

35 **Abstract**<br>36 Many mo<br>37 rice (*Oryz*<br>38 soft comr<br>39 (*Lilium lc*<br>40 componer<br>41 developm<br>42 developm 36 Many monocot plants have high social and economic value. These include grasses such as<br>37 rice (*Oryza sativa*), wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), which produce<br>38 soft commodities for many foo 37 rice (*Oryza sativa*), wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), which produce<br>38 soft commodities for many food and beverage industries, and ornamental flowers like lily<br>39 (*Lilium longiflorum*) and 38 soft commodities for many food and beverage industries, and ornamental flowers like lily<br>39 (*Lilium longiflorum*) and orchid (*Oncidium Gower Ramsey*), which represent an important<br>40 component of international flower 39 (*Lilium longiflorum*) and orchid (*Oncidium Gower Ramsey*), which represent an important<br>40 component of international flower markets. There is constant pressure to improve the<br>41 development and diversity of these spe 40 component of international flower markets. There is constant pressure to improve the development and diversity of these species with a significant emphasis on flower development, and this is particularly relevant consid development and diversity of these species with a significant emphasis on flower<br>development, and this is particularly relevant considering the impact of changing<br>environments on reproduction and thus yield. MADS-box prote development, and this is particularly relevant considering the impact of changing<br>environments on reproduction and thus yield. MADS-box proteins are a family of<br>transcription factors that contain a conserved 56 amino acid 43 environments on reproduction and thus yield. MADS-box proteins are a family of<br>44 transcription factors that contain a conserved 56 amino acid MADS-box motif. In plants,<br>45 attention has been devoted to characterisation transcription factors that contain a conserved 56 amino acid MADS-box motif. In plants,<br>attention has been devoted to characterisation of this family due to their roles in inflorescence<br>and flower development, which holds 45 attention has been devoted to characterisation of this family due to their roles in inflorescence<br>46 and flower development, which holds promise for the modification of floral architecture for<br>47 plant breeding. This ha and flower development, which holds promise for the modification of floral architecture for<br>
47 plant breeding. This has been explored in diverse angiosperms, but particularly the dicot<br>
48 model *Arabidopsis thaliana*. Th plant breeding. This has been explored in diverse angiosperms, but particularly the dicot<br>model *Arabidopsis thaliana*. The focus of this review is on the less-well characterised roles of<br>the MADS-box proteins in monocot f model *Arabidopsis thaliana*. The focus of this review is on the less-well characterised roles of<br>the MADS-box proteins in monocot flower development and how changes in MADS-box<br>proteins throughout evolution may have contr 49 the MADS-box proteins in monocot flower development and how changes in MADS-box<br>50 proteins throughout evolution may have contributed to creating a diverse range of flowers.<br>51 Examining these changes within the monocot 50 proteins throughout evolution may have contributed to creating a diverse range of flowers.<br>
51 Examining these changes within the monocots can identify the importance of certain genes<br>
52 and pinpoint those which might

51 Examining these changes within the monocots can identify the importance of certain genes<br>52 and pinpoint those which might be useful in future crop improvement and breeding strategies.<br>53<br>54 **Introduction**<br>56 **Introduct** 52 and pinpoint those which might be useful in future crop improvement and breeding strategies.<br>53<br>54 **Introduction**<br>56 **The grass family, Poaceae, diverged from other Poales around 55-70 million years ago<br>57 <b>The grass fa** 54 55 56 57 58 59 60 55 56 57 58 59 60 61 55 **Introduction**<br>56<br>57 The grass far<br>58 (Bommert *et*<br>59 determinants of<br>60 genes and providing varie<br>62 identify pathw 57 58 59 60 61 62 63 The grass family, Poaceae, diverged from other Poales around 55-70 million years ago<br>
(Bommert *et al.*, 2005). The inflorescence morphology of grasses is one of the major<br>
determinants of yield and is thus a key breeding 58 (Bommert *et al.*, 2005). The inflorescence morphology of grasses is one of the major<br>59 determinants of yield and is thus a key breeding target (Bommert *et al.*, 2005). Identifying<br>50 genes and proteins that are invol 59 determinants of yield and is thus a key breeding target (Bommert *et al.*, 2005). Identifying<br>60 genes and proteins that are involved in flower development and their behaviour in high-<br>51 yielding varieties and varietie

genes and proteins that are involved in flower development and their behaviour in high-<br>
sidentify pathways that can be targeted for the improvement of important crops.<br>
62 identify pathways that can be targeted for the im identify pathways that can be targeted for the improvement of important crops.<br>62 identify pathways that can be targeted for the improvement of important crops.<br>63<br>64 Much of our knowledge of flower structure, morphology a 62 identify pathways that can be targeted for the improvement of important crops.<br>63 Much of our knowledge of flower structure, morphology and genetics ha<br>65 through study of the model dicotyledonous plants *Arabidopsis th* 64<br>65<br>66<br>67<br>68 64 Much of our knowledge of flower structure, morphology and genetics has been gained<br>65 through study of the model dicotyledonous plants *Arabidopsis thaliana* and *Antirrhinum*<br>66 majus. Arabidopsis flowers contain 4 con 65 through study of the model dicotyledonous plants *Arabidopsis thaliana* and *Antirrhinum* majus. *Arabidopsis* flowers contain 4 concentric whorls of organs including 4 sepals, 4 petals, 6 stamen and 2 fused carpels. In 66 *majus*. *Arabidopsis* flowers contain 4 concentric whorls of organs including 4 sepals, 4 petals, 6 stamen and 2 fused carpels. In general, flowers in the grasses share a similar structure, but exhibit some key differe 67 6 stamen and 2 fused carpels. In general, flowers in the grasses share a similar structure, but exhibit some key differences. The rice spikelet comprises a single fertile floret that contains 2 68 exhibit some key differences. The rice spikelet comprises a single fertile floret that contains 69 lemma and palea in whorl 1, two lodicules in whorl 2, six stamens in whorl 3 and a pistil in<br>
70 whorl 4 (Figure 1A). In addition, there are two pairs of repressed bracts: rudimentary glumes<br>
71 and sterile lemmas (Zha whorl 4 (Figure 1A). In addition, there are two pairs of repressed bracts: rudimentary glumes<br>and sterile lemmas (Zhang *et al.*, 2013). The identity of the palea and lemma has caused a lot<br>of debate (Bell, 1991; Clifford 71 and sterile lemmas (Zhang *et al.*, 2013). The identity of the palea and lemma has caused a lot of debate (Bell, 1991; Clifford, 1987). Their morphology is very similar except for three vascular strand in the lemma comp 72 of debate (Bell, 1991; Clifford, 1987). Their morphology is very similar except for three vascular strand in the lemma compared to two in palea (Ambrose *et al.*, 2000), and a higher density of trichomes and more stoma vascular strand in the lemma compared to two in palea (Ambrose *et al.*, 2000), and a higher<br>density of trichomes and more stomata in the lemma compared to the palea (Ambrose *et al.*,<br>2000). The palea is considered a prop density of trichomes and more stomata in the lemma compared to the palea (Ambrose *et al.*, 2000). The palea is considered a prophyll in whose axil the grass flower arises (Bell, 1991).<br>Many mutant phenotypes support the i 2000). The palea is considered a prophyll in whose axil the grass flower arises (Bell, 1991).<br>
76 Many mutant phenotypes support the interpretation that the palea and lemma are equivalent to<br>
the sepals of most other flow 76 Many mutant phenotypes support the interpretation that the palea and lemma are equivalent to<br>
77 the sepals of most other flowers (Ambrose *et al.*, 2000; Bowman, 1997; Kyozuka *et al.*, 2000;<br>
78 Prasad *et al.*, 2001; 77 the sepals of most other flowers (Ambrose *et al.*, 2000; Bowman, 1997; Kyozuka *et al.*, 2000; Prasad *et al.*, 2001; Xu *et al.*, 2017). Their function is to protect the florets and kernels from pathogens and insect a Prasad *et al.*, 2001; Xu *et al.*, 2017). Their function is to protect the florets and kernels from pathogens and insect attack and supply carbohydrates to the developing seeds (Zhang *et al.*, 2013). Lodicules play a rol 79 pathogens and insect attack and supply carbohydrates to the developing seeds (Zhang *et al.*, 2013). Lodicules play a role in opening the florets and aid in co-ordination of stamen extrusion, pollination and fertilizati 80 2013). Lodicules play a role in opening the florets and aid in co-ordination of stamen extrusion, pollination and fertilization (Bommert *et al.*, 2005; Yoshida, 2012). They are believed to be equivalent to petals in o 81 extrusion, pollination and fertilization (Bommert *et al.*, 2005; Yoshida, 2012). They are believed to be equivalent to petals in other flowers (Ambrose *et al.*, 2000; Kyozuka *et al.*, 2000; Nagasawa *et al.*, 2003). believed to be equivalent to petals in other flowers (Ambrose *et al.*, 2000; Kyozuka *et al.*, 2000; Nagasawa *et al.*, 2003). Wheat, barley and rye have spikelets that are directly attached to the main axis (Figure 1B), 2000; Nagasawa *et al.*, 2003). Wheat, barley and rye have spikelets that are directly attached<br>
84 to the main axis (Figure 1B), while other grasses have long, branched inflorescences and<br>
85 spikelets that are attached t

84 to the main axis (Figure 1B), while other grasses have long, branched inflorescences and<br>85 spikelets that are attached to lateral inflorescence branches (Zhang and Yuan, 2014). A spike<br>86 can contain up to 40 florets ( 85 spikelets that are attached to lateral inflorescence branches (Zhang and Yuan, 2014). A spike<br>
86 can contain up to 40 florets (Bommert *et al.*, 2005).<br>
87<br>
88 In rice the inflorescence meristem produces several prima can contain up to 40 florets (Bommert *et al.*, 2005).<br>87<br>88 In rice the inflorescence meristem produces seve<br>produce secondary branch meristems. Both of th<br>690 (Hoshikawa, 1989). The spikelet meristem turns<br>91 produces th 88<br>89<br>90<br>91<br>92<br>93<br>94 88 In rice the inflorescence meristem produces several primary branch meristems and they<br>89 produce secondary branch meristems. Both of these in turn produce spikelet meristems<br>80 (Hoshikawa, 1989). The spikelet meristem t 89 produce secondary branch meristems. Both of these in turn produce spikelet meristems (Hoshikawa, 1989). The spikelet meristem turns into a terminal spikelet meristem and produces the flowers (Kellogg, 2007). Maize has d 90 (Hoshikawa, 1989). The spikelet meristem turns into a terminal spikelet meristem and produces the flowers (Kellogg, 2007). Maize has distinct male (tassel) and female (ear) inflorescences (Zhang and Yuan, 2014) that are produces the flowers (Kellogg, 2007). Maize has distinct male (tassel) and female (ear)<br>inflorescences (Zhang and Yuan, 2014) that are physically separated (Figure 1C) and each<br>spikelet has a pair of florets, an upper and 92 inflorescences (Zhang and Yuan, 2014) that are physically separated (Figure 1C) and each spikelet has a pair of florets, an upper and lower one (Dreni and Zhang, 2016). The Shoot Apical Meristem (SAM) gives rise to the 93 spikelet has a pair of florets, an upper and lower one (Dreni and Zhang, 2016). The Shoot<br>94 Apical Meristem (SAM) gives rise to the terminal tassel, which has long branches and<br>95 develops male flowers. The first branc 94 Apical Meristem (SAM) gives rise to the terminal tassel, which has long branches and develops male flowers. The first branches that are produced by the apical meristem are long branches, which produce a large number of 95 develops male flowers. The first branches that are produced by the apical meristem are long<br>branches, which produce a large number of short branches. Each short branch produces a<br>single lateral branch that terminates i 96 branches, which produce a large number of short branches. Each short branch produces a single lateral branch that terminates in a spikelet (Kellogg, 2007). Ears are derived from axillary shoot meristems, have no long b 97 single lateral branch that terminates in a spikelet (Kellogg, 2007). Ears are derived from axillary shoot meristems, have no long branches and develop female flowers (Bommert *et al.*, 2005). Male and female flowers in 98 axillary shoot meristems, have no long branches and develop female flowers (Bommert *et al.*, 2005). Male and female flowers initiate one pistil, three stamens, two lodicules, a palea and a lemma. The carpel primordia i 2005). Male and female flowers initiate one pistil, three stamens, two lodicules, a palea and a lemma. The carpel primordia in the male florets and the stamen primordia in the female florets are aborted after initiation t 100 lemma. The carpel primordia in the male florets and the stamen primordia in the female<br>101 florets are aborted after initiation to produce unisexual florets (Bommert *et al.*, 2005).<br>102 101 florets are aborted after initiation to produce unisexual florets (Bommert *et al.*, 2005).<br>102

Orchids are also members of the monocotyledons, in the family Orchidaceae, but are distinct<br>
from the true grasses. Orchid flowers have a zygomorphic structure, which is very different<br>
from any of the grass floret structu 104 from the true grasses. Orchid flowers have a zygomorphic structure, which is very different from any of the grass floret structures and within the orchid family there is also great diversity (Pan *et al.*, 2014). *Onci* 105 from any of the grass floret structures and within the orchid family there is also great diversity<br>
106 (Pan *et al.*, 2014). *Oncidium Gower Ramsey*, the variety that has been frequently used for<br>
107 floral character 106 (Pan *et al.*, 2014). *Oncidium Gower Ramsey*, the variety that has been frequently used for<br>107 floral characterisation, has three types of perianth organs. In the first whorl three small sepals<br>208 can be identified, 107 floral characterisation, has three types of perianth organs. In the first whorl three small sepals<br>
108 can be identified, while in the second whorl, two petals and the very distinctive lip, or<br>
109 labellum, are found can be identified, while in the second whorl, two petals and the very distinctive lip, or<br>109 labellum, are found (Figure 1D); because the sepals and petals are not significantly different<br>110 in some plant species, they a 109 labellum, are found (Figure 1D); because the sepals and petals are not significantly different<br>
110 in some plant species, they are often called tepals. The labellum is particularly interesting<br>
111 from an evolutionar in some plant species, they are often called tepals. The labellum is particularly interesting<br>111 from an evolutionary perspective since it represents a unique floral structure that may indicate<br>112 a shift in protein func 111 from an evolutionary perspective since it represents a unique floral structure that may indicate<br>
112 a shift in protein function and interactions in the highly conserved MADS-box family<br>
113 (Mondragon-Palomino and Th 112 a shift in protein function and interactions in the highly conserved MADS-box family<br>113 (Mondragon-Palomino and Theissen, 2008). It is essential for the interaction with pollinators<br>114 and different models have been

(Mondragon-Palomino and Theissen, 2008). It is essential for the interaction with pollinators<br>
and different models have been proposed to describe the protein interactions leading to<br>
115 labellum development (Mondragon-Pa and different models have been proposed to describe the protein interactions leading to<br>115 labellum development (Mondragon-Palomino and Theissen, 2008).<br>116<br>117 Lily (Lilium longiflorum) from the monocot family Liliaceae 115 labellum development (Mondragon-Palomino and Theissen, 2008).<br>116 Lily (Lilium longiflorum) from the monocot family Liliaceae produ<br>118 sepals in the first whorl, three petals in the second whorl, six stam<br>119 three fu 117<br>118<br>119<br>120<br>121<br>122<br>123 117 Lily (*Lilium longiflorum*) from the monocot family Liliaceae produce flowers that have three sepals in the first whorl, three petals in the second whorl, six stamens in the third whorl and three fused carpels in the f sepals in the first whorl, three petals in the second whorl, six stamens in the third whorl and<br>three fused carpels in the fourth whorl (Figure 1E). In *Lilium longiflorum*, most parts of the<br>sepals and petals are still co three fused carpels in the fourth whorl (Figure 1E). In *Lilium longiflorum*, most parts of the sepals and petals are still connected to each other giving the lily flowers their distinct trumpet form and distinguishing the sepals and petals are still connected to each other giving the lily flowers their distinct trumpet<br>121 form and distinguishing them from other lily species. Similar to orchids, the sepals and petals<br>122 are almost identica 121 form and distinguishing them from other lily species. Similar to orchids, the sepals and petals<br>122 are almost identical, which earned them the general name tepals (Tzeng and Yang, 2001).<br>123 Orchid flowers probably or 122 are almost identical, which earned them the general name tepals (Tzeng and Yang, 2001).<br>
123 Orchid flowers probably originated from a flower with lily-like actinomorphic perianth with<br>
124 undifferentiated whorls of t

Orchid flowers probably originated from a flower with lily-like actinomorphic perianth with<br>
124 undifferentiated whorls of tepals (Mondragon-Palomino and Theissen, 2008).<br>
125<br>
126 The MADS-box protein family<br>
127<br>
128 Th undifferentiated whorls of tepals (Mondragon-Palomino and Theissen, 2008).<br>
125<br> **126** The MADS-box protein family<br>
127<br>
128 The MADS-box acronym is derived from MCM1 (yeast), AG (*Arabidopsi*<br>
129 (Antirrhinum) and SRF (m 126<br>127<br>128<br>129<br>130<br>131<br>132 **The MADS-box protein family**<br>
127 The MADS-box acronym is der<br>
129 (Antirrhinum) and SRF (mamm<br>
130 factor family (Lawton-Rauh *et*<br>
131 proteins are involved in diverse<br>
132 development in animals and pl<br>
133 Pelucchi *e* 128<br>128<br>130<br>131<br>132<br>133<br>134 128 The MADS-box acronym is derived from MCM1 (yeast), AG (*Arabidopsis*), DEFICIENS (Antirrhinum) and SRF (mammals), the first four proteins discovered in the transcription factor family (Lawton-Rauh *et al.*, 2000; Shore (Antirrhinum) and SRF (mammals), the first four proteins discovered in the transcription<br>130 factor family (Lawton-Rauh *et al.*, 2000; Shore and Sharrocks, 1995). The MADS-box<br>131 proteins are involved in diverse developm 130 factor family (Lawton-Rauh *et al.*, 2000; Shore and Sharrocks, 1995). The MADS-box proteins are involved in diverse developmental processes in flowering plants, cardiac muscle development in animals and pheromone resp proteins are involved in diverse developmental processes in flowering plants, cardiac muscle<br>development in animals and pheromone response in yeast (Becker and Theissen, 2003;<br>Pelucchi *et al.*, 2002; Schwarz-Sommer *et al* 

development in animals and pheromone response in yeast (Becker and Theissen, 2003;<br>133 Pelucchi *et al.*, 2002; Schwarz-Sommer *et al.*, 1990).<br>134 In plants, the MADS-box genes have been proposed to be the driving force b 133 Pelucchi *et al.*, 2002; Schwarz-Sommer *et al.*, 1990).<br>134 In plants, the MADS-box genes have been propose<br>136 In plants, the MADS-box genes have been propose<br>136 In plants (Theissen and Saedler, 2001; Yamagu 135<br>136 135 In plants, the MADS-box genes have been proposed to be the driving force behind much floral diversity (Theissen and Saedler, 2001; Yamaguchi and Hirano, 2006). Therefore, better 4 136 floral diversity (Theissen and Saedler, 2001; Yamaguchi and Hirano, 2006). Therefore, better insight into their expression and function, and their conservation in different species is<br>
138 important to inform breeding strategies targeting alterations in floral architecture. The<br>
139 MADS-box domain is highly conse 138 important to inform breeding strategies targeting alterations in floral architecture. The MADS-box domain is highly conserved across different species in dicots and monocots, which makes the functional diversity of the MADS-box domain is highly conserved across different species in dicots and monocots,<br>which makes the functional diversity of the proteins extremely interesting. In this review the<br>expression patterns and functions of MADSwhich makes the functional diversity of the proteins extremely interesting. In this review the<br>expression patterns and functions of MADS-box genes relative to flower development in six<br>different monocot species including b expression patterns and functions of MADS-box genes relative to flower development in six<br>142 different monocot species including barley, wheat, maize (*Zea mays*), rice, orchid and lily<br>143 have been compared. The cereals different monocot species including barley, wheat, maize (*Zea mays*), rice, orchid and lily<br>have been compared. The cereals barley, wheat, maize and rice are mainly cultivated for food<br>purposes, while orchid and lily have

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have been compared. The cereals barley, wheat, maize and rice are mainly cultivated for food<br>
144 purposes, while orchid and lily have economic value as ornamental plants and flowers.<br>
145 **MADS-box protein structure is co** 144 purposes, while orchid and lily have economic value as ornamental plants and flowers.<br>
145<br> **146 MADS-box protein structure is conserved between diverse plant species**<br>
147<br>
16 The MADS-box genes have been divided in t 146<br>146<br>148<br>149<br>150<br>151<br>152 **MADS-box protein structure is conserved between diverse plant species**<br>147 The MADS-box genes have been divided in two groups: Type I and Typ<br>149 Theissen, 2003). Type I genes seem to have a faster evolutionary rate than 148<br>149<br>150<br>151<br>152<br>153<br>154 The MADS-box genes have been divided in two groups: Type I and Type II (Becker and<br>149 Theissen, 2003). Type I genes seem to have a faster evolutionary rate than Type II genes. The<br>150 number of duplications of Type I gene Theissen, 2003). Type I genes seem to have a faster evolutionary rate than Type II genes. The<br>
150 number of duplications of Type I genes is higher, however, even in the shorter time frame<br>
151 (Gramzow and Theissen, 2013) number of duplications of Type I genes is higher, however, even in the shorter time frame<br>
151 (Gramzow and Theissen, 2013). In plants the Type II MADS-box genes are called MIKC-<br>
152 type genes, an acronym of the 4 differ

151 (Gramzow and Theissen, 2013). In plants the Type II MADS-box genes are called MIKC-<br>152 type genes, an acronym of the 4 different domains that have been identified in all genes of this<br>153 type (Becker and Theissen, 20 type genes, an acronym of the 4 different domains that have been identified in all genes of this<br>
153 type (Becker and Theissen, 2003).<br>
154 The MIKC-type MADS-box genes consist of a MADS-box domain, an intervening domain<br> type (Becker and Theissen, 2003).<br>
154<br>
155 The MIKC-type MADS-box gene<br>
156 (I), a K-box (K) and a C-terminal<br>
157 conserved MADS-box motif has<br>
158 activity that also plays a role in<br>
159 conserved intervening domain is<br> 155<br>155<br>156<br>157<br>158<br>160<br>161 The MIKC-type MADS-box genes consist of a MADS-box domain, an intervening domain (I), a K-box (K) and a C-terminal domain (C) (Figure 2) (Theißen *et al.*, 1996). The highly conserved MADS-box motif has 60 amino acids for 156 (I), a K-box (K) and a C-terminal domain (C) (Figure 2) (Theißen *et al.*, 1996). The highly conserved MADS-box motif has 60 amino acids for a sequence-specific DNA-binding activity that also plays a role in dimerizati 157 conserved MADS-box motif has 60 amino acids for a sequence-specific DNA-binding activity that also plays a role in dimerization and accessory factor binding. The weakly conserved intervening domain is a regulatory det 158 activity that also plays a role in dimerization and accessory factor binding. The weakly conserved intervening domain is a regulatory determinant for formation of DNA-binding dimers. The keratin-like K-box is defined b 159 conserved intervening domain is a regulatory determinant for formation of DNA-binding<br>
160 dimers. The keratin-like K-box is defined by conserved regular spacing of hydrophobic<br>
161 residues and can form amphipatic he dimers. The keratin-like K-box is defined by conserved regular spacing of hydrophobic<br>161 residues and can form amphipatic helices involved in protein dimerization, which mediate<br>162 protein-protein interactions. The most 161 residues and can form amphipatic helices involved in protein dimerization, which mediate<br>
162 protein-protein interactions. The most variable domain is located at the C-terminal end. It is<br>
163 involved in transcripti 162 protein-protein interactions. The most variable domain is located at the C-terminal end. It is<br>
163 involved in transcriptional activation and formation of multimeric transcription factor<br>
164 complexes (Becker and Th involved in transcriptional activation and formation of multimeric transcription factor<br>
164 complexes (Becker and Theissen, 2003; Fornara *et al.*, 2003; Shore and Sharrocks, 1995;<br>
2165 Zhao *et al.*, 2006a).<br>
166 Depend 164 complexes (Becker and Theissen, 2003; Fornara *et al.*, 2003; Shore and Sharrocks, 1995; Zhao *et al.*, 2006a).<br>166 Dependent on the structure of the intervening (I) domain and K-box, the MIKC-type MADS-<br>168 box protei

165 Zhao *et al.*, 2006a).<br>166 Dependent on the st<br>168 box proteins can be<br>169 type proteins. The I-167<br>168<br>169 167 Dependent on the structure of the intervening (I) domain and K-box, the MIKC-type MADS-<br>168 box proteins can be further subdivided into two categories: the MIKC<sup>c</sup>-type and the MIKC<sup>\*</sup>-<br>169 type proteins. The I-domain box proteins can be further subdivided into two categories: the MIKC<sup>c</sup>-type and the MIKC\*type proteins can be further subdivided into two categories: the MIKC<sup>c</sup>-type and the MIKC\*-<br>type proteins. The I-domain in the MIKC<sup>c</sup>-type proteins is only encoded by 1 exon, while that<br> $5$ 

type proteins. The I-domain in the MIKC $c$ -type proteins is only encoded by 1 exon, while that 169 type proteins. The I-domain in the MIKC<sup>c</sup>-type proteins is only encoded by 1 exon, while that  $5$ 

in the MIKC\*-type proteins is longer, with 4 or 5 exons (Becker and Theissen, 2003; Zhao *et* al., 2006a).<br>172 Gene duplication within the MADS-box gene family is believed to be a key process during flower evolution (Theis 171 *al.*, 2006a).<br>
172<br>
173 Gene duplic<br>
174 flower evol<br>
175 several diffe<br>
176 redundancy<br>
177 duplicated g<br>
178 series of cu 173<br>174<br>175<br>176<br>177<br>178<br>179 173 Gene duplication within the MADS-box gene family is believed to be a key process during<br>174 flower evolution (Theissen and Saedler, 2001). After gene duplication, a gene can have<br>175 several different fates. If a gene 174 flower evolution (Theissen and Saedler, 2001). After gene duplication, a gene can have<br>175 several different fates. If a gene is duplicated in its entirety, this frequently leads to functional<br>176 redundancy (Pickett a 175 several different fates. If a gene is duplicated in its entirety, this frequently leads to functional<br>176 redundancy (Pickett and Meeks-Wagner, 1995; Tautz, 1992). On the other hand, one<br>177 duplicated gene can retain 176 redundancy (Pickett and Meeks-Wagner, 1995; Tautz, 1992). On the other hand, one<br>177 duplicated gene can retain the ancestral function, while the other acquires a mutation or a<br>178 series of cumulative mutations and be duplicated gene can retain the ancestral function, while the other acquires a mutation or a series of cumulative mutations and becomes a pseudogene. In another scenario, one gene retains the ancestral function, while the o 178 series of cumulative mutations and becomes a pseudogene. In another scenario, one gene<br>
179 retains the ancestral function, while the other gains a beneficial mutation that will be<br>
180 positively selected for, which 179 retains the ancestral function, while the other gains a beneficial mutation that will be positively selected for, which results in a new function. Another possibility is that both genes acquire complementary loss-of-f 180 positively selected for, which results in a new function. Another possibility is that both genes acquire complementary loss-of-function mutations that result in the preservation of both genes as they now together retai 181 acquire complementary loss-of-function mutations that result in the preservation of both<br>
182 genes as they now together retain the original functions of their single ancestor (Lynch and<br>
183 Force, 2000). This is also 182 genes as they now together retain the original functions of their single ancestor (Lynch and<br>
183 Force, 2000). This is also referred to as the duplication-degeneration-complementation (DDC)<br>
184 model (Force *et al.* 183 Force, 2000). This is also referred to as the duplication-degeneration-complementation (DDC)<br>
184 model (Force *et al.*, 1999; Prince and Pickett, 2002). These are called non-functionalization,<br>
185 neo-functionalizati model (Force *et al.*, 1999; Prince and Pickett, 2002). These are called non-functionalization,<br>neo-functionalization and sub-functionalization, respectively (Schilling *et al.*, 2015). Most<br>major difference in the MADS-bo neo-functionalization and sub-functionalization, respectively (Schilling *et al.*, 2015). Most<br>major difference in the MADS-box gene family between species are thought to have arisen<br>from gene duplications.<br>188<br>**The role o** 

