FAMILY : LYGINOPTERIDACEAE

This group of the **Pteridospermales** was represented both in the Upper and the Lower Carboniferous periods of the Palaeozoic era. They show the following characteristic features :—

1. The stems were not strong enough to bear the weight of the foliage and were either climbers or had a straggling growth habit. They needed support to grow erect.
2. The leaves were compound and the ultimate leaf units were dissected.
3. The stem stele was either of discrete bundles or protostelic with mesarch xylem.
4. The leaf traces were also mesarch.
5. The leaf traces arise by tangential division of cauline strand.
6. The leaf traces were single but become double later.
7. The leaf had circinate ptyxis.
8. The microspores were trilete.
9. The microsporangia occur in paired synangia.
10. The seeds were cupulate.
11. The pollen chamber in the ovule was limited externally by an inverted bell-shaped sheath with a solid nucellar beak internally.
12. The ovule was surrounded by a single massive integument that was fused with the nucellus. The outer fleshy layer of the integument was not very distinct.
13. The ovule had a single vascular system.
14. The sporangia were devoid of annulus.
15. The megaspore had a very thick wall.
16. The secondary wood was soft textured with broad medullary rays.
17. The secondary xylem tracheids were long and tapering. The circular bordered pits are multiseriate and were present only on radial walls.
18. There were no mucilage canals in the stem.

The extensively investigated species *Lyginopteris oldhamia* (*Binney*) H. Potonie will be taken as a classic example to illustrate the family.

LYGINOPTERIS OLDHAMIA (BINNEY) H. POTONIE

Lyginopteris oldhamia (*Calymatotheca hoeninghausi*) was described in detail by Williamson, Scott, Brongniart, Binney, Potonie and Oliver and Scott. It was found in abundance in the coal ball horizon of Lancashire and Yorkshire. Binney (1866) described the stem of this species under the name *Dadoxylon oldhamium* which was later assigned to *Lyginodendron*. Brongniart in 1828 described its frond under the name *Sphenopteris hoeninghausi*. Potonie renamed it as *Lyginopteris oldhamia* in 1899. In 1903, Oliver and Scott showed that the seed *Lagenostoma lomaxi* belonged to *Lyginopteris oldhamia*. Later in 1929, Jongmans showed the presence of capitate glands on the cupulate envelope enclosing the seeds. Such glands were later found on the stem, fronds and the rachis. This showed that all these structures described under separate names belonged to only plant— *Lyginopteris oldhamia*. Its rachis was described under the name '*Rachiopteris aspera*' and the root as *Kaloxylon hookeri*. All these parts are now definitely known to be the various organs of *Lyginopteris*

oldhamia, which can, therefore, be regarded as a classical member of the family. The only imperfectly known part is the pollen bearing organ called *Crossotheca hoeninghausi*.

External Features (Fig. 2.1)

The stem of *Lyginopteris oldhamia* was aerial varying in diameter—from 2 mm. to 4 cm. diameter. It was frequently branched and bore adventitious roots that were probably prop roots that supported the weak stem. The leaves were spirally arranged up to 0.5 metre long. Each leaf was bipinnate to tripinnate and was once forked near its base. The pinnae were borne at right angles to the rachis and were arranged opposite to each other. The pinnae bore pinnules or leaflets that were cuneate and were arranged alternately on the ultimate branches (pinnae) of the rachis and have free veins. The petiole and the rachis were studded with capitate glands. The stem was radially symmetrical and it showed that the plants grew erect, although due to its large foliage and comparatively narrow diameter

