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# **Evolutionary history of double-stranded RNA binding proteins in plants: identification of new cofactors involved in easiRNA biogenesis**

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Running title: New DCL4 cofactors involved in easiRNA biogenesis

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## ABSTRACT

In this work, we retrace the evolutionary history of plant double-stranded RNA binding proteins (DRBs), a group of non-catalytic factors containing one or more double-stranded RNA binding motif (dsRBM) that play important roles in small RNA biogenesis and functions. Using a phylogenetic approach, we show that multiple dsRBM DRBs are systematically composed of two different types of dsRBMs evolving under different constraints and likely fulfilling complementary functions. In vascular plants, four distinct clades of multiple dsRBM DRBs are always present with the exception of Brassicaceae species, that do not possess member of the newly identified clade we named DRB6. We also identified a second new and highly conserved DRB family (we named DRB7) whose members possess a single dsRBM that shows concerted evolution with the most C-terminal dsRBM domain of the Dicer-like 4 (DCL4) proteins. Using a BiFC approach, we observed that *Arabidopsis thaliana* DRB7.2 (AtDRB7.2) can directly interact with AtDRB4 but not with AtDCL4 and we provide evidence that both AtDRB7.2 and AtDRB4 participate in the epigenetically activated siRNAs (easiRNAs) pathway.

## INTRODUCTION

The double-stranded RNA binding motif (dsRBM) is evolutionarily conserved to mediate specific interaction with double-stranded RNAs (dsRNAs) of various origin and structure, and plays critical roles in a wealth of cellular processes in prokaryotes, eukaryotes and viruses. This motif was first characterized as a 65-70 amino acids domain (St Johnston et al. 1992) that adopts an  $\alpha\beta\beta\alpha$  fold and contains conserved residues important for both structure and function (reviewed in (Chang and Ramos 2005; Masliah et al. 2013)). Several dsRBMs can also mediate protein-protein interaction allowing intramolecular packing (Sohn et al. 2007), homodimerization (Hitti et al. 2004; Yang et al. 2010), heterodimerization involving two dsRBMs (Laraki et al. 2008; Qin et al. 2010) or involving a dsRBM and other functional domains (Daniels et al. 2009; Nanduri et al. 2000; Schuldt et al. 1998).

DsRBM-containing proteins are involved in numerous cellular mechanisms ranging from localization and transport of messenger RNAs, through maturation and degradation of RNAs, to viral response and signal transduction. The animal Staufen protein is a striking example of the versatility achieved by a single dsRBM-containing protein. This protein contains no additional domain but five dsRBMs with varying affinities towards dsRNA and proteins. Staufen is essential for establishing the correct polarity of the *Drosophila* embryo by anchoring two specific maternal mRNAs, *oskar* and *bicoid*, at the opposite poles of the oocyte (St Johnston et al. 1991). The association of Staufen with the 3'UTR of *bicoid* is essential for the transport of the resulting ribonucleoprotein (RNP) complex along microtubules (Ferrandon et al. 1994), while the association of Staufen with *oskar* is more specifically involved in regulating translation after mRNA deposition (Micklem et al. 2000). More recently, STAU1 (human Staufen) was shown to bind the 3'UTRs of messengers base paired with *Alu* transcripts and to induce, with the help of UPF1 a known nonsense mediated decay factor, a specific degradation pathway (Gleghorn et al. 2013; Kim et al. 2007). STAU1 association to 5'UTR hairpins has also been shown to enhance translation of other targeted mRNAs (Dugre-Brisson et al. 2005).

DsRBM-containing proteins were also found to be tightly linked to RNA interference mechanisms. Animal Droscha and Dicer, which are part of the RNase III family, have been extensively studied for their ability to generate from dsRNA precursors, small RNA molecules involved in transcriptional or post-transcriptional gene regulation. In a pathway that is conserved in human, flies and nematodes,



Drosha is responsible for the first nuclear cleavage of microRNA precursor hairpins (Lee et al. 2003) while Dicer acts in the cytoplasm on this cleavage product to generate small RNA duplexes (Bernstein et al. 2001; Hutvagner et al. 2001). Despite the presence of a dsRBM in each of these proteins, their action requires the presence of other dsRBM-containing protein acting as cofactors. For instance, the dsRBM of Drosha seems to retain little ability to bind RNA while both dsRBMs of its cofactor, DGCR8/Pasha, are necessary to bind dsRNA while mediating the interaction with Drosha (Denli et al. 2004; Gregory et al. 2004; Han et al. 2004; Han et al. 2006; Yeom et al. 2006). Similarly, Dicer proteins are accompanied by non catalytic dsRBM-containing protein, Loquacious and R2D2 in flies (Saito et al. 2005; Tomari et al. 2004), RDE-4 in worms (Tabara et al. 2002), and TRBP and PACT in human cells (Chendrimada et al. 2005; Lee et al. 2006), that assist the processing and/or strand selection of small RNA duplexes therefore promoting the formation of the RNA induced silencing complex (RISC).

dsRBM-containing proteins are also found in plants, and most of these proteins have been linked to RNA interference or related phenomenon (Kiyota et al. 2011; Manavella et al. 2012). In the model species, *Arabidopsis thaliana*, the most studied are the four DICER-LIKE (AtDCL) proteins, which exhibit a domain organization similar to the animal Dicers, with one (for AtDCL2) or two (for AtDCL1, 3 and 4) C-terminal dsRBMs. AtDCL1 is responsible for the production of 21-nt microRNAs from Pol II precursor transcripts (Kurihara and Watanabe 2004) as well as for the production of phased cis natural antisense siRNAs, while AtDCL2 cleaves the primary convergent transcript into 24-nt duplex in this pathway (Borsani et al. 2005). AtDCL2 is also implicated in gene silencing induced by exogenous dsRNAs, as is AtDCL4 (Bouche et al. 2006; Dunoyer et al. 2007). AtDCL4 also generates phased trans-acting siRNAs (Gascioli et al. 2005) or transposon-derived 21-nt epigenetically activated small interfering RNAs (easiRNAs) (Creasey et al. 2014; McCue et al. 2012; Sarazin and Voinnet 2014) using dsRNA provided by the action of RNA-dependent RNA polymerase 6 (AtRDR6), and is also responsible for the formation of some microRNAs (Rajagopalan et al. 2006). Finally, AtDCL3 acts with RNA-dependent RNA polymerase 2 (AtRDR2) in the RNA-dependent DNA methylation (RdDM) pathway, to produce 24-nt siRNAs that guide DNA methylation, mostly to repeated sequences and transposable elements, thus participating in genome defense (Xie et al. 2004).

As for animals, some plant DCLs necessitate dsRBM-containing non-catalytic cofactors named DRB (for double stranded RNA binding). *Arabidopsis* possesses five known DRBs (AtDRB1 to 5) (Hiraguri et al. 2005), each containing two N-terminal dsRBMs. AtDRB1, also known as HYL1, is required for AtDCL1-mediated processing of miRNA precursors (Kurihara et al. 2006). AtDRB1 seems to act as a dimer and to interact with AtDCL1 via its second dsRBM (Yang et al. 2010), while the first dsRBM binds miRNA precursors as well as mature miRNA duplexes (Eamens et al. 2009; Song et al. 2007), assisting in the cleavage and in the miRNA strand selection. AtDCL4 is assisted by AtDRB4 (Nakazawa et al. 2007) and this protein seems to be essential for the *in vitro* activity of AtDCL4 (Fukudome et al. 2011). Similarly, in case of geminivirus infection, AtDRB3 seems to interact with AtDCL3, impacting the methylation of the viral genome (Raja et al. 2014). Furthermore, AtDRB2, AtDRB3 and AtDRB5 have been implicated in an atypical miRNA biogenesis pathway (Eamens et al. 2012a; Eamens et al. 2012b), and AtDRB2 and AtDRB4 affect the quantity of siRNAs acting in RdDM, suggesting a role for these two proteins in this particular pathway (Pélissier et al. 2011). More recent data, however, suggest that AtDRB2 modulates transposon element derived siRNA accumulation mostly through an indirect pathway (Clavel et al. 2015). Finally, AtDRB4 seems to have a role in resistance against pathogens, distinct from its action alongside AtDCL4 (Jakubiec et al. 2012; Zhu et al. 2013).

In this work, we reconstruct the evolutionary history of the DRB family in the Viridiplantae lineage. We discovered the presence of a new DRB family, we name DRB6, absent from Brassicaceae but present in all other vascular plant species tested. DRB1 to 6 are systematically composed of two different types of dsRBM (type 1 and 2) that have evolved under different constraints and likely fulfill complementary functions. We also uncovered a second new DRB family (named DRB7) conserved in all vascular plants and harboring a single dsRBM that evolved in a concerted manner with the second dsRBM of DCL4. We present evidence suggesting that DRB7 and DRB4 are both involved in easiRNA biogenesis.

## RESULTS AND DISCUSSION

As a first approach, we collected the sequence of all *Arabidopsis* proteins containing at least one dsRBM and no other conserved domains (here after defined as DRBs). Based on these criteria, in addition to the already described five AtDRBs (AtDRB1 to 5), two other proteins encoded by the At1g80650 and At4g00420 loci and presenting a single dsRBM, were identified. The dsRBM from these seven proteins were aligned (see Supplemental Figure S1) and used to construct a phylogenetic tree (Figure 1). This initial analysis suggests that the AtDRBs 1 to 5 are systematically composed of two types of dsRBM (Type I and II) that form a distinct clade from the Type III dsRBM present on the At1g80650 and At4g00420 proteins. This type III motif is surprisingly closely related to the second dsRBM present in the C-terminal region of the AtDCL4 enzyme (Figure 1). This second dsRBM of AtDCL4 (AtDCL4.2 in Figure 1) is the only case where a dsRBM present in a DCL protein is closely related to a dsRBM present in a DRB protein (not shown).

To test if the situation in *Arabidopsis* is representative of species in the Viridiplantae lineage, we looked for the presence of DRBs in the completely sequenced genomes of five Chlorophyte (green algae), a bryophyte, a lycophyte, four monocotyledon and twelve dicotyledon species representing the diversity of Viridiplantae (see Material and Methods for a list of species used and supplementary Table 1 for the sequence of all DRBs used in this analysis). DRBs containing at least two dsRBMs are present in all plant species while DRBs containing a single dsRBM are present in all Angiosperm but absent from the bryophyte and lycophyte species tested. No DRB could be detected in the five Chlorophyte genomes tested strongly suggesting that they are completely absent from this monophyletic phylum. This is surprising since DRBs are largely represented in animal species (Fierro-Monti and Mathews 2000; Tian et al. 2004) and a complex system of small RNAs exists in at least some Chlorophytes (Zhao et al. 2007). Based on these observations, the likely hypothesis is that RNAi machinery and DRBs were present in the common ancestor of the Viridiplantae but that DRBs were lost specifically in the Chlorophyte phylum and that the overall small RNA biogenesis process was either conserved (for *Chlamydomonas reinhardtii* and *Volvox carteri* (Zhao et al. 2007)) or lost (for the microalgae *Ostreococcus lucimarinus* (Cerutti et al. 2011)) depending on the specific Chlorophyte

lineage. Based on this, one may speculate that the Chlorophyte DICER machinery evolved to generate small RNAs without the need of DRB cofactors or that another RNA binding protein fulfill this role.

### **Evolutionary history of multiple dsRBM DRBs**

We first decided to study the evolutionary history of DRBs containing multiple dsRBMs. To do so we fused and aligned dsRBM sequences from our eighteen selected species (see above) and used this alignment (see Supplemental Figure S2) to build a phylogenetic tree (Figure 2). We observed from this analysis that plant DRBs can be grouped in four major clades that we named according to the *Arabidopsis thaliana* DRB families.

One clade represents the DRB1 family and members from this family are found in all species tested, in one or several versions. DRB1 proteins possess two dsRBMs separated by a linker of around 20 amino acids (Figure S3). The position of the first dsRBM related to the N-terminal amino acid is also constrained and 15 amino acids precede the first dsRBM in bryophyte, lycophyte and dicotyledon species while this region is of 35 amino acids for monocotyledon species. These results suggest that the position of the two dsRBMs in DRB1 proteins is important for their function. DRB1s also have, closely after the second dsRBM (less than 40 amino acids), a well-conserved arginine and lysine-rich region (KR-rich) (see Supplemental Figure S4).

A second, more complex, clade is composed of members of the DRB2-3-5 families. All members of this clade possess two dsRBMs precisely separated by a linker of 19 amino acids (Figure S3). The two dsRBMs are located at the very N-terminal region of the protein as only a single amino acid is present before the first dsRBM (Figure S3). The very high positional conservation of the dsRBMs strongly suggests that this is a critical factor for function. *P. patens* and *S. moellendorffii* DRBs are found as outgroup of this clade while vascular plants DRBs can be further divided in two subclades, one of which corresponds to the DRB2 family. The *A. thaliana* DRB3 and DRB5 proteins result from a recent segmental duplication shared by all three Brassicaceae species tested (Blanc et al. 2003) and our phylogenetic analysis supports the fact that they belong to the same family. Therefore, for simplicity and to conserve as much as possible the previous nomenclature, we suggest naming the second

subclade, the DRB3-5 family. All vascular plants possess at least one DRB2 and one DRB3-5 protein, but some species have several versions of each.

The third clade is composed of members of the DRB4 family. This family is present in all vascular plants but is absent from the two bryophyte and lycophyte genomes tested. In all vascular plants, DRB4 proteins are composed of three dsRBMs (named the DRB4A subfamily), except for Brassicaceae species (including *Arabidopsis*), where DRB4 proteins are composed of only two dsRBMs (named the DRB4B subfamily). A likely scenario to explain this situation is that the coding capacity for the first dsRBM of DRB4 was lost in the common ancestor of Brassicaceae species. A direct consequence of this observation is that the many functional analyses conducted using the *A. thaliana* DRB4 (Fukudome et al. 2011; Nakazawa et al. 2007) may not be fully representative of the situation in most vascular plants for this family. Here again the position of the three dsRBMs of DRB4A proteins is highly conserved with the exception of the linker between the first and second dsRBM of dicot DRB4A that is much more variable in length (from 35 to 299 amino acids, see Figure S3). The position of the two dsRBMs of Brassicaceae DRB4B is also well conserved (Figure S3).

