Intrinsically disordered proteins in human diseases: From polyfunctionality to multipathogenicity with intrinsic disorder

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Disclosure Statement

Speaker:

Dr. Vladimir Uversky

- Has no relevant financial relationships to disclose
- Will not be discussing unlabeled/unapproved use of drugs or products

First, a few words of gratitude

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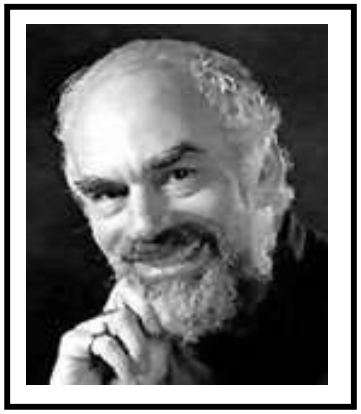

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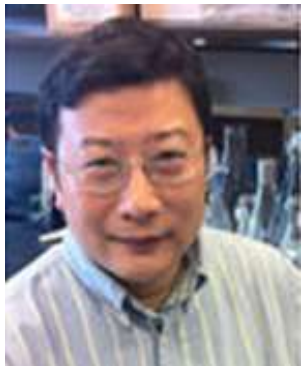

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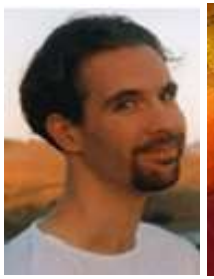
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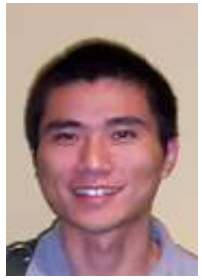
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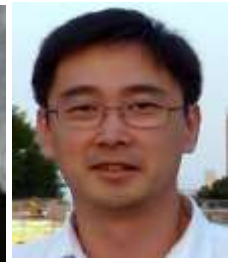
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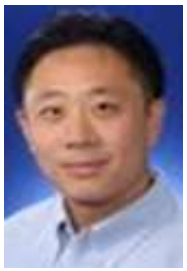
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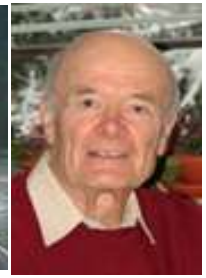
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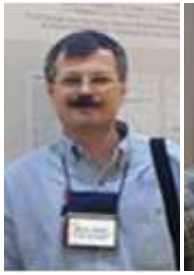
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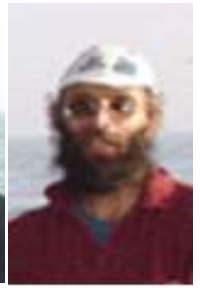
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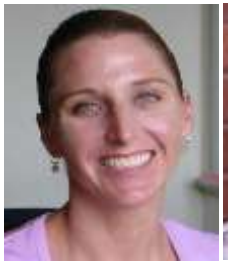

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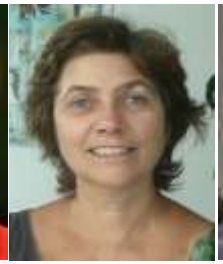
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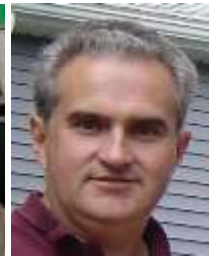
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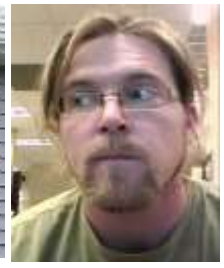
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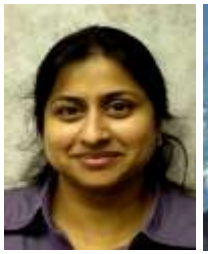

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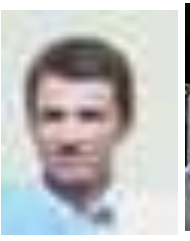

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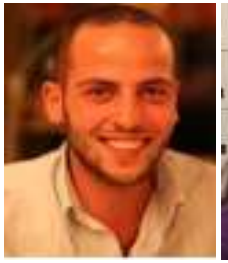

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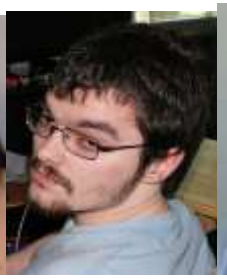

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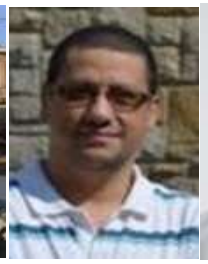

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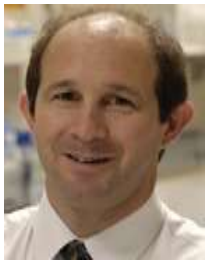

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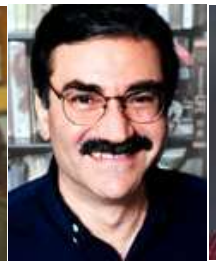

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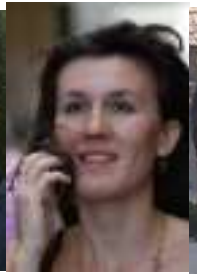

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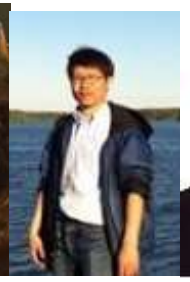

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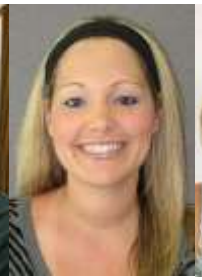

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Dream was to have this “Face Book” of my collaborators completed, but then “Autophagy-2016” happened:

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Toivonen, Luana Tomaipitinca, Dhanendra Tomar, Cristina Tomas-Zapico, Sergej Tomic, Benjamin Chun-Kit Tong, Chao Tong, Xin Tong, Sharon A. Tooze, Maria L. Torgersen, Satoru Torii, Liliana Torres-López, Alicia Torriglia, Christina G. Towers, Roberto Towns, Shinya Toyokuni, Vladimir Trajkovic, Donatella Tramontano, Quynh-Giao Tran, Leonardo H. Travassos, Charles B. Trelford, Shirley Tremel, Gemma Triola, Ioannis P. Trougakos, Betty P. Tsao, Mario P. Tschan, Hung-Fat Tse, Tak Fu Tse, Hitoshi Tsugawa, Andrey S. Tsvetkov, David A. Tumbarello, Yasin Tumtas, María J. Tuñón, Sandra Turcotte, Boris Turk, Vito Turk, Bradley J. Turner, Richard I. Tuxworth, Jessica K. Tyler, Elena V. Tyutereva, Yasuo Uchiyama, Aslihan Ugun-Klusek, Holm H. Uhlig, Marzena Ułamek-Kozioł, Ilya V. Ulasov, Midori Umekawa, Christian Ungermann, Rei Unno, Sylvie Urbé, Elisabet Uribe-Carretero, Suayib Üstün, **Vladimir N. Uversky**, Thomas Vaccari, Maria I. Vaccaro, Björn F. Vahsen, Helin Vakifahmetoglu-Norberg, Rut Valdor, Maria J. Valente, Ayelén Valko, Richard B. Vallee, Angela M. Valverde, Greet Van den Berghe, Stijn van der Veen, Luc Van Kaer, Jorg van Loosdregt, Sjoerd J.L. van Wijk, Wim Vandenberghe, Ilse Vanhorebeek, Marcos A. Vannier-Santos, Nicola Vannini, M. Cristina Vanrell, Chiara Vantaggiato, Gabriele Varano, Máté Varga, M. Helena Vasconcelos, Somya Vats, Demetrios G. Vavvas, Ignacio Vega-Naredo, Silvia Vega-Rubin-de-Celis, Anne Vehlow, Guillermo Velasco, Ariadna P. Velázquez, Francesca Velotti, Tibor Vellai, Edo Vellenga, Mireille Verdier, Panayotis Verginis, Isabelle Vergne, Paul Verkade, Manish Verma, Patrik Verstreken, Tim Vervliet, Jörg Vervoorts, Alexandre T. Vessoni, Victor M. Victor, Michel Vidal, Chiara Vidoni, Otilia V. Vieira, Richard D. Vierstra, Sonia Viganó, Helena Vihinen, Vinoy Vijayan, Miquel Vila, Marçal Vilar, José M. 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Autophagy. 2021; 17(1):1-382. One article with 2,907 co-authors

Over the years, I collaborated with more than 12,500 colleagues from more than 2,750 research organizations in 89 countries/territories

This is my interactome

Presented research would be impossible without them.

My sincere gratitude to all of them!

Outline of Talk

- Introduction of intrinsic disorder
- Manifestations of intrinsic disorder
- Disorder and protein structure-function continuum
- Intrinsically disordered proteins and neurodegenerative diseases
- Conclusions

Introduction of intrinsic disorder

Classical protein structure-function paradigm

"Lock & Key"

Current Protein Structure/ Function Paradigm

"Induced Fit"

Amino Acid Sequence

"Folding Problem"

↓

3-D Structure

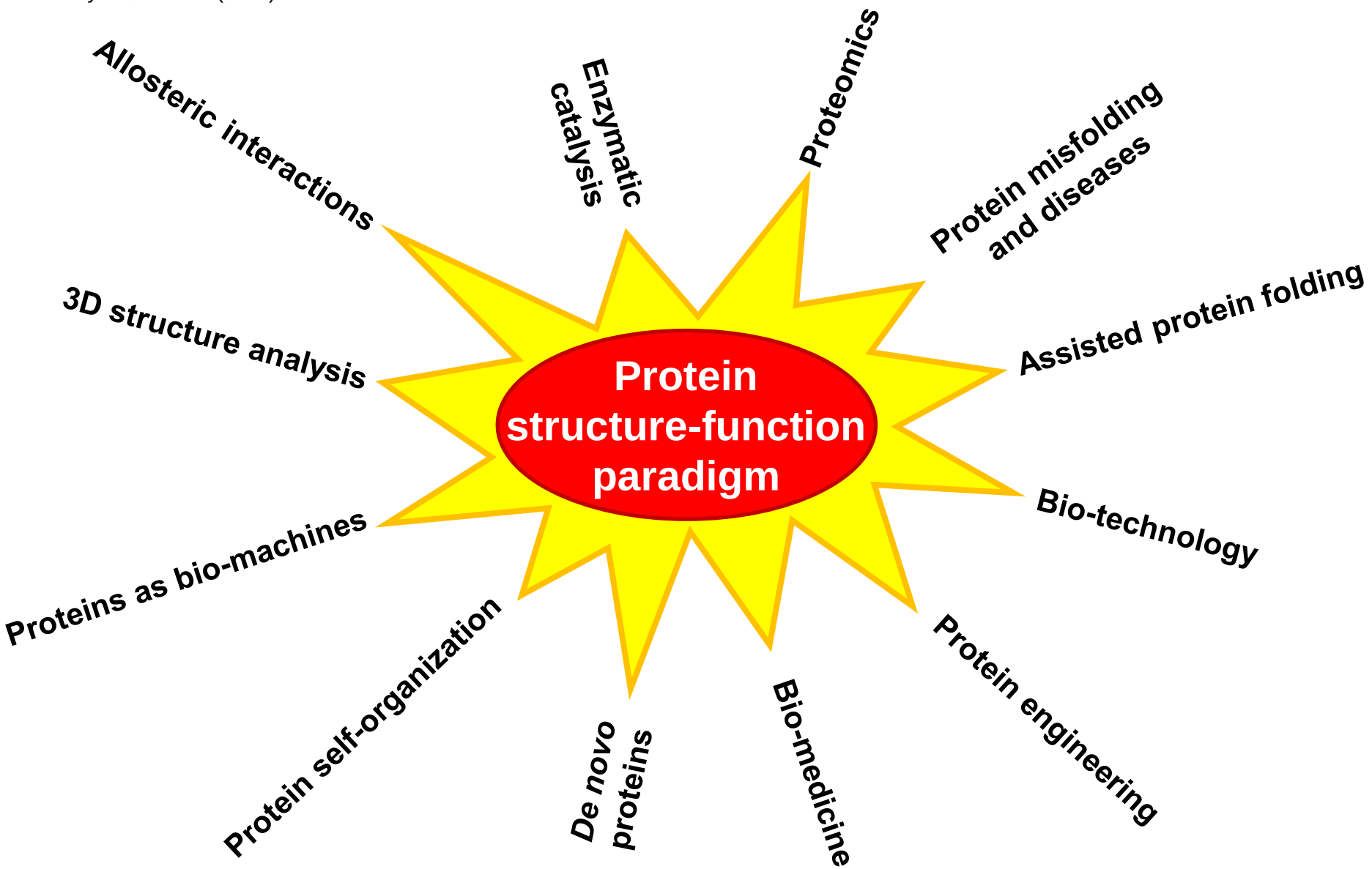
Native = Ordered

↓

Protein Function

["Lock & Key"; "Induced Fit"]

Uversky *Protein Sci.* (2002) **11:** 739



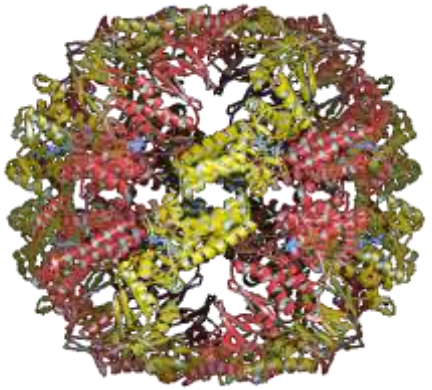
Recognition of intrinsic disorder by example

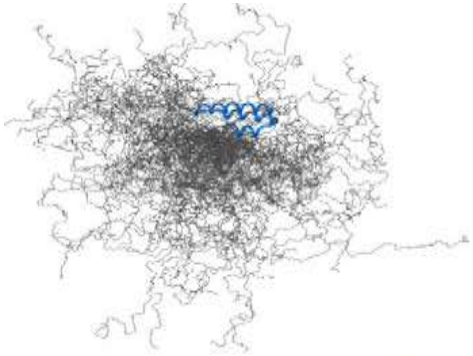
- **Many intrinsically disordered proteins were discovered as exceptions from the classical paradigm;**
- **Originally, these exceptions were rare;**
- **Phenomenon was rediscovered several times;**
- **This fact is reflected in the “paleontology” of intrinsic disorder: Originally, non-traditional proteins were called by different names.**

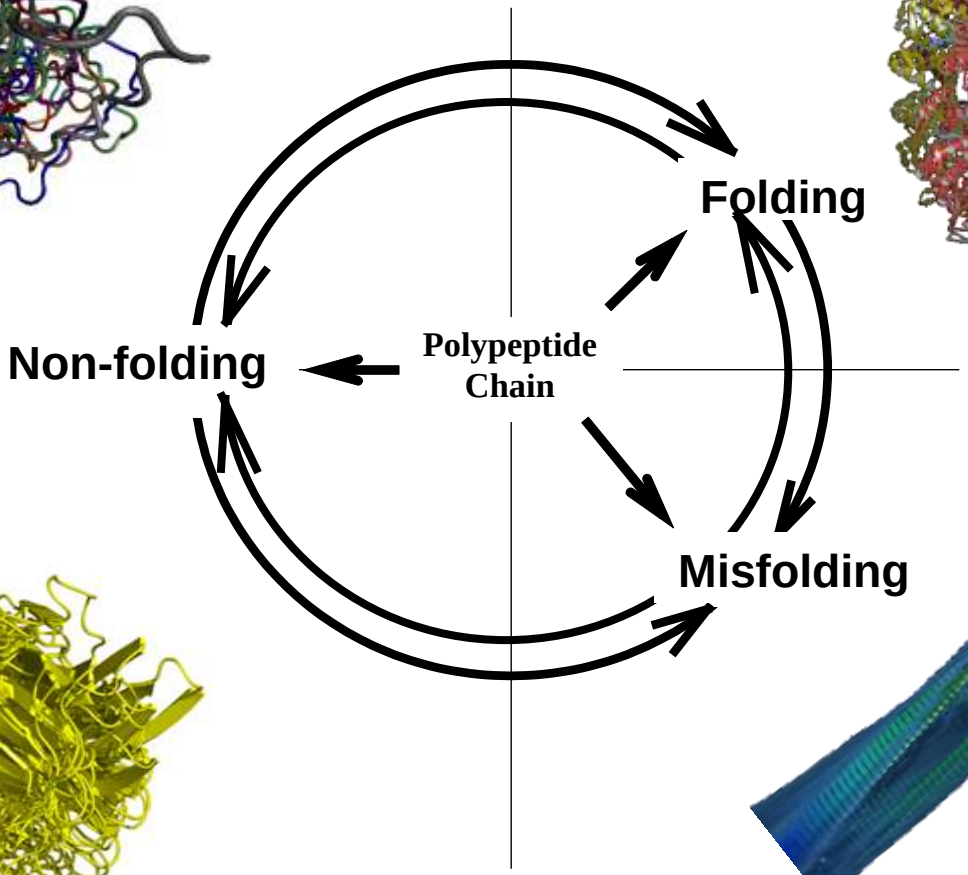
Turn of the century idea:

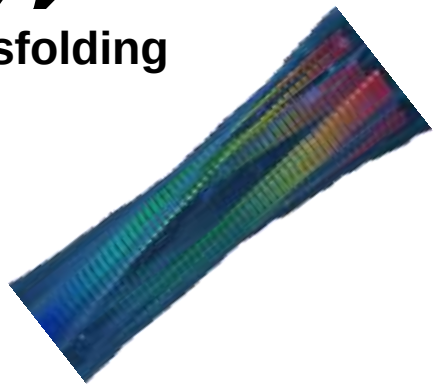
Such non-foldable or intrinsically disordered proteins are not rare exceptions, but could be abundant in nature

Fate of a polypeptide chain



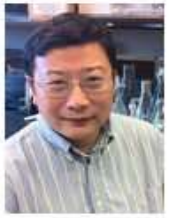






Uversky *Cell. Mol. Life Sci.* (2003) **60:** 1852

Natural abundance of intrinsic disorder

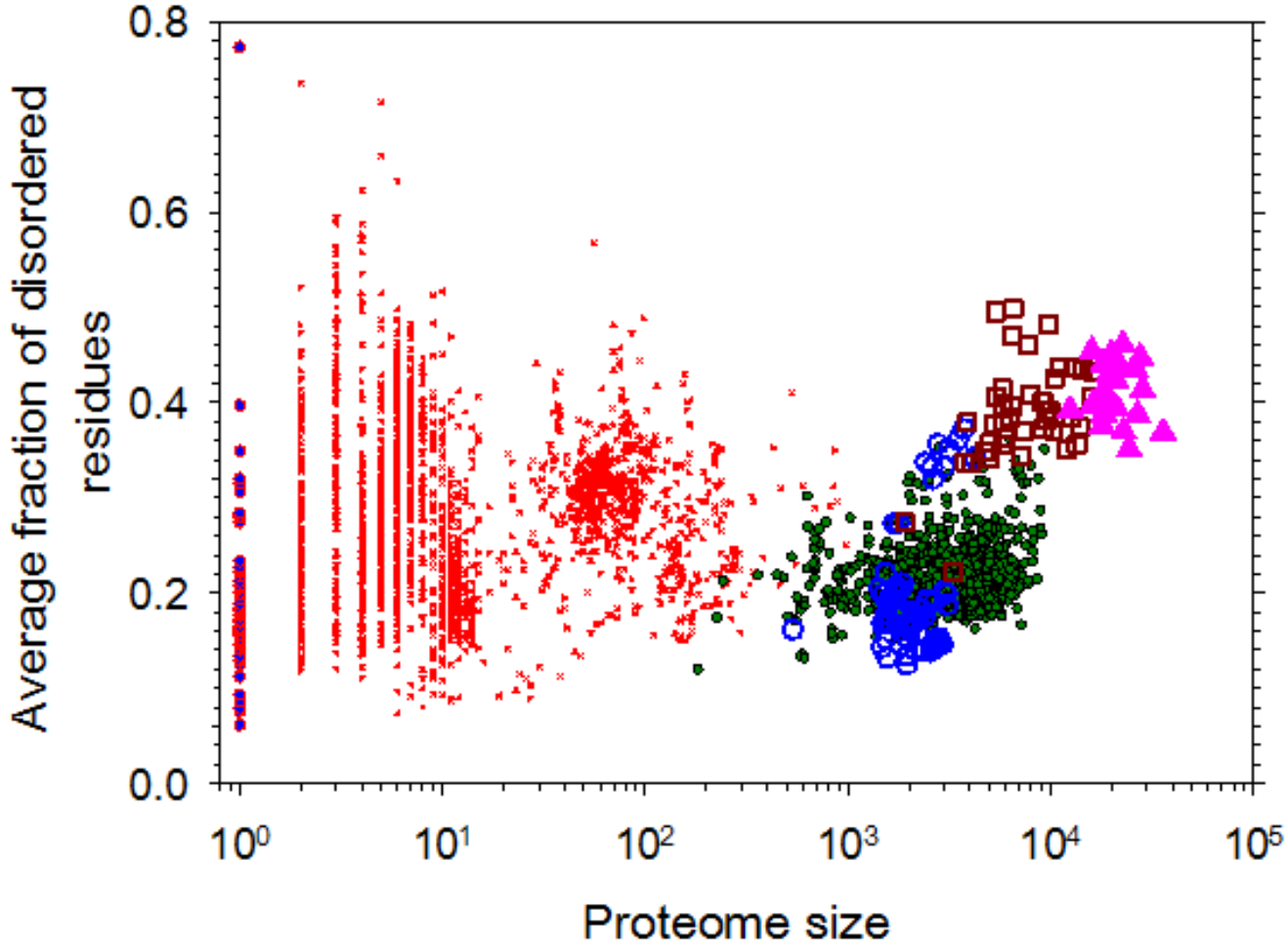


Predicted abundance of IDPs in various proteomes

Organisms	# Orgs.	# Proteins	Avg. # Proteins	% Disordered AA	%Proteins IDR >30	%Proteins Natively Unfolded
Archaea	53	536 – 4234	2052	12.5 – 35.6%	9.5 – 48.9%	3.2 – 28.6%
Bacteria	385	182 – 8172	3009	12.0 – 34.6%	11.5 – 53.7%	3.7 – 29.2%
Single-cellular Eukaryota	12	1909 – 12858	6231	27.4 – 47.1%	59.9 – 68.4%	19.2 – 43.8%
Multi-cellular Eukaryota	5	12459 – 24430	18327	35.1 – 46.1%	37.6 – 61.4%	28.3 – 42.0%

Xue *et al*. (2012) JBSD, **30**, 131

Predicted abundance of IDPs in nature



Xue *et al*. (2012) JBSD, **30**, 131

Q: Why are IDPs so abundant in different proteomes?

A: Likely to be functional

Protein structure/function relationships

Function: Lock & key
Induced fit

Function: Conformation switch

3-D Structure → (α ↔ β)

"Folding Problem"

Order → Disorder → Order

Function:
Virus/pathogen penetration
Membrane insertion
Nucleosome activation

A.A. sequence

Order → Disorder

"Non-Folding Problem"

Flexible Ensemble → Disorder → Order

Function:
Molecular recognition
Virus/phage assembly
Stepping motor

Function:
Flexible linkers
Display sites
Entropic exclusion

Dunker *et al*. (2001) *J. Mol. Graph. Model*. 19, 26

Intrinsic disorder is (almost) incompatible with catalysis, but is suited rather well for regulation, recognitions, and signaling.

Why?

Induced folding: High specificity combined with low affinity

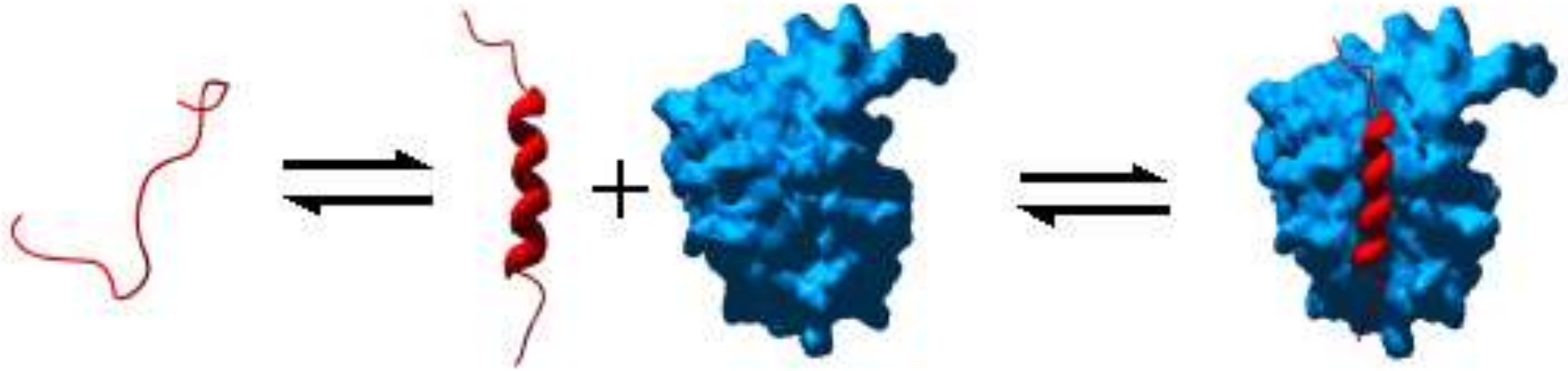
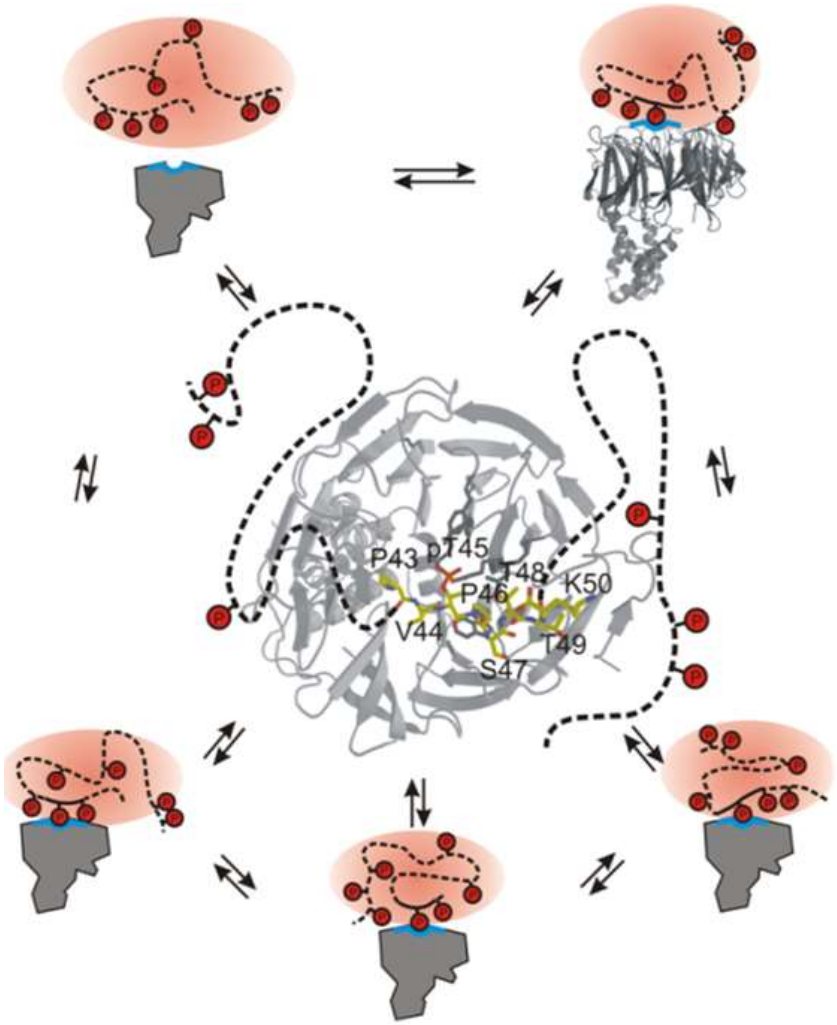


Illustration of disorder-to-order transition upon binding. This example shows the binding of a disordered region of Bad (ribbon) binding to Bcl-XL (globular). Red chain is named MoRF – molecular recognition feature.

