M. Sc. IInd Semester (Botany)

Paper-V (Pteridophytes)

Asteroxylales

By

Dr. Ratna Katiyar, Associate Professor
Department of Botany
University of Lucknow
Lucknow

Asteroxylon

Kingdom:	Plantae
Clade:	Tracheophytes
Sub-Clade:	Lycophytes
Class:	Lycopodiopsida
Order:	Drepanophycales
Family:	Asteroxylaceae Kidston & Lang
Genus:	*Asteroxylon*

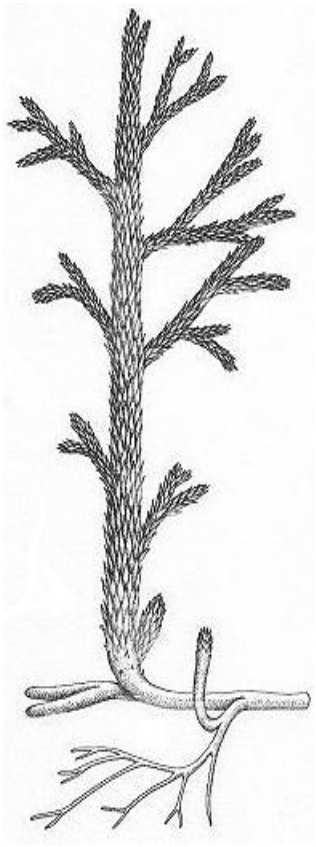

Fig. *Asteroxylon*

Introduction

Asteroxylon is an extinct genus of terrestrial vascular plant of the Lycopodiophyta, which flourished in the early Devonian period. This plant consisted of aerial, isotomously and anisotomously branching stems that reached 12 mm in diameter and 40 cm in length. The possibly procumbent aerial stems arose from a leaf-less rhizome which bore smaller-diameter, positively geotropic root-like branches. The rhizomes, which represent an independent origin of roots, reached a depth of up to 20 cm below the surface. The xylem or conducting tissue at the centre of the aerial stems is distinctly star-shaped in cross-section and has been considered an early actinostele or an "*Asteroxylon*-type" protostele. The tracheids

are of the primitive annular or helical type (called G-type also) "Leaves" – not true leaves, but protrusions – were of the form of unbranched strap-shaped enations up to 5 mm long; a single vascular trace branched from the main bundle in the centre of the stem to terminate at the base of each enation. Enations and axes bore stomata, indicating that their tissues were capable of photosynthesis.

Morphology

Aerial Axes

The aerial axes of *Asteroxylon* exhibit a maximum diameter of 12mm and possess characteristic 5mm long scale-like 'leaves' or **enations** surrounding each axis (see inset below right). *Asteroxylon* is perhaps the largest of the known plants from the chert, in life probably attaining a height above ground of about 40cm (it's rhizomes penetrating the substrate to a depth of up to 20cm). Branching is **dichotomous** and **monopodial**.

Longitudinal section of the outer cortex and epidermis of an aerial axis of *Asteroxylon mackiei* showing three non-vascularised scale-like enations or 'leaves' (**e**) (scale bar = 2mm).

One of the characteristic features of *Asteroxylon* is the scale like enations that emerge from the epidermis in a spiral arrangement around the axes. These are not true leaves since they do not possess a vascular strand (see inset right). The cuticle on both axes and enations bear abundant stomata with distinctive dark-coloured guard cells. The surface of the epidermis of the enations varies from smooth to papillate whereas that of the axes is smooth.
The cortex may be divided into a narrow outer zone of closely packed cells and a broader inner cortex that can be further subdivided into three zones: an outer and inner layer of compact cells with a trabecular middle layer of elongate cells with a well-developed inter-cellular air space network. Occasionally the inner zones of the cortex display fungal infestation. The vascular strand is quite distinctive. *Asteroxylon* possess an actinostele, in other words the vascular strand appears star shaped or stellate in transverse cross-section The xylem is exarch to locally mesarch where the protoxylem occurs at the ends of the 'lobes' of the actinostele, and displays spiral thickenings. Phloem tissue is best developed between the 'lobes' of the xylem strand. 'Leaf traces' are often seen where vascular tissue splits from the central stele. These traces end at the bases of the enations.

Sporangium

The sporangia of *Asteroxylon* were first described by Lyon (1964). Though many anatomical details remain unresolved, the sporangia are reniform (kidney-shaped), rather flattened medially, with a marginal dehiscence mechanism. The maximum dimensions for a single sporangium are 7mm by 2.5mm. Their disposition on the aerial axis is rather scattered, each sporangium being laterally attached via a stalk emerging between the angle of an enation and the main stem. *Asteroxylon*, one of the better known Rhynie plants, was originally described by Kidston and Lang (1920b) and assigned the name *Asteroxylon mackiei*. They noted fertile elements probably belonging to *Asteroxylon* within their material; however, the fertile elements of the sporophyte were not finally resolved until Lyon (1964) discovered sporangia in organic connection with the plant and he concluded that the fertile axes observed by Kidston and Lang were in fact of another new plant, *Nothia aphylla*. To date the gametophytes of *Asteroxylon* remain unknown. The overall morphology and palaeoecology of *Asteroxylon* is outlined below. "Sporangia, consisting of two kidney-shaped valves, are interspersed among the nonvascularized leaflike appendages and attached to the axis with a short pedicel. The sporangia are curved and lie close to the axis. Fertile regions of the axes alternate with sterile regions, suggesting periodic episodes of fertility.

