

Comprehensive Catalog of Currently Documented Histone Modifications

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SUMMARY

Modern techniques in molecular biology, genomics, and mass spectrometry-based proteomics have identified a large number of novel histone posttranslational modifications (PTMs), many of whose functions are still under intense investigation. Here, we catalog histone PTMs under two classes: first, those whose functions have been fairly well studied and, second, those PTMs that have been more recently identified but whose functions remain unclear. We hope that this will be a useful resource for researchers from all biological or technical backgrounds, aiding in their chromatin and epigenetic pursuits.

Outline

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Histone posttranslational modifications (PTMs) have been linked to a variety of processes, including transcription, DNA replication, and DNA damage (Kouzarides 2007; Murr 2010; for a list of reviews, see Suggested Reviews). The growing list of histone PTMs has exploded in the last several years as a consequence of the considerable advances in available antibody reagents, peptide and protein array technology, and mass spectrometry-based proteomics (Karch et al. 2013). These approaches allow for identification and quantification of histone PTMs from global or more local chromatin states, especially when combined with chromatin immunoprecipitation experiments (Han and Garcia 2013). Here, we attempt to catalog the ever-growing number of histone PTMs that have been studied over the last several years. The tables are broken down into two groups: Section 1 (Tables 1–8) lists the histone

PTMs that have been studied more and thus some functional aspects are known concerning the marks; Section 2 (Tables 9–16) lists the histone PTMs that have been detected, but in which rather limited function has been determined. The latter category of histone marks, being in their observed infancy, is very intriguing and represents a large opportunity for the chromatin biology and epigenetics communities to decipher their biological consequences and outcomes in the years to come. Histone acetylation and methylation were first discovered about 50 years ago (Allfrey et al. 1964); however, only in the last decade or so has its physiological function been uncovered. We anticipate that this will serve as a useful resource for those already working in the field, but also as motivation for those newer scientists beginning their research work in this area to continue to push the boundaries of knowledge.

Model organism key

An	<i>Aspergillus nidulans</i>
At	<i>Arabidopsis thaliana</i>
Bt	<i>Bos taurus</i>
Ce	<i>Caenorhabditis elegans</i>
Dm	<i>Drosophila melanogaster</i>
Hs	<i>Homo sapiens</i>
Mm	<i>Mus musculus</i>
Nc	<i>Neurospora crassa</i>
Rn	<i>Rattus norvegicus</i>
Sc	<i>Saccharomyces cerevisiae</i>
Sp	<i>Schizosaccharomyces pombe</i>
Tt	<i>Tetrahymena thermophila</i>
Xl	<i>Xenopus laevis</i>

Modification key

ac	acetylation	mal	malonylation
ar1	mono-ADP-ribosylation	me1	monomethylation
bio	biotinylation	me2	dimethylation
but	butyrylation	me3	trimethylation
cit	citrullination	og	O-GlcNAcylation
cr	crotonylation	oh*	hydroxylation
for	formylation	ox*	oxidation
gt*	glutathionylation	ph	phosphorylation
hib	2-hydroxyisobutyrylation	su	SUMOylation
iso	isomerization	ub	ubiquitination

* XYZ modifications are known to occur on histone proteins but have not been included in these tables at individual amino acid residues.

Table heading key

Site	A known histone PTM is indicated, based on the Brno nomenclature (Turner 2005), by the numbered amino acid residue at which it occurs followed by the abbreviation for its chemical modification (see Modification key).
Model	Refers to the model organism in which a PTM was characterized.
Enzyme	Where known, the histone-modifying enzyme (writer) that transduces a PTM is indicated. <i>Italics</i> specify the valency of modification that an enzyme can catalyze.
Function	The associated biological function of a histone PTM is indicated where known.
Reference	The key primary references where a PTM and/or its function are described are listed.

1 MORE-STUDIED HISTONE PTMS

The tables in this section list histone modifications with known functions and modifying enzymes, and primary references are indicated wherever possible (up until 2014). Distinct modification states are indicated in *italics* in the Enzyme column.

Additional modifications with currently unknown function are listed in Section 2. These modifications were obtained from a combination of sources.

The tables that constitute Section 1 have been extended from Appendix 2 in Allis et al. (2007) by Ben Garcia and Yingming Zhao, with additional input from Le Hehuang, Monika Lachner, and Marie-Laure Caparros. That appendix was based on an original setup from Lachner et al. (2003) and significantly extended by Roopsha Sengupta, Mario Richter, and Marie-Laure Caparros and verified by Patrick Trojer.

The histone modifications follow the nomenclature as proposed by Turner (2005).

Table 1. Histone H2A

Site	Model	Enzyme	Function	Reference(s)
K5ac	Hs, Sc	Tip60, p300/CBP, Hat1	Transcriptional activation	Yamamoto and Horikoshi 1997; Kimura and Horikoshi 1998; Verreault et al. 1998
K9bio		HCS Biotinidase	Acetylation and methylation dependent Involved in cell proliferation, gene silencing, and cellular response to DNA damage	Stanley et al. 2001; Kothapalli et al. 2005a; Chew et al. 2006
K7ac	Sc	Hat1, Esa1	Transcriptional activation	Suka et al. 2001
K13bio		HCS Biotinidase	Acetylation and methylation dependent Involved in cell proliferation, gene silencing, and cellular response to DNA damage	Stanley et al. 2001; Kothapalli et al. 2005a; Chew et al. 2006
K13ub	Mm	Rnf168	Part of the DNA damage response to double-stranded DNA breaks	Mattioli et al. 2012; Gatti et al. 2012
K15ub	Mm	Rnf168	Part of the DNA damage response to double-stranded DNA breaks	Mattioli et al. 2012; Gatti et al. 2012
K63ub	Mm	Rnf8	Part of the DNA damage response to double-stranded DNA breaks	Huen et al. 2007; Mailand et al. 2007
Q105me	Sc, Hs	Nop1, fibrillarin: <i>me1</i>	Ribosomal gene expression	Tessarz et al. 2014
K119ub	Dm, Hs	dRing, RING1B	Polycomb silencing UV damage response	Wang et al. 2004; Kapetanaki et al. 2006
S121ph	Sc	Mec1	DNA damage response	Wyatt et al. 2003; Harvey et al. 2005
(S122ph)	Sp	PIKK Bub1	Telomere silencing Chromosomal stability	Kawashima et al. 2010
T125ph	Sc	Mec1 PIKK	DNA damage response Telomere silencing	Wyatt et al. 2003
K126bio	Hs	HCS Biotinidase	Acetylation and methylation dependent Involved in cell proliferation, gene silencing, and cellular response to DNA damage.	Stanley et al. 2001; Kothapalli et al. 2005a; Chew et al. 2006
K126su	Sc		Transcriptional repression Blocks histone acetylation and histone ubiquitination	Nathan et al. 2006
K127bio	Hs	HCS Biotinidase	Acetylation and methylation dependent Involved in cell proliferation, gene silencing, and cellular response to DNA damage	Stanley et al. 2001; Kothapalli et al. 2005a; Chew et al. 2006
S128ph	Sc	Mec1	DNA damage response	Downs et al. 2000; Redon et al. 2003;
(S129ph)		PIKK	Telomere silencing	Wyatt et al. 2003; Downs et al. 2004
K130bio	Hs	HCS Biotinidase	Acetylation and methylation dependent Involved in cell proliferation, gene silencing, and cellular response to DNA damage	Stanley et al. 2001; Kothapalli et al. 2005a; Chew et al. 2006

Additional H2A modifications: K4ac, K21ac, K74me (Pantazis and Bonner 1981; Song et al. 2003; Aihara et al. 2004).

HCS, holocarboxylase synthetase; PIKK, phosphatidylinositol 3-kinase-related kinase.

Table 2. Histone H2AX

Site	Model	Enzyme	Function	Reference(s)
K13ub	Mm	Rnf168	Part of the DNA damage response to double-stranded DNA breaks	Mattioli et al. 2012; Gatti et al. 2012; Panier and Durocher 2013
K15ub	Mm	Rnf168	Part of the DNA damage response to double-stranded DNA breaks	Mattioli et al. 2012; Gatti et al. 2012; Panier and Durocher 2013
K63ub	Mm	Rnf8	Part of the DNA damage response to double-stranded DNA breaks	Huen et al. 2007; Mailand et al. 2007; Panier and Durocher 2013
S139ph	Hs, Sc, Dm, XI	ATM DNA-PK ATR	DNA repair M-phase related Also known as γ H2AX	Rogakou et al. 1998; Rogakou et al. 1999; Burma et al. 2001; Stiff et al. 2004; Ichijima et al. 2005; Mukherjee et al. 2006; Ward and Chen 2001
Y142ph	Hs, Mm	WSTF	DNA damage	Xiao et al. 2009

ATM, ataxia telangiectasia mutated; PK, protein kinase; ATR, ataxia telangiectasia and Rad3-related; WSTF, Williams–Beuren syndrome transcription factor.

Table 3. Histone H2B

Site	Model	Enzyme	Function	Reference(s)
K5ac	Hs		Transcriptional activation	Puerta et al. 1995; Galasinski et al. 2002
S10ph	Sc	Ste20	Apoptosis	Ahn et al. 2005
S14ph	Hs, Mm	Mst1/krs2 kinase	Apoptosis	Ajiro 2000; Cheung et al. 2003; Odegard et al. 2005
			Somatic hypermutation and class switch recombination	
K16su	Sc		Gene repression	Nathan et al. 2006
K17su	Sc		Gene repression	Nathan et al. 2006
S33ph	Dm	CTK TAF1	Transcriptional activation	Maile et al. 2004
K34ub	Sc	MSL2	Transcriptional activation	Wu et al. 2011
K120ub	Hs	RNF20/40	Cell-cycle progression in concert with SAGA for transcriptional activation through H3 methylation, DNA damage response, meiosis	Robzyk et al. 2000; Sun and Allis 2002; Kao et al. 2004; Zhu et al. 2005
K123ub	Sc	Rad6(E2) Bre1(E3); <i>ub1</i>	Telomeric silencing by lowering histone methylation at H3K4 and H3K79	Emre et al. 2005

Table 4. Histone H3

Site	Model	Enzyme	Function	Reference(s)
R2me	Hs Mm	CARM1; <i>me1, me2a</i> PRMT5; <i>me1, me2s</i> PRMT6; <i>me1, me2a</i> PRMT7; <i>me1, me2s</i>	Gene expression	Chen et al. 1999; Schurter et al. 2001; Greer and Shi 2012
T3ph	Hs At	Haspin	Centromere mitotic spindle function	Polioudaki et al. 2004; Dai et al. 2005
K4ac	Sc	GCN5, RTT109, Sir2, Hst1	Transcription activation at some promoters	Guillemette et al. 2011
K4me	Sc Ce Ds Hs Tt Ds Hs	Set1; <i>me3</i> Set-2; <i>me1–3</i> Set1; <i>me2/3</i> SETD1A; <i>me1–3</i> SETD1B Trx MLL; <i>me1–3</i> MLL2	rDNA/telomeric silencing (Sc) Germ cell maintenance Transcriptional activation (All) Transcriptional activation Trithorax activation Gene activation	Briggs et al. 2001; Roguev et al. 2001; Nagy et al. 2002; Bryk et al. 2002; Bernstein et al. 2002; Santos-Rosa et al. 2002; Lee and Skalnik 2005; Lee et al. 2007; Xiao et al. 2011 Strahl et al. 1999 Milne et al. 2002; Nakamura et al. 2002; Greer and Shi 2012

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Table 4. Continued

Site	Model	Enzyme	Function	Reference(s)
	Ds	Trr	Enhancer function	Herz et al. 2013
	Hs	MLL3; <i>me1-3</i> MLL4		
	Ce	Ash-2; <i>me1-3</i>	Germ cell specification	Beisel et al. 2002; Xiao et al. 2011
	Ds	Ash1; <i>me3</i>	Trithorax activation	
	Hs	ASH1L; <i>me1/3</i>	Gene activation	
	Hs	SETD7; <i>me1</i>	Transcriptional activation	Wang et al. 2001a; Nishioka et al. 2002a; Wilson et al. 2002; Zegerman et al. 2002
	Hs	SMYD3; <i>me2/3</i>	Transcriptional activation	Hamamoto et al. 2004
	Mm	Meisetz; <i>me3</i>	Meiotic prophase progression	Hayashi et al. 2005
T6ph	Hs	PKCβ	Inhibits AR-dependent transcription	Metzger et al. 2010
R8me	Hs	PRMT5; <i>me1, me2s</i>	Transcriptional repression	Pal et al. 2004
K9ac	Sc	SAGA GCN5	Transcriptional activation	Grant et al. 1999
	Hs	SRC1	Nuclear receptor coactivator	Spencer et al. 1997; Schubeler et al. 2000; Vaquero et al. 2004
	Dm		Transcriptional activation	Nowak and Corces 2000
K9me	Sp	Clr4; <i>me1, me2</i>	Centromeric and mating-type silencing	Bannister et al. 2001; Nakayama et al. 2001
	Nc	Dim5; <i>me3</i>	DNA methylation	Tamaru and Selker 2001
	Ce	Met-2; <i>me3</i> Mes-2; <i>me3</i>	Germ cells	Bessler et al. 2010
	Dm	Su(var)3-9; <i>me2/3</i>	Dominant PEV modifier	Czermin et al. 2001; Schotta et al. 2002; Ebert et al. 2004
	At	KRYPTONITE; <i>me2</i>	DNA methylation	Jackson et al. 2002; Jackson et al. 2004
	Mm	Suv39h1; <i>me2/3</i> Suv39h2; <i>me2/3</i>	Pericentric heterochromatin	O'Carroll et al. 2000; Rea et al. 2000; Lachner et al. 2001; Peters et al. 2001
	Hs	SUV39H1; <i>me3</i>	Rb-mediated silencing	Nielsen et al. 2001; Vandel et al. 2001
	Hs, Mm	ESET; <i>me2/me3</i> (SETDB1)	Transcriptional repression	Schultz et al. 2002; Yang et al. 2002; Dodge et al. 2004; Wang et al. 2004
	Mm, Hs	G9a; <i>me1/me2</i>	Transcriptional repression Imprinting	Tachibana et al. 2001, 2002; Ogawa et al. 2002; Xin et al. 2003
	Hs	EHMT1/GLP; <i>me1/me2</i>	Transcriptional repression	Ogawa et al. 2002; Tachibana et al. 2005
	Hs	PRDM2/RIZ1; <i>me2</i>	Tumor suppression and response to female sex hormones	Kim et al. 2003; Carling et al. 2004
S10ph	Sc	Snf1	Transcriptional activation	Lo et al. 2001
	Dm	Jil-1	Transcriptional up-regulation of male X-chromosome	Jin et al. 1999; Wang et al. 2001c
	Hs	Rsk2 Msk1 Msk2	Transcriptional activation of immediate early genes (in concert with H3-K14 acetylation)	Sassone-Corsi et al. 1999; Thomson et al. 1999; Cheung et al. 2000; Clayton et al. 2000
	Hs	IKKα	Transcriptional up-regulation	Anest et al. 2003; Yamamoto et al. 2003
	Sc, Ce	Ip11/AuroraB	Mitotic chromosome condensation	Henzel et al. 1997; Wei et al. 1999; Hsu et al. 2000
	An	NIMA	Mitotic chromosome condensation	De Souza et al. 2000
	Hs, Ce	Fyn kinase	UVB-induced MAP kinase pathway	He et al. 2005
T11ph	Hs	Dlk/ZIP	Mitosis-specific phosphorylation	Preuss et al. 2003
K14ac	Sc, Tt, Mm	Gcn5	Transcriptional activation	Brownell et al. 1996; Kuo et al. 1996
	Hs, Dm	TAF _{II} 230 TAF _{II} 250	Transcriptional activation	Mizzen et al. 1996
	Hs	p300	Transcriptional activation	Schiltz et al. 1999
	Hs	PCAF	Transcriptional activation	Schiltz et al. 1999
	Mm	SRC1	Nuclear receptor coactivator	Spencer et al. 1997
R17me	Hs, Mm	CARM1; <i>me1, me2a</i>	Transcriptional activation (in concert with H3-K18/23 acetylation)	Chen et al. 1999; Schurter et al. 2001; Bauer et al. 2002; Daujat et al. 2002

