COSMIC
Catalogue Of Somatic Mutations In Cancer

CANCER GENOMICS CONSORTIUM

Educating for Best Practices in Clinical Cancer Genomics

COSMIC - Catalogue of Somatic Mutations in Cancer

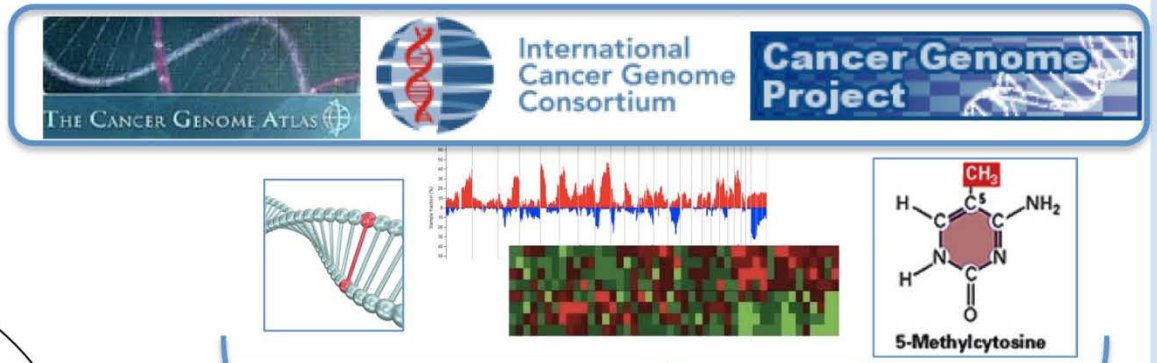
http://cancer.sanger.ac.uk/cosmic

https://academic.oup.com/nar/article-lookup/doi/10.1093/nar/gkw1121

The COSMIC Project

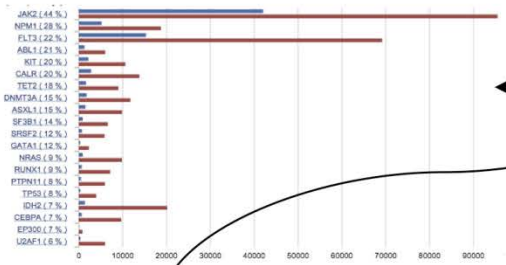
Expert knowledge curation

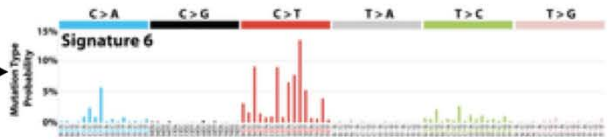
Large-scale cancer genomics

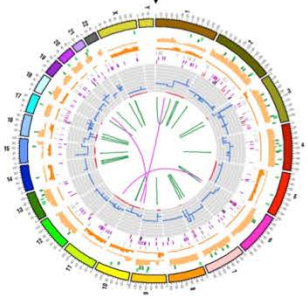


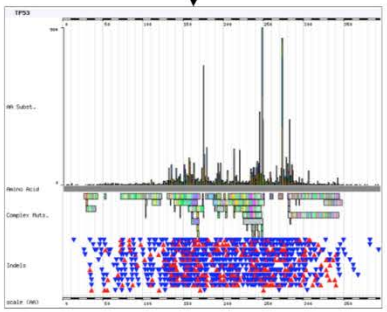
COSMIC

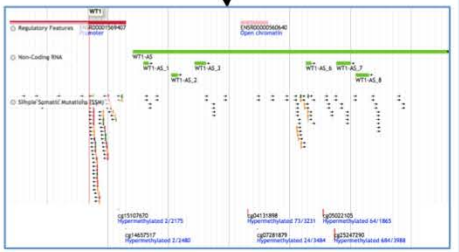
Curate, Integrate, Combine











http://cancer.sanger.ac.uk/

Data In

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Large-scale systematic screens

ICGC/TCGA/CGP

Publication datasheets

QC (data input format, details & noise)

Data Extraction

GRCh37 co-ords & allele seqs

Sample Details

QC (standardise)

ATRAC

Genic annotation (HGVS syntax)

QC (sequence and annotation checks)

Detailed genic analyses

QC *(reject ~30%)*

Deep genic data

Broad genomic data

Standardisation

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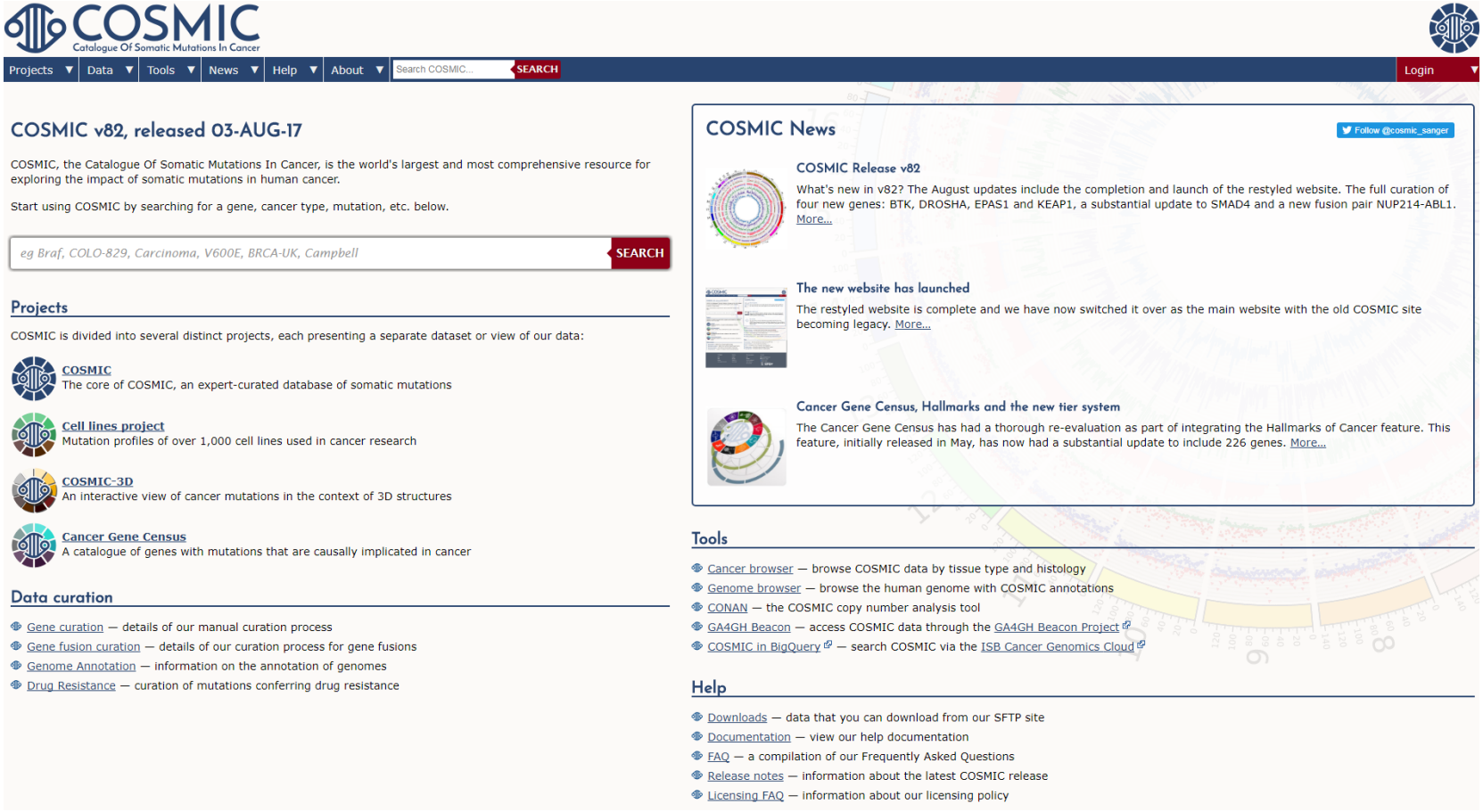
CONSORTIUM

Educating for best practices in clini cancer genomics



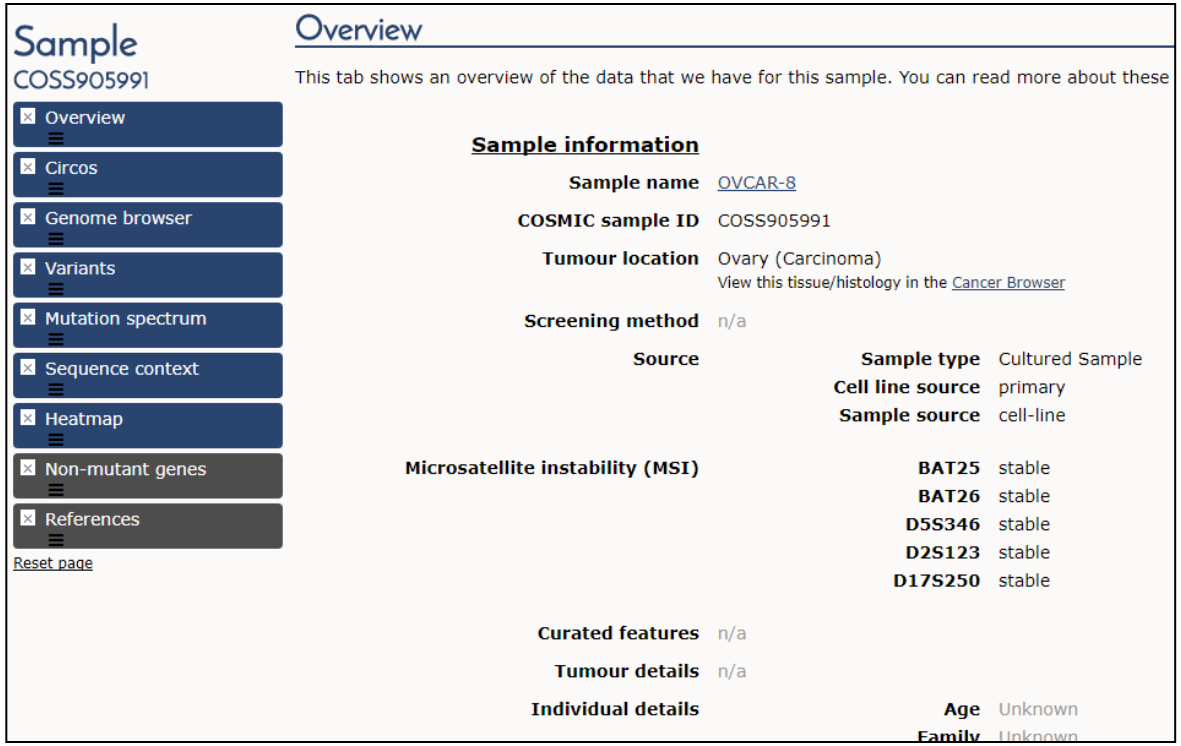
- Search for Disease, Gene, Variant, Sample, Study in either search bar
- Much information is open to public, but some features require a subscription/login.
- News window in upper right.
- Tools – Cancer Browser
- Data Curation information and details
- Release Notes – inform of new additions/advancements to COSMIC

***This is no longer the "Beta" version as of 8/1/17.

Select Data Source - COSMIC vs. Cell Lines

- Cell Lines Project and COSMIC house different data.
- To select a cell line to look into, look at the Cell Line Browser, or NCI-60 Browser if applicable

Cell Lines Data



- Once you select a cell line to view, sample page opens.
- Menu on left – click on any item in menu to navigate to that item or scroll to desired information.
  - Overview– cell line information: sample type, demographics, institute, microsatellite stability, STR Profile, Sequence stats, and Downloadable files
  - Mutation Spectrum tab – information can be matched to mutation profiles through COSMIC Home Page
  - Sequence Context tab – bases flanking mutations
  - Heatmap tab – shows frequent mutations

