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Moscow, Russia

Hierarchical Classification of Glycoside Hydrolases

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Иерархическая классификация гликозил гидролаз

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Лаборатория биоинформатики

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Enzyme Classification (IUBMB)

EC 1 – Oxidoreductases
EC 2 – Transferases
- EC 2.4 – Glycosyltransferases (including transglycosidases)
  - EC 2.4.1 – **Hexosyltransferases**
    - EC 2.4.1.10 – **Levansucrase (β-fructosyltransferase)**
    - EC 2.4.1.67 – **Galactinol-raffinose galactosyltransferase**
  - EC 2.4.2 – Pentosyltransferases

EC 3 – Hydrolases
- EC 3.2 – Glycosylases (glycoside hydrolases)
  - EC 3.2.1 – **O- and S-Glycosylases**
    - EC 3.2.1.20 – **Maltase (α-glucosidase)**
    - EC 3.2.1.22 – **Melibiase (α-galactosidase)**
    - EC 3.2.1.26 – **Sucrase (invertase, β-fructofuranosidase)**
  - EC 3.2.2 – N-Glycosylases

EC 4 – Lyases
EC 5 – Isomerases
EC 6 – Ligases

Glycoside Hydrolases = EC 3.2.1.X; X=1…>200

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Progress in the Sequence Based Classification of Glycoside Hydrolases and Their Homologues

Number of proteins	Number of families	Reference
300	36	Henrissat. *Biochem. J.* 1991, 280:309-316
480	45	Henrissat & Bairoch. *Biochem. J.* 1993, 293:781-788
950	57 (17 => 5 clans)	Henrissat & Bairoch. *Biochem. J.* 1996, 316:695-696
…	62 (19 => 5 clans)	Henrissat & Davies. *Curr. Opin. Struct. Biol.* 1997, 7:637-644
2.200	70 (…)	Coutinho & Henrissat. *CAZy server*. 1998
>20.000	101 (46 => 14 clans)	Coutinho & Henrissat. *CAZy server*. 2005
~30.000	106 (46 => 14 clans)	Coutinho & Henrissat. *CAZy server*. 2006
>30.000	110 (46 => 14 clans)	Coutinho & Henrissat. *CAZy server*. 2007

CAZy = the Carbohydrate-Active enZYmes server (http://www.cazy.org/CAZY)

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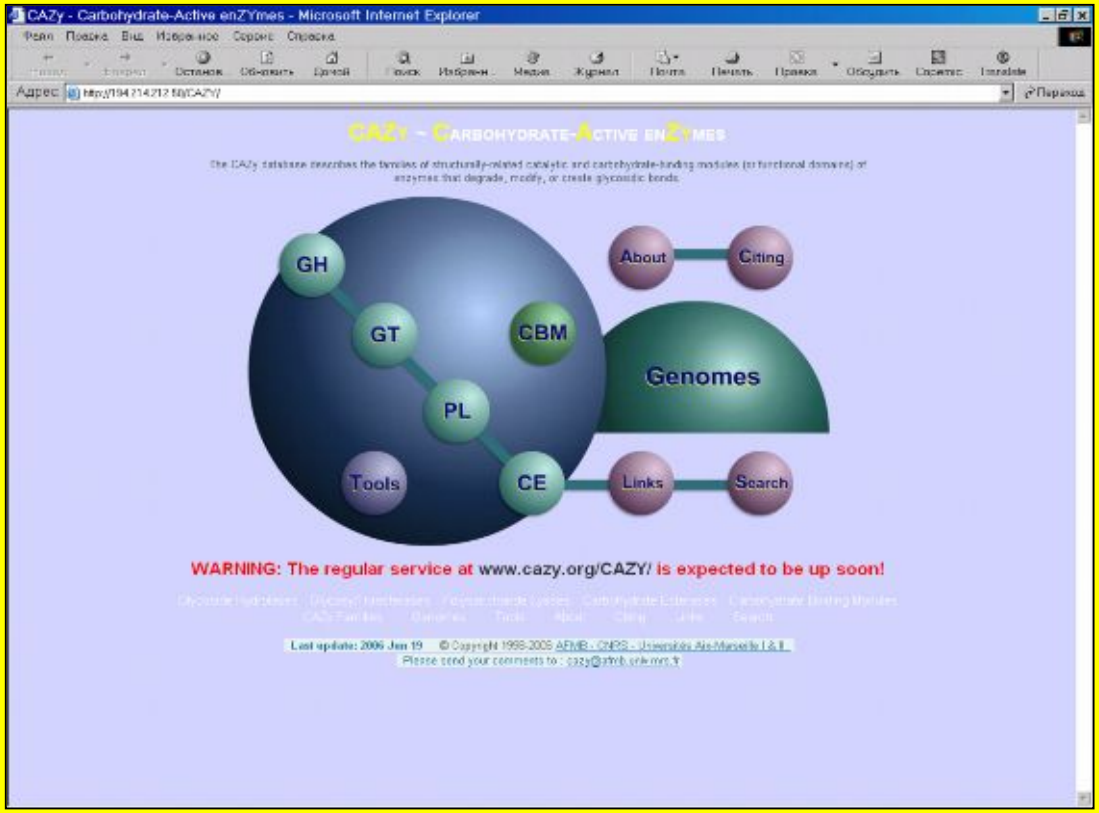
Sequence Based Classification of Glycoside Hydrolases

the Carbohydrate-Active Enzymes (CAZy) server (www.cazy.org/CAZY/)



- 30.000 protein sequences => 105 families (GH1-GH110, except GH21, GH40, GH41, GH60, and GH69)
- 46 glycoside hydrolase families => 14 clans (GH-A–GH-N)

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Clans of Glycoside Hydrolases

Clan	Families (GH)	Optical Configuration	Tertiary Structure
GH-A	**1, 2, 5, 10, 17, 26, 30, 35, 39, 42, 50, 51, 53, 59, 72, 79, 86**	**retention (equatorial orientation)**	**$(\beta/\alpha)_8$ -barrel**
GH-B	7, 16	retention (equatorial orientation)	β-jelly roll
GH-C	11, 12	retention (equatorial orientation)	β-jelly roll
GH-D	**27, 36**	**retention (axial orientation)**	**$(\beta/\alpha)_8$ -barrel**
GH-E	33, 34, 83	retention (equatorial orientation)	6-fold β-propeller
GH-F	43, 62	inversion (equatorial orientation)	5-fold β-propeller
GH-G	37, 63	inversion (axial orientation)	Not known
GH-H	**13, 70, 77**	**retention (axial orientation)**	**$(\beta/\alpha)_8$ -barrel**
GH-I	24, 46, 80	inversion (equatorial orientation)	α+β
GH-J	32, 68	retention (β-furanoside)	5-fold β-propeller
GH-K	**18, 20**	**retention (equatorial orientation)**	**$(\beta/\alpha)_8$ -barrel**
GH-L	15, 65	inversion (axial orientation)	$(\alpha/\alpha)_6$
GH-M	8, 48	inversion (equatorial orientation)	$(\alpha/\alpha)_6$
GH-N	28, 49	inversion (axial orientation)	$(\beta)_3$-solenoid

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EC 3.2.1.22

Common name: α-galactosidase

Reaction: Hydrolysis of terminal, non-reducing α-D-galactose residues in α-D-galactosides, including galactose oligosaccharides, galactomannans, and galactolipids

Molecular mechanism of hydrolyzing reaction: double displacement with overall retention of the anomeric configuration of the axial glycosidic bond

Other names: melibiase; α-D-galactosidase; α-galactosidase A; α-D-galactoside galactohydrolase; α-galactoside galactohydrolase

Systematic name: α-D-galactoside galactohydrolase

Comments: Also hydrolyses α-D-fucosides

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Glycoside hydrolase families, which include α-galactosidases