Continued

Table 4. *Continued*

Site	Model	Enzyme	Function	Reference(s)
K18ac	Sc	SAGA Ada GCN5	Transcriptional activation	Grant et al. 1999
	Hs	p300	Transcriptional activation	Schiltz et al. 1999
	Hs	CBP	Transcriptional activation (in concert with H3-R17 methylation)	Daujat et al. 2002
K23ac	Sc	SAGA	Transcriptional activation	Grant et al. 1999
	Hs	CBP	Transcriptional activation (in concert with H3-R17 methylation)	Daujat et al. 2002
R26me	Hs	CARM1; <i>me1</i> , <i>me2a</i>	In vitro methylation site	Chen et al. 1999; Schurter et al. 2001
K27ac	Sc, Dm	CBP, P300, GCN5	Enhancer function, gene expression	Tie et al. 2009; Suka et al. 2001; Creighton et al. 2010
K27me	Hs, Dm	E(z)/EZH2; <i>me3</i>	Polycomb repression	Cao et al. 2002; Czermin et al. 2002; Kuzmichev et al. 2002; Muller et al. 2002; Su et al. 2003
			Early B-cell development	
			X-chromosome inactivation	
S28ph	Hs	Aurora-B	Mitotic chromosome condensation	Goto et al. 1999; Goto et al. 2002
			UVB-induced phosphorylation	
K36me	Sc	Set2; <i>me2</i>	Gene repression	Zhong et al. 2001 Strahl et al. 2002; Kizer et al. 2005; Sun et al. 2005
K36me	Nc	Set2; <i>me2</i>	Transcription activation	Adhvaryu et al. 2005
	Sp	Set2; <i>me2</i>	Transcription elongation	Morris et al. 2005
	Ce	MES-4; <i>me2</i> MET-1; <i>me3</i>	Dosage compensation in germline Meiosis	Bender et al. 2006; Andersen and Horvitz 2007
	Dm	MES4; <i>me3</i> SET2; <i>me3</i>	Transcription elongation	Bell et al. 2007
	Hs, Mm	SETD2; <i>me1-3</i> NSD1-3; <i>me1</i> , <i>me2</i>	Transcription activation	Edmunds et al. 2008 Wang et al. 2007
	Sc, Mm, Hs	GCN5	Promoter mark on active genes	Morris et al. 2007
P38iso	Sc	Fpr4	Gene expression	Nelson et al. 2006
Y41ph	Hs	JAK2	Gene expression	Dawson et al. 2009
R43me	Hs	CARM1, PRMT6; <i>me2a</i>	Transcriptional activation	Casadio et al. 2013
			DNA replication; apoptosis	
T45ph	Sc, Hs	Cdc7, PKC	DNA replication; apoptosis	Baker et al. 2010; Hurd et al. 2009
K56ac	Sc	SPT10	Transcriptional activation; DNA damage	Xu et al. 2005; Ozdemir et al. 2005; Masumoto et al. 2005
			DNA replication	
K56me	Hs	G9a; <i>me1</i>	DNA replication	Yu et al. 2012
	Hs	Suv39h; <i>me3</i>	Heterochromatin	Jack et al. 2013
K64ac	Hs/Mm	p300	Nucleosome dynamics and transcription	Di Cerbo et al. 2014
K64me	Mm	<i>me3</i>	Pericentric heterochromatin	Daujat et al. 2009
K79me	Sc, Hs	Dot1/DOT1L; <i>me1-3</i>	Telomeric silencing, pachytene checkpoint	Feng et al. 2002; Lacoste et al. 2002; Ng et al. 2002; van Leeuwen et al. 2002; Greer and Shi 2012
			DNA damage response	
T80ph	Hs		Mitosis	Hammond et al. 2014



Table 5. Histone H3.3

Site	Model	Enzyme	Function	Reference(s)
K4me	Dm	<i>me1, me2, me3</i>	Transcriptional activation	McKittrick et al. 2004
K9me	Dm	<i>me1, me2</i>	Transcriptional repression	McKittrick et al. 2004
K9ac	Dm, Hs		Transcriptional activation	McKittrick et al. 2004; Hake et al. 2006
K14me	Dm	<i>me1, me2</i>		McKittrick et al. 2004
K14ac	Dm, Hs		Transcriptional activation	McKittrick et al. 2004; Hake et al. 2006
K18ac	Hs		Transcriptional activation	Hake et al. 2006
K23ac	Hs		Transcriptional activation	Hake et al. 2006
K27me	Dm	<i>me1, me2, me3</i>	Transcriptional repression	McKittrick et al. 2004
S31ph	Mammals		Mitosis-specific phosphorylation	Hake et al. 2005
K36me	Dm, Hs	<i>me1, me2, me3</i>	Transcriptional activation	McKittrick et al. 2004; Hake et al. 2006
K37me	Dm	<i>me1, me2</i>		McKittrick et al. 2004
K79me	Dm, Hs	<i>me1, me2</i>	Transcriptional activation	McKittrick et al. 2004; Hake et al. 2006

Table 6. CEN-H3/CENP-A

Site	Model	Enzyme	Function	Reference
G1me3	Hs	RCC1	Mitosis	Bailey et al. 2013
S7ph	Hs		Mitosis	Zeitlin et al. 2001
S16ph	Hs		Chromosome segregation during mitosis	Bailey et al. 2013
S18ph	Hs		Chromosome segregation during mitosis	Bailey et al. 2013

Table 7. Histone H4

Site	Model	Enzyme	Function	Reference(s)
S1ph	Hs, Sc	Casein kinase II	DNA damage response	Ruiz-Carrillo et al. 1975; Cheung et al. 2005; van Attikum and Gasser 2005
R3me	Hs, Sc	PRMT1; <i>me1, me2a</i> PRMT5; <i>me1, me2s</i> PRMT6; <i>me1, me2a</i> PRMT7; <i>me1, me2s</i>	Transcriptional activation	Wang et al. 2001b; Strahl et al. 2001; Greer and Shi 2012
K5ac	<i>Tt, Dm, Hs</i>	Hat1	Histone deposition	Sobel et al. 1995; Parthun et al. 1996; Taplick et al. 1998; Kruhlak et al. 2001
	Sc	Esa1/NuA4	Cell-cycle progression	Smith et al. 1998; Allard et al. 1999; Clarke et al. 1999; Miranda et al. 2006; Bird et al. 2002
K5me	Hs, Mm	ATF2	Sequence-specific transcription factor	Kawasaki et al. 2000a
	Hs	p300	Transcriptional activation	Schiltz et al. 1999; Turner and Fellows 1989
K8ac	Hs	Smyd3; <i>me1</i>	Contributes to cancer phenotype	Van Aller et al. 2012
K8ac	Hs, Mm	Y-ATF2	Excluded from Xi	Jeppesen and Turner 1993; Choy et al. 2001; Kruhlak et al. 2001; Kawasaki et al. 2000b
			Sequence-specific transcription factor	
K8me	Hs	PCAF/ p300	Transcriptional activation	Schiltz et al. 1999; Turner and Fellows 1989
	Sc	SET5; <i>me1</i>	Stress response	Green et al. 2012
K12ac	Sc, Hs	Hat1	Excluded from Xi	Jeppesen and Turner 1993; Kleff et al. 1995; Sobel et al. 1995;
			Histone deposition	Parthun et al. 1996; Chang et al. 1997; Kruhlak et al. 2001; Turner and Fellows 1989
K12me	Sc	NuA4	Mitotic and meiotic progression	Choy et al. 2001
	Sc	SET5; <i>me1</i>	Stress response	Green et al. 2012

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Table 7. *Continued*

Site	Model	Enzyme	Function	Reference(s)
K12bio	Hs	HCS Biotinidase	Decrease in response to DNA double-strand breaks Effects on cell proliferation	Stanley et al. 2001; Kothapalli et al. 2005a,b
K16ac	Mm		Excluded from Xi Cell-cycle-dependent acetylation	Jeppesen and Turner 1993; Taplick et al. 1998
	Dm	MOF	Transcriptional up-regulation of male X chromosome	Akhtar and Becker 2000; Hsu et al. 2000
	Hs, Mm	ATF2	Sequence-specific transcription factor	Kawasaki et al. 2000a; Turner 2000; Kruhlak et al. 2001; Turner and Fellows 1989; Vaquero et al. 2004
K20me	Mm, Dm	Suv4-20h1; <i>me2</i> , <i>me3</i> Suv4-20h2; <i>me2</i> , <i>me3</i>	Gene silencing	Schotta et al. 2004
	Hs, Dm	SETD8/Pr-SET7; <i>me1</i>	Transcriptional silencing Mitotic condensation	Fang et al. 2002; Nishioka et al. 2002b; Rice et al. 2002
	Dm	Ash1; <i>me2</i>	Trithorax activation in concert with H3K4 and H3K9 methylation	Beisel et al. 2002
K59me	Sc		Silent chromatin formation	Zhang et al. 2003
K59su	Hs	SUMO-1 SUMO-3	Transcriptional repression	Shiio and Eisenman 2003

Table 8. Histone H1

Site	Model	Enzyme	Function	Reference(s)
E2arn	Rn	PARP-1; <i>ar1</i>	Involved in neurotrophic activity	Ogata et al. 1980b; Visochek et al. 2005
T10ph	Hs		Mitosis specific	Chadee et al. 1995; Garcia et al. 2004; Sarg et al. 2006
			Transcriptional activation H1b	
E14arn	Rn	PARP-1; <i>ar1</i>	Involved in neurotrophic activity	Ogata et al. 1980b; Visochek et al. 2005
			Interphase specific	Chadee et al. 1995; Garcia et al. 2004; Sarg et al. 2006
S17ph	Hs		Transcriptional activation H1b	Kuzmichev et al. 2004; Daujat et al. 2005
			Blocks HP1 binding	Garcia et al. 2004; Daujat et al. 2005
R54cit	Mm	PADI4	Cellular reprogramming/nucleosome binding	Christophorou et al. 2014
T137ph	Hs		Mitosis specific	Chadee et al. 1995; Garcia et al. 2004; Sarg et al. 2006
			Transcriptional activation H1b	
T154ph	Hs		Mitosis specific	Chadee et al. 1995; Garcia et al. 2004; Sarg et al. 2006
			Transcriptional activation H1b	
S172ph	Hs		Interphase specific	Chadee et al. 1995; Garcia et al. 2004; Sarg et al. 2006
			Transcriptional activation H1b	
S188ph	Hs		Interphase specific	Chadee et al. 1995; Garcia et al. 2004; Sarg et al. 2006
			Transcriptional activation H1b	
K213ar	Rn	PARP-1; <i>ar1</i>	Involved in neurotrophic activity	Ogata et al. 1980b; Visochek et al. 2005



2 LESS-STUDIED HISTONE PTMS

Methods key

The method by which novel histone modifications have been identified is indicated by the following abbreviations:

Ab	antibody
Au	autoradiography
MS	mass spectrometry

These tables reflect modification sites that have been detected, but where no function has been assigned.

Table 9. Histone H2A^{a,b}

Site	Model	Method	Reference(s)
S1ph	Mm	Au	Pantazis and Bonner 1981
R3me3	Mm	MS	Tweedie-Cullen et al. 2012
K5hib	Mm	MS	Dai et al. 2014
K9me1; me2; suc; hib	Hs; Mm; Hs; Hs	MS	Tan et al. 2011; Tweedie-Cullen et al. 2012; Xie et al. 2012; Dai et al. 2014
R11me1, me2	Hs	MS	Waldmann et al. 2011
K13me1, ac; suc	Bt; Sc	MS	Zhang et al. 2003; Xie et al. 2012
K15ac	Bt	MS	Zhang et al. 2003
K21suc	Sc	MS	Xie et al. 2012
R29me1, me2	Hs	MS/Ab	Waldmann et al. 2011
K36ac, suc; for; hib; cr	Hs/Dm; Hs/Mm; Mm; Hs/Mm	MS	Xie et al. 2012; Wisniewski et al. 2008; Dai et al. 2014; Tan et al. 2011
Y39oh	Hs	MS	Tan et al. 2011
R42me1	Hs; Hs	MS/Ab	Tan et al. 2011
R71me1	Mm	MS	Tweedie-Cullen et al. 2012
K74ac, me1; hib	Mm; Mm	MS	Tweedie-Cullen et al. 2012; Dai et al. 2014
K75me1; hib	Bt; Mm	MS	Zhang et al. 2003; Dai et al. 2014
R77me1	Bt	MS	Zhang et al. 2003
T79ac	Mm	MS	Tweedie-Cullen et al. 2012
R88me1	Hs	MS	Tan et al. 2011
K95cr, but, pr, me1, me2; for; ub; suc; hib	Mm; Hs/Mm; Mm; Hs; Hs/Mm	MS	Tweedie-Cullen et al. 2012; Wisniewski et al. 2008; Tweedie-Cullen et al. 2009; Xie et al. 2012; Dai et al. 2014
K99me1; me2	Mm; Mm	MS	Tweedie-Cullen et al. 2012; Tweedie-Cullen et al. 2009
T101og	Hs	MS/Ab	Sakabe et al. 2010
K118for, me1, cr; for; ub, me2; hib	Hs/Mm; Hs/Mm; Mm; Mm	MS	Tan et al. 2011; Wisniewski et al. 2008; Tweedie-Cullen et al. 2009; Dai et al. 2014
K119cr; mal	Hs; Sc	MS	Tan et al. 2011; Xie et al. 2012
T120ph	Dm	Ab	Aihara et al. 2004
K125me1, cr; me2, pr; ub	Hs; Mm; Mm	MS	Tan et al. 2011; Tweedie-Cullen et al. 2012; Tweedie-Cullen et al. 2009
K127ac	Mm	MS	Tweedie-Cullen et al. 2012
K129ac	Mm	MS	Tweedie-Cullen et al. 2012

^aCarbonylation of H2A has been detected in Rn indirectly by Sharma et al. (2006).

