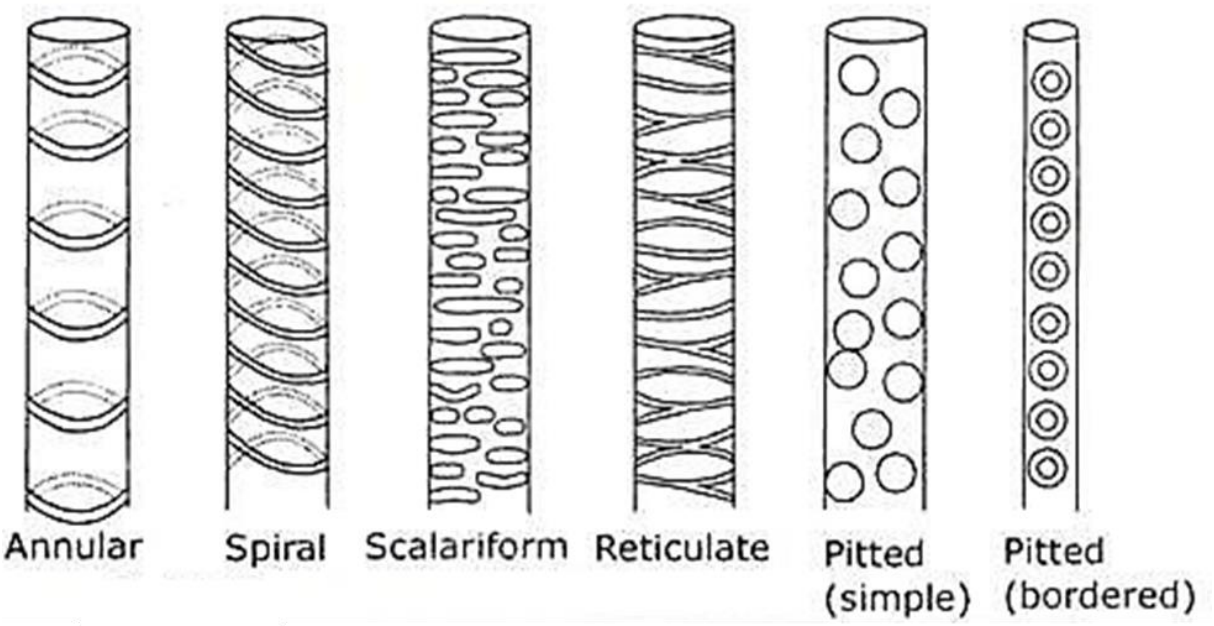
Secondary wall thickenings

The deposition of secondary wall materials occurs in such a way that various patterns are formed on the cell wall.

The following patterns are commonly noted



1. **Annular thickening**: These are ring like thickening present on the inner side of primary wall. The rest of the wall is thin.

2. **Spiral or helical thickening**: These are spiral or helical thickening of secondary wall materials. There may be more than one helix.

3. **Scalariform thickening**: The thickenings appear as parallel transverse bands like the rungs of a ladder.

4. **Reticulate thickening**: The secondary wall appears as a network as the meshes remain thin.

5. **Pitted thickening**: These are more or less circular areas, called pit, where secondary wall materials are not deposited.

Primary pit fields:

The meristematic cells and their derivatives without secondary walls have numerous deeply sunken areas on their wall. These depressions in the primary wall are termed as primary pit fields. They are also called primary pit or primordial pit where plasmodesmata exist.

In longitudinal sectional view, a primary wall with numerous sunken regions appears as beaded. In primary pit areas, the walls are thin and continuous. These primary pit field areas comprise the middle lamella and the primary wall of both adjacent cells.

Pit: These are small sharply defined more or less circular areas on the cell wall and in surface view appear as depressions in wall. In these areas, the secondary wall materials are not deposited. In contrast to primary pit, the secondary wall layers are not continuous at the pit region, i.e. the primary wall is not covered.

