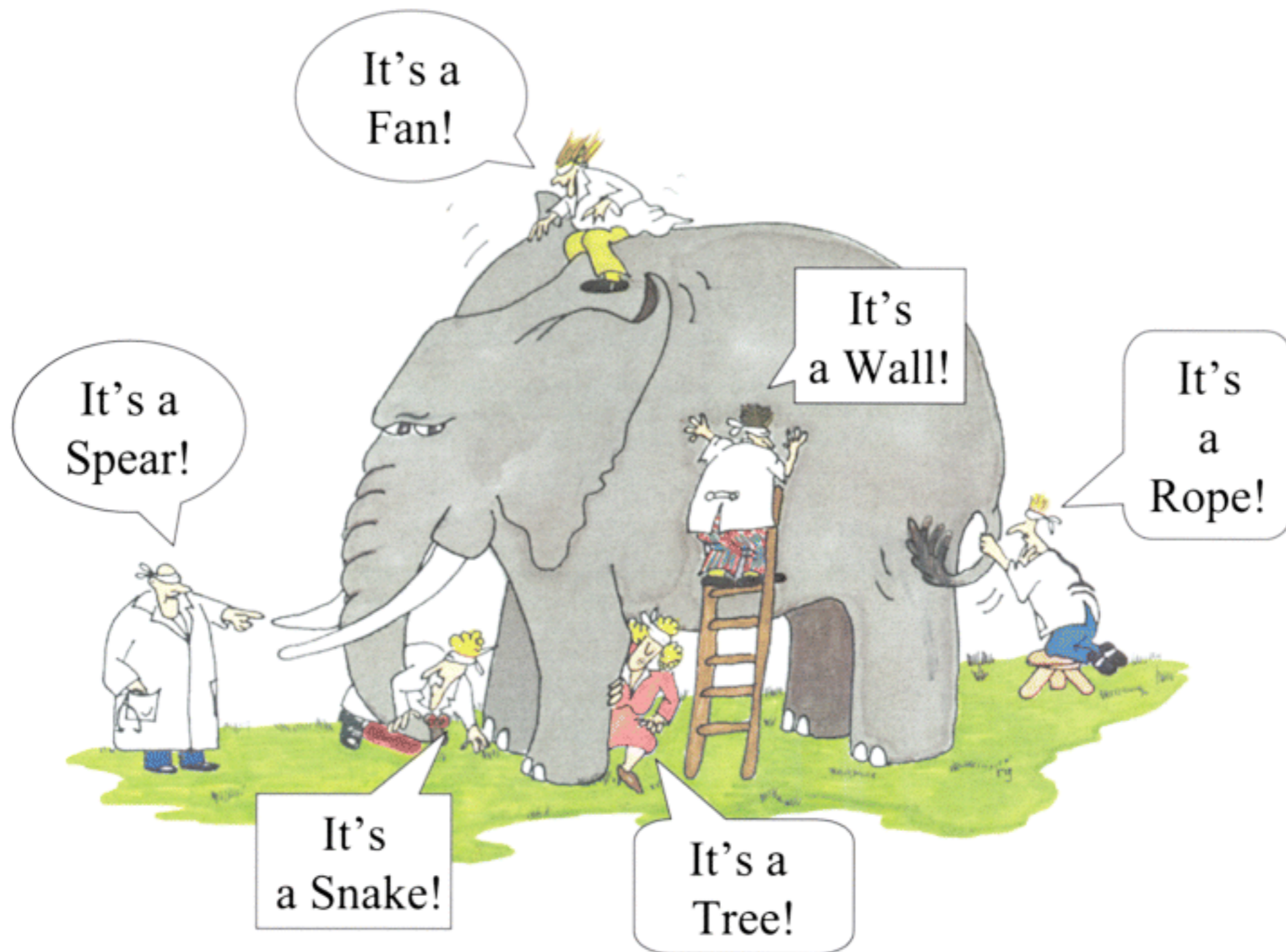


Diversity at the nuclear envelope: transcription, lamins NPCs and trypanosomes



衆瞽
摸象之圖





It's a Fan!

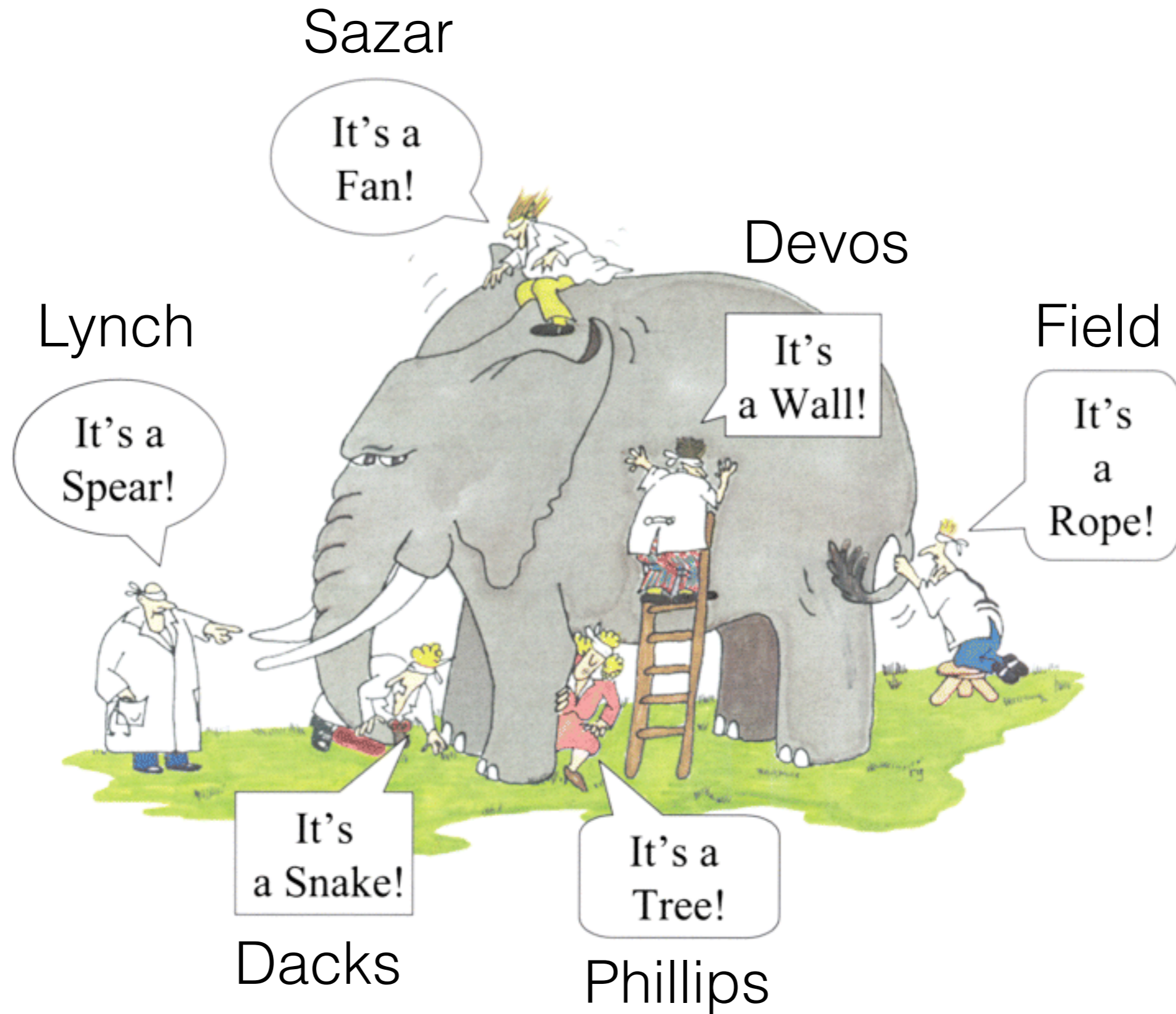
It's a Wall!

It's a Rope!

It's a Snake!

It's a Snake!

It's a Tree!



Sazar

It's a Fan!

Devos

It's a Wall!

Field

It's a Rope!

Lynch

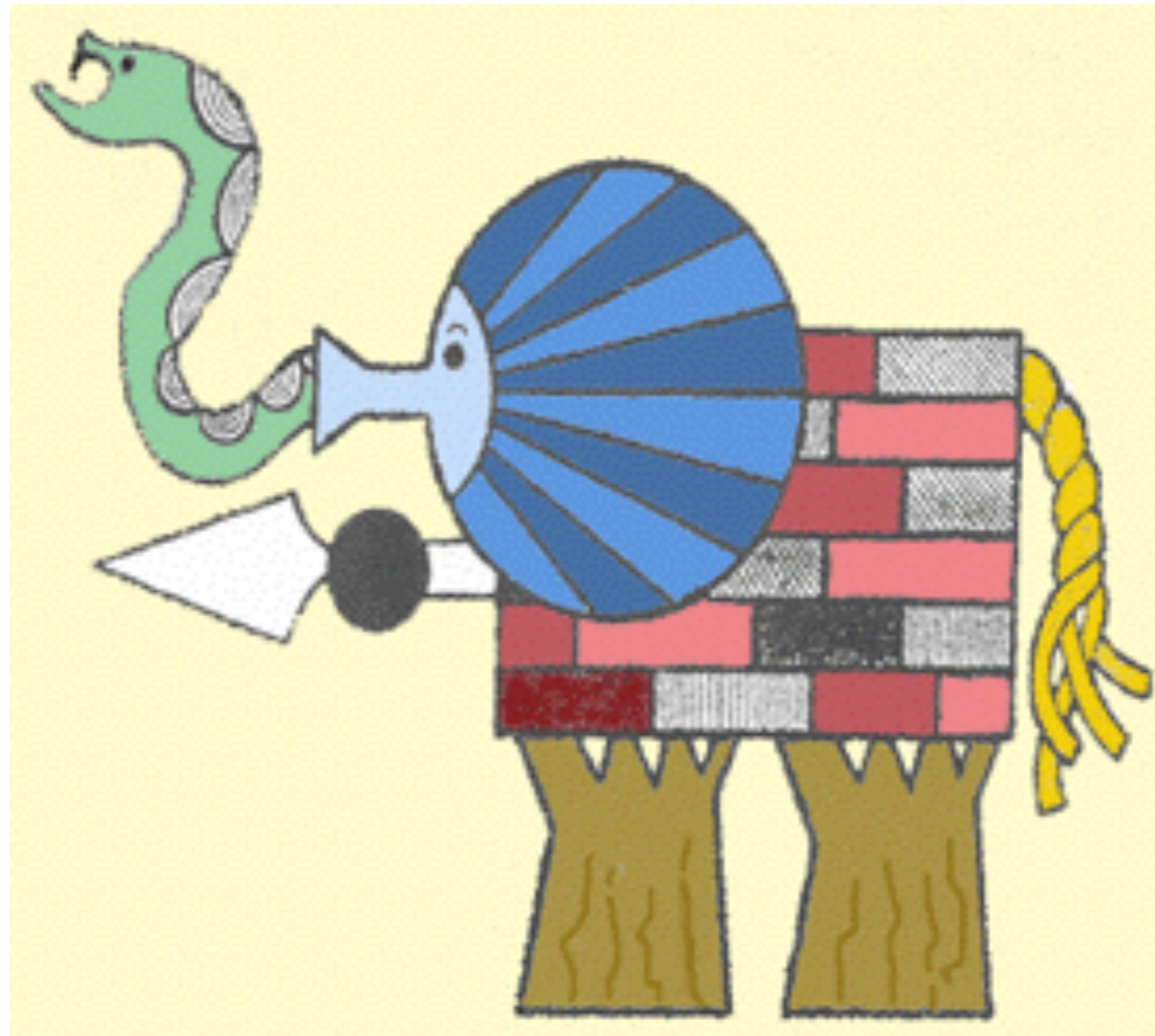
It's a Spear!

It's a Snake!

Dacks

It's a Tree!

Phillips



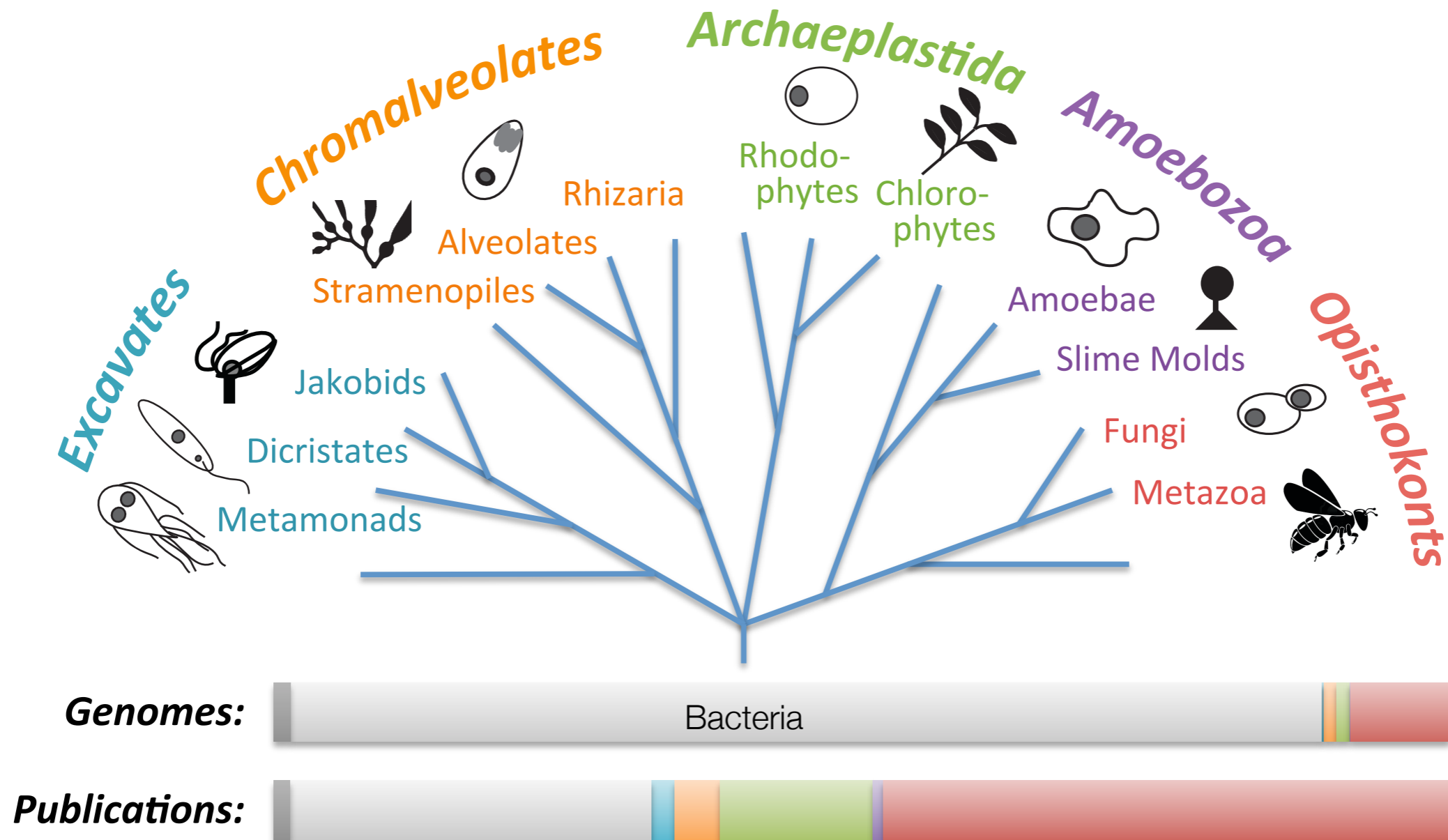
Oops!!!

Overthinking/attempts to define may
be counterproductive

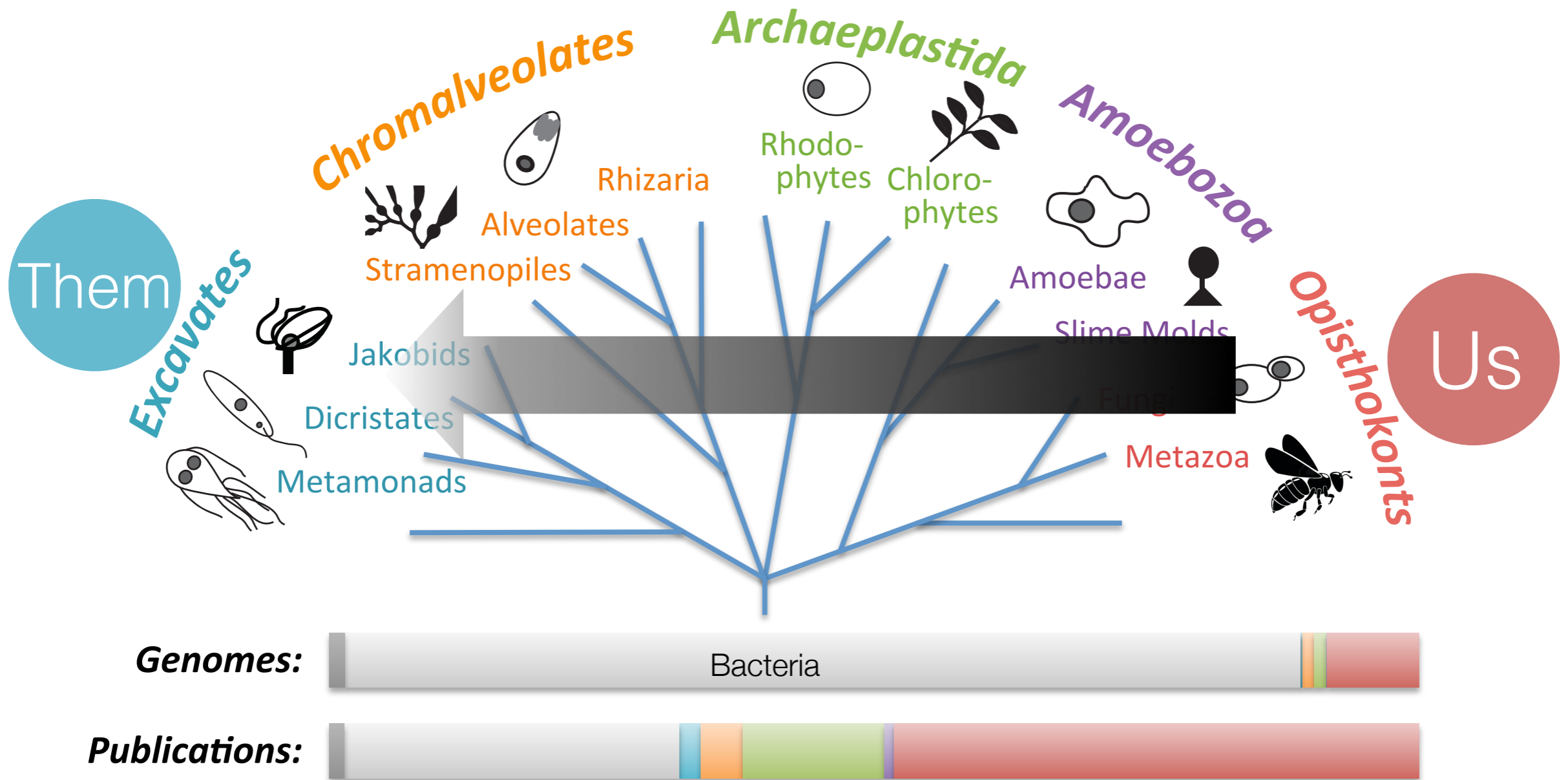
The average expert is 'roughly as accurate as a
dart-throwing chimpanzee.'

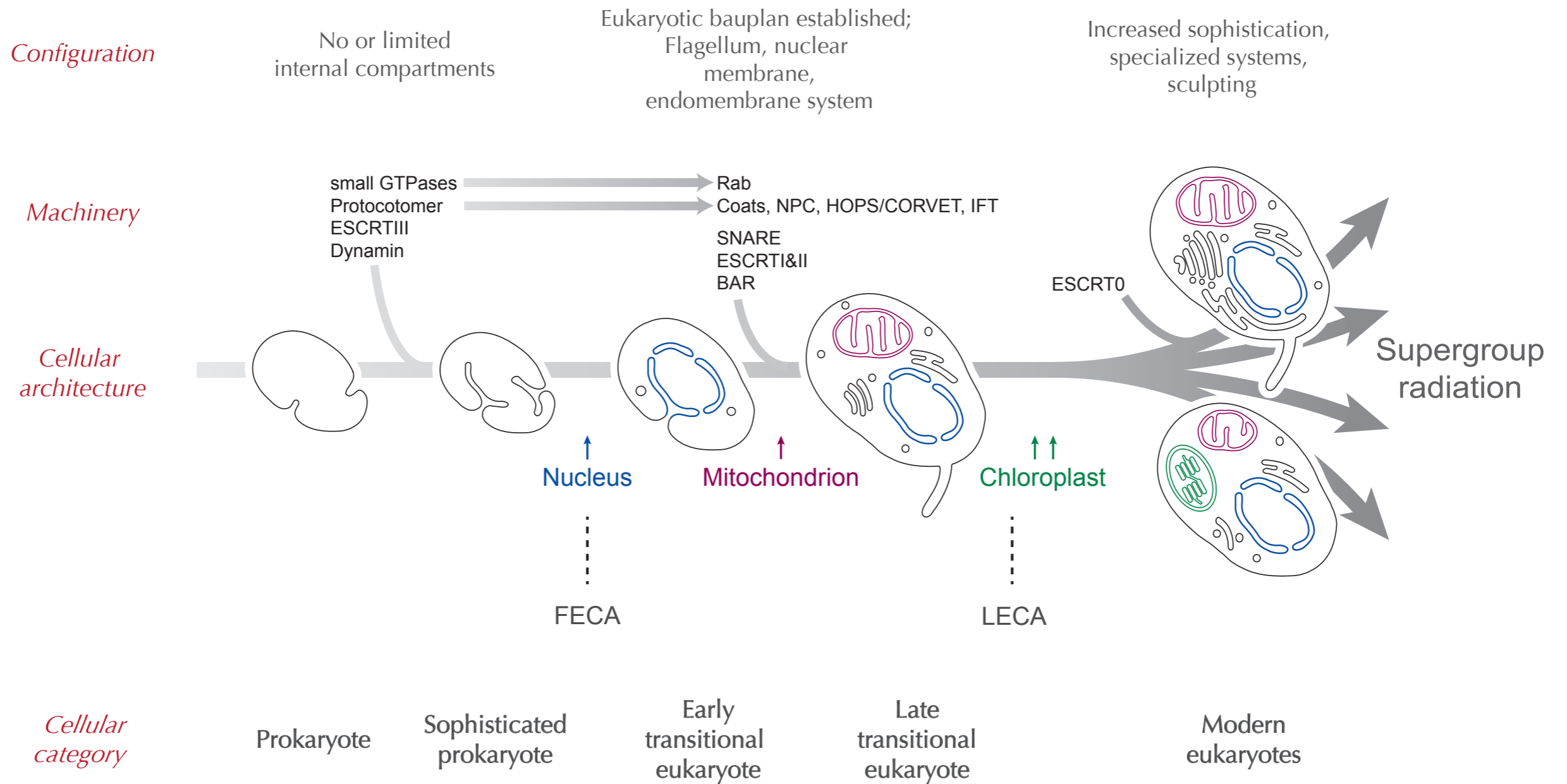
Peter Tetlock

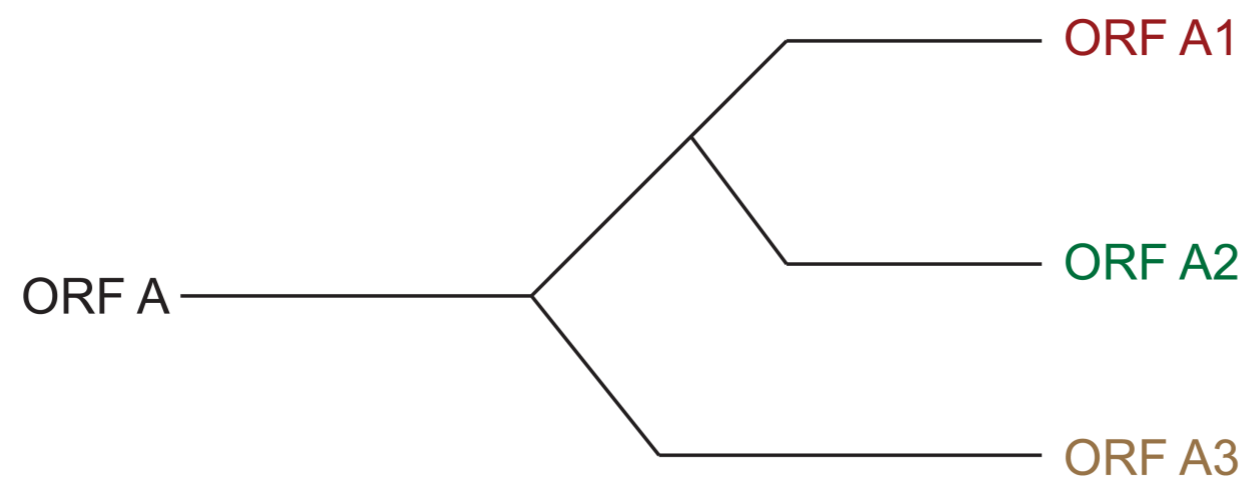
Evolutionary asymmetry

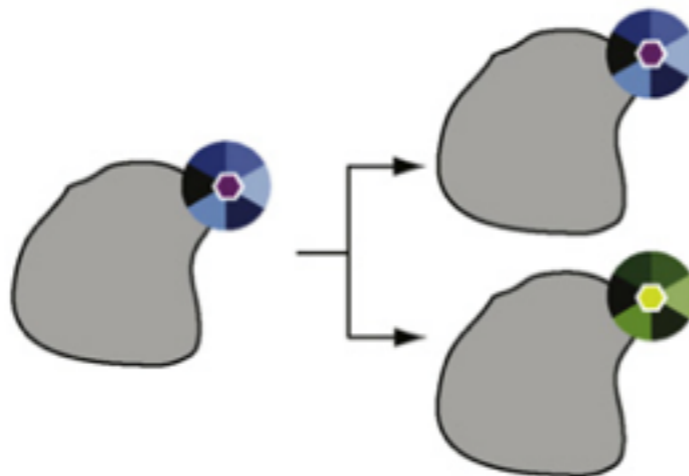
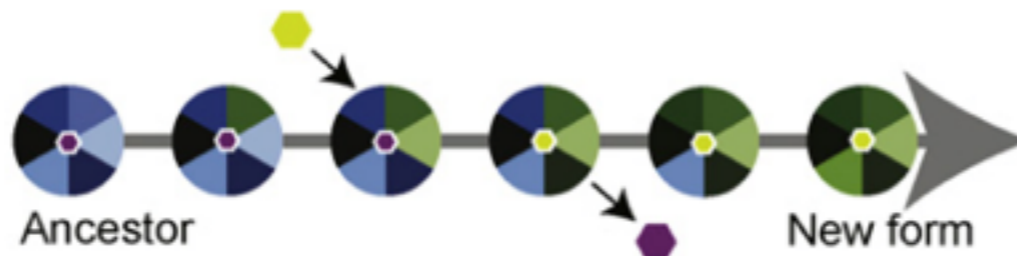
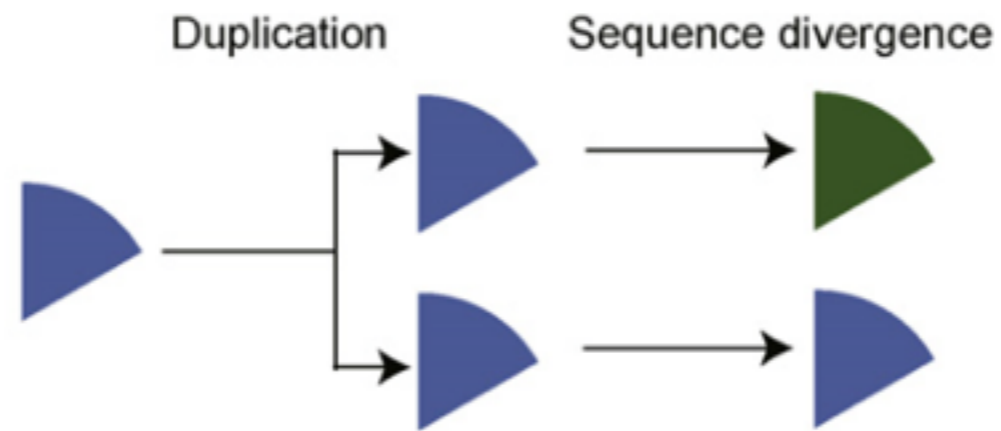
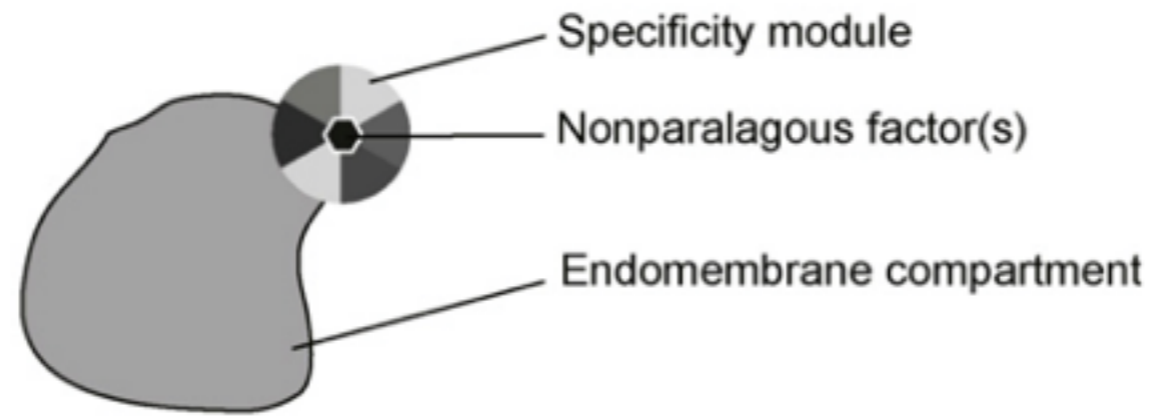


