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# 1 The Endomembrane System of the Fungal Cell

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## I. Introduction

The eukaryotic endomembrane system can be defined as all the organelles comprising both the endocytic and secretory pathways, including the endoplasmic reticulum (ER), Golgi apparatus, endosomes, multivesicular bodies, lysosomes, vacuoles, plasma membrane, and transport intermediates such as vesicles and microvesicles. These membrane-enclosed compartments form a complex intracellular system that can comprise a large percentage of the total cellular volume. To understand the interrelationships between these intracellular compartments it is helpful to consider how each might have evolved. One of the most significant advances in evolution from prokaryotes to eukaryotes was the development of extensive cellular compartmentalization (Stanier 1970), facilitated by the proliferation of internal membranes (Blobel 1980). This elaboration of internal membranes allowed for an organelle-based division of labor for the biochemistry that was previously restricted to the surface of prokaryotic cells (Becker and Melkonian 1996). This in turn allowed for the development of large cells with vastly reduced sur-

face area:volume ratios – the average eukaryotic cell is  $10^2$ – $10^3$  times greater in volume than prokaryotes (Dacks and Field 2004).

Intracellular compartments can be divided into three distinct topological groups: (1) the nucleus and cytosol, (2) mitochondria, and (3) organelles of the endomembrane system, based upon the predominant means of protein transport within each group (Blobel 1980): gated between the cytosol and nucleus via nuclear pores, transmembrane in the case of mitochondria, and mainly vesicle-mediated. Organelles are membrane-bounded compartments that contain specific chemistry. The protein constituents of each organelle define its structure and function. Since most proteins are synthesized in the cytosol, mechanisms exist for delivery of these proteins to the proper organelle. Therefore, an understanding of protein transport is inexorably connected with understanding the endomembrane system. In large part organelle homeostasis is controlled by limiting the flow of molecules both into and out of each compartment. Thus, to understand the workings of the eukaryotic cell it is fundamental to understand the defining biochemical activities for each organelle, how molecules move between them, and how the compartments are created and maintained. For the compartments that comprise the endomembrane system this is a daunting task considering all the interorganellar communication that occurs concurrently with the flow of biomaterials through the system. It is even more remarkable in fungal hyphae, perhaps the ultimate fast growing polarized eukaryotic cell. Cells of septate fungi can be upwards of 200 times longer than wide (and coenocytic *Zygomycetes* much longer than this) with a hyphal apex that extends a distance of up to four times the hyphal diameter every minute (Collinge and Trinci 1974; López-Franco et al. 1995).

While there is certainly much overlap in the strategies adopted by various eukaryotes, the

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endomembrane system of filamentous fungi has several singular structural features that set it apart from that of other higher eukaryotes. For example, the Golgi apparatus in filamentous fungi lacks stacks of membrane cisternae and does not disperse during mitosis. Also, there is a lack of structural evidence to support the existence of clathrin-coated vesicles, vectors that are responsible for the bulk of endocytosis and trans-Golgi network trafficking. Some of these differences appear to be shared between filamentous fungi and their yeast relatives while others are not (Tables 1.1–1.6). Whether these structural differences underlie significant functional differences remains to be answered and could perhaps be exploited in the design of control strategies against fungi, many of which have a significant negative impact upon humankind.

As we consider the endomembrane system of filamentous fungi, we unavoidably focus on the hyphal tip cell (Fig. 1.1) where the most obvious product of that system, polarized growth, is manifest. Additionally, in terms of morphology and ultrastructure, the hyphal tip cell is undoubtedly the most studied of all fungal cells. The overall distribution of endomembrane compartments related to the tip growth process is carefully orchestrated and maintained; and perturbation of the hyphal apex is evidenced by a rapid redistribution of cellular endomembrane components, particularly those associated with the Spitzenkörper. For further related discussion, the reader is referred to Chaps. 5 and 6 in this volume, respectively by Fischer, and by Sudbery and Court.

The present chapter was written in part to spur further inquiries in this area by bringing together disjointed sources of information. By emphasizing morphogenesis and structure we aim to draw connections between microscope-based structural knowledge and molecular data, and hope that this undertaking will generate a new perspective and appreciation for the unique qualities of the endomembrane system in filamentous fungi.

## II. Tools for Study of the Endomembrane System

The discovery and manipulation of **fluorescent reporter molecules** has revolutionized cell biology and been exploited to study fungi (Cormack 1998; Lorang et al. 2001; Czymmek et al. 2005).