Pit may be developed over primary pit field or irrespective of it, i.e. over the primary wall. A pit consists of pit cavity, pit aperture and pit membrane. The pit cavity, also called pit chamber, is the interrupted region of secondary wall. The pit aperture is the mouth or opening of the pit chamber and it lies towards the cell lumen.

The pit membrane, also termed as closing membrane, comprises the middle lamella and the two thin primary walls of two adjacent cells. The following types of pit are found on the cell wall with secondary deposition.

i. Simple pit:

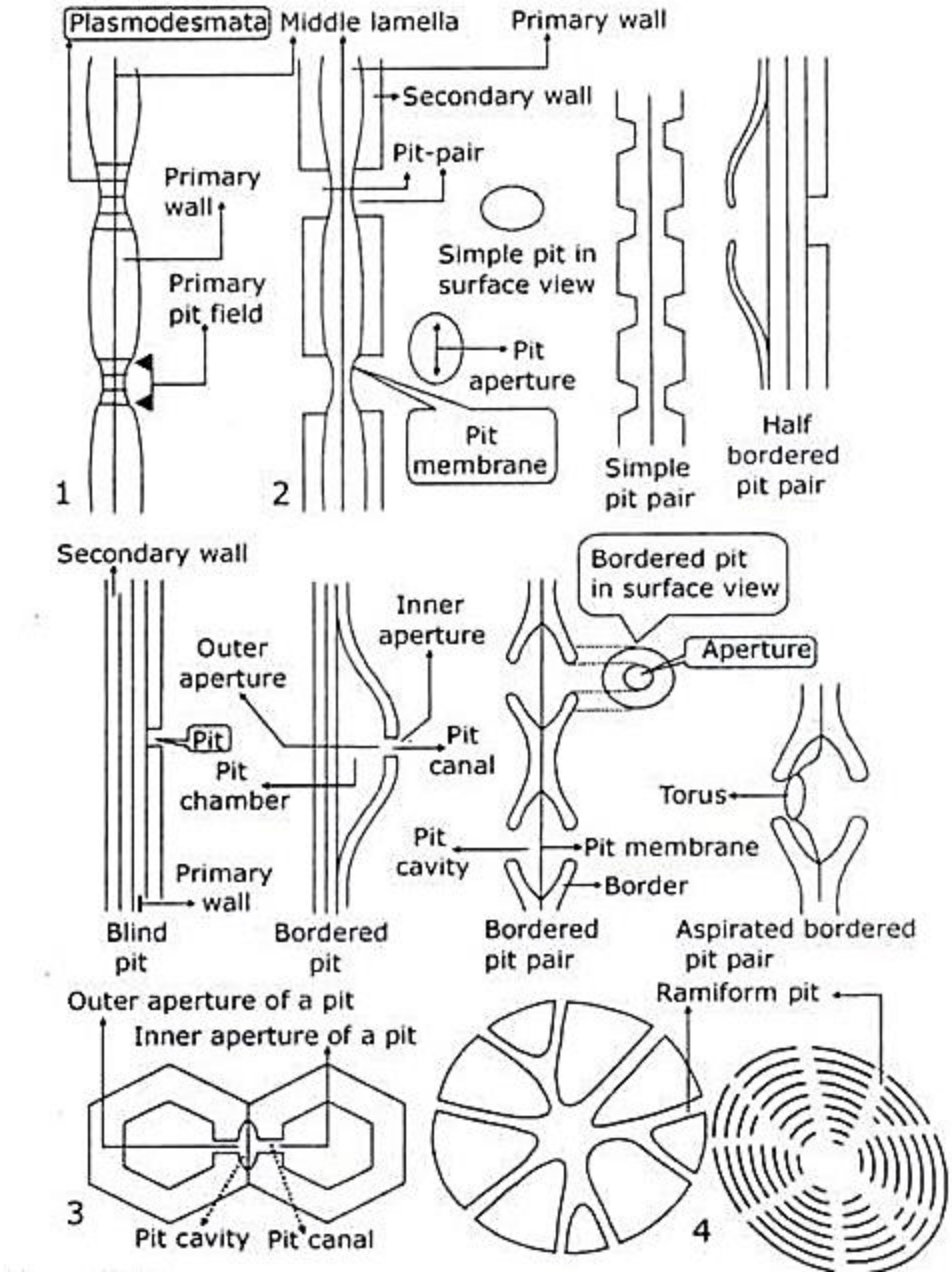
A pit is said to be simple where the secondary wall does not arch over the pit chamber and so the rim of the pit aperture contains no border. Simple pits may be of various shapes —oval, circular, pentagonal or even elongated. A simple pit consists of pit cavity, pit aperture and pit membrane where plasmodesmata exist. Simple pits are usually present in parenchyma cells.