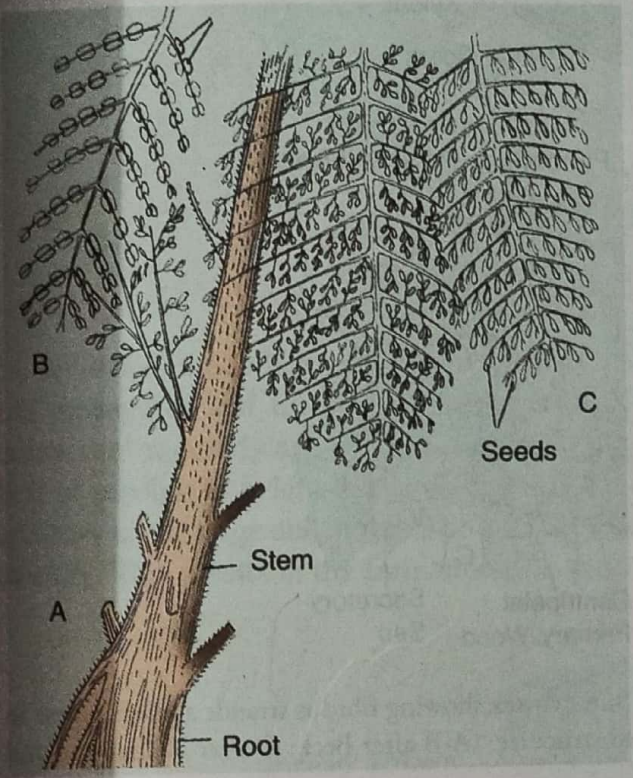

Fig. 2.1. A. Restoration of *Lyginopteris oldhamia* showing external characters. The frond on the left bears the pollen sacs on peltate leaflets (*Crossotheca*); that on the right bears seeds. Also note the stem and roots. (After Mrs. D.H. Scott)

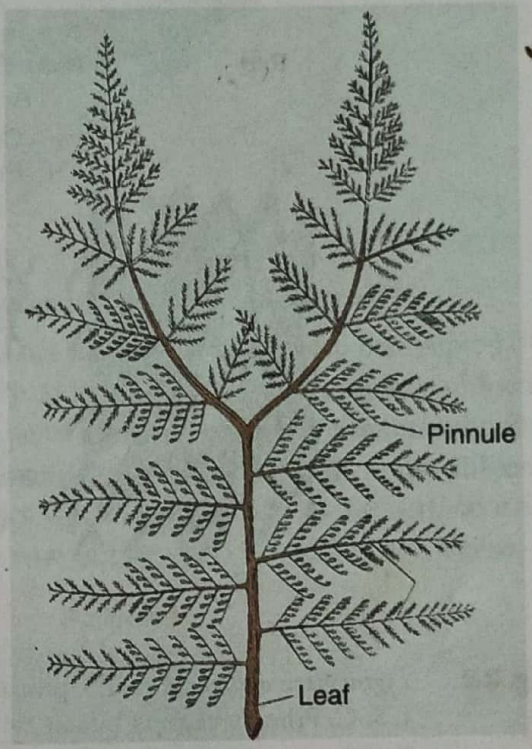

Fig. 2.1(a). B. The frond of *Lyginopteris oldhamia*.

it had to recline or depend upon support on the neighbouring plants or other objects. The prop roots which grew from among the leaves also afforded sufficient support to the stem.

Primary Structure of the Stem

The transverse sections of the stem are nearly circular in outline (Fig. 2.2). Next to the epidermis is the outer cortex which consists of radially broadened fibrous strands that form a vertical network (Fig. 2.2). In the meshes of the network are the parenchymatous cells. This system of fibrous strands affords mechanical strength to the weak stem. The inner cortex consists of ordinary parenchymatous cells. The cortex is many layered. Next to the cortex is the pericycle which consists of short cells and a number of thick walled or sclerotic cells with dark contents.

Next to the pericycle are five strands of primary vascular bundles. These are separated by parenchymatous areas. Each vascular bundle is mesarch and consists of primary phloem towards the

outer side. The cells in the phloem are small and irregularly arranged. Next to it is the cambium that is well preserved in some specimens. The xylem consists of tracheids. The tracheids of the protoxylem are spirally thickened, whereas those of the centripetal metaxylem have multiseriate bordered pits arranged on radial walls. The centrifugally developed metaxylem has scalariform tracheids. The protoxylem is surrounded on all sides by metaxylem (Fig. 2.2).

