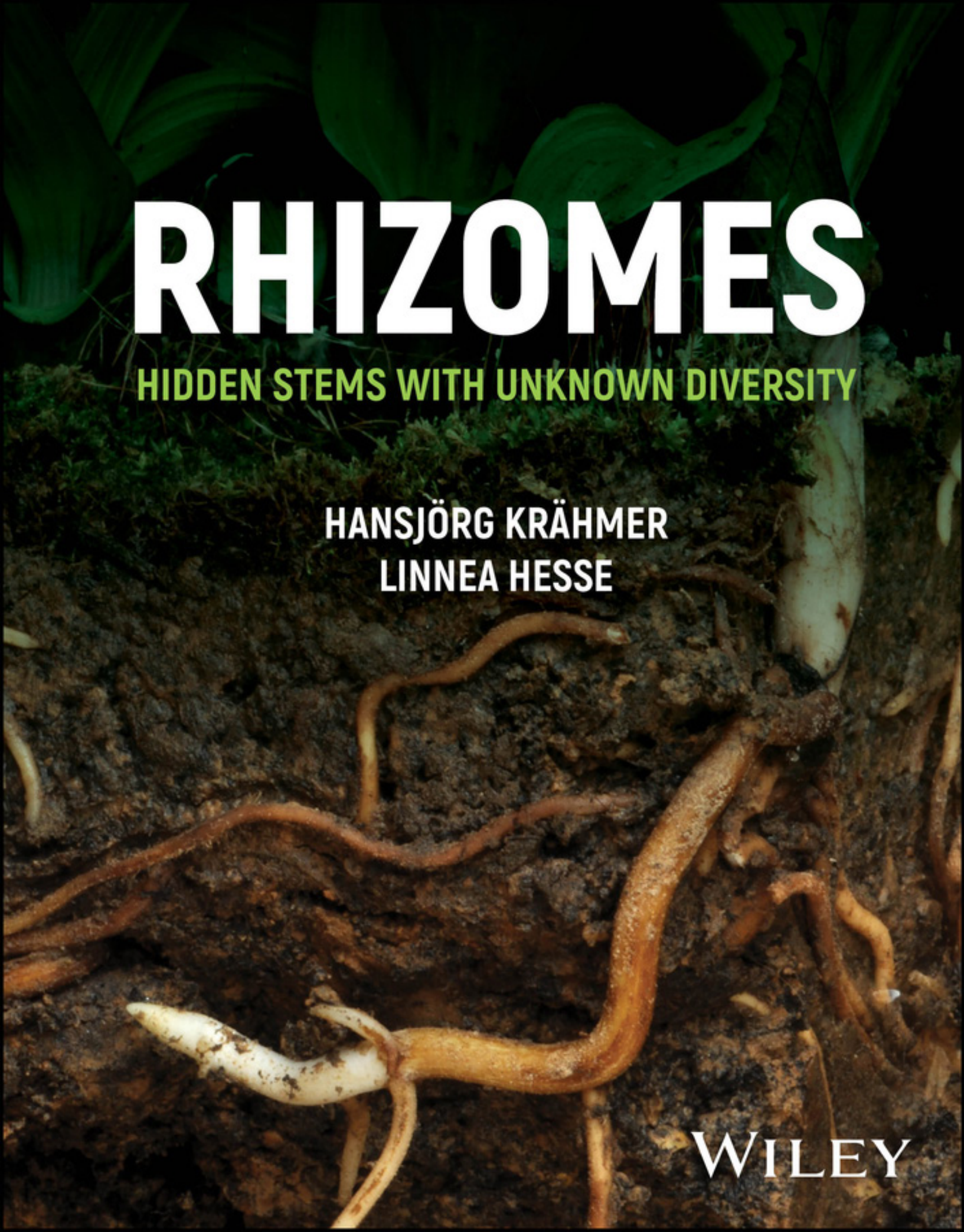
RHIZOMES
HIDDEN STEMS WITH UNKNOWN DIVERSITY
HANSJÖRG KRÄHMER
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Rhizomes

Rhizomes

Hidden Stems with Unknown Diversity

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Preface

A few years ago, an agronomy professor asked me about the difference between a root and a rhizome. To him, both looked very similar. His question was the starting point for this book. I quickly realized that a detailed histological analysis of rhizomes was missing in literature. To my surprise, the definition of a rhizome was not an easy task, and terms such as stolons, runners, corms, stem tubers and bulbs are often mixed up in literature. Very soon, I became aware of the fact that the anatomy of underground stems can differ considerably from that of above-ground stems. So far, botanists used to define just one type of stele in stems of a given species. I realized, however, that in many species stem steles may vary considerably depending on where they are formed, especially in monocots. Another so-far-accepted view was that vascular bundles are equally distributed in monocot stems. Our observations led us to the conviction that vascular bundle patterns depend on their initiation by leaf primordia in the first instance. They may indeed be equally distributed in the stem of some species. In many cases, however, they are arranged in ring-like patterns. Also, some botanists claim that the separation of a cortex and a central vascular bundle ring is not possible in monocots. Of course, species without cambia will not form round and coherent central phloem and xylem structures as they exist in many eudicots. It became, however, obvious to us that a separation of cortex and a central vascular cylinder is quite common in monocot rhizomes. Distinct borders separate both areas in several monocot species. Another intriguing phenomenon is that cells between rhizome cortex and central cylinder can stay meristematic and they can lead to secondary growth.

Some well-defined terms for roots such as endodermis and pericycle are often applied to similar structures in stems. As long as it is not clear whether vascular systems of roots and stems can be regarded as homologous, one can discuss the synonymous use of both terms. Separation layers between cortex and vascular bundle cylinder in above-ground stems look, however, often so similar to a root endodermis and contain typical Casparian strips that this term may be used unscrupulously from our point of view when highlighting the functional meaning of this layer. The most fascinating and still not completely understood vascular bundle system is that of rhizomes in the Nymphaeales order. Therefore, we placed the description of water lilies at the end of the plant orders analysed. They are often regarded as links between early angiosperms and monocots due to assumed similar vascular bundle systems. Our observations make us, however, believe that at least the vascular bundle system of *Nymphaea* species has not much in common with that of monocots and that their bundle pattern differs considerably. These are just a few aspects we became aware of within the recent years. We confirmed many results found by earlier botanists. At the same time, we regard many of our findings as new and hope our book will contribute to a better understanding of the construction of rhizomes. At the same time, we know that our overview is by far not complete. We strongly hope that our book can motivate more colleagues to look into the reasons for the modification of rhizomes as hidden and still secret stem parts in soil and water.

