Systematics and evolutionary significance of some new cryptospores from the Cambrian of eastern Tennessee, USA

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**Abstract**

The highly bioturbated mudstones of the uppermost Rome Formation and the Conasauga Group in eastern Tennessee contain an extensive palynoflora that consists primarily of nonmarine, spore-like microfossils, which are treated systematically as cryptospores because they present characters that are consistent with a charophytic origin. The following new taxa are proposed: *Adinosporus voluminosus*, *Adinosporus bullatus*, *Adinosporus geminus*, *Spissuspora laevigata*, and *Vidalagia maculata*. The lamellated wall ultrastructure of some of these cryptospores appears to be homologous to extant, crown group sphaeroecharalean liverworts and to the more basal genus, *Haplomitrium*. There is direct evidence that some of these cryptospores developed via endosporogenesis—entirely within the spore mother cell wall. The topology of enclosed spores indicates that the meiotic production of spore dyads represents the functional spore end-members, but the diaspore itself appears to be a spore packet corresponding to the contents of each original spore mother cell. Aeroterrestrial charophytes of this time period underwent sporogenesis via successive meiosis rather than simultaneous meiosis. Overall, these remains are consistent with Bower’s antithetic origin of the plant sporophyte because they present a picture of extensive and varied spore development (i.e. sporogenesis) well in advance of the occurrence of vegetative sporophytes in the fossil record.

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**1. Introduction**

This report begins documentation of the systematics of a terrestrial biota that was extensively distributed on the Laurentian continent by middle Cambrian (Series 3) time. Evidence for this early land biota is based primarily on palynological remains from rocks that appear to have formed in both estuarine and proximal marine settings from within an inner clastic belt that encircled the paleocontinent of Laurentia during much of Cambrian time (Lochman-Balk, 1971). Individual samples from these strata can be extremely abundant in terms of sheer numbers of palynomorphs; however, the morphological variability (pleomorphism) which is expressed in these spore-like cells has meant that their systematic characterization has not been straightforward. Their distribution is extensive as well; they have been recovered from around the margin of Laurentia from eastern Tennessee (Strother and Beck, 2000) to Missouri (Wood and Stephenson, 1988), to Texas (Hitchcock Fm, Strother and Baldwin, unpublished), to Arizona (Baldwin et al., 2004; Strother et al., 2004; Taylor and Strother, 2008), Nevada (Yin et al., 2013), to Idaho (Bloomington Fm, Strother, unpublished) and Wisconsin (Taylor and Strother, 2009). The purpose of this report is not to provide a comprehensive survey or overview of this microflora. Instead, what is presented here are designations of new taxa from a limited number of samples. A more comprehensive assessment of their stratigraphic and geographic distribution will be forthcoming.

If classified as sphaeromorph acritarchs, the palynomorphs described herein would be thought of as problematic, possibly marine algae, and most certainly would not be considered significant with regard to the origin of land plants. However, there are several lines of evidence with respect to geology (Baldwin et al., 2004), sporomorph morphology (Strother et al., 2004), and ultrastructure (Taylor and Strother, 2008; Taylor, 2009) that lead to their inclusion in the informal cryptospore sensu Strother and Beck (2000). Again, it is not the purpose of this report to provide another defense of the use of the term cryptospore nor is it necessary to repeat the arguments that associate these palynomorphs with the origin of land plants as originally presented by Strother et al. (2004). Subsequent work on Cambrian fossils (Taylor and Strother, 2008, 2009) in conjunction with extant studies (Brown and Lemmon, 2011; Graham et al., 2012) and especially the discovery of dyads in a basal liverwort (Renzaglia et al., 2015), continue to generally support the conclusions of Strother et al. (2004)—these palynomorphs represent spores of aeroterrestrial charophytic algae that were evolving in response to partial subaerial exposure during their life cycle.

The Cambrian cryptospores are unlike previously described cryptospore taxa from middle Ordovician (Darriwilian) and younger rocks. These younger cryptospores are recognized as such because they retain distinctive attachment geometries—either as geometrically
regular tetrads or as isomorphic, typically hilate dyads. The Cambri-
ian forms, however, generally lack geometrically regular topologies,
in which spores of similar form are arranged in symmetric tetrad or
dyad configurations. Instead, both the distinct nature of individual
spore-bodies and their physical attachment geometries are often un-
clear. In addition, Cambrian cryptospores may occur as packets of mul-
tiple spore-like bodies surrounded by one or more, synoecosomal walls
(Taylor and Strother, 2008). These facts, based on morphology, re-
veal unambiguous differences between Cambrian and younger
cryptospores. However, it is likely that these morphological differ-
ences reflect underlying biological variation in meiosis and develop-
ment during sporogenesis, rather than underlying systematic differ-
ences in evolutionary origin.

In order to place the Cambrian cryptospores within their correct
phyletic context, it is necessary to make some broad assump-
tions about functional morphology. While this not a terribly satis-
factory method, it does provide a general platform with which to
explore evolution as it was occurring in terrestrial environments
during Cambro–Ordovician time. I do not wish to claim that these
microfossils are a document of any specific evolutionary lineage
that is ancestral to the embryophytes; however, these microfossils
are relevant to the study of the origin of land plants because they are
spores derived from thalloid algal sporophytes that were evolv-
ing in response to living in subaerial settings. Phylogenists refer
to extant terrestrial algae that survive subaerial exposure as
eaeroterrestrial, and this term will be used here as well to describe
the Cambrian cryptospore producers. The assumption that these
algae were aeroterrestrial can be justified on the basis of the
spore-like character of these microfossils: they possess thick, ho-
mogeneous to multilaminate walls composed of highly refractory,
sporopollenin-like, organic compounds; they were widely dis-
persed in large numbers; they were distributed in shallow marine
to estuarine environments (reflecting freshwater and terrestrial
provenance); and their morphology (including wall ultrastructure)
parallels that of younger cryptospores and miospores. This is in ap-
position to the cyst-like characters found in marine planktonic
algae, which are typically thinner-walled and reflect a far greater
range in morphology and surface sculpture.