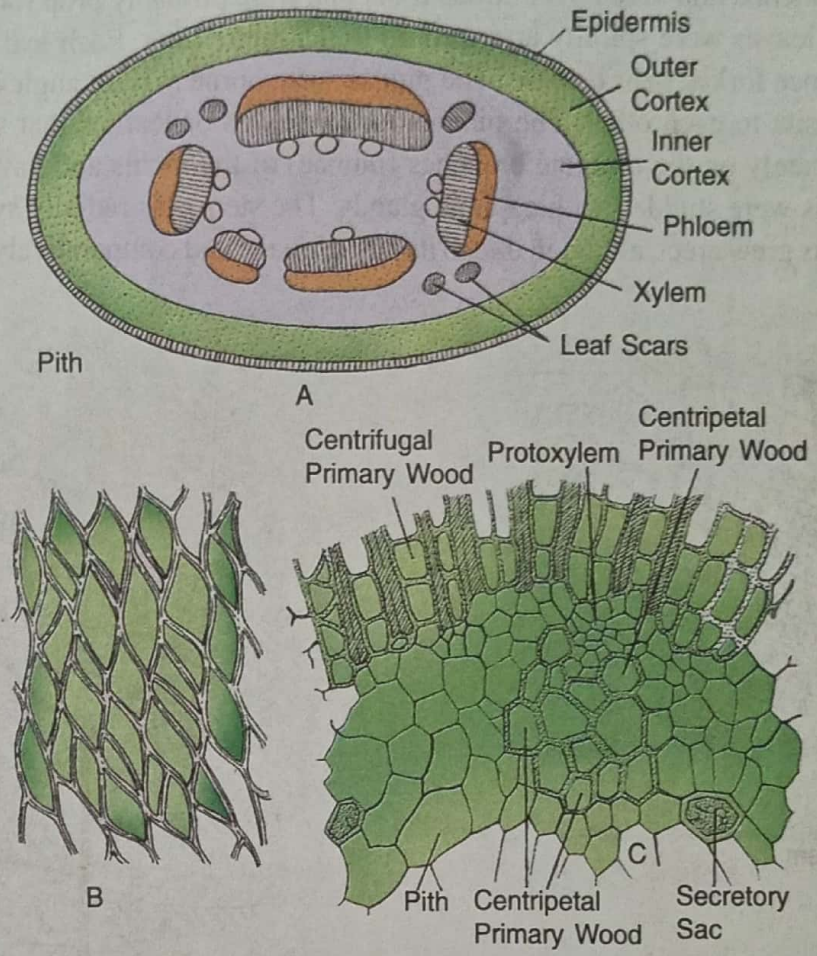

Fig. 2.2. *Lyginopteris oldhamia*, A. T.S. primary stem. B. Outer cortex showing fibrous strands as they appear in L.S. C. Primary vascular bundle showing detailed structure. (A-B after Beck; C after Williamson and Scott).

In the centre there is a large pith made up of parenchymatous cells. Scattered throughout the pith are somewhat thick-walled cells with dark contents. The number of parenchymatous and thick-walled cells is variable. The size of the pith also varies with the diameter of the stem.

Leaf Traces

A leaf trace arises by the tangential division of the cauline strand (vascular bundle of the stem). The strand traverses through the secondary wood and the cortex and divides into two in the inner cortex. These two strands again unite at the base of the petiole to form a V-shaped leaf trace. The trace traverses through the secondary xylem by way of a large ray. On the outer side of the leaf trace is a strip of secondary xylem which is considered to be its own. This wedge-shaped arc of secondary wood of the trace persists beyond the pericycle and then it starts disappearing gradually. The single trace (formed by the union of two branches in the inner cortex) traverses through the petiole and then branches into two and each branch enters the forking rachis. Later it divides to form the veins in each of the leaflets. The xylem strand of the petiole is trough-shaped with the concavity facing upwards. Sometime there are two grooves when the strand is double. The xylem is completely surrounded by phloem and on the lower side of the xylem arc there are many protoxylem groups. The outer cortex in the petiole consists of thick-walled hypodermal strands that are in continuation of those of the stem cortex. The inner cortex in the petiole consists of groups of sclereids.

