

EVIDENCE OF VASCULAR PLANTS IN THE CAMBRIAN

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During the last two decades attention has been focused on spore discoveries in Early Palaeozoic rocks, and several varied types of spores have been distinguished. While the information given by palynology agrees with the flora known in Upper and Middle Devonian, the assemblage of spores found in Lower Devonian, Silurian and Cambrian plead in favor of a more varied and advanced type of flora than the plant impressions have so far suggested. The recent discovery of Lycopodiaceous shoots in the Middle Cambrian of East-Siberia appears to confirm the evidence of palynology investigation. The purpose of this article is to emphasize the meaning of these discoveries and to discuss briefly their bearing on questions of evolution.

Our knowledge of the Devonian flora has increased importantly during the last three decades, largely as a result of the research carried out in Canada, the United States, Bohemia, Great Britain, Germany, Norway, Sweden, and Belgium. One of the most striking features is the sharp difference which appears to exist between the flora of the three main divisions of the Devonian.

As is well known, the Upper Devonian landscape foreshadows the Coal period scenery. The same groups of pteridophytes are represented by identical and

distinct genera. Preserved structures of primitive gymnosperms are also known. Some of these plants are tree-forms, with large fronds and well developed leaves. This is confirmed by palynology. Spores and pollen grains found in Upper Devonian strata show a great variety of pattern, size, and ornamentation (Naumova, 1953; Radforth and McGregor, 1954), which display affinity with filicinean, calamarian, and lycopodiaceous spores, and pollen grains of Pteridospermales, Cordaitales and Coniferales.

In the Middle Devonian, the cover of vegetation is peculiar. While members of the main races of the pteridophytes and some primitive woods of Gymnosperms are represented, most of the genera are different and simplified in habit. That is to say: though the plants show an average level of high differentiation, most of them are not tree-form, and have only minute leaves. Moreover, a few groups exist which, hitherto, have appeared to have developed during Middle Devonian: the *Proto-Articulatae*, the *Iridopteridaceae*, the *Cladoxylaceae*, etc. In a parallel way, researches on microfossils bring out a diversity of types. These, however, show less complexity of pattern than do the spores and pollen grains of the Upper Devonian (Thomson, 1952; Radforth

and McGregor, 1954). Yet, forms and types resembling filicinean, calamarian and lycopodiaceous spores have been discovered.

The vegetation in the Lower Devonian offers a sharp contrast with that of the Middle Devonian, on the basis of the record of impression so far collected. The Lower Devonian flora cover would appear to have consisted of a carpeting of slender, tufted, herbaceous and semi-aquatic plants, mostly consisting of Psilophytales or psilophyte-like forms, with a few lepidodendroid genera like *Drepanophycus* and *Protolopodendron*. The marked discrepancy observed between two floras so close in geological time as Middle and Lower Devonian, is difficult to reconcile. The absence in Lower Devonian of plant impressions positively related to any of the varied differentiated plants of the Middle Devonian is astonishing. On the other hand, the present difficulty concerning the characterization of the psilophytalean complex leads one to speculate that the latter might possibly include representative members of other phyla, in which the external morphology may have been very similar as a consequence of an adaptation to a similar set of life conditions (Leclercq, 1954).

Personal field work during the last summer has shown that the main genera of the Middle Devonian flora occur at the very beginning of the period (base of the Couvinian). So far the best known exposures are located in the upper part of the Middle Devonian (Givetian). It is now confirmed that the same differentiated flora existed through the whole sequence (Liégeois, 1953, 1955). On the other hand, in the subdivision immediately below, the Emsian (upper part of the Early Devonian), occur the monotonous undifferentiated plants of the Early Devonian. These facts provide a basis for inference that more specialized plants may have existed in Lower Devonian, simultaneously with the psilophytalean complex and lycopsids, which probably represented the dominant ecological facies of the pe-

riod. Contemporary with these, however, the precursors of the continental races which flourished in Middle Devonian may have colonized the xerophytic habitat of the Lower Devonian. Relics of these precursors have yet to be found. Field work devoted to a search for synchronous bio-facies in Lower and Middle Devonian strata is being continued in Belgium. A few examples have already been located.

The results obtained in Early Devonian palynology are extremely interesting. Thomson, in 1952, emphasized the distinctions observed between spore assemblages in Lower Devonian of Germany and Middle Devonian of Esthonia. His observations are in accord with the evidence from the megaflores hitherto collected; i.e., spores found in Middle Devonian show complex morphological features while spores that are primitive in shape and ornamentation are present in Lower Devonian (Lang, 1925; Höeg, 1942). More recently, however, Radforth and McGregor investigated sediments in Canada. They write (1954, p. 615): "Spore complexity is also a feature of floras of the Lower Devonian and Silurian periods, as indicated by the microfossils of Figs. 57 to 74. Prominence of complexity (pattern and form) is on the other hand less obvious than for the Middle and Upper Devonian rocks." The observations of Thomson, although they appear opposed to those of Radforth and McGregor, are in fact complementary. Moreover, they strengthen the suggestion that various bio-facies may have existed during the Lower Devonian, and even suggest similar conditions in Silurian.

