Pectin degrading glycoside hydrolases of family 28: sequencestructural features, specificities and evolution

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Family 28 belongs to the largest families of glycoside hydrolases. It covers several enzyme specificities of bacterial, fungal, plant and insect origins. This study deals with all available amino acid sequences of family 28 members. First, it focuses on the detailed analysis of 115 sequences of polygalacturonases yielding their evolutionary tree. The large data set allowed modification of some of the existing family 28 sequence characteristics and to draw the sequence features specific for bacterial and fungal exopolygalacturonases discriminating them from the endopolygalacturonases. The evolutionary tree reflects both the taxonomy and specificity so that bacterial, fungal and plant enzymes form their own clusters, the endo- and exo-mode of action being respected, too. The only insect (animal) representative is most related to fungal endopolygalacturonases. The present study brings further: (i) the analysis of available rhamnogalacturonase sequences; (ii) the elucidation of relatedness between the recently added member, the endo-xylogalacturonan hydrolase and the rest of the family; and (iii) revealing the sequence features characteristic of the individual enzyme specificities and the evolutionary relationships within the entire family 28. The disulfides common for the individual enzyme groups were also proposed. With regard to functionally important residues of polygalacturonases, xylogalacturonan hydrolase possesses all of them, while the rhamnogalacturonases, known to lack the histidine residue (His223; Aspergillus niger polygalacturonase II numbering), have a further tyrosine (Tyr291) replaced by a conserved tryptophan. Evolutionarily, the xylogalacturonan hydrolase is most related to fungal exopolygalacturonases and the rhamnogalacturonases form their own cluster on the adjacent branch.

Keywords: evolution/polygalacturonase/rhamnogalacturonase/ xylogalacturonan hydrolase

Introduction

Based on sequence similarities the glycoside hydrolases degrading pectin have been classified into the family 28 (Henrissat, 1991). At present, this family consists of a few enzymes, such as: (i) polygalacturonase (PG; EC 3.2.1.15) catalysing random hydrolytic cleavage of α -1,4 glycosidic bonds in pectate and other galacturonans; (ii) exopolygalacturonase (EPG; EC 3.2.1.67) catalysing the hydrolytic cleavage of one galacturonic acid residue from the non-reducing end of galacturonan; (iii) exo-poly- α -galacturonosidase (EPGD; EC 3.2.1.82) catalysing the hydrolytic cleavage of two galacturonic

acid residues from the non-reducing end of galacturonan; (iv) rhamnogalacturonase (RG; EC 3.2.1.-) catalysing the hydrolytic cleavage of α -1,2 glycosidic bonds between D-galacturonic acid and L-rhamnose; and (v) endo-xylogalacturonan hydrolase (XGH; EC 3.2.1.-) catalysing random hydrolytic cleavage of the glycosidic bond between D-galacturonic acid and L-xylose. All the family 28 members act with an inverting mechanism (Henrissat and Davies, 1997).

Pectin, as a heteropolysaccharide, is a major constituent of the middle lamella of primary cell walls of dicotyledonous plants, composed of alternating homogalacturonan-smooth and rhamnogalacturonan-hairy regions (Williamson et al., 1998; Van der Vlugt-Bergmans et al., 2000). The smooth regions are polymers of α -1,4-linked D-galacturonic acid units, partially esterified, which are split by PGs, EPGs, EPGDs, pectin lyases, pectate lyases and de-esterified by pectin methylesterases. The hairy regions consist of three different subunits, as identified in apples (Schols and Voragen, 1996): (i) subunit I is xylogalacturonan, i.e. a galacturonan backbone heavily substituted with xylose (degraded by XGH); (ii) subunit II is a short section of rhamnogalacturonan backbone with many arabinan, galactan or arabinogalactan side-chains (degraded by arabinases and galactanases); and (iii) subunit III is rhamnogalacturonan consisting of alternating rhamnose and galacturonic acid residues (degraded by RGs).

More than 100 amino acid sequences of the family 28 glycoside hydrolases are available from GenBank (Benson *et al.*, 2000) and SWISS-PROT (Bairoch and Apweiler, 2000) sequence databases. Three three-dimensional structures have already been determined, those for the RG A from *Aspergillus aculeatus* (Petersen *et al.*, 1997), PG A from *Erwinia caroto-vora* ssp. *carotovora* (Pickersgill *et al.*, 1998) and PG II from *Aspergillus niger* (Van Santen *et al.*, 1999). All adopt the so-called parallel β -helix structural domain first observed in pectate lyase C (Yoder *et al.*, 1993). This domain is a characteristic fold for a larger protein family of right-handed parallel β -helix proteins and may consist of 7–12 coils forming either three or four parallel β -sheets (Yoder and Jurnak, 1995; Jenkins *et al.*, 1998).

Comparison of the three-dimensional structure of PG with that of RG enabled the similarities and differences in their active sites to be found (Pickersgill *et al.*, 1998), which should be applicable also for the other members of family 28. The similarities in the presumed active sites as well as the overall structural similarity confirm the original classification of PGs and RGs into one sequence-based family (Henrissat, 1991) despite their very low sequence identity (about 15%).

Several comparisons of amino acid sequences of bacterial, fungal and plant polygalacturonases were performed, but in most cases either a limited number of various enzymes were used for the comparison or attention was focused only on their isolated, best conserved sequence segments (Scott-Craig *et al.*, 1990; Bussink *et al.*, 1991; Ruttkowski *et al.*, 1991; Tebbutt *et al.*, 1994; Kester *et al.*, 1996; Petersen *et al.*, 1996; Tenberge

Table I. The enzymes used in the present study

Abbreviation ^a	Source	EC	SwissProt	GenBank
Bacterial endopolygalact	uronases			
Agrtu.pg	Agrobacterium tumefaciens	3.2.1.15	P27644	M62814
Agrvi.pg	Agrobacterium vitis	3.2.1.15	P77818	U73161
Burce.pg	Burkholderia cepacia	3.2.1.15	P94293	U85788
Erwca1.pg	Erwinia carotovora	3.2.1.15	P18192	X52944
Erwca2.pg	Erwinia carotovora	3.2.1.15	P26509	X51701
Ralso.pg	Ralstonia solanacearum	3.2.1.15	P20041	M33692
Thtma.pg	Thermotoga maritima	3.2.1.15 ^b	Q9WYR8	AE001722
Bacterial exopolygalactu	ronosidases			
Erwch.epgd	Erwinia chrysanthemi	3.2.1.82	P15922	M31308
Ralso engd	Ralstonia solanacearum	3.2.1.82	053241	U60106
Theth engd	Thermognaerobacterium thermosulfurigenes	3 2 1 82 ^b	060045	U50951
Yeren.epgd	Yersinia enterocolitica	3.2.1.82 ^b	O68975	AF059505
Fungal and analygalactur	2000505			
Aspac pg	Asperaillus aculeatus	3 2 1 15	074213	A F054893
AspflA pg	Aspergitius dedicatus Aspergitius flavus	3 2 1 15	P41749	105015
AspfiR ng	Aspergillus favus	3 2 1 15	P41750	U05020
AspniA pg	Aspergillus niger	3 2 1 15	OOPAWA	V18804
AspniA.pg	Aspergillus niger	2 2 1 15	Q014W2	V18805
AspinD.pg	Aspergillus niger	2.2.1.15	Q9F4W3	11000J V64256
AspinC.pg	Aspergillus niger	3.2.1.15	Q12334	A04550 V19906
AspniD.pg	Aspergilius niger	3.2.1.15	Q9P4w2	¥ 18800
AspniE.pg	Aspergillus niger	3.2.1.15	042809	¥ 14386
Aspni1.pg	Aspergillus niger	3.2.1.15	P26213	X58892
Aspni2.pg	Aspergillus niger	3.2.1.15	P26214	X58893
Aspor.pg	Aspergillus oryzae	3.2.1.15	P35335	D14282
Asppa.pg	Aspergillus parasiticus	3.2.1.15	P49575	L23523
Asptu.pg	Aspergillus tubigensis	3.2.1.15	P19805	X58894
Botfu1.pg	Botryotinia fuckeliana	3.2.1.15	O94100	U68715
Botfu2.pg	Botryotinia fuckeliana	3.2.1.15	Q9Y7V7	U68716
Botfu3.pg	Botryotinia fuckeliana	3.2.1.15	Q9Y7V9	U68717
Botfu4.pg	Botryotinia fuckeliana	3.2.1.15	Q9Y7W0	U68719
Botfu5.pg	Botryotinia fuckeliana	3.2.1.15	Q9Y7W1	U68721
Botfu6.pg	Botryotinia fuckeliana	3.2.1.15	Q9Y7W2	U68722
Chopu.pg	Chondrostereum purpureum	3.2.1.15	P79074	D45072
Clapu1.pg	Claviceps purpurea	3.2.1.15	P78607	Y10165
Clapu2.pg	Claviceps purpurea	3.2.1.15	P78608	Y10165
Cocca.pg	Cochliobolus carbonum	3.2.1.15	P26215	M55979
Colli1.pg	Colletotrichum lindemuthianum	3.2.1.15	Q00446	X89370
Colli2.pg	Colletotrichum lindemuthianum	3.2.1.15	000104	X95457
Crnpa.pg	Cryptonectria parasitica	3.2.1.15	012593	U49710
Fusmo ng	Fusarium moniliforme	3.2.1.15	007181	L02239
Fusor1 ng	Fusarium oxysporum	3.2.1.15	013466	AB000124
Fusox2 pg	Fusarium oxysporum	3 2 1 15	074244	AF078156
Geokl ng	Geotrichum klebahnii	3 2 1 15	P87217	D89650
Kluma ng	Kluweromyces maryianus	3 2 1 15	013478	A 1000076
Ophno pg	Ophiostoma novoulmi	3 2 1 15	059934	A F052061
Penev ng	Ponicillium axpansum	3 2 1 15	050025	AF047713
Pongr1 ng	Ponicillium origoorogaum	2 2 1 15	0039925	AF047713
Pener2 ng	Penicilium griseoroseum	2.2.1.15	093885 00UD16	AF005250
Ponio no	Penicillium grisebioseum	2.2.1.15	Q90K10	AF193113
Penja.pg	Penicillum janininellum	3.2.1.15	042824	D/9960
Penol1.pg	Penicilium olsonii	3.2.1.15	Q91834	AJ245521
Penol2.pg	Penicillium olsonii	3.2.1.15	Q9Y833	AJ243522
Sacce.pg	Saccharomyces cerevisiae	3.2.1.15	P4/180	AB011818
Scisc1.pg	Sclerotinia sclerotiorum	3.2.1.15	Q12/08	L12023
Sclsc2.pg	Sclerotinia sclerotiorum	3.2.1.15	Q11134	L29040
Sclsc3.pg	Sclerotinia sclerotiorum	3.2.1.15	Q11135	L29041
Sclsc5.pg	Sclerotinia sclerotiorum	3.2.1.15	P87213	Y13669
Fungal exopolygalacturo	nases			
Asptu.epg	Aspergillus tubigensis	3.2.1.67	Q00293	X99795
Botfu.epg	Botryotinia fuckeliana	3.2.1.67	Q9UVU0	AF145229
Cocca.epg	Cochliobolus carbonum	3.2.1.67	Q00359	L48982
Fusox.epg	Fusarium oxysporum	3.2.1.67	074255	AF083075
Plant endonolvoalacturo	nases:			
Actde ng	Actinidia deliciosa	3 2 1 15	P35336	I 12010
Aroth 1 ng	Arabidonsis thaliana	3.2.1.15 3.2.1.15 ^b	022017	AC002222
Aroth2 ng	Arabidopsis thaliana	3.2.1.15 3.2.1.15b	022017	AC002333
Anath2 no	Arabidopsis inaliana	$3.2.1.13^{\circ}$	022818	AC002333
Arath 4 a c	Arabiaopsis inaliana	3.2.1.15°	004474	AC001229
Arath 5 an	Arabiaopsis inaliana	3.2.1.15°	022816	AC004005
Aratno.pg	Arabidopsis thaliana	5.2.1.15	080559	AC004005

Table I. continued

Abbreviation ^a	Source	EC	SwissProt	GenBank
Arath6.pg	Arabidopsis thaliana	3.2.1.15	O23147	AJ002532
Arath7.pg	Arabidopsis thaliana	3.2.1.15 ^b	O22935	AC002339
Arath8.pg	Arabidopsis thaliana	3.2.1.15 ^b	O48576	AC002342
Arath9.pg	Arabidopsis thaliana	3.2.1.15 ^b	O48577	AC002342
Arath10.pg	Arabidopsis thaliana	3.2.1.15 ^b	O81798	AL031135
Arath11.pg	Arabidopsis thaliana	3.2.1.15 ^b	Q38958	X98130
Arath12.pg	Arabidopsis thaliana	3.2.1.15 ^b	O22699	AC002292
Brana1.pg	Brassica napus (PG35-8)	3.2.1.15	Q42399	X95800
Brana2.pg	Brassica napus (SAC66)	3.2.1.15	Q42636	Z49971
Cucme1.pg	Cucumis melo	3.2.1.15	O81244	AF062465
Cucme2.pg	Cucumis melo	3.2.1.15	O81245	AF062466
Cucme3.pg	Cucumis melo	3.2.1.15	O81246	AF062467
Glyma1.pg	Glycine max	3.2.1.15	Q9SWS3	AF128266
Glyma2.pg	Glycine max	3.2.1.15	Q9SWS2	AF128267
LycesA.pg	Lycopersicon esculentum (fruit; PG2A)	3.2.1.15	P05117	X04583
Lyces1.pg	Lycopersicon esculentum (TAPG1)	3.2.1.15	O22311	AF001000
Lyces2.pg	Lycopersicon esculentum (TAPG2)	3.2.1.15	Q96487	AF001001
Lyces3.pg	Lycopersicon esculentum (TAPG3)	3.2.1.15	O22310	AF000999
Lyces4.pg	Lycopersicon esculentum (TAPG4)	3.2.1.15	Q96488	U70481
Lyces5.pg	Lycopersicon esculentum (TAPG5)	3.2.1.15	O22313	AF001003
Lyces6.pg	Lycopersicon esculentum (TAPG6)	3.2.1.15	O22610	AF029230
Maldo.pg	Malus domestica	3.2.1.15	P48978	L27743
Medsa.pg	Medicago sativa (MSPG3)	3.2.1.15	O82019	Y11118
Peram.pg	Persea americana	3.2.1.15	Q02096	X66426
Prupe1.pg	Prunus persica (PRF5)	3.2.1.15	P48979	X76735
Prupe2.pg	Prunus persica (Feicheng)	3.2.1.15	O82586	AF095577
Prupe3.pg	Prunus persica (genomic)	3.2.1.15	Q43063	X77231
Rubid.pg	Rubus idaeus (fragment)	3.2.1.15	O65886	AJ224147
Plant exopolygalacturonases				
Arath1.epg	Arabidopsis thaliana (flower)	3.2.1.67	P49063	X72292
Arath2.epg	Arabidopsis thaliana (flower)	3.2.1.67	O65401	X73222
Arath3.epg	Arabidopsis thaliana (flower)	3.2.1.67 ^b	O65905	AJ003135
Arath4.epg	Arabidopsis thaliana (flower)	3.2.1.67	P49062	X72291
Arath5.epg	Arabidopsis thaliana (flower)	3.2.1.67 ^b	O48729	AC002505
Arath6.epg	Arabidopsis thaliana	3.2.1.67 ^b	O49721	AL021713
Arath7.epg	Arabidopsis thaliana	3.2.1.67 ^b	O49319	AC002334
Plant nollen nolvgalacturonas				
Crvia nn	Cryptomeria japonica	3 2 1 15	P43212	D29772
Gosha pp	Gossynium barbadense	3 2 1 15	039766	LI09805
Goshi pp	Gossyptum barbauense Gossyptum hirsutum	3 2 1 15	039786	U09717
Medsa pp	Medicago sativa (P73)	3 2 1 15	040312	U20431
Nicta pp	Nicotiana tabacum	3 2 1 15	005967	X71020
Salgil nn	Salix gilgiana (flower)	3 2 1 15	Q05507	AB029457
Salgi2 nn	Salix gilgiana (flower)	3 2 1 15	O9MBB9	AB029458
Salgi3 nn	Salix gilgiana (flower)	3 2 1 15	O9MBB8	AB029450
Salgi4 nn	Salix gilgiana (flower)	3 2 1 15	O9MBB7	AB029460
Brana pen	Brassica napus (Sta 44-4)	3 2 1 67 ^b	P35337	I 19879
Oenor pep	Denothera organensis	3 2 1 67	P24548	Not
Oenoi.pep	Oenomera organensis	5.2.1.07	124540	available
Phlpr pep	Phloum protonse	3 2 1 67 ^b	09XG86	A 1238848
Zeamal nen	Zea mays	3 2 1 67	P26216	X57627
Zeama? pen	Zea mays	3 2 1 67	P35338	X64408
Zeama3 nen	Zea mays	3 2 1 67	P35339	X66422
Zeamas.pep	Ecu muys	5.2.1.07	1 55557	100422
Insect polygalacturonase				
Phaco.pg	Phaedon cochleariae (mustard beetle)	3.2.1.15	O97400	Y17906
Rhamnogalacturonases				
AspacA.rg	Aspergillus aculeatus	3.2.1	Q00001	L35499
AspniA.rg	Aspergillus niger	3.2.1	P87160	X94220
AspniB.rg	Aspergillus niger	3.2.1	P87161	X94221
Botfu.rg	Botryotinia fuckeliana	3.2.1	P87247	U62397
Xylogalacturonan hydrolase				
AsptuA.xgh	Aspergillus tubingensis	3.2.1 -	O9UUZ2	AJ249460
1	1 0		<	

^aThe terminations of abbreviations for the individual enzyme specificities are as follows: pg, endopolygalacturonase; epg, exopolygalacturonase; epg, exopolygalacturonase; pp, pollen exopolygalacturonase; rg, rhamnogalacturonase; xgh, xylogalacturonan hydrolase. ^bFor these members the EC number was assigned only based on sequence similarities.

et al., 1996; Huang and Allen, 1997; Hadfield *et al.*, 1998; Stratilová *et al.*, 1998; Gognies *et al.*, 1999; Wubben *et al.*, 1999; Torki *et al.*, 2000). Thus, the regions comprising the residues 178_NTD, 201_DD, 222_GHG and 256_RIK (unless otherwise specified, all amino acid numbering throughout the text corresponds to the open reading frame of *A.niger* PG II) (Bussink *et al.*, 1990) have been found to be strictly conserved in all PGs, EPGs and EPGDs, with the Asp180, Asp201, Asp202, His223, Arg256 and Lys258 being probably involved in their active site (Rexová-Benková and Mračková, 1978; Pickersgill *et al.*, 1998; Van Santen *et al.*, 1999; Armand *et al.*, 2000). However, in RGs these regions are 193_gID, 215_De, 237_sgG and 269_miK (*A.aculeatus* RG mature enzyme numbering) (Kofod *et al.*, 1994); the His223 of polygalacturonase is replaced by Gly238 of RG.

