atoms at an average distance of 3.335 Å [4 × Ba(2)–O(1), 2.910(16) Å; 4 × Ba(2)–O(2), 3.592(9) Å; and 8 × Ba(2)–O(w5), 3.419(7) Å]. Eight chlorine atoms form square antiprisms around Ba(3) which share with each other a square face [4 × Ba(3)–Cl(1), 3.435(5) Å; and 4 × Ba(3)–Cl(2), 3.235(3) Å]. This brings the Ba(3) atoms to within 2.76 Å of each other. However, the Ba(3) atoms have an occupancy factor of 0.5, which means that statistically only every other Ba(3)-site is occupied, and therefore the Ba(3) atoms actually do not have to be in this close contact.

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Early Silurian Spore Tetrads from New York: Earliest New World Evidence for Vascular Plants?

Abstract. *Several taxa of abundant cutinized trilete spores from earliest Silurian shale in New York predate by almost an entire period vascular land plant megafossils. Paleoecological evidence suggests that these spores may represent vascular land or semiaquatic plants but a bryophytic origin cannot be precluded on the basis of spore characters. An algal origin is considered unlikely.*

Extracted samples of the Medina Group (Lower and Middle Llandovery, basal Silurian) of western New York have yielded abundant spore tetrads that may provide some of the earliest evidence for the presence of vascular land plants. This record, to our knowledge, is preceded only by the recent discovery of rare triradiate spores, tracheids, plant tissues, and cuticle fragments from the Middle Ordovician (Llanvirnian Sarka Formation) of the Bohemian Massif (*1*). If the Bohemian remains can be authenticated, they will provide the earliest evidence of vascular plants (*2*).

Sandstone and shale of the Medina Group are exposed in a section along the Niagara River, about 11 km to the north of Niagara Falls at the Robert Moses Power Plant site. In this region, the Medina Group overlies the Late Ordovician Queenston Formation. The basal unit of the Medina is the Whirlpool Sandstone ("White Medina"); above it (in ascending order) are the Power Glen Formation ("Gray Medina") and the Grimsby Formation ("Red Medina"). The uppermost Medina Group unit is the Thorold Sandstone, above which is the Neahga Shale.

Berry and Boucot (*3*) review the available evidence for correlation of these Silurian units. Neither the Medina units nor the Queenston or Thorold formations of this area have yielded zonable invertebrate megafossils (*3*). All are considered to be largely nonmarine, estuarine, or very nearshore marine on the basis of their physical characteristics, their lithofacies relationships with richly fossiliferous, zonable, wholly marine units occurring to the west on the northern rim of the Michigan Basin, or the extreme rarity and restriction to certain limited horizons of marine invertebrate megafossils. Microfossil evidence (discussed below) and the presence of infrequent marine invertebrates (*4*) suggest that the shales of the Medina Group were indeed deposited in a marine environment, although possibly near shore in a situation unsuited for the presence of abundant marine shelly invertebrate megafossils.

Shale from the Whirlpool, Power Glen, and Grimsby of the Medina Group, as well as from the Queenston and Neahga, were extracted for plant spores and other organic microfossils, by using several of the chemical and other methods described in detail by Gray (*5*) (Table 1). No organic microfossils of any type were recovered from three extracted samples of the Queenston; marine organic microfossils including scolecodonts, acritarchs, and chitinozoans were, however, recovered from the Neahga [see also (*6*)].

The three Medina Group samples provided spore tetrads (*6*) and other organic microfossils in a hash of organic material, much of which appears to be highly carbonized. Other organic objects suggestive of plant origin, such as cuticular tissues of the type common in abundantly sporiferous Late Silurian samples from Gotland (*7*), were not found in any of the samples. The Gotland samples, however, have spore tetrads reminiscent of the simple tetrahedral type described herein, in addition to single spores with triradiate laesurae.