GH4 – α-galactosidase from *Escherichia coli* and bifunctional enzymes with α-galactosidase and α-glucosidase (EC 3.2.1.20) activities from *Thermotoga maritime* and *Thermotoga neapolitana*
+ 6-phospho-α-glucosidases (EC 3.2.1.122) from Eubacteria
+ 6-phospho-β-glucosidases (EC 3.2.1.86) from Eubacteria

GH27 – mainly α-galactosidases from Eukaryota (animals, plants, fungi, etc.) and some Eubacteria
+ α-N-acetylgalactosaminidases (EC 3.2.1.49) from Eukaryota (animals and fungi)
+ isomalto-dextranase (EC 3.2.1.94) from *Arthrobacter globiformis*

GH36 – mainly α-galactosidases from Eubacteria and Eukaryota (fungi and plants)
+ α-galactosyltransferases (EC 2.4.1.67 and EC 2.4.1.82) from plants
+ α-N-acetylgalactosaminidase from *Clostridium perfringens*
+ ORFs from *Sulfolobus solfataricus* and *Sulfolobus tokodaii*

clan GH-D

GH57 – α-galactosidases from *Pyrococcus furiosus* and *Thermococcus alcaliphilus*
+ α-amylases (EC 3.2.1.1), amylopullulanase (EC 3.2.1.41), and 4-α-glucanotransferases (EC 2.4.1.x) from Eubacteria and Archaea

GH110 – α-galactosidase from *Bacteroides fragilis*

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Family GH27

Subfamily 27a:

- plant α-galactosidases: *Arabidopsis*, *Carica*, *Coffea*, *Cyamopsis*, *Glycine*, *Helianthus*, *Hordeum*, *Lycopersicon*, *Oryza*, *Petunia*, *Phaseolus*, and *Senna*
- α-galactosyltransferase from *Ajuga reptans*
- animal α-galactosidases and α-N-acetylgalactosaminidases: *Anopheles*, *Apis*, *Ateles*, *Brugia*, *Caenorhabditis*, *Ciona*, *Danio*, *Drosophila*, *Gallus*, *Homo*, *Mus*, *Rattus*, *Takifugu*, and *Tetraodon*
- fungal and yeast α-galactosidases: *Aspergillus*, *Ganoderma*, *Gibberella*, *Magnaporthe*, *Mortierella*, *Penicillium*, *Phanerochaete*, *Saccharomyces*, *Schizosaccharomyces*, *Thermomyces*, *Torulaspora*, *Trichoderma*, *Ustilago*, and *Zygosaccharomyces*
- α-N-acetylgalactosaminidase from *Acremonium* sp.
- ORFs from *Dictyostelium discoideum* and *Toxoplasma gondii*
- bacterial α-galactosidases: *Cellvibrio mixtus*, *Clostridium josui*, *Pseudomonas fluorescens*, *Saccharopolyspora erythraea*, and *Streptomyces coelicolor*
- bacterial ORFs: *Bacteroides*, *Fibrobacter*, *Microbulbifer*, *Porphyromonas*, and *Streptomyces*

Subfamily 27b:

- plant ORFs: *Arabidopsis thaliana* and *Oryza sativa*
- bacterial ORFs: *Bacillus halodurans*, *Bifidobacterium longum*, *Kineococcus radiotolerans*, and *Ruminococcus albus*

Subfamily 27c:

- α-galactosidase from *Trichoderma reesei*
- ORF from *Aspergillus nidulans*

Unclassified proteins

- isomalto-dextranase from *Arthrobacter globiformis*
- bacterial ORFs: *Bacteroides thetaiotaomicron* and *Streptomyces avermitilis*

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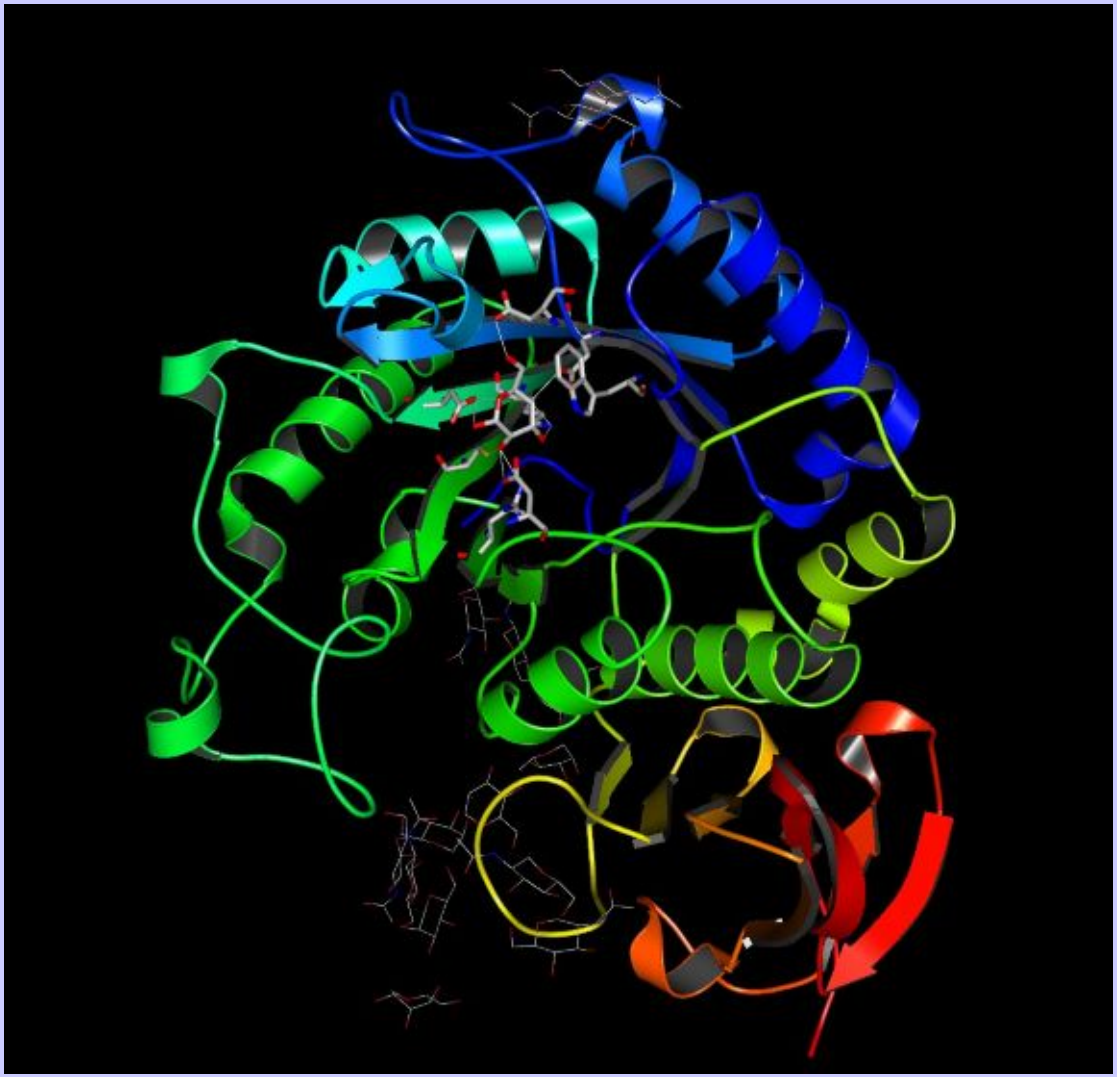
Tertiary Structure of GH27 Glycosidases

(*Trichoderma reesei* α-galactosidase)



GH27N

N-terminal catalytic $(\beta/\alpha)_8$-domain
(TIM barrel-type structure)

GH27C

C- terminal domain
(β-sandwich fold,
Greek key motif)

