



Devonian smooth-walled tasmanids and new insights of life-cycle descriptions through fluorescence microscopy

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Abstract

Fossil microspherules suspected to be marine algal cysts of varying mineralogy are abundant in Paleozoic deposits worldwide. Positive identification of remineralized microspherule fossils is problematic and long debated, particularly for tasmanid species. Several hundred silica-rich microspherules were retrieved through complete maceration of black shale samples from the Givetian Oatka Creek Formation of the Appalachian Basin. Microspherules were analyzed visually through transmitted, incident light, and fluorescence microscopy. The structural features of these microspherules are evident and are interpreted to be *Tasmanites sinuous*. The images presented herein are the first fluorescence images showing in detail the life cycle stages of the genus *Tasmanites*. This work also confirms that this tasmanid species does extend into the Givetian as suspected from prior research.

Keywords: fluorescence microscopy, marine algal cysts, pellicle cysts, resting cyst, *Tasmanites*

Introduction

The presence of mineralized, walled, spheroidal microfossils in Paleozoic rocks is ubiquitous worldwide. In Laurasian deposits, microspherules ranging in size from 40µm to 500µm in diameter, with and without ornamentation, single to multi-layered outer walls, and have been reported to occur in higher abundance throughout black shales ranging in age from Middle Devonian to Early Mississippian in both Gondwana and Laurentia (Revill *et al.* 1994, Caplan & Bustin 1996, Paris *et al.* 2000, Schieber & Baird 2001, Vigran *et al.* 2008, Wicander & Playford 2008, Chamberlain *et al.* 2016, Mouro *et al.* 2016, Lelono 2019). Due to high variability of paleoenvironments of the Devonian Appalachian Seaway, the mineralogy of preserved microspherules varies widely rendering the visualization of internal identifying structures of certain marine algae cysts difficult, thus, making their taxonomic assignment problematic at best.

The marine algal cyst *Tasmanites* is prolific in the Devonian Appalachian Seaway. *Tasmanites* cysts have been reported to occasionally maintain a high amount of sedimentary organic matter (e.g., telalginite; Ryder *et al.* 2013, Hackley *et al.* 2017, Liu *et al.* 2019a), others preserve as pyrite (Provo 1976, Schieber & Baird 2001, Kus *et al.* 2012, Liu *et al.* 2019b), calcite (Bruner *et al.* 2015, Li & Schieber 2015), calcite and pyrite (Chamberlain *et al.* 2016), and silicates (Schieber 1996, Schieber & Baird 2001, Bruner *et al.* 2015, Li & Schieber, 2015, Liu *et al.* 2019b, 2020, Bartlett *et al.* 2022). Where deposits render organic-rich cysts that can be retrieved and identified through traditional palynological processes identification is relatively simple and straightforward, however, many Middle to Late Devonian deposits contain strictly mineralized spherules which are observed through thin section analysis or complete rock maceration. Where the preservation of cysts is mineralized entirely with opaque minerals, like pyrite, observations of internal structures are inhibited, and researchers are reliant on a limited number of specimens retrieved through digestion processes.

While the preservation of *Tasmanites* as clear to translucent silica-rich forms have been reported in several Appalachian sequences (Schieber 1996, Schieber & Baird 2001, Bruner *et al.* 2015, Li & Schieber 2015, Liu *et al.* 2019b, 2020, Bartlett *et al.* 2022) these investigations are primarily limited to paleoenvironmental implications around

Tasmanites abundances, their preservation and inferred thermal maturity of host rock, rather than systematics at a species level. Further, these marine algal cysts often shattered in thin section, thus, where internal structural analysis is required for identification, many assignments are incomplete and/or questioned. This paper seeks to expand upon Bartlett *et al.*'s (2022) fluorescent microscopic approaches by including these first reported images of pellicle, resting, and expanded cyst stages. The Prasinophyceae is a large, poly- or paraphyletic group of single-celled, flagellate green algae hypothesized to have diverged early in chlorophyte phylogeny (Lewis and McCourt, 2004). The life history of several species of Pyramimonadales includes a unique non-motile stage characterized by the formation of organic-walled cyst-like structures termed phycomata. The alga remains metabolically active within the phycoma and undergoes vegetative reproduction; as a result, the phycoma increases in size over time. Prasinophycean phycomata have decay-resistant walls and thus have preservation potential as fossils (Quintavalle & Playford, 2006); the oldest persuasive specimens come from the Precambrian and are more than 1.2 Ga old (reviewed in Teyssèdre 2006). The majority of fossil phycomata have been described from strata deposited in marine or brackish water, but there are also several reports of these structures from freshwater deposits (Dotzler *et al.* 2007).