The Medinan spore tetrads are most often dark brown, or even opaque, and quite brittle. They are arranged in the conventional tetrahedral tetrad configuration (Fig. 1) common to the development of most modern pollen and to some spores of both vascular and nonvascular plants, which indicates that the precursor spore mother cell underwent meiotic division. The individual spores are arranged in two planes and appear to be at the apices of a pyramidal tetrahedron. Where individual spores have broken away from the tetrad, a generally distinct, clearly marked triradiate scar is present, with the simple rays extending to the equator of the spore. The tetrads range in size from approximately 18 to 50 μm, most being in excess of 20 μm, and have a smooth, faintly scabrate, or microspinous surface (Figs. 1 and 2). Some few appear to be reticulate (Fig. 1). A denser marginal coloration on some of the spores suggests real differences in wall thickness or even the possibility of an equatorial thickening. These morphologic variations appear to indicate a greater diversity of spore taxa than have been previously recorded from the Llandovery. Some clusters of spore tetrads may have come directly from sporangia without breaking up into individual tetrad units, although such clusters may also indicate clumping of the type that is known to occur among the pollen of certain modern plants (*8*).

Spore tetrads are common to abundant as compared with other organic microfossils in both the Whirlpool and Power Glen formations; in the Grimsby, however, spore tetrads are rare compared with other microfossils (Table 1). The other recognizable organic micro-

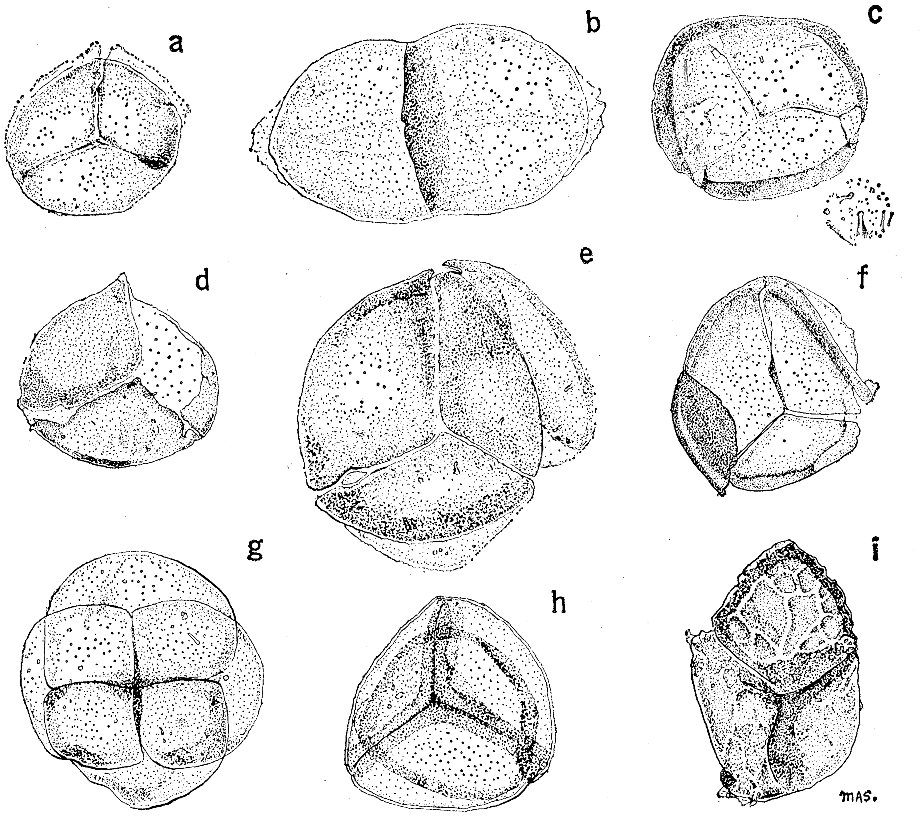

Fig. 1. Organic microfossils from the Medina Group (Lower Llandovery) of New York (× 750). Specimens illustrated are all from the Power Glen Formation. (a, c–i) Plant spores. (b) Dyad, of unknown affinity. (a, d) Single spores with distinct triradiate scar: (a) with remnants of possible perispore; (d) part of proximal surface bounded by triradiate scar broken away. (c) Spore with distinct triradiate scar, an apparent equatorially thickened wall, and small surface clavae shown in greater detail in generalized enlargement. (e, f) Spores with remnants of other members of the spore tetrad still adhering; (e) appears to have surface clavae similar to those of (c). (g–i) Spore tetrads in tetrahedral configuration: (i) tetrad with surface reticulum.

fossils (acritarchs, scolecodonts, chitinozoans) are considered to be of marine origin. Their presence, if indigenous, supports the conclusion that the Medina shales are marine, although the generally low abundance of most forms and the scarcity of marine invertebrates argue for a nearshore origin (*9*).

