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 *Vidalgea maculata*. The lamellated wall ultrastructure of some of these cryptospores appears to be homologous to extant, crown group sphaerocarpacean 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.

Keywords: Laurentia; palynology; origin of land plants; Rogersville Shale; successive meiosis

1. Introduction

1 This report begins documentation of the systematics of a terrestrial biota that was
2 extensively distributed on the Laurentian continent by middle Cambrian (Series 3) time.
3 Evidence for this early land biota is based primarily on palynological remains from rocks
4 that appear to have formed in both estuarine and proximal marine settings from within an
5 inner clastic belt that encircled the paleocontinent of Laurentia during much of Cambrian
6 time (Lochman-Balk, 1971). Individual samples from these strata can be extremely
7 abundant in terms of sheer numbers of palynomorphs, however, the morphological
8 variability (pleomorphism) which is expressed in these spore-like cells has meant that
9 their systematic characterization has not been straightforward. Their distribution is
10 extensive as well; they have been recovered from around the margin of Laurentia from
11 eastern Tennessee (Strother and Beck, 2000) to Missouri (Wood and Stephenson, 1988),
12 to Texas (Hitchcock Fm, Strother and Baldwin unpublished), to Arizona (Baldwin et al.,
13 2004; Strother et al., 2004; Taylor and Strother, 2008), Nevada (Yin et al., 2013), to
14 Idaho (Bloomington Fm, Strother unpublished) and Wisconsin (Taylor and Strother,
15 2009). The purpose of his report is not to provide a comprehensive survey or overview of
16 this microflora. Instead, what is presented here are designations of new taxa from a
17 limited number of samples. A more comprehensive assessment of their stratigraphic and
18 geographic distribution will be forthcoming.

19 If classified as sphaeromorph acritarchs, the palynomorphs described herein would be
20 thought of as problematic, possibly marine algae, and most certainly not considered
21 significant with regard to the origin of land plants. However, there are several lines of
22 evidence with respect to both geology (Baldwin et al., 2004) and sporomorph
23 morphology (Strother et al., 2004) and ultrastructure (Taylor, 2009; Taylor and Strother,
24 2008) that lead to their inclusion in the informal group, cryptospores *sensu* Strother &
25 Beck (2000). Again, it is not the purpose of this report to provide another defense of the
26 use of the term, *cryptospore*, nor is it necessary, to repeat the arguments that associate
27 these palynomorphs with the origin of land plants as originally presented by Strother et
28 al. (2004). Subsequent work on Cambrian fossils (Taylor and Strother, 2009; 2008) in
29 conjunction with extant studies (Brown and Lemmon, 2011; Graham et al., 2012) and
30 especially the discovery of dyads in a basal liverwort (Renzaglia et al., in press), continue
31 to generally support the conclusions of Strother et al. (2004) – these palynomorphs

1 represent spores of aeroterrestrial charophytic algae that were evolving in response to
2 partial subaerial exposure during their life cycle.

3 The Cambrian cryptospores are unlike previously described cryptospore taxa from
4 middle Ordovician (Darriwilian) and younger rocks. These younger cryptospores are
5 recognized as such because they retain distinctive attachment geometries – either as
6 geometrically regular tetrads or as isomorphic, typically hilate dyads. The Cambrian
7 forms, however, generally lack geometrically regular topologies, in which spores of
8 similar form are arranged in symmetric tetrad or dyad configurations. Instead, both the
9 distinct nature of individual spore bodies and their physical attachment geometries are
10 often unclear. In addition, Cambrian cryptospores may occur as packets of multiple
11 spore-like bodies surrounded by one or more, synoecosporal walls (Taylor and Strother,
12 2008). These facts, based on morphology, reveal unambiguous differences between
13 Cambrian and younger cryptospores. However, it is likely that these morphological
14 differences reflect underlying biological variation in meiosis and development during
15 sporogenesis, rather than underlying systematic differences in evolutionary origin.

16 In order to place the Cambrian cryptospores within their correct phylogenetic context,
17 it is necessary to make some broad assumptions about functional morphology. While this
18 not a terribly satisfactory method, it does provide a general platform with which to
19 explore evolution as it was occurring in terrestrial environments during Cambro-
20 Ordovician time. I do not wish to claim that these microfossils are a document of any
21 specific evolutionary lineage that is ancestral to the embryophytes, however, these
22 microfossils are relevant to the study of the origin of land plants because they are spores
23 derived from thalloid algal sporophytes that were evolving in response to living in
24 subaerial settings. Phycologists refer to extant terrestrial algae that survive subaerial
25 exposure as, aeroterrestrial, and this term will be used here as well to describe the
26 Cambrian cryptospore producers. The assumption that these algae were aeroterrestrial
27 can be justified on the basis of the spore-like character of these microfossils: they
28 possess thick, homogeneous to multilaminate walls composed of highly refractory,
29 sporopollenin-like, organic compounds; they were widely dispersed in large numbers;
30 they were distributed in shallow marine to estuarine environments (reflecting freshwater
31 and terrestrial provenance); and their morphology (including wall ultrastructure) parallels

1 that of younger cryptospores and miospores. This is in apposition to the cyst-like
2 characters found in marine planktonic algae, which are typically thinner-walled and
3 reflect a far greater range in morphology and surface sculpture.

4 Ultrastructural studies of Cambrian cryptospores (Strother et al., 2004; Taylor, 2009;
5 Taylor and Strother, 2008; 2009) have already shown that many of these early forms
6 possess laminated walls, some of which appear homologous with those of the crown
7 group (Forrest et al., 2006) liverworts *Riccia* and *Sphaerocarpos* (Strother, 2010) and the
8 primitive liverwort, *Haplomitrium gibbisiae* (Renzaglia et al., in press). This indicates that
9 embryophytic spore characters in streptophyte lineages were evolving prior to the origin
10 of the first embryophyte sporophytes *sensu stricto*, (i.e. biaxial sporophytes that develop
11 from a multicellular embryo (Niklas, 1997; Niklas and Kutschera, 2010). In a direct
12 reading of the fossil record, spores appear before sporophytes. This idea is not new, in
13 fact, it is a fundamental thesis of Bower's antithetic hypothesis for the origin of the plant
14 sporophyte, in which he proposed that the plant spore must have preceded the evolution
15 of a vegetative sporophyte (Bower, 1908). "Spores before sporophytes," has been more
16 recently championed in cytological studies of sporogenesis in extant bryophytes, which
17 show accelerated onset of cytokinesis in combination with the retarded application of
18 sporopolleninous sporoderm during spore development (Brown and Lemmon, 2011).
19 Thus, some living bryophytes directly support earlier suppositions about the
20 developmental "transfer" of sporopollenin from zygote to (meio)spore wall (Graham,
21 1985; Hemsley, 1994). Studies of meiosis and zygote development in *Coleochaete* also
22 strongly support the ideas of Bower (Graham, 1984; Graham, 1985; Graham, 1993). A
23 thorough understanding of heterochrony and sporogenesis in both bryophytes and
24 charophytes is now essential for guiding our interpretation of fossil cryptospores
25 recovered from Ordovician and Cambrian strata (Strother et al., 2004; Strother et al.,
26 2015).

