Volatile Glycosylation in Tea Plants: Sequential Glycosylations for the Biosynthesis of Aroma β -Primeverosides Are Catalyzed by Two Camellia sinensis Glycosyltransferases

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Volatile glycosylation in tea plants: Sequential glycosylations for the biosynthesis of aroma

23 β-primeverosides are catalyzed by two *Camellia sinensis* glycosyltransferases

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39 One-Sentence Summary:

40 Two glycosyltransferases catalyze sequential glycosylations of volatiles important for 41 tea aroma quality, leading to stable accumulation of the volatiles as the water-soluble 42 β -primeverosides.

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43 **Footnotes**

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58 Abstract

Tea plants (Camellia sinensis) store volatile organic compounds (VOCs; monoterpene, 5960 aromatic, and aliphatic alcohols) in the leaves in the form of water-soluble diglycosides, 61 primarily as β -primeverosides (6-O- β -D-xylopyranosyl- β -D-glucopyranosides). These 62VOCs play a critical role in plant defenses and tea aroma quality, yet little is known 63 about their biosynthesis and physiological roles in planta. Here we identified two UDP-glycosyltransferases (UGTs) from C. sinensis: UGT85K11 (CsGT1) and 64 65 UGT94P1 (CsGT2), converting VOCs into β -primeverosides by sequential 66 glucosylation and xylosylation, respectively. CsGT1 exhibits a broad substrate 67 specificity toward monoterpene, aromatic and aliphatic alcohols to produce the 68 respective glucosides. On the other hand, CsGT2 specifically catalyzes the xylosylation 69 of the 6'-hydroxy group of the sugar moiety of geranyl β -D-glucopyranoside, producing 70geranyl β -primeveroside. Homology modeling, followed by site-directed mutagenesis of 71CsGT2, identified a unique isoleucine 141 residue playing a crucial role in sugar donor 72specificity toward UDP-xylose. The transcripts of both CsGTs were mainly expressed in 73young leaves, along with β -primeverosidase (β -PD) encoding a diglycoside-specific 74glycosidase. In conclusion, our findings reveal the mechanism of aroma 75 β -primeverosides biosynthesis in C. sinensis. This information can be used to preserve 76 tea aroma better during the manufacturing process and to investigate the mechanism of 77plant chemical defenses.

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79 Introduction

Plants emit volatile organic compounds (VOCs), such as monoterpenes (C10), 80 81 sesquiterpenes (C15), phenylpropanoids (C9), norisoprenoids (C16), aromatic esters, or 82 green leaf alcohols (C6), in response to attacks by insect herbivores, mechanical 83 wounding, or endogenous developmental cues. In general, VOCs are considered not 84 only to be chemical defense compounds transmitting biological signals to the 85 environment (Arimura et al., 2009), but also important commercial products because 86 they influence the quality and character of dietary foods and beverages as aromas. Tea, 87 manufactured from Camellia sinensis (Fig. 1A), is the most popular beverage in the 88 world, and is classified as black, green or oolong tea based on the manufacturing 89 processes (withering, rolling, and fermentation), which affects the composition and 90 quantity of aroma compounds (Balentine et al., 1997; Graham, 1992). For instance, 91 black tea is produced by full fermentation, during which tea metabolites artificially react 92 with endogenous enzymes (e.g., polyphenol oxidases and β -glucosidases). Floral tea 93 aroma is one of the crucial components to evaluate the value and quality of tea products. 94 The floral aroma caused by linalool, geraniol, 2-phenylethanol (2-PE) and benzyl 95 alcohol are predominant flavor volatile compounds in oolong tea and black tea, whereas 96 (Z)-3-hexenol adds a grassy note to green tea (Kawakami et al., 1995; Kumazawa and 97 Masuda, 2002). However, fresh leaves of C. sinensis barely emit a slightly green note 98 before they are processed for tea. This is because aroma volatiles in tea leaves are accumulated typically as water-soluble glycoside form. Since the first report on the 99 100 isolation of benzyl β -D-glucopyranoside (benzyl-glc) (Yano et al., 1991), various aroma

101 glycosides have been identified in fresh tea leaves (Kobayashi et al., 1994). The 102 chemical structure of most glycosides was shown to be β -primeveroside 103 $(6-O-\beta-D-xylopyranosyl-\beta-D-glucopyranoside; Guo et al., 1993, 1994; Moon et al.,$ 104 1994, 1996), suggesting that a common biosynthetic machinery for the conjugation of 105 β -primeveroside to aroma volatiles exists. Previous quantitative analysis of aroma 106 glycosides in tea leaves demonstrated that levels of aroma β -primeverosides are 107 three-fold higher than monoglycosides (Wang et al., 2000), indicating that sequential 108 sugar conjugating reactions to aroma volatiles (glucosylation followed by xylosylation) 109 occur in tea leaves. Highly diverse aroma volatiles, such as benzyl alcohol, 2-PE, 110 (Z)-3-hexenol, linalool and geraniol, are stored as β -primeverosides in the leaves of C. 111 sinensis (Guo et al., 1993, 1994; Moon et al., 1994, 1996). Aromatic alcohols, such as 112 benzyl alcohol and 2-PE, serve as attractants for both parasitic and predatory insects for 113 herbivores and (Z)-3-hexenol released from herbivore-damaged tissue has also been 114 found to induce defense responses in neighboring plants (Pichersky and Gershenzon, 1152002; Sugimoto et al., 2014). Monoterpene alcohols such as geraniol and linalool have 116 potential activity toward microorganisms and fungi and geraniol also has a potent 117 apoptosis-inducing activity in plant cells (Pattnaik et al., 1997; Izumi et al., 1999). 118 Mizutani et al. (2002) reported that a β -primeverosidase (β -PD) from C. sinensis 119 specifically hydrolyzes aroma β -primeverosides into primeverose (disaccharide unit) 120 and aroma volatile (aglycone unit). The data support the idea that aroma β -PDs are the 121key enzymes responsible for the production of chemical defense compounds against 122pathogens and herbivores as well as for the characteristic aromas of tea products. Thus,

123 it is of particular interest to understand the biosynthesis and physiological role of aroma 124 β -primeverosides in *C. sinensis*. However, corresponding genes for biosynthesis of 125 volatile β -primeverosides have so far not been reported.

126 Previous attempts to over-produce volatile compounds in plants by over-expressing 127 genes that are responsible for the biosynthesis of aglycones often resulted in the 128 accumulation of respective glycosides. For example, ectopic expression of Clarkia 129breweri (S)-linalool synthase (LIS) in Petunia hybrida resulted in the accumulation of 130 (S)-linalyl β -D-glucopyranosides ((S)-linalyl-glc) (Lücker et al., 2001) and transgenic 131 Arabidopsis plants expressing a strawberry terpene synthase (FaNES1) produced 132 (S)-linalool, nerolidol, and the glycosylated derivatives (Aharoni et al., 2003). Moreover, 133 relieving a bottleneck in the endogenous eugenol pathway by heterologous 134 over-expression of a *P. hybrida* coniferyl alcohol acetyltransferase (*PhCFAT*) gene 135resulted in up to 7- and 22-fold increase in the levels of eugenol, and its glycoside 136 (eugenyl-glc), respectively, in leaves of transgenic aspen plants (Koeduka et al., 2013). 137 These results suggest that glycosylation of volatiles is a general phenomenon in land 138 plants.

Here we demonstrate the biochemical and molecular characteristics of two UDP-glycosyltransferases (UGTs) from *C. sinensis*, UGT85K11 (CsGT1) and UGT94P1 (CsGT2), responsible for the sequential glucosylation and xylosylation in the biosynthesis of volatile β -primeverosides (Fig. 1B). In addition, we discuss the physiological roles that volatile metabolites might play in plants, based on the distribution of aroma precursors and spatiotemporal expression pattern of these UGT

- 145 genes in C. sinensis.
- 146
- 147
- 148 **Results**

149 Organ-specific composition in aroma monoglycosides and diglycosides

150Aroma monoglycosides and diglycosides were extracted from fresh leaves and 151stems at two developmental stages (young and mature) of C. sinensis. Various 152 β -primeverosides, as well as monoglycosides of aroma compounds in tea leaves, were 153quantified by liquid chromatography-mass spectrometry (LC-MS) (Fig. 2). The results 154show that geranyl β -primeveroside (geranyl-pri) and linalyl β -primeveroside 155(linalyl-pri) were the two primary aroma glycosides that were detected mainly in young 156 organs, leaves and stems, respectively. These data also suggest that the metabolic 157activity of the glycosylation machinery responsible for the biosynthesis of aroma 158 β -primeverosides is higher in growing young tissues. As the tea leaves grew, the total 159amounts of 2-phenylethyl β -primeveroside (2PE-pri), benzyl β -primeveroside 160 (benzyl-pri), and (Z)-3-hexenyl β -primeveroside (hexenyl-pri) increased in the mature 161 leaves, whereas those of geranyl-pri and linalyl-pri decreased (Supplemental Table S1). 162Since the overall fresh weight of the mature leaves was approximately four times larger 163 than in young leaves, the apparent concentrations of geranyl-pri and linalyl-pri were 164 substantially decreased in mature leaves. The results suggested that these two 165 β -primeverosides were further metabolized to unknown chemical forms or were 166 transferred from young leaves to other parts of the plant.

168 Identification of Arabidopsis UGT85A3 showing trans-glucosylation activity 169 toward volatiles

170of monoglucosides Concurrent occurrence and primeverosides of the 171corresponding volatiles in tea leaves suggested that primeverosides are biosynthesized via two sequential glycosylations steps, an initial glucosylation, followed by 172173 xylosylation rather than by direct conjugation of the primeverosyl moiety to the 174volatiles. We therefore searched for glucosyltransferases potentially responsible for the 175first glucosylation step in aroma β -primeveroside biosynthesis. For several classes of 176 specialized metabolites, the biosynthetic genes are often found co-expressed 177(Fukushima et al., 2011). Transcriptome expression profiles and co-expression analysis 178became powerful tools for prediction of the biosynthetic genes constituting the 179metabolic pathway (Fukushima et al., 2011, Ginglinger et al., 2013, Usadel et al., 2009). However, a co-expression analytical tool for *C. sinensis*, a non-model plant, 180 181 are not yet available. For identification of the glucosyltransferases catalyzing the first 182 glucosylation of volatiles, we surveyed UGTs co-expressing with structural genes for 183 monoterpene biosynthesis in Arabidopsis by ATTED II (http://atted.jp), which is a 184 database developed to identify functionally related genes by co-expression. 185 By using geraniol/nerol 10-hydroxylase gene (At2g45580; CYP76C3) and linalool 186 synthase gene (At1g61680; AtLIS) (Ginglinger et al., 2013; Mizutani et al., 1997; 187Obayashi et al., 2011) as probes, we found that the expression profiles of Arabidopsis 188 UGT85A3 (At_UGT85A3, At1g22380; r = 0.873) exhibits relatively high correlation

with *AtLIS and CYP76C3* (Supplemental Fig. S1). *In vitro* functional characterization of At_UGT85A3 was performed using UDP-glucose as a sugar donor and geraniol or (*Z*)-3-hexenol as a sugar acceptor revealed that At_UGT85A3 produced geranyl-glc from geraniol and hexenyl-glc from (*Z*)-3-hexenol (Supplemental Fig. S2 and Supplemental Fig. S3). These data demonstrate that At_UGT85A3 is capable of catalyzing the glucosylation of monoterpene alcohols and aliphatic alcohols.

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196 Identification of a *C. sinensis* UGT catalyzing the first glucosylation step for 197 volatile β -primeveroside.

198 To isolate C. sinensis UGTs responsible for the first glucosylation step in volatile 199 β -primeveroside biosynthesis, a cDNA library constructed from a mixture of leaves, 200 stem and roots of C. sinensis (Mizutani et al., 2002) was screened with digoxigenin 201(DIG)-labeled At_UGT85A3. Two rounds of screening identified four novel UGTs, 202 which were individually expressed in Escherichia coli and subjected to enzyme activity 203 assays using UDP-glucose as a sugar donor and a variety of volatile alcohol acceptors. 204We found that one of the UGTs, named CsGT1, catalyzes glucosylation of geraniol as 205shown by the appearance of a product peak at the retention time of 10.2 min with m/z206 361 ([M + HCOO]⁻), both values of which correspond to those of authentic geranyl-glc 207(Fig. 3A and Fig. 3B). CsGT1 was assigned as Cs_UGT85K11 by the committee 208responsible for naming UDP-glucuronosyltransferases (Mackenzie et al., 1997).

209 The maximum velocity (V_{max}) and estimated apparent K_m values of CsGT1 for 210 geraniol were 332.1 ± 8.1 nkat mg⁻¹ protein and 44.2 ± 3.0 µM, respectively (Table 1). 211The sugar acceptor specificity of CsGT1 was surveyed using six aroma alcohols and 212two flavonoids found in the leaves of C. sinensis. CsGT1 was active toward all six 213volatiles with relative activities: geraniol (100%), eugenol (84%), (Z)-3-hexenol (62%), 214benzyl alcohol (48%), 2-PE (9.2%), and linalool (1.4%), whereas CsGT1 did not accept 215quercetin or cyanidine as substrates (Fig. 3C). On the other hand, CsGT1 showed clear 216 preference to UDP-glucose (100%) as a sugar donor compared to UDP-galactose (15%), 217UDP-xylose (n.d.), and UDP-glucuronic acid (n.d.) when geraniol was used as a sugar 218 acceptor (Fig. 3D). Taken together, these data indicate that CsGT1 preferentially 219 glucosylates volatiles using UDP-glucose as a specific sugar donor but exhibits a broad 220 substrate specificity for sugar acceptors.

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222 Identification of orthologous UGTs of CsGT1 from various plants

223 Volatile glycosides are reported in different plant species, including apricot, peach, 224yellow plum (Krammer et al., 1991), grape berries (Günata et al., 1985), kiwi (Young 225and Paterson, 1995), strawberry (Roscher, et al., 1997), raspberry (Pabst et al., 1991), 226 and tomato (Marlatt, et al., 1992). Based on these general observations, we searched for 227UGTs in the NCBI Genbank (www.ncbi.nlm.nih.gov) based on amino acid sequence 228similarities with CsGT1 (accession number: AB847092). We found homologous UGTs 229broadly represented throughout the angiosperm plant lineages. We cloned another five 230Vv_UGT85A28, UGTs from grapevine vinifera: Vv UGT85A33. (Vitis 231Vv_UGT85A30), sweet potato (Ipomoea batatas: Ib_UGT85A32), and snapdragon 232(Antirrhinum majus: Am_UGT85A13), and experimentally characterized the 233 recombinant enzymes by the procedure used for CsGT1. They exhibited volatile 234 glycosylating activities similar to CsGT1, including the production of geranyl-glc and 235 hexenyl-glc (Supplemental Fig. S2 and S3). These data show that UGTs with structural 236 similarities, capable of catalyzing the first glucosylation step of aroma diglycosides 237 such as β -primeverosides are widely conserved in various plant lineages.

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239 Purification of *C. sinensis* UGT catalyzing the second xylosylation step

240To identify the UGT that is responsible for the second step (6-O-xylosylation for 241glucose moiety of aroma monoglucoside) which is the conversion of aroma glucosides 242to aroma β -prime verosides, xylosyltransferase from young tea leaves was purified based 243on the xylosylation activity using geranyl-glc as a substrate at each step. The 244purification of the xylosyltransferase through seven purification steps resulted in 24513.0-fold enrichment (Supplemental Table S2). Protein purity was assessed by 246SDS-PAGE, followed by silver staining (Supplemental Fig. S4). Each excised protein 247band was subjected to LC-MS/MS to determine the partial amino acid sequence. De 248novo analysis (PEAKS Software, www.bioinfor.com) identified three peptide sequences 249(Fig. S 5A). Using the three peptide sequences (FPEVEKVELEEALPK, GLVVEGWAPQAR, and EEIEEIAHGLELSMVNFIWVVRFPEVEK) obtained from a 250251single protein band, the corresponding cDNA was surveyed by a tBLASTn search in a 252C. sinensis EST database constructed by 454 GS-FLX (Roche) (Ohgami et al. 2014). 253Contig134, encoding a partial UGT gene, was identified as the most likely candidate 254gene. A cDNA clone was isolated, carrying the sequence of contig134 in a

1362-bp ORF encoded a polypeptide of 453 amino acid residues (calculated M.W:
51.3 kDa). The encoded polypeptide was named CsGT2, which was assigned as
UGT94P1 by the committee responsible for naming UDP-glucuronosyltransferases
(Mackenzie et al., 1997).

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260 **Biochemical characterization of the xylosyltransferase**

261To test whether CsGT2 catalyzes the xylosylation of aroma glucosides into 262 aroma β -primeverosides (Fig. 4A), we performed heterologous expression of CsGT2 in 263E. coli (Supplemental Fig. S6A) and in vitro enzymatic assays with recombinant CsGT2, 264UDP-xylose as a sugar donor and geranyl-glc as a sugar acceptor. Figure 4B shows that 265CsGT2 produced a new peak with a retention time at 4.9 min. This peak was identical to 266 the authentic geranyl-pri, which was structurally determined to be xylosylated at the 267C-6'position of the glucoside moiety by nuclear magnetic resonance spectroscopy 268(NMR) (Guo et al, 1993). These results demonstrate that CsGT2 specifically catalyzes the xylosylation toward the C-6' position of geranyl-glc. The V_{max} and estimated 269apparent $K_{\rm m}$ values of CsGT2 were determined to be 60.0 ± 4.8 nkat mg⁻¹ protein and 270271 $78.1 \pm 19.6 \mu$ M, respectively (Table I). The substrate specificity of CsGT2 was 272determined using four aroma glucosides and one non-natural glucoside as sugar 273acceptors. CsGT2 was active toward all four aroma glucosides with the following relative activities: geranyl-glc (100%), 2-phenylethyl β -D-glucopyranoside (2PE-glc) 274275(16%), linalyl-glc (12%), and eugenyl-glc (2%), but not toward the non-natural 276*p*-nitrophenyl β -D-glucopyranoside (*p*NP-glc) (Fig. 4C). It is important to mention that

277 CsGT2 did not exhibit any activity toward monoterpene alcohols (volatile aglycones).

278 On the other hand, investigation of the specificity of CsGT2 toward various 279 sugar donors using geranyl-glc as a sugar acceptor revealed that CsGT2 preferentially 280 used UDP-xylose (100%) as a sugar donor, while a weak activity was detected with 281 UDP-glucose (30%) and no apparent activity for UDP-glucuronic acid or 282 UDP-galactose (Fig. 4D). These results demonstrate that CsGT2 preferentially catalyzes 283 the xylosylation of aroma glucosides, leading to the formation of aroma 284 β -primeverosides.

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286 Homology modeling and mutagenesis analysis of CsGT2

287 The sugar donor specificity of UGTs is dictated by a small number of amino 288 acid residues (Osmani et al., 2008, Noguchi et al., 2009, Ono et al. 2010a). The residues 289are located in three distinct domains: N-terminal, middle, and C-terminal (PSPG-box) 290(Sayama et al., 2012). To gain insights into the molecular mechanism of UDP-xylose 291specificity of CsGT2, we constructed a structural model of CsGT2 by homology 292 modeling (Discovery Studio 3.5, Accelrys). The crystal structures of the 293glycosyltransferases, At_UGT72B1 (PDB code: 2vce) and Mt_UGT85H2 (PDB code: 2942pq6), were selected as templates for their similarities to CsGT2. In addition, we used 295the three-dimensional (3D) structure of the sugar donor, UDP-2F-Glc, and the crystal 296 structure of grape UDP-glucose:flavonoid 3-O-glycosyltransferase VvGT1 (PDB code: 297 2c1z) (Offen et al., 2006). In the constructed homology model, Ile141 was identified as 298a candidate residue for the control of sugar donor specificity because it is located 299proximal to UDP-xylose (Fig. 5A and Fig. 5E). This unique Ile141 was found to be 300 conserved in two xylosyltransferases specific for flavonoid glycosides, kiwi F3GGT1 301 (Ile136) and *Arabidopsis* UGT79B1 (Ile142) (Montefiori et al.. 2011. 302 Yonekura-Sakakibara et al., 2012) (Table II). In contrast, various amino acid residues 303 occupy this position in other structurally similar glycosyltransferases, including 304 Ipomoea purpurea UGT79G16 (Thr138), Sesamum indicum UGT94D1 (Ser140), 305 Veronica persica UGT94F1 (Ala144), and Solanum lycopersicum Nonsmoky 306 glycosyltransferase 1 (Sl NSGT1) (Val145) (Table II) (Morita et al., 2005, Noguchi et 307 al., 2008, Ono et al., 2010b, Tikunov et al., 2013). To assess the functional relevance of 308 Ile141 for the specificity toward UDP-xylose, a CsGT2-I141S mutant was generated by 309 site-specific mutagenesis, in which Ile141 was replaced by a Ser residue. CsGT2-I141S 310 was heterologously expressed in E. coli (Supplemental Figure S6B). Compared with 311 wild-type CsGT2, the mutant exhibited significantly lower activity with UDP-xylose 312 but higher activity with UDP-glucose (Fig. 5C and Fig. 5D). These experiments 313 identified Ile141 as the crucial residue responsible for the sugar donor specificity of 314 CsGT2 for UDP-xylose.

