

THE OLDEST STOMATA (PARACYTIC) WITH PAIRED GUARD CELLS

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ABSTRACT

Stomata of the lycopod *Drepanophycus spinaeformis* were collected by Lang (1932) in Early Devonian strata of Siegenian age (390-374 million years ago). They are reinterpreted on the basis of a study of stomata from younger (Emsian, Givetian, Frasnian) collections. These plants are shown to have a paracytic stomatal apparatus. Lang therefore found the oldest example of paired guard cells and the oldest occurrence of paracytic stomata among vascular plants.

INTRODUCTION

THE publication of the Silver Jubilee Volume of *The Palaeobotanist* certainly justifies submitting a paper on cuticular pattern in an early vascular land plant. It is appropriate because of the many papers including cuticular pattern that have appeared in *The Palaeobotanist*, the official publication of the Birbal Sahni Institute of Palaeobotany. One hopes that the Journal will have a long and productive future.

The impetus for the present account is a paper by Chaloner (1970) entitled "The rise of the first land plants" given at the XI International Botanical Congress in Seattle, 1969. Therein Chaloner (p. 356, 359) remarked that the oldest preserved stomata yet recorded were found in *Zosterophyllum myretonianum* (Lele & Walton, 1961) of Gedinnian age (oldest Stage of Devonian, 395-390 million years ago). These stomata apparently consisted of a single guard cell and its enclosed pore. Whether the plants had a single guard cell or preservation had destroyed the radial walls between two guard cells is unknown. To date no Gedinnian plants with paired guard cells have been described.

Chaloner (1970) also suggested that the stomata Lang (1932) found in the lycopod *Drepanophycus spinaeformis* were the oldest to illustrate paired guard cells. The age of Lang's specimen is Siegenian (390-374 million years ago).

In a recent report on cuticles of *Drepanophycus spinaeformis* from Emsian (374-370 MYA), Givetian (365-359 MYA) and

Frasnian (359-353 MYA) strata of New York and Canada, Stubblefield and I (1978) confirmed that the species does have paired guard cells throughout its stratigraphic range. However, after a careful study of our material, we found it necessary to reinterpret the description by Lang (1932).

DESCRIPTION

Samples of the cuticle of *Drepanophycus spinaeformis* from one Middle Devonian locality will suffice for a description of its stomata. Pl. 1, fig. 1 illustrates randomly distributed stomata and elongate and polygonal epidermal cells. Pl. 2, fig. 3 shows a well preserved stoma that can be described using the terminology of Stace (1965). The pore is centrally located and is surrounded by a pair of reniform guard cells (g). The radial walls (r) separating the guard cells are distinct. Around the guard cells, and conforming to their shape, are two subsidiary cells (s) whose radial walls are also indicated (r). The poral walls (p) of the guard cells are darkened. Metcalfe and Chalk (1950) applied the term paracytic to a stomatal apparatus of this type. The whole stomatal apparatus consists of two distinct guard cells surrounded by two distinct subsidiary cells, and a central pore (aperture).

In both Pl. 1, fig. 1 and Pl. 2, fig. 3 a ring of epidermal cells may appear to encircle the stomatal apparatus. This ring seems to result from divisions in the epidermal cells immediately adjacent to the stomatal apparatus. In Pl. 2, fig. 3 arrow (ew) indicates

a wall formed by such a division in a large epidermal cell. Another dark, poorly preserved wall can be seen in the epidermal cell to the right. Other examples are seen in Pl. 1, fig. 1 (arrows).

Pl. 2, fig. 4 is an illustration of a stoma of *Drepanophycus spinaeformis* copied from Lang (1932, his fig. 12). The pore, somewhat enlarged by tearing, is surrounded by a pair of guard cells (g). The poral wall of the guard cells is darkened (p) and the epidermal walls (e) of the guard cells are distinct. Radial walls (r) of both guard and subsidiary cells are parallel to the long axes of the stomatal apparatus. One of the illustrations by Lang (1932, his fig. 71) is reproduced here as Pl. 1, fig. 2. It shows divisions of surrounding epidermal cells like those found often in our material (Pl. 1, fig. 1; Pl. 2, fig. 3).