Ultrastructural studies of Cambrian cryptospores (Strother et al.,
2004; Taylor and Strother, 2008, 2009; Taylor, 2009) have already
shown that many of these early forms possess laminated walls,
some of which appear homologous with those of the crown group
(Forrest et al., 2006) liverworts Riccia and Sphaerocarpus
(Taylor, 2010) and the primitive liverwort, Haplomitrium gibbisa
(Renzaglia et al., 2015). This indicates that embryophytic spore characters in
strephtyple lineages were evolving prior to the origin of the first em-
byrophyte sporophytes sensu stricto (i.e. biaxial sporophytes that devel-
op from a multicellular embryo (Niklas, 1997; Niklas and Kutschera,
2010)). In a direct reading of the fossil record, spores appear before spo-
rophytes. This idea is not new, in fact, it is a fundamental thesis of
Bower’s atheriotic hypothesis for the origin of the plant sporophyte,
in which he proposed that the plant sporophyte must have preceded the
evolution of a vegetative sporophyte (Bower, 1908). “Spores before
sporopores,” has been more recently championed in cytological
studies of sporogenesis in extant bryophytes, which show accelerat-
ed onset of cytokinesis in combination with the retarded application of
sporopollenin sporoderm during spore development (Brown and
Lemmon, 2011). Thus, some living bryophytes directly support
earlier suppositions about the developmental “transfer” of sporopollenin from zygote to (meio)spore wall (Graham, 1985; Hemsley,
1994). Studies of meiosis and zygote development in Coleochaete
also strongly support the ideas of Bower (Graham, 1984, 1985,
1993). A thorough understanding of heterochrony and sporogenesis
in both bryophytes and charophytes is now essential for guiding our
interpretation of fossil cryptospores recovered from Ordovician and
Cambrian strata (Strother et al., 2004, 2015).

1.1. Endosporogenesis and the interpretation of cryptospore morphology

Plate I, 1, exemplifies a fundamental problem with how to interpret
and describe systematically Cambro–Ordovician cryptospores. This fos-
sil consists of a spherical wall (cell) within which occur both a
sporophyte dyad and an incompletely (?) formed tetrads. How does one deal with this systematically? In a biological sense, this specimen
consists of a spore mother cell (SMC) that underwent a series of nuclear
divisions (preceded by DNA endoreduplications) along with successive
cytokinesis to produce two distinct spore clusters—a dyad and an in-
completely formed tetrad. More specifically, after a first mitotic division,
the resultant nuclei migrated away from each other, with one undergo-
ing a single subsequent mitosis (resulting in a dyad), but the other di-
viding twice to produce an apparent tetrad of spores. The specimen in
Plate I, 2, is similar, but here the two endosporic products appear
more similar to each other—probably incompletely formed tetrads.
Spore cell walls formed only after the first mitosis and subsequent nu-
clear migration.

All of this spore development occurred endogenously, entirely
within the SMC, hence it can be viewed as an example of
endosporogenesis. This form of successive meiosis occurs when mi-
tosis becomes temporally decoupled from cytokinesis, establishing
a classic case of heterochrony. It can happen through an acceleration
of chromosomal duplication and nuclear division (mitosis), or via a
retardation of cytokinesis and cell wall formation. Although we can-
not be certain of the spore ploidy, it is most probable that the SMC it-
self was either diploid or polyploid before meiosis began, but that the
resultant spores were all haploid.

Taxonomic precedent among paleobotanists has been to segregate
cryptospore dyads and tetrads into different taxa at the genus level
(Strother, 1991; Richardson, 1996); however, in this case, one would
certainly argue that both the enclosed dyad and tetrad in Plate I, 1,
must belong to the same biological species. A parallel condition occurs
in the late Cambrian cryptospore. Agamachates casearius Taylor and
Strother, 2008, which consists of spore packets that may contain differ-
cent numbers of what are, ultimately, dyads. The result of this under-
standing is that the application of taxonomic distinctions between
tetrads and dyads, while perhaps warranted on strictly morphological
grounds, is not to be trusted to demarcate biological species.

While it is possible to find individual geometrically regular tetr-
rads and dyads in large populations of Cambrian cryptospores (e.g.
Figs. 14g and 15b in Baldwin et al., 2004, and Pl. 1.2 in Taylor and
Strother, 2009), such individuals are not particularly characteristic
of the populations as a whole. Given our current level of stratigraphic
sampling, therefore, abundant isometric tetrads first occur in the
Darriwillian of Saudi Arabia (Strother et al., 1996, 2015; Le Hérisé
et al., 2007). This indicates that pre-Darriwillian cryptospores were pro-
duced by organisms utilizing successive meiosis and that simultaneous
meiosis in sporopores first evolved during the Dapingian–
Darriwillian interval. This decoupling of mitosis and cytokinesis has
combined with multiple episodes of wall formation to produce spores
and spore pairs which are not isomorphic. Thus, the morphology of
Cambrian cryptospores appears highly variable, especially when com-
pared to younger forms. And this variability places the Cambrian
cryptospores clearly outside the acceptable morphologic range of
miospores derived from embryophytes, whose synapomorphies are de-
defined on characters stemming from simultaneous meiosis.

