
Early Land Plants

H. P. Banks

Phil. Trans. R. Soc. Lond. B 1985 **309**, 197-200

doi: 10.1098/rstb.1985.0078

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Early land plants

BY H. P. BANKS

Plant Biology, Plant Science Building, Cornell University, Ithaca, New York 14853, U.S.A.

After three decades of vigorous research on the Siluro-Devonian floras neither interest nor productivity is slackening. Some newer developments and comments on the two previous papers are listed here to highlight the varied disciplines and approaches that are being brought to bear on Silurian–early Devonian floras.

(i) Banks (1981) reported wounds, probably inflicted by chewing microarthropods, in axes of *Psilophyton dawsonii* repaired by the formation of a periderm. Unreported evidence indicates wounding and repair stimulated by piercing and sucking activity of other animals. These observations complement the work of Kevan *et al.* (1975) on arthropods and damage to plants that are found in the Rhynie Chert, and that of Shear *et al.* (1984) on a new terrestrial fauna from eastern New York. Interest in plant–animal interrelationships will attract a new group of scholars to the study of Siluro-Devonian plants. Particularly important will be the maceration of large quantities of rock.

(ii) Stubblefield & Banks (1983) found oomycetous fungi within cells in the cellularly permineralized aerial axes of *Psilophyton dawsonii*. Rayner (1983) reported apparent fungal bodies in the spines on compression specimens of *Sawdonia ornata*. These reports supplement that by Kevan *et al.* (1975) on the fungi in the Rhynie Chert. Whether the fungi were parasitic or saprophytic, or were mycorrhizal as suggested by Pirozynski & Malloch (1975), is unclear on the basis of present evidence. Sherwood-Pike & Gray (1985) have isolated hyphae and spores of higher fungi from macerates of mid to late Silurian rocks from Gotland. Other fragments appear to be coprolites of arthropods that include fragments of hyphae. They suggest that fungi and microarthropods may have served as terrestrial decomposers during late Silurian. Pratt *et al.* (1978) reported septate fungi in earliest Silurian. These introductory works imply a productive future in the study of Siluro-Devonian terrestrial fungi.

(iii) Hueber (1982) reported at the A.I.B.S. meeting at Pennsylvania State University the discovery of tubes in the central strand of *Taenioocrada dubia*, a plant that has always been considered to be a typical tracheophyte. The walls of the tubes, as viewed with scanning electron microscopy, consist of an inner, microporate layer, an outer, meshwork layer and a helical, spongy layer between the two. This is quite unlike walls of tracheids and implies that *T. dubia* is no tracheophyte. Schweitzer (1983) has suggested that *Taenioocrada* was an intertidal plant. True tracheids have not been found in *Rhynia major* (Edwards 1980) nor in *Nothia aphylla*, (Lyon 1964) both from the Rhynie Chert bed. Thus one can speculate on the existence in the Devonian of a group of plants with remarkably tracheophyte-like morphology but non-tracheophyte anatomy. Ultimately the data may lead to the erection of a new Division or Subdivision. *T. dubia* underscores the importance of detailed studies of each early land plant before drawing final conclusions as to its affinity.

(iv) The lycopod genus *Baragwanathia*, long associated with the Siegenian Stage, and lately with the Ludlow (Garratt & Rickards 1984), has now been recorded by Heuber (1983) in the Emsian of Canada. If the Ludlow occurrence is sustained, we have another example of

evolutionary stasis. This early occurrence may also suggest that tracheophytes arose polyphyletically from their presumed algal ancestors, the *Rhynia*- and trimerophyte types on the one hand and the zosterophylls and lycopods on the other.

(v) Limited work in biogeochemistry, for example, Niklas & Gensel (1976), which should be confirmed and extended, supports previously suggested relationships among groups of early land plants.

(vi) The global distribution of early floras is widening, for example, to Antarctica and China. I suggest that ultimately the Devonian floras of northern and southern palaeohemispheres will be shown to be remarkably alike (see, for example, Fairon-Demaret 1974; Hueber 1983).

(vii) Some workers, such as Dianne Edwards (this symposium), are now making serious attempts to determine the palaeogeography–ecology of the early plants. Team research, for example, by Thorez *et al.* (1977) is modelling sedimentary basins on the basis of sedimentological and palaeontological (spores, conodonts, ostracodes, acritarchs, scolecodonts) evidence that produces a detailed biostratigraphic zonation and palaeogeographical reconstruction.

(viii) The study of megafossils of early land plants has progressed to the stage where the time of appearance of various anatomical and morphological characteristics is known and the plants themselves can be grouped into Assemblage Zones comparable to those erected by palynologists (Chaloner & Sheerin 1979; Banks 1980).

