Glycosylphosphatidylinositol-Anchored Proteins in *Arabidopsis* and One of Their Common Roles in Signaling Transduction

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Diverse proteins are found modified with glycosylphosphatidylinositol (GPI) at their carboxyl terminus in eukaryotes, which allows them to associate with membrane lipid bilayers and anchor on the external surface of the plasma membrane. GPI-anchored proteins (GPI-APs) play crucial roles in various processes, and more and more GPI-APs have been identified and studied. In this review, previous genomic and proteomic predictions of GPI-APs in *Arabidopsis* have been updated, which reveal their high abundance and complexity. From studies of individual GPI-APs in *Arabidopsis*, certain GPI-APs have been found associated with partner receptor-like kinases (RLKs), targeting RLKs to their subcellular localization and helping to recognize extracellular signaling polypeptide ligands. Interestingly, the association might also be involved in ligand selection. The analyses suggest that GPI-APs are essential and widely involved in signal transduction through association with RLKs.

**Keywords:** glycosylphosphatidylinositol (GPI), GPI-anchored protein (GPI-AP), receptor-like kinase (RLK), ligand, signaling transduction

**GLYCOSYLPHOSPHATIDYLINOSITOL (GPI) MODIFICATION AND GPI-ANCHORED PROTEIN (GPI-AP) BIOSYNTHESIS**

The GPI oligosaccharide structure is ubiquitous among eukaryotes with a common minimal backbone consisting of three mannoses, one non-N-acetylated glucosamine (GlcN), and inositol phospholipid, which covalently links the carboxyl terminus (C terminus) of GPI-APs to the lipid bilayer (Figure 1A) (Stevens, 1995; Oxley and Bacic, 1999; Kinoshita and Fujita, 2016). Catalyzed by a series of enzyme complexes, GPI biosynthesis starts with a lipid molecule at the rough side of the endoplasmic reticulum (ER), and this then flips and the synthesis is completed on the luminal side of the ER (Figure 1C) (Stevens, 1995; Takeda and Kinoshita, 1995; Kinoshita and Fujita, 2016). The typical GPI-AP precursors possess a common structure that lead them to be modified by GPI moieties inside endomembrane systems: amino-terminal (N-terminal) hydrophobic signal peptides lead them to enter the ER lumen, and during translation and maturation, C-terminal hydrophobic signals are recognized and cleaved at the ω position by a series of catalytic complexes, where the peptide bond is replaced by a bond with ethanolamine phosphate (Figures 1A–C) (Eisenhaber et al., 1998; Kinoshita, 2014a; Kinoshita and Fujita, 2016).

The GPI moiety allows these GPI-APs, which possess no transmembrane region, to be anchored to membrane lipid bilayers. Compared to transmembrane association, GPIanchoring has its advantages: GPI-AP shedding and release due to the presence of GPI-specific phospholipases (PLC)
makes this association reversible in mammalian cells (Orihashi et al., 2012; Fujihara and Ikawa, 2016). In plants, although similar shedding and release mechanisms are indicated as various GPI-APs were identified in cell walls, thus far, no GPI-specific PLC has been identified yet (Bayer et al., 2006; Yeats et al., 2018). However, a bacterial phosphatidylinositol-specific PLC (PI-PLC) has been used for shedding GPI-APs from lipid bilayers in vitro and identifying them by further proteomic analysis in Arabidopsis (Borner et al., 2003; Elortza et al., 2003; Takahashi et al., 2016; Yeats et al., 2018).

**IMPORTANCE OF GPI ANCHORING FOR GPI-APS**

GPI-APs and their GPI moieties were demonstrated to be crucial for diverse developmental processes in mammals and in plants, because development was found to be broadly and severely affected if GPI moiety biosynthesis is disrupted (Kawagoe et al., 1996; Gillmor et al., 2005; Kinoshita, 2014b; Bundy et al., 2016).

As the most noticeable feature, GPI anchoring was thought to be essential for the functions of GPI-APs, and their enzymatic activities or subcellular localizations could be altered by the removal of the GPI moiety (Tozeren et al., 1992; Butikofer et al., 2001; Davies et al., 2010). However, there are exceptions: the GPI anchoring of ZERZAUST and FLA4/SOS5 was shown to be dispensable for their functions in Arabidopsis (Vaddepalli et al., 2017; Xue et al., 2017).

GPI moieties also play crucial roles for driving the transient, relatively ordered membrane domains rich in sphingolipids and sterols, which are called lipid rafts or microdomains, to their target regions (Saha et al., 2016; Sezgin et al., 2017; Hellwing et al., 2018; Lebreton et al., 2018). In mammalian and yeast cells, GPI-APs are co-clustered and organized in a mixture of monomers and cholesterol-dependent nanoclusters in the same lipid raft. These exit the ER in vesicles distinct from other secretory proteins and are predominantly sorted to the apical surface to serve in protein trafficking and signaling transduction (Eisenhaber et al., 1998; Morsomme et al., 2003; Legler et al., 2005; Muniz and Zurzolo, 2014; Miyagawa-Yamaguchi et al., 2015; Sezgin et al., 2017). In Arabidopsis, although GPI modification was found essential for protein delivery from the ER to the plasma membranes (Zavaliev et al., 2016), the lipid raft mechanism has not been well revealed yet.

**PREDICTION AND IDENTIFICATION OF GPI-APS IN ARABIDOPSIS**

To identify GPI-APs, various bioinformatics tools were developed, generally depending on the prediction of a specific...
hydrophobic region at the C terminus. Examples are big-PI Plant Predictor (http://mendel.imp.ac.at/sat/gpi/gpi_server.html) (Eisenhaber et al., 1998), PredGPI (http://gpcr2.biocomp.unibo.it/gpipe/info.htm) (Pierleoni et al., 2008), GPI-SOM (http://gpi.unibe.ch/) (Fankhauser and Maser, 2005), and fragAnchor (Poisson et al., 2007). According to the latest genomic scanning by these tools, among lower and higher eukaryotes, about 0.21% to 2.01% of total proteins from diverse families are predicted to be modified by GPI moieties, and the percentage in Arabidopsis is 0.83% (Eisenhaber et al., 2001; Poisson et al., 2007). In the meantime, proteomic assays, which depend on cleavage from membranes by bacterial PI-PLC treatment in vitro and enrichment in particular membrane fractions, were performed to compare proteomic data to bioinformatic data. To date, more than 300 GPI-APs have been identified in Arabidopsis (Borner et al., 2002; Borner et al., 2003; Elortza et al., 2003; Bayer et al., 2006; Takahashi et al., 2016).

Arabidopsis GPI-APs identified in 2003 (Borner et al., 2003; Elortza et al., 2003) and 2016 (Takahashi et al., 2016) are assembled in Tables 1 and 2, respectively, and their functions are discussed.

