OBSERVATIONS ON THE SPORANGIA OF HORNEOPHYTON LIGNIERI (Kidston and Lang) BARGHOORN AND DARRAH 1938.*

A. A. BHUTTA

Department of Botany, University of the Punjab, New Campus, Lahore.

Introduction

The Rhynie Chert (Aberdeenshire, Scotland) was discovered by Dr. Mackie in 1912 who in 1916 published the first illustrations of sections of two of the plants without naming or describing them. Thereafter, Kidston and Lang (1917-21) in their successive papers on the Rhynie flora described four vascular plants and a number of Thallophytes:

The vascular plants described are:-

- (a) Rhynia gwynne-vaughani
- (b) Rhynia major
- (c) Hornea lignieri
- (d) Asteroxylon mackiei

Barghoorn & Darrah (1938) pointed out that the name *Hornea* was pre-occupied by a living member belonging to the family Sapindaceae and they proposed the name *Horneophyton* for this plant.

Kidston & Lang (1920) recorded that the epidermal cells, of sporangia of *Horneophyton lignieri*, were thickened on their outer tangential and radial walls. Furthermore, they regarded these broad flat tipped sporangia as being indehiscent and indicated certain irregularities in the sporangial walls which they accounted for by accidental contraction, probably due to dryness.

El-Saadwy (1966) has recently described a few sporangia of *Horneophyton*, larger in size than those described by Kidston & Lang (1920), which had branched columella. He noticed some apparent differentiation between the epidermal cells of the broad apical ends which are better preserved than those of the lateral walls which have stomata. In contrast to Kidston & Lang (1920) he thought that dehiscence probably took place by means of an apical slit on the "broad concave ends". However, no detailed description was given but emphasized the need for further investigation for arriving at a plausible conclusion.

^{*} This paper is a part of a Ph.D. thesis submitted to the University of Wales, Cardiff, United Kingdom.

28 A.A. BHUTTA

It is interesting to note that Lemoigne (1966) has recently described a "bryophytic sporogonium" from the Rhynie deposit, which is similar in size and shape to a *Horneophyton lignieri* sporangium (having a single columella) but apparently differing from it in having an "operculum" and in containing larger spores measuring upto 150µ.

In view of the conflicting reports in palaeobotanical literature it was decided to study the structure of apical region of *Horneophyton lignieri* sporangium and its possible mechanism of dehiscence.

Materials and Methods

The material used in the present studies was collected over a period of years by Dr. A. G. Lyon who generously handed this over to the writer for further investigation. This consisted of a selection of Rhynie Chert blocks containing sporangia of *Horneophyton lignieri*.

- (a) Peel sections of sporangia were prepared as described by Joy. Willis & Lacey (1956) using 40% "Analar" Hydrofluoric acid for etching and 0.075 mm. cellulose acetate film (Clarifoil) for peeling. All the peel sections were mounted in "Duramount" 244 (Cormack Chemicals).
- (b) Ground sections of sporangia were prepared on an electrically driven Model C.H.3 "Cutrock" machine adjustable both for grinding and cutting purposes.
- (c) Photomicrograph and critical observational work were both carried out with the aid of binocular Zeiss Photomicroscope. Negatives were made on Ilford Pan F films and developed in "Acutal" (Paterson). From these, untouched prints were subsequently made.

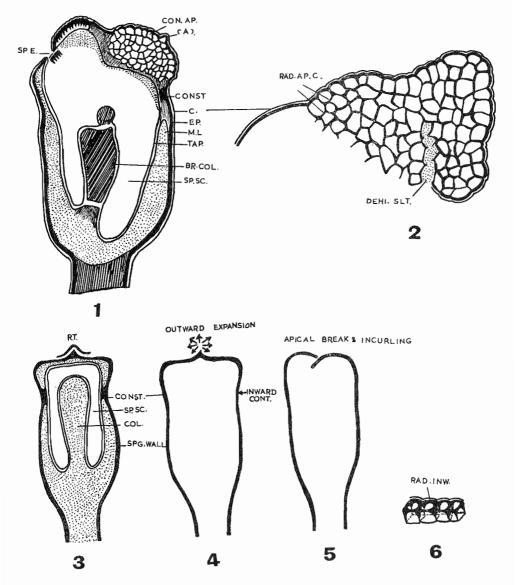
All the ground and peel sections and slides are preserved in the Botany Department, University College of South Wales and Monmouthshire, Cardiff, United Kingdom.

