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REVIEW ARTICLE

Polarity, planes of cell division, and the evolution of plant multicellularity

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Abstract

Organisms as diverse as bacteria, fungi, plants, and animals manifest a property called "polarity." The literature shows that polarity emerges as a consequence of different mechanisms in different lineages. However, across all unicellular and multicellular organisms, polarity is evident when cells, organs, or organisms manifest one or more of the following: *orientation*, *axiation*, and *asymmetry*. Here, we review the relationships among these three features in the context of cell division and the evolution of multicellular polarity primarily in plants (defined here to include the algae). Data from unicellular and unbranched filamentous organisms (e.g., *Chlamydomonas* and *Ulothrix*) show that cell orientation and axiation are marked by cytoplasmic asymmetries. Branched filamentous organisms (e.g., *Cladophora* and moss protonema) require an orthogonal reorientation of axiation, or a localized cell asymmetry (e.g., "tip" growth in pollen tubes and fungal hyphae). The evolution of complex multicellular meristematic polarity required a third reorientation of axiation. These transitions show that polarity and the orientation of the future plane(s) of cell division are dyadic dynamical patterning modules that were critical for multicellular eukaryotic organisms.

Keywords Algae · Asymmetric cell division · Dynamical patterning modules · Meristems · Symmetry breaking · Volvocines

The ability to reduce everything to simple fundamental laws does not imply the ability to start from those laws and reconstruct the universe – P. W. Anderson (1972)

Introduction

Cell division in specific directions is critical to the determination of multicellular form because planes of division establish directions of growth. The specification of the plane of division is a consequence, or at least a correlate, of cell polarity, i.e., the plane of cell division is prefigured by mechanisms that rely on some form of cellular polarity. Yet, comparative analyses of diverse organisms with rigid cell walls (i.e., bacteria, algae, land plants, and fungi) indicate that the mechanisms that establish polarity (designated henceforth as POL) and the mechanisms that define the location of the future cell wall (FCW) can differ even among closely related organisms (Niklas 2000; Niklas 2014; Niklas et al. 2013). In addition, POL can be evoked by internal cytoplasmic asymmetries and by external stimuli, e.g., gravity and unidirectional light. For this reason, Hernández-Hernández et al. (Hernández-Hernández et al. 2012) and Benítez et al. (2018) designated POL and FCW as plant dynamical patterning modules

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(DPMs), which are defined as sets of conserved gene products and molecular networks that operate in conjunction with the physical morphogenetic and patterning processes they mobilize (Hernández- Hernández et al. 2012; Newman and Bhat 2009; Newman et al. 2009). Normal cell division requires that POL and FCW operate in a coordinated manner, wherein POL establishes a spatial reference system in which FCW reliably operates. Among multicellular organisms, orderly cell division typically takes place in one or more directions with respect to the body axis. Therefore, POL must establish different spatial reference systems, even if the mechanism responsible for POL is invariant at the cellular level. A profoundly central (but as yet not fully answered) question is, How is POL achieved in unicellular organisms and how did it evolve in conjunction with the emergence of multicellular organisms?

Our goal is to address this question by focusing on polyphyletic photosynthetic eukaryotes (i.e., algae and land plants). This focus is justified because (1) a broad phylogenetic survey is required if our hypothesis is correct (viz POL and FCW are achieved in different ways by different lineages), (2) most photosynthetic eukaryotes produce rigid cell walls whose size, shape, and geometry can be used to infer POL and FCW growth patterns, and (3) all algal lineages contain unicellular species, which provide an opportunity to examine the unicellular-to-multicellular evolutionary transformation. In addition, among these multicellular organisms, POL is typically established by meristems consisting of one or many cells (e.g., moss gametophores and flowering plants, respectively) (Fig. 1). Finally, phylogenetic analyses of the land plants and their algal relatives (collectively called the streptophytes) provide reliable contexts to trace evolutionary trends, from unicellular to complex multicellular taxa (Li et al. 2018; Palmer et al. 2004). Thus, photosynthetic eukaryotes provide useful diverse clades with which to pursue our objectives.

In the following, we review data showing that POL and FCW are established by different mechanisms, thereby reaffirming that they are distinct DPMs. We then review what is currently known about the evolution of POL and FCW and show that changes in intracellular gradients tend to be the first discernable manifestation of POL. We also compare POL in plants and fungi with POL in metazoans and prokaryotes. We conclude with speculations on how POL contributed to the evolution of multicellularity and apical meristems. Throughout, we draw a sharp distinction between the manifestations of POL and the mechanisms responsible for it because one challenge in identifying the mechanisms evoking POL is determining whether the phenomenology observed around or within cells is the result of POL or its cause.

POL and its ambiguities

The word "polarity" was first used in biology by G. J. Allman when discussing hydroid regeneration (Allman 1864). Although the word is now widely used, its meaning is context-driven and sometimes ambiguous. Consider two filamentous algae, *Spirogyra* and *Ulothrix*. In both, FCW is invariably transverse giving rise to an unbranched filament with two ends or "poles." However, in contrast to *Spirogyra* filaments, *Ulothrix* filaments are tethered to a substrate by a holdfast cell formed when a zoospore attaches to a substrate and undergoes asymmetric cell division. Here, the polarity of the filament as a whole is the result of two different expressions of polarity (the asymmetry of zoospore division and the subsequent symmetry of vegetative cell division). Although *Spirogyra* and *Ulothrix* are both unbranched filamentous organisms, their POL is not equivalent, e.g., *Spirogyra*'s polarity results from a single plane of division, whereas *Ulothrix*'s polarity includes asymmetric ends. For similar reasons, the word polarity is commonly used descriptively to specify orientation, or the direction of a process or activity. In doing so, *polarity*, *direction*, *orientation*, and even *symmetry*, are nearly interchangeable, and thus easily conflated.

Other difficulties occur because POL can be weak or strong, and sometimes reversible. For example, POL is not discernable in coccoid bacteria or in the eggs of many algae, whereas experiments using the asexual propagules of liverworts (gemmae) show that the capacity to form rhizoids on either side decreases over time (Haberlandt 1914). Similarly, cuttings of moss gametophores can generate rhizoids at their base and protonema at their top, but POL is reversed by inverting their orientation (Fitting 1938; Westerdijk 1906), a phenomenology observed for stem cuttings of vascular plants (Vöchting 1878; Wulff 1910; Zimmermann 1923), but not for roots (Warmke and Warmke 1950). Experiments using fern gametophytes show that POL during regeneration is associated with physiological gradients, particularly differences in osmotic concentrations (e.g., Gratzy-Wardengg 1929 and Albaum 1938), and when fern gametophytes are sliced transversely, regeneration POL is invariably apical (Fig. 2).

Despite its spatiotemporal complexity, the literature shows that POL becomes morphologically evident when one or more of the three features occurs: (1) *orientation* with respect to a spatial frame of reference (e.g., gravity or light), (2) *axiation* in a direction relative to orientation (e.g., cell elongation or expansion), and (3) *asymmetry* with respect to orientation or axiation (e.g., oblique cell division).

POL at the cellular level

The relationship between POL and FCW in unicellular organisms is illustrated with *Chlamydomonas* and *Polytoma*,

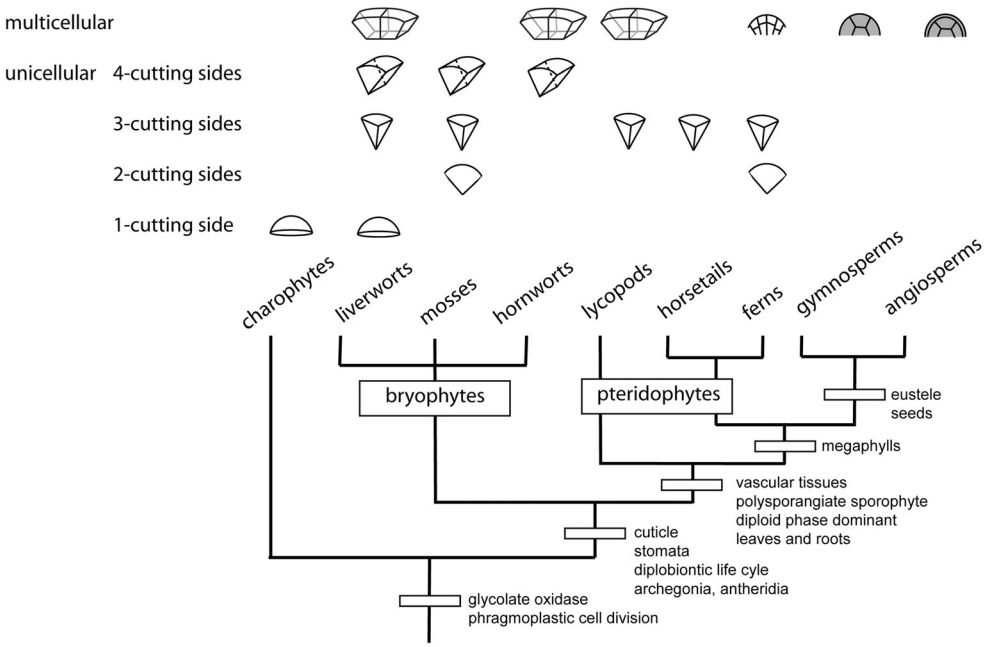

Fig. 1 A phylogeny of apical meristems. A schematic of streptophyte phylogenetic relationships and the appearance of apical meristems within different lineages. Within the charophycean algae, the apical meristem is a single, hemispherical cell with one cutting side (e.g., *Chara*; see also Fig. 7c). Within the nonvascular land plants (bryophytes), unicellular apical meristems with one, two, three, and four cutting sides occur (e.g., *Physcomitrella*; see also Fig. 7e) as well as simple multicellular meristems consisting of two cells with eight cutting sides. Within the seedless vascular plants (pteridophytes), unicellular apical meristems with two or three sides persist (e.g., *Equisetum*) in addition to simple and more complex multicellular meristems (e.g., the lycopod *Selaginella* and ferns, respectively). Large multicellular meristems occur within the seed plants (shaded areas blocked within lines denote multicellular domains). Data for bryophytes taken from Parihar (1961); data for vascular plants taken from Bierhorst (1971)

wherein the FCW is typically longitudinal with respect to the anterior-posterior cell axis, i.e., the cell is symmetrically bisected. However, the spindle apparatus sometimes rotates through a right angle before or during division such that the FCW is transverse to the original cell axis (e.g., Mosbacher 1929; see also Fritsch 1965). Cytoplasmic asymmetries occur also as a consequence of gravity. For example, proplastids occupy the upper half of *Equisetum* spores and the vegetative cells of the lycopod *Isoetes* and the alga *Enteromorpha* (Müller-Stoll 1952; Nienburg 1924; Stewart 1948). In *Equisetum*, the FCW bisects the spore beneath the proplastids (Nienburg 1924).

