## Centrosome control of the cell cycle

## Stephen Doxsey<sup>1</sup>, Wendy Zimmerman<sup>2</sup> and Keith Mikule<sup>1</sup>

<sup>1</sup>Program in Molecular Medicine, University of Massachusetts Medical School, Worcester, Massachusetts 01605, USA

<sup>2</sup>Department of Molecular and Cellular Biology, Harvard University, Cambridge Massachusetts 02138, USA Corresponding author: Doxsey, Stephen (stephen.doxsey@umassmed.edu).

Trends Cell Biology vol. 15, issue 6, June 2005.

## Fully referenced version of Table 1 from the published article.

Ubiquitination and	Aik3 <sup>27</sup>	PPP4R2 <sup>62</sup>	Separase <sup>85,86</sup>
protein degradation	Drf3 <sup>28</sup>	Chaperonins	topoisomerase llα <sup>87</sup>
$APC^1$	EB1 <sup>29</sup>	Hsp70 <sup>63,64</sup>	Mitotic exit/MEN
$BimA^2$	$Eg2^{30}$	Hsp73 <sup>44</sup>	Bfa1p/Bub2p*88,89
CDC16 <sup>3</sup>	FAK <sup>31</sup>	Hsp90 <sup>13,65</sup>	Cdc14p* <sup>90</sup>
CDC27 <sup>3</sup>	Fes/Fps <sup>32</sup>	Apoptosis related	Cdc14A <sup>91,92</sup>
Cut1*4	Katanin <sup>33</sup>	caspase 3 <sup>66</sup>	Cdc14B <sup>91</sup>
Dorfin <sup>5</sup>	Mps1p <sup>34</sup>	DAP-like kinase <sup>67</sup>	Cdc15p*93
ecm29p <sup>6</sup>	Nek2 <sup>35</sup>	Irod/lan5 <sup>68</sup>	Dbf2* <sup>94</sup>
Fzy/Cdc20 <sup>7,8</sup>	Nek2A <sup>36</sup>	pim-1 <sup>69</sup>	mob1p*95
Fzr/Cdh1 <sup>7</sup>	Nek2B <sup>37</sup>	Rb <sup>70</sup>	Nud1p*96
MDM2 <sup>9</sup>	NIMA/Fin1p* <sup>38</sup>	Spi1 <sup>71</sup>	Tem1p*89
$MUBPy^{10}$	NPM/B23 <sup>39</sup>	Spi2 <sup>71</sup>	Cytokinesis/SIN
pmt3p* <sup>11</sup>	Nuf <sup>40</sup>	Survivin <sup>66</sup>	Bvr4p* <sup>97,98</sup>
20S proteosome <sup>12,13</sup>	p160ROCK <sup>41</sup>	DNA damage	Cdc7p*98,99
p19(SKIP1) <sup>14</sup>	R1 <sup>42</sup>	checkpoint	Cdc16p*97
SCF <sup>14,15</sup>	Sced <sup>43</sup>	Brca1 <sup>72</sup>	Cdc11p*100
PA700 <sup>13</sup>	TCP-1 <sup>44</sup>	Chk1 <sup>47</sup>	Dma1p*101
PA28 <sup>13</sup>	TTK <sup>44</sup>	Chk2 <sup>48,73</sup>	Ibd1p*102
Parkin <sup>16</sup>	zyg-1 <sup>45</sup>	p53 <sup>63</sup>	sid1p*90
RASSF1A <sup>17</sup>	CDKs and cyclins	MAPK pathway	sid2p kinase* <sup>103</sup>
Ubiquitin <sup>13</sup>	CDK1 <sup>46</sup>	Erk1 <sup>74</sup>	sid4p* <sup>99</sup>
UBP-t2 <sup>18</sup>	CDK2 <sup>47,48</sup>	Erk2 <sup>36,74</sup>	spg1p* <sup>97,99</sup>
UCH/CeUBP130 <sup>19</sup>	cyclin A <sup>49</sup>	JNK <sup>75</sup>	PTP-BL <sup>104</sup>
Vihar E2-C <sup>20</sup>	cyclin B <sup>50,51</sup>	Mek <sup>76</sup>	Transcriptional
Nuclear transport/	cyclin E <sup>52</sup>	MLK3 <sup>77</sup>	regulators
Spindle assembly	Mitotic regulators	MKK <sup>78</sup>	Casein kinase 2 <sup>105</sup>
Ran <sup>21</sup>	CARB <sup>53</sup>	p38MAPK <sup>79</sup>	HDAC1 <sup>106</sup>
RanBPM <sup>22</sup>	Cdc25B <sup>54</sup>	Slt2p(Mpk1p)* <sup>80</sup>	Id1 <sup>107</sup>
Ndc1p* <sup>23</sup>	Inh2 <sup>55,56</sup>	Spindle checkpoint	Pie-1 <sup>108</sup>
RanBP1 <sup>24</sup>	polo kinase <sup>57,58</sup>	Esp1*81	mRNA/mRNA
Cytoskeletal	plo1p*59	GapCenA <sup>82</sup>	processing
regulators	PP1 <sup>60</sup>	HsMAD1 <sup>83</sup>	CPB <sup>109</sup>
Aurora/Aik <sup>25</sup>	PP4 <sup>61</sup>	hMad2 <sup>84</sup>	cyclin B mRNA <sup>109</sup>
Aurora 2 <sup>26</sup>	ΓΓ4		

