Chapter

Phloem: Cell Types, Structure, and Commercial Uses

Marcelo R. Pace

Abstract

Phloem is the vascular tissue in charge of transport and distribution of the organic nutrients. The phloem is also a pathway to signaling molecules and has a structural function in the plant body. It is typically composed of three cell types: sieve elements, parenchyma, and sclerenchyma. The sieve elements have the main function of transport and typically have lost their nuclei and other organelles in the course of their specialization. Hence, the sieve elements rely on specialized neighboring parenchyma cells to sustain all of their physiological function and activities. All cell types of the phloem may vary morphologically and in their distribution in the tissue, and this diversity is taxonomic and functionally informative. The phloem can be of primary or secondary origin, being derived from either procambium or cambium, respectively. Some vascular plant lineages have exclusive primary phloem, such as the lycophytes, ferns, and the monocotyledons, and the sieve elements will be long living in these taxa. In plants with secondary growth, the secondary phloem is formed, and typically the primary phloem collapses. Because new secondary phloem is constantly formed, the longevity of sieve elements in the secondary plant body is much more reduced. In this chapter, the structure of the phloem and its cell types are described in detail and also some of the known commercial uses of this tissue.

Keywords: sieve tube, sieve tube element, companion cells, bark

1. Introduction

Phloem is the vascular plant tissue responsible for the transport and distribution of sugars produced by the photosynthesis. Since the plant is a continuum, phloem will be found in the external part of root cylinders (**Figure 1a**), in the stem vascular bundles (**Figure 1b**) and in the abaxial part of the venations of every single leaf (**Figure 1c**). While the most common is to have the phloem external to the xylem in roots and stems and abaxial in leaves, some exceptions exist and are usually taxon specific. The phloem found in the inside is named internal or intraxylary phloem (**Figure 1b**).

As a constitutive tissue in the plant body, phloem functions extrapolate its main function of sugar transport, including transport of signalizing molecules such as mRNAs, hormones, defenses from biotic and abiotic agents, sustenance of the organs, gas exchange, and storage of many ergastic materials, such as starch, calcium oxalate crystals, and tannins. Parenchymatic cells of the phloem can also give rise to new meristems, such as the phellogen or cork cambium. All vascular plants have phloem, which typically includes specialized living conducting cells

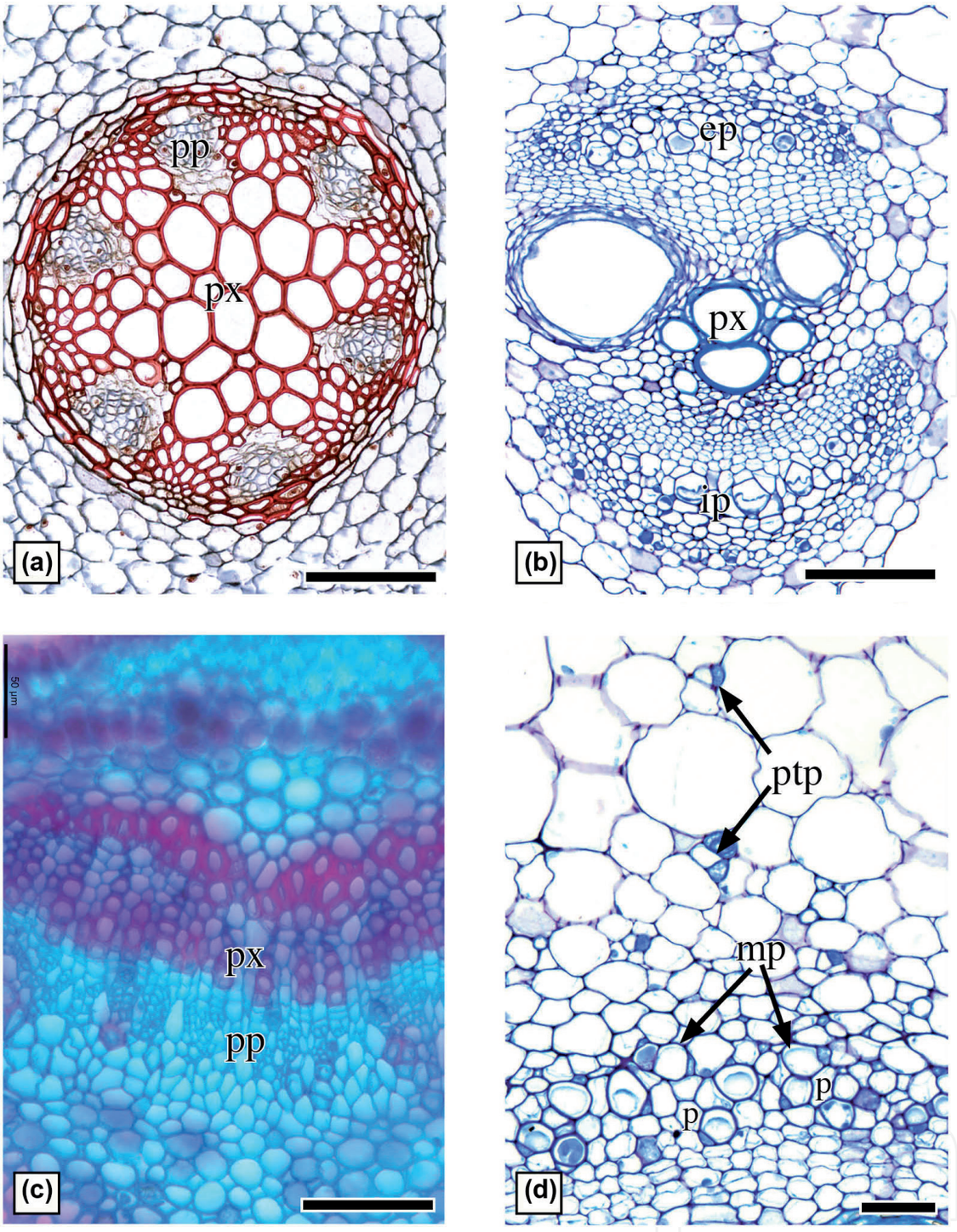

Figure 1.
Location of the primary phloem in different organs and its cell composition. (a) Ranunculus acris (Ranunculaceae). Root transverse section (TS), exarch structure, six strands of primary phloem alternating with the six protoxylem poles. (b) Bicollateral vascular bundle of a squash, Cucurbita pepo (Cucurbitaceae) TS. On the top is the external phloem, and on the bottom is the intraxylary or internal phloem. (Picture credit to Solange Mazzoni Viveiros). (c) Detail of the leaf midrib vascular cylinder of Tetrapterys mucronata (Malpighiaceae) showing primary xylem on the top and primary phloem on the bottom. (Picture credit to Leyde Nayane Nunes). (d) Detail of (b), showing the protophloem on top and the metaxylem on the bottom. ep, external phloem; ip, intraxylary phloem; mp, metaphloem; p, parenchyma cell; pp, primary phloem; ptp, protophloem; px, primary xylem. Scalebars: a, c, d = 50 µm, b = 130 µm.

named sieve elements whose nucleus, ribosomes, and other organelles degenerate during maturation, making sugar transport more efficient. The life and function of these cells will then rely on closely associated parenchyma cells which support the physiological functions of these sieve elements [1]. Although typical phloem is exclusive of vascular plants, rudimentary phloem-like conducting cells are present

also in other lineages, such as the bryophyte leptoids, and even outside the plant kingdom, as the trumpet cells of the kelps and phaeophycean algae [2]. The primary phloem derives from the embryo and the apical meristem procambium throughout the life of the plant or from the cambium, in plants with secondary growth.