The fourth clade is composed of DRB proteins, with two dsRBMs, present in all vascular plants but absent in bryophyte, lycophyte and from Brassicaceae species. We named this family DRB6. Here again a likely scenario to explain this situation is that the gene coding for DRB6 emerged in the common ancestor of vascular plants but was lost much later in the common ancestor of Brassicaceae species. DRB6 proteins show two structural similarities with DRB1 proteins: a more internal positioning of the two dsRBMs compared to DRB2, DRB3-5 and DRB4 and the presence of a well-conserved arginine and lysine-rich region (KR-rich) localized after the second dsRBM (see Figure S3 and S4). Since DRB6 is absent from *A. thaliana*, nothing is known on the function of this protein at the moment. Therefore, one important conclusion from this analysis is that DRB families in *Arabidopsis* are quite atypical compared to most plant species and that conclusions reached using this species may not always be applicable to all plant lineages.

### **Evolution of dsRBMs present in multiple dsRBM DRBs**

We next decided to address questions concerning the origin and evolution of dsRBMs present in multiple dsRBM DRBs. One of our objectives is to determine if these dsRBMs can be classified in two distinct types as suggested by our initial analysis using *A. thaliana* proteins (Figure 1) and if one dsRBM of each type is always associated with DRBs of the different families. We therefore, this time, collected and aligned the different dsRBMs individually, without taking into account their protein of origin and build a phylogenetic tree using this alignment (see Supplemental Figure S5 and Figure 3). We observed that the dsRBMs indeed form two well-supported clades. The first clade (type I dsRBM) contains all dsRBMs present in the first (more N-terminal) region of DRB1, DRB2-3-5, DRB4B and DRB6 proteins and in the first and second position of the DRB4A proteins. The second clade (type II dsRBM) contains all dsRBMs present in the second (more C-terminal) region of DRB1, DRB2-3-5, DRB4B and DRB6 proteins and in the third position of the DRB4A proteins. This result suggests that two different types of dsRBM evolving under different selection pressure are always associated with the different multiple dsRBM DRBs and that a DRB with type I and II dsRBMs was already present in the plant common ancestor. Based on this result, it is likely that the RNA-binding properties of these DRBs depend on the combination of the two non-redundant types of dsRBMs that form the true RNA-binding module. In support to this conclusion, several *in vitro* studies clearly demonstrated the different RNA-binding properties of the two individual dsRBMs of plant and animal DRBs and their cooperative nature to bind efficiently RNA *in vivo* (Han et al. 2006; Micklem et al. 2000; Qin et al. 2010; Yang et al. 2010).

When analyzed separately, the DRB1 and DRB6 type I dsRBMs group in the same clade and the same is true for the type II dsRBM of these proteins (Figure 3). This result is in agreement with the structural similarities observed previously among DRB1 and DRB6 proteins (Figure 2 and S3) and support the notion that these two families, although clearly distinct, are closely related.

### **Evolutionary history of single dsRBM DRBs**

We next searched our collection of DRBs for proteins having a single dsRBM. This search was complicated by the fact that some of these proteins may merely be non-functional truncated versions of multiple dsRBM DRBs and/or result of incorrect *in silico* definition of genic organization.

Therefore, to circumvent these problems, we only retained single dsRBM DRBs that were conserved at least in two different plant species. Using this criterion, a single family of mono dsRBM DRBs was identified that we named DRB7 (Figure 4). This family includes proteins coded by the At1g80650 and At4g00420 (renamed AtDRB7.1 and AtDRB7.2) that possess a dsRBM closely related to the second (closest to the C-terminal end) dsRBM of DCL4 (Figure 1). DRB7 proteins are found in all vascular plants but are absent from the bryophyte and lycophyte species tested. To precise the evolutionary link between DRB7 and DCL4, we collected and aligned their dsRBMs (see Supplemental Figure S6) and used this alignment to build a phylogenetic tree (Figure 4, see also Supplementary Table 1 for a list of DRB7 and DCL4 sequences used). This analysis strongly suggests that the single dsRBM of DRB7 and the second dsRBM of DCL4 evolved in a concerted manner. This can be inferred from the fact that all plant DRB7 sequences are not found in a single clade (that would be distinct from a second DCL4 clade) but rather that DRB7 and DCL4 sequences from monocotyledon and DRB7 and DCL4 sequences from dicotyledon species form two distinct clades (Figure 4). Therefore, it is likely that both dsRBMs have a common origin and that both proteins were present in the common ancestor of vascular plants but also that DRB7 and DCL4 sequences evolved from the common ancestor in a concerted manner in the mono- and dicotyledon lineages. Although the DRB7 function is for the moment unknown, our results can best be explained if DRB7 proteins cooperates with DCL4 in a yet to define pathway.

#### **Impact of AtDRB7 loss of function on known AtDCL4 *in vivo* substrates.**

AtDRB4 is a well-characterized cofactor of AtDCL4 and is important for the biogenesis of tasiRNAs and some miRNAs (Adenot et al. 2006; Rajagopalan et al. 2006). To determine if one or both of the two AtDRB7 proteins could also participate as AtDCL4 cofactor in these two pathways, we selected *Arabidopsis* mutants defective in the production of AtDRB7.1, AtDRB7.2 or both proteins. Figure 5 shows that, as expected, several AtDRB4/AtDCL4-dependent small RNAs (tasiRNAs, miRNA822, miRNA839) underaccumulate in *drb4* but are present at a level similar to wild-type in the single (*drb7.1* or *drb7.2*) or double (*drb7.1/drb7.2*) mutant lines. Similarly, polIV-dependent siRNA accumulation, that was previously shown to be decreased in *drb4* and *dcl4* mutants (Pélissier et al.

2011), is not affected in *drb7* mutants (Figure 5 and data not shown). The introduction of *drb7* mutations into the *drb4* background does not enhance the *drb4* molecular phenotype (Figure 5) further suggesting that if AtDRB7 is indeed a cofactor of AtDCL4, it is not involved in these pathways.

Recently, AtDCL4 has been implicated in transcription termination of an endogenous *Arabidopsis* gene named FCA (Liu et al. 2012). To determine if *Arabidopsis* AtDRB7 proteins could be involved as a AtDCL4 cofactor in this process, we performed QRT-PCR to monitor the levels of FCA read-through products in single and double *drb7* mutant lines compared to two *dcl4* null mutant lines (*dcl4-2* and *dcl4-5*). However, in contrast to published results (Liu et al. 2012), we were not able to observe a significant increase of FCA read-through products in the two *dcl4* mutant lines nor in single and double *drb7* mutant lines (Figure S7). We were therefore unable to document a role for AtDRB7 in these putative AtDCL4-dependent transcription termination events.

Recently, a new class of epigenetically activated siRNAs from transposable elements (easiRNAs), whose production depends on AtDCL4, AtDCL2 and AtRDR6, has been described (Creasey et al. 2014; McCue et al. 2012; Sarazin and Voinnet 2014). These 21-22 nucleotides easiRNAs are abundant in the DECREASED DNA METHYLATION 1 (*ddm1*) mutants (Creasey et al. 2014; McCue et al. 2013; McCue et al. 2014; Nuthikattu et al. 2013), as well as in the vegetative nucleus of pollen grains and dedifferentiated plant cell cultures (Slotkin et al. 2009; Tanurdzic et al. 2008). We therefore tested if one or both AtDRB7 proteins could be involved in the biogenesis of easiRNAs. By far, the major contributor of easiRNAs is represented by the *Athila* family of retrotransposons. The internal domain downstream of the *Athila* gag-pol-encoding ORF, also known as Transcriptionally Silent Information (TSI), is particularly prone to produce 21-22 nt easiRNAs (McCue et al. 2014; Slotkin 2010). While *Athila* full-length transcripts initiate within the 5' LTR region, specific TSI transcription originates from internal sequences and was associated with three different types of transcripts (Steimer et al. 2000). Using two different probes located in the TSI 3' part (within the TSI-A region as defined in (Steimer et al. 2000)), we observed that 21-nt easiRNAs were not significantly affected by the loss of AtDRB7.2 or AtDRB4 (Figure 6A and B). However, a strong increase in AtDCL3-dependent 24 nucleotides siRNAs was noted in *ddm1 drb7.2* and *ddm1 drb4* double mutants, and in the *ddm1 drb4 drb7.2* triple mutant compared to the *ddm1* mutant (Figure 6A and B). Such a situation is analogous to



what was observed when the easiRNA pathway is perturbed in a *ddm1 rdr6* double mutant and could reflect a switch from AtRDR6/AtDCL4 towards AtRDR2/AtDCL3 processing of the templates (Creasey et al. 2014; Sarazin and Voinnet 2014). Interestingly, a substantial overaccumulation of AtDCL2-dependent 22-nt easiRNAs in the *drb4*, but not *drb7.2*, mutated plants was also observed suggesting that AtDCL2 loading on AtRDR6-derived templates becomes facilitated only when the AtDRB4 cofactor is lost. Monitoring the accumulation of easiRNAs targeting the 5' part of TSI, we observed a similar situation for 21- and 22-nt but not 24-nt easiRNAs (Figure 6A and B). Indeed, no massive shift to 24-nt siRNAs was observed; only a modest increase of 24-nt easiRNAs occurs in *ddm1 drb4* and *ddm1 drb4 drb7.2* mutants compared to *ddm1* (Figure 6A and B). To explain this discrepancy, it should be noted that TSI transcription is rather complex as three main TSI transcripts accumulate, two polyA<sup>+</sup> RNAs of 5000 and 2500 nucleotides and a polyA<sup>-</sup> RNA of 1250 nucleotides. While these transcripts overlap within the TSI 3' region, only the 5000-nt RNAs can be detected with a 5' specific-probe (Steimer et al. 2000). Additionally, the Athila2 and 6A subfamilies are the main suppliers of easiRNAs (Nuthikattu et al. 2013), and the TSI 5' part probes can only detect Athila6A members-derived easiRNAs while the 3' probes can detect a wider range of Athila2 and 6A subfamilies loci-derived easiRNAs. These differences in targeting specificity for the 5' and 3' probes are likely to be at the origin of the differences in easiRNAs populations we observed. Elucidating the complex mechanisms involved in easiRNA biogenesis is a challenging topic (Sarazin and Voinnet 2014) and would certainly benefit from the identification reported here of new cofactors impacting this pathway, such as the AtDRB7.2 and AtDRB4 proteins.

TSI-specific easiRNAs are preferentially incorporated into AGO1 and regulate target genes displaying complementary sequences (McCue et al. 2013; McCue et al. 2014). This is the case for the Athila6A derived AMS-specific easiRNAs (Figure 6A) that strongly downregulate the AMS gene in *ddm1* plants (McCue et al., 2013). Figure 6C confirms such impact on AMS mRNA levels, and also shows that this downregulation was not changed in our double or triple mutant plants. A similar result was obtained for another known easiRNA target, the LACS7 transcript (McCue et al. 2013) indicating that modification of small RNAs pattern in *ddm1 drb4*, *ddm1 drb7.2* or *ddm1 drb4 drb7.2* mutants does not impact targets of easiRNAs.

Using the same probes, no variation in small RNA populations was observed when using *drb7.1* instead of *drb7.2* background (Figure S8), suggesting that in contrast to AtDRB7.2, AtDRB7.1 is not involved in easiRNA biogenesis but possibly in another yet to define DCL4-dependent pathway.

#### **AtDRB7.2 is interacting with AtDRB4 but not with AtDCL4**

To test if AtDRB7.2 could interact directly with AtDCL4, a situation that could explain the concerted evolution signature of Figure 4, we used a BiFC strategy. Using as positive control the expected AtDRB4-AtDCL4 interaction, we observed that AtDRB7.2 interacts strongly with AtDRB4 but not directly with AtDCL4 (Figure 7, for additional positive and negative controls of the BiFC experiment see Figure S9 and S10). This result, combined to our inability to pull-down AtDCL4 using a tagged version of AtDRB7.2 (data not shown), suggest that AtDRB7.2 exists mainly, *in vivo*, in complex with AtDRB4 and not with AtDCL4. Therefore, since the concerted evolution signature is apparently not based on a direct contact between the two proteins, it is tempting to propose that AtDRB7.2 and AtDCL4 cooperate to bind a common ligand. However, our genetic results (see Figure 5 and 6) suggest that none of the tested AtDCL4 end-products (including 21-nt easiRNAs) are affected by the loss of AtDRB7.2. Surprisingly, the absence of AtDRB4 does not modify the accumulation of 21-nt easiRNAs either (Figure 6), suggesting that AtDCL4 is able to generate 21-nt easiRNAs without involving those DRBs and that the concerted evolution signature we observed in Figure 4 cannot be explained by the cooperative binding of AtDCL4 and AtDRB7.2 to easiRNA precursor molecules. Therefore, the molecular origin of this signature is yet to be determined and could result from the cooperative or competitive binding of both proteins to a common RNA ligand yet to identify or occurring in specific and/or discrete cell types.

#### **Conclusion**

By retracing the evolutionary history of DRB proteins in plants we were able to identify two new families we named DRB6 and DRB7. The earlier discovery of the DRB6 family was impaired by its absence in the model species *Arabidopsis*. DRB6 share structural similarities with DRB1 and it is tempting to speculate that it could also be involved in the production of miRNAs, except in

Brassicaceae where, other DRBs (such as AtDRB2, AtDRB3 and AtDRB5; Eamens et al., 2012a; Eamens et al, 2012b) could play its part.

Determining precisely the role of DRB7 proteins will require more work. We show here that one of the two Arabidopsis DRB7 proteins (AtDRB7.2) is involved, in combination with AtDRB4, in the easiRNA pathway, by inhibiting the accumulation of DCL3-dependent 24nt siRNAs from easiRNA-generating loci. However, the increased accumulation of those 24nt siRNAs in *drb4* or *drb7* mutant background has no impact on the regulation of easiRNA target accumulation. How AtDRB7 and AtDRB4, in association or not with DCL4, negatively regulate the accumulation of those 24nt siRNAs remains to be determined. One possibility is that AtDRB4/AtDRB7 may be inhibitors of DCL3 activity. This inhibitory effect can be mediated through a direct interaction with DCL3 that will either compete for binding of DCL3 cofactors or directly inhibit its processing on particular substrate. Alternatively, AtDRB4/AtDRB7 may directly sequester specific dsRNA precursors, thereby preventing their access and processing by DCL3. Finally, given that this inhibitory effect is only observed in a *ddm1* mutant background, it is also possible that this mutation triggers a change in the homeostasis of either DCL3, its cofactor(s), or of factor(s) required for the production of these particular polIV-dependent dsRNAs. This change may, in turn, makes DCL3-mediated processing more susceptible to the presence or absence of AtDRB4/AtDRB7. This is particularly striking in the *drb4* mutant background where opposite molecular phenotypes are observed for 24nt TSI 3'part-derived siRNA in presence or absence of DDM1 (Figures 5 and 6). Although the reason for this difference is currently unknown, one interesting factor to test would be DRB2 as increased accumulation of several polIV-dependent siRNA were previously observed in *drb2* mutant background (Clavel et al. 2015; Pélissier et al. 2011). Although closely related to AtDRB7.2, AtDRB7.1 does not seem to be involved in any small RNA pathway tested so far and its function will also need to be further investigated in the future.

