LATE ORDOVICIAN – EARLY SILURIAN TERRESTRIAL BIOTAS
OF VIRGINIA, OHIO, AND PENNSYLVANIA:
AN INVESTIGATION INTO THE EARLY COLONIZATION OF LAND

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the College of Arts and Sciences of Ohio University

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This dissertation entitled

LATE ORDOVICIAN – EARLY SILURIAN TERRESTRIAL BIOTAS
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AN INVESTIGATION INTO THE EARLY COLONIZATION OF LAND

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Late Ordovician – Early Silurian terrestrial biotas of Virginia, Ohio, and Pennsylvania: an investigation into the early colonization of land (284 pp.)

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An early phase in the colonization of land is documented by investigation of three fossil compression biotas from Passage Creek (Silurian, Llandoverian, Virginia), Kiser Lake (Silurian, Llandoverian, Ohio), and Conococheague Mountain (Ordovician, Ashgillian, Pennsylvania). A framework for investigation of the colonization of land is constructed by (1) a review of hypotheses on the origin of land plants; (2) a summary of the fossil record of terrestrial biotas; (3) an assessment of the potential of different continental depositional environments to preserve plant remains; (4) a reevaluation of Ordovician-Silurian fluvial styles based on published data; and (5) a review of pertinent data on biological soil crusts, which are considered the closest modern analogues of early terrestrial communities. The three studied biotas are non-paradigmatic biotas, defined here as biotas whose components escape unequivocal taxonomic assignment because their features preclude assignment to any known group, or compare them to several known groups without allowing further distinction.

The Passage Creek biota consists of rich, morphologically and anatomically diverse fossil assemblages. They demonstrate that a well-developed groundcover was already present at the beginning of the Silurian, occupying river floodplains. This groundcover consisted principally of thalloid organisms and the diversity of terrestrial
communites included cyanobacteria, as well as organisms characterized by complex internal organization, the affinities of which remain unresolved. The Kiser Lake fossils consist of carbonaceous compressions, one of which compares to liverwort leaves and lichen rhizines. The same sediments yield scraps of cellular tissue and the earliest spores assignable to ascomycetes. These are preserved in peritidal carbonate sediments. The Conococheague Mountain biota includes rich compression assemblages from transitional shallow marine and deltaic facies. Such deposits usually harbor mixtures of marine and continental fossils, rendering interpretation of the ecology of original organisms difficult. These three biotas contain the oldest macrofossils of terrestrial (Passage Creek) and potentially terrestrial (Conococheague Mountain, Kiser Lake) organisms and demonstrate that diverse communities including complex forms were present much earlier than previously thought. The thalloid morphology represents a transitional stage in the evolution of complexity among terrestrial primary producers from exclusively microbial photosynthesizers to complex embryophytes with axial morphology.

Approved: Gar W. Rothwell

Distinguished Professor of Environmental and Plant Biology
PREFACE

When I started this study, it seemed a relatively straightforward undertaking: searching for the origin of land plants by looking at fossils. However, as I progressed in familiarizing myself with the present state of knowledge in the field, in understanding the thinking of those who had tackled this subject before me, in producing new data from fossils, and in organizing all of these into written text, I started realizing that my original pursuit was targeting only one aspect within the very tip of a vast iceberg representing the fundamental process of colonization of land surfaces by life. That this iceberg consisted of a multitude of aspects and facets frozen together as a collection of facts and observations scattered within a blurry matrix of unknown. That these facts and observations represented the accumulation of results from work by numerous people, over many years, in a very diverse array of fields of research: paleobiology, molecular biology, genetics, developmental and structural biology, biochemistry, phylogenetics, stratigraphy, sedimentology, and geochemistry. And that the answer to my initial question could only be found by melting the whole iceberg down into consistent, organized knowledge, to clarify the connections and add the missing parts between all of these facts and observations, as well as to uncover new facts and link them to what is already known.

Consequently I broadened my perspective and started by building up an epistemologic framework for my pursuit. This meant defining the nature of problems engendered by the features of the fossils that I was studying; understanding what we mean by plants and land plants, and what we think currently about their phylogeny;
summarizing the ideas, as well as the present state of knowledge on the colonization of land and early terrestrial biotas. I added an assessment of the potential of different sedimentary depositional environments for preserving remains of terrestrial biotas, and summarized knowledge of the structure and ecology of biological soil crusts (the most likely modern analogues of early terrestrial ecosystems), as stepping stones. Within this framework I could formulate hypotheses and begin looking at fossil biotas.

The results are both frustrating and encouraging. The fossils do not give up their secrets willingly. The mode of preservation represents a redoubtable obstacle to understanding their nature. But this can be overcome by detailed characterization of the fossils coupled with actualistic experimental work on morphologically similar modern groups. Additional fossil material present in abundance at several new unexplored localities can reveal better preservation and add to the characteristics documented so far. Features preserved in the fossils studied here nevertheless provide evidence for the diversity of early terrestrial life and allow for establishing a minimal date for the advent of complex life on land. But more importantly, these results show that fossils hold great potential for clarifying this crucial chapter in the history of life, of which we have only written the first pages.
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1. INTRODUCTION: THE SYSTEMATIC PARADIGM AND NON-PARADIGMATIC BIOTAS

The overwhelming majority of studies of compression floras operate within a well-constrained system whereby the systematic affinities of the fossils are known at the onset of the work, usually down to the class or family level, and quite often in even greater taxonomic detail. Within this system of knowledge, such studies are aimed at better characterizing, understanding, and classifying the plants. Subsequent approaches can then assess plant diversity and richness. At a more general level, this epistemological paradigm, whereby the systematic affinities of fossils are known a priori down to a certain level (ergo, systematic paradigm), underlies the greater part of paleobiological studies. In this work I am introducing a few of the comparatively rare biotas that force us outside of that systematic paradigm, henceforth termed non-paradigmatic, and I am using a polyphasic method that integrates information from multiple techniques for reconstructing and interpreting the structure of fossils in the absence of a systematic framework.

In contrast to fossil biotas that fall within the systematic paradigm, non-paradigmatic fossil assemblages present a major challenge – there is no a priori knowledge of the systematic affinities of the organisms, not even at the kingdom level. Ediacaran biotas of the late Neoproterozoic and Early Cambrian are particularly well-known examples of non-paradigmatic assemblages for which Peterson et al. (2003) provide an insightful discussion of their potential relationships and problematic. Within the systematic paradigm, some level of knowledge of systematic affinities provides a
consistent framework for subsequent inquiry and inference. By contrast, in non-paradigmatic assemblages readily observable features of the fossils do not allow an *a priori* assessment of their systematic relationships. This knowledge handicap associated with non-paradigmatic biotas sets the starting point of scientific inference at a much more fundamental level, and upsets the usual patterns of logical reasoning. For instance, when studying a frond compression we know that it represents a plant which is potentially assignable to a definite number of systematic groups based on gross morphology and prior taxonomic knowledge. Starting from this knowledge basis, we expect to see epidermal cell patterns and stomata in the cuticle, we expect to find a certain type of diaspores in reproductive structures, and if cross-sections of the carbonaceous material reveal any trace of the original internal organization we can compare it with the search image that we have for the internal structure of the leaf. For non-paradigmatic assemblages such a logical framework is not available either because an extant analogue cannot be readily identified, or because the fossils display features that are common to several living groups. As a consequence, observed structures cannot be easily or directly compared to known structures of an extant group. This precludes even the most basic systematic assignments, which in turn affects interpretation of the structures, creating a logical deadlock.

Seen in this light, attempts to characterize and classify organisms of non-paradigmatic biotas are akin to trying to understand alien life forms from another planet. However, compared to a hypothetical, but live alien biota, non-paradigmatic fossil biotas feature an added aggravating complication in the form of alterations that affect the structure of organisms due to the diagenetic processes associated with different modes of
fossilization. I nevertheless argue that, rather than rendering non-paradigmatic biotas unattractive and pushing them to the periphery of our scientifically explorable universe of knowledge, this situation makes them particularly attractive objects of investigation, for two distinct reasons. One is philosophical, with practical ramifications: non-paradigmatic biotas challenge the very bases of the way we make systematic assignments in paleobiology, and their study can contribute to reshaping fundamental patterns of inference that operate in understanding enigmatic traces of life from this planet or elsewhere. The other important reason for investigating non-paradigmatic biotas resides in the fact that they are associated with pivotal, but not very well understood, moments in the evolution of life (e.g., Ediacaran biotas and the radiation of metazoans). Therefore, they very likely hold crucial information that could lead to a better understanding of such moments, provided the potential logical stalemate built into their very nature can be broken. It is proposed that that the key to the eventual understanding of non-paradigmatic biotas resides in (i) careful and comprehensive characterization of the fossils, coupled with (ii) detailed comparative actualistic work.
2. SEQUEL TO INTRODUCTION: PLANTS AND LAND PLANTS

How do we define plants? As Stewart and Rothwell (1993) carefully acknowledge, botanists do not agree as to what should be included in the plant kingdom. Moreover, few authors, even among those working at the boundaries of the plant kingdom, explicitly define plants and, as is often the case when definitions are avoided, this favors a rather loose usage of terms. All of these result in a great amount of confusion, especially when tackling such a problem as the origin of land plants, because if there is no consensus on what are the *plants*, what then are the *land plants*? A good illustration of this situation is provided by Gray and Boucot’s (1977) definition of land plants, as photosynthetic organisms that customarily live on land and whose relations are to other *plants* living on land. Accepted by Graham (1993) as a reasonable working definition, it clearly shows that land plants can only be as well defined as plants, as a group, are defined.

As my work deals with some very early terrestrial organisms, I deemed it necessary to have an overview of the current understanding on this issue. Without trying to give a complete account of the evolution of thinking on the definition of plants, and without trying to encompass the whole range of current ideas on the subject, in the following I show a few ways of understanding the concept of *plant*. This selection is the result of a clearly directed choice, and reflects the focus of my readings on works dealing with the colonization of land. In doing this, I am also trying to find out what the different authors see as *land plants*. 
Probably one of the most popular college-level textbooks on general botany in the United States today, Raven et al.’s “Biology of Plants” (1999) describes plants as eukaryotic photosynthetic organisms adapted for a life on the land, multicellular, with cells containing vacuoles and surrounded by a cellulosic cell wall. However, by including only bryophytes and vascular plants in the group, the authors implicitly equate plants with embryophytes. The immediate outcome is that land plants are also only embryophytes. They nevertheless point out that green algae are clearly very closely related to plants, that the Coleochaetales and Charales among the Charophyceae most closely resemble plants, and that plants were probably derived from an extinct charophycean. Ligrone et al. (2000) adopt the same view, equating plants and land plants to embryophytes, as do Graham and Wilcox (2000).

At the opposite pole, Kenrick and Crane (1997) in their book on the origin and early diversification of land plants, follow the ideas of Copeland (1956) giving a very inclusive definition of plants. In their view plants (Chlorobiota) include green algae (Chlorophyta sensu lato) and embryophytes. But at the same time they equate land plants with embryophytes, thus leaving all other plants that live on land (e.g., soil green algae, chlorophycean lichen symbionts) in a state of systematic conflict. Bateman et al. (1998) do not define the plants, but their discussion of the relationship between land plants and green algae, specifically the Charophyceae, implies that they follow the same idea of land plant-embryophyte equivalence.

One of the foremost students of land plant phylogeny today, Graham (1993) in her book on the origin of land plants carefully discusses the definition of land plants. By agreeing that terrestrial algae having acquired unambiguous adaptations to land can be
described as land plants, Graham implies that *plants* are more than embryophytes. However, she considers that charophyceans and embryophytes form a clade, and therefore when she talks about the charophycean ancestor of plants this implies that plants are either just embryophytes, or embryophytes plus charophyceans, or embryophytes plus some of the charophyceans, all of which contradict the implication above, that plants include embryophytes plus terrestrial algae. Aside from this, for *land plants* Graham recognizes the difficulty of defining the concept when faced with the dichotomy between modern (green) algae and embryophytes. Depending at what level in the charophycean-embryophyte clade the transition to terrestrial environments occurred, land plants could designate anything between embryophytes plus some of the charophyceans, on one hand, and just some of the embryophytes, on the other hand. She considers there is basis for speculation that the first embryophytes were inhabitants of shallow water rather than terrestrial habitats, in which case just some of the embryophytes would qualify as land plants.

In their work on early embryophytes, Graham and Gray (2001) talk about embryophytic land plants. This implies that they assume the existence of non-embryophytic land plants. Therefore land plants, and hence plants, are equivalent to embryophytes plus some other group(s). In the same line of thought, Renzaglia et al. (2000) equate green plants to streptophytes, the group defined by Jeffrey (1982) as charophyceae plus embryophytes.

Just considering these few examples it is clear that we are far from reaching a consensus in the definition of the concept of plant. Because of this, different authors refer to different entities when talking about land plants. Fortunately, aside from this
principally nomenclatural problem, groups of real organisms, extant and fossil, exist and have characters that allow us to study them and to infer their phylogenetic relationships, irrespective of what names we prefer to use in designating them. Keeping with this point of view, instead of trying to reach a debatable conclusion on the subject, at least for the purpose of this text I will use the more general phrases “terrestrial biotas” or “terrestrial organisms” to designate non-animal organisms living on land and the systematic affinities of which are unresolved.
3. PREVIOUS HYPOTHESES ON EARLY LAND PLANTS

3.1. ORIGIN OF EMBRYOPHYTES

For those who equate land plants to embryophytes, two main competing hypotheses, their roots in the nineteenth century, have been put forward to explain the advent of the embryophytes. Both stemmed from the necessity to understand the phylogeny of bryophytes as compared to vascular plants. These two hypotheses can be regarded as the first important step in our quest to understand the colonization of land by life, and Graham (1993), Stewart and Rothwell (1993), and Kenrick and Crane (1997) give extensive accounts and references on the historic development of both hypotheses. I will therefore limit myself at stating the core ideas and principal implications of each of them.

The Homologous Hypothesis is also known as the transformation hypothesis and was elaborated mainly through the thinking of Celakovský, Pringsheim, Bower, Potonié, Hallier, Tansley, Fritsch and Church. According to the homologous hypothesis, vascular plants and bryophytes evolved from algal ancestors with a diplobiontic life cycle (two multicellular phases) and isomorphic alternation of phases (such as the extant *Ulva*). In this perspective, bryophytes and vascular plants represented two different lineages evolved from the same or different algal ancestors (and therefore the hypothesis does not exclude polyphyly of embryophytes), the bryophytes by reduction of the sporophyte and retention of it on the gametophyte, and the vascular plants by progressive reduction of the gametophyte.
The Antithetic Hypothesis, also known as the interpolation hypothesis, was developed largely by Celakovsky and Bower. This hypothesis proposes that the ancestor of bryophytes and vascular plants was an alga with haplobiontic life cycle (multicellular gametophyte and unicellular sporophyte represented by the zygote, such as those known in extant *Chara* or *Coleochaete*). Then bryophytes and, later on, polysporangiophytes evolved by delay in meiosis and intercalation of mitotic divisions in the sporophyte (leading to multicellular sporophytes), and further elaboration and independence of the sporophyte. It follows from this that if we take parsimony for a valid criterion, embryophytes are monophyletic, with bryophytes paraphyletic to the polysporangiophyte clade.

Extensive ultrastructural studies on green algae and embryophytes in the second half of the twentieth century, such as those of Stewart and Mattox (1975, 1978), started clarifying the phylogenetic relationships among different groups of green algae. This resulted in more solid evidence supporting earlier suggestions by Pringsheim, Bower, and Jeffrey that the charophycean algae and, in particular, the Charales and Coleochaetales, are more closely related to embryophytes than to other green algal groups. As both the Charales and the Coleochaetales have haplobiontic life cycles, these findings supported the antithetic theory for the origin of embryophytes. With the development of numerical cladistics as a method of assessing phylogeny in the same period, these phylogenetic ideas, as well as the two hypotheses, came to be tested. A plethora of studies using morphological, ultrastructural, and molecular data, or combinations of these looked into the phylogeny of algae and basal embryophytes. Graham (1993), Kenrick and Crane (1997), and Graham and Wilcox (2000) give extensive references and detailed accounts.
on the history of the research and the evolution of thought. The present state of knowledge in the field is best summarized by Graham and Wilcox (2000). Corroborating data developed by Mishler et al. (1994), they propose two major evolutionary lineages of green algae, one including the ulvophyceans, trebouxiophyceans, and chlorophyceans (the UTC clade), and the other comprising the charophyceans and the embryophytes (the CE clade). A basal polytomy including these two major lineages and prasinophyceans reflects the present lack of understanding of relationships among modern prasinophyceans. In this respect it is very important to note that Graham and Wilcox (2000) point out that the two clades (UTC and CE) are currently thought to have evolved from distinct types of unicellular flagellates related to modern prasinophyceans which are very likely a polyphyletic group. However, the CE clade, which is well supported by the latest ultrastructural (Cook et al., 1997), cytokinetic (Brown and Lemmon, 1997), and molecular data (Graham, 1993; Mishler et al., 1994; McCourt et al., 1996; Lewis et al., 1997; Bhattacharya and Medlin, 1998), is in accord with the tenets of the antithetic hypothesis.

If the CE clade as a whole is quite well supported, relationships within it and within the embryophyte clade are less well resolved. Different studies point at either Coleochaete, the Charales, or a clade comprising both Coleochaete and the Charales, as the sister group to embryophytes, and no conclusive opinion has been reached as yet on the issue (Graham and Wilcox, 2000). The relationships between the different bryophyte lineages and the fossil and extant polysporangiophytes within the Embryophyta are another subject of debate. Even though the embryophyte clade is well supported, it is not clear which of the bryophyte lineages is basal in the clade, and which lineage (or
lineages) represents the sister group to polysporangiophytes. Different studies resulted in
more or less conflicting results, and Goffinet (2000) recently reviewed all this work (and
gives an extensive list of references), showing how different are the results of analyses
based on very diverse types of data. However, in the conclusions he suggests that the
most recent phylogenetic reconstructions of relationships among extant embryophyte
lineages converge toward a hypothesis where hornworts are the most basal lineage, while
mosses and liverworts form a clade sister to the polysporangiophytes.

Supporting a sister group relationship between extant embryophytes and
charophyceans, the results of modern cladistic analyses (e.g., Mishler et al., 1994;
McCourt et al., 1996; Cook et al., 1997; Brown and Lemmon, 1997; Lewis et al., 1997;
Bhattacharya and Medlin, 1998) provide the theoretic basis for hypotheses proposing,
more or less explicitly, the evolution of the basic embryophytic characters in groups of
freshwater charophyceans. Continued research is presently dedicated to studying the
extant charophyceans and embryophytes in order to further test these hypotheses.
However, even if it were demonstrated to represent the true phylogeny of the
embryophytes, the hypothesized relationship would still leave the early phases of
embryophyte evolution unresolved. Also, such questions as what was the composition of
early terrestrial biotas; what were the ecological relationships among the constituents of
these communities; what were the systematic relationships and the ecology of early
terrestrial organisms; from what type of organism did the embryophytes evolve, remain
unanswered. As stressed by almost every author who has approached the phylogeny of
embryophytes, all of these problems would have probably been overridden if fossils of
the earliest embryophytes were found. Unfortunately, the fossil record is wanting of very
early embryophytes, and the earliest forms known to us are already too evolved to shed light onto the issue.
3.2. SYMBIOSIS

For those who equate plants to the whole green algal clade, if indeed it is a clade, the earliest land plants could have been terrestrial green algae. There seems to be a quite wide agreement on the fact that photosynthetic autotrophs as primary producers were among the first organisms to colonize the land. Yet we know almost nothing about the level of organization or the systematic position of these early terrestrial colonizers. Several authors have suggested that terrestrial microorganisms were already present in the Precambrian (Barghoorn, 1977; Siegel, 1977; Campbell, 1979; Gay and Grandstaff, 1980). Golubic and Campbell (1979) proposed that prokaryotic communities may have colonized the land surface as long ago as the early Precambrian, and Wright (1985) considered that the land surface may have been initially colonized by preadapted intertidal organisms, in the early Precambrian. However, to date, most of the evidence for life in terrestrial environment prior to the earliest known polysporangiophytes (Cooksonia, upper Early Silurian) is largely circumstantial and will be discussed later.

Somewhat aside from the mainstream thinking in terms of antithetic vs. homologous hypotheses, a quite different point of view as to what types of organisms formed the earliest terrestrial biotas was proposed by Jeffrey (1962) and subsequently much elaborated by Pirozynski and Malloch (1975). Based on the widespread occurrence of the mycotrophic habit in extant embryophytes, Jeffrey (1962) was the first to suggest that the evolution of fungus-alga symbioses might have played a role in the early stages of the colonization of land. In his view these early associations, later to evolve into mycotrophic vascular plants, would have been dominated by the (chlorophycean) alga
that used the more efficient fungal hyphae for absorption and conduction of nutrients that such early associations. Even though he admitted the possibility of algae already colonizing terrestrial environments before the advent of embryophytes, he excluded these algae from the potential ancestors of the embryophytes. Jeffrey envisioned at least the early phases of the alga-fungus association as developing with the “feet in freshwater”.

Initially unaware of Jeffrey’s novel idea, but following a similar line of thinking, in a seminal paper Pirozynski and Malloch (1975) took the next step forward and postulated that it was mycotrophism that made terrestrial plant life and evolution possible. As Jeffrey’s ideas previously, their hypothesis was inspired by the quasi-ubiquity of fungal symbionts in the form of mycorrhizae in extant embryophytes, and on examples from the fossil record. They thought that if most present-day plants need fungal associations for survival, it is unlikely that organisms no better adapted to life in the terrestrial environment could have arisen and evolved without an even greater dependence on fungi. Their contention was that the colonization of land and the evolution of plants (and by plants they probably referred to embryophytes) was possible only through the establishment of symbiotic associations of semi-aquatic algae and aquatic fungi.

Pirozynski and Malloch suggest that the first alga-fungus associations formed in an aquatic or semi-aquatic environment and compare them to present-day associations between filamentous algae and water molds (Spirogyra or Vaucheria and Pythium). For the photobiont in the ancestral association they prefer charophyceans. For the mycobiont, even though they talk about oomycetes, they refer in fact to what are today arbuscular mycorrhizal fungi, assigned later by Pirozynski and Dalpé (1989) to the family
Glomaceae of the Zygomycetes, and recently grouped into their own phylum, Glomeromycota (Schussler et al., 2001). As for the type of association they assume that the ancestral one was an endotrophic association, but at the same time a loose one, the fungus being not incorporated into the algal spores. Such associations would have resulted in advantages with respect to survival in the terrestrial environment. Desiccation was avoided by production of oils as a result of the photobiont-mycobiont interaction, as in the associations between fungi and the gametophytes of the liverwort *Pellia* and of *Lycopodium*. These associations were also capable of more efficient uptake and assimilation of nutrients (such as nitrogen and phosphorus), through the mycobiont.

Pirozynski and Malloch’s (1975) hypothesis is extremely important and brings a fresh breath to the thinking on embryophyte origins by introducing a novel concept of terrestrial colonist and proposing fungal associations as an obligate step in the evolution of embryophytes. The association involving two symbiotic components, the alga and the fungus, is seen as better adapted for the colonization of land than each of its components individually. They even go so far as to propose that the association was so necessary that the first plants could be considered as partly composed of a fungus. Discussing this hypothesis in her book on the origin of land plants, Graham (1993) considers there is not enough evidence in support of it, but nevertheless agrees that symbiotic associations between early land plants and fungi might have been frequent.
3.3. AQUATIC OR TERRESTRIAL?

All of the above hypotheses have something in common: they all envision aquatic multicellular algal ancestors for the lineages leading to embryophytes. Most of the nineteenth century hypotheses were centered on origin from marine algal ancestors. With the introduction of charophyceans as possible algal ancestors to the embryophytes, the focus of evolutionary theories switched to the freshwater environments. Jeffrey (1962) for example, was among those to dismiss the idea of direct colonization of the land by littoral intertidal algae. Although he admitted the presence of some soil algae before the advent of embryophytes, Jeffrey proposed the origin of embryophytes from chlorophyceans associated with fungi, via a freshwater transition stage. Graham (1993) also dismissed the possibility of land plants evolving from seaweeds on beaches, and instead proposed that land plants arose most directly from freshwater charophyceans, and therefore implicitly at the margins of freshwater basins/streams. She dismissed the hypothesis that some charophyceans might have passed through one or several phases of terrestrial life, based on evidence that freshwater environments rather than terrestrial selection pressures influenced the development of the advanced/derived morphologies and reproductive features of charophytes. Also, Graham (1993) considered the presence of the embryophytic habit (which she equated to matrotrophy, the retention on and nutrition of the zygote by the gametophyte) in charophyceans evidence that first embryophytes inhabited shallow water. In contrast, gametangia are considered to have evolved after matrotrophy, more likely as a result of terrestrial selection pressures. Later on, Renzaglia et al. (2000) viewed the transitional streptophytes poised at the extremity
of the terrestrial landscape (probably already inhabited), and therefore having evolved from aquatic forms. Graham and Gray (2001) suggested that the transition to land of embryophytes from charophycean ancestors most likely occurred in ephemeral freshwater habitats. Even Pirozynski and Malloch’s (1975) bold hypothesis suggested that the first alga-fungus associations formed in an aquatic or semi-aquatic environment.

Another important change of perspective in approaching the origin and evolution of early terrestrial biotas is that proposed by the hypotheses of Stebbins and Hill (1980). If the great majority of authors approaching the origin of embryophytes agreed upon the presence of some form of photoautotrophic life on land considerably earlier than the advent of the earliest embryophytes, all of them envisioned the latter as evolving from marine or freshwater aquatic, or semi-aquatic algae. Contrary to this line of thinking, Stebbins and Hill (1980) dismissed the dogma that land plants are derived directly from aquatic algae. Instead, they introduced the novel idea that the algal lineage leading to embryophytes started with unicellular forms that inhabited aquatic interstices in moist soils, and continued with derivatives of these which acquired multicellularity also in association with a terrestrial rather than an aquatic life. According to Stebbins and Hill, embryophytes are derived from charophyceans, but not from any of their modern representatives. Suggesting that this evolution occurred on land, on moist soil surfaces, rather than in the water, they implied that extant charophyceans represent secondarily aquatic forms.

In very general terms, Stebbins and Hill’s (1980) ideas were rooted in the hypothesis that adaptations specific to life on land are much more likely to have developed as a result of selective pressures of the terrestrial environment, rather than due
to evolution in the aquatic environment. In support of their hypothesis, Stebbins and Hill (1980) brought several arguments. (1) The absence of zoospores in Zygnematales, Charales and some species of *Klebsormidium* would be best explained by derivation of this group from terrestrial ancestors. Zoospores being most efficient as form of asexual reproduction in water, their loss would not be disadvantageous for algae living in terrestrial habitats. (2) Conjugation as the mode of sexual reproduction in Zygnematales would represent a remnant of past terrestrial existence, characterized by a lack of water to facilitate movement of motile gametes. All other aquatic green algae in which sexual reproduction is known produce motile gametes. They compare this situation to that observed in Phycomycetes, the terrestrial groups of which have evolved a form of conjugation similar to that known in Zygnematales, whereas aquatic forms produce motile gametes. (3) A three-dimensional plant body (as known in *Coleochaete* and Charales) is more likely to have evolved as a result of terrestrial selective pressures, because it would have had a higher adaptive value on land by conferring resistance to strong light and drought (buffering them through several cell layers). (4) The different charophycean lineages are considered long branches resulting from numerous extinctions, based on the great differences among these lineages. Stebbins and Hill considered that this would be best explained by evolution in a very dynamic environment, i.e. the terrestrial environment, that favors higher rates of evolution, and more frequent radiations and extinctions than the less dynamic aquatic environment. For comparison, they suggested that chlorophycean lineages, having evolved in the stable aquatic environment, show a lesser amount of divergence. (5) Two of the main adaptations for plant life on land, resistance to desiccation and the development of support tissues, could not have
been triggered in aquatic algae because they are disadvantageous to life in water. Cuticle in the aquatic environment would restrict the exchanges between the organism and the surrounding medium (aquatic algae and even the submerged parts of secondarily aquatic angiosperms don’t have a cuticle). Rigid support tissue, including lignified vascular tissue, would greatly reduce the flexibility required for life in water. In other words for larger, multicellular aquatic algae to colonize the land, they would have needed to already have developed these adaptations (among others), but developing them while still in the aquatic environment would have been disadvantageous. The larger and more complex an aquatic alga, the more reduced would have been the likelihood of it colonizing land.
3.4. SUMMARY

Starting with the earliest coherent hypotheses of the nineteenth century, the main stream of thinking in terms of the colonization of land was focused on explaining the advent of vascular plants from marine algae. It is in this context that the two competing hypotheses, the homologous hypothesis (1a), and the antithetic hypothesis (1b) were advanced. With the accumulation of evidence for embryophyte monophyly and for a sister group relationship between the embryophytes (i.e., bryophytes plus vascular plants) and some of the charophytes, the focus of evolutionary hypotheses switched toward an aquatic origin of embryophytes from freshwater charophycean algae (2). A change of perspective was introduced by the ideas of Pirozynski and Malloch (1975) on the crucial role played by fungal associations in the colonization of land by photoautotrophs (3). But even their hypothesis envisioned the early phases of this evolution taking place in an aquatic or semi-aquatic environment. Stebbins and Hill (1980) were the first to propose the origin of embryophytes in terrestrial charophyceans, which themselves derived on land from unicellular green algae (4).
4. PRESENT STATE OF KNOWLEDGE OF EARLY TERRESTRIAL BIOTAS

The fossil record as we know it today provides abundant evidence that by the Early Devonian terrestrial ecosystems were varied and had reached a high degree of complexity. Several embryophyte lineages were already present and diversified: the rhyniophytoids and rhyniophytes, the trimerophytes, the zosterophylls and the lycophytes. Edwards (2000) considered “Lycophytina sensu lato” a separate lineage, probably to accommodate Baragwanathia as representing the lycophyte lineage already diverged from the zosterophylls. Quite expectedly, these ecosystems also included highly diversified fungal and animal components (Taylor and Taylor, 2000; Shear and Selden, 2001). On the other hand, the microfossil record of terrestrial biotas goes much further back, into the Middle Ordovician, or even earlier. Due to these characteristics of the fossil record, in reviewing the present state of knowledge of early terrestrial biotas, I will focus mainly on the period of time preceding the Devonian, and look at the Ordovician and the Silurian. I will also discuss earlier circumstantial evidence that relates to life in the terrestrial environment.