Tasmanites (Tasmanaceae) is an algal microfossil which occurs in many marine facies from the Cambrian to the Miocene (Martín-Closas 2003). Haplotypic features are frequently absent, but the surface may occasionally be covered by numerous, regularly spaced punctae. Ultrathin sections of the wall show concentric banding and two types of pores which traverse the wall in a radiating pattern in modern prasinophytes and several species of exceptionally preserved fossil forms (Jux 1968, Tel'nova 2012). The affinities of *Tasmanites* have remained in doubt since the original description by Newton in 1875, however, most researchers now consider these microfossils to represent the phycomata of planktonic prasinophytes. Guy-Ohlson (1988), using a variety of techniques, was able to demonstrate the life history of *Tasmanites* based on specimens of Toarcian (Early Jurassic) age from southern Sweden. Her investigation substantiates the affinities of *Tasmanites* with the modern prasinophycean algae *Pachysphaera*, *Halosphaera*, and *Pterosphaera*.

Tasmanites fossils are most commonly preserved as organic-rich or telalginite compressed cysts usually ranging from 100 to 600 µm in diameter (Ryder *et al.* 2013; Hacklet *et al.* 2017, Liu *et al.* 2019a), however, they have been found in their uncompressed form within certain deposits where infilling and remineralization may occur, leaving behind microspherules that are dominated by pyrite (Provo 1976, Schieber & Baird 2001, Kus *et al.* 2012, Liu *et al.* 2019b), silicates (Schieber 1996, Schieber & Baird 2001, Bruner *et al.* 2015, Li & Schieber 2015, Liu *et al.* 2019b, 2020, Bartlett *et al.* 2022), and calcite (Bruner *et al.* 2015, Li & Schieber 2015, Chamberlain *et al.* 2016). Many of these spherules have been reported as near perfect spherules. Schieber & Baird (2001) hypothesize that the spheroids are preserved in their original form due to settling into areas where sediments contain a large amount of water and the low sedimentation rates where they are deposited allowed for mineral replacement prior to any compaction of the forms. While examination of *Tasmanites* is possible through traditional approaches with sedimentary organic matter, the microfossils that are preserved through complete remineralization have been questioned in their affinity. Marine algal cysts within several deposits of the Appalachian Seaway have undergone such pathways and analysis of specimens comprised of both opaque and transparent minerals have been problematic. The Devonian Appalachian Basin, which spans from Alabama northeasterly to Greenland, was part of a retroarc foreland that developed adjacent and parallel to the Acadian Orogenic belt, a mountain chain built by the oblique collision of the North American continental margin with the Avalon terrane and beginning its formation in the Middle Devonian and terminating in the Late Devonian (van Staal *et al.* 2009). The dominant controls on the deposition of black shales in the Devonian Appalachian Basin have often been attributed to global eustatic changes or tectonic events or both (Ver Straeten *et al.* 1997, Werne *et al.* 2002, Sageman *et al.* 2003, Arthur & Sageman 2005, Brett *et al.* 2011). At the time of deposition, the beds studied herein were formed during a time of relative tectonic quiescence (Filer 2002, Arthur & Sageman 2005).