27 *1.1 Endosporogenesis and the interpretation of cryptospore morphology*

28 Plate I, 1 exemplifies a fundamental problem with how to interpret and describe
29 systematically Cambro-Ordovician cryptospores. This fossil consists of a spherical wall
30 (cell) within which occur both a cryptospore dyad and an incompletely (?) formed tetrad.

1 How does one deal with this systematically? In a biological sense, this specimen consists
2 of a spore mother cell (SMC) that underwent a series of nuclear divisions (preceded by
3 DNA endoreduplications) along with successive cytokinesis to produce two distinct spore
4 clusters - a dyad and an incompletely formed tetrad. More specifically, after a first
5 mitotic division, the resultant nuclei migrated away from each other, with one undergoing
6 a single subsequent mitosis (resulting in a dyad), but the other dividing twice to produce
7 an apparent tetrad of spores. The specimen in Plate I, 2 is similar, but here the two
8 endosporic products appear more similar to each other – probably incompletely-formed
9 tetrads. Spore cell walls formed only after the first mitosis and subsequent nuclear
10 migration.

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

19 Taxonomic precedent amongst paleobotanists has been to segregate cryptospore dyads
20 and tetrad into different taxa at the genus level (Strother, 1991; Richardson, 1996;);
21 however, in this case one would certainly argue that both the enclosed dyad and tetrad in
22 Plate I, 1-2 must belong to the same biological species. A parallel condition occurs in the
23 late Cambrian cryptospore, *Agamachates casearius* Taylor & Strother 2008, which
24 consists of spore packets that may contain different numbers of what are, ultimately,
25 dyads. The result of this understanding is that the application of taxonomic distinctions
26 between tetrads and dyads, while perhaps warranted on strictly morphological grounds, is
27 not to be trusted to demarcate biological species.

28 While it is possible to find individual geometrically regular tetrads and dyads in large
29 populations of Cambrian cryptospores (e.g. Figs. 14g and 15b in Baldwin et al., 2004,
30 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 Darriwilian of Saudi Arabia (Le Hérisse et al., 2007; Strother et al., 1996; Strother et al. 2015). This indicates that pre-Darriwilian cryptospores were produced by organisms utilizing successive meiosis and that simultaneous meiosis in streptophytes first evolved during the Dapingian-Darriwilian 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 compared to younger forms. And this variability places the Cambrian cryptospores clearly outside the acceptable morphologic range of miospores derived from embryophytes, whose synapomorphies are 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 appear to each be dyads, the B-B' pair also appear 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 specimen (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 geometrically irregular cryptospores (Taylor, 2009; Taylor and Strother, 2008; 2009). This knowledge of underlying wall structure has led to the recognition that spore

1 characters related to development are essential to the interpretation of morphology, a
2 view that is reinforced by modern studies in bryophyte sporogenesis (Brown and
3 Lemmon, 2011). I have tried to present a reasonable defense of a streptophytic origin to
4 the Cambrian cryptospores, based on their laminated construction, that appears
5 plesiomorphic in the embryophytes (Blackmore and Barnes, 1987). Thus, ultrastructure
6 as viewed with the transmission electron microscope (TEM) has been the critical tool
7 permitting the general systematic placement of these problematic microfossils.

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

18 **2. Materials and Methods**

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

26 In this report, the following samples were used as a source for plate illustrations: from
27 the JOY No. 2 well, samples J2-1518 (Rogersville Shale), J2-1541 (Rogersville Shale),
28 J2-1571 (Rogersville Shale), J2-1578 (Rogersville Shale), J2-1580s (Rogersville Shale),
29 J2-1587s (Rogersville Shale), J2-1803 (Pumpkin Valley Shale); from the Thorn Hill
30 Section, samples SB01-14 (Rome Formation), SB01-17 (Rogersville Shale); from the

1 Grand Canyon, GC96-10A (Bright Angel Shale, Thunder Falls, Tapeats Creek drainage),
2 GC10-3 (Bright Angel Shale, Red Canyon section). A generalized stratigraphic section
3 for eastern Tennessee and for the Grand Canyon is presented in Figure 1.

4 Samples were processed using standard palynological techniques as described in Barss
5 and Williams (1973). At the Palaeobotany Laboratory at Boston College, approximately
6 10 g of rock sample were placed in a 250 ml Teflon beaker with about 125 ml of
7 concentrated (52%) HF. After several days the samples were rinsed multiple times in
8 deionized water, treated in warm dilute HCl if needed, and oxidized by short (typically 2
9 to 20 minutes) treatment in either dilute HNO₃ or Schultze's solution. The oxidized
10 residues were then cleaned with a heavy liquid (gravity) separation using ZnCl₂ solution
11 adjusted to a specific gravity of 2.0. Screening treatments varied from sample to sample,
12 but the recovery of palynomorphs < 20µm in diameter is assured only by eliminating
13 screening altogether, so processing of these samples typically includes a 10 or 20µm
14 screened fraction together with an unscreened fraction.

15 Slides for transmitted white light microscopy (LM) were mounted in glycerine jelly.
16 White light digital images were obtained by mounting a Nikon D1x body onto the photo-
17 tube of a Zeiss Universal microscope. Exposure was controlled with a coplanar electronic
18 shutter mounted between the condenser and the field stop. Color balance was set using
19 the *Camera Raw* module in Adobe Photoshop. Image background brightness was set to
20 fall between 218 and 224. This results in a medium light gray background without
21 introducing overly stretched tones in the specimen image itself. Some dust was removed
22 using the *Spot Healing Brush Tool*.

23 Samples for scanning electron microscopy (SEM) were placed directly onto SEM stubs
24 marked with a grid to facilitate the locating of individual specimens. Samples were
25 scanned on an Amray 1600 series SEM with a tungsten filament operated at 15 to 20 keV.
26 Digital images on the Amray SEM were acquired by attaching a Fujifilm S1 Pro digital
27 camera back to the analog photographic port and taking a time exposure to match the
28 scan rate on the oscilloscope. The resultant RGB images were processed Adobe
29 Photoshop, using the *Dust & Scratches>Noise>Filter* menu to remove noise and
30 *Levels>Adjustments>Image* menu to set image tonal range.