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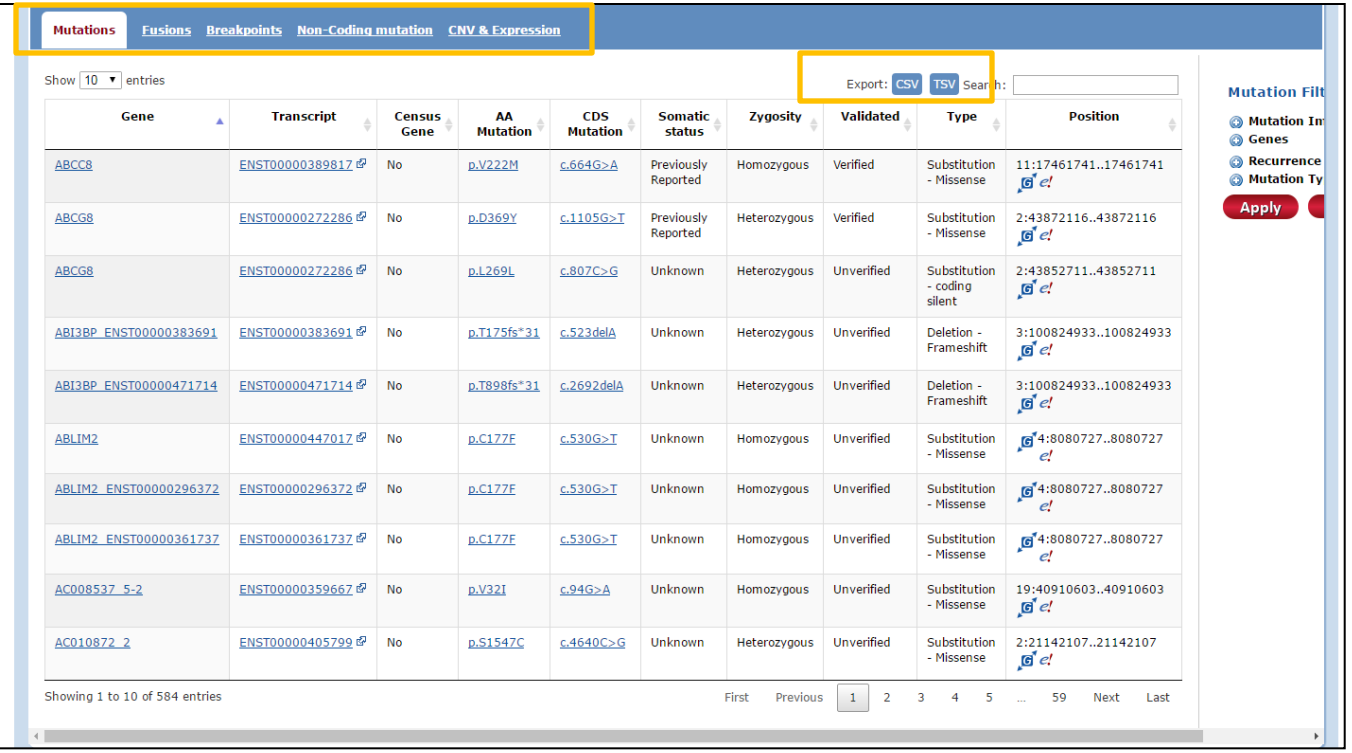
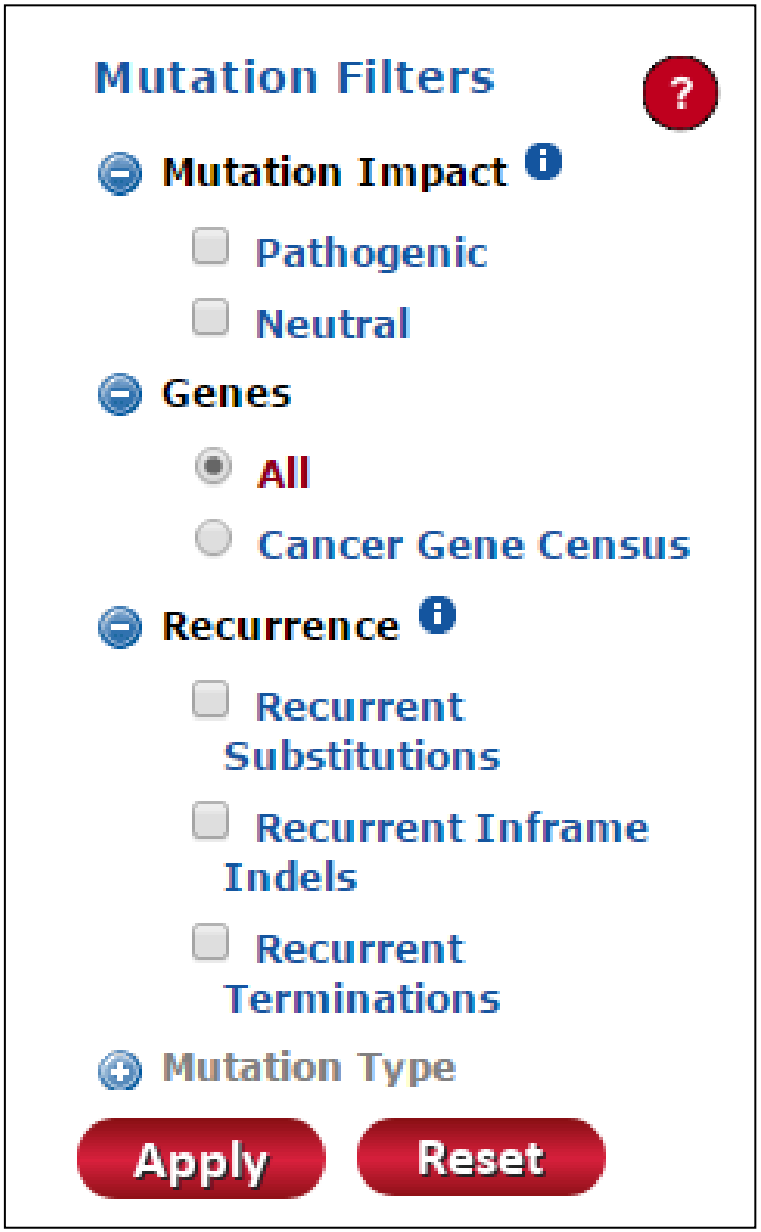
Cell Lines Variants tab



- Can view by variant type – tabs in window
  - Breakpoints: search by hg38 coordinates
- Exportable in .TSV and .CSV
- Click on Gene name to go to gene page
- Click on mutation nomenclature to go to mutation page – can determine mutation recurrence in cell lines dataset and pathway involvement

Mutation Filters

- Scroll right to see expandable mutation filters.



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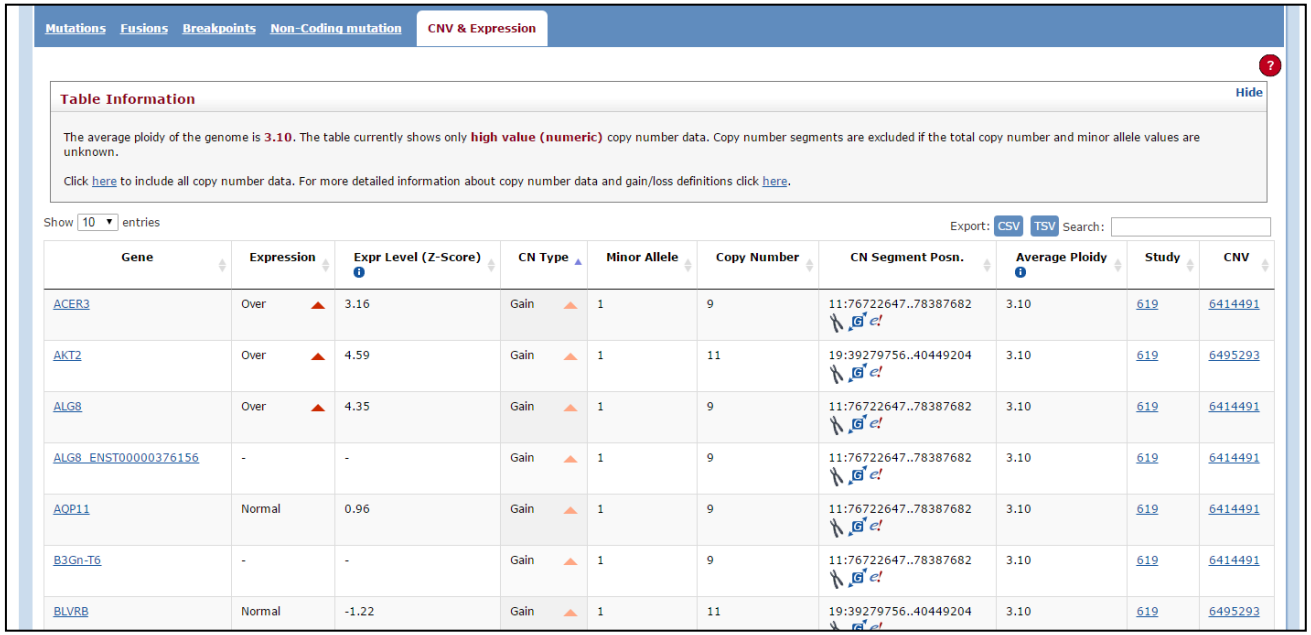
CNV and Expression Data

- Under/over expression
  - Z-Score
- CN Type
  - Minor allele
  - Copy number observed
  - Hg38 coordinates
- Average Ploidy



Mutations | Fusions | Breakpoints | Non-Coding mutation | CNV & Expression

Table Information Hide

The average ploidy of the genome is **3.10**. The table currently shows only **high value (numeric)** copy number data. Copy number segments are excluded if the total copy number and minor allele values are unknown.

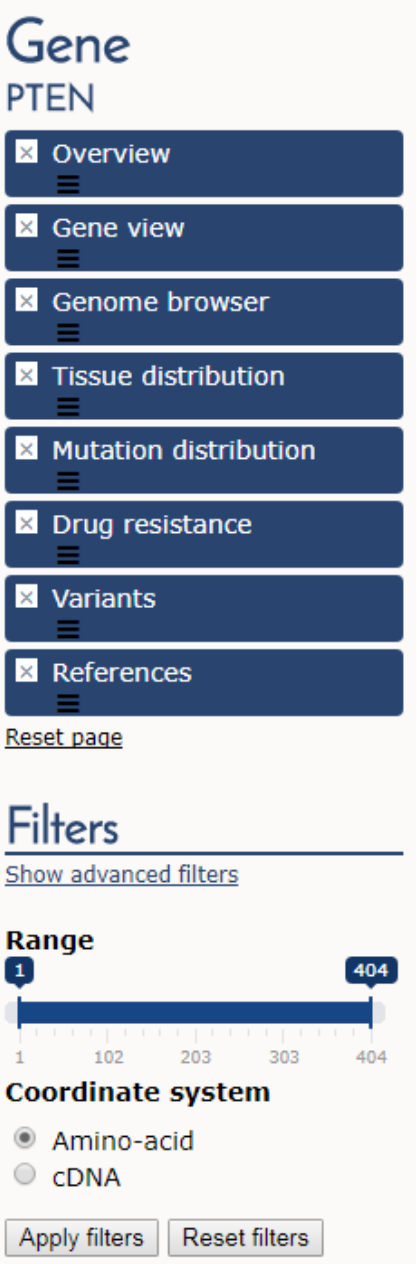
Click here to include all copy number data. For more detailed information about copy number data and gain/loss definitions click here.

Show 10 entries Export: CSV TSV Search:

Gene	Expression	Expr Level (Z-Score)	CN Type	Minor Allele	Copy Number	CN Segment Posn.	Average Ploidy	Study	CNV
ACER3	Over	3.16	Gain	1	9	11:76722647..78387682	3.10	619	6414491
AKT2	Over	4.59	Gain	1	11	19:39279756..40449204	3.10	619	6495293
ALG8	Over	4.35	Gain	1	9	11:76722647..78387682	3.10	619	6414491
ALG8_ENST00000376156	-	-	Gain	1	9	11:76722647..78387682	3.10	619	6414491
AQP11	Normal	0.96	Gain	1	9	11:76722647..78387682	3.10	619	6414491
B3Gn-T6	-	-	Gain	1	9	11:76722647..78387682	3.10	619	6414491
BLVRB	Normal	-1.22	Gain	1	11	19:39279756..40449204	3.10	619	6495293

Searching in COSMIC

- Search by disease type – brings you to Cancer Browser – see slides 24-30
- Search by gene – brings you to search results page that can link to gene/mutation overview (same format as Cell Lines Project)
- Search by mutation – bring you to mutation overview page (same format as Cell Lines Project)
- All data are derived directly from a cited data source
  - Usually a PubMed ID



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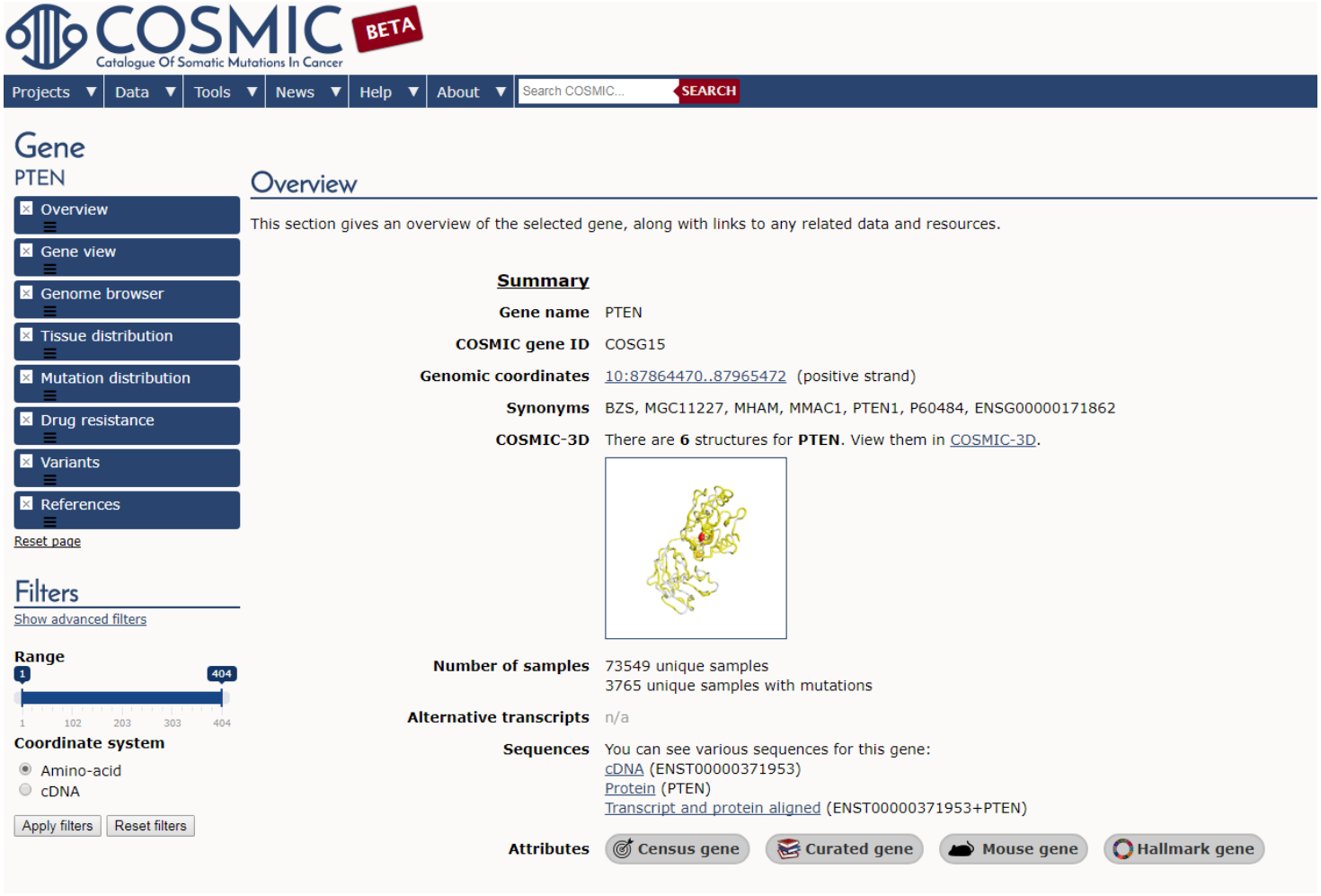
Gene Overview Page

- Several Items on Menu on left panel
  - Gene view – view domains within gene and where mutations reside
  - Genome browser - view genomic context
  - Overview – general information
  - Tissue – expression/mutations in each tissue type
  - Distribution – what kind of mutations observed?
  - Drug Resistance – do mutations confer drug resistance
  - Variants – table of observed variants in gene
  - References – curated references for gene