## **METHODS**

### **Sequence selection, multiple sequences alignments and phylogenetic reconstruction**

Twenty-three species representing the diversity of the Viridiplantae lineage were searched for the presence of DRBs. At the root of the lineage, we have selected five chlorophytes (*Chlamydomonas reinhardtii*, *Volvox carteri*, *Coccomyxa subellipsoidea*, *Micromonas pusilla* and *Ostreococcus lucimarinus*), one bryophyte (*Physcomitrella patens*), and one lycophyte (*Selaginella moellendorffii*). The four monocotyledons species we have selected (*Sorghum bicolor*, *Zea mays*, *Setaria italica* and *Oryza sativa*) are representative of the three major subclades of this lineage. For the analysis of the DRB7 family, we used the *Brachypodium distachyon* instead of the *Oryza sativa* protein due to a sequence quality problem for this gene in *O. sativa*. To represent the dicotyledons, we used twelve species, one at the root of this lineage (*Aquilegia coerulea*), one at the root of the Pentapetalae (*Mimulus guttatus*) an outgroup of the Malvidae (*Eucalyptus grandis*), seven Malvidae species representing the four major subclades of this group (*Citrus sinensis*, *Theobroma cacao*, *Thellungiella halophila*, *Brassica rapa*, *Arabidopsis thaliana*, *Populus trichocarpa* and *Ricinus communis*) and two Fabidae species representing the two subclades of this group (*Cucumis sativus*, *Phaseolus vulgaris*). Blast searches were performed starting from known *Arabidopsis* dsRBMs. However, to make sure we did not miss any DRBs, each time a new dsRBM was found in a given species it was itself used as a probe in a new BLAST search. By using this iterated BLAST procedure we are very confident that we did not miss any dsRBM containing proteins and that we have collected all DRBs in species we have studied.

Sequences were aligned using the multiple sequence comparison by log-expectation (MUSCLE v3.7) software (Edgar 2004). Alignment shading was obtained using BOXSHADE v3.21. Trees were reconstructed using the fast maximum likelihood tree estimation program PHYML (Guindon and Gascuel 2003) using the LG amino acids replacement matrix (Le and Gascuel 2008). Statistical support for the major clusters were obtained using the approximate likelihood-ratio test (aLRT) (Anisimova and Gascuel 2006).

### **Plant material and plant growth conditions**

The *drb4-1* and *ddm1-2* mutant lines are in Col0 background and were described previously (Curtin et al. 2008; Jeddeloh et al. 1999). The *drb7.2* mutant corresponds to a GABI-Kat line (GK-525B11; background Col0) bearing a tDNA insertion into the 3<sup>rd</sup> intron of the At4g00420 gene. The *drb7.1* mutant in the Nössen (No) genetic background was obtained from the “RIKEN *Arabidopsis* transposon mutants” resources (PST 12013) and contains a Ds insertion into the 2<sup>nd</sup> exon of the At1g80650 gene. Absence of DRB7.1 and 7.2 transcripts was ascertained by semi-qRT-PCR using exon-specific primers surrounding the integration sites. Double *drb7.1 drb7.2* mutant lines were obtained by crossing and a Col x No crossed line was used as control. Plant seeds were stratified for two to four days at 4°C before growth in chambers on soil at 23°C under a 16h-light/8h-dark cycle.

### **RNA isolation and hybridization**

Total RNA was extracted as described in (Pélissier et al. 2004), using immature floral inflorescences (stages 1-12) or aerial parts from 2 weeks-old seedlings. For the detection of small RNAs, 15µg of total RNA samples were heat-treated in 1.5 volume of standard formamide buffer and loaded on a 15% polyacrylamide (19 :1 acrylamide :bis-acrylamide) – 8.3M urea - 0.5X TBE gel and separated by electrophoresis. The samples were electroblotted to hybond-NX membranes (GE healthcare) and fixed following a carbodiimide-mediated cross-linking procedure (Pall et al. 2007). Pre-hybridization and hybridization was carried out in 5X SSC, 20mM Na<sub>2</sub>HPO<sub>4</sub> pH7.2, 7% SDS, 2X Denhardt solution, 50mg/ml herring DNA at 50°C. Filters were washed twice with 3X SSC, 5% SDS at 50°C for 10 min, followed by one to two washes with 1X SSC, 1% SDS at 50°C for 10 min. Signals were visualized by autoradiography or by using a phosphorimager (Molecular Imager FX; Bio-Rad) for quantification. Sequences of the different probes used are given in Table S2.

### **QRT-PCR analysis**

2 µg of total RNA were DNase treated using the Promega RQ1 kit following manufacturer's recommendations. 0.2 µg of treated RNA was reverse transcribed using PrimeScript RT reagent kit (Perfect real time, Takara) in a final volume of 10 µl, using either a mix of oligodT and random hexanucleotides or a mixture of gene specific primers for fca 3' end analysis experiments (rt7-R and

act2-R). One  $\mu$ l of cDNA was used for amplification, using the Eco Real-Time system (Illumina) and SYBR Premix Ex Taq II (Tli RnaseH Plus) (Takara) in a final volume of 15  $\mu$ l. Actin2 RNA was used as input control to normalize the expression levels, with a minimum of two biological repeats per experiments. Primers used can be found in Table S2.

### **BiFC constructs**

DRB4 and DRB7.2 open reading frames flanked by AttB1 and AttB2 sites (see Table S2 for primer sequences) were amplified from *Arabidopsis* cDNA clones (Columbia ecotype), cloned into Gateway vector pDONR221 using BP recombination (Invitrogen), and sequenced. An LR reaction between the entry vector and the complete set of four pBiFP vectors (Azimzadeh et al., 2008) produced the final expression vectors, where coding sequences are cloned in fusion with the N- and C-terminal parts of YFP (Hu et al., 2002), either as N-terminal or C-terminal fusions, under the control of the cauliflower mosaic virus 35S promoter. cDNA of DCL4 was cloned, in fusion with the N- and C-terminal parts of YFP, either as N-terminal or C-terminal fusions under the control of its endogenous promoter, in pB7GW34 vector using the “MultiSite Gateway Three-Fragment Vector Construction Kit” (Invitrogen). For fluorescence complementation tests, all eight compatible combinations between protein pairs (i.e., providing both parts of the YFP) were assayed in transient expression. A C-terminal fusion of the Glutathion S-transferase (GST) with the C-terminal part of the YFP (kindly provided by N. Lukhovitskaya, IBMP, France) was used a negative control with the appropriate compatible combination of DCL4, DRB4 or DRB7.2 YFP fusions.

### **Transient assay in *Nicotiana benthamiana* leaves**

Each expression vector was introduced in *Agrobacterium tumefaciens* strain GV3101 by electroporation. *Agrobacterium* bacterial cultures were incubated overnight at 28°C with agitation. Each culture was pelleted, and resuspended in 10mM MgCl<sub>2</sub>, 200 $\mu$ M Acetosyringone buffer to an OD<sub>600</sub> of 1.5 and put 2 hrs under gentle agitation at room temperature. To enhance transient expression of BiFC fusion proteins, the P19 viral suppressor of RNA silencing was coexpressed (Voinnet et al.,

2003). Equal volumes of each bacterial culture were mixed before infiltration and YFP fluorescence was scored 3 to 4 d post-infiltration with a confocal microscope (LSM780, ZEISS).

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## FIGURE LEGENDS

Figure 1: Phylogenetic analysis of Double Stranded RNA binding Motifs (dsRBMs) of *Arabidopsis thaliana* Double stranded RNA Binding proteins (DRB) and of the DiCer-Like 4 protein (DCL4) (see Table S1 for protein sequences and Figure S1 for the alignment). Selected informative statistical supports (approximate likelihood-ratio test (aLRT) data) are indicated. A schematic representation of the position of the different conserved domains in each DRB family is presented (see also Figure 3 and S3).

Figure 2: Phylogenetic analysis of the DRB proteins having multiple dsRBMs. The phylogenetic tree was obtained by fusing and aligning the dsRBMs of 110 DRB proteins from 18 plant species (see Table S1 for protein sequences and Figure S2 for the alignment). Selected informative statistical supports (approximate likelihood-ratio test (aLRT) data) are indicated. Names of the different DRB families are indicated with a schematic representation of the position of the different conserved domains in each family (see also Figure S3). The classification as type I or type II dsRBM was obtained by analyzing the individual motifs (see Figure 3). Species codes are the following: Pp: *Physcomitrella patens*, Sm: *Selaginella moellendorffii*, Sb: *Sorghum bicolor*, Zm: *Zea mays*, Si:

*Setaria italic*, Os: *Oryza sativa*, Ac: *Aquilegia coerulea*, Mg: *Mimulus guttatus*, Eg: *Eucalyptus grandis*, Cs: *Citrus sinensis*, Tc: *Theobroma cacao*, Th: *Thellungiella halophila*, Br: *Brassica rapa*, At: *Arabidopsis thaliana*, Cus: *Cucumis sativus*, Pv: *Phaseolus vulgaris*, Pt: *Populus trichocarpa*, Rc: *Ricinus communis*.

Figure 3: Phylogenetic analysis of individual dsRBMs present in multiple dsRBM DRBs. Selected informative statistical supports (approximate likelihood-ratio test (aLRT) data) are indicated (see Table S1 for protein sequences and Figure S5 for the alignment). Names of the different DRBs are indicated in which the last number after the dot (1, 2 or 3) denotes the position of the dsRBM in the protein (1 being the most N-terminal). The two different clades define the two types of dsRBM (I or II). The color code defined here was used in the schematic presentation of the DRB families in Figure 2. Species codes are as in Figure 2.

Figure 4: Phylogenetic analysis of individual dsRBMs present in the single dsRBM DRB7 family and in the most C-terminal region of the DCL4 family. Selected informative statistical supports (approximate likelihood-ratio test (aLRT) data) are indicated (see Table S1 for protein sequences and Figure S6 for the alignment). Bd: *Brachypodium distachyon*

Figure 5: Impact of AtDRB7 loss of function on known AtDCL4 *in vivo* substrates. DRB4, but not DRB7 proteins, is required for proper accumulation of polIV-dependent siRNAs (TSI), tasiRNAs and DCL4-dependent miRNAs (miR822 and 839). Total RNA extracts from immature flowers were blotted and hybridized sequentially with the indicated probes. While DCL1-dependent miRNA171 is unaffected in all mutant combinations, significant change in small RNA level/pattern is observed in the *drb4* mutant background only; no additional impact is visible when *dr7.1* and *drb7.2* mutations are combined with *drb4*. Because Col0 was used as control following introgression of the *drb7.1* Nössen (No) mutant allele into *drb4 drb7.2* line, three individual plants of the progeny were analyzed to minimize potential effects of mixed genetic backgrounds. Values for 21-nt RNA accumulation (or 24-



nt for TSI 3' part probe 2) are normalized to U6 RNA and are expressed as a ratio relative to the wild-type control plants. Variation of more than 1,5 fold are highlighted in bold.

Figure 6: Impact of AtDRB7.2 loss of function on the easiRNA pathway and on targets of the easiRNA pathway. A. To properly compare easiRNA accumulation patterns, total RNAs of immature floral inflorescences were extracted from Col0 or siblings segregating from a single *ddm*<sup>-/-</sup> *drb4*<sup>+/-</sup> *drb7.2*<sup>+/-</sup> parental plant. Blotted RNAs were probed with the indicated probes. AtDRB4 and AtDRB7.2 both impact the processing of easiRNA precursors. As expected AtDRB4 also impact the production of tasiRNA (*tas2*) and a AtDCL4-AtDRB4 dependent miRNA (*mir822*) but none of the two proteins impact a AtDCL1-AtDRB1 dependent miRNA (*mir171*). For *tas2*, 21nt AtDCL4-dependent tasiRNAs are reduced in *drb4* and low levels of 22-24nt species accumulate due to compensatory functions of AtDCL2/AtDCL3, as expected when AtDCL4 activity is reduced on *tas2* precursor (Gascioli et al., 2005). B. Accumulation of 22- and 24-nt siRNAs relative to the 21-nt level. Hybridization results from only one of the two TSI 5' or 3' probes are shown as both probes in each case, gave similar results. Values are means derived from two individual siblings (A.) +/- SEM and are given relative to *ddm1* set arbitrarily to 1. C. qRT-PCR analyses of AMS and LACS7 expression in different genetic backgrounds. Targeting of AMS and LACS7 mRNAs by AGO1-loaded 21nt-siRNAs in *ddm1* plants is not affected by the additional *drb4* and *drb7.2* mutations. Values normalized to *actin2* are means derived from three individual siblings (only two for triple mutants) +/- SEM and are represented relative to Col0 set arbitrarily to 1.

Figure 7 : BiFC visualization of AtDRB7.2 interaction with AtDRB4. Shown are confocal images of *Nicotiana benthamiana* epidermal cells coinfiltrated with Agrobacterium cultures harboring different combination of expression vectors (indicated on the left of the panels). Scale bars and the position of nucleus are shown. Positive control for the BiFC experiment corresponds to coexpression of AtDRB4 and AtDCL4, fused to the indicated YFP moieties (one example of two different combinations is shown). As previously reported (Hiraguri et al., 2005; Zhu et al., 2013), AtDRB4 was found to be associated with AtDCL4 in the nucleus. YFP complementation was also observed when AtDRB7.2

and AtDRB4 were coexpressed (one example of two different combinations is shown) and showed similar nuclear localization as the one observed with AtDRB4 and AtDCL4. By contrast, none of the combinations between AtDRB7.2 and AtDCL4, nor any of the negative controls involving GST fusion as one of the partner (not shown), gives a visible fluorescent signal. For additional positive and negative controls of the BiFC experiment see Figure S9 and S10.

## **SUPPLEMENTARY MATERIAL**

Table S1: Sequence of the proteins used in this study.

Table S2: Sequence of the primers used in this study.

