NOTES ON BELGIAN SPECIMENS OF *SPOROGONITES*

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ABSTRACT

Specimens of *Sporogonites exuberans* from the Lower Devonian of Belgium are shown to be borne by a presumed thallus-like structure. The general habit of the plant and lack of vascular tissue suggest bryophytic rather than psilophytic relationships.

DURING the summer of 1958 I enjoyed the privilege of collaborating with Professor Suzanne Leclercq in a study of certain of her excellent collections of Middle Devonian plants from eastern Belgium. In order to extend my knowledge of Lower and Upper Devonian floras several days were devoted to an examination of the rather vast collections in the Brussels Natural History Museum that have been gathered in recent years by Dr. Stockmans. These collections are among the finest to be found in any institution today for the geologic period they represent and are deserving of far more time than I was able to devote to them. However, my attention was particularly attracted to certain specimens of *Sporogonites* which seemed to shed some light on the habit of this interesting but problematical genus and it seemed desirable to record these observations without further delay. I am grateful to Dr. Stockmans for granting me permission to describe and illustrate several specimens in the Brussels collections and to Professor Leclercq for the use of her laboratory and photographic facilities.

Sporogonites exuberans was first described by Halle in 1916 and was discussed in further detail in 1936, his account being based on specimens from the Lower Devonian of Norway. A second species, *S. chapmani*, was described by Lang and Cookson (1930) from the early Devonian Walhalla series of Victoria. Their fossils consist of a slender stalk 0·75 mm. wide, unbranched, bearing a capsule-like structure which tapers to a rounded point. The capsule itself is 2·5 mm. wide and 5 mm. long, or 7·5 mm. including the widened region of the stalk. They also recognized *S. chapmani* forma *minor* for specimens with a smaller capsule, its diameter being 1·5 mm. and the length, including the flared portion of the stalk, is about 5 mm. They were unable to demonstrate spores or cellular structure; if correctly attributed to *Sporogonites*, the chief interest in these specimens lies in the greatly extended geographical range. Since then Cookson (1949) has described somewhat smaller sporangia from the Lower Devonian of Lilydale, Victoria, which are doubtfully referred to *Sporogonites*. Croft & Lang (1942) have described specimens from the Lower Old Red sandstone of Wales in which they were able to demonstrate the presence of spores which average about 20 μ in diameter and the presence of stomata in the epidermis of the upper part of the stalk. Belgian specimens have been described by Lang (1937) and Stockmans (1940) and these will be considered in further detail below.

The now rather well-known Norwegian specimens described by Halle consist of a pyriform sporangium borne on a slender unbranched stalk. He was able to demonstrate that the lower half of the sporangium is sterile while the upper half consists of a multi-layered wall, the cell structure of which was well preserved in part, and a dome-shaped mass of spores. The central core is not preserved but it is thought that a columella was originally present. The spores measure 20 to 25 μ and were numerous in what was probably a single-chambered sporangium; the mode of dehiscence is unknown.

In his first detailed account of the fossil Halle (1916a) inclined towards the view that it was most closely allied with the bryophytes but in 1936 he expressed the feeling that " it appears on the whole probable that *Sporogonites* represents part of a Pteridophyte belonging or related to the Psilophytales ". This shift in opinion resulted largely from the discovery of the Rhynie plants and their influence on morphological thought, and in particular, to the supposed similarity of *Sporogonites* to *Horneophyton* with its columelate sporangium. It is also pertinent to the present account to note that Halle figured a " thallus-like " fragment (1936, PL. 4, FIG. 7) tentatively attributed to *Sporogonites* and he noted that " it suggests comparison

with the rhizome of *Rhynia* or, perhaps even more strongly, with the curious protocorm-like rhizome of *Hornea* (*Horneophyton*)". The fossil referred to is actually a very small fragment and I think inadequate to the comparison mentioned.

Sporogonites exuberans was first recorded from Belgium by Lang in 1937 and on the basis of admittedly minor differences he referred to the Belgian specimens as *S. exuberans* forma *belgica*. In 1940 Stockmans mentioned it and figured several specimens in his study of the Lower Devonian plants of Belgium. All of the specimens considered in the present account are from the Emsien (upper) division of the Lower Devonian and were collected at the Bois de Bescaille quarry at Estinnes-au-Mont which is located shortly east of Mons.

