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ON *SPOROGONITES* HALLE : A MORPHOLOGIC, TAXONOMIC AND PHYLOGENETIC APPRAISAL

D. C. BHARADWAJ

Birbal Sahni Institute of Palaeobotany, 53, University Road, Lucknow-226 007, India

ABSTRACT

All the information regarding *Sporogonites* Halle, available from descriptions and illustrations by various authors has been analysed, evaluated and synthesized to arrive at a composite picture of the plant. It has been concluded that *Sporogonites* is the earliest known bryophyte which had a hygrophyllous, liverwort-like, gametophytic (?) thallus bearing a large number of sporophytic (?) stalks (setae) terminating into obovoid or clavate capsules with an upper, continuous, spore-containing part and a lower, sterile, photosynthetic portion. The structure and organization of the capsule combines features of the two primitive subclasses of Musci but without columella. The presence of lignified vascular tissue in the stalk or the thallus has not been substantiated. An emended diagnosis and a reconstruction based upon the synthesized information has been given for the genus.

Key-words — Bryophyte, *Sporogonites*, Morphology, Taxonomy, Phylogeny, Lower Devonian.

साराँश

स्पोरोगोनाइटिस हाले का आकारिकीय, वर्गीकरणिक एवं जातिवृतीय आकलन – दिनेश चन्द्र भारद्वाज

विभिन्न लेखकों के वर्णनों एवं चित्रों से स्पोरोगोनाइटिस हाले के बारे में प्राप्त जानकारी इस पौधे के संग्रथित स्वरूप को समझने के लिए विश्लेषित, मूल्यांकित तथा संश्लेषित की गई है। यह निष्कर्षित किया गया है कि स्पोरोगोनाइटिस प्राचीनतम् विदित ब्रायोफ़ाइट है जिसका आर्द्रतोद्भिदी, लिवरवर्ट-सदृश, युग्मकोद्भिदी थैलस अनेक बीजाणु-उद्भिदी ?वृन्त (स्फोटिकावृन्त) उत्पन्न करता है जिनके अग्र सिरे प्रतिअंडाकार अथवा मुदगराकार संपुटों में परिवर्तित हो जाते हैं। इन संपुटों का ऊपरी भाग पूर्णतया बीजाणुयुक्त तथा निचला भाग अबंध्य एवं प्रकाश-संश्लेषी होता है। संपुट की संरचना एवं संगठन मसाई के दो आद्य उपसंवर्गों के लक्षणों से मिलते हैं परन्तु ये स्तम्भिका रहित हैं। वृन्त अथवा थैलस में लगुडित संवहनी ऊतक की उपस्थिति अभिपुष्टित नहीं है। संश्लेषित जानकारी पर आधारित इस वंश के लिए एक संशोधित निदान भी प्रस्तुत किया गया है।

INTRODUCTION

SPOROGONITES Halle happens to be among the few earliest spore bearing plant fossils known from the Lower Devonian, preceded only by *Cooksonia* Lang and possibly *Baragwanathia* Lang & Cookson, which have been known from the uppermost Silurian (Downtonian). However, while *Cooksonia* and *Baragwanathia* are established as vascular plants having a conducting strand of annular tracheids, *Sporogonites* is considered to be non-vascular.

Halle (1916a) found the nearest analogy of *Sporogonites* in the sporogonia of the Bryophyta. He compared its organization comprising a stalk bearing at the tip a swollen organ containing spores with the seta and capsule respectively, as found in the Bryales. However, three decades later, Halle (1946), inspite of having held earlier that " both in habit and in the relation of sporogenous to sterile tissue, the massive capsule of *Sporogonites* more closely resembles the sporogonium of a Bryophyte than any known type of Pteridophytic sporogonium " and " even if it should be proved that the capsule

of *Sporogonites* does not possess a columella, this would not necessarily invalidate the comparison with a sporogonium since a columella is not always present even in the Bryales (*Archidium*)", changed his inclination in favour of psilophytalean affinity for *Sporogonites*. He presumed that the "thallus-like" fragment from which stalks like those of *Sporogonites* ensued, suggests comparison with the protocorm-like rhizome of *Hornea* (*Horneophyton*). Summing up his final view, Halle (1936, p. 622) said, "it appears on the whole probable that *Sporogonites* represents part of a Pteridophyte belonging or related to the Psilophytales but its resemblance to a sporogonium may at the same time be regarded as significant, especially in combination with the columellate sporogonium of the better preserved *Hornea lignieri*".