IoEve, IoDpp and	Structural/scaffold	TACC1 <sup>199</sup>	HSET <sup>247</sup>
IoTld mRNA <sup>110</sup>	proteins	TACC2 <sup>199</sup>	Kar3p* <sup>248</sup>
Maskin <sup>109</sup>	Actin <sup>147,148</sup>	TACC3 <sup>199,200</sup>	Kinesin <sup>249</sup>
Translin <sup>111</sup>	hAKAP220 <sup>149</sup>	TACC4 <sup>201</sup>	$Xklp2^{250}$
G1/S regulation	AKAP350 <sup>124,150</sup>	Tekt1 <sup>202</sup>	Lis1 <sup>251</sup>
p21 <sup>66</sup>	Asp <sup>151</sup>	Vimentin <sup>203</sup>	myosin-V <sup>252</sup>
plk2/sak <sup>112,113</sup>	CCCAP <sup>152</sup>	Vinculin <sup>204</sup>	Ncd <sup>253</sup>
Wnt signaling	Cenexin <sup>153</sup>	ZYG-9 <sup>197</sup>	Nudel <sup>254</sup>
$APC^{114}$	Centriolin <sup>154</sup>	ZYG-12 <sup>205</sup>	p22dynactin <sup>255,256</sup>
Casein kinase 1 <sup>115,116</sup>	Centrosomin <sup>155,156</sup>	$4.1/4.1R^{206,207}$	p150Glued <sup>257</sup>
GSK-3 <sup>117</sup>	CEP110 <sup>157</sup>	$14$ -3-3 $\varepsilon$ $^{208}$	Pavarotti <sup>258</sup>
Membrane receptor	C-Nap1 <sup>158</sup>	$14-3-3 \gamma^{208}$	Calcium binding
signaling	Cik1p* <sup>159</sup>	MAPs	Calmodulin <sup>259,260</sup>
CCD41/EPCR <sup>118</sup>	Cnm67p* <sup>160</sup>	BIK1* <sup>209</sup>	Caltractin/centrin <sup>261,262</sup>
cAMP receptor	CP309 <sup>161</sup>	Bld10p <sup>210</sup>	Cdc31p* <sup>263</sup>
protein Rll <sup>119</sup>	DdCP224 <sup>162</sup>	CP60 <sup>211</sup>	Centrin <sup>264-266</sup>
fyn kinase <sup>120</sup>	CPAP <sup>163</sup>	CP190 <sup>212</sup>	Rng2p* <sup>267</sup>
GDI-2 <sup>121</sup>	Cut11p* <sup>164</sup>	CPAP <sup>213</sup>	
kar5p* <sup>122</sup>	$\delta$ tubulin <sup>165</sup>	CPAP Dom 1 n * <sup>167</sup>	Other proteins
PI 3-kinase <sup>123</sup>	DISC1 <sup>166</sup>	Dam1p* <sup>167</sup> EB1 <sup>214,215</sup>	AlphaB-crystallin <sup>268</sup>
PKA <sup>124,125</sup>	Duo1p* <sup>167</sup>	EB1	Basonuclin <sup>269</sup> BBS4 <sup>270</sup>
PKB/AKT <sup>117</sup>	ε tubulin <sup>165</sup>	γ tubulin/Tub4p* <sup>216,217</sup>	BBS4 <sup>-1.5</sup>
PKC βII <sup>126</sup>	GIFP <sup>168</sup>	Spc97p*/GCP2 <sup>218,219</sup>	BN46/51 <sup>271</sup>
PKC $\varepsilon^{127}$	Kar1p* <sup>169,170</sup>	Spc98*/GCP3 <sup>219,220</sup>	Ceap- $11^{272}$
PKC $\theta^{128}$	LGN <sup>171</sup>	GCP5 <sup>221</sup>	Ceap- $16^{272}$
SOCS-1 <sup>129</sup>	Miranda <sup>172</sup>	GCP6 <sup>221</sup>	CLIC4 <sup>273</sup>
Other kinases/	Mps2* <sup>173</sup>	Xgrip109 <sup>222</sup>	CTCF <sup>274</sup>
phosphatases	Mar 2 - * 174	Xgrip210 <sup>223</sup>	Cytocentrin <sup>275</sup>
LK6 <sup>130</sup>	Mps3p* <sup>174</sup>	Huntingtin <sup>224</sup>	DISC1 <sup>276</sup>
MAK-V/Hunk <sup>131</sup>	Nep98p* <sup>175</sup>	MAP1 <sup>225,226</sup>	Hec1 <sup>277</sup>
MARK4 <sup>132</sup>	Ninein <sup>176</sup>	$MAP1B^{227}$	ID1 <sup>107</sup>
Nm23-R1 <sup>133</sup>	MNudeE <sup>177</sup>	MAP2 <sup>225</sup>	MacroH2A1 <sup>278</sup>
Pim-1 <sup>69</sup>	Nuf2* <sup>178</sup>	XMAP215 <sup>228,229</sup>	Nuf <sup>279</sup>
PTP-BL <sup>104</sup>	Odf2 <sup>179</sup>	Mast <sup>230</sup>	Nuf2 <sup>277</sup>
PYK2 <sup>134</sup>	OFD1 <sup>180</sup>	MIR1 <sup>231</sup>	Orc2 <sup>280</sup>
WARTS/h-warts <sup>135,136</sup>	Paxillin <sup>181</sup>	Msps <sup>232</sup>	mPARD6a <sup>281</sup>
Golgi regulation	PCM-1 <sup>182</sup>	$NuMA^{233,234}$	PGs1 <sup>282</sup>
GAPcenA <sup>82</sup>	pericentrin A <sup>183,184</sup>	p93Dis1* <sup>235</sup>	$\mathrm{PIBF}^{283}$
PSKH1 <sup>137</sup>	pericentrin B <sup>185,186</sup>	pp39mos <sup>236</sup>	presenilin 1, 2 <sup>284</sup>
Other enzymes	PUMA-1 <sup>187</sup>	Stu2p* <sup>237</sup>	Ribonucleoprotein <sup>285</sup>
α enolase <sup>138</sup>	S100b <sup>188</sup>	Tau <sup>238</sup>	Rsp1p* <sup>183</sup>
MBD3 <sup>106</sup>	SNAD <sup>189</sup>	TPX2 <sup>239,240</sup>	$SAS-4^{286}$
NTKL <sup>139</sup>	Sp77 <sup>190</sup>	RABP1 <sup>17</sup>	SLMAP <sup>287</sup>
PARG <sup>140</sup>	Sp83 <sup>190</sup>	RHAMM <sup>241</sup>	SPD-2 <sup>288</sup>
PARP <sup>141</sup>	Spc29p* <sup>191</sup>	Spastin <sup>242</sup>	Speriolin <sup>289</sup>
hPARP-3 <sup>142</sup>	Spc42p* <sup>192</sup>	Motor proteins	Synaptotagmin IX <sup>290</sup>
6-PGDase <sup>143</sup>	Spc72p* <sup>193,194</sup>	Centractin/Arp1 <sup>243</sup>	TINA <sup>291</sup>
RUVBL1/TIP49a <sup>144</sup>	Spc90p*195	Dynein <sup>244</sup>	TSG101 <sup>292</sup>
SPO14*/PLD <sup>145</sup>	Spc110p*/Nuf1* <sup>195,196</sup>	Eg5 <sup>245</sup>	Vik1p* <sup>293</sup>
Tankyrase <sup>146</sup>	TAC-1 <sup>197</sup>	FLA10 <sup>246</sup>	·r
1 ankyrase	D-TACC <sup>198</sup>		

Viral proteins and<br/>infectious agentsChlamydia<br/>trachomatis  $^{296}$ HSV-2-VP16  $^{299}$ Adenovirus $^{294}$ Gag  $^{297}$ tsutsugamushi  $^{300}$ African SwineHIV-1 Nef  $^{298}$ SV40 virus  $^{301}$ Fever virus p50 $^{295}$ HSV-2-UL46  $^{299}$ SV40 T antigen  $^{301}$ 

## References

- 1 Kurasawa, Y. and Todokoro, K. (1999) Identification of human APC10/Doc1 as a subunit of anaphase promoting complex. *Oncogene* 18 (37), 5131-5137
- Mirabito, P.M. and Morris, N.R. (1993) BIMA, a TPR-containing protein required for mitosis, localizes to the spindle pole body in Aspergillus nidulans. *J Cell Biol* 120 (4), 959-968