A split set of samples from the JOY-2 core were processed by Dave Bodman at the University of Sheffield. The majority of these samples were screened at 20µm, and not oxidized in Schultze's solution, so these samples, for the most part, contained only larger specimens and clusters. Samples processed at Sheffield are designated with an "s" suffix added to the well depth sample number.

3. Systematic Paleontology

Domain: Eukarya Woese et al. (1990)

Eukaryotic Super-group: ARCHAEPLASTIDA Adl et al. (2005)

Phylum: CHLOROPHYTA Pascher (1914) emend. Lewis & McCourt (2004)

Subphylum: CHAROPHYTA Migula (1897) emend. Karol et al. (2001)

Informal taxon, Anteturma: CRYPTOSPORITES Richardson, Ford & Parker (1984)

ADINOSPORUS Strother, *gen. nov.*

Type: Adinosporus voluminosus Strother, sp. nov.

Diagnosis: Packets of one or more inaperturate, sub-spherical, 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 multi-laminate 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

1 be the starting point for multiple sets of attached cells. Many tetrads appear to have this
2 form of paired dyads recognizable by size differences between pairs and by the somewhat
3 adpressed and mutually compressed, flattened contact areas between vesicles within a
4 pair. But the arrangement of paired sets is not absolute, as solitary and odd-numbered
5 polyads are quite common. Although folds in the walls are common, they are rarely
6 broadly arcuate in appearance, but are more often thinner and somewhat sinuous, or
7 ropey, possibly reflecting simple compression of the wall during diagenetic flattening.
8 Folds are a reflection of the entire membrane plus vesicle complex, so that folds
9 themselves may include one or more of the wall laminae.

10 These forms differ from leiospherids in several distinct ways. Species of *Adinosporus*
11 are not perfectly spherical in either their attached or separated form, but are more or less
12 subspherical in shape. The color is not the light to medium yellow that is more typical of
13 thinner-walled acritarchs; these forms appear more robust than most acritarch species,
14 indicating either a generally thicker wall or reflecting differences in primary chemical
15 composition of the wall. Folding of the vesicle wall in the leiosphaerids tends to form
16 broad arcuate folds which may extend for the entire diameter of the vesicle. This is never
17 the case with *Adinosporus* which forms more narrow, sinuous folds. *Leiosphaeridia*, as
18 originally established by Eisenack (1958), also has a pylome, which, although not always
19 expressed in species of *Leiosphaeridia*, is completely lacking in *Adinosporus*.
20 *Synsphaeridium* differs in possessing thinner walls, a spherical (rather than discoidal)
21 shape to the discrete vesicles, lack of clear attachment thickenings and lack of enclosing
22 envelopes, membranes or synoecosporal walls.

23 ***Adinosporus voluminosus* Strother, sp. nov.**

24 *Holotype*: Original slide number J2-1571/B, England Finder location H57,
25 photomicrographs Plate I, 3C', 4.

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

27 *Type locality*: Joy No. 2 well, depth 1571', location N35.93° W84.27°, Oak Ridge
28 National Laboratories, Oak Ridge Tennessee, USA.

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

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

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

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

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

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

27 Dyads or apparent dyads are a common packet form (Plate I, 17-25). Once again,
28 however, there is considerable variation in the distinct nature of individual enclosed
29 spore-bodies. Plate I, 17 exhibits one aspect of this variability as this image shows a
30 distinct dyad pair in close association with a pseudodyad. This pseudodyad is confirmed

1 as such by a continuous margin and folds (F, arrow) that cross the equatorial plane. The
2 darkened region of the equatorial plane appears to mark a potential plane of division,
3 corresponding to a division that actually did take place in the adjacent dyad. Many dyads
4 contain internal, thickened bands (TB, arrows) that appear to mark these sites of potential
5 division planes (Plate I, 3, 20-23). Yet, in many cases, the internal walls and exact spore-
6 body configurations remain ambiguous, as in Plate I, 18. In other specimens, the very
7 nature of the wall itself, which comprises numerous ropey folds expressing the
8 underlying multilamellate nature of the sporoderm, obscures the exact articulation of
9 internal spore-bodies. This effect can be seen in Plate I, 19 and 24 in which the walls are
10 highly folded. When such folds are narrower (Plate I, 25), or less numerous, (Plate I, 20-
11 23) the delineation of the spore-bodies is more obvious. Dyads may also be flattened
12 along their axial plane, producing nearly circular forms (Plate I, 26).

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

20 *Adinosporus voluminosus* also occurs in the Rome Formation and two examples are
21 illustrated in Plate II, 4, 5. This occurrence has some biostratigraphic significance as the
22 Rome has long been considered to be of Early Cambrian age, which is now Series 2,
23 Stage 4 (Figure 1).

24 ***Adinosporus bullatus* Strother, sp. nov.**

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

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

28 *Type locality:* Sample of the Lower Shale Member of the Rogersville Shale, immediately
29 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, *bull*, refers to the knob-like bulbils that characterize this species.

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

Description: Bulbils 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 graduated 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 bulbils 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 bulbils varies from specimen to specimen, ranging from one or two per vesicle to perhaps 12 to 20 for an entire packet. They are typically 2 to 3 µm in diameter with a height of up to 1 µm. Somewhat similar thickenings are described by Wood & Benson (2000) in the Triassic *Plaesiodyctyon 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 synoecosporal 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. bullata*. 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 Tapeats 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.

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 to 29 μm .

1 *Discussion:* *Adinosporus geminus* could represent an end-member of morphological
2 variation associated with *A. voluminosus*; however, these planar dyad sets are distinctive
3 enough to be recognized consistently. The morphological range in variation for the
4 species is expressed in Plate III, 1-7, which include the species holotype (Plate III, 1) and
5 a population of paratypes from the type slide. The holotype shows the tight folds which
6 characterize the underlying laminated sporoderm. All these specimens display a dark
7 equatorial band where each of the spore-bodies in a pair meet. The thickened contact
8 region within each dyad may give the appearance of a pseudodyad – i.e. they may
9 sometimes represent an incomplete wall between the two spore-bodies. This feature is
10 most apparent in Plate III, 6. The dyad pairs tend to line up precisely along these
11 thickened zones, often giving the appearance of an asymmetrically thickened planar
12 tetrad (Plate III, 2). The suture between each dyad pair should be distinct in order to be
13 included in this species. This can be seen clearly in Plate III, 2, 3 and 5. In Plate III, 7, the
14 two dyad pairs have partially separated, forming an acute angle between them.

15 ***SPISSUSPORA*** Strother, *gen. nov.*

16 *Type:* *Spissuspora laevigata* Strother, *sp. nov.*

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

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

23 ***Spissuspora laevigata*** Strother, *sp. nov.*

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

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

26 *Type locality:* Joy No. 2 well, depth 1578', location N35.93° W84.27°, Oak Ridge
27 National Laboratories, Oak Ridge, Tennessee, USA.