Evolutionary asymmetry

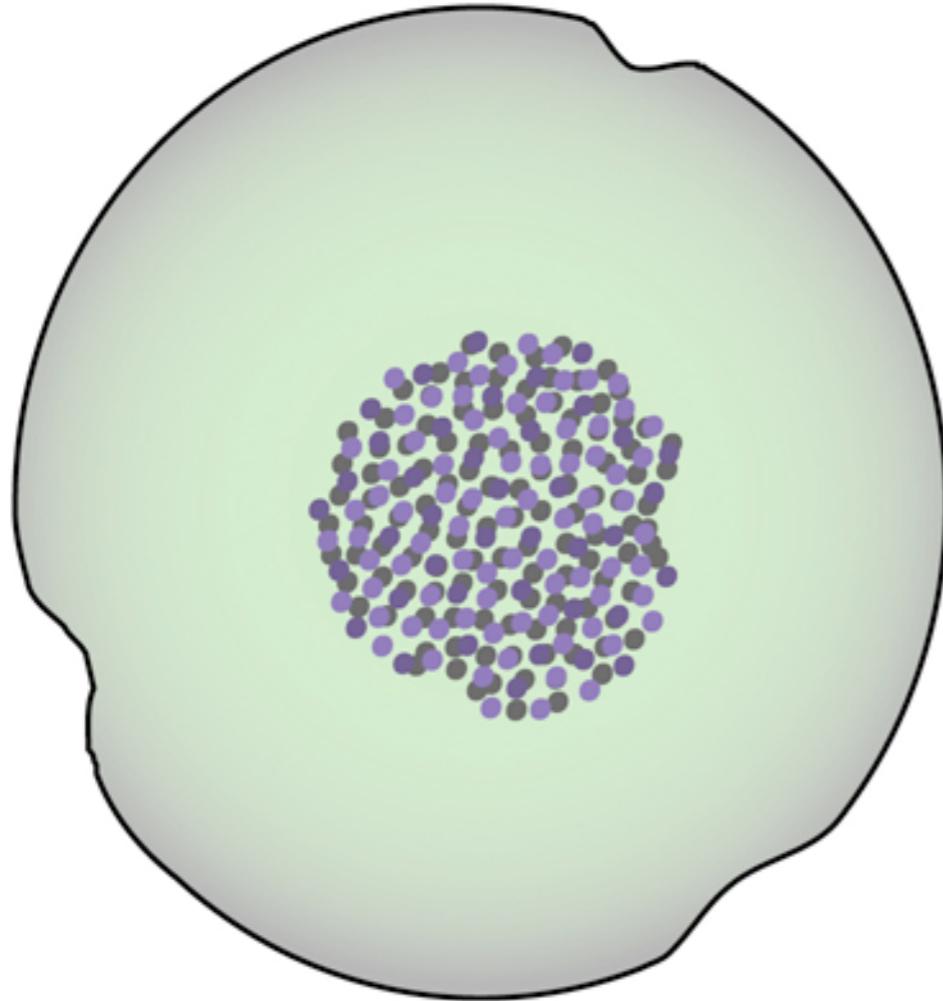




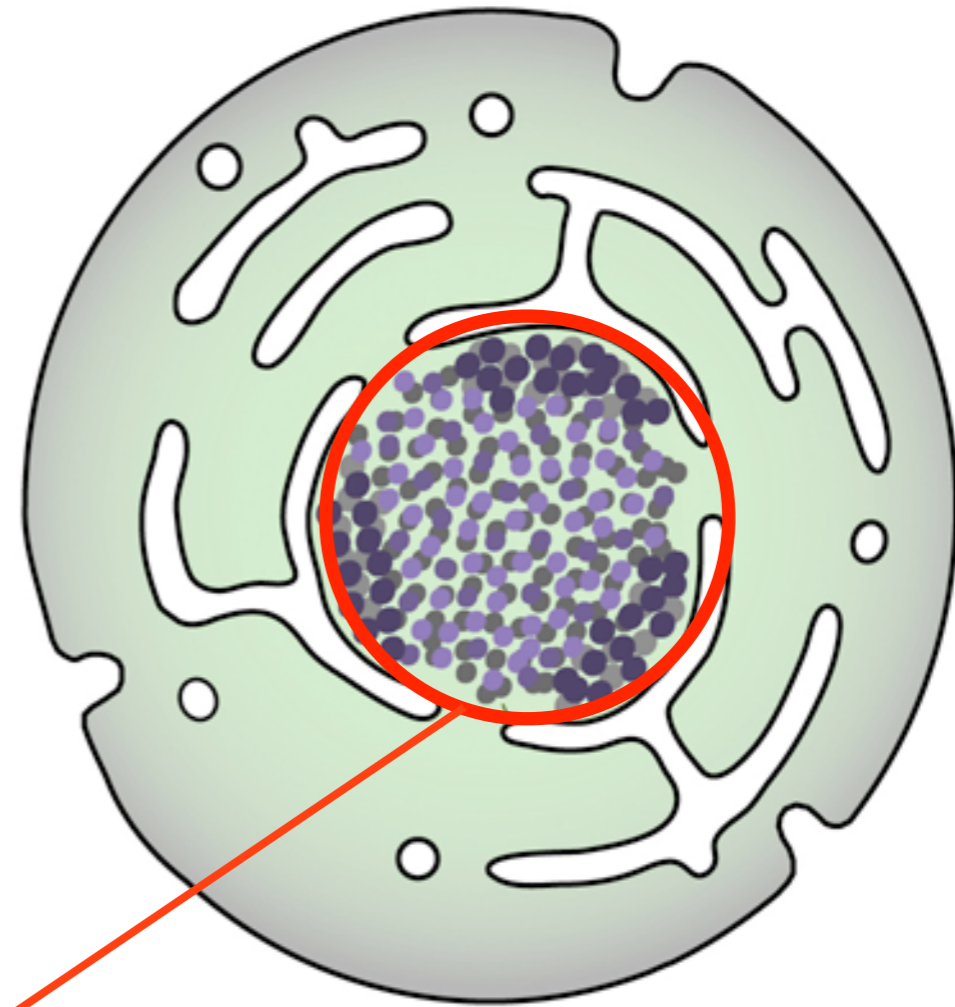




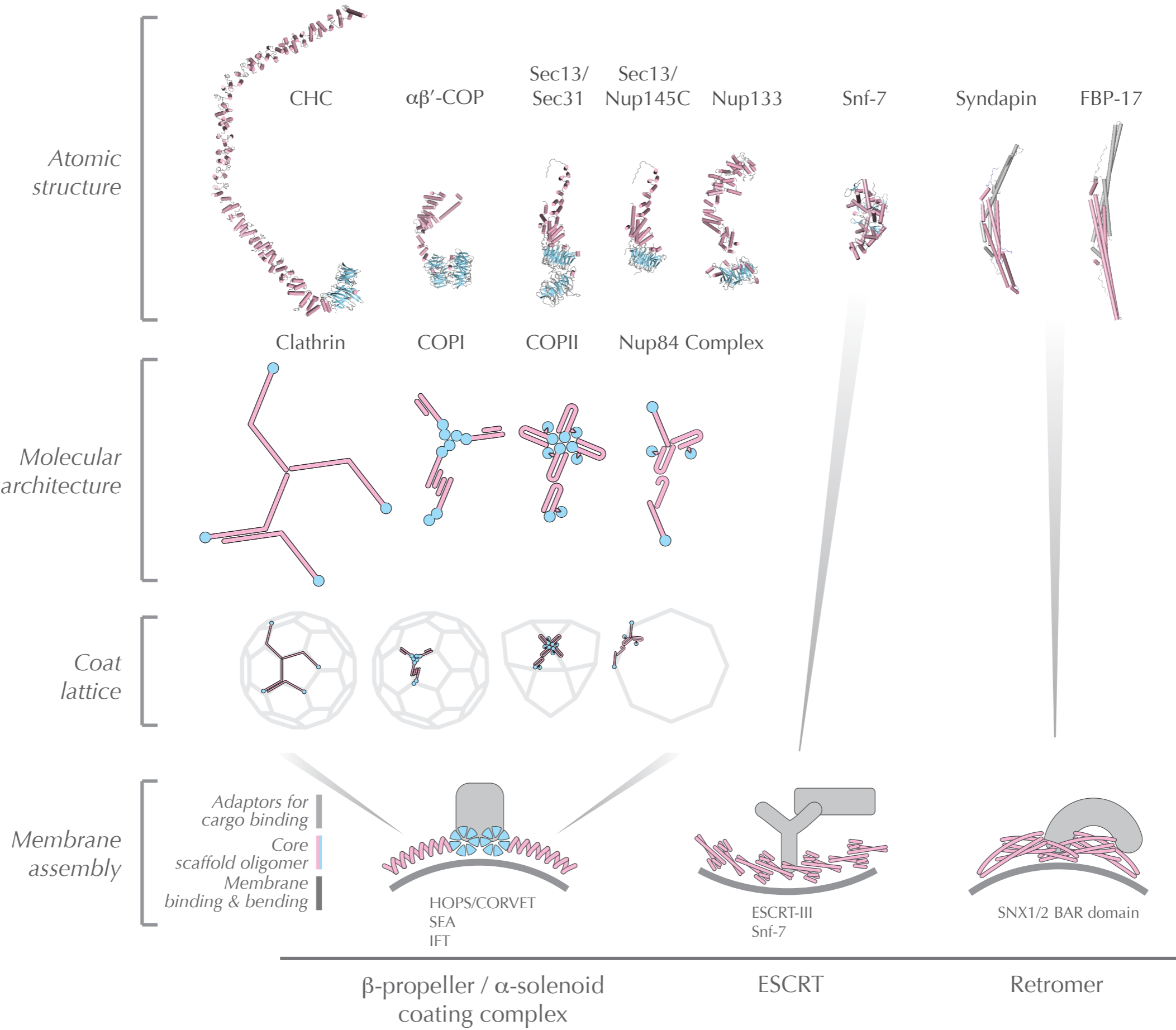
Prokaryote



Modern Eukaryote

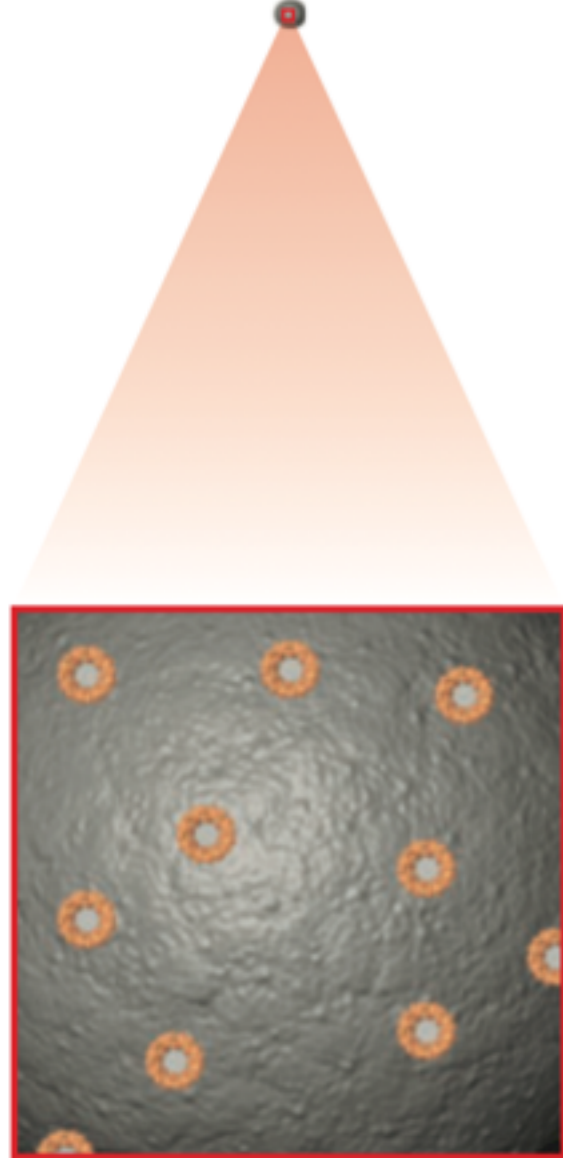


NPC
KAPs
Lamin

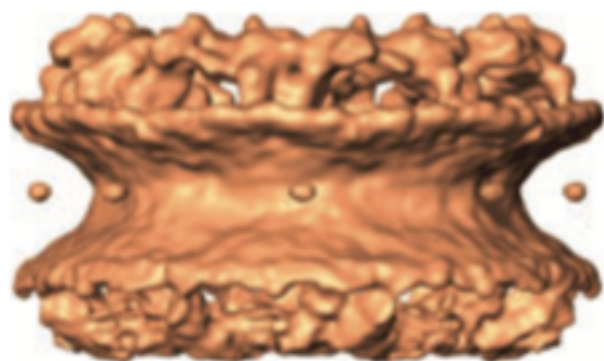


Human fibroblast nucleus

$R = 5 \mu\text{m}$

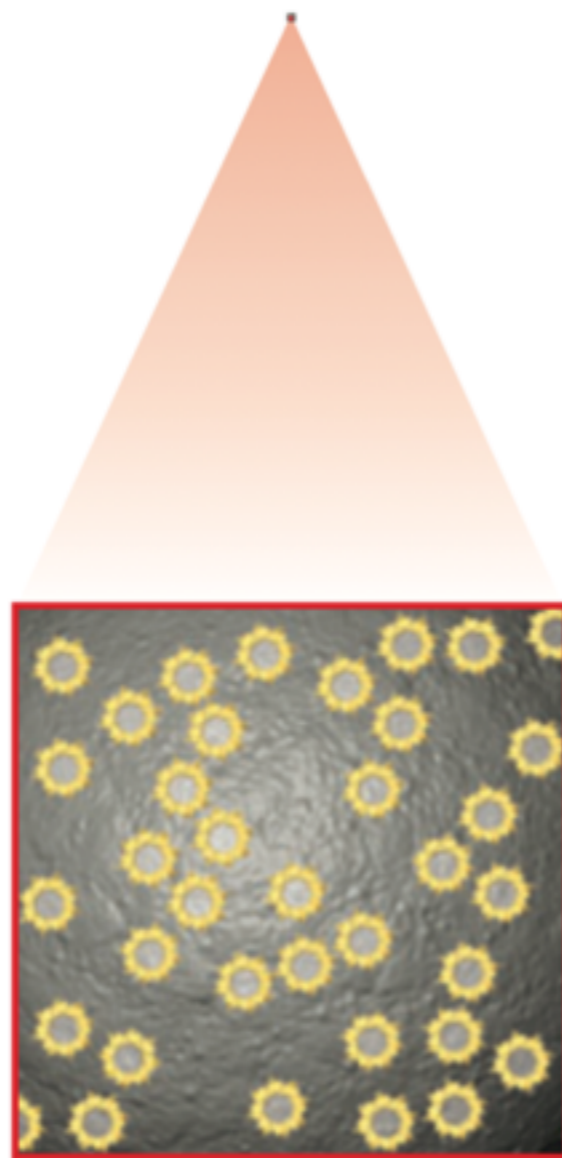


1 μm

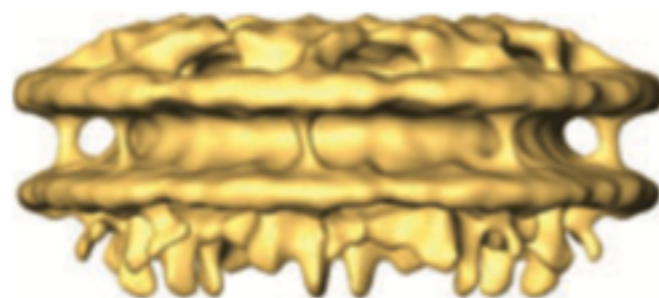


Dictyostelium discoideum nucleus

$R = 1.5 \mu\text{m}$

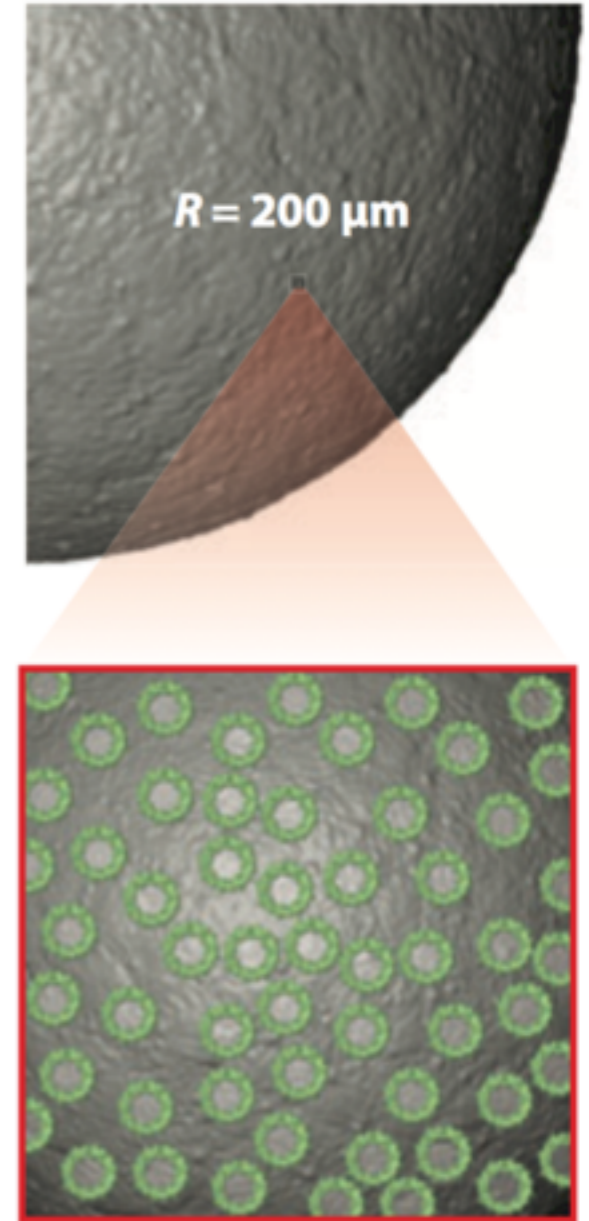


1 μm

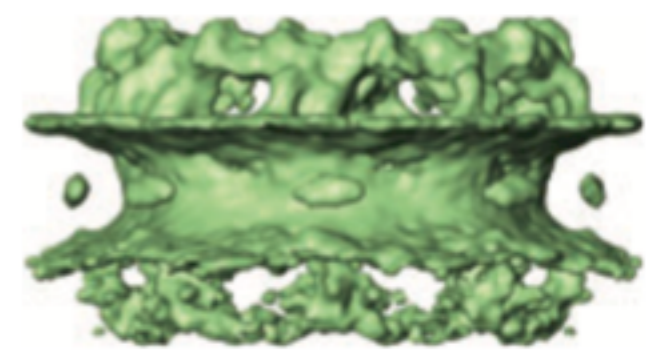


Xenopus laevis oocyte nucleus

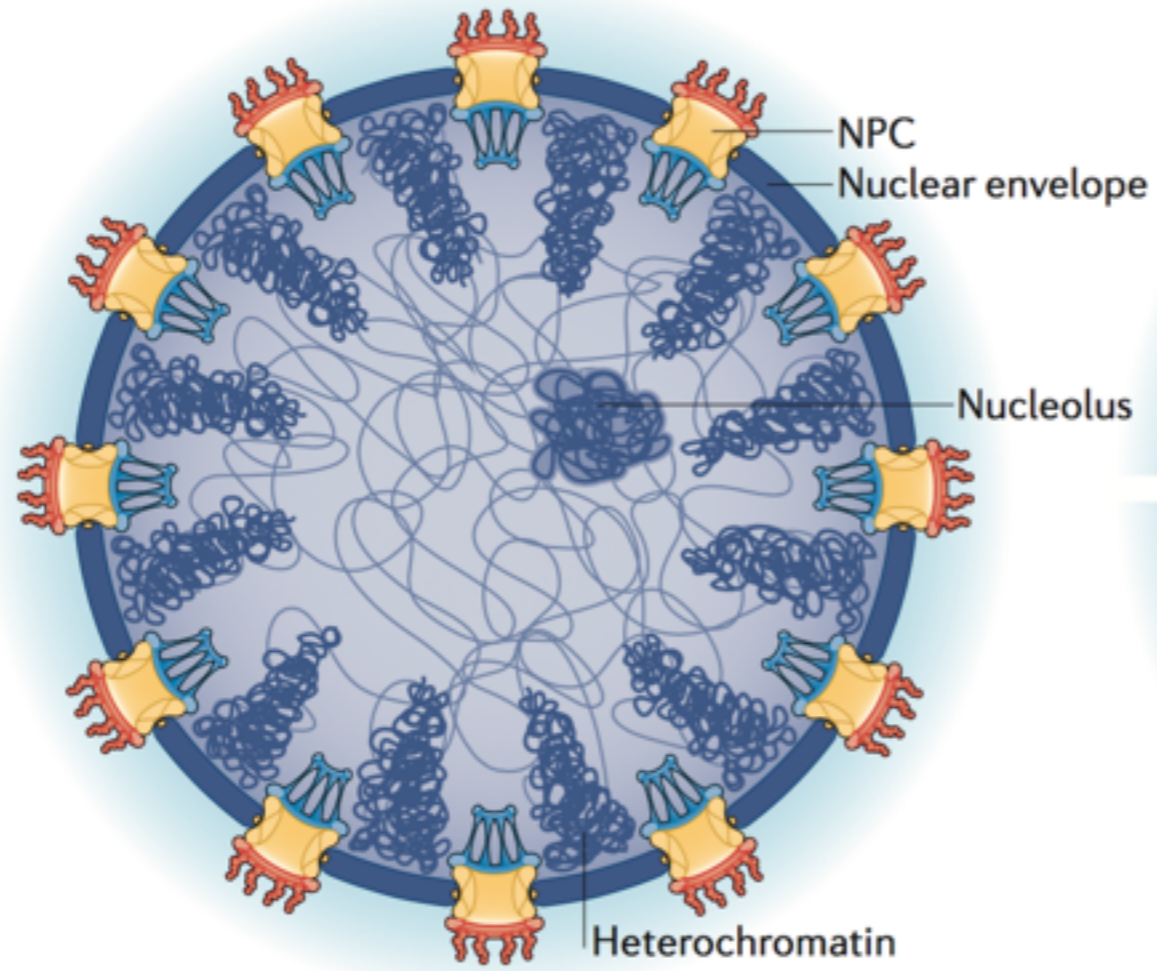
$R = 200 \mu\text{m}$



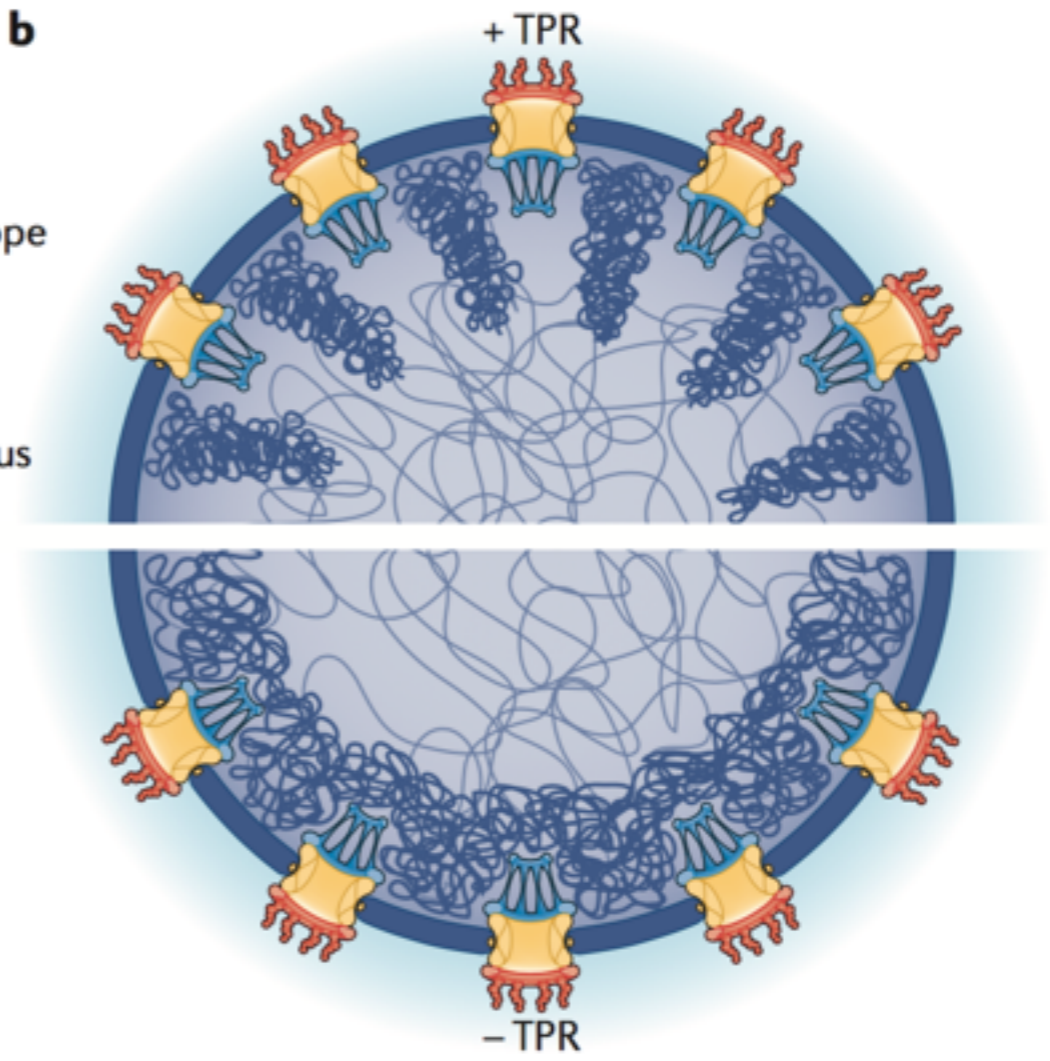
1 μm

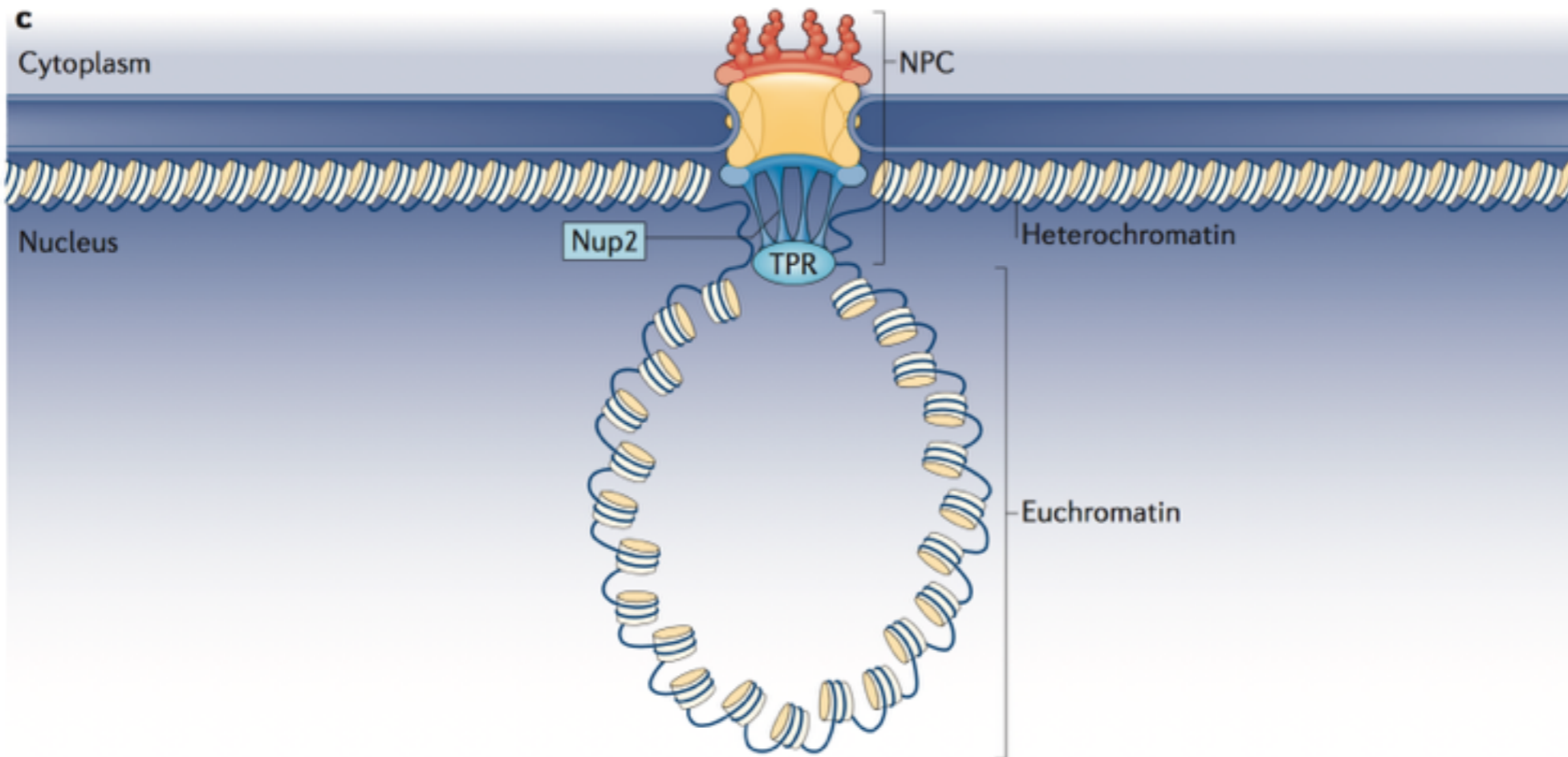


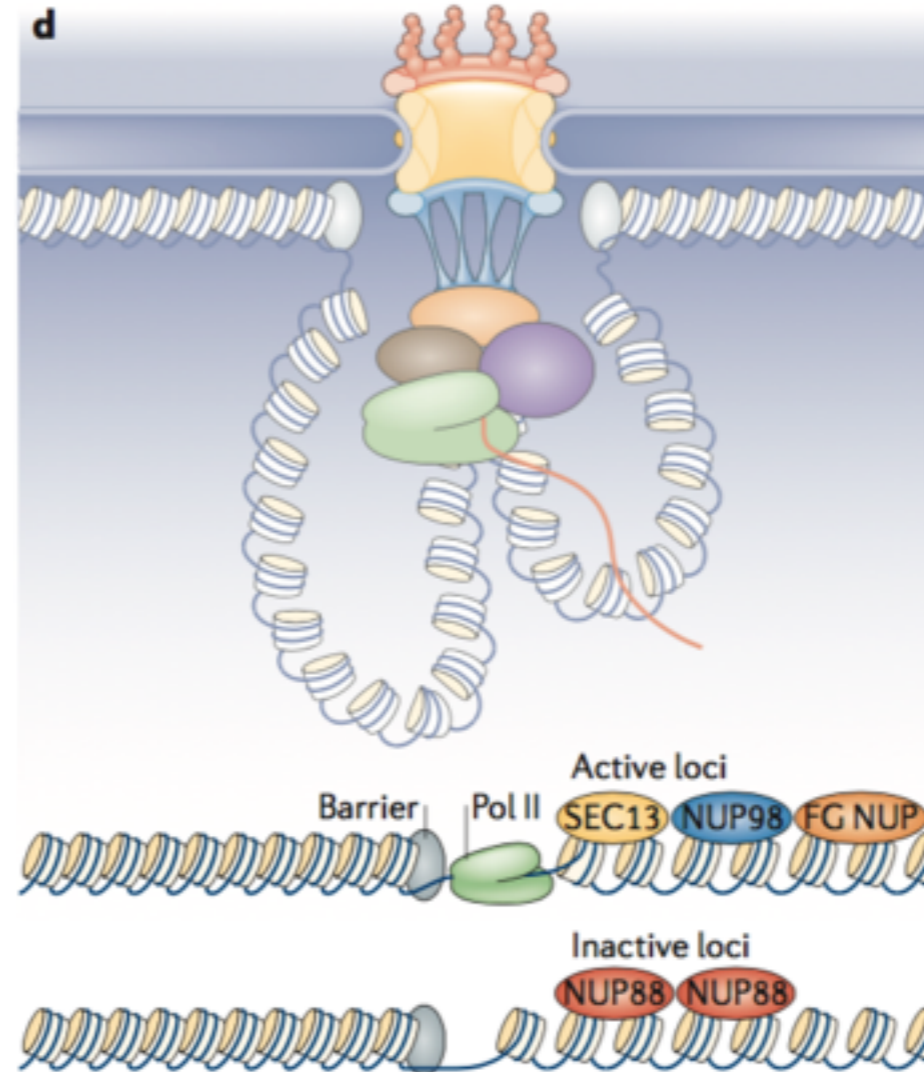
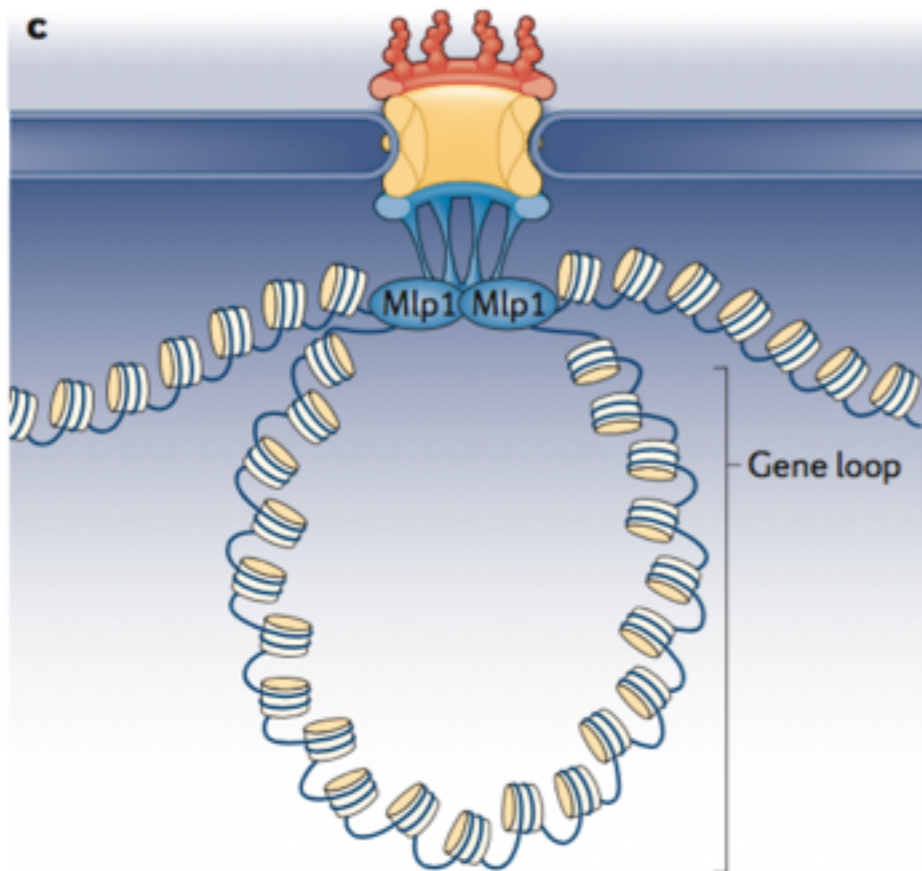
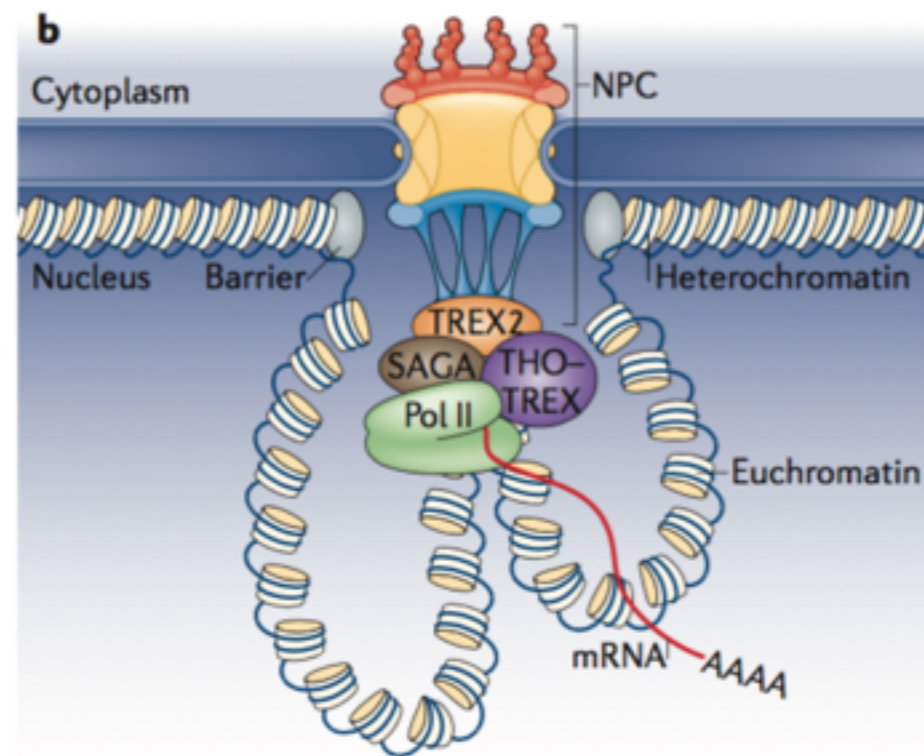
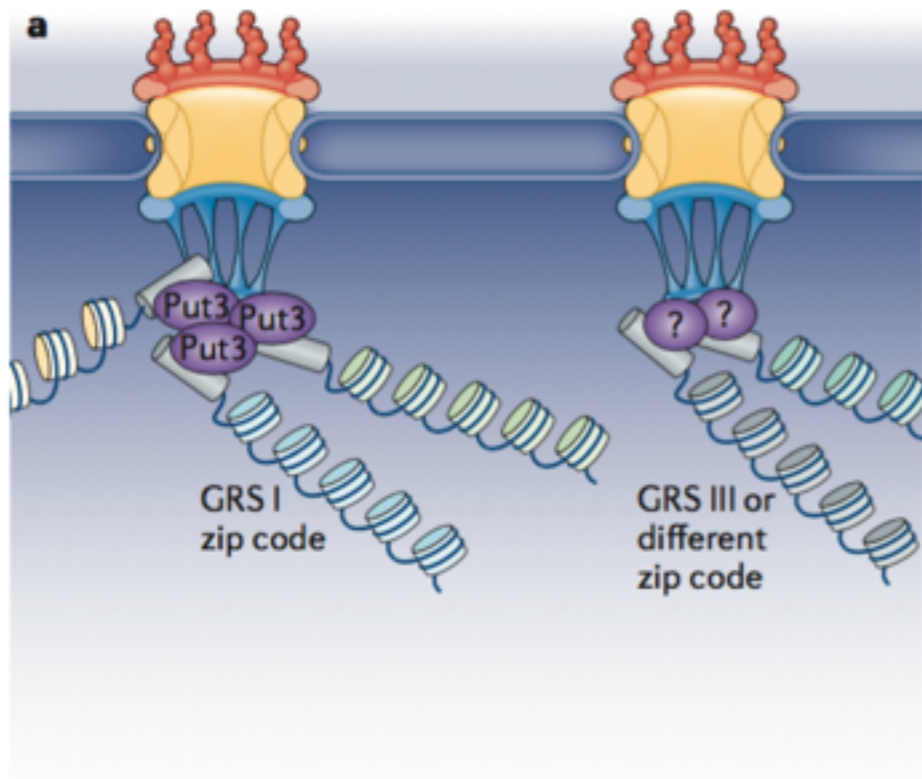
a



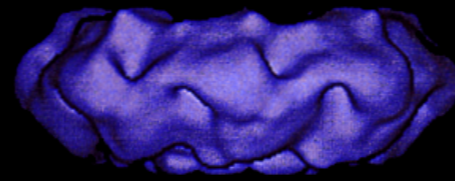
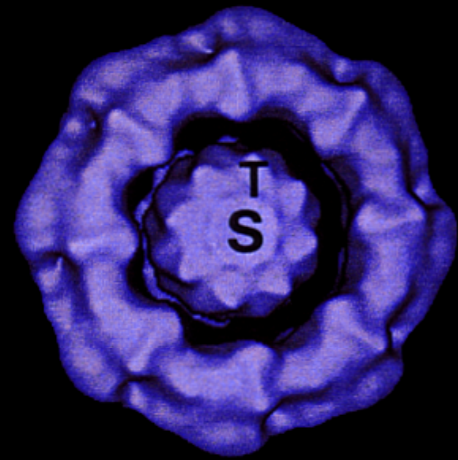
b



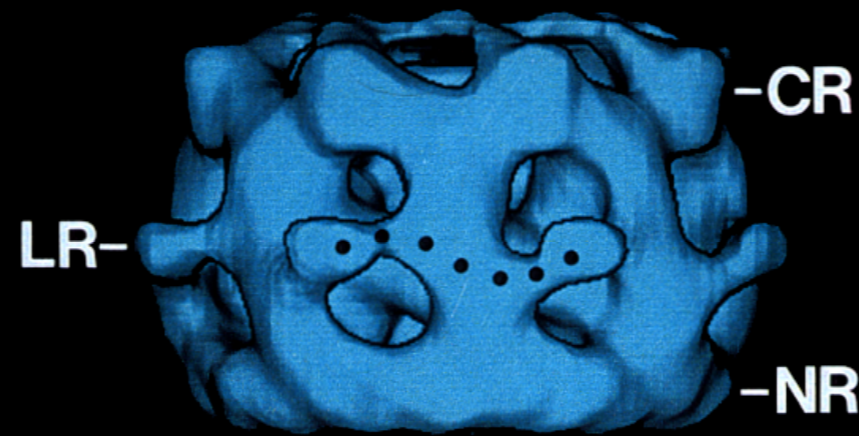
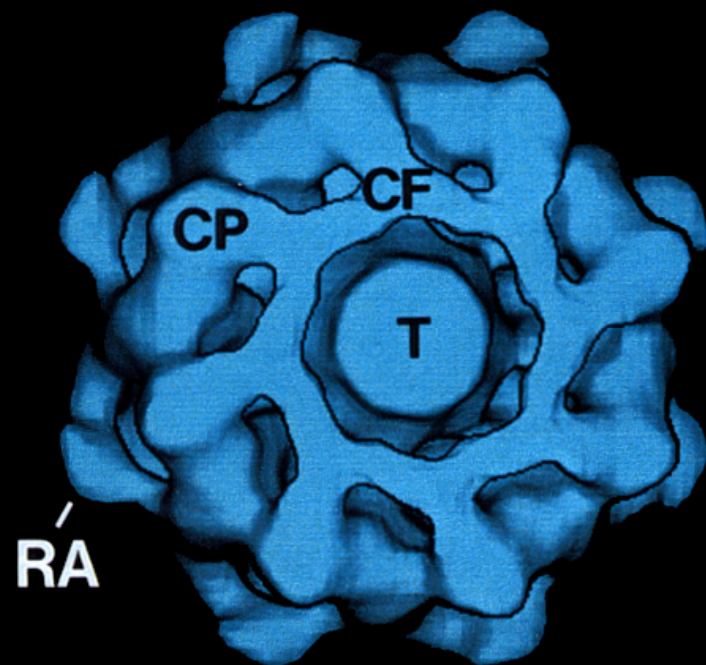




Animal and fungal nuclear pore complexes have species specific structures, but similar protein compositions



Yeast



Rat

Trypanosomes are highly divergent

African



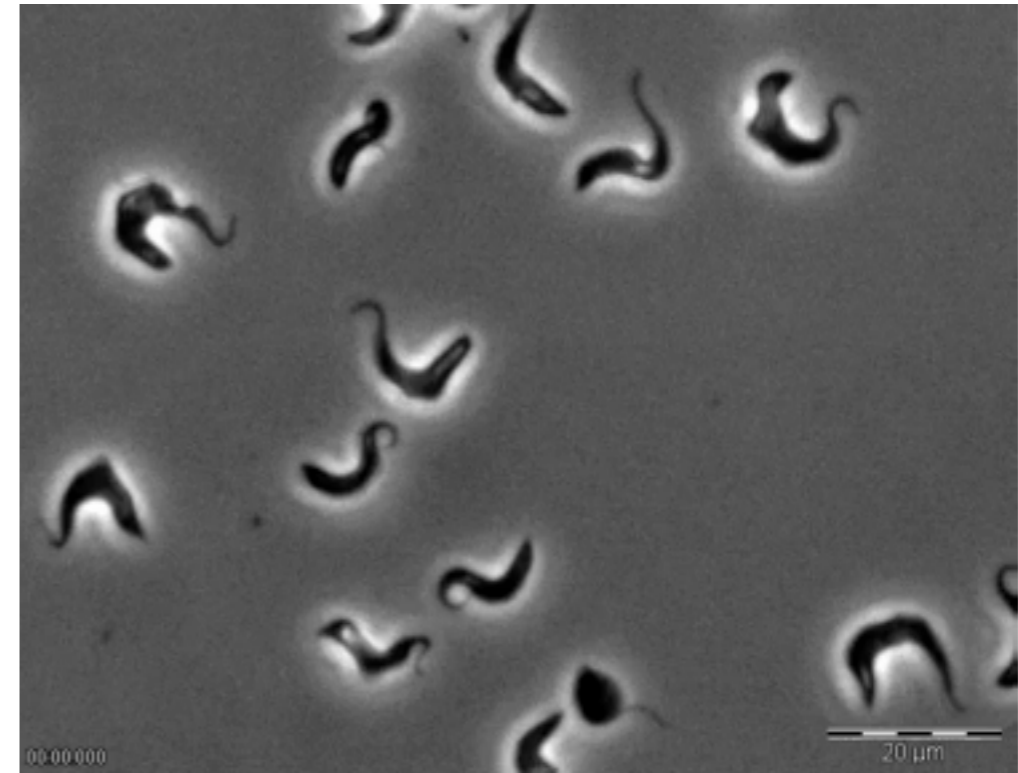
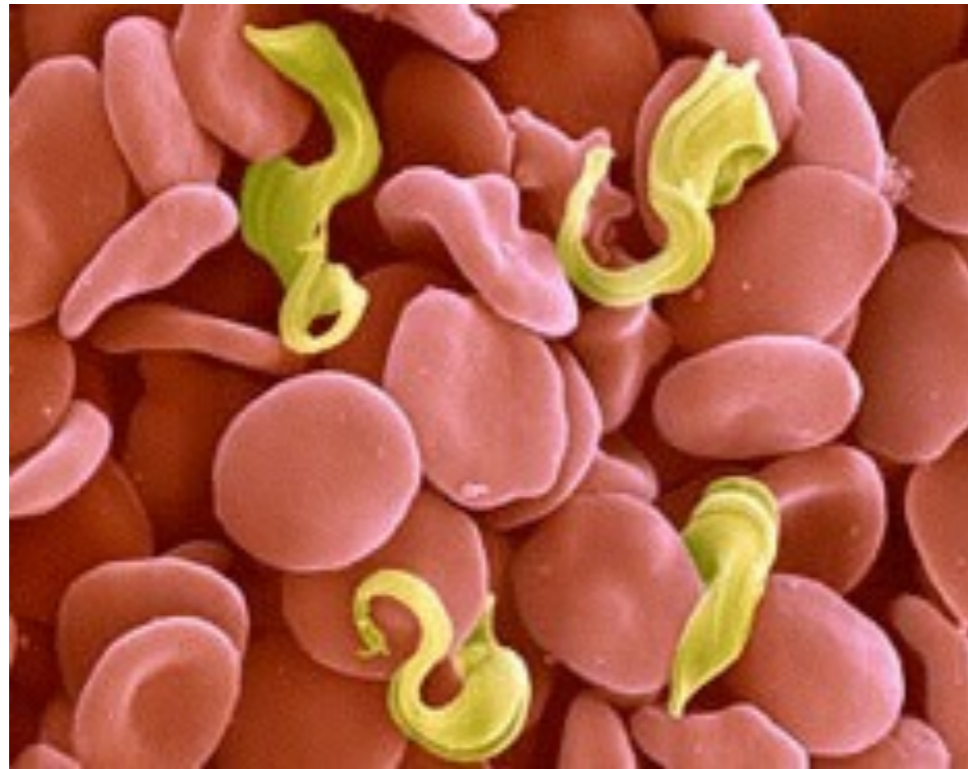
American



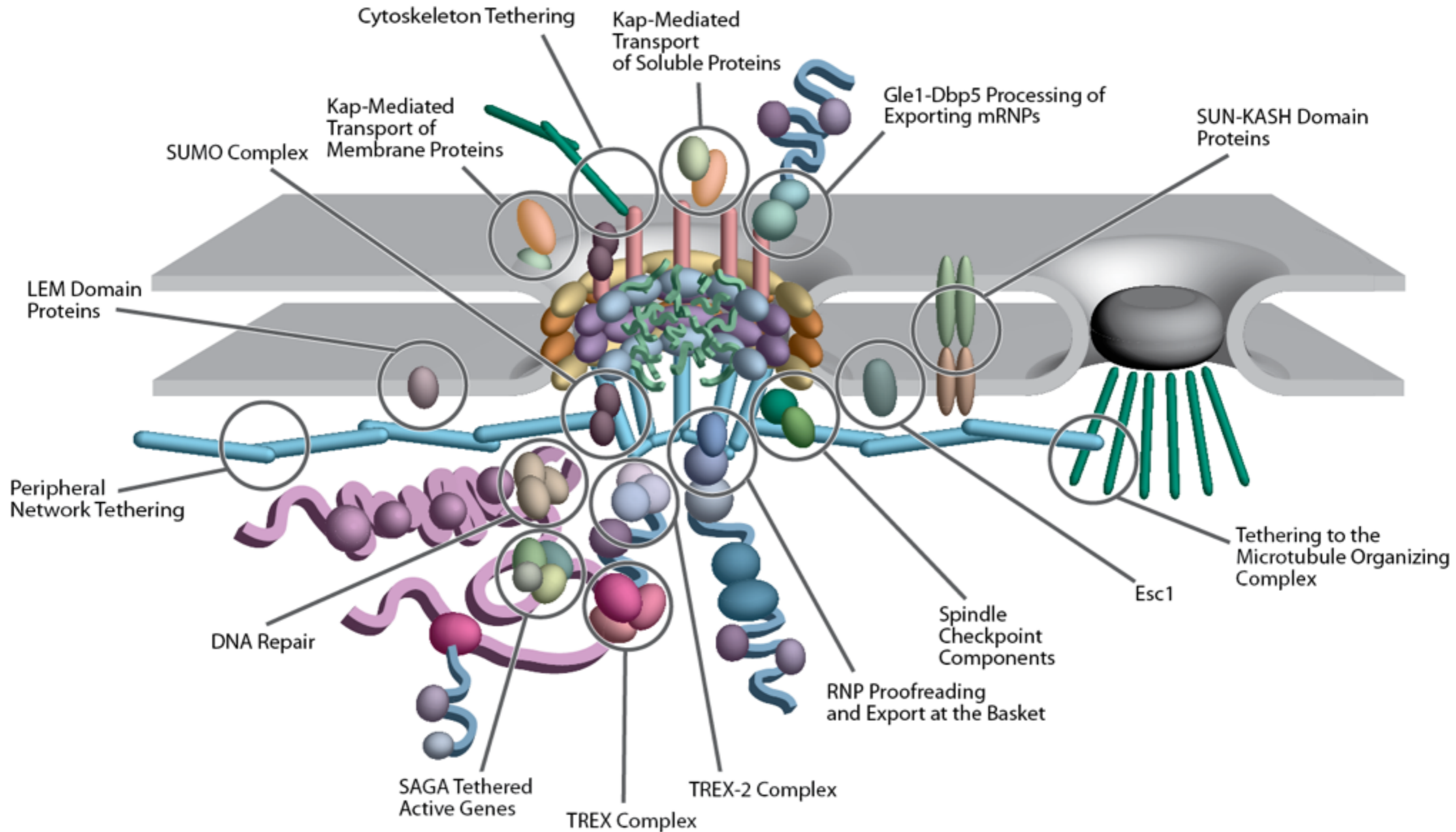
Leishmania

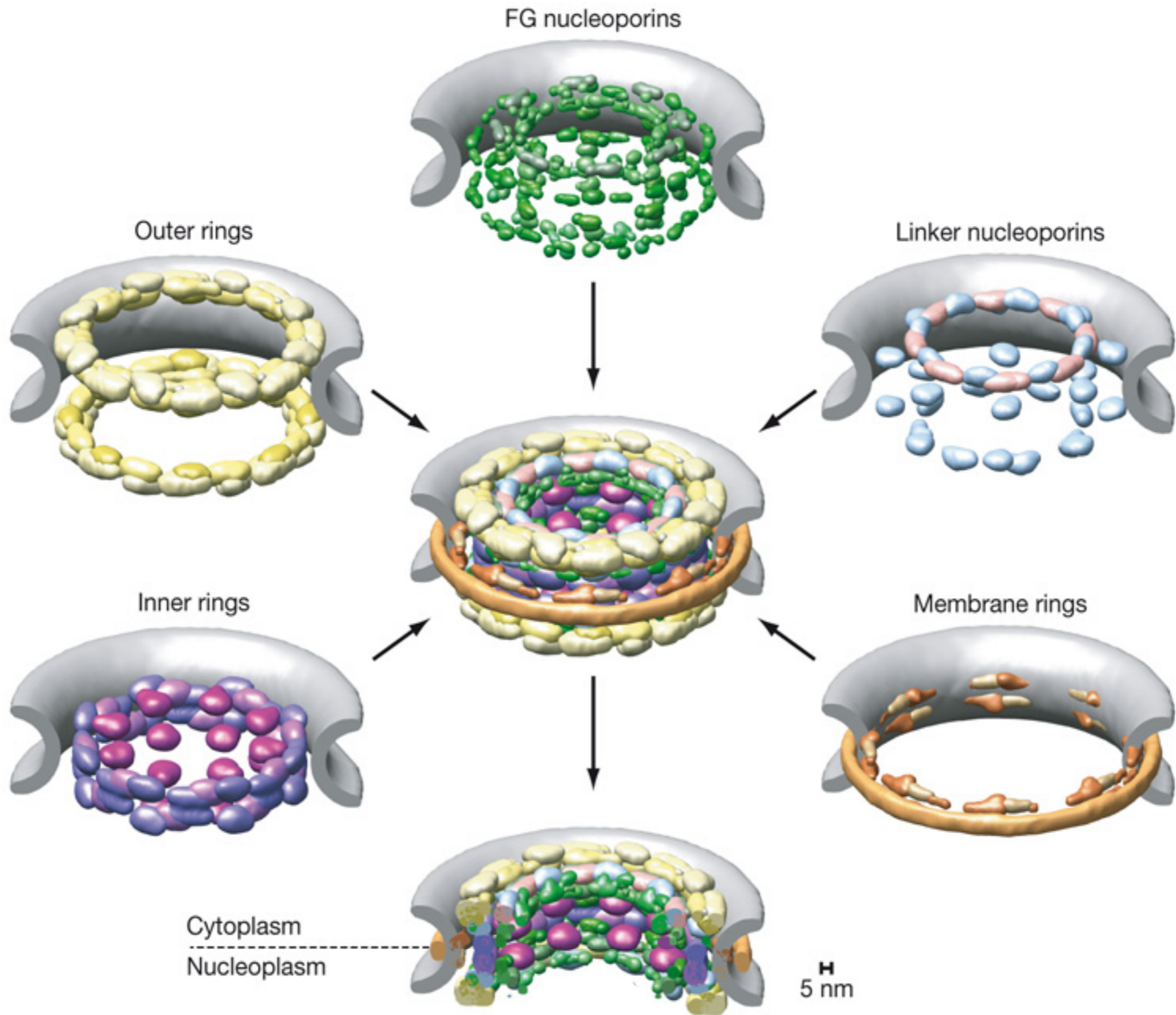


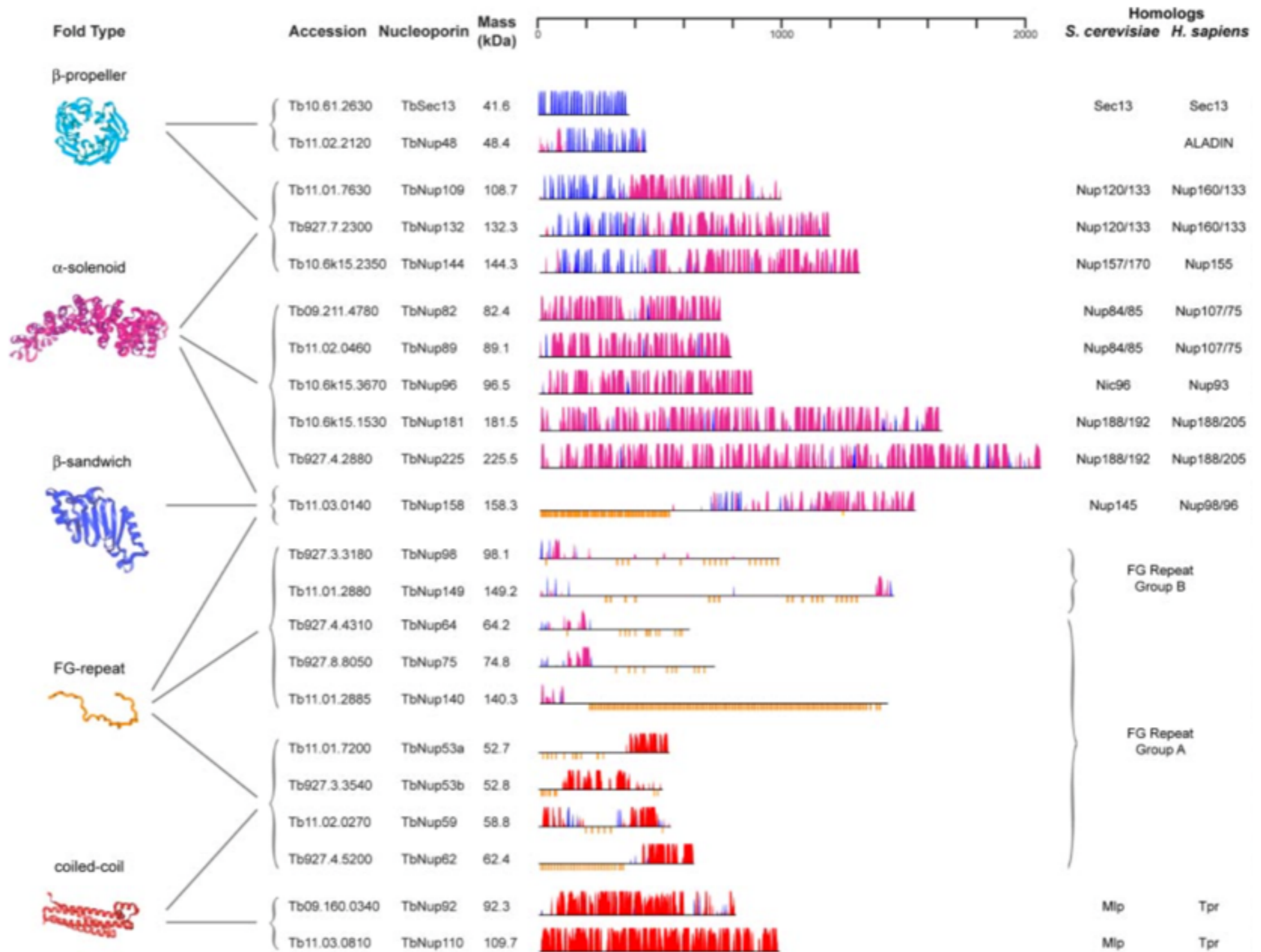
Trypanosomes are highly divergent



The nuclear pore complex and the nuclear envelope







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Tb11.02.2120	+	Aladin		1.1e-12	
Tb09.160.2360	+	Rae1		9.4e-32	
Tb10.6k15.2350	+	Nup155		5.4e-24	
Tb11.02.0460	+	Nup107		0.02	
Tb10.6k15.3670	+	Nup93		0.0012	
Tb1927.4.2880	+	Nup205		0.96	
Tb11.03.0140	+	Nup96/98		0.0012	
Tb11.01.7200	+	Nup62		8.2e-05	
Tb927.4.5200	+	Nup54		1.2e-08	
Tb927.3.3180	–	–	+	0.016	FG repeats
Tb927.3.3540	–	–	+	2.1	FG repeats
Tb11.02.0270	–	–	+	0.16	FG repeats
Tb11.01.2880	–	–	+	1.1	FG repeats
Tb927.4.4310	–	–	+	3.4	FG repeats
Tb927.8.8050	–	–	+	4	FG repeats
Tb11.01.2885	–	–	+	0.0009	FG repeats
Tb11.03.0810	–	–	+	5.8	
Tb10.6k15.1530	–	–	–	ND	
Tb09.211.4780	–	–	–	ND	
Tb09.160.0340	–	–	–	ND	
Tb11.01.7630	–	–	–	ND	
Tb927.7.2300	–	–	–	ND	

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		Opisthokonts				Excavates				
		Dipterans		Vertebrates		Diplomonads	Heterolobosea	Parabasalids	Kinetoplastids	
		Ag	Am	Dm	Hs	Gl	Ng	Tv	Tb	Lm
LOCALIZATION	NUP									
	Gle1	x	x	x	x		x			
	Aladin	x		x	x		x		x	x
Cytoplasmic fibrils	Nup88	x	x	x	x					
	Nup214	x	x	x	x		x			x
	Nup358	x	x	x	x					
Scaffold	Nup160	x	x	x	x		x			
	Nup133	x	x	x	x		x			
	Nup107	x	x	x	x	x	x	x	x	x
	Nup75	x	x	x	x		x			
	Nup43	x	x	x	x					
	Nup37	x	x	x	x					
	Seh1	x	x	x	x		x		x	x
	Sec13	x	x	x	x	x	x	x	x	x
	Nup205	x	x	x	x		x	x	x	x
	Nup188	x	x	x	x					
	Nup155	x	x	x	x	x	x	x	x	x
	Nup93	x	x	x	x		x	x	x	x
	Nup35	x	x	x	x	x		x		
Transmembrane	Ndc1	x		x	x			x		
	Pom121				x					
	Gp210	x	x	x	x		x	x		
	Pom152									
	Pom34									
Nuclear ring	Nup96-98	x		x	x	x	x	x	x	x
	Rae1	x	x	x	x	x	x		x	x
Central	Nup62	x	x	x	x		x	x	x	x
channel	Nup58	x	x	x	x		x			x
	Nup54	x	x	x	x	x	x	x	x	x
Nuclear	Nup50	x	x	x	x		x			
basket	Nup153		x	x	x		x			
	TPR	x	x	x	x		x			
Nups in supergroup		31				23				

