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HISTOLOGICAL INVESTIGATIONS OF THE SECONDARY PHLOEM OF GYMNOSPERMS

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HISTOLOGICAL INVESTIGATIONS OF THE SECONDARY PHLOEM OF GYMNOSPERMS

PROEFSCHRIFT
TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWKUNDE
OP GEZAG VAN DE RECTOR MAGNIFICUS, IR. F. HELLINGA,
HOOGLERAAR IN DE CULTUURTECHNIEK,
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DOOR

R. W. DEN OUTER

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STELLINGEN

I

De differentiatie van het vertikale systeem van de bast, loopt parallel met de reductie van de baststralen.

Dit proefschrift

II

De eiwitcellen in de bast van het *Chamaecyparis pisifera* type, vertonen meer overeenkomst met de begeleidende cellen van de Angiospermen, dan de eitwitcellen in de bast van het *Pseudotsuga taxifolia* type.

Dit proefschrift

III

De term mergstralen moet uitsluitend gebruikt worden voor primaire stralen, terwijl secundaire stralen, baststralen genoemd moeten worden, wanneer zij in het secundaire phloëem voorkomen en houtstralen wanneer zij in het secundaire xyleem voorkomen.

IV

Bij de bast van Gymnospermen is, in tegenstelling met de bast van Angiospermen, de mate van aanwezigheid van bastvezels karakteristiek voor het ontwikkelingsstadium van het vertikale systeem.

ZAHUR, M.S., Cornell Univ. Agr. Exp. St. Mem. 358 (1959)

V

De opvatting van STRASBURGER dat stippels tussen eiwithoudende- en zetmeelhoudende systemen zouden ontbreken, is gebleken onjuist te zijn.

STRASBURGER, E., Über den Bau und den Verrichtungen der Leitungsbahnen in den Pflanzen. Jena (1891)

VI

De criteria, welke GREGUSS aanlegt bij de rangschikking van de houtstralen van de Gymnospermen in verschillende ontwikkelingsstadia, gelden niet voor de baststralen.

GREGUSS, P., Xylotomische Bestimmung der heute lebenden Gymnospermen. Budapest (1955)

Proefschrift van R. W. DEN OUTER
Wageningen, 23 juni 1967.

VII

Bij de indeling in typen, zijn bij de bast de stralen wel van belang en bij het hout niet.

Dit proefschrift

VIII

De *Vaccinium* fase van het *Dicranum* vegetatietype, welke volgens MEISEL-JAHN o.a. ontstaat na bebossing van door anthropogene invloeden uit het *Querceto-Betuletum* ontstane heidevelden met *Pinus sylvestris*, doorloopt maximaal 5 en niet 4 stadia.

MEISEL-JAHN, S., Angewandte Pflanzensoziologie; Die Kiefern-Forstgesellschaften des Nordwestdeutsche Flachlandes (1955)

IX

De „topsterfte" in *Pinus sylvestris* bossen in Nederland heeft als voornaamste oorzaak het niet aangepast zijn van deze houtsoort aan het hier te lande heersende klimaat.

X

De verkeersveiligheid in Nederland kan verhoogd worden, indien de Verzekeringsmaatschappijen zouden weigeren ingevoerde tweedehands wagens te verzekeren.

CONTENTS

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1. INTRODUCTION

To gain an insight into the structure of the secondary phloem of Gymnosperms, primarily the different cell types with regard to their appearance, differentiation and degree of development, have to be described. Special attention has been paid to the presence or the absence of pits, i.e. the location of connections between adjacent cells; in particular amount, kind and location of these pits have been examined. Through these pits an easy movement of assimilates from one cell to another, is possible.

The term 'pit' is used in a broad sense, that is to indicate a cavity or a thin place in the cell wall. In primary walls such pits will also be called 'primary pit-fields'. More specifically, the cavities in parenchyma-cell walls will be called pits, those in sieve-cell walls, between adjacent sieve cells, will be called sieve areas. Consequently the cell types are dependent upon pit-contact between these cells for food-conducting functions. The different arrangements of these cell types are investigated, also the directions in which this movement of assimilates may take place.

Many statements have been made about food-conduction pathways. The way in which the main transport of food is directly related to the arrangement and the structure of the cell types and the importance of special combinations of different kinds of cell types, have been pointed out. Thus, apart from the comparative anatomy, some physiological aspects have also been alluded to. All these statements about food-conducting pathways require evidence from experiments with tracers etc. So in this thesis only a cytological basis for physiological investigations has been created.

Further both the interrelationship between the different cell types and the combination of their occurrence have been studied. An attempt has been made to classify the Gymnosperms into a small number of different types, based on the characteristic structure of their secondary phloem. Though the arrangement of the cells in the different Gymnosperms varies widely, each of these species belongs to one of the main types or is to be considered as an intermediate between two of those types. The phloem rays turned out to be most important in classifying the various phloem types, in contrast with the wood rays.

The different types of secondary xylem are arranged and classified in view of dead elements: tracheids, libriform fibres and vessel members. These are determining for a special wood species; they are, except for the libriform fibres, essential to the water-conducting function of the xylem. These elements develop, differentiate and modify in the course of time, according to the changing ecologic situations.

The living part of the wood, the parenchymatous part and the wood rays in particular, also develop, but they are not essential to the vertical water-conducting system but they provide for the horizontal conduction of water and assimilates. The wood rays are not interrelated and they do not interfere with the dead cells, which are determining for a special type of wood species. Therefore the wood rays are not essential in classifying woody species into several evolutionary stages, if only the wood is considered.

This is entirely different with the phloem, which is mainly composed of living cells. It is a close, complex and active system; one of its functions is the conduction of assimilates, mainly by the sieve cells, throughout the plant body; here the living phloem rays play a prominent part. A classification of the different Gymnosperm woods, based on the structure of the secondary phloem, is hardly possible without considering the phloem rays.

Though it will appear that the phloem rays and the axial system of the phloem show different evolutionary trends, the former are still essential to the classification as mentioned above. Apart from the rays and the axial system of the secondary phloem, the so-called 'Strasburger albuminous cells' are also important in this connection. They are intimately associated with the sieve cells, which are considered to be the most important element of the secondary phloem.

2. MATERIAL AND METHODS

2.1. SLIDES

The 9 families of the Gymnosperms and the different genera belonging to these families, are:

Cycadaceae
Encephalartos
Microcycas
Cycas
Zamia
Macrozamia
Ceratozamia

Ginkgoaceae
Ginkgo

Araucariaceae
Agathis
Araucaria

Podocarpaceae
Acmopyle
Dacrydium
Microcachrys
Microstrobus
Phyllocladus
Podocarpus
Saxegothaea

Taxaceae
Amentotaxus
Austrotaxus
Pseudotaxus
Taxus
Torreya

Cephalotaxaceae
Cephalotaxus

Cupressaceae
Actinostrobus
Austrocedrus
Callitris
Calocedrus
Neocallitropsis
Chamaecyparis
Cupressus
Diselma
Fitzroya
Fokienia
Juniperus
Libocedrus
Papuacedrus
Pilgerodendron
Tetraclinis
Thuja
Thujopsis
Widdringtonia

Taxodiaceae
Athrotaxus
Cryptomeria
Cunninghamia
Glyptostrobus
Metasequoia
Sciadopitys
Sequoia
Sequoiadendron
Taiwania
Taxodium

Pinaceae
Abies
Cathaya
Cedrus
Keteleeria
Larix
Picea
Tsuga
Pseudolarix
Pseudotsuga
Pinus

Samples of stems of several Gymnosperm wood species were taken: in particular the anatomical and the cytological features of the secondary phloem are investigated and occasionally those of the xylem.

These wood species are:

Cycadaceae	*Cycas circinatum* L.
Ginkgoaceae	*Ginkgo biloba* L.
Araucariaceae	*Agathis spec.*
	Araucaria araucana K. KOCH
Podocarpaceae	*Podocarpus nerifolius* D. DON
	Dacrydium elatum WALL.

	Sciadopitys verticillata SIEB. et ZUCC.
Taxaceae	*Taxus baccata* L.
	Torreya nucifera SIEB. et ZUCC.
	Cephalotaxus harringtonia R. SMITH
Cupressaceae	*Chamaecyparis pisifera* ENDL. var. *plumosa* OTTO
	Biota spec.
	Cupressus sempervirens L.
	Juniperus chinensis L.
	Juniperus communis L.
	Fitzroya cupressoides JOHN.
	Libocedrus decurrens TORR.
	Thuja plicata LAMB.
	Thujopsis dolabrata SIEB. et ZUCC.
	Cryptomeria japonica D. DON
Taxodiaceae	*Cunninghamia lanceolata* HOOK
	Metasequoia glyptostroboides HU et CHENG
	Taxodium distichum A. RICH.
	Sequoiadendron giganteum BUCHH.
Pinaceae	*Abies concolor* HOOPES
	Tsuga canadensis CARR.
	Cedrus libani A. RICH.
	Larix decidua Hopes
	Pseudolarix kaempferi GORD.
	Picea spec.
	Pseudotsuga taxifolia BRITT.
	Pinus sylvestris L.

Also some samples of the *Chlamydospermae* were examined, viz.:

Ephedraceae	*Ephedra spec.*
Gnetaceae	*Gnetum gnemon* L.

With chisel and hammer pieces of wood and bast are cut from the different stems at a height of about one yard above the trunk base; these pieces were taken in different seasons of the year.

For some cytological reactions it was necessary to make sections immediately after cutting the samples, while for the normal anatomical studies the samples were killed and fixed first in formalin alcohol or Carnoy and next cut and stained. Transverse, tangential (tg.) and radial (rd.) sections, varying from 10 to 60 microns, were made with a sharp razor or with a sliding microtome. During the winter, when the cambium is inactive, the bast does not become detached from the xylem when making the sections, whereas it does happen in samples taken during the spring.

These sections were subjected to treatment with one or more staining procedures and chemical reactions listed below.

Kaiser's gelatine-glycerine used for direct imbedding without preliminary treatment or after suitable staining procedures (JOHANSEN, 1940).

Eau de Javelle (REINDERS, 1961): by this treatment non-transparent tissues were decolourized and the protoplasts became transparent; thus a transparent material is obtained in which the pits were very distinct, particularly if stained with haemalaun afterwards.

Haematoxyline for staining unlignified tissues, (JOHANSEN, 1940).

Phloroglucine and hydrochloric acid for staining lignified tissues (REINDERS, 1961).

Haemalaun staining for both lignified and unlignified tissues (JOHANSEN, 1940).

Cotton blue for staining the nucleus and the plasma (JOHANSEN, 1940).

Aniline blue for the staining of callose (JOHANSEN, 1940).

Iodine for the indication of the presence of starch (JOHANSEN, 1940).

Sudan III for the staining of cork (JOHANSEN, 1940).

Benzidine reagent according to GLICK (1963) for indicating the presence of the enzyme peroxydase, based on the oxidation of benzidine by the enzyme.

Fast green according to the method by ALFERT and GESCHWIND (RAUEN, 1964), a selective staining of basic protein in nuclei.

Chloramine T Schiff reagent according to BURSTONE (1955).

Alloxane Schiff reagent according to RAUEN (1964).

Ninhydrin Schiff reagent according to RAUEN (1964). The three last mentioned reactions are used to indicate protein. Terminal and lateral amino groups of the peptide chain form a coloured compound.

Fuchsine, gold orange and light green for the staining of plasma and nuclei.

Demonstration of acid phosphatase according to FREY (1954) and GOMORI (1939, 1941). This enzyme is always present where transport of organic materials occurs.

Maceration was performed according to JEFFREY (JOHANSEN, 1940).

A few wood species with a great difference in hardness of the phloem layers were embedded in polyaethylene- glycol, before making slides.

2.2. DRAWINGS

The schematic drawings were made with the help of a Leitz Laborlux microscope; sometimes a drawing-prisma was used.

2.3. TERMS USED

Most of the terms used are defined according to the 'International Glossary of Terms used in Wood Anatomy' (1957), e.g.:

Albuminous cell — A parenchymatous cell with much protoplasm, with apparently a large nucleus, mostly without starch and with extensive pit-contact with the sieve cells. They are physiologically but not ontogenetically associated with the sieve elements. When they occur in the vertical system they are called phloem-albuminous cells; when they occur in the rd. system, the term ray-albuminous cell will be used.

Bark — A nontechnical term used to cover all the tissues outside the xylem cylinder. In older trees usually divisible into inner (living), cf. secondary phloem, and outer (dead), cf. rhytidome.

Bark, early — The bark formed during the earlier stages of the season.

Bark, late — The bark formed during the later stages of the season.

Bast — See secondary phloem.

Cambium — The actively dividing layer of cells, which lies between and gives rise to, secondary xylem and secondary phloem.

Cambial initial — An individual cell of the cambium, i.e. fusiform initial and ray initial.

Cambial zone — A term of convenience for the layer of varying width composed of cambial initials and their undifferentiated derivatives.

Cambium, cork — See phellogen.

Cell — A chamber or compartment containing or having contained a protoplast.

Companion cell — A sister cell of a sieve-tube member, intimately connected with it and retaining the nucleus and dense cytoplasm. The cell is physiologically and ontogenetically associated with a sieve-tube member.

Cork — A nontechnical term for phellem.

Cortex — The primary ground tissue of a stem or root between epidermis and vascular cylinder.

Crystal cell — A fusiform parenchymatous cell, not divided into compartments by septa, containing several crystals.

Crystalcell strand — A crystal cell divided into compartments by septa.

Crystalliferous cell — Any cell containing one or more crystals.

Fibre, bast — A long, narrow cell of the bast, other than parenchyma, sclereids and sieve cells, usually thick-walled, directly formed from the cambium.

Fibre-sclereid — A fibrelike sclereid.

Fibre-tracheid — A fibrelike tracheid; commonly thick-walled with a small lumen, a pointed end and bordered pits.

Fusiform initial — A cambial initial giving rise to an axial element of xylem or phloem; it is spindleshaped (fusiform) as seen in tangential section.

Growth layer — A layer of bark or wood, apparently produced during one growing period; frequently divisible into early and late bark or wood.

Growth ring — In bark and wood a growth layer, as seen in cross section.

Growth ring boundary — The outer limit of a growth ring.

Half-heterogeneous phloem ray — A phloem ray partly composed of parenchyma cells and albuminous cells and partly, either exclusively of parenchyma cells, or exclusively of albuminous cells.

Heterogeneous phloem ray — A phloem ray composed of parenchyma cells and albuminous cells.

Homogeneous phloem ray — A phloem ray composed of exclusively parenchyma cells or exclusively albuminous cells.

Intercellular canal, radial — A tubular intercellular space of interminable length, extending across the grain in a radial direction, enclosed in a ray.

Intercellular space — A space between cells.

Meristem — A tissue capable of active cell division, thereby adding new cells to the plant body.

Parenchyma — Tissue composed of mostly thin-walled cells of different forms, like brick-shaped, isodiametric, fusiform, cylindrical, egg-shaped; formed in the phloem from fusiform cambial initials, mostly by later transverse divisions of the daughter cells (phloem-parenchyma cells) or from ray initials (ray-parenchyma cells); they have pits.

Parenchyma, ray — Parenchyma constituting either the wood rays or the phloem rays, wholly or in part.

Parenchyma strand — An axial series of two or more parenchyma cells derived from a single fusiform cambial initial.

Periderm — (= secondary cork) The layers which replace the epidermis as the impermeable covering of the older stems, consisting of phellem, phellogen and phelloderm.

Phellem — (= cork) A tissue produced externally by the phellogen in a stem or root. The cell walls are generally suberized; in thick-walled cells, there may be additional lignified layers towards the cell lumen. Unsuberized cells of the phellem are known as phelloid cells.

Phelloderm — A tissue that generally resembles cortial parenchyma in appearance, but which consists of the inner derivatives of the phellogen.

Phellogen — (=cork cambium) The meristematic layer that produces the periderm; phellem towards the outside, phelloderm towards the inside.

Phelloid cell — Unsuberized cell of the phellem.

Phloem — The principal food-conducting tissue of the vascular plants. It occurs both as primary and as secondary tissue and it is usually, but not always, associated with xylem. The secondary phloem is separated from the secondary xylem by the cambium, from which it is derived. The basic types of cells of which it is composed are sieve elements, parenchyma cells, fibres and sclereids.

Phloem, primary — The first-formed phloem, differentiated below the apical meristem, before a definite cambium can be recognized.

Phloem, secondary — (=bast) The part of the bark formed by the cambium.

Phloem ray — A ribbonlike aggregate of cells formed by the ray initials and extending radially in the phloem.

Pit — (=primary pit-fields) A cavity or thin place in the primary cell-wall. More specifically, the cavities in parenchyma-cell walls would be called pits or primary pit fields; those in sieve-cell walls would be called sieve areas.

Pit, simple — A pit in which the cavity becomes wider, or remains of constant width, or only gradually narrows during the growth in thickness of the secondary cell wall.

Pit, bordered — A pit in which the membrane is overarched by the secondary cell wall.

Protoplast — The mass of protoplasm enclosed by a cell wall.

Ray, phloem — See phloem ray.

Ray initial — A cambium initial giving rise to a ray cell.

Ray tracheid — A tracheid forming a part of a ray; mostly forming rows of 1–3 cells high on both sides of the wood ray parenchyma cells, which constitute the middle of the ray.

Rhytidome — The innermost phellem and the tissues isolated by it; often consisting of different periderm layers enclosing pockets of cortial or phloem tissues. A technical term for the outer bark.

Ring, growth — In bark and wood a growth layer, as seen in cross section.

Ring boundary, growth — The outer limit of a growth ring.

Sclereid — A strenthening cell that is not parenchymatous, but which has thick, often lignified secondary walls and which often lacks a protoplast when mature. Sclereids vary in shape, are formed from parenchymatous cells and often branched.

Semi-heterogeneous phloem ray — See half-heterogeneous phloem ray.

Semi-sieve area — A combination of a sieve area and a pit (primary pit-field).

Sieve-area — (=sieve field) A depressed area in the wall of sieve cells and sieve-tube members, perforated by a sieve-like cluster of minute pores through which the protoplast is connected with that of a contiguous sieve element. In sieve-tube members the sieve areas are usually specialized by a more or less pronounced enlargement of the connecting strands, in particular those on the end walls. Both, the sieve cells and the sieve-tube members are commonly associated with callose cylinders.

Sieve cell — A long, slender, conducting cell of the phloem, mostly enucleate at maturity, which is provided with relatively unspecialized sieve areas of the same degree of specialization, lying on the radial walls and especially on the tapering ends of the cells that overlap those of other sieve cells.

Sieve plate — A specialized part of the wall, mostly of the end wall of a sieve-tube member, that has a solitary sieve area (simple sieve plate), or several closely placed sieve areas, often arranged in a scalariform or reticulate manner (compound sieve plate).

Sieve tube — A food-conducting tube of the phloem formed of an axial series of sieve-tube members. Sieve plates are found on the end walls of the sieve-tube members.

Sieve-tube member — A long conducting cell of the phloem that forms one of a series of similar cells arranged end to end to form a sieve tube. The members are enucleate at maturity, and certain sieve areas are more specialized than others, the former being mainly located on either the traverse or the inclined end walls, to form the sieve plates.

Stone cell — An approximately isodiametric sclereid.

Tracheid — An imperforate wood cell with bordered pits on all walls, to congeneric elements.

Wood — (=xylem) The principal strengthening and water-conducting tissue of stems and roots characterized by the presence of tracheary elements (vessel-members and tracheids).

Wood, early — (=spring wood) The less dense, first-formed part of the growth ring, with larger cells.

Wood, late — (=autumn wood, summer wood). The denser, later-formed part of the growth ring, with smaller cells.

3. THE DIFFERENT CELL TYPES IN THE SECONDARY PHLOEM

In the secondary phloem of the Gymnosperms, sieve cells and parenchymatous cells always occur apart from one or more of the following cell types: crystalcell strands, sclereids, stone cells, albuminous cells and phloem fibres.

A periderm is always formed in the older phloem. All the above mentioned cells are produced by the cambium cells (fig. 1).

3.1. The cambium cells

The cambium contains fusiform cambial initials and ray initials, (Reinders and Prakken, 1964; Esau, 1964). It is single-layered and it produces radial rows of xylem elements towards the inside and rows of phloem elements towards the outside. These newly deposited elements still have a general resemblance to the initials from which they have originated. They have to differentiate to their definite form. Consequently it is very difficult to indicate the layer of cambium proper within the active cambium, so the whole area of undifferentiated cells is called: the cambial zone. This zone is larger in the active cambium than in the inactive cambium during the winterrest period.

3.1.1. Fusiform cambial initials

The fusiform cambial initials are thin-walled and they contain much plasma with a distinct nucleus. The initials are longitudinally elongated and radially flattened. In radial sections they are more or less rectangular, in tangential sections tapering or pointed at the end and sometimes forming a roof-like pattern in this way (fig. 1).

As seen in a tangential section, they lie mostly unarranged, that is, the cambium is nonstratified. They may either produce new xylem-elements or phloem-elements by forming tangential walls or they may multiply in a tangential direction, thus producing new cambium cells. To this purpose an oblique traverse wall originates in the middle of the cell (Bannan, 1951, 1965). The two halves develop and grow in this sliding position so that after some time two cambium cells lie in tangential juxtaposition. The active cambium cell has an extremely thin wall, to such an extent that, making sections, the xylem and the phloem get detached. During the winterrest period the wall is much thicker and as strong as the contiguous elements of the phloem; consequently the xylem and the phloem do not loosen in the sections now.

3.1.2. Ray initials

The phloem rays and the wood rays, respectively, originate in a special section of the cambium which is called the ray-meristem, consequently consisting of ray initials. This meristem is not composed of elongated cells like the earlier described fusiform cambium initials, but of initials which are very similar to the ray cells into which they differentiate. There is both a continuous formation of new ray initials in the cambium and a continuous loss (BARGHOORN, 1940). Besides, the ray initials themselves may differentiate, forming phloem rays, gradually changing their cell shape. Another possibility is that the albuminous cells of the phloem rays are formed before the ray-parenchyma cells, while the ray initial, after a short time of inactivity produces either more albuminous cells or both ray-parenchyma cells and albuminous cells (BANNAN 1951, 1953, 1965).

3.2. SIEVE CELLS

The sieve elements are the basic food-conducting elements of the secondary phloem. We may distinguish the less specialized sieve cells as they occur in the Gymnosperms, and the more specialized sieve tubes in the Angiosperms. The sieve cells are elongated cells. In cross section their shape varies from oval to rectangular, while their lumen is either as small as that of the phloem-parenchyma cells or smaller. They are of the same length as the fusiform cambial initials. They neither sclerify nor dilate (ESAU 1964). In contrast to the secondary phloem in the Angiosperms, the secondary phloem in the Gymnosperms, and in the *Pinaceae* in particular, consists mainly of sieve cells, up to 90%. Nuclei are more often found in the mature sieve cells of the Gymnosperms, than in the sieve-tube members of the Angiosperms (EVERT and ALFIERI, 1965). The sieve areas are very thin parts of the walls with perforations or pores through which the protoplasts of contiguous cells are interconnected. They are restricted to the rd. walls. On the overlapping ends of the cells are more sieve areas than in the centre, whereas they hardly occur on the tg. walls (HEPTON and PRESTON, 1960). The walls are thin, achromatic and seldom lignified. Only the walls of the *Pinaceae* show a secondary thickening of especially the rd. walls. The contents of the sieve cells consist of a clear liquid. Starch is present in most cases and protoplasm occurs in the living sieve cells close to the cambium. Later there is only a small cytoplasmic layer present against the wall. Nuclei are to be found in the young, immature cells and also often in the older, mature sieve cells.

Usually the sieve cells remain functional for one vegetation period only, although in several Gymnosperms they may live longer but generally not longer than two or three years. When the sieve cells have become nonfunctional, they usually collapse in a typical manner and the enlarging phloem-parenchyma cells partly take their place.

A thin layer of callose may occur against the wall of the pores of the sieve areas. At the end of the growing season and during the winter rest the amount of callose is augmented considerably and callose plugs may be formed, constricting the sieve areas completely (ULLRICH, 1963; GRILLOS and SMITH, 1959; EVERT and DERR, 1964). The thin layer of callose, as to be seen in functional sieve cells, is probably formed because of a delay in the process of fixing (ESAU and CHEADLE, 1965). Later these callose plugs dissolve again. Mutual contact in a tangential direction through pits is usually impossible because the sieve areas occur mainly on the radial walls. As the sieve cells overlap each other, not ending at the same height, assimilates may be more easily conducted in a longitudinal and tangential direction than in a radial direction. Pit-contact with the phloem-parenchyma cells is scarce, but a contact with both the ray-parenchyma cells and the ray-albuminous cells exists by means of groups of pits on their mutual radial walls. Summarizing we may say that the sieve cells of the Gymnosperms resemble the parenchyma cells, but that they possess some characteristic features to distinguish them. A mature, functioning sieve cell often has a necrotic nucleus, no ordinary starch, but often a carbohydrate, staining red with iodine.

The sieve elements of *Monocotyledoneae* probably do not store this carbohydrate, but so-called granules, which also occur in the vascular Cryptogams (LAMOUREUX, 1961). They do not possess specialized sieve plates as the Angiosperms, but sieve areas, i.e. clusters of specialized pits. By protoplasma strands through the pores of these sieve areas, the protoplasts in the adjacent cells are connected with each other (HEPTON and PRESTON, 1960). These strands are encased by callose; they are wider and more prominent than the plasmodesmata through the pits of the parenchyma cells.

Slime, a proteinaceous substance, is hardly present, or entirely lacking, in some *Dicotyledoneae*, *Monocotyledoneae* and the vascular Cryptograms, but it is abundant in the sieve-tube elements of most *Dicotyledoneae* (LAMOUREUX, 1961), and in the immature Gymnosperm sieve cells. EVERT and ALFIERI (1965) revealed that mature sieve cells of Gymnosperms contain internal strands which are derived ontogenetically from the slime bodies of immature cells. These strands traverse the cell and run from cell to cell through sieve-area pores. The sieve cells have parietal cytoplasm, which can be plasmolyzed even after the tonoplast itself has disappeared (CURRIER, ESAU and CHEADLE, 1955). To the opinion of DULOY, MERCER and RATHGEBER (1961) though, this parietal layer is no cytoplasm, but either plasmalemma or tonoplast. The thin non-lignified walls often show nacreous thickenings; only in the *Pinaceae* a secondary thickening of the walls is to be seen, though SRIVASTAVA (1963b) has suggested that the nacreous thickenings may be similar to the secondary walls of the sieve cells in the *Pinaceae*.

The sieve areas occur almost exclusively on the radial walls. Maybe the *Cycadaceae* are the only exception in this respect (RUSSOW, 1882 and STRASBURGER, 1891). LAMOUREUX (1961) concludes that the sieve elements of the vascular Cryptograms are sieve cells as in the Gymnosperms, but the pores and the connecting strands in the sieve areas are smaller than those in the Gymnosperms and considerably smaller than those in the Angiosperms. In his opinion the sieve cells of the Gymnosperms are more specialized than those in the vascular Cryptogams. Some primitive Angiosperms possess sieve cells instead of sieve-tube members and consequently lack sieve plates as seen in the more advanced species (BAILEY and SWAMY, 1949). A survey of literature (HEMENWAY, 1911, 1913; HUBER, 1939; CHEADLE, 1948) shows that there is entire agreement as to the fact that the sieve cell is considered as a primitive conducting element and the sieve-tube members of the Angiosperms are more specialized elements, as originated from the sieve cells phylogenetically by gradual decrease in length of the end walls and in the amount of sieve areas on these walls. This phenomenon is concomitant with a decrease in number of the sieve areas on the radial walls. In addition ZAHUR (1959) reports a correlation between the shortening of the end walls and both the increase in size of the pores of the compound sieve plates on these walls and the decrease in length of the sieve-tube members.

It is well known (BAILEY, 1944; TIPPO, 1946; CHEADLE, 1953) that the length of the xylem elements, e.g. vessel members, is a reliable criterion in determining the degree of evolutionary specialization of a certain wood species. The shortening of these xylem elements is correlated to the decrease in length of the fusiform cambium initials, but not to the shortening of the sieve elements in the *Dicotyledoneae* secondary phloem (ESAU and CHEADLE, 1955), because there are two different reasons for this gradual decrease in length of the sieve elements during their evolution (ZAHUR, 1959): namely by a decrease in length of the individual fusiform initials and also by the appearance of secondary septa in the sieve-tube member mother cells. The longer meristematic activity of the sieve-tube member mother cells in the *Dicotyledoneae*, in comparison with a shorter similar activity in the *Monocotyledoneae*, is also considered to be a trend of specialization. In the Gymnosperms the sieve cell mother cells differentiate into sieve cells within a short time.

For a long time several controversial opinions existed about the permeability of cytoplasm in sieve-tube elements. STRASBURGER (1891) and SCHUMACHER (1939) concluded that the mature and still functioning sieve-tube elements respond to plasmolyzing reagents.

CURTIS and ASAI (1939) noted that plasmolizing is only possible if special precautions have been taken; HUBER and ROUSCHAL (1938) and ABBE and CRAFTS (1939) believed the cytoplasm not capable of being plasmolyzed.

Eventually CURRIER, ESAU and CHEADLE (1955) demonstrated that this cytoplasm can be plasmolyzed and deplasmolyzed as well.

3.3. PARENCHYMATOUS ELEMENTS

Apart from the sieve cells, the parenchymatous elements of the secondary phloem are also important. These elements are:

Phloem-parenchyma cells, idioblasts, ray-parenchyma cells, sclereids (originated from the parenchyma cells) and the so-called Strasburger albuminous cells. The last two elements belong to a special group of parenchymatous cells; they will be discussed separately.

3.3.1. Phloem-parenchyma cells

Phloem-parenchyma cells are always present. They are axially extended and usually combined with sister cells into strands (fig. 2 and 7). The scarcely present, undivided phloem-parenchyma cells, the fusiform phloem-parenchyma cells, are less longer than the cambium cells from which they have originated. Consequently the individual parenchyma cells of the phloem-parenchyma strands are much shorter. In a longitudinal section the parenchyma cells are oval-shaped or rectangular; in cross section they are oval-shaped or circular (fig. 3). In the older phloem they are no longer cylindrical, but spindle-shaped. Inwards of the periderm the cells are living, functional, and thin-walled; occasionally however the walls may be thickened but never lignified. There is a distinct nucleus and cytoplasm, while starch often occurs, especially in the dormant period. In addition chloroplasts occur and different ergastic materials are stored like tannins, yellow and brownish products of unknown substance, resins, gums, oil, latices etc. (ESAU, 1964; REINDERS and PRAKKEN, 1964; STRASBURGER, 1965). Single parenchyma cells with similar contents, as oil cells and tannin cells, are called idioblasts. Crystals often occur as calcium oxalate. Such crystal-containing phloem-parenchyma cells often form crystalcell strands.

Unlike the secondary phloem of the Angiosperms, the secondary phloem of the Gymnosperms possesses a relatively small amount of phloem parenchyma, while usually early phloem has less parenchyma cells than the late phloem (HUBER, 1939; 1949). Generally the phloem-parenchyma strands are more or less tg. stratified. An easy food transport through pits is mainly possible in a longitudinal and in a tangential direction, because many large pits occur on both the radial walls of two adjacent phloem-parenchyma cells and on the walls to the ray-parenchyma cells. On the traverse walls of two cells situated above each other, many pits occur which are much smaller. On the mutual tangential walls, however, of two phloem-parenchyma cells there are only a few pits, while they are lacking completely on the tangential walls joining sieve cells.

3.3.2. Ray-parenchyma cells

Unlike the phloem-parenchyma cells which are vertically extended, the parenchyma cells of the ray are radially extended (fig. 2, 14 and 50). The ray-parenchyma cells also show a typical arrangement, different from the arrangement, of phloem-parenchyma cells because they have originated from different cambium initials, namely from ray-initials. Their shape is more or less rectangular in cross and radial sections, wheras it is almost isodiametrical in tangential sections. The radial extension of the cells suits their food-conducting function very well, i.e. food transport in a radial direction. The longer the cells, the fewer the traverse walls and probably the easier the food transport. Farther from the cambium, the cells are rounded off, but otherwise they change little. In the dilatation areas, if the ray dilates, their shape changes, especially when ray-parenchyma cells contact a layer of phloem fibres. Then a so-called contact sclerosis may take place. The usually thin walls of the cells thicken on the mentioned spots and they lignify, though generally the cells remain functional and alive.

A distinct nucleus and protoplasm is present and furthermore the contents usually consist of starch with occasionally calcium oxalate crystals. The original round shape of the nucleus in the cambial zone, gradually becomes oval or even stretched, farther from the cambial zone.

Ray-parenchyma cells possess pits: many large pits occur on the radial walls to the phloem-parenchyma cells and often groups of smaller pits on the walls to the sieve cells; on the mutual tangential walls again many pits, while on the mutual cross walls and on the walls to the albuminous cells, groups of smaller pits occur.

Intercellular canals, situated between the radial rows of ray-parenchyma cells, are usually radially extended. Pits connected to pits of the adjacent cell, debouch in these canals, while there also may be blind pits. In the vicinity of the tangential wall, these intercellular canals may enlarge considerably, forming intercellular areas, especially in the older phloem.

3.4. SCLEREIDS AND STONE CELLS

Sclereids originate from parenchyma cells (REINDERS and PRAKKEN, 1964). Many intermediate forms between thickwalled parenchyma cells and genuine well developed sclereids are to be found. Sclereids may occur as isodiametric stone cells, as irregularly shaped sclereids, but also as fibre-sclereids which resemble the phloem fibres (HOLDHEIDE, 1951; EVERT, 1963). However, phloem fibres originate from the cambium directly, whereas the sclereids arise via the parenchyma cells, which are reactivated in a later stage; they grow and their walls thicken. If the thickening is equable, stone cells arise, whereas fibre-sclereids are formed when typical tip growth is present. When growing, the tip often has to avoid an obstacle, in this way forming a bend in the fibre-sclereid (fig. 2). The wall is thick with often a distinct layering, while the walls, of the fibre-sclereids in particular, are lignified.

Stone cells usually have many ramified pit canals and their contents may consist of tannins and crystals. The fibre-sclereids however, have fewer pit canals, which usually are not ramified.

As sclereids initiate from parenchymatous cells, they do not occur close to the cambium, but often in two year old phloem layers and in the ones more outwards, whereas phloem fibres are already present in the functional phloem. Whether sclereids occur or not and in what number, varies with the species. Fibre-sclereids occur in the bands of parenchyma cells between the layers of sieve cells in the early phloem, whereas stone cells occur more often in the dilatation tissues. Phloem fibres occur in tangential layers, alternated by layers of other phloem cells. Several contiguous tangential layers of phloem fibres may constitute the boundary between the late phloem and the early phloem. Stone cells originated from the phloem-parenchyma cells, differ from those originated from ray-parenchyma cells, in many respects.

Both stone cells and fibre-sclereids have a pit-contact with the other elements of the secondary phloem, similar to pit-contact of the parenchyma cells from which they have originated. The number of the pits, however, is much reduced.

3.5. ALBUMINOUS CELLS

The secondary phloem of the Gymnosperms possesses albuminous cells and no companion cells, whereas it usually is the other way round in the Angiosperms.

In the protophloem of the Angiosperms, the companion cells are frequently lacking (ESAU, CHEADLE and GIFFORD, 1953) and also in the secondary phloem of some primitive Angiosperms, while the vascular Cryptogams have neither companion cells nor albuminous cells (LAMOUREUX, 1961). The term 'albuminous cell' is not well chosen; it is in fact a misnomer. STRASBURGER (1891) who used this term for the first time, thought these cells to be rich in proteins, but they are not. It is true that they stain deeper with dyes than ordinary parenchyma cells do; they often have denser protoplasm with a conspicuous nucleus; and their shape is usually elongated. Therefore BARGHOORN (1940) described them as 'erect cells'. However, not all the erect cells are albuminous cells. The term 'companion cells' would be inappropriate too, as the companion cells are ontogenetically associated with the sieve-tube elements and the albuminous cells are not, anyway not in the Gymnosperms. In several *Dicotyledoneae* however, parenchyma cells occur, which are ontogenetically and probably also physiologically, associated with the sieve-tube elements (CHEADLE and ESAU, 1958; EVERT, 1960). They might be considered as intermediate between the albuminous cells of the Gymnosperms and the companion cells of the Angiosperms, because they are not yet genuine companion cells but are more or less associated with the sieve-tube members. Though, as stated above, the term 'albuminous cell' is not appropriate and many intermediate forms between albuminous cells and companion cells occur, we continue to use the term 'albuminous cells' for those cells which are physiologically associated with the sieve elements, but not ontogenetically. STRASBURGER (1891) states that the albuminous cells remain active as long as the sieve cells; they collapse simultaneously. GRILLOS and SMITH (1959) think that some albuminous cells live longer; i.e., those which are not directly connected to the sieve cells; in this case they occur in radial plates of cells. Towards the cambium the height of these cells decreases gradually, and eventually they form phloem rays. Consequently in this stage the rays consist of albuminous cells only. But these cells are probably no genuine albuminous cells, for by definition albuminous cells must have direct connections to the sieve cells. SRIVASTAVA (1963b) has noted that these cells always contain starch, they enlarge in the older phloem and they are in this stage very similar to the ordinary parenchyma cells. Consequently, he too does not use the term albuminous cells in this case but parenchyma cells. ESAU (1964) thinks that genuine albuminous cells cannot contain starch; so the above mentioned erect cells may be intermediate forms between ordinary parenchyma cells and albuminous cells. Even to the opinion of SRIVASTAVA (1963b) not all the erect cells at the margins of heterogeneous rays are albuminous cells, but those containing starch and lacking sieve areas on the walls facing the sieve cells, are ordinary parenchyma cells. His investigations are carried out with material collected both in the active and in the dormant season; he thinks it unlikely that the albuminous cells store starch in the active period (also STRASBURGER, 1891). Consequently, only the erect cells at the margins of the heterogeneous phloem rays, which do not contain starch, are called albuminous cells by SRIVASTAVA.

In our slides, however, we did found starch in some erect cells, with also semi-sieve areas on the walls facing the sieve cells. This is not unlikely as the sieve cells commonly contain starch and there may be a physiological relationship between both cell types.

Albuminous cells are always present. Within the vertical system either singly, scattered between the parenchyma cells, or in longitudinal strands of two or more albuminous cells above each other (fig. 46); in the horizontal system either as more or less erect cells on both the upper and the lower side of the phloem ray (fig. 2, 14 and 15) or in between the ray- parenchyma cells. The latter are called the ray-albuminous cells and the former, occuring in the vertical system, are called the phloem-albuminous cells.

The phloem-albuminous cells may be bordered by the sieve cells on one side only, but more often on both tangential sides. Regarding their shape they resemble the common phloem-parenchyma cells, usually however, they have more protoplasm and a round, conspicuous nucleus, which seems to be larger than the more spindle-shaped or oval nuclei of normal parenchyma cells. Their contents also differ from that of the common parenchyma cells. They live for a much shorter period than the parenchyma cells, so that both the phloem-albuminous cells and the ray-albuminous cells soon lose their protoplasm and their nucleus, collapsing in a typical way.

Pit-contact of the albuminous cells also differs from that of the phloem-parenchyma cells. Phloem-albuminous cells have only a few pits on both the mutual traverse walls to the phloem-parenchyma cells, hardly any or no pit-contact at all on the radial walls to both the phloem-parenchyma cells and the ray-parenchyma cells, but many groups of pits on the tangential walls between the phloem-albuminous cells and the sieve cells. The albuminous cells on both sides of the rays are often rectangularly shaped and extended in a longitudinal direction. These cells hardly have any contact with each other on the tangential walls; on the cross walls to the ray-parenchyma cells and on the radial walls to the sieve cells, groups of small pits occur. There are many pits to the phloem-parenchyma cells in the mutual radial walls. In the functional phloem these cells contain much protoplasm and a conspicuously large nucleus. Both the nucleus and the protoplasm disappear rather suddenly before the cells collapse. They live as long as the sieve cells do.

3.6. PHLOEM FIBRES

The phloem fibres already occur in the functional phloem, as they initiate directly from the fusiform cambial initials and not from the phloem-parenchyma cells like sclereids do (fig. 50). In the Angiosperms the phloem fibres are often surrounded by crystalcell strands; they form bundles of 2–5 cells in width, which do not contain crushed sieve cells or parenchyma cells as distinct from the sclereids (HOLDHEIDE, 1951). In the Gymnosperms they usually occur in tangential layers of one cell in width, though they may be wider, but never more then three cells in width (fig. 52, 69). These layers of phloem fibres usually alternate regularly with layers of other phloem elements, e.g. in the Gymnosperms showing an ordinary sequence. In cross sections the fibres are 3-6 angular, mostly rectangular (fig. 66, 69), often with a conspicuous middle lamella. The secondary walls are hardly stratified; already close to the cambium they are often lignified with a gelatinous layer. Their lumen is small.

The fibres show a typical, intrusive growth; they strengthen the bast, and may become very long. The phloem fibres are interconnected by quite a few of wall perforations, resembling bordered pits. There are many pits to the ray-parenchyma cells and very few pits to the sieve cells. The pit canal is mostly unramified. The fibres are not divided.

