

# PIN proteins and the evolution of plant development

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**Many aspects of development in the model plant *Arabidopsis thaliana* involve regulated distribution of the hormone auxin by the PIN-FORMED (PIN) family of auxin efflux carriers. The role of PIN-mediated auxin transport in other plants is not well understood, but studies in a wider range of species have begun to illuminate developmental mechanisms across land plants. In this review, I discuss recent progress in understanding the evolution of PIN-mediated auxin transport, and its role in development across the green plant lineage. I also discuss the idea that changes in auxin biology led to morphological novelty in plant development: currently available evidence suggests major innovations in auxin transport are rare and not associated with the evolution of new developmental mechanisms.**

## Auxin transport, PIN proteins, and development

The hormone auxin (see [Glossary](#)) has long been recognized as an important regulator of plant growth, but a veritable avalanche of data in recent years has demonstrated that auxin is involved in almost every aspect of plant development [1,2]. A key element in auxin function is its tightly regulated distribution by a specialized transport system ([Box 1](#)) [3]. PIN-family auxin efflux carriers form a major part of this system, and are thought to control the direction and quantity of transport in many cells ([Box 1](#)) [4]. The mutant phenotypes and expression patterns associated with PIN proteins suggest they are important regulators of development, and a large number of reports have described their function in many processes, although largely restricted to the model plant *Arabidopsis thaliana*. However, recent studies have begun to dissect the role of auxin transport in a wider range of land plants. Given its importance in angiosperms, it has been proposed that major innovations in auxin biology led to some of the radical innovations in body plans seen during land plant evolution [5,6]; advances in the availability of sequence data and in the use of non-angiosperm model species mean that it is possible to begin to assess the validity of this hypothesis. Here, I assess whether innovations in PIN-mediated auxin transport could have

contributed to the evolution of plant development, by examining the evolution of auxin transport as a phenomenon and PIN proteins as a major component of that phenomenon.

## General features of PIN protein evolution

A remarkable aspect of the PIN family is the existence of several clades with highly divergent structural forms, which points to the intriguing evolutionary history of PIN proteins. It has been proposed that the short-looped, endoplasmic reticulum (ER)-localized protein type ([Box 2](#)) was the ancestral PIN form within land plants [7–9], but a recent analysis of PIN evolution using deeper and wider sampling has overturned this view [10]. Notably, canonical PIN proteins ([Box 2](#)) are present in all land plant groups including liverworts ([Figure 1](#)), firmly demonstrating that the canonical structure is ancestral [10]. Canonical PIN proteins from the liverwort *Marchantia polymorpha* and the moss *Physcomitrella patens* have a similar loop structure, comprising approximately 35 identifiable motifs arranged in the same order ([Box 2](#)); strongly implying that the same structure was present in the ancestral canonical PIN protein [10]. Canonical proteins from vascular plant PIN clades (hereafter these clades are named as in [10]) have loops containing most, but not all motifs, suggesting a process of subfunctionalization between PIN proteins that allowed specialization as their copy number increased. All the available evidence suggests that noncanonical PIN proteins evolved repeatedly and independently from within the canonical lineage, primarily in angiosperms, and probably represent neofunctionalization events, given the extent of the divergence ([Figure 1](#)) [10]. The general pattern of evolution in PIN structure has been essentially a conservative one, punctuated by a few extreme events of reductive evolution giving rise to noncanonical PIN proteins. There has been surprisingly little positive evolution in PIN structure, with few significant innovations in the loop structure, such as new motifs or rearrangements of existing ones [10]. Even in the longest loops (PINN from monilophytes), the innovation is merely tandem repetition of motifs already present in the canonical loop [10]. Despite this general structural conservation, it is nevertheless true that PIN proteins have a complex evolutionary history, the consequences of which are not currently clear ([Figure 1](#)). Below, I examine how PIN-mediated auxin transport may regulate development in major taxonomic groups, and whether changes in PIN complement, function, or expression could have contributed to their morphological evolution.