Fluorescent protein tagging methods have aided greatly investigations of the endomembrane system of other eukaryotes (Hanson and Köhler 2001). These probes can be used to determine the subcellular distribution of a given molecule as well as assess its mobility and potential protein–protein interactions. In addition, fluorescent protein markers can be used to label specific compartments, monitoring their size, shape, mobility and time-resolved changes that occur during development or in response to environmental stimuli. For example, a yeast deletion library was used in conjunction with a background strain with a plasma membrane-targeted GFP to identify genes required for precise delivery of this protein to its proper destination (Proszynski et al. 2005). These types of studies could do much to advance our understanding.

Recent advances in gene targeting and the development of fusion PCR for gene-tagging have combined to make large-scale gene and genome manipulation feasible in *Neurospora crassa*, *Aspergillus nidulans*, and *A. fumigatus*. First, disruption of the non-homologous end joining DNA repair pathway (NHEJ), by deletion of the KU70 or KU80 genes, essentially eliminates the historically difficult problem of inefficient gene targeting in these fungi (Ninomiya et al. 2004; da Silva Ferreira et al. 2006; Krappman et al. 2006; Nayak et al. 2006). For example, in *A. nidulans* cells lacking KU70 or KU80, ~90% of transformants are

**Table. 1.1.** (on page 3–4) Endoplasmic reticulum proteins in fungi. *A. nidulans* (An) ER proteins were identified by tBlastn of the An genome ([http://www.broad.mit.edu/annotation/genome/aspergillus\\_nidulans/](http://www.broad.mit.edu/annotation/genome/aspergillus_nidulans/)) using *S. cerevisiae* (Sc) proteins. Sc proteins were obtained from Gene Ontology annotation for yeast endoplasmic reticulum ([www.yeastgenome.org](http://www.yeastgenome.org)). Proteins were further defined by forward and reverse tBlastn and blastp between Sc and An genomes, tBlastn of An proteins against the An genome, and tBlastn and blastp of An and Sc proteins to all Fungal Genome Initiative (FGI) genomes (<http://www.broad.mit.edu/annotation/fgi/>)

**Table. 1.2.** (on page 5–7) Golgi proteins. *A. nidulans* (An) ER proteins were identified by tBlastn of the An genome ([http://www.broad.mit.edu/annotation/genome/aspergillus\\_nidulans/](http://www.broad.mit.edu/annotation/genome/aspergillus_nidulans/)) using *S. cerevisiae* (Sc) proteins. Sc proteins were obtained from Gene Ontology annotation for yeast golgi ([www.yeastgenome.org](http://www.yeastgenome.org)). Proteins were further defined by forward and reverse tBlastn and blastp between Sc and An genomes, tBlastn of An proteins against the An genome, and tBlastn and blastp of An and Sc proteins to all Fungal Genome Initiative (FGI) genomes (<http://www.broad.mit.edu/annotation/fgi/>)