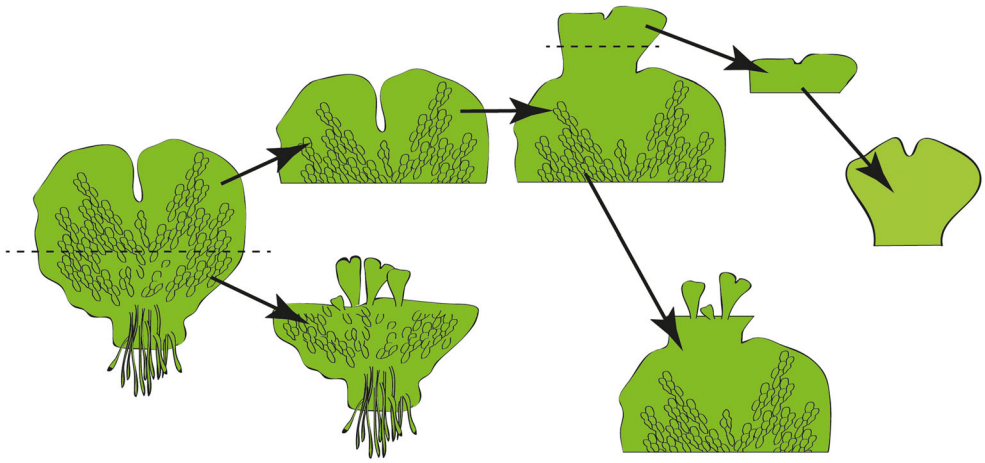

Fig. 2 Polarity in fern regeneration. Schematic of fern prothallus (gametophyte) regeneration. The heart-shaped prothallus has a multicellular apical meristem in its apical notch and produces rhizoids at the opposite end (figure on left). When bisected transversely (dashed line), the apical portion regenerates a miniature version and fails to produce rhizoids at the opposite end. The basal portion generates multiple miniature prothalli (middle figures). This pattern reiterates if the apical portion is bisected again (figures to the right). Redrawn from Albaum (1938)

Cytoskeletal POL that involves the cytoskeleton-plasma membrane-cell wall continuum also occurs in multicellular plants. For example, Miehe (1905) plasmolyzed the filaments of *Cladophora* to pull protoplasts away from cell walls (thereby breaking all intercellular connections) and observed protoplasts to enlarge, emerge from their walls, and regenerate filaments, producing rhizoids at their base and new cells above (Czaja 1930; Miehe 1905). Borowikow (1914) succeeded in reversing this POL by centrifugation. Rhizoids formed opposite the centrifugal "pole." Similar results are reported for the red alga *Griffithsia* (Schechter 1935). Centrifugation of the eggs of metazoan ascidians results in embryonic monstrosities after fertilization (Conklin 1915).

Experiments with morphologically complex coenocytic algae provide additional insights about the effects of gravity on POL. For example, the foliose thallus of *Bryopsis* is attached to a substrate by rhizoid-like outgrowths. This morphology is completely reversed when plants are inverted, i.e., the thallus forms rhizoids and the rhizoids form a new thallus (Noll 1888; Winkler 1900). Steinecke (1925) showed that cytoplasmic contents "reshuffle" during inversion. *Caulerpa* responds similarly (Dostál 1926; Janse 1906; Janse 1910), even with respect to its diageotropic "rhizomes" (Zimmermann 1923). A recent intracellular transcriptomic atlas of *Caulerpa* reveals an acropetal transcript distribution from the "rhizome" into the "leaf," which conforms roughly to a transcription-to-translation pattern (Ranjan et al. 2015; see also Menzel 1996). Thus, morphological and molecular POL is correlated.

For sessile organisms, gravity provides a reliable and ubiquitous geocentric "cue" as a spatial framework to establish POL. However, gravity is only one among many abiotic signals that can align POL, as indicated by extensive experiments using the cytologically symmetric eggs of the brown alga *Fucus*. When fertilized, the zygote develops a cell wall 2 h after fertilization, and a rhizoid 12 h later. Investigations show that the direction of light provides the strongest cue to establish zygotic POL (Fig. 3). Rhizoids always form on the side opposite the light source and FCW is perpendicular to the source (Brawley and Wetherbee 1981; Nienburg 1922a; Nienburg 1922b). Using polarized light, Jaffe (1956) showed that rhizoids typically develop in the plane of polarization. Without light, the point of sperm entry establishes a default POL (Hable and Kropf 2000; see also Kropf et al. 1999), as in the brown alga *Cystosira* (Knapp 1931). Additional studies show that zygote cell wall asymmetry also influences POL and FCW (Goodner and Quatrano 1993; Quatrano and Shaw 1997). An additional phenomenon is the "group effect" (Rosenwinge 1889). When zygotes are juxtaposed, rhizoids form on the side facing neighbors (Bloch 1943; Whitaker 1940). POL is also rheotropically sensitive (i.e., *Fucus* rhizoids form downstream of moving water at pH 6.5 (Bentrup and Jaffe 1968)), which is consistent with POL being influenced by a gradient of an extruded (as yet, unidentified) molecular signal. Thus, POL in this system manifests a "distributed causality."

POL and bioelectric fields

All cells generate electrical potential differences whose polarities can be changed. For example, inversion of *Ceratopteris* spores results in a gravity-dependent polar calcium current in less than 25 s (Salmi et al. 2011). Further, *Fucus* zygotes POL are affected by unilateral light, which relocates Ca^{2+} channels (see Fig. 3c) thereby changing Ca^{2+} levels and establishing asymmetric electrical POL (reviewed in Cove et al. 1999). In an elegant experiment, Jaffe (Jaffe 1966) placed *Fucus* zygotes in a capillary tube, illuminated them from one end (so that all of the zygotes were polarized in the same direction), measured the voltage difference across the tube during embryo development, and showed that electrical POL and morphological POL are correlated (Fig. 4).

Bioelectric fields are generated by asymmetries in charge-carrying ions. The ions can be viewed as chemicals that generate the electric fields by carrying charge, and chemicals that regulate the electric fields. The distinction can be ambiguous because generators of bioelectric fields can have regulatory functions as well as generate small bioelectric fields. In general, the bioelectric fields are generated by an asymmetry in H^+ (e.g., pH) caused by the action of asymmetrical proton-translocating ATPases on the plasma membrane, and/or plasma membrane-localized redox chains involving reactive oxygen species (see Harold 1986, 2001, 2014; Bell et al. 2009).

Multicellular organisms manifest a similar correlation between electrical and morphological POL. For example, Lund and Rosene (1947) recorded the electrical currents around the alga *Pithophora*, which flow along the lengths of individual cells, between adjoining cells, and along the entire length of the filament, all aligned with the growing apices of the filament and its lateral branches (Fig. 5). Scott and Martin (1962) recorded electrical currents over the surfaces of bean seedling roots, which changed configuration asymmetrically in a few minutes when vertical roots were placed horizontally. Changes were prominent over the "dorsal" side in the region of the apical meristem; the current direction remained unchanged along more proximal regions and along the entire lower surface (thereby mirroring a geotropic response). Reorientation also produced an asymmetrical current pattern at the root cap. No change in current pattern and no gravitropism occur in roots growing in media with submicromolar Ca^{2+} concentrations (see also Collings et al. 1992).

Logically, if bioelectric fields cause morphological POL, it should be possible to change POL by changing the direction of bioelectric fields. Although such experiments are difficult to perform, Lund and coworkers (Lund et al. 1945)

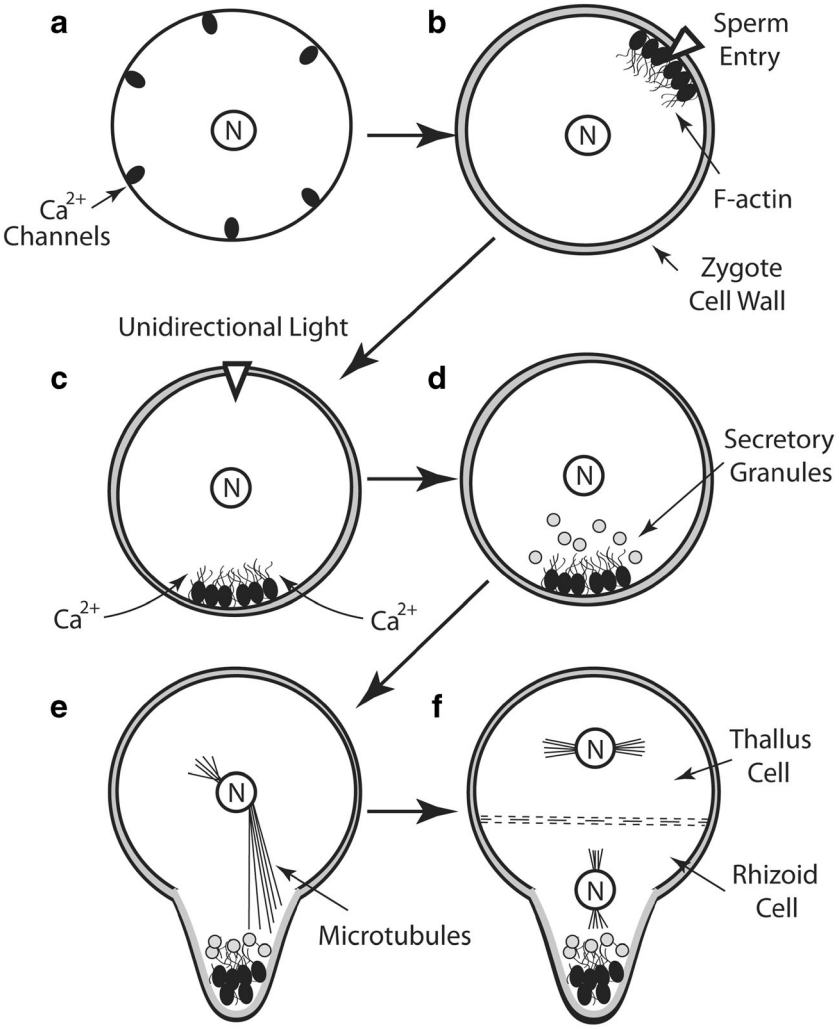

Fig. 3 Polarity in *Fucus* zygotes. The establishment of polarity and asymmetric cell division in *Fucus* zygotes. Ion channels and Ca^{2+} receptors are symmetrically distributed before fertilization (**a**) but are transported by F-actin to the site of sperm entry (**b**) and relocate to the opposite side of a unidirectional light source where localized ion channels elevate intracellular Ca^{2+} levels (**c**). Polarity becomes fixed as a result of secretory vesicle transport to the site of Ca^{2+} channels (**d**) and the cytoplasmic (and cell wall) asymmetry at the rhizoid pole continues to direct F-actin transport and directs the orientation of the spindle for the first cell division (**e**, **f**). N nucleus. Adapted from Cove et al. (1999)