2. Phloem cell types

The phloem is a complex tissue and is formed typically by three cell types, the sieve elements, the parenchyma cells, and the sclerenchyma cells (**Figure 2a–d**). Sclerenchyma cells might sometimes be absent in primary and/or secondary phloem. The presence, quantities, and arrangements of these cell types in the tissue commonly vary and may be taxonomic informative [3, 4]. Lists depicting these variations in all phloem cell types are of ultimate importance for complete bark descriptions [5]. What follows is a description of these three major cell types in the phloem.

2.1 Conducting phloem cells

Sieve element is a general term that encompasses all conducting cells of the phloem, both sieve cells and sieve tube elements [1, 6]. The name sieve derives from the strainer appearance given to the cells by the presence of numerous pores crossing their bodies (**Figure 2c**). These pores are specialized plasmodesmata of wider diameter, and the sieve areas are basically specialized primary pit fields [7]. The sieve pores are usually lined up with callose, which were shown to be related with the formation of the sieve pores in angiosperms, although not in gymnosperms [8]. Large amounts of callose deposit in the sieve areas also when the sieve element loses conductivity, suffers injury, or becomes dormant. Callose in gymnosperms is typically wound callose [8]. Callose can be easily detected with aniline blue under fluorescence or resorcin blue [9] (**Figure 2b** and **c**).

Sieve elements have only primary walls, but sometimes this wall can be very thick receiving the name of nacreous walls (**Figure 2d**) [10] and can be present in all major vascular plant lineages [1]. Nacreous walls can be very thick, and some authors have proposed they would be secondary walls [1, 8]. Nacreous walls can almost occlude the entire lumen of the sieve element (**Figure 2d**); hence, its presence needs to be considered in experiments of sugar translocation. Such thick walls might be related to resistance to high turgor pressures within the sieve elements. Nacreous walls seem to have a strong phylogenetic signal and are much more common in some families, such as *Annonaceae*, *Calycanthaceae*, and *Magnoliaceae* [10].

There are basically two types of sieve elements: sieve cells and sieve tube elements. The sieve tube elements are distinguished by the presence of sieve plates, that is, sieve areas with wider and more abundant sieve pores, usually in both extreme ends of the cells, while sieve cells lack sieve plates [1, 6, 8]. A group of connected sieve tube elements form a sieve tube [8]. According to this concept, lycophytes and ferns have sieve cells [1]. However, because of the many differences in the morphology and distribution of protoplasm organelles and chemical substances between the sieve elements of gymnosperms and vascular cryptogams, Evert [8] suggests the use of "sieve cell" as exclusive to the gymnosperms, leaving the more general term "sieve element" to the lycophytes and ferns.

The longevity of sieve elements varies. In many species it is functional for just one growth season, while for other species they can be functional a couple of years, or in the case of plants that lack secondary growth, they will be living for the entire