3.7. PERIDERM

The periderm or secondary cork, is initiated after the phellogen is formed from a layer of mature, living, phloem-parenchyma cells (fig. 10, 11, 58, 59). The phellogen produces dead cells towards the outside (phellem) and living cells towards the inside, the phelloderm (ESAU, 1964; REINDERS, 1964). The phellem may be homogeneous, i.e. composed of one type of cell, but in the Gymnosperms it often is heterogeneous as in *Picea abies* and in *Pinus sylvestris* where layers of stone phellem alternate with layers of soft phellem and phlobaphen phellem.

The cells outside the periderm are separated from the living phloem and then die, because there is no longer any supply of food and water. In cross sections the various layers of the periderm show an arched pattern in which the more recently deposited layers are continuous with the older ones. The innermost layer of phellem and the dead phloem isolated by it, form together the rhytidome. The different cells undergo a cytological and a chemical change before they are separated from the living phloem (HOLDHEIDE, 1951).

In most cases the parenchyma cells increase in size, crushing the sieve cells completely, which often collapse before, e.g., in the *Pinaceae* (fig. 10, 11), whereas the *Cupressaceae* show the opposite possibility; the parenchyma cells collapse and the sieve cells remain intact (fig. 58 and 59).

Stone cells often arise before the periderm is formed. A second, chemical change before the separation from the living phloem, is the lignification of the walls of almost all the parenchyma cells. So we find outside the periderm empty, dead parenchyma cells with lignified walls. The cells are either crushed sieve cells with much enlarged parenchyma cells, or open sieve cells with crushed parenchyma cells.

4. DISTRIBUTION AND ARRANGEMENT OF CELL TYPES IN THE AXIAL SYSTEM OF THE SECONDARY PHLOEM

4.1. The sieve cells

The sieve cells are elongated, as stated in a preceding chapter. They possess sieve areas, varying in size, shape and number, but almost always restricted to the radial walls, and particularly to the inclined radial walls at the end of the cells. Judging by the way in which these sieve areas are located, the adjacent sieve cells should be able to transport assimilates through pits, both in a longitudinal and in a tangential direction, but not in a radial direction. On the tangential walls however, small groups of pits do occur, which are always connected to the opposite pits in the walls of contiguous phloem-albuminous cells only. The latter, though lying within the parenchymatous cell layer, hardly have any pit-contact with the parenchyma cells, consequently a transport of assimilates through pits from sieve cells to parenchyma cells in a radial direction is hardly possible via these albuminous cells. No other pit-contact of these sieve cells in a radial direction seems to be present. But in a tangential direction the sieve cells possess, in addition to the sieve areas, connecting them to adjacent sieve cells, semi-sieve areas on the radial walls to the ray-albuminous cells and often groups of pits to the ray-parenchyma cells. Sieve cells have no pit-contact with any of the other cell types in the secondary phloem, viz. sclereids, phloem fibres, crystalcell strands, and the cells of the phelloderm. The sieve cells, deposited by the cambium are arranged in radial rows and also often in tangential layers, but the amount of deposited sieve cells varies.

4.1.1. Sieve cells arranged in broad bands

The cambium may deposit very broad bands of sieve cells, to such an amount, that they become the basic elements of the axial system of the secondary phloem (fig. 3). Though several tangential layers of sieve cells are situated against each other, food transport in a radial direction does not seem possible. The scattered phloem rays, perpendicular to the tangential and longitudinal transport system of the sieve cells, are in this case heterogeneous, which implies that they possess ray-albuminous cells in addition to parenchyma cells. Only sieve cells and ray-albuminous cells are interconnected by means of semi-sieve areas on their mutual radial walls. Due to the great number of phloem rays and to the length of the sieve cells, every sieve cell may have pit-contact with at least one ray-albuminous cell. In some wood species, belonging to the *Pinaceae*, the sieve cells are also connected to the ray-parenchyma cells and consequently assimilates can also be conveyed via pits directly to the radial conducting ray-parenchyma cells. If the axial system of the secondary phloem consists primarily of sieve cells, occasionally one or two irregular tangential layers of parenchyma cells per growth layer occur scattered within the mass of sieve cells. These cell types have no pit-contact with each other.

4.1.2. Sieve cells arranged into tangential bands

A second possibility, different from the above mentioned, in which extremely wide bands of sieve cells are produced by the cambium, is that, in which narrower bands of sieve cells are deposited; 1–3 cells wide radially (fig. 42 and 43). Within these bands the food transport through pits seems to be restricted to the longitudinal and the tangential directions; there is pit-contact between these bands and the phloem rays, here consisting of parenchyma cells only. The mentioned bands of sieve cells alternate with bands of parenchyma cells of equal width.

4.1.3. Sieve cells arranged into tangential layers of one cell wide

The sieve cells may also be deposited as tg. layers of one cell wide, in between a one cell wide layer of phloem fibres and a layer of parenchyma cells. This structure is to be seen in the wood species with an orderly sequence as in the *Taxaceae*, the *Cupressaceae* and the *Taxodiaceae* (fig. 51, 66, 69). These one cell wide layers of sieve cells are not interconnected directly, because these layers are always separated by a layer of phloem fibres and a layer of parenchyma cells. Consequently there is probably an independent longitudinal and a tangential food transport through pits within the layer of sieve cells and the layer of parenchyma cells. Tangentially they are connected to the parenchyma cells of the phloem rays, which are homogeneous in this case. These rays are also connected to the 1 cell wide layers of phloem fibres and of parenchyma cells.

4.2. THE PARENCHYMA CELLS

Next to the sieve cells, the parenchyma cells are most important. Not only because of their storage of ergastic substances and because they may differentiate into fibresclereids or into stone cells, strengthening the older bast, but above all, because the living components of the older phloem are mainly parenchyma cells. By then the sieve cells have been nonfunctional for a long time already and usually they are collapsed as well. The parenchyma cells can also be deposited by the cambium in various amounts.

4.2.1. Scattered among sieve cells

They may be deposited as very irregular, narrow tg. layers or singly, lying scattered among the sieve cells (fig. 3, 4). These scattered cells, however, are all interconnected by pits, in this way forming a parenchyma-cell net among the sieve cells. This parenchyma-cell net is also connected with the phloem rays (fig. 17).

4.2.2. In tangential bands

The parenchyma cells may also form tangential bands with a few phloem fibres and albuminous cells, but no sieve cells. Usually these bands are 2–3 cell wide with a food transport possibility through pits in a longitudinal and tangential direction.

4.2.3. *In layers of one cell wide*

This arrangement is present in those wood species where the sieve cells also occur in one cell wide tangential layers, in this way constituting the so-called 'orderly sequence' (fig. 51). These parenchyma cells are closely interconnected, by numerous large pits particularly occurring on the radial walls. They hardly have any pit-contact with the albuminous cells within these layers and no pit-contact at all with the sieve cells.

Consequently the parenchymatous cells consisting here of several tangential layers separated from each other, should be able to an independent food transport in a longitudinal and a tangential direction. The speed of movement of assimilates in parenchyma cells is probably much slower than that in sieve cells; at best the parenchyma cells constitute a secondary or auxiliary conducting system. These different layers are interconnected by the radial food conducting system, the parenchyma cells of the phloem rays. Though the ray-parenchyma cells in the three above mentioned cases are identical, which implies that the radial transport system is similar, the longitudinal and the tangential food conducting system varies from: a parenchyma-cell net, composed of scattered parenchyma cells via wider tangential bands of parenchyma cells, to layers of one cell wide. In the young, active phloem, both the sieve cells and the parenchyma cells are very important, but in the older bast only the parenchyma cells remain alive. The sieve cells have become nonfunctional and are often completely collapsed. On the other hand the parenchyma cells have increased in size with a rounder shape on cross sections and they may store many ergastic substances like starch, crystals, tannins, resins etc. Then the living axial system consists of parenchymatous cells only with many intercellular spaces between them, while of the sieve cells and the albuminous cells only remnants are to be seen.

If the secondary phloem is composed primarily of sieve cells, the differences between the younger and the older secondary phloem are most striking, as in the *Pinaceae* (fig. 3 and 5), whereas they are less pronounced in the wood species with an orderly sequence as in the *Cupressaceae* (fig. 51 and 53).

4.3. THE ALBUMINOUS CELLS

Adjacent albuminous cells hardly have any pit-contact with each other, consequently they do not form a closed system of interconnected cells. On the other hand they do have pit-contact with the adjacent sieve cells and usually a less pronounced contact with the adjacent parenchyma cells.

The albuminous cells may occur: in long longitudinal strands in the phloem-parenchyma bands; scattered or in short longitudinal strands in the parenchyma cell layers; either on one side or on both sides of the ray-parenchyma cells; in between the ray-parenchyma cells; as 1–2 cell high rays of albuminous cells; as a combination of the above mentioned possibilities.

4.4. THE PHLOEM FIBRES

The phloem fibres can be deposited by the cambium in different ways:

4.4.1. *Scattered among the parenchyma cells (fig. 42)*

They are not interconnected but they are connected to the phloem-parenchyma cells in the younger bast.

4.4.2. *Arranged in tangential layers of 1 cell wide*

This is the prevailing possibility (fig. 51). These layers are always included by layers of sieve cells of the same width, but they are not connected to the latter. On the other hand a pit-contact in a tangential direction is present and a pit-contact between these layers of phloem fibres and the phloem rays is also present. The fibres may vary in shape and in thickness of the walls.

4.4.3. *Arranged in tangential bands of 2–3 cells wide*

The phloem fibres may also be deposited as rd. wider tg. bands which are not connected to each other. Pits are present in the tangential walls between the fibres. These wider bands occur in the secondary phloem of the species with an orderly sequence and in particular near the growth ring boundary.

4.5. GROWTH RINGS

As a rule the cambium deposits more xylem than phloem and the amount of phloem varies widely in the different wood species. The annual increment of the secondary phloem, the annual growth rings, are usually still to be distinguished in the older phloem. In hardwood species the parenchyma cells prevail in the late phloem, whereas the early phloem consists mainly of sieve cells (HOLDHEIDE, 1951). The growth ring boundary is often formed by parenchyma cells, so that the parenchyma cells are adjacent to the wide sieve cells of the spring phloem. In soft wood species the parenchyma cells usually do not occur at the growth ring boundary. So here the growth ring boundary is formed by the transition from narrow, late sieve cells to wide, spring sieve cells. In several *Pinaceae* a more or less tangential layer of parenchyma cells is often present in the centre of the annual ring. Also sclereids are very helpful in determining this boundary, because they mainly occur in the early phloem.

In many wood species where an orderly sequence of the secondary phloem is present as for instance in the *Cupressaceae*, the annual increment consists of one or more, but mostly of two of such series (HUBER, 1939, 1949). The number of these series however, is dependent on the age of the individual plant, on the species and also on weather conditions. It often occurs that a growing season is ended by two adjacent layers of phloem fibres, instead of the normal procedure of one layer only. The width of the annual ring is often very narrow, 0.2–0.3 mm. However, young fast growing trees possess wider growth rings than older trees, which grow more slowly. The width of the annual growth ring is nog constant, it decreases by the collapse of the sieve cells. But in the *Cupressaceae* where the sieve cells hardly collapse, this width remains almost constant. By the different changes in the older growth rings, the ray-parenchyma cells may be partly pushed aside, thus forming a phloem ray which is irregular in cross section. These curves in the phloem rays may also be used to locate the annual growth boundaries.

In the older secondary phloem, many parenchyma cells sclerify, forming complete stone cell nests, as for instance in *Abies alba*. Eventually the periderm is initiated.

5. THE PHLOEM RAYS AND THE WOOD RAYS

5.1. THE PHLOEM RAYS

5.1.1. *Structure*

The Gymnosperms possess uniseriate phloem rays, i.e., the rays are one cell wide in tangential direction, but they are usually several cells high. The phloem ray can be homogeneous, heterogeneous or semi-heterogeneous.

5.1.2. *Development*

SRIVASTAVA (1963b) has noted that the kind of the formed phloic elements are dependent on the fusiform cambial initials whose height may either increase, decrease or remain constant. In this way sieve cells, strands of tannin-containing parenchyma cells and crystalcell strands, originate from the increasing or from the regular fusiform initials, whereas the albuminous cells, the starch-containing 'albuminous' cells, crystal cells and different other kinds of parenchyma cells are derivatives of the declining tiers of fusiform initials. It is also possible that the regular tiers of initials differentiate into declining tiers and eventually into phloem rays, composed of exclusively albuminous cells. In a later stage the albuminous cells become marginal cells, while starch-containing cells originate in the middle of the rays. BRAUN (1955a) and GRILLOS and SMITH (1959) conclude that the height of the phloem rays increases till a certain maximum is attained, which remains almost constant afterwards. This height is not only dependent on the age but also on the vitality of the species concerned.

There are several possibilities of ray formation in the secondary phloem of the Gymnosperms. The upper part of a fusiform cambium initial may be separated by a transverse wall from the rest of the initial, forming a ray initial in this way, or a radial wall may be formed in the middle of the cambium initial, separating a segment from it, which may become a ray initial. This is shown by BANNAN (1953) in *Chamaecyparis*. SRIVASTAVA (1963b) also believes this to be a common mode of ray formation. A fusiform initial may also be segmented by several transverse walls and some or even all segments may be converted into ray initials (BANNAN, 1951, 1965; BARGHOORN, 1940, 1941b). According to BANNAN (1951, 1955) particularly the fusiform initials with little contact to the rays, are differentiated into ray initials.

Most rays however, originate from declining radial plates of initials, one cell in width, or from gradually declining fusiform initials. While declining, such fusiform initials deposit mostly elements on the phloem side (CHRYSLER, 1913; BARGHOORN, 1940), consequently, the declining radial plates on the xylem side are much shorter than those on the phloem side. This change of regular tiers into declining tiers and eventually into phloem rays goes with a change of the cell types, originated by these phloic initials. When these tiers are only a few cells high, i.e., in the first stage of ray formation, only the albuminous cells, or only starch-containing parenchyma cells remain. In a later stage the albuminous cells in the heterogeneous rays have obtained their marginal position and the starch containing parenchyma cells occur in the middle of the rays. The increase in height of the rays is caused by the formation of transverse or oblique divisions in the parenchyma cells and by the addition of new ray initials at the margins of the rays and also by the fusion of two phloem rays, because the fusiform initials between them shorten and gradually disappear. A decrease in height may be caused by the loss of some ray initials (BARGHOORN 1940, 1941b); the latter usually are marginal initials. The ray may be cut in two by the loss of a ray initial in the centre and by the intrusion of a fusiform initial into the vacated space.

So during the development of a ray the height increases because the number of the rows of cells is increasing, whereas the width remains constant, i.e. always uniseriate, except in those rays where radial resin canals occur. As stated above, a one cell high phloem ray of *Pseudotsuga taxifolia*, for instance, consists of a radial row of albuminous cells; by division a two cell high ray is formed, still consisting of albuminous cells exclusively. Only when the ray becomes three or more cells high, ordinary ray-parenchyma cells do occur in the centre of the ray. Originally both the albuminous cells and the parenchyma cells possess an abundance of protoplasm with a conspicuous nucleus. The ray-parenchyma cells elongate in a radial direction further from the cambium. The amount of protoplasm has remained constant; it has a parietal position or it may form strands from the cell wall to the nucleus. The cell shape becomes more oval. The albuminous cells which originally have much protoplasm and a large nucleus, lose both protoplasm and nucleus rather suddenly, further from the cambium, without a stretching of the cells. Gradually the empty cells collapse. The common wall between an albuminous cell and a ray-parenchyma cell remains intact, but the longitudinal walls fold back into a typical S-shape. Eventually a compact mass of collapsed cells is left. Consequently the older phloem ray consists of living parenchyma cells with collapsed nonfunctional albuminous cells on both sides of the ray (fig. 15, 16).

In places where ray-albuminous cells occur on the phloem side, narrow, mostly dead tracheids occur on the xylem side; where ray-parenchyma cells occur on the phloem side, wood-ray parenchyma cells occur on the xylem side (fig. 14).

Species like *Chamaecyparis pisifera* with homogeneous phloem rays and homogeneous wood rays, show a development resembling that of *Pseudotsuga taxifolia;* the only difference is that rays of the former are composed of parenchyma cells only (fig. 60). Both ray-tracheids and ray-albuminous cells are lacking; consequently the structure of the ray close to the cambium is almost similar to the structure further from the cambium, although the ray-parenchyma cells further from the cambium are rounded off and are no longer rectangular in radial sections, like the cells close to the cambium. In addition, the nucleus has become oval (fig. 61, 62).

5.1.3. *Phylogenetic stages*

The thickening of the walls of the wood ray-parenchyma cells and also but not to such an extent, the pitting on the radial walls of these cells with the elements of the axial system, are important factors in determining the developmental stage of the considered species of the Gymnosperms (GREGUSS, 1955).

The characteristics stated above are less important if we try to classify the different families by means of the phloem rays. There is a certain trend for a gradual thickening of the transverse and radial walls of the phloem ray-parenchyma cells in different families. The walls of the parenchyma cells of the phloem ray in the *Pinaceae* for instance, are thicker than the corresponding walls in the *Ginkgoaceae*, but the transition is a very gradual one; furthermore the tangential walls remain rather thin. More characteristic is the cell shape, the pitting and the structure of the phloem ray. Besides the structure and the arrangement of the different cell types in the axial system of the secondary phloem, are determining as well.

We may distinguish 5 different phylogenetic stages (fig. 73):

1. The phloem rays are homogeneous, consisting exclusively of procumbent parenchyma cells which all have pit-contact with both the parenchyma cells and the sieve cells of the axial system. The axial system is composed of narrow, one cell wide, tangential cell layers forming an orderly sequence, while the phloem-albuminous cells lie scattered in between the parenchyma cells.

2. The phloem rays are homogeneous with procumbent ray-parenchyma cells, with more or less erect marginal parenchyma cells. All the ray-parenchyma cells, the sieve cells and the parenchyma cells of the axial system are interconnected. The axial system consists of rather wide tangential bands of sieve cells, alternated with bands of phloem-parenchyma cells in which long longitudinal strands of phloem-albuminous cells occur.

3. The phloem rays are semi-heterogeneous, phloem-albuminous cells are scarcely present. The axial system consists mainly of sieve cells which are connected to both the parenchyma cells and the albuminous cells of the rays. One irregular tangential layer of phloem-parenchyma cells is deposited within one growth layer. There is pit-contact between phloem-parenchyma cells and both the cell types of the phloem ray.

4. The phloem rays are heterogeneous. The axial system consists mainly of sieve cells which are connected to both the parenchyma cells and the albuminous cells in the rays. One irregular tangential layer of parenchyma cells is deposited within one growth layer. There is pit-contact between phloem-parenchyma cells and both the cell types of the phloem ray.

5. The phloem rays are heterogeneous. The axial system consists mainly of sieve cells which are connected to the ray-albuminous cells only and not to the parenchyma cells in the centre of the rays. The phloem-parenchyma cells constitute a parenchyma cell net. There is pit-contact between phloem-parenchyma cells and both the cell types of the phloem ray.

5.2. THE WOOD RAYS

5.2.1. *Structure*

Usually the wood rays of the Gymnosperms are uniseriate too; they are called homogeneous if they are composed of exclusively procumbent parenchyma cells and heterogeneous if ray-tracheids occur on both sides of the ray.

The family to which a specific wood species belongs, is determining for the wood ray type, as can be seen in the following list:

		phloem ray	wood ray
Cycadaceae	*Cycas circinatum* L.	homogeneous	homogeneous
Ginkgoaceae	*Ginkgo biloba* L.	,,	,,
Podocarpaceae	*Podocarpus nerifolius* D. Don	,,	,,
Taxaceae	*Taxus baccata* L.	,,	,,
Cupressaceae	*Chamaecyparis pisifera* Endl.	,,	,,
,,	*Thuja plicata* Lamb.	,,	,,
,,	*Thujopsis dolabrata* Sieb. et Zucc.	,,	,,
Taxodiaceae	*Taxodium distichum* A. Rich.	,,	,,
,,	*Cryptomeria japonica* D. Don	,,	,,
Pinaceae	*Abies concolor* Hoopes.	heterogeneous	,,
,,	*Pseudolarix kaempferi* Britt.	,,	,,
,,	*Tsuga canadensis* Carr.	±heterogeneous	±heterogeneous
,,	*Cedrus libani* A. Rich.	,,	,,
,,	*Larix decidua* Mill.	heterogeneous	heterogeneous
,,	*Picea spec.*	,,	,,
,,	*Pseudotsuga taxifolia* Britt.	,,	,,
,,	*Pinus sylvestris* L.	,,	,,

It is evident from the list above, that the species of the first mentioned families possess both homogeneous phloem rays and homogeneous wood rays. Heterogeneous rays occur in the *Pinaceae* for the first time. In *Abies concolor* and in *Pseudolarix kaempferi* only the phloem rays are heterogeneous, whereas the wood rays are still homogeneous. In *Tsuga canadensis* and in *Cedrus libani* both phloem rays and wood rays, are semi-heterogeneous, i.e. that the albuminous cells in the phloem ray and the tracheids in the wood ray are not continuous, but can be interrupted or can be lacking completely on one side. In species like *Larix decidua, Pseudotsuga taxifolia* and *Pinus sylvestris* both ray types are entirely heterogeneous.

5.2.2. *Development*

The heterogeneous wood ray of species belonging to the *Pinaceae, Pseudotsuga taxifolia* for example, develops as follows (fig. 13). In a primary stage it is only one row high, consisting exclusively of ray-tracheids; it becomes two rows high after division, still exclusively composed of tracheids and it is only after a radially extended row of parenchyma cells has differentiated between these tracheids, that the ray develops into its definite form and structure. After repeated divisions of the parenchyma cells, at last a ray has been developed which is composed out of many rows of ray-parenchyma cells with one row of tracheids on both the upper and the lower side of the ray. Occasionally two or more rows of tracheids may occur and it is even possible to find a row of tracheids in between the parenchyma cells.

Tracheids do not always form the beginning of the ray of the *Pinaceae* (BANNAN, 1934; THOMPSON, 1910). In *Tsuga canadensis* for instance, a one cell high ray in the xylem may be composed of parenchyma cells, whereas in the phloem it may consist of albuminous cells. A two cell high ray in the xylem may be composed of a row of parenchyma cells bordered by a row of tracheids and in the phloem it is composed of two rows of albuminous cells (fig. 34).

6. TYPES OF SECONDARY PHLOEM BASED ON ARRANGEMENT OF CELL TYPES

The cell types, as described in the preceding chapter, can occur in various combinations, to be classified into three main groups. These three groups differ in many respects and will be discussed separately. In this thesis they will be called the three main types of secondary phloem. Some species, though belonging to one of the three above mentioned types, already show features of the next type and may be considered as intermediate forms.
The three groups are:

6.1. SECONDARY PHLOEM CONSISTING OF BROAD BANDS OF SIEVE CELLS (*PSEUDOTSUGA TAXIFOLIA* TYPE)

The species in this group, all belonging to the *Pinaceae*, show a phloem consisting mainly of sieve cells in which the few parenchyma cells occur either in discontinuously tangential bands, or scattered between the sieve cells, forming a parenchyma-cell net. Several intermediate forms are possible between these two extremes.
The phloem rays of all the species, belonging to this type, are heterogeneous or semi-heterogeneous. The sieve cells, adjacent to the phloem rays, have either pit-contact with the albuminous cells only, or in some cases with both the albuminous cells and parenchyma cells of the rays.

The secondary phloem of the Douglas-fir is, in our opinion, the most characteristic of this bast type. It has a net of phloem-parenchyma cells, heterogeneous phloem rays, while the sieve cells have pit-contact with the ray-albuminous cells only. It is considered to be the primary stage in the phylogenetic sequence of the secondary phloem, seen in respect of this study. The secondary phloem of some wood species belonging to this type and of several intermediate forms between this first stage and the next one of *Ginkgo biloba*, will be described individually.

6.1.1. *Pit-contact between sieve cells and phloem rays via the albuminous cells (fig. 18)*

Apart from *Pseudotsuga taxifolia* BRITT., also *Pinus sylvestris*, *Larix decidua* and *Abies concolor* among others belong to this group.

6.1.1.1. *Pseudotsuga taxifolia* BRITT. (fig. 2 to 18 inclusive)

No tangential layering of the different cells is to be seen in the phloem of *Pseudotsuga taxifolia*. The secondary phloem consists mainly of sieve cells; only close to the cambial zone are these cells arranged in regular tangential layers (fig. 3 and 4). They possess large sieve areas which do not lie closely together and are restricted to the radial walls. The phloem rays are heterogeneous. The albuminous cells have pit-contact with the ray-parenchyma cells, the phloem-parenchyma cells and the sieve cells. The ray-parenchyma cells have only pit-contact with the phloem-parenchyma cells. Parenchyma cells lie scattered among the sieve cells, forming discontinuous and irregular tangential layers. The cells within such a layer are connected to one another by pits, forming a parenchyma-cell net. These nets are also interconnected in a radial direction.

The phloem-parenchyma cells have, when touching each other, pits on the radial, traverse and tangential walls, but they have no pits on the mutual tangential walls to the sieve cells. Though there are wide layers of sieve cells, every sieve cell might have contact with a ray-albuminous cell, because the phloem rays traverse this mass of sieve cells frequently and the sieve cells are long cells.

Presumably no direct movement of food is possible here through pits from sieve cells to ray-parenchyma cells, but only via the ray-albuminous cells because the sieve cells hardly have any connections with ray-parenchyma cells (fig. 7). Through the latter a radial food transport may be possible. After a short time the sieve cells and the albuminous cells collapse simultaneously (fig. 8 and 9). The longitudinal walls of the ray-albuminous cells fold back in a typical S-shape; a formless mass of these crushed cells remains on both sides of the phloem ray. The ray-parenchyma cells on the borders of the ray become more or less hexagonal, while the cells in the centre increase in size. A distinct pit-contact with the phloem-parenchyma cells still exists.

Because most of the sieve cells collapse, by then the axial system of the older phloem consists of parenchyma cells, which are still alive and functional and increasing in size (fig. 8). Some of the parenchyma cells differentiate as sclereids, fibre-sclereids, or as stone cells. Although within these particular strands vertical food transport is hampered, on the whole sclereids hardly effect the food transport, because of the density of the parenchyma cell net. The sclereids only appear after the second year (GRILLOS and SMITH, 1959) and lie scattered between the parenchyma cells; they taper and usually their walls become very thick, crushing the other cells. Crystalcell strands also occur, mainly close to the growth ring boundaries.

In the course of time the parenchyma cells initiate a periderm. The cells outside this periderm decline and die; all the sieve cells are crushed by the parenchyma cells which enlarged before they are cut off from the living cells (fig. 10, 11). Thus the tissue outside the periderm consists of areas of crushed sieve cells, parenchyma cells, sclereids, one or two crystalcell strands, and large intercellular spaces.

Apart from the above mentioned parenchyma cells, some other types of parenchyma cells are to be found in the secondary phloem of Douglas-fir.

We find five basic types, viz.:

1. Apart from the ray-parenchyma cells, in the axial system of the secondary phloem ordinary unspecialized parenchyma cells occur, which originated from fusiform cambial cells, divided into many smaller cells by transverse walls. These cells often occur in a more or less tangential band, sometimes at the end

of the growth layer. Fast grown trees sometimes show two of these bands in an early and in a late stage of the growing season. A parenchyma cell net is formed. Apart from starch they also store resinous and tanniniferous products. They enlarge in the older phloem and may differentiate into sclereids after the second growth layer. In an early stage these sclereids may still contain a nucleus, cytoplasm and resin, but later on all this is absent.

2. Parenchyma cells originated from cambium initials, without traverse septation. In this case the parenchyma cells are approximately of the same length as the original fusiform cambium initials. They often contain resin, but no tannins, while simple crystals are abundant. The parenchyma cells collapse after the crystal formation, but they are still easily to distinguish in the older phloem, because of their contents of resins and crystals.
3. 'Erect albuminous cells'. Phloem-parenchyma cells, similar to those mentioned under 1., but with the following distinctions:

During the winter rest period they contain neither resins nor tannins but only starch; they possess primary pit fields opposite the sieve areas of the adjacent sieve cells; they die after the sieve cells disorganize; usually they do not occur in long longitudinal strands as with type 1., but more often in radial plates, which are originally four cells high, but gradually decrease in height nearer to the cambium. They may have originated from cambium initials, which form wood rays on the xylem side. In the latter mentioned case the radial plates are usually two cells high and show a similarity to phloem rays, consisting exclusively of erect ray-albuminous cells. Such parenchyma cells often connect the albuminous cells of two phloem rays, lying above each other. Thus parenchyma cells belonging to type 3., resemble albuminous cells; in our opinion they should be considered as albuminous cells. Pit-contact of 'erect albuminous cells' with the sieve cells is more intense in younger trees than in older trees (GRILLOS and SMITH, 1959).

4. Parenchyma cells, similar to the above mentioned 'erect albuminous cells', but lacking pit-contact with the sieve cells. They contain neither resins, nor tannins and they do not collapse simultaneously with the sieve cells, but shortly after.
5. Ray-parenchyma cells, radially stretched, increasing gradually in size in the older phloem, while the radial parenchyma strands become separated by the enlarging intercellular spaces. They store much starch, but little resin and tannin, as far as uniseriate phloem rays are concerned, as a matter of fact they are usually uniseriate.

Although the sieve cells of many Conifers remain functional for one year only, the *Pinaceae* are exceptional and so is *Pseudotsuga taxifolia*. During the second year the 'definite' callose cylinders are deposited and this is only possible in living cells. Early in the growing season all the formed callose is dissolved; later, during the following growing season, they are deposited again; first in the growth layer of the preceding year; namely on the half sieve areas between sieve cells and albuminous cells and between sieve cells and 'erect albuminous cells' and at last on sieve areas between the sieve cells. This callose is called 'definitive callose'. Shortly after, 'dormancy callose' plugs are deposited on the sieve areas within the growth layer of the present year. During the winter period the callose masses in both growth layers remain and are dissolved again during the following year.

Thus for every sieve cell there is a callose deposit on the sieve areas twice; first during the first growing season, dissolving when the next season starts, second during the second growing season another deposit of callose, the so-called 'definitive callose' is formed which, however, also gradually disappears in the following growing season.

Summary:

Bark: well developed.

Outside the periderm: the sieve cells collapse. Only phloem-parenchyma cells and ray-parenchyma cells remain, apart from sclereids and an occasional crystalcell strand.

Growth layers: distinct.

Mechanical tissue: phloem fibres are lacking, but instead sclereids occur, originated from phloem-parenchyma cells; besides some crystalcell strands are present.

Sieve cells: the most common cells of the secondary phloem are sieve cells; they form the bulk of the axial system. No direct pit-contact is present between sieve cells and ray-parenchyma cells. There is an intensive pit-contact between two adjacent sieve cells on their mutual radial walls and between sieve cells and albuminous cells.

Albuminous cells: albuminous cells in the axial system are scarce; instead ray-albuminous cells occur on both sides of the phloem ray. They have pit-contact with the sieve cells, the phloem-parenchyma cells and the ray-parenchyma cells.

Phloem-parenchyma cells: they are scarcely present, they do not form regular tangential layers of cells between the sieve cells. They form a parenchyma cell net. There is a direct mutual pit-contact between this net and the ray-parenchyma cells.

Phloem-rays: phloem rays and wood rays are predominantly heterogeneous.

6.1.1.2. *Pinus sylvestris* L. (fig. 19, 20 and 21)

Bark: well developed.

Outside the periderm: the sieve cells are completely collapsed and only wall remnants can be found in this stage. The axial system is formed by phloem-parenchyma cells with an occasional crystalcell strand.

Growth layers: rather distinct.

Mechanical tissue: crystal cells hardly occur, while sclereids and phloem fibres are lacking completely.

Sieve cells: they constitute the most abundant cell type of the secondary phloem and they are able to transport food in both a longitudinal and a tangential direction. Via the ray-albuminous cells, they have contact with the ray-parenchyma cells. No direct pit-contact is present between sieve cells and ray-parenchyma cells. The sieve cells collapse after a functioning period of one or two years (fig. 21).

Albuminous cells: mainly present as ray-albuminous cells on either side of the phloem ray. They are longitudinally stretched, especially in the cambial zone. They have pit-contact with the sieve cells, phloem-parenchyma cells and ray-parenchyma cells.

Phloem-parenchyma cells: the parenchyma cells lie either scattered among the sieve cells or arranged into irregular tangential bands (fig. 19). They form a net of parenchyma cells and have pit-contact with the phloem rays via the albuminous cells and the ray-parenchyma cells. In the older phloem food transport is only possible via the parenchyma cells, viz. the phloem-parenchyma cell net and the ray-parenchyma cells.

Phloem rays: the phloem ray is heterogeneous with ray-albuminous cells, remarkably stretched in a longitudinal direction (fig. 20). Especially between the ray-parenchyma cells, intercellular spaces are found, stretched in a radial direction, probably they do not occur between the ray initials. The wood ray is also heterogeneous; often the ray-parenchyma cells are accompanied by several rows of ray-tracheids.

6.1.1.3. *Larix decidua* MILL. (fig. 22, 23 and 24)

The secondary phloem of *Larix decidua* shows a structure intermediate between *Tsuga canadensis* and *Pseudotsuga taxifolia.*

Bark: well developed.

Outside the periderm: the sieve cells are completely collapsed. Only parenchyma cells, crystalcell strands and sclereids are present.

Growth layers: indistinct.

Mechanical tissue: many crystalcell strands occur, particularly in the growth ring boundary. In the older phloem fibre-sclereids originate, as seen in *Pseudotsuga taxifolia* and stone-cell nests are also formed as in *Abies concolor, Tsuga canadensis* and *Cedrus libani.*

Sieve cells: as in all *Pinaceae* the phloem tissue consists mainly of sieve cells, having contact with the ray-parenchyma cells via the ray-albuminous cells. No direct pit-contact is present between the sieve cells and ray-parenchyma cells. The sieve cells are more or less collapsed after the second year, causing a tangential rupture of the tissue structure.

Albuminous cells: mainly present as ray-albuminous cells. They occur on both sides of the phloem ray and have pit-contact with the sieve cells, the phloem-parenchyma cells and the ray-parenchyma cells.

Phloem-parenchyma cells: the parenchyma cells lie scattered between the sieve cells, or are arranged into discontinuous tangential layers (fig. 22 and 23). All these cells form a more or less closed parenchyma cell net. There is pit-contact between this net and both the ray-parenchyma cells and the ray-albuminous cells.

Phloem rays: the phloem rays and the wood rays are both heterogeneous (fig. 24).

6.1.1.4. *Abies concolor* HOOPES (fig. 25 to 29 inclusive)

Bark: well developed.

Outside the periderm: the sieve cells are completely collapsed, where as the parenchyma cells increase in size before they are cut off.

Growth layers: distinct. In the functioning phloem there is also a pronounced distinction between the wider spring sieve cells and the narrower summer sieve cells.

Mechanical tissue: many crystalcell strands are present. In the older phloem stone-cell nests are formed.

Sieve cells: the secondary phloem consists mainly of sieve cells. A longitudinal and a tangential food transport through pits is possible through the sieve cells to the ray-parenchyma cells, via the ray-albuminous cells. No direct pit-contact is present between sieve cells and ray-parenchyma cells.

Albuminous cells: mainly present as ray-albuminous cells, on either side of the phloem ray. They have pit-contact with the sieve cells, the phloem-parenchyma cells and the ray-parenchyma cells.

Phloem-parenchyma cells: the phloem-parenchyma cells are arranged in more or less tangential layers of one cell wide. In these layers there is quite a number of crystal cells to be found (fig. 25). A parenchyma cell net is lacking; therefore the layers which occur mainly in between the wider spring sieve cells and the narrower summer sieve cells, have no direct pit-contact. An intimate pit-contact with both the albuminous cells and the ray-parenchyma cells is present.

Many of the parenchyma cells differentiate into stone cells in the older phloem. In this way large nests of these cells make the older bast very hard, while they also disturb the tangential layering. The masses of stone cells lie scattered between the soft cell types, viz. the phloem-parenchyma cells and the partly crushed sieve cells.

Phloem rays: the phloem ray is heterogeneous, the wood ray is homogeneous. Thus in the cambial zone erect albuminous cells are deposited on the phloem side along both sides of the ray-parenchyma cells; only procumbent wood ray-parenchyma cells are formed on the xylem side (fig. 27).

The ray-albuminous cells, which probably have the same functional relationship to the sieve cells as the companion cells have to the sieve tubes, here, as in all above mentioned examples, possess an additional function as conducting cells in the food transport system from sieve cell to ray-parenchyma cell and vice versa. These albuminous cells however, disorganize after a short time and only a narrow strip of crushed cells remains, all along the ray-parenchyma cells (fig. 28 and 29). As the sieve cells collapse simultaneously, only the parenchymatous cells remain.

6.1.2. *Pit-contact between sieve cells and all phloem ray elements* (Tsuga canadensis *subtype*)

The four above described species are all examples of the *Pseudotsuge taxifolia* type. On the other hand some species, though still belonging to the *Pseudotsuga taxifolia* type, differ slightly from it. The sieve cells of this group do not only have pit-contact with the ray-albuminous cells, but also with the ray-parenchyma cells (fig. 36). This group will be called the *Tsuga canadensis* subtype. Except for *Tsuga canadensis*, the species belonging to this type are among others:

6.1.2.1. *Tsuga canadensis* CARR. (fig. 30 to 36 inclusive)

Bark: well developed.

Outside the periderm: the sieve cells are completely crushed and the parenchyma cells have increased in size.

Growth layers: indistinct or absent.

Mechanical tissue: crystalcell strands are present. In the older phloem nests of sclereids occur.

Sieve cells: the axial system consists mainly of sieve cells. They have pit-contact with both the albuminous cells and the parenchyma cells of the phloem ray. Radial and longitudinal transport of food through pits is possible.

Albuminous cells: mainly as ray-albuminous cells. They occur irregularly and may even be absent on one side of the phloem ray in places, or occasionally on both sides. Pit-contact is present between these cells and the sieve cells, the phloem-parenchyma cells and the ray-parenchyma cells. In the older phloem the ray-albuminous cells are collapsed, while the nonfunctional sieve cells have hardly decreased in size. Phloem-albuminous cells occur more often in this type.

Phloem-parenchyma cells: they are rather regulary arranged in tangential layers, more regular than in *Cedrus* (fig. 30, 37). These tangential layers are independently situated and separated by sieve cells; they have no pit-contact with the latter. There is no parenchyma-cell net. Pit-contact exists between phloem-parenchyma cells and both ray-albuminous cells and ray-parenchyma cells.

Phloem rays: the phloem ray and the wood ray are semi-heterogeneous; the ray-albuminous cells, respectively wood-ray tracheids, occur either on one side of the rays or on both sides, or they may be absent (fig. 32, 34). Intercellular spaces occur between the elements of the phloem ray, the ray initials and the elements of the wood ray. Because the ray-albuminous cells may be absent at several places, it seems understandable that the sieve cells have pit-contact with both the ray-albuminous cells and the ray-parenchyma cells (fig. 32, 35 and 36).

6.1.2.2. *Cedrus libani* A. RICH. (fig. 37 and 38)

Bark: well developed.

Outside the periderm: the sieve cells are completely collapsed; phloem-parenchyma cells and ray-parenchyma cells, stone cells and some crystalcell strands remain.

Growth layers: indistinct.

Mechanical tissue: crystalcell strands occur, while in the older phloem some of the parenchyma cells differentiate into stone cells.

Sieve cells: the structure of the secondary phloem is almost similar to that of *Tsuga canadensis.*

Albuminous cells: mainly as ray-albuminous cells. They are not always present on both sides of the phloem ray and may even be absent altogether. There is a pit-contact with the sieve cells, the phloem-parenchyma cells and the ray-parenchyma cells. Phloem-albuminous cells regularly occur.

Phloem-parenchyma cells: within an annual growth layer one or two continuous layers of parenchyma cells occur between the sieve cells (fig. 37). The former are not entirely tangential as in the *Cupressaceae*, but they tend to a radial direction several times. Besides many crystals are deposited in several parenchyma cells so that crystalcell strands are formed, mostly at the growth ring boundary. The different layers of parenchyma cells are separated from each other and there is no parenchyma cell net. By means of wide pits the phloem-parenchyma cells are connected to both the ray-albuminous cells and the ray-parenchyma cells. In the older phloem some parenchyma cells differentiate into stone cells.

Phloem rays: the phloem rays and the wood rays are semi-heterogeneous.

6.1.2.3. *Picea spec.* (fig. 39, 40 and 41)

The secondary phloem of *Picea spec.* resembles that of *Pseudotsuga taxifolia* more than *Tsuga canadensis* and *Cedrus libani* do. Still it belongs to the *Tsuga canadensis* subtype because there is pit-contact between sieve cells and all the elements of the phloem ray.

Bark: well developed.

Outside the periderm: the sieve cells collapse completely. Only parenchyma cells and stone cells remain.

Growth layers: indistinct or absent.

Mechanical tissue: occasionally stone cells occur. Chrystalcell strands and sclereids are almost lacking.

Sieve cells: the axial system is formed mainly of sieve cells which show a regular layering. These cells have contact with both the ray-albuminous cells and the ray-parenchyma cells (fig. 40, 41). The further from the cambial zone, the more sieve cells disorganize. The sieve cells of the early phloem collapse later than those of the late phloem of the same growth layer, but eventually their radial walls fold together into a typical S-shape, while a shift in tangential direction takes place.

