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Lower Palaeozoic Sporomorphs: Their Stratigraphical Distribution and Possible Affinities [and Discussion]

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Lower Palaeozoic sporomorphs: their stratigraphical distribution and possible affinities

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Richardson & Ioannides (1973) speculated on possible bryophytic affinities of some Silurian dispersed spores. Later, at the International Palynological Congress in Cambridge (1980) I discussed the close morphological similarities of some Silurian and early Devonian spores to those from mosses and liverworts. In particular the dispersed miospore genera *Streelispora* and *Aneurospora* are similar to the spores of the extant liverwort *Anthoceras* and spores of some species of the extant moss genus *Encalypta* to fossil spores of *Emphanisporites*. If such similarities are indicative of affinity then many of the Silurian spores may have belonged to early bryophytic ancestors. As mosses and liverworts are not usually preserved as fossils, such an explanation would help to explain the major discrepancy between the number of dispersed Silurian and Lower Devonian miospore species and the few species of land plants known.

Table 1 plots the numerical distribution of sporomorphs in the Lower Palaeozoic. There is evidence that most of the spores were derived from land plants but an asterisk indicates where some of the included species are marine, or are possibly marine. Simple plants, some of which have been compared to blue-green algae, occur in Precambrian terrestrial and marine deposits and are referred to as cryptarchs (Diver & Peat 1979). The fossils in categories 1 to 3 are regarded as of uncertain nature, are here called cryptospores, and are found in rocks of non-marine origin (Strother & Traverse 1979) and near-shore marine sediments (Miller & Eames 1982). The asterisk in column one indicates that some of these forms may be sphaeromorph acritarchs but the sporomorphs tend to have more robust walls. The asterisk in column 2 (cross tetrads) indicates that these particular forms have only been found in marine strata but as they occur in tetrads they differ from 'normal' acritarchs. The dyads have also been found in continental and marine strata. Dr D. John (British Museum, Natural History) tells me that such dyads are unknown among modern freshwater algae. Tetrahedral tetrads (column 4) occur possibly in the Caradocian of Libya (Gray *et al.* 1982) and certainly in the Ashgillian (Vavrdova 1982). I have also seen them in Ashgillian rocks in Libya (dating by acritarchs and chitinozoa, S. G. Molyneux and F. Paris, unpublished). The lower Llandovery is typified by cryptospores including 'permanent' cross tetrads along with tetrahedral tetrads and the latter are also 'permanent', that is, not normally separated into single spores. If these tetrads are forcibly separated (Gray *et al.* 1982, figures 5–6) the individual grains resemble those of the dispersed spore genus *Ambitisporites*. Dispersed spores of this genus first appear in the Llandovery (around the lower–middle Llandovery boundary, (Berry, in Gray & Boucot 1971)) and in the upper Llandovery and younger strata 'permanent' tetrads are uncommon. This marks a second distinct phase in miospore development (Richardson & Lister 1969, table 6) the beginning of dispersed laevigate trilete spores. The third major phase was the beginning, and rapid growth,

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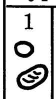
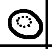
† Dr Richardson had not seen Professor Gray's typescript before submitting this written discussion item. The contribution from Dr Richardson published here constituted 'invited discussion' at the meeting. Professor Gray has accordingly been given the right of reply without a response from Dr Richardson.

of sculptured trilete spores, a development which began, according to present data, in the upper Wenlock. Both in England and Wales and North Africa there was a rapid increase in sculptured forms (figures in brackets) in the 'Ludlovian' and Downtonian. The cause of this sculptural diversity is unknown but sculpture is also present in alete cryptopolar spores (column 6). Trilete spores occur in some mosses, while many modern mosses have spores that are alete but have a more or less circular area covered by a thin membrane over one pole.