Hansjörg Krähmer

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I also thank my colleagues at Bayer AG who gave me access to literature and to plant material. Of particular mention are Stephan Engels, Vanessa Kroker and Hans-Georg Schumacher who assisted me again with plant material just like with my previous books. Other colleagues who kindly provided me with specimens were Alicia Cirujeda from the Departamento de Sistemas Agrícolas, Forestales y Medio Ambiente in Zaragoza, Spain, and Simon Pfanzelt from the Botanical Garden München-Nymphenburg, Germany.

Elisabeth Graaff of the Rheinlandgemüse Hydro GmbH & Co. KG in Vettweiß, Germany, discussed with me the propagation of rhubarb illustrated with several instructive pictures.

Again, I experienced the professional support from my counterparts in Wiley I was already familiar with from the preparation of other books before.

Finally, I would like to stress that I could only complete my contributions to our book with the backing of my wife Ulrike. On many of our walks, she stimulated me to collect plants and to analyse them. She was often the first to detect a species I was looking for. Ulrike tolerated all my investments in plant material I privately bought from garden centres, and she accepted that I spent many days just with dissecting plants and writing book chapters, thereby more or less neglecting the rules of a regular family life.

Part I

Introduction

1

Introduction

1.1 The Role of Rhizomes in Agriculture and Pharmacology

Plant rhizomes play an important role in agriculture and in food production. Some vegetables such as asparagus form rhizomes. This is also the case for some sugar cane varieties (Matsuoka and Garcia 2011). Rhizome tubers of potatoes, of yams (*Dioscorea* species) and of ginger (*Zingiber officinale* Roscoe) are consumed as food.

Several plant rhizomes produce natural substances which are used as drugs or drug precursors. Pharmacognosy books and books on medicinal plants are full of examples such as a textbook by Singh and Sharma (2020). In this book, compounds derived from rhizomes of *Asparagus*, *Colocasia*, *Curcuma*, *Dioscorea* and *Zingiber* species are described.

Many troublesome weeds spread via rhizomes such as purple nutsedge: *Cyperus rotundus* L., quackgrass: *Elymus repens* (L.) Gould, cogongrass: *Imperata cylindrica* (L.) P. Beauv, johnsongrass: *Sorghum halepense* (L.) Pers. or itch grass: *Rottboellia cochinchinensis* (Lour.) Clayton.

1.2 Characterization of Rhizomes in Literature

A rhizome is defined by Bell (2008) as 'A stem growing more or less horizontally below ground level. Rhizomes tend to be thick, fleshy or woody, and bear scale leaves or less often foliage leaves, or the scars when these leaves have been lost; they also bear adventitious roots most frequently at the nodes'. Troll (1935) stresses that rhizome internodes are stunted. Also, he highlights homorhizy as characteristic of rhizomes. He does, however, not mention the horizontal growth. This makes sense as the rhizomes of several plant species do not grow horizontally as we will show later.

The amount of comparative English synoptic literature on rhizomes is quite restricted.

Only few articles discuss general characteristics of rhizomes. One is Holm's article on the application of the term 'rhizome' (1929).

Burkill (1960) claims that the term rhizome was introduced to science by the British botanist Ker-Gawler without any reference. According to Burkill, a rhizome is characterized by its cauline nature, by horizontality and by thickness. The term thickness is, however, not specified. Ehrhart (1787) uses the term rhizoma for *Polypodium oreopteris* syn *Oreopteris limbosperma* (All.) Holub and makes clear that this fern rhizome is different from a root.

Unfortunately, most classical textbooks on plant anatomy just contain a few lines on rhizomes. Esau (1977) even does not mention them. Troll's German textbook on general botany (1973) is an exception insofar as it provides a few detailed and illustrated explanations. In volume 1 (1935) and volume 3 (1943) of his 'Comparative Anatomy of Higher Plants', Troll devotes several chapters to rhizome characteristics, especially to adventitious roots. Von Guttenberg (1968) created various histological illustrations on the formation of rhizome roots.

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In Arber's book on monocotyledons (1925), rhizomes are only referred to briefly. Her grass book (1934) contains a few details on bamboo and grass rhizomes. Other classical anatomy compilations of monocot plant orders or families contain short paragraphs on the anatomy of rhizomes only. Metcalfe (1971), for example, lists just a few general characteristics of the rhizomes of sedges. The general morphology of grass rhizomes is described by Metcalfe (1960) in two sentences only. His first statement 'Grass rhizomes, in species where these subterranean stems are well developed, are essentially similar in structure to the culms' can, however, no longer be supported. Kraehmer (2019) demonstrates that underground stems of some grasses may look quite different compared with above-ground culms. Tomlinson (1961, 1969, 1982) characterizes rhizomes of representatives in the Zingiberales order or in the former group Helobiae. Cutler (1969) reserves a few lines for representatives of the former Juncales order. Ayensu (1972) discusses the characterization of rhizomes in the order Dioscoreales on two pages.

Some of these authors admit that structures of monocot rhizomes deserve further investigations. When it comes to the description of the outer part of the stele and to the growth of the rhizome, Metcalfe (1971) concludes 'The reader's attention is drawn to this, more in the hope that the subject will receive further investigation on ontogenic lines than because the author feels certain about it'.

On the other side, it must be stressed here that several anatomical rhizome descriptions of selected species or groups were published within the last decades. This is the case for several agricultural weeds such as for *Cyperus* species, *Elymus repens* (L.) Gould syn *Agropyron repens* (L.) P. Beauv., *Imperata cylindrica* (L.) Raeusch., *Rottboellia cochinchinensis* (Lour.) Clayton, *Sorghum halepense* (L), for invasive weeds such as *Arundo donax* L., for aquatic monocots or for bamboo. Literature on these groups was summarized by Kraehmer and Baur (2013) and Kraehmer (2016, 2019). A more systematic and comparative approach to the anatomy of rhizomes was provided for a few groups such as, for example, for the family Iridaceae (Rudall 1984) or for Marantaceae (Tomlinson 1961).