Moreover, Stratilová *et al.* (Stratilová *et al.*, 1996) have described the potential role for a tyrosine residue in the function of a PG by chemical modification and spectrophotometric titration. The eventual position of this tyrosine was proposed by comparison of 36 different PG sequences which revealed a strictly conserved tyrosine residue equivalent to Tyr291 of *A.niger* PG II (Stratilová *et al.*, 1998).

Despite all these partial findings a serious deep analysis of all available amino acid sequences of the glycoside hydrolase family 28 is still lacking. Moreover, the family 28 is a quickly growing family of enzymes (more than 100 members). The need for this study may be supported also by running genome projects that yield numerous sequences of putative proteins having similarity to those of the family 28. Therefore, the aim of the present study was to: (i) compare as many as possible amino acid sequences of the members of this family of glycoside hydrolases; (ii) describe their evolutionary relationships in detail; and (iii) reveal their similarities and differences that would allow one to discriminate between them.

Materials and methods

The enzymes belonging to the glycoside hydrolase family 28 involved in the present study are listed in Table I. The listing for this family provided by the CAZy web-server (April 2000) (Coutinho and Henrissat, 2000) served as a base. The following enzyme specificities are represented: polygalacturonase; exopolygalacturonase; exopolygalacturonosidase; rhamnogalacturonase; and endoxylogalacturonan hydrolase. The sequences were retrieved from the GenBank (Benson *et al.*, 2000) and SWISS-PROT (Bairoch and Apweiler, 2000) sequence databases.

All sequence alignments were performed using the program CLUSTAL W (Thompson et al., 1994) and then manually tuned where applicable. In some cases the hydrophobic cluster analysis method (Gaboriaud et al., 1987; Callebaut et al., 1997) was applied in order to detect or support weaker sequence similarities. The method used for building the evolutionary trees was the neighbour-joining method (Saitou and Nei, 1987). The Phylip format tree output was applied using the bootstrapping procedure (Felsenstein, 1985); the number of bootstrap trials used was 1000. The trees were drawn with the program TreeView (Page, 1996). The BLAST tool (Altschul et al., 1990) was also used for sequence similarity searches. Threedimensional structure modelling was performed using the SWISS-MODEL automated protein modelling server (Guex and Peitsch, 1997; Guex et al., 1999) according to the instructions given there (http://www.expasy.ch/swissmod/). The experimentally determined three-dimensional structures

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were retrieved from the Protein Data Bank (Berman *et al.*, 2000). The protein structures were displayed by the program WebLabViewerLite (Molecular Simulations, Inc.)

Results and discussion

Conserved sequence regions and invariant residues of polygalacturonases

In this study 115 amino acid sequences of PGs, EPGs and EPGDs were compared. One sequence represents the insects (animals), the one from the phytophagous mustard beetle *Phaedon cochleariae* (Girard and Jouanin, 1999), whereas all the others belong to bacteria, fungi and plants (Table I) that form the three main groups. No polygalacturonase from archaeal origin is known. The group of plant enzymes covers 19 members of a gene family encoding PGs and EPGs in *Arabidopsis thaliana* (Torki *et al.*, 2000).

The amino acid sequence alignment of all 115 PG, EPG and EPGD sequences (Figure 1; the colour version of Figure 1 can be found at the URL: http://nic.savba.sk/~umikstef/PGs) confirmed that there are four strictly conserved sequence segments with one invariantly conserved residue, Tyr291, as recognized previously (e.g. Stratilová *et al.*, 1998). Remarkably there was only one further amino acid residue, Gly228, strictly conserved in all these enzymes (Pavenicová, 2000). This glycine is positioned close to the C-terminus of the third conserved region (222_GHG). Structurally, it is located in the seventh turn between the β -sheets PB1 and PB2a of *A.niger* PG II (Van Santen *et al.*, 1999); however, as yet no function has been assigned to it.

The first segment, 178_NTD, consists of two strictly conserved residues, Asn which is substituted in one PG from *Penicillium griseoroseum* (Pengr2.pg) by His and the totally conserved Asp, and the almost invariantly conserved (93.0%) Thr179 in the middle. The threonine was replaced in all bacterial EPGDs by either Gly or Ala, and in four fungal enzymes (Botfu3.pg, Botfu6.pg, Fusox1.pg and Fusox.epg) by serine. Moreover, the enzyme from *Thermotoga maritima*, declared in the GenBank as a putative EPGD, contains the substitution Gly—Asn which is not in accordance with the rest of the bacterial EPGDs. However, as will be shown later, this protein also lacks the other sequence features characteristic of bacterial EPGDs and goes well with the bacterial PGs (Figure 1).

The second segment, 201_DD, is exclusively conserved in all polygalacturonases with specific amino acid residues neighbouring at both sides of this dipeptide. All bacterial and plant enzymes together with most of fungal EPGs have the glycine at the N-terminal side of 201_DD, while all fungal PGs (including the PG from insect) contain a glutamine in that position. Concerning the C-terminal side of the second segment, there is a cysteine residue conserved in all plant and fungal polygalacturonases, the insect PG as well as the two bacterial enzymes (Agrtu.pg and Yeren.epgd).

In the third segment, 222_GHG, there is an almost invariantly conserved (94.8%) Gly222 followed by two totally conserved His and Gly. The former glycine was replaced in one of the two fungal PGs from *Colletotrichum lindemuthianum* and all four known fungal EPGs by serine as well as in the enzyme from *T.maritima*. The fourth conserved segment, 256_RIK, contains a highly conserved (87.0%) Ile257 in addition to the strictly conserved Lys and Arg which is replaced by His in the insect PG. The isoleucine was not conserved in two

Evolution of glycoside hydrolase family 28

Agrtu.pg					1,1	1,2b- 1,3-		2,1- MATAT	
Agrvi.pg	AKD-G	GSLDPADADGK-	SPHPDQMRLQAAIDG	AGGAVKLVPGAEG	QDAFLSGPLSLKSGV	/LWIDKGVTLFASRDPKDYDSGAG	GTANSS-	STKTGKPLIMAKDT	26
Burce.pg Erwcal.pg	AFASDSRTVSEPKAP-S	ATSTPOWSSSTA-	TSTIQKALNNSG	OGKAVKLSAGSS-	-SVFLSGPLSLPSGVS	N-IVLKLEKGFTLKGSPAQ SLLIDKGVTLRAVNNAKSFENAPS:	PSS	GAMLTGSNLSNL	11
Erwca2.pg	SDSRTVSEPKTP-S	SSTTLKADSSTA-	TSTIQKALNNDD	QGKAVRLSAGST-	-SVFLSGPLSLPSGVS	SLLIDKGVTLRAVNNAKSFENAPS:	SGVVDK	NGKG DAFITAVST	23
Thtma.pg	PIR-G	SVDSVDGNPA- VNLLDFGARGD-	GRTDSSESFX	AGQAVKLVKGSAG RAIEELSKOGGGRLI	ESGFLSGSLKLKSGV: VPEGVFLTGPIHLKS	ILWIDTGVTLFASRNPADYDNGLG IELHVKGTIKFIPDPERYLPVV-	- LTRF-EG	NDKSENALIVARDT IELYNYSPLVYALDSENV	15
Erwch.epgd	AVPKV-I	INITQYGAKGD-	GTTLNTSAIQKAIDASP	TGERIDVPAG	VFKTGALWLKSD	MULLOGATLLGSDNAADYPDA	YKIYSYVS-	QVRPASLLNAIDK	24
Ralso.epgd	TOUTITOCTADCTDCDNT.T	YNVARLGARGD-	GATLNTAVIQKAIDESAGTST	TAYGERVLIPADDAS	GAVFVSGALFLRSN	LEVAEGATLRGSANAVDYPLAKG	YQLYSYFT-	NATDDRRPPSLLNALSP	29
Yeren.epgd	AKPQI-V	VNVRDFGAIDD-	GKTLNTKAIQQAIDS	PGARVEIPAG	- TYKSGALWLKSD	INLOAGAILLGSENPDDYPAG	YRLYPYST-	-SQ-VGQKSAPLISTVST IERPASLINAIDP	27:
Aspac.pg	TEEIAKRAT	TTTTSG	SNGASSASKSKTSSSTIV-	LSNVAVPSG	-TTLDLTKLNDGT	HVIESGETTEGYK	E X S	GPLISVSGSDL	212
Aspf1A.pg Aspf1B.pg	D	DSWTTTS	KSGKTSSSTIT- SACASASAKSSSNIV-	LSNIEVPAG	-ETLDLTGLNDGT	TITESTTESYK	EWE	GPLISVSGTNI	90
AspniA.pg	SDFTKRS	ST TTTD	SESKTSSDIV-	LKDITVPAG	-ETLNLKDLNDGT	TVTREGTTTMEYE	EMD	GPLLRISGKDI	101
AspniE.pg AspniC.pg	T	-SSTRTS	KSGKSSBSTIT- SEGASKASKSKTSBSTIY-	LONIAVPAG	-ETLDLTGLKKGT	TVINEGETTNGYK	ENK	GPLISMSGTDI	95
AspniD.pg	G-T	TTTTTE	YASISSAVASSNIL-	LSNINAPAS	-STIDLTGLQTGA	AVIRAGETTRGDTY	DSD	FDPIVISGTDV	22
Aspnil.pg	SEFAKKAS	STATETS	ASEASESISSESDVV-	LSSIEVPAG	-TTLDLTDLNDGT	TITREGETTSRGYK	EWS	GPLVSVSGTDI	11.
Aspni2.pg	EARD	DSSTRTT	KAGKAKSSTIT-	LNNIEVPAG	-TTLDLTGLTSGT	KVINEGTTTNQYE	E N A	GPLISMSGEHI	9
Asppa.pg	ELEARD	DS TTTS	AADAKSGKTSSSTIT-	LSNIEVPAG	-ETLDLTGLNDGT	TVINSGETTINGYK	- ENE	GPLISVSGTNI	91
Asptu.pg	EARG	-STWKT	KAGKAGSTIT-	LDNIEVPAG	-TTLDLTGLTSGT	KVIFEGTTTFDYE	ENA	GPLISMSGKDI	9
Botfu2.pg	A	AG T P S	TAATALASKTTSSTIT-	LDSVVVPAG	-TTLDLTGLKTGT	KVIRQGTATEGYS	ENS	GPLISISGQDI	101
Botfu3.pg	PNTPEPA	-GTATA	YADIADIIASTNIV-	LDNISAPAS	-STIDLOKLODGS	TVTPSGTTSPGTTA	DSD	FDPIVVKGTDI	250
Botfu5.pg	T	TT TESC	SGGASSASKSKSSSSIII-	LSALAVPSG	-TTLDLTGLTKGT	TVIREGITTRGYE	ENS	GPLVSVSGTDI	12:
Botfu6.pg Chopu.pg	T	TASTASV	VDDA VDDA	AIVINNVFAPSG	-SSIDLTGVKAGT	TITPAGKTTPGFTN	DSS	FEPIKLGGSGI	9.
Clapul.pg	VSRAAALSGA	ADSTSD	VAQAIQKKASSSTIT-	LRNLKVPAG	-KTLDLSNLSDGT	RVINTGRTTRGYQ		GPLIAMSGKNL	10
Clapu2.pg Cocca.pg	SGLDARD	ADSTESD	IQKKTSSSTIT- 	LRNLKVPAG	-KTLDLSDLNDGT	RVIFTGRTTFEYQ	ENE	GPLIAVSGTNI	10
Colli1.pg	ELKAR A	ASTTTD	AASAIKGKAS TTIV-	LNNIAVPAG	-TTLDMTGLKSGT	HVSFSGKTTFGYK	E N E	GPLISFSGSNV	9
Colliz.pg Crnpa.pg	ASK	KSSTETD	AKTAMSKKTSBTDIV- AAAVSKSKASBATIT-	LNGIKVPAG	-QTLDLTGLRDGT	KVTFKGTTTFGYK	ENA	GPLISVSGTDI	94
Fusmo.pg	DP	P-SVTE	YSGLATAVSSEKNIV-	LNGFQVPTG	-KQLDLSSLQNDS	TVTFKGTTTTATTA	DND	FNPIVISGSNI	9
Fusox2.pg	DP	35STTTD	AATAIKNKAGSSTIT-	LNGFQVPTG	-KALDLSKLKDGA -TTLDLTKLNDGT	HVIRGKTTRATTA	DND	FDPIVISGNGI	9. 9
Geokl.pg	GDLQARGS	SA VEKD	IAGKKSSSIT-	LENIAVPAG	-QTLDLTGLAKGT	VVTPAGTTTPGYK	EWA	GPLISVSGDSI	9
Ophno.pg	LAERAT	rsatesc	GGLSNAATVT-	LNNVAVPSG	- TTLDLSKLADGA	TVNFVGQVTFGYD	ENV	GPLVSISGKNI	94 11
Penex.pg	GS	SA SYSG	TSGAAAALAGKAGSSSIT-	LNNVVVPAG	-TTLDLTGLASGT	KVIPEGTTTPGYK	Q#A	GPLISISGTNI	10
Pengr2.pg	TDLVERGSS	SS TETS	KAGKSSESTIV-	LDNIKVPAG	-ETLDLSKLKSGT	KVIEKGETTLGYK	EWE	GPLVSVSGTSI	10
Penja.pg	SDLTKKSSS	ST TPSS	SASASASKSSSTIV-	LSNIEVPAG	-KTLDLTDLKDGT	KVIFEGTTTEGYK	E N S	GPLIKISGSDI	10
Penol2.pg	PKLEERAT	TS TESC	SAGASSASKSKTASATIV-	LSAVAVPSG	-TTLDLTGLNDGT	TVIPEGETTEGYK	EWS	GPLVSVSGTDI	111
Sacce.pg	BKRD	DSTLTG	SSLSSLSTVKKASSIV-	IKDLTVPAG	-QTLDLTGLSSGT	TVTPEGTTTPQYK	ENS	GPLISISGSKI	9
Sclsc2.pg	VEKRAG	GS TSG	SSGAAAAIKSKASSATIV-	ISAVAVPSG	-TTLDLTGLKSGT	HVVFEGTTTFGYE	EWY	GTLVSVSGTDI	11
Scisc3.pg	NEKRAG	GSSTESG	SSGAAAAIKSKASSATIV-	ISAVAVPSG	- TTLDL/TGL&SGT	HVVFEGTTTFGYE	EWY	GPLVSVSGTDI	11
Asptu.epg	PKK-PF	FRPLPTSOSRDK-	- TSHVR - SHGDGTDDSDYILSALBO NHOO	KVVFDEDK	-EYIIGTALNMTFI	KNIDLEVIGTILEINDID	YWOAN	SPECCEONATTR	13
Botfu.epg	PKHKSARPNV-QF	FHPKSLDTPAPSPAARTK-	-TYVK-SSGNGTDDSPAIMSALHE WEGG-	HVIFSKGV	-TYLIGTAMDWTFI	KHIDLDIQGELLPSDDTA	YNEAN	SPERVPORATSP	15
Cocca.epg Fusox.epg	PHV-EA	FLPGKASSVPGSRNK- AAPYGTGKAFPASPARSRK	- TOMLK - ALGGGKDDSANILSAVKQ - SINGG - DFAYVNPGKGKNVDDAFSILKAFKK - SKGG -	HVVFPKGQ	-QFTIGTALDLTFI -KYSIASPLDLTWI	MGIDLDIQGTIQUINDTD		SPROVPORATTP SPROVPORATTP	13
Actde.pg	ASK-TV	VNVDDPGAKGD-	G-RDDTKAFEKAMKAASSSTS-	SAVLLVPK	-KNYLVRPISFSGP-5	KS-GLTMQIYGTIEASDDRS	DYRK	DGRHNLVFDSVONL	17
Arath1.pg	AQ-SY	YNVLSFGAKPD-	GKTDATKAFNAVNOTASASSR-	PVTIVVPKG	-RFLLR-SVTFDGSK	KPKPVTFRIDGTLVAPADYR	VIG	NEDYWIFFQHLDGI	11.
Arath3.pg	ART-SL	LNVLSFGANPN-	GIVESAKAFSDAMDAA GVED-	SVVIYVPKG	-RYLVSGEVRFEGES	KSREITLRIDGTLIGPODYS	LLG	KKENNFSFSGVHNV	12
Arath4.pg	AMP-SF	FNVQRYGARGD-	GRADATKS FLTANSLASGSRA-	RAMVYVPRG	-TYLVK-NLVFWGP-	KN-IITFKNDGTLVAPANYW	DIG	NSGYWILFAKVNRI	12
Arath6.pg	A-S-TV	VSVSNFGAKGD-	GKTDDTQAFKKAKKASSING-	VTTFLVPKG	-KTYLLKSTRFRGP-	KS-LRNFQILGTLSASTKRS	DYK	DKNHWLILEDVNNL	15
Arath7.pg	TPT-TV	VSVSDFGAKGD-	GITDISKAPUNARKKASSSNG-	AVNLLVPKG	-NTYLLKSIQLTGP-	NS-ILTVQIFGTLSASQKRS	DYK	DISKNIMFDGVNNL	15
Arath9.pg	NGQ-IY	YDVLKFGAEGN-	GITDDSKTFVKAMSAMGGSGGN	SKTFLIPSN	-QTFLLQPLTFQGP-	KSPSVQVKFDGKIVAPINKA	AWSE-S	KLFRWVSFKEIIGL	11
Arathl0.pg	YGK-NY	YNVLNFDAKGD-	GOTDDSEAFLOANTAAGGDGD	IKTLLIPSG	-KTFLLOPTVFQGP-	KSSSIKVQLDGTIVAPSDKF	AWSD-P	ISRMNIKFSTVSGL	10
Arath12.pg	VQPPPTPLPLQPVEDSQ-QF	FNVLDFGAKGD-	GMSDDTOAFEAAMASASKVEA-	STMIIPPD	-YIFLVGPISFSGPY	QAN-IVFQLEGMIVAPTDTE	SWGG	GLMWWIEFTKLSGI	21
Branal.pg Brana2.pg	S-S-TV	VSVSNFGAKGD-	GKTDDTQAFKKAHKKASSTNG-	VTTFLIPKG	-KTYLLKSIRFRGP-	KS-LRSFQILGTLSASTKRS	DYSN	DENHALILEDVNNL	16
Cucme1.pg	GGL-TF	FDIVNLGAKPD-	GKTDASHALQSAMARASSTV-	ASTVYVPKG	-RFYVQ-SGNFIGP-	NYNSITFLINGTLVASSNFK	VLA	KSRTWISFSRINGL	11
Cucne2.pg	API-TF	FNVVDFGAKPNN FNVDDVGAKPNN	IKIDSSKAFESANKOAFSSSR- G-EDDTEAFKETWDAFSSTN-	AATIYVPKA	-KFYIY-SATFKGP-	KNNVITLQMDGTLVAPPNFH	LTA	QSKTWIIFRQVNGV	14.
Glyma1.pg	AT-SF	FNVLDYGAKGD-	GHADDTKAFEDAMAAA KVEG-	STMVVPSG	-SVFLVKPISFSGPN	EPN-IVFQLDGKIIAPTSSE	AWGS	GTLOWLEFSKLNTI	13
Glyma2.pg LycesA.pg	AT-TF	PNVLDYGAKDG- INVLSEGAKDD-	GHADDTKAFONANVAASKVEG-	STMVVPSG	-SVFLVKPISFSGPN	EPN-IVFQLDGKIIAPTGSA	AWGS	GTLONLEFSKLNKI	13
Lyces1.pg	NTN-IY	YNVQNYGAKSD-	GKTDSSKAFLNAMAAA ASNK-	PSTINVPIG	-KYLIH-NANFNGQT	KSKAITMHIDGTLLAPSDYN	VIG	NEENWIKFEKVNGL	11
Lyces2.pg	NTN-IY	YDVQNYGAKSD- YNVQNYGAKSD-	GKIDSSKAFLNAMAAASASNT- GETDSSEAFLSAMSAASASTS-	PSTINVPMG	-KYLIH-NANFNGQT -NYLIR-NAYFNGKR	KSKAITMHIDGTLLAPSDYN	VIG	NEENWIKFEKVNAL	11
Lyces4.pg	NTIY	YNVQNFGAQSN-	GKIDSTKAFLSSMG-PSMGFYE	RLHYYVPRG	-NYLIR-NIYFNGQT	KSNAIAIHIDGTLLAPSDYN	AID	NDGSWIKFEKVNRV	11
Lycess.pg	IY VM-FL	LNVINFGAKSD-		SSTIYVPRG	-IFLVK-QAYFKG-K	NNNPIIFRIDGSIVAPFDYN	VIG	NDGNWITFENVNGV NEKNWILFOGVDGV	11
Maldo.pg	PAK-TI	ISVDDPGAKGN-	G-ADDTQAFVKAKAASSSG	AMVLVVPQ	-KNYLVRPIEFSGP-	KS-QLTLQIYGTIEASEDRS	-IYK-	DIDHMLIFDNVONL	18
Peram.pg	PDT-DI	ISVDDFGARGD-		GSVLIVPEN	-KNYLLKQITFSGP-	KS-DLRVKIRGTIEASSDQS	DWV-GH	NRKRWIEFEDISNL	17
Prupel.pg	PL-TY	YNVASLGAKAD-	GKTDSTKAFLSAMAKASASMN-	PGVIYVPAG	-TFFLR-DVVFSGP-	KNNAITFRIAGTLVAPSDYR	VIG	NAANWIFFHHVNGV	11
Prupe3.pg	SVK-TI	ISVANFGAKGN-		AIVLVVPQ	-KTYLVRPIEFSGP-	KS-HLTMQIYGTIEASDDRS	VIGK	DVTHMLIFDNVQSL	17
Rubid.pg			TR	AHVLLVPK	-KNYLVKPITFSGP-	KS-KLTMQIYGSIEASDDRS	VYSK	DLYHWIIFDNVRNL	6
Arath1.epg Arath2.epg	A-AV	VDVKASGAKGD- LDVKASGAKGD-	GKTDDSAAFAAAKKEASAAG 	STITVPKG	-EYMVE-SLEFKGP-	KGP-VTLELNGNFKAPATVK	-TTKPH	AGNIDFENIADF	15
Arath3.epg	A	AEVFTIGSSSG-	SDITQALLKARTSA QSSSP	SKVVIPKG	-EFKLG-EIEMRGP-	KAP-IEVTLQGTVKADGNAI	QGKE	KWVVFGNIDGF	10
Arath4.epg	NPT-VY	YDITKFGAVGD-	GSTNTFKAFLNTHIQVADSPVF	ATLLVPKG	-TFLAG-PVIFAGP-	KSK-VTVNVIGTIIATTS	GYATP	EMPLPERVDNL	13
Arath6.epg		g	AFVAANDKAPKSSSS	SVNLIIPRG	-EFSVG-SLRFSGP-	TNV-SNLTVRVKASTDLS	KYRSG	GGWIQFGWINGL	5
Arath7.epg Cryia.np	IRKVENSRHDAIN-IF	FDVRNYGARAD- FNVEKYGAVGD-		RSTVYIPSG	- IFYLR-QVTFSGP-	KSS-ITFFIRGTLLAPRNPY	AINQE	EWILFKYVDNL	12
Gosba.pp	A-FD	DVVAKFGAKAD-	GKTDLSKPFLDANKEA ASVTF	STVVIPKG	-TYLLS-KVNLEGP-	KAP-IEINVQGTIQAPADPS	AFKDP	NWVRFYSVENF	11
Goshi.pp Medsa.pp	A-FD	DVVAKFGAKAD- LDISKFGGKPM-	GKTDLSKPFLDARKEASASVTP SDIGOALTSANNEASASTTA	STVVIPKG	-TYLLS-KVNLEGP-	KAP-IEINVQGTIQAPADPS	AFKDP	ECHEREL MOUT	11
Nicta.pp	G-VF	FDITKYGANSN-	ADISEALLNARKEA OSTSF	STIVIPKG	-TFTMN-QVKLEGP-	KSP-LELQIQATLKAPSDPS	QLKVG	ENLTVNKLDQF	11.
Salgil.pp Salgi2.pp	G-VF	FDVTKYGGKQ FDVTKYGGKF	DITAALTNAKKDA ASTKF	SKVRIPSG	-TYSLR-QVTLAGP-	KSA-IELQVNGILKAPVNPD	QFSGG	HWNFRYIDHL	11
Salgi3.pp	G-VL	LDVTKYDGKE	DITEALNNARKDA ASTNF	SKVLIPSG	-TYSLR-QVTLAGP-	KAA-IELQVDGILKAPVNPD	QFSGG	SWVDFRHVDQL	11
Salgi4.pp Brana.pep	G-VF	AEVFTAGGRE	DITEALNNARKDADASTNF SDITAAVLKATTSASOAPAF	SKVHIPSG	-TYSLR-QVTLAGP- -DFKLG-ETVMTGP-	KAA-IELQVDGILKAPVDPN KSP-IEFTLQGNVKTDGGST	QFSGG	HWVDFSHVDQL 	11:
Oenor.pep			DSTOALTTANKEA ASASP	STILVPKG	-NFAVG-LITLEGP-	KSS-IGLQLQGTLKAPADPS	KIKGL	GWINLNKIDLL	7
Zeamal.pep	ADG-TY PGG-SF	FDITKLGAKPD-	GKTDSTKEVEEAKASASGGT-G	KOTILIPEG	-DFLTG-PLNFTGP- -DFLVG-OLNFTG-P	KGD-VTIKLDGNLLSSNDLA	KYKAN QYKDH	WIEIMRIKKL	11:
Zeama2.pep	PGG-SF	FDITKLGASGN-	GKTDSTKAVQEAMASA GGT-G	KQTILIPKG	-DFLVG-QLNFTG-P	KGD-VTIQVDGNLLATTDLS	QYKEH	GNWIEILRVDNL	13
Phace ng	PGG-SF	-STISSASGN-	FDOM		- DFLVG - FLNFIG - P	TITEDOVTIONLLATIOLS	QYKDH	GREAT CONTRACTOR	130
		-W1100	VSATTVPERIDIA-	- + GIALIE + PPRJ		ATA A A A A A A A A A A A A A A A A A A		OPLURVKGKAI	