# major difference in the MADS-box gene family between species are thought to have arisen<br>187 from gene duplications.<br>188<br>189 **The role of MIKC<sup>c</sup>-type MADS-box proteins in the ABCDE model of flower<br>190 development**<br>191<br>192 The role of MIKC<sup>c</sup>-type MADS-box proteins in the ABCDE model of flower

187 from gene duplications.<br>188<br>**189 The role of MIKC<sup>c</sup>.<br>190 development**<br>191<br>192 The floral organ identit<br>193 different classes based c<br>194 al. 1989 1991: Coapar 189<br>190<br>191<br>192<br>193<br>194 The role of MIKC<sup>e</sup>-type MADS-box proteins in the ABCDE model of flower<br>190 development<br>191 The floral organ identity MADS-box genes of the MIKC<sup>e</sup>-type have been divided into five<br>193 different classes based on their home 190 **development**<br>
191<br>
192 The floral org<br>
193 different class<br>
194 al., 1989, 199<br>
195 The A- and E-<br>
196 and E-class pr<br>
197 E-class compl 192<br>193<br>194<br>195<br>196<br>197<br>198 The floral organ identity MADS-box genes of the  $M$ KC<sup>c</sup>-type have been divided into five The floral organ identity MADS-box genes of the MIKC<sup>c</sup>-type have been divided into five<br>different classes based on their homeotic function: class A, B, C, D and E genes (Bowman *et<br>al.*, 1989, 1991; Coen and Meyerowitz, 1 different classes based on their homeotic function: class A, B, C, D and E genes (Bowman *et al.*, 1989, 1991; Coen and Meyerowitz, 1991; Theißen, 2001; Weigel and Meyerowitz, 1994). The A- and E-class protein complexes sp al., 1989, 1991; Coen and Meyerowitz, 1991; Theißen, 2001; Weigel and Meyerowitz, 1994).<br>The A- and E-class protein complexes specify sepals in the first whorl. Complexes of A-, B-<br>and E-class proteins specify petals in th 195 The A- and E-class protein complexes specify sepals in the first whorl. Complexes of A-, B-<br>
196 and E-class proteins specify petals in the second whorl (Honma and Goto, 2001). B-, C- and<br>
197 E-class complexes specif 196 and E-class proteins specify petals in the second whorl (Honma and Goto, 2001). B-, C- and E-class complexes specify stamens in the third whorl and C- and E-class protein complexes specify carpels in the fourth whorl 197 E-class complexes specify stamens in the third whorl and C- and E-class protein complexes specify carpels in the fourth whorl (Coen and Meyerowitz, 1991; Honma and Goto, 2001). D-class proteins specify ovules together 198 specify carpels in the fourth whorl (Coen and Meyerowitz, 1991; Honma and Goto, 2001). D-<br>
199 class proteins specify ovules together with E-class genes (Figure 3) (Angenent and Colombo,<br>
1996; Becker and Theissen, 200 class proteins specify ovules together with E-class genes (Figure 3) (Angenent and Colombo, 1996; Becker and Theissen, 2003; Colombo *et al.*, 1995; Li *et al.*, 2011; Theissen and Saedler, 2001; Wang *et al.*, 2015a). Ano 200 1996; Becker and Theissen, 2003; Colombo *et al.*, 1995; Li *et al.*, 2011; Theissen and Saedler, 2001; Wang *et al.*, 2015a). Another group of genes, phylogenetically related to the B-class genes was identified and wa 201 Saedler, 2001; Wang *et al.*, 2015a). Another group of genes, phylogenetically related to the B-class genes was identified and was named the B<sub>sister</sub> or Bs genes (Becker *et al.*, 2002). 202 B-class genes was identified and was named the Bsister or Bs genes (Becker *et al.*, 2002). 203 Genes in this class are mainly expressed in female reproductive organs, especially in the ovules (Becker *et al.*, 2002; Becker and Theissen, 2003; Munster *et al.*, 2001). All of these genes also fall into separate cl 204 ovules (Becker *et al.*, 2002; Becker and Theissen, 2003; Munster *et al.*, 2001). All of these<br>205 genes also fall into separate clades, named after the first proteins identified (Figure 4). The<br>206 genes in the SQUAgenes also fall into separate clades, named after the first proteins identified (Figure 4). The<br>
genes in the SQUA-clade all determine either inflorescence or floral meristem identity and<br>
some have additional A-type funct genes in the SQUA-clade all determine either inflorescence or floral meristem identity and<br>
207 some have additional A-type functions, while genes in the DEF/GLO clade have class B<br>
208 functions (Theißen *et al.*, 1996). 207 some have additional A-type functions, while genes in the DEF/GLO clade have class B<br>
208 functions (Theißen *et al.*, 1996). The AG-clade consists of an AG- and an AGL11 (or STK)-<br>
210 **The ABCDE model in monocots**<br>
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functions (Theißen *et al.*, 1996). The AG-clade consists of an AG- and an AGL11 (or STK)-<br>209 lineage and the class E genes are all part of the SEP/AGL2-clade.<br>210<br>211 **The ABCDE model in monocots**<br>212<br>213 MADS-box genes 209 lineage and the class E genes are all part of the SEP/AGL2-clade.<br>
210<br>
211 The ABCDE model in monocots<br>
212<br>
213 MADS-box genes involved in flower development have been s<br>
214 species. In monocots, most research has b 211<br>212<br>213<br>214<br>215<br>216<br>217 The **ABCDE model in monocots**<br>
212<br>
213 MADS-box genes involved in flo<br>
214 species. In monocots, most rese<br>
215 Comparing the expression patter<br>
216 monocot species provides inform<br>
217 evolution may have affected dif<br>
21 213<br>214<br>215<br>215<br>216<br>217<br>218<br>219 213 MADS-box genes involved in flower development have been studied in a wide variety of<br>214 species. In monocots, most research has been undertaken in rice, wheat and maize.<br>215 Comparing the expression patterns and funct species. In monocots, most research has been undertaken in rice, wheat and maize.<br>
215 Comparing the expression patterns and functions of MADS-box floral genes in different<br>
216 monocot species provides information on the 215 Comparing the expression patterns and functions of MADS-box floral genes in different monocot species provides information on the differences in their morphology and how evolution may have affected different floral str 216 monocot species provides information on the differences in their morphology and how<br>217 evolution may have affected different floral structures and floral diversity among these<br>218 species. While rice, wheat and barley evolution may have affected different floral structures and floral diversity among these<br>species. While rice, wheat and barley have a similar floral pattern, the flowers in orchid and<br>lily are very different. The emergence species. While rice, wheat and barley have a similar floral pattern, the flowers in orchid and<br>
219 lily are very different. The emergence of unique organs like the labellum in orchid and the<br>
220 differentiation between m 219 lily are very different. The emergence of unique organs like the labellum in orchid and the<br>
220 differentiation between male tassels and female ears in maize are also interesting to be<br>
221 elucidated. Comparing the e differentiation between male tassels and female ears in maize are also interesting to be<br>
221 elucidated. Comparing the expression and function of the ABCDE MADS-box genes within<br>
222 these monocot species provides an inte elucidated. Comparing the expression and function of the ABCDE MADS-box genes within<br>
222 these monocot species provides an interesting opportunity to elucidate more about their role<br>
223 in shaping these different floral

these monocot species provides an interesting opportunity to elucidate more about their role<br>
223 in shaping these different floral structures.<br>
224 **A-class genes**<br>
226 In *Arabidopsis* and *Antirrhinum*, the A-class gene in shaping these different floral structures.<br>
224<br>
225 **A-class genes**<br>
226<br>
227 In *Arabidopsis* and *Antirrhinum*, the A-cl<br>
228 transition from vegetative to reproductive<br>
229 the regulation of fruit maturation (Fornar 225<br>225<br>226<br>227<br>228<br>229<br>230 225 **A-class genes**<br>
226<br>
227 In *Arabidopsis*<br>
228 transition from<br>
229 the regulation<br>
230 some level of 6<br>
231 function (Zhar<br>
232 within the clas --<br>227<br>228<br>229<br>230<br>231<br>232<br>233 In *Arabidopsis* and *Antirrhinum*, the A-class genes *AP1* and *SQUA* are responsible for the transition from vegetative to reproductive growth, determination of floral organ identity and the regulation of fruit maturatio transition from vegetative to reproductive growth, determination of floral organ identity and<br>
229 transition of fruit maturation (Fornara *et al.*, 2004). Their orthologues in monocots have<br>
230 some level of conservatio 229 the regulation of fruit maturation (Fornara *et al.*, 2004). Their orthologues in monocots have<br>
230 some level of conservation, but there is some divergence in sequence, expression pattern and<br>
231 function (Zhang and 230 some level of conservation, but there is some divergence in sequence, expression pattern and<br>
231 function (Zhang and Yuan, 2014). In the core eudicots there are two different gene clades<br>
232 within the class A genes function (Zhang and Yuan, 2014). In the core eudicots there are two different gene clades<br>
232 within the class A genes: euAP1 and euFUL, which have arisen from a duplication event that<br>
233 coincided with the origin of th within the class A genes: euAP1 and euFUL, which have arisen from a duplication event that<br>
coincided with the origin of this angiosperm group (Litt and Irish, 2003; Shan *et al.*, 2007). In<br>
non-core eudicots and monocot 233 coincided with the origin of this angiosperm group (Litt and Irish, 2003; Shan *et al.*, 2007). In non-core eudicots and monocots, only sequences that are similar to euFUL genes have been found and these have been term 234 non-core eudicots and monocots, only sequences that are similar to euFUL genes have been<br>
235 found and these have been termed 'FUL-like' genes (Litt and Irish, 2003). The monocot FUL-<br>
27 235 found and these have been termed 'FUL-like' genes (Litt and Irish, 2003). The monocot FUL-<br>7

236 like genes fall into two successively branching clades, which indicates another duplication in<br>
237 the gene lineage (Litt and Irish, 2003).<br>
238 The FUL-like and the euFUL sequences have a highly conserved motif in t the gene lineage (Litt and Irish, 2003).<br>
238<br>
239 The FUL-like and the euFUL sequen<br>
240 (Figure 5), the FUL-like or paleoAP1<br>
241 euAP1 sequences (Litt and Irish, 2003)<br>
242 in their C-terminus: RRNa-LaLT/N<br>
243 transcri 239<br>240<br>241<br>242<br>243<br>244<br>245 239 The FUL-like and the euFUL sequences have a highly conserved motif in the C-terminus (Figure 5), the FUL-like or paleoAP1 motif (L/MPPWML), which has not been found in the euAP1 sequences (Litt and Irish, 2003). euAP1 240 (Figure 5), the FUL-like or paleoAP1 motif (L/MPPWML), which has not been found in the euAP1 sequences (Litt and Irish, 2003). euAP1 sequences have two distinct conserved motifs in their C-terminus: RRNa-LaLT/NLa and C euAP1 sequences (Litt and Irish, 2003). euAP1 sequences have two distinct conserved motifs<br>
242 in their C-terminus: RRNa-LaLT/NLa and CFAT/A. These motifs contain an acidic<br>
243 transcription activation domain and a farne in their C-terminus: RRNa-LaLT/NLa and CFAT/A. These motifs contain an acidic<br>
243 transcription activation domain and a farnesylation signal (Chen *et al.*, 2008; Fornara *et al.*,<br>
2004; Litt and Irish, 2003). Both of th transcription activation domain and a farnesylation signal (Chen *et al.*, 2008; Fornara *et al.*, 2004; Litt and Irish, 2003). Both of these motifs have not been observed in FUL-like and euFUL sequences. It is suggested t 244 2004; Litt and Irish, 2003). Both of these motifs have not been observed in FUL-like and<br>245 euFUL sequences. It is suggested that the euAP1 motif has arisen via a translational<br>246 frameshift from the euFUL/FUL-like m

euFUL sequences. It is suggested that the euAP1 motif has arisen via a translational<br>
246 frameshift from the euFUL/FUL-like motif. This frameshift may have resulted in different<br>
247 functions for the euAP1 proteins (Litt frameshift from the euFUL/FUL-like motif. This frameshift may have resulted in different<br>
247 functions for the euAP1 proteins (Litt and Irish, 2003).<br>
248 The rice genome contains four A-class genes, *OsMADS14*, *OsMADS15* 247 functions for the euAP1 proteins (Litt and Irish, 2003).<br>
248 The rice genome contains four A-class genes,  $OsM$ <br>
250  $OsMADS20$ . Northern blot and in situ hybridization<br>
251 expressed in the apical region of the floral m 249<br>250<br>251<br>252<br>253<br>254<br>255 The rice genome contains four A-class genes, *OsMADS14*, *OsMADS15*, *OsMADS18* and *OsMADS20*. Northern blot and in situ hybridization analysis showed that *OsMADS15* is expressed in the apical region of the floral merist 250 *OsMADS20*. Northern blot and in situ hybridization analysis showed that *OsMADS15* is expressed in the apical region of the floral meristem and subsequently accumulates in the developing lemma and palea (Kyozuka *et a* 251 expressed in the apical region of the floral meristem and subsequently accumulates in the developing lemma and palea (Kyozuka *et al.*, 2000). Expression becomes restricted to the palea, lemma and lodicules after diff developing lemma and palea (Kyozuka *et al.*, 2000). Expression becomes restricted to the palea, lemma and lodicules after differentiation of the spikelet organs (Figure 5B) (Kyozuka *et al.*, 2000), which is similar to *A* 253 palea, lemma and lodicules after differentiation of the spikelet organs (Figure 5B) (Kyozuka *et al.*, 2000), which is similar to *AP1* (Fornara *et al.*, 2003). T-DNA insertional lines that lead to loss-of-function m *et al.*, 2000), which is similar to *AP1* (Fornara *et al.*, 2003). T-DNA insertional lines that lead<br>
255 to loss-of-function mutants of *OsMADS15* show smaller paleas, while a single nucleotide<br>
256 mutation in *OsMADS1* to loss-of-function mutants of *OsMADS15* show smaller paleas, while a single nucleotide<br>
256 mutation in *OsMADS15* leads to degenerative paleas and occasional pseudovivipary (Wang *et*<br>
257 al., 2010; Wu *et al.*, 2017). mutation in *OsMADS15* leads to degenerative paleas and occasional pseudovivipary (Wang *et* al., 2010; Wu *et al.*, 2017). Overexpression of *OsMADS15* causes early internode elongation, shoot-born crown root development, *al.*, 2010; Wu *et al.*, 2017). Overexpression of *OsMADS15* causes early internode elongation, shoot-born crown root development, reduced plant height and early flowering (Lu *et al.*, 2012). Northern blot and in situ hy 258 shoot-born crown root development, reduced plant height and early flowering (Lu *et al.*, 2012). Northern blot and in situ hybridization analysis showed that *OsMADS14* expression is similar to that of *OsMADS15*, and 269 2012). Northern blot and in situ hybridization analysis showed that *OsMADS14* expression is<br>
260 similar to that of *OsMADS15*, and is initially detectable in the whole region of the floral<br>
261 meristem during flower 260 similar to that of *OsMADS15*, and is initially detectable in the whole region of the floral<br>261 meristem during flower development, and subsequently becomes restricted to the primordia of<br>262 glumes, lemma and palea ( meristem during flower development, and subsequently becomes restricted to the primordia of<br>262 glumes, lemma and palea (Pelucchi *et al.*, 2002). In mature flowers the expression of<br>263 *OsMADS14* is detectable in the rep 262 glumes, lemma and palea (Pelucchi *et al.*, 2002). In mature flowers the expression of *OsMADS14* is detectable in the reproductive organs (Figure 5B) (Moon *et al.*, 1999b; Pelucchi *et al.*, 2002). A loss-of-function 263 *OsMADS14* is detectable in the reproductive organs (Figure 5B) (Moon *et al.*, 1999b;<br>264 Pelucchi *et al.*, 2002). A loss-of-function T-DNA insertion mutant in *OsMADS14* showed no<br>265 phenotype in the field, while e 264 Pelucchi *et al.*, 2002). A loss-of-function T-DNA insertion mutant in *OsMADS14* showed no<br>265 phenotype in the field, while ectopic expression leads to early flowering at the callus stage<br>266 (Jeon *et al.*, 2000b; W 265 phenotype in the field, while ectopic expression leads to early flowering at the callus stage (Jeon *et al.*, 2000b; Wu *et al.*, 2017). Double mutant *osmads14osmads15* plants fail to produce secondary branches and sp 266 (Jeon *et al.*, 2000b; Wu *et al.*, 2017). Double mutant *osmads14osmads15* plants fail to produce secondary branches and spikelets and only leaf-like organs are observed (Wu *et al.*, 2017). The single mutant phenotyp 267 produce secondary branches and spikelets and only leaf-like organs are observed (Wu *et al.*, 268 2017). The single mutant phenotype of *OsMADS14* and that of the double mutant suggest that its function is largely redu 268 2017). The single mutant phenotype of *OsMADS14* and that of the double mutant suggest that<br>269 its function is largely redundant with other genes, such as *OsMADS15*. Analysis of<br>8 269 its function is largely redundant with other genes, such as *OsMADS15*. Analysis of 270 heterozygous double mutants suggests that OsMADS14 and OsMADS15 went through sub-<br>271 functionalization and acquired partially overlapping functions (Wu *et al.*, 2017). They work<br>272 together in a dose-dependent mann 271 functionalization and acquired partially overlapping functions (Wu *et al.*, 2017). They work together in a dose-dependent manner by antagonizing C-class genes and both determine floral meristem fate (Wu *et al.*, 2017 272 together in a dose-dependent manner by antagonizing C-class genes and both determine floral<br>
273 meristem fate (Wu *et al.*, 2017). OsMADS14 mainly regulates the identities of the lodicule<br>
274 and stamens, while OsMA 273 meristem fate (Wu *et al.*, 2017). OsMADS14 mainly regulates the identities of the lodicule<br>274 and stamens, while OsMADS15 is mainly responsible for the empty glumes, palea and lemma<br>275 (Wu *et al.*, 2017). *OsMADS18* 274 and stamens, while OsMADS15 is mainly responsible for the empty glumes, palea and lemma<br>
275 (Wu *et al.*, 2017). *OsMADS18* has a different expression pattern compared to the other *AP1*<br>
276 orthologues. Northern blo (Wu *et al.*, 2017). *OsMADS18* has a different expression pattern compared to the other *AP1* orthologues. Northern blot and in situ hybridization analysis revealed expression in roots, leaves and flowers with a strong si orthologues. Northern blot and in situ hybridization analysis revealed expression in roots,<br>
277 leaves and flowers with a strong signal in the inflorescence (Fornara *et al.*, 2003; Masiero *et*<br>
278 *al.*, 2002; Pelucchi leaves and flowers with a strong signal in the inflorescence (Fornara *et al.*, 2003; Masiero *et al.*, 2002; Pelucchi *et al.*, 2002). *OsMADS18* expression levels are maximal when the plant reaches the reproductive stage *al.*, 2002; Pelucchi *et al.*, 2002). *OsMADS18* expression levels are maximal when the plant reaches the reproductive stage (Fornara *et al.*, 2003), but are absent from the lodicules and the sterile glumes in mature flo reaches the reproductive stage (Fornara *et al.*, 2003), but are absent from the lodicules and the sterile glumes in mature flowers (Pelucchi *et al.*, 2002). Fornara *et al.* (2004) described an RNAi line of *OsMADS18* th 280 sterile glumes in mature flowers (Pelucchi *et al.*, 2002). Fornara *et al.* (2004) described an RNAi line of *OsMADS18* that showed no visible phenotype, while a recent RNAi line described by Wu *et al.* (2017) showed 281 RNAi line of *OsMADS18* that showed no visible phenotype, while a recent RNAi line<br>282 described by Wu *et al.* (2017) showed only a low seed setting rate. Overexpression of<br>283 *OsMADS18* induces precocious initiation described by Wu *et al.* (2017) showed only a low seed setting rate. Overexpression of *OsMADS18* induces precocious initiation of axillary shoot meristems and early transition to flowering (Fornara *et al.*, 2004). These *OsMADS18* induces precocious initiation of axillary shoot meristems and early transition to flowering (Fornara *et al.*, 2004). These results suggest that OsMADS18 is possibly not required for specifying floral organ iden 284 flowering (Fornara *et al.*, 2004). These results suggest that OsMADS18 is possibly not required for specifying floral organ identity but may be involved in promoting the differentiation of the vegetative shoot or seed required for specifying floral organ identity but may be involved in promoting the differentiation of the vegetative shoot or seed development together with OsMADS14 and OsMADS15 (Formara *et al.*, 2004; Wu *et al.*, 2017 differentiation of the vegetative shoot or seed development together with OsMADS14 and<br>
287 OsMADS15 (Fornara *et al.*, 2004; Wu *et al.*, 2017). Yeast-2-Hybrid and BiFC experiments<br>
288 have shown that OSMADS18 forms hete 287 OsMADS15 (Fornara *et al.*, 2004; Wu *et al.*, 2017). Yeast-2-Hybrid and BiFC experiments<br>
288 have shown that OsMADS18 forms heterodimers with OsMADS14, OsMADS15,<br>
289 OsMADS8, OsMADS7, OsMADS6 and OsMADS47 (Masiero have shown that OsMADS18 forms heterodimers with OsMADS14, OsMADS15, OsMADS8, OsMADS7, OsMADS6 and OsMADS47 (Masiero *et al.*, 2002; Wu *et al.*, 2017), but does not form homodimers (Wu *et al.*, 2017), revealing a conserv 289 OsMADS8, OsMADS7, OsMADS6 and OsMADS47 (Masiero *et al.*, 2002; Wu *et al.*, 2017),<br>290 but does not form homodimers (Wu *et al.*, 2017), revealing a conserved aspect between<br>291 monocots and dicots (Fornara *et al.*, 290 but does not form homodimers (Wu *et al.*, 2017), revealing a conserved aspect between monocots and dicots (Fornara *et al.*, 2004). Both OsMADS14 and OsMADS15 have been shown to interact with each other and OsMADS1, a 291 monocots and dicots (Fornara *et al.*, 2004). Both OsMADS14 and OsMADS15 have been<br>292 shown to interact with each other and OsMADS1, and can also form homodimers, (Lim *et al.*,<br>2000; Wu *et al.*, 2017). The expressio 292 shown to interact with each other and OsMADS1, and can also form homodimers, (Lim *et al.*, 2000; Wu *et al.*, 2017). The expression of *OsMADS20* was detected in shoots and seeds by RT-PCR (Lee *et al.*, 2003b), but R 2000; Wu *et al.*, 2017). The expression of *OsMADS20* was detected in shoots and seeds by<br>
294 RT-PCR (Lee *et al.*, 2003b), but RNAi lines show no observable phenotype (Wu *et al.*, 2017).<br>
295 The quadruple mutant of *o* RT-PCR (Lee *et al.*, 2003b), but RNAi lines show no observable phenotype (Wu *et al.*, 2017).<br>
295 The quadruple mutant of *osmads14 osmads15 osmads18 osmads20* does not display a more<br>
296 severe phenotype than the The quadruple mutant of *osmads14 osmads15 osmads18 osmads20* does not display a more<br>
296 severe phenotype than the double mutant *osmads14 osmads15*, suggesting that OsMADS14<br>
297 and OsMADS15 are sufficient for specifyi

296 severe phenotype than the double mutant *osmads14 osmads15*, suggesting that OsMADS14<br>297 and OsMADS15 are sufficient for specifying palea, lemma and lodicule identity in rice florets<br>298 (Wu *et al.*, 2017).<br>299 In ma 297 and OsMADS15 are sufficient for specifying palea, lemma and lodicule identity in rice florets<br>
298 (Wu *et al.*, 2017).<br>
299 In maize, *ZAP1* was identified as the *AP1* orthologue because of the sequence similarities 298 (Wu *et al.*, 2017).<br>299<br>300 In maize, *ZAP1* w.<br>301 the similar express<br>302 in male and femal<br>303 northern blot analy  $300$ <br> $301$ <br> $302$ <br> $303$ 300 In maize, *ZAP1* was identified as the *AP1* orthologue because of the sequence similarities and<br>301 the similar expression pattern to *Arabidopsis* (Mena *et al.*, 1995). *ZAP1* mRNA was detected<br>302 in male and femal 301 the similar expression pattern to *Arabidopsis* (Mena *et al.*, 1995). *ZAP1* mRNA was detected<br>302 in male and female inflorescences and the husk leaves that surround the developing ear using<br>303 northern blot analysi 302 in male and female inflorescences and the husk leaves that surround the developing ear using<br>303 northern blot analysis (Figure 5B) (Mena *et al.*, 1995). ZAP1 is expressed in lemma, palea and<br>9 303 northern blot analysis (Figure 5B) (Mena *et al.*, 1995). *ZAP1* is expressed in lemma, palea and 304 lodicules, similar to *OsMADS14* and *OsMADS15* (Li *et al.*, 2014). *ZMM4* and *ZMM15* have<br>305 also been identified as orthologues of rice *OsMADS14*; *ZMM28* is the orthologue of rice<br>*OsMADS18* (Table 1) (Li *et al* 305 also been identified as orthologues of rice *OsMADS14*; *ZMM28* is the orthologue of rice *OsMADS18* (Table 1) (Li *et al.*, 2014; Zhao *et al.*, 2011). *ZMM4* and *ZMM15* are not expressed in young tissues, but accumu 306 *OsMADS18* (Table 1) (Li *et al.*, 2014; Zhao *et al.*, 2011). *ZMM4* and *ZMM15* are not expressed in young tissues, but accumulate after the transition from vegetative to reproductive growth in developing apical and expressed in young tissues, but accumulate after the transition from vegetative to reproductive<br>growth in developing apical and lateral inflorescences (Danilevskaya *et al.*, 2008). Expression<br>of *ZMM4* and *ZMM15* was not 308 growth in developing apical and lateral inflorescences (Danilevskaya *et al.*, 2008). Expression of *ZMM4* and *ZMM15* was not found in any of the embryonic tissues, but low levels of expression in husk, stalk, mature 309 of *ZMM4* and *ZMM15* was not found in any of the embryonic tissues, but low levels of expression in husk, stalk, mature leaf and root were detected by MPSS analysis, in situ hybridization and promotor:GUS analysis (Da 310 expression in husk, stalk, mature leaf and root were detected by MPSS analysis, in situ<br>311 hybridization and promotor:GUS analysis (Danilevskaya *et al.*, 2008). The expression profile<br>312 of *ZMM15* is similar to tha 311 hybridization and promotor:GUS analysis (Danilevskaya *et al.*, 2008). The expression profile of *ZMM15* is similar to that of *ZMM4* but overall has a low expression level (Danilevskaya *et al.*, 2008). When both gene 312 of *ZMM15* is similar to that of *ZMM4* but overall has a low expression level (Danilevskaya *et al.*, 2008). When both genes are overexpressed only *ZMM14* mediates early flowering, which may suggest that *ZMM15* has