Andrews (1960) while examining the Belgian specimens of *Sporogonites* in Dr Stockman's collection noted the striking parallel arrangement of stalks. This led to his suspicion that such a condition implied attachment of the stalks to some other plant organ. Upon re-examination of the specimens, he could recognize the stalks attached to a carbonaceous film of significant extent which he tentatively named, "thallus". Finally he summed up assuming tentatively that *Sporogonites* was a non-vascular plant consisting of an irregularly shaped flat thallus which bore many slender, upright, unbranched axes each bearing a terminal sporogonium. His conclusion has been (1960, p. 88) "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".

Sporogonites appears to have been the most ancient, likely bryophytic fossil to be of special interest for one who is both a Bryologist and a Palaeobotanist. Hence, I have attempted to synthesize here, the information available from the works of various authors for a fuller understanding of the nature and structure of the genus. In this appraisal of its morphology and taxonomy I have accepted the various author's conclusions that their material does belong to one genus where *prima facie* all the specimens do seem to agree in organization with the type, rather closely.

DESCRIPTION

Sporogonites Halle, 1916a

Remarks — Halle (1916a) gave a short diagnosis of *Sporogonites* and in another publication (1916b) a fuller account along with the diagnosis quoted below:

Diagnosis —" Spore-producing body consisting of a simple-stalk and terminal capsule. Stalk 0·5 mm in diameter and up to at least 50 mm long faintly striated longitudinally. Capsule elongatedly obovoid or clavate, 6-9 mm long and 2-4 mm in diameter in the thickest part, with a rounded apex and a tapering base, gradually merging into the thicker upper part of the stalk. Basal part of the capsule with probably 12 elevated striae passing over into the stalk. The thickest part of the capsule with probably 12 longitudinal furrows of varying strength, half of the number being broader and deeper than the others, and the two kinds regularly alternating. The lower part of the capsule sterile throughout, the upper part consisting of three different zones: a wall of several layers of cells, a thick sporogenous tract forming a complete dome covering the top of the columella. Spores tetrahedral-globular, 0·020-0·025 mm in diameter, with a cutinized wall showing a fine dotted sculpture".

Type Species — *Sporogonites exuberans* Halle, 1916a.

Type Horizon & Locality — Lower Devonian; Lake Roeragen, Norway.

Type Material from Roeragen, Norway — *1. Halle, 1916b, pl. 3, figs 10, 11* — The specimen is a completely flattened impression. It consists of a ±50 mm long and 0·5 mm broad stalk and an elongatedly obovate capsule, 6 mm long and 2·5 mm in broadest width. The stalk and capsule are not sharply demarcated as the latter gradually widens from the top of the stalk. The fine striations borne on the stalk continue into the basal part of the capsule as 4 to 5 furrows are seen in surface view. Near about the middle of the capsule there is a distinct break separating the apical rounded part from the basal part.

2. Halle, 1916b, pl. 3, figs 12, 13 — The specimen is an impression. The capsule is short, pear-shaped imperceptibly passing into the stalk. The basal half of capsule shows four longitudinal ridges with 3 grooves

in between them and these continue from middle of the capsule down into the stalk.

3. Halle, 1916b, pl. 3, fig. 14 — This specimen was found to be petrified and has provided valuable information regarding the inner structure of the basal part of the capsule and the stalk (Halle, 1936, pl. 3, figs 8-10; pl. 4, figs 5, 6). The surface of the basal half of the capsule shows 4 ridges and 3 intervening grooves.

4. Halle, 1916b, pl. 3, fig. 15 — The specimen has been found to be preserved in a carbonized state with its apical part containing spores. The stalk and the capsule are seen continuous with each other. In this specimen also the basal and the apical part of the capsule are separated by a break.

This specimen was subsequently found partly petrified and hence, amnable to sectioning which has revealed (Halle, 1936, pl. 3, figs 2-7) well preserved internal structure especially of the capsule wall and the columellaless sporiferous cavity enclosed by the wall. Between the apical and the basal part of the capsule a deep and wide channel is evident on the two lateral sides.

5. Halle, 1916b, pl. 3, figs. 16, 17 — In this specimen the apical part of the capsule is almost hemispherical and separated from the basal part by a distinct constriction. The latter seems, though not very clearly in the photographs, to have had ridges and grooves on the surface.

