Early Silurian nonmarine animal remains and the nature of the early continental ecosystem

JANE GRAY **and** ARTHUR J. BOUCOT

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An assemblage of animal remains, the oldest from undoubted nonmarine beds, with structures attributable to at least one possible terrestrial animal, has been recovered in deposits of Early Silurian, Rhuddanian age, from the Central Appalachians. Other elements of a terrestrial ecosystem are plants at a nonvascular, possible liverwort-like, level of organization, and ascomycetes, predominantly terrestrial saprophytic and parasitic fungi (the oldest known). Together they provide evidence that pre-tracheophytic land plants and fungi, in association with invertebrates, occupied continental habitats by at least the earliest Silurian. While no evidence suggests that these organisms existed in a single community, they provide the earliest fossil record for the coexistence of varied organisms in the nonmarine ecosystem. Terrestrial invertebrates may have co-occurred with the earliest mid-Ordovician embryophytes although no fossil evidence for invertebrates exists before the Late Ordovician/Early Silurian. In view of the limited embryophytic dependence of many soil invertebrates, a preembryophytic evolution for them is consistent with the postulated significance of the soil habitat in terrestrialization and the evolution of feeding strategies among nonpredatory terrestrial invertebrates from microphytophagy to detritivory to herbivory as some emerged from within soils to soil litter to the soil surface. Detritivory can be regarded as a derivative extension of microphytophagy, since detritivores only consume detritus 'processed' by microorganisms and may be selecting microorganisms from detrital substrates as the basis of their nutrition.

Key words: terrestrial ecosystem evolution, nonmarine arthropods, soils, microphytophagy, detritivory

Jane Gray, Department of Biology, University of Oregon, Eugene, OR 97403, U.S.A.
Arthur J. Boucot, Department of Zoology, Oregon State University, *Corvallis*, OR 97331, U.S.A.

Introduction

Not uncommonly, paleontologists are confronted with problematic plant and animal remains particularly in older parts of the geologic column. During the past century, a steady stream of new and unique organisms has come to light, particularly from the marine Precambrian and Cambrian.

Until recent years there was little reason to suppose that Early Paleozoic nonmarine strata would provide significant data on their own unique assemblages of organisms. The prevailing view was that, even if pre-Devonian nonmarine organisms had existed there was little possibility for recovering evidence of them. The result: neglect. Published data on Early Paleozoic continental organisms and the development of the early continental ecosystem thus remain meagre despite our own concerted efforts beginning over 20 years ago (Gray & Boucot 1971).

Early stages of continentalization are still enigmatic because of ambiguities concerning the environment and potential routes by which organisms may have come to land. Much speculation, largely uninhibited by factual information, attaches to such questions as the nature of the earliest nonmarine organisms; the timing of continentalization; the resources available to sustain life in freshwaters and on land; how organisms coped with apparently hostile environments of the land surface; the paths to continentalization; and what habitats are most likely to have preceded full terrestrialization.

New fossil evidence has demonstrated that the record of land plant life, at post-algal level of organization, commenced in the early Middle Ordovician (Gray *et al.* 1982; J. Gray, H. McClure, and A.J. Boucot, unpublished) at least 60–70 Ma (million years) earlier than was previously taken for granted. This has conspicuously narrowed the vast interval separating life's beginnings in the sea from the apparent initiation of colonization in nonmarine habitats but still leaves unaccounted for a 'fallow' gap of millions of years.

The fossils largely responsible for the change in view on the antiquity and character of early continental ecosystems are microscopic plant remains, commonly the original substances of the organisms themselves, freed from rocks by chemical digestion using methods traditionally employed by pollen analysts and palynologists (Gray 1965).

The animal remains considered in this paper are the first and oldest to be discovered serendipitously in fluvial deposits in intimate association with spores of these land plants and fungal spores. These fragmented remains indicate that the animals were small, even tiny – microinvertebrates that might have sequestered themselves beneath rocks, dwelt interstitially within the soil, or lived in cyanobacterial, algal or bryophytic mats on the soil surface.

Invertebrate paleontologists have paid scant attention to tiny organic fragments of cuticle and tiny body parts of microfossils recovered by chemical digestion of rocks, traditionally stressing complete specimens. At Gilboa, New York, for example, apart from the few spectacular complete or nearly complete animal remains, most of the late Middle Devonian Gilboa material consists of fragments, as with the animal remains described here, of which only about 5% or less are identifiable (W.A. Shear, personal communication to JG, 1987). These fragmented remains of small fossil invertebrates often present a challenge to the paleontologist because invertebrate zoologists generally have tended to neglect the morphological details of cuticle and body parts of small animals. Though problematic and presently unidentified, such enigmatic remains should not be ignored in terms of their evolutionary and environmental implications.

With regard to the variety of animal remains recovered from the Early Silurian Tuscarora Formation, there are morphological reasons to believe they are primarily arthropodan. Inability to taxonomically assign these fragments to any higher taxa in no way detracts from their significance or importance as evidence for nonmarine organisms, nor even as evidence for animal diversity. One need but look to the example provided by Early Paleozoic continental trace fossils, whose affinities similarly are commonly uncertain or unknown. No one questions their utility nor the need to document them as part of the record.

Together with plant and fungal remains, these tiny animal fragments provide significant and provocative evidence for Early Silurian continental colonization, an area where information is greatly needed. Together the remains provide several essential elements of a functional ecosystem: plant autotrophs, recyclers, and animal heterotrophs. No evidence exists that these components were integrated into a single 'community' despite their association in the same stratigraphic unit.

This paper has several missions: (1) To present a preliminary account of some of the Early Silurian organic remains – the oldest bona fide fossil evidence for nonmarine animals; (2) to review evidences for pre-Late Devonian nonmarine animals as a basis for framing hypotheses about the timing of 'continentalization' and 'terrestrialization'; **(3)** to consider from among some of the potential avenues to terrestrialization – the marine littoral, the freshwater and the interstitial soil – which seems most likely within environmental scenarios hypothesized for the late Precambrian and Early Paleozoic when initial stages of terrestrialization likely occurred; and (4) to speculate about the ecology of animals and other organisms most likely to have taken part in the development of nonmarine ecosystems and full terrestrialization.

The nonmarine environment

The nonmarine environment consists of a complex of ecosystems united less by shared characteristics than the fact that they are not marine. The equivalent terms 'nonmarine' and 'continental' both refer to (1) dry-land, surface (epigeal) terrestrial habitats, (2) wholly aquatic, 'freshwater' standing and running water habitats that include waters of salinities greatly exceeding normal seawater as well as water with low levels of dissolved salts, and (3) habitats that bridge the dry-ground and wholly aquatic, such as swamps and bogs. Additional to these familiar 'surface' habitats, continental environments also include the less conspicuous, often overlooked soil habitat and the soil biota complex. This habitat is of most interest within the context of this paper.

Soils may be regarded as a component of the terrestrial ecosystem and its most characteristic feature, or as an independent ecosystem with its own permanent organisms as well as temporary taxa also found in the dry-ground surface terrestrial and freshwater ecosystems. In soils, freshwater organisms include microfauna and meiofauna, in the micron and low millimeter size range, that live interstitially within the water between soil particles (in water-filled soil capillaries) or in films of water surrounding soil particles. This soil water fauna, or ground-water fauna, includes purely aquatic organisms, some confined to this habitat, some also occupying surface waters, as well as those active only in the presence of water but capable of surviving periodic desiccation.

