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A PALAEOBOTANICAL POT-POURRI

Abstract

This study, the third in the series of virtual issues of *Palaeontology*, examines the contributions the journal has made to the field of palaeobotany from 1961 onwards. I offer a personal selection of six papers representing four decades of research, with a range of specific geographical (Canada, Australia, China), temporal (Mesozoic, Devonian, Silurian) or more general (cycads, palynology, stratigraphy) focus.

Key words

Palaeobotany, palynology, cycads, early land plants, Devonian, Silurian

A quick flick through the archive of all 57 volumes of *Palaeontology* proved not that onerous as there were relatively few palaeobotanical contributions, but producing a short list was mind-numbing. As compensation on the entertainment side, my selection is a fossil plant equivalent of Desert Island Discs (for those not devotees of BBC Radio 4, this is the programme in which famous people select eight pieces of music they would wish to listen to when marooned on a desert island). Thus, here a scientific theme is replaced by a personal one. My choice includes papers by giants in their fields for which I have a very high regard, on subjects of interest to my own research area (early land plants) and even one on

which I am a co-author (see Table 1) . I would not go as far as pianist Moura Limpany's selection of all eight of her own recordings.

I begin with Professor Tom Harris ' presidential address on fossil cycads (Harris 1961). Professor Harris was the most influential Mesozoic palaeobotanist of his generation and my PhD external examiner. The cycads are a small group of gymnosperms with a fragmentary fossil record. This was critically reviewed in the paper, and attention drawn to morphological similarities in pinnate leaf construction to another group of Mesozoic gymnosperms, the Bennettiales, now extinct and probably not closely related. He recognized the importance of cuticular characters, particularly stomata in distinguishing the leaves, and also of reconstructing whole plants based on fragments of leaves, trunks and reproductive organs. His own reconstruction uniting *Nilssonia* leaves, catkin-like *Beania* female cones and *Androstrobus* male cones remains a favourite of textbooks and undergraduate lectures. Surprisingly little further progress has been made in succeeding years and in all aspects of such studies one is reminded of Harris' quote (p.318), "When you have found out all you can hope to see and interpreted all visible things in a satisfactory way, however sensible it may be to stop, you make a great mistake if you do." Sound advice for all palaeontologists, except perhaps the fourth year PhD student.

John Richardson and I have worked together for the past 50 years. My second paper, Richardson and Lister (1969), emphasizes the importance of

palynology in correlation with continental rocks, when combined with detailed circumscription and illustration of the spores themselves. The spores, together with the sometimes exceedingly well-preserved plant assemblages in the succession through the essentially fluvial rocks of the latest Silurian and the Lower Devonian of the Welsh Borderland and South Wales, provide a unique record of an early diversification of vascular plants that can be correlated with other events on the Old Red Sandstone Continent and even further afar. Thus this and subsequent papers by Richardson and his students lend credence to the contention at the end of the paper that there are “some indications that even in this area spores may eventually provide significant stratigraphic contributions”.

While stratigraphy figures in the title of my third choice, Harlan Banks' paper extends much further than a mere listing of plant taxa in a stratigraphic framework, which extends from the Silurian into the Devonian (Banks, 1972). Banks, together with Henry Andrews, was responsible for the renaissance of interest in Lower Devonian palaeobotany in the 1960s and 1970s, and I began my studies on British plants at Cornell in 1964. The paper includes critical assessment of not only the ages of the tracheophytes, but also their vascular status, and again emphasized the role of spores in dating as well as documenting the presence of vascular plants even in absence of megafossils. He reviewed the preservation of almost all Silurian plants in marine rocks and consequently speculated on the habitats (river plains, coastal flats and even salt-marshes) and palaeophysiology/ecology of these and basal Devonian examples. The paper also encompassed as land plants non-vascular nematophytes, a group in which I

am particularly interested today as part of the biological crusts (cryptogamic covers) comprising algae, cyanobacteria and cryptophytes which preceded a land vegetation dominated by vascular plants. I am less convinced of his hypothesis that charophytes were also adapted for life on land.