Gene Overview Page

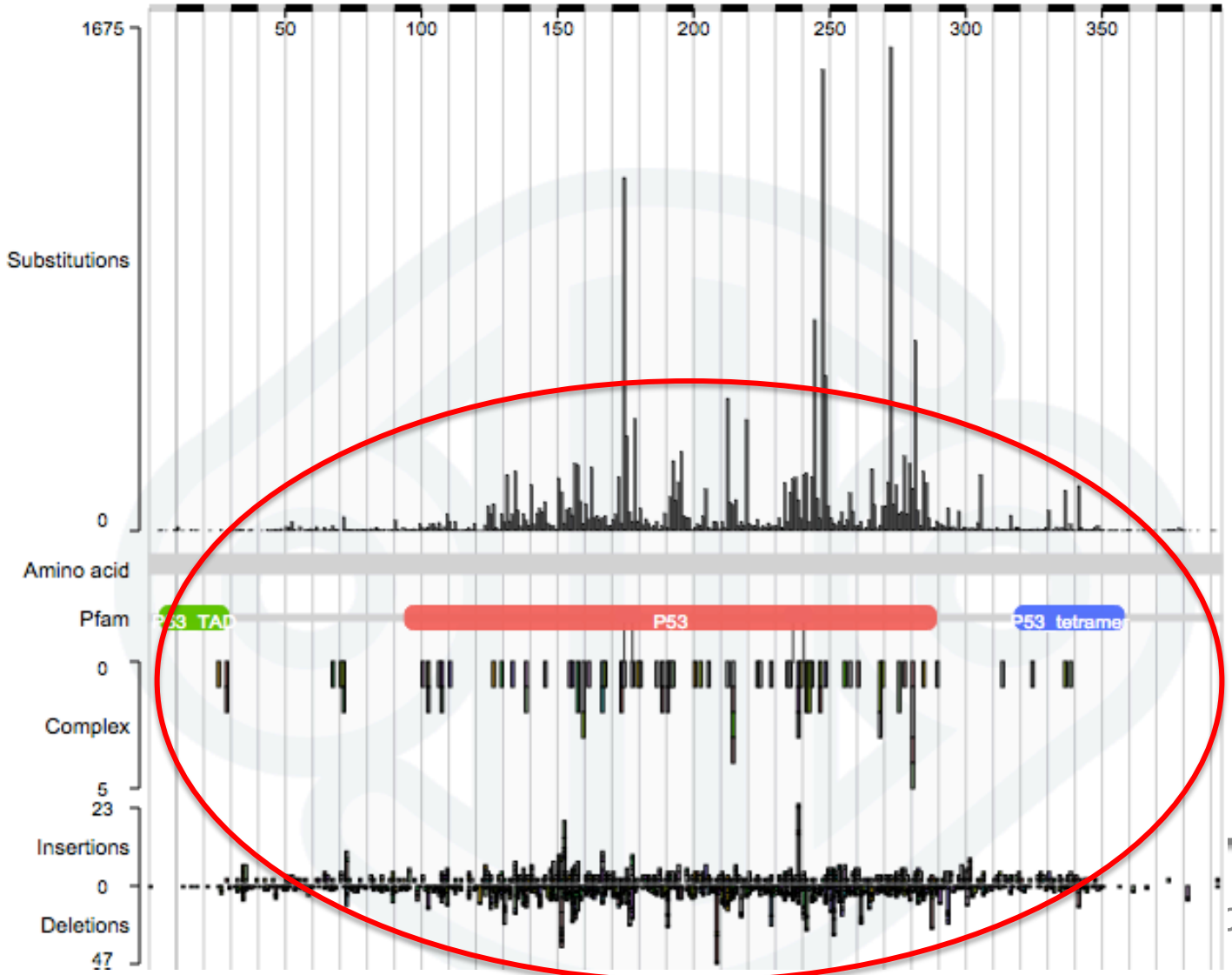


Navigate the gene page by selecting an item from the left menu or scrolling through page.

p53 – an inactivating mutation profile

p53 is oncogenic when its activity is destroyed by inactivating mutations: ***Loss - of - function***.

including substitutions, insertions and deletions which cause an early STOP codon



Nonsense subs

TAT TGG CTA GTA CAT

Tyr Trp Leu Val His

TAT TGA CTA GTA CAT

Tyr STOP

Frameshift Indels

TAT TGG CTA GTA CAT

Tyr Trp Leu Val His

TAC TCG GCT AGT ACA T

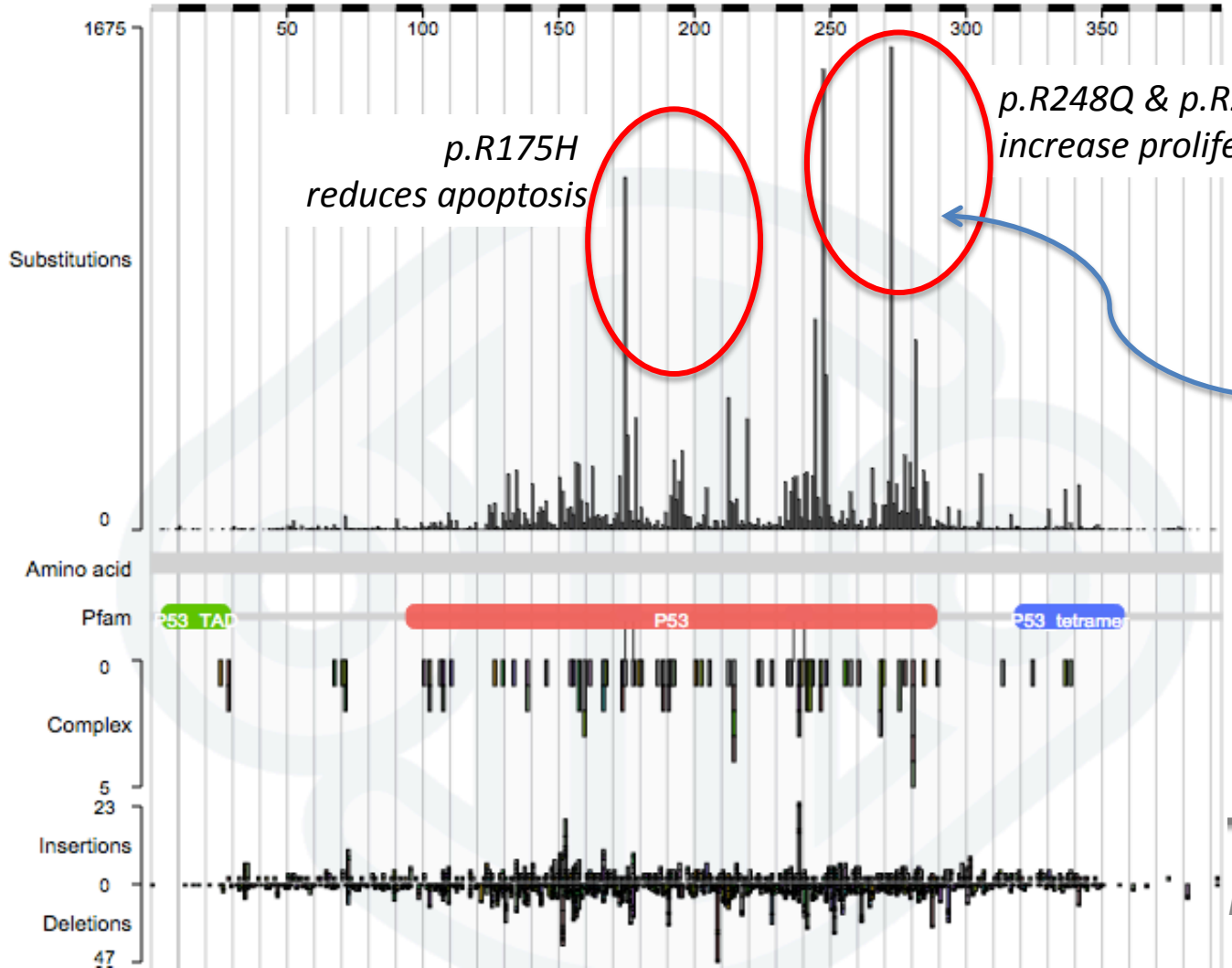
Tyr Ser Ala Ser Thr

cer genomics

p53 – dominant missense mutations

However, specific p53 mutations also show ***Gain – of – function***

- key missense substitutions cause an increase in malignancy
- and cause resistance to chemotherapies (eg cisplatin)



p.R175H
reduces apoptosis

p.R248Q & p.R273H/C
increase proliferation & invasiveness

Missense (R273H)

GTG CGT GTT
Val Arg Val

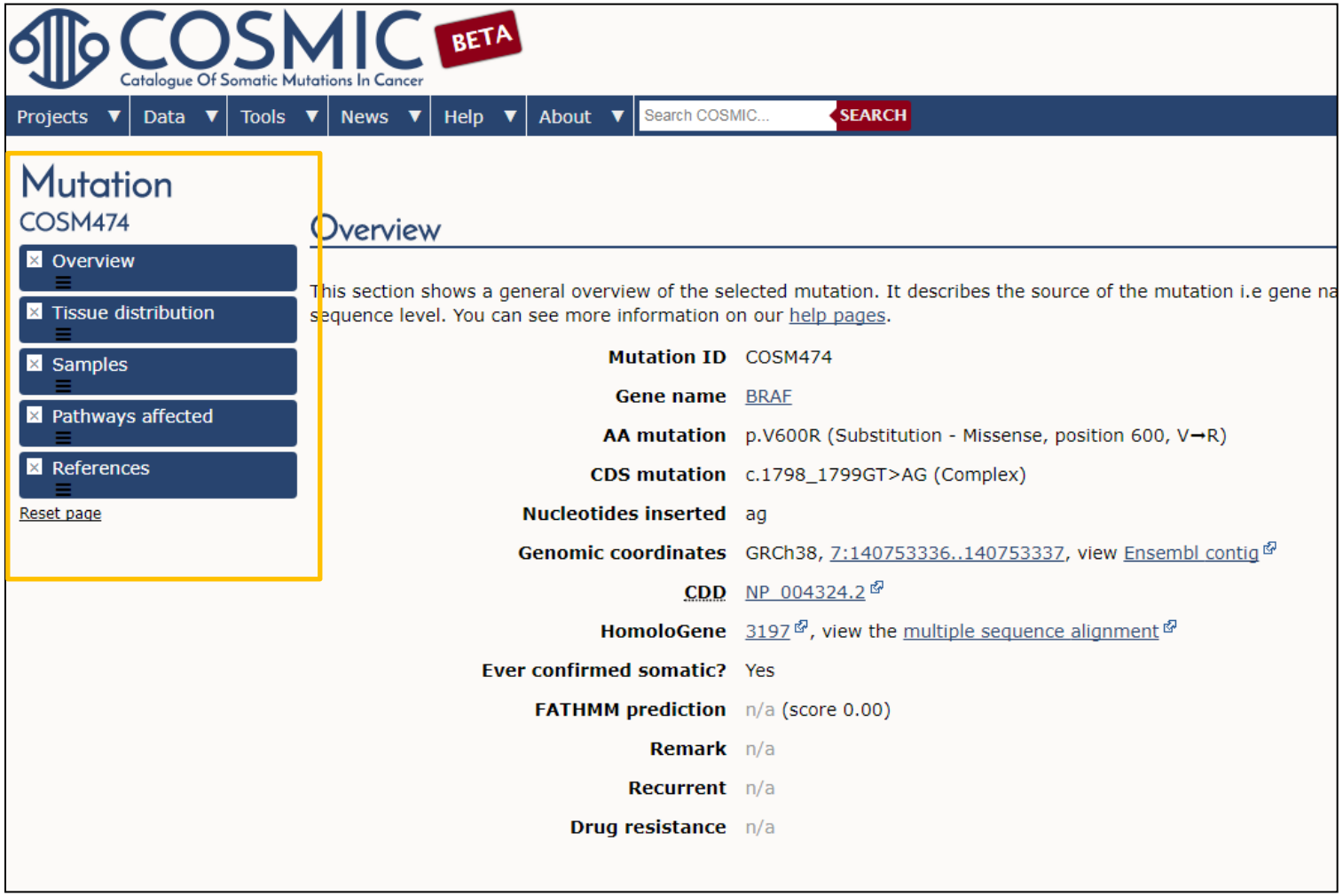
GTG CAT GTT
Val His Val

p53 is a DNA binding protein, affecting the work of many other genes – GOF mutations alter how p53 binds to DNA, changing its checkpoint function

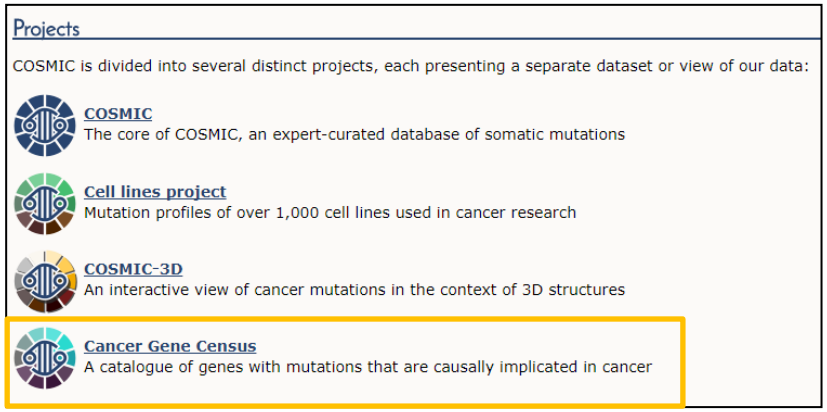
Mutation Overview

- Overview – general mutation information
- Tissue distribution – mutation frequency in tissue types
- Samples – table of affected samples
- Pathways Affected – table of affected pathways
  - Click link to go to WikiPathways
- References – links to relevant publications

Mutation Overview Page



Cancer Gene Census



- Main Links under "Projects" Section on COSMIC home page.
- List is in table format and (with license) is exportable in .CSV or .TSV format.
- Genes marked as Hallmarks of Cancer have more functional descriptions available
  - Click on 