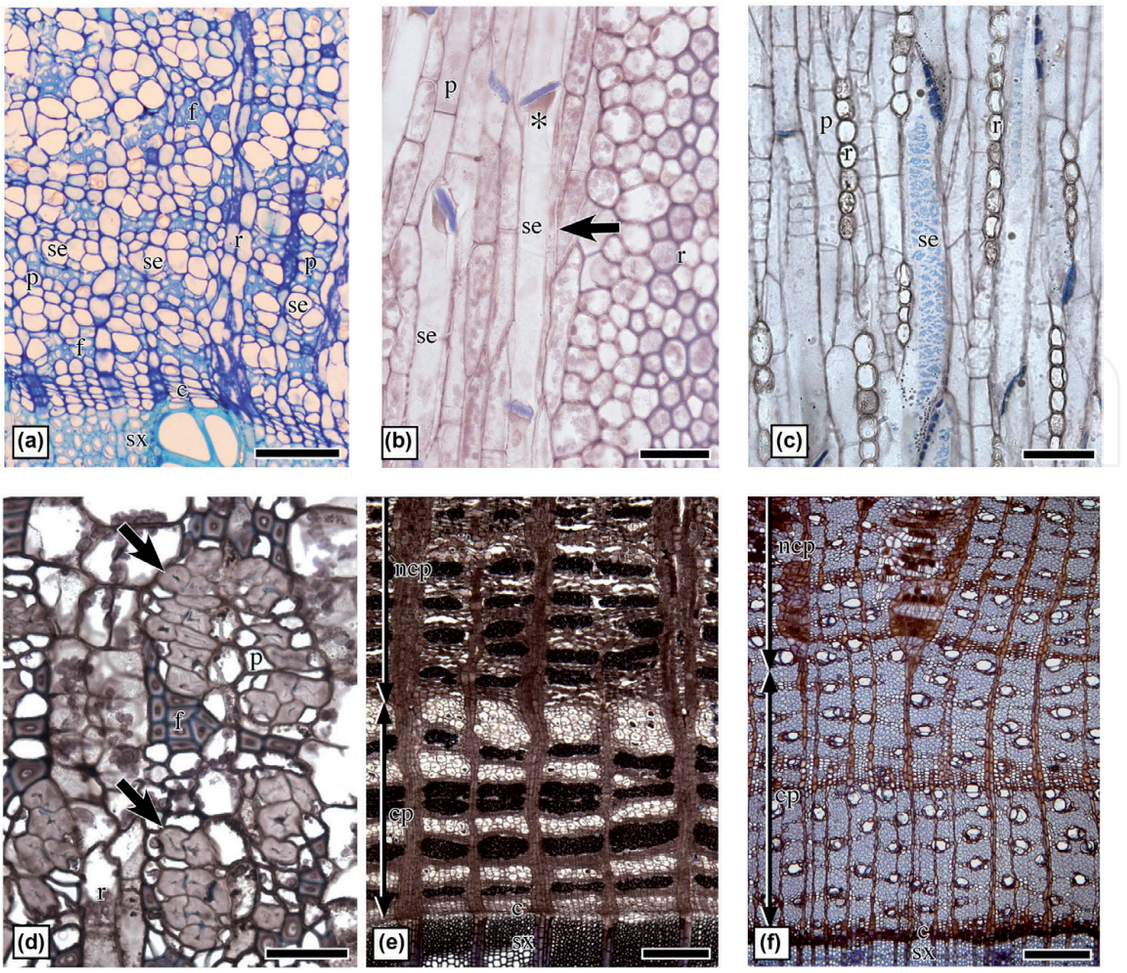

Figure 2.
General aspects of the secondary phloem. (a) Composition of the secondary phloem of Luehea divaricata (Malvaceae) TS, showing sieve tube elements (se) in clusters, axial parenchyma cells (p), fiber clusters (f), and rays (r). (b) Longitudinal tangential section (LT) of Cordia caffra (Boraginaceae) showing sieve tube element (se), companion cells (arrow), multiseriate ray (r), and axial parenchyma (p). Note callose staining with resorcin blue evidencing the slightly inclined simple sieve plates. Note also the P-protein (asterisk) next to the sieve plate. (c) LT of the secondary phloem of Castanea dentata (Fagaceae) showing sieve tube elements (se) with inclined, compound sieve plates and numerous lateral sieve areas of narrower pores, unicellular rays (r), and axial parenchyma (p). (d) TS of Talauma sp. (Magnoliaceae) showing sieve tube elements in clusters, with conspicuous nacreous walls, parenchyma cells (p), clusters of fibers (f), and rays (r). (e) Secondary phloem of maple, Acer saccharum (Sapindaceae), showing the conducting phloem (cp), where sieve tubes and companion cells are turgid, and the nonconducting phloem (ncp), with collapsed sieve tubes. (f) Secondary phloem of Carya cordiformis (Juglandaceae) showing a phloem formed by a background of fibers where solitary to multiple of two sieve tubes are scattered, with sieve-tube-centric and diffuse-in-aggregate axial parenchyma. Note that no collapse is seen in the nonconducting phloem of Carya. c, cambium; sx, secondary xylem. Scalebars: a = 100 μm, b-d = 50 μm, e, f = 200 μm.

plant life spam. Palm trees would perhaps be the plants with the oldest conducting sieve tube elements, since some reach 200 years [11]. In other plants, on the other hand, the sieve elements collapse a few cells away from the vascular cambium, corresponding to a fraction of the mm. In a mature tree, most of the secondary phloem will generally be composed of sieve elements no longer conducting. This region is called nonconducting phloem, in opposition to the area where sieve elements are turgid and conducting, called conducting phloem [5, 8] (**Figure 2e** and **f**). The term collapsed and noncollapsed phloem and functional and nonfunctional phloem are not recommended, since in some plants the nonconducting phloem keeps its sieve elements intact (**Figure 2f**), and although large parts of the phloem may not be conducting, the tissue as a whole is certainly still functioning in storage, protection, and even dividing or giving rise to new meristems, such as the phellogen and the dilatation meristem of some rays [5, 8].

2.1.1 Sieve cells and Strasburger cells

Sieve cells are typically very elongated cells with tapering ends (**Figure 3b**), which lack sieve plates, that is, lack an area in the sieve element where the pores are of a wider diameter. Even though the sieve areas may be more abundant in the terminal parts of the sieve cells, the pores in these terminal areas are of the same diameter as those of the lateral areas of the sieve element. Sieve cells lack P-protein in all stages of development. The sustenance of the sieve cells is carried by specialized parenchyma cells in close contact with the sieve elements, with numerous plasmodesmata, which maintain the physiological functioning of the sieve cells, including the loading and unloading of photosynthates. These cells are known either as albuminous cells or Strasburger cells. The name albuminous was initially coined given the proteinaceous appearance of these cell's contents. However, because the high protein content is not always present, the name Strasburger cell, paying tribute to its discoverer Erns Strasburger, is recommended over albuminous cells [5, 12]. Strasburger cells in the secondary phloem can be either axial parenchyma cells, as is common in *Ephedra* [13], or ray parenchyma cells, as is common in the conifers (**Figure 3c**) [14]. More commonly, the most conspicuous Strasburger cells in conifers are the marginal ray cells which are elongated (**Figure 3c**) and have a larger number of symplastic contact with the sieve cells [14]. Sometimes declining axial parenchyma cells also acts as Strasburger cells in *Pinus* [14]. The only reliable character to distinguish a Strasburger cell from an ordinary cell is the presence of conspicuous connections [14]. In the primary phloem, parenchyma cells next to the sieve cells are those which act as Strasburger cells.

2.1.2 Sieve tube elements and companion cells

A synapomorphy of the angiosperms is the presence of sieve tube elements and companion cells, both sister cells derived from the asymmetrical division of a single mother cell. In some instances, these mother cells can divide many times, creating assemblages of sieve tube elements and parenchyma cells

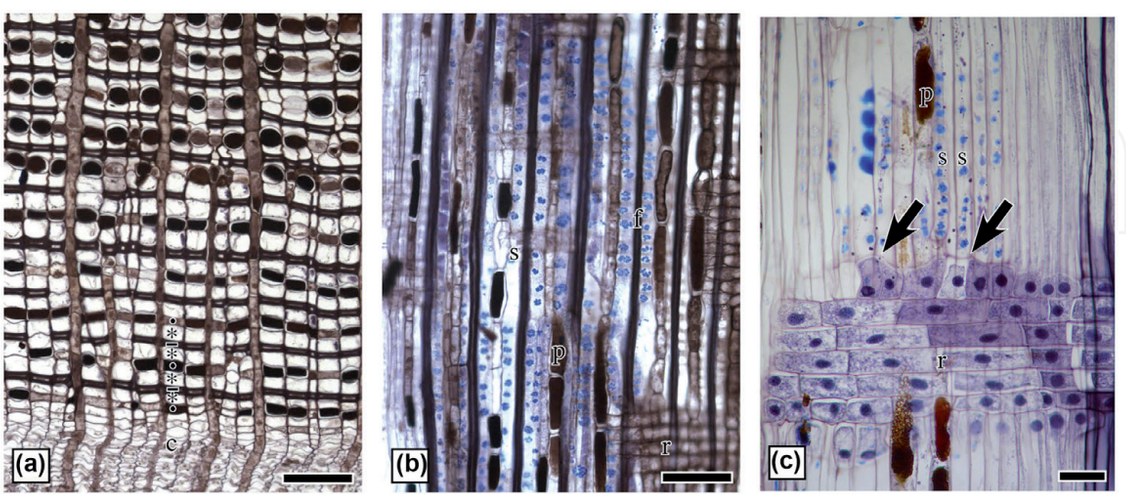

Figure 3.
*The secondary phloem of conifers. (a) Transverse section of the secondary phloem of Sequoia sempervirens (Cupressaceae) showing alternating tangential bands of sieve cells, axial parenchyma, and fibers, interrupted by uniseriate rays. (b). Longitudinal radial section (LR) of the secondary phloem of Sequoia sempervirens (Cupressaceae) showing alternating tangential bands of sieve cells, axial parenchyma, and fibers, interrupted by uniseriate rays. Sieve pores distributed across the walls of long sieve cells. (c). LR section of Pinus strobus (Pinaceae) showing the elongated marginal ray cells in close contact with the sieve cells. These are the Strasburger cells. f and rectangular symbol = fibers, s and * = the sieve cells, p and dot = axial parenchyma cells rich in tannins. Scalebars: a, b = 100 μm, c = 50 μm.*

ontogenetically related [15]. Sieve tube elements have specialized areas in the terminal parts of the sieve elements in which a sieve plate is present (**Figures 2b** and **c**). Within the sieve plate, the pores are much wider than those of the lateral sieve areas, evidencing a specialization of these areas for conduction [16]. In *Cucurbita*, the pores in the sieve plate have up to 10 μm in diameter, while the pores in the lateral sieve areas are of about 0.1 μm [7, 17]. The protoplast of sieve tube elements contain a specific constitutive protein called P-protein (P from phloem, also known as slime; **Figure 2b**), which in some taxa (e.g., *Leguminosae*) is nondispersive and can be seen as coagula inside of the sieve element [18].