Are the spore tetrads the reproductive structures of vascular plants of terrestrial or perhaps semiterrestrial origin? Are any deductions possible from the microfossil assemblage or from the environmental occurrence and morphology of the spores that support their reference to early vascular plants?

There are no credible pre-Silurian megafossils attributable to vascular plants. Spores, tracheids, plant tissues, and cuticle fragments have, however, been reported from the Middle Ordovician of Bohemia (*1*), although this occurrence is yet to be authenticated. Within the Silurian, the few megafossils attributed to vascular plants commonly lack definitive criteria such as cutinized spores, tracheids, and epidermal cuticle with stomates; such remains are known only from Late Silurian occurrences in Britain (*10*), Czechoslovakia (*11*), Podolia (*12*), and New York (*13*). However, dispersed spores with distinct triradiate scars whose vascular plant origin is commonly assumed are more abundant and more widely recorded from the Silurian of Pennsylvania [(*14*); see also Table 1, Bloomsburg Formation], New York (*6, 15, 16*), Virginia (*17*), Libya (*18*), Britain (*19*), Spain (*20*), Algeria (*21*), and Gotland and Scania (*7*). Although additional Silurian vascular plant megafossils may be discovered, it is a reasonable assumption from their known very limited fossil record that dispersed Silurian spores will always outnumber megafossil remains, just as younger spores and pollen occur more commonly than coeval plant megafossils because they are produced more abundantly and are dispersed more widely in marine and nonmarine sedimentary rocks. The earliest, generally accepted evidence for a vascular land flora is the presence of a few isolated spores from the Lower Silurian (near the Early Llandovery–Middle Llandovery boundary) of Libya (*18*). The recently reported occurrence of spores and other microscopic remains attributed to land vascular plants in the Middle Ordovician of Bohemia (*1*) predates acceptable megafossil remains by possibly 40 million years. The scarcity of credible vascular land-plant megafossils cannot in itself constitute prima facie evidence that widespread and abundant dispersed spores do not have a vascular plant source.

In attempting to determine the affinities of dispersed Silurian spores with vascular plants, lack of supporting evidence from vegetative and other remains throws the burden of proof mainly on spore characters. Neither the presence of spores in tetrad groups, nor the presence of a proximal triradiate scar, nor the presence of a cutinized cell wall that will withstand the rigors of preservation and chemical extraction is definitive evidence that isolated spores were produced by vascular plants (*2*), although the correlation between these features and the spores of living vascular land plants is high (*22*). Certain algae, especially among the red algae (Rhodophyta; subclass Florideae) produce tetrasporangia with four nonmotile spores in tetrahedral configuration that may bear rudimentary triradiate scars. Although phycologists have expressed skepticism that any *living* red algae (*23*) possess spores capable of preservation similar to the Silurian spores here described, it would be unwise to conclude that Silurian shallow-water or nonmarine algae possessing such wall structures did not exist. The known record of fossil red algae provides little help, for all Paleozoic red algae are lime-secreting forms. Coralline algae belonging to the Rhodophyta are common in the Late Cretaceous and Tertiary, but only one genus is known from the Silurian (*24*). The known fossil record together with certain highly specialized reproductive features suggests a very long geologic history for the red algae (*25*), for which the spores described here might provide some evidence. Nor can the possibility of a bryophytic origin for these Silurian spores be ignored. This group produces cutinized spores in tetrahedral tetrads; individual spores may display a proximal triradiate scar. Bryophytes have a megafossil record that stretches well into the middle Paleozoic (*26*), although spores attributed to bryophytes are first recognized in the early Mesozoic. Both records probably poorly reflect the geologic history of this group of nonvascular land plants. Although it is tempting to conclude that the abundant, simple Early Silurian spore tetrads from the Medina Group represent the dispersed reproductive structures of primitive vascular plants, a more comprehensive survey of algal and bryophytic reproductive structures, both living and fossil, is necessary before a completely definitive statement is possible concerning the affinities of our Silurian material on the basis of spore morphology alone.