In the apical part of the capsule, Halle (1916b) found a greenish brown mass of spores similar to those found in the specimen figured by him in pl. 3, fig. 15. Halle (1916b) describes the spores from both these specimens to have been perfectly similar, 0·020-0·025 mm in diameter and of tetrahedrally rounded type. The spore surface is stated to be having a fine, dotted sculpture.

Synthesis of Descriptive Features — A meticulous study of the type material by Halle (1916b, 1936) has provided most of the morphological information about the capsule which happens to be the principle object of interest and also about the anatomy of the apical part of the stalk. The important descriptive features of the genus as revealed from the study made by Halle are:

1. The capsule is an elongated obovate, or pear-shaped body with distinct constriction, channel or breakage near or slightly above the middle part; one end of the capsule is free and the other tapers down into a slender stalk.

2. The basal half of the capsule shows on the surface in one plane, a number (4 to 6) of striations (furrows) continuing down on to the stalk.

3. The apex of the capsule is generally more rounded than conical.

4. In the two petrified specimens with inner structure of capsule preserved partly, the basal part is seen to be composed of parenchymatous cells. In one of the specimens (Halle, 1936, pl. 3, fig. 9), the basal sterile zone is well below the median constriction. The apical part is full of spores. The sporiferous region is bounded by a peripheral wall of a number of layers of small and thick-walled cells. The cells of the inner layers of the wall are comparatively thinner-walled and larger than in the outer layers. The outer cells of the peripheral wall appear vertical and palisade-like with curious papilla-like projections in the top portion but as one traces them down the capsule laterally these are progressively isodiametric and ultimately rectangular as seen in a vertical section.

5. The capsule cavity is wholly filled with spores. There is no evidence of any mass of sterile tissue or even an empty space projecting into the sporiferous region.

6. The spores are 20-25 μm in diameter and circular in polar view but pyramido-hemispherical in equatorial view. The tetrads appear to be tetrahedral. The spores have " fine dotted sculpture " on the spore surface.

7. The stalk is slender and the longest known attached to a capsule, measures 30 mm in length. The basal end not being attached to any other structure, this length may not represent the total extent.

8. From a petrified specimen described by Halle (1936, pl. 3, figs 8-10; pl. 4, fig. 6) the internal organization of the stalk is now known to have consisted of an outer zone of narrow thick-walled cells surrounding a core of larger cells which are thin-walled and only slightly elongated. In some of these cells, apparently in the peripheral region of the central strand, granulation or pitting was observed by Halle (1936, pl. 4, fig. 6), but he considered it to be probably an accidental feature. He concluded that

neither in the solid basal part of the capsule nor the stalk, could any vascular elements be recognized.

9. Associated with the capsules of *Sporogonites exuberans*, Halle (1916b) found a curious "thallus-like" fragment with a number of stalks arising from it. These, like the capsule stalks, showed no lignified conducting tissue. The surface of the thallus-like fragment is rough, possibly with some sort of tomentum.

Additional descriptive information from other studies—Halle (1916b, pl. 3, figs 23-32) described one capsule which also was included by him in *Sporogonites exuberans*. However, for reasons detailed later in this paper, it has been considered preferable not to identify it with *S. exuberans* and instead designate it as cf. *Sporogonites* sp. (cf. Stockmans, 1940).

In this specimen the capsule is petrified and lacks the stalk but of which an unmistakable occurrence is indicated by a straight 30 mm long, elevated streak of a ferruginous substance attached to the base of the capsule. The capsule is elongatedly obovoid measuring 9 mm in length and 3·5 mm in maximum width a little above the middle part from where the width decreases both ways. The apex of the capsule appears to have broken, yet a roundly conical shape of the apex is surmisable. The basal part bears 5-6 fine ridges. On the surface of the wide middle part five longitudinal furrows, three alternatingly wide and shallow and two narrow and deep, are seen on the exposed half. The whole circumference might be bearing 12 furrows. As seen in a v.s. of the upper part of the capsule, the lower fourth part has uniform structure consisting of vertically elongated cells as seen in its middle. In the upper three fourth part, three zones can be distinguished. The outer zone is the capsule wall composed of several layers of vertically elongated cells. This zone domes the sporiferous middle zone which in turn domes a structureless central column. The limit between the sporiferous and the central zone is not very marked. The spores have been inferred to measure 20 μm on average.