Cancer Gene Census

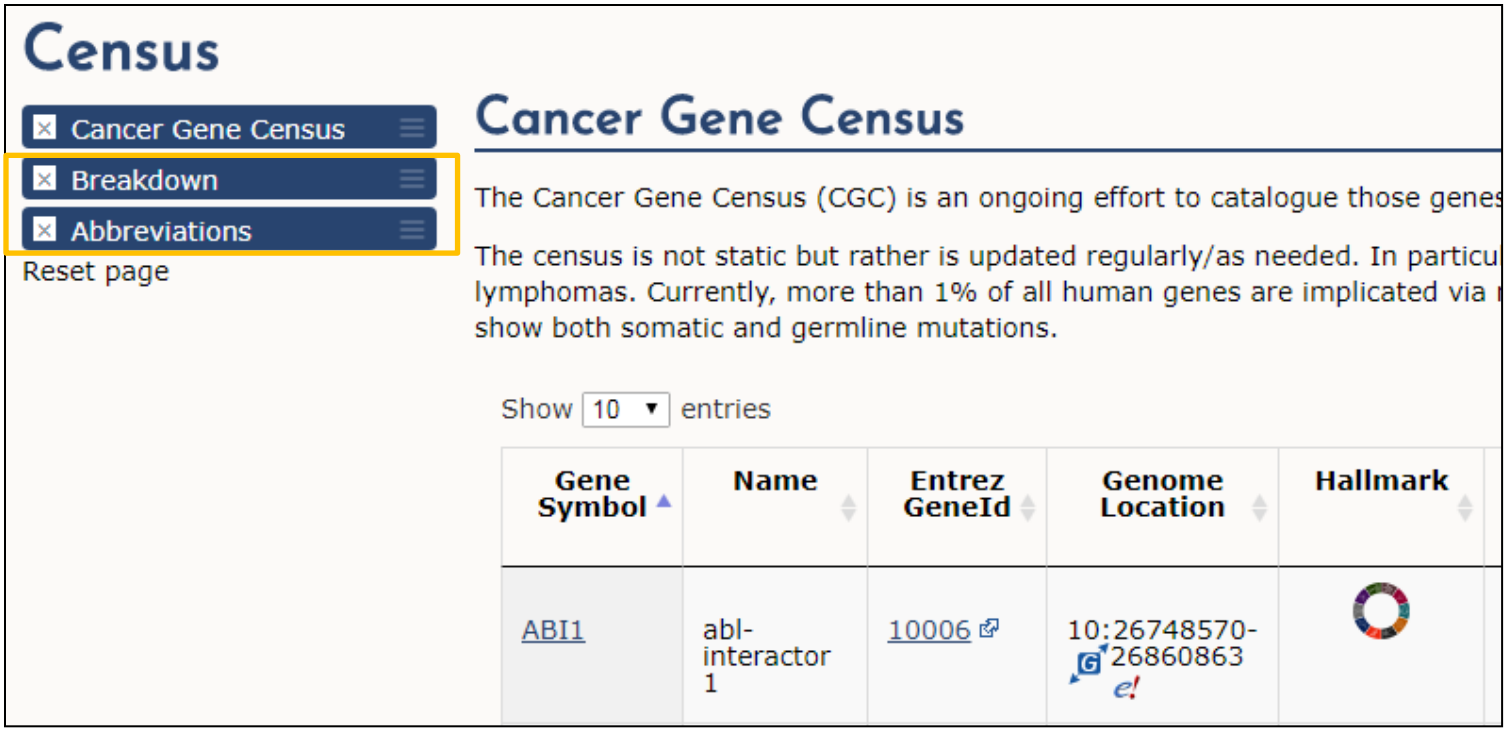
The Cancer Gene Census (CGC) is an ongoing effort to catalogue those genes for which mutations have been causally implicated in cancer. The original census and analysis was published in Nature Reviews Cancer.

The census is not static but rather is updated regularly/as needed. In particular we are grateful to Felix Mitelman and his colleagues in providing information on more genes involved in uncommon translocations in leukaemias and lymphomas. Currently, more than 1% of all human genes are implicated via mutation in cancer. Of these, approximately 90% have somatic mutations in cancer, 20% bear germline mutations that predispose to cancer and 10% show both somatic and germline mutations.

Show 10 entries Export: CSV TSV Search:

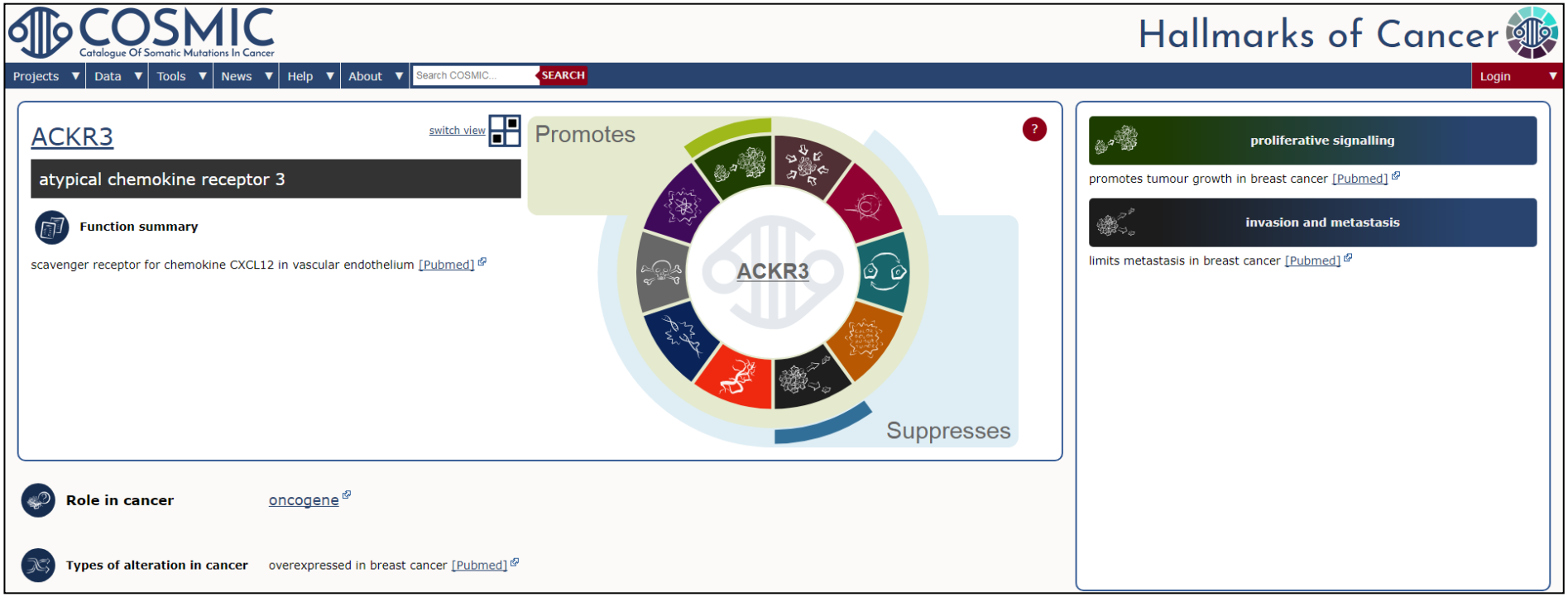
Gene Symbol	Name	Entrez GeneId	Genome Location	Hallmark	Chr Band	Somatic	Germline	Tumour Types(Somatic)	Tumour Types(Germline)	Cancer Syndrome	Tissue Type	Molecular Genetics	Role in Cancer	Mut Typ
ABI1	abl-interactor 1	10006	10:26748570-26860863		10p11.2	yes		AML			L	Dom	TSG; fusion	T
ABL1	v-abl Abelson murine leukemia viral oncogene homolog 1	25	9:130835447-130885683		9q34.1	yes		CML; ALL; T-ALL			L	Dom	oncogene; fusion	T; Mis
ABL2	c-abl oncogene 2; non-receptor tyrosine kinase	27	1:179107718-179143044		1q24-q25	yes		AML			L	Dom	oncogene; fusion	T
ACKR3	atypical chemokine receptor 3	57007	2:-		2q37.3	yes		lipoma			M	Dom	oncogene; fusion	T
ACSL3	acyl-CoA synthetase long-chain family	2181	2:222908773-222941654		2q36	yes		prostate			E	Dom	fusion	T

Cancer Gene Census



- Click on buttons near the top of the browser or scroll down to see the "Breakdown" of the types of gene abnormalities in the Census or abbreviations used in the table.

Hallmarks of Cancer



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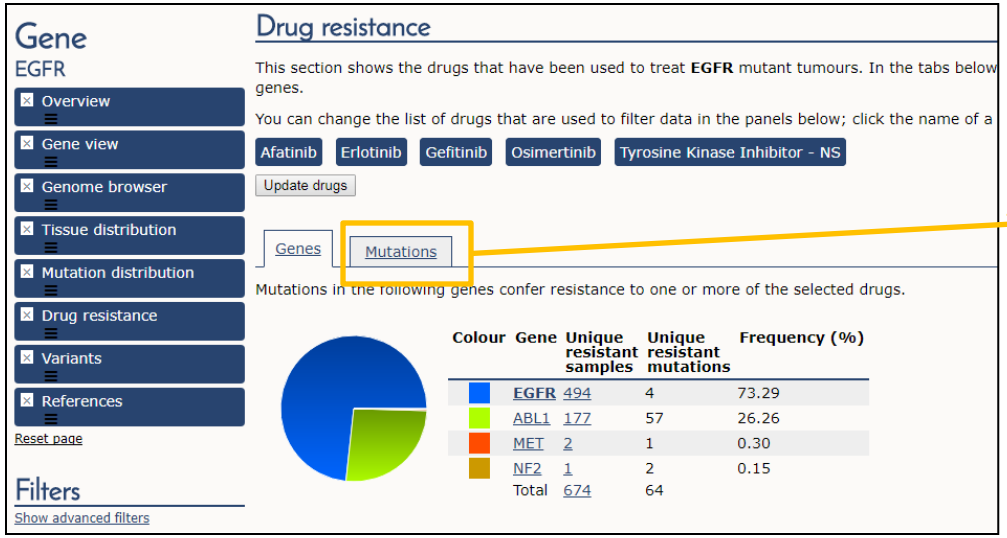
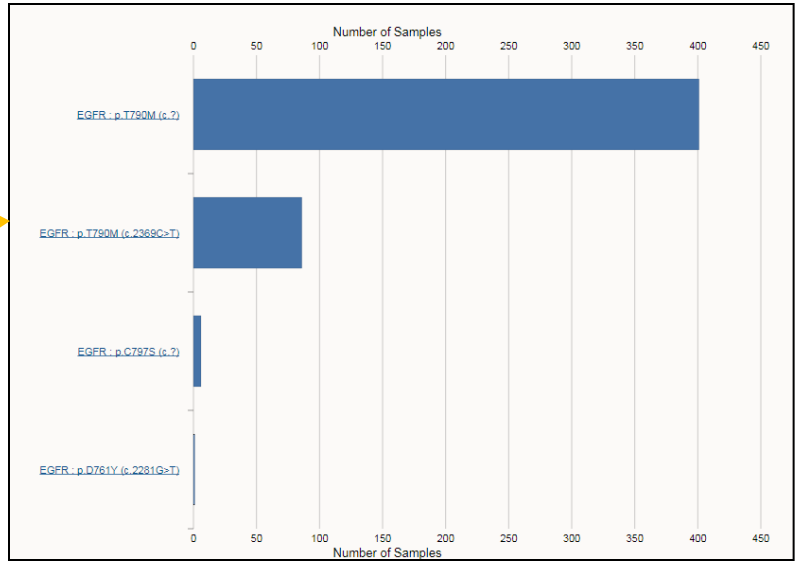
Drug Resistance

- Main Link under “Data Curation” section on COSMIC home page.
- Resistance Data are available for 12 genes:
  - ABL1, ALK, BRAF, EGFR, ESR1, FLT3, KIT, MAP2K1, MAP2K2, PDGFRA, SMO, MET
- Table to view drug and resistance mutation frequency

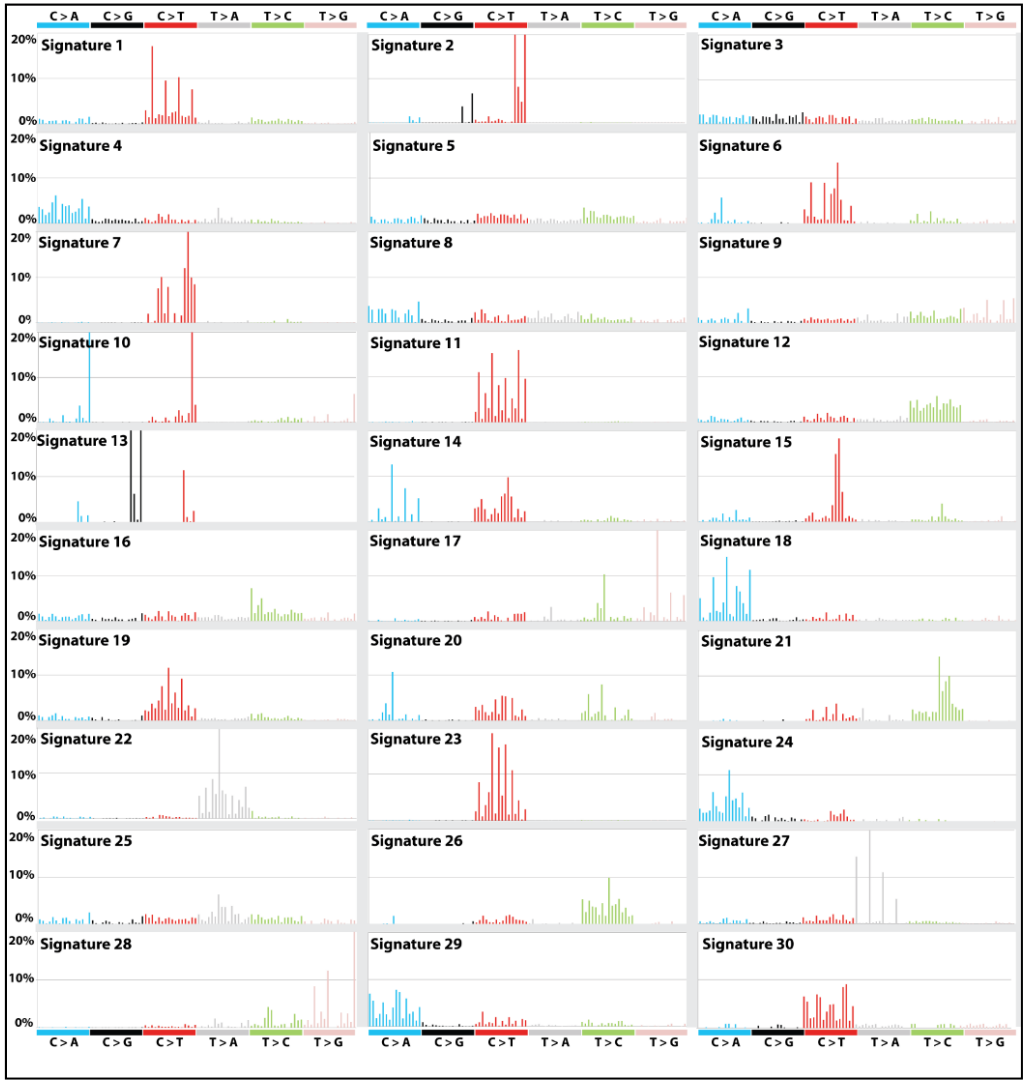
Drug Resistance

- Manually curated list of genes that can carry resistance mutations to particular drugs.
- Click on gene name in table to see Gene Page. Scroll down to to the drug resistance section





Mutational Signatures



- Selection under "Data" in top banner.
- Describes mutational signatures in detail and specifies diseases that carry each mutational signature.