Figure S1: Alignment of the *Arabidopsis thaliana* dsRBMs present in DRB proteins and in the most C-terminal region of the DCL4 protein. Names of the different DRBs are indicated followed by a number (1 or 2) indicating the position of the dsRBM in the protein (1 being the most N-terminal). At1g80650 and At4g00420 have a single dsRBM. This alignment was used to build the phylogenetic tree of Figure 1.

Figure S2: Alignment of the fused dsRBMs present in multiple dsRBM DRBs used to build the phylogenetic tree of Figure 2.

Figure S3: Positioning of the dsRBMs in the different DRB families. The average size (in amino acids) of the linker regions before the first dsRBM and connecting internal dsRBMs is presented (with standard deviations) for each category except for the most variable linkers (V\*) where only the lower and higher sizes are presented.

Figure S4: Identification of conserved Arginine-Lysine rich (RK-rich) region in proteins from the DRB1 (A) and DRB6 (B) families. In A, only the DRB1 second dsRBM and its immediate flanking region is shown. In B, only the DRB6 C-terminal end is shown. Species codes are as in Figure 2.

Figure S5: Alignment of individual dsRBMs present in multiple dsRBM DRBs used to build the phylogenetic tree of Figure 3. Species codes are as in Figure 2.

Figure S6: Alignment of individual dsRBMs present in the single dsRBM DRB7 family and in the most C-terminal region of the DCL4 protein family. This alignment was used to build the phylogenetic tree of Figure 4. Species codes are as in Figure 2.

Figure S7: Impact of AtDCL4 and AtDRB7 losses on the transcription termination of FCA. No significant change in read-through transcription was observed for the mutant lines tested, using seedlings (A) or immature flowers (B) total RNAs as template. Primers used are diagnostic for the rt7 region (Liu et al. 2012), several hundred base pairs downstream of the FCA polyA termination signal. Actin2 is used for normalization and the accurate control Col0, No or Col x No is set arbitrarily to 1. Values are means derived from at least two biological repeats +/- SEM, except for individual siblings segregating from *drb4 +/- drb7.1 +/- drb7.2 -/-* plants.

Figure S8: AtDRB7.1 loss of function has no impact on the processing of easiRNA precursors. Blotted RNAs were probed with the indicated probes; U6 RNA was used as loading control.

Figure S9: Negative controls of the BIFC experiments. Negative controls using a GST protein fused to the N- or C-terminal part of YFP fragments (YFP<sup>N</sup> or YFP<sup>C</sup>) in combination with the complementary AtDCL4 (A), AtDRB4 or AtDRB7.2 (B) YFP fusions. The fusion of the YFP fragment was always done at the C-terminus of the GST while the fusion of the complementary YFP fragment was done either at the N-terminus (for example YFP<sup>N</sup>-AtDCL4) or C-terminus (for example AtDRB7.2- YFP<sup>N</sup>) of the three tested proteins. (C). Negative controls using additional swaps (other than the ones shown in Figure 7) of AtDCL4 and AtDRB7.2 YFP fusion proteins. (D) Negative controls of AtDRB7.2 and AtDRB4 fusion YFP co-expressed with cucumber mosaic virus 2b protein (CMV2b) (Wang et al.

2004) corresponding YFP fusion. Scale bars and the position of nucleus are shown. BIFC experiments were done as explained in Figure 7 and in the Material and Methods section.

Figure S10: Positive controls of the BIFC experiments. New swaps (other than the ones shown in Figure 7) were done to challenge the positive interaction between AtDRB4 and AtDRB7.2. We fused this time the C-terminal part of YFP to the C-terminus of AtDRB4 and the N-terminal part of YFP to the C-terminus of AtDCL7.2 (A) and the C-terminal part of YFP to the N-terminus of AtDRB4 and the N-terminal part of YFP to the N-terminus of AtDCL7.2 (B). (C) A positive control showing the expected interaction between cucumber mosaic virus 2b protein (CMV2b) and importing alpha1 (NbIMP- $\alpha$ 1) (Wang et al. 2004). (D) Same experiments as in Figure 7 but showing a broader view. Scale bars and the position of nucleus are shown. BIFC experiments were done as explained in Figure 7 and in the Material and Methods section.

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Figure 1

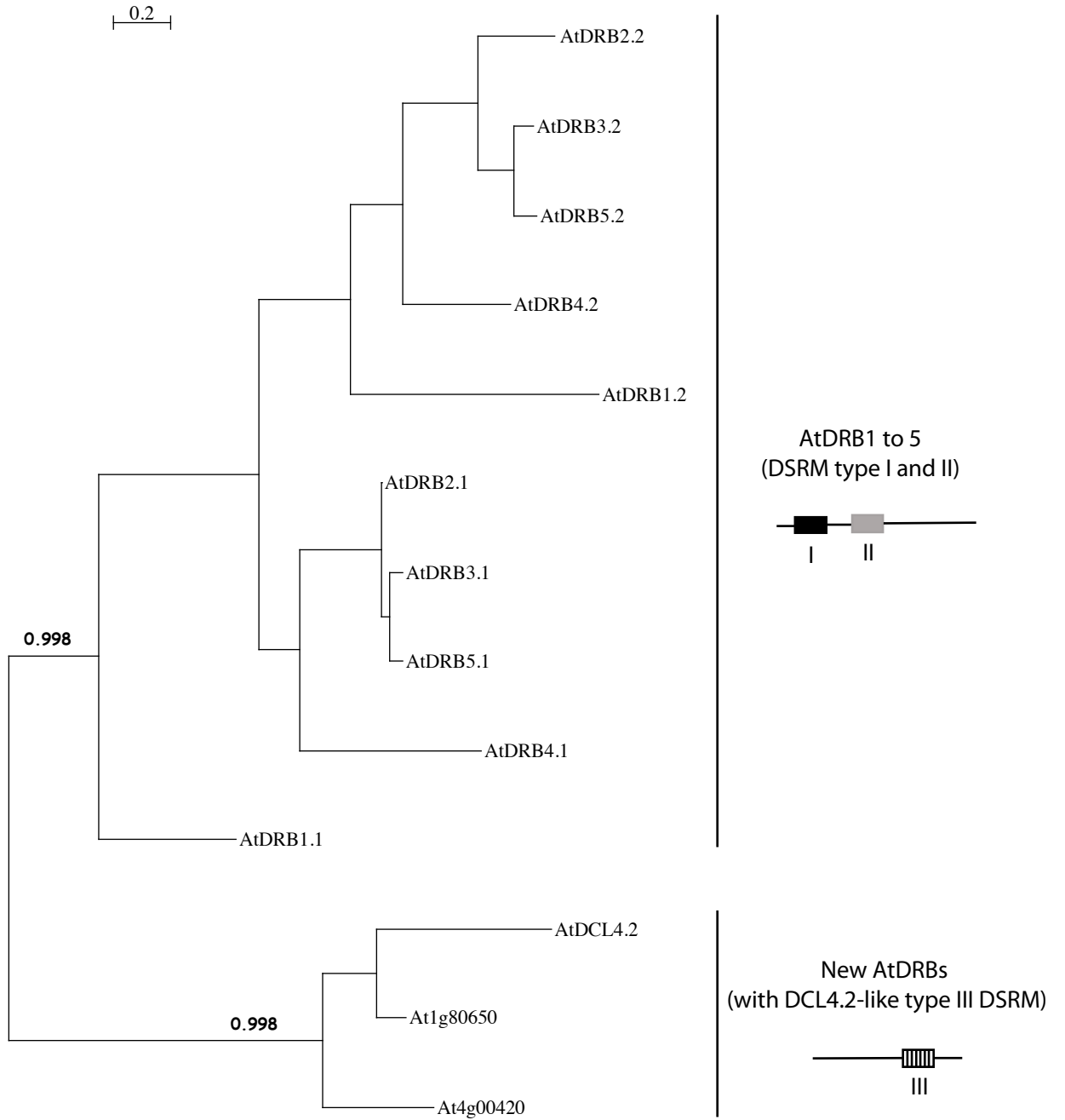


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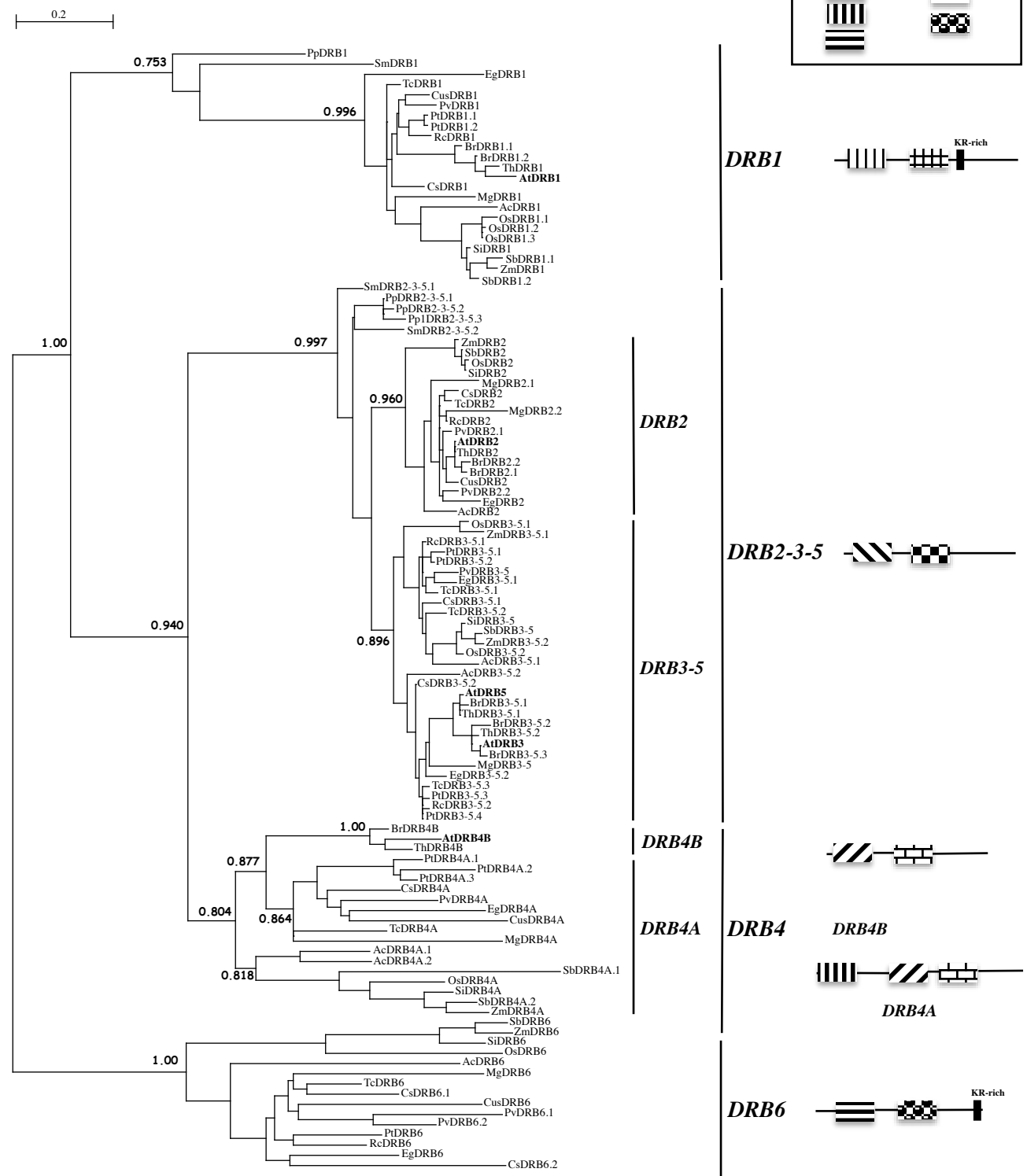


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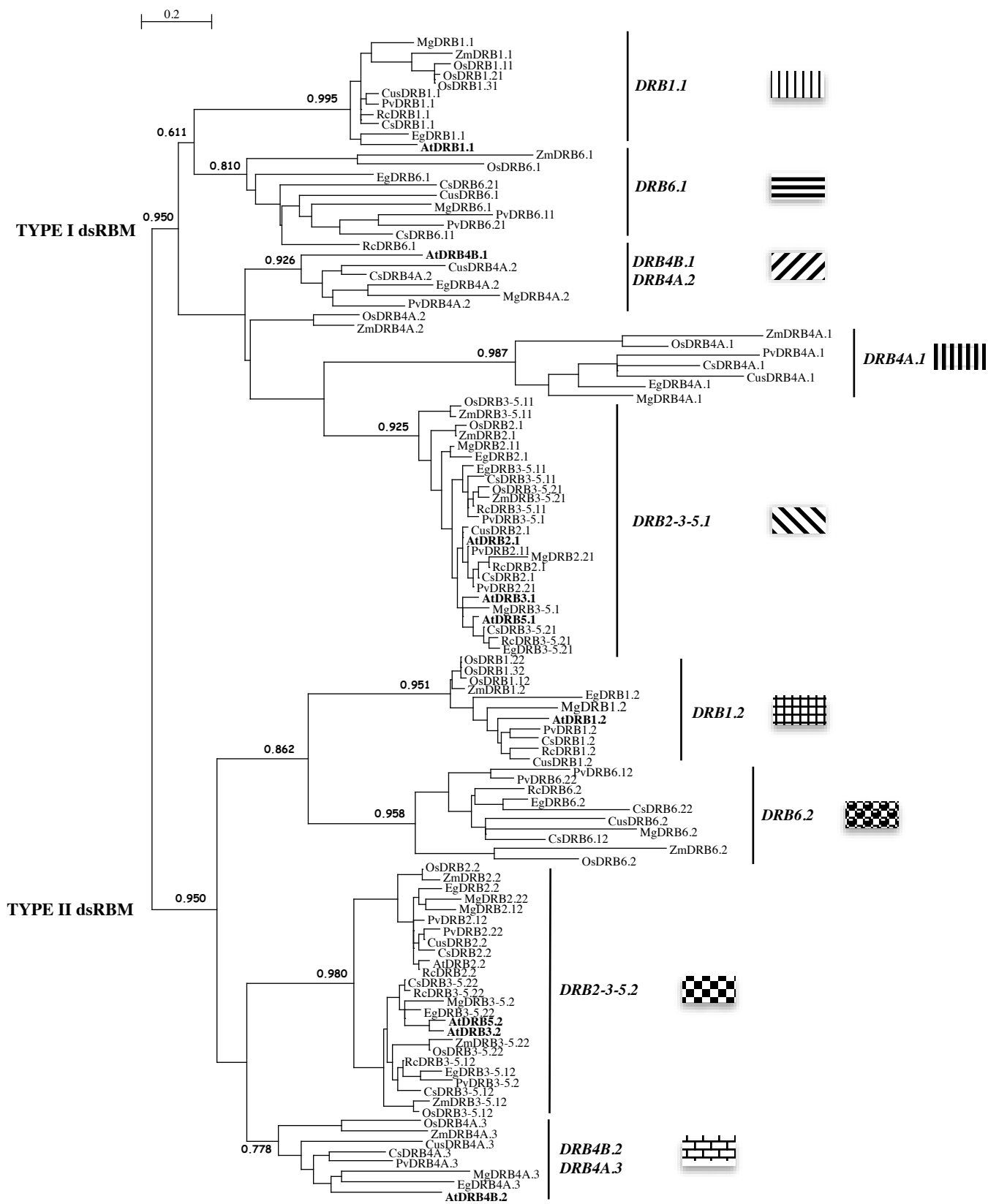