313 *al.*, 2008). When both genes are overexpressed only ZMM14 mediates early flowering, which may suggest that ZMM15 has a function similar to but weaker than ZMM14 (Danilevskaya *et al.*, 2008).<br>315 *al.*, 2008).<br>316 Th 314 may suggest that ZMM15 has a function similar to but weaker than ZMM14 (Danilevskaya *et al.*, 2008).<br>316<br>317 The expression patterns of the barley A-class genes do not correspond to those of *SQUA* and<br>318 *AP1*, impl 315 *al.*, 2008).<br>
316<br>
317 The expres<br>
318 *AP1*, impl<br>
319 hybridizati<br>
320 the express<br>
321 detectable,<br>
322 Subsequen 317<br>318<br>319<br>320<br>321<br>322<br>323 317 The expression patterns of the barley A-class genes do not correspond to those of *SQUA* and *AP1*, implying that they are not functional equivalents (Schmitz *et al.*, 2000). In situ hybridization, RT-PCR and northern *AP1*, implying that they are not functional equivalents (Schmitz *et al.*, 2000). In situ<br>
1319 hybridization, RT-PCR and northern blot analysis showed that at the awn primordium stage<br>
1320 the expression of *HvBM18* (al 319 hybridization, RT-PCR and northern blot analysis showed that at the awn primordium stage<br>320 the expression of *HvBM18* (also known as *BM3*) and *HvBM14* (also known as *BM5*) is hardly<br>321 detectable, while *HvBM15* 320 the expression of *HvBM18* (also known as *BM3*) and *HvBM14* (also known as *BM5*) is hardly<br>321 detectable, while *HvBM15* (also known as *BM8*) expression is strong (Schmitz *et al.*, 2000).<br>322 Subsequently the thr 321 detectable, while *HvBM15* (also known as *BM8*) expression is strong (Schmitz *et al.*, 2000).<br>322 Subsequently the three genes are expressed in all organ primordia and the vascular system of<br>323 the barley floret thr 322 Subsequently the three genes are expressed in all organ primordia and the vascular system of<br>323 the barley floret throughout inflorescence development (Schmitz *et al.*, 2000).  $HvBM14$  and<br>324  $HvBM15$  are specific fo 323 the barley floret throughout inflorescence development (Schmitz *et al.*, 2000). *HvBM14* and *HvBM15* are specific for these tissues, while *HvBM18* is also expressed in all other tissues, similar to its orthologue in *HvBM15* are specific for these tissues, while *HvBM18* is also expressed in all other tissues, similar to its orthologue in rice *OsMADS18* (Figure 5B) (Schmitz *et al.*, 2000). *HvBM14* shows a marked increase in transcr similar to its orthologue in rice *OsMADS18* (Figure 5B) (Schmitz *et al.*, 2000). *HvBM14*<br>shows a marked increase in transcript abundance during the induction of the reproductive<br>phase, similar to *OsMADS18* (Fornara *et* shows a marked increase in transcript abundance during the induction of the reproductive<br>327 phase, similar to *OsMADS18* (Fornara *et al.*, 2004). *HvBM14* is the equivalent of the *VRN1*<br>328 gene in other temperate cerea 327 phase, similar to *OsMADS18* (Fornara *et al.*, 2004). *HvBM14* is the equivalent of the *VRN1* gene in other temperate cereals and is generally not expressed in non-vernalized winter barleys, but is induced by vernali 328 gene in other temperate cereals and is generally not expressed in non-vernalized winter<br>329 barleys, but is induced by vernalization (Trevaskis *et al.*, 2003). Spring barley lines carrying<br>330 dominant spring VRN-HI 329 barleys, but is induced by vernalization (Trevaskis *et al.*, 2003). Spring barley lines carrying<br>330 dominant spring *VRN-H1* alleles or with homozygous recessive *VRN-H2* alleles have low<br>331 levels of *HvBM14* expre 330 dominant spring *VRN-H1* alleles or with homozygous recessive *VRN-H2* alleles have low<br>331 levels of *HvBM14* expression (Trevaskis *et al.*, 2003). Trevaskis *et al.* (2003) suggest that<br>332 *HvBM14* expression might 331 levels of *HvBM14* expression (Trevaskis *et al.*, 2003). Trevaskis *et al.* (2003) suggest that *HvBM14* expression might be controlled by activation and repression to respond to vernalization, which has been suggeste *HvBM14* expression might be controlled by activation and repression to respond to vernalization, which has been suggested previously in wheat (Sasani *et al.*, 2009; Tranquilli and Dubcovsky, 2000; Yan *et al.*, 2003).<br>33 333 vernalization, which has been suggested previously in wheat (Sasani *et al.*, 2009; Tranquilli<br>334 and Dubcovsky, 2000; Yan *et al.*, 2003).<br>335<br>336 Orthologues of the rice genes *OsMADS14*, *OsMADS15* and *OsMADS18* h

and Dubcovsky, 2000; Yan *et al.*, 2003).<br>335<br>Orthologues of the rice genes *OsMADS*<br>337 wheat and have been termed *WFUL1* 336<br>337 336 Orthologues of the rice genes *OsMADS14*, *OsMADS15* and *OsMADS18* have been found in wheat and have been termed *WFUL1* (corresponding to *VRN1*), *WFUL2* and *WFUL3* 10 337 wheat and have been termed *WFUL1* (corresponding to *VRN1*), *WFUL2* and *WFUL3*

338 respectively (Table 1)(Kinjo *et al.*, 2012). In situ hybridization, RT-PCR and qRT-PCR<br>339 determined that *WFUL3* is expressed in the spikelet primordia and throughout the spikelet<br>340 meristem. *WFUL1* and *WFUL2* a 339 determined that *WFUL3* is expressed in the spikelet primordia and throughout the spikelet<br>340 meristem. *WFUL1* and *WFUL2* are only expressed in the basal part of the spikelet meristem.<br>341 *WFUL1* is expressed in le 340 meristem. *WFUL1* and *WFUL2* are only expressed in the basal part of the spikelet meristem.<br>341 *WFUL1* is expressed in leaves at the vegetative phase, in young spikes and in all floral organs<br>342 after floral organ d *WFUL1* is expressed in leaves at the vegetative phase, in young spikes and in all floral organs<br>
after floral organ development, while the expression of *WFUL2* is reduced in stamens and<br>
undetectable in pistils (Figure 5 342 after floral organ development, while the expression of *WFUL2* is reduced in stamens and undetectable in pistils (Figure 5B) (Kinjo *et al.*, 2012). This corresponds to the expression pattern and function of *OsMADS14* 343 undetectable in pistils (Figure 5B) (Kinjo *et al.*, 2012). This corresponds to the expression pattern and function of *OsMADS14* and *OsMADS15* in rice and *ZAP1* in maize, indicating that this diversification of func 344 pattern and function of *OsMADS14* and *OsMADS15* in rice and *ZAP1* in maize, indicating<br>345 that this diversification of function has also occurred in the common ancestor of all the<br>346 mentioned grasses (Murai, 2013 that this diversification of function has also occurred in the common ancestor of all the mentioned grasses (Murai, 2013). Overexpression of *WFUL1* and *WFUL2* leads to early flowering phenotypes (Adam *et al.*, 2007; Kin 346 mentioned grasses (Murai, 2013). Overexpression of *WFUL1* and *WFUL2* leads to early<br>347 flowering phenotypes (Adam *et al.*, 2007; Kinjo *et al.*, 2012). *WFUL1* has been suggested to<br>348 have a function in phase tra 347 flowering phenotypes (Adam *et al.*, 2007; Kinjo *et al.*, 2012). *WFUL1* has been suggested to have a function in phase transition in leaves and providing flowering competency (Murai, 2013; Murai *et al.*, 2003). *WFU* have a function in phase transition in leaves and providing flowering competency (Murai, 2013; Murai *et al.*, 2003). *WFUL3* seems to have a function in floral meristem development together with *WFUL2*, while *WFUL2* has 2013; Murai *et al.*, 2003). *WFUL3* seems to have a function in floral meristem development<br>350 together with *WFUL2*, while *WFUL2* has a specialised function in development of the outer<br>351 floral organs (Kinjo *et al.* 1350 together with *WFUL2*, while *WFUL2* has a specialised function in development of the outer<br>
1351 floral organs (Kinjo *et al.*, 2012). Yeast-two or three-hybrid analysis showed that WFUL2<br>
1352 interacts with the B-c

351 floral organs (Kinjo *et al.*, 2012). Yeast-two or three-hybrid analysis showed that WFUL2 interacts with the B-class proteins WAP3 and WPI and the E-class proteins WSEP and WLHS1, while WFUL1 and WFUL2 both interact w 352 interacts with the B-class proteins WAP3 and WPI and the E-class proteins WSEP and<br>353 WLHS1, while WFUL1 and WFUL2 both interact with WSEP (Kinjo *et al.*, 2012).<br>354 *OMADS10*, the *AP1* orthologue in orchid, is almo WLHS1, while WFUL1 and WFUL2 both interact with WSEP (Kinjo *et al.*, 2012).<br>354 *OMADS10*, the *AP1* orthologue in orchid, is almost undetectable in flower bud<br>developmental stages and during flower maturation, as shown b 355<br>355<br>356<br>358<br>359<br>360<br>361 *OMADS10*, the *AP1* orthologue in orchid, is almost undetectable in flower buds of early developmental stages and during flower maturation, as shown by RT-PCR (Chang *et al.*, 2009). In mature flowers, *OMADS10* is expres 356 developmental stages and during flower maturation, as shown by RT-PCR (Chang *et al.*, 2009). In mature flowers, *OMADS10* is expressed in the labellum, carpel, anther cap and stigmatic cavity (Figure 5B) (Chang *et al* 2009). In mature flowers, *OMADS10* is expressed in the labellum, carpel, anther cap and stigmatic cavity (Figure 5B) (Chang *et al.*, 2009). It is also strongly detected in vegetative leaves. This expression pattern is di 358 stigmatic cavity (Figure 5B) (Chang *et al.*, 2009). It is also strongly detected in vegetative<br>359 leaves. This expression pattern is different from those of A-function genes in *Arabidopsis*,<br>360 *Antirrhinum* and th 359 leaves. This expression pattern is different from those of A-function genes in *Arabidopsis*,<br>360 *Antirrhinum* and the grasses, but is similar to that found in the *AP1* orthologues in lily,<br>361 *LMADS5* and *LMADS6* 360 *Antirrhinum* and the grasses, but is similar to that found in the *AP1* orthologues in lily, *LMADS5* and *LMADS6* (Chang *et al.*, 2009). Ectopic expression of *OMADS10* in *Arabidopsis* induced an early flowering ph *LMADS5* and *LMADS6* (Chang *et al.*, 2009). Ectopic expression of *OMADS10* in *Arabidopsis* induced an early flowering phenotype, but no homeotic conversions of floral organs (Chang *et al.*, 2009). Aside from *LMADS5* 362 induced an early flowering phenotype, but no homeotic conversions of floral organs (Chang *et al.*, 2009). Aside from *LMADS5* and *LMADS6* there is one more A-class MADS-box gene in lily: *LMADS7*. Northern blot analy *al.*, 2009). Aside from *LMADS5* and *LMADS6* there is one more A-class MADS-box gene in lily: *LMADS7*. Northern blot analysis showed that *LMADS5* and *LMADS6* were strongly expressed in vegetative stem and leaves and c 364 lily: *LMADS7*. Northern blot analysis showed that *LMADS5* and *LMADS6* were strongly expressed in vegetative stem and leaves and carpels and weakly in the other three floral organs (Chen *et al.*, 2008). *LMADS7* exp 265 expressed in vegetative stem and leaves and carpels and weakly in the other three floral organs (Chen *et al.*, 2008). *LMADS7* expression was absent in vegetative leaves and in any of the four organs of the flower, bu organs (Chen *et al.*, 2008). *LMADS7* expression was absent in vegetative leaves and in any of<br>367 the four organs of the flower, but was detected in the vegetative stem and the inflorescence<br>368 meristem (Chen *et al.*, 367 the four organs of the flower, but was detected in the vegetative stem and the inflorescence<br>368 meristem (Chen *et al.*, 2008). The expression pattern of *LMADS5*, 6 and 7 is mostly different<br>369 from that of other ge 368 meristem (Chen *et al.*, 2008). The expression pattern of *LMADS5*, 6 and 7 is mostly different<br>369 from that of other genes in the SQUA clade, with the exception of the A-class MADS-box<br>370 genes in orchid (Figure 5B) 369 from that of other genes in the SQUA clade, with the exception of the A-class MADS-box<br>370 genes in orchid (Figure 5B). Ectopic expression of the A-class lily genes in *Arabidopsis*<br>371 results in early flowering pheno 370 genes in orchid (Figure 5B). Ectopic expression of the A-class lily genes in *Arabidopsis*  371 results in early flowering phenotypes and floral organ conversions such as carpelloid sepals and staminoid petals (Chen *et al.*, 2008). Functional complementation analysis showed that<br>ectopic expression of these genes could rescue an *ap1* mutant phenotype in *Arabidopsis*<br>(Chen *et al.*, 2008). Based on their ex 373 ectopic expression of these genes could rescue an *ap1* mutant phenotype in *Arabidopsis*<br>374 (Chen *et al.*, 2008). Based on their expression pattern and ectopic expression analysis it was<br>375 suggested that they have

374 (Chen *et al.*, 2008). Based on their expression pattern and ectopic expression analysis it was<br>375 suggested that they have a function in flower induction, initiation and formation (Chen *et al.*,<br>376 2008).<br>377 In ri suggested that they have a function in flower induction, initiation and formation (Chen *et al.*,<br>376 2008).<br>377 In rice, only *OsMADS18* shows a different expression pattern compared to other A-class<br>379 genes, whereas al 376 2008).<br>
377<br>
378 In rice<br>
379 genes,<br>
380 also no<br>
381 duplica<br>
382 *OsMAl*<br>
383 have a 378<br>378<br>380<br>381<br>382<br>383<br>384 378 In rice, only *OsMADS18* shows a different expression pattern compared to other A-class genes, whereas all the A-class genes in barley have a different expression pattern. There is also no *OsMADS20* orthologue in barl genes, whereas all the A-class genes in barley have a different expression pattern. There is<br>also no  $OsMADS20$  orthologue in barley, maize or wheat. In maize there has been a<br>duplication event resulting in  $ZMM4$  and  $ZMM15$ , 380 also no *OsMADS20* orthologue in barley, maize or wheat. In maize there has been a duplication event resulting in *ZMM4* and *ZMM15*, and both appear to be orthologues of *OsMADS14*. In wheat, only *WFUL2* has the ascr 381 duplication event resulting in *ZMM4* and *ZMM15*, and both appear to be orthologues of *OsMADS14*. In wheat, only *WFUL2* has the ascribed A-class function. *WFUL1* and *WFUL3* have a different expression pattern and *OsMADS14*. In wheat, only *WFUL2* has the ascribed A-class function. *WFUL1* and *WFUL3* have a different expression pattern and function. The A-class genes in orchid and lily have a completely different expression patter have a different expression pattern and function. The A-class genes in orchid and lily have a<br>
sompletely different expression patterns to their orthologues in grasses and *Arabidopsis*.<br>
Loss-of-function or knock-down mut completely different expression patterns to their orthologues in grasses and *Arabidopsis*.<br>
385 Loss-of-function or knock-down mutants are currently missing for most of the A-class genes<br>
386 in maize, barley, wheat, orch Loss-of-function or knock-down mutants are currently missing for most of the A-class genes<br>
in maize, barley, wheat, orchid and lily, which could lead to a better understanding of their<br>
function.<br> **388**<br> **B-class genes**<br>

in maize, barley, wheat, orchid and lily, which could lead to a better understanding of their<br>
1888<br> **B-class genes**<br> **B** 387 function.<br>
388<br>
389 **B-class g**<br>
390<br>
391 B-class g<br>
392 2003), an<br>
393 2003; Mu 389<br>389<br>391<br>392<br>393<br>394 **B-class genes**<br>
390 **B-class genes**<br>
392 2003), and inc<br>
393 2003; Munster<br>
394 by a gene dup<br>
395 lineages: the L<br>
396 which consists 391<br>392<br>393<br>394<br>395<br>396<br>397 391 B-class genes determine the identity of petals and stamens in *Arabidopsis* (Fornara *et al.*, 2003), and increasing evidence suggests this is an ancestral function (Becker and Theissen, 2003; Munster *et al.*, 2001). 2003), and increasing evidence suggests this is an ancestral function (Becker and Theissen, 2003; Munster *et al.*, 2001). Similar to the A-class genes, the B-class genes have been shaped by a gene duplication event close 2003; Munster *et al.*, 2001). Similar to the A-class genes, the B-class genes have been shaped<br>by a gene duplication event close to the base of the crown group angiosperms, creating two<br>lineages: the DEF-like lineage whic by a gene duplication event close to the base of the crown group angiosperms, creating two<br>395 lineages: the DEF-like lineage which consists of AP3-like proteins and the GLO-like lineage,<br>396 which consists of PI-like prot 395 lineages: the DEF-like lineage which consists of AP3-like proteins and the GLO-like lineage,<br>396 which consists of PI-like proteins (Figure 6B) (Becker and Theissen, 2003; Winter *et al.*,<br>397 2002a; Zahn *et al.*, 20

which consists of PI-like proteins (Figure 6B) (Becker and Theissen, 2003; Winter *et al.*, 2002a; Zahn *et al.*, 2005b).<br>398<br>**AP3-like genes**<br>400<br>In higher eudicots, an euAP3 motif is found in the AP3-like proteins, but a 2002a; Zahn *et al.*, 2005b).<br>398<br>**AP3-like genes**<br>400<br>401 In higher eudicots, an euAl<br>eudicots and non-eudicots.<br>403 observed in their sequences<br>highly conserved sequence 399<br>400<br>401<br>402<br>403<br>404 399 *AP3-like genes*<br>400<br>401 In higher eudice<br>402 eudicots and no<br>403 observed in thei<br>404 highly conserve 401<br>402<br>403<br>404 401 In higher eudicots, an euAP3 motif is found in the AP3-like proteins, but absent in non-core eudicots and non-eudicots. Instead a highly conserved paleoAP3 motif (YGxHDLRLA) is observed in their sequences (Figure 6A) ( eudicots and non-eudicots. Instead a highly conserved paleoAP3 motif (YGxHDLRLA) is<br>
403 observed in their sequences (Figure 6A) (Kramer *et al.*, 1998). AP3-like proteins also have a<br>
404 highly conserved sequence motif i 403 observed in their sequences (Figure 6A) (Kramer *et al.*, 1998). AP3-like proteins also have a highly conserved sequence motif in the K box (Q/HYExM) (Kramer *et al.*, 1998; Tzeng and 12 404 highly conserved sequence motif in the K box (Q/HYExM) (Kramer *et al.*, 1998; Tzeng and Yang, 2001). Only one DEF-like gene has been found in most monocots, so it is presumed<br>that no gene duplication event happened here, except for orchids, where the gene duplication<br>seems to have occurred in the DEF-clade in that no gene duplication event happened here, except for orchids, where the gene duplication<br>seems to have occurred in the DEF-clade instead of the GLO-clade (Table 1) (Chen *et al.*,<br>2012). The paleoAP3 motif seems to hav seems to have occurred in the DEF-clade instead of the GLO-clade (Table 1) (Chen *et al.*, 2012). The paleoAP3 motif seems to have significant sequence diversification in the GLO-like lineage after duplication, where it ha 2012). The paleoAP3 motif seems to have significant sequence diversification in the GLO-<br>
409 like lineage after duplication, where it has been termed a PI-like motif (Figure 6A) (Kramer *et*<br>
410 *al.*, 1998; Moon *et al.* like lineage after duplication, where it has been termed a PI-like motif (Figure 6A) (Kramer *et al.*, 1998; Moon *et al.*, 1999a). The observation of these different motifs in the monocot B-<br>class MADS-box genes shows tha al., 1998; Moon *et al.*, 1999a). The observation of these different motifs in the monocot B-<br>class MADS-box genes shows that AP3 homologues were highly conserved in most monocots<br>during evolution and that they are more cl

during evolution and that they are more closely related to the lower eudicots than to the higher<br>eudicots (Tzeng and Yang, 2001).<br>414 In rice, *OsMADS16* is a member of DEF-clade and expression is detected in lodicule and<br> during evolution and that they are more closely related to the lower eudicots than to the higher<br>eudicots (Tzeng and Yang, 2001).<br>414<br>In rice, *OsMADS16* is a member of DEF-clade and expression is detected in lodicule and<br> eudicots (Tzeng and Yang, 2001).<br>
414<br>
415 In rice, *OsMADS16* is a member<br>
416 stamen primordia from initiation<br>
417 hybridization (Figure 6B) (Fornara<br>
418 DEF- and GLO-like proteins, like<br>
419 which might have originate 415<br>416<br>417<br>418<br>420<br>421 In rice, *OsMADS16* is a member of DEF-clade and expression is detected in lodicule and<br>
416 stamen primordia from initiation onwards, as revealed by RNA blot analysis and in situ<br>
417 hybridization (Figure 6B) (Fornara *e* 416 stamen primordia from initiation onwards, as revealed by RNA blot analysis and in situ<br>
417 hybridization (Figure 6B) (Fornara *et al.*, 2003; Moon *et al.*, 1999a; Nagasawa *et al.*, 2003).<br>
418 DEF- and GLO-like prot 417 hybridization (Figure 6B) (Fornara *et al.*, 2003; Moon *et al.*, 1999a; Nagasawa *et al.*, 2003).<br>418 DEF- and GLO-like proteins, like AP3 and PI in *Arabidopsis*, form obligate heterodimers,<br>419 which might have orig 418 DEF- and GLO-like proteins, like AP3 and PI in *Arabidopsis*, form obligate heterodimers,<br>419 which might have originated after the gymnosperm-angiosperm split but before the monocot-<br>420 eudicot split (Davies *et al.* which might have originated after the gymnosperm-angiosperm split but before the monocot-<br>eudicot split (Davies *et al.*, 1996; Goto and Meyerowitz, 1994; Winter *et al.*, 2002b). The<br>interaction between proteins of the G eudicot split (Davies *et al.*, 1996; Goto and Meyerowitz, 1994; Winter *et al.*, 2002b). The<br>interaction between proteins of the GLO- and the DEF-clade is conserved, as shown by the<br>interaction of OsMADS16 with OsMADS4 an interaction between proteins of the GLO- and the DEF-clade is conserved, as shown by the<br>interaction of OsMADS16 with OsMADS4 and OsMADS2 by yeast-two-hybrid analysis<br>(Moon *et al.*, 1999a; Yao *et al.*, 2008). They form interaction of OsMADS16 with OsMADS4 and OsMADS2 by yeast-two-hybrid analysis<br>
423 (Moon *et al.*, 1999a; Yao *et al.*, 2008). They form a heterodimer and may auto-regulate their<br>
424 own expression (Yadav *et al.*, 2007), (Moon *et al.*, 1999a; Yao *et al.*, 2008). They form a heterodimer and may auto-regulate their<br>
424 own expression (Yadav *et al.*, 2007), similar to AP3 and PI in *Arabidopsis* (Krizek and<br>
425 Meyerowitz, 1996). The fun 424 own expression (Yadav *et al.*, 2007), similar to AP3 and PI in *Arabidopsis* (Krizek and Meyerowitz, 1996). The function of *OsMADS16* seems to be well conserved between rice and *Arabidopsis* (Yamaguchi and Hirano, 2 *Arabidopsis* (Yamaguchi and Hirano, 2006). A loss-of-function mutant of *OsMADS16*, known as *spwl* (*superwoman1*), shows the homoetic transformation of stamens into carpels and lodicules into palea-like organs (Nagasawa Arabidopsis (Yamaguchi and Hirano, 2006). A loss-of-function mutant of *OsMADS16*,<br>
Acta and lodicules into palea-like organs (Nagasawa *et al.*, 2003). Similarly, *SILKY1*, the *AP3*<br>
orthologue in maize, is required for 427 known as *spw1 (superwoman1)*, shows the homoetic transformation of stamens into carpels<br>428 and lodicules into palea-like organs (Nagasawa *et al.*, 2003). Similarly, *SILKY1*, the *AP3*<br>429 orthologue in maize, is re and lodicules into palea-like organs (Nagasawa *et al.*, 2003). Similarly, *SILKY1*, the *AP3* orthologue in maize, is required for the normal development of lodicules and stamens. *SILKY1* is expressed in the centre of th orthologue in maize, is required for the normal development of lodicules and stamens.<br> *SILKYI* is expressed in the centre of the floral meristem after the lemma and palea primordia<br>
have initiated as well as in lodicules *SILKY1* is expressed in the centre of the floral meristem after the lemma and palea primordia<br>
have initiated as well as in lodicules and stamens throughout their development (Ambrose *et*<br>
al., 2000). A loss-of-function have initiated as well as in lodicules and stamens throughout their development (Ambrose *et al.*, 2000). A loss-of-function mutation of *SILKY1* results in homeotic transformations of stamens to carpels and lodicules to l al., 2000). A loss-of-function mutation of *SILKY1* results in homeotic transformations of stamens to carpels and lodicules to lemma- or palea-like organs (Ambrose *et al.*, 2000). OSMADS16 also seems to interact with OsMA 433 stamens to carpels and lodicules to lemma- or palea-like organs (Ambrose *et al.*, 2000).<br>434 OsMADS16 also seems to interact with OsMADS3 (C-class), OsMADS15 (A-class),<br>435 OsMADS8 (E-class) and OsMADS6 (AGL6-like) (L

0SMADS16 also seems to interact with OsMADS3 (C-class), OsMADS15 (A-class), OsMADS8 (E-class) and OsMADS6 (AGL6-like) (Lee *et al.*, 2003a).<br>
In wheat, two homeologous genes of *WAP3* (*TaMADS#51* and *TaMADS#82*) on<br>
chro 435 OsMADS8 (E-class) and OsMADS6 (AGL6-like) (Lee *et al.*, 2003a).<br>436 In wheat, two homeologous genes of *WAP3 (TaMADS#51* chromosomes 7B and 7D respectively were identified as AP3-like I<br>438 (Hama *et al.*, 2004). *WAP* 436 In wheat, two homeologous genes of *WAP3 (TaMADS#51* and *TaMADS#82)* on chromosomes 7B and 7D respectively were identified as AP3-like B-class genes (Table 1) (Hama *et al.*, 2004). *WAP3/TaMADS#51* expression is only 437 chromosomes 7B and 7D respectively were identified as AP3-like B-class genes (Table 1)<br>438 (Hama *et al.*, 2004). *WAP3/TaMADS#51* expression is only detected in young spikes at the<br>438 (Hama *et al.*, 2004). *WAP3/Ta* 438 (Hama *et al.*, 2004). *WAP3/TaMADS#51* expression is only detected in young spikes at the

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floral organ development stage, while *WAP3/TaMADS#82* expression was lower in young<br>spikes, but higher in spikes at heading stage (Figure 6B) (Hama *et al.*, 2004).<br>441 The DEF-like genes in orchid are subdivided into fou spikes, but higher in spikes at heading stage (Figure 6B) (Hama *et al.*, 2004).<br>
441 The DEF-like genes in orchid are subdivided into four different clades (Mond<br>
443 and Theissen, 2008). *OMADS3* (clade 2), one AP3-like 442<br>443<br>444<br>445<br>446<br>447<br>448 The DEF-like genes in orchid are subdivided into four different clades (Mondragon-Palomino<br>
and Theissen, 2008). *OMADS3* (clade 2), one AP3-like gene in orchid, does not contain the<br>
C-terminal motif, which differs from t and Theissen, 2008). *OMADS3* (clade 2), one AP3-like gene in orchid, does not contain the C-terminal motif, which differs from the other B-class genes found so far (Figure 6) (Hsu and Yang, 2002). The conserved K box sequ C-terminal motif, which differs from the other B-class genes found so far (Figure 6) (Hsu and Yang, 2002). The conserved K box sequence (QYQRM), however, is present (Hsu and Yang, 2002; Tsai and Chen, 2006). Its expression Yang, 2002). The conserved K box sequence (QYQRM), however, is present (Hsu and Yang, 2002; Tsai and Chen, 2006). Its expression can be detected in all four floral organs as well as in vegetative leaves as shown by a combi 2002; Tsai and Chen, 2006). Its expression can be detected in all four floral organs as well as<br>
in vegetative leaves as shown by a combination of RT-PCR and Northern analysis (Hsu and<br>
Yang, 2002) which is different from 447 in vegetative leaves as shown by a combination of RT-PCR and Northern analysis (Hsu and Yang, 2002) which is different from other B-class genes that show specific expression in flowers (Figure 6B). Yeast-two-hybrid ana Yang, 2002) which is different from other B-class genes that show specific expression in flowers (Figure 6B). Yeast-two-hybrid analysis showed that OMADS3 is able to form strong homodimers (Hsu and Yang, 2002; Tsai and Che flowers (Figure 6B). Yeast-two-hybrid analysis showed that OMADS3 is able to form strong<br>homodimers (Hsu and Yang, 2002; Tsai and Chen, 2006). Three other DEF-like genes are<br>found in orchid; *OMADS12* (clade 4), *OMADS5* ( 450 homodimers (Hsu and Yang, 2002; Tsai and Chen, 2006). Three other DEF-like genes are<br>451 found in orchid; *OMADS12* (clade 4), *OMADS5* (clade 1) with expression in sepals and petals<br>452 and *OMADS9* (clade 3) which is 451 found in orchid; *OMADS12* (clade 4), *OMADS5* (clade 1) with expression in sepals and petals<br>452 and *OMADS9* (clade 3) which is highly expressed in petals and absent in vegetative tissues;<br>453 (Figure 6B) (Chang *et* and *OMADS9* (clade 3) which is highly expressed in petals and absent in vegetative tissues ;<br>
(Figure 6B) (Chang *et al.*, 2010; Hsu *et al.*, 2015). OMADS5 and OMADS9 may play a<br>
different role in the formation of the se 453 (Figure 6B) (Chang *et al.*, 2010; Hsu *et al.*, 2015). OMADS5 and OMADS9 may play a different role in the formation of the sepal, petal and labellum (Chang *et al.*, 2010). The difference for petal and lip formation m 454 different role in the formation of the sepal, petal and labellum (Chang *et al.*, 2010). The difference for petal and lip formation may be due to the expression of *OMADS5* in the petal and its absence in the lip. OMAD difference for petal and lip formation may be due to the expression of *OMADS5* in the petal<br>and its absence in the lip. OMADS5 may have a negative role in regulating labellum<br>formation (Chang *et al.*, 2010) which was fu 456 and its absence in the lip. OMADS5 may have a negative role in regulating labellum formation (Chang *et al.*, 2010) which was further supported by the reduced expression of *OMADS5* in lip-like sepals and lip-like pet 457 formation (Chang *et al.*, 2010) which was further supported by the reduced expression of *OMADS5* in lip-like sepals and lip-like petals of peloric orchid mutants of *O. Gower Ramsey* (Chang *et al.*, 2010). OMADS5 an *OMADS5* in lip-like sepals and lip-like petals of peloric orchid mutants of *O. Gower Ramsey* (Chang *et al.*, 2010). OMADS5 and OMADS9 are able to form homodimers and heterodimers with each other and with OMADS3 (Chang 459 (Chang *et al.*, 2010). OMADS5 and OMADS9 are able to form homodimers and heterodimers<br>460 with each other and with OMADS3 (Chang *et al.*, 2010). *OMADS12* is weakly expressed in<br>461 stamen, but strongly expressed in with each other and with OMADS3 (Chang *et al.*, 2010). *OMADS12* is weakly expressed in stamen, but strongly expressed in the carpel (Hsu *et al.*, 2015). Its expression is completely absent in the sepal, petal and labell