^b5-Hydroxylation of lysine residues has been reported for canonical histones (H2A, H2B, H3, and H4) by Unoki et al. (2013).

Table 10. Histone H2AX

Site	Model	Method	Reference
K118ub	Mm	MS	Tweedie-Cullen et al. 2009
K119ub	Mm	MS	Tweedie-Cullen et al. 2009

Table 11. Histone H2A.Z

Site	Model	Method	Reference(s)
K4ac; me1	Hs;	MS;	Tweedie-Cullen et al. 2009;
	Hs/Mm	MS/Ab	Binda et al. 2013
K7ac; me1	Hs;	MS;	Bonenfant et al. 2006;
	Hs/Mm	MS/Ab	Binda et al. 2013
K11ac	Hs	MS	Bonenfant et al. 2006
K13ac	Mm	MS	Tweedie-Cullen et al. 2009
K120ub	Mm	MS	Ku et al. 2012
K121ub	Mm	MS	Ku et al. 2012
K125ub	Mm	MS	Ku et al. 2012

Table 12. Histone macroH2A

Site	Model	Method	Reference(s)
K17me1	Hs	MS	Chu et al. 2006
K115ub	Hs	MS	Ogawa et al. 2005; Chu et al. 2006
K122me2	Hs	MS	Chu et al. 2006
T128ph	Hs	MS/Ab	Chu et al. 2006; Bernstein et al. 2008
K238me1	Hs	MS	Chu et al. 2006
K238me2	Hs	MS	Chu et al. 2006

Table 13. Histone H2B

Site	Model	Method	Reference(s)
E2arn	Rn	Au	Ogata et al. 1980a
K5me1; cr; for; hib; suc	Bt; Hs; Hs/Mm; Hs/ Mm; Hs	MS	Zhang et al. 2003; Tan et al. 2011; Wisniewski et al. 2008; Dai et al. 2014; Weinert et al. 2013
	Mm	MS	Tweedie-Cullen et al. 2009
S6ph	Mm	MS	Tweedie-Cullen et al. 2009
K11ac; cr	Sc; Hs/Mm	MS	Jiang et al. 2007; Tan et al. 2011
K12me1, cr; me3; hib	Hs; Mm; Mm	MS	Tan et al. 2011; Tweedie-Cullen et al. 2012; Dai et al. 2014
K15ac; me1, cr	Hs	MS	Tan et al. 2011
K16ac; cr	Sc; Hs	MS	Jiang et al. 2007; Tan et al. 2011
T19ac	Mm	MS	Tweedie-Cullen et al. 2012
K20me1, cr; hib	Hs; Mm	MS	Tan et al. 2011; Dai et al. 2014
K21but	Sc	MS	Zhang et al. 2009
K23me1, cr; me2; hib	Hs; Bt; Mm	MS	Tan et al. 2011; Zhang et al. 2003; Dai et al. 2014
K24hib	Mm	MS	Dai et al. 2014
K34for; cr; suc; me1; hib	Hs/Mm; Hs/Mm; Sc/ Hs; Mm; Mm	MS	Wisniewski et al. 2008; Tan et al. 2011; Xie et al. 2012; Tweedie-Cullen et al. 2012; Dai et al. 2014
	Hs	MS/Ab	Sakabe et al. 2010
S36og	Hs	MS/Ab	Sakabe et al. 2010
K37me1	Sc	MS	Zhang et al. 2009
E38me2	Sc	MS	Zhang et al. 2009
Y37oh	Hs	MS	Tan et al. 2011
K43me1; for; hib; suc	Bt; Hs/Mm; Mm; Hs	MS	Zhang et al. 2003; Wisniewski et al. 2008; Dai et al. 2014; Weinert et al. 2013
	Hs/Mm; Sc/Dm; Hs/ Mm	MS	Wisniewski et al. 2008; Xie et al. 2012; Dai et al. 2014
K57me1; ac; hib	Hs; Mm; Mm	MS	Tan et al. 2011; Tweedie-Cullen et al. 2012; Dai et al. 2014
E64me2	Sc	MS	Zhang et al. 2009
S76ph	Mm	MS	Tweedie-Cullen et al. 2009
K79me1	Hs	MS	Tan et al. 2011
K85ac; me1; suc; hib	Bt; Hs; Hs; Hs/Mm	MS	Zhang et al. 2003; Tan et al. 2011; Weinert et al. 2013; Dai et al. 2014
	Mm	MS	Tweedie-Cullen et al. 2009
S88ph	Mm	MS	Tweedie-Cullen et al. 2009
T89ph	Mm	MS	Tweedie-Cullen et al. 2009
S92ph	Mm	MS	Tweedie-Cullen et al. 2009
K99me1	Hs	MS	Tan et al. 2011
K108for; cr; ub; ac; hib; suc	Hs/Mm; Mm; Mm; Hs/Mm; Mm	MS	Wisniewski et al. 2008; Tweedie-Cullen et al. 2012; Tweedie- Cullen et al. 2009; Dai et al. 2014; Park et al. 2013
	Mm	MS	Tweedie-Cullen et al. 2009
S113ph	Mm	MS	Tweedie-Cullen et al. 2009
K116for, me1; suc, mal; ac; hib; cr	Hs; Hs/Dm; Mm; Hs/ Mm; Mm	MS	Tan et al. 2011; Xie et al. 2012; Tweedie-Cullen et al. 2012; Dai et al. 2014; Montellier et al. 2013
	Hs; Hs/Dm/Mm; Mm; Hs/Mm	MS	Tan et al. 2011; Xie et al. 2012; Tweedie-Cullen et al. 2009; Dai et al. 2014
K120for; suc; ac, ub; hib	Hs; Hs/Dm/Mm; Mm; Hs/Mm	MS	Tan et al. 2011; Xie et al. 2012; Tweedie-Cullen et al. 2009; Dai et al. 2014
K125ac	Mm	MS	Tweedie-Cullen et al. 2012

Also, 5-hydroxylation of lysine residues has been reported (Unoki et al. 2013).

Table 14. Histone H3

Site	Model	Method	Reference(s)
K4cr; hib; ac	Hs/Mm; Mm; Hs	MS	Tan et al. 2011; Dai et al. 2014; Garcia et al. 2007
T6ac	Tt	MS	Britton et al. 2013
K9cr; hib	Hs/Mm; Mm	MS	Tan et al. 2011; Dai et al. 2014
S10ac; og	Sc/Mm/Hs	MS; Ab; Ab	Britton et al. 2013; Zhang et al. 2011
K14suc; but; hib	Hs; Sc; Mm	MS	Xie et al. 2012; Zhang et al. 2009; Dai et al. 2014
K18cr; for; me1; hib	Hs/Mm; Hs/Mm; Mm; Mm	MS	Tan et al. 2011; Wisniewski et al. 2008; Garcia et al. 2005; Dai et al. 2014
T22ac	Sc/Dm/Hs	MS	Britton et al. 2013
K23cr; for; pr; hib; suc	Hs/Mm; Hs/Mm; Sc; Hs/Mm; Mm	MS	Tan et al. 2011; Wisniewski et al. 2008; Zhang et al. 2009; Dai et al. 2014; Park et al. 2013
K27cr; but; hib; suc	Hs/Mm; Sc; Mm; Mm	MS	Tan et al. 2011; Zhang et al. 2009; Dai et al. 2014; Park et al. 2013
S28ac	Mm	MS	Britton et al. 2013
T32og	Hs	MS	Fong et al. 2012
K36hib	Mm	MS	Dai et al. 2014
R52me1	Sc/Bt	MS	Hyland et al. 2005
R53me1	Sc/Bt	MS	Hyland et al. 2005
Y54ac	Tet	MS	Britton et al. 2013
K56cr; for; suc; mal; pr; ub; hib	Hs/Mm; Dm/Mm/ Hs; Sc; Mm; Hs/Mm	MS	Tan et al. 2011; Xie et al. 2012; Zhang et al. 2009; Tweedie-Cullen et al. 2009; Dai et al. 2014
E59me2	Sc	MS	Zhang et al. 2009
R63me1	Hs/Mm	MS	Tan et al. 2011
K64for; hib; ac; me1	Hs/Mm; Mm; Sc; Hs	MS	Wisniewski et al. 2008; Dai et al. 2014; Garcia et al. 2007
K79suc; for; cr; ub; hib; ac	Sc/Dm/Mm/Hs; Hs/ Mm; Mm; Mm; Hs/ Mm; Hs	MS	Xie et al. 2012; Wisniewski et al. 2008; Tweedie-Cullen et al. 2012; Tweedie-Cullen et al. 2009; Dai et al. 2014; Garcia et al. 2007
T80ac	Mm	MS	Tweedie-Cullen et al. 2012
R83me1, me2	Mm	MS	Tweedie-Cullen et al. 2012
S86ph	Mm	MS	Tweedie-Cullen et al. 2012
T107ph	Mm	MS	Tweedie-Cullen et al. 2012
C110gt	Hs/Mm	Indirect chemical labeling	Garcia-Gimenez et al. 2013
K115ac; but	Sc/Bt; Mm	MS	Hyland et al. 2005; Tweedie-Cullen et al. 2012
T118ph	Sc/Bt	MS	Hyland et al. 2005
R128me1	Hs/Mm	MS	Tan et al. 2011
K122suc; for; me2; hib; cr	Hs; Hs/Mm; Mm; Hs/ Mm; Mm	MS	Tan et al. 2011; Wisniewski et al. 2008; Tweedie-Cullen et al. 2009; Dai et al. 2014; Montellier et al. 2013
K134me1	Mm	MS	Tweedie-Cullen et al. 2012

Also, 5-hydroxylation of lysine residues has been reported (Unoki et al. 2013).

Table 15. Histone H4

Site	Model	Method	Reference(s)
R3me3	Mm	MS	Tweedie-Cullen et al. 2012
K5cr; me3; pr; but; hib	Mm/Hs; Mm; Hs; Mm	MS	Tan et al. 2011; Tweedie-Cullen et al. 2012; Chen et al. 2007; Dai et al. 2014
K8cr; pr; but; hib	Mm/Hs; Hs; Mm	MS; MS; MS/Ab	Tan et al. 2011; Chen et al. 2007; Dai et al. 2014
K12cr; for; suc; pr; but; hib	Mm/Hs; Hs; Hs; Mm	MS	Tan et al. 2011; Wisniewski et al. 2008; Xie et al. 2012; Chen et al. 2007; Dai et al. 2014
K16cr, me1; pr; pr; but; hib	Mm/Hs; Mm; Hs; Mm	MS	Tan et al. 2011; Tweedie-Cullen et al. 2012; Chen et al. 2007; Dai et al. 2014
R17me1, me2	Mm	MS	Tweedie-Cullen et al. 2012
R17me1, me2, me3	Mm	MS	Tweedie-Cullen et al. 2012
K20ac	Sc	MS	Garcia et al. 2007

Continued

Table 15. *Continued*

Site	Model	Method	Reference(s)
K31for; suc; hib; me1; pr	Hs; Sc/Dm/Mm/Hs; Hs/Mm; Hs/Mm/ Sc; Hs	MS	Tan et al. 2011; Xie et al. 2012; Dai et al. 2014; Garcia et al. 2007; Chen et al. 2007
R23me3	Mm	MS	Tweedie-Cullen et al. 2012
R35me1	Hs	MS	Tan et al. 2011
K44pr; hib	Hs; Mm	MS	Chen et al. 2007; Dai et al. 2014
S47og; ph	Hs; Sc/Bt	MS/Ab; MS	Sakabe et al. 2010; Hyland et al. 2005
Y51oh	Hs	MS	Tan et al. 2011
R55me1	Hs	MS	Tan et al. 2011
K59me1, for; hib	Hs; Mm/Hs; Mm	MS	Tan et al. 2011; Wisniewski et al. 2008; Dai et al. 2014
R67me1	Hs	MS	Tan et al. 2011
K77me1; suc; for; hib; ac; pr; cr	Hs; Sc/Dm/Mm/Hs; Mm/Hs; Hs/Mm; Sc/Bt; Hs; Mm	MS	Tan et al. 2011; Xie et al. 2012; Wisniewski et al. 2008; Dai et al. 2014; Hyland et al. 2005; Chen et al. 2007; Montellier et al. 2013
K79for; suc, ac; hib; pr	Hs; Dm/Mm; Mm; Hs/Mm; Hs	MS	Wisniewski et al. 2008; Xie et al. 2012; Tweedie-Cullen et al. 2012; Dai et al. 2014; Chen et al. 2007
Y88ox; ph	Hs; Mm	MS	Tan et al. 2011; Tweedie-Cullen et al. 2009
K91ac; for; suc; cr; hib; pr	Hs; Hs; Dm/Mm/Hs; Mm; Hs/Mm; Hs	MS	Tan et al. 2011; Wisniewski et al. 2008; Xie et al. 2012; Tweedie-Cullen et al. 2012; Dai et al. 2014; Chen et al. 2007
R92me1	Sc/Bt	MS	Hyland et al. 2005

Also, 5-hydroxylation of lysine residues has been reported (Unoki et al. 2013).