Modern soils vary in development depending on their geographic distribution. Many with a well-developed profile, are a complex mix of weathered and unweathered rock materials derived from the substratum and organic debris in various stages of decomposition derived both from surface and subsurface life. Soils in immature stages of development – deficient in organic matter and surface litter – provide the most likely models for early terrestrial soils. They are hypothesized to provide the most likely habitat for organisms that bridged the nonmarine aquatic-dry-ground terrestrial ecosystems in the Precambrian or Early Paleozoic.

Soil and soil litter organisms, unlike soil-surface organisms, include few herbivores that feed on undecomposed green plant tissues and comparatively few carnivores. Most derive sustenance from decayed or partially decayed plant materials and/or the microorganisms for which these decaying tissues provide the substrate.

Early Paleozoic nonmarine and potential terrestrial organisms

Pre-Middle Ordovician. — Scattered evidences for nonmarine fossils exist from the Archaeozoic to the Early-Middle Ordovician. Some of the Precambrian records are said to be from lacustrine deposits. None involves a proven terrestrial habitat well away from the intertidal shoreline. The earliest, Archaeozoic record, consists of varied evidences for limnic cyanobacterial stromatolites (Buick 1992). Jackson (1973) and Jackson *et al.* (1978) present geochemical and isotopic data suggesting that some Proterozoic bitumens were derived from nonmarine, possibly terrestrial algae, such as green algae. Campbell (1979) draws compelling parallels between modern procaryotic desert crust organisms and possibly similar materials from the Precambrian. Golubic & Campbell (1979) compare the similar morphologies of a modern microbial lithophyte with a Proterozoic organism that might have been an intertidal lithophyte. Hofmann *et al.* (1980) describe some Proterozoic stromatolites they interpret as having lived intertidally. Beeunas & Knauth (1985) provide Proterozoic isotopic data consistent with the existence of terrestrial autotrophs. Knauth & Horodyski (1992) report Middle and Late Proterozoic occurrences of cyanobacteria that they interpret as terrestrial, using both paleontological and isotopic evidence (see Kerr 1992, for a figure of the fossils).

Robbins *et al.* (1985) described minute problematic fossils that resemble fecal pellets made by freshwater, planktonic microcrustaceans such as copepods, benthic polychaetes, and ciliates from Precambrian and Cambrian age deposits. Precambrian lake deposits as old as 1.3 Ga (billion years) yielded the above problematica, as have still older Proterozoic rocks (as old as 1.9 Ga) that might be either lacustrine or marine. Archaeozoic samples, however, have not produced such problematica.

Several intriguing 'limnic' habitats in the Cambrian and Early-Middle Ordovician appear to have unique, enigmatic arthropods lacking close relations with coeval marine taxa: (1) Early Cambrian finely laminated 'lacustrine' beds from Bohemia (Chlupač & Havlíček 1956; I. Chlupač and M. Konzalova unpublished); (2) Early Cambrian 'limnic' deposits from Siberia (Bergström 1979, 1980); and (3) Early-Middle Ordovician varve-like deposits from Tennessee. These last were laid down in a cenote-like basin (Laurence 1944: although differently interpreted by Caster & Brooks 1956) at a time of lowered sealevel in an area that on paleogeographic grounds may have been many kilometers from the sea.

Although the sediments at these three localities may be of 'nonmarine' type, for none of their unique arthropods is there absolute certainty about their nonmarine origin. There is no way to know that marine animals could not themselves have moved into these environments from elsewhere or have been transported there by purely physical agencies. The unique locality in each case, plus the rarity of specimens raises problems in interpretation.

No coeval Precambrian, Cambrian or Ordovician body fossil evidence exists for dry ground animals. This habitat may be represented by trace fossils *Climactichnites* and *Protichnites* from the barren, cleanly washed sands of the Late Cambrian Mount Simon Sandstone of the upper Mississippi Valley (Raasch 1939). Raasch originally attributed these traces to marine aglaspids possibly capable of venturing onto land. But because aglaspid body fossils and traces never co-occur, Raasch later suggested (personal communication to J.G., 1985, cited in Gray 1988a) that such an attribution 'now seems highly speculative'. Yochelson & Fedonkin (1992) attributed *Climactichnites* from eastern as well as mid-western North America to an unknown marine organism feeding on low intertidal sand organisms and/or detritus. Although proof that a marine metazoan made *Climactichnites* is lacking, the possibility that its maker was a marine organism behaving like limuloids that venture onto land from shallow-water, nearshore habitats to feed and breed seems more likely than the alternative possiblity that the trace maker had something to do with the development of the nonmarine ecosystem.

Middle Ordovician through Early Silurian. — Beginning in the Middle Ordovician, microfossils provide continuous evidence for terrestrial plant life at a post-algal/pre-tracheophytic level of organization (Gray 1991; Gray & Shear 1992; J. Gray, H. McClure, and A.J. Boucot, unpublished).

No coeval continuous sequence of potential nonmarine, limnic or terrestrial animals exists so early in time. A single record of trace fossils from Late Ordovician deposits interpreted as paleosols by Retallack (1985) and Retallack & Feakes (1987) may be evidence for soil inhabiting arthropods. These paleosols are immediately subjacent to the animal-bearing Early Silurian beds in central Pennsylvania reported on herein. The simple burrows, of a type frequently associated with nonmarine deposits, are not assigned to any taxon even at phylum level, and provide no independent insight into the specific kind(s) of animals that produced them. The authors invoked arthropods, such as millipedes, merely because millipedes are known to have been among earliest nonmarine burrowing invertebrates compatible with the interpretation of a seasonally dry environment. If these deposits are correctly interpreted as paleosols with associated caliche, and the structures are burrows, they would provide conclusive evidence for Late Ordovician terrestrial animals that approach in age the mid-Ordovician pre-tracheophytic embryophytes.

Eurypterids of potentially nonmarine origin are virtually unknown before the Wenlock, but at least one specimen of Llandovery age from the Tuscarora Formation comes from either a nonmarine or brackish-estuarine environment (Boucot *et al.* 1994) at Kishacoquillas Gap some 32 km (20 miles) northwest of Millerstown. Because the depositional environment of the Tuscarora varies from fluvial at Millerstown to interbedded fluvial/littoral-marine or fluvial/tidal-marine at Kishacoquillas Gap, the environment of the eurypterid-bearing bed is uncertain. The absence of associated marine mega-or microfossils tends to favor a nonmarine depositional environment. Other eurypterid occurrences from Pennsylvania and New York are from potentially nonmarine beds of essentially equivalent age (Boucot *et al.* 1994).

Late Silurian through Middle Devonian. — The first more-or-less continuous records for multicellular nonmarine, continental animals subsequent to these described herein, begin in the Late Silurian.

Potentially the oldest is the enigmatic arthropod *Pseudarthron* described by Selden & White (1983) from a single, incomplete specimen from the Slot Burn Formation of Lesmahagow, Scotland. Selden & White (1983) assigned the Slot Burn Formation to the Ludlow and Wellman & Richardson (1993) to the early Wenlock although a late Llandovery age is not precluded by the data they present. In the absence of associated marine fossils, Selden & White (1983) concluded that 'Pseudarthron was probably a member of a fresh- or brackish-water, vagrant epifaunal benthos'. However, the locally widespread palynological evidence summarized by Wellman & Richardson (1993) indicates a freshwater, limnic environment for the arthropod- and spore-bearing beds. Associated vertebrates in the Slot Burn Formation are environmentally nondiagnostic, because they include some forms that occur in both marine and nonmarine environments, as do the eurypterids.