461 stamen, but strongly expressed in the carpel (Hsu *et al.*, 2015). Its expression is completely<br>462 absent in the sepal, petal and labellum (Hsu *et al.*, 2015). This indicates that clade 4 in *O*.<br>463 *Gower Ramsey* d 462 absent in the sepal, petal and labellum (Hsu *et al.*, 2015). This indicates that clade 4 in *O.*<br>463 *Gower Ramsey* does not appear to affect perianth differentiation (Hsu *et al.*, 2015).<br>464 In lily, the *LMADS1* ge *Gower Ramsey* does not appear to affect perianth differentiation (Hsu *et al.*, 2015).<br>
464 In lily, the *LMADS1* gene is the functional counterpart of *AP3* in *Arabidopsis*<br>
466 (Tzeng and Yang, 2001) with conserved fun 465<br>466<br>467<br>468<br>469<br>471 166 In lily, the *LMADS1* gene is the functional counterpart of *AP3* in *Arabidopsis* (Table 1)<br>166 (Tzeng and Yang, 2001) with conserved function in regulating petal and stamen development.<br>167 *LMADS1* is expressed in a Transaction in regulating petal and stamen development.<br>
466 LMADS1 is expressed in all four floral whorls, but the protein is only detected in petals and<br>
468 stamens, as revealed by Western blot analysis, suggesting post *LMADS1* is expressed in all four floral whorls, but the protein is only detected in petals and<br>
468 stamens, as revealed by Western blot analysis, suggesting post-transcriptional regulation<br>
469 (Tzeng and Yang, 2001). *L* 468 stamens, as revealed by Western blot analysis, suggesting post-transcriptional regulation (Tzeng and Yang, 2001). *LMADS1* transcripts were also strongly detected in late-developing carpels (Tzeng and Yang, 2001). Yeas 469 (Tzeng and Yang, 2001). *LMADS1* transcripts were also strongly detected in late-developing carpels (Tzeng and Yang, 2001). Yeast-two-hybrid analysis showed that LMADS1 can form strong homodimers, similar to OMADS3 (Hs 2470 carpels (Tzeng and Yang, 2001). Yeast-two-hybrid analysis showed that LMADS1 can form<br>
471 strong homodimers, similar to OMADS3 (Hsu and Yang, 2002; Tsai and Chen, 2006; Tzeng<br>
2472 et al., 2004; Tzeng and Yang, 2001) 471 strong homodimers, similar to OMADS3 (Hsu and Yang, 2002; Tsai and Chen, 2006; Tzeng<br>  $et al., 2004$ ; Tzeng and Yang, 2001). The highly conserved paleoAP3 motif (YGSHDLRLA)<br>  $14$ 472 *et al.*, 2004; Tzeng and Yang, 2001). The highly conserved paleoAP3 motif (YGSHDLRLA)

was found at the C-terminus of LMADS1 (Figure 6A). Within the K box, the highly<br>
474 conserved sequence (QYEKM) was also identified (Tzeng and Yang, 2001).<br>
475<br>
476 Briefly, wheat has two *AP3* homeologues showing differe conserved sequence (QYEKM) was also identified (Tzeng and Yang, 2001).<br>475<br>Briefly, wheat has two *AP3* homeologues showing different expression p<br>indicating divergent functions. A series of duplication events in orchid ar 476<br>477<br>478<br>480<br>481<br>482 476 Briefly, wheat has two *AP3* homeologues showing different expression patterns, possibly indicating divergent functions. A series of duplication events in orchid are proposed to form 4 different clades of AP3-like B-cl indicating divergent functions. A series of duplication events in orchid are proposed to form<br>478 4 different clades of AP3-like B-class genes with functional diversification which may<br>479 contribute to the development of 4 different clades of AP3-like B-class genes with functional diversification which may<br>
479 contribute to the development of the unique orchid floral structure, the labellum. Unlike the<br>
480 A-class genes, lily AP3-like ge 479 contribute to the development of the unique orchid floral structure, the labellum. Unlike the<br>480 A-class genes, lily AP3-like genes now show more similarity with the AP3-like genes in<br>481 grasses and *Arabidopsis* th

A-class genes, lily AP3-like genes now show more similarity with the AP3-like genes in<br>
481 grasses and *Arabidopsis* than with those in orchid.<br>
482<br> **PI-like genes**<br>
484<br>
485 Several GLO-like genes have been identified i 181 grasses and *Arabidopsis* than with those in orchid.<br>
182 **PI-like genes**<br>
183 **PI-like genes**<br>
184 Several GLO-like genes have been identified in rice al., 2010; Chen et al., 2012; Chung et al., 1995;<br>
187 proteins of 483<br>484<br>485<br>486<br>487<br>488<br>489 483 *PI-like genes*<br>484 **Several GLO-**<br>486 *al.*, 2010; Che<br>487 proteins of th<br>488 (Figure 6).<br>489 In rice the PI-485<br>486<br>487<br>488<br>489<br>490<br>491 Several GLO-like genes have been identified in rice, barley, wheat, maize and lily (Chang *et al.*, 2010; Chen *et al.*, 2012; Chung *et al.*, 1995; Hama *et al.*, 2004; Munster *et al.*, 2001); proteins of the GLO-like li

ab. al., 2010; Chen *et al.*, 2012; Chung *et al.*, 1995; Hama *et al.*, 2004; Munster *et al.*, 2001);<br>proteins of the GLO-like lineage have a conserved PI-motif in their C-terminal domain<br>(Figure 6).<br>489 In rice the PI-l proteins of the GLO-like lineage have a conserved PI-motif in their C-terminal domain<br>488 (Figure 6).<br>489<br>490 In rice the PI-like genes *OsMADS2* and *OsMADS4* are mainly expressed in lodicules, stamens<br>491 and carpels (Fi 488 (Figure 6).<br>489<br>490 In rice the 1<br>491 and carpels<br>492 function of<br>493 (Kang and<br>494 RNAi know<br>495 second wh 490<br>491<br>492<br>493<br>494<br>495 190 In rice the PI-like genes *OsMADS2* and *OsMADS4* are mainly expressed in lodicules, stamens<br>
191 and carpels (Figure 6B) (Chung *et al.*, 1995; Fornara *et al.*, 2003; Kyozuka *et al.*, 2000). The<br>
192 function of *Os* 491 and carpels (Figure 6B) (Chung *et al.*, 1995; Fornara *et al.*, 2003; Kyozuka *et al.*, 2000). The function of *OsMADS2* is similar to that of PI in *Arabidopsis*, based upon RNAi analysis (Kang and An, 2005; Prasad a function of *OsMADS2* is similar to that of PI in *Arabidopsis*, based upon RNAi analysis (Kang and An, 2005; Prasad and Vijayraghavan, 2003; Yadav *et al.*, 2007; Yao *et al.*, 2008). RNAi knock-down lines of *OsMADS2* sh 493 (Kang and An, 2005; Prasad and Vijayraghavan, 2003; Yadav *et al.*, 2007; Yao *et al.*, 2008).<br>494 RNAi knock-down lines of *OsMADS2* showed continued growth of the distal region of<br>495 second whorl organs forming an e 494 RNAi knock-down lines of *OsMADS2* showed continued growth of the distal region of second whorl organs forming an elongated bract-like structure, but no apparent changes in stamen shape (Yadav *et al.*, 2007; Yao *et a* second whorl organs forming an elongated bract-like structure, but no apparent changes in<br>
496 stamen shape (Yadav *et al.*, 2007; Yao *et al.*, 2008; Yoshida *et al.*, 2007). *OsMADS2* is<br>
497 transiently expressed early 496 stamen shape (Yadav *et al.*, 2007; Yao *et al.*, 2008; Yoshida *et al.*, 2007). *OsMADS2* is<br>497 transiently expressed early in all floral tissues and later strongly expressed in early stamen<br>498 primordia as shown by transiently expressed early in all floral tissues and later strongly expressed in early stamen<br>primordia as shown by in situ hybridization (Kyozuka *et al.*, 2000; Yadav *et al.*, 2007).<br>Similar expression levels are dete primordia as shown by in situ hybridization (Kyozuka *et al.*, 2000; Yadav *et al.*, 2007).<br>
499 Similar expression levels are detected in developing lodicules and stamens, but are later<br>
500 substantially reduced in diffe 499 Similar expression levels are detected in developing lodicules and stamens, but are later substantially reduced in differentiating stamens (Kyozuka *et al.*, 2000; Yadav *et al.*, 2007). *OsMADS4* transcription activa substantially reduced in differentiating stamens (Kyozuka *et al.*, 2000; Yadav *et al.*, 2007).<br>
501 *OsMADS4* transcription activation occurs very early and uniformly during spikelet meristem<br>
initiation (Chung *et al.*, 501 *OsMADS4* transcription activation occurs very early and uniformly during spikelet meristem<br>502 initiation (Chung *et al.*, 1995; Yadav *et al.*, 2007). During floret organ development high<br>503 levels of *OsMADS4* expr 502 initiation (Chung *et al.*, 1995; Yadav *et al.*, 2007). During floret organ development high<br>
503 levels of *OsMADS4* expression occur in stamen and carpel with reduced expression in<br>
504 differentiating lodicules (Ya 503 levels of *OsMADS4* expression occur in stamen and carpel with reduced expression in differentiating lodicules (Yadav *et al.*, 2007). RNAi lines of *OsMADS4* showed no phenotypic alterations, indicating that OsMADS4 a 504 differentiating lodicules (Yadav *et al.*, 2007). RNAi lines of *OsMADS4* showed no phenotypic<br>505 alterations, indicating that OsMADS4 and OsMADS2 might be acting redundantly in stamen<br>506 specification (Yao *et al.*, 505 alterations, indicating that OsMADS4 and OsMADS2 might be acting redundantly in stamen<br>506 specification (Yao *et al.*, 2008; Yoshida *et al.*, 2007). Supporting this, in the double knock-<br>15 506 specification (Yao *et al.*, 2008; Yoshida *et al.*, 2007). Supporting this, in the double knock507 down mutants of *OsMADS2* and *OsMADS4* the stamens were transformed into carpel-like<br>508 organs (Yao *et al.*, 2008; Yoshida *et al.*, 2007). Moreover, the lodicules in these double<br>509 mutants also showed a complete organs (Yao *et al.*, 2008; Yoshida *et al.*, 2007). Moreover, the lodicules in these double<br>mutants also showed a complete homeotic conversion to bract-like organs, suggesting that<br>OsMADS4 plays a minor role in determinin

mutants also showed a complete homeotic conversion to bract-like organs, suggesting that<br>
510 OsMADS4 plays a minor role in determining lodicule identity (Yao *et al.*, 2008; Yoshida *et*<br>
511 *al.*, 2007).<br>
512 The *PI* o 510 OsMADS4 plays a minor role in determining lodicule identity (Yao *et al.*, 2008; Yoshida *et* al., 2007).<br>512 The PI orthologs ZMM18, ZMM29 and ZMM16 in maize show an expression pattern similar to that of *OsMADS2* and 11 *al.*, 2007).<br>
512<br>
513 The *PI* orth<br>
514 to that of<br>
515 orthologue<br>
516 (Munster *e*<br>
517 primordia<br>
518 lodicules ( 513<br>513<br>515<br>516<br>517<br>518<br>519 513 The *PI* orthologs *ZMM18*, *ZMM29* and *ZMM16* in maize show an expression pattern similar<br>514 to that of *OsMADS2* and *OsMADS4* (Figure 6B) (Fornara *et al.*, 2003). *ZMM16* is the<br>515 orthologue of *OsMADS2*, while 514 to that of *OsMADS2* and *OsMADS4* (Figure 6B) (Fornara *et al.*, 2003). *ZMM16* is the orthologue of *OsMADS2*, while *ZMM18* and *ZMM29* are orthologous to *OsMADS4* (Table 1) (Munster *et al.*, 2001). These maize ge orthologue of *OsMADS2*, while *ZMM18* and *ZMM29* are orthologous to *OsMADS4* (Table 1)<br>
(Munster *et al.*, 2001). These maize genes are expressed in lodicules, stamens and carpel<br>
primordia in male and female infloresce 516 (Munster *et al.*, 2001). These maize genes are expressed in lodicules, stamens and carpel primordia in male and female inflorescences and later are restricted only to stamen and lodicules (Whipple *et al.*, 2004). ZMM primordia in male and female inflorescences and later are restricted only to stamen and lodicules (Whipple *et al.*, 2004). ZMM16 was also weakly detected in vegetative organs (Munster *et al.*, 2001). The observation of s 518 lodicules (Whipple *et al.*, 2004). *ZMM16* was also weakly detected in vegetative organs (Munster *et al.*, 2001). The observation of some different expression patterns of *ZMM16* from *ZMM18* and *ZMM29* suggest that 519 (Munster *et al.*, 2001). The observation of some different expression patterns of *ZMM16* from *ZMM18* and *ZMM29* suggest that different degrees of selection pressures led to a functional diversification of the genes 520 from *ZMM18* and *ZMM29* suggest that different degrees of selection pressures led to a functional diversification of the genes (Munster *et al.*, 2001). The gene pair *ZMM18* and *ZMM29* appear to have originated by a 521 functional diversification of the genes (Munster *et al.*, 2001). The gene pair *ZMM18* and *ZMM29* appear to have originated by a gene duplication event (Munster *et al.*, 2001). Using an electrophoretic mobility shif *ZMM29* appear to have originated by a gene duplication event (Munster *et al.*, 2001). Using<br>
an electrophoretic mobility shift assay (EMSA), Whipple *et al.* (2004) showed that ZMM16<br>
forms obligate heterodimers to bind 523 an electrophoretic mobility shift assay (EMSA), Whipple *et al.* (2004) showed that ZMM16 forms obligate heterodimers to bind DNA. They also showed that neither SILKY1, nor ZMM16 alone could bind DNA, while SILKY1 and 524 forms obligate heterodimers to bind DNA. They also showed that neither SILKY1, nor ZMM16 alone could bind DNA, while SILKY1 and ZMM16 together could bind DNA, indicating that the heterodimer is necessary for DNA bindi ZMM16 alone could bind DNA, while SILKY1 and ZMM16 together could bind DNA, indicating that the heterodimer is necessary for DNA binding. *WPI1* and *WPI2* in wheat are orthologous to *OsMADS4* and *OsMADS2*, respectively. indicating that the heterodimer is necessary for DNA binding. *WPI1* and *WPI2* in wheat are orthologous to *OsMADS4* and *OsMADS2*, respectively. *WPI1* is expressed in the primordia of the stamen and lodicules as shown b orthologous to *OsMADS4* and *OsMADS2*, respectively. *WPII* is expressed in the primordia of<br>the stamen and lodicules as shown by in situ analysis (Table 1, Figure 6B) (Hama *et al.*,<br>2004). The alloplasmic wheat with a d the stamen and lodicules as shown by in situ analysis (Table 1, Figure 6B) (Hama *et al.*, 2004). The alloplasmic wheat with a deficiency of *WPII* showed pistillody, the change of stamens into pistil-like structures, sugg

2004). The alloplasmic wheat with a deficiency of *WPII* showed pistillody, the change of stamens into pistil-like structures, suggesting that WPII plays a role in floral organ identity (Hama *et al.*, 2004).<br>
532 *OMADS8* 530 stamens into pistil-like structures, suggesting that WPI1 plays a role in floral organ identity<br>
531 (Hama *et al.*, 2004).<br>
532 *OMADS8* is the only GLO-like gene identified in *O. Gower Ramsey* (Table 1) with expres 531 (Hama *et al.*, 2004).<br>532 *OMADS8* is the only<br>534 detected in vegetativ<br>535 *et al.*, 2015). OMAI<br>536 OMADS9, while it<br>537 Ectopic expression o 533<br>533<br>535<br>536<br>537<br>538<br>538 *OMADS8* is the only GLO-like gene identified in *O. Gower Ramsey* (Table 1) with expression detected in vegetative leaves, roots and all floral organs (Figure 6B) (Chang *et al.*, 2010; Hsu *et al.*, 2015). OMADS8 was una detected in vegetative leaves, roots and all floral organs (Figure 6B) (Chang *et al.*, 2010; Hsu *et al.*, 2015). OMADS8 was unable to form homodimers or heterodimers with OMADS5 or OMADS9 , while it does however form het *et al.*, 2015). OMADS8 was unable to form homodimers or heterodimers with OMADS5 or OMADS9, while it does however form heterodimers with OMADS3 (Chang *et al.*, 2010). Ectopic expression of *OMADS8* in *Arabidopsis* conve 536 OMADS9, while it does however form heterodimers with OMADS3 (Chang *et al.*, 2010).<br>537 Ectopic expression of *OMADS8* in *Arabidopsis* converted sepals into petal-like organs (Chang<br>*et al.*, 2010). Based on these fin 537 Ectopic expression of *OMADS8* in *Arabidopsis* converted sepals into petal-like organs (Chang *et al.*, 2010). Based on these findings in *O. Gower Ramsey*, Chang et al. (2010) proposed that the presence of at least O *et al.*, 2010). Based on these findings in *O. Gower Ramsey*, Chang et al. (2010) proposed that<br>the presence of at least OMADS3/8/5 and/or OMADS9 is required for sepal and petal<br>16 539 the presence of at least OMADS3/8/5 and/or OMADS9 is required for sepal and petal

formation, whereas the presence of OMADS3/8/9 and the absence of OMADS5 are likely to<br>541 be required for labellum formation (Chang *et al.*, 2010).<br>542 *LMADS8* and *LMADS9* were identified as the *PI* orthologs in *Liliu* be required for labellum formation (Chang *et al.*, 2010).<br>
542 *LMADS8* and *LMADS9* were identified as the *PI* ortho<br>
544 (Chen *et al.*, 2012). qRT-PCR analysis revealed that *LM*<br>
and second whorl tepals in young and 543<br>544<br>545<br>546<br>548<br>549 *LMADS8* and *LMADS9* were identified as the *PI* orthologs in *Lilium longiflorum* (Table 1)<br>
(Chen *et al.*, 2012). qRT-PCR analysis revealed that *LMADS8* is highly expressed in the first<br>
and second whorl tepals in you 544 (Chen *et al.*, 2012). qRT-PCR analysis revealed that *LMADS8* is highly expressed in the first<br>545 and second whorl tepals in young and mature flowers, but is absent in vegetative leaves, roots<br>546 and stem (Chen *et* and second whorl tepals in young and mature flowers, but is absent in vegetative leaves, roots<br>
and stem (Chen *et al.*, 2012). The expression pattern of *LMADS9* is very similar to that of<br> *LMADS8* (Figure 6B). As seen i 546 and stem (Chen *et al.*, 2012). The expression pattern of *LMADS9* is very similar to that of *LMADS8* (Figure 6B). As seen in *Arabidopsis* AP3 and PI, and OsMADS4 and OsMADS16 in rice, LMADS8 and LMADS9 are able to f *LMADS8* (Figure 6B). As seen in *Arabidopsis* AP3 and PI, and OsMADS4 and OsMADS16<br>in rice, LMADS8 and LMADS9 are able to form heterodimers with the AP3-like LMADS1<br>proteins, and can also form homodimers and heterodimers in rice, LMADS8 and LMADS9 are able to form heterodimers with the AP3-like LMADS1<br>proteins, and can also form homodimers and heterodimers with each other as shown by yeast-<br>two-hybrid analysis (Chen *et al.*, 2012). The f proteins, and can also form homodimers and heterodimers with each other as shown by yeast-<br>two-hybrid analysis (Chen *et al.*, 2012). The function of LMADS8 and LMADS9 seems to be<br>involved in tepal formation and to a minor two-hybrid analysis (Chen *et al.*, 2012). The function of LMADS8 and LMADS9 seems to be<br>involved in tepal formation and to a minor extent in early stamen formation (Chen *et al.*,<br>2012). Interestingly, *LMADS9* is a trunc 551 involved in tepal formation and to a minor extent in early stamen formation (Chen *et al.*, 2012). Interestingly, *LMADS9* is a truncated version of *LMADS8*, missing the PI-motif in the C-terminal region (Figure 6A) ( 2012). Interestingly, *LMADS9* is a truncated version of *LMADS8*, missing the PI-motif in the<br>553 C-terminal region (Figure 6A) (Chen *et al.*, 2012). Ectopic expression of *LMADS8* and<br>554 *LMADS9* in *Arabidopsis* parti C-terminal region (Figure 6A) (Chen *et al.*, 2012). Ectopic expression of *LMADS8* and *LMADS9* in *Arabidopsis* partially converts sepals into petal-like organs (Chen *et al.*, 2012). Overexpression of *LMADS8* in the *p LMADS9* in *Arabidopsis* partially converts sepals into petal-like organs (Chen *et al.*, 2012).<br>
555 Overexpression of *LMADS8* in the *pi* mutant of *Arabidopsis* completely rescued the<br>
phenotype, while overexpression

Overexpression of *LMADS8* in the *pi* mutant of *Arabidopsis* completely rescued the phenotype, while overexpression of *LMADS9* only partially rescued the phenotype (Chen *et al.*, 2012).<br>558 Overall, the PI-like B-class phenotype, while overexpression of *LMADS9* only partially rescued the phenotype (Chen *et* al., 2012).<br>558<br>Overall, the PI-like B-class genes in the grasses seem to have a conserved expression pattern<br>560 and function. On 557 *al.*, 2012).<br>
558 Overall, th<br>
560 and function<br>
561 interaction<br>
562 floral struc<br>
563 defining Pl<br>
564 and, possit 559<br>560<br>561<br>562<br>563<br>565 559 Overall, the PI-like B-class genes in the grasses seem to have a conserved expression pattern<br>560 and function. Only one PI-like gene is found in orchid, with a different protein-protein<br>561 interaction pattern and fu and function. Only one PI-like gene is found in orchid, with a different protein-protein<br>561 interaction pattern and function, indicating that the B-class genes are essential for the unique<br>562 floral structure of orchids interaction pattern and function, indicating that the B-class genes are essential for the unique<br>
floral structure of orchids (Chang *et al.*, 2010). Even though LMADS9 does not have the<br>
defining PI-motif at its C-terminu floral structure of orchids (Chang *et al.*, 2010). Even though LMADS9 does not have the defining PI-motif at its C-terminus, it does not seem to have lost its interaction possibilities and, possibly may have retained its defining PI-motif at its C-terminus, it does not seem to have lost its interaction possibilities<br>
and, possibly may have retained its function (Chen *et al.*, 2012).<br>
565<br> **The Bsister-genes are phylogenetically closely re** 

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9564 and, possibly may have retained its function (Chen *et al.*, 2012).<br>
565<br>
566 **The Bsister-genes are phylogenetically closely related to t<br>
different functions<br>
569 Close relatives of B-class genes have been identifie** 566<br>567<br>568<br>569<br>571<br>572 567<br>568<br>569<br>570<br>571<br>572<br>573 The Baister-genes are phylogenetically closely related to the B-class genes but have different functions<br>569<br>Close relatives of B-class genes have been identified in various species including rice, maize, barley and wheat 568 **different functions**<br>569 Close relatives of B-<br>571 barley and wheat are<br>572 female reproductive<br>573 by gene duplication 570<br>571<br>572<br>573 570 Close relatives of B-class genes have been identified in various species including rice, maize, barley and wheat and have been termed the  $B_{\text{sister}}(B_s)$  genes. They are mainly expressed in female reproductive organs, barley and wheat and have been termed the  $B<sub>sister</sub>$  ( $B<sub>s</sub>$ ) genes. They are mainly expressed in 571 barley and wheat and have been termed the  $B_{\text{sister}}(B_s)$  genes. They are mainly expressed in female reproductive organs, especially ovules. The two lineages were most likely generated by gene duplication (Becker and T 572 female reproductive organs, especially ovules. The two lineages were most likely generated<br>573 by gene duplication (Becker and Theissen, 2003; Munster *et al.*, 2001). Compared with the B-<br><sup>17</sup> 573 by gene duplication (Becker and Theissen, 2003; Munster *et al.*, 2001). Compared with the B-

class genes, B<sub>sister</sub> genes share a shorter I domain, a sub-terminal PI-motif-derived sequence<br>and in some cases a paleoAP3 motif in the C-terminal region (Figure 7A) (Becker *et al.*,<br>2002). In *Arabidopsis*, two B<sub>sist</sub> 575 and in some cases a paleoAP3 motif in the C-terminal region (Figure 7A) (Becker *et al.*, 2002). In *Arabidopsis*, two  $B_{\text{sister}}$  genes have been identified, *ABS* and *GOA* (Becker *et al.*, 2002; Mizzotti *et al.*, 2002). In *Arabidopsis*, two B<sub>sister</sub> genes have been identified, ABS and GOA (Becker *et al.*, 2002). In *Arabidopsis*, two B<sub>sister</sub> genes have been identified, *ABS* and *GOA* (Becker *et al.*, 2002; Mizzotti *et al.*, 2012; Nesi *et al.*, 2002). *ABS* is expressed in the endothelial layer of the inner integuments 2002; Mizzotti *et al.*, 2012; Nesi *et al.*, 2002). *ABS* is expressed in the endothelial layer of the<br>
inner integuments of mature ovules and is necessary for inner integument differentiation (Nesi<br> *et al.*, 2002). *GOA* 578 inner integuments of mature ovules and is necessary for inner integument differentiation (Nesi<br>
579 *et al.*, 2002). GOA has a broad expression pattern in ovule primordia and in ovules, which<br>
580 later is restricted *et al.*, 2002). *GOA* has a broad expression pattern in ovule primordia and in ovules, which<br>1580 later is restricted to the outer integuments (Prasad *et al.*, 2010). It has functions in ovule outer<br>1581 integument devel