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316 Gene expression and phylogenetic analysis of CsGT1 and CsGT2

317 The tissue specificity of the glycosylation of volatiles was assessed by 318 quantitative real-time polymerase chain reaction (qRT-PCR) performed with specific 319 organs of *C. sinensis* (leaves from young to fully mature stage, stems, roots and 320 flowers). Both *CsGT1* and *CsGT2* were highly expressed in young leaves, where β -PD 321 was also found to be highly expressed (Fig. 6). During leaf maturation, the expression 322 of *CsGT1* and *CsGT2* decreased, which is consistent with the accumulation profile of 323 β -primeverosides (Fig. 2).

324 Sequence analysis indicated that CsGT1 and CsGT2 only share 27% amino 325acid identity. Phylogenetic analysis showed that CsGT1 and CsGT2 belong to different 326 clades, OG2 and OG8, respectively (Yonekura-Sakakibara and Hanada, 2011) (Fig. 7). 327 CsGT1 showed high similarity to cassava UGT85K4, and UGT85K5 involved in the 328 biosynthesis of cyanogenic glucosides (Kannangara et al., 2011). In contrast, CsGT2 329 constitutes a new member of the so-called "sugar-sugar UGT" or glycoside-specific 330 glycosyltransferase (GGT) group that specifically catalyzes glycosylation at the sugar 331 moiety of various phytochemical glycosides (but not aglycones), including the morning 332 glory Dusky (UGT79G16), and tomato NSGT1 involved in the glucosylation of 333 anthocyanin and volatile glycosides, respectively (Morita et al., 2005, Tikunov et al., 334 2013).

335

336 Tissue localization of a selected aroma glycosidic precursor

337 The preferential expression of the two *CsGTs* in young leaves is consistent 338 with the accumulation of β -primeverosides in plant tissue (Fig. 2). To gain further 339 insights into the biological role of aroma glucosides and aroma β -primeverosides, MS 340 imaging analysis was conducted to localize the metabolites in the young leaves at the 341 cellular level. The specific signals, with a molecular weight of m/z 417, 284 and 340 342 corresponding to hexenyl-pri, hexenyl-glc and geranyl-glc respectively, were 343 preferentially detected in the epidermal layer of C. sinensis leaves, indicating a highly 344 regulated distribution of the aroma glycosidic precursor (Supplemental Fig. S7). 345346 347Discussion 348 CsGT1 and CsGT2 catalyze the two glycosylation steps of volatile monoterpenes 349 and alcohols 350 The broad substrate specificity of CsGT1 for sugar acceptors substantiates the 351structural diversity of the β -primeverosides of monoterpenes and primary alcohols 352 known to accumulate in leaves of C. sinensis (Fig. 2). CsGT1 belongs to the UGT85 family and shows similarities in structure and function to kiwi AdGT4 and grape 353 354VvGT14, VvGT16, VvGT17, and VvGT19 that were recently shown to catalyze the 355glucosylation of small terpenes and primary alcohols that are accumulated as glycosides 356 in ripe kiwi and grapes (Bönisch et al., 2014a; Bönisch et al., 2014b; Yauk et al., 2014). 357 It is noteworthy that AdGT4, VvGT14, and VvGT16 also have broad substrate 358 specificities toward volatile sugar acceptors (Bönisch et al., 2014a; Yauk et al., 2014). 359 Taken together, our data and these studies support the notion that the machinery behind 360 the glucosylation of monoterpenes and primary alcohols is fairly conserved among 361 phylogenetically discrete various plant species (tea, kiwi, grapevine, Arabidopsis, 362 snapdragon, and sweet potato) (Supplemental Fig. S2 and Supplemental Fig. S3) 363 (Bönisch et al., 2014a; Yauk et al., 2014). The estimated apparent K_m of CsGT1 for 364 geraniol (44 µM) was comparable to those of other volatile UGTs isolated from kiwi

365 and grape (AdGT4 for (Z)-3-hexenol: 57.0 µM; VvGt14, VvGT15a, VvGT15b, 366 VvGT15c, and VvGT16 for citronellol: 9, 29, 55, 20, and 108 µM, respectively). These 367 UGTs were found highly expressed in young tea leaf, ripe kiwi, and grape where 368 aroma glucosides are dominantly accumulated. Furthermore, the concentration of 369 substrates, (Z)-3-hexenol in ripe kiwi, citronellol in grape, and geraniol in young tea 370 leaves were determined to be at least 0.8, 1.0, and 5.8 mM, respectively (Bönisch et al., 371 2014a; Yauk et al., 2014). Their relatively lower substrate specificity toward volatile 372 sugar acceptors, compared to those of previously characterized non-volatile UGTs, 373 might reflect their promiscuous biochemical nature, recognizing structurally diverse 374substrates. Taken together, UGT85-related enzymes play a role in the formation of 375 aroma glucosides in various plants.

376 On the other hand, CsGT2 was identified as a novel UGT that specifically 377 catalyzes 6-O-xylosylation of the sugar moiety of aroma monoglucosides, the second 378 step of glycosylation in the biosynthesis of β -primeverosides (Fig. 4A). CsGT2 belongs 379 to the GGT cluster (OG8), with regio-specificity for the C-2 hydroxy or C-6 hydroxy 380 group of sugar moieties of various phytochemical glycosides (Noguchi et al., 2008). 381 CsGT2 is phylogenetically related to tomato NSGT1 (Sl_NSGT1), which catalyzes the 382 third 2-O-glucosylation of volatile-derived diglycosides (Tikunov et al., 2013) (Fig. 7). 383 The majority of UGTs within this GGT cluster catalyze sugar-sugar glycosylation of 384 various phytochemicals e.g., flavonoids, triterpenoids, and lignans (Morita et al., 2005; 385Noguchi et al., 2008; Sawada et al., 2005; Shibuya et al., 2010; Yonekura-Sakakibara et 386 al., 2014). Therefore, it is conceivable that an ancestral GGT has adapted to accommodate structurally diverse specialized metabolites that often exist only in particular plant lineages while maintaining its unique regio-specificity for the sugar moiety. The biochemical activities of GT1 and GT2 suggest their participation in the biosynthesis of aroma β -primeverosides in tea plants.

391

392 Sugar donor specificity of CsGT2 for UDP-xylose

393 UGTs usually show exclusive sugar donor specificity, which is determined by 394 a small number of amino acid residues proximal to the bound sugar donor in the 395substrate binding pocket (Noguchi et al. 2009; Ono et al., 2010a; Osmani et al., 2008). 396 These crucial residues for sugar donor specificity are located in three distinguishable 397 regions such as the N-terminal, middle, and C-terminal regions (Sayama et al., 2012). 398 Mutagenesis experiments (Ile141 \rightarrow Ser141) revealed that the unique Ile141 of CsGT2 399 located in the middle region is a residue determining the specificity toward UDP-xylose. 400 The fact that the CsGT2-I141S mutant had considerably higher specificity for 401 UDP-glucose supports the notion that the xylosyltransferase evolved from a 402 glucosyltransferase by the acquisition of the crucial Ile141. It should be noted that an Ile 403 residue, which corresponds to Ile141 in CsGT2, is also present in the mid-region of the 404 3-O-glycoside:2"-O-xylosyltransferases (kiwi Ac_F3GGT1 two flavonoid and 405 Arabidopsis UGT79B1), but Arabidopsis flavonol not in 406 3-O-glucoside:2"-O-glucosyltransferase (UGT79B6) (Table II) (Yonekura-Sakakibara et 407 al., 2012, 2014). These data suggest that the recognition mechanism for UDP-xylose by 408 CsGT2 is similar to those of xylosyltransferases from kiwifruit and Arabidopsis,

409 although these two UGTs specifically recognize flavonoid glycosides as their sugar410 acceptors.

411 The hydrophobic bulky side chain of the Ile residue possibly contributes to 412 the unique sugar donor specificity of CsGT2 for UDP-xylose, by hindering the access of 413 sugar donors with a functional group at the C6 position (UDP-glucose, UDP-galactose, 414 and UDP-glucuronate) to the substrate pocket of GGT xylosyltransferases. In contrast, 415the CsGT2-I141S mutant showed a preference for UDP-glucose instead of UDP-xylose, 416 as a sugar donor (Fig. 5C and Fig. 5D). Therefore, the hydroxy group of Ser141 could 417 contribute to the recognition of UDP-glucose via a hydrogen bond with the C6 hydroxy 418 group of UDP-glucose (Fig. 5B and Fig. 5F). Conversely, the fact that the CsGT2-I141S 419 mutant failed to use UDP-xylose as a sugar donor suggests that the hydroxy group of 420 the side chain of the Ser141 prevents binding to UDP-xylose because of a lack of the C6 421 functional group in the sugar donor binding pocket, probably via hydrophilic properties. 422 The bulky side chain of the Ile may structurally be required to form an appropriate sugar 423 donor-binding pocket for UDP-xylose (Fig. 5G and Fig. 5H).

424 Soybean Sg-1^a (Gm_UGT73F4) of the OG1 cluster is a xylosyltransferase 425 involved in the biosynthesis of triterpenoid soyasaponins but has no Ile residue 426 corresponding to Ile141 of CsGT2. Instead, Sg-1^a has a unique Ser residue (Ser138) in 427 the middle domain found essential for its sugar donor specificity towards UDP-xylose 428 (Sayama et al., 2012). Therefore, our findings indicate that the typical sugar donor 429 specificity of CsGT2 and Sg-1^a for UDP-xylose results from convergent evolution 430 because i) Sg-1^a and CsGT2 are phylogenetically remote GGTs specialized for

431structurally different substrates (glycosides of large triterpenes vs. small volatile 432monoterpenes, respectively) but with the same sugar donor specificity for UDP-xylose, 433 and ii) replacement of Ile141 with a Ser residue in the CsGT2-I141S mutant resulted in 434 a significant decrease in specificity for UDP-Xylose (Fig. 5C), whereas replacement of Ser138 with Gly residue in Sg-1^a (S138G) converted the xylosylating activity into a 435glucosylating activity (Sayama et al., 2012). These findings not only highlight the 436 437 plasticity of sugar donor specificity of UGTs, but demonstrate that the metabolic 438 specialization is a consequence of the lineage-specific differentiation of the enzymes.

439

440 Putative physiological roles of CsGT1 and CsGT2 in volatile metabolism

441 The predominant gene expression of the two CsGTs into young tea leaves, together 442with the localization of geranyl-pri, 2PE-pri, and hexenyl-pri in young leaves of C. 443 sinensis, suggests that these VOCs play physiological roles in this tissue. Given that 444 VOCs are chemical defense precursors against fungi and herbivores, CsGTs and β -PD 445play vital roles in the storage and release of C. sinensis VOCs, respectively. Based on 446 these data, we propose a plausible volatile metabolism in tea plant where tissue damage 447caused by herbivores would allow geranyl-pri to encounter extracellular β -PD, resulting 448 in the rapid release of geraniol into the air, without *de novo* biosynthesis (Fig. 8). It is of 449 particular interest to reveal the sophisticated defense system and whether the molecular 450evolution of the second enzyme CsGT2 is coupled to the evolution of β -PD, which 451specifically hydrolyzes diglycosides but is inactive against monoglycosides (Mizutani et 452al., 2002).

453Linalyl-pri dominantly accumulated in stems, while geranyl-pri accumulated in 454leaves, (Fig. 2). However, CsGT1 exhibited less activity towards linalool compared to 455geraniol while CsGT2 showed weaker activity for linalyl-glc than geranyl-glc. 456 Moreover, both CsGT1 and CsGT2 were predominantly expressed in young leaves 457rather than stem (Fig. 6). These data suggest that geraniol and linalool are separately 458biosynthesized in leaves and stems of tea plants, respectively and that members of an 459unknown class of glucosyltransferases specifically catalyze glucosylation of linalool 460 and linalyl-glc. This notion is supported by recent reports that kiwi AdGT4 and grape 461 VvGT14, which are UGT85-class glucosyltransferases for volatiles, also showed little 462 enzyme activity towards linalool in contrast to their preferred substrate, geraniol 463 (Bönisch et al., 2014b; Yauk et al., 2014). Since CsGT1, AdGT4 and VvGT14 464 commonly exhibited substrate preference to the primary alcohols geraniol and 465 (Z)-3-hexenol over the tertiary alcohol linalool, there might be a structural feature of 466 substrate recognition that is shared by these enzymes. All together, these data suggest 467 the possibility that the molecular machinery for volatile glycosides could be distinct in 468 leaves and stems of the tea plant.

Various plant species use the glycosylation of specialized metabolites to increase their solubility, which constitutes a primary strategy to accumulate metabolites operating as defensive compounds against herbivores and pathogens. At the same time, glycosylation of the metabolites facilitates the transport of the resulting glycosides to specific compartments, where they are stored separately from hydrolyzing enzymes glycosidases. For instance, tissue damage by insect attack or pathogen infection triggers

475the production of the phytotoxin 4-dihydroxy-1,4-benzoxazin-3-one (DIBOA) and its 7-methoxy derivative benzoxazinoid by a β -glucosidase that hydrolyzes the stored form 476 477DIMBOA-glucoside (Frey al.. 2009). Similarly, glucosinolates et 478 $(\beta$ -thioglucoside-*N*-hydroxysulfates) are precursors of the isothiocyanates and nitriles 479 known as "mustard oil bomb" against insects. These glucosinolates are 480 compartmentalized into S-cells, whereas the myrosinases that hydrolyze glucosinolates 481 are only expressed in myrosin cells (Koroleva et al., 2010). Tissue damage by insects elicits the hydrolysis of glucosinolates by myrosinases and the accumulation of 482 483 isothiocyanates and nitriles.

484 On the other hand, volatile alcohols and monoterpenes are mainly stored in the 485 form of diglycosides. Interestingly, various sugars (i.e., xylose, arabinose, apiose, and 486 rhamnose) could be attached to monoglycosides of VOCs as a second sugar molecule 487 (Tikunov et al., 2013, Bönisch et al., 2014b). This observation suggests that the second 488 sugar moiety of the glyco-conjugated VOCs further increases stability that leads to the 489 accumulation of such glyco-conjugated VOCs. Calculation of the cLogP (low value 490 indicates high water solubility) revealed that the two sequential glycosylation reactions 491 supporting the conversion of geraniol into geranyl-pri are associated with a stepwise increase in hydrophilicity, from 2.97 to 2.00 (geranyl-glc) and from 2.00 to 0.46 492493 (geranyl-pri). The cLogP value significantly depends on the sugar type at the 494 non-reducing end, as well as the sugar number (Tsukada et al. 2006). Furthermore, the 495existence of exoglycosidases that cleave disaccharide primeverose into glucose and 496 xylose has not been established in tea or other plants. Therefore, the xylosylation of

497 geranyl-glc by CsGT2 shown in this study should substantially contribute to the 498 increase in water solubility and the endurance against exoglycosidases. In addition, the 499 increase in water solubility of geraniol through glycosylation may be related to the fact 500 that geraniol and other monoterpene alcohols exhibit high apoptosis-inducing activity in 501plant cells (Izumi et al., 1999). This toxic nature of geraniol necessitates precise control 502of its biosynthesis and conversion into mono- and diglycosides by CsGT1 and CsGT2, 503 respectively for the accumulation of defensive geranyl-pri upon potential attacks by 504herbivores.

505

506 Conclusion

507 β -Primeverosides are the most abundant form of aroma diglycosides in C. sinensis, and 508they are commercially and physiologically important for tea aroma quality in dietary 509 beverages, and for chemical defense against herbivores in tea plant. Here we 510demonstrated through metabolic profiling of aroma glycosides in the plant, the 511enzymatic characterization and the transcript analysis that CsGT1 and CsGT2 catalyze 512the sequential glucosylation and xylosylation of aromas, respectively, leading to 513production of aroma β -primeverosides. The transcripts of the two CsGTs and β -PD in 514young tea leaves, together with the localization of geranyl-pri in epidermal cells of 515young tea leaves, strongly support the potent physiological role of VOCs in chemical 516 defense primarily in this tender tissue. Here we report identification and 517characterization of molecular machineries for the biosynthesis of β -primeverosides of 518tea aroma. Our findings provided not only molecular insights into volatile metabolism

519 in *C. sinensis*, but also crucial molecular tools for controlling tea aroma quality and for 520 understanding of a sophisticated chemical defense system elaborated during plant 521 evolution.

522

523

524 Materials and Methods

525 Chemicals

526 *p*NP-pri, eugenyl-pri, and 2PE-pri were kindly provided by Prof. Usui and Dr. 527Murata (Shizuoka University, Japan) (Murata et al., 1999). Geranyl-pri and linalyl-pri were prepared as described (Guo et al., 1993, 1999). pNP-glc, cyanidin 3-O-glucoside 528529chloride, and quercetin 3-O-glucoside were purchased from Sigma-Aldrich 530 (www.sigmaaldrich.com). Other glucosides were chemically synthesized using the 531procedure for 2PE-glc as previously described (Ma et al., 2001). UDP-xylose was obtained from CarboSource Services at the University of Georgia (Athens, USA). Other 532533chemicals were purchased from Sigma-Aldrich and Wako Pure Chemical Industries 534(www.wako-chem.co.jp/english/).

535

536 **Plant Materials**

537 Young leaves of *C. sinensis* var. *sinensis* cv. Yabukita were harvested at the 538 Center for Education and Research of Field Sciences, Shizuoka University and at Tea 539 Research Center, Shizuoka Prefectural Research Institute of Agriculture and Forestry 540 (Shizuoka, Japan). The young and mature developmental stages of leaves and stems were defined as follows: young leaves, which are the first, second, and third leaves (plucking part for high grade tea products); mature leaves, which are the fourth and fifth leaves; stem, which are green young non-lignified part between the 3rd leaf and 5th leaf; branch, which are brown lignified old part (Fig. S8). All plant materials were quickly frozen in liquid nitrogen and stored at -80° C prior to use.

546

547 Quantification of endogenous aroma glycosides in *C. sinensis*.

548Three point five grams (fresh weight) of leaves and stems at two 549developmental stages (young and mature) of C. sinensis were finely crushed in a tissue 550mill (TK-AM5, www.e-taitec.com) suspended in 80% methanol (30 ml) and filtrated. 551The filtrate was concentrated *in vacuo* and separated with *n*-hexane. The aqueous layer 552was concentrated in vacuo, dissolved in distilled water and purified with Oasis HLB 553(3cc, Waters; www.waters.com). The glycosidic fractions were concentrated in vacuo 554and dissolved in distilled water prior to GC-MS analysis. Detailed procedures for 555LC-MS analysis condition are given in Supplemental Materials and Methods S1.

556

557 Identification of CsGT1

558 Full-length cDNA clone of *CsGT1* was isolated by a screen with full-length 559 DIG-labeled mixed probes for At_UGT85A, in a cDNA library derived from *C. sinensis* 560 previously described (Mizutani et al., 2002). Library screening was performed under a 561 low stringency condition as described in Yonekura-Sakakibara et al. (2000), and 562 Noguchi et al. (2008, 2009). The screening probes of At_UGT85A were DIG-labeled by PCR using gene-specific oligonucleotides (Supplemental Table S3). More than 50 positive clones were obtained in approximately 5,000,000 plaques after two rounds of screening. The cDNA fragments of positive clones were sequenced by conventional primer walking method with BigDye-terminator version 3.1 cycle sequencing kit (Life Technologies; www.lifetechnologies.com). Among these clones, a full-length cDNA for the *CsGT1* gene was identified by blastx search based on sequence similarities with At UGT85A3.