Plate I, 3, demonstrates the problem of variability in packet topology
and spore morphology that occurs within what must be a biologically
unique species. The illustrated sample consists of three pairs of spore-
like packets which are aligned linearly. The A-A' pair appears to each
be dyads, the B-B' pair also appears to be dyads, but they differ in size
and shape from the A-A' pair. Finally, the largest pair set, C-C' appears
grossly as dyads, but with an indeterminate number of interior spore-
bodies present in each member of the pair. Even the least complex spec-
imen (A) shows both a darkened, equatorial thickening (ET arrow)
delineating the dyad boundary in addition to a transverse thickened band (TB arrow). This cryptospore cluster represents, in a nutshell, the inherent difficulty in constructing a taxonomy that incorporates such a wide range of sporomorph morphology and topology. Thus, the taxonomy that follows represents a compromise: one that is inherently “lumped” in overall style, but with the inclusion of particular morphological end-members into separate, disjunct taxa.

1.2. Ultrastructure and the generation of cryptospore systematics

Several recent works concerning the sporoderm ultrastructure of Cambrian cryptospores have provided the basis of an improved understanding of the topology of genetically irregular cryptospores (Taylor and Strother, 2008, 2009; Taylor, 2009). This knowledge of underlying wall structure has led to the recognition that spore characters related to development are essential to the interpretation of morphology, a view that is reinforced by modern studies in bryophyte sporogenesis (Brown and Lemmon, 2011). I have tried to present a reasonable defense of a streptomphytic origin to the Cambrian cryptospores, based on their laminated construction, that appears plesiomorphic in the embryophytes (Blackmore and Barnes, 1987). Thus, ultrastructure as viewed with the transmission electron microscope (TEM) has been the critical tool permitting the general systematic placement of these problematic microfossils.

Ultrastructure also plays an essential role in the interpretation of morphology for the purpose of generating a reasonable lower-level taxonomy for these forms, which is the primary purpose of this report. In general, the Cambrian material is quite opaque in transmitted visible light (Baldwin et al., 2004; Strother et al., 2004). This is not necessarily due to carbonization that is associated with thermal maturation. Rather, the walls of most of the cryptospores studied in this report are composed of one or more laminae that are highly folded back on themselves, creating thick accumulations of wall material (Taylor, 2009). These contorted laminae overlap each other to create dense, thick walls that are only marginally translucent in visible light, although they are generally translucent to near infrared light (e.g. Plate 1, 2).

2. Materials and methods

A series of samples comes from both core and outcrop in eastern Tennessee, USA. The principal source of these samples is from a core from the JOY No. 2 well (Hasson and Haase, 1988) from the Oak Ridge National Laboratory [ORNL] in Oak Ridge Tennessee, US. This core was sampled on site late in 2001 and again in 2007. The study of core samples was supplemented with field collections made by Gordon Wood in 1981, plus additional field samples collected from the Thorn Hill section (Byerly et al., 1986) together with John Beck in 2001, and later and by John Beck and Brian Pedder in 2008.

In this report, the following samples were used as a source for plate illustrations: from the JOY No. 2 well, samples J2-1518 (Rogersville Shale), J2-1541 (Rogersville Shale), J2-1571 (Rogersville Shale), J2-1578 (Rogersville Shale), J2-1580s (Rogersville Shale), J2-1587s (Rogersville Shale), J2-1803 (Pumpkin Valley Shale); from the Thorn Hill Section, samples SB01-14 (Rome Formation), SB01-17 (Rogersville Shale); from the Grand Canyon, GC96-10A (Bright Angel Shale, Thunder Falls, Tapeats Creek drainage), GC10-3 (Bright Angel Shale, Red Canyon section). A generalized stratigraphic section for eastern Tennessee and for the Grand Canyon is presented in Fig. 1.

Samples were processed using standard palynological techniques as described in Barss and Williams (1973). At the Palaeobotany Laboratory at Boston College, approximately ten grams of rock sample was placed in a 250 ml Teflon beaker with about 125 ml of concentrated (52%)
HF. After several days, the samples were rinsed multiple times in deionized water, treated in warm dilute HCl if needed, and oxidized by short (typically 2–20 minutes) treatment in either dilute HNO₃ or Schulze’s solution. The oxidized residues were then cleaned with a heavy liquid (gravity) separation using ZnCl₂ solution adjusted to a specified concentration. The oxidized residues were then cleaned with a heavy liquid by ZnCl₂ solution adjusted to a specific gravity of 2.0. Screening treatments varied from sample to sample, but the recovery of palynomorphs was set to fall between 218 and 224. This results in a medium light fraction.

Slides for transmitted white light microscopy were mounted in glycine jelly. White light digital images were obtained by mounting a Nikon D1x body onto the photo-tube of a Zeiss Universal microscope. Exposure was controlled with a coplanar electronic shutter mounted onto the photo-tube of a Zeiss Universal microscope. Ni kon D1x body onto the photo-tube of a Zeiss Universal microscope. 

3. Systematic paleontology

Domain: Eukarya Woese et al. (1990)
Eukaryotic Super-group: ARCHAEPLASTIDA Adl et al. (2005)
Subphylum: CHLOROPHYTA Migula (1897) emend. Karol et al. (2001)
Informal taxon, Anteturma: CRYPTOSPORITES Richardson, Ford and Parker (1984)

ADINOSPORUS Strother, gen. nov.
Type: Adinosporus voluminosus Strother, sp. nov.
Diagnosis: Packets of one or more inaperturate, subspherical, spore-like cells closely adpressed into various geometric arrangements; walls composed of one or more laminae, each of which may be highly folded; individual wall laminae may enclose two or more of the spore-like cells; walls robust without perforations or large arcuate folds; packet margins typically convex in plan view; internally thickened bands, often transverse to attached spore-bodies are common. Etymology: From the Greek, adinos, meaning thick, dense, crowded, referring to the multilaminate walls.