Photosynthetic organisms in the form of chroococcalean and oscillatorialean cyanobacteria are known in the fossil record from the oldest microbial communities that occur in water-laid deposits older than 3 billion years (Schopf, 2000). Even though this record is far from complete, it shows a good continuity of the cyanobacterial lineage and further advent of photosynthetic eukaryote lineages in the aqueous realm throughout the Archaean, Proterozoic, and early Phanerozoic eons (Knoll, 1992, 1994; Schopf, 2000). Our understanding of the colonization of land is far less complete due to a paucity of
reliable data concerning the very first phases of this crucial event of the evolution of life. Photosynthetic autotrophs as primary producers were certainly among the first organisms to colonize the land. Yet we know little about the level of organization or the systematic position of these early terrestrial colonizers. Several authors have suggested that terrestrial microorganisms were already present in the Precambrian (Barghoorn, 1977; Siegel, 1977; Campbell, 1979; Gay and Grandstaff, 1980). Golubic and Campbell (1979) proposed that prokaryotic communities may have colonized the land surface as long ago as the early Precambrian, and Wright (1985) considered that the land surface may have been initially colonized by preadapted intertidal organisms, in the early Precambrian. More recently, Watanabe et al. (2000) presented geochemical evidence in support of the existence of terrestrial ecosystems 2.6 billion years ago, from Archaean paleosols of South Africa.

In terms of direct evidence, the earliest known terrestrial organisms are represented by the filamentous microfossils of uncertain affinity reported by Horodyski and Knauth (1994) from 1.2 billion and 800 million year old rocks in California. Between these and the earliest known larger plant fragments of the Late Silurian, the fossil record of terrestrial photoautotrophs is represented by dispersed remains of putative or certain land plant origin starting in the Middle Ordovician (Strother et al., 1996; Edwards, 2000; Wellman and Gray, 2000): cryptospores, sheets of cells or fragments of “cuticle”, and a variety of smooth and ornamented tubes.
4.1. THE DISPERSED MICROFOSSIL RECORD

Dispersed microfossils are the earliest remains assignable to terrestrial biotas known in the fossil record. They are traditionally included in three main categories: (1) cryptospores and spores, (2) fragments of cuticle with cellular patterns and fragments of cellular tissue, (3) and tubes (smooth or ornamented/banded). The term cuticle is used here with the same meaning as defined by Chaloner et al. (1974), that is, in the broad sense of an outer resistant covering. In addition to the three main types of dispersed microfossils I will also discuss the fossil record of fungal spores and hyphae which potentially represent a part of the fossil record of early terrestrial biotas. Figures 4.1 and 4.2 show the first occurrences and stratigraphic ranges of different types of dispersed microfossils, compiled from Pratt et al. (1978), Sherwood-Pike and Gray (1985), Edwards (1993), Strother et al. (1996), Edwards et al. (1998), Edwards (2000), Redecker et al. (2000), Wellman and Gray (2000), Kotyk et al. (2002), Tomescu and Rothwell (2004), and references therein.

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, and they have been compared to a wide range of fossil and living groups by different authors (e.g., Edwards, 1982, 1986; Gray and Boucot, 1977; Banks, 1975a, b; Kroken et al., 1996; Kodner and Graham, 2001; Graham and Gray, 2001; Graham, 2002; Graham et al., 2002). However, to date 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 based on (1) their resilience to degradation, and on (2) the fact that in some cases they have been recovered from continental (fluvial) deposits. Resilience 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 limited to terrestrial organisms. Acritarchs, dinoflagellates, prasinophyceans and other algal cysts, chitinozoans, fungal spores, and eurypterid cuticle, among others, are also resistant to palynological extraction techniques. This suggests that resilient 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 in some instances cryptospores, tubular fossils and cuticle-like fragments have been recovered from fluvial deposits (e.g., Wellman et al., 2003) can be, and has been, used as evidence for their origin in non-marine organisms. However, their dispersed nature precludes unequivocal attribution to organisms occupying specific continental environments (i.e., freshwater vs. terrestrial).
4.1.1. Cryptospores and Spores

Tetrads, dyads, and monads, naked or enclosed within a laevigate or variously ornamented envelope, in which case they are also called “fused”, are known as cryptospores. Termed cryptospores in order to differentiate them from embryophyte spores in a period when their systematic affinities were debated, they are now widely accepted as direct evidence for the presence of terrestrial embryophytes (Strother, 2000; Edwards and Wellman, 2001; Graham and Gray, 2001). Until recently the cryptospore stratigraphic record started in the Llanvirnian (Middle Ordovician) (Strother et al., 1996). However, Strother (2000) and Strother and Beck (2000) report cryptospore monads, dyads, and tetrads, naked or enclosed in an envelope, from Middle Cambrian deposits of Arizona and Tennessee. Between the Middle Cambrian and the Llanvirnian (early Middle Ordovician), no other cryptospore assemblages with tetrads and dyads are known. Strother (2000, p. 5) also describes “probable trilete spores” from the Middle Cambrian (Figures 4.1, 4.2) locality in the Rogersville Shale of Tennessee. This suggests that embryophytes were present much earlier than previously documented by macrofossil evidence, and potentially sets a minimum age for the earliest embryophytes, 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. Aside from this very early and as yet equivocal occurrence, the earliest trilete spores are known from the Llanvirnian.
4.1.2. Fragments of Cuticle and Cellular Tissue

Anisomorphic, astomatous cuticles with a reticulum of flanges showing no preferred alignment (Edwards and Wellman, 1996) are also known from the Llanvirnian on (Figures 4.1, 4.2). Such cuticles were initially described by Lang (1937) in relation to the thalloid organism *Nematothallus*, but study of Lang’s material by Strother (1993) concluded that these cuticles were actually not attached to the lectotype. They were not observed as parts of other *Nematothallus* species erected by Strother (1988). Similar cuticles are recorded from thalloid Devonian megafossils of uncertain affinity (*Spongiophyton, Protosalvinia*) (Edwards and Wellman, 1996). Edwards (1982), Edwards and Rose (1984), and Edwards (1996) thoroughly described, classified, and named such dispersed cuticles, but the generic name of *Nematothallus*-type cuticles is still used sometimes to refer to this type of dispersed remains. The resilience of these cuticles has been used to suggest that they might have represented adaptations for survival in terrestrial habitats, but probably for organisms other than plants, as preliminary chemical analyses provide evidence against similarities with fossil plant cuticles (Edwards and Wellman, 2001).

Fragments of cuticle unequivocally assignable to higher land plants are known as early as the Wenlockian (Silurian). They consist of fragments displaying well defined, rectangular or lenticular cellular patterns, occasionally with attached spores, that derive from sporangia (sporangial cuticle), and of fragments showing aligned cells and stomata (starting in the Pridolian), derived from axial fossils (Edwards and Wellman, 2001).
Fragments of cellular tissue have a much longer stratigraphic record, being present in the Neoproterozoic (Samuelsson and Butterfield, 2001). These authors describe them as sheet-forming spheroids, whereas Strother et al. (1996) report them from the Middle Ordovician as clusters of spore-like cells. The origin of the fragments of cellular tissue is uncertain and when discussing it one should certainly take into account a wide range of organisms, including aquatic, marine organisms. Tomescu and Rothwell (2002) describe fragments of cellular tissue at least two cells layers thick from Llandoverian sediments preserving compression-impression mesofossils compared to liverwort or lichen appendages and containing also ascomycetous spores. Based on these co-occurrences, they compare the tissue fragments to algal or plant parenchymatous tissue, or fungal pseudoparenchymatous tissue.

4.1.3. Tubular Microfossils

Smooth tubular structures are known starting with the Ashgillian, whereas ornamented tubes appear in the Llanvirnian (Wellman and Gray, 2000), and tubes with internal banded thickenings are known from the Llandoverian (Edwards and Wellman, 2001) (Figures 4.1, 4.2). Smooth tubes of equal size or forming two size classes, and sometimes also internally banded tubes, occur in the enigmatic organisms *Nematothallus*, *Prototaxites*, *Nematasketum*, and *Nematoplexus*. Although they strikingly resemble tracheids, internally banded tubes differ from tracheids in that their wall between the thickenings is much thicker than in a tracheid and appears to have the same composition as the thickening (Edwards and Wellman, 1996). Citing evidence of banded tubes
growing on or within tissues of higher land plants, Edwards and Wellman (2001) hypothesized that they might represent pathogens or decomposers of the plants. Banks (1975a and b), Gray and Boucot (1977), Pratt et al. (1978), Gray (1985), Wellman and Gray (2000), Edwards and Wellman (2001), and Graham and Gray (2001), thoroughly discuss and review the possible origins of tubular structures, and particularly banded tubes.

The earliest tracheids are known from the late Ludlowian (Edwards and Davies, 1976). They were described from unbranched axes occurring in combination with dichotomously branching axes sometimes bearing *Cooksonia*-type sporangia. Although the stratigraphic record of genus *Cooksonia* extends to the late Wenlockian (Edwards et al., 1983), the age of the earliest *Cooksonia* specimen with *in situ* observed tracheids is much younger: Gedinnian (Early Devonian) (Edwards et al., 1992).

### 4.1.4. Fungal Hyphae and Spores

In a previous review of the fossil record of the Glomaceae, Pirozynski and Dalpé (1989) considered the earliest record of glomacean fungi, although somewhat equivocal, to be from the Silurian of Estonia (by Locquin, 1981). Unseptate hyphae and spores assigned to glomalean fungi are described from Llandeilian (Middle Ordovician) rocks of Wisconsin by Redecker et al. (2000) (Figures 4.1, 4.2). They compared the fossils to modern arbuscular mycorrhizal fungi (Glomales, Zygomycetes), suggesting that these fungi may have played a crucial role in facilitating the colonization of land by plants. This report represents the earliest occurrence of dispersed remains assignable to the group
of mycorrhizal fungi, and also the earliest occurrence of dispersed remains assignable to a group of terrestrial fungi. Based on this occurrence of mycorrhizal fungi long before the first known occurrence of vascular plants, Redecker et al. (2000) suggested that these fungi were participating in either mycorrhiza-like associations with non-vascular plants, or in *Geosiphon*-like associations with cyanobacteria.

Pratt et al. (1978) report the earliest septate filaments of fungal affinity, occurring as dispersed fragments or interwoven into dense mats, from the Llandoverian (Early Silurian). Some of the filaments display flask-shaped branches and the authors compare them to those seen in extant Fungi Imperfecti, interpreting them as evidence for the presence of higher fungi. Sherwood-Pike and Gray (1985) describe septate, branched hyphal filaments, and also multiseptate spores assignable to the ascomycetes, from the Late Silurian (Ludlovian) of Gotland, Sweden. Tomescu and Rothwell (2002) have described the earliest multiseptate ascomycete spores from the Llandoverian of Ohio.

Permineralized fungi are known from the Early Devonian Rhynie Chert. They include chytridiomycetes (Taylor et al., 1992, 1994), ascomycetes (Taylor et al., 1999), arbuscular mycorrhizal fungi (Taylor et al., 1995a), and even lichen-like organisms (Taylor et al., 1995b, 1997).
4.2. THE MESO- AND MACROFOSSIL RECORD

Embryophytes are the only group of non-animal terrestrial organisms that exhibit features directly pointing to an aerial living environment – stomata. Furthermore, all modern embryophytes are terrestrial or secondarily aquatic. For these reasons, meso- and macrofossils have been interpreted as terrestrial because they either had been preserved in terrestrial sediments, or they had an external morphology reminiscent of embryophytes, or both. The axial habit of a fossil had been sometimes considered sufficient to place it in the terrestrial fossils if it occurred in concurrence with recognizable embryophyte fossils, even in marine settings (e.g., Edwards and Feehan, 1980). However, the earliest known embryophytes are relatively highly derived (polysporangiophytes), and older dispersed microfossils assignable to embryophytes give no information about the living environments of less derived embryophytes. Therefore, in my opinion, the only ways to ascertain a terrestrial embryophyte are to document stomata, or to find it in situ, in terrestrial deposits.

4.2.1. Embryophytes and Polysporangiophytes

The earliest occurrence of unequivocal embryophytes, reported from late Wenlockian strata (Figures 4.1, 4.2) in Ireland consists of polysporangiophytes (Edwards and Feehan, 1980; Edwards et al., 1983). The synapomorphy that defines polysporangiophytes is the presence of axial, branching sporophytes that bear multiple sporangia (Kenrick and Crane, 1991). The group includes vascular plants (tracheophytes), as well as extinct non-vascular taxa. In the late Wenlockian of Ireland
dispersed fertile and sterile dichotomously branching axes, some of them assignable to
genus *Cooksonia*, are preserved in marine sediments. Genus *Cooksonia* is also linked to
the earliest known occurrences of tracheids and vascular plants (Edwards and Davies,

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 comprehensive review of the fossil record of bryophytes by Krassilov and
Schuster (1984) showed that the only taxon in this group that is known from pre-
Devonian rocks is *Sporogonites*. Reported from the Late Silurian (Walhalla Group,
Victoria, Australia), *Sporogonites* has an uncertain systematic position within the
bryophytes due to the combination of characters it exhibits, which does not meet the
criteria for assignment to any of the extant bryophyte groups. Krassilov and Schuster
(1984) also mentioned genus *Prahepaticites* described from the Late Silurian of
Ukraine, noting that the relationships of the fossil to bryophytes, or even land plants, are
ambiguous. Studying the ultrastructure of the spores of *Parka decipiens*, Hemsley (1989)
compared them to liverwort spores, but made no inference based on this as to the
affinities of this problematic fossil.
Problematic carbonaceous tubes lacking internal anatomy (*Eohostimella*) were described by Schopf et al. (1966) from nearshore marine deposits of late Llandoveryan age in Maine. They interpreted *Eohostimella* as an erect, possibly terrestrial plant, and geochemical studies by Niklas (1976c) have suggested a vascular plant-like chemistry for these fossils. *Eohostimella* occurs in nearshore marine sediments and consists of carbonaceous tubes 1-2 mm in diameter and 1-2 cm long, devoid of any internal anatomy. The occurrence in marine deposits and the inconclusive morphology and anatomy of the fossils renders the placement of *Eohostimella* among the plants highly questionable.

Several other reports of lower Paleozoic land plant macrofossils are controversial, or subsequent research has shown these putative plants to represent different animal groups (Kenrick et al., 1999, and references therein).

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). By the end of the Ludlowian all of the main groups of polysporangiophytes are present. 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, it is not until the Early Devonian that we see the first record of a polysporangiophyte assemblage from unequivocally terrestrial deposits. The Lochkovian Brown Clee Hill and Targrove Quarry assemblages of the Welsh Borderland are described from fluvial sequences, but are thought to represent transported plant material (Edwards and Fanning, 1985; Edwards et al., 1994; Edwards, 1996). Before these, there are two reports of polysporangiophytes in allochthonous or at
least para-autochtonous assemblages from the Pridolian. The depositional environment of the Freshwater East (Dyfed, Wales) assemblage (Edwards, 1979) is interpreted as intertidal, whereas that of the Perton Lane (Hereford and Worcester, England) assemblage is considered fluvio-marine (Fanning et al., 1991). Although such assemblages 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.

To date, the Pragian-early Emsian Rhynie Chert biota remains the oldest known fossil community including embryophytes preserved in situ (Figures 4.1, 4.2). The plants were colonizing the floodplain and associated ponds of a river system, and the whole communities were fossilized by permineralization in silica provided by hot springs fed by a fault zone (Rice et al., 2002; The Rhynie Chert Research Group, 2002, http://www.abdn.ac.uk/~gmi265/profiles/rhynie/analogues.htm).

### 4.2.2. Nematophytes

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 (Figure 4.2). 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.

Fossil species assigned to the nematophytes are known from rocks as young as the Devonian. Upon describing the genus *Nematothallus*, Lang (1937) suggested the erection of class Nematothallales to include *Nematothallus* and the previously described *Prototaxites* (*Nematophyton*). *Prototaxites* has since been assigned to the fungi (Hueber, 2001; Boyce et al., 2004), but other taxa have been subsequently described and included in the nematophytes: *Nematasketum* and *Nematoplexus*. The feature that unites all these taxa is an internal anatomy consisting of tubes of different types and sizes. *Nematothallus* was originally described as thin, thalloid incrustations of variable shape, consisting of (1) tubes of two orders of width, (2) cuticle exhibiting a pseudo-cellular pattern (hence the much used phrases “*Nematothallus*-type cuticle”, or “nematophyte cuticle”), and (3) spores of various sizes. Because no unequivocal anatomical relationship between the three types of remains could be ascertained, Strother (1993) emended Lang’s diagnosis of the type species, *Nematothallus pseudo-vasculosa*, retaining only the bimodal tubular construction as diagnostic. Prior to this, Strother (1988) had erected the informal, presumably protistan, group Paraphyta to include the nematophytes.

The early- to mid-Llandoverian organisms of the Massanutten Sandstone of Virginia (Pratt et al., 1978) are the earliest macrofossils known from terrestrial (fluvial) sediments. However, although all studies approaching them (Pratt et al., 1978; Niklas and Pratt, 1980; Niklas and Smocovitis, 1983) recognized their terrestrial origin, they failed to recognize in them the earliest macrofossil assemblage, and as a consequence
overlooked the external morphology of the fossils to study directly the dispersed microfossils obtained by bulk maceration of the fossiliferous rocks. Based on the affinities of the dispersed microfossils, Pratt et al. (1978) assigned the thalloid fossils to the nematophytes considering them the oldest known non-marine, and probably terrestrial, plants. The two subsequent studies on the Massanutten Sandstone fossils (Niklas and Pratt, 1980; Niklas and Smocovitis, 1983) also referred to the remains as plants.

Another nematophyte occurrence (*Nematothallus, Prototaxites*) is reported from late Wenlockian to Ludlovian strata in the Bloomsburg Formation of Pennsylvania (Strother, 1988), which is roughly contemporaneous with the oldest *Cooksonia* (Figure 4.2). The Bloomsburg Formation represents fluvial (Hoskins, 1961; Epstein and Epstein, 1969; Faill 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 confidently characterize the depositional environment at the fossil locality, but current interpretations and the age of the rocks place these fossils among the oldest macrofossil occurrences of potentially terrestrial organisms.

**4.2.3. Algae**

Unequivocal terrestrial algae are unknown in the pre-Devonian fossil record. The only candidate for a terrestrial alga would be the photobiont of the lichen-like
Spongiophyton (discussed below), but its affinities are as yet unresolved, and it could represent an alga as well as a cyanobacterium.

The oldest known Charophyceans occur in the Late Silurian (Feist and Grambast-Fessard, 1991): Praesycidium siluricum represents a charophyte oogonium. By the Early Devonian charophytes oogonia show important diversity, and a permineralized charalean, Paleonitella, is known from the Rhynie Chert (Edwards and Lyon, 1983). The enigmatic Parka decipiens, known from the Late Silurian and Early Devonian has been compared to Coleochaete (Niklas, 1976a, 1976b). Similarities between the two include the thalloid morphology, the green algal-like chemical composition of Parka, and the reproductive structures. However, reviewing previous work on the affinities of Parka, Graham (1993) noted that there are also differences: the thallus of Parka is at least two cell layers thick, the reproductive structures of Parka contain a large number of spores as opposed to one oogonium/zygote in Coleochaete. Another difficulty in assessing the affinities of Parka is that the exact nature of the spores (meiotic vs. mitotic products) is not well understood because they lack the characteristic haptotypic marks. However, the fact that Parka produced resistant spores is generally taken as an indication of an adaptation to desiccation (Hemsley, 1994).

4.2.4. Fungi and Lichens

Unequivocal fungal macrofossils are unknown before the Devonian. The oldest fungal macrofossils were described from the Pragian-early Emsian Rhynie Chert. They include an ascomycete (Taylor et al., 1999), and a lichenized fungus of putative
zygomycete affinity (Taylor et al., 1995a, 1997). The fungal diversity revealed by the Rhynie Chert biota, which also includes chytrids and mycorrhizal fungi (Taylor et al., 1992, 1994, 1995b), correlates with the early occurrences of dispersed fungal microfossils suggesting that a high degree of diversity had been reached by fungi prior to the Devonian.

The only Silurian macrofossil occurrences of putative fungi are those of Prototaxites (Figure 4.2). The genus is reported by Lang (1937) from several Pridolian localities, but the earliest known occurrence is in the Upper Wenlockian and consists of axes assigned to Prototaxites by Edwards et al. (1983). Known mainly from the Devonian, Prototaxites is an axial fossil of considerable size (the largest known specimen is 17 ft long and 4 ft in diameter at the base) with the internal anatomy consisting of three types of hyphae. Strother (1988) reported fragments assignable to Prototaxites from the Bloomsburg Formation, at the Wenlockian-Ludlovian boundary. Considered by successive authors to represent conifer-like rotted wood, a lichen, an alga, and a fungus, Prototaxites has been assigned by Hueber (2001) to the fungi after thorough review of previous work and study of a large number of specimens. Hueber considered Prototaxites represented the sporophore of a saprobiic fungus possessing an extensive filamentous perennial soma.

The oldest occurrences of lichen macrofossils are in the Early Devonian. The Rhynie Chert produced Winfrenatia, a cyanolichen preserved as permineralizations (Taylor et al., 1995a, 1997). The photobiont of Winfrenatia is most similar to coccoid cyanobacteria of the Gloecapsa and Chroococcidiopsis type, whereas affinities of the mycobiont are closer to the Zygomycetes (Taylor et al., 1997). Spongiophyton, an
enigmatic Early and Middle Devonian fossil, has been previously interpreted as a lycopod, a potential phaeophycean alga, and a thalloid plant (Chaloner et al., 1974; Niklas and Chaloner, 1976, and references therein). Studying permineralized *Spongiophyton* material, Stein et al. (1993) proposed that in fact it represented a lichen with a branched tubular thallus consisting of a reticulate medulla of septate hyphae enveloped in a thick cortex perforated by pseudocyphellae. Comparing the short cup-shaped branches seen in *Spongiophyton* to apothecia, they also suggested that the mycobiont of *Spongiophyton* was an ascomycete.
4.3. THE FOSSIL RECORD OF TERRESTRIAL ANIMALS

Shear and Selden (2001) compiled a thorough review of fossil evidence for the presence of animals in early terrestrial ecosystems. The earliest unequivocal terrestrial animal assemblage is known from the Pridolian of Ludford Lane (England) and consists of several taxa. Here the animal remains, mixed with rhyniophytoid plant fragments, are found in tidal deposits. As in the case of fungal fossils, the systematic diversity of animals in the Pridolian (arachnids, centipedes, and scorpions) is consistent with older occurrences of trace and body fossils of putative terrestrial animal origin (Shear and Selden, 2001 and references therein), suggesting a diversification of land animals earlier than the Late Silurian. Putatively terrestrial animal trackways and dispersed fragments are known from earlier, Caradocian rocks of England (Johnson et al., 1994), and in the Llandoverian of Pennsylvania (Gray and Boucot, 1994). The available evidence is not conclusive as to whether these fossils represent terrestrial, amphibious or aquatic fauna. Occurrences of probable freshwater arthropods have been reported from Ordovician non-marine deposits (reviewed in Retallack, 2000).
4.4. INDIRECT EVIDENCE ON EARLY TERRESTRIAL BIOTAS

Several authors have suggested that terrestrial microorganisms were present in the Proterozoic. Wright (1985) proposed that the land surface may have been initially colonized by pre-adapted intertidal organisms early in Precambrian times. Campbell (1979) described organic-rich paleosols in the 2.4 billion year old Early Proterozoic Blind River Formation of Ontario and related them to the presence of prokaryotic soil crusts. More recently, Watanabe et al. (2000) presented geochemical evidence in support of the existence of terrestrial ecosystems 2.65 billion years old from Late Archean paleosols of South Africa. Similar evidence, in the form of organic carbon, was reported from the 2.45 billion year old Elliot Lake paleosols in Ontario (Gay and Grandstaff, 1980), and from the 2.78 billion year old Mount Roe paleosol in Australia (Rye and Holland, 2000). Studying 2.2 billion year old laterite profiles of the Hekpoort paleosol in South Africa, Beukes et al. (2002) presented evidence for the presence of abundant terrestrial biomass suggesting continent-wide microbial colonization of land.

Based on isotopic studies carried out on the Middle Proterozoic Mescal Limestone (Arizona), Beeunas and Knauth (1985) inferred that the subaerial environment was a biologically active zone (i.e., some form of ground cover was present) 1.2 billion years ago. The results of this study were considered controversial by Vahrenkamp and Rossinsky (1987), but later Horodyski and Knauth (1994) reported the earliest direct evidence of terrestrial life from the Mescal Limestone and from the younger, 800 million year old Late Proterozoic Beck Spring Dolomite (California). The fossils represent organisms of bacterial/cyanobacterial affinity.
Some potential evidence for life in the early paleosols comes from sedimentary structures. Retallack et al. (1984), and Retallack (1986a) described Precambrian paleosols (Dwaal Heuvel Formation, Transvaal) that contain rounded clay aggregates (crumb peds) encrusted by a thin rind of iron and manganese, which is better developed on the top than the bottom of the ped. These are similar to microbially produced rock varnish, thought to be fixed from atmospheric dust by fungi and bacteria. However, modern iron-manganese varnish occurs on the upper, but not lower, sides of exposed pebbles not only within soils, but also in streams and lakes (Dorn and Oberlander, 1982).

Another type of circumstantial evidence comes from the fact that Precambrian paleosols are more clay-rich and deeply weathered than a hypothetical initial stage of grains simply loosened from bedrock by physical and chemical weathering. Without the presence in soils of microbial life to stabilize the grains, they would have been easily washed away, and clay would not have formed in place (Retallack, 1986b).

In Cambrian deposits, traces of supratidal microbes are reported by Southgate (1986) from phoscretes in Australia. However, as pointed out by Siegel (1977) and Golubic and Campbell (1979), these microbial traces are very similar in soils and shallow marine or lacustrine deposits.

In a paleosol of the Late Ordovician (Ashgillian) Juniata formation (Pennsylvania), Retallack (1986b) recorded invertebrate burrows, and inferred that plants should have been present as well providing food for the animals that dug the burrows. The same paper described structures that may be due to the presence of plants from the late Ordovician (Caradocian or Ashgillian) paleosol in the Dunn Point Formation (Nova Scotia). Here putative traces of diagenetically modified organic matter are found in
mounds that are interpreted as sediments stabilized against erosion by clumps of non–vascular land plants.
4.5. **IN SITU TERRESTRIAL BIOTAS**

The oldest known terrestrial biota preserved *in situ* is that of the Rhynie Chert (Figures 4.1, 4.2). World-famous for exquisite cellular preservation of the fossils, this Early Devonian (Pragian) biota (Rice et al., 1995) includes terrestrial and freshwater 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 (floodplain, 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 (Figure 4.2). 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 they 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 zostero phylls and *Renalia*), more ephemeral near-channel environments (preferentially occupied by trimerophytes), and fully terrestrial riparian environments (with *Spongiophyton* and *Prototaxites*), that the authors tentatively related to contrasting life-history strategies.

The Rhynie Chert and Battery Point Formation biotas 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 multiple trophic levels (primary producers, decomposers, detritivores, and carnivores), 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., multi-storied vegetation and, arguably, herbivory).

The presence of herbivory in the Rhynie Chert and Battery Point Formation biotas is a debated issue. Using the 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, based on plant damage and dispersed coprolites containing plant fragments that are reported in the Rhynie Chert and Battery Point Formation biotas.
4.6. SUMMARY AND DISCUSSION

The well characterized *in situ* terrestrial biotas of the Early Devonian not only are 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.