Even in lineages of angiosperms where vessels were lost and tracheids re-evolved, such as *Winteraceae* in the *Magnoliids* and *Trochodendraceae* in the *eudicots*, sieve elements and companion cells are present [19], suggesting the independent evolution of these two plant vascular tissues derived from the same meristem initials. Since the sieve tube element loses its nucleus and ribosomes, the companion cell is the cell responsible for the metabolic life of the sieve elements, including the transport of carbohydrates in and out the sieve elements [7]. Companion cells may be arranged in vertical strands, with two to more cells (**Figure 2b**). Other parenchyma cells around the sieve tube integrate with the companion cells and can also act in this matter [7]. Typically, the cells closely related with the sieve tube elements die at the same time as the sieve element loses conductivity.

Sieve tube elements vary morphologically. The sieve plates can be transverse to slightly inclined (**Figure 2b**) or very inclined (**Figure 2c**) and contain a single sieve area (**Figure 2b**) or many (**Figure 2c**). When one sieve area is present, the sieve plate is named simple sieve plate, while when two to many are present, the sieve plates are called compound sieve plates. Compound sieve plates typically occur in sieve tube elements with inclined to very inclined sieve plates (**Figure 2c**). In addition, sieve elements with compound sieve plates are typically longer than those with simple sieve plates. Evolution to sieve elements of both sieve area types has been recorded in certain lineages, such as in *Arecaceae*, *Bignoniaceae*, and *Leguminosae* [5, 20], and to the present it is not still clear why the evolution of distinct morphologies would be or not beneficial. The only clear pattern is that compound sieve plates appear in long sieve elements [1], and phloem with a lot of fibers generally has compound sieve plates [20].

2.2 Parenchyma

In the primary phloem, just one type of parenchyma is present and typically intermingles with the sieve elements (**Figure 1d**). In the secondary structure, there are two types of parenchyma: axial parenchyma and ray parenchyma (**Figures 2b**, **c**, **3b**, **c**), derived, respectively, from the fusiform and ray initials of the cambium.

The axial parenchyma in conifers commonly is arranged in concentric, alternating layers (**Figure 3a** and **b**). These parenchyma cells contain a lot of phenolic substances, which were viewed as a defense mechanism against bark attackers [21]. In Gnetales, the phloem axial parenchyma appears to be intermingling with the sieve cells (**Figure 4a**) [22]. Some of these axial parenchyma cells act as Strasburger cells [13].

In angiosperms, the distribution of the axial phloem parenchyma is more varied, and it may appear as a background tissue where other cells are dispersed or may be in bands (**Figure 4b** and **c**) and radial rows or sieve-tube-centric (**Figure 4d**) [5, 20]. The distribution of axial phloem parenchyma is commonly related to the abundance of fibers or sclereids. In species with more fibers, it is common to have a more organized arrangement of the parenchyma. For example, in *Robinia pseudoacacia* (*Leguminosae*) there are parenchyma bands in either side