Relationships

Asteroxylon is rather more anatomically complex than the other known Rhynie chert plants. The plant is considered a true lycophyte (a group of plants which includes the 'club mosses') based on the structure of its apical meristem (Hueber 1992) together with the characteristic exarch actinostele and the lateral disposition of the sporangia. The spirally thickened and reticulate cell walls of the xylem cells are also typical of lycophytes (Kenrick & Crane 1991). Modern lycophytes are also characterised by their enations or microphylls which possess a single vascular strand. In *Asteroxylon* the vascular trace stops at the base of the enations which may suggest the plant represents an intermediate stage in the evolution of lycopsid leaves.

Palaeo-ecology

Asteroxylon is quite commonly encountered in a number of chert beds and apparently formed a significant component of the Rhynie flora during the Early Devonian. Its rhizomes are usually found traversing plant litter and the plant is primarily found to occur *in situ* with two or more other genera, commonly *Nothia*, *Rhynia* and *Aglaophyton* and occasionally *Ventarura*. It seems therefore that *Asteroxylon* primarily lived as part of a diverse plant community rather than as monotypic stands (Powell *et al*. 2000b).

The fact that *Asteroxylon* possesses an extensive, substrate-penetrating 'root' system suggests it was capable of exploiting larger volumes of water and nutrients than the other Rhynie plants. Also the presence of microphylls increase the surface area of the aerial axes. This would have created a larger photosynthetic surface and with the greater density of stomata the plant possesses would also have meant greater efficiency in gaseous exchange and transpiration. It is likely that *Asteroxylon* could tolerate quite dry habitats compared with most of the other Rhynie flora

Zosterophyllum

Kingdom:	Plantae
Clade:	Tracheophytes
Clade:	Lycophytes
Plesion:	Zosterophylls
Genus:	*Zosterophyllum* Penh. (1892)

Zosterophyllum was a genus of Silurian-Devonian vascular land plants with naked branching axes on which usually kidney-shaped sporangia were arranged in lateral positions. It is the type genus for the group known as zosterophylls, thought to be part of the lineage from which modern lycophytes evolved. More than 20 species have been described.

The diagnostic features of the genus have changed since its first description in 1892, as the original species (*Zosterophyllum myretonianum*) has become better known, and as other species have been discovered. *Zosterophyllum* is a vascular plant. The axes (stems) are naked, lacking leaves or outgrowths ("enations"). When branching occurs, the branches are either isotomous (equally sized) or pseudomonopodial (one branch is larger than the other but still clearly involves division of the original axis rather a distinct side growth). The sporangia are upright on short stalks. In face view, they are flattened, usually kidney-shaped (reniform). They open (dehisce) along the top forming two equally sized valves. Sporangia are grouped into a compact spike in which they are either helically arranged or form distinct rows (e.g. *Z. llanoveranum*). *Z. myretonianum* is thought to have been semiaquatic.

Taxonomy

The genus *Zosterophyllum* was erected in 1892 by David P. Penhallow for the type species *Zosterophyllum myretonianum*, based on fossils found at Myreton quarry near Dundee, Scotland, in Lower Devonian rocks (from about 419 to 393 million years ago).

Species with radially symmetrical spikes of sporangia have been placed in subgenus *Zosterophyllum*, those with bilaterally symmetrical spikes in subgenus *Platyzosterophyllum*. Hao and Xue in 2013 used the absence of terminal sporangia to place some species, such as *Z. llanoveranum*, in the paraphyletic order Gosslingiales, a group of zosterophylls considered to have indeterminate growth, with fertile branches generally showing circinate vernation (initially curled up). Other species, such as *Z. myretonianum*, were not placed in the order, as they did not have terminal sporangia.

Phylogeny

A cladogram published in 2004 by Crane et al. places the species of *Zosterophyllum* in a paraphyletic stem group of broadly defined "zosterophylls", basal to the lycopsids (living and extinct clubmosses and relatives). On this view, the genus is not monophyletic.

A cladistic analysis by Hao and Xue in 2013 agreed that *Zosterophyllum* is not monophyletic, with the three species of *Zosterophyllum* they included falling into different clades, some being closer to the Gosslingiales than others. Their analysis differed in producing a monophyletic clade of zosterophylls (their Zosterophyllopsida).