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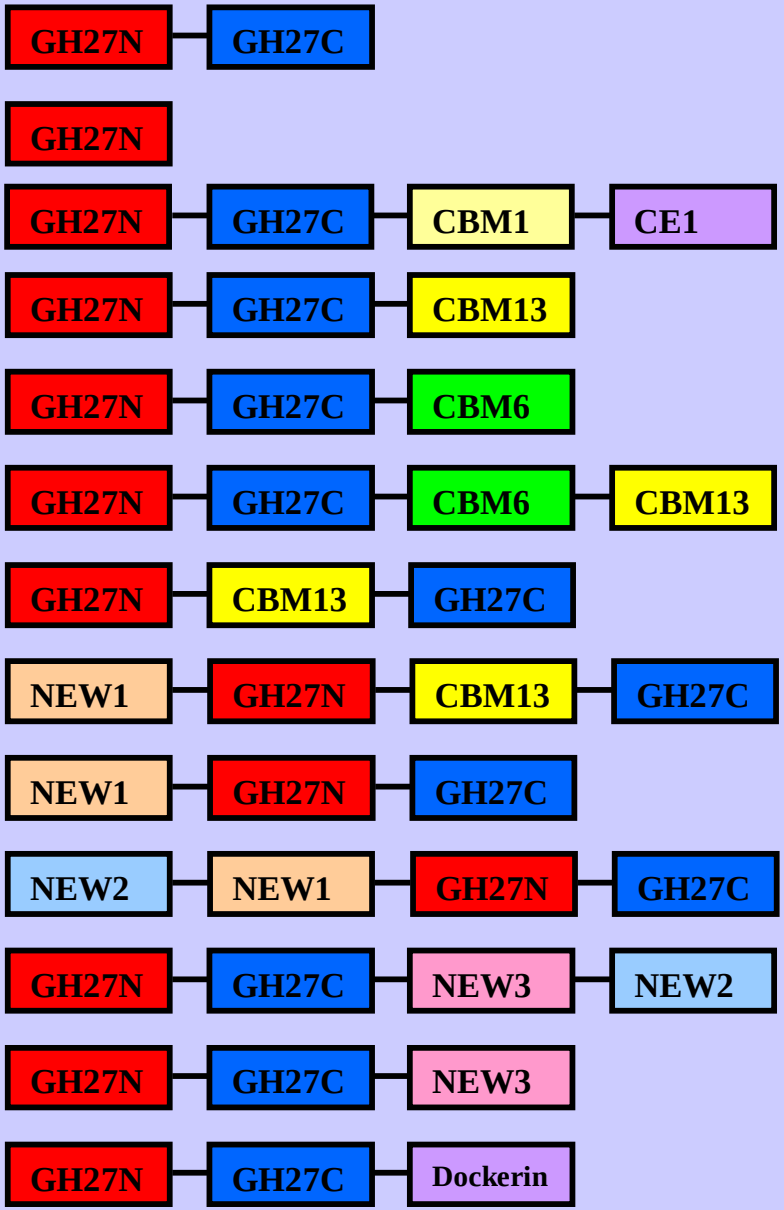
Domain structure of proteins of the GH27 family

according to Naumoff D.G. Phylogenetic analysis of α-galactosidases of the GH27 family. Molecular Biology (Engl Transl), 2004, 38(3):388-399.
PDF: http://bioinform.genetika.ru/members/Naumoff/MB2004E.pdf



GH27N	N-terminal domain of GH27 family
GH27C	C -terminal domain of GH27 family
CE1	CE1 domain of carbohydrate esterases
CBM1	Carbohydrate-binding module CBM1
CBM6	Carbohydrate-binding module CBM6
CBM13	Carbohydrate-binding module CBM13
Dockerin	Dockerin I domain
NEW1	Uncharacterized domain
NEW2	Uncharacterized domain (NPCBM)
NEW3	Uncharacterized domain

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Family GH36

Subfamily GH36A:

– bacterial α-galactosidases: *Azotobacter*, *Bacillus*, *Geobacillus*, *Bifidobacterium*, *Carnobacterium*, *Clostridium*, *Enterococcus*, *Erwinia*, *Escherichia*, *Geobacillus*, *Klebsiella*, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Novosphingobium*, *Oenococcus*, *Pediococcus*, *Ruminococcus*, *Streptococcus*, *Streptomyces*, *Thermoanaerobacter*, *Treponema*, *Vibrio*, and *Yersinia*

– fungal α-galactosidases: *Absidia*, *Aspergillus*, *Gibberella*, *Penicillium*, and *Trichoderma*

Subfamily GH36B:

– bacterial α-galactosidases: *Burkholderia*, *Leptospira*, *Streptomyces*, *Thermotoga*, *Thermus*, and *Vibrio*

Subfamily GH36C:

– plant alkaline α-galactosidases or seed imbibition proteins: *Arabidopsis*, *Brassica*, *Cicer*, *Cucumis*, *Hordeum*, *Lycopersicon*, *Malus*, *Oryza*, and *Persea*

– plant α-galactosyltransferases: *Alonsoa*, *Arabidopsis*, *Cucumis*, *Medicago*, *Oryza*, *Pisum*, *Stachys*, and *Vigna*

– fungal ORFs: *Aspergillus*, *Coccidioides*, *Cryptococcus*, *Gibberella*, *Magnaporthe*, *Neurospora*, and *Ustilago*

– ORF from *Toxoplasma gondii*

– α-galactosidase from *Bifidobacterium breve*

– bacterial ORFs: *Bifidobacterium longum*, *Bacteroides fragilis*, and *Bacteroides thetaiotaomicron*

– ORFs from *Sulfolobus solfataricus* and *Sulfolobus tokodaii*

Subfamily GH36D:

– α-N-acetylgalactosaminidase from *Clostridium perfringens*

– bacterial ORFs: *Aeromonas*, *Clostridium*, *Escherichia*, *Photorhabdus*, and *Streptococcus*

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Four conserved regions in proteins of the α-galactosidase superfamily, containing Asp residues

MEL1_YEAST	65	GYKYIILDDCWS	141	NRVDYLKYDNCY	204	WRMSGDV	258	WNDLDNL	GH27
AGAL_PHAVU	106	GYQYINIDDCWG	184	WGIDYLKYDNCE	242	WRTTGDI	274	WNDPDML	
NAGA_HUMAN	71	GYTYLNIDDCWI	148	WKVDMLKLDGCF	212	WRNYDDI	248	WNDPDML	
AGL1_BIFLO	48	GWDTLVIDIDWY	178	WGLDFLKVDDMQ	240	WRISDDL	272	WADADMV	
AGL3_HYPJE	234	GYDLCSLDSGWQ	339	WGVDMLKLDFLT	407	MRTDQDL	451	YPDMDAL	
IMD_ARTGO	100	GYDIACTD-GWI	219	LGVPYLRIDFLS	290	VRINADA	338	ILDGDFM	
AGAL_LACPL	367	GIEMFVLDDGWF	478	VPIDYIKWDMNR	551	QSWPSDN	584	GTSPDEL	GH36A
AGL2_HYPJE	375	GIKLFVLDDGWF	496	ASISYVKWDNNR	561	HIWTSDD	594	SAVPNGQ	
AGL7_ASPFU	413	GAGYFVIDAGWY	524	YGVGYFKFDYNI	595	LQSSSDQ	626	WAYPQPA	
AGAL_THEMA	213	PFEVFQIDDAYE	319	MGYRYFKIDFLF	382	MRIGPDT	423	LNDPDCL	GH36B
AGAL_VIBPA	227	DLEWVLLDDGYQ	341	WGVELFKLDANY	404	MRVSDDV	436	QIDPDCA	
AGL3_STRCO	329	GLKWAVLDDGWQ	438	WGYEGLKIDGQH	512	QYPSSDP	540	SYSGDHV	
AGAL_SULSO	256	RLNWVIIDDGWQ	360	RDFDLVKVDNQW	421	MRNSIDY	454	YPDYDMF	GH36C
AGAL_BIFBR	339	PVSWVLIDDGWS	458	AGVDFVKVDSQS	523	TRTSDDF	556	HCDWDMF	
GALT_VIGAN	251	APRFVVIDDGWQ	476	TGVTGVKIDVIH	544	GRVGDDF	585	QPDWDMF	
NAGA_CLOPE	253	TLDAFVVDDGWA	355	YDISYWKIDGML	429	IQTSQDV		...	GH36D
ORF1_CLOPE	515	PIDSYVVDDGWH	634	FDIDYWKLDGFA	715	IQNSQDT		...	
ORF1_ECOLI	297	ALDAFLLDDGWD	393	EHITSFKLDGMG	458	WRQGDDI		...	
ORF2_CLOPE	112	PKGIIMIDDGWS	220	YGVDGFKFDAGD	286	HSWEYNG	344	ALMPMMQ	GH31
XYLQ_LACPE	297	PLDVFHFDCFWQ	406	MGVDSFKTDFGE	474	IQYTGAA	534	LLSSHSR	
XYLS_SULSO	250	PLDVIVLDWRYW	345	LGIDAYWLDASE	423	ISWSGDV	483	TFCPILR	
LYAG_HUMAN	397	PLDVQWNDLDYM	510	VPFDGMWIDMNE	611	GHWTGDV	666	AFYPFMR	