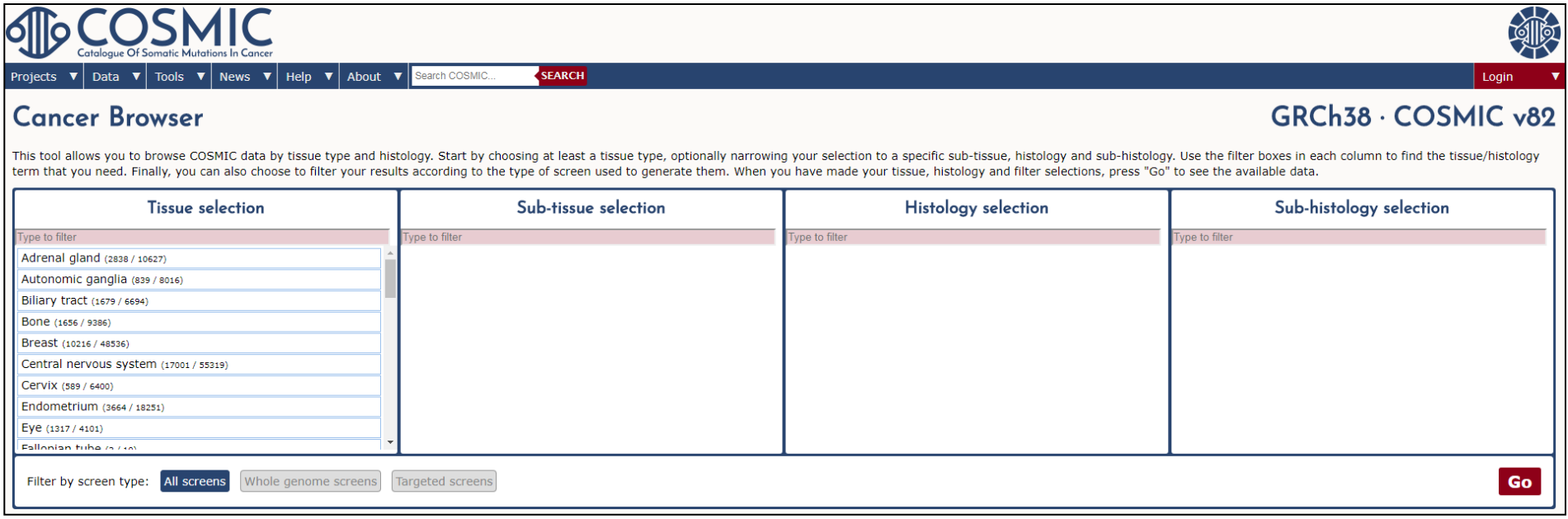
GRCh37 Cancer Archive

- If your lab has not converted to hg38, there is an option to view GRCh37/hg19 information on COSMIC.
- Under “Projects” in top banner, select GRCh37 archive to see legacy site.

Data Curation

- Other links under Expert Curation section on home page
  - **Gene Curation:** list of all genes with deep curation completed. Curation details included on Curated Genes page. Click on gene to go to gene page.
  - **Gene Fusion Curation:** list of all gene fusions with deep curation completed for solid tumors. Click on pair of gene to go to fusion overview page.
    - Fusion Overview page – information about in what kind of tissue fusion was observed and PMID.
  - **Genome Annotation**: Information and parameters used to analyze data.
  - **Drug Resistance:** See slides 19-20.

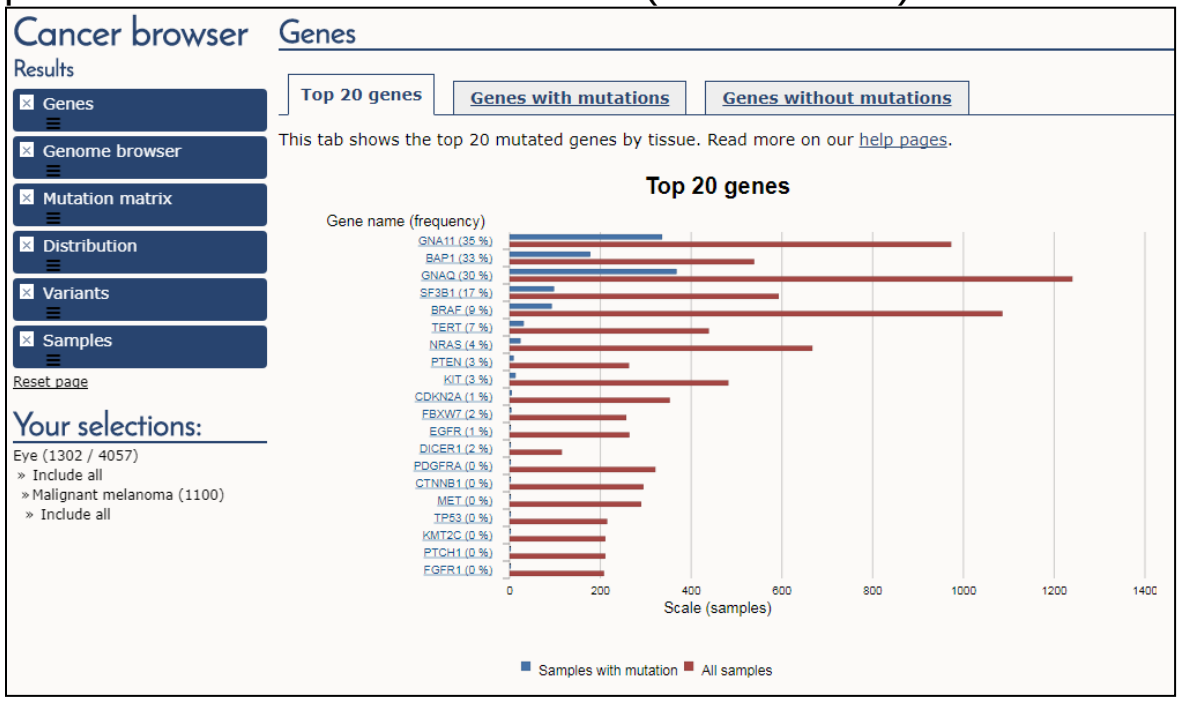
Cancer Browser



- Main link under “Tools” on home page
- Select tumor of interest by tissue and histology
- Press ‘Go’ in lower right corner of window

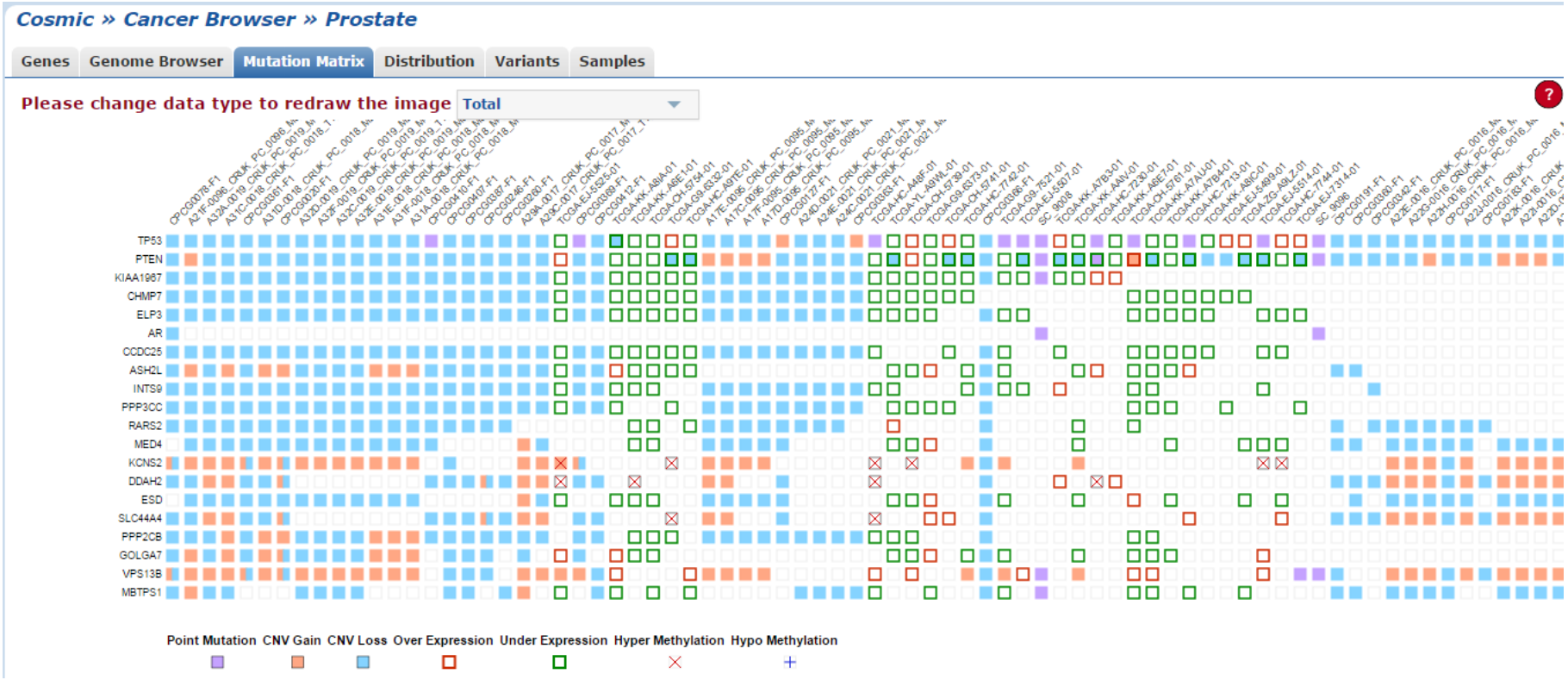
Cancer Browser

- Opens to bar graph of top 20 mutated genes in your selected type of cancer.
- In table format you can view and filter genes with and without mutations by mutation frequency or number of samples tested.
  - Exportable in .CSV or .TSV format (with license)

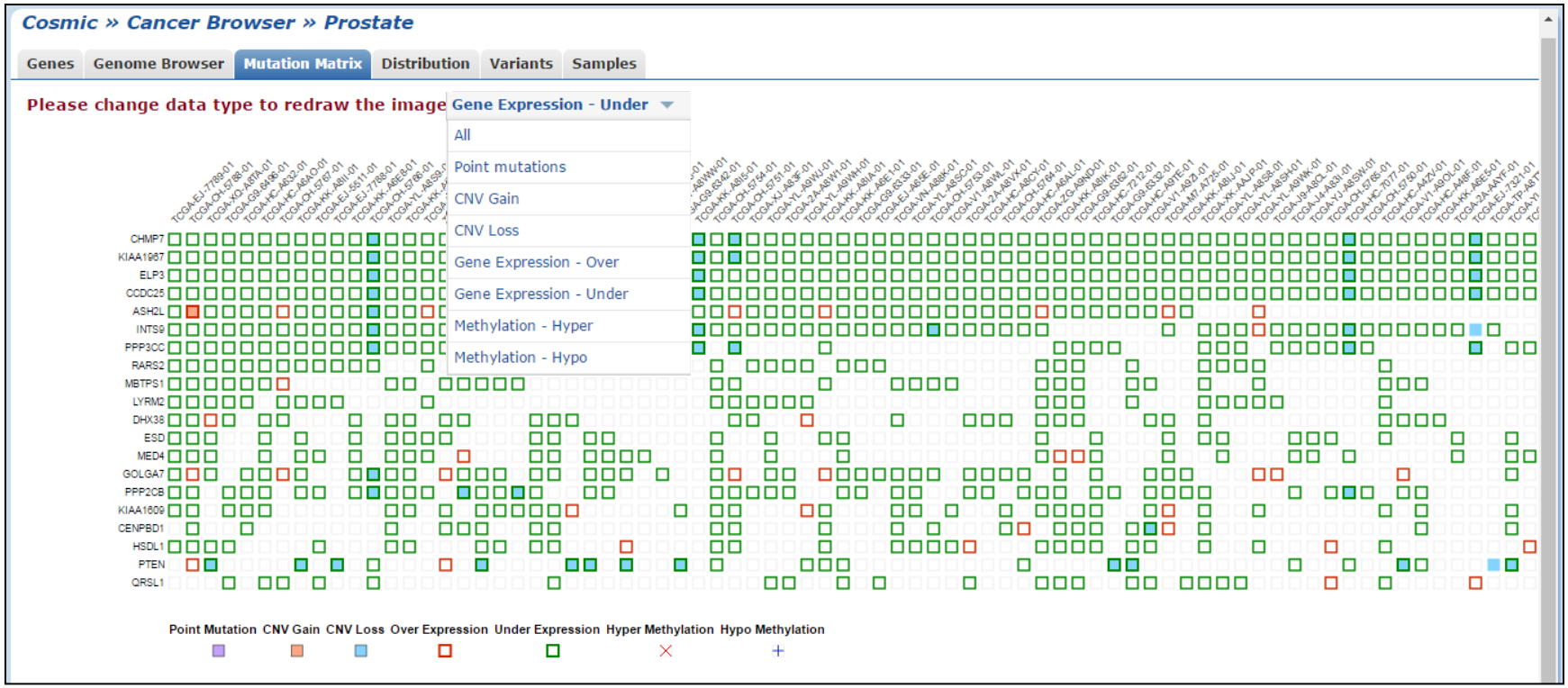


Cancer Browser

- Can view genome browser in cancer browser window.
- Mutation matrix – top 20 mutations by sample



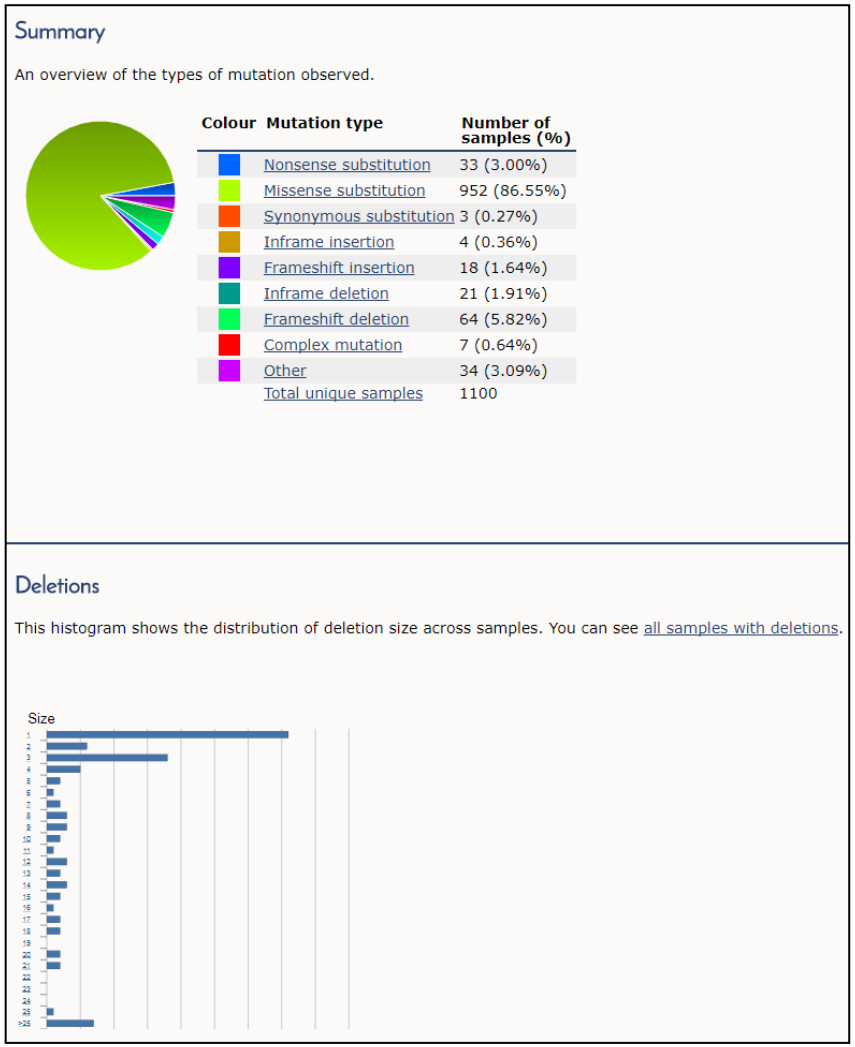
Cancer Browser: Mutation Matrix



- Can redraw image using drop-down menu on top of window to view data based on a certain mutation type.