Results and Discussion

(A.) The structure of the apical region of the sporangium of Horneophyton

During the course of present investigations a large number of *Horneophyton* sporangia were studied both from peel and ground sections. They confirm to the descriptions of Kidston & Lang (1920) and El-Saadwy (1966) in their external features.

In an empty bicolumellate sporangium one of the top broad ends was found to possess a "dome" shaped appearance (see Fig. I and Text-fig. I). A break seen in

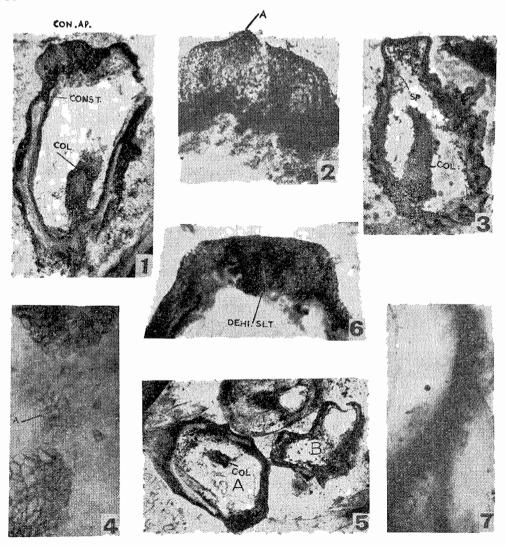


EXPLANATION OF TEXT-FIGURES

Text-figure I. A median L.S. of *Horneop¹ yton lignieri* bicolumellate sporangium. (A), raised cell of the "dome"; BR. COL., branched columella; C, cuticle; CON. AP., "convex apex"; CONST., constriction; EP., epidermis; M.L., middle sporangial wall; SP.E; split end and SP. SC.; spore sac. (Based on

Text-figure 2. Drawing of a portion of the apical region of a dehisced sporangium. DEHI. SLT.; dehiscence slit; RAD. APC, radially thickened cells. (Based on fig. 6).

Text-figures 3-6. Showing diagramatic representation of mechanism of dehiscence in *Horneophyton* sporangium. COL., dolumella; CONST., constricted region: INWARD. CONT., inward contraction; R.T., region with inwardly projected "wedge" shaped thickenings; RAD. INW. radial and inward projections; SP. SC., spore sac and SPG. WALL, sporangial wall.



EXPLANATION OF PLATE

A median L.S. of an empty bicolumellate sporangium of *Horneophyton lignieri* X 13. COL., columella; GON. AP., convex apical end: CONST., constricted region. (Ground section No. 19). Fig. 1. Figs. 2 and 4. The vonvex apical end in fig. 1 is shown enlarged X 55. A., raised apical cell which is encircled by few cells in (X60) fig. 4 (Ground section No. 19).

- A median L.S. of another sporangium. The top end is slightly curled in. X 20. COL., columella and SP., spores. (Ground section No. 26).

 Section of sporangia X12. Sporangium A shows top broad end while the second sporangium B Fig. 3. Fig. 5.
- which is branched. One of the branch is with concave end and the second is with flat top end (Ground section No. 27).
 The top end of the sporangium A shown in fig. 5 is enlarged X 50. DEHI. SLT.; dehiscence
- Fig. 6.
- It shows "wedge" shaped thickenings X 180. It can also be seen in fig. 6B. Fig. 7.

a como con trapago a traballa de la como traballa de la como de la

31

the walls of other branch of the sporangium would suggest that spores probably escaped through this opening. The "domed" apex of the first branch shows no evidence of a break and appears to be in its original condition. A few branched columellate sporangia of the plant have also been described by Kidston & Lang (1920). It is however, interesting to note that El-Saadwy (1966) found a sporangium which had upto five branches of the columella.