Lang and Cookson (1930) identified two specimens as *Sporogonites chapmani* and *S. chapmani* cf. *minor*, from the Walhalla Series, eastern Victoria in Australia, surmised to be of early Devonian age. Both the specimens are incrustations but only the external features are known.

S. chapmani Lang & Cookson — The specimen is about 2·5 cm long. The slender unbranched stalk is straight and about 0·75 mm wide. The stalk widens gradually to form the basal region of the terminal capsule-like structure. The basal part is 2·5 mm long and the upper part is 5 mm long and 2·5 mm wide. The apical part of the capsule tapers to a rounded point. The widened region of the stalk exhibits on the surface exposed, longitudinally running, four ridges separated by shallow grooves. These ridges die out gradually, passing downwards on to the narrow stalk. There is a definite boundary between the base of the capsule-like body and the widened end of the stalk, the line indicating this being slightly convex downwards. The middle of the capsule shows breakage as if by crushing of the capsule during fossilization. The capsular portion seems to have a thick wall enclosing a continuous cavity. No spores could be recovered.

S. chapmani, f. *minor* Lang & Cookson is a smaller form agreeing in general organization with *S. chapmani*.

Lang (1937) described specimens of *Sporogonites* from Grès de Wépion, Belgium, as *S. exuberans* f. *belgica*. His best specimens showed typical stalks about 0·5 mm wide and up to 4 cm long lying more or less parallel and ending in capsules of 6-7×2 mm size. The preservation was poor.

Stockmans (1940) recorded *Sporogonites* from a number of other localities in Belgium. From Dave he found capsules of different sizes, one with a rounded apex being 3·75 mm wide and 10 mm in length. From Thuin, he has illustrated *Sporogonites* sp., a capsule distinctly divisible outwardly into a bluntly ovate upper part and an obovate basal part. The upper part bears 3 deep, long furrows on the surface in view, i.e. 6 furrows in circumference. In a specimen from 'Teinne aux pires' only the basal half with its four ridges in surface view has remained while the apical part is missing. In the rather richly represented locality of 'Estinnes-au-Mont' east of Mons, in a well preserved capsule he observed horizontal rows of flat epidermal cells arranged like bricks in a wall. In most of the capsules the ± middle, horizontal band is seen very well. Most of the capsules have a conical

tip. Stockmans examined the stalks for possible vascular tissue but found no trace of it.

Croft and Lang (1942) studied a few specimens from Llanover a short distance south of Abergavenny, occurring in the Senni beds of England and Wales which are of late Lower Old Red Sandstone (Siegenian) age. In one of the specimens, an over 1 mm wide and 3 mm long piece of stalk widens to form the basal region of the terminal capsule which is 3·5 mm broad and 7 mm long. Out of this length about 2 mm high is the sterile basal region and 5 mm high fertile region. The line of junction between the two regions is clearly demarcated. The apex is rounded. The basal region is free from any organic crust and three ridges are seen distinctly in surface view. There are some indications of the fertile region having been bounded by a fairly thick wall. In the second specimen, the fertile region has a mass of 17·5-25 μm sized spores with reticulate sculpture of low muri. They were also able to see sparingly distributed simple stomata with two, curved guard-cells in an epidermis of elongated cells having pointed ends, on the upper part of the stalk and its passage into the basal portion of capsule, In a third, much smaller, pear-shaped specimen the apex of the fertile region is very broadly rounded. The basal sterile part is only 1·5 mm high and the fertile part is 2·5 mm high.

Andrews (1960) examined the rich, Belgian collections of *Sporogonites* made by Stockmans near Estinnes-au-Mont from beds of Emsien (upper) division of the Lower Devonian. His study revealed some specimens where the erect stalks were apparently attached to a carbonaceous film — thallus. In a few cases the base of the stalks, in direct organic connection with the thallus, was slightly flared. Stalks were seen arising beyond the margin of the thallus on one side. The thallus was measured to be 14 cm long and up to 3 cm wide in one case and 5×7 cm in another case. The thallus shows irregular preservation which according to Andrews (1960) suggests that it was thin, thalloid organ. He further surmised that the thallus was a relatively fragile structure and quickly decayed leaving only the stalks. In one case the aggregation of stalks measured up to 10 cm leading to the assumption that they could be even longer. Andrews has also interpreted the absence of capsule from many of the stalks to be due to the possibility of the capsules having been easily detached or released by an abscission mechanism. However, this does not seem to be true in view of the varying lengths of stalks found attached to the capsules.

