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Wetlands before tracheophytes: Thalloid terrestrial communities of the Early Silurian Passage Creek biota (Virginia)

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ABSTRACT

Early Silurian (Llandoverian) macrofossils from the lower Massanutten Sandstone at Passage Creek in Virginia represent the oldest known terrestrial wetland communities. Fossils are preserved as compressions in overbank deposits of a braided fluvial system. Specimens with entire margins and specimens forming extensive crusts provide evidence for in situ preservation, whereas pre-burial cracks in the fossils demonstrate subaerial exposure. Developed in river flood plains that provided the wettest available environments on land at the time, these communities occupied settings similar to present-day riverine wetlands. Compared with the latter, which are continuously wet by virtue of the moisture retention capabilities of soils and vegetation, Early Silurian flood-plain wetlands were principally abiotically wet, depending on climate and fluctuations of the rivers for moisture supply. Varying in size from <1 cm to >10 cm, fossils exhibit predominantly thalloid morphologies but some are strap-shaped or form crusts. Their abundance indicates that a well-developed terrestrial groundcover was present by the Early Silurian. Morphological and anatomical diversity of specimens suggests that this groundcover consisted of several types of organisms and organismal associations, some characterized by complex internal organization. Earlier microfossil finds at Passage Creek corroborate an image of systematically diverse but structurally simple communities, consisting only of primary producers and decomposers. Ten to fifteen million years older than the oldest previously known complex terrestrial organisms (e.g., *Cooksonia*), they provide a new perspective on the early stages of land colonization by complex organisms, whereby the earliest terrestrial communities were built by a guild of thalloid organisms and associations of organisms comparable to extant biological soil crusts.

Keywords: macrofossils, fluvial, Llandovery, complex, diversity, soil crusts, braided.

INTRODUCTION

In the modern world, the term "wetlands" brings to mind lush vegetation and water-rich soils. We tend to think that wetland ecosystems result primarily from high volumes of relatively constant moisture input. In reality, the moisture retention capabilities of the system play an equally important role as moisture input, and it is largely because of the abundant vegetation, with its soil-forming and water retention capacities, that wetlands are the continuously water-soaked environments that we know today.

This has been the situation for a good part of the interval since life colonized land surfaces, especially since the advent of lignophytes (Algeo et al., 2001). By contrast, during the earliest stages of land colonization, before the formation of organic soils and the development of a thick, multistoried groundcover, wetland landscapes must have been of a distinctly different nature. Until recently, a notably scarce fossil record for the earliest phases of terrestrial plant community development has left a distinct gap in our understanding of how wetlands developed through time. However, a growing body of new micro- and macrofossil evidence from basal Phanerozoic deposits now provides an opportunity to fill this hiatus. In this paper we review the oldest known wetland biotas, introduce recently discovered macrofossils from the Llandoverian of Virginia, and explore their implications for the evolution of wetland ecosystems and terrestrial life.

THE OLDEST WETLAND BIOTAS

Biotas of the Rhynie Chert and Battery Point Formation

The oldest currently known wetland biota preserved in situ is that of the Rhynie Chert (Fig. 1). World famous for exquisite cellular preservation of the fossils, this Early Devonian (Pragian) biota (Rice et al., 1995) includes terrestrial and fresh-water communities. Trewin et al. (2003) provide a comprehensive compilation of information on the genesis and environments of the Rhynie Chert. Communities of the Rhynie Chert occupied several ecological niches within a river system (flood plain, ponds, and lakes). Plants, animals, algae, cyanobacteria, and fungi are preserved as autochthonous or allochthonous assemblages by hydrothermal activity. The hot springs provided a source of silica-rich solutions to permineralize the organisms. Extensive studies of the different organisms in the Rhynie Chert have accumulated evidence that this biota includes most of the elements of the modern trophic chain (primary producers, decomposers, detritivores, and carnivores) and features several types of mutualistic as well as antagonistic associations (Taylor and Taylor, 2000; Shear and Selden, 2001, and references therein).

Only slightly younger, the Emsian (Early Devonian) Battery Point Formation of Gaspé (Quebec, Canada) preserves another well-documented wetland biota (Fig. 1). Hotton et al. (2001) produced detailed reconstructions of terrestrial communities inhabiting different environments of a fluvial-deltaic landscape on a tidally influenced coastal plain. Based on the distribution of compressed remains, those authors defined three types of fossil associations correlated with different environments inferred from sedimentary facies. These correlations suggested clade-based niche partitioning among dysaerobic wetland sites within interdistributary basins (dominated by zosterophylls and *Renalia*), more ephemeral near-channel environments (preferentially occupied by trimerophytes), and fully terrestrial riparian environments (with *Spongiophyton* and *Prototaxites*), which the authors tentatively related to contrasting life-history strategies.

The biotas of the Rhynie Chert and Battery Point Formation provide solid evidence that by the end of the Early Devonian diverse and complex wetland communities were present in fluvial systems. Although ancient, these communities reveal that Early Devonian ecosystems already had differentiated into
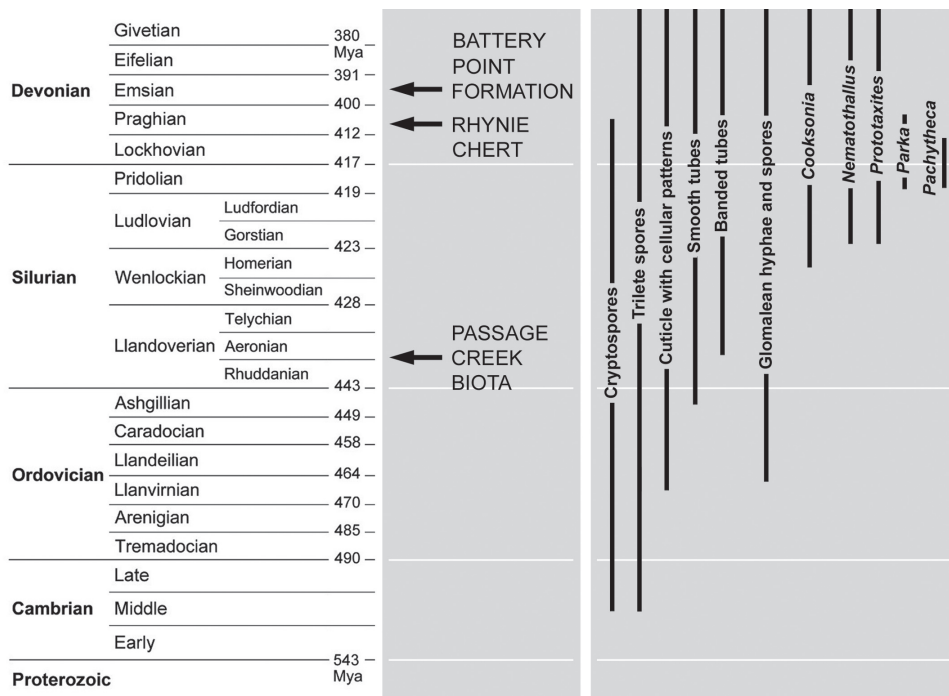

Figure 1. Stratigraphic ranges of microfossil types and macrofossil taxa considered in discussions of the colonization of land, and positions of localities significant for the fossil record of early wetland communities. Absolute ages from Palmer and Geissman (1999).

multiple trophic levels and that they were partitioned into several ecological niches occupied by organisms within the same trophic level (at least for the primary producers). In fact, by the Pragian riverine wetlands harbored communities that lacked only few of the physiognomic and trophic attributes of their modern counterparts (e.g., multistoried vegetation and, arguably, herbivory).

The presence of herbivory in the Rhynie Chert and Battery Point Formation biotas is a debated issue. Using a very restrictive definition of herbivory—as being exerted only by animals that routinely feed on leaves, shoots, and roots of living plants—Shear and Selden (2001, p. 49) have questioned the presence of this trophic level in the two biotas. On the other hand, use of a more inclusive definition allowed Labandeira (2002) to infer herbivory represented by boring, piercing and sucking, and spore consumption, on the basis of plant damage and dispersed coprolites containing plant fragments that are reported in the Rhynie Chert and Battery Point Formation biotas.

Not only are these well-characterized Early Devonian wetland biotas quite complex ecologically, but they also comprise phylogenetically derived primary producers: the bulk of the preserved biomass is contributed by a combination of non-tracheophytic and tracheophytic polysporangiophytes. Among embryophytes, a clade most commonly equated to Kingdom Plantae in modern systematics, polysporangiophytes form the crown group characterized by branching sporophytes bearing more than one sporangium. Defined as a clade by the presence of a multicellular sporophyte in the life cycle, embryophytes include three bryophytic clades (liverworts, hornworts, and mosses) in positions basal to and/or sister to the polysporangiophytes. Such phylogenetic relationships suggest that the fossil record should preserve wetland communities older than the Rhynie Chert and Battery Point Formation, and which would include earlier, bryophytic stages of embryophytic evolution. However, in the pre-Devonian fossil record microfossil evidence for embryophytes is not paralleled by abundant terrestrial and wetland macrofossils or by in situ preservation.

