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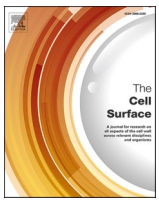

The plasma membrane – cell wall nexus in plant cells: focus on the Hechtian structure

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ABSTRACT

Across all kingdoms of life, cells secrete an extracellular polymer mesh that in turn feeds back onto them. This entails physical connections between the plasma membrane and the polymer mesh. In plant cells, one connection stands out: the Hechtian strand which, during plasmolysis, reflects the existence of a physical link between the plasma membrane of the retracting protoplast and the cell wall. The Hechtian strand is part of a larger structure, which we call the Hechtian structure, that comprises the Hechtian strand, the Hechtian reticulum and the Hechtian attachment sites. Although it has been observed for more than 100 years, its molecular composition and biological functions remain ill-described. A comprehensive characterization of the Hechtian structure is a critical step towards understanding this plasma membrane-cell wall connection and its relevance in cell signaling. This short review intends to highlight the main features of the Hechtian structure, in order to provide a clear framework for future research in this under-explored and promising field.

Hechtian structure landmarks: attachment sites, reticulum and strands

In 1877, De Vries coined the term "plasmolysis" for the "separation of the living protoplasm from the cell wall by dehydrating substances" (De Vries, 1877). Today, we use this term for the separation of the protoplast from the cell wall. Plasmolysis reveals contact sites between the plasma membrane and the cell wall (reviewed e.g. by Oparka, 1994; Lang-Pauluzzi, 2000): as water flows out of the cell and the protoplast shrinks, the plasma membrane of the retracting protoplast appears to remain physically attached to the cell wall, forming strand-like structures. How this is achieved has been a long-standing question and is still not clarified today.

These strand-like structures are often called "Hechtian strands", honoring their detailed description by Hecht (Hecht, 1912), even though they have already been observed earlier on (Pringsheim, 1854). In this review, we would like to stress that the connection between the protoplast and the cell wall is a more complex structure than classically pictured, for which we propose the name "Hechtian structure" (Figs. 1 and 2).

The Hechtian structure is comprised of three parts: (i) the Hechtian attachment sites (HATSs), which are thought to be discrete cortical regions of plasma membrane – cell wall connections (Pont-Lezica et al., 1993) (Fig. 1A,B,E); (ii) the Hechtian reticulum, which is the branched network of membranes located just beneath the cell wall in plasmolysed cells (Hecht, 1912) (Fig. 1C-E); and (iii) the Hechtian strand that is a thin plasma membrane tube that goes through the periplasmic space, connecting the retracting protoplast to the cell wall via the Hechtian reticulum and the HATSs (Hecht, 1912) (Fig. 1A,B,E,F). In fact, the Hechtian reticulum may be viewed as a cluster of HATSs, although this would need to be investigated. In some cases, Hechtian strands can be branched.

Note that in addition to these plasmodesmata-unrelated Hechtian structures described above, there are also plasmodesmata-related Hechtian strands (Hecht, 1912), ensuring plasma membrane continuity through plasmodesmata during plasmolysis (Fig. 1F). In this review, we focus on plasmodesmata-unrelated Hechtian structures.

The Hechtian structure has been identified in a wide range of photosynthetic organisms (Fig. 2) including the unicellular algae *Closterium acerosum* (Domozych et al., 2003), the moss *Physcomitrella patens* protonema cells (Harant & Lang, 2020), and different tracheophyte cells such as epidermal onion (Pont-Lezica et al., 1993; Lang-Pauluzzi &

Abbreviations: HATSs, Hechtian attachment sites.