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	Aladin	x		x	x		x		x	x
Cytoplasmic fibrils	Nup88	x	x	x	x					
	Nup214	x	x	x	x		x			x
	Nup358	x	x	x	x					
Scaffold	Nup160	x	x	x	x		x			
	Nup133	x	x	x	x		x			
	Nup107	x	x	x	x	x	x	x	x	x
	Nup75	x	x	x	x		x			
	Nup43	x	x	x	x					
	Nup37	x	x	x	x					
	Seh1	x	x	x	x		x		x	x
	Sec13	x	x	x	x	x	x	x	x	x
	Nup205	x	x	x	x		x	x	x	x
	Nup188	x	x	x	x					
	Nup155	x	x	x	x	x	x	x	x	x
	Nup93	x	x	x	x		x	x	x	x
	Nup35	x	x	x	x	x		x		
Transmembrane	Ndc1	x		x	x			x		
	Pom121				x					
	Gp210	x	x	x	x		x	x		
	Pom152									
	Pom34									
Nuclear ring	Nup96-98	x		x	x	x	x	x	x	x
	Rae1	x	x	x	x	x	x		x	x
Central channel	Nup62	x	x	x	x		x	x	x	x
	Nup58	x	x	x	x		x			x
	Nup54	x	x	x	x	x	x	x	x	x
Nuclear basket	Nup50	x	x	x	x		x			
	Nup153		x	x	x		x			
	TPR	x	x	x	x		x			
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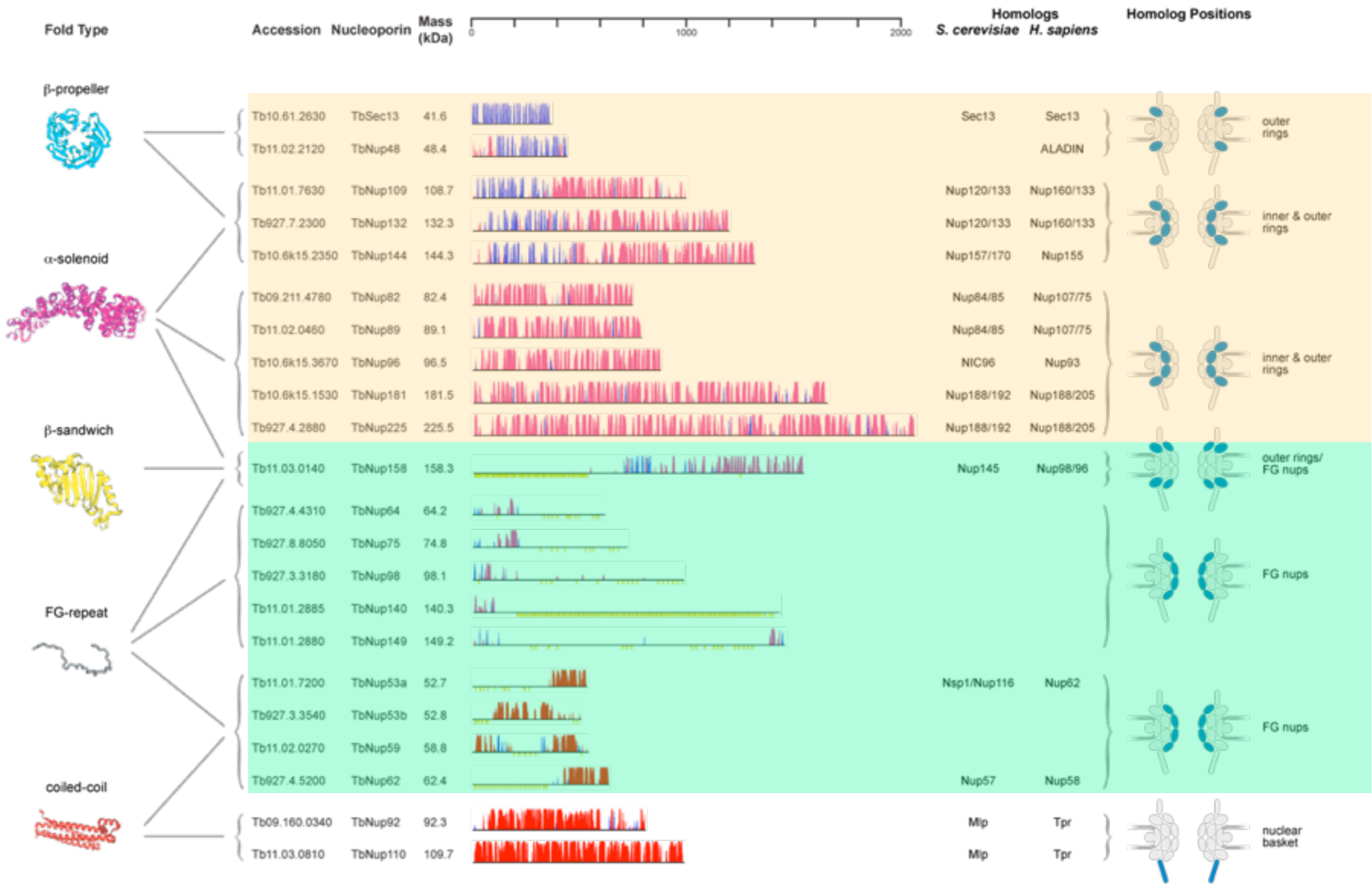
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	Nup214	x	x	x	x		x			x
	Nup358	x	x	x	x					
Scaffold	Nup160	x	x	x	x		x			
	Nup133	x	x	x	x		x			
	Nup107	x	x	x	x	x	x	x	x	x
	Nup75	x	x	x	x		x			
	Nup43	x	x	x	x					
	Nup37	x	x	x	x					
	Seh1	x	x	x	x		x		x	x
	Sec13	x	x	x	x	x	x	x	x	x
	Nup205	x	x	x	x		x	x	x	x
	Nup188	x	x	x	x					
	Nup155	x	x	x	x	x	x	x	x	x
	Nup93	x	x	x	x		x	x	x	x
	Nup35	x	x	x	x	x		x		
Transmembrane	Ndc1	x		x	x			x		
	Pom121				x					
	Gp210	x	x	x	x		x	x		
	Pom152									
	Pom34									
Nuclear ring	Nup96-98	x		x	x	x	x	x	x	x
	Rae1	x	x	x	x	x	x		x	x
Central channel	Nup62	x	x	x	x		x	x	x	x
	Nup58	x	x	x	x		x			x
	Nup54	x	x	x	x	x	x	x	x	x
Nuclear basket	Nup50	x	x	x	x		x			
	Nup153		x	x	x		x			
	TPR	x	x	x	x		x			
Nups in supergroup		31				23				



Classes of nucleoporins

Scaffold

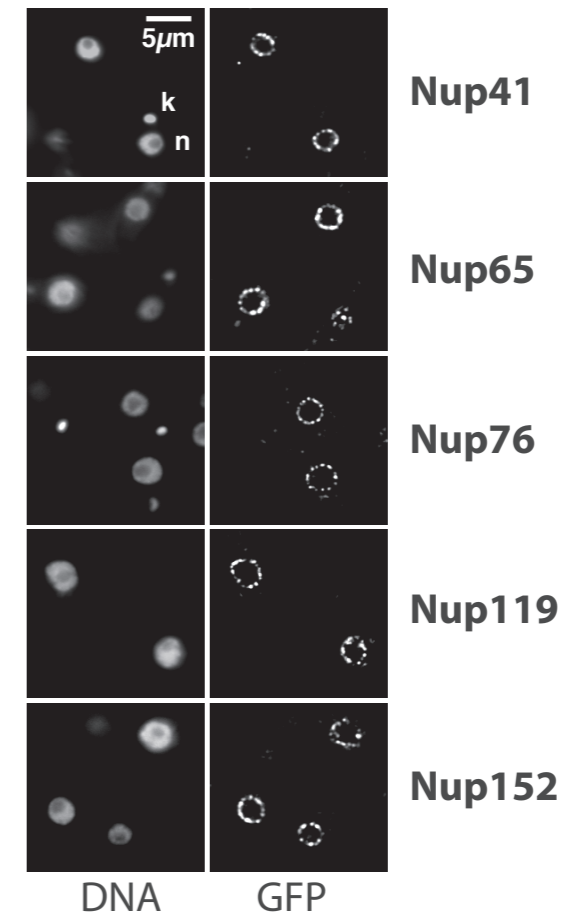
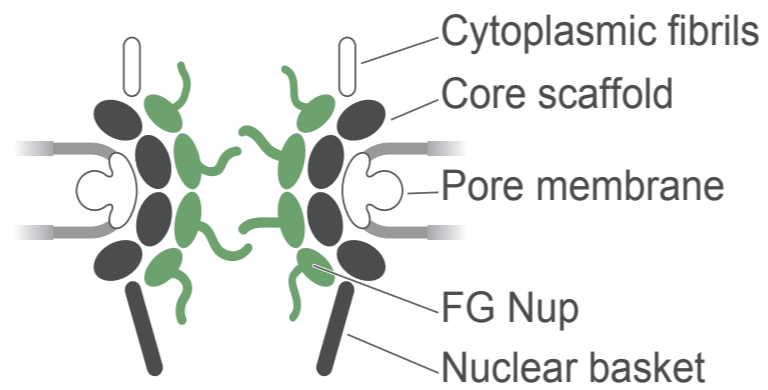
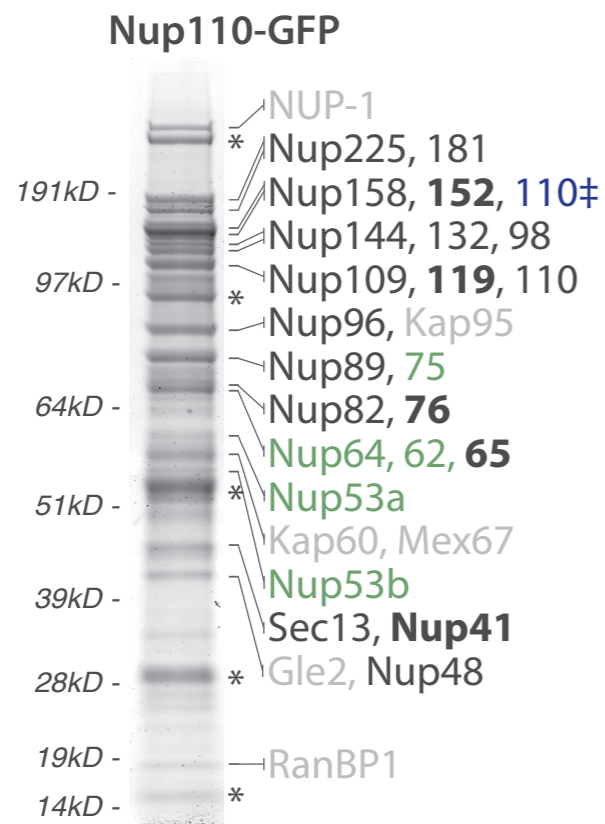
FG repeat

Only 3 major fold types

β-propellers

α-solenoid

Disordered FG-repeat



Accession no.	Nucleoporin	Mass (kDa)	Predicted secondary structure/No. of amino acids	Fold type	Potential orthologs	
					Yeast	Vertebrates
Tb927.10.2320	Nup41	41.2		β-propeller	Nup82	Nup43
Tb927.10.3810	Nup65	64.8		RRM TMD	Nup53/59	Nup35
Tb927.8.6250	Nup76	75.5		coiled coil	Nup82	Nup88
Tb927.11.9780	Nup119	118.8		β-propeller/α-solenoid	Nup157/170	Nup155
Tb927.10.9650	Nup152	152.9		β-propeller/α-solenoid	Nup120/133	Nup133/160

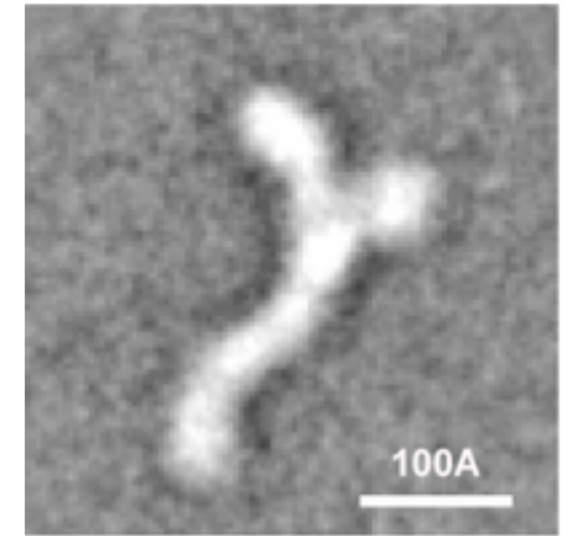
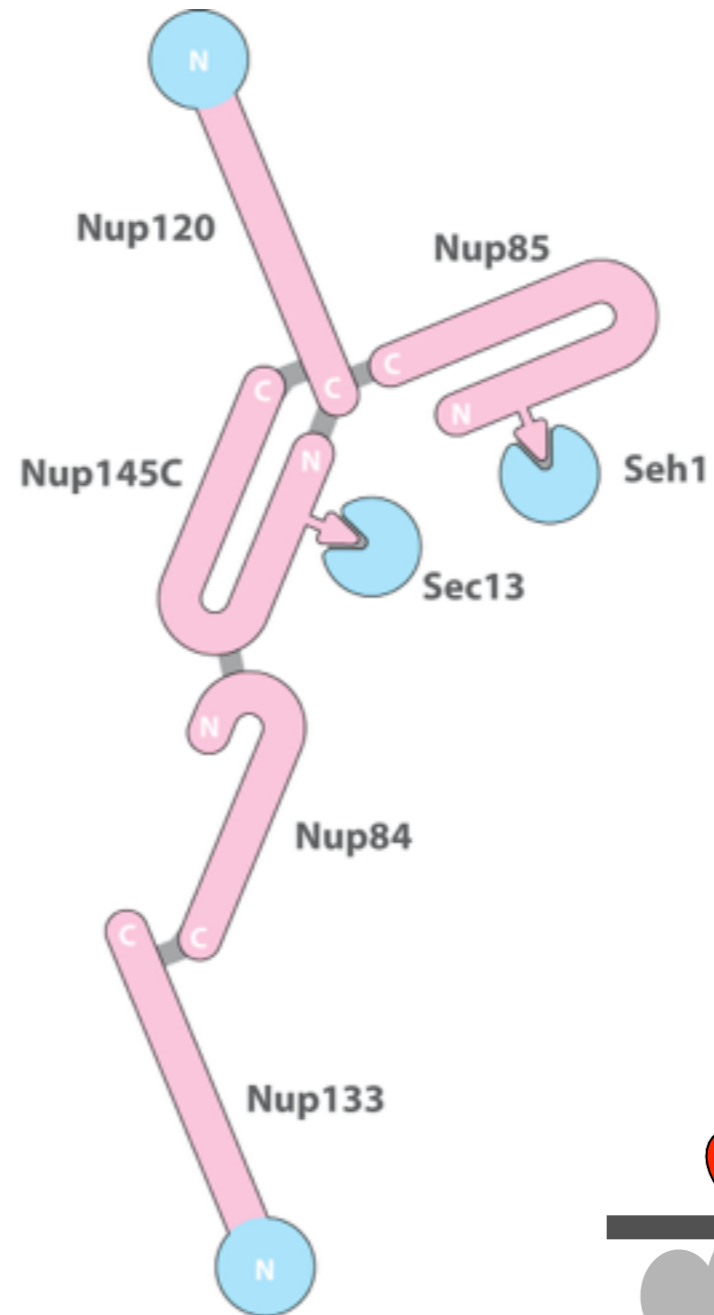
NUP84 complex



β -propeller

α -solenoid

both

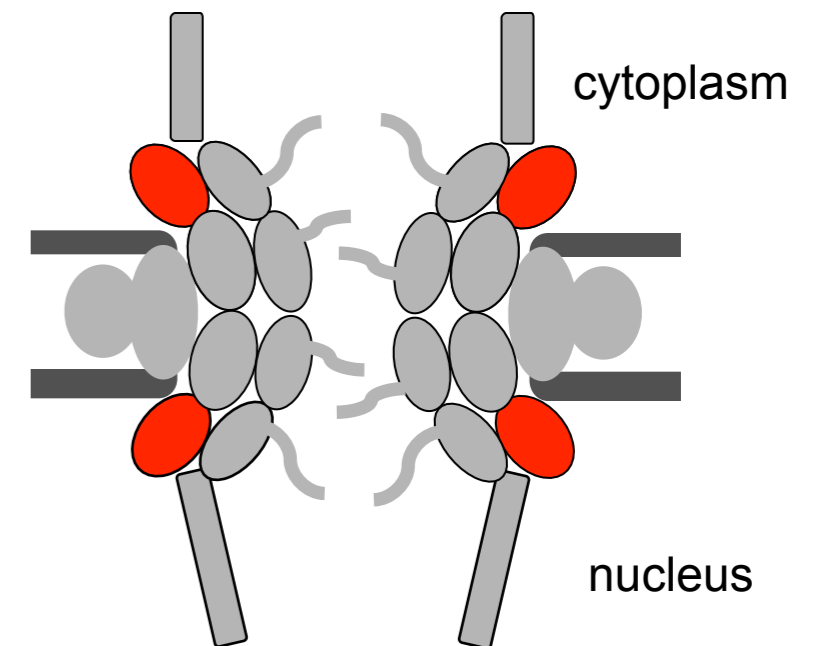


Y-shaped, 7-protein complex

Forms the two outer rings of the NPC

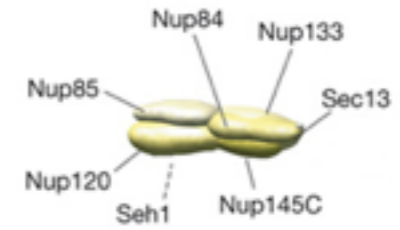
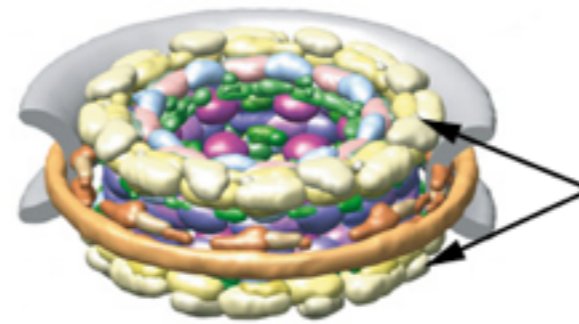
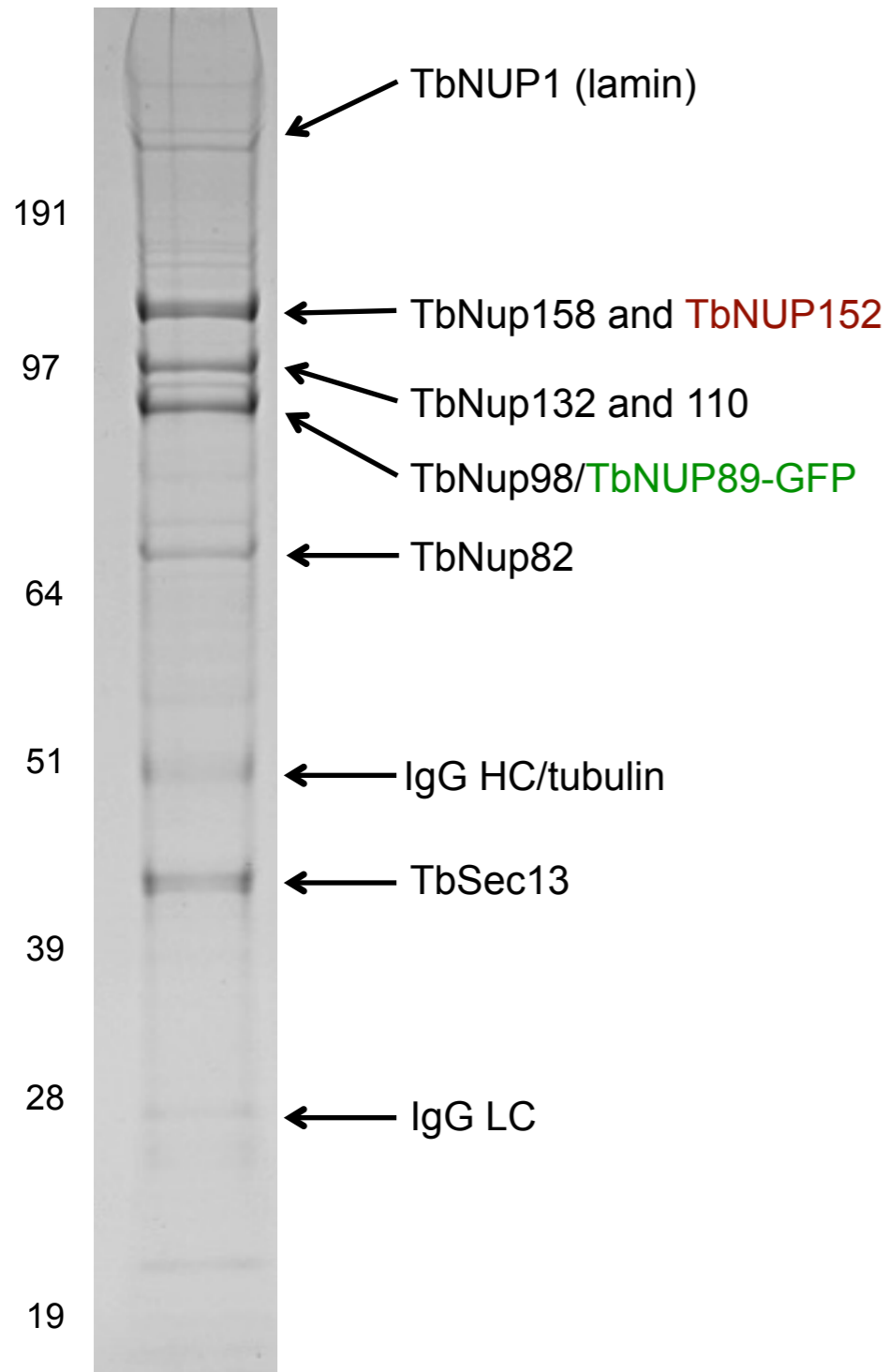
Present in 16 copies in the NPC

Shares a common ancestor with vesicle coating complexes



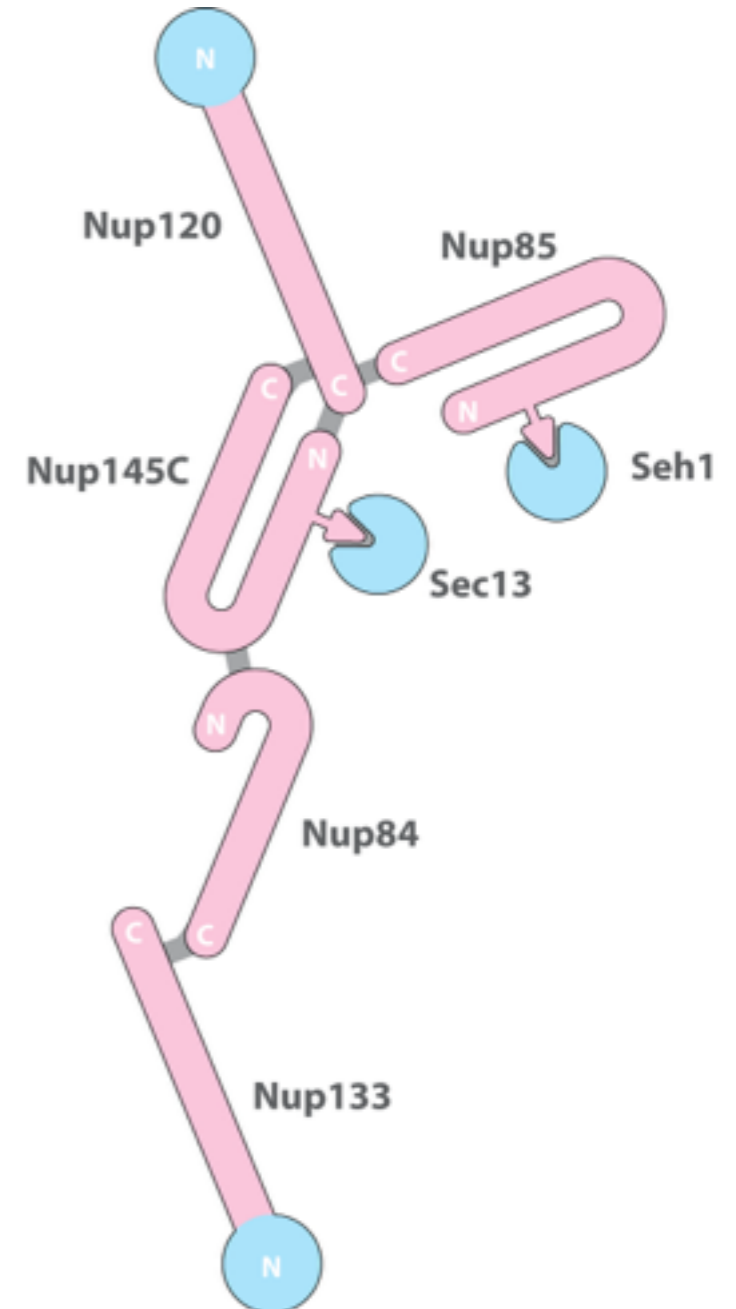
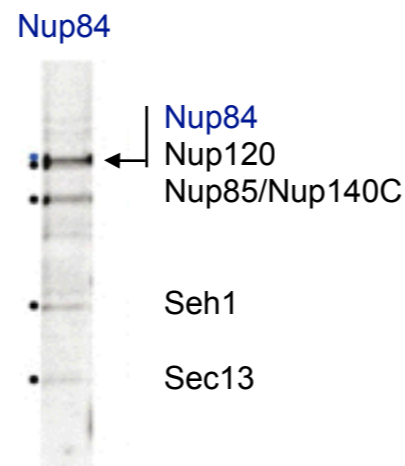
NUP84 complex pullout

TbNUP89-GFP



S. cerevisiae equivalents

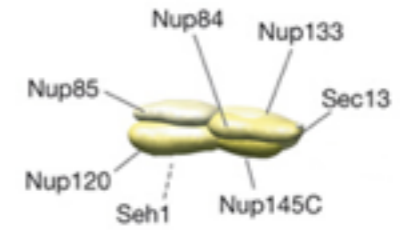
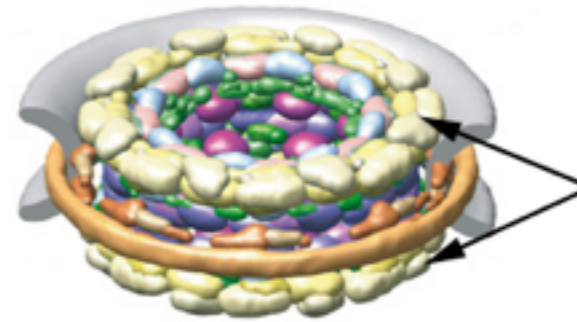
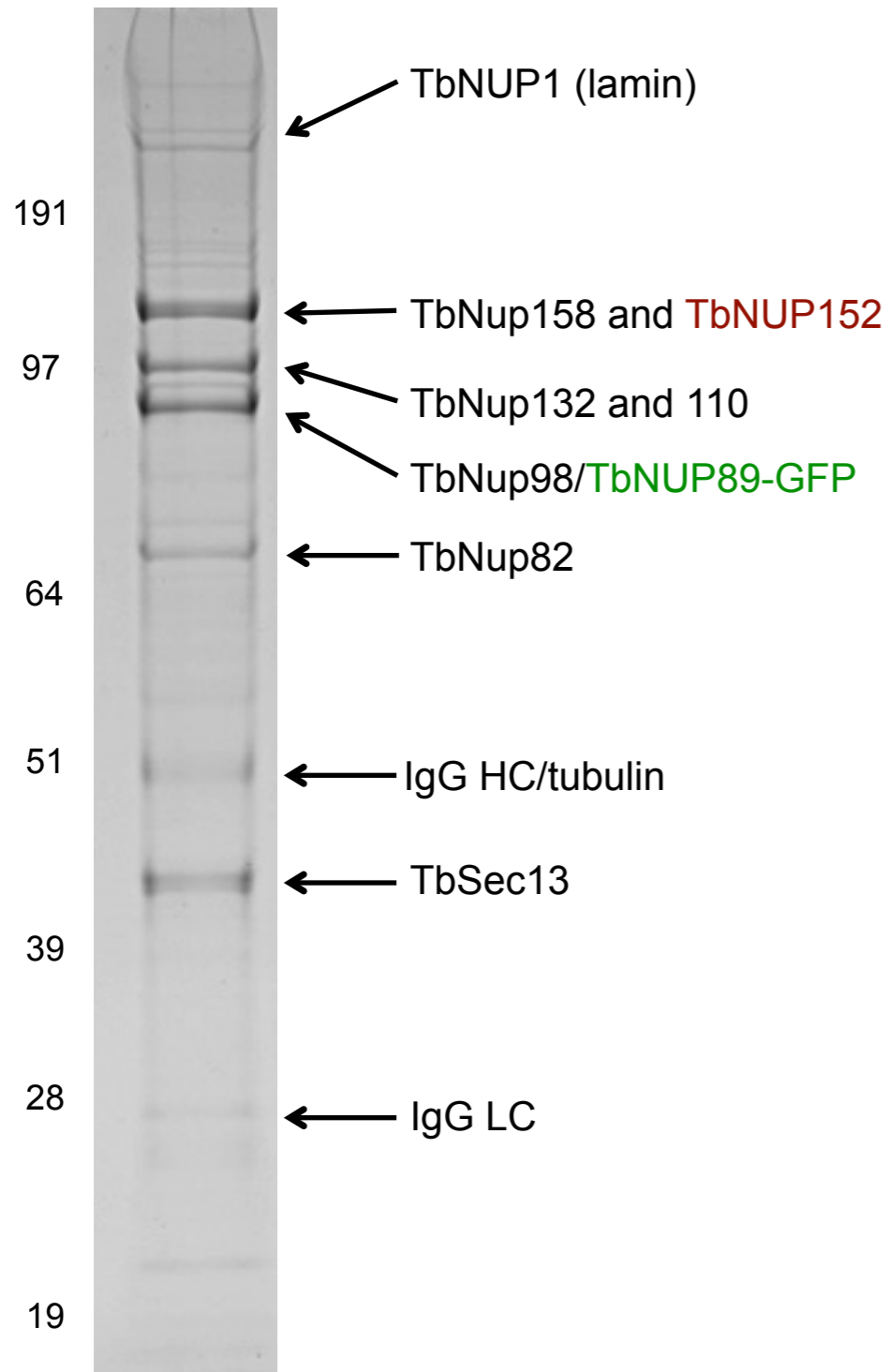
TbNup158 = ScNup145
TbNup152 = to be determined
 TbNup132 = ScNup120/133
 TbNup110 = ScMlp
 TbNup98 = FG repeat, Group B
TbNup89 = ScNup84/85
 TbNup82 = ScNup84/85
 TbSec13 = ScSec13



Nups41 and 152 appear to be trypanosome specific

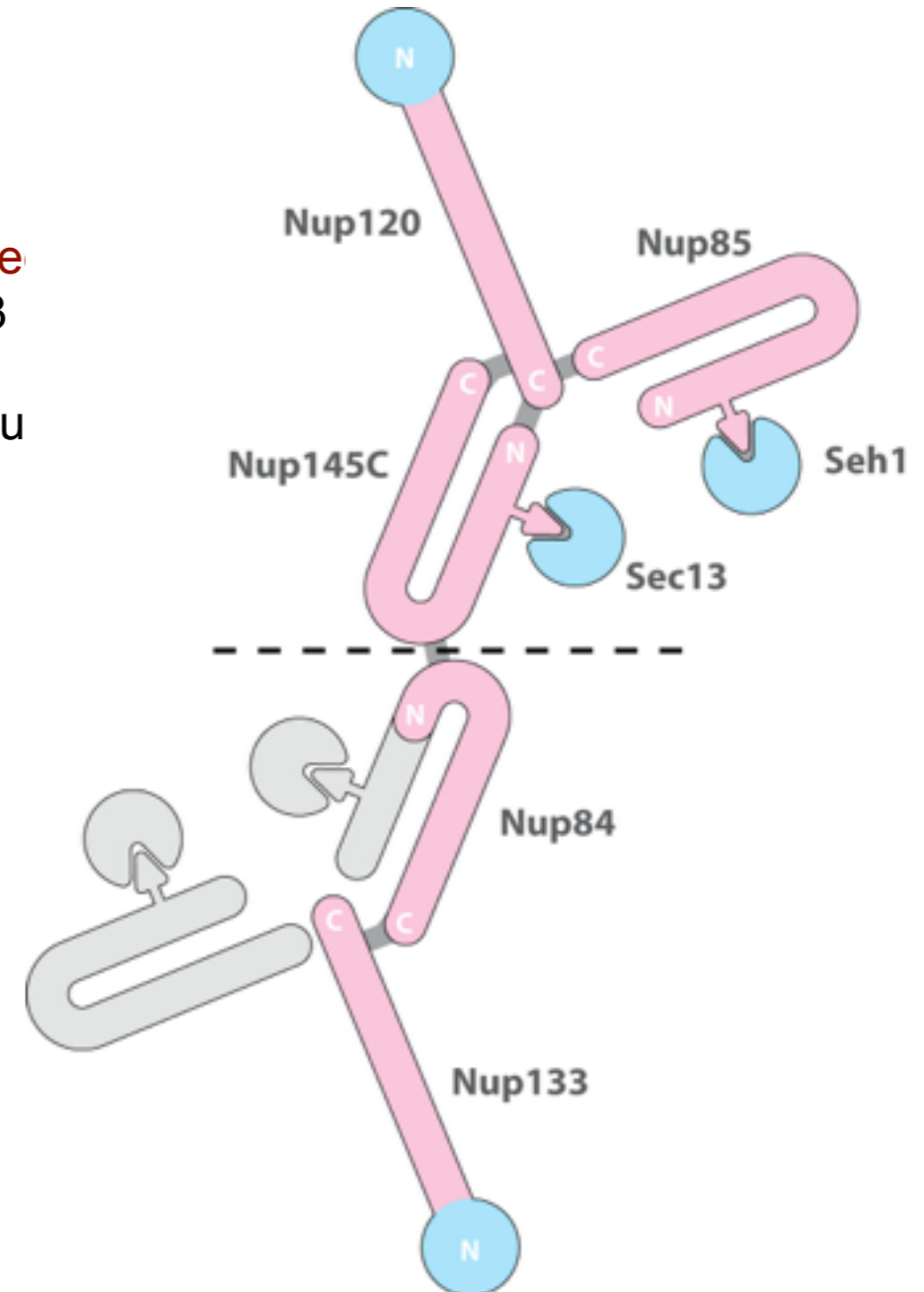
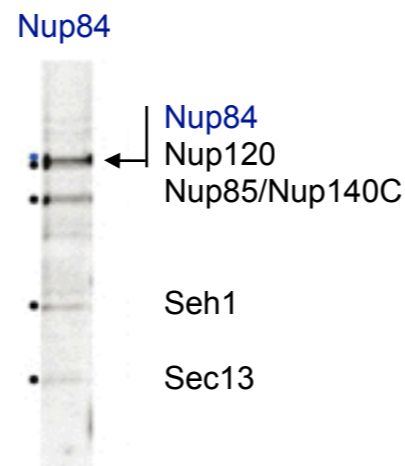
NUP84 complex pullout

TbNUP89-GFP

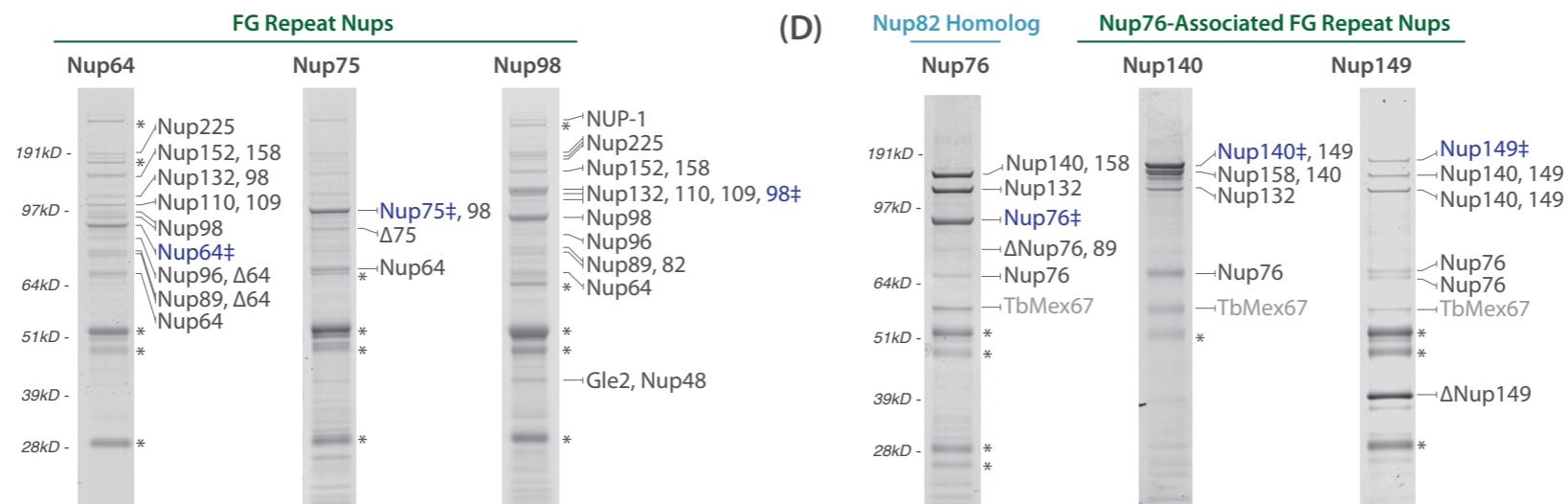
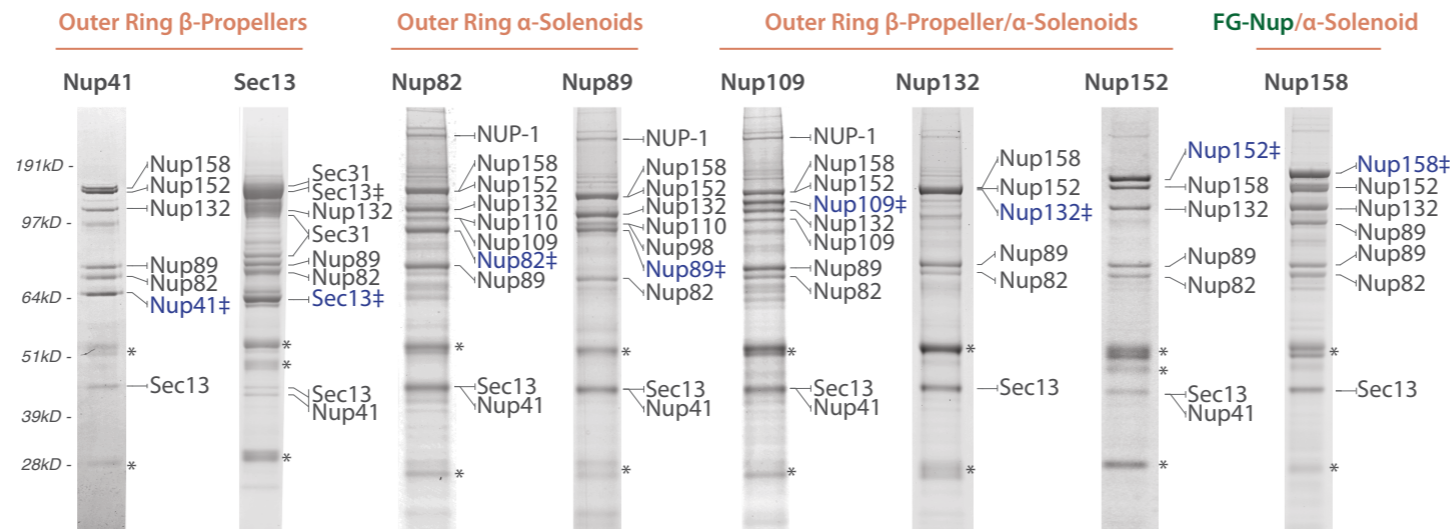
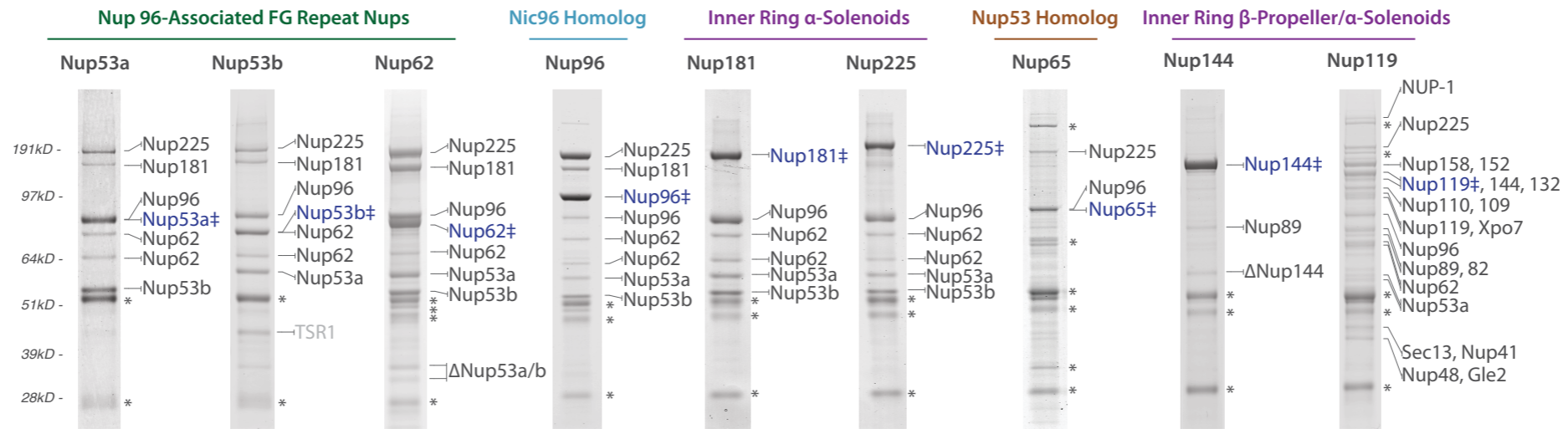


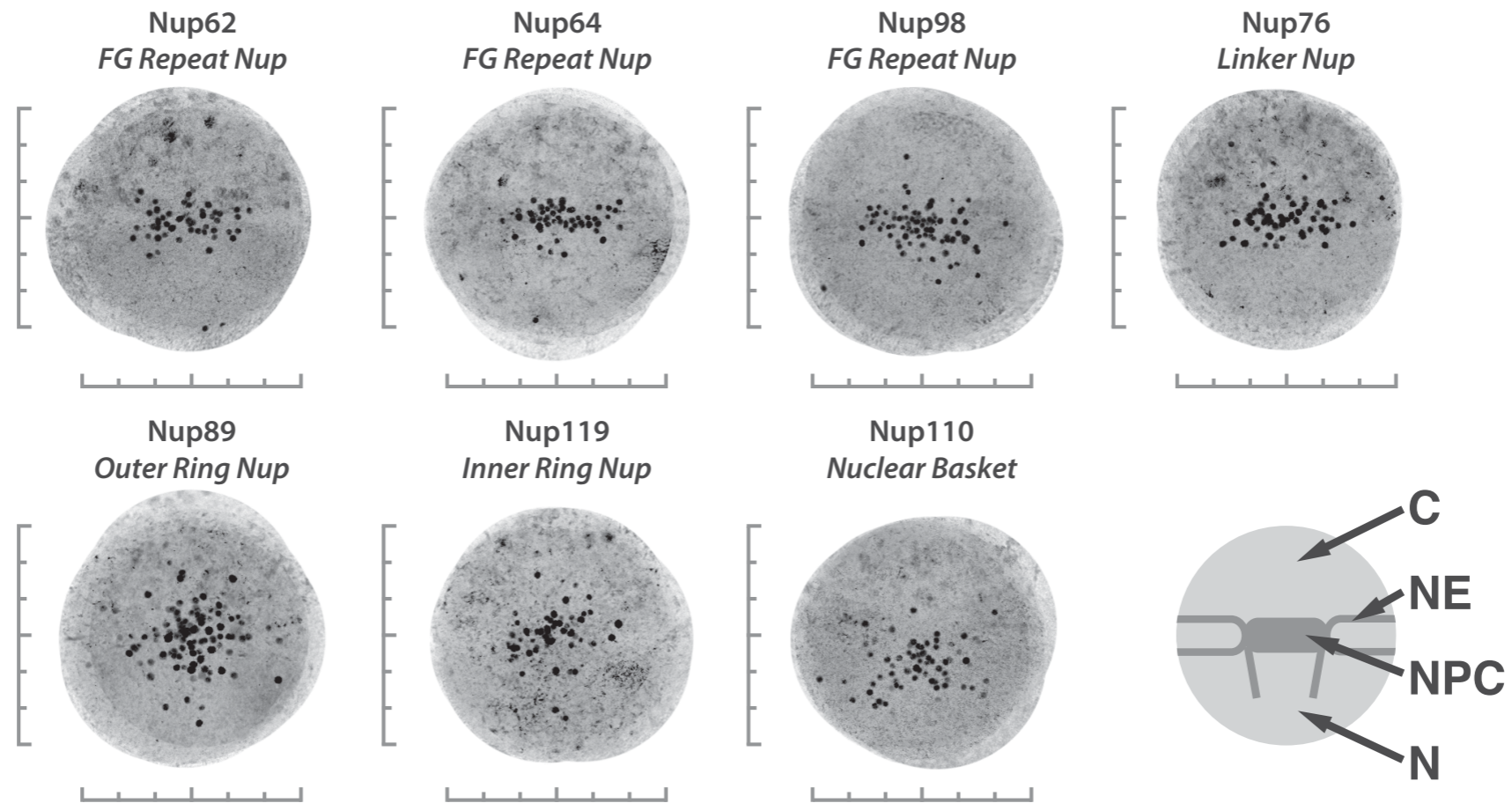
S. cerevisiae equivalents

TbNup158 = ScNup145
TbNup152 = to be determine
 TbNup132 = ScNup120/133
 TbNup110 = ScMlp
 TbNup98 = FG repeat, Grou
TbNup89 = ScNup84/85
 TbNup82 = ScNup84/85
 TbSec13 = ScSec13

