

Occurrence of Endodermis with a Casparian Strip in Stem and Leaf

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I. Abstract

It is well known that an endodermis with casparian strip always occurs in roots, but few people are aware that it also occurs in stems and leaves of some vascular plants. The rather sparse literature on endodermis in aerial organs was last included in a review in 1943. The present compilation, which does not consider hydathodes, nectaries, or other secretory structures, emphasizes distribution of cauline and foliar endodermis with casparian strip. It occurs unevenly among major taxa: quite common in rhizomes and leaves among pteridophyte groups, with exceptions; absent in gymnosperm stems but found in leaves at least among some conifers; in stems of at least 30 mostly herbaceous angiosperm families, but far less common in leaves, where it is mostly reported from petioles. Etiolation can induce casparian strips in stems and petioles of some herbaceous plants, but results from leaf blades are questionable. There are recent reports of an endodermis with casparian strip in leaves of both woody and herbaceous taxa. The physiological function, if any, of a casparian strip in aerial organs remains unknown.

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II. Introduction

Roots in the primary state of growth have an endodermis, the specialized innermost cell layer of the cortex. Newly mature endodermal cells always have a casparian strip (c.s.), the narrow to broad band of suberin encircling the anticlinal (radial or transverse) cell walls. Contact with adjoining strips seals the endodermis as a whole, and thus water and dissolved substances must enter the protoplast, which to some extent controls what passes in and out of the stele.

The endodermis may remain permanently in this primary state (stage 1) or, in an older root zone, it may deposit a thin suberin layer inside the entire wall (stage 2), a condition that persists in some species. In still other species, the endodermis progresses to stage 3 by depositing a secondary cell wall over the suberin. This added wall material may be either uniformly thick or asymmetrically thickened (U-shaped) toward the stele, and it may or may not be lignified. In stages 2 and 3 the c.s. is covered and no longer detectable. Guttenberg (1943) and Van Fleet (1961) considered these three endodermal stages in detail.

The hypodermis, the outermost cell layer of the cortex, may also exhibit anatomical features, including a c.s., that are remarkably similar to those of the endodermis. These features are collectively called the "exodermis." It is restricted to roots, where it is common but not universal. The exodermis is not considered further here, but a recent original contribution and point of entry into the literature is provided by Damus et al. (1997).

Turning to aerial organs, an endodermis with c.s. appears to be uncommon in general in vascular plants but to have uneven distribution among the major taxa. It is common in stems, rhizomes, and leaves among pteridophytes, uncommon to absent among gymnosperms, and widespread but of spotty occurrence among angiosperms (Guttenberg, 1943). The cauline and foliar endodermis usually remains at stage 1, advances to stage 2 in a few species, but rarely reaches stage 3.

Van Fleet (1950, 1961) defined the endodermis by functional rather than anatomical characteristics. He therefore regarded the endodermis as common in aerial organs, where the presence of a c.s. marks only one variation among others with similar function, such as the starch sheath in the stem and the bundle sheath around foliar vascular bundles. Among his list of monocots with an aerial endodermis, therefore, he did not specially indicate those marked by a c.s. (Van Fleet, 1942). Guttenberg (1943), in contrast, used the term "endodermis" only if a c.s. was present. He did, however, include non-c.s. cell layers ("endodermoide") in his comprehensive review of the endodermis and similar layers around vascular tissue.

This brief review deals with the aerial endodermis, a poorly known anatomical feature. Standard plant anatomy texts (Cutter, 1971; Esau, 1965; Fahn, 1990; Mauseth, 1988) report briefly that a stem endodermis exists, but only Cutter (1971) and Mauseth (1988) make bare mention of it for the leaf. Primary and secondary (non-textbook) sources on endodermis in aerial organs are sparse, mostly old, and often in sources considered obscure and/or generally unavailable.

III. Pteridophytes

Among the several vascular plant groups that constitute the Pteridophyta, a foliar endodermis with c.s. is common in some but rare or absent in others. Some of the 19th- and early 20th-century studies that recorded such information were mentioned by Ogura (1938), but a review of all endodermis literature was presented by Guttenberg (1943). Concerning Pteridophytes, he concluded that most representatives with an aerial endodermis and c.s. remain in stage 1

(thin cellulosic wall with c.s.), some attain stage 2 (c.s. plus the cell wall partially or completely covered by a suberized thickening), but none show stage 3 (lignified secondary cell wall).

Guttenberg's summary table (1943: 111) included family-level distributions. Keeping in mind that the sample is often small for a particular taxon, he stated that no foliar endodermis occurs in Selaginellaceae, Isoetaceae, Ophioglossaceae, or Marattiaceae. A stage 1 endodermis is found in Equisetaceae, Lycopodiaceae, Osmundaceae, Marsileaceae, and Salviniaceae. He indicated that among various unnamed families of Filicalean ferns, there is a mixture of taxa with stage 1 and stage 2 endodermis.