(ix) Lycopods show a wider range of leaf morphology in Devonian than today. *Leclercqia complexa* (Banks *et al.* 1972), whose leaves terminate in five sharply pointed tips, is the extreme and more and more specimens, assumed to be *Protolepidodendron scharyanum*, are proving to be *Leclercqia* (Fairon-Demaret 1974, 1980). This genus is also the first lycopod, extinct or extant, in which homospority is accompanied by ligules, which have been demonstrated on both sterile and fertile leaves by Grierson & Bonamo (1979). Evolutionary stasis is also illustrated among lycopods. *Drepanophycus spinaeformis* ranges from Siegenian into Frasnian, (Banks & Grierson 1968) *Baragwanathia* from Ludlow (if confirmed) into Emsian, *Leclercqia* from Emsian into Givetian.

(x) Complex anatomical structure had evolved by Emsian. The trimerophyte *Psilophyton dawsonii* (Banks *et al.* 1975) apparently has alternating zones of profuse, close, vegetative branching followed by more distantly spaced fertile branches. The vascular strand becomes remarkably enlarged just below the vegetative branching and then breaks up into the numerous traces that supply individual branches some of which are tiny, some larger. Above this branching, the vascular column regains its normal size and gives off small traces alternately to fertile branches. This pattern is far removed from what is known about the simple rhyniophytes. Similarly, the pitting on tracheid walls in *P. dawsonii* is advanced (Hartman & Banks 1980). Scalariform bordered pit pairs are the basic type of pitting present. But strands of secondary wall connect the pit borders causing the apertures of each pit pair to appear multiaperturate. This interpretation is confirmed by scanning electron microscope studies and by thin sections (2 µm) of demineralized axes embedded in resin.

(xi) The soil-binding properties of these early plants would seem to be minimal. Rhyniophytes lack roots; trimerophytes have not been demonstrated to possess roots. Zosterophylls may have produced occasional root-like (rhizophore) organs (Banks & Davis 1969; Edwards 1970). Roots have been demonstrated in the lycopod *Drepanophycus spinaeformis* (Rayner 1984). However they are adventitious and although each branches several times they do not constitute a true root system such as appears in Frasnian and perhaps Middle Devonian strata as well. Because they

penetrated well into the soil below the rhizome, they certainly anchored the plant and contributed to the binding of the soil.

(xii) Remy & Remy (1980) have produced the first credible fossil evidence of the gametophytic phase of a terrestrial plant with their description of a gametangiophore bearing antheridia and sperms found in the Rhynie Chert.

(xiii) Gray (this symposium) has suggested that Ordovician–early Silurian permanent tetrads may indicate a bryophytic level of evolution earlier than the first vascular plants. This interpretation gives new meaning to these perplexing tetrads.

