

**Роль
сателлитсвязывающих
белков в
высокоуровневой
организации хроматина**

Уровни упаковки генома

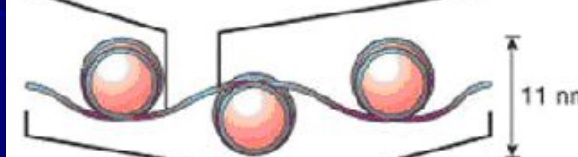
Интерфаз
а

Двойная спираль



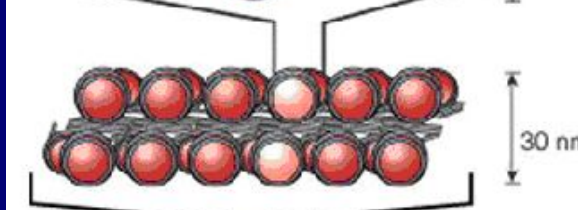
2 нм 1x

10 нм фибрилла



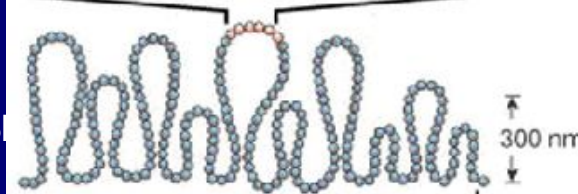
10 нм 6x

30 нм фибрилла



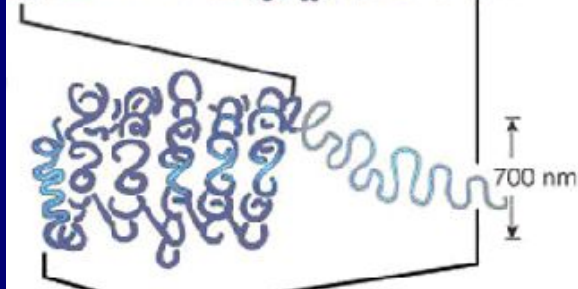
30 нм фибрилла 40x

Петельные домены



Петельные домены 700x

Фрагмент
конденсированной
хромосомы



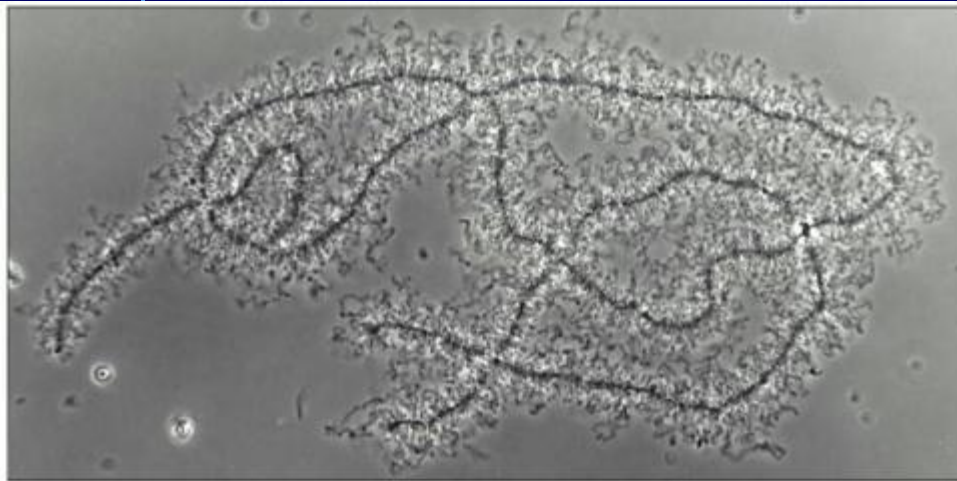
Метафазная
хромосома



Из статьи:
Controlling the double helix
Gary Felsenfeld and Mark Groudine
Nature 421, 448-453

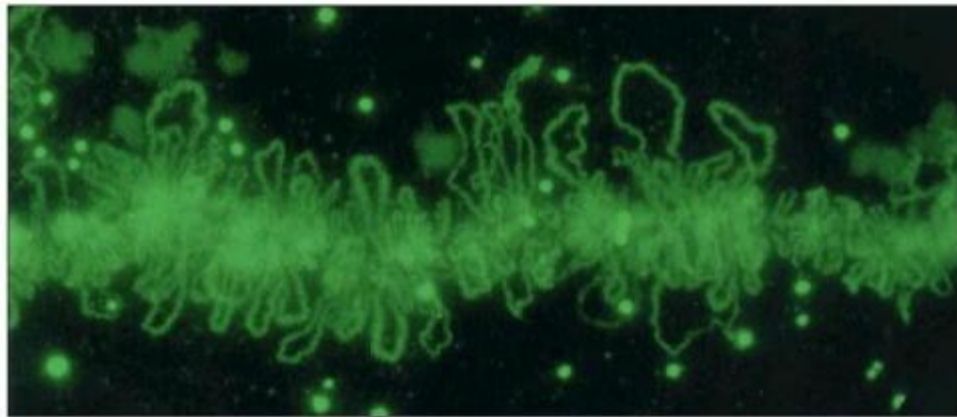


Хромосомы типа ламповых щеток



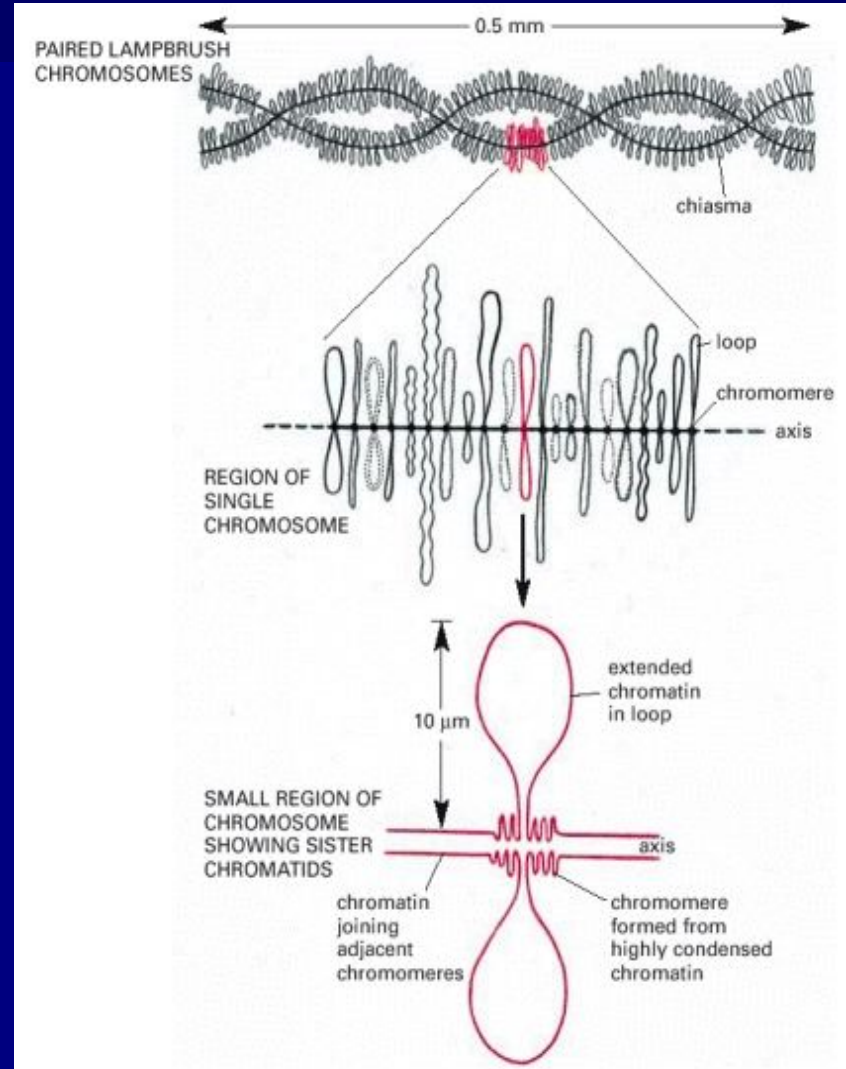
(A)

0.1 mm



(B)

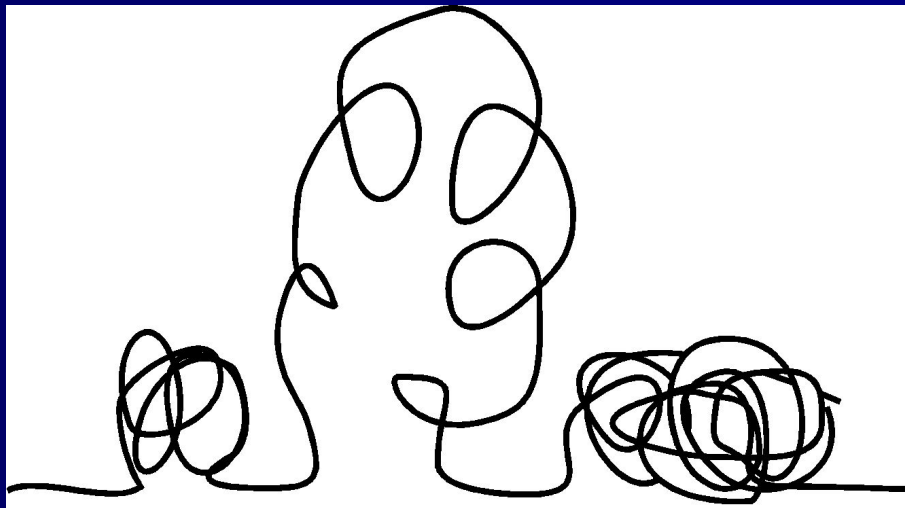
20 μm



Доменная гипотеза организации эукариотического генома

Весь геном построен из однотипных блоков - доменов, которые могут включать один или несколько генов

Домены в целом находятся под контролем особых регуляторных систем, которые контролируют их транскрипционный статус на уровне упаковки (более компактной или менее компактной) всего домена в интерфазной хромосоме



Активный домен

Неактивный домен

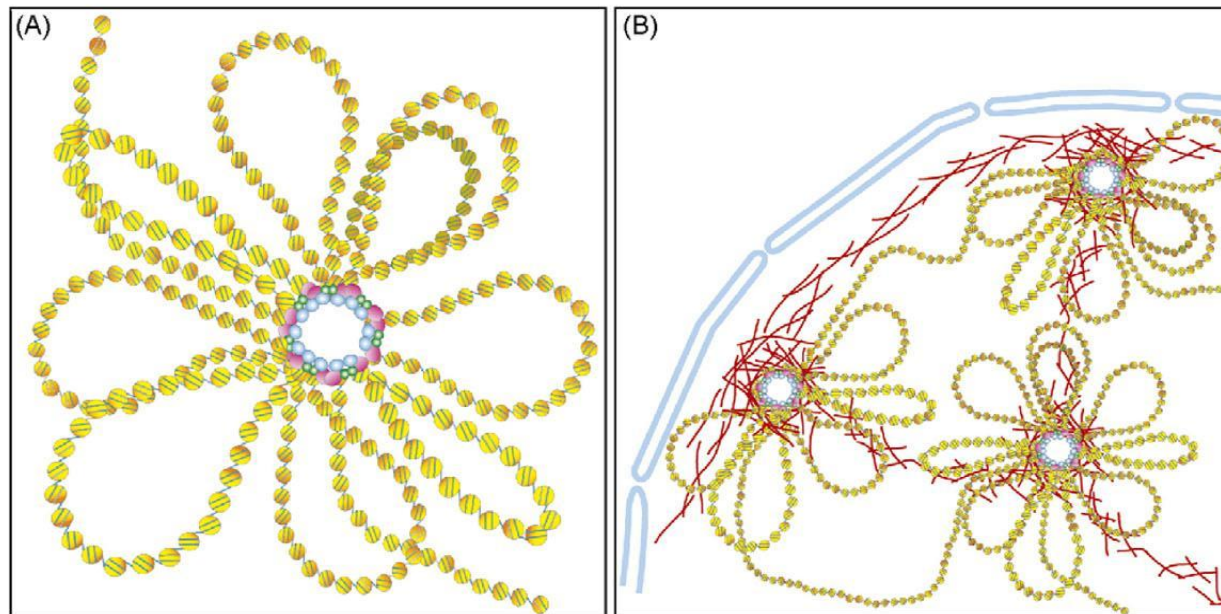
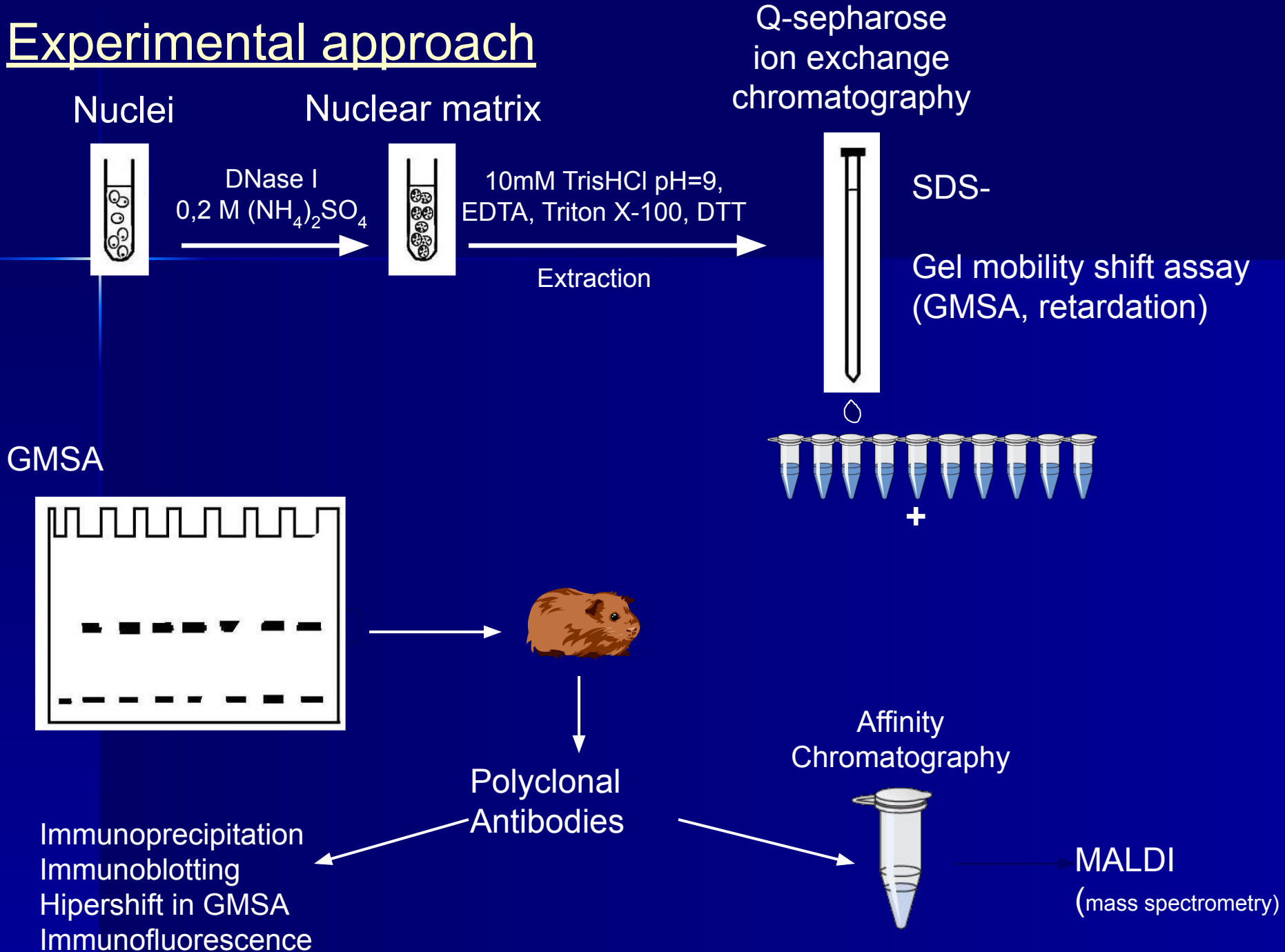


Fig. 1. Insulator elements organize the chromatin fiber in the nucleus by establishing separate compartments of higher-order chromatin structure. (A) Domains of open chromatin (yellow nucleosomes) are flanked by insulators (pink, blue and green spheres) that interact together to form a loop. (B) Diagram showing part of a nucleus with compartmentalized chromatin, anchored in part to the nuclear periphery by interactions of the insulators with the nuclear lamina (red lines).

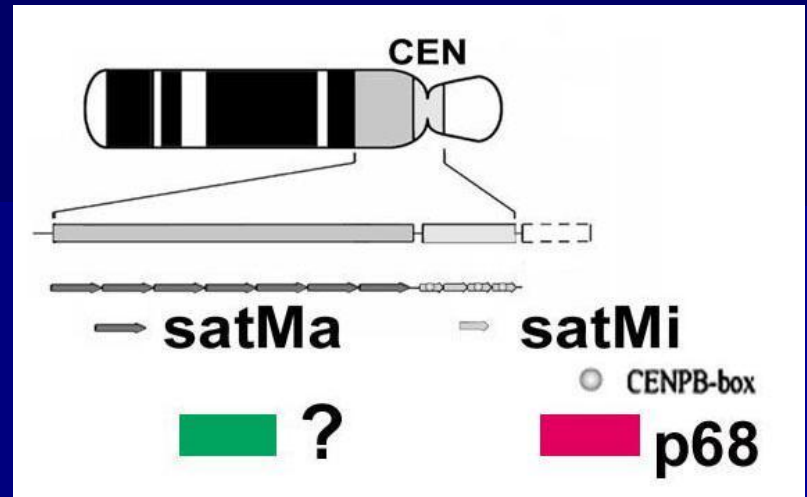
Insulator elements organize the chromatin fiber in the nucleus by establishing separate compartments of higher-order chromatin structure. (A) Domains of open chromatin (yellow nucleosomes) are flanked by insulators (pink, blue and green spheres) that interact together to form a loop. (B) Diagram showing part of a nucleus with compartmentalized chromatin, anchored in part to the nuclear periphery by interactions of the insulators with the nuclear lamina (red lines).

