. With the Rheic Ocean continuing to narrow, Laurasia and Gondwana were geographically contiguous, with Armorica lying between them. Paleontologic and sedimentological evidence points to a fairly uniform global climate during the Late Devonian.

In terms of Devonian microphytoplankton and miospore assemblages, the Late Devonian has received the greatest attention. However, some of the early studies were stratigraphically/chronologically imprecise, or their assemblages were poorly preserved or inadequately illustrated, such that they are not readily applicable to paleobiogeographic syntheses (Molyneux *et al.*, 2013).

Mississippian paleogeography was little changed from the Late Devonian. Laurasia was still located between *ca.* 30° north and *ca.* 30° south of the equator, and the Rheic Ocean between Laurasia and Gondwana continued to narrow as Gondwana moved northward and began colliding with Laurasia in the onset to the final stage in the formation of Pangaea.

In general, the literature on North American Mississippian microphytoplankton and miospore studies is sparse. Mullins and Servais (2008) discussed the global diversity of Carboniferous microphytoplankton and noted that the majority of studies describe Tour-

naisian assemblages, and, moreover, that most of these are from paleoequatorial to high paleolatitudes of the southern hemisphere. Although publications concerning Mississippian miospores are extensive, relatively few of these are based upon North American successions (Heal and Clayton, 2008).

Microphytoplankton assemblages

Molyneux *et al.* (2013) provide a comprehensive list of all publications that incorporate descriptions and illustrations of Late Devonian microphytoplankton assemblages. In addition, several papers have dealt with the biogeographical distribution of microphytoplankton during this time interval (e.g., Wood, 1984; Vanguetaine, 1986; Vavrdová and Issacson, 1997, 1999, 2000; Colbath, 1990; Clayton *et al.*, 2002).

Analysis of the published literature indicates that Late Devonian microphytoplankton can be divided into (a) a cosmopolitan element characterizing the low paleolatitudes of North America, Armorica, northern Africa, Iran, Australia, and North China; and (b) a more endemic component confined to the higher paleolatitudes of South America. There is also evidence for occasional incursions of the high-paleolatitude assemblages into the low paleolatitudinal regions of North America and northern Perigondwana (Molyneux *et al.*, 2013).

A substantial number of the Frasnian and Famennian acritarchs and prasinophytes present in the Saverton Shale are characteristic of the low paleolatitudes or are cosmopolitan in distribution. These include, among others, *Cymatiosphaera ambotrocha*, *C. perimembrana*, *Polyedryxium embudum*, *P. pharaone*, *Gorgonisphaeridium absitum*, *G. ohioense*, *G. plerispinosum*, *G. winslowiae*, *Lophosphaeridium segregum*, *Navifusa bacilla*, *Puteoscorium sprucegroveense*, *Stellinium comptum*, *S. micropolygonale*, and *U. winslowiae* (Molyneux *et al.*, in press).

Interestingly, *Marahnites brasiliensis*, *M. mosesii*, *Umbellasphaeridium deflandrei*, and *U. saharicum* – all common constituents of the high-latitude microphytoplankton – were dispersed into the lower latitudes during the Late Devonian (as evidenced by their occurrence in several sections in North America and elsewhere), but were not identified in the Saverton Shale microphytoplankton assemblage (see Molyneux *et al.*, 1984; Wood, 1984; Playford and McGregor, 1993; Vavrdová and Isaacson, 1999).

The Mississippian microphytoplankton assemblages can be characterized as significantly reduced in diversity compared to those of the Late Devonian. Furthermore, the assemblages are typically dominated by leiospheres, tasmanitids, and small, morphologically simple acanthomorphic acritarchs such as *Lo-*

phosphaeridium, *Micrhystridium*, and *Veryhachium*; however, representatives of *Cymatiosphaera*, *Gorgonisphaeridium*, *Stellinium*, and *Unellium* have also been reported (Mullins and Servais, 2008).

The composition of the Hannibal microphytoplankton assemblage is not indicative of any particular latitudinal region. It consists primarily of leiospheres and both identifiable and indeterminate species of *Micrhystridium*, which dominate the acritarch component; also, specimens of *Gorgonisphaeridium ohioense*, *G. winslowiae*, and *Veryhachium trispinosum* occur, albeit infrequently (Fig. 2). Except for *G. winslowiae*, which is apparently restricted to the lower palaeolatitudes, the other microphytoplankton taxa are reputedly distributed globally. Heal and Clayton (2008) recorded a somewhat more diverse microphytoplankton assemblage from the Hannibal Shale in Missouri, than we report from Illinois. Their assemblage is dominated by leiospheres, tasmanitids, and acanthomorphic acritarchs. Most of the acritarchs identified in the Hannibal Shale, although common in the Late Devonian, are known to persist into the Mississippian, with a wide paleogeographic distribution.

Miospore assemblages

The most striking attribute of the conspicuously impoverished miospore assemblages retrieved from the Saverton Shale (S) and the Hannibal Shale (H) samples is their content – almost exclusively and in one or both formations – of the cosmopolitan or virtually cosmopolitan species *Auroraspora macra* (S, H), *Emphanisporites rotatus* (S), *Grandispora cornuta* (S), *Indotriradites explanatus* (S), *Retispora lepidophyta* (S), *Retusotriletes incohatus* (S, H), *Teichertospora torquata* (S), *Vallatisporites hystricosus* (S), and *Verrucosisporites niditus* (S, H). This palynologic cosmopolitanism is surely a manifestation of the uniformity of global terrestrial floras during Devonian and earliest Mississippian time. In particular, Streeel and Marshall (2006, p. 490) noted that, during the Devonian–Mississippian transitional interval, Euramerica and Western Gondwana were in sufficiently close proximity or connection to facilitate floristic interchange.

Clearly, the Saverton–Hannibal miospore assemblages, such as they are, comply with those known from coeval Euramerican palynofloras, as indeed can be inferred from the findings of Heal and Clayton (2008) and Heal *et al.* (2009). Later Carboniferous and Permian floras, as documented globally, testify to a steadily accelerating, climatically driven trend toward phyto-provincialism – megascopically and palynologically well expressed – that culminated, for instance, in the development of the Permian *Glossopteris* Flora

of Gondwana, together with the other taxonomically distinctive, coeval floras of the northern hemisphere (e.g., Chaloner and Lacey, 1973).

Summary and conclusions

A diverse palynofloral suite, comprised of 38 acritarch and prasinophyte species (including two new species and one new combination), and 14 miospore species (one of which is new, and another a new combination), was recovered from the Upper Devonian (Strunian; LN miospore Zone) Saverton and Lower Mississippian (Kinderhookian) Hannibal shales in Pike County, southwestern Illinois, U.S.A. The microphytoplankton and miospore assemblage from the Saverton Shale is abundant, diverse, and moderately well preserved, whereas that of the Hannibal reflects a significant decline in acritarch and prasinophyte diversity, as well as miospore abundance and diversity, resulting in an overall depauperate palynoflora.