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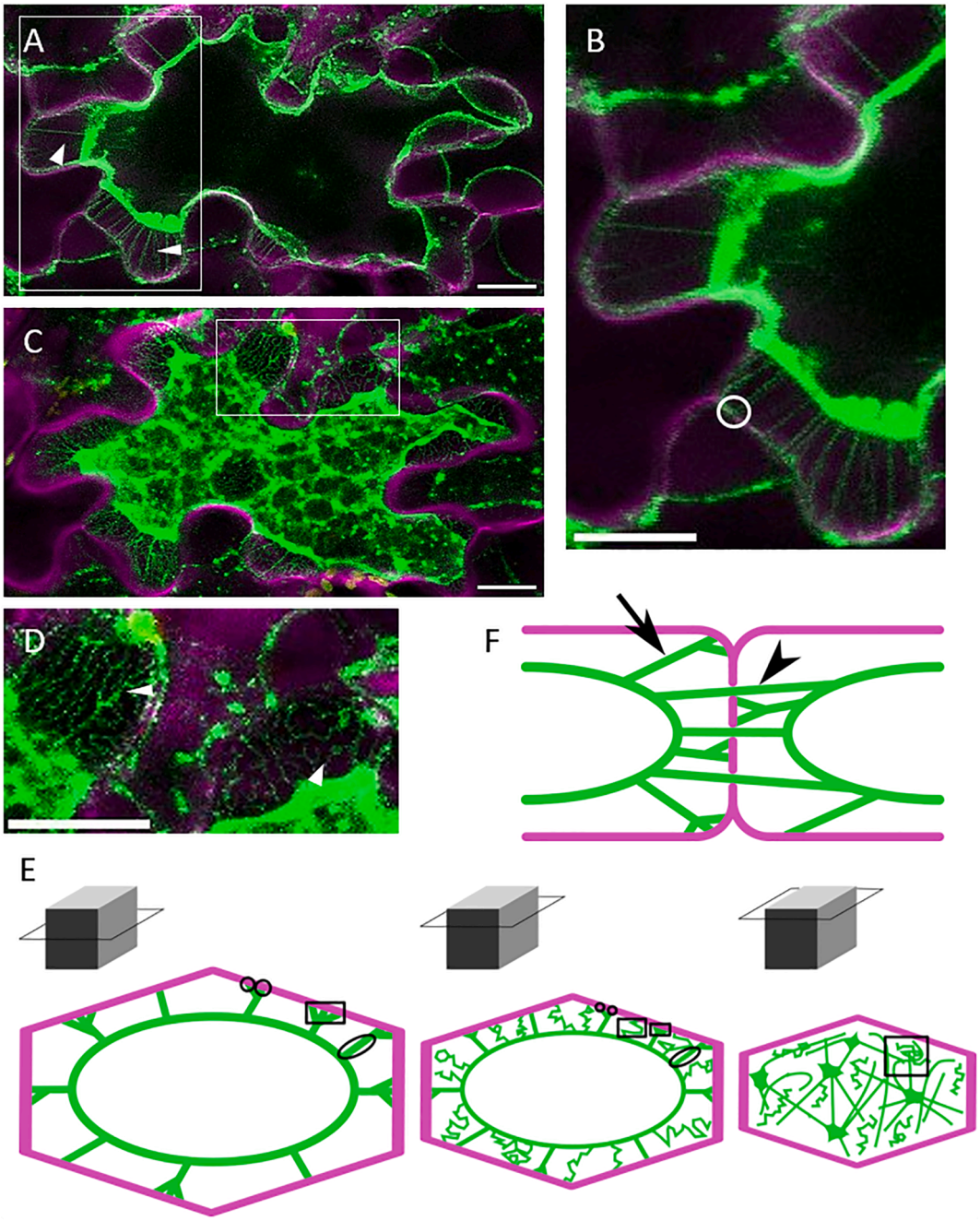

Fig. 1. Plasmolysis of *Nicotiana benthamiana* pavement cell reveals Hechtian strands in the periplasmic space and Hechtian reticulum beneath the cell wall. **A** Plasmolysed pavement cell at 10μm from cell surface showing the plasma membrane mainly detached at the lobes. Upon plasmolysis, the protoplast's plasma membrane (green) is detached from the wall (magenta) and it is possible to observe Hechtian strands as thread-like plasma membrane strands in the periplasmic space (white arrowheads). Not all the plasmolysed areas exhibit Hechtian structures. **B** Inset (area framed in A) showing the Hechtian strands at higher magnification. The location of a HATSs is indicated with a white circle. **C** Maximum intensity projection of 5μm depth showing the Hechtian reticulum just beneath the cell wall of a plasmolyzed pavement cell. **D** Inset (area framed in C) showing the Hechtian reticulum in detail containing thick, wavy tubular structures, and branched tubular structures with cisternae adjacent to the cell surface (white arrowheads). **E** Illustration of a plasmolysed cell revealing the Hechtian structure: the Hechtian attachment sites (black circles) are continuous with the retracting protoplast via the Hechtian reticulum (black rectangle) and Hechtian strand (black oval). From left to right: midplane section, a plane closer to the wall and a plane just beneath the cell wall of a plasmolysed cell. The cell wall is depicted in magenta, the plasma membrane in green. **F** Schematic representation of plasmodesmata-related and -unrelated Hechtian strands. The plasmodesmata-unrelated Hechtian strands (arrow) continue into the Hechtian reticulum, which ends with HATSs at the cell wall. The plasmodesmata-related Hechtian strands (arrowhead) ensure membrane continuity between adjacent cells by connecting the two retracting protoplasts through plasmodesmata. Note that both might ensure contact to the cell wall: while the plasmodesmata-unrelated Hechtian strands contact the cell wall head on at HATSs, the plasmodesmata-related Hechtian strands might contact the cell wall laterally at plasmodesmata. Four-week-old *N. benthamiana* plants were transiently transformed with *Agrobacterium tumefaciens* carrying the construct *pPDF1::LTI6B-mCitrine* to label the plasma membrane. Images were acquired 3 days post-infiltration with a SP8 Leica confocal microscope. The cells were plasmolyzed for 30 min in glycerol 10 %. Green: Signal from *LTI6B-mCitrine* channel (λ excitation: 514nm, λ emission: 529–600nm, detector gain: 600V, laser: 30%, objective: 25x/ water /NA: 0.95). Magenta: Calcofluor staining of the cell wall, only anticlinal walls' signals are shown. (λ excitation: 405nm, λ emission: 430–475nm, detector gain: 400V, laser: 5 %, objective: 25x/ water /NA: 0.95). Scale bar: 15μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