Vaccinia virus 302

Wolbachia pipientis 303

- Tugendreich, S. et al. (1995) CDC27Hs colocalizes with CDC16Hs to the centrosome and mitotic spindle and is essential for the metaphase to anaphase transition. *Cell* 81 (2), 261-268
- 4 Kumada, K. et al. (1998) Cut1 is loaded onto the spindle by binding to Cut2 and promotes anaphase spindle movement upon Cut2 proteolysis. *Curr Biol* 8 (11), 633-641
- Niwa, J. et al. (2001) A novel centrosomal ring-finger protein, dorfin, mediates ubiquitin ligase activity. *Biochem Biophys Res Commun* 281 (3), 706-713
- Gorbea, C. et al. (2004) Characterization of mammalian Ecm29, a 26S proteasome-associated protein that localizes to the nucleus and membrane vesicles. *J Biol Chem* 279 (52), 54849-54861
- Raff, J.W. et al. (2002) The roles of Fzy/Cdc20 and Fzr/Cdh1 in regulating the destruction of cyclin B in space and time. *J Cell Biol.* 157 (7), 1139-1149f
- **8** Kallio, M.J. et al. (2002) Rapid microtubule-independent dynamics of Cdc20 at kinetochores and centrosomes in mammalian cells. *J Cell Biol* 158 (5), 841-847
- 9 Carroll, P.E. et al. (1999) Centrosome hyperamplification in human cancer: chromosome instability induced by p53 mutation and/or Mdm2 overexpression. *Oncogene* 18 (11), 1935-1944
- Berruti, G. and Martegani, E. (2002) mUBPy and MSJ-1, a deubiquitinating enzyme and a molecular chaperone specifically expressed in testis, associate with the acrosome and centrosome in mouse germ cells. *Ann N Y Acad Sci* 973, 5-7
- Tanaka, K. et al. (1999) Characterization of a fission yeast SUMO-1 homologue, pmt3p, required for multiple nuclear events, including the control of telomere length and chromosome segregation. *Mol Cell Biol* 19 (12), 8660-8672
- Gordon, C. (2002) The intracellular localization of the proteasome. *Curr Top Microbiol Immunol* 268, 175-184
- Wigley, W.C. et al. (1999) Dynamic association of proteasomal machinery with the centrosome. *J Cell Biol* 145 (3), 481-490
- Gstaiger, M. et al. (1999) Association of human SCF(SKP2) subunit p19(SKP1) with interphase centrosomes and mitotic spindle poles. *Exp Cell Res* 247 (2), 554-562
- Freed, E. et al. (1999) Components of an SCF ubiquitin ligase localize to the centrosome and regulate the centrosome duplication cycle. *Genes Dev* 13 (17), 2242-2257
- Zhao, J. et al. (2003) Parkin is recruited to the centrosome in response to inhibition of proteasomes. *J Cell Sci* 116 (Pt 19), 4011-4019
- Song, M.S. et al. (2005) The centrosomal protein RAS association domain family protein 1A (RASSF1A)-binding protein 1 regulates mitotic progression by recruiting RASSF1A to spindle poles. *J Biol Chem* 280 (5), 3920-3927
- Lin, H. et al. (2000) Divergent N-terminal sequences target an inducible testis deubiquitinating enzyme to distinct subcellular structures. *Mol Cell Biol* 20 (17), 6568-6578
- Lee, J. et al. (2001) A deubiquitinating enzyme, UCH/CeUBP130, has an essential role in the formation of a functional microtubule-organizing centre (MTOC) during early cleavage in C. elegans. *Genes Cells* 6 (10), 899-911

<sup>\*</sup> non-vertebrate proteins

<sup>#</sup> some proteins could appear in multiple categories

- Mathe, E. et al. (2004) The E2-C vihar is required for the correct spatiotemporal proteolysis of cyclin B and itself undergoes cyclical degradation. *Curr Biol* 14 (19), 1723-1733
- Keryer, G. et al. (2003) Part of Ran is associated with AKAP450 at the centrosome: involvement in microtubule-organizing activity. *Mol Biol Cell* 14 (10), 4260-4271
- Nakamura, M. et al. (1998) When overexpressed, a novel centrosomal protein, RanBPM, causes ectopic microtubule nucleation similar to gamma-tubulin. *J Cell Biol* 143 (4), 1041-1052
- Chial, H.J. et al. (1998) Saccharomyces cerevisiae Ndc1p is a shared component of nuclear pore complexes and spindle pole bodies. *J Cell Biol* 143 (7), 1789-1800
- Di Fiore, B. et al. (2003) Mammalian RanBP1 regulates centrosome cohesion during mitosis. *J Cell Sci* 116 (Pt 16), 3399-3411
- Kimura, M. et al. (1997) Cell cycle-dependent expression and spindle pole localization of a novel human protein kinase, Aik, related to Aurora of Drosophila and yeast Ipl1. *J Biol Chem* 272 (21), 13766-13771
- Zhou, H. et al. (1998) Tumour amplified kinase STK15/BTAK induces centrosome amplification, aneuploidy and transformation. *Nat Genet* 20 (2), 189-193
- Kimura, M. et al. (1999) Cell cycle-dependent expression and centrosome localization of a third human aurora/Ipl1-related protein kinase, AIK3. *J Biol Chem* 274 (11), 7334-7340
- Peng, J. et al. (2003) Disruption of the Diaphanous-related formin Drf1 gene encoding mDia1 reveals a role for Drf3 as an effector for Cdc42. *Curr Biol* 13 (7), 534-545
- Morrison, E.E. et al. (1998) EB1, a protein which interacts with the APC tumour suppressor, is associated with the microtubule cytoskeleton throughout the cell cycle. *Oncogene* 17 (26), 3471-3477
- Roghi, C. et al. (1998) The Xenopus protein kinase pEg2 associates with the centrosome in a cell cycle-dependent manner, binds to the spindle microtubules and is involved in bipolar mitotic spindle assembly. *J Cell Sci* 111 ( Pt 5), 557-572
- Xie, Z. et al. (2003) Serine 732 phosphorylation of FAK by Cdk5 is important for microtubule organization, nuclear movement, and neuronal migration. *Cell* 114 (4), 469-482
- Takahashi, S. et al. (2003) Role for Fes/Fps tyrosine kinase in microtubule nucleation through is Fes/CIP4 homology domain. *J Biol Chem* 278 (49), 49129-49133
- McNally, F.J. et al. (1996) Katanin, the microtubule-severing ATPase, is concentrated at centrosomes. *J Cell Sci* 109 (Pt 3), 561-567
- Fisk, H.A. and Winey, M. (2001) The mouse Mps1p-like kinase regulates centrosome duplication. *Cell* 106 (1), 95-104
- Fry, A.M. et al. (1998) A centrosomal function for the human Nek2 protein kinase, a member of the NIMA family of cell cycle regulators. *Embo J* 17 (2), 470-481
- Lou, Y. et al. (2004) Nek2A specifies the centrosomal localization of Erk2. *Biochem Biophys Res Commun* 321 (2), 495-501
- Fry, A.M. et al. (2000) The NIMA-related kinase X-Nek2B is required for efficient assembly of the zygotic centrosome in Xenopus laevis. *J Cell Sci* 113 ( Pt 11), 1973-1984
- 38 Krien, M.J. et al. (2002) The fission yeast NIMA kinase Fin1p is required for spindle function and nuclear envelope integrity. *Embo J* 21 (7), 1713-1722
- Tokuyama, Y. et al. (2001) Specific phosphorylation of nucleophosmin on Thr(199) by cyclin-dependent kinase 2-cyclin E and its role in centrosome duplication. *J Biol Chem* 276 (24), 21529-21537
- Rothwell, W.F. et al. (1998) Nuclear-fallout, a Drosophila protein that cycles from the cytoplasm to the centrosomes, regulates cortical microfilament organization. *Development* 125 (7), 1295-1303
- Chevrier, V. et al. (2002) The Rho-associated protein kinase p160ROCK is required for centrosome positioning. *J Cell Biol* 157 (5), 807-817
- Takada, S. et al. (2000) Identification of ribonucleotide reductase protein R1 as an activator of microtubule nucleation in Xenopus egg mitotic extracts. *Mol Biol Cell* 11 (12), 4173-4187
- 43 Stevenson, V.A. et al. (2001) Centrosomes and the Scrambled protein coordinate microtubule-independent actin reorganization. *Nat Cell Biol* 3 (1), 68-75
- Brown, C.R. et al. (1996) Molecular chaperones and the centrosome. A role for TCP-1 in microtubule nucleation. *J Biol Chem* 271 (2), 824-832
- O'Connell, K.F. et al. (2001) The C. elegans zyg-1 gene encodes a regulator of centrosome duplication with distinct maternal and paternal roles in the embryo. *Cell* 105 (4), 547-558
- Pockwinse, S.M. et al. (1997) Cell cycle independent interaction of CDC2 with the centrosome, which is associated with the nuclear matrix-intermediate filament scaffold. *Proc Natl Acad Sci U S A* 94 (7), 3022-3027