The Siluro-Devonian of Australia has yielded compressions of the oldest vascular plants so far collected. These remains reveal plants of different types, habits and habitats. Besides the *Yarravia* and *Hedeia* of uncertain systematic position, there are representative members of the psilophytales-complex and the differentiated *Baragwanathia* (Lang and Cookson, 1935). The occurrence of two phyla: Psilophytales and Lycopsida in Siluro-

Devonian suggests the possible co-existence of other races of vascular plants in that period (Leclercq, 1954). As has been noted, this suggestion receives the support of palynology (Radforth and McGregor, 1954).

The Cambrian megaflores has until recently yielded no evidence, although palynology has argued for the existence of varied vascular plants. According to Reissinger (1939) and Naumova (1949), the spores found in the blue-clay of Lower Cambrian of Kunda in Esthonia and of Pre-Baltique in U.S.S.R. are cutinized; generally very small in size; 15 up to 27 microns (exceptionally 75 microns); regular in shape, round or oval; and smooth or slightly grained, irregularly multi-folded, with triradiate marking more or less distinct. In greater contrast are the spores found in the Upper and Middle Cambrian of Kashmir, Spiti, and the Neobolus shale from Salt Range in India. If the majority of these are round or oval in shape, triangular forms are not uncommon (Jacob, 1953). A coarse network ornamentation, continuous membranous wing and even bladders (?) are observed (Ghosh and Bose, 1950; Ghosh, Sen and Bose, 1951; Ghosh and Bose, 1952; Jacob, 1953). The size of the spores generally varies from 5 to 50 microns with the largest ones ranging from 25 to 130 microns. Most of the samples are geologically authenticated by the characteristic fauna (trilobites and brachiopods) of the horizons (Jacob, 1953 a and b). So far, at least, fifty types of spores have been distinguished.

Such a remarkable variety of spores in Cambrian sediments is impressive and certainly unexpected. Moreover, besides the spores Reissinger (1939), Ghosh and Bose (1950), Ghosh, Sen, Bose (1951), Ghosh and Bose (1952), and Jacob (1953 a-b) have found tiny fragments of woody elements, which, despite poor preservation, show scalariform and pitted (simple and bordered pits) tracheids.

The conclusion to be drawn from these facts was that varied types of vascular

plants existed in Early Palaeozoic. However, scepticism was prevalent among scientists. It was suspected that the samples of rocks were probably contaminated by younger sediment. That is why Indian workers repeatedly checked their results, and this always with success. Nevertheless the persistent lack of floral remains in Cambrian came into conflict with palynology. Furthermore, the existence of such a simple group of vascular plants as the Psilophytales in Upper Silurian supported the hypothesis that this may have represented the starting point of terrestrial plant life. Fortunately, the discrepancy between micro-flora and mega-flora is now in process of vanishing.

In the Middle Cambrian of East Siberia a lycopodiaceous plant has been discovered (Kryschtowitch, 1953). The geological age of the deposit is determined by the following fauna: *Prohedinia attenuata* Lerm, *Ptychoparia tchadensis* N. Tchern, *Anomocariodes limbataeformis* Lerm and *Hyagnostus truncatus* (Brögg). According to the author this fauna corresponds in age to the West European zone with *Paradoxides forchammeri* from the Middle Cambrian. He writes as follows:

"The plant material consists of 4 impressions of shoots, the fragments of which are 4 up to 8.5 cm. long, and 8 to 13 mm. broad. The surface of the axis is covered fairly evenly with oblong thickenings in regular arrangement. The thickenings are extended upwards and downwards by thin stripes giving the whole shoot a wrinkled appearance. In addition the surface of the shoot is minutely granulated. The shoot is densely covered with thin and delicate appendages (leaves) which are up to 9 mm. long. On the impressions the edge of the shoot is uneven, as if dentate due to the form of the thickenings and the arrangement of the appendages. In some places it is possible to trace a thin stripe, a vascular bundle right out to the base of the thickenings. . . ." "Attempts to isolate the cuticle or epidermis through mazeration or to obtain a colodion impression have not been successful."

Kryschtowitch points out that the Cambrian plant differs very much from the typical psilophytes (*Psilophyton*, *Rhynia*, *Hornea*, *Asteroxylon*) and may rather

be compared with *Drepanophycus* and *Baragwanathia*. He says: "In its sculpture our plant very much resembles *Drepanophycus spinaeformis*; in the latter, however, the appendages look like thorns, while appendages (leaves) in *Baragwanathia* very much resemble those of *Aldanophyton antiquissimum*" (the new plant name). Consequently Kryschtofowitch comes to the conclusion that the Cambrian plant "... seems rather to show that it belongs to the primitive lycopodiales, not to the psilophytes." In accordance with the lack of sporangia and anatomy, the author separates the new plant under a new genus which, he says, may be a provisional name.