O.Markovič and Š.Janeček

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| Agrtu.pg | RATG
 | G- | -AGRRKPVRAR
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 |
 | HLVSÄHK | TOLLGPTIRMAASWTIHPOG-EEDLTA | 58
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| Burce.pg | TITGTG
 | AIDG- | -DGQD
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| Erwcal.pg | TNSG
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 | IQINKSK | -NFTLYNVSLINSPNFHVVPSD-GDGFTA | 213
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| Erwca2.pg
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-RGGSLVTSGPNANRLT
 | -WELAA
 | DAKVKKLKQNTPRL
 | IQINKSK | - NFTLYNVSLINSPNFHVVFSD-GDGFTA | 213
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| Thtma.pg | AITGS
 | GVLDGS | ADNEH
 | WWPWKGKKDFGWKEGLPN
 | QEDVKKLKEMAERGTPVEERVFGKGHYLRPSF
 | VQFYRSR | -NVLVEGVKIINSPMW VHPVL-SENVII | 226
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| Erwch.epgd | NSSAVGT
 | FKNIRIVGKGIIDG- | -NGWKRS ADAKDELGNTL
 | PQYVKSD
 | NSKVSKDGI-LAKNQVA
 | AAVATG | MDTKTAYSQRRSSLVTLRG-VQNAYI | 337
 |
| Theth.epgd | DVYGNTIQYQ
 | NIRTVGHGVING- | -NGWARKG-TDTIDEVGNRL
-NGWAQVSSKDTSVPIDDQF
 | DOYOKGN
 | ASKWSTLGV-LAKSQML
SSNISTTAKNH-LALNO
 | AAQAEAGGT | LDSTRNANYYSNRRSSLATFRG-ARQIYF | 412
 |
| Yeren.epgd | NNSKPGT
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 | PQYVASK
 | NSKVHEDGI-LAKNQVE
 | KAVSDG | MDLKNAYGQRRSSLMTLRG-VENVYL | 344
 |
| Aspac.pg | TITG
 | AS-GHSING- | -DGSR
 | -WMDGEG
 | GGKTKPK
 | AAHSLTN | SVISGLKIVNSEVQVFSVAG-SDYLTL | 179
 |
| Aspf1B.pg | TVTQ
 | AS-GAKIDG- | -DGSR
 | -WWDGKG
 | GRTKPKES
 | YVHKLDS
OYPOLES | SSITGLQIYNTEVQGFSIQSDNLNI
PTITGLHVXNSEVOVFSVOGNDVHL | 263
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| AspniA.pg | TVTQ
 | SS-DAVLDG- | -NGAK
 | WDGEG
 | KPP
 | YAHDLDD | SKISGLYIKNTRVQAISVESDNLVI | 167
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| Aspni8.pg
AspniC.pg | TVKQ
 | AS-GAKINA- | -DGAR
 | - WEDGKG
 |
 | QAHKLDQ | SSITGLKVYNTEVQGFSILADHLTI | 160
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 | -YWDGEG
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 | VVKDMY | -NSKIENLNILNWEVHSFEIEN-TEYLTI | 289
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| AspniE.pg
Aspnil.pg | TVTG
 | AD-GAYING- | -DGSR
 | - WWDGEG
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 | YAHDLTS | STISGIVIONSBVOVFSIDG-STYLTM | 179
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| Aspni2.pg | TVTG
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 | - WWDGKG
 | TSG-KKKPKFF
 | YAHGLDS | | 161
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Aspna.pg | KVQQ
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 | -WORKG
 | GN
 | YAHKLDS | SSITGLQIYNTWQGFSIQSDNLNI | 163
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| Asptu.pg | TVTG
 | AS-GHLINS- | -DGAR
 | -WWDGKG
 | TSG-KKKPKFF
 | YAHGLDS | | 161
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| Botful.pg
Botfu2.pg | TVKG
 | AS-GSKLDG- | -QGAK
 | - YWDGKG
 | KPP
 | YAHSLKG | -KSTISGINILNSEVQVFSING-ASGLTL | 183
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| Botfu3.pg | TITG
 | AA-GHVIDG- | -NGAA
 | -YWDGQG
 | SNGGTDKPDHPP
 | WKDVV | -NGVISNLNIQNWPTHSFDITG-AQGLTV | 225
 |
| Botfu4.pg | KVAGSN
 | AD-TAILNG- | -NGAS
 | -YWDGEG
 | KPP
 | QAHDLTD | SLIETLTILNPPVQVFSING-VSNLEL | 193
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| Botfu6.pg | TVTA
 | EP-DAIIDG- | -NGQV
 | -YWDGLG
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 | AAKKLIG | GSIIENLYIONWEVHLFTITG-AVGLTI | 162
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| Chopu.pg | NFVGAD
 | HIFDG- | -NGAL
 | - YMDGKG
 | NGTHKPHP
 | LKIKGSG | TYKKFEVLNSDAQAISVGPTDAHLTL | 157
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| Clapu2.pg | KVSG
 | SP-GNIID#- | -EGQR
 | - MCDGKG
 | DKK
 | NAHDLIN | SEIRNLNVLNTWAHAFSISH-AENLGI | 167
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| Cocca.pg | KVVG
 | AS-GHTIDA- | -AGQK
 | WWDGKG
 | XPP
 | YAHSLTT | SSISGLNIKNTEVQAFSING-VTGLTL | 163
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| Colli2.pg | AVEG
 | AS-GSLIS | -EGER
 | -NWDGKG
 | GNGGKKKP
 | KVK-IND | STINGLATIN TRYUAPSING-AANLGV
GSITGLRVKNTRAHGPSINS-VKGLKG | 162
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| Crnpa.pg | EVTG
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 | WWDGEG
 | SNGGKTKPKM
 | YAHSLKQ | STIHNLKVKNTEVOFMSINS-ATDLNV | 169
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| Fusox1.pg | TITG
 | AS-GHVIDG- | -NGPA
 | -YWDGEG
 | HTT

 | VVQKTTG
VVKKTTG | NSKITNLNIQNWEVHSFDITG-SSOLTI
NSKITNLNIQNWEVHSFDITG-SSOLTI | 164
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| Fusox2.pg | LIEG
 | AA-GHSIDK- | -EGKR
 | WIDGKG
 | SNGGKKKPKFF
 | SAHSLKN | | 161
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| Kluma.pg | KVVG
 | KS-GHLLDG- | -GGSR
 | - WWDGKG
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 | YAHKLQN
SLRLTGN | SNIQGLOVYNTEVQAFSILSDHLTL
SDVGGLOIKNTEIOAISVNS-SSDTVI | 164
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| Ophno.pg | TVQG
 | AS-GAVFNA- | -NGAR
 | WWDGXG
 | SGKTKPK##
 | YAHGLTN | SKILNLSIKNTRIQAVSING-DGLTI | 176
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| Penex.pg
Pengrl.pg | QVSG
 | AS-GHLIDG- | -QGSR
 | - WWDGEG
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 | FAHSLKG | SSTITGLNIKDSPVQVPSISG-SSGLTI | 177
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| Pengr2.pg | NVSG
 | AS-GHVVNG- | -GGPS
 | - NMDGKG
 | TNGGKKKPKFP
 | YAHGLDN | SNISGLNVKNTRVQGFSVQADHLVL | 168
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| Penja.pg
Penoll.pg | TVEA
 | AD-GAVINA- | -DGSR
 | -WWDGEG
 | TNGGKTKPKPP
 | YAHSLDD | STISGLNIKNTEVQAFSIQSDNLII | 170
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| Penol2.pg | TVKG
 | AS-GATLNG- | -DGSR
 | -WWDGKG
 | SNGGKTKPKFF
 | YAHKMFS | STISDIHIVNSDVQVFSING-ATDLTL | 178
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| Sacce.pg | SVVG
 | AS-GHTIDG- | -QGAK
 | - WWDGLG
 |
 | KLALTGT | SKVTGLNIKNAPHOVFSINK-SDLTI | 160
 |
| Sclsc2.pg | TVTG
 | TS-GSVLDG- | -NGAK
 | -YWDGKG
 |
 | YAHSLKG | -KSSINNVKILNSEVQGFSINS-ASGLTL | 183
 |
| Sclsc3.pg | TVTG
 | AS-GSILDG- | -NGGK
 | -YMDGKG
 | TNGGKTKPKFT
 | YAHSLKG | KSSINNVKILNSPEEGFSINS-ASGLTL | 183
 |
| Asptu eng | NOLOGEDVININGG
 | GTTNG- | -NGRD
 | - XHDGEG-
 |
 | AAHNLIS | STIENIYILNPEVQVPSIDN-ANGLTI | 183
 |
| Botfu.epg | KLGGEDVFMYGG
 | GTLNG- | -NGQT
 | WYDYYA
 | SNIYALRPVL
 | IGIDGLK | -DSILSDLVLRYSBOYYNFIAN-SSNVVY | 222
 |
| Cocca.epg | FQLGGKDINVYGG
 | GT LDG- | -NGQA
 | WYDLYA
 | KDIYILRPIL
 | FGLIGAK | -NAKISDLKFRYSROWYTLVAN-SSOVVF | 210
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| Actide pg | REIGGRUININGD
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| | RVEGG
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 | LTIEDAH | -GLIMSNLRMRNRRIGSTLSST-ARTELI | 216
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| Arath1.pg | RVEGG
 | GTING-
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 | LTIEDAH
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- HVIVKNL&IENAQIHVSFN- AVNQA
- NVVVSGLTSINSQMPHVVING & WNVKL
- NIKISGLTSINSQKPHIVIDN- SNNVNI
- NVKLKGVLSLNSQLPHLAINE & MIKE
- NVLKGLSSFNSQMMVTVHH-SSNVRI | 216
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NGGHN- 97-G- AXS
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- NUVVSGILSILSSQMFHVVING - SUNVNI
- NIKISGLTSINSQKFHIVIDN - SUNVNI
- XVILSGLSSPNQMMVVINH- SUNVNI
- ZVVLSGLTSINSQTTHLVINS - SUNVIV
- ZVILSGLSSPNQMMVTVINS - SUNVIV
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- NVLIKSLSSQLFHING - SNNVNI
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- NILNVKNLRVKNAQQIQISIEK - SNVVPV
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- VVXLIGULSSGLFHINTAR - SVNIKI
- VVVXIGTISSGTHHVING - SVNVH
- NILVVKNLKVKNQQIQISIEK - SVKVFV
- DLIVKILERER - SVKVFV
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- NVLISGLSSPNSQMHVTVHH - SNNVNI
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- DLMTIDIFNSFNNHISISE - KRVQL
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Evolution of glycoside hydrolase family 28