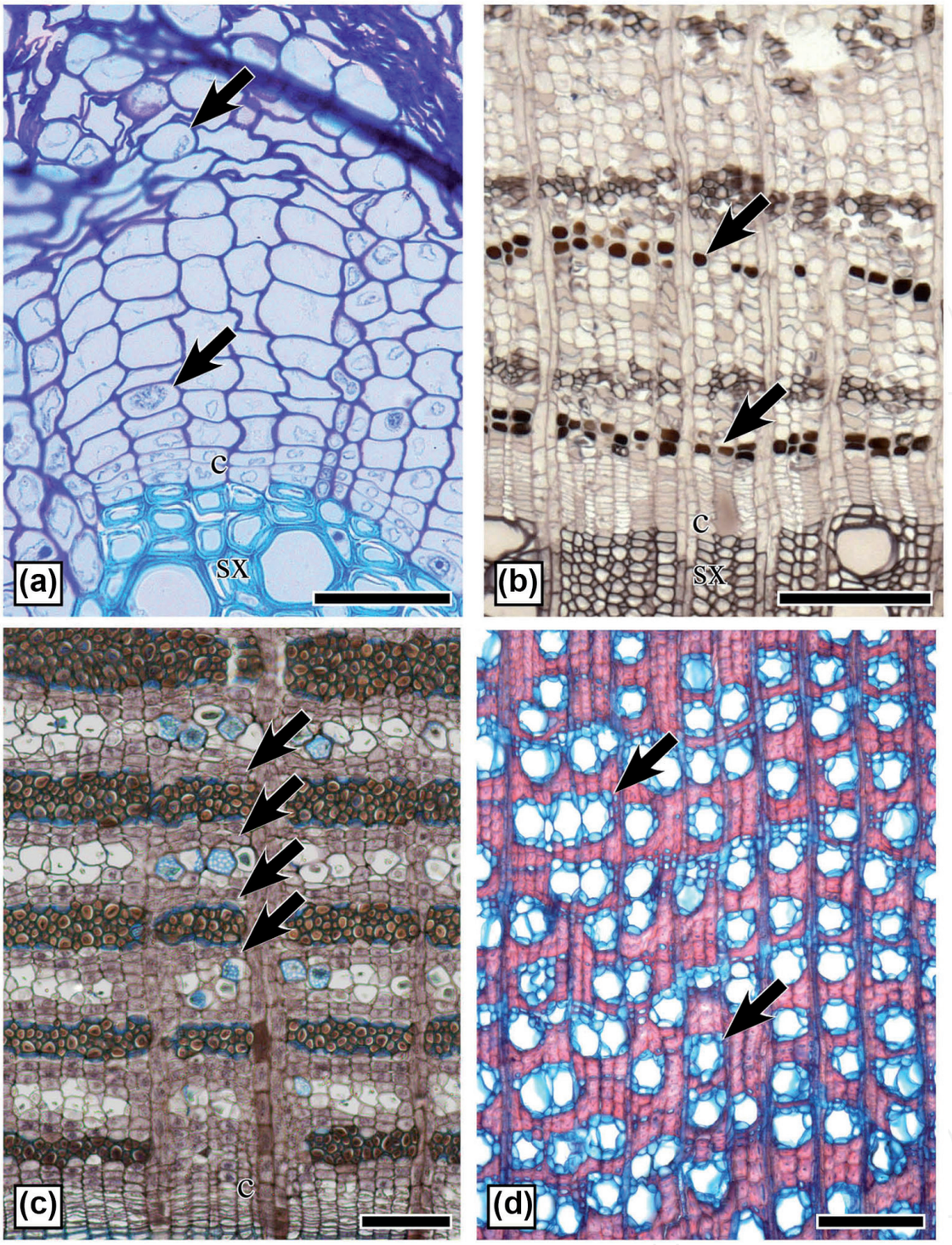

Figure 4.
Phloem axial parenchyma distribution in secondary phloem. (a) Ephedra tweediana (Ephedraceae) TS, showing sieve cells interspersed by axial parenchyma cells (arrows). Six to five cells away from the cambium, the sieve cells already lose conductivity and collapse with axial parenchyma cells enlarging (top arrow). (b) Lannea discolor (Anacardiaceae) TS showing axial parenchyma with tannins arranged in narrow bands (arrows). There are also other parenchyma cells with less content dispersed in the phloem. Note also the fibers in concentric bands. (c) Robinia pseudoacacia (Leguminosae) TS showing bands of axial parenchyma associated with the fiber bands and sieve tube elements in clusters with simple sieve plates staining with resorcin blue. (d) Fridericia nigrescens (Bignoniaceae) TS with sieve tubes surrounded by sieve-tube-centric axial parenchyma. The tissue background corresponds to the fibers. c, cambium; sx, secondary xylem; c, cambium; sp, secondary phloem; sx, secondary xylem. Scalebars: a = 50 μm; b, d = 200 μm; c = 100 μm.

of the concentric fiber bands (**Figure 4c**). When very large quantities of sclerenchyma are present, such as in the secondary phloem of *Carya* (*Juglandaceae*) or in *Fridericia*, *Tanaecium*, *Tynanthus*, and *Xylophragma* (*Bignoniaceae*), the

sieve-tube-centric parenchyma appears (**Figure 4c**) and, as the name suggests, is surrounding the sieve tubes [8, 20, 23].

Although collectively described and referred to as axial phloem parenchyma, it is important to note that in many plants there will be distinct groups of phloem parenchyma within the phloem with quite different ergastic contents and therefore presumed different functions. Some of these specialized parenchyma cells may be considered secretory structures. Within a single plant, it is not uncommon that while some cells have crystals (especially when in contact with sclerenchyma), others have tannins, starch, and other substances. In apple trees (*Malus domestica*, *Rosaceae*) three types of axial parenchyma have been recorded: (1) crystal-bearing cells, (2) tannin- and starch-containing cells, and (3) those with no tannin or starch, which integrate with the companion cells [15].

Within bands of axial parenchyma, canals with a clear epithelium may be formed in many plant groups such as *Pinaceae*, *Anacardiaceae*, *Apiales*, a feature with strong phylogenetic signal. Some phloem parenchyma cells also act in the sustenance and support of the sieve elements, even when not derived from the same mother cell [7]. In longitudinal section, the axial phloem parenchyma may appear fusiform (not segmented) or in two up to several cells per strand [5].

While the phloem ages and moves away from the cambium, its structure dramatically change, and typically axial parenchyma cells enlarge (**Figures 4a** and **b**, **6c**), divide, and store more ergastic contents toward the nonconducting phloem. In plants with low fiber content, the dilatation undergone by the parenchyma cells typically provokes the collapse of the sieve elements. The axial parenchyma in the nonconducting phloem can dedifferentiate and give rise to new lateral meristems. In plants with multiple periderms, typically new phellogens are formed within the secondary phloem, compacting within the multiple periderms large quantities of dead, suberized phloem. In plants with variant secondary growth, especially lianas, new cambia might differentiate from axial phloem parenchyma cells [24]. In the Asian *Tetrastigma* (*Vitaceae*), new cambia were recorded differentiating from primary phloem parenchyma cells [25].

2.3 Sclerenchyma

Sclerenchymatic cells are those with thick secondary walls, commonly lignified. Sclerenchyma can be present or not in the phloem, and when present it typically gives structure to the tissue. For instance, a phloem with concentric layers of sclerenchyma cells is called stratified (**Figures 2e**, **3a**, and **4c**) [5]—not to be confused with storied, regarding the organization of the elements in tangential section. In Leguminosae, bands of phloem are associated to the concentric fiber bands (**Figure 4c**).

Older phloem shows more sclerification than younger phloem, and the sclerenchyma may also act as a barrier to bark attackers [21]. The sclerenchyma is typically divided in two categories: fibers and sclereids. These cell types differ mainly in form and size, but origin has also been used to distinguish them [26].

2.3.1 Fibers

Fibers are long and slender cells, derived from meristems, the fiber primordia [1, 26, 27]. In the primary phloem, fiber caps are sometimes found in association with the protophloem (**Figure 5a**) and are named protophloem fibers. Since only an ontogenetic study can evidence whether these fibers indeed differentiate within the protophloem, a term coined in the nineteenth century German and American literature, pericyclic fibers, has been recommended to be used instead of primary phloem

fibers or perivascular fibers [5]. In the monocotyledons, fibers are commonly an important component of the vascular bundles (**Figure 5b–d**). Commonly these fibers are associated with the phloem (**Figure 5b**), but they might also be associated with the xylem (**Figure 5c**) or be central in the vascular bundle (**Figure 5d**). These fibers are not, however, understood as part of either phloem or xylem; although they are of vascular nature, they differentiate directly from procambium.

2.3.2 Sclereids

Sclereids may have different forms and sizes (**Figure 6a–c**). Within the phloem, they are more typically square or polygonal (stone cells) and contain numerous pits and conspicuous pit canals. Holdheid [26] defines that a sclereid is a cell derived from the belated sclerification of a parenchyma cell, and that is in fact the rule in the majority of cases (**Figure 6a** and **b**). However, there are lineages in which the sclereids differentiate very close to the cambium (e.g., *Pleonotoma*, *Bignoniaceae*, **Figure 6c**; [20]), and it would be untrue to claim that the derivatives had a stage as a mature parenchyma cell [1]. In these cases, the form is enough to define the sclereid.