Oldfield *et al*. *Biochemistry* (2005) **44**: 12454

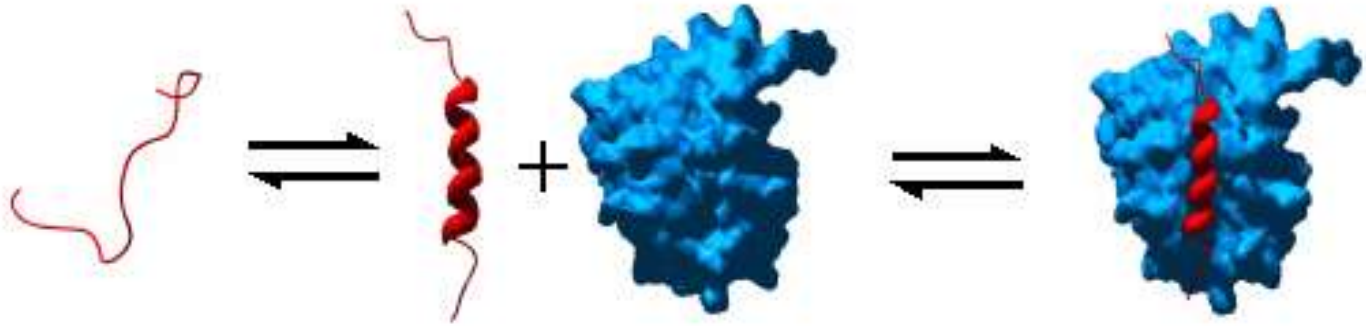
IDPs play staccato: “Polyelectrostatic” model



Dynamic complex of pSic1 and Cdc4. Multiple sub-optimal binding motifs in pSic1 interact with the binding pocket of Cdc4 in a dynamic equilibrium.
J Mol Recognit. (2010) 23, 105-116.

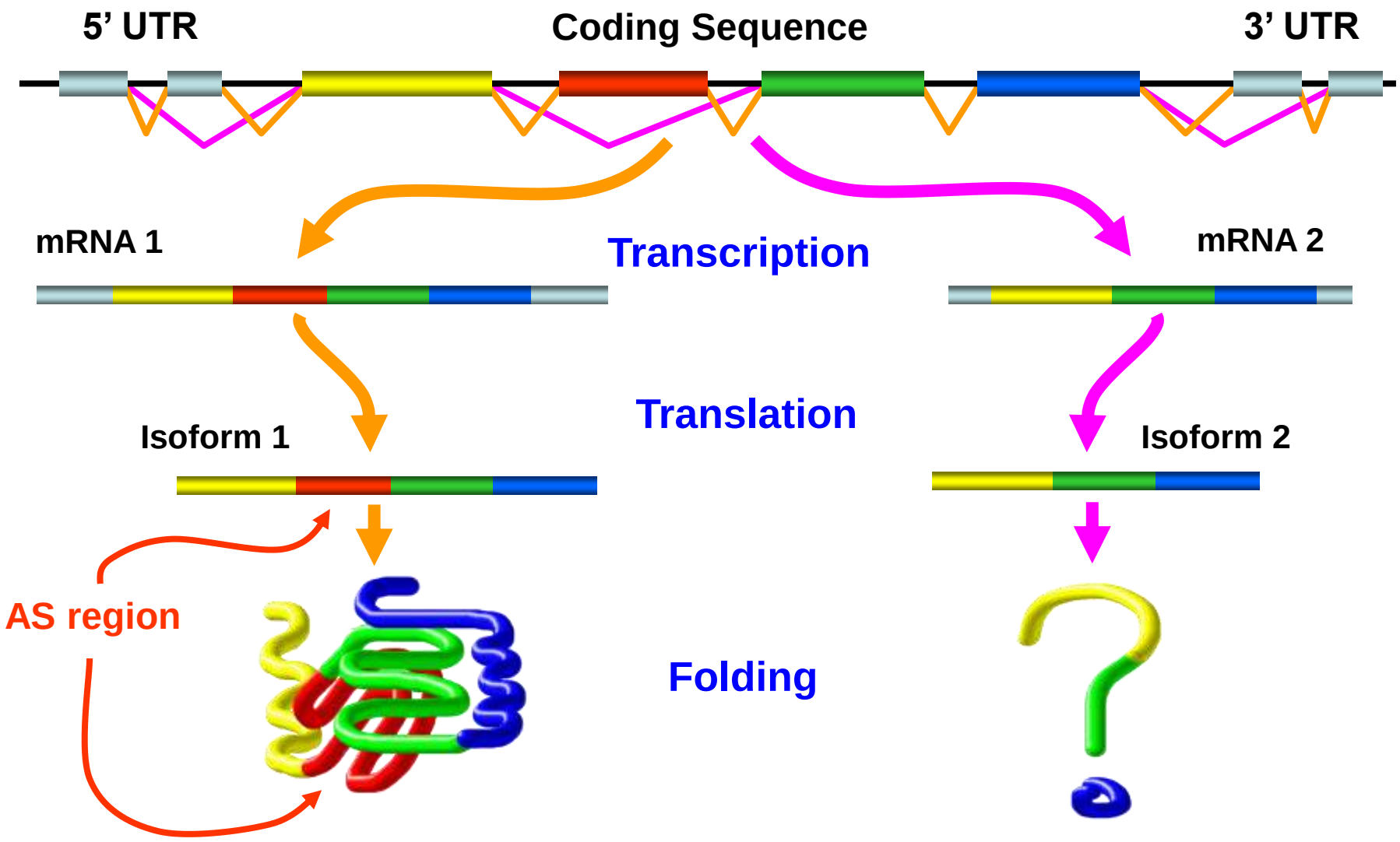
Mittag T., Forman-Kay J. (2010) J. Mol. Recognit. 23 (2) 105-116

Modes of IDP interactions #1



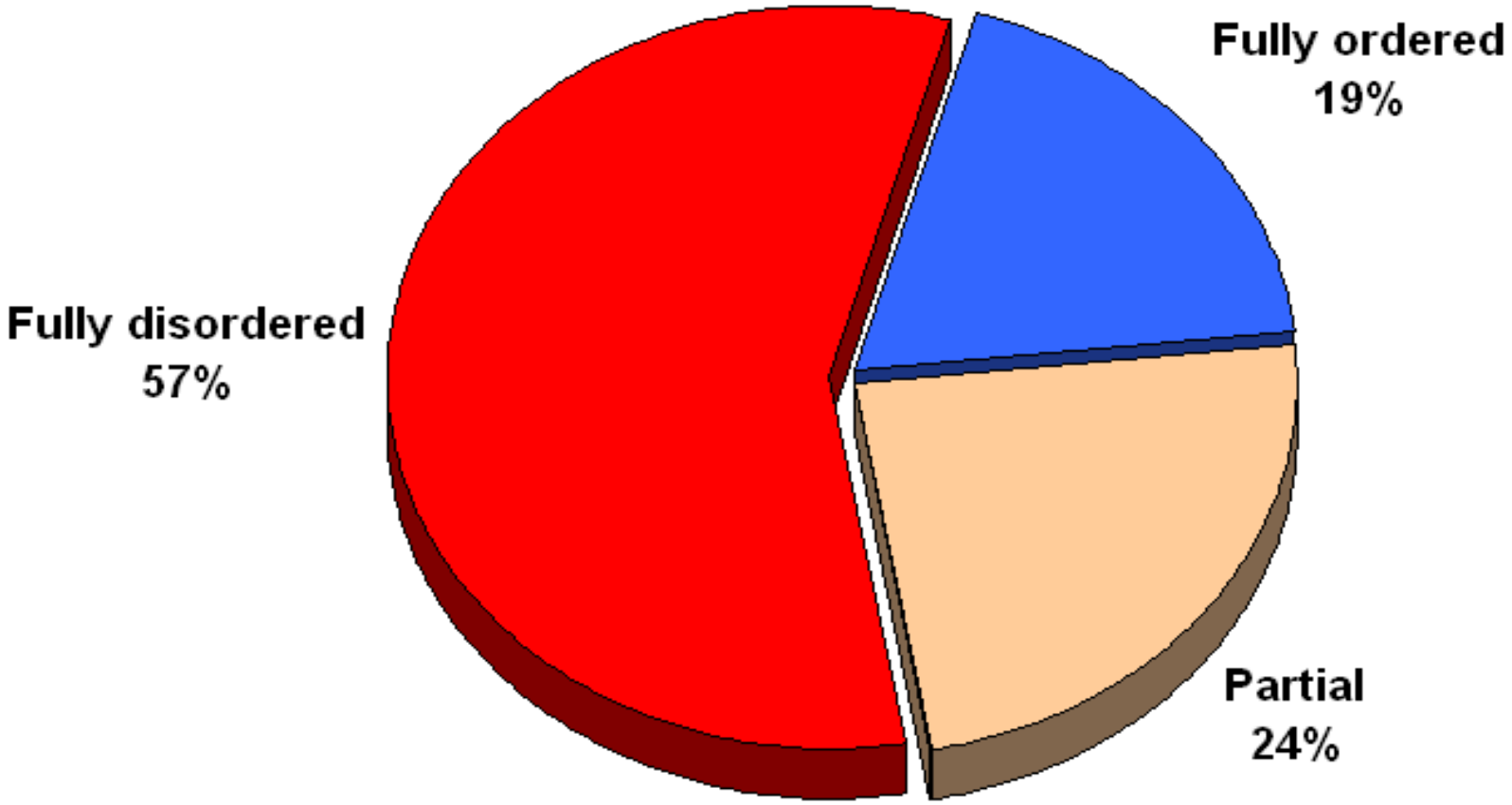
Intrinsic disorder and alternative splicing

Alternative Splicing



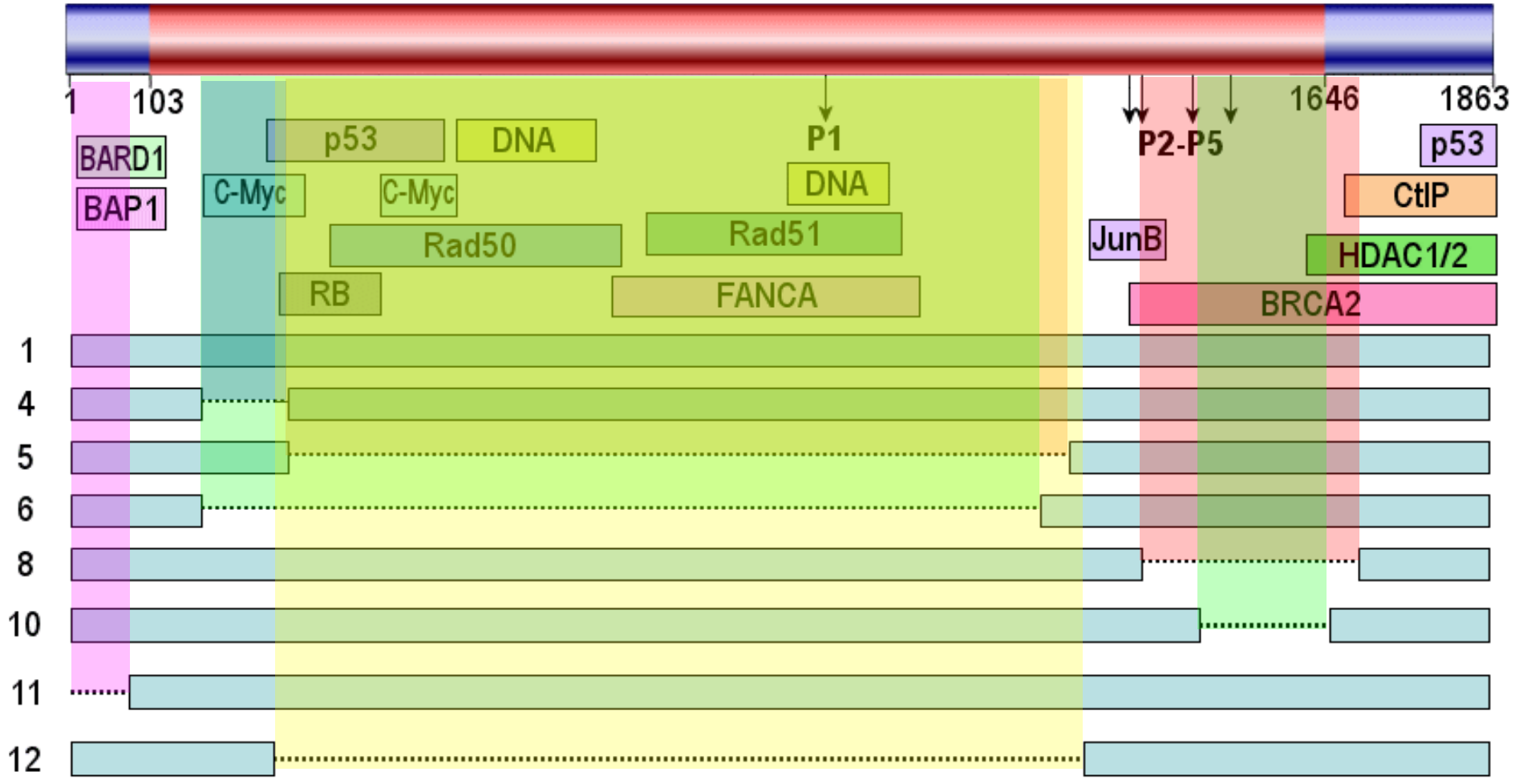
Abundance of disorder in alternatively spliced regions

Distribution of structurally characterized AS regions

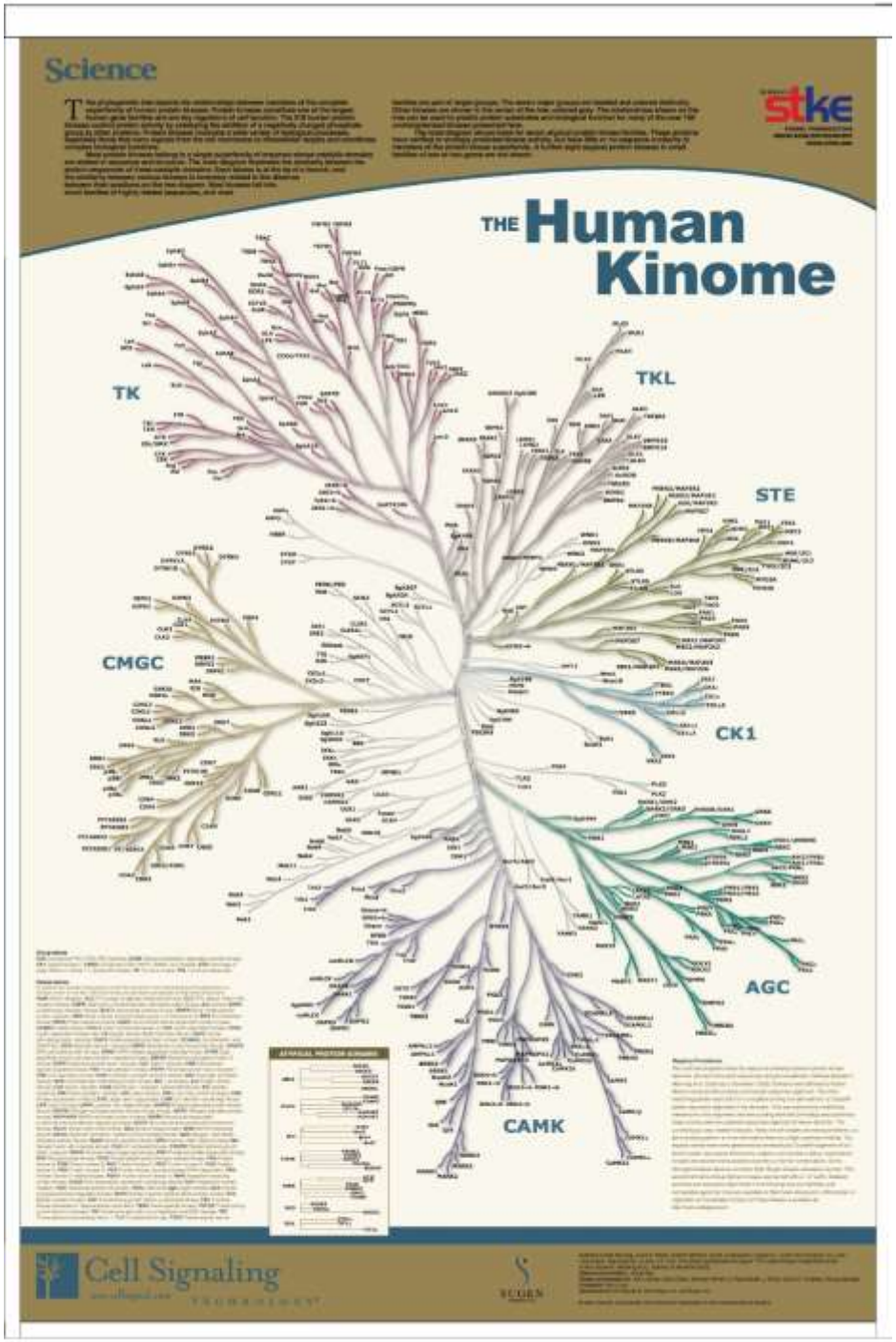


Romero *et al*., *PNAS* (2006), 103: 8390

Functional regulation via AS: Breast Cancer Protein 1 (BRCA1)



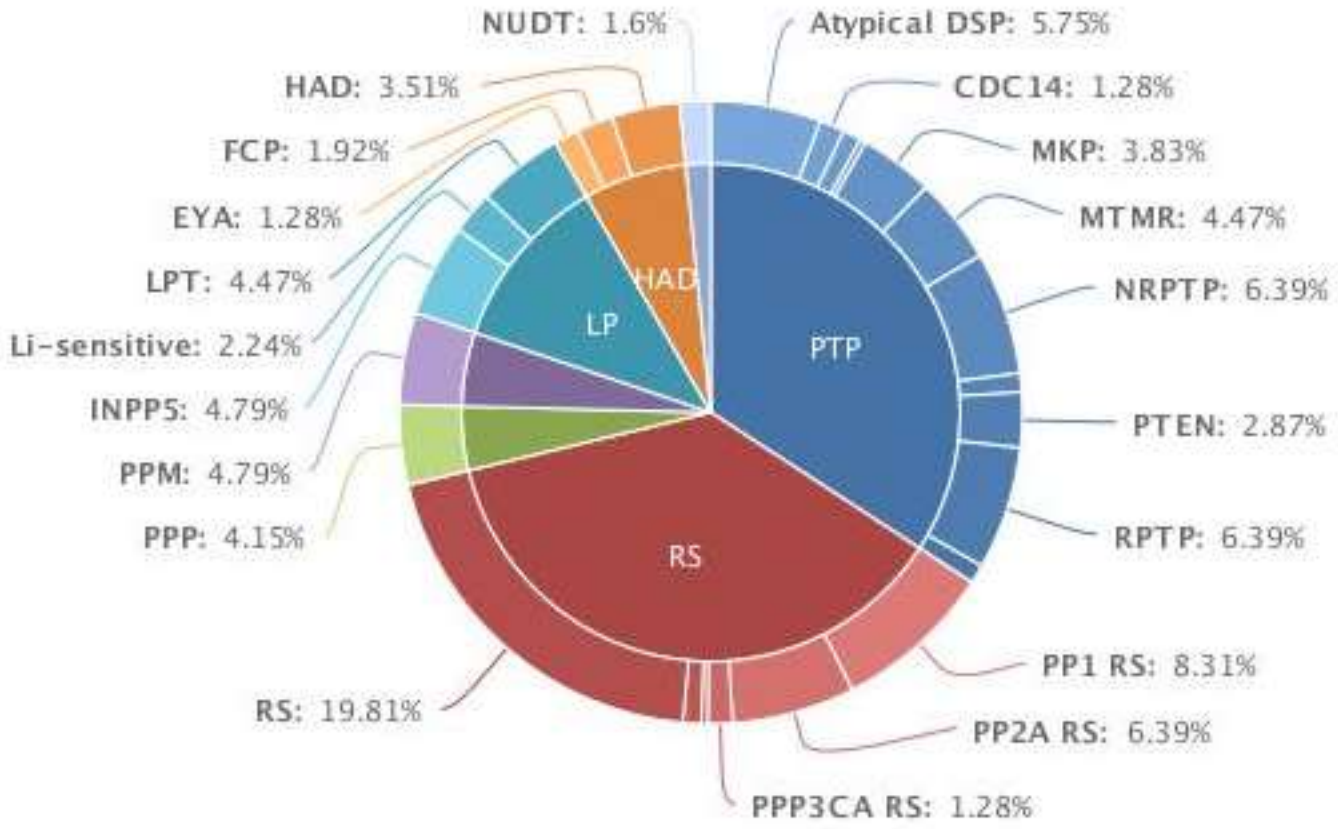
Intrinsic disorder and PTMs



The entire set of 518 protein kinases in the human genome makes up one of the largest of all human gene families. These enzymes catalyze the phosphorylation of proteins, specifically serine/threonine and tyrosine residues – an important reaction that regulates key cellular functions like cell division, metabolism, and apoptosis in normal and disease states. This makes kinases key therapeutic targets in several diseases such as cancer, neurodegeneration, behavioral disorders, diabetes, and cardiovascular diseases.

https://evolutionofalabrat.wordpress.com/2015/11/13/the-human-kinome/

Human phosphatome



In humans, there are about 245 proteins either containing a phosphatase domain or experimentally characterized as regulatory subunits.

http://hupho.uniroma2.it/ufo.php

Phosphorylation & intrinsic disorder

- **>>75% of eukaryotic proteins can be phosphorylated;**
- **Each human protein kinase serves ~30 substrates;**
- **Each human phosphatase is expected to dephosphorylate ~61 clients;**
- **Few proteins ± phosphate in PDB;**
- **In PDB, nearly all eukaryotic protein sites without phosphate are natively disordered;**
- **Regions of intrinsic disorder commonly have phosphorylation sites;**

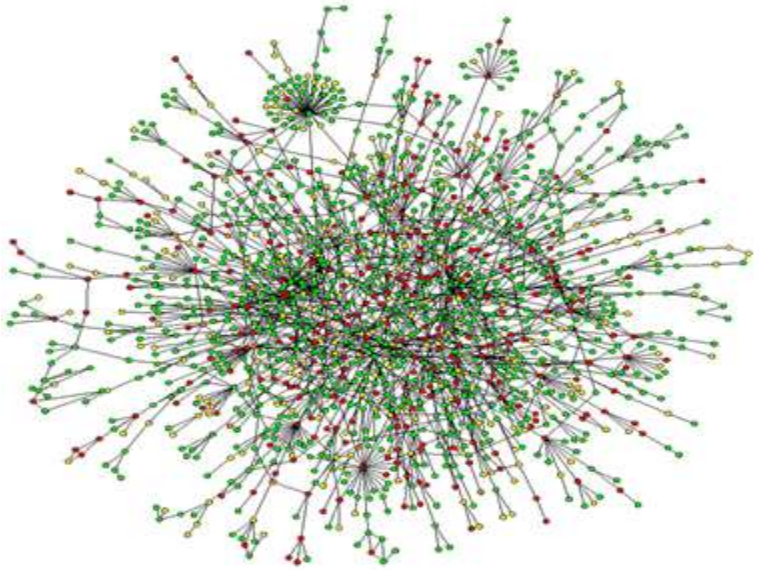
Posttranslational Modifications & Protein Intrinsic Disorder

- Phosphorylation, acetylation, ubiquitination, regulated proteolytic cleavage, etc. very often (always?) occur in regions of intrinsic disorder.

- Flexibility of intrinsic disorder facilitates (enables?) binding to the active site of the modifying enzyme.

