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Langoxylon asterochlaenoideum Stockmans: Anatomy and relationships of a fern-like plant from the Middle Devonian of Belgium

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Abstract

Restudy of Stockmans' [Stockmans, F., 1968. Végétaux Mésodévoniens récoltés aux confins du Massif du Brabant (Belgique). Mém. Mus. Roy. Hist. Nat. Belg. 159, 1-49.] Middle Devonian *Langoxylon asterochlaenoideum* clarifies many details of its anatomy. The main axis has a large multi-ribbed actinostele from which traces of two size classes depart in an irregular helix to decurrent lateral appendages. Most laterals are branch-like and supplied by major traces that are initially terete, expand distally, become bilaterally ridged, and then radially fluted just before appendage separation. Other minor traces supplied ultimate appendage- or leaf-like organs, which have smaller terete traces that fork and contract distally. Inner metaxylem of the main axis and branches consists mostly of apparent xylem parenchyma. Primary xylem is mesarch with two types of protoxylem strands. Protoxylem of the main axis appears to consist only of tracheids and occurs as several strands in each of the deeply cleft actinostele ridges (i.e., of the 'radiating' type). Protoxylem of lateral appendages occurs only at the tips of the xylem ridges (i.e., of the 'permanent' type) and has a core of parenchyma cells surrounded by protoxylem tracheids. This latter type has been called a peripheral loop (boucle périphérique) and shows minimal cell elongation. It differs from protoxylem lacunae of similar-appearing iridopterid taxa where parenchyma is absent and stretching of central tracheids results in their destruction to produce a vertical cavity. These multiple forms of protoxylem architecture might be useful for systematics of euphyllophytes. Where preserved, primary phloem is concentric. The cortex has inner parenchymatous and outer fibrous zones. *Langoxylon* bears only a superficial resemblance to *Asteropteris* and *Asterochlaena*, to which Stockmans compared his genus, and seems to be unrelated to them or to iridopterids like *Ibyka*, *Arachnoxylon*, *Iridopteris*, and *Compsocradus*, or the lignophyte *Stenokoleos*. *Langoxylon* compares with Middle Devonian archaeopterid progymnosperms like *Actinopodium* and *Actinoxylon*, but has a mixture of anatomical characters that were previously used to subdivide Euphyllophytina into Moniliformopses and Radiatopses types. *Langoxylon* is thus a 'fern-like' Middle Devonian euphyllophyte of uncertain phylogenetic relationship. Its most important contribution is to stimulate further investigations of the characters used to reconstruct early plant phylogeny.

Keywords: *Langoxylon*; Devonian; fern; progymnosperm; iridopterid; archaeopterid; Moniliformopses; Radiatopses; Euphyllophytina; Belgium

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1. Introduction

The Devonian represents a key time period in the evolution of terrestrial ecosystems as new, more complex plant growth and organizational patterns evolved. This period is marked by the emergence of new clades, such as the euphyllophyte groups of monilophytes (Moniliformopses with permanent protoxylem groups) and lignophytes (Radiatopses, in part, with radiate protoxylem groups). The re-investigation of anatomically preserved Devonian plants is particularly important because the primary characters used to delineate these groups are anatomical (e.g., Beck and Stein, 1993; Kenrick and Crane, 1997a,b; Berry and Stein, 2000; Cordi and Stein, 2005). In addition, these are the founding populations of early terrestrial communities that are marked by rapid increases of spatial complexity related to the rise of developmental innovations such as leaves, roots, pseudomonopodial apical growth of tall axes, and lateral meristems that compensated for the mechanical, physiological, and hydraulic conductance needs of ever taller and larger plants.

Studies of plants from the Devonian give us a better sense of the vertical and horizontal structure of successive early plant communities and help establish links between anatomically-preserved remains and time-equivalent compressed, morphologically-preserved plants with the prospect of ultimately creating whole-plant reconstructions within an ecological context. Each new increment of data helps us reconstruct the evolutionary scenarios that led to the rise of clades defined by key innovations and test the phylogenetic frameworks on which our studies of plant evolution rest.

In this context, our re-examination of Stockmans' (1968) *Langoxylon asterochlaenoideum* is pertinent because this Middle Devonian species, which is based upon a single incompletely described anatomical specimen, has features that span the characters of both Moniliformopses (iridopterid subgroup of Cladoxylopsida *sensu* Cordi and Stein, 2005) and Radiatopses (lignophyte subgroup *sensu* Doyle and Donoghue, 1986; Beck and Stein, 1993) types of euphyllophytes (of Kenrick and Crane, 1997a). Our detailed anatomical redescription of *Langoxylon*, therefore, provides a means to assess the proposed uniqueness of characters currently used to define each group and to investigate the impact of this new information on interpretations of early vascular plant phylogenies.

Langoxylon asterochlaenoideum Stockmans (1968) was described from a permineralized axis collected in Middle Devonian beds of Belgium. Stockmans placed it as an early coenopterid fern intermediate between *Asteropteris* from the Mid-Upper Devonian and *Asterochlaena* from the Permian. During our 1970–1973 investigations of several Middle and Upper Devonian plants from New York with similar anatomy (i.e., *Ibyka*, *Triloboxylon*, *Rhymokalon*; Skog and Banks, 1973; Scheckler, 1975a,b) it became necessary to restudy Stockmans' specimen in order to add some detail to his description. The specimen was made available to us through the kindness of Dr. Paul Sartenaer, Directeur de Paléontologie de l'Institut Royal des Sciences Naturelles de Belgique (IRSNB) à Bruxelles (Director of Paleontology, Royal Institute of Natural Sciences of Belgium, Brussels) who also consented to our further preparation of the axis. Our new preparations confirm most of Stockmans' original description, clarify some parts that were previously obscure, affirm its validity as a genus, and enable us to make several new observations that clarify better its possible relationships.

2. Materials and methods

Langoxylon is based on a single permineralized axis (IRScNB specimen no. 107303) 14 cm long and roughly 1.4 cm in diameter (Plate I, 1) that was collected from an excavation for a tower foundation along the Charleroi-Bruxelles channel at Ronquières in the Province of Hainaut, Commune de Braine-le-Comte, Belgium, (M. Fairon-Demaret, personal communication). This site was called Ronquières, tour du plan incliné — tête amont and is the source of all the fossils described from Ronquières in Stockmans (1968). The fossiliferous horizon lies within the Alvaux Member of the Bois de Bordeaux Formation (Formation du Bois de Bordeaux, Membre d'Alvaux; Bultynck et al., 1991). At Ronquières the Alvaux Member consists of gray shales, sandstones and sandy limestones with numerous fragmentary plant remains, capped by a thin deposit of calcareous and dolomitic sediments. The Alvaux Member is overlain by red rocks of the Mazy Member (Membre de Mazy). Based on brachiopods and ostracods these rocks are Givetian (upper Middle Devonian); traditionally the Alvaux Member is regarded as Gvb (middle to upper Givetian; Bultynck et al., 1991).

Permineralization is mostly by iron pyrites (pyrite and marcasite crystal morphs) but the central parts of main axis xylem and some lateral appendages are infiltrated with gray dolomite that has caused some loss of cellular detail. Apparent secondary mineralization by pyrite has also split portions of the main axis xylem resulting in further loss of detail in these areas. Stockmans prepared seven polished transverse faces, which he numbered according to his figure 6 (Stockmans, 1968) and our Plate I, 1, and two longitudinal