570

571 Enzyme purification of a xylosyltransferase specific for monoglucoside-bound

572 volatiles

All procedures were performed at 4°C. The composition of the purification 573574buffers and solutions for peptide analysis is described in Supplemental Table S4. Tea 575leaves (100 g) were finely chopped, crushed in a tissue mill (Taitec) suspended in 100 576ml buffer A and centrifuged (20,000 $\times g$; 30 min). The supernatant was collected, and 577ammonium sulfate was added up to 30% saturation. The mixture was centrifuged 578 $(20,000 \times g; 30 \text{ min})$, the supernatant collected, and ammonium sulfate was added up to 57970% saturation, followed by another centrifugation (20,000 $\times g$; 30 min). The pellet was 580dissolved in buffer B and dialyzed against buffer B for complete removal of the 581ammonium sulfate. Purification of active fractions was performed using the following 582columns;: HiTrap DEAE FF (5 ml, GE Healthcare; www.gelifesciences.com), HiTrap Q 583FF (5 ml), Macro-prep Ceramic Hydroxyapatite Type III (5 ml, Bio-Rad; 584www.bio-rad.com), HiTrap Blue HP (1 ml), and Mono Q 5/50 GL (1 ml). At each

585 purification step, the eluted fractions were tested for xylosyltransferase activity toward 586 geranyl-glc by LC-MS, and the active fractions were pooled before the next purification 587 step. Detailed procedures are given in Supplemental Materials and Methods.

588

589 Identification of the peptide sequence of CsGT2 by LC-MS/MS

590 Purified proteins were separated by SDS-PAGE and stained by Silver staining, 591the major bands were excised from the gel and destained with solution F. Proteins in the 592gel pieces were reduced and alkylated in solutions G and H, respectively, followed by 593solution H. After serial washes with the wash solution F and acetonitrile, the proteins 594were digested with trypsin (Promega; www.promega.com). The tryptic peptides were 595extracted from the gel pieces with solution I, and the extract was concentrated in vacuo. 596 The concentrated solution was centrifuged $(20,000 \times g; 10 \text{ min})$ and the supernatant was 597 analyzed by LC–MS/MS (Supplemental Materials and Methods). All peptide mass data 598 were analyzed using the Peaks software (Bioinformatics Solutions).

599

600 Identification of full-length CsGT2 cDNA

Since contig134 had a partial ORF of *CsGT2*, the full-length sequence of *CsGT2* cDNA was obtained from fresh young tea leaves using gene-specific
CsGT2-Race-FW and CsGT2-Race-RV oligonucleotides, using the SMARTer cDNA
RACE cDNA amplification kit (Clontech; www.clontech.com) and PrimeStar HS
polymerase (TAKARA BIO; www.takara-bio.com), according to manufacturer's
instructions. The amplified products were gel purified and ligated into pJET 1.2 vector

607 using the CloneJET kit (Thermo Fisher Scientific; www.thermoscientificbio.com).

608

609 Heterologous expression of recombinant UGT proteins

610 Total RNA was extracted from fresh young leaves of C. sinensis using 611 RNeasy Plant Mini kit (Qiagen; www.qiagen.com), according to the manufacturer's 612 instructions. cDNA was reverse-transcribed from 1 µg of total RNA with SuperScript III 613 (Life Technologies). Full-length cDNA fragments of CsGT1 and CsGT2 genes were 614 amplified from cDNA of C. sinensis cv. Yabukita by RT-PCR, using gene-specific 615 oligonucleotides (Supplemental Table S3). In vitro mutagenesis of the CsGT2 gene was 616 performed by recombinant PCR with specific mutagenic oligonucleotides 617 (Supplemental Table S3) as previously described (Noguchi et al. 2009). For their 618 expression in E. coli, the generated amplicons were ligated into the pENTR/D-TOPO 619 vector (Life Technologies), and the sequence was verified. They were subcloned into the 620 pET15b expression vector (Merck Millipore; www.merckmillipore.com) and 621 transformed into E. coli BL21 (DE3) (TOYOBO; www.toyobo-global.com). The 622 recombinant proteins produced by E. coli BL21 were quantified by Bradford method (Bradford, 1976) with BSA as the standard, and separated by SDS-PAGE. The 623 624 expressed recombinant proteins were immunologically detected in the gels by western 625blotting as described previously (Sayama et al., 2012).

626

627 Enzyme assay of CsGT1 and CsGT2

628

For relative activity assays of CsGT1 and CsGT2, the enzymatic reaction

629 mixture (50 µL) consisted of 100 mM sugar acceptor, 2 mM sugar donor, 50 mM 630 potassium phosphate buffer, pH 8.0, and enzyme. The enzyme assays were initiated 631 after pre-incubation of the mixture without the enzyme at 30°C for 5 min. After 632 incubation at 30°C for 10 min, the reaction was stopped by the addition of 50 μ L of 633 ice-cold methanol. The same assay conditions were used for determination of the kinetic 634 parameters of CsGT1 and CsGT2 except that the sugar acceptor geranyl-glc was used 635 instead of geraniol and at six different concentrations from 1.25-250 µM. The enzymatic 636 products were analyzed by LC-MS analysis (Materials and Methods S1). The apparent 637 $K_{\rm m}$ and $V_{\rm max}$ values for each sugar donor and the sugar acceptor (geraniol) were 638 determined by a saturating substrate concentration by fitting the initial linear velocity 639 data to a Michaelis-Menten equation using nonlinear regression analysis in the 640 Kaleidagraph software (www.synergy.com).

641

642 Homology modeling

643 The construction of a 3D model according to CsGT2 was conducted using the 644 Discovery Studio (DS) 3.5 (http://accelrys.com/). The crystal structures of 645 At_UGT72B1 (PDB code: 2vce), Mt_UGT85H2 (PDB code: 2pq6), and VvGT1 (PDB 646 code: 2c1z), and the 3D structure of the sugar donor UDP-2-F-Glc, were used as 647 templates. The initial structure of CsGT2 was constructed using the multiple homology 648 modeling protocols of the DS3.5 MODELER module. The resulting CsGT2 structure 649 was inserted in the UDP-2F-Glc bound in VvGT1, and the sugar moiety of UDP-2F-Glc 650 was replaced with a xylose. Structure optimization of the initial complex model 651 (CsGT2-UDP-Xyl) was performed using molecular mechanics and dynamics simulation
652 with the CHARMm force field of DS3.5. On the other hand, the 3D structure of the
653 CsGT2 (I141S) mutant was first constructed by replacing Ile141 with a serine residue.
654 After insertion of UDP-2F-Glc bound to VvGT1, the fluoride atom of UDP-2F-Glc was

655 converted to a hydroxy group to generate the model complex, CsGT2 (I141S)-UDP-Glc,

which was optimized by the same procedure used for CsGT2-UDP-Xyl.

657

658 Quantitative real-time PCR (qRT-PCR) of CsGTs and β -PD

659 The qRT-PCR was performed as previously described (Noguchi et al., 2008). 660 In brief, the cDNA was prepared from multiple organs and tissues of C. sinensis. The 661 CsGT1, CsGT2, β -PD, and 18S rRNA were quantified by real-time PCR using specific 662 primers (Supplemental Table S3) and a Power SYBR Green PCR kit (Qiagen) on a 7500 663 Real-Time PCR system (Life Technologies). The transcription levels were quantified 664 using the ddCT threshold cycle method, and normalized to the expression level of an 665 internal standard (18S rDNA). The results are presented as the means \pm SE of three 666 independent experiments.

667

668 **Phylogenetic analysis**

The amino acid sequences of UGTs (Supplemental Table S5) were aligned
based on codon position using ClustalW bundled in MEGA6 (Tamura et al. 2013). All
sites containing gaps and missing data were eliminated from the remaining analysis.
Unrooted phylogenetic trees were reconstructed by neighbor-joining methods from the

673	translated amino acid sequences. The neighbor-joining tree was reconstructed by
674	MEGA6, and the matrix of evolutionary distances was calculated by Poisson correction
675	for multiple substitutions. The reliability of the reconstructed tree was evaluated by a
676	bootstrap test for 1,000 replicates.
677	
678	GenBank accession numbers
679	Sequence data from this article can be found in GenBank/EMBL under the
680	following accession numbers: UGT85K11 (AB847092) and UGT94P1 (AB847093).
681	
682	
683	Supplemental Data Files
684	Supplemental Figure S1. Co-expression analysis of AtLIS, CYP76C3 and UGT85A3
685	by ATTEDII (Gene coexpression database, http://atted.jp/) with Ver. C4.1.
686	Supplemental Figure S2 . Enzymatic activity of CsGT1 homologs for (<i>Z</i>)-3-hexenol.
687	Supplemental Figure S3. Enzymatic activity of CsGT1 homologs for geraniol.
688	Supplemental Figure S4. Purified enzymes catalyzing the second xylosyltransferase
689	(CsGT2).
690	Supplemental Figure S5. Partial peptide sequence of CsGT2.
691	Supplemental Figure S6. Recombinant proteins of a series of CsGTs.
692	Supplemental Figure S7. Imaging MS of young fresh leaves of C. sinensis.
693	Supplemental Figure S8. Harvesting individual tissues for quantification of
694	endogenous aroma glycosides and quantitative real-time PCR (qRT-PCR) of CsGT1,

695 *CsGT2* and β -*PD*.

696 Supplemental Figure S9. Multiple sequence alignment of protein sequences of
697 UGT-glucosyltransferase OG2 and OG8 family. The alignment was performed using
698 ClustalW2.1.

699 Supplemental Table S1. Summary of fresh weight and amounts of aroma
700 β-primeverosides in young leaves and mature leaves of *C. sinensis*.

701 Supplemental Table S2. Summary of the purification of CsGT2 from young fresh

702 leaves of *C.sinensis*.

703 Supplemental Table S3. Gene specific primers used for 5', 3'-RACE, amplification of

full-length genes from *C. sinensis*, construction of CsGT2-I141S or real-time PCR.

705 Supplemental Table S4. Composition of the buffers and solutions for purification and

706 identification of CsGT2 protein.

Supplemental Table S5. GenBank accession numbers used for the construction of the
phylogenetic tree in Figure 7.

709

Supplemental Materials and Methods. Detailed description of the experimental
procedure in this study.

712

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- 952

953

954 **Figure legends**

Figure 1. Metabolism of volatile organic compounds in *Camellia sinensis*. A) Photo of young leaves. (B) Biosynthesis pathway of geranyl β -primeveroside (geranyl 6-*O*- β -D-xylopyranosyl- β -D-glucopyranoside) from geraniol. CsGT1 (UGT85K11) and CsGT2 (UGT94P1) are the two glycosyltransferases that are shown to catalyze the sequential glucosylation and xylosylation of geraniol, respectively, in this work (Bold arrows).

961

962 Figure 2. Quantification of aroma monoglycosides and diglycosides in fresh tea 963 leaves Ten glycosides were used as authentic standards to quantify endogenous 964 glycoside in young leaves, young stems, mature leaves, and mature stems of C. sinensis: 965benzyl β -D-glucopyranoside (benzyl-glc), benzyl β -primeveroside (benzyl-pri), geranyl 966 β -D-glucopyranoside (geranyl-glc), geranyl β -primeveroside (geranyl-pri), 967 (Z)-3-hexenyl β -D-glucopyranoside (hexenyl-glu), (Z)-3-hexenyl β -primeveroside 968 (hexenyl-pri), linalyl β -D-glucopyranoside (linalyl-glc), linalyl β -primeveroside 969 (linalyl-pri), 2-phenylethyl β -D-glucopyranoside (2PE-glc), and 2-phenylethyl 970 β -primeveroside (2PE-pri). Data are presented as mean \pm SD (n = 3).

971

972 **Figure 3. Biochemical characterization of CsGT1 and At_UGT85As.** A) CsGT1 973 catalyzes the glucosylation of geraniol to produce geranyl β -D-glucopyranoside 974 (geranyl-glc). B) LC-MS analysis of the enzymatic product of CsGT1 (UGT85K11) and 975 At_UGT85A3 (At1g22380) compared with the authentic standard (geranyl-glu). C) 976 Relative activity of CsGT1 toward sugar acceptors (geraniol, linalool, eugenol, benzyl 977 alcohol, (*Z*)-3-hexenol, 2-PE, quercetin, and cyanidin). D) Relative activity of CsGT1 978 toward sugar donors (UDP-glucose, UDP-xylose, UDP-galactose, and UDP-glucuronic 979 acid). Data are presented as mean \pm SD (n = 3).

980

981 Figure 4. Biochemical characterization of CsGT2. A) CsGT2 (UGT94P1) catalyzes 982 the xylosylation of geranyl-glc into geranyl β -primeveroside (geranyl 983 $6-O-\beta$ -D-xylopyranosyl- β -D-glucopyranosides). B) LC-MS analysis of the enzymatic 984 product of CsGT2 (UGT94P1) compared with an authentic standard (geranyl-pri) (r.t. = 985 4.9 min). C) Relative activity of CsGT2 toward sugar acceptors (geranyl-glc, linalyl-glc, 986 eugenyl-glc, 2PE-glc, and pNP-glc). D) Relative activity of CsGT2 toward sugar donors 987 (UDP-glucose, UDP-xylose, UDP-galactose, and UDP-glucuronic acid).

988

989 Figure 5. Structural Comparison on the sugar-donor specificity of CsGT2 and its 990 mutant, CsGT2 (I141S). A) Homology model of UDP-xylose-bound CsGT2. B) Homology model of UDP-glucose-bound CsGT2 (I141S). For homology models, 991 992 important amino acid residues on the active site are drawn at the stick form and 993 UDP-sugars at the ball and stick form. Carbon atoms are colored in green for UGT 994 amino acid residues and in cyan for UDP-sugars. Oxygen atoms are red, nitrogen atoms 995are blue, and phosphorus atoms are orange. Plausible hydrogen bonds are indicated by 996 the red dotted lines. To simplify the visibility of the models, the structure of a sugar

997 acceptor is removed. C) Relative activity of CsGT2 and CsGT2 (I141S) toward 998 UDP-xylose with geranyl-glc as a sugar acceptor. D) Relative activity of CsGT2 and 999 CsGT2 (I141S) toward UDP-glucose with geranyl-glc as a sugar acceptor. Data are 1000 presented as mean \pm SD (n = 3). E) Schematic representations of UDP-sugar recognition of with CsGT2 (WT) and UDP-xylose (schematic model of Fig. 5A). F) 1001 Schematic representations of UDP-sugar recognition of with CsGT2 (I141S) and 1002 1003 UDP-glucose (schematic model of Fig. 5B). G) Schematic representations of UDP-sugar recognition of with CsGT2 (I141S) and UDP-xylose. H) Schematic 1004 1005representations of UDP-sugar recognition of with CsGT2 (WT) and UDP-glucose.

1006

1007 Figure 6. Relative transcript abundance of *CsGT1*, *CsGT2*, and β -*PD* in various 1008 organs (young leaves, matures leaves, stem, root, and flower) of *C. sinensis*. 1009 Transcript abundance was measured by qRT-PCR and normalized to the internal 1010 reference *ribosomal 18S*. The expression level of each gene in the stem was set at 1.0. 1011 Data are presented as mean \pm SD (n = 3).

1012

Figure 7. Phylogeny of UGT-glucosyltransferase OG2 and OG8 family. All other UGT sequences were for *Arabidopsis thaliana* available on The Arabidopsis Information Resource (TAIR) website. High bootstrap values (>750) are indicated on the branches (1000 replicates). The Vv_UGT85A28 described here was found to be identical to VvGT14 (Bönisch et al., 2014b).

- 1019 Figure 8. Schematic illustration of a mode-of-action of CsGT1, CsGT2, and β -PD
- 1020 in the volatile metabolism in *C. sinensis*.
- 1021

Table 1. Kinetic parameters of CsGT1 (UGT85K11) and CsGT2 (UGT94P1).					
	substrate	$\kappa_{ m m}$	V_{\max}	$V_{\rm max}/K_{\rm m}$	
enzymes		μM	nkat g-1 protein	nkat g ⁻¹ µM ⁻¹	
CsGT1 (UGT85K11)	geraniol	44.2 ± 3.0	332.1± 8.1	7.5± 0.5	
CsGT2 (UGT94P1)	geranyl β-⊡- glucopyranoside	78.1 ± 19.6	60.0 ± 4.8	0.77 ± 0.2	
Data are presented as mean \pm SD (n = 3)					

		substrate specificity			
GGT (OG8)	species	sugar donor	sugar acceptor	positi on	sequence alignment
CsGT2 (UGT94P1)	Tea (C. sinensis)	UDP- xylose	Volatile mono-glucoside	6'	ipavqim <u>i</u> tgat 141
AcF3GGT1	Kiwifruit (A. chinensis)	UDP- xylose	Flavonoid galactoside	2'	iksvnyc <u>i</u> ispa 136
UGT79B1	A. thaliana	UDP- xylose	Flavonoid glucoside	2'	aktvcfn <u>i</u> vsaa 142
UGT79B6	A. thaliana	UDP- glucose	Flavonoid glucoside	2'	vksvnfi <u>t</u> isaa 135
UGT94D1	Sesame (S. indicum)	UDP- glucose	Lignan glucoside	6'	ipamvfl <u>s</u> tgaa 140
UGT94F1	V. persica	UDP- glucose	Flavonoid glucoside	2'	spsvwfm <u>a</u> sgat 144
Dusky (UGT79G16)	Morning glory (I. purpurea)	UDP- glucose	Flavonoid glucoside	2'	iksvfys <u>t</u> ispl 138
NSGT1	Tomato (S. lycopersicum)	UDP- glucose	Volatile di-glycoside	2'	ihaimfy <u>v</u> ssts 145

Table 2. Comparison of substrate specificity of GGTs in OG8 cluster



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Figure 3. Biochemical characterization of CsGT1 and At_UGT85As. A) CsGT1 catalyzes the glucosylation of geraniol to produce geranyl β -D-glucopyranoside (geranyl-glc). B) LC-MS analysis of the enzymatic product of CsGT1 (UGT85K11), At_UGT85A1 (At1g22400), and At_UGT85A3 (At1g22380) compared with the authentic standard (geranyl-glu). C) Relative activity of CsGT1 toward sugar acceptors (geraniol, linalool, eugenol, benzyl alcohol, (Z)-3-hexenol, 2-phenylethanol, quercetin, and cyanidin). D) Relative activity of CsGT1 toward sugar donors (UDP-glucose, UDP-xylose, UDP-galactose, and UDP-glucuronic acid). Data are presented as mean \pm SD (n = 3).



Figure 4. Biochemical characterization of CsGT2. A) CsGT2 (UGT94P1) catalyzes the xylosylation of geranyl-glc into geranyl β -primeveroside (geranyl 6-*O*- β -D-xylopyranosyl- β -D-glucopyranosides). B) LC-MS analysis of the enzymatic product of CsGT2 (UGT94P1) compared with an authentic standard (geranyl-pri) (r.t. = 4.9 min). C) Relative activity of CsGT2 toward sugar acceptors (geranyl-glc, linalyl-glc, eugenyl-glc, 2PE-glc, and *p*NP-glc). D) Relative activity of CsGT2 toward sugar donors (UDP-glucose, UDP-xylose, UDP-galactose, and UDP-glucuronic acid).