The Saverton microphytoplankton assemblage shows a high degree of similarity to other North American Upper Devonian palynofloras, notably to the New Albany Shale, Ohio Shale, and Bedford Shale of Kentucky (Huysken *et al.*, 1992), the Bedford Shale and Berea Sandstone of Ohio (Molyneux *et al.*, 1984), and the Bakken Formation of southern Saskatchewan, Canada (Playford and McGregor, 1993). Interestingly, several coeval formations, such as the Antrim Shale of Indiana (Wicander and Loeblisch, 1977), and the Chagrin, Cleveland, and Bedford shales of Ohio (Wicander, 1974), are in close geographic proximity, but lack significant numbers of co-occurring species. This seeming disparity is very likely due to the naming of many new species on the basis of minor morphological differences and/or only a few specimens. Globally, the Saverton microphytoplankton assemblage displays the closest similarity to the Famennian Hongguleleng Formation of China (Lu-Li chang and Wicander, 1988). It also has many stratigraphically long-ranging and geographically widespread species in common with other Late Devonian assemblages, such as those reported from Europe, the Middle East, South America, and Australia. The Hannibal microphytoplankton assemblage contains the same morphologically simple and stratigraphically long-ranging taxa that are found globally in Lower Mississippian strata, together with a few taxa, notably *Gorgonisphaeridium ohioense* and *G. winslowiae*, that possibly extend from the Devonian into the Early Mississippian.

The Saverton miospore assemblage features a number of species known to be restricted to the latest

Devonian, and that serve as reliable index fossils for that time interval, in particular, *Retispora lepidophyta*. The Hannibal miospore assemblage is both less abundant and diverse than its microphytoplankton counterpart, and is suggestive of an Early Mississippian age.

Sedimentologic and paleontologic/palynologic evidence indicates that the Saverton and Hannibal shales were deposited in a normal marine, low-energy, somewhat offshore environment within the Illinois Basin, which was positioned in the low equatorial latitude at that time.

Acknowledgments

Sincere thanks are here expressed to the following individuals and institutions. Reed Wicander thanks Central Michigan University for his sabbatical and the University of Queensland School of Earth Sciences (Head, Professor Paulo Vasconcelos) for providing research facilities during his visit. Both authors thank Leanne Goodwin (PDT Architects, Brisbane) for drafting Figure 1. We also thank Professor Geoffrey Clayton, Department of Geology, Trinity College, Ireland and Dr. Stewart Molyneux, British Geological Survey, United Kingdom for their critical review of the manuscript and for their useful suggestions for its improvement.

References

- Note.*- Following conventional practice, the bibliographic listing hereunder excludes "taxa-only references;" i.e., those that are cited in the text solely as adjuncts to taxonomic names and without page references (e.g., *Indotriradites* Tiwari, 1964 emend. Foster, 1979).
- Al-Ameri, T.K. 1983. Acid-resistant microfossils used in the determination of Palaeozoic palaeoenvironments in Libya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 44, 103-116.
- Allen, K.C. 1965. Lower and Middle Devonian spores of north and central Vestspitsbergen. *Palaeontology*, 8, 687-748.
- Avkhimovitch, V.I., Byvsheva, T.V., Higgs, K., Streel, M. and Umnova, V.T. 1988. Miospore systematics and stratigraphic significance of Devonian-Carboniferous boundary deposits in the European part of the USSR and Western Europe. *Courier Forschungsinstitut Senckenberg*, 100, 169-191.
- Avkhimovitch, V.I., Chibrikova, E.V., Obukhovskaya, T.G., Nazarenko, A.M., Umnova, V.T., Raskatova, L.G., Manturova, V.N., Loboziak, S. and Streel, M. 1993. Middle and Upper Devonian miospore zonation of Eastern Europe. *Bulletin du Centre de Recherches Elf Exploration Production*, 17, 79-147.

- Azcuy, C.L. and di Pasquo, M. 2005. Early Carboniferous palynoflora from the Ambo Formation, Pongo de Mainique, Peru. *Review of Palaeobotany and Palynology*, 134, 153-184.
- Bain, A. and Doubinger J. 1965. Etude d'un microplancton (Acritarches) du Dévonien supérieur des Ardennes. *Bulletin du Service de la Carte Géologique d'Alsace et de Lorraine*, 18, 15-30.
- Balme, B.E. 1988a. Miospores from Late Devonian (early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B*, 209, 109-166.
- Balme, B.E. 1988b. *Teichertospora* n. gen., an endoreticulate miospore from the Late Devonian of Western Australia. *Senckenbergiana lethaea*, 69, 159-169.
- Barreda, V.D. 1986. Acritarcos givetiano–frasnianos de la Cuenca del Noroeste, provincia de Salta, Argentina. *Revista Española de Micropaleontología*, 18, 229-245.
- Becker, G., Bless, M.J.M., Streel, M. and Thorez, J. 1974. Palynology and ostracode distribution in the Upper Devonian and basal Dinantian of Belgium and their dependence on sedimentary facies. *Mededelingen Rijks Geologische Dienst, Nieuwe Serie*, 25, 9-99.
- Bharadwaj, D.C., Tiwari, R.S. and Venkatachala, B.S. 1970. An Upper Devonian microflora from New Albany Shale, Kentucky, U.S.A. *The Palaeobotanist*, 19, 29-40.
- Byvsheva, T.V. 1985. Spores from deposits of the Tournaisian and Viséan stages of the Russian Plate. In: Menner, V.V. and Byvsheva, T.V. (eds.), *Atlas of spores and pollen of Phanerozoic oil- and gas-bearing strata of the Russian and Turanian plates. Trudy Vsesoiuznogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Neftianogo Instituta (VNIGNI)*, 253, 80-158. (In Russian).
- Chaloner, W.G. and Lacey, W.S. 1973. The distribution of late Palaeozoic floras. In: Hughes, N.F. (ed.), *Organisms and continents through time. Special Papers in Palaeontology*, 12, 271-289.
- Clayton, G. 1996. Mississippian miospores. In: Jansonius, J. and McGregor, D.C. (eds.), *Palynology: principles and applications, volume 2*. American Association of Stratigraphic Palynologists Foundation, Dallas, 589-596.
- Clayton, G., Wicander, R. and Pereira, Z. 2002. Palynological evidence concerning the relative positions of northern Gondwana and southern Laurussia in latest Devonian and Mississippian times. In: Wyse Jackson, P.N., Parkes, M.A. and Wood, R. (eds.), *Studies in Palaeozoic palaeontology and biostratigraphy in honour of Charles Hepworth Holland. Special Papers in Palaeontology*, 67, 45-56.
- Clayton, G., Paterson, N., Mason, C.E., Etensohn, F., Lierman, R.T., Goodhue, R., Rooney, A. and Wicander, R. 2012. Palynostratigraphy and palynofacies of Upper Devonian rocks in the Appalachian Basin, U.S.A. *Program and Abstracts, A Joint Meeting of the 45th Annual Meeting of AASP – The Palynological Society and Meeting of the CIMP – Commission Internationale de la Microflore du Paléozoïque Subcommissions, 21-25 July 2012, Lexington, Kentucky, U.S.A.*, 16-17.
- Colbath, G.K. 1990. Devonian (Givetian–Frasnian) organic-walled phytoplankton from the Limestone Billy Hills reef complex, Canning Basin, Western Australia. *Palaeontographica Abteilung B*, 217, 87-145.
- Collinson, C. 1961. The Kinderhookian Series in the Mississippi Valley. *Kansas Geological Society 26th Annual Field Conference Guidebook, Report of Investigations*, 27, 100-109.
- Collinson, C., Becker, L.E., James, G.W., Koenig, J.W. and Swann, D.H. 1967. Illinois Basin. In: Oswald, D.H. (ed.), *International symposium on the Devonian System. Alberta Society of Petroleum Geologists*, 1, 940-962.
- Collinson, C., Scott, A.J. and Rexroad, C.B. 1962. Six charts showing biostratigraphic zones and correlations based on conodonts from the Devonian and Mississippian rocks of the Upper Mississippi Valley. *Illinois State Geological Survey Circular*, 328, 1-32.
- Conkin, J.E., Conkin, B.M. and Pike, J.W. 1965. Mississippian foraminifera of the United States. Part 2 – The Hannibal Formation of northeastern Missouri and western Illinois. *Micropaleontology*, 11, 335-359.
- Cramer, F.H. 1964. Microplankton from three Paleozoic formations in the province of Leon, N.W. Spain. *Leidse Geologische Mededelingen*, 30, 253-361.
- Day, J. and Witzke, B.J. 2012. Timing of Upper Devonian marine flooding events and episodes of organic-rich Sweetland Creek, Grassy Creek and Saverton Shale deposition in the Iowa and N.W. Illinois Basin. *Geological Society of America, Abstracts with Programs*, 44(6), 7.
- Day, J., Witzke, B.J., Rowe, H. and Ellwood, B. 2009. Preliminary results of high-resolution investigation of Upper Devonian (late Frasnian–Famennian) relative sea level and climate record from the subsurface of the Iowa and Western Illinois Basins. *Geological Society of America, Abstracts with Programs*, 41(4), 27.
- Deflandre, G. 1945. Microfossils des calcaires Siluriens de la Montagne Noir. *Annales de Paléontologie*, 31, 39-75.
- Deunff, J. 1955. Un microplancton fossile Dévonien à hystriosphères du continent Nord-Américain. *Bulletin de Microscopie Appliquée, Série 2*, 5, 136-149.
- Deunff, J. 1961. Quelques précisions concernant les hystriosphères du Dévonien du Canada. *Compte Rendu Sommaire des Séances de la Société géologique de France*, 8, 1961, 216-218.
- Deunff, J. 1966. *Recherches sur les microplanctons du Dévonien (Acritarches et Dinophyceae)*. Thèse Université Rennes, 168 pp.
- Deunff, J. 1981. Observations préliminaires sur le paléophytoplancton de la coupe de Caffiers (Givetien–Frasnien du Boulonnais, France). *Annales de la Société géologique du Nord*, 100, 65-71.
- Dorning, K.J. 1981. Silurian acritarch distribution in the Ludlovian Shelf Sea of South Wales and the Welsh Borderland. In: Neal, R.G. and Brasier, M.D. (eds.), *Microfossils from Recent and fossil shelf seas*. Ellis Horwood Ltd., Chichester, 31-36.
- Eisenack, A. 1938. Hystriospheriden und verwandte Formen im baltischen Silur. *Zeitschrift für Geologieforschung und Flachlandsgeologie*, 14, 1-30.
- Evitt, W.R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystriospheres, and acritarchs, I, II. *Proceedings of the United States National Academy of Sciences*, 49, 158-164, 298-302.
- Fatka, O. and Brocke, R. 2008. Morphological variability and method of opening of the Devonian acritarch *Navifusa*