ii. Ramiform pit:

Ex. Cydonia fruit. In the transverse section of very thick walled brachysclereids, the simple pit appears as a canal on the cell wall. Some of them have the form of branches due to coalescence with the neighbouring canals. These branched shaped pits are ramiform pit.

iii. Bordered pit:

It is found in lignified fibres, tracheids and trachea. In these pits, the pit cavity is partly enclosed by over-arching of the secondary cell wall, which is revealed in longitudinal section. In surface view, bordered pits appear as two concentric rings where the inner circle is the pit aperture and the outer circle forms the border.



A bordered pit is thus composed of:

(1) Pit chamber, formed by the over-arching of secondary cell wall, and pit aperture, the shape of which may be circular, oval or linear;

(2) The middle lamella or pit membrane or closing membrane.

Sometimes the overarching of secondary wall may be very thick to form a canal – termed pit canal, which lies between the pit chamber and cell lumen. Therefore, the pit canal has two

openings – outer aperture, which lies towards the cell wall and inner aperture, which is the other opposite opening towards the cell lumen.

The size and shape of pit chambers and inner apertures depend on the thickness of secondary wall. The pit chambers and outer apertures are always circular in outline in thick wall. The shape of inner aperture varies, it may be elliptical, narrowed and elongated, and slit like. The length of the narrow and elongated inner aperture may be less than the margin of pit cavity or equal to the limit of the cavity.

The length may also be much elongated than the limit of pit chamber and in this case the pit canal is funnel shaped. In a pit pair, where both the inner apertures are elongated beyond the margin of pit cavity, the apertures are crossed in appearance in face view. In the wood fibres (e.g. Magnolia, Populus) these 'crossed pit apertures' are very conspicuous.

In some gymnospermous wood like Pinus, Cedrus etc. the closing membrane between the bordered pit pairs is thickened at the middle. The thickened portion is termed torus, which is more or less disc shaped and wider than the pit aperture. The torus remains suspended by microfibrils. The microfibrils are loosely arranged and radially oriented to form a raised border over the closing membrane where the tori are present.

The raised border is known as Margo that appears as a thick circular border around the torus. There are many perforations in the Margo. Studies with Electron microscope confirm the porous nature of Margo though it was discovered as early as in 1913 by Bailey with the aid of a light microscope. In Cedrus the torus has fringed margin- a characteristic feature that distinguishes it from other genera

In gymnosperm, where the vessels are usually absent, conduction of water occurs mainly through the bordered pits of tracheids. The torus is apparently impermeable. Usually the torus occupies the median position and so water can move freely.

The pit membrane is flexible and during water movement, the torus swings. During swinging, torus may be at the lateral position where it blocks the pit aperture and thus prevents the flow of water. In conifers, bordered pits regulate the flow of water with the help of torus that acts as the valve.

The shape and arrangements of bordered pit in tracheary elements may vary and accordingly the following three types are noted:

(a) Scalariform pitting:

In this type, the bordered pits are either linear or elongated and arranged in regular transverse bands like a ladder (ex. Magnolia).

(b) Opposite pitting:

Here the pits are either elongated or circular or elliptic in outline and arranged in horizontal rows; when such pits are crowded, the outline of pits become either rectangular or square (ex. Liriodendron).

