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PERIDERMAL ACTIVITY (WOUND REPAIR) IN AN EARLY DEVONIAN (EMSIAN) TRIMEROPHYTE FROM THE GASPÉ PENINSULA, CANADA

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ABSTRACT

An unattached axis, cf. *Psilophyton dawsonii*, is cellularly preserved in pebbles found adjacent to those that include *Psilophyton dawsonii* Banks, Leclerq & Hueber, 1975. The axis shows clear evidence of periderm formation in part of its surface that may have been chewed by arthropods. It seems to be the oldest evidence yet discovered of any kind of periderm formation. Its age is late Emsian, a stage that extended from 374 to 370 million years ago.

Key-words — Peridermal activity, *Psilophyton*, Early Devonian, Gaspé Peninsula, Canada.

सारांश

कनाडा में गॅस्पे प्रायद्वीप से एक प्रारंभिक डिवोनियन (ऍम्सियन) ट्राइमेरोफ़ाइट में परिचर्म-सक्रियता (घाव-पूर्ति) – हार्लन पी० बैंक्स

जिन गुटिकाओं में साइलोफ़ाइटॉन डॉसोनाई बैंक्स, लैक्लर्क एवं ह्यूबर, 1975 पाया जाता है उन्हीं के समीपवर्ती अन्य गुटिकाओं में साइलोफ़ाइटॉन डॉसोनाई से संदर्भित एक असंलग्न अक्ष कोशिकीयत :परीरक्षित है। यह अक्ष अपनी सतह के एक भाग पर आँशिक परिचर्म बनने का स्पष्ट प्रमाण व्यक्त करती है जो कि शायद आर्थोपोड्स द्वारा चबायी हुई हो। अभी तक अन्वेषित किसी भी प्रकार की परिचर्म निर्माण का यह प्राचीनतम् प्रमाण प्रतीत होता है। इसकी आयु उत्तर ऍम्सियन है जो कि 37 करोड़ 40 लाख से 37 करोड़ वर्षों तक विस्तृत एक चरण है।

INTRODUCTION

THE publication of a preliminary report in the Surange Commemorative volume on early evidence of peridermal activity is an appropriate tribute to Dr Surange because it provides another link in the chain of evidence that documents evolution among early vascular plants. This type of evidence has marked Dr Surange's long and productive career. His data have enabled him to make new interpretations and to contribute significantly to our understanding of fossil plants. One hopes his contributions will continue following retirement as Director of the Birbal Sahni Institute of Palaeobotany.

There is another justification for this report. It records the first appearance of a biocharacter, periderm. Thus it records an innovation in the fossil record. Until now the oldest periderm was that found in the presumed progymnosperm *Triloboxylon arnoldii* Matten, 1974 (syn. *T. halli* Scheckler & Banks, 1971) of Middle Devonian, mid-Givetian age. The periderm in *Triloboxylon* is apparently natural periderm (Esau, 1977, p. 192, fig. 12.1). The present report of wound periderm in cf. *Psilophyton dawsonii* suggests a much earlier origin of peridermal activity, if not natural periderm. Two current papers have suggested the use of such innovations in biostratigraphic studies of Devonian plants. Chaloner and Sheerin (1979), in a general paper on Devonian macrofossils, analyzed the time of appearance of 42 vegetative and reproductive characters. Their bar diagrams, illustrating the appearance of these innovations in successively younger strata, demonstrate clearly the potential usefulness of single characters in biostratigraphy. Banks (1980) used time of appearance of biocharacters to supplement a biostratigraphic zonation of Upper Silurian-Devonian strata that is based on assemblages of genera of megafossils. He starts with a *Cooksonia* Assemblage Zone I (late Ludlow-Gedinnian) and continues to a *Rhacophyton* Assemblage Zone VII (mid Famennian-mid post Famennian Devonian). The biocharacters are useful especially when one has a collection of unidentifiable axes from continental strata of uncertain stratigraphic position. If the collection includes some secondary xylem, the strata can, at present, be no older than Eifelian-early Givetian (Assemblage Zone IV); or if it includes seeds, the strata are no older than mid-Famennian (Zone VII). The biocharacters thus extend the usefulness of Plant Generic Assemblage Zones.