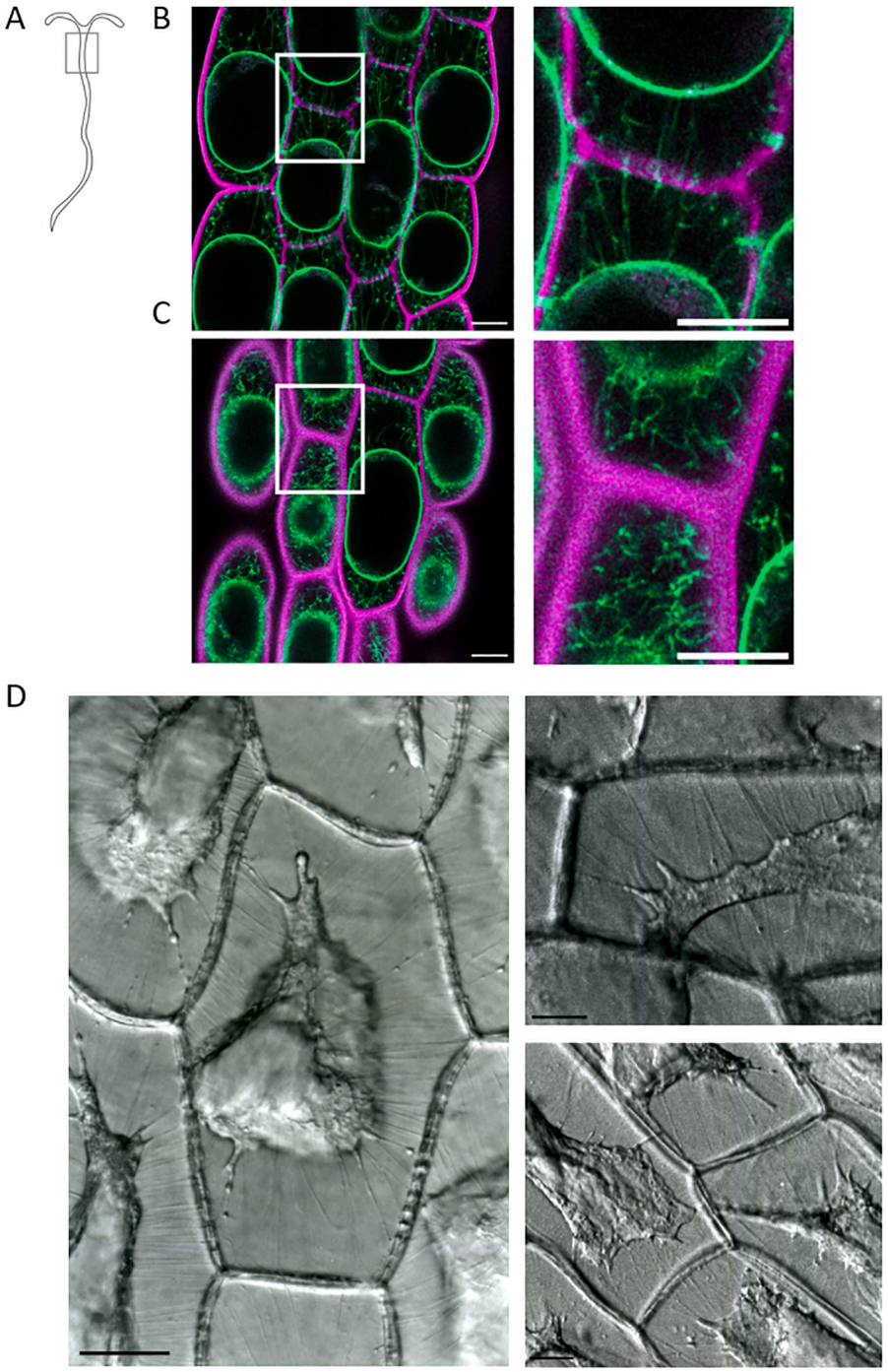

Fig. 2. The Hechtian structure in different plant species. **A** Plasmolysed *Arabidopsis thaliana* hypocotyl (box) reveals the Hechtian structure (B,C). **B** A midplane section shows Hechtian strands that continue into the Hechtian reticulum close the the cell wall. Boxed area magnified on the right. **C** A section closer to the cell wall shows the Hechtian reticulum. Boxed area magnified on the right. Scale bars: 10μm. B, C show single confocal sections, the cell wall signal is pseudocolored in magenta, the membrane signal in green. **D** Plasmolysed epidermal onion cells showing Hechtian strands. The epidermis was peeled free from an onion bulb scale and plasmolysed in 1 kmol.m^{-3} $CaCl_2$. Bright field images acquired by Rafael Pont-Lezica. Hoffman optics. Scale bar: 10μm. Seven days old in vitro grown Arabidopsis thaliana seedlings (p35S::LTI6B-GFP, ecotype WS), were propidium-iodide stained and mounted in water between a slide and a coverslip, separated by spacers. The water was replaced by D-Sorbitol solution by sucking the water out with a tissue paper on one side, and supplying 0.6 M D-Sorbitol solution with a pipette at the edge of the coverslip on the other side. The plants were imaged on a LSM980 (ZEISS, Jena) upright confocal microscope with airyscan detection, 35 min after the Sorbitol solution was added. Objective: water immersion Plan-Apochromat 20x/1.0. GFP channel (plasma membrane): 488nm laser at 1.8%, dual band detection filter: BP420-480 + BP495-550, detector master gain: 850V, digital gain 1.0. PI channel (cell wall): 561nm laser at 0.5%, dual band detection filter: BP495-550 + BP570-630, detector master gain: 850V, digital gain 1.0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Gunning, 2000; Fig. 2B) and *Tradescantia virginiana* cells (Lang et al., 2004); *Gynkgo biloba* callus (Buer et al., 2000) or *Nicotiana tabacum* BY-2 cells (Yoneda et al., 2020). The presence of Hechtian structures is classically used in Arabidopsis to validate the plasma membrane localization of proteins and visualize plasma membrane-cell wall attachments (e.g. Hématy et al., 2007; Barbosa et al., 2023). The Hechtian structure has also been observed in other walled organisms such as the oomycetes *Saprolegnia ferax* and *Achlya ambisexualis*, and the ascomycete *Neurospora crassa* (Bachewich & Heath, 1997).

Characteristics of the Hechtian structure

