Supplementary Information

The AAA+ chaperone VCP disaggregates Tau fibrils and generates aggregate seeds

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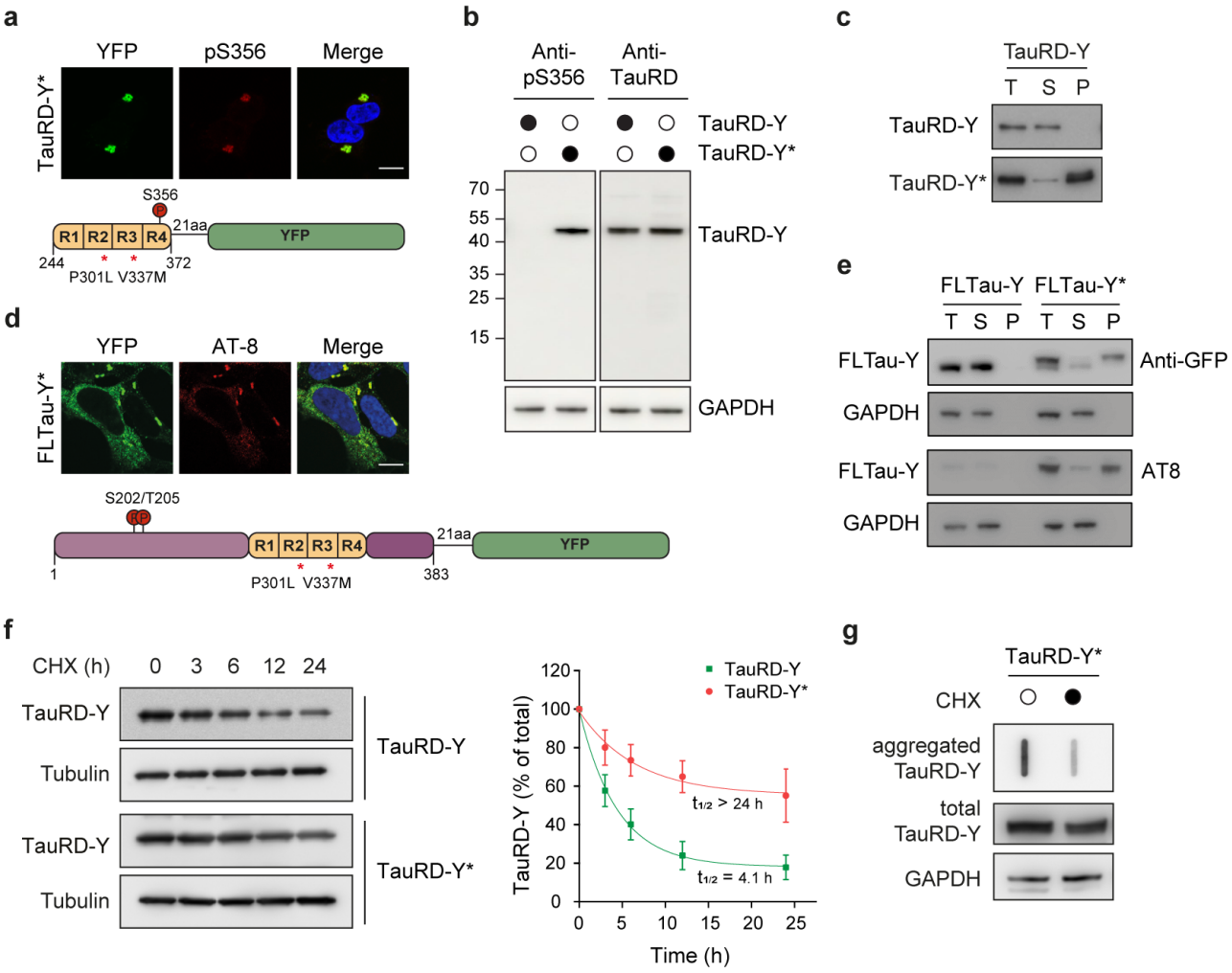
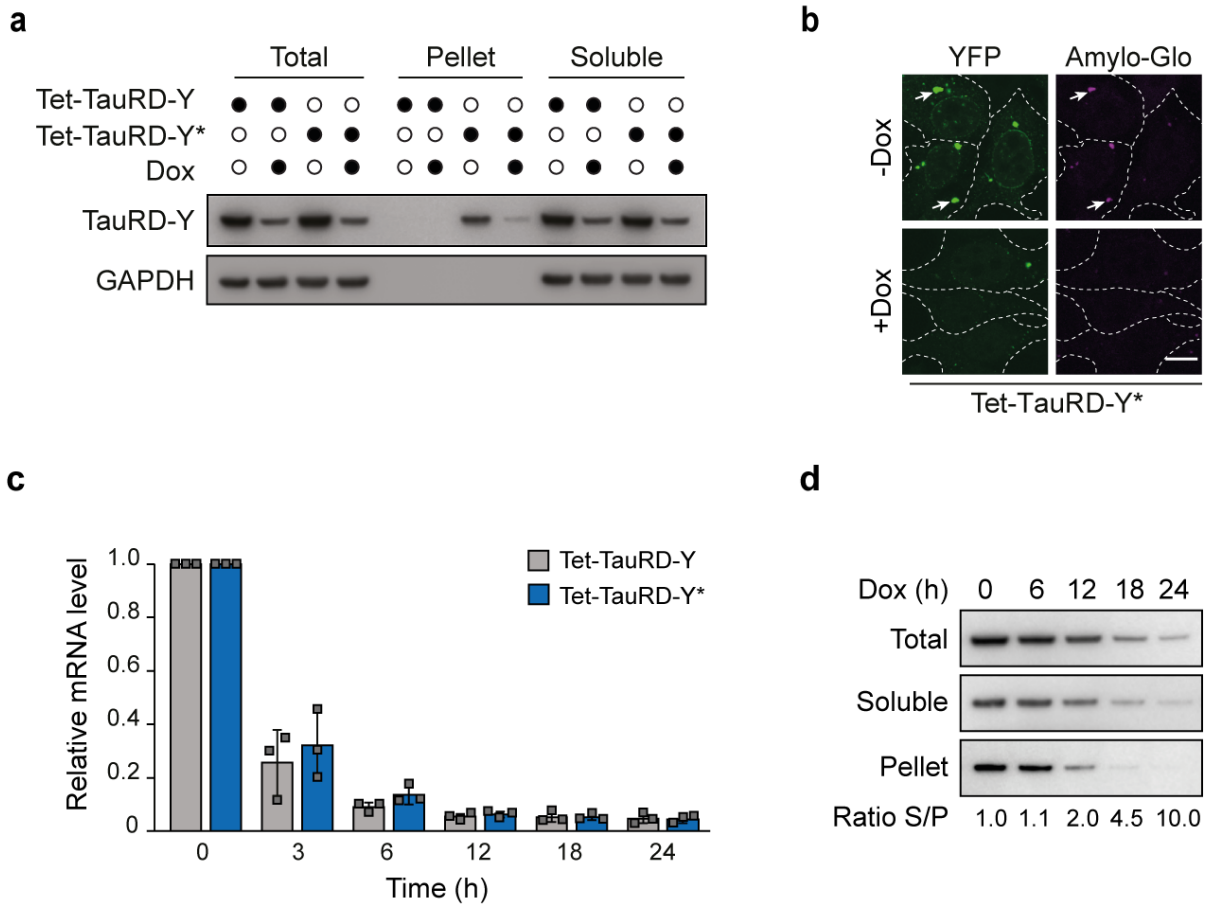
Supplementary information includes 10 Supplementary Figures and 1 Table



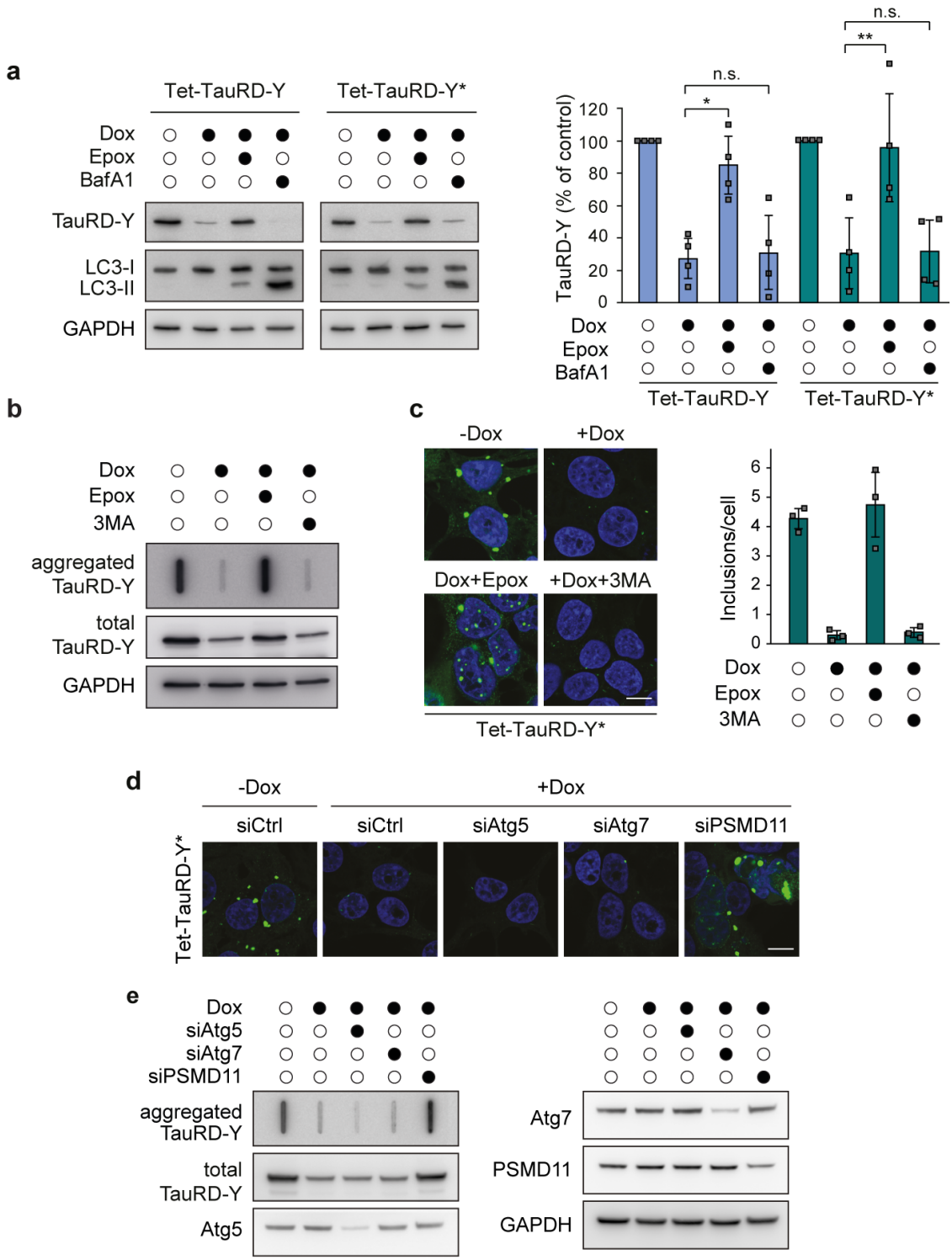
Supplementary Fig. 1: Tau aggregation and clearance in a constitutive expression model.

