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Silurian Trilete Spores and Spore Tetrads from Gotland: Their Implications for Land Plant Evolution

Abstract. *Land-plant type spores occur in argillaceous limestones and platform graptolitic mudstones of Wenlock-Ludlow age in Sweden. Analysis of the stratal sequence demonstrates that occurrence of abundant spores is a function of depositional ecology, particularly water depth and shoreline proximity. This ecological analysis and the seeming absence of any correlation between the first appearances of abundant spores and megafossils of land-plant type raise the possibility that land plants evolved far earlier than the megafossil record suggests.*

The island of Gotland, situated in the Baltic Sea about 100 km east of the Swedish mainland, is the classic region for Silurian invertebrate megafossil remains. Especially noteworthy are the excellent exposures of unmetamorphosed bedrock in the coastal cliffs and elsewhere, with their abundance of unusually well preserved invertebrate remains that have claimed the attention of naturalists since the beginning of the 18th century. These rocks have also yielded rock-forming calcareous algae (*1*) and have proved to be rich in planktonic marine organic microfossils, such as chitinozoans (*2*).

Because the Gotland Silurian sequence appears to be wholly marine and has always been interpreted as having been deposited some distance from the nearest shoreline, the seeming absence of land plant remains is not unexpected (*3*). Nevertheless, the time interval during which these rocks were deposited appears to have been critical in the evolution of land (vascular) plants, all of whose earliest pre-Devonian remains are recovered from marine strata.

The purpose of this report is to call attention to a variety of microscopic plant remains recovered from a sampling of the Silurian sequence of Gotland and adjacent Scania (Table 1) (*4*) and whose source would appear to be land plants, even if it cannot be demonstrated from their morphology and environment of occurrence that they stem from land vascular plants (*5*). Insofar as it is possible from observations made to date, it is also our purpose to provide new information on the rate of evolution of plants producing land-plant type spores and to add to the growing body of paleoecological data regarding the early environments of possible land plants.

Although the Gotland trilete spores and spore tetrads are not the oldest known (*6–8*), they are important additions to the growing number of widespread, durable pre-Devonian spores of the land-plant type that predate megafossil remains attributed to land and to land vascular plants. Their excellent preservation matches that of the other Gotland Silurian fossils; they are also among the more abundant and diversified pre-Pridoli spore assemblages of which there is published record (*9*), particularly in the Burgsvik Sandstone, where trilete spores and spore tetrads are most common.

The Gotland Silurian sequence includes well-dated strata of late Llandovery through Ludlow age, units that represent essentially the upper half of the Silurian (Fig. 1). These rocks were deposited in a marine, reef-controlled, warm-water regime near the western edge of the Russian Platform (*10*); platform graptolitic mudstones crop out to the southwest in Scania and on the island of Bornholm, and occur to the south in boreholes drilled in northern Poland and in Germany. The uppermost Silurian (late Ludlow to Pridoli) beds in Scania consist of shallow water marine carbonate rocks and mudstones grading up into high intertidal or nonmarine red beds essentially lacking megafossils (*11*).

The Gotland Silurian is normally thought of as a marine carbonate sequence having little connection with fossils of possible nearshore or nonmarine origin. However, the varying plant spore distribution, correlated with the varying acritarch abundance and diversity (Table 1), is consistent with the conclusion that some of the rock units were deposited under deeper water than others (or that some were deposited at different distances from the shoreline, or under different conditions of marine current activity). The evidence that supports this conclusion has been given elsewhere (*7*). The water depth–shoreline correlation provided by the organic microfossils from the Gotland

Standard series	Gotland	Scania
Pridoli		Öved Sandstone
	Sundre Beds	
	Hamra Beds	Öved-Ramsåsa Siltstone
Ludlow	Burgsvik Beds and Eke Beds	
	Hemse Beds	
	Klinteberg Beds	
	Mulde Beds	
	Halla Beds	
	Slite Beds	
Wenlock	Högklint Beds	
	Upper Visby Beds	
	Lower Visby Beds	
Llandovery Upper		

Fig. 1. Correlation of the Silurian stratigraphic units from Gotland and Scania, together with their position relative to the standard Silurian sequence.

and Scanian samples is independently substantiated by the co-occurring invertebrates (Table 1) and by classic geologic evidence: a number of the strata yield information on animal communities and lithology that indicates a varying water depth and proximity to the shoreline. The Gotland-Scanian Silurian is thus suited to provide data with which to test the hypothesis that the reported Silurian plant occurrences and abundance (both megafossil and microfossil) may be in significant part a function of sampled physical environments, rather than a direct function of the evolution and abundance of vascular (or land) plants in the Silurian (*8*).