Table 16. Histone H1

Site	Model	Method	Reference(s)
S1ph	Hs	MS	Garcia et al. 2004
E2arn	Rn	Au	Ogata et al. 1980b
T3ph	Hs	MS	Garcia et al. 2004
K12me1	Hs	MS	Lu et al. 2009
E14arn	Rn	Au	Ogata et al. 1980b
K16ac; me1, me2; for	Hs/Mm; Hs/Mm	MS	Wisniewski et al. 2007 Wisniewski et al. 2008
T17ph	Hs	MS	Garcia et al. 2004
K21ac; me1	Hs; Mm	MS	Wisniewski et al. 2007; Tweedie-Cullen et al. 2012
K22hib	Mm	MS	Dai et al. 2014
K25hib	Mm	MS	Dai et al. 2014
K26hib	Mm	MS	Dai et al. 2014
S30ph	Hs	MS	Garcia et al. 2004
K33ac; me2, for; cr; ub; hib	Hs; Mm; Hs/Mm; Mm; Mm	MS	Wisniewski et al. 2007; Tweedie-Cullen et al. 2012; Tan et al. 2011; Tweedie-Cullen et al. 2009
S35ph; ac	Hs; Mm	MS	Garcia et al. 2004; Tweedie-Cullen et al. 2012
K45ac;ub; hib; for; suc	Hs; Hs; Hs/Mm; Mm	MS	Wisniewski et al. 2007; Dai et al. 2014; Wisniewski et al. 2008; Park et al. 2013
K48ac	Hs	MS	Wisniewski et al. 2007
S50ac	Mm	MS	Tweedie-Cullen et al. 2012
K51ac; me1; hib	Hs; Mm; Hs/Mm	MS	Wisniewski et al. 2007; Tweedie-Cullen et al. 2012; Dai et al. 2014
K54me1	Hs	MS	Tan et al. 2011
K62ac; for; hib; suc	Hs; Hs/Mm; Hs/Mm; Hs	MS	Garcia et al. 2004; Wisniewski et al. 2008; Dai et al. 2014; Weinert et al. 2013
K63ac; me1; for; cr; hib	Hs; Hs; Hs/Mm; Hs/ Mm; Hs	MS	Wisniewski et al. 2007; Lu et al. 2009; Wisniewski et al. 2008; Tan et al. 2011; Dai et al. 2014
K64ac	Hs	MS	Tan et al. 2011
K66for	Hs/Mm	MS	Wisniewski et al. 2008

Continued

Table 16. Continued

Site	Model	Method	Reference(s)
S72ph	Hs	MS	Garcia et al. 2004
Y73oh	Hs	MS	Tan et al. 2011
K74for; hib	Hs/Mm; Mm	MS	Wisniewski et al. 2008; Dai et al. 2014
K80hib	Mm	MS	Dai et al. 2014
K81me1	Hs	MS	Lu et al. 2009
K83for	Hs	MS	Tan et al. 2011
K84for; cr; hib	Hs/Mm; Hs/Mm; Hs/Mm	MS	Wisniewski et al. 2008; Tan et al. 2011; Dai et al. 2014
K85ac	Hs	MS	Wisniewski et al. 2007
S87ph ^a	Hs	MS	Garcia et al. 2004
K87for ^a	Hs	MS	Wisniewski et al. 2007
K89ac, for; cr; suc; hib	Hs; Hs; Mm; Hs	MS	Wisniewski et al. 2007; Tan et al. 2011; Park et al. 2013; Dai et al. 2014
K92me1	Hs	MS	Tan et al. 2011
K96ac; me1; me2; for; cr; hib; suc	Hs; Hs; Mm; Hs/Mm; Hs; Hs/Mm; Mm	MS	Wisniewski et al. 2007; Lu et al. 2009; Tweedie-Cullen et al. 2012; Wisniewski et al. 2008; Tan et al. 2011; Dai et al. 2014; Park et al. 2013
K101me1	Hs	MS	Lu et al. 2009
K105me1; suc	Hs; Mm	MS	Lu et al. 2009; Park et al. 2013
K107me1	Hs	MS	Lu et al. 2009
K109me2; for; hib	Mm; Hs/Mm; Mm	MS	Tweedie-Cullen et al. 2012; Wisniewski et al. 2008; Dai et al. 2014
S112ac	Mm	MS	Tweedie-Cullen et al. 2012
K118me1	Hs	MS	Lu et al. 2009
K120hib; suc	Mm; Mm	MS	Dai et al. 2014; Park et al. 2013
K128hib	Mm	MS	Dai et al. 2014
K131me1	Hs	MS	Tan et al. 2011
K135hib	Mm	MS	Dai et al. 2014
K140for	Hs/Mm	MS	Wisniewski et al. 2008
T145ph	Hs	MS	Garcia et al. 2004
T146ph	Hs	MS	Garcia et al. 2004
K147me1; hib	Hs; Mm	MS	Lu et al. 2009; Dai et al. 2014
K150me1	Hs	MS	Tan et al. 2011
K158cr; hib	Hs/Mm; Mm	MS	Tan et al. 2011; Dai et al. 2014
K159for	Hs/Mm	MS	Wisniewski et al. 2008
T164ph	Hs	MS	Wisniewski et al. 2007
K167cr; hib	Hs; Mm	MS	Tan et al. 2011; Dai et al. 2014
T179ph	Hs	MS	Garcia et al. 2004
K187me1	Hs	MS/Ab	Weiss et al. 2010
K201me1	Hs	MS	Tan et al. 2011
K212hib	Mm	MS	Dai et al. 2014
K226me1	Hs	MS	Tan et al. 2011

Pham (2000) found an enzyme that ubiquitinates histone H1

^aH1S87 and H1K87 represent different histone H1 variants.

REFERENCES

- Adhvaryu KK, Morris SA, Strahl BD, Selker EU. 2005. Methylation of histone H3 lysine 36 is required for normal development in *Neurospora crassa*. *Eukaryot Cell* **4**: 1455–1464.
- Ahn SH, Cheung WL, Hsu JY, Diaz RL, Smith MM, Allis CD. 2005. Sterile 20 kinase phosphorylates histone H2B at serine 10 during hydrogen peroxide-induced apoptosis in *S. cerevisiae*. *Cell* **120**: 25–36.
- Aihara H, Nakagawa T, Yasui K, Ohta T, Hirose S, Dhomae N, Takio K, Kaneko M, Takeshima Y, Muramatsu M, et al. 2004. Nucleosomal histone kinase-1 phosphorylates H2A Thr 119 during mitosis in the early *Drosophila* embryo. *Genes Dev* **18**: 877–888.
- Ajro K. 2000. Histone H2B phosphorylation in mammalian apoptotic cells. An association with DNA fragmentation. *J Biol Chem* **275**: 439–443.
- Akhtar A, Becker PB. 2000. Activation of transcription through histone H4 acetylation by MOF, an acetyltransferase essential for dosage compensation in *Drosophila*. *Mol Cell* **5**: 367–375.
- Allard S, Utley RT, Savard J, Clarke A, Grant P, Brandl CJ, Pillus L, Workman JL, Cote J. 1999. NuA4, an essential transcription adaptor/histone H4 acetyltransferase complex containing Esa1p and the ATM-related cofactor Tra1p. *EMBO J* **18**: 5108–5119.

- Allfrey VG, Faulkner R, Mirsky AE. 1964. Acetylation and methylation of histones and their possible role in the regulation of RNA synthesis. *Proc Natl Acad Sci* **51**: 786–794.
- Allis CD, Jenuwein T, Reinberg D. eds. 2007. *Epigenetics*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.
- Andersen EC, Horvitz HR. 2007. Two *C. elegans* histone methyltransferases repress lin-3 EGF transcription to inhibit vulval development. *Development* **134**: 2991–2999.
- Anest V, Hanson JL, Cogswell PC, Steinbrecher KA, Strahl BD, Baldwin AS. 2003. A nucleosomal function for I κ B kinase- α in NF- κ B-dependent gene expression. *Nature* **423**: 659–663.
- Bailey AO, Panchenko T, Sathyan KM, Petkowski JJ, Pai PJ, Bai DL, Russell DH, Macara IG, Shabanowitz J, Hunt DE, et al. 2013. Posttranslational modification of CENP-A influences the conformation of centromeric chromatin. *Proc Natl Acad Sci* **110**: 11827–11832.
- Baker SP, Phillips J, Anderson S, Qiu Q, Shabanowitz J, Smith MM, Yates JR 3rd, Hunt DE, Grant PA. 2010. Histone H3 Thr 45 phosphorylation is a replication-associated post-translational modification in *S. cerevisiae*. *Nat Cell Biol* **12**: 294–298.
- Bannister AJ, Zegerman P, Partridge JF, Miska EA, Thomas JO, Allshire RC, Kouzarides T. 2001. Selective recognition of methylated lysine 9 on histone H3 by the HP1 chromo domain. *Nature* **410**: 120–124.
- Bauer UM, Daujat S, Nielsen SJ, Nightingale K, Kouzarides T. 2002. Methylation at arginine 17 of histone H3 is linked to gene activation. *EMBO Rep* **3**: 39–44.
- Beisel C, Imhof A, Greene J, Kremmer E, Sauer E. 2002. Histone methylation by the *Drosophila* epigenetic transcriptional regulator Ash1. *Nature* **419**: 857–862.
- Bell O, Wirbelauer C, Hild M, Scharf AN, Schwaiger M, MacAlpine DM, Zilbermann F, van Leeuwen F, Bell SP, Imhof A, et al. 2007. Localized H3K36 methylation states define histone H4K16 acetylation during transcriptional elongation in *Drosophila*. *EMBO J* **26**: 4974–4984.
- Bender LB, Suh J, Carroll CR, Fong Y, Fingerman IM, Briggs SD, Cao R, Zhang Y, Reinke V, Strome S. 2006. MES-4: An autosome-associated histone methyltransferase that participates in silencing the X chromosomes in the *C. elegans* germ line. *Development* **133**: 3907–3917.
- Bernstein BE, Humphrey EL, Erlich RL, Schneider R, Bouman P, Liu JS, Kouzarides T, Schreiber SL. 2002. Methylation of histone H3 Lys 4 in coding regions of active genes. *Proc Natl Acad Sci* **99**: 8695–8700.
- Bernstein E, Muratore-Schroeder TL, Diaz RL, Chow JC, Changolkar LN, Shabanowitz J, Heard E, Pehrson JR, Hunt DE, Allis CD. 2008. A phosphorylated subpopulation of the histone variant macroH2A1 is excluded from the inactive X chromosome and enriched during mitosis. *Proc Natl Acad Sci* **105**: 1533–1538.
- Bessler JB, Andersen EC, Villeneuve AM. 2010. Differential localization and independent acquisition of the H3K9me2 and H3K9me3 chromatin modifications in the *Caenorhabditis elegans* adult germ line. *PLoS Genet* **6**: e1000830.
- Binda O, Sevilla A, LeRoy G, Lemischka IR, Garcia BA, Richard S. 2013. SETD6 monomethylates H2AZ on lysine 7 and is required for the maintenance of embryonic stem cell self-renewal. *Epigenetics* **8**: 177–183.
- Bird AW, Yu DY, Pray-Grant MG, Qiu Q, Harmon KE, Megee PC, Grant PA, Smith MM, Christman MF. 2002. Acetylation of histone H4 by Esa1 is required for DNA double-strand break repair. *Nature* **419**: 411–415.
- Bonenfant D, Coulot M, Towbin H, Schindler P, van Oostrum J. 2006. Characterization of histone H2A and H2B variants and their post-translational modifications by mass spectrometry. *Mol Cell Proteomics* **5**: 541–552.
- Briggs SD, Bryk M, Strahl BD, Cheung WL, Davie JK, Dent SY, Winston F, Allis CD. 2001. Histone H3 lysine 4 methylation is mediated by Set1 and required for cell growth and rDNA silencing in *Saccharomyces cerevisiae*. *Genes Dev* **15**: 3286–3295.
- Britton LM, Newhart A, Bhanu NV, Sridharan R, Gonzales-Cope M, Plath K, Janicki SM, Garcia BA. 2013. Initial characterization of histone H3 serine 10 O-acetylation. *Epigenetics* **8**: 1101–1113.
- Brownell JE, Zhou J, Ranalli T, Kobayashi R, Edmondson DG, Roth SY, Allis CD. 1996. *Tetrahymena* histone acetyltransferase A: A homolog to yeast Gcn5p linking histone acetylation to gene activation. *Cell* **84**: 843–851.
- Bryk M, Briggs SD, Strahl BD, Curcio MJ, Allis CD, Winston F. 2002. Evidence that Set1, a factor required for methylation of histone H3, regulates rDNA silencing in *S. cerevisiae* by a Sir2-dependent mechanism. *Curr Biol* **12**: 165–170.
- Burma S, Chen BP, Murphy M, Kurimasa A, Chen DJ. 2001. ATM phosphorylates histone H2AX in response to DNA double-strand breaks. *J Biol Chem* **276**: 42462–42467.
- Cao R, Wang L, Wang H, Xia L, Erdjument-Bromage H, Tempst P, Jones RS, Zhang Y. 2002. Role of histone H3 lysine 27 methylation in Polycomb-group silencing. *Science* **298**: 1039–1043.
- Carling T, Kim KC, Yang XH, Gu J, Zhang XK, Huang S. 2004. A histone methyltransferase is required for maximal response to female sex hormones. *Mol Cell Biol* **24**: 7032–7042.
- Casadio F, Lu X, Pollock SB, LeRoy G, Garcia BA, Muir TW, Roeder RG, Allis CD. 2013. H3R42me2a is a histone modification with positive transcriptional effects. *Proc Natl Acad Sci* **110**: 14894–14899.
- Chadee DN, Taylor WR, Hurta RA, Allis CD, Wright JA, Davie JR. 1995. Increased phosphorylation of histone H1 in mouse fibroblasts transformed with oncogenes or constitutively active mitogen-activated protein kinase kinase. *J Biol Chem* **270**: 20098–20105.
- Chang L, Loranger SS, Mizzen C, Ernst SG, Allis CD, Annunziato AT. 1997. Histones in transit: Cytosolic histone complexes and diacetylation of H4 during nucleosome assembly in human cells. *Biochemistry* **36**: 469–480.
- Chen D, Ma H, Hong H, Koh SS, Huang SM, Schurter BT, Aswad DW, Stallcup MR. 1999. Regulation of transcription by a protein methyltransferase. *Science* **284**: 2174–2177.
- Chen Y, Sprung R, Tang Y, Ball H, Sangras B, Kim SC, Falck JR, Peng J, Gu W, Zhao Y. 2007. Lysine propionylation and butyrylation are novel post-translational modifications in histones. *Mol Cell Proteomics* **6**: 812–819.
- Cheung P, Tanner KG, Cheung WL, Sassone-Corsi P, Denu JM, Allis CD. 2000. Synergistic coupling of histone H3 phosphorylation and acetylation in response to epidermal growth factor stimulation. *Mol Cell* **5**: 905–915.
- Cheung WL, Ajiro K, Samejima K, Kloc M, Cheung P, Mizzen CA, Beeser A, Etkin LD, Chernoff J, Earnshaw WC, et al. 2003. Apoptotic phosphorylation of histone H2B is mediated by mammalian sterile twenty kinase. *Cell* **113**: 507–517.
- Cheung WL, Turner FB, Krishnamoorthy T, Wolner B, Ahn SH, Foley M, Dorsey JA, Peterson CL, Berger SL, Allis CD. 2005. Phosphorylation of histone H4 serine 1 during DNA damage requires casein kinase II in *S. cerevisiae*. *Curr Biol* **15**: 656–660.
- Chew YC, Camporeale G, Kothapalli N, Sarath G, Zemleni J. 2006. Lysine residues in N-terminal and C-terminal regions of human histone H2A are targets for biotinylation by biotinidase. *J Nutr Biochem* **17**: 225–233.
- Choy JS, Tobe BT, Huh JH, Kron SJ. 2001. Yng2p-dependent NuA4 histone H4 acetylation activity is required for mitotic and meiotic progression. *J Biol Chem* **276**: 43653–43662.
- Christophorou MA, Castelo-Branco G, Halley-Stott RP, Oliveira CS, Loos R, Radzisheuskaya A, Mowen KA, Bertone P, Silva JC, Zernicka-Goetz M, et al. 2014. Citrullination regulates pluripotency and histone H1 binding to chromatin. *Nature* **507**: 104–108.
- Chu F, Nusinow DA, Chalkley RJ, Plath K, Panning B, Burlingame AL. 2006. Mapping post-translational modifications of the histone variant MacroH2A1 using tandem mass spectrometry. *Mol Cell Proteomics* **5**: 194–203.
- Clarke AS, Lowell JE, Jacobson SJ, Pillus L. 1999. Esa1p is an essential histone acetyltransferase required for cell cycle progression. *Mol Cell Biol* **19**: 2515–2526.
- Clayton AL, Rose S, Barratt MJ, Mahadevan LC. 2000. Phosphoacetylation of histone H3 on *c-fos*- and *c-jun*-associated nucleosomes upon gene activation. *EMBO J* **19**: 3714–3726.