(c) Alternate pitting:

In this type the round or oval pits are arranged in diagonal rows and on crowding, the outline of the pit may be hexagonal (ex. Salix).

iv. Aspirated pit:

In these pits, the torus occupies the lateral position. It blocks the outer aperture of pit canal. The pit membrane loses flexibility and thus the pit becomes nonfunctional. It is found in the heartwood of Pinus.

v. Pit pair:

In a functional pit, a pit on one wall must coincide in position with a pit in the wall of adjacent cell. These two pits along with the pit membrane, present in between them, form a structural and functional unit-termed pit pair.

In a pit pair:

(1) The two complementary pits may be simple-termed simple pit pair;

(2) The two complementary pits are bordered – termed bordered-pit-pair;

(3) A bordered pit coincides with simple pit-termed half bordered pit; and

(4) A large pit is complemented by two or more pits – known as unilateral compound pitting.

vi. Blind pit:

When a pit is not complemented by any pit on the adjacent wall, it is termed as blind pit. These pits are nonfunctional and may occur opposite to intercellular spaces.

vii. Vestured pit:

These pits are characterized by the presence of some minute projections in the pit chamber. These outgrowths originate at the side wall of the pit cavity and pit aperture by the accumulation of cytoplasmic materials.

The projections form sculpturing of various shapes. They are found in the secondary tracheary elements of some members of Leguminosae, Cruciferae, Myrtaceae and Caprifoliaceae. Vestured pits are considered to be advanced, as they are present in developed xylem.

Some specialized cell wall structures

1. Trabeculae:

Trabeculae are bar or rod-like radial projections of the cell wall. They extend across the cell lumen in radial direction and so occur in radial rows. Sometimes these small bars may extend up to the phloem through cambium. They occur frequently in the tracheids of conifers (ex. Abies), rare elsewhere.

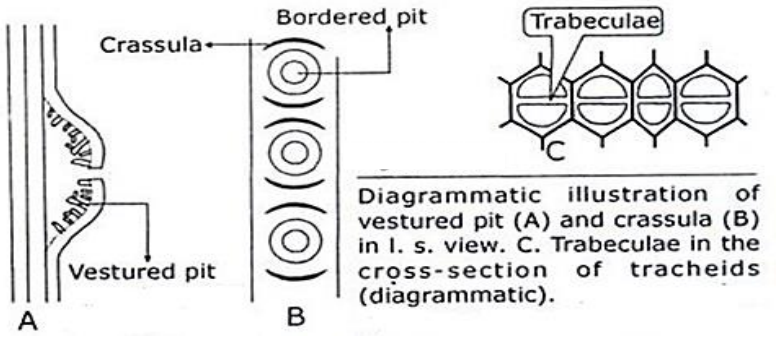
2. Crassulae:

These are linear or crescent shaped thickening present along the upper and lower margins of individual or small group of bordered pits. The primary wall and middle lamella, at the rims of primary pit-field thickens to form crassulae. These thickenings may surround or partly encircle individual bordered pits.

The deposition of secondary wall materials is interrupted at the regions of crassulae and they are visible when stained properly. Therefore, crassulae represent the elevated rim of primary pit-fields. Crassulae were also named as ‘Bars of Sanio’ or ‘Rims of Sanio’, but now a days these terms are of little use. They are commonly found in gymnospermous tracheids, ex. Pinus.

3. Wart structures:

Small wart like structures of 0.1 pm to 0.5 pm in diameter are found to be present lining the inner surface of secondary wall of conifer tracheids. They are also present in the fibres and vessels of dicots. They are supposed to be the remnants of protoplast or the remnant of lignin precursors, which deposited on the inner wall of tracheids, fibres and vessels to form warts.



Diagrammatic illustration of vestured pit (A) and crassula (B) in l. s. view. C. Trabeculae in the cross-section of tracheids (diagrammatic).