1580 later is restricted to the outer integuments (Prasad *et al.*, 2010). It has functions in ovule outer integument development and the regulation of fruit longitudinal growth (Prasad *et al.*, 2010; Yang *et al.*, 2012) integument development and the regulation of fruit longitudinal growth (Prasad *et al.*, 2010;<br>
582 Yang *et al.*, 2012).<br>
583<br>
584 The Bsister genes form three subclades in monocots: OsMADS29, OsMADS30 and<br>
585 OsMADS31 ( 582 Yang *et al.*, 2012).<br>583<br>584 The Bsister genes<br>585 OsMADS31 (Yang<br>586 genome (Table 1).<br>587 developing seeds, 789 7B) (Yang *et al.*, results in reduced 584<br>585<br>586<br>587<br>588<br>589<br>590 The Bsister genes form three subclades in monocots: OsMADS29, OsMADS30 and<br>585 OsMADS31 (Yang *et al.*, 2012), which are named after the three B<sub>sister</sub> genes found in the rice<br>586 genome (Table 1). Expression analysis sh 585 OsMADS31 (Yang *et al.*, 2012), which are named after the three B<sub>sister</sub> genes found in the rice<br>586 genome (Table 1). Expression analysis showed that *OsMADS29* expression is restricted to<br>587 developing seeds, while genome (Table 1). Expression analysis showed that *OsMADS29* expression is restricted to developing seeds, while *OsMADS30* is expressed throughout all organs in the plant (Figure 7B) (Yang *et al.*, 2012). Suppressed expr developing seeds, while *OsMADS30* is expressed throughout all organs in the plant (Figure 7B) (Yang *et al.*, 2012). Suppressed expression of *OsMADS29* by an antisense construct results in reduced and delayed cell degrad 7B) (Yang *et al.*, 2012). Suppressed expression of *OsMADS29* by an antisense construct<br>results in reduced and delayed cell degradation of the nucellar projection, abnormal<br>endosperm development and altered seed morpholog 589 results in reduced and delayed cell degradation of the nucellar projection, abnormal<br>590 endosperm development and altered seed morphology (Yin and Xue, 2012), indicating that<br>591 *OsMADS29* is important for the degra 690 endosperm development and altered seed morphology (Yin and Xue, 2012), indicating that  $OsMADS29$  is important for the degradation of the nucellar projection and the nucellus. Yeast-two-hybrid analysis showed that OsMADS 591 *OsMADS29* is important for the degradation of the nucellar projection and the nucellus.<br>592 Yeast-two-hybrid analysis showed that OsMADS29 interacts with all five E-class MADS-box<br>593 genes and both AGL6-like MADS-box S92 Yeast-two-hybrid analysis showed that OsMADS29 interacts with all five E-class MADS-box genes and both AGL6-like MADS-box genes (Nayar *et al.*, 2014). It also interacts with A-class OsMADS14 and OsMADS18, C-class OsM spaces and both AGL6-like MADS-box genes (Nayar *et al.*, 2014). It also interacts with A-<br>class OsMADS14 and OsMADS18, C-class OsMADS3 and B<sub>sister</sub> protein OsMADS31 and<br>forms homodimers (Nayar *et al.*, 2014). *OsMADS30* class OsMADS14 and OsMADS18, C-class OsMADS3 and B<sub>sister</sub> protein OsMADS31 and<br>595 forms homodimers (Nayar *et al.*, 2014). *OsMADS30* lacks the characteristic B<sub>sister</sub> motifs<br>696 (Becker *et al.*, 2002; Yang *et al.*, 595 forms homodimers (Nayar *et al.*, 2014). *OsMADS30* lacks the characteristic B<sub>sister</sub> motifs (Becker *et al.*, 2002; Yang *et al.*, 2012) and has a different C-terminal due to the insertion of a mobile element (OsME) 596 (Becker *et al.*, 2002; Yang *et al.*, 2012) and has a different C-terminal due to the insertion of a<br>597 mobile element (OsME), which has altered function and expression profile (Figure 7A)<br>598 (Schilling *et al.*, 20 597 mobile element (OsME), which has altered function and expression profile (Figure 7A)<br>598 (Schilling *et al.*, 2015). In maize, *ZMM17* has been identified as a B<sub>sister</sub> gene; *ZMM17* is<br>599 expressed in all organ pri 598 (Schilling *et al.*, 2015). In maize, *ZMM17* has been identified as a B<sub>sister</sub> gene; *ZMM17* is<br>
599 expressed in all organ primordia of the female spikelet, but later restricted to the ovule and the<br>
400 developing 599 expressed in all organ primordia of the female spikelet, but later restricted to the ovule and the developing silk as determined by northern hybridization analysis (Becker *et al.*, 2002; Yang *et al.*, 2012). *WBsis* 600 developing silk as determined by northern hybridization analysis (Becker *et al.*, 2002; Yang *et al.*, 2012). *WBsis* was classified as a B<sub>sister</sub> gene and part of *OsMADS29*-like clade in wheat because of the high 601 *al.*, 2012). *WBsis* was classified as a B<sub>sister</sub> gene and part of *OsMADS29*-like clade in wheat because of the high sequence similarity with *OsMADS29* and *OsMADS31* (Yamada et al., 2009). *WBsis* is expressed in 602 because of the high sequence similarity with *OsMADS29* and *OsMADS31* (Yamada et al., 2009). *WBsis* is expressed in the endothelial layer of the inner integument of the ovule, similar to *ABS* in *Arabidopsis*, weak 2009). *WBsis* is expressed in the endothelial layer of the inner integument of the ovule,<br>
similar to *ABS* in *Arabidopsis*, weak expression is also detected in the nucellus and the outer<br>
integument (Mizzotti *et al.*, 604 similar to *ABS* in *Arabidopsis*, weak expression is also detected in the nucellus and the outer<br>integument (Mizzotti *et al.*, 2012; Yamada *et al.*, 2009; Yang *et al.*, 2012).<br>606 605 integument (Mizzotti *et al.*, 2012; Yamada *et al.*, 2009; Yang *et al.*, 2012).

607 All B<sub>sister</sub> genes discussed here show a similar expression pattern, except *OsMADS30* which<br>608 also has a diverged function. No B<sub>sister</sub> genes have been thoroughly investigated in barley,<br>610 **C**- **and D-class gene** 

608 also has a diverged function. No B<sub>sister</sub> genes have been thoroughly investigated in barley,<br>609 orchid and lily.<br>610 **C**- **and D-class genes**<br>612 **C-** class genes in eudicots specify the plant reproductive organs al 609 orchid and lily.<br>
610<br>
611 **C- and D-class**<br>
612<br>
613 **C-class genes i**<br>
614 with the B-class<br>
615 negative regulat<br>
616 2015b) Upon t 611<br>612<br>613<br>614<br>615<br>616 611 **C- and D-class genes**<br>612 <br>C-class genes in eudie<br>614 with the B-class genes<br>615 negative regulation of<br>616 2015b). Upon the dise<br>617 *Petunia* in regulating of<br>618 function (Angenent *et* --- 613<br>614 615<br>616 617 618 619 613 C-class genes in eudicots specify the plant reproductive organs alone (carpels) or together with the B-class genes (stamens) (Fornara *et al.*, 2003). They also seem to be involved in the negative regulation of A-clas with the B-class genes (stamens) (Fornara *et al.*, 2003). They also seem to be involved in the negative regulation of A-class MADS-box genes (Gustafson-Brown *et al.*, 1994; Wang *et al.*, 2015b). Upon the discovery of th 615 negative regulation of A-class MADS-box genes (Gustafson-Brown *et al.*, 1994; Wang *et al.*, 2015b). Upon the discovery of the function of the MADS-box genes *FBP7* and *FBP11* in *Petunia* in regulating ovule organ i 616 2015b). Upon the discovery of the function of the MADS-box genes *FBP7* and *FBP11* in *Petunia* in regulating ovule organ identity, the ABC model was extended to incorporate a D function (Angenent *et al.*, 1995; Colo *Petunia* in regulating ovule organ identity, the ABC model was extended to incorporate a D<br>function (Angenent *et al.*, 1995; Colombo *et al.*, 1995). D-gene function is involved in the<br>determination of the identity of th film function (Angenent *et al.*, 1995; Colombo *et al.*, 1995). D-gene function is involved in the determination of the identity of the central meristem, the progenitor tissue of the placenta and the ovules (Angenent and determination of the identity of the central meristem, the progenitor tissue of the placenta and<br>
the ovules (Angenent and Colombo, 1996). Both C- and D-class genes belong to the AG-like<br>
subfamily and have arisen through

the ovules (Angenent and Colombo, 1996). Both C- and D-class genes belong to the AG-like<br>subfamily and have arisen through a gene duplication event close to base of the angiosperm<br>emergence (Becker and Theissen, 2003).<br>62 621 subfamily and have arisen through a gene duplication event close to base of the angiosperm<br>622 emergence (Becker and Theissen, 2003).<br>623 C- and D-class proteins can be distinguished by the structure of the N-terminal emergence (Becker and Theissen, 2003).<br>623 C- and D-class proteins can be distinguis<br>625 box. In D-lineage, a glutamine at position<br>626 C-lineage (Figures 7 and 8) (Dreni *et al.*,<br>627 also have a non-polar hydrophobic res 624<br>625<br>626<br>627<br>628<br>629<br>630 624 C- and D-class proteins can be distinguished by the structure of the N-terminal part of the K-<br>625 box. In D-lineage, a glutamine at position 105 is conserved, while this residue is not found in<br>626 C-lineage (Figures 625 box. In D-lineage, a glutamine at position 105 is conserved, while this residue is not found in C-lineage (Figures 7 and 8) (Dreni *et al.*, 2007; Kramer *et al.*, 2004). Most D-lineage proteins also have a non-polar 626 C-lineage (Figures 7 and 8) (Dreni *et al.*, 2007; Kramer *et al.*, 2004). Most D-lineage proteins also have a non-polar hydrophobic residue at position 106, whereas C-lineage proteins have a polar residue at that pos 627 also have a non-polar hydrophobic residue at position 106, whereas C-lineage proteins have a polar residue at that position (Dreni *et al.*, 2007). Monocot D-lineage proteins have a specific single amino acid insertio 628 polar residue at that position (Dreni *et al.*, 2007). Monocot D-lineage proteins have a specific single amino acid insertion at position 90 and at position 113 there is a histidine residue. Both of these are not pres 629 single amino acid insertion at position 90 and at position 113 there is a histidine residue. Both<br>630 of these are not present in C-lineage proteins (Dreni *et al.*, 2007). Furthermore there is a<br>631 conserved AG moti 630 of these are not present in C-lineage proteins (Dreni *et al.*, 2007). Furthermore there is a conserved AG motif I and AG motif II in the C-terminal region of AG-like proteins, which can be found in C- and D-class prot 631 conserved AG motif I and AG motif II in the C-terminal region of AG-like proteins, which<br>632 can be found in C- and D-class proteins (Kramer *et al.*, 2004). A nine-amino acid motif<br>633 downstream of the AG motif II i

632 can be found in C- and D-class proteins (Kramer *et al.*, 2004). A nine-amino acid motif downstream of the AG motif II is specific for D-class proteins (Hsu *et al.*, 2010) (Figures 8 and 9).<br>635 In rice, two duplicate 633 downstream of the AG motif II is specific for D-class proteins (Hsu *et al.*, 2010) (Figures 8 and 9).<br>635 and 9).<br>635 In rice, two duplicated C-class genes *OsMADS3* and *OsMADS58* have partially subfunctionalized (Ta 634 and 9).<br>635<br>636 In rice<br>637 subfunc<br>638 high se<br>639 hybridi: 636<br>637<br>638<br>639 636 In rice, two duplicated C-class genes *OsMADS3* and *OsMADS58* have partially subfunctionalized (Table 1) (Kang *et al.*, 1995; Yamaguchi *et al.*, 2006). *OsMADS3* shows high sequence similarity and expression with *A* 637 subfunctionalized (Table 1) (Kang *et al.*, 1995; Yamaguchi *et al.*, 2006). *OsMADS3* shows<br>638 high sequence similarity and expression with *Arabidopsis AG* (C-class gene). In situ<br>639 hybridization showed that *OsMA* 638 high sequence similarity and expression with *Arabidopsis AG* (C-class gene). In situ<br>hybridization showed that *OsMADS3* is strongly expressed in stamen primordia, while<br>19 639 hybridization showed that *OsMADS3* is strongly expressed in stamen primordia, while

640 *OsMADS58* is expressed at a lower level uniformly throughout the floral meristem (Dreni *et al.*, 2011). After the differentiation of the third whorl organ, both *OsMADS3* and *OsMADS58* have a similar expression pro *al.*, 2011). After the differentiation of the third whorl organ, both *OsMADS3* and *OsMADS58* have a similar expression profile in the filament and the anther wall and a stable expression level in the carpel and ovule pr have a similar expression profile in the filament and the anther wall and a stable expression<br>for level in the carpel and ovule primordia (Dreni *et al.*, 2011). *OsMADS3* plays a predominant<br>role in stamen specification, for the carpel and ovule primordia (Dreni *et al.*, 2011). *OsMADS3* plays a predominant role in stamen specification, with knock-out mutants by T-DNA insertion (*mads3-3*) exhibiting stamens completely or incompletely tra 644 role in stamen specification, with knock-out mutants by T-DNA insertion ( $mads3-3$ ) exhibiting stamens completely or incompletely transformed into lodicules while carpels developed normally (Dreni *et al.*, 2011; Yamagu 645 exhibiting stamens completely or incompletely transformed into lodicules while carpels developed normally (Dreni *et al.*, 2011; Yamaguchi *et al.*, 2006). Even though *osmads58* insertional mutants showed no drastic developed normally (Dreni *et al.*, 2011; Yamaguchi *et al.*, 2006). Even though *osmads58* insertional mutants showed no drastic phenotype (Dreni *et al.*, 2011), *osmads3-3 osmads58* double mutants showed a complete loss insertional mutants showed no drastic phenotype (Dreni *et al.*, 2011), *osmads3-3 osmads58* double mutants showed a complete loss of reproductive organ identity and floral meristem determinacy (Dreni *et al.*, 2011). The 648 double mutants showed a complete loss of reproductive organ identity and floral meristem<br>649 determinacy (Dreni *et al.*, 2011). The size of the floral meristem also strongly increased and<br>650 the combination of these 649 determinacy (Dreni *et al.*, 2011). The size of the floral meristem also strongly increased and the combination of these features resulted in an enlarged third whorl. In half of the florets, the carpel was replaced by 650 the combination of these features resulted in an enlarged third whorl. In half of the florets, the carpel was replaced by a small green lemma/palea-like structure (Dreni *et al.*, 2011). Based on these results it seem 651 carpel was replaced by a small green lemma/palea-like structure (Dreni *et al.*, 2011). Based<br>652 on these results it seems that OsMADS3 and OsMADS58 work redundantly, with the<br>653 contribution of OsMADS3 being more im 652 on these results it seems that OsMADS3 and OsMADS58 work redundantly, with the contribution of OsMADS3 being more important (Dreni *et al.*, 2011). OsMADS3 and OsMADS58 genetically interact with the B-class gene OsMAD 653 contribution of OsMADS3 being more important (Dreni *et al.*, 2011). OsMADS3 and OsMADS58 genetically interact with the B-class gene OsMADS16 and together they play a key role in suppressing indeterminate growth within

654 OsMADS58 genetically interact with the B-class gene OsMADS16 and together they play a<br>655 key role in suppressing indeterminate growth within floral meristem in the third whorl<br>656 primordia (Yun *et al.*, 2013).<br>657 655 key role in suppressing indeterminate growth within floral meristem in the third whorl<br>656 primordia (Yun *et al.*, 2013).<br>657 *WAG1* and *WAG2* are classified as C-function genes in *Triticum aestivum* (Table 1)<br>659 656 primordia (Yun *et al.*, 2013).<br>657 *WAG1* and *WAG2* are clas<br>659 (Hirabayashi and Murai, 200<br>660 Zhao *et al.*, 2006a). Althoug<br>661 and *OsMADS3* respectively,<br>662 2013; Wei *et al.*, 2011). Me<sub>3</sub><br>663 wheat genome on 658<br>659<br>660<br>661<br>662<br>663<br>664 *WAG1* and *WAG2* are classified as C-function genes in *Triticum aestivum* (Table 1) (Hirabayashi and Murai, 2009; Meguro *et al.*, 2003; Murai, 2013; Shitsukawa *et al.*, 2007; Zhao *et al.*, 2006a). Although they share 659 (Hirabayashi and Murai, 2009; Meguro *et al.*, 2003; Murai, 2013; Shitsukawa *et al.*, 2007; Zhao *et al.*, 2006a). Although they share high level sequence similarity to rice *OsMADS58* and *OsMADS3* respectively, they 27 660 Zhao *et al.*, 2006a). Although they share high level sequence similarity to rice *OsMADS58* and *OsMADS3* respectively, they have different expression patterns and functions (Murai, 2013; Wei *et al.*, 2011). Megur 661 and *OsMADS3* respectively, they have different expression patterns and functions (Murai, 2013; Wei *et al.*, 2011). Meguro *et al.* (2003) detected three homeologues of *WAG1* in the wheat genome on the group one chr 662 2013; Wei *et al.*, 2011). Meguro *et al.* (2003) detected three homeologues of *WAG1* in the wheat genome on the group one chromosomes (1A, 1B and 1D) by Southern blot analysis, while Wei *et al.* (2011) found three wheat genome on the group one chromosomes (1A, 1B and 1D) by Southern blot analysis,<br>
while Wei *et al.* (2011) found three homeologues of *WAG2* on the group two chromosomes<br>
(2A, 2B and 2D). *WAG1* expression is low dur 664 while Wei *et al.* (2011) found three homeologues of *WAG2* on the group two chromosomes (2A, 2B and 2D). *WAG1* expression is low during initiation of floral organ primordia, but transcripts accumulate in developing 665 (2A, 2B and 2D). *WAG1* expression is low during initiation of floral organ primordia, but transcripts accumulate in developing spikes at the booting to heading stage seen by Northern blot analysis, suggesting it is i 666 transcripts accumulate in developing spikes at the booting to heading stage seen by Northern<br>667 blot analysis, suggesting it is involved in floral organ development rather than differentiation<br>668 (Meguro *et al.*, 2 667 blot analysis, suggesting it is involved in floral organ development rather than differentiation (Meguro *et al.*, 2003). In situ hybridization showed that *WAG1* and *WAG2* are detected in the stamen, carpel and ovul 668 (Meguro *et al.*, 2003). In situ hybridization showed that *WAG1* and *WAG2* are detected in the stamen, carpel and ovule (Figure 8B) (Yamada *et al.*, 2009). Ectopic expression of the *WAG1* and *WAG2* genes induced p 669 stamen, carpel and ovule (Figure 8B) (Yamada *et al.*, 2009). Ectopic expression of the *WAG1* and *WAG2* genes induced pistilloid stamens in alloplasmic wheat, which suggests they participate in ectopic ovule formatio 670 and *WAG2* genes induced pistilloid stamens in alloplasmic wheat, which suggests they participate in ectopic ovule formation in these structures (Yamada *et al.*, 2009).<br>672 671 participate in ectopic ovule formation in these structures (Yamada *et al.*, 2009).

673 The maize orthologues of rice *OsMADS3* are *ZMM2* and *ZMM23*, and *OsMADS58* is *ZAG1* (Table 1) (Li *et al.*, 2014; Münster *et al.*, 2002; Schmidt *et al.*, 1993; Theißen *et al.*, 1995). *ZAG1* is expressed early (Table 1) (Li *et al.*, 2014; Münster *et al.*, 2002; Schmidt *et al.*, 1993; Theißen *et al.*, 1995).<br> *CAGI* is expressed early in stamen and carpel primordia as shown by RNA blot analysis and<br>
in situ hybridization (Sch *ZAG1* is expressed early in stamen and carpel primordia as shown by RNA blot analysis and<br>in situ hybridization (Schmidt *et al.*, 1993). *ZMM2* is mainly expressed in the anthers (Figure<br>8B) (Li *et al.*, 2014; Mena *et* 676 in situ hybridization (Schmidt *et al.*, 1993). *ZMM2* is mainly expressed in the anthers (Figure 8B) (Li *et al.*, 2014; Mena *et al.*, 1996). Analysis of loss-of-function mutants showed that *ZAG1* determines the flo 8B) (Li *et al.*, 2014; Mena *et al.*, 1996). Analysis of loss-of-function mutants showed that<br>8678 ZAGI determines the floral meristem, while ZMM2 participates in regulating the formation of<br>8679 stamens and carpels (Mena *ZAG1* determines the floral meristem, while *ZMM2* participates in regulating the formation of stamens and carpels (Mena *et al.*, 1996; Wei *et al.*, 2011). The orchid genes, *OMADS4* and *OMADS2* are both placed in the 679 stamens and carpels (Mena *et al.*, 1996; Wei *et al.*, 2011). The orchid genes, *OMADS4* and *OMADS2* are both placed in the AG-clade, with *OMADS4* having a C-class function and *OMADS2* a D-class function (Table 1) *OMADS2* are both placed in the AG-clade, with *OMADS4* having a C-class function and *OMADS2* a D-class function (Table 1) (Hsu *et al.*, 2010). qRT-PCR analysis showed that *OMADS4* is expressed in stamens, the stigmatic 681 *OMADS2* a D-class function (Table 1) (Hsu *et al.*, 2010). qRT-PCR analysis showed that 682 *OMADS4* is expressed in stamens, the stigmatic cavity and ovule (Figure 8B) (Hsu *et al.*, 2010), which is similar to that o *OMADS4* is expressed in stamens, the stigmatic cavity and ovule (Figure 8B) (Hsu *et al.*, 2010), which is similar to that of AG in Arabidopsis (Yanofsky et al., 1990). Yeast-two-hybrid analysis showed that OMADS4 and OMA 2010), which is similar to that of *AG* in *Arabidopsis* (Yanofsky et al., 1990). Yeast-two-<br>hybrid analysis showed that OMADS4 and OMADS2 can form homodimers and<br>heterodimers with each other (Hsu *et al.*, 2010). *LMADS10* hybrid analysis showed that OMADS4 and OMADS2 can form homodimers and heterodimers with each other (Hsu *et al.*, 2010). *LMADS10*, the C-class gene in Lily, is expressed in stamens and carpels (Hsu *et al.*, 2010). This i 685 heterodimers with each other (Hsu *et al.*, 2010). *LMADS10*, the C-class gene in Lily, is<br>686 expressed in stamens and carpels (Hsu *et al.*, 2010). This is very similar to the expression<br>687 pattern in *Oncidium Gowe* expressed in stamens and carpels (Hsu *et al.*, 2010). This is very similar to the expression pattern in *Oncidium Gower Ramsey* (Figure 8B). Ectopic expression of *LMADS10* in *Arabidopsis* caused early flowering and prod 687 pattern in *Oncidium Gower Ramsey* (Figure 8B). Ectopic expression of *LMADS10* in *Arabidopsis* caused early flowering and produced small, curly leaves and floral organ conversions like carpelloid sepals (Hsu *et al. Arabidopsis* caused early flowering and produced small, curly leaves and floral organ<br>
conversions like carpelloid sepals (Hsu *et al.*, 2010). Overexpression of *OMADS4* in<br> *Arabidopsis* only showed a moderate early flo

689 conversions like carpelloid sepals (Hsu *et al.*, 2010). Overexpression of *OMADS4* in<br>690 *Arabidopsis* only showed a moderate early flowering phenotype with no homeotic floral<br>691 organ changes (Hsu *et al.*, 2010).<br> *Arabidopsis* only showed a moderate early flowering phenotype with no homeotic floral<br>691 organ changes (Hsu *et al.*, 2010).<br>692 Rice has two duplicated D-lineage genes: *OsMADS13* and *OsMADS21* (Table 1) (Dreni *et al.* 691 organ changes (Hsu *et al.*, 2010).<br>692 Rice has two duplicated D-lineage<br>694 2007; Kramer *et al.*, 2004). *OsM*<br>695 cell layer of the carpel wall. Its e<br>696 in the integuments (Lopez-Dee of<br>697 ovule primordia develo 693<br>694<br>695<br>696<br>697<br>698 Rice has two duplicated D-lineage genes: *OsMADS13* and *OsMADS21* (Table 1) (Dreni *et al.*, 2007; Kramer *et al.*, 2004). *OsMADS13* is expressed in the ovule primordium and the inner cell layer of the carpel wall. Its e 2007; Kramer *et al.*, 2004). *OsMADS13* is expressed in the ovule primordium and the inner cell layer of the carpel wall. Its expression persists during development of the ovule, mainly in the integuments (Lopez-Dee *et* 695 cell layer of the carpel wall. Its expression persists during development of the ovule, mainly<br>696 in the integuments (Lopez-Dee *et al.*, 1999). In a *Tos17* insertion mutant of *OsMADS13*,<br>697 ovule primordia develo 696 in the integuments (Lopez-Dee *et al.*, 1999). In a *Tos17* insertion mutant of *OsMADS13*, ovule primordia developed into carpelloid structures that grew out of the carpel, giving rise to ectopic styles and stigmas ( 697 ovule primordia developed into carpelloid structures that grew out of the carpel, giving rise to<br>698 ectopic styles and stigmas (Dreni *et al.* (2007); Yamaki *et al.* (2011). The *osmads3-3*<br>699 *osmads13* double mut 698 ectopic styles and stigmas (Dreni *et al.* (2007); Yamaki *et al.* (2011). The *osmads3-3* osmads13 double mutant showed a complete loss of floral meristem determinacy inside the fourth whorl, while the *osmads13 osmad* 699 *osmads13* double mutant showed a complete loss of floral meristem determinacy inside the<br>690 fourth whorl, while the *osmads13 osmads58* double mutant showed a similar but milder<br>691 phenotype (Dreni *et al.*, 2011; 700 fourth whorl, while the *osmads13 osmads58* double mutant showed a similar but milder phenotype (Dreni *et al.*, 2011; Li *et al.*, 2011). OsMADS13 interacts with the E-class MADS-box proteins, OsMADS7 and OsMADS8, and 701 phenotype (Dreni *et al.*, 2011; Li *et al.*, 2011). OsMADS13 interacts with the E-class MADS-<br>
702 box proteins, OsMADS7 and OsMADS8, and is involved in ovule specification and floral<br>
703 meristem determinacy (Dreni box proteins, OsMADS7 and OsMADS8, and is involved in ovule specification and floral<br>
meristem determinacy (Dreni *et al.*, 2007; Fornara *et al.*, 2003; Yamaguchi and Hirano,<br>
2006). RT-PCR and in situ hybridization showe 703 meristem determinacy (Dreni *et al.*, 2007; Fornara *et al.*, 2003; Yamaguchi and Hirano, 2006). RT-PCR and in situ hybridization showed that *OsMADS21* is expressed at low levels in the inner two whorls of the flower 2006). RT-PCR and in situ hybridization showed that *OsMADS21* is expressed at low levels<br>
705 in the inner two whorls of the flower and ovules, its expression overlaps with that of<br> *OsMADS13* (Arora *et al.*, 2007; Dreni 705 in the inner two whorls of the flower and ovules, its expression overlaps with that of *OSMADS13* (Arora *et al.*, 2007; Dreni *et al.*, 2007). The *OSMADS21* expression is in two 21 706 *OsMADS13* (Arora *et al.*, 2007; Dreni *et al.*, 2007). The *OsMADS21* expression is in two whorls of the flower which differs from other D-lineage genes, which are ovule-specific<br>
708 (Figure 9B) (Dreni *et al.*, 2007), it is also highly expressed in developing kernels (Arora *et al.*,<br>
709 2007; Dreni *et al.*, 708 (Figure 9B) (Dreni *et al.*, 2007), it is also highly expressed in developing kernels (Arora *et al.*, 2007; Dreni *et al.*, 2007). T-DNA insertional mutants of *OsMADS21* show no aberrant phenotype while osmads13 osma 2007; Dreni *et al.*, 2007). T-DNA insertional mutants of *OsMADS21* show no aberrant phenotype while osmads13 osmads21 double mutants showed no more severe phenotypes than the *osmads13* single mutant and upregulation of phenotype while os*mads13 osmads21* double mutants showed no more severe phenotypes<br>
711 than the *osmads13* single mutant and upregulation of *OsMADS21* resulted in partial<br>
712 complementation of *osmads13* phenotype, bu 711 than the *osmads13* single mutant and upregulation of *OsMADS21* resulted in partial<br>712 complementation of *osmads13* phenotype, but ovule development was not completely<br>713 restored (Dreni *et al.*, 2007; Dreni *et* 712 complementation of *osmads13* phenotype, but ovule development was not completely restored (Dreni *et al.*, 2007; Dreni *et al.*, 2011). These results suggest that *OsMADS21* has lost its function in determining ovule

