

PRIMERS ON CHROMATIN

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CROSS-TALK

heterochromatin

Position SET

HP1

NURD

siRNA

CENP-A

RSC

SNF

SWI

H4

H3

H1

silence

HAT

tails

organization

landscape

switch

linkers

telomere

repair

divide

30nm

Crystal structure of the nucleosome core particle at 2.8 Å resolution

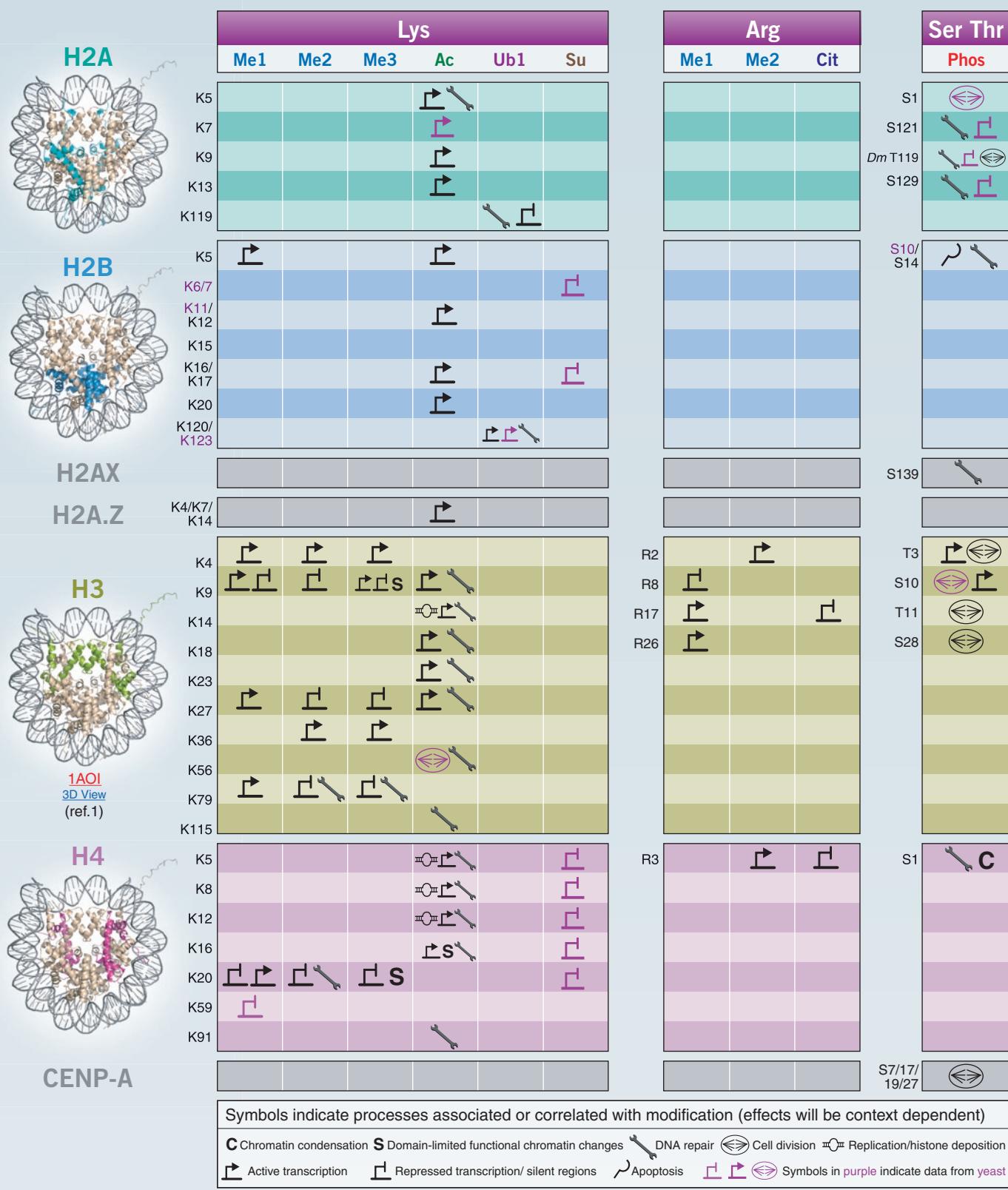
Karolin Luger, Armin W. Mader, Robin K. Richmond, David P. Sargent, & Timothy J. Reinberg, *Nature*, 409, 195-199, 2000