Figure 5. Structural Comparison on the sugar-donor specificity of CsGT2 and its mutant, CsGT2 (I141S). A) Homology model of UDP-xylose-bound CsGT2. B) Homology model of UDP-glucose-bound CsGT2 (I141S). For homology models, important amino acid residues on the active site are drawn at the stick form and UDP-sugars at the ball and stick form. Carbon atoms are colored in green for UGT amino acid residues and in cyan for UDP-sugars. Oxygen atoms are red, nitrogen atoms are blue, and phosphorus atoms are orange. Plausible hydrogen bonds are indicated by the red dotted lines. To simplify the visibility of the models, the structure of a sugar acceptor is removed. C) Relative activity of CsGT2 and CsGT2 (I141S) toward UDP-xylose with geranyl-glc as a sugar acceptor. D) Relative activity of CsGT2 and CsGT2 (I141S) toward UDP-glucose with geranyl-glc as a sugar acceptor. Data are presented as mean \pm SD (n = 3). E) Schematic representations of UDP-sugar recognition of with CsGT2 (I141S) and UDP-glucose (schematic model of Fig. 5A). F) Schematic representations of UDP-sugar recognition of with CsGT2 (I141S) and UDP-sylose. H) Schematic representations of UDP-sugar recognition of with CsGT2 (I141S) and UDP-xylose. H)



Figure 6. Relative transcript abundance of *CsGT1*, *CsGT2*, and β -PD in various organs (young leaves, matures leaves, stem, root, and flower) of *C. sinensis*. Transcript abundance was measured by qRT-PCR and normalized to the internal reference *ribosomal 18S*. The expression level of each gene in the stem was set at 1.0. Data are presented as mean \pm SD (n = 3).



Figure 7. Phylogeny of UGT-glucosyltransferase OG2 and OG8 family. All other UGT sequences were for *Arabidopsis thaliana* available on The Arabidopsis Information Resource (TAIR) website. High bootstrap values (>750) are indicated on the branches (1000 replicates). The Vv_UGT85A28 described here was found to be identical to VvGT14 (Bönisch et al., 2014b).



Figure 8. Schematic illustration of a mode-of-action for the metabolism of aroma volatiles by CsGT1, CsGT2, and β -PD in *C. sinensis.*

Supplemental Materials and Methods

LC-MS conditions for quantification of endogenous aroma glycosides in C. sinensis. LC-MS analysis of ten aroma glycosidic precursors was performed on LCMS-2010A system (Shimadzu; www.shimadzu.com) equipped with Capcell Pak UG120 C₁₈ reversed phase column (2.0 mm i.d. x 150 mm, 5 µm, Shiseidou; hplc.shiseido.co.jp/e) and electrospray operating conditions were used the followings: dry gas 1.5 l/min, capillary voltage 1.5 kV, dry gas temperature 250°C. The endogenous aroma glycosides were quantified with the SIM negative mode. For benzyl-glc, benzyl-pri, 2PE-glc, 2PE-pri, (Z)-3-hexenyl-glc and (Z)-3-hexenyl-pri, the glycosidic fractions of were subjected to the LC-MS using gradient elution with aqueous formic acid (0.1%,v/v) as solvent A and acetonitrile as solvent B at a flow rate of 0.2 ml/min at 40°C. The gradient condition started with isocratic conditions of 16% of solvent B for 5 min and then increased up to 29% of solvent B for 24.5 min. The m/z293 ion for benzyl-glc (tR 10.5 min), the m/z 425 ion for benzyl-pri (tR 14.9 min) the m/z 307 ion for 2PE-glc (*tR* 18.3 min), the *m*/*z* 439 ion for 2PE-pri (*tR* 22.4 min) The *m*/*z* 285 ion for (Z)-3-hexenyl-glc (tR 21.6 min), the m/z 417 ion for (Z)-3-hexenyl-pri (tR 26.3 min) and the m/z 456 ion for pNP-pri (tR 8.2 min) as a internal standard. For geranyl-glc, geranyl-pri, linalyl-glc and linalyl-pri, the glycosidic fractions of were subjected to the LC-MS using gradient elution with aqueous formic acid (0.1%,v/v) as solvent A and acetonitrile as solvent B at a flow rate of 0.2 ml/min at 40°C. The gradient condition started with 7% of solvent B then increased up to 30% of solvent B for 4 min and keep 30% of solvent B for 13 min. The m/z 339 ion for geranyl-glc (tR 14.5 min) and linalyl-glc (tR 13.0 min), and the m/z 471 ion for geranyl-pri (tR 11.9 min) and linalyl-glc (tR 11.0 min)

Enzyme purification of a xylosyltransferase specific for monoglucoside-bound

volatiles

The enzyme solution was applied to a HiTrap DEAE FF (5 ml, GE Healthcare) equilibrated with buffer B and eluted by a linear gradient of NaCl (0 to 340 mM) of buffer B. The active fraction was equilibrated with buffer C using an Amicon Ultra-15 centrifugal filter device (Mr 30,000 cutoff; Millipore). Then, the enzyme fraction was applied to a HiTrap Q FF (5 ml, GE Healthcare) and eluted with a linear gradient of NaCl (0 to 1 M) of buffer C. The active fractions was equilibrated with buffer D and applied to a Macro-prep Ceramic Hydroxyapatite Type III (5ml, Bio-Rad), and eluted with a linear gradient of NaCl (0 to 1 M) in buffer D. The active fraction was equilibrated with buffer E, applied to a HiTrap Blue HP (1 ml, GE Healthcare) and eluted with a linear gradient of NaCl (0 to 2 M) of buffer E. The active fraction was equilibrated with buffer C and applied to a Mono Q 5/50 GL (1 ml, GE Healthcare) and eluted with a linear gradient of NaCl (0 to 1 M) of buffer E. The active fraction was equilibrated with buffer C and applied to a Mono Q 5/50 GL (1 ml, GE Healthcare) and eluted with a linear gradient of NaCl (0 to 1 M) of buffer C. Peptide sequences were analyzed by Nano-LC-TOF MS.

Nano-LC-MS/MS analysis of partial peptide sequences of purified CsGT2

Peptide assignments were performed using an LC-ESI-LIT-q-TOF mass spectrometer equipped with NanoFrontier eLD System (Hitachi High-Technologies, www.hitachi-hitec.com) and а nano-flow HPLC. NanoFrontier nLC (Hitachi High-Technologies). The LIT-TOF and CID modes were used for MS detection and peptide fragmentation, respectively. The trypsin-treated sample (10 µl) was injected, and the peptides were trapped on a C18 column, Monolith Trap (50 µm × 150 mm, Hitachi High-Technologies). Peptide separation was achieved using a packed nano-capillary column (capillary-Ex nano mono cap, 0.05 × 150 mm, GL Science, Japan) at a flow rate of 200 nl/min. The peptides were eluted using an acetonitrile gradient (A: 2% acetonitrile containing 0.1% formic acid; B: 98% acetonitrile containing 0.1% formic acid; 0 min with A = 98%, B = 2%, followed by 60 min with A = 60%, B = 40%). All peptide mass data were analyzed using Peaks software (Bioinformatics Solutions Inc., www.bioinfor.com) and the MASCOT database (Matrix Science, www.matrixscience.com).

LC-MS analysis of CsGTs enzymatic products

Enzymatic reaction mixtures by UGT enzymes were analyzed by LC-MS using Shimadzu LCMS-2010A (www.shimadzu.com) system with negative electrospray ionization mode; dry temperature, 250°C; a flow rate, 0.2 ml/min and column oven temperature, 40 °C. HPLC separation was performed according to the following conditions: Analysis of CsGT1 enzymatic products was performed using a CAPCELL PAK C₁₈ UG120 column (2.0 mm I.D.×150 mm; 5 μ m) (Shiseido, hplc.shiseido.co.jp/e/) and elution was started with 15% solvent B, following a linear gradient flow up to 90% in 15 min (solvent A: H₂O containing 0.05% (v/v) formic acid, B: acetonitrile) Analysis of CsGT2 enzymatic products was performed using a CAPCELL PAK C₁₈ UG120 column (2.0 mm; 5 μ m) (Shiseido) and elution was started with 15% solvent B (0-2 min) following a linear gradient flow up to 60% in 8 min (solvent A: H₂O containing 0.05% (v/v) formic acid, B: H_2O containing 0.05% (v/v) formic acid, B: H_2O containing 0.05% (v/v) formic acid, B: acetonitrile) Analysis of CsGT2 enzymatic products was performed using a CAPCELL PAK C₁₈ UG120 column (2.0 mm I.D.×75 mm; 5 μ m) (Shiseido) and elution was started with 15% solvent B (0-2 min) following a linear gradient flow up to 60% in 8 min (solvent A: H₂O containing 0.05% (v/v) formic acid, B: acetonitrile)

Subcloning of CsGT1 and CsGT2 to pET15b vector for *E.coli* expression

The amplified cDNA fragments of CsGT1 and CsGT2 genes were subcloned into pENTR/D-TOPO vector (Life Technologies; www.lifetechnologies.com), and then digested with *Xho*I and *BgI*II for CsGT1, and *Nde*I and *BamH*I for CsGT2 and the resulting DNA fragments were ligated into a pET-15b vector (Merck Millipore; www.merckmillipore.com) previously digested with *Xho*I and *BamH*I for CsGT1, and *Nde*I and *BamH*I for CsGT2, respectively. The resulting plasmids were named pET-15b-CsGT1 and pET-15b-CsGT2, which encoded an N-terminal in-frame fusion of CsGT1 and CsGT2, respectively, with a Hisx6 tag. The inserted fragments were sequenced to confirm the absence of PCR errors and transformed into *E. coli* BL21(DE3) (TOYOBO; www.toyobo-global.com).

Subcloning of CsGT2 (I141S) to pET15b vector

According to the previously published method of Noguchi et al. (2007), in vitro mutagenesis of the CsGT2 gene was performed using recombinant PCR with the pENTR-Directional-TOPO vector (Life Technologies) containing the wild-type CsGT2 cDNAs as the templates and the specific mutagenic oligonucleotide primer set (CsGT2-134-I141S-FW and CsGT2-134-I141S-Rv) (Supplemental Table S2) to obtain the CsGT2-I141S mutant. The amplified fragment containing the I141S mutation was digested with Ndel and Bg/II, and the resulting DNA fragments were ligated with pET-15b at Ndel and BamH site as described above. The introduced mutation was verified by DNA sequencing of both strands. The resulting CsGT2-I141S fragment was inserted in the expression vector pET-15b as described above.

E.coli expression and purification of recombinant CsGT1 and CsGT2

The transformant cells were precultured at 37°C for 16 hr in a Luria-Bertani broth containing 50 µg/mL ampicillin. Twenty milliliters of the pre-culture was then inoculated into 200 mL, then further incubated at 22°C for 20 hr with Overnight Express Autoinduction System 1 (Merck Millipore) for expression of recombinant proteins. All subsequent operations were conducted at 0 to 4°C. The recombinant *E. coli* cells were harvested by centrifugation (7000*g*, 15 min), washed with distilled water, and resuspended in buffer F containing 20 mM imidazole. The cells were disrupted at 4°C by five cycles of ultrasonication. The cell debris was removed by centrifugation (7,000*g*, 15 min). Polyethyleneimine was slowly added to the supernatant solution to a final concentration of 0.12% (v/v). The mixture was allowed to stand at 4°C for 30 min, followed by centrifugation (7,000*g*, 15 min). The supernatant was applied to a HisTrap HP column (1 mL; GE Healthcare) equilibrated with buffer F containing 20 mM imidazole. The column was washed with buffer F containing 20 mM imidazole.

the enzyme was eluted with buffer F containing 200 mM imidazole. The active column-bound fractions were concentrated and desalted using Vivaspin 30,000 MWCO (GE Healthcare), followed by substitution with buffer G. The expressed recombinant proteins in the gels were separated by SDS-PAGE and visualized by using PAGE Blue 83 (Cosmo Bio; www.cosmobio.co.jp/index_e) and His · Tag monoclonal antibody (mouse, Merck Millipore) and ECL Anti-mouse IgG Horseradish Peroxidase-linked Whole antibody (sheep, GE Healthcare) respectively. Chemical luminescence derived from the recombinant proteins was detected by using Chemi-Lumi One Ultra (Nacalai tesque; www.nacalai.co.jp/english/) in Molecular Imager ChemiDoc XRS+ (BioRad; www.bio-rad.com/)

Preparation of cryosections of tea leaf for MS imaging

For MS imaging analysis, cryosections of the young tea leaf were prepared as described elsewhere. Briefly, tea leaves were embedded in SCEM embedding medium (Leica, Tissue-Tek www.leica-microsystems.com) in а Cryomold (Sakura Finetek. www.sakura-finetek.com/) and desiccated in vacuo for 5 min at ambient temperature. The leaves were frozen by placing the mold containing tea leaves embedded in the medium on a block of dry ice for 15 min. Longitudinal sections of the leaves in 5 µm thickness were cut using a cryotome (Cryostar NX70, Thermo Scientific; www.thermosci.jp) with blade and block temperatures of -20 and -25 °C, respectively, and the sections were transferred onto a glass slide coated with indium tin oxide (Bruker Daltonics; www.bruker.jp). The sections were dried in 50 ml tubes containing dried silica gel. The cryosections were uniformly sprayed with a solution of 50 mg/ml dihydrobenzoic acid (DHBA) in 70% methanol containing 0.1% trifluoroacetic acid using a 0.2-mm caliber airbrush (Procon Boy FWA Platinum; Mr. Hobby, Japan), air-dried for 10 min and mounted on a MALDI target plate.

MALDI-MS imaging analysis

Longitudinal sections of seeds were selected for MS imaging analysis, performed by MALDI-TOF-MS/MS (Ultraflextream III, Bruker Daltonics). Parameters of the laser shots were as follows: laser diameter, 15 μ m; raster, 15 μ m; laser power, 3_mid; laser power boost, 50%. Data from 100 laser shots were obtained at each position using the FlexImaging software program (Bruker Daltonics). The spectra were acquired in the positive mode. For MS/MS analysis, the parent ion of (*Z*)-3-hexenyl-pri (*m*/*z* 417), (*Z*)-3-hexenyl- glu (*m*/*z* 284) and geranyl-glc (*m*/*z* 340) were monitored for a peak tolerance of 0.5 kDa. A cutoff value of 50% was used for the production of the images. The instrument was calibrated in the positive ion mode in the low-mass range using a mixture of selected chemical standards (DHBA and 4-hydroxycinnamic acid) prior to data acquisition. Authentic (*Z*)-3-hexenyl-pri was used as a reference compound. The images of the parent ion were overlaid onto bright-field images of the corresponding leaf sections with the use of FlexImaging software.

Supplemental Tables

<u>·</u> ··	aroma glycosides (µg g ⁻¹ fresh weight)		total amounts of aroma glycosides (µg)		
_	young leaves mature leaves		young leaves	mature leaves	
			(FW 0.192 ± 0.016 g)	(FW 0.808± 0.057 g)	
benzyl-glc	0.46 ± 0.022	0.044 ±0.01	0.088 ± 0.008	0.036 ± 0.008	
2PE-glc	0.22 ± 0.010	0.098 ±0.03	0.042 ± 0.004	0.079 ± 0.025	
hexenyl-glc	0.65 ± 0.030	0.609 ±0.11	0.125 ± 0.012	0.493 ± 0.096	
linalyl-glc	n.d.	n.d.	nd	nd	
geranyl-glc	0.092 ± 0.015	0.101 ±0.01	0.018 ± 0.003	0.081 ± 0.010	
benzyl-pri	1.75 ± 0.082	2.031 ±0.20	0.336 ± 0.032	1.64 ± 0199	
2PE-pri	13.0 ± 0.61	8.78 ±1.9	2.50 ± 0.24	7.09 ± 1.63	
hexenyl-pri	3.04 ± 0.14	1.505 ±0.23	0.584 ± 0.056	1.22 ± 0.21	
linalyl-pri	7.19 ± 1.20	0.079 ±0.06	1.38 ± 0.26	0.064 ± 0.049	
geranyl-pri	18.6 ± 0.67	3.789 ±0.84	3.57 ± 0.32	3.06 ± 0.72	

Supplemental Table S1. Summary of fresh weight and amounts of aroma β -primeverosides in young leaves and mature leaves of *C.sinensis*.

	Total protein	Total activity	Specific activity	Yield	Purification fold	
	(mg)	(mU)	(mU mg⁻¹)	(%)	(-fold)	
1. Crude extract	681	457	0.67	100.0	1.0	
2. 30-70%(NH ₄) ₂ SO ₄	616	414	0.67	90.5	1.0	
3. HiTrap DEAE	63	39	0.62	8.5	0.9	
4. HiTrap Q	30	29	0.97	6.3	1.4	
5. Hydroxyapatite	5.4	8.7	1.61	1.9	2.4	
6. HiTrap Blue	0.34	1.1	3.23	0.24	4.8	
7. Mono Q	0.15	1.3	8.67	0.28	13	

Supplemental Table S2. Summary of the purification of CsGT2 from young fresh leaves of *C.sinensis*

One unit activity was defined as the amount of enzyme biosynthesized 1 μ mol of geranyl β -primeveroside per minute at 30°C. Specific activity and purification fold were calculated from the activity data.

Supplemental Table S3. Gene specific primers used for 5', 3'-RACE, amplification of full-length genes from *C.sinensis*, construction of CsGT2-I141S or real-time PCR.

gene specific primers	Primer sequences
At_UGT85A1-Dig-Fw	5'-ATGGGATCTCAGATCATTCATAACT-3'
At_UGT85A1-Dig-Rv	5'-TTAATCCTGTGATTTTTGTCCCA-3'
At_UGT85A3-Dig-Fw	5'-ATGGGATCCCGTTTTGTTTCTAACGAA-3'
At_UGT85A3-Dig-Rv	5'-TTACGTGTTAGGGATCTTTCCCAA-3'
CsGT2-Race-FW	5'- GGCTGCTCATATTGCATGGGTATGGCTA-3'
CsGT2-Race-RV	5'-CGACAGGGTAGGAGAGAGAGGACTGGTTGT-3'
CACC-Xhol-CsGT1-FW	5'-CACCCTCGAGATGGGTAGCAGAAAGCAG-3'
CsGT1- <i>BgI</i> II-stop-RV	5'-AGATCTTTAGTATTGCTCACAATAGTGAAGAGC-3'
CACC-Ndel-CsGT2-FW	5'-CACCCATATGGATTCAAAAAAGAGCAAAATG-3'
CsGT2- <i>BamH</i> I-RV	5'-GGATCCTAATTTTTGAGCAACTTCACATC-3'
CsGT2-134-I141S-FW	5'-GCAGTCCAGCTCATGAGTACCGGAGCCACG-3'
CsGT2-134-I141S-RV	5'-CGTGGCTCCGGTACTCATGAGCTGGACTGC-3'
qRT-CsGT1-FW2	5'-TGTCCAAAGAGGCATTTTCC-3'
qRT-CsGT1-RV2	5'- AAGGATGGCATGTCCTTGAG-3'
qRT-CsGT2-FW2	5'-CGCAGTCCAGCTCATGATTA-3'
qRT-CsGT2-RV2	5'-TCAACAAAGTGGCGAAACTG-3'
qRT- <i>β-PD</i> -FW	5'-AAGGATCCCCAGAGGGTCTA-3'
qRT- <i>β-PD</i> -RV	5'-TCCGAACCTTTGGGTGTAAC -3'
qRT-Cs18SrRNA-FW	5'-CACGGGGAGGTAGTGACAAT-3'
qRT-Cs18SrRNA-RV	5'-CCTCCAATGGATCCTCGTTA-3'

Supplemental Table S4. Composition of the buffers and solutions for purification and identification of CsGT2 protein

Buffer/Solution	Composition
Buffer A	100 mM Tris-HCI (pH 7.5) containing 10 mM sodium ascorbate, 5 mM dithiothreitol, 1 mM phenylmethylsulfonyl, 1 mM EDTA, 0.1% CHAPS, 0.1% (v/v) 2-mercaptoethanol, 5% (w/v) polyvinylpolypyrrolidone and 10% (w/v) DOWEX1x2(Cl ⁻)
Buffer B	20 mM Tris-HCI (pH 8.0) containing 0.1% (v/v)
	2-mercaptoethanol
Buffer C	20 mM borate buffer (pH 9.0) containing 0.1% (v/v) 2-mercaptoethanol
Buffer D	5 mM potassium phosphate buffer (pH 6.8) containing 0.1% (v/v) 2-mercaptoethanol
Buffer E	20 mM potassium phosphate buffer (pH 6.8) containing
	0.1% (v/v) 2-mercaptoethanol
Solution F	25 mM NH₄HCO₃/acetonitrile (1:1 v/v)
Solution G	10 mM dithiothreitol/50 mM NH ₄ HCO ₃
Solution H	55 mM iodoacetoamide/50 mM NH ₄ HCO ₃
Solution I	50% acetonitrile containing 1% formic acid

Supplemental Table S5. GenBank accession numbers used for construction of the phylogenetic tree in Figure 7.