The Catskills deltaic sequences have been studied, the subsequent reports on the lithology, stratigraphy, and geochemistry of the beds that recorded a series of five transgressive/regressive cycles, each of a few million years duration. The Devonian mudrocks of western and central New York State are part of the Catskill Delta Complex, dominated by siliciclastic material eroded from the Acadian orogen (Arthur & Sageman 2005, Ver Straeten *et al.* 2011). These shale deposits alternate from dark gray organic-rich shale and light gray organic-poor shale (Sageman *et al.* 2003, Arthur & Sageman 2005, Ver Straeten *et al.* 2011, Haddad *et al.* 2018, Kelly *et al.* 2019, He *et al.* 2020). The Oatka Creek Formation, the uppermost formation of the Marcellus Group, is an organic-rich black shale deposit suspected to have been deposited under anoxic conditions (Werne *et al.* 2002). Subsurface thermal maturation for the Marcellus Group Formations have reported $CAI_{min}:CAI_{max}$ of 2:2; %R_o of 0.5, and an R_o of 38 (Weary *et al.* 2000).

Material & Methods

The Oatka Creek Formation was sampled at 50 cm intervals throughout the entirety of the 9 m thick deposit at outcrops in LeRoy, New York (Fig. 1). These shale samples were processed through a complete digestion methodology detailed in Meehan *et al.* (2020). The resulting fluids containing macerated rock sediments were then run through a series of nested sieves (500, 355, 212, 90, and 63 μm), dried at room temperature ($\sim 20^\circ\text{C}$), specimen search was made from all sieve ranges.

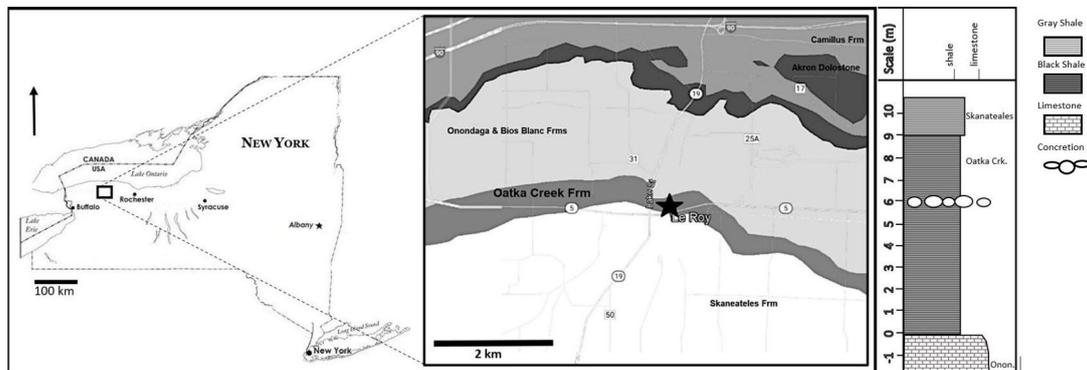


FIGURE 1. Large scale map of New York state denoting the location of the study area within the region; detail inset of the study location of sampling in Oatka Creek in the city of LeRoy, New York; generalized stratigraphic section of Eifellian to Givetian formations of LeRoy, New York found within Oatka Creek.

Microspherules retrieved from the Oatka Creek Formation were imaged with a digital transmitted light microscope and fluorescence images acquired with a Zeiss LSM 710 confocal microscope using a 20 x Plan Apochromat, 0.8NA objective. Laser lines and detector ranges information are embedded in image metadata and uploaded as supplementary data which is easily processed through Zeiss ZEN lite free software (www.zeiss.com/microscopy/int/products/microscope-software/zen-lite.html).

Results

Transmitted and Incident Light Microscopy

Plates 1–2 show single specimen images with varying points of focus on the specimen under transmitted and/or overhead light effect on microspherules. The transmitted light imaging quality varies depending on the specimen and focal point on the three-dimensional object. Internal components, internal spheroidal structure(s), of microspherules are evident in $\sim 50\%$ of specimens (Figs. 2–3); of this set of microspherules $\sim 90\%$ showed evidence of internal structures ranging in size from 2–10 μm (Fig. 2: 1–3; Fig. 3: 1–2). The remaining 10% contained substantially larger internal structures (Fig. 2: 3a–3c). Fig 2: 3a–b show a large internal structure that appears to be either multiple smaller structures fused together, or a single structure preserved during the process of division. External textures and/or ornamentation are rare on all specimens; this surface probably corresponds to the vesicle surface. Occasional pits resemble vesicle surface markings associated with the tubular canals, or punctae, commonly observed in vesicle walls of the prasinophyte microalga *Tasmanites* by Burden *et al.* (2002) and Chamberlain *et al.* (2016) (Fig. 2: 2a, 2d; Fig. 3: 2b). there is wide variability in tasmanitid punctation, however, no specimens observed showed punctae with a discernable pattern. Five specimens were retrieved that appear to either be fused during preservation (Fig 3: 1a–1c) or undergoing budding or fission (Fig. 2: 3a–3e). In addition, the small, circular pits visible on the specimen's surface appear similar to structures interpreted as punctae. We therefore interpret these features in our specimens as punctae.