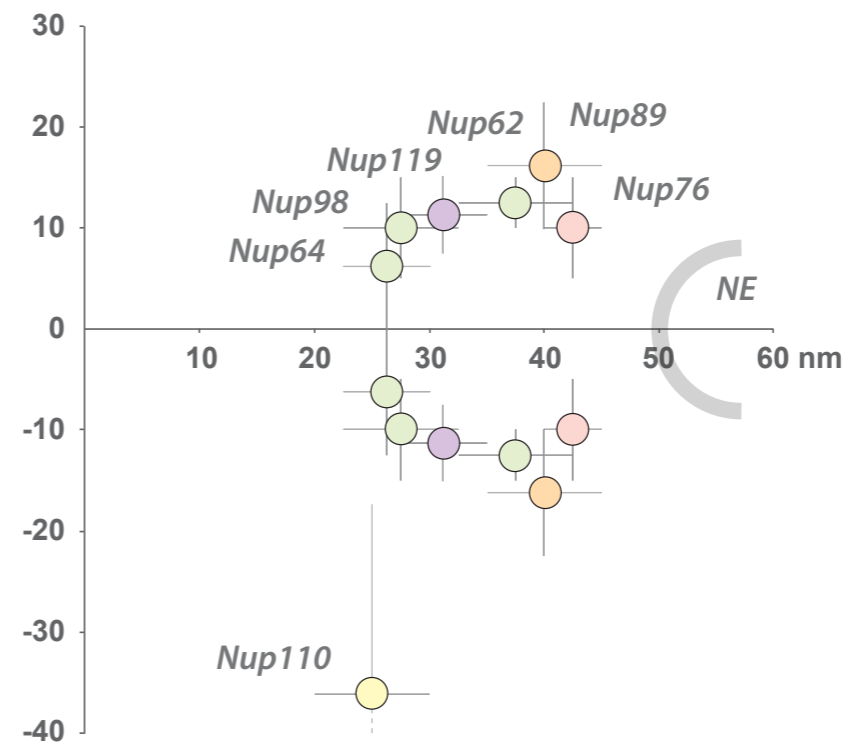


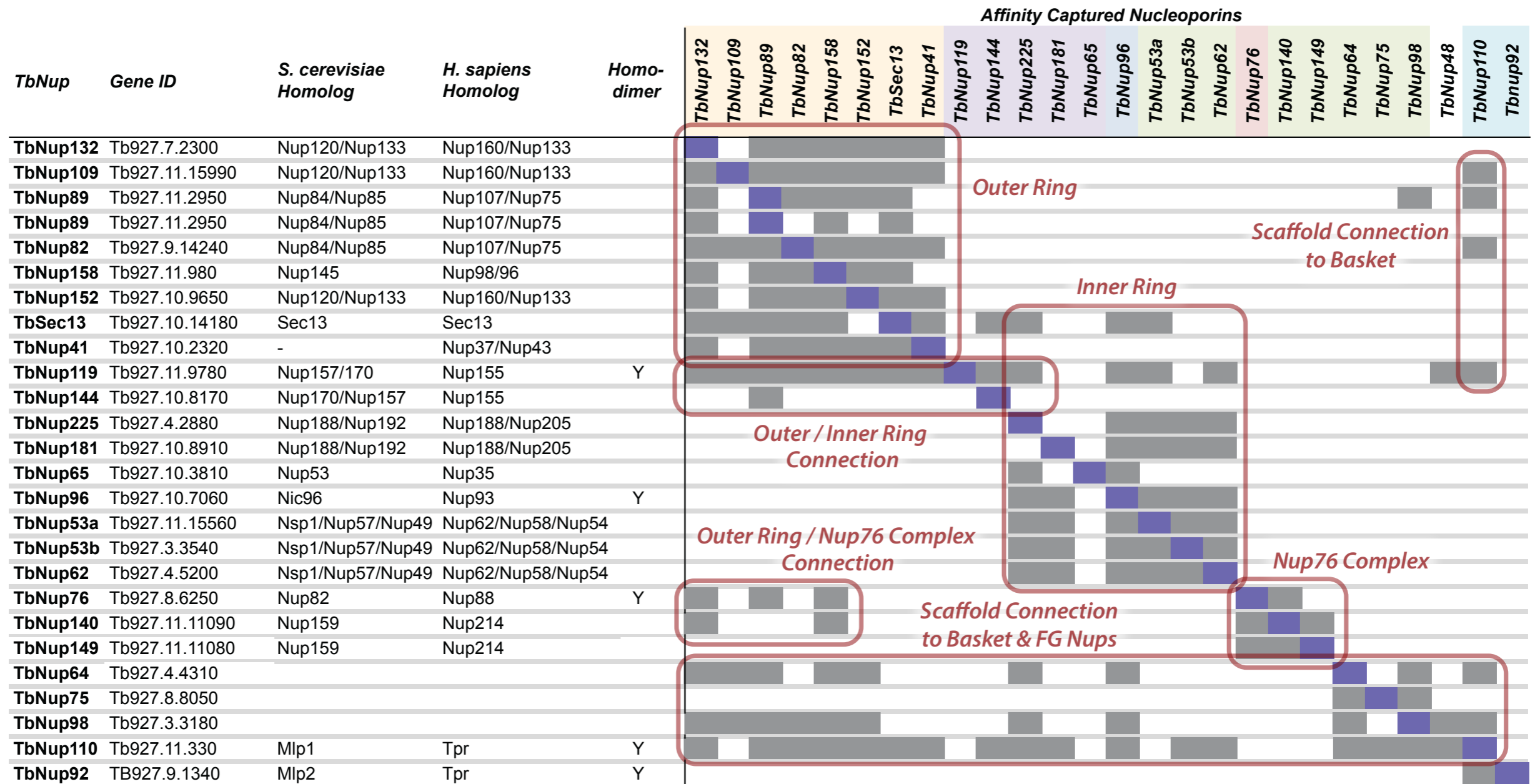
Nups41 and 152 appear to be trypanosome specific





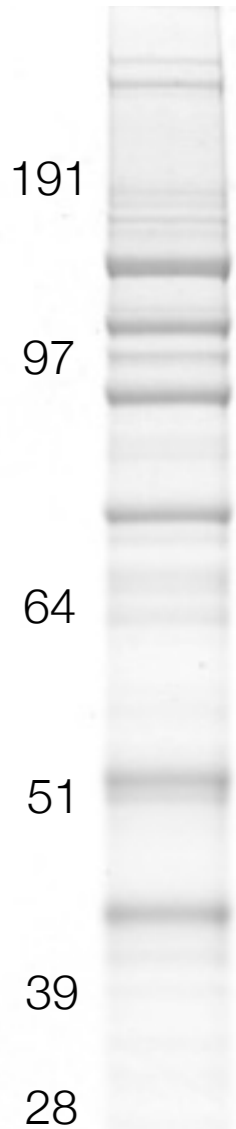
Nup	R ave	R Err	N (R)	Z ave	Z Err	N (Z)
Nup62	37.5	5.0	26	±12.5	2.5	52
Nup64	26.3	3.8	21	±6.2	6.3	58
Nup98	27.5	5.0	41	±10.0	5.0	94
Nup76	42.5	2.5	30	±10.0	5.0	60
Nup89	40.0	5.0	43	±16.2	6.3	120
Nup119	31.2	3.8	37	±11.3	3.8	65
Nup110	25.0	5.0	23	-36.2	18.8	73





Many subcomplexes have conserved and divergent units

Nup82-GFP



TbNup84
Complex

ScNup84
Complex

HsNup106-170
Complex

TbNUP-1 (lamin)

X

✓

TbNup158

ScNup145

HsNup96/98

TbNup152

ScNup120

HsNup160/133

TbNup132

ScNup133

HsNup160/133

TbNup109

X

X

TbNup82-GFP

ScNup84

HsNup107/75

TbNup89

ScNup85

HsNup107/75

Tubulin

ScSeh1

HsSeh1

TbSec13 +

ScSec13

HsSec13

TbNup41

X

HsNup43??

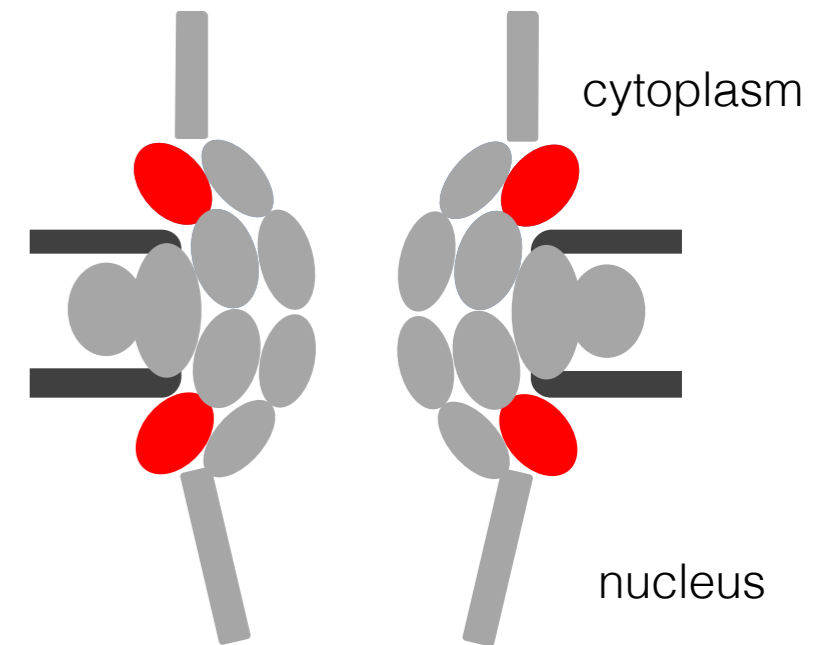
TbALADIN

X

HsNup37

X

HsALADIN



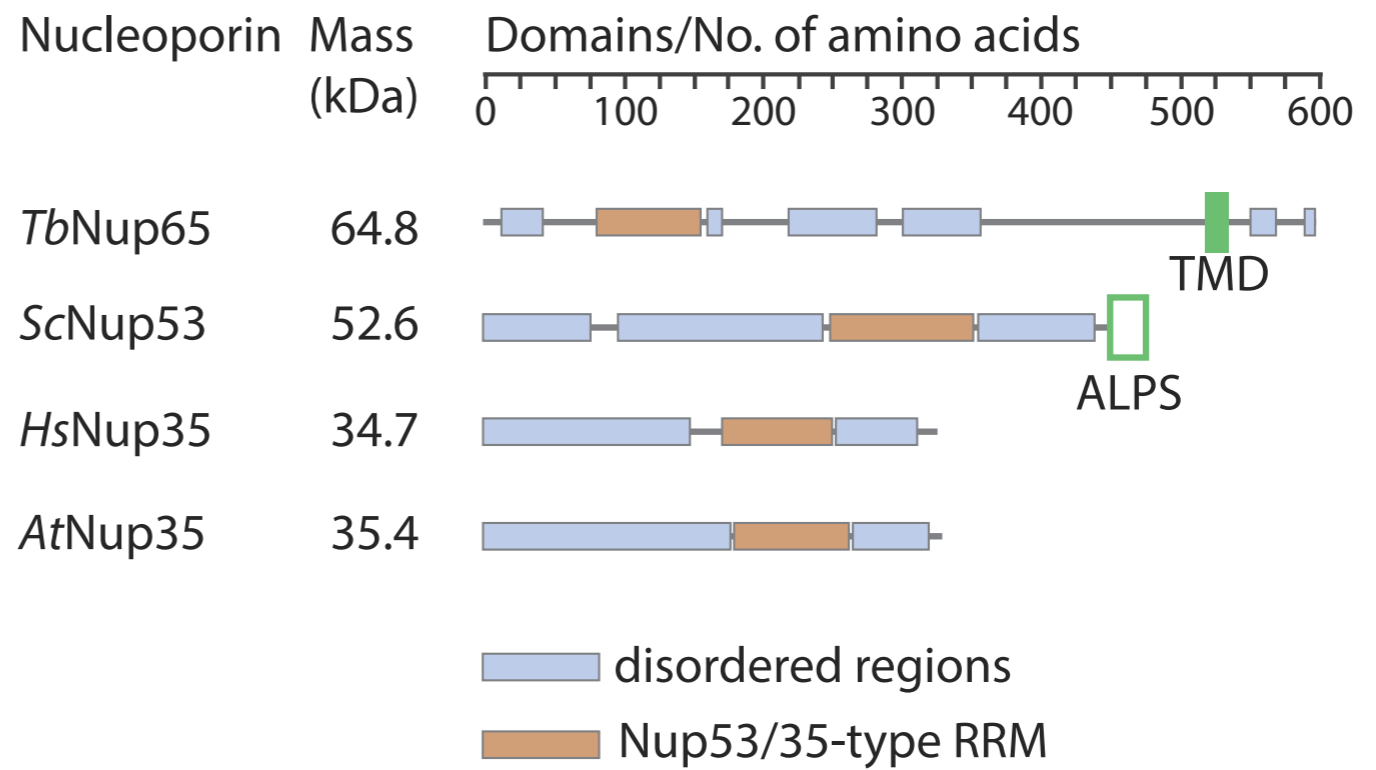
Sup Pel

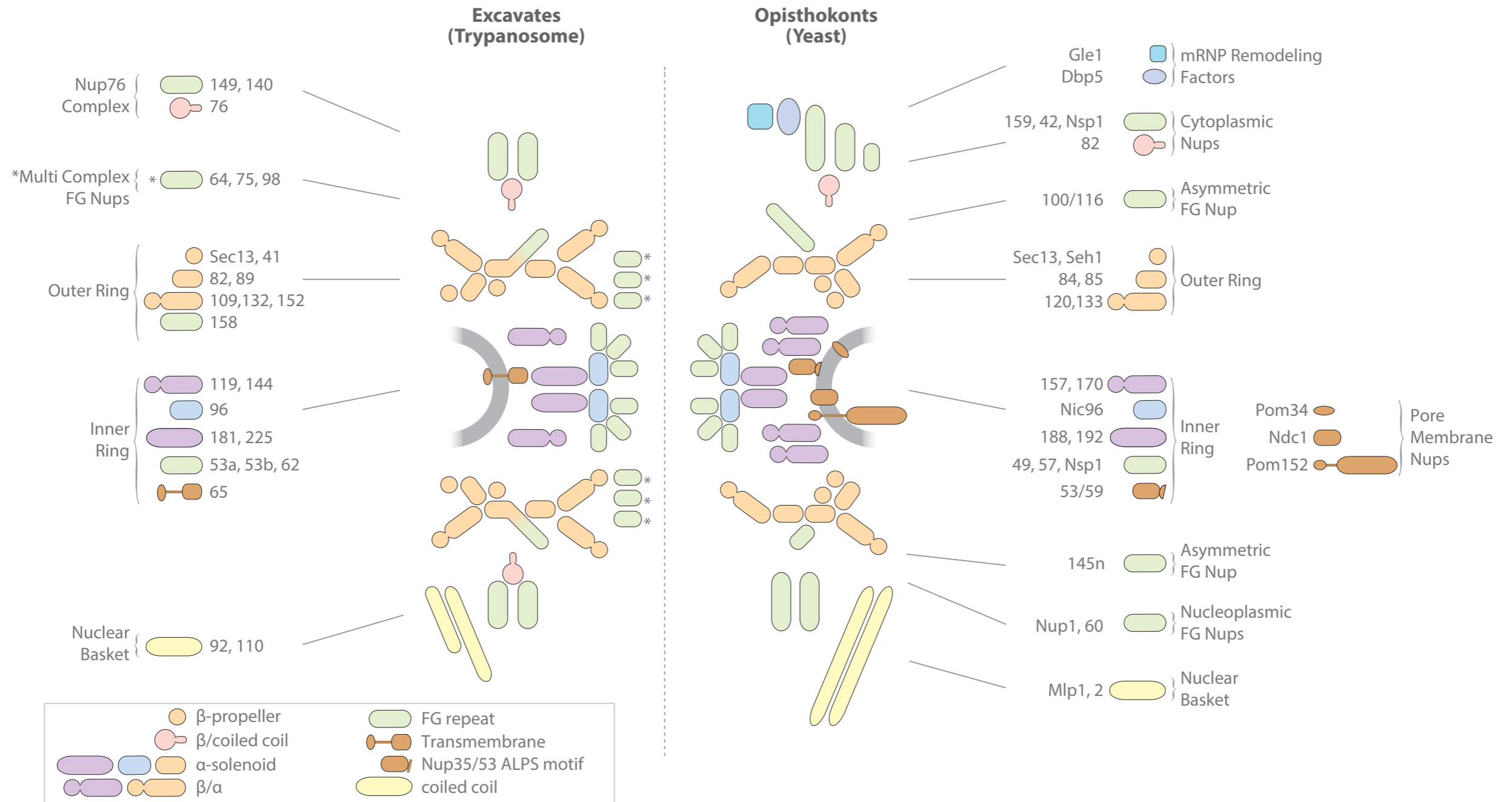


Nup65

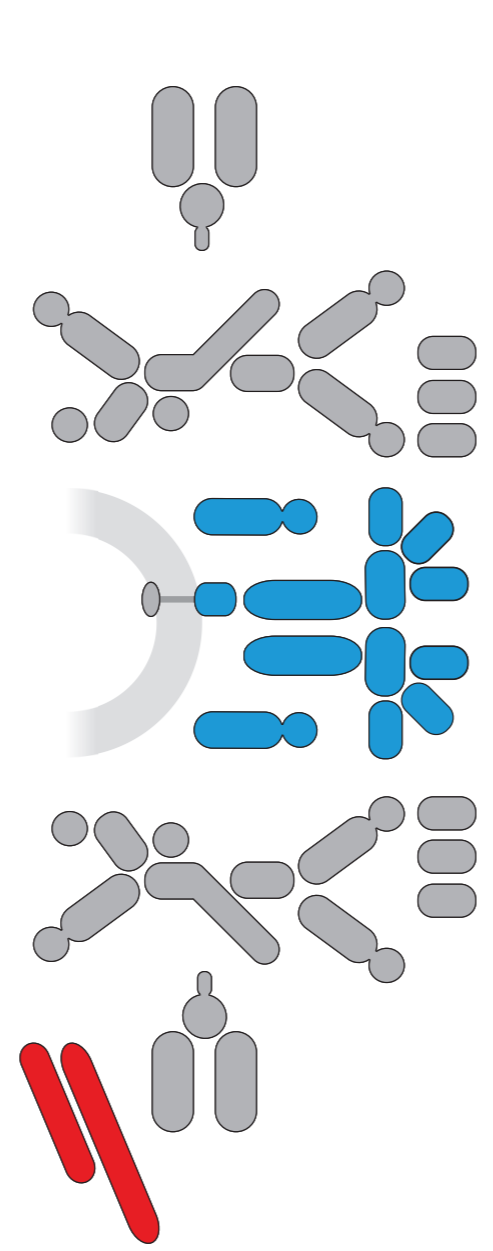
Nup89

Tb927.7.4760

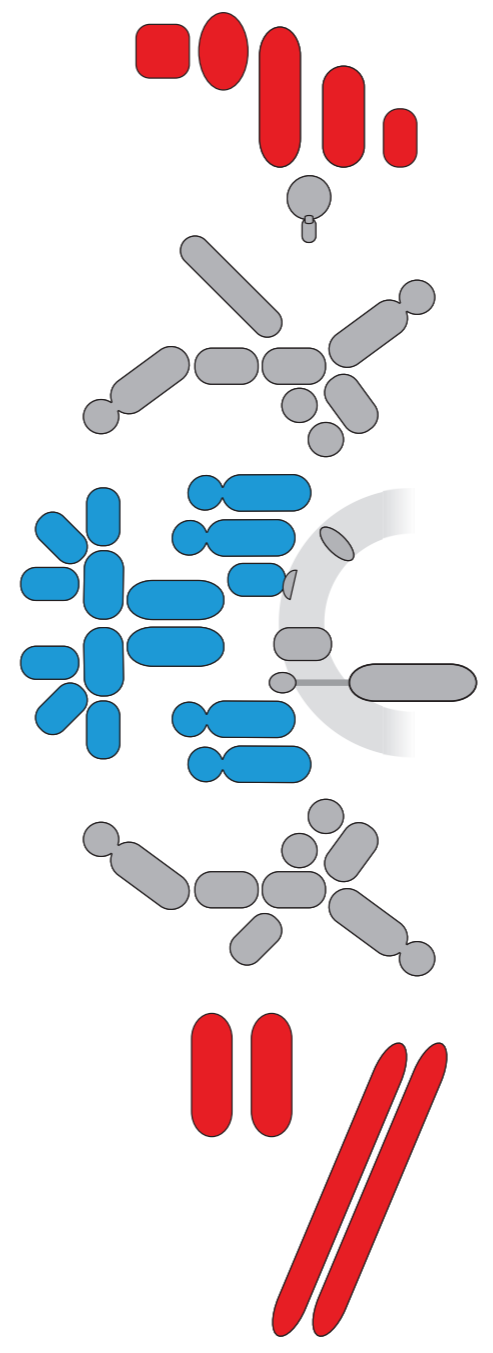


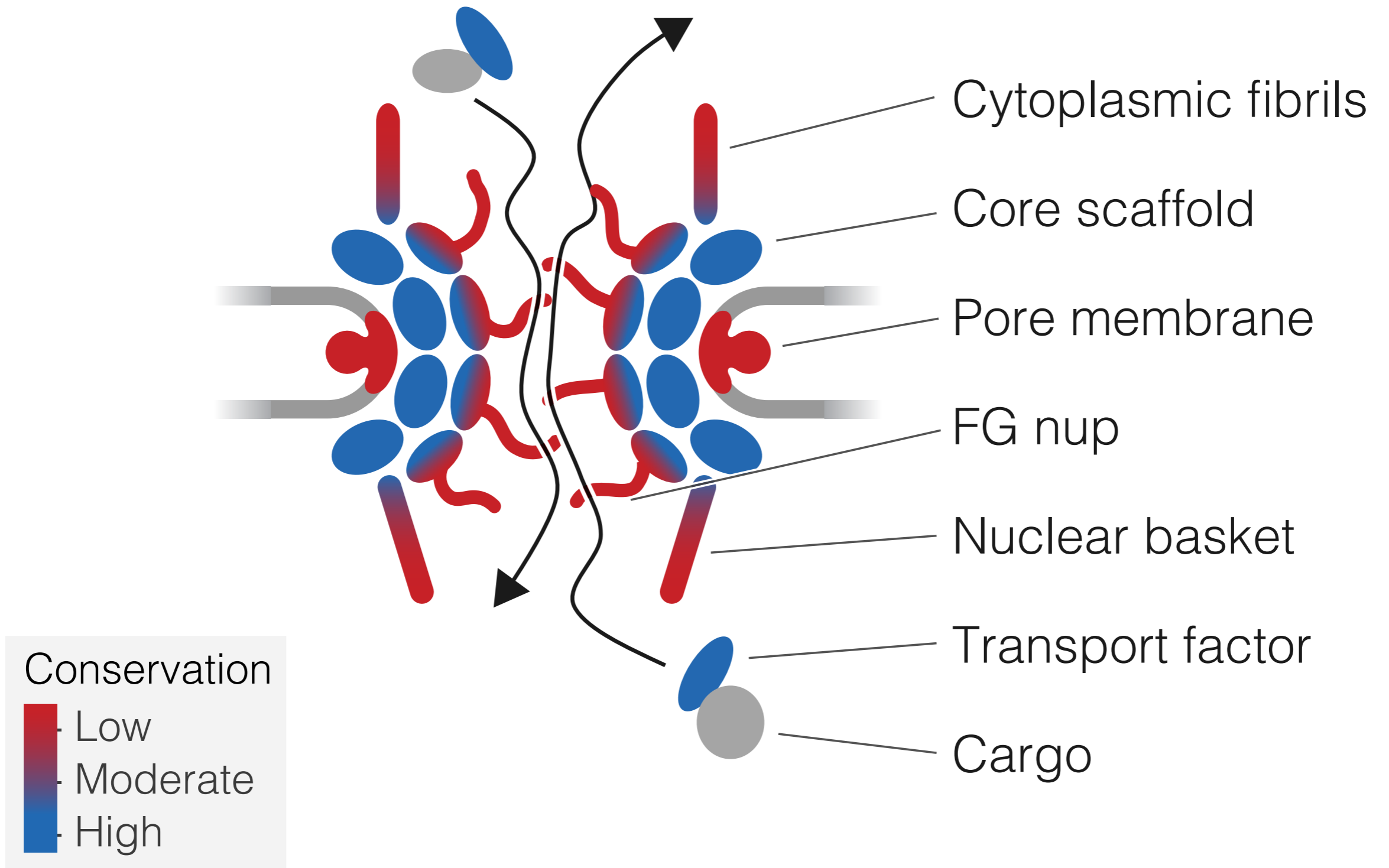


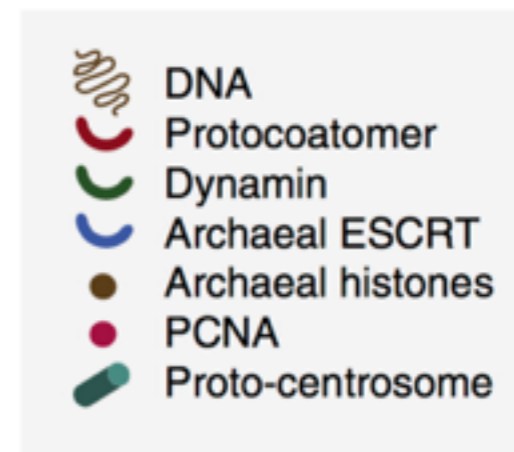
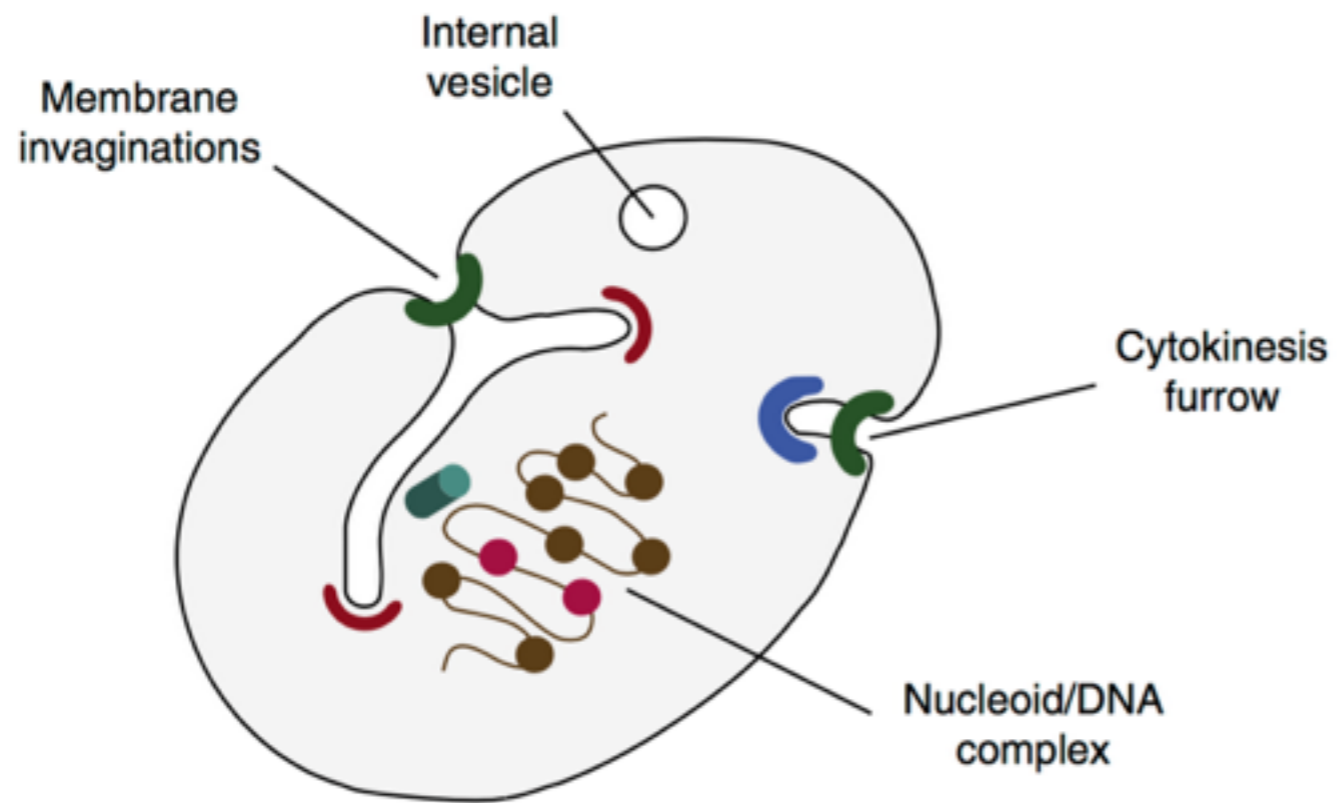
**Excavates
(Trypanosome)**



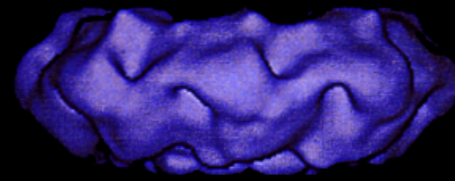
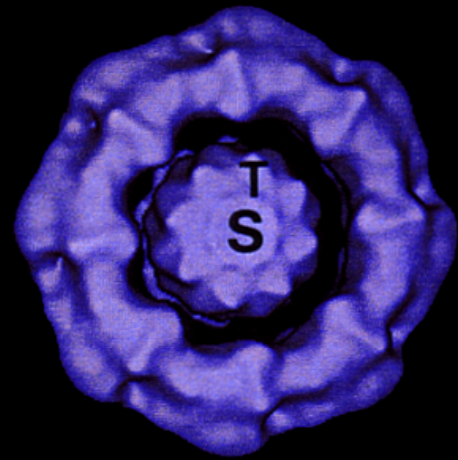
**Opisthokonts
(Yeast)**



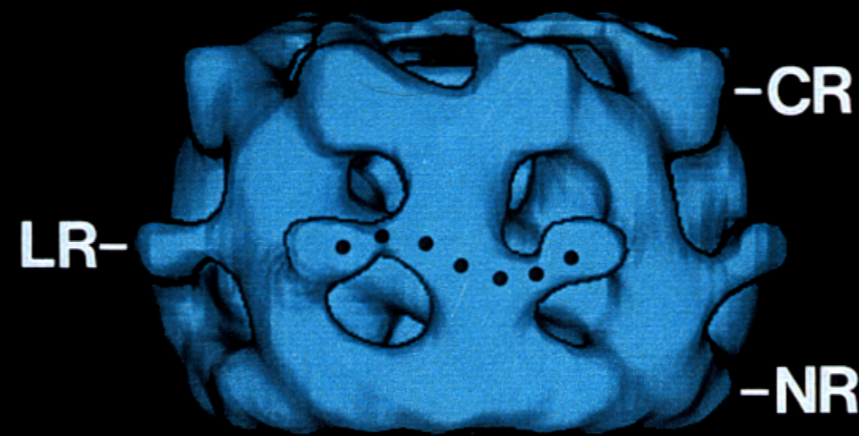
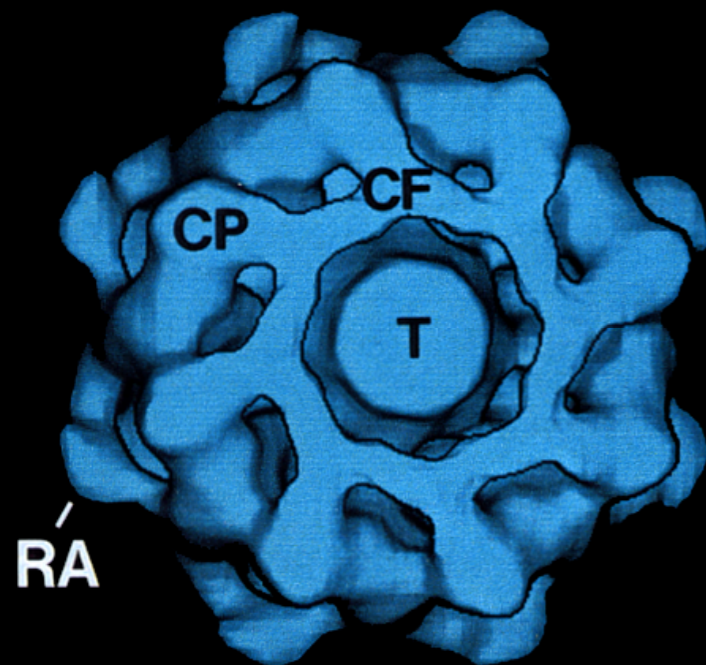




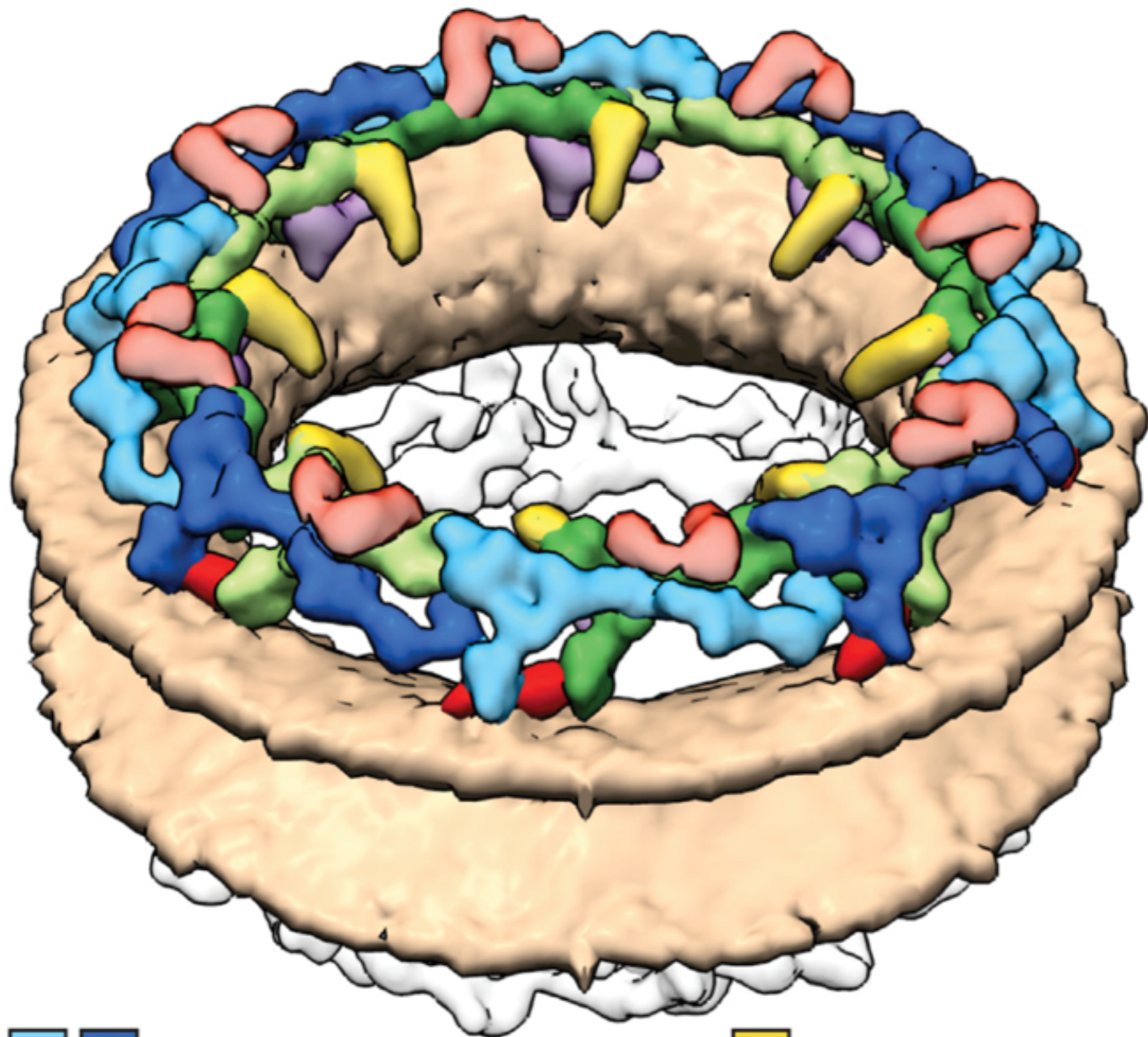
Animal and fungal nuclear pore complexes have species specific structures, but similar protein compositions







Yeast





Rat




  Outer Nup107 subcomplex

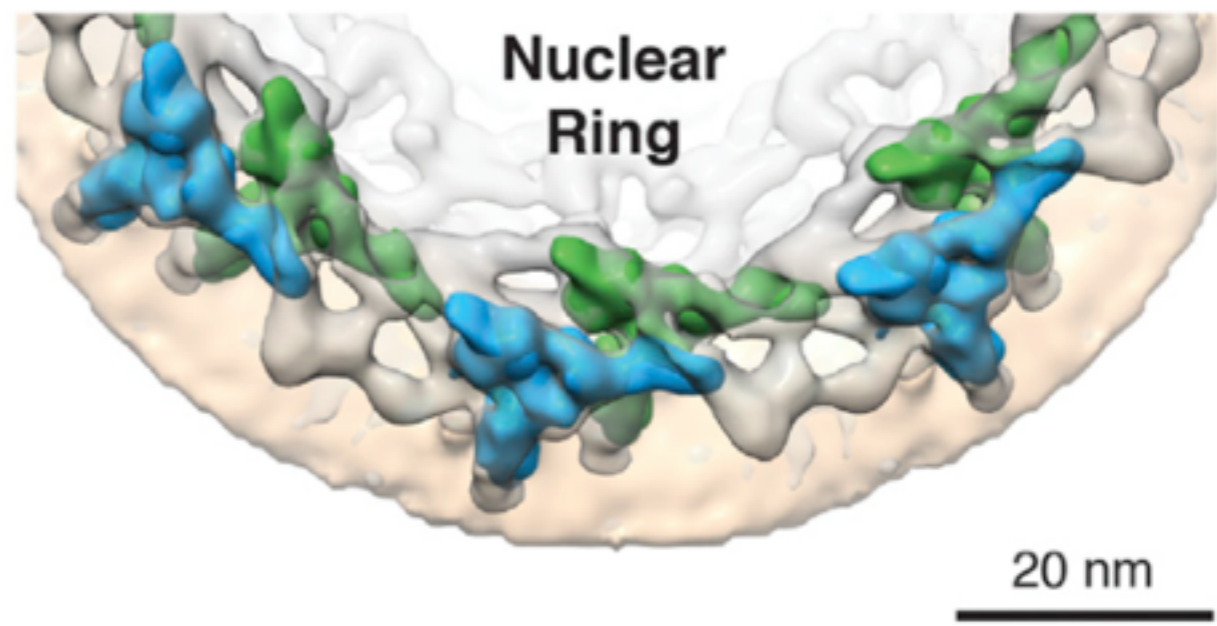
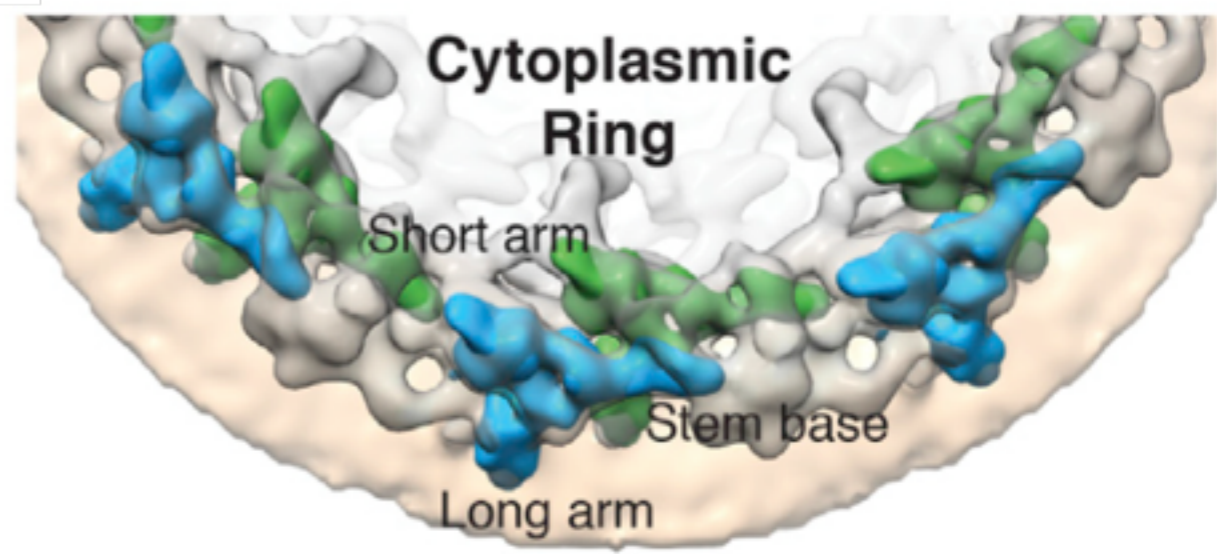
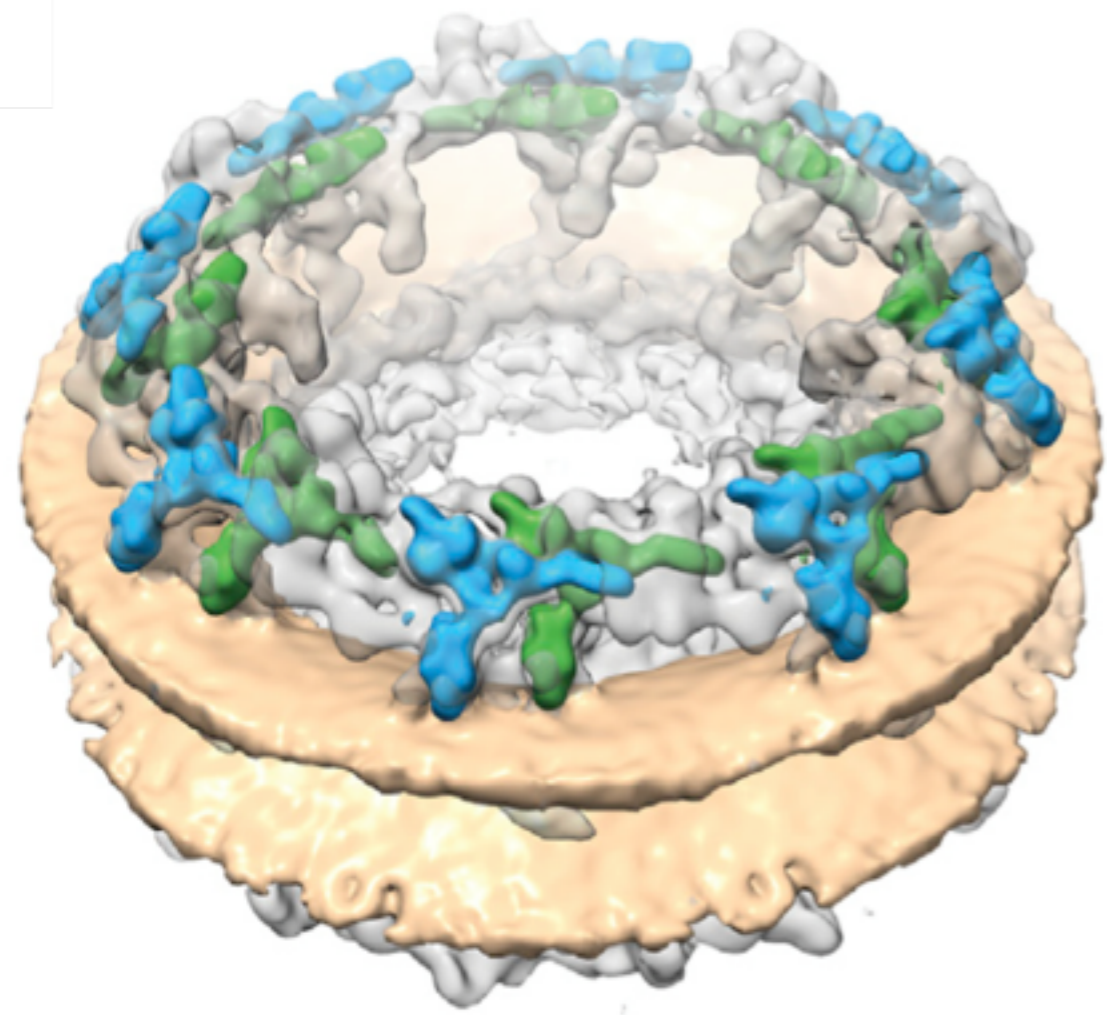
  Inner Nup107 subcomplex

 Nup214 subcomplex

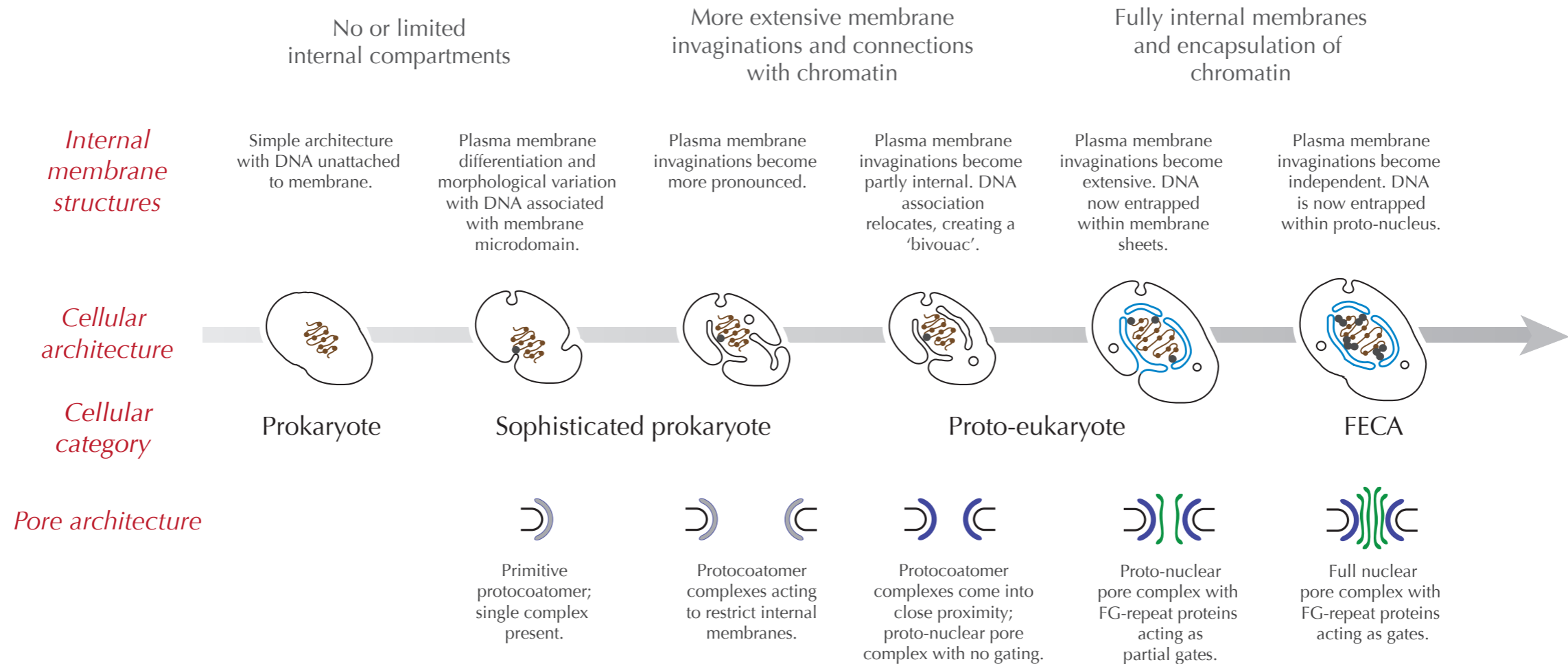
 POM121 region

 Nup358 region

 Nup188 region



How did the nuclear envelope arise?