Discussion: Spore-like cells do not generally form geometrically regular packets as the size of individual spore-bodies may vary within the packet; contacts between individual spore-bodies may appear indistinct or characterized by darker zones or bands, rather than discrete walls; walls appear thick, often dark, especially in central areas where they overlap. Spore margins, while they approach a circular outline and are always smooth, are typically somewhat irregular in outline. The basic unit of paired sets of cells seems to be the starting point for multiple sets of attached cells. Many tetrads appear to have this form of paired dyads recognizable by size differences between pairs and by the somewhat adpressed and mutually compressed, flattened contact areas between vesicles within a pair. But the arrangement of paired sets is not absolute, as solitary and odd-numbered polyads are quite common. Although folds in the walls are common, they are rarely broadly arcuate in appearance, but are more often thinner and somewhat sinuous, or ropey, possibly reflecting simple compression of the wall during diagenetic flattening. Folds are a reflection of the entire membrane plus vesicle complex, so that folds themselves may include one or more of the wall laminae.

These forms differ from leiospherids in several distinct ways. Species of Adinosporus are not perfectly spherical in either their attached or separated form but are more or less subspherical in shape. The color is not the light to medium yellow that is more typical of thinner-walled acritarchs; these forms appear more robust than most acritarch species, indicating either a generally thicker wall or affecting simple compression of the wall. Folding of the vesicle wall in the leiosphaerids tends to form broad arcuate folds which may extend for the entire diameter of the vesicle. This is never the case with Adinosporus which forms more narrow, sinuous folds. Leiosphaeridia, as originally established by Eisenack (1958), also has a pylem, which, although not always expressed in species of Leiosphaeridia, is completely lacking in Adinosporus. Synsphaeridium differs in possessing thinner walls, a spherical (rather than discoidal) shape to the discrete vesicles, lack of clear attachment thickenings and lack of enclosing envelopes, membranes, or syncocosporal walls.
Adinosporus voluminosus Strother, sp. nov.

Holotype: Original slide number J2-1571/8, England Finder location H57, photomicrographs Plate I, 3C, 4.

Repository: Harvard University Paleobotanical Collection (HUPC) No. 65846.

Type locality: Joy No. 2 well, depth 1571’, location N35.93” W84.27”, Oak Ridge National Laboratories, Oak Ridge Tennessee, USA.

Type stratum: Rogersville Shale (Conasauga Group).

Etymology: From the Latin voluminosus, meaning full of folds, of many volumes.

Diagnosis: Surface laevigate, often blotchy; spore-body margins smooth, but flexuous, irregular, not typically rigid or of consistent curvature around the entire margin.

Description: Packets may be solitary, clumped, or in more-or-less geometrically regular, planar rows. A population of 50 spore packets from sample J2-1578 (slide J2-1578.1) had a mean width of 20.9 µm, a range of 12–34 µm, with a standard deviation of 4.5 µm. Specimens were effectively sampled at random, as the graduated reticule was not realigned during measurement.

Discussion: Adinosporus voluminosus is the most common species in the Laurentian assemblages studied thus far from the Bright Angel Shale (Baldwin et al., 2004; Strother et al., 2004) and from the Conasauga Group. The blotchy nature of the wall is probably due to variations in thickness in the wall, which itself may be composed of multiple, internally folded laminae (Taylor and Strother, 2008). For many packets, it has been difficult to count the number of attached cells, but many forms occur as dyads and tetrads. The species holotype (Pl. I, 3 C) is associated with a set of six packets arranged in two rows. Plate I, 4, shows the holotype cropped from its neighbors. It demonstrates the overall irregular to nearly spherical form of each member of the dyad pair.

Packet morphology ranges considerably, as exemplified in Plate I, 3. Although tetrads (Plate I, 5–14) are not the most common packet form, neither are they particularly rare. Tetrads may be more or less planar (Plate I, 5–9), but they range into configurations that can be almost tetrahedral (Plate I, 10, square (Plate I, 11), or irregularly flattened (Plate I, 12–13). They may be tightly compact as in Plate I, 6, 10, and 14, or more open, as in Plate I, 8, and 9. Sometimes, it is not possible to determine exactly how many individual spore-bodies are contained within the packets (Plate I, 3, 15–17). It is not uncommon to observe what appear to be triads comprised of a single larger cell closely adpressed to a dyad pair. This configuration can be seen in Plate I, 15, but is most obvious in Plate I, 16.

Dyads or apparent dyads are a common packet form (Plate I, 17–25). Once again, however, there is considerable variation in the distinct nature of individual enclosed spore-bodies. Plate I, 17, exhibits one aspect of this variability as this image shows a distinct dyad pair in close association with a pseudodyad. This pseudodyad is confirmed as such by a continuous margin and folds (F, arrow) that cross the equatorial plane. The darkened region of the equatorial plane appears to mark a potential plane of division, corresponding to a division that actually did take place in the adjacent dyad. Many dyads contain internal, thickened bands (TB, arrows) that appear to mark these sites of potential division planes (Plate I, 3, 20–23). Yet, in many cases, the internal walls and exact spore-body configurations remain ambiguous, as in Plate I, 18. In other specimens, the very nature of the wall itself, which comprises numerous ropey folds expressing the underlying multilamellate nature of the sporoderm, obscures the exact articulation of internal spore-bodies. This effect can be seen in Plate I, 19 and 24, in which the walls are highly folded. When such folds are narrower (Plate I, 25), or less numerous, (Plate I, 20–23), the delineation of the spore-bodies is more obvious. Dyads may also be flattened along their axial plane, producing nearly circular forms (Plate I, 26).