Secondary Structure of the Stem (Fig. 2.3)

Next to the two cortical layers is the periderm, then pericycle, crushed primary phloem and then the secondary vascular tissue. The secondary cylinder surrounds the primary xylem and it is traversed

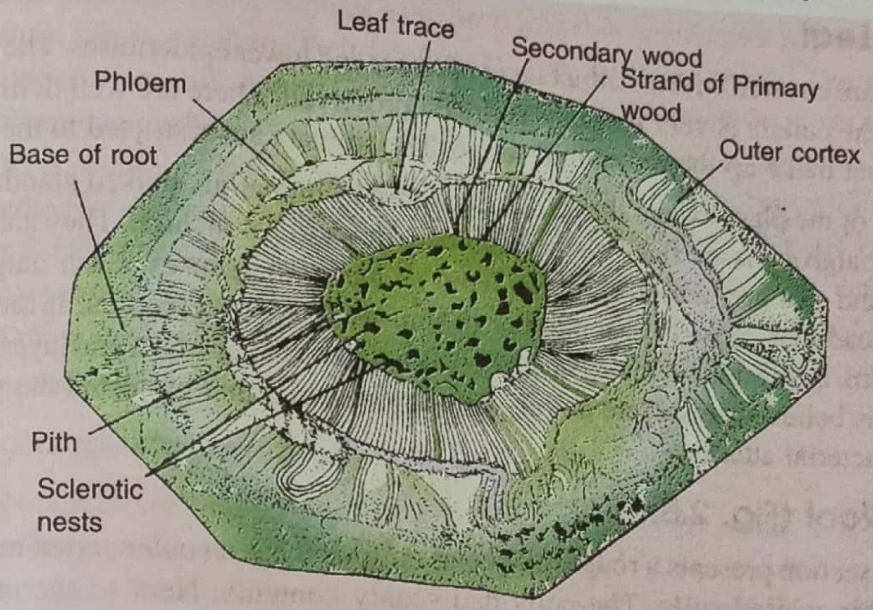

Fig. 2.3. *Lyginopteris oldhamia*. T.S. stem showing secondary structure (After Scott).

by secondary medullary rays that may be narrow or wide. That secondary ring is also interrupted by the passage of leaf trace that originates from the primary xylem strand. The secondary phloem consists of regularly arranged cells and in a transection a line of phloem cells is continuous with the line of secondary xylem tracheids below, formed by the same cambial cell. The cells in the phloem are alternately large and small. The smaller ones divide by a wall at right angles to the vertical row of cells. This results in the formation of a short transverse row of two or more small cells. These

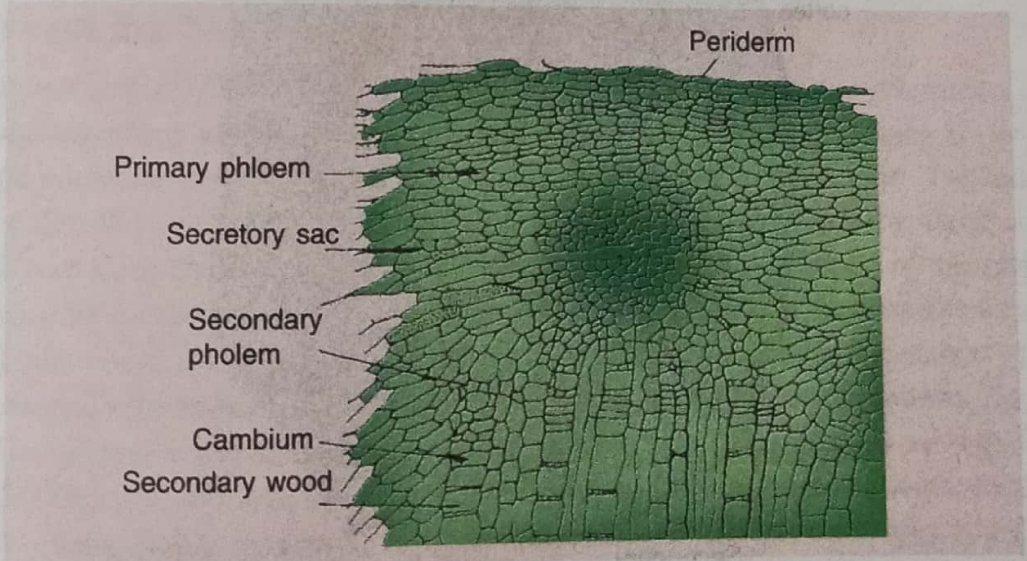

Fig. 2.4. *Lyginopteris oldhamia*. T.S. stem showing details of secondary vascular bundle. (After Williamson and Scott.

cells later become suberised. Next to the secondary phloem is the cambium. The secondary xylem is next to the cambium and forms a narrow zone in stems with smaller diameter and a comparatively wide zone in thicker stems. It consists of large tracheids with multiseriate bordered pits arranged on the radial walls. The bordered pits have angular borders. The secondary xylem rays are 1-12 cells wide and a few to many cells in height. The pits are irregularly arranged.

