(SS36) Continents before vascular plants

Date: August 24
Place: Room 5333 (oral)
Organizers: Dianne Edwards, Jennifer Morris & Charles Wellman
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Purpose: There is a growing body of evidence relating to both fresh water and terrestrial habitats that there were diverse communities of photosynthetic organisms growing on continents prior to the colonization of land by vascular plants. Participants include Cyanobacteria and algae, often associated in biofilms or crusts, and lichens, as well as the earliest embryophytes that show some of the characteristics of bryophytes. Evidence based on micro- meso- and megafossils, trace fossils as well as geochemical and isotopic signatures will be reviewed in the context of gradually changing lithosphere and atmosphere.
We welcome contributions involving all aspects of terrestrial landscapes and colonization before and during the early stages of the evolution of vascular plants.

Oral Presentation

Aug. 24 [PM2] Room: 5333

Chairs: Dianne Edwards, Jennifer Morris

14:30-15:10 **[Keynote] Understanding the early terrestrial palynological record: decay experiments and their taphonomic implications** SS36-O01 (567)

Charles Wellman, Linda Graham, Louise Lewis,Wilson Taylor

15:10-15:30 **Diversity in enigmatic Cambrian cryptospores: phylogenetic divergence or paleofloristic differentiation?** SS36-O02 (516)

Wilson A. Taylor

15:30-15:50 **Chemostratigraphy, depositional environments and the pre-tracheophyte fossil record at the continental - marine transition** SS36-O03 (526)

Alexandru M.F. Tomescu, Gregory C. Nadon, Lisa M. Pratt, Gar W. Rothwell

Aug. 24 [PM3] Room: 5333

Chair: Charles Wellman

16:20-17:00 **[Keynote] Lang's nematophytes revisited** SS36-O04 (113)

Dianne Edwards, Rosemarie Honegger, Lindsey Axe

17:00-17:20 **Cryptospores and the algal plant transition** SS36-O05 (615)

Paul K. Strother

17:20-17:40 **Dispersed cryptospores reunited with their parent plants: clues from the Lower Devonian on pre-vascular vegetation** SS36-O06 (349)

Jennifer L. Morris, Dianne Edwards, John B. Richardson, Lindsey Axe

SS36-O01 (567)

Understanding the early terrestrial palynological record: decay experiments and their taphonomic implications

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It is generally assumed that terrestrial environments harboured microbial communities long before the appearance of land plants sometime during the Mid Palaeozoic. Until recently evidence for such biotas (fossil, sedimentological, geochemical) was extremely rare. However, palynological investigation of ancient terrestrial deposits is yielded abundant and exciting new evidence for early terrestrial life. This includes evidence from the Cambrian-Ordovician of Oman, the Torridonian of Scotland (ca. 950 Ma) and the Nonesuch Shale of the USA (ca. 1100 Ma). The palynological preparations yield diverse palynomorph assemblages consisting of unicellular prokaryotes and eukaryotes (sheathes, filaments, tubular structures and sphaeromorphs - including encysted forms, clusters and enclosed clusters). Some forms are unexpectedly large, including sphaeromorphs exceeding 400 µm in diameter, and others exhibit surprisingly complex wall structure. Tantalizing structural elements indicate the presence of larger, possibly multicellular organisms. Unfortunately, the biological affinities of the vast majority of these palynomorphs are largely unknown. However, exceptional preservation in phosphate is widespread in the Torridonian and is providing additional evidence that is helping in the interpretation of the dispersed palynomorphs. The Torridonian also preserves abundant sedimentary structures interpreted as representing subaerial microbial mats, and the palynomorph assemblages from these sediments contain autochthonous wefts of these mats (associated with various cyanobacteria). Together the new fossil evidence is beginning to reveal the nature of the complex microbial communities of organisms that inhabited terrestrial (subaerial and freshwater aquatic) environments that existed prior to the appearance of land plants. The palynomorphs probably in the main represent autochthonous elements that accumulated in aquatic environments and represent free-living benthic and planktonic freshwater organisms. However, some elements may represent allochthonous elements transported into these depositional environments from terrestrial subaerial habitats. By the Mid Ordovician dispersed land plant spores (often termed cryptospores) appear in palynological preparations. They occur in large numbers worldwide, forming similar assemblages that persist for some 30 million years. These dispersed spores are considered to represent the first land plants (embryophytes). They are interpreted as plants at a ‘bryophyte-like’ grade or organization, that were probably ecological generalists and hence cosmopolitan. This talk will discuss the results of a collaborative project aimed at critically reviewing the fossil evidence for the earliest terrestrial microbial biota. We consider the nature and biological affinities of the earliest terrestrial microbial fossils based on detailed morphological and ultrastructural analysis of the fossils, comparisons with extant organisms, and taphonomic experiments on extant material.

Keywords: Precambrian, Cambrian, Ordovician, Embryophytes, land plants.

SS36-O02 (516)

Diversity in enigmatic Cambrian cryptospores: phylogenetic divergence or paleofloristic differentiation?