Often, Adinosporus voluminosus occurs as packets of an indeterminate number of enclosed or tightly adherent spore-bodies which are grouped into clusters (Plate II, 1–6). Packets within clusters can be fairly tightly associated (Plate II, 1, 2) or they may be more loosely associated (Plate II, 3). Plate II, 6, illustrates an isolated packet which is clearly lacking a synocoecsoral wall enclosing the entire spore set. This quality, that is the presence or absence of an enclosing envelope, varies considerably, as often, when viewed in transmitted light, the individual packets do appear to be enclosed Plate II, 1–3.

Adinosporus voluminosus also occurs in the Rome Formation and two examples are illustrated in Plate II, 4, 5. This occurrence has some biotaxonomic significance as the Rome has long been considered to be of early Cambrian age, which is now Series 2, Stage 4 (Fig. 1).

Adinosporus pullatus Strother, sp. nov.

Holotype: Original sample SB01-17, slide number NHM/08/1810, England Finder location M33, photomicrograph Plate II, 7.

Repository: Harvard University Paleobotanical Collection (HUPC) No. 65847.

Type locality: Sample of the Lower Shale Member of the Rogersville Shale, immediately below contact with the Craig Limestone Member was taken from a roadcut along US 25E at N 36.38”, W 83.44”. This outcrop is part of the classic section at Thorn Hill, Tennessee, USA, described in Byerly et al. (1986).

Type stratum: Rogersville Shale (Conasauga Group).

Etymology: From the Latin bulla, refers to the knob-like bulbls that characterize this species.

Diagnosis: Surface laevigate with one or more darker bulbls, squarish to rounded, from 1 to 3 µm in width, embedded within the laminated wall.

Description: Bulbls generally few, one or two per spore-body, sometimes more.

A population of 50 specimens from sample SB01-17 (slide NHM/08/1810) measured across the diameter of individual spore-bodies had a mean width of 20.5 µm, a range of 11–34 µm, with a standard deviation of 4.1 µm. Specimens were effectively sampled at random, as the graduaded reticule was not realigned during measurement.

Discussion: The knobby form appears to be a variant upon A. voluminosus, for there is no distinguishable difference in size or other salient features. The bulbls do not necessarily occur on all the vesicles within a cluster, but the knobby ornament is easily recognizable and so is helpful in distinguishing the species. The number of bulbls varies from specimen to specimen, ranging from one or two per vesicle to perhaps 12–20 for an entire packet. They are typically 2–3 µm in diameter with a height of up to 1 µm. Somewhat similar thickenings are described by Wood and Benson (2000) in the Triassic Plaeisiodictyon mosellanum spp. bullatum, a chlorococcalean algal with inferred fresh to brackish water distribution.

The species holotype, illustrated in Plate II, 7, appears as a planar tetrad with a surrounding synocoecsoral wall. The wall appears to surround the entire tetrad as evidenced by its continuity across spore-bodies (arrow). The characteristic mottled appearance associated with the lamellated wall of Adinosporus is still quite evident in A. pullata. Packets show a similar variety of clustered arrangements: a large dyad (Plate II, 8); larger clusters (polyads) (Plate II, 9), paired dyads (Plate II, 10), single pseudo-dyads (Plate II, 11), and smaller clusters (Plate II, 12). The species occurs sporadically throughout the Rogersville Shale, but it is especially common in some samples of equivalent age from the Bright Angel Shale in the Grand Canyon, Arizona. Examples from sections at Red Canyon (Plate II, 9) and Tepazts Creek in the Grand Canyon (Plate II, 12) are illustrated here for comparison.

Adinosporus geminus Strother, sp. nov.

Holotype: Original slide J2-1578/A SEM, England Finder location Q34/4, photomicrograph Plate III, 1.

Repository: Harvard University Paleobotanical Collection (HUPC) No. 65848.

Type locality: Joy No. 2 well, depth 1578’, location N35.93” W84.27”, Oak Ridge National Laboratories, Oak Ridge Tennessee, USA.

Type stratum: Rogersville Shale (Conasauga Group).

Etymology: From the Latin geminus, twin-born.

Diagnosis: A quartet of spore-like organic-walled microfossils comprised of two pairs (dyads) adpressed laterally; spore attachment
within dyad pairs characterized by thickened medial zone without distinct suture; dyad margins may show a medial cleft or be smooth, effectively forming an ellipsoidal margin; suture between dyad pairs distinct and complete, but not typically characterized by thickenings; walls of medium but variable thickness, often characterized by ropey folds; individual spore-bodies subspherical flattened to subcircular ranging to hemispherical in outline.

**Description:** The walls are typically of medium density and may contain slightly sinuous wrinkles (folds) emanating medially and running normal to the medial plane of attachment; a darker, broadly arcuate, equatorial thickening (contact thickening) separates each spore of each dyad pair, but the two dyads are typically adpressed laterally without obvious structural modification, so they appear more distinct from each other than do individual spores within each dyad pair.
Plate III. Adinosporus geminus Strother, gen. et sp. nov. The scale bar represents 10 μm in all images. Figured specimens are considered to be paratypes if they occur on the same prepared slide as the holotype.

5. Paratype. Specimen demonstrating marginal thinning (arrow) which is due to the underlying lamellate nature of the sporoderm. Sample J2-1578, slide J2-1578/SEM, England Finder location X45, Rogersville Shale.
7. Paratype. Another smaller pair which remains only partially attached. Sample J2-1578, slide J2-1578/SEM, England Finder location G38/4, Rogersville Shale.