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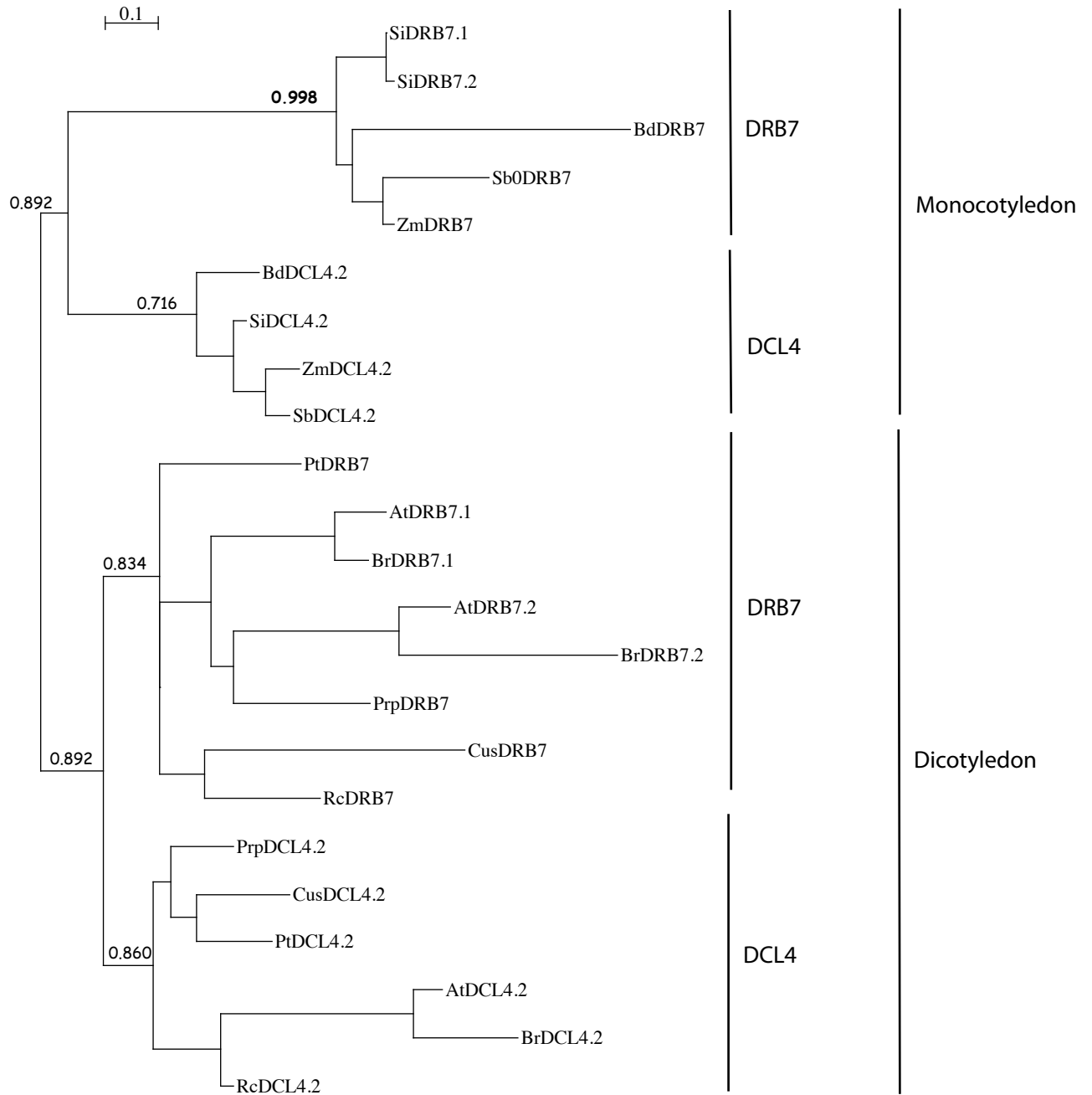
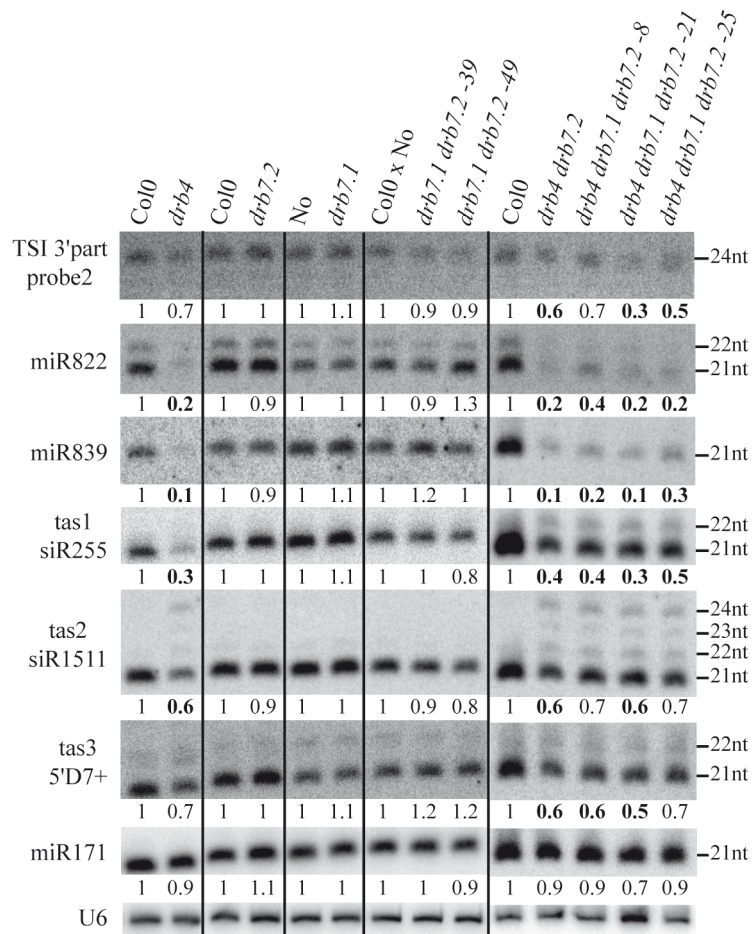


Figure 5





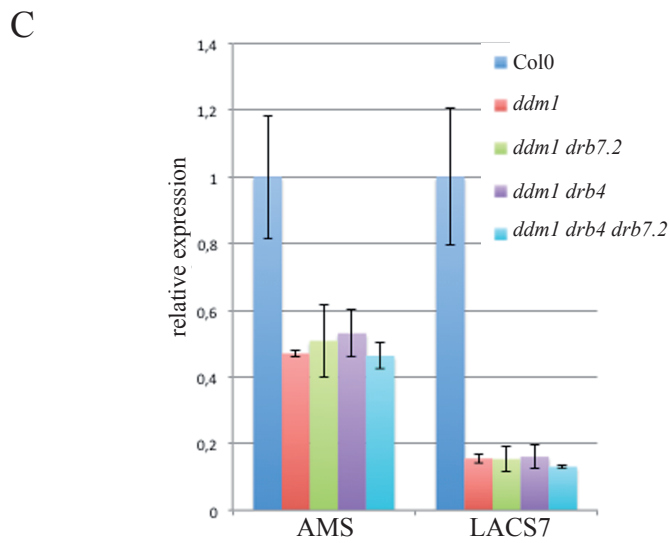
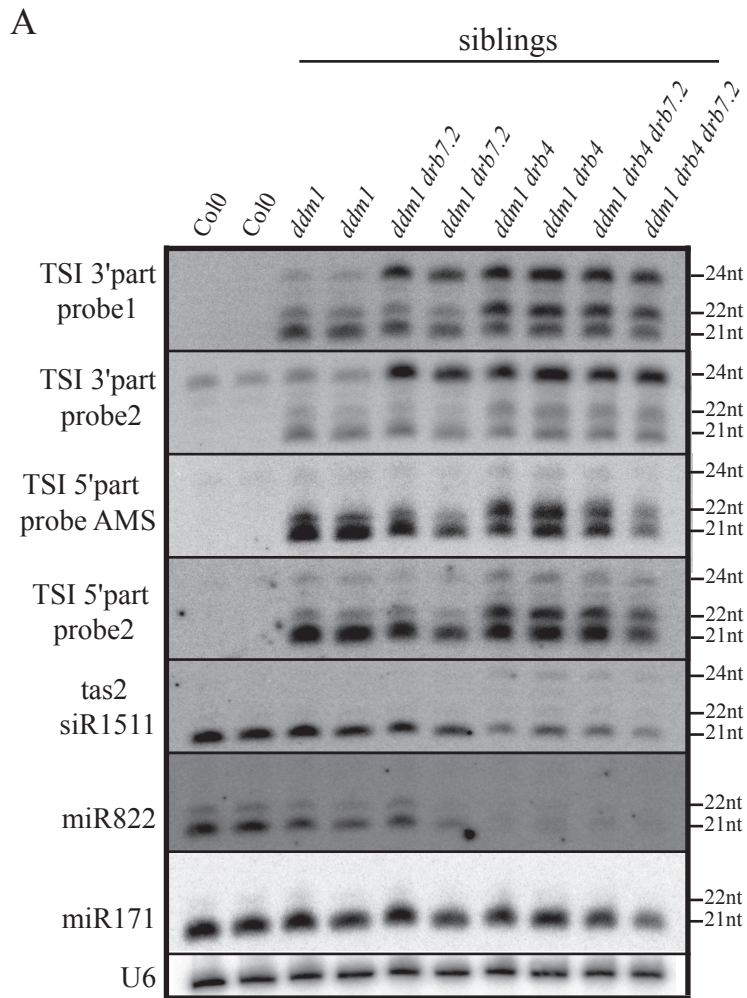
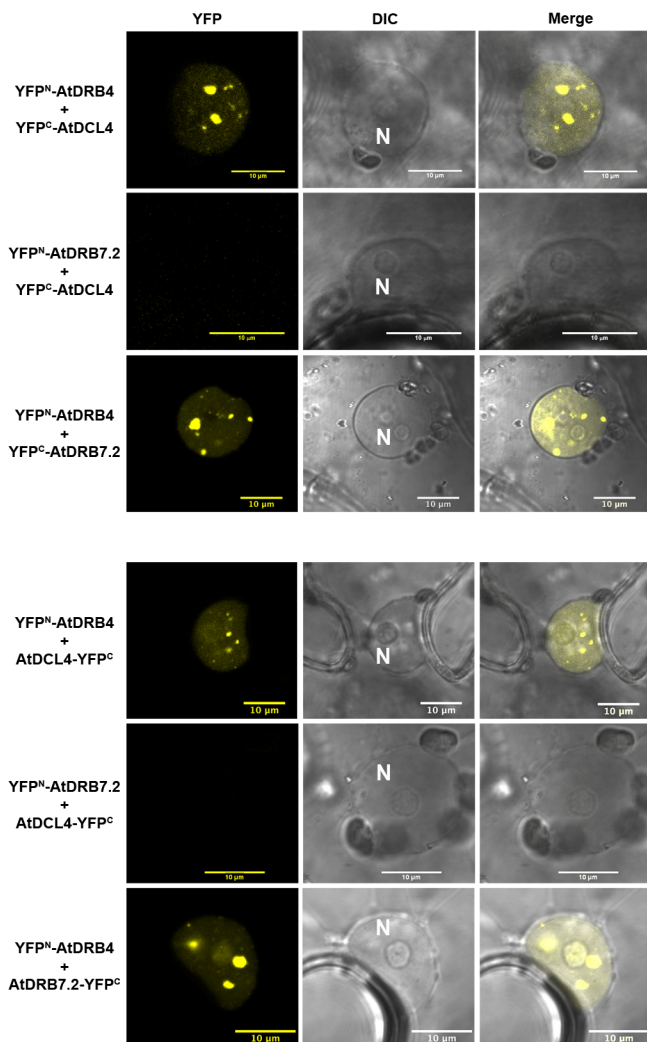


Figure 6

Figure 7



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AtDRB1-2 1 CKNLLOEYAOKMNYAIPLYQCQKVETLGRVTFTCVEIG-----GIKYTGAA-TRTKKDAEISAGRTALLAI
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Figure S1



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Figure S2

Figure S3

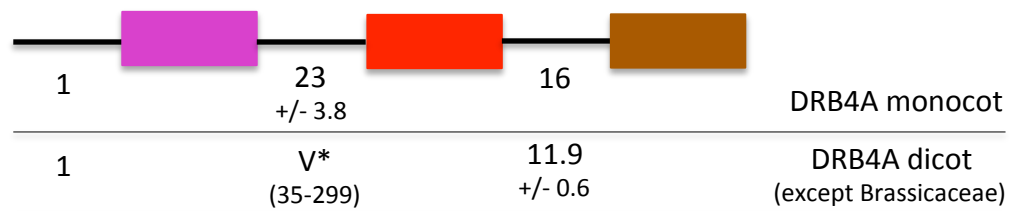
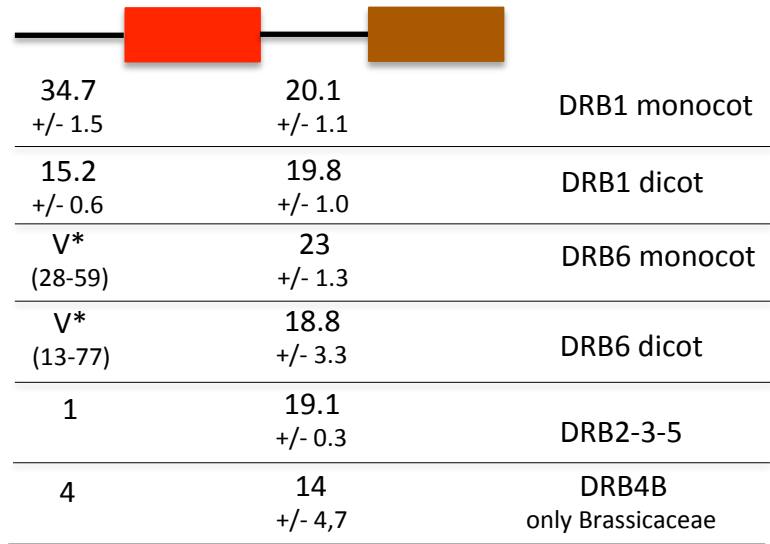