Albuminous cells: they occur mainly as ray-albuminous cells. There is pit-contact ot the sieve cells, to the phloem-parenchyma cells and to the ray-parenchyma cells.

Phloem-parenchyma cells: there is a more or less coherent tangential layer of parenchyma cells in the centre of the growth ring. There is no pit-contact to the sieve cells, but only to the ray-albuminous cells and to the ray-parenchyma cells. There is no parenchyma cell net.

Phloem rays: the phloem ray and the wood ray are heterogeneous.

6.2. SECONDARY PHLOEM CONSISTING OF BANDS OF SIEVE CELLS AND BANDS OF PARENCHYMA CELLS (*GINKGO BILOBA* TYPE)

This type shows a regular pattern of alternating, rather wide, tangential bands of parenchyma cells and of sieve cells. Apart from *Ginkgo biloba*, the species of the *Cycadaceae* and the *Araucariaceae* belong to this type and some of the *Podocarpaceae* and the *Taxaceae*. The species belonging to the *Taxaceae* however, are already to be considered as intermediate forms between the *Ginkgo biloba* type and the next group of the *Chamaecyparis pisifera* type. Apart from the description of *Ginkgo biloba*, as characteristic for this group, short descriptions will be given of *Podocarpus nerifolius* and *Taxus baccata*, successively.

6.2.1. Ginkgo biloba *L.* (*fig. 42 to 47 inclusive*)

This species belongs to the family *Ginkgoaceae*. The secondary phloem consists of phloem-parenchyma cells, sieve cells, some phloem fibres and some crystal cells and phloem-albuminous cells. Though an orderly sequence does not yet exist, but a distinct tangential layering is present. Bands of parenchyma cells, 1–3 cells wide in radial extent, alternate with bands, 1–2 cells wide, of sieve cells (fig. 42, 43 and 44).

Bark: well developed.

Outside the periderm: neither the sieve cells nor the parenchyma cells collapse. Thus the bast outside the periderm resembles the older bast.

Growth layers: indistinct or absent.

Mechanical tissue: some very large cells are formed. Thick-walled phloem fibres, with a very small lumen, occur in the parenchyma cell band. These fibres hardly interfere with the food transport, because there are so few of them and because the parenchyma band is more than 1 cell wide. The phloem fibres have pores on the same walls as the parenchyma cells have, but not so many of them. In reference to the structure of the wall which is clearly layered, the fibres resemble the stone cells, particularly on cross sections, but they have originated from the cambium initials and their structure is also fibrous, so obviously they are phloem fibres.

Sieve cells: the volume taken by all the sieve cells is almost equal to that taken by the parenchyma cells. The sieve cells are wide and possess many large oval-shaped, radially stretched sieve areas on the radial walls. They have pit-contact with the phloem-albuminous cells and the ray-parenchyma cells, but hardly any contact with the phloem-parenchyma cells. Though the band of sieve cells is 1–2 cells wide, the possibility exists that every individual sieve cell is connected to an albuminous cell.

Albuminous cells: they occur in the phloem-parenchyma cell bands. They do not lie scattered between the parenchyma cells, but they form long longitudinal strands of cells which are not part of parenchyma-cell strands. They have pit-contact with the sieve cells and also with the phloem-parenchyma cells and even with the ray-parenchyma cells. They collapse in a typical way after the sieve cells have become nonfunctional.

Phloem-parenchyma cells: these cells occur in bands, 1–3 cells wide. These bands, more or less tangential, are intimately connected to the phloem rays (fig. 45, 47). There is also pit-contact between phloem-albuminous cells and phloem-parenchyma cells, but not with the sieve cells.

Phloem rays: both the phloem ray and the wood ray are homogeneous. The ray-parenchyma cells are rather high, almost erect, particularly the border cells and those in the cambial zone. These cells also have a distinct pit-contact with both the sieve cells and the phloem-parenchyma cells. Intercellular spaces occur in a radial direction in the phloem rays, traversing the cambium and continuing into the wood rays. They do not widen in the older bast farther from the cambium; on the contrary they are more or less crushed.

Summarizing we have two bands of cells, viz. one of sieve cells and one of parenchyma cells, with phloem fibres and phloem-albuminous cells in the latter band. Between the mentioned bands two ways of food transport seem to be possible:

a. In a tangential direction to the phloem rays within the bands and from there to the adjacent band;

b. In a radial direction directly between two adjacent bands, viz. via the phloem-albuminous cells.

These albuminous cells still resemble the ordinary parenchyma cells except for their pitting and their collapse; they are less specialized than those in the *Cupressaceae*. Thus the separation between the two cell types radially, is not so distinct as in the *Cupressaceae*.

Outside the zone near the cambium the structure of the secondary phloem changes, partly because the phloem-albuminous cells collapse in a typical way and partly because the phloem-parenchyma cells increase considerably in size when large crystals originate within these cells. On the other hand there is hardly any collapse of the sieve cells, while the other parenchyma cells do not enlarge much (fig. 46).

So in the older phloem the different tangential bands of phloem-parenchyma cells have no direct contact with each other but only via the phloem rays.

6.2.2. Podocarpus nerifolius *D. DON*

Podocarpus nerifolius belongs to the *Podocarpaceae*, systematically between the *Ginkgoaceae* and the *Taxaceae*. As far as the anatomy of its secondary phloem is concerned, it is also intermediate between the *Ginkgoaceae* and the *Taxaceae*. Some species of this family resemble *Ginkgo biloba* with a secondary phloem consisting of bands of parenchyma cells and of sieve cells; others have layers of phloem fibres as well, whereas species with a more or less orderly sequence (and thus resembling *Taxus baccata*), also occur.

Podocarpus nerifolius has tangential layers of phloem fibres. Besides several bands of sieve cells and parenchyma cells alternate without a single layer of phloem fibres between them. Also *Dacrydium* belongs to this family. *Dacrydium fonkii* has an axial system, consisting of sieve cells and parenchyma cells as in *Ginkgo biloba*. *Dacrydium elatum* has phloem fibres scattered in the bands of parenchyma cells, while the *Podocarpus* species show the beginning of an orderly sequence (LIESE and MATTE, 1962).

This rhythm is very irregular in *Podocarpus nerifolius* and in *Podocarpus blumei* as either the layers of phloem fibres are lacking occasionally, or are interrupted by parenchyma cells, whereas the secondary phloem of *Podocarpus rumphii* shows an orderly sequence similar to that of *Taxus baccata*.

Bark: not very well developed.

Growth layers: absent or indistinct.

Mechanical tissue: composed of tangential layers of fibres. These layers may be absent, or they may be interrupted by parenchyma cells.

Sieve cells: they are not the predominant cells of the bast and they occur in tangential layers or bands. There is pit-contact with the phloem-albuminous cells and with the ray-parenchyma cells. Pit-contact with the phloem-parenchyma cells is scarce.

Albuminous cells: they occur in long longitudinal strands, between the phloem-parenchyma cells. They have mainly pit-contact with the sieve cells, but also with the phloem-parenchyma cells and very little contact with the ray-parenchyma cells. They collapse simultaneously with the sieve cells, or just after the sieve cells have become nonfunctional.

Phloem-parenchyma cells: they occur in tangential layers or bands. Pit-contact with the phloem ray-parenchyma cells, but also with the phloem-albuminous cells, although the number of pits is smaller here, compared with *Ginkgo biloba*.

Phloem rays: both the phloem rays and the wood rays are homogeneous. The parenchyma cells of the phloem ray are more or less erect or 'square' as in *Ginkgo biloba*.

6.2.3. Taxus baccata L. (*fig. 48 and 49*).

Taxus baccata is an intermediate between *Ginkgo biloba* and *Chamaecyparis pisifera*. Though a distinct orderly sequence is present as in *Chamaecyparis pisifera*, many deviations are to be seen, in particular near the growth ring boundary. Here, two or even three layers of parenchyma cells, instead of one, are surrounded by the sieve cells. So, regarding the amount of parenchyma, the secondary phloem of *Taxus baccata* resembles that of *Ginkgo biloba*, and regarding the tangential layering and the orderly sequence, it resembles the secondary phloem of *Chamaecyparis pisifera*.

Bark: well developed.

Outside the periderm: the sieve cells and the albuminous cells have collapsed, whereas the parenchyma cells have enlarged before they were cut off by the periderm.

Growth layers: indistinct. More fibres occur near the growth ring boundary than elsewhere in the growth ring.

Mechanical tissue: phloem fibres lie not irregularly scattered as in *Ginkgo biloba*, but only within the one cell wide layers of crystal cells. The number of the phloem fibres is small. The pits of the crystal cells and phloem fibres are restricted to the rd. walls.

Sieve cells: the sieve cells are arranged in one cell wide tangential layers. They have pit-contact with one another, with the ray-parenchyma cells and with the phloem-albuminous cells as well. Transport of assimilates through pits via the albuminous cells, seems also possible in a radial direction between the layers of sieve cells and the layers of parenchyma cells, in contrast to the situation in *Chamaecyparis pisifera*, where the only possible contact of a parenchyma cell with the layer of sieve cells is via the phloem rays.

Albuminous cells: they occur in the layers of the parenchyma cells, mostly in longitudinal strands. There is pit-contact to the phloem-parenchyma cells and to the sieve cells. The sieve cells and the albuminous cells collapse almost simultaneously.

Phloem-parenchyma cells: one or two tangential layers of parenchyma cells are surrounded by sieve cells. There is pit-contact to other parenchyma cells and to the ray-parenchyma cells and the albuminous cells. Instead of layers of phloem fibres as in *Chamaecyparis pisifera*, one cell wide layers of parenchyma cells occur with an abundance of minuscule crystals, with occasionally one or two phloem fibres.

Phloem rays: both the phloem rays and the wood rays are homogeneous. The ray-parenchyma cells are rather high, especially on both the upper and the lower side of the rays, but they are not erect or 'square' like in *Ginkgo biloba*. Outside the cambial zone they become more radially stretched with a pronounced pit-contact with phloem-parenchyma cells in particular.

6.3. SECONDARY PHLOEM CONSISTING OF A REGULAR SEQUENCE OF ALTERNATING CELL TYPES (*CHAMAECYPARIS PISIFERA* TYPE)

The secondary phloem in this group of species consists of regularly alternating tangential layers of cells, in the sequence: parenchyma cells – sieve cells – phloem fibres – sieve cells – parenchyma cells etc. No wide bands of parenchyma cells and sieve cells occur as in the previous type, but always isolated layers, one cell in width. *Chamaecyparis pisifera* is considered to be characteristic of this type. In addition, there are several species, more or less different from *Chamaecyparis pisifera*, presenting intermediate forms between *Chamaecyparis* and *Ginkgo biloba*. Some examples are: *Thuja plicata, Thujopsis dolabrata, Taxodium distichum, Cryptomeria japonica.*

A short description of all mentioned species will be given successively.

6.3.1. Chamaecyparis pisifera *ENDL. var.* plumosa *OTTO.(fig. 50 to 65 inclusive).*

The number and the size of the pits occurring between two adjacent elements of the secondary phloem are essential for the movement of assimilates. The interconnection between parenchymatous elements is all too obvious. As the phloem-parenchyma cells are arranged in tangential layers, one cell wide, (fig. 51, 52, 53 and 54), food transport will be possible within these layers, which are also connceted to the phloem rays. Within these phloem rays an unhampered food transport is possible in a radial direction; therefore, it must be possible that water and assimiltates are easily conveyed from the phloem rays to the tangential layers of parenchyma cells and vice versa.

The sieve cells, also arranged in layers one cell wide, allow a food transport in a longitudinal and in a tangential direction, towards the phloem rays and vice versa (fig. 64).

The layers of the phloem fibres show a similar structure. There is pit-contact within the tangential layers, but the layers themselves are not interconnected.

All the assimilates, stored in both the wood rays and the phloem rays, are conveyed through the ray-parenchyma cells in a radial direction together with the added assimilates from the sieve cells; via the rays they reach the different tangential layers of phloem elements, which are isolated from each other. The phloem ray consists of radial rows of parenchyma cells. In the xylem the ray-parenchyma cells have a direct contact with the tracheids by means of wide half-bordered pits; in the phloem by pits with all the different cell types (fig. 55). Every individual ray-parenchyma cell itself is connected to a sieve cell, to a phloem-parenchyma cell and to a phloem fibre. Phloem-albuminous cells lie scattered among the phloem-parenchyma cells within the tangential layers. The sieve cells are active for a short time only, after which they become non-functional. The albuminous cells, probably having a function comparable to that of the companion cells in the Angiosperms, also disorganize soon, almost simultaneously with the sieve cells. This fact could explain the lack of pit-contact of the phloem-albuminous cells with the radially extended ray-parenchyma cells; the pits would be superfluous. In *Chamaecyparis pisifera* the dead sieve cells collapse more or less in the older phloem, though not to the same extent as in *Pseudotsuga taxifolia.* The parenchyma cells stay alive and increase a little in size. They do not receive assimilates from the sieve cells, as the latter are not active any longer. The phloem ray is still functioning and as pit-contact between ray-parenchyma cells and phloem-parenchyma cells is present, assimilates are transported through pits via this way. The phloem fibres, meant to strengthen the tissue, increase somewhat in size in the older phloem, but their walls do not thicken very much.

They soon lose their contents and die, so food transport to this cell type is not necessary any more. In the older phloem pit-contact between the ray-parenchyma cells and the phloem fibres on the radial walls, is hardly visible (fig. 56). Neither are nuclei and plasma, except in the parenchyma cells. Because these parenchyma cells have increased in size, their amount of plasma has diminished relatively and the form of the nuclei has changed. They are no longer circular as in the early phloem, but more oval or stretched; they even seem to have decreased in size.

Bark: well developed.

Outside the periderm: the phloem-parenchyma cells collapse completely, while in comparison the sieve cells disorganize less and remain almost intact (fig. 58 and 59).

Growth layers: not always very easy to distinguish. At the growth ring boundary the tangential layer of fibres is mostly more than one cell wide in radial direction.

Mechanical tissue: well developed, composed of tangentially arranged layers of phloem fibres. These fibres are much elongated, radially flattened, with pits on the radial walls only.

Sieve cells: the sieve cells, also arranged in one cell wide tangential layers, allow a food transport in a longitudinal and a tangential direction. There is pit-contact with other sieve cells, with the ray-parenchyma cells and with the phloem-albuminous cells; not with the phloem-parenchyma cells.

Albuminous cells: phloem-albuminous cells lie scattered in the parenchyma cell layers. They have mainly pit-contact with the sieve cells, both on the tangential outer wall and on the tangential inner wall. They hardly have any pit-contact with the phloem-parenchyma cells. The albuminous cells and the sieve cells collapse simultaneously.

Phloem-parenchyma cells: the phloem-parenchyma cells are also arranged in tangential layers, one cell wide. There is pit-contact with other phloem-parenchyma cells and with the ray-parenchyma cells, but not with the sieve cells and hardly any contact with the phloem-albuminous cells. In the older phloem only the tangential layers of phloem-parenchyma cells and the ray-parenchyma cells remain alive. The annual increment hardly changes in width, because the sieve cells are hardly crushed and the parenchyma cells hardly increase in size.

Phloem rays: the phloem rays and the wood rays are both homogeneous, consisting of radially stretched parenchyma cells. These cells have pit-contact with one another and with all the other cell types of the bast. In the rays there are intercellular spaces running in a radial direction from the wood ray through the ray initials, to the phloem ray. The pits in the traverse walls, which are wider in the wood ray than in the phloem ray, debouch into these spaces joining the pores of the adjacent cells; blind pits hardly occur.

6.3.2. Thuja plicata *LAMB. (fig. 66, 67 and 68)*

Thuja plicata belongs to the *Cupressaceae*. The secondary phloem resembles that of *Chamaecyparis pisifera* in many respects. The only difference is caused by the phloem fibres, which have thicker walls (fig. 66). The pits of these fibres are not restricted to the radial walls, but there is also some pit-contact with the sieve cells in a radial direction. The intercellular canals are also more pronounced, in particular in the older phloem (fig. 67, 68). In some places large intercellular spaces are to be seen, thus isolating the different radial rows of ray-parenchyma cells from each other.

6.3.3. Thujopsis dolabrata *Sieb. et Zucc.*

Thujopsis dolabrata belongs to the *Cupressaceae*. The anatomical structure of the secondary phloem is almost similar to that of *Thuja plicata*. The phloem fibres are not so thick-walled and they rather resemble those of *Chamaecyparis pisifera.*

6.3.4. Taxodium distichum *A. Rich. (fig. 69, 70 and 71)*

Bark: well developed.

Outside the periderm: the sieve cells collapse completely, while the parenchyma cells usually have enlarged somewhat.

Mechanical tissue: well developed, composed of tangential layers of fibres. Although a pronounced orderly sequence still exists, occasionally, instead of phloem fibres, layers of phloem-parenchyma cells occur, containing only one or two phloem fibres. The layers of phloem fibres consist of fibres which vary widely in thickness (fig. 69). In some layers they may be large, very thick-walled and radially extended, whereas also layers occur with rather thin-walled fibres, tangentially extended. Both types of fibres and the parenchyma cells possess pits on the radial walls mainly.

Sieve sells: arranged in tangential layers, one cell wide. They have pit-contact to each other and to the ray-parenchyma cells by means of groups of small pits on the radial walls (fig. 70). They have no pit-contact with the adjacent layer of phloem fibres, whereas some contact with the phloem-parenchyma cells is possible via the albuminous cells. The sieve cells hardly disorganize in the older phloem (fig. 71).

Albuminous cells: they lie scattered between the phloem-parenchyma cells. The layer of sieve cells and the layer of parenchyma cells are connected via the albuminous cells, though less than in *Ginkgo biloba* and in *Taxus baccata.*

Phloem-parenchyma cells: the phloem-parenchyma cells have pit-contact with each other, with the ray-parenchyma cells, some contact with the albuminous cells and no pit-contact at all with the sieve cells.

Occasionally, a layer of phloem fibres is replaced by a layer of parenchyma cells. In that case tangential layers of parenchyma cells alternate with layers of sieve cells, which resembles the bast of *Ginkgo biloba.*

Phloem rays: the ray consists of radially extended cells, with a distinct pit-contact with both the phloem-parenchyma cells, the phloem fibres and the sieve cells. The phloem ray and the wood ray are both homogeneous. Intercellular spaces, extended in radial direction, occur in the phloem rays, in the ray initials and in the wood rays as well; in the older phloem they may enlarge to such an extent, that the radial rows of phloem-parenchyma cells are almost detached from one another.

6.3.5. Cryptomeria japonica *D. Don*

The structure of the secondary phloem of *Cryptomeria japonica* is almost similar to that of *Taxodium distichum.* There is a distinct tangential layering, but the different cell types do not alternate so regularly any longer. Thus no pronounced orderly sequence is present. The phloem fibres often are very thin-walled, or entirely missing. In this case sieve cells alternate with parenchyma cells, or several sieve cell layers are linked together. Yet layers of phloem fibres also occur, consisting of almost square phloem fibres. In addition sclereids occur in the older phloem as stone cells. This structure of the secondary phloem: several layers of sieve cells alternated by layers of parenchyma cells with stone cells in places, resembles the phloem of *Ginkgo biloba.* But regarding the transport system of assimilates through pits, the secondary phloem of *Cryptomeria japonica* resembles *Taxodium distichum* and the *Cupressaceae.*

The following table gives a summary of the pit-contact between the different elements and the characteristics of the secondary phloem of the described species.

		Chamaecyparis pisifer	*Thuja plicata*	*Thujopsis dolabrata*	*Cryptomeria japonica*	*Taxodium distichum*	*Taxus baccata*	*Ginkgo biloba*	*Abies alba*	*Cedrus libani*	*Tsuga canadensis*	*Larix decidua*	*Picea spec.*	*Pseudotsuga taxifolia*	*Pinus sylvestris*
Wood ray	homogeneous	+	+	+	+	+	+	+	+	±	±	−	−	−	−
	heterogeneous	−	−	−	−	−	−	−	−	±	±	+	+	+	+
Phloem ray	homogeneous	+	+	+	+	+	+	+	−	±	±	−	−	−	−
	heterogeneous	−	−	−	−	−	−	−	+	±	±	+	+	+	+
Tangential layering	regular	+	+	+	±	+	+	±	±	−	−	±	±	−	−
	irregular	−	−	−	±	−	−	±	±	+	+	±	±	+	+
Phloem fibres (PhF)	tg. layers	+	+	+	+	+	c	−	−	−	−	−	−	−	−
	scattered	−	−	−	−	−	−	+	c	c	c	c	−	c	c
Sclereids (SCL)		−	−	−	−	−	+	+	+	+	+	+	+	+	−
Ray-albuminous cell (RAC)		−	−	−	−	−	−	−	+	+	+	+	+	+	+
Phloem-alb. cell (PhAC)		+	+	?	+	+	+	+	−	−	−	−	−	−	−
Collapse outside the periderm of	SC	−	−	±	±	±	±	−	+	+	±	+	+	+	+
	PC	+	+	−	−	−	−	−	−	−	−	−	−	−	−
	PhAC	+	+	?	+	+	+	+	−	−	−	−	−	−	−
Phloem-parenchyma cell (PC); pit-contact with	RAC	−	−	−	−	−	−	−	+	?	+	+	+	+	+
	PhRPC	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	PhAC	−	−	?	−	−	−	±	−	−	?	−	−	−	−
	SC	−	−	−	−	−	−	−	−	−	−	−	−	−	−
	PhF	−	−	−	−	−	−	±	−	−	−	−	−	−	−
	SCL	−	−	−	−	−	±	+	+	+	+	+	+	+	−
Phloem-ray parenchyma cell (PhRPC); pit-contact with	RAC	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	PhAC	−	−	?	−	−	−	−	−	−	?	−	−	−	−
	SC	+	+	+	+	+	+	+	−	+	+	−	+	−	−
	PhF	+	+	+	+	+	+	−	−	−	−	−	−	−	−
	SCL	−	−	−	−	−	+	−	+	+	+	+	+	+	−
	PC	+	+	+	+	+	+	+	+	+	+	+	+	+	+

		Chamaecyparis pisifera	*Thuja plicata*	*Thujopsis dolabrata*	*Cryptomeria japonica*	*Taxodium distichum*	*Taxus baccata*	*Ginkgo biloba*	*Abies alba*	*Cedrus libani*	*Tsuga canadensis*	*Larix decidua*	*Picea spec.*	*Pseudotsuga taxifolia*	*Pinus sylvestris*
Sieve cells (SC); pit-contact with	RAC	–	–	–	–	–	–	–	+	+	+	+	+	+	+
	PhRPC	+	+	+	+	+	+	+	–	+	+	–	+	–	–
	PhAC	+	+	+	+	+	+	+	–	–	–	–	–	–	–
	PhF	+	+	±	–	–	–	–	–	–	–	–	–	–	–
	SCL	–	–	–	?	–	–	–	+	–	?	?	?	+	–
	PC	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tangential layers of sieve cells	1 cell wide	+	+	+	+	+	+	±	–	–	–	–	–	–	–
	more c. wide	–	–	–	±	–	–	±	+	+	+	+	+	+	+
Sieve areas	large	+	+	–	–	±	–	+	+	+	±	+	+	+	±
	small	–	–	+	+	±	+	–	–	–	–	–	–	–	±
Ray-albuminous cell (RAC); pit-contact with	PhRPC	–	–	–	–	–	–	–	+	+	+	+	+	+	+
	PhAC	–	–	–	–	–	–	–	–	–	?	–	–	–	–
	SC	–	–	–	–	–	–	–	+	+	+	+	+	+	+
	PhF	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	SCL	–	–	–	–	–	–	–	–	–	+	?	?	–	–
	PC	–	–	–	–	–	–	–	+	?	+	+	+	+	+
Phloem-albuminous cell (PhAC); pit-contact with	RAC	–	–	–	–	–	–	–	–	–	?	–	–	–	–
	PhRPC	–	–	?	–	–	–	–	–	–	?	–	–	–	–
	SC	+	+	+	+	+	+	+	–	–	–	–	–	–	–
	PhF	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	SCL	–	–	–	?	–	–	+	–	–	–	–	–	–	–
	PC	–	–	?	–	–	–	±	–	–	?	–	–	–	–
Radial inter-cell. spaces	between PhRPC	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	between RhRPC and RAC	–	–	–	–	–	–	–	+	–	±	+	±	±	–
	between WRPC	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	between WRPC and WRT	–	–	–	–	–	–	–	+	+	+	+	+	+	+

Legends (see also page 72):

+ = present
- = absent
? = doubtfull
c = crystalliferous cell

7. THE PHYLOGENETIC STAGES OF THE BAST TYPES

7.1. COMPARISON OF THE STRUCTURE OF THE DIFFERENT SECONDARY PHLOEM TYPES

Information on pit-contact between the different cell types is given in the table of chapter 6.

Comparing the secondary phloem of the Gymnosperms with that of the Angiosperms, the relatively simple structure of the former is striking. The cells are deposited by the cambium in radial rows and usually in tangential layers as well. This tangential layering remains visible for a long time. In many species tangential layers of different cell types alternate regularly.

The vertical system of the secondary phloem is always composed of sieve cells and parenchyma cells; in addition phloem fibres, sclereids, crystalcell strands and resin ducts may occur. The horizontal system consists of uniseriate phloem rays which are either homogeneous or heterogeneous. If the phloem rays enclose resin ducts, they are multiseriate.

As a rule, the arrangement of the elements deposited by the cambium, as described above, is hardly interrupted by the enlargement of cells, the forming of stone cell nests, or irregularly shaped phloem fibres etc. The *Taxaceae*, *Cupressaceae* and *Taxodiaceae* in particular, possess a secondary phloem with an orderly sequence. Companion cells are always lacking in the Gymnosperms, instead albuminous cells occur. Albuminous cells occur either on both sides, or on one side of the phloem rays (*Pseudotsuga taxifolia* type and *Tsuga canadensis* subtype), in long longitudinal strands among the parenchyma cells (*Ginkgo biloba* type), scattered among the parenchyma cells (*Chamaecyparis pisifera* type), or as a combination of ray-albuminous cells and phloem-albuminous cells (some species belonging to the *Pseudotsuga taxifolia* type).

The phloem-parenchyma cells mainly occur in longitudinal strands which are arranged in the following ways:

a. In the *Taxaceae*, *Cupressaceae* and *Taxodiaceae* in one cell wide tangential layers, separated by tangential layers of sieve cells (*Chamaecyparis pisifera* type); the cells within each layer are interconnected and they have pit-contact with the phloem rays as well.

b. Phloem parenchyma may also be arranged in a different way, as in the *Pinaceae* (*Pseudotsuga taxifolia* type).

The axial system consists of sieve cells and every year one or two, more or less continuous, tangential layers of parenchyma cells are formed between the sieve cells. In cross sections is to be seen that these tangential layers are not composed of parenchyma cells only; they are interrupted by sieve cells, or they suddenly shift into a radial direction. Often all these parenchyma cells are interconnected; thus forming not only an intertwined tangential structure, but a parenchyma cell net, because all the different, more or less tangential zones, are also connected to each other. Pit-contact between sieve cells and ray-parenchyma cells is lacking in species belonging to the *Pseudotsuga taxifolia* type, but it is present in species belonging to the *Tsuga canadensis* subtype.

Although many tg. sieve cell layers lie against each other, contact with the ray-parenchyma cells is much more complicated (*Pseudotsuga taxifolia* type), than in the phloem of the *Chamaecyparis pisifera* type, because the only possible way of contact is via the ray-albuminous cells. It is a remarkable fact that the parenchyma cell net, though permeated by sieve cells, is not directly connected to the latter, but only via the phloem rays.

In a later stage, farther from the cambium, the sieve cells become non-functional and some phloem-parenchyma cells sclerify, hampering the transport of assimilates in places. The remaining living elements in the secondary phloem are by then, both ray-parenchyma cells and phloem-parenchyma cells.

7.2. CHARACTERISTICS OF THE DIFFERENT PHYLOGENETIC STAGES

A survey of the descriptions of the secondary phloem in different woodspecies of the Gymnosperms, as given in the preceding pages, shows that apparently some features are characteristic in classifying them, according to their evolutionary stage.

These characteristics are:

a. the arrangement and the distribution of the cell types;
b. the structure of the phloem rays;
c. the type of the albuminous cells and the way in which they are arranged;
d. the presence or the absence of phloem fibres, crystalcell strands, crystal cells, sclereids, fibres and stone cells;
e. the distribution of the parenchyma cells;
f. pit-contact between components of the axial system and the phloem rays;
g. the changes in the older phloem;
h. the changes of the bast outside the periderm.

7.3. THE DIFFERENT PHYLOGENETIC STAGES

By means of the above mentioned characteristics, 4 different categories can be distinguished which may be classed in 3 stages of evolution:

I. *Pseudotsuga taxifolia* type;
Ia. *Tsuga canadensis* subtype;
II. *Ginkgo biloba* type;
III. *Chamaecyparis pisifera* type.

The following 3 species form a gradual transition from the *Chamaecyparis pisifera* type to the *Ginkgo biloba* type.

Thuja plicata still has an orderly sequence, but in *Taxodium distichum* some irregularities occur: e.g., mostly a parenchyma-cell layer is followed by another parenchyma-cell layer. In *Cryptomeria japonica* these irregularities are more pronounced; phloem fibres may be lacking, layers of sieve cells may alternate with layers of parenchyma cells, or several tangential layers of parenchyma cells may lie against each other. Anyhow, the orderly sequence becomes less pronounced and the function of the phloem fibres becomes less significant. Though there still is an independent food transport through pits within the different cell-type layers, these tangential layers become wider.

Considering the sequence: *Pinus sylvestris, Pseudotsuga taxifolia, Picea spec., Tsuga canadensis, Ginkgo biloba, Taxus baccata, Chamaecyparis pisifera,* the following features are noticeable:

a. the structure of the axial system gradually changes from a system mainly composed of sieve cells with scarce, almost scattered, parenchyma cells forming a parenchyma cell net, to a system with a very regular tangential layering and an arrangement of the different cell types, with a pronounced orderly sequence, containing much parenchyma.

So the number of parenchyma cells increases, while the amount of sieve cells decreases.

b. First, ray-albuminous cells occur on both sides of the heterogeneous phloem rays (*Pseudotsuga taxifolia*); then either on the lower side or on the upper side of the semi-heterogeneous phloem rays (*Tsuga canadensis*). These ray-albuminous cells always have pit-contact with both the parenchyma cells and the sieve cells. When ray-albuminous cells occur on the phloem side, either wood-ray tracheids occur on the xylem side (*Pseudotsuga taxifolia*), or ordinary wood-ray parenchyma cells (*Abies concolor*).

Eventually the ray-albuminous cells gradually disappear and instead the phloem-albuminous cells appear. First in long longitudinal strands, occuring in the 1–3 cell wide tg. parenchyma-cell layers, in this way interfering with the tangential transport of assimilates within a single band of parenchyma cells, only if the bands are one cell wide. Besides, both cell types have pit-contact with each other, so a direct movement of assimilates through pits is possible between sieve cells and phloem-parenchyma cells via the phloem-albuminous cells (*Ginkgo biloba*). At last, scattered phloem-albuminous cells occur singly within one cell wide tangential layers of parenchyma cells, distinctly isolated. Though they do interfere with the transport system in places, they do not cut off a whole layer of parenchyma cells in a tangential direction, because they do not form long longitudinal strands (*Chamaecyparis pisifera*).

c. Only sclereids occur in e.g. *Pseudotsuga taxifolia, Abies concolor,* and *Picea,* followed by both sclereids and phloem fibres (*Cryptomeria japonica*), scattered phloem fibres between the phloem-parenchyma cell bands (*Ginkgo biloba*), tangential layers of very thick-walled fibres alternating with relatively thin-walled fibres (*Taxodium distichum*) and eventually phloem fibres of the same thickness occuring in regular one cell wide tangential layers (*Chamaecyparis pisifera*).

Usually, sclereids and phloem fibres do not occur together in the same species. Crystalcell strands are present in the *Pseudotsuga taxifolia* type; crystals are present in special, much enlarged cells in the *Ginkgo biloba* type, while crystal cells are lacking in the *Chamaecyparis* type, but then sometimes crystals are present in some radial walls.

d. Outside the periderm the *Pseugotsuga taxifolia* type shows a collapse of the sieve cells, changing via the *Ginkgo biloba* type, with hardly any collapse of the phloem elements, towards a collapse of the phloem-parenchyma cells in the *Chamaecyparis pisifera* type.

It appears that certain characteristics always occur in the same combinations. When the phloem rays are heterogeneous, ray-albuminous cells occur, but also some phloem-albuminous cells may be present; in this case the wood rays are also heterogeneous, with some homogeneous exceptions. Crystalcell strands are always present and sclereids occur instead of phloem fibres. The axial system is composed of sieve cells with little scattered parenchyma, arranged in discontinuous tangential layers; a parenchyma cell net is often formed. Outside the periderm the sieve cells collapse instead of the parenchyma cells.

When both the phloem rays and the wood rays are homogeneous, exclusively phloem-albuminous cells are present. The secondary phloem is distinctly layered; it has mostly an orderly sequence. The bands of sieve cells are narrow in radial extent; the different tangential layers of parenchyma cells have no contact with each other; there are many phloem fibres. Outside the periderm the parenchyma cells collapse.

Summarizing we may state that the different types of secondary phloem belonging to the 9 families of the Gymnosperms, are to be classified into three different categories; one of these categories has one subtype. These three categories or types may be considered as three subsequent stages of evolution. This sequence is: *Pseudotsuga taxifolia, Tsuga canadensis, Ginkgo biloba* and *Chamaecyparis pisifera.*

a. Considering first of all, the secondary phloem itself, leaving the phloem rays out of consideration, the axial system appears to change gradually in the above mentioned sequence. In *Pseudotsuga taxifolia* a homogeneous, relatively primitive axial system is present, consisting almost exclusively of sieve cells, with scattered parenchyma cells among them and hardly any phloem-albuminous cells. Thus hardly any differentiation of functions. When the sieve cells, after a functional period of one, or sometimes two years, die and eventually collapse, the few scattered phloem-parenchyma cells remain alive with sclereids to strengthen the structure.

Considering the sequence via *Tsuga canadensis* and *Ginkgo biloba* up to *Chamaecyparis pisifera,* it appears that the number of parenchyma cells increases gradually, the ray-albuminous cells disappear and instead phloem-albuminous cells occur. The latter form continuous longitudinal strands in the secondary phloem of the *Ginkgo biloba* type; in the *Chamaecyparis pisifera* type they lie scattered, occasionally in groups of one to three cells but usually single This last form of the phloem-albuminous cells, singly between other cell types, shows some resemblance with the situation of the companion cells in the Angiosperms. That is, these short parenchymatous cells, with much protoplasm, a distinct nucleus, with pit contact to one or two sieve cells and a simultaneous collapse with these sieve cells, are comparable with the short companion cells of the Angiosperms, originated from cambium initials from which a small lenticular part is separated along the side, while the rest differentiates into a sieve-tube member and which are considered as the most primitive Angiosperm companion cells (HUBER and GRAF, 1955; ZIEGLER, 1955c). In *Chamaecyparis pisifera* the entire complex of the secondary phloem has a permanent food conducting function in a longitudinal and in a tangential direction, because it is composed of alternating one-cell wide cell layers which are to be considered as independent food-conducting canals.

When the sieve cells and the albuminous cells collapse simultaneously, only the phloem-parenchyma cells and the ray-parenchyma cells remain active. Within these tangential layers of parenchyma cells, the albuminous cells form a barrier but they hardly interfere with food transport because they lie scattered. But they do hamper food transport, in a tangential direction in particular, when the phloem-albuminous cells form long longitudinal strands, like in the *Ginkgo biloba* type, and the tangential bands of parenchyma cells are not more then 1 cell wide. So it seems preferable that the bands are wider than one cell, which they usually are.

Apart from the parenchyma cells, after the collapse of the sieve cells the only food-conducting cells, specialized phloem fibres, remain active, which has an extra advantage, because now parenchyma cells have not to differentiate into sclereids to strengthen the tissue. Thus we notice a differentiation of functions; in *Chamaecyparis pisifera* this is not due to an orderly sequence, but to the fact that the different cells are specialized, adopting different functions.

In the Angiosperms a similar differentiation is to be seen. Besides the phloem-albuminous cells in *Chamaecyparis pisifera* show a greater resemblance to the companion cells in the Angiosperms, than the ray-albuminous cells of the *Pseudotsuga taxifolia* type do. This is caused by the facts that the phloem-albuminous cells, in contrast with the ray-albuminous cells, hardly have any pit-contact with the ray-parenchyma cells; they do not lie scattered amid the parenchyma cells and they are more intimately associated to the sieve cells than the ray-albuminous cells are. Besides they are probably not functioning as canals, transporting assimilates from sieve cells to ray-parenchyma cells, like some ray-albuminous cells do.

Although the Angiosperms do not possess an orderly sequence, it seems likely that they have attained this differentiation via an orderly sequence, for only after a highly specialized differentiation, a pronounced tg. arrangement of the different kinds of cells is nog necessary any longer.

b. In the classification, as described above, the phloem rays have been left out of consideration. Classifying the wood species by means of the structure of the xylem, the wood rays are always left out. The xylem mainly consists of dead cells; its main functions are transport of water and strengthening of the plant body. The living elements of the xylem, the wood parenchyma and the wood rays have a different function, almost independent from the axial system. The phloem shows two living systems, both with a food-conducting function, though in different directions. There is a close relationship between these two systems, but it may be possible that the evolutionary stages of the axial system of the phloem and of the ray system differ widely. Considering the phloem rays separately, we notice a phylogenetical reduction parallel with the evolutionary stages of the axial system (fig. 72 and 73). In the *Chamaecyparis pisifera* type, the phloem ray consists of procumbent parenchyma cells; in the *Ginkgo biloba* type it still consists of procumbent parenchyma cells, but with square or erect cells on the margins, cells with probably the same function as the procumbent rd. stretched cells, but with a larger contact area with the longitudinally stretched cells of the axial system. In the subtype *Tsuga canadensis*, the procumbent parenchyma cells are only partly associated with erect albuminous cells, but in the *Pseudotsuga taxifolia* type, all the phloem rays are heterogeneous. Apart from the apparently close physiological association to the sieve cells (simultaneous collapse), the ray-albuminous cells probably play a part in the transport of assimilates, namely as a link between the vertical and the horizontal system. In the subtype *Tsuga canadensis* the procumbent parenchyma cells have a similar function, but in the *Pseudotsuga taxifolia* type only the ray-albuminous cells have this linking function to the sieve cells. Thus food transport from the phloem rays to the sieve cells and vice versa, is only possible then via the ray-albuminous cells, whereas the radial transport is only possible via the procumbent parenchyma cells in the phloem rays.

These highly specialized phloem rays are present in a primitive, relatively unspecialized axial system, like in the *Pseudotsuga taxifolia* type, with almost exclusively sieve cells and hardly any specialized phloem-parenchyma cells, comparable to the albuminous cells in the rays. So the axial system and the phloem rays show opposite tendencies in evolution stages: the less reduced the phloem rays, the less developed the axial system of the secondary phloem; the more homogeneous the axial system, the more heterogeneous the phloem rays, (*Pseudotsuga taxifolia* type) and on the other hand: the more homogeneous the phloem rays, the more heterogeneous the axial system of the secondary phloem (*Chamaecyparis pisifera* type).

The parallelism of a differentiation of the axial system of the secondary phloem and a simplification of the structure of the phloem rays, implies the close relationship of both systems; in any case a much closer one than existing between the axial system of the xylem and the wood rays. The three phylogenetic stages of the phloem rays and of the axial system may be characterized and classified as follows:

I. *Pseudotsuga taxifolia* type.

The phloem rays are heterogeneous like the wood rays. Resin ducts are present. This type possesses the most complicated, least reduced phloem rays, in contrast with a simple, homogeneous axial system, composed of mainly sieve cells. The families, belonging to this group, are monoecious (*Pinaceae*), living in the northern hemisphere.

II. *Ginkgo biloba* type.

The phloem rays consist of procumbent parenchyma cells, with square, more or less erect, parenchyma cells on the margins; the phloem rays are homogeneous and so are the wood rays. The axial system of the secondary phloem shows a simple orderly sequence; tangential rather wide bands of sieve cells alternate with bands of phloem-parenchyma cells. Long strands of phloem-albuminous cells are present.

The families, belonging to this phylogenetic stage, are dioecious (*Ginkgoaceae*, *Araucariaceae* and some species belonging to the *Podocarpaceae* and to the *Taxaceae*), living in the southern hemisphere.

III. *Chamaecyparis pisifera* type.

All the ray-parenchyma cells are procumbent; the phloem ray is much reduced; both the phloem ray and the wood ray are homogeneous. The axial system is highly differentiated; it has an orderly sequence with only scattered phloem-albuminous cells. In some respects the secondary phloem of this type resembles that of the Angiosperms. The arrangement of the leaves is helical or opposite. The genera, belonging to this group, are monoecious, living in East Asia and in North America (*Cupressaceae*, *Taxodiaceae* and some species belonging to the *Taxaceae* and *Podocarpaceae*, HOUTZAGERS, 1954).