A recently published book designed for archaeologists in the first instance provides an interesting compilation of a few facts and principal considerations on rhizomes (Hather 2017). It contains some findings we will elaborate on here more in detail. Also, we will try to cover many aspects not specified in this book with a 'detailed description of the morphological and anatomical characters used in the identification of charred vegetative parenchymous organs'.

A number of terms for stem modifications are used in literature without precise definitions.

A clear distinction between rhizomes, runners and stolons is for example not easy. Troll (1935) defines a runner as a lateral shoot of basal leaves that develops in a peculiar form insofar as it grows along the soil surface and that it has prolonged internodes. In his chapter on potato runners, he distinguishes, however, between below-ground and above-ground runners. He uses the term stolon in this context also. Bell and Tomlinson (1980) discuss the term rhizome in a general way including organs such as stolons, offsets, or suckers which may intergrade with tubers and corms. We will try to find criteria which allow a distinction between several existing rhizome modifications.

Unfortunately, we can only use selected species here for general conclusions. We will try to describe rhizomes of lycophytes, ferns and monocot, eudicot, ANA grade and magnoliid species separately. We will then concentrate on differences between these groups.

We will begin with lycophyte and fern rhizomes as these plant groups are assumed to be related with the evolutionary early tracheophytes. We will continue with monocot rhizomes as these often differ considerably from above-ground stems. The anatomical differences between dicot rhizomes and above-ground stems are less pronounced in many cases as we will see. Among the gymnosperms, rhizomes are only those found in the Gnetaceae family (McLean 1950).

1.3 Rhizome Anatomy

Rhizomes of many eudicots can be divided into an outer cortex and an inner central bundle cylinder. Falkenberg (1876) discusses the question if this distinction is also possible for monocot stems as bundles in monocots may be distributed all over the stem section. This question can, however, be answered easily for most rhizomes as Von Guttenberg (1943) explained and as we will see later in our book.

The innermost cortex cells of rhizomes often differentiate into a sheath that can appear in different modifications. This sheath, for example, can be differentiated as a starch sheath or as an endodermis with Casparian strips. It is often part of a boundary that is differentiated in a characteristic way. Lateral roots may arise from this boundary. In consequence, some authors use the same boundary terminology for roots and rhizomes. Following Esau (1977), we believe that the undifferentiated use of the two terms endodermis and pericycle is not always justified, neither for above-ground stems nor for rhizomes.

Many authors have applied these terms for stems in the past. Troll (1943) uses the terms endodermis and pericycle when describing below-ground and above-ground stem boundaries.

Von Guttenberg (1943) applies the term endodermis in his German overview of plant sheaths to all kinds of sheaths in roots, stems and leaves. He even provides a list of plant orders with an endodermis in shoots ('Sproßendodermen'). With others, he uses it as a functional term. In some cases, he calls non-suberized sheaths starch sheaths. He clearly distinguishes, however, an endodermis from the exodermis of roots which he defines as a hypodermal layer following the rhizodermis in his book on primary roots of angiosperms (Von Guttenberg 1968). He admits on the other side that some scientists actually named the exodermis 'outer endodermis' in the 19th century.

A few molecular biologists see similarities between the root endodermis and the exodermis (Geldner 2013). Based on the existence of Casparian strips, these similarities could justify the classification of the exodermis as a layer with the function of an endodermis.

Leersten (1997) highlights the occurrence of an endodermis in stems and leaves and provides an update on 20th-century literature. He stresses that from his point of view, the term endodermis can just be defined based on its function as a border.

On the other side, position and ontogeny often lead to the use of different expressions for structures which are similar to an endodermis: the exodermis as a hypodermal sheath, the mestome sheath as a special layer in leaves, the starch sheath as a border between cortex and vascular cylinders in many stems.

The identification of an endodermis is rather easy in roots. Initially, it contains lignin and at later developmental stages suberin which can easily be stained. For stems, it is, however, more complicated. A recent overview of the endodermis in angiosperm shoots (Seago 2020) claims the occurrence of sheaths with Casparian strips in 95 plant species. Its depictions often show, however, cells in a secondary or tertiary stage but not true Casparian strips as defined, for example, by Evert (2006) or Esau (1977). Also, this paper does not reflect on the ontogeny of sheaths and the position of an endodermis in stems when compared with that in roots.

Some authors attribute the monocot endodermis meristematic properties leading to secondary growth as, for example, in *Cyperus* rhizomes (De Menezes et al. 2005). Kroemer (1903) and Bond (1930) report on dividing endodermis cells in dicot roots. Also, endodermis and endodermis-like structures of angiosperms are often associated with meristematic cell layers. Esau (1977), however, stresses that the endodermis is usually uniseriate with the exception of a few dicot species with secretory canals. She defines a structure that is usually associated with the endodermis of roots and shows a meristematic character: the pericycle. She defines the pericycle as the limiting layer of the stele. Within the root, it arises from the same part of the apical meristem as vascular tissues. Some authors call this layer pericambium as, for example, Von Guttenberg (1968).

The pericycle of eudicot and monocot roots can easily be defined. It surrounds the coherent elements in the case of actinostelic centres and forms the outer layer of the stele. It is located between endodermis and stele.

The definition of a pericycle in above-ground eudicot stems becomes, however, much more complicated when considering various stem specificities. Vascular bundles often do not form a coherent vascular bundle cylinder. Endodermises, endodermoids and starch sheaths can often not be identified in stems at all.

Foster and Gifford (1974) make clear that 'the pericycle is not present in all vascular plants' and that the 'so-called pericycle in the stems of many angiosperms is actually the outermost portion of the primary phloem'. Metcalfe and Chalk (1965) use the terms pericycle and pericyclic regularly for stems despite declaring in their introduction: 'In the stems of many plants, the "pericycle" is not clearly defined, nor, in fact, is there any general agreement concerning the precise meaning of this term. There is, nevertheless, a portion of the stem between the inner boundary of the primary cortex and the outer part of the primary phloem in which mechanical elements usually arise'. Stover (1934) uses the term pericycle for peripheral sclerenchyma layers in grass stems. His understanding of a pericycle has nothing in common with the definition of a layer of meristematic cells.

