



## 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. Aero-terrestrial 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 group, cryptospores *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 aero-terrestrial 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 (Darrivillian) and younger rocks. These younger cryptospores are recognized as such because they retain distinctive attachment geometries—either as geometrically

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regular tetrads or as isomorphic, typically hilate dyads. The Cambrian 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 unclear. In addition, Cambrian cryptospores may occur as packets of multiple spore-like bodies surrounded by one or more, synoecospore walls (Taylor and Strother, 2008). These facts, based on morphology, reveal unambiguous differences between Cambrian and younger cryptospores. However, it is likely that these morphological differences reflect underlying biological variation in meiosis and development during sporogenesis, rather than underlying systematic differences in evolutionary origin.

In order to place the Cambrian cryptospores within their correct phylogenetic context, it is necessary to make some broad assumptions about functional morphology. While this not a terribly satisfactory 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 evolving in response to living in subaerial settings. Phycologists refer to extant terrestrial algae that survive subaerial exposure as aeroterrestrial, 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, homogeneous to multilaminate walls composed of highly refractory, sporopollenin-like, organic compounds; they were widely dispersed 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 apposition 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 *Sphaerocarpos* (Strother, 2010) and the primitive liverwort, *Haplomitrium gibbisiae* (Renzaglia et al., 2015). This indicates that embryophytic spore characters in streptophyte lineages were evolving prior to the origin of the first embryophyte sporophytes *sensu stricto* (i.e. biaxial sporophytes that develop from a multicellular embryo (Niklas, 1997; Niklas and Kutschera, 2010)). In a direct reading of the fossil record, spores appear before sporophytes. This idea is not new, in fact, it is a fundamental thesis of Bower's antithetic hypothesis for the origin of the plant sporophyte, in which he proposed that the plant spore must have preceded the evolution of a vegetative sporophyte (Bower, 1908). "Spores before sporophytes," has been more recently championed in cytological studies of sporogenesis in extant bryophytes, which show accelerated 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 1, 1, exemplifies a fundamental problem with how to interpret and describe systematically Cambro–Ordovician cryptospores. This fossil consists of a spherical wall (cell) within which occur both a cryptospore dyad and an incompletely (?) formed tetrad. 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 incompletely formed tetrad. More specifically, after a first mitotic division, the resultant nuclei migrated away from each other, with one undergoing a single subsequent mitosis (resulting in a dyad), but the other dividing twice to produce an apparent tetrad of spores. The specimen in Plate 1, 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 nuclear 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 mitosis 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 cannot be certain of the spore ploidy, it is most probable that the SMC itself 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 tetrad 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 1, 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 different numbers of what are, ultimately, dyads. The result of this understanding 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 tetrads 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 Darriwilian of Saudi Arabia (Strother et al., 1996, 2015; Le Hérisse et al., 2007). 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 1, 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 specimen (A) shows both a darkened, equatorial thickening (ET arrow)

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