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

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

2 *Diagnosis:* Walls solid, spore-bodies within a cluster are usually quite similar in
3 diameter.

4 *Description:* A population of 42 specimens from sample J2-1578 (slide J2-1578.1) had a
5 mean diameter of 15.8 μm , a range of 10 – 23 μm , with a standard deviation of 2.3 μm .
6 Specimens were effectively sampled at random, as the graduated reticule was not
7 realigned during measurement.

8 *Discussion:* This genus stands apart from *Adinosporus* because the distinctly rounded
9 spores never possess folds or wrinkles on the surface. The spore margin is not
10 particularly distinct and does not form any sort of rim or apparent equatorial thickening
11 that is so often seen in *Adinosporus*. These features are probably related to the underlying
12 wall structure, which does not appear to be laminated, but rather more homogeneous.
13 Thus, the walls of *Spissuspora* are never folded or crumpled. Instead, the wall surface
14 may appear blotchy or irregularly pitted (Plate IV, 1, 4).

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

24 ***VIDALGEA*** Strother, *gen. nov.*

25 *Type:* *Vidalgea maculata* Strother, *sp. nov.*

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

1 *Etymology*: In honor of the palynologist Gonzalo Vidal.

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

7 ***Vidalgea maculata*** Strother, *sp. nov.*

8 *Holotype*: Original slide J2-1803/B2, England Finder location G49/4, photomicrograph
9 in Plate IV, 1-2,

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

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

13 *Type stratum*: Pumpkin Valley Shale (Conasauga Group).

14 *Etymology*: From the Latin, *macula*, spot, mark reflecting the mottled nature of the wall.

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

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

27 *Discussion*: *Vidalgea maculata* is characterized on the basis of its peculiar mottled wall
28 type and the overarching spherical shape of the spore-bodies. The outermost granulate

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

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

12 **4. Discussion**

13 *4.1 Early cryptospore morphology*

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

26 In spite of the ultrastructural character of the Cambrian forms, which clearly points to
27 laminated walls as the plesiomorphic state for the embryophytes, endoreduplication and
28 successive meiosis point toward the charophyceans as the producers of the Cambrian
29 cryptospores. Graham et al. (2012) have shown recently that extant aeroterrestrial
30 *Coleochaete*, in response to desiccation, produces resistant laminae, supplementing the

1 primary cell walls surrounding vegetative cells. The inclusion of spores produced within
2 the existing walls of a SMC, can also be construed as an adaptation to subaerial
3 conditions. This condition of meiotic products developing inside the SMC, constitutes a
4 form of endosporogenesis. This is distinct from plant endospory, which refers to the
5 commencement of gametophyte development when it occurs within a spore wall.

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

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

30 *4.2 Cryptospores and the origin of land plants*

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

12 There are a number of features of the Cambrian cryptospores that support Bower's
13 theory that vegetative tissues of the sporophyte generation evolved after sporogenous
14 tissues of the sporophyte. His argument for the selective pressure to evolve vegetative
15 tissues was that the developing spores would have required more nutrient than was
16 available in the initial SMC. In other words, a single zygote can only cleave a finite
17 number of times before the distribution of cytoplasm becomes too dilute for continued
18 viability. Many of the Cambrian cryptospores, are quite small (Plate I, 16, 21, 22) yet
19 their morphologies continue to reflect the presence of thickened bands that characterize
20 the larger forms. Thus, there does appear to be a morphological continuum between
21 spores (and spore packets) of different sizes, as they kept dividing down to diameters of
22 less than 10µm.

23 Cambrian cryptospores were probably not formed in unilocular sporangia, at least not
24 in the sense of a mass of cells enclosed within a vegetative layer (wall). In Plate I, 1 and
25 2, the spherical SMC has retained its primary cell wall. The inclusion of spores produced
26 within the SMC cell wall is indicative of endosporogenesis, in which spore formation has
27 occurred entirely within the generative cell and the spores have been retained inside the
28 wall. Both the spherical shape and the obviously resistant chemical nature of the SMC
29 wall, indicate that, in this case, the SMC was likely to have existed as an isolated,
30 independent cell. Even though many of the spore-packets of *Adinosporus voluminosus*

1 and *A. bullatus* occur in clusters (e.g. Plate II, 5, 9, 12), they never seem to take on a
2 gross form that might be interpreted as having formed within a unilocular sporangium.

3 **5. Conclusion**

4 The sheer abundance of these microfossils implies that some ancestral streptophytes
5 were well-established by Middle Cambrian (Series3) time and that some form of
6 diversified, plant-like cover existed on the land surface some 50 Myr in advance of the
7 first rhyniophytoids. Plenty of spores were being produced, but seemingly in the absence
8 of any sporophytic hosts. On the basis of fossil remains, (Strother, 2010) has argued that
9 thalloid gametophytes may have preceded the origin of the full sporophytic phase in the
10 evolving streptophyte lineage that lead to the embryophytes. This is supported by
11 experimental evidence of desiccation resistance found in aeroterrestrial *Coleochaete*
12 (Graham et al., 2012) and the occurrence of multicellular spore “thalli” recently found in
13 Dapingian strata in Utah (Vecoli et al., in press). Phylogenomic studies indicate that
14 arthropods began radiation into terrestrial habitats long before the Silurian origin of
15 rhyniophytoids (Wheat and Wahlberg, 2013). They must have been eating something.

16 The developmental sloppiness that has produced such wide morphological and
17 topological variation in the Cambrian cryptospores has been, and continues to be, an
18 impediment to their description and classification. Nevertheless, the palynomorphs
19 described herein do conform to a hypothetical evolutionary series that begins with a
20 *Coleochaete*-style of meiosis, which is characterized by DNA endoreduplication within a
21 diploid zygote. In *Coleochaete*, each meiospore produced results in a motile, flagellated
22 zoospore. That zoospore has been replaced in these Cambrian examples, by a thick,
23 multilaminated, environmentally resistant wall, surrounding a non-motile spore. That
24 wall seems to be homologous to the spore walls of the early land plants. During the
25 Cambrian these spores were highly variable in terms of morphology and configuration,
26 directly reflecting their origin through successive meiosis. The extant land plants, at the
27 bryophyte grade, evolved several development schemes that appear during sporogenesis
28 and function to precisely determine the topological position of meiospores produced
29 through simultaneous meiosis. These include pre-prophase bands and quadralobing of the
30 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 Darriwilian (mid-Ordovician) Hanadir Member (Strother et al., 2015).