- Creyghton MP, Cheng AW, Welstead GG, Kooistra T, Carey BW, Steine EJ, Hanna J, Lodato MA, Frampton GM, Sharp PA, et al. 2010. Histone H3K27ac separates active from poised enhancers and predicts developmental state. *Proc Natl Acad Sci* **107**: 21931–21936.
- Czermin B, Schotta G, Hulsman BB, Brehm A, Becker PB, Reuter G, Imhof A. 2001. Physical and functional association of SU(VAR)3–9 and HDAC1 in *Drosophila*. *EMBO Rep* **2**: 915–919.
- Czermin B, Melfi R, McCabe D, Seitz V, Imhof A, Pirrotta V. 2002. *Drosophila* enhancer of Zeste/ESC complexes have a histone H3 methyltransferase activity that marks chromosomal Polycomb sites. *Cell* **111**: 185–196.
- Dai J, Sultan S, Taylor SS, Higgins JM. 2005. The kinase haspin is required for mitotic histone H3 Thr 3 phosphorylation and normal metaphase chromosome alignment. *Genes Dev* **19**: 472–488.
- Dai L, Peng C, Montellier E, Lu Z, Chen Y, Ishii H, Debernardi A, Buchou T, Rousseaux S, Jin F, et al. 2014. Lysine 2-hydroxyisobutyrylation is a widely distributed active histone mark. *Nat Chem Biol* **10**: 365–370.
- Daujat S, Bauer UM, Shah V, Turner B, Berger S, Kouzarides T. 2002. Crosstalk between CARM1 methylation and CBP acetylation on histone H3. *Curr Biol* **12**: 2090–2097.
- Daujat S, Zeissler U, Waldmann T, Happel N, Schneider R. 2005. HP1 binds specifically to Lys26-methylated histone H14, whereas simultaneous Ser27 phosphorylation blocks HP1 binding. *J Biol Chem* **280**: 38090–38095.
- Daujat S, Weiss T, Mohn F, Lange UC, Ziegler-Birling C, Zeissler U, Lappe M, Schubeler D, Torres-Padilla ME, Schneider R. 2009. H3K64 trimethylation marks heterochromatin and is dynamically remodeled during developmental reprogramming. *Nat Struct Mol Biol* **16**: 777–781.
- Dawson MA, Bannister AJ, Gottgens B, Foster SD, Bartke T, Green AR, Kouzarides T. 2009. JAK2 phosphorylates histone H3Y41 and excludes HP1 α from chromatin. *Nature* **461**: 819–822.
- De Souza CB, Osmani AH, Wu LP, Spotts JL, Osmani SA. 2000. Mitotic histone H3 phosphorylation by the NIMA kinase in *Aspergillus nidulans*. *Cell* **102**: 293–302.
- Di Cerbo V, Mohn F, Ryan DP, Montellier E, Kacem S, Tropberger P, Kallis E, Holzner M, Hoerner L, Feldmann A, et al. 2014. Acetylation of histone H3 at lysine 64 regulates nucleosome dynamics and facilitates transcription. *eLife* **3**: e01632.
- Dodge JE, Kang YK, Beppu H, Lei H, Li E. 2004. Histone H3-K9 methyltransferase ESET is essential for early development. *Mol Cell Biol* **24**: 2478–2486.
- Downs JA, Lowndes NE, Jackson SP. 2000. A role for *Saccharomyces cerevisiae* histone H2A in DNA repair. *Nature* **408**: 1001–1004.
- Downs JA, Allard S, Jobin-Robitaille O, Javaheri A, Auger A, Bouchard N, Kron SJ, Jackson SP, Cote J. 2004. Binding of chromatin-modifying activities to phosphorylated histone H2A at DNA damage sites. *Mol Cell* **16**: 979–990.
- Ebert A, Schotta G, Lein S, Kubicek S, Krauss V, Jenuwein T, Reuter G. 2004. Su(var) genes regulate the balance between euchromatin and heterochromatin in *Drosophila*. *Genes Dev* **18**: 2973–2983.
- Edmunds JW, Mahadevan LC, Clayton AL. 2008. Dynamic histone H3 methylation during gene induction: HYPB/Setd2 mediates all H3K36 trimethylation. *EMBO J* **27**: 406–420.
- Emre NC, Ingvarsdottir K, Wyce A, Wood A, Krogan NJ, Henry KW, Li K, Marmorstein R, Greenblatt JF, Shilatifard A, et al. 2005. Maintenance of low histone ubiquitylation by Ubp10 correlates with telomere-proximal Sir2 association and gene silencing. *Mol Cell* **17**: 585–594.
- Fang J, Feng Q, Ketel CS, Wang H, Cao R, Xia L, Erdjument-Bromage H, Tempst P, Simon JA, Zhang Y. 2002. Purification and functional characterization of SET8, a nucleosomal histone H4-lysine 20-specific methyltransferase. *Curr Biol* **12**: 1086–1099.
- Feng Q, Wang H, Ng HH, Erdjument-Bromage H, Tempst P, Struhl K, Zhang Y. 2002. Methylation of H3-lysine 79 is mediated by a new family of HMTases without a SET domain. *Curr Biol* **12**: 1052–1058.
- Fong JJ, Nguyen BL, Bridger R, Medrano EE, Wells L, Pan S, Sifers RN. 2012. β -N-Acetylglucosamine O-GlcNAc is a novel regulator of mitosis-specific phosphorylations on histone H3. *J Biol Chem* **287**: 12195–12203.
- Galasinski SC, Louie DF, Gloor KK, Resing KA, Ahn NG. 2002. Global regulation of post-translational modifications on core histones. *J Biol Chem* **277**: 2579–2588.
- Garcia BA, Busby SA, Barber CM, Shabanowitz J, Allis CD, Hunt DF. 2004. Characterization of phosphorylation sites on histone H1 isoforms by tandem mass spectrometry. *J Proteome Res* **3**: 1219–1227.
- Garcia BA, Busby SA, Shabanowitz J, Hunt DF, Mishra N. 2005. Resetting the epigenetic histone code in the MRL-lpr/lpr mouse model of lupus by histone deacetylase inhibition. *J Proteome Res* **4**: 2032–2042.
- Garcia BA, Hake SB, Diaz RL, Kauer M, Morris SA, Recht J, Shabanowitz J, Mishra N, Strahl BD, Allis CD, et al. 2007. Organismal differences in post-translational modifications in histones H3 and H4. *J Biol Chem* **282**: 7641–7655.
- Garcia-Gimenez JL, Olaso G, Hake SB, Bonisch C, Wiedemann SM, Markovic J, Dasi F, Gimeno A, Perez-Quilis C, Palacios O, et al. 2013. Histone h3 glutathionylation in proliferating mammalian cells destabilizes nucleosomal structure. *Antioxid Redox Signal* **19**: 1305–1320.
- Gatti M, Pinato S, Maspero E, Soffientini P, Polo S, Penengo L. 2012. A novel ubiquitin mark at the N-terminal tail of histone H2As targeted by RNF168 ubiquitin ligase. *Cell Cycle* **11**: 2538–2544.
- Goto H, Tomono Y, Ajiro K, Kosako H, Fujita M, Sakurai M, Okawa K, Iwamatsu A, Okigaki T, Takahashi T, et al. 1999. Identification of a novel phosphorylation site on histone H3 coupled with mitotic chromosome condensation. *J Biol Chem* **274**: 25543–25549.
- Goto H, Yasui Y, Nigg EA, Inagaki M. 2002. Aurora-B phosphorylates histone H3 at serine28 with regard to the mitotic chromosome condensation. *Genes Cells* **7**: 11–17.
- Grant PA, Eberharther A, John S, Cook RG, Turner BM, Workman JL. 1999. Expanded lysine acetylation specificity of Gcn5 in native complexes. *J Biol Chem* **274**: 5895–5900.
- Green EM, Mas G, Young NL, Garcia BA, Gozani O. 2012. Methylation of H4 lysines 5, 8 and 12 by yeast Set5 calibrates chromatin stress responses. *Nat Struct Mol Biol* **19**: 361–363.
- Greer EL, Shi Y. 2012. Histone methylation: A dynamic mark in health, disease and inheritance. *Nat Rev Genet* **13**: 343–357.
- Guillemette B, Drogaris P, Lin HH, Armstrong H, Hiragami-Hamada K, Imhof A, Bonnell E, Thibault P, Verreault A, Festenstein RJ. 2011. H3 lysine 4 is acetylated at active gene promoters and is regulated by H3 lysine 4 methylation. *PLoS Genet* **7**: e1001354.
- Hake SB, Garcia BA, Kauer M, Baker SP, Shabanowitz J, Hunt DF, Allis CD. 2005. Serine 31 phosphorylation of histone variant H3.3 is specific to regions bordering centromeres in metaphase chromosomes. *Proc Natl Acad Sci* **102**: 6344–6349.
- Hake SB, Garcia BA, Duncan EM, Kauer M, Dellaire G, Shabanowitz J, Bazett-Jones DP, Allis CD, Hunt DF. 2006. Expression patterns and post-translational modifications associated with mammalian histone H3 variants. *J Biol Chem* **281**: 559–568.
- Hamamoto R, Furukawa Y, Morita M, Iimura Y, Silva FB, Li M, Yagyu R, Nakamura Y. 2004. SMYD3 encodes a histone methyltransferase involved in the proliferation of cancer cells. *Nat Cell Biol* **6**: 731–740.
- Hammond SL, Byrum SD, Namjoshi S, Graves HK, Dennehey BK, Tackett AJ, Tyler JK. 2014. Mitotic phosphorylation of histone H3 threonine 80. *Cell Cycle* **13**: 440–452.
- Han Y, Garcia BA. 2013. Combining genomic and proteomic approaches for epigenetics research. *Epigenomics* **5**: 439–452.
- Harvey AC, Jackson SP, Downs JA. 2005. *Saccharomyces cerevisiae* histone H2A Ser122 facilitates DNA repair. *Genetics* **170**: 543–553.
- Hayashi K, Yoshida K, Matsui Y. 2005. A histone H3 methyltransferase controls epigenetic events required for meiotic prophase. *Nature* **438**: 374–378.
- He Z, Cho YY, Ma WY, Choi HS, Bode AM, Dong Z. 2005. Regulation of ultraviolet B-induced phosphorylation of histone H3 at serine 10 by Fyn kinase. *J Biol Chem* **280**: 2446–2454.
- Hendzel MJ, Wei Y, Mancini MA, Van Hooser A, Ranalli T, Brinkley BR, Bazett-Jones DP, Allis CD. 1997. Mitosis-specific phosphoryla-