The Hechtian structure and HATSs in particular, are attractive candidates as a nexus between the cell wall, the plasma membrane, the cytoskeleton, and the endoplasmic reticulum (Wyatt & Carpita, 1993). Several complex structural interactions have been described inside of cells, including reported molecular interactions between the cytoskeleton and the plasma membrane (Liu et al., 2015b), the cytoskeleton and the endoplasmic reticulum (Hamada et al., 2014), as well as between the endoplasmic reticulum and the plasma membrane (Wang et al., 2017). Moreover, numerous studies dealing with the molecular interactions between the cell wall and the plasma membrane have been performed in order to identify the linkers: receptor-like kinases, arabinogalactan proteins, and formins are among the proteins highlighted to act as linkers (reviewed in Liu et al., 2015a). The composition of the Hechtian structure suggests that a complex nexus could exist at HATSs.

There is evidence for the presence of cytoplasm within the Hechtian strands, as measured by esterase activity in oat coleoptiles (Drake et al., 1978), *Pteridium* protoplasts (Attree & Sheffield, 1985) and tobacco cells (Chang et al., 1996). However, Oparka (1994) did not measure esterase activity in onion epidermis. This discrepancy may be partially explained by Hechtian strands of different widths, among which the thinner ones could exclude the cytoplasm.

The Hechtian reticulum, as well as some Hechtian strands, contain endoplasmic reticulum as evidenced by electron microscopy images (Oparka, 1994) and 3,3′-dihexyloxacarbocyanine iodide staining (Oparka, 1994; Lang-Pauluzzi & Gunning, 2000) of plasmolysed onion epidermal cells; and the fluorescent endoplasmic reticulum marker HDEL in *Arabidopsis thaliana* and *Nicotiana benthamiana* Hechtian strands (Cheng et al., 2017).

The presence of cytoskeleton within the Hechtian reticulum and Hechtian strands is controversial due to the difficulties of preservation of cortical actin microfilaments (Lang-Pauluzzi & Gunning, 2000) and induced depolymerization of microtubules (Cheng et al., 2017) during plasmolysis. Both actin microfilaments and microtubules can be present in Hechtian strands in onion (Lang-Pauluzzi & Gunning, 2000), as well as in Arabidopsis (Cheng et al., 2017). However, the disruption of the cytoskeleton does not abolish the formation of Hechtian strands (Lang-Pauluzzi & Gunning, 2000). On the contrary, Domozych et al., 2003 reported the absence of cytoskeleton from the Hechtian strands of the algae *Closterium acerosum*, as assayed by TEM and fluorescence staining observations.

Electron microscopy images of *T. virginiana* leaf epidermal cells show that the membranous tubes of the Hechtian reticulum along the cell wall are embedded by cell wall elements (Lang et al., 2004), and an accumulation of callose has been identified around the Hechtian reticulum (Lang et al., 2004), suggesting that callose might be involved in the attachment of the Hechtian reticulum to the cell wall.