Pro

Euk



Membrane capper



Fenestrations



Subunit duplication



FG Gate



More gating



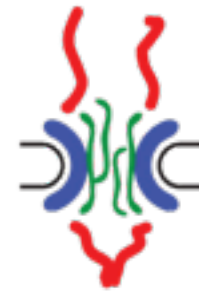
Additional fxn



Asymmetry



More asymm



More elaboration

pre-FECA/FECA



Membrane capper



Fenestrations



Subunit duplication



FG Gate



More gating

LECA/post-LECA



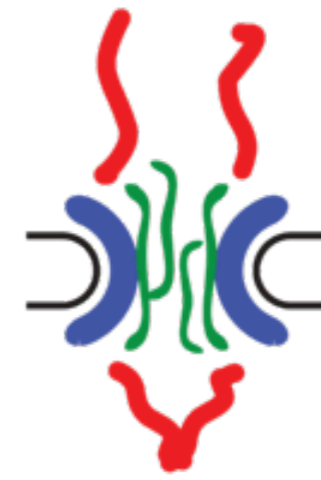
Additional fxn



Asymmetry

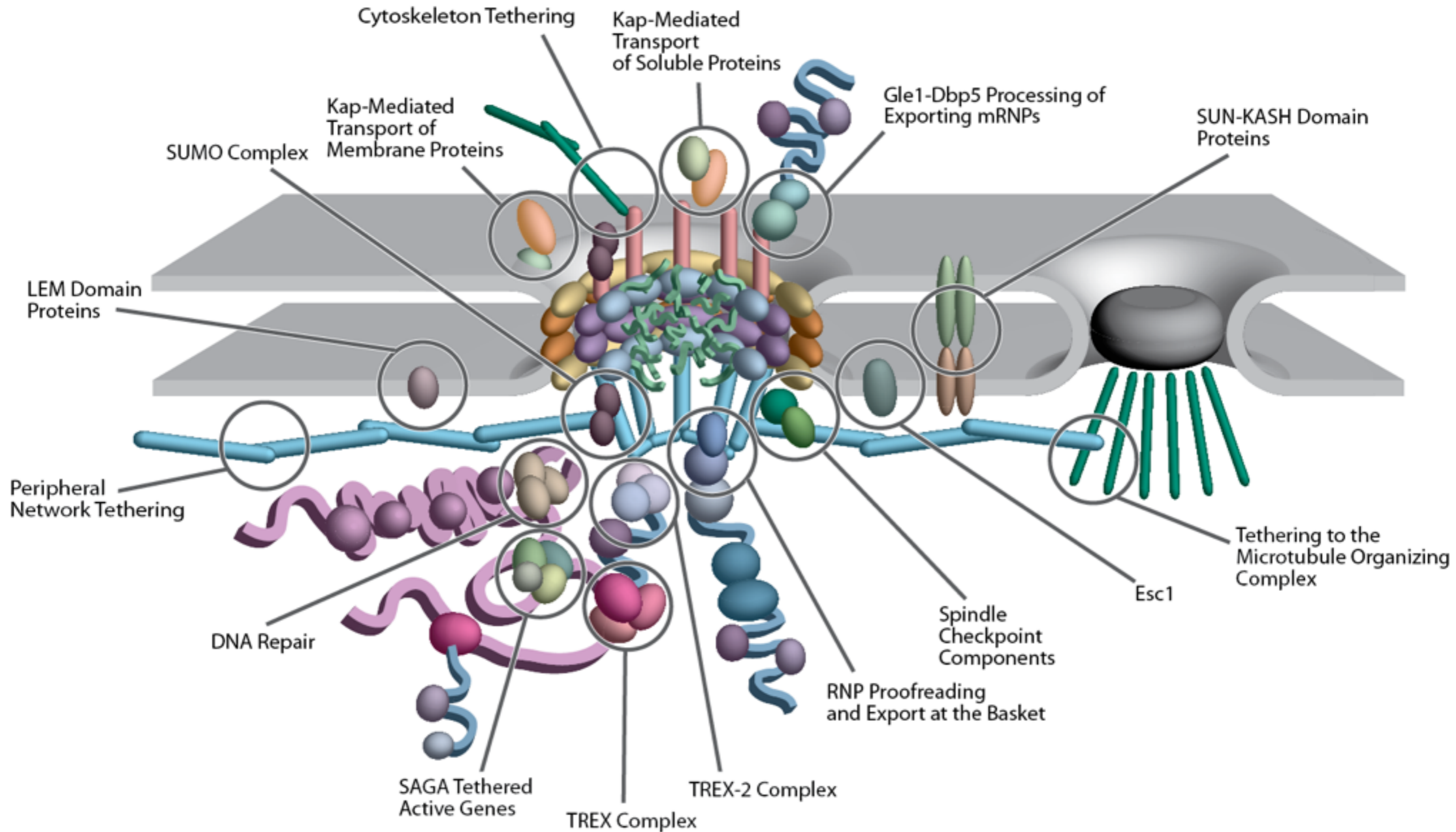


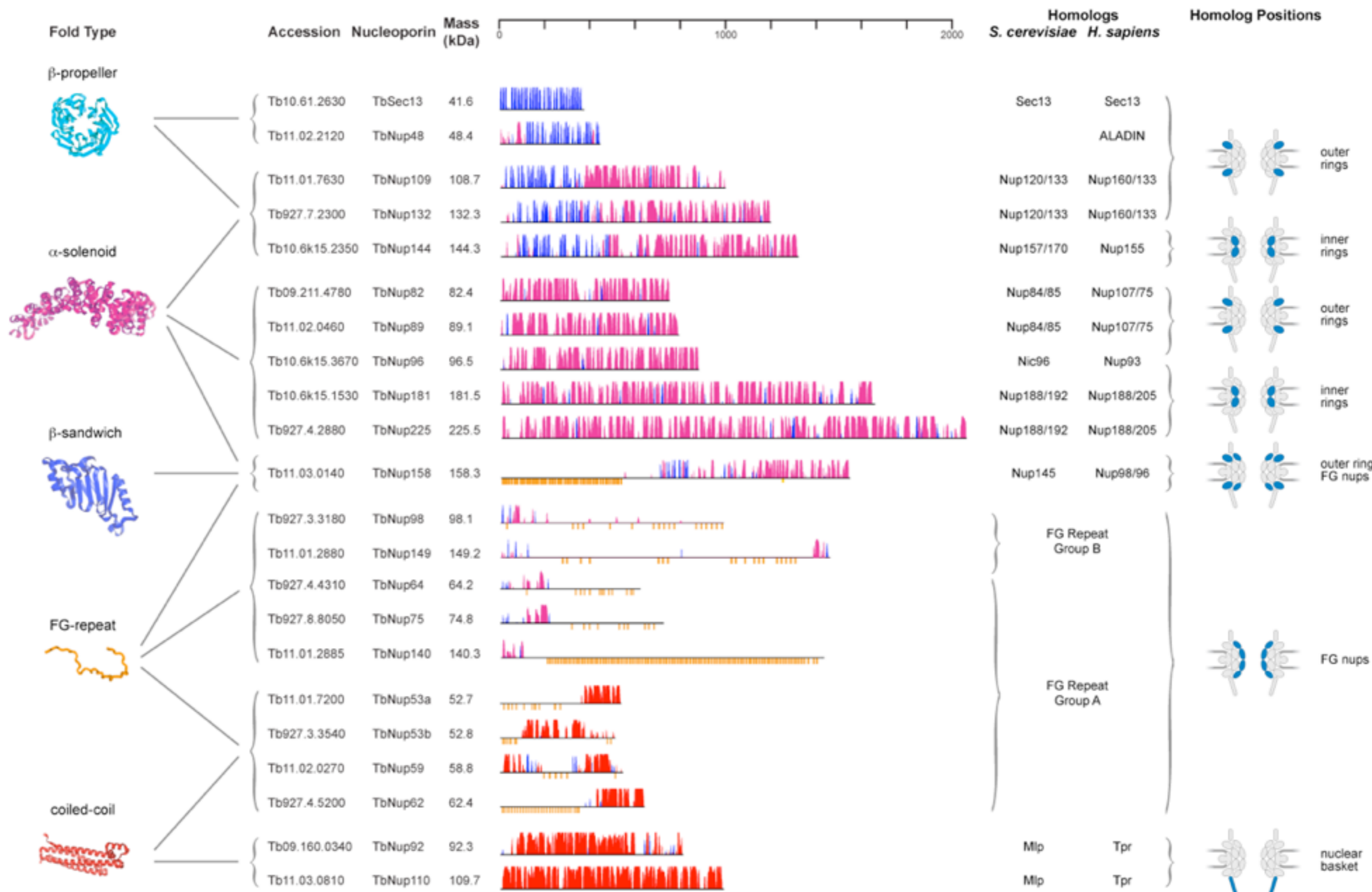
More asymm

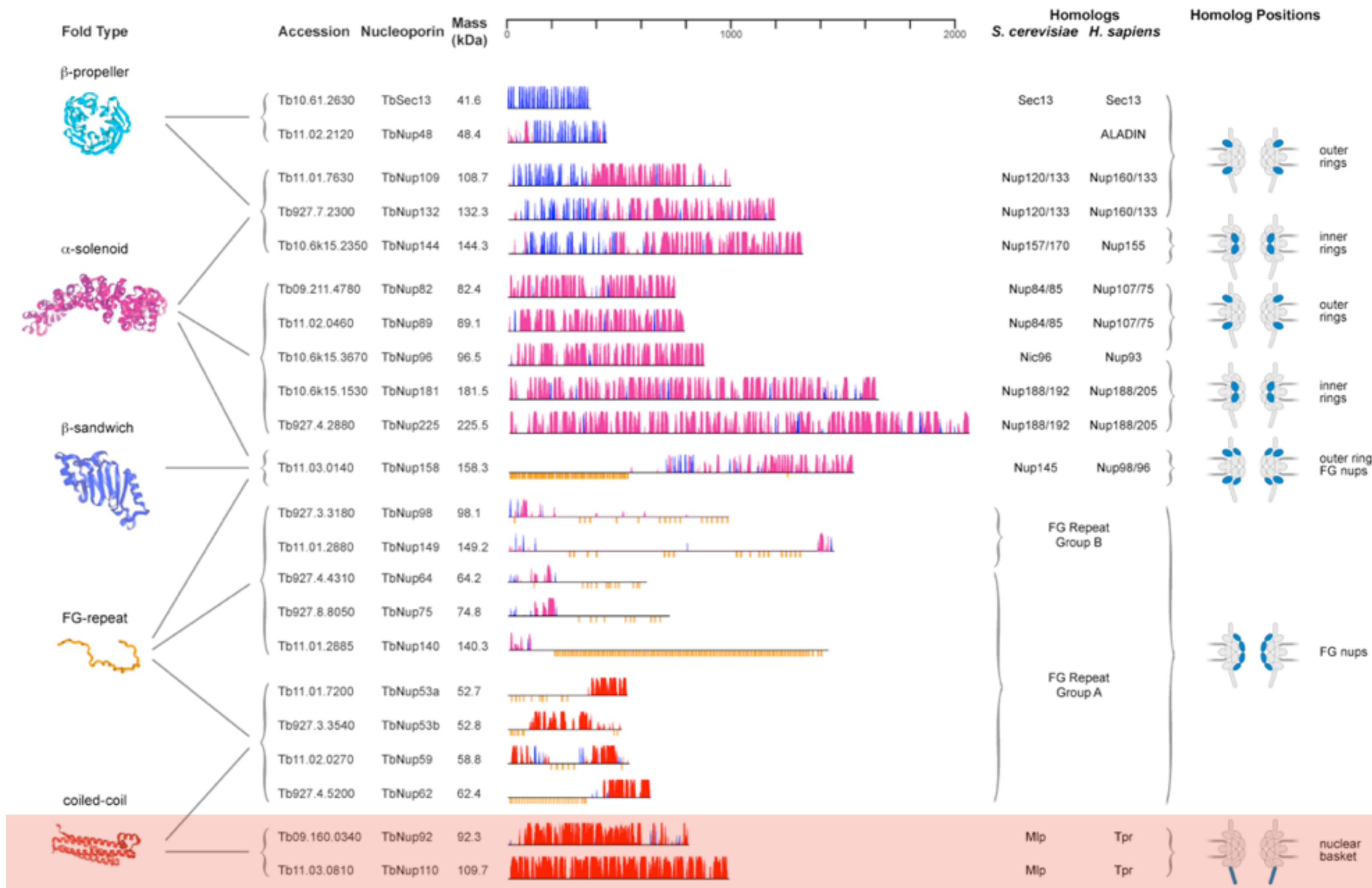


More elaboration

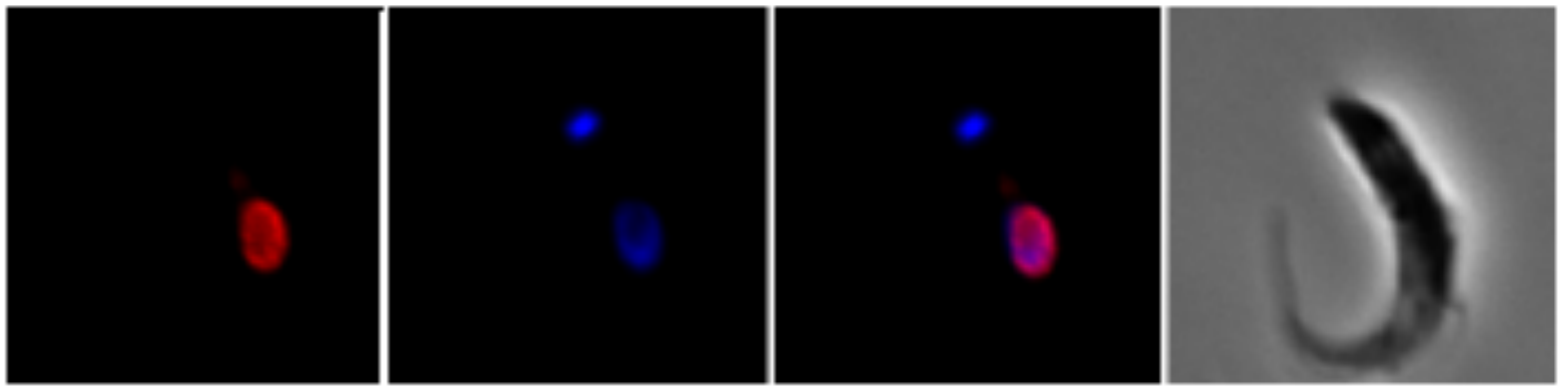
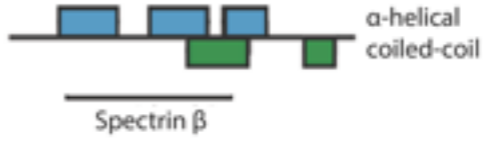
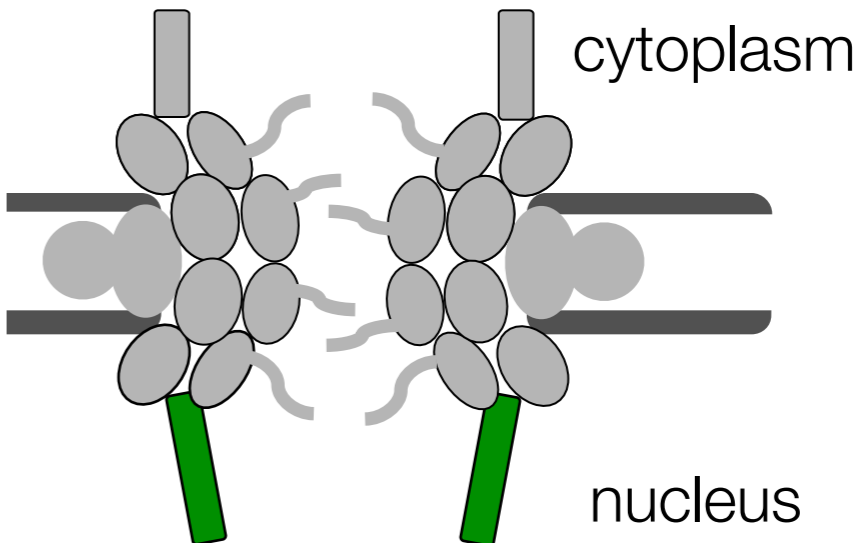
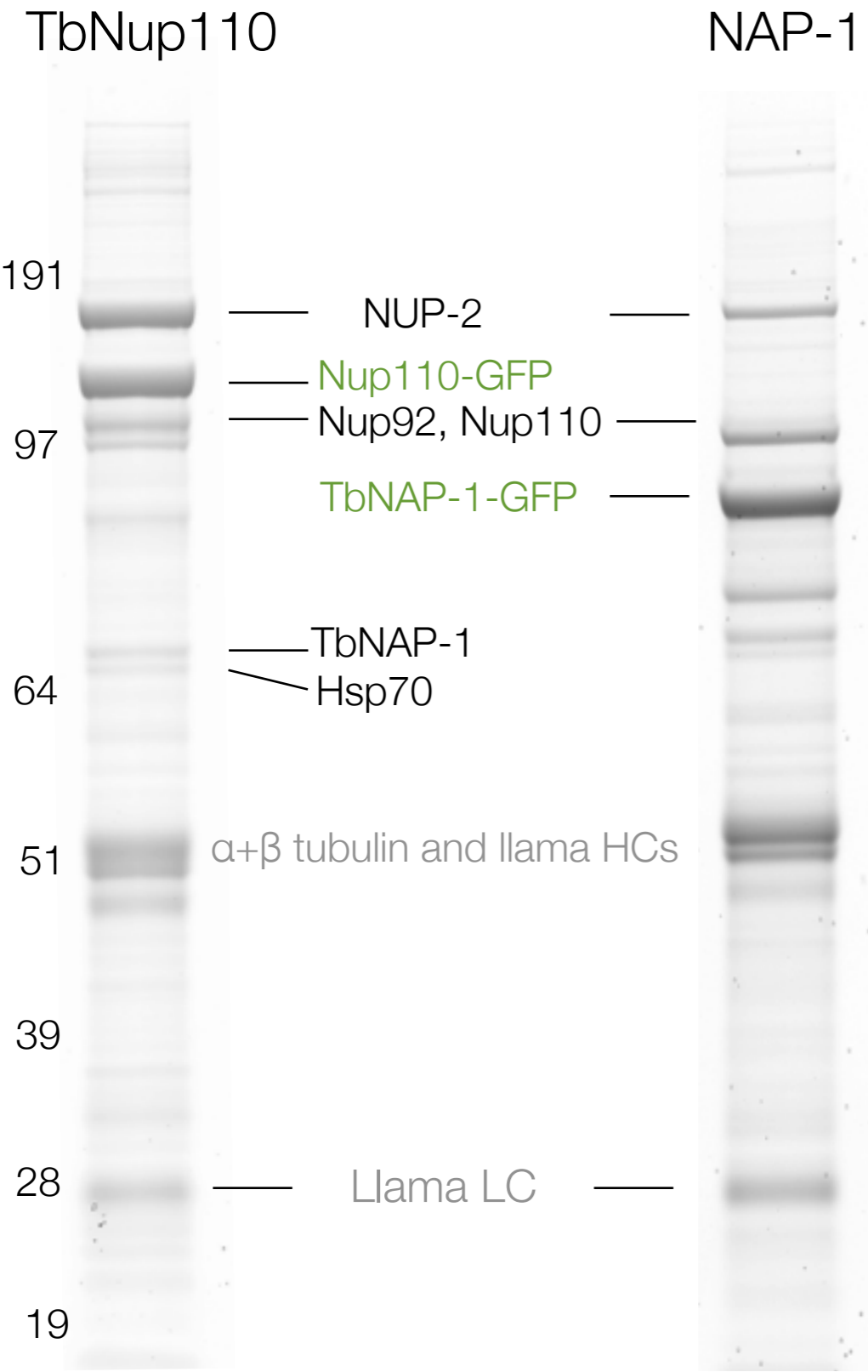
The nuclear pore complex and the nuclear envelope



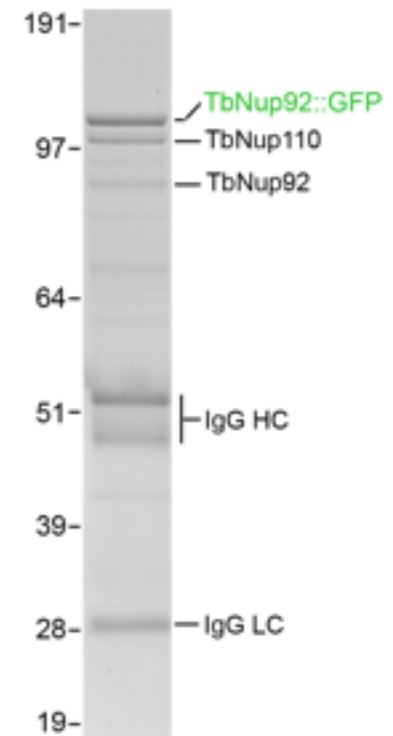
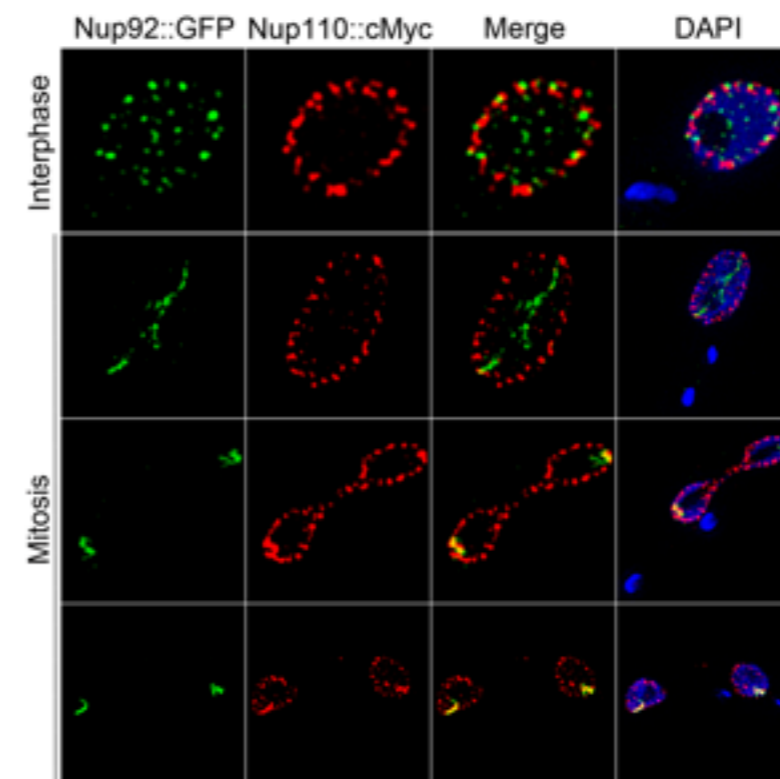
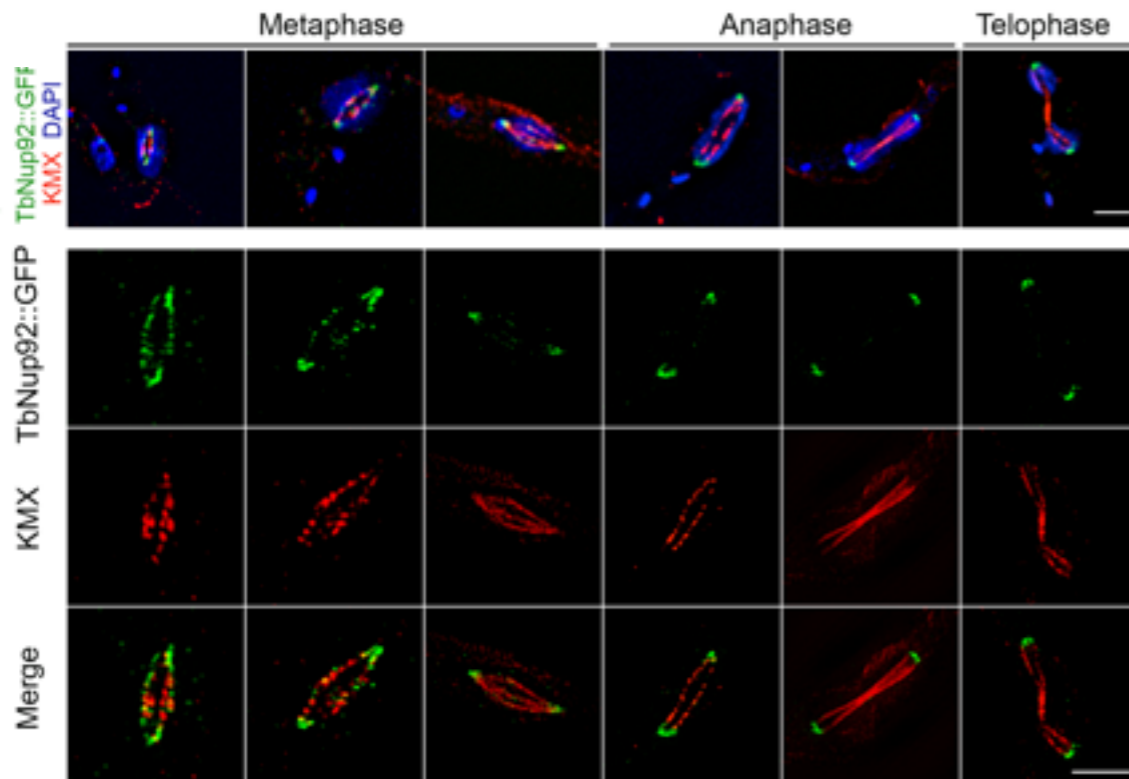
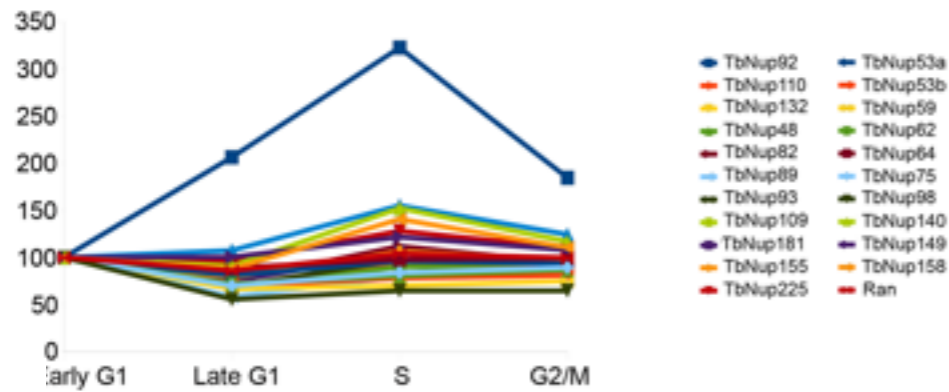


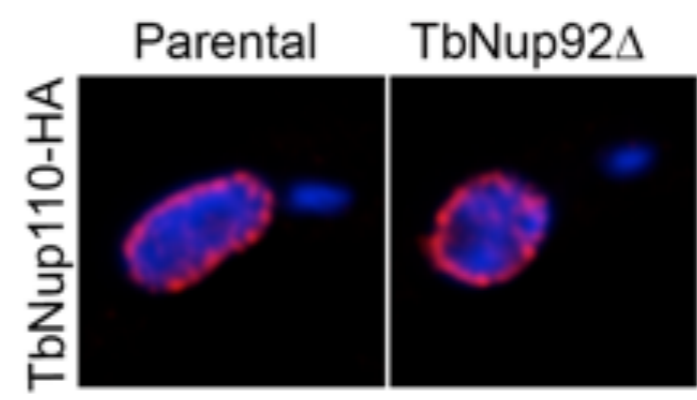
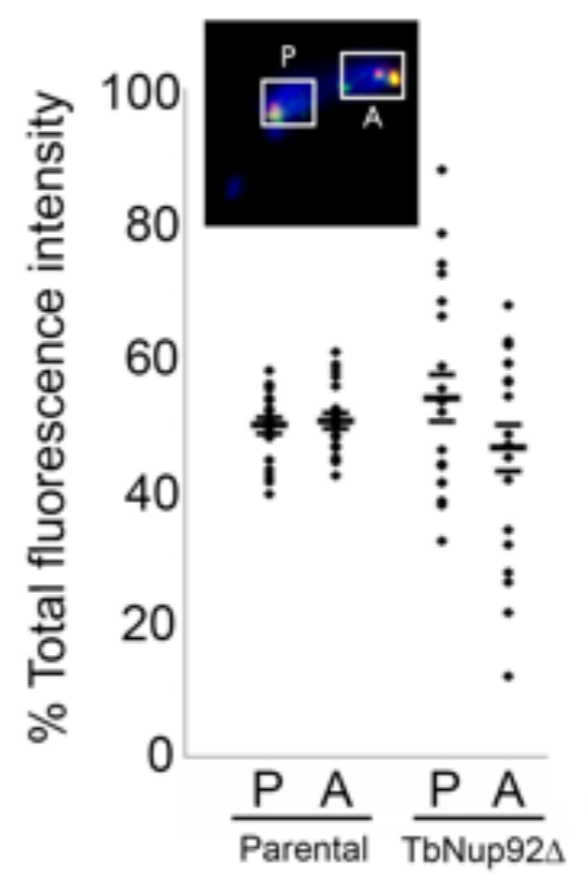
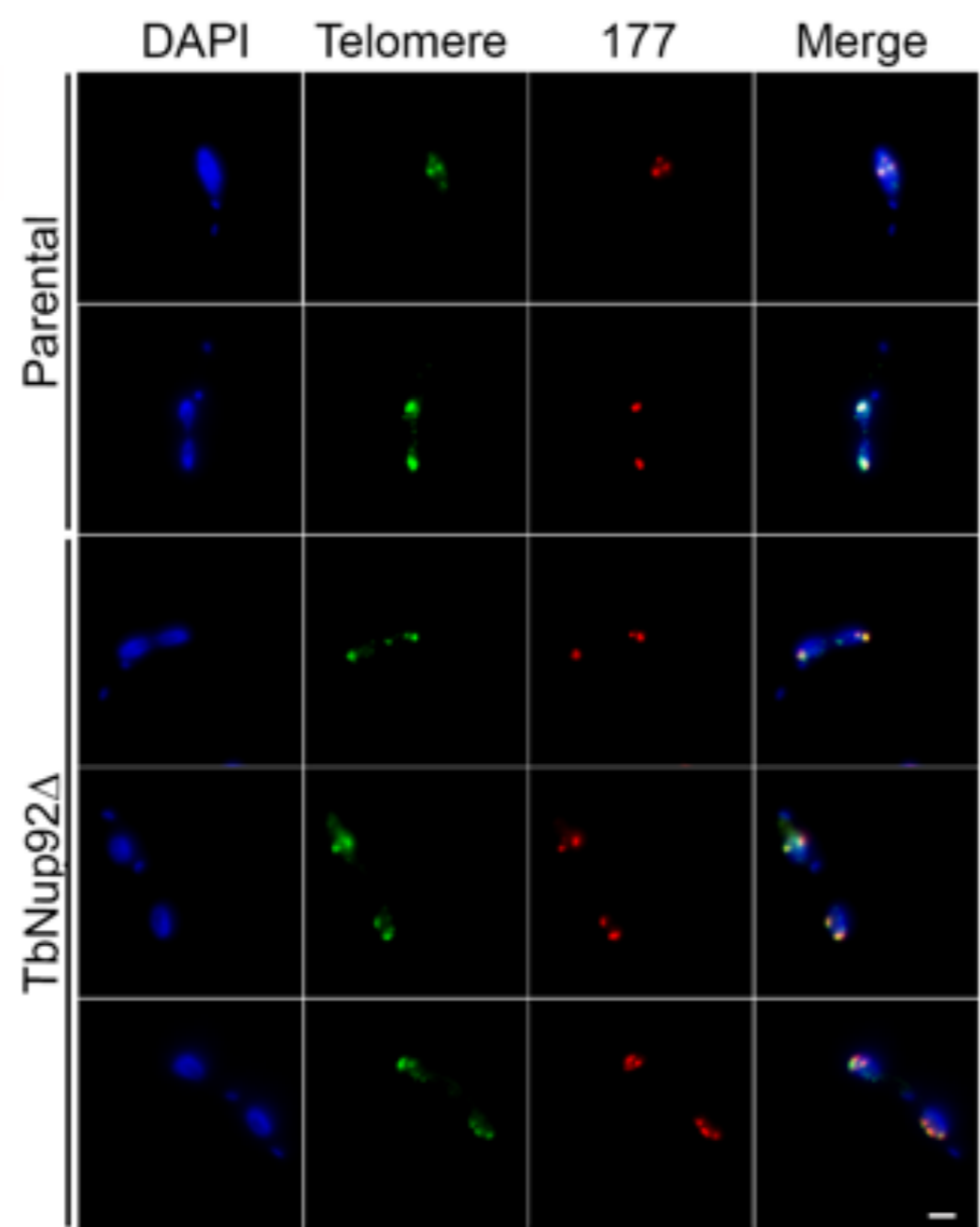


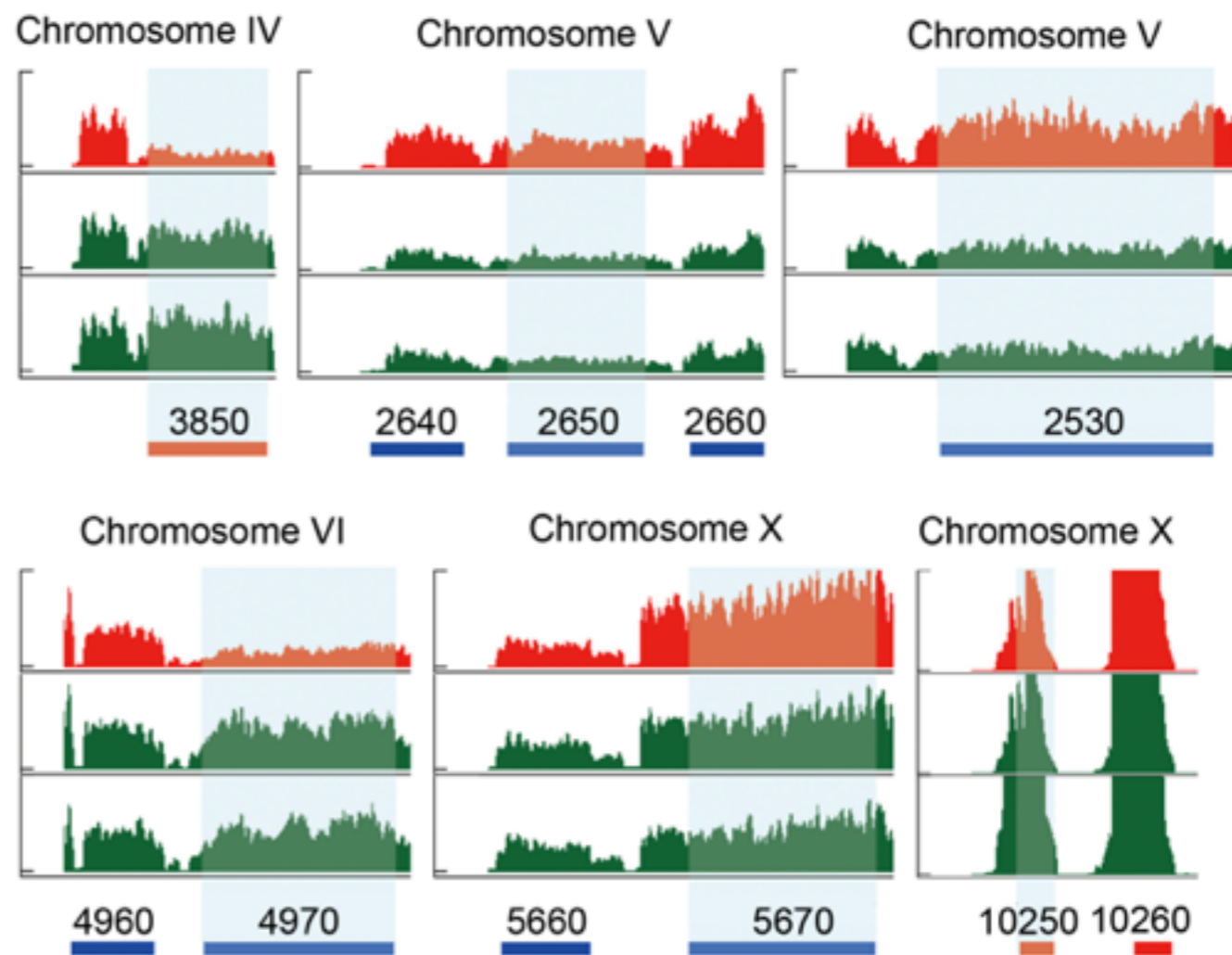
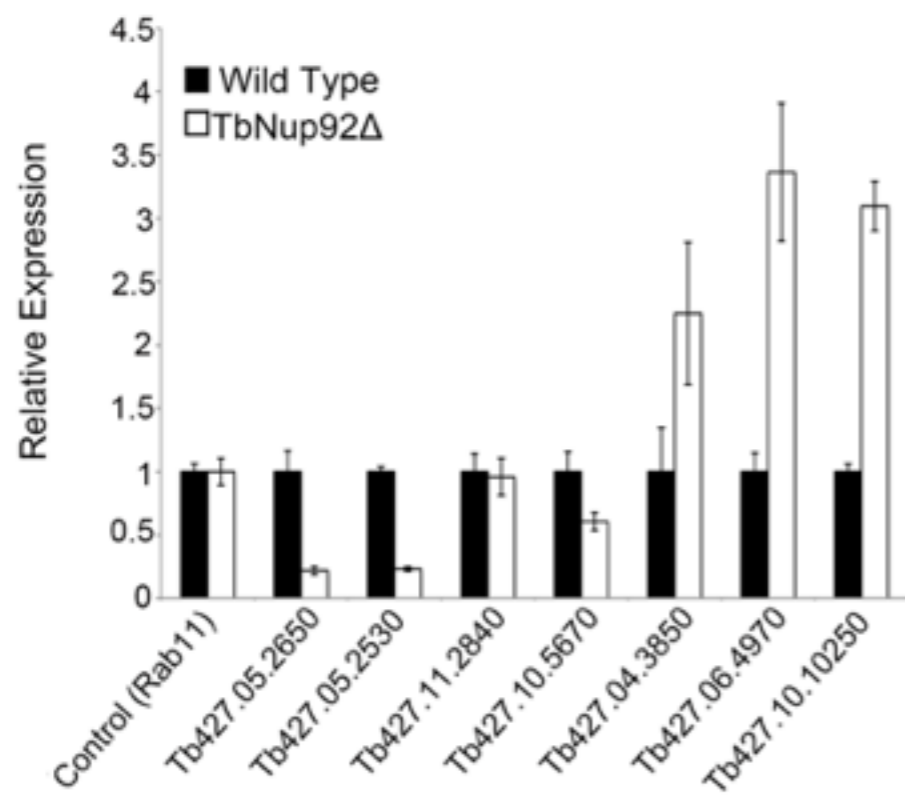
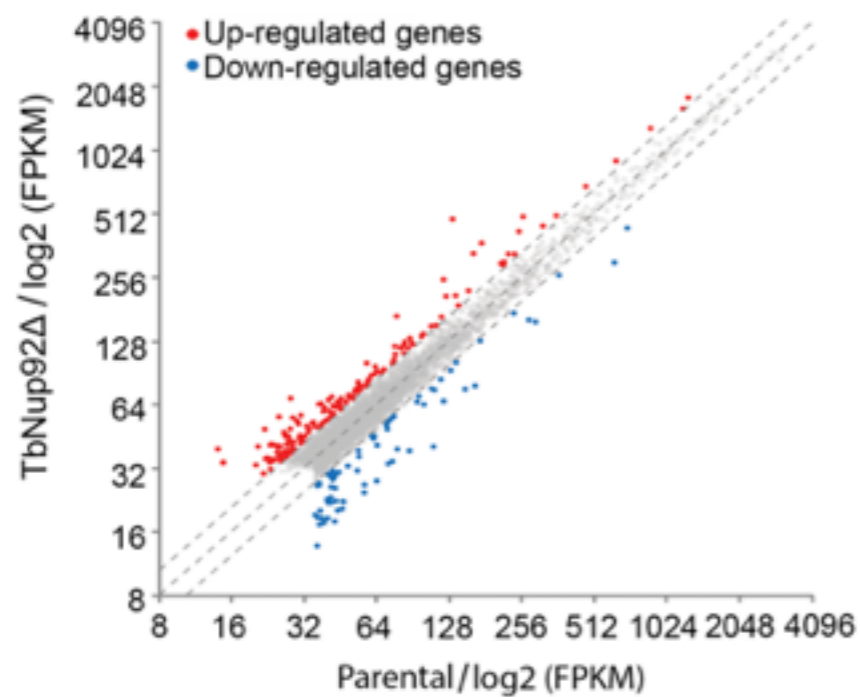
TbNup110 interacts with TbNup92, NUP-2 and NAP-1



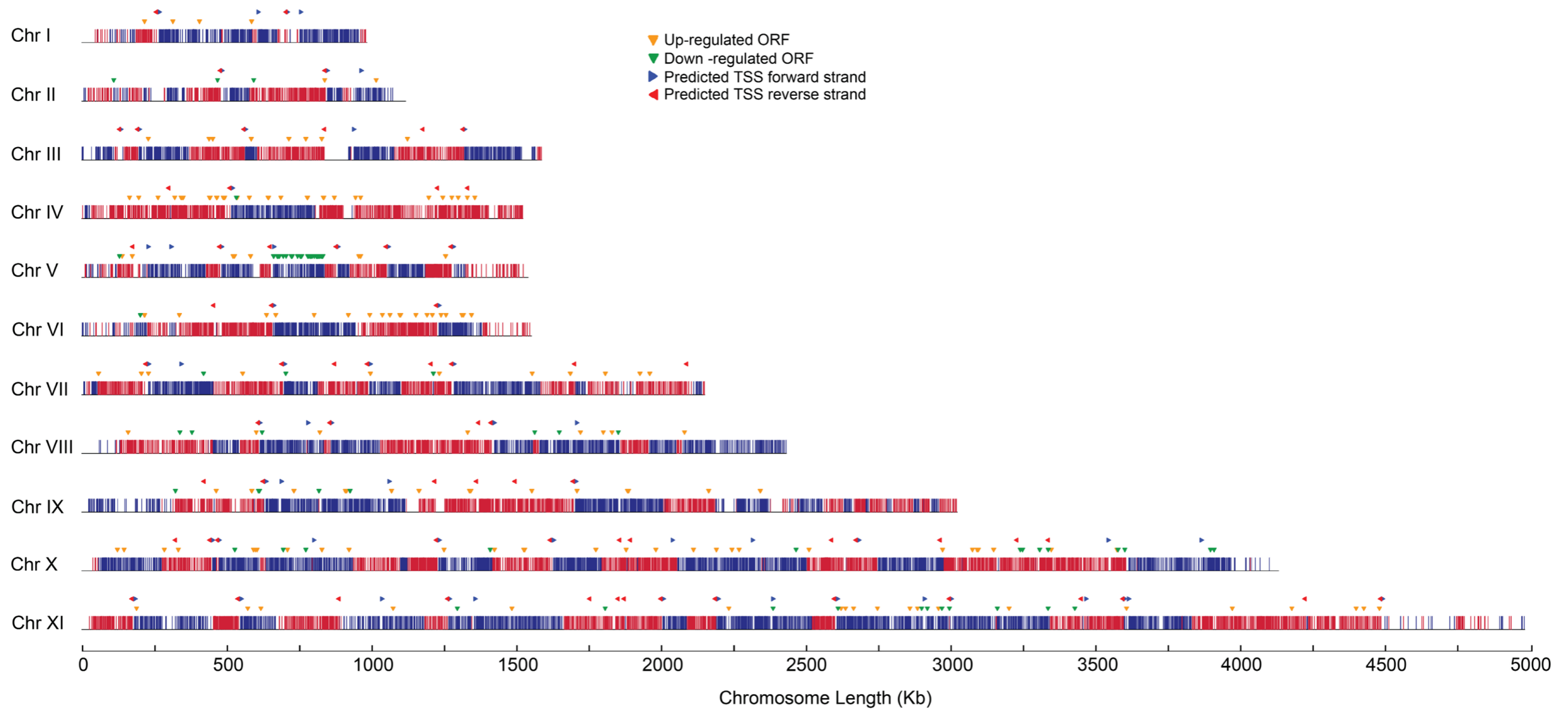
TbNup92 is a cell cycle-regulated protein and associates with the spindle



