

Additional Table 1. Targets of Cdk1^a.

Common, systematic name	Biological function	Cdk1 phosphorylation sites and consequence of phosphorylation	Reference
<i>Regulation of Cdk1 activity</i>			
Cln1, YMR199W	G1 cyclin	The exact phosphorylation sites have not been mapped, but phosphorylation of Cln1 is thought to target it for degradation by the SCF	[1-3]
Cln2, YPL256C	G1 cyclin	Alanine substitution of T311, T381, S396, T405, S427, T430 and S518 inhibits degradation by the SCF	[1-3]
Cln3, YAL040C	G1 cyclin	Alanine substitution of S468 prevents degradation by the SCF, but other phosphorylation sites may exist	[2, 4, 5]
Clb6, YPR119W	S cyclin	The exact phosphorylation sites have not been mapped, but phosphorylation by Cdk1 (and Pho85) is thought to target Clb6 for destruction by the SCF	[6]
Far1, YJL157C	CKI	Phosphorylation of S87 targets Far1 for degradation	[7]
Sic1, YLR079W	CKI	Sic1 harbors nine Cdk1 consensus sites (T2, T5, T33, T45, S69, S76, S80, T173, and S191) and phosphorylation of at least six of these sites targets Sic1 for degradation	[3, 8-10]
Swe1, YJL187C	Protein kinase	Phosphorylation of T45, S56 ^b , S63 ^b , T74 ^b , S105 ^b , S111, T121, T124, S127 ^b , S133, S136 ^b , T196, S201, S263, S266 ^b , T367 ^b , T373, T384 ^b depends on Cdk1. Alanine substitution of all these sites resulted in	[11, 12]

reduced kinase activity of Swe1. In addition, phosphorylation of Swe1 by Cdk1 on unknown residues is involved in its degradation

Mih1, YMR036C	Protein phosphatase	Phosphorylation sites have not been mapped, and the consequences of phosphorylation are not clear, but probably affect the phosphatase activity towards Y19 of Cdk1.	[13]
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DNA replication

Sld2, YKL108W	Replication factor	Cdk1 phosphorylates Sld2 on a number of residues, but especially phosphorylation of T84 stimulates binding to Dpb11 and contributes to initiation of DNA replication	[14-17]
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Sld3, YGL113W	Replication factor	Alanine substitution of T600 and S622 is lethal; phosphorylation of Sld3 stimulates binding to Dpb11 and initiation of replication	[14, 16]
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Pol12, YBL035C	Alpha- primase complex	Phosphorylation sites have not been mapped, but phosphorylation of Pol12 is thought to inhibit its interaction with chromatin	[18, 19]
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Cdc6, YJL194W	Replication factor	Simultaneous alanine substitution of T7, T23 and S43 stabilizes Cdc6 by preventing degradation by the SCF. Alanine substitution of T134 and S372 also stabilizes Cdc6, possibly by preventing degradation by the APC	[20]
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Orc2, YBR060C	Replication factor	Orc2 contains six optimal Cdk1 sites (S16, T24, T70, T174, S188, S206), but <i>in vivo</i> phosphorylation sites have not been mapped, except S188, the phosphorylation of which may inhibit ATP binding by Orc5	[21]
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Orc6, YHR118C	Replication factor	Orc6 contains four optimal Cdk1 sites (S106, S116, S123, T146), but exact phosphorylation sites have not been mapped; alanine substitution of Cdk1 sites has revealed that phosphorylation of Orc6 is important for prevention of re-replication	[21, 22]
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Mcm3, YEL032W	Replication factor	Phosphorylation of at least 5 Cdk1 sites in the NLS portion of Mcm3 results in nuclear export of the entire Mcm2-7 complex	[23]
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Dpb2, YPR175W	Replication factor	The main phosphorylation site is thought to be S144, and alanine substitution of S144 in combination with S125 and S616 reduces the interaction between Dpb2 and Pol2	[22, 24]
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Anaphase promoting complex