In going through the 16 trays of *Sporogonites* specimens in Dr. Stockmans' collections, my attention was drawn particularly to the parallel arrangement of the sporangium-bearing stalks, a feature that may be clearly noted in all of the specimens figured herewith. Dozens of specimens present this arrangement, far too many to be accounted for by mere chance aggregation. Lang noted this feature on the single specimen at his disposal and in referring to the axes (sporangiophores) he commented that " Their close association, parallel position and similar direction seem against chance carriage of isolated specimens but there is nothing to show the complete form and mode of growth of the plant " (1937, p. 2). After observing this feature in dozens of specimens I could not avoid the suspicion that the parallel arrangement (*see especially* FIG. 4) implied attachment to some other plant organ. In going back through the collections a second time several specimens were found which confirmed this suspicion beyond a doubt. It is only fair to note that the collection deserves more careful study than I was able to devote to it and, in view of what is now known, further collecting would certainly be appropriate.

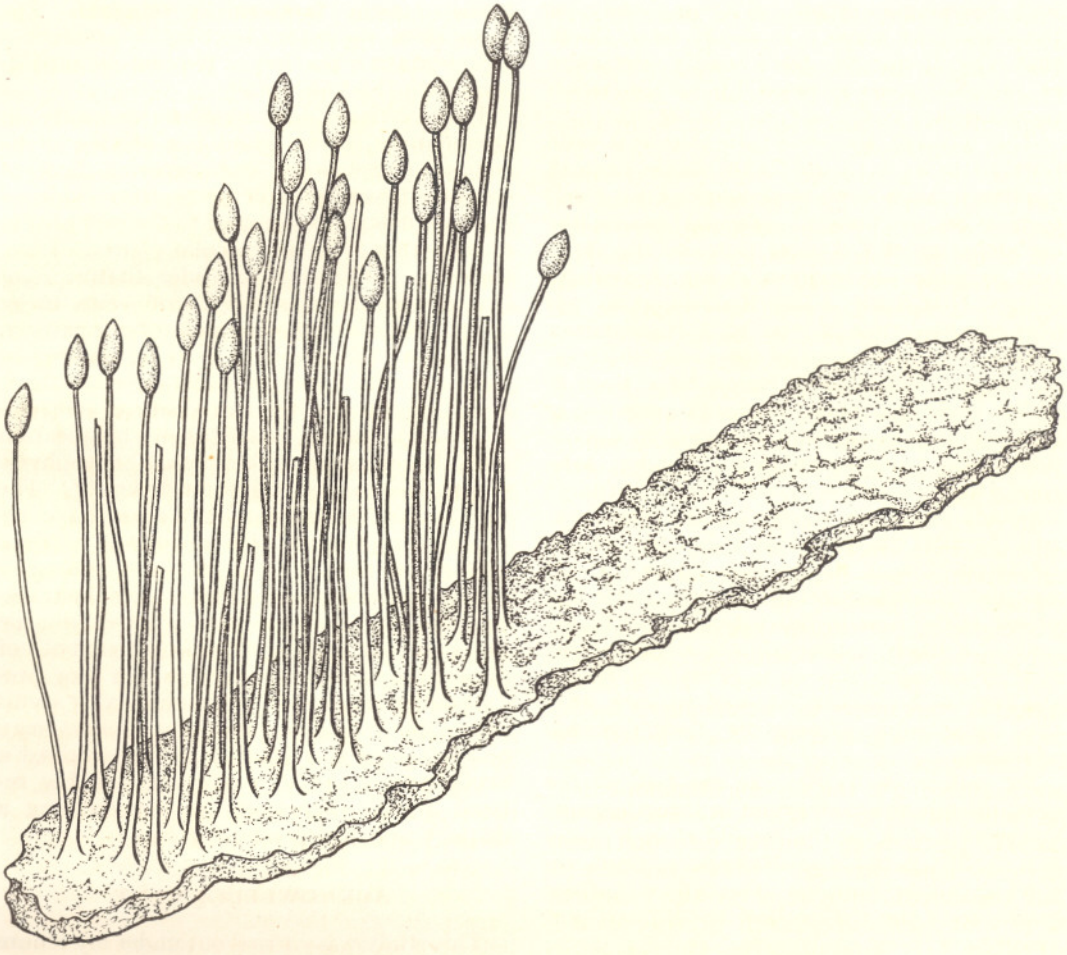
The plant impressions are black against a grayish black shale which renders effective photographic illustration rather difficult. They were photographed under glycerin, having been coated first with a very thin film of cellulose acetate (" peel ") solution to prevent the rock from absorbing the glycerin and becoming discoloured. It seems most convenient now to consider the specimens individually. The numbers are those of the Paleobotanical Department, Brussels Museum of Natural History.