a Immunofluorescence staining of TauRD-Y* cells with an antibody against Tau phosphorylation at S356 (red) and YFP fluorescence of TauRD-Y (green). Scale bar, 10 µm. **b** Analysis of Tau S356 phosphorylation in lysates of TauRD-Y and TauRD-Y* cells by immunoblotting. Total TauRD-Y was detected using antibody against TauRD. **c** Solubility of TauRD-Y in TauRD-Y and TauRD-Y* cells at steady state, determined by fractionation of cell lysate by centrifugation, followed by immunoblotting with anti-GFP antibody. T, total cell lysate, S, supernatant, P, pellet. **d** Immunofluorescence staining of full-length Tau (FLTau-Y) in aggregate-containing FLTau-Y* cells with AT-8 antibody specific for Tau phosphorylation at S202/T205 (red) and YFP fluorescence of TauRD-Y (green). Scale bar, 10 µm. **e** Solubility of phosphorylated FLTau-Y in FLTau-Y and FLTau-Y* cells at steady state analyzed as in (c). Immunoblotting was with AT-8 antibody (bottom) and anti-GFP (top). GAPDH served as loading control. **f** Turnover of TauRD-Y in TauRD-Y and TauRD-Y* cells upon cycloheximide (CHX) shut-off (CHX; 50 µg/mL). Left, anti-GFP immunoblots to determine TauRD-Y levels. Tubulin served as loading control. Right, exponential fits of CHX chase data and corresponding half-lives ($t_{1/2}$). Mean ± s.d.; n=3. **g** Filter trap analysis of aggregated TauRD-Y upon CHX chase for 24 h. Aggregated and total TauRD-Y levels were determined by anti-GFP immunoblotting. GAPDH served as loading control.



Supplementary Fig. 2: TauRD-Y aggregation and clearance upon inhibition of expression in a Tet-regulated TauRD-Y expression system.

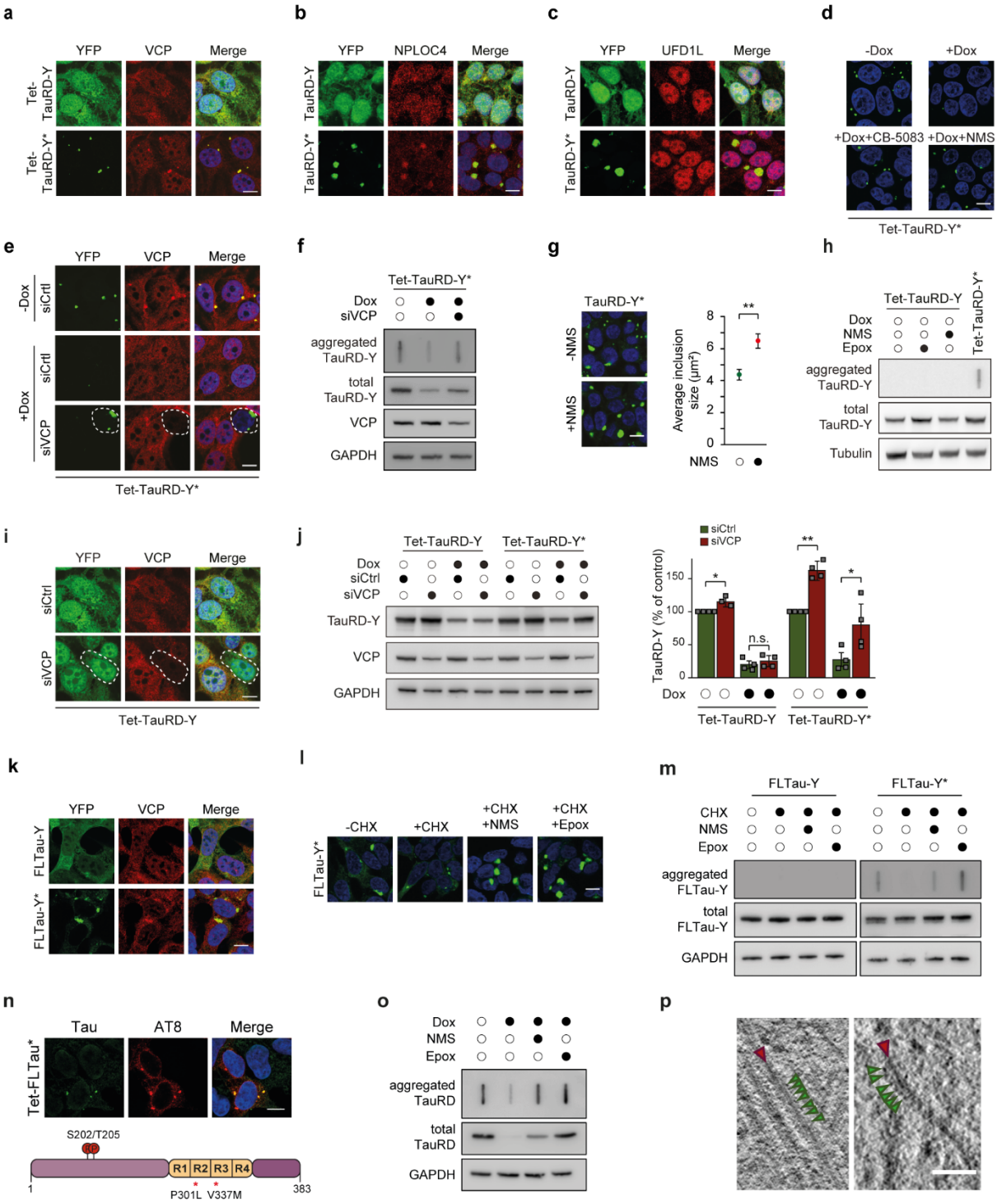
a Solubility of TauRD-Y in Tet-TauRD-Y and Tet-TauRD-Y* cells upon addition of 50 ng/mL doxycycline (Dox) for 24 h. Cell lysates were fractionated as in Supplementary Fig. 1c. TauRD-Y was detected with anti-GFP antibody. GAPDH served as loading control. **b** Representative fluorescence images of Tet-TauRD-Y* cells treated with Dox for 24 h showing staining of TauRD-Y inclusions (green) with Amylo-Glo (magenta). White dashed lines indicate cell boundaries. Scale bar, 10 µm. **c** Quantitative PCR analysis of TauRD-Y mRNA in Tet-TauRD-Y and Tet-TauRD-Y* cells treated with Dox for 0, 3, 6, 12, 18 and 24 h. mRNA levels were normalized to the reference gene *RPS18*. Mean ± s.d.; n=3. **d** Solubility of TauRD-Y in Tet-TauRD-Y* cells upon addition of Dox for the indicated times. Normalized ratios of TauRD-Y in soluble (S) and pellet (P) fractions are stated.



Supplementary Fig. 3: Effect of UPS and autophagy inhibition on TauRD-Y levels and aggregate clearance.

a Analysis of TauRD-Y levels in Tet-TauRD-Y and Tet-TauRD-Y* cells treated for 24 h with doxycycline (Dox; 50 ng/mL) alone or in combination with Epoxomicin (Epox; 50 nM) or