The Pre-Devonian Fossil Record

Microfossil evidence in the form of putative trilete spores from the Middle Cambrian Rogersville Shale in Tennessee (Strother, 2000) suggests that embryophytes were indeed present much earlier than previously documented by macrofossil evidence. This sets a minimum age for the earliest embryophytes (Fig. 1), but the marine depositional environment of the rocks (Rankey et al., 1994) leaves open all three alternatives for the origin of the spores, from an ecological standpoint: marine, freshwater, or terrestrial environments. The embryophyte macrofossil record begins much later, in the late Wenlockian (Fig. 1), and consists of polysporangiophytes (e.g., *Cooksonia*; Edwards and Feehan, 1980), rather than the bryophytic grade forms predicted by modern systematic studies (Mishler and Churchill, 1985). Attempts to document bryophytes in the earliest macro- and mesofossil embryophyte assemblages (Edwards, 2000) have been

frustrated until now by the fragmentary state of fossils. Claims of bryophytic-grade plants based on a few problematic Ordovician fossils (reviewed by Retallack, 2000) have not been substantiated by further results. Current perceptions also are hampered by relatively narrow definitions of bryophyte-grade plants that are based on extant taxa, and that do not accommodate the inclusion of organisms exhibiting novel combinations of characters.

The Late Silurian witnessed rapid radiation and geographic expansion of embryophytes, as documented by the list of Silurian and Early Devonian fossil localities compiled by Edwards and Wellman (2001). At least some of these fossils represent terrestrial plants very likely growing in wetland communities, and the considerable taxonomic diversity displayed by embryophytes as early as the Late Silurian suggests that such communities were quite complex. However, all of these pre–Rhynie Chert embryophyte assemblages are allochthonous, and although they provide a broad idea of the types of plants, the transported state of the fossils restricts our ability to characterize the communities in which they grew.

Embryophytes are not the only macroscopic organisms found in the early terrestrial fossil record. Nematophytes and other problematic macrofossils sometimes considered in discussions of land plant origins (e.g., *Pachytheca*, *Parka*, briefly reviewed by Taylor, 1988), are also known as early as the Silurian. Of these, nematophytes appear earliest in the fossil record, and include several taxa characterized principally by a tubular internal organization. The biological relationships of nematophytes have been tentatively placed with different extant groups of algae and fungi, or with groups that have no living descendants, but a lack of preserved reproductive structures has frustrated attempts to conclusively resolve their systematic affinities. The oldest macrofossil nematophyte occurrence *(Nematothallus, Prototaxites)* is reported from late Wenlockian to Ludlovian strata in the Bloomsburg Formation of Pennsylvania (Strother, 1988) and is roughly contemporaneous with the oldest *Cooksonia* (Fig. 1). The Bloomsburg Formation represents fluvial (Epstein and Epstein, 1969; Fail and Wells, 1974; Dennison and Wheeler, 1975; Retallack, 1985; Driese et al., 1992) and tidally influenced (Epstein, 1993) settings at different locations. Detailed sedimentological studies will be needed to characterize the depositional environment at the fossil locality with confidence, but current interpretations and the age of the rocks place these fossils among the oldest macrofossil occurrences of both potentially terrestrial and wetland organisms. Problematic carbonaceous tubes lacking internal anatomy *(Eohostimella)* were described by Schopf et al. (1966) from nearshore marine deposits of late Llandoverian age in Maine, and geochemical studies by Niklas (1976) have suggested a vascular plantlike chemistry for these fossils. However, the marine depositional environment and the inconclusive morphology and anatomy have precluded unequivocal taxonomic assignment of *Eohostimella*. Although animals are not the focus of this paper, it is worth mentioning that occurrences of probable fresh-water arthropods have been reported from Ordovician nonmarine deposits (review in Retallack, 2000), and that the earliest

unequivocal terrestrial animals (arachnids, centipedes, and scorpions) are known in the Pridolian (Shear and Selden, 2001).

A wide diversity of cuticle-like fragments and tubes that apparently lack extant counterparts also occur as dispersed microfossils as early as the Middle Ordovician (Fig. 1), and they have been compared with a wide range of fossil and living groups by different authors (e.g., Edwards, 1982, 1986; Gray and Boucot, 1977; Banks, 1975a, 1975b; Kroken et al., 1996; Kodner and Graham, 2001; Graham and Gray, 2001). However, their biological relationships remain largely unresolved because of a lack of diagnostic systematic characters and the dispersed nature of these fossils. Together with cryptospores and spores, cuticle-like fragments and tubes are traditionally associated with land organisms on the basis of (1) their resistance to degradation, and (2) their occasional recovery from continental (fluvial) deposits.

Resistance to degradation is interpreted as reflecting origin in desiccation-resistant organisms, or parts of organisms (Graham and Gray, 2001) that otherwise may have been submerged. Nevertheless, it is noteworthy that resistant microfossils (i.e., not degradable by palynological extraction techniques) are not produced exclusively by terrestrial organisms. They also occur as acritarchs, dinoflagellates, prasinophyceans and other algal cysts, chitinozoans, fungal spores, and eurypterid cuticle, among others. This indicates that resistant, fossilizable substances are not limited to organisms living in desiccation-prone environments, and therefore their presence alone cannot be used as evidence for life in terrestrial environments. More biochemical and geochemical studies on the different types of such resilient substances and their distribution among extant and fossil taxa are needed before this statement can be made with any degree of certainty. The fact that cryptospores, tubular fossils, and cuticle-like fragments have sometimes been recovered from fluvial deposits can be, and has been, used as evidence for their origin in nonmarine organisms. However, their dispersed nature precludes unequivocal attribution to organisms occupying specific continental environments (i.e., fresh-water versus terrestrial).

The Immediate Challenge

Prior to the late Wenlockian the fossil record of terrestrial organisms is so incomplete that the search for wetland biotas becomes synonymous with the search for terrestrial life. Communities of terrestrial microorganisms in the form of cyanobacteria and bacteria were probably established relatively early in the Precambrian, as has been proposed by numerous authors (e.g., Barghoorn, 1977; Siegel, 1977; Campbell, 1979; Golubic and Campbell, 1979; Gay and Grandstaff, 1980), and Retallack (2001) provides a comprehensive review of the types of evidence accumulated to date. Such communities may have produced the microfossils of uncertain affinities reported by Horodyski and Knauth (1994) from paleokarst cavities in 1.2 billion and 800 million year old rocks in California. It is natural to think that early terrestrial microbial communities would have thrived in the wettest available environments, in the proximity of marine and fresh-water bodies. Therefore, they probably represent the first terrestrial wetland communities.

The challenge before us today is to discover the origins of complex terrestrial life, and to decipher the succession of wetland communities that has culminated in the establishment of modern wetlands. Colonization of land by complex organisms appears to be a Phanerozoic phenomenon that may be intimately associated with the evolution of new clades and of new mutualistic associations (Pirozynski and Malloch, 1975; Pirozynski, 1981; Selosse and Le Tacon, 1998; Knoll and Bambach, 2000). In the interval between the establishment of terrestrial microbial communities and the first macrofossils of terrestrial organisms (e.g., *Cooksonia*), the fossil record previously has yielded only dispersed microfossils traditionally but not conclusively associated with land organisms (as discussed above). The newly recognized macrofossil evidence from this interval that is introduced below provides a first opportunity to begin to fill this gap by providing an organismal context for understanding the microfossil evidence, and by establishing a paleoecological framework for the most ancient complex terrestrial communities.

THE PASSAGE CREEK BIOTA

One notable exception to the general paucity of terrestrial macrofossils prior to the Wenlockian is the Passage Creek biota (Fig. 1). The Early Silurian (Llandoverian) lower Massanutten Sandstone preserves at Passage Creek, in Virginia, the oldest macroscopic evidence for complex terrestrial groundcover. Embedded in fine-grained partings representing overbank deposition in a braided river system, the Passage Creek fossils are the remains of wetland communities occupying riverine flood plains (see sections on the age and depositional environments of the fossil assemblages below).

Previous Studies

This locality, first reported by Pratt et al. (1975a, 1975b), is well known for microfossils, but it also yields the oldest macrofossil assemblages known from nonmarine deposits. Fossils occur in the lower member of the Massanutten Sandstone, the age of which is early–middle Llandoverian (Early Silurian). Pratt et al. (1978) were the first to study the fossils of the Massanutten Sandstone carefully. They mention and briefly describe macroscopic compressions up to several centimeters in length, exhibiting foliose habit or axial construction, and that tend to be fragmented, with irregular outlines. However, after clearing and examination of coalified matter with scanning electron microscopy (SEM), the compressions showed no internal cellular preservation or external details. The study by Pratt et al. (1978) focuses on organic residues obtained by bulk maceration of rock fragments. These authors describe several types of dispersed microfossils: smooth and banded tubular elements, cuticular and cellular sheet fragments, trilete spores, spore tetrads, cryptospores, and septate hyphal filaments, sometimes apparently associated in different

combinations. Because of the fluvial origin of the fossiliferous rocks, Pratt et al. (1978) consider this fossil assemblage to represent the oldest evidence of nonvascular, thalloid land plants, which they compare to nematophytes.

In a subsequent study, Niklas and Pratt (1980) subjected carbonaceous compressions from the Massanutten Sandstone to biogeochemical analyses and found small amounts of chemical constituents that they interpreted as potential degradative by-products of a lignin-like moiety. Niklas and Smocovitis (1983) studied shale partings from Passage Creek containing small (0.26–2.75 mm) compressions. Macerating individual fossils, they described cuticle-like fragments and three types of tubular elements, including an interesting fragment of tissue that incorporates longitudinally aligned smooth and banded tubes. On the basis of the disposition of the tubes (several smooth walled tubes surrounding two to three larger banded tubes), and by analogy with present-day embryophytes, they tentatively interpreted the strand of tubular cells as conducting tissue. The authors nevertheless emphasize that until more is known about anatomy and morphology, the systematic affinities of organisms represented by the fossils will remain conjectural.