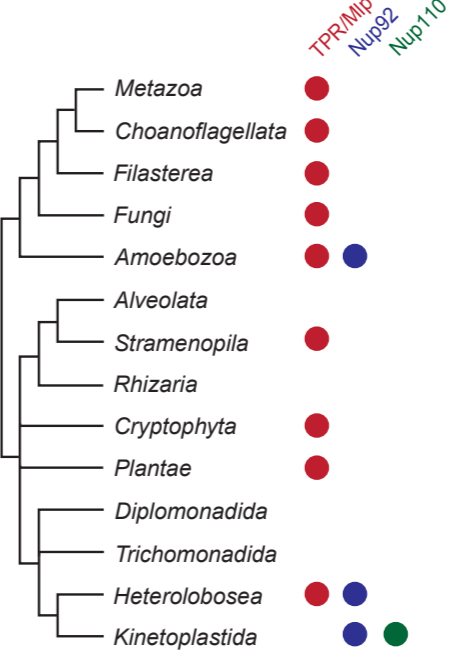
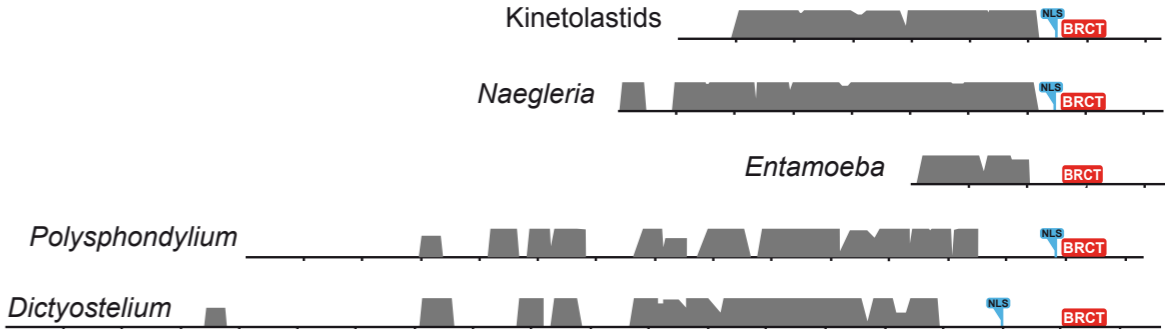
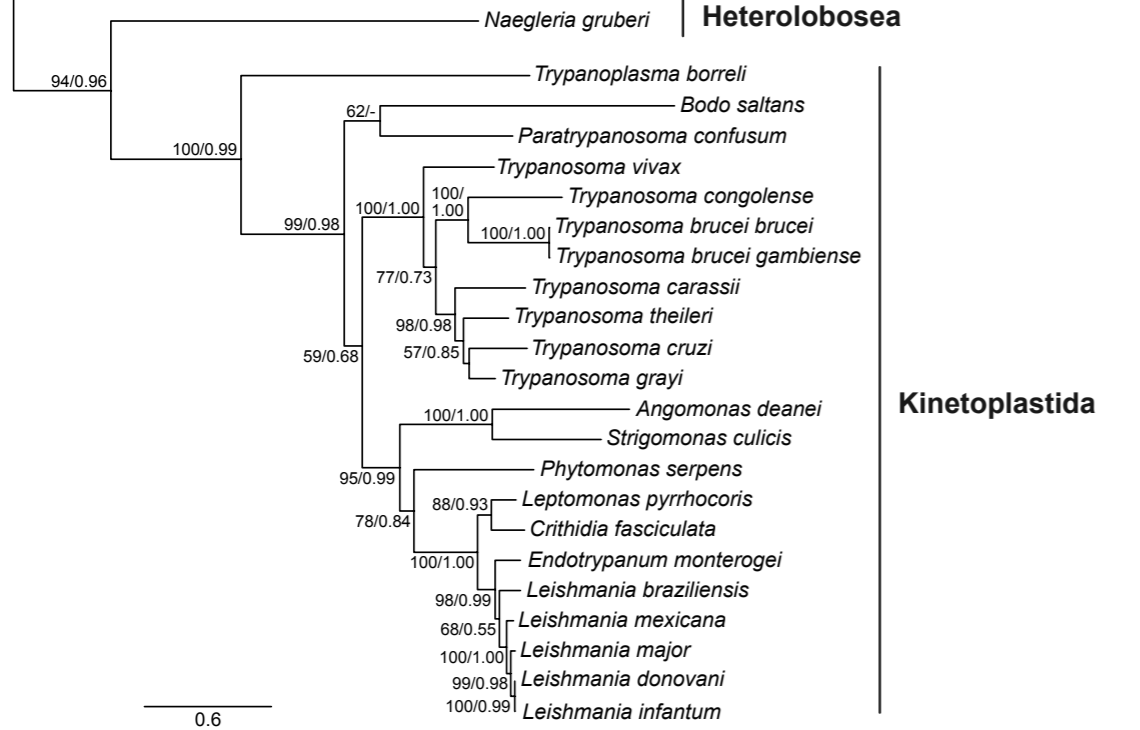
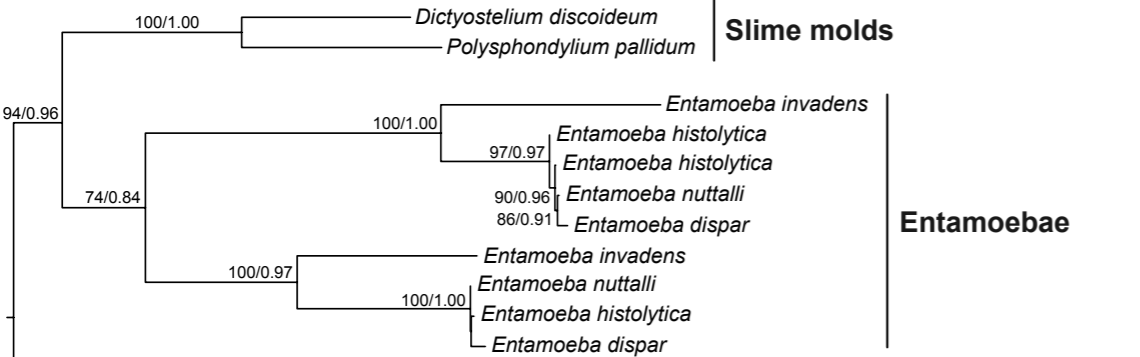




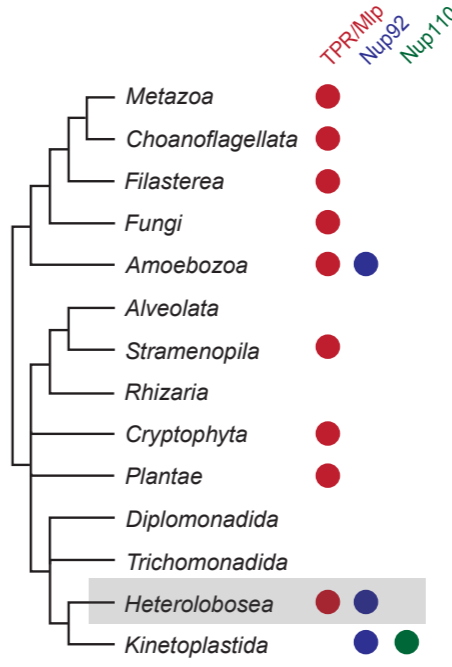
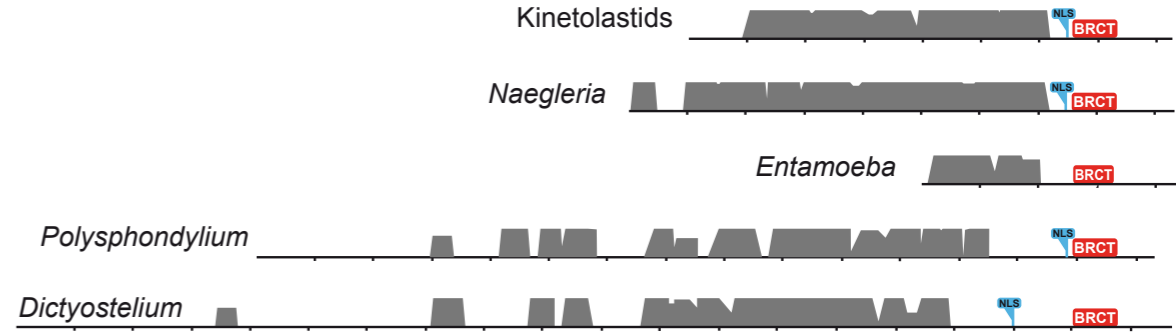
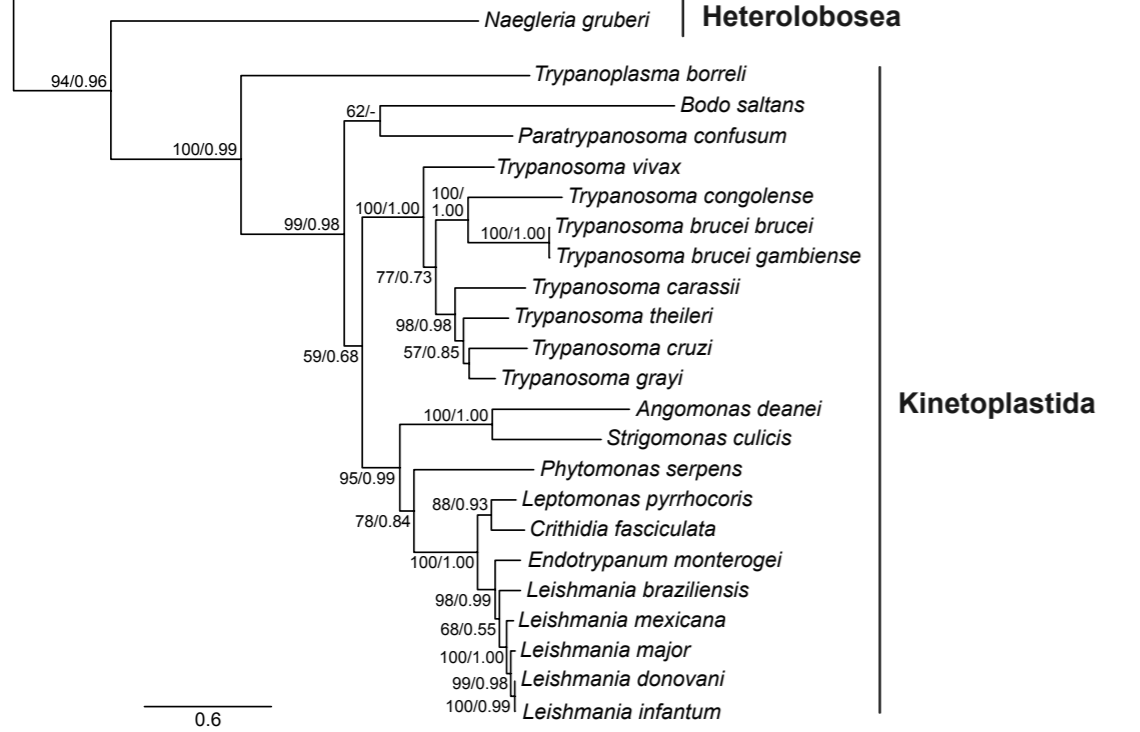
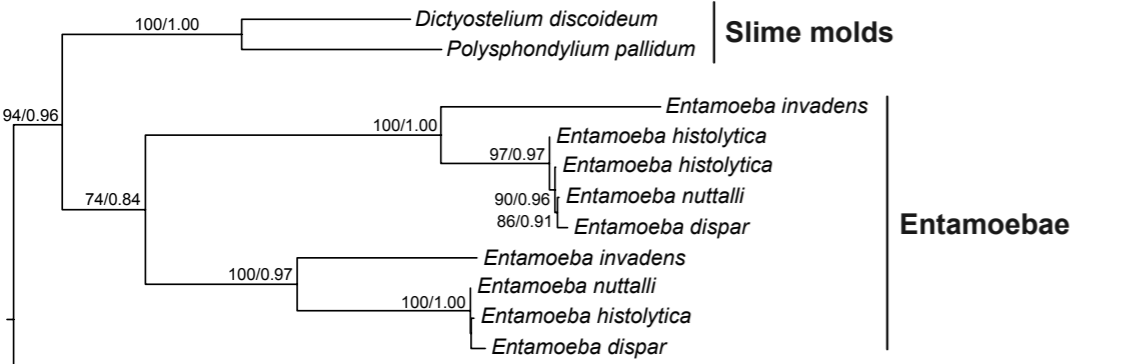
TbNup92 modulates mRNA levels, but not promoter activity



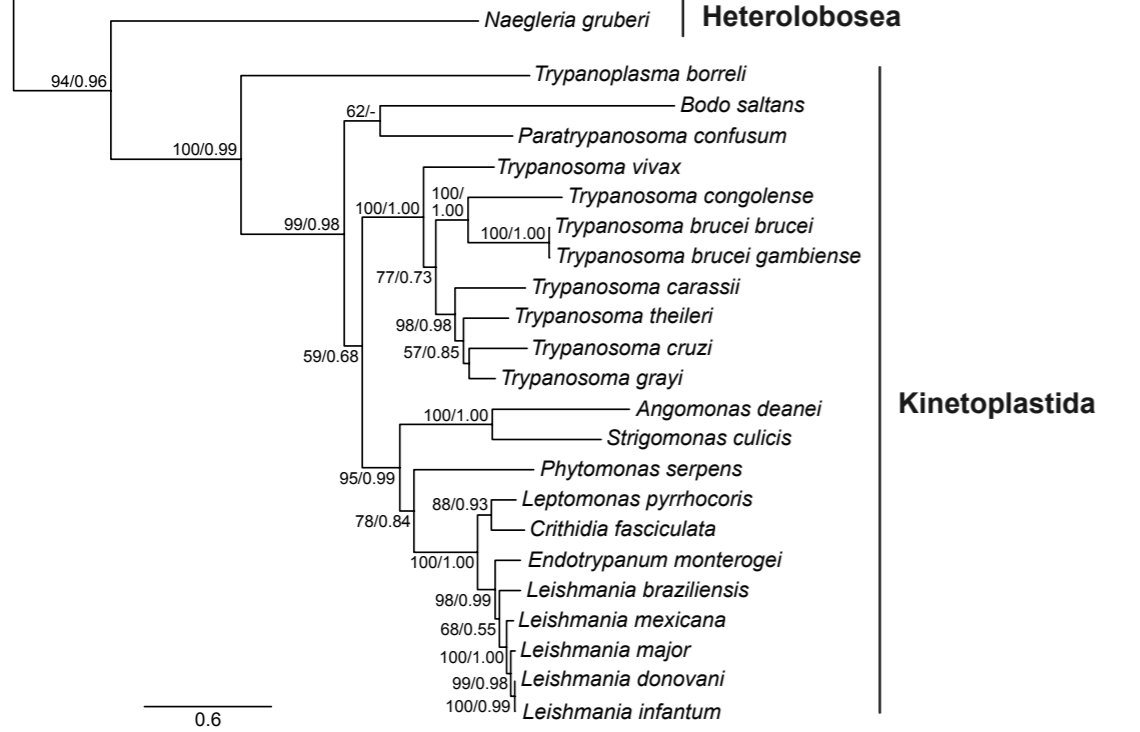
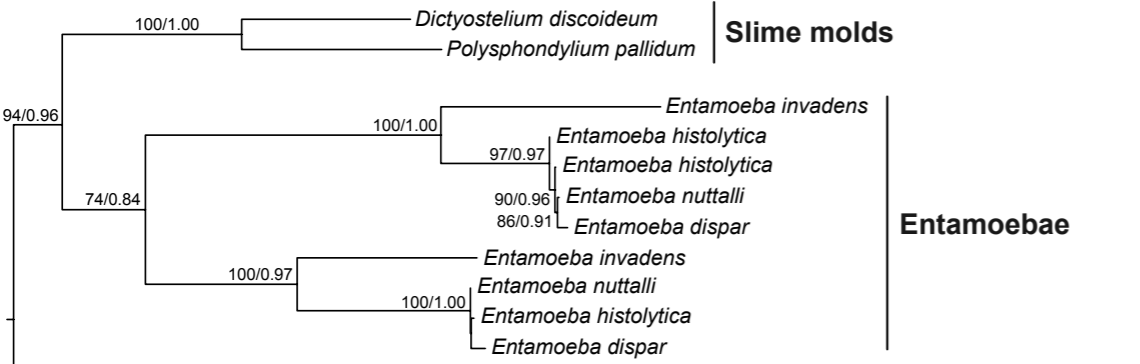
Evolution of TbNup92



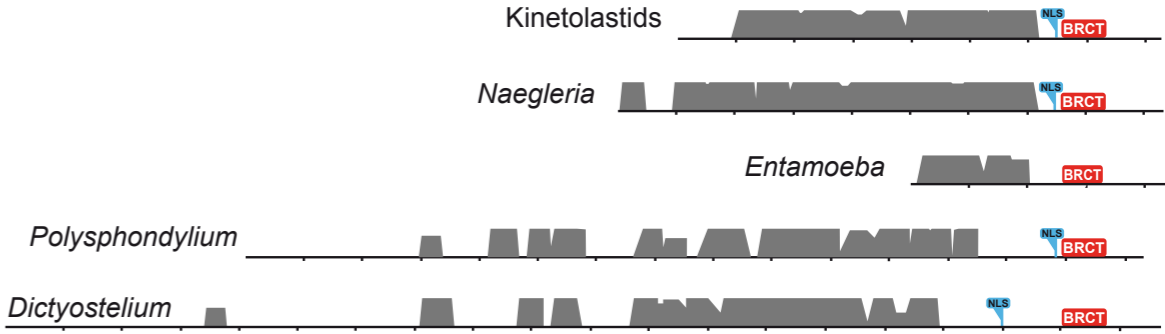
Evolution of TbNup92



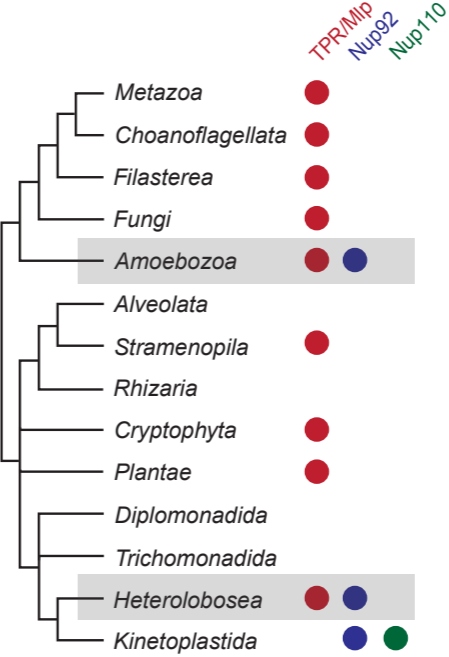
Evolution of TbNup92



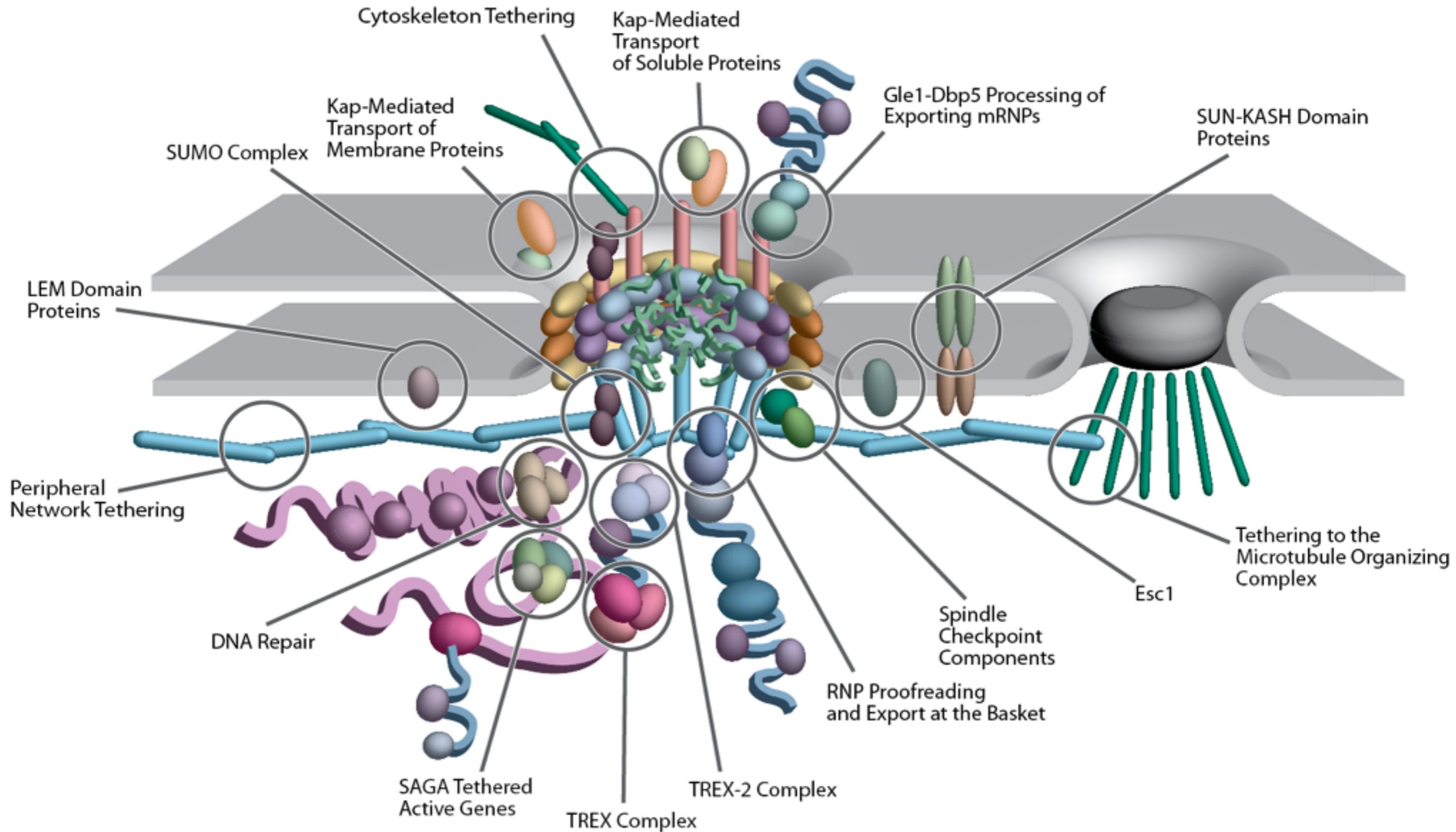
Amoebozoa



Excavata

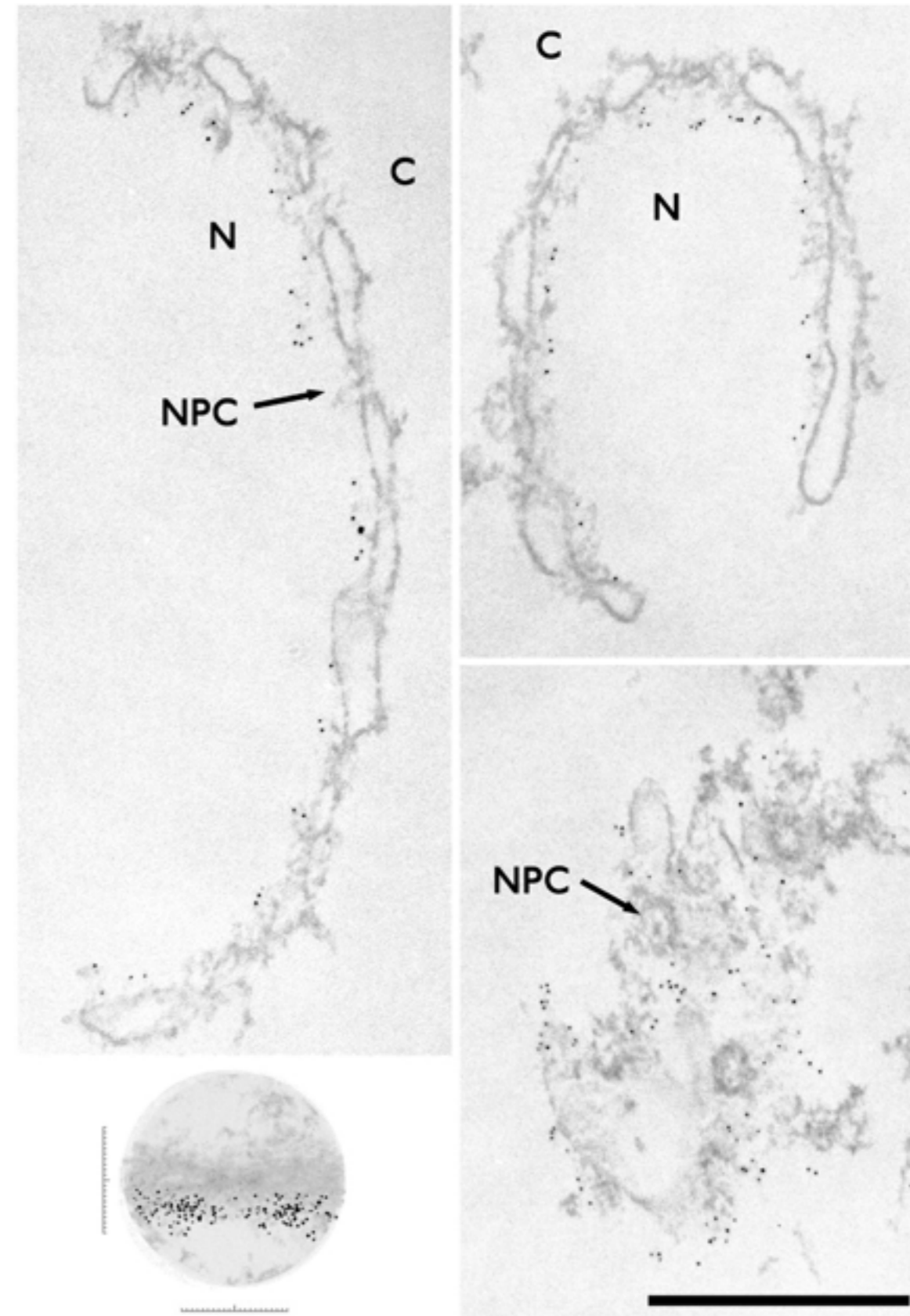
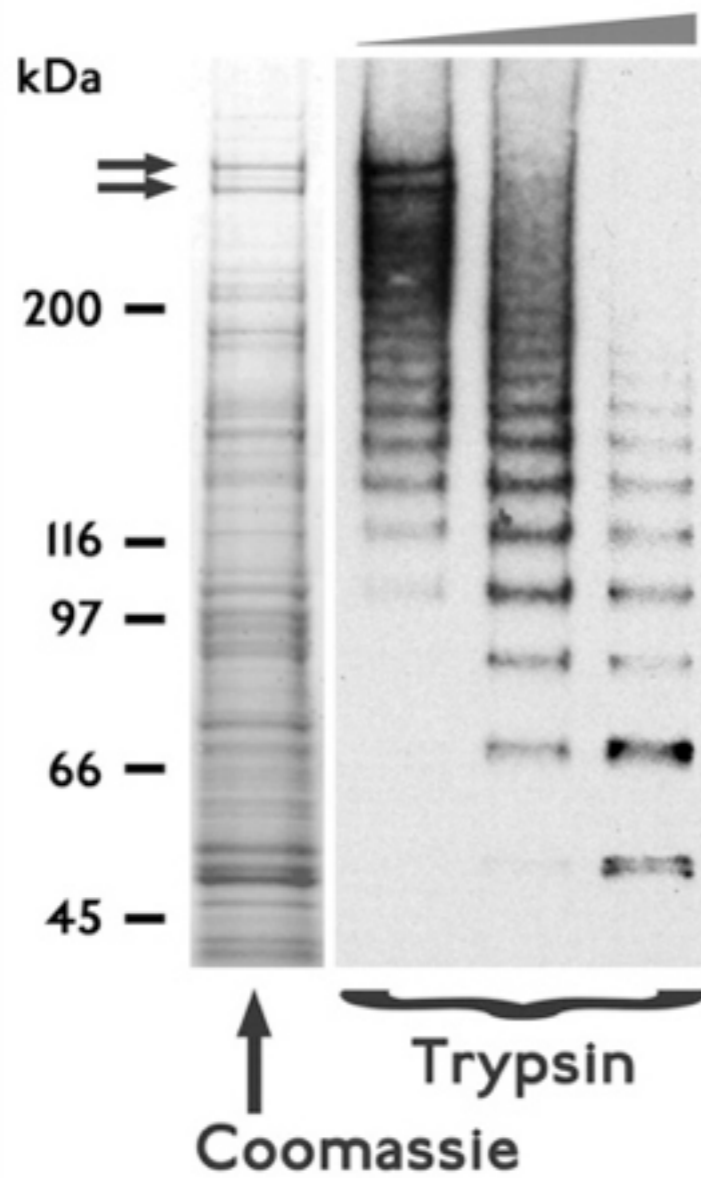
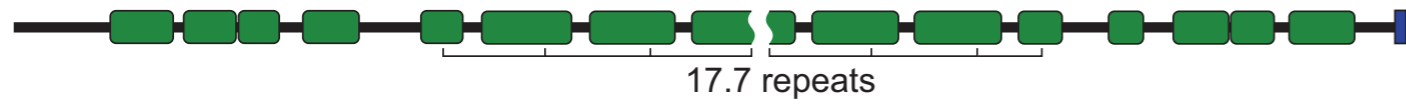


The nuclear pore complex and the nuclear envelope

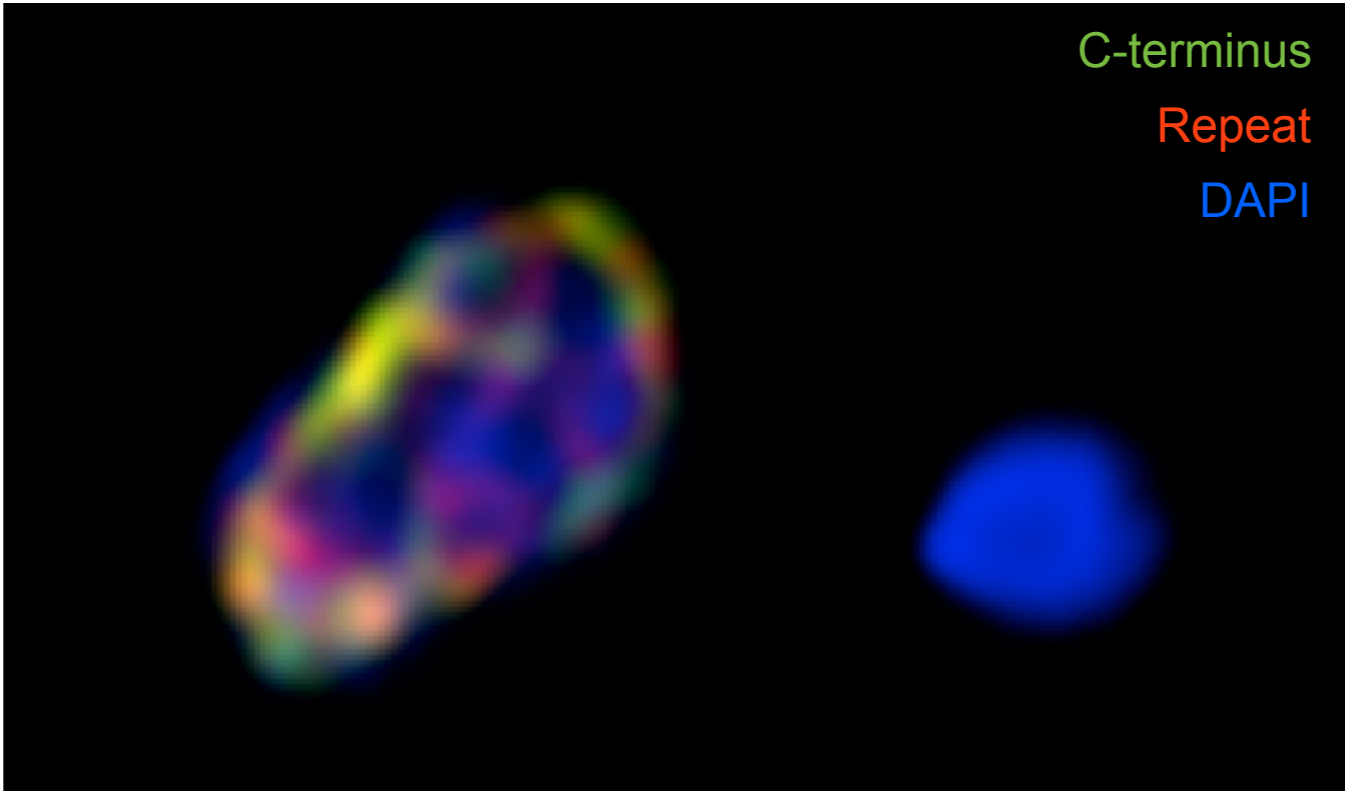
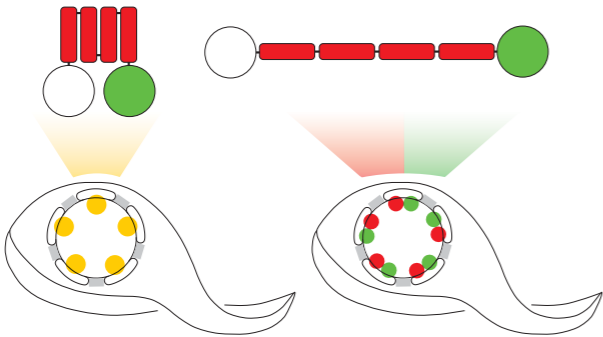
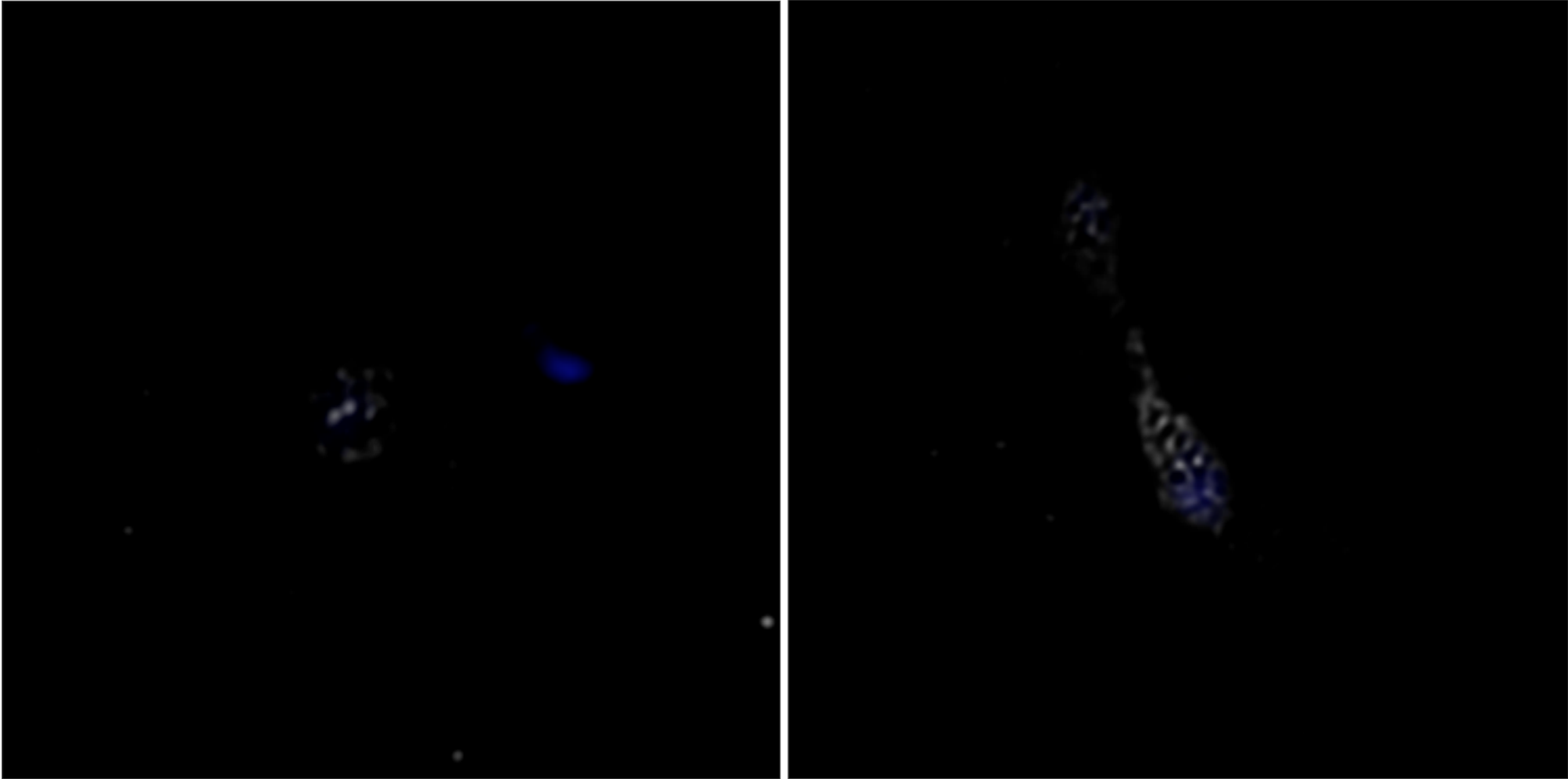


NUP-1

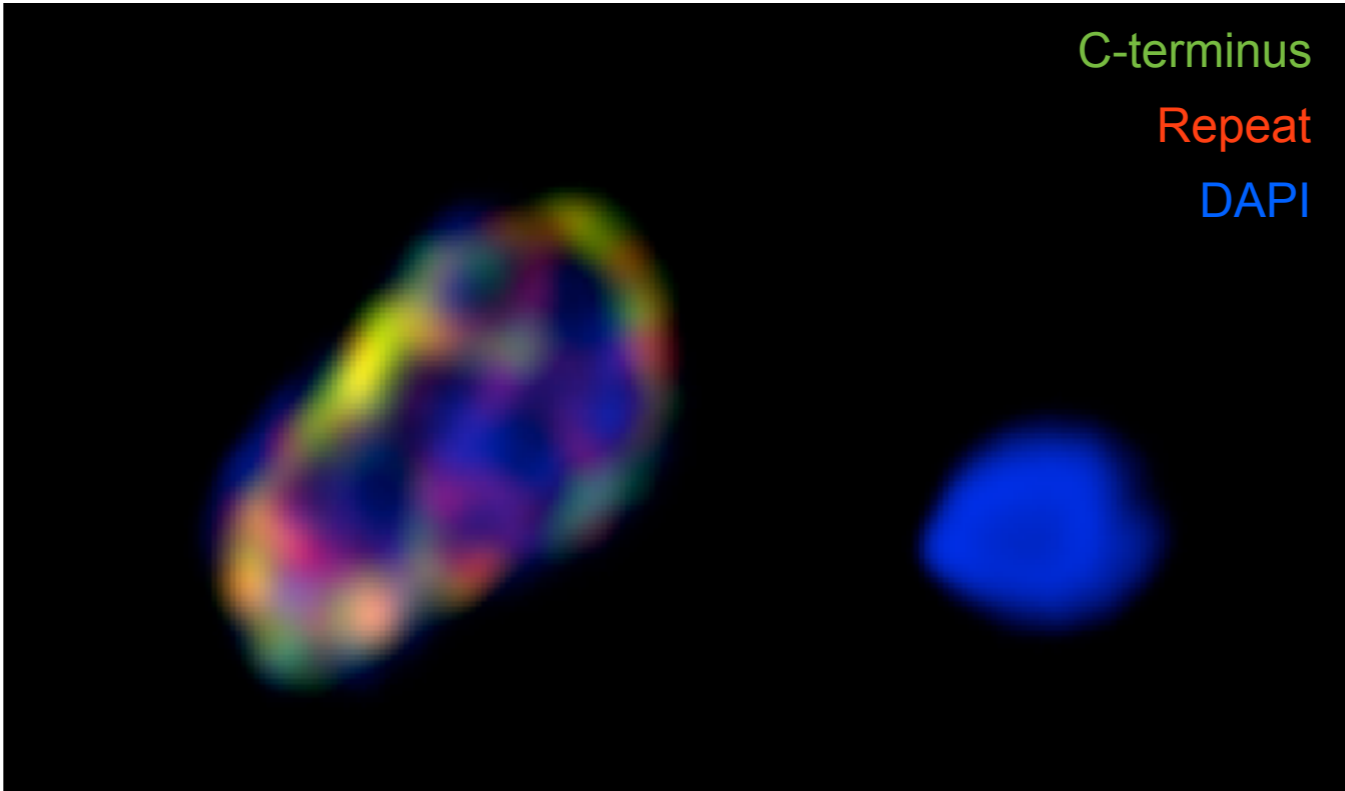
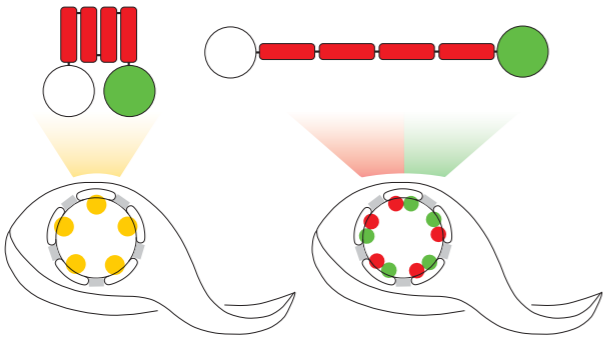
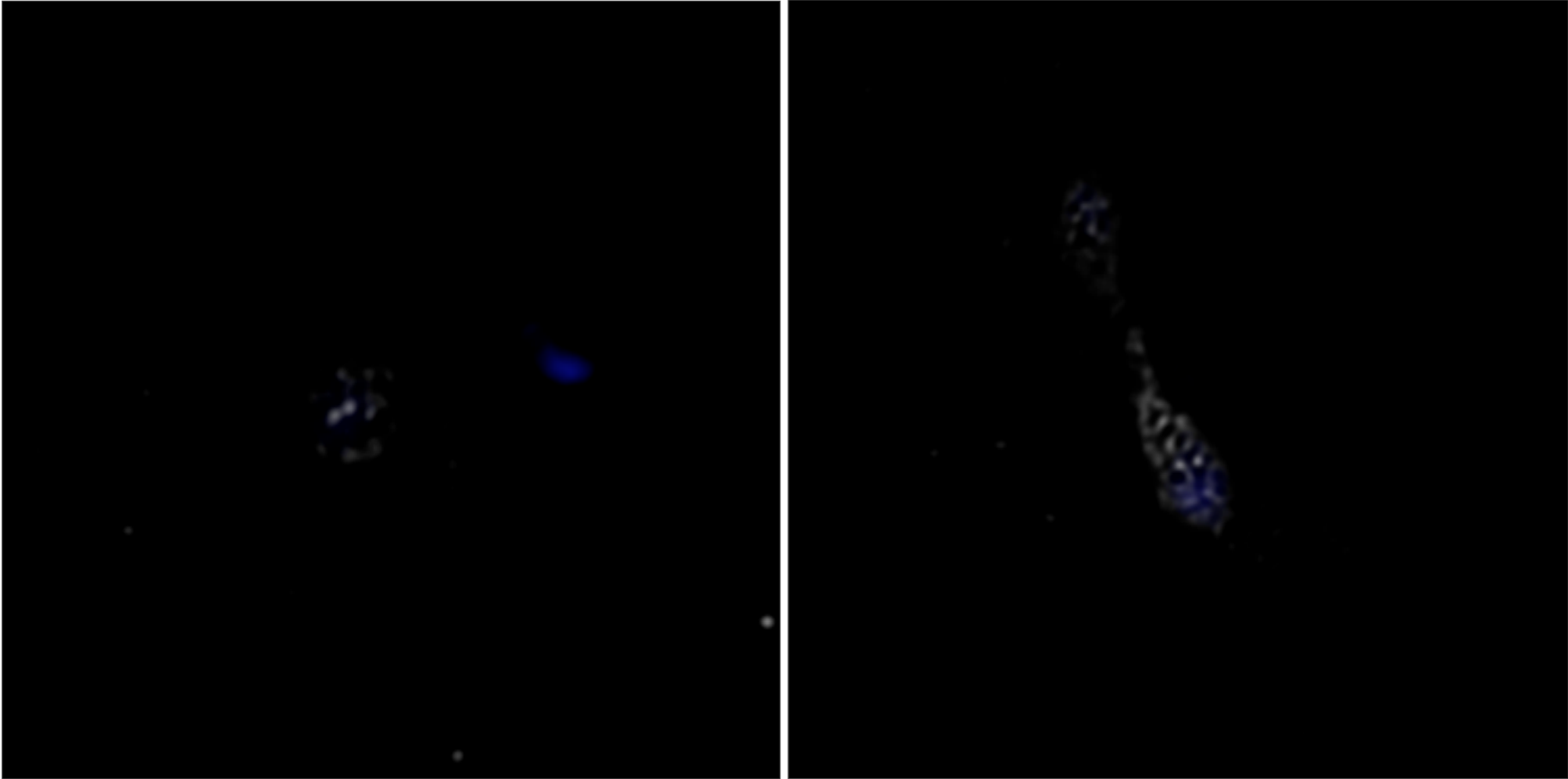
~450kDa