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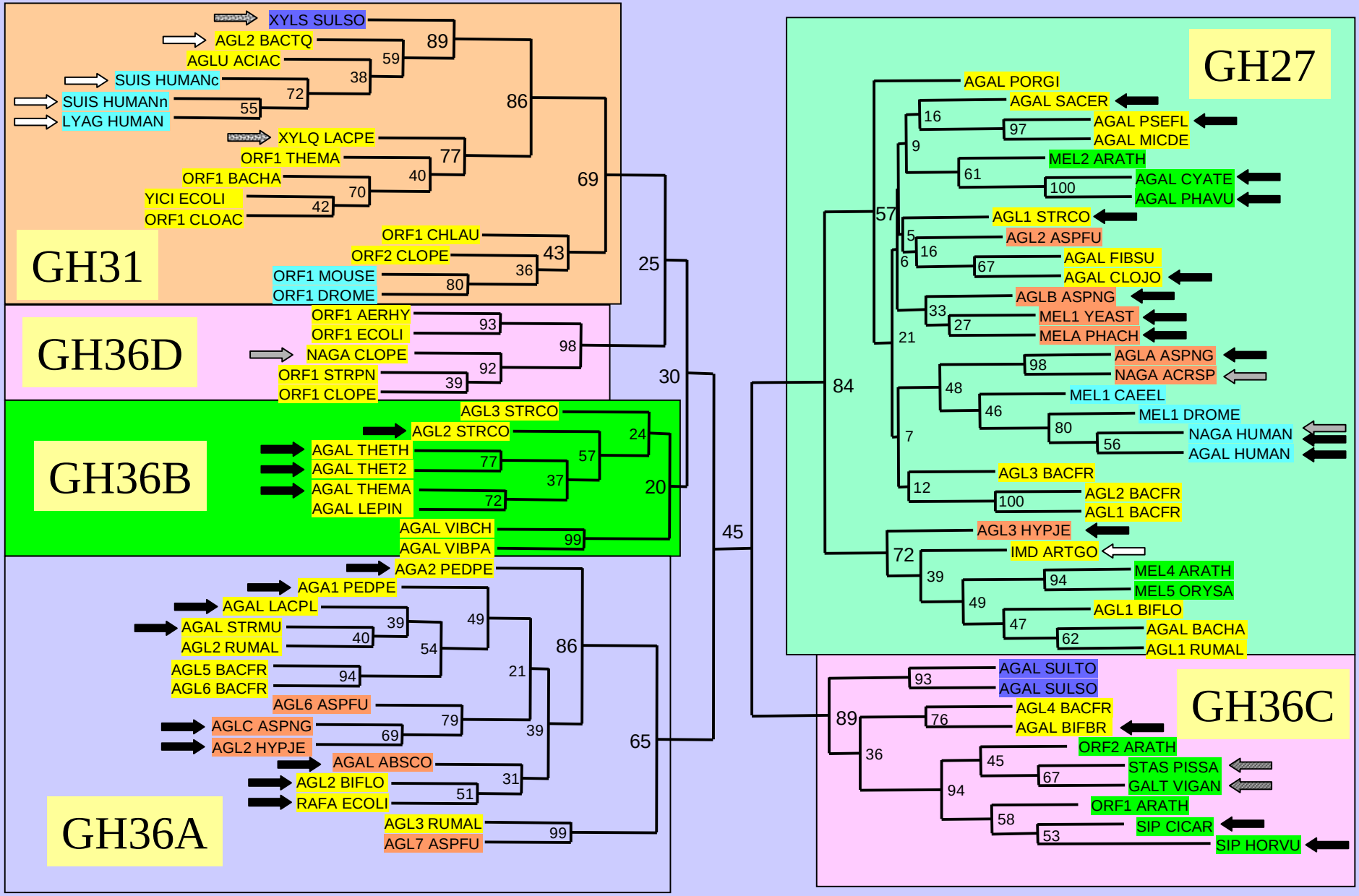
The neighbor-joining phylogenetic tree of the α-galactosidase superfamily



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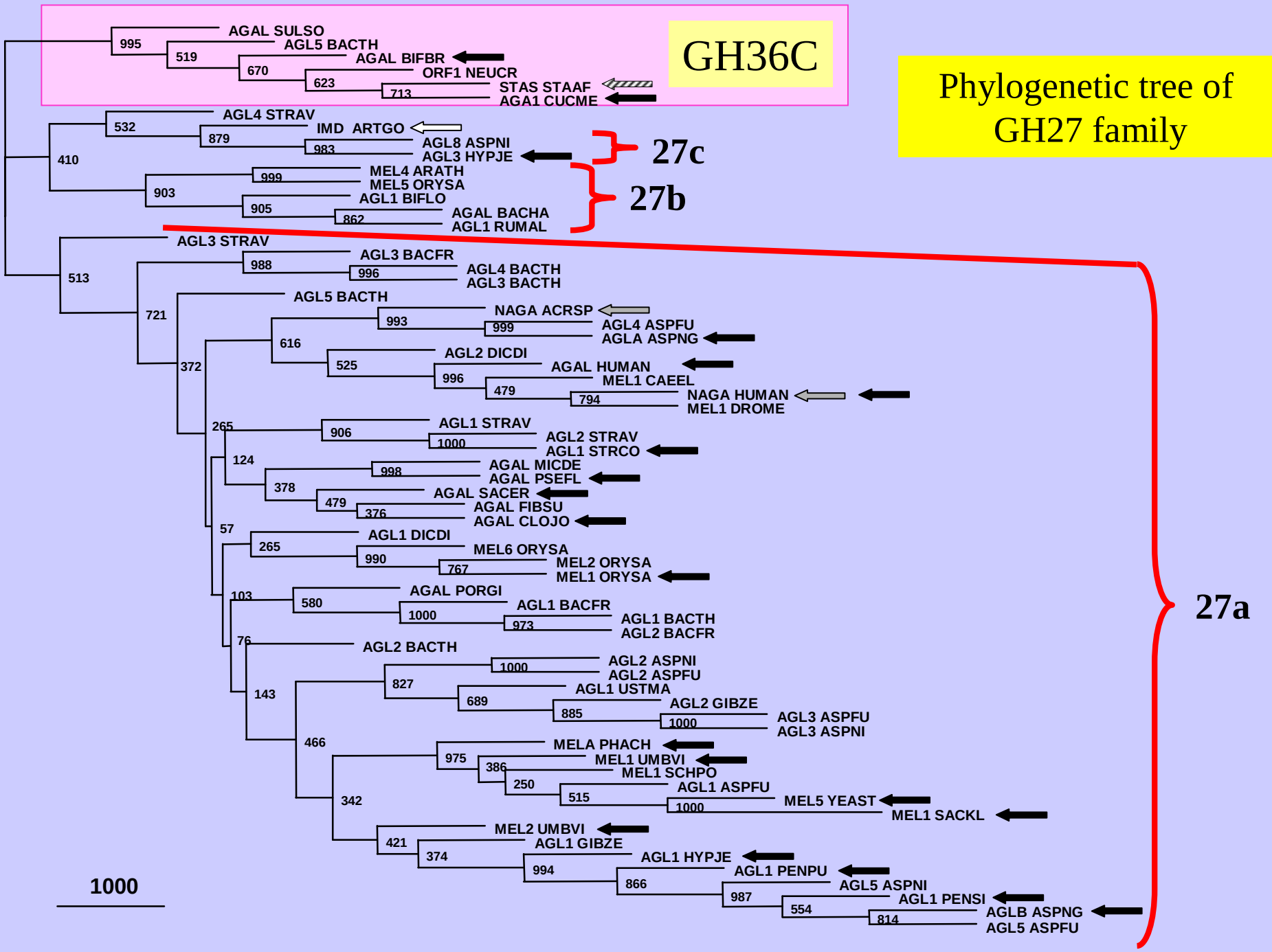