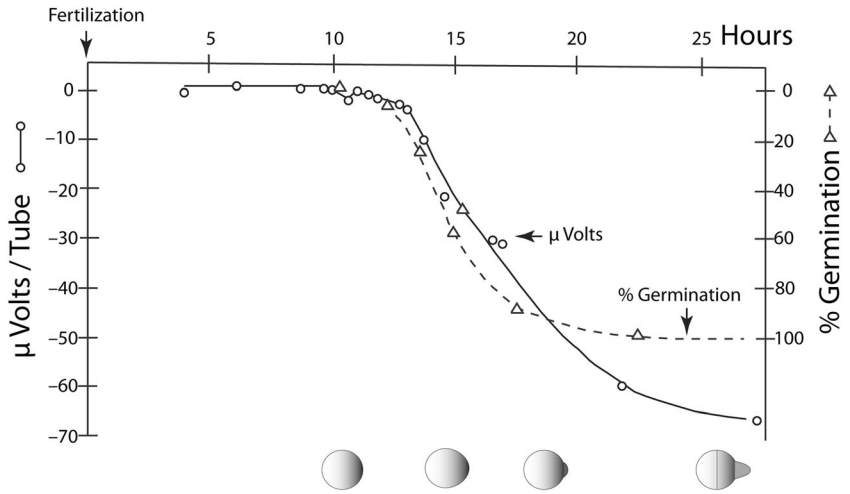

Fig. 4 *Fucus* electrical and morphological polarities. Nomograph of the relationship between electrical and morphological polarity, and the percentage of *Fucus* zygote germination over a time course of 25 h. *Fucus* zygotes were placed in a capillary tube and exposed to a unilateral light source at one end to polarize and synchronize germination. The intensity of the electrical field across the length of the tube was measured over the course subsequent development. As the percentage of germination increased the voltage differential increased, reaching its maximum at 100% germination at approximately the same time the first zygotic division occurred (see four drawings at bottom). Redrawn from Jaffe (1966)

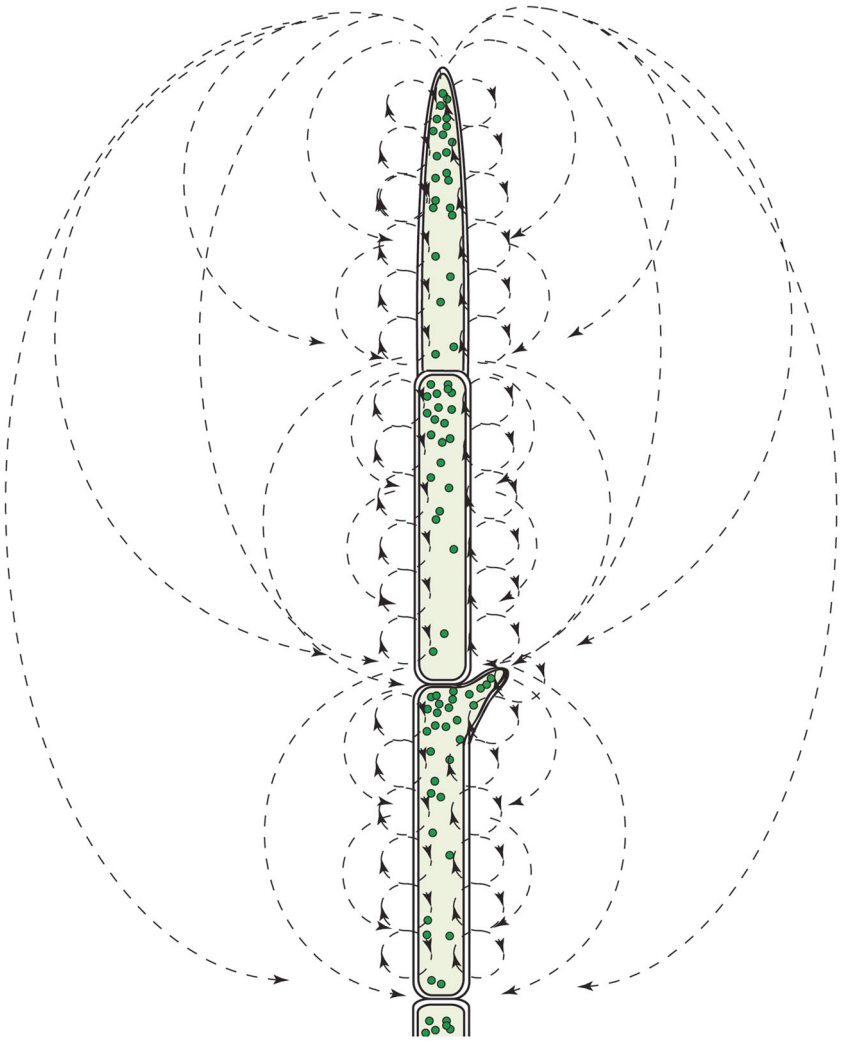

Fig. 5 Electrical polarity. Schematic of the electrical field generated by and around a branching filament of the green alga *Pithophora*. Currents form around individual cells, groups of cells, and along the entire length of the filament (dashed lines with arrows denote + to – current directions). Note the currents generated around the asymmetric cell second from the bottom (see Fig. 6a). Redrawn from Lund and Rosene (1947)

completely inhibited the growth in length by passing an electric current upward along the length of onion roots, whereas a current in the opposite direction had no observable effect.

POL and intercellular connections

Once multicellularity was achieved in which one or more cells was surrounded and not in direct contact with the external medium, bidirectional POL became increasingly necessary. Benítez and coworkers (Benítez et al. 2018) have drawn attention to the importance of intercellular POL facilitated by cytoplasmic connections, e.g., the plasmodesmata of land plants, septal pores of fungi, and trumpet cells of brown kelps (Bloemendal and Kuck 2013; Hernández- Hernández et al. 2012; Terauchi et al. 2015). Ultrastructural studies reveal that intercellular distribution of connections can provide rapid asymmetric bidirectional nutrient and signaling molecule transport (e.g., photosynthates and IAA, respectively). For example, Nagasato and coworkers (Nagasato et al. 2017) report that fluorescent dyes move faster basipetally than acropetally in the brown alga *Halopteris congesta*. Likewise, Kitagawa and Fujita (2013) observed unidirectional transport of the photoconvertible dye Dendra2 in *Physcomitrella* protonema. Intercellular connections exist in the sister group of the land plants, the charophycean algae (e.g., *Chara zeylanica*). However, they are less specialized than those in the land plants (Cook et al. 1997).

Different taxa have the capacity to precisely control the distribution of intercellular connections (Imaichi and Hiratsuka 2007; Imaichi et al. 2018) and their aperture size thereby controlling cytoplasmic fluxes and concentration gradients (Christensen et al. 2009; Sager and Lee 2014). The aperture size of land plant plasmodesmata is regulated by the deposition and degradation of callose within the walls around plasmodesmata (De Storme and Geelen 2014). Callose turnover involves several protein families including GLUCAN SYNTHASE LIKE (GSL) proteins and β-glucanases, which

respectively synthesize and degrade callose (De Storme and Geelen 2014; Guseman et al. 2010; Ruan et al. 2004; see also Benítez et al. 2018). The amount of callose around plasmodesmata is correlated with the genetic expression of GSLs and β-glucanases, and the intercellular migration of signaling molecules (Benitez-Alfonso et al. 2013; Guseman et al. 2010; Ruan et al. 2004; Vatén et al. 2011). For example, using an inducible knockdown mutation of *GSL8*, Han and coworkers reported that the reduced callose deposition at plasmodesmata in *Arabidopsis* hypocotyls enhances IAA diffusion. The loss of an asymmetric IAA distribution prevented differential cell elongation between the shaded and unshaded sides of the hypocotyl required for a normal phototropic response (Han et al. 2014). These and other observations (e.g., Brunkard and Zambryski 2017) indicate that the regulation of plasmodesmata apertures affects IAA transport, the establishment of IAA concentration gradients, and thus POL at the organismic level. However, this is still an open avenue of research because the probe used by Han and collaborators (2014) is blind to any IAA within membraneous compartments and previous work shows that cell-cell auxin transport is not always inhibited when plasmodesmata are severed (Cande and Ray 1976; Drake et al. 1978). Moreover, there are other molecules involved in PD integrity and gating, such as myosins and actin cytoskeleton (Reichelt et al. 1999; Volkmann et al. 2003), which could be interacting with callose in complex ways.

POL and intracellular IAA gradients

Auxins, particular indole-3-acetic acid (IAA), are crucial in land plant development (Zažímalová et al. 2014). IAA mobility is driven mainly by active transport into and out of cells, but auxin influx can also result from the passive diffusion of the protonated form of IAA across the plasma membrane. Active influx is mediated by the transport of the dissociated, anionic form (IAA−) by a permease $2H^+$-IAA co-transporter (e.g., AUX1), whereas active efflux of IAA requires auxin anion efflux carriers. Several protein families are known to transport IAA in *Arabidopsis thaliana*, but the PIN-FORMED (PIN) constitutes the best studied efflux carrier family. *Arabidopsis* has eight PIN transporters, most of which localize at the plasma membrane (Feraru and Friml 2008). These proteins are actively sorted to specific domains of the plasma membrane and can thus anisotropically direct auxin effluxes (Adamowski and Friml 2015; Blilou et al. 2005; Feraru and Friml 2008; Wisniewska et al. 2006). PIN polar localization within cells gives rise to polar cell-to-cell transport, which can scale up to tissue- and organ-level patterning. Indeed, *pin* mutations alter IAA patterning and have significant phenotypic effects, e.g., changes in the morphology of shoot and root apical meristems (Blilou et al. 2005; Okada et al. 1991).

The study of PIN intracellular dynamics has uncovered some of the biochemical and physical regulators of IAA polar transport. Interestingly, evidence suggests that PINs are important to regulate their own POL, possibly via coupled feedbacks (Geldner 2009; Hernández- Hernández et al. 2018; Niklas and Kutschera 2012). Mechanical forces acting at the tissue and plasma membrane level also seem to regulate PIN localization, and therefore IAA polarization patterns. Specifically, there is evidence that the localization of the auxin transporter PIN1 and microtubule array orientation respond to a shared upstream biomechanical regulator as evidenced by mathematical modeling consistent with a biophysical coupling feedback loop between auxin transport in shoot apical meristems, i.e., the orientation of the microtubule cytoskeleton, which is correlated with PIN1 orientation, is affected by biomechanical stress fields (Heisler et al. 2010).