Incongruence between the age of the earliest known land plants and the much older age of the earliest dispersed remains of putative land plant origin emphasizes the paucity of data concerning the former and represents a significant gap in our knowledge. In terms of phylogeny, this lack of data has led to a bias in most of the current approaches of land plant phylogeny toward untested hypotheses. These hypotheses are based mainly on different types of molecular data from extant organisms and some take into account the chemistry of compounds considered characteristic of terrestrial plants. The latest
molecular (Graham, 1993; Mishler et al., 1994; McCourt et al., 1996; Lewis et al., 1997; Bhattacharya and Medlin, 1998), ultrastructural (Cook et al., 1997), and cytokinetic (Brown and Lemmon, 1997) studies dealing with the phylogeny of land plants agree on their sister-group relationship to members of either the Coleochaetales or the Charales of the charophycean green algae. A recently developed approach (Kroken et al., 1996; Kodner and Graham, 2001; Graham, 2002; Graham et al., 2002) attempts to relate the different types of dispersed material described from the fossil record to dispersed material obtained from known extant taxa. This is realized by subjecting living material to treatments which mimic the processes that affect terrestrial organic matter from its deposition, through diagenesis and until after the physico-chemical processing techniques used to extract it from the rocks. This approach has shown similarities between dispersed microfossils traditionally associated with early land plants and acetolysis-resistant bryophyte tissues.

The same incongruence applies if we look beyond plants, at the fossil record of early terrestrial biotas as a whole. This is also characterized by an important gap between microfossils, on one hand, and meso-/macrofossils on the other hand. If putative terrestrial microfossils have been described from rocks as old as the Precambrian, the earliest meso-/macrofossils studied as such are late Wenlockian.

It is clear that the strongest evidence for the advent of terrestrial life or for the evolution of land plants would be the fossil remains of the organisms that originated early in the colonization of land. Potentially, these fossils could be present in rocks older than the Middle Ordovician that represent depositional environments favorable to the development and preservation of plants. It has been suggested by several authors (Gray
and Boucot, 1977; Stebbins and Hill, 1980; Krassilov and Schuster, 1984; Graham, 1993; Kenrick, 2000; Wellman and Gray, 2000) that the scarcity of early terrestrial fossils reflects a preservational bias, their poor potential for preservation resulting from the lack of resilient substances such as cutin, lignin, or other related compounds. Therefore, only the most resilient parts of these early terrestrial organisms were preserved as dispersed microfossils, whereas the organisms as a whole, considered too fragile, were not preserved. However, the instances where very fragile plants and structures are preserved (sometimes exceptionally) are not so rare in the fossil record, and structures as ephemeral as apical meristematic cells, pollen tubes, pollination droplets, cellular organelles, and even chromosomes are sometimes preserved (e.g., Good and Taylor, 1972; Rothwell, 1972a, 1977; Millay and Eggert, 1974; Niklas et al., 1978; Brack-Hanes and Vaughn, 1978). Also, resistant microfossils that withstand palynological extraction techniques are not limited to terrestrial organisms (see section 4.1).

In my opinion, the incongruence seen in the fossil record of early terrestrial biotas, and our lack of knowledge of the earliest terrestrial ecosystems, have more to do with the size of the organisms involved and with the lack of an effective search image for these organisms. This is best illustrated by the treatment of the Llandoverian macrofossils in the Massanutten Sandstone (Pratt et al., 1978). They represent not only the earliest terrestrial macrofossils, but also the earliest to be preserved in situ in terrestrial sediments. However, being thalloid and not axial, like typical embryophytes, they were not analyzed as whole organisms/communities. Rather, they were macerated from the sediments as dispersed microfossils, and compared to the nematophytes, a
hypothesized extinct group that represents an evolutionary (and probably also a conceptual) dead end.

The lack of an appropriate search image amplifies, in the case of the earliest land plants, a problem rooted in the very method that underlies the science of paleontology (including paleobotany). Paleontologists usually find out about fossil occurrences as a result of their discovery by other people and in most of the cases the other people are not even paleontologists; there are also the situations of the famous, classic fossil localities that have been known for centuries already. On the other hand, paleontologists rarely go out with the specific aim of finding a particular fossil occurrence, for example in order to test an evolutionary hypothesis. This is also the reason why paleontology is sometimes accused of being just descriptive and not using the scientific method, i.e., putting forward hypotheses and then finding proof that either supports or rejects them. However, there are notable exceptions in which paleontologists have set out with the specific goal to find particular fossils. These resulted in the documentation of the considerable diversity and widespread distribution of Precambrian life (by E.S.Barghoorn and his collaborators, reported in a plethora of papers) or the reconstruction of the earliest seed plants (by Gillespie et al., 1981).

Thus, it may be that the macrofossil record of early terrestrial life does not match the microfossil record because the macrofossils may have been overlooked. Conceptual leaps lead to advancement in science, and in paleontology/palaeobotany these leaps are made principally in terms of search image. Although the problem of the preservational bias is important, the small size of these early terrestrial colonizers undoubtedly adds another bias to the fossil record. Besides rendering them more likely to be destroyed
before fossilization, the small size also diminishes the chances of the fossils being noticed by field workers. The dispersed nature of the evidence that we now possess on land plants does not foster the construction of search images for these organisms. Kenrick (2000) cautioned against the use of a search image based on modern bryophytes, that would be unproductive in the search for early land plants. The fossil record is known to have produced new combinations of characters and new character states (Edwards, 2000) reflected in organisms whose features place them out of any of the groups known in the present biota. The example of Prototaxites is illustrative for this type of taxonomic indetermination. A Devonian organism whose systematic position has been long time debated even though it certainly did not go unnoticed, producing “logs” up to 17 ft in length and 4 ft in diameter, Prototaxites was only very recently classified in the Kingdom Fungi by Hueber (2001).
5. RATIONALE FOR THE STUDY

Current hypotheses on the colonization of land have been shaped by three main lines of thinking: (1) the early conception that vascular plants (tracheophytes) evolved from algae, and the resulting tendency of equating land plants to vascular plants; (2) the idea that embryophytes, i.e., bryophytes plus polysporangiophytes, including tracheophytes and non-vascular transitional forms with branching sporophytes, are closely related to charophycean green algae and evolved in freshwater, an idea that pervades most modern hypotheses; (3) the generalized tendency of looking at embryophyte evolution in terms of organismal evolution. These lines of thinking have helped understanding evolution within the embryophytes and refining concepts of early tracheophytes. In the same time, they have resulted in a conceptual subordination of the evolution of terrestrial communities to the evolution of embryophytes, so that early terrestrial communities are seen principally as a result of the advent of embryophytes, built by, and around the embryophytes. By focusing on evolution at the organismal level, these hypotheses have taken evolution out of its natural context, overlooking the central fact that embryophytes evolved within communities. As a consequence, we have no conclusive information on the make-up of the earliest terrestrial communities, the systematic position and the relationships among the organisms in these communities, or how embryophytes evolved. Several facts and ideas can help us find answers to these and other questions related to the early colonization of land. (1) Modern systematics places embryophytes in a sister-group relationship to charophycean green algae. (2) It has been hypothesized that embryophyte evolution is tightly linked to fungal associations.
This finds support in the occurrence of microfossils of putative embryophyte and fungal affinity very early in the fossil record. (3) Another hypothesis proposes that embryophytes evolved on land, from unicellular green algae. Bateman et al. (1998) considered the transition to land of prokaryotic and simple eukaryotic oxygen producers and fungi an essential precursor to the embryophytic life history. Accumulating evidence that terrestrial communities existed long before the advent of embryophytes supports this hypothesis. If we put together the previous three hypotheses, a new hypothesis emerges that states embryophytes evolved from charophycean ancestors on land, in communities dominated by mycobiont - photobiont associations, as a result of interactions within these associations. Within this framework, the study of early terrestrial biotas as communities of interacting organisms becomes central not only to understanding the colonization of land, but also the evolution of embryophytes.
5.1. WORKING HYPOTHESES

In contrast to the previous, organism-centered hypotheses, the new hypothesis emphasizes community-level ecology for understanding evolution of early terrestrial biotas, and the origin of embryophytes. In this hypothesis, association with fungi plays an important role in the colonization of land by photoautotrophs. Early terrestrial biotas were dominated by mycobiont - photobiont associations of the type seen in extant microbiotic crust communities, lichens, and mycorrhizal associations. It is hypothesized that in the first phases of the colonization, association with fungi played an important role in creating a suitable environment for the survival of charophycean green algae and the subsequent evolution of embryophytic photobionts. In this context, the advent of embryophytes, most of which depend on mycorrhizal associations of some kind, is seen as occurring in and from these associations (i.e., on land). Communities similar to the microbiotic crusts, and particularly the lichenicolous microbiotic crusts, with their good water-retention potential, would have provided the perfect environment for early embryophytes of the type hypothesized by Pirozynski (1981). Pirozynski (1981) suggested that the early embryophytes may have been characterized by long-lived, mycotrophic subterranean gametophytes devoid of chlorophyll. These would have acted as resting stages through periods of adverse conditions, with exposed, cuticularized, photosynthetic sporophytes infrequently, or sporadically, being produced during periods of optimal conditions.

At the level of organismal interactions, two main evolutionary scenarios can be imagined. In a "homologous" scenario, evolution in early terrestrial associations could
have evolved from rather loose initial interactions in two divergent directions, one toward symbioses where the mycobiont maintains and controls the photobiont as in extant lichens, and one toward symbioses dominated by the photobiont that uses the mycobiont, as in mycorrhizal associations. In an "antithetic" scenario, early terrestrial associations can be hypothesized to have evolved from a lichen-type, mycobiont-dominated type of interaction, toward mycorrhizal-type, photobiont-dominated associations.

At the scale of community structure, the successional patterns seen in the development of extant microbiotic crusts may serve as models for the evolutionary succession that led to the colonization of land and the advent of embryophytes. This is in accord with the ideas of Price (1988), who gave an evolutionary spin to the theory of facilitation suggesting that in the broadest sense ecology recapitulates phylogeny. As suggested by successional studies in microbiotic crusts (Anderson et al., 1982b; Johansen et al., 1984; Johansen and St.Clair, 1986; St.Clair and Johansen, 1993), the early terrestrial ground cover could have evolved through successive stages, from cyanobacterial mats to communities dominated by algae and fungi in different types of associations, and to the advent and eventual dominance of embryophytes.

This view departs from earlier organism-centered hypotheses of evolution and moves the emphasis of scientific inquiry to understanding the interactions and coevolution of organisms, and the community-level ecology and evolution in early terrestrial biotas.
5.2. APPROACH

My approach to the paleobiological questions and hypotheses outlined above followed an inductive path that went from constraining a time period significant for the evolution of terrestrial life and the advent of land plants, through identifying rocks deposited in sedimentary environments with good potential of incorporating and preserving the biota, and defining a search image for the fossils, to sampling the rocks and analyzing the fossils using various techniques.

**Time.** A survey of the important benchmarks in the fossil record of terrestrial life shows that land masses witnessed a transition from exclusively microbial communities, hypothesized by numerous authors and potentially represented by filamentous microfossils described from the latest Precambrian (Horodyski and Knauth, 1994), to communities of complex organisms, such as the polysporangiophytes and animals, at the end of the Silurian. In terms of embryophyte evolution, the microfossil record starts in the mid-Ordovician, and possibly earlier, whereas the oldest macrofossils are derived polysporangiophytes known from the mid-Silurian. Considering these two perspectives, the interval including the Middle and Late Ordovician and the Early Silurian, roughly between 470 and 420 million years ago, appears to have witnessed events of high significance for the subject of the present study.

**Rocks.** Except for the stomata present on embryophytes, no features are preserved in the fossil record that would unequivocally identify fossils as organisms of the aerial realm. Presence in microfossils of compounds that withstand palynological extraction techniques, such as sporopollenin, is often considered to indicate that their
producers lived on land. However, such compounds are not limited to terrestrial dwellers (see section 4.1), and therefore cannot be used to unequivocally infer a terrestrial origin for dispersed microfossils recovered from marine deposits. This limits the search for early terrestrial life to rocks deposited in continental settings, be they fully continental (e.g., fluvial), or marginal (e.g., intertidal). An assessment of these rocks and their potential for preserving plant fossils is presented below (section 6).

**Search Image.** My working hypotheses point to biological soil crusts as the most likely modern analogue of early terrestrial communities that witnessed the advent of embryophytes, both in terms of morphology and taxonomic make-up, as well as in terms of ecology and physiology. This is the search image that I use in the field, and in order to understand these closest extant analogues I reviewed the features of biological soil crusts that present relevance to my study (section 7).
6. FACIES MODELS FOR \textit{IN SITU} PRESERVATION OF LAND PLANTS

In order to develop models for settings favorable to the \textit{in situ} preservation of the earliest land plants, I undertook a review of modern sedimentary environments of continents and continental margins, looking also at examples of their ancient analogs. Such an approach should certainly take into account the bias introduced by the profound influences that the modern vegetal cover has on some of the modern settings, such as fluvial and tidal mudflat environments. It is this direction of inquiry that this section tries to approach. In doing this, I first considered the modern sedimentary environments and then tried to find ancient analogs for them. Therefore use of terms such as marsh, peat and coal in the text applies to the periods of time where the vegetational aspects implied by these terms existed.

The fossil biota most extensively analyzed in this study, at Passage Creek (Virginia), is preserved in rocks that lack a recent and detailed sedimentological analysis but have been interpreted as braided river deposits. A hypothesis put forward by Schumm (1967, 1968) and reiterated by Cotter (1978) proposed that the Early/Late Silurian boundary records a transition of fluvial styles worldwide from principally braided rivers, to principally meandering rivers, that represents the result of the development of a groundcover with significant bank-stabilizing capacities. Because this could hold important implications for the main topic of this study, early terrestrial biotas, I revisited the fluvial styles of select Ordovician and Silurian formations (section 6.4.) as a partial test of the hypothesis.
6.1. MINIMAL REQUIREMENTS FOR PRESERVATION OF IN SITU PLANT MATERIAL

It is unclear whether cutin and lignin, compounds with high preservation potential, were present in the earliest embryophytes, but cellulose was undoubtedly a significant component of the cell walls of these plants. A linear polymer of glucose anhydride units, cellulose is insoluble in water, dilute alkali, most organic acids and most common solvents (alcohols, chloroform, acetone, benzene etc.), and it is not susceptible to oxidation except under extreme conditions (Gray, 1965).

However, the alteration of organic matter in the early stages of diagenesis is largely controlled by the activities of microorganisms and burrowing animals. Degradation of the cell wall (aero- or anaerobically) is characterized primarily by loss of cellulose (Barghoorn, 1949). In an oxidizing environment, microorganisms biochemically eliminate the bulk of the carbohydrates (cellulose, hemicellulose) in the early stages of diagenesis (Degens, 1965). If paleosols with animal burrows are known only starting with the uppermost Ordovician (Ashgillian) (Retallack and Feakes, 1987), Selden and Edwards (1989) hypothesized that land surfaces in the Paleozoic were at least partially covered by microbial mats, predominantly cyanobacterial initially. Bacteria would have also been present as decomposers in these early terrestrial communities. Fungi, probably the most important decomposers in terrestrial ecosystems, are thought to have already reached high diversity as early as 600 million years ago (Redecker et al., 2000; Berbee and Taylor, 2001).
The rate of degradation of plant material due to microbiological activity is usually most rapid in warm, moist, highly aerobic environments (Barghoorn, 1949). However, at any stage in the decomposition of plant materials, burial or submergence and a limitation of the oxygen supply can help to arrest biochemical decomposition (Gray, 1965). Even though in anaerobic conditions bacteria slowly degrade residual organic materials and their decomposition products (Gray, 1965), wet environments and particularly oxygen-deficient ones, greatly reduce plant tissue degradation rates (Barghoorn, 1949).

According to this author, if mineralization of plant remains occurs at a stage when cellulosic structural residues are still retained (as is apparently often the case), the infiltration and precipitation of minerals (calcium carbonate, silica) may cause a fixation of structure which retains a large measure of biological detail in mineral form. Organic matter, chemically modified, may be retained in higher or lower percentages as well.

Some unsuitable rocks can be quickly eliminated from the list of likely candidates. Due to their age, lower Paleozoic sedimentary rocks are more likely to have experienced metamorphism. In rocks which are too strongly affected even by low-grade metamorphic processes (especially thermal alteration), all organic material will be carbonized (Kerp, 1990) rendering the plant remains unsuitable for analysis. Still, there are many lower Paleozoic rocks that have not been metamorphosed. Sandstone embedding of plant fossils may damage them as a result of compaction, since sand grains will make imprints that may have severe consequences considering the fragility and reduced size of the plant remains. Pyrite formation may affect the vegetal material in the same way (Kerp, 1990).
Taking into account all of these aspects, the minimal requirements for *in situ* preservation of the earliest land plants are: (1) rapid burial in (2) fine-grained sediment and (3) early onset of anaerobic conditions. A fourth requirement has to be added, even though it does not necessarily control preservation, namely a terrestrial substrate on which the plants could grow. It is this fourth requirement that, for *in situ* material, rules out all aqueous sedimentary environments and limits the search to those that imply at least temporary subaerial exposure.
6.2. SEDIMENTARY ENVIRONMENTS

The earliest land plants were at the bryophyte grade, therefore zooidogamous and needing a certain amount of moisture for fertilization to take place. This suggests that very arid environments should also be ruled out of this survey. However, extensive microbiotic crusts are known to be central to resource dynamics in many arid ecosystems (Evans and Johansen, 1999), such as the Colorado Plateau, the Great Basin, or the Sonoran and Mojave Deserts. These communities include prokaryotes, fungi, algae and bryophytes, usually hosted by lichen crusts. They prove that the actual amount of moisture required for effective algal and bryophyte reproduction and survival may be as low as the one provided by dew retention in the microbiotic crusts. Terrestrial microbial communities are known to thrive presently even in conditions as extreme as those of the arid soils of the Antarctic dry valleys (Burkins et al., 2000). However, even though onset of anaerobic conditions exists theoretically in both these types of arid sedimentary environments, the likelihood is low and therefore these environments are not discussed here. The sedimentary environments discussed include fluvial, deltaic, barrier-island, carbonate and evaporite environments. The review of these environments is based mainly on the papers published by various authors in Walker (1984) and Walker and James (1992), and to a lesser extent on Reading (1986).
6.2.1. Fluvial Systems (Rust and Koster, 1984; Walker and Cant, 1984)

In fluvial systems deposition outside the main channel (overbank deposition) in levees and especially floodbasins takes place during flood stages when the river overtops its banks, and leads to vertical accretion. Near the main channel vertical accretion is principally silty and cross-laminated, whereas farther from the river deposits are finer, muddy, and floodwater stagnation may occur, resulting in the deposition of back-swamp clays. These deposits have good potential for in situ plant preservation. They provide a good substrate for the development of plants, as well as the appropriate material that would preserve the plant material by covering it. When present, floodwater stagnation leads to the onset of anaerobic conditions. In post-Silurian river systems, flood basins and levees tend to be abundantly vegetated and vertical accretion can result in the formation of coal seams.

In the stratigraphy of meandering systems an elongated sand bodies are bounded below and on both sides by flood basin fines. Given continuous supply and subsidence, this geometry will form a series of successive point bar sand bodies interbedded with shales. The general facies sequence for meandering rivers is fining upwards, with overbank deposits (vertical accretion) overlying laterally accreted in-channel deposits. The model contains a coarse lag at the base, overlain by successive trough cross-bedding, small scale trough cross-lamination with occasional interbedded horizontal lamination and finally by siltstones and mudstones of the vertical accretion deposits, with root traces, desiccation cracks and caliche-like concretions (under more arid conditions) or coal seams (under more humid circumstances). The more sinuous the meandering of the river,
the higher the proportion of fine, vertical accretion deposits in the overall alluvial stratigraphy and the higher the potential for preservation of *in situ* plant remains.

*Braided fluvial systems* suppose a more active sedimentation, and therefore higher deposition rates than those in meandering systems. This means faster burial of the plant remains and thus better preservation potential. However, deposition in these systems is predominantly sand or gravel. The finer material (silt and clay) tends to be transported through the system without accumulation and floodplain sedimentation generally occurs only during major floods. Even if the finer material bypasses the fluvial system it may still be found downstream, in a delta. However, muddy braided river systems are also known. The scarcity of fine-grained sediments and the fact that processes are more dynamic than in meandering systems (comparatively rapid lateral migration of channels) result in vertical accretion deposits that are thinner, less commonly deposited, and only rarely preserved. In the Brahmaputra flood basin, clay is deposited by flood waters at a rate of only 2 cm or less per year but the abundant vegetation still forms 1-4 m thick peat deposits.

Fine-grained vertical accretion deposits, although thinner than in meandering systems, form the top of sand flat facies sequences in braided systems. In the summary sequence developed for the Devonian Battery Point Sandstone (Quebec) by Cant and Walker (1976) the vertical accretion deposits include cross-laminated siltstones interbedded with mudstones. The complete sequence has a channel-floor lag overlain by poorly defined trough cross-bedding, well defined trough cross-bedding, large sets of planar-tabular cross-bedding, small sets of planar-tabular cross-bedding with isolated scour fills and finally the vertical accretion deposits.
Although considerably less frequent, braided rivers are known also from muddy depositional settings (e.g., Lorenz and Nadon, 2004). Mudstone facies in overbank deposits of such settings preserve mottling and root structures consistent with alteration of the sediments by pedogenic processes.

Braided systems are responsible for the deposition of coarse alluvial deposits, but also of finer sequences. The coarser sediments less commonly bear fines, which lowers even more the potential for preservation of vegetal remains. However, thick (but laterally impersistent) coals occur sometimes even within intermontane, conglomeratic alluvial deposits. Vertical accretion mudstones present in the topmost parts of sequences in Carboniferous distal gravelly braided fluvial deposits are known to contain transported and in situ plant material. It is generally considered that braiding is more common in semi-arid or arid areas, where the scarcity or lack of vegetation would tend to store rainfall and regulate runoff. This is thought to apply to landscapes before the advent of land plants as well.

Anastomosed systems are similar to braided systems as concerns their channel network, but have more sinuous and, what is more important, more stable channels. This situation is the result of a rapidly elevating base level that causes high rates of aggradation, deposition of fines and stabilization of river channel patterns. This allows for accumulation and preservation of vertical accretion deposits in flood basins. The geometry of the deposits includes thick vertically accreted sand bodies bounded by fine wetland facies. This setting is very favorable to the in situ preservation of plant material: modern anastomosed systems preserve vegetal remains in a variety of facies, such as silty
levee facies (mainly roots), clay and silty clay flood pond facies, muddy back-swamp facies and peat bog facies.

Overall, fluvial systems have a high potential for preservation of *in situ* plant remains in flood basin deposits. In *meandering systems* the increased potential due to higher proportion of fine-grained deposits is counterbalanced by lower sedimentation rates (i.e., slower burial) and scarcer occurrences in the lower Paleozoic geologic record. It is generally considered that most of the pre-Silurian rivers were braided, as a consequence of the lack of well-established terrestrial vegetation that would have stabilized riverbanks. *Braided systems* present the advantages of higher sedimentation rates (and therefore more rapid burial) and of more frequent occurrences in lower Paleozoic deposits, but in their case fine, vertical accretion deposits are preserved and occur in lower proportions. *Anastomosing systems* allow accumulation of larger quantities of fine deposits than braided systems and probably have higher sedimentation rates (faster burial) than meandering systems. The revised anastomosed luvial facies model proposed by Nadon (1994) includes relatively rare coals, but abundant crevasse splay, and marsh sediments favorable to the preservation of plant material.

**6.2.2. Deltaic Systems** (Miall, 1984; Rust and Koster, 1984)

Deltaic systems presently include environments characterized by rich vegetal populations. In the general model of the progradational phase of delta growth, the sedimentary sequence is capped by topset delta marsh sediments that include a mosaic of mud, peat, or fluvial deposits.
In river-dominated deltaic systems the marshy delta floodplain forms by filling with sediment of the interdistributary bays, characterized by muddy sedimentation. The deposits contain shells and are bioturbated which indicates nutrient richness. Pre-Devonian river-dominated deltas are mainly fan deltas, built by braided distributary networks that were predominant before the advent of terrestrial vegetation. Modern fan deltas tend to occur in arctic or arid environments, where the abundance of coarse bedload, the lack of vegetation, and the variable river discharge favor unstable braided distributary networks. Pebbly sands and gravels are common to dominant components of the delta plain.

The subaerial area of tide-dominated deltaic systems consists largely of tidal flats comprising mainly fine-grained deposits. The sedimentation rates are high and fine sediments are introduced in large quantities into the delta marsh between the distributaries by overbank flooding during high tides.

The deltaic floodplain provides good conditions for the preservation of in situ plant remains in wave-dominated deltaic systems as well. This is shown by the sequence stratigraphy of the wave-dominated deltaic deposits of the Early Devonian Bokkeveld Group in South Africa. Here vegetal remains are present in distributary mouth bar and floodplain facies (Tankard and Barwis, 1982). While the plants in the distributary mouth bar facies are very probably transported, in the floodplain facies, plant remains are accompanied by root traces, which suggests in situ preservation.

In summary, deltaic systems are generally rich in fine sediments containing a rich organic component. These sediments form nutrient-rich substrates favorable to land plant growth in the delta plain, as well as in interdistributary bays, where marine influences are
not too strong. The sedimentation rates are high, providing rapid burial of the organic matter. Some deltaic systems therefore have high potential for in situ preservation of plant remains. However, there are also a few problems with these systems. First, if pre-Devonian deltas were mainly fan-deltas, then they are characterized by much lower proportions of fine sediments and therefore less likely to provide sedimentary environments favorable to the in situ preservation of plant remains. Second, vertical deltaic build-up that preserves the topmost, finer part of the deltaic sequences only occurs if the rates of sedimentation and subsidence are in approximate balance. Subsidence rates slower than sedimentation rates lead to seaward progradation of the delta and reworking of the abandoned lobes with limited preservation of the topmost finer deposits and the plant remains therein. Due to the large variability of deltaic settings, a facies model that would fit all possible deltaic sedimentary sequences was not developed to date, but facies models for the different delta types are discussed by Elliott (1986).

6.2.3. Barrier-Island – Strand-Plain Systems (Reinson, 1984)

Within the barrier-island system, marshy areas favorable to plant growth and preservation occur in flood tidal deltas and around the lagoons (including the areas adjacent to the barrier area). If filled with sediment or in a regressive setting, the whole body of water behind the barrier can evolve into a marsh. The organic deposits that accumulate within these areas (peat/coal) are usually thin. They are formed by vegetation inhabiting the sand flats and mud flats of the lagoonal margin, washover flats or abandoned/mature flood tidal deltas. These back-barrier deposits are preserved by
transgressive barrier-shoreline migrations. However, they are preserved only if a relatively rapid transgression drowns the barrier in place and leads to a stepwise retreat of the barrier shoreline, as is the case with the Late Cretaceous Horseshoe Canyon Formation in Alberta (Rahmani, 1983). The general transgressive facies model is characterized by subtidal and intertidal back-barrier facies and does not show a fining-upwards or coarsening-upwards trend.

When preserved, back-barrier deposits of barrier-islands have a high potential for in situ preservation of plant remains, as proved by coal occurrences in the lagoonal sequences of Carboniferous deposits in Kentucky and West Virginia (Horne and Ferm, 1978), and by plant remains in the Cretaceous lagoonal deposits of the St. Mary River Formation in Alberta (Young and Reinson, 1975).

6.2.4. Carbonate and Evaporite Systems (James, 1984; Schreiber, 1986; Kendall, 1992)

Extensive tidal mats develop in the intertidal zone of low-energy tidal flats in carbonate systems. The upper limit of distribution of the mats coincides with the upper limit of the intertidal zone in arid areas. In areas of high rainfall, mats are prolific in the supratidal zone that retains a sufficient amount of moisture. Algal mats also develop in the landward parts of the supratidal zone and into low-lying terrestrial environments where the two intergrade, forming algal marshes in regions of high rainfall.

The preservation potential of the mats is low, as oxidizing conditions represent the norm in the intertidal and supratidal zones. The mats usually rot away during burial
leaving just characteristic structures such as fenestral porosity. As sedimentation is mainly composed of storm deposits, the algal mats in the supratidal zone are preserved only when covered with sediment deposited during particularly intense storms. The resulting sequence is one composed of alternating algal mats and storm layers. Periods characterized by high storm incidence are therefore likely to favor the preservation of the plant material by rapid burial. Carbonate cementation may help in this process by sealing the pores and thus reducing oxidation, but carbonate cements more often destroy plant fossils. Algal mats may be exceptionally preserved by silicification, as shown by the numerous findings of Precambrian biota (e.g., Barghoorn and Tyler, 1965; Knoll, 1984). Silicification may often be more important to a better preservation than rapid burial. Algal mats also develop in the intertidal and supratidal zones of evaporite systems, but unless permineralized or otherwise preserved during life or early in their burial history, which happens in some areas, they decay forming algal peat.