Beyond their molecular composition, Hechtian structures are physical objects: Hechtian strands are thin and tense. They appear straight and mostly deprived of wavy curves, likely because they remain under tension as the protoplast contracts (Fig. 1A-B and Fig. 2B,D). Tensions of individual Hechtian strands of $\sim 20\mu$m in length were determined to be on the order of $\sim$ 1pN by optical microsurgical techniques in *Nicotiana tabacum* and *Gynkgo biloba* callus cells (Buer et al., 2000); a value that is two orders of magnitude higher than the tensile strength of the plasma membrane measured in NIH-3 T3 mouse fibroblasts (Tan et al., 2011). The cross-sectional diameter of Hechtian strands ranges between 100nm and 200nm upon incipient plasmolysis, and decreases to a range of 20 to 40nm after long-term plasmolysis in onion epidermis (Oparka et al., 1994). Their density and diameter may vary with the degree of plasmolysis (Lang et al., 2004). Hechtian strands have been reported to be thicker close to the protoplast than close to the cell wall in *Tradescantia virginiana* leaf epidermal cells (Lang et al., 2004).

During deplasmolysis, Hechtian strands are thought to be reincorporated into the plasma membrane (Lang-Pauluzzi & Gunning, 2000). Furthermore, Johnson-Flanagan & Singh (1986) noted that in cold hardened cells, new sets of strands or rivulets of membranes could be formed with each new plasmolysis/deplasmolysis cycle. These data suggest that the Hechtian structure is dynamic and versatile.

Conclusive evidence is still lacking, but the nexus of cell wall, plasma membrane, cytoskeleton and endoplasmic reticulum in the Hechtian structure and in particular at HATSs, makes them attractive candidates for signaling centers.

The contribution of the Hechtian structure to signaling

The cell wall - plasma membrane interface is a critical site for detecting stimuli generated by changes in water status, membrane tension and cell wall properties (Haswell & Verslues, 2015), caused in part by abiotic and biotic stresses. In this regard, HATSs could serve as hubs to centralize molecular components involved in the perception and consequent signaling triggered by changes in water potential, such as mechanosensitive channels and osmosensors.

There is some evidence for the importance of the Hechtian structure in cell wall integrity sensing: new cell wall has been reported to be produced along the old cell wall even during plasmolysis if the Hechtian structure is present. In contrast, when the Hechtian structure is disrupted, the new cell wall was instead observed to be synthesized along the protoplast outline (Schindler et al., 1989, Yoneda et al., 2020). Hechtian structures may also maintain cell polarity by anchoring the plasma membrane to the cell wall preventing slippage (Pont-Lezica et al., 1993).

Additionally, the Hechtian structure may be involved in the response to cold stress, as evidenced by the formation of Hechtian strands in *Closterium Acerosum* in response to cooling (Domozych et al., 2003), and the increased density of strands in cold-hardened *Gynkgo biloba* callus cells (Buer et al., 2000).

Finally, functional plasma membrane-cell wall connections are relevant for successful pathogen defense. For instance, the plant defense signaling protein NDR1, that limits electrolyte leakage in response to *Pseudomonas syringae pv. tomato* DC3000 infection, has been suggested to be involved in plasma membrane-cell wall adhesion (Knepper et al., 2011). Moreover, when the Hechtian structure was apparently impaired with RGD-peptides treatments in Pea or Cowpea cells infected with fungi they are not host for; plant immune responses including callose deposition and ROS production were decreased, whereas fungal penetration efficiency was increased (Mellersh et al., 2002).

While these examples show an implication of the Hechtian structure in signaling, plant scientists still have a lot of work to do to understand the role of the Hechtian structure in signaling.

The Hechtian structure as an integrator of mechanical signaling?

Whether the Hechtian structure could also serve as a hub for mechanotransduction still remains enigmatic. It has been hypothesized, that the connections between the cell wall and the plasma membrane may serve as “plasmalemmal control centers”, accumulating not only plasma membrane and cell wall, but also mechanosensory ion channels, cytoskeleton and regulatory molecules (Pickard, 1994). The presence and maintenance of Hechtian strands reflects the strength of the attachment to the cell wall, as the bulk of the protoplast shrinks.

Therefore plasma membrane-cell wall linkers may be able to transmit mechanical signals from the cell wall to the plasma membrane, in particular to mechanosensitive elements, such as ion channels, or cytoskeletal elements (Pont-Lezica et al., 1993; Ackermann & Stanislas, 2020; Hamant et al., 2019). Hence, Hechtian strands and HATSs can be regarded as specialized structures for perceiving mechanical signals at the cell surface and triggering the transduction pathways. The presence of nano/microdomains in the plasma membrane and cell wall supports this idea.

