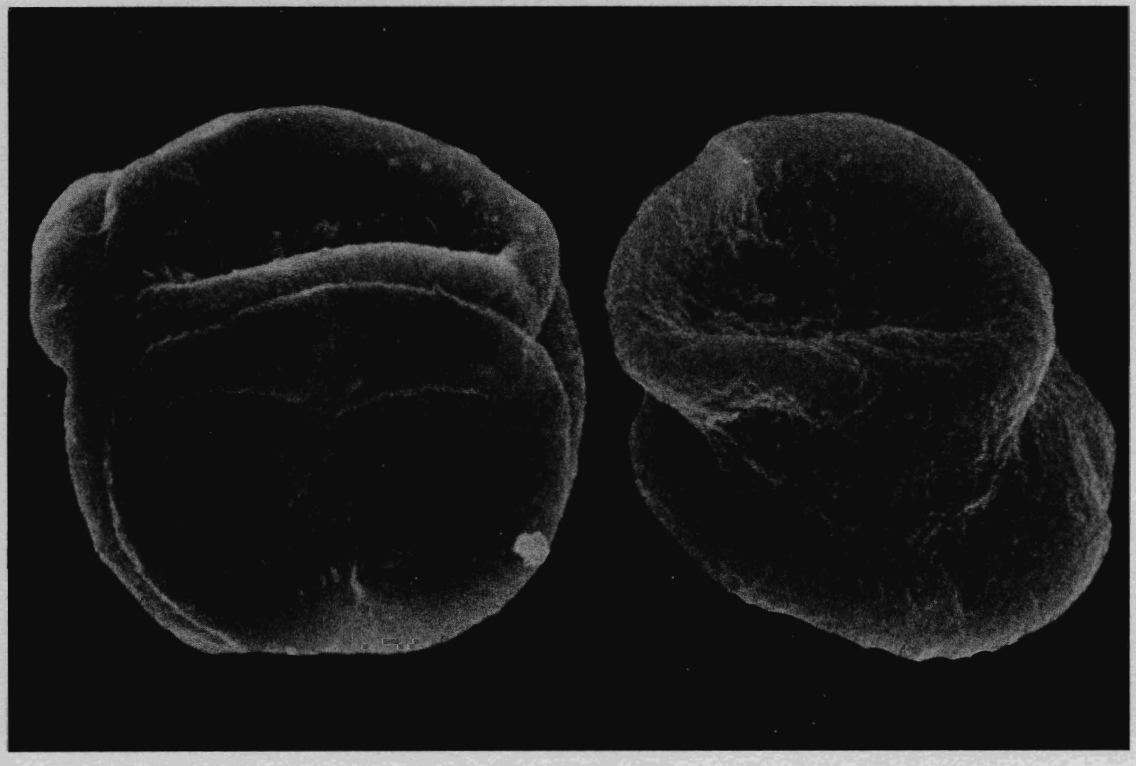
SPECIAL PAPERS IN PALAEONTOLOGY · 55

Studies on early land plant spores from Britain



THE PALAEONTOLOGICAL ASSOCIATION

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SPECIAL PAPERS IN PALAEONTOLOGY NO. 55

STUDIES ON EARLY LAND PLANT SPORES FROM BRITAIN

EDITED BY

CHRISTOPHER J. CLEAL

with 23 text-figures, 28 plates and 7 tables

THE PALAEONTOLOGICAL ASSOCIATION

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PREFACE

ONE of the key topics in modern palaeobotany is the early development of terrestrial vegetation between the Ordovician and Early Devonian. It is significant for understanding the evolution of higher plants, as well as for its impact on the development of the terrestrial environment, which in turn affected the evolution of higher animals, especially the vertebrates and arthropods. Plants not only stabilized the terrestrial environment, but also provided food and shelter for many of these animals. It is almost certain that, if plants had not first invaded the land, there could not have been the subsequent development of an extensive land fauna, that eventually gave rise to man.