The sporangium is 4 mm. long and 2 mm. broad with a dome (A) 1 mm. in diameter and 0.7 mm. in height. A raised central cell at its tip is distinctly visible. This is encircled by 8-10 cells. The remaining epidermal cells of the dome are similar to those of the broad flat or concave ends of sporangia described by Kidston & Lang (1920) and El-Saadwy (1966). The central region of the top end, around the raised cell, has a radius of 0.2 mm, is about 0.1-0.2 mm. high. The "wcdge" like radially projected thickenings are particularly clear in this region (see Fig. 5B and 7).

The epidermal cells of the sporangium apex are angular (25-70 μ in size) without air spaces. Their outer tangential walls are thickened (see Figs. 1-6 and Text-figs 1-2) while their radial walls nave inwardly projecting "wedge" shaped thickenings (see Fig. 7) on the other hand th inner tangential walls of epidermal cells are thin. The cells at the top seem to be relatively more rigid. There are however, no stomata present here. The cells along the basal sides, of the "dome" shaped structure, become slightly elongated (44 x 87 μ) and are more like the epidermal cells of the lateral walls of the sporangium which are quite elongated and variable in size (usually 150-200 μ long and 40-50 μ broad). El-Saadwy (1966) has reported the occurrence of stomata in this place. The epidermal cells of the lateral walls also have thickenings (see Fig. 5A) that project inwardly (cf. Kidston & Lang, 1920, El-Saadwy 1966) but not forming peculiar "wedge" shaped structures found in the cells at the top "broad ends".

The lateral sporangial walls towards the base of the "broad tip" are usually constricted. The out-lines of these cells in the constricted region become indistinct (see Figs. 1, 3 and 5A). Above this region the sporangial cells gradually widen out again to their original dimension upto the periphery of the top end, before becoming slightly thinner again in the middle of the top region. This has been observed in a number of specimens and is particularly clear when the upper end is viewed in median longitudinal section (see also Kidston & Lang, 1920; Plate IX, Fig. 59).

Most of the dehisced sporangia when seen in median longitudinal sections (Fig. 5B) have somewhat concave tops (cf. El-Saadway, 1966) while others especially those containing spores have more or less flat tops (see Figs. 3, 5,A and 6 also cf. Kidston & Lang 1920, Plat IX, Fig. 59). It seems likely that both the "flat" and "concave" appearances of the top ends have resulted either from incurling of the top region following dehiscence or may be due to the plane of section. It is very

Jan 37 32 + below White resided

32 A.A. BHUTTA

difficult to demonstrate this feature by peel sections alone and perhaps El-Saadwy (1966) did not notice this character because he did not have access to ground sections of sporangia of the plant. A sporangium apex cut in longitudinal or in oblique median longitudinal section has a wall which appears nearly as broad as that of the rest of sporangial wall giving it a somewhat "flat" appearance. In a median longitudinal section of a dehisced sporangium the top end will tend to look rather "concave". Some of the sporangia figured by Kidston & Lang (1920) contain spores and are probably undehisced. The sporangium shown (in Kidston & Lang, 1920; Plat IX, Fig. 58.) has a slightly convex rather than concave or flat apical region. Sections cut in a sub or oblique median longitudinal plane could result in an apex appearing flat.

(B) Probable Mechanism of Dehiscence

Kidston & Lange (1920) thought that the sporangia of the plant were indehiscent. While El-Saadwy (1966) assumed that a dehiscence slit occurred in the top broad "concave" ends but he was uncertain about the precise mechanism.

It is likely that sporangia of the plant underwent differential contraction (probably through drying cf. Kidston & Lang, 1920) particularly in the region of the lateral wall of sporangia just below the "dome". This may have set up stresses in the "convex" surface of the apex (where the cells are thickened both peripherally and radially) which eventually brought about splitting probably at more than three points.

As has been mentioned, the top cells are thickened at their outer peripheries and have inwardly projecting "wedge" shaped thickenings at their corners. The wall structure of these cells could account for their observed tendency to curl inwards after the breakage in the sporangial wall. In this way, the "convex" appearance of the tops of dehisced sporangia could be explained. The suggested dehiscence mechanism of these sporangia is shown diagramatically in Text-figures 3-6.