The X-ray crystal structure of the nucleosome core particle of chromatin shows atomic detail how the histone protein octamer is assembled and how 146 base pairs of DNA are organized into a superhelix around it. Both histone/histone and histone/DNA interactions depend on the histone fold domains and additional, well-ordered structure elements extending from this motif. Histone amino-terminal tails pass over and between the pyres of the DNA superhelix to contact neighbouring particles. The lack of uniformity between multiple histone/DNA-binding sites causes the DNA to deviate from ideal superhelix geometry.

To accompany the Focus on Chromatin appearing in this issue of *Nature Structural & Molecular Biology*, a series of primers has been specially prepared that covers the wealth of knowledge in four areas of chromatin research. These areas include functions associated with covalent histone modifications, the enzymes that mediate these modifications, modules that recognize chromatin, and the ATP-dependent chromatin-remodeling complexes. In such a complex field, the information has inevitably been somewhat simplified. As an example, the correlation between modifications and functions are often context dependent. For instance, H3K9 methylation has been associated with transcriptional activation when present in the coding region of the gene, but has also been associated with repression. The reference list provides further reading and details, as do the Reviews and Perspective in this issue. Although there are many informative structures in this field, space constraints allowed only representative structures to be shown, followed by reference citations for related structures ('3D REF' column). The primers can be used as a stand-alone resource — feel free to tear them out of the issue or print out the PDF versions and modify or add to them yourself as new data emerge. The online versions of the primers contain hyperlinks to the Protein Data Bank as well as 3D view links that allow structural visualization.