- Krämer, A. et al. (2004) Centrosome-associated Chk1 prevents premature activation of cyclin-B–Cdk1 kinase. *Nature Cell Biology* 6 (9), 885-891
- Tsvetkov, L. et al. (2003) Polo-like kinase 1 and Chk2 interact and co-localize to centrosomes and the midbody. *J Biol Chem* 278 (10), 8468-8475
- Buendia, B. et al. (1992) Regulation of the microtubule nucleating activity of centrosomes in Xenopus egg extracts: role of cyclin A-associated protein kinase. *J Cell Biol* 116 (6), 1431-1442
- Bailly, E. et al. (1989) p34cdc2 is located in both nucleus and cytoplasm; part is centrosomally associated at G2/M and enters vesicles at anaphase. *Embo J* 8 (13), 3985-3995
- Debec, A. and Montmory, C. (1992) Cyclin B is associated with centrosomes in Drosophila mitotic cells. *Biol Cell* 75 (2), 121-126
- Hinchcliffe, E.H. et al. (1999) Requirement of Cdk2-cyclin E activity for repeated centrosome reproduction in Xenopus egg extracts. *Science* 283 (5403), 851-854
- McShea, A. et al. (2000) Identification of CIP-1-associated regulator of cyclin B (CARB), a novel p21-binding protein acting in the G2 phase of the cell cycle. *J Biol Chem* 275 (30), 23181-23186
- Dutertre, S. et al. (2004) Phosphorylation of CDC25B by Aurora-A at the centrosome contributes to the G2-M transition. *J Cell Sci* 117 (Pt 12), 2523-2531
- Eto, M. et al. (2002) Inhibitor-2 regulates protein phosphatase-1 complexed with NimA-related kinase to induce centrosome separation. *J Biol Chem* 277 (46), 44013-44020
- Leach, C. et al. (2003) Phosphorylation of phosphatase inhibitor-2 at centrosomes during mitosis. *J Biol Chem* 278 (28), 26015-26020
- Logarinho, E. and Sunkel, C.E. (1998) The Drosophila POLO kinase localises to multiple compartments of the mitotic apparatus and is required for the phosphorylation of MPM2 reactive epitopes. *J Cell Sci* 111 (Pt 19), 2897-2909
- Golsteyn, R.M. et al. (1995) Cell cycle regulation of the activity and subcellular localization of Plk1, a human protein kinase implicated in mitotic spindle function. *J Cell Biol* 129 (6), 1617-1628
- Bahler, J. et al. (1998) Role of polo kinase and Mid1p in determining the site of cell division in fission yeast. *J Cell Biol* 143 (6), 1603-1616
- Andreassen, P.R. et al. (1998) Differential subcellular localization of protein phosphatase-1 alpha, gamma1, and delta isoforms during both interphase and mitosis in mammalian cells. *J Cell Biol* 141 (5), 1207-1215
- Helps, N.R. et al. (1998) Protein phosphatase 4 is an essential enzyme required for organisation of microtubules at centrosomes in Drosophila embryos. *J Cell Sci* 111 ( Pt 10), 1331-1340
- Hastie, C.J. et al. (2000) A novel 50 kDa protein forms complexes with protein phosphatase 4 and is located at centrosomal microtubule organizing centres. *Biochem J* 347 Pt 3, 845-855
- Brown, C.R. et al. (1994) Both viral (adenovirus E1B) and cellular (hsp 70, p53) components interact with centrosomes. *J Cell Physiol* 160 (1), 47-60
- Rattner, J.B. (1991) hsp70 is localized to the centrosome of dividing HeLa cells. *Exp Cell Res* 195 (1), 110-113
- Lange, B.M. et al. (2000) Hsp90 is a core centrosomal component and is required at different stages of the centrosome cycle in Drosophila and vertebrates. *Embo J* 19 (6), 1252-1262
- Li, F. et al. (1999) Pleiotropic cell-division defects and apoptosis induced by interference with survivin function. *Nat Cell Biol* 1 (8), 461-466
- Preuss, U. et al. (2003) DAP-like kinase, a member of the death-associated protein kinase family, associates with centrosomes, centromers, and the contractile ring during mitosis. *Eur J Cell Biol* 82 (9), 447-459
- Sandal, T. et al. (2003) Irod/Ian5: an inhibitor of gamma-radiation- and okadaic acid-induced apoptosis. Mol Biol Cell 14 (8), 3292-3304
- Bhattacharya, N. et al. (2002) Pim-1 associates with protein complexes necessary for mitosis. *Chromosoma* 111 (2), 80-95
- Thomas, R.C. et al. (1996) Translocation of the retinoblastoma gene product during mitosis. *Exp Cell Res* 223 (2), 227-232
- Rothbarth, K. et al. (2001) Intracellular location and nuclear targeting of the Spi-1, Spi-2 and Spi-3 genederived serine protease inhibitors in non-secretory cells. *Eur J Cell Biol* 80 (5), 341-348
- Hsu, L.C. and White, R.L. (1998) BRCA1 is associated with the centrosome during mitosis. *Proc Natl Acad Sci U S A* 95 (22), 12983-12988

