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ABSTRACTS

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ON POLLEN ULTRASTRUCTURE IN CRETACEOUS AND PALEOGENE PLATANOIDS

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Presently in situ pollen grains are studied in eleven platanoid species: *Aquia brookensis* Crane, Pedersen, Friis & Drinnan *Platananthus potomacensis* Friis, Crane & Pedersen, *Hamatia elknekensis* Pedersen, Crane & Drinnan, Sarbaya radiata Krassilov & Shilin, *Quadriplatanus georgianus* Magallón-Puebla, Herendeen et Crane, *Platananthus hueberi* Friis, Crane et Pedersen, *P. scanicus* Friis, Crane et Pedersen, *Archaranthus krassilovii* N. Maslova et Kodrul, *Tricolpopollianthus burejensis* Krassilov, *Platananthus speirsae* Pigg & Stockey, *Platanites hybridicus* Forbes, *Chemurnautia staminosa* N. Maslova, *Platananthus synandrus* Manchester, *Macginistemon mikaneides* (MacGinitie) Manchester and *Platanus neptuni* (Ettings.) Buzek, Holy & Kvacek. Pollen wall ultrastructure was studied in in situ pollen grains of two platanaceous species, Archaranthus krassilovii from the Maastrichtian – Lower Paleocene of Amur Province and Chemurnautia staminosa from the Upper Paleocene – Lower Eocene of Kamchatka. These species maintain an intermediate position in respect to the general evolutionary tendencies reflected in the fossil records of platanoid pollen grains, in particular (1) an increase in pollen grain dimensions, (2) a more uniform surface reticulum in recent forms relative to a differentiation of mesocolpium areas with larger lumina decreasing toward the colpi in ancient forms and (3) a lighter "vitalized" construction of pollen wall in recent forms, with small cavities in ectexine and a thinner foot layer. In *A. krassilovii,* the colpi are bordered with a sexinal ridge, a feature shared with *Platananthus scanicus, P. speirsae*, and *P. synandrus*, but lacking in other fossil platanoids as well as in extant *Platanus*. In the Cretaceous and Paleogene platanoids (*Aquia brookensis, Platananthus potomacensis, Hamatia elknekensis, Platananthus hueberi, P. scanicus*) the endexine is heterogenous (structureless-granulate or granulate-lamellate) in the apertural region. In *Archaranthus krassilovii* and *Chemurnautia staminosa*, the endexine is two-layered over both the apertural and inaperural regions, with the granulate and lamellate layers fairly distinct throughout due to their different electronic densities. The endexine of *Platananthus speirsae* and *P. synandrus* is poorly preserved. In extant species, the endexine is poorly differentiated, its detailed structure needs further investigations.

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FIRST STEPS ON LAND – ORGANISMAL EVOLUTION IN EARLY TERRESTRIAL BIOTAS*

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Photosynthetic autotrophs represent today the fuel at the base of the trophic pyramid in the greatest majority of ecosystems, and as such during much of Earth's history they fueled the evolution of life. It is not surprising therefore that they have made the main focus of studies of the colonization of land. A survey of the evidence available to date on the beginnings of terrestrial life reveals a diverse assortment of data. (1) Geochemical and sedimentological studies provide indirect evidence that photosynthetic autotrophs were present on land in the Archean, 2.6 billion years ago, suggesting that they formed microbial mats. (2) Direct fossil evidence implies that the Archean and Proterozoic terrestrial colonists were organisms of cyanobacterial and possibly algal affinities. (3) Embryophyte spores are known from the mid-Ordovician, and possibly as early as the mid-Cambrian. Dispersed tubular and cuticle-like microfossils traditionally associated with early land plants, sometimes occur in association with the spores. (4) Land plant macrofossils of polysporangiophytes and tracheophytes (e.g., *Cooksonia*) occur from the mid-Silurian onward.

The empirical framework provided by these data delineates a large-scale evolutionary pattern in the early history of photosynthetic terrestrial organisms. Starting with the initial colonization of land by microorganisms, this pattern is marked by two major evolutionary events: the advent of embryophytes between the mid-Cambrian and the mid-Ordovician, and the appearance of polysporangiophytes and tracheophytes before the Late Silurian. These represent progressive steps in the evolution of organismal complexity by accumulation of evolutionary innovations within the guild of primary producers. Closely followed by evolutionary radiations, these events increased biological diversity and engendered community turnover on land. Seen through the prism of organismal complexity, the appearance of embryophytes marked the transition from microbial life to complex life forms, by opening the way for anatomical differentiation within the organismal body. The advent of polysporangiophytes and tracheophytes subsequently added a new dimension to the photoautotrophic world by introducing two features with crucial roles for the complex architecture of the plant sporophytes that dominate modern canopies: the capacity to branch and conducting tissues.