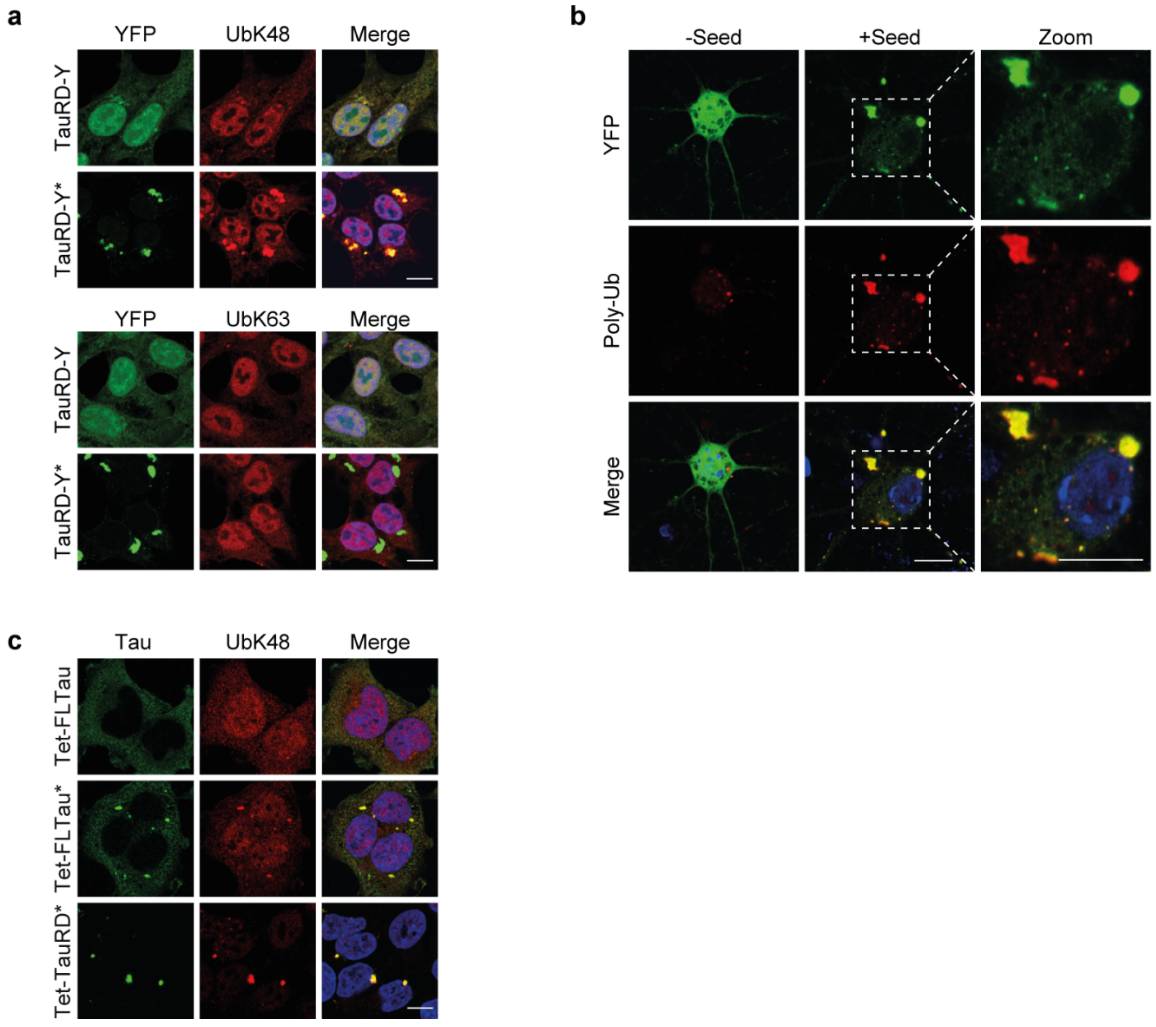
Bafilomycin A1 (BafA1; 50 nM). TauRD-Y and LC3 levels were determined by immunoblotting against GFP and LC3B respectively. GAPDH served as loading control. Mean ± s.d.; n=4. *p<0.05 (Tet-TauRD-Y: + Dox vs + Dox + Epox, p=0.0114), **p<0.01 (Tet-TauRD-Y*: + Dox vs + Dox + Epox, p=0.0026); n.s. non-significant (Tet-TauRD-Y: + Dox vs + Dox + Epox, p= 0.6422; Tet-TauRD-Y*: + Dox vs + Dox + Epox, p= 0.8799) from two-tailed Student's paired t-test. **b** Filter trap analysis of Tet-TauRD-Y* cells treated for 24 h with Dox alone or in combination with Epoxomicin (Epox; 50 nM) or 3-methyladenine (3MA; 5 mM). Aggregated and total TauRD-Y was detected with anti-GFP antibody. **c** Left, representative images of Tet-TauRD-Y* cells treated for 24 h with Dox alone or, in combination with Epoxomicin (Epox; 50 nM) or 3MA (5 mM). Scale bar, 10 μm. Right, quantification of TauRD-Y foci. 100-200 cells analyzed per experiment. Mean ± s.d.; n=3. **d** Representative images of Tet-TauRD-Y* cells transfected with non-targeted (Ctrl) siRNA or siRNA against Atg5 (50 nM), Atg7 (50 nM) and PSMD11 (25 nM). 72 h after transfection, doxycycline (Dox; 50 ng/mL) was added for another 24 h where indicated. Scale bar, 10 μm. **e** Filter trap analysis of Tet-TauRD-Y* cells transfected with siRNAs and treated with Dox as stated in (d). TauRD-Y was detected by immunoblotting with anti-GFP antibody.



Supplementary Fig. 4: Aggregation specific stabilization of Tau by VCP inactivation.

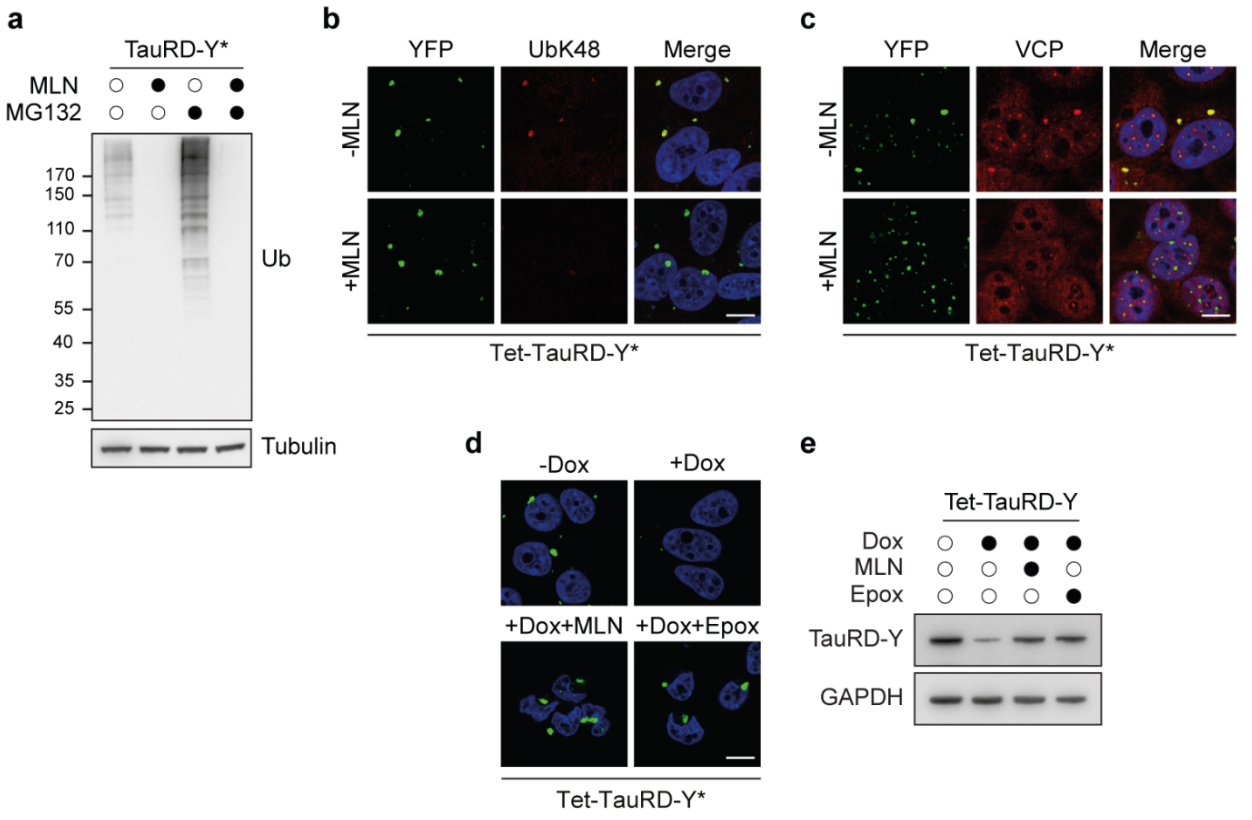
a Immunofluorescence staining of VCP (red) and YFP fluorescence of TauRD-Y (green) in Tet-TauRD-Y and Tet-TauRD-Y* cells. **b** and **c** Immunofluorescence staining of NPLOC4 (b) (red) and UFD1L (c) (red) in TauRD-Y and TauRD-Y* cells. Scale bars, 10 µm. **d** Representative images of Tet-TauRD-Y* cells treated for 24 h with doxycycline (Dox; 50 ng/mL) alone or in

combination with CB-5083 (1 μM) or NMS-873 (NMS; 2.5 μM). Scale bar, 10 μm. **e** Immunofluorescence staining of VCP (red) in Tet-TauRD-Y* cells treated with non-targeted (Ctrl) or VCP siRNA for 96 h. Doxycycline (Dox; 50 ng/mL) was added for the last 24 h. Dashed lines indicate a cell with reduced VCP levels. Scale bar, 10 μm. **f** Filter trap analysis of aggregated TauRD-Y in Tet-TauRD-Y* lysates treated as in (d). Aggregated and total TauRD-Y was analyzed by anti-GFP immunoblotting. GAPDH served as loading control. **g** Size increase of TauRD-Y inclusions upon VCP inhibition. Representative images of TauRD-Y* cells treated for 24 h with NMS-873 (NMS; 5 μM) and quantification of average inclusion size (μm^2). 200-400 cells analyzed per experiment. Mean ± s.d.; n=5. **p<0.01 (p= 0.0022) from two-tailed Student's paired t-test. **h** Filter trap analysis of Tet-TauRD-Y cells treated for 24 h with Epoxomicin (Epox; 50 nM) or NMS-873 (NMS; 2.5 μM) where indicated. Tet-TauRD-Y* lysate was used as control. TauRD-Y was detected by immunoblotting with anti-GFP antibody. **i** Immunofluorescence staining of VCP (red) and YFP fluorescence of TauRD-Y (green) in Tet-TauRD-Y cells transfected with non-targeted (Ctrl) or VCP siRNA for 96 h. Dashed lines indicate a cell with reduced VCP levels. Scale bar, 10 μm. **j** Left, analysis of TauRD-Y level in Tet-TauRD-Y and Tet-TauRD-Y* cells transfected for 96 h with non-targeted (Ctrl) or VCP siRNA where indicated. Doxycycline (Dox; 50 ng/mL) was added for the last 24 h. TauRD-Y was detected by immunoblotting with anti-GFP antibody. Right, quantification of TauRD-Y immunoblot. Mean ± s.d.; n=4. *p<0.05 (Tet-TauRD-Y - Dox: siCtrl vs siVCP, p= 0.0218; Tet-TauRD-Y* + Dox: siCtrl vs siVCP, p= 0.0156); **p<0.01 (Tet-TauRD-Y* - Dox: siCtrl vs siVCP, p= 0.0023); n.s. non-significant (Tet-TauRD-Y + Dox: siCtrl vs siVCP, p= 0.0539) from two-tailed paired Student's t-test. **k** Immunofluorescence staining of VCP (red) and YFP fluorescence of FLTau-Y (green) in FLTau-Y and FLTau-Y* cells. Scale bar, 10 μm. **l** Representative images of FLTau-Y* cells treated for 24 h with cycloheximide (CHX; 50 μg/mL) alone or in combination with NMS-873 (NMS; 2.5 μM) or Epoxomicin (Epox; 100 nM). Scale bar, 10 μm. **m** Filter trap analysis of lysates from FLTau-Y and FLTau-Y* cells treated for 24 h with Dox alone or in combination with NMS-873 (NMS; 2.5 μM) or Epoxomicin (Epox; 50 nM). Aggregated and total FLTau-Y levels were determined by immunoblotting against GFP. GAPDH served as loading control. **n** Immunofluorescence staining of full-length Tau (FLTau) in aggregate-containing Tet-FLTau* cells with Tau (green) and Tau S202/T205 phosphorylation specific AT-8 (red) antibody. Scale bar, 10 μm. **o** Filter trap analysis of lysates from Tet-TauRD* cells treated for 24 h with Dox alone or in combination with NMS-873 (NMS; 2.5 μM) or Epoxomicin (Epox; 50 nM). Aggregated and total TauRD levels were determined by immunoblotting against myc and TauRD, respectively. GAPDH served as loading control. **p** Examples of two TauRD-Y fibrils from a representative 1.4 nm thick tomographic slice of a TauRD inclusion from neurons. Red arrows indicate TauRD-Y fibrils and green arrows indicate globular densities along fibrils. Scale bar, 40 nm.