Material and Methods

Fossils occur in the lower Massanutten Sandstone, along Route 678 at the gap of Passage Creek in Shenandoah County, 6 km southeast of Strasburg, Virginia, USA (38º56'N; 78º18'W) (see Figure 1 in Pratt et al., 1978). The Llandoverian sedimentary succession is well exposed in road cuts and on the slopes of Green Mountain. Lithology of the formation consists of thick and very hard sandstone beds and discontinuous, finely to thickly laminated fossiliferous siltstone, and very fine sandstone with minor shale, forming discontinuous partings (Fig. 2). Thickness of the partings ranges from a few centimeters to over 10 cm. The somewhat softer shale tends to weather back from the surface, and the hardness of the adjacent sandstone beds renders sampling difficult, especially along road cuts. Sampling the more extensive outcrops on the slopes of Green Mountain allowed us to maximize the size of shale samples and consequently the surface of bedding planes exposed in them. Two distinct siltstone and shale partings 15–25 cm thick were sampled on their whole thickness, 0.8–1 m of length, and depths ranging from 0.3 to 0.8 m. Samples thus obtained totaled hundreds of fossils visible on freshly split surfaces, and considerably more on the closely spaced (1–5 mm) unexposed bedding planes. This was important for observations on the size and morphology of the fossils, as well as on their patterns of spatial distribution.

The abundant macrofossils are preserved as compressions that form black carbonaceous films of varying thicknesses. Fresh breaks in the rock usually reveal most of each compression on the bedding plane, where the outlines of the fossils seem angular and fragmentary at first glance. However, this appearance is often misleading. Due to the low fissility of the rock and to the position of the fossils, which are rarely perfectly flat, the original margins of the fossils most often remain unexposed. The cause for this is very likely the sedimentary microstructure of the fossiliferous siltstones that reflects irregular sedimentation at the millimeter and centimeter scale. Careful degagement of both part and counterpart is therefore needed to uncover the original outline of each fossil. Prior to degagement rock samples were placed in 20% hydrofluoric acid for 1–2 min. This enhanced the contrast between the fossils and the surrounding mineral matrix, and softened the surface layer of the sample, allowing for easier preparation. Degagement was then performed under a dissecting microscope, with the samples immersed in water, using dissecting needles and a scalpel. Most of the images that document external morphology of the fossils were taken with the samples immersed in water.

The carbonaceous material of the compressions is very brittle. Because of profuse fissuring it tends to disaggregate into minute pieces upon maceration of the rocks, prohibiting separation of whole fossils from the sedimentary matrix. Therefore, we documented internal organization of the fossils from individual unitary carbonaceous fragments removed by hand from the compressions, or obtained by bulk maceration. When accompanied by mineral matrix, the fragments were passed through 40% hydrofluoric acid to remove siliceous sediment, and then rinsed in distilled water. Other carbonaceous fragments were recovered from bulk maceration of small pieces of fossiliferous rock.

The fragments were subjected to different treatments depending on the investigation techniques that were to be utilized. Some fragments were bleached using household-grade sodium hypochlorite for eight to nine days, followed by progressive rinsing in distilled water, dehydration in a graded ethanol series and xylene, and mounting on microscope slides with Eukitt

Figure 2. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. Fossiliferous siltstone and very fine sandstone (between arrows) forms relatively thin, finely laminated, and discontinuous partings separating the sandstone beds at Green Mountain. Hammer for scale, 27.5 cm.

(Calibrated Instruments, Hawthorne, New York). For SEM the carbonaceous fragments were dehydrated in ethanol, mounted on aluminum stubs, and gold-coated. Thin sectioning for light microscopy was performed in parallel with ultra-thin sectioning for transmission electron microscopy (TEM). Carbonaceous fragments dehydrated in an ethanol series were immersed in propylene oxide and subsequently embedded in Epon-type resin (Electron Microscopy Sciences, Fort Washington, Pennsylvania). Thin sections (0.5–0.7 µm) and ultra-thin sections (60–80 nm) were cut using glass knives on a Reichert Ultracut microtome. Thin sections were mounted on glass slides for light microscopy, using Eukitt, and ultra-thin sections were picked on copper grids. Experiments showed that fixation prior to resin embedding, and staining of ultra-thin sections on the copper grids have no influence on the quality of the sections or differential contrast of the images. Therefore these procedures were omitted.

Imaging of the specimens was realized with Leaf Lumina (Leaf Systems Inc., Southboro, MA), and PhotoPhase (Phase One A/S, Frederiksberg, Denmark) digital scanning cameras, using a macro lens mounted on a Leitz Aristophot bellows camera, or using the Aristophot in conjunction with a Zeiss WL compound microscope for light microscopy. Scanning electron microscopy was performed on a Zeiss DSM 962 digital scanning microscope, and ultra-thin sections were observed and imaged at 80 kV using a Zeiss transmission electron microscope. Specimens are reposited in the Ohio University Paleobotanical Herbarium as numbers 15980–16001.

Extensive systematic studies of the Passage Creek fossils are in course of completion. Because of the specifics of both the methods used and the fossil preservation, such studies are time-consuming and will be the focus of future publications. The results presented here are based on qualitative surveys of the samples and on the most significant finds of the fossil characterization work completed to date. Visual survey of all available specimens allowed us to broadly constrain the size range of fossils, as well as to assess morphological diversity within the assemblages. Internal organization of the fossils was observed on thin sections from 35 distinct unitary fragments out of which 16 came from five individual fossils, and 19 were recovered by bulk maceration of small samples. Even at this stage, the finds nevertheless allow us to build an unforeseen picture of some of the earliest wetland biotas that we considered of high interest for the broad paleoecological and evolutionary foci of the present volume.

Diversity and Structure of Early Silurian Wetland Communities

The external morphology and internal anatomy of the macrofossils in the Passage Creek assemblages, as well as the wide spectrum of dispersed microfossils described by Pratt et al. (1978) in association with the macrofossils, all contribute to an image of considerable diversity of the Llandoverian wetland communities. The organic material in the fossils exhibits a variety of textures, and the fossils occur as crusts or discrete specimens displaying ellipsoidal, lobed, elongated, and irregular morphologies, as well as a wide range of sizes. Examination of the internal organization of the fossils reveals several distinct types of construction, and indicates the presence of complex organisms.

Morphological Diversity of Macrofossils

Macrofossils range in size from smaller than 1 mm to over 11 cm in greatest dimension (Figs. 3A–D, 4A–F). At least two different general types of textures have been observed in the compressions (Fig. 3C at arrows). One type is represented by more-or-less smooth, relatively thick, black and continuous organic films, while the other is characteristic of much thinner films with profuse small-scale discontinuities that form a checkered, salt-and-pepper pattern and give the appearance of gray color. Most of the fossils for which we documented external morphology exhibit rounded outlines suggestive of very little or no fragmentation. Sometimes the edges of the fossils are recurved. For example, the edges of the fossil in Figure 4B go down into the matrix (arrows). Some of the fossils display numerous cracks in the carbonaceous material that are identical to those that form in modern biological soil crusts (Fig. 3C at arrowhead). Careful observations showed that the cracks in the fossils are not related to discontinuities of the surrounding rock. This demonstrates that the cracks formed prior to burial in sediment and fossilization of the organisms, and therefore most likely resulted from desiccation due to subaerial exposure.

Morphologically, a first distinction can be made between largely continuous crusts and discrete fossils. The largest dimension of a continuous crust observed to date is 11 cm (Fig. 3D) and is limited by the size of the rock sample. The crust displays highly irregular voids with sizes ranging from less than 1 mm to several cm in size. Both types of texture outlined above occur in this crust, but the limits between them are difficult to determine.

