

CATEGORY A — PLANT ANATOMY AND PHYSIOLOGY

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Hydrophytic and xerophytic designations are given to plants with adaptations to water-dominated or water-scarce environments, respectively. Species within each classification share characteristics due to similar ecological and habitat challenges rather than evolutionary homology. As such, the hydrophyte and xerophyte taxa are polyphyletic and may include structural disparities between members (Raven, 2003). This work looks at the adaptations in a sampling of different hydrophytes (pleuston, elodeid) and xerophytes (succulent, woody, epiphyte, grass) with an emphasis on the differences between the two. Given the large variety of hydrophytes and xerophytes, the features described here are not necessarily be common to all plants within the given group, nor are the morphological and anatomical adaptations found in nature limited to those described here.

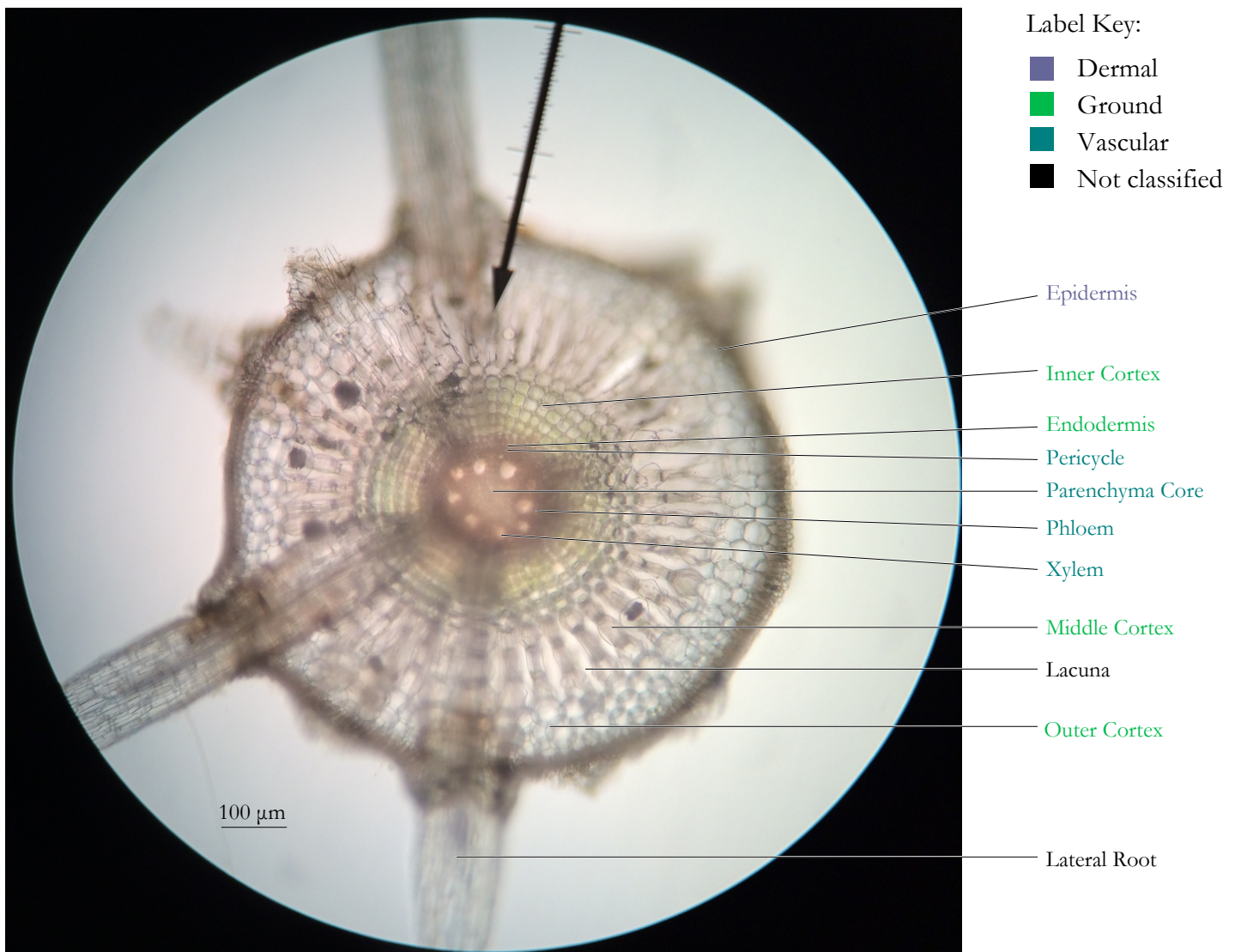


Figure 1: Transverse section of *Eichhornia crassipes* root

The section was prepared by hand, left unstained, and viewed at 100x magnification (10x objective).

The roots of *Eichhornia crassipes*, a pleuston hydrophyte, are made for floating rather than anchoring. The middle cortex is composed of aerenchyma and lacunae (intercellular air cavities) that confer flexibility and buoyancy to the root. The lacunae also provide a pathway for the rapid and energetically inexpensive exchange of gases

(e.g. oxygen and ethylene) between the submerged root system and the above-water shoot system. Due to its unrestricted access to water, *Eichhornia* has poorly developed vascular tissues and absorptive surfaces; a single, large element constitutes the xylem in each vascular bundle and root hairs are entirely absent from the thin-walled and uni-layered epidermis (Pandey & Chadha, 1998).