However, IAA also acts to loosen the cell-wall and to modify localized responses to mechanical forces (Braybrook and Peaucelle 2013; Feraru et al. 2011; Heisler et al. 2010; Hernández- Hernández et al. 2018; Zwiewka et al. 2015). Further, PINs appear to directly or indirectly regulate proteins involved in endocytosis and vesicle formation, and therefore PIN intracellular transport and polar localization in the membrane. Some of the molecules potentially involved in this second feedback loop are GNOM (a vesicle transport regulator), PINOID (a AGC-kinase that regulates PIN polarity), and rho-GTPases affecting endocytosis and actin filament assembly: (Benjamins et al. 2001; Geldner 2009; Kleine-Vehn et al. 2008; Lehman et al. 2017; Lin et al. 2013; Lin et al. 2012; Reinhardt et al. 2003; Sukumar et al. 2009). Collectively, our current knowledge suggests that mechanical and chemical factors act as a physico-genetic module to initiate, amplify, and maintain the polarization patterns of the PIN auxin efflux carriers (Geldner 2009; Hernández- Hernández et al. 2018).

Although there are clear differences between the molecules involved in plant and animal POL, some common elements and dynamical motifs are recognizable in these two independently evolved systems. For example, rho-GTPases are key factors in the polarization processes in plants, yeast, and animals, wherein they help organize actin filaments guiding more activated GTPases (Geldner 2009; Lin et al. 2013; Lin et al. 2012). As further discussed below, the Rho family is a central player in the PAR (partitioning defective complex) cytoskeletal scaffolding apparatus underlying planar cell polarity in animals. However, the main pattern emerging from the comparison of intracellular-to-intercellular polarity in different lineages is that plant and animal systems rely on the spontaneous generation of POL from the amplification of small spatial differences, possibly initiated by diffusion and amplified by physico-genetic modules of diverse molecular identities (Geldner 2009).

FCW and POL

A general theory predicting FCW remains elusive. Hofmeister (1863) noted that cell growth precedes division and that FCW normally forms at 90° angle to the longitudinal axis of dividing cells. This observation is consistent with how cells divide in *Spirogyra*, *Ulothrix*, and the red alga *Bangia*. However, cell growth need not precede FCW (e.g., palintomy in *Volvox*) and "Hofmeister's rule" is violated frequently (e.g., oblique walls in moss protonema). Plateau (1873) predicted that FCW minimizes the new wall's surface area, an idea promulgated by Berthold (1886) and Errera (1888). Although Sachs (1878) agreed that new walls often meet old walls at 90° angles, even when requiring curved walls, he rejected the minimum surface area hypothesis, which was nevertheless recapitulated by D'Arcy Thompson (Thompson and Whyte 1942).

The idea that FCW is influenced by mechanical forces can be traced to Kny (1902), who applied unidirectional pressure on dividing cells and observed mitotic figures to rotate 90° such that FCW was parallel to the direction of the applied force. More recent experiments confirm that externally applied compression affects FCW (e.g., Lintilhac and Vesecky 1984). However, it is not clear whether *endogenous* mechanical forces generate FCW patterns, and, it is difficult to conceive of how mechanical forces per se dictate FCW in unicellular organisms, although they do affect FCW patterns in tissues (e.g., Beauzamy et al. 2015; Louveaux et al. 2016).

Regardless of how the FCW is prefigured, changes in POL are required to produce even simple body plans such as a branched filament. For example, in the green alga *Cladophora*, branching is achieved by the formation of a localized outgrowth in the cell wall, which subsequently forms a new cell by forming an oblique cell wall at its base (Fig. 6a; see also Fig. 5). Using the coenocytic yellow-green alga *Vaucheria*, Kataoka (1975) found that blue light stimulated localized outgrowth attended by an outward electrical current (lasting 1 hour) that reversed direction and continued as the new branch developed. *Physcomitrella* protonema branch similarly (Fig. 6b, c), and produce a unicellular apical meristem initiated by a subsequent oblique division forming a pyramidal cell with three "cutting faces" (see Fig. 7e). In each case, POL must change within a cell. It is worth noting that the formation of branches in *Cladophora*, *Vaucheria*, and *Physcomitrella* protonema differs from that of how transverse walls normally form because it requires a localized reduction in the yield stress of a previously formed wall and the localized delivery of new wall materials to the extruding tip. Both processes occur in other algae, fungal hyphae, and in numerous specialized biological systems, e.g., the formation of *Spirogyra* conjugation tubes and the "tip growth" of pollen grains, branched unicellular trichomes, and root hairs (see Geitmann and Ortega 2009, and Majda et al. 2017).

FCW, POL, and meristems

Our review of POL and FCW and the appearance of land plant meristems (see Fig. 1) suggests a simple scenario for the evolution of land plant multicellularity and localized meristematic activity: (1) polarity in the unicellular ancestor involved an antero-posterior cytoskeleton-plasma membrane-cell wall asymmetry, which provided an invariant reference system for FCW (Fig. 7a), (2) this ancestral polarity served as a reference system for FCW in the filamentous body plan of its descendants that achieved ID unidirectional cell division (Fig. 7b), (3) a systemic "organismic" POL was subsequently achieved with an intercellular transport system, (4) with the acquisition of a sessile growth habit, systemic POL provided a context within which cytoskeletal POL could shift FCW from 1D to 2D and subsequently to 3D (Fig. 7c–e), and (5) regional domains of POL and FCW activity evolved into more complex meristems (Fig. 7e, f), particularly in terms of intercellular domains created by plasmodesmatal networks (Ligrone and Duckett 1998; Imaichi and Hiratsuka 2007; Imaichi et al. 2018).

A critical aspect of this scenario is the appearance of systemic POL permitting FCW to change direction within a cell. This form of POL may not have been difficult to achieve because a sessile growth habit provides a "global" framework for POL. This is evident even at the unicellular level when zygotes and zoospores attach to a substrate, undergo uneven transverse cell division, and produce a rhizoid at one end (see Fig. 3e, f). The presence of bioelectric fields around simple filamentous sessile algae provides evidence for systemic asymmetric antero-posterior POL (see Fig. 5). It is not unreasonable therefore to assume that this POL will be amplified and "internalized" with increasing body size because of the necessity for bi-directional transport. In a very real sense, the evolution of multicellularity drove the evolution of POL and FCW just as the evolution of POL and FCW drove the evolution of more complex multicellularity.

Currently, little is known about the genetics involved in the 1D-to-2D or a 2D-to-3D transition. However, a recent study highlights in importance of the CLAVATA peptide and a receptor-like kinase pathway in the land plants (Whitewoods et al. 2018). This system is unknown among the green algae (which achieve 1D and 2D polarity; see Fig. 7b, c). It is thus unique to the land plants. Using the 2D protonema-to-3D gametophore transition in *Physcomitrella* (see Fig. 7d, e), Whitewoods and coworkers report that 3D fails in the absence of the CLAVATA peptide and a receptor-like kinase pathway (Whitewoods et al. 2018). While on this topic, Skopelitis et al. (2017) have demonstrated that sharp developmental boundaries associated with foliar leaf dorsiventrality can be generated by the threshold-based readout of counter-gradients of mobile small RNAs. This system is analogous to morphogen systems in animal systems.

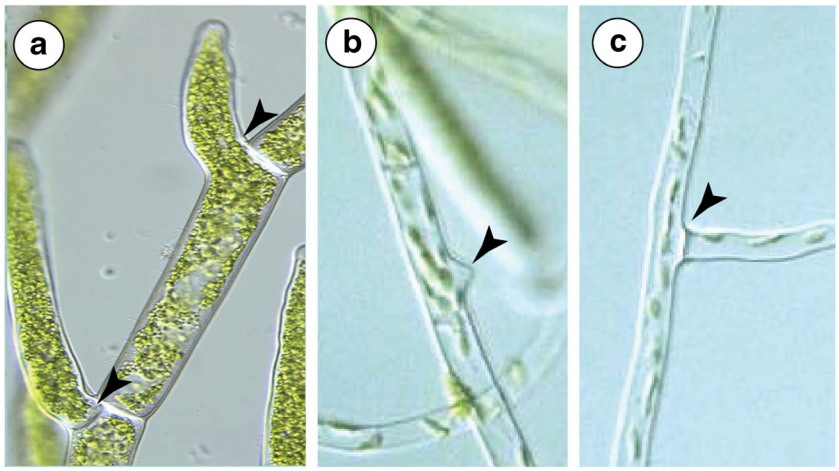

Fig. 6 Asymmetric cell divisions. Asymmetric cell divisions in the filaments of the green alga *Cladophora* (**a**) and moss protonema (**b**, **c**). **a** Arrowheads indicate where asymmetric division is beginning (upper arrow) and where it has occurred (lower arrow). The oblique wall at the base of the lateral filament (bottom arrow) differs in orientation from the transverse wall just above it. **b**, **c** As in the case of *Cladophora*, asymmetric division in the moss protonema begins as a lateral bulge (**b**) that extends in length before a wall is formed at the base of the branch (see Fig. 7d)

Plasticity of POL in volvocine algae

Unlike most multicellular algae and land plants, volvocine algae can undergo morphogenetic movements that are similar to gastrulation in metazoans (Höhn and Hallmann 2011; Höhn and Hallmann 2016; Matt and Umen 2016), because even when attached to each other, their cells are not cemented by rigid materials. Initially cells are attached by numerous cytoplasmic bridges (CBs), the result of incomplete cytokinesis, which appear to be functionally analogous, but not homologous to plasmodesmata. This flexible association (different from the transient cadherin-based attachments of embryonic animal cells) permits the cell sheets to undergo inversion (Höhn and Hallmann 2011; Hoops et al. 2005). In addition to the uncharacteristic (for plants) cell-sheet flexibility, the individual cells of volvocines (in contrast to their unicellular relative, *Chlamydomonas*) lack rigid cell walls but have a flexible glycocalyx, enabling active cell shape changes that accompany and apparently promote inversion. This plasticity of orientation, axiation, and asymmetry in cells that start out with intrinsic polarity permits these organisms to employ POL in way akin to that in animal embryos.

As in metazoan embryos, folding or bending of the volvocine cell sheet is achieved by changes in cell shape and concerted movements of cells with respect to the CB system. But unlike most gastrulating animal embryos, cell division is completed before the beginning of inversion. Furthermore, the cells, being directly connected to one another, do not change their position relative to their neighbors, so migration or intercalation is not involved. This makes the reorientation of POL, accompanied by changes in cell size and shape, the basis of morphogenesis in these algae.