The specimen shown in Figure 1 and Text-figure 1 is undouhtedly a sporangium of *Horneophyton* although it shows certain resemblances with a bryophytic sporogonium in that it possesses a columella and an "operculum" like 'dome' shaped apex. A rather similar specimen with a single columella was also described from the Rhynie Chert by Lemoigne (1966) but it differed in the size of its spores which were stated to measure about 150 μ. In describing it he said, "Certes cet appareil sporifère a beaucoup de resemblances avec celui d'Horneophyton mais il en diffère quant à la dimension des spores". Lemoigne has not provided any magnification for his figure but on the basis of measurements given it has been estimated that it represents an enlargement of about X32. Although the illustration is of a rather poor quality, it is possible to distinguish dark bodies which seem to represent the spores. Assuming

the dimensions of the sporangium given by him correct, the largest spores in his figure measure about 65 μ . It seems likely, therefore, that he made an error in his measurements. As spore tetrads of *Horneophyton* do not exceed 80 μ in diameter in ground sections of sporangia (cf. Bhutta, 1969). His specimen does not, in fact, show any clear distinction between his supposed "operculum" and rest of the sporangium. The fact that there appears to be an "operculum" is only due to the oblique plane of section of his specimen. Moreover, it is imperfectly preserved (cf. Kidston & Lang, 1920, Plate IX, Fig. 59). The present comparison and evidence suggests that Lemoigne's (1966) "sporogonium" is probably just a sporangium of *Horneophyton lignieri*, but in order to confirm this, it would, of course be necessary to examine the actual specimen.

Acknowledgements

I am very much obliged to Prof. G.F. Asprey, University College, Cardiff for providing me with the facilities of work in his Department. Sincere thanks are due to Dr. A.G. Lyon for his advice, criticism and encouragement during studies. I also express my indebtedness to him for providing the material and making available to me his personal collection of literature.

I am also grateful to Dr. M.S. Zahur who very kindly read the manuscript.

References

- Barghoorn, E.S. and Darrah, W.C. 1938. *Horneophyton*, a necessary change of name for *Hornea*. Havard Univ. Bot. Mus. Leaflets, 6: 142-144.
- Bhutta, A.A. 1969. Studies in the flora of the Rhynie Chert. Ph.D. Thesis, University of Wales. (2 vol.)
- El-Saadwy. 1966. Studies in the flora of the Rhynie Chert. Ph. D. thesis, University of Wales.
- Joy, K.W.; A.J. Willis and W.S. Lacey. 1956. A rapid cellulose peel technique in Palaeobotany. Ann. Bot., N.S., 20: 835-837.
- Kidston, R. and W.H. Lang. 1917. On Old Red Sandstone plants showing structure from the Rhynie chert Bed, Aberdeenshire. Part I. *Rhynia gwynne-vaughani*, Kidston and Lang. Trans. Roy. Soc. Edin., **51**: 761-784.
- 1920. On Old Red Sandstone plants showing structure from the Rhynie chert Bed, Aberdeenshire. Part II. Additional notes on *Rhynia gwynne-vaughani*, Kidston and Lang; with description of *Rhynia major*, n.sp., and *Hornea lignieri*, n.g.n.sp. Trans. Roy. Soc. Edin., **52**: 603-627.

34 A.A. BHUTTA

- ————1920. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Abserdeenshire. Part. III. *Asteroxylon mackiei* Kidston nd Lang, Trans. Roy. Soc. Edin., **52**: 643-680.
- -----1921. On Old Red Sandstone plants showing structure from the Rhynie chert Bed. Aberdeenshire. Part IV. Restoration of the vascular cryptogams and discussion of their brearing on the general morphology of the Pteridophyta and the origin of the organisation of Land plants. Trans. Roy. Soc. Edin., 52: 831-854.
- Lemoigne, M.Y. 1966. Sur un sporogone de Bryale D'age Devonian. Bulletin Mensuel, de la Société Linneenne de Lyon. 35 me. Année, No. 1, 13-16.
- Mackie, W. 1916. The rock series of Craigbeg and Ord Hill, Rhynie, Aberdeenshire. Trans. Edin. Geol. Soc. 10: 205-236.