Formins and membranes: anchoring cortical actin to the cell wall and beyond

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INTRODUCTION
Formins (FH2 proteins) are a large family of evolutionarily conserved eukaryotic proteins participating in actin and microtubule organization. Land plants have three formin clades, with only two – Class I and II – present in angiosperms. Class I formins are often transmembrane proteins, residing at the plasmalemma and anchoring the cortical cytoskeleton across the membrane to the cell wall, while Class II formins possess a PTEN-related membrane-binding domain. Lower plant Class III and non-plant formins usually contain domains predicted to bind RHG GTPases that are membrane-associated. Thus, some kind of membrane anchorage appears to be a common formin feature. Direct interactions between various non-plant formins and integral or peripheral membrane proteins have indeed been reported, with varying mechanisms and biological implications. Besides of summarizing new data on Class I and Class II formin-membrane relationships, this review surveys such “non-classical” formin-membrane interactions and examines which, if any, of them may be evolutionarily conserved and operating also in plants. FYVE, SH3 and BAR domain-containing proteins emerge as possible candidates for such conserved membrane-associated formin partners.

Keywords: formin, actin, plasmalemma, endomembranes, cell polarity, endocytosis, vesicle trafficking

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VARIETY OF MECHANISMS CAN ATTACH FORMINS TO MEMBRANES
The functionality (or value, in the neo-Darwinian terms) of a protein critically depends on its (intracellular) location, reminiscent of the well-known truth concerning real estate. Aside of regulating gene expression with far-reaching downstream effects, a protein can hardly exert a membrane-related function without physically associating with membranes. This may be accomplished by diverse mechanisms: by membrane insertion in integral membrane proteins, by direct binding (possibly following a post-translational
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Formins associated with membranes

FIGURE 1 | Possible mechanisms of formin-membrane attachment.

Protein domains are drawn roughly to scale based on the sequences of proteins listed in parentheses (including Arabidopsis locus identifiers and/or GenBank or Uniprot accession numbers; interacting protein pairs were chosen based on cited literature). Formins are shown in shades of blue, their interactors in shades of orange, cytoplasmic side of the membrane faces down. Complex stoichiometry is speculative in the absence of data. (A) Direct insertion into the membrane, as in plant Class I formins (Arabidopsis AtFH1, At3g25500). (B) Peripheral membrane binding, as in plant Class II formins (Arabidopsis AtFH14, At1g31810). (C) Interaction with a peripheral membrane protein, such as a RHO GTPase or a FBAR protein (left: mouse mDia1, NP_031884.1 and Cdc42, NP_033991.1; right: human DAAM1, XP_005267487.1, and FB17 GMR1.2). (D) Interaction with an integral membrane protein, as in mammalian formins binding to CD21 (human FHOS, NP_037373.2, and CD21, NP_000260.5).

The only formins experimentally proven to be integral membrane proteins are the members of the plant Class I clade. Outside plants, secretory and transmembrane peptides were predicted only in several uncharacterized invertebrate and protist formins, without experimental proof that these proteins are membrane-located, albeit in one Caenorhabditis case there is at least cDNA evidence that the gene is expressed (Grunt et al., 2008). Some metazoan formins can also bind to membranes peripherally, similar to plant Class II formins. Drosophila Diaphanous, a prototype member of the large metazoan Diaphanous related formin (DRF) clade (Goode and Eck, 2007), directly binds PtdIns(4,5)P2 through an N-terminal basic domain. However, its membrane association requires simultaneous binding to a RHO GTPase (see below), i.e., binding a membrane phosphoinositide alone does not yet make the formin a peripheral membrane protein (Bousoo et al., 2013).

Association of fungal and metazoan formins with membranes is thus usually indirect, mediated by binding to peripheral or integral membrane proteins. Numerous formin interactors have been identified, most of them cytoplasmic (Aspenström, 2010). The best characterized membrane-associated ones are notorious formin regulators – the small GTPases of the RHO family, which can attach to membranes thanks to their hydrophobic post-translational modifications. Many formins, including fungal ones and metazoan DRFs, contain a conserved N-terminal GTPase binding domain (GBD/FH3) whose binding to an active (GTP-loaded) RHO alleviates autoinhibition mediated by a C-terminal autoinhibitory domain (Watanabe et al., 1997). The GBD/FH3 domain is probably evolutionarily ancient, although it appears to be absent in plants (Rivero et al., 2005).