As already stated above, monocot rhizomes and above-ground monocot stems do not form coherent xylem or phloem layers at all. It is impossible therefore to find coherent 'primary phloem or xylem' in monocots.

On the other side, separation layers between a cortex and a central bundle cylinder are quite common in monocot rhizomes. Their origin can, however, not be associated with an endodermis or a pericycle in a root as we believe.

The term pericycle is also used in descriptions of the rhizome of ferns. The position and function of fern pericycles are, however, quite different from that of pericycles in eudicot and monocot roots. Ogura (1972) defines the fern pericycle as 'a zone between the phloem and the endodermis, consisting of one or more parenchyma layers which are more or less larger than the cells of the phloem or endodermis'.

We will discuss the term pericycle in Chapter 11 and at the end of our book again (Chapter 22).

The boundary layer between the rhizome cortex and the central vascular bundle cylinder is sometimes accompanied by a primary thickening meristem (PTM, Rudall 1991). Roots often arise from this boundary.

Weber (1936) distinguishes between different types of species with stem-borne roots:

- dicot representatives with roots arising from the hypocotyl,
- plants with roots at nodes,
- those with roots at internodes,
- species with roots at buds.

Rhizome boundaries often differ considerably from root boundaries. Mangin (1882) proposes the term 'couche dictyogyogène' or dictyogenous layer for the rhizome cortex border with the intention to characterize its special anatomy. The Greek word δίκτυον means 'net'. The term can therefore be translated as a 'net-forming layer'. The resulting layers of vascular bundles and fibres are the result of anomalous thickening and of root extensions. We will show examples later. Other than Von Guttenberg (1968), we do not regard the dictyogenous layer as equivalent to the pericycle.

Boundaries are often not found at early rhizome stages and not in all monocot rhizomes. The anatomy of borders can vary considerably during plant development. In many cases, an endodermis, endodermoid or starch sheath is only formed at advanced developmental stages.

The secondary formation of roots requires meristematic cells such as the cells of the pericycle in the root. Within *Arabidopsis* roots, the role of pericycle cells was investigated on a gene expression level. The pericycle is regarded today as a site where plant stem cells are able to generate new tissues (Perez-Garcia and Moreno-Risueno 2018).

When using terms for stem sheaths separating cortex and central vascular cylinders, we often tend to follow Tomlinson (1969), Metcalfe (1971), Rudall (1984), Kraehmer and Baur (2013) and Kraehmer (2019) who prefer the term endodermoid instead of endodermis when analysing organs other than roots. We use this term especially for rhizomes in which we cannot find characteristic Casparian strips with our methods employed when they just look like starch sheaths or when the border between cortex and cylinder is not closed. Some authors called border layers between cortex and cylinder phloeoterma (Von Guttenberg 1968).

It should be noticed here that earlier Marantaceae rhizome descriptions of Tomlinson (1961) contain the term endodermis whereas later ones (1969) use the term endodermoid presumably due to changing insights.

The inner bundle sheath of many grass leaves has characters of an endodermis (Brown 1958). Schwendener (1890) had called these sheaths mestome sheaths. Again, this term has to do with its special location within a leaf. Also, its surrounding is quite different from that of an endodermis in roots.

Unfortunately, the term endodermoid is not accepted by several scientists. Van Fleet (1961), for example, was a strong opponent of it. We will try here to justify our view on terminologies used for boundaries between cortex and central cylinder of monocot rhizomes based on our own findings.

Also, we will demonstrate that the structure of underground monocot rhizomes is usually quite different from that of regular aerial stem parts.

Some above- or near-ground stems may adopt or keep features of underground rhizomes (Bell and Tomlinson 1980) such as the formation of stem-borne roots. This fact makes it difficult to distinguish in a clear way between rhizomes and regular, above-ground stems.

A very exact definition is apparently not always possible. It appears that scientists from the 18th and 19th centuries were already aware of this. The word rhizome contains the Greek origin ῥίζα (rhiza), meaning root, and tells us presumably just that a rhizome looks similar to a root.

1.4 Genomics of Rhizomes

Within the last decade, molecular geneticists have started to analyse molecular mechanisms

and signalling processes leading to stolon and rhizome initiation and development (Guo et al. 2019). Gene mapping data and transcriptome sequencing results were published for several rhizome-producing species such as *Phyllostachys praecox* (Wang et al. 2010), *Oryza* species (Hu et al. 2011), *Phragmites australis* (He et al. 2012), *Miscanthus* species (Kim et al. 2014), *Sorghum* species (Zhang et al. 2014) and for *Nelumbo nucifera* (Yang et al. 2015).

We will reserve a chapter for the discussion of these new insights into molecular regulatory mechanisms in rhizomes.

Rhizome-producing species may form large colonies or groups of genetically identical individuals. Examples are bamboo forests (Fig. 1.1) or clones of perennial weeds in arable fields such as of perennial *Cyperus* species or of *Sorghum halepense*. Advantages and disadvantages of such 'uniform' units will be discussed later.

Figure 1.1 Little bamboo forest of *Phyllostachys flexuosa* clones in the Botanical Garden of Frankfurt am Main (Germany).

Many open questions and a missing up-to-date overview on rhizomes make it worthwhile from our point of view to summarize all these aspects and to provide a compilation that shows what rhizomes of different plant groups have in common and which features are species- or group-specific.

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2

Evolution of Rhizomes and Their Distinction from Similar Plant Organs

2.1 Rhizomes of Early Vascular Plants

Plant rhizomes developed quite early in evolution. Some plant species found in the 396-million-year-old Scottish Rhynie Chert lacked roots (Kenrick 2002). Absorption of water and nutrients was presumably achieved by rhizoids on prostrate stems or early rhizomes. A developmental distinction between rhizomes and stems is often not possible in these findings. The extinct Devonian group Zosterophyllophyta was characterized by much branched rhizomes. Dormant meristematic regions in these rhizomes were able to develop into erect stems. Rhizomes of species in the genus *Asteroxylon* (Lycopodiopsida) were leafless unlike stems. The stem bundle pattern differed from that of rhizomes. Carboniferous horsetails of the genus *Calamites* developed thick, horizontal rhizomes of up to 40 cm diameter with roots in whorls at nodes.