Intrinsic disorder in protein-protein interaction networks

When key-and-lock does not work: Hub proteins



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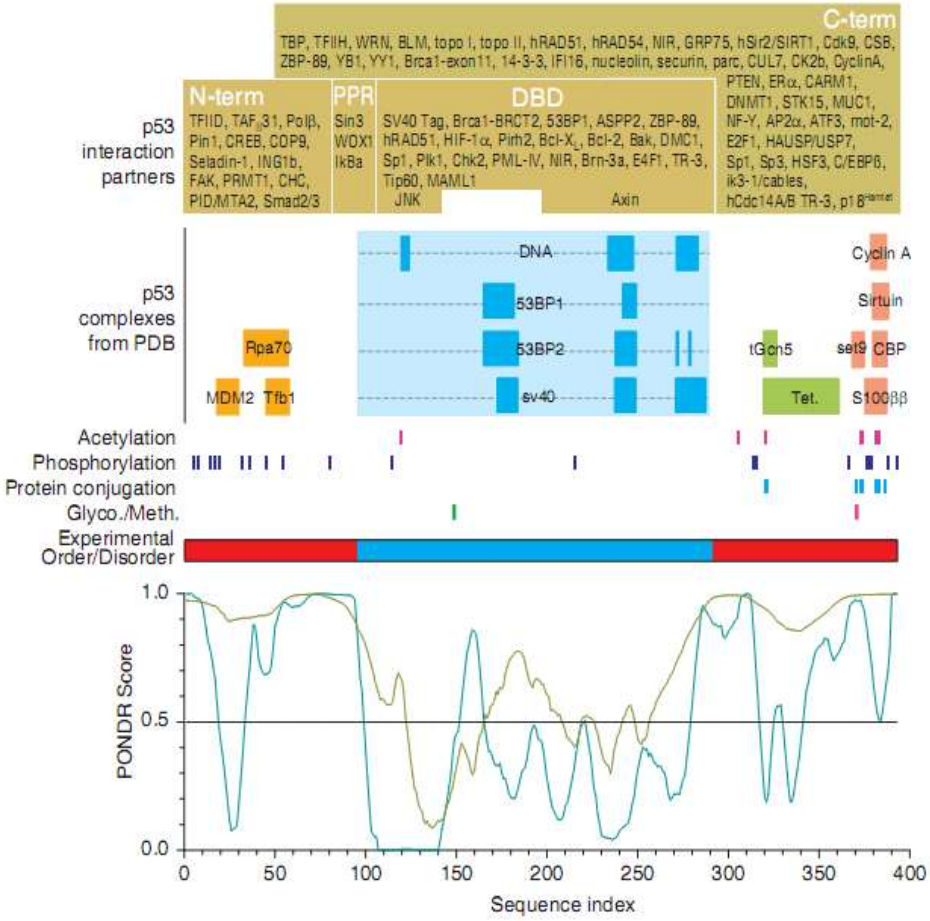
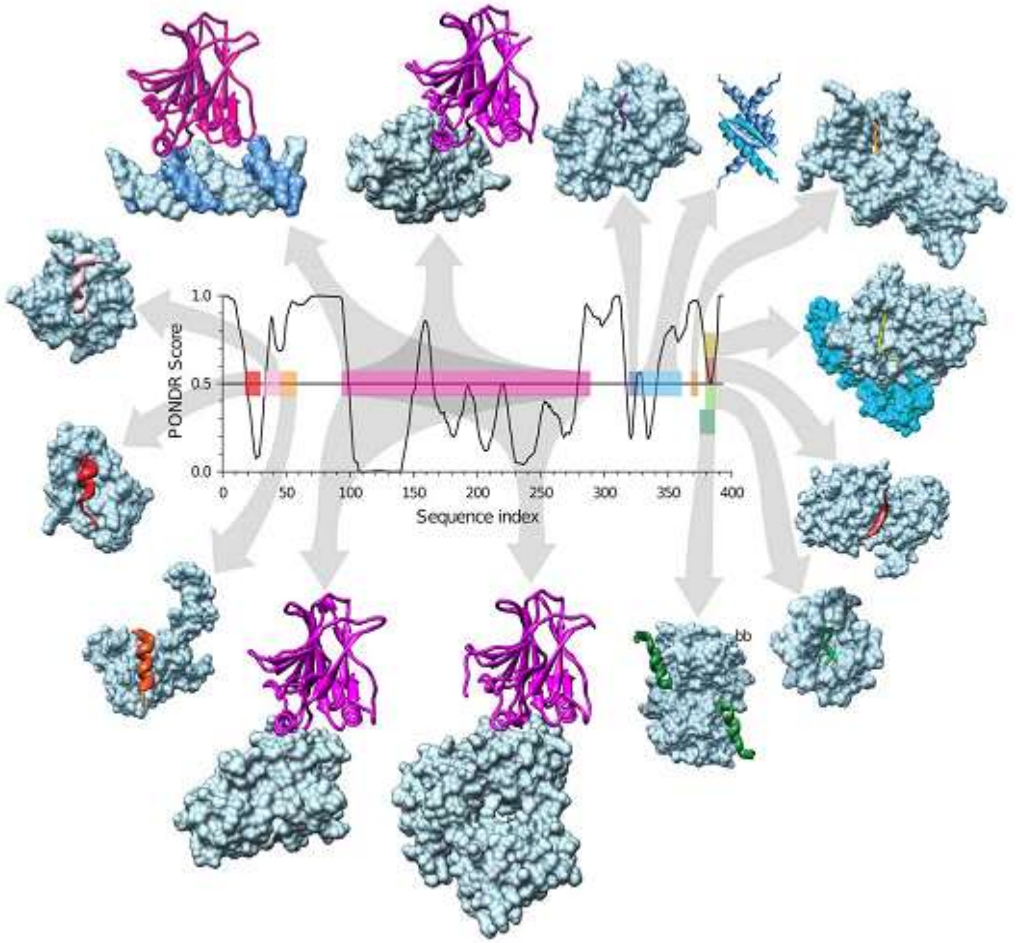
Binding promiscuity: Hubs

- Protein-Protein Interaction (PPI) networks typically have a few proteins (hubs) binding to many partners, but with most proteins binding to few partners.
- Standard lock and key mechanisms do not readily accommodate binding to multiple partners.
- Intrinsic disorder is crucial for PPI networks.
- Hubs are either disordered by themselves or interact with disordered partners.

Dunker et al. *FEBS J.* (2005) 272: 5129

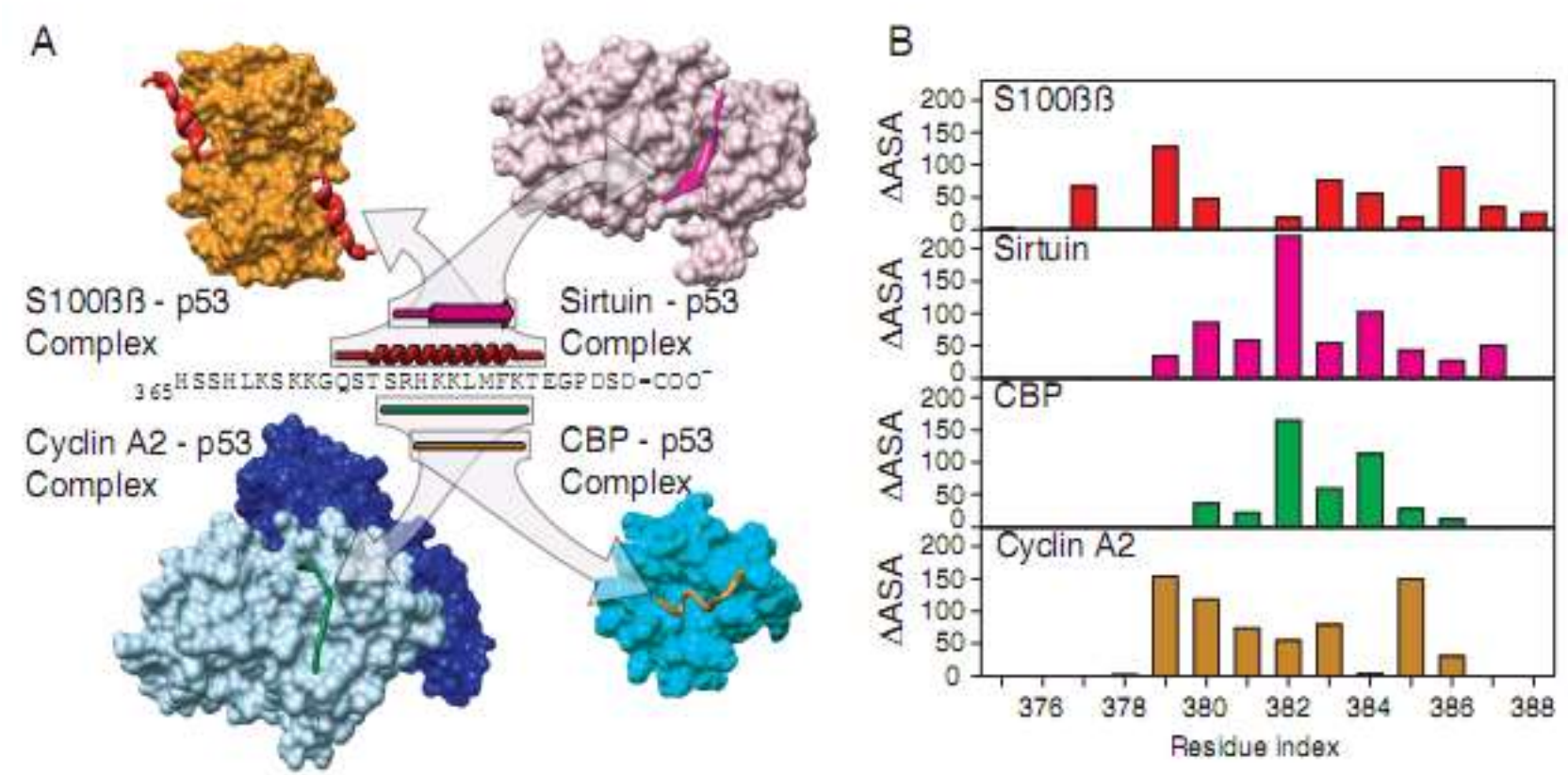
Binding promiscuity:
p53 one-to-many binding scenario





Uversky *et al*. (2008) *Ann. Rev. Biophys. Mol. Biol.* 37, 215
Oldfield *et al*. (2008) *BMC Genomics*, 9, S1

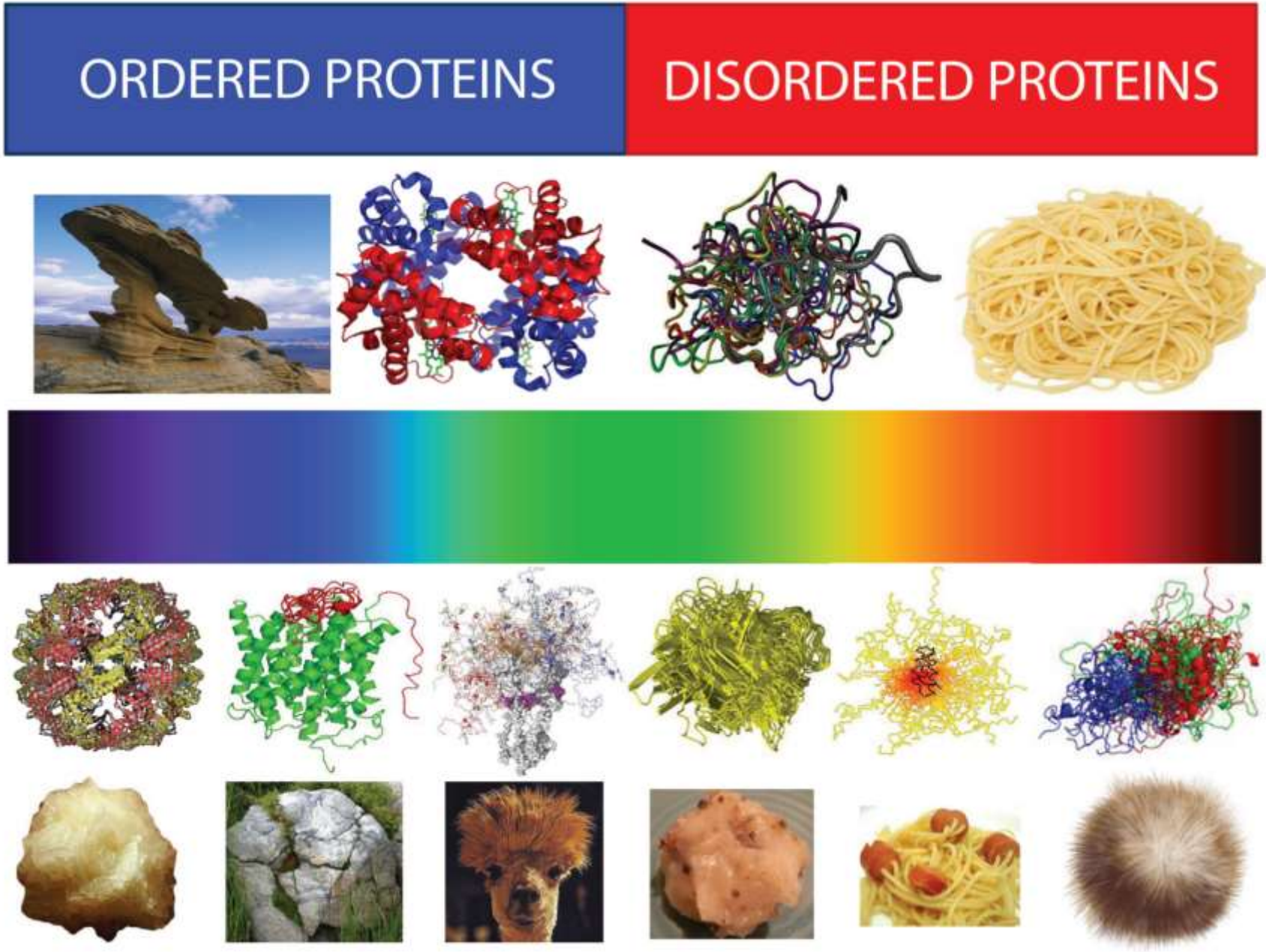
Binding plasticity:
p53 C-terminal Domain



Uversky et al. (2008) ***Ann. Rev. Biophys. Mol. Biol.*** **37, 215**

Protein structure-function continuum

Structural heterogeneity of IDPs or spectroscopy of intrinsic disorder



Uversky (2013) *Protein Science.* 22(6):693-724

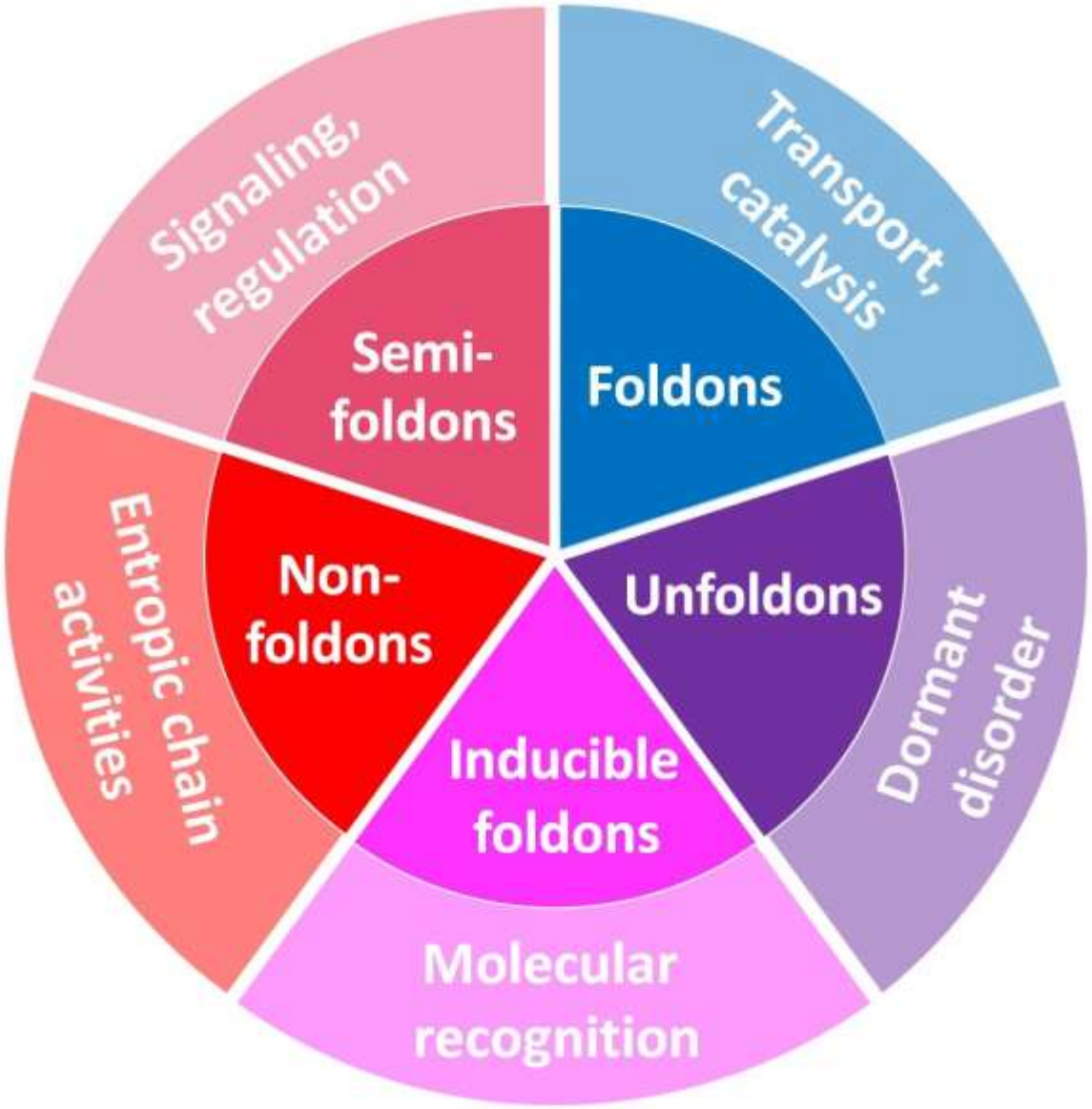
Structural heterogeneity of IDPs

IDPs can be described as various combinations of differently folded regions:

- Foldons (independent foldable units of a protein)
- Inducible foldons (disordered regions that can fold at least in part due to the interaction with binding partners)
- Inducible morphing foldons (disordered regions that can fold differently at interaction with different binding partners)
- Non-foldons (non-foldable protein regions)
- Semi-foldons (regions which are always in semi-folded state)
- Unfoldons (regions that undergo an order-to-disorder transition to become functional)

Uversky (2013) *Biochim Biophys Acta* **1834**, 932

Different functions of foldons and Co.

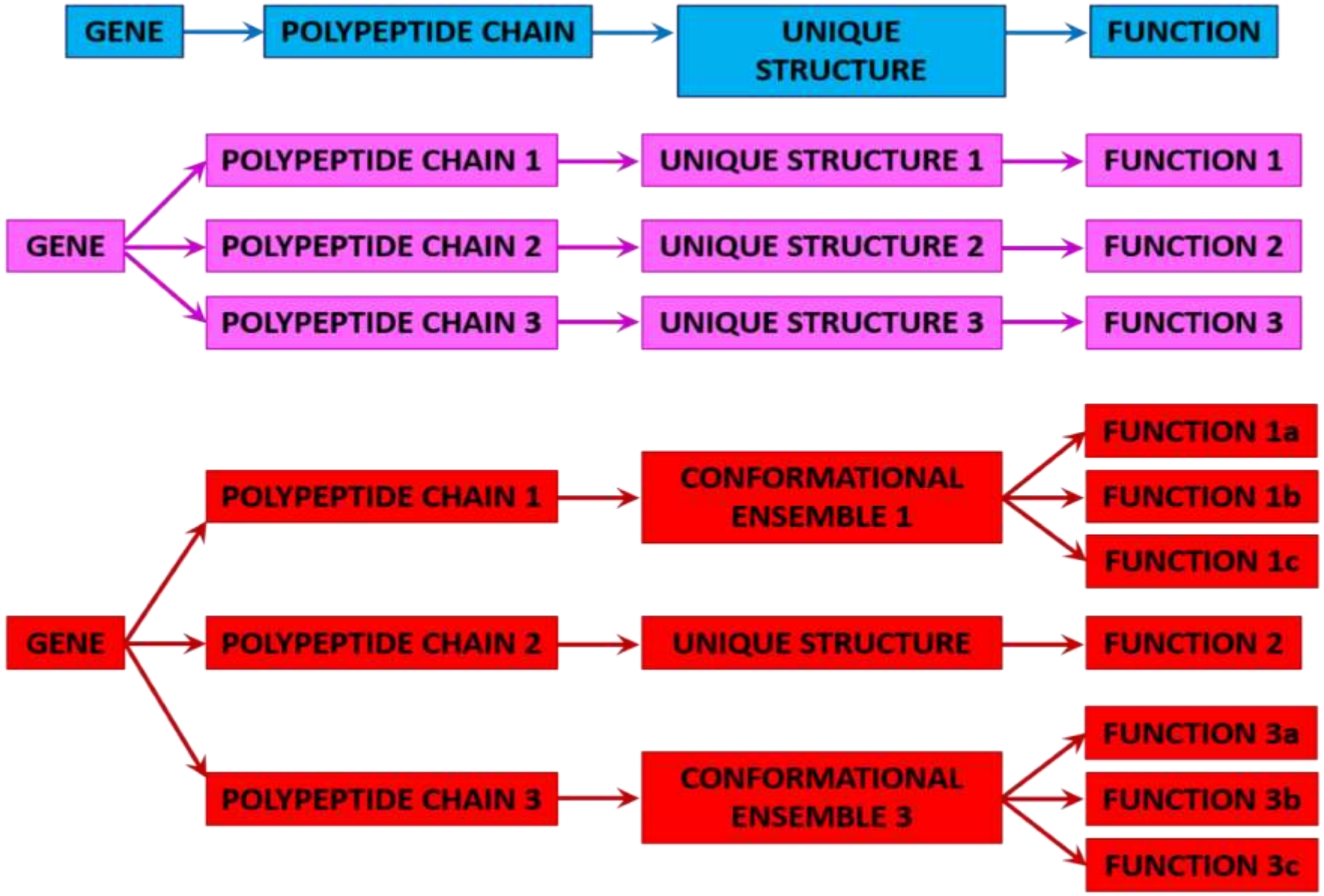


Uversky (2015) *FEBS Journal*. **282** (7) 1182-1189

Protein structure-function continuum: Proteoforms

- The major part of the complexity of the biological machinery is determined by protein variability rather than results from a high number of distinct genes (although he human genome contains about **21,000** protein-encoding genes, but the total number of proteins in human cells is estimated to be between **250,000** to **1,000,000**);
- Typical protein exists as an ensemble of proteoforms; i.e., different molecular forms in which the protein product of a single gene can be found, including changes due to genetic variations, alternatively spliced mRNA and PTMs

Uversky (2016) *International Journal of Molecular Sciences*.**17**(11), 1874



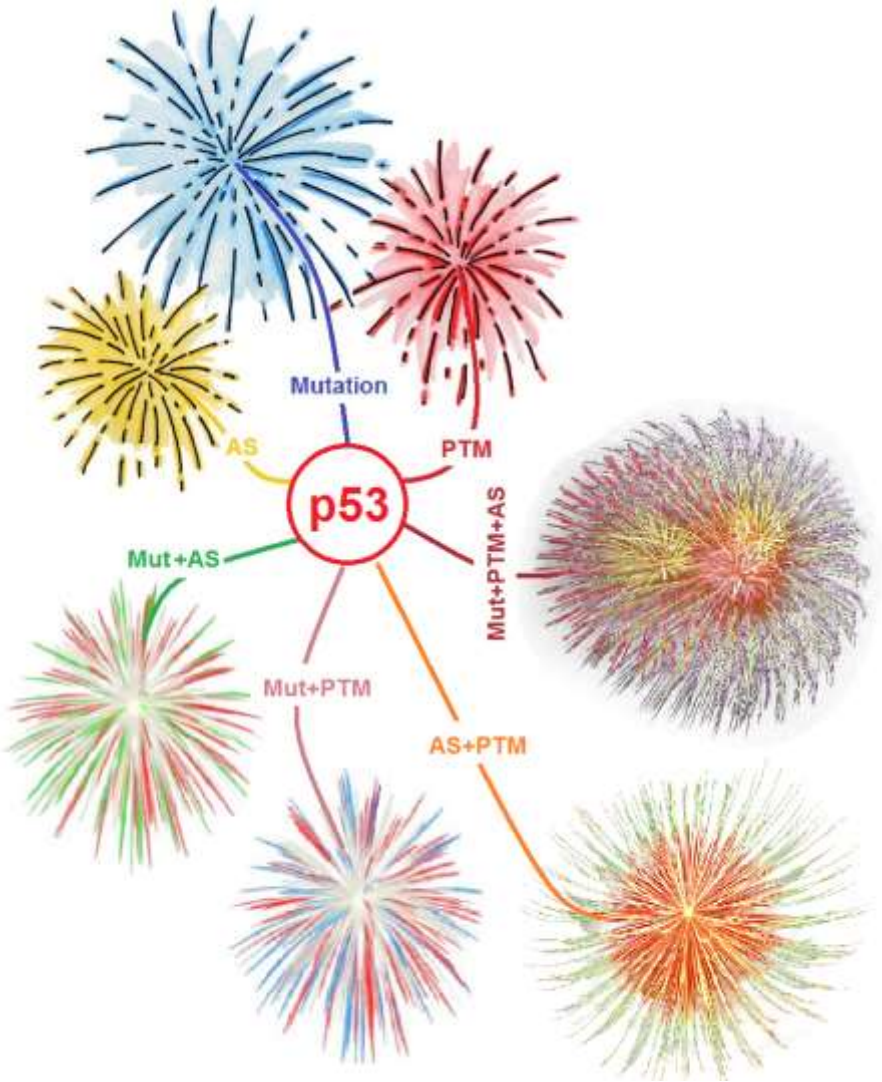
Uversky (2016) *International Journal of Molecular Sciences*.**17**(11), 1874

Protein structure-function continuum: Different types of proteoforms

Uversky (2016) *International Journal of Molecular Sciences*.**17**(11), 1874

- Basic (or intrinsic, or conformational) proteoforms – reflection of the fact that any protein exist as a dynamic conformational ensemble, members of which have different structures and potentially can have different functions.
- Inducible proteoforms originating due to the various alterations (mutations, PTMs, or consequences of alternative splicing) of the canonical protein sequence and representing a mixture of these various forms. Any member of the inducible (or modified) proteoform (i.e., any mutated, modified, or alternatively spliced form) is a conformational proteoform itself since it also represents a structural ensemble.
- Functioning proteoforms – reflection of the fact that protein function, interaction with specific partners, or placement inside the natural cellular environment can affect structural ensemble of both basic and induced proteoforms.

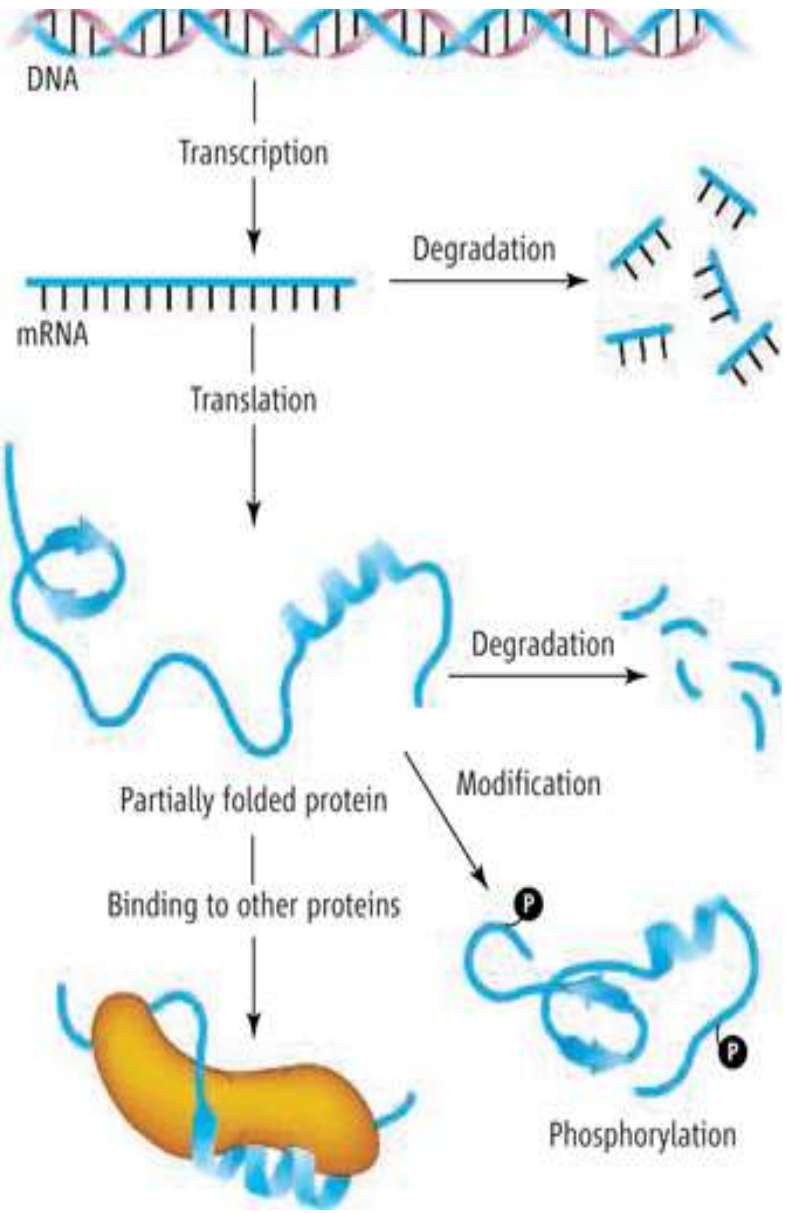
Firework representation of protein structure-function continuum



Uversky (2016) *International Journal of Molecular Sciences*.**17**(11), 1874

Intrinsic disorder inside the cell: Controlled chaos

Controlled chaos



The availability and abundance of intrinsically disordered proteins inside a cell is under tight control.