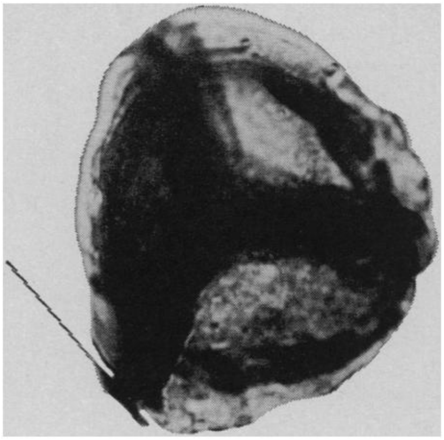

Fig. 2. Microphotograph of a spore tetrad (magnification, approximately × 1200). [Harrison Howard]

Although many Silurian spores, including our Medinan specimens, are unaccompanied by confirming plant remains (tracheids, cuticle), Evitt (*16*) finds cuticle fragments in the Maplewood Shale (New York), where spores are also reported by Cramer (*15*), and similar fragments plus spores and tracheids in the Williamson Shale (New York), both of Late Llandovery age and only a little younger than our Medinan material. If the complex of characters taken to define the vascular plant condition did not arise until the Silurian (*27*), it would appear that they arose almost simultaneously. On a theoretical basis, however, one might speculate that in the shallow-water marine or semiterrestrial state, which may have preceded full land entry by many millions of years, cutinized spores able to withstand periodic desiccation and thus ensure reproduction might well have appeared prior to either the vascular system or the cutinized epidermal wall so necessary for wholly land existence. In this connection, the apparent absence of cutinized spores in the wholly aquatic modern algae, as well as the loss through reduction of a cutinized wall in pollen of living vascular plants whose pollen operates completely submerged (*8, 28*), is noteworthy. Since cutinization primarily assures against desiccation, there is no functional reason for wholly submerged spores or pollen to be cutinized. The presence of a cutinized wall in our Early Silurian spores strongly suggests that they belonged to either terrestrial or semiaquatic plants, which, in the latter case, bore their sporangia out of water.

If a widespread, nearshore, shallow marine or nonmarine primitive vascular flora existed during the Early Silurian, as we hypothesize, its remains might be expected to be extremely abundant in sedimentary rocks from localities representing that environment, as opposed to samples from areas either farther away on the dry land or farther offshore in deeper water. However, previously reported rare Llandovery through Ludlow age spore occurrences are from relatively offshore marine environments; common to abundant latest Silurian (Pridoli age) spores, by contrast, are from relatively nearshore marine environments. None represents wholly continental environments. This coincidence raises the possibility (*29*) that the published record of Silurian spore occurrences to date reflects environmental control (and inadequate sampling) as much as evolution and development of the Silurian flora in time. The examination of over 75 diverse Early and Late Silurian rocks from New York, Pennsylvania, Ohio, and Sweden [Gotland

Table 1. Age, location, and organic microfossil content (c, common; r, rare) of extracted Silurian rock samples from New York and Pennsylvania.