- bacilla* (Deunff, 1955) Playford, 1977. *Review of Palaeobotany and Palynology*, 148, 108-123.
- Filipiak, P. 2004. Miospore stratigraphy of upper Famennian and Lower Carboniferous deposits of the Holy Cross Mountains (central Poland). *Review of Palaeobotany and Palynology*, 128, 291-322.
- Filipiak, P. 2005. Late Devonian and Early Carboniferous acritarchs and prasinophytes from the Holy Cross Mountains (central Poland). *Review of Palaeobotany and Palynology*, 134, 1-26.
- Foster, C.B. and Balme, B.E. 1994. Ultrastructure of *Teichotospora torquata* (Higgs) from the Late Devonian: oldest saccate palynomorph. In: Kurmann, M.H. and Doyle, J.A. (eds.), *Ultrastructure of fossil spores and pollen*. Kew, Royal Botanic Garden, 87-97.
- Gao Lianda. 1986. Late Devonian and Early Carboniferous acritarchs from Nyalam County, Xizang (Tibet), China. *Review of Palaeobotany and Palynology*, 47, 17-30.
- Ghavidel-syooki, M. 1994. Upper Devonian acritarchs and miospores from the Geirud Formation in central Alborz Range, northern Iran. *Journal of Sciences, Islamic Republic of Iran*, 5, 103-122.
- Ghavidel-syooki, M. 2001. Palynostratigraphy and paleogeography of the Late Devonian in northeastern Esfahan City, central Iran. In: Goodman, D.K. and Clarke, R.T. (eds.), *Proceedings of the IX International Palynological Congress, Houston, Texas, U.S.A., 1996*. American Association of Stratigraphic Palynologists Foundation, Dallas, 37-51.
- Ghavidel-syooki, M. and Owens, B. 2007. Palynostratigraphy and palaeogeography of the Padeha, Khoshyeilagh, and Mobarak formations in the eastern Alborz Range (Kopet-Dagh region), northeastern Iran. *Revue de Micropaléontologie*, 50, 129-144.
- González, F. 2009. Reappraisal of the organic-walled microphytoplankton genus *Maranhites*: morphology, excystment, and speciation. *Review of Palaeobotany and Palynology*, 154, 6-21.
- González, F., Moreno, C. and Playford, G. 2011. The Gondwana-Laurussia convergence process: evidence from the Middle Mississippian (Viséan) palynostratigraphic record. *Geological Magazine*, 148, 317-328.
- González, F., Playford, G. and Moreno, C. 2005. Upper Devonian biostratigraphy of the Iberian Pyrite Belt, southwest Spain. Part one: miospores. *Palaeontographica Abteilung B*, 273, 1-51.
- Gray, J. and Boucot, A.J. 1972. Palynological evidence bearing on the Ordovician–Silurian paraconformity in Ohio. *Geological Society of America Bulletin*, 83, 1299-1314.
- Guennel, G.K. 1963. Devonian spores in a Middle Silurian reef. *Grana Palynologica*, 4, 245-261.
- Hacquebard, P.A. 1957. Plant spores in coal from the Horton Group (Mississippian) of Nova Scotia. *Micropaleontology*, 3, 301-324.
- Hashemi, H. and Playford, G. 1998. Upper Devonian palynomorphs of the Shishtu Formation, Central Iran Basin, east-central Iran. *Palaeontographica Abteilung B*, 246, 115-212.
- Heal, S. and Clayton, G. 2008. The palynology of the Hannibal Shale (Mississippian) of northeastern Missouri, U.S.A. and correlation with Western Europe. *Palynology*, 32, 27-37.
- Heal, S., Paterson, N., Eble, C., Mason, C.E., Goodhue, R., Larsson, N. and Clayton, G. 2009. Preliminary palynological results from the Late Devonian–Early Mississippian of Morehead and adjacent areas. In: Ettensohn, F.R., Lierman, R.T. and Mason, C.E., *Upper Devonian–Lower Mississippian clastic rocks in northeastern Kentucky: evidence for Acadian alpine glaciation and models for source-rock and reservoir-rock development in the eastern United States*. American Institute of Professional Geologists-Kentucky Section, Spring Field Trip, April 18, 2009, 42-52.
- Higgs, K. 1975. Upper Devonian and Lower Carboniferous miospore assemblages from Hook Head, County Wexford, Ireland. *Micropaleontology*, 21, 393-419.
- Higgs, K.T., Avkhimovitch, V.I., Loboziak, S., Maziane-Serraj, N., Stempien-Salek, M. and Streel, M. 2000. Systematic study and stratigraphic correlation of the *Grandispora* complex in the Famennian of northwest and eastern Europe. *Review of Palaeobotany and Palynology*, 112, 207-228.
- Higgs, K., Clayton, G. and Keegan, J.B. 1988. Stratigraphic and systematic palynology of the Tournaisian rocks of Ireland. *Geological Survey of Ireland Special Paper*, 7, 1-93.
- Higgs, K.T., Finucane, D. and Tunbridge, I.P. 2002. Late Devonian and Early Carboniferous microfloras from the Hakkari Province of southeastern Turkey. *Review of Palaeobotany and Palynology*, 118, 141-156.
- Higgs, K.T., Prestianni, C., Streel, M. and Thorez, J. 2013. High resolution miospore stratigraphy of the Upper Famennian of eastern Belgium, and correlation with the conodont zonation. *Geologica Belgica*, 16, 84-94.
- Howe, W.B. 1961. The stratigraphic succession in Missouri. *Missouri Geological Survey and Water Resources, 2nd Series*, 40, 1-185.
- Huysken, K.T., Wicander, R. and Ettensohn, F.R. 1992. Palynology and biostratigraphy of selected Middle and Upper Devonian black-shale sections in Kentucky. *Michigan Academician*, 24, 355-368.
- Jacobson, S.R. 1979. Acritarchs as paleoenvironmental indicators in Middle and Upper Ordovician rocks from Kentucky, Ohio, and New York. *Journal of Paleontology*, 53, 1197-1212.
- Jäger, H. 2002. Palynology of the Lower Carboniferous (Mississippian) Kammquartzite Formation in the Rhenohercynian Zone, Germany. *Senckenbergiana lethaea*, 82, 609-637.
- Johnson, J.G., Klapper, G. and Sandberg, C.A. 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America Bulletin*, 96, 567-587.
- Kedo, G.I. 1957. The stratigraphy and spore-pollen groups of the Carboniferous of Byelorussian SSR. *Doklady Akademii Nauk SSSR*, 115, 1165-1168. (in Russian).
- Koenig, J.W., Martin J.A. and Collinson C.W. 1961. Day 2 Field Trip. *Kansas Geological Society 26th Annual Field Conference Guidebook, Report of Investigations*, 27, 65-67.
- Kremp, G.O.W. 1965. *Morphologic encyclopedia of palynology: an international collection of definitions and illustrations of spores and pollen*. Program in Geochronology, University of Arizona, Contribution, 100, xiii + 185 pp. University of Arizona Press, Tucson.