<i>S. cerevisiae</i>	<i>A. nidulans</i>	Other fungi <sup>a</sup>
Endoplasmic reticulum membrane proteins		
SEC61 translocation complex		
SBH1, SBH2	AN0417	Ci, Cg, Nc, Mg, Bc, Ss
SSS1	AN4589	Bc, Ss, Mg, Ci, Cg, Ro, Nc, Cn
SEC61, SSH1	AN7721	Ci, Ss, Nc, Cg, Mg, Cn, Ro, Bc
		(8e <sup>-14</sup> , 5e <sup>-19</sup> ) (2.6e <sup>-16</sup> ) (1e <sup>-123</sup> , 5e <sup>-50</sup> )
SEC63 pre-secretory protein translocation complex		
SEC62	AN6269	Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
SEC63	AN0834	Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
SEC66	AN1442	Ss, Nc, Cg, Mg, Ci, Bc, Cn, Ro
SEC72	AN10987	Ci, Nc, Mg, Cg, Bc, Ss, Ro, Cn
		(4e <sup>-24</sup> ) (5e <sup>-32</sup> ) (2e <sup>-09</sup> ) (7e <sup>-07</sup> )
Other ER membrane proteins		
VPS64 ( <i>cytoplasm</i> → <i>vacuole protein targeting</i> )	AN4632	Ci, Nc, Ss, Mg, Bc, Cg, Ro
HSD1 ( <i>unknown function</i> )	AN3177	Ci, Bc, Mg, Cg, Nc, Ss, Cn, Ro
PHO86 ( <i>packaging PHO84 into COPII vesicles</i> )	None	None
NPL4 ( <i>complex w/CDC48, UFD1</i> )	AN0295	Ci, Ss, Cg, Bc, Nc, Mg, Ro, Cn
ERI1 ( <i>GPI-GnT complex</i> )	AN8536	Mg, Bc, Nc, Ss, Cg, Ci
CUE1 ( <i>recruits UBC7, protein degradation</i> )	AN5900	Ci, Bc, Ss, Mg, Nc, Cg, Cn
ERG28 ( <i>interacts w/ERG6, -26, -27</i> )	AN5862	Ci, Bc, Ss, Nc, Cg, Mg, Ro, Cn
DER1 ( <i>ER-associated protein degradation</i> )	Contig 109 <sup>b</sup>	Nc, Mg, Ci
CSG2 ( <i>mannosylation</i> )	AN0674	Ci, Ss, Bc, Mg, Nc, Cg, Ro, Cn
YET1, YET2, YET3 ( <i>HuBAP31 homolog</i> )	AN0819	Ci, Nc, Cg, Mg, Ss, Bc, Ro
STE14 ( <i>farnesyl Cys-COOH methyltransferase</i> )	AN6162	Ci, Nc, Cg, Mg, Ro, Bc, Cn, Ss
BIG1 ( <i>cell wall β-glucan content</i> )	AN5684	Bc, Ci, Ss, Mg, Cg, Nc
ERD1 ( <i>retention of luminal ER proteins</i> )	AN5682	Nc, Mg, Cg, Ss, Bc, Ci, Cn
ERD2 ( <i>binds HDEL motif in ER proteins</i> )	AN11226	Ss, Bc, Nc, Ci, Mg, Cg, Cn, Ro
Novel additional ERD2 homolog	AN4528	Nc, Bc, Mg, Ss, Cg, Cn
VPH2 ( <i>vacuolar-ATPase assembly</i> )	None	None
VMA21 ( <i>vacuolar-ATPase assembly</i> )	AN2975 <sup>c</sup>	Ss, Mg, Cg
VMA22 ( <i>vacuolar-ATPase assembly</i> )	AN4766 <sup>d</sup>	Nc, Mg, Cg, Ci, Bc, Ro, Ss
MCD4 ( <i>GPI anchor synthesis</i> )	AN7049	Ci, Bc, Cg, Nc, Ss, Mg, Ro
RCR1 ( <i>chitin deposition in cell wall</i> )	AN1001	Ci, Cg, Nc, Ss, Mg, Bc, Ro
KAR5 ( <i>nuclear membrane fusion</i> )	AN1771	Ci, Mg, Bc, Cg, Nc, Ss
FRT1 ( <i>calcineurin substrate</i> )	Not found	MGG_09764?
FRT2 ( <i>interacts with FRT1</i> )	None	None
		(2e <sup>-05</sup> → 0.028) (2e <sup>-18</sup> → 0.68) (0.0 → 6e <sup>-51</sup> ) (1e <sup>-126</sup> → 1e <sup>-27</sup> ) (2e <sup>-30</sup> → 3e <sup>-06</sup> ) (0.79)
Endoplasmic reticulum luminal proteins		
ZRG17 ( <i>possible zinc uptake function</i> )	AN1076	Ci, Bc, Ss, Mg, Nc, Cg
PGA2 ( <i>maturation of GAS1, PHO8</i> )	AN0597 <sup>e</sup>	Mg, Nc, Ci, Ss, Bc
PGA3 ( <i>maturation of GAS1, PHO8</i> )	AN6366	Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
INP54 ( <i>ptdins 4,5-bisphosphate-5-phosphatase</i> )	AN11023	Ci, Ss, Mg, Nc, Cg, Bc, Ro
		(1e <sup>-24</sup> ) - (3e <sup>-55</sup> ) (6e <sup>-06</sup> )
Disulfide bond formation		
ERV2 ( <i>PI 4,5-bisphosphate-5-phosphatase</i> )	AN3759	Ci, Nc, Mg, Ss, Bc
EPS1 ( <i>PDI1-related protein</i> )	AN5970	Ci, Ss, Bc, Cg, Nc, Mg, Ro
PD11, EUG1 ( <i>protein disulfide isomerase</i> )	AN7436	Ci, Nc, Cg, Ss, Mg, Bc, Ro, Cn
		(1e <sup>-44</sup> → 1e <sup>-35</sup> ) (0.0 → 5e <sup>-32</sup> ) (1e <sup>-179</sup> → 3e <sup>-73</sup> )