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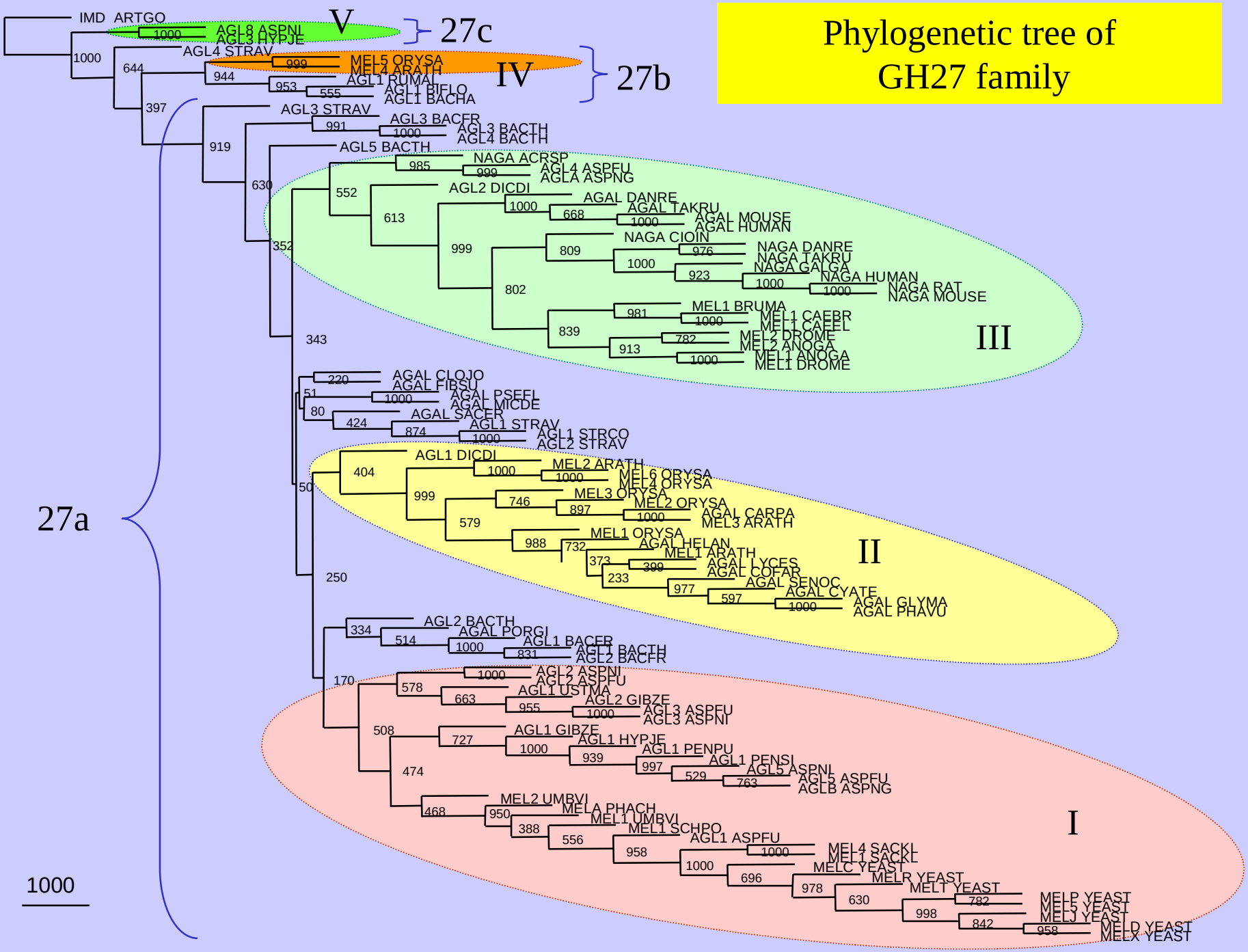
Phylogenetic tree of GH27 family



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Families of the α-galactosidase superfamily and family GH97

Family	GH27	GH31	GH36A	GH36B	GH36C	GH36D	GH97
Clan	GH-D	None	GH-D	GH-D	GH-D	GH-D	None
COG/KOG	KOG2366	COG1501 KOG1065	COG3345	COG3345	None	None	None
Known enzymatic activities	EC 2.4.1.x EC 3.2.1.22 EC 3.2.1.49 EC 3.2.1.94	EC 2.4.1.x EC 3.2.1.3 EC 3.2.1.10 EC 3.2.1.20 EC 3.2.1.48 EC 4.2.2.13	EC 3.2.1.22	EC 3.2.1.22	EC 2.4.1.67 EC 2.4.1.82 EC 3.2.1.22	EC 3.2.1.49	EC 3.2.1.20
Molecular mechanism	Retaining	Retaining	Retaining	Not known	Not known	Not known	Not known
Origin	**Eukaryota:** Alveolata Fungi Metazoa Mycetozoa Viridiplantae **Eubacteria:** Acidobacteria Actinobacteria Bacteroidetes Fibrobacteres Firmicutes Proteobacteria	**Eukaryota:** Alveolata Entamoebidae Euglenozoa Fungi Metazoa Mycetozoa Rhodophyta Viridiplantae **Eubacteria:** Acidobacteria Actinobacteria Bacteroidetes Cyanobacteria Firmicutes Proteobacteria Spirochaetes Thermotogales Thermus **Archaea:** Crenarchaeota Euryarchaeota	**Eukaryota:** Fungi **Eubacteria:** Actinobacteria Bacteroidetes Firmicutes Proteobacteria Spirochaetes	**Eubacteria:** Acidobacteria Actinobacteria Deinococcus Proteobacteria Spirochaetes Thermotogales Thermus	**Eukaryota:** Alveolata Fungi Viridiplantae **Eubacteria:** Actinobacteria Bacteroidetes **Archaea:** Crenarchaeota	**Eubacteria:** Firmicutes Proteobacteria	**Eukaryota:** Metazoa (?) **Eubacteria:** Acidobacteria Actinobacteria Bacteroidetes Firmicutes Planctomycetes Proteobacteria **Archaea:** Euryarchaeota