- tion of histone H3 initiates primarily within pericentromeric heterochromatin during G2 and spreads in an ordered fashion coincident with mitotic chromosome condensation. *Chromosoma* **106**: 348–360.
- Hsu JY, Sun ZW, Li X, Reuben M, Tatchell K, Bishop DK, Grushcow JM, Brame CJ, Caldwell JA, Hunt DE, et al. 2000. Mitotic phosphorylation of histone H3 is governed by Ipl1/aurora kinase and Glc7/PP1 phosphatase in budding yeast and nematodes. *Cell* **102**: 279–291.
- Huen MS, Grant R, Manke I, Minn K, Yu X, Yaffe MB, Chen J. 2007. RNF8 transduces the DNA-damage signal via histone ubiquitylation and checkpoint protein assembly. *Cell* **131**: 901–914.
- Hurd PJ, Bannister AJ, Halls K, Dawson MA, Vermeulen M, Olsen JV, Ismail H, Somers J, Mann M, Owen-Hughes T, et al. 2009. Phosphorylation of histone H3 Thr-45 is linked to apoptosis. *J Biol Chem* **284**: 16575–16583.
- Hyland EM, Cosgrove MS, Molina H, Wang D, Pandey A, Cottee RJ, Boeke JD. 2005. Insights into the role of histone H3 and histone H4 core modifiable residues in *Saccharomyces cerevisiae*. *Mol Cell Biol* **25**: 10060–10070.
- Ichijima Y, Sakasai R, Okita N, Asahina K, Mizutani S, Teraoka H. 2005. Phosphorylation of histone H2AX at M phase in human cells without DNA damage response. *Biochem Biophys Res Commun* **336**: 807–812.
- Jack AP, Bussemer S, Hahn M, Punzeler S, Snyder M, Wells M, Csankovszki G, Solovei I, Schotta G, Hake SB. 2013. H3K56me3 is a novel, conserved heterochromatic mark that largely but not completely overlaps with H3K9me3 in both regulation and localization. *PLoS One* **8**: e51765.
- Jackson JP, Lindroth AM, Cao X, Jacobsen SE. 2002. Control of CpNpG DNA methylation by the KRYPTONITE histone H3 methyltransferase. *Nature* **416**: 556–560.
- Jackson JP, Johnson L, Jasencakova Z, Zhang X, PerezBurgos L, Singh PB, Cheng X, Schubert I, Jenuwein T, Jacobsen SE. 2004. Dimethylation of histone H3 lysine 9 is a critical mark for DNA methylation and gene silencing in *Arabidopsis thaliana*. *Chromosoma* **112**: 308–315.
- Jeppesen P, Turner BM. 1993. The inactive X chromosome in female mammals is distinguished by a lack of histone H4 acetylation, a cytogenetic marker for gene expression. *Cell* **74**: 281–289.
- Jiang L, Smith JN, Anderson SL, Ma P, Mizzen CA, Kelleher NL. 2007. Global assessment of combinatorial post-translational modification of core histones in yeast using contemporary mass spectrometry. LYS4 trimethylation correlates with degree of acetylation on the same H3 tail. *J Biol Chem* **282**: 27923–27934.
- Jin Y, Wang Y, Walker DL, Dong H, Conley C, Johansen J, Johansen KM. 1999. JIL-1: A novel chromosomal tandem kinase implicated in transcriptional regulation in *Drosophila*. *Mol Cell* **4**: 129–135.
- Kao CF, Hillyer C, Tsukuda T, Henry K, Berger S, Osley MA. 2004. Rad6 plays a role in transcriptional activation through ubiquitylation of histone H2B. *Genes Dev* **18**: 184–195.
- Kapetanaki MG, Guerrero-Santoro J, Bisi DC, Hsieh CL, Rapic-Otrin V, Levine AS. 2006. The DDB1-CUL4^{DDB2} ubiquitin ligase is deficient in xeroderma pigmentosum group E and targets histone H2A at UV-damaged DNA sites. *Proc Natl Acad Sci* **103**: 2588–2593.
- Karch KR, Denizio JE, Black BE, Garcia BA. 2013. Identification and interrogation of combinatorial histone modifications. *Front Genet* **4**: 264.
- Kawasaki H, Taira K, Yokoyama K. 2000a. Histone acetyltransferase (HAT) activity of ATF-2 is necessary for the CRE-dependent transcription. *Nucleic Acids Symp Ser* **2000**: 259–260.
- Kawasaki H, Schiltz L, Chiu R, Itakura K, Taira K, Nakatani Y, Yokoyama KK. 2000b. ATF-2 has intrinsic histone acetyltransferase activity which is modulated by phosphorylation. *Nature* **405**: 195–200.
- Kawashima SA, Yamagishi Y, Honda T, Ishiguro K, Watanabe Y. 2010. Phosphorylation of H2A by Bub1 prevents chromosomal instability through localizing shugoshin. *Science* **327**: 172–177.
- Kim KC, Geng L, Huang S. 2003. Inactivation of a histone methyltransferase by mutations in human cancers. *Cancer Res* **63**: 7619–7623.
- Kimura A, Horikoshi M. 1998. Tip60 acetylates six lysines of a specific class in core histones in vitro. *Genes Cells* **3**: 789–800.
- Kizer KO, Phatnani HP, Shibata Y, Hall H, Greenleaf AL, Strahl BD. 2005. A novel domain in Set2 mediates RNA polymerase II interaction and couples histone H3 K36 methylation with transcript elongation. *Mol Cell Biol* **25**: 3305–3316.
- Kleff S, Andrulis ED, Anderson CW, Sternglanz R. 1995. Identification of a gene encoding a yeast histone H4 acetyltransferase. *J Biol Chem* **270**: 24674–24677.
- Kothapalli N, Camporeale G, Kueh A, Chew YC, Oommen AM, Griffin JB, Zempleni J. 2005a. Biological functions of biotinylated histones. *J Nutr Biochem* **16**: 446–448.
- Kothapalli N, Sarath G, Zempleni J. 2005b. Biotinylation of K12 in histone H4 decreases in response to DNA double-strand breaks in human JAr choriocarcinoma cells. *J Nutr* **135**: 2337–2342.
- Kouzarides T. 2007. Chromatin modifications and their function. *Cell* **128**: 693–705.
- Kruhlik MJ, Hendzel MJ, Fischle W, Bertos NR, Hameed S, Yang XJ, Verdin E, Bazett-Jones DP. 2001. Regulation of global acetylation in mitosis through loss of histone acetyltransferases and deacetylases from chromatin. *J Biol Chem* **276**: 38307–38319.
- Ku M, Jaffe JD, Koche RP, Rheinbay E, Endoh M, Koseki H, Carr SA, Bernstein BE. 2012. H2A.Z landscapes and dual modifications in pluripotent and multipotent stem cells underlie complex genome regulatory functions. *Genome Biol* **13**: R85.
- Kuo MH, Brownell JE, Sobel RE, Ranalli TA, Cook RG, Edmondson DG, Roth SY, Allis CD. 1996. Transcription-linked acetylation by Gcn5p of histones H3 and H4 at specific lysines. *Nature* **383**: 269–272.
- Kuzmichev A, Nishioka K, Erdjument-Bromage H, Tempst P, Reinberg D. 2002. Histone methyltransferase activity associated with a human multiprotein complex containing the Enhancer of Zeste protein. *Genes Dev* **16**: 2893–2905.
- Kuzmichev A, Jenuwein T, Tempst P, Reinberg D. 2004. Different EZH2-containing complexes target methylation of histone H1 or nucleosomal histone H3. *Mol Cell* **14**: 183–193.
- Lachner M, O'Carroll D, Rea S, Mechtler K, Jenuwein T. 2001. Methylation of histone H3 lysine 9 creates a binding site for HP1 proteins. *Nature* **410**: 116–120.
- Lachner M, O'Sullivan RJ, Jenuwein T. 2003. An epigenetic road map for histone lysine methylation. *J Cell Sci* **116**: 2117–2124.
- Lacoste N, Utley RT, Hunter JM, Poirier GG, Cote J. 2002. Disruptor of telomeric silencing-1 is a chromatin-specific histone H3 methyltransferase. *J Biol Chem* **277**: 30421–30424.
- Lee JH, Skalnik DG. 2005. CpG-binding protein (CXXC finger protein 1) is a component of the mammalian Set1 histone H3-Lys4 methyltransferase complex, the analogue of the yeast Set1/COMPASS complex. *J Biol Chem* **280**: 41725–41731.
- Lee JH, Tate CM, You JS, Skalnik DG. 2007. Identification and characterization of the human Set1B histone H3-Lys4 methyltransferase complex. *J Biol Chem* **282**: 13419–13428.
- Lo WS, Duggan L, Emre NC, Belotserkovskaya R, Lane WS, Shiekhattar R, Berger SL. 2001. Snf1—A histone kinase that works in concert with the histone acetyltransferase Gcn5 to regulate transcription. *Science* **293**: 1142–1146.
- Lu A, Zougman A, Pudelko M, Bebenek M, Ziolkowski P, Mann M, Wisniewski JR. 2009. Mapping of lysine monomethylation of linker histones in human breast and its cancer. *J Proteome Res* **8**: 4207–4215.
- Mailand N, Bekker-Jensen S, Fastrup H, Melander F, Bartek J, Lukas C, Lukas J. 2007. RNF8 ubiquitylates histones at DNA double-strand breaks and promotes assembly of repair proteins. *Cell* **131**: 887–900.
- Maile T, Kwoczyński S, Katzenberger RJ, Wassarman DA, Sauer F. 2004. TAF1 activates transcription by phosphorylation of serine 33 in histone H2B. *Science* **304**: 1010–1014.
- Masumoto H, Hawke D, Kobayashi R, Verreault A. 2005. A role for cell-cycle-regulated histone H3 lysine 56 acetylation in the DNA damage response. *Nature* **436**: 294–298.

- Mattiroli F, Vissers JH, van Dijk WJ, Ikpa B, Citterio E, Vermeulen W, Martijn JA, Sixma TK. 2012. RNF168 ubiquitinates K13–15 on H2A/H2AX to drive DNA damage signaling. *Cell* **150**: 1182–1195.
- McKittrick E, Gafken PR, Ahmad K, Henikoff S. 2004. Histone H33 is enriched in covalent modifications associated with active chromatin. *Proc Natl Acad Sci* **101**: 1525–1530.
- Mitzger E, Imhof A, Patel D, Kahl B, Hoffmeyer K, Friedrichs N, Muller JM, Greschik H, Kirfel J, Ji S, et al. 2010. Phosphorylation of histone H3T6 by PKCB(I) controls demethylation at histone H3K4. *Nature* **464**: 792–796.
- Milne TA, Briggs SD, Brock HW, Martin ME, Gibbs D, Allis CD, Hess JL. 2002. MLL targets SET domain methyltransferase activity to *Hox* gene promoters. *Mol Cell* **10**: 1107–1117.
- Miranda TB, Sayegh J, Frankel A, Katz JE, Miranda M, Clarke S. 2006. Yeast Hsl7 (histone synthetic lethal 7) catalyses the in vitro formation of ω -N^G-monomethylarginine in calf thymus histone H2A. *Biochem J* **395**: 563–570.
- Mizzen CA, Yang XJ, Kokubo T, Brownell JE, Bannister AJ, Owen-Hughes T, Workman J, Wang L, Berger SL, Kouzarides T, et al. 1996. The TAF_{II}250 subunit of TFIID has histone acetyltransferase activity. *Cell* **87**: 1261–1270.
- Montellier E, Boussovar F, Rousseaux S, Zhang K, Buchou T, Fenaille F, Shiota H, Debernardi A, Hery P, Jamshidikia M, et al. 2013. Chromatin-to-nucleoprotamine transition is controlled by the histone H2B variant TH2B. *Genes Dev* **27**: 1680–1692.
- Morris SA, Shibata Y, Noma K, Tsukamoto Y, Warren E, Temple B, Grewal SI, Strahl BD. 2005. Histone H3 K36 methylation is associated with transcription elongation in *Schizosaccharomyces pombe*. *Eukaryot Cell* **4**: 1446–1454.
- Morris SA, Rao B, Garcia BA, Hake SB, Diaz RL, Shabanowitz J, Hunt DE, Allis CD, Lieb JD, Strahl BD. 2007. Identification of histone H3 lysine 36 acetylation as a highly conserved histone modification. *J Biol Chem* **282**: 7632–7640.
- Mukherjee B, Kessinger C, Kobayashi J, Chen BP, Chen DJ, Chatterjee A, Burma S. 2006. DNA-PK phosphorylates histone H2AX during apoptotic DNA fragmentation in mammalian cells. *DNA Repair* **5**: 575–590.
- Muller J, Hart CM, Francis NJ, Vargas ML, Sengupta A, Wild B, Miller EL, O'Connor MB, Kingston RE, Simon JA. 2002. Histone methyltransferase activity of a *Drosophila* Polycomb group repressor complex. *Cell* **111**: 197–208.
- Murr R. 2010. Interplay between different epigenetic modifications and mechanisms. *Adv Genet* **70**: 101–141.
- Nagy PL, Griesenbeck J, Kornberg RD, Cleary ML. 2002. A trithorax-group complex purified from *Saccharomyces cerevisiae* is required for methylation of histone H3. *Proc Natl Acad Sci* **99**: 90–94.
- Nakayama J, Rice JC, Strahl BD, Allis CD, Grewal SI. 2001. Role of histone H3 lysine 9 methylation in epigenetic control of heterochromatin assembly. *Science* **292**: 110–113.
- Nakamura T, Mori T, Tada S, Krajewski W, Rozovskaia T, Wassell R, Dubois G, Mazo A, Croce CM, Canaani E. 2002. ALL-1 is a histone methyltransferase that assembles a supercomplex of proteins involved in transcriptional regulation. *Mol Cell* **10**: 1119–1128.
- Nathan D, Ingvarsdottir K, Sterner DE, Bylebyl GR, Dokmanovic M, Dorsey JA, Whelan KA, Krsmanovic M, Lane WS, Meluh PB, et al. 2006. Histone sumoylation is a negative regulator in *Saccharomyces cerevisiae* and shows dynamic interplay with positive-acting histone modifications. *Genes Dev* **20**: 966–976.
- Nelson CJ, Santos-Rosa H, Kouzarides T. 2006. Proline isomerization of histone H3 regulates lysine methylation and gene expression. *Cell* **126**: 905–916.
- Ng HH, Xu RM, Zhang Y, Struhl K. 2002. Ubiquitination of histone H2B by Rad6 is required for efficient Dot1-mediated methylation of histone H3 lysine 79. *J Biol Chem* **277**: 34655–34657.
- Nielsen SJ, Schneider R, Bauer UM, Bannister AJ, Morrison A, O'Carroll D, Firestein R, Cleary M, Jenuwein T, Herrera RE, et al. 2001. Rb targets histone H3 methylation and HP1 to promoters. *Nature* **412**: 561–565.
- Nishioka K, Chuikov S, Sarma K, Erdjument-Bromage H, Allis CD, Tempst P, Reinberg D. 2002a. Set9, a novel histone H3 methyltransferase that facilitates transcription by precluding histone tail modifications required for heterochromatin formation. *Genes Dev* **16**: 479–489.
- Nishioka K, Rice JC, Sarma K, Erdjument-Bromage H, Werner J, Wang Y, Chuikov S, Valenzuela P, Tempst P, Steward R, et al. 2002b. PR-Set7 is a nucleosome-specific methyltransferase that modifies lysine 20 of histone H4 and is associated with silent chromatin. *Mol Cell* **9**: 1201–1213.
- Nowak SJ, Corces VG. 2000. Phosphorylation of histone H3 correlates with transcriptionally active loci. *Genes Dev* **14**: 3003–3013.
- O'Carroll D, Scherthan H, Peters AH, Opravil S, Haynes AR, Laible G, Rea S, Schmid M, Lebersorger A, Jerratsch M, et al. 2000. Isolation and characterization of *Suv39h2*, a second histone H3 methyltransferase gene that displays testis-specific expression. *Mol Cell Biol* **20**: 9423–9433.
- Odegard VH, Kim ST, Anderson SM, Shlomchik MJ, Schatz DG. 2005. Histone modifications associated with somatic hypermutation. *Immunity* **23**: 101–110.
- Ogata N, Ueda K, Hayaishi O. 1980a. ADP-ribosylation of histone H2B. Identification of glutamic acid residue 2 as the modification site. *J Biol Chem* **255**: 7610–7615.
- Ogata N, Ueda K, Kagamiyama H, Hayaishi O. 1980b. ADP-ribosylation of histone H1 identification of glutamic acid residues 2, 14, the COOH-terminal lysine residue as modification sites. *J Biol Chem* **255**: 7616–7620.
- Ogawa H, Ishiguro K, Gaubatz S, Livingston DM, Nakatani Y. 2002. A complex with chromatin modifiers that occupies E2F- and Myc-responsive genes in G₀ cells. *Science* **296**: 1132–1136.
- Ogawa Y, Ono T, Wakata Y, Okawa K, Tagami H, Shibahara KI. 2005. Histone variant macroH2A12 is mono-ubiquitinated at its histone domain. *Biochem Biophys Res Commun* **336**: 204–209.
- Ozdemir A, Spicuglia S, Lasonder E, Vermeulen M, Campsteijn C, Stunnenberg HG, Logie C. 2005. Characterization of lysine 56 of histone H3 as an acetylation site in *Saccharomyces cerevisiae*. *J Biol Chem* **280**: 25949–25952.
- Pal S, Vishwanath SN, Erdjument-Bromage H, Tempst P, Sif S. 2004. Human SWI/SNF-associated PRMT5 methylates histone H3 arginine 8 and negatively regulates expression of ST7 and NM23 tumor suppressor genes. *Mol Cell Biol* **24**: 9630–9645.
- Pantazis P, Bonner WM. 1981. Quantitative determination of histone modification H2A acetylation and phosphorylation. *J Biol Chem* **256**: 4669–4675.
- Park J, Chen Y, Tishkoff DX, Peng C, Tan M, Dai L, Xie Z, Zhang Y, Zwaans BM, Skinner ME, et al. 2013. SIRT6-mediated lysine desuccinylation impacts diverse metabolic pathways. *Mol Cell* **50**: 919–930.
- Parthun MR, Widom J, Gottschling DE. 1996. The major cytoplasmic histone acetyltransferase in yeast: Links to chromatin replication and histone metabolism. *Cell* **87**: 85–94.
- Peters AH, O'Carroll D, Scherthan H, Mechtler K, Sauer S, Schofer C, Weipoltshammer K, Pagani M, Lachner M, Kohlmaier A, et al. 2001. Loss of the *Suv39h* histone methyltransferases impairs mammalian heterochromatin and genome stability. *Cell* **107**: 323–337.
- Pham AD, Sauer F. 2000. Ubiquitin-activating/conjugating activity of TAF_{II}250, a mediator of activation of gene expression in *Drosophila*. *Science* **289**: 2357–2360.
- Polioudaki H, Markaki Y, Kourmouli N, Dyalynas G, Theodoropoulos PA, Singh PB, Georgatos SD. 2004. Mitotic phosphorylation of histone H3 at threonine 3. *FEBS Lett* **560**: 39–44.
- Preuss U, Landsberg G, Scheidtmann KH. 2003. Novel mitosis-specific phosphorylation of histone H3 at Thr11 mediated by Dlk/ZIP kinase. *Nucleic Acids Res* **31**: 878–885.