The references included by Guttenberg (1943) were either unillustrated or documented by drawings. Since his review, a good light micrographic illustration of a stage 2 foliar endodermis in *Adiantum* appeared in Wylie (1948). More detailed examples of foliar endodermis, some with quite obvious c.s. and others with a faint c.s., have been shown by transmission electron microscopy in 23 taxonomically broadly distributed fern species, and a few other pteridophytes (Warmbrodt, 1984; Warmbrodt & Evert, 1978, 1979a, 1979b). As in Guttenberg's 1943 summary, these more recent studies reveal a range from no detectable endodermis to stage one and stage two examples.

IV. Gymnosperms

Among gymnosperms there are no reports of endodermis with c.s. in the stem, perhaps because they are all woody, with an early onset of secondary growth. Examples of foliar endodermis with c.s. are problematic. Napp-Zinn (1966: 156–162) devoted a substantial section of his book to the considerable literature on the “vascular bundle sheath” but reported that only three of the approximately 50 references he included had mentioned a c.s. Chamberlain (1935) merely stated as a generalization, without specific documentation, that conifer leaves commonly have a c.s. Lederer (1955) mentioned, but did not illustrate, an endodermis with c.s. in any of the broad array of gymnosperms he surveyed. Keng and Little (1961) examined freehand sections of pine needles stained with safranin and fast green, and presented anatomical observations in tabular form for 42 species and hybrids. Their few photomicrographs did not include any of the four species they listed as having an endodermis with a “prominent” c.s.: *Pinus echinata*, *P. jeffreyi*, *P. ponderosa*, and *P. taeda*. In addition to these species, they listed some other species and hybrids as having a “not prominent” c.s.

Napp-Zinn (1966) did not cite Buchholz (1951), who described the anatomy of an unusually broad, flat pine leaf from a southeast Asian species provisionally identified as *Pinus krempfi*. Buchholz mentioned, but did not illustrate, an “endodermal sheath with distinct Casparian [*sic*] strips.”

In a developmental study of *Pseudotsuga menziesii* leaves, Owens (1968) showed photomicrographs of cross sections in which the endodermis was conspicuous but no c.s. was evident. The text, however, stated that a c.s. as broad as the entire anticlinal walls stained light red with safranin after the leaf had fully elongated.

Soar (1922) has been most often cited by later workers for information on gymnosperm foliar endodermis. She did not mention a c.s. in describing leaf anatomy of 11 species of conifers, but she said that endodermal cells in all of them had the entire radial and transverse walls impregnated by a lignocellulose core with suberin superimposed, whereas the tangential walls were variously structured (e.g., with suberin patches or uniformly thin lignification) so that they could be water-permeable to some degree. She concluded from this that the foliar endodermis impedes, but does not stop, the passage of water from the foliar stele to the cortex.

Other investigators, both in the older (Plaut, 1910) and the newer (Gambles & Dengler, 1973; Scholz & Bauch, 1973; Carde, 1978) literature, did not detect a c.s. in their studies of conifer leaves. Among gymnosperms, therefore, those published observations documented by illustrations support the view that there is no c.s. in the form of a narrow ribbon but that other anatomical specializations of the bundle sheath (endodermis) cell wall occur in some taxa. In contrast, there is no documentation for the species stated by Buchholz (1951), Lederer (1955), and Keng and Little (1961) to have a foliar endodermis with distinct c.s. The report by Owens (1968) is intermediate; he showed a conspicuous endodermis in which the c.s. is not evident, but his black and white photomicrographs possibly just did not show the stated red staining reaction.

V. Angiosperms

Among angiosperms, Metcalfe and Chalk (1979) listed 25 dicotyledonous families in which an endodermis with c.s. has been recorded from the stem. Guttenberg (1943) had earlier tabulated 33 dicotyledonous families with cauline and foliar endodermis, and his text also mentioned a few monocotyledonous families with this feature. About 10% of angiosperm families are therefore included, although it must be remembered that very few taxa per family have been studied.

It cannot be assumed that because a stem endodermis with c.s. occurs, a similar configuration also occurs in the leaf. Bond (1931), for example, found a stem endodermis in eight species of *Piper* (Piperaceae) but reported it as absent from petiole and leaf lamina. Generalizations about a particular family are therefore premature, except perhaps for Bonnetiaceae (Dickison & Weitzman, 1996) as discussed later in this section. It can be said that virtually all of the families listed are wholly or mostly herbaceous, and that in the few primarily woody ones the reports are almost all from herbaceous taxa (the woody family Bonnetiaceae, again, is an exception).