restored (Dreni *et al.*, 2007; Dreni *et al.*, 2011). These results suggest that *OsMADS21* has lost<br>
tis function in determining ovule identity, presumably because of its redundancy with<br> *OsMADS13* (Dreni *et al.*, 2007 714 its function in determining ovule identity, presumably because of its redundancy with  $OsMADS13$  (Dreni et al., 2007; Fornara et al., 2003; Yamaguchi and Hirano, 2006).<br>716 The closest relative to the *Arabidopsis* D-fun *OsMADS13* (Dreni *et al.*, 2007; Fornara *et al.*, 2003; Yamaguchi and Hirano, 2006).<br>
716 The closest relative to the *Arabidopsis* D-function gene *STK* in wheat is *WSTK*, also<br>
718 TaAG-3 (Table 1) (Paolacci *et al.*, 717<br>718<br>719<br>720<br>721<br>722<br>723 The closest relative to the *Arabidopsis* D-function gene *STK* in wheat is *WSTK*, also known as TaAG-3 (Table 1) (Paolacci *et al.*, 2007; Zhao *et al.*, 2006a). Yeast-two-hybrid analysis has shown that WSTK forms a comp TaAG-3 (Table 1) (Paolacci *et al.*, 2007; Zhao *et al.*, 2006a). Yeast-two-hybrid analysis has shown that WSTK forms a complex with the E-class protein WSEP (Murai, 2013; Shitsukawa *et al.*, 2007; Yamada *et al.*, 2009). 279 shown that WSTK forms a complex with the E-class protein WSEP (Murai, 2013; Shitsukawa<br>
270 *et al.*, 2007; Yamada *et al.*, 2009). RT-PCR assays showed that it is expressed in pistils with<br>
271 strong expression in t *et al.*, 2007; Yamada *et al.*, 2009). RT-PCR assays showed that it is expressed in pistils with<br>
strong expression in the developing ovule (Yamada *et al.*, 2009). In situ hybridization showed<br>
WSTK mRNA in the ectopic o 721 strong expression in the developing ovule (Yamada *et al.*, 2009). In situ hybridization showed<br>722 WSTK mRNA in the ectopic ovules and pistil-like stamens of alloplasmic wheat, suggesting a<br>723 role in ovule formation WSTK mRNA in the ectopic ovules and pistil-like stamens of alloplasmic wheat, suggesting a<br>role in ovule formation (Yamada *et al.*, 2009). There are presumably three homeologues of<br>*WSTK* in the wheat genome (Yamada *et* role in ovule formation (Yamada *et al.*, 2009). There are presumably three homeologues of *WSTK* in the wheat genome (Yamada *et al.*, 2009; Zhao *et al.*, 2006a). The closest relative to *OsMADS21* in wheat has been iden *WSTK* in the wheat genome (Yamada *et al.*, 2009; Zhao *et al.*, 2006a). The closest relative to *OsMADS21* in wheat has been identified as *TaAG-4* (Paolacci *et al.*, 2007). *TaAG-4* has weak expression in stamens and v *OsMADS21* in wheat has been identified as *TaAG-4* (Paolacci *et al.*, 2007). *TaAG-4* has weak expression in stamens and very high expression in pistils as shown by RT-PCR (Paolacci *et al.*, 2007). *ZAG2* and *ZMM1* hav expression in stamens and very high expression in pistils as shown by RT-PCR (Paolacci *et al.*, 2007). ZAG2 and ZMM1 have been identified as D-class genes in maize (Li *et al.*, 2014; Schmidt *et al.*, 1993; Theißen *et a al.*, 2007). *ZAG2* and *ZMM1* have been identified as D-class genes in maize (Li *et al.*, 2014;<br>
Schmidt *et al.*, 1993; Theißen *et al.*, 1995). *ZAG2* is a floral specific gene, but expressed later<br>
in floral primordi Tata Schmidt *et al.*, 1993; Theiβen *et al.*, 1995). *ZAG2* is a floral specific gene, but expressed later<br>
in floral primordia than the C-class gene *ZAG1*. Expression of *ZAG2* is largely restricted to<br>
the developing in floral primordia than the C-class gene *ZAG1*. Expression of *ZAG2* is largely restricted to<br>
the developing ovules and the inner carpel face as determined by in situ hybridization<br>
(Schmidt *et al.*, 1993). qRT-PCR sho the developing ovules and the inner carpel face as determined by in situ hybridization (Schmidt *et al.*, 1993). qRT-PCR showed that *OMADS2* in *O. Gower Ramsey* is expressed in the stigmatic cavity and the ovary, but is 731 (Schmidt *et al.*, 1993). qRT-PCR showed that *OMADS2* in *O. Gower Ramsey* is expressed in the stigmatic cavity and the ovary, but is undetectable in sepals, petals, the labellum and stamens (Figure 9B) (Hsu *et al.*, the stigmatic cavity and the ovary, but is undetectable in sepals, petals, the labellum and<br>
stamens (Figure 9B) (Hsu *et al.*, 2010). Ectopic expression of *OMADS2* shows the same<br>
phenotype as *LMADS10*, except there ar 733 stamens (Figure 9B) (Hsu *et al.*, 2010). Ectopic expression of *OMADS2* shows the same<br>
734 phenotype as *LMADS10*, except there are no floral organ conversions (Hsu *et al.*, 2010).<br> *LMADS2* was identified as the Dphenotype as *LMADS10*, except there are no floral organ conversions (Hsu *et al.*, 2010).<br> *LMADS2* was identified as the D-class protein in *Lilium longiflorum* (Tzeng *et al.*, 2002). It<br>
was exclusively expressed in th *LMADS2* was identified as the D-class protein in *Lilium longiflorum* (Tzeng *et al.*, 2002). It was exclusively expressed in the carpel, more specifically in the ovule as seen by RNA blot analysis (Tzeng *et al.*, 2002). was exclusively expressed in the carpel, more specifically in the ovule as seen by RNA blot analysis (Tzeng *et al.*, 2002). LMADS2 can form heterodimers with LMADS10 and both can also form homodimers as shown by yeast-two 2737 analysis (Tzeng *et al.*, 2002). LMADS2 can form heterodimers with LMADS10 and both can<br>
2738 also form homodimers as shown by yeast-two-hybrid analysis (Hsu *et al.*, 2010). Ectopic<br>
2739 expression of *LMADS2* in Ar 738 also form homodimers as shown by yeast-two-hybrid analysis (Hsu *et al.*, 2010). Ectopic<br>
739 expression of *LMADS2* in Arabidopsis caused early flowering and floral organ conversion of<br>
740 sepals and petals to carpel %739 expression of *LMADS2* in Arabidopsis caused early flowering and floral organ conversion of sepals and petals to carpel- and stamen-like structures (Tzeng *et al.*, 2002).<br>22 740 sepals and petals to carpel- and stamen-like structures (Tzeng *et al.*, 2002).

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742<br>743<br>744<br>745<br>746<br>747 The gene duplication event of C-class genes is also seen in some grasses, for instance, in<br>
T43 maize, leading to three different C-class genes and possible subfunctionalization (Dreni and<br>
T44 Kater, 2014). In contrast, o maize, leading to three different C-class genes and possible subfunctionalization (Dreni and<br>
744 Kater, 2014). In contrast, only one C-class gene and one D-class gene have currently been<br>
745 found in *O. Gower Ramsey* an Kater, 2014). In contrast, only one C-class gene and one D-class gene have currently been<br>
found in *O. Gower Ramsey* and *L. longiflorum*, but their expression patterns are highly<br>
conserved compared with those of *Arabid* 

Found in *O. Gower Ramsey* and *L. longiflorum*, but their expression patterns are highly<br>
conserved compared with those of *Arabidopsis* and rice.<br> **E-class genes**<br> **E-class genes**<br> **E-class genes**<br> **E-class genes**<br> **E-cl** conserved compared with those of *Arabidopsis* and rice.<br>
747 E-class genes<br>
748 E-class genes belong to *AGL2*-subfamily and specify flow<br>
750 order protein complexes with the class A, B or C protein<br>
751 2003; Pelaz *et* 747 **E-class genes**<br>
748 **E-class genes 1**<br>
750 order protein c<br>
751 2003; Pelaz *e*<br>
752 contributes to<br>
753 formation or t<br>
754 Theissen and 749<br>750<br>751<br>752<br>753<br>754<br>755 E-class genes belong to *AGL2*-subfamily and specify flower organ identity by forming higher-<br>order protein complexes with the class A, B or C proteins respectively (Becker and Theissen,<br>2003; Pelaz *et al.*, 2000; Theißen order protein complexes with the class A, B or C proteins respectively (Becker and Theissen, 2003; Pelaz *et al.*, 2000; Theißen, 2001). This ability to form tetrameric complexes also contributes to the development of flor 2003; Pelaz *et al.*, 2000; Theißen, 2001). This ability to form tetrameric complexes also<br>
2003; Contributes to the development of floral quartets to control sepal, petal, stamen and carpel<br>
2003; Theissen and Saedler, 20 contributes to the development of floral quartets to control sepal, petal, stamen and carpel<br>formation or their equivalents in grasses (Becker and Theissen, 2003; Fornara et al., 2003;<br>Theissen and Saedler, 2001). In *Arab* 753 formation or their equivalents in grasses (Becker and Theissen, 2003; Fornara *et al.*, 2003; Theissen and Saedler, 2001). In *Arabidopsis, SEP1/2/3/4* have been identified as E-class genes (Huang *et al.*, 1995; Ma *e* T54 Theissen and Saedler, 2001). In *Arabidopsis*, *SEP1/2/3/4* have been identified as E-class genes (Huang *et al.*, 1995; Ma *et al.*, 1991; Mandel and Yanofsky, 1998). *SEP1*, *SEP2* and *SEP4* are expressed in all fou genes (Huang *et al.*, 1995; Ma *et al.*, 1991; Mandel and Yanofsky, 1998). *SEP1*, *SEP2* and *SEP4* are expressed in all four whorls of the flower, with SEP4 showing higher expression in the central dome (Ditta *et al.*,

*SEP4* are expressed in all four whorls of the flower, with SEP4 showing higher expression in<br>the central dome (Ditta *et al.*, 2004; Flanagan and Ma, 1994; Savidge *et al.*, 1995). *SEP3* is<br>only expressed in the inner th the central dome (Ditta *et al.*, 2004; Flanagan and Ma, 1994; Savidge *et al.*, 1995). *SEP3* is<br>
only expressed in the inner three whorls (Mandel and Yanofsky, 1998).<br> *AGL2*-like genes were deduced to have undergone a g only expressed in the inner three whorls (Mandel and Yanofsky, 1998).<br>
759<br>
760 *AGL2*-like genes were deduced to have undergone a gene duplication e<br>
761 of the extant angiosperms, and after the divergence between exta<br>
2 760<br>761<br>762<br>763<br>765<br>765<br>765 *AGL2*-like genes were deduced to have undergone a gene duplication event before the origin<br>
of the extant angiosperms, and after the divergence between extant gymnosperms and<br>
angiosperms, creating the SEP3- and LOFSEP-li 761 of the extant angiosperms, and after the divergence between extant gymnosperms and angiosperms, creating the SEP3- and LOFSEP-lineages (Malcomber and Kellogg, 2005; Zahn *et al.*, 2005a). Furthermore, SEP3- and LOFSEP-262 angiosperms, creating the SEP3- and LOFSEP-lineages (Malcomber and Kellogg, 2005; Zahn *et al.*, 2005a). Furthermore, SEP3- and LOFSEP-lineages may have undergone more gene duplication events in the grasses, leading to 763 Zahn *et al.*, 2005a). Furthermore, SEP3- and LOFSEP-lineages may have undergone more gene duplication events in the grasses, leading to three LOFSEP lineages: OsMADS1-, OsMADS5- and OsMADS34-clades and two SEP3-lineag 264 gene duplication events in the grasses, leading to three LOFSEP lineages: OsMADS1-, OsMADS5- and OsMADS34-clades and two SEP3-lineages: OsMADS7- and OsMADS8-clade (Malcomber and Kellogg, 2005; Zahn *et al.*, 2005a). I 765 OsMADS5- and OsMADS34-clades and two SEP3-lineages: OsMADS7- and OsMADS8-<br>
266 clade (Malcomber and Kellogg, 2005; Zahn *et al.*, 2005a). In addition, two motifs (SEPI and<br>
367 SEPII) that consist of hydrophobic and po 766 clade (Malcomber and Kellogg, 2005; Zahn *et al.*, 2005a). In addition, two motifs (SEPI and SEPII) that consist of hydrophobic and polar residues were observed in AGL2-like proteins (Vandenbussche *et al.*, 2003; Zahn The 767 SEPII) that consist of hydrophobic and polar residues were observed in AGL2-like proteins<br>
768 (Vandenbussche *et al.*, 2003; Zahn *et al.*, 2005a). Clade-specific changes in these motifs can<br>
769 be seen, for inst 768 (Vandenbussche *et al.*, 2003; Zahn *et al.*, 2005a). Clade-specific changes in these motifs can<br>
769 be seen, for instance, the OsMADS5-clade in grasses have lost the final 12-15 amino acids<br>
770 within the SEPII moti the seen, for instance, the OsMADS5-clade in grasses have lost the final 12-15 amino acids<br>within the SEPII motif, possibly caused by a recent gene duplication followed by a frameshift<br>mutation (Vandenbussche *et al.*, 200 770 within the SEPII motif, possibly caused by a recent gene duplication followed by a frameshift<br>771 mutation (Vandenbussche *et al.*, 2003; Zahn *et al.*, 2005a).<br>772<br>*LOFSEP-lineage*<br>23 771 mutation (Vandenbussche *et al.*, 2003; Zahn *et al.*, 2005a).<br>772<br>*LOFSEP-lineage* 

# 772 773 *LOFSEP-lineage*

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775<br>776<br>777<br>778<br>780<br>781 775 *OsMADS1-clade*<br>
776 *OsMADS1*, one<br>
777 meristem determi<br>
778 specific-cell type<br>
779 detected in the flo<br>
780 and weakly in the<br>
781 (Figure 10B) (C<br>
782 Overexpression *OsMADS1*, one well-characterised E-class gene in rice, plays an important role in floral<br>meristem determination and controls the differentiation and proliferation of palea and lemma<br>specific-cell types (Jeon *et al.*, 200 meristem determination and controls the differentiation and proliferation of palea and lemma<br>specific-cell types (Jeon *et al.*, 2000a; Prasad *et al.*, 2005). The expression of *OsMADS1* is<br>detected in the floral meriste 178 specific-cell types (Jeon *et al.*, 2000a; Prasad *et al.*, 2005). The expression of *OsMADS1* is<br>
179 detected in the floral meristem during early flower development, and later in the palea, lemma<br>
1780 and weakly in detected in the floral meristem during early flower development, and later in the palea, lemma<br>
and weakly in the carpel shown by northern blot analysis, RT-PCR and in situ hybridization<br>
(Figure 10B) (Chung *et al.*, 199 2780 and weakly in the carpel shown by northern blot analysis, RT-PCR and in situ hybridization<br>
781 (Figure 10B) (Chung *et al.*, 1994; Kobayashi *et al.*, 2010; Prasad *et al.*, 2001).<br>
782 Overexpression of *OsMADS1* ca 781 (Figure 10B) (Chung *et al.*, 1994; Kobayashi *et al.*, 2010; Prasad *et al.*, 2001).<br>782 Overexpression of *OsMADS1* caused stunted panicles, irregular positioned branches and<br>783 spikelets and the rudimentary glumes Overexpression of *OsMADS1* caused stunted panicles, irregular positioned branches and spikelets and the rudimentary glumes were transformed into palea/lemma-like structures (Prasad *et al.*, 2005; Prasad *et al.*, 2001). restand the rudimentary glumes were transformed into palea/lemma-like structures<br>
784 (Prasad *et al.*, 2005; Prasad *et al.*, 2001). Different mutants of *OsMADS1* have been<br>
785 investigated. Jeon *et al.* (2000a) repor 784 (Prasad *et al.*, 2005; Prasad *et al.*, 2001). Different mutants of *OsMADS1* have been<br>785 investigated. Jeon *et al.* (2000a) reported that *lhs-1* (*leafy hull sterile1*), which contains two<br>786 missense mutations investigated. Jeon *et al.* (2000a) reported that *lhs-1 (leafy hull sterile1)*, which contains two<br>786 missense mutations in *OsMADS1* MADS-domain, showed a loss of floral meristem<br>787 determination and transformation of missense mutations in *OsMADS1* MADS-domain, showed a loss of floral meristem<br>determination and transformation of palea and lemma into leaf-like structures. Similarly,<br>other *OsMADS1* mutants such as *osmads1*-z and *nsr* determination and transformation of palea and lemma into leaf-like structures. Similarly,<br>
788 other *OsMADS1* mutants such as *osmads1-z* and *nsr (naked seed rice)* showed the<br>
789 transformation of the lemma, palea and other *OsMADS1* mutants such as *osmads1-z* and *nsr (naked seed rice)* showed the transformation of the lemma, palea and lodicules into leaf-like structures (Chen *et al.*, 2006; Gao *et al.*, 2010). OsMADS1 was shown to transformation of the lemma, palea and lodicules into leaf-like structures (Chen *et al.*, 2006;<br>
Gao *et al.*, 2010). OsMADS1 was shown to interact with the A-class proteins OsMADS14<br>
and OsMADS15, the B-class protein OsM 790 Gao *et al.*, 2010). OsMADS1 was shown to interact with the A-class proteins OsMADS14<br>
2010 and OsMADS15, the B-class protein OsMADS16, the C-class proteins OsMADS3 and<br>
2000 OsMADS88 and the AGL-like protein OsMADS6 ( 291 and OsMADS15, the B-class protein OsMADS16, the C-class proteins OsMADS3 and<br>
292 OsMADS58, the D-class protein OsMADS13, the E-class proteins OsMADS7 and<br>
2000, Moon *et al.*, 1999b). Two maize homologs of *OsMADS1*, 792 OsMADS58, the D-class protein OsMADS13, the E-class proteins OsMADS7 and OsMADS8 and the AGL-like protein OsMADS6 (Cui *et al.*, 2010; Hu *et al.*, 2015; Lim *et al.*, 2000; Moon *et al.*, 1999b). Two maize homologs of 0SMADS8 and the AGL-like protein OsMADS6 (Cui *et al.*, 2010; Hu *et al.*, 2015; Lim *et al.*, 2000; Moon *et al.*, 1999b). Two maize homologs of *OsMADS1*, *ZMM8* and *ZMM14* are thought to determine the alternative ident 2000; Moon *et al.*, 1999b). Two maize homologs of *OsMADS1*, *ZMM8* and *ZMM14* are<br>
795 thought to determine the alternative identity of the upper vs the lower floret within each<br>
596 spikelet primordium (Becker and Thei thought to determine the alternative identity of the upper vs the lower floret within each<br>spikelet primordium (Becker and Theissen, 2003; Cacharrón *et al.*, 1999). Their expression<br>was only detectable in the upper floret 796 spikelet primordium (Becker and Theissen, 2003; Cacharrón *et al.*, 1999). Their expression was only detectable in the upper floret, but not in the lower floret of the developing spike, shown by in situ hybridization ( was only detectable in the upper floret, but not in the lower floret of the developing spike,<br>
shown by in situ hybridization (Figure 10B) (Cacharrón *et al.*, 1995; Cacharrón *et al.*, 1999).<br> *ZMM14* expression is lower 2798 shown by in situ hybridization (Figure 10B) (Cacharrón *et al.*, 1995; Cacharrón *et al.*, 1999).<br>
2799 ZMM14 expression is lower than that of ZMM8 and is stronger in the carpels than in the other<br>
1798 tissues (Cacha *ZMM14* expression is lower than that of *ZMM8* and is stronger in the carpels than in the other<br>tissues (Cacharrón *et al.*, 1999). The function of barley *HvBM1* (also known as *BM7*) remains<br>to be elucidated. The expres tissues (Cacharrón *et al.*, 1999). The function of barley *HvBM1* (also known as *BM7*) remains<br>to be elucidated. The expression of *HvBM1* is seen in the floret meristem at the distal part of<br>the awn primordium. As flore

801 to be elucidated. The expression of *HvBM1* is seen in the floret meristem at the distal part of<br>802 the awn primordium. As floret development continues, expression is detected in the lemma<br>803 and palea, in the lodicu the awn primordium. As floret development continues, expression is detected in the lemma<br>and palea, in the lodicules and the ovule, but not in the anther (Schmitz *et al.*, 2000).<br>Wheat has three homeologues of *OsMADS1* and palea, in the lodicules and the ovule, but not in the anther (Schmitz *et al.*, 2000).<br>
804 Wheat has three homeologues of *OsMADS1* called *WLHS1* located on chromosome<br>
805 and 4C (Shitsukawa *et al.*, 2007). In situ Wheat has three homeologues of *OsMADS1* called *WLHS1* located on chromosomes 4A, 4B and 4C (Shitsukawa *et al.*, 2007). In situ hybridization analysis showed that the expression of *WLHS1* is initially detectable in the 805 and 4C (Shitsukawa *et al.*, 2007). In situ hybridization analysis showed that the expression of *WLHS1* is initially detectable in the inflorescence axis at inflorescence meristem initiation (Shitsukawa *et al.*, 2007 806 *WLHS1* is initially detectable in the inflorescence axis at inflorescence meristem initiation (Shitsukawa *et al.*, 2007). During floral organ differentiation, their expression signals are 24 807 (Shitsukawa *et al.*, 2007). During floral organ differentiation, their expression signals are detected in the spikelet axis at the most proximal position (Shitsukawa *et al.*, 2007). Later, their expression was observed in the glume, lemma and palea until maturity of the floral organs (Shitsukawa *et al.*, 2007). S 809 their expression was observed in the glume, lemma and palea until maturity of the floral organs (Shitsukawa *et al.*, 2007). Shitsukawa *et al.* (2007) showed that expression of *WLHS1*-*B* is much lower than that of organs (Shitsukawa *et al.*, 2007). Shitsukawa *et al.* (2007) showed that expression of *WLHS1*-*B* is much lower than that of *WLHS1*-*A* and -*D*. WLHS1-B and WLHS1-D interact with B-class WAP3 and WPI2 and all E-class 811 *B* is much lower than that of *WLHS1-A* and  $-D$ . WLHS1-B and WLHS1-D interact with B-<br>
812 class WAP3 and WPI2 and all E-class genes, with the exception of WLHS1-A (Shitsukawa *et*<br>
81. al., 2007). It has been suggest 812 class WAP3 and WPI2 and all E-class genes, with the exception of WLHS1-A (Shitsukawa *et al.*, 2007). It has been suggested that the lack of interaction with WLHS1-A is due to the loss of the K box in WLHS1-A (Davies al., 2007). It has been suggested that the lack of interaction with WLHS1-A is due to the loss<br>
814 of the K box in WLHS1-A (Davies *et al.*, 1996; Shitsukawa *et al.*, 2007). Overexpression of<br>
815 *WLHS1* homeologues in

814 of the K box in WLHS1-A (Davies *et al.*, 1996; Shitsukawa *et al.*, 2007). Overexpression of *WLHS1* homeologues in *Arabidopsis* showed no phenotype for *WLHS1-A* and early flowering and late production of terminal f *WLHS1* homeologues in *Arabidopsis* showed no phenotype for *WLHS1-A* and early flowering<br>and late production of terminal flowers for *WLHS1-B* and *-D* (Shitsukawa *et al.*, 2007).<br>817<br>*OsMADS5-clade*<br>The function of the and late production of terminal flowers for *WLHS1-B* and *–D* (Shitsukawa *et al.*, 2007).<br>818 *OsMADS5-clade*<br>819 The function of the *LOFSEP* gene *OsMADS5* has remained a mystery because<br>820 detectable phenotype in eit 818<br>819<br>820<br>821<br>822<br>823<br>824 818 *OsMADS5-clade*<br>819 The function of<br>820 detectable pheno<br>821 except for the lo<br>822 dissection (Agrav<br>823 suggest one role of<br>824 *OsMADS1* and *C*<br>825 genes. Furthermo The function of the *LOFSEP* gene *OsMADS5* has remained a mystery because of no<br>820 detectable phenotype in either panicles or vegetative organs in loss-of-function mutants,<br>821 except for the lodicules being more tightly detectable phenotype in either panicles or vegetative organs in loss-of-function mutants,<br>except for the lodicules being more tightly attached to the lemma and palea upon spikelet<br>dissection (Agrawal *et al.*, 2005). Rece except for the lodicules being more tightly attached to the lemma and palea upon spikelet dissection (Agrawal *et al.*, 2005). Recent findings using genetic and molecular approaches, suggest one role of *OsMADS5* is to red dissection (Agrawal *et al.*, 2005). Recent findings using genetic and molecular approaches,<br>suggest one role of *OsMADS5* is to redundantly regulate spikelet morphogenesis together with<br>*OsMADS1* and *OsMADS34*, by positi state of *OsMADS5* is to redundantly regulate spikelet morphogenesis together with<br>824 *OsMADS1* and *OsMADS34*, by positively regulating the other MADS-box floral homeotic<br>825 genes. Furthermore, OsMADS1, OsMADS5 and OsMA 824 *OsMADS1* and *OsMADS34*, by positively regulating the other MADS-box floral homeotic<br>825 genes. Furthermore, OsMADS1, OsMADS5 and OsMADS34 can form protein-protein<br>826 interactions with other MADS-box floral homeotic

genes. Furthermore, OsMADS1, OsMADS5 and OsMADS34 can form protein-protein<br>interactions with other MADS-box floral homeotic members, which is a typical, conserved<br>activity of plant SEP proteins (Wu *et al.*, 2018).<br>828<br>ZMM 326 interactions with other MADS-box floral homeotic members, which is a typical, conserved<br>327 activity of plant SEP proteins (Wu *et al.*, 2018).<br>328<br>329 *ZMM3* (maize) was classified as a member of the OsMADS5-clade in activity of plant SEP proteins (Wu *et al.*, 2018).<br>828 *ZMM3* (maize) was classified as a member of with unknown function (Malcomber and Kello<br>831 *TaSEP-6* as an orthologue of *OsMADS5*, locar<br>832 wheat genome. Northern --<br>829<br>830<br>831<br>832<br>833<br>834 *ZMM3* (maize) was classified as a member of the OsMADS5-clade in the LOFSEP-lineage<br>with unknown function (Malcomber and Kellogg, 2005). Paolacci *et al.* (2007) identified<br>*TaSEP-6* as an orthologue of *OsMADS5*, located with unknown function (Malcomber and Kellogg, 2005). Paolacci *et al.* (2007) identified TaSEP-6 as an orthologue of *OsMADS5*, located on chromosomes 7A, 7B and 7D in the wheat genome. Northern blot analysis, RT-PCR and q

*TaSEP-6* as an orthologue of *OsMADS5*, located on chromosomes 7A, 7B and 7D in the<br>wheat genome. Northern blot analysis, RT-PCR and qRT-PCR showed that it is expressed in<br>all floral organs, but at very high levels in glu wheat genome. Northern blot analysis, RT-PCR and qRT-PCR showed that it is expressed in<br>all floral organs, but at very high levels in glumes, lemma and palea (Paolacci *et al.*, 2007).<br>834<br>*OsMADS34-clade*<br>Unlike other *SE* assa all floral organs, but at very high levels in glumes, lemma and palea (Paolacci *et al.*, 2007).<br>
834 *OsMADS34-clade*<br>
835 *OsMADS34-clade*<br>
836 Unlike other *SEP*-like genes involved in controlling flower developmen 835<br>835<br>836<br>837<br>838<br>839<br>840 835 *OsMADS34-clade*<br>836 Unlike other *SEF*<br>837 *(PANICLE PHYTC*<br>838 spikelet developme<br>839 showed altered in<br>840 secondary branch<br>841 spikelet morpholo Unlike other *SEP*-like genes involved in controlling flower development, *OsMADS34* (*PANICLE PHYTOMER2* [*PAP2*]), one *LOFSEP* gene, is required for rice inflorescence and spikelet development (Gao *et al.*, 2010; Kobay 837 (*PANICLE PHYTOMER2* [*PAP2*]), one *LOFSEP* gene, is required for rice inflorescence and spikelet development (Gao *et al.*, 2010; Kobayashi *et al.*, 2010; Lin *et al.*, 2014). *osmads34-1* showed altered inflorescen 838 spikelet development (Gao *et al.*, 2010; Kobayashi *et al.*, 2010; Lin *et al.*, 2014). *osmads34-1* showed altered inflorescence shape with increased primary branch number and decreased secondary branch number. In ad 839 showed altered inflorescence shape with increased primary branch number and decreased<br>840 secondary branch number. In addition, *osmads34-1* showed fewer spikelets and changed<br>841 spikelet morphology, containing elonga 840 secondary branch number. In addition, *osmads34-1* showed fewer spikelets and changed<br>841 spikelet morphology, containing elongated sterile lemmas with lemma/palea-like features<br>25 841 spikelet morphology, containing elongated sterile lemmas with lemma/palea-like features<br>25 642 (Gao *et al.*, 2010)(Gao et al., 2010). Recently *OsMADS34/PAP2* was shown to be involved in the transition from vegetative to reproductive development via specifying inflorescence meristem identity together with three 843 the transition from vegetative to reproductive development via specifying inflorescence<br>
844 meristem identity together with three  $API/FUL$ -like genes  $OsMADS14$ ,  $OsMADS15$  and<br>  $OsMADS18$  (Kobayashi et al., 2012). These fin meristem identity together with three *AP1/FUL*-like genes *OsMADS14*, *OsMADS15* and *OsMADS18* (Kobayashi et al., 2012). These findings clearly show that OsMADS34 is a positive regulator of inflorescence meristem identit