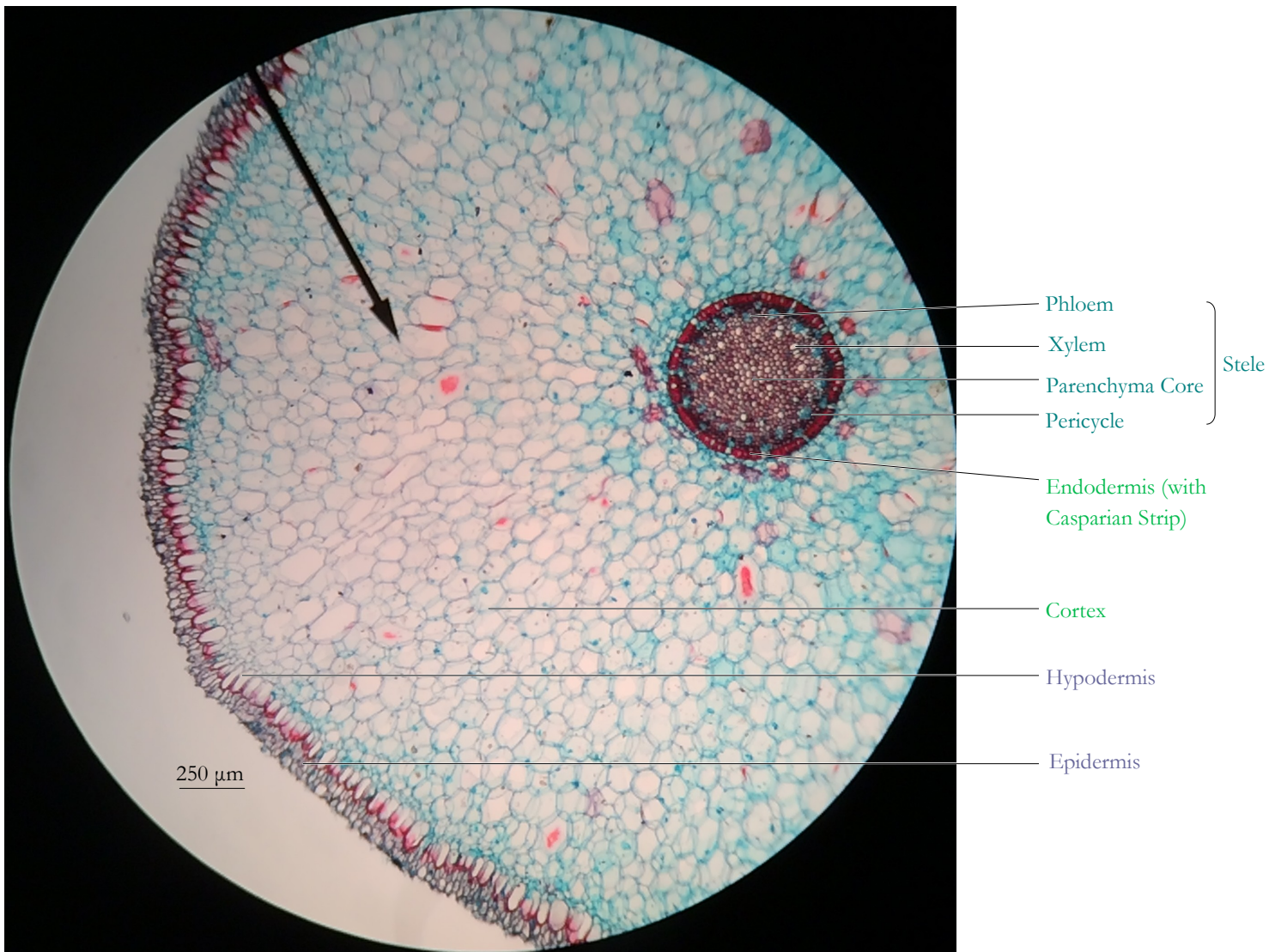


Figure 2: Transverse section of *Phalaenopsis* member aerial root

The section was prepared by hand, stained with Safranin O and Fast Green FCF, and viewed at 40x magnification (4x objective).

Phalaenopsis exhibits root succulence, adapting to xeric conditions by retaining water. The cells of the cortex are large and parenchymatous, reflecting their function in water storage (figure 2). Evaporative water loss is reduced by the radially elongated, multi-layered epidermis and the sclerenchymatous hypodermis. The dermal tissues also serve a protective function, reducing damage to internal tissues from high light intensities. Lignified tissues (stained red) of the hypodermis and stele provide mechanical support to the water-heavy cortex. *Phalaenopsis*'s larger size and lack of lateral root extensions reduces its surface area to volume ratio, in turn reducing the rate of water loss through the root surface. Vascular tissues are well developed and represented by numerous bundles (Pandey & Chadha, 1998).

Micro Differences in Root Structure

The hydrophyte's epidermis is thinner than that of the xerophyte. Lignified tissues are present in the xerophyte, while aerenchyma is present in the hydrophyte. Surface area to volume ratio is lower in the xerophyte.