Somewhat younger are a variety of arthropods (problematic myriapods, phyllocarids, eurypterids) and agnathans from the lacustrine Cowie Formation, Stonehaven Group of Cowie, Scotland (Almond 1985), originally assigned to the Pndoli. On the basis of spores it is now considered to be of late Wenlock to early Ludlow age (Marshall 1991). The associated diplopod, possibly the oldest known, is potentially terrestrial, though its poor preservation precluded conclusive determination of its morphology and habitat.

McNamara & Trewin (1993) have described an arthropodan body fossil from a mixed braided fluvial and aeolian sandsheet environment of the Tumblagooda Sandstone, Western Australia. Although the age is not precise, the presence of simple trilete spores in the Tumblagooda and its relations with the overlying Dirk Hartog Formation of Ludlow age, suggests an early to mid-Late Silurian age. This single specimen interpreted to be .a euthycarcinoid, co-occurs with a rich, as yet undescribed trace fossil assemblage that includes 'extensive trackways thought to have been made by a number of different types of arthropods, including eurypterids' (McNamara & Trewin 1993: p. 319; Trewin 1993). McNamara & Trewin (1993) Interpret their euthycarcinoid *Kalbarria* as a potential ancestor of the hexapods, as well as being early enough in time to fulfill that role.

Whereas McNamara & Trewin (1993: p. 332) attribute both the euthycarcinoid and eurypterid trackways to aquatic animals, they indicate that they were made subaerially by animals 'able to walk out of water' (see also Trewin, 1993). The ability of such aquatic arthropods to forage and breed on land, much as modern limuloids, suggests it to be an ancient adaptation. If the traces noted by Trewin (1993) and McNamara & Trewin (1993) are those of eurypterids, they provide one of the older records for freshwater eurypterids.

The latest Silurian, Pndoli, of the Welsh Borderland, has produced remains of one entire specimen of a trigonotarbid arachnid plus body parts and abundant cuticles attributed to terrestrial centipedes. These occur with land plant remains (*Cooksonia* and other rhyniophytoids), and a predominance of nonmarine aquatic arthropod fragments, including eurypterids, scorpions and kampecarid myriapods (Jeram et *al.* 1990) all transported into a nearshore marine environment where they occur with a restricted marine fauna (Jerarn *et al.* 1990).

Despite the limitations of the Late Silurian body fossil record, the morphological complexity and taxonomic diversity of varied Late Silurian and Early Devonian nonmarine trace assemblages in minerogenic substrates, some originally interpreted as marine, but now shown to be consistent with a freshwater origin (Webby 1968; Trewin 1976; Allen & Williams 1981; Bradshaw 1981; Gevers & Twomey 1982; Pollard & Walker 1984; Pollard 1985; Walker 1985; Woolfe 1990; Trewin 1993; McNamara & Trewin 1993) as well as in organic substrates (Kidston & Lang 1921; Kevan *et al.* 1975; Banks 1981; Banks & Colthart 1993) exceeds the variety of known, coeval, potential trace makers.

Early to Middle Devonian assemblages include a variety of evidence for continental and particularly terrestrial animal life. Terrestrial arthropods from the mid-Early Devonian Rhynie Chert include collembolans, an actinedid (= prostigmatid) mite, and trigonotarbids (Kevan *et al.* 1975; Rolfe 1980). A least one aquatic crustacean is known (Gray 1988a).

Scorpions from the Early Devonian (early-middle Siegenian) Beartooth Butte Formation, Wyoming, U.S.A., have a morphology most compatible with a terrestrial habitat (A. Jeram, personal communication, 1993). Some have regarded the Beartooth Butte Formation as marine but interpretation of the scorpion as terrestrial is compatible with the absence of any evidence for marine invertebrates in the Beartooth Butte and distant location from any potential shoreline (see Gray, 1988a: pp. 24, 135, for environmental discussion of the Beartooth Butte Formation).

The Early Emsian Battery Point Sandstone produced an archaeognathid (bristletail) insect (Labandeira *et al.*, 1988), a wingless member of the thysanurans that include modern machilids. Labandeira (personal communication, 1993) is presently finding a variety of arthropod fragments from this same unit.

Early Emsian arthropleurids and trigonotarbid arachnids are found at Alken an der Mosel together with aquatic, perhaps brackish, perhaps freshwater, eurypterids and scorpions (Starmer 1970, 1976, 1977).

The Givetian age Panther Mountain Formation at Gilboa includes spiders, trigonotarbids and other arachnids (Selden *et al.* 1991; Shear *et al.* 1987), prostigmatid ('endeostigmatid') and oribatid mites (Norton 1985; Norton *et al.* 1988), arthropleurids, pseudoscorpions, centipedes, and an archaeognath (bristletail) (Shear & Kukalova-Peck 1990). Although the 'aquatic scorpion' *Tiphoscorpio hueberi* from the Panther Mountain Formation has been reassigned to the arthropleurids (Selden & Shear 1992), terrestrial scorpions are found at Gilboa (Jeram 1993).

In addition to the arthropods cited above, Almond (1985) has discussed a number of apparently terrestrial myriapod-like arthropods from the late Wenlock-Ludlovian, Gedinnian & Siegenian of the Lower Old Red Sandstone of Scotland, and freshwater bivalves, gastropods, crustaceans and vertebrates (Starmer 1976, 1977; Rolfe 1980; Gray 1988a) are found in Early to Middle Devonian assemblages.

Animal, plant and fungal remains from the Tuscarora Formation

Locality, stratigraphy, and depositional environment

The fossil-bearing rocks are in the basal portion of the Tuscarora Formation, immediately north of Millerstown, Harrisburg region, central Pennsylvania, exposed in a roadcut on U.S. Highway 22. The animal, plant and fungal fossils were recovered from thin mudstone partings separated by and interlayered with a thick sequence of clean quartzites.

In this area the Tuscarora Formation is underlain by the Late Ordovician Juniata Formation with a sharp basal contact that could represent a minor disconformity. It intergrades with the overlying Rose Hill Formation that contains marine ostracodes belonging to late Llandovery Zones C_3–C_6. The Tuscarora does not contain age-diagnostic marine invertebrates. Its gradational relations with the overlying Rose Hill Formation indicate it to be of Llandovery, earlier Llandovery age (Berry & Boucot 1970). Spore assemblage type indicates that it is assignable to Microfossil Assemblage Zone I (Gray 1985); morphometric analysis of average spore diameters is consistent with a Rhuddanian age (Gray 1988b).

The Tuscarora Formation crops out widely in central Pennsylvania and neighboring states to the south. It represents a variety of nearshore shelf, coastal and fluvial environments (Cotter 1982, 1983; Smith 1970; Yaekel 1962). Where the unit is exposed in central Pennsylvania, including Millerstown, it is concluded to have been 'deposited solely in alluvial fan and braided fluvial systems' (Cotter 1982, 1983). Yaekel's (1962) paleocurrent analysis and comparisons made by Smith (1970) between deposits of the Tuscarora and the modern South Platte-Platte Rivers in Nebraska and Colorado support Cotter's conclusions about the depositional environment. This information is consistent with the total absence of marine fossils or of shallow water, nearshore marine trace fossils such as Arthrophycus, in the lower half of the formation where animal remains were obtained. Absence of marine microfossils such as spiny and ornamented acritarchs or chitinozoans, is consistent with lack of salt wedge transport upstream into the Millerstown freshwater environment.