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=FUNCTIONS ASSOCIATED WITH COVALENT HISTONE MODIFICATIONS



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HISTONE-MODIFYING ENZYMES

REPRESENTATIVE STRUCTURE	PROTEIN	TARGET	DOMAIN	3D REF	PROTEIN	TARGET	DOMAIN	3D REF	
Histone acetyltransferases (HATs)									
<i>Tt</i> Gcn5 5GCN 3D View	Gcn5	H3K9/14/18/23/27, H2B	2–9	Sc Hpa2	H3K14		12		
	PCAF & GCN5L	H3K9/14/18	10,11	Sc Hat1	H2AK5/7, H4K5/12		13		
GNAT family									
<i>Sc</i> Esa1 1FY7 3D View	Sc Esa1 (TIP60)	H2A, H4	14,15	HBO1	H4K5/8/12		16		
	MOZ & MORF/ Sc Sas3	H3K14/23	(Sas3)	MOF/Dm Mof/ Sc Sas2	H4K16			17	
MYST family									
<i>Sc</i> Rtt109 1W22 3D View	Sc Rtt109	H3K56		CBP/p300	H2AK5, H2BK12/15 H3K14/18, H4K5/8/12			See note	
Histone deacetylases (HDACs)									
<i>HDAC8</i> 1O9S 3D View	Sc Rpd3	H2A, H2B, H3, H4K5/8/12ac	0		Hst3 & 4	H3K56ac	0		
	HDAC8 ^b	H3ac, H4ac	19–21	SIRT1 ^b	H3K9ac, H4K16ac, H1ac		0	23	
<i>Sc</i> Hos1 & Hos2 Sc Hos3 Sc Hda1 	Sc Hos1 & Hos2	H3ac, H4ac		Sc SIRT2	H3K9ac, H4K16ac		0	27	
	Sc Hos3	H2BK11/16ac, H4K12ac		Sc Hst2	H4K16ac		0	22–26	
	Sc Hda1	H3, H2BK11/16ac		Sc Sir2	H3K56ac, H4K16ac		0	28	
Histone methyltransferases (HMTs)									
SET domain lysine HMTs									
<i>SET7/9</i> 1ORI 3D View	Sc Set1 ^a , SET1A & 1B	H3K4	29	Sp Clr4	H3K9	33,34			
	MLL1-4 ^a	H3K4	30	Dm E(z) & EZH2	H3K27(EZH2, H1bK26) ^a				
<i>Ash1</i> ^a 2Q8E 3D View	Ash1 ^a	H3K4		SET2	H3K36	35,36			
	SUV39H1 & H2	H3K9		NSD1	H3K36				
<i>ESET/SETDB1</i> 1O9S 3D View	ESET/SETDB1	H3K9		SMYD2	H3K36				
	Nc DIM-5	H3K9	31,32	SUV420H1 & H2	H4K20				
<i>RIZ1</i> 1O9S 3D View	RIZ1	H3K9		SET7/9	H3K4	37–41			
	G9a	H3K9		SET8/PR-SET7	H4K20			42,43	
<i>EuHMTase1</i> 1O9S 3D View	EuHMTase1	H3K9							
Non-SET domain lysine HMTs									
<i>PRMT1</i> 1O9S 3D View	Sc Dot-1 & DOT1L	H3K79	44,45						
Arginine HMTs									
<i>CARM1</i> 1O9S 3D View	CARM1	H3R2/17/26	46,47	PRMT5	H3R8/H4R3		46		
	PRMT1/Sc Hmt1	H4R3	48,49	PRMT6	H3R2		47		
Histone demethylases									
LSD1/BHC110									
<i>LSD1</i> 2H94 3D View	LSD1/BHC110	H3K4me1/2, H3K9me1/2	50–54						
JmjC family demethylases									
<i>JMJD2A</i> 2Q8E 3D View	Dm Lid/JARID1A,B,C,D	H3K4me2/3		UTX	H3K27me2/3				
	JHDM2a & b	H3K9me1/2		JMJD2A & C	H3K9/36me2/3				
<i>JMJD2D</i> 2Q8E 3D View	JMJD2D	H3K9me2/3		JHDM1a & b	H3K36me1/2				
	JMJD2B	H3K9me3		JMJD6	H3R2me2, H4R3me2				
PROTEIN	TARGET	3D REF	PROTEIN	TARGET	3D REF	PROTEIN	TARGET	3D REF	
Ubiquitin ligases				Kinases					
<i>BMI-RING1B</i> 2CKL 3D View	BMI-RING1B	H2AK119	60,61	ATM/ATR/DNA-PK (<i>Sc</i> Mec1/Tel1)	H2AXS139 (<i>Sc</i> H2AS129)		Sc Aurora B & <i>Sc</i> Snf1	H3S10	64–66
	RNF20/40	H2B		MST1 (<i>Sc</i> Ste20)	H2BS14 (<i>Sc</i> H2BS10)		Dm Nhk1	Dm H2T119	
<i>Cul4-DDB-Roc1</i> 2DEY 3D View	Cul4-DDB-Roc1	H3/H4		Haspin	H3T3		ZIP	H3T11	
	<i>Sc</i> Rad6/Bre1	H2BK123	62	MSK1&2	H3S10	63	<i>Sc</i> CK II & Sps1	H4S1	
Deiminases									
<i>PADI4</i> 2DEY 3D View	PADI4	H3R2/8/17/26, H4R3	67,68	PRMT	JmjC	PHD	RRM	Fbox	Bromodomain
				SWIRM	JmJN	TPR	SET		Zinc finger
				WWWP	KIX	Sir2-like	Post-SET		Chromodomain
				Ankyrin	BAH	Tudor	Pre-SET		MYST
				WW	HDAC	SANT	(any type)		Acetyltransferase
									Other conserved domain
									Methyl-binding (MBD)
									Other conserved domain
									Amino oxidase domain
Prolyl Isomerases									
<i>Sc Fpr4</i>				Proteins mammalian except <i>Sc</i> , <i>S. cerevisiae</i> ; <i>Sp</i> , <i>S. pombe</i> ; <i>Nc</i> , <i>N. crassa</i> ; <i>Tt</i> , <i>T. thermophila</i> ; <i>Dm</i> , <i>D. melanogaster</i> . Enzymes may have different <i>in vitro</i> , <i>in vivo</i> or context-dependent targets, and may have higher efficiency for one residue over others.					
				Additional structures both awaiting publication and published (e.g. CBP/p300) are available in the protein databank. The human HDACs and other structures in this family are discussed in ref. 28 and references therein.					