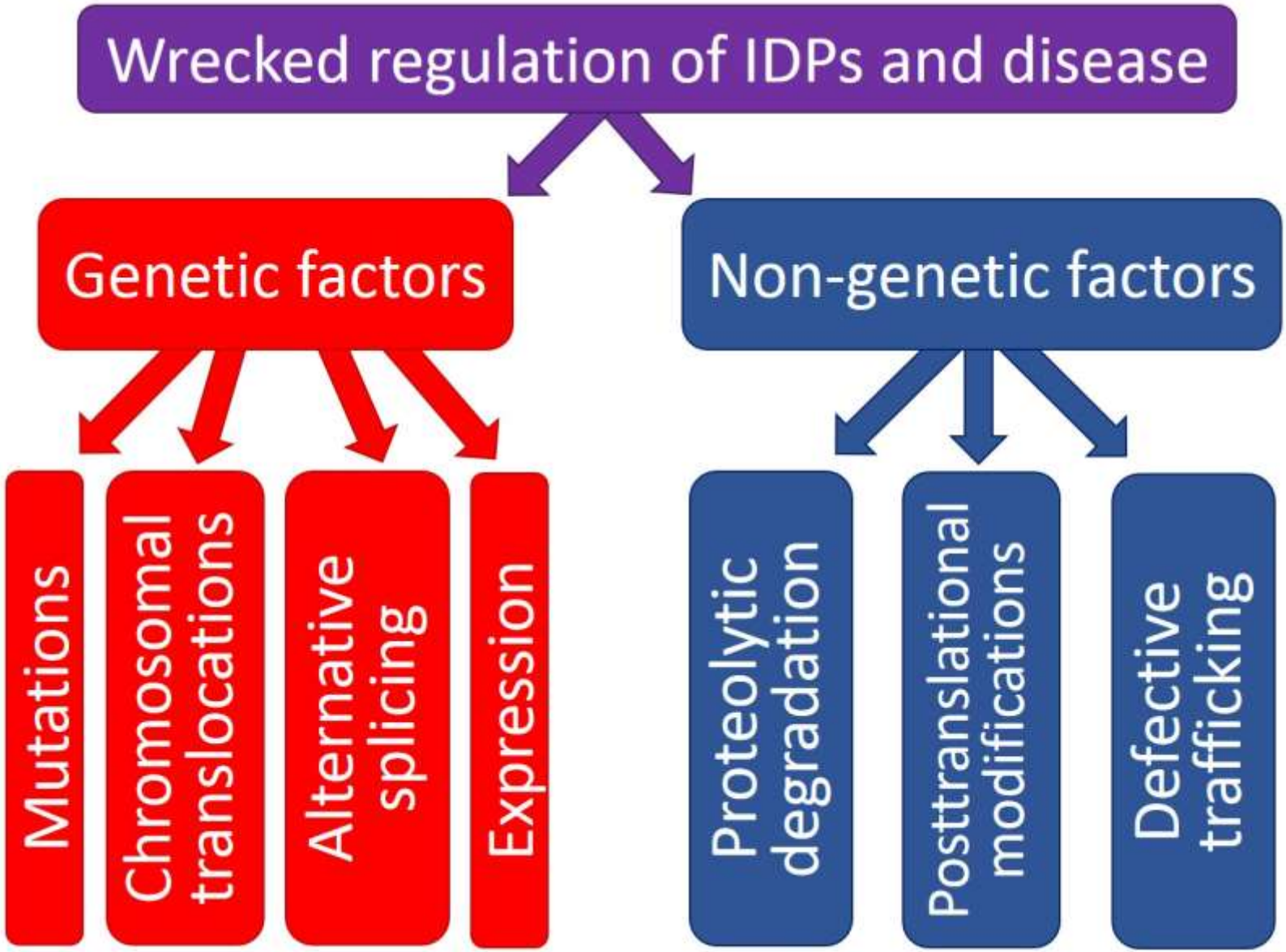
Disorder management inside the cell. As a result of fast mRNA degradation, slow translation of mRNA into protein, and fast protein degradation, the overall amount of intrinsically disordered proteins inside a cell is less, and their half-lives are generally shorter, than those of ordered proteins. However, some disordered proteins can be present at high quantities and for long periods of time if they are modified (such as by phosphorylation) or interact with some specific binding partners.

Gsponer J., Futschik M.E., Teichmann S.A., Babu M. (2008) *Science* 322 (5906), 1365

Uversky V.N., Dunker A.K. (2008) *Science* 322 (5906), 1340

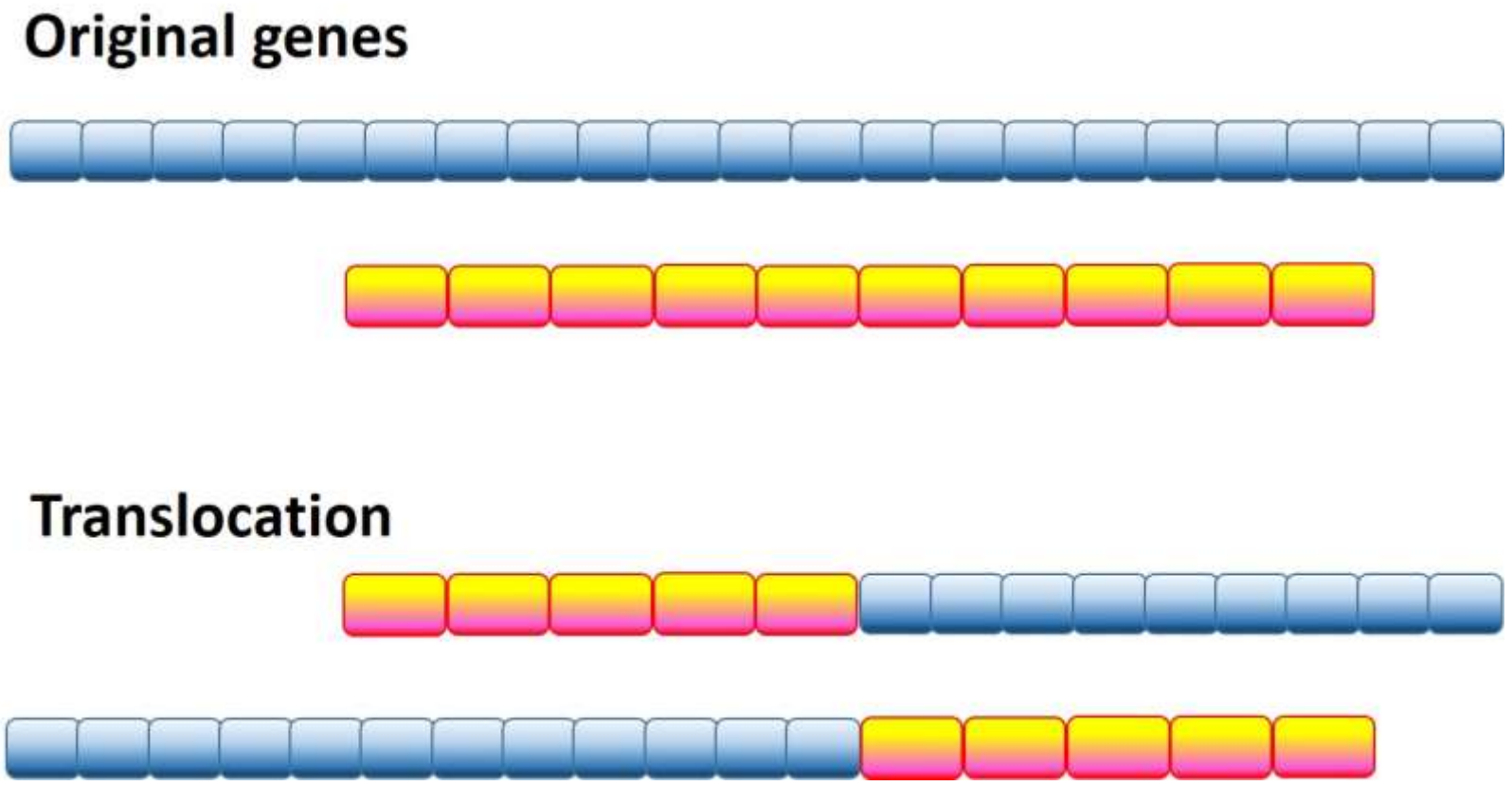
Uncontrolled chaos:

Intrinsic disorder and human diseases or D^2 concept

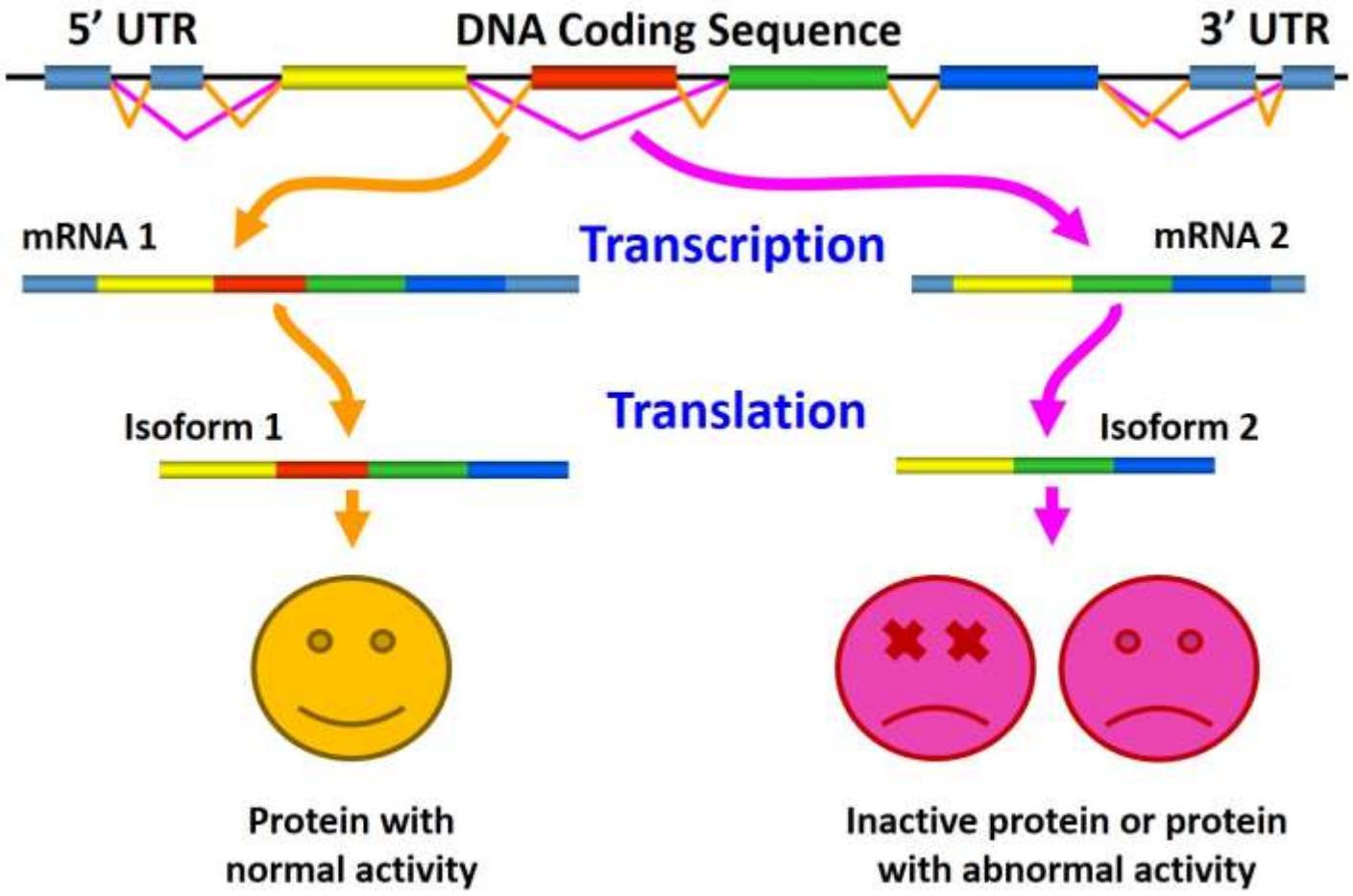


Uversky (2014) *Frontiers in Molecular Biosciences: Protein Folding, Misfolding and Degradation*. **1** (article 6) 1-24.

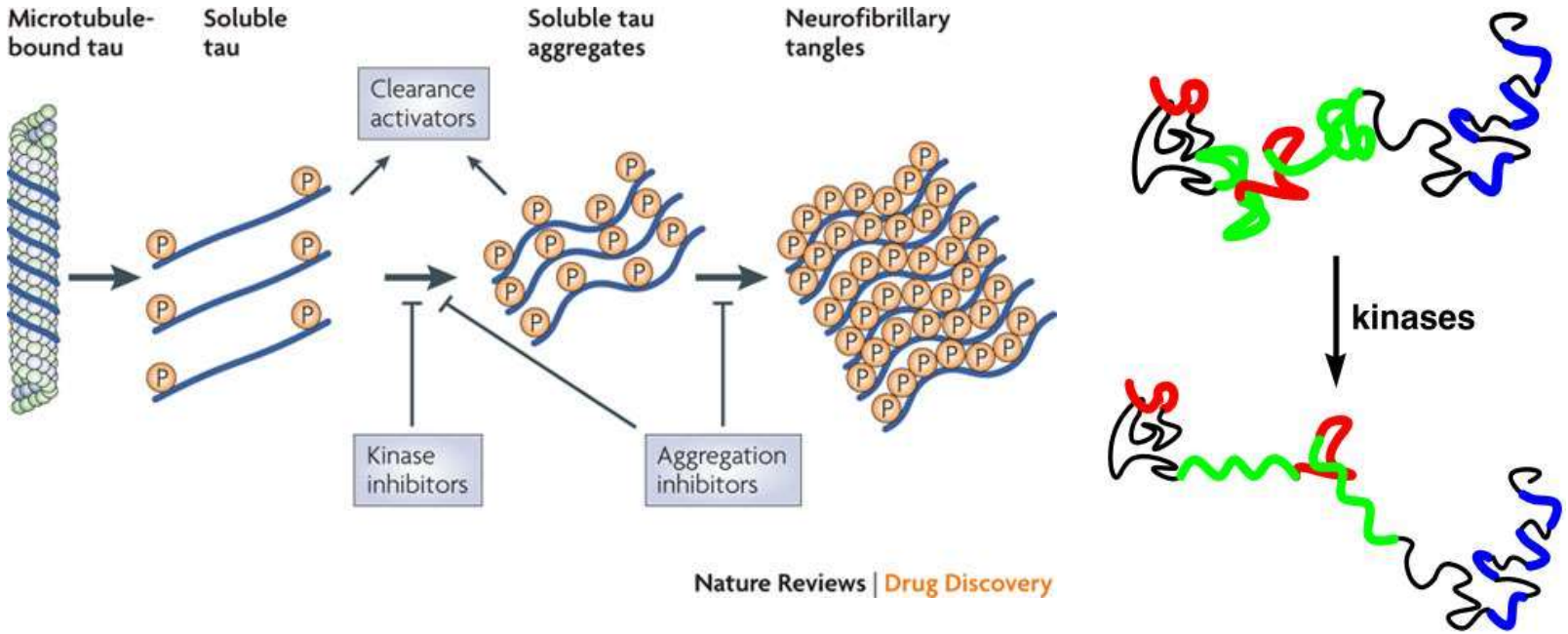
Chromosomal translocation



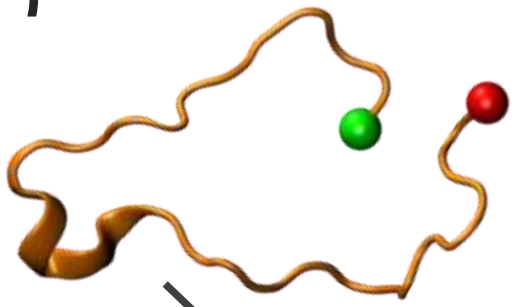
Aberrant alternative splicing

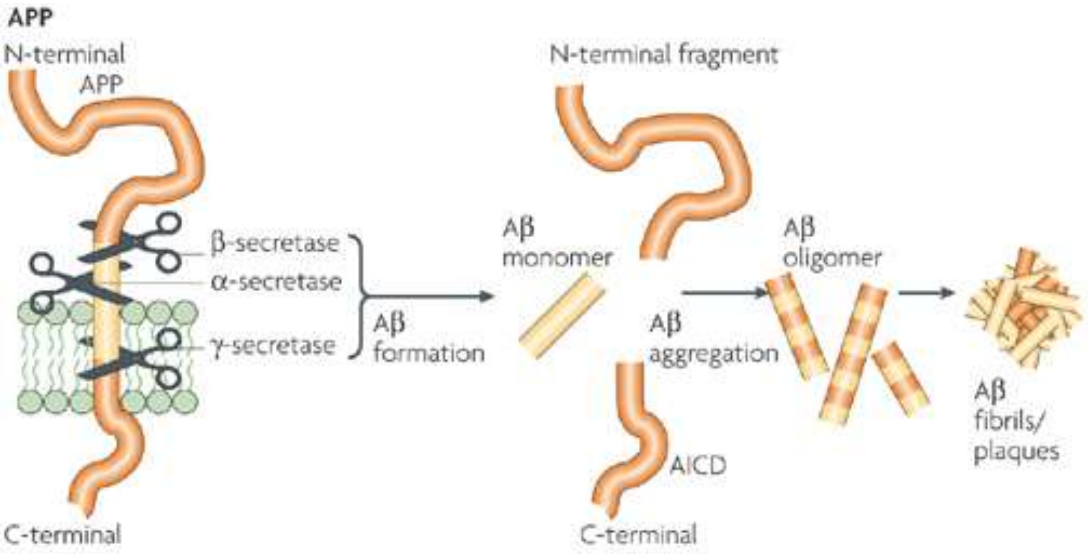


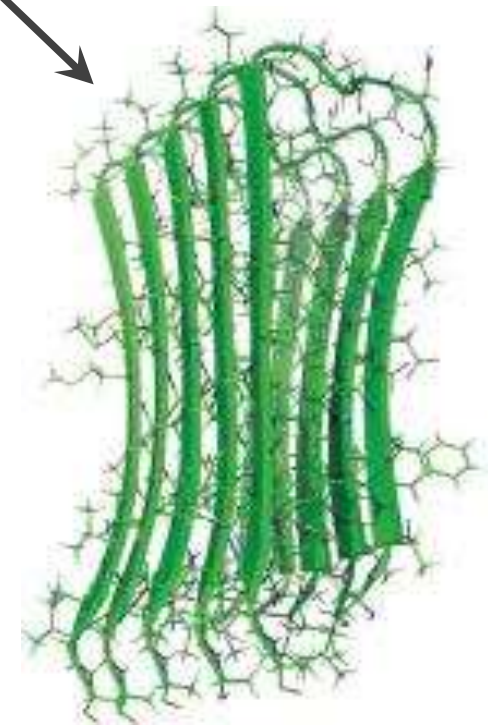
Aberrant posttranslational modifications of tau and AD



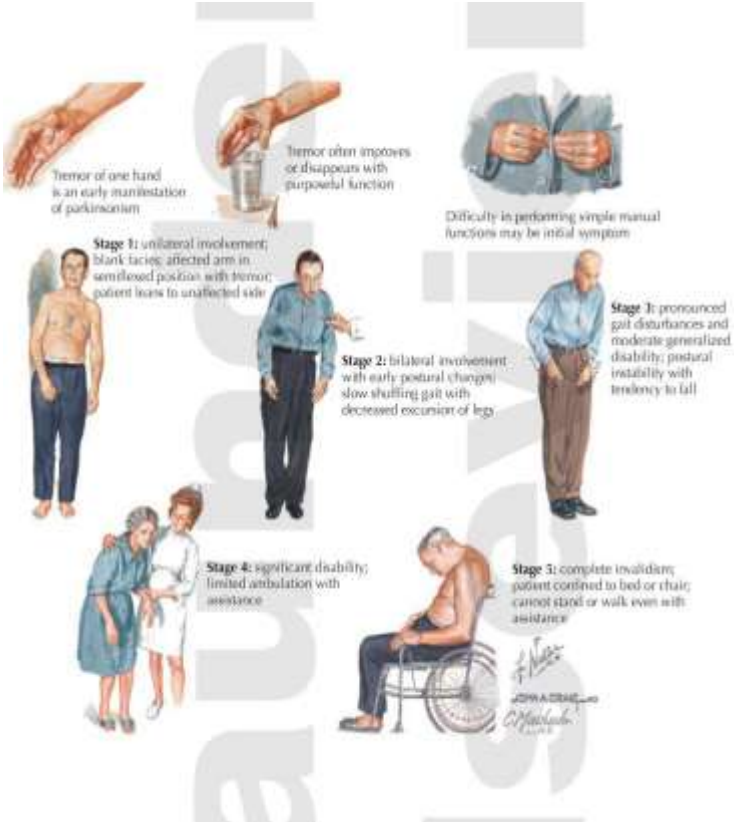
Aberrant proteolytic degradation of Aβ and AD





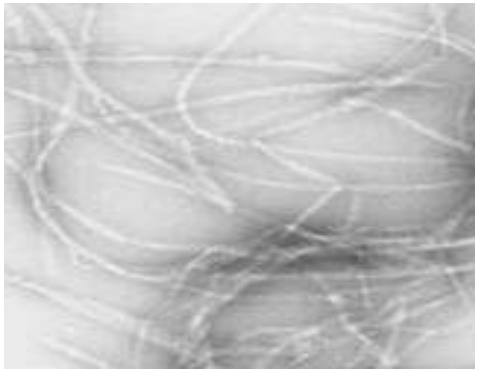


Parkinson’s disease

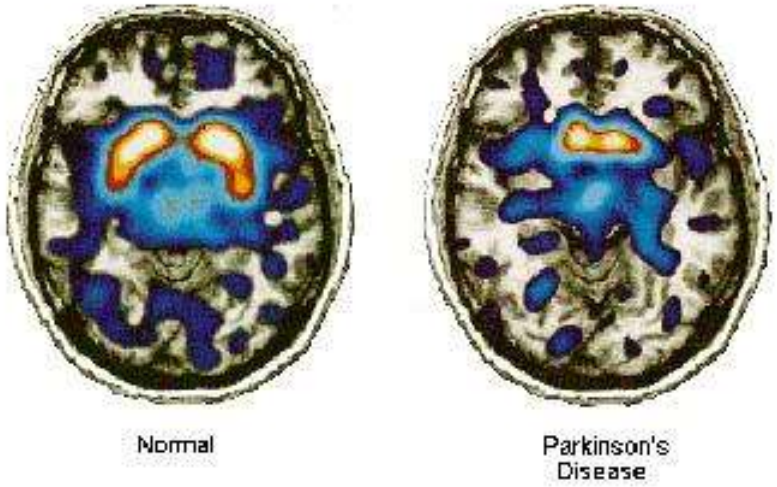


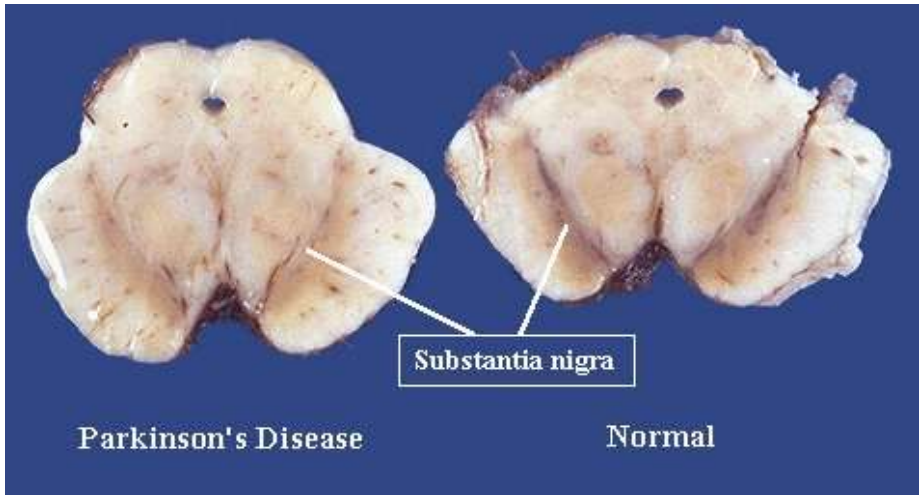
Parkinson's diseases as a protein deposition disorder

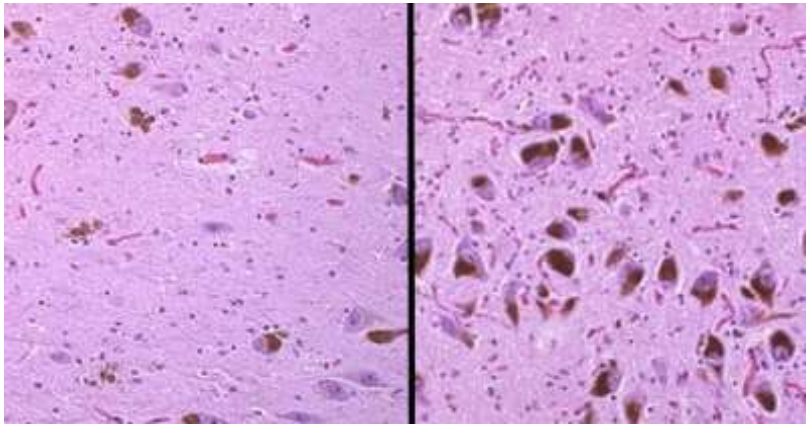
- Second most common neurodegenerative disease
- An "environmental" disease (pesticides and metals)
- Due to the death of **dopaminergic neurons** in the ***substantia nigra***
- Pathological hallmark is intracellular proteinaceous inclusions called **Lewy bodies** and **Lewy neurites**