Apparently, modified stems took over the role of roots which developed later.

The role of modern tracheophyte rhizomes must be seen differently. Rhizomes of monocot and eudicot species evolved independently from the above-mentioned extinct plant groups.

2.2 Rhizomes as Characteristic Attributes of Different Plant Growth Forms

Scientists of the early 20th century tried to characterize plants according to their life and growth forms. Raunkiaer (1934) for example classified plants according to their ability to survive unfavorable seasons with either drought or cold temperature. He grouped plants based on the arrangement of buds or shoot apices in the air (phanerophytes), close to the ground (chamaephytes), in the soil surface (hemicryptophytes) or buried in the ground (cryptophytes) and regarded annuals as a separate group. One subgroup was defined as "rhizome-geophytes." Characteristics of many cryptophytes are underground organs such as bulbs, tubers and other storage organs. A recent review highlights the complexities of belowground organs in geophytes (Tribble et al. 2021). It stresses that geophytism has evolved multiple times in different plant groups.

Prostrate, above-ground shoots, so-called runners, are typical of the hemicryptophyte group. Unfortunately, some species develop above-ground runners and horizontal shoots often entering the ground, which may also be called stolons. Raunkiaer (1934) mentions in this context some *Epilobium* species, *Urtica dioica* L., *Lysimachia vulgaris* L. or representatives of the Lamiales order.

Troll (1935, 1973) uses the term geophyte for perennial plants with storage organs and regeneration buds below or near ground. He distinguishes between three forms of storage shoots: rhizomes, bulbs and tubers.

Rhizomes: Hidden Stems with Unknown Diversity, First Edition. Hansjörg Krähmer and Linnea Hesse.
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German speaking botanists created a large number of new terms in the attempt to classify plant growth forms in the last century. Examples are the classification of different growth forms of shrubs (Rauh 1938), of forbs and of trees (Kästner and Karrer 1995; Krumbiegel 2002). Some of the terms employed were never translated from German into English or they are not used by papers written in English. We will try to explain why this is the case for selected terms such as the term pleiocorm as defined in Section 2.3.

2.3 Glossary and Distinction of Rhizomes from Similar Plant Features

Based on definitions of Anderson (1999), Barclay (2002), Bell (2008), Simpson (2010) and Kraehmer and Baur (2013) we try to define now a few characteristic organs which allow their distinction from rhizomes. The literature definitions of runners and stolons and the synonymous use of these terms lead to some doubts, and we prefer to use them separately for practical reasons:

- **rhizome: below ground stem with roots and morphologically or histologically differing from above ground stems.**
  The rhizomes of many different plant species do not grow horizontally as the rhizome definition of Bell (2008) claims. In the following chapters, we will show a number of examples with vertical rhizomes or rhizomes growing in all directions. Also, we believe that a few specific characteristics allow the distinction of rhizomes from above ground stems, such as the lack of chlorophyll, the development of roots along whole rhizomes and missing flowers.
- **rhizome tuber: a thickened below ground rhizome portion.**
  We would like to use the term rhizome tuber for thickened underground stems in accordance with Gregory (1965). Unfortunately, it is quite difficult to define in a measurable way what thick and thin means in this context.
- **aerial rhizome: above ground, rooted and more or less horizontally growing stem portion.**
  This form of above ground rhizomes occurs in some plant groups such as orchids or *Monstera* species and has to be regarded as an exception of the rule that rhizomes are below ground stems. Traditionally, these organs were, however, defined as rhizomes by many botanists. This is why we include them in our list of rhizome types even if this may not look logic.
- **caudex**: "**a short, thick**, vertical or branched **perennial stem**, underground or at/near ground level" (Simpson 2010). A caudex sample is shown in Fig. 2.4. A more detailed description follows in part 4 (Fig. 14.10).
- **rootstock:** "a **general term for an underground stem** or shoot" (Simpson 2010). This term is often equivalent to the term rhizome.
- **stolon: below-ground stem that forms a chain of internodes**, roots and cataphylls at nodes, and forms the next internode from the terminal bud at the last node in the chain.
  The term stolon is presumably derived from the Greek word στόλος (cohort, armada, entourage). Below-ground stems of potato are usually called stolons.
  With Gregory (1965), **we define here stolons as a special form of rhizomes**.
  Stolons are usually round and elongated. They often do not contain a closed cambium that results in secondary thickening.
- **runner:** prostrate, **above-ground chain of internodes**, forming new plants at each node, and giving rise to the next internode from an axillary bud in the leaf axil (one of two axillary buds at each node). Examples are strawberry, creeping buttercup (*Ranunculus repens* L., Fig. 2.1a) or ground-ivy (*Glechoma hederacea* L., Fig. 2.1c).
- **We do not regard runners as rhizomes.**

The runners of some species such as bermudagrass, *Cynodon dactylon* (L.) Pers. (Fig. 2.1b) or spider plant, *Chlorophytum comosum* (Thunb.) Jacques (Fig. 2.1d) are often called stolons as we also did when describing grasses in previous books (Kraehmer and Baur 2013; Kraehmer 2019). The spider plant produces flowers at nodes (Fig. 2.1d). This fact makes it necessary to differentiate above ground runners from below-ground stems which usually do not flower.

Stolons are not only formed by eudicots and by monocots. They are also characteristic of some fern species such as of *Nephrolepis exaltata* (L.) Schott (Fig. 2.2b).

Barclay (2002) creates a difference between the terms stolon and runner as he connects stolons with foliage leaves and runners with scale leaves. We regard this distinction as artificial as runners of strawberries and of bermudagrass both develop foliage leaves.