So in reference to the phylogenetic stage of the axial system and the reduction of the phloem rays, the sequence starts with stage I with an almost homogeneous axial system and ray-albuminous cells, differentiating via stage II to stage III, with a highly specialized axial system and with phloem-albuminous cells (*Chamaecyparis pisifera* type), comparable with the companion cells of the Angiosperms.

Jeffrey (1905) demonstrated that probably the course of the evolution of the *Coniferales* had gradually led to the complete loss of the resin canals. The ancestral forms are provided with anastomosing resin canals, e.g. *Pinus* (belonging to the *Pseudotsuga taxifolia* type), whereas they are lacking in the more recent species, e.g. *Abies*, *Ginkgo* and *Chamaecyparis* (*Ginkgo biloba* type and *Chamaecyparis pisifera* type). The wood rays of e.g. *Pinus*, *Picea* and *Pseudotsuga* (*Pseudotsuga taxifolia* type) possess marginal ray-tracheids, generally interpreted as favouring the radial movement of water in the xylem; they are probably necessary because the bordered pits of the wood-tracheids occur mainly on the radial walls. STRASBURGER (1891) and JEFFREY (1905) emphasized that the *Coniferales* constitute a group which has undergone reduction in the course of time, consequently complex structural features are more apt to be characteristic of the ancestral forms than of the more recent forms. They consider ray tracheids as primitive. As ray-albuminous cells often occur in combination with ray tracheids, the ray-albuminous cells of the phloem rays are also primitive in their opinion. GREGUSS (1953) and PENHALLOW (1903) on the other hand assume that the presence of these ray tracheids marks a high stage of evolution.

8. DISCUSSION

8.1. AXIAL SYSTEM

Considering the evolutionary sequence of the axial system in the secondary phloem of Gymnosperms and afterwards of that of Angiosperms, it appears that in the first stage the secondary phloem of Gymnosperms lacks a tangential layering of the different cell types, though occasionally more or less distinct tangential rows of parenchyma cells are present. Though several investigators have described the regular tangential layers of parenchyma cells in the secondary phloem of the *Pinaceae* (HUBER and LIESE, 1963), this phenomenon is not present in all the *Pinaceae*. According to STRASBURGER (1891) and GRILLOS and SMITH (1959), the regular tangential layers of parenchyma cells might be lacking in young stems, but this does not agree with the slides, taken from full grown trees, which are examined by us; because also here regular tangential layers are lacking and only very irregular layers of parenchyma cells occur (*Pseudotsuga taxifolia* type).

In the *Ginkgo biloba* type, irregular, rather wide bands of parenchyma cells, alternate with bands of sieve cells. In the *Chamaecyparis pisifera* type a very regular and strict orderly sequence is to be seen. Within a growth layer, the size of the phloem fibres decreases in radial extent during the growing season. Besides, HUBER (1949) has demonstrated that within the first orderly sequence of a growth layer, the first layer of sieve cells tends to widen from 1, to 2 or 3 cells in width; he believed that the closed area of sieve cells in the early phloem of the *Pinaceae*, has developed from this increase of the first sieve-cell layer of the *Chamaecyparis pisifera* type. *Larix decidua* has an early phloem of exclusively sieve cells and a late phloem of alternating bands of sieve cells and bands of parenchyma cells. *Larix decidua* looses its needles in the autumn; so then more parenchyma cells are necessary to store assimilates. Because this necessity does not exist for the other *Pinaceae*, this may be the reason for the formation of only one or sometimes two layers of parenchyma cells p.a. during the summer, as e.g. in *Picea spec.* (HUBER 1949).

There are, however, many evergreen *Pinaceae* with a late phloem showing a structure similar to that of *Larix decidua* and with an early phloem, containing much parenchyma. We may also state that the late phloem of *Larix decidua* resembles the phloem of *Ginkgo biloba* in some respects. A more pronounced and strictly tangential layering is found in the *Chamaecyparis pisifera* type though, particularly in the first orderly sequence of the growth layer, when many assimilates have to be transported, more sieve cells may be formed. Thus an evolution towards the *Ginkgo biloba* type and consequently an evolutionary trend opposite to the trend as described by HUBER. Probably not from *Chamaecyparis pisifera* type towards *Pseudotsuga taxifolia* type (HUBER, 1949), but the other way round, from *Pseudotsuga taxifolia*, via *Ginkgo biloba* towards *Chamaecyparis pisifera* type.

Some primitive Angiosperms show this tangential layering of *Chamaecyparis* *pisifera* as well, like *Austrobaileya* (*Magnoliaceae*), where tangential layers of sieve cells regularly alternate with layers of parenchyma cells (BAILEY and SWAMY, 1949). HOLDHEIDE (1951) has demonstrated that also in *Berberis*, *Ribes*, *Pyrus* and *Euonymus*, similar regular bands of parenchyma cells occur, adjacent to bands of sieve tubes.

We may consider all these species, and also *Austrobaileya* to belong to a type of Angiosperms with a simplified orderly sequence. In all the other Angiosperms however, this orderly sequence does not longer exist.

8.2. ALBUMINOUS CELLS AND COMPANION CELLS

Parallel to the change in the general structure of the axial system of the secondary phloem, there is also a gradual modification to be noted from albuminous cell to companion cell and in addition a gradual change of the sieve elements.

Considering the evolution from albuminous cell to companion cell first of all, the following features have been noted:

Companion cells are probably present in all the Angiosperms. HOLDHEIDE (1951) believes that *Pyrus communis* e.g. has no companion cells, but HUBER and GRAF (1955) and EVERT (1960) have demonstrated that each sieve-tube member does possess a small companoin cell and that this does not apply to *Pyrus communis* only, but probably to all Angiosperms.

There still appear to be some Angiosperms in which companion cells are definitely absent like in *Austrobaileya* (BAILEY and SWAMY, 1949); these species do not possess genuine sieve tubes, but sieve cells, consequently without sieve plates.

The companion cells occur in different forms:

1. short companion cells originate from cambium initials, from which a small lenticular part is separated from the side part of the cell, or from the end; this part differentiates into a companion cell, while the remaining part of the same initial differentiates into a sieve-tube member, like in *Liriodendron*.
2. originated from a sieve-tube member mother cell, separated from the prospective sieve-tube member by a longitudinal wall. In this case they are of approximately the same length as the sieve-tube members themselves.
3. this long, undivided companion cell precursor, may be subdivided into several smaller companion cells by the formation of two to four transverse walls; in this way a strand of companion cells is formed.
4. apart from the above mentioned transverse walls, also longitudinal walls may be formed within this long companion cell: in this way plates of companion cells originate.
5. several companion cells, associated with one sieve-tube member, but separated from each other; like in *Magnolia*, *Eucalyptus*, *Tilia*.

Apart from the companion cells, restricted to the Angiosperms, the albuminous cells occur in all the soft wood species, and according to HOLDHEIDE (1951), also in most hard wood species, probably even in all of them. These albuminous cells form, together with ordinary parenchyma cells, strands of cells. Physiologically they resemble the companion cells, in contrast with the ordinary sister-parenchyma cells. The difference between two sister-cells within one special strand of parenchyma cells may not be too significant (HOLDHEIDE, 1951; HUBER and GRAF, 1955). As stated above, some Angiosperms also appear to possess specialized parenchyma cells (albuminous cells), which show a more intimate association with the sieve-tube members than the ordinary parenchyma cells. In the more primitive Angiosperms, relatively few companion cells and many albuminous cells occur. The latter preferably join as many sieve cells or sieve-tube members as possible and besides do not disturb food conduction within the layers of parenchyma cells. This ideal situation exists if tangential layers of sieve cells regularly alternate with tangential layers of parenchyma cells. In the secondary phloem of the *Ginkgo biloba* type this structure is not jet attained; here the albuminous cells occur in long longitudinal strands within bands of parenchyma cells.

Only in the highly specialized *Chamaecyparis pisifera* type this situation is attained, where the parenchyma cells no longer have a strengthening function, but layers of phloem fibres fulfil this function, and where, in addition, the albuminous cells lie scattered among the parenchyma cells, arranged in one-cell wide tangential layers, included by two layers of sieve cells; thus phloem-albuminous cells join the sieve cells at both the tangential outer wall and the tangential inner wall (*Chamaecyparis pisifera*).

Eventually, relatively late, a companion cell may be formed out of the sieve-tube member mother cell by a vertical wall; probably these companion cells first alternate with the sieve-tube members, as seen in a radial direction, while later the former may also occur at other walls, than only at the tangential walls of the sieve-tube members (HUBER and GRAF, 1955). Several features, characteristic of the Angiosperms, are present in *Gnetum*. The phloem-albuminous cells are intimately connected to the sieve cells, to such an extent that according to THOMPSON (1919), they have to be called companion cells, though ontogenetically they are not correlated with the sieve cells, because they have originated from different tiers of cambium initials. In addition many of them do not collapse simultaneously with the sieve cells. So the term 'companion cells' is not appropriate here, but 'albuminous cells' among parenchyma cells; we may suggest the possibility that these albuminous cells are a transitional stage between genuine albuminous cells and companion cells.

The sieve elements decrease in length during their evolution, as will be discussed later. Thus in the Angiosperms, the number of the albuminous cells are not sufficient any longer for the shortened sieve-tube members; now genuine companion cells are separated from the sieve-tube members themselves. Originally the latter are probably lenticularly separated, short, companion cells and later the long companion cells occur, separated from the sieve-tube member mothercell by a long vertical wall. Divided companion cells and segments of them must be considered as derivatives (HUBER and GRAF, 1955). ZIEGLER (1955c) also concluded that the companion cells belonging to his type A (much shorter than the sieve-tube member) are the most primitive, whereas his type B (the companion cells and the sieve-tube members are of the same length) and C (similar to type B, but segmented into smaller companion cells by transverse walls) are derivatives.

Esau (1947) has also demonstrated the correlation in the cytology of some parenchyma cells and companion cells and the sieve-tube members, in *Vitis* and *Eucalyptus*. Slime bodies are characteristic of young, not yet entirely differentiated sieve tubes of the *Dicotyledoneae*. In *Vitis* these slime bodies also occur in the companion cells. Although the companion cells have not been investigated in all species, it is generally accepted that they possess a dense mass of protoplasm; this is not a meristematic feature, as the young companion cells have a thinner, less staining protoplasm, than the older ones. Possibly many companion cells of the *Dicotyledoneae* have slime bodies, probably not so much pronounced as in *Vitis*, but more dispersed. Slime bodies are also found in the phloem parenchyma of *Eucalyptus* (Esau, 1947); possibly these parenchyma cells are more specialized, more physiologically associated with the sieve-tube members than the ordinary parenchyma cells; they may be even ontogenetically associated with these sieve-tube members. Here again these cells may be considered as intermediate forms, between phloem-parenchyma cells and albuminous cells, and between albuminous cells and companion cells.

Evert (1960, 1963) has also found distinct, though short, companion cells in *Pyrus* and in addition parenchyma cells, differentiated from the same phloic initials as the sieve-tube members. These parenchyma cells, ontogenetically associated with the sieve-tube members, could easily be distinguished from the companion cells, but hardly from the other parenchyma cells, because though these parenchyma cells collapse in the older phloem, most of the ordinary parenchyma cells also do. Also Esau and Cheadle (1955) have found parenchyma cells, ontogenetically associated with the sieve-tube members.

Though companion cells are lacking in *Austrobaileya* (Bailey and Swamy, 1949), the above described special parenchyma cells may be present, as demonstrated in the *Calycanthaceae* by Cheadle and Esau (1958). Though the latter are not companion cells, they neither are albuminous cells, because of their ontogenetic relationship with the sieve-tube members. The phloem-albuminous cells, in the Gymnosperms ontogenetically independent of the sieve cells, may evolve into the companion cells of the Angiosperms, via these ontogenetically associated parenchyma cells. It is quite possible that in the Angiosperms, ordinary phloem-albuminous cells may occur together with these special ontogenetically associated parenchymatous cells, besides the normal companion cells.

Not only in the phloem but also in the xylem, parenchymatous cells appear to be closely associated with the empty vessels which have lost their contents of protoplasm (Resch, 1954); not only during the differentiation process, but also in their mature stage. Possibly they are necessary to prevent air embolism in the water column of the vessels. Ziegler (1955) has noted that these parenchymatous cells show a high phosphatase activity, but otherwise they cannot be distinguished from ordinary parenchyma cells regarding their contents of starch, their shape, their amount of protoplasm etc. They lie regularly scattered in the xylem. According to ZIEGLER, these cells rich in enzymes, may be responsible for the dephosphorization of hexosephosphates formed during the phosphorization of starch. So these cells are able to deliver saccharides to the vessels (bleeding of *Acer spec.*).

Summarizing we may notice:

The erect ray-albuminous cells (*Pseudotsuga taxifolia* type) disappear; instead many long strands of phloem-albuminous cells (*Ginkgo biloba* type) occur. These strands of phloem-albuminous cells decrease in length (*Chamaecyparis pisifera* type); a transitional stage to the Angiosperms is attained like in *Gnetum* and the *Austrobaileya* type, still possessing sieve cells and albuminous cells, followed by the normal Angiosperms with genuine companion cells. First the latter are still short, lenticularly separated from the sieve-tube member mother cells, while the secondary phloem shows a simplified orderly sequence; afterwards long undivided companion cells are formed as long as the sieve-tube members themselves and eventually divided ones. Though albuminous cells still occur in the Angiosperms, their number decreases gradually.

8.3. SIEVE ELEMENTS

The sieve elements gradually change as well. Specialization of these elements can be discussed from a cytologic and from a morphologic point of view.

8.3.1. *Cytologic specialization*

If an evolutionary trend is to be noted in the changes of sieve elements in primitive, lower developed, species to those in higher developed species, the most primitive sieve elements resemble more or less, specialized parenchyma cells, like the most primitive albuminous cells do. During the cytologic specialization from parenchyma cell to sieve element, the parenchyma cell gradually gets a less conspicuous nucleus, it produces less starch; it stains less intensely with dyes and callose is formed. The plasmodesmata increase in size, forming permanent connections between two adjacent cells. In addition the parenchyma cells adapt to a food-conducting function, which is not caused by higher permeability of the protoplasts, as in a functioning sieve cell the protoplasm can still be plasmolyzed (CURRIER, ESAU and CHEADLE, 1955). Concomitant with this cytologic specialization of the protoplast, the physiological association between sieve elements and parenchyma cells, containing a nucleus, becomes more intimate. In almost all plants special parenchyma cells are associated physiologically with sieve elements, but the association increases and in the Angiosperms it has become so strong that not only both cell types, sieve-tube members and companion cells, are ontogenetically associated, but even their protoplasm shows a pronounced resemblance (ESAU, 1947, 1954).

Parallel to this phenomenon, also the sclereids, differentiated from parenchyma cells, disappear and special phloem fibres, with a strengthening function, are formed.

8.3.2. *Morphologic specialization*

Apart from this cytologic specialization of the sieve elements, also a morphologic one is to be noted as is shown by CHEADLE and WHITFORD (1941) in the *Monocotyledoneae;* probably it is also present in the *Dicotyledoneae;* (HUBER, 1939). During this process, the length of the sieve elements concerned, decreases gradually, in the same way, as described for xylem elements by TIPPO (1946). It must be borne in mind that the shortened xylem vessel members have originated from shortened cambium initials and that the same cambium initials have also formed the sieve elements. These sieve-tube members however, may be divided by secondary transverse walls into still shorter segments; consequently in the phloem, sieve elements may be present, which are much shorter than the cambium initials from which they have originated (ESAU, CHEADLE and GIFFORD, 1953). In the Gymnosperms long sieve cells are to be seen (*Pseudotsuga taxifolia* type). Via the *Chamaecyparis pisifera* type, *Austrobaileya* and the Angiosperms with sieve cells and albuminous cells, those Angiosperms which possess sieve-tube members and in addition to some albuminous cells many companion cells, the long sieve cells become shorter and they are gradually converted into rather long sieve-tube members. Originally the transverse walls between two sieve elements are very oblique, but they become more horizontal during their evolutionary process. Simultaneously the position of the pits changes; first scattered, later arranged in clusters; these clusters of pits become sieve areas, occurring on the oblique transverse wall between sieve-tube members in particular; these sieve areas form compound sieve plates and eventually simple sieve plates occur on the, in this stage horizontal transverse walls. Due to this shortening process of the sieve-tube members (BAILEY, 1954; MÄGDEFRAU, 1953), their chance of joining an albuminous cell has decreased; therefore genuine companion cells are formed.

The sieve elements of *Pyrus* may be considered as intermediate between the Gymnosperm-and the common Angiosperm sieve elements. According to HOLDHEIDE (1951) companion cells are lacking in *Pyrus* and according to HUBER (1939) even all the *Pomoideae* do not possess sieve-tube members but sieve cells. EVERT (1960, 1963) however, has demonstrated that in *Pyrus*, the sieve areas on the end walls are definitely different, from those on the longitudinal walls; consequently the sieve elements in *Pyrus* are sieve-tube members and not sieve cells; they are long and slender with very oblique end walls on which compound sieve plates occur; these features are characteristic of relatively primitive sieve-tube members in the Angiosperms (CHEADLE, 1948).

9. SUMMARY

An investigation of the secondary phloem of the different species of the Gymnosperms shows that there are 3 different categories to be distinguished, which may be classed in 3 evolutionary stages. Features, characteristic in classifying them, are:

a. the structure of the axial system;
b. the arrangement of the parenchyma cells;
c. the structure of the phloem rays;
d. pit-contact between the phloem rays and the cells of the axial system;
e. the type of the albuminous cells and the way in which they are arranged;
f. the presence or absence of phloem fibres, crystallcell strands, crystal cells, sclereids and stone cells;
g. the changes in the older phloem;
h. the changes of the bast outside the periderm.

The 3 different categories are:

I. *Pseudotsuga taxifolia* type.

Some of the *Pinaceae* belong to this type.

The axial system is composed primarily of sieve cells with a few scattered parenchyma cells, which form a parenchyma-cell net of interconnected cells throughout the axial system. The phloem rays are heterogeneous; the radially stretched ray-parenchyma cells in the middle of the rays, do not have pit-contact with the sieve cells. The latter are connected to the ray-parenchyma cells, via the ray-albuminous cells only. The albuminous cells occur almost exclusively as ray-albuminous cells, although some phloem-albuminous cells are present. Crystalcell strands regularly occur and in the older phloem also sclereids are present. Outside the periderm only parenchyma cells, crystalcell strands and sclereids are left; the sieve cells are completely disorganized.

Ia. *Tsuga canadensis* subtype.

The other *Pinaceae*, are grouped in this type. This type may be considered as a subtype of the *Pseudotsuga taxifolia* type; it differs from it, because all the elements of the phloem ray, both the ray-parenchyma cells and the ray-albuminous cells, are connected to the different elements of the axial system, i.e. the sieve cells and the phloem-parenchyma cells. Besides the phloem rays are semi-heterogeneous. Phloem-albuminous cells are scarce.

II. *Ginkgo biloba* type.

The *Cycadaceae*, *Araucariaceae* and a part of the *Podocarpaceae* and *Taxaceae* belong to this group. The axial system is composed half of sieve cells and half of parenchyma cells. They constitute 1–3 cell wide tangential bands, which alternate regularly. The phloem rays are homogeneous, with marginal cells which are not entirely procumbent, but more or less longitudinally

stretched. The ray-parenchyma cells have pit-contact with both the phloem-parenchyma cells and the sieve cells. Only phloem-albuminous cells occur; they form long longitudinal strands lying within the phloem-parenchyma cell bands. There is pit-contact between phloem-albuminous cells and both the sieve cells and the phloem-parenchyma cells of the axial system. Occasionally phloem fibres occur in the bands of parenchyma cells. Outside the periderm neither the parenchyma cells, nor the sieve cells collapse entirely.

III. *Chamaecyparis pisifera* type.

The *Cupressaceae, Taxodiaceae* and a part of the *Taxaceae* and *Podocarpaceae,* belong to this group. The axial system consists of regular tangential cell layers, arranged in a fixed order of phloem fibres, sieve cells, parenchyma cells, sieve cells, phloem fibres etc., the so-called orderly sequence. The phloem-albuminous cells lie usually scattered among the parenchyma cells, singly, never in long longitudinal strands. The phloem rays are homogeneous. Each cell of the phloem ray is connected to all the elements of the axial system. There is no parenchyma-cell net. Phloem fibres, some crystalcells and crystals in the cell-wall are present. Outside the periderm the parenchyma cells collapse, whereas the sieve cells remain almost intact.

These 3 types form 3 evolutionary stages. Considering the sequence, *Pseudotsuga taxifolia, Tsuga canadensis, Ginkgo biloba* and *Chamaecyparis pisifera,* the following features are noticeable:

a. The structure of the axial system changes from about 90% sieve cells and some scattered parenchyma cells, to an axial system with a very regular tangential layering, with a pronounced orderly sequence and with much parenchyma.

b. First ray-albuminous cells and a few phloem-albuminous cells are present; then only phloem-albuminous cells forming long longitudinal strands, resembling ordinary parenchyma cells as far as their pitting is concerned, and eventually scattered phloem-albuminous cells, distinctly isolated from the phloem-parenchyma cells, singly within one cell wide tangential layers of parenchyma cells.

c. First only sclereids, then sclereids and scattered phloem fibres, followed by a stage of only scattered phloem fibres and eventually phloem fibres of the same thickness, forming tangential layers of one cell wide.

d. Outside the periderm a collapse of the sieve cells (*Pseudotsuga taxifolia* type), changing via the *Ginkgo biloba* type with hardly any collapse of the phloem elements, towards collapse of the phloem-parenchyma cells, instead of the sieve cells (*Chamaecyparis pisifera* type).

e. First heterogeneous phloem rays, with no pit-contact between ray-parenchyma cells and sieve cells; then all the elements of the heterogeneous rays have pit-contact with all the elements of the axial system. *Tsuga canadensis* type with semi-heterogeneous phloem rays; *Ginkgo biloba* type with homogeneous rays bordered by more or less erect parenchyma cells and at last *Chamaecyparis* *pisifera* type with homogeneous phloem rays of which all the ray-parenchyma cells are procumbent.

So in reference to the evolutionary stage of the axial system and the reduction of the phloem rays, the phylogenetic sequence starts with stage I with an almost homogeneous axial system and ray-albuminous cells, and a complex heterogeneous phloem ray, differentiating via stage II to stage III, with a highly specialized axial system with phloem-albuminous cells and a relatively simple, reduced homogeneous phloem ray. The reduction of the phloem rays runs parallel with the differentiation of the axial system.

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SAMENVATTING

Uit het onderzoek van het secundaire phloëem van verschillende Gymnospermen blijkt, dat zij te rangschikken zijn in drie typen, die onderscheiden kunnen worden in weer drie ontwikkelingsstadia. Bij deze indeling zijn de volgende eigenschappen van de bast van belang:

a. de samenstelling van het vertikale systeem;
b. de rangschikking van de parenchymcellen;
c. de struktuur van de baststralen;
d. het stippelkontakt tussen de verschillende celtypen van de baststralen en die van het vertikale systeem;
e. de rangschikking der eiwitcellen en het type daarvan;
f. de aanwezigheid resp. afwezigheid van bastvezels, kristalcellenvezels, kristalcellen, sklereiden en steencellen;
g. de veranderingen die de oudere bast ondergaat;
h. de veranderingen van de bast, buiten het periderm.

De drie onderscheiden typen zijn:

I. *Pseudotsuga taxifolia* type.

Hiertoe behoort een gedeelte van de *Pinaceae*.

Het vertikale systeem is opgebouwd uit zeefcellen, waartussen verspreid liggende parenchymcellen voorkomen, die een parenchymcelnet vormen. Dit parenchymcelnet doorkruist de grondmassa van zeefcellen in alle richtingen.

De baststralen zijn heterogeen. De radiaal gestrekte parenchymcellen in het centrum van de baststraal hebben geen stippelkontakt met de zeefcellen. Deze laatste hebben alleen stippelkontakt met de straal-eiwitcellen.

De eiwitcellen komen bijna uitsluitend voor als straal-eiwitcellen, hoewel ook phloëem-eiwitcellen aanwezig zijn.

Kristalcellenvezels komen regelmatig voor, terwijl in de oudere bast ook sklereiden aanwezig kunnen zijn.

Buiten het periderm zijn de zeefcellen volledig gekollabeerd en blijven alleen de parenchymcellen, kristalcellenvezels en sklereiden intakt.

Ia. *Tsuga canadensis* subtype.

De rest van de *Pinaceae* behoort tot dit subtype van het *Pseudotsuga taxifolia* type.

De verschillen met het vorige type zijn:

Straal-eiwitcellen en radiaal gestrekte straal-parenchymcellen, hebben beide stippelkontakt met alle elementen van het vertikale systeem; dus zowel met de zeefcellen als met de parenchymcellen;

De baststralen zijn half-heterogeen.

II. *Ginkgo biloba* type

De *Cycadaceae*, *Araucariaceae* en een gedeelte van de *Podocarpaceae* en van de *Taxaceae*, behoren tot dit type.

Het vertikale systeem bestaat voor ongeveer de helft uit parenchymcellen en voor de helft uit zeefcellen. Beide celtypen vormen 1–3 cellen brede tangentiale banden, die elkaar regelmatig afwisselen.

De baststralen zijn homogeen, maar de randcellen hiervan zijn veel hoger dan de centraal gelegen parenchymcellen; zij zijn in radiale doorsnede niet rechthoekig, maar bijna vierkant. De straal-parenchymcellen hebben stippelkontakt met alle celtypen van het vertikale systeem.

Alleen phloëem-eiwitcellen zijn aanwezig; zij vormen lange longitudinale reeksen van cellen en zij bevinden zich in de parenchymcelbanden. Zij hebben onderling stippelkontakt en ook met de celtypen van het vertikale systeem.

Hier en daar komen in de parenchymcel-banden bastvezels voor.

Buiten het periderm zijn de zeefcellen en parenchymcellen slechts weinig gekollabeerd.

III. *Chamaecyparis pisifera* type

De *Cupressaceae*, *Taxodiaceae* en een gedeelte van de *Taxaceae* en van de *Podocarpaceae*, behoren tot dit type.

Het vertikale systeem bestaat uit 1 cel brede tangentiale lagen, die elk uit een ander type cellen zijn samengesteld. Deze tangentiale lagen hebben een vaste rangschikking, namelijk in de volgorde: bastvezels, zeefcellen, parenchymcellen, zeefcellen, bastvezels enz.; zij vormen een zogenaamd 'vierenritme'.

Alleen phloëem-eiwitcellen komen voor. Deze liggen verspreid tussen de phloeem-parenchymcellen; zij vormen nooit, lange longitudinale reeksen van cellen.

De baststralen zijn homogeen. Elke straal-parenchymcel heeft stippelkontakt met alle elementen van het vertikale systeem.

Er is geen parenchymcelnet; bastvezels, enige kristalcellen en kleine kristallen in de celwanden zijn aanwezig.

Buiten het periderm kollaberen de parenchymcellen, terwijl de zeefcellen min of meer intakt blijven.

Deze drie typen kunnen beschouwd worden als drie ontwikkelingsstadia. Wanneer wij de reeks *Pseudotsuga taxifolia, Tsuga canadensis, Ginkgo biloba* en *Chamaecyparis pisifera* beschouwen, vallen de volgende punten hierbij op:

a. de struktuur van het vertikale systeem verandert van ongeveer 90% zeefcellen, (waarbij de rest wordt ingenomen door verspreid liggende parenchymcellen), in een vertikaal systeem met een zeer regelmatige tangentiale gelaagdheid, het 'vierenritme', waarbij juist veel parenchym aanwezig is.

b. eerst zijn bijna uitsluitend straal-eiwitcellen aanwezig, waarnaast slechts enkele phloëem-eiwitcellen, vervolgens komen alleen phloëem-eitwitcellen voor in lange longitudinale reeksen, die wat hun stippeling betreft, nog op gewone parenchymcellen lijken en tenslotte, binnen de tangentiale parenchymcellagen verspreid liggende phloëem-eiwitcellen, die geen stippelkontakt meer hebben met de parenchymcellen.

c. eerst komen alleen sklereiden voor, vervolgens sklereiden en enkele verspreid liggende bastvezels, gevolgd door een stadium, waarin alleen bastvezels voorkomen. Deze bastvezels hebben ongeveer dezelfde dikte en vormen 1 cel brede tangentiale lagen.

d. bij het *Pseudotsuga taxifolia* type kollaberen buiten het periderm de zeefcellen, terwijl de parenchymcellen intakt blijven. Bij het *Ginkgo biloba* type treedt bijna geen kollaps op buiten het periderm, noch van de zeefcellen, noch van de parenchymcellen. Tenslotte treffen wij bij het *Chamaecyparis pisifera* type buiten het periderm een kollaps aan van de parenchymcellen, terwijl hier de zeefcellen min of meer intakt blijven.

e. eerst zijn de baststralen heterogeen, terwijl geen stippelkontakt aanwezig is tussen straal-parenchymcellen en zeefcellen (*Pseudotsuga taxifolia* type); vervolgens hebben alle celtypen van de heterogene baststraal stippelkontakt met al de elementen van het vertikale systeem, terwijl de baststralen hier half heterogeen zijn (*Tsuga canadensis* type); nu volgt het *Ginkgo biloba* type met homogene baststralen, waarbij de randcellen in radiale doorsnede bijna vierkant zijn en tenslotte het *Chamaecyparis pisifera* type met homogene baststralen waarin alle parenchymcellen liggend zijn.

Beschouwen wij de differentiatie van het vertikale systeem en tegelijkertijd de reductie van de baststralen, dan zijn de basttypen te rangschikken in een reeks van ontwikkelingsstadia, beginnend met type I. Type I heeft een homogeen, weinig gedifferentieerd vertikaal systeem, straal-eiwitcellen en gecompliceerde heterogene baststralen. Dit type I gaat via type II, over in type III met een zeer gespecialiseerd vertikaal systeem en relatief eenvoudige, gereduceerde, homogene baststralen. De reductie van de baststralen loopt parallel met de differentiatie van het vertikale systeem.

REFERENCES

ABBE, L.S. and A.S. CRAFTS	1939	Phloem of White pine and other Coniferous species. Bot. Gaz. **100**:695–722.
BAILEY, I.W.	1925	Some salient lines of specialisation in tracheary pitting, I, Gymnosperms. Ann. Bot. **39**:587–597.
BAILEY, I.W.	1954	Contributions to Plant Anatomy. Chron. Bot. Comp. Waltham, Mass.
BAILEY, I.W. and B.G.L. SWAMY	1949	The morphology and relationships of *Austrobaileya*. J. Arnold Arb. **30**:211–226.
BANNAN, M.W.	1934	Origin and cellular character of xylem rays in Gymnosperms. Bot. Gaz. **96**:260–281.
BANNAN, M.W.	1951	The reduction of fusiform cambial cells in *Chamaecyparis* and *Thuja*. Can. J. Bot. **29**:57–67.
BANNAN, M.W.	1953	The reduction of fusiform cambial cells in *Chamaecyparis* and *Thuja*. Can. J. Bot. **31**: 63–74.
BANNAN, M.W.	1955	The vascular cambium and radial growth in *Thuja occidentalis* L. Can. J. Bot. **33**: 113–138.
BANNAN, M.W.	1965	Ray contacts and rate of anticlinal division in fusiform cambial cells of some *Pinaceae*. Can. J. Bot. **43**: 487–507.
BARGHOORN, E.S.	1940	Origin and development of the uniseriate ray in *Coniferae*. Bull. Torrey Bot. Club **67**: 303–328.
BARGHOORN, E.S.	1941 a	The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons, II: Modification of the multiseriate and uniseriate rays. Am. J. Bot. **28**: 273–282.
BARGHOORN, E.S.	1941 b	The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons, III: The elimination of rays. Bull. Torrey Bot. Club **68**: 317–325.
BEHNKE, H.D.	1965	Über das Phloem der *Discoreaceae* unter besonderer Berücksichtigung ihrer Phloem-becken. Ztschr. für Pflanzen-Physiologie **53**: 97–125.
BRAUN, H.J.	1955 a	Beitrag zur Entwicklungsgeschichte der Markstrahlen. Bot. Studien **4**: 73–131.
BRAUN, H.J.	1955 b	Entstehung und Veränderung netzigen Borkenmuster. Ztschr. für Bot. **43**: 205–242.
BRAUN, H.J.	1959	Die Vernetzung der Gefässe bei *Populus*. Ztschr. für Bot. **47**: 421–434.
BRAUN, H.J.	1963	Die Organisation des Stammes von Bäumen und Stäuchern. Stuttgart, 162 p.
BRAUN, H.J. and R.W. DEN OUTER	1965	Die unterschiedlichen Beziehungen der Holzstrahlen zum Hydrosystem als wesentliches Differenzierungsprinzip. Ztschr. für Bot. **52**: 539–571.
CHEADLE, V.I.	1948	Observations on the phloem in the *Monocotyledoneae*, II: Additional data on the occurrence and phylogenetic specialization in structure of the sieve tubes in the metaphloem. Am. J. Bot. **35**: 129–131.
CHEADLE, V.I.	1956	Research on xylem and phloem. Progress in fifty years. Am. J. Bot. **43**: 719–731.
CHEADLE, V.I. and K. ESAU	1958	Secondary Phloem of *Calycanthaceae*. Univ. Cal. Publ. Bot. **29**: 397–504.
CHEADLE, V.I. and N.B. WHITFORD	1941	Observations on the phloem in the *Monocotyledoneae*. Am. J. Bot. **28**: 623–627.

Chrysler, M.A.	1913	The origin of the erect cells in the phloem of the *Abietineae*. Bot. Gaz. **56**: 36–50.
Courtot, Y. and L. Baillaud	1958	Quelques modalites du rythme de la differation dans le fibre des Cupressacees. Ann. Sc. Univ. Besançon, 2 serie, Bot. **12**: 53–57.
Crafts, A.S.	1939	The relation between structure and function of phloem. Am. J. Bot. **266**: 172–177.
Crafts, A.S. and H.B. Currier	1963	On the sieve tube function. Protoplasma **57**: 188–202.
Currier, H.B., K. Esau and V.I. Cheadle	1955	Plasmolytic studies on phloem. Am. J. Bot. **42**: 68–81.
Curtis, O.F. and G.N. Asai	1939	Evidence relative to the supposed permeability of sieve tube protoplasm. Am. J. Bot. **26**: 165–175.
Dallimore, W. and A.B. Jackson	1966	A Handbook of *Coniferae* and *Ginkgoaceae*. Fourth Edition. Revised by S.G. Harrison, Publ. Edward Arnold Ltd., London, 729 p.
Duloy, M., F.V. Mercer and N. Rathgeber	1961	Studies on translocation, II: Submicroscopic anatomy of the phloem. Aust. J. Biol. Sci. **14**: 506–518.
Eicke, R.	1964	*Ginkgo biloba.* Entwicklungsstand des Holzes und seines Feinbaus. Ber. dtsch. bot. Ges. **77**: 379–385.
Engelman, E.M.	1963	Fine structure of the proteinaceous substance in sieve tubes. Planta **59**: 420–426.
Engelman, E.M.	1965	Sieve element of *Impatiens sultanii*, II: Developmental aspects. Ann. Bot. **29**: 103:118.
Engelman, E.M.	1965	Sieve element of *Impatiens sultanii*, I: Wound reaction. Ann. Bot. **29**: 83–101.
Esau, K.	1947	Sieve tube inclusions. Am. J. Bot. **34**: 224–233.
Esau, K.	1950	Development and structure of the phloem tissue. Bot. Rev. **16**: 67–114.
Esau, K.	1954	The present status of knowledge on trends of specialization in the phloem tissue. 8 Congress Int. Bot. Paris **7/8**: 279–281.
Esau, K.	1962	Development of sieve plate pores. Bot. Gaz. **123**: 233–243.
Esau, K.	1964	Plant Anatomy, 735 p.
Esau, K.	1965	Fixation images of sieve element plastids in *Beta*. Proc. Nat. Academy Sci. **54**: 429–437.
Esau, K.	1965	On the anatomy of the woody plant. Cellular Ultrastructure of Woody plants: 35–49.
Esau, K. and V.I. Cheadle	1955	Significance of cell divisions in differentiating secondary phloem. Acta Bot. Neerl. **4**: 348–357.
Esau, K. and V.I. Cheadle	1958	Wall thickening in sieve elements. Proc. Nat. Acad. Sci. **44**: 546–553.
Esau, K. and V.I. Cheadle	1961	An evaluation of studies on ultrastructure of sieve plates. Pros. Natl. Acad. Sci. (U.S.) **47**: 1716–1726.
Esau, K. and V.I. Cheadle	1965	Cytologic studies on phloem. Univ. Cal. Publ. Bot. **36**: 253–344.
Esau, K., V.I. Cheadle and H.B. Currier	1957	Physiology of the Phloem. Ann. Rev. Plant Phys. **8**: 349–374.
Esau, K., V.I. Cheadle and E.M. Grifford	1953	Comparative structure and possible trends of specialization of the phloem. Am. J. Bot. **40**: 9–19.
Esau, K., V.I. Cheadle and E.B. Risley	1962	Development of sieve plate spores. Bot. Gaz. **123**: 233–243.
Eschrich, W.	1964	Physiology of sieve tube callose. Ber. dtsch. bot. Ges. **77**: 368.

ESCHRICH, W.	1965	Physiologie der Siebröhren Kallose. Planta **65**: 280–300.
ESCHRICH, W. H. B. CURRIER, S. YAMAGUCHI and R. B. M. NAIRN	1965	Der Einfluss verstärkter Kallose Bildung auf den Stoffentransport in Siebröhren. Planta **65**: 49–64.
EVANS, N. T. S., M. EBERT and J. MOORBY	1963	A model for the translocation of photosynthate in the Soybean. J. Exp. Bot. **14**: 221–231.
EVERT, R. F.	1960	Phloem structure in *Pyrus communis*. Univ. Cal. Publ. Bot. **32**: 127–194.
EVERT, R. F.	1963	Ontogeny and Structure of the secondary phloem in *Pyrus malus*. Am. J. Bot. **50**: 8–37.
EVERT, R. F.	1963	The cambium and seasonal development of the phloem in *Pyrus malus*. Am. J. Bot. **50**: 149–159.
EVERT, R. F. and F. J. ALFIERI	1965	Ontogeny and structure of Coniferous sieve cells. Am. J. Bot. **52**: 1058–1066.
EVERT, R. F. and W. F. DERR	1947	Slime substance and strands in sieve elements. Am. J. Bot. **34**: 45–52.
EVERT, R. F. and W. F. DERR	1964	Slime substance and strands in sieve elements. Am. J. Bot. **51**: 875–880.
EVERT, R. F. and W. F. DERR	1964	Callose substance in sieve elements. Am. J. Bot. **51**: 552–560.
EVERT, R. F. and L. MURMANIS	1965	Ultrastructure of the secondary phloem of *Tilia americana*. Am. J. Bot. **52**: 95–106.
FREY, G.	1954	Aktivität und Lokalisation von saurer Phosphatase in den vegetativen Teilen einiger Angiospermen und einiger Samen. Ber. schweiz. bot. Ges. **64**: 390.
GLICK, D.	1959	Methods of biochemical analysis, Vol. I–VII. New York, 1954–1959.
GLICK, D.	1963	Quantitative chemical techniques of Histo- and Cytochemistry, Vol. I–II. New York, 1961–1963.
GOMORI, G.	1939	Microtechnical demonstration of fosfatase in tissue sections. Proc. Soc. Exp. Biol. and Med. (NY) **42**: 23–26.
GOMORI, G.	1941	Distribution of acid fosfatase in the tissues under normal and under pathologic conditions. Arch. Path. **32**: 189–199.
GREGUSS, P.	1955	Xylotomische Bestimmung der heute lebenden Gymnospermen. Budapest.
GREGUSS, P.	1959	Holzanatomie der europäischen Laubhölzer und Sträuchern. Budapest.
GRILLOS, S. J. and F. H. SMITH	1959	The secondary phloem of the Douglas fir. Forest Science **5**: 377–388.
HEMENWAY, A. F.	1911	Studies on the phloem of the Dicotyledons, I: Phloem of the *Juglandaceae*. Bot. Gaz. **51**: 131–135.
HEMENWAY, A. F.	1913	Studies on the phloem of the Dicotyledons. Bot. Gaz. **55**: 236–243.
HEPTON, C. E. L. and R. D. PRESTON	1960	Electron microscopic observations of the structure of sieve connections in the phloem of Angiosperms and Gymnosperms. J. Exp. Bot. **11**: 381–394.
HILL, G. P.	1962	Exudation from *Aphid* stylets. J. Exp. Bot. **13**: 144–151.
HOLDHEIDE, W.	1951	Anatomie mitteleuropäischer Gehölzrinden. In H. Freund's Handbuch der Mikr. in der Technik **5**: 193–367. Umschau verlag Frankfurt-am-Main, Germany.
HOLDHEIDE, W. and B. HUBER	1952	Ähnlichkeiten und Unterschiede in Feinbau von Holz und Rinde. Holz als Roh- und Werkstoff **10**: 263–268.
HOUTZAGERS, G.	1954	Houtteelt der gematigde luchtstreek. Deel I, de Houtsoorten. Zwolle, 576 p.