Although the potential for *in situ* preservation of plant material exists in carbonate systems, it is very dependent upon post-sedimentation phenomena (e.g., diagenesis). Generally, facies models do not record the supratidal facies because of the rarity of their preservation. Evaporite deposits, with the incumbent uncertainties related to their environment of genesis are even more difficult to assess as to their potential for preservation of *in situ* plant remains. However, it is interesting to note that the lower Purbeck sequence in Dorset considered to represent mostly intertidal and supratidal facies, includes carbonaceous shales (termed dirt beds) with *in situ* tree stumps on an erosion surface.
6.3. SUMMARY – PRESERVATION POTENTIAL OF DEPOSITIONAL ENVIRONMENTS

There is good potential for preservation of *in situ* plant remains in fluvial, deltaic, barrier-island – strand-plain, carbonate, and evaporite systems. Fluvial systems generally have a high potential for preservation of *in situ* plant material in the flood basin deposits. The proportion in which these fine, vertical accretion sediments relative to the coarser lateral accretion sediments are deposited and preserved varies depending on the type of fluvial system. Highly meandering and anastomosing systems tend to accumulate and preserve higher proportions of vertical accretion sediments than braided systems, which are thought to have been more frequent before the advent of land plants.

Deltaic systems also have high potential for preservation of *in situ* plant material. There is a lot of variability in deltaic systems, but their interdistributary bays generally have high sedimentation rates of fine, nutrient-rich sediments (favorable to the installation of land plants). Balanced rates of subsidence and sedimentation preserve the topmost, finer part of the deltaic sequences. Due to the high variability of deltaic systems no general model was developed for them.

If preserved by rapid, stepwise transgressions, back-barrier deposits of barrier-islands have high potential for *in situ* preservation of plant remains. No generalized facies model was developed to date for barrier-island deposits. The tidal facies of carbonate and evaporite systems may preserve *in situ* plant remains, but the potential for that is lower than in the previous systems and depend more on diagenetic processes.

Although this paper deals with depositional environments, it shouldn't be forgotten that
diagenesis often plays an important role in the preservation of plant material. Exceptional structural preservation of plant material occurs in concretions (carbonate, siliceous, pyretic, etc.) that are the results of diagenetic processes.

These conclusions show that more work needs to be done in order to develop facies models for the *in situ* preservation of plant remains. More detail needs to be added to the systems discussed above, mainly with respect to sedimentation rates in the different depositional environments within a system, and by the inclusion of data from ancient deposits and of data on diagenetic processes. Further refinement of the models could even lead to a quantitative assessment and classification of their potential for the *in situ* preservation of plant remains, which would be of great help in the continued search for the earliest land plants.
6.4. REVISITING ORDOVICIAN AND SILURIAN FLUVIAL STYLES

A quarter of a century ago, Cotter (1978) published a study evaluating Paleozoic fluvial styles as reflected in the Central Appalachian terrigenous sequences. The results of his study documented a mid-Paleozoic (post Early Silurian) change of fluvial style from exclusively braided to a mixture of braided and meandering. Cotter interpreted these results as supporting the hypothesis put forward earlier by Schumm (1967, 1968), that such changes in fluvial style were the result of the advent and diversification of vascular land plants. This hypothesis was drawn from observations of the significant bank-stabilizing effects of present vegetation, and their considerable influence on modern fluvial styles.

Schumm’s hypothesis was consistent with knowledge of the evolution of land plants and of fluvial styles in ancient and modern river deposits at the time. However, the last twenty-five years have brought a wealth of information on the evolution of land plants that resulted in pushing back in geologic time the moment of appearance of terrestrial organisms. Presently, there is evidence (represented by trilet spores, the hallmark of the embryophytic condition), that embryophytes, the group including all extant land plants (bryophytes and tracheophytes) had evolved by the mid-Ordovician, and possibly as early as the Cambrian (Strother, 2000). A well-developed ground cover is now considered to have been present very probably by the Early Silurian in the wettest available terrestrial habitats, emerged areas of the fluvial systems (Tomescu and Rothwell, 2004).
Ongoing study of this ancient ground cover suggests that it was very likely morphologically and ecologically similar to modern mutualistic associations known as microbiotic crusts, or biological soil crusts. Today microbiotic crusts include bacteria, cyanobacteria, fungi, algae, lichens, and bryophytes forming loose associations, and occur principally in desert areas, where environmental conditions are unfavorable for the establishment of higher plants. Here, the crusts play a major role in soil formation, in stabilizing the soil and preventing erosion (Belnap and Lange, 2001). If the Early Silurian groundcover was indeed similar to microbiotic crusts, then it must have played the same kind of roles in floodplain settings or their equivalents in the river systems where it occurred, and thus may have influenced fluvial styles.

These recent finds suggest that Schumm’s (1967, 1968) hypothesis needs reevaluation, or at least some refining. Also, since publication of the initial study by Cotter (1978), the field of fluvial sedimentology has witnessed important theoretical developments that allow better assessment and interpretation of sedimentological information. Hence the purpose of this section to survey published occurrences of Ordovician and Silurian fluvial sequences in an attempt to assess fluvial style based on an updated set of criteria. I will first introduce the criteria and discuss their value in inferring fluvial style. Then I will present the Ordovician and Silurian occurrences of fluvial deposits surveyed for this study. The results of the survey will be summarized in tables that I will subsequently use to draw conclusions on the fluvial style of Ordovician and Silurian rivers. But, before all of these, a review of Cotter’s (1978) work and results is necessary.
6.4.1. E. Cotter’s Analysis

The study by Cotter (1978) had two parts. The first part surveyed published reports on fluvial sequences and records fluvial styles as interpreted by the original authors, with the aim of uncovering potential patterns of distribution of fluvial styles through geologic time. The second part looked at eight formations of fluvial origin in Pennsylvania to assess fluvial style and ascertain potential patterns.

As pointed out by the author, the survey of published reports was not exhaustive. Cotter did not re-interpret data presented by the original authors, and he only recorded the interpretations of original authors that were clearly stated in terms of braided vs. meandering. He found 122 such interpretations published between 1961 and 1977, and covering the Precambrian and the whole Phanerozoic. Among the 122, 65 were interpreted as braided and 57 as meandering, and Cotter’s results showed 0% meandering streams in the Ordovician, based on one published report, and 40% meandering streams in the Silurian, based on five reports. He then inferred an increase in the proportion of meandering beginning in the Silurian, but not without mentioning the shortcomings of his dataset: interpretations by different authors using different conceptual models, and under-representation of some periods. Indeed, just one published interpretation for the Ordovician renders futile any interpretation of what changed between the Ordovician and the Silurian in terms of fluvial styles.

Aware of the problems of the survey, Cotter engaged in a study of fluvial formations based on outcrops in central Pennsylvania (Figure 6.1.A). The underlying assumption of the second part of his study was that such an approach would eliminate the
complicating factors that affected the results of his literature survey, by looking at formations deposited in similar tectonic settings and using the same conceptual model. Cotter looked at eight formations ranging Late Ordovician through Late Pennsylvanian (Figure 6.1.B), using a three-fold scheme proposed by Brown (1973) which distinguishes three fluvial systems: braided, coarse-grained meanderbelt, and fine-grained meanderbelt. Among braided systems, Cotter further separates sheet-braided from channel-braided at width/thickness = 20. His results showed sheet-braided rivers in the Late Ordovician-Early Silurian, and oscillations between channel-braided and fine-grained meanderbelt systems in the Late Devonian-Late Pennsylvanian. He interpreted these results as reflecting a mid-Paleozoic change in fluvial style from nearly all braided systems to a mixture of braided and meandering systems.

Without attempting to address all of the problems of Cotter’s second approach, I will just comment below on a few important aspects of his work that render the results unreliable.

1) Cotter’s dataset excluded from the analysis an interval of at least 60 million years between the late Llandoverian (top of the Tuscarora Formation), and the Late Devonian (base of the Catskill Formation). Although there is an objective reason for this omission (the absence of fluvial deposits in the study area for that interval), it leaves out of the analysis a time span as long as the whole Tertiary.

2) Cotter mentioned using Brown’s (1973) scheme, but does not detail this usage. In fact, except for the width/thickness ratio mentioned above, he did not define an explicit and consistent set of criteria to distinguish between fluvial styles. A look at
Brown (1973) reveals that he did not develop or follow consistently a well-defined set of criteria either. Instead, he constructed a table of the “spectrum of features along idealized fluvial systems” (Brown, 1973, p. 12; Figure 6.2), and then erected idealized descriptive depositional models for the three fluvial styles. Only three of Brown’s criteria can be applied in outcrops: sand/mud ratio, sand body geometry and association, and the presence of levees (although identification of the latter in outcrops is problematic).

This explains Cotter’s lack of a well-defined set of criteria. However, careful reading of his descriptions of the eight formations reveals the features he used to distinguish among fluvial styles. These were the coarse/fine sediment ratio, the width/thickness of genetic units, the presence/absence of fining-upward trends in textures and structures, and the frequency of planar cross-lamination.

3) During the interval taken into consideration in this study (Late Ordovician – Pennsylvanian) the Appalachian basin was influenced by glaciations and sea-level oscillations that undoubtedly affected fluvial styles (considerable changes in climate, base level, subsidence, etc.). Cotter (1978) mentioned some of these influencing factors, but did not take them into consideration in his interpretation.

6.4.2. Materials and Method

At the time Cotter’s paper was written the implicit criteria he used were the best available, but since that time numerous studies have improved our knowledge of the different fluvial styles and their reflection in outcrops. This is why I am reiterating a
survey of fluvial sequences, focusing however only on the Ordovician and Silurian. Like Cotter’s, my survey relies on published reports, but I try to interpret fluvial styles based on the information provided by the authors. To do this, I have developed a set of criteria based on sedimentary characteristics that taken alone or in concert are likely to reflect fluvial style.

6.4.2.1. Criteria

My analysis follows largely the guidelines set up by Friend (1983), who developed a set of practical criteria to be used in assessing and classifying fluvial styles. Where necessary, I also used ideas and comments from earlier similar attempts by Brown (1973) and Jackson (1978), to define and discuss criteria.

Grain size

Two tightly related usages have been given to grain size in assessing fluvial style. Within sequences, at the scale of the lithologic unit, grain size can be used to interpret units in terms of transport-mode, distinguishing between bed-transport units (coarser), and suspension-transport units (finer).

At a higher degree of generalization, a simplified version of the grain-size criterion can be applied at the sequence scale. The overall proportion of coarser-grained sediment to finer-grained sediment in a fluvial sequence has been used to infer gross transport-mode and channel sinuosity within the river system. High proportions of coarse deposits are interpreted as representing less sinuous, braided systems depositing mainly
bed-transport units, and high proportions of fine-grained sediments as produced by more sinuous, meandering systems that deposit considerably more suspension-transport units.

Proportions of grain sizes in rock sequences provide the most general and probably the least reliable criterion used in inferring fluvial channel patterns. This is because they are controlled not only by a multitude of depositional factors, but also by the degree of preservation of sedimentary sequences in a given tectonic setting (rates of aggradation vs. degradation/erosion). Friend (1983) cautioned against the use of grain size proportions by themselves as an index of channel pattern, citing examples of problems and exceptions in the application of this criterion. However, he also pointed out that it may prove useful in the absence of diagnostic sedimentary structures, therefore I recorded it where available, to be used in conjunction with other types of evidence.

Grain size is a quantitative or semi-quantitative criterion, and its application raises the problem of setting absolute values for drawing the line between coarser and finer units. Friend (1983) distinguished between sand-grade or coarser units, interpreted as bed-load deposits, and medium silt or finer units, representing suspension-load deposits. However, he pointed out that this was an arbitrary, subjective limit, for which different authors may set different values. In this analysis I am making the same distinction, between coarse units (sand-grade or coarser), and fine units (silt-grade or finer).

Distinction between principally coarse-grained and principally fine-grained sequences can be delicate where the proportion of the two types are not very different. Brown (1973) distinguished braided rivers as characterized by medium- to coarse-grained sand and gravel highly common, and silt-grade and finer material rare. Friend (1983) distinguishes between “mainly bed-transport deposits”, “mainly suspension deposits”,


and an intermediate “bed-transport and suspension deposits”, without defining clear-cut boundary values for the proportion of bed- to suspension-load deposits. Because most of the papers surveyed in this study do not provide exact values for coarse/fine proportions, and absolute values of this proportion do not carry a direct significance with respect to fluvial style, I recorded only semi-quantitative data (very high, high, equal, low).

**Coarse sediment body geometry**

Friend (1983) pointed out that the recognition of channels is a major step in the analysis of fluvial deposits. Whereas ribbon sandstone bodies can be interpreted in terms of presence of fixed channels within a channelized flow context, sheet sandstones are more difficult to interpret as they can result from both channelized flow (in mobile channel belts), and non-channelized flow. Further distinctions within sheet sandstones are based on identification of channels and sedimentary structures that may or may not be preserved or observable, therefore a first distinction needs to be made between ribbon- and sheet sandstones when looking at sandstone body geometry. The width/depth ratio of the sandstone body is used for making this distinction, and absolute boundary values of this ratio used by different authors vary widely, from 15 to 100. However, the surveyed papers provide only qualitative data on this characteristic of the sedimentary sequences, if at all. Qualitative descriptions of the authors were consequently used in the data set, and in several instances they could be verified on published photographs.
**Channel geometry and behavior**

Depending on the measure in which channels can be recognized and sedimentary structures are observable, channel geometry and behavior, and sandstone body geometry are interrelated criteria.

Where channels can be identified, their geometry (width/depth ratio and shape) and behavior can be used to interpret channel pattern. Brown (1973) distinguished between discontinuous, lenticular, or tabular channel fill units he considered characteristic of braided rivers, and channel fill units asymmetric in cross section that he attributed to meanderbelts. Looking at channel behavior, Friend (1983) made a first distinction between fixed channel, generating ribbon sandstones, and mobile channel belts that produce sheet sandstone bodies. Based on the channel migration mode as revealed by sedimentary structures within sheet sandstones, he further distinguished between steady lateral migration reflecting meandering rivers, and steady and switching migration, characteristic of both meandering and braided rivers.

Very few of the surveyed papers mention channels apart from information on basal scour or cut-and-fill structures. When they do, quantitative data are lacking except for two cases, and most of the existing data is qualitative (e.g., “broadly lenticular genetic units” in Cotter, 1978, p. 366). When available, such qualitative information was recorded in the data base.

**Particular sedimentary structures**

For each of the structures, frequencies of occurrence were recorded semi-quantitatively: rare, present, frequent or abundant. When authors only mention presence
of a type of structure, without commenting on its frequency, that type was recorded as “present”.

**Basal scouring.** In the absence of data on channel geometry and spatial association, the frequency of basal scouring indirectly reflects channel behavior. Abundant basal scours can be interpreted as characterizing systems with highly unstable, laterally migrating channels. Lateral migration occurs in both meandering and braided streams (Friend, 1983), but while in meandering systems migration is steady in one direction (at least for some period of time) and is accompanied by characteristic structures (epsilon cross stratification), braided channels tend to switch direction more or less randomly. When basal scouring can be followed for some length in an exposure, its extent and relief can also give some indication on channel geometry.

**Shale intraclasts.** These also reflect the amount of scouring, and therefore indirectly channel migration. Where fine-grained sediment is rare in the fluvial sequences the presence of shale intraclasts in abundance can be interpreted as reflecting highly unstable, migrating channels that eroded most of the overbank deposits in the system. Their presence is also important in that it speaks of the existence in the system of such overbank settings characterized by fine sedimentation, and thus provides a record of flood plain deposits.

**Structureless sandstone/conglomerate bodies.** Friend (1983) gave five possible interpretations for structureless sheet-sandstone bodies where channels cannot be identified: non-channelized flow (sheetflood), channel width/depth ratio too high, sediment grain-size too uniform, bad outcrop (wrongly oriented, small), or major reworking of channel fill units.
**Horizontal bedding.** In sand-grade sediments (including coarse sandstones with pebbles) horizontal bedding indicates upper-flow-regime conditions. According to Lorenz and Nadon (2002) it forms on channel floors in fast flowing shallow water, and is present in significant amounts in ancient fluvial deposits that have been interpreted as braided.

**Planar cross bedding.** Occurs in gravel tabular bodies (bars, bedforms), as well as in sandy bedforms, and downstream- and lateral-accretion macroforms (Miall, 1996). It is generally considered to be characteristic of braided reaches, especially where point bar deposits (epsilon cross stratification) are absent.

**Trough cross bedding.** Produced by the migration of 3-D dunes, trough cross bedding represents deposition in channels and does not really carry a significance in terms of fluvial style. Their frequency was recorded just in order to provide a term of comparison to frequencies of horizontal bedding and planar cross bedding.

**Epsilon cross stratification.** The hallmark of point bar deposits and hence high sinuosity reaches, epsilon cross stratification is not recorded *per se* in any of the surveyed papers. In his short description of sedimentary structures of the Juniata Formation, Cotter (1978) mentioned mudstone lining foreset laminae that could be interpreted to represent inclined heterolithic stratification. However, in the absence of a more detailed description of the structures, there is no certainty that they represent point bar deposits.

**Fining-upward “cycles”.** Associated by Allen (1970) to his point-bar model, fining-upward sequences are not exclusively characteristic of meandering reaches, but they are also present in channel-fill deposits of low-sinuosity reaches (Galloway, 1981) and in floodplain facies of braided reaches (Nanson and Croke, 1992). When compared to the
fining-upward sequences of point bar deposits, those of braided reach floodplains usually exhibit abrupt boundaries between the coarse basal sediments and the fine upper section (Nanson and Croke, 1992). Although fining-upward sequences are recorded in the surveyed papers, no such level of detail is available. The occurrences were nevertheless recorded in the data set.

**Mud cracks.** Characteristic of subaerially exposed areas of fine sediment deposition, their frequency of preservation can be interpreted as a gross index for the surfaces occupied by such processes in the zone of influence of stream deposition. As their preservation necessitates not only subaerial exposure of fine unconsolidated sediment, but also rapid burial without scouring, high frequencies of mud cracks can also be used as an indication for flashy, highly and rapidly variable hydrograph.

**Paleocurrent distributions.** Local-level distribution of current directions, namely their degree of dispersion can be used to separate high sinuosity reaches (high current dispersions) from low sinuosity reaches (low scatter of current directions).

### 6.4.2.2. Formations

Without being exhaustive (due to the limited physical time), the survey documents nine Ordovician and Silurian formations based on 16 published papers. Five of the formations are from the Appalachian Basin, three from Norway, and one from Ireland, and their stratigraphic distribution is summarized in Table 6.1, along with the number of publications that provided data on each formation.
6.4.3. Results

Results of the survey are summarized in Tables 6.2-6.9, and they are detailed below starting with the formations of the Appalachian Basin (in stratigraphic order), and continuing with those from Norway and Ireland.

**Bald Eagle/Oswego Formation, Late Ordovician** (Table 6.2). Data available on the Bald Eagle/Oswego is rather scarce. It is generally characterized by very high proportions of coarse, sand-grade deposits that form sheets. Basal scouring and shale intraclasts are present, but their frequencies are not recorded. Both horizontal and cross bedding are frequent, mainly planar cross bedding. Paleocurrent directions are available only as outcrop-level vector means (Yeakel, 1962), and cannot be used to infer dispersion of flow directions. The very high abundance of sandstone, along with the high frequencies of horizontal bedding and planar cross bedding would suggest a braided fluvial style, but the absence of any indication on body geometry recommends caution.

**Juniata Formation, uppermost Ordovician** (Table 6.3). The proportion of coarse sediment in the Juniata varies considerably, from high abundance of sandstones in proximal facies, to low in the distal facies. Sandstone body geometry is not described, but published photographs illustrate sheet sandstones. Cotter (1978) mentions “broadly lenticular genetic units“ (p. 366), but interpretation of these data in terms of channel geometry is precluded by the absence of concurrent basal scouring and any quantitative data. Shale pebble conglomerates are frequent in distal facies (Yeakel, 1962), suggesting erosion of fine-grained portions in the river system, consistent with the presence of fine-grained facies with some frequency in the system. As in the case of the Bald Eagle,
horizontal bedding is frequent, and planar cross-bedding is abundant in the Juniata. Frequent mud cracks (at least in proximal facies) can be an indication of migrating channels and/or recurrent flash floods. Paleocurrent distribution is again available only as vector means (Yeakel, 1962), and therefore not useful in assessing fluvial style. The variable, sometimes low proportions of coarse sediment caution against immediate interpretation of the sheet sandstones as products of braided streams, the more so as channel geometry is rarely suggested. A mention of mudstone lining foreset laminae (Cotter, 1978) could represent inclined heterolithic stratification characteristic of point bar lateral accretion in meandering streams, but this needs verification.

**Tuscarora Formation, early-middle Llandoveryan (Early Silurian)** (Table 6.4). The Tuscarora is the best documented of the nine studied formations. It features overall very high proportions of sheet sandstones, sometimes conglomeratic. Cotter (1978, 1983) provides information that suggests broad and shallow channels (sheet channel geometry). Abundant basal scouring suggests frequent and important lateral migration in the river system within mobile channel belts. The frequent basal scouring, as well as the presence and sometimes abundance of shale intraclasts speaks of the potential presence in the system of more fine-grained facies than the observed coarse/fine unit proportions would suggest. The abundance of structureless sandstones in the context of the sheet geometry discussed above could indicate frequent non-channelized flow, assuming that the absence of structures is genuine, and not just cryptic bedding resulting from uniform grain size. All of the bedding types (horizontal, planar cross-bedding, and trough cross-bedding) seem to be frequent at least locally. Although fining-upward cycles are recorded by several authors, they cannot be interpreted in terms of fluvial style in the absence of
additional detailed information. Paleocurrent distributions are presented as largely unimodal by Whisonant (1977), but Folk (1960) showed weakly unimodal dispersions, and the measurements published by Yeakel (1962) exhibited considerable scatter at some localities. The information available for the Tuscarora is consistent with the traditional image of braided systems. Quantitative data on channel geometry, as well as careful study of the architecture of sedimentary units in outcrops would considerably strengthen this interpretation.

Shawangunk Formation, Early to basal “Middle” Silurian (Table 6.5). The basal part of the Shawangunk is laterally equivalent to the finer-grained Tuscarora Formation. The Shawangunk includes very high proportions of coarse, conglomeratic and sand-grade sediment in the lower and upper members, and somewhat lower (but still high) proportions of coarse-grained units in the middle member, forming sheet bodies. Epstein and Epstein (1972) mentioned sheets of coarse sediments in the Minsi Member (lower Shawangunk). Epstein (1993) recorded lenticular beds (sheet channels?) in all three members, and for the upper member gives one of the two more direct descriptions of channel geometry (“shallow channels are abundant”, p. L22). Basal scouring was abundant (hence the description of channel geometry), and shale intraclasts are frequent. Throughout the formation no structureless coarse units are mentioned, and horizontal and trough cross-bedding are most abundant, although planar cross-bedding is present and sometimes frequent. The lower member included fining-upward sequences and mud cracks, and paleocurrent distribution was said to be largely unimodal, although no detailed data are available. Assuming that the abundant shallow channels correspond to the lenticular beds described in the formation, and considering the abundance of basal
scouring, braided streams with wide shallow channels can be tentatively inferred as producers of the Shawangunk. The abundance of horizontal bedding, the frequency of planar cross-bedding, and the unimodal paleocurrent distributions support this interpretation, but quantitative data and architectural information on the sedimentary sequences are still needed.

**Bloomsburg Formation, Ludlowian (Late Silurian)** (Table 6.6). Information available on the Bloomsburg is very scarce. The coarse/fine sediment ratio is highly variable at among localities. Basal scouring is abundant, and shale intraclasts are present, as well as fining-upward sequences and mud cracks. Horizontal bedding seems to be the most frequent bedding type, but trough cross-bedding is also documented. Paleocurrent distribution in southeastern New York is bimodal, suggestive of tidal influences (Epstein, 1993). Interpretations based on such scarce data would be highly unreliable.

**Ringerike Group, Late Silurian, Oslo Graben, Norway** (Table 6.7). It includes three formations, the Sundvollen, Stubdal, and Holmestrand, all three representing fluvial sedimentation. **Sundvollen Formation, early-middle Ludlowian**—Information available on the Sundvollen suggests a braided style (frequent basal scouring and shale intraclasts, abundant structureless coarse units, frequent horizontal bedding and presence of planar cross-bedding, unimodal paleocurrent distribution). However, the relatively high proportion of fine sediment (roughly equal to that of coarse sediment), as well as the absence of any information on coarse unit and channel geometry, preclude reliable interpretation. **Stubdal Formation, late Ludlowian**—The Stubdal exhibits characteristics very similar to the Sundvollen formation, but features very high coarse/fine ratios. This, together with the mention of broad, shallow channels (Turner,
Holmestrand Formation, Pridolian-Lochkovian—Very sparse data available on this formation preclude any reliable information in terms of fluvial style.

Mweelrea Group undivided, Llanvirnian (Middle Ordovician), South Mayo Inlier, Ireland (Table 6.8). Pudsey (1984) described very high proportions of coarse sediment forming sheets with abundant trough cross-bedding and very rare horizontal and planar cross-bedding. Basal scouring was present, and the author described lenticular sedimentary units defined by changes in grain-size. Channel geometry is somewhat characterized, as Pudsey mentioned on one hand lenticular sedimentary units, “no deep channels, but only wide shallow scours” (p. 153), and on the other two clear examples of channels, 1.5 and 2 m deep, with steep and even undercut walls. One of the channels was cut into channel-fill sandstone and the other into fine-grained deposits, and both are filled with massive coarse-grained sediment. However, as width of the two channels is not given it is hard to include them in an interpretation of fluvial style. Current dispersion is unimodal, but with considerable scatter. Fluvial style was interpreted by Pudsey as braided with mainly sheet-flow, based on the very high proportions of coarse units, inferred low water/channel depth, and unimodality of the current dispersions. However, the absence of data on channel width weakens his interpretation.
6.4.4. Discussion

This survey of Ordovician and Silurian fluvial sequences relies on the information published by the different authors. Such an approach is heavily dependent upon the type, quality, and degree of detail of this information. The main problem with the information is its age. Most of the surveyed papers are old enough to have been published at times when most of the ideas that underlie what today we call fluvial sedimentology were only beginning to be formulated, if not simply unknown.

The data available are highly skewed toward lithology, and with a few exceptions (Smith, 1970; Turner, 1974; Pudsey, 1984) structures and facies are not given the importance they hold today. For example, in several of the papers trough cross-bedding is not differentiated from planar cross-bedding, and the two are collectively referred to as cross-bedding. Information on the geometry of sediment bodies is minimal. Except for the two channels reported by Pudsey (1984) no quantitative data is given, and even qualitative data on channel geometry is very rare (Turner, 1974; Epstein, 1993). In most cases qualitative channel geometry was only inferred from information on basal scouring or other indirect evidence, where available. Where it is not a result of the timing of publication with respect to recent advances in fluvial sedimentology, this situation very likely reflects the mainly lithostratigraphic focus of some of the surveyed publications.

Summarizing, the collected data set (Tables 6.2-6.8) is characterized by a general absence of quantitative information, a frequent lack of detail on sedimentary structures, and a complete absence of information on the spatial (vertical, but also lateral) relationships among sediment bodies at outcrop scale. This precludes reliable
interpretations of fluvial style based on the published information, and Table 6.9 summarizes this situation and the results of this survey.

The formations included in the survey have also been given different interpretations by the some authors, but available time did not allow a review of these interpretations. However, the fact that the units of the Appalachian Basin crop out along a large geographic area, as well as the long time interval represented by Shawangunk sedimentation, indicate that these units represent multiple river systems, the fluvial styles of which may have varied laterally and in time. Such a situation could possibly accommodate all or most of the interpretations given to the different formations, as shown by the work of Cotter (1983) on the Tuscarora. Studying the different facies of the formation and their geographic distribution in Pennsylvania, Cotter was able to reconstruct the geographic distribution of different depositional environments along the northwest dipping paleoslope of the Llandoverian Taconic foreland. His reconstruction shows a southeast to northwest facies change from 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.

To my knowledge, no detailed sedimentological study has been published recently on the alluvial sequences of the Appalachian Basin. The results of the present survey show how little we know on the fluvial styles characteristic of the rivers that deposited these units, in spite of the sometimes numerous publications that describe them. These results underscore the need for modern detailed field studies in order to understand the depositional environments and sedimentation history of an important part of the Lower Paleozoic of the Appalachian Basin.
7. BIOLOGICAL SOIL CRUSTS

Biological soil crusts, also known as microbiotic crusts, are described as thin crusts at the surface of the soil, consolidated by microorganisms, lichens and bryophytes (St.Clair and Johansen, 1993), as water-stable surface soil aggregates held together by algae, fungi, lichens, and mosses (Johansen, 1993), or as consolidated matrices of lichens, cyanobacteria, mosses and algae, that grow on soil surfaces (Evans and Johansen, 1999).

In my hypothesis, biological soil crusts are important in the search for the origin of land plants, because their composition and formation represent the closest extant analogue of the earliest types of ground cover and respectively of their mode of apparition. The climactic ground cover before the advent of land plants was probably very similar to the recent algal and lichen crusts, installed after colonization by bacteria and cyanobacteria. One of the most important effects of an organically active soil cover is represented by the biochemical weathering of the mineral matter by soluble organic compounds (Wright, 1985). Adding to the effects of physico-chemical factors, this leads to the weathering of rocks and sediments, a first step in soil formation. Beside that, the development of crusts with nitrogen fixation, as well as the contribution to the organic matter content through their primary productivity, led to accumulation of humus in the weathered substrate. Humus improves fertility and helps in better moisture retention. All these factors concurred in providing a favorable environment for the advent of land plants – soil.