Discrete fossils fall into two main morphological classes: (1) fossils with roughly isodiametric outlines that we term thalloid (Fig. 4A–D), and (2) elongated, strap-shaped fossils (Fig. 4E, 4F). Thalloid fossils largely dominate the assemblages at Passage Creek. They range from less than 1 cm up to several centimeters across, and often display rounded margins and more-or-less pronounced lobes (lobe sinuses at arrowheads on Figures 4A–D). We have documented specimens with deltoid (Fig. 4A, 4D) and oval (Fig. 4C) outlines, as well as compressions with more irregular outlines (Fig. 4B, 4D). Some of the fossils exhibit short protrusions (Fig. 4A, 4C, 4D, at arrows) that may have been involved in attachment of the organisms to the substrate. However, additional specimens that display this type of feature need to be studied, and anatomical evidence for differentiation of an attachment structure needs to be substantiated. The surface of the compressions sometimes reveals differences in the thickness of organic matter, as seen in Figure 4A between the thicker (darker) central part of the specimen and the thinner (lighter) two margins that diverge from the base. The thickness of the fossils rarely exceeds 50 µm. Other morphological features, such as potential reproductive structures, are absent from the studied specimens.
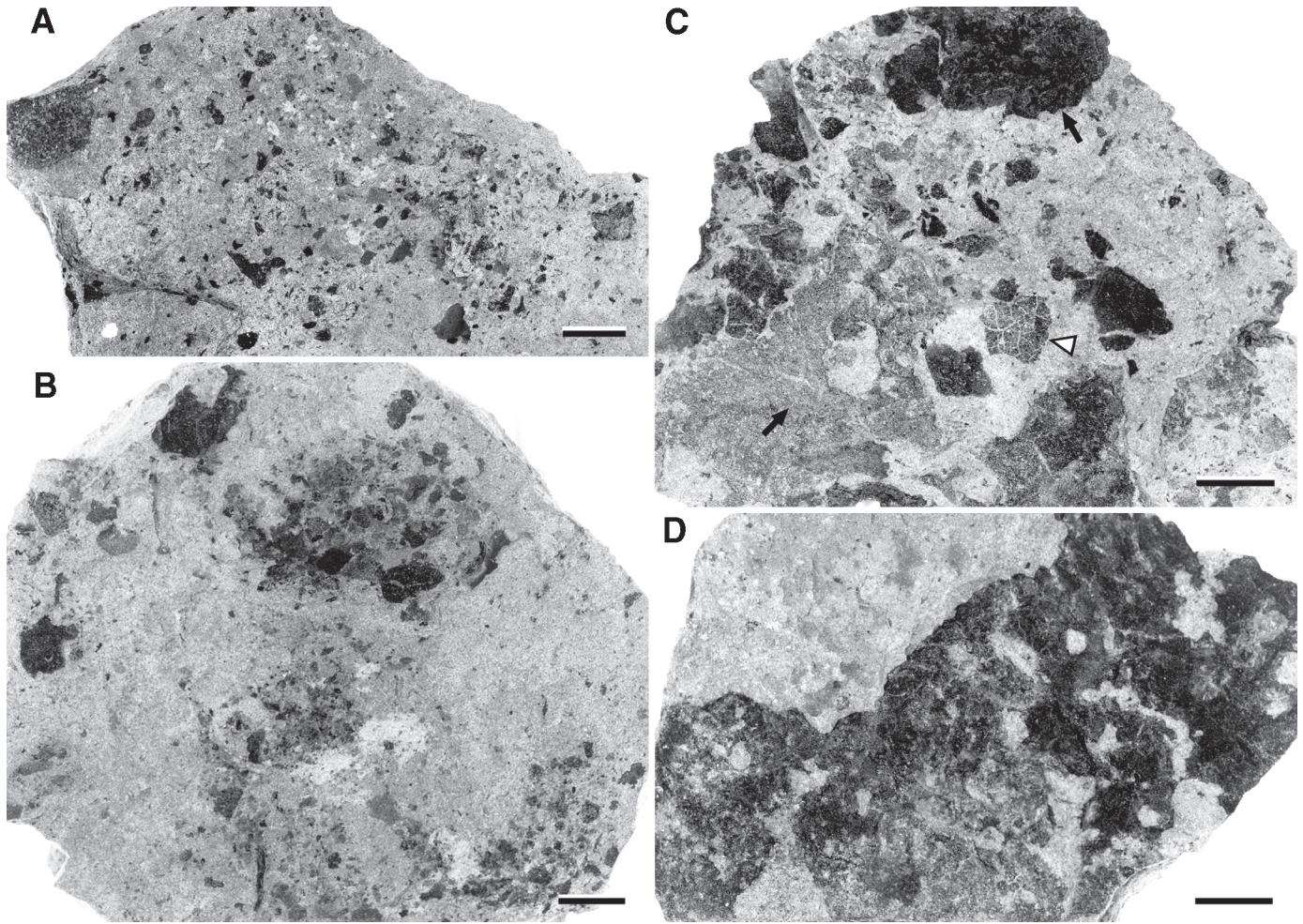
Figure 3. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. Decimeter-scale patterns of fossil arrangement on bedding planes. (A) Predominance of small-sized fossils, evenly distributed. OUPH 15980. (B) Predominance of small-sized fossils, forming agglomerations. OUPH 15981. (C) Predominance of larger fossils. Two different types of texture can be observed: one is represented by thicker, black, and continuous compressions with definite margins (upper arrow), while the other is characteristic of thinner compressions with profuse small-scale discontinuities (lower arrow), sometimes lacking definite margins. Some of the fossil crusts display cracks (arrowhead) indicative of desiccation due to subaerial exposure. OUPH 15982. (D) Extensive carbonaceous crust. The limit at the upper left is not the edge of the fossil, but rather mineral matrix overlying the fossil. OUPH 15983. All scale bars 1 cm.

Elongated, strap-shaped fossils are quite rare at Passage Creek. Their morphology bears resemblance to axial forms usually associated to embryophytes. However, axial external morphology implies axial arrangement of anatomical features both at the outside and inside the body part, and is generally associated with radial symmetry. The ends of the two elongated fossils found so far at Passage Creek (Fig. 4E, 4F) exhibit no conclusive evidence for breaking from longer organisms, and until we find evidence for radial symmetry and axial anatomy they cannot be considered axial. A similar approach was taken by Strother (1988) in describing ribbon-shaped *Nematothallus* specimens from the Bloomsburg Formation, which he termed taenioid. At Passage Creek strap-shaped fossils are considerably thicker than thalloid ones and can reach 160 µm. The two fossils are 5.6 × 0.6 cm and

8 × 1.2 cm in size, and exhibit somewhat wavy margins. While the smaller fossil (Fig. 4E) is slightly curved, with apparently rounded terminations, the larger one (Fig. 4F) is straight and displays a two-pronged termination (the other end is truncated by the edge of the rock sample).

Internal Organization

Thin sectioning of the carbonaceous material has shown that sections 0.5–0.7 µm thick are translucent and appear colored in hues of brown, whereas sections thicker than 0.9 µm are opaque and black. Sectioning, together with scanning electron microscopy, also revealed dramatic effects of diagenesis that obscured the cellular structure of the original organisms. The internal anatomy of macrofossils as observed in light microscopy of
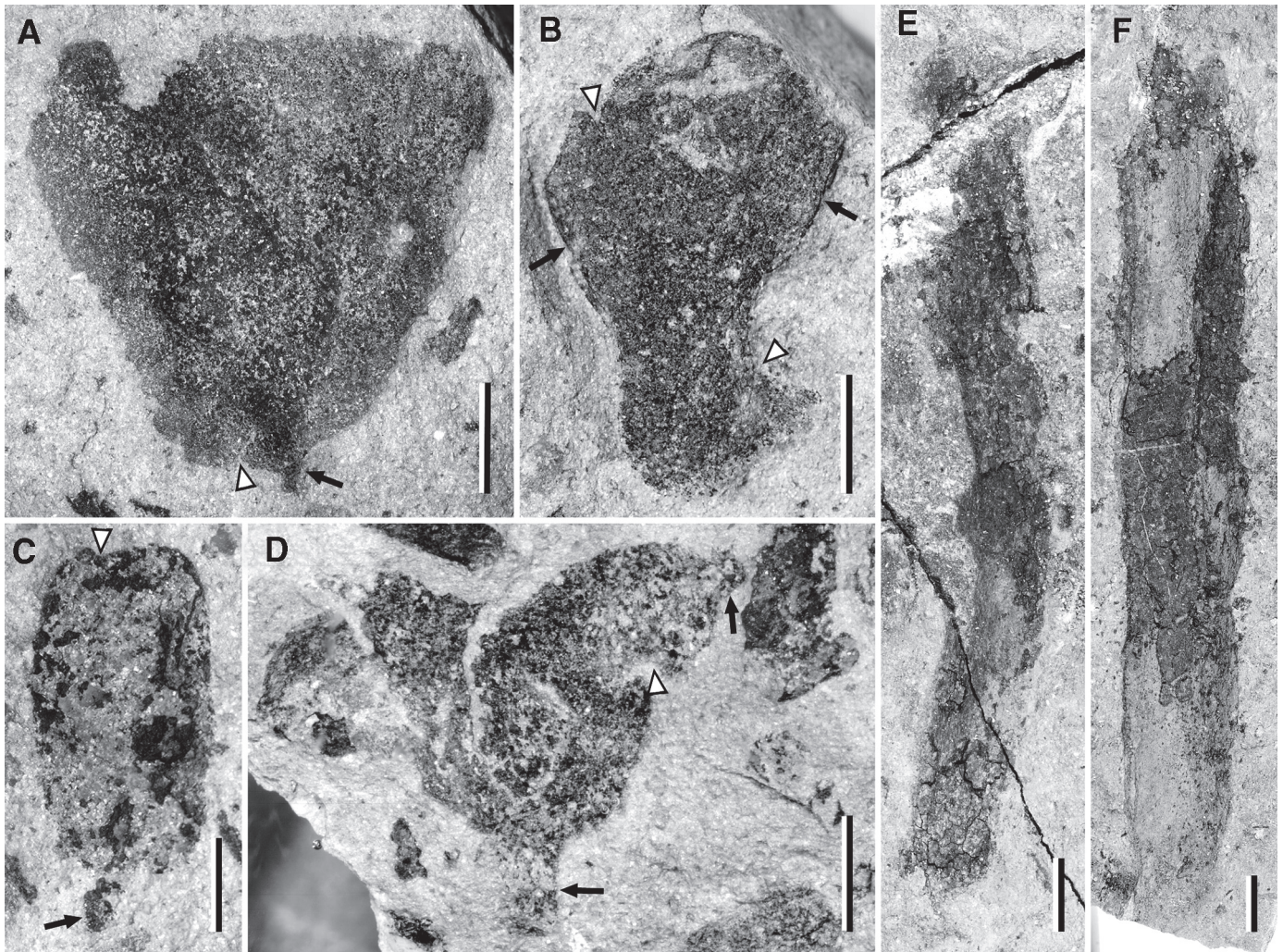
Figure 4. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. Thalloid (A–D), and strap-shaped (E, F) macrofossils. (A) Thalloid specimen with a deltoid shape, undulating margins, a possible attachment protrusion (arrow), and a strongly incised lobe sinus (arrowhead). It displays a thicker and darker central area and thinner areas along the two margins that diverge from the base; the upper left side feature is an artifact of rock splitting, and not an actual lobe, as shown by degagement of the counterpart of the fossil. OUPH 15984. Scale bar 5 mm. (B) Thalloid specimen with irregular shape, lobes (lobe sinuses at arrowheads), and edges recurved down into the mineral matrix (at arrows). OUPH 15985. Scale bar 5 mm. (C) Oval thalloid specimen with possible attachment protrusion (arrow) and very shallow lobation (lobe sinus at arrowhead). OUPH 15986. Scale bar 2 mm. (D) The central part of the image shows two partly overlapping thalloid specimens, one with a deltoid shape and a possible attachment protrusion (lower arrow), and the other with a possible attachment protrusion (upper arrow) and lobed (lobe sinus at arrowhead). OUPH 15987. Scale bar 2 mm. (E) Strap-shaped specimen with rounded terminations. OUPH 15988. Scale bar 5 mm. (F) Strap-shaped specimen with a two-pronged termination. OUPH 15989. Scale bar 5 mm.