Formins can bind some other peripheral membrane proteins. The N-terminal portion of mammalian FMNL1, a classical GBD/FH3 containing formin, interacts with AHNK (desmoyokin), a huge phosphoprotein binding the plasmalemma as a part of a larger multiprotein complex (Haase, 2007; Dempsey et al., 2012). Rather than attaching itself to the membrane via AHNK, the formin, bound to a RHO GTPase, participates in recruiting AHNK from the cytoplasm to the plasmalemma.
Another SH3-containing transmembrane protein, the osmosen- 
that themselves can nucleate actin FYVE domain-containing proteins, including the Spir proteins 
malian formins with compartments of the endomembrane system 
with a coiled coiled motif in between (Roberts-Galbraith and Gould, 2010). A mammalian homolog of CIP4, a prototype protein of this family originally identified as a Cdc42 (RHO GTPase) effector, interacts with the DAAM1 formin via its SH3 domain, raising thus the possibility that other SH3-containing proteins may bind formins as well (Aspenström et al., 2006).

This is not surprising, as SH3 domains associate with proline-rich proteins (Alexandropoulos et al., 1995), and the major- ity of formins contain an extremely Pro-rich domain, termed FH1, in front of the hallmark FH2 domain. Indeed, the same study identified a Src family non-receptor tyrosine kinase as a DAAM1 binding partner, confirming thereby previous observ- 
ations that other metaoxan formins can bind Src (Uetz et al., 1996).

SH3 domain-containing proteins often interact with integral 
membrane proteins, and some are themselves inserted into mem- 
branes, such as, e.g., the budding yeast protein Fes1p (not to be 
confused with the fusion yeast formin Fusi1) which can bind to the Bni1p and Bnr1p formins via its SH3 domain (Tong et al., 2002). Another SH3-containing transmembrane protein, the osmosen- 
or Sho1p, participates in a larger protein complex with Bni1p and 
and can be found elsewhere (e.g., Chesarone et al., 2010; Yang 
and Srivik, 2011; Vaškovitcová et al., 2013). What follows is 
a summary of biological implications of the formin-membrane 
interactions discussed in the previous section.

Some of these mechanisms may localize formins within the 
plane of the plasmalemma, participating thus in the control of cell 
polarity, or delimiting cell surface domains with increased mem- 
brane expansion or turnover (including polar or tip growth; for 
the concept of “activated cortical domains” in plant cells compare 
Záskk et al., 2009). Phosphoinositide interaction of Drosophila 
Diaphanous is required for targeting the formin to the epithelial 
apical membrane (Rousso et al., 2013), and interaction with the 
F-BAR protein CIP4 may inhibit Diaphanous in lateral and basal 
membrane domains (Yan et al., 2013). However, other metaoxan F- 
BAR proteins may stimulate formin activity while connecting 
the plasmalemma and the cortical cytoskeleton during actin-driven membrane tubulation and ruffling (Toguchi et al., 2010) or dur- 
ing formation of dendritic spines in neurons (Wakita et al., 2011). Aspergillus formin interactor MesA promotes formin localization 
to growing tips of hyphae (Pearson et al., 2004), reminiscent of 
the function of some plant formins in tip growth (see below). Similarly, formin-containing complexes of budding yeast Fus1p 
localize at the tip of mating protrusions, or “shmoos” (Nelson 
et al., 2004). In zebras, complexes involving RH3, a DTF type 
formin and Antxr2a exhibit polar localization at the plasmalemma and contribute to division plane positioning (Castanon et al., 2013).