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## Glossary

**Angiosperms:** ‘flowering plants’; a monophyletic clade of vascular plants distinguished by the production of seeds within an enclosed ovary; by far the most abundant and diverse group of land plants.

**Apoplast:** the space occupied by the plant cell walls, which forms a continuous network surrounding every cell in a plant.

**Auxin:** auxin (indole-3-acetic acid, IAA) is a small but ubiquitous signaling molecule in plant development, named from the Greek *auxein* ‘to grow’.

**Bryophytes:** collective name for liverworts, mosses, and hornworts, three ancient plant groups that diverged from vascular plants early in land-plant evolutionary history. It is generally thought that they do not form a monophyletic clade, but rather a paraphyletic grade with respect to vascular plants (e.g., [18]) (Figure 1, main text); the exact interrelation of these groups to each other remains unclear. However, they have several common features, including a dominant gametophytic phase.

**Charales:** one of the major orders of charophyte algae (Figure 1, main text). It includes multicellular species with complex development and has long been assumed to be the sister group to land plants, but their relation is currently uncertain.

**Charophytes:** collective name for algae in the streptophyte lineage that form a monophyletic clade together with land plants. Not a monophyletic group in themselves, but a paraphyletic grade with respect to land plants (Figure 1, main text).

**Chlorophytes:** monophyletic group of species that form one of the two major divisions of the green algae, the other being streptophytes.

**Clade:** group of organisms (or genes, proteins) that includes all the descendants of a common ancestor; clades are by definition monophyletic.

**Coleochaetales:** one of the major orders of charophyte algae (Figure 1, main text); includes multicellular species with development of intermediate complexity.

**Euphyllophytes:** clade of vascular plants that contains monilophytes and spermatophytes (Figure 1, main text).

**Gametophyte:** the haploid phase of a plant life cycle; grows from haploid spores released by the diploid sporophyte phase and produce gametes that will fuse together to form a new diploid sporophyte phase. In spermatophytes, the gametophytic phase is severely reduced.

**Gymnosperms:** theoretically paraphyletic group of all spermatophytes minus the angiosperms; produce ‘naked’ seeds. However, extant gymnosperms (conifers, gnetales, cycads, and *Ginkgo*) are generally thought to form a monophyletic clade within the broader spermatophyte clade (Figure 1, main text).

**Hornworts:** see ‘Bryophytes’.

**Klebsormidiales:** one of the major orders of charophyte algae (Figure 1, main text). Development is limited to the production of unbranched filaments of cells.

**Liverworts:** see ‘Bryophytes’.

**Lycophytes:** ‘club mosses’; a clade of vascular plants that forms the sister group to the euphyllophytes (Figure 1, main text).

**Monilophytes:** clade of vascular plants that includes ferns and their allies, including horsetails (Equisetopsida) (Figure 1, main text).

**Monophyletic group:** one that contains all the species (or genes or proteins) descended from a common ancestor.

**Neofunctionalization:** one possible outcome of gene duplication, in which the function of the ancestral function is retained by one duplicate, while the other gains a new function not present in the ancestral gene.

**Paraphyletic group:** one that contains all the species (or genes, proteins) derived from a common ancestor, minus a given monophyletic subgroup. See, for instance, ‘Bryophytes’.

**Spermatophytes:** ‘seed plants’; a clade of vascular plants that produce true seeds; includes the gymnosperms and angiosperms (Figure 1, main text).

**Sporophyte:** the diploid phase of a plant life cycle, formed by fusion of haploid gametes. Undergoes meiosis to produce haploid spores, which in turn produce haploid gametophytes.

**Streptophytes:** monophyletic group of species that form one of the two major divisions of the plant kingdom, the other being chlorophytes; includes land plants and charophyte algae.

**Subfunctionalization:** one possible outcome of gene duplication, in which the function of the ancestral gene is divided between the duplicated copies.

**Tracheophytes/vascular plants:** clade of land plants defined by the presence of lignified vascular elements; includes lycophytes and euphyllophytes (Figure 1, main text).

**Zygnematales:** one of the major orders of charophyte algae (Figure 1, main text). Most species form unbranched filaments of cells.