NUP-1 forms a cage



NUP-1 forms a cage

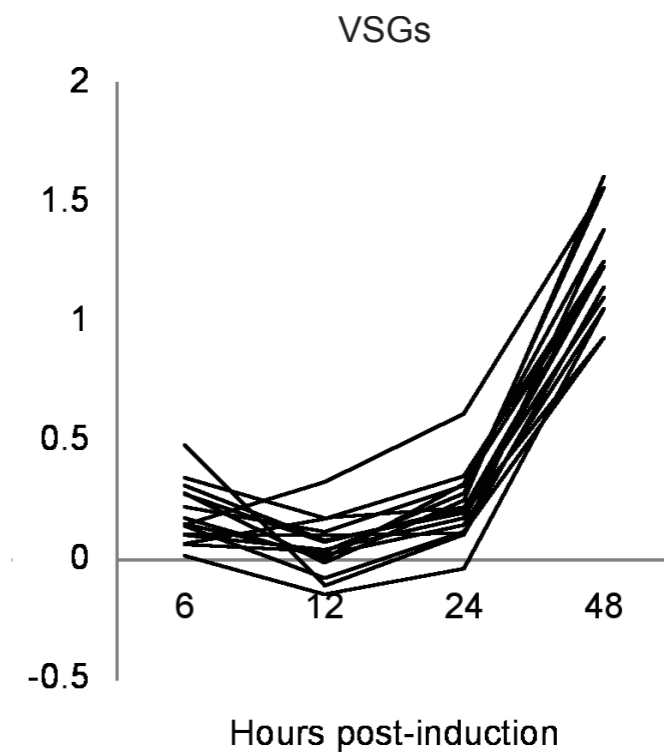
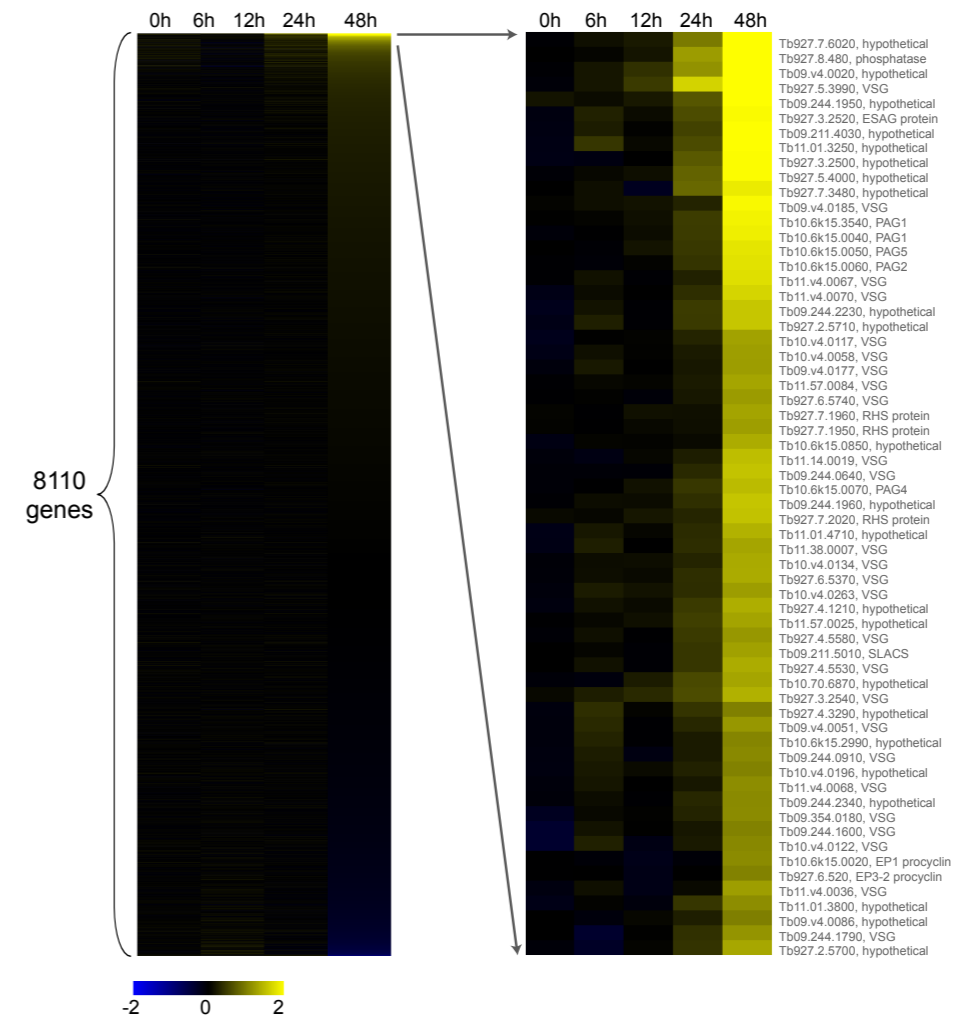
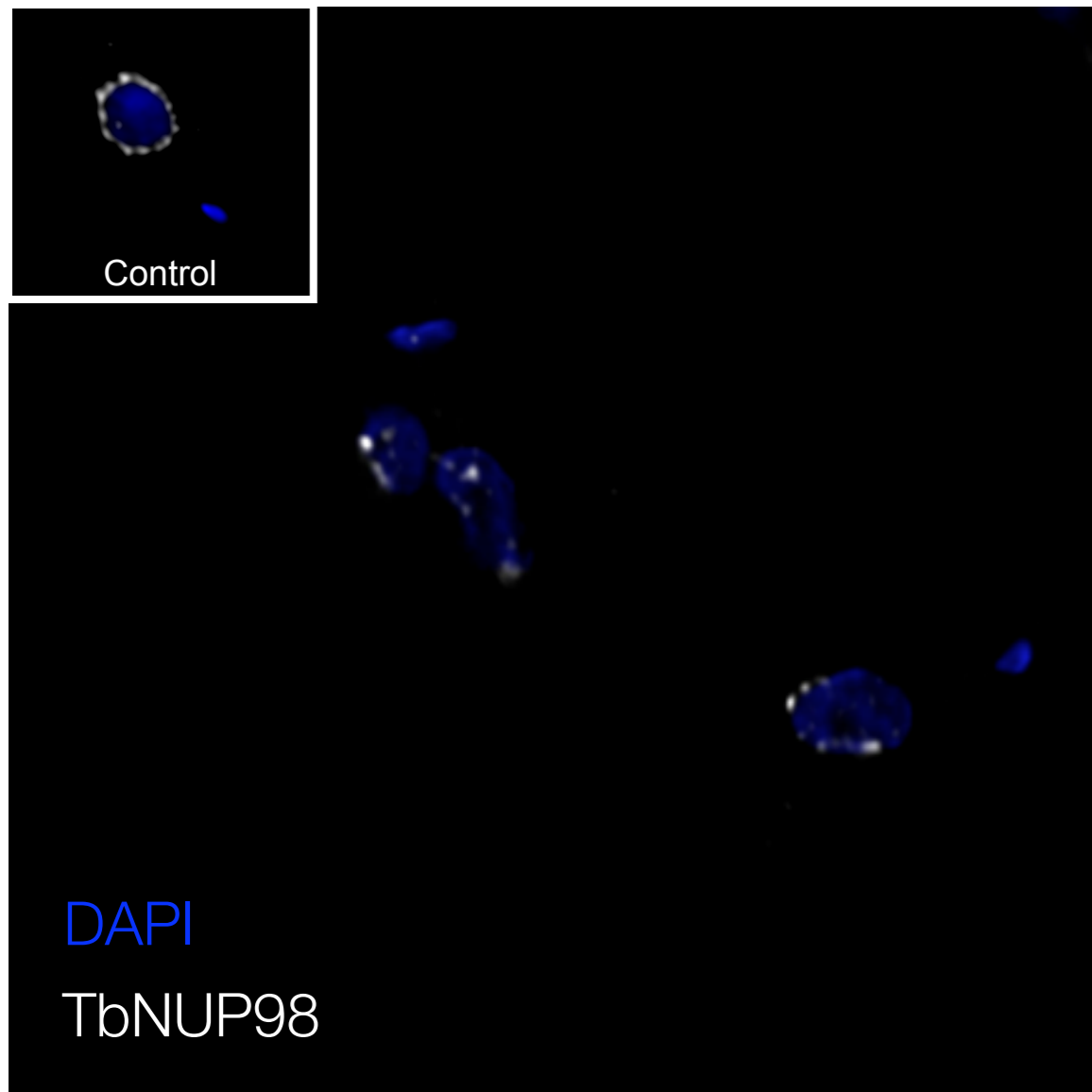


C-terminus

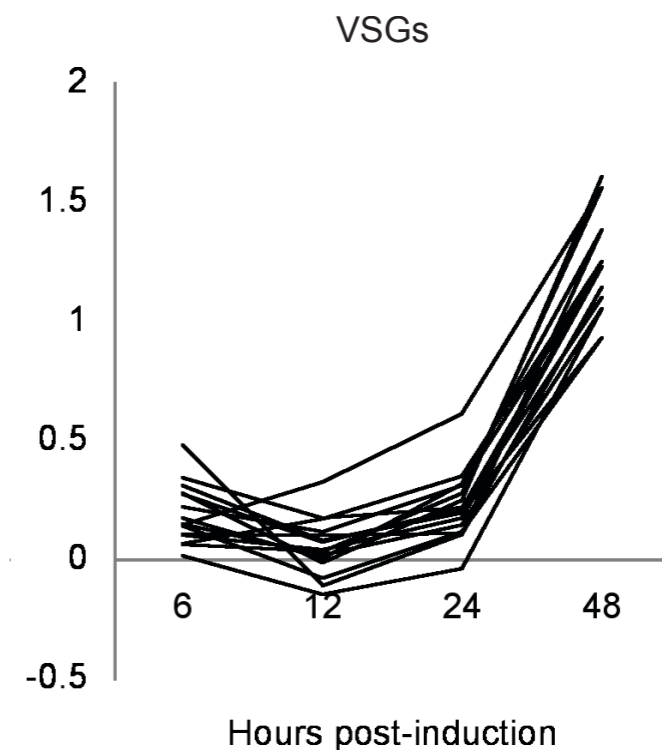
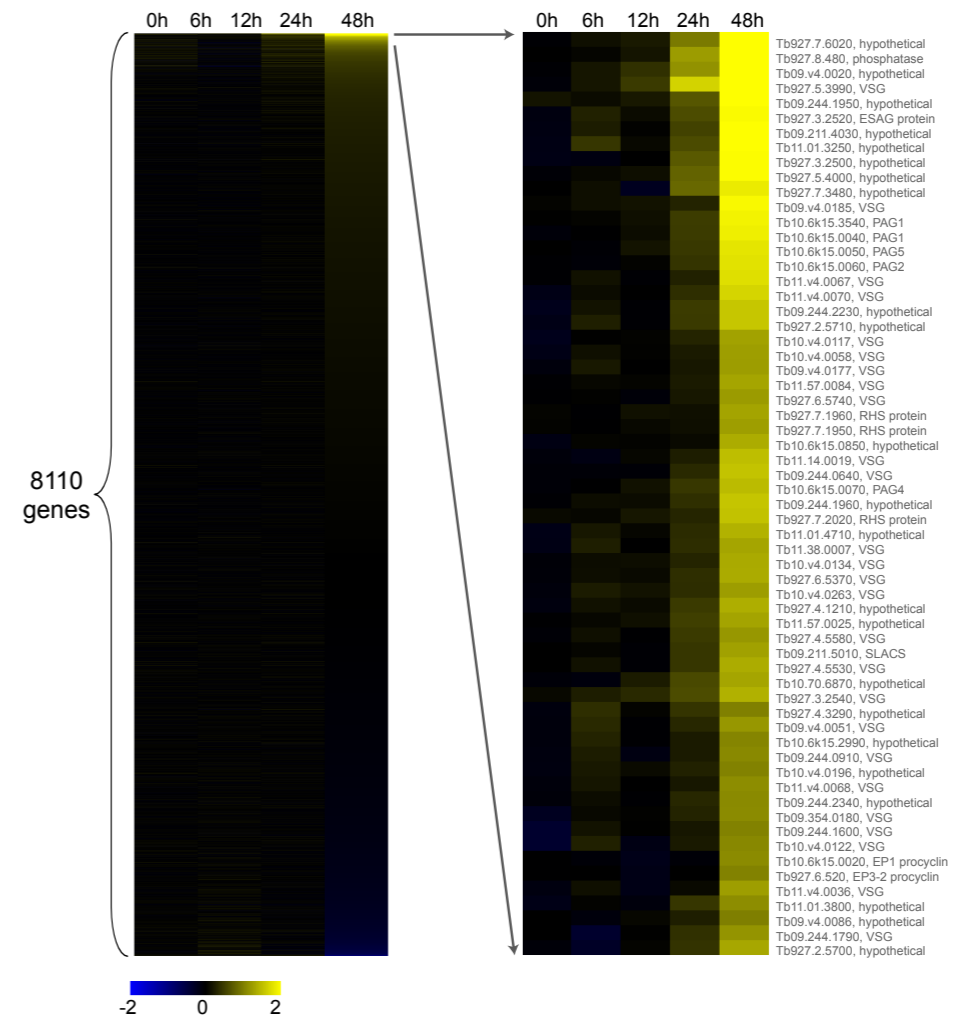
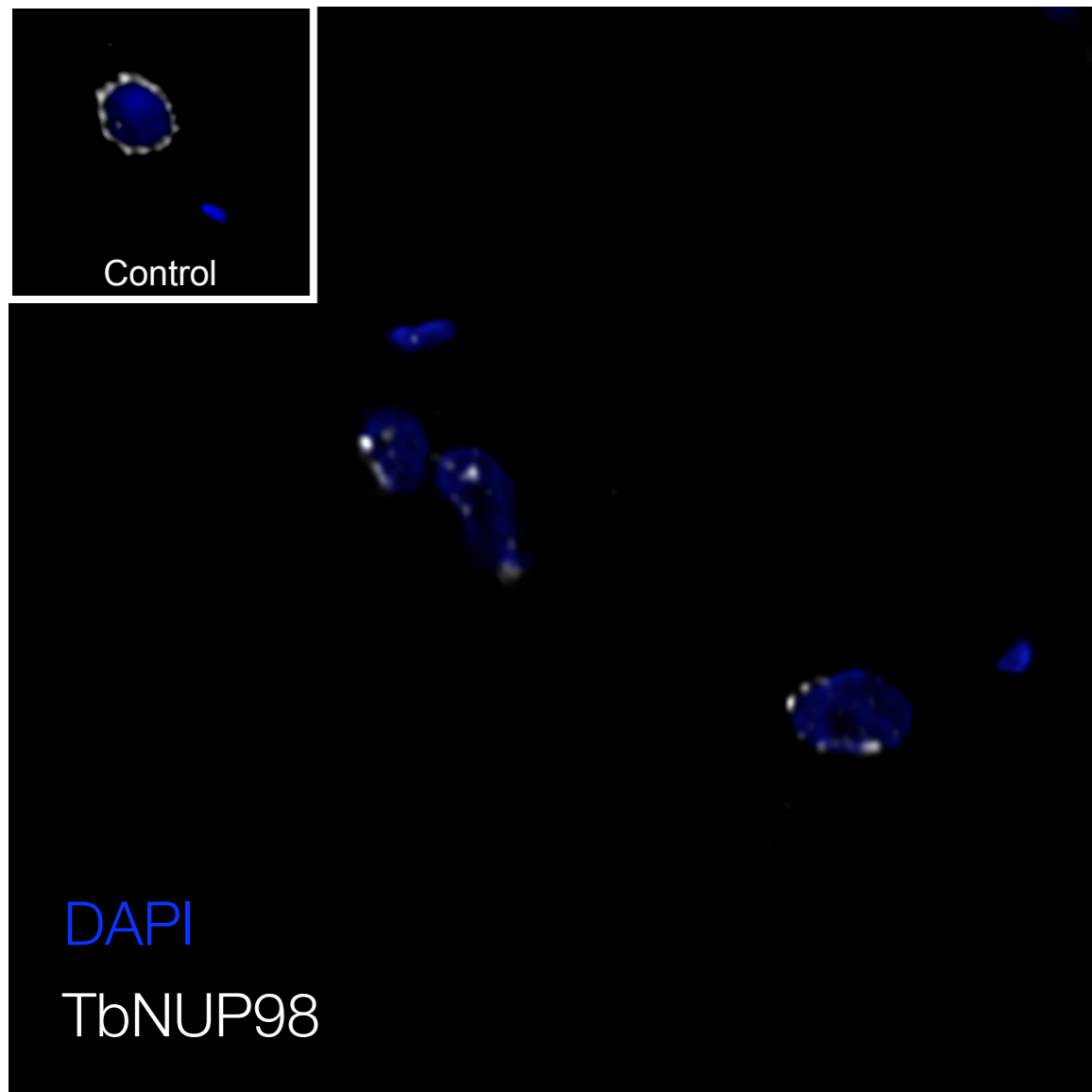
Repeat

DAPI

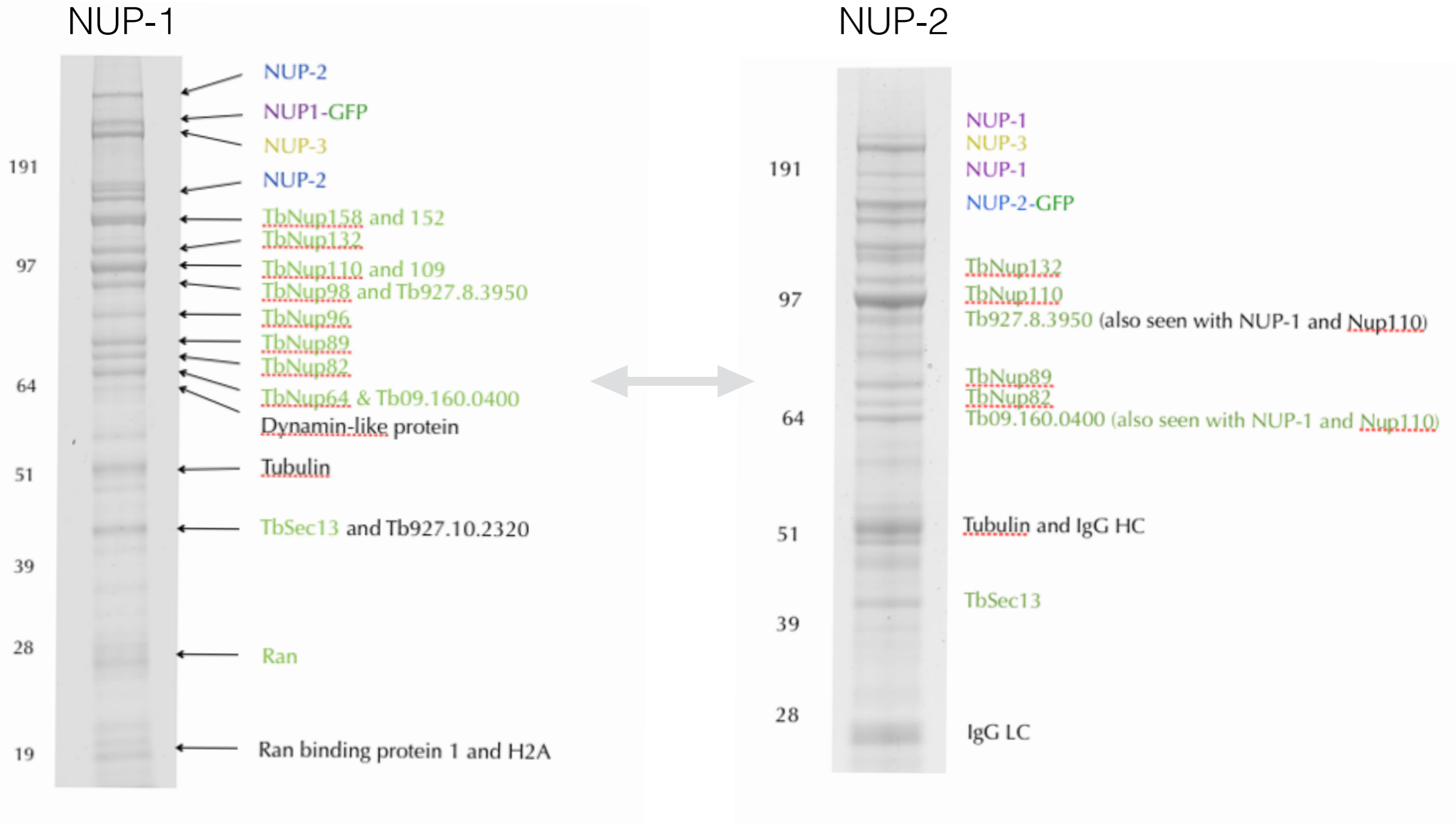
Nuclear pore positioning and VSG repression requires NUP-1



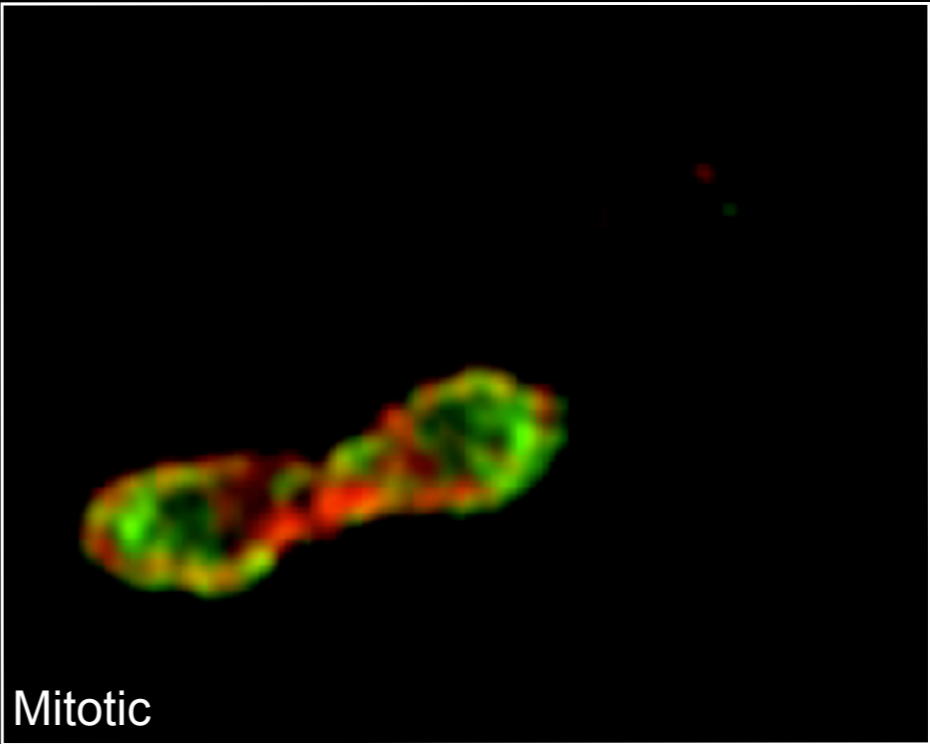
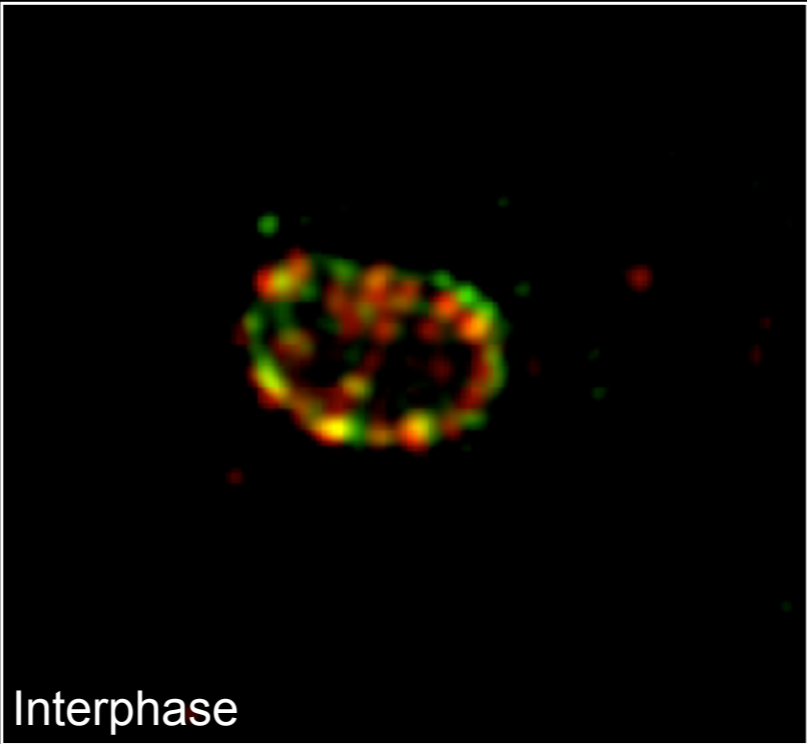
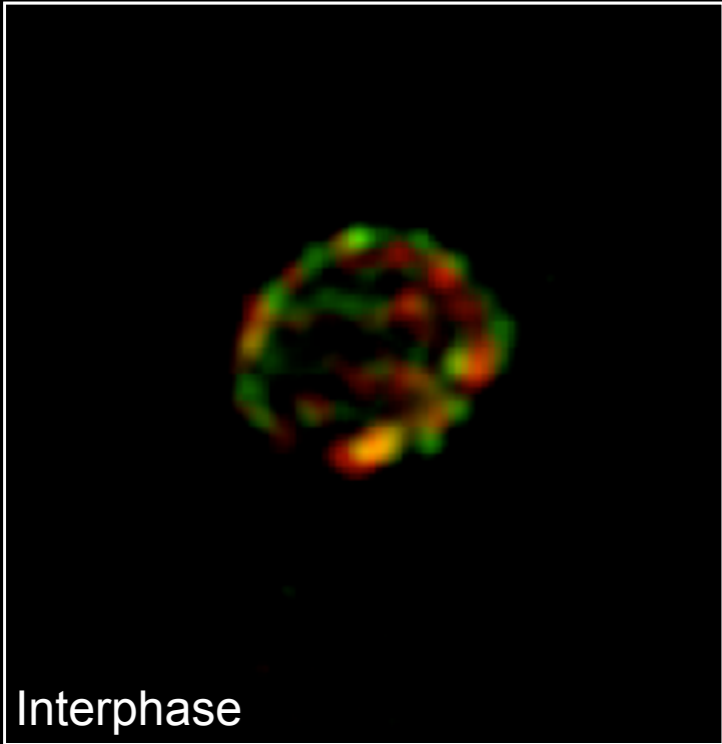
Nuclear pore positioning and VSG repression requires NUP-1



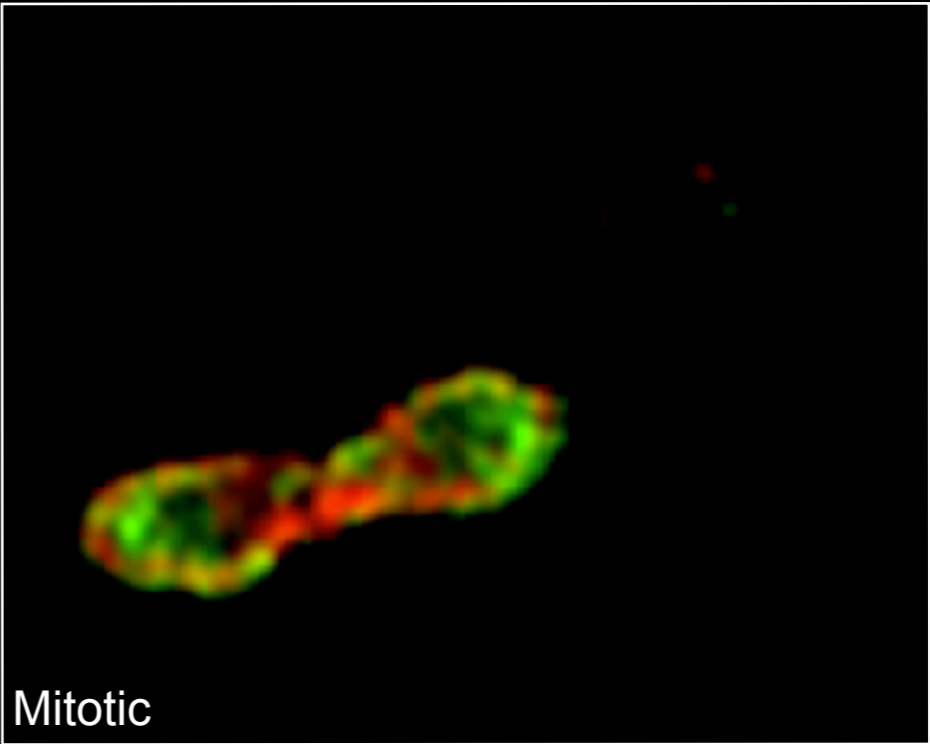
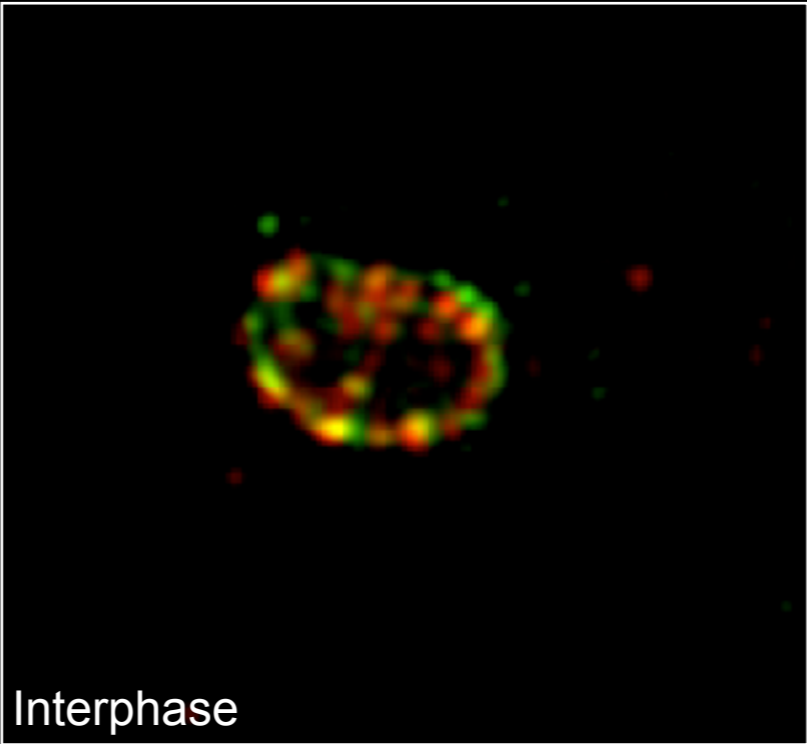
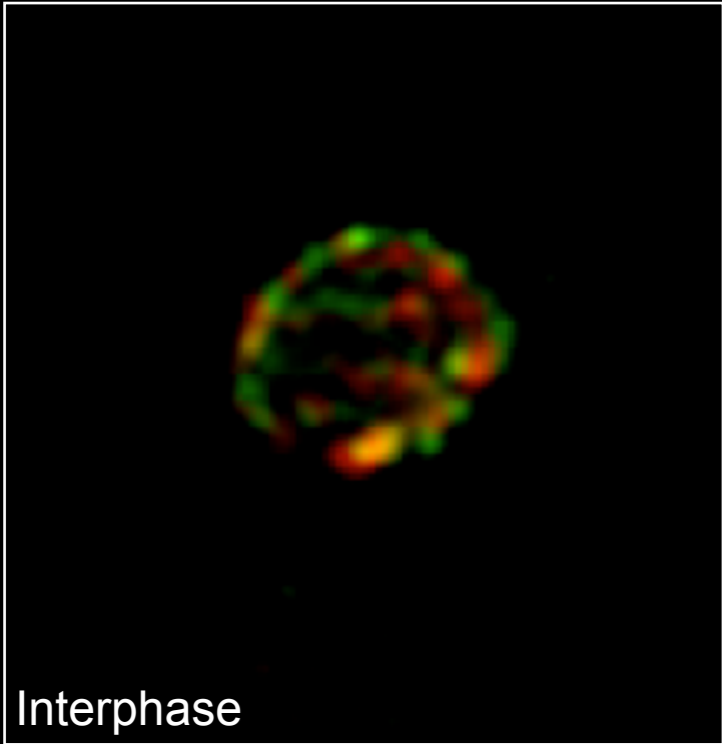
NUP-1 interacts with the NPC and additional IF proteins