A peculiar endodermis-like layer was described by Lyshede (1989) in the seedling axis of *Cuscuta pedicillata*, a parasitic angiosperm. Before the seedling contacts a host plant, its "endodermis" often appears densely stained, and in the lower (caudate) part of the seedling the endodermal cells develop intrusive wall folds that form "cristae" within the cell lumen. Lyshede speculated that this cell layer, which does not develop a casparian strip, transfers material from dying cortical and epidermal cells to the stele while at the same time resisting collapse in order to maintain the normal turgor of sieve tubes in the phloem.

In some experimental studies, a c.s. has been induced in etiolated stems of plants (especially herbaceous legumes) placed in darkness for some time. A few earlier references on this topic were cited by Van Fleet (1950), who also reported on his own experiments on etiolation-induced c.s. in the stem and foliar endodermis of some plants placed in darkness. Among several varieties of *Raphanus sativus* he noted that a lamina c.s. "rarely developed." His results on several other species were mentioned rather vaguely. For instance, two species of *Senecio* (*S. obovatus* and *S. aureus*) were said to have developed a well-defined c.s., but he did not distinguish among the aerial organs. Also, he said that *Helianthus annuus*, *Lactuca sativa*, *Brassica napus*, and *B. oleracea* "were like radish [*Raphanus*]" but left unstated whether or not this included a laminar c.s. He concluded that his results support the hypothesis that there is a commonality among vascular/cortex boundary cell layers in root, stem, and leaf. The evidence for induction of a c.s. in leaf blade vascular bundle sheath cells is equivocal, and reinvestigation is therefore needed.

In the leaf, reports of a petiole and midrib endodermis should perhaps be considered separately from those of vascular bundles in the lamina, because petiole and midrib are more stem-like than leaflike in structure and function. Guttenberg (1943) cited several published examples from the petiole, as did Napp-Zinn (1973–1974). Mylius (1913), for example, reported endodermis from several taxa of three dicot and three monocot families, all of which appear to have been described from the petiole. It is usually not stated in the literature whether or not a petiolar c.s. is accompanied by a laminar c.s. Cordemoy (1923) is perhaps the only investigator to report an endodermis with c.s. from the stem and fused leaf base (analogous to the petiole) of species of *Casuarina* (dicot family Casuarinaceae), and then to mention its absence from the free part of the lamina.

Early in this century, Holm (1907a) described leaf anatomy of representatives of six genera of Rubiaceae. Four *Galium* species had an aerial endodermis with c.s.: for two species (*G. pilosum* and *G. triflorum*) he specifically said that “all nerves” have a parenchyma sheath of small rectangular cells with the c.s. “very plainly visible,” whereas for *G. circaezans* and *G. latifolium* he merely said that they agreed with the other two species, which implies that they also had foliar endodermis with c.s. His drawings show the c.s. as thickened dots on the radial walls.

Holm (1907b) also described the anatomy of *Dianthera americana* and *Ruellia ciliosa* (Acanthaceae). The former had an endodermis with c.s. in both stem and leaf bundles (illustrated in drawings but not mentioned in text), and the latter had what he called an “open endodermis,” an arc of cells with c.s. above the xylem but absent next to the phloem. This configuration accompanied each of the five bundles in the midrib, but the c.s. did not continue with the bundles when they branched into the lamina.

The most cited study of a foliar endodermis in angiosperms is that of Trapp (1933) on Plantaginaceae. Among the two genera of this family, he investigated *Littorella lacustris* and eight species of *Plantago*. Freehand sections cut from basal, median, and apical areas of fresh mature and juvenile leaves were stained with gentian violet or Sudan III. All nine species had an endodermis with c.s. around all veins, even the smallest ones. In four species (*Littorella lacustris*, *P. coronopus*, *P. lanceolata*, *P. major*) the endodermis remained in stage 1; in the other five species (*P. alpina*, *P. arborescens*, *P. argentea*, *P. maritima*, *P. raoulii*) a stage 2 endodermis formed later.

Teaching slides of *Plantago major* leaf cross sections in the Botany Department collection at Iowa State University show an exceedingly slender c.s. (0.3–0.4 μm wide) in foliar endodermal cells around all vein orders, including the midvein. Although staining red with safranin, in contrast to the fast green-stained primary endodermal wall, attempts to show the threadlike c.s. in black-and-white photomicrographs were unsuccessful. These sections do, however, verify Trapp's observations on one species.

Van Fleet (1950) reported on some monocot leaves. In *Carex laeviconica* and *Scirpus atrovirens* (Cyperaceae), and in two species of grasses (*Oplismenus hirtellus*, *Pennisetum villosum*), he found that a c.s. appeared first in mestome sheath cells, followed by deposition of the characteristic U-shaped asymmetrical wall of the mature mestome cells.