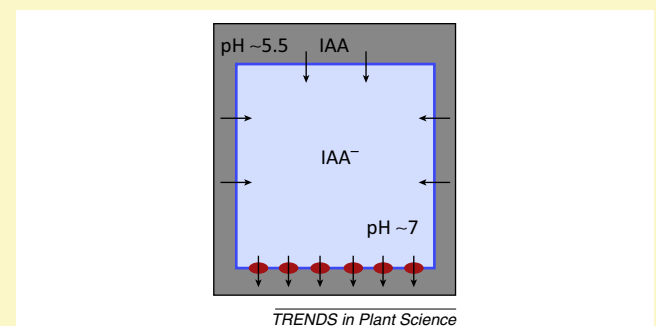
## Auxin transport and PINs in algae

Given the presence of canonical PINs in liverworts, most innovation in PIN structure must have occurred in the algal ancestors of land plants (Figure 1). Auxin is certainly

## Box 1. Auxin transport

Historically, ‘auxin transport’ referred to the phenomenon of observable auxin movement through plant tissues, which was an early discovery in the auxin field [70]. Given that this detectable movement usually only occurs in one direction through a tissue, it is often described as polar auxin transport (PAT). In this review, PAT is used exclusively in this sense: that is, ‘bulk’ polar movement of auxin through a tissue, typically assayed by tracking radiolabeled auxin molecules. Much debate initially surrounded the nature of PAT: whether it could be diffusive in nature, or whether it was an active process, or indeed whether it occurred in phloem vessels [71]. The chemiosmotic hypothesis later provided a convincing cellular framework for understanding PAT [72,73]. In the cytoplasm (pH ~7) auxin molecules are largely deprotonated and, as charged molecules, cannot pass through the plasma membrane; thus, efflux carriers are required to move auxin out of cells (Figure 1). However, in the apoplast (pH ~5.5), a higher proportion of auxin molecules are protonated and can move freely into cells (Figure 1). Therefore, the observed polarity of auxin transport was predicted to be a consequence of polar localization of auxin efflux carriers [72,73].

The subsequent discovery of polarly localized PIN proteins [57–59,74] that act as efflux carriers for auxin [75] confirmed the essence of the chemiosmotic hypothesis. Two other types of auxin carrier have also been identified: ATP-dependent ABCB transporters, which are apolarly localized, and probably function in basal auxin mobilization, and AUX/LAX influx carriers that help to load auxin into cells in regions of high auxin concentration (reviewed in [76]). The expression and activity of PIN and ABCB proteins in *Arabidopsis* implies the widespread existence of shorter-range patterns of intercellular auxin transport, which may or may not be polar. Therefore, it must be stressed that the absence of detectable PAT in a tissue does not mean that there is no auxin transport. The discovery that some PIN proteins, along with the novel PILS family of putative auxin carriers [77], are localized to ER membranes has further clouded the meaning of ‘auxin transport’, because it seems that there is also intracellular movement of auxin between cell compartments (Box 2). In this review, ‘auxin transport’ is broadly used as shorthand for any active, carrier-mediated intercellular transport of auxin, irrespective of polarity and/or detectability.



**Figure 1.** The chemiosmotic theory of polar auxin transport. Neutrally charged indole-3-acetic acid (IAA) molecules in the apoplast (gray) can move into the cell through any membrane. However, negatively charged auxin molecules in the cytoplasm (light blue) can only exit the cell by the action of specific efflux carriers, in this case, polarly localized (red ovals).

present in both charophyte and chlorophyte algae [11] and the gradual evolution of auxin signaling, homeostasis, and transport mechanisms can be tracked through charophyte algae [12,13]. PIN sequences have been identified from *Klebsormidium flaccidum* (Klebsormidiales; KfPIN) and *Spirogyra pratensis* (Zygnematales; SpPIN), but not from genome sequences of chlorophyte algae, suggesting that PINs are a streptophyte-specific innovation (Figure 1) [8,12,13]. However, from such limited data, it is difficult to conclude much about the evolution of PIN proteins in algae. The mutual level of dissimilarity between KfPIN,

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