- Takada, S. et al. (2003) Drosophila checkpoint kinase 2 couples centrosome function and spindle assembly to genomic integrity. *Cell* 113 (1), 87-99
- Verlhac, M.H. et al. (1993) MAP kinase becomes stably activated at metaphase and is associated with microtubule-organizing centers during meiotic maturation of mouse oocytes. *Dev Biol* 158 (2), 330-340
- 75 MacCorkle-Chosnek, R.A. et al. (2001) Cell cycle regulation of c-Jun N-terminal kinase activity at the centrosomes. *Biochem Biophys Res Commun* 289 (1), 173-180
- Liu, X. et al. (2004) The MAP kinase pathway is required for entry into mitosis and cell survival. Oncogene 23 (3), 763-776
- Swenson, K.I. et al. (2003) A new identity for MLK3 as an NIMA-related, cell cycle-regulated kinase that is localized near centrosomes and influences microtubule organization. *Mol Biol Cell* 14 (1), 156-172
- Shapiro, P.S. et al. (1998) Activation of the MKK/ERK pathway during somatic cell mitosis: direct interactions of active ERK with kinetochores and regulation of the mitotic 3F3/2 phosphoantigen. *J Cell Biol* 142 (6), 1533-1545
- Liu, J. et al. (2004) Serine-threonine kinases and transcription factors active in signal transduction are detected at high levels of phosphorylation during mitosis in preimplantation embryos and trophoblast stem cells. *Reproduction* 128 (5), 643-654
- Mazzoni, C. et al. (1993) The SLT2 (MPK1) MAP kinase homolog is involved in polarized cell growth in Saccharomyces cerevisiae. *J Cell Biol* 123 (6 Pt 2), 1821-1833
- Jensen, S. et al. (2001) A novel role of the budding yeast separin Esp1 in anaphase spindle elongation: evidence that proper spindle association of Esp1 is regulated by Pds1. *J Cell Biol* 152 (1), 27-40
- 82 Cuif, M.H. et al. (1999) Characterization of GAPCenA, a GTPase activating protein for Rab6, part of which associates with the centrosome. *Embo J* 18 (7), 1772-1782
- Jin, D.Y. et al. (1998) Human T cell leukemia virus type 1 oncoprotein Tax targets the human mitotic checkpoint protein MAD1. *Cell* 93 (1), 81-91
- Howell, B.J. et al. (2000) Visualization of Mad2 dynamics at kinetochores, along spindle fibers, and at spindle poles in living cells. *J Cell Biol* 150 (6), 1233-1250
- Chestukhin, A. et al. (2003) Processing, localization, and requirement of human separase for normal anaphase progression. *Proc Natl Acad Sci U S A* 100 (8), 4574-4579
- Nakamura, T. et al. (2002) Cut1/separase C-terminus affects spindle pole body positioning in interphase of fission yeast: pointed nuclear formation. *Genes Cells* 7 (11), 1113-1124
- Barthelmes, H.U. et al. (2000) Active DNA topoisomerase IIalpha is a component of the salt-stable centrosome core. *J Biol Chem* 275 (49), 38823-38830
- Fraschini, R. et al. (1999) Budding yeast Bub2 is localized at spindle pole bodies and activates the mitotic checkpoint via a different pathway from Mad2. *J Cell Biol* 145 (5), 979-991
- Pereira, G. et al. (2000) The Bub2p spindle checkpoint links nuclear migration with mitotic exit. *Mol Cell* 6 (1), 1-10
- Guertin, D.A. et al. (2000) The role of the sid1p kinase and cdc14p in regulating the onset of cytokinesis in fission yeast. *Embo J* 19 (8), 1803-1815
- Kaiser, B.K. et al. (2004) Xenopus Cdc14 alpha/beta are localized to the nucleolus and centrosome and are required for embryonic cell division. *BMC Cell Biol* 5 (1), 27
- Bembenek, J. and Yu, H. (2001) Regulation of the anaphase-promoting complex by the dual specificity phosphatase human Cdc14a. *J Biol Chem* 276 (51), 48237-48242
- Cenamor, R. et al. (1999) The budding yeast Cdc15 localizes to the spindle pole body in a cell-cycle-dependent manner. *Mol Cell Biol Res Commun* 2 (3), 178-184
- Frenz, L.M. et al. (2000) The budding yeast Dbf2 protein kinase localises to the centrosome and moves to the bud neck in late mitosis. *J Cell Sci* 113 Pt 19, 3399-3408
- Salimova, E. et al. (2000) The S. pombe orthologue of the S. cerevisiae mob1 gene is essential and functions in signalling the onset of septum formation. *J Cell Sci* 113 ( Pt 10), 1695-1704
- Gruneberg, U. et al. (2000) Nud1p links astral microtubule organization and the control of exit from mitosis. *Embo J* 19 (23), 6475-6488
- 97 Cerutti, L. and Simanis, V. (1999) Asymmetry of the spindle pole bodies and spg1p GAP segregation during mitosis in fission yeast. *J Cell Sci* 112 ( Pt 14), 2313-2321
- Li, C. et al. (2000) Byr4 localizes to spindle-pole bodies in a cell cycle-regulated manner to control Cdc7 localization and septation in fission yeast. *J Biol Chem* 275 (19), 14381-14387
- Chang, L. and Gould, K.L. (2000) Sid4p is required to localize components of the septation initiation pathway to the spindle pole body in fission yeast. *Proc Natl Acad Sci U S A* 97 (10), 5249-5254