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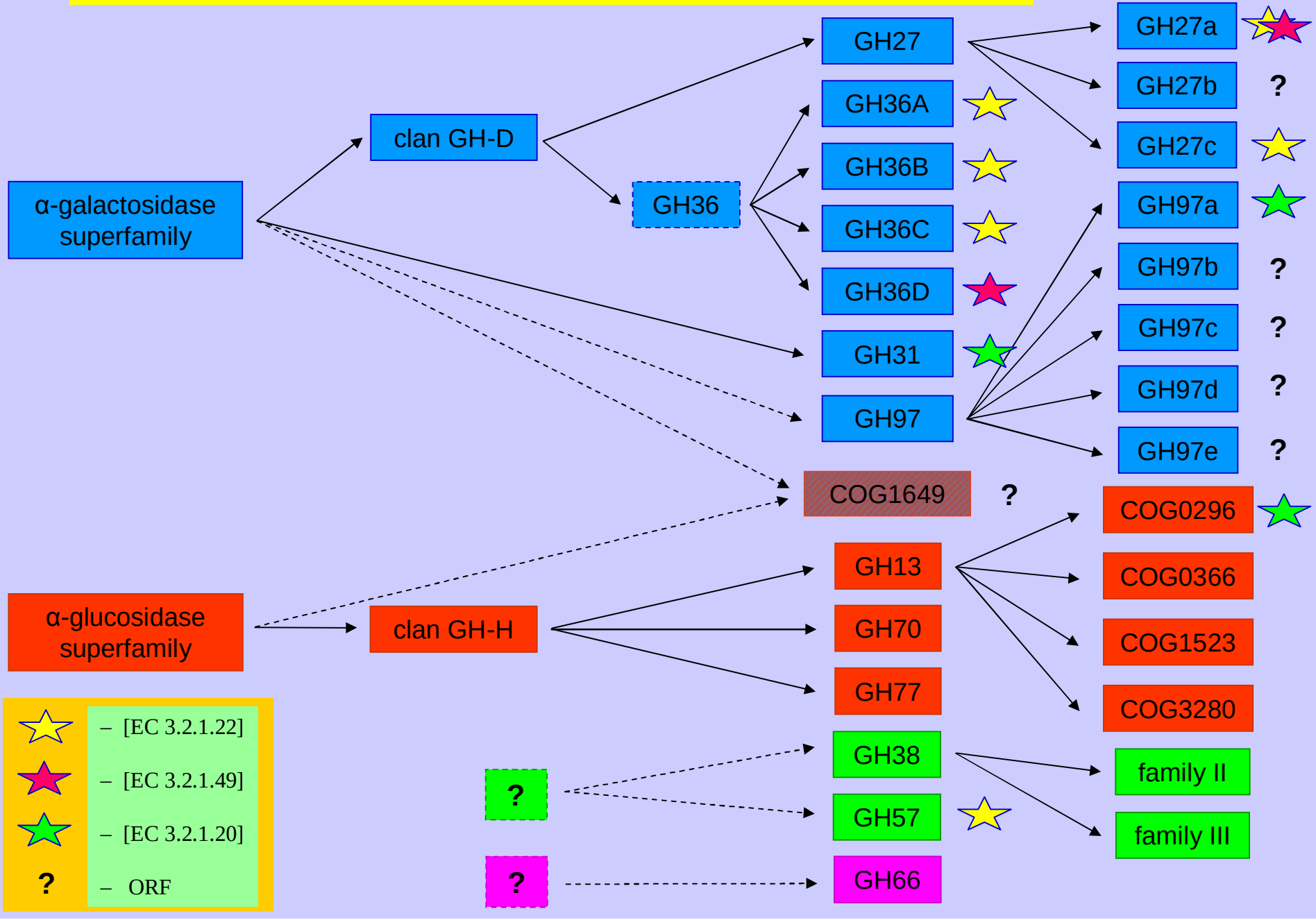
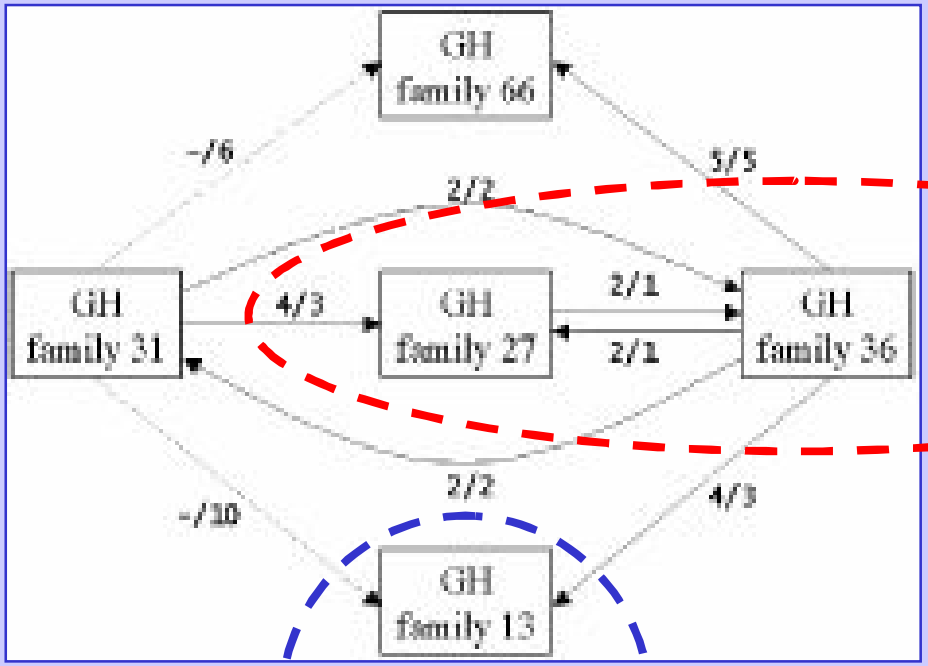
$(\beta/\alpha)_8$-barrel-type retaining α-D-glycopyranosidase families



Rigden DJ. Iterative database searches demonstrate that glycoside hydrolase families 27, 31, 36, and 66 share a common evolutionary origin with family 13. *FEBS Lett.* 2002, 523(1-3):17-22.