Obviously precise times of first appearance of biocharacters will change as new localities are visited, as techniques are applied more widely to the collections, and as better preserved specimens are found. The present report of peridermal activity under a wound, in plants from Emsian strata, is an example. There is even earlier evidence of wounding. Kidston and Lang (1921, pp. 832-835) observed cellular reaction to wounding in *Rhynia gwynne-vaughanii* and *R. major*. The Rhynie chert in which *Rhynia* occurs is now regarded as of Siegenian-Emsian age, whereas cf. *Psilophyton dawsonii* of the present paper is from latest Emsian strata. *Rhynia* does not, however, show any evidence of the production of radial rows of tabular cells that could be called periderm. Regardless of changes that may be made in the timing of these innovations, one still expects to see a gradual appearance of new characters in successively younger strata.

MATERIALS AND METHODS

Psilophyton dawsonii, the present material, and some as yet undescribed axes were found permineralized in limey cobbles that were included in coarse sandstones. The sandstones outcropped along a beach (Banks, Leclerq & Hueber, 1975). The organic matter (cell walls) of the plants is translucent brown in thin section and in peels. The matrix surrounding the axes is light gray, fine-grained limestone (calcilutite) (Hartman & Banks, 1980). The cell lumens are filled by calcite crystals and the unpreserved inner cortex of the axes is filled either by coarse calcite crystals or by lime mud similar to that which surrounds the axes. The slides used in the present study were made by standard coal ball peeling techniques. They are filed in the Cornell University Paleobotanical Collection under Type no. 263.

LOCALITY AND STRATIGRAPHY

The cobbles occur in cliffs along the south shore of Gaspé Bay, eastward from Douglastown, Province of Quebec, Canada. Additional details are given in Banks, Leclerq & Hueber (1975) and Hartman and Banks (1980). The cobble-containing strata belong to the *Grandispora* subzone of McGregor (pers. comm., 1979) or the *Psilophyton* Assemblage zone of Banks (1980). This places the cobbles in uppermost Emsian strata (McGregor, 1977). Palynological and megafossil zonations are compared in Table 1 of Hartman and Banks (1980).

DESCRIPTION

Psilophyton dawsonii is cellularly preserved (petrified) in calcite cobbles and pebbles. Many of its organs were preserved intact, in organic connection. Only its base (? rhizome) remains to be found. Some cobbles and pebbles are filled exclusively with *P. dawsonii* whose branches are attached at various levels along the stem; some enclose unattached lengths of axes that are indistinguishable from *P. dawsonii*, along with other axes that are as yet unidentified. A pebble of the latter type includes an axis here labelled only cf. *P. dawsonii*, because it is unattached. The pebble was peeled in order to trace an unidentified axis. An incidental by-product in those peels is a series of 28 transverse sections of the axis of cf. *P. dawsonii*. These peels encompass one entire surface wound that was repaired by the production of periderm (Pl. 1, fig. 1). The first peel shows one margin of the wound and the last shows the opposite margin. No longitudinal sections were made, nor can they be made now because the entire wound has been peeled.

The wounded axis, as preserved, is slightly elliptical in outline. Its longest diameter is 1·25 mm. The tangential extent of the wound as seen in Pl. 1, fig. 1 (area delimited by vertical bars) approximates 0·9 mm. It occupies approximately one third of the circumference of the axis. Hypodermal outer cortex composed of collenchymatous cells is the only tissue of the axis that is preserved. The thick-walled cells are called collenchyma because longitudinal sections of *Psilophyton dawsonii* and other unidentified axes regularly show their end walls to be transverse or slightly oblique and because the initiation of phellogen in the collenchyma shows that they were alive at maturity. The collenchyma cells are of varying sizes and appear to have rounded outlines. Examination of their apparent compound middle lamella shows that they were angular and fitted closely together. They are three to four cells in radial extent in the unwounded axis (Pl. 1, fig. 1). Inner cortex, phloem and xylem have been lost during preservation. Epidermis too is rarely preserved. The 28 peels (assuming perhaps 15 to 20 peels per mm) suggest that the vertical extent of the wound was 1·5 mm. If so, its outline was slightly elliptical, with its long axis oriented vertically.