On the other hand, there are cases where long and slender cells derive from previously mature parenchyma cells and are morphologically difficult to distinguish from fibers. In these cases, these cells are called fiber sclereids and may be even in concentric layers, such as in apple trees and pears (*Malus domestica* and *Pyrus*

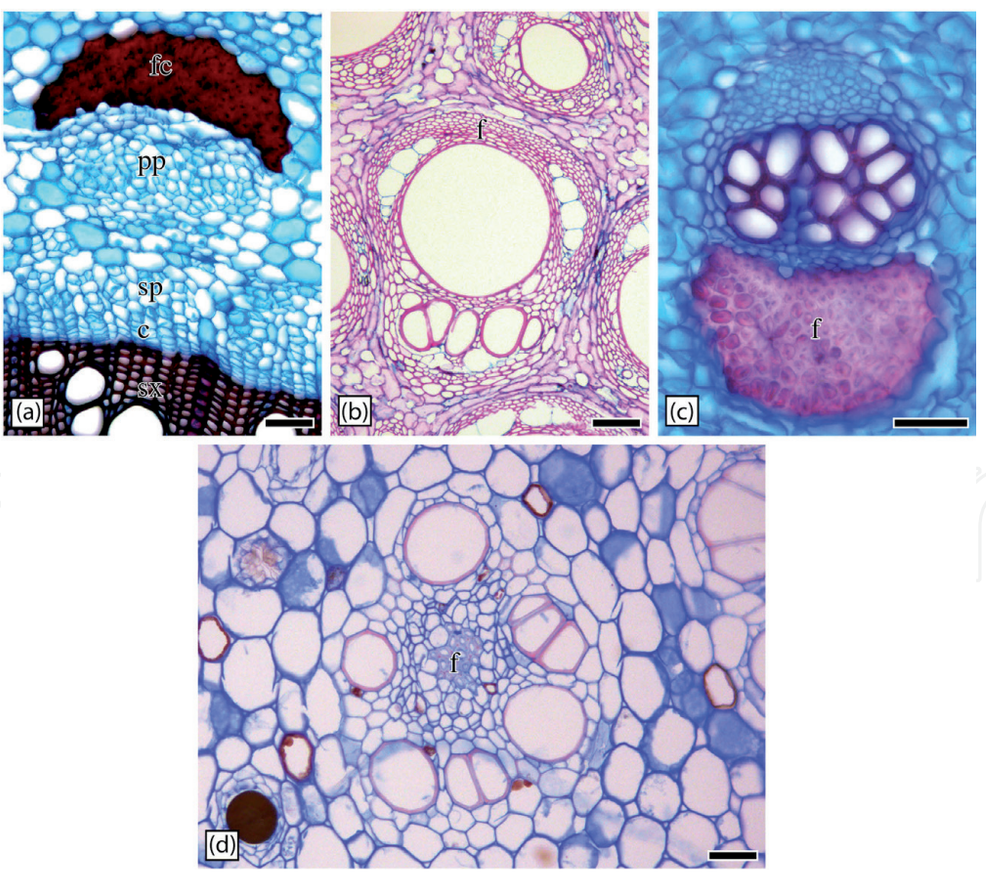

Figure 5.
Vascular fibers associated to eudicot and monocot primary structure. (a) Pericyclic fiber cap (fc) and primary phloem (pp) in Perianthomega vellozoi (Bignoniaceae). Secondary phloem (sp) beginning to be produced. Vascular bundles in monocotyledons. (b) Vascular bundle in the climber Calamus manan (Arecaceae) with fibers toward the phloem side. Phloem in two strands around a wide metaxylem vessel. (c) Vascular bundle of Vellozia alata (Velloziaceae), with fiber cap toward the xylem side. Phloem on the top side of the picture. (Picture credit to Marina Blanco Cattai). (d) Amphivasal bundle of Philodendron with fibers in the center of the vascular bundle and phloem surrounding it. Scalebars: a, b = 100 μm, c, d = 50 μm.

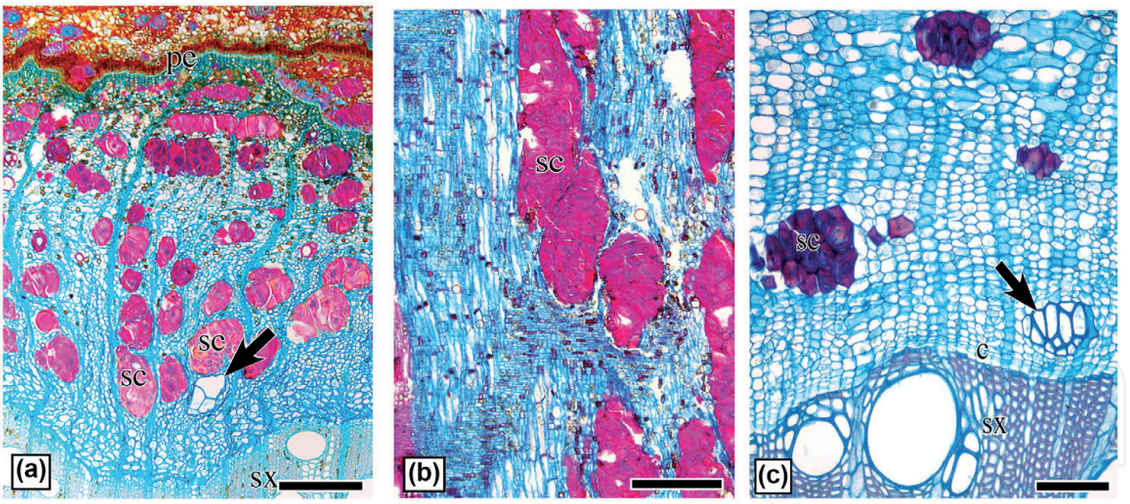

Figure 6.
Sclereids in the secondary phloem. (a) Sclereids (sc) differentiate from parenchyma cells (arrow) in the nonconducting phloem of Heteropterys intermedia (Malpighiaceae) TS, forming large clusters. (b) Longitudinal radial section of Heteropterys intermedia (Malpighiaceae) showing the sclereid masses. (c) In Pleonotoma tetraquetra (Bignoniaceae), the sclereids differentiate (arrow) close to the cambium within the conducting phloem. c, cambium; pe, periderm; sc, sclereid; sx, secondary xylem. Scalebars: a, b = 400 μm, c = 250 μm.

communis, respectively; [15]). Sclereids can also develop with different arrangements in the phloem, being isolated and scattered or in clusters (**Figures 6a–c**) [5].

2.4 Rays

The rays in the conducting phloem have typically the same organization in terms of width, height, and cellular composition as the secondary xylem. In this respect the rays vary from uniseriate to multiseriate (**Figure 7a**) and may be homocellular or heterocellular (**Figure 7b**). Homocellular rays are those composed of cells of one shape, all procumbent or all upright (common in many shrubs). Heterocellular rays are those where more than one cell shape is present together (**Figure 7b**). Ray composition is appreciated in radial sections.

Because the vascular cambium produces much more xylem to the inside than phloem to the outside, phloem rays typically greatly dilate toward the periphery of the organ (**Figure 7c**). It is not uncommon that a dilatation meristem longitudinal to the cambium forms in some barks (**Figure 7c**), especially in families with very wide, wedge-like rays such as the *Malvaceae*. Plants with unicellular rays very rarely have dilatation by cell division [15, 26]. Instead, they have great lateral expansion of their single cells. Ray width can be only determined in tangential sections.

Rays are typically exclusively parenchymatic; however, in many species sieve elements appear in the rays and are called ray sieve cells or radial sieve cells [5, 28, 29]. These cells were recorded connecting two different sieve tubes (collections of sieve tube elements). Ray sieve elements seem to be present in taxa where perforated ray cells have been also recorded [30].