Morphotaxonomic Synthesis — The various studies of *Sporogonites* tend to lead to the view that the plant had a flat basal thallus composed of a soft and easily decomposed tissue presumed to be thin and parenchymatous. The thallus bore many, erect, uprising, slender, invariably unbranched stalks quite close to each other.

The stalks appear to have occasionally had a flared base attached to the thallus. The stalk apparently lacked vascular strand in the conventional sense. However, it had a cortex of thicker-walled, narrower cells and a central strand of thinner-walled, broader cells. Presumably the compact cortex gave the strength to more than 10 cm long yet only 0·5-1·0 mm thick slender stalks to stand upright. The central strand of thin-walled cells might have conducted water from and to the developing sporogonium. The sort of pitting seen in some walls of the cells in the central strand might have been a reality and possibly aiding in the conduction of water through a very much simplified or primitive conductive mechanism. The central strand continued right into the basal sterile part of the capsule. The epidermis on the widened apical part of the stalk was composed of vertically elongated cells with sparsely distributed, small stomata having two kidney-shaped guard cells. The stomata were presumably functional and their presence suggests that at least partly the stalk was aerial and the stomata permitted gaseous exchange presumably for photosynthesis and moisture economy regulation.

The basal, sterile part of the capsule and the widened top of the stalk, bore 3-6 ridges alternating with grooves, as seen in one view. It is presumed that such ridges were present as well on the side not in view. In some cases the ridges and grooves or furrows have been seen on the apical part of the capsule. The basal sterile part has always been noted to be shorter vertically as compared to the sporiferous upper part. Curiously, though characteristically, the median

transverse region of the capsule shows a deep channel (Halle, 1936, pl. 3, fig. 2), a constriction, a band or a breakage along or above the basal sterile region. The apex of the capsule is rounded in *S. exuberans*, conical in *S. chapmani* and usually acutely conical in *S. exuberans* f. *belgica*.

Internally, the upper part of the capsule was wholly full of spores in tetrahedral tetrads as well as free, without any indication of a columella or any structure akin to it. The capsule wall was several cell layers thick peripherally. The cells were small and thick-walled outwards and larger and thin-walled inwards. The epidermal cells were vertical and palisade-like with papilla-like projections in the apical region of the capsule but progressively isodiametric to rectangular laterally in the case of *S. exuberans*. Stockmans has illustrated horizontally rectangular cells of the capsule epidermis in surface view.

The spores of *S. exuberans* are pyramido-hemispherical with a circular equator. They have been seen united in tetrahedral tetrads. No trilete mark has been noted by Halle or Croft and Lang (1942) although a faint indication of it is seen in the spore on the extreme right basal corner of the figure given by Halle (1916b, pl. 3, fig. 20). The surface sculpture has been described by Halle (1916b) as finely dotted but described and illustrated by Croft and Lang as reticulate with low muri. The difference in the two descriptions might be of interpretation only. The spores have been found to measure about 20 μm (17·5-25 μm).

Regarding the mode of dehiscence, there seems to be some indication in the type specimen with the apical half of the capsule having broken off along the median transverse area during fossilization and lying separated from the remaining basal portion. This condition is also indicated in both the specimens illustrated by Lang and Cookson (1930, pl. 11, figs 11-14) as *S. chapmani* and *S. chapmani* f. *minor*. In some other specimens as well (Stockmans, 1940, pl. 4, figs 6, 8), there are indications of the same phenomenon. Moreover, in a Belgian specimen (Stockmans, 1940, pl. 8, fig. 2) the capsular part appears to have been separated and shed before fossilization resulting into preservation of only the basal sterile part bearing longitudinal striations. Obviously there is evidence suggestive for a kind of operculate dehiscence of the capsule. So far, no annulus or other structural indication of the mode of dehiscence has been observed in any of the longitudinal sections available. Thus, it is apparent that the capsule was basically cleistocarpic. However, there seems to have been initiated a localization of the region of dehiscence in the median portion where irregular gelatinization of the middle lamella between the peripheral cells might have occurred late, as the capsule ripened, to effect a sort of opercular dehiscence. The jagged, free, lower margin of the capsule top in the type specimen seems to indicate such a likelihood. One might as well conjecture another possibility if the deep furrows on the apicular, fertile region of the capsule in *Sporogonites* sp., and cf. *Sporogonites* sp. played a part in longitudinal dehiscence of the capsule comparable to that in *Andreaea*.