Pl. 1, figs 1 and 2 illustrate peel no. 16, approximately half way through the wound. The axis as a whole appears to retain an elliptical outline, although the depth of the wound and the amount of secondary tissue produced give the impression that the outer cortex had sunken into the empty space left by the loss of inner cortex and phloem, tissues that typically are missing from *Psilophyton dawsonii* in these cobbles and pebbles. The wound is capped by necrosed cells (Pl. 1, figs 1, 2, horizontal arrows) filled with organic debris. This layer may represent a closing layer that formed after the wounding and prior to the initiation of phellogen. Below this layer thin-walled cork cells (phellem) are clearly distinguishable. Still deeper, but in the same radial rows, the cells are thicker-walled. They may be phelloderm. Two cells in which phellogen may have been initiated are indicated in Pl. 1, fig. 2 by arrows. These thicker-walled cells suggest that phellogen was initiated in the collenchyma of the outer cortex. Although the number varies in the different rows, there were sometimes seven of the thicker-walled and an equal number of thin-walled cells in one radial row.

Examination of Pl. 1, fig. 1 suggests the possibility that the wound may have been deeper from the center to its left margin than at its right margin. The unwounded cortex on the right appears to be continuous with that underneath the right margin of the wound where a few cells appear to be undivided and otherwise unchanged by the injury (Pl. 1, fig. 1, arrow). Their slightly sunken position relative to their normal position in an unwounded stem can be explained either by pressure from the newly forming secondary tissue or by some collapse during fossilization. To the left of these unmodified cortical cells the radial alignment of the innermost cells is either slightly distorted or possibly they are not peridermal cells, in which case the wound is shallower on the right side. Pl. 1, fig. 1 also demonstrates that the wound is shallower at its margins and deeper near the center. Similarly, the first and last peels of the series of 28 demonstrate a thinning of the wound at the margins at right angles to those figured here. Thus the three-dimensional shape of the wound and of the periderm was like that of a shallow dish. The total thickness of the periderm was about 0·5 mm.

DISCUSSION

Wounding in Devonian plants and periderm formation have both been the subject of recent publications. Kevan, Chaloner and Savile (1975) reviewed the wounds seen in *Rhynia* by Kidston and Lang (1921a) in their analysis of the interrelationships between early terrestrial arthropods and plants. Scheckler and Banks (1972) summarized the natural periderm they had found in *Triloboxylon*, *Tetraxylopteris* and *Proteokalon*. The present paper contributes to both subjects.

The wounds in *Rhynia* (Kidston & Lang, 1921a, p. 834) were dark, necrosed areas or areas in which the necrosed tissue had disappeared, leaving a cavity. Cells around the area were often enlarged, reoriented, and/or characterized by some thin walls that indicated recent mitotic divisions. All of these changes must have occurred prior to the death of the cells, and none is related to the fungal activity that is found elsewhere in the stems. The wounded areas varied from limited regions on the surface to large areas extending to the center of the stem. Neither Kidston and Lang nor subsequent authors seem to have observed rows of tabular cells such as characterized natural periderm (Esau, 1977, p. 184, fig. 12.1A; Scheckler & Banks, 1971) and wound periderm (Esau, 1977, p. 184, fig. 12.1B; present paper, Pl. 1, figs 1, 2). Thus the wounds in cf. *Psilophyton dawsonii* are unique among early Devonian plants.

The feature newly described here, a wound accompanied by wound periderm, is described as such because of the limited area it covers, approximately $0{\cdot}9 \times 1{\cdot}5$ mm on the surface and 0·5 mm in depth. Further, the radial rows of mostly tabular cells reflect the kind of stimulus that a wound produces as an initiator of mitotic activity. Finally the shallow area involved is comparable to small wounds observed among extant plants. None of our wounded axes other than the one described here shows any sign of a natural periderm. Nor did we find any natural periderm in the original material of *Psilophyton dawsonii* (Banks, Hueber & Leclerq, 1975). Instead, one always finds only the small surface area of disrupted cells underlain by radial rows of peridermal cells.

It is inappropriate in a short note to review the extensive literature on wounding and its repair. Reference to Esau (1977, chapt. 12) and the papers cited at the end of her chapter on periderm will perhaps suffice. It is clear that wounding produces a chemical stimulus capable of initiating mitotic divisions. It is unclear how far this stimulus can be transmitted radially from cell to cell, if at all. The precise alignment of divisions in one cell with similar divisions in adjoining cells implies the emplacement of some sort of pattern over all cells in an area. The limited extent of periderm formation in many wounds implies that another chemical control is exerted to bring about a cessation of activity. Some plants, at least, require that the surface of a wound be sealed over by the accumulation of necrosed cells and by living cells that become cutinized and suberized. That layer in the present plant may be represented by the dark debris on the surface of the wound (Pl. 1, fig. 2, horizontal arrows). Phellogen can be formed after the sealing by the initiation of mitotic activity in living, though apparently mature cells. In the present case the phellogen probably formed in cells at the inner edge of the cortical collenchyma tissue.