In Table 1, 248 genes predicted to encode GPI-APs in 2003 have been listed. Some corrections have been made, as some of them could not be found in databases or turned out to encode non-coding RNA. However, according to more recent experimental data, genes not included in 2003 also turned out to encode GPI-APs, such as At1g09460, At2g30933, At2g03505, and At4g13600 (Simpson et al., 2009), LORELEI (Tsukamoto et al., 2010), and XYP2 (Motose et al., 2004). Interestingly, due to recent achievements on alternative splicing, transcriptional variants of SK33 (Zhou, 2019a) and CRK10 (Grojean and Downes, 2010) have been found to encode GPI-APs besides their ordinarily reported proteins (Figure 2). Alternative splicing largely enhanced the diversity of transcriptome and proteome, and more and more genes (up to 80% according to recent RNA-seq achievements) have been found to be alternatively spliced in Arabidopsis, which could greatly increase the abundance of GPI-APs (Wang et al., 2009; Flichkin et al., 2010; Severing et al., 2011; Reddy et al., 2013; Lee and Rio, 2015; Bush et al., 2017).

In addition, 163 GPI-APs were predicted in 2016, and those not included in Table 1 are listed in Table 2. In this study, a large proportion of possible GPI-APs were discounted as typical GPI-APs in spite of being predicted to possess a GPI signal at the C terminus by various bioinformatics tools. Some of those discounted were transmembrane proteins, such as PIN3 and PIN4 and some receptor-like kinases (RLKs), and the other were cytoplasmic proteins without N-terminal secretory signal peptide, such as SNARE family proteins (listed at the end of Table 2).

FUNCTIONAL DIVERSITY OF GPI-APS IN ARABIDOPSIS

GPI-APs listed in Tables 1 and 2 are from diverse families, such as cell wall structure proteins, proteases, enzymes, receptor-like proteins (RLPs), lipid transfer proteins, and GPI-anchored peptides, which imply a functional diversity of GPI-APs: indeed, they were found functional in most processes, such as cell wall composition, cell wall component synthesis, cell polar expansion, stress responses, hormone signaling responses, pathogen responses, stomatal development, pollen tube elongation, and double fertilization in Arabidopsis.

Among these GPI-APs, the arabinogalactan protein (AGP) family, LORELEI family, COBRA family, and some RLKs, were better characterized. AGP family proteins are ubiquitous cell wall components anchoring on the plasma membrane throughout the Plant Kingdom and abundantly decorated at their Hyp residues by arabinogalactan polysaccharides, which make them be one of the most complex families of macromolecules in plants and play roles in various processes (Schultz et al., 2000; Ellis et al., 2010; Marzec et al., 2015; Showalter and Basu, 2016; Losada and Herrero, 2019; Palacio-Lopez et al., 2019). COBRA families were reported to be involved in various processes by regulating cell wall synthesis in plants (Hochholdinger et al., 2008; Caö et al., 2012; Niu et al., 2015; Niu et al., 2018). LORELEI family proteins associate with cell surface RLK, which is essential not only for ligand recognition but also for RLK transport (Capron et al., 2008; Duan et al., 2010; Tsukamoto et al., 2010; Meng et al., 2012; Yu et al., 2012; Li et al., 2015; Li et al., 2016; Liao et al., 2017; Stegmann et al., 2017; Feng et al., 2018; Guo et al., 2018; Yin et al., 2018).

INVolVEMENT OF GPI-APs IN SIGNALING TRANSDUCTION IN ARABIDOPSIS

In Arabidopsis, hundreds of RLKs, which possess extracellular ligand recognition domains and intracellular kinase domains, control a wide range of processes, including development, disease resistance, hormone perception, and self-incompatibility (Shiu and Bleecker, 2001; Muschietti and Wengier, 2018; Wei and Li, 2018). Their association with extracellular ligands, including phytohormones, signaling polypeptides, and pathogen molecules, leads to the phosphorylation of the intracellular kinase domain, which consequently activate cytoplasmic signaling components and switch on response mechanisms (Figure 3A) (Pearce et al., 2001; Asai et al., 2002; Geldner and Robatzek, 2008; Murphy et al., 2012; Breiden and Simon, 2016; Yamaguchi et al., 2016; Chardin et al., 2017).

By summarizing the functional mechanism of those listed GPI-APs in Tables 1 and 2, a group of GPI-APs from various families was found to share a common mechanism of action involving RLK-related signal transduction (Table 3). The same mechanism has been reported in mammalian cells, for example, that GPI-anchored CD14 possessing leucine-rich repeats (LRR) region associates with not only Toll-like receptor TLR4 to perceive their polypeptide ligand lipopolysaccharide (LPS) leading them to activate mitogen-activated protein kinase (MAPK) cascades (Wright et al., 1990; Schumann, 1992; Zanoni et al., 2011; Li X. et al., 2015) but also TLR3 to perceive viral double-stranded RNA (dsRNA) leading them to activate (Vercammen et al., 2008). This common mechanism
TABLE 1 | A review of predicted GPI-APs updated from (Borner et al., 2003; Elortza et al., 2003).