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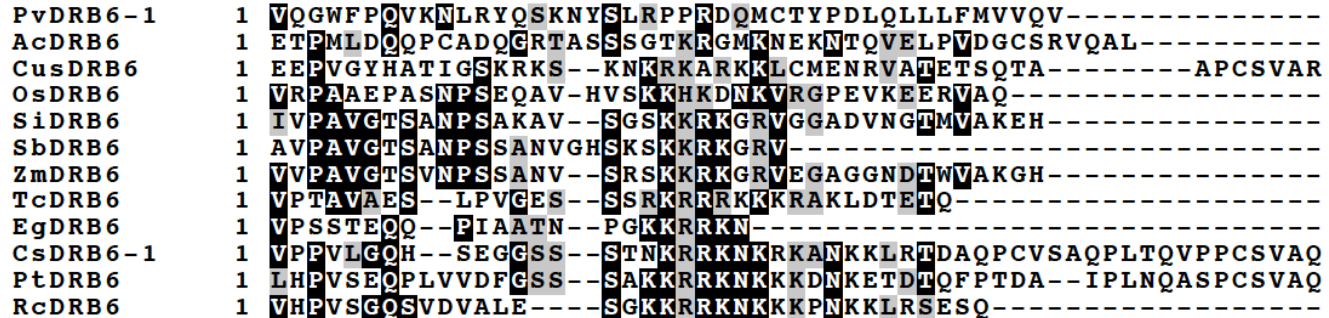
A



B

KR-rich region

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Figure S5

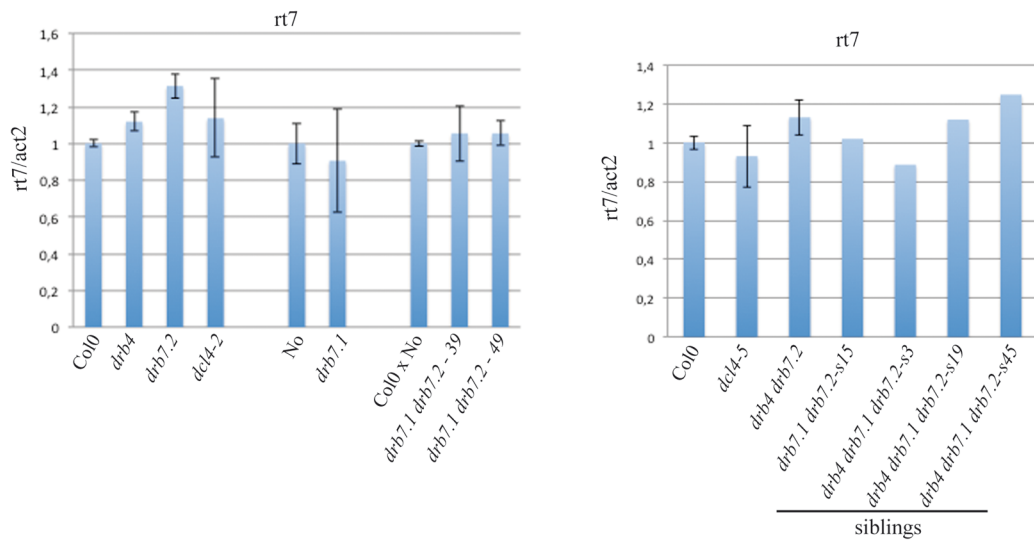
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BrDRB7-2 1 AREOLYKLCGVRHWKAPLYTFNODGPDNTKLFKVEVSVIKEASGITVLECFGDPHNKKKIAAEQAAEVALWFL
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Figure S6

A



B

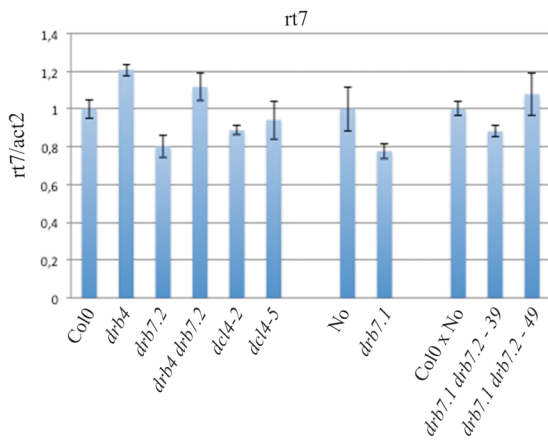


Figure S7

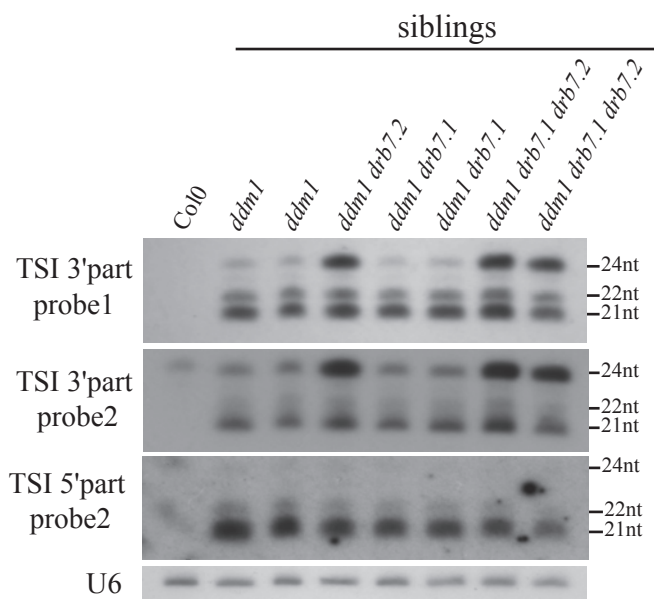


Figure S8

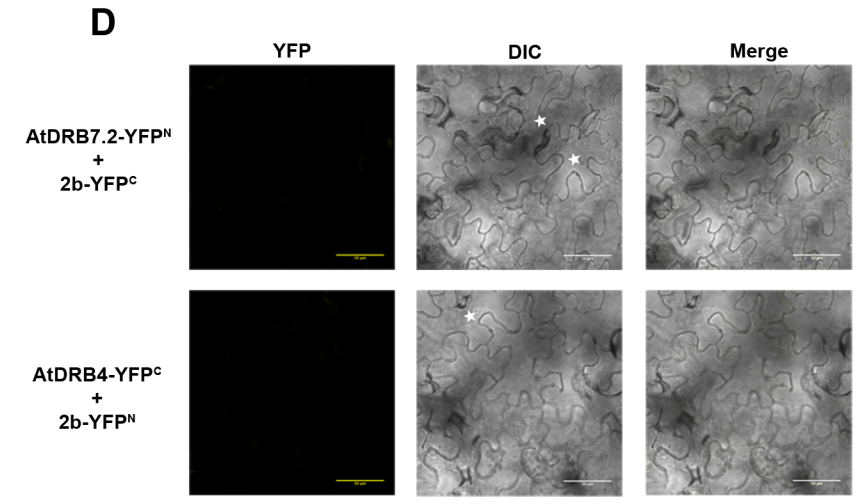
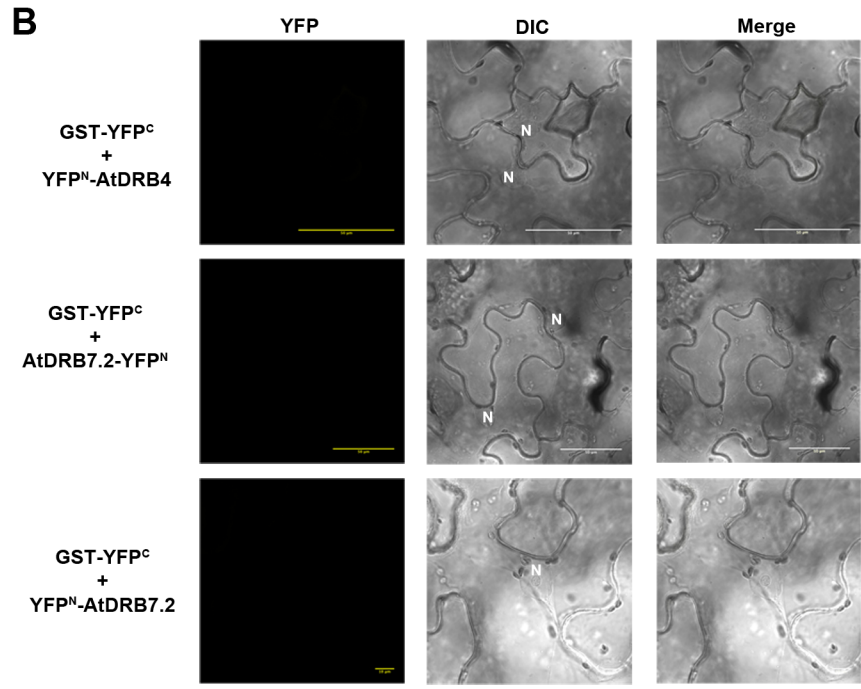
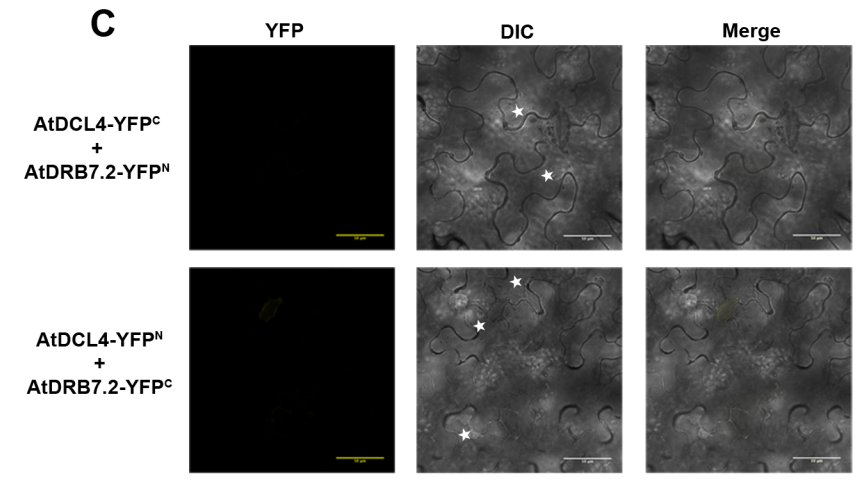
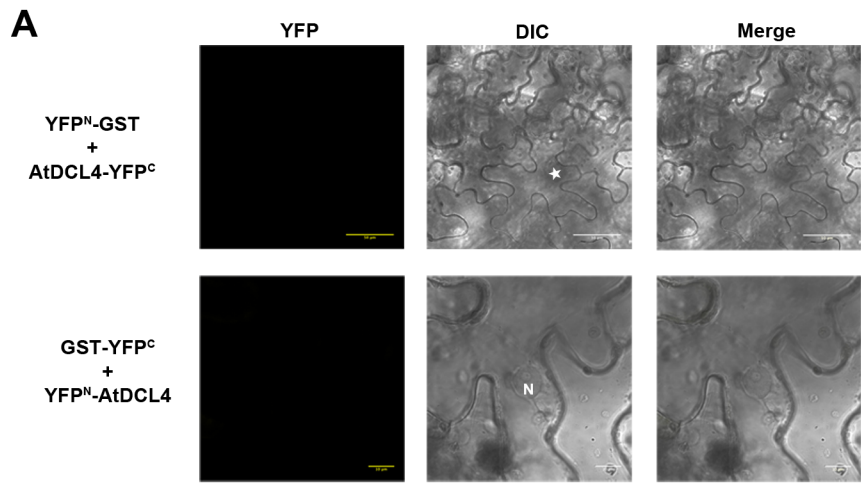


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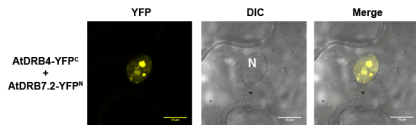
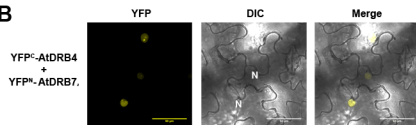
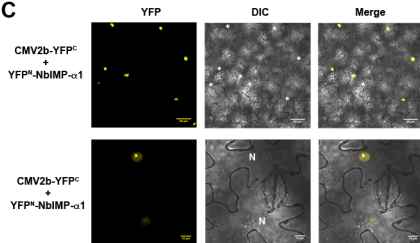
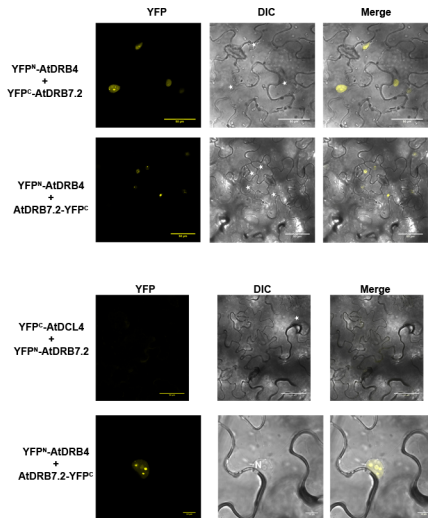
**A****B****C****D**

