

## THE QUESTIONABLE ORIGIN OF EARLY LAND PLANTS FROM ALGAE

F. P. JONKER

Laboratory of Palaeobotany and Palynology, The State University of Utrecht  
Heidelberglaan 2, The Netherlands

### ABSTRACT

The paper deals with the rise of terrestrial plant life in the Early Devonian. The view is developed that apart from Psilophytes some algal groups may have given rise to (semi-) land plants. (Semi-) land algae, however, have not been successful in competition with land invading Tracheophytes and became extinct after a relatively short existence.

*Key-words* — Algae, Early land plants, Terrestrial vegetation, Psilophytes, Early Devonian.

### सारांश

प्रारंभिक स्थलीय पौधों का शैवालों से संदिग्ध उद्भव — एफ़० पी० यौन्कर

प्रस्तुत शोध-पत्र प्रारंभिक डिवोनियन में स्थलीय पादप-जीवन के उत्कर्ष से सम्बन्धित है। यह विचार व्यक्त किया गया है कि साइलोफ़ाइटियों के अतिरिक्त कुछ शैवालीय समूहों से भी (अर्ध) भू-पादपों का विकास हुआ हो। तथापि, स्थलाक्रांता ट्रेकियोफ़ाइटियों के मुकाबले में (अर्ध) स्थलीय शैवाल सफल नहीं रहे तथा अपेक्षया अल्पकालिक अस्तित्व के पश्चात् विलुप्त हो गये।

**I**N what I presume was his final paper, J. M. Schopf (1978) showed that the till then enigmatic, North-American, Devonian genus *Foerstia* White belonged to the Phaeophyta and should be regarded as a marine "furoid". The presumed spore, or megaspore, tetrads represented egg cells of which the coats were resistant. These eggs, borne in fucoidal conceptacles, might be forerunners of the more reduced oocytes that occur in modern Fucales. The thallus of *Foerstia* lacks a cuticle and it has internal filamentous pseudo-tissue like *Fucus* and other fucoidal brown algae.

A year later, Jonker (1979) developed the view that the Early Devonian members also of the enigmatic genus *Prototaxites* Dawson were Rhodophyta-Nemalionales with stout, erect, branched, winged cauloids, the wings in some places expanding into phylloids, while terminal phylloids also occurred. The phylloids were described before as *Nematothallus* Lang and the cystocarps as *Pachytheca* J. D. Hook.

The two above mentioned papers prove again that some knowledge of modern larger algae, their life form, and their reproduction and life cycle is needed in studying and interpreting Silurian and Devonian plant megafossils which are too often attributed to Psilophytes or other Pteridophytes.

Another question in connection with these fossils, however, arises, in regard to which problem numerous suppositions have been published, viz., did these algae represent early land plants or at least temporarily emerged and at other times submerged plants. The sudden rise of land plants in the Devonian, belonging to different divisions of Pteridophytes, is apparent. It is, generally, attributed to a gradual, genesis of atmospheric conditions suitable to terrestrial plant life. It might be that this atmospheric change also produced a certain effect on some groups of algae, giving rise to different groups of land algae, or at least algae transitional from water plants to land plants, but then apparently to unsuccessful (semi) land plants that be-

came extinct after a relatively short existence.

With regard to both *Foerstia* and *Prototaxites*, Gray and Boucot (1977) argued that the "Nematophytalean tracheid-like tubes" as found in the cauloids and phylloids of these genera, may have had a functional role similar to that of tracheids, i.e. they may have been water conductors, a circumstance only expected in a land plant or possibly in an emergent aquatic. They attributed the two genera, together with *Protosalvinia* Dawson in which genus they included *Foerstia*, to the *Nematophytales* Lang, an order of land algae and more or less intermediate between water and land plants or between algae and vascular plants.

In his above mentioned paper Schopf (1978) strongly opposed to Gray and Boucot's concept with regard to *Foerstia*. *Foerstia* should be regarded as a marine furoid and, according to him, there is no evidence that these plants have ever been anything but marine. *Foerstia* remains have never been reported from a nonmarine association and this statement contrasts with Gray and Boucot's view when they compared marine occurrences with that of occasional pieces of drift wood of *Callixylon*.