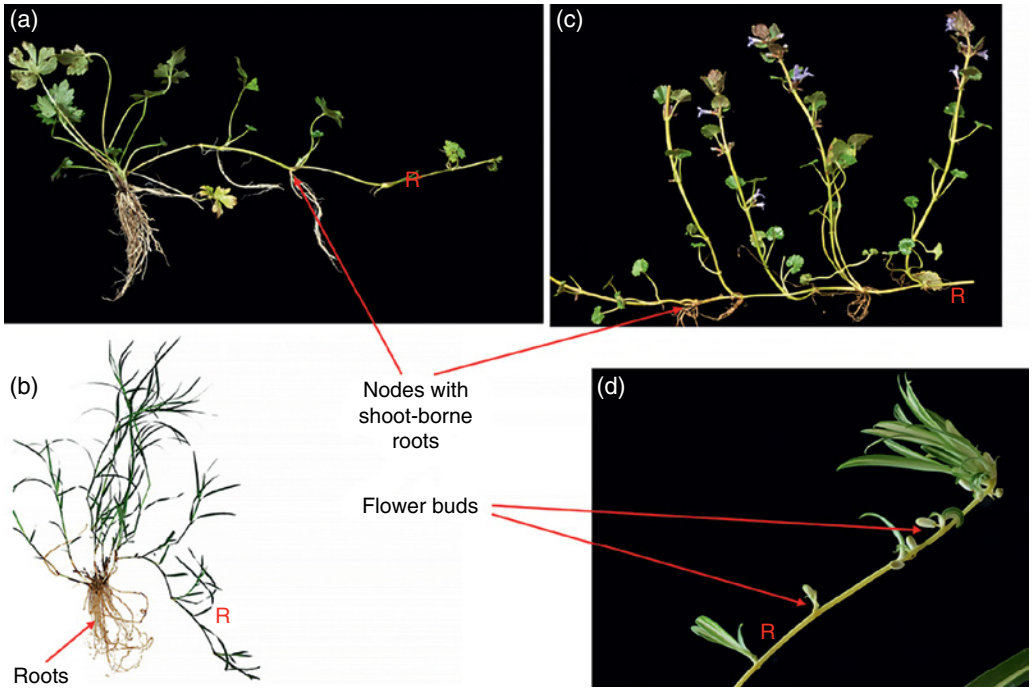

Figure 2.1 Runners of dicots and monocots. New plants and roots arise at nodes. (a) *Ranunculus repens*; (b) *Cynodon dactylon*; (c) *Glechoma hederacea*; (d) *Chlorophytum comosum* with leaves and flower buds at nodes. R runners.

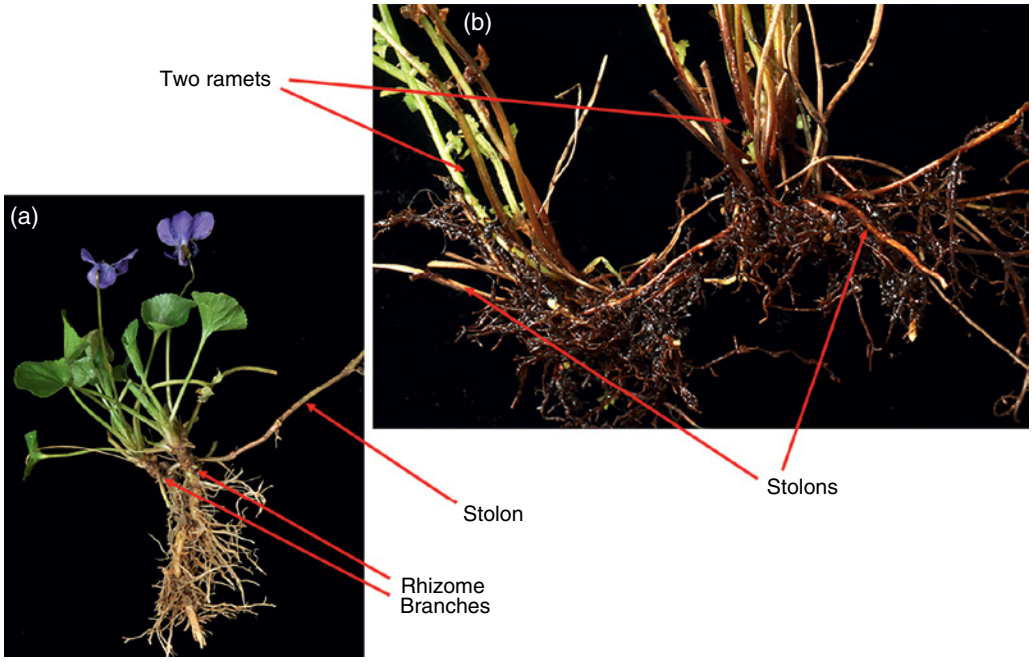

Figure 2.2 (a) *Viola odorata* with branched rhizome and stolon; (b) stolons of the fern *Nephrolepis exaltata*.

Scales are rather characteristic of rhizomes. Stevens (1966) shows that literature often uses different terms for the same organs with different examples.

Stolons and runners are elements of the vegetative propagation of tracheophytes which can lead to large clones. Each individual of such a clone is called a ramet. We will discuss this phenomenon in a separate chapter (Chapter 19).

We would like to stress already here that a few species produce runners and stolons as well as rhizomes such as *C. dactylon* or *Viola odorata* L. The rhizomes of *V. odorata* by the way often grow vertically as Fig. 2.2 demonstrates.