^a In complexes, COMPASS for Set1, EZH2 in PRC complexes.

^b Please see further reading for the full set of mammalian HDACs.

=HISTONE RECOGNITION DOMAINS=

REPRESENTATIVE STRUCTURE

STRUCTURE	PROTEIN	TARGET	CD REF	PROTEIN	TARGET	CD REF
Bromodomain						
GCN5 	Sc Gcn5	H4K16ac	5,6	CBP/p300	?	140
	PCAF	H4K16ac	10	Sc Bdf1/BRD8/dBrd8	H4ac	
	TAF1	H4ac	18	Polybromo/BAF180	H3ac	
	hBRG1	H3K14ac	69,70	Sc Rsc1,2,4	H3K14ac (Rsc4)	71 (Rsc4)
	Sc Snf2	H3ac/H4ac		Dm NURF301/BPTF	?	81 (BPTF)
1E6I 3D View	Sc Sth1	?		hACF1/dACF	?	

Chromodomain

	HP1/Swi6	H3K9me2/3	72,73	dMi-2/CHD3/CHD4/CHD5	?	
	PC1/PC2/Polycomb/LHP1	H3K27me3, H3K9me3	74,75	CHD6/CHD7/CHD8/CHD9	?	
	CHD1	H3K4me1/3	76	hBAF155	?	
	<i>Sc Chd1</i>	?	101,102	dMrg15/hMRG15, <i>Sc Eaf3</i> ^a	H3K36me, H3K4me	77
	dTip60/hTIP60, MOF, Esa1	?	17 (<i>Dm</i> MOF)	CDY1	H3K9me2/3	
	<i>Sp Clr4</i> , SUV39H1	H3K9me	33 (Clr4)			

PHD

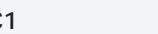
 Yng1 2JMJ 3D View	BHC80	H3K4me0	78	hACF1/dACF	Core histones	
	Yng1	H3K4me2/3	79	Ash1	?	
	ING2	H3K4me2/3	80	JMJD2A/2B/2C	?	
	BPTF/ <i>Dm</i> NURF301	H3K4me2/3	81	JHDM1a/b	?	
	NSD1	?		JARID1C	H3K9me3	
	MLL	?		dMI-2/CHD3/CHD4	?	

Tudor

 2IG0 3D View	JMJD2A	H3K4me3/H4K20me3	55	ESET/SETDB1	H3K9	
	53BP1	H4K20me1/2	82	JMJD2B/2C	?	
	Sp Crb2	H4K20me2	82	PHF20	H4K20me2	

	PROTEIN	TARGET	3D REF
MBT			
L(3)MBT L1	L(3)MBTL1	H1bK26me1/2, H4K20me1/2	89
	SCML2	?	90
	SFMBT	H3K9me1/2, H4K20me1/2	
	PHF20L1	H3K4me1, H4K20me1	
10Z2 3D View			