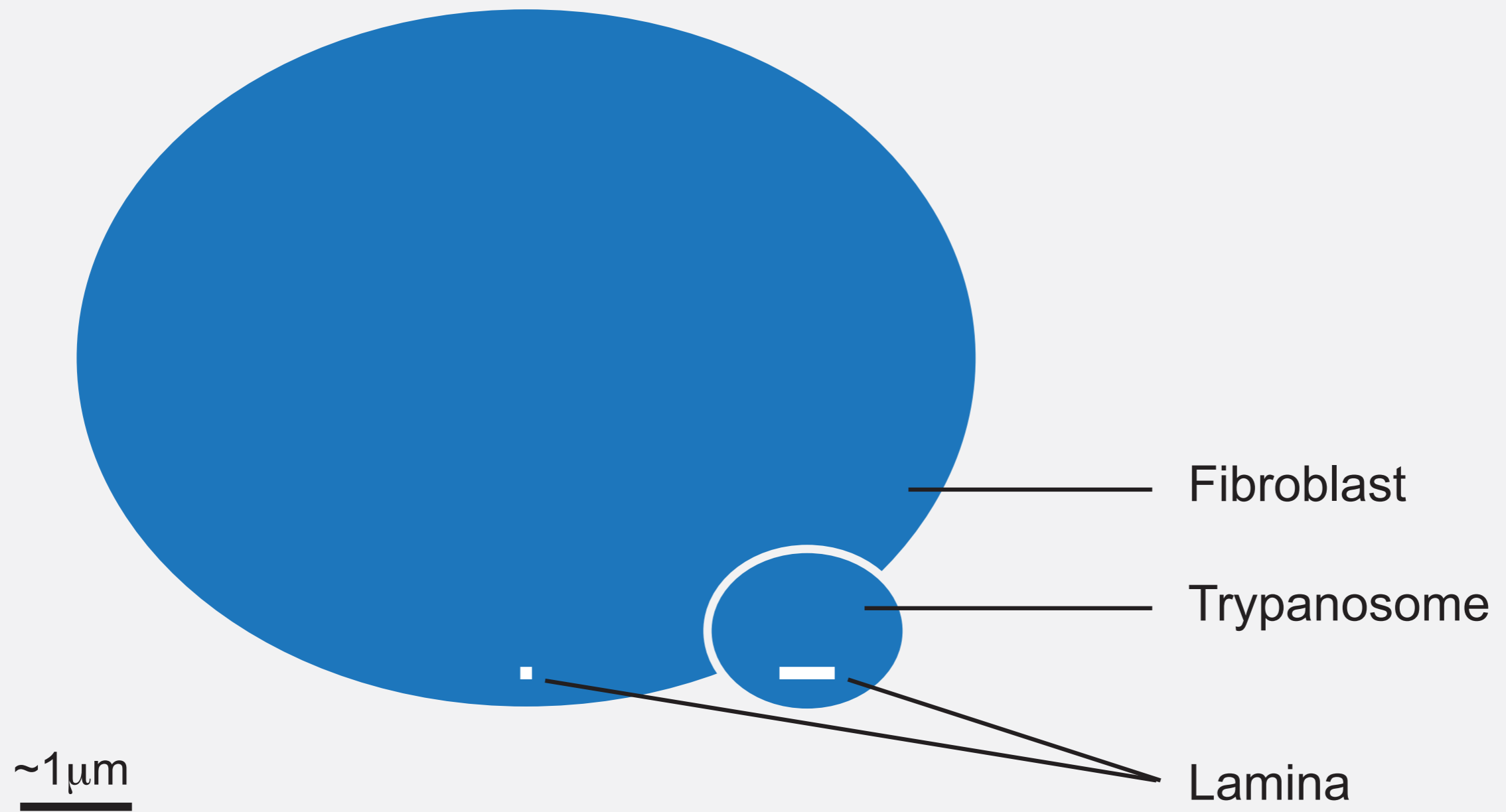
NUP-1 | NUP-2



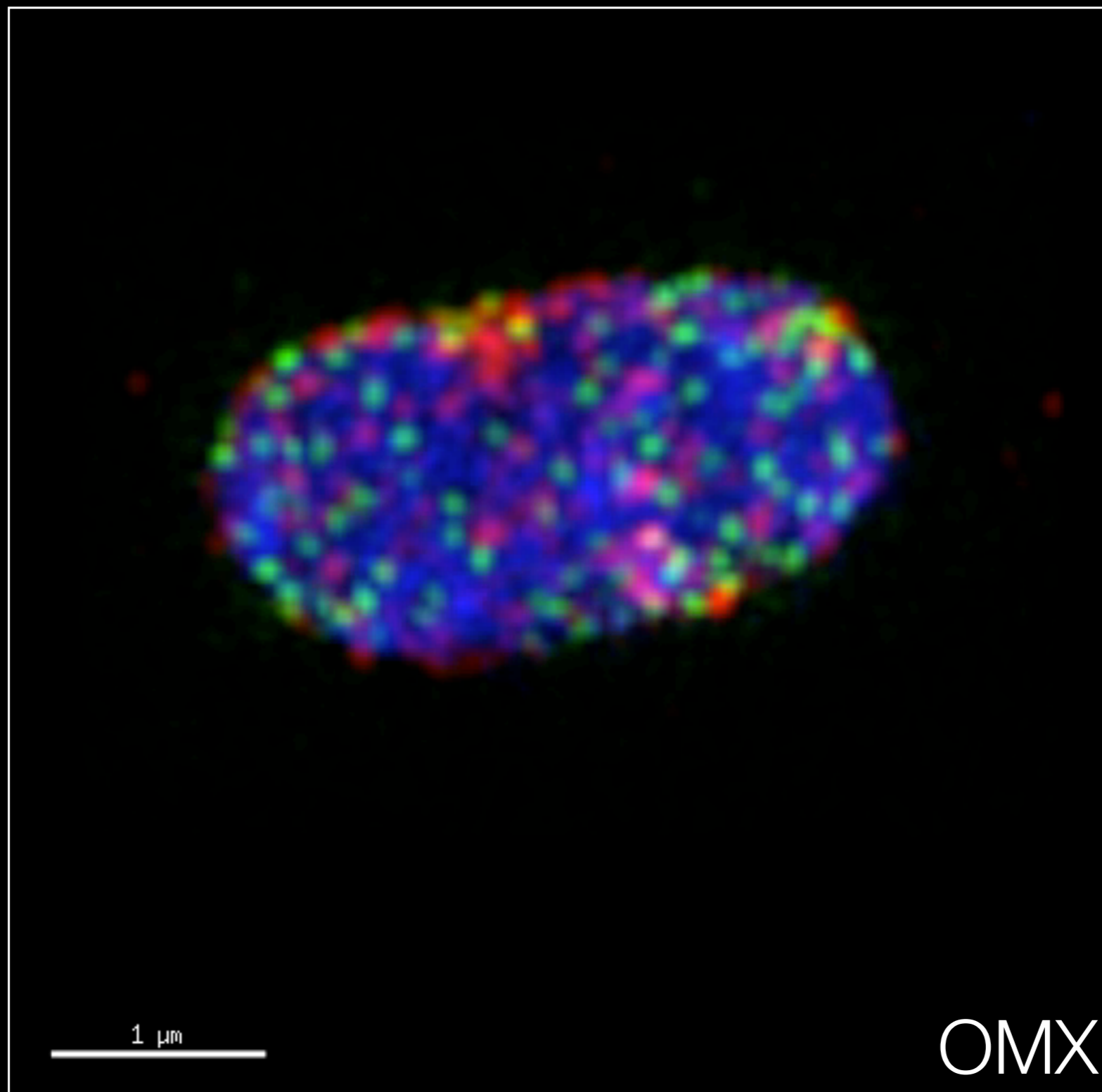
NUP-1 | NUP-2



Relative dimensions of human and trypanosome nuclei and lamina proteins

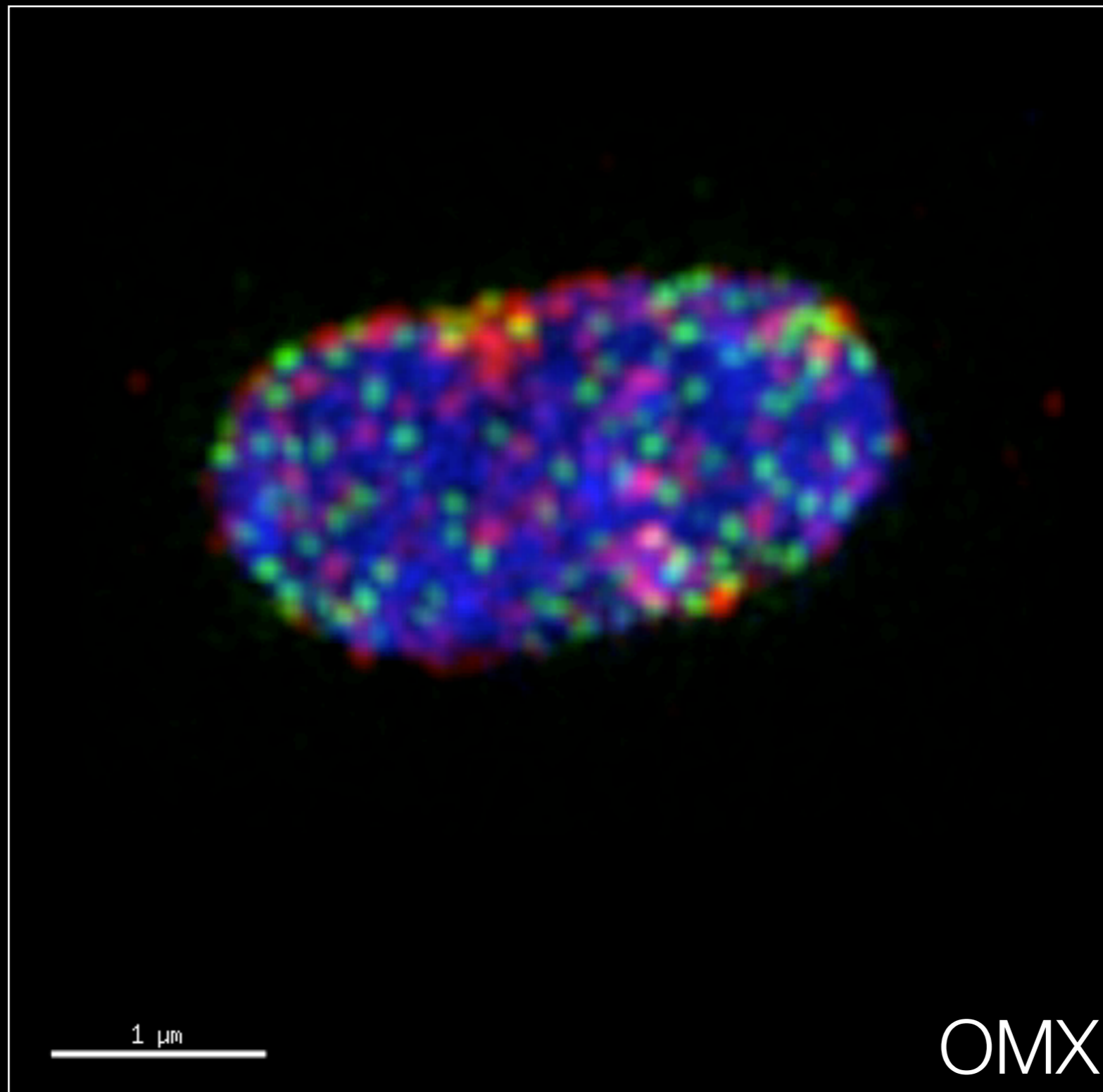


NPC | NUP-1 | DNA



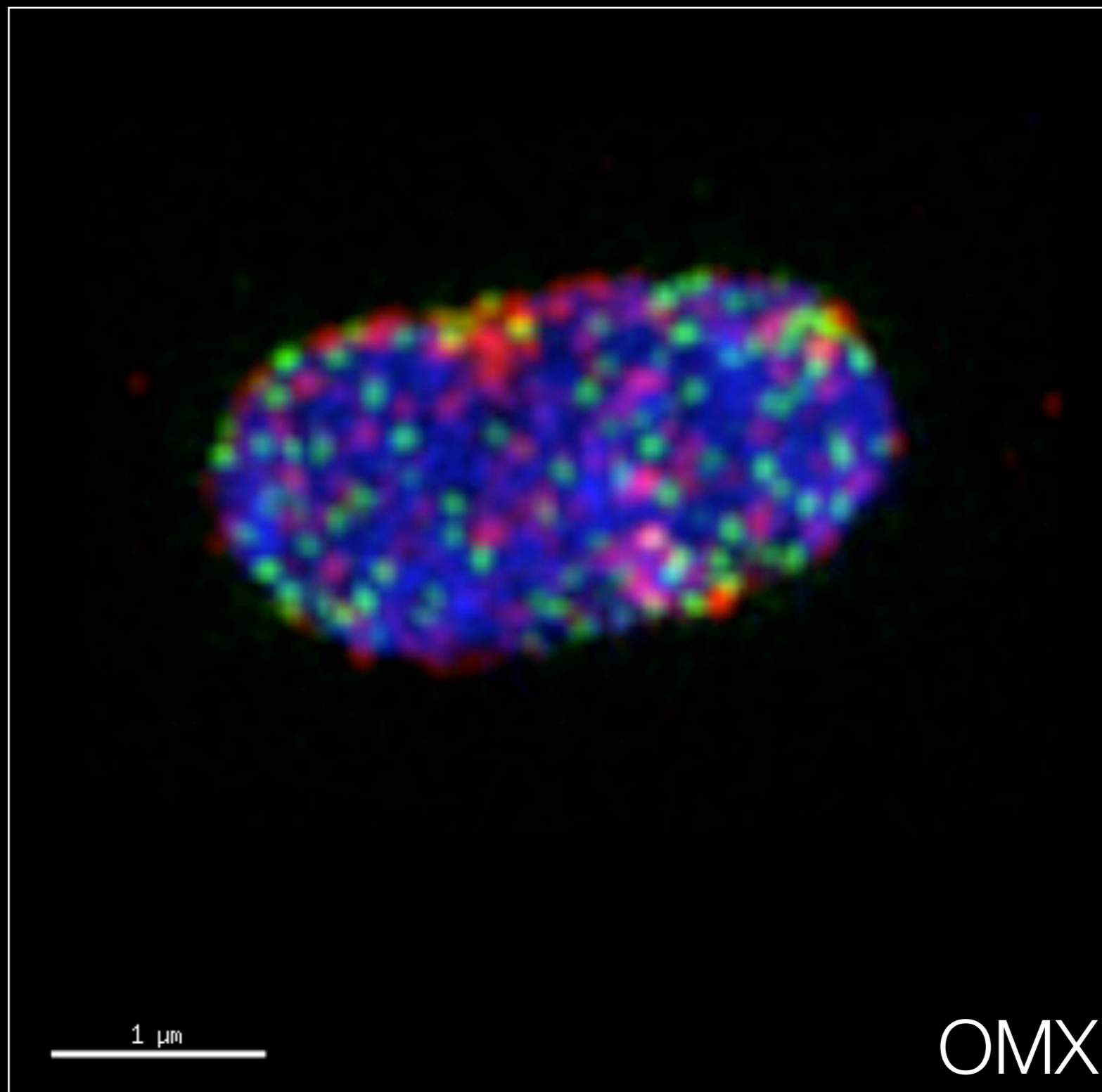
NPC: Nup98 C-terminus
NUP-1: C-terminus

NPC | NUP-1 | DNA

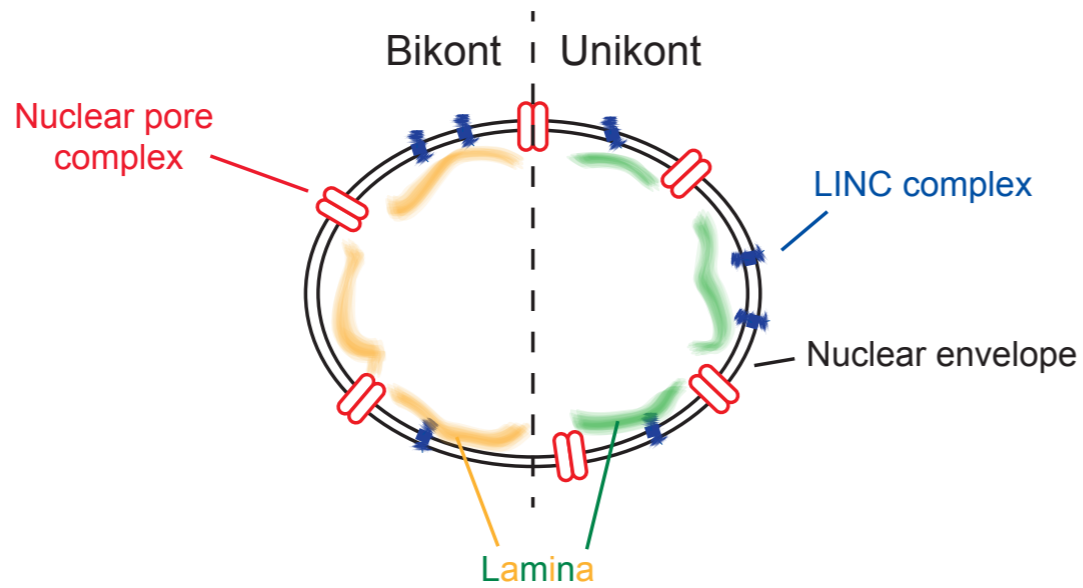


NPC: Nup98 C-terminus
NUP-1: C-terminus

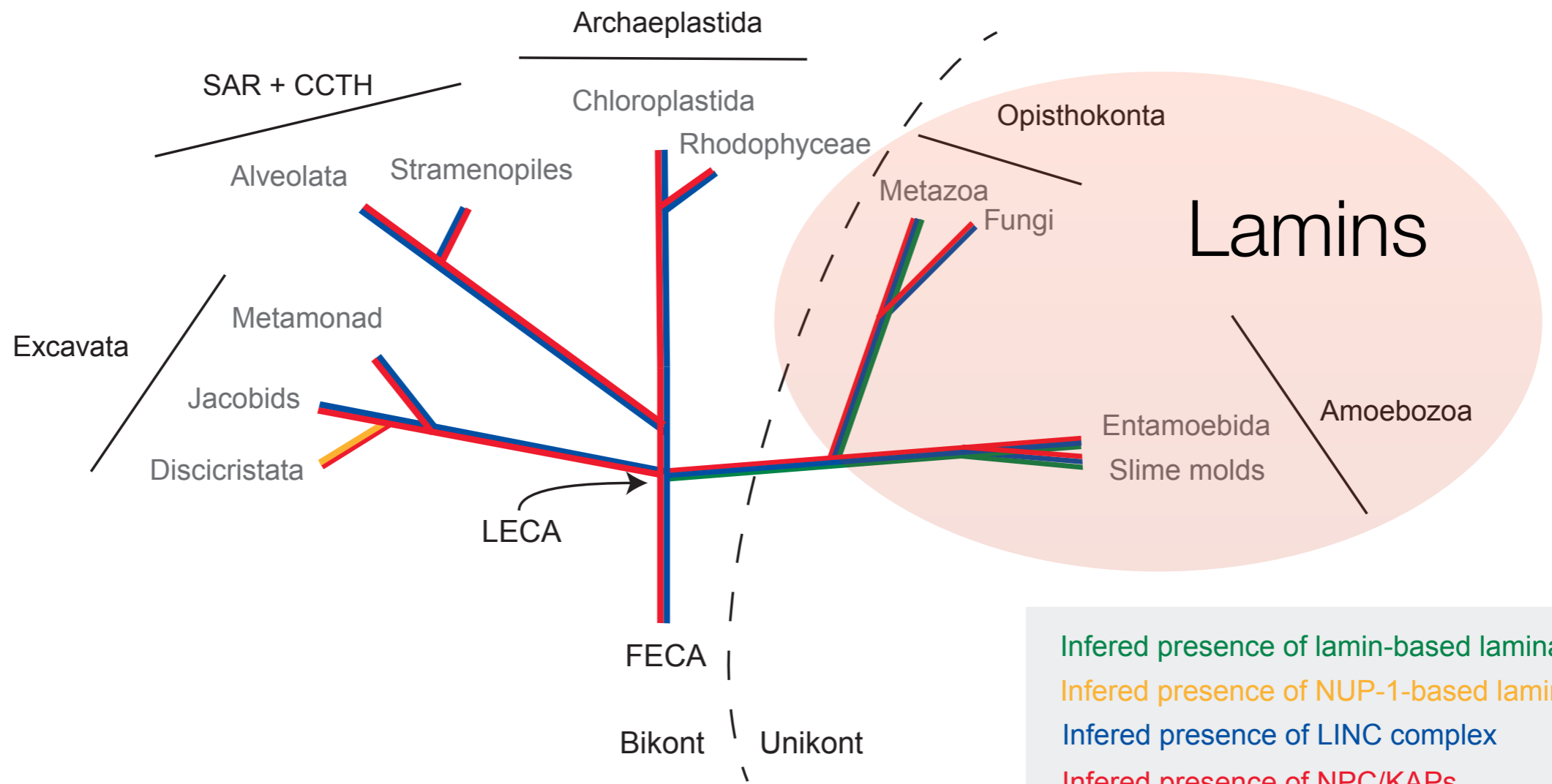
NPC | NUP-1 | DNA



NPC: Nup98 C-terminus
NUP-1: C-terminus

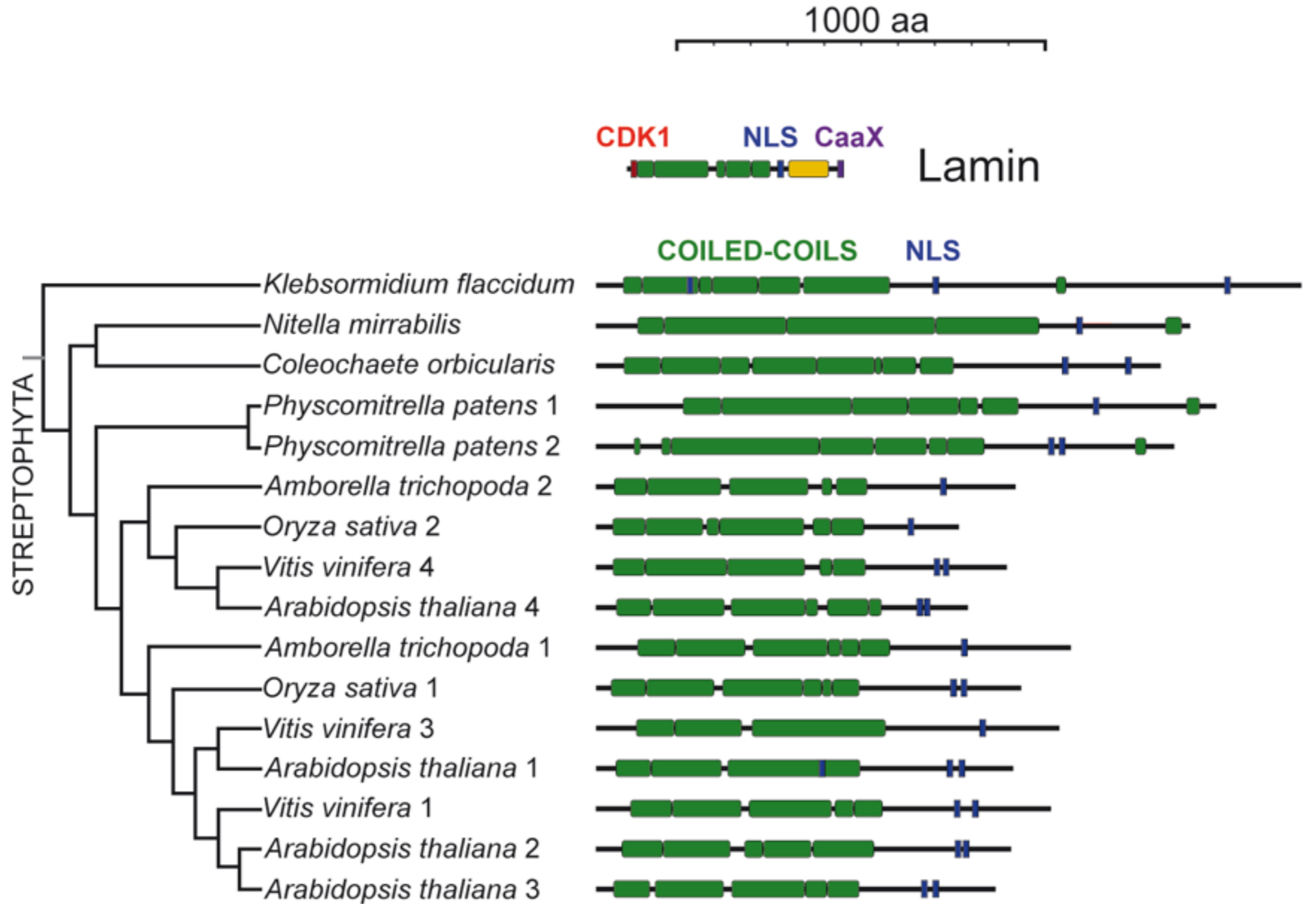


~60kDa

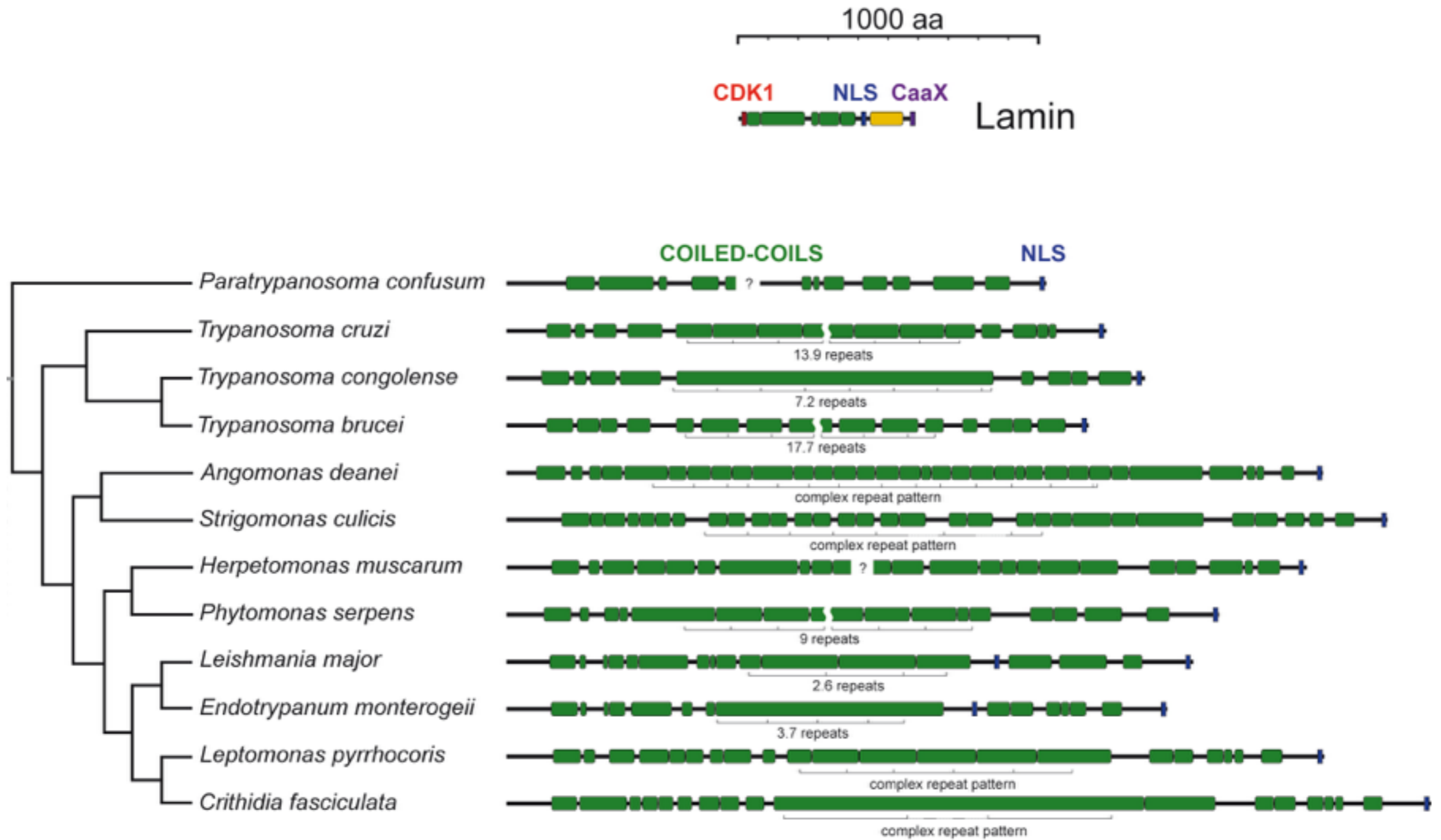


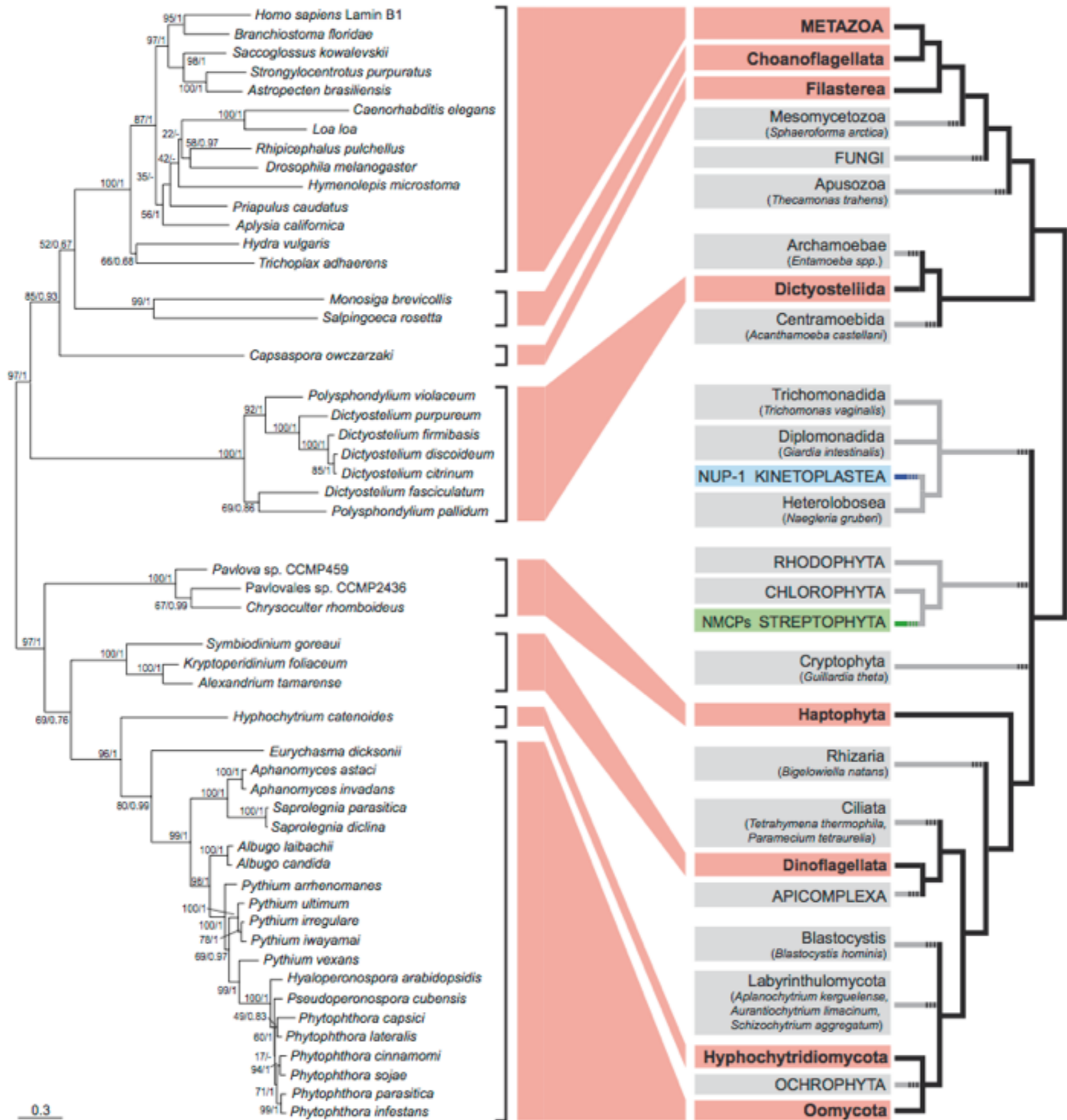
Inferred presence of lamin-based lamina
 Inferred presence of NUP-1-based lamina
 Inferred presence of LINC complex
 Inferred presence of NPC/KAPs

NMCPs (nuclear matrix constituent proteins)

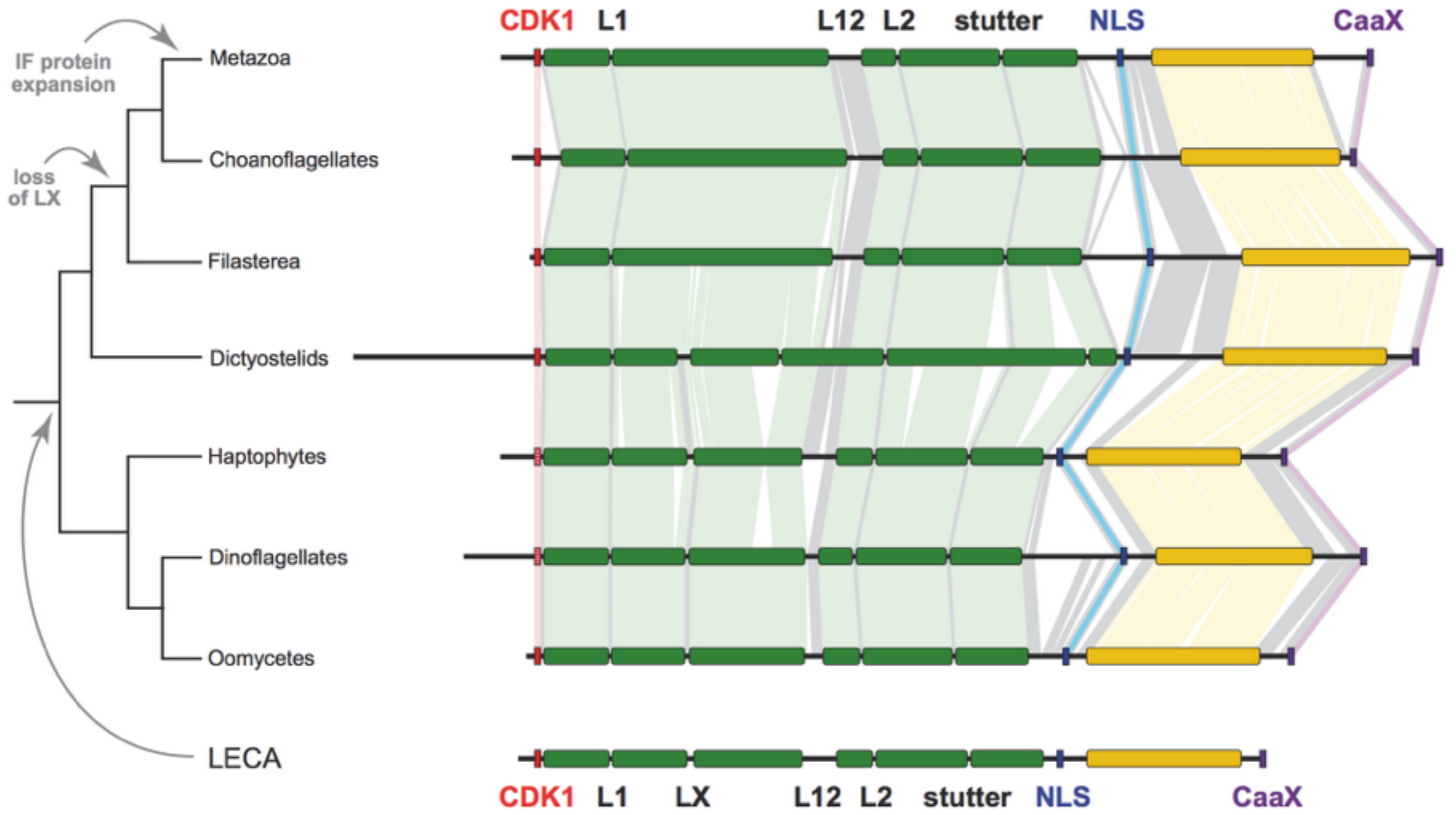


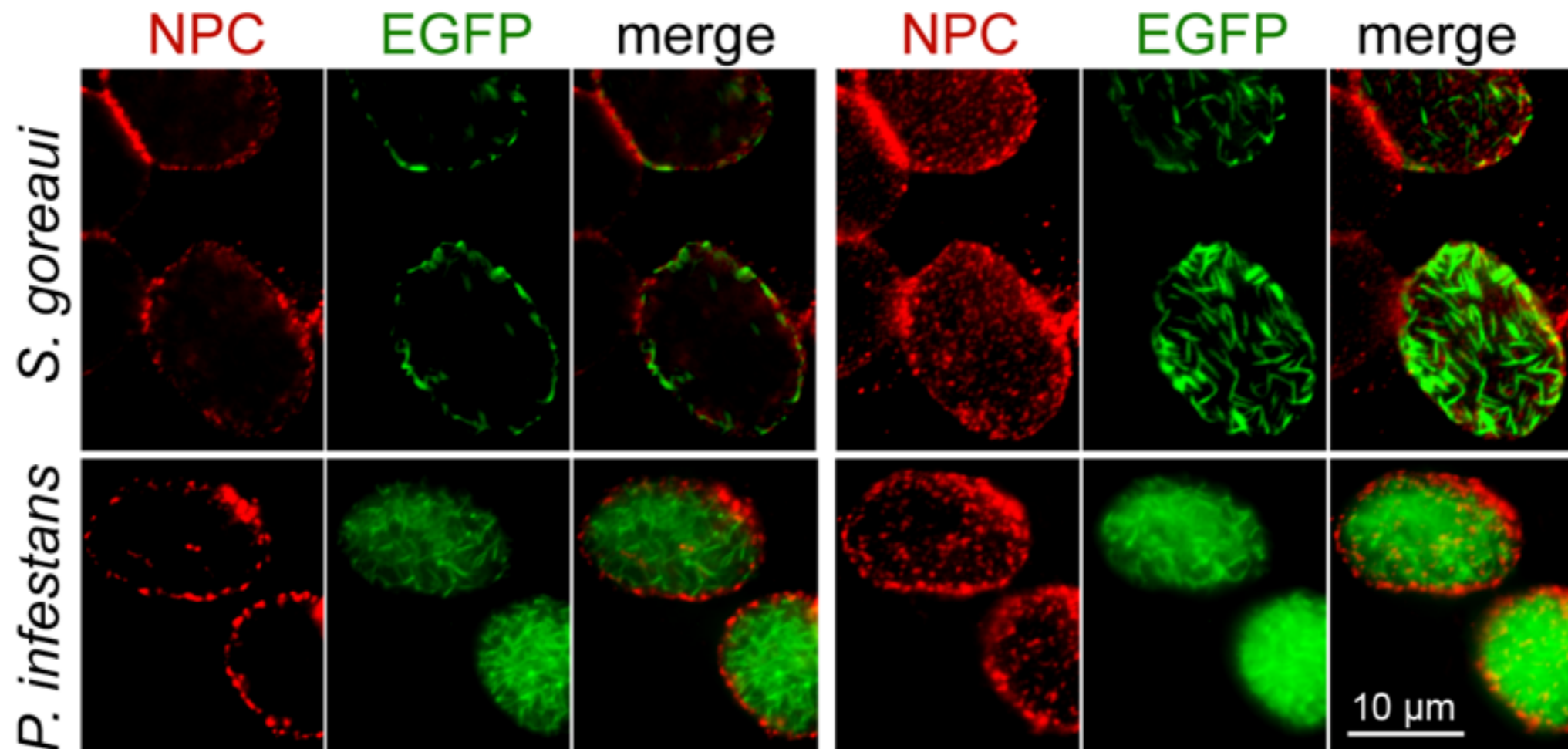
NUP-1





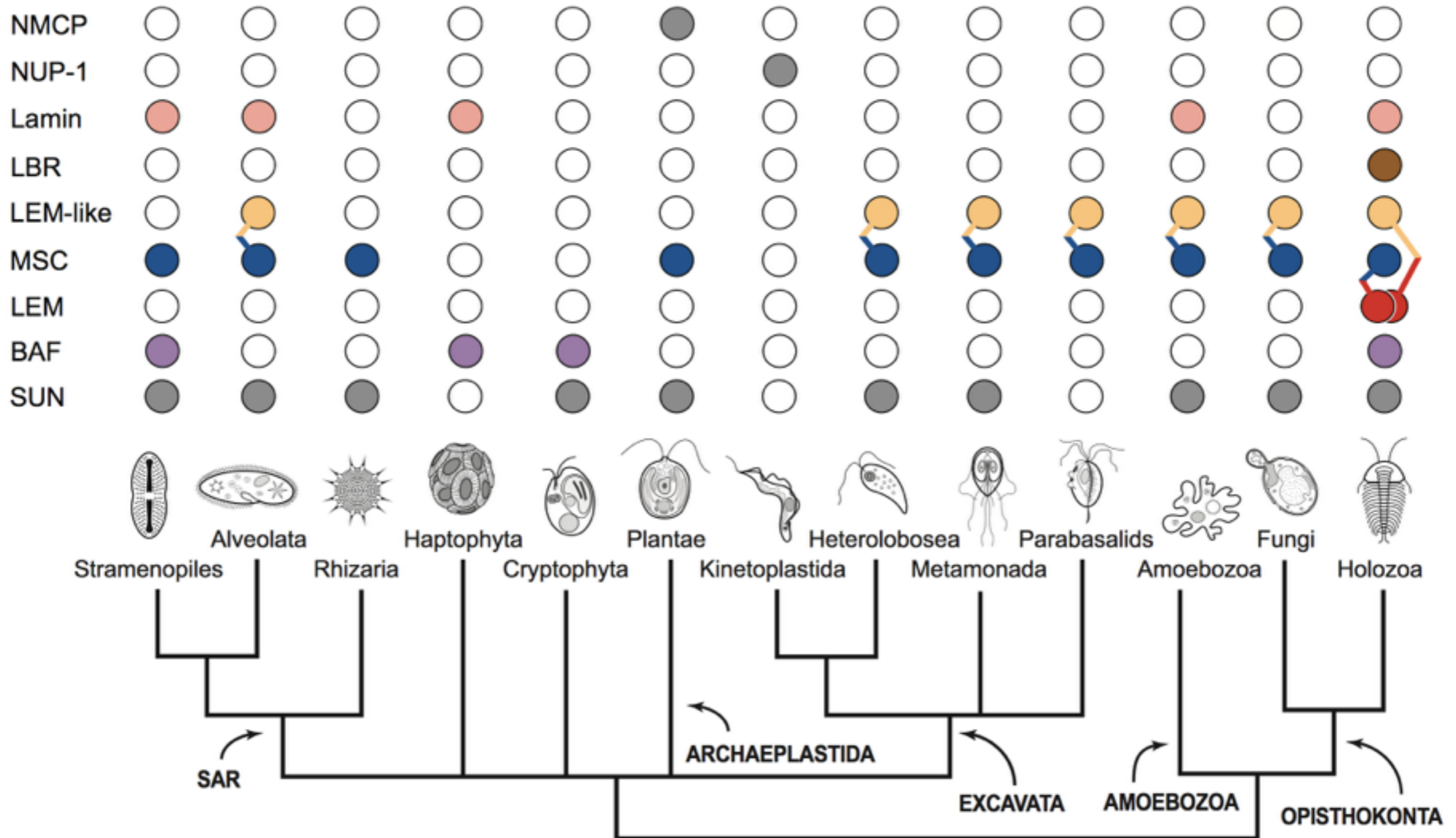
0.3



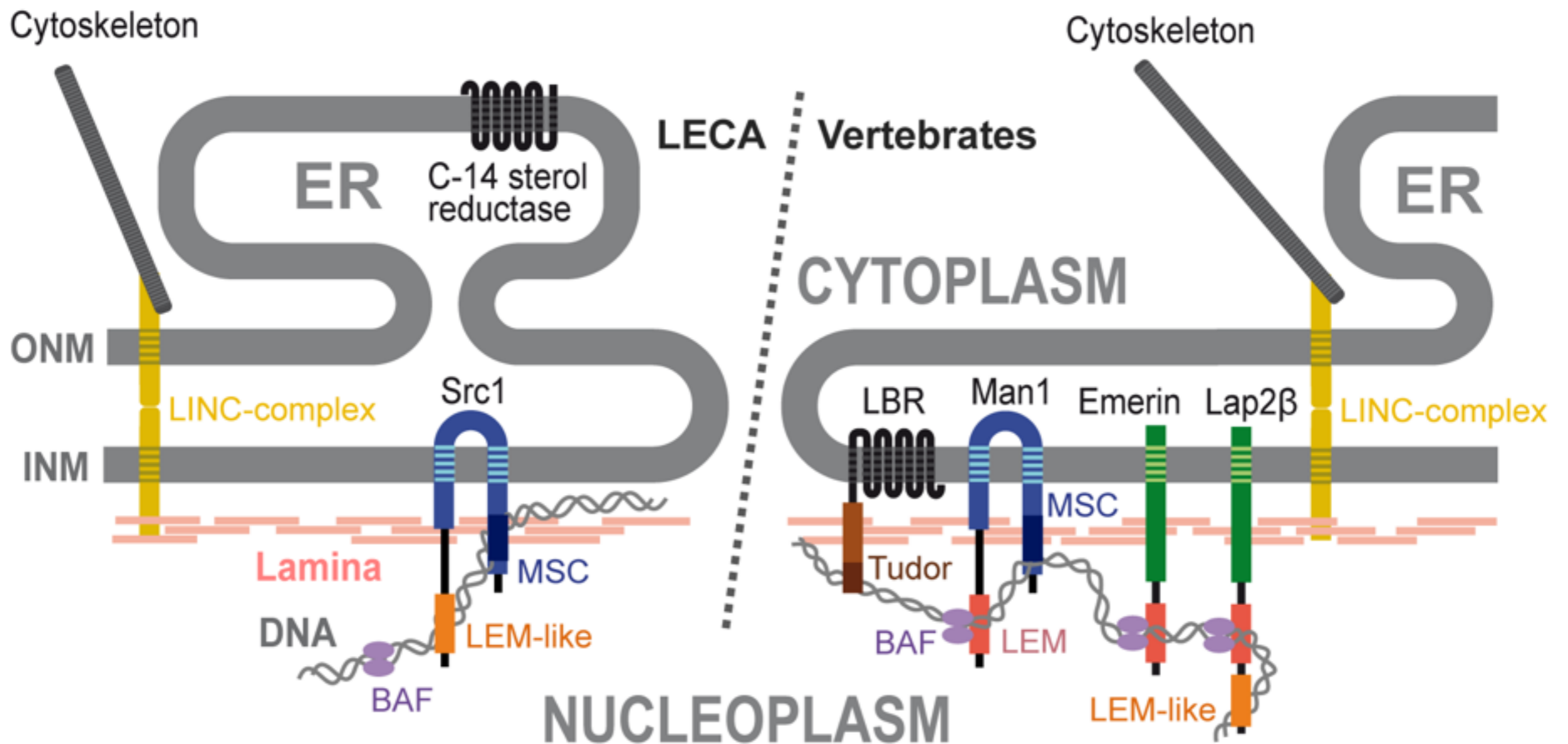


Dinoflagellate *Symbiodinium goreau*
 Oomycete *Phytophthora infestans*

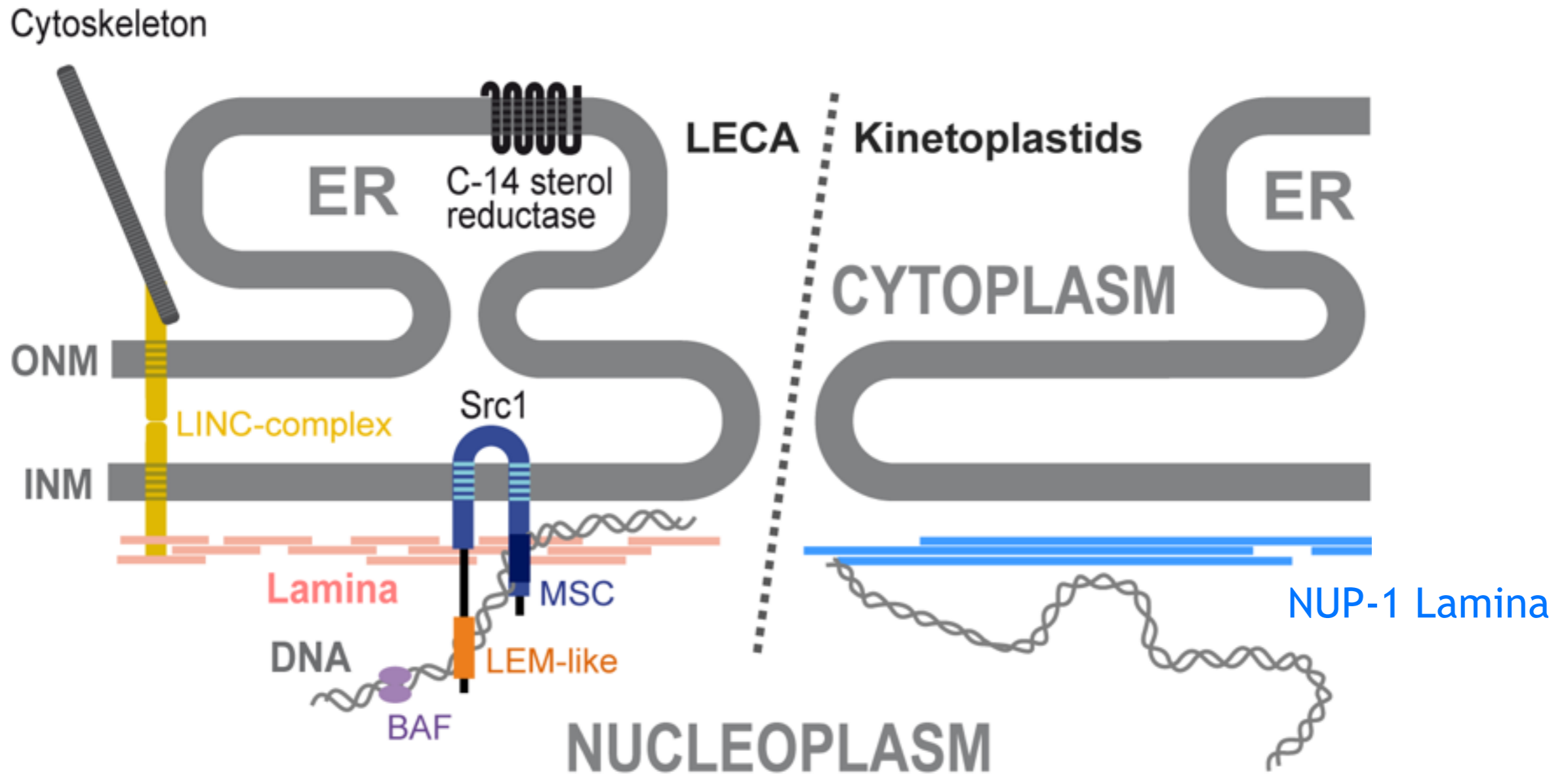
Evolution of the nuclear envelope

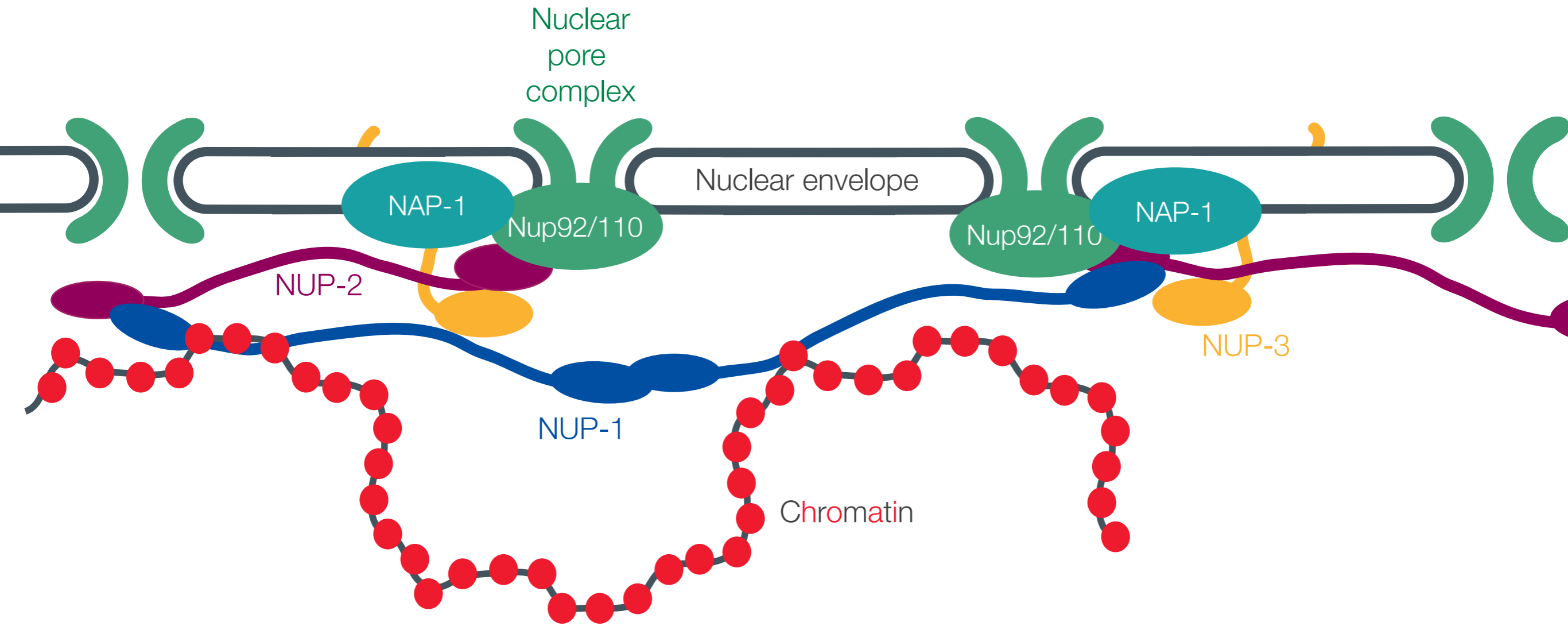


Evolution of the nuclear envelope

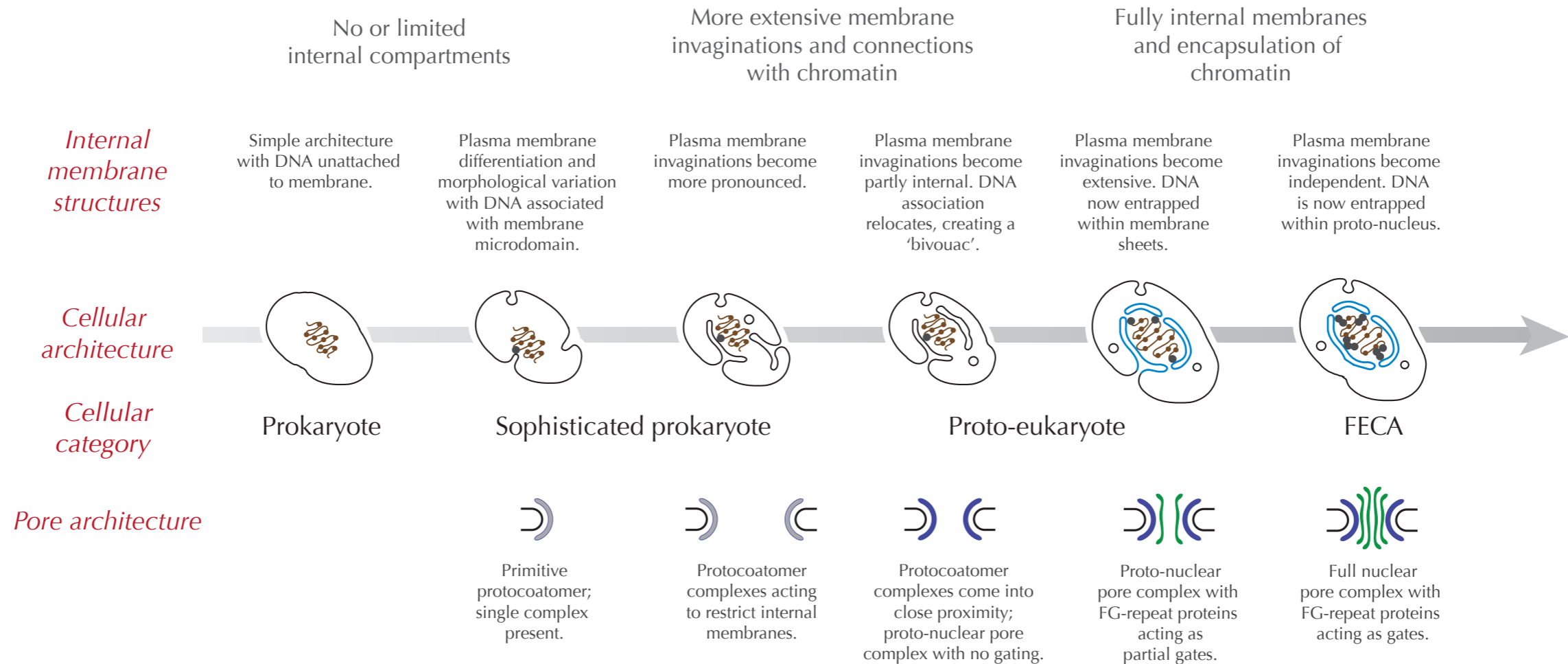


Evolution of the nuclear envelope





How did the nuclear envelope arise?



Conclusions

Trypanosome NPC is symmetrical, lacking the cytoplasmic mRNA export machinery.

Alternative mechanisms for membrane attachment.

Subunit flexibility within NPC substructures.

Alternate lamina systems in trypanosomes and plants.

Original lamina most likely lamin system.

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The Leverhulme Trust



Coulson plot generator
<http://sourceforge.net/projects/coulson/>

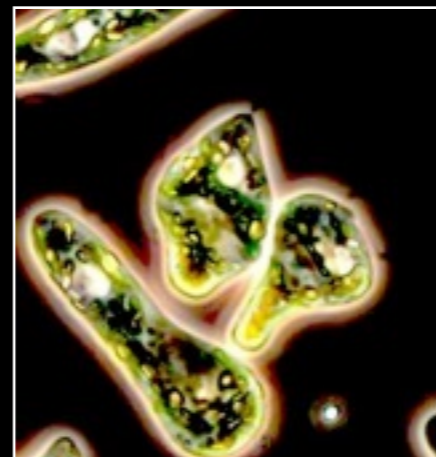


Euglena genome project
<http://euglenadb.org>



RNAit
<http://trypanofan.bioc.cam.ac.uk/trypanofan/main/>

Euglena gracilis



Trypanosoma brucei



Dundee