3. Structure and development of primary and secondary phloem

3.1 Primary phloem

The primary phloem derives from the embryo in the seed and the procambium from the organ's apices. Similarly to the primary xylem, the primary phloem is

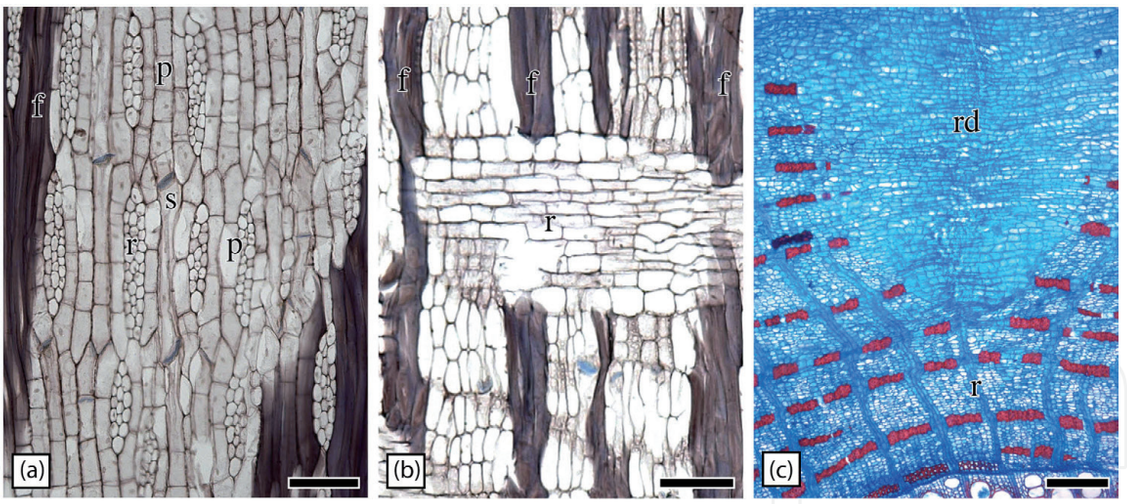

Figure 7.
Rays in the secondary phloem. (a) Longitudinal tangential section of Brachylaena transvaalensis (Asteraceae) showing storied structure, biseriate to triseriate rays (r), sieve tube elements with simple sieve plate (s) and axial parenchyma cells composed of 4–5 cells, and fibers. (b) Longitudinal radial section of Brachylaena transvaalensis (Asteraceae) showing heterocellular rays (r), with body procumbent and one row of marginal square cells. Fibers (f) in bands. (c) Ray dilatation (rd) by the formation of a dilatation meristem in the center of the ray in Perianthomega vellozoi (Bignoniaceae). f, fiber; p, axial parenchyma cell; r, ray; s, sieve tube element. Scalebars: a, b = 100 μm, c = 300 μm.

divided in protophloem and metaphloem (**Figure 1d**), with the protophloem differentiating first, while the plant is still elongating, and the metaphloem differentiating last. The phloem is always exarch, independently of the organ. Protophloem sieve elements sometimes lack companion cells, such as in *Arabidopsis*, and in this case the sieve elements are sustained by other neighboring parenchyma cells. Commonly, the protophloem quickly becomes obliterated and loses function. In plants without secondary growth, the metaphloem will be conducted during the entire life of the plant, as in the monocotyledons (**Figure 5b–d**) [11]. Different vascular plant lineages display different arrangements of the primary xylem and phloem, depending on the stele type. Two main types of steles exist, the protostele and the siphonostele. In the protostele, the entire center of the organ is composed of vascular tissue (**Figure 1a**), with the phloem in strands alternated with a central xylem in the protostele, haplostele, and actinostele (**Figure 1a**), while primary phloem is interspersed in the protostele plectostele [6]. The roots of all the vascular plants are protostelic (**Figure 1a**). The stems, however, can vary. In the lycophytes, they are always protostelic, while in the ferns (monilophytes) they might be protostelic, such as in *Psilotum*, or in all other range of siphonostelic steles [31]. The siphonostele evolved in concert with the macrophytes and resulted in the formation of a central pith derived from the ground meristem. No lineage displays as much diversity in the primary vasculature architecture as do the ferns. In the seed plants, that is, gymnosperms and angiosperms, the stem stele is always a syphonostele, either a eustele, where discrete vascular bundles form a concentric ring, or the atactostele, a type of stele exclusive of the monocotyledons where the bundles are scattered in the entire stem center. Some lineages of eudicotyledons and *Magnoliids* have evolved another subtype of siphonostele, the polycyclic eustele, where more than one ring of bundles is present, such as in *Piperaceae* and *Nyctaginaceae*.

The primary phloem is simpler than the secondary phloem and is basically formed by sieve elements and parenchyma cells (**Figure 1a–d**). Fiber caps are commonly present, and they might be phloematic (**Figure 5a**). For a discussion on their origin, check the section on fibers above. The position of the phloem is typically external or abaxial to the xylem, but in some lineages the bundles are bicollateral

(**Figure 1b**), and phloem is present both inside and outside (abaxial and adaxial), while in amphivasal bundles, the xylem encircles the phloem (**Figure 5d**), as in the secondary vascular tissues of some *Asparagales* [32, 33] and *Iridaceae* corms [34]. In some plant families and orders, intraxylary phloem (perimedullar phloem islands) is a synapomorphy, such as in the order *Myrtales* and in the families *Apocynaceae* and *Convolvulaceae* [35]. These phloem strands are initially primary, but a cambium can differentiate between the protoxylem and the phloem strands and develop secondary tissues inside of the pith.

3.2 Secondary phloem

Being derived from the cambium, the secondary phloem will share a number of characteristics with the secondary xylem. For instance, it is divided in an axial and radial system. The axial system is composed of sieve elements, axial parenchyma cells, and fibers, and the radial system is formed by rays, which are typically parenchymatic (**Figure 2a–c**). Similar to secondary xylem, the secondary phloem can be storied (**Figure 7a**) or non-storied (**Figure 2b** and **c**), depending whether the cambial mother cells are organized in tiers or not.

Some trees will have growth rings, with an early and a late phloem, both in temperate and tropical regions, but their characterization is only possible with periodical collections [5]. Sometimes, but not always, the fiber band width gives a hint on the presence of growth rings or the formation of very small sieve elements in the late phloem [1, 5].

3.2.1 Secondary phloem of gymnosperms

In conifers (except Gnetales) the secondary phloem is typically marked by an alternation of axial cell types (**Figure 3a** and **b**), uniseriate rays, and, in many lineages, axial and radial resin canals (e.g., *Pinaceae* and *Cupressaceae*). In the *Pinaceae*, the phloem is marked by the presence of an alternation of sieve cells and bands of axial parenchyma with phenolic contents, some also with druses. In the nonconducting phloem of *Pinaceae*, sclereids differentiate. In all other conifers, in addition to the alternation of parenchyma bands and sieve cells, fiber bands are present (**Figure 3a** and **b**). Therefore, sieve cells, parenchyma cells with phenolic content, and bands of fibers appear in alternation in non-*Pinaceae* and Gnetales conifers, including *Araucariaceae*, *Cupressaceae*, *Podocarpaceae*, *Taxaceae*, and *Taxodiaceae* [8, 21]. Another marked difference of these conifers compared to *Pinaceae* is that they contain a lot of crystals in their cell walls, including in Gnetales (see New World *Ephedra*; [36]), while in *Pinaceae* they are exclusively inside of idioblastic cells.