*OsMADS18* (Kobayashi et al., 2012). These findings clearly show that OsMADS34 is a positive regulator of inflorescence meristem identity and spikelet meristem identity as well as a suppressor of elongation of the glumes ( bositive regulator of inflorescence meristem identity and spikelet meristem identity as well as<br>a suppressor of elongation of the glumes (Kobayashi *et al.*, 2010; Kobayashi *et al.*, 2012).<br>848<br>In maize and wheat, the fun a suppressor of elongation of the glumes (Kobayashi *et al.*, 2010; Kobayashi *et al.*, 2012).<br>848<br>In maize and wheat, the function of *OsMADS34* homologs have not been elucidated, and c<br>850 expression data is reported. Tw 849<br>850<br>851<br>852<br>853<br>854<br>855 In maize and wheat, the function of *OsMADS34* homologs have not been elucidated, and only<br>expression data is reported. Two maize homologues of *OsMADS34*, *ZMM24* and *ZMM31* are<br>expressed in early developing tassels and expression data is reported. Two maize homologues of *OsMADS34*, *ZMM24* and *ZMM31* are<br>expressed in early developing tassels and ears, and *ZMM24* shows high expression throughout<br>ear development (Danilevskaya *et al.*, expressed in early developing tassels and ears, and *ZMM24* shows high expression throughout ear development (Danilevskaya *et al.*, 2008). *TaSEP-5* was identified as the orthologue of *OsMADS34* in wheat and its three ho ear development (Danilevskaya *et al.*, 2008). *TaSEP-5* was identified as the orthologue of *OsMADS34* in wheat and its three homeologues are located on chromosomes 5A, 5B and 5D with high expression level at the early sp *OsMADS34* in wheat and its three homeologues are located on chromosomes 5A, 5B and 5D<br>with high expression level at the early spike developmental stages, which decreases, but<br>increases again in spikes at the booting and h

with high expression level at the early spike developmental stages, which decreases, but<br>increases again in spikes at the booting and heading stages (Paolacci *et al.*, 2007). Notably,<br>*TaSEP-5* is highly expressed in the increases again in spikes at the booting and heading stages (Paolacci *et al.*, 2007). Notably, TaSEP-5 is highly expressed in the glumes, lemma and palea (Paolacci *et al.*, 2007). Orchid and lily To date there is no dire *TaSEP-5* is highly expressed in the glumes, lemma and palea (Paolacci *et al.*, 2007).<br>857 *Orchid and lily*<br>859 *To date there is no direct genetic evidence showing the function of the <i>OsMADS1-*<br>860 *OMADS11* in orchid. 858<br>859<br>860<br>861<br>862<br>863 858 *Orchid and lily*<br>859 To date there is<br>860 *OMADS11* in or<br>861 and stigmatic c<br>862 shown by RT-P<br>863 phenotypes and<br>864 were identified<br>865 orthologue, wh To date there is no direct genetic evidence showing the function of the *OsMADS1*-like gene<br>
860 *OMADS11* in orchid. *OMADS11* is highly expressed in the sepal, petal, lip, carpel, anther cap<br>
861 and stigmatic cavity and *OMADS11* in orchid. *OMADS11* is highly expressed in the sepal, petal, lip, carpel, anther cap<br>and stigmatic cavity and has no expression signal in vegetative leaves and stamens as was<br>shown by RT-PCR. Ectopic expression and stigmatic cavity and has no expression signal in vegetative leaves and stamens as was<br>
862 shown by RT-PCR. Ectopic expression of *OMADS11* in *Arabidopsis* showed early flowering<br>
863 phenotypes and smaller, curled le 862 shown by RT-PCR. Ectopic expression of *OMADS11* in *Arabidopsis* showed early flowering<br>
863 phenotypes and smaller, curled leaves (Chang *et al.*, 2009). In lily, *LMADS3* and *LMADS4*<br>
864 were identified as E-class 863 phenotypes and smaller, curled leaves (Chang *et al.*, 2009). In lily, *LMADS3* and *LMADS4* were identified as E-class genes (Table 1) (Tzeng *et al.*, 2003). *LMADS4* is a *SEP1/2* orthologue, which is expressed in t were identified as E-class genes (Table 1) (Tzeng *et al.*, 2003). *LMADS4* is a *SEP1/2* orthologue, which is expressed in the inflorescence meristem, floral buds of different developmental stages and in all four whorls o orthologue, which is expressed in the inflorescence meristem, floral buds of different developmental stages and in all four whorls of the flower (Chang *et al.*, 2009; Tzeng *et al.*, 2003). *LMADS4* is also expressed in t 866 developmental stages and in all four whorls of the flower (Chang *et al.*, 2009; Tzeng *et al.*, 2003). *LMADS4* is also expressed in the vegetative leaf and in the inflorescence stem (Tzeng *et al.*, 2003). *Arabidops* 2003). *LMADS4* is also expressed in the vegetative leaf and in the inflorescence stem (Tzeng *et al.*, 2003). *Arabidopsis* plants with ectopic expression of *LMADS4* were indistinguishable from the wild type plants (Tzen *et al.*, 2003). *Arabidopsis* plants with ectopic expression of *LMADS4* were indistinguishable<br>
from the wild type plants (Tzeng *et al.*, 2003).<br>
870<br>
871 **SEP3-lineage**<br>
872<br>
873 **OsMADS7-clade**<br>
874 **OsMADS7** has redu

1869 from the wild type plants (Tzeng *et al.*, 2003).<br>
1870<br>
1872<br>
1873 *OsMADS7-clade*<br>
1874 *OsMADS7* has redundant function in specifyir<br>
1875 suggested by the observation that *OsMADS7* a 871<br>872<br>873<br>874<br>875 871 *SEP3-lineage*<br>872 <u>*OsMADS7-clas*<br>874 *OsMADS7* has<br>875 suggested by the sugges</u> ---<br>873<br>874<br>875 873 *OsMADS7-clade*<br>874 *OsMADS7* has response to the suggested by the 874 *OsMADS7* has redundant function in specifying rice flower development with *OsMADS8*, as suggested by the observation that *OsMADS7* and *OsMADS8* share almost identical expression 26<br>26 875 suggested by the observation that *OsMADS7* and *OsMADS8* share almost identical expression<br>26 patterns (Kang *et al.*, 1997; Pelucchi *et al.*, 2002). *OsMADS7* and *OsMADS8* are expressed<br>early in the floral meristem where the lodicule and stamen primordia develop (Kang *et al.*,<br>1997; Pelucchi *et al.*, 2002). Su early in the floral meristem where the lodicule and stamen primordia develop (Kang *et al.*, 1997; Pelucchi *et al.*, 2002). Subsequently they are expressed in lodicules, developing stamen and carpel primordia throughout f 1997; Pelucchi *et al.*, 2002). Subsequently they are expressed in lodicules, developing stamen<br>
and carpel primordia throughout floret development (Figure 10B) (Kang *et al.*, 1997; Pelucchi<br> *et al.*, 2002). Overexpressi and carpel primordia throughout floret development (Figure 10B) (Kang *et al.*, 1997; Pelucchi *et al.*, 2002). Overexpression and knockdown of *OsMADS7* shows similar phenotypes to that of *OsMADS8* (Cui *et al.*, 2010; J *et al.*, 2002). Overexpression and knockdown of *OsMADS7* shows similar phenotypes to that of *OsMADS8* (Cui *et al.*, 2010; Jeon *et al.*, 2000b; Kang *et al.*, 1997). Knock-down of both *OsMADS7* and *OsMADS8* resulted 881 of *OsMADS8* (Cui *et al.*, 2010; Jeon *et al.*, 2000b; Kang *et al.*, 1997). Knock-down of both *OsMADS7* and *OsMADS8* resulted in late flowering and homeotic transformation of lodicules, stamens and carpels into pal *OsMADS7* and *OsMADS8* resulted in late flowering and homeotic transformation of lodicules,<br>stamens and carpels into palea/lemma-like structures, while knockdown of *OsMADS7* or<br>*OsMADS8* using RNAi only showed mild pheno stamens and carpels into palea/lemma-like structures, while knockdown of *OsMADS7* or<br>884 *OsMADS8* using RNAi only showed mild phenotypes (Cui *et al.*, 2010). In vitro and in vivo<br>885 assays showed that OsMADS7 interacts

*OsMADS8* using RNAi only showed mild phenotypes (Cui *et al.*, 2010). In vitro and in vivo assays showed that OsMADS7 interacts with OsMADS8 and OsMADS1 and can form homodimers (Cui *et al.*, 2010).<br>887 *ZMM6* in maize is assays showed that OsMADS7 interacts with OsMADS8 and OsMADS1 and can form<br>
886 homodimers (Cui *et al.*, 2010).<br>
887<br>
2*MM6* in maize is weakly expressed in all organs of the upper and lower floret during the<br>
inflorescen 886 homodimers (Cui *et al.*, 2010).<br>887<br>888 *ZMM6* in maize is weakly exp<br>inflorescence development and<br>890 the embryo during maize ke<br>891 Cacharrón *et al.*, 1999; Lid *et a*<br>892 showed no obvious developmer<br>In barley, 888<br>889<br>890<br>891<br>892<br>893 *ZMM6* in maize is weakly expressed in all organs of the upper and lower floret during the inflorescence development and strongly expressed in the endosperm transfer cell region and the embryo during maize kernel developme

inflorescence development and strongly expressed in the endosperm transfer cell region and<br>
890 the embryo during maize kernel development (Figure 10B) (Cacharrón *et al.*, 1995;<br>
Cacharrón *et al.*, 1999; Lid *et al.*, 2 890 the embryo during maize kernel development (Figure 10B) (Cacharrón *et al.*, 1995;<br>Cacharrón *et al.*, 1999; Lid *et al.*, 2004). Loss-of-function of ZMM6 with a Mutator-insertion<br>showed no obvious developmental defect 891 Cacharrón *et al.*, 1999; Lid *et al.*, 2004). Loss-of-function of *ZMM6* with a *Mutator*-insertion<br>892 showed no obvious developmental defects in the kernel (Lid *et al.*, 2004).<br>893 In barley, *HvBM7* (also known as 892 showed no obvious developmental defects in the kernel (Lid *et al.*, 2004).<br>893 In barley, *HvBM7* (also known as *BM9*) expression has been found in an<br>894 lemma or palea and later also in lodicules and the carpel (Fi In barley, *HvBM7* (also known as *BM9*) expression has been found in anthers, but not in the lemma or palea and later also in lodicules and the carpel (Figure 10B) (Schmitz *et al.*, 2000). The wheat SEP-like protein WSEP 894 lemma or palea and later also in lodicules and the carpel (Figure 10B) (Schmitz *et al.*, 2000).<br>895 The wheat SEP-like protein WSEP has three homeologues in the wheat genome on<br>896 chromosomes 7A, 7B and 7D (Paolacci 895 The wheat SEP-like protein WSEP has three homeologues in the wheat genome on chromosomes 7A, 7B and 7D (Paolacci *et al.*, 2007; Shitsukawa *et al.*, 2007). Just before initiation of the lodicule, stamen and carpel fo 896 chromosomes 7A, 7B and 7D (Paolacci *et al.*, 2007; Shitsukawa *et al.*, 2007). Just before initiation of the lodicule, stamen and carpel formation, *WSEP* expression was detected in whorls 2, 3 and 4 (Shitsukawa *et a* initiation of the lodicule, stamen and carpel formation, *WSEP* expression was detected in whorls 2, 3 and 4 (Shitsukawa *et al.*, 2007). In all subsequent stages, expression was also detected in the palea of the floret (F whorls 2, 3 and 4 (Shitsukawa *et al.*, 2007). In all subsequent stages, expression was also detected in the palea of the floret (Figure 10B). qRT-PCR showed that there is no difference in expression between the three home detected in the palea of the floret (Figure 10B). qRT-PCR showed that there is no difference<br>
in expression between the three homeologues (Shitsukawa *et al.*, 2007). Overexpression of<br> *WSEP* in *Arabidopsis* showed earl 900 in expression between the three homeologues (Shitsukawa *et al.*, 2007). Overexpression of *WSEP* in *Arabidopsis* showed early flowering and four to five curled leaves phenotypes for all three homeologues (Shitsukawa WSEP in *Arabidopsis* showed early flowering and four to five curled leaves phenotypes for all three homeologues (Shitsukawa *et al.*, 2007). The strong expression of *WSEP* not only during floral organ differentiation, bu 902 three homeologues (Shitsukawa *et al.*, 2007). The strong expression of *WSEP* not only during<br>903 floral organ differentiation, but also after floral organ determination, suggests that *WSEP*<br>904 genes are involved in 903 floral organ differentiation, but also after floral organ determination, suggests that *WSEP* genes are involved in both floral organ differentiation but also in their subsequent development (Chang *et al.*, 2009; Mura 904 genes are involved in both floral organ differentiation but also in their subsequent<br>
905 development (Chang *et al.*, 2009; Murai, 2013; Shitsukawa *et al.*, 2007). WSEP interacts with<br>
906 the A-class WAP1, the B-cla 905 development (Chang *et al.*, 2009; Murai, 2013; Shitsukawa *et al.*, 2007). WSEP interacts with<br>
906 the A-class WAP1, the B-class WAP3 and WPI2, the C-class WAG1 and WAG2, the D-class<br>
907 WSTK and all E-class genes, 906 the A-class WAP1, the B-class WAP3 and WPI2, the C-class WAG1 and WAG2, the D-class<br>
907 WSTK and all E-class genes, except WLHS1-A (Shitsukawa *et al.*, 2007).<br>
908 *OsMADS8-clade*<br>
909 *OsMADS8-clade* 907 WSTK and all E-class genes, except WLHS1-A (Shitsukawa *et al.*, 2007).<br>908 *OsMADS8-clade*<br>909 *OsMADS8-clade* 

909<br>1 909 *OsMADS8-clade*  910 The expression pattern of the *OsMADS8* homologue in maize *ZMM27* is similar to that of *ZMM6*, showing weak expression during development of the inflorescence and strong expression during maize kernel development (Li 2*XMM6*, showing weak expression during development of the inflorescence and strong expression during maize kernel development (Lid *et al.*, 2004). Further, loss of function of *ZMM27* in a *Mutator*-insertional mutant di expression during maize kernel development (Lid *et al.*, 2004). Further, loss of function of *ZMM27* in a *Mutator*-insertional mutant did not induce obvious defects and neither did the double mutant with *ZMM6* (*Lid et* 2*MM27* in a *Mutator*-insertional mutant did not induce obvious defects and neither did the double mutant with *ZMM6* (*Lid et al., 2004*). *TaMADS1* was identified as the *OsMADS8* orthologue in wheat, with the three hom 914 double mutant with *ZMM6 (Lid et al., 2004). TaMADS1* was identified as the *OsMADS8* orthologue in wheat, with the three homeologues located on chromosomes 5A, 5B and 5D (Paolacci *et al., 2007)*. Northern blot analys 915 orthologue in wheat, with the three homeologues located on chromosomes 5A, 5B and 5D<br>916 (Paolacci *et al.*, 2007). Northern blot analysis and in situ hybridization showed that they are<br>917 uniformly expressed in the 916 (Paolacci *et al.*, 2007). Northern blot analysis and in situ hybridization showed that they are<br>917 uniformly expressed in the spikelet primordia and later confined to the carpels and stamens<br>918 (Zhao *et al.*, 2006b

917 uniformly expressed in the spikelet primordia and later confined to the carpels and stamens<br>
918 (Zhao *et al.*, 2006b). Overexpression of *TaMADS1* in *Arabidopsis* showed mild to severe<br>
919 phenotypes with early flo (Zhao *et al.*, 2006b). Overexpression of *TaMADS1* in *Arabidopsis* showed mild to severe<br>
phenotypes with early flowering and abnormal floral organs (Zhao *et al.*, 2006b).<br>
920<br>
921 Orchid and lily<br>
Expression of the Os 919 phenotypes with early flowering and abnormal floral organs (Zhao *et al.*, 2006b).<br>920 *Orchid and lily*<br>922 Expression of the *OsMADS7*-like gene in orchid, *OMADS6*, is abundant in the<br>923 labellum, carpel, anther ca 921<br>922<br>923<br>924<br>925<br>926<br>927 921 *Orchid and lily*<br>
922 Expression of t<br>
923 labellum, carpe<br>
924 PCR (Figure 10<br>
925 in early floweri<br>
926 flowers and hor<br>
927 like structures<br>
928 almost identical Expression of the *OsMADS7*-like gene in orchid, *OMADS6*, is abundant in the sepal, petal, labellum, carpel, anther cap and stigmatic cavity, and weak in the stamen, as shown by RT-<br>PCR (Figure 10B) (Chang *et al.*, 2009) 923 labellum, carpel, anther cap and stigmatic cavity, and weak in the stamen, as shown by RT-<br>
924 PCR (Figure 10B) (Chang *et al.*, 2009). Overexpression of *OMADS*6 in *Arabidopsis* resulted<br>
925 in early flowering, two 924 PCR (Figure 10B) (Chang *et al.*, 2009). Overexpression of *OMADS*6 in *Arabidopsis* resulted<br>925 in early flowering, two to four small curled leaves, terminal flowers composed of two to three<br>926 flowers and homeotic 925 in early flowering, two to four small curled leaves, terminal flowers composed of two to three<br>
926 flowers and homeotic conversions of sepals into carpel-like structures and petals into stamen-<br>
927 like structures ( Flowers and homeotic conversions of sepals into carpel-like structures and petals into stamen-<br>
927 like structures (Chang *et al.*, 2009). In lily, *LMADS3* is a *SEP3* orthologue, which shows<br>
almost identical expression 927 like structures (Chang *et al.*, 2009). In lily, *LMADS3* is a *SEP3* orthologue, which shows<br>928 almost identical expression to that of the *OsMADS1*-like gene in lily, *LMADS4* (Tzeng *et al.*,<br>929 2003). Northern bl almost identical expression to that of the *OsMADS*1-like gene in lily, *LMADS4* (Tzeng *et al.*, 2003). Northern blot analysis showed that *LMADS3* is expressed in the inflorescence meristem and later in all four floral o 2003). Northern blot analysis showed that *LMADS3* is expressed in the inflorescence meristem and later in all four floral organs, but absent in vegetative leaves (Tzeng *et al.*, 2003). Overexpression of *LMADS3* in *Arab* meristem and later in all four floral organs, but absent in vegetative leaves (Tzeng *et al.*, 2003). Overexpression of *LMADS3* in *Arabidopsis* resulted in early flowering, two to three small curled rosette leaves and tw 2003). Overexpression of *LMADS3* in *Arabidopsis* resulted in early flowering, two to three small curled rosette leaves and two curled cauline leaves (Tzeng *et al.*, 2003). Inflorescence determinacy was lost, as was prod 932 small curled rosette leaves and two curled cauline leaves (Tzeng *et al.*, 2003). Inflorescence<br>933 determinacy was lost, as was production of terminal flowers at the end of the inflorescence<br>934 that had two to three

determinacy was lost, as was production of terminal flowers at the end of the inflorescence<br>
934 that had two to three carpels.<br>
935<br>
936 **AGL6-like genes**<br>
937<br>
938 The *AGL6* subfamily is thought to be sister to the E-cl 934 that had two to three carpels.<br>935<br>936 AGL6-like genes<br>937<br>The AGL6 subfamily is thou<br>939 Theissen, 2003). Rijpkema et<br>940 ABCDE model. Arabidopsis 936<br>937<br>938<br>939<br>940<br>941 936 **AGL6-like genes**<br>
937 The AGL6 subfar<br>
939 Theissen, 2003). I<br>
940 ABCDE model. A<br>
941 have various dives<br>
942 described so far (I 938<br>939<br>940<br>941<br>942 938 The *AGL6* subfamily is thought to be sister to the E-class AGL2-like genes (Becker and Theissen, 2003). Rijpkema et al (2009) proposed adding *AGL6*-like genes to the E-class of the ABCDE model. *Arabidopsis* has two 939 Theissen, 2003). Rijpkema et al (2009) proposed adding *AGL6*-like genes to the E-class of the<br>940 ABCDE model. *Arabidopsis* has two AGL6-like genes: *AGL6* and *AGL13*, both of which<br>941 have various divergent functi 940 ABCDE model. *Arabidopsis* has two AGL6-like genes: *AGL6* and *AGL13*, both of which<br>941 have various divergent functions in the plant, although no loss-of-function mutants have been<br>942 described so far (Dreni and Zh 941 have various divergent functions in the plant, although no loss-of-function mutants have been<br>942 described so far (Dreni and Zhang, 2016). AGL6 in *Arabidopsis* can interact with some type I<br>28 942 described so far (Dreni and Zhang, 2016). AGL6 in *Arabidopsis* can interact with some type I MADS proteins, which is unusual for  $MIKC^c$ -type MADS proteins (Dreni and Zhang, 2016).

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MADS proteins, which is unusual for MIKC<sup>c</sup>-type MADS proteins (Dreni and Zhang, 2016).<br>
944 AGL6-like proteins have a C-terminus with two short, but highly conserved regions named<br>
945 AGL6-I and AGL6-II motifs (Ohmori *e* AGL6-like proteins have a C-terminus with two short, but highly conserved regions named<br>AGL6-I and AGL6-II motifs (Ohmori *et al.*, 2009).<br>946<br>In monocots the *AGL6* family has four well-defined clades: *AGL*6-I to *AGL6*-AGL6-I and AGL6-II motifs (Ohmori *et al.*, 2009).<br>
946<br>
1 In monocots the *AGL6* family has four well-define<br>
2 Zhang, 2016). Orchid sequences are part of the *A*<br>
2 Zhang, 2016). The *AGL6*-I clade in grasses can<br>
2 ZAG3 947<br>948<br>949<br>950<br>952<br>953 947 In monocots the *AGL6* family has four well-defined clades: *AGL6*-I to *AGL6*-IV (Dreni and Zhang, 2016). Orchid sequences are part of the *AGL6*-III and *AGL6*-IV clade (Dreni and Zhang, 2016). The *AGL6*-I clade in 2016). Orchid sequences are part of the AGL6-III and AGL6-IV clade (Dreni and Zhang, 2016). The *AGL6*-I clade in grasses can be further subdivided in two branches: *ZAG3/OsMADS6* and *OsMADS17* (Dreni and Zhang, 2016). Li 949 Zhang, 2016). The *AGL6*-I clade in grasses can be further subdivided in two branches:<br>950 ZAG3/OsMADS6 and OsMADS17 (Dreni and Zhang, 2016). Li *et al.* (2010) proposed a<br>4-auplication event that gave rise to these cl 27 950 *ZAG3/OsMADS6* and *OsMADS17* (Dreni and Zhang, 2016). Li *et al.* (2010) proposed a duplication event that gave rise to these clades may have occurred before the diversification of grasses . The *OsMADS17* clade is duplication event that gave rise to these clades may have occurred before the diversification<br>952 of grasses . The *OsMADS17* clade is characterised by 25 amino acid substitutions, most of<br>953 them located in the K-domain 952 of grasses . The *OsMADS17* clade is characterised by 25 amino acid substitutions, most of them located in the K-domain and the C-terminal domain. *OsMADS6*-like sequences in grasses have a highly conserved motif (MLGW

them located in the K-domain and the C-terminal domain. *OsMADS6*-like sequences in<br>954 grasses have a highly conserved motif (MLGWVL) that is different in *OsMADS17*-like genes<br>(VMGWPL) (Figure 10A) (Reinheimer and Kellog grasses have a highly conserved motif (MLGWVL) that is different in *OsMADS17*-like genes<br>
955 (VMGWPL) (Figure 10A) (Reinheimer and Kellogg, 2009).<br>
956<br>
957 The expression pattern of *AGL*6-like genes in plants shows cle 955 (VMGWPL) (Figure 10A) (Reinheimer and Kellogg, 2009).<br>956<br>957 The expression pattern of *AGL6*-like genes in plants sh<br>evolutionary changes (Reinheimer and Kellogg, 2009).<br>959 integument of the ovule is ancestral, and 957<br>958<br>959<br>960<br>961<br>962<br>963 957 The expression pattern of *AGL6*-like genes in plants shows clear differences reflecting<br>958 evolutionary changes (Reinheimer and Kellogg, 2009). Their expression in the inner<br>959 integument of the ovule is ancestral, 958 evolutionary changes (Reinheimer and Kellogg, 2009). Their expression in the inner integument of the ovule is ancestral, and is also seen in the gymnosperms. Expression in the floral meristem was acquired in angiosper 959 integument of the ovule is ancestral, and is also seen in the gymnosperms. Expression in the<br>960 floral meristem was acquired in angiosperms and expression in the second whorl organs was<br>961 acquired in monocots. Earl

960 floral meristem was acquired in angiosperms and expression in the second whorl organs was<br>
961 acquired in monocots. Early in grass evolution a new expression domain emerged in the palea<br>
962 (Reinheimer and Kellogg, 961 acquired in monocots. Early in grass evolution a new expression domain emerged in the palea<br>962 (Reinheimer and Kellogg, 2009).<br>963 Rice has two AGL6-like genes: *OsMADS6* and *OsMADS17*, which have different expressi 962 (Reinheimer and Kellogg, 2009).<br>
963 Rice has two *AGL*6-like genes: *C*<br>
965 patterns (Ohmori *et al.*, 2009;<br>
966 hybridization showed that *OsMA*<br>
967 later in the emerging palea prim<br>
968 palea, lodicules, ovule in 964<br>965<br>966<br>967<br>968<br>969 964 Rice has two *AGL6*-like genes: *OsMADS6* and *OsMADS17*, which have different expression patterns (Ohmori *et al.*, 2009; Reinheimer and Kellogg, 2009). RT-PCR and in situ hybridization showed that *OsMADS6* is expres patterns (Ohmori *et al.*, 2009; Reinheimer and Kellogg, 2009). RT-PCR and in situ<br>hybridization showed that *OsMADS6* is expressed in the floral meristem at early stages and<br>later in the emerging palea primordium (Li *et* hybridization showed that *OsMADS6* is expressed in the floral meristem at early stages and<br>14ter in the emerging palea primordium (Li *et al.*, 2010). It is also detected in developing<br>1668 palea, lodicules, ovule integum 967 later in the emerging palea primordium (Li *et al.*, 2010). It is also detected in developing palea, lodicules, ovule integuments, carpels and weakly in lemma (Figure 11B) (Dreni and Zhang, 2016; Li *et al.*, 2010). Mu palea, lodicules, ovule integuments, carpels and weakly in lemma (Figure 11B) (Dreni and Zhang, 2016; Li *et al.*, 2010). Mutants of *OsMADS6* (also called *mfo1*), showed disturbed palea and lodicule identities and had e 269 Zhang, 2016; Li *et al.*, 2010). Mutants of *OsMADS6* (also called *mfo1*), showed disturbed palea and lodicule identities and had extra carpels or spikelets (Ohmori *et al.*, 2009). *mfo1 lhs1* double mutant resulte palea and lodicule identities and had extra carpels or spikelets (Ohmori *et al.*, 2009). *mfo1*<br>
1*hs1* double mutant resulted in a severe phenotype including the loss of spikelet meristem<br>
1972 determinacy, suggesting th *lhs1* double mutant resulted in a severe phenotype including the loss of spikelet meristem determinacy, suggesting that together with OsMADS1, OsMADS6 determines floral organ and meristem identities (Li *et al.*, 2010; Oh 972 determinacy, suggesting that together with OsMADS1, OsMADS6 determines floral organ<br>
973 and meristem identities (Li *et al.*, 2010; Ohmori *et al.*, 2009). This also suggests that<br>
974 OsMADS6 has a very similar func 973 and meristem identities (Li *et al.*, 2010; Ohmori *et al.*, 2009). This also suggests that OsMADS6 has a very similar function to the E-class genes, which regulate the development of all four whorls and floral meriste 974 OsMADS6 has a very similar function to the E-class genes, which regulate the development<br>
975 of all four whorls and floral meristem determinacy (Li *et al.*, 2010). OsMADS6 can also form<br>
976 protein complexes with r 975 of all four whorls and floral meristem determinacy (Li *et al.*, 2010). OsMADS6 can also form<br>
976 protein complexes with rice B-, D- and E-class proteins in Yeast-two-Hybrid assays, which<br>
29 976 protein complexes with rice B-, D- and E-class proteins in Yeast-two-Hybrid assays, which<br>29 977 resemble the complexes formed by E-class genes with A-, B- and C-class proteins in *Arabidopsis* (Lee *et al.*, 2003a; Moon *et al.*, 1999b; Seok *et al.*, 2010). OsMADS6 also interacts with the D-class protein OsMADS *Arabidopsis* (Lee *et al.*, 2003a; Moon *et al.*, 1999b; Seok *et al.*, 2010). OsMADS6 also<br>interacts with the D-class protein OsMADS13 and B<sub>sister</sub>-class protein OsMADS29 (Favaro *et<br>al.*, 2002; Nayar *et al.*, 2014). T 979 interacts with the D-class protein OsMADS13 and B<sub>sister</sub>-class protein OsMADS29 (Favaro *et al.*, 2002; Nayar *et al.*, 2014). Together with B-class proteins it specifies lodicule identity (Dreni and Zhang, 2016). Os *al.*, 2002; Nayar *et al.*, 2014). Together with B-class proteins it specifies lodicule identity (Dreni and Zhang, 2016). OsMADS6 also represses the A-class genes *OsMADS14* and *OsMADS15. OsMADS17* is expressed in the fl 981 (Dreni and Zhang, 2016). OsMADS6 also represses the A-class genes *OsMADS14* and *OsMADS15*. *OsMADS17* is expressed in the floral meristem and later becomes restricted to the lodicule primordia and is also detected in 982 *OsMADS15*. *OsMADS17* is expressed in the floral meristem and later becomes restricted to the lodicule primordia and is also detected in the anther wall (Figure 11B) (Reinheimer and Kellogg, 2009). Suppression of *OsM* the lodicule primordia and is also detected in the anther wall (Figure 11B) (Reinheimer and<br>
1984 Kellogg, 2009). Suppression of *OsMADS17* by RNAi did not result in any morphological<br>
1985 abnormalities (Ohmori *et al.*,