| Group               | Sub-group                      | Total | Gene No. | Name   | Descriptions                                                                                                                                 |
|---------------------|--------------------------------|-------|----------|--------|---------------------------------------------------------------------------------------------------------------------------------------------|
| AGP                 | Classical AGP                  | 17    | At1g68725| AGP19  | AGP17-19 encode a subclass of lysine-rich AGPs, among which AGP18 was reported to be essential for the initiation of female gametogenesis both at the sporophytic and gametophytic levels, and AGP19 functions in cell division and expansion (Acosta-Garcia and Vielle-Calzada, 2004; Sun et al., 2005; Yang et al., 2007; Yang et al., 2011; Zhang et al., 2011a; Zhang et al., 2011b). |
| AGP                 |                                 |       | At4g37450| AGP18  | AGP6 and AGP10 are co-expressed and co-localized in pollen grains and pollen tubes and essential for pollen grain development and pollen early germination, possibly because they are essential components of the nexine layer in pollen cell wall (Levitin et al., 2008; Coimbra et al., 2009; Coimbra et al., 2010; Costa et al., 2013; Palareti et al., 2016). |
| AGP                 |                                 |       | At2g23130| AGP17  | AGP17-19 encode a subclass of lysine-rich AGPs, among which AGP18 was reported to be essential for the initiation of female gametogenesis both at the sporophytic and gametophytic levels, and AGP19 functions in cell division and expansion (Acosta-Garcia and Vielle-Calzada, 2004; Sun et al., 2005; Yang et al., 2007; Yang et al., 2011; Zhang et al., 2011a; Zhang et al., 2011b). |
| AGP                 |                                 |       | At5g14380| AGP6   | AGP6 and AGP10 are co-expressed and co-localized in pollen grains and pollen tubes and essential for pollen grain development and pollen early germination, possibly because they are essential components of the nexine layer in pollen cell wall (Levitin et al., 2008; Coimbra et al., 2009; Coimbra et al., 2010; Costa et al., 2013; Palareti et al., 2016). |
| AGP                 |                                 |       | At4g09030| AGP10  | AGP10 is essential for the degeneration of synergid cells, which guide the pollen tube attraction after acceptance of the unique pollen tube, and for prohibition of polytubey (Pereira et al., 2016a; Pereira et al., 2016b). |
| AGP                 |                                 |       | At4g09030| AGP3   | AGP3 is essential for the degeneration of synergid cells, which guide the pollen tube attraction after acceptance of the unique pollen tube, and for prohibition of polytubey (Pereira et al., 2016a; Pereira et al., 2016b). |
| AGP                 |                                 |       | At5g01700| AGP11  | AGP11 is essential for the degeneration of synergid cells, which guide the pollen tube attraction after acceptance of the unique pollen tube, and for prohibition of polytubey (Pereira et al., 2016a; Pereira et al., 2016b). |
| AG peptides         | (Schultz et al., 2004), a group of GPI-anchored arabinogalactan polypeptides | 12    | At3g13520| AGP12  | AGP12 is essential for the degeneration of synergid cells, which guide the pollen tube attraction after acceptance of the unique pollen tube, and for prohibition of polytubey (Pereira et al., 2016a; Pereira et al., 2016b). |
| FLAs (fasciclin-like AGPs) |                               | 16    | At5g55730| FLA1   | FLA1 is involved in lateral root initiation and shoot regeneration potentially by regulating cell-type specification (Johnson et al., 2011). |
| FLAs (fasciclin-like AGPs) |                               |       | At4g12730| FLA2   | FLA2 is specifically expressed in pollen grains and tubes and involved in microspore development potentially through the regulation of cellulose deposition (Li et al., 2010). |
| FLAs (fasciclin-like AGPs) |                               |       | At2g24450| FLA3   | FLA3 is specifically expressed in pollen grains and tubes and involved in microspore development potentially through the regulation of cellulose deposition (Li et al., 2010). |
| FLAs (fasciclin-like AGPs) |                               |       | At3g46550| FLA4/SOS5 | FLA4/SOS5 is directly associated with cell wall RLKs FEI1/2 to perceive environmental stimuli in apoplast by altering its conformation and association with FEI1/2. This complex could regulate cell wall synthesis and composition by collaborating with CESA5. Interestingly, this regulation could also be controlled by ethylene and ABA with unclear mechanism. Surprisingly, the absence of GPI anchors only affected their PM localization but not their function (Harpaz-Saad et al., 2012; Seifert et al., 2014; Basu et al., 2016; Griffiths et al., 2016; Xue et al., 2017; Turupcu et al., 2018). |

(Continued)
| Group                  | Sub-group                              | Total | Gene No.     | Name              | Descriptions                                                                 |
|-----------------------|----------------------------------------|-------|--------------|-------------------|-----------------------------------------------------------------------------|
| Extensin related      | Extensin related                       | 7     | A1g02405     | Proline-rich protein |                                                                             |
|                       |                                       |       | A1g70990     | Proline-rich protein |                                                                             |
|                       |                                       |       | A4g16140     | Proline-rich protein |                                                                             |
|                       |                                       |       | A5g11990     | Proline-rich protein |                                                                             |
|                       |                                       |       | A3g006750    | Hydroxyproline-rich glycoprotein family protein |                              |
|                       |                                       |       | A1g23040     | Hydroxyproline-rich glycoprotein family protein |                              |
|                       |                                       |       | A5g49280     | Hydroxyproline-rich glycoprotein family protein |                              |
| Phytocyanins          | Stellacyanin like                      | 4     | A5g20230     | BCB/ SAG14         | Regulates lignin biosynthesis induced by oxidative stress (Ezaki et al., 2005; Kim et al., 2011; Ji et al., 2015; Tang et al., 2016). |
| ([Nersissian et al., 1998]) |                                      |       | A2g31050     | Copredoxin superfamily protein |                                           |
|                       |                                       |       | A2g28720     | Copredoxin superfamily protein |                                           |
|                       |                                       |       | A5g26330     | Copredoxin superfamily protein |                                           |
|                       |                                       |       | A1g22480     | Copredoxin superfamily protein |                                           |
|                       |                                       |       | A1g72230     | Copredoxin superfamily protein |                                           |
|                       |                                       |       | A3g27200     | Copredoxin superfamily protein |                                           |
|                       | Uclacyanin like                        | 8     | A2g23300     | UCC1               | UCC1, UCC2 and UCC3 encode copper binding proteins (Nersissian et al., 1998). | |
|                       |                                       |       | A2g47790     | UCC2               |                                                                             |
|                       |                                       |       | A3g60280     | UCC3               |                                                                             |
|                       |                                       |       | A3g60270     | Copredoxin superfamily protein |                                           |
|                       |                                       |       | A5g07475     | Copredoxin superfamily protein |                                           |
|                       | ENODL (early nodulin like)             | 17    | A5g3870      | ENODL1             | Catalyzes the formation of pyroglutamic acid at the N-terminus of several peptides and proteins (Schilling et al., 2007). |
|                       |                                       |       | A4g27520     | ENODL2             |                                                                             |
|                       |                                       |       | A4g28365     | ENODL3             |                                                                             |
|                       |                                       |       | A4g32490     | ENODL4             |                                                                             |
|                       |                                       |       | A3g18590     | ENODL5             |                                                                             |
|                       |                                       |       | A1g49840     | ENODL6             |                                                                             |
|                       |                                       |       | A1g78000     | ENODL7             |                                                                             |
|                       |                                       |       | A1g66460*    | ENODL8             |                                                                             |
|                       |                                       |       | A3g20570     | ENODL9             |                                                                             |
|                       |                                       |       | A2g23990     | ENODL11            |                                                                             |
|                       |                                       |       | A4g30590     | ENODL12            |                                                                             |
|                       |                                       |       | A5g25090     | ENODL13            |                                                                             |
|                       |                                       |       | A2g25060     | ENODL14            |                                                                             |
|                       |                                       |       | A4g31840     | ENODL15            |                                                                             |
|                       |                                       |       | A3g01070     | ENODL16            | ENODL14 and ENODL15 directly interact with RLK FERONIA and regulate maternally controlled male-female communication and fertilization (Escobar-Restrepo et al., 2007; Hou et al., 2016). |
|                       |                                       |       | A5g15350     | ENODL17            |                                                                             |
|                       |                                       |       | A1g08500     | ENODL18            |                                                                             |
|                       |                                       |       | A5g60920     | COBRA/ COB          | Classified as unknown/hypothetical in Borner et al. (2003). Involved in starch mobilization and reproductive progresses (Khan et al., 2007). |
| COBRA family          | COBRA family                           | 10    | A3g02210     | COBL1              |                                                                                   |
| ([all 12 COBRA members, except COBL5, was predicted to be GPI-AP (Roudier et al., 2002)]) | |       | A3g29810     | COBL2              |                                                                                   |
|                       |                                       |       | A5g15630     | COBL4/ IRX6        | Localizes on plasma membrane polarly and regulates cell wall biosynthesis and cellulose microfibrils in Arabidopsis and tomato (Schindelman et al., 2001; Roudier et al., 2003). Its regulation responses to various stresses potentially by involving in jasmonic acid-related signaling pathway (Ko et al., 2006; Dinneny et al., 2008; Sorsk et al., 2019). |
|                       |                                       |       | A1g09790     | COBL6              | Plays a role in the deposition of crystalline cellulose in secondary cell wall structures during seed coat epidermal cell differentiation, and the regulation is independent of the FEI-SOS pathway (Ben-Tov et al., 2015; Ben-Tov et al., 2018). Participates in regulating secondary cell wall biosynthesis (Taylor-Teeples et al., 2015; Niu et al., 2018). |
|                       |                                       |       | A3g16860     | COBL8              |                                                                                   |
|                       |                                       |       | A5g20080     | COBL10             |                                                                                   |
|                       |                                       |       | A4g16120     | COBL7/ SEB1        |                                                                                   |
|                       |                                       |       | A4g27110     | COBL11             |                                                                                   |
|                       |                                       |       | A5g49270     | COBL9/ DER8/ SHV2   |                                                                                   |
| (Continued)
### TABLE 1 | Continued