<i>S. cerevisiae</i>	<i>A. nidulans</i>	Other fungi <sup>a</sup>
MPD1 (inhibits CNE1 chaperone activity)	AN0248	Ci, Nc, Mg, Ss, Bc, Cg, Ro, Cn
ER chaperones/unfolded protein response		
SHR3 (ER packaging chaperone)	AN1845	Ci, Ss, Bc, Mg, Nc
ERJ5 (co-chaperone, DnaJ-like domain)	AN5770	Ci, Mg, Cg, Bc, Nc, Ss, Ro, Cn
ORM1, ORM2 (unfolded protein response)	AN1933	Ci, Cg, Ss, Bc, Mg, Nc, Cn, Ro
ERO1 (oxidative protein folding)	AN1510	Ci, Ss, Bc, Mg, Nc, Cg, Ro, Cn
FES1 (HSP70 nucleotide exchange factor)	AN6543	Cg, Mg, Ci, Nc, Ss, Bc, Ro, Cn
LHS1 (HSP70 family chaperone)	AN0847	Ci, Ss, Bc, Nc, Mg, Cg, Cn, Ro
SIL1 (KAR2 nucleotide exchange factor)	BC1G_08026.1 <sup>f</sup>	Bc, Cg, Nc, Mg
KAR2/BIP (ATPase, chaperone)	AN2062	Ci, Bc, Ss, Nc, Mg, Cg, Ro, Cn
CPR5 (ER cyclophilin)	AN4467	Cg, Nc, Ss, Ro, Ci, Bc, Mg
HRD1 (ubiquitin-protein ligase for ERAD)	AN1488	Ci, Ss, Bc, Cg, Nc, Mg, Cn
CNE1 (calnexin, ER chaperone)	AN3592	Ci, Nc, Cg, Mg, Ss, Bc, Cn, Ro
HLJ1 (co-chaperone for HSP40)	AN4441	Ss, Bc, Cg, Mg, Nc, Ci, Ro
JID1 (probable HSP40 co-chaperone)	Contig 51 <sup>g</sup>	Ss, Bc, Nc, Ci, Mg, Ro
YDJ1 (DnaJ co-chaperone for HSP70, -90)	AN2731	Ci, Ss, Bc, Cg, Nc, Mg, Ro, Cn
Other ER and ER-associated proteins		
SWR1 (SWI2/SNF2-related ATPase)	AN9077	Ci, Ss, Nc, Cg, Bc, Mg, Ro, Cn
SWC3 (SWR1 complex)	AN3834	Ci, Bc, Ss, Cg, Mg, Nc
MSC1 (unknown function)	AN4940	Ci, Nc, Mg, Bc, Ss, Cg, Cn
MSC2 (cation diffusion facilitator family)	AN5347	Ci, Nc, Ro, Bc, Mg, Ss, Cg, Cn
MSC7 (unknown function)	AN6636	Ci, Bc, Cg, Mg, Nc, Ss, Ro, Cn
SLC1 (1-acyl-glycerol-3-PO <sub>4</sub> acyltransferase)	AN6139	Ci, Cg, Nc, Bc, Ss, Mg, Cn, Ro
ARE1, ARE2 (acyl-CoA:sterol acyltransferase)	AN4208	Ss, Mg, Nc, Ci, Cg, Bc, Cn
<b>Novel additional ARE1/2 homolog</b>	AN6159 <sup>h</sup>	Ci, Ss, Bc, Cg, Nc, Mg, Ro, Cn
MNL1 (α-mannosidase-like protein)	AN11163	Ci, Bc, Ss, Mg, Cg, Nc, Bc, Ro, Cn

<sup>a</sup> Listed are fungi in which one or more putative orthologs occur. Order of fungi and corresponding range of e-values indicate relative strength of homology to An sequence. Bc *Botrytis cinerea*, Cg *Chaetomium globosum*, Ci *Coccidioides immitis*, Cn *Cryptococcus neoformans*, Mg *Magnaporthe grisea*, Nc *Neurospora crassa*, Ro *Rhizopus oryzae*, Ss *Sclerotinia sclerotiorum*.

<sup>b</sup> Sc DER1 found an unnamed hypothetical ORF in An (contig 109, nt 132344–133047). Sc DER1 found putative orthologs in three other fungi; its closest relative is NCU00146 (3e<sup>-10</sup>).