- Krapp, A. et al. (2003) Mitotic hyperphosphorylation of the fission yeast SIN scaffold protein cdc11p is regulated by the protein kinase cdc7p. *Curr Biol* 13 (2), 168-172
- Guertin, D.A. et al. (2002) Dma1 prevents mitotic exit and cytokinesis by inhibiting the septation initiation network (SIN). *Dev Cell* 3 (6), 779-790
- Lee, J. et al. (1999) Ibd1p, a possible spindle pole body associated protein, regulates nuclear division and bud separation in Saccharomyces cerevisiae. *Biochim Biophys Acta* 1449 (3), 239-253
- Sparks, C.A. et al. (1999) Sid2p, a spindle pole body kinase that regulates the onset of cytokinesis. *J Cell Biol* 146 (4), 777-790
- Herrmann, L. et al. (2003) The protein tyrosine phosphatase PTP-BL associates with the midbody and is involved in the regulation of cytokinesis. *Mol Biol Cell* 14 (1), 230-240
- Pietromonaco, S.F. et al. (1995) Identification of enzymatically active Ca2+/calmodulin-dependent protein kinase in centrosomes of hemopoietic cells. *Blood Cells Mol Dis* 21 (1), 34-41
- Sakai, H. et al. (2002) MBD3 and HDAC1, two components of the NuRD complex, are localized at Aurora-A-positive centrosomes in M phase. *J Biol Chem* 277 (50), 48714-48723
- Hasskarl, J. et al. (2004) The helix-loop-helix protein ID1 localizes to centrosomes and rapidly induces abnormal centrosome numbers. *Oncogene* 23 (10), 1930-1938
- Mello, C.C. et al. (1996) The PIE-1 protein and germline specification in C. elegans embryos. *Nature* 382 (6593), 710-712
- Groisman, I. et al. (2000) CPEB, maskin, and cyclin B1 mRNA at the mitotic apparatus: implications for local translational control of cell division. *Cell* 103 (3), 435-447
- Lambert, J.D. and Nagy, L.M. (2002) Asymmetric inheritance of centrosomally localized mRNAs during embryonic cleavages. *Nature* 420 (6916), 682-686
- Castro, A. et al. (2000) Part of Xenopus translin is localized in the centrosomes during mitosis. *Biochem Biophys Res Commun* 276 (2), 515-523
- Hudson, J.W. et al. (2001) Late mitotic failure in mice lacking Sak, a polo-like kinase. *Curr Biol* 11 (6), 441-446
- Warnke, S. et al. (2004) Polo-like kinase-2 is required for centriole duplication in mammalian cells. *Curr Biol* 14 (13), 1200-1207
- Olmeda, D. et al. (2003) Beta-catenin regulation during the cell cycle: implications in G2/M and apoptosis. *Mol Biol Cell* 14 (7), 2844-2860
- Brockman, J.L. et al. (1992) Cell cycle-dependent localization of casein kinase I to mitotic spindles. *Proc Natl Acad Sci U S A* 89 (20), 9454-9458
- Sillibourne, J.E. et al. (2002) Centrosomal anchoring of the protein kinase CK1delta mediated by attachment to the large, coiled-coil scaffolding protein CG-NAP/AKAP450. *J Mol Biol* 322 (4), 785-797
- Wakefield, J.G. et al. (2003) A role for glycogen synthase kinase-3 in mitotic spindle dynamics and chromosome alignment. *J Cell Sci* 116 (Pt 4), 637-646
- Fukudome, K. and Esmon, C.T. (1995) Molecular cloning and expression of murine and bovine endothelial cell protein C/activated protein C receptor (EPCR). The structural and functional conservation in human, bovine, and murine EPCR. *J Biol Chem* 270 (10), 5571-5577
- De Camilli, P. et al. (1986) Heterogeneous distribution of the cAMP receptor protein RII in the nervous system: evidence for its intracellular accumulation on microtubules, microtubule-organizing centers, and in the area of the Golgi complex. *J Cell Biol* 103 (1), 189-203
- Ley, S.C. et al. (1994) Distinct intracellular localization of Lck and Fyn protein tyrosine kinases in human T lymphocytes. *J Cell Biol* 125 (3), 639-649
- Shisheva, A. et al. (1995) Pericentriolar targeting of GDP-dissociation inhibitor isoform 2. *Eur J Cell Biol* 68 (2), 143-158
- Beh, C.T. et al. (1997) KAR5 encodes a novel pheromone-inducible protein required for homotypic nuclear fusion. *J Cell Biol* 139 (5), 1063-1076
- Kapeller, R. et al. (1993) Internalization of activated platelet-derived growth factor receptor-phosphatidylinositol-3' kinase complexes: potential interactions with the microtubule cytoskeleton. *Mol Cell Biol* 13 (10), 6052-6063
- Keryer, G. et al. (1993) A high-affinity binding protein for the regulatory subunit of cAMP-dependent protein kinase II in the centrosome of human cells. *Exp Cell Res* 204 (2), 230-240
- Diviani, D. et al. (2000) Pericentrin anchors protein kinase A at the centrosome through a newly identified RII-binding domain. *Curr Biol* 10 (7), 417-420

- Chen, D. et al. (2004) Centrosomal anchoring of protein kinase C betaII by pericentrin controls microtubule organization, spindle function, and cytokinesis. *J Biol Chem* 279 (6), 4829-4839
- Takahashi, M. et al. (2000) Association of immature hypophosphorylated protein kinase cepsilon with an anchoring protein CG-NAP. *J Biol Chem* 275 (44), 34592-34596
- Passalacqua, M. et al. (1999) Protein kinase C-theta is specifically localized on centrosomes and kinetochores in mitotic cells. *Biochem J* 337 (Pt 1), 113-118
- Vuong, B.Q. et al. (2004) SOCS-1 localizes to the microtubule organizing complex-associated 20S proteasome. *Mol Cell Biol* 24 (20), 9092-9101
- Kidd, D. and Raff, J.W. (1997) LK6, a short lived protein kinase in Drosophila that can associate with microtubules and centrosomes. *J Cell Sci* 110 (Pt 2), 209-219
- Korobko, E.V. et al. (2004) Subcellular localization of MAK-V/Hunk protein kinase expressed in COS-1 cells. *Cell Biol Int* 28 (1), 49-56
- Trinczek, B. et al. (2004) MARK4 is a novel microtubule-associated proteins/microtubule affinity-regulating kinase that binds to the cellular microtubule network and to centrosomes. *J Biol Chem* 279 (7), 5915-5923
- Roymans, D. et al. (2001) Identification of the tumor metastasis suppressor Nm23-H1/Nm23-R1 as a constituent of the centrosome. *Exp Cell Res* 262 (2), 145-153
- Rodriguez-Fernandez, J.L. et al. (2002) LFA-1 integrin and the microtubular cytoskeleton are involved in the Ca(2)(+)-mediated regulation of the activity of the tyrosine kinase PYK2 in T cells. *J Leukoc Biol* 71 (3), 520-530
- Morisaki, T. et al. (2002) WARTS tumor suppressor is phosphorylated by Cdc2/cyclin B at spindle poles during mitosis. *FEBS Lett* 529 (2-3), 319-324
- Nishiyama, Y. et al. (1999) A human homolog of Drosophila warts tumor suppressor, h-warts, localized to mitotic apparatus and specifically phosphorylated during mitosis. *FEBS Lett* 459 (2), 159-165
- Brede, G. et al. (2000) Characterization of PSKH1, a novel human protein serine kinase with centrosomal, golgi, and nuclear localization. *Genomics* 70 (1), 82-92
- Johnstone, S.A. et al. (1992) Enolase is present at the centrosome of HeLa cells. *Exp Cell Res* 202 (2), 458-463
- Di, Y. et al. (2003) Cloning and characterization of a novel gene which encodes a protein interacting with the mitosis-associated kinase-like protein NTKL. *J Hum Genet* 48 (6), 315-321
- Ohashi, S. et al. (2003) Subcellular localization of poly(ADP-ribose) glycohydrolase in mammalian cells. *Biochem Biophys Res Commun* 307 (4), 915-921
- Kanai, M. et al. (2000) Poly(ADP-ribose) polymerase localizes to the centrosomes and chromosomes. *Biochem Biophys Res Commun* 278 (2), 385-389
- Augustin, A. et al. (2003) PARP-3 localizes preferentially to the daughter centriole and interferes with the G1/S cell cycle progression. *J Cell Sci* 116 (Pt 8), 1551-1562
- Kindzelskii, A.L. et al. (2004) 6-phosphogluconate dehydrogenase and glucose-6-phosphate dehydrogenase form a supramolecular complex in human neutrophils that undergoes retrograde trafficking during pregnancy. *J Immunol* 172 (10), 6373-6381
- Gartner, W. et al. (2003) The ATP-dependent helicase RUVBL1/TIP49a associates with tubulin during mitosis. *Cell Motil Cytoskeleton* 56 (2), 79-93
- Rudge, S.A. et al. (1998) Relocalization of phospholipase D activity mediates membrane formation during meiosis. *J Cell Biol* 140 (1), 81-90
- Smith, S. and de Lange, T. (1999) Cell cycle dependent localization of the telomeric PARP, tankyrase, to nuclear pore complexes and centrosomes. *J Cell Sci* 112 (Pt 21), 3649-3656
- Schloss, J.A. et al. (1977) Myosin subfragment binding for the localization of actin-like microfilaments in cultured cells. A light and electron microscope study. *J Cell Biol* 74 (3), 794-815
- 148 Cande, W.Z. et al. (1977) A comparison of the distribution of actin and tubulin in the mammalian mitotic spindle as seen by indirect immunofluorescence. *J Cell Biol* 72 (3), 552-567
- Reinton, N. et al. (2000) Localization of a novel human A-kinase-anchoring protein, hAKAP220, during spermatogenesis. *Dev Biol* 223 (1), 194-204
- Schmidt, P.H. et al. (1999) AKAP350, a multiply spliced protein kinase A-anchoring protein associated with centrosomes. *J Biol Chem* 274 (5), 3055-3066
- do Carmo Avides, M. and Glover, D.M. (1999) Abnormal spindle protein, Asp, and the integrity of mitotic centrosomal microtubule organizing centers. *Science* 283 (5408), 1733-1735