Lang (1932) interpreted the stomata of *Drepanophycus spinaeformis* (Pl. 2, fig. 4) to consist only of two large guard cells (the cells we call subsidiary-s). If we accept this interpretation, the poral walls are very thick (Pl. 2, fig. 4, g plus p). To account for this thickness Lang assumed that cuticle extended from the radial walls down into the stomatal aperture (pore) where it flattened and almost filled the aperture. If his interpretation were correct, these stomata would today be called anomocytic (no subsidiary cells). However, a careful comparison of our many stomata (Pl. 2, fig. 3) with figure 12 of Lang (Pl. 2, fig. 4) shows that he had two subsidiary cells, two guard cells, a pore, radial walls on both guard and subsidiary cells, and poral and epidermal walls on the guard

cells. There is no difference between our stomatal apparatus and that found by him. Therefore both fit the description of a paracytic stomatal apparatus.

DISCUSSION

Paracytic stomata are well-known among Mesozoic Bennettitaleans (Florin, 1951, p. 293). Florin used the term syndetocheilic for them. We prefer paracytic because of the ontogenetic development of stomata in *Drepanophycus spinaeformis* is unknown. Stidd and Stidd (1976), who described paracytic stomata in Carboniferous pteridosperms, suggested that they were perhaps the oldest examples of this type of apparatus. Now it appears that Devonian examples are even older. Our oldest collection of *D. spinaeformis* that yielded cuticle with paracytic stomata is Emsian but the material described by Lang was collected in older Siegenian strata.

At present *Drepanophycus spinaeformis* from the Siegenian of Scotland is the oldest vascular land plant from which paired guard cells and paracytic stomata have been described. This report does not preclude the existence of still older examples if and when they are found.

ACKNOWLEDGEMENTS

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REFERENCES

- CHALONER, W. G. (1970). The rise of the first land plants. *Biol. Rev.*, **45**: 353-377.
- FLORIN, R. (1951). Evolution in cordaites and conifers. *Acta Horti. Bergiani*, **15**: 285-388.
- LANG, W. H. (1932). Contributions to the study of the Old Red Sandstone Flora of Scotland. VIII. On *Arthrostigma*, *Psilophyton*, and some associated plant remains from the Strathmore beds of the Caledonian Lower Old Red Sandstone. *Trans. Roy. Soc. Edinburgh*, **57**: 491-521.
- LELE, K. M. & WALTON, J. (1961). Contributions to the knowledge of '*Zosterophyllum myretonianum*' Penhallow from the Lower Old Red Sandstone of Angus. *Trans. Roy. Soc. Edinburgh*, **64**: 469-475.
- METCALFE, C. R. & CHALK, L. (1950). *Anatomy of the Dicotyledons*. Oxford Clarendon Press. **2**.
- STACE, C. A. (1965). Cuticular studies as an aid to plant taxonomy. *Bull. Br. Mus. Nat. Hist. (Bot.)*, **4**: 1-78.
- STIDD, L. L. O. & STIDD, B. M. (1976). Paracytic (syndetocheilic) stomata in Carboniferous seed ferns. *Science*, **193**: 156-157.
- STUBBLEFIELD, S. & BANKS, H. P. (1978). The cuticle of *Drepanophycus spinaeformis*, a long-ranging Devonian lycopod from New York and eastern Canada. *Am. J. Bot.*, **65**: 110-118.

EXPLANATION OF PLATES

PLATE 1

1. *Drepanophycus spinaeformis*, sheet of cuticle bearing impressions of elongate and polygonal epidermal cells and stomatal apparatus. Arrows indicate stomatal apparatus surrounded by an apparent ring of epidermal cells. Middle Devonian — Givetian stage. Prattsville, N.Y. Slide no. C.U.P.C. 252.1. $\times 115$.

2. Same species. Fig. 71 of Lang (1932). This figure copied from Lang, illustrates that stomata in his material also were sometimes surrounded by a ring of epidermal cells. Arrows (ew) indicate walls produced following the division of epidermal cells. No. 928. $\times 400$.