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7. References

- Adl, S.M., Simpson, A.G.B., Farmer, M.A., Andersen, R.A., Anderson, O.R., Barta, J.R., Bowser, S.S., Brugerolle, G., Fensome, R.A., Fredericq, S., James, T.Y., Karpov, S., Kugrens, P., Krug, J., Lane, C.E., Lewis, L.A., Lodge, J., Lynn, D.H., Mann, D.G., McCourt, R.M., Mendoza, L., Moestrup, O., Mozley-Standridge, S.E., Nerad, T.A., Shearer, C.A., Smirnov, A.V., Spiegel, F.W., Taylor, M.F.J.R., 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *Journal of Eukaryotic Microbiology* 52, 399–451. doi:10.1111/j.1550-7408.2005.00053.x
- Baldwin, C.T., Strother, P.K., Beck, J.H., Rose, E., 2004. Palaeoecology of the Bright Angel Shale in the eastern Grand Canyon, Arizona, USA, incorporating sedimentological, ichnological and palynological data. *Geological Society, London, Special Publications* 228, 213–236. doi:10.1144/GSL.SP.2004.228.01.11

- 1 Barss, M.S., Williams, G.L., 1973. Palynology and nannofossil processing techniques.
2 Geological Survey of Canada, Paper 73-26, 1–25.
- 3 Blackmore, S., Barnes, S.H., 1987. Embryophyte spore walls: origin, development, and
4 homologies. *Cladistics* 3, 185–195. doi:10.1111/j.1096-0031.1987.tb00506.x
- 5 Bower, F.O., 1908. The origin of a land flora: a theory based on the facts of alternation.
6 Macmillan and Co., Limited, London.
- 7 Brown, R.C., Lemmon, B.E., 2011. Spores before sporophytes: hypothesizing the origin
8 of sporogenesis at the algal-plant transition. *New Phytologist* 190, 875–881.
9 doi:10.1111/j.1469-8137.2011.03709.x
- 10 Byerly, D.W., Walker, K.R., Diehl, W.W., Ghazizadeh, M., Johnson, R.E., Lutz, C.T.,
11 Schoner, A.K., Simmons, W.A., Simonson, J.C.B., Weber, L.J., Wedekind, J.E., 1986.
12 Thorn Hill: A classic Paleozoic stratigraphic section in Tennessee. *Geological Society of*
13 *America Centennial Field Guide -- Southeastern Section*, 131-136.
- 14 Eisenack, A. 1958. *Tasmanites* Newton 1875 und *Leiosphaeridia* n. g. als Gattungen der
15 *Hystriosphæridea*. *Palaeontographica*, Abt. A, 110, 1-19.
- 16 Forrest, L.L., Davis, E.C., Long, D.G., Crandall-Stotler, B.J., Clark, A., Hollingsworth,
17 M.L., 2006. Unraveling the evolutionary history of the liverworts (Marchantiophyta):
18 multiple taxa, genomes and analyses. *The Bryologist* 109, 303–334.
- 19 Graham, L.E. 1984. *Coleochaete* and the Origin of Land Plants, 1984. *American Journal*
20 *of Botany* 71, 603-608.
- 21 Graham, L.E., 1985. The origin of the life cycle of land plants: A simple modification in
22 the life cycle of an extinct green alga is the likely origin of the first land plants. *American*
23 *Scientist* 73, 178–186.
- 24 Graham, L.E., 1993. *Origin of Land Plants*. John Wiley & Sons, Inc., New York.
- 25 Graham, L.E., Arancibia-Avila, P., Taylor, W.A., Strother, P.K., Cook, M.E., 2012.
26 *Aeroterrestrial Coleochaete* (Streptophyta, Coleochaetales) models early plant adaptation
27 to land. *Am. J. Bot.* 99, 130–144. doi:10.3732/ajb.1100245

- 1 Hasson, K.O., Haase, C.S., 1988. Lithofacies and paleogeography of the Conasauga
2 Group, (Middle and Late Cambrian) in the Valley and Ridge province of east Tennessee.
3 Geological Society of America Bulletin 100, 234–246. doi:10.1130/0016-
4 7606(1988)100<0234:LAPOTC>2.3.CO;2
- 5 Hemsley, A.R., 1994. The origin of the land plant sporophyte: an interpolational
6 scenario. Biological Reviews 69, 263–273. doi:10.1111/j.1469-185X.1994.tb01270.x
- 7 Karol, K.G., McCourt, R.M., Cimino, M.T., Delwiche, C.F., 2001. The closest living
8 relatives of land plants. Science 294, 2351–2353. doi:10.1126/science.1065156
- 9 Le Hérissey, A., Al-Ruwaili, M., Miller, M., Vecoli, M., 2007. Environmental changes
10 reflected by palynomorphs in the early Middle Ordovician Hanadir Member of the Qasim
11 Formation, Saudi Arabia. Revue de Micropaléontologie 50, 3–16.
12 doi:10.1016/j.revmic.2007.01.010
- 13 Lewis, L.A., McCourt, R.M., 2004. Green algae and the origin of land plants. American
14 Journal of Botany 91, 1535–1556.
- 15 Lochman-Balk, C., 1971. The Cambrian of the craton of the United States, in: Holland,
16 C.H. (Ed.), Cambrian of the New World. Wiley-Interscience, London, pp. 79–167.
- 17 Migula, W., 1897. Die Characeen Deutschlands, Oesterreichs und der Schweiz, in:
18 Rabenhorst, L. (Ed.), Kryptogamen-Flora Von Deutschland, Oesterreich Und Der
19 Schweizfl. E. Kummer, Leipzig, pp. 1–766.
- 20 Niklas, K.J., 1997. The Evolutionary Biology of Plants. The University of Chicago Press,
21 Chicago.
- 22 Niklas, K.J., Kutschera, U., 2010. The evolution of the land plant life cycle. New
23 Phytologist 185, 27–41. doi:10.1111/j.1469-8137.2009.03054.x
- 24 Pascher, A., 1914. Ueber Flagellaten und Algen. Ber. Deutsch Bot. Ges. 32, 136–160.
- 25 Renzaglia, K., Crandall-Stotler, B., Pressel, S., Duckett, J., Schuette, S., Strother, P.K.,
26 Permanent spore dyads are not 'a thing of the past': on their occurrence in the liverwort
27 *Haplomitrium*. Botanical Journal of the Linnean Society (in press).

1 Richardson, J.B., 1996. Lower and middle Paleozoic records of terrestrial palynomorphs,
2 in: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. AASP
3 Foundation, Houston, pp. 555–574.

4 Richardson, J.B., Ford, J.H., Parker, F., 1984. Miospores, correlation and age of some
5 Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and
6 Angus). *Journal of Micropalaeontology* 3, 109–124. doi:10.1144/jm.3.2.109

7 Strother, P.K., 1991. A classification schema for the cryptospores. *Palynology* 15, 219–
8 236. doi:10.1080/01916122.1991.9989397

9 Strother, P.K., 2010. Thalloid carbonaceous incrustations and the asynchronous evolution
10 of embryophyte characters during the Early Paleozoic. *International Journal of Coal*
11 *Geology* 83, 154–161. doi:10.1016/j.coal.2009.10.013

12 Strother, P.K., Al-Hajri, S., Traverse, A., 1996. New evidence for land plants from the
13 lower Middle Ordovician of Saudi Arabia. *Geology* 24, 55–58.