- Lane, H.R. and Brenckle, P.H. 2005. Type Mississippian subdivisions and biostratigraphic succession. In: Heckel, P.H. (ed.), *Stratigraphy and biostratigraphy of the Mississippian Subsystem (Carboniferous System) in its type region, the Mississippi River Valley of Illinois, Missouri, and Iowa. Illinois State Geological Survey Guidebook*, 34, 76-105.
- Le Hérissé, A. and Deunff, J. 1988. Acritarches et prasino-phycees (Givetian supérieur-Frasnien moyen) de Ferques (Boulonnais-France). In: Brice, D. (ed.), *Le Dévonien de Ferques, Bas-Boulonnais (N. France). Biostratigraphie du Paléozoïque, Université de Bretagne Occidentale*, 7, 103-152.
- Le Hérissé, A., Servais T. and Wicander, R. 2000. Devonian acritarchs and related forms. *Courier Forschungsinstitut Senckenberg*, 220, 195-205.
- Li, J., Servais, T., Yan, K. and Zhu, H. 2004. A nearshore-offshore trend in the acritarch distribution of the Early–Middle Ordovician of the Yangtze Platform, South China. *Review of Palaeobotany and Palynology*, 130, 141-161.
- Lister, T.R. 1970. A monograph of the acritarchs and Chitinozoa from the Wenlock and Ludlow series of the Ludlow and Millichope areas, Shropshire, Part 1. *Palaeontographical Society Monographs*, 124, 1-100.
- Lu Li-chang and Wicander, R. 1988. Upper Devonian acritarchs and spores from the Hongguleleng Formation, Hefeng district in Xinjiang, China. *Revista Española de Micropaleontología*, 20, 109-148.
- Luber, A.A. and Waltz, I.E. 1941. Atlas of microspores and pollen grains of the Palaeozoic of the USSR. *Trudy Vsesoiuznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta*, 139, 1-75. (in Russian).
- Martel, A.T., McGregor, D.C. and Utting, J. 1993. Stratigraphic significance of Upper Devonian and Lower Carboniferous miospores from the type area of the Horton Group, Nova Scotia. *Canadian Journal of Earth Sciences*, 30, 1091-1098.
- Martin, F. 1981. Acritarches du Famennien inférieur à Villers-sur-Lesse (Belgique). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, no. 2, 52, 1-49.
- Martin F. 1982. Acritarches et chitinozoaires de la partie supérieure du Frasnien dans un affleurement au nord immédiat de Frasnien (Belgique). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, no. 2, 54, 1-17.
- Martin, F. 1985. Acritarches du Frasnien supérieur et du Famennien inférieur du nord méridional du Bassin de Dinant (Ardenne belge). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, no. 2, 55, 1-57.
- Maziane, N., Higgs, K.T. and Streel, M. 1999. Revision of the late Famennian miospore zonation scheme in eastern Belgium. *Journal of Micropalaeontology*, 18, 17-25.
- McGregor, D.C. 1973. Lower and Middle Devonian spores of eastern Gaspé, Canada. *Palaeontographica Abteilung B*, 142, 1-77.
- McGregor, D.C. and Playford, G. 1990. Morphology and distribution of the miospore *Teichertospora torquata* comb. nov. in the Upper Devonian of Euramerica and Australia. *Palynology*, 14, 7-18.
- McGregor, D.C. and Playford, G. 1992. Canadian and Australian Devonian spores: zonation and correlation. *Geological Survey of Canada Bulletin*, 438, 1-125.
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. and Turland, N.J. (eds. and compilers) 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress, Melbourne, Australia, July 2011. Regnum Vegetabile*, 154, xxx + 240 pp. Koeltz Scientific Books, Koenigstein, Germany.
- Melo, J.H.G. and Loboziak, S. 2003. Devonian–Early Carboniferous miospore biostratigraphy of the Amazon Basin, northern Brazil. *Review of Palaeobotany and Palynology*, 124, 131-202.
- Melo, J.H.G. and Playford, G. 2012. Miospore palynology and biostratigraphy of Mississippian strata of the Amazonas Basin, northern Brazil. Part Two. *American Association of Stratigraphic Palynologists, Contributions Series*, 47, 91-201.
- Molyneux, S.G., Delabroye, A., Wicander, R. and Servais, T. 2013. Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton. In: Harper, D.A.T. and Servais, T. (eds.), *Early Palaeozoic biogeography and palaeogeography. Geological Society, London Memoir*, 38, 357-390.
- Molyneux, S.G., Manger, W.L. and Owens B. 1984. Preliminary account of Late Devonian palynomorph assemblages from the Bedford Shale and Berea Sandstone Formations of central Ohio, U.S.A. *Journal of Micropalaeontology*, 3, 41-51.
- Mullins, G.L. and Servais, T. 2008. The diversity of the Carboniferous phytoplankton. *Review of Palaeobotany and Palynology*, 149, 29-49.
- Ottone, E.G. 1996. Devonian palynomorphs from the Los Monos Formation, Tarija Basin, Argentina. *Palynology*, 20, 105-155.
- Pereira, Z., Matos, J., Fernandes, P. and Oliveira, J.T. 2008. Palynostratigraphy and systematic palynology of the Devonian and Carboniferous successions of the South Portuguese Zone, Portugal. *Memórias Geológicas do Instituto Nacional de Engenharia, Tecnologia e Inovação*, 34, 1-181.
- Pérez Loinaze, V. 2008. Systematic palynological study of the Cortaderas Formation (Mississippian), Río Blanco Basin, Argentina. Part two. *Ameghiniana*, 45, 421-441.
- Playford, G. 1964. Miospores from the Mississippian Horton Group, eastern Canada. *Geological Survey of Canada Bulletin*, 107, 1-47.
- Playford, G. 1976. Plant microfossils from the Upper Devonian and Lower Carboniferous of the Canning Basin, Western Australia. *Palaeontographica Abteilung B*, 158, 1-71.
- Playford, G. 1977. Lower to Middle Devonian acritarchs of the Moose River Basin, Ontario. *Geological Survey of Canada Bulletin*, 279, 1-87.
- Playford, G. 1981. Late Devonian acritarchs from the Gneudna Formation in the western Carnarvon Basin, Western Australia. *Géobios*, 14, 145-171.