Agrtu.pg	b 4,3 AASTXIAPHDSP	5,1 5,2b 5,3 GFNPESSRNVMISGVRFSV	6,1 2a 6,1 2a GIAVKAGKRGPDGEI	6,2b 6,3	7,1 GLVIGSEMS	7, 2a- 7,2b 7,3- GGWHDVTVED%DMIG	8,1	166
Agrvi.pg Burce.pg	WGIKTLSPSAVYTRPDYASPPETTPDKLTPATSFTPDTVK DGVWTYANPNRNASGDD	GFDPGQSSKVVLAYSAISTCO AIDIIGTOTATIKN LLDTCO	HVAIKAGGDK	PSTRMTFAHNRFYY	MSVUSETD	AGVDGIHVYDLVMDGHD	SPNGNGLEIKSDT	380
Erwcal.pg	WKTTEKTPSTAR	GIDPMSSKNITIAHSNISTC	NVAIKAYKGR	SETRNISILHNEFGT	MSIGSET	MOVYNVTVDDLIMTG	TINGLRINSDK	311
Ralso.pg	WGIKTVTPSLAYAVAGYKEPSGSTPDKVTPATEFTPETVK	DGFDPGQSTNVVLAYSYINTCO	HVAVKASSG	PTRNLLFAHNHFYY	LSICSETN		SSAGNGLEINSDA	370
Thuma.pg Erwch.epgd	ADVTIRNPANHGIMFLESENVVENSVIHOTFNAM	GIDPESEKYMLIEKERPDIG GVERGESONIMVFNSVFDIG	SINTAAGMGODAO	-KOEPSONNILFNNFFRH	-GLVIQSEMS	GGWRNVVARNNVYMN	VERALELETNS	332
Ralso.epgd	GDVTL/INPAFHGVMFVESENMVFANTVTQTFDING NVNGLVIGDGLUVINPSFHTISVSNSONVUNOLIASTVDING	GVEFCHSSNAVVFNNFIDSOD	NINFAAGQGKNYE-	-GGAPQQYAMIFNNYMREGH	-GVVACSHTG	AWIQDILAEDNVMFM	TDNGLELNSTP	539
Yeren.epgd	AGFTVRNPAFHGIMNLENHNVVANGLIHQTYDAN	GIEFGESONVMVFNNFFDTG	SINEAAGTGEKAO-	EQEPMKGAMLFNNYFRMCH	-AIVTGSHTG	AWIEDILAENNVMYL	TDIGLEARSTS	471
Aspac.pg AspflA.pg	KDITIDNSDGD-DNGGH TDVTIDNSAG-TA	DARDIGTSTYVTISGATVYNOD DARDVGSSTYINIDGATVYNOD	VAVNSGE	NIYESGGY SG	LSIGSVGGRS	-D-NTVKNVTPVDSTIIN	SDNGVRINTNI	279
Aspf1B.pg	TDITIDNSDGD-NNGGHN	TARDVSESNGVYITGANVKNO	LAINSGE	NIEFTGAT SGG	ISIGSIGNRD	-T-NTVKNVKVADSTVVD	SDNGIRINTIS	265
AspniB.pg	TDVTIDNSAG-TSKGH	DAPDIGOSTYITIDGATVYNO	DCLAINSGE	HITETNGYADGGH	LSIGSVGGRD	-D-NTVKNVTFIDSTVSD -D-NTVNDVTISNSKVLN	SENGVEINTVY	267
AspniC.pg AspniD.pg	TDITVDNTDGDTDDLAAN SGLILNNTAGDAANSKSDGDPAAH	DGEDIGESTYITITGAEIYNOD DGEDIKOSDFLTLSNSWVHNOD	CVAINSGE	SIVVDNLYSYGGH	LSIGSVGGRD LSIGSIGGKS	-D-NTVKNVTFYDVNVLK -N-NTVDGVTFSNSQVIN	SQQAIRINTIY SENGERINSNA	281 397
AspniE.pg Aspnil.pg	EDITIDNTDGD-DGEAA NDFTIDNSDGD-DNGGH	DGEDIGDSTYITITGANVYNOD DGEDISESTGVYISGATVKNOD	VAVNSGE	NIYESGGV SG	LSICSVGGRS	-D-NTVKNVTFYDSDIKS -D-NTVKNVTISDSTVSN	SQNGVRIBTIY	279
Aspni2.pg	TDVTINNADGD-TQGGHT TDVTINNAGG-TQ	DATOVGNSVGVNIIKPWVHNOD	LAVNSGE	NINFIGGT IG H	LSIGSVGDRS	-N-NVVKNVTIEHSTVSN	SENAVRINTIS	261
Asppa.pg	TDVTIDNSAG-TABGHN	DATDIGSSTYINIDGATVYNC	TATNIGS	HITEINGY DG	LSIGSVGGRS	-D-NTVEDVTISNSKVVN	SQNGVRINTVY	262
Asptu.pg Botful.pg	SNINIDNSAGDAGSLGH	DARDVGNSVGVNIIKPWVHNCH	LAINSGE	GITTTGGTASG	LSIGSVGGRS LSIGSVGGRS	-D-NTVSDIIIESSTVKN	SENAVELETVS	261 284
Botfu2.pg Botfu3.pg	ININIDNSAGDAGSLGH SGLTLDNSAGDAPNSASGDDPAAH	DAPDINLSONIFISGAIVKNOD GEDISGSDSVTLKDIVVKNOD	DOVAVNSGT	NITTIGGNASCON	LSIGSVGGRSGT LSIGSVGGKS	GA-NDVKDVRFLSSTVQK -N-NTVSGVTFSDSTITN	STNGVEVETVS SONGSEESNS	276 333
Botfu4.pg	AYITVDASAGDSLG	DATDIGASDTVLIEYATVYNOD	VATNSGS	NIIPKNGY SGGH	LSICSVGGRS	-N-NTVDTVSFLSSTVTK	SVOGIRISTIA	292
Botfu6.pg	QNLVLNNTAGDAPNAASGTLAAAHN	GEDVSSSSNTIIKNTQVFNC	VAVISON	NITIDGLYSSG	LSICSVGGKS	-N-NNVTNITFKNSELVN	SSNGARINSNS	270
Clapul.pg	PNVNIDDSAGD-SLGGH	GEDUS-ANNVTIONSIVKNO GEDIGNSNGVTISGESVRNO	E+MAINSGT	NITEVNGFSG	ISIGSIATG LSIGSVGGRS	KHVSNVVIKGNTVTR -S-NIVKGVHIANSKVTK	SMYGVENSAOR SMNGIRISTIA	255
Clapu2.pg Cocca.pg	FNVNIDDSAGD-TQGGH DRITIDNSAGDSAGA-Her	GYDIGNSNGVTISG SVRNO DAVDIGSSSGITISNANIKNO	Devainsgi	NITEVNGFSSGGH	LSICSVGFRS VSICSVGGRK	-S-NTVKGVHIANSKVTK -D-NTVKGVVVSGTTIAN	SMYGVRIETIA SDNGVRIETIS	268
Collil.pg	YDVSVDNSAGDSAG	DAPDVGSSTGVYISGADVKNOD	DOLAVNSOT	NITERGT SG	LSIGSVGGRK	-D-NVVKSVSITNSKIIN	SDNGVRINTVA	262
Crnpa.pg	IDVIMDNSAGASKG	APDVGQSEDVIISGAVINO	LAINSGT	NITTSGSSTG	LSICSVGGRS	-D-NTVKTVSITNSKIIN	SQNGVRINTVY	268
Fusno.pg Fusox1.pg	SGLILDNRAGDKPNAKSGSLPAAH SGLILDNRLGDKPNAKSGSLPAAH	GEDISSSDHVTLDNNHVYNCD GEDISSSDHVTLDNIHVYNCD	E VAVISGT	NIVVSNMYSSOG	LSIGSVOCKS LSIGSVOCKS	-D-NVVDGVQFLSSQVVN -N-NVVNGVQFLDSQIVN	SONGERINSNS SENGERINSNS	272
Pusox2.pg Geokl.pg	YGVHMDNSLGDSLGG-HN SNILVDNRAGD-KA	DATDVGSSTGVYISGAVVKNOD	E-LAINSGT	HITFONGESCOM	LSIGSVGGRS	-D-NTVKTVRILNSSISN	SDNGVRINTVS	261
Kluma.pg	HDVTIDNRDGDKDNLGHN	DGEDVGNVNNVTIENSHVYNCD	F INVISOT	GVYFKNNY SG	ASICSVGLRS	-N-NVVDTVYFENNQIVN	SDNGLRINTIQ	260
Ophno.pg Penex.pg	TDMTIDSSAGDSAGG-HO SGVTIDNKNGDTNSLGH	DGFDIGTSKNIIIDGAKVYNOD DGFDIGDSDSITITGATVYNOD	E-VAVNSGT	KITPONGLASGE	LSIGSVGGRS LSIGSVGGRS	-D-NTVDTVTFYNSQIKN -N-NVVETVHISSTQVVN	SVNGIBVEGTV SQNGVEVEAVS	276
Pengr1.pg Pengr2.pg	SGITVDTADGDSNGGH	DARDVGSSNGVYITSPIVHNOD DARDVGSSTYITISNANIKNOD	E-LAVNIGT	HITTOOT SO	ISIGSVGGRS	-D-NTVDGVTVESTIKD	SDNGVRINTVY	275
Penja.pg	DGVTIDNSDGD-ENGGH	DGEDISESTGVTIRNAVVKNOD	IAINSGO	NIYTGGT SGGN	LSIGSVGGRD	-D-NTVKNVTITDSTVTD	SANGVRINTVY	270
Penoll.pg Penol2.pg	SGITVDNRDGDTDEGGH	DAEDVGESTYITISNANIKNOD	E-LAVNSGT	DITTTGGLSG	LSIGSVGGRD LSIGSVGGRS	-D-NTVKNVTISDSTVSN -N-NDVANVIIENSQIQD	SINGIEINTIY SINGVRINTVY	269
Sacce.pg Sclscl.pg	SDITIDIRDGD-SAGGHN SGITIDNSAGNS	DGEDVGSSSNVLIGGETVYNG DAEDVGSSTDITISGANVONOD	E IAVNSGS	TIKENNNYSYNGH	ISVUSVOGRS LSIGSVOGRS	-D-NTVNGFWAENNHVIN -D-NVVSDVIIESSTVKN	SDNGLRINTVE SANGVERETVL	260
Sclsc2.pg	SGITIDNSAGNSLGH	DARDVGSSTDITISGANVONCO	LAINSGT	GITTTGGTSSGGH	LSIGSVGGRS	-D-NVVSDVIIESSTVKN	SANGVEINTVS	282
Scisc3.pg	NNVTINASAGDTGSLGH	DGEDIGDSTSVTITGANVYNOD	DEVAINSGT	GITPSGGV_SC	LSVGSVGGRS	-D-NIVQTVNFENSEIKN	SQNGVEINTVS SQNGVEINTIS	282
Asptu.epg	DGIDISGYSKSDNE	GENTYRSNNIVIONSVINNG	F VSFRPNST	NILVQNLHENGS	ISVUSLGQYKDE	VDIVENVYVYNISMFN	ASDMARTRVIEP	307
Cocca.epg	SNIDIFGDSKSKNPAK	GROTTESDNIVIGNSVINNG	VSPKPNST	NILVONLVENGS	ISVGSLGQYPGE	VDIVENILVRNISMSN	ASDGARINVWP	325
Pusox.epg	SDLELEAKSINGVKIAR	GHDTYRSDRIVIONSVIDNT	DEVERKPRST	NVVVQNLV@NGSH	ISVESLGQYKGE	TDIVENLYIYNISMSN	ASDGARINVEP	315
Arathl.pg	OGVKVLAAGNS	GIHVQSSSSVSIFNTKISTC	DPVSIGPGTN	GLWIENVAGP	ISIGSLGKDSVE	SEVONVTVKTVTFTG	TINGVELNING	274
Arath2.pg Arath3.pg	DGVKVSADENSP EDVRIIAPDESP	DGIHVESSHSVHITNSRIGTER DGIHIQLSTDIEVRNASIKTER	DEISIGPGST	NVFIQTIRSGPEN	ISIGSLGRAEEE ISIGSLAKSIEE	QUVDNVTVSNVDFMG QUVENVTVKNAVFVR	TNNGVRINTNG TDNGLRINSNP	287
Arath4.pg	ENVRIRAPSGS Provide the second se	GIHVQSSSGVTISGGTIATC	DGIALSOGSR	NIWIERVN GP	ISIGSLGDYANE	EGVONVTVTSSVFTK	TQNGVRISTMA	282
Arath6.pg	SNVEITAPGDSP	GIHITNTONIRVSNSDIGTC	DGISIEDGTQ	NLQIFDLT GPGH	ISIGSLGDDNSB	AYVSGINVDGAKFSE	SDNGVRIBTEO	326
Arath7.pg Arath8.pg	SNVVVTAPADSPA	GINISESSDVDIYDTVIGTC	Delsiesgsg	NVQINDIT%GPGH	ISIGSLGDDNS# ISVGSVGRDGEE	SIVENVQVTNSTFIR	TDNGVELNTMO TDNGASLSTMP	319
Arath9.pg Arath10.pg	TKIKLVAPEDSP SNINLFAPETS	GINISGSSDVDVYDTFIGTCI GIDISDSTNINIFDSTIGTCI	DEVAINNGSV	NINITRMNSGPGH	ISVGSLGRDGER	SIVENVQVTNETFFR	TONGVRINTEP TINGAR INTER	268
Arathl1.pg	NNITISSPENSP	GIHLQNTRNVEIQHSNIA	DEVSIQTGSS	NVHIHHIN GPGH	ISIGGLGKDKSV	AVSDIIVEDISION	TLAGVRIETNO	326
Branal.pg	KNVKITAPGD	GIHIVATKNIRISNSDIGTC	DelSIEDGSQ	NVQINDLTAGPGH	ISIGSLGDDNSP	AYVSGIDVDGATLSE	TDNGVRINTNO	320
Brana2.pg Cucme1.pg	KNVKITAPGDSPO OGVKVLAASNSPO	DGIHIVATKNIRISNSDIGTCI DGIHVERSSNVTILNSNIRTCI	SISIEDGSQ	NVQINDLTAGPGH	ISIGSLGDDNSK ISIGSLGKWWEE	AYVSGINVDGATLSE AGVENVTLKTAHFKG	TDNGVRIBTEQ TMNGVRIBSKG	328
Cucme2.pg	ERLNIYAPANS PH	GIDLEETSYVTILDSNIGT	DGISVGPGTS	NVLIQNIY GPG	ISIGSLORKER	NEVONVTVQSERLKK	TONGVEIDSEG	304
Glyma1.pg	SGISVSSPGDSP2	GIHLQNSQNVVIYSSTLA	DEVSIQTESS	DIYVHNVN GPGH	ISICSLGRENTS	ASVRNVTVRDVTIQN	TLTGVRIBTEO	312
Glyma2.pg LycesA.pg	SGISVSSPGDSPA SNLMINASAKSPA	DGIHLQNSQNVVIYSSTLASO DGVHVSNTQYIQISDTIIGTC	DEISIVSGSQ	DIYVHNVN%GPGH	ISIGSLGRENT? ISIGSLGSGNSE	A%VRNVTVRDVTIQN AYVSNVTVNEAKIIG	TLTGVEINTRO AENGVEINTRO	300
Lyces1.pg	QGVKVSAPGNBP	GIHVKSSSGVSIMKSQIGTO GIHVKLSSGVSINSHIGTO	DEISIGPGTS	NLWIEGIAGPON	ISICSLGWKOOF	LOVONVTVKTVTFSG	TINGVIPUITIA	27
Lyces3.pg	QGLKVSAPGDBP	GIHVKLSSGVSIMKSQIGTG	DEISIGPONS	NLWIEGIA GP	ISIGSLOWKKO	SEVQNVTIKTVTFSG	TTNGVEVETEA	27
Lyces5.pg	QGVKVLSPGN8P	GIHVQSSSGVSIRNSNIGTG	SISIGPGNS	NLWIEGIASCP	ISIGSLGWESKE	QUVQNVIVKTVTFTG	TONGVEVETRA	275
Lyces6.pg Maldo.pg	QGVKVYAPGESPS SELTVTAPEDSPS	DGIHVQLSSDISILNSIISTC DGIHVTNTONITISSSVIGTC	SUSIGPGTS	RVQATDITSGPG	CISICSLAKDFEE CISICSLGEDGSE	AGVQNVTVKSVMFMN DHVSGVFVNGAKLSG	TONGVRINTNG TSNGLRINTNK	282
Medsa.pg	DSVTITAPVTS	GIHIGRSTDVKVLNTNIATC	VSLGDGSR	QITVQNVN%GPE	C ISVGSLGKYPKE	EAVERVLVKNTTITN	TDNGVRIKTEP	275
Prupel.pg	QGVRVSRSGNSP	GIHVOMSSGVTILNSKIATG	VSIGPGTS	NLWIEGVASGPG	GISICSLGKEQEE	AGVONVTVKTVTFSG	TONGLAIRS	283
Prupe2.pg Prupe3.pg	QGVRVSASGNSP SHLTVTAPEDSP	GIHVQMSSGVTILNSKIATO	SIGPGTS	RVQATDITSGP	ISIGSLGREQER	DHVSGVFVNGAKISG	TONGLETINSWG TSNGVRINTWO	282
Rubid.pg	SYLTVTAPETSP	GIHVANTONITISNSIIGT	ESIVSGSQ	NVQASSIT	ISIGSLGEOGSI	DRVSKVTVNGAKISG	TMNGVRINT	220
Arath1.epg Arath2.epg	TDIGIDAPPESI	GIHIGRSNGVNLIGAKIKTG	VSIGDGTE	NLIVENVEGP	GISIGSLARYPNE	QPVKGVTVRKELIKN	TDNGVRINTWP	320
Arath3.epg Arath4.epg	NNIKIVAPEDSPO ONIKLTAPAESPO	GIHLGRSDGIKILNSFIST GIHLSNADNVSILDSTIAT	EISVGDGMK	NLHVEKVT%GP&	G ISVGSLGRYGHI G LSVGSLGKYKNE	QDVSGIKVINTLQE	TDNGLRINTWP	272
Arath5.epg	TGVTITAPSDSP	GIRMGSSSNIQISNTNIGTO	TAILSGTT	KLNISNINAGP	ISVESLGKNKDE	KDVKDLFVRDVIFNG	TSDGIRIRTWE	285
Arath7.epg	TGVTITAPGD	GIKIGKSSHMQIYNVTIGTO	IAILDGTS	NLDISDVR GPC	ISVGSLGRYKE	KNVQGLTVRNSIING	TTDGLRIRT	230
Cryja.pp Gosba.pp	IGISITAPRDS	GIDIFASKNFHLOKNTIGTG GIHMGKSEGVNIIASDIKTC	ISIGDGTK	NIVIEDLIEGP	ISIGSLGRENSE ISIGSLGKFONE	AEVSYVHVNGAKFID EPVEGIKISNSTITN	TONGLAISTRO TSNGARISTRP	311
Goshi.pp Medsa.pp	ERLKIEAPDES	GIHMGKSEGVNIIASDIKTG GIHMGKSTDVKILNTNIGT	ISIGDGTK	NMVIKEITGPG	ISIGSLGKFON	EPVEGIKISNTITN	TSNGARIETHP	283
Nicta.pp	IRPNVSAPANEP	GIHVSRSSSVNITDSNFSTG	ISVGDETE	QLYITRVT3GPG	ISVGSLGGNPD	KPVVGVFVRNSTFTN	TDNGVRINTEP	27
Salgi1.pp Salgi2.pp	QHPTVTAPAE	TOGINIGRSTGIYIIDSKIGTG	DSISVGDGTE	ELHVIRVINGPO	ISVGSLGRYPN	KPVSGIFVKNaTISN	TANGVELISSEP	280
Salgi3.pp Salgi4.pp	OHFINIARGES	GIHIGQSTGIYIIDSNIGTCI GIHIGRSTGIYIIDSKIGTCI	SISVGDGTE	ELHVTGVTSGP	ISVGSLGRYPNS ISVGSLGRYPNS	KPVSGIFVKNTISN KPVSGIFVKNTISN	TANGVRINSHP TANGVRINSHP	280
Brana.pep	DNIKIIAPAES	GIHLGR BGVKILNTKIATC	DESISVGDGMK	NINTERVVSGP	ISVESLERYEW	QDVTDITVKN TLEG	TSNGLAISTMP	272
Phlpr.pep	KDVTITAPGDSP	DGIHIGDSSKVTITDTTIGTC	ISIGPGST	GLNITGVT GP	ISVGSLGRYKD	KDVTDITVKN VLKK	STNGLSISSE	271
Zeamal.pep Zeama2.pep	KDVTVTAPGD KDVTVTAPGD	DGIHMGDSSGITITNTVIGVG DGIHMGDSSGITITNTVIGVG	DEISIGPGTS	KVNITGVT%GP6	ISIGSLGRYKDI ISIGSLGRYKDI	KDVTDINVKDWTLKK KDVTDINVKDWTLKK	TMFGVRINAME TMFGVRINAME	295
Zeama3.pep	KDVNVTAPGD#P	GIHMGDSSGVTITNTVIGVG	DEISIGPGTS	KVNITGVT%GPG	ISIGSLGRYKD	KDVTDINVKDETLKK	TANGVRINANE	295
Phace.pg	SGWNIDVSQGDKDALGH	GEDINTTDOL/TIEDTVVKNO	INCOT	NFLENNLDESG	LSLSVOTSHE	IK-NTVRNVTPSNSVVRK	SRNGIHISTTY	263