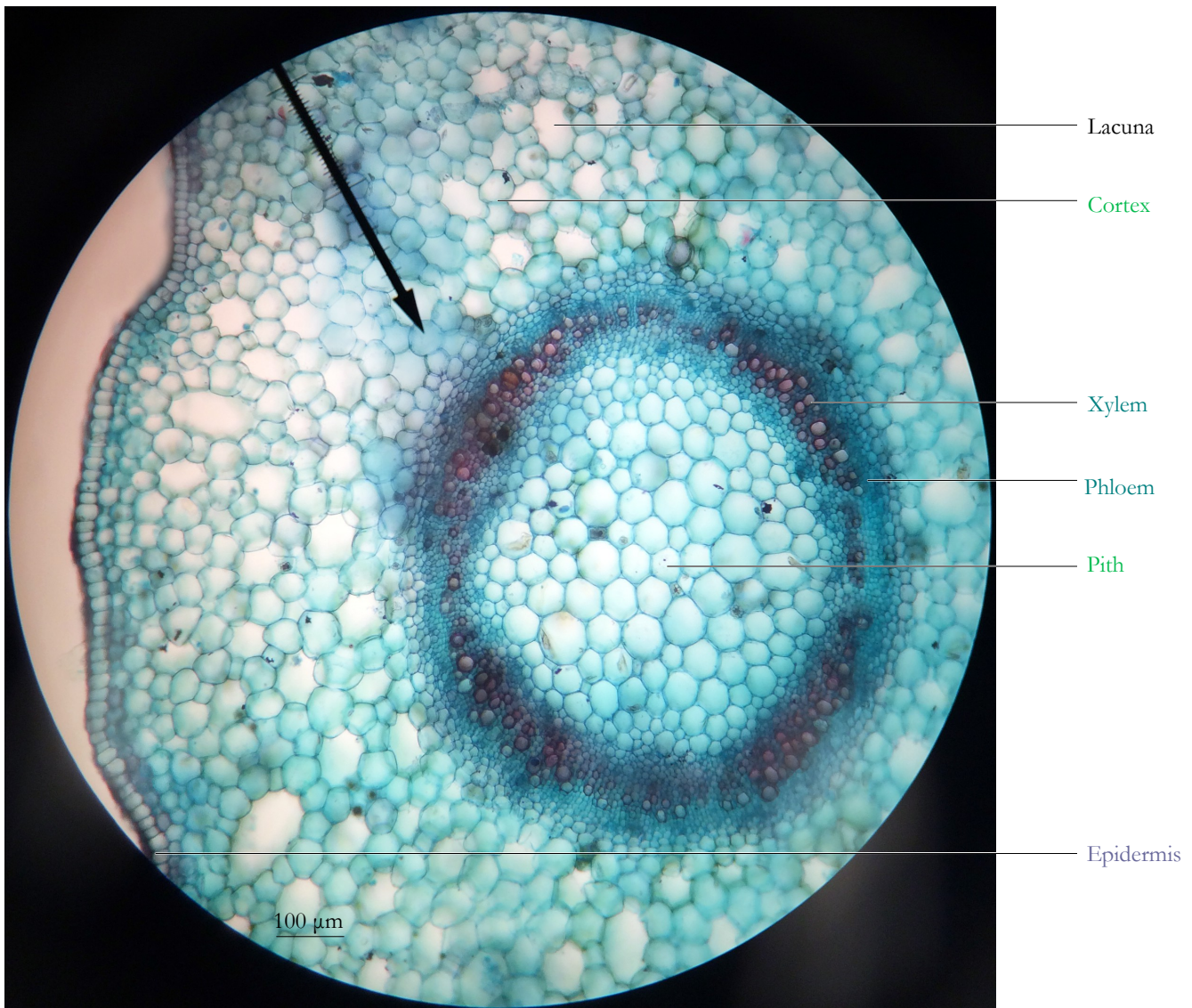


Figure 3: Transverse section of *Ludwigia repens* stem

The section was prepared by hand, stained with Safranin O and Fast Green FCF, and viewed at 100x magnification (10x objective).

Ludwigia repens is a submerged (elodeid) vascular hydrophyte. Its lack of emergent structures makes gas/nutrient acquisition and distribution throughout the plant body particularly important. The lacunae support the establishment of an oxygen and carbon dioxide gradient between the photosynthetic leaves and the stem or roots. Also, the thin-walled epidermis facilitates gas exchange and water/nutrient absorption directly from the water. The uptake of water across the general plant body reduces the need for water transport, hence the poorly developed xylem. Once again, aerenchyma tissue can be found in the cortex region. The thin-walled, uniseriate aerenchyma helps in maximizing sunlight exposure by providing buoyancy and keeping the plant upright.

The sample has stained mostly blue, indicating a lack of mechanical tissue (figure 3). Sclerenchyma is unnecessary due to the inflated lacuna and the constant availability of water, which generates turgor pressure in plant cells. Mechanical tissues are also prone to breakage due to water stress. The uncutinized epidermis and the spongy aerenchyma of *Ludwigia* are suitable for hydric conditions since they promote resource acquisition/exchange and allow the stem to bend in the case of a current. (Pandey & Chadha, 1998)

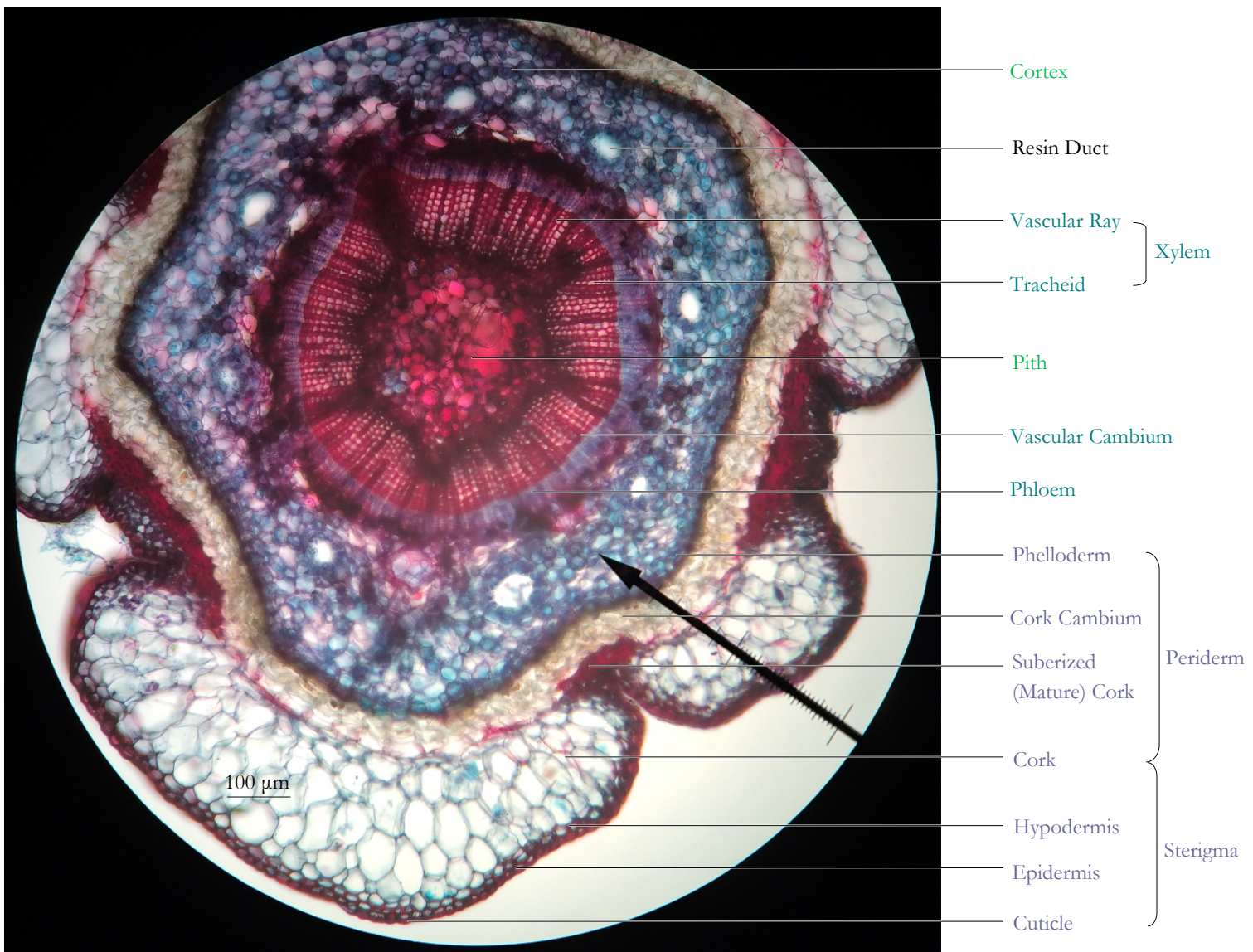


Figure 4: Transverse section of 1-year-old *Picea* member stem

The section was prepared by hand, stained with Safranin O and Fast Green FCF, and viewed at 100x magnification (10x objective).