14 Strother, P.K., Beck, J.H., 2000. Spore-like microfossils from Middle Cambrian strata:
15 expanding the meaning of the term cryptospore, in: Harley, M.M., Morton, C.M.,
16 Blackmore, S. (Eds.), *Pollen and Spores: Morphology and Biology*. The Royal Botanic
17 Gardens Kew, pp. 413–424.

18 Strother, P.K., Traverse, A., Vecoli, M., 2015. Cryptospores from the Hanadir Shale
19 Member of the Qasim Formation, Ordovician (Darriwilian) of Saudi Arabia: taxonomy
20 and systematics. *Review of Palaeobotany and Palynology* 212, 97–110.
21 doi:10.1016/j.revpalbo.2014.08.018

22 Strother, P.K., Wood, G.D., Taylor, W.A., Beck, J.H., 2004. Middle Cambrian
23 cryptospores and the origin of land plants. *Memoirs of the Association of Australasian*
24 *Palaeontologists* 29, 99–113.

25 Taylor, 2009. Laminae in palynomorph walls from the Middle Cambrian-Early
26 Devonian. *Review of Palaeobotany and Palynology* 156, 7–7.
27 doi:10.1016/j.revpalbo.2008.09.008

- 1 Taylor, W.A., Strother, P.K., 2008. Ultrastructure of some Cambrian palynomorphs from
2 the Bright Angel Shale, Arizona, USA. *Review of Palaeobotany and Palynology* 151, 41–
3 50. doi:10.1016/j.revpalbo.2008.01.012
- 4 Taylor, W.A., Strother, P.K., 2009. Ultrastructure, morphology, and topology of
5 Cambrian palynomorphs from the Lone Rock Formation, Wisconsin, USA. *Review of*
6 *Palaeobotany and Palynology* 153, 296–309. doi:10.1016/j.revpalbo.2008.09.001
- 7 Vecoli, M., Beck, J.H., Strother, P.K., 2015. Palynology of the Ordovician Kanosh Shale
8 at Fossil Mountain, Utah. *Journal of Paleontology* (in press).
- 9 Wheat, C.W., Wahlberg, N., 2013. Phylogenomic insights into the Cambrian explosion,
10 the colonization of land and the evolution of flight in arthropoda. *Systematic Biology* 62,
11 93–109. doi:10.1093/sysbio/sys074
- 12 Woese, C.R., Kandler, O., Wheelis, M.L., 1990. Towards a natural system of organisms:
13 proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National*
14 *Academy of Sciences* 87, 4576–4579. doi:10.1073/pnas.87.12.4576
- 15 Wood, G.D., Benson, D. G., 2000. The North American occurrence of the algal
16 coenobium *Plaesiodyctyon*: Paleogeographic, paleoecologic, and biostratigraphic
17 importance in the Triassic. *Palynology* 24, 9–20.
- 18 Wood, G.D., Stephenson, J.T., 1988. Cambrian palynomorphs from the warm-water
19 provincial realm Bonnetterre and Davis Formations of Missouri and Arkansas (Reelfoot
20 rift area): Biostratigraphy, paleoecology, and thermal maturity, in: Gregg, M., Palmer,
21 J.R., Kurtz, V.E. (Eds.), *Field Guide to the Upper Cambrian of Southeastern Missouri*.
22 University of Missouri Press, Rolla, pp. 84–102.
- 23 Yin, L., Zhao, Y., Bian, L., Peng, J., 2013. Comparison between cryptospores from the
24 Cambrian Log Cabin Member, Pioche Shale, Nevada, USA and similar specimens from
25 the Cambrian Kaili Formation, Guizhou. China. *Science China: Earth Sciences*, 56, 703–
26 709.

27
28 Plate and Figure captions

1 Figure 1. Stratigraphic column for the sampled sections. The lithostratigraphic units
2 mentioned in the text are in bold. The Series/Stage boundaries are estimates based on the
3 known ranges of Laurentian trilobite biozones. The Tonto Group is probably deposited
4 entirely within the *Glossopleura* biozone, corresponding to Series3, Stage 5. The age of
5 the Rome Formation is constrained only to within the *Ollenellus* biozone, which is
6 probably Series 2.

7

Plate I. *Adinosporus voluminosus* Strother, gen. et sp. nov. The scale bar in all images is 10 μm - except for 4, 21 and 22 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.

1. Tetrad (T) and dyad (D) of spores contained within the original spore mother cell (SMC arrow). This specimen exemplifies the inherent problem in correlating morphological pleomorphism with biological provenance, as a single generative cell contains two topologically different cryptospore packets. Note that the SMC wall differs in character from the cryptospores held inside. Sample J2-1587s, Rogersville Shale.

2. Packets of two tetrads preserved within a single generative cell (SMC arrow). The tetrads are indistinctly divided and are recognized as such by interior bands, rather than by discrete walls, although the two packets remain distinct. Photographed in infrared light (830nm). Sample J2-1580s, Rogersville Shale.

3. *Adinosporus voluminosus* Strother, gen. et sp. nov. Cluster of six packets that includes the holotype, labeled C'. This population demonstrates the inherent variability in topology of *Adinosporus*, including common morphological features of the taxon such as transverse bands (TB arrow) and apparent equatorial thickenings (ET arrow) where spore-bodies are in close contact.

4. *A. voluminosus* Strother, gen. et sp. nov. Holotype. Note the conspicuous folds (F arrows) that indicate the multilaminate underlying nature of the spore wall. Sample J2-1571, slide J2-1571/B, England Finder location H57.

5. Tightly-adherent planar tetrad configuration, sample J2-1578, Rogersville Shale.

6. An infrared (830nm band pass filter) image of this planar tetrad reveals both the indistinct nature of the interior spore walls in addition to the folds (F arrow), which portray the underlying laminated nature of the spore wall. Sample J2-1587s, Rogersville Shale.

7. This planar tetrad shows spore-bodies of similar size, but with slightly different degrees of separation. Sample J2-1587s, Rogersville Shale.

8. This planar tetrad shows well-separated spore-bodies, which appear to represent two dyads of different size. Sample SB01-17, Rogersville Shale.