Formins also associate with the endomembrane system and 
participate in vesicle trafficking. The above-described metaoxan 
Supiformin complexes engage in actin-dependent vesicle trans- 
port, possibly via actin nucleation on vesicle membranes (see 
Kerkhoff, 2011; Dietrich et al., 2013). Formins, bound to RHO 
GTPases, also participate in spatially restricted endocytosis and 
in endosome dynamics in both yeasts (Gachet and Hyams, 2005; 
Presser et al., 2011) and metazoa, where interaction with Src 
appears to be contributing as well (Gasman et al., 2003). It has to be 
noted, though, that all the endosome- and endocytosis-associated formins described so far contain the GBDFH3 domain which can 
engage in endocytosis regulation also outside the formin context, 
as in the Entamoeba EhNCABP166, which lacks the FH2 domain 
(Campos-Parra et al., 2010). The F-BAR family formin interactors 
to are also predominantly involved in endocytosis (Feng et al., 
2010), as well as in autophagy, also an endosome-dependent pro- 
cess (Huet al., 2009). The F-BAR domain’s ability to increase 
or stabilize membrane curvature may play an important role in 
generating endocytic membrane vesicles, a process facilitated by 
dynamin (Roberts-Galbraith and Gould, 2010).
While most reports on formin-endomembrane associations point to endocytotic pathways or compartments, genetic data from fission yeast suggest that the For3 formin participates in exocytosis, as a synthetic thermosensitivity phenotype was observed upon combining mutations affecting For3 and Mug33, a transmembrane protein involved in polarized secretion and co-localizing with the exocyst complex (South et al., 2011). Also the formin binding partner AHNAK has been implicated in the delivery of Ca2+-channels to the plasmalemma repair of cell membrane lesions, i.e., in processes that, on the first glance, appear to be exocytosis-driven, albeit they have a non-separable endocytotic component as well (Idone et al., 2008).

To summarize, numerous lines of evidence point to formins being involved in various aspects of endosome trafficking or endomembrane system organization. Recent reports even indicate that the ER associated formin INF2 (Chhabra et al., 2009) participates in the division of mitochondria, which involves a dynamin-related protein (Korobova et al., 2013), and other formins contribute to actin rearrangements involved in Toxoplasma apicoplast division (Jacot et al., 2013). However, as most of the reported interactions involve proteins so far found only in opisthokonts, it remains to be seen if similar mechanisms operate also in plants.

### Membrane-associated Formins in Plants: The Known and the Possible

Insertion of typical plant Class I formins into membranes, as well as membrane association of PTEN domain-containing formins, is experimentally well documented. As far as biological function is concerned, plant formins, often plasmalemma-associated, participate in the division of mitochondria, which involves AHNAK and other FYVE domain-containing proteins, such as Spir (FYVE) and F-BAR-SH3. F-BAR-SH3 domains are often found in plant SH3 domain-containing proteins, such as Fus1, which has an analogous BAR-SH3 domain layout with a plant-specific shorter BAR domain instead of FBAR (see BAR-SH3).

| Protein or domain(s) | Non-plant query | Land plant candidates | Notes |
|---------------------|----------------|----------------------|-------|
| AHNAK               | NP_001611.1 (human AHNAK isoform 1) | N.A. | Best plant BLAST hit with E-value 5e-06 only matches a low complexity region of AHNAK |
| Spr (FYVE)          | NP_001246101.1 (Drosophila spr isoform F) | N.A. | Many plant FYVE domain protein exist; for candidate selection see text. |
| other FYVE          | cd00066 (FYVE domain) | A1qg33240, FAB1A A2gi4270, FAB1B | |
| F-BAR-SH3           | NP_0042111 (human CIP4) | N.A. | No bona fide plant F-BAR domains but several proteins have an analogous BAR-SH3 domain layout with a plant-specific shorter BAR domain (cd07607) instead of FBAR (see BAR-SH3). |
| Fus1 (SH3)          | NP_009903 (Saccharomyces cerevisiae Fus1p) | N.A. | No additional Arabidopsis paralogs identified by Blast with AtFus1 query. |
| other BAR-SH3       | cd07607 (BAR domain of the plant SH3 domain-containing protein) | A1qg31440, AtSH3P1 A0qg34680, AtSH3P2 A0qg8060, AtSH3P9 | |
| Antxr2              | XP_005165376.1 (zebrafish Antxr2 isoform X1) | N.A. | No additional Arabidopsis paralogs identified by Blast with AtSH3P3 query. |
| MesA                | G80BR2.2 (Aspergillus nidulans MesA) | N.A. | |
| Grid2               | NP_0010510.2 (human Grid2) | N.A. | PDZ domain in the formin partner required for binding, not found in plant formins. |
| CD21                | NP_0100659.1 (human CD21 isoform 1) | N.A. | PKD2 homologs found in Micromonas and volvocalcine algae. |
| PKD2                | NP_0328873 (mouse polycystin-2) | N.A. | |

GenBank/UniProt accession numbers are provided for protein sequences used as queries, and NCBI conserved domain database accessions for domains. N.A. not available (not found in standard Blast searches of the Viridiplantae section of the NCBI protein database using the listed non-plant sequences as queries). For proteins and domains where land plant candidates were found, only Arabidopsis proteins are shown (referred to using standard A. thaliana locus nomenclature), albeit non-Arabidopsis homologs without experimental data exist as well.
lacking AtFH1 have more dynamic microtubules (Rosero et al., 2013).