Genuine vascular plant megafossils bearing on the question of vascular plant evolution are very rare (*8*); they are known to occur with certainty only in marine beds of Pridoli age in Great Britain. Analysis of limited Silurian land-plant type spore assemblages (*12, 13*) indicates that spore frequency and morphologic diversity begin at a low level during the Early Silurian and increase steadily through the period to give rise to a relatively rich, diversified Early Devonian flora. Microfossil evidence thus appears to reinforce the megafossil evidence that suggests that vascular plants first arose in the Silurian, more or less immediately before their first definitive megafossil remains are found in the Pridoli (*14*). However, an increasing number of occurrences of pre-Devonian trilete spores and spore tetrads are turning up in rocks of Early Silurian and Late Ordovician age on a worldwide basis (*6–8*). In addition, the spore-bearing rocks reported are largely derived from marine sequences that grade from relatively deep, more offshore environments in the oldest beds to relatively shallow, more nearshore environments in the youngest beds. This suggests the alternate possibility of an extended pre-Devonian evolution for land (vascular) plants well before the first appearance of unequivocal vascular plant remains in the latest Silurian.

The data in Table 1 show that the relative abundance and stratigraphic and geographic distribution of spores in the Gotland-Scanian sequence generally correlate with the grain size of the sedimentary rock and with the relative abundance and stratigraphic and geographic distribution of other types of organic microfossils. These correlations bear on questions of the evolution of the spore-bearing plants. Spores are either rare or absent in sand-sized rocks (such as calcarenites) lacking a significant silt and clay size fraction, with which most spores sediment. Spores may be common to abundant, rare, or absent in rocks with silt and clay size fractions, but are invariably common to abundant only in rocks with a significant silt and clay size fraction. When spores are rare or absent, acritarchs or chitinozoans are usually common to abundant; when spores are common to abundant, acritarchs or chitinozoans are most often rare to common. Spores are rare or absent in rocks assigned to benthic assemblage 2 (Table 1) or to deeper water, more offshore positions, regardless of rock grain size, an observation that agrees well with the benthic assemblage distribution and abundance of

Table 1. Relative abundance of organic microfossils, benthic assemblage position, and gross lithology of Gotland-Scanian Silurian rocks. Samples examined in each unit represent localities throughout Gotland and Scania. Relative abundances (A, abundant; C, common; R, rare) are no reflection of absolute abundances of organic microfossils, which vary widely from sample to sample. Occurrences of microfossils marked by extremely low absolute abundance are indicated by P (present), and blank spaces indicate absence. Unless otherwise indicated by L (Laufeld), the relative frequencies and sample content are based on samples analyzed by Gray. Benthic assemblages 1 and 2 are believed to represent respectively high and low intertidal positions, with a maximum depth range in the Silurian of no more than 10 m between mean high and mean low water. Benthic assemblage 3 is thought to extend to a depth no greater than the lower limit of the photic zone (~ 70 m); it is characterized by abundant calcareous algae and abundant reef formation. Benthic assemblages 4 and 5 are believed to extend out to the limits of the continental shelf, with a depth range of 175 to 200 m (*12, 13*). Dual assignment indicates uncertainty in position; absence of fossils, absence of diagnostic fossils, or evidence of possible redeposition of fossils in some cases preclude exact assignment. Abbreviations used in lithology: I, argillaceous calcarenite; II, calcareous siltstone; III, oolitic limestone; IV, argillaceous limestone; V, calcarenite; VI, thin-bedded limestone.