Experimental approach



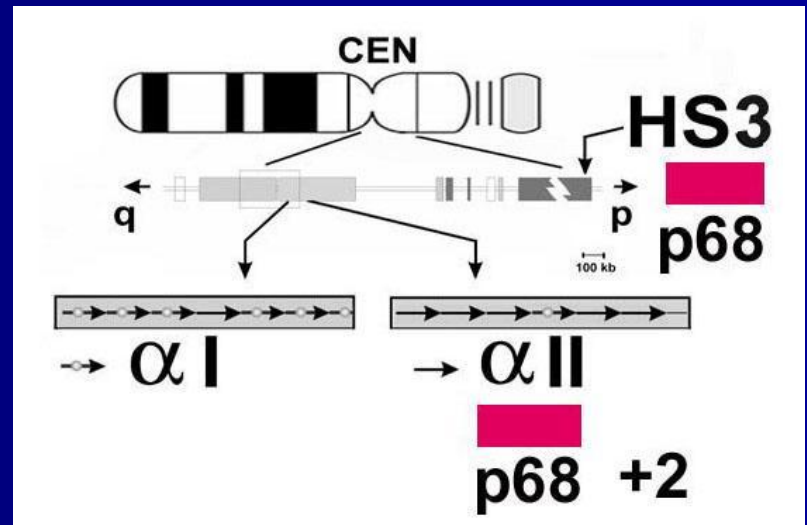
Mus

Mus musculus

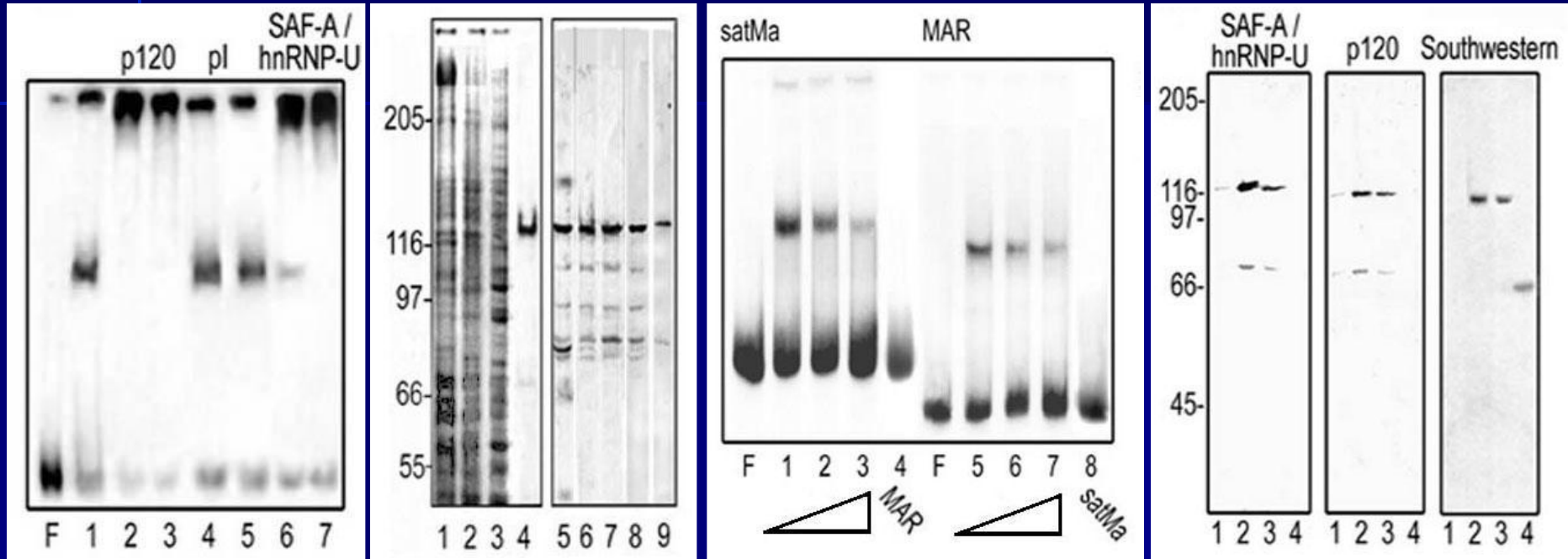


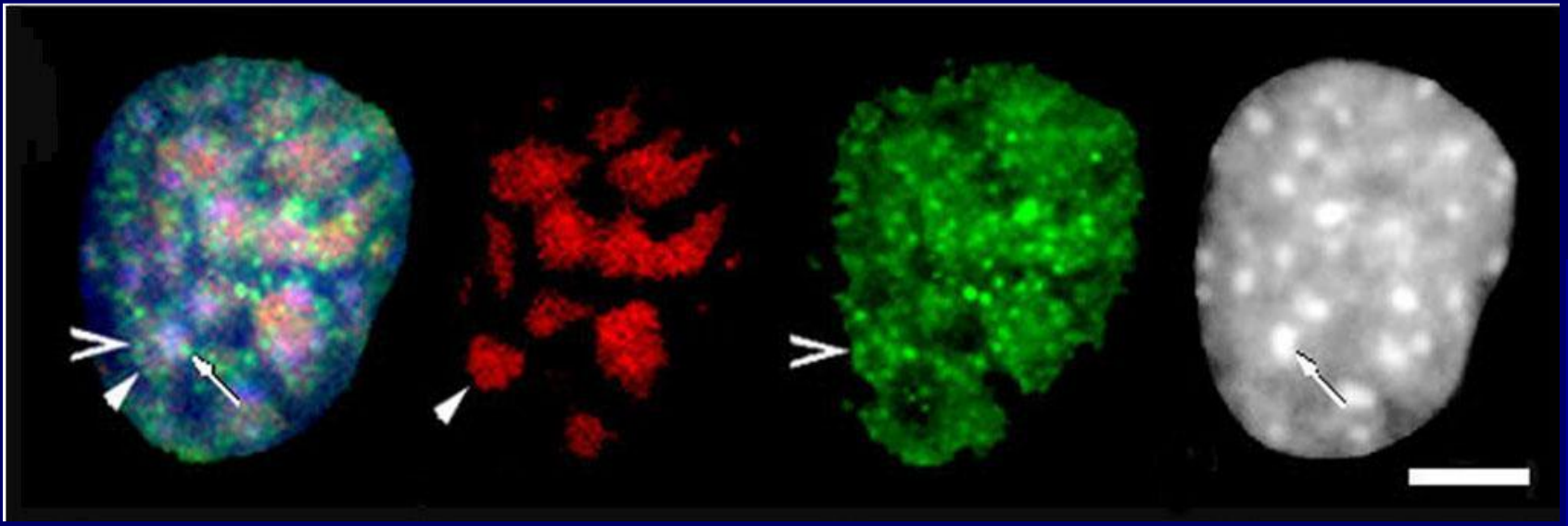
Homo

Homo sapiens



Saf-a/hnRNP U





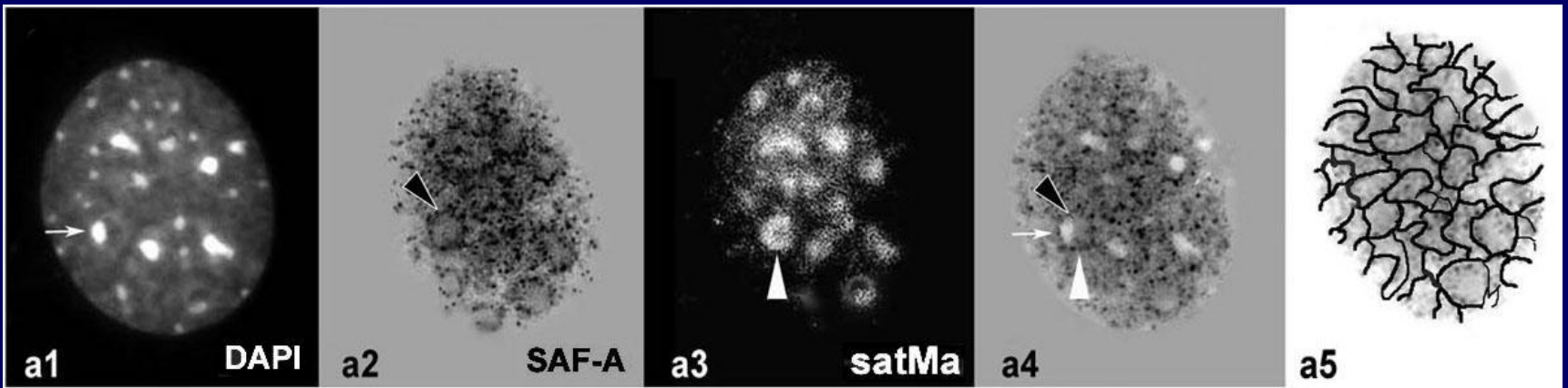
satMa FISH



Saf-a IF



DAPI



a1

DAPI

a2

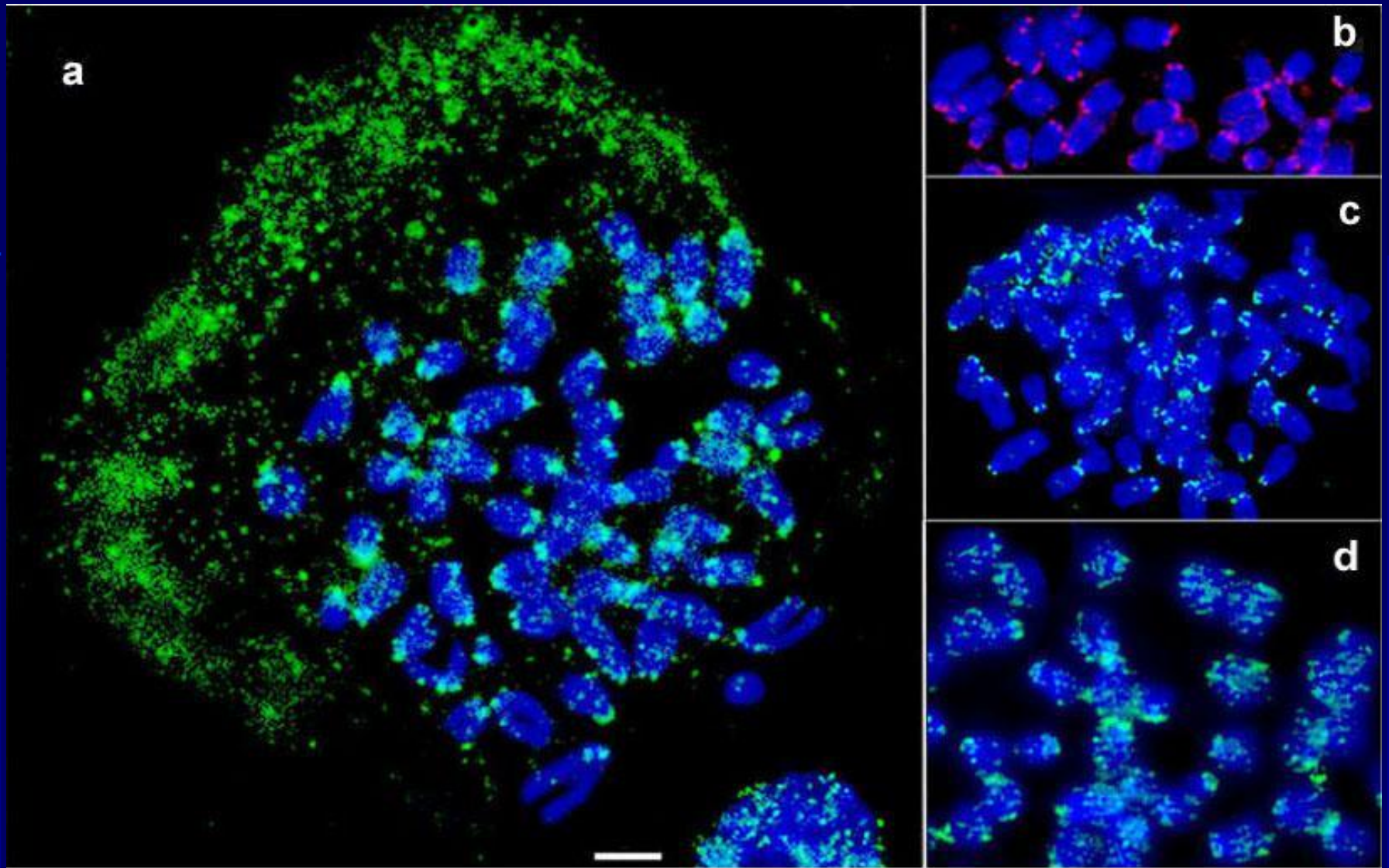
SAF-A

a3

satMa

a4

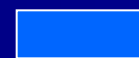
a5



Saf-a



- CENP-B



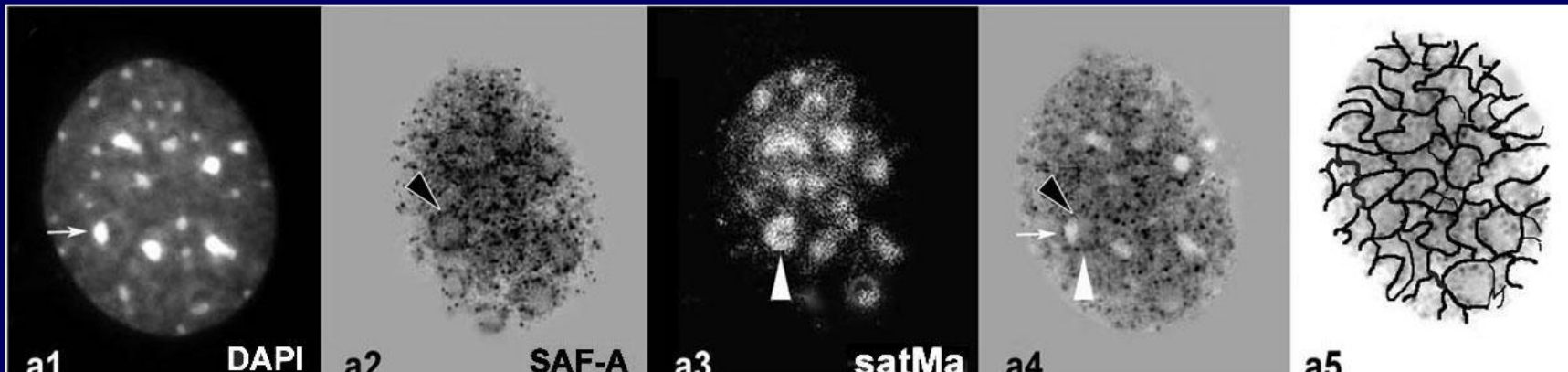
- DAPI

Saf-a/hnRNP U domain structure

```

001  MSSSPVNVKk1KVSe1KEeLKKRRLSDKGLKAe1MEr1QAE3ALDDEEAGGR
051  PAMEPGNGSLDLGGDSAGRSGAGLEQEAAAGGDEEEEEEEEEEEEGISALD
101  GDQMEELGEENGAAGAADSGPMEEEEEAASEDENGDDQGFQEGEDELGDEEE
151  GAGDENGHGEQQPQPPATQQQQPQQQQRGAAKEAAGKSSGPTSLFAVTVE3AP
201  PGARQGQQQAGGKKKAEGGGGGGRPGAPAGDGKTEQKGGDKKRGVVKRPRE
251  DHGRGYFEYIEENKYSRAKSPQPPVEEEDHFDLDTVCLDTYNCDLHFKI
301  SRDRLSASSLTMESFAFLWAGGRASYGVSKGKVCFEMKVTEKIPVRHLYT
351  KDIDIHEVRIGWSLTTSGMLLGEEEFSGYSLKGIKTCNCETEDYGEKFD
401  endVITCFANFESDEVELSYAKNGODLGVAFKISKEVLAGRPLFPHVLCH
451  NCAVEFNFGQKEKPYFPIPEEYTFIQNVPLEDRVRGPKGPEEKKDCEVVM
501  MLgLPgAgkTTWVTKHAENPGKYNILGTNTIMDKMMVAGFKKQMDTGTK
551  LNTLLQRAPQCLGKFIEIAARKKRNFILDQTNVSAAAQRRKMCLFAGFQR
601  KAVWCPKDEDYKQNecRTQKKAIEVEGKDLPEHAVLKMKGNTLPEVAECFCCDEI
651  TYVELQKEEAQKLLLEQYKEESKKALCCPPEKKQNTGSKKSNKNKSGKNQFN
701  GGGHRGRGGLNNecMNMRGGNFRGGAPGNRGGYNRRGNMPQRGGGGGGSGGIGYP
751  YPRAPVFPGRGSYSNRGNYNRGGMPNRGNYNQNFRRGRGNRRGYKNQSQGY
801  NQWQQGQFWGQKPWSQHYHQGYNM
    
```

DNA binding (residues 001-201)
 NTPase (residues 351-451)
 c-coiled (residues 601-701)
 RNA binding (residues 701-801)



Saf-a/hnRNP U specifically interacts with β -actin in the nucleus

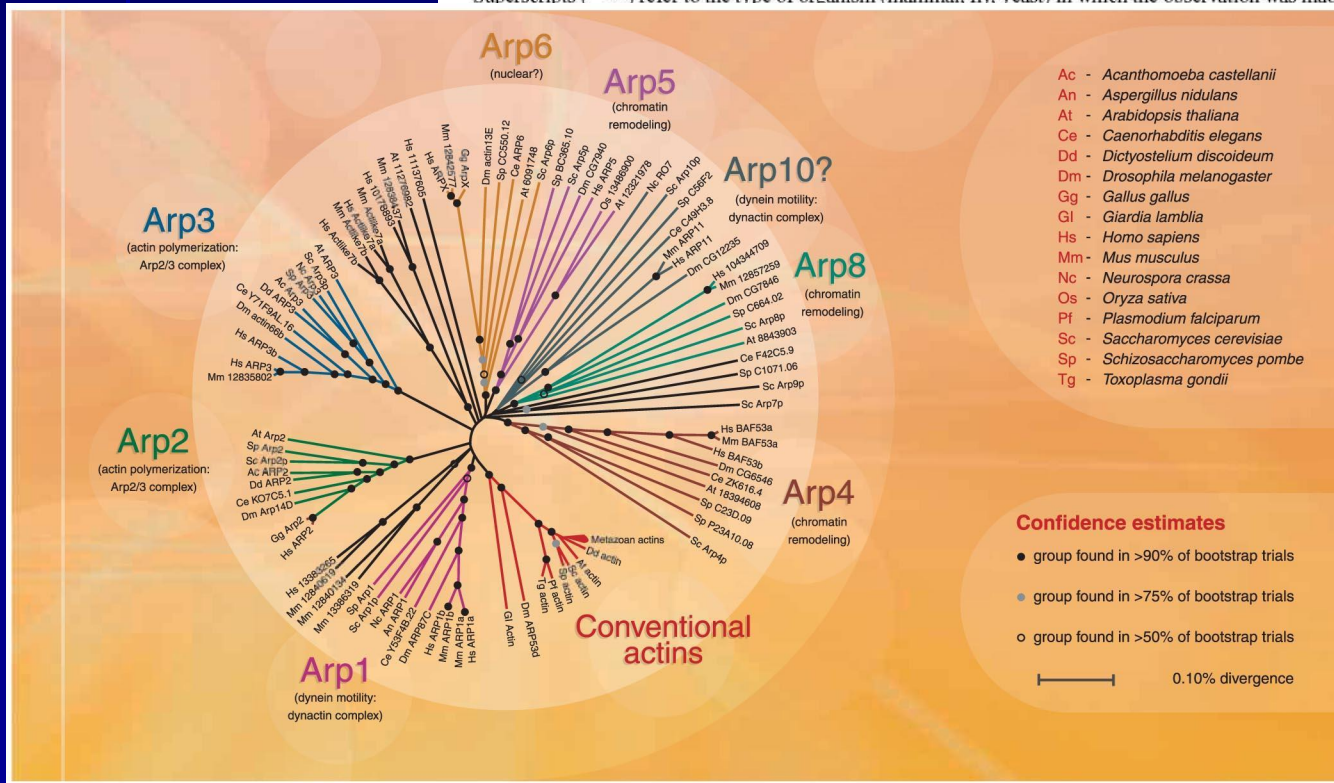
Actin and hnRNP U cooperate for productive transcription by RNA Polymerase II
Kukalev A et al., Nature, 2005



Table 1. Summary of functional information for actin subfamilies

Actin subfamily	Organisms?	Localization	Essential In yeast?	Function
Actin	Human→ <i>Giardia</i> (Ubiquitous?)	Cytoplasm ^{MFY} , nucleus ^M	Y	Cell motility/transport ^{MFY} , polarity ^{MFY} , chromatin remodeling ^{MY}
Arp1	Human→yeast	Cytoplasm ^{MFY}	N (spindle alignment)	Dynein motor function (dynactin complex ^{MFY})
Arp2	Human→yeast, <i>Arabidopsis</i>	Cytoplasm ^{MFY}	Y	Actin polymerization (Arp2/3 complex ^{MFY})
Arp3	Human→yeast, <i>Arabidopsis</i>	Cytoplasm ^{MFY}	Y	Actin polymerization (Arp2/3 complex ^{MFY})
Arp4	Human→yeast, <i>Arabidopsis</i>	Nucleus ^Y	Y	Chromatin remodeling (SWI/SNF ^M , INO80 ^Y , NuA4 ^Y , histone acetyltransferase ^{YM})
Arp5	Human→yeast, <i>Arabidopsis</i>	Nucleus ^Y	Y	Chromatin remodeling (INO80 complex ^Y)
Arp6	Human→yeast, <i>Arabidopsis</i>	Nucleus ^{FY}	N	Localized to heterochromatin ^F
Arp8	Human→yeast, <i>Arabidopsis</i>	Nucleus ^Y	N	Chromatin remodeling (INO80 complex ^Y)
Arp10	Likely human→yeast	Cytoplasm ^{MY}	?	Dynein motor function (dynactin complex ^{M,N,crassa})
Orphans				
Arps 7,9	<i>S. cerevisiae</i> , <i>S. pombe</i> (Arp 9)	Nucleus ^Y	Y/Y	Chromatin remodeling (SWI/SNF ^Y , RSC complex ^Y)

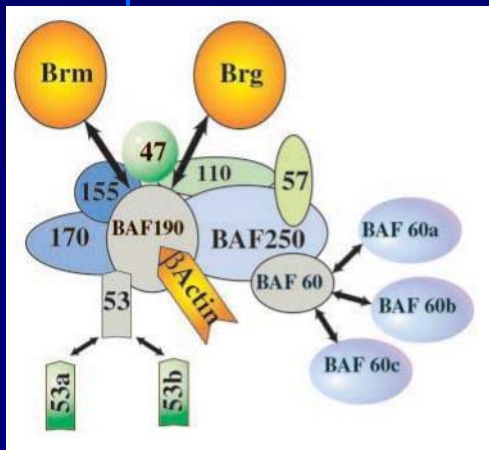
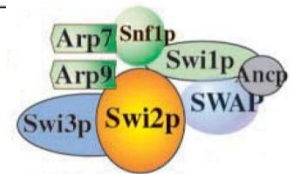
Superscripts (^{M,FY}) refer to the type of organism (mammal, flv. yeast) in which the observation was made. The ARP10 subfamily is italicized to indicate that human ARP11 is part of dynactin and that *Neurospora crassa* ARP10 is of a conserved subfamily.



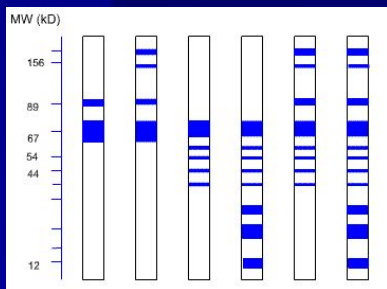
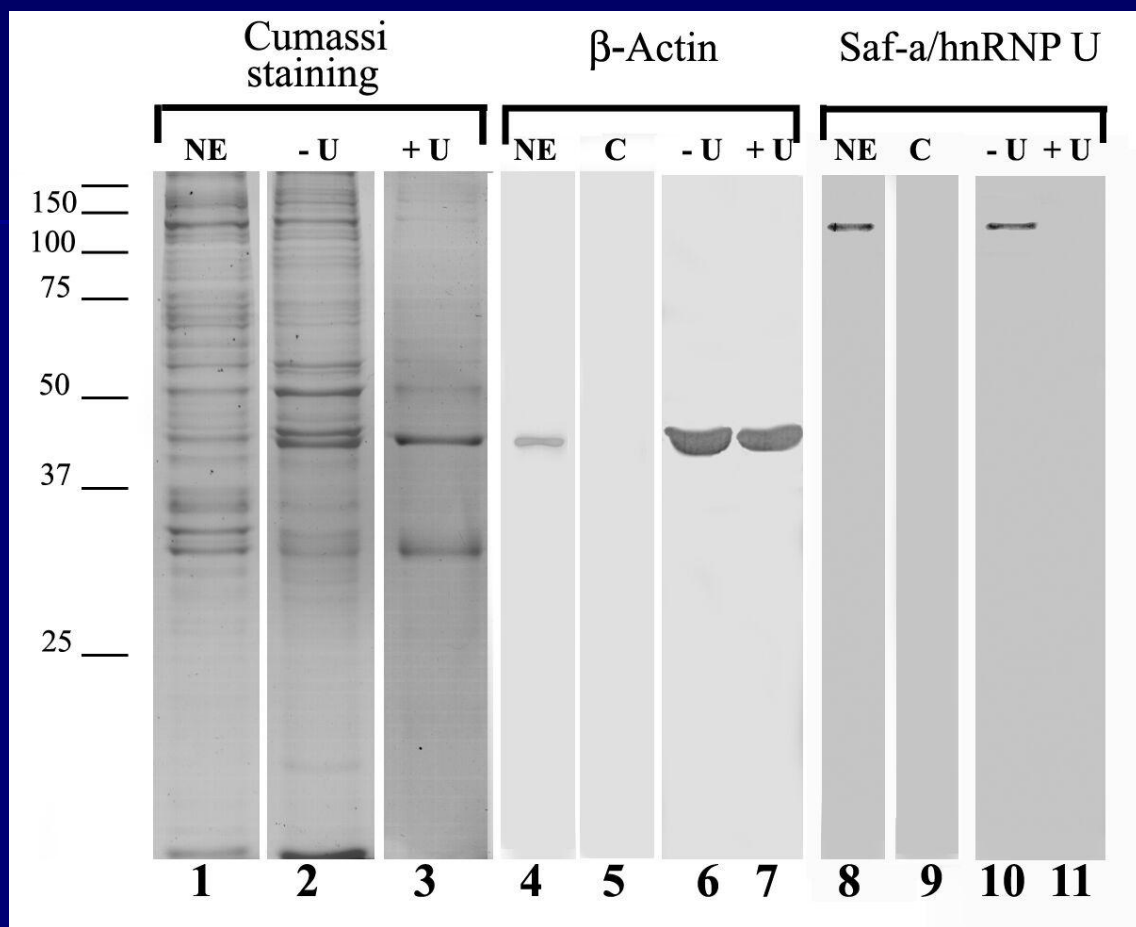
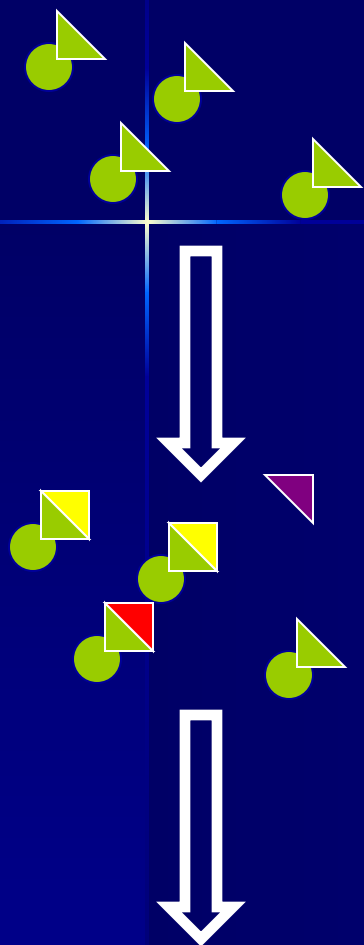
ces Genome Database (

TABLE 1 Chromatin modifying complexes

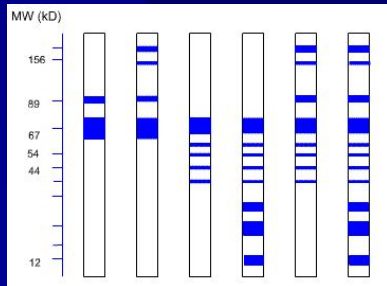
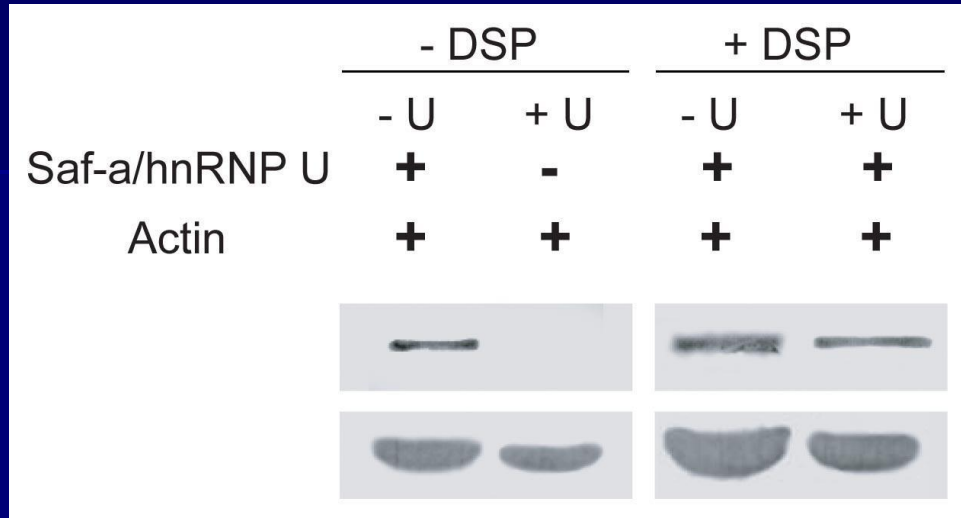
Name	Organism	Actin	Arps	ATPase	Acetylase/ deacetylase	Comments and references
SWI/SNF	<i>S. cerevisiae</i>	No	Arp7,9	SWI2/SNF2	No	(44, 45, 138, 139)
Rsc	<i>S. cerevisiae</i>	No	Arp7,9	Sth1	No	(19, 50)
INO80	<i>S. cerevisiae</i>	Act1	Arp4,5,8	Ino80	No	Phospholipid biosynthesis; helicase activity. (15, 33)
NuA4	<i>S. cerevisiae</i>	Act1	Arp4	None	Acetylase	Esa1 acetylase is essential for cell cycle progression. Arp4 binds histones in vitro and is involved in epigenetic control of transcription. (16, 38, 39, 140)
BAF	Mammals	Yes	BAF53a or b	Brg1 or hBrm	No	Heterogeneous complex. Contains BAF250. (13, 24, 25)
PBAF	Mammals	Yes	BAF53a	Brg1	No	Absence of BAF250. Only Brg1 ATPase present. (141)
p400	Mammals	Yes	BAF53	P400 TAP54 α,β	N/A	ATPase and helicase activity. Shared subunits with Tip60 complex. (18)
Tip60	Mammals	Yes	BAF53	TAP54 α,β	Acetylase	ATPase and helicase activity. Links HAT activity to DNA repair and apoptosis. (17)
NuRD	Mammals	No	No	Mi-2	Deacetylase	Involved in gene silencing. (142–144)
RSF	Mammals	No	No	hSNF2h	No	Facilitates transcription from chromatin templates. Has nucleosome remodeling and spacing activities. (142)
LSH	Mammals	?	?	LSH	?	Member of SNF2/RAD54 family of proteins. Lsh $^{-/-}$ mice die perinatally. (145, 146)
BAP	<i>D. melanogaster</i>	Yes	BAP55	Brahma	No	Maintains homeotic gene expression. (14, 29)
Domino	<i>D. melanogaster</i>	?	?	Domino	?	Identified in a genetic screen for hematopoietic disorders. (32)
ACF	<i>D. melanogaster</i>	No	No	ISWI	No	Assembles periodic nucleosome arrays. (143)
NURF	<i>D. melanogaster</i>	No	No	ISWI	No	Disrupts nucleosome arrays. Pyrophosphatase. (60, 61, 147)
CHRAC	<i>D. melanogaster</i>	No	No	ISWI	No	Remodels chromatin, displaces nucleosomes in <i>cis</i> . (62, 148)



Saf-a/hnRNP U co-precipitated with b-actin



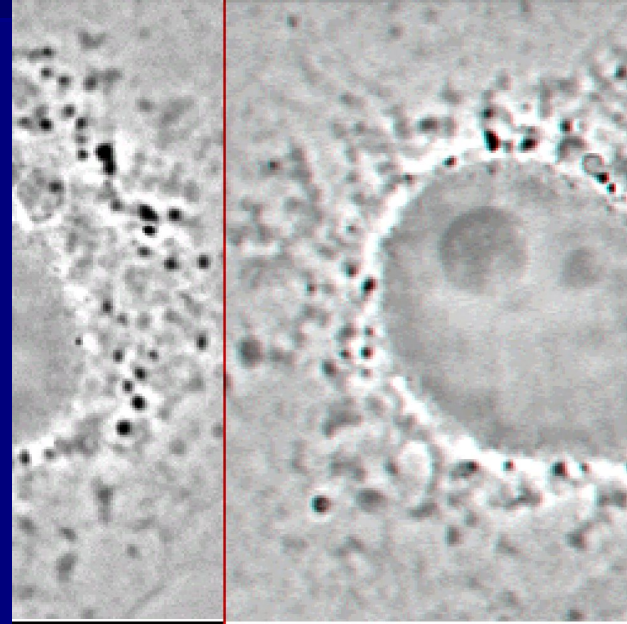
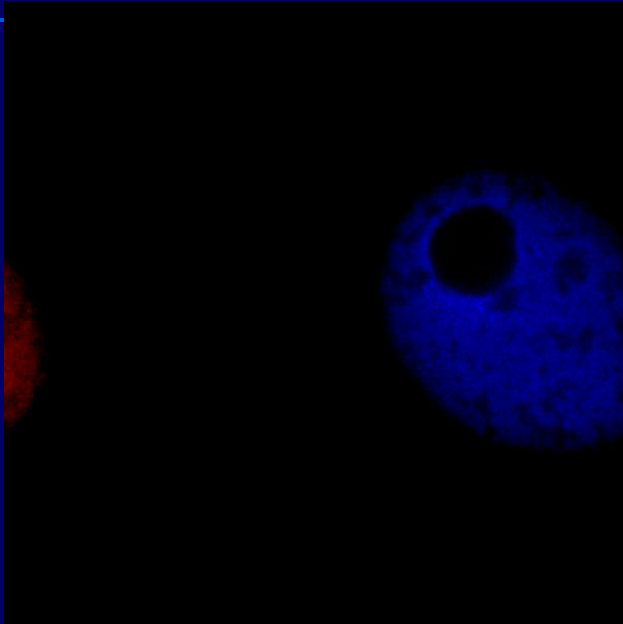
Actin binds Saf-a/hnRNP U *in vivo*