A nonrigid extracellular matrix appears after inversion, but its absence beforehand means that volvocine cells, unlike those of typical plants, can readily change their shape. During inversion, *V. carteri* cells are spindle-shaped, flask-shaped, or columnar, whereas those of *V. globator* are spindle-shaped, teardrop-shaped, paddle-shaped, or pencil-shaped in different regions at different stages. In all cases, the cells are intrinsically polarized, much the same as the unicellular *Chlamydomonas*, with the nucleus located at the apical end, below the site of the incipient flagella, with the chloroplast at the basal end. The position of the CB system changes relative to these components during inversion of the cell sheets, moving from a mid-cellular location to the basal portion of the coupled cells in *V. globator* (Höhn and Hallmann 2011).

A physical model presented by Höhn et al. (2015) highlights the "generic" similarities (in the sense of being predictable from the physics of nonliving materials (Newman and Comper 1990)) of these POL-dependent morphogenetic movements to those of animal systems, notwithstanding the added constraint in the volvocines of conservation of nearest-neighbor relationships.

Comparison of POL in metazoans and prokaryotes

Although this Review focuses on POL in photosynthetic eukaryotes, comparison with the POL DPM in animal and certain bacterial systems helps to specify the particularities of our main subjects. Animal cells exhibit two distinct kinds of polarity, apicobasal (A/B) and planar cell polarity (PCP). The first serves to make the cell surface nonuniform by inserting different sets of integral membrane proteins on different portions (e.g., apical, basolateral) of the plasma membrane. The second changes the shape of the cell or the orientation of a surface appendage (e.g., a bristle, a cilium). In the

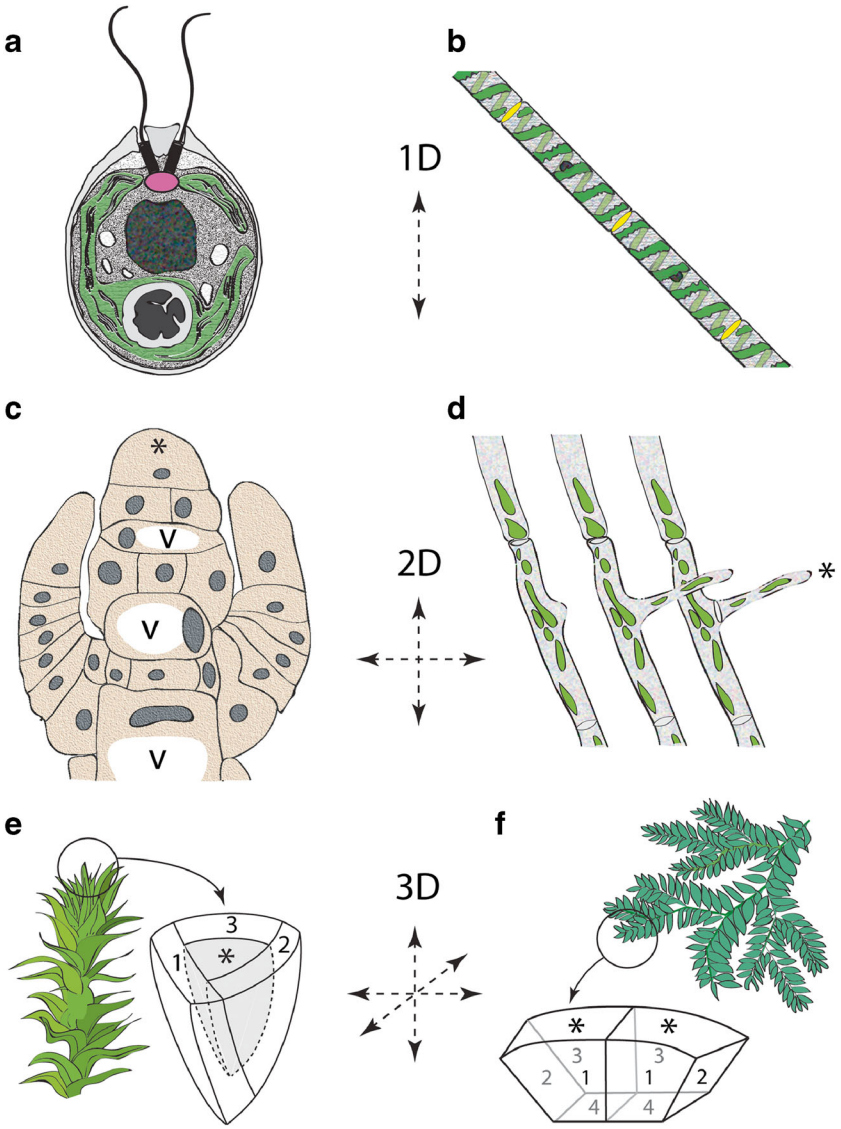

Fig. 7 Evolution of POL and FCW. Schematics of unicellular and multicellular plants arranged to illustrate a scenario for the evolution of land plant multicellularity and apical meristems with increasing complexity. Centered dashed lines and arrows denote planes of division (1D, 2D, and 3D). The organisms depicted here are not intended to suggest phylogenetic relationships. **a** POL and FCW in unicellular algae are established by an asymmetric cytoskeleton-plasma membrane-cell wall continuum (e.g., *Chlamydomonas*). FCW occurs in only one plane. **b** POL and FCW in a simple unbranched alga are also established by asymmetric cytoskeletons and cell-to-cell end wall. FCW occurs in only one plane. **c**, **d** Among sessile plants, POL becomes systemic at the organismic level by means of localized apical growth (denoted by *) and intercellular transport. Adjustment of POL at the cellular level can reorient FCW to achieve cell division in two directions (e.g., 2D in *Chara*, *Cladophora*, and moss protonema) (see Fig. 6). **e**, **f** POL in apical cells (denoted by *) reposition FCW to achieve two or more "cutting sides" (indicated by numbers). Systemic POL and FCW are coordinated within the plant body by intercellular symplastic transport and signaling systems (e.g., plasmodesmata and IAA, respectively). V vacuole

multicellular context these are manifested as two different POL-type DPMs (Newman and Bhat 2009), POL_a, which leads, for example, to the formation of lumens in clusters of cell (Bedzhov and Zernicka-Goetz 2014), and POL_p, which by enabling cell-cell intercalation, leads to the tissue reshaping phenomenon known as convergent extension (Skoglund and Keller 2010).

Both A/B and PCP are elicited in animal cells by the metazoan-specific short-range morphogen Wnt (Karner et al. 2006a; Karner et al. 2006b), via a common cytoskeletal scaffolding complex termed PAR (Lang and Munro 2017), though using some different adaptor molecules. Polarity is stabilized in animal tissues by interactions of cells with their neighbors and extracellular matrices via transmembrane cadherin and integrin proteins (Allam et al. 2018). Plant cells lack the PAR complex and these surface molecules. However, their PINs serve analogous polarity-inducing functions. Interestingly, however, two of the key components of PAR,

the Rho family kinase Cdc42, a cell cycle regular, and the calcium-dependent scaffolding protein MO25 (also called Cab29) are both present in yeast, where they are similarly involved in polarity generation (Halatek et al. 2018; Mendoza et al. 2005). Other enzymes conserved between yeast and metazoans are also suspected of participating in establishing polarity (Lee et al. 2018), suggesting deep divergence between cell polarization in plants, on the one hand, and opisthokonts, the group comprising fungi, metazoans, and unicellular holozoans, on the other.

Polarity in prokaryotes has been well-studied (Bowman et al. 2011; Dworkin 2009). One illuminating comparison to plants involves the myxobacteria, which exhibit changes in polarity at the single-cell level, changing reversibly from a round, symmetrical form, the spore, to a rod-shaped vegetative form (LaRossa et al. 1983). These cells also undergo multicellular morphogenesis (swarming and fruiting body formation) (Hartzell 2016; Kaiser 2008; Whitworth and American Society for Microbiology. 2008; Yang and Higgs 2014), exhibiting therefore the POL DPM as well. A cell wall stabilizes the shape asymmetry of the developmentally competent bacteria (as in most plant cells, but unlike the cells of volvocine algae and animals during their developmental stages). Unlike multicellular plants, however, the cell wall does not cement the cells together, but allows for gliding, with nearest neighbors continually changing.

In *Myxococcus xanthus*, a model myxobacteria, the molecular components associated with cellular differentiation and communication are integrated in a regulatory network that includes transcription factors, membrane proteins, protein kinases, scaffold proteins, and enzymes (Arias Del Angel et al. 2018). POL in myxobacteria is more like that of animal embryos, where the cells are also independently mobile, than the volvocines, where the cells are harnessed together by systems of cytoplasmic bridges. As we have seen, the uses of polarity in typical multicellular plants are unlike any of these.

Conclusions: POL, ion channels, and symmetry breaking

Following the advice of George Gore (1878), our review of the literature leads us to conclude that asymmetry in cytosolic ion concentrations resulting from changes in ion channel and pump location, activity, or type is an ancient phylogenetically common denominator with which to achieve POL and thus orient FCW. If correct, the "default" ancestral condition was a unicellular organism lacking a structurally polarized cytoskeleton enveloped by a more or less uniform cell membrane and a more or less uniform cell wall (e.g., coccoidal prokaryotes, *Fucus* eggs). This cytoskeleton-plasma membrane-cell wall symmetry was broken evolutionarily in different ways to achieve more complex POL and FCW. In some lineages, asymmetry relied on external cues (e.g., gravity or light). In others, asymmetry evolved as a consequence of morphological and physiological specializations, such as flagella at the anterior end of the cell (e.g., *Chlamydomonas*). With the advent of simple multicellularity POL and FCW involved interas well as intracellular gradients. Complex multicellularity and meristematic growth were achieved by the ability to manifest 1D to 2D and then 3D POL and FCW.

Symmetry breaking in the streptophytes likely involved Ca^{2+} channels and pumps. Ca^{2+} fluxes are associated with every example of POL thus far reported in this clade. The regulation of cytoplasmic Ca^{2+} is a major link between bioelectrical signaling and cellular activity. However, calcium is a cytotoxin for organisms relying on phosphate metabolism for energy because it binds with phosphate to form hydroxyapatite (Wayne 2009). Therefore, phosphate-dependent organisms have to prevent high concentrations of calcium in extracellular spaces from mixing with cytosolic phosphate. This is achieved by Ca^{2+} pumps that maintain low cytosolic Ca^{2+} levels. With the evolution of Ca^{2+} channels, calcium could serve as an efficient signaling molecule because of its potential toxicity and low intracellular concentration. Only three components are necessary: (1) gated calcium channels for the rapid intra- and extracellular transport of messenger ions, (2) Ca^{2+} pumps and sequestering proteins to restore the resting level of Ca^{2+} and regulate signal durations, and (3) regulatory molecules able to sense intracellular Ca^{2+} concentrations. Ionic channels that extrude Ca^{2+} and deliver external K^+ exist in prokaryotes (Hille 1992). Consequently, given their ancestral capacities to redistribute proteins, the first eukaryotes had only to change membrane proteins to control cytoplasmic Ca^{2+}.