Animal remains

Animal remains are of three principal types: a) minute, spinose, seta-like structures, b) varied cuticles, some spinose, some with other ornamentation and c) tracheid-like tubes (Figs 1A–D, 2A–C, 3 are typical examples). Many are arthropod-like, meaning they are more like remains one would anticipate from arthropods than any currently existing animals in other phyla. Others are similar to eurypterid cuticle and at least one appears to represent the jaw fragment of an annelid worm.

Remains are not provided with a formal set of Linnaean binomina, since to do so would probably cause difficulty for future workers who may recover some of the whole organisms from which these fragments were derived.

With regard to the arthropod-like remains, there is the possibility that they belong to an extinct higher taxon or taxa. Body fossil evidence for nonmarine animals to which these remains could belong are singularly sparse during this interval of time, as detailed above. Complicating the problem of properly identifying fragmentary animal remains is the lack of comprehensive work on, and illustration of, modern arthropod exoskeletons at magnifications of 500–2000 times. This limited number of available high magnification studies provide far too small a sample to decide whether or not these basal Silurian animal fragments are truly unique and morphologically distinct from modern arthropod structures.

The putative setae (Figs 1A–B, 2B–C) consist of a central shaft, generally unornamented basally, but distally bearing numerous spinose protuberances that taper to a point, and tend to be restricted to either side of the shaft, rather than being randomly distributed over the entire distal surface. Surfaces of both the minute spinose protuberances and the shaft appear smooth at magnifications up to x 5000. The whole structure is strikingly similar to the bipectinate tactile setae seen in various arthropods (G.W. Krantz, personal communication, 1987).

Cuticles (Figs 1C, 2D) consist of a number of different types, some spinose but differentiated by spine length, form and distribution. In some, spines are scattered on the cuticle surface; in others, spines are arranged in regular rows. In the illustrated examples, the long smooth spines taper to a sharp point. Cuticle fragments with variable spinose edges have also been recovered. Variability may reflect derivation from a variety of plates belonging to a single organism or to different organisms.

Tracheae-like structures (Figs 2A, **3)** closely resemble arthropod tracheae found in groups such as chilopods, diplopods, onychophorans and arachnids rather than insects and crustaceans (M. Locke, personal communication, 1987). Locke wrote that these structures are 'probably tracheae rather than tracheoles because of their size'. Similar structures are common in Ludlovian samples from Gotland (Fig. 2A). These remains provide the first body fossil evidence for pre-latest Silurian-earlier Devonian probable air-breathing, terrestrial animals. The smooth, annular rings with relatively 'rectangular' cross-sections, are characteristic of these structures (Figs 2A, **3).**

Plant remains

Abundant spores in the Tuscarora Formation are attributed to post-algal/pre-tracheophytic plants at possible bryophyte (hepatic) grade of organization (Gray 1984, 1985, 1991). Such spores are agents of dispersal as well as reproduction. They are abundant in horizons that yield animal remains, as well as in many other beds that contained few or no animal remains. Attribution to land plants rests in part on their morphology and

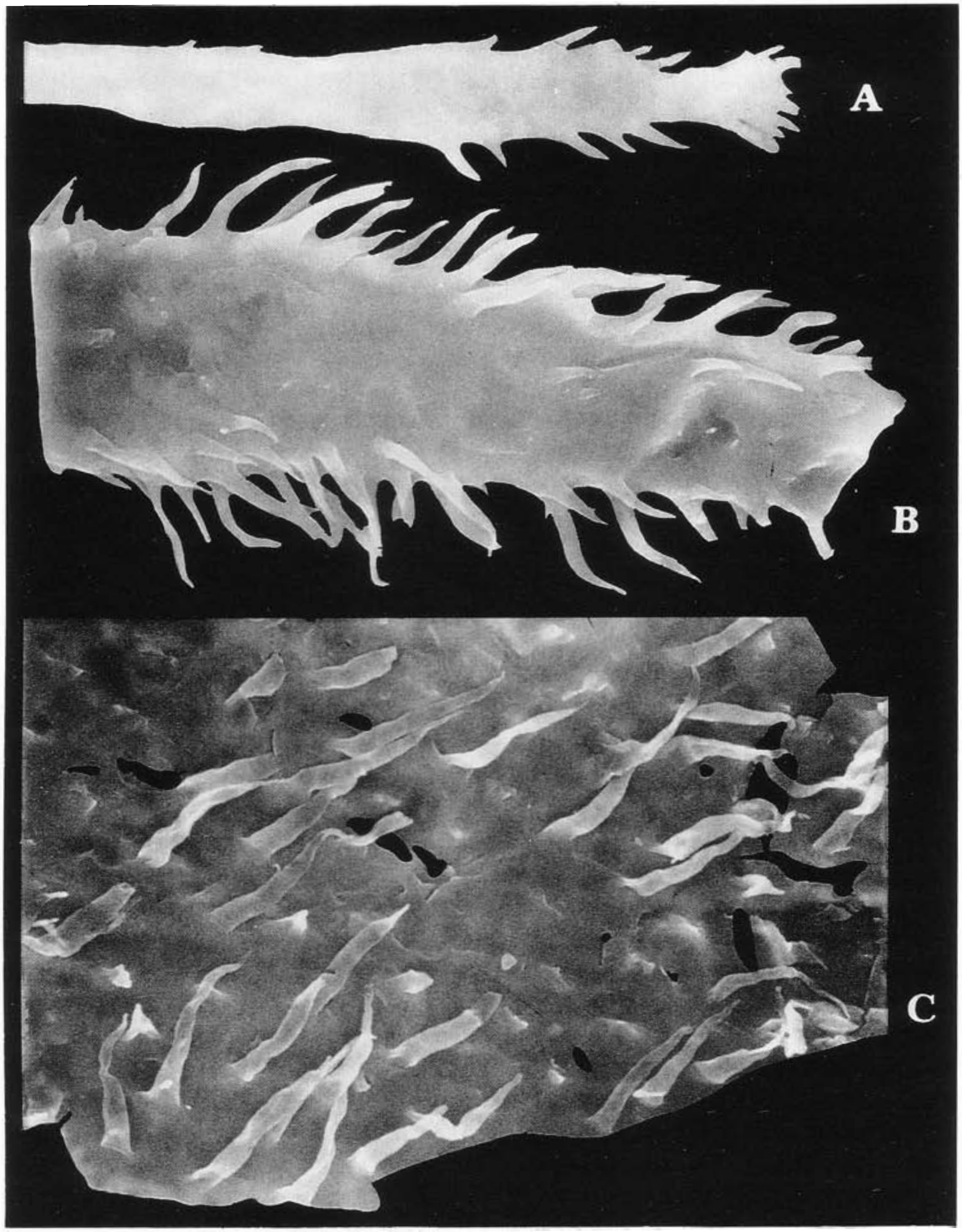

Fig. 1. Scanning electron micrographs of arthropod-like fragments from the lower part of the Tuscarora Formation, Millerstown, Pennsylvania. ❑A. Seta-like structure with numerous, laterally directed, smooth spines (× 1500) inclined distally at about a sixty degree angle. Note absence of spines on the proximal part of the shaft. ❑B. Fragment of a larger seta-like structure, showing the nature of the tapering, smooth spines (× 1500).❑C. Cuticle fragment, with scattered, smooth spines (× 1500). Note a few short spines among the long ones.

in part on their distribution in a similar spectrum of depositional environments in which pollen and spores of extant plants occur, including shallow-water, nearshore marine deposits, fluvial rocks such as the lower Tuscarora Formation, and inland limnic deposits (Wellman & Richardson 1993) some distance from shoreline. At Millerstown, in the overlying marine Rose Hill Formation, spores are rare to uncommon compared with the Tuscarora, consistent with transportation offshore by wind and/or water.