<sup>c</sup> Sc VMA21 did not find the An ortholog, but did find the putative Mg ortholog, MGG\_09929 (2e<sup>-05</sup>). MGG\_09929, in turn, found Sc VMA21 (1.6e<sup>-07</sup>) and the putative An ortholog, AN2975 (0.008).

<sup>d</sup> Sc VMA22 did not find the An ortholog, but did find the putative Ss ortholog, SSIG\_13727 (e=11.0). SSIG\_13727, in turn, found Sc VMA22 (0.097) and the putative An ortholog, AN4766 (3.1).

<sup>e</sup> Sc PGA2 did not find an An homolog, but did find the putative Ci ortholog, CIMG\_00038.2 (1e<sup>-04</sup>). CIMG\_00038.2, in turn, found Sc PGA2, and a putative An ortholog, AN0597. The An gene did not find PGA2 in Sc, but found the same five putative orthologs in other fungi as were found by CIMG\_00038.2.

<sup>f</sup> Sc SIL1 did not find an An homolog, but did find the putative Bc ortholog, BC1G\_08026.1 (8e<sup>-12</sup>). BC1G\_08026.1, in turn, found Sc SIL1 (1.3e<sup>-10</sup>) and putative orthologs in three other fungi, but not in *A. nidulans*.

<sup>g</sup> Sc JID1 found an unnamed hypothetical ORF in An (contig 51, nt 221952–222362). Sc JID1 found putative orthologs in other fungi; its closest relative is SSIG\_11303 (2e<sup>-10</sup>).

<sup>h</sup> Sc ARE1 and ARE2 are strongly related paralogs (1.3e<sup>-155</sup>). The An ortholog of ARE1/ARE2 is AN4208 (0.0). Reciprocal blastp of the Sc genome finds ARE1 (2.2e<sup>-67</sup>) and ARE2 (4.2e<sup>-57</sup>). In addition, An possesses one paralog, AN6159, that shows moderate similarity to AN4208 (2.3e<sup>-31</sup>), and to the Sc ARE1/2 paralogs (5.7e<sup>-21</sup> and 3e<sup>-30</sup>, respectively).