Pathology of Parkinson's disease:
Neurodegeneration

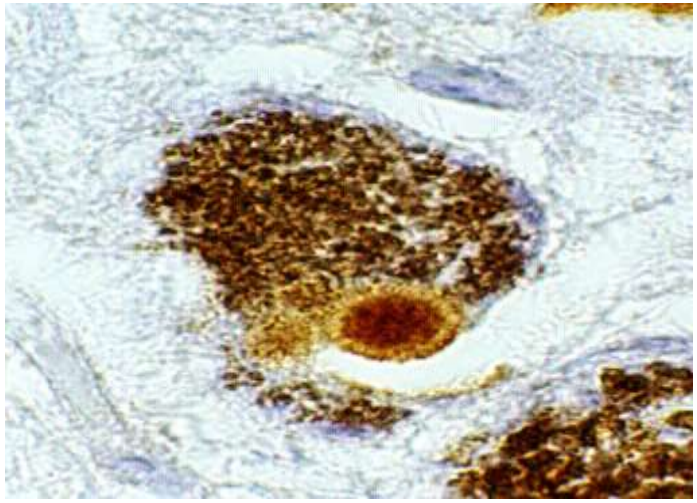


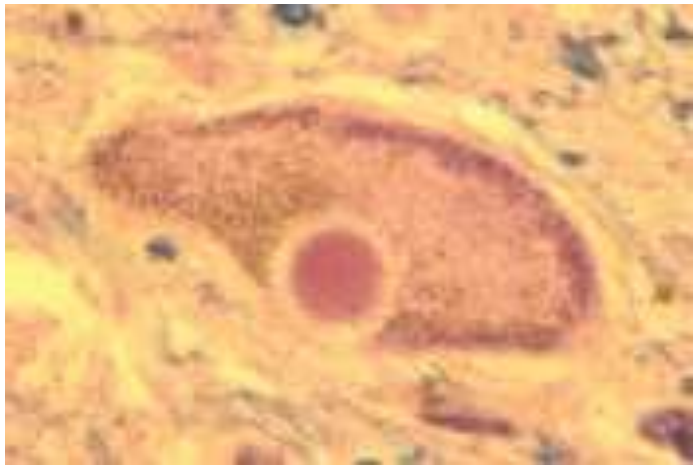


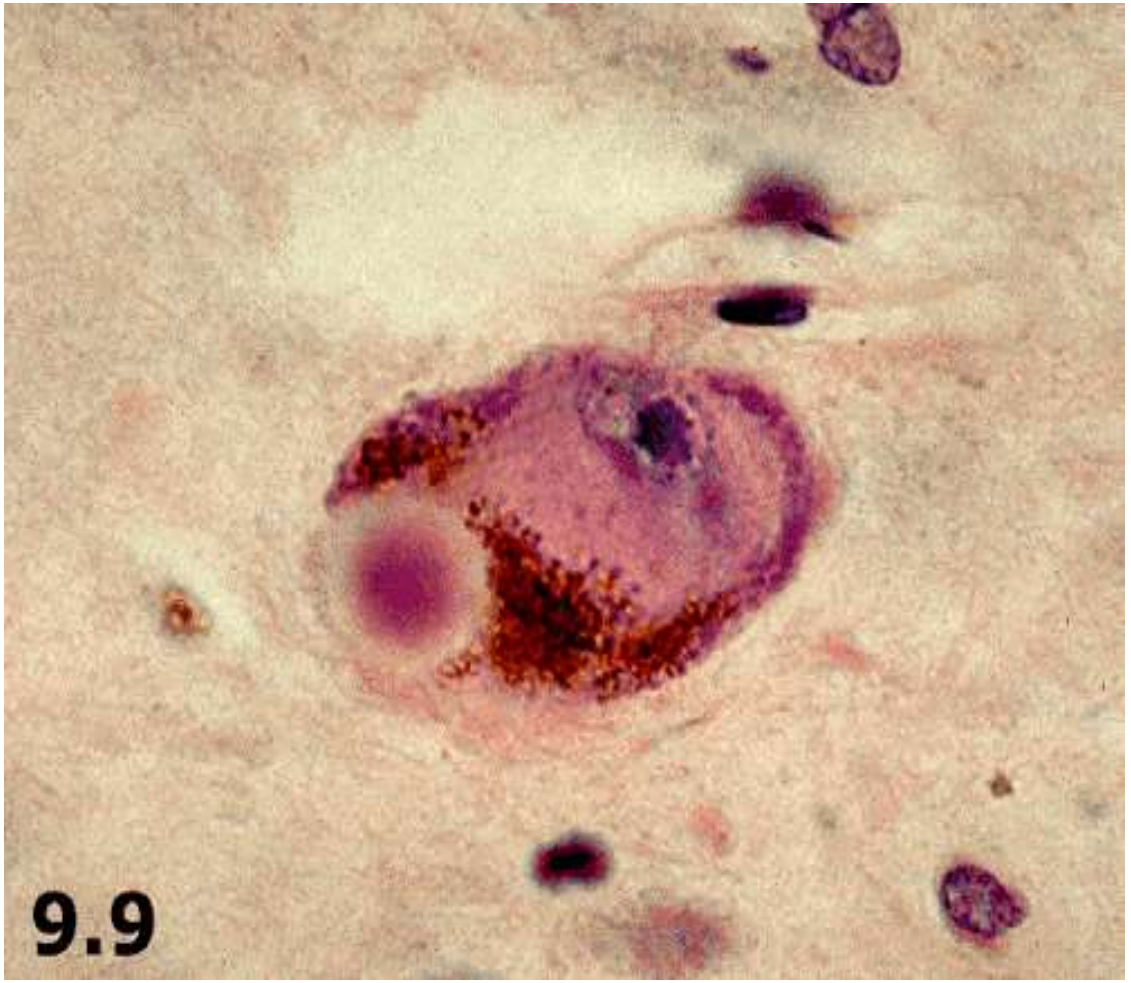


Pathology of Parkinson's disease:

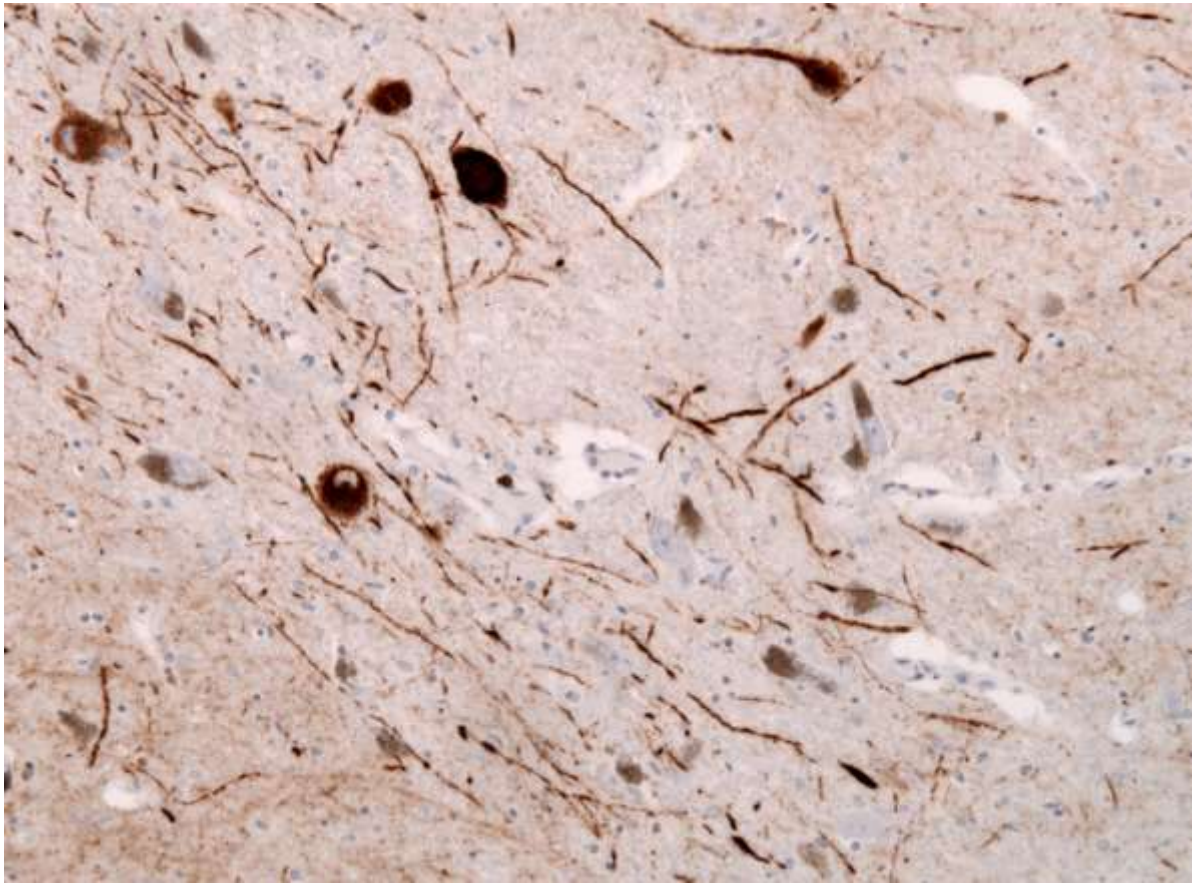
Lewy bodies in *substantia nigra*







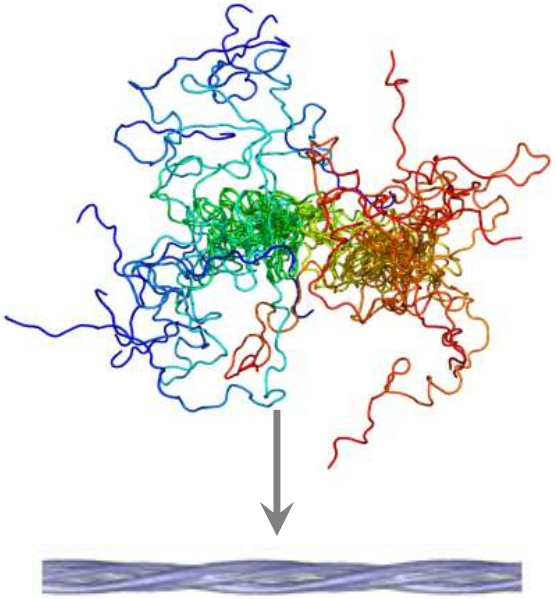
Lewy neurites: Another pathological culprit



Synucleinopathies:

α-Synuclein-containing inclusions

LB – Lewy body (PD)
LN – Lewy neurite (PD)
GCI - glial cytoplasmic inclusions (MSA)
NCI - neuronal cytoplasmic inclusions (NBIA1)
AF – axonal spheroids (NBIA1)



LB LN GCI NCI AF

Protein Misfolding Diseases:
Synucleinopathies

Diseases with neuronal inclusions

Normal aging

Parkinson's disease

- **Idiopathic**
- **Neurotoxicant-induced (incidental)**
- **Familial**
  - **With α-synuclein point mutations**
  - **With α-synuclein gene triplication**
  - **With mutations in other proteins**
- **Pure autonomic failure**
- **Lewy body dysphagia**

Amyotrophic lateral sclerosis

- **Familial**
- **Sporadic**

Parkinsonism plus syndromes

- **Sporadic**
  - **Progressive supranuclear palsy**
  - **Olivoponto cerebrellar atrophy (Shy-Dragger syndrome)**
  - **Cortical-basal ganglionic degeneration**
  - **Sporadic pallidal degeneration**
  - **Bilateral striatopallido dentate calcinosis**
  - **Parkinsonism with neuroacanthocytosis**
- **Familial**
  - **Familial diffuse Lewy body disease**
  - **Familial dementia with swollen achromatic neurons and cortico-basal inclusion bodies**

Parkinsonism plus syndromes (continued)

- **Familial (continued)**
  - **Frontotemporal dementia with parkinsonism linked to chromosome 17**
  - **Associated with psychiatric disturbances**
  - **Associated with respiratory disturbances**
  - **Associated with dystonia**
  - **Associated with myoclonus and seizures**
- **Familial progressive supranuclear palsy**

Alzheimer's disease

- **Sporadic**
- **Familial with APP mutation**
- **Familial with PS-1 mutation**
- **Familial with other mutations**
- **Familial British dementia**

Down's syndrome

Amyotrophic lateral sclerosis-parkinsonsim/dementia complex of Guam

Prion diseases

Ataxia telangiectatica

Meige's syndrome

Lewy body diseases

- **Dementia with Lewy bodies**
- **Pure form - transitional/limbic**
- **Pure form - neocortical**
- **Diffuse Lewy body disease**
- **Common form**
- **Pure form**

Lewy body diseases

- **Lewy body variant of Alzheimer's disease**
- **Incidental Lewy body disease**
- **Lewy body dementia**
- **Senile dementia of Lewy body type**
- **Dementia associated with cortical Lewy bodies**

Neuroaxonal dystrophies

- **Neurodegeneration with brain iron accumulation, type I (Hallervorden-Spatz syndrome or adult neuroaxonal dystrophy)**

Motor neuron disease

Tauopathies

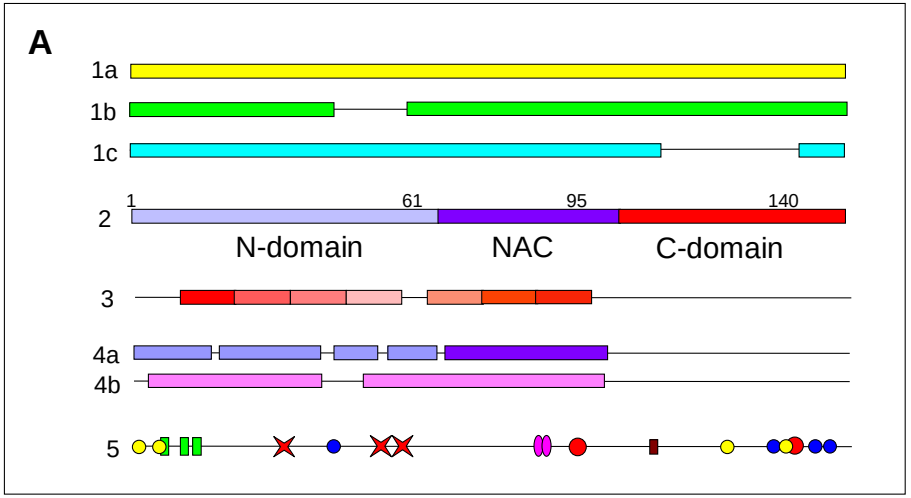
- **Frontotemporal degeneration/dementia**
- **Pick's disease**
- **Post-encephalitic parkinsonism**
- **Dementia pugilistica**
- **Argyrophilic grain disease**
- **Corticobasal degeneration**

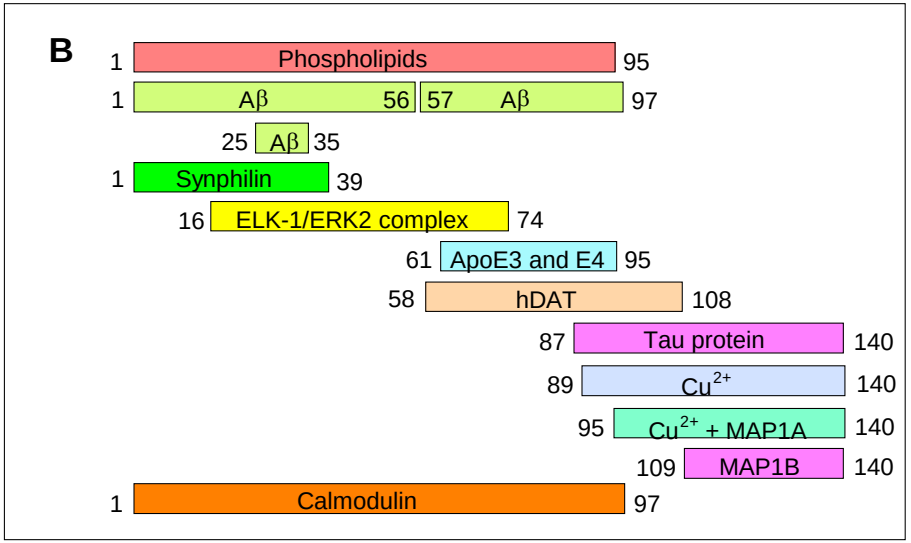
Diseases with neuronaland glial inclusions

Multiple system atrophy

- **Shy-Drager syndrome**
- **Striatonigral degeneration (MSA-P)**
- **Olivopontocerebellar atrophy (MSA-C)**

What is so special about α-synuclein?



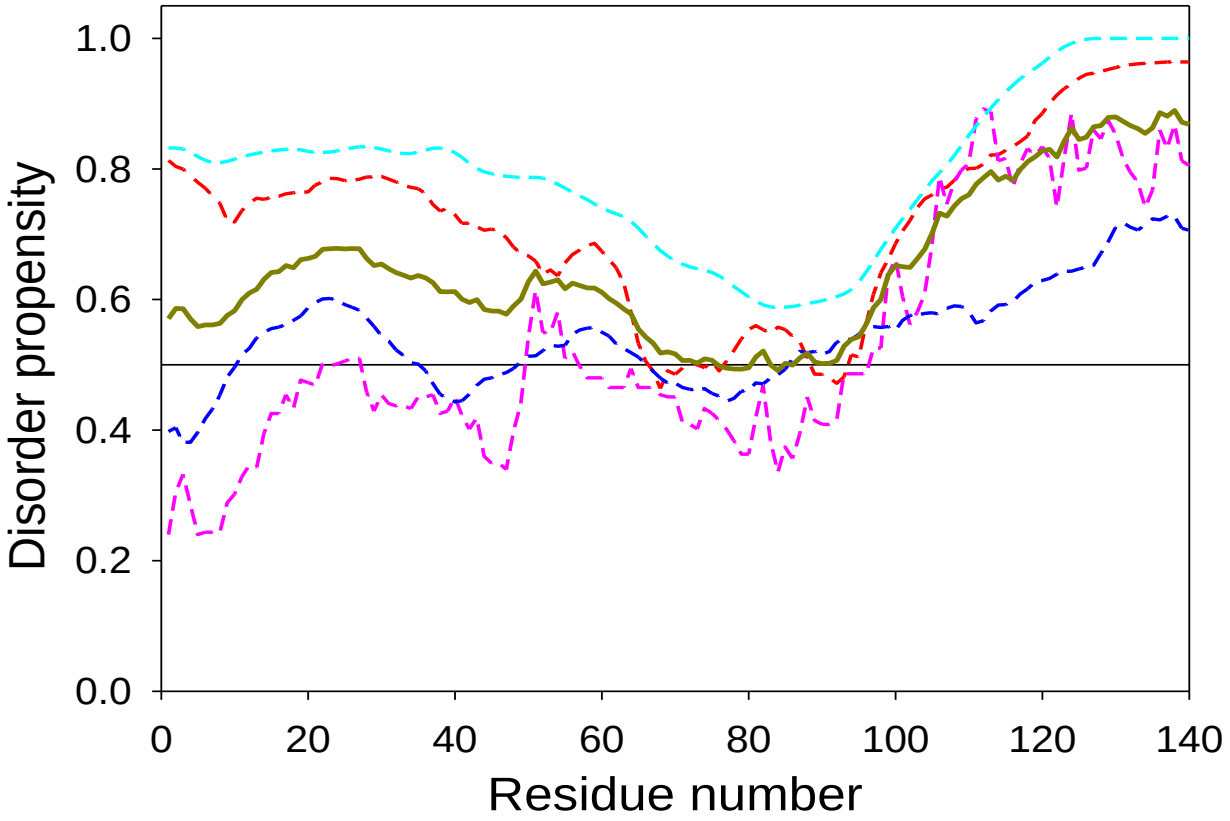


Plot A shows three AS isoforms of α-synuclein (1a, 1b, and 1c); three formal structural domain (2); seven imperfect repeats (3); predicted (4a) and experimentally determined α-helices (4b); PTM sites: oxidative methionines (yellow circles) and tyrosines (blue circles); phosphorylation sites (red circles); ubiquitination (green boxes); sumoylation (brown box); tTG crosslinking sites (red ovals); and PD-related mutations (three red stars)

Plot B represents interaction domains responsible for binding of several ligands and proteins. The numbers on the bars correspond to the residues in α-synuclein sequence (modified from Dev K. K., Hofele K., Barbieri S., Buchman V. L. and van der Putten H. (2003) *Neuropharmacology* 45, 14-44).

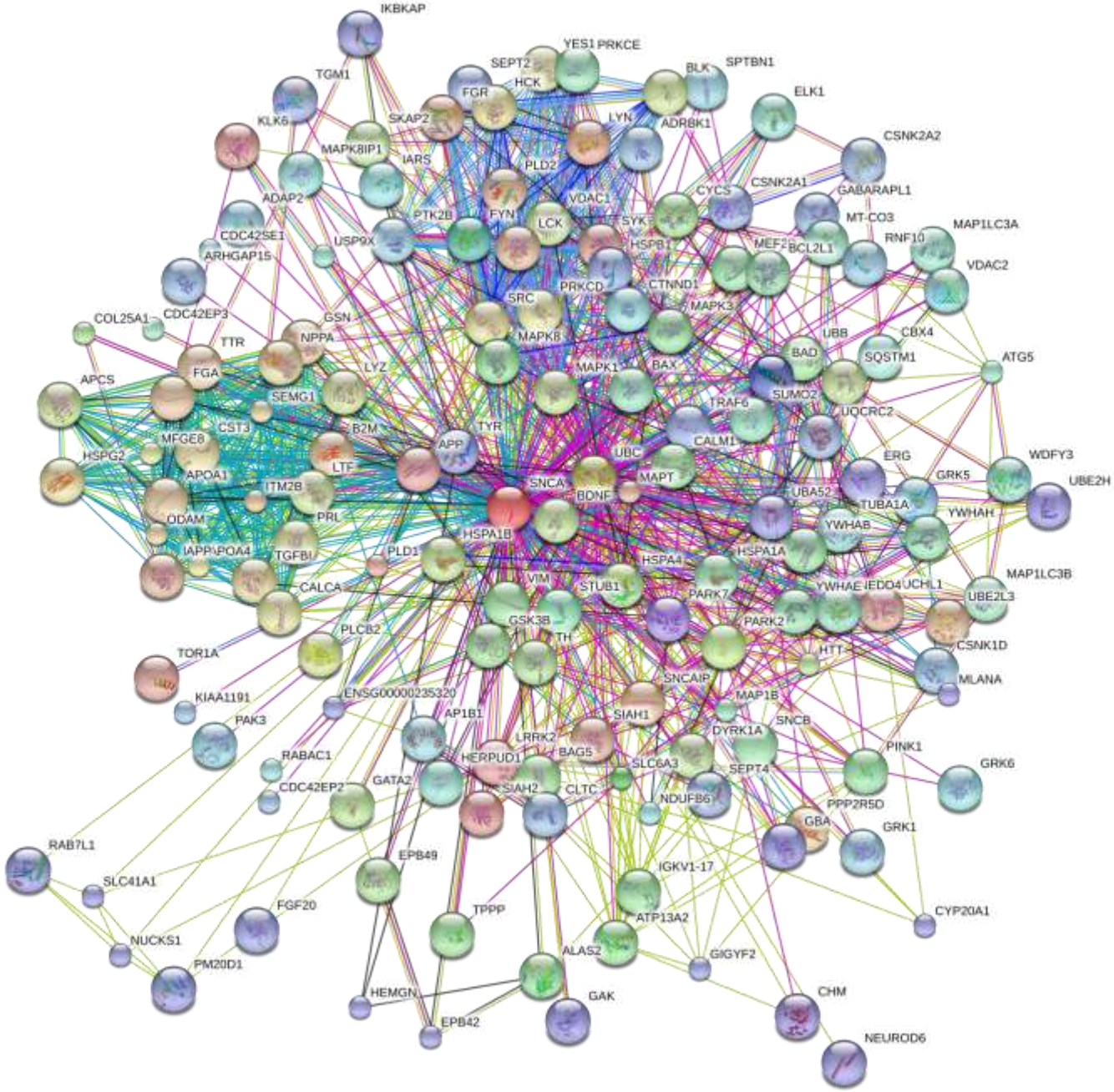
Uversky (2008) *Curr. Prot. Pept. Sci*, **9**, 507

α-Synuclein is a natively unfolded protein

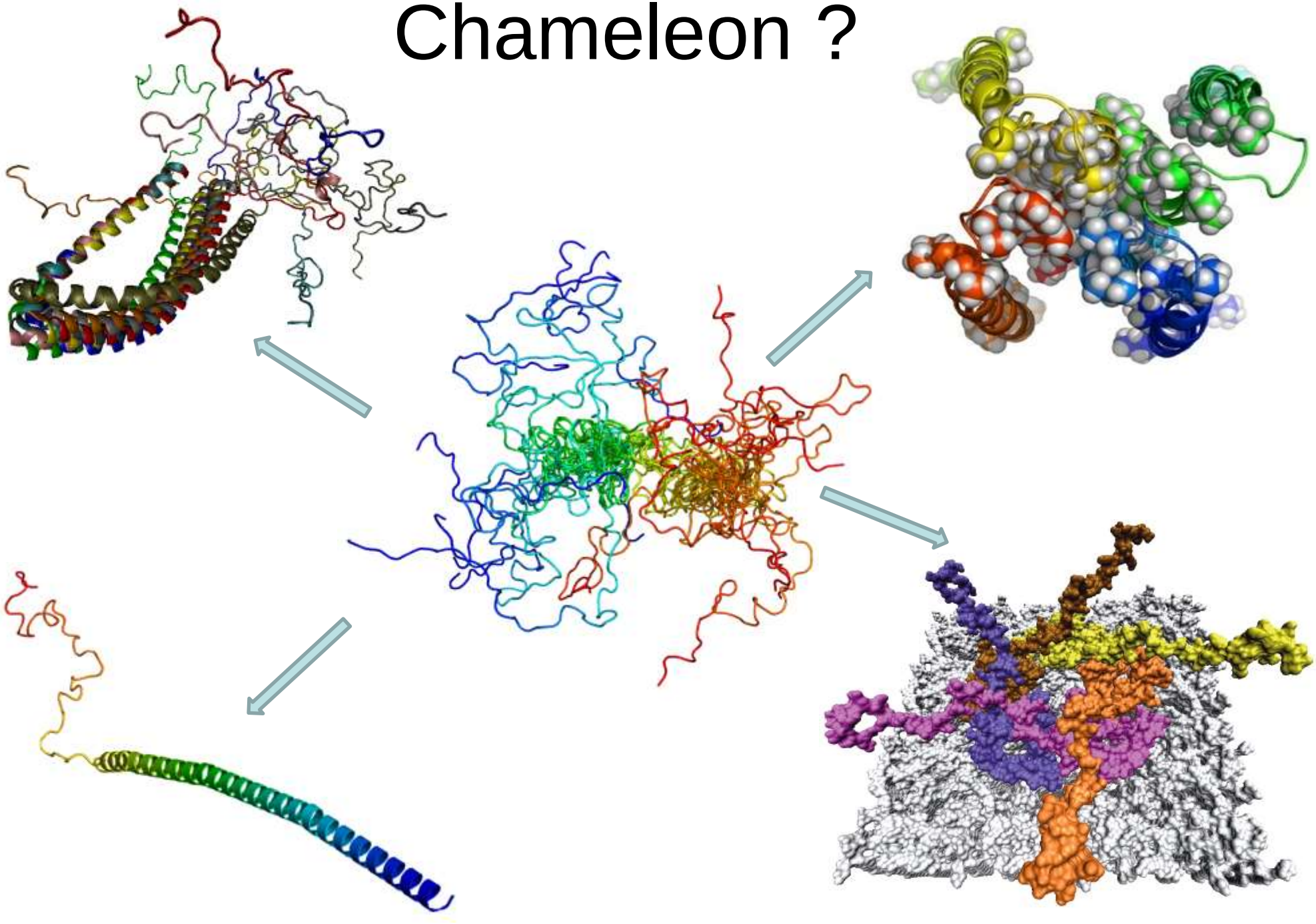


Intrinsic disorder propensity in human α-synuclein estimated by IUPred (pink dashed line); RONN (blue dashed line); PONDR VSL2 (red dashed line) and PONDR VL3 (cyan dashed line). Solid dark yellow line represents the averaged results.