Because any mechanical, electrical, or chemical change in the plasma membrane is, in theory, capable of opening Ca^{2+} channels, calcium can serve as a "secondary" messenger in a vast constellation of metabolic processes (Weber 1976). Extensive research on plants shows that Ca^{2+} channels become activated (followed by dramatic increases in cytosolic Ca^{2+}) by mechanical perturbation (e.g., vibration and touch), growth-altering substances (e.g., brassinosteroids and jasmonates), and abiotic factors (e.g., light and gravity). Thus, Ca^{2+} channels permit diverse kinds of stimuli to evoke similar or identical responses.

What is unclear is how cells discriminate among different stimuli. Theoretically, we expect organisms to evolve signal-specific sensory systems permitting them to respond in adaptively different ways to different environmental cues. This may help to explain why there are many different kinds of Ca^{2+} channels that may trigger different subcellular systems. Each channel is a protein, made up of one or more polypeptides forming a hydrophilic pore in a membrane. Although each allows Ca^{2+} to pass relatively unimpeded at a rate of about 10^6 s^{-1} or more (Wayne 2009), channels can be either nonselective, or highly selective for Ca^{2+} depending on their

pore size and the charge density of their binding sites—properties that depend on protein structure, which can vary among channels. Thus, many types of Ca^{2+} channels can occupy the same membrane. This variation in protein structure and size provides a mechanism whereby different signals can be perceived and redirected differently.

Finally, because the origins of POL and FCW are polyphyletic and have been achieved in different ways in different lineages, each is a true dynamical patterning module. Since differential gene expression within a cell is incapable of achieving either and since it is obvious that both occur in unicellular organisms, changes in either or both modules must rely on changes in gene expression patterns using internal or external cues. One example of the latter is the blue light receptor aureochrome (AUREO) found in photosynthetic stramenopiles (see Takahashi 2016). Within this clade, AUREO participates in rhizoid formation (e.g., *Fucus*), cell shape regulation (e.g., *Vaucheria*), and chloroplast movement (e.g., *Vaucheria*). Takahashi and coworkers reported that AUREO1 has a bZIP domain and a light-oxygen-voltage domain that operate as a transcription factor, binding to a specific *cis* element consensus sequence TGACGT when cells are irradiated with blue light (Takahashi et al. 2007). It was further shown that under oxidative conditions AUREO1 forms a dimer at its bZIP region by means of disulfide bonds (Hisatomi et al. 2014). Although the genes that AUREO activates or silences are currently unknown, it is clear that AUREO is involved in a diverse range of morphogenetic responses affecting POL and FCW in a large clade of eukaryotic organisms.

> "*Every event has many surrounding antecedents, and they may be divided into those which are separable from the event, and those which are not; and the cause of an event is always to be found amongst the inseparable ones only. In ordinary language, the most probable cause of an event is, a priori, that circumstance which, in the greatest number of cases, immediately precedes or accompanies it.*" — Gore (1878)

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

References

Adamowski M, Friml J (2015) PIN-dependent auxin transport: action, regulation, and evolution. Plant Cell 27:20–32. https://doi.org/10.1105/tpc.114.134874

Albaum HG (1938) Normal growth, regeneration and adventitious outgrowth formation in fern prothallia. Am J Bot 25:37–44

Allam AH, Charnley M, Russell SM (2018) Context-specific mechanisms of cell polarity regulation. J Mol Biol 430:3457–3471

Allman GJ (1864) Report on the present state of our knowledge of the reproductive system in Hydroida. Rept British Assoc Adv Sci 1863: 351–426

Arias Del Angel JA, Escalante AE, Martinez-Castilla LP, Benitez M (2018) Cell-fate determination in *Myxococcus xanthus* development: network dynamics and novel predictions. Develop Growth Differ 60:121–129. https://doi.org/10.1111/dgd.12424

Beauzamy L, Louveaux M, Hamant O, Boudaoud A (2015) Mechanically, the shoot apical meristem of *Arabidopsis* behaves like a shell inflated by a pressure of about 1 MPa. Front Plant Sci 6:1038. https://doi.org/10.3389/fpls.2015.01038

Bedzhov I, Zernicka-Goetz M (2014) Self-organizing properties of mouse pluripotent cells initiate morphogenesis upon implantation. Cell 156:1032–1044. https://doi.org/10.1016/j.cell.2014.01.023

Bell E, Takeda S, Dolan L (2009) Reactive oxygen species in growth and development. In del Río LA,Puppo A (eds) Reactive oxygen species in plant signaling. Springer, Berlin pp 43–55

Benítez M, Hernández- Hernández V, Newman SA, Niklas KJ (2018) Dynamical patterning modules, biogeneric materials, and the evolution of multicellularity in plants. Frontiers in Plant Science. https://doi.org/10.3389/fpls.2018.00

Benitez-Alfonso Y, Faulkner C, Pendle A, Miyashima S, Helariutta Y, Maule A (2013) Symplastic intercellular connectivity regulates lateral root patterning. Dev Cell 26:136–147. https://doi.org/10.1016/j.devcel.2013.06.010

Benjamins R, Quint A, Weijers D, Hooykaas P, Offringa R (2001) The PINOID protein kinase regulates organ development in *Arabidopsis* by enhancing polar auxin transport. Development 128:4057–4067

Bentrup FW, Jaffe LF (1968) Analyzing the "group effect": rheotropic responses of developing *Fucus* eggs. Protoplasma 65:25–35

Berthold GDW (1886) Studien über protoplasmamechanik. A. Felix, Leipzig

Bierhorst DW (1971) Morphology of vascular plants. In: The Macmillan biology series. Macmillan, New York

Blilou I, Xu J, Wildwater M, Willemsen V, Paponov I, Friml J, Heidstra R, Aida M, Palme K, Scheres B (2005) The PIN auxin efflux facilitator network controls growth and patterning in *Arabidopsis* roots. Nature 433:39–44. https://doi.org/10.1038/nature03184

Bloch R (1943) Polarity in plants. Bot Rev 9:261–310

Bloemendal S, Kuck U (2013) Cell-to-cell communication in plants, animals, and fungi: a comparative review. Naturwissenschaften 100:3–19. https://doi.org/10.1007/s00114-012-0988-z

Borowikow GA (1914) La polarité renverse le *Cladophora glomerate*. Bull Jard Bot Pierre Grand 14:475–481

Bowman GR, Lyuksyutova AI, Shapiro L (2011) Bacterial polarity. Curr Opin Cell Biol 23:71–77. https://doi.org/10.1016/j.ceb.2010.10.013

Brawley SH, Wetherbee R (1981) The biology of seaweeds. In: Lobban CS, Wynne MJ (eds) Cytology and ultrastructure. Blackwell, Oxford, pp 248–299

Braybrook SA, Peaucelle A (2013) Mechano-chemical aspects of organ formation in *Arabidopsis thaliana*: the relationship between auxin and pectin. PLoS One 8:e57813. https://doi.org/10.1371/journal.pone.0057813

Brunkard JO, Zambryski PC (2017) Plasmodesmata enable multicellularity: new insights into their evolution, biogenesis, and functions in