The stem of *Picea* is modified to reduce water loss. A thick, waxy cuticle covers the stem surface to limit transpiration, acting as a barrier to diffusion (figure 4). The sterigmata (needle extensions) sheathe the stem and lengthens the diffusion pathway to further reduce evaporative water loss. The epidermal and mature cork tissues of *Picea* are highly lignified to resist wilting. Mechanical strengthening of the sterigmata also serves to allow photosynthesis during drought conditions, as the needles would otherwise wilt and cease to function. The scale-like shape of the sterigmata decreases their surface area to volume ratio and evaporative water loss. Vascular tissues, especially xylem, are well-developed and abundant (Schweingruber et al., 2007).

Micro Differences in Stem Structure

Cells of the xerophyte, most notably those of the cortex and vascular cylinder, are smaller than the cells of the hydrophyte. Cell walls take up a greater portion of the xerophyte's volume than the hydrophyte's volume. This can be attributed to both the xerophyte's vulnerability to wilting and the hydrophyte's subsistence on an excess of water. Vascular tissues are more numerous in the xerophyte, forming a wider ring than that of the vascular tissues in the hydrophyte. Vessels are also more compactly arranged and well-developed in the xerophyte, reflecting a greater need to distribute water. Lignification is absent in the hydrophyte and extensive in the xerophyte. Cutin, periderm and lateral growth are present in the xerophyte but absent in the hydrophyte.

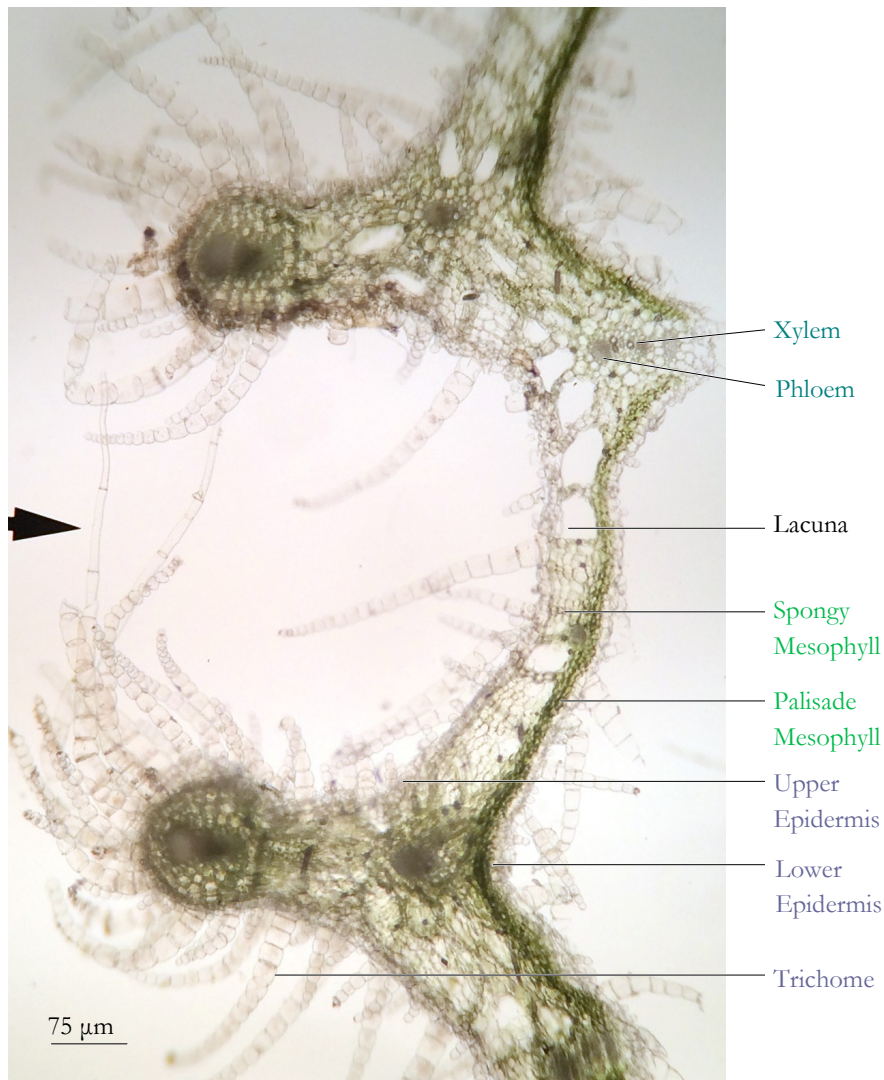


Figure 5: Transverse section of *Pistia stratiotes* leaf

The section was prepared by hand, left unstained and viewed at 100x magnification (10x objective).

Micro Differences in Leaf Structure

Pistia is a pleuston that exhibits adaptations for living at the air-water interface. The spongy mesophyll is aerated by lacunae which, once again, provide buoyancy and gas exchange (figure 6). The leaf lacunae, being continuous with the air spaces of the stem and root, facilitate the generation of an oxygen and carbon dioxide gradient. Photosynthesis drives an increase in O_2 partial pressure in the lacunae, while respiration drives a decrease in O_2 partial pressure in the stem and roots. Diffusion then favors the roots, providing oxygen to the submerged parts of the plant. The reverse occurs for the exchange of CO_2 (Pandey & Chadha, 1998; Raven, 2003).