- Playford, G. 1983. The Devonian miospore genus *Geminospora* Balme 1962: a reappraisal based upon topotypic *G. lemurata* (type species). *Association of Australasian Palaeontologists Memoir*, 1, 311-325.
- Playford, G. 1991. Australian Lower Carboniferous miospores relevant to extra-Gondwanic correlations: an evaluation. *Courier Forschungsinstitut Senckenberg*, 130, 85-125. (imprinted 1990).
- Playford, G. 1993. Miospores and organic-walled microphytoplankton characteristic of strata contiguous with the Devonian–Carboniferous boundary. *Compte Rendu, Douzième Congrès International de Stratigraphie et de Géologie du Carbonifère–Permien, Buenos Aires, September 1991*, 1, 127-160.
- Playford, G. 2009. Review of Devonian palynology, Canning Basin. In: Playford, P.E., Hocking, R.M. and Cockbain, A.E., Devonian reef complexes of the Canning Basin, Western Australia. *Geological Survey of Western Australia Bulletin*, 145, Appendix 3, 441-444.
- Playford, G. and Dettmann, M.E. 1996. Spores. In: Jansonius, J. and McGregor, D.C. (eds.), *Palynology: principles and applications, volume 1*. American Association of Stratigraphic Palynologists Foundation, Dallas, 227-260.
- Playford, G. and Dring, R.S. 1981. Late Devonian acritarchs from the Carnarvon Basin, Western Australia. *Special Papers in Palaeontology*, 27, 1-78.
- Playford, G. and McGregor, D.C. 1993. Miospores and organic-walled microphytoplankton of Devonian–Carboniferous boundary beds (Bakken Formation), southern Saskatchewan: a systematic and stratigraphic appraisal. *Geological Survey of Canada Bulletin*, 445, 1-107.
- Playford, G. and Melo, J.H.G. 2012. Miospore palynology and biostratigraphy of Mississippian strata of the Amazonas Basin, northern Brazil. Part One. *American Association of Stratigraphic Palynologists, Contributions Series*, 47, 1-89.
- Potonié, R. and Kremp, G. 1954. Die Gattungen der paläozoischen Spores dispersae und ihre Stratigraphie. *Geologisches Jahrbuch*, 69, 111-194.
- Rauscher, R. 1969. Présence d'une forme nouvelle d'acritarches dans le Dévonien de Normandie. *Compte Rendu de l'Académie des Sciences de Paris*, 268D, 34-36.
- Reaugh, A.B. 1978. A new species of *Cymatiosphaera* (Acritarcha) with constant field tabulation from the Devonian of Tennessee. *Palaeontology*, 21, 835-846.
- Richardson, J.B. and McGregor, D.C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Geological Survey of Canada Bulletin*, 364, 1-79.
- Riegel, W. 2008. The Late Palaeozoic phytoplankton blackout – Artefact or evidence of global change? *Review of Palaeobotany and Palynology*, 148, 73-90.
- Sarmiento, R. 1957. Microfossil zonation of Mancos Group. *American Association of Petroleum Geologists Bulletin*, 41, 1683-1693.
- Scott, A.J. and Collinson, C. 1961. Conodont faunas from the Louisiana and McCraney Formations of Illinois, Iowa and Missouri. *Kansas Geological Society 26th Annual Field Conference Guidebook, Report of Investigations*, 27, 110-141.
- Servais, T., Vecoli, M., Jun Li, Molyneux, S.G., Raevskaya, E.G. and Rubinstein, C.V. 2007. The acritarch genus *Veryhachium* Deunff 1954: taxonomic evaluation and first appearance. *Palynology*, 31, 191-203.
- Smith, A.H.V. and Butterworth, M.A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Special Papers in Palaeontology*, 1, 1-324.
- Staplin, F.L. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology*, 4, 392-424.
- Staplin, F.L., Jansonius, J. and Pocock, S.A.J. 1965. Evaluation of some acritarchous hystriosphere genera. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 123, 167-201.
- Stockmans, F. and Willièrè, Y. 1960. Hystriosphères du Dévonien belge (sondage de l'Asile d'aliénés à Tournai). *Senckenbergiana lethaea*, 41, 1-11.
- Stockmans, F. and Willièrè, Y. 1962a. Hystriosphères du Dévonien belge (sondage de l'Asile d'aliéné à Tournai). *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 71, 41-77.
- Stockmans, F. and Willièrè, Y. 1962b. Hystriosphères du Dévonien belge (sondage de Wépion). *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 71, 83-99.
- Stockmans, F. and Willièrè, Y. 1963. Les hystriosphères ou mieux les acritarches du Silurien belge. Sondage de la Brasserie Lust à Courtrai (Kortrijk). *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 71, 450-481.
- Stockmans, F. and Willièrè, Y. 1966. Les Acritarches du Dinantien du sondage de l'Asile d'aliénés à Tournai. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 74, 462-477.
- Stockmans, F. and Willièrè, Y. 1967. Les Acritarches du Dinantien du sondage de Vieux Leuze à Leuze (Hainaut, Belgique). *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 75, 233-242.
- Stockmans, F. and Willièrè, Y. 1969. Acritarches du Famennien inférieur. *Académie royale de Belgique, Classe des Sciences*, 38, 1-63.
- Stockmans, F. and Willièrè, Y. 1974. Acritarches de la "Tranchée de Senzeille" (Frasnien supérieur et Famennien inférieur). *Académie royale de Belgique, Classe des Sciences*, 41, 1-79.
- Streel, M. 1986. Miospore contribution to the Upper Famennian–Strunian event stratigraphy. *Annales de la Société géologique de Belgique*, 109, 75-92.
- Streel, M. 2009. Upper Devonian miospore and conodont zone correlation in Western Europe. In: Königshof, P. (ed.), *Devonian change: case studies in palaeogeography and palaeoecology*. *Geological Society, London, Special Publications*, 314, 163-176.
- Streel, M., Higgs, K., Loboziak, S., Riegel, W. and Steemans, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardennes-Rhenish regions. *Review of Palaeobotany and Palynology*, 50, 211-229.
- Streel, M. and Loboziak, S. 1996. Middle and Upper Devonian miospores. In: Jansonius, J. and McGregor, D.C. (eds.), *Palynology: principles and applications, volume*