Cdh1, YGL003C	APC activator	Simultaneous alanine substitution of S16, S42, T157 and T173 results in defects in SPB separation; phosphorylation of S16, S42, S227, S239 and S436, and T176 abolishes the interaction between Hct1 and APC, thus inhibiting APC activation	[25-27]
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Acm1, YPL267W	Cdh1 inhibitor	Phosphorylation of S37, S48, S102, S202 (not a Cdk1 consensus site) and S161 may stabilize Acm1, protecting it from proteasome-mediated destruction; alanine substitution of the full CDK consensus sites (S3, S31, S48, S102, T161) results in nuclear accumulation and enhanced degradation of Acm1	[28-30]
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Cdc16, YKL022C	APC component	Alanine substitution of S44, S59, S95, S103, T115, T406 (<i>cdc16-6A</i> allele) inhibits binding of Cdc20 to the APC and thereby APC activation, leading to mitotic delay	[31]
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Cdc23, YHR166C APC component Alanine substitution of the minimal Cdk1 site (S59) exacerbated the defect of *cdc16-6A* and *cdc27-5A* mutants [31]

Cdc27, YBL084C APC component Alanine substitution of the Cdk1 sites S267, T304, S328, T351, T397 (the *cdc27-5A* allele) prevents Cks1 binding to the APC and leads to mitotic delay [31]

Pheromone signaling

Ste20, YHL007C PAK family kinase The exact Cdk1 phosphorylation sites have not been mapped, but phosphorylation of Ste20 by Cdk1 may inhibit Ste20, thus restricting pheromone signaling to the G1 phase of the cell cycle [32, 33]

Ste5, YDR103W Adaptor Alanine substitution of 8 Cdk1 sites (T4, S11, T29, S43, S69, S71, S81, T102) triggers aberrant pheromone arrest outside G1, possibly because phosphorylation by Cln-Cdk1 promotes SCF-mediated degradation of Ste5 [34, 35]

Transcription

Ace2, YLR131C Transcription factor Alanine substitution of T575, S701 and S714 results in constitutive nuclear localization of Ace2 [36, 37]

Smp2, YMR165C Transcription inhibitor Alanine substitution of S110, S114, S168, S602, T723, S744, S748 results in derepression of transcription of ER-localized phospholipid biosynthesis enzymes, which may support nuclear membrane synthesis [38, 39]

Whi5, YOR083W Transcription inhibitor Whi5 is phosphorylated on at least 16 sites *in vivo* (10 Cdk1 consensus sites and 6 non-consensus sites); phosphorylation of Whi5 induces release from SBF and exclusion from the nucleus [40-42]

Swi6, YLR182W	Transcription factor	Phosphorylation of S160 promotes nuclear export	[43]
Swi5, YDR146C	Transcription factor	Phosphorylation of S646 and S664 promotes nuclear export	[44]
Fkh2, YNL068C	Transcription factor	Phosphorylation of S683 and T697 promotes the interaction with Ndd1 to activate transcription	[45]
Ndd1, YOR372C	Transcription factor	Phosphorylation of T319 enhances the interaction with Fkh2, thus promoting transcription	[46, 47]
Stb1, YNL309W	Transcription factor	The exact phosphorylation sites have not been mapped, but phosphorylation by Cln-Cdk1 may abrogate the interaction between Stb1 and Swi6 and may release Stb1 from promoter regions	[48-50]
Pho2, YDL106C	Transcription factor	Phosphorylation of S230 promotes the interaction between Pho2 and Pho4 to induce transcription	[51]
Msa1, YOR066W	Transcription factor	Alanine substitution of S54 and T84 results in its nuclear localization	[52]

Initiation of anaphase, FEAR, MEN

Pds1, YDR113C	Securin	S37, S71, S212, S278, S292, S304 are phosphorylated <i>in vivo</i> ; phosphorylation of both S37 and S71 inhibits degradation by degradation by the APC, while phosphorylation of S212, S278 and S304 is thought to be important for the interaction between Pds1 and Esp1 and nuclear import of the Pds1-Esp1 complex	[53, 54]
Cdc5, YMR001C	Polo kinase	Phosphorylation of T242 contributes to activation of Cdc5	[55]