In view of the above described enhancement in the knowledge of *Sporogonites*, the generic diagnosis given by Halle (1916a) is emended here as follows:

Sporogonites Halle emend.

Emended Diagnosis — Plant consisting of a basal, flat thallus apparently of thin and delicate tissue bearing on its tomentaceous surface numbers of slender, leafless, unbranched, parallel stalks, 0·5 to 1·0 mm in diameter and upto 10 cm or more in length. The base of stalk expanded. The cortex of the stalk made up of narrow, elongated thick-walled cells and the interior composed of larger, thin-walled, pitted cells. Stalk surface faintly striated *vis-a-vis* ridged longitudinally. Stalk tip widened to form the base of a longish obovoid, or clavate capsule with a rounded to acute-conical apex. Widened stalk-tip bearing sparsely distributed simple stomata on the surface and grooves and ridges in continuation with those on the capsule. The basal, sterile part of the capsule demarcated variously along its boundary with the wider fertile, apical part. Capsule full of tetrahedral spore tetrads as well as free circular spores when preserved, protected by a several cell layers thick peripheral wall. Spores having finely reticulate sculpture. Capsule cleistocarpic with occasional breakage round the middle part.

Sporogonites Halle emend., as known at present is represented by the following taxa.

1. *S. exuberans* Halle — Recorded from Roeragen (Lower Devonian), Norway and Llanover (Lower Devonian), Great Britain.

2. *S. chapmani* Lang & Cookson — Recorded from Early Devonian, Australia.

3. *S. chapmani* var. *minor* Lang & Cookson — Recorded from Early Devonian, Australia.

4. *S. belgica* Lang emend. — Emended Diagnosis: Thalli forming mats and stalks arising from its surface slender, unbranched, bearing oval capsules with acutely conical tips. The apical and basal part separated by a median, wide band.

Lectotype — Stockmans, 1940, pl. 4, fig. 8 from Lower Devonian of Belgium.

Sporogonites sp.— Recorded from Lower Devonian of Belgium.

cf. *Sporogonites* sp.— Recorded from Roeragen (Lower Devonian), Norway.

Affinities

There is hardly any doubt that *Sporogonites* lacks a conductive strand of the kind which characterizes the accepted vascular plants. Obviously, it cannot be identified as a member of the Pteridophyta. The presence of columella in the sporiferous cavity has not been established and the thallus-like fragment is really an irregular, structureless, delicate expansion rather than something similar to the protocorm-like rhizome of the kind found in *Horneophyton*. These facts negativate any reference of *Sporogonites* to Psilopsida.