| Group   | Sub-group | Total | Gene No.    | Name         | Descriptions                                                                                                                                                                                                 |
|---------|-----------|-------|-------------|--------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| GDPDL   |           | 6     | At1g66970   | GDPDL1/SHV3- | Homologue of the extracellular domain of RLK GDPDL2/SHV3-Like2/SVL2. Possesses the capacity to hydrolyze glycerophosphodiesters, which is stimulated by Ca$^{2+}$ in Arabidopsis, and plays an important role in various physiological processes (Cheng et al., 2011). |
|         |           |       | At1g66980   | SHV3-        |                                                                                                                                                                                                             |
|         |           |       | At4g26690   | GDPDL3/SHV3  |                                                                                                                                                                                                             |
|         |           |       | At3g20520   | GDPDL5       | SHV3 and GDPDL4 are involved in primary cell wall organization, which regulates cell polar expansion by coordinating proton pumping and cellulose synthesis (Parker et al., 2000; Hayashi et al., 2008; Yeats and Somerville, 2018; Yeats et al., 2018). |
|         |           |       | At3g20520   | GDPDL4/SHV3  |                                                                                                                                                                                                             |
|         |           |       | At5g55480   | GDPDL5/SLV1  |                                                                                                                                                                                                             |
|         |           |       | At5g58050   | GDPDL6/SLV4  |                                                                                                                                                                                                             |
|         |           |       | At5g58170   | GDPDL7/SLV5  |                                                                                                                                                                                                             |
| HIPL    |           | 3     | At1g74790   | ZERZAUST,   | Shown in Borner et al. (2003) but could not be found in databases                                                                                                                                              |
|         |           |       | At5g39970   | ZET          | Carbohydrate-binding X8 domain superfamily protein                                                                                                                                                           |
|         |           |       | At5g62630   | PDCB1       | Regulates the gating of plasmodesmata and the plasmodesmatal transport through plasmodesmal callose degradation (Zavaliev et al., 2016).                                                                         |
|         |           |       | At2g19440   | ZETH         | Homolog of ZET and works redundantly with ZET (Vaddepalli et al., 2019).                                                                                                                                      |
|         |           |       | At1g26450   | BG_PPAP     |                                                                                                                                                                                                             |
|         |           |       | At1g64760   | ZERZAUST,   | Carbohydrate-binding X8 domain superfamily protein                                                                                                                                                           |
|         |           |       | At3g04010   | ZET          | Required for cell wall organization during tissue morphogenesis potentially by being mediated by RLKs. Interestingly, the presence of GPI anchor is dispensable for its function (Fulton et al., 2009; Vaddepalli et al., 2017; Vaddepalli et al., 2019). |
|         |           |       | At3g13560   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At3g24330   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At4g29360   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At4g31140   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g18220   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g20870   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g42720   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g56590   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g58090   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g58480   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g64790   | ZET          |                                                                                                                                                                                                             |
|         |           |       | At5g42100   | BG_PPAP     | Regulates the gating of plasmodesmata and the plasmodesmatal transport through plasmodesmal callose degradation (Zavaliev et al., 2016).                                                                         |
|         |           |       | At5g61130   | PDCB1       | PCDB1-PDCB3, At1g69295, and At3g58100 encode a subgroup of X8-domain containing GPI-APs, which localize to the plasmodesmata and predicted to bind callose (Sim physician et al., 2009; Zavaliev et al., 2016). |
|         |           |       | At5g08000   | PDCB2       |                                                                                                                                                                                                             |
|         |           |       | At1g18650   | PDCB3       |                                                                                                                                                                                                             |
|         |           |       | At1g69295   | PCDB3       |                                                                                                                                                                                                             |
|         |           |       | At1g69295   | PCDB3       |                                                                                                                                                                                                             |
|         |           |       | At1g58100   | PCDB3       |                                                                                                                                                                                                             |
|         |           |       | At1g09960   | BG_PPAP     | At1g09960, At2g30933, At2g03505, and At4g13600 encode a subgroup of X8-domain-containing GPI-APs (Sim physician et al., 2009) but not included in Borner et al. (2003). |
|         |           |       | At2g30933   | BG_PPAP     |                                                                                                                                                                                                             |
|         |           |       | At2g03505   | BG_PPAP     |                                                                                                                                                                                                             |
|         |           |       | At4g13600   | BG_PPAP     |                                                                                                                                                                                                             |
| Polygalacturonase | 1 |       | At3g15720   | BG_PPAP     | Regulates the gating of plasmodesmata and the plasmodesmatal transport through plasmodesmal callose degradation (Zavaliev et al., 2016).                                                                         |
| Pectate lyases | 3 |       | At3g53190   | PMR6         | Required for fungal infection progress and effects cell wall composition through pectin synthesis (Vogel et al., 2002; Vogel et al., 2004).                                                                     |
|         |           |       | At3g54920   | PMR6         | Pectin lyase-like superfamily protein                                                                                                                                                                          |
|         |           |       | At5g04310   | PMR6         | Pectin lyase-like superfamily protein                                                                                                                                                                          |