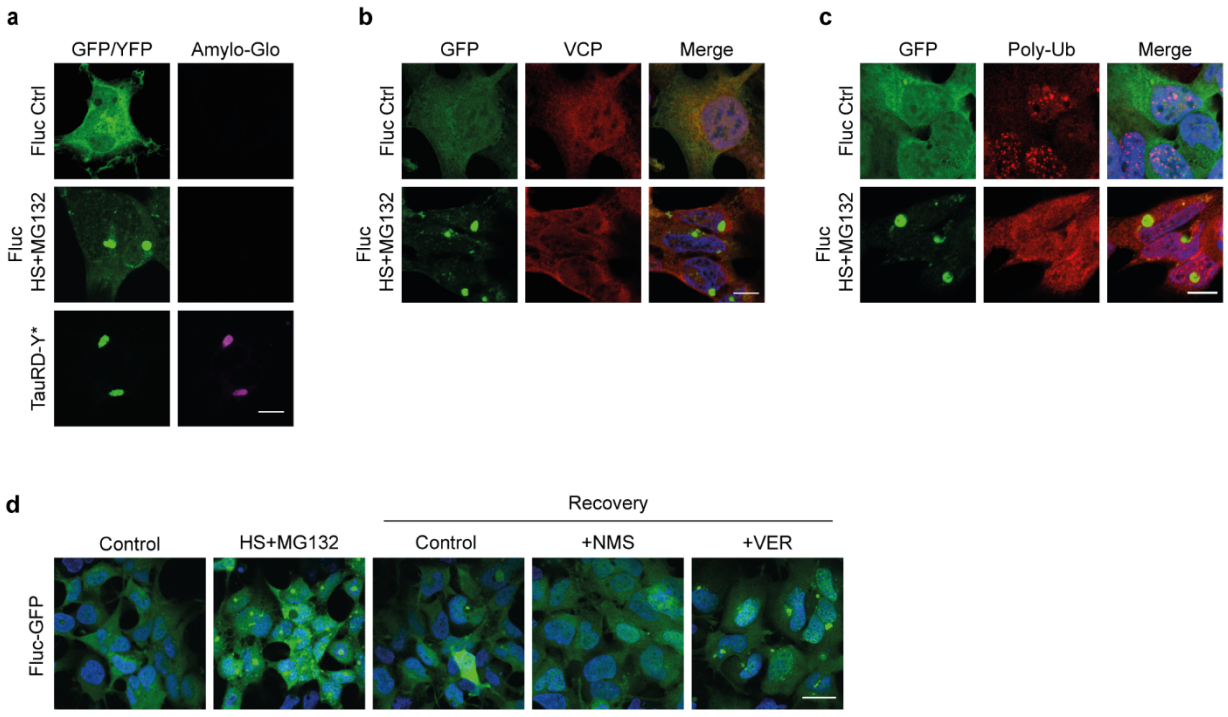
Supplementary Fig. 5: Ubiquitylation of TauRD-Y aggregates.

a Immunofluorescence staining of (top) ubiquitin-K48 (UbK48) (red) and (bottom) ubiquitin K63 (UbK63) (red) chains and YFP fluorescence of TauRD-Y (green) in TauRD-Y and TauRD-Y* cells. Scale bars, 10 µm. **b** Immunofluorescence staining of ubiquitylated proteins (FK2 antibody) (red) in primary neurons expressing TauRD-Y (green) and treated with TauRD containing lysates (+Seed) where indicated. Scale bars, 20 µm. **c** Immunofluorescence staining of ubiquitin-K48 (UbK48) (red) chains and Tau (green) in Tet-FLTau, Tet-FLTau* and Tet-TauRD* cells. FLTau was detected using Tau-5 and TauRD using anti-myc antibody. Scale bar, 10 µm.



Supplementary Fig. 6: Role of ubiquitylation in TauRD-Y disaggregation.

a Analysis of ubiquitylated protein levels in lysates of TauRD-Y* cells treated with the ubiquitin activating enzyme E1 inhibitor MLN7243 (MLN; 0.5 µM) alone or in combination with proteasome inhibitor MG132 (1 µM) for 14 h. Ubiquitylated proteins were detected by immunoblotting against ubiquitin. Tubulin served as loading control. **b** Immunofluorescence staining of ubiquitin-K48 chains (UbK48) (red) and **c** VCP (red) in Tet-TauRD-Y* cells treated with MLN7243 (MLN; 0.5 µM) for 12 h. Scale bars, 10 µm. **d** Representative images of Tet-TauRD-Y* cells treated for 24 h with doxycycline (Dox; 50 ng/mL) alone or in combination with MLN7243 (MLN; 0.5 µM) or Epoxomicin (Epox; 50 nM). Scale bar, 10 µm. **e** Analysis of TauRD-Y levels in Tet-TauRD-Y cells treated for 24 h with Dox, MLN7243 and Epoxomicin as in (d). GAPDH served as loading control.



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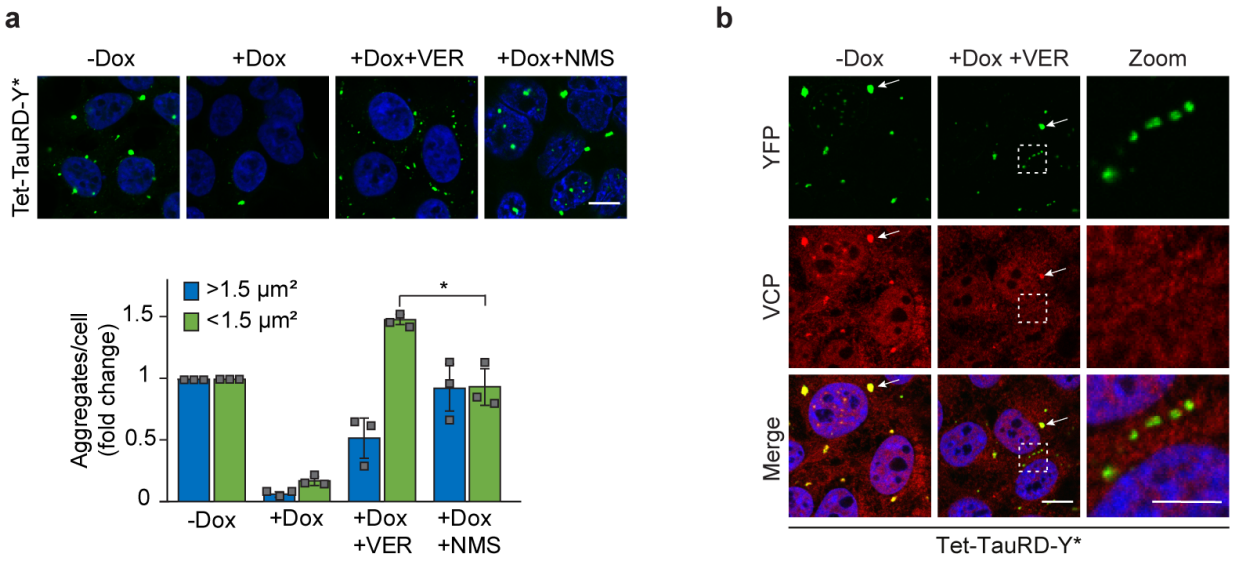
167 **Supplementary Fig. 7: Effect of VCP inhibition on firefly luciferase (Fluc) disaggregation.**
168 **a** Fluc-GFP expressing cells maintained at 37 °C (Fluc Ctrl) or heat-stressed at 43 °C in presence
169 of 5 µM MG132 for 2 h (Fluc HS) were stained with the amyloid-specific dye Amylo-Glo
170 (magenta). TauRD-Y* cells were used as control. Amylo-Glo fluorescence was imaged with
171 similar exposure settings in all panels. Scale bar, 10 µm. **b** Immunofluorescence staining of VCP
172 (red), and **c** ubiquitylated proteins (FK2 antibody) (red) in Fluc-GFP cells treated as in (a). Scale
173 bars, 10 µm. **d** Effect of VCP and Hsp70 inhibition on Fluc-GFP disaggregation. Fluc-GFP
174 aggregation was induced as in (a). Cells were then shifted to MG132 free media and allowed to
175 recover at 37 °C for 8 h in presence of NMS-873 (NMS; 2.5 µM) and VER-155008 (VER; 10
176 µM) where indicated. Scale bar, 30 µm.