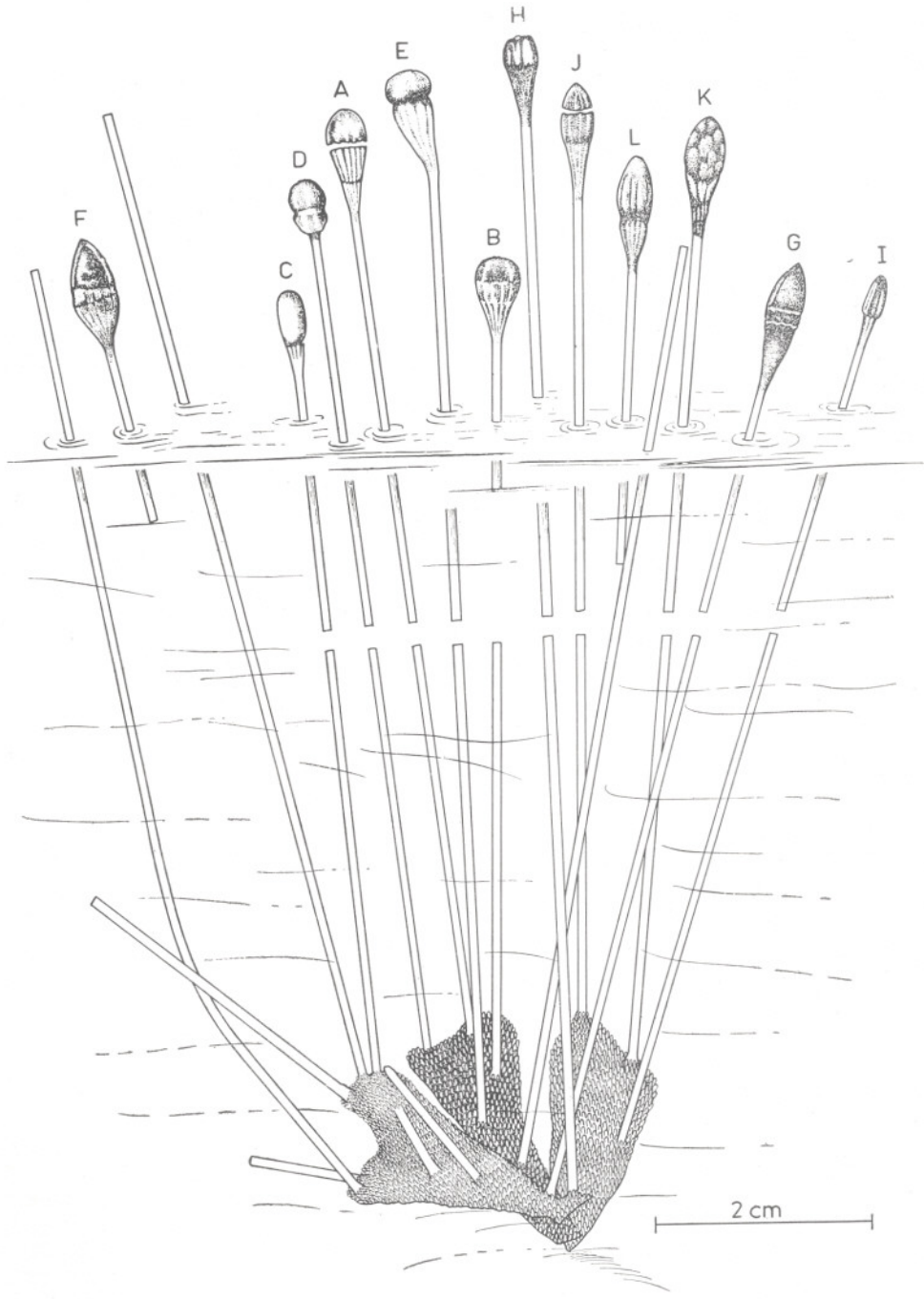
As understood at present, *Sporogonites* is assumed to have had a prostrate, expanded, non-vascular thallus with papillate or lamellate upper surface. From this surface a large number of thin, unbranched stalks each bearing terminally an obovoid, ovaloid or clavate capsule partly filled with spores, arose. Now we may consider the morphology and homologies of each of the three components separately.

Thallus — The thallus-like fragment illustrated by Halle (1916a, 1936) appears to have a definite shape. There seems to be a narrowed posterior end, gradually expanding and apparently dividing into two unequal portions anteriorly. This shape agrees more or less with the usual shape of a liverwort frond. The stalks are seen arising from the anterior as well as the posterior portions. In the Belgian specimens, where Andrews (1960) has identified a carbonaceous film as the remanent of the thallus, no shape is recognizable. Its surface seems to be uneven. In the Norweigan specimen as well, Halle (1916a) noticed a peculiar ruggedness of the surface apparently caused by a sort of tomentum. Such a surface could be due to the presence of closely-set, small papillae (cf. *Dumortiera velutina*) or lamellae (cf. *Anthoceros punctatus*). The rather shapeless thallus of Belgian material might be due to overlapping, crowded, filmy fronds which on fossilization were so closely appressed as to lose their outline and the whole mass appears like a sheet or mat. The few uncovered spaces between the fronds have presumably given the " spotty " appearance noted by Andrews (1960) in one of the films.

Stalks — Even, an about 2·5 cm long frond illustrated by Halle (1916a, pl. 3, fig. 36) as many as 8 or 9 stalks appear to be arising from various locations on it. Obviously the thallus was a prolific producer of stalks *vis-a-vis* fruiting bodies. The stalks are slightly wider at the base but otherwise slender and unbranched in spite of their pretty good lengths which in similar psilophyte sporangial stalks (e.g. *Cooksonia*) would often be forked. Internally the stalk had a sort of tissue differentiation with a central column of thinner-walled longish cells surrounded by a several cells deep cortex of thicker-walled elongated cells. The apical part of the stalk progressively widened and continued further up as the sterile basal part of the capsule. The tissue was continuous, without any internal or external separation of the apical part of the stalk with the basal part of the capsule. The surface of the apical, wider portion had elongated epidermal cells with tapering ends and simple stomata having two guard-cells, sparsely distributed among them.