Abbreviation	Plant species		Accession NO
Ad_GT4	Actinidia deliciosa	fuzzy kiwifruit	AIL51400
At_UGT79B1	Arabidopsis thaliana	Arabidopsis	NP_200217
At_UGT79B6	Arabidopsis thaliana	Arabidopsis	NP_200212
At_UGT85A3	Arabidopsis thaliana	Arabidopsis	NP_173655
Bp_UGT94B1	Bellis perennis	daisy	Q5NTH0
Cm_F7G2RhaT	Citrus maxima	pomelo	Q8GVE3
Cr_UGT3	Catharanthus roseus	madagascar periwinkle	BAH80312
Cr_UGT4	Catharanthus roseus	madagascar periwinkle	BAH80313
Cr_UGT85A23	Catharanthus roseus	madagascar periwinkle	F8WLS6
Cs_F7G6RhaT	Citrus sinensis	orange	NP_001275829
Cs_UGT1_UGT85K11	Camellia sinensis	tea plant	BAO51834
Cs_UGT2_UGT94P1	Camellia sinensis	tea plant	BAO51835
Gj_UGT85A24	Gardenia jasminoides	gardenia	F8WKW1
Gm_SGT3_UGT91H4_RhaT	Glycine max	soybean	NP_001240857
lb_UGT85A32	Ipomoea batatas	sweet potato	BAO51842
lp_UGT79G16	Ipomoea purpurea	morning glory	Q53UH5
Me_UGT85K4	Manihot esculenta	cassava	AEO45781
Me_UGT85K5	Manihot esculenta	cassava	AEO45782
Mt_UGT85H2	Medicago truncatula	barrel clover	XP_003618665
Nh_Rt	Nierembergia sp. NB17	cupflower	BAC10994
Pd_UGT85A19	Prunus dulcis	almond	ABV68925
Ph_Rt (UGT79A1)	Petunia x hybrida	petunia	CAA50376
Sb_UGT85B1	Sorghum bicolor	sorghum	XP_002463518
Si_UGT94D1	Sesamum indicum	sesame	BAF99027
SI_NSGT1	Solanum lycopersicum	tomato	AGO03777
Sr_UGT85A8	Stevia rebaudiana	stevia	AAR06913
Sr_UGT85C1	Stevia rebaudiana	stevia	AAR06922
Sr_UGT85C2	Stevia rebaudiana	stevia	AAR06916
Vp_UGT94F1	Veronica persica	persian speedwell	BAI44133
VvGT16	Vitis vinifera	grapevine	XP_002263158
Vv_UGT85A28 (VvGT14)	Vitis vinifera	grapevine	BAO51844
Vv_UGT85A30	Vitis vinifera	grapevine	NP_001277170
Vv_UGT85A33	Vitis vinifera	grapevine	NP_001277168

Supplemental Figures



(8-OH linalyl-glc)

Supplemental Figure S1. Co-expression analysis of AtLIS, CYP76Cs and UGT85A3 by ATTDII (Gene coexpression database, http://atted.jp/) with Ver. C4.1.



Supplemental Figure S2. Enzymatic activity of CsGT1 homologs for (*Z*)-3-hexenol. *In vitro* characterization of UGT85s toward (*Z*)-3-hexenol with tea plant (CsGT1; UGT85K11), Arabidopsis (At_UGT85A3), grapevine (*Vitis vinifera*: Vv_UGT85A33, Vv_UGT85A28, Vv_UGT85A30) and snapdragon (*Antirrhinum majus*: Am_UGT85A13). LC-MS analysis of the enzymatic product of CsGT1 (UGT85K11), At_UGT85A1, At_UGT85A3, Vv_UGT85A33, Vv_UGT85A30) and Am_UGT85A13 compared to the authentic standard ((*Z*)-3-hexenol).


Supplemental Figure S3. Enzymatic activity of CsGT1 homologs for geraniol. *In vitro* characterization of UGT85As toward geraniol with grapevine (*Vitis vinifera*: Vv_UGT85A33, Vv_UGT85A28, Vv_UGT85A30), sweet potato (*Ipomoea batatas*: Ib_UGT85A32), snapdragon (*Antirrhinum majus*: Am_UGT85A13). LC-MS analysis of the enzymatic product of Vv_UGT85A33, Vv_UGT85A28, Vv_UGT85A30 and Am_UGT85A13 and Ib_UGT85A32 compared to the authentic standard (geranyl-glu).



Supplemental Figure S4. Purified enzymes catalyzing the second xylosyltransferase (CsGT2). SDS-PAGE analysis of each active fraction obtained from purification steps. Lane 1; crude enzyme, lane 2; ammonium sulfate, lane 3; HiTrap DEAE FF, lane 4; HiTrap Q FF, lane 5; Macro-prep Ceramic Hydroxyapatite Type III, lane 6; HiTrap Blue HP, lane 7; Mono Q 5/50 GL. SDS-PAGE was staining by a silver staining methods (Sil-best stain one, Nacalai, Kyoto, Japan)

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Sequence	Charge	Observed m/z	Mr (Calc)
			1755 000 1
FPEVEKVELEEALPK	+3	586.3224	1755.9294
AT 1917 AUX D A 3 D	. •	0.44.050	4004 0000
GLVVEGWAPQAR	+2	641.852	1281.6829
RETERTALICI EL CMUNETATUDEDEURU			
FETEFIAHGTETSMANEIMAAKELEAFK	+4	840 4036	3357 6948
		0-0.4000	0+001.0040

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1	ENEHSEIIQW	LDNKGEYSTL	FVSFGSEYFM	SKEEIEEIAH	GLELSMVNFI
51	WVVRFPEVEK	VELEEALPKG	FIDRVGER <mark>GL</mark>	VVEGWAPQAR	ILTHSSTGGF
101	VSHCEWNSVL	ESLKFGVPMV	AIPMQYEQPL	NAKLVEEVGV	AAEVNRDING
151	RLNREEIAQV	IRKVVVEKSG	EDIRIKARIF	GDKIRMKGDE	EIDEAVEVLL
201	QLCKDVKLLK	NSNFIEIFKW	VEKVFYFYFI	LFYWVVWYTN	SLIRLYTSRR
251	STNIVFDHVV	LVLDLVALFF	IYIYRFTIIG	VIVSSFCSID	TGGILNMV

Supplemental Figure S5. Partial peptide sequence of the CsGT2. LC-MS/MS analysis of the partial peptide sequences of CsGT2 (UGT94P1) that purified from tea leaves. A) Three peptide sequences were exactly identified with tea EST database contig 13. B) Predicted amino acid sequence of tea EST database contig 134. Red letters show identical peptides with tea EST database and LC-MS/MS analytical results.



Supplemental Figure S6. Recombinant proteins of a series of CsGTs. Specific bands responsible of CsGT1 and CsGT2 (A), and CsGT2-I141S proteins (B) were detected around the size marker of 50kDa in SDS-PAGE, are roughly consistent with the estimated molecular size of CsGT1 (55.7 kDa) and CsGT2 (51.1 kDa), respectively. These specific bands were immunologically confirmed to be the recombinant CsGTs by Western blotting analysis.



Supplemental Figure S7. Imaging MS of young fresh leaves of *C.sinensis*. Specific signal (red; m/z 417) corresponding to (*Z*)-3-hexenyl-pri. Specific

signal (orange; m/z 284) corresponding to (Z)-3-hexenyl-glc. Specific signal (green; m/z 340) corresponding to geranyl-glc.



Supplemental Figure S8. Harvesting individual tissues for quantification of endogenous aroma glycosides and quantitative real-time PCR (qRT-PCR) of CsGTs and β -PD. The young and mature developmental stages of leaves and stems were defined as follows: young leaves, which are the first, second, and third leaves (plucking part for high grade tea products); mature leaves, which are the fourth and fifth leaves; stem, which are green young non-lignified part between the 3rd leaf and 5th leaf; branch, which are brown lignified old part.

		10	20	30	40	50	60	70	
					.				
Vv_UGT85A28_VvGT14	1	М	GSMEKPHAN	CIPYPAQGH	INPMIKLAKLI	IFRGERITFVN	TEFNHTRLLK	KAQGPN	56
Vv_UGT85A30	1	MAM	AEKPRPHAN	CVPFPAQGH	INPMMKLAKLI	I <mark>HKGF</mark> HITFVN	TEFNHQRLLK	SRGPN	58
Ad_GT4	1	MGSA	GMPEK PHAN	CLPYPAQGH	ITEMIKLAKLIK	ISKGEHVTEVN	TEFNHKRLLF	SRGPD	59
Cr_UGT85A23	1	MGSLSSS	DYSKK <mark>D#</mark> A	CIPYPAQGH	INPMIKLAKLI	IY <mark>KGF</mark> HITFVN	TEFNHKRLLF	KSRGSD	62
Gj_UGT85A24	1	MGSI	SLPEKHHA	CIPYPAQGH	INPMIKLAKILI	HKGEHITEVN	TEFNHKRLLK	SRGPD	59
Ib_UGT85A32	1	MGSLS	SELDK	CIPYPAQGH	INPMIKLAKILI	HKGEHIITEVN	TEFNHRREF	RTRGPE	60
At_UGT85A3	1	MGSRFV	SNEQK	CVPYPAQGH	INPMMKVAKLU	IVKGEHVTEVN	IVYNHNRI	RSRGAN	61
Sr_UGT85A8	1	MASI	AEMQK <mark>DH</mark> AI	CIPYPAQGH	INPMMQFAKLI	IFKGEHISFVN	NHY <mark>NH</mark> KRLQF	RSRGLS	59
Pd_UGT85A19	1	MSPV	ASKEKPHA	FVPF PAQGH	INEMIQUAKIIIN	IYKGEHIITEVN	TEFNIKRMLE	SQCSH	59
Vv_UGT85A33	1	MGSV	TASDKD	LIPYPAQGH	VNEMI KLAKLII	INKGEFVSEVN	TEYNEKRLLF	RSRGPN	59
VvGT16	1		-MGDKD:V	CIPFPAQGH	KEM KIAKLIN	YRGEHITEVN	TEFNIKRULF	RSREPH	54
Mt_UGT85H2	1	MGN	FANRK	MIPYPVQGH	NLFK AALIN	ILREPHILTEVN	HEYN: KRULK	SREPK	58
Me_UGT85K4	1	MGSI	SPQKPINA	LVPYPAQGH	VNILMQUGKLIN		ILEHN: RRUIF	REQE	59
Me_UGT85K5	1	MGSL	ASEIPERA	LVPYPAQGH	VNPLMQLGKLI	ISRGETTEVN	TEHNERRITE	REQE	59
Cs_UGT1_UGT85K11	1	M	GSRKQIDHA	CVPFPAQGH		ISRGETTIEVN	ILEFINERRI LÇ	SKEPE	56
Sr_UG185C1	1	MDQMAK	IDERRET	FIFFPAQSH	KCM KIARIII			ASGETQ	61
SF_UG185C2	1	MDAMA	DDDD	FIFFPAQSH TUDEDCOCUT			DF DINOF LE	SSGPR	60
	1	MGSNA	PPPPTI V				DERVINOLEI		6U 61
	1	MGVFG5	-MCSKETAL	MINUTER			PREADEN	TNIFD	54
Tp UCT79C16	1	MC	SOATTVIM	MYDWECVAL	TCFFDUANKUZ	CHENDING T T	DENTOSE		57
ND D+	1	MG	FNERVILLA	MEDEENE		CUCIENT	ASCINASIDIDE		56
$\frac{1}{2}$	1	MENEMK	HONDATION	MEREEAFOR			ASCINGUE	MT NGA	50 61
Ce F7C6PhaT	1	MHADSNOHHKMOTES	AFADOLIN	MEGEEGEG	SPEVOISNER	STHEVKVSDET	ADONT DETKS	SST.N	68
	1	MD	SKKSKWMM			NUMBER	MDTNT.TSTKK	אחיידס	57
Si UCT94D1	1	MD	TREESTREE	MERWIAHCH	ISAFTETAKSTZ	KRNDVIYTCS	SOVNENSTSK	NMSSK	57
Bp UGT94B1	1	MDSK	TDSKTFRV	MTEWTAYSH	ISRFUVFAKBUT	NHNDHUYTCS	SOTEMOYIKK	INTITSO	59
Cm F7G2RhaT	1	MDT	KHODKSII	MIRWIAHER		SOGNOHUYOCS	PNNLOSEGE	NVEKN	58
Cr UGT3	1	MATEOO	OASTSCKT	MEDWLAFGH	ISSELOLAKKUS	SDREPYFYICS	UPTNLDSTKN	IKTNON	61
Cr UGT4	1	MATEOO	EAPNSLKII	MERWIAFOR	VSPETOTAKKUS	SDREEYIYICS	PINLDSIKN	NISON	61
S1 NSGT1	1	££	IKENS	LFRWLGF	VNPETATAKKI	SKMNOH YOLS	PIILKSIKE	TLDKN	58
Vp UGT94F1	1	MEK	EEAKMFKII	MFEWLAHCH	IFPFLELAKTLS	SKRNOTHACS	TAINLDSIKS	NLAND	58
Gm SGT3 UGT91H4 RhaT	1	MDSVALNGK	SNDKPL	MLEWLAMGH	IYPYFEVAKIL?	QKCHFVTFIN	SPKNIDRMPK	TPKHL	64
		80	0.0						
		00	90	100	110	120	130	140	J
		····	90 	100	110 	120	130 • • • • • • • • • • • •		J
Vv_UGT85A28_VvGT14	57	S-LNG PT5Q5	90 ett<mark>i</mark>p<mark>dgl.p</mark> i	100 SNVDATK	110 . Q dip<mark>sf</mark>castkf	120 (NCTAPERRIA	130 AK <mark>I</mark> NDRG	140 	110
Vv_UGT85A28_VvGT14 Vv_UGT85A30	57 59	S-LNGIPTI9QI S-LRGIPSI9QI	90 ETIPDGLPP ETIADGLPP	100 . SNVDAN SDIDAN	110 . QDIPSICASTKF QDVPSICASTHN	120 NCTAPERRIA NDCTAPERDIA	130 AKINDRG AKINDTSS	140 skv	, 110 116
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4	57 59 60	S-LNGPPT503 S-LRGPPT503 S-LTGPS1503	90 ETIPDGLPI ETIADGLPI ETIPDGLPI	100 SNVDAN SDIDAN SDIDAN	110 DIPSICASTKF DVPSICASTHN DFIPSICESTRF	120 NCTAPERRIAL NCTAPERDAL NCTGPERQAL	130 AKUNDRG AKUNDTSS GKUNNTVS	skv	, 110 116 117
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23	57 59 60 63	S-LNGPT3Q3 S-LRGPP3Q3 S-LTGPS3Q3 S-LTGPH3Q3 S-LKGPH3Q3	90 ETIPDGLPI ETIADGLPI ETIPDGLPI KTIPDGLPI	100 SNVDAH SDIDAH SDIDAH SDVDAH	110 DIPSICASTKF DVPSICASTHA DFIPSICESTRF DDIPSICESTTI	120 NCIAPERRIA NCIAPERRIA NCIAPERDIA NCIGPERDIA NCIGPERDIA	130 AKUNDRG AKUNDTSS GKUNNTVS QKUNDTSS	SKV SGV SEV	, 110 116 117 120
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 rb-UGT85A24	57 59 60 63 60	S-LNGDFT905 S-LRGDFT905 S-LTGDFS905 S-LTGDFS905 S-LKGDHS505 A-LNGDHS505 A-LNGDHS505	90 ETIPDGLPP ETIPDGLPP ETIPDGLPP KTIPDGLPP KTIPDGLPP	100 SNVDAR SDIDAR SDIDAR SDVDAR SDVDAR	110 DIPSICASTRE DVPSICASTRE DVPSICASTRE DIPSICESTRE DIPSICESTTI DIPSICESTTI	120 NCTAPERRIA NCTAPERDIA NCTAPERDIA NCTGPERQUI NCTGPERQUI RCTDPERNIA	130 AKUNDTSS GKUNNTVS GKUNNTVS QKUNDTSS AEUNGPSS		110 116 117 120 117
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Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2	57 59 60 61 62 60 60 55 59	S-INGPPT3Q3 S-IRGPPS3Q3 S-IRGPS5Q3 S-IRGPS5Q3 A-INGPP53Q3 A-INGPP53Q3 A-IDGPP53Q3 A-IDGPP53Q3 A-IDGPP5R3 S-IDGPS5Q3 A-IDGPP5R3 S-IDGPP5R3 A-IDGPP5R3 A-IDGPP5R3	ETIPOGLED ETIPOGLED ETIPOGLED KTIPOGLED ETIPOGLED ESIPOGLED YSIPOGLED ETIPOGLED ETIPOGLED ETIPOGLED ESIPOGLED	100 SNVDARK SDIDARK SDIDARK SDUDARK SDVDARK SDADARK SNAEAR SDADARK SDADARK VDADARK	110 DIPSICASTRI DVPSICASTRI DVPSICESTRI DIPSICESTTI DIPSICESTSI DIPSICESTSI DIPSICESTSI DIPSICESTPI DIPSICESTPI DIPSICESTPI DIPSICESTPI DVPTICOSVRI	120 	130 ARUNDRG AKUNDTSS QKUNDTSS QKUNDTSS ARUNDTAV QRIVTR ATUNG TKUNSS TKUNSS AKUNDAPS AKUNDAPS	140 	110 116 117 120 117 118 117 114 115 117 112
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4	57 59 60 61 62 60 60 55 59 60	S-ING	ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ESIPOGLP ETIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP	100 SNVDAM SDIDAM SDIDAM SDVDAM SDVDAM SDVDAM SDADAM SDADAM SDADAM ME-GDGDV8(ME-GDGDV8(TDADAM	110 DIPSICASTRE DOVESICASTRE DIPSICESTRI DIPSICESTRI DIPSICESTRI DIPSICESTSI DIPSICESTSI DIPSICESTSI DIPSICESTPE DIPSICESTPE DIPSICESTPE DIVSISSTRE	120 	130 AKUNDRG GKUNDTSS GKUNNTVS QKUNDTSS AFUNGPSS QRIVTR ARUNDTAV TKUNSS TKUNDPSY AKUNDAPS TRUNDAPS TRUNDAPS	140 	110 116 117 120 117 118 117 114 115 117 112 116 115
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K5	57 59 60 61 62 60 60 55 59 60	S-LNGPF5QS S-LRGPS5QS S-LRGPS5QS S-LRGPS5QS S-LRGPS5QS A-LNGPS5QS A-LDGPS5QS A-LDGPS5QS A-LDGPS5QS A-LDGPS5QS A-LDGPS5QS A-LDGPS5QS F-DGPD5QS F-DGPD5QS	ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP SIPOGLP ETIPOGLP ETIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP EAIPOGLP EAIPOGLP	100 S	110 DDIPSICASTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICESTRE DDIPSICSTRE DHVPSISDSTRE	120 	130 AKUNDRG GKUNDRG QKUNDTSS QKUNDTSS QRUVTR QRIVTR TKUNSS TKUNDPSY AKUNDAPS AKUK	14(110 116 117 120 117 118 117 114 115 117 112 116 115 115
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Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 VvGT16 Mt_UGT85A3 VvGT16 Mt_UGT85K1 Me_UGT85K1 Me_UGT85K1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT9B1 At_UGT79B1 At_UGT79B1 At_UGT79B1 Cs_F7G6RhaT Cs_UGT2_UGT94P1 Si_UGT94D1 Bp_UGT94D1 Bp_UGT94F1 Cr_UGT3 Cr_UGT4 S1_NSGT1 Vp_UGT94F1 Cr_UGT4_UCT PAL	57 59 60 60 60 60 55 90 60 57 60 61 61 60 55 90 60 57 60 61 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 60 57 60 61 57 77 62 61 61 57 77 62 63 57 77 57 75 75 85 61 57 77 57 75 75 75 75 75	S-INGPF5Q5 S-IRGPS5Q5 S-IRGPS5Q5 S-IRGPS5Q5 S-IRGPS5Q5 S-IRGPS5Q5 A-IDGPS5Q5 A-IDGPS5Q5 A-IDGPS5Q5 A-IDGPS5Q5 A-IDGPS5Q5 F-IDGPD5Q5 F-IDGPD5Q5 F-IDGPD5Q5 F-IDGPD5Q5 F-IDGPD5Q5 F-IDGPD5Q5 F-IDG	ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ETIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP ESIPOGLP POUS ESIPOGLP POUS ESIPOGLP PS-VDGLP PS-VDGLP PS-VDGLP PH-VEGLP PH-VEGLP PH-VEGLP PS-SPELP PH-VEGLP PS-SPELP PN-SPOLP PN-SPOLP PN-SPOLP PY-LHELP ES-PELP	100 SNVDAM SDIDAM SDIDAM SDVDAM SDVDAM SDADAM SS	110 DDIPSICASTH DDIPSICASTH DDIPSICESTR	120 	130 AKUNDRG	140 	110 116 117 120 117 120 117 118 117 118 117 114 115 117 112 116 115 115 115 115 115 116 115 116 115 117 112 116 117 118 118

Supplemental Figure S9. Multiple sequence alignment of protein sequences of UGT-glucosyltransferase OG2 and OG8 family. The alignment was performed using ClustalW2.1.