In the present-day succession of biological soil crusts, installation and early development of the crust with microbes and lichens are followed by the installation of
mosses and finally of vascular plants, as the soil grows richer in organic matter. The earliest organic soils probably had the installation of a biological soil crust as a starting point that triggered subsequent production and accumulation of organic matter. Wright (1985) considers that the nearest possible analogues of the pre-late Silurian soil cover are those developed under lichens or moss cushions. Such soils (showing little mixing of the organic and mineral fractions and thin humus) are now seen only in settings in which higher plants are not prominent and would not represent the spectrum possible in the past. Once the land plants evolved, they not only thrived on stable soils, but also spread on their incipient stages, the microbiotic crusts. The installation of the earliest land plants would have represented thus the corresponding last successional stage in the development of the Paleozoic biological soil crusts.

The term cryptogamic crust was first introduced by Kleiner and Harper (1972). Other terms were also used to designate the same biological phenomenon: microfloral crust (Loope and Gifford, 1972), microphytic crust (West, 1990) or cryptobiotic crust (Belnap, 1993). On the other hand, St.Clair and Johansen (1993) recommend the usage of the term microbiotic crust instead of all others.

Microbiotic crusts are found today in various ecosystems: mesic environments, tropical and temperate deserts, as well as polar regions. In North America, they are most prevalent in the semiarid steppe regions in the Great Basin, Colorado Plateau, and Columbia Basin. They also extend into the hotter, more arid deserts in the southwestern regions of the United States.
Microbiotic crusts are very important in soil formation and stabilization and in the improvement of soil fertility. On primary substrates, algae trigger soil formation by promoting the weathering of silicate minerals. This is done by (1) the retention of water and (2) the production of carbonic acid as a result of photosynthesis (Metting, 1981).

Wilson and Jones (1983) have shown that lichens participate in the biochemical weathering of rocks and minerals, principally due to the activity of the mycobiont and in particular to the excretion of organic acids during growth. Many crustose lichens (and particularly their fungal components) generate oxalic acid and a variety of weak phenolic acids. The weathering effects from crustose lichens are similar to those observed in soils formed under cool temperature climates (where biochemical weathering is predominant); in both instances there is active breakdown of primary minerals combined with a virtual absence of well–ordered weathering products. Intense chemical weathering was ascertained in the immediate vicinity of the hyphae.

In early stages of soil formation, microbiotic crusts are the main factor of soil stabilization that results in a reduction of soil erosion (Snyder and Wullstein, 1973; St.Clair and Johansen, 1993). The crusts and the algae they contain help in the establishment of a stable soil structure through accretion of colloids, extracellular polysaccharides from filamentous sheaths, and individual and colonial mucilage. Soil particles aggregate around the colloids leading to an improved infiltration and percolation of water that reduces erosion. Algal crusts help in the preservation of the integrity of mature soils, as well (Metting, 1981).
Microbiotic crusts are also the only source of soil fertility in the very early stages of soil development. They improve the cation exchange capacity of the soils through contributions of organic material and by reducing the erosion of silts and clays (St.Clair and Johansen, 1993). Crust growth represents the avenue for the incorporation of organic carbon in sediments via photosynthesis. The higher the carbon content of the soil, the higher the proportion of heterotrophic metabolism and, thus, the higher the microbiological immobilization of nitrogen (West and Skujins, 1977).

Nitrogen is the element most commonly found in least supply (in forms available for higher plant nutrition) in xeric environments (West and Skujins, 1977). It is incorporated in sediments (soils) through nitrogen fixation by bacteria (Azotobacter-like), cyanobacteria (free-living or lichenized), and algae. According to Snyder and Wullstein (1973), mosses were not proven to fix nitrogen. These authors showed that numerous cyanobacteria fix nitrogen in pure cultures: most of them are in the Nostocales and a few in the Stigonematales; several of these occur in crusts on desert soils. In most of the nitrogen–fixing lichens, phycobionts are Nostocales.

In order to carry out nitrogen fixation, cyanobacteria need a minimum amount of moisture. West and Skujins (1977) considered that in xeric environments dew provides enough moisture for this process. On the other hand, Snyder and Wullstein (1973) have shown that in desert regions, nitrogen fixation by cryptogamic crusts occurs only during moist periods.

Even though the nitrogen content of soils associated with algal and lichen crusts is significantly greater than in other instances, the desert cryptogamic crusts appear to produce relatively small amounts of assimilable nitrogen. However, this is, essential to
the survival of the slow-growing biota in these environments (Snyder and Wullstein, 1973). Furthermore, accumulation of humus by microbiotic crusts through the incorporation of organic carbon and nitrogen, and the moisture it holds, leads to the establishment of a soil layer favorable to the installation of higher plants.
7.2. BIOTIC COMPONENTS OF SOIL CRUSTS

Cyanobacteria, bacteria, algae, fungi, lichens, and bryophytes are all reported from microbiotic crusts. As the different systematic groups present are still unequally studied, the available information is unbalanced from this point of view.

**Cyanobacteria** are favored by soils of higher pH (Flechtner et al., 1998). Microbiotic crusts include *Microcoleus*, *Phormidium*, *Plectonema*, *Schizothrix*, *Nostoc*, *Tolypothrix*, and *Scytonema* among the most common genera. *Microcoleus vaginatus* (Vaucher) Gomont is probably the most widespread species of microbiotic crusts (Johansen, 1993); however, in hot desert crusts *Schizothrix* is better represented (Cameron, 1960).

Most freshwater algal divisions are represented. Flechtner et al. (1998) reported high level of algal diversity in the microbiotic crusts of the central desert of Baja California (Mexico) – 66 species. In the cold winter semi-deserts of northeastern Great Basin (Utah), microbiotic crusts total up to 240 kg algal biomass·ha⁻¹.

*Chlorophytes* are abundant and ubiquitous in microbiotic crusts. They are distributed across the entire pH range, as are the *bacillariophytes* (diatoms); however, both groups are not very well studied in these occurrences. Other algal groups present are *eustigmatophytes*, *chrysophytes*, *xanthophytes*, and *euglenophytes* (Flechtner et al., 1998). *Rhodophytes* are reported from soils (Metting, 1981), but their presence in microbiotic crusts has not been recorded. In their review of microbiotic crusts, Evans and Johansen (1999) provided a list of the most common algae and cyanobacteria in North American deserts.
**Lichens** are common components of soil crust communities and sometimes account for a significant percentage of the ground cover of the crusts. According to Snyder and Wullstein (1973), some lichens are found only associated with mosses. Squamulose (minutely foliose), crustose, fruticose, and foliose types are present. The latter two are mainly vagrant (unattached); they tend to become entangled with detritus and may become temporarily attached to the soil during wet periods (St.Clair et al., 1993). These authors provide an annotated list of soil crust lichen taxa of the intermountain area of the western United States, and another list with species of soil crust lichens encountered in different environments.
7.3. TYPES OF BIOLOGICAL SOIL CRUSTS

Johansen (1993) wrote about three main types of crusts based on their general morphology: smooth and flat crusts, rough crusts, and uneven (pedicled) crusts. As this author pointed out, the type of crust at a particular location depends on the soil substrate and process of development. Biotic components also vary with the crust type: (1) smooth and flat crusts are dominated by algae; they are typical of areas of ephemeral ponding; (2) rough, uneven crusts are lichenized when mature and usually occur on silty, often saline soils of flat basins; (3) pedicled crusts are either mainly algal or lichenized; pedicles attain 6 cm in height; they typically occur in erodible soils on land with some topographic relief, or in shallow soil pockets in slickrock habitats (e.g. areas of exposed sandstone).

The morphology of the crust surface varies from flattened, polygonal, possessing a rough, undulating surface, to pedicled (St.Clair and Johansen, 1993) and types of crusts are defined on the basis of this microtopography. The different morphologic crust types may also reflect succession, as flat crusts of some areas are thought to represent the early stages of rough or pedicled crusts (Johansen, 1993).

Another classification (Eldridge and Greene, 1994) defined three main types of microbiotic crusts on the basis of their position with respect to the soil surface: (1) hypermorphic crusts developed above ground, on stable soil substrates, and comprise mainly mosses and liverworts; these are the most susceptible to disturbance; (2) perimorphic crusts spread at ground, both above and below the soil surface; their principal components are crustose, squamulose, foliose lichens and to a lesser extent endedaphic and epedaphic algae; they have intermediate tolerance to disturbance; (3)
cryptomorphic crusts are developed below ground, mainly by cyanobacteria, algae, and filamentous fungi; these are the most tolerant to disturbance because of their less exposed position.

Rain crusts are very thin and fragile cryptomorphic crusts, often cyanobacterial, that are common in areas with sporadic ponding of water. Between rain events their surface cracks and curls upward (Metting, 1991). They can be seen as initial stages in the formation of microbiotic crusts.

The different types of crusts can occur associated in different proportions depending on the substrate and on the degree of colonization by biota. For example, Anderson et al. (1982a) described cryptomorphic to perimorphic crusts developed on fine-grained (silty) soils. A cemented layer that they called a vesicular layer, which is resistant to trampling disturbance, subtends these crusts. When dry, the soil cracks, as well as the crust, revealing a polygonal surface structure. On gypsiferous soils, which are very poor in supporting vascular plant growth, highly lichenized perimorphic crusts often develop.
7.4. BIOLOGICAL SOIL CRUSTS AND THE ABIOTIC ENVIRONMENT

Microbiotic crusts have been shown to develop faster on silty soils with high electrical conductivity and rich in phosphorous (Anderson et al., 1982a). Crust buildup is also positively correlated with soil alkalinity (Johansen and St.Clair, 1986). Johansen (1993) noted that cyanobacteria are absent in acidic soils, whereas soils of pH 8-9 are capable of supporting vigorous microbiotic crust communities.

In the present day, microbiotic crusts are best developed in arid regions, where low water availability prevents continuous plant cover, allowing large areas of the soil surface to be exposed to direct sunlight (Metting, 1991). Part of this resistance is due to that of soil algae. Some algae are able to resist prolonged periods without water; they are well adapted for existence in environments and climatic zones where moisture is the primary limiting factor. Buried, resting stages of soil-surface algae have been proven to remain viable for nearly a century (Metting, 1981). This is because soil algae are able to utilize gaseous water in order to maintain metabolic functions, in approximately the same way as lichens do (Lange et al., 1970). Moreover, some green algae and cyanobacteria can survive temperatures >100°C when dormant in dry soil (Metting, 1981).

On the other hand, in the cold winter semi-deserts of northeastern Great Basin (Utah), crusts cover the soil (up to 70% of the surface of the soil) shortly after snow melt (West and Skujins, 1977). Here the crusts are made of lichen-moss matrix with cyanobacteria.

In addition to their resistance, algae are easily dispersed, as air currents constitute a constant source of algal propagules. Among algae, green algae are known to be able to
live at lower nutrient levels than other algae in soils (Metting, 1981). Most microbiotic crust algae live generally within the top centimeter of the soil, with the highest concentrations at the surface (*endedaphic*). The only commonly *epedaphic* taxa found in deserts are *Nostoc* taxa (Evans and Johansen, 1999).

The lichens growing on the soil are known as *terriculous* (Evans and Johansen, 1999). A few associations characteristic of soil crusts have been observed (Snyder and Wullstein, 1973). (1) Some lichens are found only associated with mosses – mosses provide a more favorable environment with greater moisture and/or a more nutrient-rich substrate; lichens supply some usable nitrogen to mosses. (2) Lichens (*Dermatocarpon*) form interspecific associations with free-living cyanobacteria. Lichens resist surface erosion, consolidate the soil, offering protection to the free-living algal communities; cyanobacteria provide some of the necessary nitrogen to lichens. (3) Epiphytic cyanobacteria and/or associated bacteria may form associations with mosses and lichens.
7.5. SUCCESIONAL PATTERNS IN BIOLOGICAL SOIL CRUSTS

Soil algae and cyanobacteria play the major role in the initiation of crust development. Particularly, filamentous cyanobacteria form a mat on the soil surface during times of moist, moderate weather. This mat consolidates the soil under it (Johansen, 1993). According to Metting (1981), the succession of soil colonization begins with algal crusts that are further lichenized. St.Clair and Johansen (1993) also show that after disturbances there is first recovery of cyanobacteria and then recovery of lichens and mosses. However, studies of the colonization of the ash from Mount St. Helens by Rayburn et al. (1982) showed that cyanobacteria are not obligate, ubiquitous colonizers. In desert environments lichen crusts are often seen as the climatic climax, although in some instances, e.g., in parts of the Sahara, algal crusts have been proven to be stable (Metting, 1981).

In their study of the effects of fire disturbance on microbiotic crusts of a desert shrubland area of Utah, Johansen et al. (1984) examined some patterns of recovery following disturbance. Algae were the first crust organisms to invade the burned area and achieved full recovery within five years after the fire. In contrast, lichen and moss species recolonized at a much slower rate. Among lichens, the first to re-establish were those with specialized asexual propagules containing both symbionts (Collema). Only one of the several moss species living on unburned areas re-established in the burned ones in the five years following the fire (Pterygoneurum). Even seven years after the fire the recovery of lichens and mosses was incomplete in terms of both biomass and
community composition. The recovery would probably have been even slower in the
presence of grazers to trample the crusts.

Recovery from grazing in a microbiotic soil crust community was studied by
Johansen and St.Clair (1986) in the same desert shrubland area of Utah. The grazed area
had been protected from grazing for seven years before being compared with an adjacent
area that has been protected for twenty years. Their results demonstrate that the algal
community had essentially recovered in the seven years following removal of livestock
from the range, whereas the lichen and moss communities were still in the process of
recovery. The significantly greater amount of a particular lichen species (*Dermatocarpon
lachneum*) in the more recently grazed area as compared to the area protected from
grazing was hypothesized to represent an intermediate successional stage in the recovery
process.

Anderson et al. (1982b) found that lichens and mosses had become fairly well
established after a 14-17 year period of protection from grazing on Utah winter ranges.
Exclosures protected for 37-38 years showed little change in the moss flora, though
lichen diversity was greater than in the 14-17 year old exclosures. This contrasts with
Johansen and St.Clair's (1986) results, but the latter suggested that the faster recovery of
the algal component in the soil crusts of their study may be the result of precipitation
above the mean during the period of their study. The higher level of precipitation may
have accelerated the crust recovery effect, at least for its algal component. A study by
Johansen (1984) showed that excessive soil moisture affects differently the varied groups
of organisms that constitute the soil crust. He compared the composition of an algal soil
crust in the Great Basin desert (Utah) before and after a hundred-year storm. The storm
event induced a dramatic increase of soil moisture, from a mean of 3.9% before the storm to one of 20.6% after the storm. It generated significant changes in the composition and biomass of the soil crust community. But rather than a simple increase in all species present, the algal community showed increases in some groups and decreases in others. *Anabaena, Nostoc, Phormidium*, as well as the whole group of chlorophytes, showed significant increases, whereas diatom numbers dropped dramatically. This suggests that such events, which are not rare on a larger time scale, may strongly influence the succession in microbiotic crusts by “resetting the counter” of species proportions at a relative “zero” from time to time. However, this has to be verified by further studies on how quick the crust communities recover after such events.

Johansen and St.Clair (1986) pointed out that the conclusions reached by Anderson et al. (1982b) may actually have a more general applicability than theirs: in drier areas or drier years development of the algal soil microbiotic crusts following grazing disturbance might take longer than the seven-year period observed by them.

In conclusion, recovery of soil microbiotic crusts from disturbance follows several trends. Algae are the most resistant component to disturbance and are also the quickest to recover. Lichens and mosses are slower to recover. Whereas lichens and mosses may take as long as 14-17 years to recover, the algal component of the crusts may take less than seven years to recover, especially if recovery is favored by precipitation above the mean of the region.
8. THE KISER LAKE BIOTA

8.1. MATERIAL AND METHODS

Fossils were recovered from a sample taken at 87.6 m of depth in drill core no. 3061, drilled in 1991 for the Division of Geological Survey (Ohio Division of Natural Resources) and located at the Ohio Geological Sample Repository, Horace R. Collins Laboratory. The core was drilled on the beach at the eastern end of Kiser Lake, in Kiser Lake State Park, Champaign County, Ohio, 40°11’09”N, 83°57’13”W (Figures 8.1, 8.2). As discussed below, the sample is attributable to the Brassfield Formation of middle Llandoverian age.

The drill core was split longitudinally and one half remained at the Ohio Geological Sample Repository as a voucher specimen. The other half (Figure 8.3.A) was analyzed in the Paleobotany Laboratory at Ohio University. The fossil material occurs in a thin brown shale lamina (up to 2 mm thick) within calcareous dolomite, where it forms a few black patches scattered on the split surface of the rock. Most of these patches are submillimetric and just two of them exceed 4 mm, hence the term mesofossils. Most of the patches appear amorphous, but under closer examination a few of them exhibit a consistent morphology. The fossils are preserved as coalified compressions and impressions on the shale surfaces on both part and counterpart (Figures 8.3.B, C). They consist of impressions covered by very thin black films that are profusely fissured and broken into angular fragments (Figure 8.4). The minute fragments (generally between
20-80 µm) often flake off of the rock surface leaving delicate outlines of the fossils (Figure 8.4 at arrowheads).

Fossils were observed in oblique reflected illumination using a Zeiss microscope. High resolution images were captured via a MicroLumina digital scanning camera (Leaf Systems, Bedford, Mass.) and a PhotoPhase digital scanning camera (Phase One A/S, Frederiksborg, Denmark). Due to considerable relief of the rock surface and small size of the specimens, the outlines of the fossils are not immediately apparent on these images. In order to render a better image of the specimens, outlines of the part and counterpart were traced on composite digital images created from images taken at several focal planes (Figure 8.5). To avoid interpretive errors, only the most reliable compression and impression outlines were traced. Following tracing of compression-impressions, the two drawings corresponding to the part and counterpart were superimposed, rendering a more complete image of the fossil (Figure 8.6).

Following imaging of the fossils as described above, shale containing the counterpart of the fossils was processed using palynological techniques with the aim of recovering the fragments of coaly film and any other palynomorphs embedded in the mineral matrix of the shale. Processing involved hydrochloric and hydrofluoric acid digestion, alkali (NaOH) removal of soluble organic matter, nitric acid oxidation, and heavy liquid flotation (ZnCl₂, 1.9 g·cm⁻³). Acid maceration of the shale produced abundant amorphous organic matter. However, after dissolution and cleaning of the latter with alkali and nitric acid, very few palynomorphs were left. This was to be expected considering the small sample size (< 0.7 cm³ of shale) and minute fragments of coaly
film. Permanent microscope slides were mounted using Eukitt (Calibrated Instruments, Hawthorne, N.Y.) xylene-soluble mounting medium.

All type, cited and figured material has been deposited in the Ohio University Paleobotanical Herbarium, Athens, Ohio, under the accession numbers OUPH 14495, 14496.
8.2. LOCALITY, STRATIGRAPHIC CONTEXT, AND AGE

At the depth the fossils were found, the rock is calcareous dolomite, yellowish-gray, with coarse crystalline dolomite and calcareous cement, and thin, wavy to irregular bedding. The fossils were embedded in a 2-3 mm thick lamina of brown shale. As shown by the well log for core no. 3061 on file at the Division of Geological Survey (Ohio Division of Natural Resources), the sample belongs to Sub-Lockport undifferentiated rocks of the Early Silurian, and comes from 0.8 m above the contact of the sub-Lockport with underlying Late Ordovician rocks. The Late Ordovician is undifferentiated, and the Ordovician - Silurian contact is gradational over approximately 0.3 m.

"Sub-Lockport undifferentiated" and "Upper Ordovician undifferentiated" are generic terms based almost exclusively on lithology and used extensively in the expeditive description of drill cores. In this part of Ohio the Ordovician – Silurian boundary is designated in drill cores at the sometimes gradational transition between more shaly, silty facies (Ordovician) and calcareous (limestone, dolomite) facies (Silurian). For a first approximation, the use of these terms allows rapid orientation within the laterally restricted sedimentary sequences seen in drill cores. However, this information lacks the stratigraphic resolution needed in this study for assessing the age and depositional environment of the samples. Better characterization of the stratigraphic position of our sample can be derived from a number of studies that address the geology of the Silurian in Ohio.
As pointed out by Janssens (1977), Silurian rocks of Ohio are sometimes difficult to correlate, even over relatively short distances, because of facies changes. Hansen (1998) stressed that although they have undergone much study and subdivision, Silurian rocks of Ohio are still incompletely understood. He attributed this to significant lateral changes in rock types and thicknesses, and to the lack of good exposures. Where the shale component of the carbonate rocks between the Ordovician and the Lockport Group is absent, these similar stratigraphic units become indistinguishable (Janssens, 1977). The generic name “Sub-Lockport” is used to designate such Early Silurian sedimentary sequences below the Lockport Group.

According to Kleffner et al. (1989), the most complete stratigraphic succession at the Ordovician-Silurian boundary in west-central Ohio includes the Preachersville Member of the Drakes Formation, the Centerville beds, and the Belfast Member of the Brassfield Formation. However, the same authors pointed out that this complete succession does not occur everywhere in west-central Ohio because the Centerville beds are not present at all locations throughout the region. The Preachersville Member and the Belfast Member, which is also absent at places, are well dated by fossils to the Late Ordovician and Early Silurian respectively. However, the fauna of the Centerville beds does not presently allow a definitive attribution of this unit to either the Late Ordovician or the Early Silurian (Kleffner, personal communication, 2002). According to Kleffner et al. (1989), the unit is similar to the underlying Late Ordovician Drakes Formation. Both are characterized by a high content of shale and silty material. However, the lithology of the undifferentiated Late Ordovician of the drill core as described in the log for well no. 3061 is also mainly shale. Taking into account that in drill cores the Ordovician –
Silurian boundary is usually defined at the first appearance of carbonate, this suggests that the uppermost part of what is described as Ordovician in the core may in fact represent the Centerville unit. Our sample, taken at 0.8 m above the Ordovician – Silurian contact can therefore be assigned with a reasonable degree of certainty, to either the Belfast Member of the Brassfield Formation (if present in the area), or to the Brassfield Formation proper (Figure 8.7). According to O'Donnell (1967), the age of the Belfast Member is middle Llandoverian (Early Silurian) and it corresponds more precisely to the A₄ brachiopod zone. The same author showed that the base of the Brassfield Formation is dated at various locations in Ohio and Kentucky to the A₄–B₁ brachiopod zones. Therefore, the age of the fossils is middle Llandoverian – Figure 4.1.

The area that is today Ohio was in tropical latitudes during the Silurian, just south of the 15°S parallel (Scotese and McKerrow, 1990). It was covered by shallow, epeiric seas during the Llandoverian (Berry and Boucot, 1970). Sedimentation in the area is represented mainly by carbonate rocks with minor terrigenous sedimentary inputs, as upland areas (i.e., the Late Ordovician Taconic mountains) were far to the east (Hansen, 1998). During the time interval that encompasses the Ordovician – Silurian boundary, the region witnessed at least two regressive-transgressive cycles that generated unconformities in the stratigraphic record. The fall in sea level at the end of the Ordovician, attributed by Berry and Boucot (1973) to glaciation in the Southern Hemisphere, eventually exposed most of the region corresponding to western Ohio before the first Llandoverian transgression. Uppermost Ordovician rocks (the Drakes Formation) correspond to very shallow water or tidal flat environments (O’Donnell, 1967; Hansen, 1997). The emergence and erosion of Ordovician rocks before the
beginning of Silurian deposition is documented by unconformable contacts between different Late Ordovician and Early Silurian units, some of which are absent at different localities (O’Donnell, 1967; Kleffner et al., 1989; Mark Kleffner, personal communication, 2002), and by the presence of reworked Ordovician material in the Belfast Member (Rexroad cited in Gray and Boucot, 1972; Mark Kleffner, personal communication, 2002). Gray and Boucot (1972) documented a very shallow marine (if not terrestrial) hiatus at the Ordovician – Silurian boundary on the east side of the Cincinnati Arch, based on the relative abundance of putatively terrestrial palynomorphs, as compared to marine palynomorphs, in the rocks immediately below and above the boundary.

The palynology of the Ordovician – Silurian boundary in Ohio has been studied by Gray and Boucot (1972). These authors used the palynomorph contents below and above the Ordovician – Silurian paraconformity to infer shallowing marine environments (not excluding subaerial exposure) in the time period encompassing the boundary. In a series of articles, Taylor (1995, 1996, 1997) analyzed ultrastructure and its functional and evolutionary implications, for spore tetrads and dyads recovered from Late Ordovician - Early Silurian deposits of southern Ohio.

The top of the Centerville Formation, also composed of tidal flat deposits (Riddle, 1991), is thought to record another unconformable contact with the overlying Belfast Member of the Brassfield Formation (Kleffner et al., 1989). These authors base this interpretation on the distribution and reworking of microfossils and lithic evidence and attribute the regression to a eustatic sea level fall in the Rhuddanian, or to the uplift of the Cincinnati Arch.
Riddle (1991) interpreted the Brassfield Formation as a carbonate bank to reefal-lagoonal deposit. On the paleogeographic map of Droste and Shaver (1983, p. 18), Champaign County falls on the limit between land and sea for the period of deposition of the first half of the Brassfield Formation. In an analysis of the Brassfield in southwestern Ohio, Hendricks (1983) found evidence that deposition of the Brassfield Formation generated a complex carbonate facies mosaic, in response to an irregular, shallow sea-floor profile. Based on litho- and biofacies, he suggested that the Belfast Member at the base of the Brassfield Formation represents tidal flat deposition and argues that conditions were periodically intertidal, and that isolated supratidal exposure surfaces may have existed in the region at the time. A third regression may account for the probable unconformable contact at the top of the Belfast member, suggested by Rexroad et al. (1965), O’Donnell (1967) and Hendricks (1983).

The evidence presented so far points to the conclusion that nearshore marine to intertidal and even locally supratidal conditions were generalized in the west-central Ohio region throughout the time period spanning the uppermost Ordovician and the beginning of the Silurian (middle Llandoveryan). Summarizing these geologic data we conclude that the stratigraphic position of our sample is generally consistent with a middle Llandoveryan age, characterized by sedimentation occurring in a subtidal to supratidal environment.
8.3. DESCRIPTION OF FOSSILS

Names will be validated by subsequent publication.

8.3.1. *Quasihepatica*

INCERTAE SEDIS

Genus *Quasihepatica* new genus

**Type species.** *Quasihepatica multifida* new species, by monotipy (Figures 8.3-8.6, 8.9).

**Diagnosis.** Tuft of flat, elongated, branching lobes that diverge from a central, somewhat linear zone. Lobes divide twice producing long, narrow segments; first division anisotomous; second, apical division isotomous. Segments narrowing significantly immediately distal to each branching from the lobes. Forking sinuses rounded. Narrow segments divide producing acute sinuses. Preserved as fragmentary, millimetric-scale compressions and impressions of palmate or fan-shaped outline.

**Etymology.** From Latin, *quasi-*, almost, and Hepaticae for liverworts, emphasizing similarity with dissected liverwort leaves.

**Occurrence.** As for the species.

**Discussion.** See discussion of *Quasihepatica multifida* below.
*Quasihepatica multifida* new species (Figures 8.3-8.6, 8.9)

**Diagnosis.** As for the genus.

**Description.** *Quasihepatica multifida* represents fragmentary remnants of a larger entity, preserved as compressions and impressions of black, carbonaceous filmy material. The crossing of compressions and impressions at several places on the rock surface (Figure 8.6) suggests a three-dimensional morphology for the organism. The size of the fossil slightly exceeds 5 mm. The coaly films are profusely fissured and flake off the rock surface easily. Specimens display a tuft of palmate or fan-shaped outline. Flat, elongated first order lobes diverge from a central, somewhat linear zone. The lobes divide at least twice. The first branching is anisotomous, whereas the second, apical branching is isotomous. Branching angles are wide and markedly rounded. At each branching a dramatic reduction in width occurs. Segments departing from the lobes narrow significantly, immediately distal to each branching. They are very elongate and narrow, and broken apically. The narrow segments fork isotomously at acute angles.

Width could be measured for only one of the first order lobes: 392 µm at the level of the branching. Second order branches (two measured) are 211 and 262 µm wide at the level where they branch to produce long, narrow segments (third order branches). The latter, as well as some second-order branches, are 37 – 82 µm wide (mean = 54.6 µm; n = 7) at the base and taper very gradually down to 16 – 46 µm (mean = 29.0 µm; n = 7). The longest uninterrupted feature, comprising a first order lobe with second- and third-order branches (Figure 8.6), is 2.1 mm long. The first order lobe is 563 µm long and the larger second order branch is 512 µm long; the longest third order branch is 1096 µm.
**Etymology.** From Latin, *multifida*, branched several times.

**Holotype.** Compression-impression in drill core sample OUPH 14495, Figures 8.3-8.6, 8.9. Middle Llandoverian. Base of Brassfield Formation. Drill core extracted from well no. 3061, on beach at the eastern end of Kiser Lake, in Kiser Lake State Park, Champaign County, Ohio, USA, 40°11'09"N, 83°57'W, at 87.6 m of depth.