- Kenedy, A.A. et al. (2003) Identification and characterization of the novel centrosome-associated protein CCCAP. *Gene* 303, 35-46
- Lange, B.M. and Gull, K. (1995) A molecular marker for centriole maturation in the mammalian cell cycle. *J Cell Biol* 130 (4), 919-927
- Gromley, A. et al. (2003) A novel human protein of the maternal centriole is required for the final stages of cytokinesis and entry into S phase. *J Cell Biol* 161 (3), 535-545
- Li, K. and Kaufman, T.C. (1996) The homeotic target gene centrosomin encodes an essential centrosomal component. *Cell* 85 (4), 585-596
- Petzelt, C. et al. (1997) The centrosomal protein centrosomin A and the nuclear protein centrosomin B derive from one gene by post-transcriptional processes involving RNA editing. *J Cell Sci* 110 ( Pt 20), 2573-2578
- Ou, Y.Y. et al. (2002) CEP110 and ninein are located in a specific domain of the centrosome associated with centrosome maturation. *J Cell Sci* 115 (Pt 9), 1825-1835
- Fry, A.M. et al. (1998) C-Nap1, a novel centrosomal coiled-coil protein and candidate substrate of the cell cycle-regulated protein kinase Nek2. *J Cell Biol* 141 (7), 1563-1574
- Page, B.D. and Snyder, M. (1992) CIK1: a developmentally regulated spindle pole body-associated protein important for microtubule functions in Saccharomyces cerevisiae. *Genes Dev* 6 (8), 1414-1429
- Schaerer, F. et al. (2001) Cnm67p is a spacer protein of the Saccharomyces cerevisiae spindle pole body outer plaque. *Mol Biol Cell* 12 (8), 2519-2533
- Kawaguchi, S. and Zheng, Y. (2004) Characterization of a Drosophila centrosome protein CP309 that shares homology with Kendrin and CG-NAP. *Mol Biol Cell* 15 (1), 37-45
- Graf, R. et al. (2000) Dictyostelium DdCP224 is a microtubule-associated protein and a permanent centrosomal resident involved in centrosome duplication. *J Cell Sci* 113 ( Pt 10), 1747-1758
- Hung, L.Y. et al. (2000) Protein 4.1 R-135 interacts with a novel centrosomal protein (CPAP) which is associated with the gamma-tubulin complex. *Mol Cell Biol* 20 (20), 7813-7825
- West, R.R. et al. (1998) cut11(+): A gene required for cell cycle-dependent spindle pole body anchoring in the nuclear envelope and bipolar spindle formation in Schizosaccharomyces pombe. *Mol Biol Cell* 9 (10), 2839-2855
- 165 Chang, P. and Stearns, T. (2000) Delta-tubulin and epsilon-tubulin: two new human centrosomal tubulins reveal new aspects of centrosome structure and function. *Nat Cell Biol* 2 (1), 30-35
- Morris, J.A. et al. (2003) DISC1 (Disrupted-In-Schizophrenia 1) is a centrosome-associated protein that interacts with MAP1A, MIPT3, ATF4/5 and NUDEL: regulation and loss of interaction with mutation. *Hum Mol Genet* 12 (13), 1591-1608
- Hofmann, C. et al. (1998) Saccharomyces cerevisiae Duo1p and Dam1p, novel proteins involved in mitotic spindle function. *J Cell Biol* 143 (4), 1029-1040
- Kalnins, V.I. et al. (1985) Assembly of glial intermediate filament protein is initiated in the centriolar region. *Brain Res* 345 (2), 322-326
- Biggins, S. and Rose, M.D. (1994) Direct interaction between yeast spindle pole body components: Kar1p is required for Cdc31p localization to the spindle pole body. *J Cell Biol* 125 (4), 843-852
- Spang, A. et al. (1995) The Cdc31p-binding protein Kar1p is a component of the half bridge of the yeast spindle pole body. *J Cell Biol* 128 (5), 863-877
- Du, Q. et al. (2001) A mammalian Partner of inscuteable binds NuMA and regulates mitotic spindle organization. *Nat Cell Biol* 3 (12), 1069-1075
- Mollinari, C. et al. (2002) Miranda, a protein involved in neuroblast asymmetric division, is associated with embryonic centrosomes of Drosophila melanogaster. *Biol Cell* 94 (1), 1-13
- Munoz-Centeno, M.C. et al. (1999) Saccharomyces cerevisiae MPS2 encodes a membrane protein localized at the spindle pole body and the nuclear envelope. *Mol Biol Cell* 10 (7), 2393-2406
- Jaspersen, S.L. et al. (2002) Mps3p is a novel component of the yeast spindle pole body that interacts with the yeast centrin homologue Cdc31p. *J Cell Biol* 159 (6), 945-956
- Nishikawa, S. et al. (2003) Nep98p is a component of the yeast spindle pole body and essential for nuclear division and fusion. *J Biol Chem* 278 (11), 9938-9943
- Bouckson-Castaing, V. et al. (1996) Molecular characterisation of ninein, a new coiled-coil protein of the centrosome. *J Cell Sci* 109 ( Pt 1), 179-190
- Feng, Y. et al. (2000) LIS1 regulates CNS lamination by interacting with mNudE, a central component of the centrosome. *Neuron* 28 (3), 665-679