Cancer Browser: Distribution

- Distribution of mutations within your selected cancer type.
- Substitutions are described similarly base>base (not shown)
- Indels described by size in bps (Insertions displayed similar to deletions)



Summary

An overview of the types of mutation observed.

Colour	Mutation type	Number of samples (%)
	Nonsense substitution	33 (3.00%)
	Missense substitution	952 (86.55%)
	Synonymous substitution	3 (0.27%)
	Inframe insertion	4 (0.36%)
	Frameshift insertion	18 (1.64%)
	Inframe deletion	21 (1.91%)
	Frameshift deletion	64 (5.82%)
	Complex mutation	7 (0.64%)
	Other	34 (3.09%)
	Total unique samples	1100

Deletions

This histogram shows the distribution of deletion size across samples. You can see all samples with deletions.

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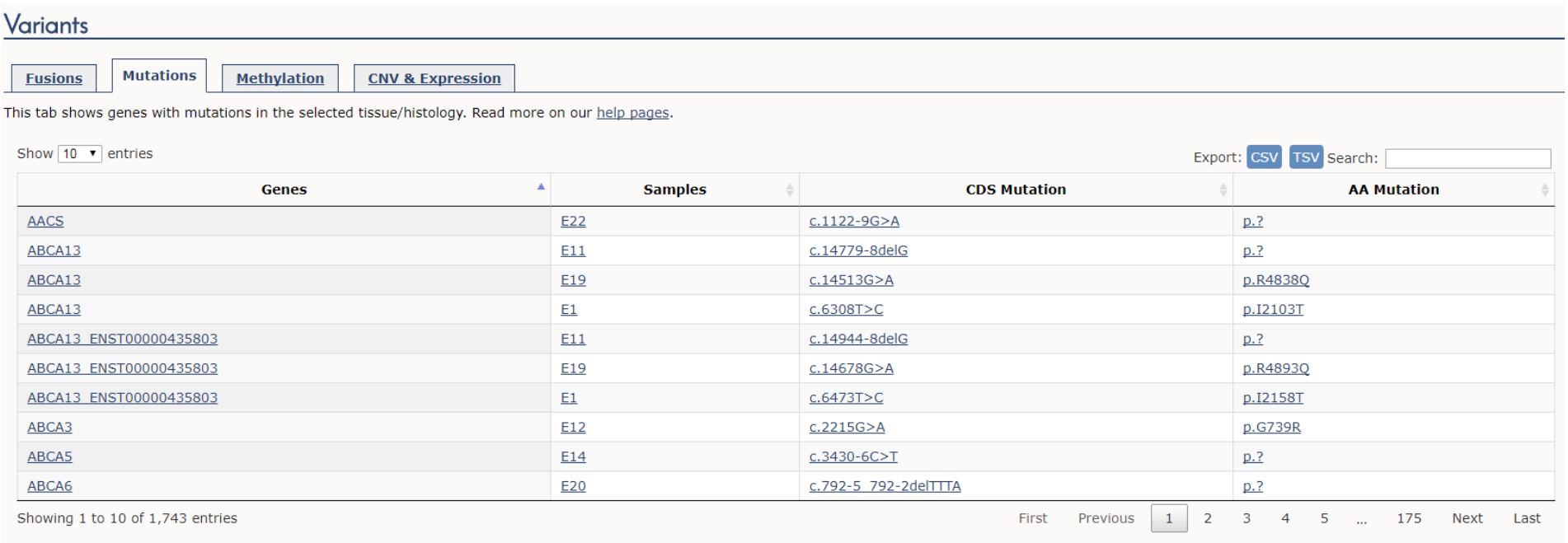
Cancer Browser: Variants

- Observed Fusions, Mutations, Methylation status, and CNV/Expression data given in table format.
  - Exportable in .CSV and .TSV format (with license)
  - Click on mutations for mutation overview
  - Click on fusion pairing for Fusion overview
  - Click on gene for gene overview.



Variants

Fusions | Mutations | Methylation | CNV & Expression

This tab shows genes with mutations in the selected tissue/histology. Read more on our help pages.

Show 10 entries Export: CSV TSV Search:

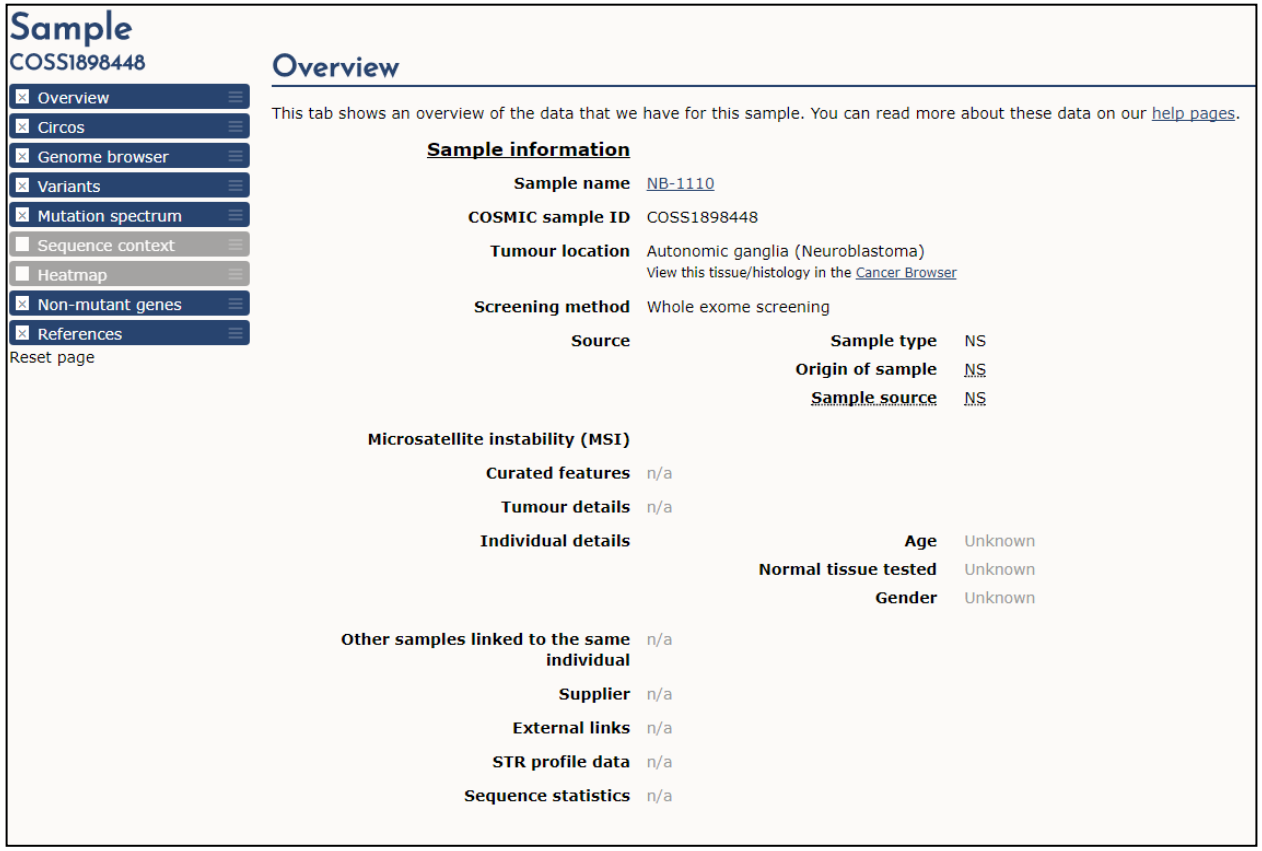
Genes	Samples	CDS Mutation	AA Mutation
AACS	E22	c.1122-9G>A	p.?
ABCA13	E11	c.14779-8delG	p.?
ABCA13	E19	c.14513G>A	p.R4838Q
ABCA13	E1	c.6308T>C	p.I2103T
ABCA13_ENST00000435803	E11	c.14944-8delG	p.?
ABCA13_ENST00000435803	E19	c.14678G>A	p.R4893Q
ABCA13_ENST00000435803	E1	c.6473T>C	p.I2158T
ABCA3	E12	c.2215G>A	p.G739R
ABCA5	E14	c.3430-6C>T	p.?
ABCA6	E20	c.792-5_792-2delTTTA	p.?

Showing 1 to 10 of 1,743 entries First Previous 1 2 3 4 5 ... 175 Next Last

Cancer Browser: Samples

- Table of mutated and non-mutated samples
  - Exportable in .TSV or .CSV (with license)
  - Click on sample ID for sample overview page

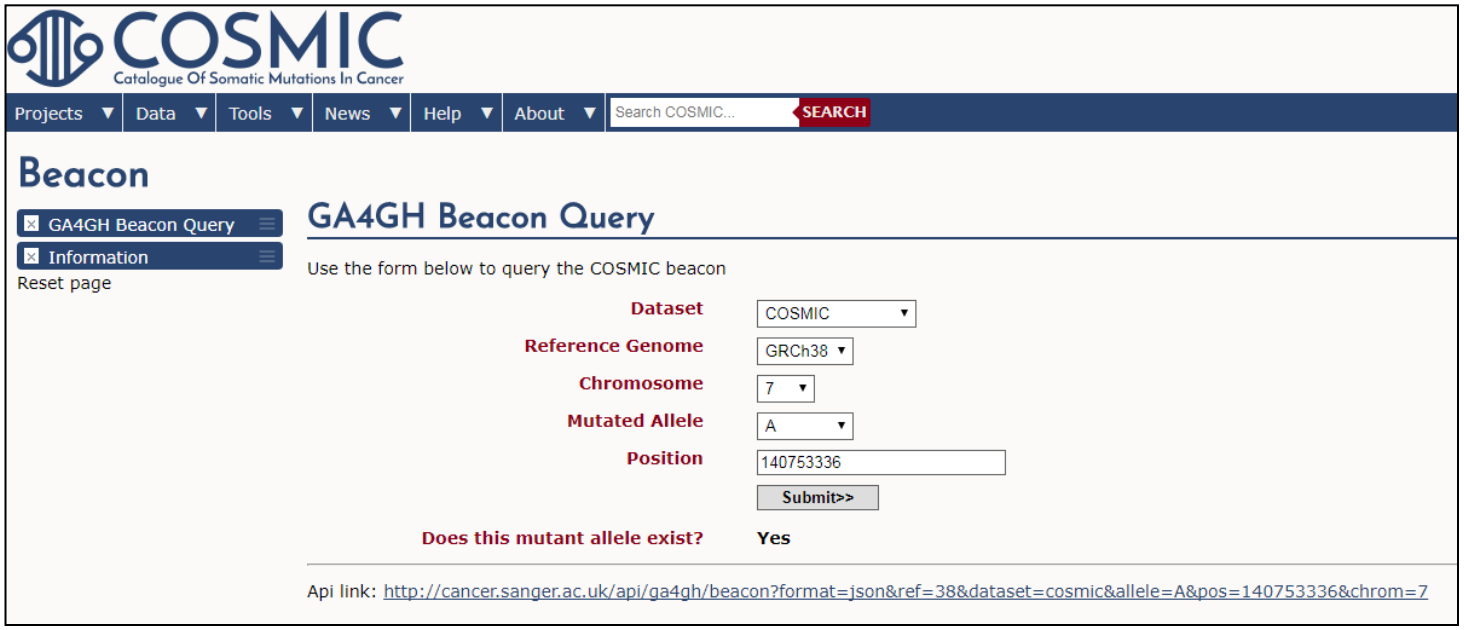
Sample Overview Page



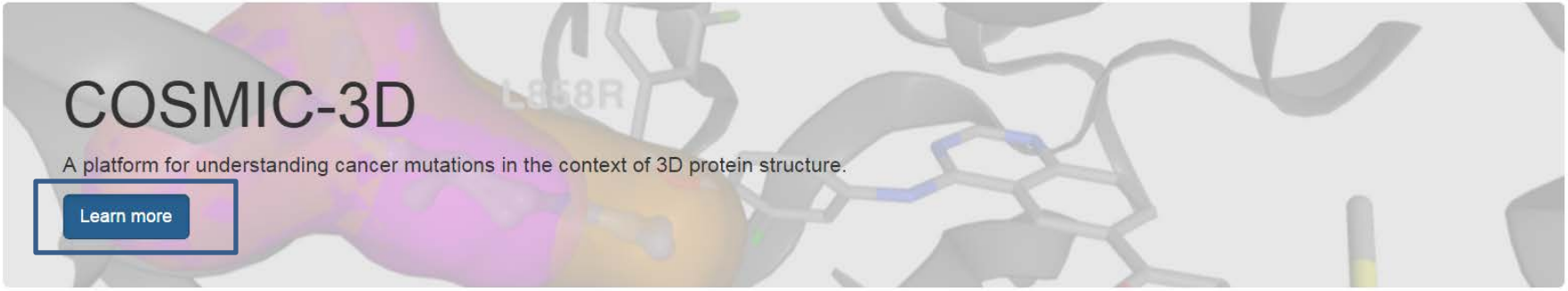
- Click on menu on left side of page or scroll to desired information
- Primary reference(s) and/or large study name are available in the reference section

GA4GH Beacon

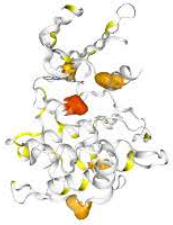
- Main link under “Tools” on COSMIC home page
- GA4GH = Global Alliance for Genomics and Health – see Information section
- Shared URL format for query
  - http://cancer.sanger.ac.uk/api/ga4gh/beacon/query?chrom=?;pos=?;allele=?
- Can query if COSMIC or Cell Lines Project has observed a specific mutation at a designated genomic locus.