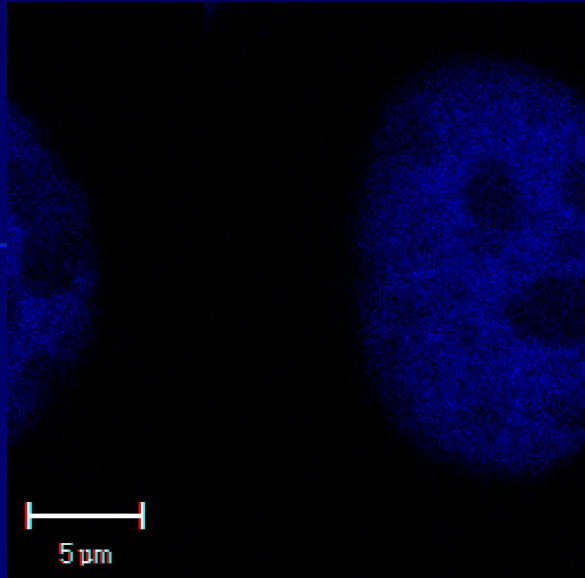
Saf-a/GFP fusion proteins



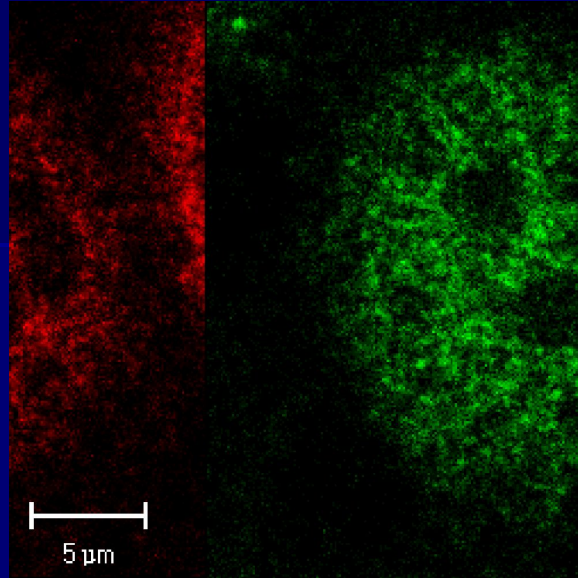
1-823 a/a



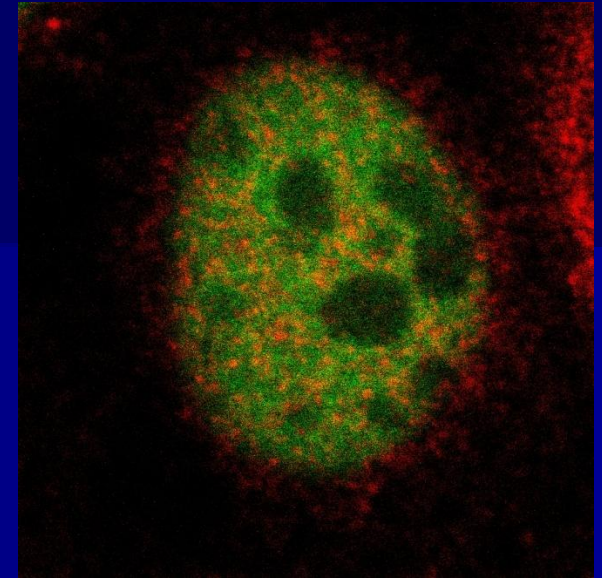
Actin co-localised with fusion Saf-a-GFP in HeLa cells



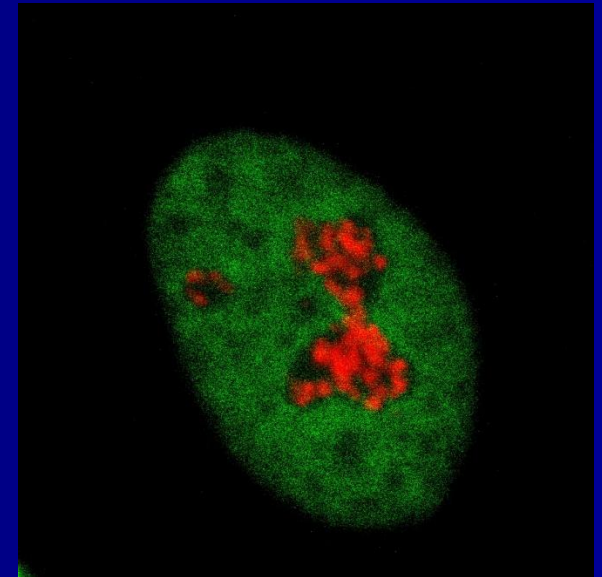
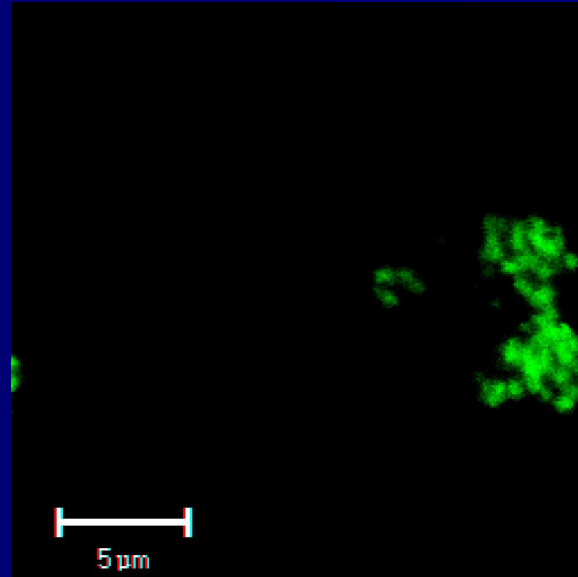
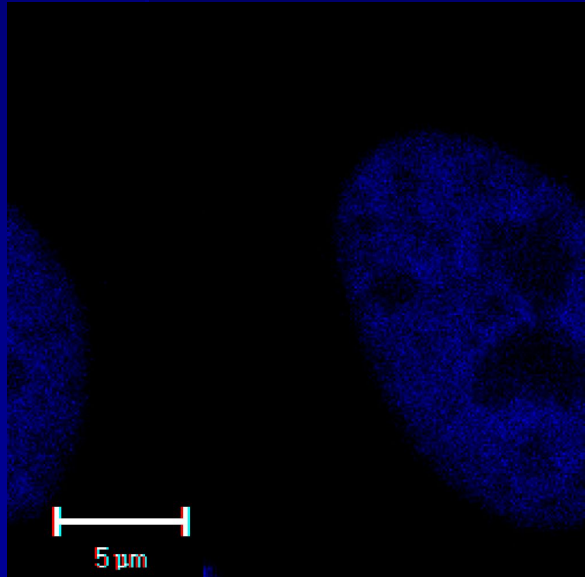
Saf-a FL/pEGFP-N1



β -Actin/Fibrillarlin



Merged

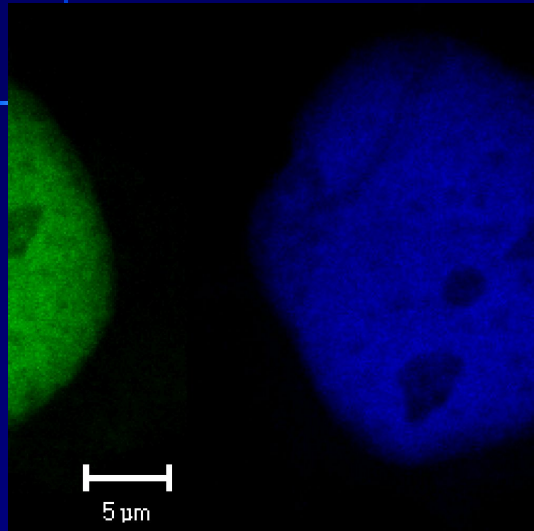


Saf-a N1-12/GFP fusion protein

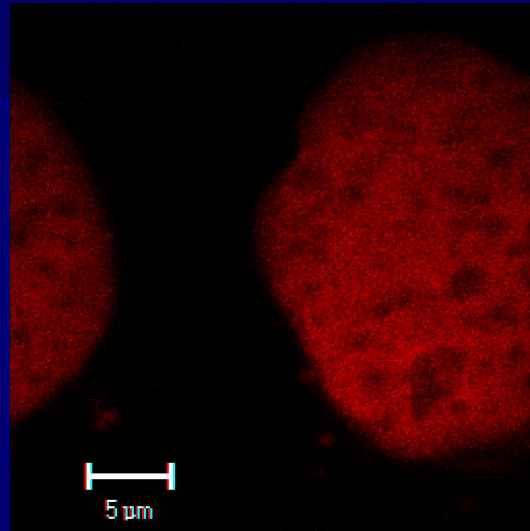
Saf-a N1-12



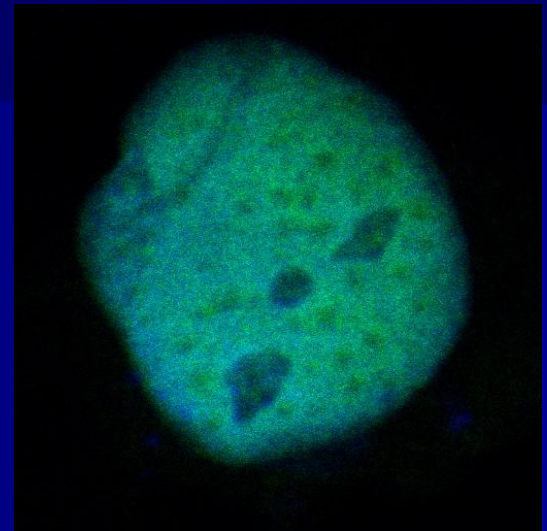
1-250 a/a - DNA-binding region



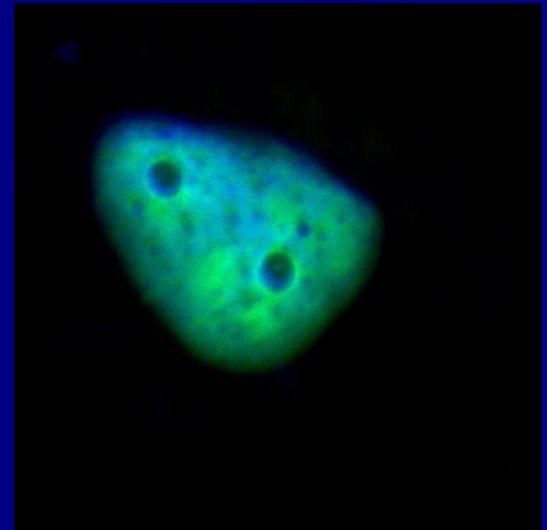
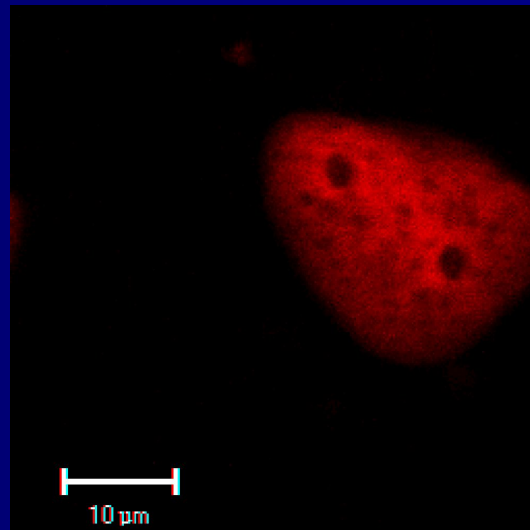
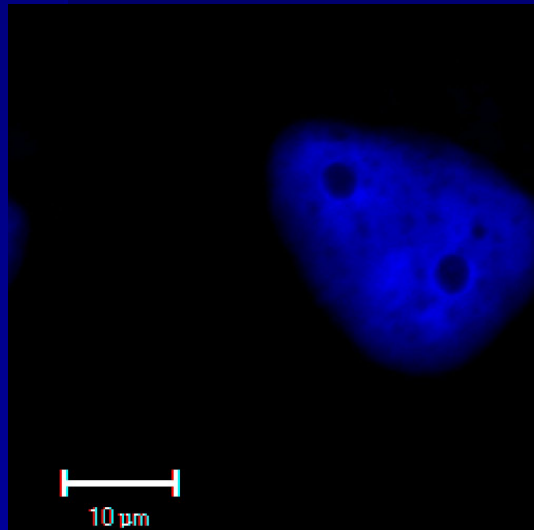
Saf-a 21-22/pEGFP-N1



DAPI



Merged

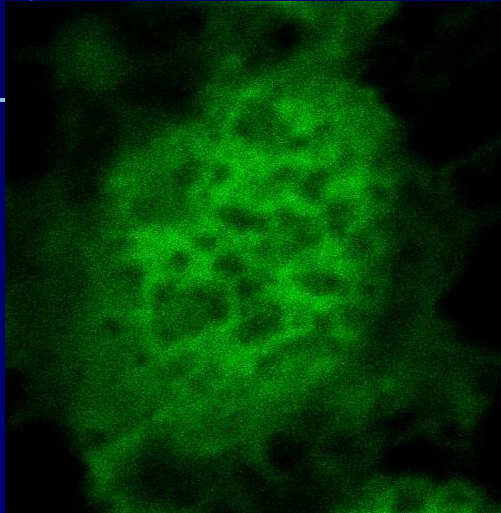


Saf-a 21-22/GFP fusion protein

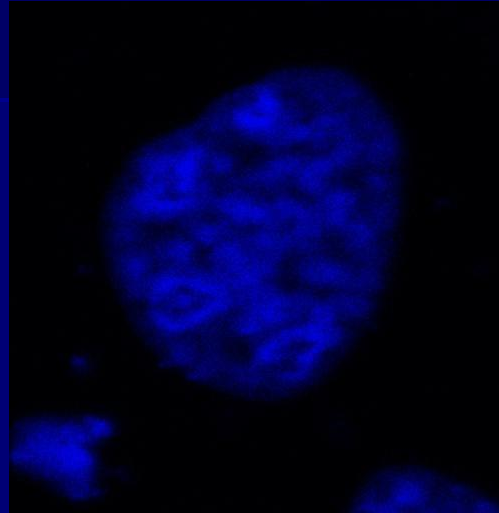
Saf-a 21-22



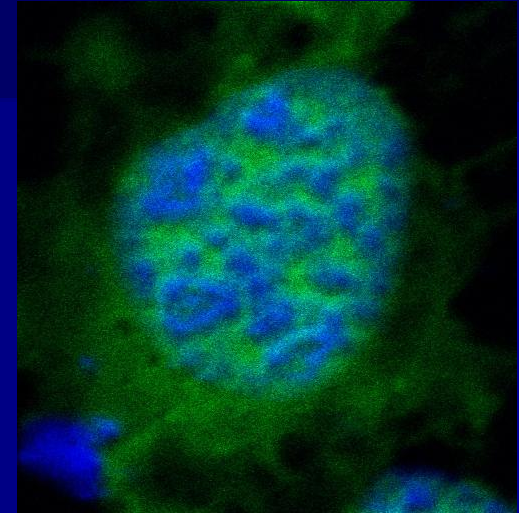
250-550 a/a - middle part, potential NTP binding domain



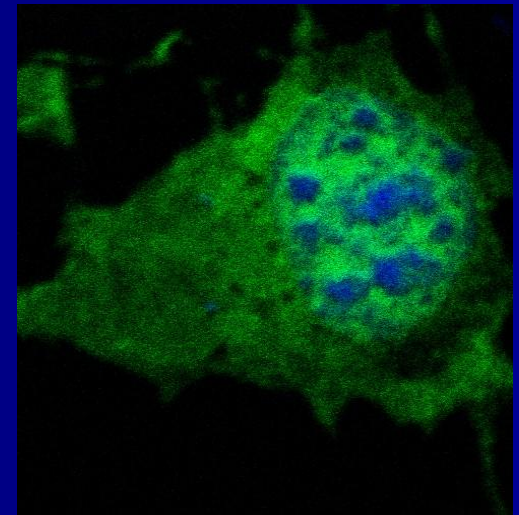
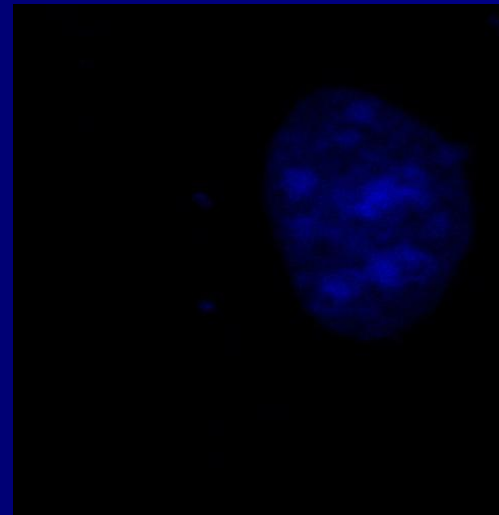
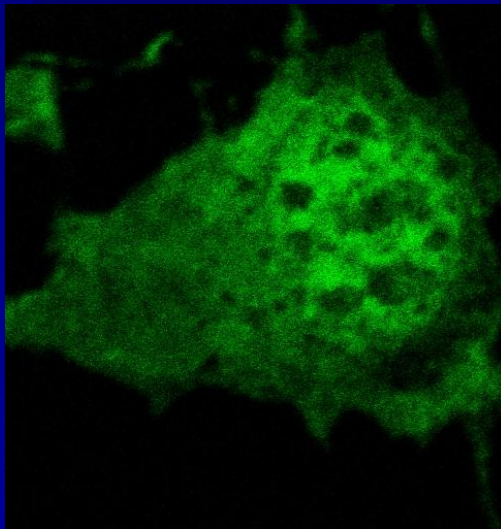
Saf-a 21-22/pEGFP-N1



DAPI



Merged

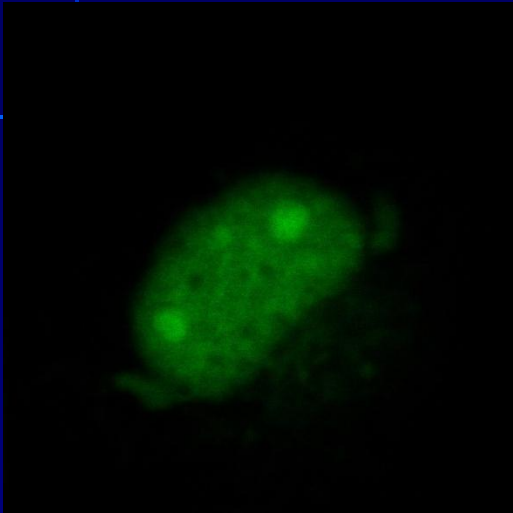


Saf-a 31-N3/GFP fusion protein

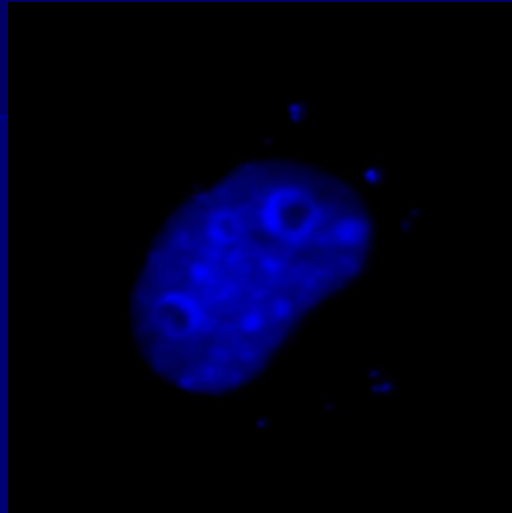
Saf-a 31-N3



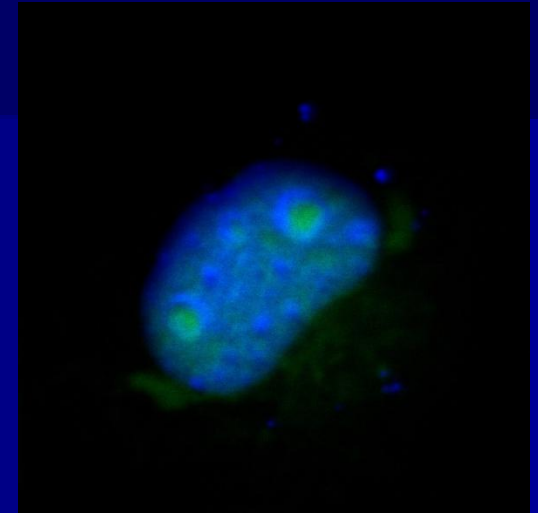
550-823 a/a - RNA-binding region



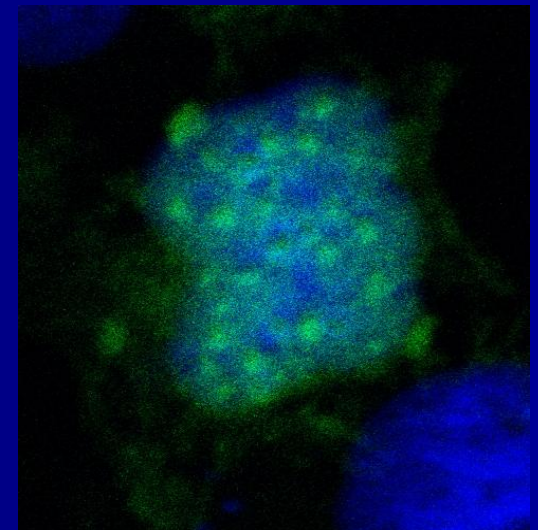
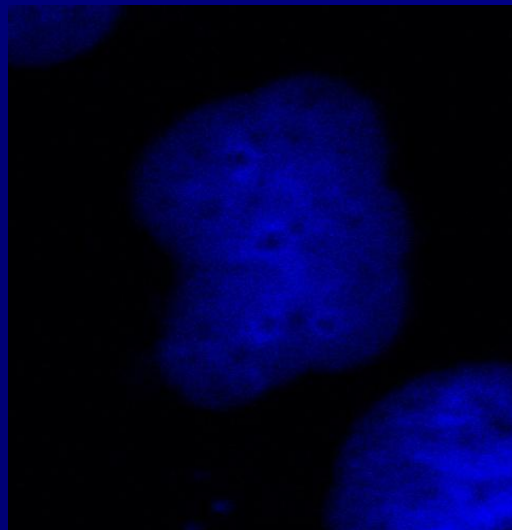
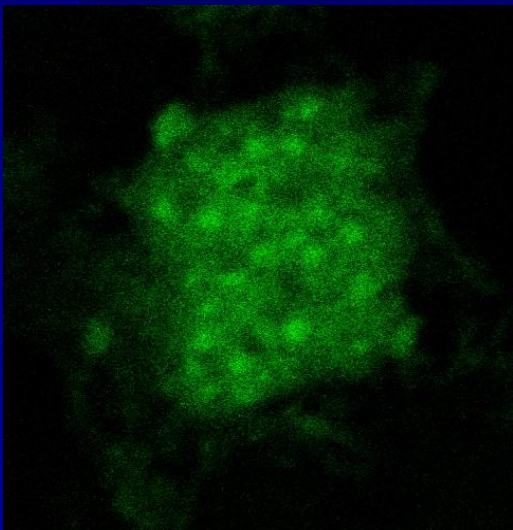
Saf-a 31-N3/pEGFP-N1



DAPI



Merged



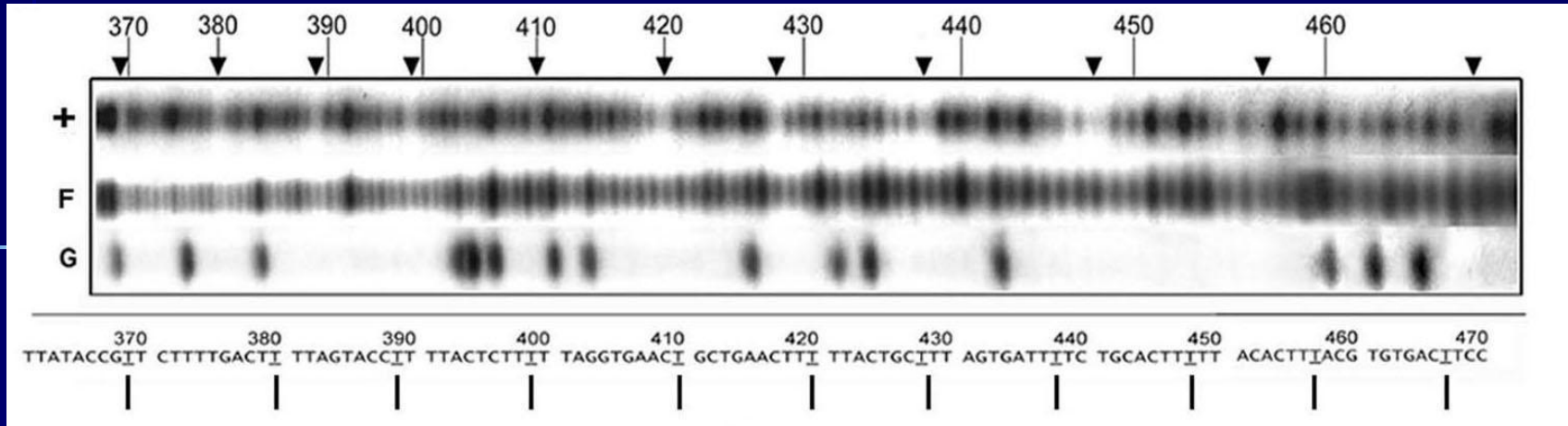
QRTQK motif presents in other nuclear and cytoplasmic proteins

QRTQK

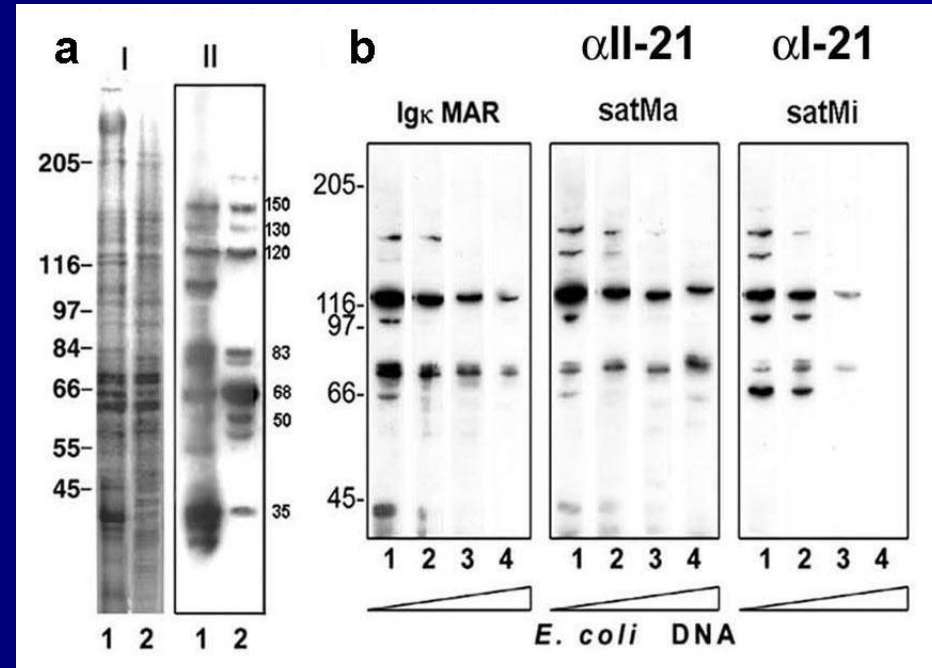
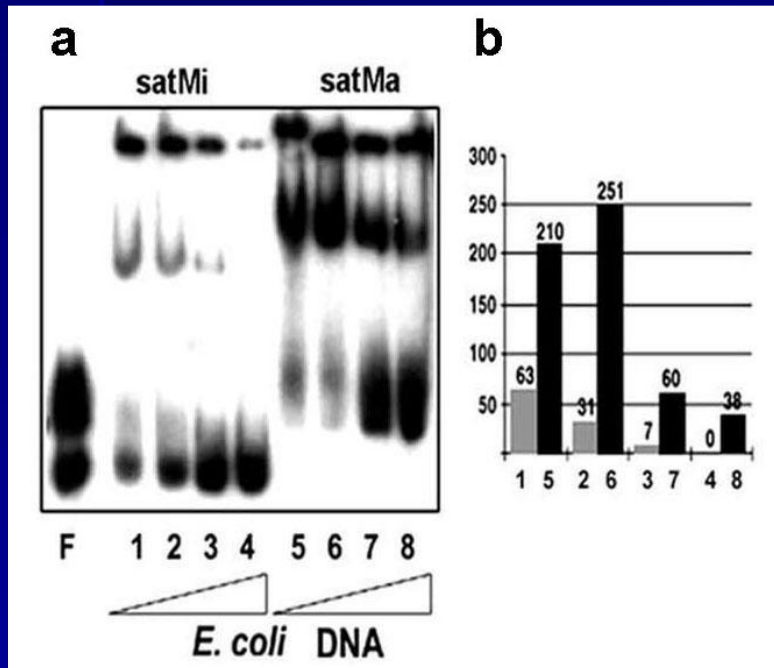
Hrp65-2	507	NQRPQKAA	Chironomus tentants
SAF-A Human	611	KQRTQKKA	Homo sapiens
SAF-A Xenopus	557	KE RT QKKS	Xenopus laevis
RNA polymerase	56	KE RT QK KK	Plasmodium falciparum
Matrin CYP Danio	363	M QRT QKAK	Danio rerio
Matrin CYP Rat	363	M QRA Q R M R	Rattus norvegicus
S6 ribosomal protein	195	K QRT Q K NK	Homo sapiens
Slac2c	784	K QRT Q V QT	Homo sapiens
Desmoplakin	1608	K QRT Q E EEL	Homo sapiens

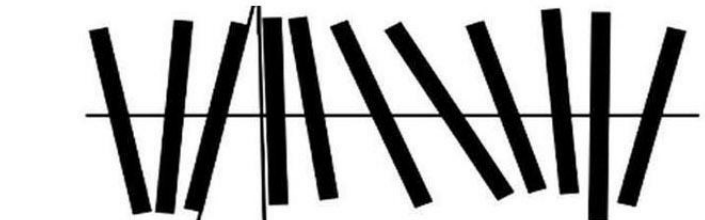
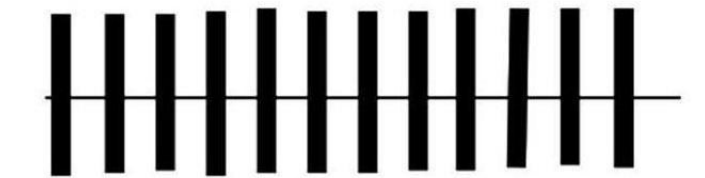
Hrp65-2 (CAC42828 - C. tentants), SAF-A Human (NM_031844 - Homo sapiens, NP_058085 - Mus musculus), SAF-A Xenopus (AAD02820 - Xenopus laevis), DNA-dependent RNA polymerase (NP_701124 - Plasmodium falciparum), Matrin cyclophilin Danio (AAH44189 - Danio rerio), Matrin Cyclophilin Rat (AAC00191 - Rattus norvegicus), S6 ribosomal protein (Q9YGF2 - Oncorhynchus mykiss, NP_989152 - Xenopus tropicalis, NP_990556 - Gallus gallus, CAC69540 - Elaphe sp., AAH27620 - Homo sapiens, AAH10604 - Mus musculus), Desmoplakin (XP_225259 - Rattus norvegicus, NP_004406 - Homo sapiens, BC033467 - Mus musculus), Slac2c (BAC15555 - Homo sapiens, AAP94626 - Rattus norvegicus, Q8K3I4 - Mus musculus).

