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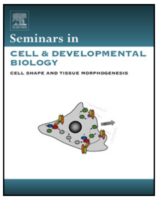

Review

Seeing the endomembrane system for the trees: Evolutionary analysis highlights the importance of plants as models for eukaryotic membrane-trafficking

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ABSTRACT

Plant cells show many signs of a unique evolutionary history. This is seen in the system of intracellular organelles and vesicle transport pathways plants use to traffic molecular cargo. Bioinformatic and cell biological work in this area is beginning to tackle the question of how plant cells have evolved, and what this tells us about the evolution of other eukaryotes. Key protein families with membrane trafficking function, including Rabs, SNAREs, vesicle coat proteins, and ArfGAPs, show patterns of evolution that indicate both specialization and conservation in plants. These changes are accompanied by changes at the level of organelles and trafficking pathways between them. Major specializations include losses of several ancient Rabs, novel functions of many proteins, and apparent modification of trafficking in endocytosis and cytokinesis. Nevertheless, plants show extensive conservation of ancestral membrane trafficking genes, and conservation of their ancestral function in most duplicates. Moreover, plants have retained several ancient membrane trafficking genes lost in the evolution of animals and fungi. Considering this, plants such as *Arabidopsis* are highly valuable for investigating not only plant-specific aspects of membrane trafficking, but also general eukaryotic mechanisms.

Contents

1. Introduction

Plants have an incredibly important role in human society, as sources of sustenance, shelter, inspiration, and medicine. Understanding the diversity, history and biology of plants is one of the longest-standing pursuits of science and one that continues to be actively pursued today. Following the paths set forth by Linneaus and Hooke, biologists are using sophisticated computational and genomic methods to delve into the evolutionary history and systematics of the plant lineage (herein defined as embryophytes/land plants), and using powerful microscopy and molecular biology methods to examine the underlying processes of plant life at the cellular level.

The membrane trafficking system (MTS) underlies functions necessary for all eukaryotic cells. It comprises organelles such as the endoplasmic reticulum (ER), Golgi apparatus, and endosomes, as well as proteins that mediate transport of cargo among the compartments and the plasma membrane (PM), typically through vesicles [1]. These organelles, and the molecular machinery encom-

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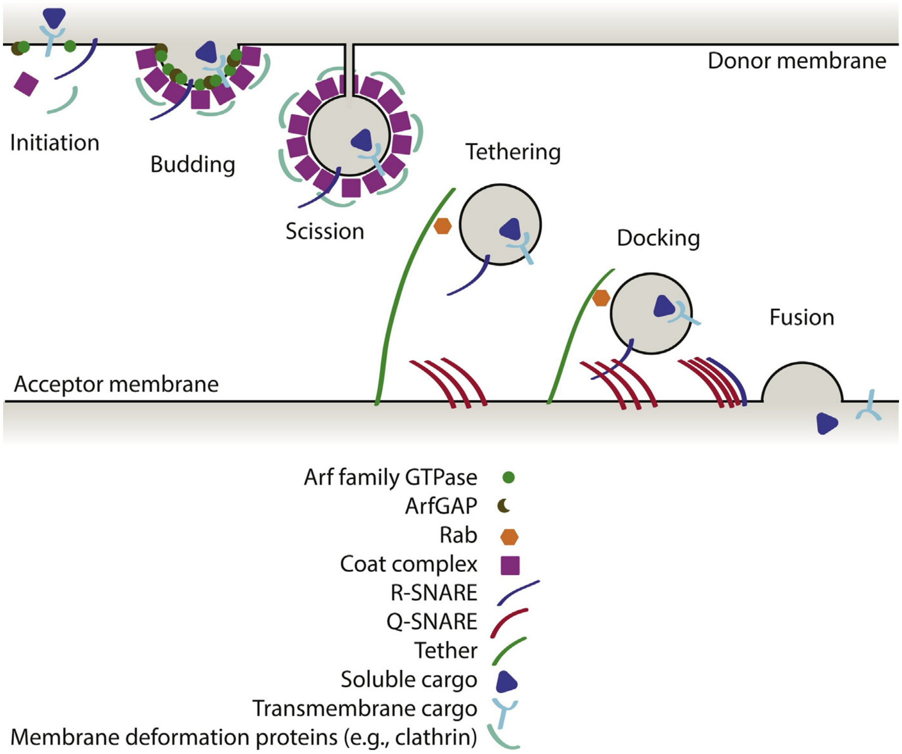