Net1 (Cfi1), YJL076W	RENT complex	Net1 is phosphorylated <i>in vivo</i> on 19 sites, and the <i>net1-3cdk</i> mutant carrying alanine substitution of 3 Cdk1 consensus sites (S166, T212, S252) fails to release Cdc14	[56]
Spo12, YHR152W	Nucleolar protein	Alanine substitution of S118 and S125 results in mitotic delay, but also in synthetic lethality when combined with an <i>lte1Δ</i> mutation	[57]
Lte1, YAL024C	Putative GEF	The exact phosphorylation sites have not been mapped, but Lte1 phosphorylation by Cdk1 is thought to be required for its localization to the bud cortex, although a mutant with alanine substitution of five (T317, T614, S630, S667, T793) out of a total of nine potential Cdk1 sites displayed no phenotype	[58]
Cdc15, YAR019C	Protein kinase	Alanine substitution of 7 Cdk1 consensus sites results in more robust mitotic exit without affecting kinase activity	[59]

DNA repair, checkpoint, telomere maintenance

Srs2, YJL092W	DNA helicase	Alanine substitution of seven Cdk1 consensus sites (T604, S698, S879, S938, S893, S950, and S965) leads to defects in damage-induced formation of Sgs1-Mre11 and Srs2-Mre11 subcomplexes and sensitivity to MMS, and inefficient DNA repair	[60-62]
Dna2	Nuclease	Phosphorylation in its NLS sequence results in nuclear import	[52]
Sae2, YGL175C	Nuclease	Phosphorylation of S267 increases Sae2 nuclease activity to resect DSBs	[63]
Yen1,	Holliday	Alanine substitution of S679 results in its nuclear	[52]

YER041W	junction resolvase	accumulation	
Cdc13, YDL220C	Telomere capping	Phosphorylation of T308 recruits the telomerase complex to telomeres resulting in telomere elongation; may also promote subsequent phosphorylation of S306 by Mec1. T336 is also phosphorylated, but the consequence remains unknown	[64, 65]
Mer2, YJR021C	Meiotic DSB formation	Phosphorylation of S30 and S271 promotes Spo11-mediated formation of DSBs at meiotic recombination hotspots	[66-68]
Rad9, YDR217C	Adaptor	Alanine substitution of 18 N-terminal sites reduces Rad53 activation under low zeocin concentrations, but has no effect on Rad53 activation at high zeocin concentrations	[69]
Rad53, YPL153C	Checkpoint kinase similar to mammalian Chk2	Aspartate substitution of S774 results in increased sensitivity to calcofluor white, indicating an involvement of Rad53 in cell morphogenesis; alanine substitution of S774 resulted in enhanced checkpoint adaptation in the presence of DNA damage	[70, 71]
Psy4, YBL046W	Regulatory subunit of a phosphatase involved in the repair of cross-linked DNA	Alanine substitution of T320 results in its nuclear localization	[52]

Regulation of SPBs, kinetochores, mitotic spindle

Ase1, Microtubule T55, S64, S198, T675, S707, S803, S819 are potential [22, 72-74]

YOR058C	associated protein	phosphorylation sites, and dephosphorylation of Ase1 is involved in spindle midzone organization	
Ask1, YKL052C	DASH complex	Alanine substitution of S216 and S250 exacerbates temperature-sensitivity when combined with the additional mutation of a temperature-sensitive <i>ask1-3</i> allele	[75]
Bir1, YJR089W	Passenger complex	Alanine substitution of nine sites (S383A, S395A, S552A, S587A, S667A, T684A, S688A, T735A, and T747A) prevents localization of Ndc10 to the spindle at anaphase	[76]
Cnm67, YNL225C	SPB outer plaque	Phosphorylation of Cnm67 may contribute to asymmetric localization of dynein	[77]
Fin1, YDR130C	Intermediate filament protein	Alanine substitution of the full CDK consensus sites (S36, S54, T68, S117, S148) localizes Fin1 to the spindle before anaphase and impairs efficient chromosome segregation	[22, 78]
Kar9, YPL269W	Karyogamy protein	Phosphorylation of S197 and S496 contributes to asymmetric loading of Kar9 onto SPBs	[79, 80]
Mps1, YDL028C	Protein kinase	Phosphorylation of T29 stabilizes Mps1 and contributes to SPB duplication	[81]
Nud1, YOR373W	SPB outer plaque	Unknown	[82]
Sli15, YBR156C	Passenger complex	Alanine substitution of S335, S373, S427, S437, S462 and T474 results in aberrant localization of Sli15-Ipl1 to the mitotic spindle	[83]