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	8,2a	8,2b 8,3	9,1		9, 2a- 9,2b-	9,3	10,1	10, 10, 2a 2b 10,3	
Agrtu.pg Agrvi.pg	RSRGGMVGN SRGGKVTN	ITMRRVLLDGVQT VLXEDV@MRNVAF	ALSANAH PLVFDTR	HEDADGHDDWVQSRM SDKTGDRIPDFSGI1	VPAPVNDGTPFVDGI VRNLRYTGSTTGSG	TVEDVEIRNLAHAAGVF: GHVVLRGIRDDAHYO	LGLPDVPSATSLSATSP PLGLFLDTIO	IVSHDPSAVATPPIM FDGAOPLLVCSADPAEK	274 480
Burce.pg Erwcal.pg	TAKDSGATTG SAAGVVNG	VTTRNTSMRNVQQ VRTSNVVMKNVAK	PFLFTYA	ASGTGG-ALPIIAN WEKKEGSNVPDWSDI	TIDNVIATATK	QQGAIIGLSNSLMGVPK: GVVVLNGENAKK	GDTGISITNSQIS	GGKAFSVTDGELQLG	421
Erwca2.pg	SNAGVVNG	VRESNVVMKNVAK	PIVIDT	TEKKEGSNVPDWSDI	FKDVTSETK	GVVVLNGENAKK	-PIEVTMKNVK	LTSDSTWQIKNVNVKK-	402
Thtma.pg	RRGGYMEN	IFTIDNVAVNVSE	EVIRINLR	DNEEGEYLPVVRS	VFVKNLKATGGK	RIMIFLGYKANKOKN YAVRIEGLENDYVKD	- PLTITLDNVV	FDGTLPAFEGSHYGGPA -VLLEFGQLGMENVIMNGS	470
Erwch.epgd	AIGGGAHG	IVERNSAMKNLAK	QAVIVTLS	ADNNGTIDYTPAKVI	PARFYDFTVKNV	TVQDSTGSNP	AIEITGDSSK	DIWHSQFIFSNMKLSGVSP	559
Theth.epgd	GNGGGARN	ITTRDSALAYITOND	GSPFLLTDG	SSALPTDTSNWAPD	SARPRDITVENS-TV	NGSKKYAI	MFQGAPDG	FDYNITFNNVFFGAG	658 589
Yeren.epgd	TIGGGARN	VTERNNAMRDLAK	-QVMVMTLD	ADSNANIDYPPAKI	PAQFYDFTLKNV	TVDNSTGKNP	SIEIKGDTAN	KAWHRLVHVNNVQLNNVTP	566
Aspf1A.pg	DATGTVSN	VKPEDITLSGITK	-MGLIVEQD	MEN-GSPTGTET-	NGIKVSDIT	-FDKVTGTVESD	-ATDINILGGSG	STDWTWSGVSITGG	348
AspriB.pg AspniA.pg	GATGSVSG DATGTVED	ITESNIQLSGISD	-NGIVIEQD	NKN-GGPTGKPT MEN-GDPTGTES	TGVPITDLT	-VNGVTGSVASK	-ATPVNILGGKG	SESDWTWKGVSISGG SESDWTWSGIDITGG	351 353
AspniB.pg AspniC.pg	GKTGTVEN GDTGSVSE	VKREDITLSDISK VTRHEIAFSDATD	-WGIVVEQD -WGIVIEQD	MEN-GSPTGTRT	NGVKVEDIT	- FKKVTGSVKSS	-GTDINILAGSG	SSSNUTHSGVDVTGG	345
AspniD.pg	DTTGEVYN	VKYENITLSGISD	-WGIDIQQD	NEN-GGATGDPT	NGVKIENIS	- FVNVKGTMSD	-GKDYYILSGDG	SSSNFVFTDVDITGG	482
Aspnil.pg	KETGDVSE	IT SNIQLSGITD	-XGIVIEQD	YEN-GSPTGTES-	TGIPITDVT	-VDGVTGTLEDD	-ATOVXILCODG	SSIDWIWIDVDVIGG	363 353
Aspni2.pg Aspor.pg	GATGSVSE DATGTVSN	ITTSNIVMSGISD VKREDITLSGITK	-YGVVIQQD -YGLIVEQD	HED-GKPTGKPT HEN-GSPTGTPT	NGVTIQDVK	-LESVTGSVDSG	-ATEINLLSGSG	SSDWTHDDVKVTGG STGLTHSGVSITGG	347 348
Asppa.pg	GATGTVSN	VKPEDITLSGITK	-YGLVVEQD	EN-GSPTGTET	NGITVSGIT	- FEKVIGTVESD	-ATDIVILLGSG	STONTESGVSITGG	348
Botful.pg	GATGSVSG	VTXKDITLSGITS	- W GVVVQQD	KN-GSPTGTPT	SGVPITDVT	-FSNVKGTVASG	-ATNVYVLSAK	SGWSWD-VSVSGG	367
Botfu3.pg	GTIGTIEN	VTYSNIKMSNISD	-WGIDVQQD	NLN-GGPTGEPT	NGVKISGIT	- FSSVTGTTTDD	- AYNYYVL GSG	SSDITTTDVSISGG	359 419
Botfu4.pg Botfu5.pg	GDTGTVNN GDTGTVSG	VENDDITLSSISK ITNSGITLSGITD	-YGILIEQN -YGITVNQN	DG-GDLHGDET DGTSGEET	TGVPITDLT	-IKNISGTGAVSS-S -LENITGTVEST	-GYDVVIVEGST	SEKSWTWSSVAVTGG	380
Botfu6.pg	ETTGFISN	ITYSNIKLTNIDT	- GIDVOOD	LN-GGPTGEPT-	NGVIIENIL	- FENVVGTAAAS	-ARNYEVLAGEG	SSNIKESGVKITGG	356
Clapul.pg	GAKGAVSD	VVYDNISLSDISG	-VGIVVQQD	KN-GKPTGKPT	TGVPITNIT	-VNKVTGNVKPG	-GTNVQVL GSS	SS NGWTWTDNKVVDG	354
Cocca.pg	GAEGAVSD GATGSVSD	ITTENITLENIAK	-MGIAIEÖD	NKN-GKPTGNPT	TGVPITNLT	-LKNVAGSVTGS	GANVHIL%GSS GTEI¥VL%GKG	SSAKGWIWIDNKIVDG SSSGWNWSGVSITGG	355 349
Collil.pg Colli2.pg	GATGPVSD KKTGSVSG	ITESGITLSNIAK	-WGIVIEQD -KGIVIQQD	MEN-GSPTGKET MEN-GSPTGKET	SGVPISGLT	-LSKISGSVSSS -IKNVKGSVASK	- ATPVXILSAS	TNWKMSGVSVTGG	346
Crnpa.pg Busmo.pg	DATGSVSD	VTYSGITLSGITN	- GIVIEQD	EN-GSPTGTET	TGVPITGLT	-VSKVTGSVASS	-ATDVYILSGKG	SSGWKWSGNSVTGG	354
Fusox1.pg	GTIGTIAN	VINCNISLINISK	- GVDVQQD	LN-GGPTGKPT	NGVKISGIK	-PIKVIGIVASS	-AQDWYIL GDG	S-SGUTESGNAITGG	356
Pusox2.pg Geck1.pg	GATGSVSD GATGSVSG	VKRODITLSNIAK	-WGIDVQQD	MEN-GSPTGTPT MRN-GGPTGNPT	NGVENTDVT	- INKVTGTVSSPA - FINIHGSVKSS	-GTEVXILSAN -GTNAXLLSGSG	SKNWINNNKVTGG SSSNWTNSKINVKGG	346 350
Kluma.pg Ophno.pq	KATGSVNN GTIKG	VHELSNTISGIRK VTENKITLSGITN	- GIVVETD - GVLIEON	NSN-GSTTGT G	SKVPITNFE	-VDGLTGSVDSS	-AYRVKIFVAG	ASKWTWKNVDITGG	344
Penex.pg Pengrl pg	GATGTIKG	VTPODITLSGITS	-OGITIRQE	TN-SGYTGST	TGVPITGLT	-LNNVHGTVTSK	-GTDITIESGSS	AS SGWTWTKVAVSGG	365
Pengr2.pg	KATGAVSD	VTRSNIKLSNIAK	-YGIVIEQD	QN-GSPTGKPT-	TGVPITGLK	-VEKVTGTVKSS	-GTDVWILGASG	S-KNWIWTGNSVTGG	361 354
Penja.pg Penoll.pg	DATGSVSD KAKGEVAD	VTUSDITVSGITD VTUSNIELSNIAK	-WGIVIEQD -WGIVIEQD	MEN-GSPTGTPT MEN-GSPTGKPT	SGVPITDLT	-VKGITGSVESD	AVEVWILNGDD	ASSDWTWSGVDITSG SESDWTWSGNKVSGG	356 355
Penol2.pg Sacce.pg	EATGSVKN GATGTVTN	VTYKDITLSGITK VNFISNKISGIKS	-YGIVIEQD -YGIVIE	MEN-GSPTGTRT MLN-SKTTGTAT	DGVPITDLT	-LDGVKGTVASS	GTNVXILSAEG	ASSDWTWDGVSVSGG	365
Scisci.pg	GATGSVSG	VTYKDITLSGITS	QUVIEQD	NEN-GSPTGKPT-	SGVPITGVT	-LSNVHGTVSSS	-ATNVYVLSAK	SCWTWD-VNVTGG	365
Sclsc3.pg	GATGSVSG	VTYKDITLSGITS	-YGVVIEQD	EN-GSPTGKET-	SGVPITVVT	-LSNVHGTVSSS	-ATNVYVLSAK	SGWIND-VNVTGG	365
Asptu.epg	GTPSALSADLOGGGSGSVKN	VINSGITLSGITD	-MGIIVNQA	CONT-AGST-	NGVAISKFI	- LDNVTGTVESG	-ATNIXIESGSG	SUTNETESGVSVTGG	368
Botfu.epg	NTASALSGDLOGGGGSG RVNN	ITEDTMYIDNVDY	AIEVDQ	GOKNL-THELEFP-	SPLTITDII	- FRNFTGKTSTKY-Q	- POIGTFASST	SV-NNIVASGIDVLSP	428
Fusox.epg	GVETAFQSLLNOGGGLGRVRN	VIEDGRIVENVDI	AITITQ	GOKNO-TIONEFP		- MKNEWGTVSTKY-D	PRVGYVV3SSF	RSSTSWLRILKSRFQ	421
Actde.pg	GGSGSASN	IKPONVEMHNVEN	PIIIDQN	DODKP OBOS-	SAVQVKNVV	QNIKGTSAS	NVAITFDSKR	FPSQGIVLEDVDLEIE	431
Arath2.pg	KDSNSRARN	IVEQUINMEMVEN	PIIIDQH	XaLHKPaPKQE-	SGVKVSNVR	- MEDIHGTSNT	EVAVLLDSSKE	KPSTGIVMDDVNLVSV	373
Arath3.pg Arath4.pg	RHSNGEVER RPSRGEVNN	VRELGAIMVNVSY VVERNLIMNNVEN	PILIDQN	MAPGDSSAPSQE MAPNGKGAPRQS	SGIKINDVI SGVKISGVT	-XSGIMGTSAT	EIAIKMD@SEK	VPETGIRMQAINLTSY NHETGLRLQDIKLTYM	372 369
Arath5.pg Arath6.pg	RQSTGFVRN GGSGTAKN	VLEONLIMKNVON	PIIVDQN PIIID	APSNQ GAPKQG	SGVKISQVV	-WRNIQGTSRT	QQALTFDSRS	NPPQAIRLHDIKLTFN YPPOGIVLENVKIKGG	367
Arath7.pg	GGSGTASN	IIPQNIQMDNVKN	PIIIDQD	D-KSKSTTEK-	SAVQVKNVV	-YRDISGTSAS	ENAITFN SKN	YP QGIVLDRVNIKGG	404
Arath9.pg	NGKGYARN	ILPKDLTFRESKN	PIIIDQN	VD-KGRLDVEE-	SAVAISNVI	-TDIRGTSQR	NEIIKIDSSEV	TYAKDIVLDKIDIATV	353
Arath10.pg Arath11.pg	GGQGYARN GGLGVVKN	ISPTDITLVNTKN LTPSNIQVKDVKV	PIIIDQH	MID-KGRLTEE WEDKSKEKNQT	SAVAISNVK RAVSISGVK	- WDFRGTSSN	KNAITLKSSET	THEVDVVMDGIDITMA VP9MDVDLMDIRLRPS	342
Arath12.pg Branal.pg	GGIGSVKG GGSGTAKN	ILESNIQLTEVQL	PIVID PIIID	MEDHSK MINHT	SAVSVEGVT	-YEKIRGT-YT	VKPVHFASDS	FPSIDVQLSGIELKP-	492
Brana2.pg	GGSGTAKN	IKPONIRMONVEN	PIIIDQN	D-KDKAEQOE-	SAVQVNNVV	-WRNIQGTSAT	-DVAIMFNSVK	YP2QGIVLENVNIKGG	413
Cucnel.pg Cucnel.pg	RPSTGRAKN	IRECHITMIDVEN	PIVINQN	YOPHNQGAPGKE-	SGIKISDVT	-XEDINGTSAT	EVGINFERSPA	RPANEIRLKDVKLIFK FPAKGIVLENVQLTYK	367 391
Cucne3.pg Glymal.pg	GGKGYAQN GGSGSVQN	IIPONIVMDNVTN IMPSNVQVSGVQT	PIIIMQN PISIDQY	NGDOKEP STOOA NGDGGR SRNES	DAVAVSNVM SAVAVSGIH	-XQNIRGTSAS	EVAVKFDSSKS	VPSQGILLQDINLVHK LPSSGITLDTIQLES-	429 395
Glyma2.pg LycesA.pg	GGSGSVQN GGSGOASN	IMPSNVQVSGVQI	PILIDQY	DGGKSRNES	SAVAVSAIH	-YVNIKGT-YT	KQPIYFASDN	LPATGITLDTIRLES-	391
Lyces1.pg	RPSNGFVRN	VLPOHIVMVNVKN	PIIIDQN	PNHQ SEPHKG -	SGIKISDVT	-YQDIHGTSAT	EVAVKLDSKS	NPSSGITLEDVNLSYQ	364
Lyces3.pg	RPSNGWVRN	VLROHIVMVNVKN	PIIIDQN	WAPNHQ SAPHKG-	SSVKISDVT	-YODIHGTSAT	KVAVKIDSKR	NP3SGITLEDLNLSYN	364
Lyces4.pg Lyces5.pg	RPSNGFVRN RPSSGFVRH	VLEOHIVMSNVON	PIIIDQN	WAPNHE SAPNOG	SGVKISDVT	-WEDINGTSAT	EIAVKLD%SKT	NPESGITLEDVNLSYK NPESGITLDNVNLSYK	362
Lyces6.pg Maldo.pg	RPSTGEVNN GGSGSATN	VLEQHVAMIDVEN	PIVIDQN PIIID	PYNKNSPGQV- NODHKTK-DSKOOK	SGVKVSDVT	- WODINGSSAT	RVAMEFDSER	NPSKGIKLEDVNLSYK	369
Medsa.pg	SSPG-TSPITD	MHREDIIMVNVIN	QE	SPWNQSKLV-	PSKIKISKVI	- KNIRGTSKT	KDGVVLISKS	FPEDAVELNNVALTFN	367
Prupel.pg	RPSTGPARN	IL QHATMVNVEN	PIVIDQH	MEPDNKGEPGQV	SGVQISDVT	-XEDIHGTSAT	EVAVKFD3SKS	SPAQGYIVGNINLVGN HPEREIKLEDVKLTYK	420 368
Prupe2.pg Prupe3.pg	GGSGSASN	ILEQHATMVNVEN IVEQNVEMNDVTN	PIVIDQH PIIIDQN	BEPDNK GEPGQV BEDHKNK - DETRQR	SGVQISDVT	-YEDIHGTSAT	EVAVKFD%SPK	HPSSEIKLEDVKLTYK VPSOGIVLONIOLONA	368
Rubid.pg	GGSGMASN	IVEQNIEMNDVTN	@IIIDQN	DTSDKRK KQQS-	KAVKVQNVL	-YKNIRGTSAS	KYAIAFDSSKS	IP QGIVLQNVQLHK-	315
Arath1.epg Arath2.epg	-GSP-PGIASN	ILLEDITMDNVSL	2VLIDQB	YSPYGHSKAGV	PSKVKLSDVT	-IKGIKGTSAT	KVAVKLMASKG	VPSTNIALSDINLVHN VPSTNIALSDINLVHN	410
Arath3.epg Arath4.epg	SAA	IHREDIILKDVSN	PILIDQE	BEPWNQSRGC	ASTIKLVNIS	- KNIRGTSGN	KDAVKLLSKG	YPSONVEIGDIDIKYN VPSOGVNVVDVNLDVV	360
Arath5.epg	SSAS-KILVSN	FVYENIQMIDVGK-	PINIDQ3	PHPPSEHEI	R-KSHVQIQDLK	-LKNIYGTSKN	KVAVNLQ SKS	FP KNVELIDINIKQN	373
Arath7.epg	KSVS-QISVSN	FLAENIQMINVGN-	PIVIDQC	PHGQ DSPGK	Y-ASHVQIKDVK	-YNNIWGTSTS	KEALKMQ SKT	FPSQDVELSNINLHYV	376
Gosba.pp	-GEH-GGAVSE	IHREDITMNNVSS	BITID	PWNKSKKNE-	SAVQ1QDVT ESKVKLSNIS	- KNIRGTSAT	PEAIKFISGS	MPEKDIKLSDISLKLT SPEONVELADIDIOHN	403 370
Goshi.pp Medsa.pp	-GEH-GGAVSE DAPG-TITVSD	IHEEDITMNNVSS	PILIDQC	PWNK SKKNE - YPWNQ SKKN -	ESKVKLSNIS PSKIKLSKIS	- KNIRGTSAL	PEAIKFISSGS	SPEGNVELADIDIKHN VPEDGVELNNVDLKFN	370 369
Nicta.pp Salgil co	-ASH-PGVVND	WHEEDIIVONVSN-		NEPPNKNKDL-	PSQVKISKVS	- QNIKGTSRT	QDAVSLLRSKG	VPSEGIEVGDIDITYS	362
Salgi2.pp	-DLY-GGVASN	MHREDIVMNNVQN-	PILLD	YEPHNQSLKA-	PSKVKISDVS	-KNIRGTSAT	PVVVKLASSG	IPSEKVELANINLLYS	367
Salgi3.pp Salgi4.pp	-DLY-GGDASN	MHREDIVMNNVQN		PWNQSSLKS	PSKVKISDVS PSKVKISDVS	- FKNIRGTSAT	PVVVKLASSGG	IPSEKVELADINLVYS IPSEKVELADINLVYS	367 367
Brana.pep Cenor.pep	SAA	HTEDIILNKVSN	PILIDQE	PWNQSNKNK-	PSTIKLVDIT	- FRNIRGTSEN	KDAVKLLSSKG	HPENVEIGDINIEYT FPENGVELADIDLTYS	360
Phlpr.pep Zeamal per	DAKS-PLTASK	LTYENVEMEDVGY-	PIIID	PNKI TSKG-	-DSARVTVKDVT	- FRNITGTSST	PEAVSLLSSDK	QPONGVTMNDVKIEYS	366
Zeama2.pep	DAAS-VLTVSK	IHYENIKMEDSAN-	PIFIDM9	PNKL TANG-	-ASKVTVKDVT	- KNITGTSST	PEAISLLETAK	VPSTGATMDDVNVEYS	383
Phaco.pg	0FRGRYPWRM	LTESNIAMEGIWE	-WAVNVE	KK-GKPTGIFU	ASKVIVKDVT	-EEKVTGTLTGE-F	PEAVNLL TAK	IPHIGVINDDVNIKYS	383
				7			W. W. W.	- Marchington and Andre	