Although somewhat out of chronological order, I turn now to Tims and Chambers' (1984) paper on Australian plants. My all-time palaeobotanical hero, W. H. Lang had written a paper with Isabel Cookson, (the formidable Australian palaeobotanist for whom *Cooksonia* is named), on Silurian plants from Victoria. The assemblage included the pre-lycophyte *Baragwanathia* whose levels of organization did not conform to the evolutionary sequence recorded in Laurentia, and so it was with some relief that the graptolites originally used to date the assemblage actually indicated a Lower Devonian age. Complacency was shattered when it was found that there were actually two horizons with similar plants separated by some 1700 m of unfossiliferous rock, the lower one, again dated by graptolites, as Silurian. Tims and Chambers (1984) described plants from both horizons, including new species of *Salopella* and *Dawsonites*, genera also known from the present Northern Hemisphere. Thus, the anomaly remains, and the enigma has deepened by the finding of zosterophylls and possibly lycophytes in the Upper Silurian of Arctic Canada, at a time when the vegetation preserved in similarly aged rocks elsewhere on the Old Red Sandstone Continent was at a rhyniophyte grade of organization.

Also from Canada (Restigouche River, New Brunswick) is the vascular plant, *Chaleuria cirrosa* (Andrews *et al.*, 1974). It was from this broad

geographical area on the shores of the Gaspé Peninsula that the oldest publications on early land plants were produced by Dawson in the mid-nineteenth century. *Chaleuria* occurs towards the top of the fossiliferous horizons in rocks now dated by spores as uppermost Lower Devonian and is noteworthy as the oldest heterosporous plant, with some sporangia in the terminal parts containing numerous small spores (30-48 µm) and other numerous larger examples (60-156 µm). Spores also differ in ornament and have been placed in different genera in the *sporae dispersae* (*Apiculiretusispora* v. *Cyclogranisporites*). Separation of the sexes in this way is considered an essential early step in the evolution of the seed habit. It is seen today only in the fern *Platyzoma*, where the small spores develop into free-living green, male gametophytes and the largest into free-living female ones. A similar life history is thus inferred for *Chaleuria*, although in the fossil, intriguingly a third type of sporangium with mixtures of the two types is recorded, perhaps indicating an even earlier stage in the evolution of heterospory with variation in the nature of sporocytes within a single sporangium.

Access to Chinese fossils has transformed our palaeontological world. An excellent example is palaeobotany, and I was privileged to publish one of the first publications based on the Lower Devonian assemblage from Yunnan (Li and Edwards 1992). It marked the start of a long collaboration with Professor Li Cheng-Sen at the Institute of Botany in Beijing, who together with Professor Hao Shou-Gang and his students, had made extensive collections of the Posongchong flora, beautifully summarised by Hao and Xue (2013). The flora is very diverse (28 genera; 35 species), with extraordinary levels of disparity that do

not fit comfortably into existing taxonomic frameworks. *Adoketophyton subverticillatum* is an excellent example. It was a leafless plant with terminal cones (strobili) in which each laterally attached bivalve sporangium was subtended by a fan-shaped bract (the latter missing in *Zosterophyllum*), while the subtending stems differed in the developmental sequence of water-conducting cells when compared with the zosterophyll lineage. Such a combination of characters does not occur in the major early vascular plant lineages, except perhaps the Barinophytales. It provides an example of the high endemicity in the Posongchong flora, and the provincialism that culminated in the emergence of the late Palaeozoic Cathaysian flora.

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TABLE 1. Contents.

1. Harris (1961) <i>The fossil cycads.</i>
2. Richardson and Lister (1969) <i>Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales.</i>
3. Banks (1972) <i>The stratigraphic occurrence of early land plants.</i>
4. Tims and Chambers (1984) <i>Rhyniophyta and Trimerophytina from the early land flora of Victoria, Australia.</i>
5. Andrews <i>et al.</i> (1974) <i>An apparently heterosporous plant from the Middle Devonian of New Brunswick.</i>
6. Li and Edwards (1992) <i>A new genus of early land plants with novel strobilar construction from the Lower Devonian Posongchong Formation, Yunnan Province, China.</i>