Saf-a/hnRNP U DNA binding

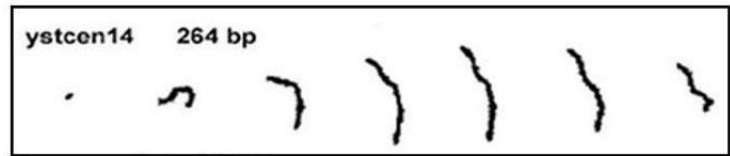
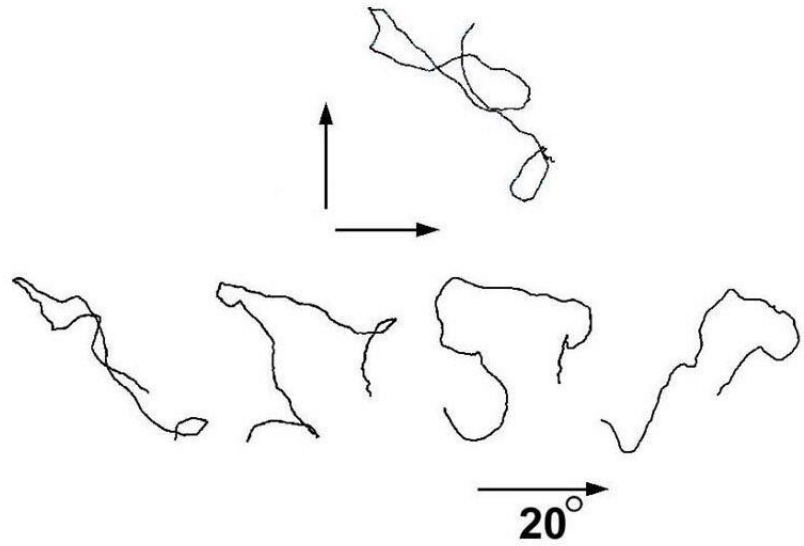
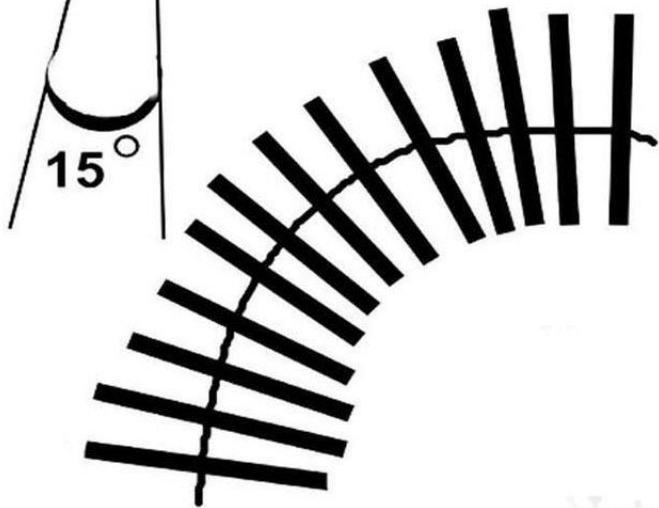


Southwestern blot

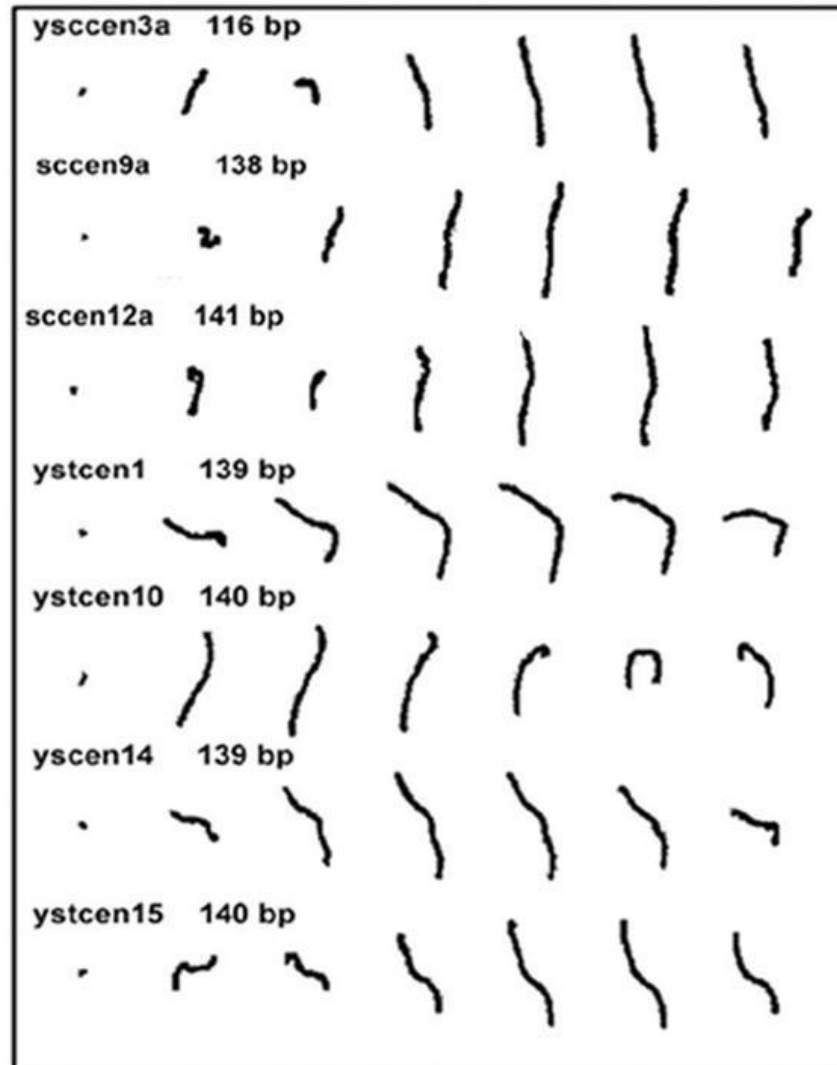




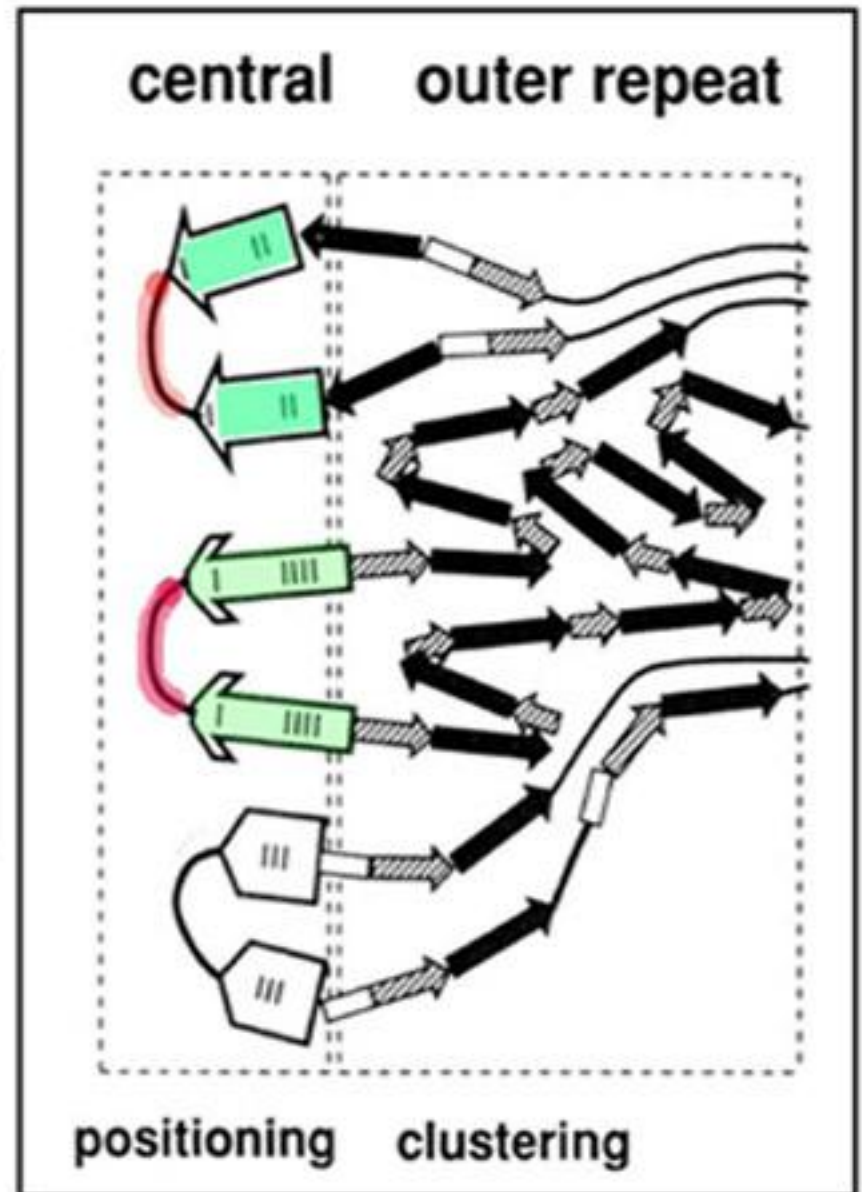
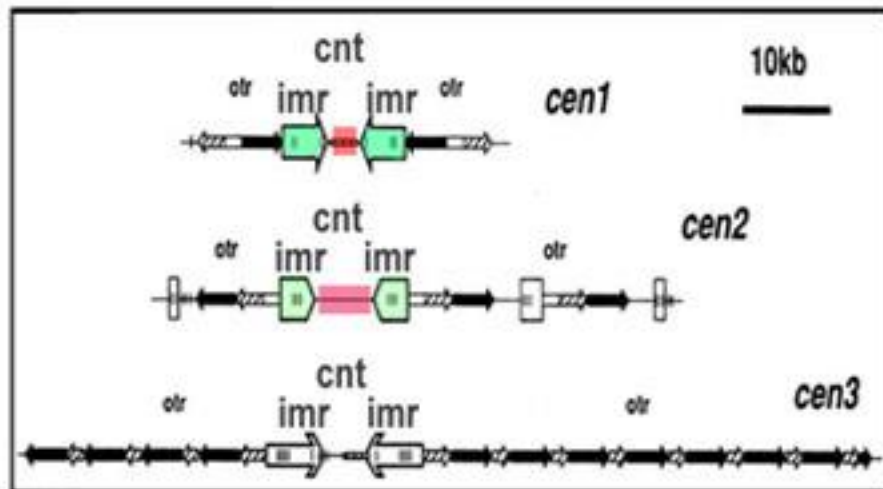
wedge

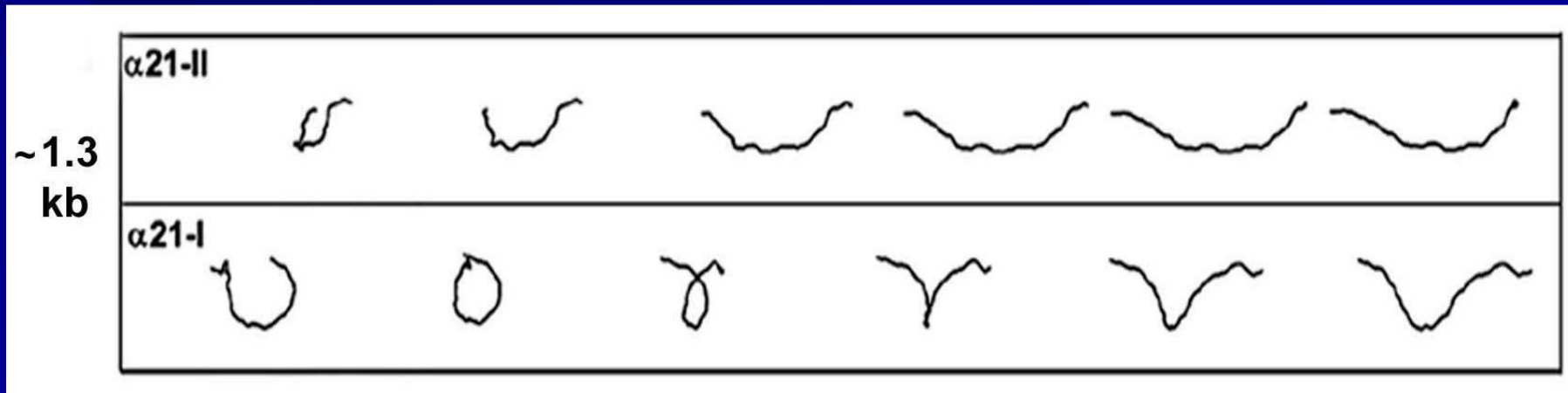
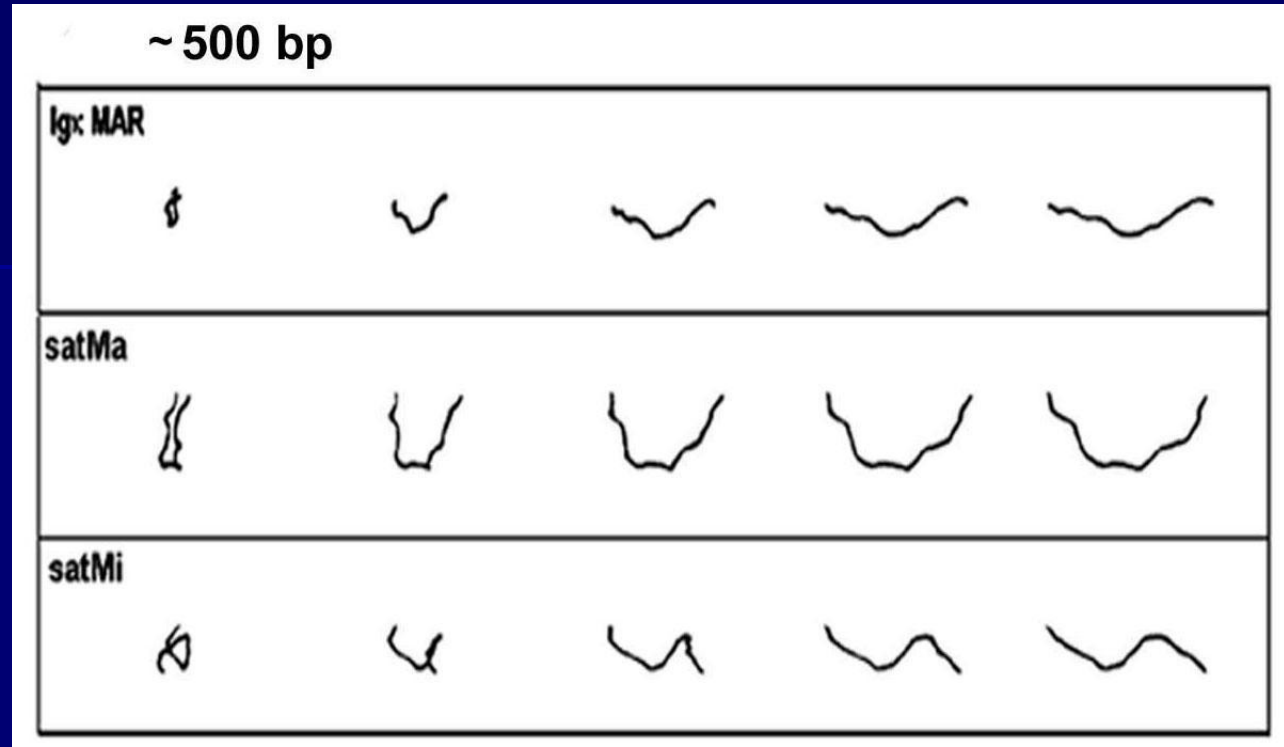
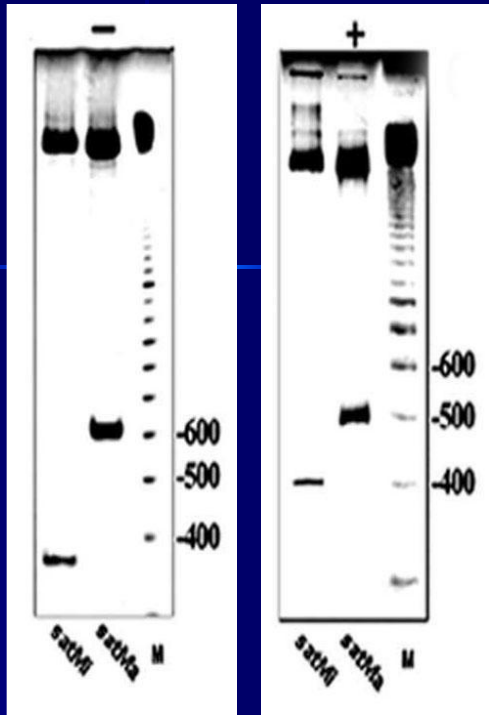


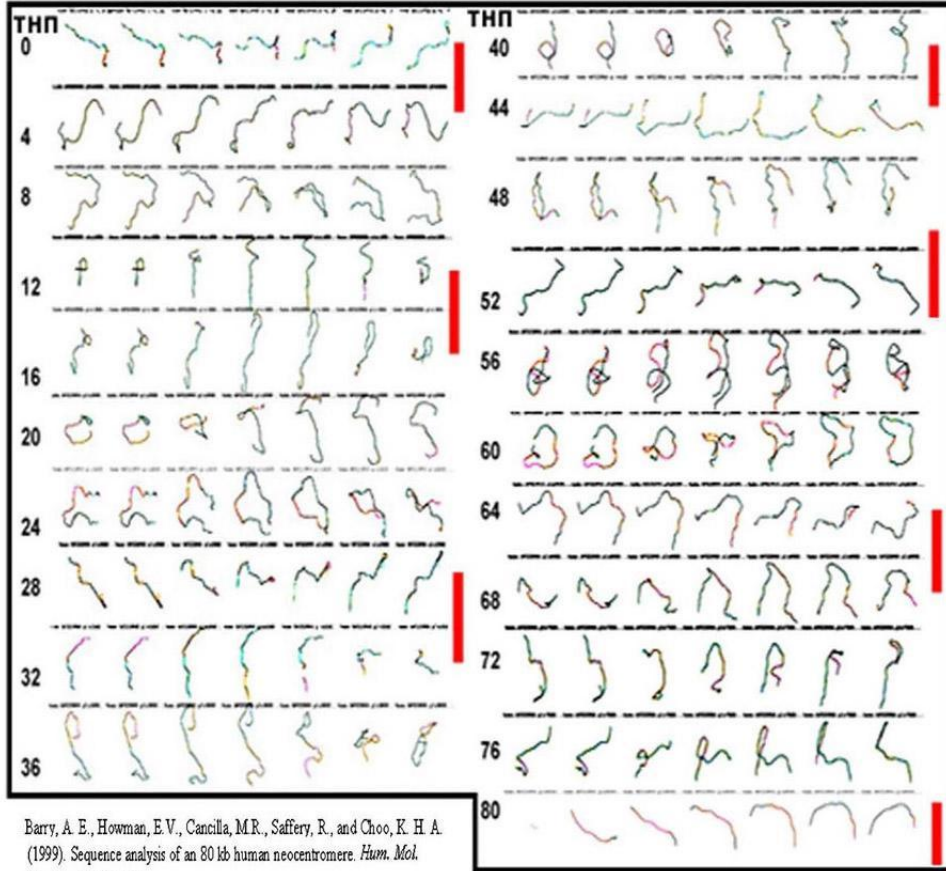
S.cerevisiae



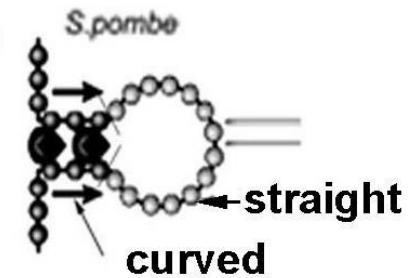
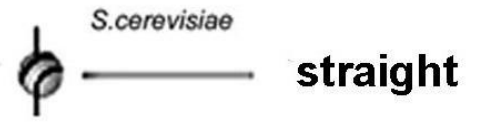
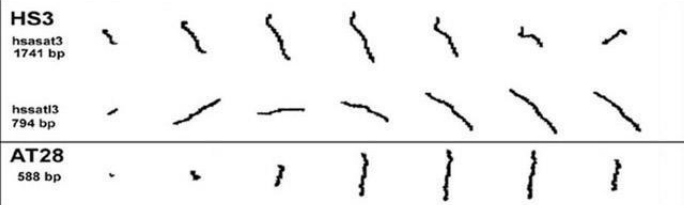
S.pombe



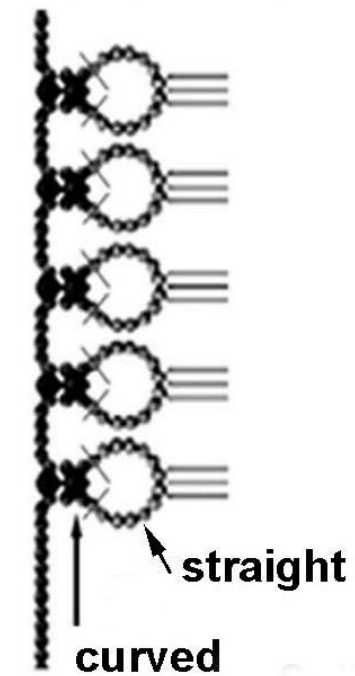


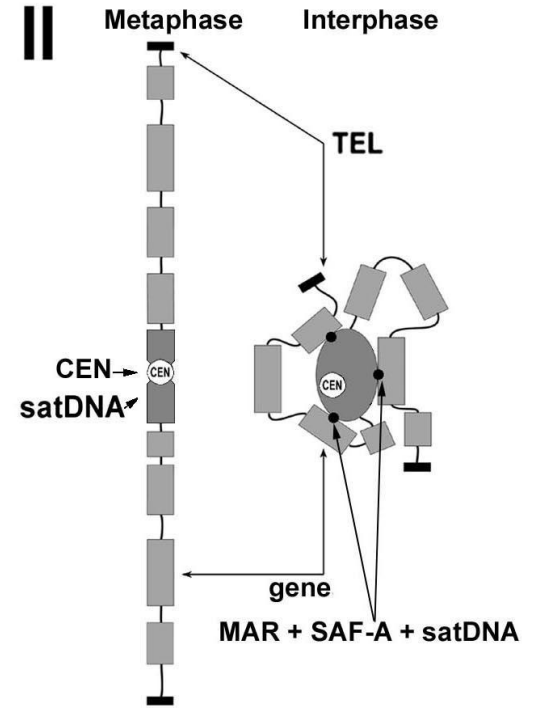
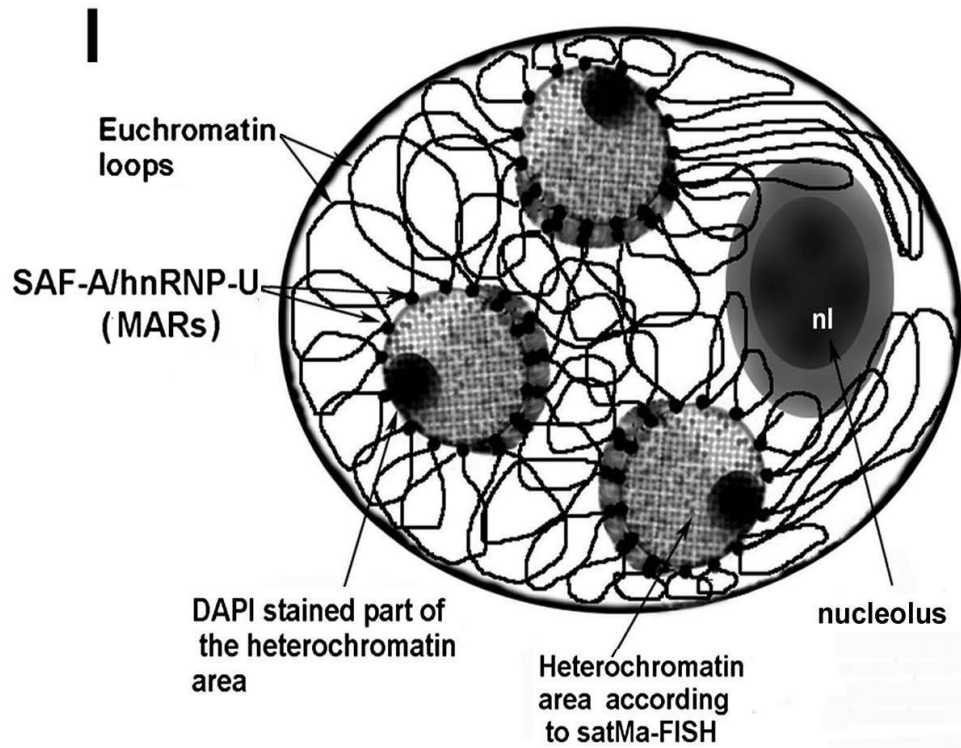


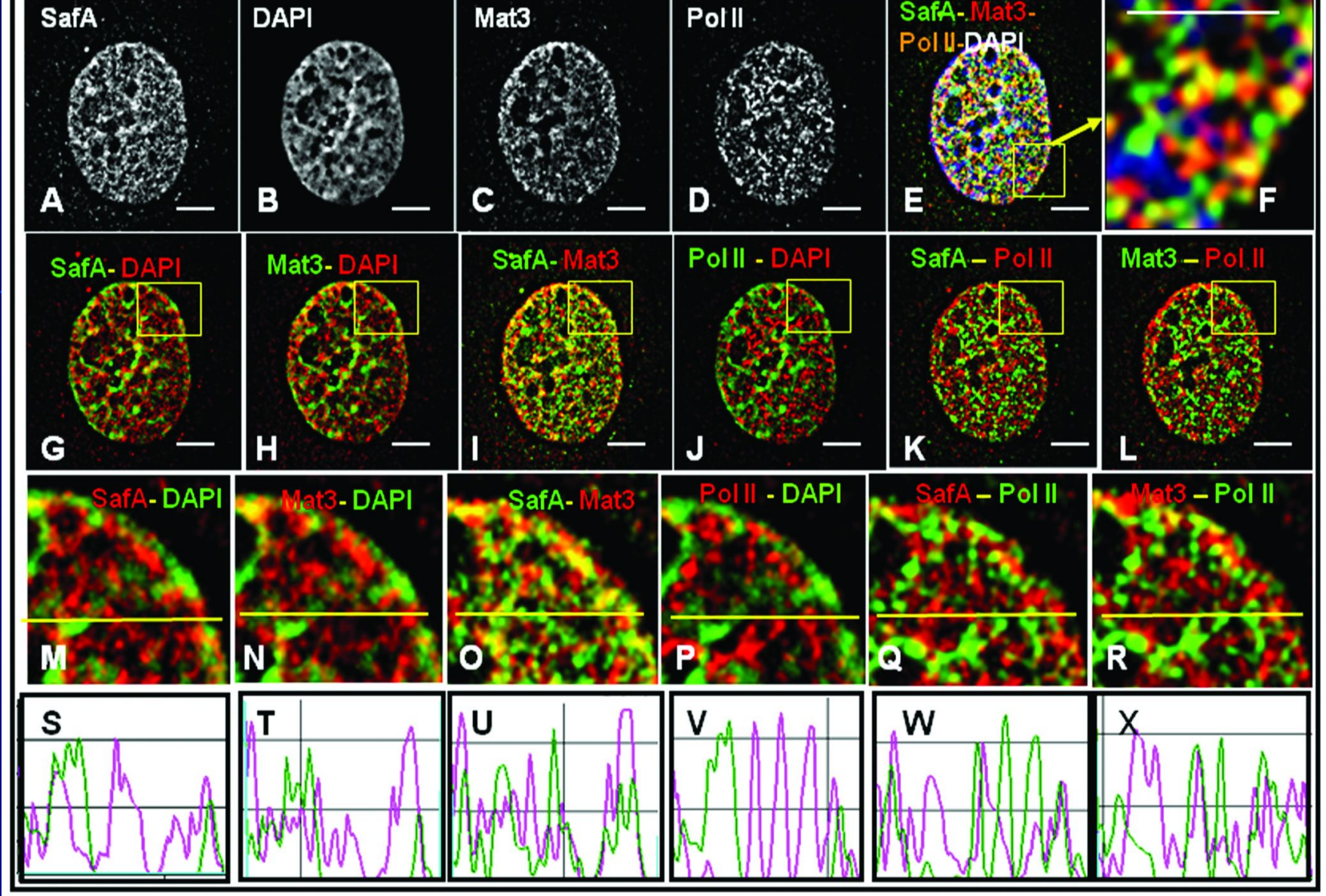
Barry, A. E., Howman, E. V., Cancilla, M. R., Saffery, R., and Choo, K. H. A. (1999). Sequence analysis of an 80 kb human neocentromere. *Hum. Mol. Genetics*, 8, 217-227.