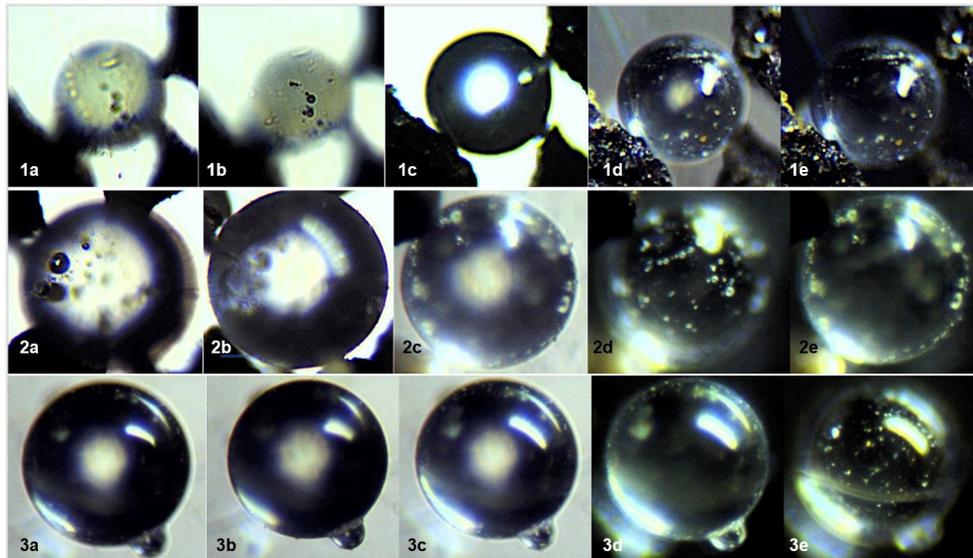


FIGURE 2. Transmitted and incident light images of silica-rich microspherules retrieved from the Oatka Creek Formation, Leroy, New York. Internal to external (left to right) focal point shift imaging approach allows for internal structures at different points within the tasmanid to be imaged: 1a–e: internal pyritic inclusions imaged throughout single tasmanid, inclusions interpreted to be portions of gamete stage internal structures; 2a–e, surface punctae visible (2a) in addition to internal pyritic inclusions; 3 a–e conjoined or splitting tasmanid containing internal pyritic inclusions. Images taken at a magnification of 10x, average diameter of all cysts, 125 μm .