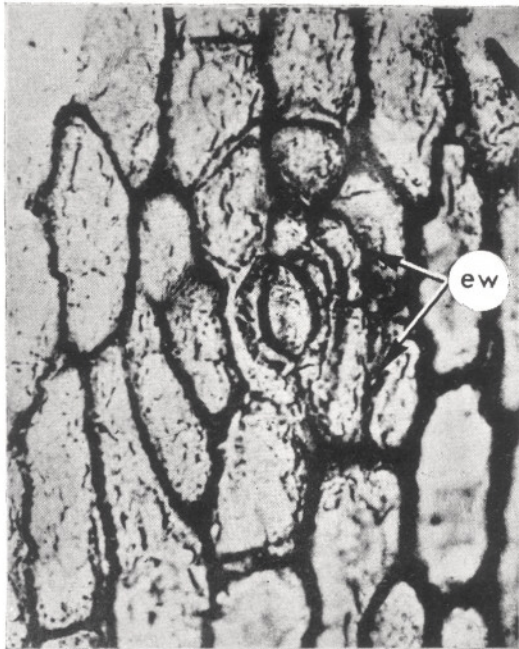
PLATE 2

3. *Drepanophycus spinaeformis*, one well-preserved paracytic stoma. Stomatal apparatus consists of pore, a pair of guard cells, and a pair of subsidiary cells. Some epidermal cells outside the subsidiary cells appear to have divided recently. p, poral wall of guard cell; g, guard cell; r, radial walls of guard cell and of subsidiary cell; s, subsidiary cell; ew, wall formed by recent division of epidermal cell outside subsidiary cell. Middle Devonian — Givetian Stage. Prattsville, N.Y. Slide no. C.U.P.C. 252.4. $\times 656$.

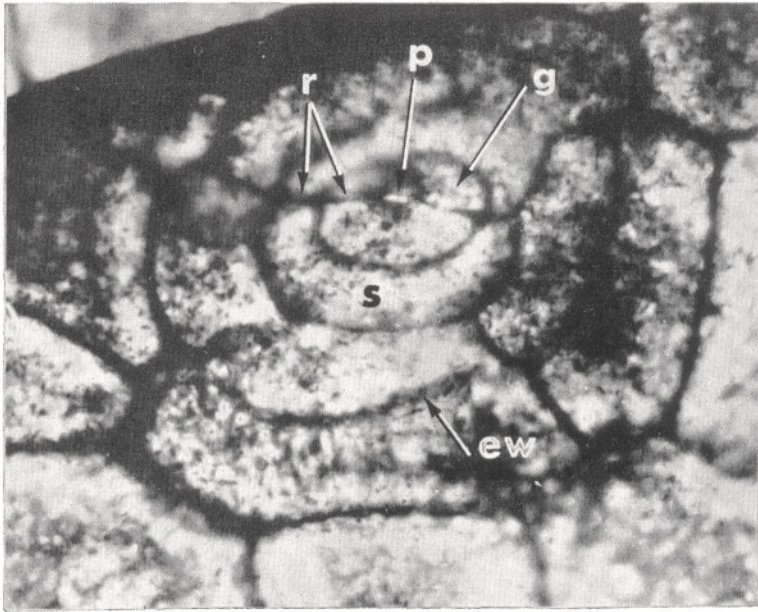
4. Same species. Fig. 12 Lang (1932). This figure, copied from Lang, illustrates a stoma like ours. Symbols are the same as for fig. 3. e, epidermal wall of guard cell. No. 936. $\times 640$.



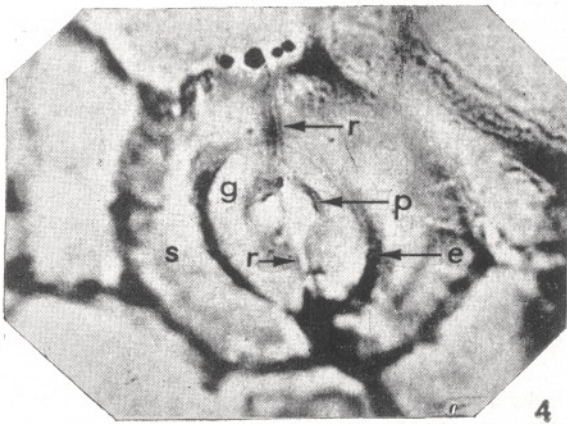
1



2



3



4

PLATE 2