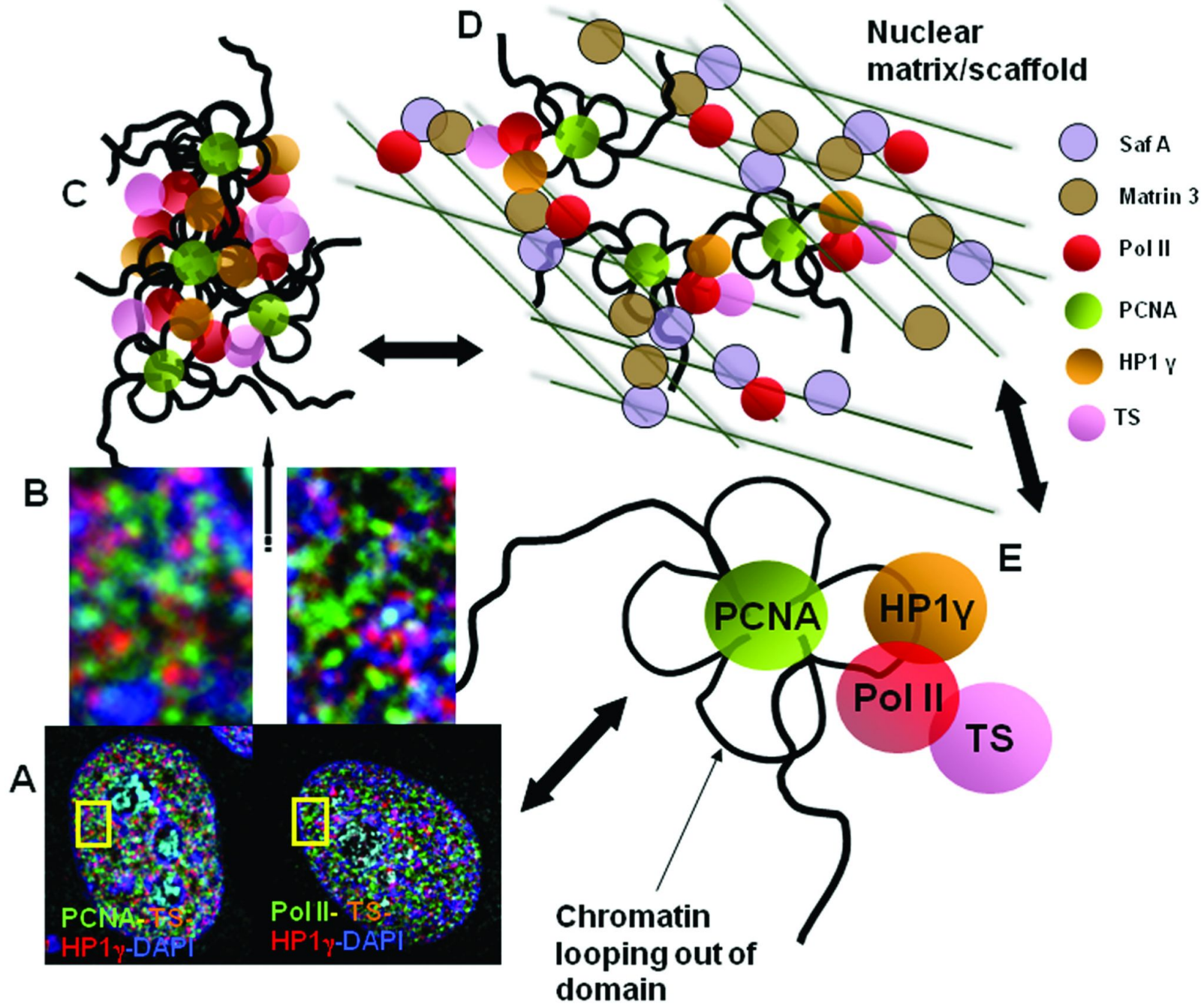
D.melanogaster, H.sapiens



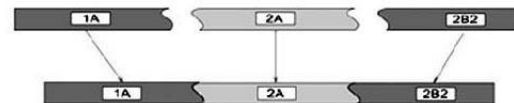




Identifying Functional Neighborhoods within the Cell Nucleus: Proximity Analysis of Early S-Phase Replicating Chromatin Domains to Sites of Transcription, RNA Polymerase II, HP1 γ , Matrin 3 and SAF-A
 MalyavanthamBerezney, J Cell Biochem. 2008



1

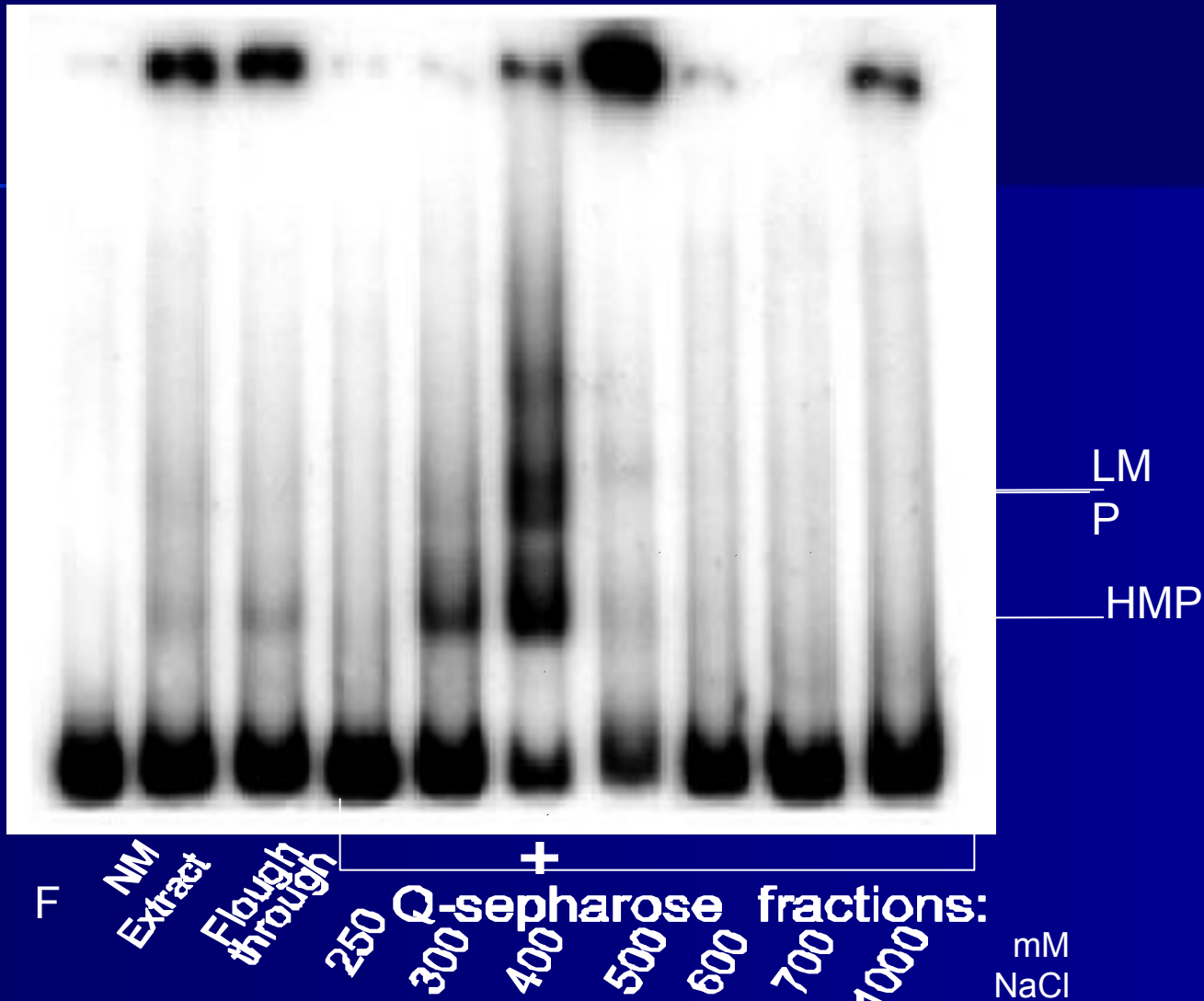


2

Hnfh200 P19246	----- LQ 2
Hnf66 Q16352	----- LQ 2
RATlama 1072002	----- LQ 2
Hkert1 Q14525	----- HQ 2
mTRF2 NP_033379	HAGGGGSSDSSGRAASRRASRSGGRARRRHEPGLGGAERGAGEARLEE 50
	↑ Dim
Hnfh200 P19246	ALN-----DRFAGYIDK-----VRQLEAHNRSLEV 27
Hnf66 Q16352	GLN-----DRFAVFIEK-----VHOLETCNRALEL 27
RATlama 1072002	ELN-----DRLAVYIDR-----VRSLETEHAGLRL 27
Hkert1 Q14525	FLN-----DRLASYLEK-----VRQLERDN-AELL 26
mTRF2 NP_033379	AVNRAVVLKFFYFHEALRAFSSRYRDFRQIRDINQALLVRPLGKEHTVSRL 100
	* : : : *
Hnfh200 P19246	TSALREIRAQLEGH-----AVEYODLLNVKHALDIEIAAYRKL 66
Hnf66 Q16352	TAALREIRAQYES-----LAEYODLLNVKHALDIEIAAYRKL 65
RATlama 1072002	ADALQELRAQHED-----QVEYQELLDIKLALDHEIHAYRKL 65
Hkert1 Q14525	NQVLNETRQYEA-----LVEYQVLLDVRARLECEINTYRSL 64
mTRF2 NP_033379	LRVNQCLSRIEEENLDCSFDHEALTPLESAINVLEHIKTEFTLTDSHV 150
	. . . * . . . : : : . . . * : . . .
Hnfh200 P19246	EGEE-----70
Hnf66 Q16352	EGEE-----69
RATlama 1072002	EGEE-----69
Hkert1 Q14525	ESED-----68
mTRF2 NP_033379	ESSRKLVKAAVVICIKNKEFEKASKILKKYHNSKPTTQKLRDLDLNIIR 200
	* . .
Hnfh200 P19246	-----VKNHALDIEIAA
Hnf66 Q16352	-----VKNHALDIEIAA
RATlama 1072002	-----VKNHALDIEIAA
Hkert1 Q14525	-----VKNHALDIEIAA
mTRF2 NP_033379	EKNLAHPVIGNFSYEVFQKHLRFLESHLDDTEPYLLTHAKKALKSESAA 250
	* * * * *
	↑ Dim
Hnfh200 P19246	-----LTAALREIRAQYESLA-
Hnf66 Q16352	-----LTAALREIRAQYESLA-
RATlama 1072002	-----LTAALREIRAQYESLA-
Hkert1 Q14525	-----LTAALREIRAQYESLA-
mTRF2 NP_033379	SSTNRESKHPEPVEKFLREPPRQPQNPPATGIZRTLKAAPKALSTAQDSE 300
	* . : * : * : : * :
mTRF2 NP_033379	AAFAKLDQKDLVLANLASPSSPAHKYKRPKDEHESAAPAEGEGSSSRQP 350
mTRF2 NP_033379	RNSPMTISRLLLEEDSQSTEPSPGLNSSHEAMSASKPRALNQPHPGKPK 400
Hnfh200 P19246	-----
Hnf66 Q16352	-----
RATlama 1072002	-----LADALQELRAQHEDQV-
Hkert1 Q14525	-----LADALQELRAQHEDQV-
mTRF2 NP_033379	KASKDKWNSPNGLEEKVWLEEDQLFEVQAPGEDRSSSLTRKQKUTIEES 450
	* * * : * * * :
	↑ Myh
mTRF2 NP_033379	EWVKDGVRRKYEGENWAAISKSYPFVNRATAVHIKDRURTHKLGHI 495
	↑ Myh

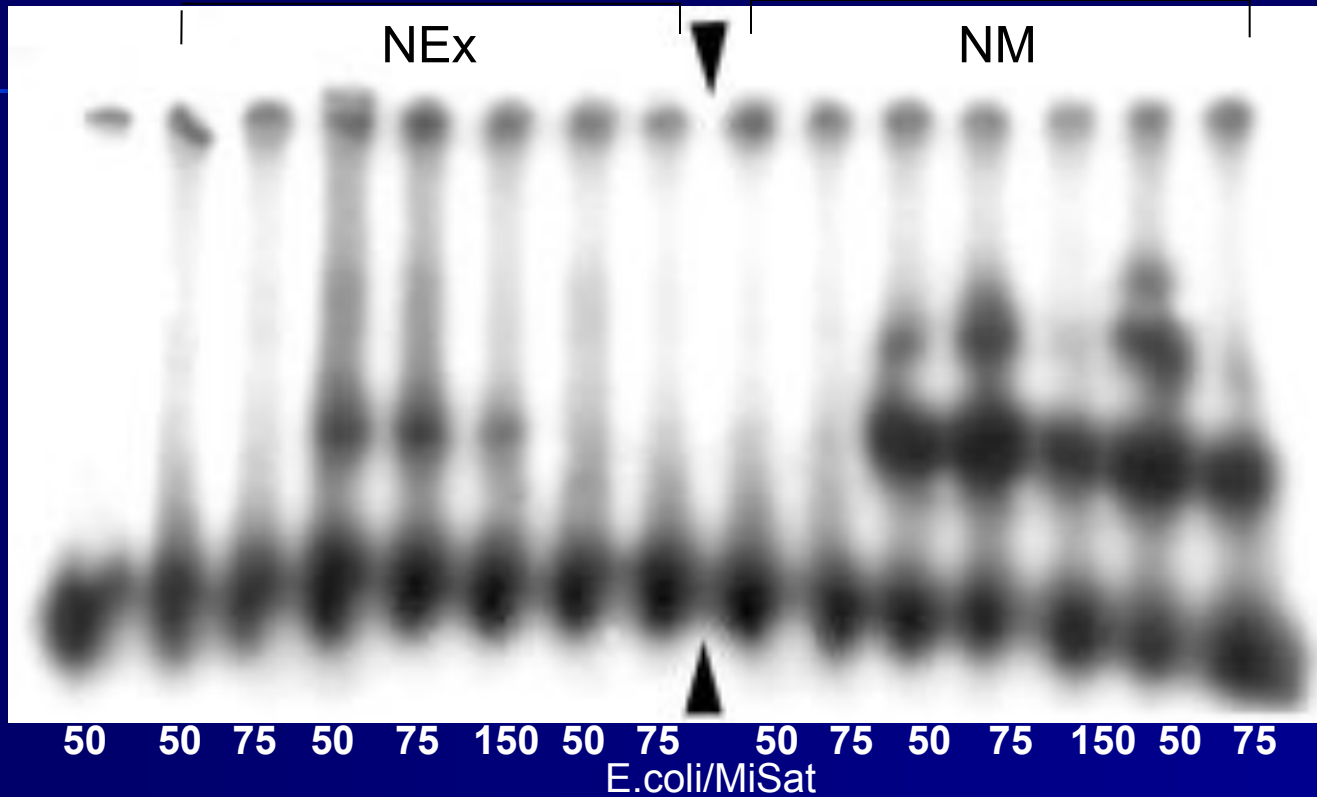
TRF2 sp domen

Homo sapiens



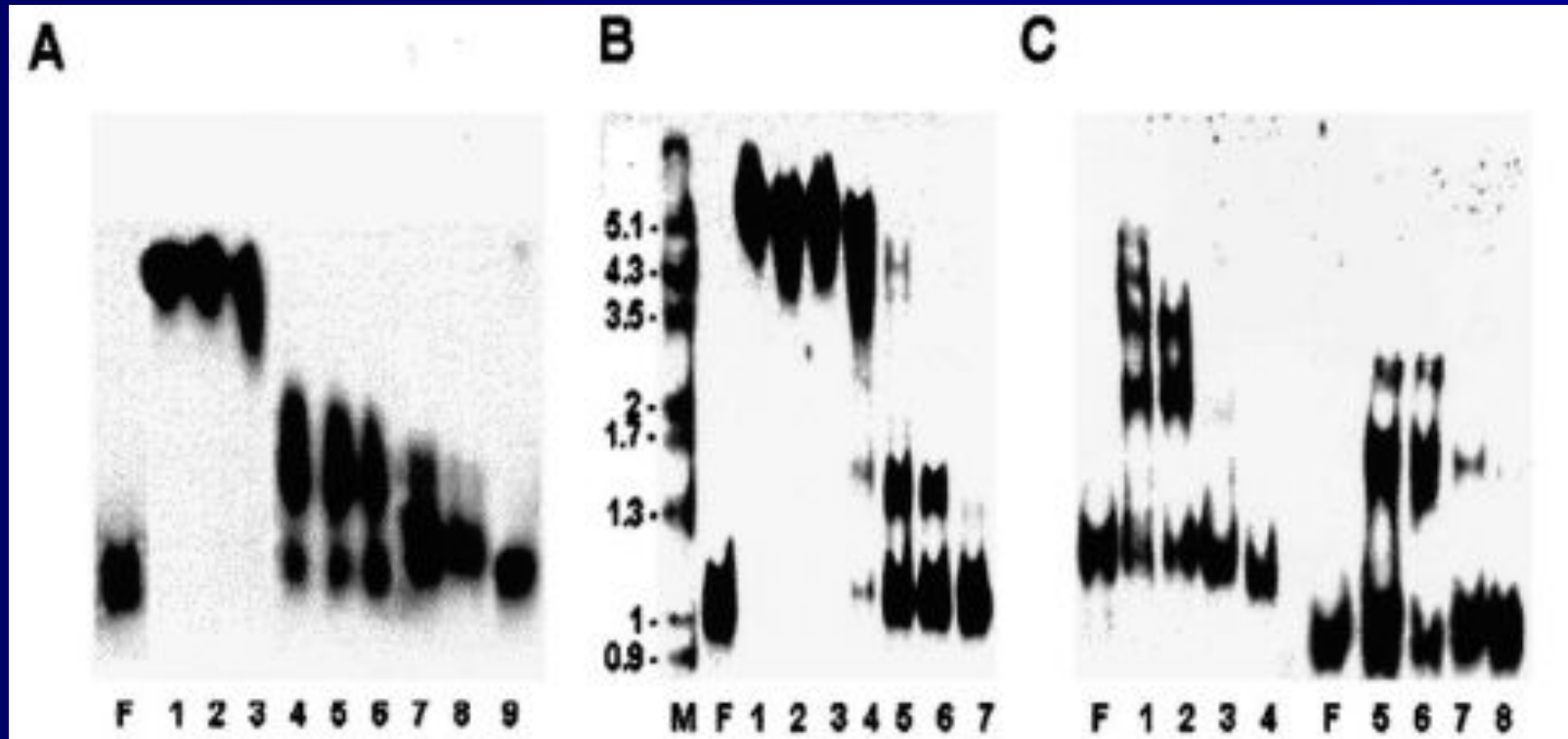
- ЯМ человека связывает центромерную альфа-сателлитную ДНК