Table 1. To show the distribution of Lower Palaeozoic sporomorph taxa

	taxa total	cryptospores			miospores			
		1	2	3	4	5	6	
								
Downton	36(21)		* 2(1)	2(0)		30(17)	4(3)	
Ludlow	23(11)		* 2(1)		1(0)	16(7)	4(3)	
U. Wenlock	12(3) 9(3)				1(1)	9(1) 5(0)	} 3(2)	←
L. Wenlock	6(0)					5(0)	1(0)	
M.–U. Llandovery	6(1)	1(1)	1(0)	2(0)	1(0)	1(0)		
L.–M. Llandovery H.	2(0)					2(0)		←
Rhuddanian M. & E.	11(6)	* 4(4)	4(2)	2(0)	1(0)			
Ashgillian V. Caradocian G.	1(0)				1(0) 1(?)			←
L. Ordovician								
Cambrian								
		✓	✓	?				
Precambrian continental cryptarchs								

Records from the upper Llandovery are based on new data (J. B. Richardson, unpublished) and those from the Wenlock and above are based on Richardson & Ioannides 1973). Figures in brackets indicate the numbers of sculptured species. G., Gray *et al.* 1982; H., Hoffmeister 1959; M. & E., Miller & Eames 1981; V., Vavrdova 1982.

Thus the table shows three major events in sporomorph distribution in the Lower Palaeozoic. First, the appearance of tetrahedral tetrads (upper Ordovician) and later accompanied in the Rhuddanian (lower Llandovery) by a distinct microflora of cryptospores most of which were continental in origin; second, the appearance of dispersed trilete spores (lower–middle Llandovery); and third, the development of sculptured trilete spores (Upper Wenlock).

Spores closely resembling those of the genus *Ambitisporites* have been found *in situ* in sporangia borne by dichotomizing (*Cooksonia*-like) axes (Edwards & Fanning, this symposium). The sporangia occur in alluvial deposits of lower Gedinnian age of the Welsh Borderland. It may be important that such spores closely resemble those prised from some of the earliest known

(?Caradocian) permanent tetrads. Did *Cooksonia*-like plants already exist in the Upper Ordovician? Or did these 'permanent' tetrahedral tetrads represent plants ancestral to *Cooksonia*? Or were *Ambitisporites*-like spores produced by several different plants?

Finally, Silurian and Lower Devonian spore sequences show closely similar patterns of development in southern Britain (Laurasia) and north Africa (Gondwana) a fact which should be considered in assessing claims (Gray *et al.* 1982) of 'late Llandovery–early Wenlock vascular megafossils (lycophytes and *Psilophyton*)'.

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Discussion

JANE GRAY. Richardson wants to compare the dispersed spores of the moss *Encalypta* to the fossil trilete spore taxon *Emphanisporites*. Spores of *Encalypta* known to me (Erdtman 1965; Boros & Járai-Komlódi 1975; Horton 1983) have aperture systems or sculpture patterns that are distinct from that of essentially all species of *Emphanisporites*. *Encalypta ciliata* (Hedw.) Hoffm., to which Richardson evidently refers, bears some superficial resemblance to one Devonian species of *Emphanisporites* (*E. erraticus*), not to *any Emphanisporites* of Silurian age. Most of the Silurian species of *Emphanisporites* are not heteropolar to the extent that one or two of the Devonian species are. The basic differences in sculpture among a number of fossil taxa now assigned to *Emphanisporites* raises the question of whether all fossil spore taxa referred to *Emphanisporites* should be included within that taxon merely because of some superficial similarities. The Silurian *Emphanisporites* species do not find a counterpart in *Encalypta* nor can it be stated as Richardson does, that all species of *Emphanisporites* are similar to some *Encalypta*. *Streelispora* and *Aneurospora* are fossil spore taxa whose spores are beset with varied types of ornamentation: spines, warts, cones, etc. Some extant species of *Anthoceros* (and *Phaeoceros*) also have variously shaped 'processes' including spines, warts, cones, etc. But then a similar spore type is also found among the vascular cryptogams. What does this 'prove' about the affinities of *Aneurospora* and *Streelispora* spores? It does not follow, based on possible similarities of one or two taxa that 'many of the Silurian [trilete] spores may have belonged to early hepatic and, or bryophytic ancestors'. However, since I have raised the possibility that many of the obligate spore tetrads with perisporal membranes might have affinities with hepatics, and that these spore types preceded the vascular level of spore morphology, I would be the last one to deny the possibility that some of the late Silurian spores (or other trilete spores of the Palaeozoic) might be of bryophytic origin, and I have addressed this question in my paper in the present volume. I am, however, dubious that a strong case can be made for assigning many of the heavily ornamented late Silurian spore types to bryophytes, because of spore ornamentation types which they may also share with spores of vascular cryptogams.