		1	150	160	170	180	190	200	210	
Vv UGT85A28 VvGT14	111	PEVTCHESD		LDAAOEL	enedillwia	SACCEMAYVOY	 RSLIDKGFT	PLKDESYTTN	 IG-Y ^{ID} D 17	16
Vv UGT85A30	117	PPVTCIVSD		LKAAEEL	GIPEVFFWTT	SACCEFMGYVQY	RHLIDRGFF	PLKDESCLTN	G-н о 18	32
Ad GT4	118	PPVSCVVSD	GVMS	LDAABEL	GIPOVLEWTI	SVCGFMAYVHY	RNLIEKGYT	PLKDVSYVTN	IG-Y<mark>I</mark>D 18	33
Cr_UGT85A23	121	PPVSCVVSD	AVMSET	IS <mark>AA</mark> QELI	DIPEVLEWTE	SACCVLGYM#Y	AQLIDKGLT	PLKDASYFSN	IG-FID 18	86
Gj_UGT85A24	118	PPVSCIVSD	GVMSET	le <mark>aa</mark> ael	GVPEILFWTT	SACGFLGYMHY	AKLIEKGLT	Plkdasylsn	IG-YIE 18	33
Ib_UGT85A32	119	PPVSCIVSD	GVMSIT	VDAAEEL	GIPEVLEWTI	SACCFLGYMHF	TQLLDKGYT	PLKDESYLTN	IG-YIE 18	34
At_UGT85A3	118	PEVSCIVSD	GSMSET	LDVAEEL	GVEEIHEWTI	SACGFMAYLHF	YLFIEKGLC	PVKDASCITK	E-Y D 18	33
Sr_UGT85A8	115	PEVSCHISD	GVMSIT	LQ‡‡ERF	CIPEVIEWTE	SACCFLAYTHY	RDLVDKEYI	PLKOTNDUTN	IG-YNE 18	30
Pd_UGT85A19	110	PEVTERVAD	GVSSBT		GIPEVILEWIT	SACELMGYVQY	YRLIEKGLT	PFKDAKDFAN	G-YPD 18	1
VV_UG185A33	113	PEVSCIVSD	COMONT	IDAAKERE		SACCENTRET	RNLIKKGLI	PLODESCISM	IG-YND 18	53 19
W+ 11GT85H2	117	PEVICINS	CCMSDT		ELENVIJEN	SACSLLNVM:F	RSEVERGIT	DEKDESYLTN		22
Me UGT85K4	116	PRITCHISD	GVMADA	IDAARHF	GILEIORWIT	SACEFMAYL	IELVRRGIV	PFKDESFTHD	G-тир 18	31
Me UGT85K5	116	PPITCIISD	GVMADA	IDAARHF	GIPEIOFWIT	SACGFMAYLHH	IELVRRGIV	PFKDESFLHD	G-т<u>г</u>д 18	31
Cs UGT1 UGT85K11	119	PGVTCVVSD	GAMNIJA	MK <mark>AA</mark> EEA	GIPEVQEWTA	SACC FMGYLHY	PQLVQRGIF	PFKDESFQSD	G-S<mark>D</mark>D 18	34
sr_ugr85C1	116	-PATCIICD	GCMTHAI	N-TIR <mark>AA</mark> EKLI	NIEVILEWIM	ia <mark>acc</mark> fmafyqa	KVLKEKEIV	PVKDETYLTN	IG-YND 18	33
Sr_UGT85C2	112	-PPTCIISD	GFLSVF	TID <mark>AA</mark> KKL	GIPVMMYWIII	A <mark>ACC</mark> FMGFY <mark>H</mark> I	HSLIEKGFA	Plkdasyltn	ig-y<mark>n</mark>d 17	8
Sb_UGT85B1	122	PEVTCVVGD	VVMTIGA	AA <mark>AA</mark> REA	GIPEVQEETA	SACGLLGYLHY	GELVERGLV	PFRDASLLAD	DDYND 18	88
At_UGT79B1	114	PDLVFYD	SAH-WI	PEI <mark>A</mark> KPI	GAKTVCENIV	SAASIALSLVP	SAEREVIDG	KEMSGEE <mark>I</mark> AK	T-P G 17	7
At_UGT/9B6	1107	PDLUFFD	FAH-WI	PEIAREY	EVKSVNEIHI	SAACVAISFVP		-GRSQDD <u>H</u> GS	T-PPG 10	0
IP_UGT/9GI6	112		FTH-WL	PSLARKI	GIKSVEYSUL	SPLMHGYALSP	ERRVVG	KQLTEADMMK	D-DC 17	10
Ph R + IICT79A1	114	PHEVLED	FACENT	PKM2NGL		VALSTAFLTCP	ARVIEPK	KYPSLEDMKK	P-Pig 17	16
Cs F7G6RhaT	123	PHEVEED	FTHYWL	PGLVGSOL	GIKTVNISVE	SAISOAYLVVP	ARKLNN-	SLAD	S-PDG 18	32
Cs UGT2 UGT94P1	112	PDLVIYD	VSPSWA	QSTALSF	DIPAVQLMII	GATVASFGQHM	ікн	CGSV	7E 16	51
si_ugr94d1	111	PDLVLYD	FLQSWA	SEE <mark>A</mark> ESQI	NIRAMVELSI	GAAAISFIMYH	WFE	TRPE	се 16	50
Bp_UGT94B1	114	PHLVIYD	FNQLWA	PEVASTL	HIPSIQLLSC	CVALYALDAHL	ҮТК	P <mark>I</mark> DE	EN-LAK 16	66
Cm_F7G2RhaT	114	PTLVMYD	LFQPMA	AE <mark>AA</mark> YQYI	DIAAILIJLPI	SAVACSFLL:N	IVN	PSLK	 16	52
Cr_UGT3	116	PDLIIYD	LHQPWT	EALASRHI	NTEAVSESTM	INAVSFAYVMHM	FMN	PGI-	E 16	54
Cr_UGT4	116	PDLUIHD	VHQQWT	AVLASKQI	NULAWSISSIM	NAVSFAYIM:M	FMQ	PGS-	E 16	
SI_NSGTI Vo UCT94F1	115		GEQPWV		N HAIMSYVS Gedevaldaas	STSCLAILINQ	F.TH		LTS 16)/ :2
Gm SGT3 UGT91H4 RhaT	118		FAAAWV	TPTAKSYI	NTECAHYNTT	PAFNKVFFDPP	КDК		TASTC 17	12
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	1 7 7	2	20 	230	240	250	260	270	280 	
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Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad GT4	177 183 184	2 TVVDWIEG- TVVDWIEA- TVIDWIEG-	20 mkgir Mkgvr Megir	230 KDIESBIRTTI RDIESBIRTTI KDIESBIRTTI	240 DP-DDIMLDF NP-DDIVVNF DP-NDIMLDF	250 . AMGELERARKA AMGEVERANDA VLSETKNTHRS	260 SAIIFNTFD SAILLNTFD SAILLNTFD	270 AIJEQEVLDAI EIJEHEVLQAI KIJEHOVLEPI	280 APMYP 24 STMFP 25 ASMFP 25	14 50
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr UGT85A23	177 183 184 187	2 TVVDWIPG- TVVDWIPA- TVIDWIPG- OVIDWIPG-	20 MKGIRI MKGVRI MEGIRI MEGIRI	230 KDIESEIRTTI RDIESEIRTTI KDIESEIRTTI RDIETEIRTTI	240 DP-DDIMLDF NP-DDIVVNF DP-NDIMLDF NP-DEYMIKF	250 	260 SATTENTED SATTENTED SATTENTED SATTENTED SATVENTED	270 Aleqevidai Subheviqai Kidhqviepi Sidesevidsi	280 Apmyp 24 STMFP 25 ASMFP 25 STLLP 25	4 50 51
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24	177 183 184 187 184	2 TVVDWTEG- TVVDWTEA- TVIDWTEG- QVIDWTEG- QSIDWTEG-	20 MKGIRU MEGIRU MEGIRU MKDIRU	230 KDISSIRTTI RDISSIRTTI KDISSIRTTI RDISSIRTTI RDISTIRTTI KDISSIRTTI	240 DP-DDIMLDE NP-DDIVVNE DP-NDIMLDE NP-DEYMIKE NP-DEYMIKE	250 . AMGELERARKA AMGEVERANDA VLSETKNTHRS ILQETERSKKA VLQETERAKKA	260 SALLENTED SALLENTED SALLENTED SALLENTED SALVENTEQ SALLENTEQ	270 ALEQEVLDAI SIEHEVLQAI KIEHQVLEPI SHESEVIDSI SHEDDVINAI	280 APMYP 24 STMFP 25 ASMFP 25 STLLP 25 SAILP 25	14 50 51 54
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32	177 183 184 187 184 185	2 TVVDWIEG- TVVDWIEA- TVIDWIEG- QVIDWIEG- QSIDWIEG- TELDWVKG-	20 MKGIRU MEGIRU MEGIRU MKDIRU MKGIRU	230 KDIESTIRTTI RDIESTIRTTI KDIESTIRTTI RDIETTIRTTI KDIESTIRTTI RDIESTIRTTI	240 DP-DDIMLDE NP-DDIVVNE DP-NDIMLDE NP-DEYMIKE NP-DDYMVKE NP-DEYMLKE	250 	260 SALLENTED SALLENTED SALLENTED SALLENTED SALLENTED SALLENTED SALLENTED SALLENTED	270 ANGQEVLDAI SMGHEVLQAI KIGHQVLEPI SMGEVIDS SMGDVINAI ANGHEAIMAI	280 APMYP 24 STMFP 25 ASMFP 25 STLLP 25 SATLP 25 SATLP 25 OSMLP 25	14 50 51 54 51
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3	177 183 184 187 184 185 184	2 TVVDWTEG- TVVDWTEA- TVIDWIEG- QVIDWIEG- QSIDWIEG- TELDWVKG- TVIDWIES-	20 MKGIRU MKGVRU MEGIRU MKDIRU MKGIRU MNNVKU	230 RDLESDIRTTI KDLESDIRTTI KDLESDIRTTI KDLESDIRTTI RDLESDIRTTI	240 DP-DDIMLDE NP-DDIVVNE DP-NDIMLDE NP-DEYMIKE NP-DEYMIKE NP-DEYMLKE NP-DEYMLKE	250 	260 SATIPATED SATIPATED SATIPATED SATUDATEQ SATUDATEQ SATUDATEQ SATUDATEQ SATUDATED SATUDATED	270 ALEQEVIDAI MAEVIQAI MAEVIQAI SIASHEVIDSI BIESEVID BIESEVID B	280 APMYP 24 STMFP 25 ASMFP 25 SATLP 25 SATLP 25 QSMLP 25 QSTLP 25	14 50 51 51 52
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8	177 183 184 187 184 185 184 185	2 TVVDWEG- TVVDWEA- TVIDWEG- QVIDWEG- QSIDWEG- TELDWVKG- TVIDWES- TSIDWEG-	20 MKGIRU MEGIRU MEGIRU MKDIRU MNNVKU MKNIRU	230 KOLESGIRTTI ROLESGIRTTI KOLESGIRTTI ROLESGIRTTI ROLESGIRTTI KOLESGIRTTI KOLESGIRTTI	240 DP-DDIMLDF NP-DDIWLDF NP-DDIWLDF NP-DYMIKF NP-DYMVKF NP-DEYMIKF NP-DEYMLKF NP-NDIMLNF DI-NDIMLNF	250 	260 SATIFNTFD SATILNTFD SATILNTFD SATILNTFQ SATILNTFQ SATILNTFD SATILNTFD SATILNTFD VATILNTFD	270 ALCEVIDAT CILDHEVLOAT KALHQVLEP DASEVIDST JACDVINAT ALCHEATMAN DACHDITQSM ALCKDSITPU	280 APMYP 24 STMFP 25 ASMFP 25 SATLP 25 SATLP 25 QSMLP 25 QSTLP 25 TALNP 24	14 50 51 51 51 51
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19	177 183 184 187 184 185 184 185 184 181	2 TVVDWEG- TVVDWEA- TVIDWEG- QVIDWEG- QSIDWEG- TVIDWES- TSIDWEG- TEIDWEG-	20 MKGIRU MEGIRU MEGIRU MKDIRU MKDIRU MKNIRU MKNIRU	230 KOLESGIRTI ROLESGIRTI KOLESGIRTI ROLESGIRTI ROLESGIRTI KOLESGIRTI KOLESGIRTI KOLESGIRTI	240 DP-DDIMLDF NP-DDIVUNF DP-NDIMLDF NP-DYMKR NP-DYMKR NP-DYMKR NP-DYMKR DI-NDIMLNY DP-NDIMLNY DP-NDIMLHY	250 AMGELERARKA AMGEVERANDA VLSETKNTHRS ILQETERAKKA VLQETERAKKA ILQETGRARRA VVREACRTKRA FLIETEAIPKG MVSETERSKKA	260 SAILNTFD SAILNTFD SAILNTFD SAILNTFO SAILNTFO SAILNTFO SAILNTFD SAILNTFD SAILNTFD	270 ALCOUNDAT CHARLOULDAT CHARLOULDAT CHARLOULDAT CHARLOULDAT CHARLOULDAT ALCOUNDAT ALCOUNDAT ALCOUNDAT	280 APMYP 24 STMFP 25 ASMFP 25 STILP 25 STILP 25 QSMLP 25 QSTLP 25 LAINP 24 STILP 24	14 50 51 51 51 18
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33	177 183 184 187 184 185 184 185 184 181 182 184	2 TVVDWEG- TVVDWEA- TVIDWEG- QVIDWEG- QSIDWEG- TELDWKG- TVIDWES- TSIDWEG- TEIDWEG- TVVDFVGK	20 MKGIRI MKGVRI MEGIRI MKDIRI MKDIRI MKNIRI MKNIRI MKVRI KKTIRI	230 RDLESDIRTTI KDLESDIRTTI KDLESDIRTTI KDLESDIRTTI KDLESDIRTTI KDLESDIRTTI KDLESDIRTTI KDFESDIRTTI KDFESDIRTTI	240 DP-DDIMLDF NP-DDIVUNF DP-NDIMLDF NP-DYMIKF NP-DYMKKF NP-DYMKKF NP-NDIMLNF DI-NDIMLNF DI-NDIMLNF DI-NDIMLNF DI-NDIMLNF	250 	260 SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED	270 ALCOUNDAT CLOHEVLOAT KALHQVLEP DASEVIDST DADDVINAT ALCHEATMAT DADDITOST ALCOUNDAT ALCOUNDAT ALCOUNDAT	280 APMYP 24 STMFP 25 ASMFP 25 STILP 25 STILP 25 QSMLP 25 QSTLP 25 LAINP 24 STILP 24 STILP 24	14 50 51 52 51 18 19 52
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2	177 183 184 187 184 185 184 181 182 184 179 183	2 TVVDWEG- TVVDWEA- TVIDWEG- QVIDWEG- QVIDWEG- TELDWVKG- TVIDWES- TSIDWEG- TEIDWEG- TVVDFVGK TIIDWVEG- TKVDWEG-	20 MKGIRU MKGVRU MEGIRU MKDIRU MKDIRU MKNIRU MKNIRU MKNIRU MKNMRU IKNIRU	230 RDLESFIRTTI KDLESFIRTTI KDLESFIRTTI KDLESFIRTTI KDLESFIRTTI KDLESFIRTTI KDFESFIRTTI KDFESFIRTTI RDFESFIRTTI RDFESFIRTTI	240 DP-DDIMLDF NP-DDIMLDF NP-DDIWLDF NP-DDYMKE NP-DEYMKE NP-NDIMLNF DI-NDIMLNF DI-NDIMLHY DL-NDIMLHY DPSDHFMLDF DPSDHFMLDF	250 	260 SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SATIENTED SCIENTED	270 ALCOUNT AL	280 STMFP 24 STMFP 25 SSTLP 25 SSTLP 25 SSTLP 25 CSMLP 25 CSMLP 24 SSTLP 25 SSMFP 24 SSMFP 25	4 50 51 52 51 52 52 52 52 52 52 52
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4	177 183 184 187 184 185 184 181 182 184 179 183 182	2 TVVDWEG- TVVDWEG- QVLDWEG- QVLDWEG- TELDWEG- TVLDWEG- TVLDWEG- TVVDFVEGK TILDWEG- TVVDFVEGK TILDWEG- TKVOWEG- TKVOWEG-	20 MKGIRU MKGVRU MEGIRU MKDIRU MKDIRU MKNIRU MKNIRU MKNIRU MKNRU LKNFRU MPNMKU	230 KOLESSIRTTI ROLESSIRTTI ROLESSIRTTI ROLESSIRTTI ROLESSIRTTI ROLESSIRTTI ROFESSIRTTI ROFESSIRTTI ROFESSIRTTI ROFESSIRTTI ROFESSIRTTI ROFESSIRTTI	240 DP-DDIMLDF NP-DDIMLDF NP-DDIMLDF NP-DEYMIKF NP-DEYMIKF NP-DEYMIKF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLDF NP-NDIMLF	250 	260 SATIENTED SATURTED SATURTED SATURTED SATURTED SATURTED SATURTED SATURTED SATURTED SCURNED SCURNED	270 ALCOUNT AL	280 STMFP 24 STMFP 25 SASMFP 25 SASMFP 25 SATLP 25 OSSMLP 25 CALP 25 SSMFP 24 SATLP 25 SSMFP 25 SSMFP 25 ARYS 24	14 50 51 52 51 52 52 52 52 50 50
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K5	177 183 184 187 184 185 184 185 184 182 184 179 183 182 182	2 TVVDWEG- TVVDWEG- QVDWEG- QVDWEG- TVDWEG- TVDWEG- TVDWEG- TVDWEG- TVVDFVEGK TIIDWEG- TKVWEG- TKVWEG- QVDFEG- QVDFEG-	20 MKGIRU MKGURU MKGIRU MKDIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU	230 NOIESEIRTTI ROIESEIRTTI ROIESEIRTTI ROIESEIRTTI ROIESEIRTTI ROIESEIRTTI ROFESEIRTTI ROFESEIRTTI ROFESEIRTTI ROFESEIRTTI ROFESEIRTTI ROMESEIRVTI ROMESEIRVTI	240 DP-DDIMLDF NP-DDIMLDF NP-DEYMKF NP-DEYMKF NP-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLFF DV-NDIMLFF DV-NDIMFDF DV-NDIMFDF	250 	260 SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED DALLATED DALLATED	270 AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT AMOCVUDAT	280 APMYP 24 STMFP 25 ASMFP 25 SATLP 25 SATLP 25 SATLP 25 QSTLP 25 QSTLP 24 SATLP 24 SATLP 24 SATLP 24 SATLP 24 AARYS 24 AARYS 24	4 50 51 52 51 52 51 52 52 50 52 50 52 50 52 50 52 50 52 50 52 50 52 52 52 52 52 52 52 52 52 52 52 52 52
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11	177 183 184 187 184 185 184 185 184 182 184 179 183 182 182 182	2 TVVDWEG- TVVDWEG- QVIDWEG- QVIDWEG- QVIDWEG- TVIDWEG- TVIDWEG- TVVDFVEGK TIIDWVG- TKVDFVEGK TIIDWVG- QVDFUG- QVDFUG- TVIDWEG-	20 MKGIRU MKGVRU MEGIRU MKDIRU MKNIRU MKNIRU MKNIRU KKTIRU MKNIRU LKNFRU MPNMKU MPNMKU MRNIRU	230 KDIESFIRTT RDIESFIRTT RDIESFIRTT RDIESFIRTT RDIESFIRTT RDIESFIRTT RDIESFIRTT RDFESFIRTT RDFESFIRTT RDFESFIRTT RDFESFIRTT RDFESFIRTT RDFESFIRTT RDMESFIRVT RDMESFIRVT RDMESFIRTT	240 DP-DDIMLDF NP-DDIMLDF NP-DEYMIKF NP-DEYMIKF NP-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLEF DV-NDIMEDF DV-NDIMEDF DP-NDIMEDF DP-NDIMENF	250 	260 SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED DALLATED SALLATED SALLATED SALLATED	270 AME OEVLOAT AME OEVLOAT AME OEVLOAT AME HEVLOAT AME HEALMAN AME HEALMAN AME HEALMAN AME NOVLOAT AME OEVVOAT AME OEVVOAT AME OEVLOAT AME OEVLOAT THE HOVLOAT	280 APMYP 24 STMFP 25 STMFP 25 SATLP 25 SATLP 25 SATLP 25 OSTLP 25 SATLP 24 SATLP 24 SATLP 24 SATLP 25 SSMFP 24 SATLP 25 AARYS 24 AARYS 24 ASKFH 25	4 50 51 52 52 52 50 52 50 52 50 52 50 52 50