GH-D

GH-H

clans

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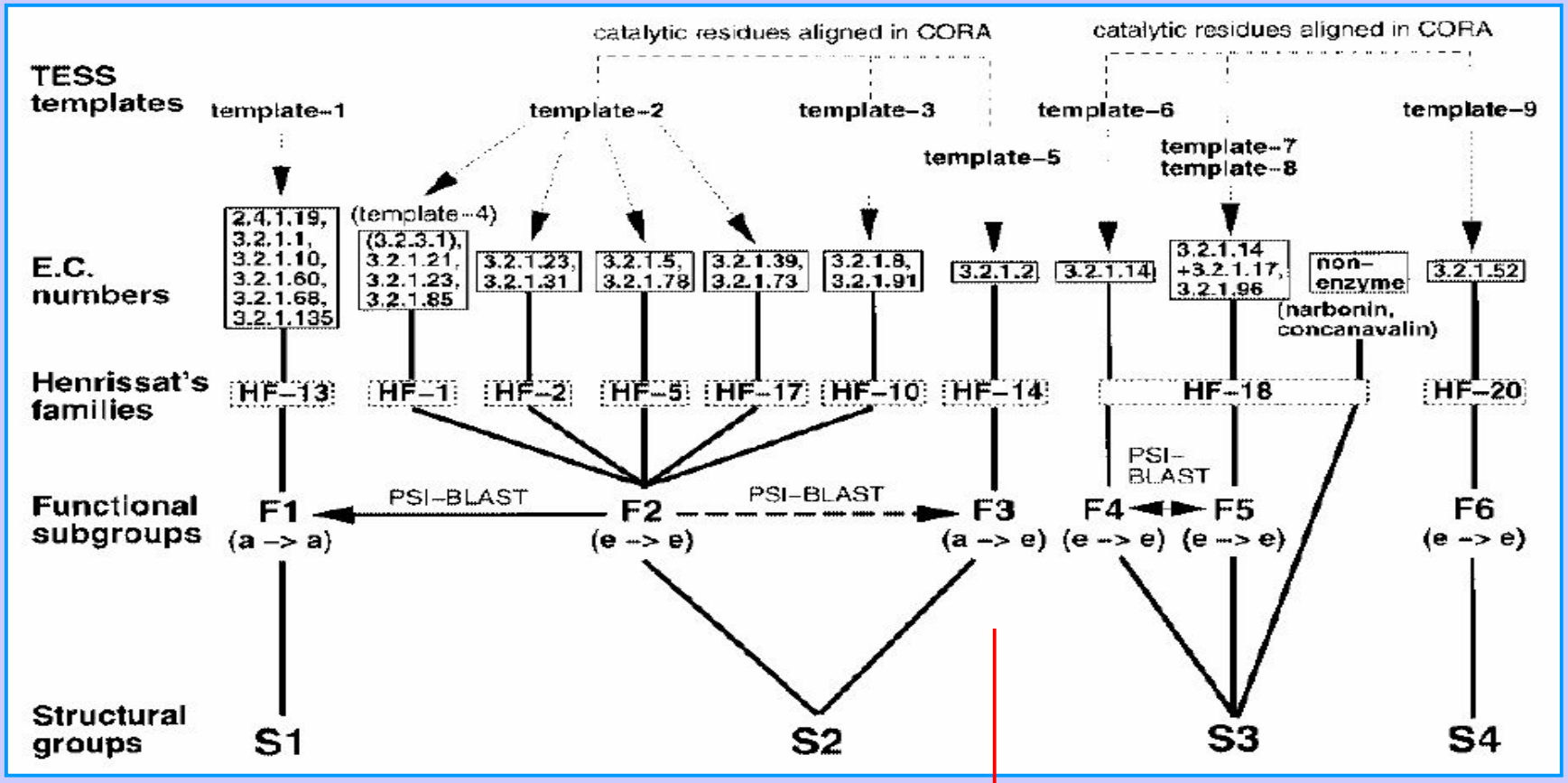
Nagano N, Porter CT, Thornton JM. The $(\beta/\alpha)_8$ glycosidases: sequence and structure analyses suggest distant evolutionary relationships. Protein Eng. 2001, 14(11):845-855.



clans: GH-H GH-A ? GH-K

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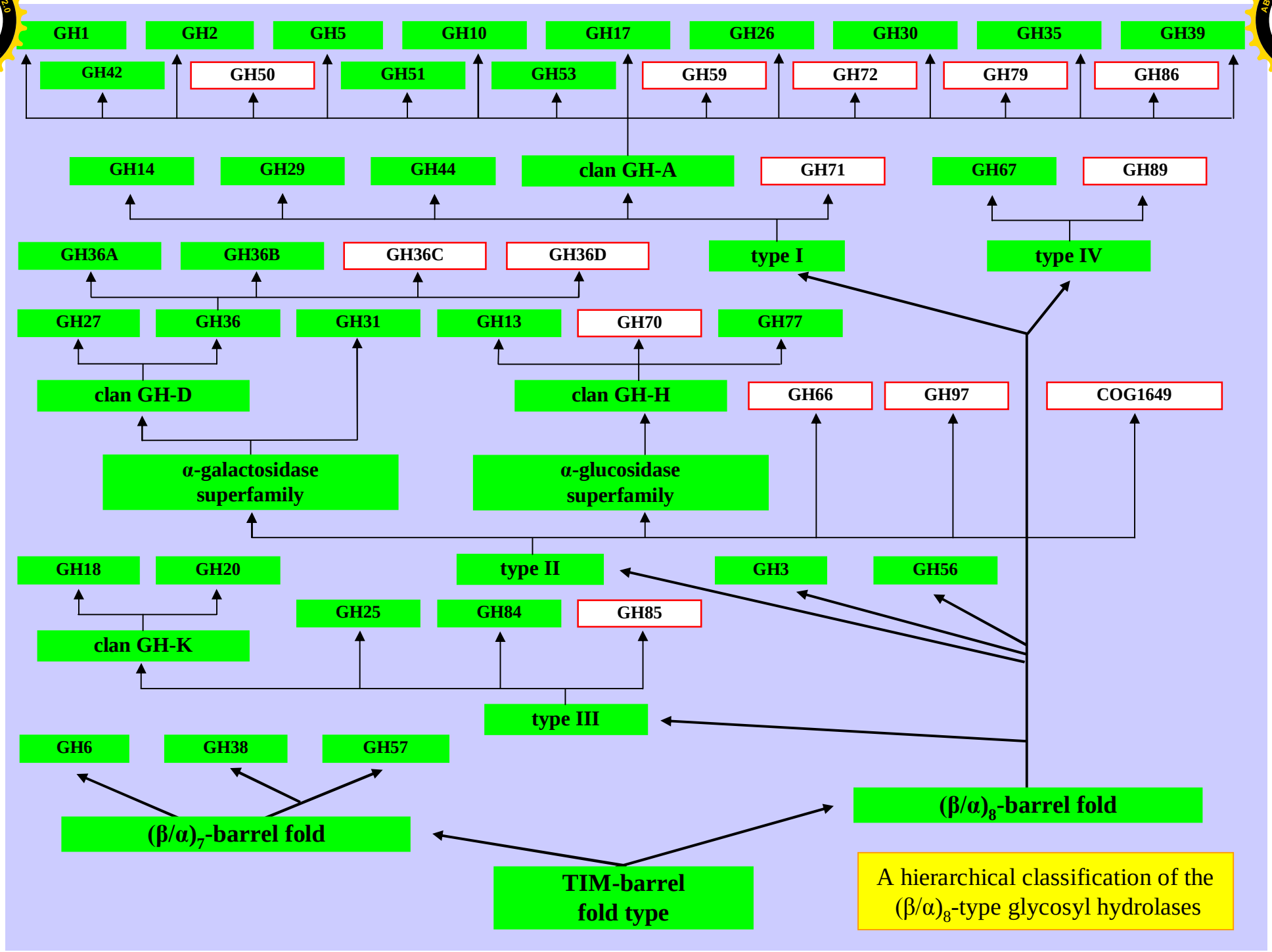
GH1
GH2
GH5
GH10
GH17
GH26
GH30
GH35
GH39
GH42
GH50
GH51
GH53
GH59
GH72
GH79
GH86
GH14
GH29
GH44
clan GH-A
GH71
GH67
GH89
GH36A
GH36B
GH36C
GH36D
type I
type IV
GH27
GH36
GH31
GH13
GH70
GH77
clan GH-D
clan GH-H
GH66
GH97
COG1649
α-galactosidase superfamily
α-glucosidase superfamily
GH18
GH20
type II
GH3
GH56
GH25
GH84
GH85
clan GH-K
type III
GH6
GH38
GH57
(β/α)8-barrel fold
(β/α)7-barrel fold
TIM-barrel fold type
A hierarchical classification of the (β/α)8-type glycosyl hydrolases

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Clans of Glycoside Hydrolases