The cause of the wound in *Psilophyton* is worthy of speculation. Kidston and Lang (1921b, p. 895) attributed the wounds in *Rhynia* (other than those resulting from obvious fungal activity) to prolonged exposure to external factors associated with volcanic activity. Kevan *et al.* (1975) reviewed the evidence for terrestrial animals, small, simple arthropods, in the Rhynie chert and concluded that the damage may have been caused by chewing or by sucking animals. This seems a more likely explanation of the wounds in *Rhynia* than various external factors. *Psilophyton*, unfortunately, is not accompanied by any animalian remains. Nevertheless chewing arthropods that were extant at the time seem to be the most likely explanation for its lesions. A possible sequence of events can be postulated. First, epidermis and cortex were damaged over a small area by chewing arthropods. Some cells died and some may have produced suberin and cutin, resulting in an outer closing layer. Then innermost collenchyma cells of the outer cortex were stimulated to mitotic activity, forming a phellogen. This meristem then produced the phellem and phelloderm cells, illustrated in Pl. 1, figs 1 and 2. Evidence that the wound was mostly superficial and repaired rather quickly is provided by the normal-appearing cortex beneath one edge of the periderm (Pl. 1, fig. 1, right side, arrow).

Natural periderm appears to have evolved at least by mid-Givetian, as shown by the presumed progymnosperm *Triloboxylon arnoldii* Matten, 1974 (syn. *T. halii* Scheckler & Banks, 1971). Its degree of complexity is such that discovery of natural periderm in older Eifelian strata probably awaits only the discovery of well-preserved specimens and the application of careful techniques to them. The present report of wound periderm suggests that at least the potential for natural periderm formation existed as early as Emsian (upper Lower Devonian strata) time. It also indicates that the hypodermal cells of *Psilophyton* were living at maturity and capable of resumption of meristematic activity (Esau, 1965, chart 14). Finally, the same evidence supports the original description of thick-walled cells in the outer cortex of *Psilophyton* as collenchyma and not sclerenchyma.

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REFERENCES

BANKS, H. P. (1980). Floral assemblage zones in the Siluro-Devonian, pp. 1-24, in Dilcher, D. and Taylor, T. N. (Eds) — *Biostratigraphy of Fossil Plants: Successional and Paleoecological Analyses*. Dowden, Hutchinson and Ross, Inc. Stroudsburg, Pa.

BANKS, H. P., LECLERQ, S. & HUEBER, F. M. (1975). Anatomy and morphology of *Psilophyton dawsonii*, sp. n. from the late Lower Devonian of Quebec (Gaspé), and Ontario, Canada. *Palaeontogr. Amer.*, **8**: 75-127.

CHALONER, W. G. & SHEERIN, A. (1979). Devonian macrofloras, in House, M. R., Scrutton, C. T. and Bassett, M. G. (Eds) — *The Devonian System: A Palaeontological Association International Symposium*. Spec. Papers in Palaeontol., **23**: 145-161.

ESAU, K. (1965). *Plant Anatomy*. 2nd edn. John Wiley & Sons, Inc. New York. 767 pp.

ESAU, K. (1977). *Anatomy of Seed Plants*. 2nd edn. John Wiley & Sons, Inc. New York. 550 pp.

HARTMAN, C. M. & BANKS, H. P. (1980). Pitting in *Psilophyton dawsonii*, an Early Devonian trimerophyte. *Amer. J. Bot.* (in press).

KEVAN, P. G., CHALONER, W. G. & SAVILLE, D. B. O. (1975). Inter-relationships of early terrestrial arthropods and plants. *Palaeontology*, **18**: 391-417.

KIDSTON, R. & LANG, W. H. (1921a). On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Pt. IV. Restorations of the vascular cryptogams, and discussion of their bearing on the general morphology of the Pteridophyta and the origin of the organization of land plants. *Trans. R. Soc. Edinb.*, **52**: 831-854.