Figure S10

**Table S1:** Sequence of the proteins used in this study. Species codes are as in Figure 2 and 4

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>PpDRB1

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K

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>SiDRB1

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>PtDRB1.1

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>PtDRB1.2

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>BrDRB1.1

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>BrDRB1.2

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>EgDRB1

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>ThDRB1

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>CsDRB1

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>TcDRB1



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>AcDRB1

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>MgDRB1

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>PvDRB1

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>RcDRB1

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>CusDRB1

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>ZmDRB1

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>AtDRB2

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>AtDRB3

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>AtDRB5

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>PpDRB2-3-5.3

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>PpDRB2-3-5.2

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>PpDRB2-3-5.1

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>SmDRB2-3-5.1

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>SmDRB2-3-5.2

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>OsDRB2

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>OsDRB3-5.2

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>OsDRB3-5.1

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S S L K Q S N I R T T V S P L V F D L W I V C H G G D V F V V V W C S A G G A Q G A R R R R R R G A G A C G R R Q G A R R A E A A G R L R R R R W  
R R E G G G V S T E E A S R R R V L F V R H V A V Q T S M G A S V A A A A G G R T Q D T A S P A P A A A A S G G V R L P S R R R R A G A R A E E G  
R R A G A H A A R R H A A R Q G G R R N A A A D A V L L R A V L P P R R R R R P D E A L R R R R R V P R A A G G E R P F S D P G L R R A T V A A A A  
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>SbDRB2

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>SbDRB3-5

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G K E G C T G S S T S P A E E H N T L T V P S S T T Q S S L H K L E P N E D E Q T L Q A G L K Q A H E Q Q L M P S S S C V S P L V T A Q N S V Q R K H Y  
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>SiDRB2

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P L P P P A A R T Q Q L P P L M S H P P I R M A S P V R I P A S P M F G P S A P V Q G P K P V M S V Q L K D V Q Q S R R E P V K P V I P V Q V K  
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>SiDRB3-5

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S E L K Q L P R V G E P S S S S C P S D Q D D E E H E Q A I V T R T L A S L N L A N G G K T L H Q K E K Q S N N R P S S R S Y A K P N P S S Y R S H L  
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E A A P G L P R Y F S P Y P V T F V P R S P L P A T V P K I H E R R Q D H A E T V E F P D A A V F S Q Y G D Q H K F Q G K E D C T G T S A S P C P R S G S  
S S T A H P S L Q K R D P N E E K E T L G S K H A E P N K S Q G Q P K S S P S W V N P S I P A H G S I Q R K H Y T S S V Q H D D P P Q T S R S S L P E L  
W S S R S P A A P R S G A A V P V N S P V S G Y Q R H P W L A A S V T V R T A V P V C S A R P N A V N T P G E A A R V R P I A Q N C L D P E T P R N  
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>PtDRB3-5.3

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>PvDRB2.2

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>PvDRB3-5

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>RcDRB3-5.2

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>RcDRB3-5.1

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>CusDRB2

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>ZmDRB2

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>ZmDRB3-5.1

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>ThDRB4B

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>TcDRB4A

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>MgDRB4A

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>PvDRB4A

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>ZmDRB4A

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>OsDRB6

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>SbDRB6

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>SiDRB6

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>PtDRB6

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>EgDRB6

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>CsDRB6.1

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>CsDRB6.2

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>TcDRB6

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>AcDRB6

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>MgDRB6

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>PvDRB6.2

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>PvDRB6.1

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>RcDRB6

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>CusDRB6

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>ZmDRB6

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>AtDRB7.1 (At1g80650)

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>AtDRB7.2 (At4g00420)

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>OsDRB7

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>SbDRB7

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>SiDRB7.1

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>SiDRB7.2

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>PtDRB7

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>BrDRB7.1

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>BrDRB7.2

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>PrpDRB7

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>RcDRB7

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>CusDRB7

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>ZmDRB7

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>BdDRB7 30297

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>AtDCL4

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>BdDCL4

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>SiDCL4

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NVDFKDDALYRVLDAASANLSLMDYINISELEELIGYKFKHKGALLQAFVHPSFNKHSGGCYQRMFLGDAVLEYL  
MVSYLAYSAYPDLKPGQITDLKSLAVNNTSFAYVAIKKSMHKYLIKDSKYLMAAVNKFENYFNLSNSEKDLSEEPAC  
KVLGDIVESC VGAVLLDSGFNLNHAWKLMMLLPILSFCMDHINPLRELRELCQNGFDLGLPKPIKADGEFHV  
VEVNVNGKMSCTAANQNSKHARKLAAQDTLSKLNKYGYKHKSLEELRTATKKEPELIGYDEEPIKVDGVPLE  
MKNLQMNNGEMEENIFFGNNEAFFIGRSATSIQRTGEDNKVDRNDANNGRINKSNVVTQNGCLPRGEAAKINKKEY  
HGDMVHKTARSFLYELCAANYWKPPPEFELCKDEGPSHLRKFCTCKVLVQIMGPSATLLECYSDPKLQKKAQEAHA  
QGALWCLKQLGYLPKDETHV

>ZmDCL4 (incomplete)

MQVLGDIVESC VGAVLLDSGFNLNHVWKLMLMLLPILSFCGMHIDPMRELRETCQYNGFDLGLPEPTKYNGEFH  
VKVEVNINGKMISCTAANRNSKDARKVAAQETLSKLNKYGYKHKRKSLLEEILRSTTKKESELIGYDEEPINVEDDID  
MQMNNLLINGERTSIQSTAGDNKVDKNDANSGRNNKSNVVMQNGCLPRGATDKINQKEYHGDMVRKTARSFLYE  
LCAANYWKPPPEFELCNDEGPSHLRKFCTCKVLIEITGTSVSLLECYSDPKLQKRAAQEAHAEGALWYLKHLGYLPRD  
ENRF

>SbDCL4 (incomplete)

MEHFVELPPELCSLKITGFSKDMGSSLSLLPSLMCRLENLLVAIELKNVMSSYFPEASQISASGILEALTTERCLERISL  
ERLEVLGDAFLKYVVGHRNFISYEGLEDEGQLTRRRSDIVNSNLYELSIRRNQVYIRDQHFEPTQFFALGRPCKVVC  
NPDREATLHPKNIDPDRRENCNLRCKSHHWLHRKTIADVVESSLGAFIVECGFKAFAFLRWIGIKVDFENSALY  
RVLDASSTNLSLMNYMNISELEELIGYTFKHKGALLQAFVHPSFNKHSGGCYQRMFLGDAVLDYLMASYLSAYP  
DLKPGQLTDLKSLALNNNSFAYVAVKKSIIHKYLIKDSKSLTAAINKFQNYVNLSSSEKDLLEEPTCPKVLGDIVESC  
GAVLLDSGFNLNHVWKLMLMLLPILSFCGMHIDPMRELREICQYNGFELGLPKPTEDNGEFHVKEVNIDGKMIS  
CTAANRNSKDARKVAAQEAALLKLNNGYKHKRKSLLEEILRATTKKESELIGYDEEPINVEDDIQMKNLLINGEMEG  
NIFQNKVSLNGRSETSIQSTTGDNKVDKNDANNGRNNKSNVVMQNGCLPRGATDKTNQREYHGDMVRKTARS  
FLYELCAANYWKPPDFELCKGEGPSHLRKFCTCKVLIQITGTSATLLECYSDPKLQKKAHEHAEGALWYLKQLGY  
LPKDDYRV

>PrpDCL4

MDDAGTSSPSDQGASSGADDVLVESGAGALKSDKDPKRVARKYQLELCKRALEENIIVYLGTCGCKTHIAVLLIYE  
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KVYSVEDKEELYHFVSSPVITVYNYGPVIRNTSSHYTSYCTKLEQIKRQCIEELSKKTNDYQSVRSKLLNRMHDSI  
LFCLESLGLWGALKASHILLNGDHFERNELMEEEGNNGDDTACVNYLTRADDILATDCLRDAIAADLSCVEILKEPF  
FSRKLRLIGILSSFRLQQNMKCIIFVNRVVTASSLSYILQRLKFLASWKCDFLVGVHSRLMSMSRKKMNIILDKFRS  
GELNLLIATKVGEEGLDIQTCCLVIRFDLPETVASFIQSRGRARMPQSEYAFVNSGNQKELDLIEKFRKDEDKMNM  
EIAFRSSDTFIGSEDRIYKVDSSGASISSGYSISLLHQYCSKLPHEFYFDPNPKFFFLDDLGGTICHILPSNAPIHQIVS  
TQQSSMEDAKKDAKLAIEELHKLALSDYLLPQQSNPVEELMLDSSSDSTEDEDSRAELHEMLVPAALKEPW  
SNSEDHVSLSYYLKFNPVPEDRYKSFGLFVKAPLVEAESMELDLHLAHSRSMTELVPVSGFAEFGKDEILLAQNF  
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SDIRLASGYKSISDVKNLSVYAPYKSTFYFITDVVQERNAYSYPKDSGTLSYVDHLIKKFHHLKYPEQQLLHAKPLFC  
LHNLHNRKQEDSGPQLDEYFIDLPELCELKVLAFSKDIGSSISLLPSIMHLENLLVAIELKHVLSVSFPEGAEVT  
AERVLEALTTEKQERFSLELLEILGDAFLKFAVGRHFLLHDSLEDEGLTRKRSNVVNNNSLFLKATRSNLQVYIR  
DQSFEPQFFALGRPCPRICGKETIGAIQGLCSVVNHTNSSEVRCCKGHHWLYKTIADVVESSLGAFVVDVSGFKA  
ATAFLRWIGIQVDFEPSQVTEVCIASRYIPLSACMDIAAENSLGYQFVHKGALLQAFVHPSYNKHGGGCYQRLFL  
GDAVLDYLYSYLVYVYKPKPGQLTDLRSVSVNNAFANVAVDRSFHKFLICDSGSLSEAIKVYVDFIDTPASERGL  
LDGPKCPKSLGDLVESLGAILLDTGFNLNRVWEIMLSFLKPIMSFSSLQSPIRELRQLCAHTWDLRFLPSKKGKT  
YSIQATVEGNNVRATASSTSLNKKDAIRICAKLIFAELKAQGNIPKTKSLEEVKSSSEMEAKLIGYDETPIDVLPDV



IGFDKLVQEPICRRNFNSKMHKEERNGDSSCIKPVLPQPPSFEAVKIQPRYQVWSISQIFLLSENLPGGSHKATARA  
RLYEICAANYWEPPLFECCNEEGPSHLKLFTEKVVVIEEAPDMILECFGSPHGNKAAAEEHAAEGALWYLRNGGY  
ISSD

>CusDCL4

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TKFRSGELNLLIATKVGEEGLDIQTCCLVIRFDLPETVSSFIQSRGRARMPQSEYAFVLVDSGNEKELGLINEFRKDEN  
RMDREIYSRSSNETFDSHEESIYRVASTGASITSGRSISLLHEYCSKLPHDDYFDPKPQFSYYDDLGGTVCHVNLPSN  
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ELHEMIFPAALKESWTGSGYLVLYCYHIKCTPDRDRNYKEGFLFVKAPLPQEAERMGLEHLHARGRSVMVNLIPS  
GVVLEEEITQAESFQEMFLKVIDRLEFVQEIPLRNNASRSVSSSYLLLPIMIFHDNEGSLFIDWNVIRRLSSKIF  
QNDAQLVKGATASDTHLMLYDGHRRSSDIENSLVYVPYKGEFFVTNIERGKNGHSQYKNSGFSHFELKTKFGI  
HLNYPEQPLLRAKPLFLLHNWLHNKREDSEARHLEEFIELPPEVCQLKIIGFSKDIGSSISLLPSIMHRLNLLVAI  
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NLLKLATRKNLQVYIRDQPFEPQFYLLGRPCPRICNEETSKDIHSHDDATNNAKANETKCSKGHHWLQKKTISDV  
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SYHKHGGGQYRLEFLGDAVLDYLITSYLYSAYPKLPGQLTDLRSVFRNEAFANVAVDVRFYKFLLCDSTSLSDI  
KSYVHFIAKAPFERDSLEQPRCPKALGDLVSSVAVLVDTGDFMNCVWKIMLSFIDPIMSFGFQLSPIRDITEFCQ  
NCGWKLKFNSSKMEGYYSVKAIEVKGGNFHATASANRRKKAIAANLILTKLAKGFIPEVNSLEKILKSSKMM  
EPKLGIDETPSITIDQVDNGHRTLNVLEFSSEHSDPRMHCVDNNEPVRITRISKMLVSSSRTAGEQLKPAFEGHDS  
PTDLQSSSVGRSGKTTARSRLYEVCANHWNRPSFDCMNEEGPSHLKMFTYKVVLEIEEAPDTIFEFFGAPHLKKK  
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>PtDCL4

MSGGHVTGEHSSLSVGGTNRVSSSIVGDGEESGSLQRTEKDPKMARKYQLELCKKALEENIIVYLTGCGKTH  
IAVLLIYEMGHLIRQPQKSACVFLAPTVALVHQQAKVIEDSTDFKVGICYGKSNRLKTHSSWEKEIEQNEVLVMTPO  
ILYLNLSHSFIKMDLIALLIFDECHHAQVKSHPYAQIMKVFYKNNNDGKLPRIFGMTASPVVKGASSRENLPRESINS  
LENLLDAKVSVEDKEELECFAVSPVIRVYLYGPVANGTSSSYEAYNILEGVKRQCIVEIGKKTGDNQSLESLRSTK  
RMLIRMHENIIFCLENLGLWGALQACRILLSGDHSEWALIEAEGNTSDVSMCDRYLNQATNVFAADCTRDGVT  
NVSQVEVLKEPFFSRKLLRLIEILSNFRLQPDMKCIVFNRIVTARSLSHILQNLKFLTQSWKCDFLVGVHSGLKMSR  
KTMNVILERFRTGKLNLLATKVGEEGLDIQTCCLVIRFDLPETVASFIQSRGRARMPQSEYVFLVDSGNQKERDLIE  
KFKIDEARMNIEICDRSRETDFDSIEEKIYKVHATGASITSGLSISLLQYCSKLPHDEYFDPKPKFFYFDDSEGTVCHI  
ILPSNAPTHKIVGTPQSSIEVAKKDAACKAIEQLHLKALGSEFLPQEDTNELELVSSSDNDCEDKDSRGELREMLV  
PAVLKESWTELEKPIHLNSYIEFCVPEPDRYKQFGLFLKAPLPLEADKMSLELHARGRSVMTKLVPSGLSKFST  
DEITHATNFQELFLKAILDRSEFVHEVPLGKDALSKSCPTFYLLPVIFHVSERRVTVDWEIIRCLSSPVFKNPAN  
AVDKGILPSNDCLQLANGCSSIRDVENSIVYTPHQKFFYFITNIVPEKNGDSPCKGSNTRSHKDHLTTTFGIHLRYPE  
QPLLRAKQLFCLRNLLCNRRKEDSELQELDEHFVDLAPELCELKIIGFSKDIGSSISLLPSVMHRLNLLVAIELKCILS  
ASFSEGDKVTAHRVLEALTTEKQCERLSLERLETLDGDAFLKFAVGRHFFLLHDTLDEGELTRKRSNAVNNNSLFLK  
ASRNNLQVFIRDQFPDPYQFFALGHPCPRICTKESEGTHSQCGSHVTGQAKGSEVRCCKGHHWLHNKTVSDVVEA  
LIGAFVLVDSGFKAIAFLRWIGIKVDFDSSQVINICQASRTYAMLNPSMDLATLENLLGHQFLYKGLLQAFVHPSH  
KNGGGCYQRLEFLGDAVLDYLITSYLFVYPKMKPGHLTDLRSVLVNNRAFASVAVDRSFHEYLICDSDALSAATKK  
FVDFVRTPKSERRLLEGPKCPKVLGDLVSSVGAILLDTGFDLNIHWKIMLSFLNPISFSNLQINPVRELKELCQSH  
NWDVEVPASKKGRTFSDVTLGKDMNISASANSNKEAIRMASEKIYARLKDQGLIPMTNSLEEVLRNSQKMEA  
KLIGYDETPIDVALDAHGFENSKIQEPFGINCSYEVDRDSCPPRFEAVDAWSLSPLDFTGGQPSEATGDLRCDRDVLIT  
GKVDLGTARSRLREICAANSWKPPSFECCTEEGPSHLKSFTYKVVVEIEEAPEMSFEVCGSPQMKKAAAEDAEG  
ALWYLKHQRHLS