Fig. 1. Schematic of a generalized vesicle trafficking pathway, adapted from [5]. Vesicle traffic begins with initiation of vesicle formation at the donor membrane, followed by budding, scission, uncoating, tethering, docking, and finally fusion. These steps are mediated by pathway-specific members of large protein families, including Rabs, SNAREs, and Heterotetrameric Adaptor Complex (HTAC) components.

passing the MTS are largely conserved in all eukaryotes [2]. And, thus the MTS is relevant to understanding eukaryotic cell biology, from human diseases, both congenital and infectious, to the healthy working of macroscopic and microscopic organisms critical to terrestrial, marine, and freshwater ecosystems [3,4].

The basic membrane-trafficking process involves various protein families that mediate the stages typical to vesicle transport pathways [5] (Fig. 1). Small GTPases (Sar1 or Arf), or specific lipids effect recruitment of vesicle coat proteins composing the COPI, COPII, or Adaptin complexes [6], which are required for packaging of cargo proteins into the nascent vesicle. ArfGAPs are GTP-activating proteins for Arfs, and are involved in both positive and negative regulation of vesicle transport [7]. After budding and scission, vesicles are transported towards their target membrane where they are recognized by tethering proteins, such as components of multi-subunit tethering complexes. The final stage involves binding of SNARE proteins on the vesicle membrane to those on the target membranes, leading to membrane fusion [8]. In addition, members of the Rab family of small GTPases act as molecular switches that allow the coordinated organelle-specific action of other membrane trafficking proteins, including tethers [9]. This model of vesicular trafficking generally holds true for membrane-trafficking across eukaryotes and among different trafficking pathways between the endomembrane organelles. However, the specificity of the pathways depends on which members of the proteins families just described are involved, and it is here that the intriguing variation exists between eukaryotes.

This variation is investigated from an evolutionary perspective by addressing two complementary questions: (1) What aspects of the membrane-trafficking system are common to all eukaryotes, and (2) what aspects evolved uniquely in the various lineages. The latter question informs our understanding of cellular physiology in specific eukaryotes, whether humans, parasites, or agricultural crops. The former question allows us to assemble a general understanding of eukaryotic cellular biology. Addressing these questions involves integration of genomic and cell biological data, and distinguishing the broadly conserved, and thus general, features from those aspects that are lineage-specific.

Herein we address the evolution of the MTS in plants, focusing on the relevance of plants for understanding membrane trafficking in other eukaryotes. At the outset, the MTS in plants appears to be highly specialized, bringing into question the relevance of plants to understanding general eukaryotic membrane trafficking mechanisms. The most striking specializations include loss of numerous ancient Rab proteins (section 3), and duplication and modification of many membrane trafficking proteins (section 4), as well as apparent conglomeration of the *trans*-Golgi network and early endosomal compartments, and the presence of a cell plate for cytokinesis (section 5). However, we argue that in each of these cases core eukaryotic membrane trafficking mechanisms remain largely intact, and once the homology of the specialized components is clear, their seemingly outlying biology can be integrated in a larger context of membrane-trafficking cell biology. Moreover, several ancient membrane trafficking proteins have been remarkably conserved in plants, while lost in other prominent model eukaryotes (Section 6). Overall, we suggest that the conservation of pan-eukaryotic machinery in plants makes them valuable model systems for understanding the cell biology of membrane-trafficking in a general eukaryotic context.

2. The eukaryotic ancestor as a starting point for understanding the evolution of membrane trafficking in plants

To place the trafficking systems of plants in context, the relationship of the plant lineage to other eukaryotes needs to be clarified, as does knowledge about the membrane-trafficking system of the last eukaryotic common ancestor (LECA) (*i.e.*, the common ancestor of

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