(Continued)
TABLE 1 | Continued

| Group             | Sub-group | Total | Gene No. | Name     | Descriptions                                                                                                                                 |
|-------------------|-----------|-------|----------|----------|---------------------------------------------------------------------------------------------------------------------------------------------|
| Proteases         | Aspartyl proteases | 10    | A1g05840 | A36      | A36 and A39 co-localize with GPI-anchored COBL10 and involved in pollen tube germination, vitality, and pollen tube guidance (Gao et al., 2017; Gao et al., 2017). |
|                   |           |       | A1g08210 | A39      |                                                                                                                                             |
|                   |           |       | A1g535280|          |                                                                                                                                             |
|                   |           |       | A1g65240 |          |                                                                                                                                             |
|                   |           |       | A1g27760 |          |                                                                                                                                             |
|                   |           |       | A1g02740 |          |                                                                                                                                             |
|                   |           |       | A1g51330 |          |                                                                                                                                             |
|                   |           |       | A1g51350 |          |                                                                                                                                             |
|                   |           |       | A4g35880 |          |                                                                                                                                             |
|                   |           |       | A5g10080 |          |                                                                                                                                             |
|                   | Metalloproteases | 5     | A1g24140 | AT3-MMP  | This subgroup of proteases contribute to the MAMP-triggered callose deposition in response to the bacterial flagellin peptide flg22, which suggests their involvement in the pattern-triggered immunity in interactions with necrotrophic and biotrophic pathogen (Zhao et al., 2017). |
|                   |           |       | A1g59970 | AT5-MMP  |                                                                                                                                             |
|                   |           |       | A1g70170 | AT2-MMP  |                                                                                                                                             |
|                   |           |       | A2g45040 | AT4-MMP  |                                                                                                                                             |
|                   |           |       | A4g16640 | AT1-MMP  |                                                                                                                                             |
|                   | Cys proteases | 1     | A3g43960 |          | Regulates root hair elongation (Lin et al., 2011).                                                                                           |
| LTPL (lipid transfer-like protein) |            | 26    | A1g06450 | LTPG3    | LTPG1, LTPG2, LTPG5, and LPTG6 are involved in cuticular wax export or accumulation in epidermal cells and during pathogen defense (Debono et al., 2009; Kim et al., 2012; Guo et al., 2013; Edstam and Edqvist, 2014; Fahlgberg et al., 2019). |
|                   |           |       | A1g18280 | LTPG1/    |                                                                                                                                             |
|                   |           |       | A1g27950 | LTPG     |                                                                                                                                             |
|                   |           |       | A3g43720 | LTPG2    |                                                                                                                                             |
|                   |           |       | A3g22600 | LTPG5    |                                                                                                                                             |
|                   |           |       | A1g55260 | LTPG6    |                                                                                                                                             |
|                   |           |       | A1g62790 |          |                                                                                                                                             |
|                   |           |       | A1g73890 |          |                                                                                                                                             |
|                   |           |       | A2g13830 |          |                                                                                                                                             |
|                   |           |       | A2g27130 |          |                                                                                                                                             |
|                   |           |       | A2g44290 |          |                                                                                                                                             |
|                   |           |       | A2g44300 |          |                                                                                                                                             |
|                   |           |       | A2g48130 | LTPG15   | Involved in suberin monomer export in seed coats (Lee and Suh, 2019).                                                                       |
|                   |           |       | A2g48140 | EDA4     |                                                                                                                                             |
|                   |           |       | A1g36150 |          |                                                                                                                                             |
|                   |           |       | A3g22611 |          | Does not exist                                                                                                                                 |
|                   |           |       | A3g58550 | LTPG4    |                                                                                                                                             |
|                   |           |       | A4g08670 |          |                                                                                                                                             |
|                   |           |       | A4g12360 |          |                                                                                                                                             |
|                   |           |       | A4g14805 |          |                                                                                                                                             |
|                   |           |       | A4g14815 |          |                                                                                                                                             |
|                   |           |       | A4g22630 |          |                                                                                                                                             |
|                   |           |       | A4g22640 |          |                                                                                                                                             |
|                   |           |       | A5g09137 |          |                                                                                                                                             |
|                   |           |       | A5g13900 |          |                                                                                                                                             |
|                   |           |       | A5g64080 | XYP1     | XYP1 and XYP2 function as mediators of inductive cell-cell interaction in vascular development (Motosose et al., 2004). XYP2 was not shown in (Borner et al., 2003) due to its alternative splicing. |
|                   |           |       | A2g18320 | XYP2     |                                                                                                                                             |
| SKU5-Similar family |            | 4     | A4g12420 | SKU5     | SKU5 is involved in root directional growth (Sebrock et al., 2002), and this group of genes is redundantly essential for root development by regulating cell polar expansion and cell wall synthesis (Zhou, 2019a, Zhou, 2019b). SKS3 was not shown in Borner et al. (2003) due to alternative splicing. |
|                   |           |       | A4g25240 | SKS1     |                                                                                                                                             |
|                   |           |       | A5g51480 | SKS2     |                                                                                                                                             |
|                   |           |       | A5g48450 | SKS3     |                                                                                                                                             |
| RLP               | RLK3 like (DUF26) | 5     | A1g63550 |          | This subgroup of RLPs homolog with the extracellular region of a group of cysteine-rich RLKs (CRKs).                                             |
|                   |           |       | A1g63580 |          |                                                                                                                                             |
|                   |           |       | A5g41280 |          |                                                                                                                                             |
|                   |           |       | A5g41290 |          |                                                                                                                                             |
|                   |           |       | A5g41300 |          |                                                                                                                                             |
| PRKs like         |            | 3     | A1g20030 |          | This subgroup of pathogenesis-related thaumatin superfamily proteins are similar with the extracellular region of an osmotin/thaumatin-like protein kinase PRSK (PR5-like receptor kinase) (Wang et al., 1996; Abdin et al., 2011). |
|                   |           |       | A4g36010 |          |                                                                                                                                             |
|                   |           |       | A4g38660 |          |                                                                                                                                             |
| Lectin like       |            | 1     | A1g07460 |          | Homologue of L-type lectin receptor kinase III, 1 (LECRK-III, 1)                                                                           |