2. American Association of Stratigraphic Palynologists Foundation, Dallas, 575-587.
- Streel, M. and Marshall, J.E.A. 2006. Devonian–Carboniferous boundary correlations and their paleogeographic implications for the assembly of Pangaea. In: Wong, Th.E. (ed.), *Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy*, Utrecht, The Netherlands, 10-16 August 2003, Royal Netherlands Academy of Arts and Sciences, 481-496.
- Stricanne, L., Munnecke, A., Pross, J. and Servais, T. 2004. Acritarch distribution along an inshore-offshore transect in the Gorstian (lower Ludlow) of Gotland, Sweden. *Review of Palaeobotany and Palynology*, 130, 195-216.
- Sullivan, H.J. 1964. Miospores from the Lower Limestone Shales (Tournaisian) of the Forest of Dean Basin, Gloucestershire. *Compte Rendu, 5^{ème} Congrès International de Stratigraphie et de Géologie du Carbonifère, Paris, 1963*, 3, 1249-1259.
- Sullivan, H.J. 1968. A Tournaisian spore flora from the Cementstone Group of Ayreshire, Scotland. *Palaeontology*, 11, 116-131.
- Tappan, H. 1968. Primary production, isotopes, extinctions and the atmosphere. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 4, 187-210.
- Taugourdeau-Lantz, J. 1960. Sur la microflore du Frasnien inférieur de Beaulieu (Boulonnais). *Revue de Micropaléontologie*, 3, 144-154.
- Thompson, T.L. 1986. Paleozoic succession in Missouri, Part 4 – Mississippian system. *Missouri Department of Natural Resources, Division of Geology and Land Survey, Report of Investigations*, 70, 1-189.
- Traverse, A. 2007. *Paleopalynology, second edition*. xvii + 813 pp. Springer, Dordrecht.
- Turnau, E., Avkhimovitch, V.I., Byvsheva, T.V., Clayton, G., Higgs, K.T. and Owens, B. 1994. Taxonomy and stratigraphical distribution of *Verrucosiporites nitidus* Playford, 1964 and related species. *Review of Palaeobotany and Palynology*, 81, 289-295.
- Turner, R.E. 1986. New and revised acritarch taxa from the Upper Devonian (Frasnian) of Alberta, Canada. *Canadian Journal of Earth Sciences*, 23, 599-607.
- Turner, R.E. 1991. New acritarch taxa from the Middle and Upper Devonian (Givetian–Frasnian) of western Canada. *Canadian Journal of Earth Sciences*, 28, 1471-1487.
- Upshaw, C.F. 1964. Palynological zonation of the Upper Cretaceous Frontier Formation near Dubois, Wyoming. In: Cross, A.T. (ed.), *Palynology in oil exploration. Society of Economic Paleontologists and Mineralogists, Special Publication*, 11, 153-168.
- Van der Zwan, C.J. 1980. Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. III. Palynology of Devonian–Carboniferous transition sequences, with special reference to the Bantry Bay area, Co. Cork. *Review of Palaeobotany and Palynology*, 30, 165-286.
- Vanguetaine, M. 1986. Late Devonian and Carboniferous acritarch stratigraphy and paleogeography. *Annales de la Société géologique du Nord*, 105, 93-102.
- Vanguetaine, M., Declairfayt, T., Rouarth, A. and Smeesters, A. 1983. Zonation par acritarches du Frasnien supérieur–Famennien inférieur dans les bassins de Dinant, Namur, Herve et Campine (Devonien supérieur de Belgique). *Annales de la Société géologique de Belgique*, 106, 121-171.
- Vavrdová, M., Bek, J., Dufka, P. and Isaacson, P. 1996. Palynology of the Devonian (Lochkovian to Tournaisian) sequence, Madre de Dios Basin, northern Bolivia. *Věstník Českého geologického ústavu*, 71, 333-349.
- Vavrdová, M. and Isaacson, P. 1997. Affinities of Late Devonian acritarchs from the Madre de Dios Basin, northern Bolivia. In: Fatka, O. and Servais, T. (eds.), *Acritarcha in Praha 1996. Proceedings of the International Meeting and Workshop. Acta Universitatis Carolinae, Geologica*, 40, 683-693.
- Vavrdová, M. and Isaacson, P. 1999. Late Famennian phyto-geographic provincialism: evidence for a limited separation of Gondwana and Laurentia. In: Feist, R., Talent, J.A. and Daurer, A. (eds.), *North Gondwana: Mid-Paleozoic terranes, stratigraphy and biota. Abhandlungen der Geologischen Bundesanstalt*, 54, 453-463.
- Vavrdová, M. and Isaacson, P. 2000. Palynology of selected Devonian strata, Western Gondwana. *Zentralblatt für Geologie und Paläontologie, Teil 1: Allgemeine, angewandte, Regionale und Historische Geologie*, 1999, 799-821.
- Vecoli, M. 2000. Palaeoenvironmental interpretation of microphytoplankton diversity trends in the Cambrian–Ordovician of the northern Sahara Platform. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 160, 329-346.
- Vecoli, M. and Le Hérissé, A. 2004. Biostratigraphy, taxonomic diversity, and patterns of morphological evolution of Ordovician acritarchs (organic-walled microphytoplankton) from the northern Gondwana margin in relation to palaeoclimatic and palaeogeographic changes. *Earth-Science Reviews*, 67, 267-311.
- Wicander, E.R. 1974. Upper Devonian–Lower Mississippian acritarchs and prasinophycean algae from Ohio, U.S.A. *Palaeontographica Abteilung B*, 148, 9–43.
- Wicander, E.R. 1975. Fluctuations in a Late Devonian–Early Mississippian phytoplankton flora of Ohio, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 17, 89-108.
- Wicander, R., Clayton, G., Marshall, J.E.A., Troth, I. and Racey, A. 2011. Was the latest Devonian glaciation a multiple event? New palynological evidence from Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 305, 75-83.
- Wicander, E.R. and Loeblich, A.R., Jr. 1977. Organic-walled microphytoplankton and its stratigraphic significance from the Upper Devonian Antrim Shale, Indiana, U.S.A. *Palaeontographica Abteilung B*, 160, 129-165.
- Wicander, R. and Playford, G. 1985. Acritarchs and spores from the Upper Devonian Lime Creek Formation, Iowa, U.S.A. *Micropaleontology*, 31, 97-138.
- Wicander, R. and Wood, G.D. 1981. Systematics and biostratigraphy of the organic-walled microphytoplankton from the Middle Devonian (Givetian) Silica Formation, Ohio, U.S.A. *American Association of Stratigraphic Palynologists, Contributions Series*, 8, 1-137.
- Wicander, R. and Wright, R.P. 1983. Organic-walled microphytoplankton abundance and stratigraphic distribu-