Mus musculus



- ЯМ мыши связывает ДНК минорного сателлита

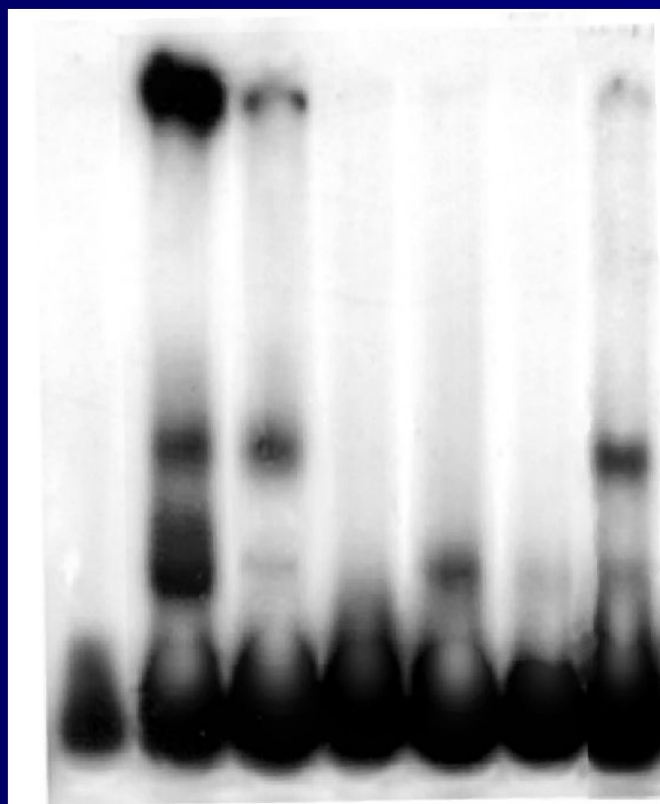
Homo sapiens



- ЯМ человека связывает прицентромерный сателлит 3

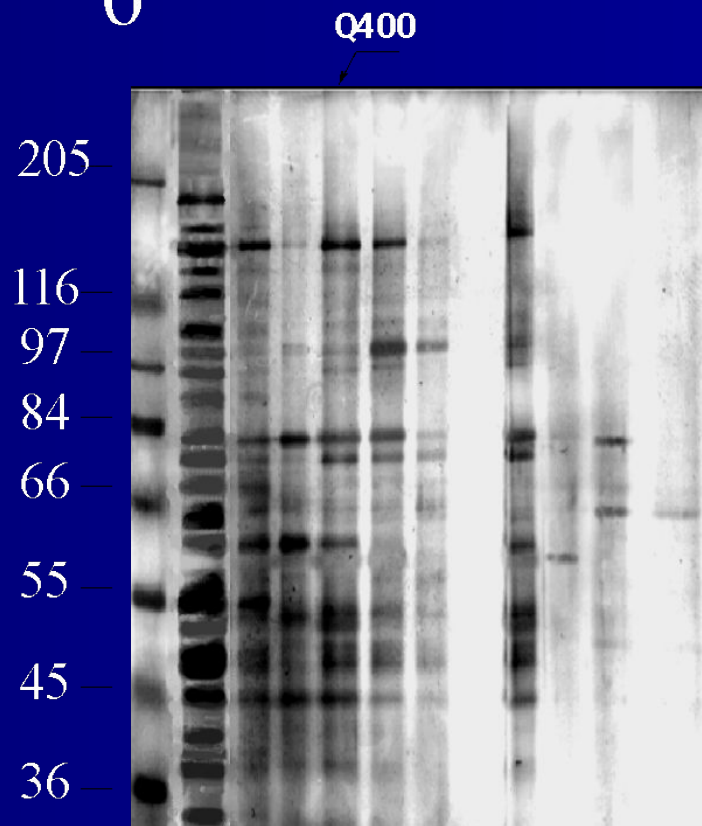
Аффинная хроматография

а



1 2 3 4 5 6 7

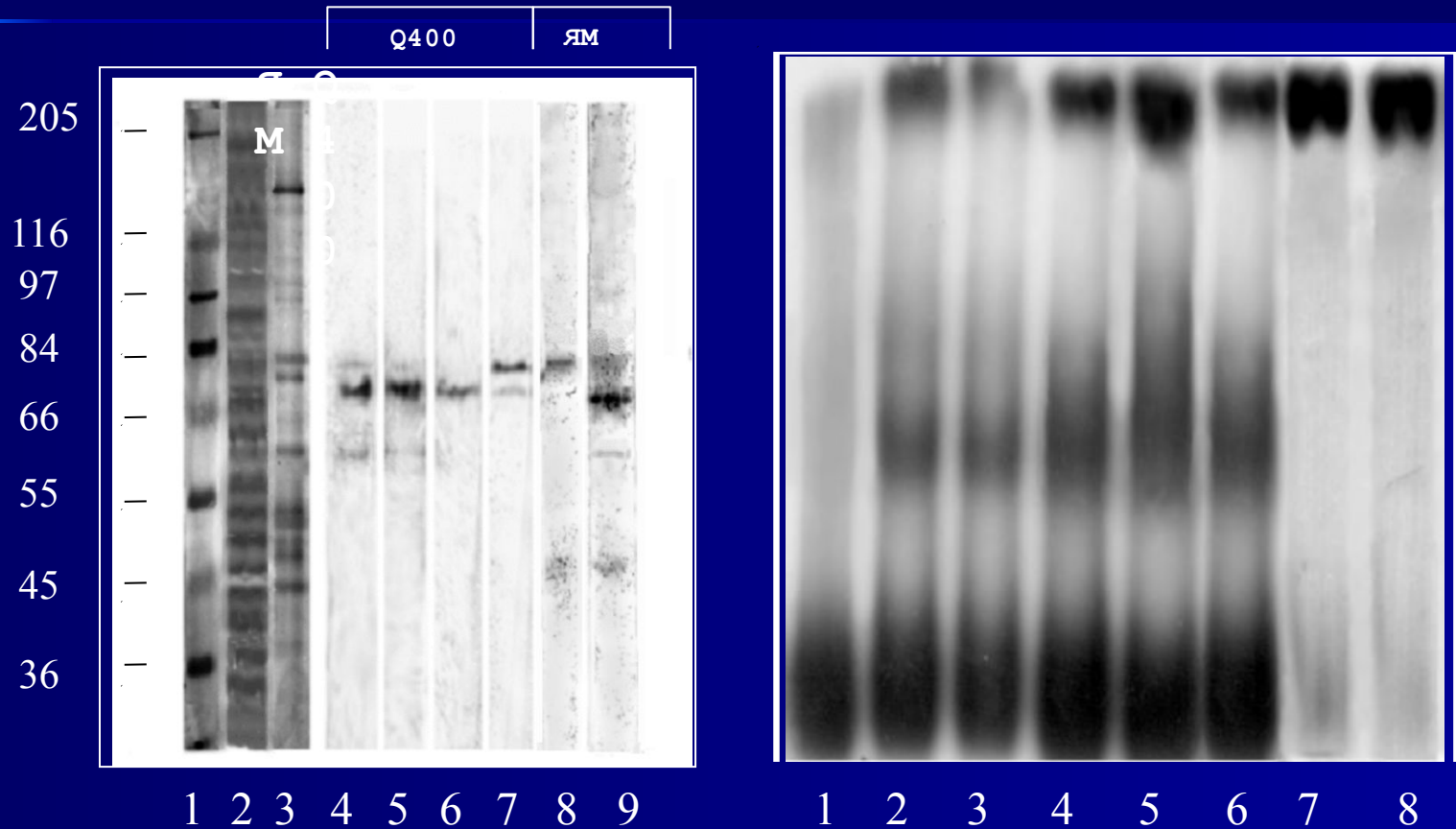
б



1 2 3 4 5 6 7 8 9 10 11

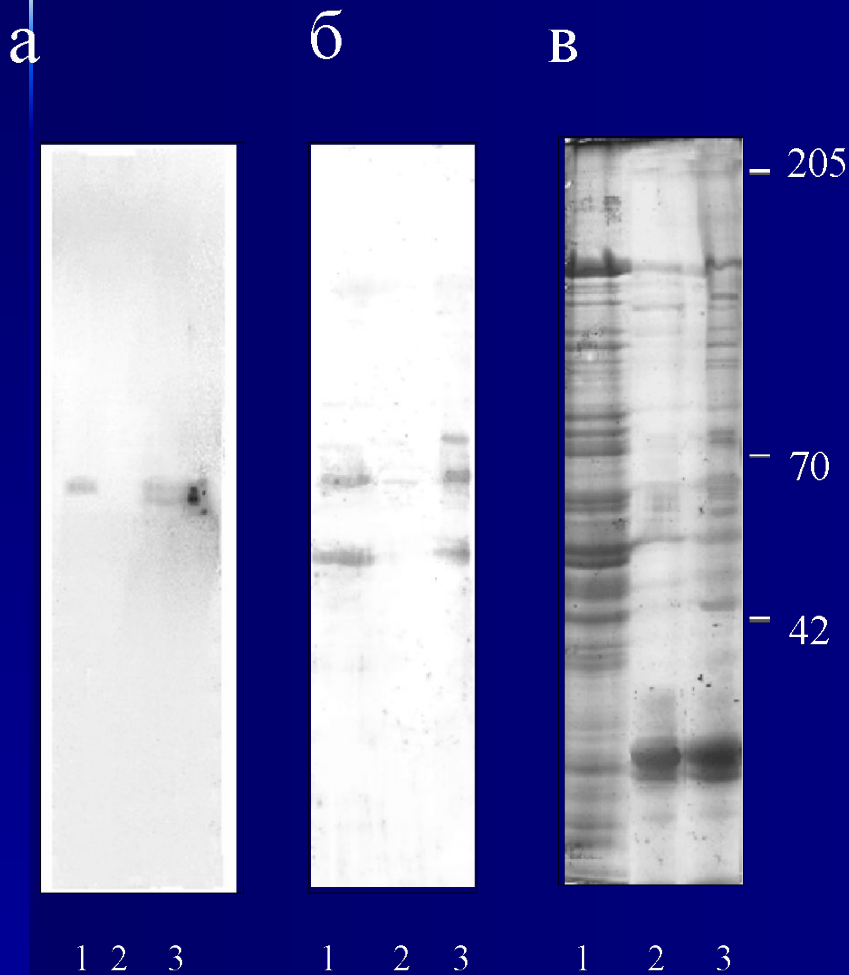
- Белок 70 кДа ЯМ человека связывает α -сат ДНК

Получение АТ



- Поликлональные АТ распознают белки массой р80, р70 и р57

Саузвестерн гибридикация

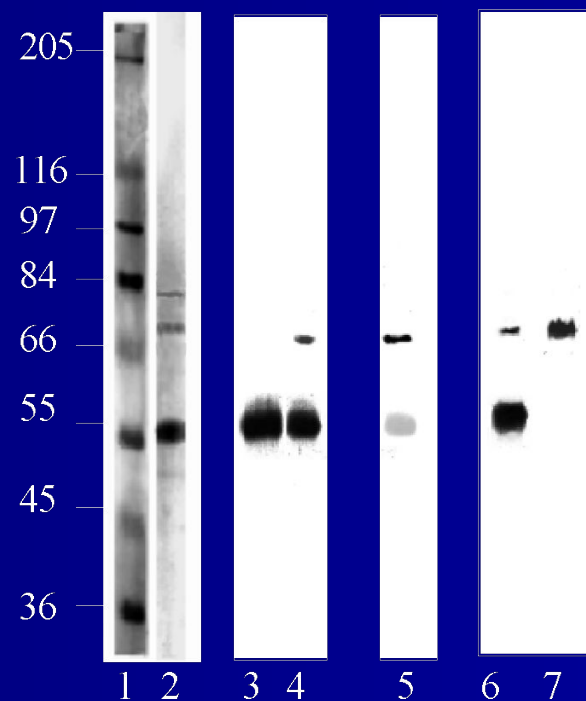
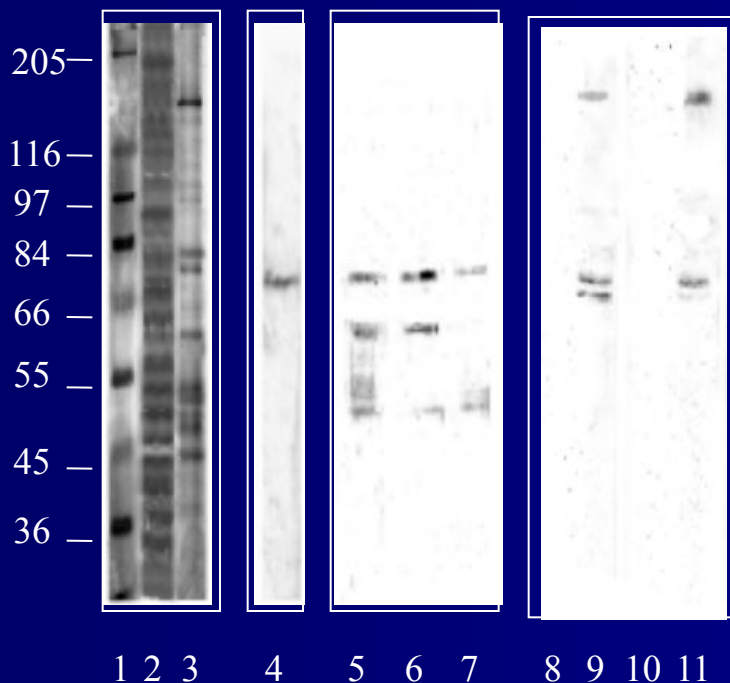


- Среди белков, распознаваемых сывороткой именно р70 отвечает за связывание с ДНК

Выявление IFA детерминанты

6

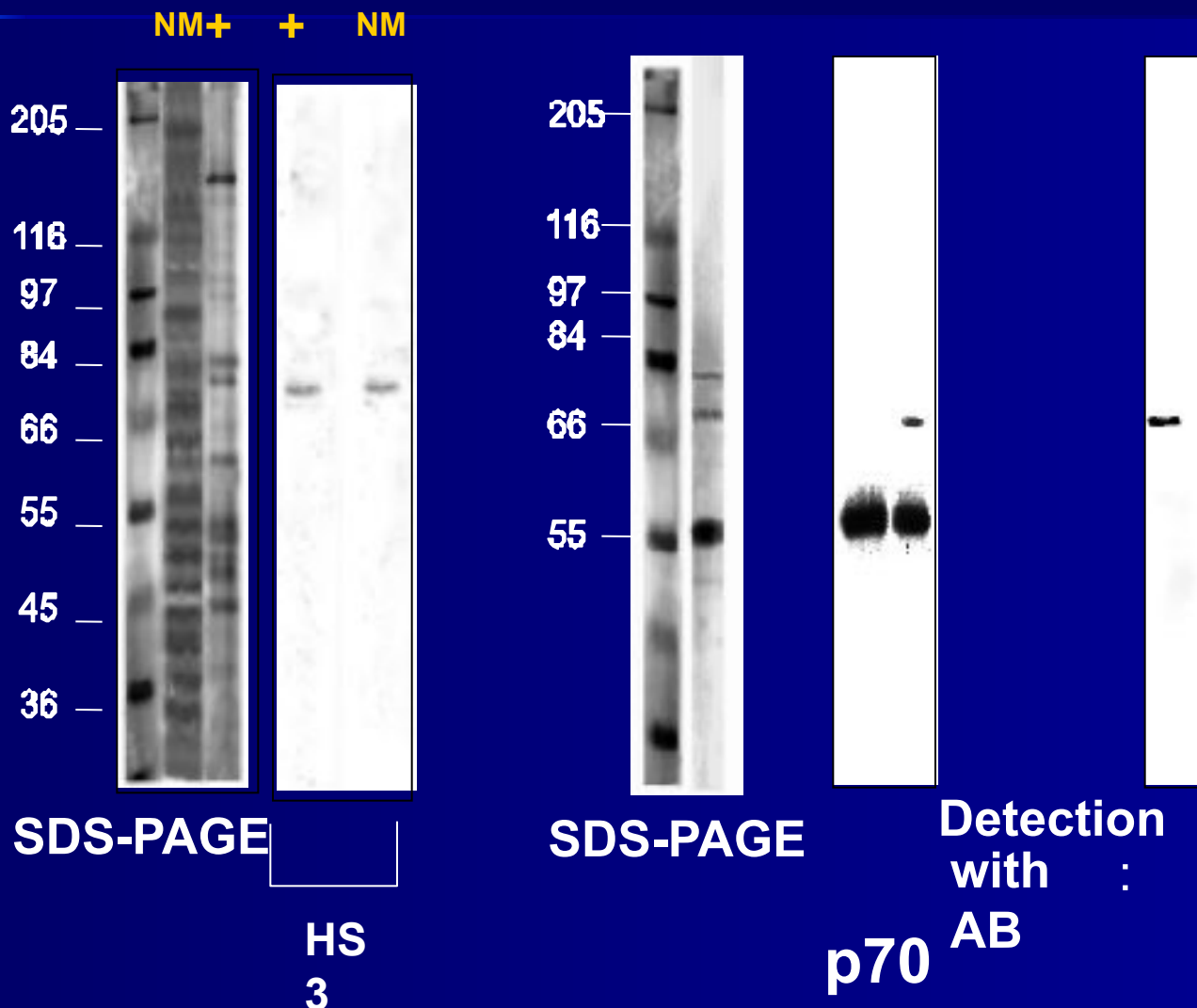
а

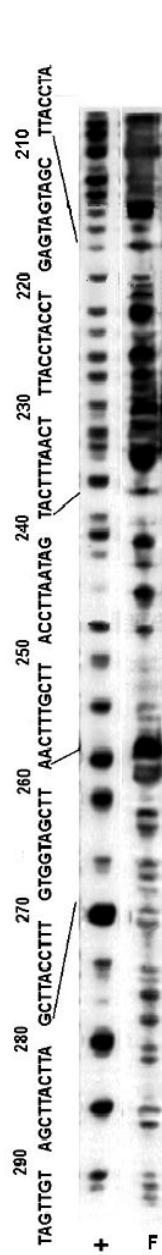
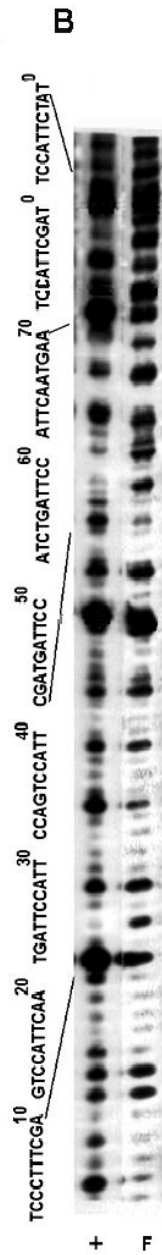
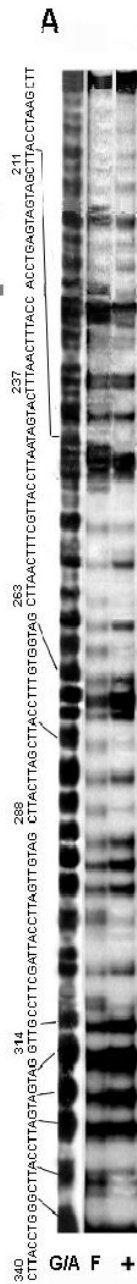


ДНК E. Coli

- Белок p70 обладает общей антигенной детерминантой с белками промежуточных филаментов

P70 связывает α -сат ДНК и ДНК сателлита 3





TCCCTTTCGA 11
TCCATTCAA⁰TG ATTC⁰CATT CCAG⁰TC 36
CATT⁰CGAT⁰GAT⁰TCC⁰ATCTGATCCA 61
TTCA⁰ATGA⁰ATCC⁰ATTCG⁰ATT CC⁰ATTC 87
TATG⁰ACG⁰ATT⁰CC⁰ATTC ATT⁰CC⁰ATCT 113
GATG⁰ATG⁰ATT⁰CC⁰ATTCG⁰ATT CC⁰ATTTC 139
AA⁰TG⁰AT⁰AC⁰CA⁰TTCG⁰ATT CC⁰ATTG 162
GATG⁰ATG⁰ATT⁰CA⁰ATCA⁰ATTT ATTC 188
GATG⁰ATT⁰CC⁰ATTCG⁰AAT CC⁰ATTC 211
GATG⁰ATG⁰AG⁰TCC⁰AA TGG⁰ATTCA⁰ATTT 237
CATG⁰ATA⁰ATCC⁰ATTCG TTTC ATTC 263
GATG⁰GTG⁰TTCC⁰ATTCG⁰ATT C ATTC 288
GATG⁰TG⁰ATTCC⁰ATTAGCT CCG⁰TG 314
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GATGATGATC
 * - GATGATGATTCCATTCCGATTCCATTCC

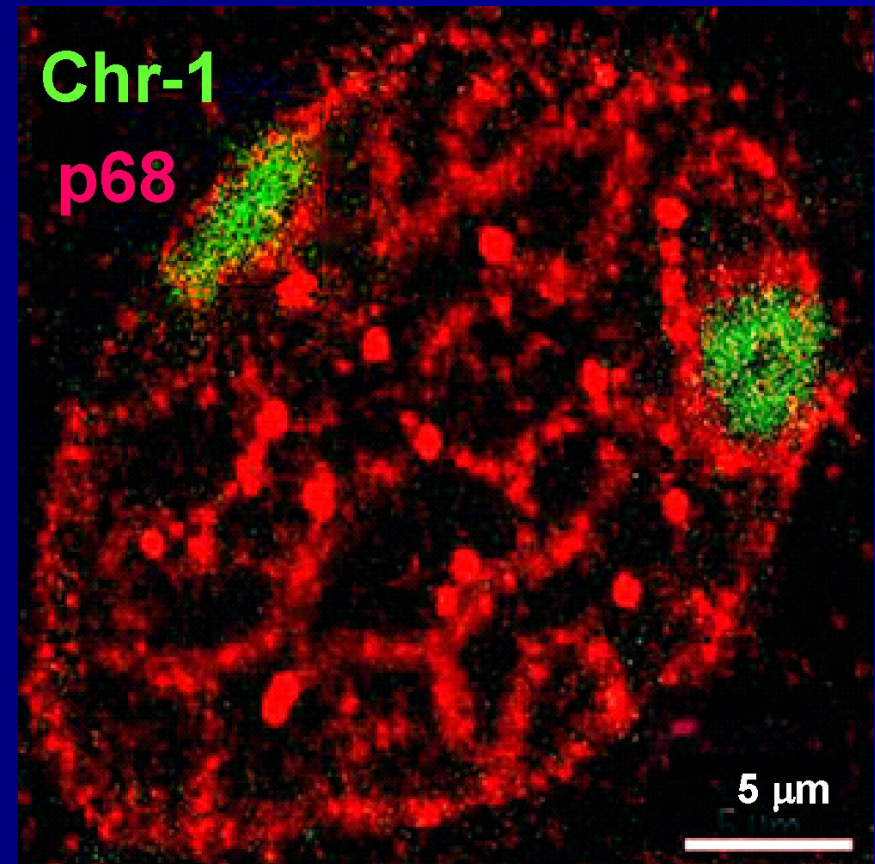
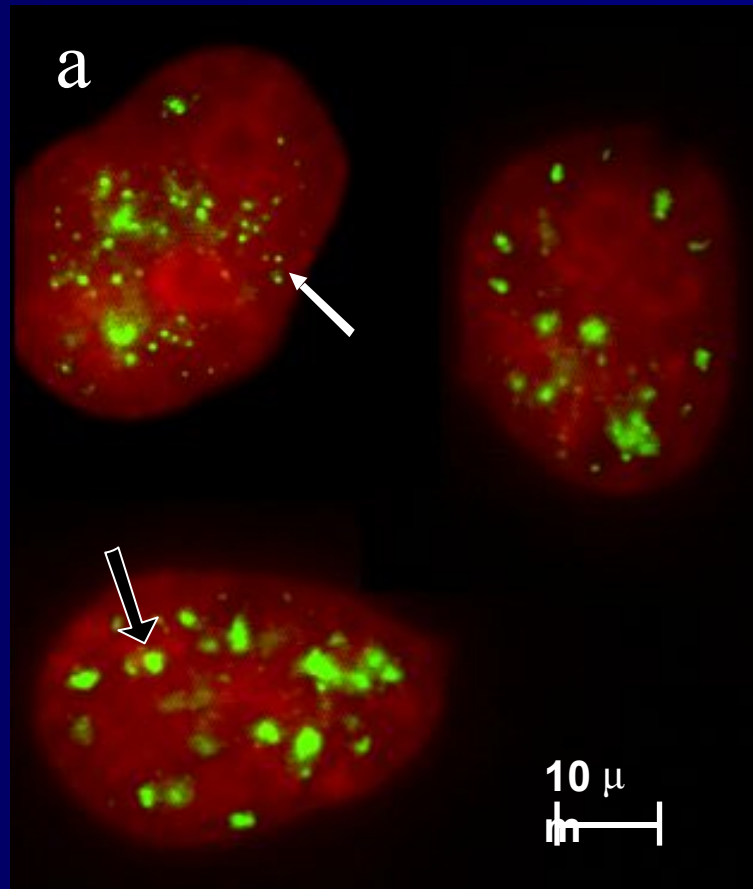
Mass-spectrometry analysis:

**p70=RNA-helicase p68=
DEAD/H box polypeptide 5**

Распределение p70 в ядре

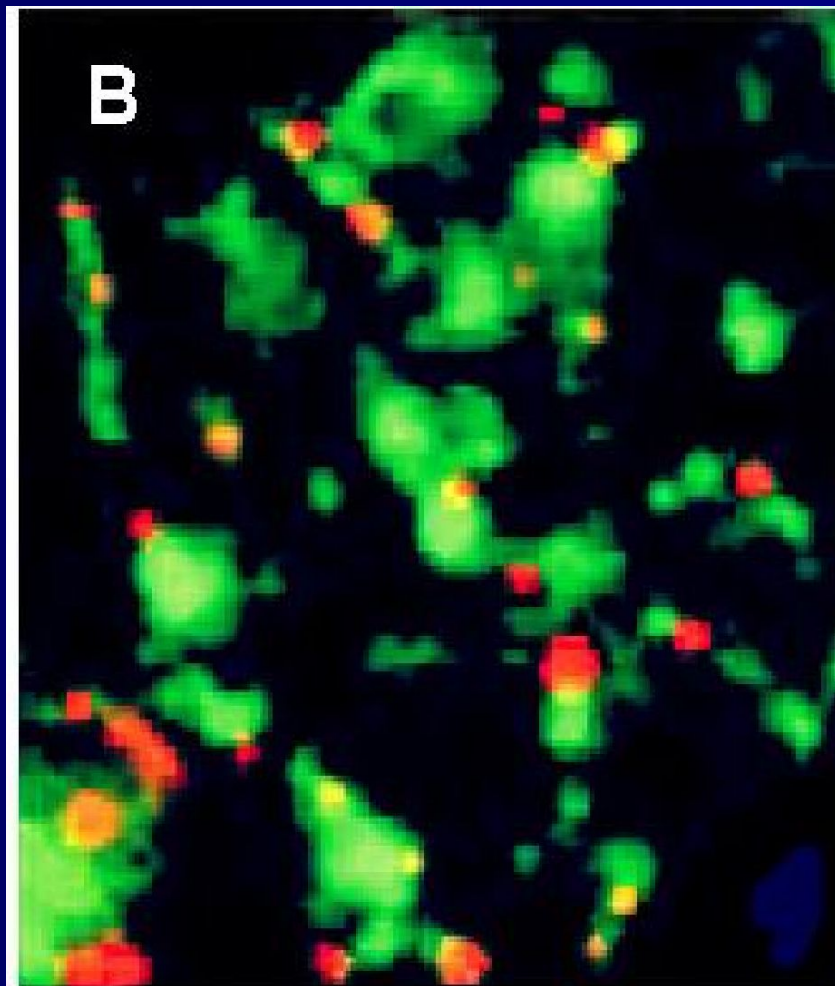
HeLa

MRC5 (сульфат аммония)