- 1 9. A planar tetrad shows well-separated spore-bodies, all of similar size. Sample SB01-
2 17, Rogersville Shale.
- 3 10. *A. voluminosus* Strother, gen. et sp. nov. Tightly-adherent square tetrad configuration,
4 note the folded nature of the sporoderm. Sample J2-1578, Rogersville Shale.
- 5 11. *A. voluminosus* Strother, gen. et sp. nov. Paratype. Tightly-adherent square tetrad
6 configuration, note the folded nature of the sporoderm. Sample J2-1571, slide J2-1571/B,
7 England Finder location X56/1, Rogersville Shale.
- 8 12. SEM image of a laterally compressed specimen, note the folds (F arrow) which are
9 evidence of an underlying laminated wall ultrastructure. Sample J2-1518, Rogersville
10 Shale.
- 11 13. SEM image of an irregular tetrad of similar spore-bodies. Sample J2-1518,
12 Rogersville Shale.
- 13 14. *A. voluminosus* Strother, gen. et sp. nov. Paratype. Tightly-adherent tetrad of
14 irregularly-shaped spore-bodies. Sample J2-1571, Rogersville Shale, slide J2-1571/B,
15 England Finder location M56/1.
- 16 15. Dyad pair with internal bands. Sample J2-1578, Rogersville Shale.
- 17 16. Small, tightly adherent triad. Sample J2-1578, Rogersville Shale.
- 18 17. Two dyads showing differing degrees of separation of their individual spore-bodies.
19 Sample J2-1578, Rogersville Shale.
- 20 18. Packet with internal thickened bands (TB arrow), which appear to demarcate potential
21 division planes. Sample J2-1578, Rogersville Shale.
- 22 19. Dyad with highly contorted sporoderm. Sample J2-1578, Rogersville Shale.
- 23 20. Dyad showing a thickened band (TB arrow) which is normal to the plane of
24 attachment between the spore pair. Sample J2-1578, Rogersville Shale.
- 25 21. Dyad showing a thickened band (arrow) which is normal to the plane of attachment
26 between the spore pair and appears to demarcate a potential further division plane.
27 Sample J2-1518, Rogersville Shale.

- 1 22. Another specimen similar to that seen in 22 but from a different sample. Sample J2-
2 1578, Rogersville Shale.
- 3 23. Smooth-wall simple dyad. Sample J2-1578, Rogersville Shale.
- 4 24. Larger dyad form with extensively folded sporoderm. Sample J2-1578, Rogersville
5 Shale.
- 6 25. Dyad configuration. Sample J2-1578, Rogersville Shale.
- 7 26. Dyad configuration but in axial compression showing the folded nature of the
8 sporoderm equatorially. Sample J2-1541, Rogersville Shale.

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

5 1. *Adinosporus voluminosus* Strother, gen. et sp. nov. Paratype. Typical cluster of
6 disorganized packets. Sample J2-1571, Slide J2-1517/B, England Finder location F56/3,
7 Rogersville Shale.

8 2. *Adinosporus voluminosus* Strother, gen. et sp. nov. Paratype. Another loosely arranged
9 cluster of packets. Sample J2-1571, Slide J2-1517/B, England Finder location Y54,
10 Rogersville Shale.

11 3. *Adinosporus voluminosus* Strother, gen. et sp. nov. Another loosely arranged cluster of
12 four packets. Sample J2-1578, Rogersville Shale.

13 4. *Adinosporus voluminosus* Strother, gen. et sp. nov. Loosely arranged set of five
14 packets from the Rome Fm, which is of Early (Series 2) Cambrian age. Sample SB01-14,
15 Rome Fm, Thorn Hill section.

16 5. *Adinosporus voluminosus* Strother, gen. et sp. nov. Another set of two dense packets,
17 also from the Rome Fm. Sample SB01-14, Rome Fm, Thorn Hill section.

18 6. *Adinosporus voluminosus* Strother, gen. et sp. nov. SEM of several compressed
19 packets. Sample J2-1578, Rogersville Shale.

20 7. *Adinosporus bullatus* Strother, gen. et sp. nov. Holotype. Specimen is essentially a
21 planar tetrad with a synoecosporal wall (arrow) that appears to enclose the entire packet.
22 Thickened bulbils (B) are the defining character for this species. Scale bar represents 5
23 μm . Sample SB01-17, slide number NHM/08/1810, England Finder location M33/0,
24 Rogersville Shale. This sample is from the Thorn Hill section.

25 8. *Adinosporus bullatus* Strother, gen. et sp. nov. Paratype. A large dyad pair. Sample
26 SB01-17, slide number NHM/08/1810, England Finder location E38/2.

27 9. *Adinosporus bullatus* Strother, gen. et sp. nov. A loose ring of packets recovered from
28 the middle Cambrian (*Glossopleura* biozone) Bright Angel Shale. From a section in Red
29 Canyon, Grand Canyon, Arizona. Sample GC10-3.

1 10. *Adinosporus bullatus* Strother, gen. et sp. nov. A paired planar dyad form. Sample J2-
2 1578, Rogersville Shale.

3 11. *Adinosporus bullatus* Strother, gen. et sp. nov. A dyad form that is completely
4 enclosed and demonstrating the ropey folding that characterizes the genus. Sample J2-
5 1578, Rogersville Shale, slide J2-1578/A/SEM, England Finder location W36/2.

6 12. *Adinosporus bullatus* Strother, gen. et sp. nov. A rosette of packets from the Bright
7 Angel Shale from a sample at Thunder Falls (Tapeats Creek drainage) in the Grand
8 Canyon, Arizona USA. Sample GC96-10 (see Strother and Beck, 2000 for locality
9 details).

10

1 Plate III. *Adinosporus geminus* Strother, gen. et sp. nov. The scale bar represents 10 μ m
2 in all images. Figured specimens are considered to be paratypes if they occur on the same
3 prepared slide as the holotype.

4 1. *Adinosporus geminus* Strother, gen. et sp. nov. Holotype. Sample J2-1578, slide J2-
5 1578/A/SEM, England Finder Location Q34/4, Rogersville Shale.

6 2. Paratype. Sample J2-1578, slide J2-1578/A/SEM, England Finder Location H60/2,
7 Rogersville Shale.

8 3. Paratype. Specimen demonstrating the transverse folds typical of the genus. Sample
9 J2-1578, slide J2-1578/SEM, England Finder location J36, Rogersville Shale.

10 4. Paratype. Sample J2-1578, slide J2-1578/A/SEM, England Finder Location D27/4,
11 Rogersville Shale.

12 5. Paratype. Specimen demonstrating marginal thinning (arrow) which is due to the
13 underlying lamellate nature of the sporoderm. Sample J2-1578, slide J2-1578/SEM,
14 England Finder location X45, Rogersville Shale.

15 6. Paratype demonstrating the smaller end of the size range. Sample J2-1578, slide J2-
16 1578/A/SEM, England Finder Location L50/3, Rogersville Shale.