>BrDCL4

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VMTPOILLHNLQHCIFIRMEWISLLILDECHHAQEQSHPYAQILKVFYKTEGVKGPRIFGMTASPVVKGGSFQSEN  
SKSINLENLLNAKVSVESNVQLDGFVSSPIVKVYYYQTAGTEASQSTNIYENMLEDIKQRCLTSLKQIDNHQTQV  
LLNMKLLKTRTHDNLISLVNLGLWGAIQAARIQLNTRNVHQPPELENNKSKICITYLSLAAEVLSSKVAKDENS  
ELISLPALKEPFFSRKLLQLIKILSAFRIEPMKCIIFVNRIVTARTLSCILNSLKLESWKSDFLVGLSSGVKMSRKS  
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KVNEEDRMNLEITSRTSEETCPRLDDEVYRVHETGACISGSSISLLYKYCSRLPHDEFFQPKPEFQFKPVDEFGGTIC  
RITLPANAPISEIVSSLLPSIEAAKNAACKAVYKLHSLGLVNLNFPDPSNEETEDELSDDEFFDFDKVEGEACSRGELY  
EMIVPDLFKQKWDPSKSCVNLQSYIYRFVPHPADRIYKFKGLFMKSPLEAETMDFDLHLAHQRSVSVKIFPKGDA

NFDNDEIRLAERFQEVALKIIFERRELITEFVPLGLQDSFRTSKSTFYLLLPINLDASESVLFVDWATIRSCLSPIFKA  
PSGLVEDMDPPVGSHLKLANGCWSIDDVKNSVVFATHKKQFYVSDICHGRNGFSAIRKSITETHLESIYNSYGVKL  
KHPLQPLLRLKPLCYVRNLLHNRKRENLEPNELEEYFIEIPPELSQLKIKGLSKDIGSSLSLLPSVMHRMENLLVAIEL  
KHMLSASIPAEVSGHRVLEALTTEKQCQERFSLERHAVLGDAFLKFAVSRHLFLHHDRLDEGELTRRRSNAVNS  
NLFRLATRRNLQVYIRDQAFDPTQFFALGHPCRVTCDEVAMKEVHSLDKVPGLLESSTGEIRCSKGHHWLHKKTIA  
DVVEALVGAFVDSGFKAIEFLKWIGINVDFESLQVRDACVASKRYMPLTTCFDLAALESLLGYKFLHKGLLQAFI  
HPSYNRHGGGCYQRLEFLGDAVLDMYTSYFFSVFVKPKPGQLTDLRSLSVNNKALANVAVSFLQRFLFCSTYL  
HDAIKDYTNFVTASPLASGPSEGPCKPKVLGDLIESFLGALFLDCGFDLNHVWRIMLSFLDPVKNSNLQLSPVKEL  
LEYCQSYKWDQEISATKKDGAFVELKVTKSSCLTASATGRNKKESTKKAQMLTNLKAHGHIKTSNPLEDVLK  
NSIRNEAKLIGYDEEPIDVDRDGLDVENLNIQDSFEEDPVTESKTSETSSSYIIRRVLTNAPPSEKEESLPQKTIKDA  
GGSIIKTAKSLLRETCVANCWKTPEFVCCGEPHAKTFSYKVILEVVDAPNMTLECYGEAKPTKKSASEQAAQAAAL  
WCLEHTGFLRR

>RcDCL4

MPDGEADISPDSSSICTVNRIAGDDDGDECNSMPQQPEKDPRKIARKYQLELCKKALEENIIVYLTGCGKTHIAV  
LLIYELGHLIRKPLKNVCVFLAPTVALVQQVRVIEQSIDFKVGVYCGNSNHLKSHRDWEKEIEQNEVLVMTPIQLLH  
TLGHSFIKMELISLLIFDECHHAQVQSSHPYAEIMKVYKTDGDKFPRIFGMTASPVVGGKASNQANLPKSINLENL  
LDAKVYSVEDNEEELFVASPVVRIYLYAPVANEKSSSYMTYFSKLEIKRKCLELHKKADSCQSLHGLQNAKKVFI  
RMHDNVVFCLENLGFWGALQACKILLSDDHFEWNALIEAEGNIDASVCDKYLAQAANMFASVCTKDCIAFDLSSV  
EVLTEPFFSRKLLRLIGILSTFRLQPNMKGIVFVNRIVTARSLSYVLQNLKFLISWKCDFLVGVHSLGKMSRKTMS  
ILEKFKTGKLNLLIATKVGEGLDIQTCCLVVRFDPETVASFIQSRGRARMPQSEYAFVDSGNQKELDIERFRRD  
EDRMNMEISSRTSNETFVSIIEKVYKVDSEGACISSAYSISLLHHYCSKLPHDEYFDPKQFFFFDDLGGTICHILPA  
NAPVHQIVGTPQSSREAAKKDAKLKAEQLHKLGSLSNLLPHEKDVNEESMLASSEPENNEGEGVRGELHEMLVP  
AVFKESLTSENWINLHSYFIKFCVPEDRIYKKGFLFIRAPLPLEAEQMELNHLACGRYVATKLVPLGCLAFHRDE  
ITQAIYFQEMFLKVILDRSDFVPEFVTLGKNSFFESSPSFYLLLPVLLCDHGNRVTVDWETVGRCLSSPVFRCVEKEC  
LPSSDCLQLANGCRSIRDIENSLVYIPHKHFFYFITNIDRGKNARSPHKCSSTSSYMEFLIQRFGIQLKYEQPLLQAK  
PLFSLHNLHNRKEDSVTQELDEYLIDFPPELCELKIIGFSKDIGSSISLLPSIMHRENLLVAIELKSLLSASFEGAE  
VTAYRILEALTTERCQERLSLERLEILGDAFLKFAVGRHLFLLHDTLDEGELTRKRSNAVNSNLLKLASRRNLQVY  
IRDQPFDPQFFALGHPCPVICTKESEGSIHSSNRNAKQENTIEVRCRSGHHWLYKKTIA DVVEALVGAFIVDSGF  
RAATAFLKWLGIRVNIEASDVTKVCLASRTFMPLAPSIDVSSLEDSLHGFVNRLVQLQAFVHPSYNKHGGGCYQR  
LEFLGDAVLDMYLSYLSVYPKPKPGLLTDLRSALVNNRAFAIVAVDRSFNEFLICDSGNLSEAIETYVNFVKRPAVE  
KDSLEGPKCPKVLGDLVESGIGAIFLDTGFDLNCIWKMLSFDPILNSSNVLLNPFRELHEFCESHKWKLFQPTLK  
RDMNFLVEAKVTGKDICLDASANNKKEAIRIASEQIIVKLDQGYIRKSNYLEEVLRSQKTDKALIGYDETPIDI  
TAHDPIGLQNLKIQDPSCSDFNPKIRSMKLTNTCSPCFIAANIQPPSPSVMVGGQPSATVAYPTSDMDKPTSAKSR  
LHDICAANCWKPLFECCYEEGPSHLKFSYKVIVEIEAAPDMILECFGAPREKKKAAAEHAAEGALWYLQHVGYL  
TVK

Supplemental Table S2

**qRT-PCR primers:**

Target	Forward primer	Reverse primer
FCA readthrough 3'end	CTAGCAGCCATGGCAAGAAT	ACGAGGGTTCGAAGTGATTG
act2	GGCTTAAAAAGCTGGGGTTF	TTGTCACACACAAGTGCATCA
TSI	GATGGGCAAAAGCCCTCGGTTTTAAATG	CTCTACCCTTTGCATTATGAATCCTT
AMS	AGCGGAGAAATGGAACAGAAGAG	CCGGAATCAAGAGGTATGGAAG
LacS7	CAAGTGCCGTAATAATCATCTGG	TCAGGTGACAAAGGAGAAGCAC

**small RNA hybridization primers:**

Target	Primer
miR822	CATGTGCAAATGCTTCCCGCA
miR839	GGGAACGATGAAAGTTGGTA
miR171	GATATTGGCGCGCTCAATCA
ta1 siR255	TACGCTATGTTGGACTTAGAA
tas2 siR1511	AAGTATCATTCGCTTGGGA
tas3 5'D7+	TGGGGTCTTACAAGGTCAAGA
U6	AGGGCCATGCTAATCTTCTC
TSI 3'part probe1	TCTAATAAGGAGAGTCAGTACTTTGGATTAACA
TSI 3'part probe2	TGGGACTTACCTTTAGCATTCTACTAAAGCT
TSI 5'part probe AMS	AATCCATCATCCTCGGATCAAA
TSI 5'part probe2	GACCTTGCAGAGTTGAGCGCCAA

**Primers for the BiFC analyses:**

DRB4-FusionCter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTTAATGGATCATGTATACAAAAGGTCAACTG	for cloning of 35S-DRB4-YFPN/
DRB4-FusionCter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTATGGCTTACAAGACGATAGGC	for cloning of 35S-DRB4-YFP <sup>NC</sup>
DRB4-FusionNter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTTAGATCATGTATACAAAAGGTCAACTGCA	for cloning of 35S-YFP <sup>NC</sup> -DRB4
DRB4-FusionNter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTATATGGCTTACAAGACGATAGGC	for cloning of 35S-YFP <sup>NC</sup> -DRB4
DRB7.2-FusionCter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTCCATGGATCTTCTCCTCCAGAG	for cloning of 35S-DRB7.2-YFP <sup>NC</sup>
DRB7.2-FusionCter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTTTCCCACGGGTTCACTGTTACC	for cloning of 35S-DRB7.2-YFP <sup>NC</sup>
DRB7.2-FusionNter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTCCGATCTTCTCCTCCAGAGTCT	for cloning of 35S-YFP <sup>NC</sup> -DRB7.2
DRB7.2-FusionNter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTTTACACGGGTTCACTGTTA	for cloning of 35S-YFP <sup>NC</sup> -DRB7.2
DCL4-FusionCter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTTAATGCGTGACGAAGTTGACTTG	for cloning of pDCL4-DCL4-YFP <sup>NC</sup>
DCL4-FusionCter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTAGCAAGGAATCCAGAATGCTTG	for cloning of pDCL4-DCL4-YFP <sup>NC</sup>
DCL4-FusionNter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTTACGTGACGAAGTTGACTTGAGC	for cloning of pDCL4-YFP <sup>NC</sup> -DCL4
DCL4-FusionNter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTATACGCAAAAGGAATCCAGAATGC	for cloning of pDCL4-YFP <sup>NC</sup> -DCL4
EYFP <sup>N</sup> -FusionNter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTTAATGGTGAGCAAGGGCGA	for cloning of pDCL4-YFP <sup>N</sup> -DCL4
EYFP <sup>N</sup> -FusionNter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTAGCCATGATATAGACGTTGTGG	for cloning of pDCL4-YFP <sup>N</sup> -DCL4
EYFP <sup>N</sup> -FusionCter Fwd	GGGGACAGCTTTCTGTACAAAGTGGGAATGGTGAGCAAGGGCGA	for cloning of pDCL4-DCL4-YFP <sup>N</sup>
EYFP <sup>N</sup> -FusionCter Rev	GGGGACAACCTTTGTATAATAAAGTTGTTTAGGCCATGATATAGACGTTGTG	for cloning of pDCL4-DCL4-YFP <sup>N</sup>
EYFP <sup>C</sup> -FusionNter Fwd	GGGGACAAGTTTGTACAAAAAAGCAGGCTTAATGGACAAGCAGAAGAACGG	for cloning of pDCL4-YFP <sup>C</sup> -DCL4
EYFP <sup>C</sup> -FusionNter Rev	GGGGACCACTTTGTACAAGAAAGCTGGGTACTTGTACAGCTCGTCCATGC	for cloning of pDCL4-YFP <sup>C</sup> -DCL4
EYFP <sup>C</sup> -FusionCter Fwd	GGGGACAGCTTTCTGTACAAAGTGGGAGACAAGCAGAAGAAGCAGGCAT	for cloning of pDCL4-DCL4-YFP <sup>C</sup>
EYFP <sup>C</sup> -FusionCter Rev	GGGGACAACCTTTGTATAATAAAGTTGTTACTTGTACAGCTCGTCCATGC	for cloning of pDCL4-DCL4-YFP <sup>C</sup>
promoterDCL4 Fwd	GGGGACAACCTTTGTATAGAAAAGTTGGTCGAACCGAGTGACGATCA	for cloning of pDCL4-DCL4-YFP <sup>NC</sup> and pDCL4-YFP <sup>NC</sup> -DCL4
promoterDCL4 Rev	GGGGACTGCTTTTTGTACAAACTTGAATTCACGATCTCACGTCCTCCTCT	for cloning of pDCL4-DCL4-YFP <sup>NC</sup> and pDCL4-YFP <sup>NC</sup> -DCL4