

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

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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-tracheophyte 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

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