Huber, B.	1937	Hundert Jahre Siebröhren Forschung. Protoplasma **29**: 132–148.
Huber, B.	1939	Das Siebröhrensystem unsere Bäume und seine jahreszeitlichen Veränderungen. Jahrb. Wissensch. Bot. **88**: 176–242.
Huber, B.	1949	Zur Phylogenie des Jahrringbaues der Rinde. Svensk Bot. Tidskr. **43**: 376–382.
Huber, B.	1951	Mikroscopische Untersuchung von Hölzern. Mikr. in der Technik (Freund) **5**: 81–192.
Huber, B.	1955	Wasserumsatz und Stoffbewegung. Fortschr. Bot. **17**: 483–508.
Huber, B. and E. Graf	1955	Vergleichende Untersuchungen über Geleitzellen der Siebröhren. Ber. dtsch. bot. Ges. **68**: 303–310.
Huber, B. and W. Liese	1963	Untersuchungen über den Feinbau des sekundären Phloems, I: *Larix decidua* Mill. Protoplasma **57**: 429–439.
Huber, B. and K. Mägdefrau	1953	Zur Phylogenie des heterogenen Markstrahlbaues. Ber. Dtsch. Bot. Ges. **66**: 116–122.
Huber, B. and E. Rouschal	1938	Anatomische und Zellphysiologische Beobachtungen am Siebröhren system der Bäume. Ber. Dtsch. Bot. Ges. **56**: 380–391.
International Association of Wood Anatomists	1957	International glossary of terms used in Wood Anatomy. Tropical Woods **107**: 1–36.
Janchen, E.	1949	Das System der Coniferen. Sitzungs ber. Oest. Akad. Wiss. Math. Nat. Kl. Abt. I, **3**: 155–162.
Jayme, G. and D. Tengel	1962	Elektronenoptische Beobachtungen über den Feinbau von Nadelholzzellen. Papier **16**: 519–524.
Jeffrey, E. C.	1905	The comparative anatomy and phylogeny of the Coniferales, part 2: The *Abietineae*. Mem. Boston Soc. Nat. History **6**: 37 p.
Jeffrey, E. C.	1940	In: Johansen D. A., Plant Microtechnique. Mc. Graw-Hill Book Company Inc. New York and London: 104.
Johansen, D. A.	1940	Plant microtechnique. Mc. Graw-Hill Book Company Inc. New York and London, 523 p.
Kaiser	1940	In: Johansen, D. A., Plant microtechnique. Mc. Graw-Hill Book Company Inc. New York and London: 119.
Kollmann, R.	1965	Zur Lokalisierung der Funktionstüchtigen Siebzellen im sekundären Phloem von *Metasequoia glyptostroboides*. Planta **65**: 173–179.
Kollmann, R. and W. Schumacher	1961	Über die Feinstructur des Phloems von *Metasequoia glyptostroboides* und seine jahreszeitlichen Veränderungen. Planta **57**: 583–607.
Kollmann, R. and W. Schumacher	1962	Über die Feinstructur des Phloems von *Metasequoia glyptostroboides* und seine jahreszeitlichen Veränderungen. Planta **58**: 366–386.
Lam, H. J.	1957	Comments on Greguss's Phylogenetical tree of plants. Blumea **8**: 528–531.
Lamoureux, C. H.	1961	Comparative studies on phloem of vascular Cryptogams. Ph. D. Doctoral Diss. Univ. Cal. Davis.
Leroy, J. F.	1960	Structure du bois et classification. Bull. Soc. Bot. France Mem.: 20–29.
Lester, H. H. and R. F. Evert	1965	Acid fosfatase activity in sieve tube members of *Tilia americana*. Planta **65**: 180–185.
Li, H. L.	1953	A reclassification of *Libocedrus* and *Cupressaceae*. J. Arnold Arb. **34**: 17–36.

LIESE, W. and V. MATTE	1962	Beitrag zur Rinden Anatomie der Gattung *Dacrydium* und *Podocarpus*. Forstwiss. Centralblatt **81**: 268–280.
MÄGDEFRAU, K.	1953	Paläobotanik. Fortschr. Bot. **14**: 99–162.
MÄGDEFRAU, K. and B. HUBER	1953	Zur Phylogenie des heterogenen Markstrahlbaues. Ber. Dtsch. Bot. Ges. **66**: 116–122.
MAZIA, D., P. A. BREWER and M. ALFERT	1953	The cytochemical staining and measurement of protein with mercuric bromophenol blue. Biol. Bull. **104**: 51–67.
MC. GIVERN, M. J.	1957	Mitochondria and plastids in sieve tube cells. Am. J. Bot. **44**: 37–48.
MENTHA, A. S. and D. C. SPANNER	1962	The fine structure of the sieve tubes of the petiole of petiole of *Nymphoides peltatum* (GMEL) O. KUNZE. Ann. Bot. **26**: 291–299.
METTENIUS, G.	1861	Beiträge zur Anatomie der Cycadeen. Abh. K. Sachs. Ges. Wiss. **7**: 565–608.
MÖLLER, J.	1882	Anatomie der Baumrinden.
PARKER, J.	1965	Strand characteristics in sieve tubes of some common tree species. Protoplasma **60**: 86–93.
PEEL, A. J.	1965	On the conductivity of the xylem of trees. Ann. Bot. **29**: 120–130.
PEEL, A. J. and P. E. WHEATHERLY	1962	Studies in sieve tube exudation through *Aphid* mouth parts: The effect of light and girdling. Ann. Bot. **26**: 633–646.
PENHALLOW, D. P.	1903	Notes on Tertiary plants. Proc. Trans. Roy. Soc. Canada **9** (sec. 4): 33–71.
PULLE, A. A.	1950	Compendium van de terminologie, nomenclatuur en systematiek der zaadplanten. Utrecht, 370 p.
RAUEN, N.	1964	Biochemisches Taschenbuch, Berlin.
REINDERS, E.	1961	Handleiding bij de Plantenanatomie. Landbouwhogeschool, Wageningen, 116 p.
REINDERS, E. and R. PRAKKEN	1964	Leerboek der Plantkunde. Amsterdam, 748 p.
RESCH, A.	1961	Zur Frage nach der Geleitzellen im Protophloem der Wurzel. Ztschr. für Bot. **49**: 82–95.
RESCH, A.	1954	Beiträge zur Cytologie des Phloems. Planta **44** :75–99.
ROUSCHAL, E.	1941	Untersuchungen über die Funktion der Siebröhren. Flora **35**: 135–200.
RUSSOW, E.	1882	Über den Bau und die Entwicklung der Siebröhren und über Bau und Entwicklung der secundairen Rinde der Dicotylen und Gymnospermen. Sitz. Ber. Dorpater Nat. Forsch. Ges. **6**: 257–327.
SCHUMACHER, W.	1939	Über die Plasmolysierbarkeit der Siebröhren Jahrb. Wiss. Bot. **88**: 545–553.
SCHWANKEL, A.	1956	Bark. Thames and Hudson, London.
SCHWERDTFEGER, F.	1957	Waldkrankheiten. Hamburg-Berlin, 485 p.
SHIMAJI, K.	1964	Structure and development of the inner bark tissue in *Abies*. J. Jap. For. Soc. **46**: 199–204.
SHIMAKURC, M.	1936	On the expansion of bast cells in Conifers. Bot. Mag. Tokio **50**: 318–323.
SITTE, P.	1961	Die submikroscopische Organisation der Pflanzenzelle. Ber. Dtsch. Bot. Ges. **74**: 177–206.
SRIVASTAVA, L. M.	1963a	Cambium and vascular derivatives of *Ginkgo biloba*. J. Arnold Arb. **44**: 165–192.
SRIVASTAVA, L. M.	1963b	Secondary phloem in the *Pinaceae*. Univ. Cal. Publ. Bot. **36**: 1–142.
STERLING, C.	1947	Organisation of the shoot of *Pseudotsuga taxifolia*

		(LAMB). BRITT., II: Vascularization. Am. J. Bot. **34**: 272–280.
STRASBURGER, E.	1891	Über den Bau und den Verrichtungen der Leitungsbahnen in den Pflanzen. Hist. Beiträge 3:1000 p. Gustav Fisher, Jena.
STRASBURGER, E.	1965	Lehrbuch der Botanik für Hochschulen.
THAINE, R.	1961	Transcellular strands and particle movement in mature sieve tubes. Nature, **192**:772.
THOMPSON, W. P.	1910	Origin of ray tracheids in the *Coniferae*. Bot. Gaz. **50**: 101–116.
THOMPSON, W. P.	1919	Companion cells in bast of *Gnetum* and Angiosperms. Bot. Gaz. **68**: 451–459.
TIPPO, O.	1946	The role of wood anatomy in phylogeny. Am. Midland Nat. **36**: 362–372.
ULLRICH, W.	1961	Zur sauerstoff abhängigkeit des Transportes in den Siebröhren. Planta **57**: 402–429.
ULLRICH, W.	1962	Beobachtungen über die Kallose ablagerung in Transportierenden und nicht Transportierenden Siebröhren. Planta **59**: 239–242.
ULLRICH, W.	1963	Über die Bildung von Kallose bei einer Hemmung des Transportes in den Siebröhren durch Cyanid. Planta **59**: 387–390.
VOLZ, G.	1952	Electronenmikroscopische Untersuchungen über die Poriengrösse pflanzlicher Zellwänden. Microscopie **7**: 251–266.
WANNER, H.	1952	Phosphatase verteilung und Kohlehydrat Transport in den Pflanzen. Planta **41**: 190.
WEATHERLEY, P. E., A. J. PEEL and G. P. HILL	1959	The physiology of the sieve tube. J. Exp. Bot. **10**: 1–16.
WEBB, J. A. and P. R. GORHAM	1965	Radial movement of C^{14} translocations from Squash phloem. Can. J. Bot. **43**: 97–103.
WOODING, F. B. P. and D. H. NORTHCOTE	1965	Association of the Endoplasmic Reticulum and the plastids in *Acer* and *Pinus*. Am. J. Bot. **52**: 526–531.
WOODING, F. B. P. and D. H. NORTHCOTE	1965	Fine structure and development of the companion cell of the phloem of *Acer pseudoplatanus*. J. Cell Biology **24**: 117–128.
YING-PE CHANG	1954	Anatomy of the common north American pulpwood barks. Tappi Monograph Series **14**.
ZAHUR, S.	1959	Comparative study of secondary phloem of 423 species of woody Dicotyledons belonging to 85 families. Cornell Univ. Agr. Exp. St. Mem. **358**: 160 p.
ZIEGLER, H.	1955a	Phosphatase Aktivität und Sauerstoffverbrauch des Nektariums von *Abutilon striatum* DICKS. Naturwissensch. **42**: 259–260.
ZIEGLER, H.	1955b	Über die Lokalisierung der sauren Phosphatase im Holz des Spitzahorns. Naturwissensch. **42**: 260.
ZIEGLER, H.	1955c	Über die Rolle des Phosphors beim Kohlehydrate Transport in der Pflanze. Vortrag auf der Tagung der dtsch. bot. Ges. in Frb. i. Br., Juni.
ZIEGLER, H.	1963	Untersuchungen über die Feinstruktur des Phloems, II: Die Siebplatten bei der Braunalge *Macrocystis pyrifera* (L.) A.G. Protoplasma **57**: 786–799.
ZIEGLER, H.	1963	Der Ferntransport organischer Stoffe in den Pflanzen. Naturwissensch. **50**: 177–186.
ZIMMERMANN, M. H.	1957	Translocation of organic substances in trees. Plant Phys.

32: 288–291 and Plant Phys. **33**: 213–217.

ZIMMERMANN, M. H. 1960 Transport in the phloem. Ann. Rev. Plant Phys. **11**: 167–190.

ZIMMERMANN, M. H. 1961 Movement of organic substances in trees. Science **133**: 73–79.

ZIJLSTRA, K. 1909 Die Gestalten der Markstrahlen in sekundären Holze. Rev. trav. bot. Neerl. **5**: 17–50.

PLATES

LEGENDS

AC	albuminous cell
CA	cambium
CrC	crystalliferous cell
GRB	growth ring boundary
Int	intercellular space
PC	parenchyma cell
PhD	phelloderm
PhF	phloem fibre
PhG	phellogen
PhM	phellem
PhR	phloem ray
PhRPC	phloem-ray parenchyma cell
SC	sieve cell
SCL	sclereid
T	tracheid
WR	wood ray
WRPC	wood-ray parenchyma cell
WRT	wood-ray tracheid

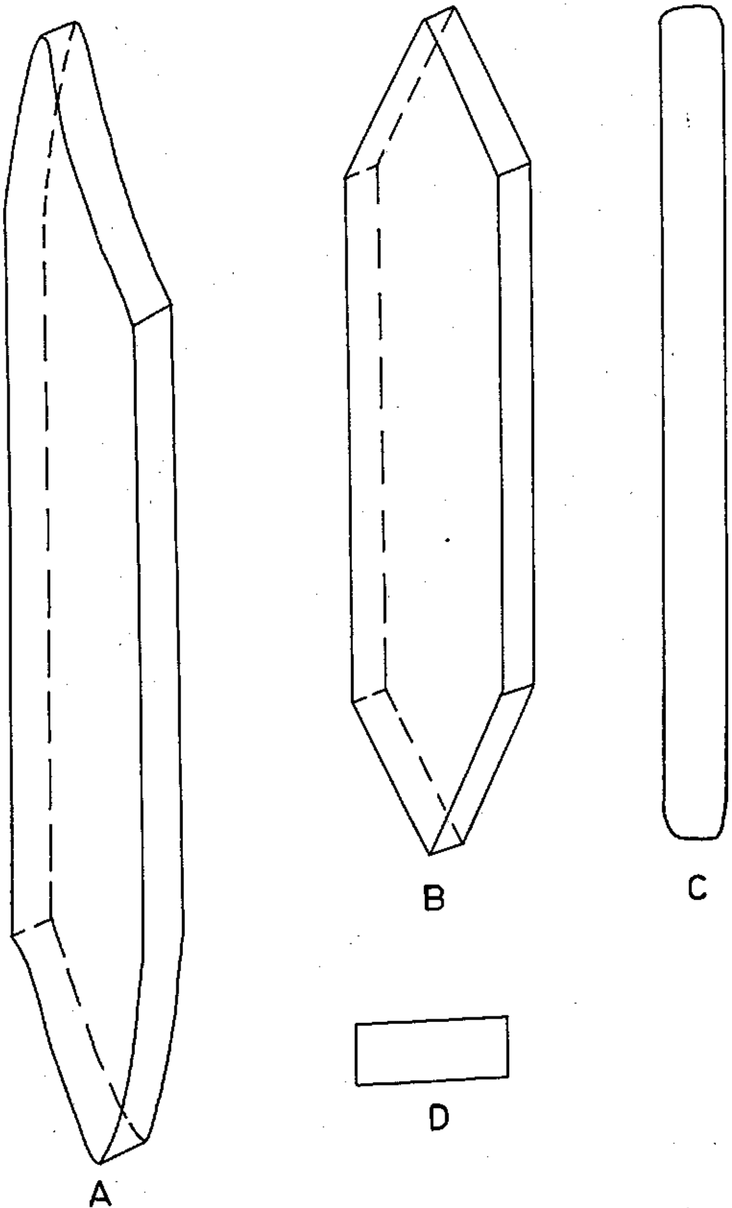


FIG. 1. Fusiform cambial initials. A and B seen from the tg. side, C in a rd. section and D in a cross section

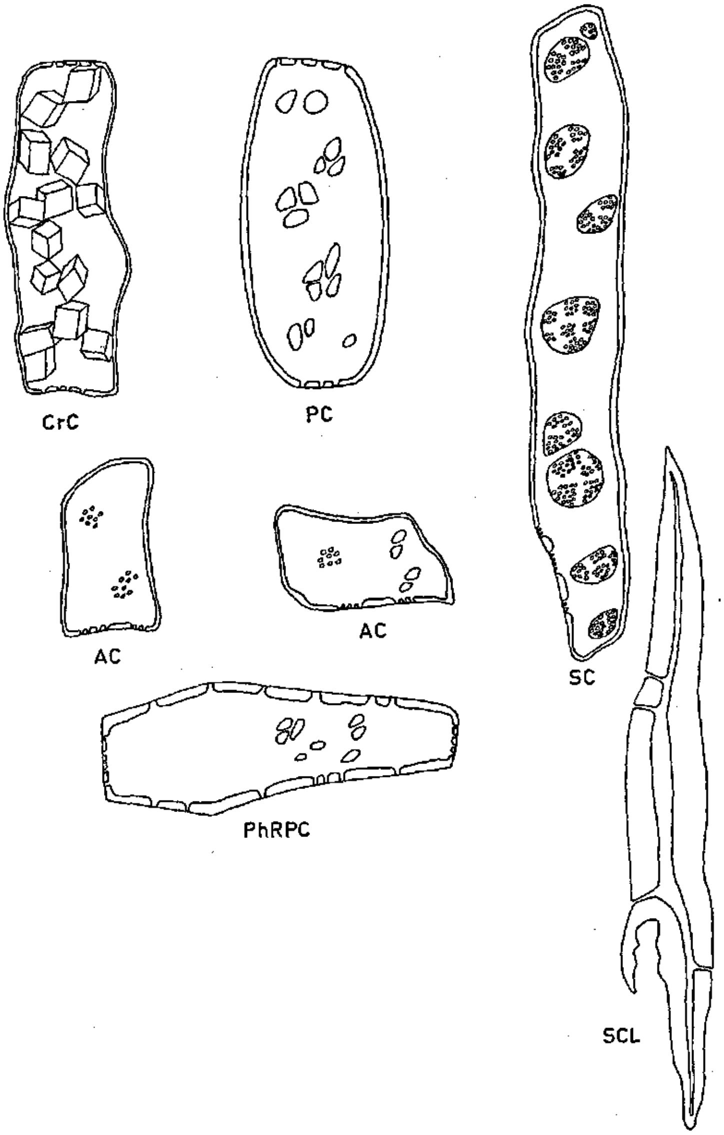


FIG. 2. *Pseudotsuga taxifolia* BRITT. Maceration. Elements of the secondary phloem

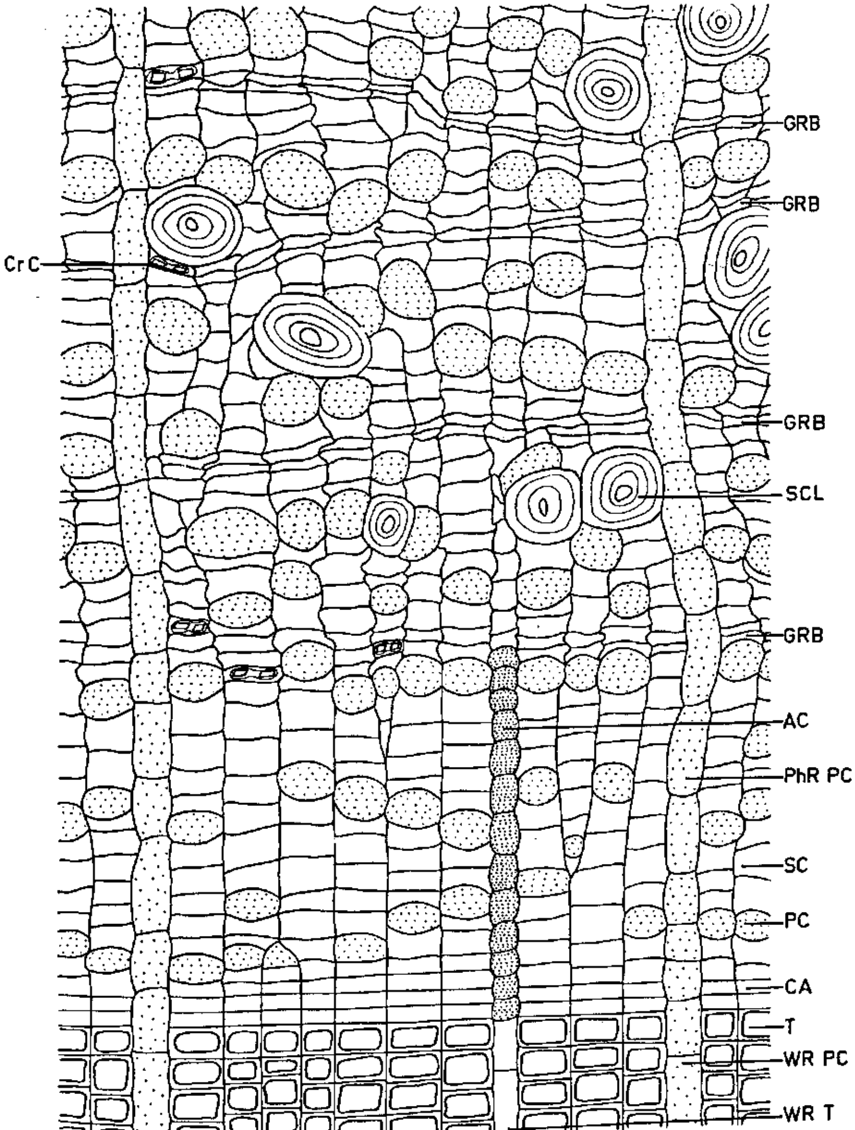


FIG. 3. *Pseudotsuga taxifolia* BRITT. Cross section of the xylem, cambium and secondary phloem. Sclereids occur in the growth rings of two years old or older. The phloem ray in the middle is cut through the row of albuminous cells. They are only alive in the growth ring of the first year; after that they collapse gradually

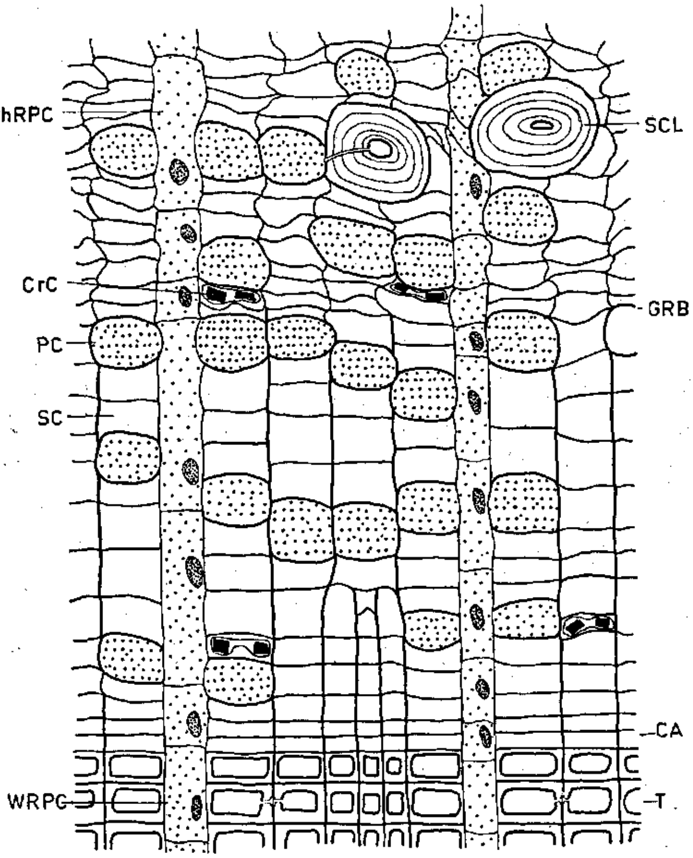


FIG. 4. *Pseudotsuga taxifolia* BRITT. Cross section of the xylem, cambium and the last two growth rings of the secondary phloem

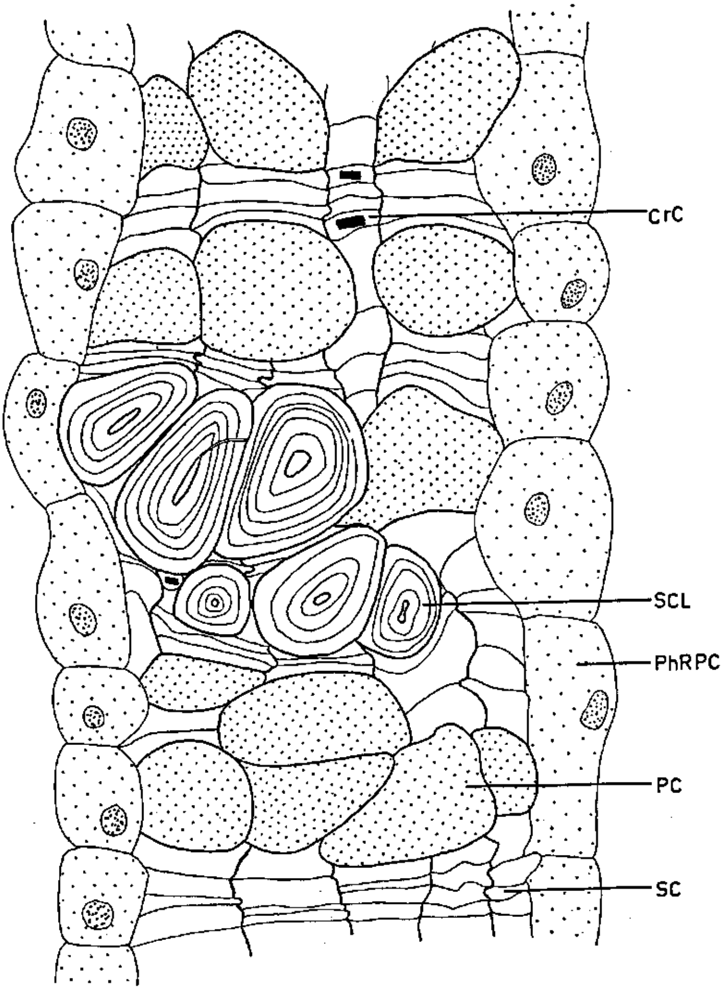


FIG. 5. *Pseudotsuga taxifolia* BRITT. Cross section of the older secondary phloem. The sieve cells are collapsed, while sclereids are differentiated from several parenchyma cells

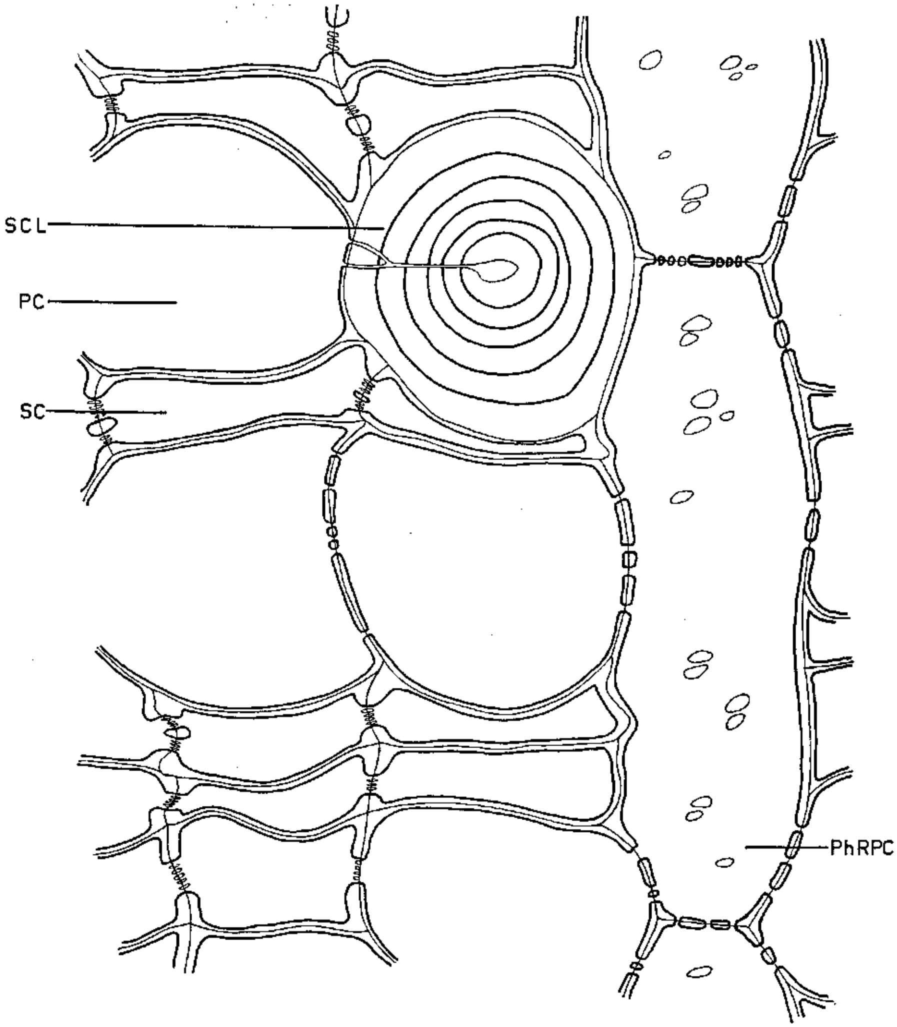


FIG. 6. *Pseudotsuga taxifolia* BRITT. Cross section showing distribution of the pits in the older phloem

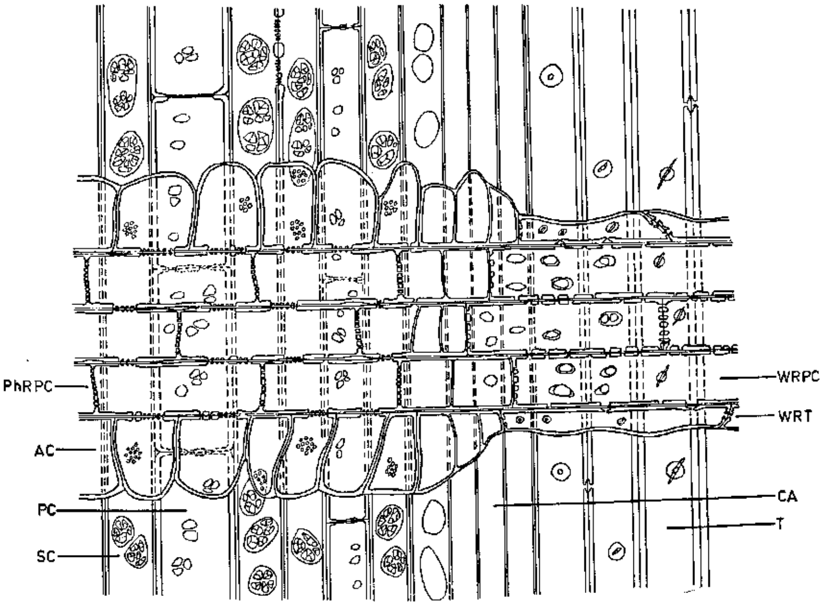


FIG. 7. *Pseudotsuga taxifolia* BRITT. Radial section showing distribution of the pits near the cambium. There is pit-contact between sieve cells and ray-albuminous cells, but not between sieve cells and ray-parenchyma cells

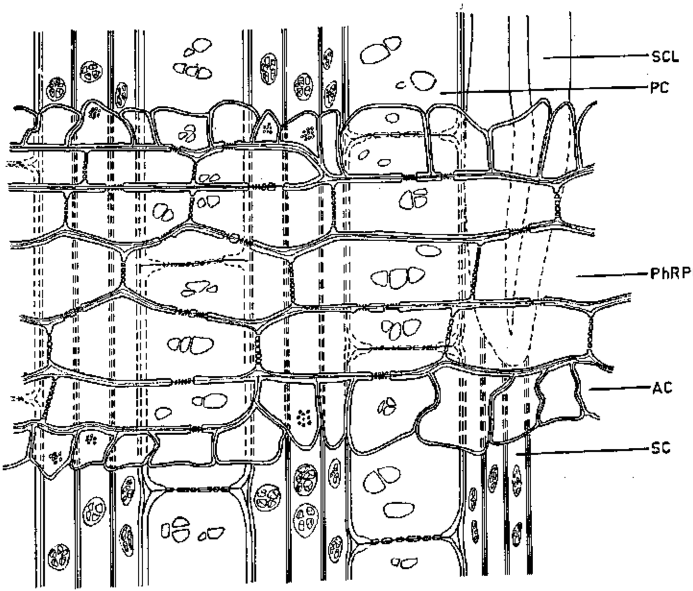


FIG. 8. *Pseudotsuga taxifolia* BRITT. Radial section showing distribution of the pits in the older phloem, attached to that of fig. 7. Far from the cambium, on the left-hand side, the ray-albuminous cells are almost entirely collapsed. The sieve cells too are collapsed, while the parenchyma cells gained in volume

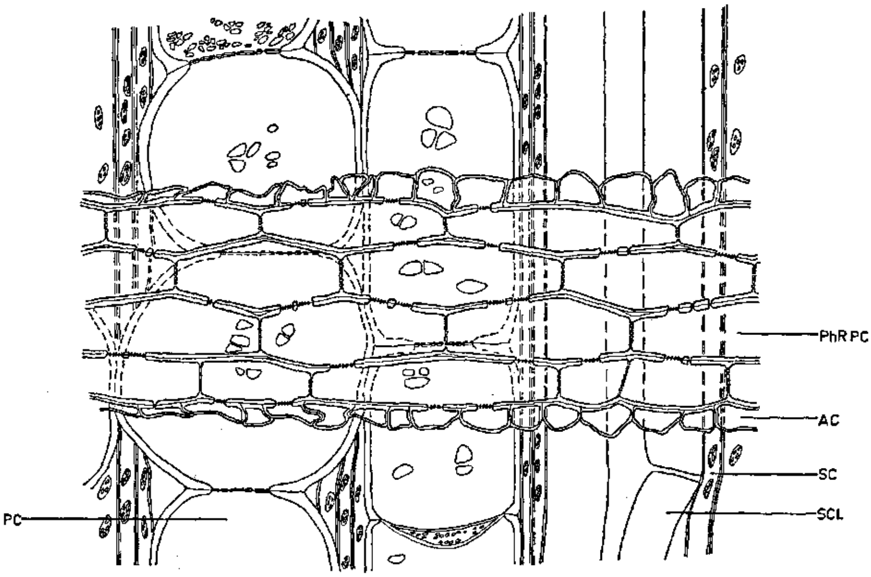


FIG. 9. *Pseudotsuga taxifolia* BRITT. Radial section of the older phloem attached to that of fig. 8, showing distribution of the pits. The cambium is on the right-hand side. Both the sieve cells and the albuminous cells are collapsed, while the parenchyma cells increased in volume. Sclereids have differentiated from parenchyma cells

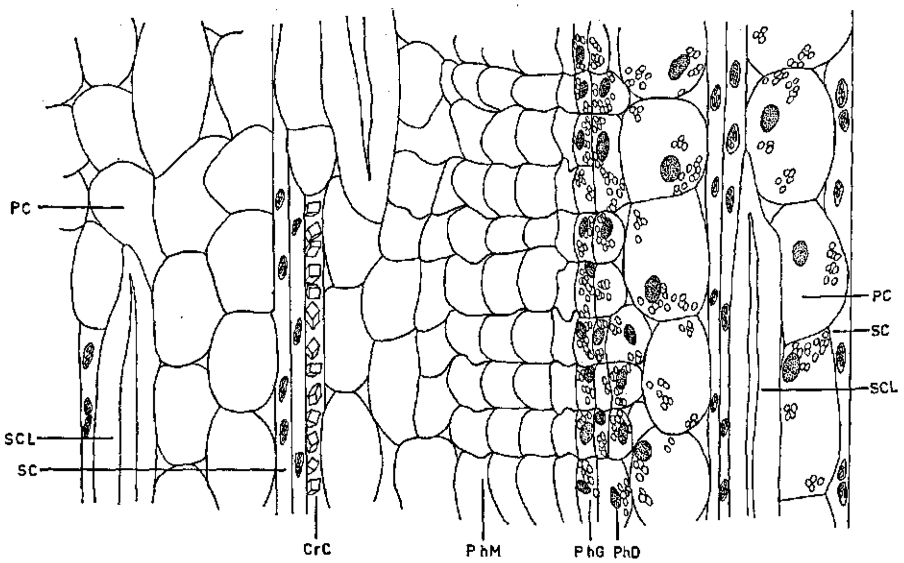


FIG. 10. *Pseudotsuga taxifolia* BRITT. Radial section of the periderm; the adjacent parenchyma cells of the living secondary phloem contain starch and possess a nucleus (right), while the dead parenchyma cells of the rhytidome (left) are empty and have lost their nuclei

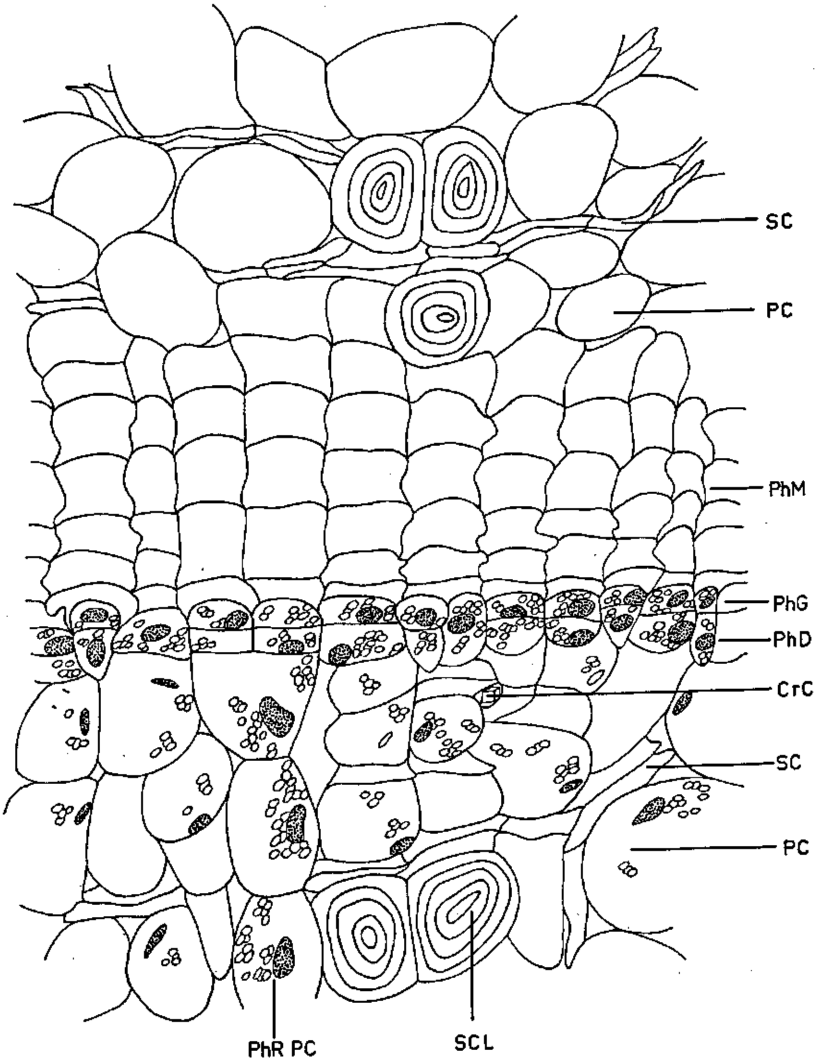


FIG. 11. *Pseudotsuga taxifolia* BRITT. Cross section of the periderm and the adjacent parenchyma cells of the living secondary phloem, containing starch and possessing a nuclei, while the dead parenchyma cells of the rhytidome (above), are empty and have lost their nuclei

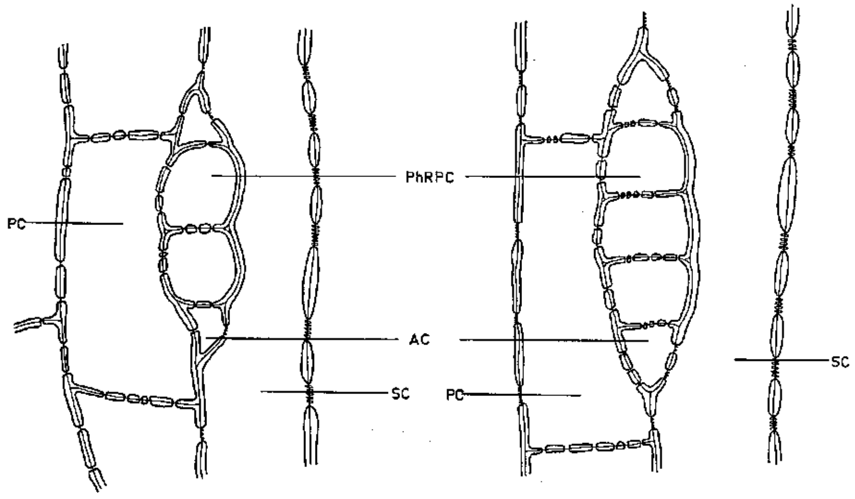


FIG. 12. *Pseudotsuga taxifolia* BRITT. Tangential section of a phloem ray near the cambial zone (right) and one in the older secondary phloem (left). Distribution of the pits. Both the phloem rays are bordered by parenchyma cells on the left-hand side and by sieve cells on the right-hand side