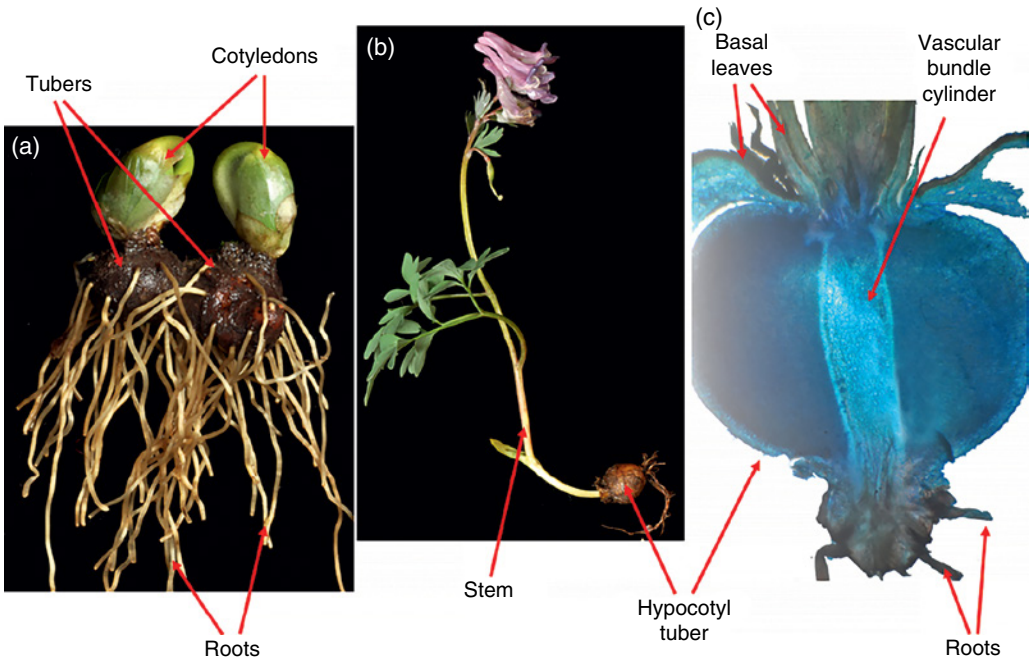

Figure 2.3 Hypocotyl tubers of (a) *Eranthis hyemalis*, (b, c) *Corydalis cava*; the picture at the right presents a longitudinal section (LS) at low magnification.

In some textbooks, all the terms stolon, rhizomes and runner are used synonymously (Judd et al. 2008). We do not follow this custom. We differentiate here clearly between above ground runners and below ground rhizomes. The anatomy of many above-ground stems may look completely different from below-ground ones as we will show. Simpson (2010) regards the rhizomes of ferns as so specific that he creates a separate, additional definition: "a horizontal stem of a fern that grows at ground level." We have come to the conclusion that not all fern rhizomes grow horizontally. It is, however, obvious that fern rhizomes are so different from those of seed plants that we cannot regard them as homologous to monocot or eudicot rhizomes.

A border case of a rhizome portion are dicot hypocotyl tubers such as that of winter aconite, *Eranthis hyemalis* (L.) Salisb. (Fig. 2.3a) of *Corydalis cava* (L.) Schweigg. & Körte (Fig. 2.3b, c), *Ranunculus bulbosus* L. (Fig. 2.4a) and of red globe radishes (Fig. 2.4b). Hypocotyls often show an anatomy very similar to roots. This is why we decided not to regard them as underground stems. More details for winter aconite were documented by Troll (1935, 1943).

In Chapters 13 and 14 we will show how some eudicot rhizomes develop and that some rhubarb species (such as *Rheum rhabarbarum* L. or *Rheum* hybrids) and some *Plantago* species start their development initially with a tuberous root or a tuberous hypocotyl first and form a rhizome later.

- **bulb:** an **underground,** perennial food storage organ consisting of a **stem axis and numerous overlapping leaf scales**; a bud with fleshy bracts or scale on a short conical stem, usually subterranean, containing food reserves.
- **corm: short swollen stem of several internodes and nodes** with either scale or foliage leaves; an example is the corm of autumn crocus, *Colchicum autumnale* L. (Fig. 2.4c) or that of taro, *Colocasia esculenta* (L.) Schott (Fig. 17.3).
- **pleiokorm/pleiocorm/pleiocormous:** a **system of** densely arranged and connected short **perennial shoots** of different ages located near the soil surface and **connected with the main tap root.**

This term was used by Meusel (1970) and Meusel et al. (1979) for special growth forms in the Caryophyllaceae family and in *Carlina* species or by Hagemann (1983, 1987) for the description of some *Hypericum* species. The terms Kormus and corm have different meanings in German and English. Kormus stands for the unit of stem, leaves and roots in German whereas a corm is a short, swollen stem as defined above in English. This fact may lead to misunderstandings. The term Pleiokorm (pleiocorm) as used by Meusel refers to stunted shoots and is in accordance with the

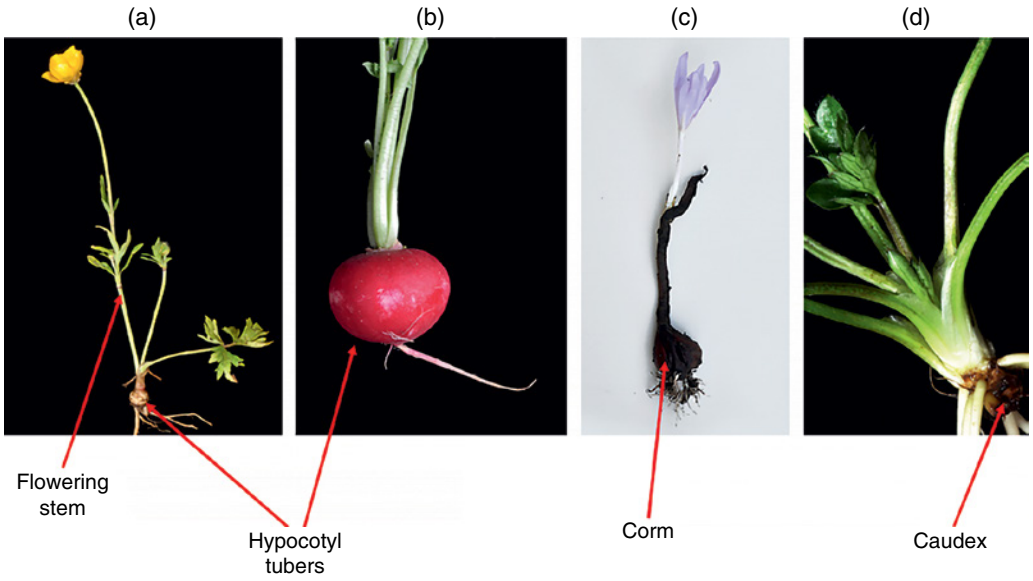

Figure 2.4 (a) Flowering *Ranunculus bulbosus* plant with hypocotyl tuber. (b) hypocotyl tuber of *Raphanus sativus* var. *sativus*. (c) Flowering *Colchicum autumnale* plant with underground corm. (d) caudex of *Ranunculus repens* L.