Kellogg, 2009). Suppression of *OsMADS17* by RNAi did not result in any morphological<br>
985 abnormalities (Ohmori *et al.*, 2009). In *mfo1* background however, it enhanced the *mfo1*<br>
986 phenotype (Ohmori *et al.*, 2009). abnormalities (Ohmori *et al.*, 2009). In *mfo1* background however, it enhanced the *mfo1*<br>
986 phenotype (Ohmori *et al.*, 2009).<br>
987<br>
988 Maize also has two *AGL6*-like genes: ZAG3 and ZAG5 (Table 1) (Mena *et al.*, 19 986 phenotype (Ohmori *et al.*, 2009).<br>987 Maize also has two AGL6-like<br>989 Reinheimer and Kellogg, 2009).<br>1990 clade and that both ZAG3 and ZA<br>991 In situ hybridization showed that<br>992 meristems, but not in the lemma<br>1993 988<br>989<br>990<br>991<br>992<br>993 Maize also has two *AGL6*-like genes: *ZAG3* and *ZAG5* (Table 1) (Mena *et al.*, 1995;<br>Reinheimer and Kellogg, 2009). It was suggested that maize had lost the AGLI/OsMADS17-<br>clade and that both *ZAG3* and *ZAG5* are ortho Reinheimer and Kellogg, 2009). It was suggested that maize had lost the AGLI/OsMADS17-<br>clade and that both ZAG3 and ZAG5 are orthologues of *OsMADS6* (Dreni and Zhang, 2016).<br>In situ hybridization showed that ZAG3 is expr clade and that both *ZAG3* and *ZAG5* are orthologues of *OsMADS6* (Dreni and Zhang, 2016).<br>991 In situ hybridization showed that *ZAG3* is expressed in both the upper and lower floral<br>meristems, but not in the lemma and s 991 In situ hybridization showed that *ZAG3* is expressed in both the upper and lower floral meristems, but not in the lemma and stamens (Thompson *et al.*, 2009). Later in development it was observed in developing lodicu 992 meristems, but not in the lemma and stamens (Thompson *et al.*, 2009). Later in development<br>
993 it was observed in developing lodicules, palea, carpel and the inner integument of the ovule<br>
994 (Figure 11B). ZAG3 inte 993 it was observed in developing lodicules, palea, carpel and the inner integument of the ovule<br>994 (Figure 11B). ZAG3 interacts with the C-class protein ZAG1 (Reinheimer and Kellogg, 2009;<br>995 Thompson *et al.*, 2009). L 994 (Figure 11B). ZAG3 interacts with the C-class protein ZAG1 (Reinheimer and Kellogg, 2009;<br>995 Thompson *et al.*, 2009). Loss-of-function of ZAG3, known as the *bearded-ear* (*bde*) mutant,<br>996 resulted in spikelets th Thompson *et al.*, 2009). Loss-of-function of *ZAG3*, known as the *bearded-ear* (*bde*) mutant, resulted in spikelets that produce more florets with more floral organs in the tassels (Thompson *et al.*, 2009). In the ear

resulted in spikelets that produce more florets with more floral organs in the tassels<br>
(Thompson *et al.*, 2009). In the ear of the mutant, the spikelets also produce more florets,<br>
which have more palea/lemma-like organs 997 (Thompson *et al.*, 2009). In the ear of the mutant, the spikelets also produce more florets,<br>998 which have more palea/lemma-like organs and sterile ovaries.<br>999 Similar to rice and maize, orchid also has two AGL6-lik which have more palea/lemma-like organs and sterile ovaries.<br>999<br>000 Similar to rice and maize, orchid also has two AGL6-like gene<br>expression pattern of *OMADS7* is extremely similar to the<br>002 AGL6-like genes in other spe 000<br>001<br>002<br>003<br>004<br>005<br>006 1000 Similar to rice and maize, orchid also has two AGL6-like genes: *OMADS7* and *OMADS1*. The<br>
1001 expression pattern of *OMADS7* is extremely similar to the E-class gene *OMADS6* and to<br>
1002 AGL6-like genes in other s 1001 expression pattern of *OMADS7* is extremely similar to the E-class gene *OMADS6* and to<br>1002 AGL6-like genes in other species, for example *AGL6* in *Arabidopsis* and ZAG3 in maize<br>1003 (Chang *et al.*, 2009). Overexp 1002 AGL6-like genes in other species, for example *AGL6* in *Arabidopsis* and *ZAG3* in maize (Chang *et al.*, 2009). Overexpression of *OMADS7* in *Arabidopsis* resulted in early flowering, producing small curled leaves 1003 (Chang *et al.*, 2009). Overexpression of *OMADS7* in *Arabidopsis* resulted in early flowering, producing small curled leaves and homeotic conversion of sepals into carpel-like structures with stigmatic papillae (Cha 1004 producing small curled leaves and homeotic conversion of sepals into carpel-like structures<br>
1005 with stigmatic papillae (Chang *et al.*, 2009). *OMADS1* shows a different expression, only in<br>
1006 the apical meriste with stigmatic papillae (Chang *et al.*, 2009). *OMADS1* shows a different expression, only in<br>1006 the apical meristem, the labellum and carpel of the flowers (Hsu *et al.*, 2003). Yeast-two-<br>1007 hybrid analysis showed t 1006 the apical meristem, the labellum and carpel of the flowers (Hsu *et al.*, 2003). Yeast-two-<br>
1007 hybrid analysis showed that OMADS1 can interact with OMADS3 (Hsu *et al.*, 2003). Ectopic<br>
1008 expression of *OMADS1* 1007 hybrid analysis showed that OMADS1 can interact with OMADS3 (Hsu *et al.*, 2003). Ectopic expression of *OMADS1* in *Arabidopsis* and tobacco resulted in reduced plant size, early flowering and loss of inflorescence d 1008 expression of *OMADS1* in *Arabidopsis* and tobacco resulted in reduced plant size, early flowering and loss of inflorescence determinacy (Hsu *et al.*, 2003). Homeotic conversions of 30 1009 flowering and loss of inflorescence determinacy (Hsu *et al.*, 2003). Homeotic conversions of

1010 sepals into carpel-like structures and petals into staminoid structures were also observed (Hsu *et al.*, 2003).<br>
1012 AGL6-like genes seem to be involved in diverse processes in all four whorls, with conserved<br>
1013 1011 *et al.*, 2003).<br>
1012<br>
1013 AGL6-like ge<br>
1014 expression and<br>
1015 function for t<br>
1016<br>
1017 **Conclusions**<br>
1018 1013<br>1014<br>1015<br>1016<br>1017<br>1018<br>1019 1013 AGL6-like genes seem to be involved in diverse processes in all four whorls, with conserved<br>
1014 expression and function in most of the species. In orchid there seems to be a specialised<br>
1015 function for these gene

expression and function in most of the species. In orchid there seems to be a specialised<br>1015 function for these genes in the labellum formation.<br>1016<br>1017 **Conclusions and perspectives**<br>1018 MADS-box ABCDE genes are cruc 1015 function for these genes in the labellum formation.<br>
1016<br>
1017 **Conclusions and perspectives**<br>
1018<br>
1019 MADS-box ABCDE genes are crucial for floral de<br>
1020 with gene duplication, sub-functionalization<br>
1021 morpho 1017<br>1018<br>1019<br>1020<br>1021<br>1022<br>1023 1017 **Conclusions and perspectives**<br>
1018 **MADS-box ABCDE** genes are<br>
1020 with gene duplication, sub-1<br>
1021 morphological forms in plants.<br>
1022 provide information on how d<br>
1023 future crop improvement.<br>
1024 In grasse 1019<br>1020<br>1021<br>1022<br>1023<br>1024<br>1025 MADS-box ABCDE genes are crucial for floral development and their evolutionary changes<br>
1020 with gene duplication, sub-functionalization and neo-functionalization led to novel<br>
1021 morphological forms in plants. Understa with gene duplication, sub-functionalization and neo-functionalization led to novel<br>1021 morphological forms in plants. Understanding the function of these MADS-box genes can<br>1022 provide information on how different flora morphological forms in plants. Understanding the function of these MADS-box genes can<br>
1022 provide information on how different floral structures originated and identify targets for<br>
1023 future crop improvement.<br>
1024 In

movide information on how different floral structures originated and identify targets for<br>1023 future crop improvement.<br>1024 In grasses, the A-class genes underwent more gene duplications and acquired functions in<br>1025 spe 1023 future crop improvement.<br>
1024 In grasses, the A-class ge<br>
1025 specifying the grass-speci<br>
1026 picture of A-class genes in<br>
1027 As in other species, the fu<br>
1028 though there may has be<br>
1029 orchids, two separate 1024 In grasses, the A-class genes underwent more gene duplications and acquired functions in specifying the grass-specific flower organs such as the palea and lodicule. Clearly the whole picture of A-class genes in grasse specifying the grass-specific flower organs such as the palea and lodicule. Clearly the whole<br>
1026 picture of A-class genes in grasses still remains to be elucidated.<br>
1027 As in other species, the function of B-class gen picture of A-class genes in grasses still remains to be elucidated.<br>
1027 As in other species, the function of B-class genes is relatively co<br>
1028 though there may has been gene duplication and sub-functio<br>
1029 orchids, 1027 As in other species, the function of B-class genes is relatively conserved in most grasses even<br>1028 though there may has been gene duplication and sub-functionalization. Exceptionally, in<br>1029 orchids, two separate d though there may has been gene duplication and sub-functionalization. Exceptionally, in orchids, two separate duplication events have led to some remarkable changes in floral structure. *OMADS3* in orchid lost the C-termin orchids, two separate duplication events have led to some remarkable changes in floral<br>1030 structure. *OMADS3* in orchid lost the C-terminal motifs of MADS-box proteins and has<br>1031 expression signal in the vegetative lea 1030 structure. *OMADS3* in orchid lost the C-terminal motifs of MADS-box proteins and has expression signal in the vegetative leaves (Hsu and Yang, 2002; Tsai and Chen, 2006). It is speculated that *LMADS1* in lily may re 1031 expression signal in the vegetative leaves (Hsu and Yang, 2002; Tsai and Chen, 2006). It is<br>
1032 speculated that *LMADS1* in lily may represent an ancestral form of the B function gene, which<br>
1033 retains the abili 1032 speculated that *LMADS1* in lily may represent an ancestral form of the B function gene, which<br>1033 retains the ability to form homodimers and regulates petal and stamen development (Tzeng<br>1034 and Yang, 2001). Notabl 1033 retains the ability to form homodimers and regulates petal and stamen development (Tzeng<br>
1034 and Yang, 2001). Notably, the  $OsMADS30$  B<sub>sister</sub> gene has gone through neo-<br>
1035 functionalization, giving it a function and Yang, 2001). Notably, the *OsMADS30* B<sub>sister</sub> gene has gone through neo-

2001). Notably, the *OsMADS30* B<sub>sister</sub> gene has gone through neo-<br>1035 functionalization, giving it a function in vegetative development instead of ovule and seed<br>1036 development (Schilling *et al.*, 2015). Until now, 1035 functionalization, giving it a function in vegetative development instead of ovule and seed<br>
1036 development (Schilling *et al.*, 2015). Until now, little is known about the Bsister genes in<br>
1037 most of the specie development (Schilling *et al.*, 2015). Until now, little is known about the Bsister genes in<br>1037 most of the species described.<br>1038 Despite gene duplication events the C- and D-class genes seem to have retained most of most of the species described.<br>
1038 Despite gene duplication even<br>
1039 function and expression patt<br>
1040 working redundantly and the<br>
1041 ovule development because o<br>
1042 *al.*, 2003; Prasad *et al.*, 200 1038 Despite gene duplication events the C- and D-class genes seem to have retained most of their<br>
1039 function and expression patterns in monocots. Sub-functionalization has lead to genes<br>
1040 working redundantly and th 1039 function and expression patterns in monocots. Sub-functionalization has lead to genes<br>
1040 working redundantly and the rice D-class gene *OsMADS21*, has lost its ability to determine<br>
1041 ovule development because o 1040 working redundantly and the rice D-class gene *OsMADS21*, has lost its ability to determine<br>
1041 ovule development because of redundancy with *OsMADS13* (Dreni *et al.*, 2007; Fornara *et*<br>
1042 *al.*, 2003; Prasad 1041 ovule development because of redundancy with *OsMADS13* (Dreni *et al.*, 2007; Fornara *et al.*, 2003; Prasad *et al.*, 2005; Yamaguchi and Hirano, 2006). Its higher expression in 31 1042 *al.*, 2003; Prasad *et al.*, 2005; Yamaguchi and Hirano, 2006). Its higher expression in

developing kernels might suggest OsMADS21 has gone through neo-functionalization and<br>1044 has a function after fertilization (Arora *et al.*, 2007).<br>1045 The E-class genes are more difficult to compare than the other class 1044 has a function after fertilization (Arora *et al.*, 2007).<br>1045 The E-class genes are more difficult to compare t<br>1046 ABCDE model as they have diversified with the<br>1047 development during evolution. The expression of 1045 The E-class genes are more difficult to compare than the other classes of genes from the<br>1046 ABCDE model as they have diversified with the function in inflorescence and spikelet<br>1047 development during evolution. The 1046 ABCDE model as they have diversified with the function in inflorescence and spikelet<br>1047 development during evolution. The expression of *OsMADS1* homologs in grasses varies from<br>1048 species to species with the deve

development during evolution. The expression of *OsMADS1* homologs in grasses varies from<br>1048 species to species with the developmental pattern of florets in the spikelet. *OsMADS1*-like<br>1049 genes may have been involved 1048 species to species with the developmental pattern of florets in the spikelet. *OsMADS1*-like genes may have been involved in morphological diversification of inflorescences during the evolution of grass species (Yamag genes may have been involved in morphological diversification of inflorescences during the<br>
evolution of grass species (Yamaguchi and Hirano, 2006).<br>
1051 Expression of *AGL*6-like genes in the palea is conserved in all sp evolution of grass species (Yamaguchi and Hirano, 2006).<br>
1051 Expression of *AGL6*-like genes in the palea is conserved i<br>
1052 could indicate that *AGL6*-like genes might play an cor<br>
1053 (Reinheimer and Kellogg, 2009). 1051 Expression of *AGL6*-like genes in the palea is conserved in all spikelet-bearing grasses. This<br>
1052 could indicate that AGL6-like genes might play an conserved role in palea development<br>
1053 (Reinheimer and Kellogg could indicate that AGL6-like genes might play an conserved role in palea development<br>1053 (Reinheimer and Kellogg, 2009). It has been proposed that AGL6-like genes may have played<br>1054 an important role in the evolution o

1053 (Reinheimer and Kellogg, 2009). It has been proposed that AGL6-like genes may have played<br>1054 an important role in the evolution of unique flower features, such as the labellum in orchids<br>1055 (Dreni and Zhang, 2016) an important role in the evolution of unique flower features, such as the labellum in orchids<br>1055 (Dreni and Zhang, 2016).<br>1056<br>Characterisation of these genes, their structure, their expression pattern and their function 1055 (Dreni and Zhang, 2016).<br>
1056<br>
1057 Characterisation of these g<br>
1058 give greater insight into the<br>
1059 can sometimes be mislea<br>
1060 confirm whether genes<br>
1061 development. In line with<br>
1062 unexplored role in m 1057<br>1058<br>1059<br>1060<br>1061<br>1062<br>1063 Characterisation of these genes, their structure, their expression pattern and their function will<br>1058 give greater insight into their role in flower development. Importantly, phylogenetic analysis<br>1059 can sometimes be m give greater insight into their role in flower development. Importantly, phylogenetic analysis<br>
1059 can sometimes be misleading, and data from functional analysis experiments are needed to<br>
1060 confirm whether genes belo can sometimes be misleading, and data from functional analysis experiments are needed to<br>1060 confirm whether genes belong in specific clades and still retain a function in flower<br>1061 development. In line with this, neo-f 1060 confirm whether genes belong in specific clades and still retain a function in flower development. In line with this, neo-functionalization likely plays a relatively important and unexplored role in monocot floral div development. In line with this, neo-functionalization likely plays a relatively important and<br>1062 unexplored role in monocot floral diversity.The identification of orthologues is currently<br>1063 heavily reliant on sequence 1062 unexplored role in monocot floral diversity.The identification of orthologues is currently<br>1063 heavily reliant on sequence similarities, but due to the many gene duplication events that have<br>1064 shaped the MADS-box heavily reliant on sequence similarities, but due to the many gene duplication events that have<br>1064 shaped the MADS-box family, some MADS-box genes in monocots have gained new roles,<br>1065 or lost their ancestral function. 1064 shaped the MADS-box family, some MADS-box genes in monocots have gained new roles,<br>1065 or lost their ancestral function. It must also be noted that most of these sequences are<br>1066 extracted from reference genomes, a 1065 or lost their ancestral function. It must also be noted that most of these sequences are extracted from reference genomes, and therefore a much greater level of diversity may be present in the pangenome that is not re extracted from reference genomes, and therefore a much greater level of diversity may be<br>1067 present in the pangenome that is not represented here. Since flower development is one of the<br>1068 major determinants for yield major determinants for yield in important crops, improving our understanding about the genes<br>
1069 major determinants for yield in important crops, improving our understanding about the genes<br>
1069 and networks involved in major determinants for yield in important crops, improving our understanding about the genes<br>
1069 and networks involved in flower development is an essential tool to help towards devising<br>
1070 new strategies for crop imp and networks involved in flower development is an essential tool to help towards devising<br>1070 new strategies for crop improvement.<br>1071 Acknowledgements<br>1073 We thank Dr. Julian Schwerdt for help with the phylogenetic ana

1070 new strategies for crop improvement.<br>
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### **Figure Legends**

**Table 1 The ABCDE genes in** *Arabidopsis* **and monocot species.** Listed are the genes in model organism *Arabidopsis* and the orthologs in monocots rice (*Oryza sativa*), maize (*Zea mays*), barley (*Hordeum vulgare*), wheat (*Triticum aestivum*), orchid (*Oncidium Gower Ramsey*) and lily (*Lilium*  l*ongiflorum*) that have been identified to date.

 **Figure 1 Rice, maize, wheat, barley, orchid and lily floral structures.** (A) A rice floret has four whorls: a lemma (le) and palea (pa) in whorl 1 that protect the floret, two lodicules (lo) in whorl 2, six stamens (sta) in whorl 3 and a carpel (ca) in whorl 4. (B) Barley and wheat florets are very similar, but only have 3 stamens. (C) Maize has two separate inflorescences, a male (tassel) and a female (ear) one. Spikelets consist of a pair of florets: the upper floret (uf) and lower floret (lf). Female florets (C, left) have a lemma, palea, two lodicules and a carpel, but no stamens. Male florets (C, right) have a lemma, palea, two lodicules and three stamens, but no carpel. Both are protected by glumes (glu). (D) Orchids have three sepals in the first whorl and two petals and a labellum (lab) in the second whorl. The third and fourth whorl are located in the column. (E) Lily has five tepals in the first and second whorl, 6 stamens in the third whorl and a carpel in the fourth whorl.

**Figure 2 Structure of MIKC-type MADS-box proteins.** MIKC-type MADS-box proteins consist of a highly conserved MADS-box domain, responsible for DNA-binding, dimerization and accessory factor binding. The Intervening domain is weakly conserved and a regulatory determinant for the formation of DNA-binding dimers. The K-box is a keratin-like domain that mediates protein-protein interactions. The C-terminal domain is the most variable domain and is involved in transcriptional activation and formation of transcription factor complexes. As an example MIKC-type proteins from maize (ZMM2), wheat (WAG2), rice (OsMADS3), orchid (OMADS4), lily (LMADS10), barley (HvBM3) and *Arabidopsis* (AG), all C-class genes, were aligned and their domains were highlighted. The C-terminal domain for AG was significantly different in sequence to that of the monocots and is therefore highlighted in a different colour. MUSCLE multiple alignment of protein sequences from the NCBI, IPK and MSU rice databases.

 **Figure 3 The ABCDE model in rice florets. The model depicts the pattern of gene expression**  required for normal whorl development. The MIKC<sup>c</sup>-type MADS-box proteins are divided in different classes: A, B, C, D and E-class. The B<sub>sister</sub> proteins are classified as B-class proteins, but have a distinct function. AGL6-like proteins are often classified together with the E-class proteins because

they have similar functions. These proteins form complexes to determine the identity of floral organs shown here in a rice floret: lemma (le), palea (pa), lodicules (lo), stamen (sta), carpel (ca) and ovule (ov).

**Figure 4 Phylogenetic analysis of ABCDE MADS-box genes from** *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.** Phylogenetic tree obtained with RAxML tree building through Geneious version 8.0 by Biomatters. Available from http://www.geneious.com. Maximum likelihood tree from 1000 bootstrap replicates. MUSCLE multiple alignment of protein sequences from the NCBI, IPK and MSU databases was used. BMGE clean up of the multiple aligment via Galaxy@pasteur (https://galaxy.pasteur.fr). The different subfamilies are represented by different colours: SQUA (orange), DEF/GLO (pink), GMM13 (blue), AG (green), AGL2 (purple), AGL6 (red). Alignments of all proteins in the different subfamilies can be found in the supplemental figures S1-7.

Figure 5 **Figure 5 Sequence alignment and expression patterns of A-class MADS-box genes in**  *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, barley, wheat, orchid and lily.** (A) The conserved FUL-like motif (LPPWML) can be found in all the monocot A-class MADSbox genes, with only minor differences. In HvBM5 and WFUL1 the Proline at the third position has been substituted by a Leucine, while the Leucine at the sixth position has been substituted for a Valine. In OsMADS20 the Proline at the third position has been substituted by a Tryptophan and in LMADS7 the Leucine at the sixth position has been substituted by an Isoleucine. (B) The expression patterns appear conserved in the grasses, with some diversity in orchid and lily. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

**Figure 6 Sequence alignment and expression patterns of B-class MADS-box genes in**  *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, barley, wheat, orchid and lily.** The B-class genes can be subdivided in two different clades: the DEF- and the GLO-clade. (A) Multiple alignment of protein sequences from the NCBI, IPK and MSU rice databases. Both clades have different motifs, a paleoAP3-motif (YGxHDLRLA) or a PI-motif (MPFTFRVQPSHPNL) respectively. HVPI and WPI1 have similar differences in the motif, as have LMADS8 and OMADS8. HvBM2, WPI2, OsMADS2 and ZMM16 also have similar differences, identifying them as homologs. LMADS9 is a truncated version of LMADS8 and does not have the PI-motif. All members of the monocot DEF-clade have a variation of the motif, except OMADS3. (B) The expression patterns of the grasses are conserved and have diversified in orchid and lily. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square

indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

Figure 7 Sequence alignment and expression patterns of B<sub>sister</sub>-class MADS-box genes in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, barley, wheat, orchid and lily.** (A) Multiple alignment of protein sequences from the NCBI, IPK and MSU rice databases. A conserved PI-derived motif can be found in the B-sister genes together with another unidentified motif downstream of the PI-derived motif. Variations in the PI-derived motif seems to divide the B-sister genes into two groups. One group consisting of ZMM17, OsMADS29, WBsis and HvBM29 has GFRLQPTQPNLQDP as the PI-derived motif. The other group consisting of OsMADS31 and HvBM31 has YKLQPL/VQPNLQE as the PI-derived motif. An unidentified TALQL motif can be found in all monocot  $B_{\text{sister}}$  genes, which is remarkably similar to the motif found in the C-class MADS-box genes (see Figure 8). OsMADS30 contains neither of the two motifs. (B) The expression pattern of B<sub>sister</sub> genes that have been investigated show conservation in the female reproductive organs. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

 **Figure 8 Sequence alignment and expression patterns of C-class MADS-box genes in**  *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.** (A) The C-class genes are very conserved throughout the entire sequence. A small distinction can be made at the C-terminus where the TALQL motif, that is also present in the B<sub>sister</sub> genes, can be found in some of the homologs. Expression of C-class genes seems to be conserved in all species. (B) The expression pattern of C-class genes are conserved across all species that have been investigated to date. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

**Figure 9 Sequence alignment and expression patterns of D-class MADS-box genes in**  *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.** (A) Multiple alignment of protein sequences from the NCBI, IPK and MSU rice databases The Cand D-class MADS-box genes in monocots can be distinguished by a conserved glutamine at position 105 and a single amino acid insertion at position 90 in the D-lineage. Remarkably, HvBM21 doesn't have a glutamine, but a leucine at position 105. It seems that most monocot genes have a glutamine insertion at position 90, except OsMADS21, that has a histidine. (B) Expression of D-class genes

seems to be conserved among all species. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

**Figure 10 Sequence alignment and expression patterns of E-class MADS-box genes in**  *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.** (A) Multiple alignment of protein sequences from the NCBI, IPK and MSU rice databases. The distinction between the two subgroups can clearly be seen, with the OsMADS1-group less related to the *Arabidopsis* SEP genes and the OsMADS7-group more closely related to the SEP genes. (B) Expression of E-class genes in very diverse, but seems to be mostly conserved among the different species. Maize seems to have distinct genes with specified expression. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

**Figure 11 Sequence alignment and expression patterns of AGL6-like MADS-box genes in**  *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.** (A) Multiple alignment of protein sequences from the NCBI, IPK and MSU rice databases. The AGL6-like genes are very conserved throughout the entire sequence. At the C-terminus (A), the motif for the OsMADS6-like genes (MLGWVL) can be distinguished, while the OsMADS17-like genes have a different motif (VMGWPL). (B) The expression pattern of AGL6-like genes seems to be conserved among the different species, with the exception of the labellum in orchid. Red squares indicate multiple genes expressed in this tissues, while orange indicates only one gene expressed in this tissue. White square indicate there is no expression and grey squares indicate no data is available about the expression in these tissues.

Supplemental Figure S1 Sequence alignment of A-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**

 Supplemental Figure S2 Sequence alignment of B-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**

 Supplemental Figure S3 Sequence alignment of Bsister-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**

 Supplemental Figure S4 Sequence alignment of C-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**

 Supplemental Figure S5 Sequence alignment of D-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**

Supplemental Figure S6 Sequence alignment of E-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**

 Supplemental Figure S7 Sequence alignment of AGL6-class proteins in *Arabidopsis, Amborella trichopoda, Populus trichocarpa***, rice, maize, wheat, barley, orchid and lily.**











 $\bf{B}$ 

A

**Class A** 





 $\, {\bf B}$ 

**Class B** 





## $\, {\bf B}$







# $\bf{B}$

**Class C** 





## $\bf{B}$





 $\, {\bf B}$ 

### **Class E**





 $\, {\bf B}$ 

**Class AGL6** 