Fig. 1. Continued.

bartu na		SDDD I INDODUCTOR	210	
Agreu.pg	DEPT NALT	DADARA DE	Economic company and the	12
Burce ng	S	STICSN	DectTTDAAT AE	50
Erwcal.ng	5	21034	grobiiirwgi 45	20
Erwca2.pg			40	02
Ralso,pg	SP-NGVHFTFGGTGPVSFAL	AIVTSSTTDVTVTGTPGTAAAVD	SKAFVPLKSVAPTSPI 52	29
Thtma.pq	RFEKLY	EGKALLK	44	4.8
Erwoh enad	TETE	I SDSO		
Ralso engd	ASTS	LEDST TRADE FRONT TO ACCESS TRADE STORES	ITERVEDAD 76	02
Theth.epgd	TYOTKIY	LKNSTFNNVVFYGSTPNYDGDOTTPVNEWHFVHSTN	IOFTGNTTOPOLPEWPSNSTA	54
Yeren.epgd	TAIM	LRDSETELRGDTPHHPSEVKK	90G 60	01
hense no	¥	Winning coact	6	-
Aspac.pg	K	STATE TO SUMS	37	78
AspflB.pg	KKSDI	SCNTP	36	66
AspniA.pg	ETSSI	SGAS	500	20
AspniB.pg	KKSSI	SOAS	SD	62
AspniC.pg	SVSD	SLAVPSGIS	5L 36	83
AspniD.pg	\$DD\$-	SNYPSSG	P 49	95
AspniE.pg	KTSSI	ENVPDDIS	37	78
Aspnil.pg	KTSDI	SENVPSGAS	36	68
Aspni2.pg	KKST/	SKNFPSVAS	36	62
Aspor.pg	KTSSI	ENVSTGAS	36	63
Asppa.pg	KTSSI	SENVPTGAS	36	63
Asptu.pg	KKST/	*KNYPSVAS	36	62
Botful.pg	KTSSI	BAGLP	38	82
Botful ng	Garage Krige	SNVDC	37 5pc	24
Botfu4 ng	KTVS	SALLS CARD	40 50 50 50 50 50 50 50 50 50 50 50 50 50	07
Bot fu5.pg	KT\$\$	STAUP	St	80
Botfu6.pg	QKES	SNYPA	SPA	71
Chopu.pg	KAGTIKSDKAKITGGQYLADQPASN	TEEMPAQDPNDPEDP	DTAMQEAEAEEAAAGNSTTSG 40	03
Clapul.pg	AKS	ANSVPAGVV	L 36	68
Clapu2.pg	ATPI	ANSRPAGVV	L 36	69
Cocca.pg	KKSS:	GLNVPSGAS	36	64
Colli1.pg	KKSS	STGIPSGSGAN	36	63
Colliz.pg	KSSTI	asgipsssgak	36	65
Crnpa.pg	RR55	SINT SGAS	36	69
Fusno.pg	C	CALLA NI	2P3 37	73
Fusion2 ng	V	WATE CON	8r5 37	11
Geokl.ng	KDSG	SOND SOND	36 271	67
Kluma.pg	SSFG	TGIPSOSGAP	36	61
Ophno, pq	KSYD	STNVPNGIS	37	79
Penex.pg	KAD	KNAPSGT	37	78
Pengr1.pg	QTSK	SKGIPSGAS	37	77
Pengr2.pg	KKSS	SGVPSGAS	36	69
Penja.pg	QTSS	SENVPSGAS	37	71
Penol1.pg	KTSSI	SKNVPSGAS	37	70
Peno12.pg	KTSS	SENVPSSAS	38	80
Sacce.pg	SSYS	SGIPSGSGAS	36	61
Scisci.pg	K1S11	GAGLPSGVR	<u>j</u>	80
Scisc2.pg	K	SUNSEP	38	80
Sciect pg	X	SUMALE SUVA	J8	80
acters.ba	K181	20041-120042	38 39	8/
Asptu.epg	DGTNDF	ESLLSVN	TATSD 43	35
Botru.epg	KGVDEA	ELNVNETGLDVT	ATTGFLGFN 45	56
Cocca.epg	CV STRUCT	ZANAEGIQSQVN	ATVEGDRGGHS 44	45
Pusox.epg	GKKPPVII	SUNID	SADPINARDIING45	54
Actde.pg	GGAAAKAI	ANNVELSE-TGVVSPH	QEEGGEEEEAS 46	67
Arath1.pg	NKPAAS	GIE-AGFFQPN	38 M	84
Aratn2.pg	HRPAQA	SDNANGSANDVVPFTP	ALKREIIIT 40	05
Araths.pg	B	GRUGLVTPSG GRACUMUDAN	39 Su	97
Arath5 ng	GRSATS	GUNDOVAVIAN	39 57	39
Arath6.pg	TA	KNANVKN-OCTVSPK	41	37
Arath7.pq	KA	STNAN	9NST 42	26
Arath8.pg	DGNKPIV	SNVYGKSINANEANG	38	81
Arath9.pg	DGNKPVVI	SNVYGKS INTNDANG	38 PED 38	81
Arath10.pg	NGGKPKVI	GQYVDGESSDTDLMRD	FKNNTSS 37	74
Arath11.pg	GGIRGLQTHQQQQAI	WNSYGKTQGPLVPSSIGY	SLRKSNIGGYYSQKVSRSYDKIEPS 47	70
Arath12.pg	VQLQYHMYDPI	WKTFGELNSATVPPID	LQIGKPARNG-VHSDHDIEL54	40
Branal.pg	KA	ENVNVKD-KGTVSPK	43	33
Ourmal pg	D01202	STVAT. OTTI OLUGION	4J	33
Cucme2.pg	NGNAKA	STNAC	39 SEPERT SET	23
Cucme3.pg	GKNDDKSAOAEAS	SKNVK	9GGG 46	61
Glymal.pg	AOETKNSNVPI	WEAYGELKTTTVPPVE	LORGNPSKEGGINSNIDSS 44	43
Glyma2.pg	AQETKNSNVPI	WEAYGEL&TKTVPPVE	LORGNPSKAGGINPKIDS 43	39
LycesA.pg	SGKPSEA	KNVHFNN-AEHVTPH	TSLEISEDEALLYNY 45	57
Lyces1.pg	NQOTEAS	EVNARGRVSGLQKPTN	SLLKS 39	92
Lyces2.pg	NQQTEA	gvnakGRVSGLQKTIN	39 JLLEN	92
Lycess.pg	N	SUNAC	St	05
Lyces5.pg	NGRAER	AVNAA CKASCERET TO	38 %L	87
Lyces6.pq	NEPAAFAS	SNVAGTTTGVIOPTS	36 2L	95
Maldo.pg	RAI	SNNVQPAY-KGVVSPR	46	60
Medsa.pg	GAPVNAI	SVNVKPILTGPTPK	TTAAEA 39	95
Peram.pg	GGKETTM	SNIVQGLLREGLSTFLFMKRRVHE	SY 46	62
Prupel.pg	NQAAES:	SHADGTTEGVVQPTS	GL 39	93
Prupe2.pg	NQAAES!	SHADGTTEGVVQPTS	39	93
Prupe3.pg	RAI	MNVKPAY-KGAVSPR	3SWGLVN 45	58
Rubid.pg	KAI	SNVNLAY-KENVSPR	3A 33	35
Arath1.epg	GKEGPAVS	SNIKPILSGKLVPAA	GTEVAKPGP 44	44
Arath2.epg	GKEGPAVS	SNIKPILSGKLVPAA	STEVAKPGP 44	45
Arath3.epg	GADGPATFI	ESNV5	39 SAPAA 39	91
Arathe con	GKIGGERKSSSGGLVGA	VIFGGKLSFPM	42 RT N	22
Arath6 eng	SSDGGRKOCONDONENUCO	SERVE AVAILABLE AVAI	40 54	62
Arath7_epg	GRDGLATA	NENVG	PRINLFLPSNIITDSNSTLEDEMOGIEOLANTTOTOPE 41	20
Cryja.pp	SGKIASELNDN ANGYPSGHVIP	KNLSPSAKRKESKSHKHPKTVMVKNMGAYDKONRTRILLGSRPPNSTNZ HO	SPSKAKLVIVHRIMPORYYPORWMSSRHCKIVHD	14
Gosba.pp	GAEPATS	LNVK	SGPVPKTPSATA	07
Goshi.pp	GAEPATS	ELNVKPITSGKLNPIP	SSGPVPKTPSATA 40	07
Medsa.pp	GAPTTAI	@TNVKPLVTGTAPV	QAPGAPAASTTATPAASKTATPAAGKSPAK 42	21
Nicta.pp	GKEGPAKS:	ENIKPSLKGKQNPPV	TASAASSS 39	96
Salgi1.pp	GSEGPAKS	SNVKPKISGIMSASG	39	93
Salgi2.pp	GSEGPAKS	RONVA	39	93
Salgiá pp	CS EGPAKS	Serve PTISGIMSASG	39	93
Brana, pen	GPDGPAKS	TNVT- PIISGIMSASG	SVGPVVKAPGKE	93
Oenor.pep	GKGGPATS	SENIK	SGSAAKAA	62
Phlpr.pep	GTNNKTMA	STNAKVTAKOVSEANT	SAA	94
Zeamal.pep	GTNNXTMA	TNAKGSTKG%LKELA	§2	10
Zeama2.pep	GTNNKTMA	TNAKGSTKG	§P 41	10
Zeama3.pep	GTNNKTMA	GENAKGSAKGSLKELA	§P 43	10
Phaco.pg	SHAS	SYVPTGYS	§ 36	67

bacterial PGs (Agrtu.pg and Thtma.pg; Ile \rightarrow Leu), all bacterial EPGDs (by Ala, Gly and Leu), four fungal PGs (Botfu2.pg, Ophno.pg, Penex.pg and Pengr2.pg; Ile \rightarrow Val) and five plant PGs (tomato abscission zone; Ile \rightarrow Val).