In some specimens of *Lyginopteris oldhamia,* internal secondary wood has also been reported. It lies internal to the primary xylem strands and is considered to have originated from a cambial strip lying just within the primary strands. It is considered to be an anomalous development.

Anatomy of Leaf

The pinules are covered with a distinct layer of upper and lower epidermises. The upper epidermis is cutinised and the cuticle is very resistant and well preserved. There are well defined palisade and spongy tissues that make up the mesophyll tissue. The stomata are restricted to the underside.

All the parts of the plant except the root are covered by numerous stalked glandular outgrowths. These glandular outgrowths are flask-shaped and may be up to 3 mm. high. They are not supplied by any vascular strand and are, therefore, considered as mere emergences. Each outgrowth bears an apical globular head that consists of a number of thin-walled secretory cells. It ranges in diameter from 0.12 – 0.4 mm. Below the secretory head there is a stalk made up of several layers of parenchyma cells. The gland is believed to secrete an oily or waxy material that protected the younger regions from fungal or bacterial attacks.

Anatomy of Root (Fig. 2.5)

A transverse section presents a roughly circular outline. It has an outer cortex made up of two to three layers of thin-walled cells. The cells had scanty contents. Next to the outer cortex is a comparatively wide inner cortex whose cells were also parenchymatous, but were full of dense contents. These are considered to be mucilaginous in nature. The endodermis and pericycle are also clearly seen in the prepared sections.

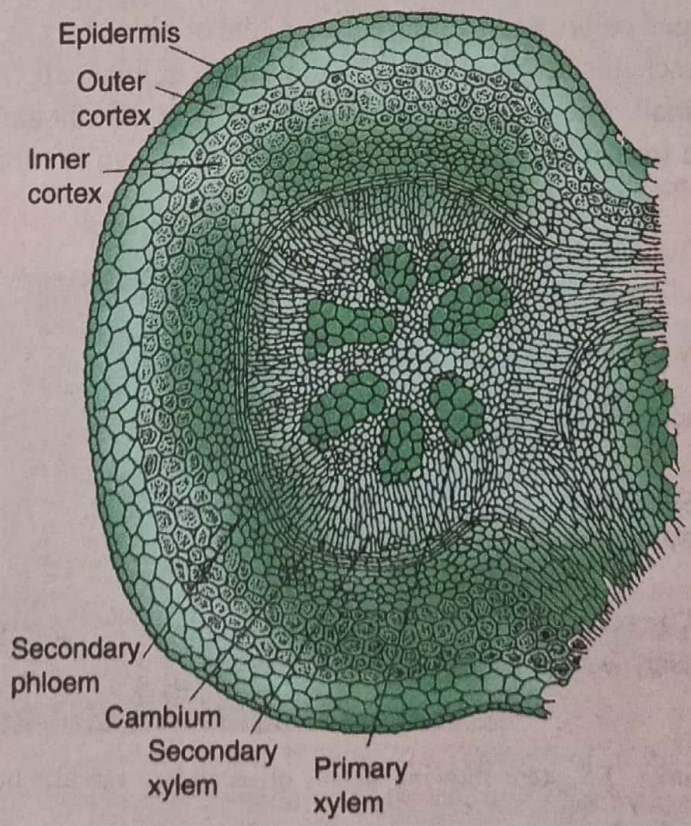

Fig. 2.5. *Lyginopteris oldhamia.*T.S. root.

Regarding its primary vasculature, the root possesses many xylem strands alternating with an equal number of phloem strands. The xylem is exarch *i.e.*, the protoxylem faces outwards and has spirally marked tracheids. The pith is scanty. The branches of root develop opposite to the protoxylem points.

The large roots show a secondary wood. It is traversed by large rays that always lie opposite to the protoxylem groups.