(Continued)
| Group                          | Sub-group                  | Total | Gene No.       | Name          | Descriptions                                                                                           |
|-------------------------------|----------------------------|-------|----------------|---------------|-------------------------------------------------------------------------------------------------------|
|                               | LysM domains               | 3     | At1g21880      | LYM1/LYP2     | LYM1 and LYM3 physically interact with the major components of bacterial cell walls and peptidoglycans and work together with a LysM RLK CERK1 to mediate perception and immunity to infection (Willmann et al., 2011). |
|                               |                            |       | At1g77630      | LYM3/LYP3     |                                                                                                       |
|                               |                            |       | At2g17120      | LYM2/LYP1     | Forms various complexes with different transmembrane RLKs from ERECTA family (ER) and/or SERKs to recognize their ligands, such as epidermal patterning factors (EPFs) and CHAL, and then to regulate stomatal development and immune response through the activation of intracellular MAPK cascade (Bundy et al., 2016; Abrash and Bergmann, 2010; Geisler et al., 2000; Geisler et al., 1998; Jakoby et al., 2006; Jorda et al., 2016; Kobe and Kajava, 2001; Lee et al., 2015; Lee et al., 2012; Lin et al., 2017; Meng et al., 2015; Rasmussen et al., 2011; Wang et al., 2008; Yan et al., 2014; Bhave et al., 2009). |
|                               |                            |       | At1g80080      | ATRLP17/TMM   | Interacts with a component of the vesicle trafficking machinery and acts as its linker with ROP2 (Jeon et al., 2008; Xu et al., 2010; Hwang et al., 2011; Hong et al., 2016). However, the presence of its GPI anchoring is doubted (Jeon et al., 2008; Yeats et al., 2018). |
|                               | Cf-2/Cf-5 like             | 3     | At1g77630      | LYP3/LYP1     |                                                                                                       |
|                               |                            |       | At2g17120      | ATRLP17/TMM   |                                                                                                       |
|                               | Other                      | 1     | At1g10375**    | Does not exist| Shown in Borner et al. (2003) but could not be found in databases.                                     |
|                               |                            |       | At4g23180***   |               | Encoded by an alternative variant of CRK10, which was believed to encode a cysteine-rich RLK (Grojean and Downes, 2010). Not shown in Borner et al. (2003) due to alternative splicing. |
| GPI-anchored peptides         | GPI-anchored peptides      | 8     | At3g01940      |               |                                                                                                       |
|                               |                            |       | At3g01950      |               |                                                                                                       |
|                               | LORELEI-like family        | 4     | At4g26468***   | LORELEI       | LLG1 chaperones transmembrane RLK FERONIA from the ER to the plasma membrane, where both LORELEI and LLG1 could associate with FERONIA to recognize extracellular ligands to regulate sperm cell release during double fertilization and early seed development (Capron et al., 2008; Duan et al., 2010; Tsukamoto et al., 2010; Meng et al., 2012; Yu et al., 2012; Li C et al., 2015; Li et al., 2016; Liao et al., 2017; Stegmann et al., 2017; Feng et al., 2018; Guo et al., 2018; Yin et al., 2018). Interestingly, LLG1 was also reported to associate with RLK FLS2 and mediate PAMP recognition (Shen et al., 2017). LORELEI was not shown in Borner et al. (2003). |
|                               |                            |       | At2g20700      | LLG2          |                                                                                                       |
|                               |                            |       | At4g28280      | LLG3          |                                                                                                       |
|                               |                            |       | At5g56170      | LLG1          |                                                                                                       |
|                               | PLC-like phosphodiesterases| 1     | At5g67130*     |               | Regulates gametophytic self-incompatibility (Qu et al., 2017). Shown as At5g67131 in Borner et al. (2003). |
|                               | Other                      | 6     | At5g07190      | SEED GENE 3   |                                                                                                       |
|                               |                            |       | At5g26200      | AT3SB         | Active in both diploid tapetum and haploid microspores and required for pollen fertility (Theerakulpisut et al., 1991; Xu et al., 1995; Luo et al., 2000). A glycine-rich protein                                                                 |
|                               |                            |       | At5g26210      | AT3S         |                                                                                                       |
|                               |                            |       | At3g07390      | BCP1          |                                                                                                       |
| Unknown/ hypothetical         |                            | 33    | At1g15460      |               |                                                                                                       |
|                               |                            |       | At1g54860      |               |                                                                                                       |
|                               |                            |       | At3g06035      |               |                                                                                                       |
|                               |                            |       | At5g19230      |               |                                                                                                       |
|                               |                            |       | At5g19250      |               |                                                                                                       |
|                               |                            |       | At1g07135      |               |                                                                                                       |
|                               |                            |       | At1g09175      |               |                                                                                                       |
|                               |                            |       | At3g04640      |               |                                                                                                       |
|                               |                            |       | At3g55790      |               |                                                                                                       |
|                               |                            |       | At1g29980      |               |                                                                                                       |
|                               |                            |       | At2g34510      |               |                                                                                                       |
|                               |                            |       | At5g14150      |               |                                                                                                       |
|                               |                            |       | At3g18050      |               |                                                                                                       |

(Continued)
GPI-Anchored Proteins Participate in Arabidopsis

Zhou

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found in both animals and plants suggests that important and common roles are played by GPI-APs in signal transduction (Figure 3B).

ASSOCIATION BETWEEN GPI-AP AND RLK

Interestingly, the association between GPI-AP and RLK could be involved in not only ligand recognition but also RLK transport and subcellular localization. One of the best characterized GPI-APs, LORELEI, not only participates in ligand recognition by associating with FERONIA but also plays a crucial role in chaperoning the transport of FERONIA from the ER to the plasma membrane (Capron et al., 2008; Duan et al., 2010; Tsukamoto et al., 2010; Meng et al., 2012; Yu et al., 2012; Li et al., 2015; Li et al., 2016; Liao et al., 2017; Stegmann et al., 2017; Feng et al., 2018; Guo et al., 2018; Yin et al., 2018) (Figure 3C). This special chaperone and transport mechanism might be due to the GPI-APs becoming involved with lipid rafts, which determine distinct protein sorting and protein traffic (Eisenhaber et al., 1998; Legler et al., 2005; Miyagawa-Yamaguchi et al., 2015; Sezgin et al., 2017).

GPI-APs appear to be important not only for ligand recognition but also essential for ligand selection. For example, RLK FERONIA recognizes ligands RALF1 or RALF22/23 when associated with GPI-anchored LORELEI or LRX5, respectively (Li C et al., 2015; Li et al., 2016; Zhao et al., 2018). This potential GPI-AP-dependent selection mechanism could greatly enhance the ligand recognition abundance of RLK but could also mediate the cross-talk between various signaling perception and transduction (Figure 3D).