cross sections can be nevertheless classified into five main types (Fig. 5A–J) based on layering and on the types and organization of organic matter within the different layers. In some instances, anatomical features observed under light microscopy in cross sections could be related to features revealed by SEM and TEM.

Type 1 (Fig. 5A). Type 1 fossils exhibit an anastomosing pattern that consists of micron-thin vertically undulating features. Representing either filaments or highly discontinuous sheets of organic matter, they form a continuous intertwining network 25–90 μm thick in the plan of the compression. The network

is denser toward the two faces of the carbonaceous film. Voids within the fossil (arrow) have consistent outlines that can be followed in serial sections.

Type 2 (Figs. 5B–D, G, 6A, 6C, 6D). This type consists of two layers of dense organic matter sometimes separated by a median region containing sporadic organic material. The two outer layers display irregular surfaces, occasional discontinuities and punctures, variable thickness (2–12 μm), tangential fissures, and may be in turn split into thinner sub-units (Figs. 5B, 6A, 6C). Figures 5C and 5D represent the part and counterpart of a

Figure 5. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. Transmitted light micrographs of cross sections illustrating the main types of internal anatomy displayed by the fossils (see text for detailed description of types). (A) Type 1. The arrow points to a void with consistent outlines that can be followed in serial cross sections. OUPH 15990. (B) Type 2. The black arrowhead indicates organic material of a different nature reflected by lighter color and different texture. The white arrowhead points to agglomeration of minute dark dots nested between the two outer layers (similar with the feature shown in SEM, Fig.5C, 5D). OUPH 15991. (C, D) Separated part and counterpart of a specimen with Type 2 anatomy. OUPH 15992 and 15993, respectively. (E) Type 3. OUPH 15994. (F) Thicker section of the same specimen as in Figure 5E, showing diaphanous organic matter in the median region (arrowhead). OUPH 15994. (G) Part of a specimen with Type 2 anatomy displaying diaphanous organic matter (light gray, at center). OUPH 15995. (H) Type 4. OUPH 15996. (I) Detail of the same specimen as in Figure 5H featuring molds of large euhedral crystals (arrowhead), and of agglomerations of very small crystals (arrow). OUPH 15996. (J) Type 5. Arrowhead indicates mold of euhedral crystal. OUPH 15997. All scale bars 20 μm.
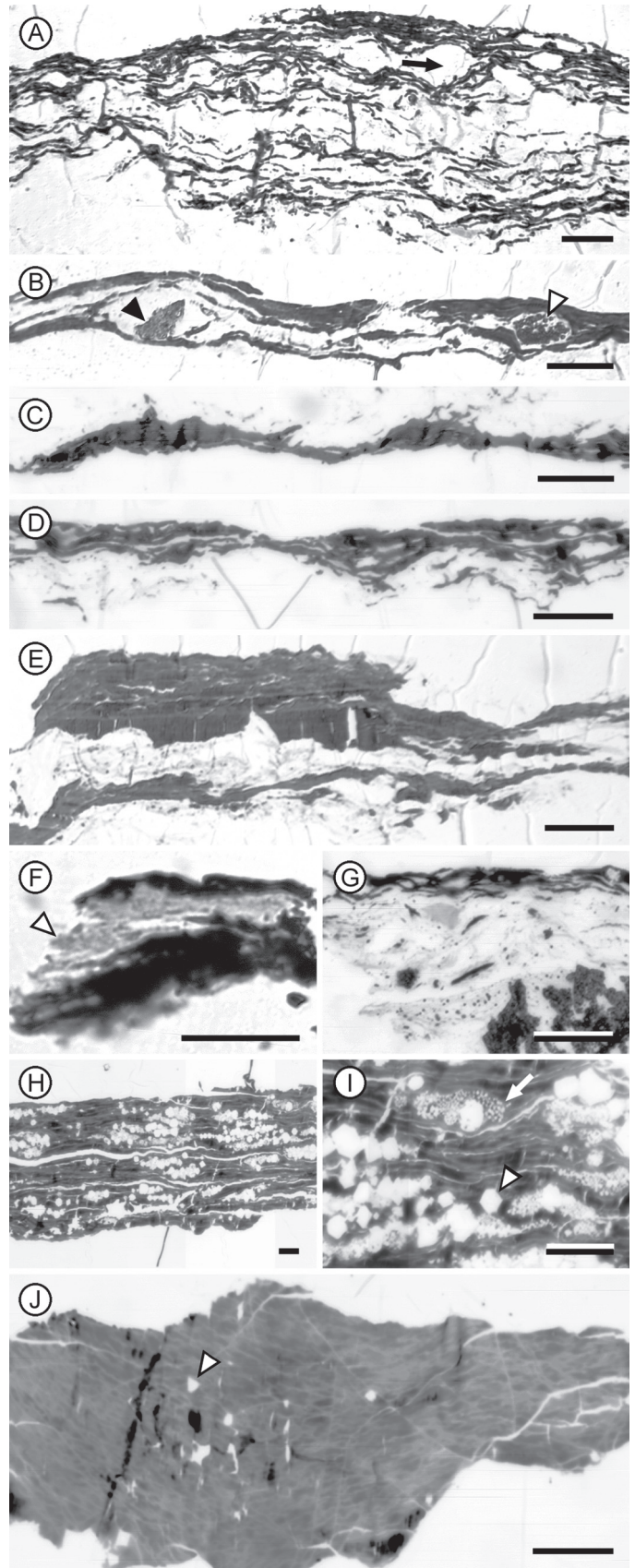
specimen with Type 2 internal anatomy. The outer layers exhibit a laminar structure consisting of largely parallel sheets (around 1 μm thick) of variable densities (lighter and darker), not very well individualized. Where the separating median region is absent the two layers appear continuous (right side of Fig. 5B). The median region has variable thickness and contains fragments similar to the outer layers, as well as organic material of an apparently different nature reflected by lighter color and different texture (Fig. 5B, black arrowhead; 5G).

Regions where minute dark dots can be seen in transverse sections are sometimes nested between the two outer layers (Fig. 5B, white arrowhead). In SEM they appear as features consisting of more-or-less regularly constricted filaments (1 μm or smaller across) with a beadlike appearance, tightly packed in a tangle with no consistent pattern (Figs. 6C at arrow, and 5D). These features are reminiscent of the packing of vesicular arbuscular mycorrhizal hyphae inside plant root cells.

Type 3 (Figs. 5E, 5F, 6B). Type 3 internal organization is similar to Type 2 in that it involves two outer layers separated by a median region (Fig. 5E). While one of the outer layers is similar to those of Type 2 fossils, the other layer (shown as the upper layer; orientation of the fossil is arbitrary) consists of two sub-layers and reaches 27 μm in thickness. The outermost sub-layer exhibits a laminar structure comparable to the one described in Type 2. The inner sub-layer is denser (darker) and massive, and has variable thickness and vertical cracks. A three-dimensional SEM image of the two sub-layers is shown in Figure 6B. The two-parted structure of the outer layer can be replaced laterally by a structure similar to that encountered in Type 2 (right side of Fig. 5E), suggesting that Type 2 and Type 3 may represent variations of the same type of internal organization.

The median region contains organic material that is less dense and very light in color, referred to here as diaphanous organic matter. Almost transparent in 0.5-μm-thick sections, it becomes

more obvious only in thicker sections (Fig. 5F at arrowhead). The presence of diaphanous organic matter (Fig. 5G) associated with the specimen shown in Figure 5D suggests that it is probably characteristic of the Type 2 internal organization as well.

Difficult to observe in light microscopy, the structure of diaphanous organic matter is revealed by TEM (Fig. 7) and demonstrates preservation of unexpected levels of detail in the organic material. The diaphanous material forms multiple discrete, mostly thin layers (100–150 nm) of homogeneous density,

but also thicker layers (460 nm, at arrow) displaying variations of density. In TEM the denser organic matter of the outer layers displays a stratified structure of tightly packed microlaminae 80–230 nm thick, with gradational boundaries between them (Fig. 7, lower right).