The only study to use transmission electron microscopy (Codaccioni, 1970) showed an endodermis with c.s. in *Mentha viridis* (Lamiaceae), *Evonymus japonicus* (Celastraceae), and *Cicer arietinum* (Fabaceae). She emphasized the stem but said, without providing evidence, that vascular bundles in the leaf lamina of these species also showed an endodermis with c.s. If this is true, *Evonymus* is a rare example of a woody plant with foliar endodermis with c.s.

In recent literature, Hufford (1992) described, but did not illustrate, the distribution of foliar endodermis with c.s. (presumably remaining at stage 1) among species of *Besseyia* and

Synthris (Scrophulariaceae). He found a c.s. in the midvein of all *Synthris* species and in all vein orders of *S. cordata*, *S. reniformis*, and *S. schizantha*; a c.s. was restricted to midvein and basal portions of secondary veins of all other species, except that it occurred only in the midrib of *S. pinnatifida*. Among *Besseyia* species, Hufford reported a c.s. from midvein and basal secondary veins of *B. alpina* and *B. bullii*, but only in the midvein of *B. rubra* and some *B. wyomingensis* specimens; three other *Besseyia* species lacked an endodermis with c.s. A foliar endodermis with c.s. is therefore quite unevenly distributed in these two genera.

Dickison and Weitzman (1996), as part of an anatomical study of members of the tropical woody family Bonnetiaceae, provide the newest report, and a photomicrograph of one example, of a foliar endodermis with c.s. in species of four genera (*Acopanea*, *Bonnetia*, *Neblinaria*, and *Neogleasonia*). The endodermis was observed around all vein orders, remained in the primary state, and its cells were filled with dark-staining deposits. In addition to the foliar endodermis, a stage 1 endodermis with c.s. occurred in the stem of *Bonnetia wurdackii*. Three other genera of Bonnetiaceae were said to lack a foliar (and presumably also a cauline) endodermis. Dickison and Weitzman (1996) remarked that this was the first example of a woody dicot family with a foliar endodermis with c.s. A possible second example, however, could be from *Evonymus japonicus* as reported by Codaccioni (1970).

VI. Conclusions

This brief review emphasizes the distribution of an endodermis with c.s. in aerial organs of vascular plants. I did not consider the c.s. associated with glands, hydathodes, and nectaries; Guttenberg (1943) and Napp-Zinn (1973–1973) provide some information on these topics. I also omitted specific references from the rather scanty 19th-century literature; citations from that period, and information gleaned from them, are in Guttenberg's comprehensive 1943 review. After Guttenberg (1943), Napp-Zinn (1966, 1973–1974) included most references on anatomical aspects of gymnosperm and angiosperm leaves. Ogura's (1972) report is disappointing because he did not mention the foliar endodermis as he did in his earlier pteridophyte compilation (Ogura, 1938). Pertinent observations from the last three decades are embedded in publications concerned primarily with other aspects, and so they are not easily located. This review is therefore not exhaustive, but I believe it is representative.

The distribution of cauline and foliar endodermis with c.s. is uneven among vascular plants. Present knowledge shows that it is common in pteridophytes but perhaps rare in gymnosperms; however, at least in conifers the entire anticlinal cell walls may act as a modified c.s. in leaves. Among angiosperms, an endodermis with c.s. is uncommon in stem and petiole, and it evidently approaches rarity in the foliar bundle sheath. A foliar endodermis with c.s. occurs chiefly among a small number of mostly herbaceous families, and in some species it may develop only after stimulation by etiolation. Dickison and Weitzman's (1996) description of a foliar endodermis with c.s. in one woody family, Bonnetiaceae, weakens the generalization that a foliar c.s. is restricted to herbaceous taxa.

Analysis of the literature does not permit the significance of the casparian strip in aerial organs to be explained. It is evident that the c.s. is far more common in pteridophytes than in gymnosperms and angiosperms—a generalization that should remain unchanged by future investigations. Perhaps this indicates that root, rhizome, stem, and leaf in pteridophytes have diverged less from some original "ur-organ" in which the stele was always strongly bounded by an endodermis with a c.s. Gifford and Foster (1989) imply as much in their brief discussion of the role of the endodermis according to the stelar theory. With increasing specialization of stem and leaf in gymnosperms and angiosperms, the anatomy of the endodermis perhaps also

changed as its functions evolved. A c.s. occurring in the foliar bundle sheath of scattered angiosperms therefore could be regarded as merely an atavism, which, if it did not interfere with function, could be tolerated by the organ. Casparian strip formation stimulated by darkness is perhaps an example of this.

These are merely speculations that emphasize the need for surveys to determine the true distribution of this easily overlooked anatomical feature. Physiological experiments also need to be devised to explore the function, if indeed there is one, of the c.s. in both stems and leaves.

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