The associations between GPI-AP and RLK could be structure independent, such as SKU5-TMK1, LRE/LLGs-FERONIA, FLA4-FEI1/FEI2, ENODL14-FERONIA, and LRX5-FERONIA, or structure dependent, such as TMM and ERECTA both possessing LRR structure at the extracellular domain and LYM1/LYM3 and CERK1 both possessing LyM structure at extracellular domain in Arabidopsis. Interestingly, the same structure dependence is also present in one of the best characterized GPI-APs in mammalian cells, CD-14, and together with its partner receptor kinases TLR3 and TLR4 all possess an LRR structure. The structure-dependent associations between GPI-APs and RLKs largely increased the curiosities of the group of GPI-anchored RLPs, which shared the same structures or sequence similarities with RLKs but lack intracellular kinase domains. They might recognize specific RLKs depending on sequence and structure similarities and form heterodimers with various

**Table 1**

| Group | Sub-group | Total | Gene No. | Name | Descriptions |
|-------|-----------|-------|----------|------|--------------|
| At4g28100 |           |       |          |      |              |
| At3g27410 |           |       |          |      |              |
| At5g49260 |           |       |          |      |              |
| At1g23050 |           |       |          |      |              |
| At1g70988 |           |       |          |      |              |
| At5g26290 | RAMCAP    |       |          |      | Hydroxyproline-rich glycoprotein family protein |
| At5g26300 |           |       |          |      | TRAF-like protein |
| At3g24518** |           |       |          |      | Natural antisense transcript overlaps with AT3G24520 |
| At5g35890 |           |       |          |      | β-galactosidase-related protein |
| At1g21090 |           |       |          |      | Cupredoxin superfamily protein |
| At1g63200 |           |       |          |      |              |
| At1g61900 |           |       |          |      |              |
| At2g28410 |           |       |          |      |              |
| At2g29680 |           |       |          |      | Zinc finger (C2H2-type) family protein |
| At3g26110 |           |       |          |      | Anther-specific protein agp1-like protein |
| At3g44100 |           |       |          |      | MD-2-related lipid recognition domain-containing protein |
| At3g58890 |           |       |          |      | RNI-like superfamily protein |
| At3g61980 | KPI-1     |       |          |      | Putative Kazal-type serine proteinase inhibitor, which is supposed to limit and control the spread of serine proteinase activity, and function during defense mechanism (Pariani et al., 2016). |
| At4g14748 |           |       |          |      | Neurogenic locus notch-like protein |
| At4g28088 |           |       |          |      |              |
| At4g28140 |           |       |          |      |              |
| At5g09210** | MIR834A |       |          |      | Encoded a microRNA of unknown function |
| At5g14190** | Does not exist |   |          |      | Shown in Borner et al. (2003) but could not be found in genomic or proteomic database actually |
| At5g16670** | Does not exist |   |          |      | Shown in Borner et al. (2003) but could not be found in genomic or proteomic database actually |
| At5g22430 |           |       |          |      | Pollen Ole 1 allergen and extensin family protein |

*Shown incorrectly in Borner et al. (2003).
**Shown in Borner et al. (2003) but does not exist in genomic or proteomic database or encodes non-coding RNA.
***Not shown in Borner et al. (2003) but could be predicted or studied as GPI-APs.
TABLE 2 | GPI-APs identified in 2016 that not included in previous study in 2003.

| Group | Sub-group | Total | Gene No. | Name | Descriptions |
|-------|-----------|-------|----------|-------|--------------|
| GPI-APs identified in 2016 that not included in previous study in 2003. | | | | | |

| Group | Sub-group | Total | Gene No. | Name | Descriptions |
|-------|-----------|-------|----------|-------|--------------|
| LTPL | (lipid transfer protein) | 3 | AT3g22620 | XYP2 | Functions as a mediator of inductive cell-cell interaction in vascular development (Motose et al., 2004). |
| | | | AT2g13820 | | |
| | | | AT4g22506 | | |
| β-1,3 Glucanases | | 3 | AT1g11820 | | O-Glycosyl hydrolase family 17 protein |
| | | | AT4g34480 | | O-Glycosyl hydrolase family 17 protein |
| | | | AT3g57240 | | |
| PLC-like phosphodiesterases | RLP | 1 | AT4g39894 | | |
| | | | AT4g18760 | | |
| Oligogalacturonide oxidase | | 2 | AT5g66680 | DGL1 | Subunit of the oligosaccharidyltransferase complex, which catalyzes N-glycosylation of nascent secretory polypeptides in the lumen of the ER (Lerouxel et al., 2005; Qin et al., 2013; Jeong et al., 2018). |
| | | | AT4g20830 | ATBBE20/OGOX1 | Required in plant immunity (Benedetti et al., 2018). |
| | | | AT5g07830 | GUS2 | Contributes to the glycosylation of AGPs (Eudes et al., 2008). |
| | | AT5g34940 | GUS3 | |
| | | AT4g18670 | LRX5 | |
| LRR extensin | | 1 | AT1g28290 | AGP31 | Involved in cell wall structure and network (Hijazi et al., 2014). |
| | | | AT1g69530 | EXPA1 | Regulates stomatal opening by altering the structure of the guard cell wall (Wei et al., 2011; Zhang et al., 2011c). |
| AQP | | 1 | AT1g22290 | | |
| | | | AT1g69530 | | |
| Expansin | | 1 | AT1g28290 | | |
| | | | AT1g69530 | | |
| PME and PMEI proteins | PME (pectin methyltransferase) | 1 | AT3g14310 | PME3 | Catalyzes the demethylsterification of pectin homogalacturonan domains in plant cell walls, and its activity could be regulated by PMEIs (Guenin et al., 2011; Senechal et al., 2015). |
| | | | AT2g31140 | PME5 | |
| | | | AT5g62360 | PMEI13 | A pectin methyltransferase inhibitor (Muller et al., 2013). |
| | | | AT3g62820 | | |
| | | | AT3g17130 | |
| | | | AT5g62350 | |
| | PMEI (pectin methyltransferase inhibitors) | 5 | AT4g30140 | CDEF1 | Possesses esterase activity and candidates for the unidentified plant cutinase for cuticle biosynthesis (Takahashi et al., 2010). |
| | | | AT5g45950 | GDSL-motif esterase/acyltransferase/lipase |
| | | | AT4g01130 | GDSL-motif esterase/acyltransferase/lipase |
| | | | AT3g16370 | GDSL-motif esterase/acyltransferase/lipase |
| | | | AT1g30600 | Subtilisin-like serine protease |
| | | | AT4g21650 | Subtilisin-like serine protease |
| | | | AT3g61820 | Eukaryotic aspartyl protease family protein |
| Proteases | | 3 | AT3g20600 | SBT3.13 | |
| | | | AT4g21650 | |
| | | | AT3g61820 | |