Plate II. Adinosporus voluminosus Strother, gen. et sp. nov. and Adinosporus bullatus Strother, gen. et sp. nov. The scale bar in all images is 10 μm—except for 7 where the scale bar represents 5 μm. Figured specimens are considered to be paratypes if they occur on the same prepared slide as the holotype.

3. Adinosporus voluminosus Strother, gen. et sp. nov. Another loosely arranged cluster of four packets. Sample J2-1578, Rogersville Shale.
4. Adinosporus voluminosus Strother, gen. et sp. nov. Loosely arranged set of five packets from the Rome Fm, which is of early (Series 2) Cambrian age. Sample SB01-14, Rome Fm, Thorn Hill section.
5. Adinosporus voluminosus Strother, gen. et sp. nov. Another set of two dense packets, also from the Rome Fm. Sample SB01-14, Rome Fm, Thorn Hill section.
7. Adinosporus bullatus Strother, gen. et sp. nov. Holotype. Specimen is essentially a planar tetrad with a synoecosporal wall (arrow) that appears to enclose the entire packet. Thickened bulbils (B) are the defining character for this species. Scale bar represents 5 μm. Sample SB01-17, slide number NHM/08/1810, England Finder location M33/0, Rogersville Shale. This sample is from the Thorn Hill section.
8. Adinosporus bullatus Strother, gen. et sp. nov. Paratype. A large dyad pair. Sample SB01-17, slide number NHM/08/1810, England Finder location E38/2.
9. Adinosporus bullatus Strother, gen. et sp. nov. A loose ring of packets recovered from the middle Cambrian (Glossopleura biozone) Bright Angel Shale. From a section in Red Canyon, Grand Canyon, Arizona. Sample GC10-3.
11. Adinosporus bullatus Strother, gen. et sp. nov. A dyad form that is completely enclosed and demonstrating the ropey folding that characterizes the genus. Sample J2-1578, Rogersville Shale, slide J2-1578/A/SEM, England Finder location W36/2.
12. Adinosporus bullatus Strother, gen. et sp. nov. A rosette of packets from the Bright Angel Shale from a sample at Thunder Falls (Tapeats Creek drainage) in the Grand Canyon, Arizona, USA. Sample GC96-10 (see Strother and Beck, 2000 for locality details).
A population of 50 specimens from sample J2-1578 (slide J2-1578/A/SEM) measured across the midpoint of the dyad pair had a mean width of 31.6 μm, a range of 18–58 μm, with a standard deviation of 7.3 μm. This corresponds to an individual cell diameter average of about 16 μm, with a corresponding range of 9–29 μm. Discussion: Adinosporus geminus could represent an end-member of morphological variation associated with A. voluminosus; however, these planar dyad sets are distinctive enough to be recognized consistently. The morphological range in variation for the species is expressed in Plate III, 1–7, which include the species holotype (Plate III, 1) and a population of paratypes from the type slide. The holotype shows the tight folds which characterize the underlying laminated sporoderm. All these specimens display a dark equatorial band where each of the spore-bodies in a pair meets. The thickened contact region within each dyad may give the appearance of a pseudodyad — i.e. they may sometimes represent an incomplete wall between the two spore-bodies. This feature is most apparent in Plate III, 6. The dyad pairs tend to line up precisely along these thickened zones, often giving the appearance of an asymmetrically thickened planar tetrad (Plate III, 2). The suture between each dyad pair should be distinct in order to be included in this species. This can be seen clearly in Plate III, 2, 3, and 5. In Plate III, 7, the two dyad pairs have partially separated, forming an acute angle between them.

**SPIUSSPORA** Strother, gen. nov.

Type: Spiusspora laevigata Strother, sp. nov.

**Holotype**: Original slide J2-1578/A/SEM, England Finder Location C27, Plate IV, 1-3.

**Repository**: Harvard University Paleobotanical Collection (HUPC) No. 65849.

**Type locality**: Joy No. 2 well, depth 1578′, location N35°9.3′ W84°27′, Oak Ridge National Laboratories, Oak Ridge, Tennessee, USA.

**Type stratum**: Rogersville Shale (Conasauga Group).

**Etymology**: From the Latin *spissus*, thick, dark, dense referring to the wall character of this taxon.

**Spiusspora laevigata** Strother, sp. nov.

**Holotype**: Slide J2-1578/A/SEM, England Finder Location C27, Plate IV, 1-3.

**Description**: Tetrad, rarely triads, pentads or higher numbers, of small, spherical spores which are tightly grouped but without clear contact modifications; walls dense, homogeneous, but sometimes somewhat blotchy in transmitted light; wall surface smooth never wrinkled or folded; tetrad may be enclosed in a thin envelope.

**Etymology**: From the Latin *laevigatus*, smooth.

**Discussion**: A population of 42 specimens from sample J2-1578 (slide J2-1578.1) had a mean diameter of 15.8 μm, a range of 10–23 μm, with a standard deviation of 2.3 μm. Specimens were effectively sampled at random, as the graduated reticule was not realigned during measurement.
Discussion: This genus stands apart from Adinosporus because the distinctly rounded spores never possess folds or wrinkles on the surface. The spore margin is not particularly distinct and does not form any sort of rim or apparent equatorial thickening that is so often seen in Adinosporus. These features are probably related to the underlying wall structure, which does not appear to be laminated, but rather
Plate V (caption on page 36).
more homogeneous. Thus, the walls of Spissuspora are never folded or crumpled. Instead, the wall surface may appear blotchy or irregularly pitted (Plate IV, 1, 4).