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178 **Supplementary Fig. 8: Role of Hsp70 in TauRD-Y disaggregation.**

179 **a** Top, Representative images of Tet-TauRD-Y* cells treated for 24 h with doxycycline (Dox; 50
180 ng/mL) alone or in combination with VER-155008 (VER; 10 µM) or NMS-873 (NMS; 2.5 µM).
181 Bottom, quantification of large (>1.5 µm^2) and small (<1.5 µm^2) TauRD-Y foci. Mean ± s.d.;
182 n=3; ~100-200 cells were analyzed per experiment. *p<0.05 (p=0.0435) from two-tailed
183 Student's paired t-test. Scale bar, 10 µm. **b** Immunofluorescence staining of VCP (red) and YFP
184 fluorescence of TauRD-Y (green) in Tet-TauRD-Y* cells treated with a combination of
185 doxycycline (Dox) and VER-155008 (VER) where indicated. White arrow points to large
186 TauRD-Y inclusions co-localizing with VCP. Dashed lines enclose TauRD-Y foci that do not co-
187 localize with VCP. Scale bar, 10 µm. Scale bar zoom, 5 µm.
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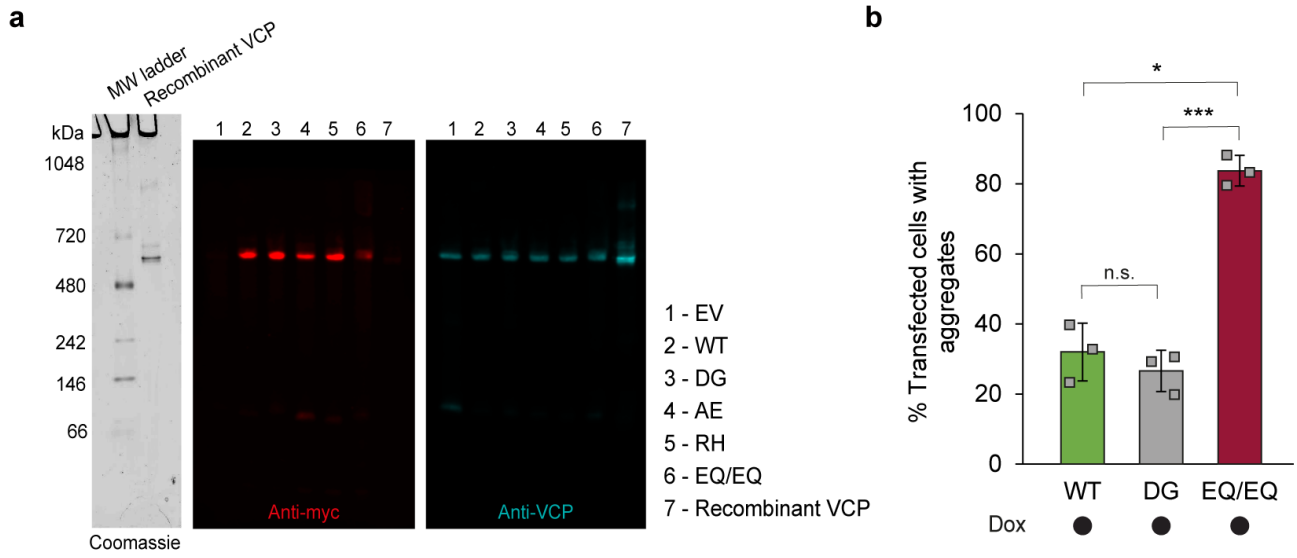
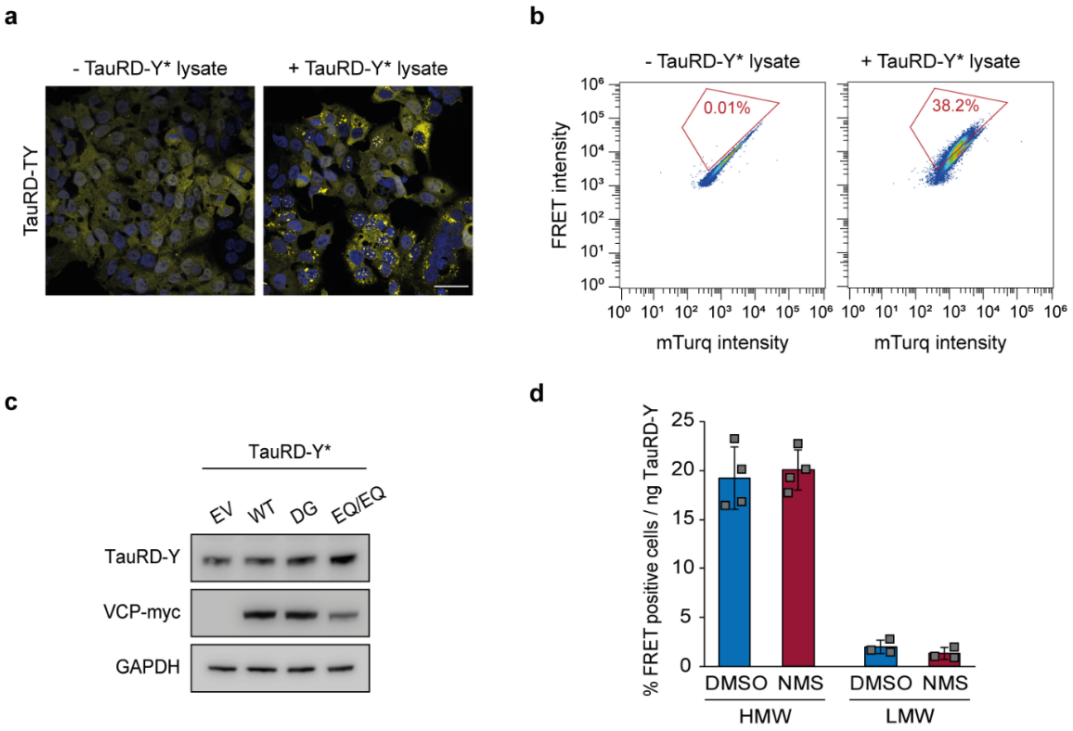


Supplementary Fig. 9: Effect of VCP mutants on Tau disaggregation.

a Native-PAGE analysis of recombinant VCP and lysates from Tet-TauRD-Y* cells transfected with empty vector (EV) and myc-tagged wild type (WT), D395G (DG), A232E (AE), R155H (RH) and E305Q/E578Q (EQ/EQ) VCP constructs. Immunoblot probed against myc (red) and VCP (cyan) is shown. Non-tagged, recombinant VCP was analyzed as control. **b** Quantification of aggregate foci in myc-positive Tet-TauRD-Y* cells transfected with myc-tagged WT, DG and EQ/EQ VCP constructs for 24 h, and treated for another 24 h with doxycycline (Dox; 50 ng/mL). Mean ± s.d.; n=3; > 100 cells analyzed per experiment; *p<0.05 (WT vs EQ/EQ p=0.0192); ***p<0.001 (DG vs EQ/EQ p=0.0008); n.s. non-significant (p=0.5646).



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201 **Supplementary Fig. 10: Analysis of seeding-competent TauRD-Y.**

202 **a** Representative images of TauRD-TY FRET reporter cells treated with TauRD-Y* lysate where
203 indicated showing TauRD-Y florescence in yellow. Scale bar, 40 µm. **b** Representative
204 pseudocolour dot plots for the analysis of FRET positive TauRD-TY cells by flow cytometry
205 upon addition of TauRD-Y* lysate. FRET intensity is plotted against mTurquoise2 (mTurq)
206 intensity and the % of FRET positive cells are indicated in red gates. **c** Analysis of TauRD-Y and
207 VCP-myc levels in TauRD-Y* cells transfected for two days with empty vector (EV) and myc-
208 tagged wild type (WT), D395G (DG) and E305Q/E578Q (EQ/EQ) VCP constructs. TauRD-Y
209 and overexpressed VCP levels were determined by immunoblotting against GFP and myc,
210 respectively. GAPDH served as loading control. **d** Comparison of seeding efficiencies of high
211 molecular weight (HMW) and low molecular weight (LMW) species obtained by size exclusion
212 chromatography of lysates from TauRD-Y* cells treated for 24 h with DMSO or NMS-873
213 (NMS; 2 µM). Mean ± s.d.; HMW n=4, LMW n=3.

Supplementary Table 1: TauRD-Y interactome in TauRD-Y* cells

List of proteins interacting with TauRD-Y in TauRD-Y* cells at steady state determined by stable isotope labelling by amino acids in cell culture (SILAC). TauRD-Y cells were used as control. Normalized SILAC ratios of TauRD-Y*/TauRD-Y [H/L] from 3 independent replicates are shown. Interactors were defined as proteins quantified in at least 2 out of 3 replicates with enrichment ≥2 fold. Proteins with known association to the ubiquitin-proteasome system are highlighted in green and VCP-cofactor complex in red. Intensity-based absolute quantification (iBAQ) values reflect measured molar protein amounts.