(Continued)
### TABLE 2 | Continued

| Group                      | Sub-group                        | Total | Gene No.   | Name          | Descriptions                                                                                                                                                                                                                                                                                                                                 |
|----------------------------|----------------------------------|-------|------------|---------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| **Others**                 |                                  | 25    | AT2g30700  |               | Disease resistance responsive                                                                                                                                                                                                                                                                                                                                                                             |
|                            |                                  |       | AT1g65870  |               | Calcineurin-like metallophosphoesterase superfamily protein                                                                                                                                                                                                                                                                                             |
|                            |                                  |       | AT5g42370  |               | Mediates high-affinity uracil and 5-fluorouracil (a toxic uracil analogue) transport (Schmidt et al., 2004).                                                                                                                                                                                                                                                                                     |
|                            |                                  |       | AT2g03530  | UPS2          | Localizes to the extracellular matrix and being considered to be involved in many physiological responses including environmental stress (Membre et al., 2003).                                                                                                                                                                       |
|                            |                                  |       | AT1g72610  | GLP1          | Glycoprotein membrane precursor GPI anchored                                                                                                                                                                                                                                                                                                         |
|                            |                                  |       | AT5g19240  |               | Possesses β-glucosidases activity and works redundantly with its homolog BGLC1 with absent GPI anchor to remove unsubstituted Glc residues from the nonreducing end of xyloglucan molecule (Sampedro et al., 2017).                                                                                                                                   |
|                            |                                  |       | AT5g04885  | BGLC3         | Pectin acetyesterase 12                                                                                                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT3g05910  | PAE12         | Galactose mutarotase-like superfamily protein                                                                                                                                                                                                                                                                                                 |
|                            |                                  |       | AT3g47800  |               | Hydroxylproline-rich glycoprotein family protein                                                                                                                                                                                                                                                                                             |
|                            |                                  |       | AT5g55730  |               | Carbohydrate esterase                                                                                                                                                                                                                                                                                                                                                     |
|                            |                                  |       | AT5g353010 | SES1          | ER localized molecular chaperone and required for heat tolerance (Guan et al., 2019).                                                                                                                                                                                                                                                                 |
|                            |                                  |       | AT5g298520 |               | Glycosyl hydrolase                                                                                                                                                                                                                                                                                                                                 |
|                            |                                  |       | AT3g07570  | Cytochrome B561 | Galacturonidase-like protein (a carbohydrate esterase)                                                                                                                                                                                                                                                                                     |
|                            |                                  |       | AT1g75680  | GHIB7         | Products UDP-glucuronic acid, which is the common precursor for arabinose, xylose, galacturonic acid, and apiose residues in cell wall biosynthesis (Reboul et al., 2011; Siddique et al., 2012).                                                                 |                                                                                                                                                                                                                             |
|                            |                                  |       | AT5g14030  |               | Inhibits both plant cell wall invertase and vacuolar invertase (Link et al., 2004).                                                                                                                                                                                                                                                                                                                                                       |
|                            |                                  |       | AT3g29360  | UGD2          | Inhibits both plant cell wall invertase and vacuolar invertase (Link et al., 2004).                                                                                                                                                                                                                                                                                                                                                       |
|                            |                                  |       | AT5g64620  | C/VIF2        | Its allantoate amidohydrolases enzymatic activity is required for nitrogen recycling from purine ring in plants (Werner et al., 2008).                                                                                                                                                                                                                                                                 |
|                            |                                  |       | AT1g68560  | XYL1          | Serine carboxypeptidase-like 35                                                                                                                                                                                                                                                                                                                                                   |
|                            |                                  |       | AT4g34180  | CYCLASE1      | Serine carboxypeptidase-like 35                                                                                                                                                                                                                                                                                                                                                   |
|                            |                                  |       | AT4g35220  | CYCLASE2      | Its allantoate amidohydrolases enzymatic activity is required for nitrogen recycling from purine ring in plants (Werner et al., 2008).                                                                                                                                                                                                                                                                 |
|                            |                                  |       | AT5g08260  | SCPL35        | Serine carboxypeptidase-like 35                                                                                                                                                                                                                                                                                                                                                   |
|                            |                                  |       | AT2g33530  | SCPL46        | Serine carboxypeptidase-like 35                                                                                                                                                                                                                                                                                                                                                   |
|                            |                                  |       | AT5g43600  | AAH-2/UAH     | Serine carboxypeptidase-like 35                                                                                                                                                                                                                                                                                                                                                   |
|                            |                                  |       | AT4g02420  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT1g3210   | ZIP11         | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT1g55910  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT5g42470  | ATNPC1-1      | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT1g70940  | PIN3          | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT2g01420  | PIN4          | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT5g55960  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
| **Not typical GPI-APs**    | **Transmembrane protein with predicted omega domain at C terminus** | **8** | AT4g15630  | CASPL1E1      | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT4g15620  | CASPL1E2      | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT4g02420  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT1g3210   |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT1g55910  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT5g42470  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT1g70940  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT2g01420  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
|                            |                                  |       | AT5g55960  |               | A negative regulator of cell death and regulates pathogen-induced symptom development in Arabidopsis (Smith et al., 2015).                                                                                                                                                                                                                                                                                          |
RLKs in the ER or Golgi bodies and then chaperone them to specific plasma membrane regions through GPI-AP-driven lipid rafts. On arrival, they select and recognize ligands and activate the intracellular signaling components. Whether the GPI-anchored RLKs encoded by transcriptional variants, such as GPI-CRK10 and its variant of CRK10, can form homodimers based on the same extracellular domains and play a role in RLK regulation, is a very interesting question.
FIGURE 3 | RLK-mediated signaling pathway and various associations between RLKs and GPI-APs. (A) Association with extracellular ligand activates and phosphorylates the intracellular kinase domain of RLK, which activates intracellular signaling components to regulate various processes. (B) GPI-AP is required for ligand recognition and its association with RLK. (C) GPI-AP is required not only for ligand recognition and its association with RLK but also for RLK localization by chaperoning its transport, and those un-chaperoned would reside in ER. (D) GPI-APs are required for ligand selection.
CONCLUSION AND PERSPECTIVES

Previous genomic and proteomic assays that predicted and identified GPI-APs from Arabidopsis have been listed. Due to recent experimental data and knowledge of alternative splicing, more and more GPI-APs have been identified, suggesting that GPI-APs in Arabidopsis might be more abundant than we expected.

Previous studies on those listed GPI-APs from diverse families were discussed, and they were found to be involved in diverse biological processes, including cell wall composition, cell wall component synthesis, cell polar expansion, hormone signaling response, stress response, pathogen response, stomata development, pollen tube elongation, and double fertilization. Those reports demonstrated the functional diversity and indispensability of GPI-APs in Arabidopsis.

Among these reports, direct associations were found between various GPI-APs and their partner cell surface RLKs, demonstrating not only participation in their ligand recognition but also essential roles in RLK transport and localization. Localization might due to specific protein sorting and protein traffic driven by GPI-AP-related lipid rafts.

Surprisingly, GPI-APs have also been shown to participate in ligand selection, which made one RLK and its downstream intracellular target activated by various ligands. Such protein cross-reactivity greatly enhanced the ligand recognition abundance of RLKs, which can also be considered as a common mechanism of cross-talk between various ligands or various signaling pathways.

In this review, the most predicted or identified GPI-APs in Arabidopsis were listed and discussed, and a common involvement of them in signaling transduction was summarized. This involvement could be very helpful for understanding the ligand-RLK signaling transduction in plants, especially for understanding the polar localization of RLKs, and the crosstalk between various ligand-RLK signaling transduction. It would be interesting to identify more associations between various GPI-APs and RLKs and study their recognition and selection of ligands and downstream intracellular signaling components in Arabidopsis.

AUTHOR CONTRIBUTIONS

KZ wrote this manuscript.

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