Within the last few years, it has become clear that plants whose spores are represented in the Tuscarora Formation populated the continents at least as far back as the Middle Ordovician (Gray *et al.* 1982) and probably the earlier Middle Ordovician (J. Gray, H. McClure, and A.J. Boucot, unpublished) perhaps replacing terrestrial cyanobacteria and green algae as the dominant autotroph in terrestrial ecosystems. These spore-producing plants were geographically widespread by the Late Ordovician or earliest Early Silurian, well in advance of the first positive evidence for tracheophytes in the mid-Late Silurian (Ludlovian of Australia: Tims & Chambers 1984). Such spores are found in localities bordering the North Atlantic in Europe and North America and within the Malvinokaffric Realm (Gray & Boucot 1972; Gray et *al.* 1982, 1986, 1992; Gray 1985, 1988b).

Fungal spores

Associated in low frequency with the spore tetrads and animal remains, are transversely multiseptate fungal spores similar in morphology to those described from the Ludlow of Gotland (Shemood-Pike & Gray, 1985). They are not accompanied by the hyphae that occurred with the spores in the Gotland sediments. The Gotland spores are ascribed on morphological grounds to the Ascomycetes because of a morphology so distinctive that it is difficult to interpret the spore type 'as anything but the conidial stage or ascospore of an Ascomycete' (Shemood-Pike & Gray 1985: p. 11). Because the Millerstown fungal spores differ in no regard from the Gotland examples, we also assign the Millerstown material to the Ascomycetes – the oldest such fossil specimens that appear to represent the higher fungi of class Ascomycetes, a predominantly terrestrial group.

Conclusions

Affinities of the Tuscarora animal microfossils. — Similar to other evidence, body and trace, from the pre-Devonian and Early Devonian, many of the animal fragments from Millerstown point toward arthropods. The organic fragments are dominated by arthropod-like materials: apparent tactile hairs, varied cuticle types, and among others, tracheae-like structures.

Although there is no particular reason to believe that arthropods were the earliest invertebrates to breach the nonmarine habitat, the durable cuticle predisposes them to fossilization compared with soft-bodied invertebrates and protistans. This may significantly bias the impression of the part played by arthropods in early continentalization. Their predisposition

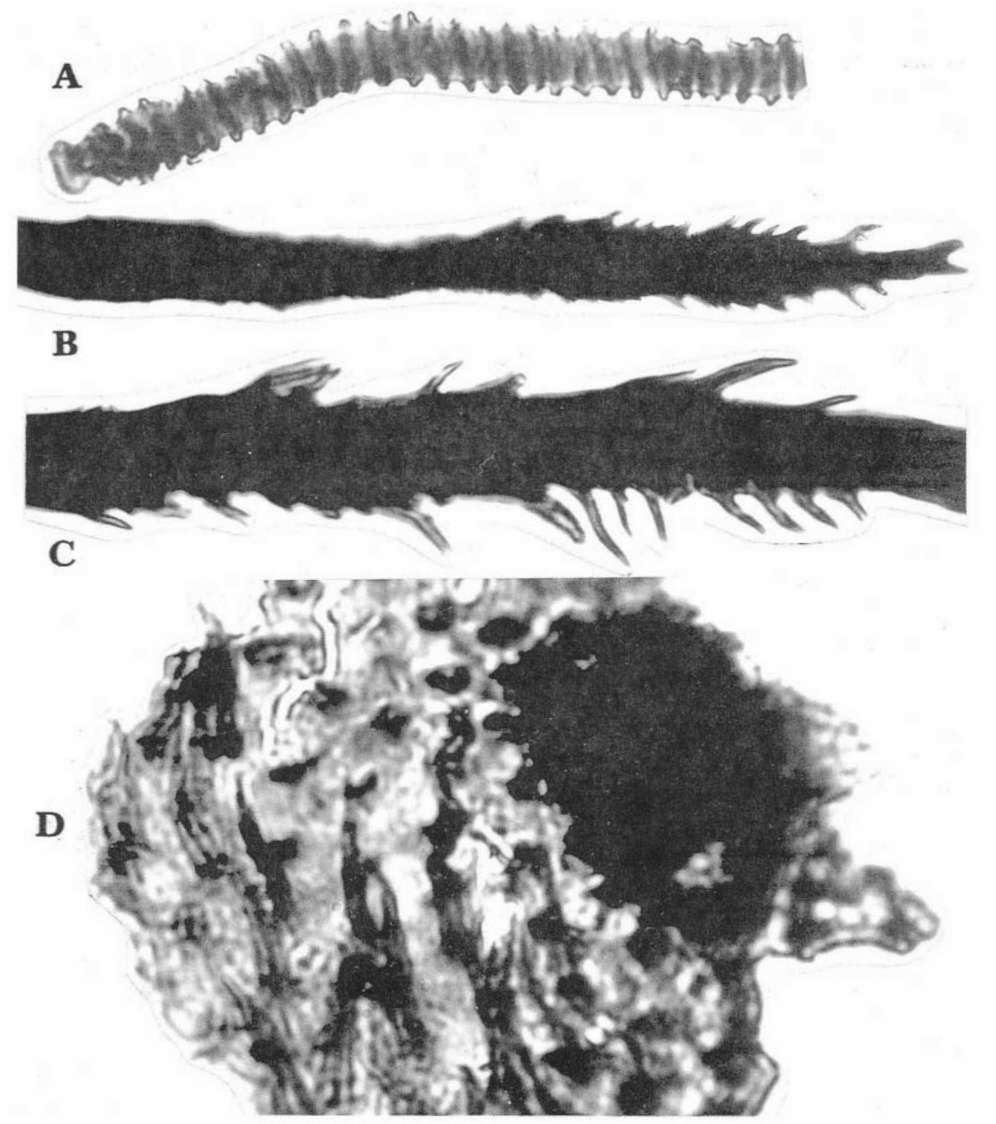

Fig. 2. Optical photographs of a tracheae-like structure from the Burgsvik Sandstone, Ludlovian, Gotland, Sweden, and arthropod-like fragments from the lower part of the Tuscarora Formation, Millerstown, Pennsylvania. □A. Portion of a tracheae-like tube showing the regular spacing of the annular rings (× 2000). □B. Seta-like structure with numerous, distal, laterally directed spines (× 800). Note the absence of spines on the more proximal portions of the shaft and the bifurcating tip. Compare with the seta-like structure of Fig. 1A. □C. Portion of the distal region of a seta-like structure with numerous, lateral spines that taper and incline distally (× 1400). □D. Spinose cuticle fragment, showing the regularly spaced, distally tapering, long and short spines, all inclined in one direction (x1400). Compare with the cuticle of Fig. 1C.

for leaving the water and venturing onto land as early as the Cambrian suggests preadaptation to early terrestrialization.