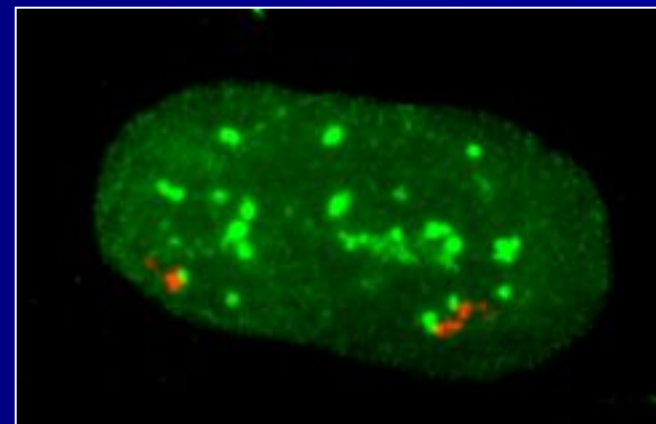


P70 по отношению к α-cat ДНК

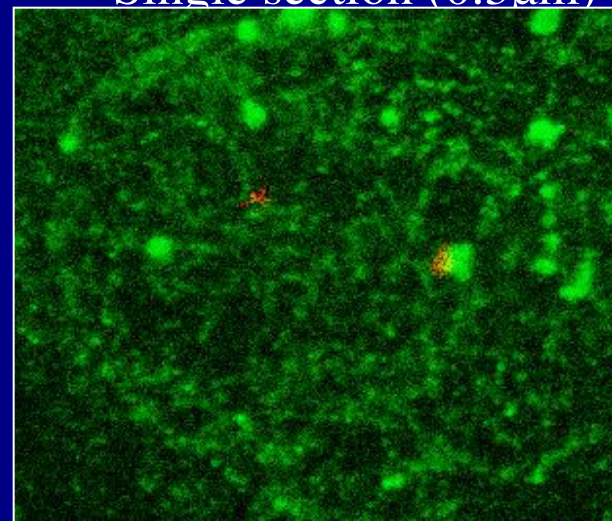
MRC5,
Upregulated
epifluorescent



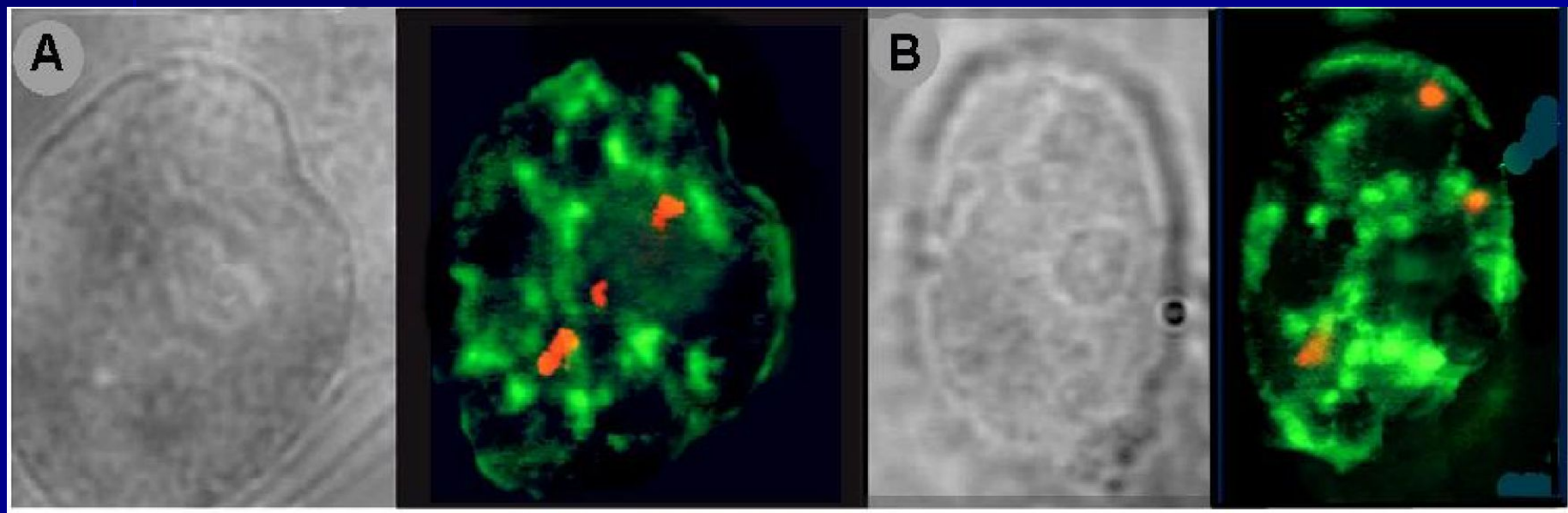
HeLa



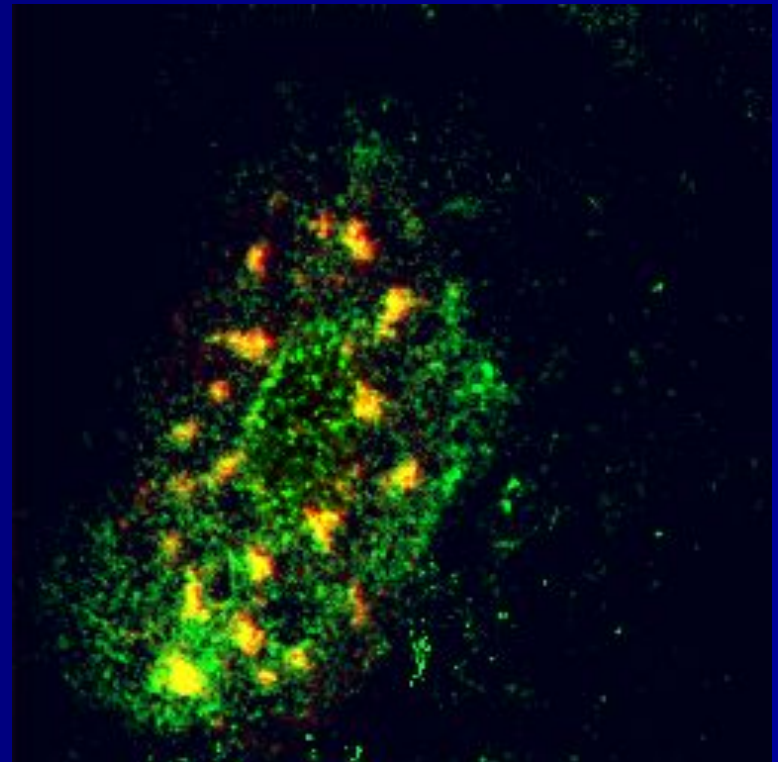
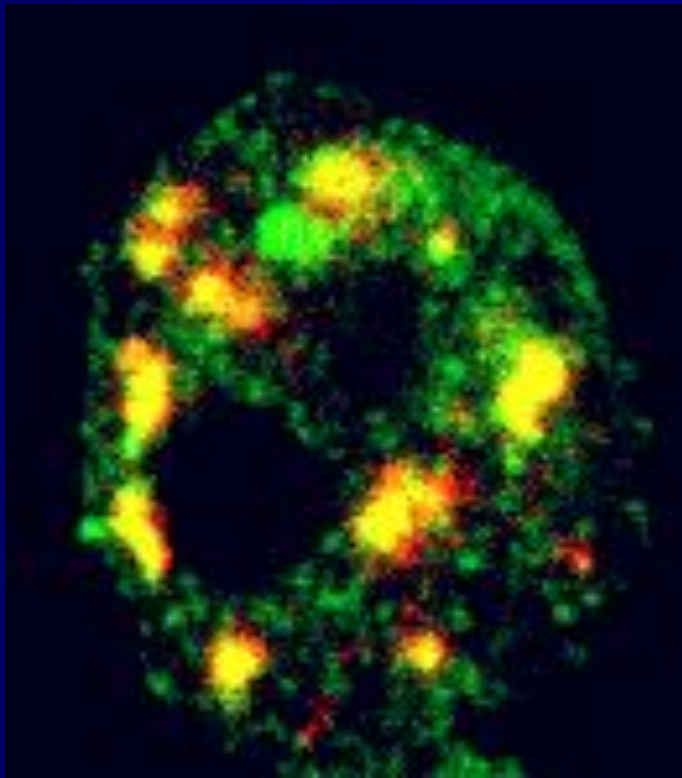
Single section (0.3 μ m)



P70 по отношению к сатЗ



Определение домена локализации p70

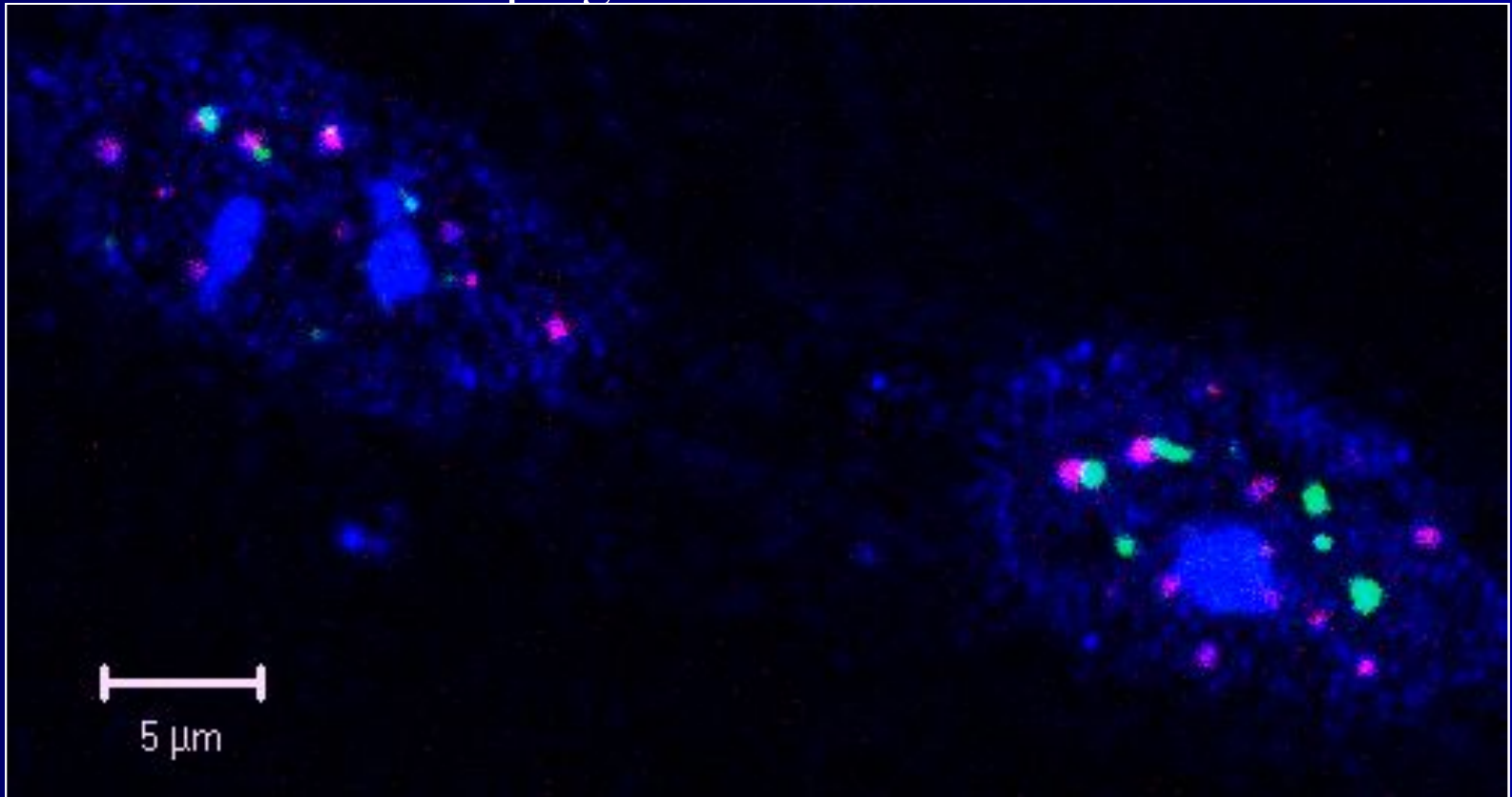


- В фибробластах и HeLa p70 находится в SC35 доменах и фибрилах между ними

In MRC5, p70 has been found in PML and SC35 domains

Upregulated

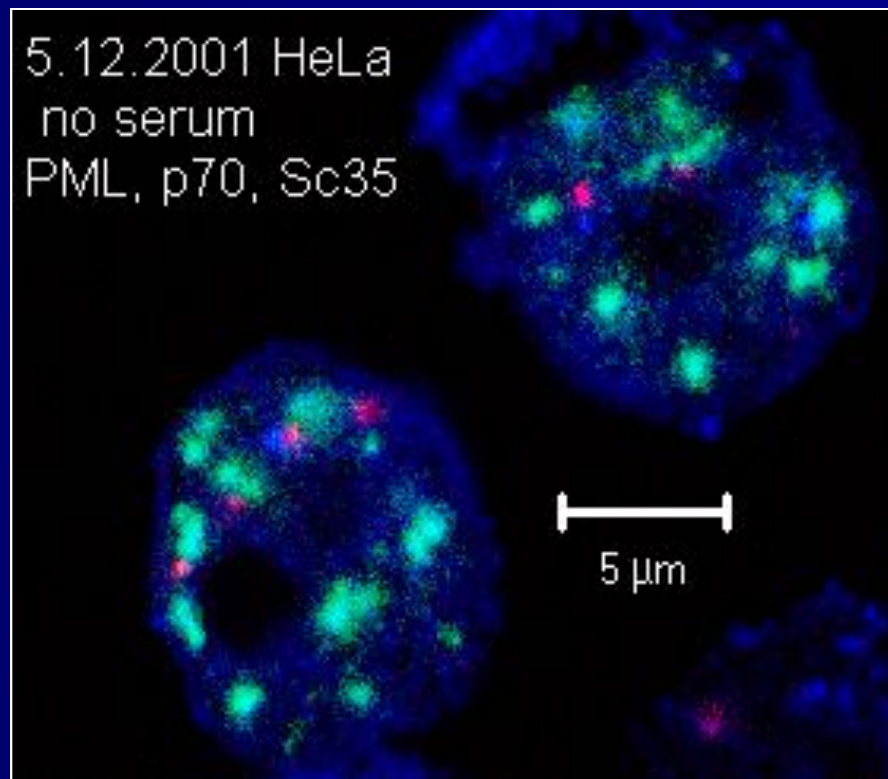
P70
Sc35
PML

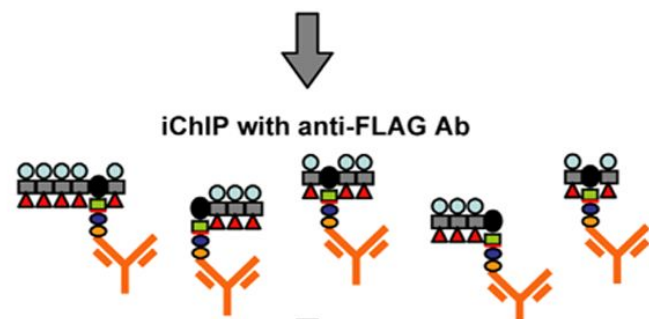
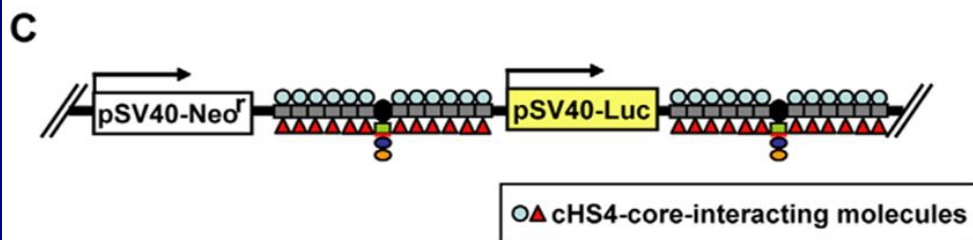
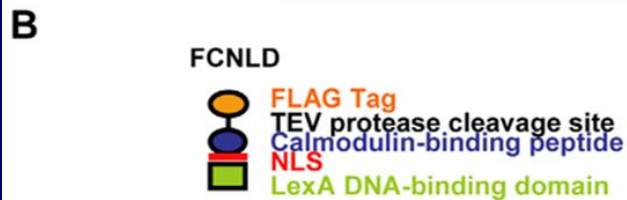
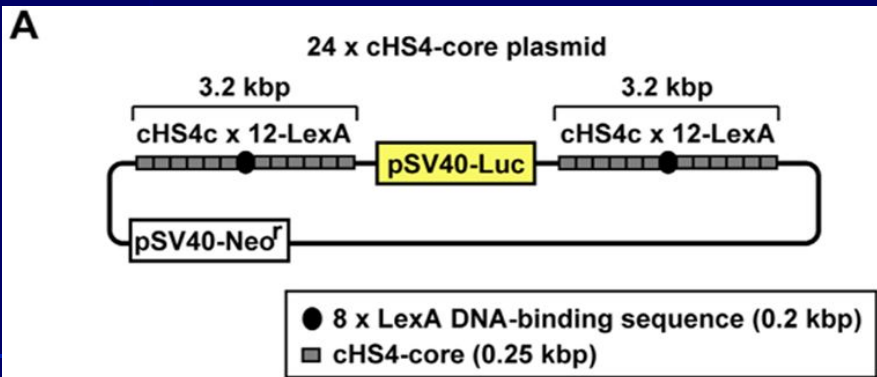


In HeLa S (SD), p70 has been found in SC 35 but not in PML

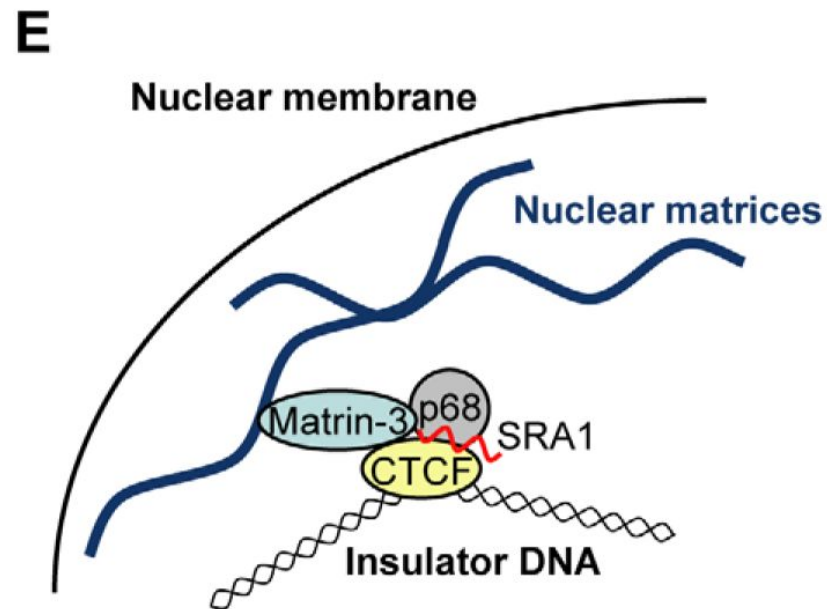
P70
Sc35
PML

HeLa S, grown in serum deprived medium





- Reverse crosslink
- SDS-PAGE
- Mass spectrometry



CCCTC-binding factor (CTCF)

Direct Identification of Insulator Components by Insertional Chromatin Immunoprecipitation

Toshitsugu Fujita, Hodaka Fujii*

PLoS ONE, 2011

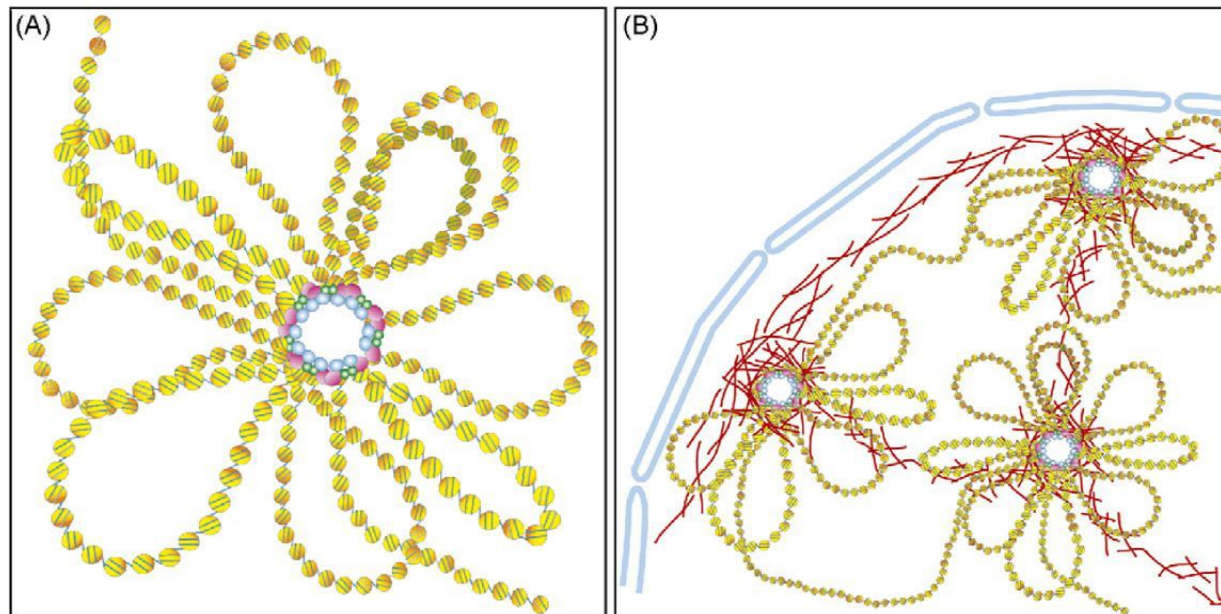


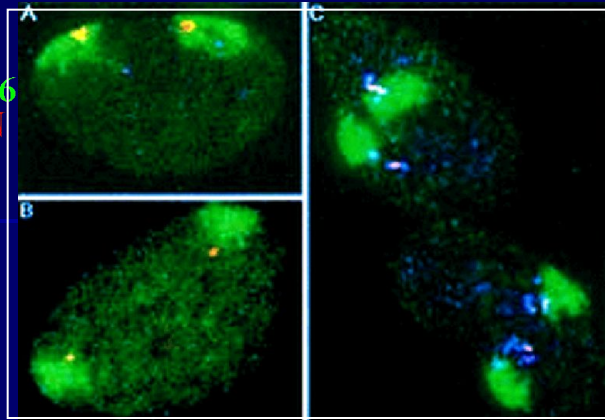
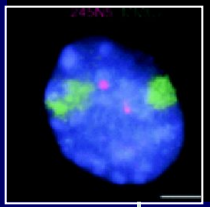
Fig. 1. Insulator elements organize the chromatin fiber in the nucleus by establishing separate compartments of higher-order chromatin structure. (A) Domains of open chromatin (yellow nucleosomes) are flanked by insulators (pink, blue and green spheres) that interact together to form a loop. (B) Diagram showing part of a nucleus with compartmentalized chromatin, anchored in part to the nuclear periphery by interactions of the insulators with the nuclear lamina (red lines).

Insulator elements organize the chromatin fiber in the nucleus by establishing separate compartments of higher-order chromatin structure. (A) Domains of open chromatin (yellow nucleosomes) are flanked by insulators (pink, blue and green spheres) that interact together to form a loop. (B) Diagram showing part of a nucleus with compartmentalized chromatin, anchored in part to the nuclear periphery by interactions of the insulators with the nuclear lamina (red lines).

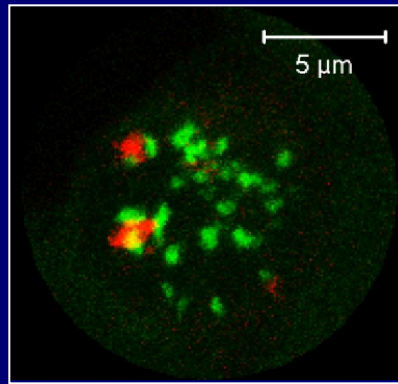
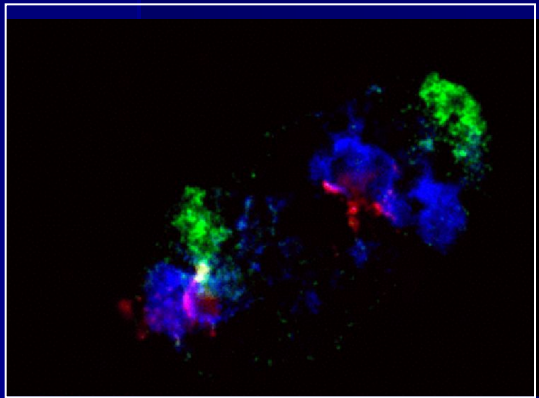
Взаимодействие хромосом в интерфазе и в митозе

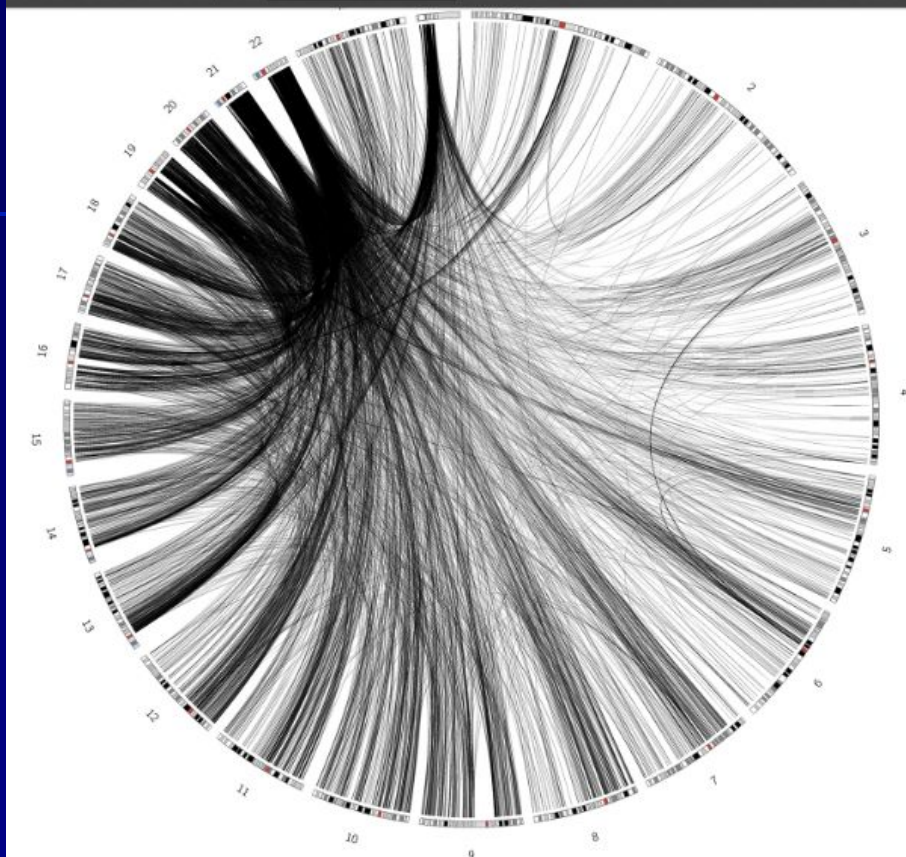
Mahy et al., 2002

Chevret et al., 2000

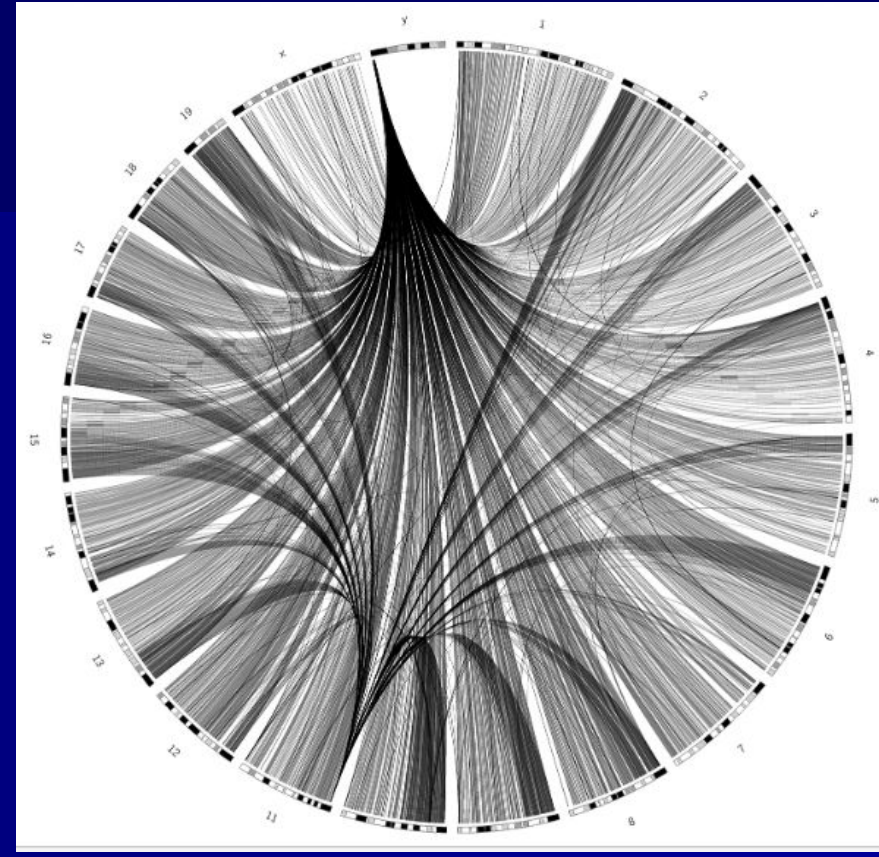


Chr 6
MHC
MHC





Контакты в области центромера и
активного хроматина



Inter-Chromosomal Contact Networks Provide
Insights into Mammalian Chromatin Organization