Tillandsia is an epiphyte of the Bromeliaceae family that has acquired xerophytic traits for living in the air. The sheet-like structures on the leaf surface (figure 7) are actually multiseriate trichomes arranged longitudinally to cover the leaf surface. *Tillandsia* relies on these trichomes to reflect light and absorb airborne water and nutrients. A number of air canals are associated with the chlorenchyma for photosynthetic gas exchange. Hydrenchyma is present for water storage, and a thick cuticle is present to reduce transpiration. In addition, stomata are sunken and covered with trichomes to reduce exposure to drying winds and create a favorable microenvironment that further decreases transpiration (Benzing, 2000).

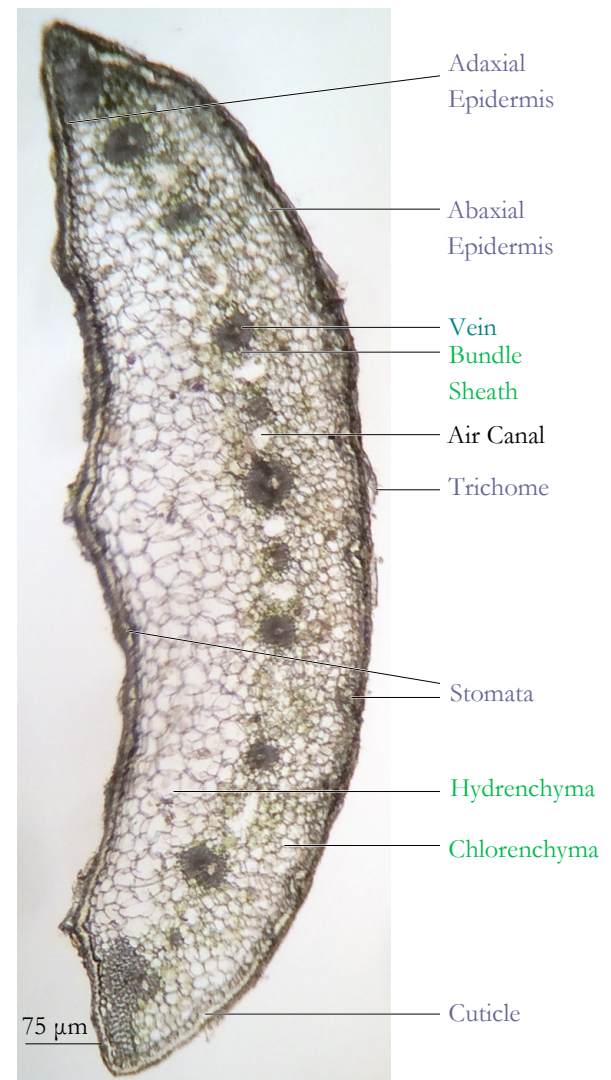


Figure 6: Transverse section of *Tillandsia* leaf

The section was prepared by hand, left unstained and viewed at 100x magnification (10x objective).

Pistia and *Tillandsia* leaves also differ in morphology. *Pistia* is furrowed in shape and exhibits leaf pubescence. The uniseriate trichomes help form extracellular air pockets along the leaf furrows and enhance buoyancy. *Tillandsia* is thicker and less wide, meaning a lower surface area to volume ratio. The thinner, broader leaves of *Pistia* maximize sun exposure and photosynthesis, while the smaller transpirational surface of *Tillandsia* promotes water retention at the expense of photosynthesis. Leaf veins are more numerous in *Tillandsia*. Vascular tissues are poorly developed in *Pistia*, consisting of phloem and a few thin-walled xylem elements.