development and immunity. Curr Opin Plant Biol 35:76–83. https://doi.org/10.1016/j.pbi.2016.11.007
Cande WZ, Ray PI (1976) Nature of cell-to-cell transfer of auxin in polar transport. Planta 129:43–52
Christensen NM, Faulkner C, Oparka K (2009) Evidence for unidirectional flow through plasmodesmata. Plant Physiol 150:96–104. https://doi.org/10.1104/pp.109.137083
Collings DA, White RG, Overall RL (1992) Ionic current changes associated with the gravity-induced bending response in roots of *Zea mays*. L Plant Physiol 100:1417–1426
Conklin EG (1915) Heredity and environment in the development of men. Norman W Harris lectures for 1914 at Northwestern University. Princeton University Press, Princeton
Cook M, Graham L, Botha C, Lavin C (1997) Comparative ultrastructure of plasmodesmata of Chara and selected bryophytes: toward an elucidation of the evolutionary origin of plant plasmodesmata. Am J Bot 84:1169–1178
Cove DJ, Hope IA, Quatrano RS (1999) Polarity in biological systems. In: Russo VEA, Cove DJ, Edgar LG, Jaenisch R, Salamini F (eds) Development. Genetics, epigenetics and environmental regulation. Springer-Verlag, Berlin, pp 507–524
Czaja AT (1930) Zellphysiologische untersuchungen an *Cladophora glomerate* Isolierung, regeneration und polarität. Protoplasma 11: 197–220
De Storme N, Geelen D (2014) Callose homeostasis at plasmodesmata: molecular regulators and developmental relevance. Front Plant Sci 5:138. https://doi.org/10.3389/fpls.2014.00138
Dostál R (1926) Zur Kenntnis der inneren Gestaltungsfaktoren bei *Caulerpa prolifera*. Ber Deutsch Bot Ges 44:56–66
Drake GA, Carr DJ, Anderson WP (1978) Plasmolysis, plasmodesmata, and the electrical coupling of oat coleoptile cells. J Exp Bot 29: 1205–1214
Dworkin J (2009) Cellular polarity in prokaryotic organisms. Cold Spring Harb Perspect Biol 1:a003368. https://doi.org/10.1101/cshperspect.a003368
Errera L (1888) Über Zellformen und Seifenblasen. Bot Centralbl 34: 395–398
Feraru E, Friml J (2008) PIN polar targeting. Plant Physiol 147:1553–1559. https://doi.org/10.1104/pp.108.121756
Feraru E, Feraru MI, Kleine-Vehn J, Martiniére A, Mouille G, Vanneste S, Vernhettes S, Runions J, Friml J (2011) PIN polarity maintenance by the cell wall in *Arabidopsis*. Curr Biol 21:338–343. https://doi.org/10.1016/j.cub.2011.01.036
Fitting H (1938) Die Umkehrbarkeit der durch Aussenfaktoren induzierten Dorsiventralität. Jahrb Wiss Bot 86:107–227
Fritsch FE (1965) The structure and reproduction of the algae vol I. Cambridge University Press, Cambridge
Geitmann A, Ortega JK (2009) Mechanics and modeling of plant cell growth. Trends Plant Sci 14:467–478. https://doi.org/10.1016/j.tplants.2009.07.006
Geldner N (2009) Cell polarity in plants: a PARspective on PINs. Curr Opin Plant Biol 12:42–48. https://doi.org/10.1016/j.pbi.2008.09.009
Goodner B, Quatrano RS (1993) *Fucus* embryogenesis: a model to study the establishment of polarity. Plant Cell 5:1471–1481. https://doi.org/10.1105/tpc.5.10.1471
Gore G (1878) The art of scientific discovery. Longmans, Green, and Co., London
Gratzy-Wardengg SAE (1929) Osmotische Untersuchungen an Farnprothallien. Planta 7:307–339
Guseman JM, Lee JS, Bogenschutz NL, Peterson KM, Virata RE, Xie B, Kanaoka MM, Hong Z, Torii KU (2010) Dysregulation of cell-to-cell connectivity and stomatal patterning by loss-of-function mutation in *Arabidopsis chorus* (glucan synthase-like 8). Development 137:1731–1741. https://doi.org/10.1242/dev.049197
Haberlandt G (1914) Zur Entwicklungsphysiologie der Rhizoiden. Sitz Akad Wiss Physik-Math Cl S.:384–401
Hable WE, Kropf DL (2000) Sperm entry induces polarity in fucoid zygotes. Development 127:493–501
Halatek J, Brauns F, Frey E (2018) Self-organization principles of intracellular pattern formation. Philos Trans R Soc Lond Ser B Biol Sci 373:20170107. https://doi.org/10.1098/rstb.2017.0107
Han X, Hyun TK, Zhang M, Kumar R, Koh EJ, Kang BH, Lucas WJ, Kim JY (2014) Auxin-callose-mediated plasmodesmal gating is essential for tropic auxin gradient formation and signaling. Dev Cell 28:132–146. https://doi.org/10.1016/j.devcel.2013.12.008
Harold FM (1986) The vital force: a study of bioenergetics. Freeman, New York
Harold FM (2001) The way of the cell: Molecules, organisms, and the order of life. Oxford University Press, Oxford
Harold FM (2014) In search of cell history: the evolution of life's building blocks. University of Chicago Press, Chicago
Hartzell T (2016) Myxobacteria. In: eLS. https://doi.org/10.1002/9780470015902.a0020391.pub2
Heisler MG, Hamant O, Krupinski U, Ohno C, Jönsson H, Traas, Meyerwitz EM (2010) Alignment between PIN1 polarity and microtubule orientation in the shoot apical meristem reveals a tight coupling between morphogenesis and auxin transport. PLoS Biol 8:e1000516. https://doi.org/10.1371/journal.pbio.1000516
Hernández- Hernández V, Niklas KJ, Newman SA, Benitez M (2012) Dynamical patterning modules in plant development and evolution. Int J Dev Biol 56:661–674. https://doi.org/10.1387/ijdb.120027mb
Hernández- Hernández V, Barrio RA, Benitez M, Nakayama N, Romero-Arias JR, Villarreal C (2018) A physico-genetic module for the polarisation of auxin efflux carriers PIN-FORMED (PIN). Phys Biol 15:036002. https://doi.org/10.1088/1478-3975/aaac99
Hille B (1992) Ionic channels of excitable membranes, 2nd edn. Sinauer Associates, Sunderland
Hisatomi O, Nakatani Y, Takeuchi K, Takahashi F, Kataoka H (2014) Blue light-induced dimerization of monomeric aureochrome-1 enhances its affinity for the target sequence. J Biol Chem 289:17379–17391. https://doi.org/10.1074/jbc.M114.554618
Höhn S, Hallmann A (2011) There is more than one way to turn a spherical cellular monolayer inside out: type B embryo inversion in *Volvox globator*. BMC Biol 9:89. https://doi.org/10.1186/1741-7007-9-89
Höhn S, Hallmann A (2016) Distinct shape-shifting regimes of bowl-shaped cell sheets - embryonic inversion in the multicellular green alga *Pleodorina*. BMC Dev Biol 16:35. https://doi.org/10.1186/s12861-016-0134-9
Höhn S, Honerkamp-Smith AR, Haas PA, Trong PK, Goldstein, RE (2015) Dynamics of a Volvox embryo turning itself inside out. Phys Rev Lett 114:178101
Hoops HJ, Nishii I, Kirk DL (2005) Cytoplasmic bridges in Volvox and its relatives. In: Baluska F, Volkmann D, Barlow PW (eds) Cell-cell channels. Eurekah.com, Georgetown, pp 1–20
Imaichi R, Hiratsuka R (2007) Evolution of shoot apical meristem structures in vascular plants with respect to plasmodesmatal network. Am J Bot 94:1911–1921
Imaichi R, Moritoki N, Solvang HK (2018) Evolution of root apical meristem structure in vascular plants: plasmodesmatal networks. Am J Bot 105:1453–1468
Jaffe L (1956) Effect of polarized light on polarity of *Fucus*. Science 123: 1081–1082. https://doi.org/10.1126/science.123.3207.1081
Jaffe LF (1966) Electrical currents through the developing *Fucus* egg. Proc Natl Acad Sci U S A 56:1102–1109
Janse JM (1906) Polarität und Organbildung bei *Caulerpa prolifera*. Jahrb Wiss Bot 42:394–460
Janse JM (1910) Über Organveränderung bei *Caulerpa prolifera*. Jahrb Wiss Bot 48:73–110

Kaiser D (2008) Myxococcus-from single-cell polarity to complex multicellular patterns. Annu Rev Genet 42:109–130. https://doi.org/10.1146/annurev.genet.42.110807.091615

Karner C, Wharton KA, Carroll TJ (2006a) Apical-basal polarity, Wnt signaling and vertebrate organogenesis. Semin Cell Dev Biol 17:214–222

Karner C, Wharton KA Jr, Carroll TJ (2006b) Planar cell polarity and vertebrate organogenesis. Semin Cell Dev Biol 17:194–203

Kataoka H (1975) Phototropism in *Vaucheria geminata*. II. The mechanism of bending and branching. Plant Cell Physiol 16:439–448

Kitagawa M, Fujita T (2013) Quantitative imaging of directional transport through plasmodesmata in moss protonemata via single-cell photoconversion of Dendra2. J Plant Res 126:577–585. https://doi.org/10.1007/s10265-013-0547-5

Kleine-Vehn J, Dhonukshe P, Sauer M, Brewer PB, Wiśniewska J, Paciorek T, Benková E, Friml J (2008) ARF GEF-dependent transcytosis and polar delivery of PIN auxin carriers in *Arabidopsis*. Curr Biol 18:526–531. https://doi.org/10.1016/j.cub.2008.03.021

Knapp E (1931) Entwicklungsphysiologische Untersuchungen an Fucaceen-Eiern. I. Zur Kenntnis der Polarität der Eier von *Cystosira barbata*. Planta 14:731–751

Kny L (1902) Über den Einfluss von Zug und Druck auf die Richtung der Scheidewände in sich theilenden Pflanzenzellen. (Zweite Mittheilung) Jahrb Wiss Bot 37:55–98

Kropf DL, Bisgrove SR, Hable WE (1999) Establishing a growth axis in fucoid algae. Trends Plant Sci 4:490–494

Lang CF, Munro E (2017) The PAR proteins: from molecular circuits to dynamic self-stabilizing cell polarity. Development 144:3405–3416. https://doi.org/10.1242/dev.139063

LaRossa R, Kuner J, Hagen D, Manoil C, Kaiser D (1983) Developmental cell interactions of *Myxococcus xanthus*: analysis of mutants. J Bacteriol 153:1394–1404

Lee ME, Rusin SF, Jenkins N, Kettenbach AN, Moseley JB (2018) Mechanisms connecting the conserved protein kinases Ssp1, Kin1, and Pom1 in fission yeast cell polarity and pivision. Curr Biol 28:84–92 e84. https://doi.org/10.1016/j.cub.2017.11.034

Lehman TA, Smertenko A, Sanguinet KA (2017) Auxin, microtubules, and vesicle trafficking: conspirators behind the cell wall. J Exp Bot 68:3321–3329. https://doi.org/10.1093/jxb/erx205

Li FW, Brouwer P, Carretero-Paulet L, Cheng S, de Vries J, Delaux PM, Eily A, Koppers N, Kuo LY, Li Z, Simenc M, Small I, Wafula E, Angarita S, Barker MS, Bräutigam A, dePamphilis C, Gould S, Hosmani PS, Huang YM, Huettel B, Kato Y, Liu X, Maere S, McDowell R, Mueller LA, Nierop KGJ, Rensing SA, Robison T, Rothfels CJ, Sigel EM, Song Y, Timilsena PR, van de Peer Y, Wang H, Wilhelmsson PKI, Wolf PG, Xu X, der JP, Schluepmann H, Wong GKS, Pryer KM (2018) Fern genomes elucidate land plant evolution and cyanobacterial symbioses. Nat Plants 4:460–472. https://doi.org/10.1038/s41477-018-0188-8

Ligrone R, Duckett JG (1998) Development of the leafy shoot in *Sphagnum* (Bryophyta) involves the activity of both apical and subapical meristem. New Phytol 140:581–595

Lin D, Nagawa S, Chen J, Cao L, Chen X, Xu T, Li H, Dhonukshe P, Yamamuro C, Friml J, Scheres B, Fu Y, Yang Z (2012) A ROP GTPase-dependent auxin signaling pathway regulates the subcellular distribution of PIN2 in *Arabidopsis* roots. Curr Biol 22:1319–1325. https://doi.org/10.1016/j.cub.2012.05.019

Lin D, Cao L, Zhou Z, Zhu L, Ehrhardt D, Yang Z, Fu Y (2013) Rho GTPase signaling activates microtubule severing to promote microtubule ordering in *Arabidopsis*. Curr Biol 23:290–297. https://doi.org/10.1016/j.cub.2013.01.022

Lintilhac PM, Vesecky TB (1984) Stress-induced alignment of division plane in plant tissues grown in vitro. Nature 307:363–364

Louveaux M, Julien JD, Mirabet V, Boudaoud A, Hamant O (2016) Cell division plane orientation based on tensile stress in *Arabidopsis thaliana*. Proc Natl Acad Sci U S A 113:E4294–E4303. https://doi.org/10.1073/pnas.1600677113

Lund EJ, Rosene HF (1947) Bioelectric fields and growth. Univ. of Texas Press, Austin

Lund EJ, Mahan RI, Hanszen AH (1945) Electric control of polar growth in roots of *Allium cepa*. Proc Soc Exp Biol Med 60:326–327

Majda M, Grones P, Sintorn IM, Vain T, Milani P, Krupinski P, Zagórska-Marek B, Viotti C, Jönsson H, Mellerowicz EJ, Hamant O, Robert S (2017) Mechanochemical polarization of contiguous cell walls shapes plant pavement cells. Dev Cell 43:290–304 e294. https://doi.org/10.1016/j.devcel.2017.10.017

Matt G, Umen J (2016) Volvox: a simple algal model for embryogenesis, morphogenesis and cellular differentiation. Dev Biol 419:99–113. https://doi.org/10.1016/j.ydbio.2016.07.014