With regard to the Tyr291 found previously to be conserved in polygalacturonases (Stratilová *et al.*, 1998), the alignment of all 115 PGs, EPGs and EPGDs known at present confirmed that this tyrosine belongs to the invariantly conserved residues of these enzymes (Figure 1).

Bacterial PGs and EPGDs

The group of bacterial PGs contains the sequences with a very low degree of mutual similarity. The seven PGs involved in the present study (Table I) exhibit only 4.7 and 11.2% identity and similarity, respectively, except for the two PGs from E.carotovora that share 96.0% sequence identity (Hinton et al., 1990; Saarilahti et al., 1990). Pair-wise similarity varies in the range between 11 and 50%, but in most cases does not reach 20%. The bacterial PG sequences have only 10 invariant residues (Asn197, Ile218, Gly248, Lys255, Gly282, Gly315, Val330 and the dipeptide 287_GV; Erwca2.pg numbering) in addition to the four well recognized conserved regions and presumably functional invariant tyrosine (Figure 1). It is worth mentioning that in Ralstonia solanacearum EPGD, this tyrosine was identified only with help of the hydrophobic cluster analysis method (data not shown) due to an inserted oligopeptide segment (Huang and Allen, 1997) absent in all other polygalacturonases (Figure 1).

On the other hand, the overall sequence similarity among bacterial EPGDs is higher (23.7% identity and 37.3% similarity), the pair-wise similarity ranging from 25 to 60%. These sequences contain not only isolated invariant residues but also several identical segments that have been found to be characteristic of bacterial EPGDs only (Figure 1). The most important segments are 202_MTL, 255_NIRI, 378_FGNS, 399_NF, 417_AW, 467_GGGA and 584_PW (Erwch.epgd numbering).

Fungal PGs and EPGs and the insect PG

Forty-three fungal PGs form a substantial part of the entire set of polygalaturonases studied in this work (Table I). Their sequences are 8.9% identical and 17.4% similar with the average pair-wise similarity of about 60% ranging from lower than 20% to higher than 90%. In the amino acid sequence alignment (Figure 1) several aromatic residues can be found as characteristic of these fungal PGs: Phe32, Phe74, Phe80, Trp85, Trp114, Trp115, Phe128, Phe129, Phe182, Phe214, Tyr272, Tyr283, Tyr326, Trp337 and Trp339 (Aspni2.pg numbering). Not all of them are conserved strictly (except of Trp115 and Phe182), but in most cases there are conservative (aromatic \rightarrow aromatic) substitutions. Of these Phe80, Trp85 and Tyr272 (or their correspondences) are present also in the fungal EPGs, and the equivalents of Trp115 (though replaced by tyrosines) may be found in the whole set of sequences shown in Figure 1. There is also one longer segment specific for fungal PGs (205_AinSG) positioned from the C-terminal side close to the active-site dipeptide 201_DD. Among the other conserved residues the two prolines, Pro148 (conserved also in the fungal EPGs) and Pro300 (not strictly conserved), could be of interest.

Fungal EPGs exhibit quite high degrees of identity (36.7%) and similarity (51.0%) with several longer conserved stretches, characteristic dipeptides and isolated invariant residues. In the N-terminal part, there is a segment starting with 60_DD and ending with 75_GG (*Aspergillus tubigensis* EPG numbering). The following regions are also typical for the EPGs from fungi: 121_SFKxxFQN, 166_LRPiL, 225_WDTYR, 248_SFKPN, 319_GGGG. In addition, Phe132, Phe133, Tyr143, Trp306, Tyr331 and Phe374 (although not invariantly conserved in all cases) as well as the two dipeptides, 355_TL and 364_LT (located in the C-terminal part), should be of importance for fungal EPGs.

With regard to the one representative of animal polygalacturonases, the insect PG from *P.cochleariae*, its sequence goes well with the fungal PGs and contains almost all sequence features characteristic of this group of PGs (Figure 1). There are 20 single residues or short segments conserved in fungal PGs that are identical with those from the insect PG.

Plant PGs and EPGs

In the group of plant polygalacturonases analysed in this study, the exact enzyme specificity has not been determined strictly due to the fact that many of them were not biochemically characterized in detail or were taken as putative proteins from sequencing the whole genome. It is not possible to say clearly in all cases whether the enzyme is a PG or EPG. There are (Figure 1) again several well conserved aromatic amino acid residues, such as Trp99 (LycesA.pg numbering), Trp157, Phe203, Trp331, Phe343 and Tyr382, as well as the other residues Ser245, Gly250, Gly269 (strictly conserved also in all bacterial PGs and EPGDs and almost in all fungal EPGs), Pro354 and Asp358 (substituted in three cases by Asn).

In agreement with the proposed classification system (Hadfield and Bennett, 1998; Torki *et al.*, 2000) the present set of 56 plant polygalacturonases can be divided into five clades: A, B, C, D, E plus the gymnosperm PG from *Cryptomeria japonica* (cedar) with a sequence without resemblance to the rest (except for the conserved sequence regions covering the active-site residues discussed above). This division is based on the evolutionary tree (Figure 2) of all polygalacturonases (Table I) reflecting the alignment shown in Figure 1. The tree will be discussed later.

The characterization of the clades and the numbering of the residues according to the consensus alignment of Torki *et al.* is used here (Torki *et al.*, 2000). For clade A, there are two exclusively specific, invariantly conserved residues Gly264 and Phe294. For clade B, there is also a characteristic Asn104 present in the Medsa.pg (from clade C), which thus exhibits an intermediary nature of clades B and C. Clade C, covering all pollen and flower PGs and plant EPGs, contains the invariant Lys176. Clades D and E are without exclusively conserved residues.

Fig. 1. Amino acid sequence alignment of all polygalacturonases. The colour version of this figure can be found at the URL: http://nic.savba.sk/~umikstef/ PGs. The abbreviations of enzyme sources are given in Table I. The 115 sequences of polygalacturonases are ordered according to their groups (from the top): bacterial PGs, bacterial EPGDs, fungal PGs, fungal EPGs, plant PGs, plant EPGs with plant pollen polygalacturonases and the insect PG. All selected residues are signified by bold. Four conserved active-site segments (178_NTD , 201_DD, 222_GHG, 256_RIK; Aspni2.pg numbering) and the invariant tyrosine (Tyr291) are highlighted by black-and-white inversion. Cysteines are coloured white and highlighted in dark grey. The residues characteristic for the individual group of polygalacturonases are highlighted in light grey. The invariant residues are signified by asterisks. The β -strands forming the 10 coils of parallel β -helix (four parallel β -sheets PB1, PB2a, PB2b and PB3) of the PG from *A.niger* (van Santen *et al.*, 1999) are indicated above the alignment blocks (the number of the coil is written in italics, while the number of the β -sheet is written in bold).



Table II. Sequence identity and	similarity	for the	clades of plant	
polygalacturonases				

Clade	Members ^a	Identity (%)	Similarity (%)
А	15	18.3	35.6
В	11	25.4	35.1
С	22	12.2	23.1
D	3	53.4	66.0
Е	4	35.1	51.8

^aThe only gymnosperm polygalacturonase from cedar (Cryja.pp) has not been classified in any of the above clades.

With regard to sequence identity and similarity in the frame of the individual clades, the values are shown in Table II. However, in general, the conserved sequence regions containing the active-site residues are conserved in plant polygalacturonases as longer segments (Figure 1).

Conserved cysteines and aromatic residues of polygalacturonases

As pointed out by the published crystal structures of polygalacturonases (Pickersgill et al., 1998; Van Santen et al., 1999) these enzymes contain some disulfide bridges stabilizing their molecules. However, the conservation of cysteines reflects taxonomy, i.e. the corresponding disulfides could be conserved only in the frames of the respective bacterial, fungal and plant groups as described above. There is only one cysteine residue conserved throughout all the polygalacturonases (Figure 1) in the position of Cys45 (Aspni2.pg).

Bacterial PG from E.carotovora has two S-S bridges, Cys41-Cys62 and Cys115-Cys125 (Pickersgill et al., 1998), but there is no conservation of cysteines in the respective positions for all bacterial PGs. Bacterial EPGDs contain an even smaller number of cysteine residues which are also without specific arrangement (Figure 1).

On the other hand, the cysteines among fungal PGs are very well conserved. Aspergillus niger PG II (Van Santen et al., 1999) has four disulfides: Cys30-Cys45, Cys203-Cys219, Cys329-Cys334 and Cys353-Cys362. While the first two bridges should be present in all fungal PGs, the one corresponding with Cys329–Cys334 is missing in the PGs from yeasts $(Cys \rightarrow Val and Cys \rightarrow Ala substitutions)$. With regard to the fourth S-S bridge, the corresponding cysteines are absent in both PGs from Claviceps purpurea and the one from Chondrostereum purpureum. The insect PG from P.cochleariae has all the cysteines in accordance with those present in the group of fungal PGs. Based on the alignment shown in Figure 1 it is possible to suppose that the fungal EPGs could contain all the four disulfides present in fungal PGs. However, the



b

position of the first cysteine from the first disulfide (Cys30-Cys45 in the fungal PGs) is shifted and corresponds to Cys50 of A.tubigensis EPG, and there is Cys-Ala substitution in EPG from Fusarium oxysporum in the position corresponding to the first cysteine of the third disulfide (Cys329; Aspni2.pg numbering). Fungal EPGs possess two additional conserved cysteines, Cys348-Cys357 (A.tubigensis EPG numbering), forming probably an extra disulfide bridge.

Since the three-dimensional structure of a plant polygalaturonase has still not been determined and the presence of disulfides in these enzymes has not been experimentally proved, the eventual S-S bridges can be proposed by analogy with fungal PGs only. Thus, plant enzymes could contain the three disulfides corresponding with the second, third and fourth disulfides of fungal PGs, positioned at Cys272-Cys289, Cys399-Cys405 and Cys427-Cys442, respectively (Lycopersicon esculentum PG A numbering). There are two exceptions, the pollen PG from *Nicotiana tabacum* with the $Cvs \rightarrow Arg$ substitution in the position corresponding with the Cys399 and the one from L.esculentum (TAPG3) with a shorter polypeptide chain. With regard to the first disulfide present in fungal PGs, all plant enzymes contain only the second cysteine, Cys103, which corresponds to Cys45 of A.niger PG II. However, there is a strictly conserved cysteine residue in all plant enzymes, Cys130 (LycesA.pg numbering), which could eventually form the S–S bridge equivalent to the first disulfide of fungal PGs. Most of the plant polygalacturonases have further cysteines, Cys186, Cys194, Cys229, Cys362 and Cys368 (LycesA.pg numbering), four of which (except for the Cys229) are absent in the PGs from clade D. Clade D, on the other hand, contains an extra cysteine corresponding with Ala317 in the LycesA.pg, which was proposed as a pollen-specific cysteine residue (Tebbutt et al., 1994; Petersen et al., 1996). This cysteine is further present in most members of clade C and in the PGs from Cucumis melo (Cucme3.pg) and Medicago sativa (Medsa.pg). Cys186 is not present in clades D, E and in the pollen PG from M.sativa (Medsa.pp). This is also the case for Cys194, which is absent in two more pollen PGs, those from Gossypium barbadense and Gossypium hirsutum. Cys229 was not observed in the sequences of PGs from A.thaliana (Arath2.pg, Arath4.pg and Arath11.pg) and Prunus persica (Prupe1.pg) as well as of EPGs from A.thaliana (Arath3.epg, Arath4.epg, Arath5.epg and Arath7.epg) and Brassica napus (Brana.pep). Both Cys362 and Cys368 are present in all plant polygalacturonases except for those from clade D and Arath4.epg, thus indicating the possibility of forming a disulfide bridge.

As far as the aromatic amino acid residues are concerned, those characteristic for the individual groups of polygalacturon-

Fig. 2. Evolutionary trees of all polygalacturonases. Both trees are based on the alignment shown in Figure 1. The abbreviations of enzyme sources are given in Table I. The branch lengths are proportional to the sequence divergence. (a) The complete tree, calculated with involving the positions with gaps in the sequence alignment, showing the relationships among the individual taxonomic (bacteria, fungi and plants) and specificity (endo- and exo-mode of action) groups as well as in the frames of all these groups. (b) The simplified tree, calculated with excluding the positions with gaps in the sequence alignment, showing the basic relationships among the individual group of polygalacturonases.

ases (PGs, EPGs and EPGDs as well as bacteria, fungi and plants) were briefly described above. The interest in these residues is due to the fact that they may be involved in binding of substrate not only in polygalacturonases (Rao et al., 1996) but also in other glycoside hydrolases, e.g. in amylases (Clarke and Svensson, 1984; Gibson and Svensson, 1986; Williamson et al., 1997). The invariantly conserved tyrosine, Tyr291 (Stratilová et al., 1993, 1998), to which also the function has been proposed (Stratilová et al., 1996), was recently confirmed by site-directed mutagenesis to be indispensable for effective catalysis constituting the subsite +1 (Pagès *et al.*, 2000). There are two further aromatic positions conserved among the different groups of polygalacturonases. These are not conserved strictly but only aromatic residues (Trp, Phe and Tyr) occur there. The first one is at Trp115, which is in all bacterial EPGDs, most fungal EPGs and three plant pollen PGs replaced by tyrosine and phenylalanine (Figure 1). The only exception is the PG from Agrobacterium tumefaciens (with a shorter polypeptide chain) that evidently does not possess an aromatic residue equivalent to Trp115. The second aromatic position corresponds with Phe271 which alternates with tyrosine (60:40%, respectively) only. The A.tumefaciens PG with a methionine residue equivalent to Phe271 exhibits an exceptional behaviour again.

Evolutionary tree of all endo- and exo-polygalacturonases

The evolutionary tree showing for the first time the relationships of a complete as possible set of sequenced polygalacturonases belonging to bacteria, fungi, plants and animals (represented by an insect) is presented in Figure 2A. The tree is based on the sequence alignment shown in Figure 1 and thus reflects the sequence similarities and differences discussed above.

Basically, the tree manifests that there are three main groups: bacteria, fungi and plants (Figure 2A), bacteria being positioned, however, between the fungal PGs and fungal EPGs. The only one representative of the animal kingdom, the insect PG from *P.cochlearie*, is included in the cluster of fungal PGs. Following this basic division of the tree, one can further see the clustering according to the endo- and exo-mode of action of these enzymes especially among the bacterial and fungal polygalacturonases and into the plant clades.

While bacterial EPGDs form their own cluster, the group of bacterial PGs is not so homogeneous reflecting the lower degree of mutual sequence similarity. The two PGs from *E.carotovora* are very closely related to each other and are located next to the pair of PGs from *Agrobacterium vitis* and *Ralstonia solanacearum*. There are three further PGs located on long branches. Two of them, those from *A.tumefaciens* and *T.maritima*, have been determined as putative PGs only (Rong *et al.*, 1991; Nelson *et al.*, 1999) so that it is not possible to correlate their position in the tree with their exact enzyme specificity. The last bacterial PG from *Burkholderia cepacia* is even more isolated which may reflect the fact that this PG is a plasmid-encoded protein (Gonzalez *et al.*, 1997).

The consequence of clear sequence differences between fungal PGs and EPGs (Figure 1) is that these two groups of polygalacturonases are well separated in the evolutionary tree (Figure 2A), both forming quite homogeneous and isolated groups. The most remarkable feature of the fungal PG part of the tree is the location of the insect PG from *P.cochlearie* (representing the animal kingdom) directly among the fungal PGs. However, this is based on the resemblance of the insect sequence to the fungal ones described above. The PG from *C.purpureum* seems to be the most distantly related member of the fungal PG group (Figure 2A) in agreement with several non-conservative substitutions in characteristic positions (Figure 1). The two PGs from yeasts are both positioned adjacent to each other thus indicating that all eventual yeast PGs would form their own separate yeast cluster in the frame of all fungal PGs. Several sub-clusters or sub-groups can be found in the fungal PG part of the tree. Based on the analysis of 35 sequences of fungal PGs Wubben *et al.* (Wubben *et al.*, 1999) have proposed five monophyletic groups of closely related PGs. The present study covering more fungal PGs (43 sequences) indicates that the number of the so-called monophyletic groups is probably higher and will even rise as more sequences become available.

As mentioned in the section dealing with the sequence comparison of plant PGs and EPGs, these enzymes have been classified into the five clades (Hadfield and Bennett, 1998; Torki et al., 2000) plus the PG from cedar (Table II). This division can also be seen from the tree (Figure 2A) where the plant polygalacturonases form clusters according to their clades and one long isolated branch leading to the cedar PG (Cryja.pp), which is the only plant gymnosperm PG. The detailed analysis of the branch arrangement in the plant angiosperm part of the tree suggested that the 'plant' branch leads to the node separating clades E, D and B on the one side from those of C and A on the other side. The only 'exception' is the clustering of the five PGs from A.thaliana (Arath1.pg-Arath5.pg) from clade A together with the three further PGs from this plant that should form clade D (Torki et al., 2000). The largest clade C (Table II) contains polygalacturonases expressed mainly in flower buds, flowers and pollen that are thought to encode the EPGs (Torki et al., 1999, 2000) with one exception, the PG from M.sativa induced by a Rhizobium strain, which was, however, originally revealed to exhibit extremely high sequence similarity to its pollen counterpart (Muñoz et al., 1998).