KIDSTON, R. & LANG, W. H. (1921b). On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Pt. V. The Thallophyta occurring in the peat bed; the succession of the plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. *Trans. R. Soc. Edinb.*, **52**: 855-902.

MATTEN, L. C. (1974). The Givetian Flora from Cairo, New York: *Rhacophyton*, *Triloboxylon* and *Cladoxylon*. *J. Linn. Soc. (Bot.)*, **68**: 303-318.

MCGREGOR, D. C. (1977). Lower and Middle Devonian spores of eastern Gaspé, Canada. II. Biostratigraphy. *Palaeontographica*, **163B**: 111-142.

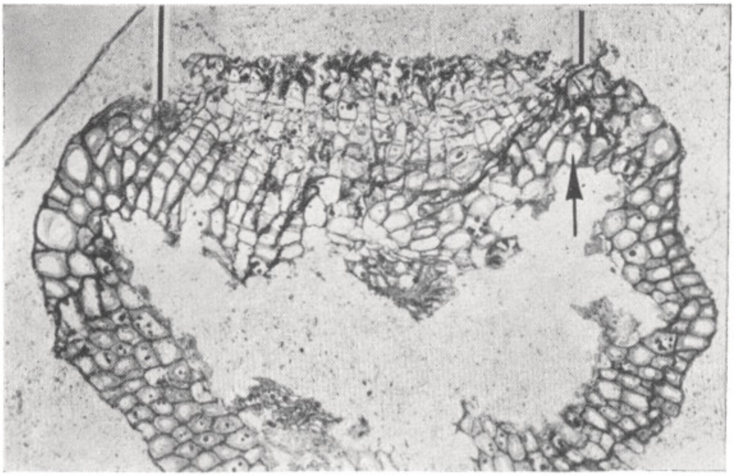
SCHECKLER, S. E. & BANKS, H. P. (1971). Anatomy and relationships of some Devonian progymnosperms from New York. *Amer. J. Bot.*, **58**: 737-751.

SCHECKLER, S. E. & BANKS, H. P. (1972). Periderm in some Devonian plants, pp. 58-64 in, Murty, Y. S., Johri, B. M., Mohan Ram, H. Y. and Varghese, T. M. (Eds) — *Advances in Plant Morphology*. Prof. V. Puri Commem. Vol. Sarita Prakashan, Meerut, India.

EXPLANATION OF PLATE

PLATE 1

1. cf. *Psilophyton dawsonii*, transverse section of axis showing cortical collenchyma and wound. Wound delimited by vertical bars. Arrow indicates normal-appearing collenchyma under right margin of wound. Inner cortex, phloem and xylem missing. Necrosed cells constitute outer surface of wound. Phellem and then phelloderm underlie necrosed cells. Slide no. C.U.P.C. 263·16. × 60.
2. same species. Axis enlarged to show the outer zone of necrosed cells, horizontal arrows, and two collenchyma cells in which phellogen may have been initiated, vertical arrows. Radial rows of phelloderm (inner) and phellem (outer) are emphasized. C.U.P.C. 263·16. × 95.



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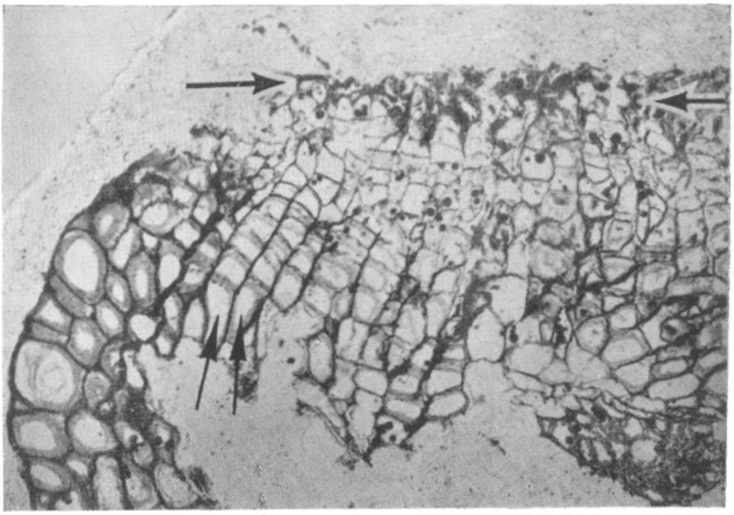

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PLATE 1