In other gymnosperms, in particular in Gnetales and Cycads, the first remarkable difference is the presence of very wide, multiseriate rays alternating with uniseriate rays. The wide rays in both groups have, however, evolved independently, since Cycads are a sister to all other gymnosperms, while Gnetales are within the conifers, as sister to the Pinaceae [31, 37]. In *Cyca* and the extinct *Cycadoidea*, sieve cells and phloem parenchyma alternate with fibers, which can be in tangential bands or not [38, 39]. In *Cyca*, the sieve cells appear in radial rolls [38], while in *Cycadoidea* there is a constant alternation of one sieve cell or phloem parenchyma to one fiber [39]. The nonconducting phloem of *Cycas* is marked by the collapse of sieve cells, enlargement of the axial parenchyma cells, ray dilatation, and sclerosis of some parenchymatic cells [38]. More than one ring of secondary phloem is present in some Cycads (e.g., *Cycas, Encephalartos*, *Lepidozamia*, and *Macrozamia*) and Gnetales (e.g., *Gnetum*), given that they have successive cambia [38, 40].

Within the Gnetales, in *Ephedra* axial parenchyma cells are interspersed with sieve cells (**Figure 4a**), and fiber may or may not be present and are typically gelatinous [36]. Fiber sclereids and/or sclereids appear in the nonconducting phloem of other species [13, 22]. In the nonconducting phloem of *Ephedra*, the sieve cells and Strasburger cells collapse with the enlargement of the axial and radial parenchyma cells (**Figure 4a**) with more ergastic contents [13]. In *Gnetum*, large areas of parenchyma sclerify, forming bands in the nonconducting phloem. The secondary phloem of *Welwitschia* is described as containing a large amount of fibers [21].

3.2.2 Secondary phloem of angiosperms

Within the angiosperms, the diversity of phloem cell type arrangements reaches its maximum. The structure can be storied (**Figure 7a**) or non-storied (**Figure 2b** and **c**); sclerenchyma can be present or lacking. The rays may be uni-, bi-, or multiseriate. A large array of secretory cells may be encountered, such as resin canals, laticifers, and mucilaginous cells. Crystalliferous parenchyma is also very common, especially when associated with fibers.

The variation in cell type arrangements can be of taxonomic interest. Sieve elements can vary in morphology and arrangement. They can be solitary (**Figure 2f**), scattered in the phloem (e.g., *Eucalyptus*, *Myrtaceae*), in clusters (e.g., *Malvaceae*; **Figures 2a**, **d** and **4c**), and in radial or tangential rows (many *Bignoniaceae*; [20]; **Figure 4d**). The functional significance of the different arrangements is unknown to date, although this is one of the features in the phloem with the strongest phylogenetic signal.

The presence, type, and arrangements of fibers and sclereids are one of the most informative characters in the bark [4]. In *Apocynaceae*, the fibers are completely absent, except in *Aspidosperma*, the sister group of all other *Apocynaceae* [35]. In *Aspidosperma*, they can appear solitary scattered across the phloem or in clusters. In some lineages, fibers appear in concentric alternating bands, as in *Leguminosae* (*Papilionoideae)*, *Mimosoideae* (**Figure 4c**) [41], *Bignoniaceae* [20], and *Malvaceae*, and this is a constant character among them.

Phloem parenchyma more commonly constitute the background tissue in the phloem but can also be distributed in bands (**Figure 4b** and **c**), radial rows, or even only around the sieve tube elements (**Figure 4d**) [5].

4. Phloem activity

The classic theory of phloem transport is that proposed by Ernst Münch [42], and it involves the formation of an osmotic pressure transport gradient, where certain zones act as sources of sugars (leaves and storage organs), while others act as sinks. Experiments showed that the concentration gradients were always seen to be positive in the direction of flow [43], supporting Münch's postulate. In a system where transport goes against the direction of transpiration, its functionality relies on the presence of a plasma membrane across the entire system to create an osmotic pressure, hence the need of a conducting system with living cells [44]. Recent studies have been refining aspects involved in the photosynthate conduction to explain long-distance transports across large trees with such a simple system [44, 45]. A direct role of intracellular calcium has also been reported in the dissolution of nondispersive P-proteins and facilitation of transport [46]. Likely, the anatomical structure of the phloem discussed in the previous sections of this chapter will prove to play a role in the system. For instance, phloem sieve element length scale with the tree sizes and sieve plate type [45]. It was also shown that sieve element's diameter, length, and pore width increase from the top to the base of the trees [47, 48].

Across the entire pathway, sugars are removed from the system to sustain all cells in the plant body. This mechanism is only possible with the concerted mechanism between sieve elements and their close related cells (Strasburger cells and companion cells), with these accompanying cells constantly channeling substances and macromolecules toward the sieve elements [44]. The Strasburger and companion cells carry the loading and unloading of the sieve elements. Given the function of loading and unloading, the companion cell-sieve tube element size ratio is directly related to being in the source or the sink of sugars [44]. For instance, in leaves the companion cells are typically much larger, for they have the high demand of constantly loading the sieve tubes. In areas of release of the sugars (unloading), the companion cells are much smaller or even absent [44].

5. Economic uses

In the economic uses, it is not always easy to distinguish the use of the phloem from that of the periderm, since both together compose the bark of a woody plant. The phloem corresponds to the inner bark, and the periderm to the outer bark. The bark has a long history of utilization, from the production of remedies [49], aphrodisiacs (yohimbe), insecticides [50], dyes, tannins [50], angostura, fibers [51], gums and resins [50], latex, and flavorings [52].

In indigenous groups from British Columbia (Canada) and Tanzania, barks from dozens of species of woody plants are used as carbohydrate food, medicine, fibers, and structural material [50, 53]. In Mexico the bark of *Ficus* is used since prehispanic times to create a type of paper called *papel amate* (from the náhuatl paper = ámatl), used, for example, to create the Aztec codices.

The rubber tree, *Hevea brasiliensis* (*Euphorbiaceae*), is known from the extraction of latex to the production of rubber. Laticifers are present in concentric rings in the secondary phloem of the rubber tree and are an important economic asset in some tropical countries. Bark residues have also been considered for mulching [53–55], to build particle boards [56, 57], as fuel, and a source of food for ruminants [52].

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Conflict of interest

The authors declare no conflict of interest.

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Author details

Marcelo R. Pace
Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico

*Address all correspondence to: marcelo.pace@ib.unam.mx

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