Continental habitats; the Tuscarora evidence. — Within the broad continental or nonmarine environment, the specific habitat occupied by any of the animals that have left their remains in the fluvial environment of the Tuscarora cannot be determined. The remains may represent organisms that lived in the freshwater environment, the surface terrestrial environment, on and within contemporary vegetation surfaces (evidences for which are provided by the spores) or within the soil environment in an interstitial manner, or any combination of these possibilities. The fragmented condition and occurrence in fluvial deposits suggests the possibility of transportation. This in turn, might point toward a previous residence in soil or in soil-surface algal or plant mats, conclusions compatible with the tiny size of the remains.

Only the tracheae-like tubes would appear to be attributable to a terrestrial, air-breathing animal, but one that may also have been a soil inhabitant. Air-breathing animals are also interpreted as having been responsible for burrows in the Late Ordovician Juniata Formation (Retallack & Feakes 1987). Both pieces of evidence suggest the presence of nonaquatic animals well in advance of more fully documented Late Silurian evidence for terrestrial animals and the significant, varied adaptive radiations in the terrestrial environment in the Devonian.

Continental ecosystem evolution: speculation and discussion

Were there Precambrian-Early Paleozoic freshwater adaptive radiations? — There are obvious theoretical reasons for believing that, apart from interstitial soil waters that could have been colonized directly across the marine/nonmarine interface, nonmarine aquatic habitats, conventionally lakes and streams, were inhabited by diverse microbiota, cyanobacteria, algae, fungi, protists and soft-bodied invertebrates long before colonization of dry ground.

Though limited and problematic, the fossil record is consistent with the theoretical possibilities of freshwater radiations among invertebrates in the Late Precambrian (Robbins et *al.* 1985) and/or in the Early Paleozoic (Bergstrom 1979, 1980). Freshwater and potentially even terrestrial radiations had apparently already occurred among cyanobacteria in the Precambrian as discussed earlier. Though undocumented by fossil evidence, terrestrial radiation may also have occurred among unicellular soil green algae by the late Precambrian or the Early Paleozoic as postulated by Stebbins & Hill (1980).

Bergstrom's (1979) hypothesis envisages Early Paleozoic radiations among many unrelated aquatic arthropod groups, with marine and freshwater taxa potentially ancestral to later Paleozoic limnic and terrestrial groups. He cites the unusual, rare, single locality, possibly limnic arthropods from Bohemia, Siberia and Tennessee as potential examples of

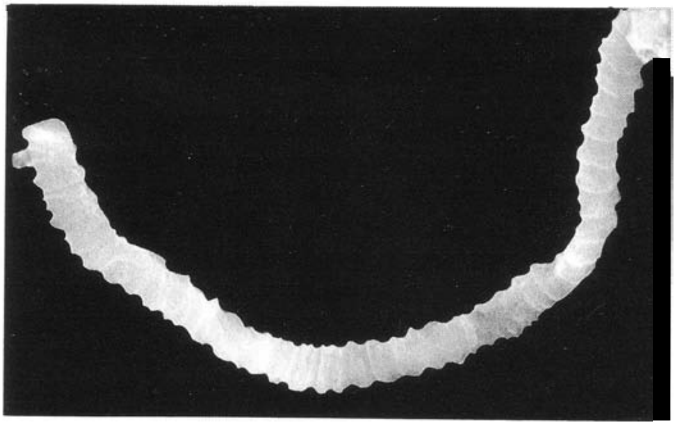

Fig. 3. Scanning electron micrograph of tracheae-like fragment from the lower part of the Tuscarora Formation, Millerstown, Pennsylvania. Note the relatively 'rectangular' cross-section of the annular rings, their relatively even spacing, and the uniform diameter along the length of the cylindrical fragment (x3000).

groups whose biological evolution may have occurred in freshwaters. He offers this as a possible explanation for their absence from older and coeval marine sediments.

Bergstrom's account raises the possibility that terrestrial arthropods presently lacking suitable marine ancestors might have been derived from a nucleus of freshwater taxa whose fossilization potential is low. Such radiations in freshwaters in combination with low probability for preservation in continental habitats might mean a permanent gap in the record for many such arthropodan groups.

Alternatively, these Early Paleozoic arthropods may represent a peculiar, marginal marine environment that has seldom been preserved, and animals that are unrepresented among normal marine biota of the Early Paleozoic.

Organisms that left only traces of their presence on clearly subaerial surfaces in the Cambrian are equally enigmatic with regard to what they were doing on land. Traces tied conclusively to nonmarine animals are unknown before the Late Silurian.

Were there Precambrian terrestrial animals? — Although it seems likely that some form of continental protistan and invertebrate life is probably as old as most marine metazoan life (Gray 1988a), the evidence for the timing of dry ground colonization is inconclusive.

The first conclusive body fossil evidence for continentalization, but not necessarily terrestrialization, are the animal body fragments from basal beds of the Tuscarora Formation at Millerstown. These animals are intermediate in time between the more complete Late Silurian through Middle Devonian animal body fossils, many attributable to modern higher taxa, and the putative Late Ordovician paleosol trace fossils whose unknown maker may not have been fully terrestrial. The close taxonomic similarity between Devonian microarthropods and modern taxa and the diversity of Early Devonian fully terrestrial animals would seem to be sufficient nonetheless to support the conclusion that continental and terrestrial animal life preceded the Late Silurian and may have been extant in the Early Paleozoic and Late Precambrian.

What does the fossil record say about rate of continentalization? — Evidence given earlier supports a beginning for continentalization and potentially terrestrialization, in the Precambrian. The fossil record provides evidence for major plant and animal adaptive radiations in the Devonian. Between these two benchmarks, the limited fossil record provides no evidence for whether continentalization and terrestrialization occurred slowly and gradually through time, or episodically and sporadically, prior to the rapid Early and Middle Devonian radiations. Whether gradual or episodic, the pre-Devonian interval of physiological and morphological adaptation must necessarily be distinguished from the apparently rapid radiations that took place in the Devonian. Such striking radiations are sometimes preceded by low diversity intervals of experimentation that 'set the stage' for more spectacular later expansions. There is no reason to believe that the spectacular radiations of the Devonian were any more the initial radiation for fully terrestrial animals than for higher land plants.

Over the years, many workers have commented on the geologically abrupt changes in terrestrial plant and animal life near the beginning of the Devonian. The more evidence becomes available, the more the apparent abruptness of this change becomes enhanced, i.e., it does not appear to be a sampling artifact, although it clearly does not mark the beginning of the continental ecosystem. Such abrupt ecosystem changes are the rule in the level bottom marine ecosystem characterized by a finite number of relatively abrupt boundaries, Ecological-Evolutionary Unit boundaries, commonly marked by extinctions and/or adaptive radiations (Boucot 1983, 1990). Within the marine ecosystem there is little understanding of the controls involved, so it is not surprising that a similar terrestrial phenomenon should be equally puzzling. It is obvious that there was a major increase in embryophytic biomass beginning in the Early Devonian with a major adaptive radiation in the tracheophytes. Lignification may have enhanced the evolutionary opportunities for dry-ground plants (Gray & Boucot 1977), all else following from it. But was the advent of lignification a chance event or not? Since there is minimal evidence for extensive herbivory (expressly the consuming of living plant tissues) involving these newly evolved embryophytes, one can suppose that the plant biomass was largely transmuted by protistan, fungal and bacterial activity into an extensive, accumulating biomass of available nutrients in the soil which in turn provided an evolutionary stimulus to increase in animal diversification and abundance.