REPRODUCTIVE STRUCTURES

Regarding the reporductive features of *Lyginopteris oldhamia* there is no doubt that it is heterosporous and heterothallic. It bears seeds. The seeds and ovules are enclosed within protective structures called the **cupules.** These cupules have been found in connection with the fronds and also bore capitate glands, which confirms their connecion with the type species. The seeds and ovules were described under a separate name *Lygenostoma lomaxi*. The dispute is regarding the pollen organs or the microsporangia that have been described under the name *Crossotheca*. The *Crossotheca* was discovered by Kidston (1905) in the form of impressions in connection with the fronds genus *Sphenopteris hoeninghausi* which is the frond of *Lyginopteris oldhamia*. Hence *Crossotheca* is now regarded as the microsporangium of this species. Some recent investigations (Andrews, 1961, pp. 135-137) have cast some doubts regarding their validity. Arnold (1948, p. 214) has suggested *Telangium* as the microsporangiate structure of *Lyginopteris*. Irrespective of a doubtful position, the *Crossotheca* is considered as the microsporangiate structure in this text.

The Microsporangium (Fig. 2.6)

The microsporangia are borne on the ultimate branches of the frond. The pinnules in these ultimate branches became flattened with slight development of lamina and bore peripheral, pendent and elongate sporangia. The microsporangium is about 3 mm. long and bilocular. Each loculus is full of several microspores that ranged 50-70 μ in diameter. The microspores show a number of cells whose identity cannot be made out. They have tri-radiate markings (trilete). The sporangia lack annulus and resemble those of *Cycas*. On dehiscence, the microspores were probably carried by wind and some of them were lodged directly on the pollen chamber. They did not develop into pollen tubes as no evidence of their formation is available uptodate. In the absence of pollen tubes the sperms must have been motile and fertilisation followed pollination. There could be no prolonged interval between the two.

The Ovule and the Seed (Fig. 2.7)

Lagenostoma lomaxi (Oliver and Scott) is a barrel-shaped and radially symmetrical ovule with a single stout integument vascularised by nine vascular strands. The integument is not lobed and forms a single complete sheath penetrated at the apex by a narrow micropyle. The integument is fused with the nucellus except near the micropylar end where it is free from the nucellus and forms a canopy that surrounds and overhangs the pollen chamber. This canopy part of the integuments is divided into nine loculi with a vascular strand extending into each. This peculiar locular structure of the canopy is believed to contain water and supply it to the seed. The integument shows two distinct regions, the external **sclerotesta** which is hard and stony and an inner fleshy **endotesta**. The **sarcotesta** or the outer fleshy layer is not distinct. External to the integument, the ovule is partially enclosed by a lobed cupule (Figs. 2.7 and 2.8), which is studded with numerous glandular outgrowths. The seeds are released from the cupule by a basal abscission mechanism. The cupule is also vascularised. The nucellus is elongate and is not vascularised. The nucellus apex has a hollow pollen chamber (Fig. 2.7) or **Lagenostome**. The pollen chamber in this ovule is conical in shape and has a central core of tissue, shaped like an inverted bell (Figs. 2.7 and 2.9). This is known as the **central column** of the pollen chamber. The pollen chamber is formed as a result of formation of flask-shaped prolongation from the nucellar tip. This prolongation extends through the micropyle in the cavity between the free part of the integument and the nucellus. The central column arises from the base of the flask-shaped pollen chamber. The column leaves only a narrow space for the reception of the pollen grains. There is also a possibility that the narrow pollen chamber is formed by the disintegration of the nucellar tissue around the central column. The pollen grains are received in the pollen chamber and perhaps

germinated there and liberated the sperms which fertilized the eggs in much the same way as in the living cycads. Long (1944) reported the female gametophytes containing several archegonia in the ovule *Lagenostoma ovoides*. *L. lomaxi* dates back to the Upper Carboniferous.

Pallet, J.M. (1966) observed the megaspore membrane resembling that of the exine of the pteridophytic spore. The outer spore wall was thick.