REFERENCES

- Banks, H. P. 1980 Floral assemblages in the Siluro-Devonian. In *Biostratigraphy of fossil plants* (ed. D. L. Dilcher & T. N. Taylor), pp. 1–24. Stroudsburg, Pa: Dowden Hutchinson & Ross.
- Banks, H. P. 1981 Peridermal activity (wound repair) in an early Devonian (Emsian) trimerophyte from the Gaspé Peninsula, Canada. *The Paleobotanist* **28–29**, 20–25.
- Banks, H. P., Bonamo, P. M. & Grierson, J. D. 1972 *Leclercqia complexa* gen. et sp. nov., a new lycopod from the late Middle Devonian of eastern New York. *Rev. Palaeobot. Palynol.* **14**, 19–40.
- Banks, H. P. & Davis, M. R. 1969 *Crenaticaulis verruculosus*, a new genus of Devonian plants allied to *Zosterophyllum*, and its bearing on the classification of early land plants. *Am. J. Bot.* **56**, 436–449.
- Banks, H. P. & Grierson, J. D. 1968 *Drepanophycus spinaeformis* Göppert in the early Upper Devonian of New York State. *Palaeontographica B* **123**, 113–120.
- Banks, H. P., Leclercq, S. & Hueber, F. M. 1975 Anatomy and morphology of *Psilophyton dawsonii*, sp. n. from the late Lower Devonian of Quebec (Gaspé) and Ontario, Canada. *Palaeontographica Americana* **8**, 77–127.
- Chaloner, W. G. & A. Sheerin 1979 Devonian macrofloras. In *The Devonian System* (ed. M. R. House, C. T. Scrutton & M. G. Bassett), Special Papers in Palaeontology no. 23, 145–161. London: Palaeontological Association.
- Edwards, D. 1970 Further observations on the Lower Devonian plant, *Gosslingia breconensis* Heard. *Phil. Trans. R. Soc. Lond. B* **258**, 225–243.
- Edwards, D. 1980 Evidence for the sporophytic status of the Lower Devonian plant *Rhynia gwynne-vaughanii* Kidston & Lang. *Rev. Palaeobot. Palynol.* **29**, 177–188.
- Fairon-Demaret, M. 1974 Nouveaux specimens du genre *Leclercqia* Banks, H. P., Bonamo, P. M. & Grierson, J. D. 1972 du Givetien (?) du Queensland (Australie) *Bull. Inst. r. Sci. nat. Belg.* **50**, 1–4.
- Fairon-Demaret, M. 1980 A propos des specimens déterminés *Protolepidodendron scharianum* par Kräusel et Weyland, 1932. *Rev. Palaeobot. Palynol.* **29**, 201–220.
- Garratt, M. J. & Rickards, R. B. 1984 Graptolite biostratigraphy of early land plants from Victoria, Australia. *Proc. Yorks. Geol. Soc.* **44**, 377–384.
- Grierson, J. D. & Bonamo, P. M. 1979 *Leclercqia complexa*: Earliest ligulate lycopod (Middle Devonian). *Am. J. Bot.* **66**, 474–476.
- Hartman, C. M. & Banks, H. P. 1980 Pitting in *Psilophyton dawsonii*, an early Devonian trimerophyte. *Am. J. Bot.* **67**, 400–412.
- Hueber, F. M. 1982 *Taeniochrada dubia* Kr. & W.: its conducting strand of helically strengthened tubes. Botanical Society of America Miscell. Pub. no. 162, 58–59.
- Hueber, F. M. 1983 A new species of *Baragwanathia* from the Sextant Formation (Emsian) Northern Ontario, Canada. *Bot. J. Linn. Soc.* **86**, 57–79.
- Kevan, P. G., Chaloner, W. G. & Saville, D. B. O. 1975 Interrelationships of early terrestrial arthropods and plants. *Palaeontology* **18**, 391–417.
- Lyon, A. G. 1964 The probable fertile region of *Asteroxylon mackiei* K. & L. *Nature, Lond.* **203**, 1082–1083.
- Niklas, K. J. & Gensel, P. G. 1976 Chemotaxonomy of some Paleozoic vascular plants. Part I: Chemical compositions and preliminary cluster analyses. *Brittonia* **28**, 353–378.
- Pirozynski, K. A. & Malloch, D. W. 1975 The origin of land plants: a matter of mycotrophism. *Biosystems* **6**, 153–164.
- Pratt, L. M., Phillips, T. L. & Dennison, J. M. 1978 Evidence of non-vascular land plants from the early Silurian (Llandoveryan) of Virginia, U.S.A. *Rev. Palaeobot. Palynol.* **25**, 121–149.
- Rayner, R. J. 1983 New observations on *Sawdonia ornata* from Scotland. *Trans. R. Soc. Edinb.* **74**, 79–93.
- Rayner, R. J. 1984 New finds of *Drepanophycus spinaeformis* Goppert from the Lower Devonian of Scotland. *Trans. R. Soc. Edinb.* (In the press.)
- Remy, W. & Remy, R. 1980 *Lyonophyton rhyniensis* nov. gen. et nov. sp., ein gametophyt aus dem chert von Rhynie (Unterdevon, Schottland). *Argumenta Palaeobotanica* **6**, 37–72.
- Shear, W. A., Bonamo, P. M., Grierson, J. D., Rolfe, W. D. I., Norton, R. A. & Smith, E. L. 1984 Early land animals in North America: Evidence from Devonian age arthropods from Gilboa, New York. *Science, Wash.* **224**, 492–494.

- Sherwood-Pike, M. & Gray, J. 1985 Silurian fungal remains: oldest records of the class Ascomycetes? *Lethaia* (In the press.)
- Stubblefield, S. P. & Banks, H. P. 1983 Fungal remains in the Devonian trimerophyte *Psilophyton dawsonii*. *Am. J. Bot.* **70**, 1258–1261.
- Schweitzer, H.-J. 1983 Die Unterdevonflora des Rheinlandes. *Palaeontographica B* **189**, 1–138.
- Thorez, J., Strel, M., Bouckaert, J. & Bless, M. J. M. 1977 Stratigraphie et paléogéographie de la partie orientale du synclinorium de Dinant (Belgique) au Famennien supérieur: un modèle de bassin sédimentaire reconstitué par analyse pluridisciplinaire sédimentologique et micropaléontologique. *Meded. Rijks Geol. Dienst., N.S.* **28**, 17–32.