The accretion of organismal complexity at the level of photosynthetic autotrophs was at least partly influenced by interactions with other groups of organisms populating the early terrestrial landscapes. (1) The co-evolution of algae and fungi within mutualistic associations has been proposed as a catalyst for the evolution of embryophytes. Abundant and diverse by the Early Devonian, fungi have been described from Silurian and even Ordovician deposits, but information on their presence prior to the Devonian is still sketchy and often is the subject of controversy. However, mid-Ordovician spores of glomalean fungi, the most important fungal group involved in modern mycorrhizal symbioses, are among the best documented fungal fossils, and support the symbiotic co-evolution hypothesis. The presence of lichens in the Early Devonian indicates that some fungal lineages were also involved in yet another distinct type of interaction with primary producers. (2) Terrestrial animals are known through body fossils from the Late Silurian. Earlier trace fossils and microfossils as old as the Late Ordovician are difficult to assign unequivocally to terrestrial dwellers. The advent of motile animal grazers and predators has been proposed as the main cause for the accelerated evolutionary tempos that led to the "Cambrian explosion" in the marine realm. By analogy, the establishment and diversification of animals on land may have represented one of the causes for the evolution and rapid diversification of polysporangiophytes and tracheophytes.

This picture clearly shows that the time interval between the mid-Cambrian – mid-Ordovician (advent of embryophytes) and the Late-Silurian (appearance of polysporangiophytes and tracheophytes) was a crucial time for the evolution of life on land. However, a careful look at the types of evidence available for terrestrial life reveals that the only unambiguous direct evidence for this period consists of dispersed microfossils: embryophyte spores, fungal hyphae and spores, and animal fragments. The dispersed state of these microfossils precludes interpretation of the habitats or the morphology of the organisms that produced them. Therefore although there is no doubt about the presence of terrestrial life, this crucial period in the evolution of life on land is extremely poorly documented, with direct evidence, in terms of the terrestriality of life, and of the morphology of organisms.

Such direct evidence comes from the Early Silurian (Llandoverian) of Virginia (USA), where the lower Massanutten Sandstone has produced abundant macrofossil assemblages that represent diverse terrestrial communities of complex thalloid organisms. Extensive sampling at the locality has produced macrofossils consisting of discrete carbonaceous compressions or more extensive crusts, with different textures, that can exceed 10 cm in size. Individual compressions are usually thalloid, but sometimes exhibit strap-shaped morphology. Their internal organization shows several distinct types characterized by complex stratification. These represent clear indications of community diversity and organismal complexity at the beginning of the Silurian, but the systematic affinities of the Passage Creek organisms pose delicate problems due to less-than-optimal fossil preservation as a result of tectonics. However, the microfossil assemblages indicate that embryophytes and fungi are among the potential producers of the fossils, and we have evidence that some of the fossils represent cyanobacterial colonies with associated bacteria. Considering all of these, our working hypothesis designates soil crusts as modern counterparts for the Early Silurian floodplain communities.

The depositional environment of fossiliferous layers indicates that the Passage Creek communities occupied substrates that experienced desiccation in river floodplains. The lower Massanutten Sandstone is interpreted as braided fluvial deposits, and the fossil assemblages occur in siltstone and shale interbeds that represent overbank deposition on elevated surfaces outside of adjacent main braid channels, in the floodplain and abandoned channels. The occurrence of extensive crusts and relatively large specimens with entire margins demonstrates that the original organisms did not undergo transport, or underwent only minimal transport, suggesting that they were native to overbank environments. Desiccation cracks observed in the sediment and fossils, and the presence of fossils with rolled-up margins demonstrate that these environments were exposed to desiccation.

The Passage Creek biota establishes an important benchmark for our understanding of the beginnings of life on land, by providing the first comprehensive image of terrestrial communities in the crucial period of time between the advent of organismal complexity in the photoautotrophic guild and the evolution of polysporangiophytes. At the beginning of the Silurian, terrestrial communities included complex organisms, were systematically diverse, and occupied the wettest environments available on land at the time, such as river floodplains. Dominated by thalloid forms, these communities were radically different from later polysporangiophytic communities that consisted mainly of plants with axial morphology. Comparable to modern soil crust communities, they provide a new and more appropriate search image for early terrestrial life. The potential presence of embryophytes, fungi, and cyanobacteria in these thalloid communities lends support to the hypothesized archetypal embryophyte morphology (thalloid gametophytes with sessile sporangia), gives a new impetus to hypotheses proposing fungus-autotroph mutualistic associations as promoters of terrestrial life evolution, and suggests that lichens may have been already present by the Early Silurian.