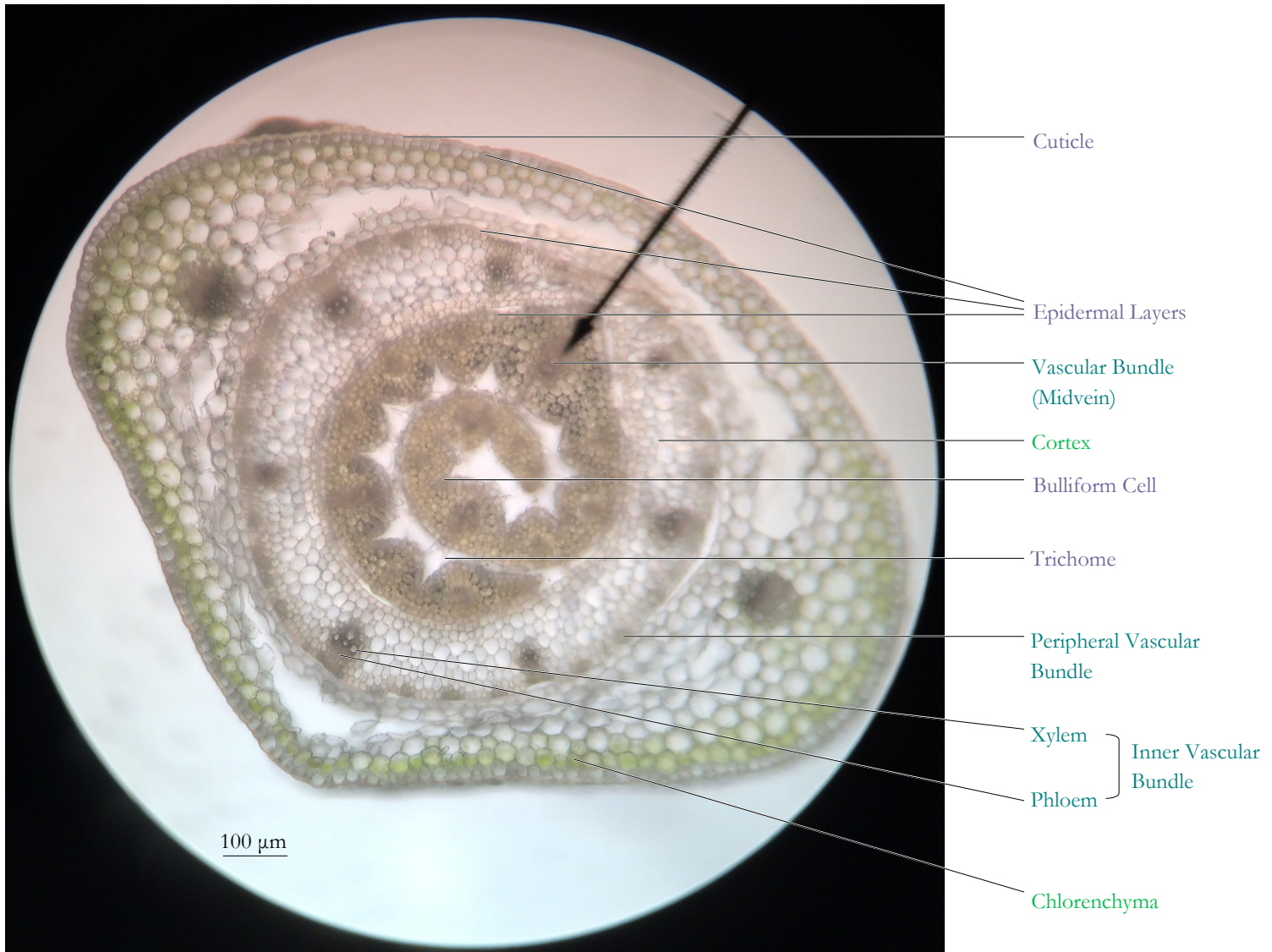


Figure 7: Transverse section of *Triticum* sheath, stem and leaf blade

The section was prepared by hand, left unstained, and viewed at 100x magnification (10x objective).

***Triticum* Features of Interest**

Triticum is a C3 grass and a major source of food around the world. Its leaf blade rolls up as a result of bulliform cell activity on the adaxial surface. Leaf rolling decreases the surface area exposed to the exterior and creates a moist local environment. Both mechanisms serve to reduce transpiration, as wind exposure would increase evaporation and air humidity would decrease it. Trichomes aid in the formation of a moist microenvironment by trapping air at the leaf adaxial surface. Transpiration is further reduced by the hollow, circular stem, the sheath, and the waxy cuticle. Vascular tissues of the stem are well developed and arranged in 2 series: the peripheral and the inner (Pandey & Chadha, 1998; Raven et al., 2003).

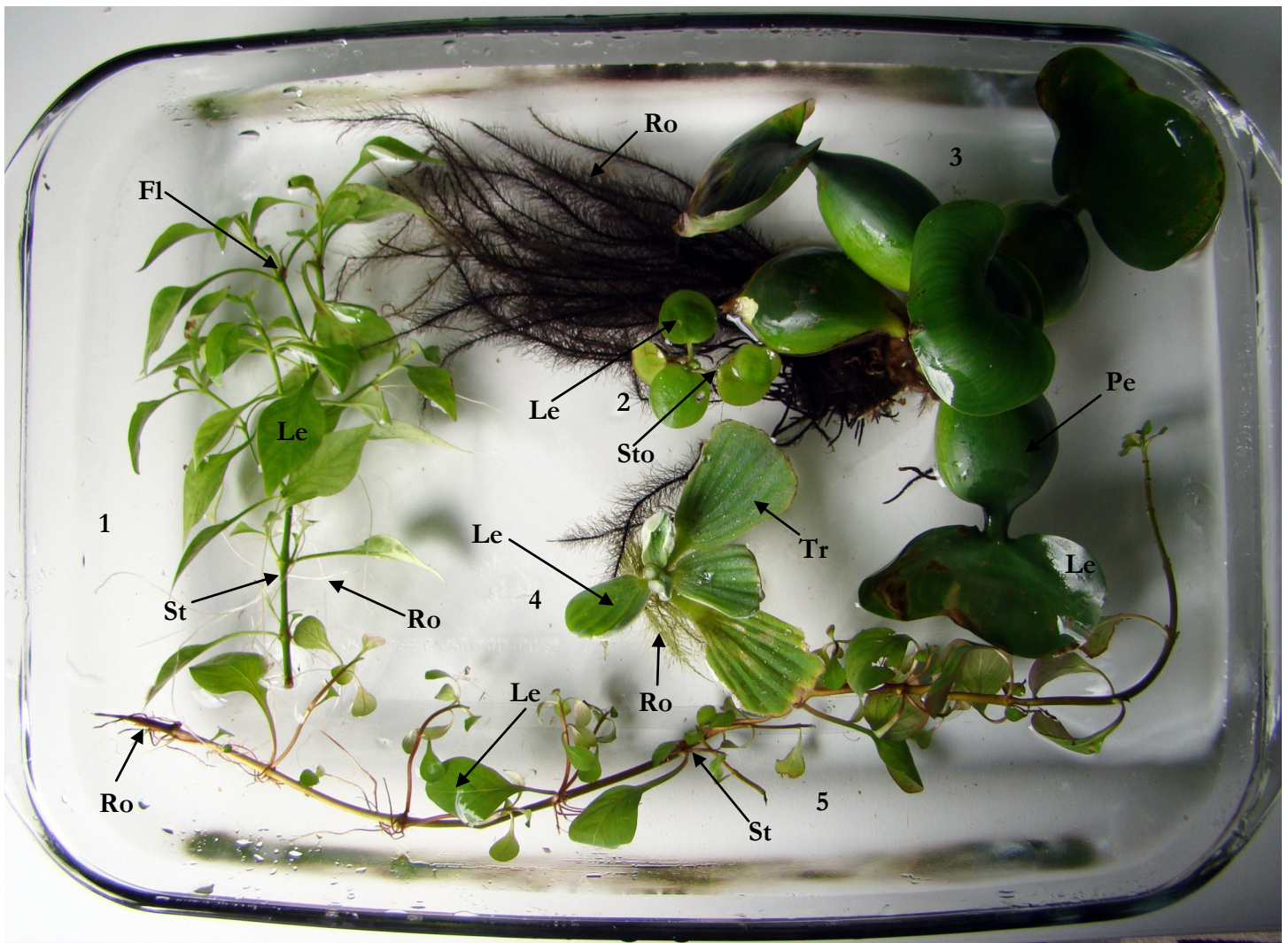


Figure 8: Frontal view of *Alteranthera* (1) and *Ludwigia repens* (5), and top view of *Limnobium laevigatum* (2), *Eichhornia crassipes* (3) and *Pistia stratiotes* (4).

Structures of interest include the root (Ro), leaf lamina (Le), flower (Fl), stolon (Sto), trichome (Tr), stem (St) and petiole (Pe).