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1	177 183 184 187 184 185 184 181 182 184 179 183 182 182 182 185 184	2 TVVDWHG- TVVDWHG- QVIDWHG- QVIDWHG- QVIDWHG- TVIDWHG- TVIDWHG- TVVDFVGCK TIIDWVG- TKVDWHG- QVDFHG- QVDFHG- TTIDWHG- MEIDWHG-	20 MKGIRU MKGVRU MKGIRU MKDIRU MKDIRU MKNIRU MKNIRU KKTIRU MKNIRU LKNFRU MPNMKU MRNIRU MKNIRU	230 KOLESSIRTTI ROLESSIRTTI ROLESSIRTTI ROLESSIRTTI KOLESSIRTTI KOLESSIRTTI KOLESSIRTTI ROFESSIRTTI ROFESSIRTTI ROFESSIRTTI ROMESSIRVTI ROMESSIRVTI ROMESSIRTTI ROMESSIRTTI ROMESSIRTTI	240 DP-DDIMLDF NP-DDIMLDF NP-DEYMKF NP-DEYMKF NP-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLNF DF-NDIMLFF DV-NDIMLFF DV-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFDF	250 	260 SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED DALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED	270 AMOOVDAT	280 APMYP 24 STMFP 25 STMFP 25 SATLP 25 SATLP 25 SATLP 25 OSTLP 25 SATLP 24 STLP 24 SSTFP 24 SSTFP 25 AARYS 24 AARYS 24 ASKFF 25 KSTFP 25	14 51 51 52 51 19 52 51 19 52 51
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K4 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C2	1777 183 184 1877 184 185 184 181 182 182 182 182 182 182 182 182 184 179	2 TVUDWEG- TVUDWEG- QVIDWEG- QVIDWEG- QVIDWEG- TVIDWEG- TSIDWEG- TVVDFVEGK TIIDWEG- TVVDFVEGK TIIDWEG- TVVDFVEGK TIIDWEG- MEIDWEG- TVIDWEG-	20 MKGIRU MKGVRU MKGVRU MKDIRU MKDIRU MKNIRU KKTIRU MKNIRU LKNFRU MPNMKU MPNMKU MRNIRU MKRIRU MKRIRU	230 KOLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROFESGIRTTI ROFESGIRTTI ROFESGIRTTI ROFESGIRVTI ROMESGIRVTI ROMESGIRVTI ROMESGIRVTI ROMESGIRVTI ROMESGIRTTI ROMESGIRTTI	240 DP-DDIMLDF NP-DDIMLDF NP-DEYMKF NP-DEYMKF NP-DEYMKF NP-NDIMLNF DP-NDIMLNF DP-NDIMLF DV-NDIMLDF DV-NDIMEDF DV-NDIMFDF DV-NDIMFDF DP-NDIMFDF DV-ND	250 	260 SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED DALLANTED DALLANTED DALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SHALLANTED SHALLANTED	270 ALLOCVIDAT ALLOCVI	280 APMYP 24 STMFP 25 STMFP 25 SATLP 25 SATLP 25 SATLP 25 OSMLP 25 OSMLP 24 STLP 24 STLP 24 SSMFP 24 SSTP 25 AARYS 24 AARYS 24 AARYS 24 AARYS 24 SSTP 25 SLRYN 24	4 50 51 52 52 52 52 52 52 52 52 52 52 52 52 52
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Vv_UGT85A3 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1 Sr_UGT85C2 Sb_UGT85B1	1777 183 184 187 184 185 184 182 184 179 183 182 182 182 182 182 182 182 182	2 TVUDWEG TVUDWEG QUDWEG QUDWEG QUDWEG TUDWEG TUDWEG TUDWEG TVUDVEG TUDWEG TUDWEG TUDWEG TUDWEG TUDWEG TUDWEG	20 MKGIRU MKGURU MKGURU MKDIRU MKDIRU MKNIRU KKTIRU MKNIRU LKNFRU MPNMKU MPNMKU MRNIRU MKRIRU MKRIRU	230 KOLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROFESGIRTTI ROFESGIRTTI ROFESGIRTTI ROFESGIRVTI ROMESGIRVTI ROMESGIRVTI ROMESGIRVTI ROMESGIRTTI ROMESGIRTTI ROMESGIRTTI	240 DP-DDIMLDF NP-DDIVNF DP-NDIVNF DP-NDIVNF NP-DEYMKF NP-DEYMKF NP-NDIMLNF DP-NDIMLNF DP-NDIMLFF DV-NDIMEDF DV-NDIMEDF DV-NDIMFDF DV-NDIMFDF DV-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFDF DP-NDIMFNF DP-NDIMFDF DP-NDIMFNF DF-DDIMFNF DF-DDI	250 	260 SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED DALLANTED DALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SHALLATED	270 ALE OEVLOAL ALE OEVLOAL ALE OEVLOAL ALE OEVLOAL ALE EVLOAL ALE EVLOAL ALE OEVLOAL ALE OEVLOAL	280 APMYP 24 STMFP 25 STMLP 25 SATLP 25 SATLP 25 OSMLP 25 OSMLP 25 OSMLP 24 STLP 24 STLP 24 SSMFP 24 SSTP 25 AARYS 24 AARYS 25	4 5 5 5 1 5
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Pd_UGT85A3 Vv_UGT85A3 Vv_UGT85A3 VvGT16 Mt_UGT85K4 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85D1 At_UGT79B1	1777 183 184 187 184 185 184 182 184 179 183 182 182 182 182 182 182 182 182	2 TVVDWHG- TVVDWHG- QVDWHG- QVDWHG- QSDWHG- TEIDWHG- TVVDFVGK TIDWHG- TVVDFVGK TIDWHG- TVVDFHG QVDFHG- QVDFHG- TVDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- YESSKVIR	20 MKGIRU MKGURU MKGURU MKDIRU MKDIRU MKNIRU KKTIRU MKNIRU LKNFRU MKNIRU LKNFRU MPNMKU MPNMKU MRNIRU MKRIRU MKRIRU MKRIRU	230 KOLESGIRTT ROLESGIRTT ROLESGIRTT ROLESGIRTT ROLESGIRTT ROLESGIRTT ROLESGIRTT ROFESGIRTT ROFESGIRTT ROFESGIRTT ROFESGIRVT KOMESGIRVT ROMESGIRVT ROMESGIRVT ROFE-LDWST ROMETCRTT	240 DP-DDIMLDF NP-DDIVVNF DP-NDIVVNF DP-NDIVVNF NP-DEYMIKF NP-DEYMIKF NP-NDIMLNF DP-NDIMLNF DP-NDIMLEF DV-NDIMEDF DV-NDIMEDF DV-NDIMEDF DV-NDIMEDF DV-NDIMEDF DP-NDILFNY TKQNYFAFEF DLN-DKVLMF DP-DDVMVSA AIGSFFDGKV	250 	260 SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED DALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SALLANTED SHALLANTED	270 ALECEVIDAT	280 APMYP 24 STMFP 25 STILP 25 SATLP 25 SATLP 25 SATLP 25 SSMLP 25 SSMLP 25 SSMFP 24 SSTIP 25 SATLP 25 SATLP 25 SARYS 24 AARYS 24 AA	
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Pd_UGT85A3 VvGT16 Mt_UGT85K19 Vv_UGT85K4 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C2 Sb_UGT85B1 At_UGT79B1 At_UGT79B6 T_UGT79C16	1777 1833 1844 1877 1844 1815 1844 1812 1822 1822 1822 1825 1824 1855 1844 1799 1899 1899 1781	2 TVVDWEG- TVVDWEG- QVDWEG- QVDWEG- QVDWEG- TVDWEG- TSDWEG- TVVDFVGK TIDWEG- TVVDFVGK TIDWEG- TVDFEG TVDFEG TVDFEG TVDFEG TVDFEG TVDFEG TVDWEG- TVDWEG- TVDWEG- TELEWVG- YESSKVLR YESSKVLR	20 MKGIRU MKGVRU MKGVRU MKDIRU MKDIRU MKNIRU MKNIRU KKTIRU MKNIRU MKNIRU MKNIRU MKNIRU MRNIRU MRNIRU MRNIRU MRNIRU MRNIRU MRNIRU MRNIRU MRNIRU	230 CLESSIRTI CDLEST CDLESSIRTI CDLESS	240 DP-DDIMLDF NP-DDIVNF DP-NDIVNF DP-NDIVNF DP-NDIVNF NP-DEYMKF NP-DEYMKF NP-NDIMLNF DP-NDIMLNF DP-NDIMLFF DV-NDIMFDF DV-NDIMFDF DV-NDIMFDF DV-NDIMFDF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-NDIFFF DV-DVF DF-DVFFF DF-DVFFF DF-DVFFF DF-DVFFF DF-DVFFF DF-DVFFF DF-DVFFF DF-DFFF DF-DVFFF DF-DFFF DF-DFFF DF-DVFFF DF-DFFFF DF-DFFFF DF-DFFF DF-DFFFF DF-DFFF DF-DFFF DF-DFFF DF-DFFF DF-DFFFF DF-DFFFF DF-DFFFF DF-DFFFF DF-DFFFF DF-DFFFF DF-DFFFF DF-DFFFF DF-DFFFFF DF-DFFFFF DF-DFFFFFF DF-DFFFFFFF DF-DFFFFFFFFFF	250 	260 SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SALLATED SHALLATED	270 ALCOUNT AL	280 APMYP 24 STMFP 25 SATLP 25 SATLP 25 SATLP 25 SATLP 25 SATLP 25 SSMFP 24 STTLP 25 SSMFP 24 SSTFP 25 SATRP 25 SARYS 24 AARYS 24 AAFFP 25 SRQYS 24 ENQFQ 22	
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Sr_UGT85A3 Vv_UGT85A33 VvGT16 Mt_UGT85H2 Me_UGT85K4 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C2 Sb_UGT85B1 At_UGT79B1 At_UGT79B1 At_UGT79B6 Ip_UGT79G16 Nb_Pt	1777 183 184 187 184 185 184 182 182 182 182 182 185 184 179 189 189 178 161 171	2 TVVDWEG TVIDWEG QVIDWEG QVIDWEG QVIDWEG TEIDWKG TEIDWKG TSIDWEG TVVDFVGK TIIDWVGC TKVDWEG TVIDWEG TVIDWEG TVIDWEG TVIDWEG TVIDWEG TVIDWEG TSLEWVG YSSKVIR YSSKVIR YSSKVIR	20 MKGIRU MKGVRU MEGIRU MEGIRU MKORRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MRNIRU MRNIRU MEGIRU MSHRU PHEAK- GHETN- AHEARG	230 KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI RDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI KDIESEIRTTI SLSFVWRKHE SLSFVWRKHE SLSFLSYPFG FTARTVMKSEI	240 DP-DDIMLDF NP-DDIVNF DP-NDIMLDF NP-DEYMKF NP-DEYMKF NP-DEYMKF NP-NDIMLNF DP-NDIMLNF DP-NDIMLFF DV-NDIMEDF DV-NDIMEDF DV-NDIMEDF DP-NDILFNYF DP-NDILFNYF AIGSFFDGKV DGTSFFERIF GDITFFDRIF	250 	260 SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SATIPNTED SHATPNTED SHA	270 ALE OEVLOAL ALE OEVLOAL AL	280 APMYP 24 STMFP 25 STILP 25 SATLP 25 SATLP 25 QSMLP 25 QSMLP 25 QSMLP 25 SSMFP 24 STILP 24 STILP 24 SSTIP 25 SATS 24 AARYS 24 AARYS 24 AARYS 24 AARYS 24 AARYS 24 AAFFP 25 SRQYS 24 ENQFQ 22 ETQFQ 23	
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Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85A1 Mme_UGT85K4 Mme_UGT85K4 Mme_UGT85K1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85B1 At_UGT79B1 At_UGT79B1 At_UGT79B1 At_UGT79B1 Cs_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Cm_F7G2RhaT Cr_UGT3 Cr_UGT4	1777 183 184 187 184 185 184 179 183 182 182 185 184 179 183 182 185 184 179 177 183 161 177 183 162 161 167 163	2 TVVDWHG- TVVDWHG- QVIDWHG- QVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVVDFVECK TIIDWVG- TVVDFVECK TIIDWVG- QVDFHG- TVVDFVGCK TVIDWGG- TVIDWGG- TVIDWGG- TVIDWGG- YSSKVVIR FDPSILHH FDHTSTSV FQTSVTSV FQTSVTSV FQTSVTSV FQTSVTSV FQTSVTSV FQFFALKIQ YEFFALVIQ YEFFALVIQ FFFKALVIS	20 MKGIRU MKGVRU MKGVRU MKGVRU MKGVRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MFNMKU MFNMKU MFNMKU MFNMKU MFNKU MFNRU MFNKU MFN	230 KDIESFIRTT RDIESFIRTT KOMESFIRTT KDIESFIRTT KDIESFIRTT KOMESFIRT KOMESFIRT KOMESFIRT KOMESFIRTT KOME	240 DP-DDIMLDF NP-DDIMLDF NP-DEYMKF NP-DEYMKF NP-DEYMKF NP-NDIMLDF DP-NDIMLNF DP-NDIMLNF DP-NDIMLPF DV-NDIMLPF DV-NDIMFDF DV-NDIMF DV-NDIMF DV-NDIMF DV-NDIMF	250 	260 SALLINTED SALLIN	270 ALCOUNT AL	280 APMYP 24 STMFP 25 STMFP 25 STLLP 25 SATLP 25 SATLP 25 SATLP 25 SATLP 24 STLP 24 STLP 24 STLP 24 STLP 24 STLP 25 SSMFP 24 SSTFP 25 SSMFP 24 SSTFP 25 SLRYN 24 AARYS 24 AARYS 24 AARYS 24 AARYS 24 STLP 25 SLRYN 24 CTOFK 24 FTOFK 24 FTOFK 24 SDLTR 22 SDLTR 22 SSTLG 22	44 60 51 52 51 88 95 22 51 56 61 12 56 61 12 56 61 12 76 60 12 12 12 12 12 12 12 12 12 12
Vv_UGT85A28_VvGT14 vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85K4 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C2 Sb_UGT85B1 At_UGT79B1 At_UGT79B1 At_UGT79B1 At_UGT79B1 Cs_F7G6RhaT Cs_UGT2_UGT94P1 Si_UGT94D1 Bp_UGT94D1 Bp_UGT94B1 Cm_F7G2RhaT Cr_UGT3 Cr_UGT4 S1_NSGT1 Vo_UGT94P1	1777 183 184 187 184 185 184 179 183 182 182 185 184 179 183 182 185 184 179 177 183 161 177 183 162 167 163 165 165	2 TVVDWHG- TVVDWHG- QVIDWHG- QVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVVDFVGK TIIDWYG- TVVDFVGK TIIDWYG- TVVDFVGK TIIDWYG- TVVDFHG- TVIDWYG- T	20 MKGIRU MKGVRU MKGVRU MKGVRU MKGVRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MKNIRU MFNMKU MPNMKU MFNMKU MFNMKU MFNMKU MFNRU MFNNU MFNNU MFNNU MFNNU MFNNU M	230 KOLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROLESSIRTT ROMESSIRV ROMESSIRV	240 DP-DJIMLDE NP-DJIMLDE NP-DEYMKE NP-DEYMKE NP-DEYMKE NP-NDIMLDE DF-NDIMLDE DF-NDIMLDE DF-NDIMLDE DV-NDIMLDE DV-NDIMEDE DV-N	250 	260 SALLINTED SALLIN	270 ALL OCTOPY ALL OCT	280 APMYP 24 STMFP 25 STMFP 25 STLLP 25 SATLP 25 SATLP 25 SSMFP 24 STLP 24 STLP 24 STLP 24 STLP 24 STLP 25 SSMFP 24 SSTFP 25 SSMFP 24 SSTFP 25 SSMFP 24 SSTFP 25 SLRYN 24 AARYS 24 AARYS 24 AARYS 24 AARYS 24 ENQFQ 23 SLRYN 24 FNQFQ 23 SLRYN 24 FNQFQ 23 SLRYN 24 FNQFQ 23 SLRYN 24 STTQFK 24 STTQFK 24 SDLTR 22 SDLTR 22 SDLTR 22 STTQFK 23 TEFSK 23 STTGK 23	44 50 51 52 51 88 95 25 15 56 61 14 85 99 11 17 60 42 22 75 00 99 19 52 51 19 55 51 19 55 51 19 55 51 19 55 51 19 55 51 19 55 55 55 55 55 55 55 55 55 55 55 55 55
Vv_UGT85A28_VvGT14 vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85A19 Vv_UGT85K4 Me_UGT85K4 Me_UGT85K5 Cs_UGT1_UGT85K11 Sr_UGT85C1 Sr_UGT85C1 Sr_UGT85C2 Sb_UGT85B1 At_UGT79B1 At_UGT79B1 At_UGT79B6 Ip_UGT79G16 Nh_Rt Ph_Rt_UGT79A1 Cs_UGT2_UGT94P1 Si_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Bp_UGT94D1 Cs_TG2RhaT Cr_UGT3 Cr_UGT4 S1_NSGT1 Vp_UGT94F1 Gm_SGT3_UGT91H4_RbaT	1777 183 184 187 184 185 184 179 183 182 182 185 184 179 183 182 185 184 179 178 161 171 175 177 183 162 161 165 165 165 165 168 3 173	2 TVVDWHG- TVVDWHG- QVIDWHG- QVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVVDFVGK TIIDWHG- TVVDFVGK TIIDWHG- TVVDFVGK TIIDWHG- TVVDFHG- QVDFHG- QVDFHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TVIDWHG- TPIEWYG- TPI	20 MKGIRJ MKGVRJ MKGVRJ MKGVRJ MKOIRJ MKNIRJ MKNIRJ MKNIRJ MKNIRJ MKNIRJ MKNIRJ MKNIRJ MKNIRJ MKNIRJ MRNIRJ MFNMKJ MFNMKJ MFNMKJ MFNKKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNKJ MFNJ MKNIRJ MFNJ MFNJ MKNIRJ MFNJ MFNJ MFNJ MFNJ MFNJ MFNJ MFNJ MFN	230 KOLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROLESGIRTTI KOLESGIRTTI KOLESGIRTTI KOLESGIRTTI KOLESGIRTTI KOLESGIRTTI ROLESGIRTTI ROLESGIRTTI ROMESGIRTTI ROMESGIRTTI ROMESGIRTTI ROMESGIRTTI ROMESGIRTTI ROMESGIRTTI ROMESGIRTTI SLSFLSYPFC DFLYIGKSFNI DFLYVFKSNS DFLYVFKSNS COLESAKNI CHEVETVYK NFCRFKSSDS NRDIPKC INYFLHLTANU FLEQLESAKNI LWERLKSDHO LGIQPIKRDDI IKRHISPNTKU	240 DP-DJIMLDE NP-DJIMLDE NP-DEYMIKE NP-DEYMIKE NP-DEYMIKE NP-NDIMLNE DP-NDIMLNE DP-NDIMLNE DP-NDIMLEE DV-NDIMLDE DV-NDIMLDE DV-NDIMFDE D	250 	260 SALLINTED SALLIN	270 ALE OEVIDAT ALE OEVIDAT ALE OEVIDAT ALE OEVIDAT ALE OEVIDAT ALE OEVIDAT ALE OSITPU ALE OSI	280 APMYP 24 STMFP 25 STLLP 25 STLLP 25 SATLP 25 SATLP 25 SATLP 25 CSMLP 25 CSMLP 24 STLP 24 STLP 24 STLP 24 STLP 25 SSMFP 24 SSTF 25 SSMFP 24 SSTF 25 SSMFP 24 SSTF 25 SSMFP 24 SSTF 25 SLRYN 24 AAFFP 25 SLRYN 24 STLR 22 SLRYN 24 AAFFP 25 SLRYN 24 AAFFP 25 SLRYN 24 STLR 22 SLRYN 24 AAFFP 25 SLRYN 24 AAFFP 25 SLRYN 24 AAFFP 25 SLRYN 24 AAFFP 25 SLRYN 24 AAFFP 25 SLRYN 24 SLRYN 24 SLR	44 50 51 52 51 52 51 52 51 52 51 52 51 52 52 52 52 52 52 52 52 52 52

