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The fern *Stauropteris oldhamia* Binney: New data on branch development and adaptive significance of the hypodermal aerenchyma

La fougère Stauropteris oldhamia *Binney : données nouvelles sur la croissance des branches et signification adaptative de la présence d'un hypoderme aérenchymateux*

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ABSTRACT

Well-preserved specimens of *Stauropteris oldhamia* are described. The material was collected in the early 1920s from the Lower Westphalian (Early Pennsylvanian) Saurue seam from Belgium. The fossil plants occur as permineralized axes fragments within a coal ball. This study confirms most of the interpretations made by previous researchers. The observation of immature axis however suggests a less regular organization than previously interpreted beyond the three first branching orders. We also highlight the presence of profusely and dichotomously branched aphlebiae, the lack of laminate organs as well as the presence of hypodermal aerenchyma in all plant parts. We interpret these features as part of a very specialized assimilatory apparatus indicating an adaptation to a humid swamp environment.

RÉSUMÉ

Nous décrivons ici des spécimens bien préservés de *Stauropteris oldhamia*. Ils ont été collectés dans les années 1920 dans la veine Saurue du Westphalien inférieur (Pennsylvannien précoce) de Belgique. Les fossiles végétaux sont trouvés perminéralisés dans des *coal-balls*. Ce travail permet de confirmer la plupart des interprétations faites par d'autres auteurs. Cependant, l'observation d'axes immatures suggère, au-delà des trois premiers ordres de ramifications, une organisation moins régulière qu'habituellement proposée. Nous mettons aussi en évidence la présence d'aphlébies densément dichotomes, l'absence d'organe plan

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ainsi que la présence d'un hypoderme aérenchymateux dans toutes les parties de la plante. Nous interprétons ces caractéristiques comme faisant partie d'un appareil assimilateur très spécialisé indiquant une adaptation à un environnement marécageux humide.

1. Introduction

The Stauropteridales are a group of Palaeozoic (Late Devonian–Carboniferous) ferns that include small herbaceous plants with a four-lobed xylem strand and a quadriseriate (branches borne alternately in pairs) or biseriate (branches borne in two rows) branching; all lack planated appendicular organs. The order is currently represented by the genera *Stauropteris* Binney (1872), *Gillespiea* Erwin and Rothwell (1989), *Rowleya* Long (1966) and putatively *Multifurcatus* Wang (2003). *Stauropteris* was formerly classified within the coenopterid ferns (Andrews and Boureau, 1970; Eggert, 1964). Subsequent authors however treated the Stauropteridales as a distinct group demonstrating an early stage in the evolution of the frond (e.g., Taylor et al., 2009). This was strongly supported by phylogenetic analyses (Corvez, 2012; Rothwell, 1999; Rothwell and Stockey, 2008).

The genus *Stauropteris* Binney, 1872 is characterized by a three-dimensional branching pattern, a slightly asymmetric cruciate protostele and the presence of vascularized aphlebiae that subtend branches (Cichan and Taylor, 1982). What kind of organ the whole branch system of *Stauropteris* represents (stem, frond?) is still unknown. The genus currently includes four species: the homosporous *S. oldhamia* Binney (1872) is the type-species; it shows a quadriseriate branching pattern; *S. burntslandica* (Bertand, 1909) and *S. berwickensis* (Long, 1966) have also a quadriseriate branching pattern but are heterosporous. The fourth species, *S. biseriata* (Cichan and Taylor, 1982), exhibits a biseriate branching pattern; its reproductive biology is unknown. The inclusion of the species *americana* in the genus (Darrah, 1941) has been questioned (Cichan and Taylor, 1982) because the four-lobed stele was not documented.

Here we describe well-preserved permineralised specimens of *Stauropteris oldhamia*, from a Lower Westphalian (Lower Pennsylvanian) locality of Belgium. The specimens allow for a better understanding of the plant organization and anatomy. New information is also provided on early ontogenetic stages and the development of branches ($N+1$ and $N+2$ axes).

2. Material and methods

This study is based on a single coal ball collected by Pr. X. Stainier and later reported by Pr. S. Leclercq (Leclercq, 1935; Stainier, 1924). It was collected from the Saurue seam in the Violette colliery, a lateral equivalent of the well-known Bouxharmont seam of the Werister colliery (Holmes and Fairon-Demaret, 1984; Leclercq, 1935). Both collieries are situated close to Liège, Belgium. The Saurue seam (Violette), synonymous with the Bouxharmont seam (Werister) and with the Grande Veine d'Oupeye seam (Cheratte) has been attributed to the Lower Westphalian A/Langsettian stage (Lower Pennsylvanian) based on the occurrence of the ammonoid *Gastrioceras listeri* Sowerby (Chaudoir et al., 1952; Lambrecht et al., 1956; Lhoest et al., 1960).

The coal ball is numbered ULg-1007 and housed in the paleobotany collections of the University of Liège. It contains a dense mass of about 10 specimens of *Stauropteris oldhamia*. This coal ball was 13 cm long and has been cut into eight slices. A total number of 1080 cellulose acetate peel sections have been prepared by S. Leclercq using the original liquid peel technique (Walton, 1928) as well as the rapid peel technique (Joy et al., 1956).

The following description refers to the branching patterns with special focus on the apical parts of one selected specimen. This specimen was selected as it is the only one showing an immature development stage. More than 600 peel sections were selected for detailed observation.

The attribution of the specimen to the species *S. oldhamia* is supported by the occurrence of a quadriseriate branching pattern, by the presence of central parenchyma separating the four primary xylem lobes in N axes (see below for branch-order terminology), of very divided aphlebiae and of an aerenchymatous hypodermis, all features formerly recognized by Bertrand (1909) and Chaphekar (1962).

3. Results

3.1. Branching and xylem anatomy

Six axis orders are present among the studied material. It is impossible to reliably assess whether the most proximal and largest axis is the main stem or not. Considering this, we choose to name N the most proximal observed axis order, and $N+1$, $N+2$, etc. the subsequent axis orders. In transverse section, all the axes appear round to oval in outline. Lower-order axes include a four-lobed xylem strand, with phloem located between the xylem arms. Two planes of symmetry can be distinguished (Fig. 1A). The main plane of symmetry, referred to as the primary plane of symmetry (PPS, Fig. 1A and D) passes through the two main phloem groups. The secondary plane of symmetry (SPS) is perpendicular to the first; it determines the direction of departure of paired $N+1$ axes, which are given off alternately.

The diameter of the basalmost axes (N-order) ranges from 3 to 5 mm along both planes of symmetry. They present a stele (about 2 mm in size, elongated in the PPS) composed of four lobes (Fig. 1A and D). The latter are arranged crosswise and separated by parenchyma in the central area. The xylem includes tracheids with a larger diameter toward the centre of the stele and tracheids with