The root systems of the submerged hydrophytes *Alteranthera* and *Ludwigia* are reduced since water and nutrients can be absorbed through the general plant body. Adventitious roots are present in *Alteranthera* (figure 8.1) and *Ludwigia* (figure 8.5), and *Ludwigia* features primary roots used for anchorage. The leaves of the submerged hydrophytes are thin and elongated to prevent breakage in moving water. For the same reason, the stem is thin and noticeably bendable in *Ludwigia*. Both *Ludwigia* and *Alteranthera* have green, photosynthetic stems, and *Alteranthera* features inflorescences at the stem axil. Though certain hydrophytes develop emergent flowers, those seen here are smaller and less colorful since they are pollinated through water rather than animals. Meanwhile, the emergent portions of the floating hydrophytes are either shiny and waxy (*Limnobium*, *Eichhornia*), indicating the presence of a cuticle, or covered in hairs (*Pistia*). The cuticle (figure 8.2 & 8.3) and leaf trichomes (figure 8.4) repel water and prevent stomatal clogging. *Eichhornia*'s petioles are bulbous and inflated while *Pistia*'s leaves are furrowed, both of which aid in buoyancy. The leaves of *Limnobium* and *Eichhornia* are broad to optimize sunlight exposure. The roots of the pleustons are thin, fibrous and flexible for movement with water currents. Vegetative propagation is accomplished in *Limnobium* through stolons (Pandey & Chadha, 1998).

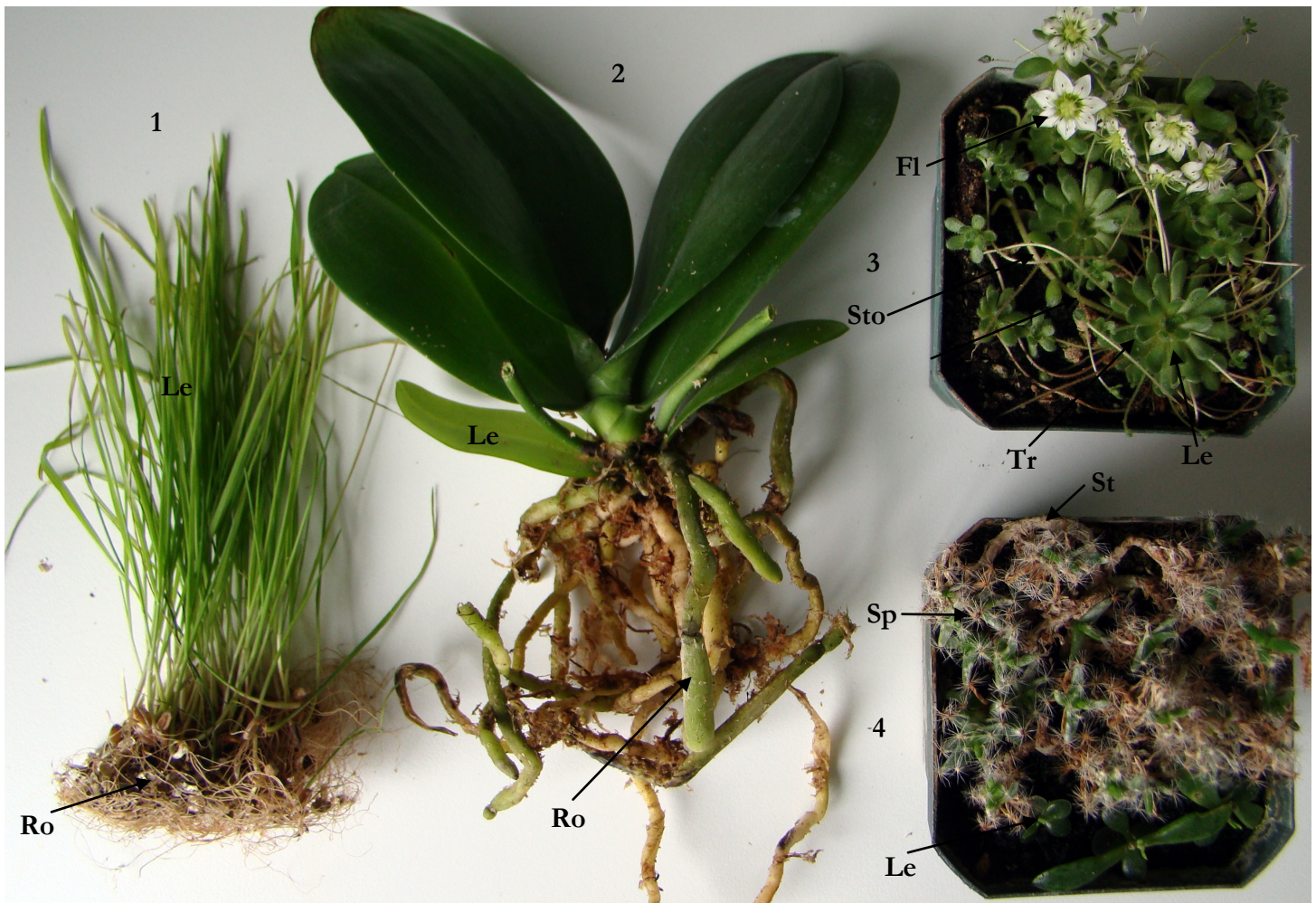


Figure 9: Frontal view of *Triticum* (1) and *Phalaenopsis* (2), and surface view of an unknown succulent (3) and *Trichodiadema stelligerum* (4).

Structures of interest include the root (Ro), leaf (Le), flower (Fl), stolon (Sto), trichome (Tr), stem (St) and spine (Sp).

The root system of *Triticum* is extensive and shallow to increase water uptake (figure 9.1). *Triticum*'s leaf blades are rolled to reduce transpiration. Leaf succulence (indicated by fleshiness) can be seen in *Phalaenopsis*, the unknown succulent and *Trichodiadema*. As well, root succulence is prominent in *Phalaenopsis* (figure 9.2). Certain roots of *Phalaenopsis* are photosynthetic (indicated by their green color) and rounded in shape to minimize transpiration through the surface. *Phalaenopsis* and *Trichodiadema* leaves are shiny due to the presence of a waxy cuticle. The cuticle reflects light, thereby lowering leaf temperature and transpiration. Trichomes can be found on the leaf surface of the unknown succulent (figure 9.3) shield it from excessive illumination and trap moisture. The spines (modified leaves) of *Trichodiadema* provide shade and further lower plant temperature to reduce transpiration. The woody growth in figure 9.4 is a means of resisting wilting and limiting transpiration. Reproduction in xerophytes is largely vegetative (e.g. through stolon growth), however, flowering may occur in suitable conditions (Pandey & Chadha 1998; G. Toole & E. Toole, 1999).