**Occurrence.** Champaign County, Ohio, USA. Middle Llandoverian.

**Discussion.** Several groups of organisms including algae, plants, graptolites, and chitin-containing animals preserve as carbonaceous compressions. However, *Quasihepatica* has morphology that is unlike any previously described fossil. Palmate shape, a dramatic reduction in width at branching points, and the wide, rounded angles of branching are reminiscent of the Late Ordovician alga *Manitobia* Fry (Fry, 1983). However, the thallus of *Manitobia* lacks the elongate ultimate order branches of *Quasihepatica*. Also, *Manitobia* and related extant algae are at least two orders of magnitude larger than *Quasihepatica*.

Several oscillatoriacean cyanobacteria including species of *Hydrocoleum* Kütz., *Dasygloea* Thwaites, or *Schizothrix* Kütz., characteristically form bundles of trichomes ensheathed together (Desikachary, 1959). These bundles divide to produce tufts of branching sheaths similar in size to *Quasihepatica* and characterized by a reduction of width at branching points. However, branching angles of these cyanobacterial taxa are almost always acute and never as rounded as those of *Quasihepatica*.

Additional evidence present in the palynologic material also speaks against a cyanobacterial origin of *Quasihepatica*. Several fragments of cellular tissue were recovered from the palynological preparations, and most of these represent
*Quasihepatica*. The largest fragment is 194 by 125 µm. The material preserves the walls of spherical cells that range 4 – 11 µm (mean = 7.8 µm) in diameter. Some of the tissue fragments consist of at least two layers of cells (Figure 8.8), suggesting algal or plant parenchymatous tissue, or fungal pseudoparenchymatous tissue. Similar and slightly larger cell agglomerates have been reported by several authors. Sheets of spheroidal cells are figured, but not described by Timofeev et al. (1976, Fig. IX.4) from the Neoproterozoic of Siberia, and by Samuelsson and Butterfield (2001, p. 243) from the Neoproterozoic of northwestern Canada. Clusters of sporelike cells (*Synsphaeridium Combaz*) are described by Strother et al. (1996), from the Middle Ordovician of Saudi Arabia. It is unclear whether any of these form multi-layered tissue like the fossils described here.

The particular type of branching exhibited by *Quasihepatica* is strikingly similar to the dissection pattern in leaves, underleaves, bracts, and perianth mouths of certain leafy liverworts (Hepaticae), such as *Plagiochila* (Dumort.) Dumort., *Ptilidium* Nees, *Trichocolea* Dumort., *Microlepidozia* (Spr.) Joerg., and *Acrobolbus* Nees. Both *Quasihepatica* and these living liverworts have broader first order lobes that divide into second- and sometimes third-order lobes that are long and narrow (Figure 8.9). Likewise, *Quasihepatica* and the living liverworts all display prominently rounded sinuses between dividing lobes. Although the overall sizes of the liverwort appendages are typically only 1/2 - 1/5 that of *Quasihepatica*, the sizes of the ultimate lobes of the living liverwort appendages (Schuster, 1966, 1969, 1980) do overlap those of the ultimate segments of *Quasihepatica*. Liverwort leaves are typically unistratose, but pluristratose leaves or leaf bases comparable to the multilayered tissues obtained from our maceration (Figure 8.8)
Smaller cells in liverwort leaves (e.g., the austral genus *Isolembidium* Schust.; Malcolm and Malcolm, 2000) fall within the size range of the larger cells in the fossil tissue fragments. However, the size and shape of cells in the tissue fragments also correspond to those seen in the pseudoparenchyma of *Palaeosclerotium pusillum* Rothwell, a fungal taxon of ascomycetous affinities (Rothwell, 1972b; Dennis, 1976).

### 8.3.2. Problematic Form with Imbricate Margin (Figures 8.10)

**Description.** This mesofossil exhibits the same type of preservation as *Quasihepatica*: compressions represented by thin, black carbonaceous film, cracked and flaking off easily, and impressions. The preservation is very fragmentary on both part and counterpart, but the general shape of the fossil suggests a rather elongated habit. The most striking feature is the margin of the fossil where compressions and impressions form a jagged edge that suggests an imbricate anatomy of the living organism. The preserved size of the compression/impression is 0.35 X 1.02 mm.

**Discussion.** The jagged edge of the fossil is reminiscent of imbricate stratification in the sheaths of nostocalean and oscillatorialean cyanobacteria such as *Petalonema* Berk., *Gloeotrichia* Ag., *Schizothrix* Kütz., *Scytonema* Ag., or *Stigonema* Ag. (Desikachary, 1959). However, the sheaths of these taxa range 24 – 115 in width, falling well below the preserved width of the fossil (0.35 mm). The jagged edge of the specimen is also reminiscent of arthropod appendages. However, no cuticular remains of possible chitin were present in the palynological preparations. Therefore, there is no
evidence that arthropods occur in the assemblage, and the affinities of this fossil are unknown.

8.3.3. Additional Fossil Material

**Carbonaceous Compressions.** The split surface of the shale exhibits several other mesofossils in the form of carbonaceous compressions with the same type of preservation as *Quasihepatica*, all smaller than 5 mm. Many of them lack consistent morphology and were not studied in detail. The largest of these mesofossils (Figure 8.11.) is 4.7 mm long and under careful examination shows longitudinally oriented coaly streaks that do not form any consistent pattern.

**Microfossils.** Organic residue extracted from the shale using palynological techniques comprises fragments of tissue (described above) and several spores. One cryptospore (23.5 μm in diameter) is an alete monad with circular, undulating ambitus (Figure 8.12). The upper surface of the cryptospore is laevigate and finely wrinkled, whereas the lower surface is ornamented with microgranules 0.5 μm in diameter, < 0.5 μm tall and 0.8 – 1.2 μm apart. As the spore is compressed and the equatorial area is locally folded over the laevigate surface, which is wrinkled itself, it is difficult to identify a subequatorial crassitude. However, the fact that the granules extend up to the ambitus, where they can be seen in lateral view, is a good indication that a subequatorial crassitude probably delimits the laevigate area from the ornamented area that extends from the lower surface across the ambitus of the cryptospore. All of the features of this
cryptospore are comparable to *Cymbohilates disponerus* Richardson, a tenuihilate cryptospore described by Richardson (1996a) in the Early Devonian Lower Old Red Sandstone of the Anglo-Welsh Basin.

Three ovoid-cylindrical, transversely multiseptate spores were present in the palynologic material. Only one of them is complete (Figure 8.13), while the two others are preserved for approximately 2/3 – 3/4 of their length. The complete spore is 36.3 μm long and the other two can be estimated to fall within the same range of length, judging by the size of the preserved fragments. The widths of the spores are 7.4, 8.4 and 12.3 μm. The complete spore displays four septa, or possibly five with the fifth one less well defined; the two incomplete spores preserve four septa. The spore walls and septa are thin and the surface of the spores lacks ornamentation. These spores have the same morphology and their sizes fall within the range of sizes of the spores described by Sherwood-Pike and Gray (1985) and interpreted as ascospores or the conidial stage of ascomycetes. They also conform to the size range of conidia and ascospores in general (Alexopoulos et al., 1996). The complete spore is more rounded at one end and it tapers somewhat at the other end. The latter is reminiscent of both the place of attachment of a conidia to a conidiophore, and to the morphology of ascospores produced within asci. Based on these lines of evidence we assign the spores to the Ascomycetes.
9. THE PASSAGE CREEK BIOTA

One notable exception to the general paucity of terrestrial macrofossils prior to the Wenlockian is the Passage Creek biota. Preserved in Early Silurian (Llandoveryan) deposits of the Appalachian Basin in Virginia, the Passage Creek biota presents the defining challenge of all non-paradigmatic assemblages: the external morphology of the fossils preserved as compressions does not allow for *a priori* assignment to any particular kingdom of life. Moreover, preliminary assessment of the internal structure of the fossils using light and electron microscopy has revealed profound diagenetic obliteration of the original anatomy (Tomescu and Rothwell, 2004), quite expectable considering the preservation as compressions. However, the challenge of this biota is all the more enticing as it includes some of the earliest macrofossils preserved in continental deposits, and the oldest known extensive macrofossil assemblages in such settings. These fossils are 15 million years older than the first vascular plant, *Cooksonia* (Edwards and Wellman, 2001), and 25 million years older than the oldest unequivocal terrestrial animal fossils (Shear and Selden, 2001), and they comprise the earliest evidence for complex life on land (Tomescu and Rothwell, 2004). As such, the Passage Creek biota could hold the key to resolving fundamental questions about the organisms involved in early stages of the colonization of land, and about the evolutionary patterns leading to the first embryophyte-dominated terrestrial biotas.
9.1. PREVIOUS STUDIES

The locality, first reported by Pratt et al. (1975a, b), is well known for microfossils, but it also yields the oldest macrofossil assemblages known from non-marine deposits. Fossils occur in the lower member of the Massanutten Sandstone, the age of which is early-middle Llandoverian (Early Silurian). All previous studies of these fossils (Pratt et al., 1978; Niklas and Pratt, 1980; Niklas and Smocovitis, 1983) acknowledge their terrestrial origin, but fail to recognize that they are the earliest megafossil assemblage. As a consequence, they generally overlook the external morphology of the fossils to study directly the dispersed microfossils obtained by bulk maceration of the fossiliferous rocks. These include cryptospores, fragments of cuticle, smooth and banded tubes, and fungal hyphae tentatively assigned to the Deuteromycetes.

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 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. 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. Studies of the Tuscarora Formation, which is stratigraphically equivalent to the lower Massanutten Sandstone, in Pennsylvania by Strother and Traverse
(1979), and Johnson (1985), reported dispersed microfossils of the same type, except for fungal hyphae. Based on the fluvial origin of the fossiliferous rocks, Pratt et al. (1978) considered this fossil assemblage to represent the oldest evidence of non-vascular, thalloid land plants. They probably used the term plants in a very inclusive manner, since at the same time they assigned the fossils to the nematophytes, a group of unresolved systematic affinities (section 4.2.2).

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 describe cuticle-like fragments and three types of tubular elements, including an interesting fragment of tissue that incorporates longitudinally aligned smooth and banded tubes. Based on the disposition of the tubes (several smooth walled tubes surrounding 2-3 larger banded tubes), and on analogy with present-day embryophytes, the strand of tubular cells was tentatively interpreted as conducting tissue. The authors nevertheless emphasized that until more is known about anatomy and morphology, the systematic affinities of organisms represented by the fossils will remain conjectural.
9.2. MATERIAL AND METHODS

9.2.1. Fossil Material

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 (38°56′43″N; 78°18′18″W; Figures 8.1, 9.1; see also 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 (Figure 9.2). The fossil assemblages are preserved in most of these numerous, finer-grained layers present at multiple levels throughout the lower Massanutten Sandstone. Thickness of the partings ranges from a few centimeters to over 10 centimeters. 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 varying between 0.3 and 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 macrofossils are preserved as abundant compressions that form black carbonaceous films of varying thicknesses on multiple bedding planes separated by millimetric clastic laminae. They are most commonly exposed as cleaved compressions (*sensu* Chaloner and Collinson, 1975) on the split bedding planes – the cleavage plane passes through the coaly material, giving two complementary compressions. Coalified compression (Schopf, 1975) is the most common mode of plant fossil preservation. Representing the prime source of evidence for the overall morphology of plants, and sometimes offering exquisite detail (e.g., the conifer pollen cone described by Hernandez-Castillo et al., 2001), macrofossil compressions are notoriously frustrating for those trying to understand the anatomical underpinnings of a particular architecture. The diagenetic processes involved lead, among others, to collapse of internal cell spaces and subsequent consolidation of the plant material (Schopf, 1975). As a result, except for thick woody fossils (e.g., twigs and tree trunks in lignite) where anatomy, although highly altered, is still recognizable, the cellular construction of tissues is most frequently obliterated to the level that only traces of the original anatomical structure are preserved. Except for a few particular instances (e.g., *Cooksonia* tracheids of Edwards and Davies, 1976; *Nematothallus* filamentous structure of Strother, 1988), the only anatomical information they offer is that of external features preserved in cuticles. Hence, studies of compressions have traditionally concentrated on the external morphology and architecture of plants, cuticular anatomy, or the spores that may be preserved in situ in sporangia (e.g., Wellman et al., 1998). Preparation techniques used in such studies typically include degagement (Fairon-Demaret et al., 1999), bulk acid maceration (Wellman and Axe, 1999), transfers (Abbott, 1950; Jones and Rowe, 1999), acetate peels
(e.g., Strother, 1988), or cuticle extraction (e.g., Kerp, 1990), and may be coupled with light- and electron microscopy.

**9.2.2. Why a Polyphasic Approach?**

The approach used to characterize the Passage Creek fossils is constrained by three attributes of this biota. One is represented by the mode of preservation as compressions, and the incumbent alteration of the morphological and anatomical information stored in the fossils. The second attribute refers to the non-paradigmatic condition of the Passage Creek biota and the associated lack of a systematic reference framework. These two conditions result in an unappealing situation whereby the information borne by fossils is altered and fragmentary, as well as not easily comparable to a particular modern group. In other words, we are trying to understand unknown organisms based on a biased set of features, without knowing the amount of bias, or the significance of the features. The first step in overcoming these constraints therefore necessarily consists of characterizing as many of the preserved morphological and anatomical features as possible in order to maximize the completeness of the information recovered from the fossils. This is best achieved by use of a polyphasic approach involving investigation of the fossils with several techniques that recover complementary information. Integration of the different types of information can then produce as complete as possible characterization of fossils, which can ultimately lead to an understanding of their affinities.
The third attribute refers to the very brittle nature of the carbonaceous material in the compressions, and to the fact that it is profusely fissured due to diagenesis. The fossils disaggregate into minute pieces upon maceration of the rocks, and therefore whole fossils cannot be extracted by acid maceration. Even when undertaken with extreme gentleness, this procedure yields only small (millimeter to submillimeter) fragments the original position of which is unknown. The transfer technique could be used instead to extract whole fossils. It involves covering of the specimen on the cleaved rock surface with a thick layer of embedding medium (e.g., bioplastic) that attaches to it, and dissolution of the mineral matrix on the opposite side of the compression until this is entirely freed from the rock. Although very effective for recovering whole fossils, this technique yields specimens attached to blocks of embedding medium and therefore not easily amenable to a polyphasic investigation which requires that the same fossil be investigated with different techniques. This requirement is met considerably easier if different fragments of the same fossil are used for the different techniques involved. An approach based on fragments eliminates the need for transfers and is not hampered by the fragmentation of the fossil compressions.

The constraints imposed by the conjunction of these three characteristics have led to use of the polyphasic method described here (Figure 9.3). It involves morphological characterization of the fossils followed by several types of microscopic investigations performed on individual unitary carbonaceous fragments removed by hand from the compressions to document the internal organization of the fossils.
9.2.3. Methods

(1) 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 low fissility of the rock, and to the position of the fossils that are rarely perfectly flat, the margins of fossils remain unexposed most often. Careful degagement of both part and counterpart is therefore needed to uncover the original outline of each fossil. Rock samples exhibiting the fossils on split bedding planes are placed in 20% hydrofluoric acid for 1-2 minutes. This removes the potential oxidation products, enhances the contrast between the fossils and the surrounding mineral matrix, and softens the surface layer of the otherwise hard siltstone or sandstone allowing for easier preparation. After neutralization in a saturated sodium bicarbonate solution, degagement is performed on both part and counterpart of the compression, under a dissecting microscope, with the samples immersed in water, and using dissecting needles, scalpels, and pipettes to gently blow away the resulting sediment. The degaged part and counterpart are imaged with the samples immersed in water, for better contrast. Images are used as background for digital tracing of the outline of the fossils under the dissecting microscope. Tracings of the part and counterpart can then be used to reconstruct the external morphology of the fossil and record detail features.

(2) Following reconstruction and characterization of the morphology, millimetric and submillimetric fragments of carbonaceous material are removed from the compressions along with part of the underlying matrix, to ensure that the whole thickness
of the fossil is available for study. Some of the fragments are cleaned in 25-30% hydrofluoric acid and 40% hydrochloric acid to eliminate the mineral fraction, rinsed, and then prepared for microscopic study following different procedures corresponding to the different investigation techniques utilized.

(3) Fragments that have not been subjected to acid cleaning are bleached using household-grade sodium hypochlorite. Preliminary experimentation has shown that whereas nitric acid and Schultze’s reagent have no apparent effect on the Passage Creek fossils over long periods of time (two weeks), in sodium hypochlorite the jet black coaly material starts changing color after a few days, and at the end of 8-9 days most fragments turn yellowish-brown and translucent. Bleaching is followed by rinsing in distilled water, undertaken progressively by replacing initially small fractions of the sodium hypochlorite solution with distilled water, and then progressively increasing the volume of the replaced fraction until completion in 3-4 hours. This is a consequence of initial experiments which have shown that bleached fragments may sometimes dissolve totally and almost instantaneously if transferred directly from sodium hypochlorite to distilled water. The fragments can be observed throughout the progressive bleaching process, and after rinsing they are dehydrated in a graded ethanol series and xylene, and mounted on permanent slides.

(4) Scanning electron microscopy (SEM) is used to document fragments that have undergone acid cleaning, as well as fragments simply removed from specimens. They are dehydrated in a graded ethanol series, pipetted onto SEM stubs, allowed to dry, and observed. Energy-dispersive X-ray spectra (EDS) can be measured in conjunction with SEM observations allowing chemical characterization of fossils. For reasons outlined
below, the non-paradigmatic status of the fossils imposes completion of a crucial additional step. Prior to SEM observation, and necessarily prior to coating of specimens (if using a microscope that requires sputter-coating), the prepared stubs are carefully scanned under a high magnification dissecting microscope and all extraneous mineral particles adhering to fossil fragments, as well as any modern contaminating organisms (e.g., fungal hyphae) are recorded. This is a very important step in a non-paradigmatic context, because it prevents potential misleading identifications of mineral features or recent contaminant organisms as fossil structures, eliminating unsupported speculation engendered by these.

Because the non-paradigmatic status of the Passage Creek biota does not allow *a priori* assumptions of systematic affinities, it leaves considerable room for identification errors potentially leading to unsupported speculation. The advantage of a polyphasic approach is that by offering multiple perspectives on the observed structures, it minimizes the risk of misidentifications. One of the often unaccounted for sources of error in this respect is represented by modern contaminants. Particularly in the case of SEM investigations that necessitate sputter-coating of samples prior to observation, this represents a real problem. Once everything is coated, it is very difficult to tell apart fossil features from possible contaminants, or even mineral particles. This may sound trivial to students of paradigmatic assemblages where the existence of a search image for the detailed structure of fossils usually renders detection of contaminants and mineral features routine. However, in a non-paradigmatic context, where there is no *a priori* knowledge of the observed features or of their significance, contaminants and even mineral particles can be easily mistaken as representing structures of the fossil, and this
may make the difference between sound science and a hoax. This is why the importance of delimiting such potentially misleading information by careful observation of specimens on the SEM stubs prior to sputter-coating needs to be emphasized. Dried and flattened fungal hyphae that grow very deep in microfissures of the weathered rock adhering to fossil compressions (Figure 9.4), would have been interpreted as features of the fossil were they not identified as contaminant material prior to coating.

(5) Fragments cleaned in hydrofluoric and hydrochloric acids are embedded for thin and ultrathin sectioning following dehydration in a graded ethanol series. They are immersed in propylene oxide and subsequently included in Epon-type resin (Electron Microscopy Sciences, Fort Washington, PA). Thin sections (0.5-0.7 µm) and ultra-thin sections (60-80 nm) are cut with an ultramicrotome. Thin sections are mounted on permanent slides for light microscopy, and ultra-thin sections are picked on copper grids for transmission electron microscopy (TEM). Experimentation on Passage Creek fossils has shown that standard TEM fixation prior to resin embedding, and staining of ultra-thin sections on the copper grids have no effect on the quality of the sections or differential contrast of the images, therefore these procedures were omitted.

After characterization of the external morphology of the fossil and removal of fragments for microscopy studies (steps 1 and 2), the part and counterpart of the rock specimen can be fit back together to cut petrographic thin sections and document the relationships between the fossil and the sedimentary matrix. Depending on size and the degree of fissility, the specimen may be partially or totally embedded in Ward’s Bio-Plastic to prevent it from falling apart.
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 macrolens mounted on a Leitz Aristophot bellows camera, or using the Aristophot in conjunction with a Zeiss WL compound microscope for light microscopy. All permanent slides for light microscopy were mounted with Eukitt (Calibrated Instruments, Hawthorne, N.Y.). Scanning electron microscopy was performed on Zeiss DSM962 and Hitachi S4000 field emission microscopes, and EDS spectra were measured on an EDX spectrometer coupled to a JEOL JSM5300 scanning electron microscope. Thin and ultra-thin sections were cut on Reichert Ultracut microtomes using glass and diamond knives, and were observed and imaged using Zeiss EM109 and Hitachi H7000 transmission electron microscopes. Specimens are reposited in the Ohio University Paleobotanical Herbarium as nos. 15980-16008.
9.3. RESULTS

Extensive systematic studies of the Passage Creek fossils are in the course of completion. Due to specifics of the methods used, and of 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 a broad constraint of the size range of fossils, and an assessment of the 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 terrestrial biotas.

9.3.1. Diversity and Structure of 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 Llandoveryan wetland communities. The organic material in the fossils exhibits different 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.

9.3.1.1. Morphological Diversity of Macrofossils

Macrofossils range in size from smaller than 1 mm, to over 11 cm in greatest dimension (Figures 9.5.A-D, 9.6.A-F). At least two different general types of textures have been observed in the compressions (Figure 9.5.C 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 external morphology was documented 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 9.6.B 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 (Figure 9.5.C 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 more-or-less continuous crusts and discrete fossils. The largest dimension of a continuous crust observed to date is 11 cm (Figure 9.5.D), and is limited by the size of the rock sample. The crust displays
highly irregular voids with sizes varying 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
gradational.

Discrete fossils fall into two main morphological classes: 1) fossils with more or
less isodiametric outlines, termed thalloid (Figures 9.6.A-D), and 2) elongated, strap-
shaped fossils (Figures 9.6.E, F). 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 9.6.A-D). We have documented specimens with deltoid (Figures
9.6.A, D) and oval (Figure 9.6.C) outlines, as well as compressions with more irregular
outlines (Figures 9.6.B, D). Some of the fossils exhibit short protrusions (Figures 9.6.A,
C, D, 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 9.6.A 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.

Elongated, strap-shaped fossils are comparatively 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 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 (Figures 9.6.E, F) 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, that 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 x 0.6 cm and 8 x 1.2 cm in size, and exhibit somewhat wavy margins. While the smaller fossil (Figure 9.6.E) is slightly curved, with apparently rounded terminations, the larger one (Figure 9.6.F) is straight and displays a two-pronged termination (the other end is truncated by the edge of the rock sample).

**9.3.1.2. Internal Organization of Macrofossils**

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 cross sections can be nevertheless classified into five main types (Figures 9.7.A-J) defined based on layering and 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 scanning and transmission electron microscopy (SEM and TEM).
**Type 1** (Figure 9.7.A)

Type 1 fossils exhibit an anastomosing pattern that consists of µm-thin vertically undulating features. Representing either filaments or highly discontinuous sheets of organic matter, they form a continuous inter-twining network 25-90 µm thick in the plane 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** (Figures 9.7.B-D, G; 9.8.A, C, D)

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 (Figures 9.7.B; 9.8.A, C). Figures 9.7.C and 9.7.D represent the part and counterpart of a specimen with Type 2 internal anatomy. The outer layers exhibit a laminar structure consisting of more-or less parallel sheets (around 1 µm thick) of variable density (lighter and darker), not very well individualized. Where the separating median region is absent the two layers appear continuous (right side of Figure 9.7.B). 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 (Figures 9.7.B, black arrowhead; 9.7.G).
Regions where minute dark dots can be seen in transverse sections are sometimes nested between the two outer layers (Figure 9.7.B, white arrowhead). In SEM they appear as features consisting of more-or-less regularly constricted filaments (1 µm or smaller across) with a bead-like appearance, tightly packed in a tangle with no consistent pattern (Figures 9.8.C at arrow, and 9.7.D). These features are reminiscent of the packing of vesicular arbuscular mycorrhizal hyphae inside plant root cells.

Type 3 (Figures 9.7.E, F; 9.8.B)

Type 3 internal organization is similar to Type 2 in that it involves two outer layers separated by a median region (Figure 9.7.E). 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, has variable thickness and vertical cracks. A three-dimesional SEM image of the two sub-layers is shown in Figure 9.8.B. 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 Figure 9.7.E), 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 (Figure 9.7.F at arrowhead). The presence of diaphanous organic matter (Figure 9.7.G) associated with the specimen
shown in Figure 9.7.D 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 (Figure 9.9) 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 (Figure 9.9, lower right).

**Type 4** (Figure 9.7.H, I)

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 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 HF dissolution for fossil extraction. Crystals fall into two size classes: the larger are more-or-less isodiametric, 4-12 µm across, whereas the smaller are 0.5 µm or smaller, and are grouped in areas the size of which is comparable to the size of the larger crystals (Figure 9.7.I at arrow). The crystal molds exhibit mainly hexagonal outlines in section (Figure 9.7.I 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** (Figure 9.7.J)

Type 5 fossils exhibit a massive structure traversed by what appears to be a very dense network of fine fissures (1 \( \mu \)m 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 post-depositional 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 9.6.E, 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 (Figure 9.10). Although the filaments appear lighter in color in reflected light (Figure 9.10.A), viewed in transmitted light they consist of denser, opaque matter (Figure 9.10.B). The filaments run more-or-less parallel to each other and to the length of the fossil, and are 30-40 \( \mu \)m wide. Some of them can be followed over lengths of around 1 mm, and show no evidence for branching.
9.3.1.3. Descriptions of Individual Fossil Specimens

Specimen BH10-13

Specimen BH10-13 produced two cleaved compressions which due to very uneven splitting preserve all the thickness of the fossil on complementary sectors of the part and counterpart. This simplified the collection of fragments and rendered separate study of part and counterpart unnecessary. The fossil is 61 mm long, 7-9 mm wide, and up to 250 µm thick, with parallel margins and rounded ends (Figure 9.6.E). Examination under the dissecting microscope shows profuse fissures and fragmentation of the carbonaceous material, but reveals few morphological details.

Fragments bleached in sodium hypochlorite exhibit a structure consisting of two types of filaments generally parallel with the long axis of the fossil, embedded within an amorphous matrix (Figures 9.10, 9.11.B). Type 1 filaments (Figure 9.11.C) are relatively rare (6% of observed filaments), uniseriate, sinuous, unbranched and can be > 600 µm long. They consist of contiguous or closely spaced spheroidal units 4.9-8.0 µm in diameter (mean = 6.4 µm; n = 14). The majority of filaments (type 2, 94%) are multiseriate. They consist of 2-4 parallel rows of closely spaced spheroids 3.1-8.0 µm in diameter (mean = 5.7 µm; n = 77) included in cylindrical structures 10.8-30.0 µm in diameter (mean = 21.2 µm; n = 70) that are unbranched, usually straight or gently curved, and sometimes > 1 mm long (Figure 9.11.F, G).

Scanning electron microscopy reveals that the spheroids that make up the filaments are aggregates of small (around 1 µm) crystals (Figure 9.11.E), and that the amorphous matrix that contains the filaments has a massive structure. In multiseriate
filaments the spaces between spheroids are filled with evenly distributed minute crystals of the same type ranging in size from < 0.5 µm to 2 µm (Figure 9.12). Energy-dispersive spectroscopy (EDS) used in conjunction with SEM indicates that the elemental composition of the spheroids is characterized by higher contents of iron and oxygen as compared to the surrounding amorphous matrix (Figure 9.13).

Thin sectioning of the carbonaceous material shows 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. Light microscopy (Figures 9.7.H, I) of sections cut perpendicular to the plane of the compression reveals a gross laminar structure disrupted by tangential fissures, and voids corresponding to crystalline aggregates that form the filaments and that were removed by acid treatments. It also shows that some of the constitutive elements of filaments are larger crystals the sizes of which fall approximately within the same range as those of spheroidal aggregates (4-12 µm). Differences in the density of the carbonaceous matrix apparent in light microscopy are better resolved in transmission electron microscopy which shows relatively well defined denser regions within a mass of less dense material (Figure 9.11.I). Spheroidal crystalline aggregates and regions with evenly distributed crystals are also resolved at a better resolution in TEM.

Both SEM and TEM reveal that crystals in the spheroidal aggregates, as well as dispersed crystals, are euhedral (have all their crystallographic faces well developed, with well-defined angles between them), indicating that they developed within the fossil. Examination of relationships between voids left by the crystals and the gross laminar
structure of the fossil (Figures 9.7.H, I) 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. SEM, and especially the outlines of crystals as seen in TEM (Figure 9.11.I), show rhombohedral crystals, which corroborate with the translucent brown color (seen in light microscopy), the Fe and O content (EDS), and the spheroidal aggregates, pointing to spherulitic siderite (FeCO₃). The cylindrical structures that incorporate the multiseriate filaments represent regions of abundant, evenly distributed and small-sized siderite crystals (Figures 9.11.I, 9.12).