Type 4 (Fig. 5H, 5I). This type consists of material with laminar structure that is disrupted by tangential fissures and crystal growth. The laminar structure is similar to that described in Type 2, with undulating darker and lighter laminae, but the thickness
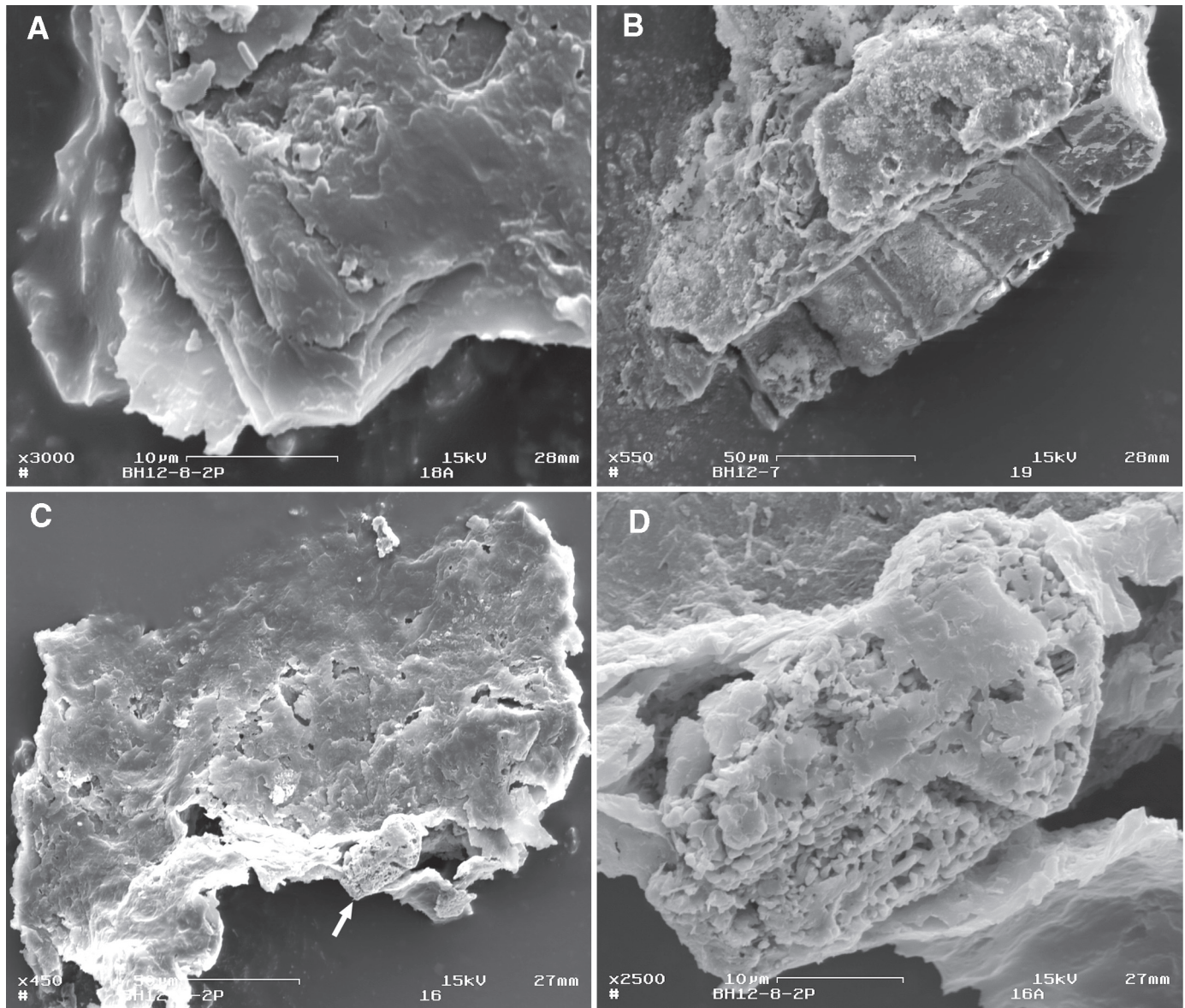

Figure 6. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. Scanning electron micrographs illustrating the three-dimensional geometry of specimens with Type 2 (A, C, and D) and Type 3 (B) internal anatomy. (A) Type 2 anatomy. Surface features (punctures, discontinuities) and irregular layering. OUPH 15998. (B) Type 3 anatomy. Thin outermost laminar sub-layer and subjacent massive layer with cracks perpendicular to layering. OUPH 15999. (C) Type 2 anatomy. Specimen with irregular, punctured surface and feature (arrow) similar to the agglomeration in Figure 5B. OUPH 15998. (D) Detail of feature in Figure 6C. OUPH 15998.

of the fossil reaches 160 µm. There are lenticular areas 10–25 µm long and 5–15 µm thick that represent molds of crystals or clusters of crystals removed during hydrofluoric acid dissolution for fossil extraction. Crystals fall into two size classes: the larger tend to be isodiametric, 4–12 µm across, whereas the smaller are 0.5 µm or smaller and are grouped in areas roughly the size of the larger crystals (Fig. 5I at arrow). The crystal molds exhibit mainly hexagonal outlines in section (Fig. 5I at arrowhead), and their euhedral habit with sharp angles indicates that they developed within the fossils by solution precipitation. Examination of relationships between voids left by the crystals and the laminar structure of the fossil demonstrates that growth of crystals was mainly disruptive. This suggests that crystal growth occurred after burial of the fossils, when it could not be accommodated through expansion of the organic material, tightly embedded in the sedimentary matrix.

Type 5 (Fig. 5J). Type 5 fossils exhibit a massive structure traversed by what appears to be a very dense network of fine fissures (1 µm or thinner) that are filled with light organic matter. The network is superimposed on a pattern of diffuse zones of darker and lighter material. Presence of a few euhedral crystal molds or voids (arrowhead) that disrupt the fissures indicates that if the fissures are the result of postdepositional deformation of the fossils, then the growth of crystals occurred after fossilization of the organic material.

Apart from the above methods of investigation, sodium hypochlorite bleaching of the carbonaceous material in the fossils can reveal recognizable structures. Such was the case with the strap-shaped specimen shown in Figure 4E, where prolonged bleaching brought the jet-black coaly material to hues of light brown, orange, and yellow, and revealed the presence of filamentous structures embedded in an apparently amorphous matrix (Fig. 8). Although the filaments appear lighter in color in reflected light (Fig. 8A), viewed in transmitted light they consist of denser, opaque matter (Fig. 8B). The filaments run roughly parallel to each other and to the length of the fossil, and are 30–40 µm wide. Some of them can be followed over lengths of around 1 mm, but show no evidence for branching.

Systematic Affinities of the Passage Creek Fossils

All of these observations reflect the presence of communities comprising primarily thalloid organisms and associations of organisms that can be aggregated into more extensive mats. Morphological and anatomical data obtained so far reveal not only diversity, but also complexity of the fossils, indicating that several types of complex organisms were present in the groundcover of Llandoverian wetlands.

Thalloid growth is not restricted to a single group of organisms but characterizes a very diverse assortment of extant and fossil groups and mutualistic symbiotic associations, all of which are potential producers of the Massanutten Sandstone fossils. These groups include cyanobacterial colonies, algae (charophyceans and others), fungi, lichens, and bryophytes (liverworts and hornworts), all of which are also encountered as constituents of the
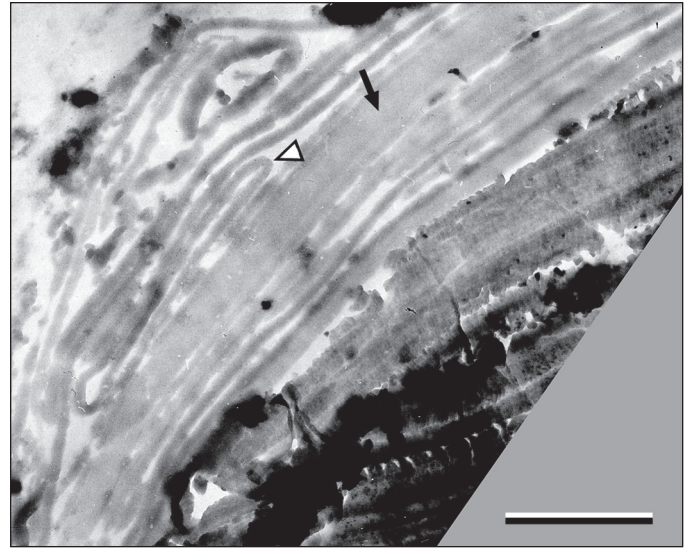

Figure 7. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. Transmission electron micrograph illustrating diaphanous organic matter (light gray) that forms multiple discrete and mostly thin layers of homogeneous density, sometimes folded (arrowhead), and thicker layers (arrow) with variations of density. Denser organic matter of the outer layers (darker, at lower right) displays a stratified structure of tightly packed microlaminae with gradational boundaries between them. OUPH 16000. Scale bar 2 µm.
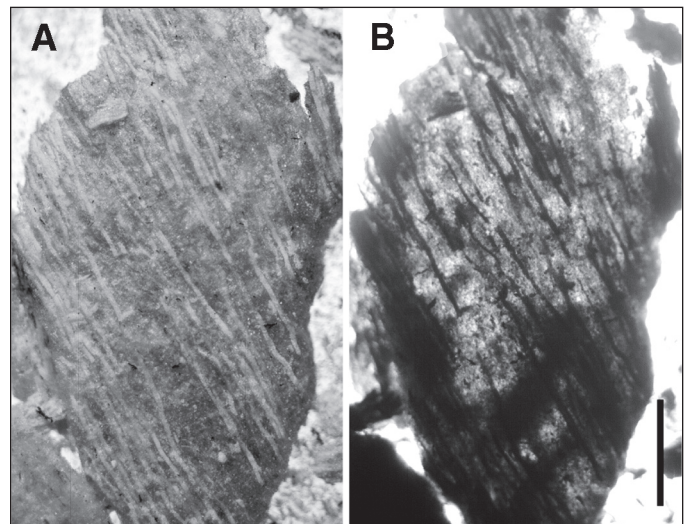
Figure 8. Lower Massanutten Sandstone, Passage Creek, Shenandoah County, Virginia, Llandoverian. A fragment of the strap-shaped specimen in Figure 4E bleached in sodium hypochlorite reveals filamentous structures more or less parallel to each other and to the length of the fossil, and incorporated in an apparently amorphous matrix. The filaments appear lighter in color in reflected light (A), but viewed in transmitted light they consist of denser, opaque matter (B). OUPH 16001. Scale bar 0.5 mm.

more loosely defined associations known as biological soil crusts, as well as the fossils *Nematothallus*, *Parka*, *Spongiophyton,* and *Protosalvinia*.