Macro Differences

There appears to be a trend toward more flexible and flaccid structures in the hydrophyte and more mechanical tissues in the xerophyte. Unlike certain xerophytes, hydrophytes do not exhibit succulence. Many adaptations in xerophytes are meant to reduce transpiration, while the adaptations of hydrophytes are in place to mitigate water stress and maximize photosynthesis. Trichomes are present to trap moist air in xerophytes and to create air pockets for buoyancy and stomatal opening in hydrophytes. It is clear that hydrophytes and xerophytes are well-suited for their environments, which may be why vegetative propagation is the dominant method of reproduction.

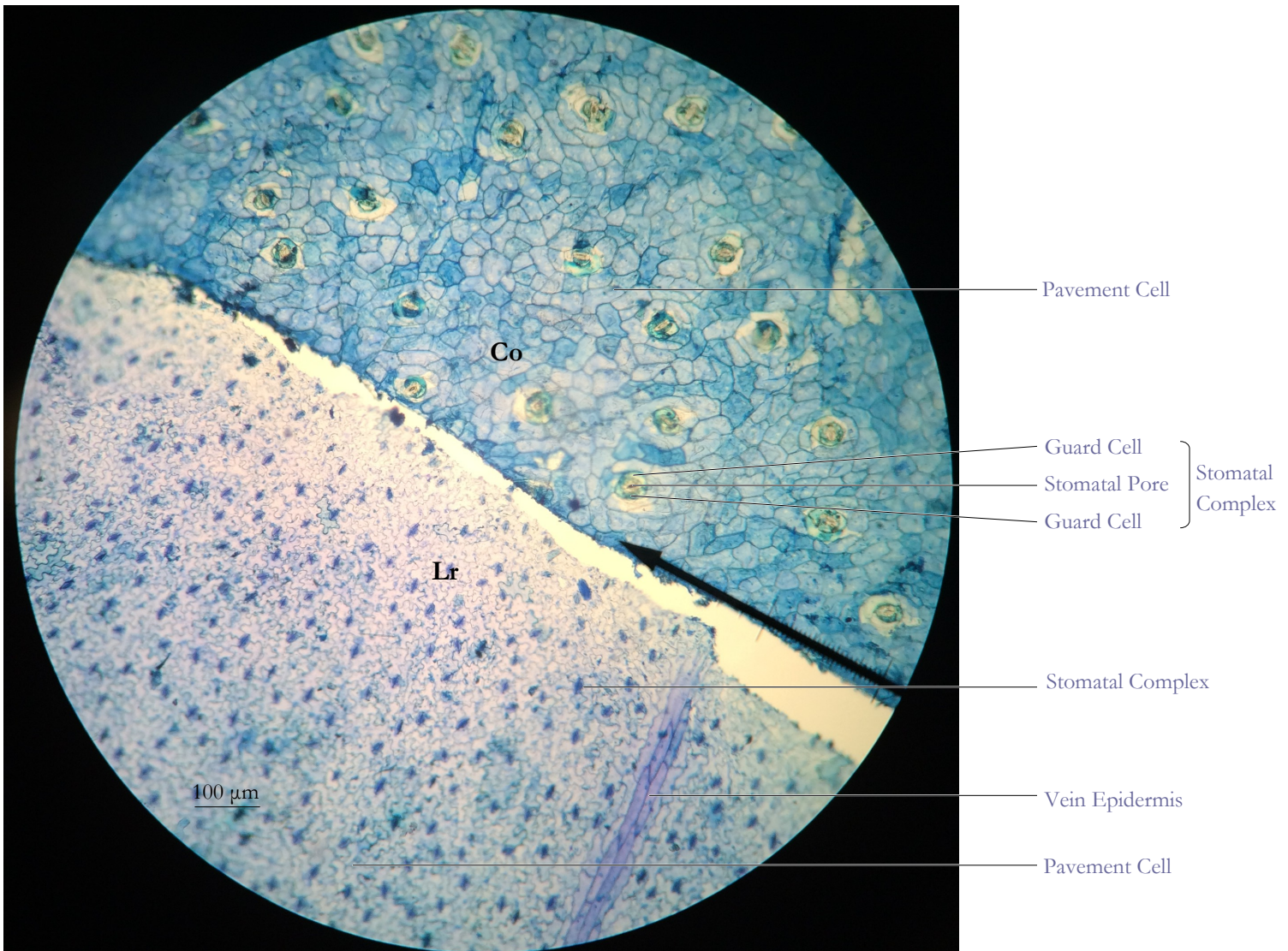


Figure 2: Stomatal peel of *Ludwigia repens* (Lr) and *Crassula ovata* (Co) leaf adaxial epidermis

The section was peeled free-hand, stained with Methylene Blue and viewed at 100x magnification (10x objective).

Micro Differences in Leaf Epidermis

Crassula ovata has a larger stomatal aperture but lower stomatal density than *Ludwigia repens*. It is worth noting that the leaves of *Crassula* also have a lower surface area (in relation to volume) to begin with. Stomatal density cannot be reduced invariably, since gas exchange is required for photosynthesis. Thus, the stomatal density seen here is most likely a function of photosynthetic requirement and how much water needs to be conserved in addition to how much water is already being conserved through other means (e.g. decreased surface area). On top of this, *Crassula* employs CAM photosynthesis, which means stomata are only open during the night anyway. Meanwhile, the hydrophyte *Ludwigia* can afford to develop abundant stomata. The function of the stomata is, however, unclear; stomata become clogged when immersed in water, and gas exchange occurs directly through the epidermis in submerged hydrophytes (). The stomata may be vestigial structures, similar to those of *Potamogeton*. Although it is interesting to speculate the evolutionary reasons for epidermal anatomy, stomatal density is by no means a definitive measure of xerophytic or hydrophytic character. Other factors such as CO₂ concentration, light intensity, photoperiod and temperature are also involved in determining stomatal density (Khan, 2001; Pandey & Chadha, 1998).

Notes:

1. Free-hand sectioning was performed following the techniques described by Glime and Wagner, 2013.
2. Sass's Safranin O and Fast Green FCF staining protocol was used