Clan	Families (GH)	Optical Configuration	Tertiary Structure
GH-A	1, 2, 5, 10, 17, 26, 30, 35, 39, 42, 50, 51, 53, 59, 72, 79, 86	retention (equatorial orientation)	$(\beta/\alpha)_8$ -barrel
GH-B	7, 16	retention (equatorial orientation)	β-jelly roll
GH-C	11, 12	retention (equatorial orientation)	β-jelly roll
GH-D	27, 36	retention (axial orientation)	$(\beta/\alpha)_8$ -barrel
GH-E	33, 34, 83	retention (equatorial orientation)	6-fold β-propeller
GH-F	43, 62	inversion (equatorial orientation)	5-fold β-propeller
GH-G	37, 63	inversion (axial orientation)	Not known
GH-H	13, 70, 77	retention (axial orientation)	$(\beta/\alpha)_8$ -barrel
GH-I	24, 46, 80	inversion (equatorial orientation)	α+β
GH-J	32, 68	retention (β-furanoside)	5-fold β-propeller
GH-K	18, 20	retention (equatorial orientation)	$(\beta/\alpha)_8$ -barrel
GH-L	15, 65	inversion (axial orientation)	$(\alpha/\alpha)_6$
GH-M	8, 48	inversion (equatorial orientation)	$(\alpha/\alpha)_6$
GH-N	28, 49	inversion (axial orientation)	$(\beta)_3$-solenoid

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β-fructosidase (furanosidase) superfamily

Family	GH32	GH43	GH62	GH68	GHLP
Clan	GH-J	GH-F	GH-F	GH-J	Not known
COG / KOG	COG1621 / KOG0228	COG3507	None	None	COG2152
Known enzymatic activities	EC 2.4.1.99 EC 2.4.1.100 EC 2.4.1.x EC 3.2.1.7 EC 3.2.1.26 EC 3.2.1.65 EC 3.2.1.80	EC 3.2.1.8 EC 3.2.1.37 EC 3.2.1.55 EC 3.2.1.99	EC 3.2.1.55	EC 2.4.1.x EC 2.4.1.9 EC 2.4.1.10 EC 3.2.1.26	Not known
Molecular mechanism	Retaining	Inverting	Not known	Retaining	Not known
Origin	**Eukaryota:** Euglenozoa Fungi Parabasalidea Viridiplantae **Eubacteria:** Actinobacteria Bacteroidetes Chloroflexi Firmicutes Fusobacteria Proteobacteria Thermotogales **Archaea:** Euryarchaeota	**Eukaryota:** Fungi Viridiplantae **Eubacteria:** Actinobacteria Bacteroidetes Firmicutes Proteobacteria Thermotogales	**Eukaryota:** Fungi **Eubacteria:** Actinobacteria Proteobacteria	**Eubacteria:** Actinobacteria Firmicutes Proteobacteria **Archaea:** Euryarchaeota	**Eukaryota:** Fungi Metazoa Viridiplantae **Eubacteria:** Actinobacteria Aquificales Cyanobacteria Firmicutes Proteobacteria Thermotogales **Archaea:** Crenarchaeota Euryarchaeota

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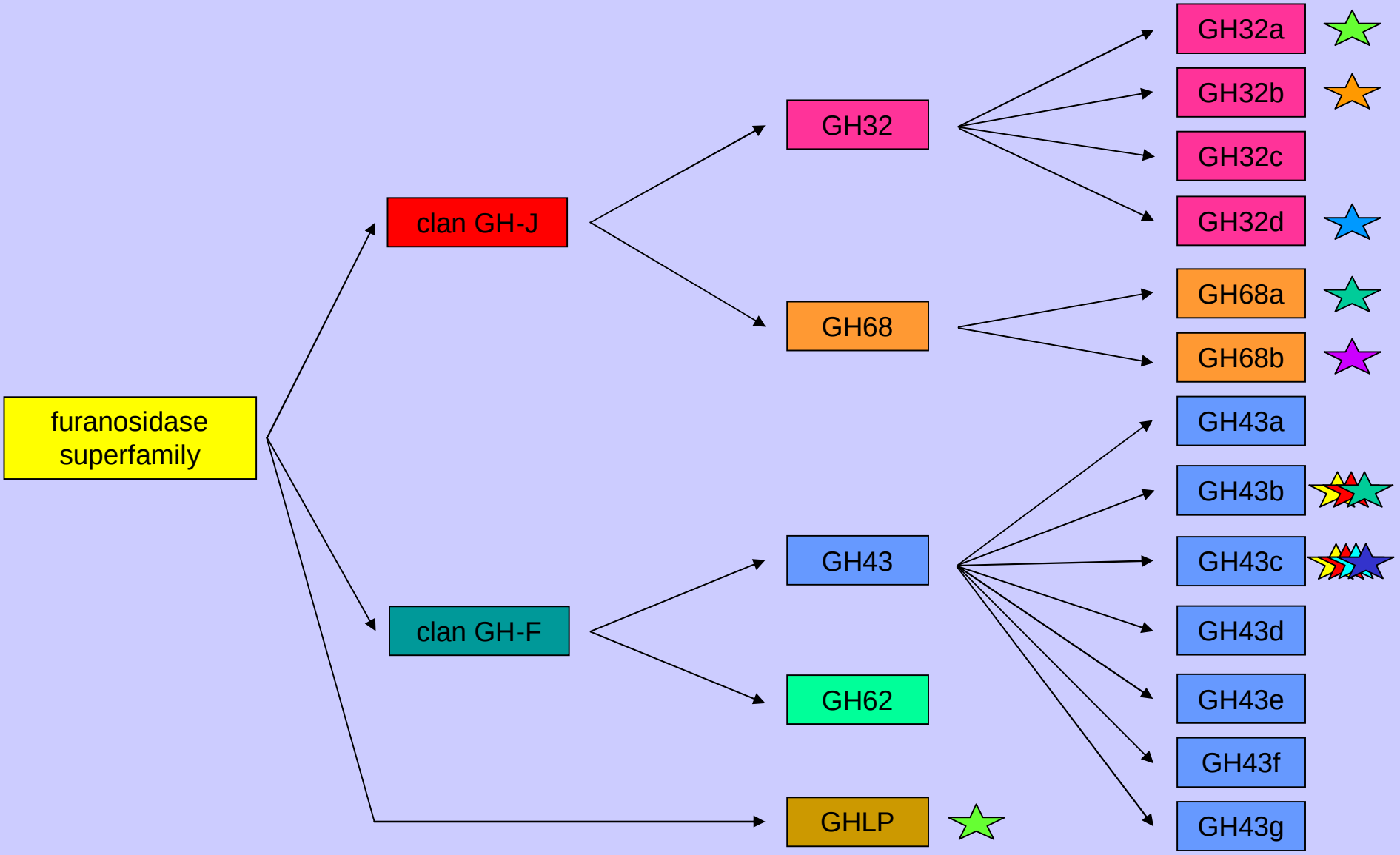
A hierarchical structure of the β-fructosidase (furanosidase) superfamily



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Clans of Glycoside Hydrolases

Clan	Families (GH)	Optical Configuration	Tertiary Structure
GH-A	1, 2, 5, 10, 17, 26, 30, 35, 39, 42, 50, 51, 53, 59, 72, 79, 86	retention (equatorial orientation)	$(\beta/\alpha)_8$ -barrel
GH-B	7, 16	retention (equatorial orientation)	β-jelly roll
GH-C	11, 12	retention (equatorial orientation)	β-jelly roll
GH-D	27, 36	retention (axial orientation)	$(\beta/\alpha)_8$ -barrel
GH-E	33, 34, 83	retention (equatorial orientation)	6-fold β-propeller
GH-F	43, 62	inversion (equatorial orientation)	5-fold β-propeller
GH-G	37, 63	inversion (axial orientation)	Not known
GH-H	13, 70, 77	retention (axial orientation)	$(\beta/\alpha)_8$ -barrel
GH-I	24, 46, 80	inversion (equatorial orientation)	α+β
GH-J	32, 68	retention (β-furanoside)	5-fold β-propeller
GH-K	18, 20	retention (equatorial orientation)	$(\beta/\alpha)_8$ -barrel
GH-L	15, 65	inversion (axial orientation)	$(\alpha/\alpha)_6$
GH-M	8, 48	inversion (equatorial orientation)	$(\alpha/\alpha)_6$
GH-N	28, 49	inversion (axial orientation)	$(\beta)_3$-solenoid

Strohmeier et al. (2004)

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