In a reply that was published shortly after the death of J.M. Schopf, Gray and Boucot (1979) stuck to their opinion and stated that a number of features, to which they now added recent biochemical data, suggest that *Foerstia* and *Protosalvinia* have been land plants or, possibly, emergent aquatics, neither furoids nor algae but representatives of a separate group of land plants as previously advocated.

With regard to *Prototaxites*, this genus was, apart from earlier attributions to seed plants, fungi or lichens, mostly attributed either to Phaeophyta-Laminariales or to a separate group of algae. But both the land plant concept and the seaweed theory have had supporters. The land plant theory or a concept in the direction of semi-aquatics gained the support of Dawson, Chiarugi, Lang, Arnold and Niklas. Supporters of the seaweed theory have been, e.g. Carruthers, Penhallow, Gothan and Weyland and especially Kräusel who argued that as marine algae of large dimensions exist at present time, there is no need to

infer the existence of large land algae in Devonian times. Brzyski (1976) was of the opinion that *Prototaxites* and *Pachythecca* were parts of the same plant. A partial fusinization of his *Pachythecca* and *Prototaxites* specimens indicates, in his opinion, that for some period of time the dead plants had not been immersed in water. Either they have been washed ashore or the water receded from their habitat. A third, according to him least likely, explanation is that it concerned land plants. In a later phase the fossilization took place in water under reductive conditions, during which the remains became pyritized. According to him the fossils in question were, consequently, at least once redeposited, and submitted to two successive stages of fossilization.

For further details and literature I refer to Jonker (1979) who himself held the opinion that the plants occurred in dense vegetations, tightly packed in muddy tidal flats or lagunes, temporarily emerged and at other times partly or totally submerged as the transport of rhodophytalean spermatia, carpospores and tetraspores require submerged conditions. He also expressed that in all probability the same way of life — water plants adapted to periods of drought and permanently or periodically completely or partly emerged — is to be attributed to the also stout and solid stems of *Taenioerada dubia* K. et W., a rather enigmatic plant but occurring in association with *Prototaxites*.

On the basis of chemical analyses Niklas (1976a) came to the conclusion that *Prototaxites loganii* Dawson (the common Early Devonian species) was either a land plant or a water plant adapted to long periods of drought. He isolated from the fossils a number of compounds considered inconsistent with algal biochemistry. His first conclusion is in accordance with Jonker's deductions, the second one, however, is in direct contradiction to an attribution to Rhodophytes. Also on the basis of organic chemical constituents Niklas (1976b) emphasized an algal affinity of *Pachythecca* which is in accordance with Jonker's view and might point to a development of cystocarps under submerged conditions.

When we evaluate the published indications of a terrestrial or of a partially

emerged nature, we may state that no value is to be set upon:

1. the solid, firm cauloids, as large and solid seaweeds even occur in modern times, especially among Phaeophytes. It, however, opens the possibility for an adaptation to periods of drought;

2. the cuticularization, which term was used for the resistant nature of the outer surface and of the tetraspore wall. A similar pseudo-cuticle and spore coat occur in many recent algae, submerged Rhodophyta-Nemalionales included;

3. conductive tubes, which occur in extant submerged Phaeophytes as well, and probably in a number of larger seaweeds belonging to other algal groups.

With regard to the last item, some tubes in *Prototaxites*, and apparently in *Foerstia* as well show annular thickening though no proof exists that these "tracheid-like tubes" were lignified. According to Schopf "they can be of diverse significance and derivation" and he doubted whether "they have anything to do with vascular protoxylem" as the internal organization is different from that of vascular plants. Gray and Boucot (1979), however, notwithstanding Schopf's arguments persist in their opinion that the "Nematophytales" have been terrestrial and that the "tracheid-like cells" had, in that connection, a functional significance regardless of their occurrence in different plant groups, just as it is true that tracheids may have arisen independently in the major plant divisions.