- tion from the Middle Devonian Columbus and Delaware Limestones of the Hamilton Quarry, Marion County, Ohio. *Ohio Journal of Science*, 83, 2-13.
- Williams, G.L., Fensome, R.A., Miller, M.A. and Sargeant, W.A.S. 2000. A glossary of the terminology applied to dinoflagellates, acritarchs and prasinophytes, with emphasis on fossils: Third edition. *American Association of Stratigraphic Palynologists, Contributions Series*, 37, 1-365.
- Willman, H.B., Atherton, E., Buschbach, T.C., Collinson, C., Frye, J.C., Hopkins, M.E., Lineback, J.A. and Simon, J.A. 1975. Handbook of Illinois stratigraphy. *Illinois State Geological Survey Bulletin*, 95, 1-261.
- Winslow, M.R. 1962. Plant spores and other microfossils from Upper Devonian and Lower Mississippian rocks of Ohio. *United States Geological Survey Professional Paper*, 364, 1-93.
- Witzke, B.J. and Bunker, B.J. 1996. Relative sea-level changes during Middle Ordovician through Mississippian deposition in the Iowa area, North American craton. In: Witzke, B.J., Ludvigson, G.A. and Day, J. (eds.), *Paleozoic sequence stratigraphy: Views from the North American craton. Geological Society of America Special Paper*, 306, 306-330.
- Wood, G.D. 1984. A stratigraphic, palaeoecologic, and palaeobiogeographic review of the acritarchs *Umbellasphaeridium deflandrei* and *Umbellasphaeridium saharicum*. *Compte Rendu, Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère, Washington/Champaign-Urbana, May 1979*, 2, 199-211.
- Wood, G.D. 1986. Some Middle Devonian (Givetian) chitinozoans and acritarchs from New York State: Preliminary results. In: Miller, M.A. (ed.), *A field excursion to Trenton Group (Middle and Upper Ordovician) and Hamilton Group (Middle Devonian) localities in New York, and a survey of their chitinozoans. American Association of Stratigraphic Palynologists Field Trip Guidebook*, 101-114.
- Wood, G.D. and Clendening, J.A. 1985. Organic-walled microphytoplankton and chitinozoans from the Middle Devonian (Givetian) Boyle Dolomite of Kentucky. *Palynology*, 9, 133-145.
- Work, D.M., Mapes, R.H. and Thompson, T.L. 1988. A new prodromitid ammonoid genus from the Hannibal Shale (Lower Mississippian) of Missouri. *Journal of Paleontology*, 62, 772-778.

Appendix: Inventory of illustrated specimens

Slide locations of individual specimens are specified by coordinates derived from a standard "England Finder" slide. Specimen catalog numbers (CM19159-CM19255 inclusive) are those of the permanent repository: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.

Recibido: abril 2013
 Revisado: junio 2013
 Aceptado: julio 2013
 Publicado: octubre 2013

Species/type	Plate/Figure number	Sample number	Slide number	England Finder	Catalog number
<i>Cymatiosphaera ambotrocha</i>					
Hypotype	1/1	1169 ASI	>20 µm6	R45/1	CM19159
Hypotype	1/2	1170 ASI	>20 µm7	K42/1	CM19160
<i>Cymatiosphaera antera</i>					
Hypotype	1/3	1169 ASI	>20 µm6	H45/4	CM19161
<i>Cymatiosphaera chelina</i>					
Hypotype	1/4	1169 ASI	>20 µm7	D40/0	CM19162
Hypotype	1/5	1169 ASI	>20 µm6	E28/1	CM19163
<i>Cymatiosphaera parvicarina</i>					
Hypotype	1/6	1169 ASI	>20 µm7	U28/3	CM19164
Hypotype	1/7	1169 ASI	>20 µm6	N36/1	CM19165
<i>Cymatiosphaera perimembrana</i>					
Hypotype	1/8	1169 ASI	>20 µm6	E41/0	CM19166
Hypotype	1/9	1169 ASI	>20 µm7	L33/4	CM19167
<i>Cymatiosphaera scitula</i>					
Holotype	1/12	1171 ASI	>20 µm6	V25/4	CM19168
Hypotype	1/13	1169 ASI	>20 µm7	E37/3	CM19169

Species/type	Plate/Figure number	Sample number	Slide number	England Finder	Catalog number
<i>Leiosphaeridia</i> spp.					
Hypotype	1/15	1169 ASI	>20 µm6	D44/3	CM19170
Hypotype	1/16	1169 ASI	>20 µm6	U42/3	CM19171
<i>Muraticavea enteichia</i>					
Hypotype	1/10	1171 ASI	>20 µm3	X36/0	CM19172
Hypotype	1/11	1171 ASI	>20 µm1	K35/3	CM19173
<i>Polyedryxium embudum</i>					
Hypotype	2/3	1169 ASI	>20 µm6	U45/0	CM19174
Hypotype	2/4	1169 ASI	>20 µm6	H27/0	CM19175
<i>Polyedryxium pharaone</i>					
Hypotype	1/14	1171 ASI	>20 µm8	U31/0	CM19176
<i>Tasmanites</i> spp.					
Hypotype	2/1	1169 ASI	>20 µm6	N43/3	CM19177
Hypotype	2/2	1169 ASI	>20 µm6	N36/0	CM19178
<i>Baltisphaeridium distentum</i>					
Hypotype	2/5	1169 ASI	>20 µm7	F38/2	CM19179
Hypotype	2/6	1169 ASI	>20 µm8	P29/0	CM19180
<i>Barathrisphaeridium chagrinese</i>					
Hypotype	4/1	1169 ASI	>20 µm8	J34/1	CM19181
<i>Estiastra culcita</i>					
Hypotype	4/2	1169 ASI	>20 µm7	K28/4	CM19182
Hypotype	4/3	1169 ASI	>20 µm7	K22/0	CM19183
<i>Gorgonisphaeridium absitum</i>					
Hypotype	3/5	1170 ASI	>20 µm6	W38/4	CM19184
Hypotype	3/6	1170 ASI	>20 µm7	F29/0	CM19185
<i>Gorgonisphaeridium elongatum</i>					
Hypotype	3/7	1169 ASI	>20 µm7	P40/1	CM19186
Hypotype	3/8	1170 ASI	>20 µm6	E24/2	CM19187
<i>Gorgonisphaeridium ohioense</i>					
Hypotype	3/9	1169 ASI	>20 µm6	T31/1	CM19188
Hypotype	3/10	1170 ASI	>20 µm7	N35/0	CM19189
<i>Gorgonisphaeridium plerispinosum</i>					
Hypotype	3/11	1169 ASI	>20 µm6	L44/1	CM19190
<i>Gorgonisphaeridium savertonense</i>					
Holotype	3/12	1169 ASI	>20 µm7	H33/4	CM19191