Mendoza M, Redemann S, Brunner D (2005) The fission yeast MO25 protein functions in polar growth and cell separation. Eur J Cell Biol 84:915–926. https://doi.org/10.1016/j.ejcb.2005.09.013

Menzel D (1996) The role of the cytoskeleton in polarity and morphogenesis of algal cells. Curr Opin Cell Biol 8:38–42

Miehe H (1905) Wachstum, Regeneration und Polarität isolierter Zellen. Ber Deutsch Bot Ges 23:257–264

Mosbacher R (1929) Sur le mode de scission de *Polytoma uvella* et ses rapports avec la division des Flagellés et le clivage cellulaire. Comptes Rendus des Séances de la Société de Biologie et des ses Filiales (Paris) 93:278–281

Müller-Stoll WR (1952) Über Regeneration und Polarität bei *Enteromorpha*. Flora 139:148–180

Nagasato C, Tanaka A, Ito T, Katsaros C, Motomura T (2017) Intercellular translocation of molecules via plasmodesmata in the multiseriate filamentous brown alga, *Halopteris congesta* (Sphacelariales, Phaeophyceae). J Phycol 53:333–341. https://doi.org/10.1111/jpy.12498

Newman SA, Bhat R (2009) Dynamical patterning modules: a "pattern language" for development and evolution of multicellular form. Int J Dev Biol 53:693–705. https://doi.org/10.1387/ijdb.072481sn

Newman SA, Comper WD (1990) Generic' physical mechanisms of morphogenesis and pattern formation. Development 110:1–18

Newman SA, Bhat R, Mezentseva NV (2009) Cell state switching factors and dynamical patterning modules: complementary mediators of plasticity in development and evolution. J Biosci 34:553–572

Nienburg W (1922a) Die Keimungsrichtung von Fucuseiern und die Theorie der Lichtperzeption. (Vorlaufige Mitteilung) Ber Deutsch Bot Ges 40:38–40

Nienburg W (1922b) Die Polarisation der Fucus-Eier durch das Licht. Wiss Meeresunters Abt Helgoland 15, N F, Abhandl 7

Nienburg W (1924) Die Wirkung des Licht auf die Keimung der *Equisetum* spore. Ber Deutsch Bot Ges 42:95–99

Niklas KJ (2000) The evolution of plant body plans — a biomechanical perspective. Ann Bot 85:411–438

Niklas KJ (2014) The evolutionary-developmental origins of multicellularity. Am J Bot 101:6–25. https://doi.org/10.3732/ajb.1300314

Niklas KJ, Kutschera U (2012) Plant development, auxin, and the subsystem incompleteness theorem. Front Plant Sci 3:37. https://doi.org/10.3389/fpls.2012.00037

Niklas KJ, Cobb ED, Crawford DR (2013) The evo-devo of multinucleate cells, tissues, and organisms, and an alternative route to multicellularity. Evol Dev 15:466–474. https://doi.org/10.1111/ede.12055

Noll F (1888) Über den Einfluss der Lage auf die morphologische Ausbildung einiger Siphoneen. Arb Bot Inst Würzburg 3:466–476

Okada K, Ueda J, Komaki MK, Bell CJ, Shimura Y (1991) Requirement of the auxin polar transport system in early stages of *Arabidopsis* floral bud formation. Plant Cell 3:677–684. https://doi.org/10.1105/tpc.3.7.677

Palmer JD, Soltis DE, Chase MW (2004) The plant tree of life: an overview and some points of view. Am J Bot 91:1437–1445. https://doi.org/10.3732/ajb.91.10.1437

Parihar NS (1961) An introduction to embryophyta. In: Bryophyta, vol 1, 4th edn. Central Book Depot, Allahabad

Plateau JAF (1873) Statique expérimentale et theéorique des liquides soumis aux seules forces moleéculaires. Gauthier-Villars, Paris

Quatrano RS, Shaw SL (1997) Role of the cell wall in the determination of two-celled *Fucus* embryos. Dev Biol 30:209–213

Ranjan A, Townsley BT, Ichihashi Y, Sinha NR, Chitwood DH (2015) An intracellular transcriptomic atlas of the giant coenocyte *Caulerpa taxifolia*. PLoS Genet 11:e1004900. https://doi.org/10.1371/journal.pgen.1004900

Reichelt S, Knight AE, Hodge TP, Baluska F, Samaj J, Volkmann D, Kendrick-Jones J (1999) Characterization of the unconventional myosin VIII in plant cells and its localization at the post-cytokinetic cell wall. Plant J 19:555–567

Reinhardt D, Pesce ER, Stieger P, Mandel T, Baltensperger K, Bennett M, Traas J, Friml J, Kuhlemeier C (2003) Regulation of phyllotaxis by polar auxin transport. Nature 426:255–260. https://doi.org/10.1038/nature02081

Rosenwinge LK (1889) Influence des agents extérieus sur l'organisation polaire et dorsiventrale des plants. Rev Gén Bot 1:53–62

Ruan YL, Xu SM, White R, Furbank RT (2004) Genotypic and developmental evidence for the role of plasmodesmatal regulation in cotton fiber elongation mediated by callose turnover. Plant Physiol 136:4104–4113. https://doi.org/10.1104/pp.104.051540

Sachs J (1878) Über die anordnung der Zellen in jüngsten Pflanzentheilen. Arb Bot Inst Würzburg 2:46–104

Sager R, Lee JY (2014) Plasmodesmata in integrated cell signalling: insights from development and environmental signals and stresses. J Exp Bot 65:6337–6358. https://doi.org/10.1093/jxb/eru365

Salmi ML, ul Haque A, Bushart TJ, Stout SC, Roux SJ, Porterfield DM (2011) Changes in gravity rapidly alter the magnitude and direction of a cellular calcium current. Planta 233:911–920. https://doi.org/10.1007/s00425-010-1343-2

Schechter V (1935) The effect of centrifuging on the polarity of an alga, *Griffithsia bornetiana*. Biol Bull 68:172–179

Scott BIH, Martin DW (1962) Bioelectric fields of bean roots and their relation to salt accumulations. Aust J Biol Sci 15:83–100

Skoglund P, Keller R (2010) Integration of planar cell polarity and ECM signaling in elongation of the vertebrate body plan. Curr Opin Cell Biol 22:589–596. https://doi.org/10.1016/j.ceb.2010.07.012

Skopelitis DS, Benkovics AH, Husbands AY, Timmermans MCP (2017) Boundary formation through a direct threshold-based readout of mobile small RNA gradients. Dev Cell 43 (3):265–273

Steinecke F (1925) Zur polarität von *Bryopsis*. Bot Arch 12:97–118

Stewart WN (1948) A study of the plastids in the cells of the mature sporophyte of *Isoetes*. Bot Gaz 110:281–300

Sukumar P, Edwards KS, Rahman A, Delong A, Muday GK (2009) PINOID kinase regulates root gravitropism through modulation of PIN2-dependent basipetal auxin transport in *Arabidopsis*. Plant Physiol 150:722–735. https://doi.org/10.1104/pp.108.131607

Takahashi F (2016) Blue-light-regulated transcription factor, Aurechrome, in photosynthetic stramenopiles. J Plant Res 129:189–197

Takahashi F, Yamagata D, Ishikawa M, Fukamatsu Y, Ogura Y, Kasahara M, Kiyosue T, Kikuyama M, Wada M, Kataoka H (2007) AUREOCHROME, a photoreceptor required for photomorphogenesis in stramenopiles. Proc Natl Acad Sci U S A 104:19625–19630. https://doi.org/10.1073/pnas.0707692104

Terauchi M, Nagasato C, Motomura T (2015) Plasmodesmata of brown algae. J Plant Res 128:7–15. https://doi.org/10.1007/s10265-014-0677-4

Thompson DAW, Whyte LL (1942) On growth and form, A new edn. The University Press, Cambridge

Vatén A, Dettmer J, Wu S, Stierhof YD, Miyashima S, Yadav SR, Roberts CJ, Campilho A, Bulone V, Lichtenberger R, Lehesranta S, Mähönen AP, Kim JY, Jokitalo E, Sauer N, Scheres B, Nakajima K, Carlsbecker A, Gallagher KL, Helariutta Y (2011) Callose biosynthesis regulates symplastic trafficking during root development. Dev Cell 21:1144–1155. https://doi.org/10.1016/j.devcel.2011.10.006

Vöchting H (1878) Über Organbildung im Pflanzenreich. Max Cohen, Bonn

Volkmann D, Mori T, Tirlapur UK, König K, Fujiwara T, Kendrick-Jones J, Baluška F (2003) Unconventional myosins of the plant-specific class VIII: endocytosis, cytokinesis, plasmodesmata/pit-fields, and cell-to-cell coupling. Cell Biol Int 27:289–291

Warmke HE, Warmke GL (1950) The role of auxin in the differentiation of root and shoot primordia from root cuttings of *Taraxacum* and *Chchorium*. Am J Bot 37:272–280

Wayne R (2009) Plant cell biology. Elsevier, Amsterdam

Weber A (1976) Synopsis of the presentations. Symp Soc Exp Biol 30:445–456

Westerdijk J (1906) Zur Regeneration der Laubmoose. Rec Trav Bot Néerl 3:1–66

Whitaker DM (1940) Physical factors of growth. Growth 4(Suppl):75–90

Whitewoods CD, Cammarata J, Venza Z, Sang S, Crook AD, Aoyama T, Wang XY, Waller M, Kamisugi Y, Cuming AC, et al. (2018). CLAVATA was a genetic novelty for the morphological innovation of 3D growth in land plants. Cur Bio (in press)

Whitworth DE, American Society for Microbiology (2008) *Myxobacteria* : multicellularity and differentiation. ASM Press, Washington

Winkler H (1900) Über Polarität, regeneration und Heteromorphose bei *Bryopsis*. Jahrb Wiss Bot 35:449–469

Wisniewska J et al (2006) Polar PIN localization directs auxin flow in plants. Science 312:883. https://doi.org/10.1126/science.1121356

Wulff E (1910) Über Heteromorphose bei *Dasycladus clavaeformis*. Ber Deutsch Bot Ges 28:264–268

Yang Z, Higgs PI (2014) Myxobacteria : genomics, cellular and molecular biology. Caister Academic Press, Norfolk

Zažímalová E, Petrášek J, Benková E (2014) Auxin and its role in plant development. Springer. In: Wien

Zimmermann W (1923) Zytologische Untersuchungen der Zelle Zeitschr Bot 15:113–175

Zwiewka M, Nodzynski T, Robert S, Vanneste S, Friml J (2015) Osmotic stress modulates the balance between exocytosis and clathrin-mediated endocytosis in *Arabidopsis thaliana*. Mol Plant 8:1175–1187. https://doi.org/10.1016/j.molp.2015.03.007