BRCT

BRCT	MDC1	H2AXPh	86,87
	<i>Sp Crb2</i>	H2APh	
	53BP1	?	
	MCPH1	H2AXPh	

14-3-3

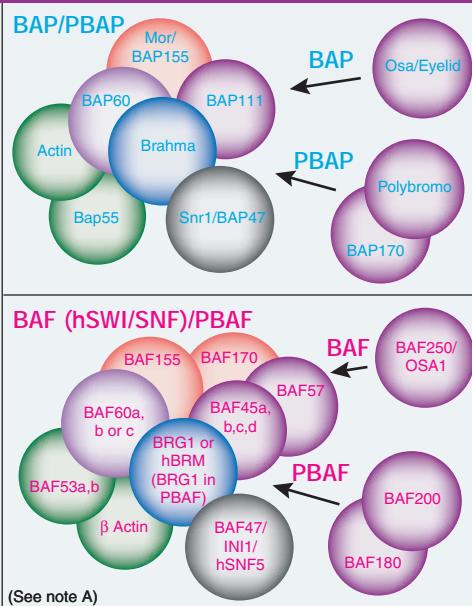
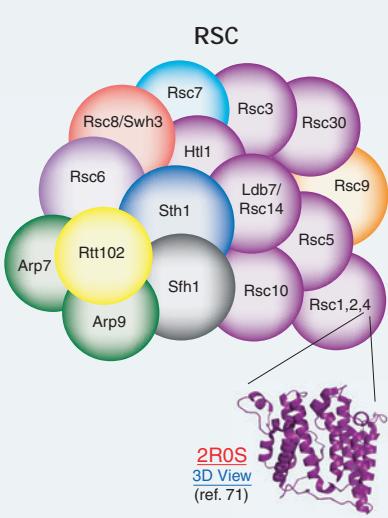
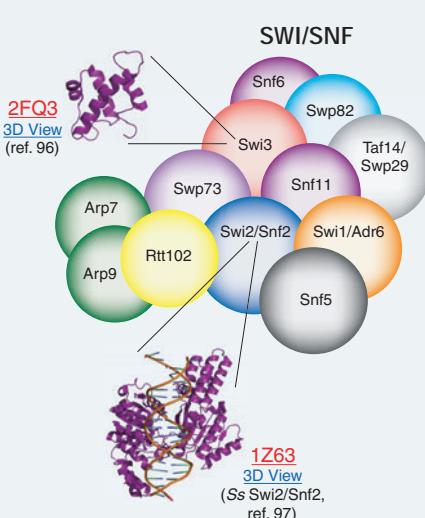
See ref. 108 for further information and examples

Question mark indicates that the exact histone binding specificity is unknown.

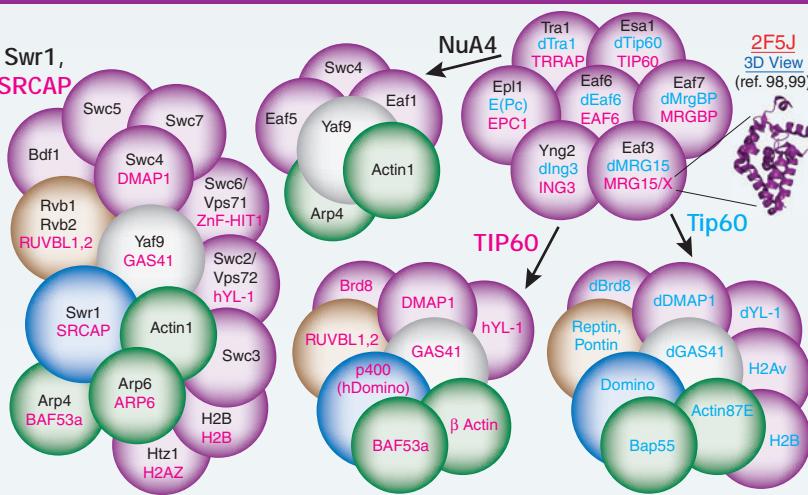
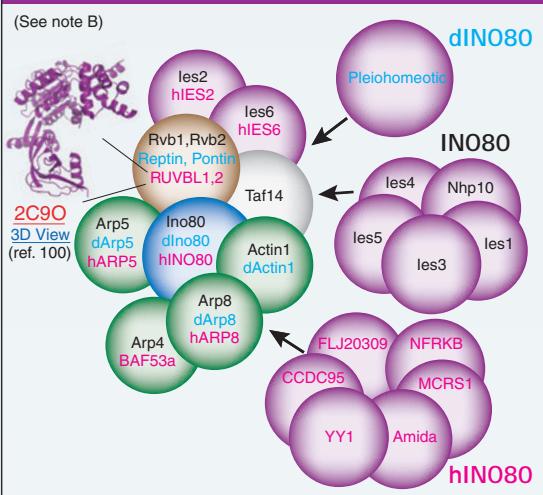
^a Chromo barrel-like motif I list is mostly limited to proteins on these pages.