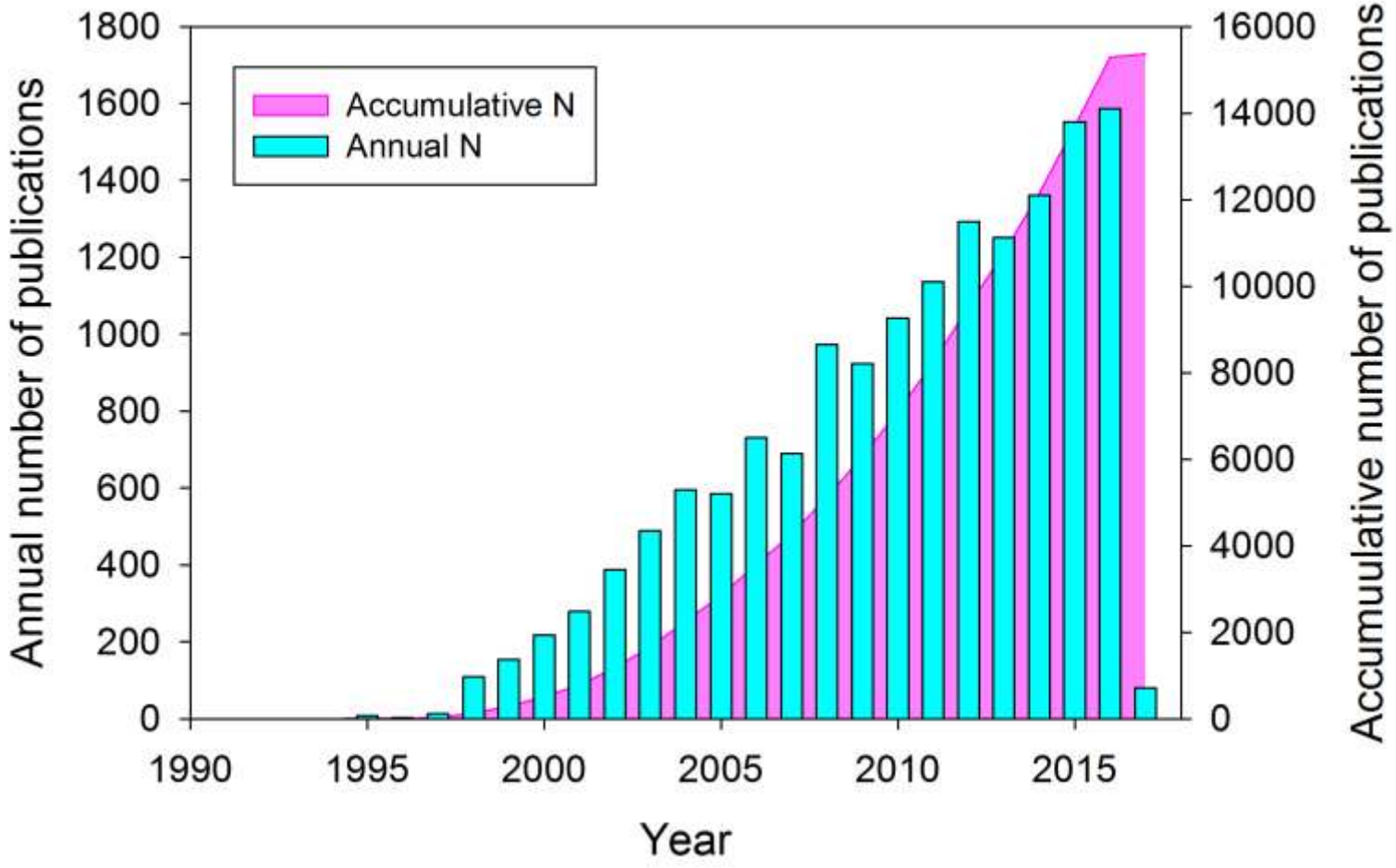
Hub ?


IKBKAP
YES1
PRKCE
SEPT2
TGM1
BLK
SPTBN1
HCK
FGR
ELK1
KLK6
SKAP2
LYN
ADRBK1
CSNK2A2
MAPK8IP1
IARS
PLD2
CSNK2A1
CYCS
GABARAPL1
ADAP2
VDAC1
PTK2B
FYN
LCK
SYK
MT-CO3
MAP1LC3A
CDC42SE1
USP9X
HSPB1
MEF2
BCL2L1
RNF10
ARHGAP15
VDAC2
PRKCD
CTNND1
SRC
MAPK3
COL25A1
CDC42EP3
GSN
MAPK8
UBB
CBX4
TTR
NPPA
BAD
SQSTM1
ATG5
FGA
LYZ
MAPK1
BAX
APCS
SEMG1
SUMO2
TRAF6
UQCRC2
CST3
B2M
TYR
CALM1
MFGE8
APP
UBC
ERG
WDFY3
HSPG2
LTF
MAPT
GRK5
UBE2H
APOA1
ITM2B
SNCA
UBA52
BDNF
TUBA1A
YWHAH
ODAM
PRL
YWHAB
HSPA1B
IAPP\POA4
TGFBI
PLD1
HSPA1A
HSPA4
MAP1LC3B
VIM
STUB1
YWHAE
IED04
UCHL1
CALCA
PARK7
UBE2L3
GSK3B
PARK2
PLCB2
TH
CSNK1D
TOR1A
HTT
SNCAIP
MLANA
KIAA1191
ENSG00000235320
MAP1B
AP1B1
SIAH1
SNCB
PAK3
DYRK1A
LRRK2
PINK1
RABAC1
BAG5
HERPUD1
SLC6A3
SEPT4
GRK6
CDC42EP2
GATA2
SIAH2
CLTC
NDUFB6
PPP2R5D
GBA
GRK1
RAB7L1
EPB49
IGKV1-17
SLC41A1
FGF20
TPPP
ATP13A2
CYP20A1
NUCKS1
ALAS2
GIGYF2
PM20D1
HEMGN
GAK
CHM
EPB42
NEUROD6

Chameleon ?

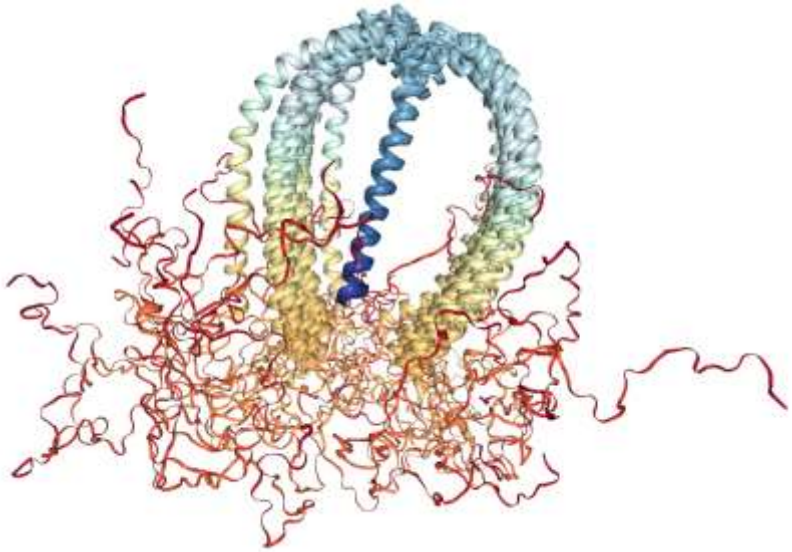


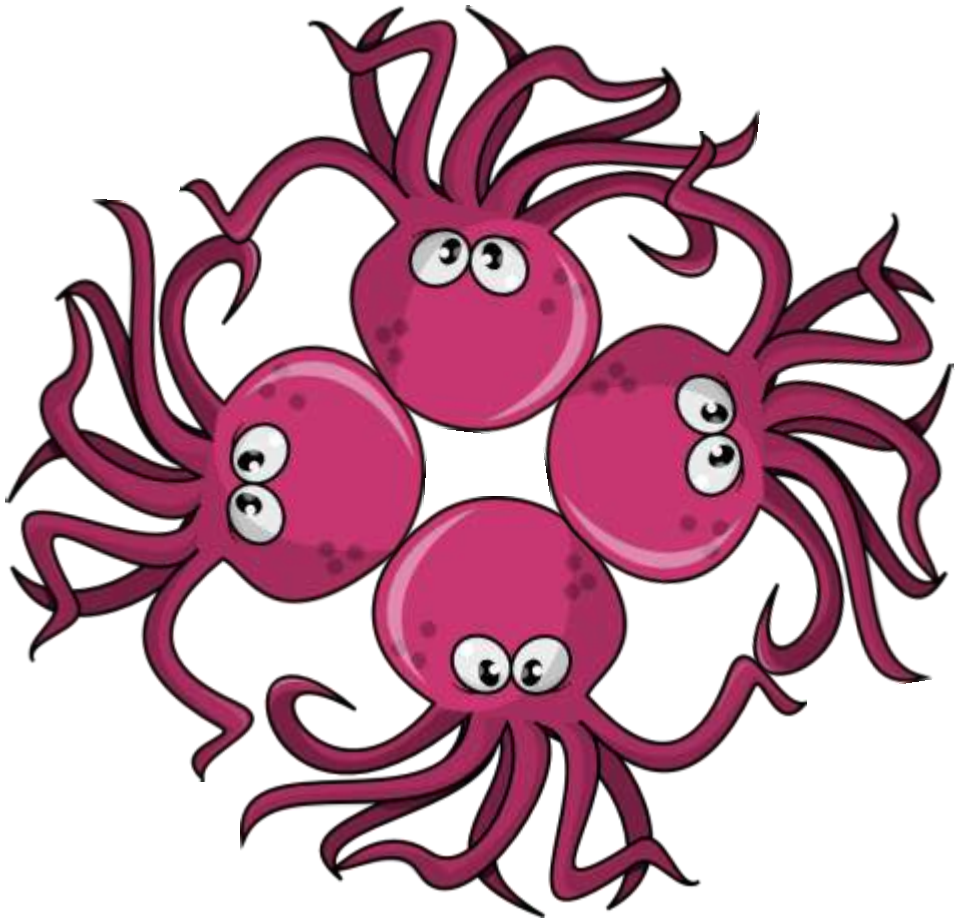
Protein with unknown function



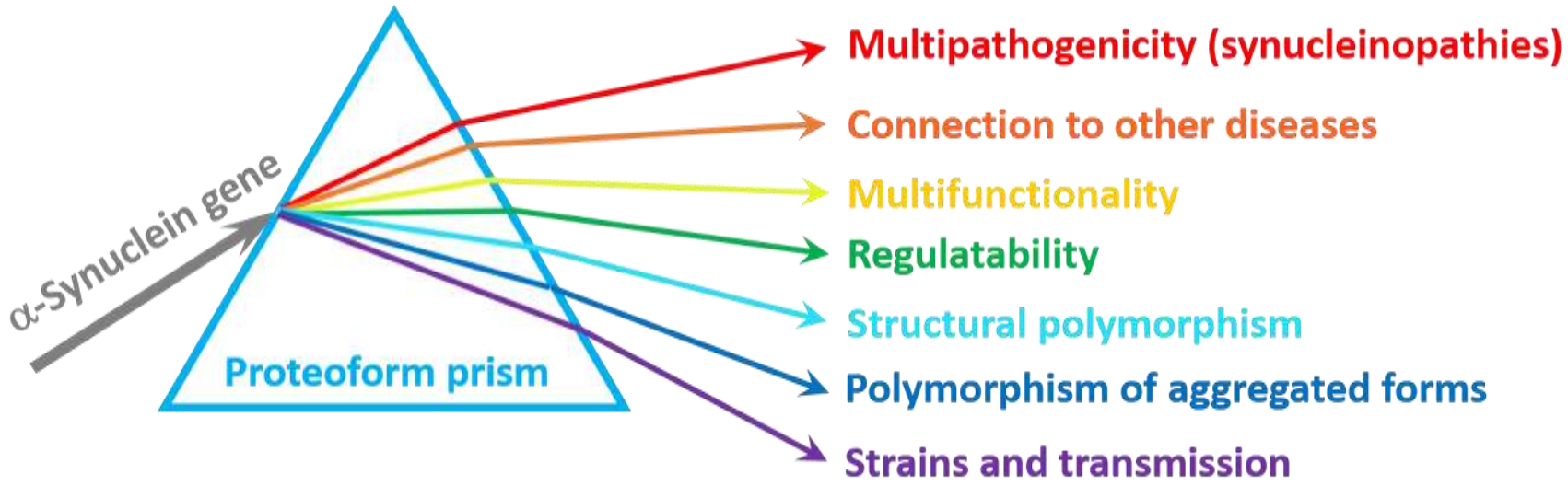
Uversky (2017) F1000 Research. 6 (F1000 Faculty Reviews), 525

Octopus view of α-synuclein functionality



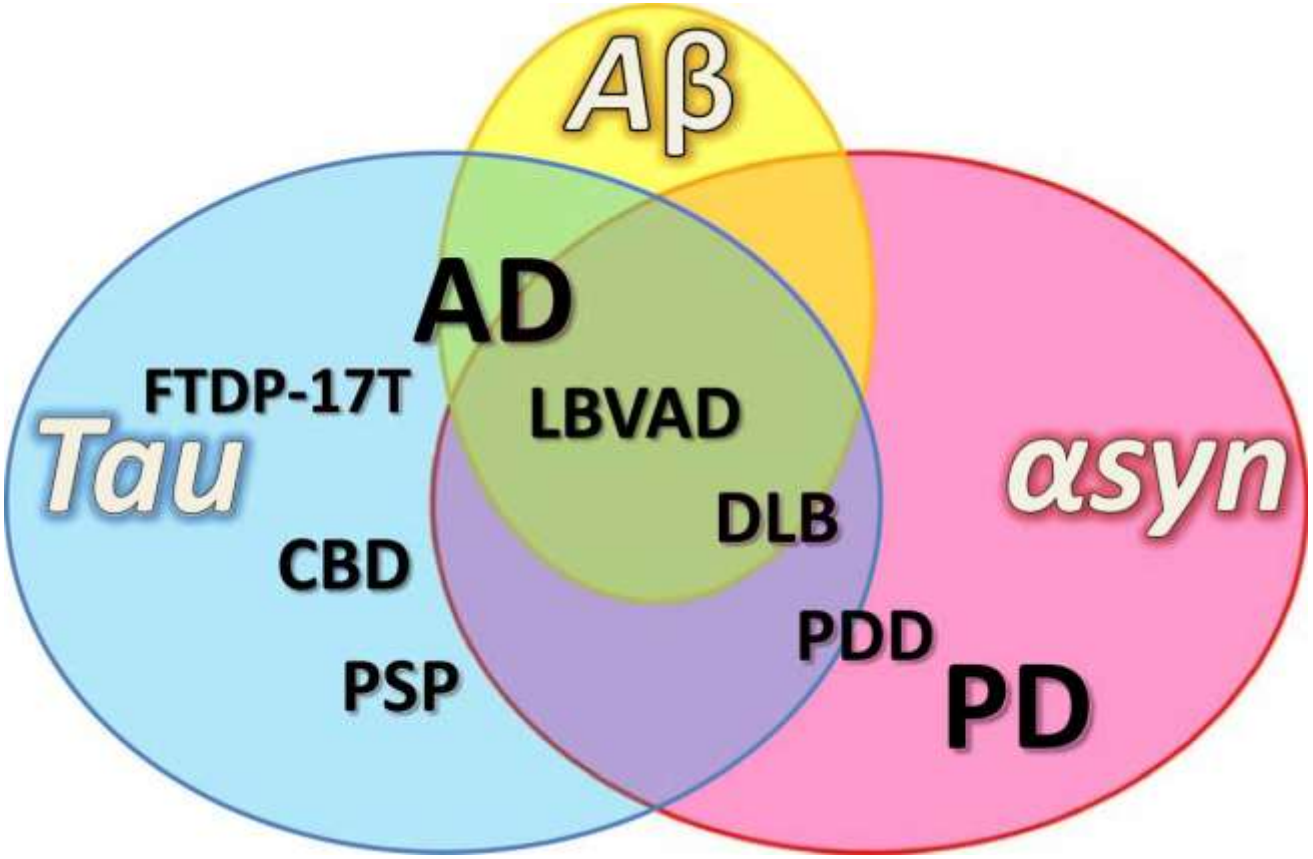


Looking at α-synuclein through the proteoform prism



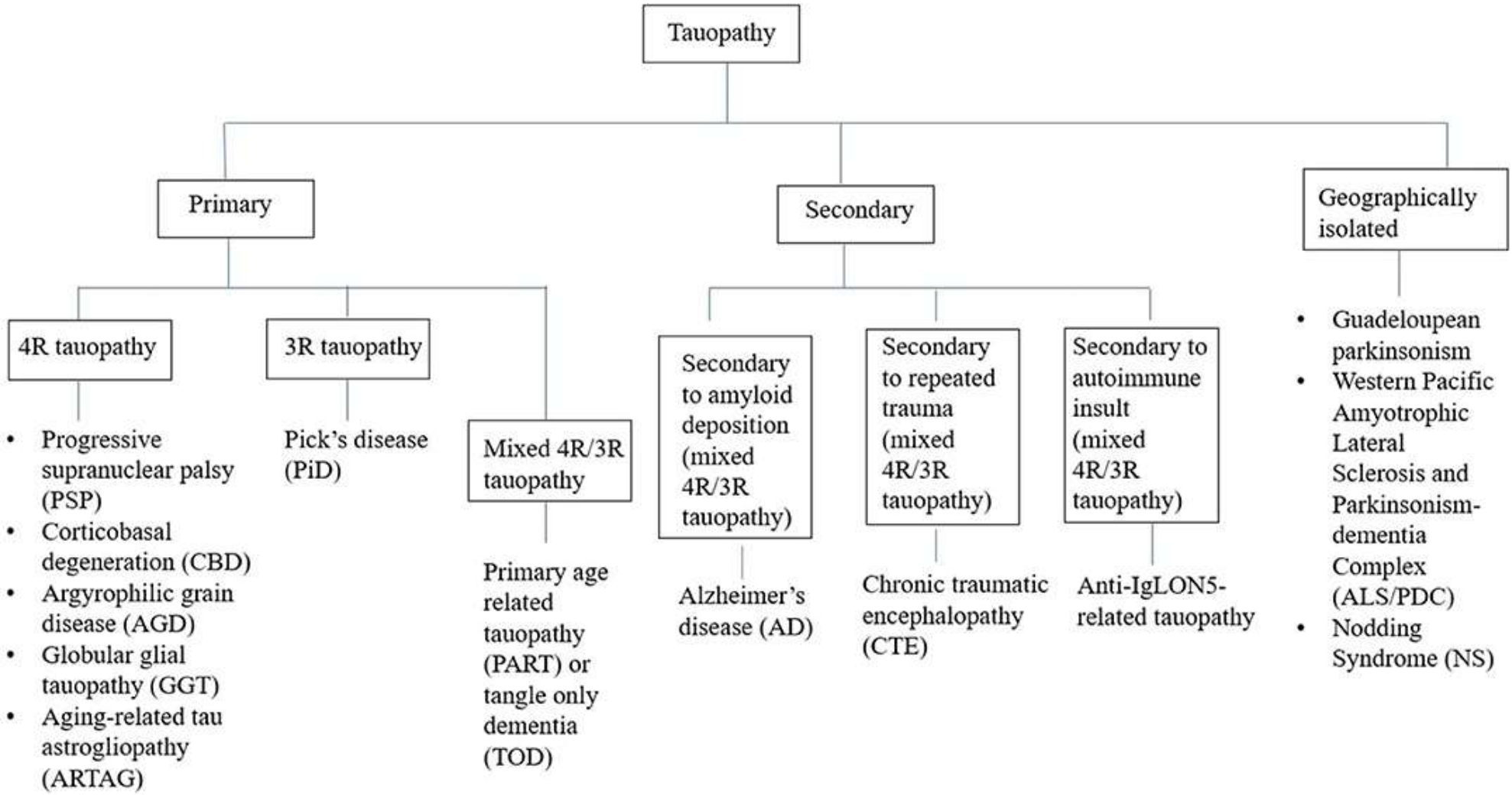
Uversky (2017) F1000 Research. 6 (F1000 Faculty Reviews), 525

α-Synuclein, Aβ, and tau: teammates in neurodegeneration



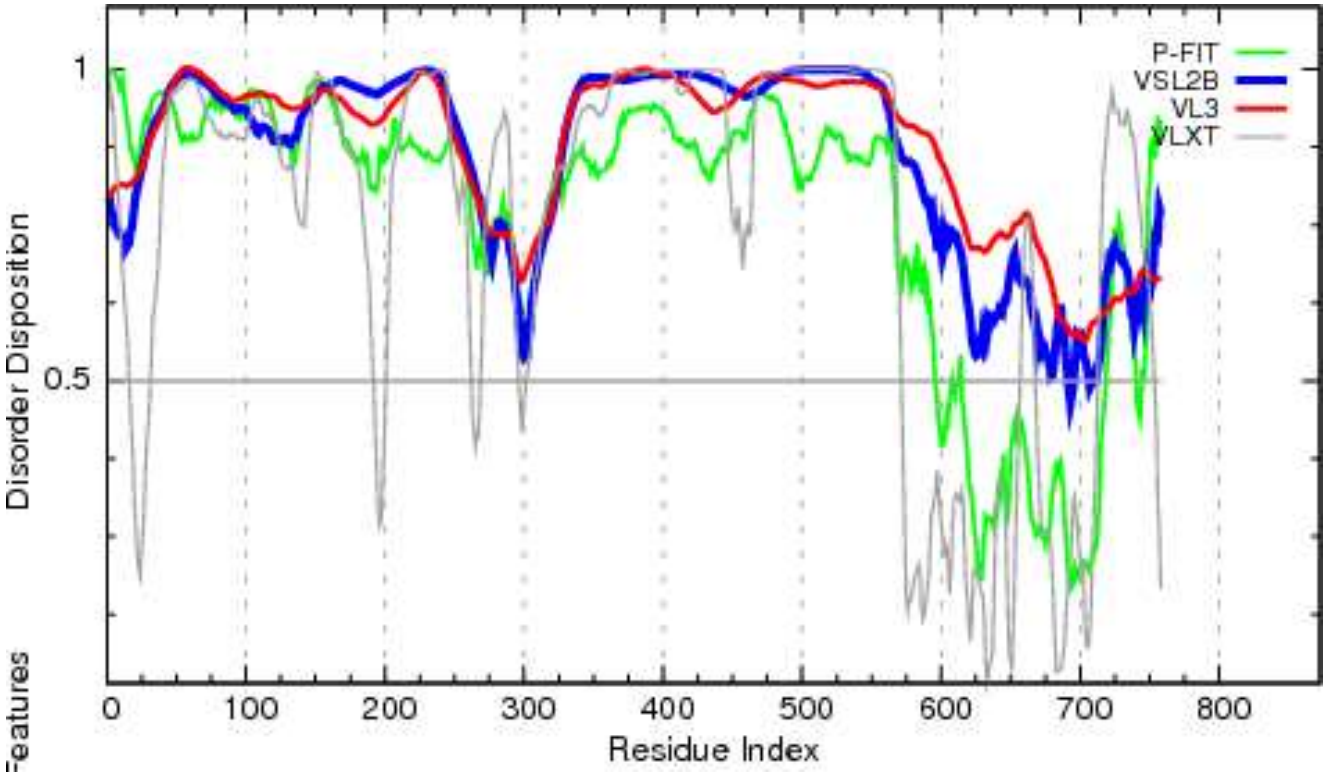
- **AD, Alzheimer's disease**
- **PD, Parkinson's disease**
- **LBVAD, Lewy body (LB) variant of AD**
- **DLB, dementia with LBs**
- **PDD, PD dementia**
- **CBD, corticobasal degeneration**
- **PSP, progressive supranuclear palsy**
- **FTDP-17T, Frontotemporal dementia with parkinsonism-17**

Classification of tauopathies

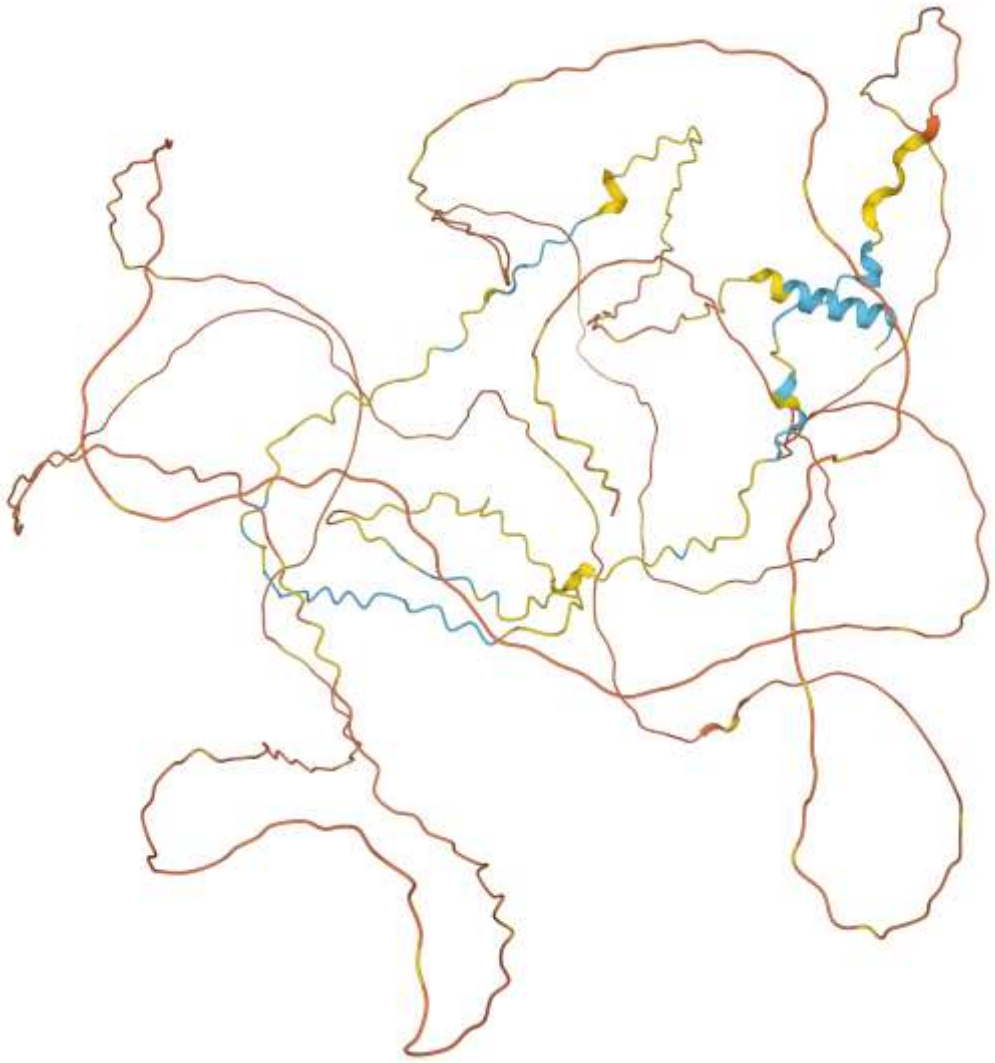


Jacky Ganguly, Mandar Jog (2020) *Front Neurol* **11**:599384

Tau as an IDP


P-FIT
VSL2B
VL3
VLXT
1
0.5
Disorder Disposition
Features
0
100
200
300
400
500
600
700
800
Residue Index