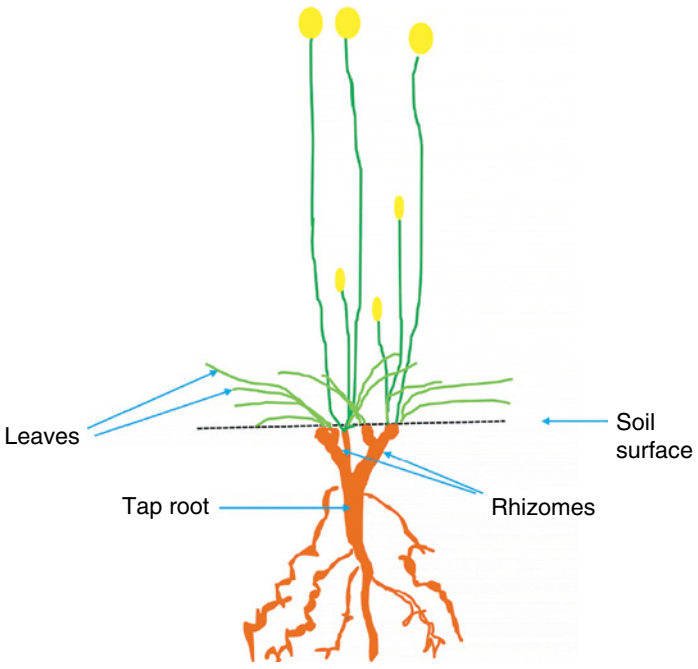

Figure 2.5 Rosulate, pleiocormous taproot-forb. *Source:* Kästner and Karrer (1995).

English meaning of corm. Kästner and Karrer (1995) described different pleiocorm-subtypes. We have selected the rosulate, pleiocormous taproot-forb as one example (Fig. 2.5) as we will use this type for the characterization of the growth form of *Plantago maritima* in Section 13.1.

A special case of rhizomes are submerged organs of wetland or aquatic plants as for example stolons analysed by Kraehmer (2016). These submerged stems are called stolons even if they are not covered by soil. They show the phenomenon of homorhizy with roots usually located at nodes (Fig. 2.6).

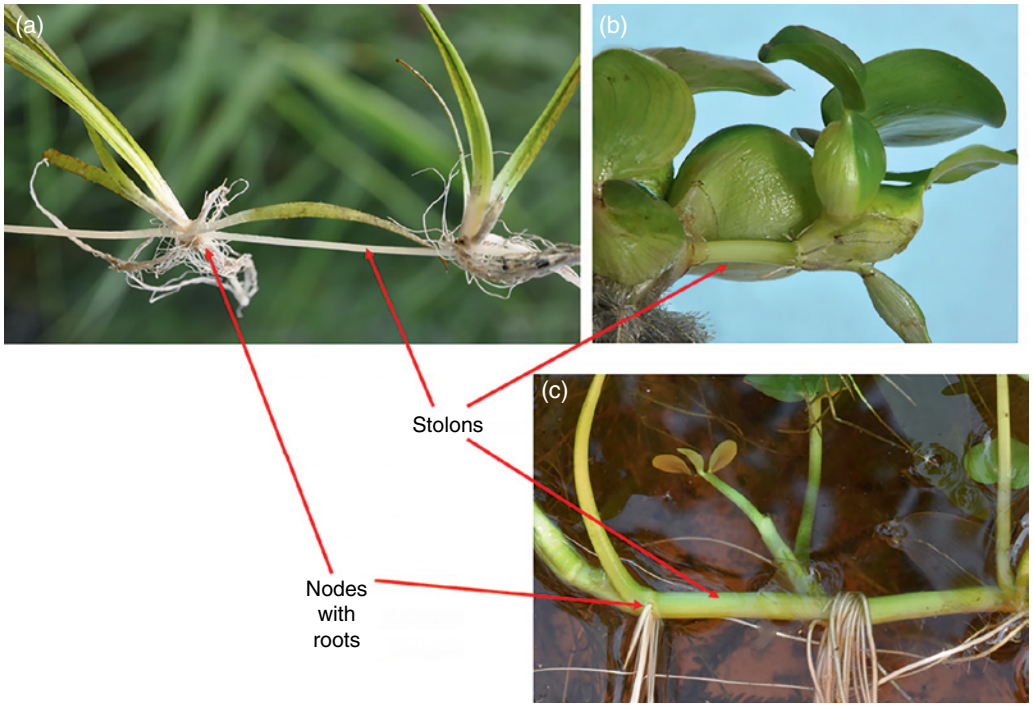

Figure 2.6 Submerged stolons of (a) *Vallisneria spiralis* L.; (b) *Eichhornia crassipes* (Mart.) Solms; (c) *Heteranthera reniformis* Ruiz & Pav.

2.4 Glossary of Terms for Characteristic Rhizome and Stem Features

In most cases, we follow the histological definitions of Esau (1977). As already outlined before, the border between cortex and the central vascular bundle cylinder requires a detailed description from our point of view.

With Esau (1977), we share the following view:

- In monocots and eudicots, the **endodermis is a sheath around a root or stem vascular cylinder.** It is the innermost layer of the cortex in roots and stems. Typical of the endodermis are so-called Casparian strips in its anticlinal walls. Usually, the endodermis is uniseriate.

With this definition, we accept that both, the exodermis of roots and the mestome sheath of leaves cannot be defined as an endodermis as these structures are not identical with the innermost layer of the cortex. They may have much in common with an endodermis such as Casparian strips and their function may be similar to that of an endodermis. They may even be coded by the same or similar genes as the endodermis. This criterion is, however, not sufficient for the definition of an endodermis from our perspective.

Von Guttenberg (1943) refers to authors who call the innermost cortex layer in stems "phloeoterma." We do not follow Onyenedum and Pace (2021) who declare: "In stems, the endodermis is typically recognized as the "starch sheath." On the other side, we will confirm the view of Seago (2020) that the endodermis is a quite common stem sheath.

The endodermis is formed from meristematic cortical cells (Esau 1977). The fully differentiated endodermis does not divide in contrast to what van Fleet (1961) claims. The ontogeny of the endodermis was already published by Von Guttenberg for different plant orders (1943).

In ferns (Polypodiopsida), **the endodermis encloses bundles or meristeles** (Ogura 1972).

- **Casparian strips or bands are special structures within primary cell walls containing lignin.** They lead to a band-like thickening of anticlinal cell walls.

In transverse sections, Casparian strips often appear as small stripes as in Fig. 2.7a.

In some cases, the actual bands can be visualized (Fig. 2.7b, c).