The stalk with its internal tissue differentiation and the terminal, widened sterile portion having stomata, has similarities with the seta in the Bryales as it continues into the apophysis of the capsule.

Capsule — The capsule body has a basal sterile part and a fertile portion above it. The fertile part has a multi-cell layered wall surrounding continuous cavity filled up with small, pyramido-hemispherical, reticulate



TEXT-FIG. 1 — Composite reconstruction of *Sporogonites* plant with the basal thalloid part having tomentatious surface and a large number of erect, unbranched, slender stalks arising from it; all the various kinds of capsules of *Sporogonites* described form the genus so far: **A-E.** From Norway (Halle, 1916b, pl. 3, figs 10, 11A, 12, 13B, 14C, 15D, 16, 17E), **F-I.** From Belgium (Stockmans, 1940, pl. 4, figs 8, 6; pl. 8, fig. 2; pl. 6, fig. 2), **J.** From Australia (Lang & Cookson, 1930, pl. 11, figs 11, 12), **K.** From Britain (Croft & Lang, 1942, pl. 11, figs 52-54), **L.** From Norway (Halle, 1916b, pl. 3, figs 24, 25).

sculptured spores having originated in tetrahedral tetrads suggesting occurrence of reduction division in their development. A little above or along the base of the fertile part, the capsule shows slight constriction, a channel or a band which is the likely region for breakage in the wall presumably for its dehiscence and the liberation of spores. The multi-cell layered capsule wall in the fertile upper part with a sterile basal part having stomata on the surface and absence of elaters, are moss-characters (the apparently continuous spore cavity is more like a ripe *Sphagnum* or *Andreaea* capsule).

In cf. *Sporogonites* sp., the longish obovoid capsule and the presence of an empty central column internally, recalls the conditions met with in ripe capsules of *Sphagnum* (Nawaschin, 1897) ready for dehiscence. As the sun dries a ripe capsule, due to transverse contraction of the wall cells, it becomes elongated and internally the delicate columella shrivels and the empty space thus created is filled up by air. On analogy, it seems that the central, tissueless column in cf. *Sporogonites* sp., was also an air-filled space. But whether there was a delicate columella which likewise shrivelled up is not certain. However, unlike *Sphagnum* the capsules of *Sporogonites exuberans*, as seen in two petrified specimens, did not have a central columella. In the case of *Sporogonites* sp., and cf. *Sporogonites* sp., the longitudinal furrows on the capsule surface in the apical part recall the lines of dehiscence in the capsule of *Andreaea*, although it is still not known if the wall was thinner or its cells were thin-walled along the furrows in the fossils specimens.

CONCLUSION

It must be recognized that there is much that we do not know about *Sporogonites*, such as the relation of stalk to the thallus which can be only imagined to be that of a thalloid gametophyte to a sporophyte stalk in a bryophyte. We know nothing about the internal structure of the capsule at an immature stage. We do not even have an absolute proof of its manner of dehiscence. However, what-so-ever we do know, makes it reasonable to regard *Sporogonites* as a bryophyte. Presumably it is like a moss combining features of the three living subclasses of Musci, as its unbranched stalk with the terminal capsule would suggest from its structure as well as organization. They apparently represent the seta and capsule of the moss sporophytic generation with the foot embedded in the prostrate thalloid structure which if gametophytic, obviously was liverwort-like as far as conjecturable from the known facts. Thus, *Sporogonites* appears to have been a unique bryophyte combining a liverwort gametophyte with a moss sporophyte. This fossil tends to suggest that the two major divisions of bryophyta could have had a common ancestor.

Reconstruction — A composite reconstruction of the plant is given in Text-fig. 1. It is based upon the organizational details of various specimens already discussed in this paper. Regarding the environment of these plants they are conjectured to have lived submerged in water. The delicate, filmy, parenchymatous thallus bearing still more delicate papillae or lamellae on the surface could have survived only under water in the Lower Devonian times when the other vegetation being mostly small-sized could not have provided highly shaded environment. Another fact pointing to hygrophyllous environment is the very slender yet pretty good length of the stalks bearing the capsules at their tips. These stalks could not have remained standing upright unless most of their lengths were submerged in water. However, the apical part of the stalk with stomata on the epidermal surface, indicates that to have been aerial. These environmental deductions have been incorporated in the reconstruction.

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