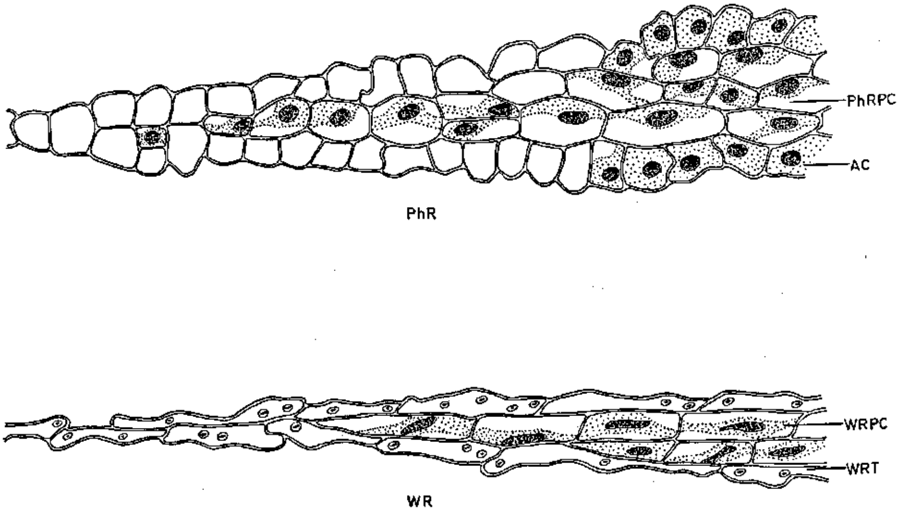
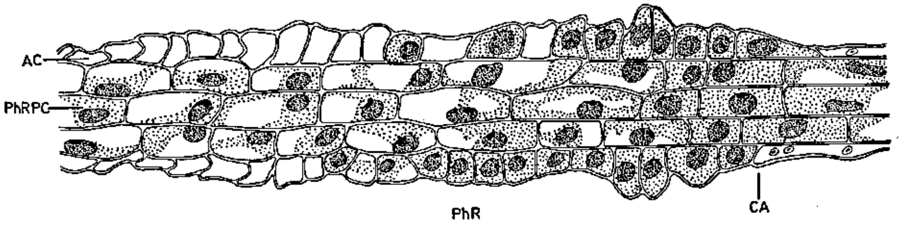


FIG. 13. *Pseudotsuga taxifolia* BRITT. Distribution of the protoplasm and the shape of the nuclei in a gradually increasing uniseriate phloem ray (above) and wood ray (below). The cambium is on the right-hand side. Only bordered pits on the radial walls of the wood-ray tracheids, are indicated



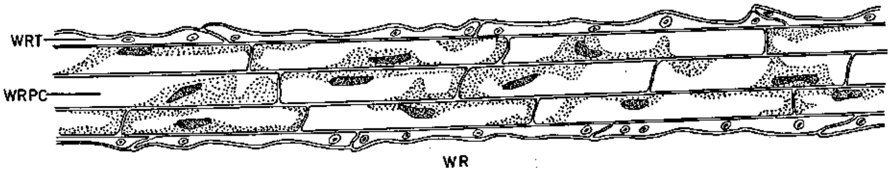


FIG. 14. *Pseudotsuga taxifolia* BRITT. Distribution of the protoplasm and the shape of the nuclei in the phloem-ray cells, the ray initials and the wood ray

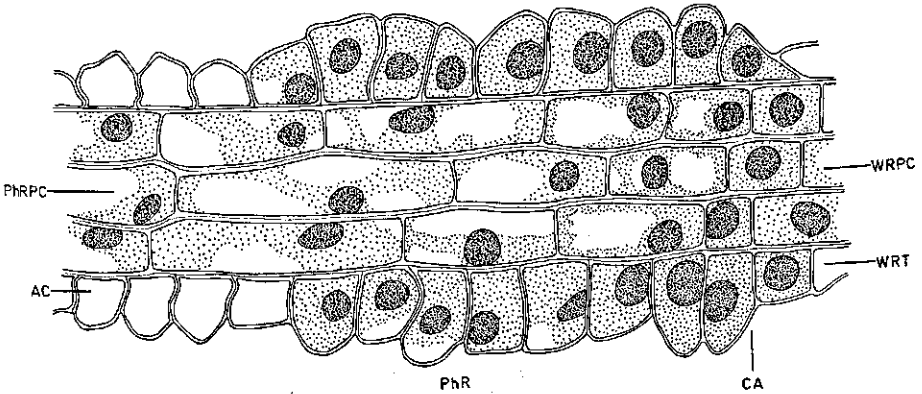


FIG. 15. *Pseudotsuga taxifolia* BRITT. Radial section showing distribution of the protoplasm and the nuclei in a phloem ray near the cambial zone. Functioning albuminous cells possess apparent large round nuclei and much protoplasm

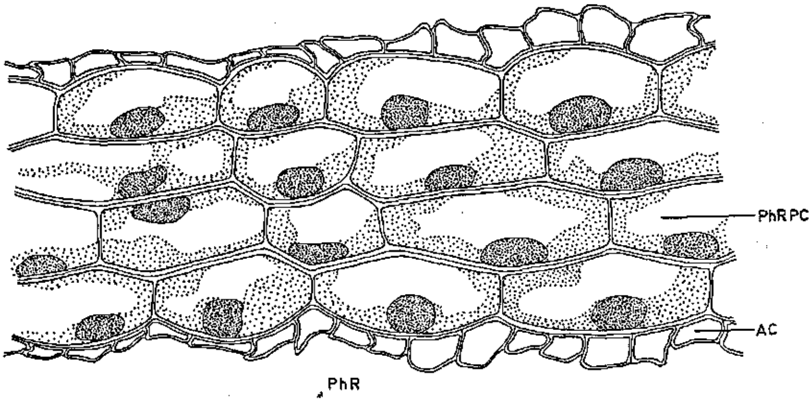


FIG. 16. *Pseudotsuga taxifolia* BRITT. Radial section of a phloem ray in the older secondary phloem. The nonfunctional albuminous cells have lost their nuclei and protoplasm; they collapse gradually. The ray-parenchyma cells are rounded off, while their nuclei are not round any more. but somewhat elongated

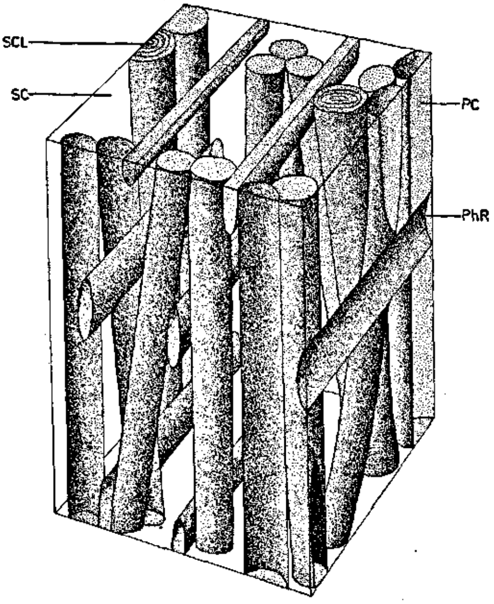


FIG. 17. *Pseudotsuga taxifolia* BRITT. Diagram showing the parenchyma cell net. The white area consists of sieve cells

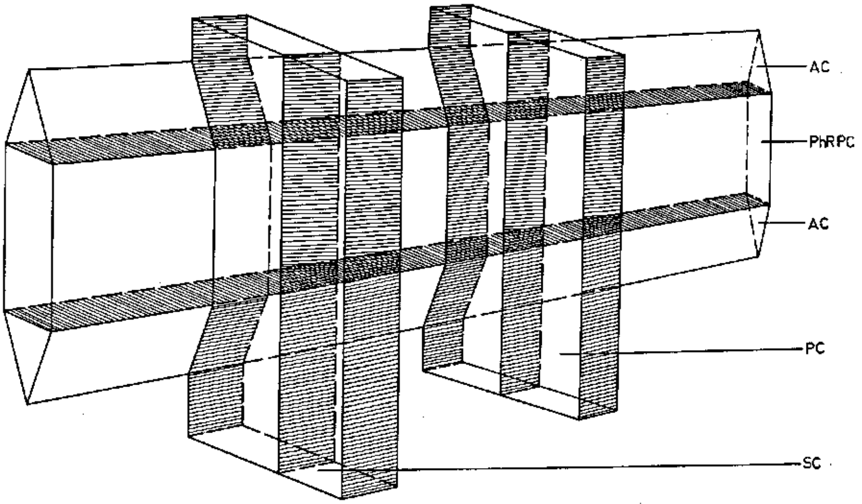


FIG. 18. *Pseudotsuga taxifolia* BRITT. Diagram, representing the contact between a phloem ray and both a layer of sieve cells (left) and a layer of parenchyma cells (right). The shaded areas represent walls, through which pit-contact is present

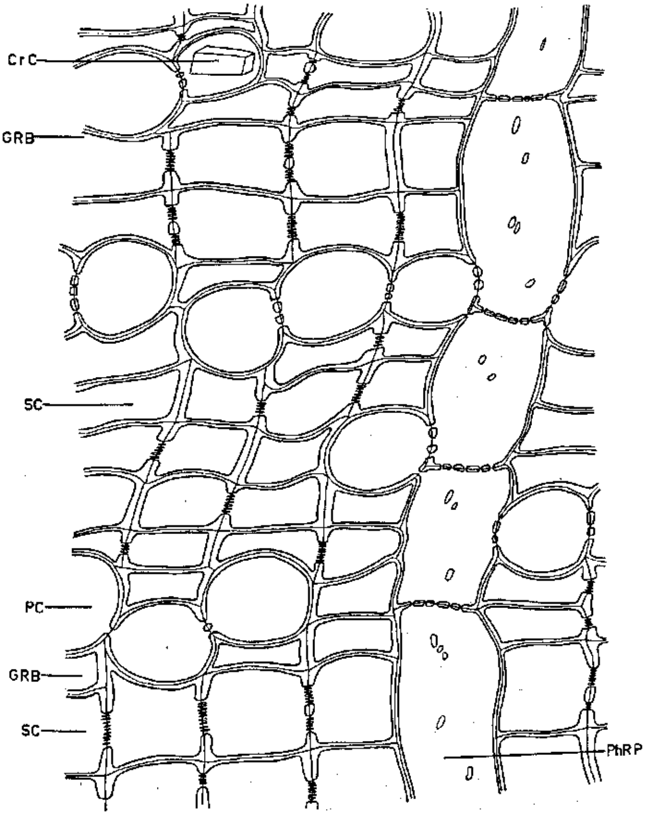


FIG. 19. *Pinus sylvestris* L. Cross section of a two year old growth ring of the secondary phloem. Mostly an irregular tangential layer of parenchyma cells is forming the border between the spring phloem and the summer phloem. In this two-year-old growth ring the parenchyma cells are somewhat rounded off, while the sieve cells are slightly collapsed

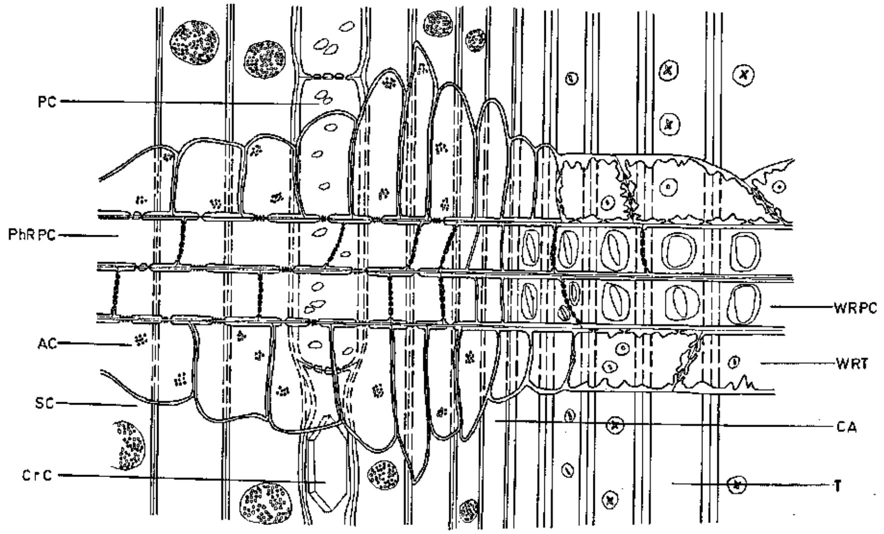


FIG. 20. *Pinus sylvestris* L. Radial section showing distribution of the pits in the secondary phloem near the cambium. The ray-albuminous cells in the cambial zone are longitudinally stretched. There is pit-contact between sieve cells and the ray-albuminous cells, but not with the ray-parenchyma cells

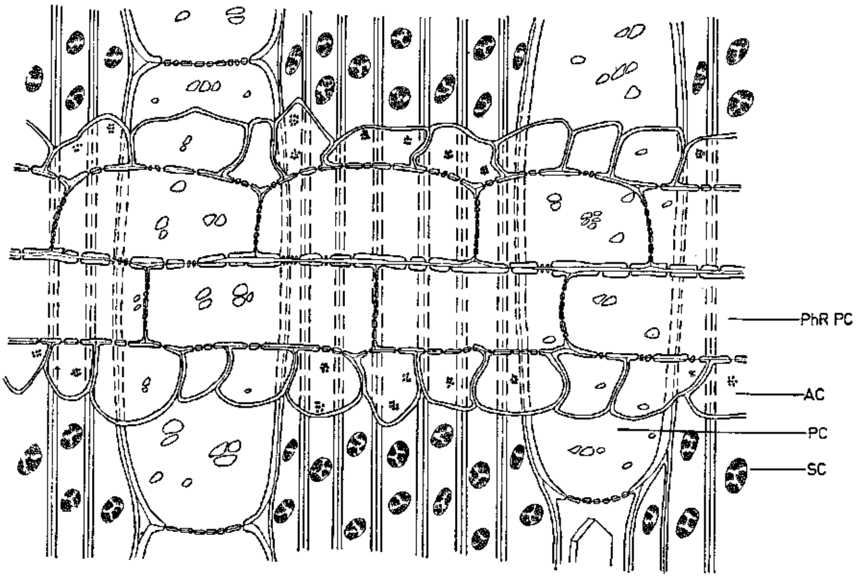


FIG. 21. *Pinus sylvestris* L. Radial section showing the distribution of the pits in the older secondary phloem. The cambium is on the right-hand side. The volume of the parenchyma cells has much increased, while the ray-albuminous cells and the sieve cells have not yet collapsed entirely

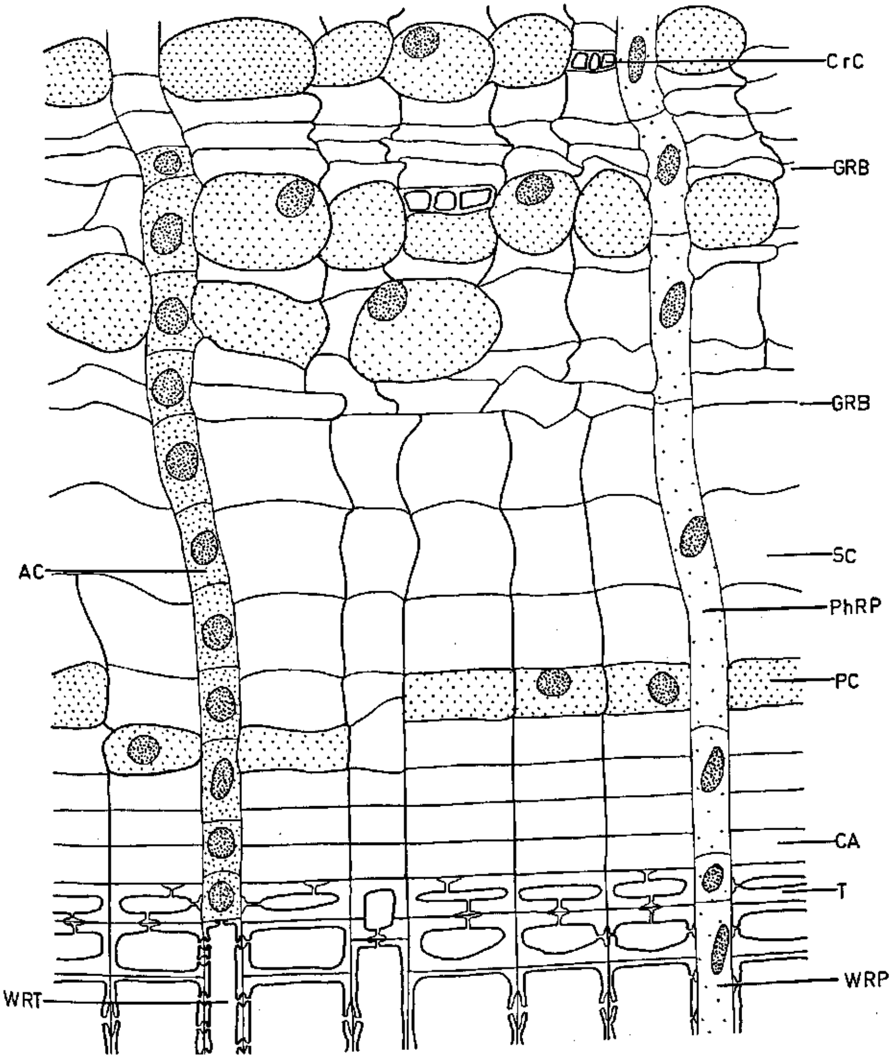


FIG. 22. *Larix decidua* MILL. Cross section of the xylem, cambium and the secondary phloem. Section of the phloem ray on the left-hand side is through the ray-albuminous cells

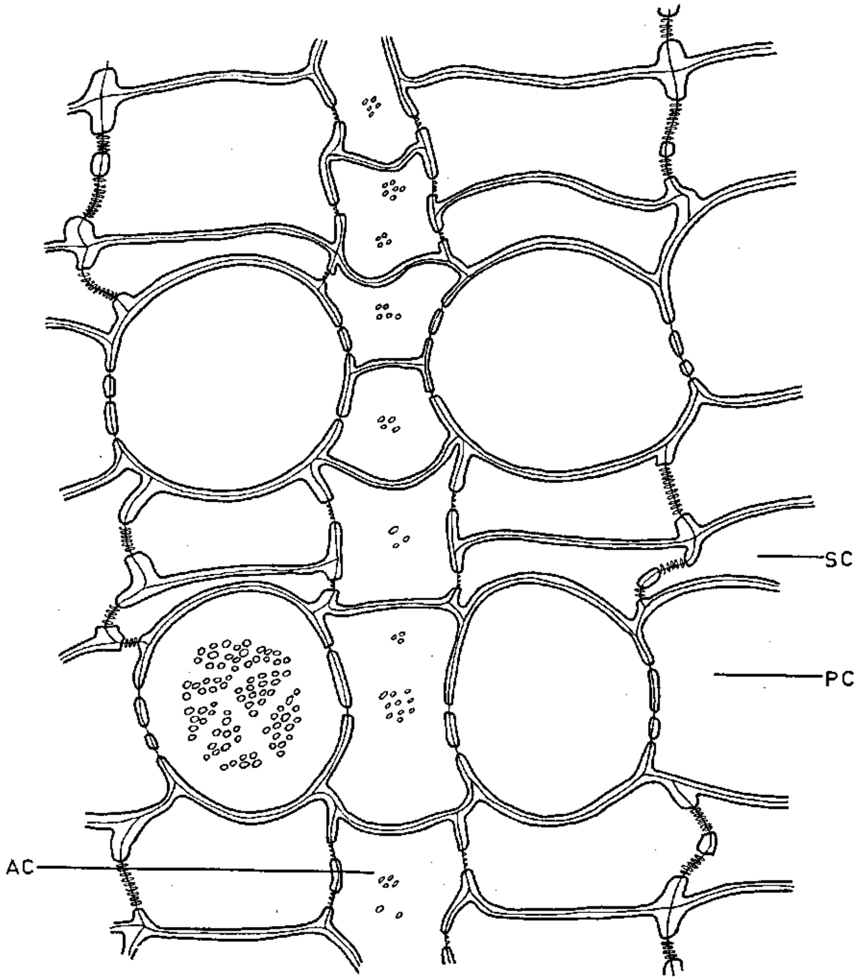


FIG. 23. *Larix decidua* MILL. Cross section showing the distribution of the pits in the older secondary phloem. The volume of the parenchyma cells has much increased, while the ray-albuminous cells and the sieve cells have not yet collapsed entirely

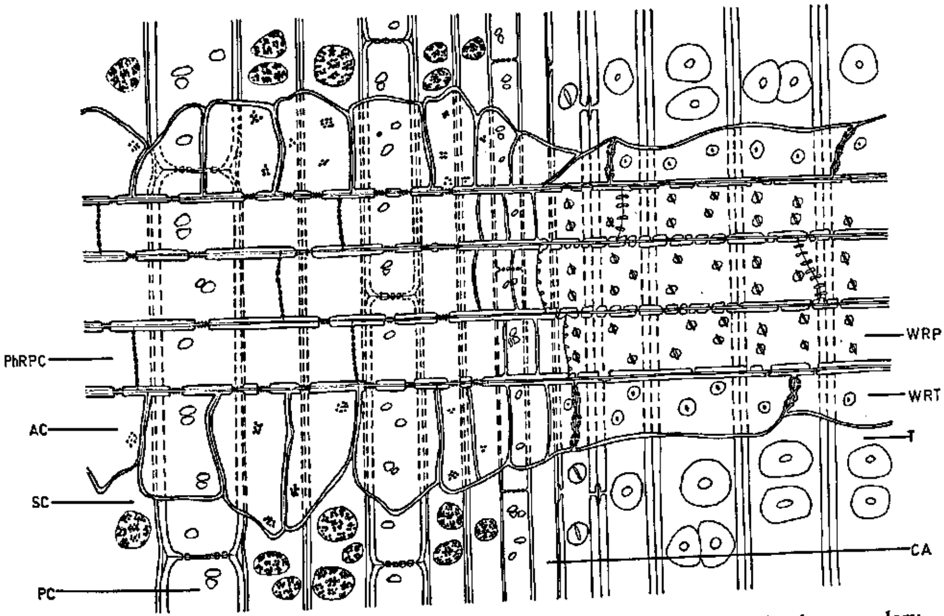


Fig. 24. *Larix decidua* Mill. Radial section showing distribution of the pits in the secondary phloem near the cambium. There is pit-contact between the sieve cells and the ray-albuminous cells, but not with the ray-parenchyma cells

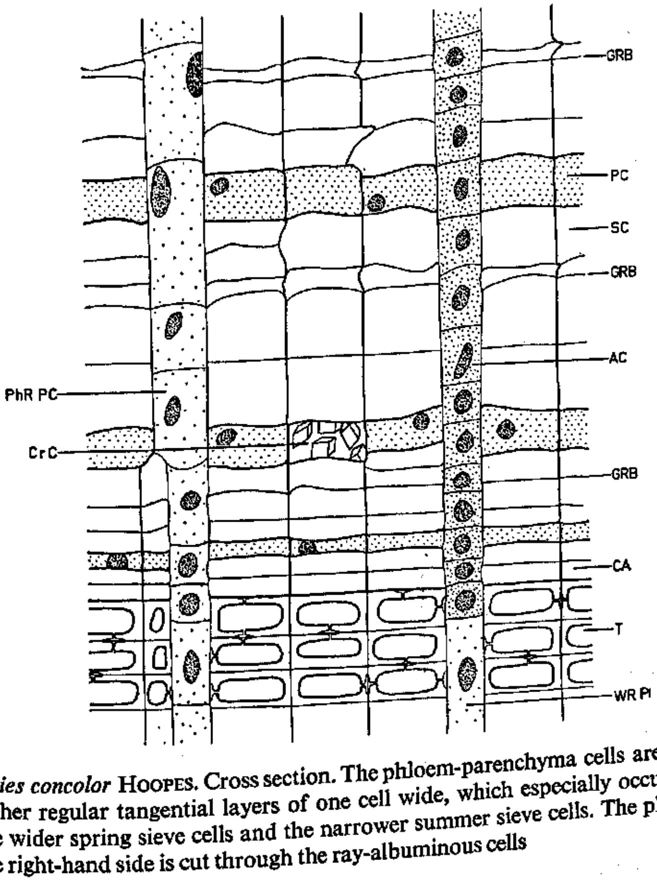


Fig. 25. *Abies concolor* Hoopes. Cross section. The phloem-parenchyma cells are arranged in rather regular tangential layers of one cell wide, which especially occur in between the wider spring sieve cells and the narrower summer sieve cells. The phloem ray on the right-hand side is cut through the ray-albuminous cells

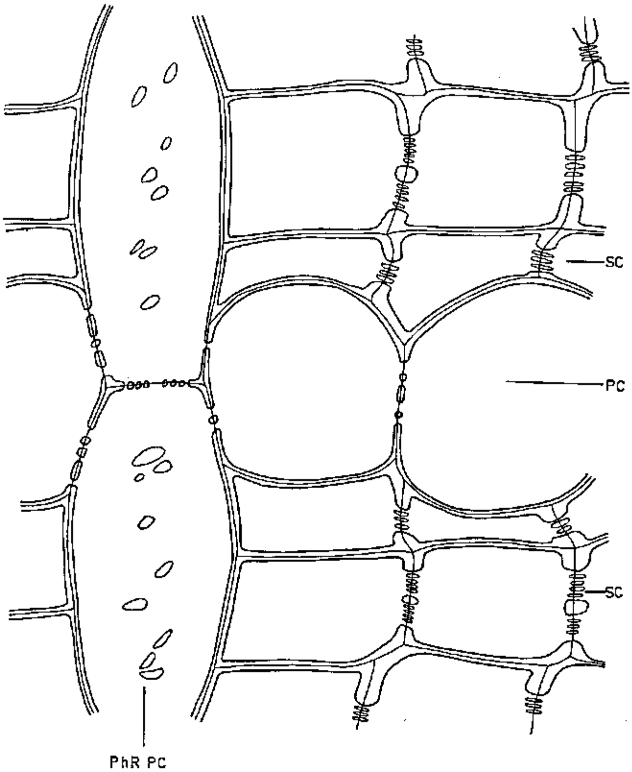


FIG. 26. *Abies concolor* HOOPES. Cross section showing distribution of the pits in the older bast. The volume of the parenchyma cells has increased

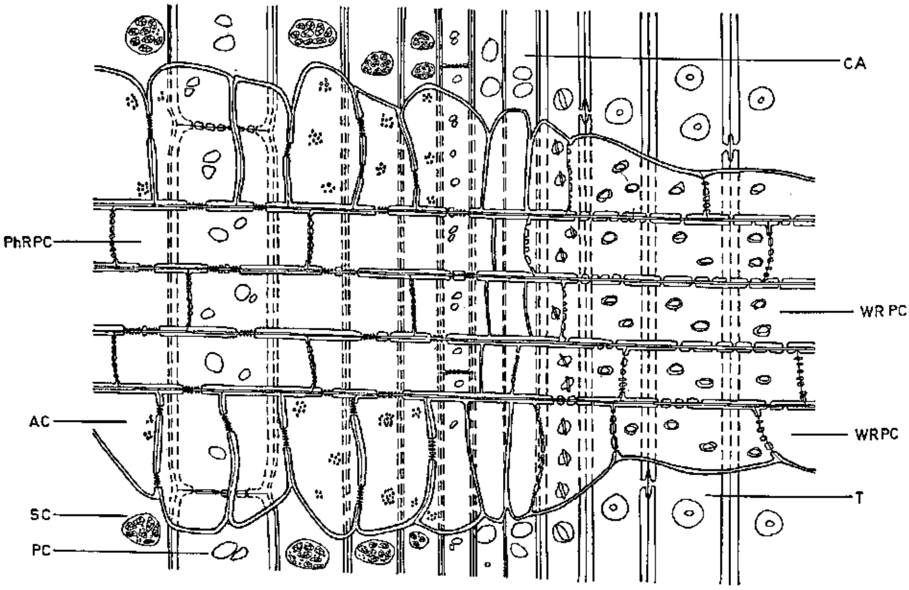


FIG. 27. *Abies concolor* HOOPES. Radial section near the cambial zone, showing distribution of the pits. The phloem ray is heterogeneous, while the wood ray is homogeneous. There is pit-contact between the ray-parenchyma cells and the ray-albuminous cells, but not between the ray-parenchyma cells and the sieve cells. Intercellular canals occur in a radial direction in the phloem ray, traversing the cambium and continuing into the wood ray

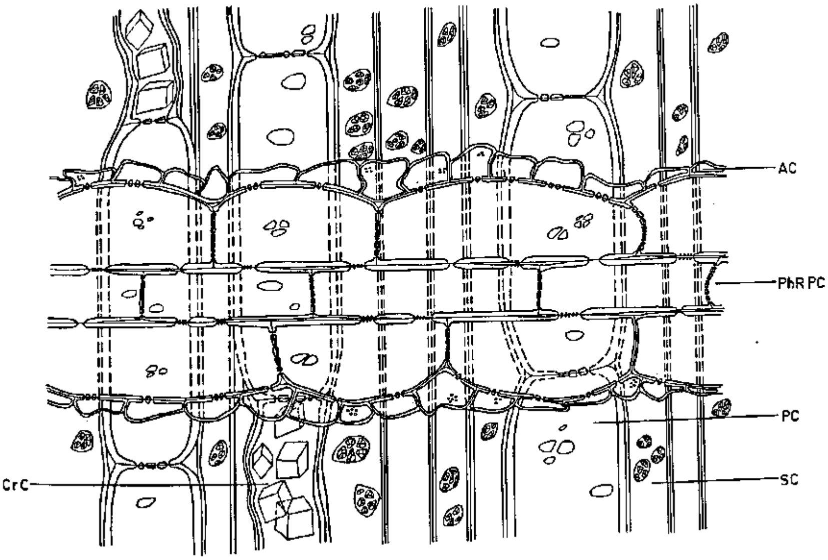


FIG. 28. *Abies concolor* HOOPES. Radial section showing distribution of the pits in the older phloem. Cambium is on the right-hand side. The ray-albuminous cells are collapsed, while the ray-parenchyma cells on the lower side and on the upper side of the heterogeneous phloem ray, are somewhat rounded

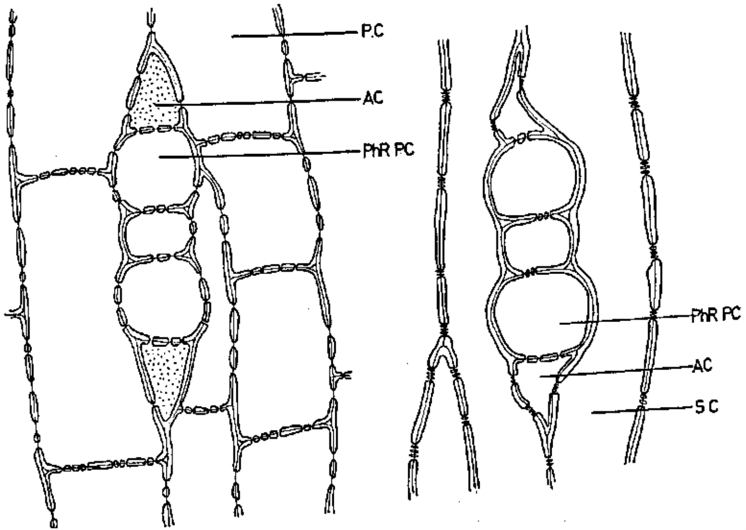


FIG. 29. *Abies concolor* HOOPES. Secondary phloem. On the left-hand side a tangential section through a layer of parenchyma cells in the functioning phloem. On the right-hand side a tangential section through a layer of sieve cells just outside the functioning phloem. There the ray-albuminous cells are already partly collapsed

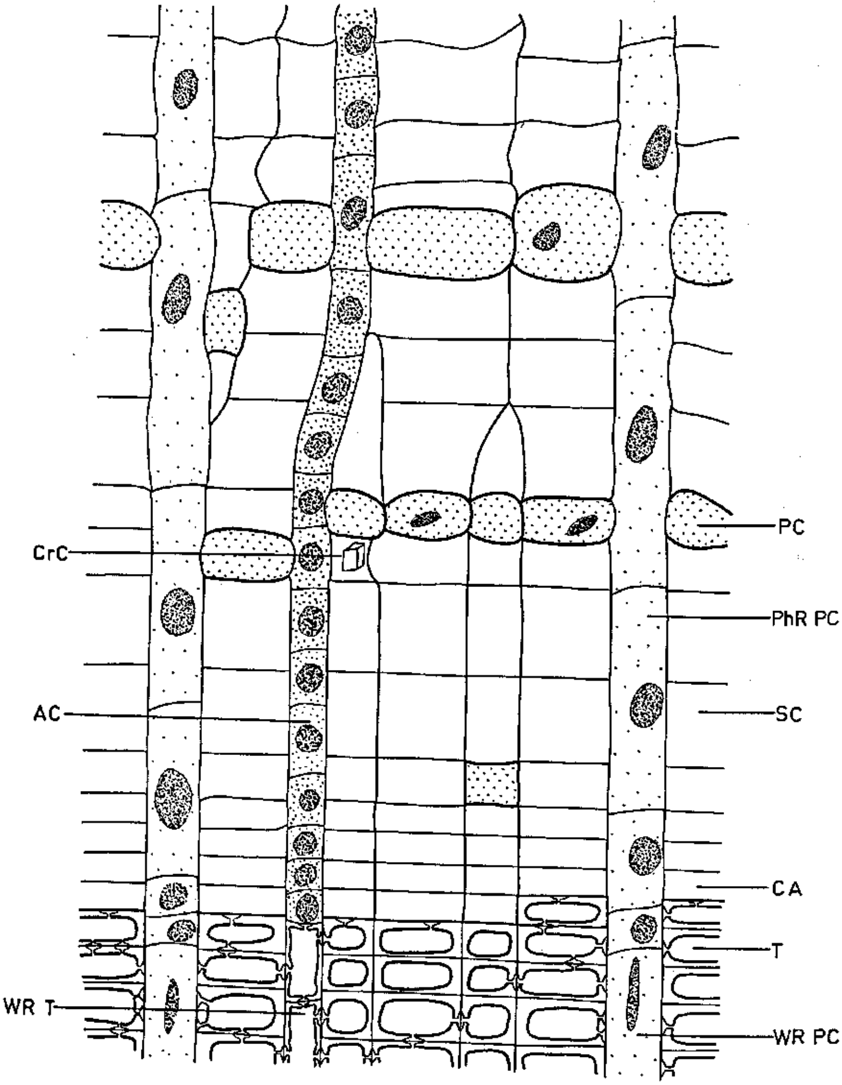


FIG. 30. *Tsuga canadensis* CARR. Cross section. Between the sieve cells there are only a small number of tangential layers of parenchyma cells; all of them one cell in width. Section of the phloem ray in the middle is through the not yet collapsed ray-albuminous cells

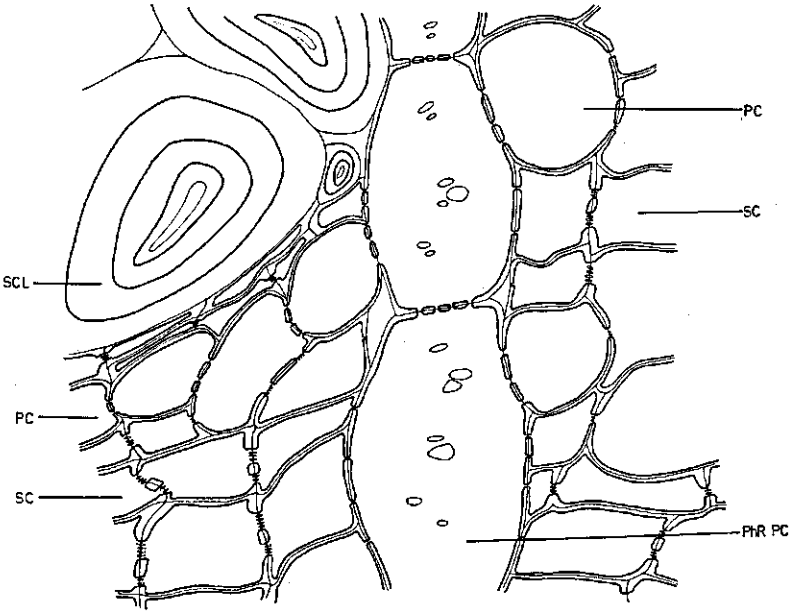


FIG. 31. *Tsuga canadensis* CARR. Cross section of the older bast. The parenchyma cells have increased in size. Some stone cells are formed out of parenchyma cells. The sieve cells are not functioning, but not yet collapsed completely

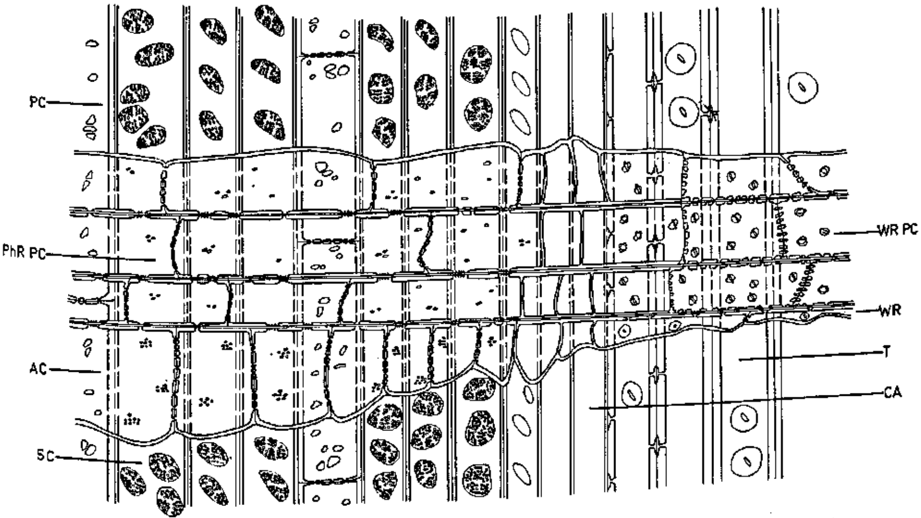


FIG. 32. *Tsuga canadensis* CARR. Radial section showing distribution of the pits near the cambial zone. Both the phloem ray and the wood ray are semi-heterogeneous. There is pit-contact between all the elements of the phloem ray and all the elements of the axial system. Intercellular canals occur in a radial direction in the phloem rays, traversing the cambium and continuing into the wood rays. They occur both between the ray-albuminous cells and the ray-parenchyma cells and between two rows of ray-parenchyma cells

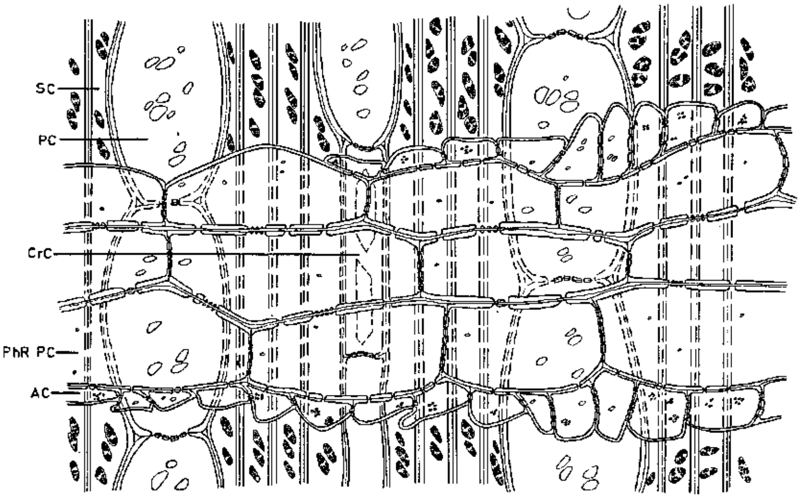


FIG. 33. *Tsuga canadensis* CARR. Radial section showing distribution of the pits in a two to three year old bast. The cambium is on the right-hand side. The phloem ray is partly heterogeneous (right) with still functioning ray-albuminous cells and partly semi-heterogeneous (left), with ray-albuminous cells already collapsed on the lower side of the ray. There the sieve cells are not functioning any longer and are collapsed partly, while the parenchyma cells increase in size

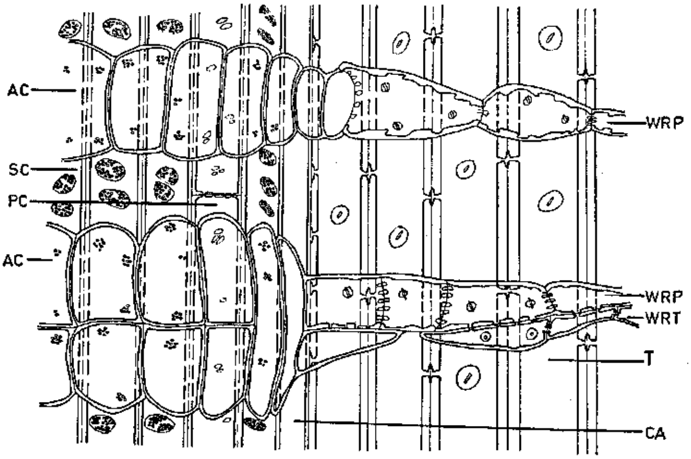


FIG. 34. *Tsuga canadensis* CARR. Radial section through two phloem rays consisting of albuminous cells only. The ray on the upper side in only one cell high and consists of ray-albuminous cells on the phloem side and of ray-parenchyma cells on the xylem side, while the other is two cells high, consisting also of ray-albuminous cells on the phloem side, but of ray-parenchyma cells and ray tracheids on the xylem side