Similar to other eukaryotic lineages, also in plants formins may be closely involved in membrane turnover or associated with endomembranes. *Physcomitrella patens* Class II formin For2A specifically localizes to PtdIns(3,5)P2-rich sites of active plasmalemma turnover (van Gisbergen et al., 2012). Overexpressed microtubule-associated Class I Arabidopsis formin AFH4 can decorate the endoplasmic reticulum and co-align it to the microtubule cytoskeleton (Deeks et al., 2010), and its relative AtFH8 is targeted to the nuclear envelope (Xue et al., 2011). Loss of tip polarity in formin-overexpressing pollen tubes (Cheung and Wu, 2004; Cheung et al., 2010) or root hairs (Yi et al., 2005), as well as irregular cell wall thickening observed in rice mutants lacking the Class II formin FHS (Yang et al., 2011) might be understood as disturbance of the eucytosol/endocytosis co-ordination. Thus, the biological implications of formin-membrane association may be conserved, and it is worth examining the molecular mechanisms underlying membrane localization of formins.

Non-classic angiosperm formins lacking the transmembrane (in Class I) or PTEN-like (in Class II) domains might heterodimerize with their membrane-bound paralogs. Surprisingly, FH2-mediated formin heterodimerization has been neither documented nor excluded yet in any organism, albeit dimerization via other domains was reported (see Čvrčková, 2012).

The Rop GTPases represent a plant branch of RHO proteins (see Mucha et al., 2011), often understood as general formin regulators. However, plant formins lack the RHO-binding GB5/FH3 domain, and the only putative RHO interaction motif found in land plant FH2 proteins is a RHO GTPase activating protein (RhoGAP)-related domain in non-angiosperm Class III formins (Grunt et al., 2008). Thus, Rops are unlikely to provide the means for direct formin-membrane binding in angiosperms, albeit they may participate in larger multi-subunit complexes.

Few, if any, clear homologs of other non-plant membrane associated formin homologs can be identified in database searches (Table 1). Two protein families may, nevertheless, deserve a closer look.

While there is no direct plant homolog of Sprt, numerous plant proteins harbor FYVE domains. The 15 FYVE-containing proteins of *A. thaliana* can be divided into five groups according to their domain architecture (Wvijal and Singh, 2010). Most of these proteins are experimentally uncharacterized, and none exhibit a significant match to any of the previously described formin interactors in BLAST searches. However, the only two experimentally characterized Arabidopsis FYVE-containing proteins encoded by the FAB1A and FAB1B genes are members of type III phosphatidylinositol 3-phosphate 5-kinase, or PIKfyve, family which has been implicated in endocytosis and actin dynamics in metazoan cells, albeit with no evidence for direct formin-membrane binding in angiosperms, albeit they may be upregulated in pollen tubes, whose growth is formin-dependent (Wang et al., 2008). Intriguingly, these proteins contain a N-terminal BAR domain, a plant-specific variant of a shorter version of the F-BAR domain; and perhaps they might represent a plant counterpart of the yeast and metazoan F-BAR formin interactors.

Last but not least, plant formins may be attached to membranes by lineage-specific mechanisms. A gene encoding a protein with unique combination of FH2 and Sec10 domains, physically linking a formin and a subunit of the membrane-associated Exocyst complex, exists in *Physcomitrella* (Grunt et al., 2008; Čvrcková et al., 2012), and the first identified plant formin interactor, FIP2 (*AtFG50000; Banno and Chua, 2000) contains a domain corresponding to the oligomerization interface of voltage-gated potassium channels, and might perhaps interact with them.

In summary, there may be more to the association of plant formins with membranes than just the transmembrane and PTEN-like domains characterizing the two angiosperm formin clades, and a comparison with non-plant systems does provide some candidates that may be worth closer investigation.

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**Table 1**

| Formin | Membrane Localization |
|--------|-----------------------|
| FYVE-containing proteins | Unknown |
| PIKfyve | Membrane-associated Exocyst complex |
| FIP2 | Membrane-associated Exocyst complex |
| Other formin interactors | Unknown |

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