Stratigraphic unit	Sample	Trilete spores and spore tetrads	Acritarchs	Chitinozoa	Benthic assemblage	Lithology
Öved-Ramsåsa Beds	1	C	A	C	2	I
	2	C	A	C	2	I
	3	C	A	C	2	I
Hamra Beds	1	P	P	L	2 3	I
	2	R	C–A	C	2 3	I
	3		P	P	2 3	I
	4	R	C–A	R–C	3	I
Eke Beds	1	P	P	L	3	I
	2	R	A	R	3?	I
	3	R	C–A	C	3	I
	4	C	C	C	3?	I
Burgsvik Beds	1	C–A	C	L	1 2	II
	2			L	3?	III
	3	L	L		1 2	III
	4		P	L	1 2	III
	5	C–A	C	L	1 2	II
	6	C–A	R–C	R	1 2	II
	7	P	P	L	1 2	III
	8	C–A	R–C	R	1 2	II
	9	C	C	C	1 2	II
Hemse Beds	1	R	A	C	2 3	IV
	2	R	A	C	3	IV
	3	R	A	R–C	3?	IV
	4	R	A	C	3	IV
Klinteberg Beds	1		P	P	3	V
Mulde Beds	1	R	A	R–C	3	IV
	2	R	A	C	3	IV
	3	R?	A	C	3?	IV
	4	R?	A	C	3 4	IV
Halla Beds	1	R?	C	C	3	IV
	2		P	L	3	V
	3	R	C	R	3	IV
	4		A	R	3	IV
Slite Beds	1		A	L	3	I
	2				2 3	VI
	3		A	R–C	3	I
	4		P	P	2	II
	5		A	R–C	3	IV
Högklint Beds	1		P		2 3	IV
Upper Visby Beds	1		A		5	IV
Lower Visby Beds	1		A	C	4	IV

Silurian spores elsewhere (*7*). Although spores are not invariably present in benthic assemblage 2 and shallower, more nearshore locations, they are only common to abundant in rocks inferred to have been deposited in these positions. The sharp dropoff in spore abundance and the correspondingly abrupt increase in acritarch and chitinozoan abundance, but particularly in acritarch diversity, begins at a position corresponding to benthic assemblage 2. Some such shallow water environments were often far from land in the Silurian (*15*), which appears to account for differences in the relative abundance of spores or acritarchs in the same environment. Despite the commonness of certain acritarch types in benthic assemblage 1 and in the shallower parts of benthic assemblage 2, a diverse assemblage of acritarchs is not usually encountered in such shallow water environments (*7, 8*).

In sum, in the Gotland units, trilete spores and spore tetrads are only common to abundant in the Burgsvik Sandstone, which on independent evidence appears to have been deposited in the most shallow water marine environment, and in the intergrading parts of the Eke Beds. Within the Burgsvik, spores are scarce in the coarser-grained beds, but common in the interbedded siltstone layers. Spores are only common in the finer-grained beds of the Eke, regardless of benthic assemblage position. Spores are also rare in the Hamra Beds of Ludlow age, which lie stratigraphically above the Burgsvik, and they are absent in the Scanian nonmarine red beds of Pridoli age. They are found with some commonness, however, in the Scanian beds of Ludlow age, which also on independent evidence are among the more shallow water Silurian deposits in the region.

The presence of common to abundant and diversified trilete spores and spore tetrads of land-plant type associated with cuticle-like and "tracheid-like" structures (*16*) in some of the Burgsvik strata appears to be an independent substantiation of at least a partly shallow water origin for some parts of this unit, especially in sampled rocks where organic microfossils of marine origin, such as chitinozoans and acritarchs, are either less common or less diversified in association with them. Notably, the beds rich in plant spores (the calcareous siltstones of the Burgsvik) lack invertebrate megafossils, although they are interbedded with oolitic limestones and sandstones containing benthic assemblage 2 marine fossils. The absence of marine megafossils from the siltstone layers of the Burgsvik suggests that the plant-rich beds may have been deposited in even shallower water than the interlayered and megafossil-bearing limestones and sandstones, a position that may have been unfavorable for the growth and preservation of marine invertebrates. Because Silurian paleogeography suggests a position for the Burgsvik Sandstone far from any shoreline of the time, it seems possible that the plant-rich beds may represent a mudflat region on which spore-producing land plants or semiaquatic plants bearing durable trilete spores and spore tetrads thrived. There is no good evidence at this time to suggest that any of the spore-bearing beds are nonmarine, since they yield some chitinozoans and acritarchs even where spores are most abundant. However, it is possible that these marine microfossils were introduced into a very high intertidal or supratidal mudflat region by storm activity. Alternatively, the land-plant type structures can be explained as due to transportation from a more shoreward position, although this seems less likely than that they came from plants indigenous to the site of deposition. The unequal distribution of the durable spores throughout the sequence argues against a marine planktonic (possibly algal) origin for them (*5*).