Slk19, YOR195W	Kinetochore protein	Unknown	[22, 82]
Spc110, YDR356W	SPB inner plaque	Phosphorylation at position 91 may be important for spindle integrity and mitotic spindle elongation; S36 may also be phosphorylated, but the function is unknown	[84]
Spc42, YKL042W	SPB central plaque	Phosphorylation on S4 and T6 mediates SPB duplication	[81]
Stu2, YLR045C	Microtubule associated protein	Unknown	[82]

Cell polarity, budding, organelle inheritance

Bem1, YBR200W	Adaptor	Phosphorylation of S72 promotes vacuole homeostasis	[85]
Bem2, YER155C	GAP	Phosphorylation sites have not been mapped. Based on similarity to Bem3, phosphorylation probably inhibits GAP activity	[86]
Bem3, YPL115C	GAP	Bem3 is phosphorylated on S195, S222, S254, S880 and possibly S585, which may inhibit GAP activity, thus contributing to actin polarization and bud emergence	[86]
Boi1, YBL085W	Adaptor	Boi1 is phosphorylated on S86, S149, T158, S229, S393, S405, S412, S540, S605, T670, T909; additional, non-Cdk1 consensus sites are also phosphorylated, potentially by Cdk1. Simultaneous alanine substitution results in defects in polarized cell	[87]

growth

Boi2, YER114C	Adaptor	Phosphorylation sites have not been mapped and no alanine substitutions of Cdk1 consensus sites have been made; based on homology to Boi1, phosphorylation of Boi2 may be involved in establishment/maintenance of cell polarity	[87]
Cdc3, YLR314C	Septin	Phosphorylation of S503 and S509 may be involved in disassembly of the old septin ring	[88]
Rga2, YDR379W	GAP	Alanine substitution of S380 in combination with S334, S692, S707, S733, S763, S770, and S772 results in cell polarity defects	[87, 89]
Shs1, YDL225W	Septin	Phosphorylation on several sites (T6, T386, S416, S441, S447) by either Cdk1 or Pho85 enhances Cdk1 inhibitory phosphorylation of Cdk1 by Swe1 later in the cell cycle	[90]
Tgl4, YKR089C	Lipid phosphatase	Phosphorylation on T675 and S890 activates its lipase activity, which mobilizes fatty acids to support initiation of bud formation in late G1	[22, 91]
Tus1, YLR425W	GEF	Simultaneous alanine substitution of S8, T13, T93, S122, S126, S163, S170, S173, S176 (all minimal Cdk1 sites), or alanine substitution of T13 and S135 (both full Cdk1 consensus sites) leads to decreased Rho1 activity and actin polymerization defects	[92]
Vac17, YCL063W	Adaptor	Alanine substitution of T149, S178, S119 and T248 results in defects in vacuole inheritance	[93]

Other

Chs2, YBR038W	Chitin synthase	Glutamate substitutions of the full Cdk1 consensus sites S14, S60, S69 and S100 resulted in constitutive ER retention of Chs2, while alanine substitutions lead to constitutive ER export	[94]
Nup53, YMR153W	Nucleoporin	Simultaneous alanine substitution of the Cdk1 consensus sites S101 and S206 ameliorated the growth defect of <i>nup170Δ</i> mutants, possibly by modulating the spindle assembly checkpoint	[95]

^a Included in this table are proteins for which Cdk1-mediated phosphorylation has been studied in at least some detail. As indicated by large-scale proteomic studies, it is likely that many more *bona fide* Cdk1 targets exist [22, 96, 97], however these potential Cdk1 substrates still await more detailed characterization to establish that they are indeed directly phosphorylated by Cdk1 *in vivo*.

^b Does not conform to the minimal Cdk1 consensus site (i.e. SP/TP).

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