What habitat is most likely for early terrestrialization? — Conceptually, from an evolutionary viewpoint, there may be abundant theoretical reasons to consider earliest continental colonization to have come in the surface freshwater ecosystem. However, a subsurface soil and associated soil litter ecosystem seems most likely to have preceded the open mode of life on the dry-ground surface and may even be posited as a likely precursor or contemporary with freshwater colonization.

Soil 'terrestrialization' prior to the Middle Ordovician advent of the embryophytes is not only appealing but highly likely. Such a subsurface ecosystem might have been present far back into the Precambrian where embryonic mineral soils with low organic content could have included a diversity of small organisms such as bacteria, cyanobacteria, fungi, algae, protistans and microarthropods and other invertebrates. Consider the biotic nature of restrictive soil environments, such as those of hot and cold deserts (Antarctica, for example), and high elevations above the tree line – habitats, together with those of bare rock faces, most likely to mimic some physical and biotic aspects of early terrestrial environments. In restrictive soil habitats the most common members of the modern soil biota include protistans, microarthropods (collembolans and mites), and such other invertebrates as rotifers, nematodes (roundworms), and tardigrades – a depauperate biota in comparison with more organic rich soils in mesic habitats (see Wallwork 1976 and Swift et *al.* 1979, for a comprehensive list of the soil fauna in all environments) but one nevertheless that includes such universally dominant soil microbiota as collembolans and mites.

Part of the soil habitat's appeal in evolution of the continental ecosystem, lies in the fact that it may have provided one of the principal pathways into nonmarine environments – freshwater and terrestrial – as an extension of the interstitial waters of estuaries, streams, and beach sands, particularly for small animals such as nematodes, annelids, hexapods (Little 1983: Tab. 10.1) and protists (Bonnet 1973). Coincidentally, a case has been made (Stebbins & Hill 1980), that moist soils and the interstitial soil habitat, presently a highly favorable environment for microscopic green algae (as well as cyanobacteria, yellow-green algae and less commonly red algae and euglenoids) may have provided the route to land for the unicellular ancestors of the charophycean green algae from which the embryophytes have evolved.

Part also lies in the fact that many soil protists and invertebrates are bacteriovores, fungivores and algivores (microphytophages), detritivores (saprophages), predators of soft-bodied microinvertebrates, or occasionally omnivores, utilizing all these resources: all these are among apparently primitive feeding strategies. Many soil microphytophages, are among the most primitive taxa within their groups. Such organisms have limited direct dependence on either group of primary land plants, bryophytes or tracheophytes, a significant consideration in view of the fact that increasingly evidences for nonmarine animals precede evidences from the fossil record for tracheophytes.

In environments of more extreme regions where tracheophytes are limited and soils are often 'raw' with limited biomass. communities tend to be simple with a rudimentary or 'poorly developed trophic structure' (Davis 1981: p. 127). In such environments, although some invertebrates browse or suck bryophytes, particularly mosses, they are more apt to graze epiphytic microbiota on their surfaces, feed on associated animals, or consume bryophytes as detritus. The last is because of the comparatively low nutrient value of living bryophyte tissues, presence of secondary compounds that inhibit feeding, and overall low digestibility due to presence of lignin-like phenolics and other cell wall components (Gerson 1982: pp. 309–312; Longton 1988: pp. 268–278, Tab. 7.11). In Antarctic terrestrial moss communities, for example, algivory 'is the only significant herbivory', and there is extensive use by primary consumers of 'dead organic material' that may include 30 to 45% of 'feces and dead microbial and invertebrate tissues' in addition to carcasses and exuviae; bryophyte material tends to accumulate because it is not readily recycled through consumption (Davis 1981: p. 140). Nevertheless, a diverse group of invertebrates has 'breach[ed] the chemical [...] defenses of bryophytes [...] and thrive on them' (Gerson 1982: p. 311). Two such groups, both invertebrates with Devonian records, are the bristletails and collembolans; these readily consume bryophytes in restrictive habitats (Gerson 1982: p. 300). The earliest bryophytes may have lacked such defenses or conceivably bryophyte-consuming animals may early have developed ways to overcome these chemical defenses.

Subsurface soil organisms also enjoy a modicum of protection from W radiation and other environmental hazards present on ground surfaces lacking significant vegetation cover. However, cyanobacterial surface mats could have provided important protection to terrestrial organisms within and underlying them (Garcia-Pichel & Castenholz 1991, 1993; Proteau *et al.* in press). Many cyanobacterial taxa of severe environments exposed to high solar irradiance possess an ultraviolet screening compound, scytonemin which, additional to its adaptive role in affording them protection from the deleterious effects of UV radiation, would 'unquestionably provide significant protection to other microorganisms living within and beneath the upper layer of sheathed cyanobacteria' (Proteau et *al.* in press). Such mats would provide protection to potential grazers as well as other autotrophs, such as green algae. Algal crusts, whether of cyanobacteria or eukaryotic microalgae also help to consolidate soil surfaces, improve water retention and provide nutrients from weathering of minerals (Metting 1990: p. 358).

Were terrestrial animals coevolved with autotrophic embryophytes? — There has been an assumption in the literature dealing with the continental habitat, particularly the terrestrial habitat, that higher autotrophs, particularly tracheophytes, **and** heterotrophs coevolved. The Tuscarora assemblage provides the earliest association of higher plants at embryophytic-level of organization, with animal remains and potentially decomposing organisms. Although the remains have been extracted from small rock samples representing the same horizon, there is no evidence for any interaction between these organisms to suggest coevolution or even that they necessarily represent a single community. The arthropod-like remains, including tracheae-like annulated tubes, occurring in association with ascomycete and embryophyte spores make it clear, nevertheless, that a complex terrestrial ecosystem was probably present.

If one accepts available fossil data to be constraining as to interpretation, autotrophic embryophytes would be inferred to have significantly preceded (at least by mid-Ordovician) either animals or saprophytes on land. Although many would find such a decoupling between plants and animals whose descendants appear to be so highly coevolved, evolutionarily unsettling, there is no reason to believe that the sequence of early terrestrialization necessarily reflected the organization of modern terrestrial ecosystems that appears to support coevolutionary arguments: tracheophytes at the base of the food chain, herbivores that feed on tracheophytes, and predators that fed on the herbivores; in other words, co-dependence of tracheophytes and invertebrate and vertebrate animals. Similar questionable assumptions may equally pertain with regard to animal-embryophyte interdependence: that some form of higher embryophytic plant life preceded the advent of animals; that early continental animals, freshwater or terrestrial, needed, directly or indirectly, the presence of embryophytic autotrophs; or that embryophytic plant life and animals co-occurred or coevolved, as often assumed for tracheophytes and animals. Indeed there are logical reasons for inferring that protists and invertebrate animals preceded the advent of embryophytes (bryophytes and tracheophytes) in terrestrial environments.