Protein ID	Protein name	Gene name	Fasta headers	Unique peptides	Mol. weight [kDa]	Norm. ratio [H/L] Rep.1	Norm. ratio [H/L] Rep.2	Norm. ratio [H/L] Rep.3	Median norm. ratio	iBAQ [H] Exp.1	iBAQ [H] Exp.2	iBAQ [H] Exp.3
Q9UNZ2;F2Z2K	NSFL1 cofactor p47	NSFL1C	sp|Q9UNZ2|NSF1C_HUMAN NSFL1 cofactor p47 OS=Homo sapi	14	40,572	42,702	80,022	11,719	42,702	59143000	112180000	13783000
Q9UQN3;A0A0	Charged multivesicular body protein 2	CHMP2B	sp|Q9UQN3|CHM2B_HUMAN Charged multivesicular body pro	4	23,906	18,201	25,514	11,839	18,201	2093000	5417800	15472000
P55072;C9IZA5	Transitional endoplasmic reticulum ATI	VCP	sp|P55072|TERA_HUMAN Transitional endoplasmic reticulum	47	89,321	16,959	43,344	6,3181	16,959	29193000	94165000	26411000
Q9UNM6;J3KN	26S proteasome non-ATPase regulatory	PSMD13	sp|Q9UNM6|PSD13_HUMAN 26S proteasome non-ATPase regu	22	42,945	17,963	16,071	13,583	16,071	9313200	17290000	5085700
Q6PEV8	Protein FAM199X	FAM199X	sp|Q6PEV8|F199X_HUMAN Protein FAM199X OS=Homo sapier	5	42,801	41,449	15,154	15,115	15,154	9838300	30031000	10267000
F8VUA2;Q9HD4	Charged multivesicular body protein 1	CHMP1A	tr|F8VUA2|F8VUA2_HUMAN Charged multivesicular body prot	5	19,531	14,648	19,186	12,293	14,648	25912000	113020000	38592000
Q15773;F5H0Y	Myeloid leukemia factor 2	MLF2	sp|Q15773|MLF2_HUMAN Myeloid leukemia factor 2 OS=Hom	6	28,147	16,867	13,819	6,564	13,819	74907000	153440000	42871000
O43242;H0YGV	26S proteasome non-ATPase regulatory	PSMD3	sp|O43242|PSMD3_HUMAN 26S proteasome non-ATPase regul	34	60,977	13,413	15,879	6,9978	13,413	21734000	50167000	10257000
O00231;J3QRY	26S proteasome non-ATPase regulatory	PSMD11	sp|O00231|PSD11_HUMAN 26S proteasome non-ATPase regul	26	47,463	13,086	22,385	7,5615	13,086	14133000	35102000	7362100
P62191;G3V4X	26S protease regulatory subunit 4	PSMC1	sp|P62191|PRS4_HUMAN 26S proteasome regulatory subunit	20	49,184	12,739	13,685	6,7346	12,739	6082800	18968000	4723500
P17480	Nucleolar transcription factor 1	UBTF	sp|P17480|UBF1_HUMAN Nucleolar transcription factor 1 OS=	22	89,405	12,209	11,585	7,1602	11,585	94071000	144030000	43389000
O14545;F8VNX	TRAF-type zinc finger domain-containin	TRAFD1	sp|O14545|TRAD1_HUMAN TRAF-type zinc finger domain-cont	12	64,84	7,2319	19,2	11,522	11,522	6914300	16022000	16301000
Q13501;E7EMC	Sequestosome-1	SQSTM1	sp|Q13501|SQSTM_HUMAN Sequestosome-1 OS=Homo sapien	16	47,687	9,6152	17,975	11,41	11,41	27933000	113830000	115270000
Q13200;C9JPC	26S proteasome non-ATPase regulatory	PSMD2	sp|Q13200|PSMD2_HUMAN 26S proteasome non-ATPase regul	46	100,2	7,2067	22,927	11,267	11,267	4555900	9942100	6380700
H0Y6K2;A0A14	Bromodomain-containing protein 2	BRD2	tr|H0Y6K2|H0Y6K2_HUMAN Bromodomain-containing protein	11	88,288	24,922	7,6855	10,958	10,958	6685300	16169000	6613700
H0YFD6;P4093	Trifunctional enzyme subunit alpha, mi	HADHA	tr|H0YFD6|H0YFD6_HUMAN Trifunctional enzyme subunit alp	29	86,371	10,902	11,422	8,175	10,902	45516000	92103000	31426000
P55036;Q5VW	26S proteasome non-ATPase regulatory	PSMD4	sp|P55036|PSMD4_HUMAN 26S proteasome non-ATPase regul	14	40,736	12,228	10,9	3,7986	10,9	19080000	82099000	8516700
Q6QNY1;J3QRU	Biogenesis of lysosome-related organell	BLOC1S2	sp|Q6QNY1|BL1S2_HUMAN Biogenesis of lysosome-related org	3	15,961	10,78	15,848	2,0051	10,78	1892700	3652000	1718300
P55084;F5GZQ	Trifunctional enzyme subunit beta, mit	HADHB	sp|P55084|ECHB_HUMAN Trifunctional enzyme subunit beta,	25	51,294	9,9693	11,079	8,0079	9,9693	65103000	128900000	39724000
P25788;G3V4X	Proteasome subunit alpha type-3	PSMA3	sp|P25788|PSA3_HUMAN Proteasome subunit alpha type-3 OS	9	28,433	3,0605	14,754	9,9671	9,9671	2846500	1743900	2866700
A8MUA9;A8MU	Small ubiquitin-related modifier 4;Sma	SUMO3;SUMO4;S	tr|A8MUA9|A8MUA9_HUMAN SMT3 suppressor of mif two 3 ho	1	15,317	8,4377	11,126		9,78185	14432000	26087000	0
Q8TAT6;I3L4U9	Nuclear protein localization protein 4 h	NPLOC4	sp|Q8TAT6|NPL4_HUMAN Nuclear protein localization protein	17	68,119	3,9291	15,451		9,69005	1208400	5604000	0
P25789;H0YM2	Proteasome subunit alpha type-4;Prote	PSMA4	sp|P25789|PSA4_HUMAN Proteasome subunit alpha type-4 OS	10	29,483	2,7706		16,307	9,5388	4339400	0	4387000
Q9UHD9	Ubiquilin-2	UBQLN2	sp|Q9UHD9|UBQL2_HUMAN Ubiquilin-2 OS=Homo sapiens OX	11	65,695	6,6843	11,794		9,23915	8201000	24600000	108990
O14818;H0Y58	Proteasome subunit alpha type-7	PSMA7	sp|O14818|PSA7_HUMAN Proteasome subunit alpha type-7 OS	14	27,887	2,6045	9,1585	10,57	9,1585	3845500	10551000	10021000
Q9UID3;E9PJ3	Vacuolar protein sorting-associated pro	VPS51	sp|Q9UID3|VPS51_HUMAN Vacuolar protein sorting-associate	11	86,041	12,8	5,2875		9,04375	603160	3513600	552200
Q14596;B7Z5R	Next to BRCA1 gene 1 protein	NBR1	sp|Q14596|NBR1_HUMAN Next to BRCA1 gene 1 protein OS=H	12	107,41		15,113	2,4528	8,7829	0	12693000	12934000
Q92890;C9JNP	Ubiquitin fusion degradation protein 1	UFD1L	sp|Q92890|UFD1_HUMAN Ubiquitin recognition factor in ER-a	9	34,5	11,411	6,134		8,7725	785590	5835400	721170
Q15008;C9J0E	26S proteasome non-ATPase regulatory	PSMD6	sp|Q15008|PSMD6_HUMAN 26S proteasome non-ATPase regul	27	45,531	7,3639	9,6008	8,555	8,555	13494000	32338000	6986900
Q96DX7	Tripartite motif-containing protein 44	TRIM44	sp|Q96DX7|TRI44_HUMAN Tripartite motif-containing protein	5	38,472	10,369	6,5983		8,48365	708170	19187000	783500
Q16643;D6R9V	Drebrin	DBN1	sp|Q16643|DREB_HUMAN Drebrin OS=Homo sapiens OX=9606	16	71,428		13,93	2,7427	8,33635	123350	13631000	6342500
A0A087X2I1;P	26S protease regulatory subunit 10B	PSMC6	tr|A0A087X2I1|A0A087X2I1_HUMAN 26S proteasome regulat	16	45,796	10,533	6,0398		8,2864	2266900	10434000	743130
P51665;H3BNT	26S proteasome non-ATPase regulatory	PSMD7	sp|P51665|PSMD7_HUMAN 26S proteasome non-ATPase regul	14	37,025	8,2466	13,713	6,6956	8,2466	9133800	34517000	6064400
P35998;A0A1W	26S protease regulatory subunit 7	PSMC2	sp|P35998|PRS7_HUMAN 26S proteasome regulatory subunit	24	48,633	7,5017	8,0742	8,5178	8,0742	8531200	12549000	5021100
B3KVL5;Q8TBK	Zinc finger CCHC domain-containing pr	ZCCHC10	tr|B3KVL5|B3KVL5_HUMAN Zinc finger, CCHC domain containi	1	20,308		7,1775	8,4956	7,83655	18527000	60508000	11466000
Q8IXW5	Putative RNA polymerase II subunit B1	RPAP2	sp|Q8IXW5|RPAP2_HUMAN Putative RNA polymerase II subuni	13	69,508	10,475	7,8181	3,3996	7,8181	1205400	8566200	4524400
P62979;J3QS3	Ubiquitin-40S ribosomal protein S27a;	RPS27A;UBB;UBC	sp|P62979|RS27A_HUMAN Ubiquitin-40S ribosomal protein S	10	17,965	9,4683	7,6945	4,1911	7,6945	3164100000	7019100000	1951400000
Q99460;A0A08	26S proteasome non-ATPase regulatory	PSMD1	sp|Q99460|PSMD1_HUMAN 26S proteasome non-ATPase regul	42	105,84	6,684	7,415	7,8358	7,415	3058500	12531000	2851500
P43686	26S protease regulatory subunit 6B	PSMC4	sp|P43686|PRS6B_HUMAN 26S proteasome regulatory subuni	21	47,366	8,4576	2,5541	6,7907	6,7907	1137200	10458000	617140
R4GMR5;K7EJR	26S proteasome non-ATPase regulatory	PSMD8	tr|R4GMR5|R4GMR5_HUMAN 26S proteasome non-ATPase reg	10	32,551	1,3779	6,6145	13,37	6,6145	491820	3751000	6211100
P0CAP2;H8Y6P	DNA-directed RNA polymerase II subuni	POLR2M;GCOM1	sp|P0CAP2|GRL1A_HUMAN DNA-directed RNA polymerase II su	4	41,739	6,9552	6,1579		6,55655	2999600	6478700	0
P49721;A0A08	Proteasome subunit beta type-2	PSMB2	sp|P49721|PSB2_HUMAN Proteasome subunit beta type-2 OS=	10	22,836	2,6138	10,075		6,3444	526870	3115400	1949400
Q9UQ35;I3L4D	Serine/arginine repetitive matrix protei	SRRM2	sp|Q9UQ35|SRRM2_HUMAN Serine/arginine repetitive matrix	44	299,61	8,8182	4,1061	6,3418	6,3418	40059000	69443000	34477000
O75487	Glypican-4;Secreted glypican-4	GPC4	sp|O75487|GPC4_HUMAN Glypican-4 OS=Homo sapiens OX=9	13	62,411	6,1176	9,697	5,2264	6,1176	12306000	31449000	4359700
Q9H307;G3V5F	Pinin	PNN	sp|Q9H307|PININ_HUMAN Pinin OS=Homo sapiens OX=9606 G	39	81,627	6,4613	5,9829	3,8631	5,9829	180190000	359840000	205880000
Q99615;K7ESP	DnaJ homolog subfamily C member 7	DNAJC7	sp|Q99615|DNJC7_HUMAN DnaJ homolog subfamily C membe	35	56,44	32,017	5,9433	3,8506	5,9433	58381000	56886000	13723000
O95816	BAG family molecular chaperone regula	BAG2	sp|O95816|BAG2_HUMAN BAG family molecular chaperone re	9	23,772	5,7371	8,5666	3,8905	5,7371	10758000	36658000	8833600
Q9BYN8	28S ribosomal protein S26, mitochond	MRPS26	sp|Q9BYN8|RT26_HUMAN 28S ribosomal protein S26, mitoch	7	24,211	5,6963	5,8954	3,1697	5,6963	15879000	55778000	11868000
P10644;K7EPB	cAMP-dependent protein kinase type I-i	PRKAR1A	sp|P10644|KAP0_HUMAN cAMP-dependent protein kinase typ	12	42,981	5,6698	8,1797	2,4289	5,6698	1804900	8873600	3456600
A0A0C4DG62;F	ADP-ribosylation factor-like protein 6-i	ARL6IP4	tr|A0A0C4DG62|A0A0C4DG62_HUMAN ADP-ribosylation facto	5	24,591	5,6534	5,8168	2,4357	5,6534	11791000	37307000	7853000
Q15545	Transcription initiation factor TFIID sut	TAF7	sp|Q15545|TAF7_HUMAN Transcription initiation factor TFIID	5	40,259	6,7383	4,5475		5,6429	1917000	3824800	262590
F5H442;Q9981	Tumor susceptibility gene 101 protein	TSG101	tr|F5H442|F5H442_HUMAN Tumor susceptibility gene 101 pro	8	40,917	6,9756	3,423		5,1993	1298100	2512100	0