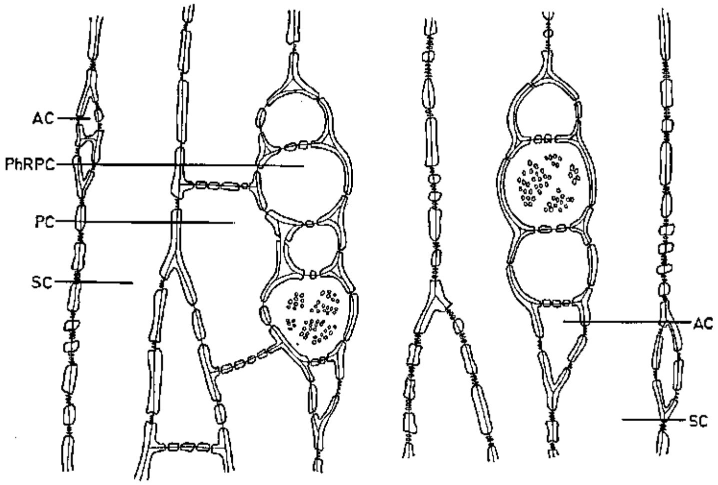


FIG. 35. *Tsuga canadensis* CARR. Tangential section showing distribution of the pits in the functioning secondary phloem. The phloem rays are both semi-heterogeneous. The phloem ray on the left is bordered by parenchyma cells and a sieve cell, while the phloem ray on the right is bordered by sieve cells on both sides

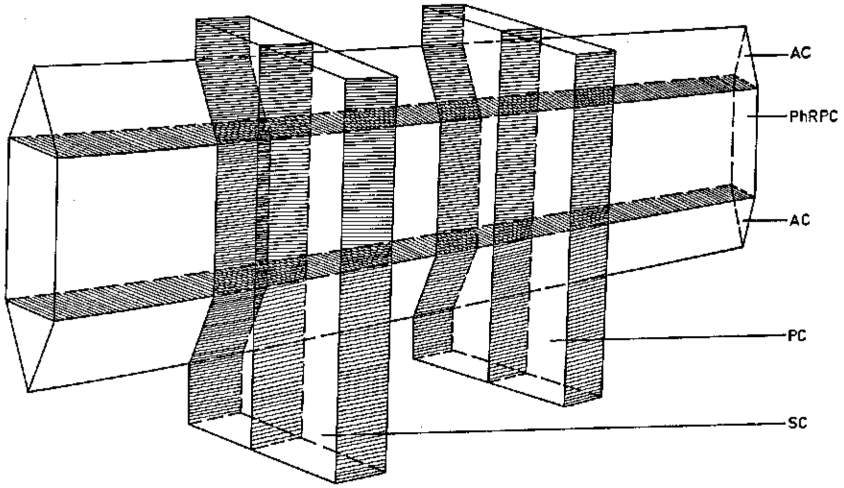


FIG. 36. Schematic drawing of a part of the bast of *Tsuga*, *Cedrus* or *Picea*. The shaded areas represent walls through which pit-contact is present. Pit-contact is shown between a phloem ray and only one tg. layer of sieve cells (left) and one layer of parenchyma cells (right). Direct transport in radial direction is not possible between two layers of sieve cells, or between a tangential layer of sieve cells and a tangential layer of parenchyma cells, only via the phloem ray. There is pit-contact between the cell types of the axial system and all the elements of the ray

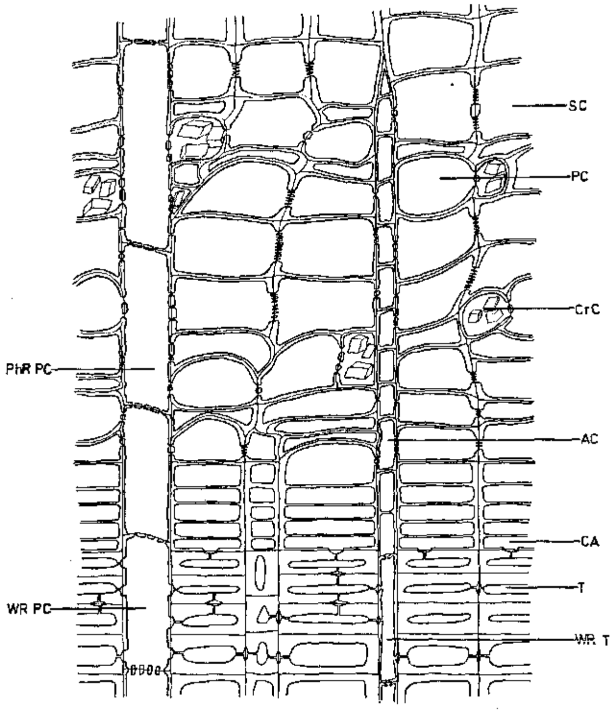


FIG. 37. *Cedrus libani* A. RICH. Cross section showing distribution of the pits near the cambial zone. Many crystals are deposited in several parenchyma cells of the irregularly formed parenchyma-cell layers. The phloem ray on the right-hand side is cut through the row of ray-albuminous cells

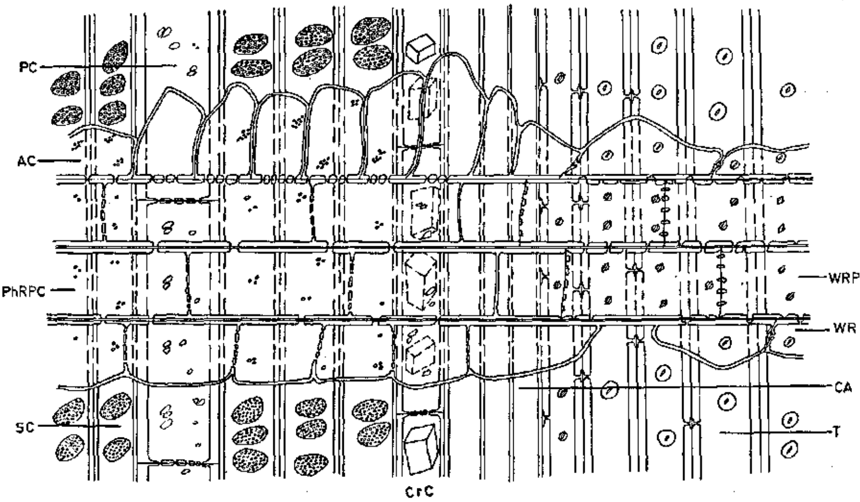


FIG. 38. *Cedrus libani* A. RICH. Radial section near the cambial zone. Both the phloem ray and the wood ray are semi-heterogeneous. Bot the ray-albuminous cells and the ray-parenchyma cells have pit-contact with all the elements of the axial system. Intercellular spaces occur in radial direction in the phloem rays, traversing the cambium and continuing into the wood rays

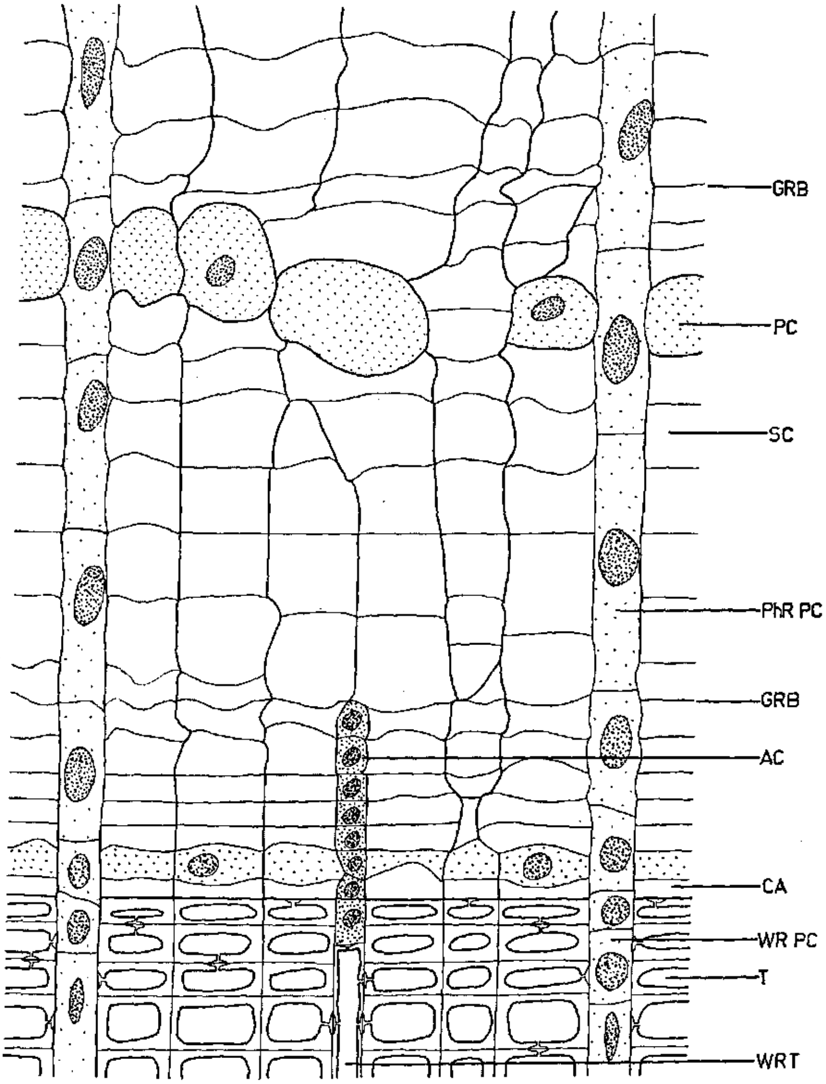


FIG. 39. *Picea spec.* Cross section. Each year one irregular tangential layer of parenchyma cells is formed. The short phloem ray in the middle is cut through the row of ray-albuminous cells

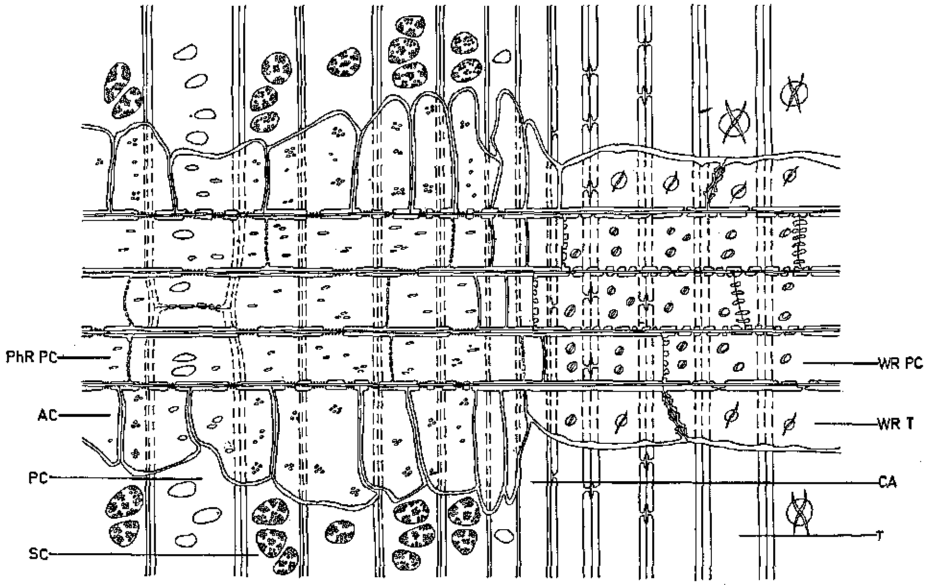


FIG. 40. *Picea spec.* Radial section near the cambial zone. Both the phloem ray and the wood ray are heterogeneous. There is pit-contact between all the elements of the phloem ray and all the cell types of the axial system. Large pits are present between ray-parenchyma cells and phloem-parenchyma cells in particular. Intercellular canals occur in the phloem ray, traversing the cambium and continuing into the wood ray

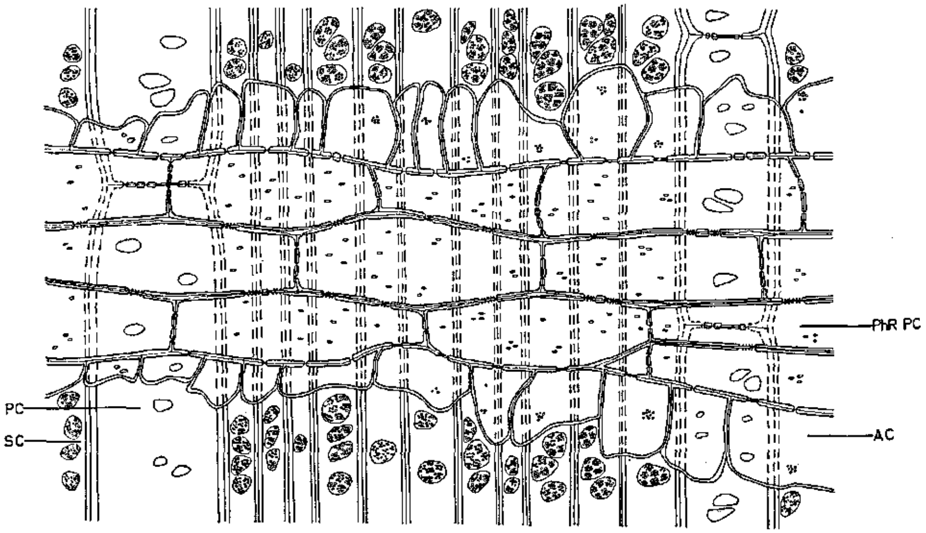


FIG. 41. *Picea spec.* Radial section showing distribution of the pits in the older bast attached to that of fig. 40. The cambium is on the right-hand side. Near the cambium the ray-albuminous cells are functioning, but they collapse already at some distance from the cambium (left-hand side of the drawing). The phloem ray, just increased in height from 5 cells to 6 cells

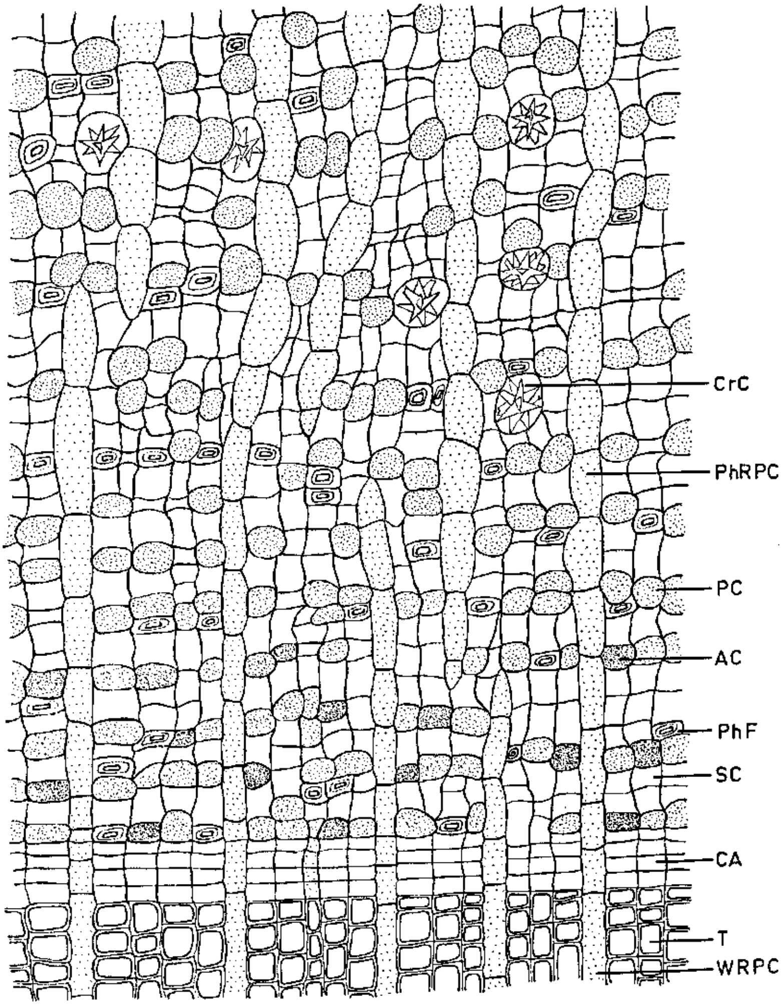


FIG. 42. *Ginkgo biloba* L. Cross section. In the older phloem the phloem-albuminous cells are collapsed, while the sieve cells disorganize only slightly. The parenchyma cells increase in size, especially the ray-parenchyma cells and those parenchyma cells in which large crystals originate

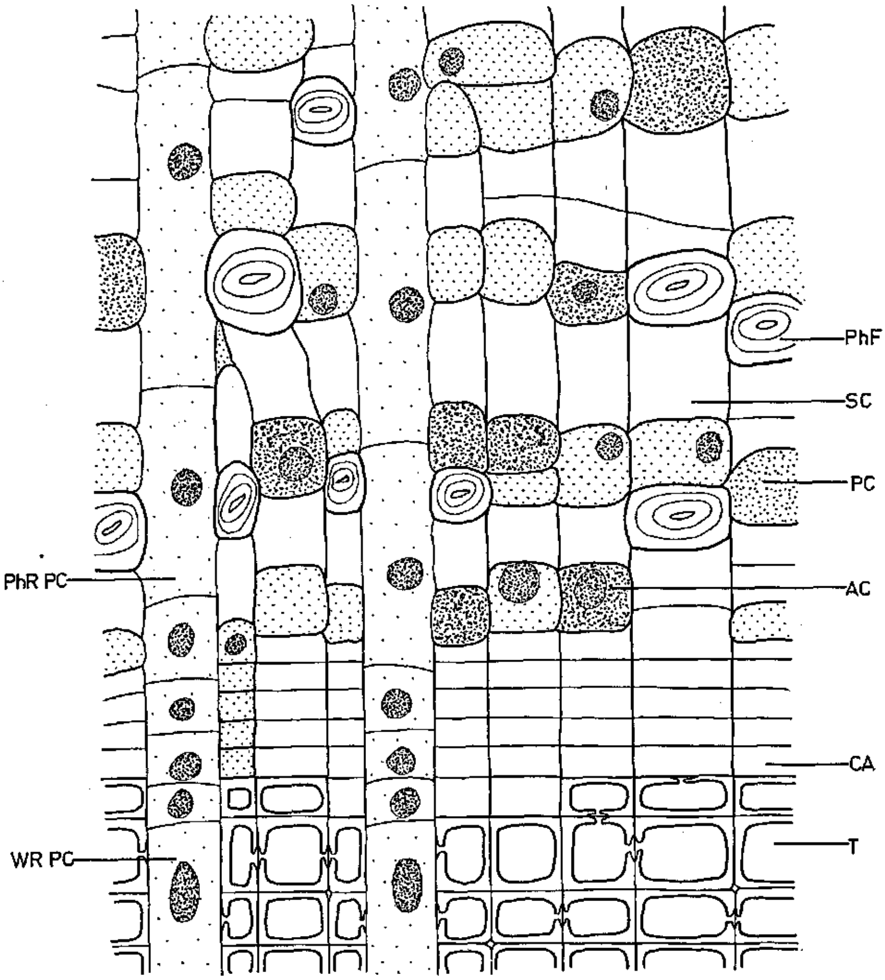


FIG. 43. *Ginkgo biloba* L. Cross section. Bands of parenchyma cells, 1–3 cells wide in radial extent, alternate with bands of sieve cells, 1–2 cells wide. In addition many phloem-albuminous cells and some phloem fibres occur in the bands of parenchyma cells

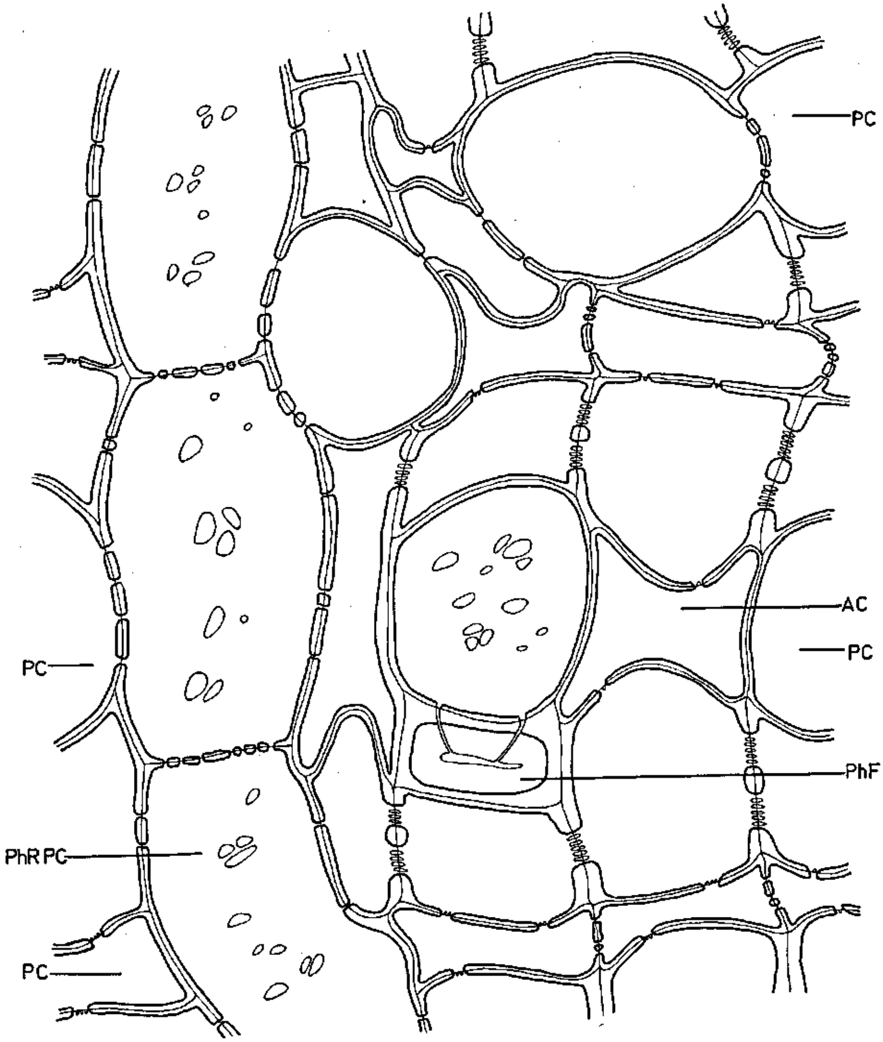


FIG. 44. *Ginkgo biloba* L. Cross section showing distribution of pits in the older secondary phloem. The phloem-albuminous cells are collapsed. On the other hand there is hardly any collapse of the sieve cells, while the volume of the parenchyma cells has increased

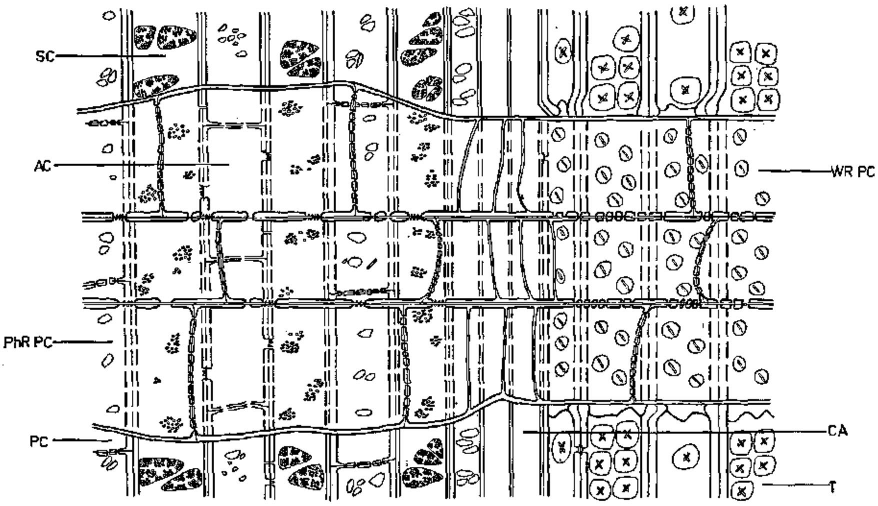


FIG. 45. *Ginkgo biloba* L. Radial section near the cambial zone. Both the phloem ray and the wood ray are homogeneous. They consist of parenchyma cells only, which have pit-contact with all the elements of the axial system. Intercellular spaces occur in a radial direction in the phloem rays, traversing the cambium and continuing into the wood rays

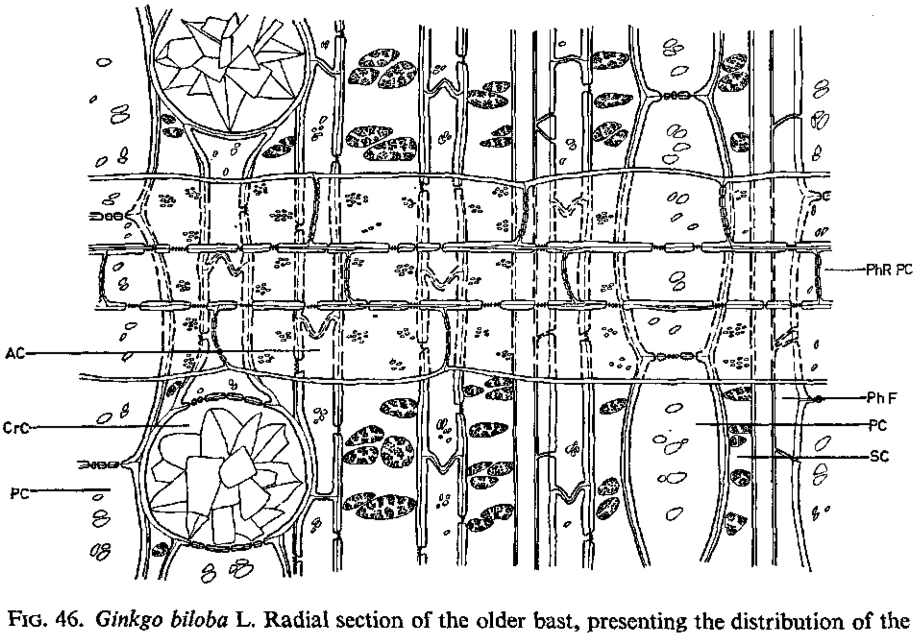


FIG. 46. *Ginkgo biloba* L. Radial section of the older bast, presenting the distribution of the pits. The parenchyma cells of the homogeneous ray have a distinct pit-contact with both the sieve cells and especially with the phloem-parenchyma cells. The parenchyma cells increase considerably in size when large crystals originate

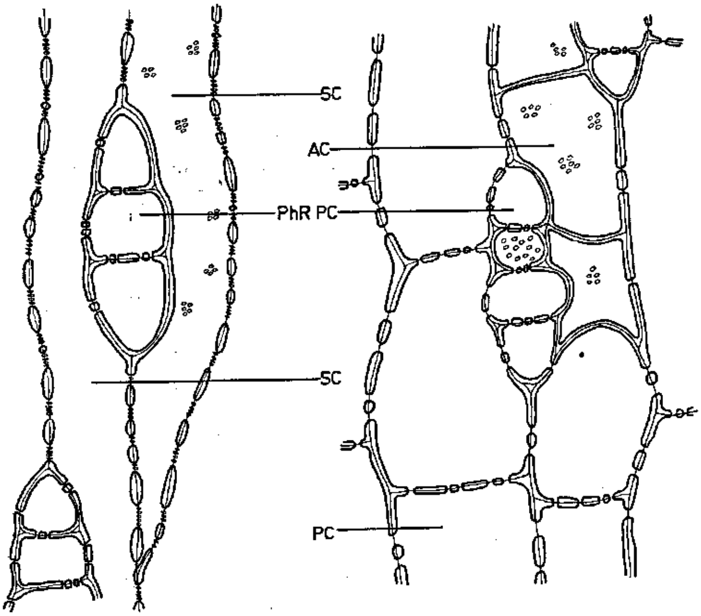


FIG. 47. *Ginkgo biloba* L. Tangential section through the functioning secondary phloem. On the left-hand side two phloem rays enclosed by sieve cells; on the right-hand side a phloem ray crossing a band of parenchyma cells

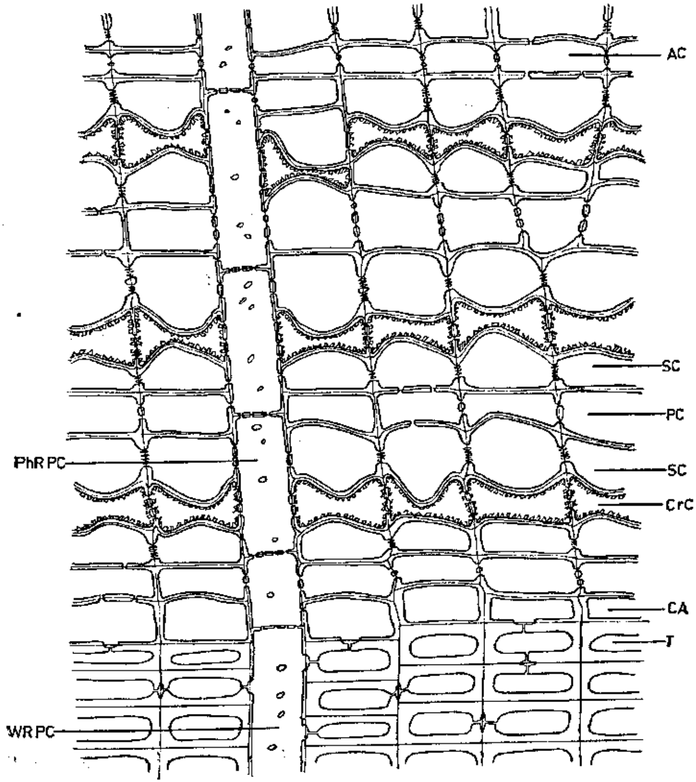


FIG. 48. *Taxus baccata* L. Cross section near the cambial zone. Instead of tangential layers of phloem fibres, there are layers of parenchyma cells with many minuscule crystals and with only a few phloem fibres

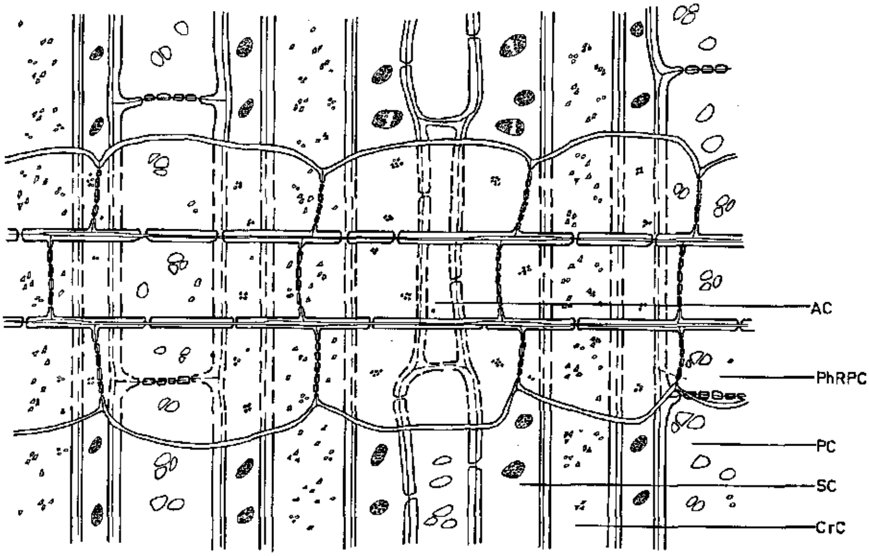


FIG. 49. *Taxus baccata* L. Radial section of the older phloem. Both the sieve cells and the phloem-albuminous cells are collapsed. The volume of the phloem-parenchyma cells and the ray-parenchyma cells, especially of those on the upper and the lower side of the homogeneous ray, is increased

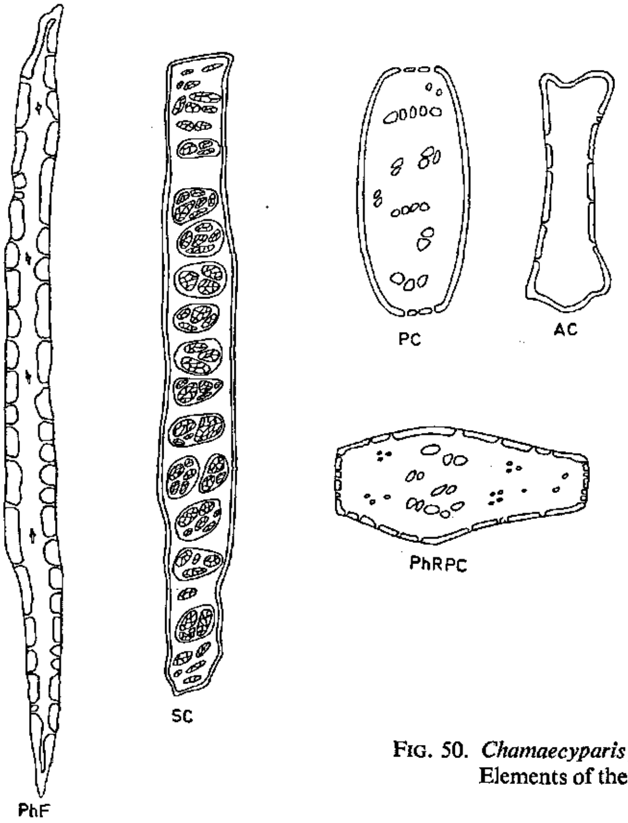


FIG. 50. *Chamaecyparis pisifera* ENDL. Maceration. Elements of the secondary phloem

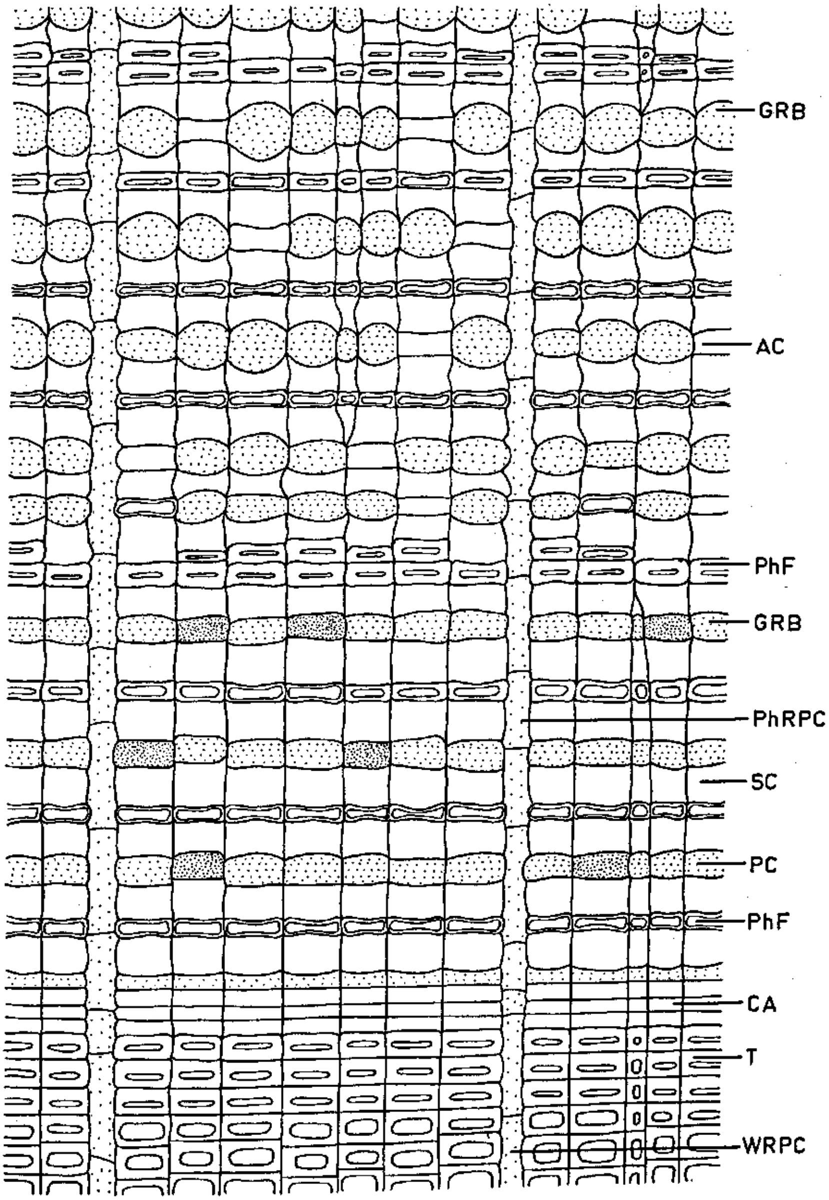


FIG. 51. *Chamaecyparis pisifera* ENDL. Cross section of the xylem, cambium and the secondary phloem. From the last growth ring boundary outwards, the volume of the parenchyma cells increases gradually, while the phloem-albuminous cells collapse

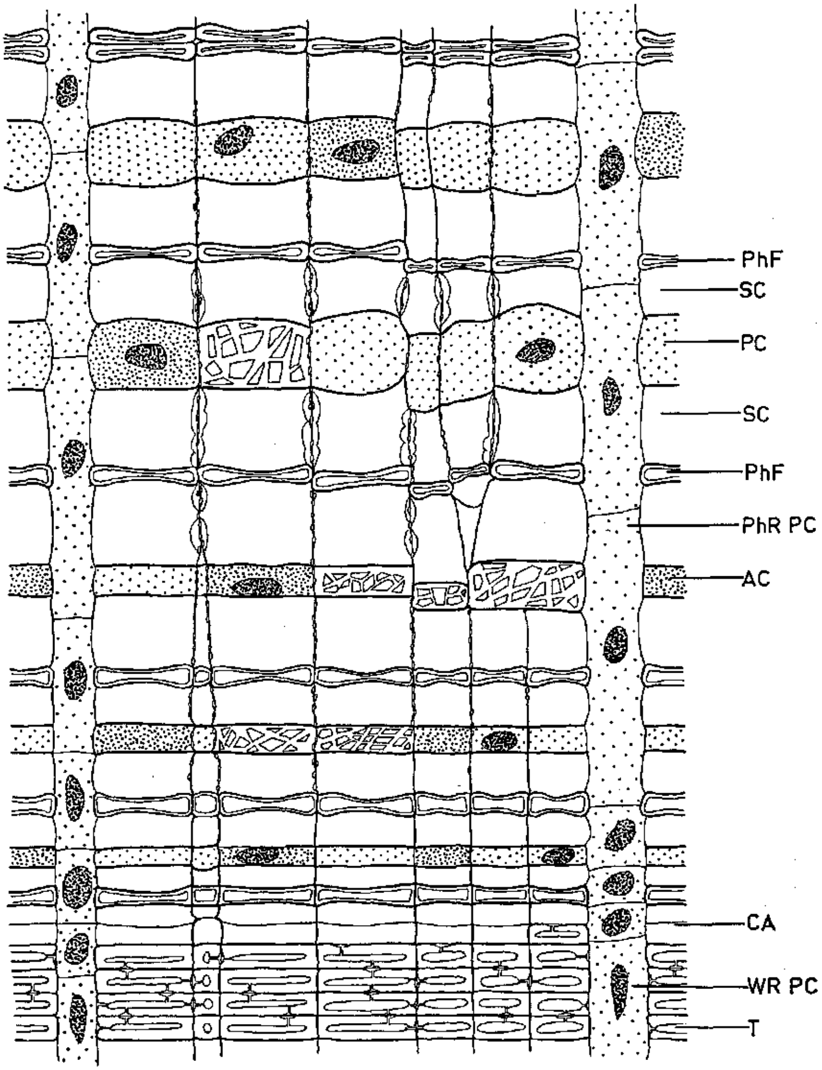


FIG. 52. *Chamaecyparis pisifera* ENDL. Cross section of the xylem, cambium and the last growth ring of the secondary phloem. Many small crystals occur in the radial walls, while callose has been deposited in the summer phloem of the last growth ring

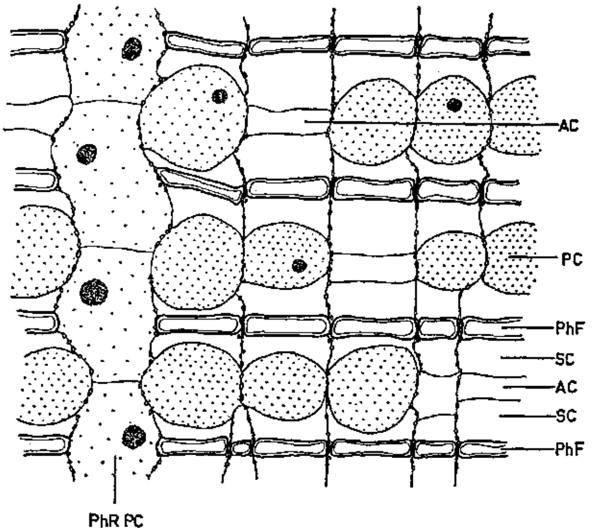


FIG. 53. *Chamaecyparis pisifera* ENDL. Cross section of the older secondary phloem. The phloem-albuminous cells are collapsed, while the volume of the parenchyma cells has increased. The figure also shows crystals in the radial walls