3D model of human Tau structure generated by AlphaFold



Model Confidence:

- Very high (pLDDT > 90)
- Confident (90 > pLDDT > 70)
- Low (70 > pLDDT > 50)
- Very low (pLDDT < 50)

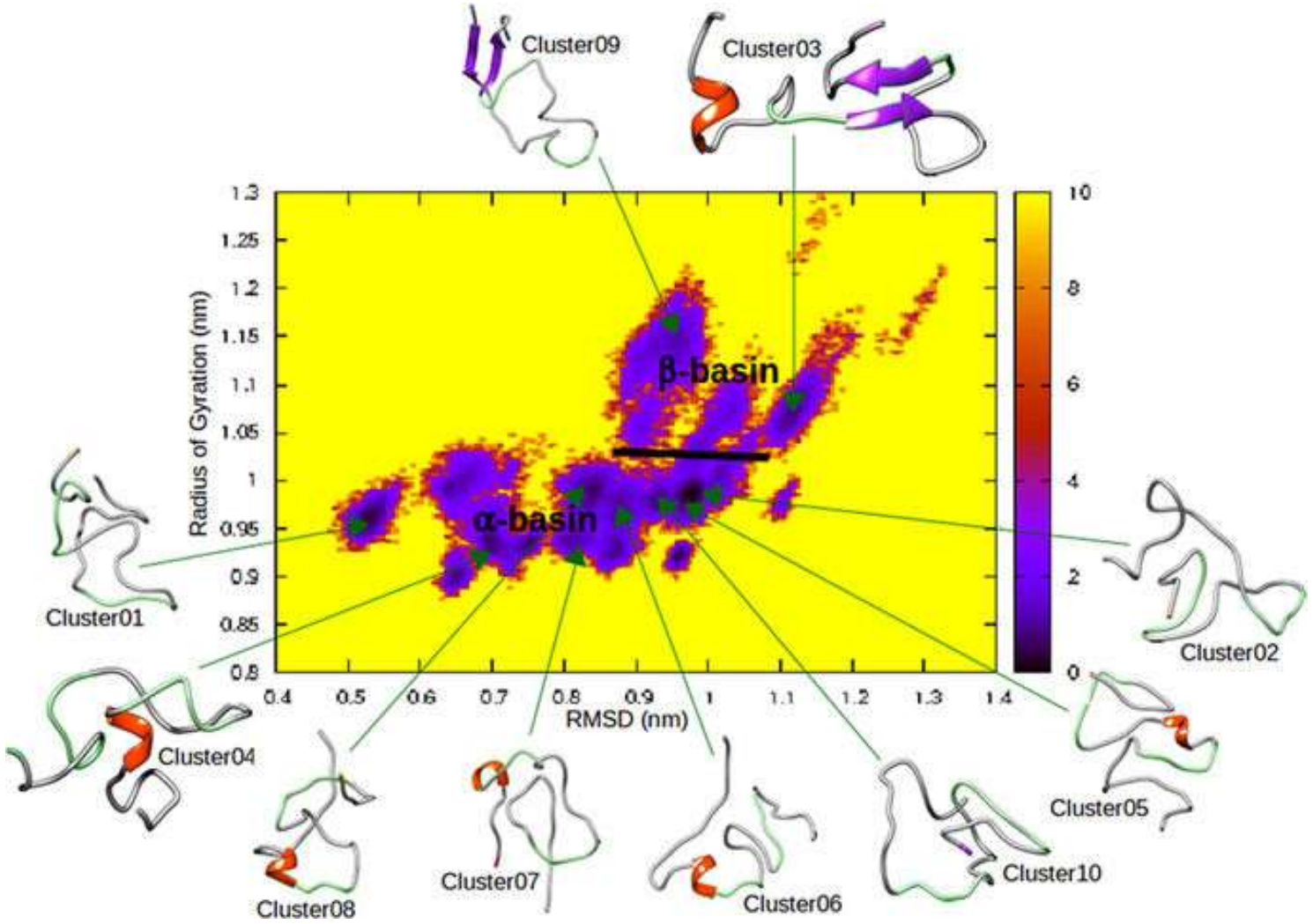
AlphaFold produces a per-residue confidence score (pLDDT) between 0 and 100. Some regions below 50 pLDDT may be unstructured in isolation.

Amyloidopathies

Pathologic accumulation of Aβ results in at least four distinct neurologic disorders that affect middle-aged and elderly adults:

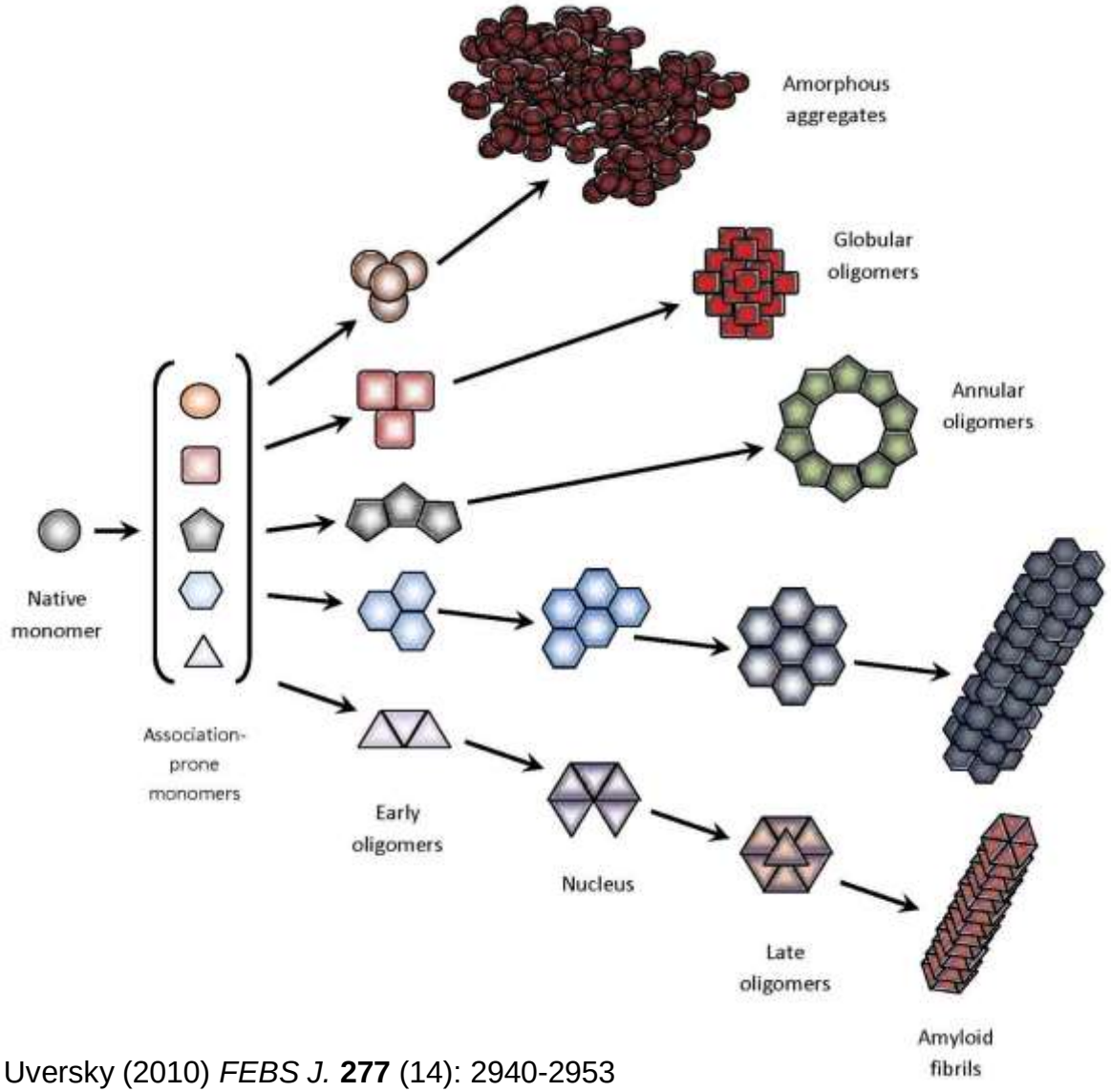
- Alzheimer disease (AD);
- Cerebral amyloid angiopathy (CAA);
- Inflammatory CAA
- Cerebral amyloidoma

Conformational ensemble of Aβ



Tran et al. (2016) Scientific Reports, 6, Article number: 21429

Multi-Facial Aggregates

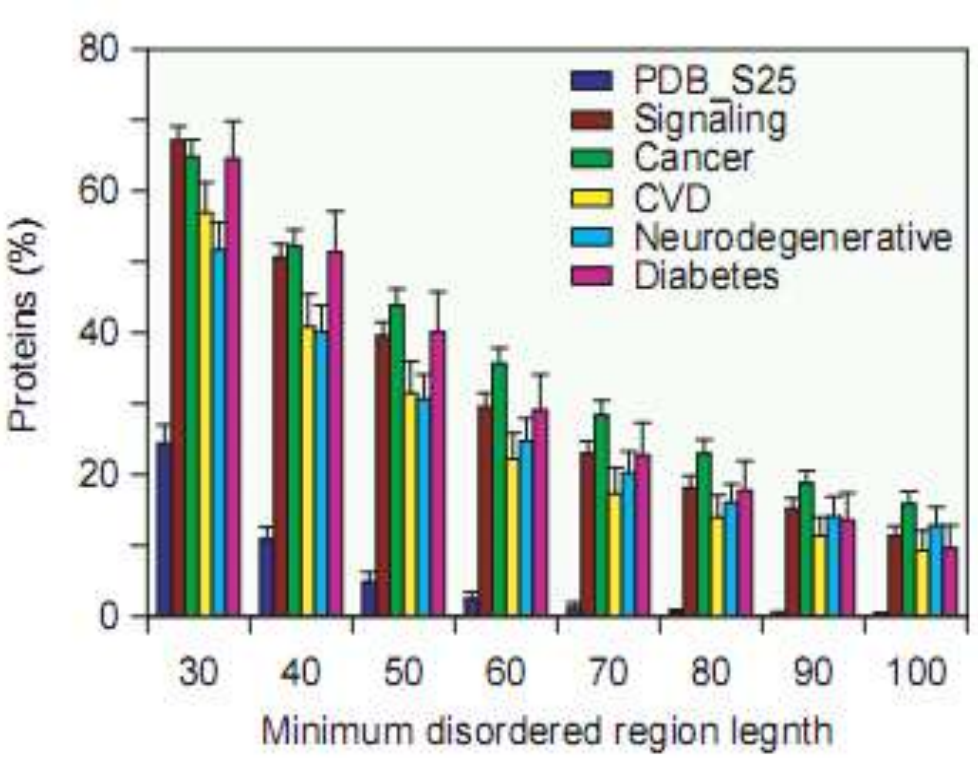


Schematic, oversimplified representation of protein self-association process. Formation of multiple association-prone monomeric forms generates multiple aggregation pathways. There are three major products of the aggregation reaction – amorphous aggregates (bottom pathway), morphologically different soluble oligomers (second and third from the top pathways) and morphologically different amyloid fibrils (two bottom pathways). Two types of soluble oligomers (spheroidal and annular) and two morphologically different amyloid fibrils are shown. Changes in color reflect potential structural changes within a monomer taking place at each elementary step. In reality, the picture is more complex and more species can be observed. Interconversions between various species at different pathways are also possible.

Uversky (2010) *FEBS J.* **277** (14): 2940-2953

From individual cases to a general picture

IDPs in human diseases



Analyzed datasets:

1,138 ordered proteins;

2,329 signaling proteins;

1,786 cancer-associated proteins;

487 CVD-related proteins;

689 proteins associated with neurodegenerative diseases;

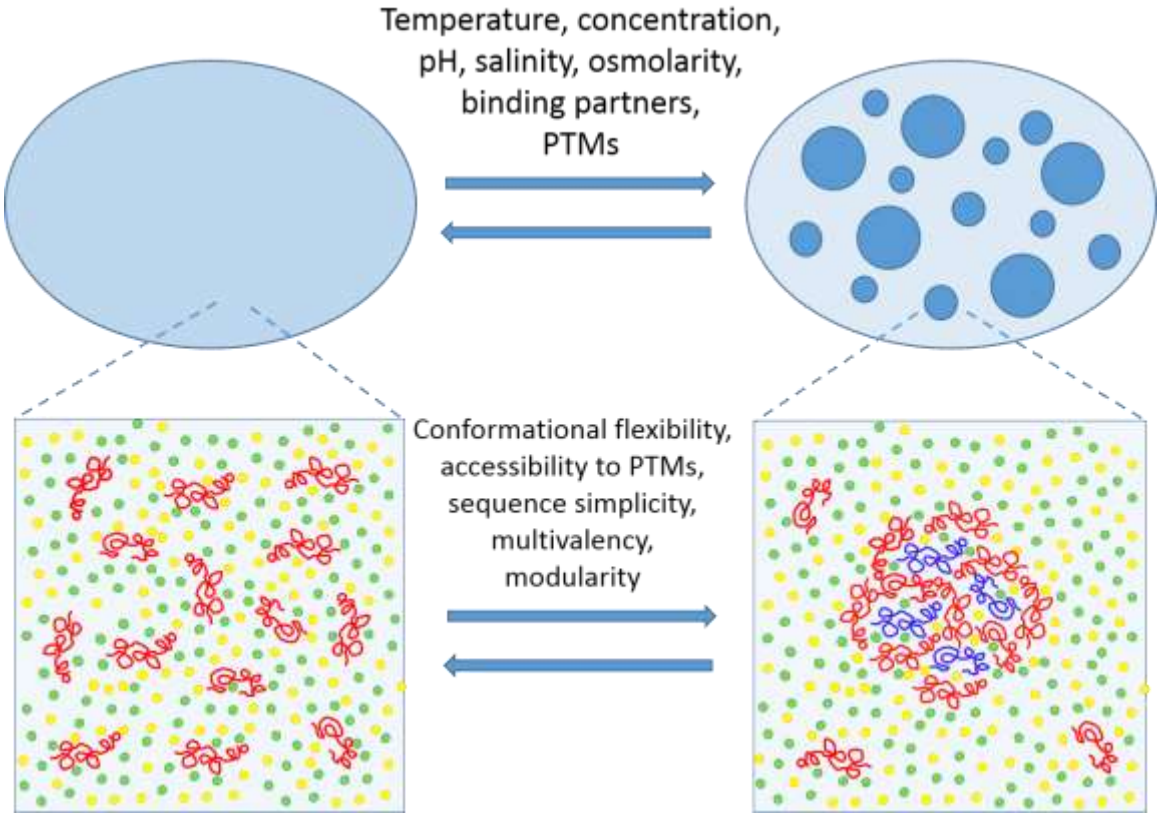
285 diabetes-related proteins

Iakoucheva et al. *J Mol Biol*. (2002) **323**:573; Cheng et al. *Biochemistry* (2006) **45**: 10448

IDPs, liquid-liquid phase transitions, and proteinaceous membrane-less organelles:

Cell as an aqueous multi-phase system

Intrinsic disorder and LLPTs



Thermodynamic factors (top) and disorder-related features controlling liquid-liquid phase transitions in protein solutions.

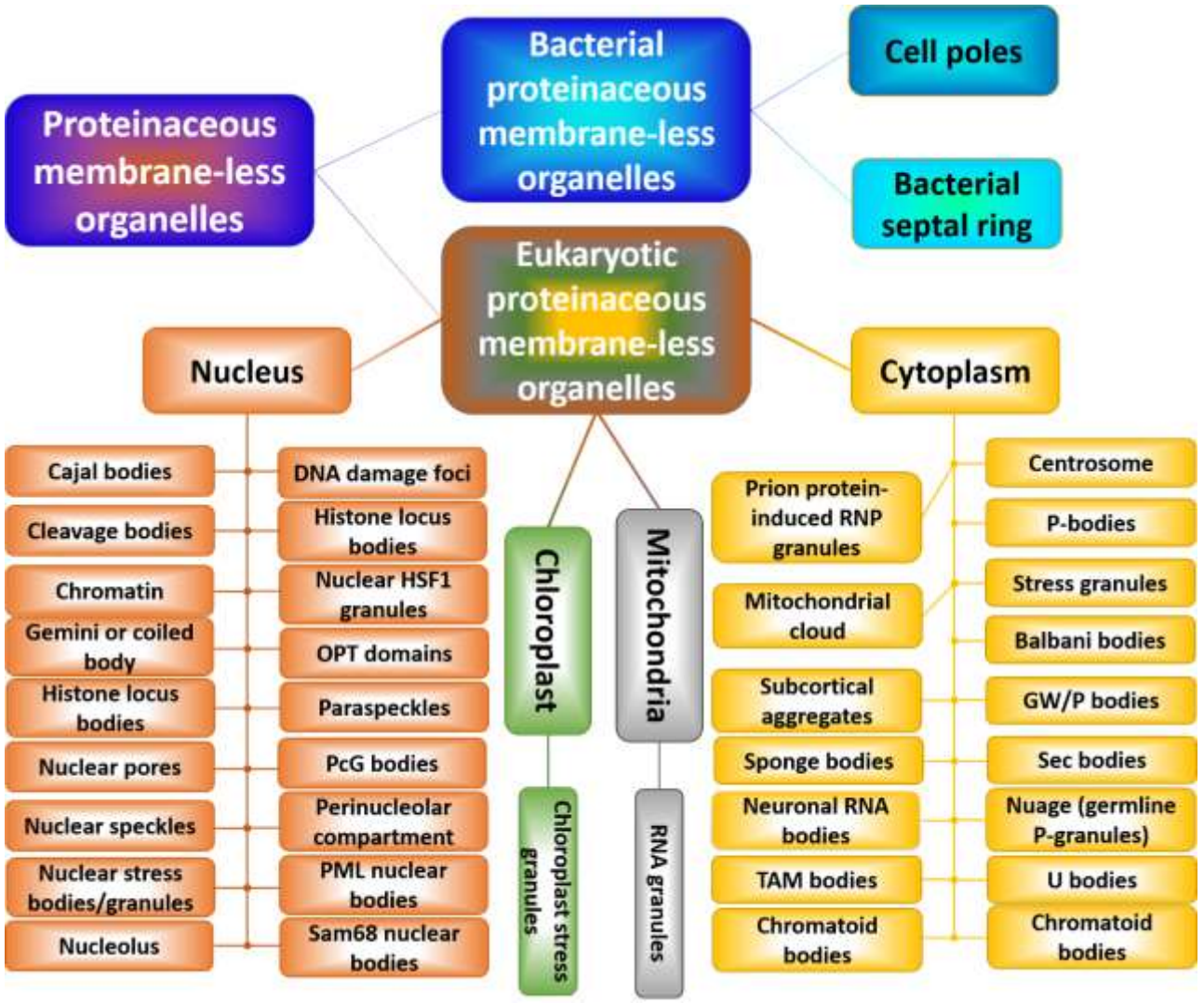
Uversky. *Curr Opin Struct Biol* (2016) **44**, 18-30

Intrinsic disorder, PMLOs, and LLPTs

- Eukaryotic cells are inhomogeneously crowded and contain various cellular bodies
- Many of these bodies are proteinaceous membrane-less organelles (PMLOs)
- PMLOs are formed as a result of highly controlled liquid-liquid phase transitions (LLPTs)
- The interior of these condensed liquid droplets represents an overcrowded milieu
- PMLOs are invariantly enriched in intrinsically disordered proteins
- Intrinsic disorder is crucial for formation, disassembly, and functionality of PMLOs

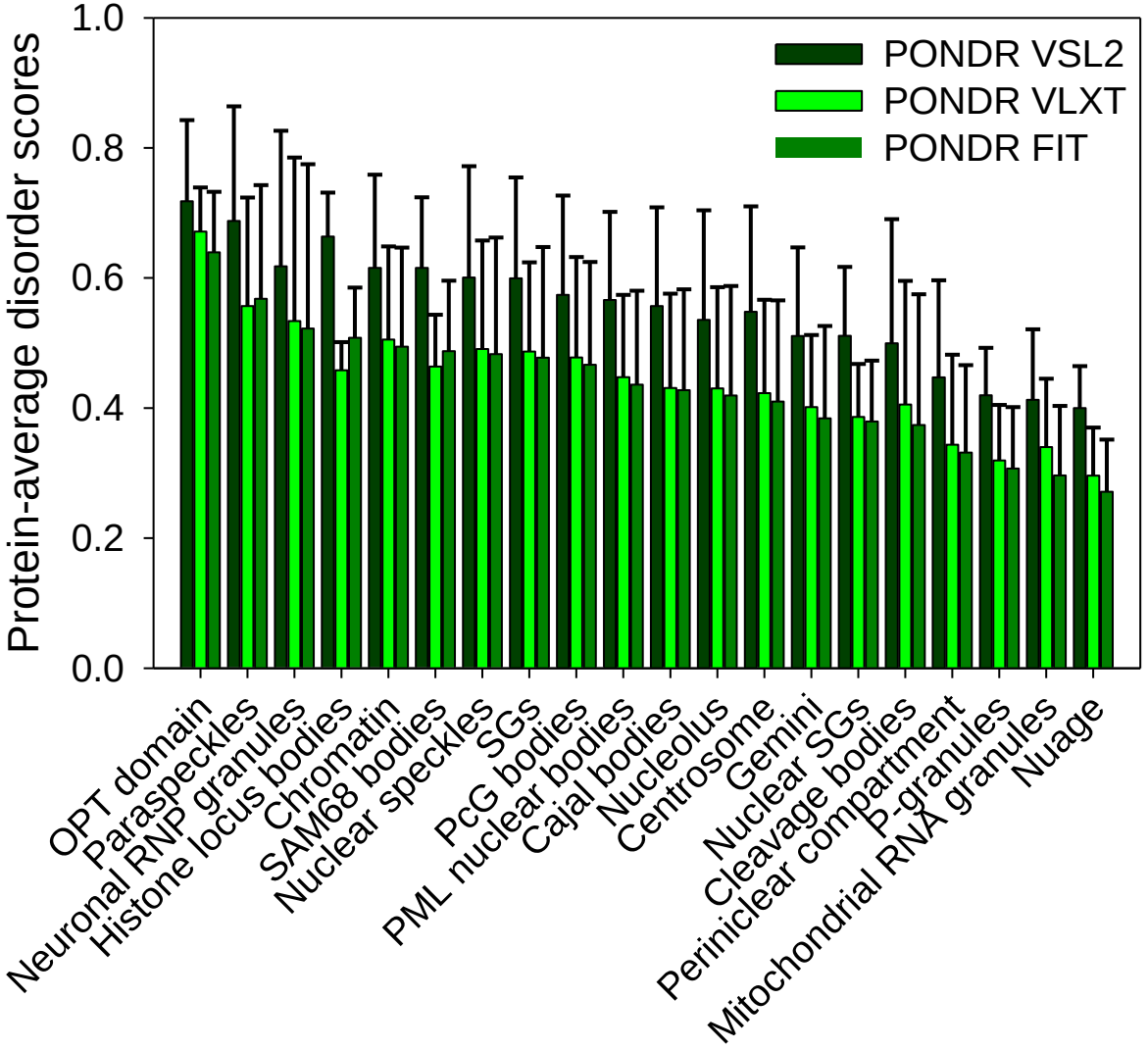
Uversky. *Curr Opin Struct Biol* (2016) **44**, 18-30

Multitude of PMLOs



Zaslavsky & Uversky (2018) *Biochemistry*. 57(17): 2437-2451.

Unfoldome of human PMLOs



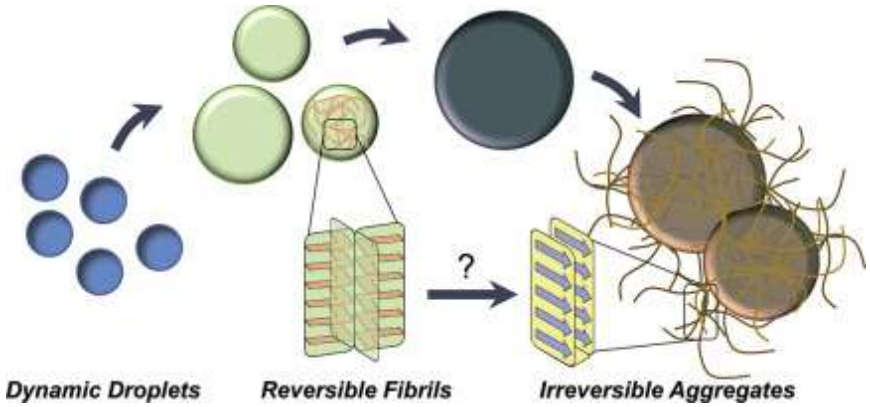
Darling et al. (2018) Proteomics. 8(5-6): e1700193 .