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Research into the tempo and timing of, and participants in, the formation of the earth's earliest terrestrial ecosystems is in its infancy. Under the best of circumstances, reconstructing past terrestrial ecosystems is much more difficult than those in the marine realm. This is compounded by the fact that our knowledge of the taxonomic affinities of organisms based solely on pre-Cambrian and Cambrian palynomorphs is sparse at best. The difficulty of identifying ancient terrestrially derived deposits (and their palynomorphs), combined with a relative lack of past efforts focused on determining the producers using all available means (e.g., wall ultrastructure) is a major reason for this. While authoritative statements on evolutionary trends or biogeography are certainly premature, it is not too early to assess what is known as a way of framing what questions may eventually yield to future insights. Three Cambrian deposits from around North America – the Bright Angel shale (Arizona, USA), the Rogersville Shale (Tennessee, USA), and the Lone Rock Formation (Wisconsin, USA) – contain terrestrially derived cryptospores (*sensu* Strother and Beck) that are broadly comparable at the level of the light microscope, but distinct from one another when examined with the transmission electron microscope (i.e., ultrastructurally). Dyads from the Bright Angel Shale are scabrate and possess multiple enclosing walls, each with a single lamina with outward directed bumps. Polyads from the same formation have multiple enclosing walls that lack the bumps. Dyads from the Rogersville Shale have an outer homogeneous wall, and each of the individual dyad members is enclosed by a single thin (23-50nm) lamina. Dyads from the Lone Rock Formation have a single lamina (44-125nm) that encloses the smallest monad units, but that is fused to the outer wall away from the contact surface. The parent plants of all were living in a tropical setting; North America in the Cambrian was located just south of the paleoequator. Thus, climate is an unlikely source of the differences. Considerably more data will need to be gathered before the relative influences of biogeography, facies, habitat, evolution, and other factors can be evaluated as possible causes of the differences. This research is ongoing.

Keywords: palynology, paleopalynology, phylogeny, terrestrial ecosystems.

SS36-O03 (526)

Chemostratigraphy, depositional environments and the pre-tracheophyte fossil record at the continental - marine transition

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The palynomorph record suggests that land plants evolved by the mid-Ordovician (ca. 470 Ma) and that eukaryotic evolution on land may have commenced as early as 1 Ga. However, direct evidence for pre-Devonian terrestrial groundcover has remained elusive. One exception is represented by Late Ordovician - Silurian assemblages of thalloid fossils at several Appalachian Basin localities in North America. These assemblages that could represent some of the missing evidence for pre-Devonian terrestrial groundcover pose a dual challenge: their taxonomic affinities and depositional environments are difficult to resolve. (1) The taxonomic affinities of fossils in these assemblages are addressed using two approaches. (i) Comparisons of stable carbon isotope signatures of fossils with those of coeval marine fossils and sediments, have confirmed the terrestrial nature of Appalachian assemblages, providing macrofossil evidence for extensive pre-tracheophytic land floras. (ii) Simulated fossilization renders extant organisms that produce thalloid morphologies directly

comparable structurally to thalloid compression fossils. Such comparisons, employed for Early Silurian assemblages in the Massanutten Sandstone (Virginia), indicate communities, built by a diverse guild of thalloid organisms, analogous to modern soil crusts. (2) Incomplete characterization of depositional environments for many Appalachian assemblages interferes with resolution of taxonomic affinities of the fossils, whose thalloid morphology characterizes taxonomically divergent groups. This hurdle is commonly encountered in sedimentary sequences that pre-date plant rooting systems: differentiation of continental (from marine) deposits is difficult in the absence of diagnostic tracheophyte or marine fossils and their trace fossils. We addressed this challenge in the Late Ordovician Bald Eagle Formation (Pennsylvania) previously shown to host terrestrial fossils. Here, limited exposures prevent more than a general shallow marine to deltaic interpretation of environments using conventional approaches (sequence stratigraphy, grain size profiles). We employ a geochemical proxy, the organic carbon:pyrite sulfur ratio (C/S), in a stratigraphic context. A comparison of 1344 C/S values from the literature shows that this proxy differentiates with accuracy between six modern depositional environments (deep marine, delta, transitional, fluvial, and lacustrine). The C/S data from the Bald Eagle Formation, adjusted to compensate for organic maturation and weathering effects, were compared to modern C/S data. This showed that the two fossil beds were deposited in small lakes and are separated by a marine interval, results easily integrated with a conventional sequence stratigraphic interpretation. Thus, a statistical approach to C/S geochemistry and stratigraphic sequences can provide independent evidence in the resolution of depositional environments.

Keywords: carbon, geochemistry, Ordovician, Silurian, sulfur.