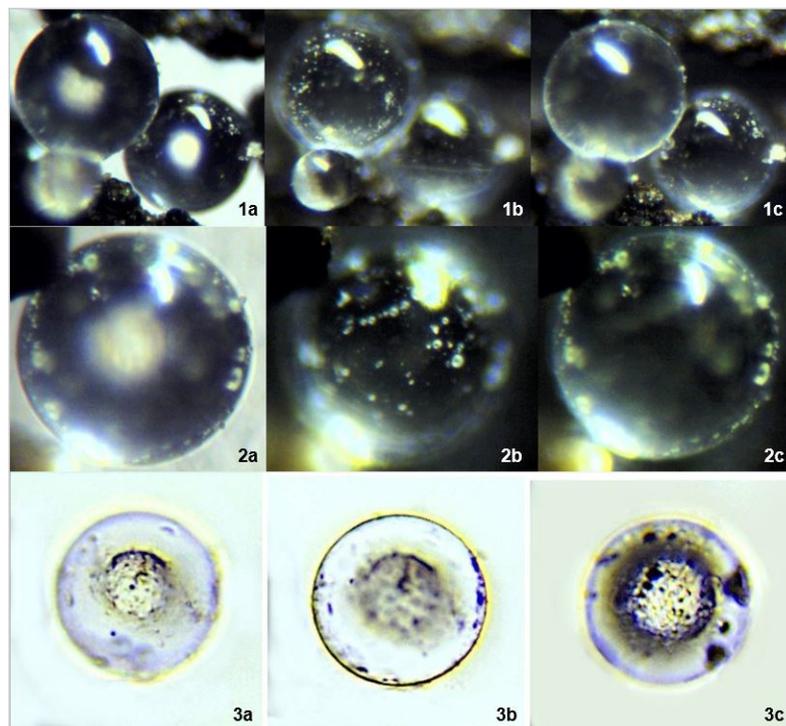


FIGURE 3. Transmitted and incident light images of silica-rich microspherules retrieved from the Oatka Creek Formation, Leroy, New York. 1a–c conjoined or splitting tasmanid containing internal pyritic inclusions, interpreted to be a dividing cyst; 2a–c single tasmanid with no pyritic inclusions but numerous surficial punctae, interpreted to be a vegetative cyst; 3a–c tasmanid with well defined internal structure interpreted to be a resting cyst. Images taken at a magnification of 10x, average diameter of all cysts, 125 μm .

Fluorescence Microscopy

Fluorescence light microscopy images (Figs. 4–5) allowed for imaging of microspherules with and without internal structures (Fig. 4 a, d) and microspherules containing internal structures (Fig. 4 b, c, e, f). Figure 2, images a and d, are cysts preserved without internal structures enclosed. Figure 4 b and c contain a single internal sphere within which appear to be additional diminutive spherules. Figure 2 e and f contain two clearly defined and separate internal

structures, within which there are additional diminutive spheres (arrows). The only portion of microspherules that would fluoresce were the internal structures, no external portion of the cysts would fluoresce. Figure 5 shows fluorescence images of microspherules believed to be internal structures expelled from cysts prior to preservation. Specimens imaged in Figure 5 contain additional internal structures like those specimens imaged in figure 4, however, possibly due to being expelled from the original cyst body, these tertiary spherules are more readily visible within these specimens. These tertiary spherules range in diameter of $\sim 1 \mu\text{m}$ - $20 \mu\text{m}$. Figure 4 b1 shows a tertiary spherule that appears to be undergoing the process of expulsion from this internal structure.

During the course of this study, several hundred individual silicate microalgae cysts were examined, and these specimens are used as a basis for the formal systematic treatment of chlorophyte (algae) taxa that is presented here.

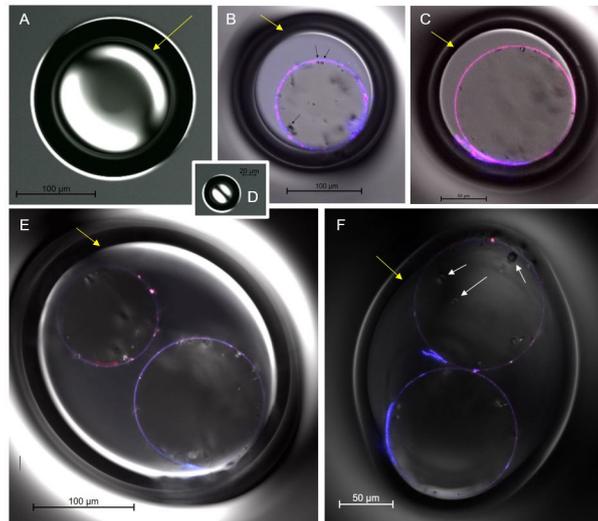


FIGURE 4. Fluorescence microscopy images of select silica-rich microspherules from the Oatka Creek Formation, Leroy, New York. Black and white arrows denote locations of diminutive spherules within endocysts. Yellow arrows denote the edge of the external wall. Average diameter of tasmanid 4a–c is $125 \mu\text{m}$; 4d diameter is $50 \mu\text{m}$; 4e tasmanid diameter is $125 \mu\text{m}$; 4f tasmanid horizontal diameter is $120 \mu\text{m}$ with a height of $\sim 130 \mu\text{m}$.