A major obstacle to studying the very earliest land plants is that, by their very nature, they were small and delicate, with a relatively low fossilization potential. Considerable progress has been made through the study of the available fragmentary macrofossils of such plants, especially by workers at the University of Wales College of Cardiff, led by Professor Dianne Edwards (e.g. Edwards and Fanning 1985; Edwards *et al.* 1986, 1992, 1994; Fanning *et al.* 1990; Edwards 1993). However, such fossils can probably give only part of the story and it has become increasingly evident that some of the gap can be filled by the study of the spores that these early plants produced. The earliest spores thought to have been produced by land plants differ from those of most living pteridophytic plants, in that they were either produced singly (monads) or in fused clusters of between two and four spores (dyads, triads and tetrads), and may be enclosed within an envelope. They are known as cryptospores following Richardson *et al.* (1984) and dominate most Ordovician and Silurian spore assemblages. Miospores that were dispersed from tetrads and have the characteristic trilete mark, as in modern pteridophytes, first appear in the Upper Llandovery, but it is only in the Lower Devonian that they come to dominate spore assemblages.

Over the years, *Palaeontology* has published a number of major contributions on early land plant palynology (e.g. Richardson and Lister 1969; Burgess 1991; Burgess and Richardson 1991; Wellman and Richardson 1993). In this volume, I have brought together four papers which were submitted recently to the journal, and which reflect various aspects of this subject. The first paper, by John Richardson, takes as its starting point some of the cryptospores discovered during his palynological work on the Lower Devonian of the Welsh Borders. The number of units in such cryptospores has been the usual way of classifying them into suprageneric groupings (turmae, subturmae, etc.) but Richardson argues that this does not produce a meaningful arrangement. He proposes that greater emphasis should instead be given to the presence or absence of an outer envelope, the degree of fusion of the units, and the sculpture. He also argues that there are two distinct types of cryptospore, which he terms eucryptospores and paracryptospores. The former are consistent units of either monads, dyads or tetrads, and are similar to spores found in some living hepatics. Although not necessarily produced by true liverworts, they probably represent the remains of plants growing in similar ephemerally wet habitats. In contrast, paracryptospores are associations of spore units with similar sculpture, but which can occur as monads, dyads, tetrads or even triads. Richardson compares these variable spore units with those produced by some living fern hybrids and he argues that it is evidence that reticulate evolution was important in the early land plants.

The biostratigraphical value of these fossils is demonstrated by the next paper, by Wellman and Richardson. The stratigraphical position of the 'Lower Old Red Sandstone' exposed near Oban in west-central Scotland relative to the better known Midland Valley sequences has for long been uncertain, due, at least in part, to the equivocal vertebrate evidence. The well preserved spore assemblages described in this paper show the sequence to be lower Lochkovian (basal Devonian) and it can thus be correlated with the lower Arbuthnott Group of the Midland Valley. The results also have a wider significance, in that the immediately overlying Lorne Lavas have provided a radiometric date (415–424 Ma), which can be regarded as a guide to the age of the Silurian–Devonian boundary.

In the third paper, Charles Wellman describes an exceptionally well preserved and diverse

assemblage of cryptospores from the upper Ordovician (Caradoc), again of the Welsh Borders. Although not the oldest known (there are records from the Llanvirn of Bohemia and Saudi Arabia), this is one of the best documented assemblages of early cryptospores. In particular it provides important information relevant to the spore zonation of these strata (Richardson 1988), especially the confirmation that true dyads occur in Richardson's stratigraphically lowest assemblage biosubzone. It also provides important evidence with which to test the palaeophytogeography proposed by Gray *et al.* (1992).

Establishing their detailed structure is central to understanding the true nature of cryptospores. Although much can be learnt by traditional optical and electron microscopy, the intimate relationship between the cryptospore units can often be difficult to determine. In the final paper of this volume, Cedric Shute, Alan Hemsley and Paul Strother have approached the problem using the new technique of confocal laser scanning microscopy (CLSM) which in effect allows very thin sections to be examined through the spores without physically cutting them. The technique was used on *in situ* cryptospores derived from a rhyniophytoid sporangium originally described by Lang (1937) from the Upper Silurian of the Welsh Borders and has yielded much information on the fine topology of the spore wall. Their evidence suggests that the dyads were released from the sporangium before the second division of meiosis, and that some of the features seen in cryptospores can be interpreted in terms of variation in timing of meiotic division, sporopollenin deposition and sporangium maturation.

All the papers in this volume have been subject to the normal refereeing used for papers submitted to *Palaeontology*.

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