- Puerta C, Hernandez F, Lopez-Arcon L, Palacian E. 1995. Acetylation of histone H2AH2B dimers facilitates transcription. *Biochem Biophys Res Commun* **210**: 409–416.
- Rea S, Eisenhaber F, O'Carroll D, Strahl BD, Sun ZW, Schmid M, Opravil S, Mechtler K, Ponting CP, Allis CD, et al. 2000. Regulation of chromatin structure by site-specific histone H3 methyltransferases. *Nature* **406**: 593–599.
- Redon C, Pilch DR, Rogakou EP, Orr AH, Lowndes NF, Bonner WM. 2003. Yeast histone 2A serine 129 is essential for the efficient repair of checkpoint-blind DNA damage. *EMBO Rep* **4**: 678–684.
- Rice JC, Nishioka K, Sarma K, Steward R, Reinberg D, Allis CD. 2002. Mitotic-specific methylation of histone H4 Lys 20 follows increased PR-Set7 expression and its localization to mitotic chromosomes. *Genes Dev* **16**: 2225–2230.
- Robzyk K, Recht J, Osley MA. 2000. Rad6-dependent ubiquitination of histone H2B in yeast. *Science* **287**: 501–504.
- Rogakou EP, Pilch DR, Orr AH, Ivanova VS, Bonner WM. 1998. DNA double-stranded breaks induce histone H2AX phosphorylation on serine 139. *J Biol Chem* **273**: 5858–5868.
- Rogakou EP, Boon C, Redon C, Bonner WM. 1999. Megabase chromatin domains involved in DNA double-strand breaks in vivo. *J Cell Biol* **146**: 905–916.
- Roguev A, Schaft D, Shevchenko A, Pijnappel WW, Wilm M, Aasland R, Stewart AF. 2001. The *Saccharomyces cerevisiae* Set1 complex includes an Ash2 homologue and methylates histone 3 lysine 4. *EMBO J* **20**: 7137–7148.
- Ruiz-Carrillo A, Wangh LJ, Allfrey VG. 1975. Processing of newly synthesized histone molecules. *Science* **190**: 117–128.
- Sakabe K, Wang Z, Hart GW. 2010. β -N-acetylglucosamine O-GlcNAc is part of the histone code. *Proc Natl Acad Sci* **107**: 19915–19920.
- Santos-Rosa H, Schneider R, Bannister AJ, Sherriff J, Bernstein BE, Emre NC, Schreiber SL, Mellor J, Kouzarides T. 2002. Active genes are trimethylated at K4 of histone H3. *Nature* **419**: 407–411.
- Sarg B, Helliger W, Talasz H, Forg B, Lindner HH. 2006. Histone H1 phosphorylation occurs site-specifically during interphase and mitosis: Identification of a novel phosphorylation site on histone H1. *J Biol Chem* **281**: 6573–6580.
- Sassone-Corsi P, Mizzen CA, Cheung P, Crosio C, Monaco L, Jacquot S, Hanauer A, Allis CD. 1999. Requirement of Rsk-2 for epidermal growth factor-activated phosphorylation of histone H3. *Science* **285**: 886–891.
- Schiltz RL, Mizzen CA, Vassilev A, Cook RG, Allis CD, Nakatani Y. 1999. Overlapping but distinct patterns of histone acetylation by the human coactivators p300 and PCAF within nucleosomal substrates. *J Biol Chem* **274**: 1189–1192.
- Schotta G, Ebert A, Krauss V, Fischer A, Hoffmann J, Rea S, Jenuwein T, Dorn R, Reuter G. 2002. Central role of *Drosophila* SU(VAR)3–9 in histone H3-K9 methylation and heterochromatic gene silencing. *EMBO J* **21**: 1121–1131.
- Schotta G, Lachner M, Sarma K, Ebert A, Sengupta R, Reuter G, Reinberg D, Jenuwein T. 2004. A silencing pathway to induce H3-K9 and H4-K20 trimethylation at constitutive heterochromatin. *Genes Dev* **18**: 1251–1262.
- Schubeler D, Francael C, Cimbara DM, Reik A, Martin DI, Groudine M. 2000. Nuclear localization and histone acetylation: A pathway for chromatin opening and transcriptional activation of the human β -globin locus. *Genes Dev* **14**: 940–950.
- Schultz DC, Ayyanathan K, Negorev D, Maul GG, Rauscher FJ III. 2002. SETDB1: A novel KAP-1-associated histone H3, lysine 9-specific methyltransferase that contributes to HP1-mediated silencing of euchromatic genes by KRAB zinc-finger proteins. *Genes Dev* **16**: 919–932.
- Schurter BT, Koh SS, Chen D, Bunick GJ, Harp JM, Hanson BL, Henschen-Edman A, Mackay DR, Stallcup MR, Aswad DW. 2001. Methylation of histone H3 by coactivator-associated arginine methyltransferase 1. *Biochemistry* **40**: 5747–5756.
- Sharma R, Nakamura A, Takahashi R, Nakamoto H, Goto S. 2006. Carbonyl modification in rat liver histones: Decrease with age and increase by dietary restriction. *Free Radic Biol Med* **40**: 1179–1184.
- Shiio Y, Eisenman RN. 2003. Histone sumoylation is associated with transcriptional repression. *Proc Natl Acad Sci* **100**: 13225–13230.
- Smith ER, Eisen A, Gu W, Sattah M, Pannuti A, Zhou J, Cook RG, Lucchesi JC, Allis CD. 1998. ESA1 is a histone acetyltransferase that is essential for growth in yeast. *Proc Natl Acad Sci* **95**: 3561–3565.
- Sobel RE, Cook RG, Perry CA, Annunziato AT, Allis CD. 1995. Conservation of deposition-related acetylation sites in newly synthesized histones H3 and H4. *Proc Natl Acad Sci* **92**: 1237–1241.
- Song OK, Wang X, Waterborg JH, Sternglanz R. 2003. An N^{α} -acetyltransferase responsible for acetylation of the N-terminal residues of histones H4 and H2A. *J Biol Chem* **278**: 38109–38112.
- Spencer TE, Jenster G, Burcin MM, Allis CD, Zhou J, Mizzen CA, McKenna NJ, Onate SA, Tsai SY, Tsai MJ, et al. 1997. Steroid receptor coactivator-1 is a histone acetyltransferase. *Nature* **389**: 194–198.
- Stanley JS, Griffin JB, Zemleni J. 2001. Biotinylation of histones in human cells. Effects of cell proliferation. *Eur J Biochem* **268**: 5424–5429.
- Stiff T, O'Driscoll M, Rief N, Iwabuchi K, Loblrich M, Jeggo PA. 2004. ATM and DNA-PK function redundantly to phosphorylate H2AX after exposure to ionizing radiation. *Cancer Res* **64**: 2390–2396.
- Strahl BD, Ohba R, Cook RG, Allis CD. 1999. Methylation of histone H3 at lysine 4 is highly conserved and correlates with transcriptionally active nuclei in *Tetrahymena*. *Proc Natl Acad Sci* **96**: 14967–14972.
- Strahl BD, Briggs SD, Brame CJ, Caldwell JA, Koh SS, Ma H, Cook RG, Shabanowitz J, Hunt DF, Stallcup MR, et al. 2001. Methylation of histone H4 at arginine 3 occurs in vivo and is mediated by the nuclear receptor coactivator PRMT1. *Curr Biol* **11**: 996–1000.
- Strahl BD, Grant PA, Briggs SD, Sun ZW, Bone JR, Caldwell JA, Mollah S, Cook RG, Shabanowitz J, Hunt DF, et al. 2002. Set2 is a nucleosomal histone H3-selective methyltransferase that mediates transcriptional repression. *Mol Cell Biol* **22**: 1298–1306.
- Su IH, Basavaraj A, Krutchinsky AN, Hobert O, Ullrich A, Chait BT, Tarakhovskiy A. 2003. Ezh2 controls B cell development through histone H3 methylation and *Igh* rearrangement. *Nat Immunol* **4**: 124–131.
- Suka N, Suka Y, Carmen AA, Wu J, Grunstein M. 2001. Highly specific antibodies determine histone acetylation site usage in yeast heterochromatin and euchromatin. *Mol Cell* **8**: 473–479.
- Sun ZW, Allis CD. 2002. Ubiquitination of histone H2B regulates H3 methylation and gene silencing in yeast. *Nature* **418**: 104–108.
- Sun XJ, Wei J, Wu XY, Hu M, Wang L, Wang HH, Zhang QH, Chen SJ, Huang QH, Chen Z. 2005. Identification and characterization of a novel human histone H3 lysine 36-specific methyltransferase. *J Biol Chem* **280**: 35261–35271.
- Tachibana M, Sugimoto K, Fukushima T, Shinkai Y. 2001. Set domain-containing protein, G9a, is a novel lysine-preferring mammalian histone methyltransferase with hyperactivity and specific selectivity to lysines 9 and 27 of histone H3. *J Biol Chem* **276**: 25309–25317.
- Tachibana M, Sugimoto K, Nozaki M, Ueda J, Ohta T, Ohki M, Fukuda M, Takeda N, Niida H, Kato H, et al. 2002. G9a histone methyltransferase plays a dominant role in euchromatic histone H3 lysine 9 methylation and is essential for early embryogenesis. *Genes Dev* **16**: 1779–1791.
- Tachibana M, Ueda J, Fukuda M, Takeda N, Ohta T, Iwanari H, Sakihama T, Kodama T, Hamakubo T, Shinkai Y. 2005. Histone methyltransferases G9a and GLP form heteromeric complexes and are both crucial for methylation of euchromatin at H3-K9. *Genes Dev* **19**: 815–826.
- Tamaru H, Selker EU. 2001. A histone H3 methyltransferase controls DNA methylation in *Neurospora crassa*. *Nature* **414**: 277–283.
- Tan M, Luo H, Lee S, Jin F, Yang JS, Montellier E, Buchou T, Cheng Z, Rousseaux S, Rajagopal N, et al. 2011. Identification of 67 histone marks and histone lysine crotonylation as a new type of histone modification. *Cell* **146**: 1016–1028.