17 7. Paratype. Another smaller pair which remains only partially attached. Sample J2-1578,
18 slide J2-1578/SEM, England Finder location G38/4, Rogersville Shale.

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1 Plate IV. *Spissuspora laevigata* Strother, gen. et sp. nov. The scale bar represents 10 μ m
2 in all images. Figured specimens are considered to be paratypes if they occur on the same
3 prepared slide as the holotype.

4 1. *Spissuspora laevigata* Strother, gen. et sp. nov. Holotype. Median focus, arrow points a
5 thin outer envelope which is largely detached from the tetrad. Sample J2-1578, slide J2-
6 1578/A/SEM, England Finder Location C27, Rogersville Shale.

7 2. *Spissuspora laevigata* Strother, gen. et sp. nov. Holotype. top focus. Sample J2-1578,
8 slide J2-1578/A/SEM, England Finder Location C27, Rogersville Shale.

9 3. *Spissuspora laevigata* Strother, gen. et sp. nov. Holotype. Image is intentionally
10 underexposed to show more clearly the thin, partially detached enclosing envelope
11 (arrow). Sample J2-1578, slide J2-1578/A/SEM, England Finder Location C27/0,
12 Rogersville Shale.

13 4. Paratype. Sample J2-1578, slide J2-1578/A/SEM, England Finder Location B39/1,
14 Rogersville Shale.

15 5. SEM image of a packet comprised of four discrete bodies. Sample J2-1578,
16 Rogersville Shale.

17 6. Elongate tetrad. Sample J2-1578, slide 1578.1, Rogersville Shale.

18 7. Paratype. Sample J2-1578, slide J2-1578/A/SEM, England Finder Location L66/0,
19 Rogersville Shale.

20 8. A somewhat more open tetrad form. Sample J2-1578, slide 1578B, Rogersville Shale.

21 9. Paratype. In this specimen one of the spore-bodies possesses a wrinkled wall, which is
22 probably a taphonomic artifact, since this is very uncommon. Sample J2-1578, slide J2-
23 1578/A/SEM, England Finder Location V29/0, Rogersville Shale.

24 10. Paratype. Arrow points to a thin membrane that is still present. Sample J2-1578, slide
25 J2-1578/A/SEM, England Finder Location W47/0, Rogersville Shale.

26 11. Paratype. Tightly bound, irregular tetrad form. Sample J2-1578, slide J2-
27 1578/A/SEM, England Finder Location B35/3, Rogersville Shale.

- 1 12. Paratype. Polyad with 6 spores. Sample J2-1578, slide J2-1578/A/SEM, England
2 Finder Location M33/2, Rogersville Shale.
- 3 13. Paratype. In this specimen there appears to be a fifth cell as part of the packet cluster.
4 Sample J2-1578, slide J2-1578/A/SEM, England Finder Location L65/3, Rogersville
5 Shale.
- 6 14. A tightly-bound cluster with five spore-like cells attached. Sample J2-1578, slide
7 1578.1, Rogersville Shale.
- 8

- 1 Plate V. *Vidalgea masculata* Strother, gen. et sp. nov. The scale bar represents 10 μ m in
2 all images. Figured specimens are considered to be paratypes if they occur on the same
3 prepared slide as the holotype.
- 4 1. *Vidalgea masculata* Strother, gen. et sp. nov. Holotype. Medial focus. Sample J2-1803,
5 Slide J2-1803/B2, England Finder Location G49/4, Pumpkin Valley Shale.
- 6 2. *Vidalgea masculata* Strother, gen. et sp. nov. Holotype. Top focus. Sample J2-1803,
7 slide J2-1803/B2, England Finder Location G49/4, Pumpkin Valley Shale.
- 8 3. Paratype, showing the interior spore body, which possess a thickened margin, and a
9 loose-fitting outer granular envelope. Sample J2-1803, slide J2-1803/B2, England Finder
10 Location F50, Pumpkin Valley Shale.
- 11 4. Paratype, showing the interior spore which is quite thick-walled and dark. Sample J2-
12 1803, slide J2-1803/B2, England Finder location F47, Pumpkin Valley Shale.
- 13 5. Paratype. Simple dyad with diffuse contents and very faintly preserved inner bodies.
14 Sample J2-1803, slide J2-1803/B2, England Finder Location Y51, Pumpkin Valley Shale.
- 15 6. Paratype. Simple dyad with only diffuse contents. Sample J2-1803, slide J2-1803/B2,
16 England Finder Location X54, Pumpkin Valley Shale.
- 17 7. Paratype Simple, tightly adherent set of three spore-like bodies of similar size (triad).
18 This image is constructed from two images in different focal planes. Sample J2-1803,
19 slide J2-1803/B2, England Finder Location F36/1, Pumpkin Valley Shale.
- 20 8. Paratype. A dyad, in which one of the cells of the dyad contains two distinct spore-like
21 inner bodies (arrows). Sample J2-1803, slide J2-1803/B2, England Finder Location R52,
22 Pumpkin Valley Shale.
- 23 9. Paratype. Triad of 3 enclosed dark, thicker-walled, inner bodies. Sample J2-1803, slide
24 J2-1803/B2, England Finder Location H43/1, Pumpkin Valley Shale.
- 25 10. Paratype. A square (planar) tetrad. Sample J2-1803, slide J2-1803/B2, England Finder
26 Location H36/2, Pumpkin Valley Shale.
- 27 11. Paratype, A square (planar) tetrad with diffuse inner bodies. Sample J2-1803, slide
28 J2-1803/B2, England Finder Location E33/4, Pumpkin Valley Shale.

- 1 12. Tetrahedral tetrad, one cell of which includes a dark inner spore-like body. Sample
2 J2-1803, slide J2-1803/A3, Pumpkin Valley Shale.
- 3 13. Paratype. showing two enclosed dyads laterally attached. The outer, synoecosporal
4 wall (arrow) clearly surrounds each dyad pair. Sample J2-1803, slide J2-1803/B2,
5 England Finder location W40/4, Pumpkin Valley Shale.
- 6 14. Another planar set of two dyads, similar to figure 13, with somewhat diffuse inner
7 bodies preserved. Sample J2-1803, slide J2-1803/A3, Pumpkin Valley Shale.
- 8 15. Irregular cluster (polyad). Sample J2-1803, slide J2-1803/A3, Pumpkin Valley Shale.
- 9 16. Paratype, showing a larger number of spore-like bodies in a cluster. Sample J2-1803,
10 slide J2-1803/B2, England Finder location J48/2, Pumpkin Valley Shale.
- 11 17. Paratype. Irregular cluster. Sample J2-1803, slide J2-1803/B2, England Finder
12 location T52/1, Pumpkin Valley Shale.
- 13 18. Irregular cluster. Sample J2-1803, slide J2-1803/A3, Pumpkin Valley Shale.

Figure 1