Species/type	Plate/Figure number	Sample number	Slide number	England Finder	Catalog number
Hypotype	3/13	1169 ASI	>20 µm6	O32/2	CM19192
Hypotype	3/14	1169 ASI	>20 µm6	V39/0	CM19193
<i>Gorgonisphaeridium winslowiae</i>					
Hypotype	3/15	1171 ASI	>20 µm8	G37/0	CM19194
Hypotype	3/16	1171 ASI	>20 µm8	G29/0	CM19195
<i>Lophosphaeridium segregum</i>					
Hypotype	2/7	1169 ASI	>20 µm6	R35/4	CM19196
Hypotype	2/8	1169 ASI	>20 µm6	V43/2	CM19197
<i>Micrhystriidium adductum</i>					
Hypotype	2/9	1169 ASI	>20 µm8	R33/1	CM19198
Hypotype	2/10	1169 ASI	>20 µm6	F32/1	CM19199
<i>Micrhystriidium stellatum</i>					
Hypotype	2/11	1169 ASI	>20 µm6	S38/2	CM19200
Hypotype	2/12	1169 ASI	>20 µm8	R32/2	CM19201
<i>Micrhystriidium</i> sp. cf. <i>M. pentagonale</i>					
Hypotype	2/13	1170 ASI	>20 µm7	K22/0	CM19202
Hypotype	2/14	1170 ASI	>20 µm6	N38/0	CM19203
Hypotype	2/15	1170 ASI	>20 µm7	F32/0	CM19204
<i>Micrhystriidium</i> spp.					
Hypotype	3/1	1169 ASI	>20 µm7	S36/2	CM19205
Hypotype	3/2	1169 ASI	>20 µm6	N40/1	CM19206
Hypotype	3/3	1172 ASI	>20 µm6	C27/3	CM19207
Hypotype	3/4	1172 ASI	>20 µm6	S28/1	CM19208
<i>Multiplicisphaeridium ramusculosum</i>					
Hypotype	4/4	1169 ASI	>20 µm6	V39/1	CM19209
<i>Navifusa bacilla</i>					
Hypotype	2/16	1170 ASI	>20 µm7	X26/1	CM19210
<i>Puteoscortum polyankistrum</i>					
Hypotype	4/5	1169 ASI	>20 µm8	L31/2	CM19211
Hypotype	4/6	1169 ASI	>20 µm7	K32/0	CM19212
<i>Puteoscortum sprucegrovense</i>					
Hypotype	4/7	1169 ASI	>20 µm7	N26/3	CM19213
Hypotype	4/8	1169 ASI	>20 µm8	C37/0	CM19214
Hypotype	4/9	1170 ASI	>20 µm8	S25/1	CM19215
<i>Stellinium comptum</i>					
Hypotype	4/10	1169 ASI	>20 µm7	K30/3	CM19216

Species/type	Plate/Figure number	Sample number	Slide number	England Finder	Catalog number
Hypotype	4/11	1169 ASI	>20 µm6	N32/2	CM19217
<i>Stellinium micropolygonale</i>					
Hypotype	4/12	1169 ASI	>20 µm6	G37/4	CM19218
Hypotype	4/13	1169 ASI	>20 µm7	R29/1	CM19219
<i>Unellium elongatum</i>					
Hypotype	4/14	1170 ASI	>20 µm6	O36/0	CM19220
Hypotype	4/15	1169 ASI	>20 µm7	M27/0	CM19221
<i>Unellium winslowiae</i>					
Hypotype	4/16	1169 ASI	>20 µm6	P46/4	CM19222
Hypotype	4/17	1169 ASI	>20 µm6	J31/4	CM19223
<i>Veryhachium arcarium</i>					
Hypotype	5/1	1170 ASI	>20 µm7	N35/4	CM19224
<i>Veryhachium cymosum</i>					
Hypotype	5/2	1169 ASI	>20 µm6	G40/3	CM19225
Hypotype	5/3	1169 ASI	>20 µm6	O40/2	CM19226
<i>Veryhachium europaeum</i>					
Hypotype	5/4	1169 ASI	>20 µm7	L32/4	CM19227
Hypotype	5/5	1169 ASI	>20 µm7	Q27/2	CM19228
<i>Veryhachium polyaster</i>					
Hypotype	4/18	1169 ASI	>20 µm7	S36/0	CM19229
<i>Veryhachium trispinosum "complex"</i>					
Hypotype	5/6	1169 ASI	>20 µm7	H33/4	CM19230
Hypotype	5/7	1169 ASI	>20 µm6	P35/3	CM19231
Hypotype	5/8	1169 ASI	>20 µm6	H27/0	CM19232
<i>Punctatisporites hannibalensis</i>					
Hypotype	5/9	1173 ASI	>20 µm4	Q33/1	CM19233
Hypotype	5/10	1172 ASI	>20 µm1	L38/0	CM19234
Hypotype	5/11	1172 ASI	>20 µm5	M36/3	CM19235
Holotype	5/12	1172 ASI	>20 µm7	Q31/0	CM19236
<i>Retusotriletes incohatatus</i>					
Hypotype	5/13	1171 ASI	>20 µm7	M35/3	CM19237
<i>Converrucosisporites</i> sp. A					
Hypotype	5/19	1169 ASI	>20 µm6	S33/0	CM19238
<i>Verrucosisporites nitidus</i>					
Hypotype	5/16	1170 ASI	>20 µm5	K42/0	CM19239
<i>Verrucosisporites</i> sp. A					

Species/type	Plate/Figure number	Sample number	Slide number	England Finder	Catalog number
Hypotype	5/14	1171 ASI	>20 µm2	Q32/4	CM19240
Hypotype	5/15	1169 ASI	>20 µm1	E31/0	CM19241
<i>Emphanisporites rotatus</i>					
Hypotype	5/17	1171 ASI	>20 µm7	V26/2	CM19242
Hypotype	5/18	1171 ASI	>20 µm4	Y23/4	CM19243
<i>Indotriradites explanatus</i>					
Hypotype	6/10	1171 ASI	>20 µm3	V37/2	CM19244
Hypotype	6/11	1171 ASI	>20 µm8	P30/3	CM19245
<i>Vallatisporites hystricosus</i>					
Hypotype	6/1	1171 ASI	>20 µm8	V25/2	CM19246
<i>Ancyrospora</i> sp. cf. <i>A. langii</i>					
Hypotype	6/4	1171 ASI	>20 µm5	L42/1	CM19247
<i>Geminospora</i> sp. A					
Hypotype	5/20	1171 ASI	>20 µm6	L34/3	CM19248
<i>Auroraspora macra</i>					
Hypotype	6/5	1169 ASI	>20 µm3	U34/2	CM19249
Hypotype	6/6	1171 ASI	>20 µm3	E42/3	CM192450
<i>Grandispora cornuta</i>					
Hypotype	6/8	1171 ASI	>20 µm8	R34/0	CM19251
Hypotype	6/9	1169 ASI	>20 µm5	Y29/0	CM19252
<i>Retispora lepidophyta</i>					
Hypotype	6/2	1171 ASI	>20 µm5	M27/0	CM19253
Hypotype	6/3	1169 ASI	>20 µm4	P45/0	CM19254
<i>Teichertospora torquata</i>					
Hypotype	6/7	1170 ASI	>20 µm5	S38/2	CM19255