An animal origin for these fossils is unlikely as none of the numerous compressions yielded by our extensive sampling exhibit consistent and regular shapes characteristic of fragments from animals with a unitary body. Cuticle-like fragments for which a possible animal origin has been discussed (Gensel et al., 1990) have been found at this locality (Pratt et al., 1978, and our observations). However, no fragments of appendages or other unequivocal animal fossils like those described by Gray and Boucot (1994) from the Tuscarora Formation are present in the microscopic fraction of maceration preparations.

Resolution of the systematic affinities of the Passage Creek thalloid fossils necessarily involves comparisons with the morphology and anatomy of all of the above organisms and associations of organisms of the thalloid guild. But before such comparisons are possible, we need to document and clarify three main types of correlations that are crucial in understanding the organisms that produced the fossils: (1) Correlation between anatomy and external morphology. This involves correlations among anatomical features revealed by different investigation techniques (cross sections, bleached specimens, SEM), and correlations between these and the external morphology of the fossils. (2) Correlation between anatomy and ultrastructure. This involves understanding the intimate structure of different types of anatomical elements, and of the relationships between them. (3) Correlation between features of the macrofossils and the components of microfossil assemblages described in the same rocks. Thorough documentation of all of these relationships is very important for understanding and reconstructing the original organisms. Such documentation will allow us to compare the fossils with different living groups of similar morphology, in order to reveal the systematic affinities of the fossils.

Even at this stage of research, we can know something about potential systematic affinities of the Passage Creek organisms from the dispersed microfossils described from the same sediments by Pratt et al. (1978), and these complement the image of diversity projected by the macrofossils. Trilete spores and tetrahedral tetrads are hallmarks of the embryophyte reproduction, and their presence in the Massanutten Sandstone microfossil assemblages suggests that embryophytes were present among the thalloid communities in the Llandoverian wetlands. This corroborates the morphology predicted for the hypothetical embryophyte archetype by Mishler and Churchill (1985), which features a thalloid gametophyte with single sessile sporangium.

The dispersed fungal hyphae are compared by Pratt et al. (1978) to dematiaceous hyphomycetes of the Fungi Imperfecti, on the basis of morphological features such as size, branching, and septation. As such they are interpreted as evidence (the earliest) for higher fungi. Presently some in the scientific community are reluctant to accept reports of earliest occurrences of dispersed fungal microfossils in the absence of conclusive evidence that sample contamination with recent material during sampling,

handling, and processing can be ruled out completely. Before this issue is addressed with scientific arguments dealing with the fossil material itself, the Passage Creek fungi need to be treated with caution. However, more recently Redecker et al. (2000) have reported dispersed glomalean hyphae and spores from the mid-Ordovician Guttenberg Formation of Wisconsin (Fig. 1), in a context that excluded the possibility of contamination with recent material (Redecker et al., 2000, p. 1921, note 16). This finding indicates that fungal groups that are presently encountered only in mycorrhizal associations with embryophytes were present long before the Silurian, and suggests that some of the thalloid bionts at Passage Creek may indeed represent or include a fungal component.

The systematic affinities of membranous cellular sheets, sometimes featuring cuticular coverings, and tubular elements with or without wall thickenings, occurring as dispersed microfossils are commonly placed with the nematophytes; as emphasized earlier, however, the systematics of such fossils remain largely unresolved. Nevertheless, Graham and Gray (2001) made an important observation by pointing out disparities between the stratigraphic record of cuticle-like fragments and tubes, thus suggesting that the two types of fossils probably originated from different types of organisms.

Structure of the Passage Creek Communities

Decimeter-scale arrangement of compression fossils on bedding planes shows several patterns. Some of the samples show a predominance of small size fossils (<5 mm) and only rare larger (>1 cm) fossils (Fig. 3A, 3B), whereas others exhibit an abundance of larger fossils around 1 cm or larger, and a few small fossils (Fig. 3C). The end member of this continuum is represented by surfaces where the compressions form extensive crusts of highly irregular outline (Fig. 3D). Fossils can be evenly distributed on the bedding planes (Fig. 3A), or they can form agglomerations a few centimeters across (Fig. 3B). The area covered by fossils is small on bedding planes where small fossils predominate (Fig. 3A, 3B), and considerably bigger where larger fossils are dominant (Fig. 3C) and in the case of crusts (Fig. 3D). Sedimentologic and taphonomic evidence indicates that at least some of the fossils at Passage Creek are preserved in situ (see section on depositional environments of the fossil assemblages). However, until in-depth treatments of the sedimentology and taphonomy of the fossiliferous layers are completed, it is difficult to estimate to what extent fossil arrangement on bedding planes can be interpreted in terms of community physiognomy.

From a trophic standpoint the Early Silurian communities at Passage Creek were relatively simple, including primary producers and probably decomposers. Primary producers at the base of the trophic structure included embryophytes, probably at a thalloid bryophytic grade of organization, as suggested by trilete spores and tetrads in the microfossil assemblages. Other groups of organisms were very likely also contributing to the biomass of this trophic level. Cyanobacteria and green algae have long been hypothesized as early terrestrial invaders (e.g., Stebbins and

Hill, 1980; Wright, 1985), and the finds of Horodyski and Knauth (1994) in the Precambrian may represent such organisms. Fungi were almost certainly present at Passage Creek as well, probably as decomposers or in associations with photoautotrophs, or both. Evidence for an animal component in the Massanutten Sandstone biota is absent from the micro- and macrofossil assemblages to date. However, Gray and Boucot (1994) recovered dispersed microfossils of animal origin along with plant and fungal spores from stratigraphically equivalent fluvial strata in the Tuscarora Formation of Pennsylvania. Shear and Selden (2001) interpret these fragments as representing fresh-water or terrestrial animals, and their presence in stratigraphically and depositionally equivalent strata leaves open the possibility that the Passage Creek biota may include an as yet unidentified animal component. Continuing study and resolution of the systematic affinities of the macrofossils is needed to clarify and substantiate these preliminary interpretations, and to shed more light on the structure of the Passage Creek communities.

Age of the Fossils

In their description of the stratigraphy of the Massanutten Sandstone along Passage Creek and in the surrounding region, Rader and Biggs (1976) recognize two distinct units. Based on stratigraphic relationships and lithology, they consider the lower unit roughly equivalent to the Tuscarora Formation, and possibly older. Previously, Yeakel (1962) had included the Massanutten Sandstone of Massanutten Mountain in his study of the Tuscarora Formation in the Central Appalachians, and Dennison and Wheeler (1975) had suggested a lower Massanutten-Tuscarora equivalence. This equivalence was inferred again by Whisonant (1977) in Virginia, and was reiterated by Pratt et al. (1978). The Passage Creek fossil assemblage occurs in the lower unit of Rader and Biggs (1976), which Pratt et al. (1978) informally named the Tuscarora member to reflect the stratigraphic equivalence.

The Tuscarora member and the Tuscarora Formation generally lack body fossils except for those reported by Pratt et al. (1978) and in this study, the biostratigraphic significance of which has yet to be assessed. The age of the Tuscarora member is consequently constrained biostratigraphically on the basis of marine assemblages in the underlying and overlying strata. These limit the age to an interval between the Ashgillian (underlying Martinsburg Formation) and the Ludlovian (top of the upper unit of the Massanutten Sandstone) (Pratt et al., 1978). Taking into account the thickness of the upper unit (Clinton Member) of the Massanutten, the latter authors consider the age of the Tuscarora member most likely early to middle Llandoverian (stages A–B). This age is in accord with that proposed for the Tuscarora Formation in Pennsylvania by Cotter (1983), i.e., early to lower-late Llandoverian (stages A–C_{2-3} of Berry and Boucot, 1970). The age of the Passage Creek fossils can therefore be placed with confidence in the Llandoverian, somewhere between the beginning of the Llandoverian and the basal late Llandoverian.

Depositional Environments of the Fossil Assemblages

Pratt et al. (1978) interpret the lower Massanutten Sandstone at Passage Creek as nonmarine, on the basis of the absence of marine fossils and nearshore indicator trace fossils (*Skolithus*, *Arthrophycus*). Although no detailed sedimentological study of the Passage Creek locality has been published, the lower Massanutten Sandstone is included in studies of the depositional environments of the Tuscarora Formation.