At the time as I moulded my concept with regard to the life form of *Prototaxites* — being rhodophytalean plants occurring tightly packed in tidal flats or lagunes, temporarily emerged and at other times submerged — into concrete form, I discussed this by letter with J. M. Schopf, who replied "... Your comments about *Prototaxites* are most interesting. I think may be, I would suppose facultatively at least, that they could invade territory well above

sea. One occurrence in Maine shows large scattered stems in a coarse cobblestone conglomerate on the slopes of Mt. Katahdin with no trace of anything marine... And I will not have any reservations about accepting an alliance of *Prototaxites* with the red algae. I think the red algae got a big lead on other kinds of plants during the Early Paleozoic and may have more or less completed their necessary environmental adaptations that time. We have had "fucoids" in disrepute for some time but the fact is that some of the forms deserve detailed study....".

My line of thought regarding the problem of the rise of land life in the Early Devonian is as follows. An existent tendency (Jonker, 1976, 1977a, 1977b) in the plant life to invade the land, was effective only after the atmospheric conditions made land life possible, and could be effective only with those plants that were firm and solid and more or less resistant against desiccation. This advantages those seaweeds that possessed an algal conductive system. The occurrence of coenocytic or septate tubes alone, either non-conducting or conductors of water or assimilates is, however, no proof of life under terrestrial conditions. Hence we may expect early land invading plants with the larger Rhodophyta and Phaeophyta.

The advantage over them, however, had those plants that when submerged, in the younger Silurian, had developed a stele. These plants are usually called primitive Psilophytes and the Psilophytes have finally been successful in invading the land and in starting an evolution in the new environment giving off evolutionary branches to Lycopods and ferns.

The land-invading algae have, apparently, not been very successful as their organization proved to be not too suitable to real land life. Unsuccessful competition with successful, more viable Tracheophytes which invaded the shore, may have caused their extinction after a relatively short existence.

## REFERENCES

- BRZYSKI, B. (1976). *Sporogonites chapmanii*, *Prototaxites lafontii*, *Prototaxites* sp. and *Pachytheca* sp. from the Devonian of Suskowola near Radom (Central Poland). *Acta Palaeobot.*, 17: 3-16.
- GRAY, J. & BOUCOT, A. J. (1971). Early vascular plants: Proof and conjecture. *Lethaia*, 10: 145-174.
- GRAY, J. & BOUCOT, A. J. (1979). The Devonian plant *Protosalvinia*. *Lethaia*, 12: 57-63.

- JONKER, F. P. (1976). Evolutionary tendencies in the Plant Kingdom since Devonian times. *Trans. Bose Res. Inst.*, **39**: 19-23.
- JONKER, F. P. (1977a). Der Tendenzbegriff: eine Anschauung gerichtet auf die Evolution im Pflanzenreich. *Ber. Deutsch. Bot. Ges.*, **90**: 391-396.
- JONKER, F. P. (1977b). The tendency concept: A view illustrated by the principal evolutionary steps in the Plant Kingdom. *24th Sir A. C. Seward Mem. Lecture*. Birbal Sahni Institute of Palaeobotany, Lucknow, India. pp. 1-9.
- JONKER, F. P. (1979). *Prototaxites* in the Lower Devonian. *Palaeontographica*, **171B**: 39-56.
- NIKLAS, K. J. (1976a). Chemotaxonomy of *Prototaxites* and evidence for possible terrestrial adaptation. *Rev. Palaeobot. Palynol.*, **22**: 1-7.
- NIKLAS, K. J. (1976b). Morphological and ontogenetic reconstruction of *Parka decipiens* Fleming and *Pachythea* Hook. from the Lower Old Red Sandstone, Scotland. *Trans. R. Soc. Edinb.*, **69**: 483-499.
- SCHOFF, J. M. (1978). *Foerstia* and recent interpretations of early vascular plants. *Lethaia*, **11**: 139-143.