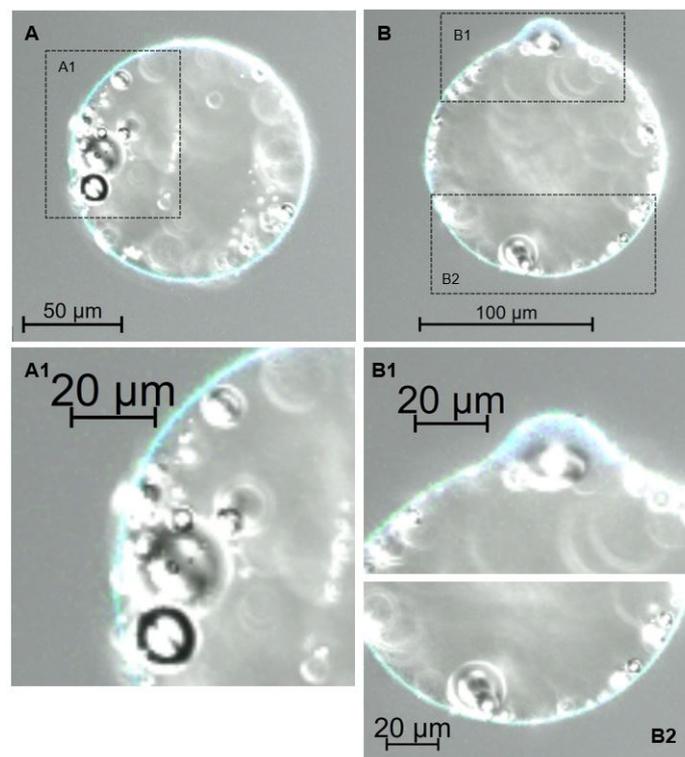


FIGURE 5. Fluorescence microscopy images of select silica-rich microspherules from the Oatka Creek Formation, Leroy, New York. 5a: tasmanid interpreted to be a gamete sack; 5b” tasmanid interpreted to be a diving stage cyst.

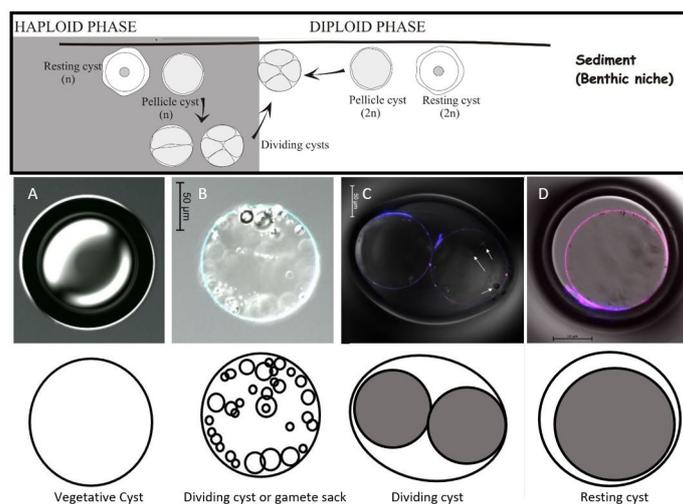


FIGURE 6. Life stage interpretative drawings based off of interpretation schematic of modern marine algal cysts (Bravo and Figueroa, 2014). 6a: image of tasmanid in a vegetative stage; 6b: image of a tasmanid in a gamete sack stage; 6c image of a tasmanid in a dividing cyst stage; 6d: image of a tasmanid in a resting cyst stage.

SYSTEMATIC DESCRIPTIONS

Super Group: Archaeplastida (Adl *et al.*)

First order subdivision: Chloroplastida (Adl *et al.*)

Second order subdivision: Prasinophytæ (Cavalier-Smith, emend Lewis & McCourt)

Order: Pterospermatales (Tappan)

Family: Tasmanitaceae (Tappan)

Genus: *Tasmanites* (Newton, emend Schopf, Wilson & Bental)