IDPs and liquid-liquid phase transitions (LLPTs)

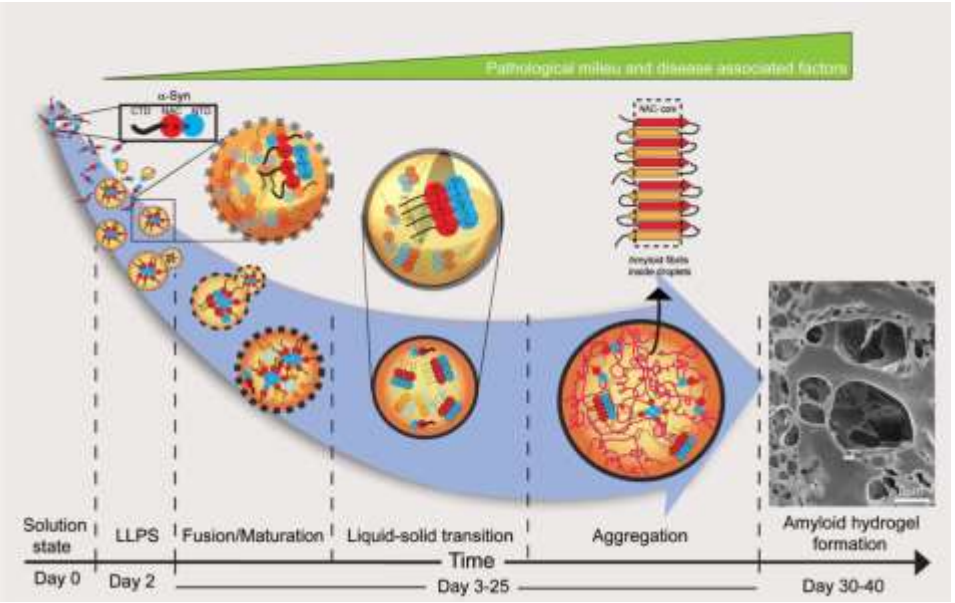
- PMLOs are many and are often formed in response to changes in the cellular environment.
- Being typically liquid in nature, these organelles can be described as products of the reversible and highly controlled LLPTs.
- Many of these PMLOs are complex coacervates containing (almost invariantly) intrinsically disordered proteins and often nucleic acids.
- It seems that lack of stable structure in major proteinaceous constituents of these organelles is crucial for the formation of phase-separated droplets.
- The liquid-like properties of phase-separated droplets could facilitate functions of their constituents, which are accumulated within droplets at high concentrations but remain dynamic.

Uversky et al. (2015) *FEBS Lett.* **589** (1):15-22

Pathological transformations in MLOs



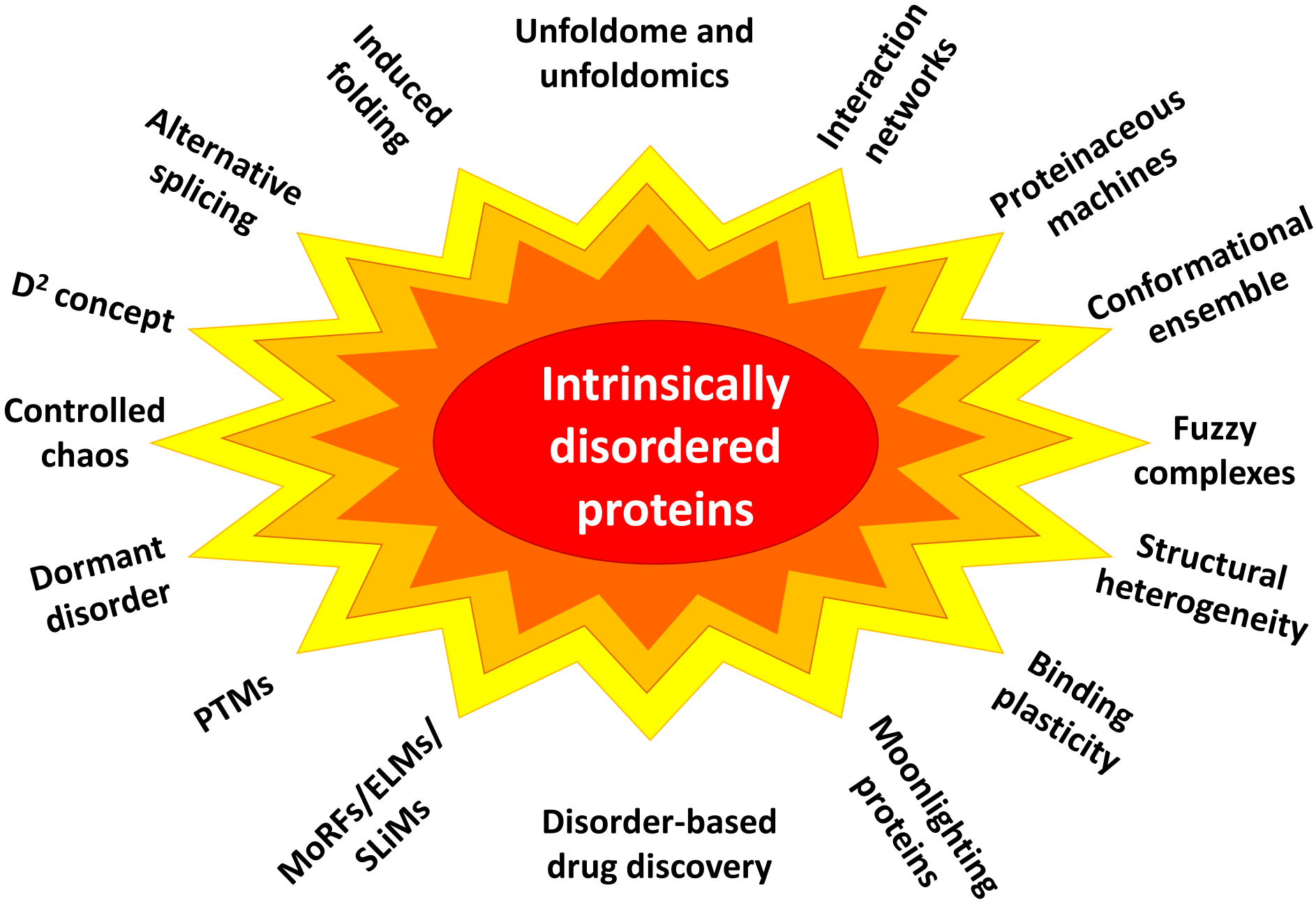
W. Michael Babinchak, Witold K.Surewicz
(2020) JMB 432 (7), 1910-1925



Soumik Ray, Nitu Singh, Satyaprakash Pandey, Rakesh Kumar, Laxmikant Gadhe, Debalina Datta, Komal Patel, Jaladhar Mahato, Ambuja Navalkar, Rajlaxmi Panigrahi, Debdeep Chatterjee, Siddhartha Maiti, Sandhya Bhatia, Surabhi Mehra, Ajay Singh, Juan Gerez, Arindam Chowdhury, Ashutosh Kumar, Ranjith Padinhateeri, Roland Riek, G Krishnamoorthy, Samir K Maji (2019)
bioRxiv 619858; doi: https://doi.org/10.1101/619858

Intrinsically disordered proteins: New concept in protein science

Uversky (2013) *Protein Science. 22 (6) 693-724*



Concluding remarks

- **Intrinsic disorder is highly abundant in various proteomes especially in their signaling proteins;**
- **Intrinsic disorder defines protein structure-function continuum;**
- **IDPs are tightly controlled in the norm;**
- **Uncontrolled chaos leads to various diseases and many disease-related proteins are IDPs;**

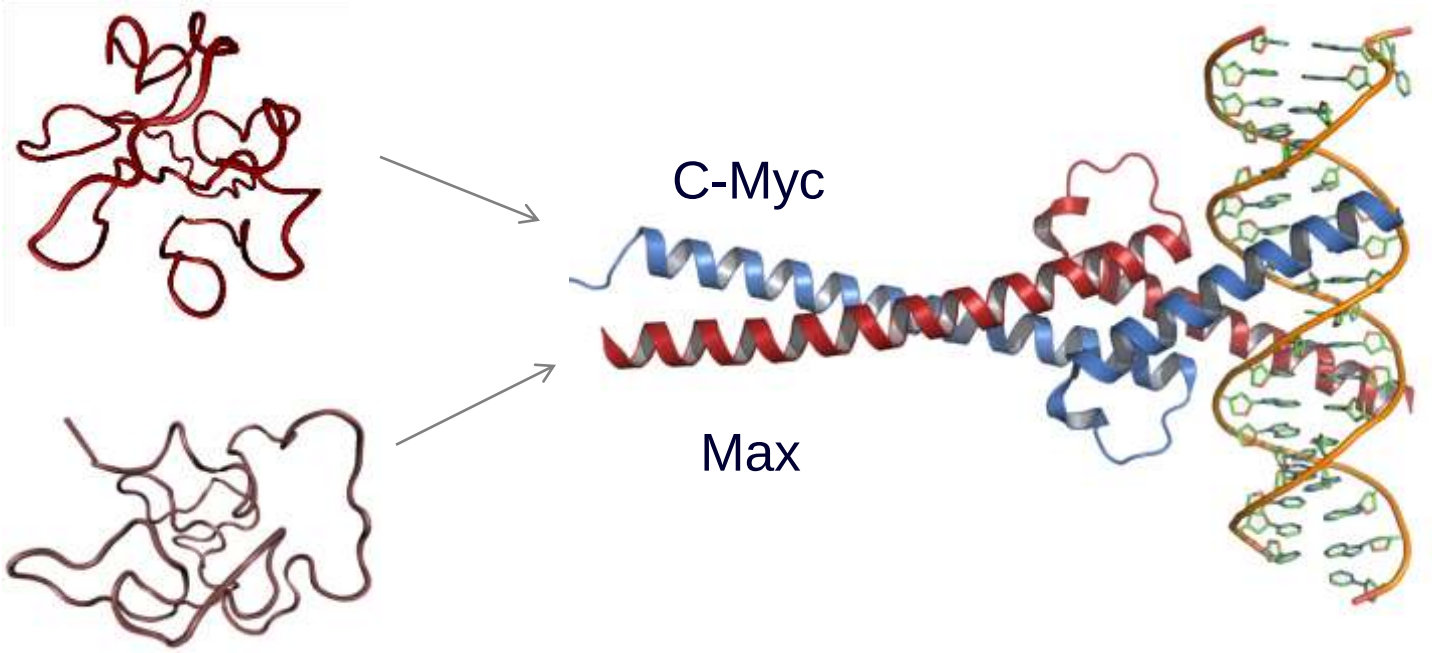
Thank you for your attention!!!

IDPs, liquid-liquid phase transitions, and proteinaceous membrane-less organelles:

Cell as an aqueous multi-phase system

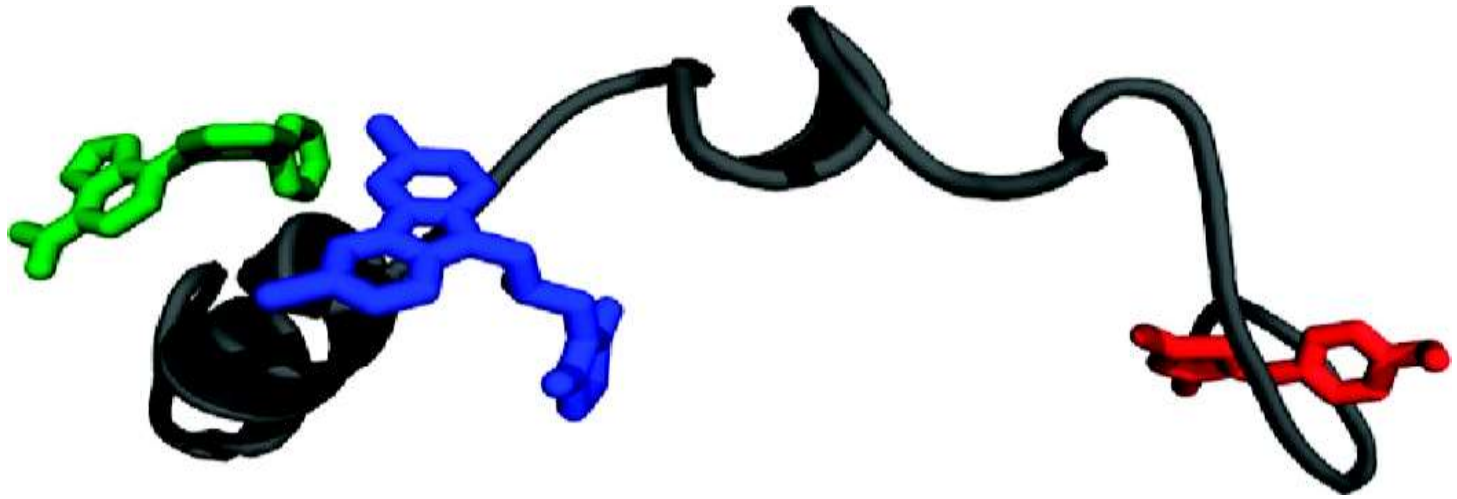
Disorder and drug discovery

c-Myc-Max complex as potential drug target



Deregulation of the c-Myc transcription factor is involved in many types of cancer. Inhibition of the dimer formation between the basic helix-loop-helix leucine zipper (bHLHZip) domain of c-Myc and a similar domain of Max is an attractive drug target. As monomers, bHLHZip proteins are intrinsically disordered but they fold on complex formation.

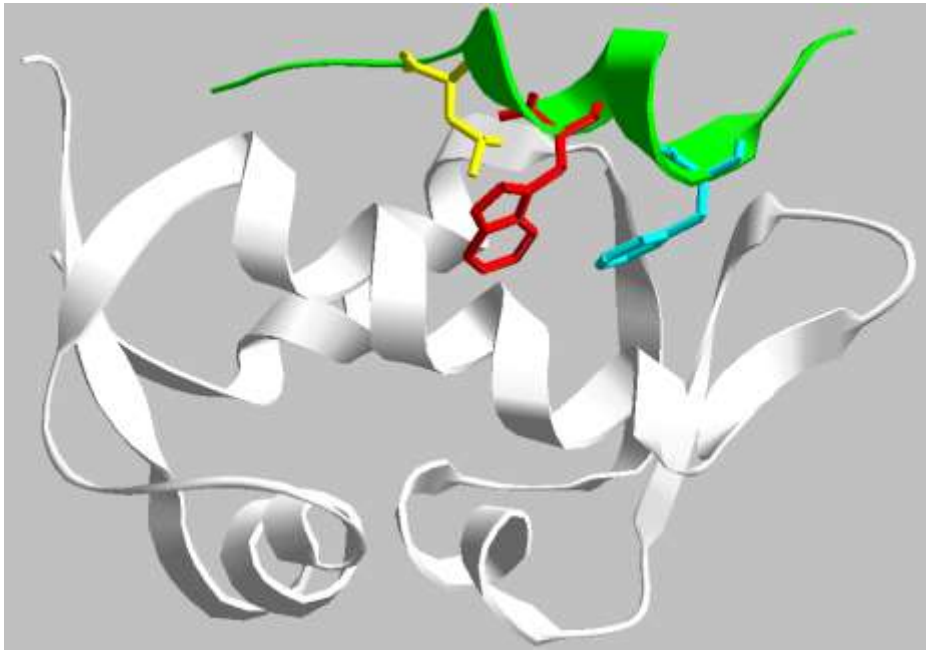
c-Myc possesses multiple independent binding sites for small-molecule inhibitors

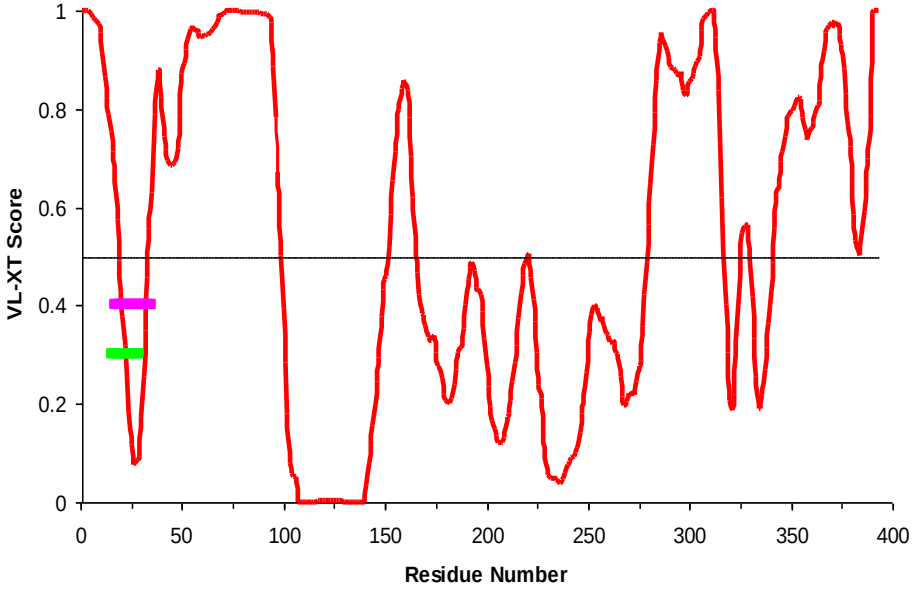


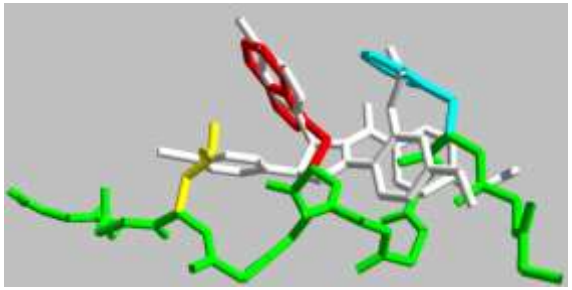
c-Myc-Max inhibitors bind to distinct ID regions of c-Myc. These binding sites are composed of short contiguous stretches of amino acids that can selectively and independently bind small molecules. Inhibitor binding induces only local conformational changes, preserves the overall disorder of c-Myc, and inhibits dimerization with Max.

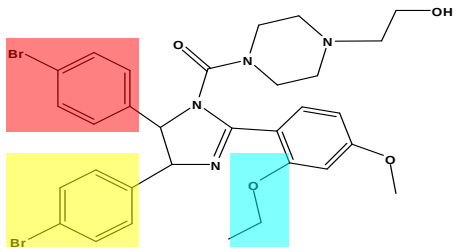
Published in: Dalia I. Hammoudeh; Ariele Viacava Follis; Edward V. Prochownik; Steven J. Metallo; *J. Am. Chem. Soc.* **2009,** 131, 7390-7401.
DOI: 10.1021/ja900616b

Protein disorder features and small molecule design: p53-Mdm2 interaction:









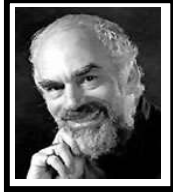
Nutlin-2

Molecular Kinetics, Inc.

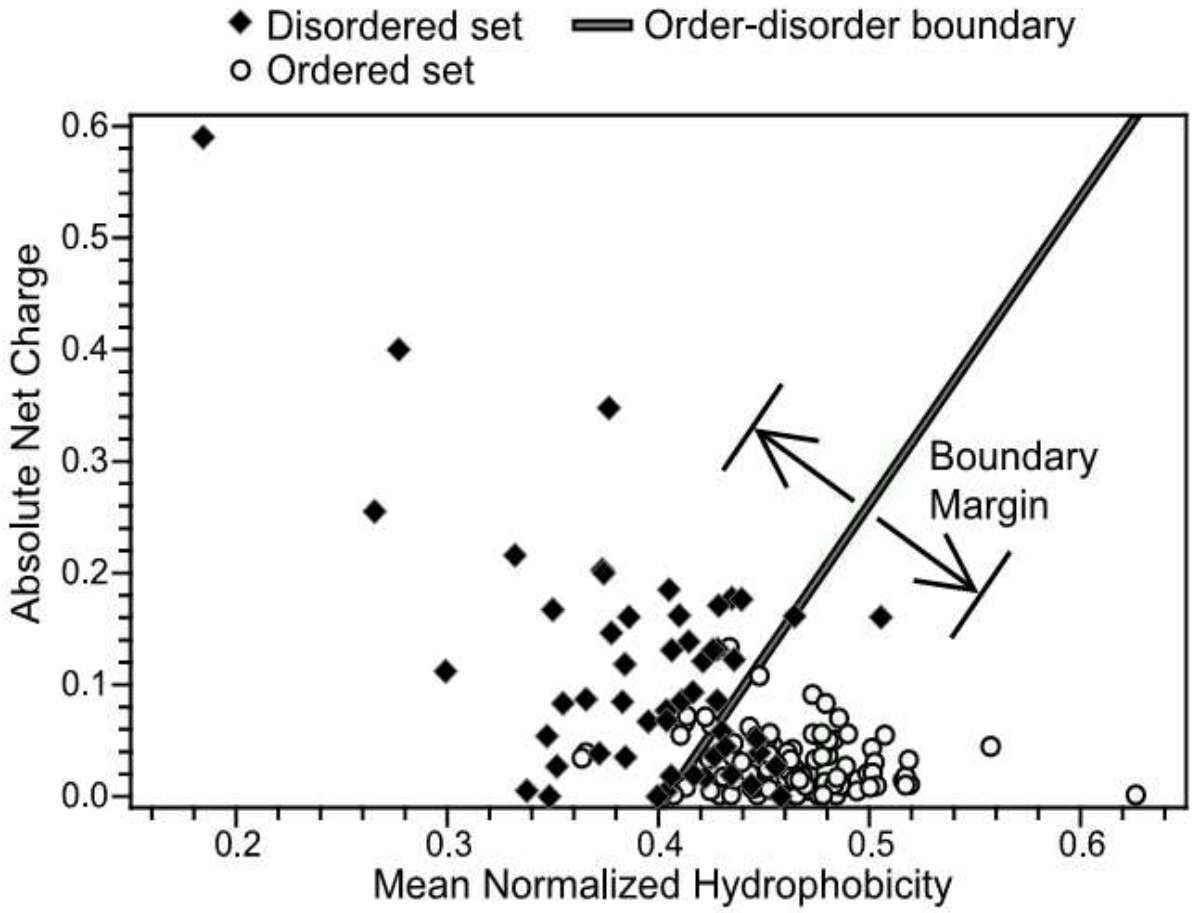
Manifestations of intrinsic disorder:

Amino acid sequence peculiarities

IDPs and “normal” proteins are different enough to be separated based on the specific features of their amino acid sequences



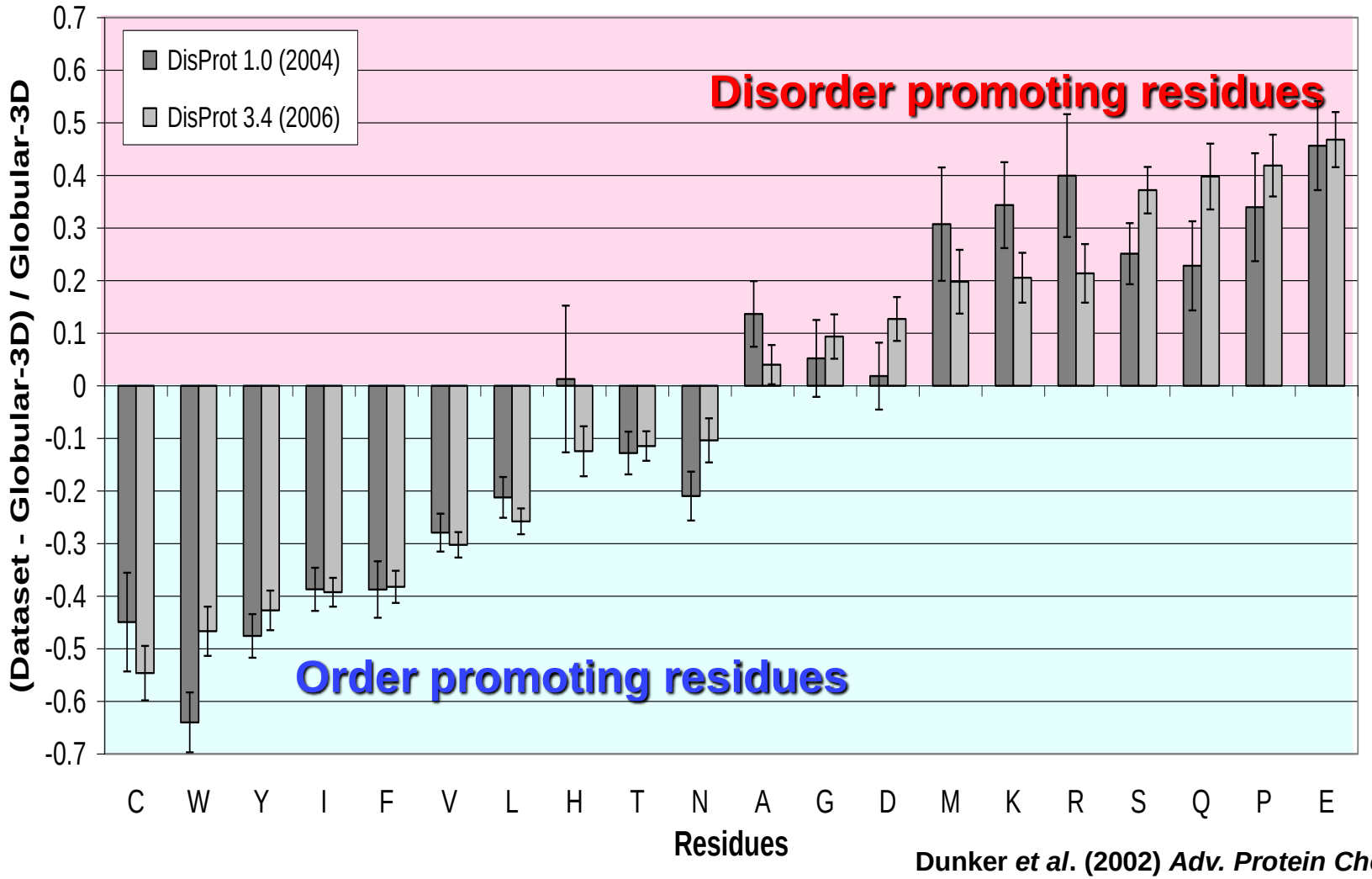
Protein non-folding: Why?



An extreme case conformationally unstable proteins are so-called natively unfolded proteins. They possess unique combination of low mean hydrophobicity and high mean net charge. High net charge leads to strong electrostatic repulsion, and low hydrophobicity means less driving force for compaction.

Uversky *et al*. (2000) *Proteins* 42, 415
Oldfield et al. (2005) *Biochemistry* 44 (37) 12454 - 12470

Amino acid determinants of protein foldability



Dunker *et al*. (2002) *Adv. Protein Chem*. 62, 25
Radivojac *et al*. (2007) *Biophys. J*. 92, 1439










www.disprot.org

DisEMBL™	Intrinsic Protein Disorder Prediction
DISOPRED2	Disorder Prediction Server
DRIPPRED	Web based predictor for disordered regions in proteins
FoldIndex©	Estimate the fold probability of a protein
GlobPlot 2	Intrinsic Protein Disorder, Domain & Globularity Prediction
IUPred	Prediction of Intrinsically Unstructured Proteins
PONDR®	Predictors of Natural Disordered Regions
PreLink	Prediction of unfolded segments in a protein sequence based on amino acid composition
RONN	Regional Order Neural Network
VL2	DisProt Predictor of Intrinsically Disordered Regions
VL3, VL3H, VL3E	DisProt Predictor of Intrinsically Disordered Regions

DisProt: Reincarnation