Several plasma membrane proteins form nanodomains of different sizes within the plasma membrane (McKenna et al., 2019). The dynamics of these nanodomains can be differentially regulated by the cytoskeleton and the cell wall; in fact, the cell wall plays a key role in the regulation of protein cluster size and lateral mobility (Martinière et al., 2012; Martinière & Zelazny, 2021; McKenna et al., 2019). Nanodomains like these could be involved in mechanosensing. For instance, in yeast, the wall mechanosensor Wsc1 forms large clusters at sites of cell wall compression (Neeli-Venkata et al., 2021). Another class of evolutionary conserved microdomains, the endoplasmic reticulum-plasma membrane contact sites, contain protein complexes involved in organelle tethering and signaling (Pérez-Sancho et al., 2016). These endoplasmic reticulum-plasma membrane contact sites have also been identified in plants, and the proteins VAP27 (a vesicular associated protein), NET3 (a NETWORKED actin binding protein C), and SYT1 (Synaptotagmin 1) have been identified as markers of these contact sites (Wang et al., 2014; Wang et al., 2016; Pérez-Sancho et al., 2015; Siao et al., 2016). SYT1 expression is strongly induced by tissue damage in Arabidopsis transcriptional reporter lines and the *syt1* mutant exhibits hypersensitivity to mechanical stress (Pérez-Sancho et al., 2015). These contact sites are often found close to the cell wall, indicating that they might coincide with HATSs (Wang et al., 2016). In fact, the Hechtian structure contains VAP27-1 and SYT1 (Wang et al., 2016; Pérez-Sancho et al., 2015). Moreover, cytoskeletal elements partially overlap with the endoplasmic reticulum-plasma membrane contact sites and influence the mobility of contact site-localized proteins (Wang et al., 2014, Siao et al., 2016). This makes the Hechtian structure an attractive candidate as a (mechano) signaling center at the nexus between the cell wall, the plasma membrane, the endoplasmic reticulum, and the cytoskeleton.

Finally, HATSs have been related to focal adhesions in animals (Schindler et al., 1989; Canut et al., 1998). Focal adhesions are discrete points in the cell, where the cytoskeleton is mechanically connected to the extracellular matrix via transmembrane proteins of the integrin family (reviewed in Iskratsch et al., 2014). The transmembrane proteins of the integrin family recognize the conserved RGD motif comprised of the amino acids Arg (R), Gly (G) and Asp (D), present on extracellular matrix proteins such as vitronectin or fibronectin (Iskratsch et al., 2014). In plants, there is some indirect evidence suggesting that HATSs might be out-competed by providing an excess of RGD in the medium (Schindler et al., 1989; Canut et al., 1998, Mellersh et al., 2002). Moreover, an RGD-binding transmembrane protein, LecRKI.9, has been identified (Gouget et al., 2006). The RGD-binding domain of this protein equally seems to titrate out HATSs (Gouget et al., 2006). Although we cannot exclude other impacts of RGD treatments on the cell physiology, this suggests one possible mechanism in which LecRKI.9 could bridge the plasma membrane to the cell wall by binding to the RGD motif in cell wall proteins. This kind of interaction between plasma membrane proteins and specific targets in the cell wall can trigger signaling and might take place at HATSs. Thus, HATSs can be considered attractive candidates as mechanotransduction hubs.

Outlook

We are only beginning to understand the complex molecular and mechanical identity of the plasma membrane-cell wall nexus. Our current understanding is based on classical, accurate characterizations of the Hechtian structure, and nurtured by cutting-edge research on the impact of the cell wall, as well as the cytoskeleton on (plasma) membrane protein dynamics. Here are some outstanding questions: What are the biological functions of the Hechtian structure? Is the distribution and density of Hechtian structures cell type specific? What are the mechanisms of plasma membrane-cell wall and cell–cell communication through the Hechtian structure? Could HATSs play a role in sensing biochemical and mechanical cues? What are the molecular components of HATSs? Finally, it would be interesting to investigate whether the apparent similarity between HATSs and focal adhesions goes beyond an attractive analogy, in particular in light of HATSs as potential sites of mechanical coupling between the cell wall and the cytoskeleton.

CRediT authorship contribution statement

Denise S. Arico: Writing – review & editing, Writing – original draft, Conceptualization. **Johanna E.M. Dickmann:** Writing – review & editing, Writing – original draft, Conceptualization. **Olivier Hamant:** Writing – review & editing, Conceptualization. **Hervé Canut:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Ackermann, F., Stanislas, T., 2020. The plasma membrane–an integrating compartment for mechano-signaling. Plants 9, 505–521.

Attree, S.M., Sheffield, E., 1985. Plasmolysis of Pteridium protoplasts: A study using light and scanning-electron microscopy. Planta 165, 151–157.

Bachewich, C.L., Heath, I.B., 1997. Differential cytoplasm-plasma membrane-cell wall adhesion patterns and their relationships to hyphal tip growth and organelle motility. Protoplasma 200, 71–86.