Remarks: *Tasmanites* is a common microalga with representatives known from the Proterozoic (Knoll & Swift 1985, Samuelson *et al.* 1999) to the modern ocean (Boalch & Guy-Ohlson 1992). Fensome *et al.* (1990) and Mullins *et al.* (2007) list of 80 and 90 species, respectively. Of these species listed, Fensome *et al.* (1990) indicate that 28 species are of Devonian age. Six of these (*T. asper*, *T. decorus*, *T. huronensis*, *T. sinuosus*, *T. sommeri*, and *T. winslowiae*) are Middle Devonian species with geographic ranges that include the western reaches of the Appalachian Seaway (Ohio, Illinois, Ontario) (Wicander 1993) and as far east as central Pennsylvania (Chamberlain *et al.* 2016). *Tasmanites* has a smooth or rough surface sphaeromorphic form lacking strong spines or other well-developed ornamentation if any at all. Members of this genus have diameters generally ranging from 40µm to 500µm. Specimens of the genus *Tasmanites* are characterized by a simple one to two-layered wall (generally ~5% of vesicle diameter); some species vesicle walls show fine, concentric laminations. Excystment occurs by means of a linear split of the vesicle. The Oatka Creek material illustrated contains several specimens which we assign to the genus *Tasmanites* based on vesicle size and morphology, wall structure, excystment pattern, and punctation.

Tasmanites sinuosus (Winslow)

Remarks: The species *sinuosus* are characterized by having spherical vesicles usually ranging from 50 µm to 400 µm in diameter with smooth to rough rugose surfaces. The vesicle wall may be punctate, unlaminated and 2 µm to 13 µm thick (~5% vesicle thickness). Of the features available for use for speciation, overall diameter of the disseminule and wall thickness are most determinable as punctae and other ornamentation are often absent. Winslow (1962) indicates

that the occurrence of *T. sinuosus* is limited to the Upper Devonian, but Wicander (1983) extended the range to the Middle Devonian, this was confirmed by Chamberlain *et al.* (2016), and herein.

Material: 283 well preserved remineralized silicate specimens (Figs. 2–5) were retrieved from all sieve ranges. Mean diameter = 110 μm ; std. dev. = $\pm 23.25 \mu\text{m}$.

Description: The specimens illustrated in Figures 2 and 3 have diameters averaging about 120 μm . Of the six Middle Devonian Appalachian Seaway tasmanitid species listed above, only *T. sinuosus* has vesicles as small as these Oatka Creek tasmanitid specimens. In addition, the specimens illustrated in Figure 4 and 5, have simple vesicle walls, which although thin compared to most tasmanitids (about 5% vesicle diameter), lie within the range of wall thickness Winslow (1962) attributes to *T. sinuosus*. The about 30% (85 specimens) had visible punctation pits. We thus suggest that these specimens most closely resemble *T. sinuosus*.

Discussion

These transparent *Tasmanites* fossils provide a unique opportunity to employ non-destructive fluorescence imaging. The images gathered of only a small subset of hundreds of microfossils appear to be snapshots of ancient prasinophytes in varying life stages. Figures 4a, d and 6c show is interpreted to be photosynthesizing vegetative cysts as there is no evidence of excystment in any specimens found. Figure 4 b and c appears to be simple cysts containing endocysts. Figure 4 e, f and figure 6 a show a cyst with an endocyst undergoing asexual reproduction, however, this splitting of the endocyst in to two clearly defined endocysts may be evidence of meiosis as well as many algae are capable of both asexual vegetative and sexual reproductive and/or inductive pathways (Moczydlowska 2010, 2016, Moczydlowska *et al.* 2011, Agić *et al.* 2015, 2016). Figure 5 and figure 6b show endocysts after excystment. Herein these endocysts that contain additional microspherules are interpreted here either a sack of offspring cells or as gametes similar to structures proposed in Moczydlowski (2010). Figure 6d is interpreted to be a resting cyst.

Conclusion

Tasmanites sinuosus is found well into the Middle Devonian throughout the Appalachian basin and its preservation varies based on varying paleoenvironmental factors that include but are not limited to oxygen availability, free ion sources in the water column, and sedimentation rates. Fluorescence microscopy is a potential non-destructive tool for speciation of microfossils where traditional palynological approaches are problematic. *Tasmanites* preserved as silica-rich spherules do contain evidence of both vegetative asexual and sexual reproduction.

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