Q14677;H0YD5	Clathrin interactor 1	CLINT1	sp|Q14677|EPN4_HUMAN Clathrin interactor 1 OS=Homo sapi	17	68,259	4,5671	5,1051		4,8361	483270	1390800	0
Q16531;F5GY5	DNA damage-binding protein 1	DDB1	sp|Q16531|DDB1_HUMAN DNA damage-binding protein 1 OS=	51	126,97	5,1552	4,8124	4,7395	4,8124	2260500	2015000	818320
O14646;H0Y8V	Chromodomain-helicase-DNA-binding	CHD1	sp|O14646|CHD1_HUMAN Chromodomain-helicase-DNA-bind	22	196,69	4,667	5,6909	3,5182	4,667	1212300	6836700	855680
G3V5Z7;P6090	Proteasome subunit alpha type;Protea	PSMA6	tr|G3V5Z7|G3V5Z7_HUMAN Proteasome subunit alpha type O	12	28,147		5,4361	3,7845	4,6103	0	986560	3211200
P17980;E9PM6	26S protease regulatory subunit 6A	PSMC3	sp|P17980|PRS6A_HUMAN 26S proteasome regulatory subuni	21	49,203	5,2382	3,8803		4,55925	2297800	7983700	563940
O00232;J3KTJ5	26S proteasome non-ATPase regulatory	PSMD12	sp|O00232|PSD12_HUMAN 26S proteasome non-ATPase regul	22	52,904	4,4642	2,2919	13,215	4,4642	5157500	5534500	3641700
P61964;V9GZ5	WD repeat-containing protein 5	WDR5	sp|P61964|WDR5_HUMAN WD repeat-containing protein 5 OS	5	36,588	2,7665	5,5202		4,14335	1116200	6218500	163100
O00487;C9JW3	26S proteasome non-ATPase regulatory	PSMD14	sp|O00487|PSDE_HUMAN 26S proteasome non-ATPase regulat	10	34,577	4,4008	3,6454		4,0231	2763600	4175800	1273000
P62195;J3QQN	26S protease regulatory subunit 8	PSMC5	sp|P62195|PRS8_HUMAN 26S proteasome regulatory subunit	23	45,626	4,5333	4,0178	2,4837	4,0178	2401900	10162000	3258800
P24928	DNA-directed RNA polymerase II subuni	POLR2A	sp|P24928|RPB1_HUMAN DNA-directed RNA polymerase II sub	51	217,17	3,9675	4,1625	3,3865	3,9675	5036400	22719000	4400000
O14974;F8VZN	Protein phosphatase 1 regulatory subu	PPP1R12A	sp|O14974|MYPT1_HUMAN Protein phosphatase 1 regulatory	15	115,28	3,6323	4,1458		3,88905	135210	738040	0
Q5VIR6;F6VX93	Vacuolar protein sorting-associated pro	VPS53	sp|Q5VIR6|VPS53_HUMAN Vacuolar protein sorting-associatec	10	79,652		2,3872	5,2434	3,8153	0	867750	158630
Q8WV44;H0Y97	E3 ubiquitin-protein ligase TRIM41	TRIM41	sp|Q8WV44|TRI41_HUMAN E3 ubiquitin-protein ligase TRIM41	5	71,669	4,3208	3,4885	3,7734	3,7734	613000	252640	1261800
F8W118;F8VV59;B7Z9C2;F8VRJ2		NAP1L1	tr|F8W118|F8W118_HUMAN Nucleosome assembly protein 1	12	24,694	3,6447	4,8952	3,4073	3,6447	4807500	20158000	2227100
E9PNW4;A0A2U	CD59 glycoprotein	CD59	tr|E9PNW4|E9PNW4_HUMAN Uncharacterized protein OS=Ho	4	11,985		4,7462	2,1357	3,44095	5131200	54954000	35045000
Q96BQ5	Coiled-coil domain-containing protein	CCDC127	sp|Q96BQ5|CC127_HUMAN Coiled-coil domain-containing pro	4	30,834	4,0401		2,7807	3,4104	3768100	3178900	697410
O43164	E3 ubiquitin-protein ligase Praja-2	PJA2	sp|O43164|PJA2_HUMAN E3 ubiquitin-protein ligase Praja-2 O	15	78,213	3,3397	6,1296	2,2392	3,3397	4791500	29710000	8235700
B8ZZD4;Q86VP	Tax1-binding protein 1	TAX1BP1	tr|B8ZZD4|B8ZZD4_HUMAN Tax1-binding protein 1 OS=Homo	14	93,609	9,5213	3,2831	3,1608	3,2831	409770	4896800	4112000
P62857	40S ribosomal protein S28	RPS28	sp|P62857|RS28_HUMAN 40S ribosomal protein S28 OS=Hom	2	7,8409	3,7217	3,2677	1,1842	3,2677	18987000	32783000	6557100
P62873;F6UT2	Guanine nucleotide-binding protein G(	GNB1	sp|P62873|GBB1_HUMAN Guanine nucleotide-binding protein	13	37,377	3,2364	4,2746	1,6165	3,2364	2812200	17175000	35389000
Q7L7X3;J3QS7	Serine/threonine-protein kinase TAO1	TAOK1	sp|Q7L7X3|TAOK1_HUMAN Serine/threonine-protein kinase TA	15	116,07	1,3856	3,2072	3,0804	3,0804	2889600	6633200	6110200
O75955;A0A14	Flotillin-1	FLOT1	sp|O75955|FLOT1_HUMAN Flotillin-1 OS=Homo sapiens OX=9	16	47,355	3,0802	3,6951	1,7534	3,0802	11366000	21730000	4780700
Q12899;A2AE4	Tripartite motif-containing protein 26	TRIM26	sp|Q12899|TRI26_HUMAN Tripartite motif-containing protein	7	62,165	4,126		2,001	3,0635	1519900	2525100	1427900
Q99986;H0YJ5	Serine/threonine-protein kinase VRK1	VRK1	sp|Q99986|VRK1_HUMAN Serine/threonine-protein kinase VR	14	45,476	3,4612	3,0568	1,1048	3,0568	2738700	26700000	18471000
C9J2Y9;P3087	DNA-directed RNA polymerase;DNA-dir	POLR2B	tr|C9J2Y9|C9J2Y9_HUMAN DNA-directed RNA polymerase subu	34	133,06	3,7497	3,0177	3,0513	3,0513	4282800	9848300	392790
H3BV80;H3BM	RNA-binding protein with serine-rich d	RNPS1	tr|H3BV80|H3BV80_HUMAN RNA-binding protein with serine-	6	24,561	3,0441	3,3076	2,5543	3,0441	139510000	204410000	94293000
Q9UBI6	Guanine nucleotide-binding protein G(	GNG12	sp|Q9UBI6|GBG12_HUMAN Guanine nucleotide-binding prote	3	8,0061	3,0438	4,9367	2,0117	3,0438	3890300	34430000	84342000
I1E4Y6;Q6Y7W	PERQ amino acid-rich with GYF domain	GIGYF2	tr|I1E4Y6|I1E4Y6_HUMAN GRB10-interacting GYF protein 2 OS	11	152,53	3,4506	2,6293		3,03995	571610	1017200	0
P16403;P1041	Histone H1.2;Histone H1.4	HIST1H1C;HIST1H	sp|P16403|H12_HUMAN Histone H1.2 OS=Homo sapiens OX=9	12	21,364	3,0264	2,2983	3,593	3,0264	103310000	303900000	129810000
P19387;H3BRR	DNA-directed RNA polymerase II subuni	POLR2C	sp|P19387|RPB3_HUMAN DNA-directed RNA polymerase II sub	10	31,441	3,0233	3,8035	2,6379	3,0233	11207000	18173000	2879500
Q5HYB6		DKFZp686J1372	tr|Q5HYB6|Q5HYB6_HUMAN Epididymis luminal protein 189 (	21	27,175	4,5555	2,9635	2,9779	2,9779	1471400	6297900	1443000
P06748;E5RI98	Nucleophosmin	NPM1	sp|P06748|NPM_HUMAN Nucleophosmin OS=Homo sapiens O	17	32,575	3,5369	2,9192	1,7384	2,9192	45741000	124660000	102380000
J3QLD9;E7EMK	Flotillin-2	FLOT2	tr|J3QLD9|J3QLD9_HUMAN Flotillin-2 OS=Homo sapiens OX=9	15	47,142	2,9067	4,1686	1,6969	2,9067	8440000	26271000	11510000
P62879;C9JIS1	Guanine nucleotide-binding protein G(	GNB2	sp|P62879|GBB2_HUMAN Guanine nucleotide-binding protein	12	37,331	2,9058	4,836	1,5201	2,9058	4881400	14551000	15388000
Q53H12;E9PC1	Acylglycerol kinase, mitochondrial	AGK	sp|Q53H12|AGK_HUMAN Acylglycerol kinase, mitochondrial O	18	47,137	1,1258	2,8627	4,0535	2,8627	4820100	15152000	13972000
Q13112	Chromatin assembly factor 1 subunit B	CHAF1B	sp|Q13112|CAF1B_HUMAN Chromatin assembly factor 1 subu	4	61,492	2,844	2,8809		2,86245	512590	77757	0
A0A087WVZ9;F	DNA-directed RNA polymerases I, II, and	POLR2E	tr|A0A087WVZ9|A0A087WVZ9_HUMAN DNA-directed RNA po	7	21,459	3,1167	2,4935		2,8051	3322300	15849000	0
Q92820	Gamma-glutamyl hydrolase	GGH	sp|Q92820|GGH_HUMAN Gamma-glutamyl hydrolase OS=Hom	8	35,964	2,8025	5,1253	2,0979	2,8025	2133200	7381800	1489700
Q96GA3;A0A07	Protein LTV1 homolog	LTV1	sp|Q96GA3|LTV1_HUMAN Protein LTV1 homolog OS=Homo sa	15	54,854	1,3874	3,0356	2,7805	2,7805	11848000	15414000	11793000
P60709;A0A2R	Actin, cytoplasmic 1;Actin, cytoplasmi	ACTB	sp|P60709|ACTB_HUMAN Actin, cytoplasmic 1 OS=Homo sapie	27	41,736	1,2178	3,5005	2,7751	2,7751	11323000	36019000	20782000
Added01;CON__	Q9U6Y5;I3L170		tr|Added01|TauYfp_HUMAN Tau Yfp	39	43,256	3,5063	2,7256	2,1606	2,7256	4130100000	8914000000	3833400000
Q99613;B5ME1	Eukaryotic translation initiation factor	EIF3C;EIF3CL	sp|Q99613|EIF3C_HUMAN Eukaryotic translation initiation fac	33	105,34	2,5577	2,8357		2,6967	855670	4670000	443520
P28066	Proteasome subunit alpha type-5	PSMA5	sp|P28066|PSA5_HUMAN Proteasome subunit alpha type-5 OS	13	26,411		3,108	2,254	2,681	713200	3627100	526020
Q9HCM4	Band 4.1-like protein 5	EPB41L5	sp|Q9HCM4|E41L5_HUMAN Band 4.1-like protein 5 OS=Homo	9	81,855	2,1785	3,0182		2,59835	227100	3722200	0
A0A087WYV5;A	Slit homolog 2 protein;Slit homolog 2 p	SLIT2	tr|A0A087WYV5|A0A087WYV5_HUMAN Slit homolog 2 protei	9	159,98	2,0219	3,1071		2,5645	487410	1400300	599630
A0A1W2PQ90;I	DNA repair protein RAD50	RAD50	tr|A0A1W2PQ90|A0A1W2PQ90_HUMAN Uncharacterized pro	25	142,94	2,5131	3,214	0,89296	2,5131	1048700	5250600	1514700
Q9H0U4;E9PLD	Ras-related protein Rab-1B;Putative Ra	RAB1B;RAB1C	sp|Q9H0U4|RAB1B_HUMAN Ras-related protein Rab-1B OS=Ho	12	22,171		2,7446	2,1603	2,45245	682330	3902100	564680
Q13823;H0YG1	Nucleolar GTP-binding protein 2	GNL2	sp|Q13823|NOG2_HUMAN Nucleolar GTP-binding protein 2 OS	18	83,654	2,5228	2,3703		2,44655	504360	3938100	57885
Q07021;I3L3Q7	Complement component 1 Q subcomp	C1QBP	sp|Q07021|C1QBP_HUMAN Complement component 1 Q subc	10	31,362	2,1285	5,1114	2,4395	2,4395	5133600	39902000	12700000
Q7Z417	Nuclear fragile X mental retardation-int	NUFIP2	sp|Q7Z417|NUFP2_HUMAN Nuclear fragile X mental retardatio	15	76,12	2,9962	2,4364	2,0328	2,4364	5829600	7837800	5467700
P08670;B0YJC4	Vimentin	VIM	sp|P08670|VIME_HUMAN Vimentin OS=Homo sapiens OX=960	45	53,651	2,4027	2,6728	1,6894	2,4027	59024000	131930000	146780000
P19525;C9JZT2	Interferon-induced, double-stranded R	EIF2AK2	sp|P19525|E2AK2_HUMAN Interferon-induced, double-strand	12	62,094	2,5648	2,384	2,0421	2,384	145870	749090	114650
Q01082	Spectrin beta chain, non-erythrocytic 1	SPTBN1	sp|Q01082|SPTB2_HUMAN Spectrin beta chain, non-erythrocy	120	274,61	2,354	5,0002	1,5658	2,354	14363000	46226000	27935000
A0A0D9SF54;A0A0D9SGF6;A0A0D9SFF6;A0A0D9SFH4;		SPTAN1	tr|A0A0D9SF54|A0A0D9SF54_HUMAN Spectrin alpha chain, n	132	282,83	2,3502	5,0256	1,4746	2,3502	16833000	62862000	26440000
P07948;E5RJ37	Tyrosine-protein kinase Lyn	LYN	sp|P07948|LYN_HUMAN Tyrosine-protein kinase Lyn OS=Homo	12	58,573		2,3857	2,2951	2,3404	0	1032300	2217900
Q9UN86;D6RA(	Ras GTPase-activating protein-binding p	G3BP2	sp|Q9UN86|G3BP2_HUMAN Ras GTPase-activating protein-bin	11	54,12	2,3338	1,3159	2,5495	2,3338	8272900	13070000	6033900
P07900;G3V2J	Heat shock protein HSP 90-alpha	HSP90AA1	sp|P07900|HS90A_HUMAN Heat shock protein HSP 90-alpha O	63	84,659	2,277	4,0858	2,008	2,277	6729400	12647000	4596800
P46013	Antigen KI-67	MKI67	sp|P46013|KI67_HUMAN Proliferation marker protein Ki-67 O	17	358,69	2,3191	2,2468	2,2169	2,2468	524560	475360	44507