As described, most specimens occur as quartets, but there are exceptions to this where there may be ambiguity. For example, in Plate IV, 4, one of the four spore-bodies is slightly elongate and appears to have an internal, thickened band that might designate a dyad. This occurs more clearly in Plate IV, 13, which appears to show a dyad attached to a set of three spore-bodies. Tetrads are typically planar (or square) (Plate IV, 4, 6–8) or somewhat irregular (Plate IV, 5, 9–12). As mentioned above, sometime there may be five spore-bodies attached (Plate IV, 13, 14) as if one member of the tetrad has continued to divide into a dyad. However, for the most part, the individual spore-bodies maintain a fairly uniform diameter within the tetrad or polyad.

Vidalgea Strother, gen. nov.

Type: Vidalgea maculata Strother, sp. nov.

Diagnosis: Spherical to subspherical spore-like cells, solitary or adpressed into regular to irregular geometric arrangements, forming packets; walls distinctly mottled, composed of one or more granular laminae, moderately translucent; outermost lamina, may enclose spore-like bodies whose walls themselves may or may not be motled.

Etymology: In honor of the palynologist Gonzalo Vidal.

Discussion: The wall character, which is a reflection of the granulate nature of the underlying laminae, is distinctive, setting Vidalgea apart from Adinosporus whose walls are darker (thicker-walled) and always smooth. In addition, Vidalgea is distinctly circular in outline, individual spore-bodies are nearly circular in plan view, never undulatory or irregular as in Adinosporus.

Vidalgea maculata Strother, sp. nov.


Repository: Harvard University Paleobotanical Collection (HUPC) No. 65850.

Type locality: Joy2 core, depth 1803; location N35.93° W84.27°, Oak Ridge National Laboratories, Oak Ridge Tennessee, USA.

Type stratum: Pumpkin Valley Shale (Conasauga Group).

Etymology: From the Latin, macula, spot, marking the mottled nature of the wall.

Diagnosis: Walls robust without perforations or large arcuate folds; spore-like cells do not generally form geometrically regular packets as the size of individual spore-bodies may vary somewhat within the packet; contacts and walls between individual spore-bodies may appear indistinct or characterized by darker zones, rather than discrete walls; packet margins always convex in plan view, never collapsed centripetally; surface mottled due to the granulate nature of the wall laminae; granules 0.4–0.7 μm in diameter appear to be an integral part of the wall construction, not applied externally as sculpture.

Description: A population of 50 specimens from slide J2–1803/A3 had a mean diameter of 26.3 μm, a range of 16–42 μm, with a standard deviation of 5.2 μm. Individual specimens were measured effectively at random as the graduated reticle was not realigned during the sampling.

Discussion: Vidalgea maculata is characterized on the basis of its peculiar mottled wall type and the overarching spherical shape of the spore-bodies. The outermost granulate wall often appears to be thin and somewhat translucent (e.g. Plate V, 3, 4, 13). The overall nature of the granulate outer wall is apparent from the specimens figured in Plate V. Fundamentally, Vidalgea maculata is not characterized by any specific number of attached spore-bodies, which can be solitary (Plate V, 3, 4) to paired (Plate V, 5, 6, 8) to triads (Plate V, 7, 9) to tetrads (Plate V, 1, 2, 7, 10–14) or polyads (Plate V, 15–18).

Plate V, 4, shows an enclosed, spore-like central body which is quite dense. This darker interior spore-body is evident in the holotype (Plate V, 2, 3) and can be seen as well in Plate V, 4, 9, 12, 17, and 18. But many specimens lack this darker inner body and these may show either a discrete inner body (Plate V, 3, 8, 13) or a more diffuse central region (Plate V, 5, 12, 14, 16, 18). In any case, it appears that a central spore-body is preserved in various stages of development/maturity throughout populations of Vidalgea.

4. Discussion

4.1. Early cryptospore morphology

Taylor and Strother (2008, 2009) presented specific hypotheses about the developmental origin of the irregular Cambrian cryptospores. The first is that they represent the end-member products of endoreduplication of DNA followed by cytokinesis, which occurred in a zygote homologous with that of Coleochaete. This allows us to interpret cryptospore morphology within the actualistic context of direct comparison with zygotic meiosis in extant charophycean algae. The second is that they formed from successive cytokinesis during zygotic meiosis, rather than simultaneous cell wall formation during meiosis. Recognizing the distinction between successive and simultaneous meiosis during sporogenesis is now critical to our interpretation of these early cryptospores. It is the fundamental characteristic that separates Darrwilian and younger cryptospores from Dapingian and older populations (Strother, 2010; Strother et al., 2015).

In spite of the ultrastructural character of the Cambrian forms, which clearly points to laminated walls as the plesiomorphic state for the embryophytes, endoreduplication and successive meiosis point toward the charophyceans as the producers of the Cambrian cryptospores. Graham et al. (2012) have shown recently that extant aeroterrestrial Coleochaete, in response to desiccation, produces resistant laminae, supplementing the primary cell walls surrounding vegetative cells. The inclusion of spores produced within the existing walls of a spore of the Coleochaete can also be construed as an adaptation to subaerial conditions. This condition of meiotic products developing inside the spore constitutes a form of endosporpogenesis. This is distinct from plant endospore, which refers to the commencement of gametophyte development when it occurs within a spore wall.