Feeding strategies of microarthropods and other animals in environments that mimic some biotic and abiotic aspects of Early Paleozoic ecosystems (hot and cold deserts, rock rubble and embryonic soils) may provide some general hints about resource utilization. A number of animals in these environments, with their scarce tracheophytes, are among the earliest terrestrial fossil animals – collembolans, bristletails and mites. If one sets aside the traditional dogma that continental animal life was ultimately dependent on tracheophytes of the Early Devonian or embryophytes of the mid-Ordovician, it is possible to think in coevolutionary terms of autotrophs and heterotrophs and in terms of a history for animal life that extends not only well below the Devonian, but well below the mid-Ordovician as well.

Such a scenario becomes increasingly likely as primitive microarthropods such as archaeognaths (bristletails) and oribatid mites have their ranges extended downward in time to join previously described actinedid mites and collembolans. Of these, the mites are 'in forms not very different from some which exist today' with the oribatid assignable to extant family Ctenacaridae (Norton 1985: p. 528) while one of the Rhynie springtails is similar to modern collembolan family Neanuridae (Kevan et *al.* 1975; Greenslade 1988) and another can be assigned to the Isotomidae (Greenslade 1988). What is interesting about the ecology of modern relatives of at least this subset of oldest terrestrial animals is their limited dependence on higher autotrophs for food or habitat and their preponderant occurrence in soil and litter (collembolans and oribatid and actinedid mites are primarily soil and litter inhabitants; bristletails live in soil and on rock scree). Microphytophagy (feeding on bacteria, algae, fungal hyphae and spores) is an ancient feeding strategy among mites – Norton (1985: p. 523) suggests that it 'was probably the ancestral one of the earliest known (Devonian) oribatid mites'. The Early Devonian actinedid *Protacarus* crani from the Rhynie Chert also belongs to a group many of whose modern representatives among 'endeostigmatid' mites are particle-feeding fungivores and algophages, although a number are nematophages (Krantz & Lindquist 1979; Norton 1985; Walter 1988). Many free-living soil nematodes in turn feed on fungus and bacteria (Southwood 1985). Although some believe that the Rhynie Chert *Protacarus* ate tracheophyte spores or pierced plant parts for their juices (Kevan et *al.* 1975; Norton 1985), it seems equally likely that they could have fed intercellularly on fungus or algae, or eaten fungal spores, as some modem 'endeostigmatids' do (Norton 1985; Walter 1988).

In the soil ecosystem, saprophagous and mycophagous mites are diverse and abundant (Norton 1985) and together with collembolans are dominant mycophages (fungivores) in most terrestrial ecosystems. While some (e.g. Krantz & Lindquist 1979) suggest that mycophagy in mites evolved from saprophagy among other pathways, Norton (1985) suggests that the lack of evidence for saprophagy among any of the early derived groups (fossil or extant), makes it seem more likely that sarcoptiform mites were ancestrally mycophagous with both saprophagy and the use of 'higher plant structural material itself derived. Bristletails subsist on algae and lichens (Eisenbeis & Wichard 1987). Many collembolans are mycophages, particularly those of soil and subsoil habitats, where the majority live; others are algivores, scavengers (saprovores) that may be selecting bacteria and fungi from detrital substrates, and a few are predators on rotifers, tardigrades and nematodes (Denis 1949; Christiansen 1964; Wallwork 1976; Vegter 1983).

The limited dependency of these primitive arthropods, directly or indirectly, on embryophytes suggests that their adaptive radiation into continental habitats could have occurred millions of years earlier than the Middle Ordovician appearance of the embryophytes. Thus, there are valid reasons for positing an evolutionary progression in feeding strategies for nonpredatory invertebrates, including arthropods and microarthropods, from mycophagy and bacteriophagy to detritivory (saprophagy) to herbivory (phytophagy).

Nonpredatory animals experience shortages of organic nitrogen that include specific proteins and/or amino acids. Nitrogen concentration is relatively high in bacteria, fungi and phytoplankton (Southwood 1972; Mattson 1980) even in comparison with tissues of highest nitrogen concentration in tracheophytes, that is flowers, fruits, seeds, leaves and cambial tissues (all absent in Early Devonian tracheophytes, with leaves and cambial tissues evolved by mid- to late Devonian). It is lowest in litter before its invasion by micro-organisms and the addition of nitrogen from rain fallout, insect frass, pollen, exuviae and so on (Mattson 1980). In addition to the fact that microorganisms have a more extensive biochemical repetory than tracheophytes, some of which is nutritionally useful to animals, they have the capacity to degrade cellulose and lignin that renders litter palatable to invertebrates most of whom cannot ingest fresh, unconditioned litter (Mattson 1980).

The increased biomass of litter following the evolution of the tracheophytes would have provided for increased concentration of microorganisms and an increase in surface and nonsurface area to be exploited by bacteria and fungi which may form a large part of the diet of saprophages such as collembolans (Wallwork 1976). This would have made the use of litter especially attractive to invertebrates, including the bulk of terrestrial arthropods that are principally detritus-microbial feeders (Southwood 1972). Effectively, detritivory (saprophagy) can be inferred to be an extension of microphytophagy rather than a separate or independent feeding strategy, in line with the concept that 'it is one thing to indicate what an animal eats, but quite another to determine the source from which it draws its nourishment' (Kevan 1968: p. 99). Thus as Kevan points out, it is decaying matter that may be ingested, 'but only micro-organisms (including fungi) may be digested'.

Despite the extreme rarity of small, poorly skeletonized or soft-bodied animals and of varied microorganisms in the fossil record, the known feeding habits of extant representatives of the soil fauna are consistent with the existence of a soil-type terrestrial ecosystem well back into the Precambrian – a fauna coevolved with the terrestrial soil microflora. Earliest possible evidences for such a microflora may be terrestrial cyanobacteria in the Precambrian. Earliest possible evidences for such a fauna are the Late Ordovician trace fossils and the earliest Silurian arthropodan-like organic fragments described herein. Because of fragmentation and small size, the remains may point toward animals of a soil habitat. However, the first well-documented fossil phase of the terrestrial ecosystem was initiated in the early Middle Ordovician with the appearance of primitive embryophytes represented by spores. Spores provide continuous evidences of a terrestrial land vegetation until the Late Silurian advent of pre-tracheophytic land plants (rhyniophytoids) and primitive tracheophytes represented by megafossils. Scattered arthropod remains – few definitely terrestrial – provide coeval evidences of nonmarine animals. These were followed in turn by the Early and Middle Devonian massive adaptive radiations of the tracheophytes roughly concurrent with radiations of varied, better skeletonized nonrnarine invertebrates. That terrestrial invertebrate evolution may appear to have occurred in tandem with tracheophyte evolution was coincidental, reflecting a significant increase in organic detritus in the soil initiated by the advent of the more recalcitrant tracheophytes.

Epilogue

Toni Hoffman had a long term interest in problematic fossils (Hoffman & Nitecki **1986**). It is appropriate to have a paper in this volume that reports on remains that provide the earliest body fossil evidences for nonmarine fossils, and the earliest potential evidence for terrestrial, air-breathing animals.

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Streszczenie

W kontynentalnych osadach wczesnego syluru z Tuscarora w Apallachach, wraz z zarodnikami przypuszczalnych roślin lądowych, występują mikroskopijne organiczne skamieniałości interpretowane przez autorów jako szczecinki i tchawki lądowych stawonogow. W nawiązaniu do tych nowych stanowisk autorzy dokonują przeglądu najstarszych znanych zespolow lądowych zwirząt i szeroko dyskutują prawdopodobne warunki życia w najpierwotniejszych ekosystemach lądowych.