<i>S. cerevisiae</i>	<i>A. nidulans</i>	<i>Other fungi<sup>a</sup></i>
<b>Golgi resident proteins</b>		
ATX2 ( <i>manganese homeostasis</i> )	AN6216	( $8.5e^{-06}$ ) Ci, Ss, Bc, Mg, Nc, Cg, Ro, Cn
ARV1 ( <i>intracellular sterol distribution</i> )	AN5868	( $1.3e^{-09}$ ) Ci, Nc, Ss, Cg, Bc, Mg
AUR1 ( <i>IPC synthase, sphingolipid synthesis</i> )	AN4991	(0.0) Ci, Ss, Bc, Cg, Nc, Ro, Cn
GDA1 ( <i>guanosine diphosphatase, GDP → GMP</i> )	AN1082	(0.0) Ci, Ss, Bc, Mg, Nc, Cg, Ro, Cn
CCC1 ( <i>vacuolar Fe<sup>2+</sup>/Mn<sup>2+</sup> transporter</i> )	AN3681	( $3.5e^{-34}$ ) Ci, Mg, Ss, Ro, Bc, Cg, Cn
<b>Novel <i>A. nidulans</i> CCC1 homolog</b>	AN4990	( $2.1e^{-31}$ ) <b>None<sup>b</sup></b>
GEF1 ( <i>chloride channel, Fe metabolism</i> )	AN2308	(0.0) Ci, Ss, Cg, Mg, Bc, Cn, Ro
<b>Novel additional GEF1 homologs<sup>c</sup></b>	AN6107	(0.0) Ci, Nc, Ss, Mg, Bc, Cg, Cn, Ro
	AN6311	(0.0) Ci, Mg, Cg, Nc, Ss, Bc, Cn, Ro
IMH1 ( <i>vesicular transport, GRIP domain</i> )	AN2480	( $9.4e^{-39}$ ) Ci, Nc, Ss, Bc, Cg, Mg, Ro
LCB4, LCB5 ( <i>sphingolipid long-chain base kinase</i> )	AN1176	(0.0) Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
ANP1 ( <i>retention of Golgi glycosyltransferases</i> )	AN10265	(0.0) Ci, Ss, Mg, Cg, Nc, Bc, Ro
VAN1 ( <i>component of mannan polymerase I</i> )	AN4395	(0.0) Ci, Mg, Cg, Bc, Nc, Ss, Ro
MNN9 ( <i>Golgi mannosyltransferase complex</i> )	AN7672	(0.0) Ci, Bc, Ss, Nc, Mg, Cg
MNN10 ( <i>Golgi membrane mannosyltransferase</i> )	AN7562	(0.0) Ss, Bc, Ci, Mg, Nc, Cg
MNN11 ( <i>Golgi mannosyltransferase complex</i> )	AN1969	( $1.5e^{-22}$ ) Ci, Cg, Nc, Ss, Mg, Bc
HOC1 ( $\alpha$ -1,6-mannosyltransferase)	AN4716	(0.0) Ci, Ss, Nc, Bc, Mg, Cg, Cn
MNN2 ( $\alpha$ -1,2-mannosyltransferase)	AN6571	(0.0) Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
MNN5 ( $\alpha$ -1,2-mannosyltransferase)	AN6857	( $4e^{-44}$ ) Ci, Bc, Ss, Mg, Nc, Cg, Cn, Ro
MNN1 ( $\alpha$ -1,3-mannosyltransferase)	AN6571 <sup>d</sup>	( $9e^{-05}$ ) Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
KRE6 ( <i>integral membrane <math>\beta</math>-1,6 glucan synthase</i> )	AN10779	(0.0) Ci, Bc, Ss, Cn
RSN1 ( <i>membrane protein, unknown function</i> )	AN8069	(0.0) Ci, Bc, Cg, Ss, Nc
DRS2 ( <i>aminophospholipid translocase</i> )	AN6112	(0.0) Ci, Bc, Cg, Nc, Mg, Ss, Ro, Cn
KEX1 ( <i>killer toxin processing, TPA carboxypeptidase</i> )	AN10184	(0.0) Ci, Ss, Nc, Mg, Bc, Cg, Cn, Ro
KEX2 ( <i>Ca<sup>2+</sup>-dependent Ser protease, proprotein convertase</i> )	AN3583	(0.0) Ci, Bc, Ss, Cg, Nc, Mg, Cn, Ro
VRG4 ( <i>Golgi GDP-mannose transporter</i> )	AN8848 <sup>e</sup>	(0.0) Ci, Bc, Ss, Mg, Nc, Cg, Ro, Cn
HVG1 ( <i>unknown function, similar to VRG4</i> )	AN9298 <sup>c</sup>	(0.0) <b>None</b>
PSD2 ( <i>phosphatidylserine decarboxylase</i> )	AN3188 <sup>f</sup>	(0.0) Ci, Ss, Cg, Mg, Bc, Cn, Ro
<b>Novel additional PSD2 homolog</b>	AN7989	(0.0) Ci
HUT1 ( <i>UDP-galactose transport to GA lumen</i> )	AN4068	(0.0) Ci, Ss, Bc, Mg, Nc, Cg, Ro, Cn
GOT1 ( <i>ER → GA transport?</i> )	AN10313	( $1e^{-07}$ ) Ci, Mg, Cg, Ss, Nc, Ro
STE13 ( <i>dipeptidyl aminopeptidase</i> )	AN2946	( $1e^{-112}$ ) Ss, Bc, Ci, Nc, Cg, Mg
PMR1 ( <i>Ca<sup>+2</sup>/Mn<sup>+2</sup> P-type ATPase</i> )	AN7464	(0.0) Ci, Ss, Bc, Mg, Nc, Cg, Cn, Ro
TUL1 ( <i>RING-finger E3 ubiquitin ligase</i> )	AN1075	( $1e^{-51}$ ) Ci, Mg, Bc, Nc, Ss, Cg, Ro, Cn
YIF1 ( <i>fusion of ER-derived COPII vesicles</i> )	AN6628	( $1e^{-22}$ ) Ci, Bc, Nc, Cg, Mg, Ss, Cn, Ro
COY1 ( <i>similar to mammalian CASP</i> )	AN0762	( $3e^{-48}$ ) Ci, Bc, Nc, Ss, Mg, Cg, Cn
SWH1, OSH2 ( <i>oxysterol-binding protein</i> )	AN9063	( $1e^{-123}$ , $1e^{-160}$ ) Bc, Nc, Ss, Mg, Ci, Cg, Ro
GMH1 ( <i>interacts with GEAI, GEA2</i> )	AN3439	( $7e^{-08}$ ) Ci, Cn



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