Age	Formation	Locality	Results
Ludlow, Late Silurian	Bloomsburg Formation	Mount Union Section, Mount Union, Pa. Field 8, Laboratory 562	Spores (r) Acritarchs (r) Chitinozoans (c)
Late Llandovery, Early Silurian	Neahga Shale	Robert Moses Power Plant Section, Niagara Falls, N.Y. Field 36; Laboratory 517	Acritarchs (c) Chitinozoans (c)
Early-Middle Llandovery, Early Silurian	Grimsby Formation "Red Medina"	Robert Moses Power Plant Section, Niagara Falls, N.Y., green beds at base of Grimsby. Field 35; Laboratory 516	Spore tetrads (r) Acritarchs (c) Chitinozoans (r) Scolecodonts (r)
Early Llandovery, Early Silurian	Power Glen Formation "Gray Medina"	Robert Moses Power Plant Section, Niagara Falls, N.Y., about 2 to 2.5 m above Field 33. Field 34; Laboratory 515	Spore tetrads (c) Acritarchs (c) Scolecodonts (r)
Early Llandovery, Early Silurian	Whirlpool Sandstone "White Medina"	Robert Moses Power Plant Section, Niagara Falls, N.Y., about 2.5 to 3 m above Queenston Formation contact. Field 33; Laboratory 514	Spore tetrads (c) Acritarchs (c) Scolecodonts (r)
Richmondian, Late Ordovician	Queenston Formation	Robert Moses Power Plant Section, Niagara Falls, N.Y., fifth green bed below Medina Group contact (about 3.3 m). Field 30; Laboratory 511	Blank
Richmondian, Late Ordovician	Queenston Formation	Robert Moses Power Plant Section, Niagara Falls, N.Y., second green bed below Medina Group contact (about 1 m). Field 31; Laboratory 512	Blank
Richmondian, Late Ordovician	Queenston Formation	Robert Moses Power Plant Section, Niagara Falls, N.Y., first green bed below Medina Group contact. Field 32; Laboratory 513	Blank

and Scania (*7*)] for organic microfossils tends to substantiate our interpretation of the importance of environmental control in the occurrence of Silurian spores, although the absence of *any* organic microfossils from many rocks where we had predicted the occurrence of spores if environment of deposition rather than evolution was the critical factor can best be explained by post-depositional alteration (*30*). Abundant spores in our Llandovery and Ludlow age samples and in other latest Silurian age samples are known only from shallow-bottom or nearshore marine environments. Truly nonmarine Early Silurian environments have not yet yielded spores, but unmetamorphosed rocks of this age capable of providing spores have not been studied by us or reported in the literature.

The possibility of environmental control of Silurian spore occurrences related to water depth and shoreline proximity is further substantiated by the inverse relationship between abundant Silurian spores, both Early and Late, and marine organic microplankton (*9*). We find that abundant spores occur in rocks deposited either landward of those containing abundant and diversified marine microplankton or in rocks consistent with very shallow-bottom conditions. Strata conventionally accepted as marine or giving evidence of more offshore or deeper water environments yield abundant marine microfossils, including acritarchs, chitinozoans, or scolecodonts, but either no spores or rare spores. The results of our preliminary work suggest that these two groups of organic microfossils have occurrence patterns that are largely mutually exclusive and that may be correlated with marine versus nonmarine or shallow marine environments (*29*).

We suggest, therefore, that the known progressive increase in the frequency and taxonomic diversity of trilete spores that occurs from the Early Silurian to the Late Silurian–Early Devonian may be largely a function of biofacies correlated with geologic environment rather than a function of organic evolution as now concluded (*19, 22*). If the orderly evolutionary sequence that appears to be represented among Silurian spores is an environmental artifact and if the Silurian spores represent vascular plants, it may yet be found that Early Paleozoic vascular plants show a trend similar to the evolutionary history of many animal groups, which exhibit far greater diversity and morphological richness in their early rather than their later history. It remains for future work to determine whether or not plant spores will be recovered in sufficient abundance from nonmarine Early Silurian or older beds to warrant the conclusion that plants had already invaded the land.

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Homograft Rejection Delayed by Treatment of Donor Tissue in vitro with Antilymphocyte Serum

Abstract. Treatment of rabbit corneal tissue in vitro with pooled rabbit serum delays the onset of corneal homograft rejection in the host. Addition of antilymphocyte serum results in a further significant delay in the onset of rejection. The mechanisms by which such treatment of donor tissues may modify the antigenic content of the material are discussed.

The use of antilymphocyte serum (ALS) (*1, 2*), as well as other immunosuppressive agents (*2, 3*) in the treatment of donor animals to modify the homograft reaction is well documented in the literature. We now report the effect of treatment of corneal donor tissue with ALS in vitro prior to its use for penetrating keratoplasty.

Horse antiserum to rabbit lympho-