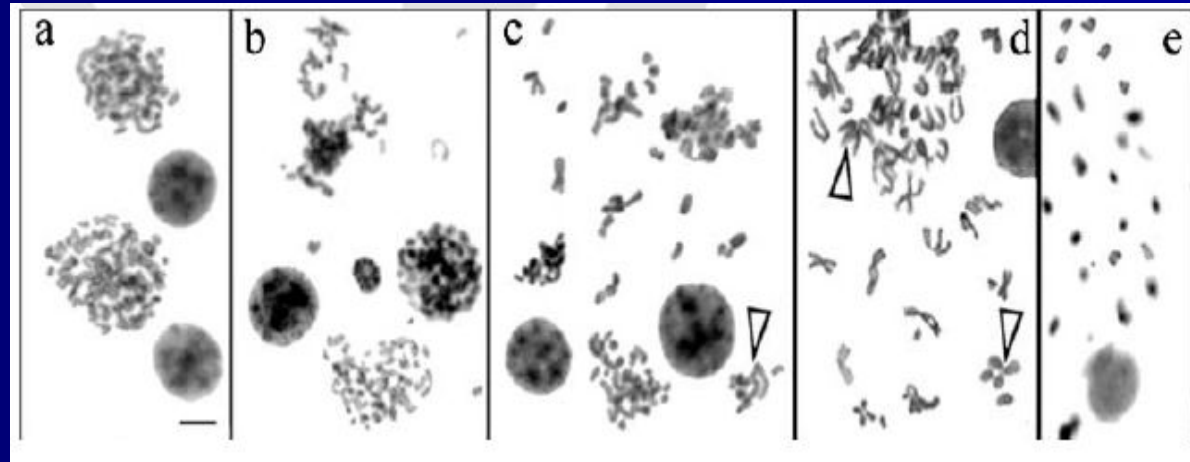
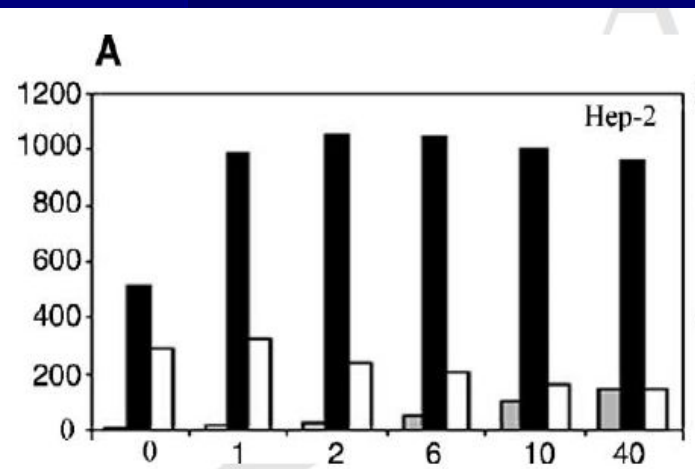
Stefanie Kaufmann, Christiane Fuchs,
Mariya Gonik, Ekaterina E. Khrameeva, Andrey
A. Mironov, Dmitriy Frishman

Агрегация хромосом

TABLE I. The Amount of the Aggregates and Aggregate/Chromosome Ratio in Mitosis Progression of GM-130 Cell Line

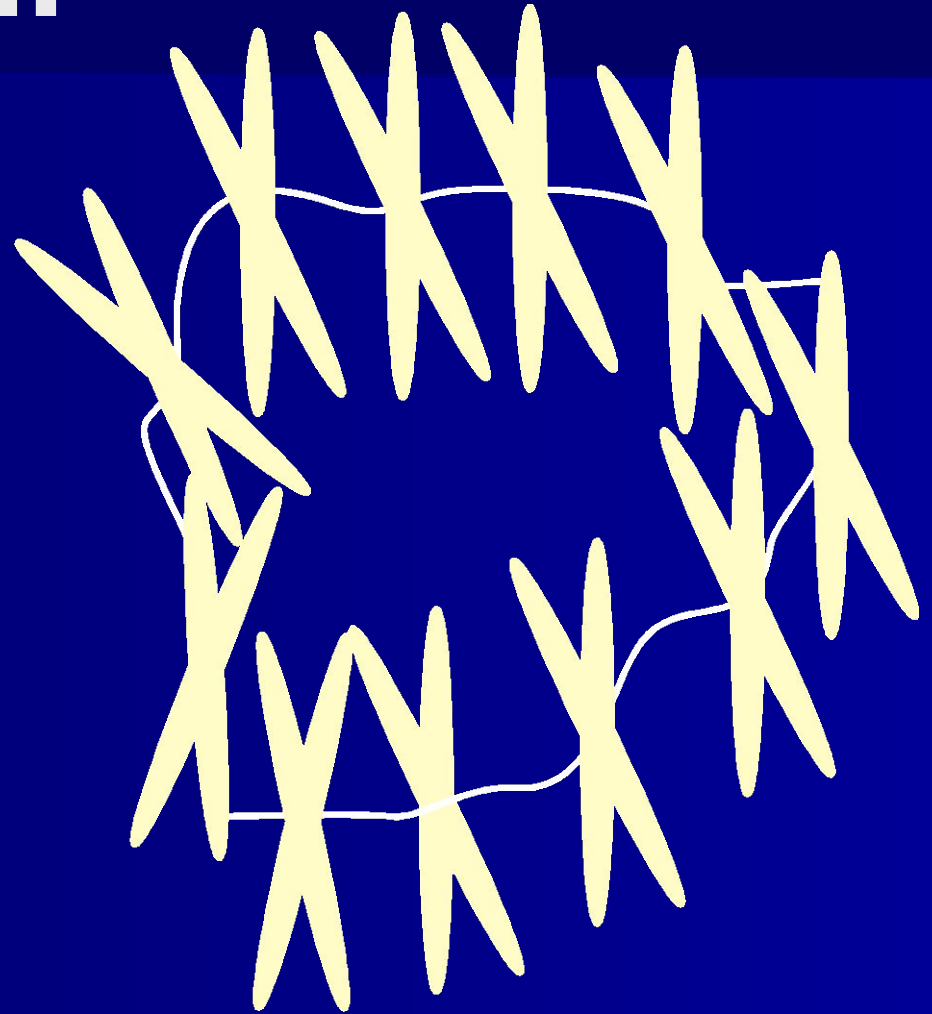
The time of incubation (hours)	0	0.3	0.7	1	2	4
The amount of the aggregates (μm^3)	166	165	118	34	3	5
Aggregates/chromosomes ratio	0.181	0.165	0.186	0.185	0.132	0.169

The time of the cells incubation after nocodazole removal in hours (see Fig. 8B). The amount of the aggregates was counted in μm^3 . The ratio of aggregates to chromosomes is in relative units.

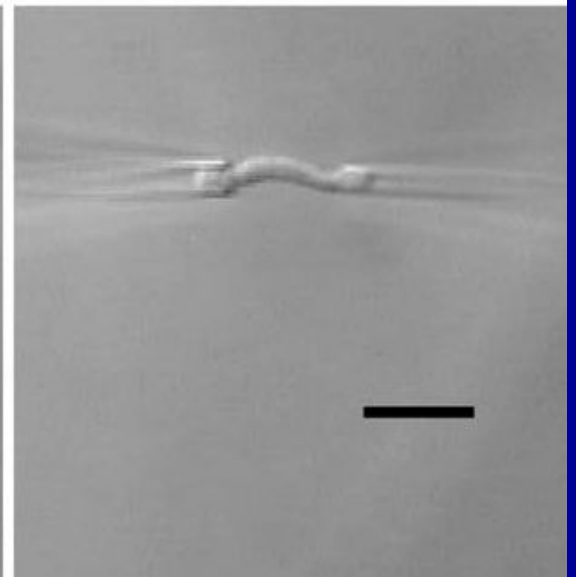
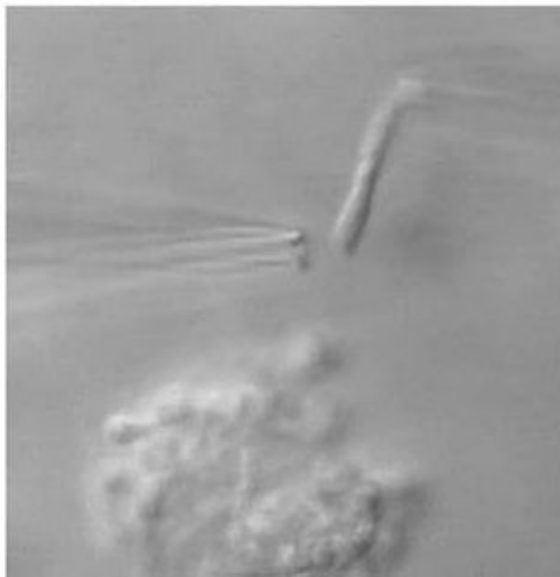
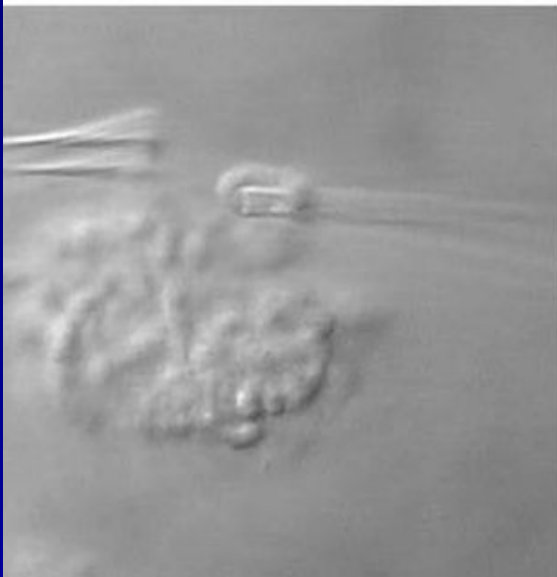
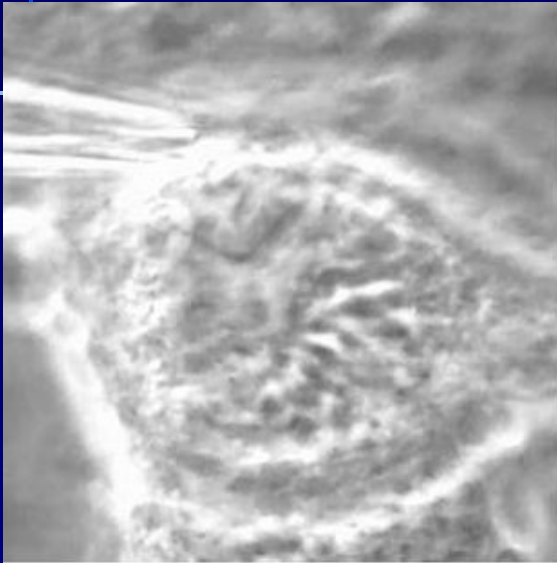


Межхромосомную нить наблюдали:

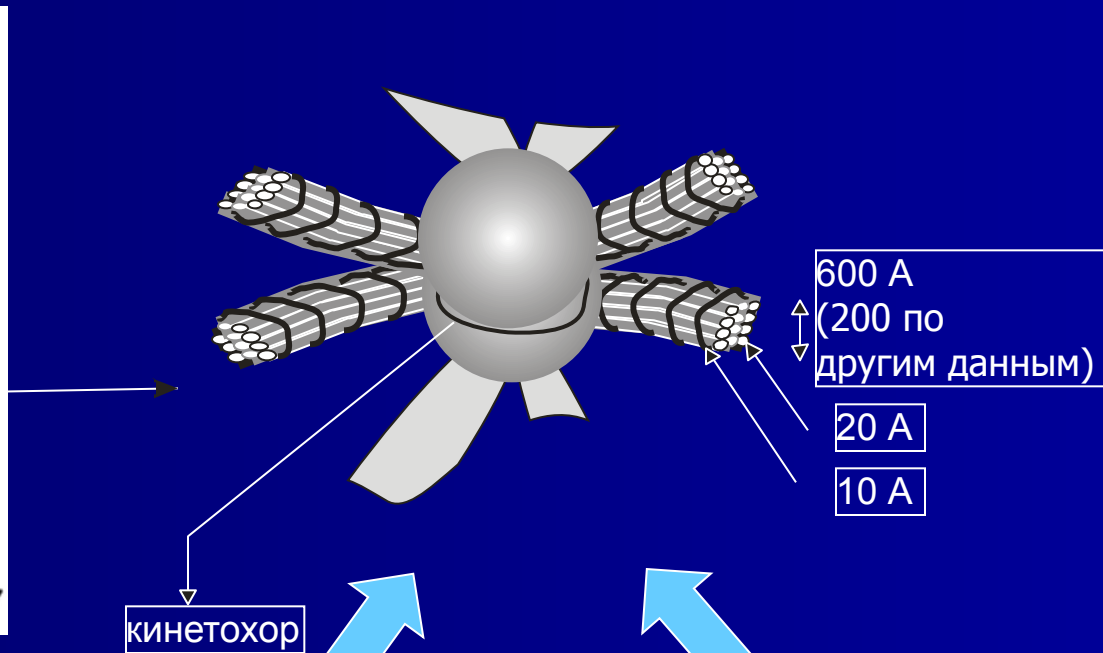
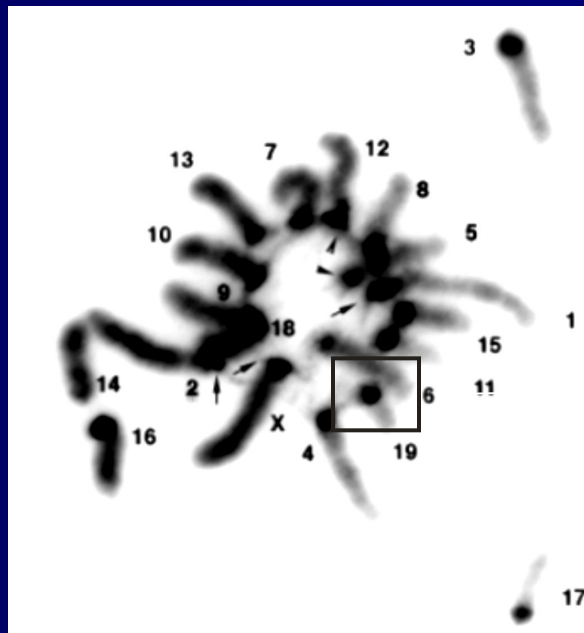
- Wilson, 1925;
- Hsu et al., 1967;
- Hoskins, 1968;
- Henderson et al.; 1973;
- Schneider 1973;
- Takayama, 1976;
- Chiarelli et al. 1977;
- Bennet et al., 1983;
- Lavany et al., 1984
- Radic et al., 1987;
- Maniotis et al., 1997;
- Nagele et al., 1998;
- Dozortsev et al., 2000;
- Saifitdinova et al., 2001
- Erukashvily et al., 2005
- Kuznetsova et al., 2007
- Marco et al., 2008



Межхромосомная нить



Состав нити



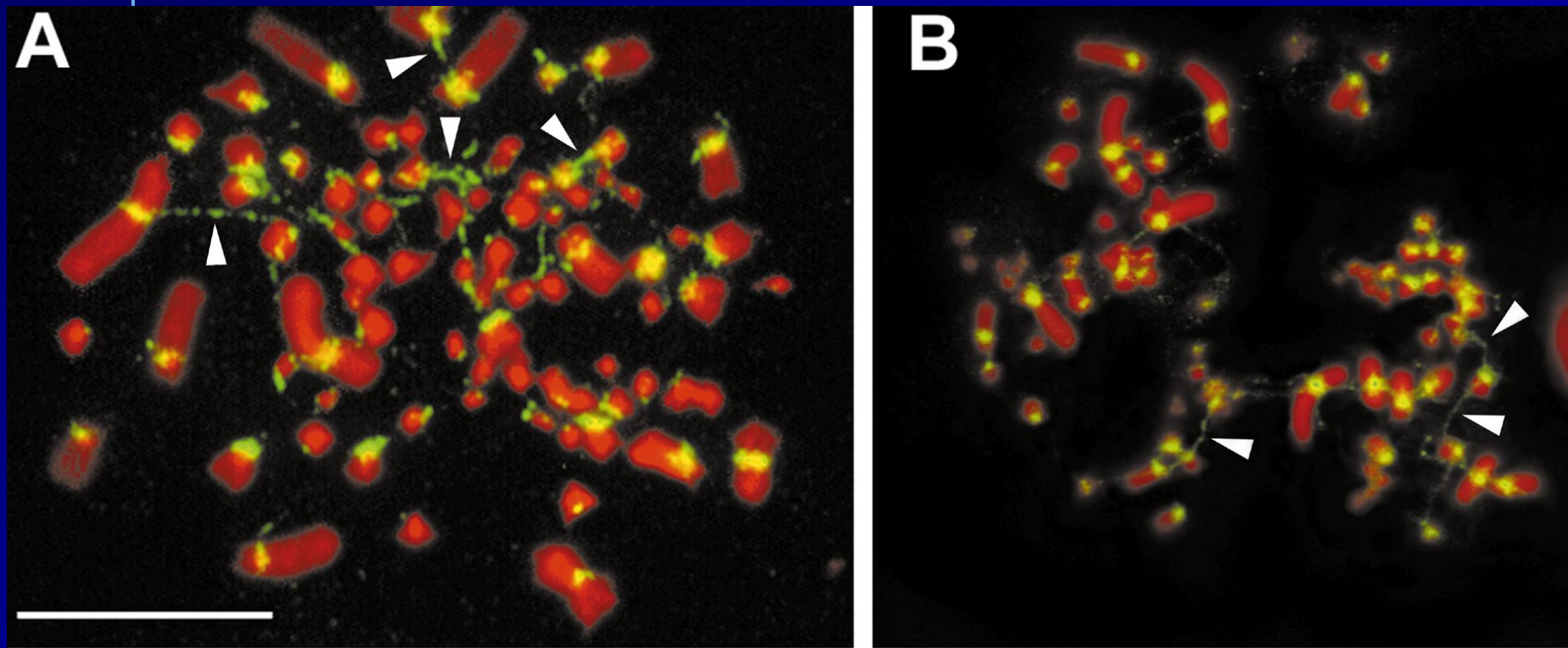
ДНК-аза – утрата связи

РНКаза и пепсин – утрата эластичности

Состав нити

- ДНК (теломерная, интерстициальная, сателлитная)
- РНК (рибосомная, мРНК)
- Белки, в т.ч. чувствительные к меркаптоэтанолу и малорастворимые

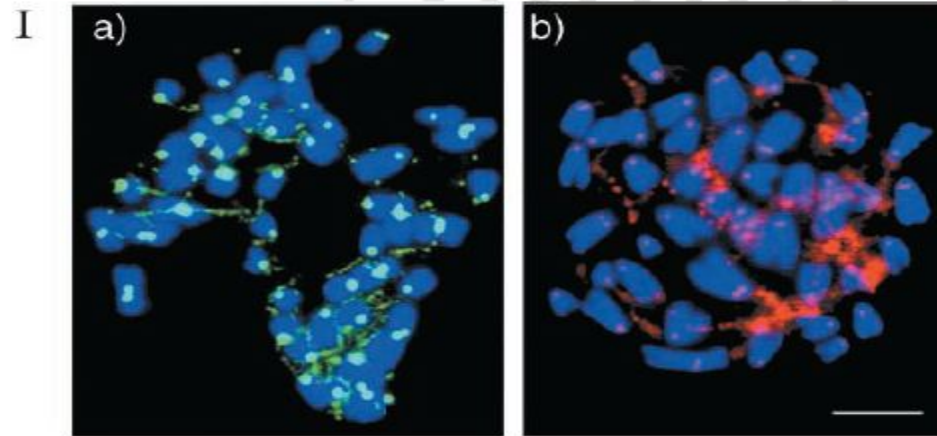
ДНК – FCP повтор зяблика



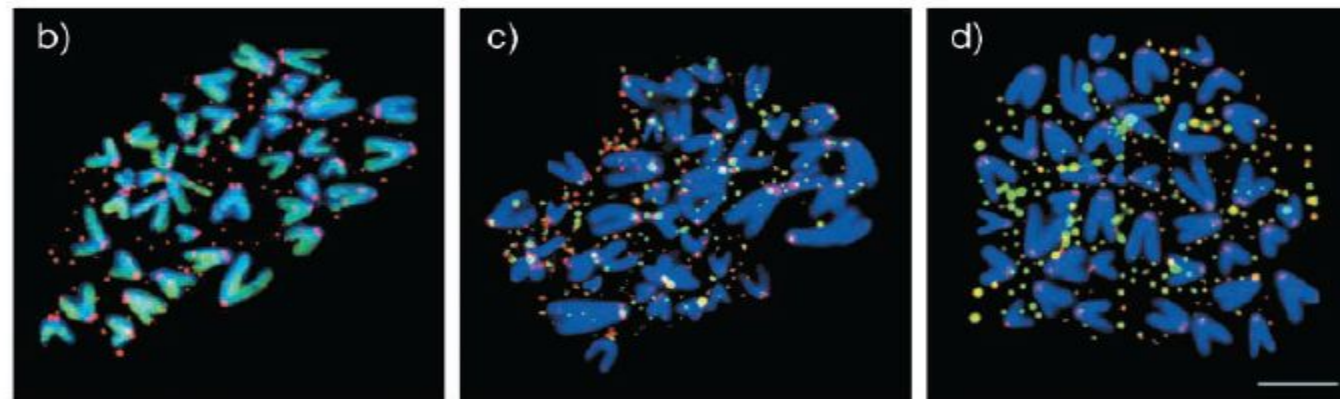
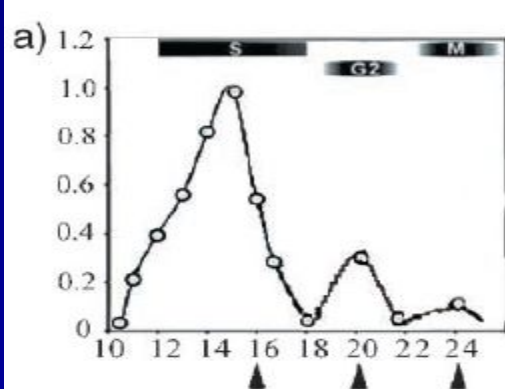
M. Musculus – позднореплицирующая ДНК

The Interchromosome Thread Composition

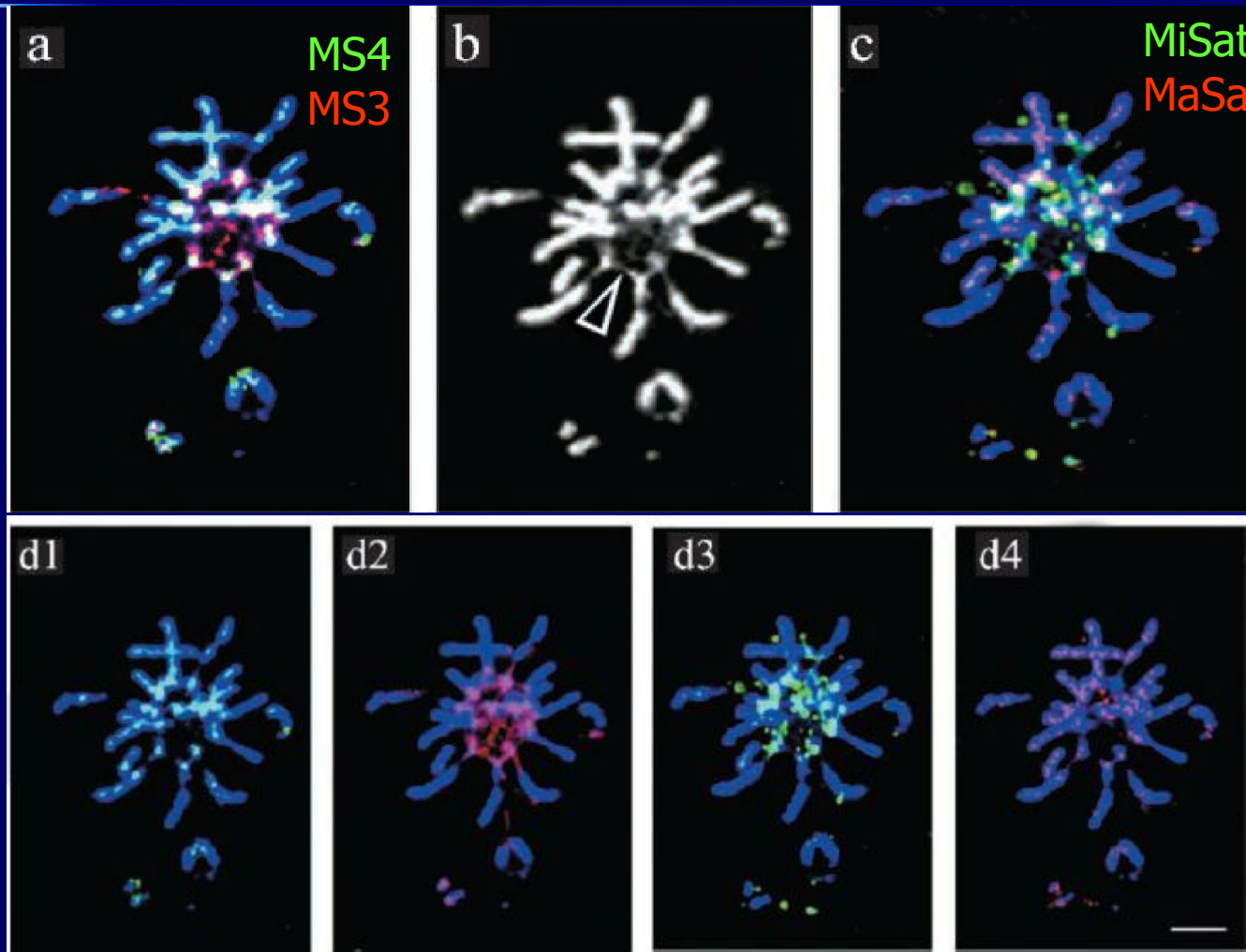
5



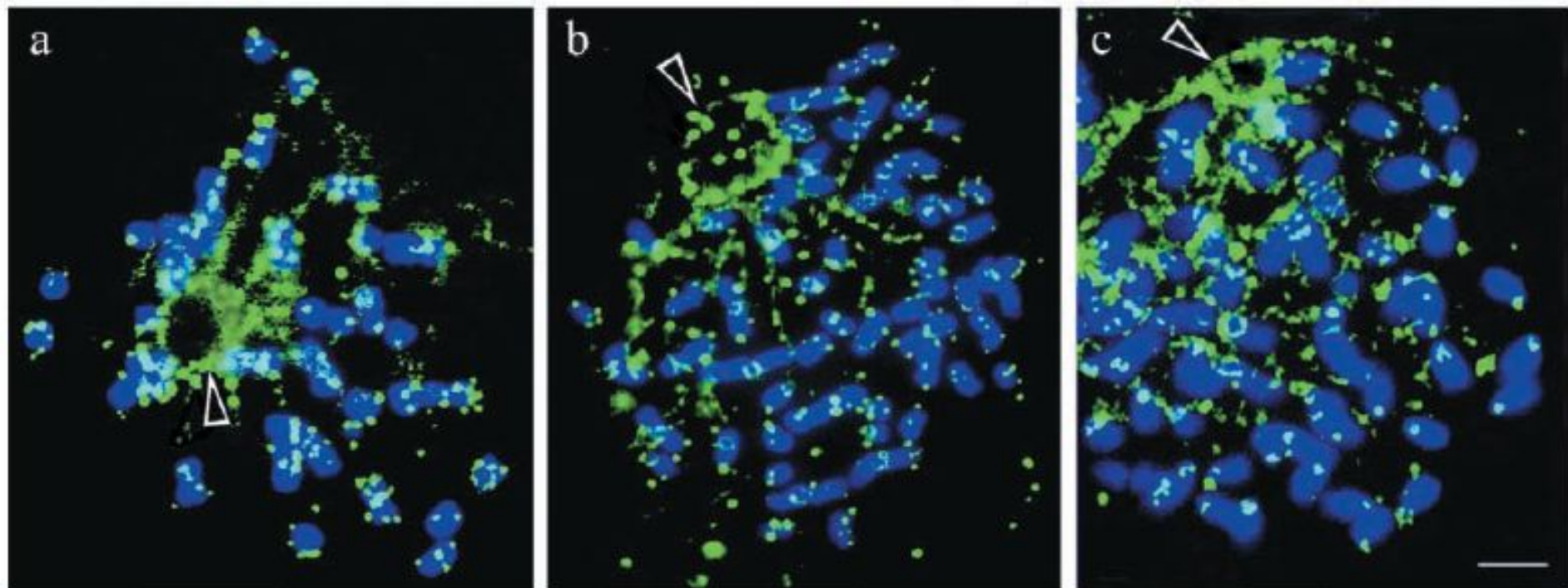
II



M. Musculus – сатДНК межхромосомной нити



Р68 в межхромосомной НИТИ



Межхромосомная нить