In an early study, Folk (1960) considered the Tuscarora in West Virginia a transitional nearshore marine to beach deposit, mainly on the basis of textural features. However, several other studies (e.g., Yeakel, 1962; Smith, 1970) strongly argue for a fluvial origin of at least most of the Tuscarora and its equivalents in Pennsylvania, New Jersey, New York, Maryland, Virginia, and West Virginia. Evidence used to support this interpretation is summarized by Fail and Wells (1974) and includes among others tabular sets of cross-beds, consistent dip directions of the cross-beds, thin, lenticular siltstones and shales, irregular bedding surfaces, abundant cut-and-fill structures, the presence of shale pebbles, and the systematic decrease in maximum pebble size in the direction of cross-bedding dip vectors. Subsequent work by Whisonant (1977), Cotter (1978), and Cotter (1983) is in agreement with the fluvial interpretation of the depositional environment. Two independent and extensive regional studies by Yeakel (1962) and Whisonant (1977) include the lower Massanutten Sandstone in their data sets. On the basis of paleocurrent directions and regional patterns of grain size distribution, both authors agree upon its location closest to the source of sediment, on a coastal plain that sloped toward the northwest.

Smith (1970) is the first to have suggested a braided style for the fluvial systems that deposited the Tuscarora, using comparisons of various sedimentary features with those of the modern South Platte and Platte Rivers of Colorado and Nebraska. His interpretation is supported by the studies of Pratt (1978) and Cotter (1978, 1983). In central Pennsylvania, Cotter (1983) interprets the basal part of the formation as beach deposits, the main body as braided-fluvial in southeastern, proximal facies, and the topmost part of the formation as coastal, sand or mud flat deposits. His paleogeographic reconstruction shows a southeast to northwest facies transition down the Llandoverian paleoslope from most proximal, alluvial fan complexes, through coastal alluvial plain facies of braided river systems, beach-strandplain, lagoon and estuary settings, to distal, shelf sand wave complexes. Cotter's (1983) reconstruction supports the paleogeographic interpretations of Yeakel (1962) and Whisonant (1977), and all provide good evidence to consider the Tuscarora as deposited by braided river systems carrying terrigenous material northwestward to the coast, from the Taconic Highlands that formed a linear source area in the southeast. The position of the lower Massanutten Sandstone in a setting proximal to the source area within this large-scale sedimentary system justifies its interpretation as deposits of braided rivers.

The macrofossils at Passage Creek occur in fine-grained partings that form thin, discontinuous layers between thicker, coarser beds of sandstone and fine conglomerate (Fig. 2). In fluvial sequences, as a result of the characteristic partitioning of sedimentation by grain size, fine-grained facies represent sedimentation outside of active channels: overbank, waning flood, or backswamp deposits (Miall, 1978, 1996). Such partitioning is very marked in braided streams and separates coarse channel deposits from finer material deposited outside active braid channels. Although "flood plain" is a term often avoided in describing the geomorphology of braided river systems, such systems include river flats – elevated surfaces within the channel tract and adjacent to active braid channels. As pointed out by Nanson and Croke (1992), once removed vertically or laterally from the proximity of active braid channels, these surfaces accumulate overbank fines in the same way as other flood plains. From the point of view the sediment partitioning by grain size such settings are therefore equivalent to the classic flood plains of meandering streams. The finer grain size of the sediments that preserve the fossils at Passage Creek (mainly siltstone to fine sandstone, with minor shale) indicates that they were deposited outside of the channels, broadly speaking in the flood plain of the river system that deposited the Massanutten Sandstone.

The preservation of fossils in flood-plain deposits does not automatically eliminate the possibility that they represent remains of fresh-water organisms transported and buried in overbank settings by flood events. The question then becomes, are the fossils autochthonous, preserved in situ and hence representing the flood-plain ecosystem, or are they allochthonous, transported material? In the latter case it would be difficult to determine whether they were transported from other locations on the flood plain, or from fresh-water ecosystems of the braid channels. Conclusive evidence in support of autochthony awaits careful sedimentological and taphonomic study of the fossiliferous layers, but several observations indicate that at least some of the Passage Creek fossils were buried in situ or underwent minimal transport. Pratt (1978) cites carbonaceous streaks perpendicular to the sedimentary lamination as evidence for in situ preservation of the fossils. Braided rivers are notorious for transporting coarse-grained bedload that acts as an extremely effective "grinding mill" on rock fragments, even over distances on the order of meters (G.C. Nadon, personal commun., 2003). Especially during floods, when it is greatly enhanced, this action would have reduced to minute fragments any organic material transported. However, several large specimens uncovered at Passage Creek by careful degagement preserve entire margins, and others form extensive organic crusts, indicating minimal, or more likely no, transport. In this context crusts with cracked surfaces were almost certainly preserved in situ.

Fossils preserved in situ on the flood plain can represent terrestrial organisms living in the aerial realm, but they also could represent fresh-water organisms of backswamp ponds or lakes. The relatively coarse texture of the sediment that incorporates the fossils (mainly siltstone and fine sand) disproves the latter

alternative: silt-grade material is not well suited for retaining the water needed to form ponds. Isotopic $\delta^{13}C$ values obtained by Niklas and Smocovitis (1983) on Passage Creek fossils range from −25.6 to −26.4, favoring a terrestrial origin for the fossils. Additional evidence is provided by desiccation cracks in the fossiliferous siltstones, and by occurrences of fossils displaying desiccation cracks (e.g., Fig. 3C, at arrowhead). All of this evidence indicates that the Passage Creek fossils represent terrestrial organisms occupying wetland settings that were at least periodically emergent, and probably submerged primarily during the floods that buried them in silty sediment.

Importance of the Passage Creek Biota

The present level of understanding of the Passage Creek biota allows for several inferences of considerable importance for the colonization of land and the role played by wetland environments. A first important conclusion is that the Passage Creek fossils represent terrestrial organisms. This interpretation was also suggested by previous workers (Pratt et al., 1978; Niklas and Pratt, 1980; Niklas and Smocovitis, 1983) and is supported by data on the depositional environments. Given their early- to mid-Llandoverian age, these fossils represent the oldest direct, macroscopic evidence for terrestrial life. Ten to fifteen million years older than the oldest previously known terrestrial organisms (polysporangiophytic embryophytes and nematophytes), the Passage Creek biota provides an unprecedented perspective for understanding the early phases of the colonization of land by macroscopic organisms.

The Passage Creek biota reveals an abundance of fossil preservation, indicating that a well-developed terrestrial groundcover was present by the Early Silurian. Developed in the flood plains of river systems, this groundcover represents communities occupying settings that are geomorphologically homologous to present-day riverine wetlands. However, compared with modern wetlands that are continuously wet by virtue of the moisture retention capabilities of soils and vegetation, the Early Silurian flood-plain wetlands were only abiotically wet, and were dependent on climate and the fluctuations of the river system for their moisture supply. Moisture retention capabilities of the groundcover were probably very limited, and the flood-plain settings were prone to desiccation between floods, as suggested by the cracks on the surface of some of the fossils. Even so, these settings provided the wettest available environments on land at the time. It is no coincidence, therefore, that these wettest environments were home to the earliest well-developed terrestrial communities of complex organisms.

Fossil assemblages preserved at Passage Creek encompass a considerable level of structural diversity, in terms of both external morphology and internal anatomy. This diversity represents evidence for the presence of systematically diverse terrestrial communities in the groundcover of Early Silurian wetlands. The different types of internal organization documented at Passage Creek indicate that these communities were built by several types of complex organisms and/or associations of organisms. Dispersed

microfossils from the same rocks provide evidence for embryophyte and probably fungal components in the biota. The observation that these organisms are thalloid provides the first direct evidence for developing an interesting new perspective on the earliest stages of the colonization of land by complex organisms.

The traditional embryophyte-focused view of the colonization of land has forged a search image for early land colonists based on one of the embryophytic synapomorphies, the axial sporophyte. However, the macrofossil record of axial sporophytes begins only in the late Wenlockian, a limit below which only tetrahedral spore tetrads and trilete spores, the microscopic embryophyte hallmarks, previously have been known. In the absence of macrofossils, spores alone do not reveal the habitat of early embryophyte growth, and the problem of terrestriality remains in the realm of hypothesis and speculation. The absence of axial sporophyte fossils and a predominance of thalloid forms in this earliest known terrestrial biota suggest that an alternative search image may provide greater success in the search for early terrestrial colonists. Rather than searching for axial sporophyte fossils in older and older deposits, a broadened focus that includes thalloid gametophytes, lichens, and other mutualistic associations such as the biological soil crusts may prove to be a more fruitful endeavor.

CONCLUSIONS

The Llandoverian Passage Creek biota of Virginia comprises the oldest macrofossil evidence for complex terrestrial life, preserved in fluvial wetland deposits. Although only preliminarily characterized, these fossils demonstrate that a well-developed, though discontinuous, groundcover was present in wetlands by the Early Silurian. This groundcover consisted of communities formed by a fairly diverse guild of thalloid organisms or associations of organisms, and of organic crusts comparable to extant biological soil crusts.

The Passage Creek biota emphasizes the importance of wetlands for the colonization of land by complex forms of life, and for the study of this process. Even though mainly abiotically wet in the absence of the considerable moisture retention capabilities conferred by soils and tracheophytic vegetation, Early Silurian river flood plains represented some of the least water-stressed environments on land at the time. As such, these wetlands offered the most favorable conditions both for the development and for the preservation of communities consisting of complex terrestrial organisms and associations of organisms. Likewise, the fossils they preserve have great potential for revealing the earliest stages of the colonization of land.

ACKNOWLEDGMENTS

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