Richardson refers to obligate tetrahedral tetrads from the Caradoc of Libya and the Ashgillian of Czechoslovakia. Ordovician spore tetrads have been reported far more widely than that (Gray & Boucot 1972; Boucot & Gray 1982). I was the first to recognize the significance of the obligate spore tetrads (Gray & Boucot 1971, 1972), their widespread geographical distribution, and their possible biostratigraphic usefulness (Gray & Boucot 1983). Before 1971 nobody perceived the significance of the obligate spore tetrads and few were looking at palynomorphs from that part of the geological column. For example, Hoffmeister's paratype slides of *Ambitisporites*, in my possession, have common smooth-walled tetrahedral tetrads plus single trilete spores. Hoffmeister (1959) totally overlooked the tetrads, not even mentioning their presence in his paper. I was the first to delimit clearly the varied microfossil assemblage zones (the time limitations of the zones and the nature of the plant spore assemblages therein) that Richardson here describes as 'phases' (Gray & Boucot 1983; Gray *et al.* 1982; Gray, this symposium). Richardson refers here to Richardson & Lister (1969, table 6) as the basis for recognition of 'a second distinct phase in miospore development...the beginning of dispersed laevigate trilete spores'. It is impossible, of course, to recognize a 'second distinct phase' until 'a first phase' is recognized as previously discussed. The data supporting a first phase was not available in 1969. Table 6 is reproduced intact below:

TOTAL NUMBER OF SPORE TAXA (PRESENT PAPER) THROUGH THE SILURIAN AND EARLY LOWER DEVONIAN

(Upper Llandoverian record from Hoffmeister (1959))

	genera	species, etc.	sculptured forms
Dittonian (Lower and Middle)	11	29	21
Downtonian	8	24	13
Ludlovian	6	15	6
Wenlockian	4	8	1
Upper Llandoverian	1	2	0

The only direct references to this table appear on their pages 209–210 and 213–214. These are as follows:

pp. 209–210. 'The spores gradually increase in variety through the Wenlock, Ludlow, Downtonian, and Dittonian (table 6) and some of this is clearly due to evolutionary changes rather than for instance distance from source areas and preservation factors.'

pp. 213–214. 'Table 6 shows a gradual increase in spore genera and species which appears to be evolutionary, and although comparison with Muller's work suggest less spore variety in holomarine sediments, the trend is consistent and repeated in Spain...and Gaspe....'

Richardson refers here to a 'third major phase': 'the beginning, and rapid growth of sculptured trilete spores a development which began, according to present data, in the upper Wenlock'. Reference to table 6, above, clearly shows the rapid increase in sculptured taxa in the Ludlovian and the Downtonian, not in the upper Wenlock. Or is the 'present data' to which Richardson refers based on information provided in Gray *et al.* 1982; Boucot & Gray 1982; Gray & Boucot 1983; and Gray, this symposium. The following statement appears in Gray

& Boucot (1983): 'Unit III (late Wenlock to Pridoli), is characterized by numerical dominance of trilete spores and by increase in diversity of spore coat patterns'.

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