Barbosa, I.C.R., De Bellis, D., Flückiger, I., Bellani, E., Grangé-Guerment, M., Hématy, K., Geldner, N., 2023. Directed growth and fusion of membrane-wall microdomains requires CASP-mediated inhibition and displacement of secretory foci. Nature Communications 14, 1626.

Buer, C.S., Weathers, P.J., Swartzlander, G.A., 2000. Changes in Hechtian Strands in Cold-Hardened Cells Measured by Optical Microsurgery. Plant Physiology 122, 1365–1377.

Canut, H., Carrasco, A., Galaud, J.P., Cassan, C., Bouyssou, H., Vita, N., Ferrara, P., Pont-Lezica, R., 1998. High affinity RGD-binding sites at the plasma membrane of Arabidopsis thaliana links the cell wall. Plant Journal 16, 63–71.

Chang, P.F.L., Damsz, B., Kononowicz, A.K., Reuveni, M., Chen, Z., Xu, Y., Hedges, K., Tseng, C.C., Singh, N.K., Binzel, M.L., et al., 1996. Alterations in cell membrane structure and expression of a membrane-associated protein after adaptation to osmotic stress. Physiologia Plantarum 98, 505–516.

Cheng, X., Lang, I., Adeniji, O.S., Griffing, L., 2017. Plasmolysis-deplasmolysis causes changes in endoplasmic reticulum form, movement, flow, and cytoskeletal association. Journal of Experimental Botany 68, 4075–4087.

De Vries, H., 1877. Eine Methode zur Analyse der Turgorkraft. Jahrb. Wiss. Bot. 14, 427–601.

Domozych, D.S., Roberts, R., Danyow, C., Flitter, R., Smith, B., Providence, K., 2003. Plasmolysis, hechtian strand formation, and localized membrane-wall adhesions in the desmid, Closterium acerosum (Chlorophyta). Journal of Phycology 39, 1194–1206.

Drake, G.A., Carr, D.J., Anderson, W.P., 1978. Plasmolysis, Plasmodesmata, and the Electrical Coupling of Oat Coleoptile Cells. Journal of Experimental Botany 29, 1205–1214.

Gouget, A., Senchou, V., Govers, F., Sanson, A., Barre, A., Rougé, P., Pont-Lezica, R., Canut, H., 2006. Lectin receptor kinases participate in protein-protein interactions to mediate plasma membrane-cell wall adhesions in Arabidopsis. Plant Physiology 140, 81–90.

Hamada, T., Ueda, H., Kawase, T., Hara-Nishimura, I., 2014. Microtubules contribute to tubule elongation and anchoring of endoplasmic reticulum, resulting in high network complexity in Arabidopsis. Plant Physiology 166, 1869–1876.

Hamant, O., Inoue, D., Bouchez, D., Dumais, J., Mjolsness, E., 2019. Are microtubules tension sensors? Nature Communications 10, 2360–2372.

Harant, D., Lang, I., 2020. Stay in touch—the cortical ER of moss protonemata in osmotic stress situations. Plants 9, 421.

Haswell, E.S., Verslues, P.E., 2015. The ongoing search for the molecular basis of plant osmosensing. Journal of General Physiology 145, 389–394.

Hecht, K., 1912. Studien über den vorgang der plasmolyse. Beitrage Zur Biologie Der Pfianzen 11, 133–145.

Hématy, K., Sado, P.E., Van Tuinen, A., Rochange, S., Desnos, T., Balzergue, S., Pelletier, S., Renou, J.P., Höfte, H., 2007. A Receptor-like Kinase Mediates the Response of Arabidopsis Cells to the Inhibition of Cellulose Synthesis. Current Biology 17, 922–931.

Iskratsch, T., Wolfenson, H., Sheetz, M.P., 2014. Appreciating force and shape-the rise of mechanotransduction in cell biology. Nature Reviews Molecular Cell Biology 15, 825–833.

Johnson-Flanagan, A.M., Singh, J., 1986. Membrane deletion during plasmolysis in hardened and non-hardened plant cells. Plant, Cell & Environment 9, 299–306.

Knepper, C., Savory, E.A., Day, B., 2011. Arabidopsis NDR1 is an integrin-like protein with a role in fluid loss and plasma membrane-cell wall adhesion. Plant Physiology 156, 286–300.

Lang, I., Barton, D.A., Overall, R.L., 2004. Membrane-wall attachments in plasmolysed plant cells. Protoplasma 224, 231–243.

Lang-Pauluzzi, I., 2000. The behaviour of the plasma membrane during plasmolysis: A study by UV microscopy. Journal of Microscopy 198, 188–198.

Lang-Pauluzzi, I., Gunning, B.E.S., 2000. A plasmolytic cycle: The fate of cytoskeletal elements. Protoplasma 212, 174–185.

Liu, Z., Persson, S., Sánchez-Rodríguez, C., 2015a. At the border: the plasma membrane-cell wall continuum. Journal of Experimental Botany 66, 1553–1563.