No. 23437 (FIG. 1). This is included to show the sporangia of which six or seven are evident on the upper half of the specimen. Although quite a number of specimens in the collection contain sporangia, there are a great many which do not; a further discussion of this point will be taken up below. There is some variation in the size of the sporangia but, in so far as comparison is possible, I see no reason to question the identification of the fossils with *Sporogonites exuberans*. It is to be hoped, however, that specimens may eventually be found in Belgium which will allow a more detailed comparison with the structurally preserved Norwegian ones.

No. 24108 (FIG. 4). This shows especially well the parallel alignment of the unbranched sporangiophores and is typical of many specimens in the collection. It is difficult to follow a single sporangiophore through its entire length although it probably could be accomplished by careful excavation with fine steel needles. However, the aggregation as a whole is about 10 cm. long and reached to the edge of the specimen so it seems safe to assume that the stalks attained a length somewhat in excess to this figure.

No. 23480 (FIGS. 5, 6). This specimen displays the attachment of the sporangiophores to the plant organ in question particularly well. Figures 5 and 6 are identical and show the fossil slightly reduced in the former and slightly enlarged in the latter, as indicated in the caption. It seemed desirable to include an untouched photo (FIG. 6) while the other has been employed to indicate clearly the outline of the structure to which the sporangiophores are attached. The dotted line in Fig. 5 indicates the margin of a carbonaceous film (to the left) with numerous sporangiophores attached along the lower half; in the following discussion the " carbonaceous film " will be referred to tentatively as a *thallus*. The left margin of the photo is the broken edge of the specimen so that its extent in that direction cannot be determined. Thus, that portion of the thallus that is preserved is 14 cm. long and 3 cm. broad at the widest point (A) where it is lobed.

No. 24113 (FIGS. 2, 3). These two figures present this specimen in the same fashion as the previous one. In Fig. 2 the dotted line represents the natural limit of the thallus and along this line it may be noted that there are numerous sporangiophores which all point



TEXT-FIG. 1 — Restoration of a portion of a plant of *Sporogonites exuberans*.

directly up. It is probable that the entire area below the dotted line represents thallus but it is somewhat " spotty "; that is, there are breaks or open places in which no carbonaceous film is present which I interpret to represent lack of preservation. If this is the case, that portion of the thallus that is preserved measures approximately 5 × 7 cm. At this point attention may be called to the dark area at the bottom of Fig. 4; it is very possible that this too represents a portion of a thallus but it is not clearly defined and does not seem to merit further comment.

DISCUSSION

The observations recorded above leave much to be discovered about *Sporogonites* but I believe we are in a somewhat better position to speculate on the habit of the plant.

It is pertinent first to refer to the stalks or sporangiophores which bear the terminal sporangia. In previous accounts Halle, Lang and Stockmans have noted the absence of any evidence of vascular tissue. There are many thousands of these stalks on the numerous specimens in the Brussels collections and I examined many of them with this point in mind and found no trace of a vascular strand. Admittedly, there is little carbonaceous matter remaining, yet the total absence of any indication of such a strand seems significant in view of the fact that Halle found none in his specimens, yet was able to demonstrate considerable cell structure in the sporangium. Although there are numerous specimens

with sporangia intact, a great many of the stalks lack them. It would seem likely that the sporangia were easily detached or possibly were released by an abscission mechanism.

The form of the structure that has been referred to as a thallus is of course critical. Specimens such as those shown in Figs. 3 and 6 show no evidence of vascular tissue; the carbonaceous film is quite thin and the apparent irregular preservation in Fig. 3 seems to suggest that it was a thin thalloid organ. If one assumes that it was of a rhizomatous nature, the dimensions of the preserved fragments are such that it would have been of rather great diameter, seemingly quite out of proportion to the slender nature of its appendages, the sporangiophores. I have been somewhat concerned over the fact that large numbers of specimens display the characteristic parallel alignment of the stalks yet in relatively few is the thallus preserved. It would seem almost certain that the latter was intact at the time of deposition of the plants and as a likely explanation it is postulated that the thallus was of a relatively fragile stucture and quickly decayed leaving only the stalks and occasionally their terminal sporangia.

At only a few points can the base of the sporangiophore be observed in direct organic connection with the thallus and at such places it is slightly flared; the other sporangiophores were in all probability attached at various points over the thallus and these basal portions have been destroyed.

It is thus tentatively assumed that the plant was a nonvascular one consisting of an irregularly shaped, flat thallus which bore many slender upright axes, the sporangiophores, which were, in turn, unbranched and bore a single, terminal sporangium. The restoration shown in Text-fig. 1 presents a representative portion of a plant in accordance with this concept.