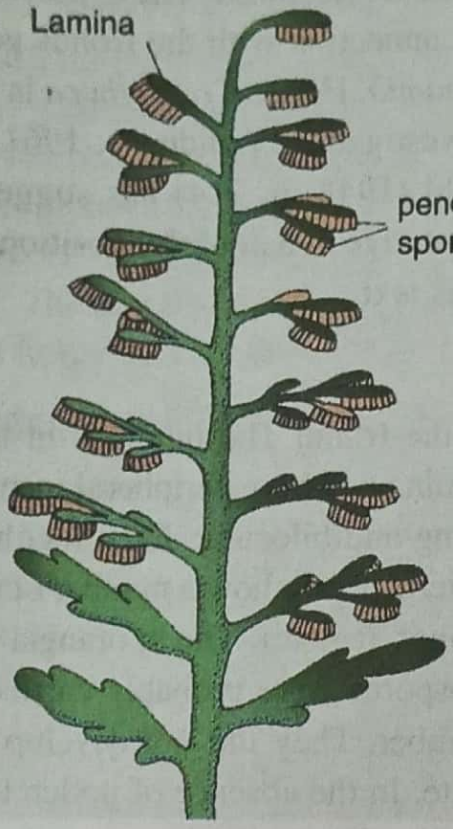

Fig. 2.6. *Lyginopteris oldhamia*. Part of a frond bearing microsporangia on the flattened pinnules. The microsporangia are pendent. The name *Corssotheca* is also given to the male organs (After Kidston).

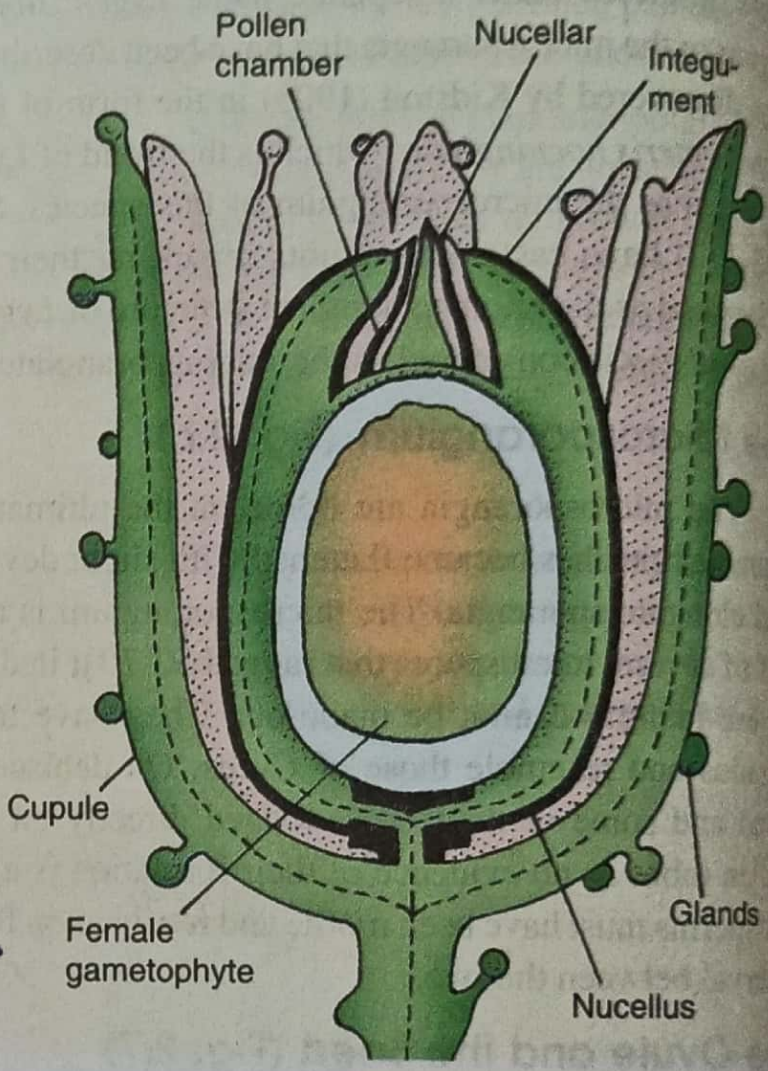

Fig. 2.7. V.S. ovule of *Lyginopteris oldhamia* (=*Langenostoma lomaxi*). Note the glands on the cupule. (After Oliver and Scott).