The unequal abundance of spores and of organic microfossils of marine origin throughout the Gotland and Scanian sections appears to correlate closely with changing environments of deposition, with spores most abundant in shallow water, fine-grained sediments and acritarchs and chitinozoans most abundant in deeper water, fine-grained sediments. Thus, there is not a linear increase in abundance and diversity of spore types up through the Gotland Silurian section, as there is in the Wenlock and Ludlow of the Welsh Borderland (*13*), but rather a close correlation between spore occurrence and water depth (shoreline proximity) as independently indicated by the marine invertebrate fossils.

The occurrence of common spores of land-plant type in the Burgsvik, in some cases associated with an uncommon and undiversified assemblage of acritarchs and with rare chitinozoans, demonstrates a situation that contrasts markedly with the occurrence of land-plant type spores in the Ludlow succession of the Welsh Borderland, where similar spores "form less than 1% of most assemblages" and are "always associated with abundant acritarchs, chitinozoa, and scolecodonts . . ." (*13*).

These observations suggest that the abundance of spores of land-plant type in the Late Silurian of Gotland and Scania is largely a function of close local environmental control. They cast doubt on the possibility that evolution played the most significant role in determining the abundance and diversity of spores in the Gotland Wenlock-Ludlow sequence and in the Scanian Ludlow-Pridoli sequence. In turn, they cast doubt on the possibility that evolution may have been the determining factor in the occurrence, abundance, and diversity of pre-Devonian spores elsewhere, where similar environmental controls may be demonstrated.

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5. There is a high correlation between the morphology of the recovered fossil spores on which this study is based and morphologies of the spores of land vascular plants. However, since a similar spore type occurs among land plants referred to the nonvascular bryophytes, there is no definitive proof at this time of a vascular origin for these spores. Since the spores of modern algae, even those produced in tetrahedral tetrads and thus potentially capable of retaining a trilete scar, are not durable-walled as are our fossil species, we do not at this time consider algae a potentially significant source of the trilete spores and spore tetrads on which this study is based.
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16. The tubular, nonseptate structures, differentially thickened in either annular or spiral manner, clearly simulate tracheids of vascular plants, although they have not been demonstrated to be tracheids, and recently A. Eisenack [*Palaeontogr. Abt. A Palaeozool. Stratigr.* **139**, 64 (1972)] has speculated that structures of the same general appearance are chitinous in composition. Similar tubular structures were first noted → W. H. Lang [*Phil. Trans. R. Soc. Lond. Ser. B* **227**, 245 (1937)] in the Nematophytales, a group which he and a number of later workers have considered to be terrestrial or semiaquatic plants. O. A. Høeg [*Medd. Nor. Svalb. Unders.* **83** (1942)] described such tubular structures in *Nematothallus* as "tracheidal tubes," saying that they are "very much like tracheids," a resemblance also noted by A. G. Lyon [*Trans. R. Soc. Edinb.* **65**, 79 (1962)] in reference to the "differentially thickened tubular cells" in the same group of plants. The important point about such structures is that they have apparently developed functionally in response to the transportation of water within the plant system or part of it, and that they do not appear to have developed in an aquatic, wholly submerged plant. This is the case regardless of what they are called or in which groups of plants they are found, including those of the Gotland Silurian, for which we do not claim a nematophytalean origin.
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Lassa Virus Isolation from Mastomys natalensis Rodents during an Epidemic in Sierra Leone

Abstract. *Lassa fever is a severe febrile illness of man, first recognized in West Africa in 1969. During an epidemic in Sierra Leone, Lassa virus was isolated for the first time from wild rodents of* Mastomys natalensis. *A high prevalence of infected* Mastomys *was found in houses occupied by patients with Lassa fever. The data presented provide the first demonstration of an extra-human cycle of Lassa virus transmission and suggest that rodent control may be an effective method of limiting the disease.*