CHROMATIN REMODELING COMPLEXES

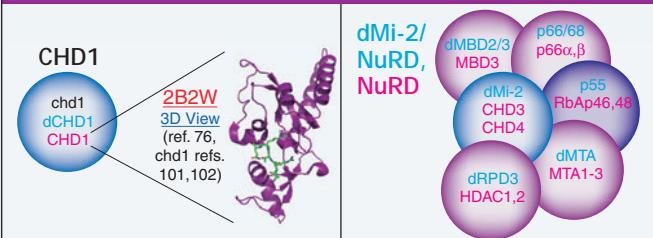
The SWI/SNF family



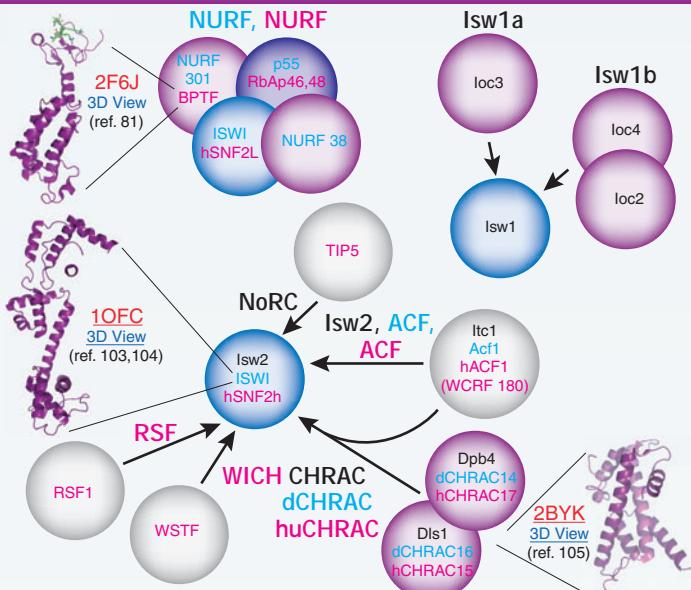
The INO80 family



The CHD/Mi-2 family



The ISWI family



Note A: The BAF complex is combinatorially assembled with interchangeable subunits¹³⁸. The situation is further complicated by the presence of 29 *swi2* homologs in the human genome, and the presence of actin-like subunits in BAF, that differ from yeast SWI/SNF or RSC.

Note B: The INO80 family name used is based on the remodeling catalytic ATPase, though the NuA4 acetyltransferase complex was identified earlier.

For EM structures see refs. 91–95.

Complex name

YEAST HOMOLOG

FLY HOMOLOG

HUMAN HOMOLOG

S. s. sootaria

- Remodeling catalytic ATPase
- Sub-family specific
- Actin-like

(Similar color sphere denotes similar subunits, i.e. Swi3 and Swh3 are related)



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