- Taplick J, Kurtev V, Lagger G, Seiser C. 1998. Histone H4 acetylation during interleukin-2 stimulation of mouse T cells. *FEBS Lett* **436**: 349–352.
- Tessarz P, Santos-Rosa H, Robson SC, Sylvestersen KB, Nelson CJ, Nielsen ML, Kouzarides T. 2014. Glutamine methylation in histone H2A is an RNA-polymerase-I-dedicated modification. *Nature* **505**: 564–568.
- Thomson S, Clayton AL, Hazzalin CA, Rose S, Barratt MJ, Mahadevan LC. 1999. The nucleosomal response associated with immediate-early gene induction is mediated via alternative MAP kinase cascades: MSK1 as a potential histone H3/HMG-14 kinase. *EMBO J* **18**: 4779–4793.
- Tie F, Banerjee R, Stratton CA, Prasad-Sinha J, Stepanik V, Zlobin A, Diaz MO, Scacheri PC, Harte PJ. 2009. CBP-mediated acetylation of histone H3 lysine 27 antagonizes *Drosophila* Polycomb silencing. *Development* **136**: 3131–3141.
- Turner BM. 2005. Reading signals on the nucleosome with a new nomenclature for modified histones. *Nat Struct Mol Biol* **12**: 110–112.
- Turner BM, Fellows G. 1989. Specific antibodies reveal ordered and cell-cycle-related use of histone-H4 acetylation sites in mammalian cells. *Eur J Biochem* **179**: 131–139.
- Tweedie-Cullen RY, Reck JM, Mansuy IM. 2009. Comprehensive mapping of post-translational modifications on synaptic, nuclear, and histone proteins in the adult mouse brain. *J Proteome Res* **8**: 4966–4982.
- Tweedie-Cullen RY, Brunner AM, Grossmann J, Mohanna S, Sichau D, Nanni P, Panse C, Mansuy IM. 2012. Identification of combinatorial patterns of post-translational modifications on individual histones in the mouse brain. *PLoS One* **7**: e36980.
- Unoki M, Masuda A, Dohmae N, Arita K, Yoshimatsu M, Iwai Y, Fukui Y, Ueda K, Hamamoto R, Shirakawa M, et al. 2013. Lysyl 5-hydroxylation, a novel histone modification, by Jumonji domain containing 6 JMJD6. *J Biol Chem* **288**: 6053–6062.
- Van Aller GS, Reynoird N, Barbash O, Huddleston M, Liu S, Zmoos AF, McDevitt P, Sinnamon R, Le B, Mas G, et al. 2012. Smyd3 regulates cancer cell phenotypes and catalyzes histone H4 lysine 5 methylation. *Epigenetics* **7**: 340–343.
- van Attikum H, Gasser SM. 2005. The histone code at DNA breaks: A guide to repair? *Nat Rev Mol Cell Biol* **6**: 757–765.
- Vandel L, Nicolas E, Vaute O, Ferreira R, Ait-Si-Ali S, Trouche D. 2001. Transcriptional repression by the retinoblastoma protein through the recruitment of a histone methyltransferase. *Mol Cell Biol* **21**: 6484–6494.
- van Leeuwen F, Gafken PR, Gottschling DE. 2002. Dot1p modulates silencing in yeast by methylation of the nucleosome core. *Cell* **109**: 745–756.
- Vaquero A, Scher M, Lee D, Erdjument-Bromage H, Tempst P, Reinberg D. 2004. Human SirT1 interacts with histone H1 and promotes formation of facultative heterochromatin. *Mol Cell* **16**: 93–105.
- Verreault A, Kaufman PD, Kobayashi R, Stillman B. 1998. Nucleosomal DNA regulates the core-histone-binding subunit of the human Hat1 acetyltransferase. *Curr Biol* **8**: 96–108.
- Visochek L, Steingart RA, Vulih-Shultzman I, Klein R, Priel E, Gozes I, Cohen-Armon M. 2005. PolyADP-ribosylation is involved in neurotrophic activity. *J Neurosci* **25**: 7420–7428.
- Waldmann T, Izzo A, Kamieniarz K, Richter F, Vogler C, Sarg B, Lindner H, Young NL, Mittler G, Garcia BA, et al. 2011. Methylation of H2AR29 is a novel repressive PRMT6 target. *Epigenetics Chromatin* **4**: 11.
- Wang H, Cao R, Xia L, Erdjument-Bromage H, Borchers C, Tempst P, Zhang Y. 2001a. Purification and functional characterization of a histone H3-lysine 4-specific methyltransferase. *Mol Cell* **8**: 1207–1217.
- Wang H, Huang ZQ, Xia L, Feng Q, Erdjument-Bromage H, Strahl BD, Briggs SD, Allis CD, Wong J, Tempst P, et al. 2001b. Methylation of histone H4 at arginine 3 facilitating transcriptional activation by nuclear hormone receptor. *Science* **293**: 853–857.
- Wang Y, Zhang W, Jin Y, Johansen J, Johansen KM. 2001c. The JIL-1 tandem kinase mediates histone H3 phosphorylation and is required for maintenance of chromatin structure in *Drosophila*. *Cell* **105**: 433–443.
- Wang H, Wang L, Erdjument-Bromage H, Vidal M, Tempst P, Jones RS, Zhang Y. 2004. Role of histone H2A ubiquitination in Polycomb silencing. *Nature* **431**: 873–878.
- Wang GG, Cai L, Pasillas MP, Kamps MP. 2007. NUP98-NSD1 links H3K36 methylation to Hox-A gene activation and leukaemogenesis. *Nat Cell Biol* **9**: 804–812.
- Ward IM, Chen J. 2001. Histone H2AX is phosphorylated in an ATR-dependent manner in response to replicational stress. *J Biol Chem* **276**: 47759–47762.
- Wei Y, Yu L, Bowen J, Gorovsky MA, Allis CD. 1999. Phosphorylation of histone H3 is required for proper chromosome condensation and segregation. *Cell* **97**: 99–109.
- Weinert BT, Schölz C, Wagner SA, Iesmantavicius V, Su D, Daniel JA, Choudhary C. 2013. Lysine succinylation is a frequently occurring modification in prokaryotes and eukaryotes and extensively overlaps with acetylation. *Cell Rep* **4**: 842–851.
- Weiss T, Hergeth S, Zeissler U, Izzo A, Tropberger P, Zee BM, Dunder M, Garcia BA, Daujat S, Schneider R. 2010. Histone H1 variant-specific lysine methylation by G9a/KMT1C and Glp1/KMT1D. *Epigenetics Chromatin* **3**: 7.
- Wilson JR, Jing C, Walker PA, Martin SR, Howell SA, Blackburn GM, Gamblin SJ, Xiao B. 2002. Crystal structure and functional analysis of the histone methyltransferase SET7/9. *Cell* **111**: 105–115.
- Wisniewski JR, Zougman A, Kruger S, Mann M. 2007. Mass spectrometric mapping of linker histone H1 variants reveals multiple acetylations, methylations, and phosphorylation as well as differences between cell culture and tissue. *Mol Cell Proteomics* **6**: 72–87.
- Wisniewski JR, Zougman A, Mann M. 2008. N^ε-formylation of lysine is a widespread post-translational modification of nuclear proteins occurring at residues involved in regulation of chromatin function. *Nucleic Acids Res* **36**: 570–577.
- Wu L, Zee BM, Wang Y, Garcia BA, Dou Y. 2011. The RING finger protein MSL2 in the MOF complex is an E3 ubiquitin ligase for H2B K34 and is involved in crosstalk with H3 K4 and K79 methylation. *Mol Cell* **43**: 132–144.
- Wyatt HR, Liaw H, Green GR, Lustig AJ. 2003. Multiple roles for *Saccharomyces cerevisiae* histone H2A in telomere position effect, Spt phenotypes and double-strand-break repair. *Genetics* **164**: 47–64.
- Xiao A, Li H, Shechter D, Ahn SH, Fabrizio LA, Erdjument-Bromage H, Ishibe-Murakami S, Wang B, Tempst P, Hofmann K, et al. 2009. WSTF regulates the H2AX DNA damage response via a novel tyrosine kinase activity. *Nature* **457**: 57–62.
- Xiao Y, Bedet C, Robert VJ, Simonet T, Dunkelbarger S, Rakotomalala C, Soete G, Korswagen HC, Strome S, Palladino F. 2011. *Caenorhabditis elegans* chromatin-associated proteins SET-2 and ASH-2 are differentially required for histone H3 Lys 4 methylation in embryos and adult germ cells. *Proc Natl Acad Sci* **108**: 8305–8310.
- Xie Z, Dai J, Dai L, Tan M, Cheng Z, Wu Y, Boeke JD, Zhao Y. 2012. Lysine succinylation and lysine malonylation in histones. *Mol Cell Proteomics* **11**: 100–107.
- Xin Z, Tachibana M, Guggiari M, Heard E, Shinkai Y, Wagstaff J. 2003. Role of histone methyltransferase G9a in CpG methylation of the Prader-Willi syndrome imprinting center. *J Biol Chem* **278**: 14996–15000.
- Xu F, Zhang K, Grunstein M. 2005. Acetylation in histone H3 globular domain regulates gene expression in yeast. *Cell* **121**: 375–385.
- Yamamoto T, Horikoshi M. 1997. Novel substrate specificity of the histone acetyltransferase activity of HIV-1-Tat interactive protein Tip60. *J Biol Chem* **272**: 30595–30598.
- Yamamoto Y, Verma UN, Prajapati S, Kwak YT, Gaynor RB. 2003. Histone H3 phosphorylation by IKK- α is critical for cytokine-induced gene expression. *Nature* **423**: 655–659.
- Yang L, Xia L, Wu DY, Wang H, Chansky HA, Schubach WH, Hickstein DD, Zhang Y. 2002. Molecular cloning of ESET, a novel histone H3-

- specific methyltransferase that interacts with ERG transcription factor. *Oncogene* **21**: 148–152.
- Yu Y, Song C, Zhang Q, DiMaggio PA, Garcia BA, York A, Carey MF, Grunstein M. 2012. Histone H3 lysine 56 methylation regulates DNA replication through its interaction with PCNA. *Mol Cell* **46**: 7–17.
- Zegerman P, Canas B, Pappin D, Kouzarides T. 2002. Histone H3 lysine 4 methylation disrupts binding of nucleosome remodeling and deacetylase (NuRD) repressor complex. *J Biol Chem* **277**: 11621–11624.
- Zeitlin SG, Barber CM, Allis CD, Sullivan KF. 2001. Differential regulation of CENP-A and histone H3 phosphorylation in G₂/M. *J Cell Sci* **114**: 653–661.
- Zhang L, Eugeni EE, Parthun MR, Freitas MA. 2003. Identification of novel histone post-translational modifications by peptide mass fingerprinting. *Chromosoma* **112**: 77–86.
- Zhang K, Chen Y, Zhang Z, Zhao Y. 2009. Identification and verification of lysine propionylation and butyrylation in yeast core histones using PTMap software. *J Proteome Res* **8**: 900–906.
- Zhang S, Roche K, Nasheuer HP, Lowndes NF. 2011. Modification of histones by sugar β -N-acetylglucosamine GlcNAc occurs on multiple residues, including histone H3 serine 10, and is cell cycle-regulated. *J Biol Chem* **286**: 37483–37495.
- Zhong S, Jansen C, She QB, Goto H, Inagaki M, Bode AM, Ma WY, Dong Z. 2001. Ultraviolet B-induced phosphorylation of histone H3 at serine 28 is mediated by MSK1. *J Biol Chem* **276**: 33213–33219.
- Zhu B, Zheng Y, Pham AD, Mandal SS, Erdjument-Bromage H, Tempst P, Reinberg D. 2005. Monoubiquitination of human histone H2B: The factors involved and their roles in HOX gene regulation. *Mol Cell* **20**: 601–611.
- Grunstein M. 1997. Histone acetylation in chromatin structure and transcription. *Nature* **389**: 349–352.
- Grunstein M. 1997. Molecular model for telomeric heterochromatin in yeast. *Curr Opin Cell Biol* **9**: 383–387.
- Grunstein M. 1998. Yeast heterochromatin: Regulation of its assembly and inheritance by histones. *Cell* **93**: 325–328.
- Henikoff S, Ahmad K. 2005. Assembly of variant histones into chromatin. *Annu Rev Cell Dev Biol* **21**: 133–153.
- Herz HM, Garruss A, Shilatifard A. 2013. SET for life: Biochemical activities and biological functions of SET domain-containing proteins. *Trends Biochem Sci* **38**: 621–639.
- Hild M, Paro R. 2003. Anti-silencing from the core: A histone H2A variant protects euchromatin. *Nat Cell Biol* **5**: 278–280.
- Jenuwein T, Allis CD. 2001. Translating the histone code. *Science* **293**: 1074–1080.
- Kimmins S, Sassone-Corsi P. 2005. Chromatin remodelling and epigenetic features of germ cells. *Nature* **434**: 583–589.
- Kurdistani SK, Grunstein M. 2003. Histone acetylation and deacetylation in yeast. *Nat Rev Mol Cell Biol* **4**: 276–284.
- Lachner M, O’Sullivan RJ, Jenuwein T. 2003. An epigenetic road map for histone lysine methylation. *J Cell Sci* **116**: 2117–2124.
- Luger K, Richmond TJ. 1998. The histone tails of the nucleosome. *Curr Opin Genet Dev* **8**: 140–146.
- Mellone BG, Allshire RC. 2003. Stretching it: Putting the CEN(P-A) in centromere. *Curr Opin Genet Dev* **13**: 191–198.
- Millar CB, Kurdistani SK, Grunstein M. 2004. Acetylation of yeast histone H4 lysine 16: A switch for protein interactions in heterochromatin and euchromatin. *Cold Spring Harbor Symp Quant Biol* **69**: 193–200.
- Nightingale KP, O’Neill LP, Turner BM. 2006. Histone modifications: Signalling receptors and potential elements of a heritable epigenetic code. *Curr Opin Genet Dev* **16**: 125–136.
- Panier S, Durocher D. 2013. Push back to respond better: Regulatory inhibition of the DNA double-strand break response. *Nat Rev Mol Cell Biol* **14**: 661–772.
- Peterson CL, Laniel MA. 2004. Histones and histone modifications. *Curr Biol* **14**: R546–R551.
- Pinder JB, Attwood KM, Dellaire G. 2013. Reading, writing, repair: The role of ubiquitin and the ubiquitin-like proteins in DNA damage signaling and repair. *Front Genet* **4**: 45.
- Reinberg D, Chuikov S, Farnham P, Karachentsev D, Kirmizis A, Kuzmichev A, Margueron R, Nishioka K, Preissner TS, Sarma K, et al. 2004. Steps toward understanding the inheritance of repressive methyl-lysine marks in histones. *Cold Spring Harbor Symp Quant Biol* **69**: 171–182.
- Sarma K, Reinberg D. 2005. Histone variants meet their match. *Nat Rev Mol Cell Biol* **6**: 139–149.
- Spencer VA, Davie JR. 2000. Signal transduction pathways and chromatin structure in cancer cells. *J Cell Biochem Suppl* **35**: 27–35.
- Sternglanz R. 1996. Histone acetylation: A gateway to transcriptional activation. *Trends Biochem Sci* **21**: 357–358.
- Turner BM. 2000. Histone acetylation and an epigenetic code. *Bioessays* **22**: 836–845.
- van Attikum H, Gasser SM. 2005. The histone code at DNA breaks: A guide to repair? *Nat Rev Mol Cell Biol* **6**: 757–765.
- Vaughn MW, Tanurdzic M, Martienssen R. 2005. Replication, repair, reactivation. *Dev Cell* **9**: 724–725.
- Wade PA, Wolffe AP. 1997. Histone acetyltransferases in control. *Curr Biol* **7**: R82–R84.
- Wade PA, Pruss D, Wolffe AP. 1997. Histone acetylation: Chromatin in action. *Trends Biochem Sci* **22**: 128–132.
- Zilberman D, Henikoff S. 2005. Epigenetic inheritance in *Arabidopsis*: Selective silence. *Curr Opin Genet Dev* **15**: 557–562.



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