Kryschtofowitch notes the findings, in the Cambrian, of a land plant, probably belonging to the lycopodiales, and various kinds of spores, and points out "That these discoveries throw a new light on the problem of the origin of land plants and permit us to trace higher cryptogames still further back in time."

While the affinity of *Aldanophyton* to the Lycopodiales can hardly be questioned, the figured specimens suggest a morphology more related to the genus *Drepanophycus* than to *Baragwanathia*. In fact there are some species within the genus *Drepanophycus* on which the appendages are more leaf-like than thorn-like. On the other hand, the form and arrangement of the thickenings on the surface of *Aldanophyton* appear to be closely comparable, in the essential features of their construction, to those of *Drepanophycus*. In view of the fragmentary condition in which the specimens are preserved, a generic discussion is not pertinent to this report.

Because the discoveries of differentiated spores and a vascular plant, in Cambrian, may be considered as among the the most interesting results of recent palaeobotanical records, we feel justified in commenting briefly on their significance.

The remarkable fact is that a lycopsid more complex in structure than the Psi-

lophytales has been found in a horizon definitely earlier than any from which the latter is known. It positively separates the origin of the lycopsids from the Psilophytales. Furthermore, the degree of differentiation exhibited by *Aldanophyton* presupposes a long evolutionary sequence prior the Cambrian. Within the limits of the lycopsids it shows the persistency of a *Drepanophycus*-like type from, at least, the Middle Cambrian to the base of Middle Devonian without much modification; that is to say, during a period of about two hundred million of years. In addition there arises the question of a probable co-existence of other phyla of vascular plants in Cambrian and even earlier. Furthermore, it accredits the Cambrian spores and their conclusion.

It is of great interest that the plant-microfossil and the megaflora show close agreement, for, in that way, the credit of palynology to predict the complexity of a flora is strengthened. Spores and pollen grains probably give a fairly adequate expression of the components of the vegetation which were flourishing during a geological period, for, by reason of their capacity to disperse, they may convey information as to types of plants which owing to their habitats have little chance to be preserved. Continental formations are generally unsuitable for preservation of plant impressions; land and fresh water deposits are peculiarly liable to destruction. These circumstances, for example, are responsible for the scarcity of our documentation on the upland plants and the fragile Bryophyta elements within the flourishing Carboniferous flora.

Similarly, the accordance of the results of palynology and plant impressions through the Early Paleozoic adds convincing support to the usefulness of spore applications for zonal analysis in economical purposes: study of stratigraphy, petroleum geology, etc.

Incidentally palynology focuses attention on the need for caution in the interpretation of ecological facies of sedimentary rocks. On the basis of a megaflora,

ecological associations may erroneously be considered as evolutionary stages. For instance the *Rhyniaceae*, upon which most of our information about the structure of the Lower Devonian plants is based, owe the simplicity of their structure *in part* to the peculiar environment to which they are adapted. Though primitive in features, they probably represent relic forms in a plant world composed of varied and more highly organized forms whose complexity we only are beginning to foresee (Leclercq, 1954). The variety of spores found in Siluro-Devonian (Radforth and McGregor, 1954) reinforces this opinion as it indicates that a vegetation more differentiated than the Psilophytales had taken possession of the land at that time.

In a wider sense palynology and plant impressions of Cambrian raise the major question of the polyphyletism of the vascular plants. They carry back to Proterozoic the fundamental preliminary process that have prepared for the differentiation of the main races, which, later, have given rise to a land flora. They indicate a more remote time for the epoch of the migration from sea to land, hitherto generally considered to have occurred during Siluro-Devonian. Moreover, the assumption that a varied flora existed in Cambrian time should adjust the flora to faunas which, in Lower Cambrian, show a burst of divers creative activity.

It is important to bear in mind that algal structures have been detected in graphitic limestones of 3000 million of years (1941, A. M. Macgregor). The alga belongs to the Stromatolites and shows well preserved graphitic, concentric laminae. The limestone belongs to the Bulawayan System in Southern Rhodesia; its age has been established by the analysis of monazites, which indicates an age of some 2650 million years (1955, A. Holmes and L. Cahen). Thus the threshold of the sedimentary rocks is crossed opening up a tremendously large field of research. If Stromatolites represent organic remains, then the enormous duration of time available for the development of distinct, un-

known ancestors throws stimulating new light on the potentialities of the original differentiation of the Plant Kingdom.

Persistence of type with imperceptible change and, from time to time, the sudden influx of new types, correlative with favorable stable geological conditions, are among the outstanding features of the history of evolution as shown by palaeontology.

On the contrary periods of profound change in fossil floras are observed in relation to major geological events as: orogenic movements, great marine transgressions, glaciations, important changes of climatic equilibrium, etc. All these perturbations must have had a far reaching influence on the evolution of plant world.

Thus the knowledge gained from the investigation of the older formations changes our perspective on the preliminary processes of plant differentiation on the earth and provokes thought and research.

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