Supplemental Figure S9. continued.

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Vv_UGT85A28_VvGT14	245	P-IMTIGPIQLL	PDQIHD	SELKLIGSNINK	EPECLKWL	DSKEPNSVVYVN	YGS-ITVMTI	2001 I 307
Vv_UGT85A30	251	P-ITTIGPLQLL	LNQMPD	NDLKSIESNLWK	FEPGCLEWL	DAKEPESVVYVN	IFGS-VTVMT	2011 v 313
Ad_GT4	252	P-IYTIGPLNLL	MNQIKE	ESLKMIGSNIN	EPMCIEWL	NSKEPKSVVYVN	IFGS-ITVMT	214 v 314
Cr_UGT85A23	255	P-IMPIGPIQIL	QNQVDD	ESLKVLGSNILWK	PEPECLEWL	DTKDPNSVVYVN	IFGS-ITVMI	10 <u>01</u> 1 317
Gj_UGT85A24	252	P-INTIGPIQFL	QKEVKD	ERLSVLGSNILW	PEPECLDWL	DSKDPNSVVYVN	IFGS-ITVMT	G<u>QI</u>V 314
Ib_UGT85A32	253	P-VYAVGPLQFL	QTQVKD	SNVRALASN	DTSCLEWL	DTKEPNSVVYVN	YGS-ITVMT	р <u>ог</u> ь 315
At_UGT85A3	252	b-AMbiGbruhtr.	VNREIEED	SEIGRMGSNIN	DETECLOWI	NTKSRNSVVYVN	FGS-ITIMT	TA<u>OP</u>L 316
Sr_UGT85A8	249	Q-IYTIGPDHMM	Q-QYVDHD	ERLKHIGSNIW	DVSCINW	DTKEPNSVVYVN	IFGS-ITVMT	(E<u>QI</u>I 312
Pd_UGT85A19	250	P-INSIGPDQLP	YSEIPSEY	NDLKAIGSNIN	PNTECLNWI	DTKEPNSVVYVN	IFGS-TTVMT	1<u>E 01</u>V 314
Vv_UGT85A33	253	P-VYSIGPLQHL	VDQISD	DRLKSMGSNLWK	DQTDCLQWL	DSKEPNSVVYVN	IEGS-ITVMES	с<u>ог</u>т 315
VvGT16	248	T-ICTVGPLPLL	LNQIPDD	NSIESN <mark>IM</mark> F	PETECLOWL	NSKQPNSVVYVN	IEGS-ITVME	PE <u>QI</u> V 308
Mt_UGT85H2	251	S-IMPIGPDPSL	LKQTPQI	HQLDSLDSNI	DTECLOWL	ESKEPGSVVYVN	IFGS-ITVMT	PEQL 314
Me_UGT85K4	250	KNIYTVOPFILL	EKGIPEI	-KSKAFRSSIN	DLSCLEWL	DKREPDSVVYVN	Yec-Vatiat	NEOLN 313
Me_UGT85K5	250	KNIYTVOPFILL	EKGIPEI	-KSKAFRSS	DLSCIEWL	DKREPDSVVYVN	Yec-Vatiat	NEOLN 313
Cs_UGT1_UGT85K11	253	N-INTIGPISLL	SKQVIDG	-EFKSLNSS	DTKCLQWL	DIKEPNSVVYVN	YGS-IIIVMII	ооник 315
Sr_UGT85C1	252	N-VYTICH QLL	LNKITQKETNN	DSYSINW	DEPECVEWI	NSKEPNSVVYVN	ises-LAV≬SI	QDUV 314
Sr_UGT85C2	246	H-INTICOPOLL	LDQIPEEKKQT	GITSLHGYSUV	DEPECTOWN	QSKEPNSVVYVN	nes-trivist	LEDMT 313
Sb_UGT85B1	257	P-INTVODIAEV	IASSDSAS	AGLAAMDISIMÇ	DTROLSWI	DGKIPAGSVVYVN	nes-mav vin	AQAR 321
At_UGT79B1	242	KPVMLTCP	VLPGSQP	NQPS	LDPQWAEWL	AKFNHGSVVFCA	ECSQPVVNK1	DOFQ 295
At_UGT79B6	225	RKVLLTCP	MLPEPDN	SKP-	LEDQWRQWI	SKFDPGSVIYCA	Les-QIILEP	DOFO 276
Ip_UGT/9G16	236	KPVLLACP.	ALPVP	SKSI	MEQKWSDWI	GKFKEGSVINCA	THES-ECTLRI	KDKFQ 286
Nh_Rt	240	KPVLLVGP	VV-PDPP	SGK-	LEEKWDAWI	NKFDAGTVINCS	iges-EnFLKI	DOIK 290
Ph_Rt_UGT/9A1	242	KPVFSNRT	RS-SGPA	SGK-	LEEKWATWL	NKFEGGTVIMCS	Fes-EnFLui	DOVK 292
Cs_F/G6RhaT	248	KPVLLTCP	LVNPEPP	SGE-		GKFPEKSVIMCS	FGS-EITFLIN	DOIR 299
Cs_UGT2_UGT94P1	227	KKVVPVCP	LVQGIDD	DE-N	DHSEIIQWI	DNKGEYSTLEVS	FIGS-EYEMSE	KEELE 278
S1_UGT94D1	225	KREVPVCP	LVQEVGC		DGND11EWL	DGKDRRSTVFSS	FIGS-EYFLSA	ANELE 277
	223	KKVLPVCP	LVQEASL	LQ-L	DHIWIMKWI		FIGS-EYILSI	DNEIE 274
Cm_F/G2RhaT	228	NETTPVCP	LIQEP	TFKV		SQKEPRSVVYAS	Hes-EYFPS	DEIH 278
Cr_UGT3	231	SKVIPVCEVIS-	LNNNDQG	QGN	DEDEITOWL	DKKSHRSSVFVS	FIGS-EYFLNF	QEIE 286
	233	REVMPVCLANSP	DNNNHQE	QSN	DGDELIQWI	ETRSERSSMENS	FIGS-EYFLNF	QEFE 291
SI_NSGTI	233	KELIPIGEDIRE	AMIDEEE		DWGTIQSWI	DKKDQLSCVIVS	FIGS-ESFLSP	QEIE 285
Vp_UGT94F1	223	KQIIPTE	LLIAN	SDE:	DEPEIMOWI	DERSERSIVIIS	FGS-ECFLSP	
Gm_SGTS_0GT91H4_RhaT	243	VPVVPVCL PPS	MQIRDVE	EEDNNE	DWVRIKD		Hes-ELELS	5ED.1. 201
		360	370	380	390	400	410	420
		360	370	380	390	400	410	420
Vy 11CT85228 VyCT14	30.8	360 	370	380 . CESATIN E	390 	400	410	420
Vv_UGT85A28_VvGT14 Vv_UGT85A30	308 314	360 EFAWGIANSNQS	370 	380 . GESAI IPE GDAAT IPE	390 PESVAETED-	400 . RGLLAGWCB	410 . QEQVITHQA	420 GGFL 369 GGFL 375
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad GT4	308 314 315	360 EFAWELANSNQS EFAWELANANLK EFAWELANSNOS	370 	380 . GESAILP GDAAILP GESAVLP	390 EFVAETED- DFVAQTKE- EFVAVTKE-	400 . RGLLAGWCF RSLLASWCF RGMLASWAF	410 . QEQVITHQA QERVITHPA	420 IGGFL 369 IGGFL 375 IGGFL 376
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23	308 314 315 318	360 EFAWELANSNQS EFAWELANSNQS EFAWELANSNQS EFAWELANSKON	370 FLWILRPDLVS FLWIIRPDLVA FLWIIRPDLVV FLWIIRPDLIS	380 	390 PEVAETED- DEVAQTKE- PEVAVTKE- EEVPETKE-	400 	410 QEQVITHQA QERVITHQA QERVITHPA QEEVIAHSS QEEVIAHSS	420 IGGFL 369 IGGFL 375 IGGFL 376 IGGFL 379
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gi UGT85A24	308 314 315 318 315	360 	370 FLWIURPDLVS FLWIIRPDLVA FLWIIRPDLVV FLWIIRPDLVS FLWIIRPDLVS	380 ESAILE GESAILE GESAULE GESSILGE GDSAILE	390 Devaeted- Devagtke- Eevautke- Eevbetke- Beljeetko-	400 RGLLAGWCE RGLLAGWCE RGLLASWCE RGLLASWCE RGLLASWCE	410 OEQVITHOA OERVITHOA OEEVIAHSS OEQVINHDA OEQVINHDA	420 GGFL 369 GGFL 375 GGFL 376 GGFL 379 GGFL 376
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32	308 314 315 318 315 316	360 	370 FLWLREDLVS FLWLREDLVS FLWLREDLVV FLWLREDLVV FLWLREDLVS FLWLREDLVS FLWLREDLVS	380 ESAILEE GDAAILE2 GESAVLEE GESSILGE GDSAILEE GDSAILEE GEAAILE	390 DIVAETED- DIVAQTKE- DIVAQTKE- EIVETKE- EIVETKD- EIJETKD-	400 RGLLAGWCE RGLLAGWCE RGMLASWCE RGLLASWCE RGMLSSWCS	410 CEQVITION CERVITION CERVITION CERVITION CERVITION CERVITION CERVITION CERVITION CERVITION	420 GGFL 369 GGFL 375 GGFL 376 GGFL 379 GGFL 376 GGFL 377
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At UGT85A3	308 314 315 318 315 316 317	360 	370 FLWLLREDLVS FLWLLREDLVA FLWLLREDLVA FLWLLREDLVS FLWLREDLVS FLWLREDLVS FLWLREDLVS	380 exating Gexating Gexating Gexating Gexating Gexating Gexating Gexating Gexating	390 PEVAETED- DEVAQTKE- PEVAVTKE- IEVETKE- PEIJETKD- PEIJETKD- IEIAETAD-	400 RGLLAGACE RGLLAGACE RGMLASACE RGLLASACE RGMLSSACE 	410 CECVITICAL CERVITICAL CERVITICAL CECVITICAL CECVITICAL CECVITICAL CECVITICAL CECVITICAL	420 GGFL 369 GGFL 375 GGFL 376 GGFL 379 GGFL 377 GGFL 377 GGFL 378
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8	308 314 315 318 315 316 317 313	360 EFAWGLANSNQS EFAWGLANSNQS EFAWGLANSKQT EFAWGLANSKKP EFAWGLANSKKP EFAWGLANSKKP EFAWGLANSKKP	370 FLWILREDLVS FLWILREDLVA FLWILREDLVA FLWILREDLVV FLWILREDLVS FLWILREDLVS FLWIRREDLVT FLWVREDSVA FLWIRREDLVG	380 exating Gexating Gexating Gexating Gbxating Gexating Gexating Gexating Gexating Gexating Gexating	390 DSVAETED- DSVAQTKE- DSVAVTKE- ESVETKE- ESLETKD- ESLETKD- ESLETKD- ESLETKE-	400 RGLLAGACE RGLLASACE RGLLASACE RGLLASACE RGLLASACE RGMLSSACE 	410 OEOVITHOA OERVITHA OERVITHA OERVITHA OERVISHA OEOVISHA OERVISHA OERVISHA OERVISHA	420 (GGFI 369 (GGFI 375 (GGFI 376 (GGFI 377 (GGFI 377 (GGFI 378 (GVPI 374
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A8 Pd_UGT85A19	308 314 315 318 315 316 317 313 315	360 EFAWGLANSNQS EFAWGLANSNQS EFAWGLANSNQS EFAWGLANSKQN EFAWGLANSKKP EFAWGLANSKKP EFAWGLANSKKD EFGWGLANSKKD	370 FLWILREDLVS FLWIIREDLVS FLWIIREDLVS FLWIIREDLVS FLWIIREDLVS FLWIREDLVS FLWIREDLVS FLWIREDVS FLWIREDVS	380 ESAI ESAI ESAU ESAU ESAU EAI EAAI EAAI EAAI EAV 2 	390 DIVAQTKE- DIVAQTKE- DIVAQTKE- DIVATKE- DIVATKE- DIVATKE- DILAETKO- DILAETKO- DILAETKO- DILAETKE- DILAETKE-	400 RGLLAGYCE RGLLASYCE RGLLASYCE RGLLASYCE RGMLSSYCS RGMLSSYCS RGMLSSYCS 	410 <u>QEOVI</u> THQA <u>QEOVI</u> THQA <u>QEOVI</u> THQA <u>QEOVI</u> THQA <u>QEOVI</u> THQA <u>QEOVI</u> THQA <u>QEOVI</u> SHQA <u>QEOVI</u> SHQA <u>QEOVI</u> SHQA <u>QEOVI</u> THQA <u>QEOVI</u> THSA	420 GGFL 369 GGFL 375 GGFL 375 GGFL 376 GGFL 376 GGFL 377 GGFL 374 GGFL 374 GGFL 374 GGFL 376
Vv_UGT85A28_VvGT14 Vv_UGT85A30 Ad_GT4 Cr_UGT85A23 Gj_UGT85A24 Ib_UGT85A32 At_UGT85A3 Sr_UGT85A3 Pd_UGT85A19 Vv_UGT85A33	308 314 315 318 315 316 317 313 315 316	360 EPAMGLANSNOS EPAMGLANANLK EFAMGLANSNOS EPAMGLANSKOT EPAMGLANSKOT EFAMGLANSKKP EFAMGLANSKKP EFAMGLANSKKP EFAMGLANSKKP	370 FLWILREDLVS FLWILREDLVA FLWILREDLVS FLWILREDLVS FLWILREDLVS FLWILREDLVS FLWILREDLVS FLWILREDLVS FLWILREDLVS	380 GESAI GESAI GESAI GESAI GEAAI GEAAI GEAAI GEAAI GEAAI GEAAI GEIAVU EEIAVU GEIAVU GEIAVU	390 DFVAQTKE- DFVAQTKE- DFVAVTKE- DFVDETKE- DFIDETKO- DFIDETKE- DFIDETKE- DFIDETKE- DFIDETKE- DFIDETKE-	400 	410 QEOVITHOA QERVITHEA QEOVITHEA QEOVITHEA QEOVITHEA QEOVITHEA QERVISHEA QEOVITHEA QEOVITHEA QEOVITHEA QEOVITHEA	420 GGFL 369 GGFL 375 GGFL 375 GGFL 376 GGFL 378 GGFL 378 GGFL 378 GGFL 374 GGFL 374 GGFL 374
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Supplemental Figure S9. continued.

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Vv UGT85A28 VvGT14	370	THNGWNSTIEGLCAGVEMICWEFFAEOOTNOCYCOTEWGVOMBIDSDVKRDEVAKLVRELMVOEK	434
Vv UGT85A30	376	THSGTNSHIPGLCCOVENTCTEFABOMENORYCOTETGVCMPIGNDVTRDBVESIVRGLMECEK	440
Ad GT4	377	THE CONSULTS IS SAVAVUOUS FAROUNDEWY COGELGTEMETOSDWEERAWERTWEEK	441
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	277		444
Gj_0GT85A24	3//	TESCHNSTIDSICSCVENICWEFFASCOUNCWFCCTAWINCDSIDANVARDSVESIVIELAVCEK	441
IL_UGT85A32	3/8	TEN <u>GWNSWIES</u> ICS <u>GVE</u> MLCWEFFABOOWNCHYACSKWGICKEIDSNVKRDEVEKIVREDIEGEK	442
At_UGT85A3	379	T <u>HCGWNST</u> IESISC <u>GVP</u> MVCMEFFAEO <u>QUNC</u> KFSCDEWEVCIEIGGD <u>VKR</u> GE <u>V</u> EAVVREIMDCEK	443
Sr_UGT85A8	375	THSGWNSTIESISNGVPMICWEFFAE00TINCRYCCVEWEICLEIDTDVKREEVEA0VREMMDGSK	439
Pd UGT85A19	377	THSCHNSTLEALCOVELLOWEFFAEOONNVRYSCTOWGICIEIDGEVKRDYIDGLVRTLYDCEE	441
Vy UGT85A33	378	THSGINSUSPECTOREFACTORYSOSENGICMETONNWARVEVERLARPIMOCEK	442
VyGT16	371	THIS CONSULTEST CARDENT CARE FAR COUNCER ACTEVICE METONN WERDAVERT WRITE CEK	435
VVGIIO	277		100
MC_UG185H2	577		441
Me_UGT85K4	3/6	S <u>HCEWNSH</u> IPCISCEKEMHCWEFFABOOWNCKYACDWKTEVBLSTNLWEBLVSIIKDMIETEI	440
Me_UGT85K5	376	S <u>HCGMNST</u> IECISGCKIMICMEFFABOOTINCKYACDVMKTCVELSTNLKREPLVSIIKPMIETEI	440
Cs_UGT1_UGT85K11	378	THCGWNSTLESICGGVEIICWEFFAEQOINCRYACTENCICMEVNHDVKRNEIVALINEMLEGDK	442
Sr UGT85C1	377	THCGWGSIIESLSAGVPMLGWESIGDORANCROMCKEWEVGMEIGKNVKRDEVEKLVRMLYEGLE	441
Sr UGT85C2	376	THCCWGSTIESLSAGVEMICKEYSWDOLWNCRYICKEWEVCLEMGTKVKRDEVKRLVOELMG-EG	439
Sb UGT85B1	385	SHORONSTITEATA ACOPUTATECHOROTUNOROLOFVICON CAOLPREVESGAVARTUREMIVEDI.	449
$\Delta + \Pi C T 7 9 B 1$	360	SHOCECSMARST MSDCOTVLUPCHCR2 TINADI MTEEMEVAUDUED-FKKCWESDOSTENAUKSWEECS	428
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Ph_Rt_UGT79A1	360	CHACTSSVIEALVNDCQVVMLEQKGDQIINAKLVSGDMEACVEINRRDEDGYFGKEDIKEAVEKVVVDVE	429
Cs_F7G6RhaT	367	CHSGFSSVTEAVISDCQLVLLELKGDCFLNSKLVAGDLKACVEVNRRDHDGHFGKEDIFKAVKTVVVDVN	436
Cs UGT2 UGT94P1	344	SHCGWNSVLESLKFGVPMVAIPMQYEOPLNAKLVEEVG-VAAEVNRD-INGRLNREEIAQVIRKVVVEKS	411
Si UGT94D1	344	SHCCMSSVMEGVYSCVEIHAVPMHLDOPFNARLVEAVG-FCEEVVRS-ROGNLDRGEVARVVKKLVMCKS	411
Bp UGT94B1	332	SHORTSSTWPSIRY OVER THAM MOTO PYNARIMETVG-ACTEVGRD-GEGRENTEP TAAVVRKVVVEDS	399
- <u>г_</u> Ст F7G2BbaT	346	SHCC/GC/GSVV/BCMVFGVPTUGVPMayBC/PSNakyVVDNG-MCMVVPRDKTNORLGCFBVARVTKHVVLOFF	414
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Supplemental Figure S9. continued.