Liu, Z., Persson, S., Zhang, Y., 2015b. The connection of cytoskeletal network with plasma membrane and the cell wall. Journal of Integrative Plant Biology 57, 330–340.

Martinière A, Lavagi I, Nageswaran G, Rolfe DJ, Maneta-Peyret L, Luu D-T, Botchway SW, Webb SED, Mongrand S, Maurel C, et al. 2012. Cell wall constrains lateral diffusion of plant plasma-membrane proteins. *Proceedings of the National Academy of Sciences of the United States of America* 109: 12805–12810.

Martinière, A., Zelazny, E., 2021. Membrane nanodomains and transport functions in plant. Plant Physiology 187, 1839–1855.

McKenna JF, Rolfe DJ, Webb SED, Tolmie AF, Botchway SW, Martin-Fernandez ML, Hawes C, Runions J. 2019. The cell wall regulates dynamics and size of plasma-membrane nanodomains in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America* 116: 12857–12862.

Mellersh, D.G., Foulds, I.V., Higgins, V.J., Heath, M.C., 2002. H_2O_2 plays different roles in determining penetration failure in three diverse plant-fungal interactions. Plant Journal 29, 257–268.

Neeli-Venkata, R., Diaz, C.M., Celador, R., Sanchez, Y., Minc, N., 2021. Detection of surface forces by the cell-wall mechanosensor Wsc1 in yeast. Developmental Cell 56, 2856–2870.

Oparka, K.J., 1994. Plasmolysis: new insights into an old process. New Phytologist 126, 571–591.

Oparka, K.J., Prior, D.A.M., Crawford, J.W., 1994. Behaviour of plasma membrane, cortical ER and plasmodesmata during plasmolysis of onion epidermal cells. Plant, Cell & Environment 17, 163–171.

Pérez-Sancho, J., Vanneste, S., Lee, E., McFarlane, H.E., del Valle, A.E., Valpuesta, V., Friml, J., Botella, M.A., Rosado, A., 2015. The arabidopsis synaptotagmin1 is enriched in endoplasmic reticulum-plasma membrane contact sites and confers cellular resistance to mechanical stresses. Plant Physiology 168, 132–143.

Pérez-Sancho, J., Tilsner, J., Samuels, A.L., Botella, M.A., Bayer, E.M., Rosado, A., 2016. Stitching Organelles: Organization and Function of Specialized Membrane Contact Sites in Plants. Trends in Cell Biology 26, 705–717.

Pickard, B.G., 1994. Contemplating the plasmalemmal control center model. Protoplasma 182, 1–9.

Pont-Lezica, R.F., McNally, J.G., Pickard, B.G., 1993. Wall-to-membrane linkers in onion epidermis: some hypotheses. Plant, Cell & Environment 16, 111–123.

Pringsheim, N., 1854. Untersuchungen über den Bau und Bildung der Pflanzenzelle. Abt 1: Grundleinen einer *Theorie der Pflanzanzelle*. Hershwald, Berlin. 1854, 12–13.

Schindler, M., Meiners, S., Cheresh, D.A., 1989. RGD-dependent Linkage between Plant Cell Wall and Plasma Membrane: Consequences for Growth. The Journal of Cell Biology 108, 1955–1965.

Siao, W., Wang, P., Voigt, B., Hussey, P.J., Baluska, F., 2016. Arabidopsis SYT1 maintains stability of cortical endoplasmic reticulum networks and VAP27-1-enriched endoplasmic reticulum-plasma membrane contact sites. Journal of Experimental Botany 67, 6161–6171.

Tan, S.C.W., Yang, T., Gong, Y., Liao, K., 2011. Rupture of plasma membrane under tension. Journal of Biomechanics 44, 1361–1366.

Wang, P., Hawkins, T.J., Richardson, C., Cummins, I., Deeks, M.J., Sparkes, I., Hawes, C., Hussey, P.J., 2014. The plant cytoskeleton, NET3C, and VAP27 mediate the link between the plasma membrane and endoplasmic reticulum. Current Biology 24, 1397–1405.

Wang, P., Richardson, C., Hawkins, T.J., Sparkes, I., Hawes, C., Hussey, P.J., 2016. Plant VAP27 proteins: Domain characterization, intracellular localization and role in plant development. New Phytologist 210, 1311–1326.

Wang, P., Hawes, C., Hussey, P.J., 2017. Plant Endoplasmic Reticulum-Plasma Membrane Contact Sites. Trends in Plant Science 22, 289–297.

Wyatt, S.E., Carpita, N.C., 1993. The plant cytoskeleton-cell-wall continuum. Trends Cell Biology. 3, 413–417.

Yoneda, A., Ohtani, M., Katagiri, D., Hosokawa, Y., Demura, T., 2020. Hechtian strands transmit cell wall integrity signals in plant cells. Plants 9, 604.