In order to re-analyse the plant part of the evolutionary tree with respect to the plant clades, a further tree was constructed (based on the alignment shown in Figure 1), however, excluding the positions with gaps. The simplified version of this tree is shown in Figure 2B. The detailed analysis of the branch arrangement in the plant part of the tree in this case suggested that the 'plant' branch leads to the node separating clade D (three PGs from A.thaliana) from the rest of the plant enzymes. The rest was then divided into well separated clades (without dividing any of them) so that clades C and A were on the one side and clades E and B were on the other side. The only gymnosperm PG from cedar was on its own long branch (adjacent to clade B) which reflected its higher dissimilarity (discussed above) with the other plant PGs which are angiosperm. With regard to bacterial and fungal parts of the tree, in the case when the positions with gaps were excluded, taxonomy was fully respected so that there were two separate branches in the tree (Figure 2B): one leading to fungal PGs and EPGs, and the other one leading to bacterial PGs and EPGDs.

Rhamnogalacturonases

The alignment of all sequenced rhamnogalacturonases is presented in Figure 3. As is well known (Coutinho and Henrissat, 2000) the RGs belong to glycoside hydrolase family 28 together with polygalacturonases although the conserved active-site regions of PGs are slightly modified in the sequences of RGs. Thus, 193_GLD (*A.aculeatus* RG numbering) corresponds

AspacA.rg AspniA.rg AspniB.rg Botfu.rg	MRGLFLLA-LGAIPALVSGQLSGSVGPLTSASTKGATKTCNILSYGAVADNSTDVGPA MPALPILA-LALAPLLVNGQLSGSVGPLTSAHSKAATKTCNVLDYGAVADNSTDIGSA MLLDKLSVLSFLGLAPIFAAAQLSGSVGPLTSASTKAATKTCNVLDYGAKADKSTDLGAP MQFGTLSALAAI-VLPAVVSAQLTGSVGPLTSRESK-ATKVCSVLDYGGKASKTSDIGPA * * * * * * * * * * * * * * * * * * *	57 57 60 58
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	ITSAWAACKSGGLVYIPSGNYALNTWVTLTGGSATAIQLDGIIYRTGTASGNMIAVTDTT LSEAWDACSDGGLIYIPPGDYAMDTWVSLSGGKATAIILDGTIYRTGTDGGNMILVENSS LASAFADCKSGGLVYVPSGDYALSTWARLSGGEAWALQIDGIIYRTGTDGGNMIYIEHSS LTSAFAACKTGGTVYVPPGDYGMSTWITLSGGSAWALKLDGIIYRTGSDDGNMIMIKHTT . * * *** *** * * ** *** *** ****	117 117 120 118
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	DFELFSSTSKGAVQGFGYVYHAEG-TYGARILRLTDVTHFSVHDIILVDAPAFHFTMDTC DFELYSNSSSGAVQGFGYVYHREGDLDGPRILRLQDVSNFAVHDIILVDAPAFHFVMDDC DFELFSSTSEGAMQGLGYEFHADDNWSGPRLLRLYEVTDFSVHDFILVDSPSFHFSLDTC DFEMYSSTSAGAIQGYGYEFHKDG-AYGARLLRFYDATNWSIHDIALVDAPQFHFSIDTC *** * * * *** ** ** ** ** ** ** ** ** *	176 177 180 177
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	SDGEVYNMAIRGGNEC <mark>CLD</mark> GIDVWGSNIWVHDVEVTNKDDCVTVKSPANNILVESIYCNW SDGEVYNMAIRGGNSC <mark>GLD</mark> GIDVWGSNIWVHDVEVTNKDDCVTVKGPANNILVESIYCNW TNGEIYNMAIRGGNHCGLDGIDVWSNNIWVHDVEVTNKDDCVTVKGPSKNILIESIYCNW VNGEVYNMIIRGGNEC <mark>GLD</mark> GIDVWGTNIWIHDVEVTNKDDCVTVKNPSDHILIEDIYCNS	236 237 240 237
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	SGCAMGSLGADTDVTDIVYRNVYTWSSNQMYMIKSNGGSGTVSNVLLENFIGHGNAYSL SGCAMGSLGADTDITDILYRNVYTWSSNQMYMIKSNGGSGTVNNTLLENFIGHGNAYSL SGCAGMGSFGSDTNVSDITYRNIYTWSSNNMMLIKSNGGSGFVENVLLENFIGHGNAYSL SGCAGMGSLGADTAISNIVYNNIYTYGSNQMYMIKSNGGSGTVSDAQFNNFIGRSNAYSL	296 297 300 297
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	DIDGYWSSMTAVAGDGVQLNNITVKNWKGTEANGATRPPIRVVCSDTAPCTDLTLEDIAI DVDSYWSSMTAVDGDGVQLSNITFKNWKGTEADGAERGPIKVVCSDTAPCTDITIEDFAM DIDSYWASMSAVDGDGVQLSNITVKNWKGTEAYGAERGPVKVVCADGAPCYDITIEDFAM NINAAWPQASKASGNGVIYENLSFNNWKGTCTSTSERGPINLLCSSTAPCTNVTITDFAI ^* *** ** *** *****	356 357 360 357
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	WTESGSSELYLCRSAYGSGYCLK-DSSSHTSY-TTTSTVTAAPSGYSATTMAADLATAFG WTESGDEQTYTCESAYGDGFCLE-DSDSTTSY-TTTQTVTTAPSGYSATTMAADLTTDFG WTEEGDSQWYSCESAYGSGYCLQ-DSDDHVSYSVTTSTVSSAPSGYSATSMAADLTTDFG GTESGSTGKYVCQNAYGSGGCLKADTDSPSAY-TTTQSWSSMPTGYEASTMAQDLATPFA ** * * * * *** *** *	414 417 419 416
AspacA.rg AspniA.rg AspniB.rg Botfu.rg	LTASIPIPTIPTSFYPGLTPYSALAG 440 TTASIPIPTIPTSFYPGLTAISPLASAATTA 448 STVSIPIPTIPTSFYPGATPYSALMANSAST 450-558 VSVSIPIPTIPTSFFPGRTPVSALMANGGKS 442-572	

Fig. 3. Amino acid sequence alignment of rhamnogalacturonases. The abbreviations of enzyme sources are given in Table I. The asterisks and dots signify the identical amino acid residues and conservative substitutions, respectively. Gaps are indicated by dashes. Cysteines are highlighted in grey and signified by bold. The four conserved active-site segments are highlighted in black-and-white inversion. The vertical arrow marks the tyrosine position (not invariantly conserved) which could correspond with the invariant tyrosine of PGs (Tyr291 of *A.niger* PG II; cf. Figure 2).

with 178_NTD (*A.niger* PG II numbering), 215_DE with 201_DD, 237_SGG with 222_GHG, and 269_MIK with 256_RIK. It means that the most significant amendments in the sequences of RGs in comparison with polygalacturonases are the lack of His223 in the third region (SGG/GHG) and hydrophilic→hydrophobic substitution in the fourth region (MIK/RIK). With regard to the invariant tyrosine residue, Tyr291, present in polygalacturonases (Figure 1), this residue may have its equivalent in RGs (Tyr301; *A.aculeatus* RG numbering); however, it seems that there is no corresponding tyrosine in the RG from *Botryotinia fuckeliana* (Figure 3).

In general, the amino acid sequences of RGs are highly similar: they exhibit mutual 48.9% sequence identity and 57.1% sequence similarity. Ten cysteines were found to be conserved in the alignment of RGs (Figure 3). Based on the determined three-dimensional structure of the RG from *A.aculaetus* (Petersen *et al.*, 1997), all the four RGs analysed in the present study should be stabilized by four disulfide bridges (Cys39–Cys65, Cys217–Cys234, Cys340–Cys346 and Cys368–Cys377) and contain two free cysteine residues (Cys176 and Cys240). Furthermore, there are 13 tyrosines, 6

phenylalanines and 4 tryptophans invariantly conserved in all four RGs, Phe169, Trp200 and Trp302 being found present in the active site of the *A.aculeatus* RG (Petersen *et al.*, 1997). Taking into account the lack of the equivalent residue of the PG-active-site histidine, there are four invariant histidines (His138, His159, His170 and His207) in the sequences of RGs (Figure 3), however, it is possible that there is no histidine in the active site of RG (Pickersgill *et al.*, 1998). This is consistent with the site-directed mutagenesis study (Armand *et al.*, 2000) indicating that His223 is not a catalytic residue in the entire glycoside hydrolase family 28, but may play an indirect role in catalysis of polygalacturonases.

Endoxylogalacturonan hydrolase

The sequence of this new member of the glycoside hydrolase family 28 was determined only recently (Van der Vlugt-Bergmans *et al.*, 2000). In contrast to RGs, the XGH sequence exhibits better similarity in the four active-site segments to polygalacturonases (205_NTD, 228_DD, 250_SHG and 284_GIK; *A.tubigensis* XGH numbering). It has the active-site DD dipeptide as well as the His251 equivalent to His223



Fig. 4. Location of the functionally important residues of polygalacturonase II from *A.niger* (A) and xylogalacturonan hydrolase from *A.tubigensis* (B). The selected residues in PG (XGH): Asp180 (Asp207), Asp201 (Asp228) and Asp202 (Asp229) coloured dark grey, and His223 (His251), Lys258 (Lys286) and Tyr291 (Tyr322) coloured black. The PG structure was retrieved from the Protein Data Bank (code: 1CZF), while the structure of XGH was modelled on the SWISS-MODEL server using the PG X-ray coordinates (1CZF) as template.

of *A.niger* PG II. It also possesses the tyrosine residue corresponding with the Tyr291 present in polygalacturonases. All this can be supported by the model of the three-dimensional structure of XGH (Figure 4) constructed using the X-ray coordinates of *A.niger* PG II (van Santen *et al.*, 1999; Protein Data Bank code: 1CZF) as template.

There is a further change in the hydropathic character of the residue in position i - 2 with respect to the invariant lysine in the four segment (256_RIK in the *A.niger* PG II versus 284_GIK in the *A.tubigensis* XGH). The transition in this position from the hydrophilic residue in polygalacturonases (Arg or His) to the hydrophobic residue in RGs (Met or Leu) via the neutral side-chain of glycine, found in XGH, should be of interest.

In order to find the most closely related family 28 sequence to that of XGH the BLAST search was used (Altschul *et al.*, 1990). It was found that the sequence of XGH exhibits the highest similarity to that of EPG from *Cochliobolus carbonum*. These two sequences have 39.9% identity and 55.4% similarity (the alignment not shown). In general, the sequence of *A.tubigensis* XGH exhibits higher similarity to the sequences of fungal EPGs than to those of fungal PGs (Van der Vlugt-Bergmans *et al.*, 2000). Remarkably, the similarity is lower to the EPG from the same organism *A.tubigensis* (53.5%) than to the taxonomically more distantly related EPG from *C.carbonum* (55.4%). Despite this pronounced sequence similarity to fungal EPGs, the XGH sequence does not contain most of the conserved regions characteristic of fungal EPGs, thus indicating its enzymatic uniqueness.

All glycoside hydrolase family 28 enzymes

Based on the analysis of available amino acid sequences of PGs, EPGDs, EPGs, RGs and XGH discussed above, a set of sequences of the family 28 members representing all the individual groups was aligned (Figure 5). It is evident that despite the overall rather low sequence similarity, each representative contains its functionally important residues in the segments equivalent to the four conserved active-site segments of PGs (178_NTD, 201_DD, 222_GHG and 256_RIK) as well as at least the conservative substitution of the Tyr291. This makes from them a common family in the frame of all glycoside hydrolases (Coutinho and Henrissat, 2000). On the other hand, there are some important changes of the residues adjacent to the residues constituting the active site, especially in RGs. In fact there are only three strictly conserved residues in common that could be functionally important in the family

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Erwca2.pg Aspni2.pg Phaco.pg LycesA.pg Erwch.epg Asptu.epg Zeamal.pep AsptuA.xgh AspacA.rg	SSCTTLKADSSTATSTIQKALNNCDQGKAVRLSAGSTSVFLSGPLSLPSGVSLLIDKGVTLRAVNNAKS DSCTFTT	107 76 73 142 225 108 106 96 95
Erwca2.pg Aspni2.pg Phaco.pg LycesA.pg Erwch.epgd Asptu.epg Zeama1.pep AsptuA.xgh AspacA.rg	FENAPSSEGVUDKNGKGEDAFITAVSTTN-SGIYGPG-TIDGQGGVKLQDKKVSWWELAA-DAKVKKLKQNTPRLIQINKSKNFTLYNVS TTTFQYEEMAGPLISMSGEHITVTGASGHLINEDGARWWDGKG-TSGKKKPKFFYAHGLDSSSITGLNIKNTP KTTFAYKEWTGPLLRVKGKAITVVGGGG-TINGNGGQL	194 148 146 215 324 190 178 174 167
Erwca2.pg Aspni2.pg Phaco.pg LycesA.pg Erwch.epgd Asptu.epg Zeama1.pep AsptuA.xgh AspacA.rg	 LINSPNFHVVFSDGDGFTAWKTTIKTPSTARATDGIDPMSSKNITIAYSNIATGODNVAIKAYKGRAETRNISILHNDF LMAFSSVQANDITFTDVTINNADGDTQGGHNTDAFDVGNSVGVNIIKPWVHNQDDCLAVNSGENIWFTGGTC VQVHSIDHSGPLTLSGWNIDVSQGDKD-ALGHNTDGFDINTTDQLTIEDTVVKNQDDCLAVNSGENFLFNNLDC SKNAQQIHIKFESGTNVVASNLMINAS	273 219 219 289 424 263 252 247 234
Erwca2.pg Aspni2.pg Phaco.pg LycesA.pg Erwch.epgd Asptu.epg Zeama1.pep AsptuA.xgh AspacA.rg	GTGHG - MSIGSETMG VYNVTVDDLKMNGTTNGLRIKSDK SAAG - VVNGVRYSNVVMKNV - AKPIVIDTVMEK	344 299 303 370 505 359 334 331 308
Erwca2.pg Aspni2.pg Phaco.pg LycesA.pg Erwch.epgd Asptu.epg Zeama1.pep AsptuA.xgh AsptaA.rg	GSNV-PDWSDITFKDVTSETKGVVVLNGENAKK-PIEVTMKNVKLTSDSTWQIKNVNVKK	402 362 457 435 435 410 406 398

Fig. 5. Amino acid sequence alignment of representative members of glycoside hydrolase family 28. The abbreviations of enzyme sources are given in Table I. Erwca2.pg represents all bacterial PGs, Aspni2.pg all fungal PGs, LycesA.pg all plant PGs, Erwch.epg all bacterial EPGDs, Aspnt.epg all fungal EPGs, Zeama1.pep all plant EPGs (including pollen PGs), AspacA.rg all RGs. Phaco.pg and AsptuA.xgh are the only representatives of PGs from insects and XGHs, respectively, so that these two enzymes are also used for comparison. The asterisks signify the identical amino acid residues and gaps are indicated by dashes. Cysteines are highlighted in grey and signified by bold. The four conserved active-site segments as well as the tyrosine invariant in all PGs (cf. Figure 2) are highlighted in black-and-white inversion. However, in RGs the strictly conserved tryptophane (Trp302 of *A.aculeatus* RG) following the Tyr301 might rather be the equivalent of the tyrosine conserved in all PGs and XGH (cf. Figure 3; for details, see text).

28, i.e. Asp180, Asp201, Lys258. This reflects very probably the fact that even closely related fungal PGs from *A.niger* have different specific kinetic parameters on polygalacturonic acid and a specific mode of action (Pavenicová, 2000). Therefore, for example, the Met150 of PG II from *A.niger* located at the subsite -2 has no strictly conserved equivalents in the frame of the entire family 28 (Figure 5) although its mutation to glutamine affected catalysis (Pagès *et al.*, 2000).

With regard to the Tyr291, which seems to be invariantly conserved in all polygalacturonases and in the XGH, the alignment of four RGs (Figure 3) indicated that there is no corresponding tyrosine in the RG from *B.fuckeliana*. However, adjacent to the Tyr301 (*A.aculeatus* RG numbering) there is a tryptophan (Trp302) which is strictly conserved in all RGs (Figure 3). Moreover, the comparison of the hydrophobic cluster analysis plots of the RG sequences with those of the PG II from *A.niger* and XGH A from *A.tubigensis* (data not shown) supports that in RGs, a tryptophan (Trp302 in *A.aculeatus* RG) replaces the role of the conserved tyrosine in polygalacturonases and XGH (Figure 5).

As far as the cysteine residues are concerned there is only one cysteine, Cys45, conserved invariantly throughout the family 28 (Figure 5). Except for the bacterial PGs and EPGDs, all the members of this family could have six cysteine residues in common corresponding with three of the four disulfide bridges (Cys203–Cys219, Cys329–Cys334 and Cys353– Cys362) present in the PG II from *A.niger*.

Based on the alignment of representative members an evolutionary tree was constructed (Figure 6) showing the mutual relationships in the frame of the entire family 28. The long branches reflect the overall rather low sequence similarity among the groups of bacterial, fungal, plant and insect PGs, EPGDs and EPGs as well as RGs and XGH. However, the taxonomy is respected so that bacterial PGs and EPGDs as well as plant PGs and EPGs are on the bacterial and plant nodes, respectively, on the neighbouring branches. As was discussed above, the insect PG is most closely related to fungal PGs represented by the PG II from *A.niger* and the XGH to fungal EPGs represented by the EPG from *A.tubigensis*. The RG A from *A.aculaetus* positioned on the longest isolated



Fig. 6. Evolutionary tree of the family 28 representatives. The tree is based on the alignment shown in Figure 5. The abbreviations of enzyme sources are given in Table I and the choice of the representatives is explained in the legend to Figure 5. The branch lengths are proportional to the sequence divergence. Numbers along branches are bootstrap values (1000 replicates). In the future the RGs and XGHs may be expected to be also divided according to the taxonomy (like the PGs, EPGs and EPGDs).

branch manifests the amendments in the sequences of RGs even in the four active-site segments.

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