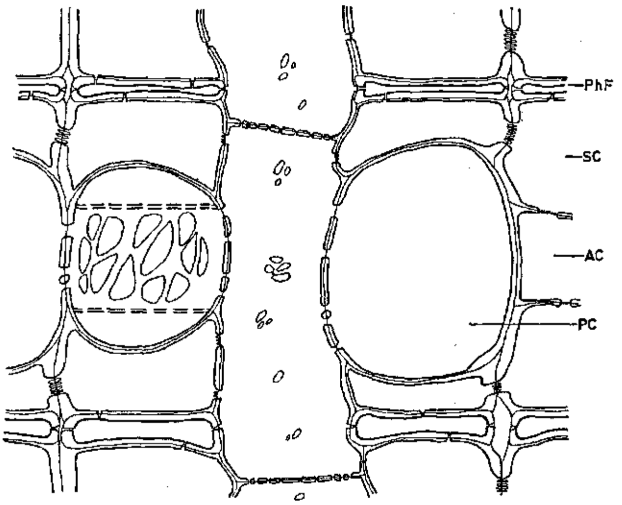


FIG. 54. *Chamaecyparis pisifera* ENDL. Cross section, showing distribution of the pits in the older phloem. The parenchyma cell on the left-hand side is cut near the transverse wall between two parenchyma cells

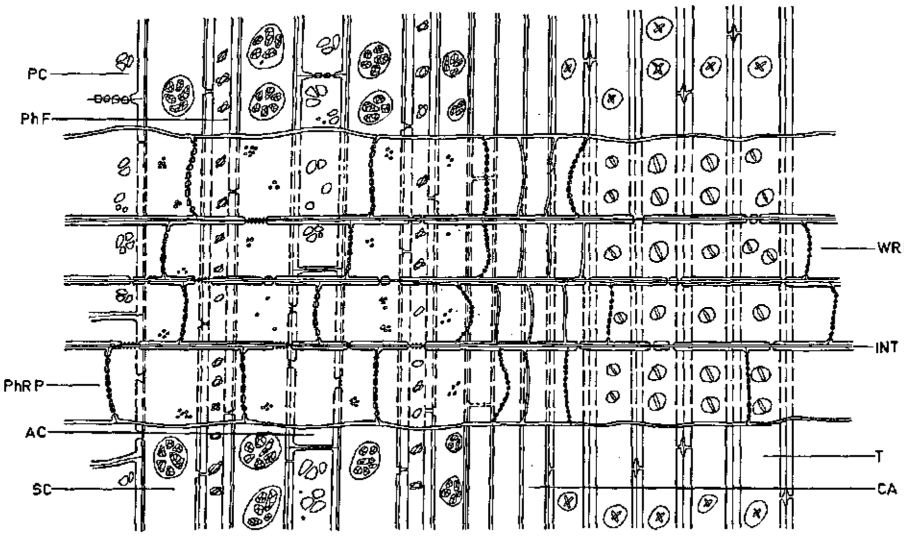


FIG. 55. *Chamaecyparis pisifera* ENDL. Radial section near the cambium showing distribution of the pits. There is pit-contact between ray-parenchyma cells and sieve cells, phloem-parenchyma cells and phloem fibres

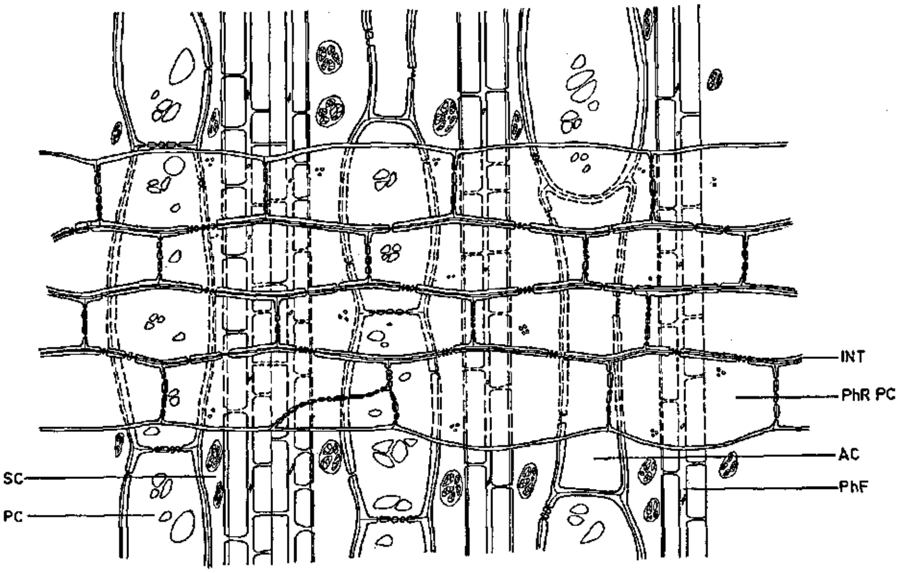


FIG. 56. *Chamaecyparis pisifera* ENDL. Radial section showing distribution of the pits in the older secondary phloem. The phloem-albuminous cells are collapsed, while the parenchyma cells are somewhat increased in size

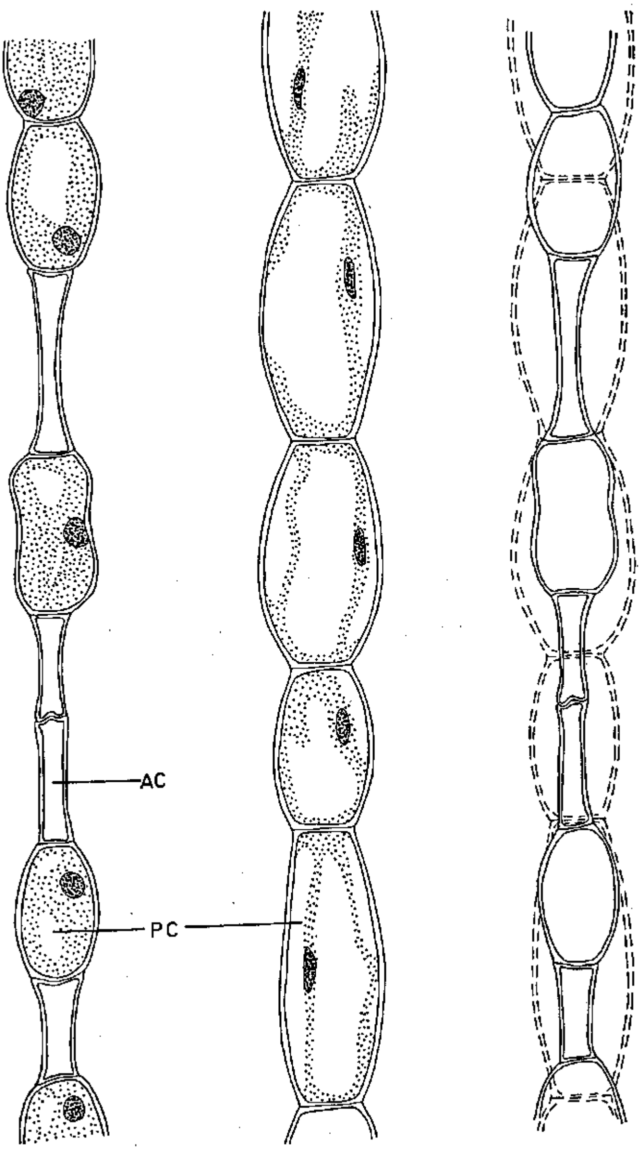


FIG. 57. *Chamaecyparis pisifera* ENDL. Two longitudinal strands of parenchyma cells and phloem-albuminous cells out of the 20th tangential layer from the cambium. On the right-hand side the two rows of one tangential layer of parenchyma cells, as they can be seen lying above one another

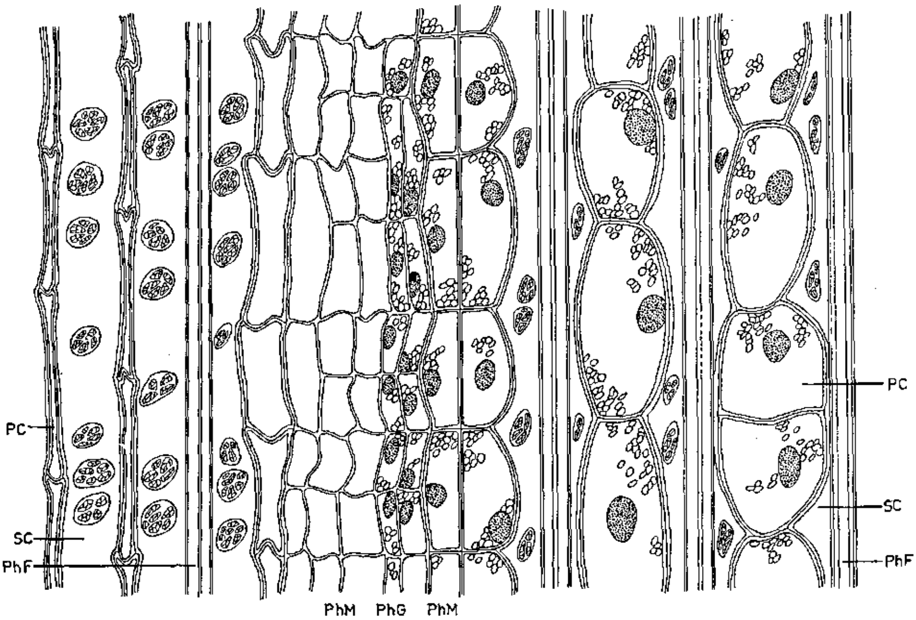


FIG. 58. *Chamaecyparis pisifera* ENDL. Radial section of the periderm. The parenchyma cells of the living secondary phloem contain starch and have nuclei (right), while the dead cells of the rhytidome are empty. Here the parenchyma cellls are collapsed and the sieve cells are not

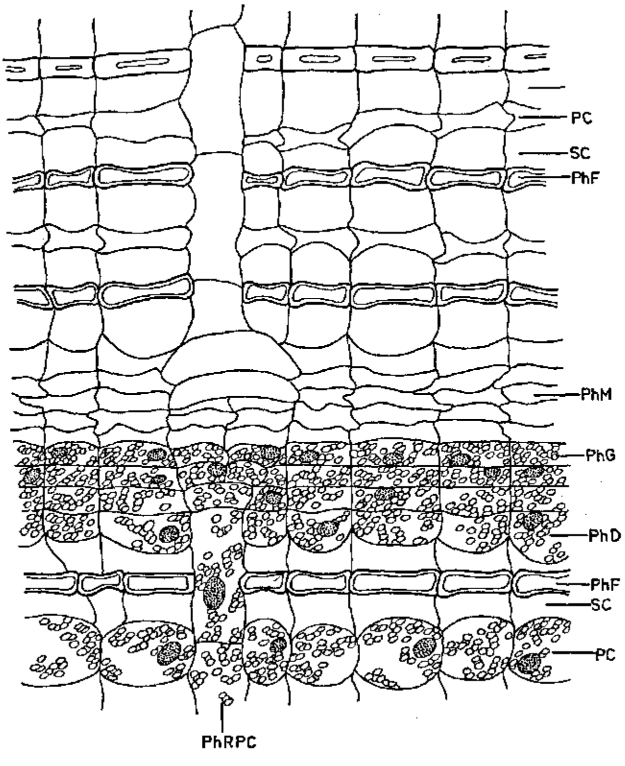
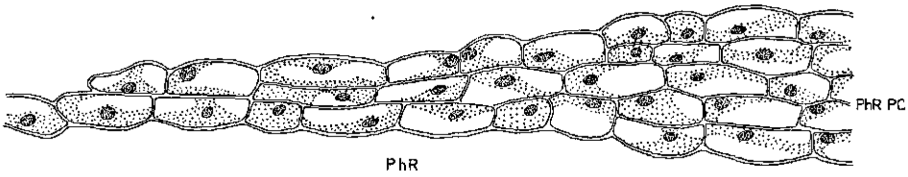


FIG. 59. *Chamaecyparis pisifera* ENDL. Cross section of the periderm. The parenchyma cells of the living secondary phloem, contain starch and nuclei (below), while the dead parenchyma cells of the rhytidome are empty (above). Outside the periderm the parenchyma cells are collapsed and the sieve cells are not



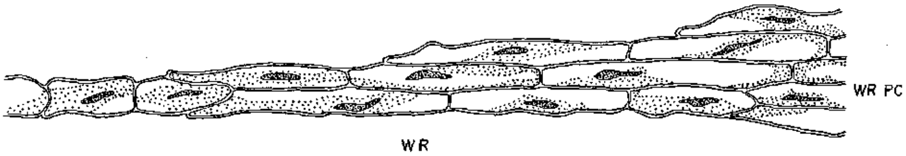
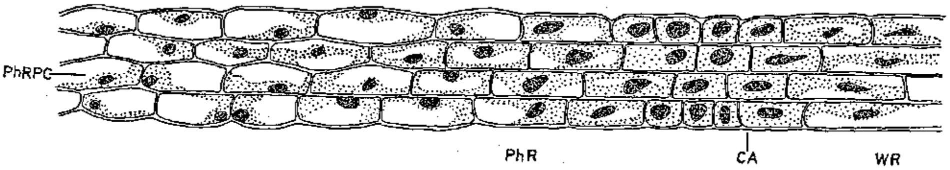


FIG. 60. *Chamaecyparis pisifera* ENDL. Distribution of the protoplasm and the shape of the nuclei in the cells of a gradually increasing phloem ray (above) and wood ray (below). The cambium is on the right-hand side



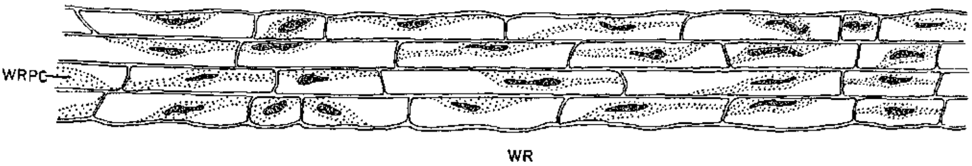


FIG. 61. *Chamaecyparis pisifera* ENDL. Distribution of the protoplasm and the shape of the nuclei in the cells of a phloem ray, in the ray initials and in the wood ray cells

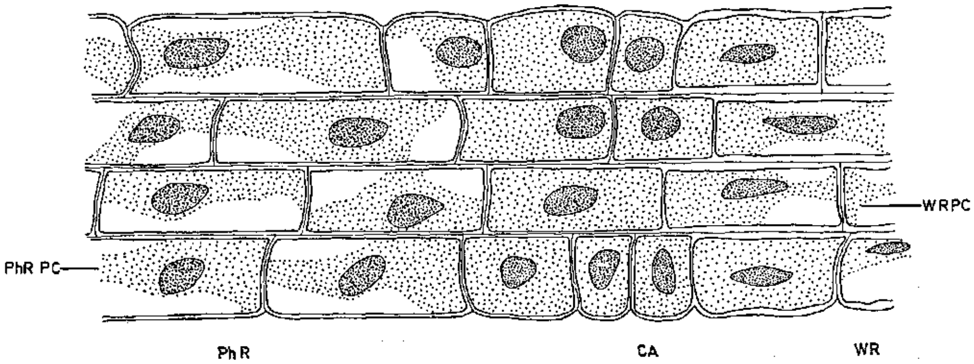


FIG. 62. *Chamaecyparis pisifera* ENDL. Radial section showing distribution of the protoplasm and the shape of the nuclei in the parenchyma cells of a phloem ray near the cambium

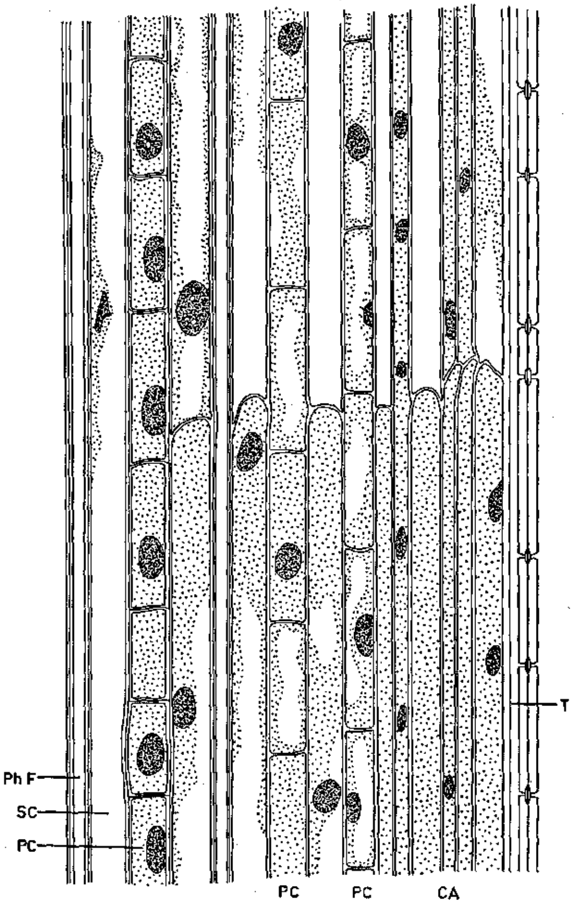


FIG. 63. *Chamaecyparis pisifera* ENDL. Radial section of the secondary phloem near the cambium showing the distribution of the protoplasm and the shape of the nuclei

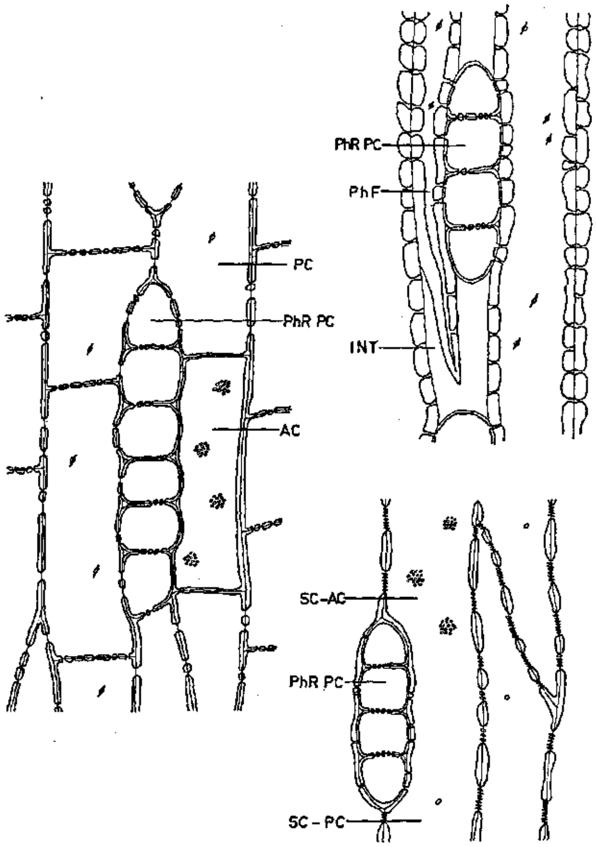


FIG. 64. *Chamaecyparis pisifera* ENDL. Tangential section showing distribution of the pits of a phloem ray crossing a parenchyma-cell layer, a phloem-fibre layer and s sieve-cell layer

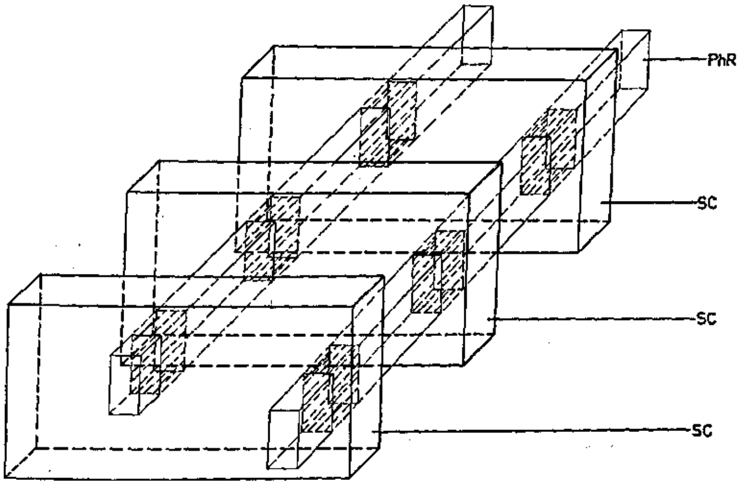


FIG. 65. *Chamaecyparis pisifera* ENDL. Diagram representing pit-contact between two phloem rays and three layers of sieve cells of the axial system. There is pit-contact between phloem ray and the layers of the sieve cells, but not between a layer of sieve cells and the adjacent layer of parenchyma cells or a layer of phloem fibres. The contact between two layers of sieve cells takes place via the ray-parenchyma cells

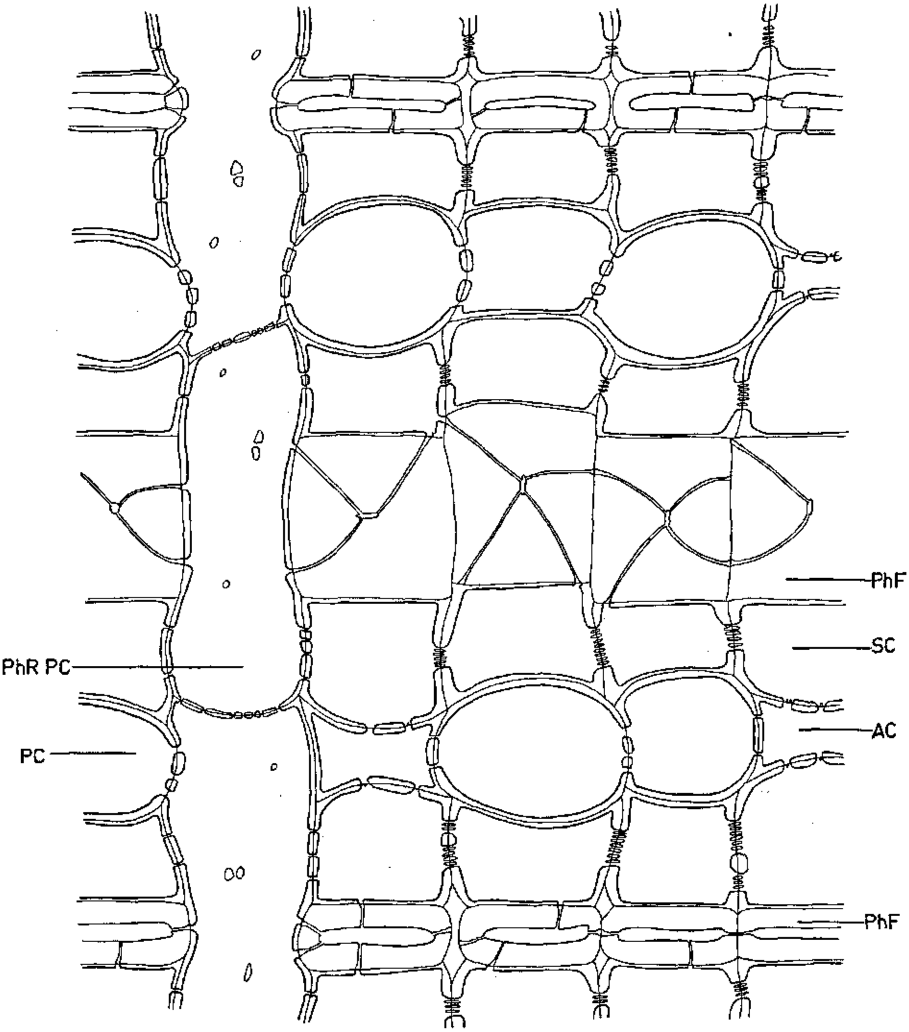


FIG. 66. *Thuja plicata* LAMB. Cross section showing distribution of the pits in the older bast. Phloem fibres with extremely thick walls alternate with fibres which have much thinner walls. The phloem-albuminous cells are collapsed completely, while the volume of the parenchyma cells have increased slightly

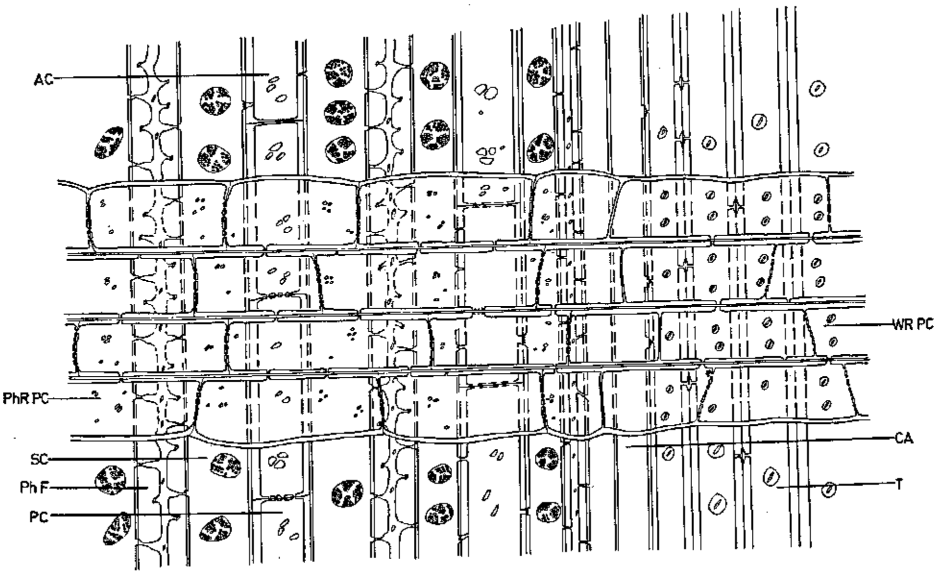


FIG. 67. *Thuja plicata* LAMB. Radial section near the cambial zone, showing distribution of the pits. Both the phloem ray and the wood ray are homogeneous. The ray-parenchyma cells have pit-contact with all the elements of the axial system. Intercellular spaces occur in radial direction in the phloem ray, traversing the cambium and continuing into the wood ray

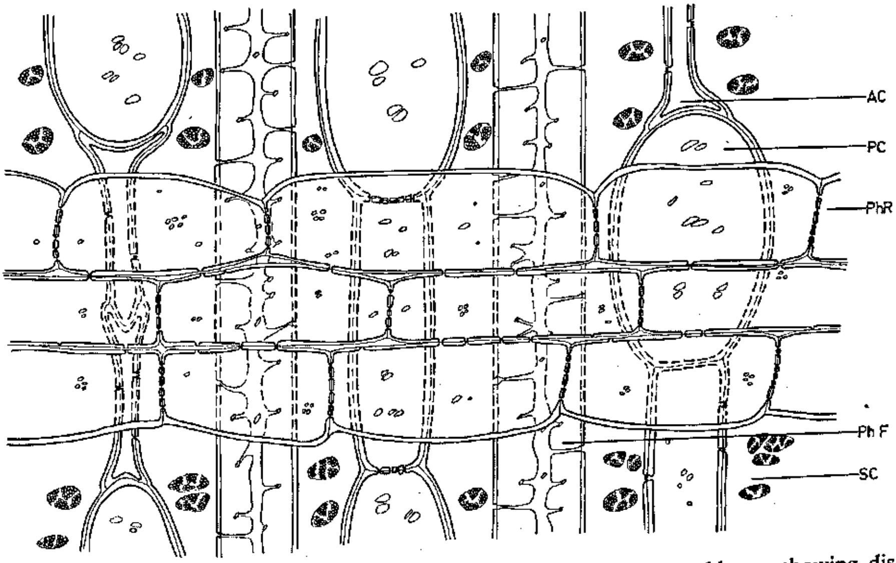


FIG. 68. *Thuja plicata* LAMB. Radial section of the older secondary phloem, showing distribution of the pits. A part of the sieve cells and all the phloem-albuminous cells are collapsed, while the volume of the parenchyma cells has increased

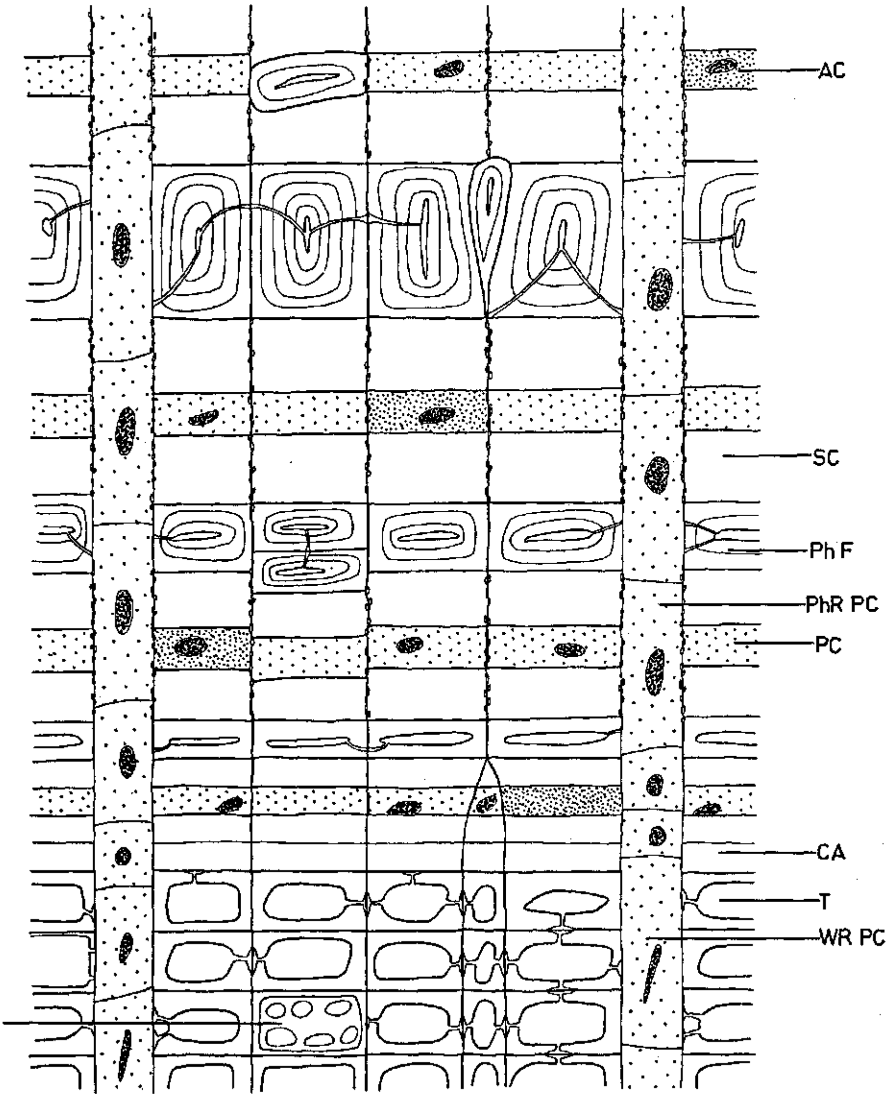


FIG. 69. *Taxodium distichum* A. RICH. Cross section. The layers of phloem fibres consist either of very thick-walled fibres, radially extended, or of smaller thin-walled fibres, tangentially extended. There are many minuscule crystals in the radial walls of both the parenchyma cells and the sieve cells

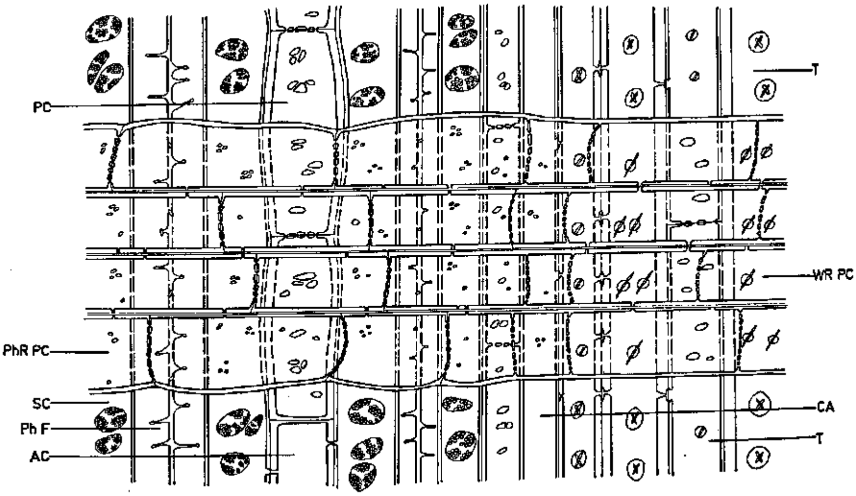


FIG. 70. *Taxodium distichum* A. RICH. Radial section near the cambial zone showing distribution of the pits. Both the phloem ray and the wood ray are homogeneous. There is pit-contact between the ray-parenchyma cells and all the elements of the axial system

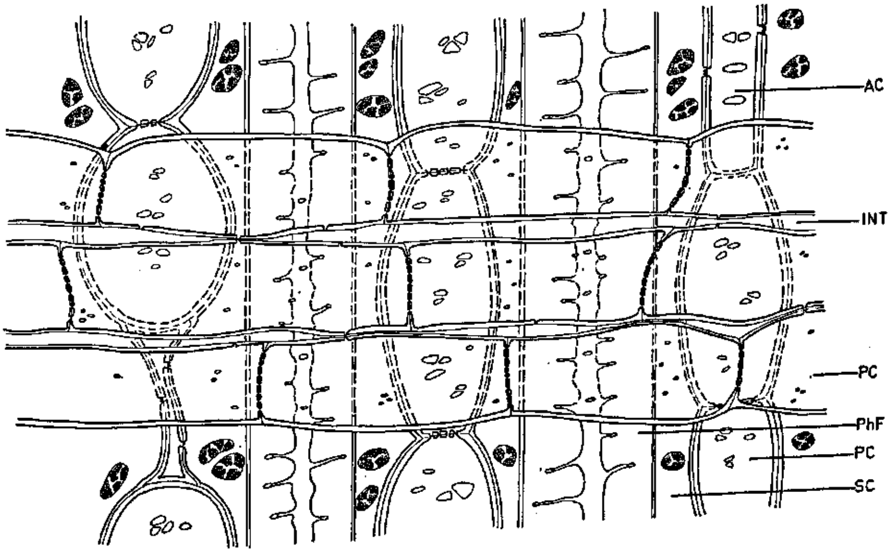
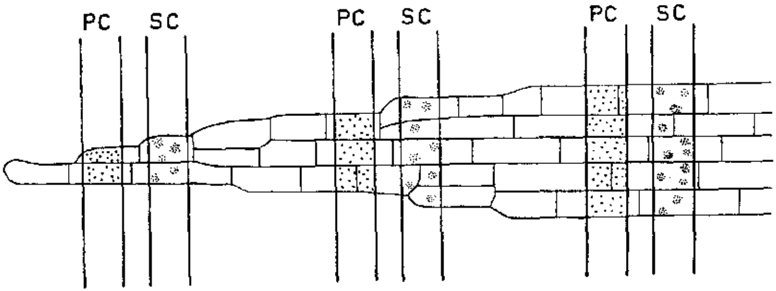
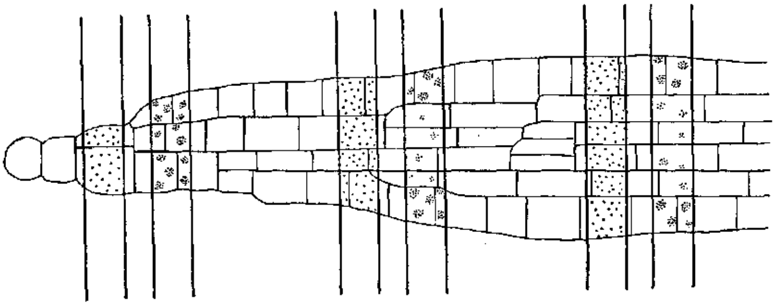


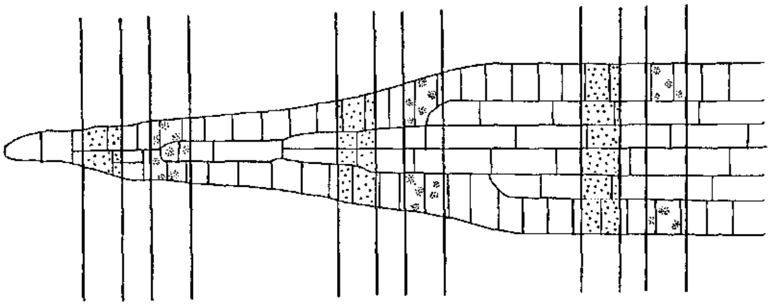
FIG. 71. *Taxodium distichum* A. RICH. Radial section of the older bast. The cambium is on the right-hand side. Both the phloem-albuminous cells and the sieve cells are collapsed, while the volume of the parenchyma cells has increased in size. The intercellular spaces, extended in radial direction, are enlarged to such an extent, that large oval intercellular spaces occur



Chamaecyparis pisifera



Ginkgo biloba



Pseudotsuga taxifolia

FIG. 72. The development of increasing phloem rays of the three main secondary phloem types; the shape of the different elements of the rays and the pit-contact of these elements to phloem-parenchyma cells and sieve cells, is represented

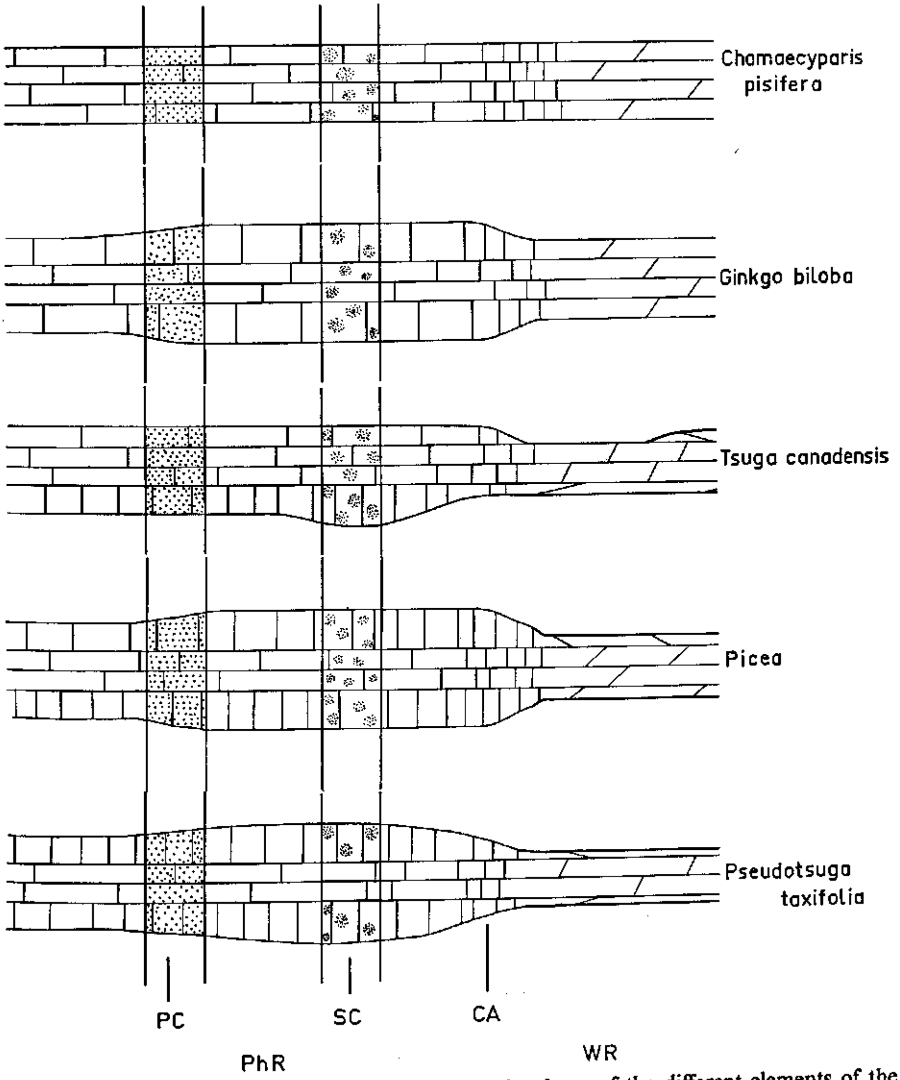


FIG. 73. The evolutionary stages of phloem rays; the shape of the different elements of the rays and the pit-contact of these elements to phloem-parenchyma cells and sieve cells of the axial system is presented.
Chamaecyparis pisifera: homogeneous phloem ray. All the ray-parenchyma cells have pit-contact with both the phloem-parenchyma cells and the sieve cells of the axial system.
Ginkgo biloba: homogeneous phloem ray in which the outer rows of ray-parenchyma cells are more longitudinally stretched than those in the centre. All the ray-parenchyma cells have pit-contact with both the phloem-parenchyma cells and the sieve cells of the axial system.
Tsuga canadensis: semi-heterogeneous phloem ray. Here the ray-albuminous cells are only present on the lower side of the phloem ray; these cells are longitudinally stretched, particularly in the cambial zone. All the elements of the phloem ray have pit-contact with both the phloem-parenchyma cells and the sieve cells of the axial system.
Picea spec.: like *Tsuga canadensis*, but the phloem ray is entirely heterogeneous.
Pseudotsuga taxifolia: the phloem ray is heterogeneous. Only the ray-albuminous cells have pit-contact with all the elements of the axial system. The ray-parenchyma cells are connected to the phloem-parenchyma cells.
From *Pseudotsuga taxifolia* up to *Chamaecyparis pisifera* a gradual reduction of the phloem rays has taken place