Lassa virus was first isolated in 1969 from three American missionary nurses who contracted a severe, hitherto undescribed febrile illness in Nigeria (*1*). Between 1969 and 1972 Lassa fever emerged as a major public health problem; four epidemics were recognized in three West African countries: Nigeria (*1, 2*), Liberia (*3*), and Sierra Leone (*4*). Although the total number of cases documented during these outbreaks was small (101 cases), the case fatality rate among hospitalized patients has been high (43 percent). In addition to the epidemic locales indicating a widespread or multifocal distribution of Lassa virus activity in West Africa, a serologic survey (*5*) has demonstrated past infection in areas where the disease has so far escaped detection. Lassa virus has a predilection for person-to-person spread within the hospital environment, with a high risk of infection in medical personnel. To date, 14 nurses and a physician have acquired Lassa fever while attending patients with the disease. The hazard to laboratory investigators is also great (*6*), and virologic studies are now confined to institutions with facilities for strict biocontainment.

In three of the four epidemics, Lassa virus was spread from person to person within a hospital environment, after introduction of the virus by a single infected patient (*1–3*). Because these were nosocomial (intrahospital) epidemics, the primary source and cycle of virus transmission in nature were not elucidated.

In September and October 1972 we investigated an outbreak of Lassa fever in the villages of Panguma and Tongo, Eastern Province, Sierra Leone (*4, 7*). In contrast to the previous nosocomial epidemics, most human cases arose in the affected communities. Although person-to-person transmission probably occurred, a nonhuman source of infection was also considered likely.

Our attention centered on wild vertebrates, since the epidemiology of viruses related to the agent of Lassa fever was known to involve rodents and bats. Lassa virus is morphologically indistinguishable from lymphocytic choriomeningitis (LCM) virus (*8, 9*) and eight other agents formerly included in the Tacaribe virus group. By complement-fixation (CF) tests, minor serologic cross reactions have been demonstrated between Lassa, LCM, and several Tacaribe group viruses (*10*). These viruses have thus been placed in a new taxonomic group designated the arenaviruses (*9*). A number of arenaviruses have been isolated from wild rodents, including: LCM virus from *Mus musculus*; Machupo virus (the agent of Bolivian hemorrhagic fever) from *Calomys callosus* in Bolivia (*11*); Junin virus (the agent of Argentinian hemorrhagic fever) from *Calomys laucha* and other species in Argentina (*12*); Tamiami virus from *Sigmodon hispidis* in Florida (*13*); and Pichinde and Amapari viruses from cricetine rodents in Colombia (*14*) and Brazil (*15*), respectively. Tacaribe virus has been isolated from *Artibeus* bats in Trinidad (*16*).

During investigations in Sierra Leone, we collected a total of 641 small vertebrates. Bats were caught in nylon mist nets set at the fringes of the affected villages. Rodents and shrews were either captured in live traps set in houses and surrounding farms and forests, or were purchased from local native trappers. We removed samples of lung, heart, spleen, kidney, blood, and, if possible, bladder urine and ectoparasites. Specimens were frozen in liquid nitrogen and returned to the Maximum Security Laboratory at the Center for Disease Control, Atlanta, Georgia, whereupon they were transferred to a mechanical freezer (– 78°C). For attempts at virus isolation, the organ pools from each animal were thawed, ground in a mortar with modified (*17*) Eagle's medium, and lightly centrifuged. We tested (*3, 7*) the supernatant fluids for virus in tube cultures of African green monkey kidney stable (Vero) cells. Cultures were inoculated with 0.1 ml of 10 percent (weight to volume) organ suspensions; 45 minutes later, maintenance medium was added, and the tubes were checked daily for cytopathic effect (CPE). Positive cultures showed typical Lassa virus CPE by day 5 or 6, whereupon they were harvested by freeze-thawing and identified by CF test. The identification of Lassa virus isolates by CF test has been described (*3, 7, 18*). The neutralization test has not been found useful for virus identification, since, in our hands, antiserums of sufficient neutralizing potency have not been produced.