It is certainly precarious to speculate on the affinities of this plant but in view of its general morphology and apparent lack of vascular tissue we have no positive evidence that justifies its assignment to the psilophytes or any other group of vascular plants. I am, therefore, inclined to consider that it is of bryophytic affinities but there seems to be no purpose in attempting a closer comparison. Just as we are finding a growing number of vascular plants in pre-Carboniferous times which, because of their diversity of morphology and anatomy, render their classification difficult, it seems likely that bryophytic plants once existed in greater diversity. The well-known discoveries of Walton have revealed the presence of liverworts of modern affinities in the Carboniferous and Neuburg's recent contribution (1956) demonstrates conclusively that mosses existed in the Permian. It is thus very likely that both of these groups of bryophytes had a long pre-Carboniferous history. In summary, it seems reasonable to assume that *Sporogonites* may be considered as a plant that had attained a bryophytic level of evolution, possibly related to the liverworts or representing a distinct and independent group.

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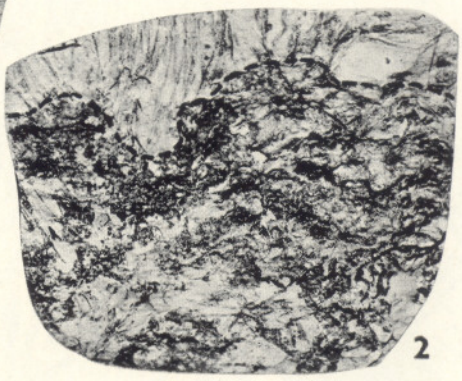

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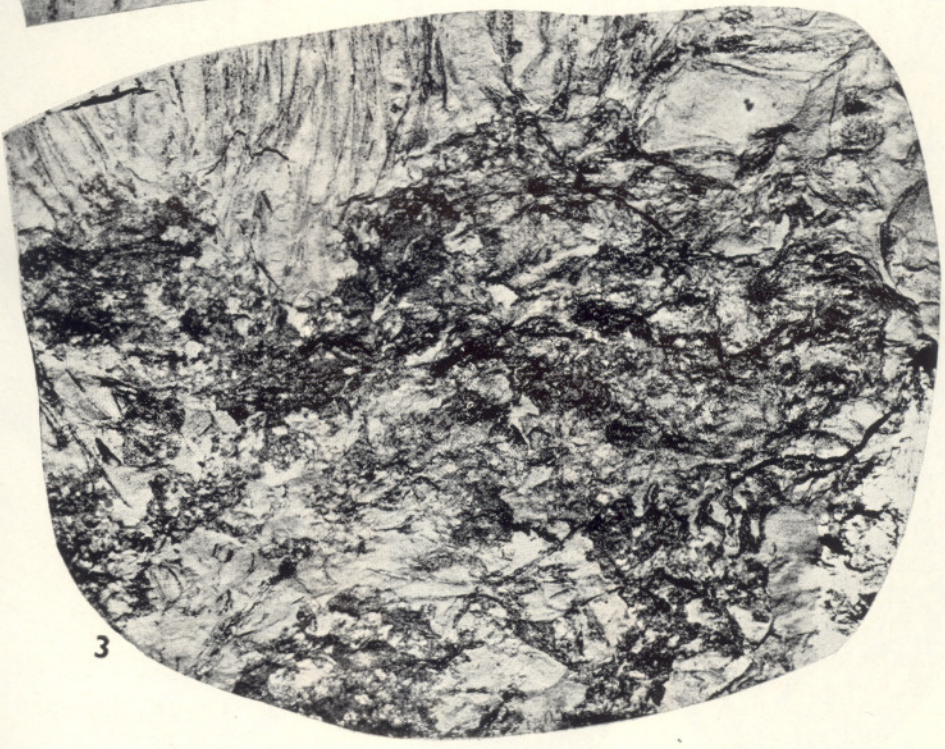

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EXPLANATION OF PLATES

Sporogonites exuberans Halle. Specimen numbers are those of the Paleobotanical Department, Natural History Museum, Brussels.

PLATE 1

1. A specimen showing sporangia. No. 23437.
2. Portion of a plant: thallus below dotted line and basal parts of sporangiophores above. No. 24113.
3. The same enlarged.

PLATE 2

4. Specimen showing parallel alignment of sporangiophores, a characteristic feature of many specimens in the Brussels collection. No. 24108.
5. Portion of a plant showing thallus to the left of the dotted line and sporangiophores to the right. No. 23480.
6. The same enlarged.