P60228;E5RGA	Eukaryotic translation initiation factor	EIF3E	sp|P60228|EIF3E_HUMAN Eukaryotic translation initiation fac	25	52,22	2,3804	2,2127	1,9171	2,2127	1089300	1573400	1367200
P49916;K7ERZ	DNA ligase 3	LIG3	sp|P49916|DNLI3_HUMAN DNA ligase 3 OS=Homo sapiens OX=	8	112,91	2,9178	2,203	2,1767	2,203	1532800	1039000	946440
Q5RKV6	Exosome complex component MTR3	EXOSC6	sp|Q5RKV6|EXOS6_HUMAN Exosome complex component MTI	6	28,235	2,3573	2,1818	2,111	2,1818	11071000	15292000	4620400
P12931	Proto-oncogene tyrosine-protein kinas	SRC	sp|P12931|SRC_HUMAN Proto-oncogene tyrosine-protein kina	8	59,834	2,168	4,1415	1,8886	2,168	748320	2601200	1702500
P63092;Q5JWF	Guanine nucleotide-binding protein G(	GNAS	sp|P63092|GNAS2_HUMAN Guanine nucleotide-binding prote	13	45,664	2,1627	4,1417	1,5402	2,1627	1488700	9048500	3740200
O75531;E9PJJ8	Barrier-to-autointegration factor;Barri	BANF1	sp|O75531|BAF_HUMAN Barrier-to-autointegration factor OS=	6	10,058	2,1605	2,4895	1,4442	2,1605	167700000	464450000	175040000
Q9Y265;E7ETR	RuvB-like 1	RUVBL1	sp|Q9Y265|RUVB1_HUMAN RuvB-like 1 OS=Homo sapiens OX=	24	50,227	1,8486	2,1597	2,5745	2,1597	2800700	6342500	382330
O14578;H7BYJ	Citron Rho-interacting kinase	CIT	sp|O14578|CTRO_HUMAN Citron Rho-interacting kinase OS=H	11	231,43	3,1776	2,1397	0,96079	2,1397	57864	292140	49921
P27986;H0YBC	Phosphatidylinositol 3-kinase regulato	PIK3R1	sp|P27986|P85A_HUMAN Phosphatidylinositol 3-kinase regul	6	83,597	1,5657	2,1169	2,5085	2,1169	745890	1116000	1210500
Q6WCQ1;J3KS	Myosin phosphatase Rho-interacting pr	MPRIP	sp|Q6WCQ1|MPRIP_HUMAN Myosin phosphatase Rho-interact	12	116,53	2,1049	2,173	0,79734	2,1049	588250	1624600	104110
P08754	Guanine nucleotide-binding protein G(	GNAI3	sp|P08754|GNAI3_HUMAN Guanine nucleotide-binding protei	15	40,532	2,0157	4,9059	2,0813	2,0813	19273000	75469000	42160000
O15234;J3KSY	Protein CASC3	CASC3	sp|O15234|CASC3_HUMAN Protein CASC3 OS=Homo sapiens C	8	76,277	2,067	2,0138	2,7423	2,067	698630	2073400	4126900
P17987;E7EQR	T-complex protein 1 subunit alpha	TCP1	sp|P17987|TCPA_HUMAN T-complex protein 1 subunit alpha C	34	60,343	1,5294	2,2873	2,0582	2,0582	485300	1703400	621710
Q5SRQ6;P6787	Casein kinase II subunit beta	CSNK2B;CSNK2B-	tr|Q5SRQ6|Q5SRQ6_HUMAN Casein kinase II subunit beta OS=H	8	26,925	2,0436	2,4349	1,2233	2,0436	5899500	15187000	987590
P08238;Q58FF	Heat shock protein HSP 90-beta	HSP90AB1	sp|P08238|HS90B_HUMAN Heat shock protein HSP 90-beta OS	64	83,263	1,9891	2,9312	2,02	2,02	7615400	29148000	15600000
O95425;A0A0J	Supervillin	SVIL	sp|O95425|SVIL_HUMAN Supervillin OS=Homo sapiens OX=96	9	247,74	1,4281	3,0818	2,0134	2,0134	360680	1636100	213390
Q14676;A2AB0	Mediator of DNA damage checkpoint pr	MDC1	sp|Q14676|MDC1_HUMAN Mediator of DNA damage checkpoi	20	226,66	2,1653	2,0075	1,5305	2,0075	303620	152960	60101
Q14008;H0YDX	Cytoskeleton-associated protein 5	CKAP5	sp|Q14008|CKAP5_HUMAN Cytoskeleton-associated protein 5	72	225,49	1,7242	2,0021	2,3599	2,0021	325010	2252600	1461800