COSMIC-3D



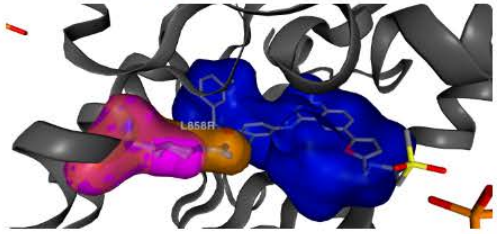
Visualise mutations



Overlay three types of cancer mutation, or a heatmap of missense recurrence, onto protein structure to add an extra dimension to COSMIC cancer genomic data.

Explore »

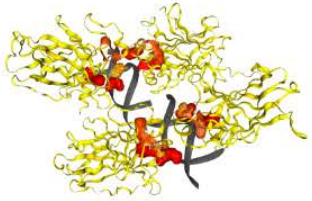
Generate hypotheses



See indicative models of missense mutants and generate hypotheses as to the effects of the mutation on protein structure and drug binding.

Explore »

Understand impact



Infer functional consequences from a different perspective on cancer mutation data.

Explore »

Getting Started

Search for a gene or protein, e.g. BRAF, EGFR, or BRCA2...

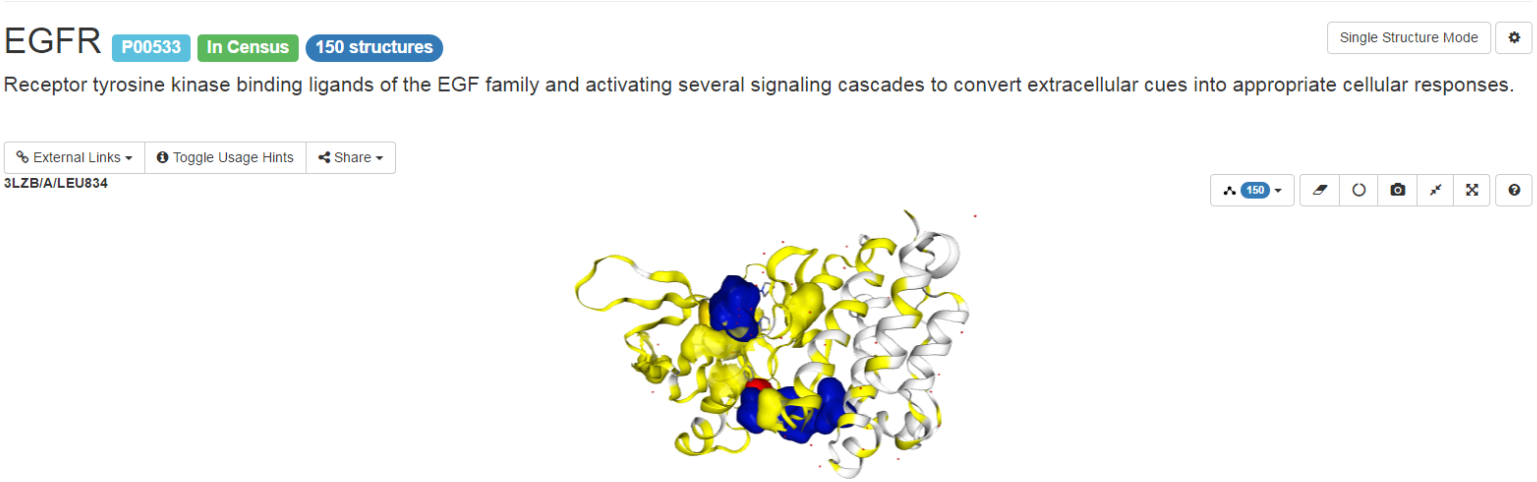
or

Show me a demo!

CANCER GENOMICS CONSORTIUM

Educating for best practices in clinical cancer genomics

COSMIC – 3D



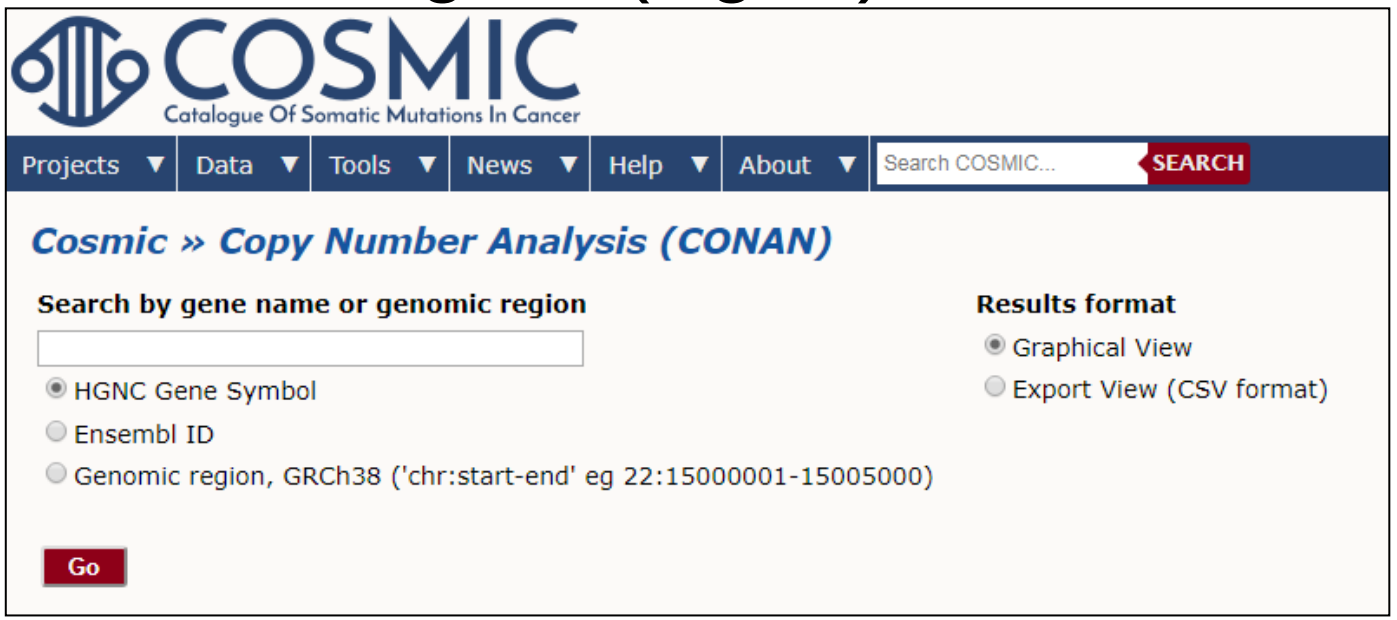
- SNV frequency depicted by yellow/orange segments
- Predicted small molecule binding sites in blue.
- Can take screenshot, pop screen out, drag mouse or click button to rotate protein structure for better view.
- Several viewing and toggle options
- Protein property information
- UniProt sequence information and mutation information integrated.
- There are so many features within this application. Check them out!

COSMIC BigQuery

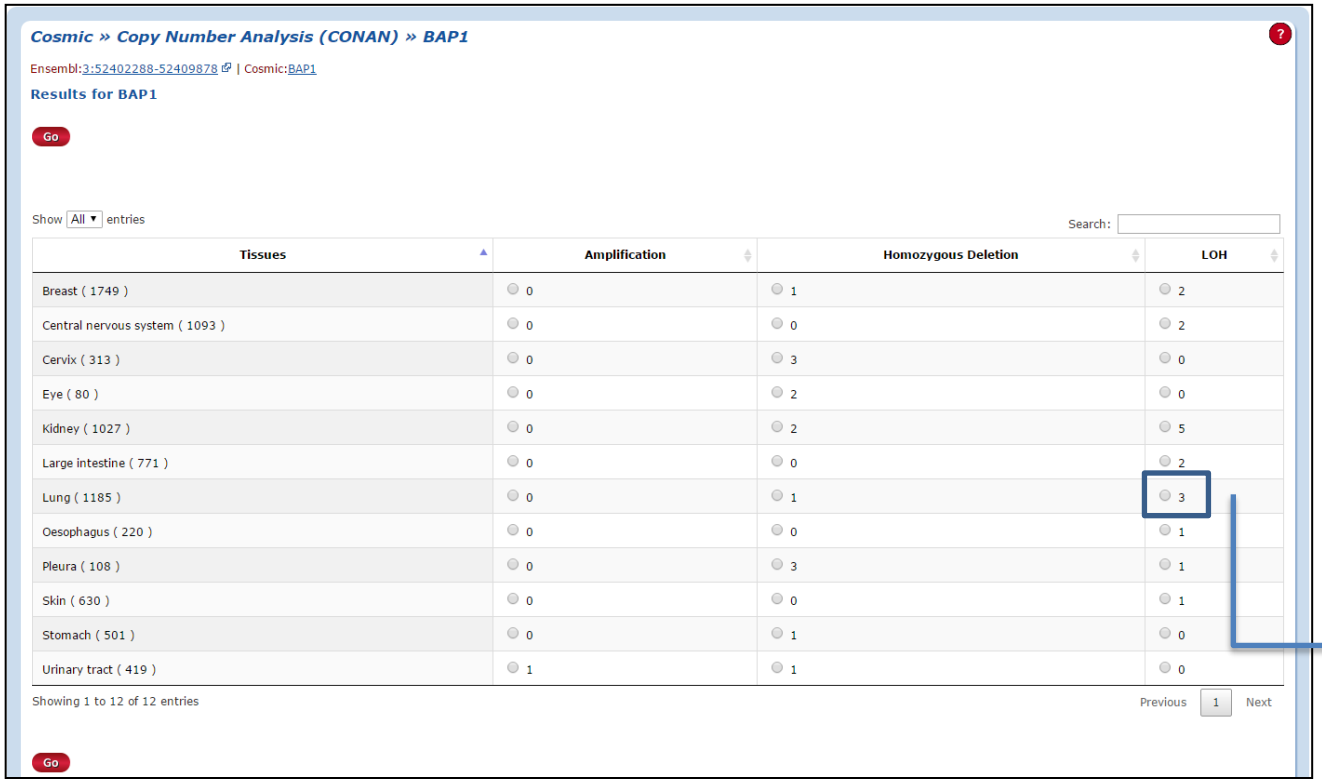
- If you have a COSMIC account, register at no charge for access to BigQuery.
- Research based queries of large datasets at minimal cost per query.
- Supports Standard SQL programming language and can be accessed by R
- http://isb-cancer-genomics-cloud.readthedocs.io/en/latest/sections/COSMIC.html

CONAN

- CONAN = COpy Number ANalysis – under “Tools” on Home page.
- Search by gene (HGNC or Ensembl) or genomic region (hg38)



CONAN



Cosmic » Copy Number Analysis (CONAN) » BAP1

Ensembl:3:52402288-52409878 | Cosmic:BAP1

Results for BAP1

Go

Show All entries

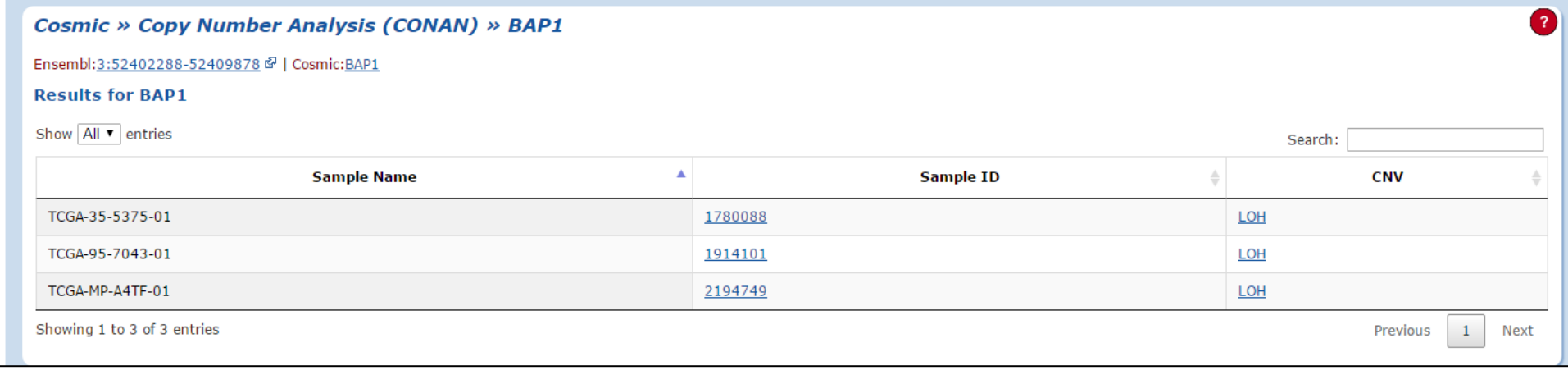
Search:

Tissues	Amplification	Homozygous Deletion	LOH
Breast (1749)	0	1	2
Central nervous system (1093)	0	0	2
Cervix (313)	0	3	0
Eye (80)	0	2	0
Kidney (1027)	0	2	5
Large intestine (771)	0	0	2
Lung (1185)	0	1	3
Oesophagus (220)	0	0	1
Pleura (108)	0	3	1
Skin (630)	0	0	1
Stomach (501)	0	1	0
Urinary tract (419)	1	1	0

Showing 1 to 12 of 12 entries

Previous 1 Next

Go



Cosmic » Copy Number Analysis (CONAN) » BAP1

Ensembl:3:52402288-52409878 | Cosmic:BAP1

Results for BAP1

Show All entries

Search:

Sample Name	Sample ID	CNV
TCGA-35-5375-01	1780088	LOH
TCGA-95-7043-01	1914101	LOH
TCGA-MP-A4TF-01	2194749	LOH

Showing 1 to 3 of 3 entries

Previous 1 Next

Data Downloads

- Main Link under “Data” on Home Page
- Need license to download data
- Depending on the data you would like to download, you may need to download off of a SFTP site using a FTP tool like WinSCP or Filezilla

Data Submission

- Under Help → Data Submission
- Using COSMIC data or describing mutation data in results