The cryptospores described here are highly variable both in shape and in attachment configuration. This implies a large degree of developmental sloppiness in both the timing and coordination of cell division and cell wall formation. But, in addition, as seen in the ten ultrastructure (Taylor and Strother, 2008, 2009; Taylor, 2009), the very nature of multilaminate wall construction apparently results in spore walls which are not particularly rigid or geometrically consistent in shape. Thus, these spore walls retain a contorted, folded character and they do not appear geometrically regular, as do typical miospores (spores derived from embryophytes that are less than 200 μm in diameter). In this aspect, the Cambrian cryptospores are different from most miospores, which may possess thicker, more homogeneous walls, or laminae which are fully fused to form robust, rigid sporoderm.

While it is possible to find individual geometrically regular tetrads and dyads in large populations of Cambrian cryptospores (e.g. Figs. 14g and 15b in Baldwin et al., 2004, and, Pl. 1, Fig. 2 in Taylor and Strother, 2009), such individuals are not particularly characteristic of the populations as a whole. Given our current level of stratigraphic sampling, therefore, abundant isometric tetrads first occur in the Darrwilian of Saudi Arabia (Strother et al., 1996, 2015; Le Hérissé et al., 2007). I interpret this to indicate that pre-Darrwilian cryptospores were produced by organisms whose sporogenesis was characterized by successive meiosis, and that simultaneous meiosis first evolved during the Dapingian–Darrwilian interval. Effectively, decoupling of spindle formation, nuclear division, and cytokinesis has combined with multiple episodes of wall formation to produce spores, and spore pairs, which are not strictly isomorphic. Thus, the morphology of Cambrian cryptospores appears highly variable with respect to younger forms.

4.2. Cryptospores and the origin of land plants

Cryptospores of Cambrian age are the direct expression of the adaptation of aeroterrestrial algae to subaerial conditions. Specifically, the
production of robust, multilaminate spore walls occurred in response to the requirement for a resting stage in the life cycle that was resistant to dehydration and oxidative degradation. But that resting stage, in the formation of spores, has now been coupled with reduction division (meiosis). If meiosis occurred during conditions of somatic exposure to desiccation, this would have encouraged the morphological features seen here with respect to enclosed development and spore wall formation—the successive application of heteropolaric wall formation applied centripetally as cell division occurred. This scenario fits the antithetic alternation theory of Bower (1908), who envisioned the origin of the embryophytic spore well in advance of the embryophytic sporophyte itself.

There are a number of features of the Cambrian cryptospores that support Bower's theory that vegetative tissues of the sporophyte generation evolved after sporogenous tissues of the sporophyte. His argument for the selective pressure to evolve vegetative tissues was that the developing spores would have required more nutrient than was available in the initial SMC. In other words, a single zygote was that the developing spores would have required more nutrient to desiccate, this would have encouraged all the morphological features that characterize the larger forms. Thus, there does appear to be a morphological continuum between spores (and spore packets) of different sizes, as they kept dividing down to diameters of less than 10 μm.

Cambrian cryptospores were probably not formed in uninuclear sporangia, at least not in the sense of a mass of cells enclosed within a vegetative layer (wall). In Plate 1, 1 and 2, the spherical SMC has retained its primary cell wall. The inclusion of spores produced within the SMC cell wall is indicative of endosporogenesis, in which spore formation has occurred entirely within the generative cell and the spores have been retained inside the wall. Both the spherical shape and the obviously resistant chemical nature of the SMC wall indicate that, in this case, the SMC was likely to have existed as an isolated, independent cell. Even though many of the spore packets of Adinosporus voluminosus and A. bullatus occur in clusters (e.g. Plate II, 5, 9, 12), they never seem to take on a gross form that might be interpreted as having formed within a uninuclear sporangium.

5. Conclusion

The sheer abundance of these microfossils implies that some ancestral streptophytes were well-established by middle Cambrian (Series 3) time and that some form of diversification, plant-like cover existed on the land surface some 50 Myr in advance of the first rhyniophyoids. Plenty of spores were being produced, but seemingly in the absence of any sporophytic hosts. On the basis of fossil remains Strother (2010) has argued that thalloid gametophytes may have preceded the origin of the full sporophytic phase in the evolving streptophyte lineage that lead to the embryophytes. This is supported by experimental evidence of desiccation resistance found in aeroterrestrial Coleochaete (Graham et al., 2012) and the occurrence of multicellular spore "thalli" recently found in Dapingian strata in Utah (Vecoli et al., 2015). Phylogenomic studies indicate that arthropods began radiation into terrestrial habitats long before the Silurian origin of rhyniophyoids (Wheat and Walsberg, 2013). They must have been eating something.

The developmental slowness that has produced such wide morphological and topological variation in the Cambrian cryptospores has been, and continues to be, an impediment to their description and classification. Nevertheless, the palynomorphs described herein do conform to a hypothetical evolutionary series that begins with a Coleochaete-style of meiosis, which is characterized by DNA endoreduplication within a diploid zygote. In Coleochaete, each meiospore produced results in a motile,flagellated zoospore. That zoospore has been replaced in these Cambrian examples, by a thick, multilaminated, environmentally resistant wall, surrounding a non-motile spore. That wall seems to be homologous to the walls of the early land plants. During the Cambrian, these spores were highly variable in terms of morphology and configuration, directly reflecting their origin through successive meiosis. The extant land plants, at the bryophyte grade, evolved several development schemes during which spore formation and function to precisely determine the topological position of meiospores produced through simultaneous meiosis. These include pre-prophase bands and quadradobling of the sporocyte, features which interact with the microtubule system to precisely position both the dividing nucleus and subsequent cytokinesis and cell wall formation (Brown and Lemmon, 2011). These are features that appear to be lacking in the Cambrian but may have been acquired during the time leading up to modern spore formation as seen by Darrwillian (mid-Ordovician) time (Strother et al., 2015).

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