**Specimen BH12-8-2**

Specimen BH12-8-2 is considerably smaller (4.7 x 3.7 mm) compared to specimen BH10-13 and split evenly, producing two cleaved compressions very similar in outline. This specimen exhibits a thalloid morphology (Figure 9.14.A, B) which is much more characteristic of the Passage Creek assemblages than Specimen BH10-13. The general shape of Specimen 2 is oval, with slightly undulating margins. A crack is present on both part and counterpart (Figure 9.14.A, white arrowhead), and a short protrusion (Figure 9.14.A, black arrowhead) may represent an attachment structure, or simply a small lobe of the thallus.

The diminutive size necessitated collection of the whole compression for fragments, from both part and counterpart of the specimen. Bleaching revealed the presence of two different types of material in both part and counterpart, but an overall lack of meaningful anatomical structures. Some of the fragments bleached in depth,
becoming brown and translucent (Figure 9.14.D), whereas others were very resistant to clearing. The latter (Figure 9.14.C) exhibit very irregular margins and occasional holes suggestive of voids formerly occupied by crystals. Although considerably thinner than specimen 1 (none of the sectioned fragments exceeded 15 µm in thickness), these fragments did not bleach in depth, but instead dissolved progressively at the margins (locally translucent; Figure 9.14.C), with the center remaining dark and opaque, until total exhaustion.

Light microscopy of sections cut perpendicular to the plane of compression shows that the counterpart has a relatively massive structure and consists of apparently homogeneous material (Figure 9.14.E, G). TEM confirms this homogeneity (Figure 9.14.I), in spite of the difficulty of obtaining good-quality sections. Occasional voids, some of them corresponding to crystalline aggregates very similar to those present in Specimen 1, are present in sections of the counterpart. By contrast, the part is characterized by a much looser organization (Figure 9.14.F, H) and features material of two different densities possibly corresponding to the two types of material (tissues?) evidenced by macerations (Figure 9.14.C, D). Dense organic material of variable thickness (dark on Figure 9.14.G, H) forms a highly irregular anastomosing network that delimits numerous lenticular and elongated voids. The dense material layer is relatively even on one side, whereas on the other side it is adjacent to a layer of less dense material. Termed diaphanous (Tomescu and Rothwell, 2004), the latter is relatively inconspicuous except for thicker sections where it becomes more apparent (Figure 9.14.H, bottom half). The diaphanous material also forms an irregular network with numerous voids and with interspersed minute elements of dense material. TEM sections of fragments of the part
reveal the homogeneous structure of the dense material (Figure 9.14.J), and fine parallel laminae at a very small scale (Figure 9.14.K) probably corresponding to the diaphanous material.

Scanning electron microscopy of fragments removed from the counterpart compression shows relatively smooth (Figure 9.15.A) to very smooth surfaces (Figure 9.15.B). In the former, the surface has a flaky appearance (Figures 9.15.A, C, D) given by occasional depressions and numerous discontinuities in very thin superimposed layers. Breaks in the fragments reveal small voids in the relatively massive structure of the material (Figure 9.15.C), or molds of spheroidal crystalline aggregates (Figure 9.15.D) also seen in thin sections and very similar to those observed in specimen BH10-13. Fracture patterns on the margins of fragments (Figure 9.15.B) suggest that a laminar structure, inconspicuous in light microscopy of thin sections or TEM, may be characteristic of the organic material in the counterpart. Fragments of the part exhibit the same flaky appearance of the surfaces, with occasional breaks and depressions (Figures 9.8.C, 9.16.A), as those of the counterpart. The voids seen in sections of the dense layer (Figures 9.14.F, H) are revealed by SEM (Figure 9.16.B), and molds of crystalline aggregates are rare. Material with a very irregular, wrinkled and foliose structure may occur associated with fragments characterized by relatively even, flaky surfaces (Figure 9.16.A, right half of the image). This association and the position of the irregular material on the opposite side of the fragment relative to the even surface suggests that this material may represent the diaphanous layer seen in light microscopy of thin sections. A feature consisting of more-or-less regularly constricted filaments (1 µm or
smaller across) with a bead-like appearance, tightly packed in a tangle with no consistent pattern, is exposed within the thickness of a fragment (Figures 9.8.C, D).
9.3.1.4. 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 more loosely defined associations known as biological soil crusts, as well as the fossil genera *Nematothallus*, *Parka*, *Spongiophyton*, and *Protosalvinia*.

An animal origin for these fossils is unlikely as none of the numerous compressions yielded by our extensive sampling exhibits 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, three main types of correlations that are crucial in understanding the organisms that produced the fossils need to be documented and clarified. 

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, involving understanding of 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. These can then allow for comparisons with the different groups of similar morphology, in order to reveal the systematic affinities of the fossils.

Even at this stage of research, some information on potential systematic affinities of organisms in the Passage Creek biota is provided by the dispersed microfossils described from the same sediments by Pratt et al. (1978), and these complement the image of diversity relayed 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 Llandoveryan 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, based on morphological features such as size, branching, and septation. As such they are interpreted as evidence (the earliest) for higher fungi. Presently there is some reluctance in circles of the scientific community in accepting reports of earliest occurrences of dispersed fungal microfossils in the absence of conclusive evidence that any possibility of contamination with recent material has been avoided during sampling, handling and processing of samples. 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 (Figure 4.1), in a context that excluded the possibility of contamination with recent material (Redecker et al., 2000, p. 1921, note 16). This 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, but as emphasized earlier, the systematics of such fossils remain largely unresolved. An important observation has nevertheless been made by Graham and Gray (2001) who pointed out
disparities between the stratigraphic record of cuticle-like fragments and tubes, suggesting that the two types of fossils probably originated from different types of organisms.

A particular case is represented by specimen BH10-13, where careful characterization of internal organization allowed for the first unequivocal systematic assignment of a macrofossil at Passage Creek. In the case of this specimen, a combination of several types of evidence reveals that the filamentous structures represent cyanobacteria whose cells have been replaced by early diagenetic siderite. (1) Filaments occur in abundance within a macroscopic carbonaceous compression corresponding to the extracellular gelatinous matrix. (2) The spherulitic siderite aggregates have a consistent size range that falls within that of cyanobacterial cells, and (3) the shapes and sizes of filaments are consistent with those of living cyanobacteria. These data ally the uniseriate type 1 filaments with nostocacean cyanobacteria (Figure 9.11.D) and the multiseriate type 2 filaments with multitrichomous oscillatoriaceans (Figure 9.11.H). (4) Additional evidence for cyanobacterial identity is provided by the mode of preservation represented by these fossils, which conforms to results of chemical, structural (Helm et al., 2000) and experimental taphonomic (Bartley, 1996) studies, all of which have stressed the characteristic resistance to degradation of cyanobacterial extracellular polymeric substances (sheath and slime) in contrast to cell contents.

Replacement of cyanobacterial cells by spherulitic siderite, which is a common product of early diagenesis in sediments of reducing environments rich in organic material (Choi et al., 2003; van Breukelen et al., 2003), is explained by a simple model for the conditions present in the fossiliferous floodplain deposits of the lower
Massanutten Sandstone. Cyanobacterial colonies living on the floodplain would have been buried in sediments and then have entered the anaerobic zone characterized by reducing conditions (as indicated by the dark grey color of the fossiliferous layers). The organic material would have promoted reduction of iron, present in abundance in such sedimentary systems, by anaerobic microbial decomposers (Nevin and Lovley, 2002; Zachara et al., 2002; van Breukelen et al., 2003; Roh et al., 2003). Because of the resilience of polymers in the extracellular matrix (Helm et al., 2000) – corresponding to the amorphous carbonaceous material of the fossil –, these decomposers concentrate on the cyanobacterial cells, resulting in precipitation of spherulitic siderite in the cells, and of dispersed siderite microcrystals within the common sheaths of multitrichomous filaments.

Morphologic convergence among living cyanobacteria and partial alteration of the original cell shape by siderite precipitation in the fossils preclude identification of the specimens with higher taxonomic precision (e.g., criteria established by Golubic and Campbell, 1979, in establishment of modern counterparts). The occurrence of two taxonomically distinct cyanobacterial populations in a common extracellular matrix is not uncommon in living microbial mats and biological soil crusts, to which the Massanutten Sandstone fossil assemblages compare closely.
9.3.1.5. 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 (Figures 9.5.A, B), whereas others exhibit an abundance of larger fossils around 1 cm or larger, and a few small fossils (Figure 9.5.C). The end member of this continuum is represented by surfaces where the compressions form extensive crusts of highly irregular outline (Figure 9.5.D). Fossils can be evenly distributed on the bedding planes (Figure 9.5.A), or they can form agglomerations a few centimeters across (Figure 9.5.B). The area covered by fossils is low on bedding planes where small fossils predominate (Figures 9.5.A, B), and considerably higher where larger fossils are dominant (Figure 9.5.C) and in the case of crusts (Figure 9.5.D).

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, before 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. As indicated by the hyphae described by Pratt et al. (1978), 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 freshwater 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.
9.3.2. 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), that Pratt et al. (1978) informally name 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 based on 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 (Figure 4.1).
9.3.3. Depositional Environments of the Fossil Assemblages

9.3.3.1. Results from Previous Work

Pratt et al. (1978) interpreted the lower Massanutten Sandstone at Passage Creek as non-marine, based on the absence of marine fossils and near-shore indicator trace fossils (Skolithus, Arthropycus). Although no detailed sedimentological study of the Passage Creek locality has been published to date, 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, based mainly on textural features. However, several other studies (among which 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 in support of this interpretation was summarized by Faill and Wells (1974) and included among others tabular sets of crossbeds, consistent dip directions of the crossbeds, 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 crossbedding dip vectors. Subsequent work by Whisonant (1977), Cotter (1978), and Cotter (1983) was in agreement with the fluvial interpretation of the depositional environment. Two independent and extensive regional studies by Yeakel (1962) and Whisonant (1977) included the lower Massanutton Sandstone in their datasets. Based on paleocurrent directions and regional patterns of grain size distribution, both
authors agreed upon its location closest to the source of sediment, on a coastal plain that sloped toward the northwest.

Smith (1970) was the first to have suggested a braided style for the fluvial systems that deposited the Tuscarora, using comparisons of various sedimentary features to those of the modern South Platte-Platte Rivers of Colorado and Nebraska. His interpretation was supported by the studies of Pratt (1978) and Cotter (1978, 1983). In central Pennsylvania, Cotter (1983) interpreted 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 showed 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 supported the paleogeographic interpretations of Yeakel (1962) and Whisonant (1977), and all provide good evidence to consider the Tuscarora was 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.
9.3.3.2. Field Observations

In the fall of 2003 I surveyed the sedimentary features of the lower Massanutten Sandstone along Passage Creek, as well as at two other exposures within the same synclinorium (Figure 9.17), in the company of Dr. Gregory C. Nadon (Department of Geological Sciences, Ohio University). The results of our survey were summarized by Dr. Nadon (personal communication, 2003).

Two of the three outcrops of the Massanutten were useful in assessing the depositional environment. The Passage Creek section and the Lookout section are both extensively exposed and sufficiently distinctive to provide insights into the depositional processes. The Passage Creek section was studied more intensively because of the abundant compression fossil content, but the Lookout section is equally instructive.

**Passage Creek Section**

The basal contact of the Massanutten Sandstone with the underlying Martinsburg Formation was not visible at the Passage Creek section. This section of the Massanutten consists of a basal quartz sandstone unit and an upper unit that contains conspicuous siltstones and shales. The deposits comprising the lower 'member' of the Passage Creek section consist of medium- to coarse-grained quartz sandstones and rare pebbly sandstones and conglomerates in beds 8-30 cm thick. Cross-bedding within the sandstones is rarely visible but where present is low-angle to planar tabular. There was one example of sigmoidal crossbedding, however, the internal laminations showed no evidence of bundling characteristic of tidal influence. Cross-lamination is equally rare.
Most of the internal structures consist of sub-horizontal to wavy laminations. Intraclasts are present but rare.

At several points within the formation, and particularly within the basal 20 m, the sandstones are interbedded with discontinuous horizons of shales or siltstones varying from <1 cm to more than 10 cm in thickness. These finer-grained deposits are well laminated within thin interbeds of medium to coarse-grained sandstones. Thin sections reveal that the shale contains elliptical, probably horizontal burrows that concentrate quartz grains. The shales and siltstones define a larger scale stacking pattern of upward fining sandstones that varies from 3-5 m in thickness. These larger groupings are generally overlain by pebbly sandstones to conglomerate. The tops of sandstone beds capped by fines are occasionally wave-rippled and many are bioturbated. Bioturbation consists primarily of horizontal to sub-horizontal unlined trails (Figure 9.18). Sizes range from less than 1 cm to more than 3 cm in width. The best exposures are on bedding planes along the margin of the creek, but careful examination of the road cuts shows that many of the beds are burrowed. No desiccation cracks in the sediment were noted in the field, but rock specimens collected for fossils preserve them (Figure 9.19.A). Some of the compression fossil also exhibit features interpreted as the results of desiccation (section 9.3.3.3).

**Lookout Section**

The Lookout section was examined only briefly, but there are significant differences between this exposure and the Passage Creek section. The basal contact with the Martinsburg is not exposed. The thickness of the section implies that the upper, fine-
grained “member” of the Massanutten Sandstone is absent at this location. The entire section exposed along the road is composed of medium- to coarse-grained sandstones in beds varying from 10-40 cm (approximately) that exhibit excellent crossbedding and cross-lamination. The shales and siltstones that are common in the Passage Creek section are absent here, while the pebbly sandstones and conglomerates are less common.

Bioturbation is less well displayed within beds of the Lookout section but there are beds that show faint vertical unlined burrows. These beds also lack internal sedimentary structures.

**Interpretation**

There are no diagnostic structures within the sediments that point to a marine depositional environment at either location. Although the basal contact is not exposed, there is no transitional sandstone unit from the Martinsburg shales, such as the homotaxial Oswego or Bald Eagle Sandstones to the west, that represent a shoaling deposit. There is no evidence of tidal indicators such as herringbone cross-stratification, bundling of laminae, or mud drapes within any of the exposures. The bioturbation is similar to that described from the broadly equivalent Juniata Formation, which is demonstrably nonmarine (Retallack, 1986b).

The strata within the Lookout section are consistent with deposition by a shallow braided fluvial system. The lack of channeling and mudstones rules out the possibility of either meandering or anastomosed fluvial conditions. The fluvial system appears to be similar to the shallow perennial stream model of Miall (1996; p. 241) and the sandy braid
plain of Sonderholm and Tirsgaard (1998). Not enough time was spent at this exposure to positively eliminate the possibility of thin eolian beds being present.

The Passage Creek section is also interpreted as a braided fluvial deposit largely on the absence of any other diagnostic criteria. The presence of the common siltstone and shale interbeds suggests this portion of the section was either marginal to the main river system represented by the Lookout section sandstones, or was part of a different river system entirely. The fine-grained deposits are interpreted to represent deposition outside of main active channels. The relative rarity of evidence for desiccation, the abundance of bioturbation, and the lack of mudstone intraclasts suggest that this section was exposed only part of the time. Within a fluvial setting, this implies a humid setting with a high water table. This setting is superficially similar to the muddy braidplain of Sonderholm and Tirsgaard (1998; cf. fig. 7).

9.3.3.3 Fossil Taphonomy

The macrofossils at Passage Creek occur in fine-grained partings that form thin, discontinuous layers between thicker, coarser beds of sandstone and fine conglomerate (Figure 9.2). 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 “floodplain” 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 floodplains. From the point of view of the sediment partitioning by grain size, such settings are therefore equivalent to the classic floodplains 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 floodplain of the river system that deposited the Massanutten Sandstone.

The preservation of fossils in floodplain deposits does not automatically eliminate the possibility that they represent remains of freshwater organisms transported and buried in overbank settings by flood events. The question then becomes: are the fossils autochthonous, preserved in situ and hence represent the floodplain 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 floodplain, or from freshwater 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 on very short distances of the order of meters (G.C. Nadon, personal communication, 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 (e.g., Figure 9.6.A), and others form extensive organic crusts, indicating minimal, or more likely no transport. In this context crusts and fossils with cracked surfaces (Figures 9.5.C, white arrowhead, and 9.19.B) were almost certainly preserved in situ.

Fossils preserved in situ on the floodplain can represent terrestrial organisms living in the aerial realm, but they also could represent freshwater 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 ranging -25.6 to -26.4, favoring a terrestrial origin for the fossils. Additional evidence is provided by desiccation cracks in the fossiliferous siltstones (Figure 9.19.A), and by occurrences of fossils displaying desiccation cracks or rolled-up margins (Figures 9.19.C, D). 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.
10. THE CONOCOCHEAGUE MOUNTAIN BIOTA – A PRELIMINARY ASSESSMENT

10.1. LOCALITY, STRATIGRAPHIC CONTEXT, AND AGE

Abundant assemblages of compression fossils occur in the Reedsville Formation and the Oswego Sandstone at the transition between the two formations, at Conococheague Mountain, Pennsylvania. The Oswego is bounded by the Reedsville Formation at the base, and the Juniata Formation at the top (Dennison and Wheeler, 1975). The Reedsville has been dated as Caradocian-Ashgillian by brachiopod biostratigraphy (Bretsky, 1970); the Juniata Formation is considered to be Ashgillian in age (Dennison and Wheeler, 1975). This stratigraphic position places the Oswego Formation in the Ashgillian, near the end of the Ordovician (Figure 4.1).

The Conococheague Mountain section was first described by Horowitz (1965), who interpreted the depositional environments as transitional from shoreline settings (uppermost Reedsville and lowest Oswego) to low-energy fluvial plain or coastal plain (lower Oswego). At a larger scale, Horowitz (1966) interpreted the Oswego as deltaic deposits marking the transition between the progressively shallower marine deposits of the Reedsville Formation, and the fluvial sedimentation of the overlying Juniata Formation. On the other hand, sedimentological studies of the Oswego Sandstone and its stratigraphic equivalent, the Bald Eagle Formation, in New York, Pennsylvania, and Virginia (Yeakel, 1962; Meckel, 1970; Faill and Wells, 1974; Rader and Biggs, 1976; Cotter, 1978) have interpreted them as fluvial, characterized it generally by very high
proportions of coarse, sand-grade deposits that form sheets. Basal scouring and shale intraclasts are present, and both horizontal and cross bedding (mainly planar cross bedding) are frequent. The very high percentage of sandstone, along with the high frequencies of horizontal bedding and planar cross bedding, suggest a braided fluvial style, but the absence of any indication on sand body geometry requires caution.

Based on the considerations above, at regional scale the Oswego/Bald Eagle can be considered to represent an upward-shallowing sequence, marginal marine grading to fluvial and floodplain settings (Dennison and Wheeler, 1975; Lehmann et al., 2000, 2001; Castle, 2001). However, the gradational aspect of the Reedsville-Oswego transition, as well as the abundance of carbonaceous compressions discovered at Conococheague Mountain, required detailed understanding of the depositional environments at this particular exposure. While a shallow marine depositional environment could have witnessed accumulation of both marine and continental material, documentation of fluvial deposition would have eliminated marine algae from the potential producers of the compressions.

In the spring of 2003, Dr. Gregory C. Nadon participated in our collecting field trip and measured over 30 m of section at Conococheague Mountain (Figure 10.1) making detailed sedimentological observations. The section comprises mainly fine-grained sandstone, and is dominated by shale only in the lower 7 meters. The sedimentological data (grain size trends, sedimentary structures) could not be used to differentiate between a shallow marine and a deltaic environment for this particular section. There are marine fossils (especially brachiopods, and some crinoids) near the base of the section, and molds of bivalve shells are present in three shale layers within the
lower 7 m of the section. The bivalves were identified as solemyoids (most probably *Psiloconcha*; John Pojeta, personal communication), which are known only from marine settings (Pojeta, 1988). All of these data are best interpreted as marine throughout most of the section, and support a shallow marine depositional environment, close to a deltaic source (G.C. Nadon, personal communication, 2003).

This environmental interpretation recommends extreme caution in the analysis of the Conococheague Mountain compressions, as shallow marine environments are known to harbor mixed assemblages consisting of autochthonous marine biota and allochthonous continental biota. This compounds the problem of systematic affinities of the carbonaceous fossils, since their non-paradigmatic condition precludes distinction between the two sources, and additional marine groups have to be considered when analyzing these affinities. As a result, work on the Conococheague Mountain biota is presently at the stage of a preliminary assessment.
10.2. FOSSIL MATERIAL

Horowitz (1965, 1966) reported minute carbonaceous fragments that he compared to charcoal, from the Ashgillian Oswego Sandstone at three localities in Pennsylvania, among them Conococheague Mountain (Doylesburg, in Horowitz’ 1965 work). The angular outlines of the fragments and their opacity, even in very thin petrographic sections, are reminiscent of charcoal, and upon infrared absorption analysis produced spectra similar to those observed from bituminous coals. These, together with the deltaic interpretation of the Oswego Sandstone by the same author, initially drew my attention to this locality.

The Oswego is exposed along a roadcut on the southeastern slope of Conococheague Mountain, in Franklin County, approximately 2.7 miles northeast of Doylesburg, Pa. (40º14’41’’N; 77º40’22’’W; Figures 8.1, 10.2, 10.3). Carbonaceous compressions occur in at least 12 layers, of different grain sizes (shale, siltstone, and sandstone), scattered throughout the section (Figure 10.1).

10.2.1. Macrofossils

The carbonaceous material is very fragmented due to transport in some beds (e.g., the sandstone in bed 64), whereas other beds (especially shales) contain larger compressions. The richest assemblages occur in beds 42 and 94. Most of the compressions are around 1 cm in size or smaller and are more or less isodiametric, thalloid (Figure 10.4), but some are slightly larger (between 1-2 cm). The carbonaceous material is very thin in all of the compressions.
A large piece of sandstone fallen from the exposure was found during fieldwork. It exhibits large relief features lined with brown material that could represent either oxidized organic material of compressions, or inorganic oxides formed/deposited preferentially on impressions (Figure 10.5.A). One of the features (Figure 10.5.B) has a radial pattern (5.5 x 6 cm in diameter) reminiscent of the trace fossils Asterosoma and Asterichnus (A. Uchman, personal communication, 2004). The other features are elongated (one of them exposed on 11 x 2.5 cm; Figure 10.5.D), or isodiametric (1 – 1.5 cm; Figure 10.5.C), and it is not clear whether they represent trace fossils, too, or they are compression fossils. The exact provenance of this rock fragment is uncertain, but the position where it was found with respect to the outcrop, as well as the granulometry, indicate that it could have come only from one of the beds 54-63. Asterosoma is a trace fossil characteristic of lower shoreface to offshore environments (Bromley and Uchman, 2003), but which is also recorded in marine to brackish-water tidal settings with minimal wave reworking (Martino and Sanderson, 1993; Greb and Chestnut, 1994) and in fan-delta complexes (Ekdale and Lewis, 1991). This would corroborate the interpretation of the Conococheague Mountain section as shallow marine and deltaic deposits; no sedimentary structures characteristic of tidal settings are present.

10.2.2. Mesofossils

Maceration of an apparently sterile sandstone fragment (bed 57) and of a shale sample including compression fossils (bed 42) yielded millimetric and sub-millimetric carbonaceous fragments. Although most of the fragments are amorphous, some of the fragments recovered from bed 42 have elongated, axial morphologies (Figure 10.6.A-E).
These axial fragments are 40-70 µm wide, flattened, and are obviously broken at both ends. Three of them exceed 1 mm in length, and the longest is 2.4 mm long. The latter (Figure 10.6.A-C) bears three bases of broken appendages; a fourth one is probably represented by the small protrusion indicated by the arrowhead in Figure 10.6.A. The shape of the appendage bases indicates that this fragment was flattened diagenetically, and suggests fan- and/or cone-shaped morphologies (especially Figure 10.6.B at arrows; Figure 10.6.C, detail of second appendage). Flattening and the short length of the fragment preclude observation of an arrangement pattern for the appendages. Another one of the axial fragments also exhibits a small protrusion (arrowhead in Figure 10.6.E).

Maceration also produced a tubular microfossil (from bed 57) with smooth walls, 560 µm long and 28 µm in diameter (Figure 10.6.F; the tube flattened and twisted during preparation and mounting).
11. DISCUSSION

Communities of terrestrial microorganisms in the form of cyanobacteria and bacteria were probably established relatively early in the Precambrian (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 freshwater bodies.

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 time interval between the establishment of terrestrial microbial communities and the first macrofossils of terrestrial organisms (i.e., *Cooksonia*), the fossil record previously has yielded only dispersed microfossils, traditionally, but not conclusively, associated with land organisms (as discussed above). The newly recognized fossil evidence from this interval that is introduced in this study provides a first opportunity to begin to fill this gap by providing an organismal context for understanding of the microfossil evidence, and by establishing a paleoecological framework for the most ancient complex terrestrial communities.
11.1. KISER LAKE BIOTA

Although the earliest known sculptured hilate monads occur in the Llandoverian (Steemans et al., 2000), *Cymbohilates disponerus* was known previously only from the Early Devonian. Richardson (1996a) originally described the species from the Lower Old Red Sandstone, and Wellman et al. (2000) reported it from a discoidal spore mass at a different locality in the same stratigraphic unit. The occurrence reported here extends the stratigraphic range of *Cymbohilates disponerus* to the Early Silurian (Llandoverian). The current opinion is that cryptospores represent good evidence for the earliest terrestrial vegetation (Richardson, 1996b; Steemans, 2000). Among cryptospores, dyads and their derivatives, the hilate monads, are most intriguing because their producers still remain unknown, mainly because of the lack of modern analogues (Wellman and Gray, 2000). Some evidence suggests that they may have been produced by rhyniophytoid plants. Wellman et al. (2000) pointed out that spores similar to *C. disponerus* have been described *in situ* by Edwards et al. (1994) from Salopella-type remains in the Early Devonian of Shropshire. Also, sporangia closest in shape to *Salopella*, which was considered a rhyniophytoid by Edwards and Richardson (1974), were found with *in situ* dyads by Fanning et al. (1991).

The earliest fossil Ascomycetes are preserved as permineralized ascocarps containing asci with ascospores, in the Early Devonian Rhynie Chert. Taylor et al. (1999) classified these fossils with the pyrenomycetous ascomycetes. The earliest known septate spores were described by Sherwood-Pike and Gray (1985) from Late Silurian (Ludlovian) sandstones of Gotland (Sweden). Those spores occurred in sandstones
deposited in environments interpreted as intertidal to supratidal. Based mainly on morphology, but also on the fact that they occurred in association with hyphae of ascomycetous affinity, the spores were interpreted as ascospores or the conidial stage of ascomycetes. Both the ascomycetous affinity assigned by Sherwood-Pike and Gray (1985) to the septate spores and hyphae from Gotland, and the pyrenomycetous affinity of the Rhynie Chert fossil (Taylor et al., 1999) were questioned by Berbee and Taylor (1993 and 2001). Using a molecular clock based on gene sequence data (18S rRNA) of 37 fungal species, calibrated with the age of fungal fossils, fossil fungus hosts and symbionts, Berbee and Taylor (1993) proposed an age of 320-180 million years for the filamentous ascomycetes. Considering that the age predicted by them was much younger than that of the septate spores of Sherwood-Pike and Gray (Ludlovian, 414-421 million years), Berbee and Taylor suggested that this discrepancy between molecular and fossil data may be due to the fact that the Ludlovian septate spores were produced either by a non-fungal organism, or by a common ancestor to the ascomycetes and basidiomycetes, present in the Silurian according to their predictions.

Following recalibration of a new molecular clock based on 18S rRNA gene sequence data using fossil occurrences and divergence times produced by earlier molecular clocks (!), Berbee and Taylor (2001) questioned the classification with the pyrenomycetous euascomycetes of the Rhynie Chert fossil by Taylor et al. (1999). They assigned a Triassic age (240 million years) to euascomycetes and suggested that the Rhynie Chert fossil represents an archiascomycete. In contrast, a more recent molecular clock study by Heckman et al. (2001) predicts a considerably older age for the Ascomycetes. Based on protein sequence data, their molecular clock was calibrated with
divergence times inferred from an earlier molecular clock study (Wang et al., 1999). Heckman et al. (2001) suggested Proterozoic ages for the Ascomycetes (around 1,200 million years) and Pyrenomycetes (around 670 million years), that would certainly accommodate both the Early Devonian pyrenomycete occurrence, and the Ludlovian and Llandoverian ascomycete occurrences. However, they also suggested a Late Proterozoic age (700 million years) for the moss/vascular plant divergence, far older than the earliest known occurrences of vascular plants or even putative land plant remains. These two studies illustrate the important discrepancies in the age predictions due mainly to the different calibration methods used for molecular clocks (discussed by Sanderson, 2003). However, as pointed out by Sherwood-Pike and Gray (1985), it is difficult to interpret the septate spores of the Swedish Ludlovian as anything but the conidial stages or ascospores of ascomycetes. In this context, the occurrence reported here extends the stratigraphic range of Ascomycetes, represented by septate spores, to the Early Silurian (Llandoveryian).