- Submitting Data to COSMIC

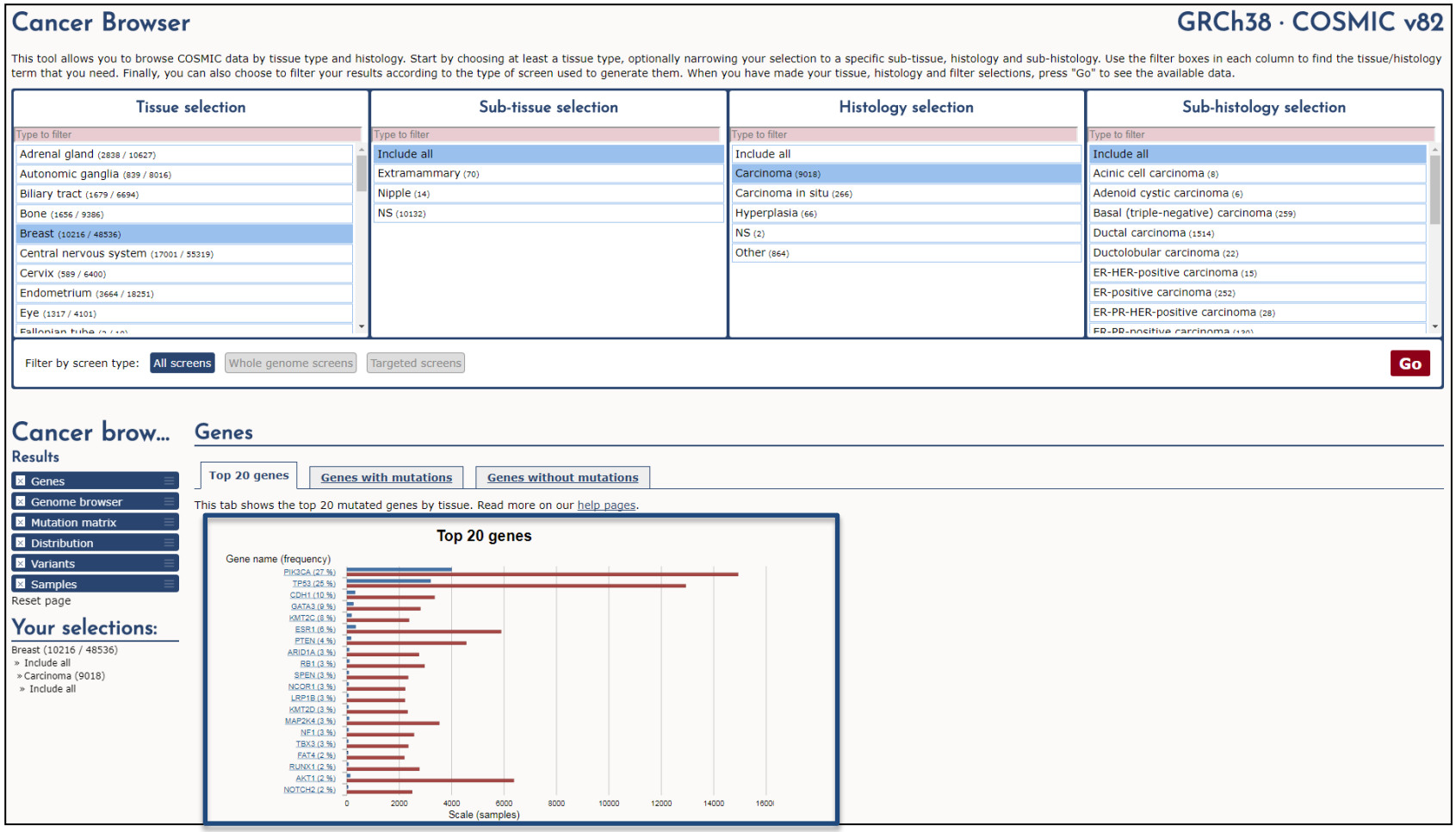
Other Links Under Data

- Genome Annotation
- Datasheets – details about COSMIC versions
- Help – links to helpful overview resources
- FAQ – Frequently Asked Questions

Scenario #1

- You are a laboratory professional trying to identify genes to put on your lab's new breast carcinoma NGS panel.
  - Cancer Browser
  - Search Cancer Gene Census

Cancer Browser Query



Search Cancer Gene Census

GRCh38 · COSMIC v8

Cancer Gene Census

The Cancer Gene Census (CGC) is an ongoing effort to catalogue those genes for which mutations have been causally implicated in cancer. The original census and analysis was published in Nature Reviews Cancer.

The census is not static but rather is updated regularly/as needed. In particular we are grateful to Felix Mitelman and his colleagues in providing information on more genes involved in uncommon translocations in leukaemias and lymphomas. Currently, more than 1% of all human genes are implicated via mutation in cancer. Of these, approximately 90% have somatic mutations in cancer, 20% bear germline mutations that predispose to cancer and 10% show both somatic and germline mutations.

Show 10 entries Export: CSV TSV Search: breast

Gene Symbol	Name	Entrez GeneId	Genome Location	Hallmark	Chr Band	Somatic	Germline	Tumour Types(Somatic)	Tumour Types(Germline)	Cancer Syndrome	Tissue Type	Molecular Genetics	Role in Cancer
AKT1	v-akt murine thymoma viral oncogene homolog 1	207	14:104770341-104792643		14q32.32	yes		breast; colorectal; ovarian; NSCLC			E	Dom	oncogene
APOBEC3B	apolipoprotein B mRNA editing enzyme catalytic subunit 3B	9582	22:38982454-38992445		22q13.1		yes		breast cancer		E	Rec	oncogene; TSG
ARID1A	AT rich interactive domain 1A (SWI-like)	8289	1:26696404-26780756		1p35.3	yes		clear cell ovarian carcinoma; RCC; breast			E	Rec	TSG; fusion
ARID1B	AT rich interactive domain 1B	57492	6:156778104-157207891		6q25.1	yes		breast; hepatocellular carcinoma			E	Rec	TSG
BAP1	BRCA1 associated protein-1 (ubiquitin carboxy-terminal hydrolase)	8314	3:52402288-52409878		3p21.31-p21.2	yes	yes	uveal melanoma; breast; NSCLC; RCC	mesothelioma; uveal melanoma		E	Rec	TSG
BRCA1	familial breast/ovarian cancer gene 1	672	17:43045678-43124096		17q21	yes	yes	ovarian	breast; ovarian	hereditary breast/ovarian cancer	E	Rec	TSG

Results from Queries

Cancer Genome Browser Query (Criteria ≥ 3% mutated) = 16 genes

- PIK3CA
- TP53
- CDH1
- GATA3
- KMT2C
- ESR1
- PTEN
- RB1
- SPEN
- ARID1A
- NCOR1
- KMT2D
- MAP2K4
- NF1
- TBX3
- LRP1B

Cancer Gene Census Query = 32 genes

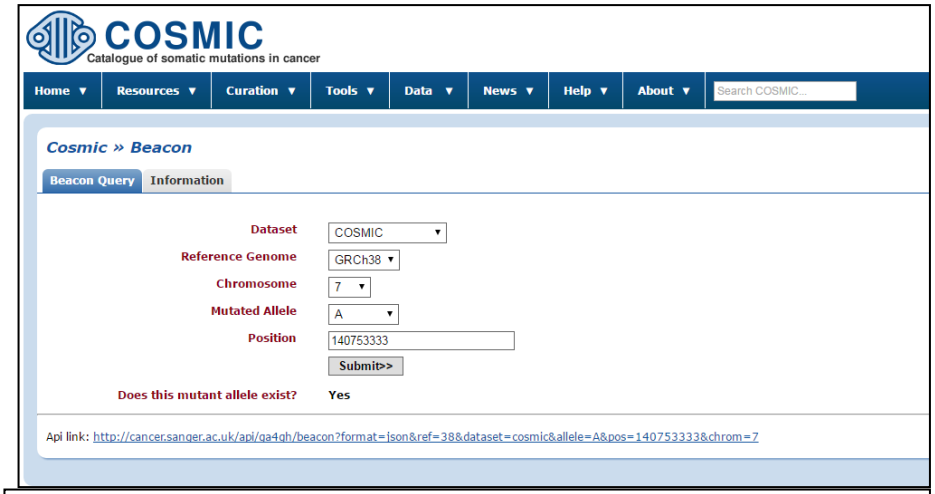
- CCND1
- KEAP1
- NOTCH1
- GATA3
- SMARCD1
- ESR1
- MAP3K13
- NCOR1
- TP53
- AKT1
- ARID1B
- TBX3
- ERBB2
- BRCA1
- BRCA2
- FOXA1
- CDKN1B
- ARID1A
- PBRM1
- SALL4
- EP300
- PIK3CA
- ETV6
- NTRK3
- CTCF
- PPM1D
- CASP8
- CDH1
- MAP3K1
- MAP3K4
- RB1
- BAP1

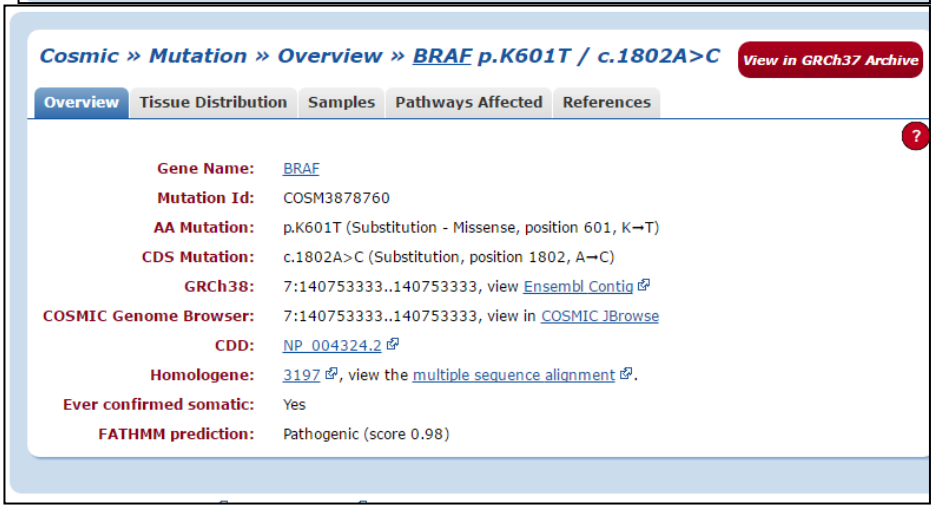
9 genes overlap between two lists = 39 total genes

Scenario #2

- A whole genome sequencing (WGS) case in your lab has a mutation that you haven't observed before. Does this mutant allele exist in COSMIC?
  - GA4GH Beacon
  - Chr7:140753333 (BRAF)
  - Mutated Allele = A

Yes – this is in COSMIC





- Mutation can be found in Genome browser on BRAF gene page or by entering the AA mutation or CDS Mutation Nomenclature

Scenario #3

- Your lab is building a Pan Cancer List based on multiple resources.
  - Cancer Gene Census

Using Data from Cancer Gene Census

- If you have a license, download as .CSV or .TSV
  - This is useful as Excel if you'd like to sort data in different ways to stratify genes based on other criteria in COSMIC's table.

- Cancer Gene Census is updated with most version releases of COSMIC.

Scenario #4

- Mate Pair sequencing has picked up a translocation your lab has not yet reported.
  - NUP98/KDM5A
  - Search in “Gene fusion curation” under Data Curation

Curated Fusions

Fusions

Gene fusions, or translocations, resulting from chromosomal rearrangements are the most common mutation class. They lead to chimeric transcripts or to deregulation of genes through juxtapositioning of novel promoter or enhancer regions.

Gene fusions are manually curated from peer reviewed publications by expert COSMIC curators. A comprehensive literature curation is completed for each fusion pair when it is released in the database. Currently COSMIC includes information on fusions involved in solid tumours. Annotation of fusions associated with leukaemias and lymphomas will be added.

Select a gene pair from the list to go to the Overview page for that fusion and see all curated fusions for that pair, as well as the tissue types in which they were found and the associated publications. Many additional data points are curated for individuals (e.g. age, gender), tumour (e.g. stage, drug response) and samples (e.g. histology, sample source). This information can be found on the Sample Overview page.

Show All ▾ entries Search: nup98

Genes	Samples	Mutations	Papers
NUP98/KDM5A_ENST00000399788	77	4	1

Showing 1 to 1 of 1 entries (filtered from 290 total entries) Previous 1 Next

- Click on fusion gene pairing to open fusion overview.
- Link to PMID and/or large scale studies on Reference tab.

Cosmic » Fusion » Overview » NUP98:KDM5A_ENST00000399788

View in GRCh37 Archive

Fusions | Tissues | References

Genes NUP98 ->KDM5A_ENST00000399788

Mutation ID	5' Partner Gene				3' Partner Gene				No. of Mutations	Mutation Frequency
	Gene Name	Last Observed Exon	Inferred Breakpoint	Inserted Sequence	Gene Name	First Observed Exon	Inferred Breakpoint	Inserted Sequence		
COSF2292	NUP98	13	1963	-	KDM5A_ENST00000399788	27	4819	-	1	25%
COSF2294	NUP98	?	?	-	KDM5A_ENST00000399788	?	?	-	3	75%
Total Mutations									**4**	**100%**

Scenario #5

- Your lab has a significant pool of data that you would like to contribute to COSMIC to enhance the knowledgebase.
  - COSMIC is exploring collaborative relationships with institutions aiming to release anonymized somatic mutation calls in COSMIC
    - COSMIC will highlight these laboratories in their webpages and strongly cite them as sources.
    - Contact COSMIC directly
      - Simon Forbes (Head of COSMIC): saf@sanger.ac.uk
      - COSMIC Helpdesk: cosmic@sanger.ac.uk

Future Features: Coming Soon

- Guide to Actionability
- Organoids
  - Data release for the Human Cancer Model Initiative
    - Better laboratory models – in preparation
- Cancer Mutation Census
  - identify driver mutations across all diseases

Online Tutorials

- COSMIC Site Overview: https://www.youtube.com/watch?v=whxlL86gnKA
- Sample Data Tutorial: https://www.youtube.com/watch?v=5dqInH8_LAo
- Cancer Browser Tutorial: https://www.youtube.com/watch?v=k477uAiKx74
- Gene Pages Tutorial: https://www.youtube.com/watch?v=2FD5RabgK6o
- Fusions Tutorial: https://www.youtube.com/watch?v=M9lLszjsuAw
- COSMIC Search Tutorial: https://www.youtube.com/watch?v=SVfloi4hfNM
- DISCLAIMER: These tutorials all provide instruction on how to use older versions of COSMIC. The latest version of COSMIC looks different and has different features.

Citation

- Forbes et al. COSMIC: somatic cancer genetics at high-resolution. Nucleic Acids Research (2017)45(D1):D777-D783. Available online: https://doi.org/10.1093/nar/gkw1121

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