SS36-O04 (113)

Lang's nematophytes revisited

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In a seminal publication in 1937, W.H. Lang not only described the then known earliest vascular plants from the lower Devonian of the Welsh Borderland, UK, the most iconic being species of *Cooksonia*, but also a new class, the Nematophytales, that he considered possessed intermediate features between algae and vascular plants and was of very general distribution in rocks of that age. Taxa included were *Prototaxites* and his new genus *Nematothallus*, a thalloid organism comprising associations of three forms of tubes covered by a cuticle bearing a reticulate pattern. More recently, cuticles with ornament and named *Cosmochlaina* have been added. Fragments of such taxa including isolated smooth and banded tubes are often recorded in palynological preparations from coeval and older rocks,while thalloid encrustations are a common feature of the latter. Ordovician occurrences possess a dearth of anatomical information, leading to much speculation as to the original nature of the biota, be it composed of algal/cyanobacterial mats or lichens. Here we present the first body fossil evidence of the nature of the tissues below *Nematothallus* and *Cosmochlaina* cuticles, albeit from Late Silurian and Early Devonian localities in the Welsh Borderland. They show a stratified organisation of hyphae, reminiscent of some lichens, but for the most part lacking evidence of photobionts. Such construction plus limited geochemical evidence indicate that complex associations of fungal hyphae were present in early terrestrial ecosystems.

SS36-O05 (615)
Cryptospores and the algal plant transition

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Cryptospore assemblages from the Hanadir Sandstone member in Saudi Arabia are dominated by forms with clear morphological homology to the spores of embryophytes. This indicates that simultaneous meiosis during sporogenesis was firmly established in plant sporophytes by Darriwilian (Middle Ordovician) time. Cryptospores found in close association as dyads and combinations within synoecosporal walls, occur in paralic settings in Cambrian and Ordovician deposits in Laurentia (North America). These palynomorphs possess a suite of characters that overlap with both the embryophytes and the charophytes; therefore, they represent an opportunity to examine the evolution of spore characters during the algal plant transition. Taylor has demonstrated that lamellated walls, similar to those found in certain extant liverworts, occur in Cambrian dyads. Other characters associated with dyad topologies indicate a predominance of successive meiosis in Cambrian cryptospores. Dyads found in the Kanosh Shale (Darriwilian) at Fossil Mountain, Utah, USA, form small thalli with distinct serial division patterns that parallel vegetative patterns seen in some chlorophyte and charophyte algae today. Intriguingly, these microfossils match Bower's century-old prediction that spores evolved in advance of the vegetative sporophyte during the antithetic origin of land plants. This same idea, "spores before sporophytes," is supported by phylogenomic studies of basal land plants and cytological studies of sporogenesis in bryophyte groups. These disparate areas of botanical research - paleobotany, morphology and molecular phylogenomics – are now converging in support of Bower's original hypothesis that the algal plant transition involved the independent evolution of both gametophytic and sporophytic phases. The origin of land plants was not a singularity in time, but rather, involved the serial acquisition of characters during the evolution of the subaerial sporophyte. It now seems likely that some key features in sporogenesis may have preceded the evolution of other sporophyte characters. This may help to explain why the plant fossil record based on meso- and megafossils, seems to lag behind the spore record by as much as 50 Myr.

Keywords: cryptospores, land plants, evolution, antithetic hypothesis.

SS36-O06 (349)
Dispersed cryptospores reunited with their parent plants: clues from the Lower Devonian on pre-vascular vegetation

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Cryptospores dominate many Ordovician to Lower Devonian palynological assemblages, both in terms of diversity and abundance, the latter in particular prior to the appearance of the first plant megafossil in Wenlock sequences. Despite this abundance, occurrences of cryptospores *in situ* are extremely rare, hence little is known about the form and affinities of the plants that produced them. Much of our understanding comes from the study of exceptionally well preserved, charcoalified mesofossils collected from two localities in the Welsh Borderland, U.K., from Upper Silurian and Lower Devonian sequences. Despite representing only a facet of early land vegetation from slightly younger sequences, they continue to make significant contributions to the understanding of the nature of cryptospore-producers, a group that were a major component of 'pre-vascular' vegetation. Here we report on several groups of sporangia and spore masses that contain permanent dyads and separating dyads. A group of sporangia with single layered walls which split into four valves contain members of the dispersed taxa *Cymbohilates horridus* complex and *Cymbohilates cymosus*. At least four different types of spinose permanent dyads have been recorded, each contained in sporangia of slightly different form assigned to a new genus, *Partitatheca*. One example has rare stomata near its base, and a single specimen (lacking a complete sporangium) was described by Kate Habgood as with bifurcating axis also bearing stomata. By contrast hilate monads are found in vast numbers in discoidal masses similar to *Cooksonia pertoni* in shape, but contained within a non-cellular layer extending into a tuft thought to represent the remains of the subtending stem, hence assigned to a new genus, *Lenticulatheca*. The apiculate spores show variation in the hilum and are assigned to the dispersed taxa *Cymbohilates variabilis*, *C. allenii* var. *allenii*, C. *allenii* var. *magnus* and *C. mesodecus*. Each mass contains a single spore species. TEM studies show a bi-layered wall, comparable with that seen in the trilete monads of the *Cooksonia pertoni* complex, whereas *in situ* *Cymbohilates horridus* have multilayered walls with the ornamented outer layer extending over the two units of the dyads. They are thus reminiscent of older dispersed permanent dyads. However the presence of stomata and a branching axis precludes inclusion of the valvate forms in the Marchantiophyta, affinities postulated for other dispersed representatives.

Keywords: early embryophytes, *in situ* spores, permanent dyads, hilate monads.