I have carefully contemplated the possibility of contamination of the microfossil sample with younger or recent material, considering that both multiseptate spores and Cymbohilates disponerus are known from younger rocks. I consider this possibility to be extremely remote, based on the fact that the sample was taken from massive rock and that Sub-Lockport rocks represent the youngest strata traversed by the drilling, except for Quaternary glacial drift deposits. Furthermore, the dark color of the microfossils even after several hours of nitric acid oxidation is entirely consistent with an advanced diagenesis undergone by organic matter of such old age.
Ascomycetes are principally terrestrial fungi (Alexopoulos et al., 1996), and hilate monads are very likely the products of terrestrial plants. These corroborate with the evidence for subaerially exposed areas in the region during Llandoveryan times, offering good support for the existence of a terrestrial biota that inhabited these areas. Considering these, as well as potential affinities suggested by morphology, the origin of the mesofossil *Quasihepatica multifida* in a terrestrial embryophyte at a bryophytic level of organization comparable to modern leafy liverworts has a certain degree of likelihood.
11.2. 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. The Passage Creek biota is 10-15 million years older than the earliest previously known terrestrial organisms (polysporangiophytic embryophytes and nematophytes), and 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 floodplains of river systems, this groundcover represents communities occupying settings that are geomorphologically homologous to present-day riverine wetlands. However, compared to modern wetlands that are continuously wet by virtue of the moisture retention capabilities of soils and vegetation, the Early Silurian floodplain 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 floodplain 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, both in terms of 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 information recovered from the two specimens, BH10-13 and BH12-8-2 (section 9.3.1.3), illustrates well the range of results obtained on the non-paradigmatic fossils of the Passage Creek biota. These results reveal the advantages of the polyphasic approach taken (sections 9.2.2, 9.2.3), and at the same time expose limitations of the different investigation techniques and problems that the approach cannot solve. The main advantage of a polyphasic approach is that it maximizes the information extracted from fossils by combining investigation techniques that provide complementary and partially overlapping perspectives on morphology and internal structure. Working on megaspores, Hemsley and Glasspool (1999) mention the necessity of relating information from SEM and TEM to achieve an accurate interpretation of the wall structure. Very important for documenting in detail all the features of the fossils, a polyphasic approach is especially suitable in the case of non-paradigmatic assemblages where it is impossible
to know in advance which of these features are significant anatomically and
taxonomically.

The overlap of complementary information produced by the different
investigation techniques employed is mainly due to their inherent limitations. Bleaching
of the coaly material can be very helpful by revealing the gross internal organization of
the fossils (Figures 9.10, Figure 9.11.B), but because of the thickness of specimens and/or
of the limitations of light microscopy, it lacks fine scale resolution. In the case of
Specimen BH10-13, light microscopy of bleached fragments could not resolve details,
such as the structure and nature of spheroids, or the structure of multiseriate filaments.
SEM shows surface features, and can relay partial images of internal structures on
fracture surfaces, at a wide range of magnifications. Additionally, energy-dispersive
spectroscopy coupled to SEM can be used to characterize the elemental chemistry of
fossils. SEM was very effective in resolving the structure of spheroids in Specimen
BH10-13, as well as the microcrystalline masses that fill the spaces between spheroids in
multiseriate filaments (Figures 9.11.E, 9.12). However, because it only shows surface
features, SEM cannot always be used to resolve internal structures. For instance, the
filaments in Specimen BH10-13 are rarely obvious in SEM (e.g., Figure 9.12), which
does not resolve details of the amorphous matrix either. Thin sectioning offers direct
insight into the internal structures of fossils starting at lower (light microscopy) and up to
very high resolutions (TEM). In Specimen BH10-13 light microscopy of thin sections
revealed the structure of filaments and the laminar gross structure of the surrounding
matrix (Figure 9.7.H, I), and TEM resolved the structure of spheroids that make up the
filaments, as well as details of the amorphous matrix (Figure 9.11.I). However, even
with the use of serial sections thin sectioning has relatively limited three-dimensional resolution.

Specimen BH10-13 is an excellent example of the power of a polyphasic approach. This specimen was particularly intriguing because of the elongated morphology suggestive of axial plant sporophytes, the earliest fossils of which are much younger, dating from the late Wenlockian (Edwards et al., 1983). By documenting in detail the filamentous structure of this fossil, our approach led to a dramatically different interpretation. Correlation of data from bleached material, SEM, energy-dispersive spectroscopy, and the study of thin sections in light microscopy and TEM, was crucial in understanding the crystals and spheroidal crystalline aggregates that make up the filaments, and it showed that they are siderite. This inference was made possible only by the conjunction of all these types of information, whereas the nature of the minerals would not have been revealed by using only one or two of the investigation techniques. Correlation of data from all investigation techniques also allowed understanding of the systematic relationships of the fossil, interpreted as a colony of cyanobacteria whose cells have been replaced by siderite during diagenesis (Tomescu et al., 2004).

The information recovered from Specimen BH12-8-2 is somewhat less revealing, and cannot be interpreted in terms of systematic relationships of the original organism, mostly due to the dramatic diagenetic alteration of anatomy which obliterated cellular details. Nevertheless, our polyphasic approach produced a most detailed characterization of the fossil that will be very useful when comparative data from experimentation on modern material becomes available. Additionally, even without directly contributing to resolution of systematic affinities, some features of the fossil provide clues to the
construction of the original organism. The presence of different types of material evidenced on bleached fragments (Figure 9.13.C, D), in thin sections (Figure 9.13.E, H), as well as in SEM (Figure 9.15.B), reflects anatomical differentiation within the organismal body even in the absence of preserved cellular anatomy. Internal anatomical differentiation has been documented on several fossils in the Passage Creek assemblages, which provide the earliest date for the occurrence of non-animal organisms characterized by internal anatomical differentiation.

Results obtained from the two specimens also illuminate significant differences in the power of resolution of the different investigation techniques among individual fossils. Bleaching of the coaly material was crucial for understanding the gross internal organization of Specimen BH10-13, which would have been much more difficult to characterize based only on thin sections and SEM. By contrast, in the case of Specimen BH12-8-2 bleaching did not produce the same quality of information, indicating instead only the presence of two different types of material. Here thin sections were more useful, especially when confirmed by SEM and TEM, by allowing distinction of three different types of material, one in the counterpart, and two in the part compression.
11.3. CONOCOCHEAGUE MOUNTAIN BIOTA

The affinities of the axial mesofossils extracted from the Conococheague Mountain samples are uncertain. They are comparable in size to early embryophyte axial mesofossils the diameters of which may fall below 100 µm: around 80 µm for *Tortilicaulis* and *Cullulitheca* (Wellman and Gray, 2000; Edwards, 2000) and close to 50 µm for the distal end of an unnamed axis bearing two sporangia (Edwards, 2000, fig. 3h). However, none of these bear lateral appendages like those present on the specimen in Figures 10.6.A-C. If the specimen represents a plant fragment, then this would be the oldest axial plant fossil. The mode of attachment of appendages would indicate that the proximal end of the specimen is narrower than its distal end. This feature would correspond to an epidogenetic segment of the embryophyte body.

The appendages are also suggestive of the bases of thecae of graptolites. According to Drs. Richard Fortey and Stig Bergstrom (personal communication, 2004), the protrusion shown in Figure 10.6.C (arrowhead) could represent a smaller, second opening just below the larger main opening represented by the appendage. This morphology (bitheca) is characteristic of dendroid graptolites. However, the bithecae should be consistently present if this is a dendroid graptolite (Richard Fortey, personal communication, 2004), but this morphology is clearly absent from the lower appendage, and probably also from the upper appendage in Figure 10.6.B. Additionally, although it is not impossible to have such a slim dendroid graptolite, the size of the specimen is unusually small.
Cross sections of the specimen may help clarify the uncertainty that plagues the systematic affinities of these mesofossils, provided diagenesis did not obliterate the original internal structure of the organisms.

The size of the smooth tube (Figure 10.6.F) falls within the size range published by Niklas and Smocovitis (1983) and by Hueber (2001) for the aseptate, unbranched skeletal tubes (hyphae) that are known as parts of the internal organization of *Prototaxites*. The latter has been reconstructed as a giant fungus by Hueber (2001), but cannot be attributed to any of the known groups of fungi because of the lack of knowledge of reproductive structures. The Ashgillian age places this microfossil among the oldest occurrences of smooth tubes, along with those described from rocks of the same age from southern Britain (Burgess and Edwards, 1991).

Correlation of the section measured by Dr. Nadon with the section of Horowitz (1965) indicates that the Oswego sandstone, as delimited by Horowitz, starts somewhere above beds 85-87 (Figure 10.1). This means that all analyzed samples at Conococheague Mountain (beds 42 and 54-63) come from the upper Reedsville Formation. The latter has been interpreted by Horowitz (1965, 1966) as representing shoreline sedimentation, interpretation confirmed by the marine fossils and trace fossils found during fieldwork and measuring of the section. Therefore, the macroscopic thalloid compressions cannot be interpreted unequivocally as remains of terrestrial organisms, and their living environments remain unclear pending additional analyses. Such analyses should employ the polyphasic method developed for the Passage Creek biota. Additionally, sulphur isotope analyses of sediments at different levels throughout the section are likely to add
precision and resolution to interpretations of depositional environments at
Conococheague Mountain.

Another important point to be made is that the Oswego Sandstone is interpreted as
low-energy coastal plain or fluvial plain sediments by Horowitz (1965, 1966). This
renders the living environments of fossils found above bed 87 less equivocal, indicating
at least a continental origin. Carbonaceous compressions occur above bed 87, in beds 94
and 98, the former harboring the second richest assemblages at Conococheague Mountain
after bed 42 in the Reedsville Formation. Work on the Conococheague Mountain section
is only at the beginning, and time available for completion of this study did not allow for
analysis of these upper fossiliferous beds, but future work will specifically target them.
12. CONCLUSIONS

12.1. UNDERSTANDING NON-PARADIGMATIC BIOTAS

Non-paradigmatic biotas are fossil biotas whose components escape unequivocal taxonomic assignment. This may happen because the features of the fossils do not allow assignment to, or inference of phylogenetic relationship with, any known group. Alternately, the non-paradigmatic condition may arise from the fact that the characteristics of fossils compare them to several known groups, without allowing further distinction. In both cases, the result is that biological thinking is taken outside the systematic paradigm, whereby a priori knowledge of systematic relationships provides a consistent logical framework for inquiry and inference. In non-paradigmatic biotas such a framework is absent which significantly upsets biological inquiry and inference. Absence of knowledge of systematic relationships precludes understanding of fossil features and of their taxonomic significance, and hence impedes assessment of systematic relationships. The way out of this conundrum can be found through detailed description of the fossils and careful comparative experimentation on modern groups. Despite the difficulty of such enterprises, the incentive for studying non-paradigmatic biotas is represented by the contributions such studies can make to basic patterns of inference involved in assessing systematic relationships, and by the fact that these biotas lie at pivotal evolutionary nodes holding the keys to many of the most fundamental evolutionary puzzles.
The polyphasic approach used here integrates information produced by various investigation techniques to characterize in detail compression fossils of the non-paradigmatic Passage Creek biota, as a first step in resolving their affinities and bringing them within the logical framework of inquiry and inference provided by the systematic paradigm. The advantages of the approach for this endeavor are two-fold: (i) the complementarity of the different techniques maximizes the level of detail of fossil characterization; and (ii) the partial overlap of results obtained through different techniques maximizes the reliability of the descriptive information providing independent perspectives on features of the fossils. Results exemplified by the two fossil specimens used here demonstrate the strength of a polyphasic approach and illustrate two important aspects. (i) The power of resolution of the different investigation techniques varies from one fossil to another within the same assemblage. A technique that proves very effective providing the key to understanding certain fossils, may offer only marginally significant information on others. This stresses the necessity of using as wide a range of investigative techniques as possible, for all fossils. (ii) The effectiveness of the approach can vary from one fossil to another within the same assemblage. In some cases it allows for taxonomic assignment, while in others assessment of systematic affinities requires additional comparative work on modern groups. However, irrespective of whether the descriptive information can be interpreted in terms of systematic relationships of fossils, detailed descriptions are crucial for comparisons with modern groups, and can offer clues on the complexity of internal organization in spite of diagenetic obliteration of cellular anatomy by diagenesis. In the case of the Passage Creek biota which contains the oldest extensive terrestrial macrofossil assemblages, such information provides a minimal age
for the advent of terrestrial organisms with complex internal organization, very important
for inferences on large-scale evolutionary events in the colonization of land.
12.2. EARLY SILURIAN TERRESTRIAL BIOTAS – NEW EVIDENCE

The fossil localities analyzed in this study provide important new evidence for the nature of early life on land, and offer particular insight into the diversity and complexity attained by terrestrial communities at the beginning of the Silurian, some 440 million years ago.

The middle Llandoverian rocks at Kiser Lake preserve the earliest occurrence of septate spores assignable to the Ascomycetes, the earliest occurrence of the hilate monad *Cymbohilates disponerus* Richardson, as well as compression-impression mesofossils with morphology reminiscent of filamentous cyanobacteria, lichen rhizines, and leafy liverwort leaves. These extend the stratigraphic range of the Ascomycetes, previously known from Late Silurian (Ludlovian) or younger deposits (Sherwood-Pike and Gray, 1985), as well as that of *Cymbohilates disponerus*, previously known from the Early Devonian of the Anglo-Welsh Basin, to the Early Silurian (middle Llandoverian). In addition to these, the Kiser Lake assemblage documents with direct evidence a new type of sedimentary setting that preserves compression mesofossils of putative terrestrial origin – the subtidal to supratidal deposits of carbonate shorelines.

The Llandoverian Passage Creek biota of Virginia comprises the oldest macrofossil evidence for complex terrestrial life. 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 floodplains. 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 floodplains 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.

Direct fossil evidence for *bona fide* terrestrial photoautotrophs is virtually unknown prior to the rise of land plants some 415 million years ago. Geochemical signatures suggest that photosynthetic organisms were present on land by the beginning of the Proterozoic, 2,600 million years ago (Watanabe et al., 2000), but no compelling fossil evidence is available for the nature of early terrestrial primary producers. Filamentous microorganisms 1,200 million year old have been reported previously from continental settings (Horodyski and Knauth, 1994), but their affinities and growth environments (epigeal vs. hypogeal) are equivocal. This study provides the first conclusive evidence for cyanobacteria known from the ground surface in a continental setting, in the Passage Creek biota, and documents a previously undescribed type of fossil preservation – replacement by diagenetic siderite.
The significance of the study extends beyond that by consolidating and improving the search image for putative terrestrial plants defined by the discoveries of Pratt et al. (1978) at Passage Creek, and by the phylogenetic hypotheses of Mishler and Churchill (1985). This image consists of thalloid carbonaceous compressions, and 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.
12.3. ORGANISMAL EVOLUTION IN EARLY TERRESTRIAL BIOTAS – AN OVERVIEW

The evidence available to date on the beginnings of terrestrial life consists of a diverse assortment of data. (1) Geochemical and sedimentological studies provide indirect evidence that photosynthetic autotrophs were present on land in the Archean, 2,600 million 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, 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 (Butterfield, 2004). 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 fossil assemblages reported in this study. These assemblages, and particularly the Passage Creek biota, establish 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 present by the Early Silurian.
REFERENCES


Friend, P.F., 1983. Towards the field classification of alluvial architecture or sequence. Special Publication of the International Association of Sedimentology 6, 345-354.


Kenrick, P., Kvacec, Z., Bengtson, S., 1999. Semblant land plants from the Middle Ordovician of the Prague Basin reinterpreted as animals. Palaeontology 42(6), 991-1002.


Table 6.1. The stratigraphic units considered in the review of fluvial styles, with their age, location, and the number of publications that provided data on each of them; AB – Appalachian Basin; I – Ireland; N – Norway.

<table>
<thead>
<tr>
<th>AGE</th>
<th>UNIT</th>
<th>PUBLICATIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td>SILURIAN</td>
<td>Pridolian</td>
<td>Holmestrand (N)</td>
</tr>
<tr>
<td></td>
<td>Ludlowian</td>
<td>Stubdal (N)</td>
</tr>
<tr>
<td></td>
<td>Wenlockian</td>
<td>Bloomsburg (AB)</td>
</tr>
<tr>
<td></td>
<td>Llandoveryian</td>
<td>Sundvollen (N)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shawangunk (AB)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tuscarora (AB)</td>
</tr>
<tr>
<td>ORDOVICIAN</td>
<td>Ashgillian</td>
<td>Juniata (AB)</td>
</tr>
<tr>
<td></td>
<td>Caradocian</td>
<td>BaldEagle/Oswego (AB)</td>
</tr>
<tr>
<td></td>
<td>Llandeilian</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Llanvirnian</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Arenigian</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tremadocian</td>
<td></td>
</tr>
</tbody>
</table>
Table 6.2. Selected published sedimentary characteristics of the Bald Eagle Formation/Oswego Sandstone, Late Ordovician, Appalachian Basin.

<table>
<thead>
<tr>
<th>Author</th>
<th>Localities</th>
<th>Coarse/Fine</th>
<th>Coarse sed. body geometry</th>
<th>Channel geometry</th>
<th>Basal scouring</th>
<th>Shale intraclasts</th>
<th>Structureless sandstone/conglomerate</th>
<th>Horizontal bedding</th>
<th>Planar cross bedding</th>
<th>Trough cross bedding</th>
<th>Fining upwards</th>
<th>Mud cracks</th>
<th>Current distrib.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yeakel (1962)</td>
<td>NY to northern VA</td>
<td>very high</td>
<td></td>
<td>freq.</td>
<td></td>
<td></td>
<td></td>
<td>cross-bedding frequent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faill &amp; Wells (1974)</td>
<td>East-central PA</td>
<td>very high</td>
<td></td>
<td>pres.</td>
<td></td>
<td></td>
<td></td>
<td>cross-bedding present</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dennison &amp; Wheeler (1975)</td>
<td>Southeastern US</td>
<td>high</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rader &amp; Biggs (1976)</td>
<td>Northern VA</td>
<td>very high</td>
<td></td>
<td>pres.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faill (1979)</td>
<td>Northeast-central PA</td>
<td>high</td>
<td></td>
<td>pres.</td>
<td></td>
<td></td>
<td></td>
<td>cross-bedding frequent</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table 6.3. Selected published sedimentary characteristics of the Juniata Formation, uppermost Ordovician, Appalachian Basin.

<table>
<thead>
<tr>
<th>Author</th>
<th>Localities</th>
<th>Coarse/Fine</th>
<th>Coarse sed. body geometry</th>
<th>Channel geometry</th>
<th>Basal scouring</th>
<th>Shale intraclasts</th>
<th>Structureless sandstone/conglomerate</th>
<th>Horizon-tal bedding</th>
<th>Planar cross bedding</th>
<th>Trough cross bedding</th>
<th>Fining upwards</th>
<th>Mud cracks</th>
<th>Current distrib.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yeakel (1962)</td>
<td>NY to northern VA</td>
<td>high (in proximal facies)</td>
<td>freq.</td>
<td>freq.</td>
<td>freq.</td>
<td>cross-bedding frequent</td>
<td>freq.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotter (1978)</td>
<td>East-central PA</td>
<td>high</td>
<td>sheet*</td>
<td></td>
<td></td>
<td>pres.</td>
<td>abund.</td>
<td></td>
<td>pres.</td>
<td></td>
<td>IHS(?)**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faill (1979)</td>
<td>Northeast-central PA</td>
<td>equal to high</td>
<td></td>
<td></td>
<td></td>
<td>pres.</td>
<td>cross-bedding abundant</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Cotter (1978) mentions “broadly lenticular genetic units” (p. 366).
** Cotter (1978) mentions “mudstone is also characteristically present along the bases of beds and lining foreset laminae” (p. 365-366).
Table 6.4. Selected published sedimentary characteristics of the Tuscarora Formation, early-middle Llandoverian (Early Silurian), Appalachian Basin; T – Tuscarora Formation.

<table>
<thead>
<tr>
<th>Author</th>
<th>Localities</th>
<th>Coarse/Fine</th>
<th>Coarse sed. body geometry</th>
<th>Channel geometry</th>
<th>Basal scouring</th>
<th>Shale intraclasts</th>
<th>Structureless sandstone/conglomerate</th>
<th>Horizontal bedding</th>
<th>Planar cross-bedding</th>
<th>Trough cross-bedding</th>
<th>Fining upwards</th>
<th>Mud cracks</th>
<th>Current distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Folk (1960)</td>
<td>WV eastern panhandle</td>
<td>very high</td>
<td>sheet</td>
<td></td>
<td>rare, in upper part</td>
<td></td>
<td>1/4 of total beds cross-bedded</td>
<td>whole member = 2 large cycles</td>
<td>weakly unimodal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(upper T.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(lower T.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yeakel (1962)</td>
<td>NY to northern VA</td>
<td>very high</td>
<td></td>
<td></td>
<td>pres.</td>
<td></td>
<td>1/2 of total beds cross-bedded</td>
<td>largely unimodal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smith (1970)</td>
<td>NY to PA</td>
<td>very high</td>
<td></td>
<td></td>
<td>abund. freq.</td>
<td>± freq.</td>
<td>± freq. abund.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whisonant (1977)</td>
<td>VA</td>
<td>abund.</td>
<td>abund.</td>
<td>abund.</td>
<td>pres. freq.</td>
<td>abund.</td>
<td>pres.</td>
<td>largely unimodal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faill (1979)</td>
<td>Northeast-central PA</td>
<td>very high</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>extensivly cross-bedded</td>
<td></td>
<td></td>
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</table>
Table 6.4. (continued)

<table>
<thead>
<tr>
<th>Author (Year)</th>
<th>Localities</th>
<th>Coarse/Fine</th>
<th>Coarse sed. body geometry</th>
<th>Channel geometry</th>
<th>Basal scouring</th>
<th>Shale intraclasts</th>
<th>Structureless sandstone/conglomerate</th>
<th>Horizontal bedding</th>
<th>Planar cross-bedding</th>
<th>Trough cross-bedding</th>
<th>Fining upwards</th>
<th>Mud cracks</th>
<th>Current distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cotter (1983)</td>
<td>PA</td>
<td>very high</td>
<td>sheet</td>
<td>sheet</td>
<td>freq.</td>
<td>freq.</td>
<td>pres.</td>
<td>freq.</td>
<td>distally</td>
<td>abund.</td>
<td>pres., 2-3</td>
<td>m thick</td>
<td></td>
</tr>
</tbody>
</table>

* Cotter (1978) mentions “in places these units consist of a single cross-laminated sandstone bed between two very thin shale beds” (p. 366).
Table 6.5. Selected published sedimentary characteristics of the Shawangunk Formation, Early to earliest “Middle” Silurian, Appalachian Basin; S – Shawangunk Formation.

<table>
<thead>
<tr>
<th>Author (Year)</th>
<th>Localities</th>
<th>Coarse/Fine</th>
<th>Coarse sed. body geometry</th>
<th>Channel geometry</th>
<th>Basal scouring</th>
<th>Shale intraclasts</th>
<th>Structureless sandstone/conglomerate</th>
<th>Horizontal bedding</th>
<th>Planar cross bedding</th>
<th>Trough cross bedding</th>
<th>Fining upwards</th>
<th>Mud cracks</th>
<th>Current distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smith (1970)</td>
<td>NY to PA</td>
<td>very high</td>
<td></td>
<td></td>
<td>abund.</td>
<td>freq.</td>
<td></td>
<td>± freq.</td>
<td>pres.</td>
<td>abund.</td>
<td></td>
<td></td>
<td>largely unimodal</td>
</tr>
<tr>
<td>Epstein &amp; Epstein (1972) Tammany Mbr. (Upper S.)</td>
<td>Eastern PA</td>
<td>very high</td>
<td></td>
<td></td>
<td>freq.</td>
<td></td>
<td></td>
<td>pres.</td>
<td>cross-bedding</td>
<td>present</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epstein (1993) Upper S.</td>
<td>Southeast NY</td>
<td>very high</td>
<td>lenticular beds, sheet*</td>
<td></td>
<td>abund.</td>
<td>pres.</td>
<td></td>
<td>pres.</td>
<td>cross-bedding</td>
<td>present</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epstein (1993) Middle S.</td>
<td>Southeast NY</td>
<td>high</td>
<td>lenticular beds</td>
<td></td>
<td>abund.</td>
<td>pres.</td>
<td></td>
<td>cross-bedding</td>
<td>present</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epstein (1993) Lower S.</td>
<td>Southeast NY</td>
<td>very high</td>
<td>lenticular beds</td>
<td></td>
<td>pres.</td>
<td>freq.</td>
<td>freq.</td>
<td>present</td>
<td>unimodal</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

* Epstein (1993) mentions “shallow channels are abundant” (p. L22).
Table 6.6. Selected published sedimentary characteristics of the Bloomsburg Formation, Ludlowian (Late Silurian), Appalachian Basin.

<table>
<thead>
<tr>
<th>Author</th>
<th>Localities</th>
<th>Coarse/Fine</th>
<th>Coarse sed. body geometry</th>
<th>Channel geometry</th>
<th>Basal scouring</th>
<th>Shale intra-clasts</th>
<th>Structureless sandstone/conglomerate</th>
<th>Horizontal bedding</th>
<th>Planar cross bedding</th>
<th>Trough cross bedding</th>
<th>Fining upwards</th>
<th>Mud cracks</th>
<th>Current distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Faill &amp; Wells (1974)</td>
<td>East-central PA</td>
<td>present</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dennison &amp; Wheeler (1975)</td>
<td>Southeastern US</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>highly variable</td>
</tr>
<tr>
<td>Epstein (1993)</td>
<td>Southeastern NY</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>
Table 6.7. Selected published sedimentary characteristics of Late Silurian formations in the Ringerike Group, Oslo Graben, Norway.

<table>
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<tr>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Holmestrand Fm. Pridolian-Lochkovian</td>
<td>very high</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>present</td>
<td>present</td>
<td>present</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stubdal Fm. Late Ludlowian</td>
<td>very high</td>
<td>sheet*</td>
<td>frequent</td>
<td>frequent</td>
<td>frequent</td>
<td>abundant</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sundvollen Fm. Early-Middle Ludlowian</td>
<td>± equal</td>
<td>frequent</td>
<td>frequent</td>
<td>abundant</td>
<td>frequent</td>
<td>present</td>
<td>present</td>
<td>abundant</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>unimodal</td>
<td></td>
</tr>
</tbody>
</table>

Table 6.8. Selected published sedimentary characteristics of the Mweelrea Group undivided, Llanvirnian (Middle Ordovician), South Mayo Inlier, Ireland.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mweelrea Group undivided Llanvirnian</td>
<td>very high sheet*</td>
<td>sheet, but also two channels, 1.5-2m deep, with steep, even undercut walls</td>
<td>pres.</td>
<td>pres.(?)**</td>
<td>very rare</td>
<td>abund.</td>
<td>present (but also coarsening upward)</td>
<td>unimodal, wide scatter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* The author mentions “no deep channels but only wide shallow scours. Sedimentation units defined by grain size changes are lenticular with convex upper and lower surfaces” (p. 153).

** The author mentions “parallel bedded units” (p. 153).
Table 6.9. Summary of results of the Ordovician and Silurian fluvial styles survey.

<table>
<thead>
<tr>
<th>AGE</th>
<th>UNIT</th>
<th>FLUVIAL STYLE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SILURIAN</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pridolian</td>
<td>Holmestrand</td>
<td>??</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Braided?</td>
</tr>
<tr>
<td>Ludlowian</td>
<td></td>
<td>??</td>
</tr>
<tr>
<td>Wenlockian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Llandoverian</td>
<td>Shawangunk</td>
<td>Braided?</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ORDOVICIAN</strong></td>
<td></td>
<td>Braided?</td>
</tr>
<tr>
<td>Tremadocian</td>
<td></td>
<td>??</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Figure 4.1. Age of the study localities, first occurrences of fossils and features associated with the colonization of land, and chronology of main organismal- and community-level events as recorded by fossils. Absolute ages from Palmer and Geissman (1999).
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<table>
<thead>
<tr>
<th></th>
<th>Braided</th>
<th>Coarse-grained Meanderbelt</th>
<th>Fine-grained Meanderbelt</th>
<th>Straight Distributary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gradient</td>
<td>High</td>
<td></td>
<td></td>
<td>Low</td>
</tr>
<tr>
<td>Channel flow</td>
<td>Unconfined</td>
<td></td>
<td></td>
<td>Confined</td>
</tr>
<tr>
<td>Discharge rate</td>
<td>Flashy</td>
<td></td>
<td></td>
<td>Continuous</td>
</tr>
<tr>
<td>Bedload/suspended load</td>
<td>High</td>
<td></td>
<td></td>
<td>Low</td>
</tr>
<tr>
<td>Sand/mud (deposit)</td>
<td>High</td>
<td></td>
<td></td>
<td>Low</td>
</tr>
<tr>
<td>Sand body (deposit)</td>
<td>Wide</td>
<td>Multilateral</td>
<td>Multistoried</td>
<td>Narrow</td>
</tr>
<tr>
<td>Levees</td>
<td>Slight</td>
<td></td>
<td></td>
<td>Prominent</td>
</tr>
</tbody>
</table>
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