- Osborne, M.A. et al. (1994) Nuf2, a spindle pole body-associated protein required for nuclear division in yeast. *J Cell Biol* 125 (4), 853-866
- Nakagawa, Y. et al. (2001) Outer dense fiber 2 is a widespread centrosome scaffold component preferentially associated with mother centrioles: its identification from isolated centrosomes. *Mol Biol Cell* 12 (6), 1687-1697
- Romio, L. et al. (2004) OFD1 is a centrosomal/basal body protein expressed during mesenchymal-epithelial transition in human nephrogenesis. *J Am Soc Nephrol* 15 (10), 2556-2568
- Herreros, L. et al. (2000) Paxillin localizes to the lymphocyte microtubule organizing center and associates with the microtubule cytoskeleton. *J Biol Chem* 275 (34), 26436-26440
- Balczon, R. et al. (1994) PCM-1, A 228-kD centrosome autoantigen with a distinct cell cycle distribution. *J Cell Biol* 124 (5), 783-793
- Zimmerman, S. et al. (2004) Rsp1p, a J domain protein required for disassembly and assembly of microtubule organizing centers during the fission yeast cell cycle. *Dev Cell* 6 (4), 497-509
- Doxsey, S.J. et al. (1994) Pericentrin, a highly conserved centrosome protein involved in microtubule organization. *Cell* 76 (4), 639-650
- Zimmerman, W.C. et al. (2004) Mitosis-specific anchoring of gamma tubulin complexes by pericentrin controls spindle organization and mitotic entry. *Mol Biol Cell* 15 (8), 3642-3657
- Li, Q. et al. (2001) Kendrin/pericentrin-B, a centrosome protein with homology to pericentrin that complexes with PCM-1. *J Cell Sci* 114 (Pt 4), 797-809.
- Esteban, M.R. et al. (1998) PUMA1: a novel protein that associates with the centrosomes, spindle and centromeres in the nematode Parascaris. *J Cell Sci* 111 ( Pt 6), 723-735
- Uchida, T. and Endo, T. (1988) Immunoelectron microscopic demonstration of S-100b protein-like in centriole, cilia, and basal body. *J Histochem Cytochem* 36 (6), 693-696
- Liu, B. and Morris, N.R. (2000) A spindle pole body-associated protein, SNAD, affects septation and conidiation in Aspergillus nidulans. *Mol Gen Genet* 263 (3), 375-387
- Hinchcliffe, E.H. and Linck, R.W. (1998) Two proteins isolated from sea urchin sperm flagella: structural components common to the stable microtubules of axonemes and centrioles. *J Cell Sci* 111 (Pt 5), 585-595
- Elliott, S. et al. (1999) Spc29p is a component of the Spc110p subcomplex and is essential for spindle pole body duplication. *Proc Natl Acad Sci U S A* 96 (11), 6205-6210
- Donaldson, A.D. and Kilmartin, J.V. (1996) Spc42p: a phosphorylated component of the S. cerevisiae spindle pole body (SPD) with an essential function during SPB duplication. *J Cell Biol* 132 (5), 887-901
- 193 Chen, X.P. et al. (1998) The yeast spindle pole body component Spc72p interacts with Stu2p and is required for proper microtubule assembly. *J Cell Biol* 141 (5), 1169-1179
- Knop, M. and Schiebel, E. (1998) Receptors determine the cellular localization of a gamma-tubulin complex and thereby the site of microtubule formation. *Embo J* 17 (14), 3952-3967
- Rout, M.P. and Kilmartin, J.V. (1990) Components of the yeast spindle and spindle pole body. *J Cell Biol* 111 (5 Pt 1), 1913-1927
- Kilmartin, J.V. et al. (1993) A spacer protein in the Saccharomyces cerevisiae spindle poly body whose transcript is cell cycle-regulated. *J Cell Biol* 123 (5), 1175-1184
- Le Bot, N. et al. (2003) TAC-1, a regulator of microtubule length in the C. elegans embryo. *Curr Biol* 13 (17), 1499-1505
- Gergely, F. et al. (2000) D-TACC: a novel centrosomal protein required for normal spindle function in the early Drosophila embryo.  $Embo\ J\ 19\ (2),\ 241-252$
- 199 Gergely, F. et al. (2000) The TACC domain identifies a family of centrosomal proteins that can interact with microtubules. *Proc Natl Acad Sci U S A* 97 (26), 14352-14357
- Piekorz, R.P. et al. (2002) The centrosomal protein TACC3 is essential for hematopoietic stem cell function and genetically interfaces with p53-regulated apoptosis. *Embo J* 21 (4), 653-664
- Steadman, B.T. et al. (2002) Transforming acidic coiled-coil-containing protein 4 interacts with centrosomal AKAP350 and the mitotic spindle apparatus. *J Biol Chem* 277 (33), 30165-30176
- Larsson, M. et al. (2000) The spatial and temporal expression of Tekt1, a mouse tektin C homologue, during spermatogenesis suggest that it is involved in the development of the sperm tail basal body and axoneme. *Eur J Cell Biol* 79 (10), 718-725
- 203 Paulin-Levasseur, M. and Brown, D.L. (1987) Vimentin dynamics during the mitogenic stimulation of mouse splenic lymphocytes. *Cell Motil Cytoskeleton* 8 (3), 227-237
- 204 Chevrier, V. et al. (1995) Identification of vinculin as a pericentriolar component in mammalian cells. *Exp Cell Res* 219 (2), 399-406

- Malone, C.J. et al. (2003) The C. elegans hook protein, ZYG-12, mediates the essential attachment between the centrosome and nucleus. *Cell* 115 (7), 825-836
- Krauss, S.W. et al. (1997) Structural protein 4.1 is located in mammalian centrosomes. *Proc Natl Acad Sci U S A* 94 (14), 7297-7302
- Gascard, P. et al. (1998) Characterization of multiple isoforms of protein 4.1R expressed during erythroid terminal differentiation. *Blood* 92 (11), 4404-4414
- Pietromonaco, S.F. et al. (1996) Association of 14-3-3 proteins with centrosomes. *Blood Cells Mol Dis* 22 (3), 225-237
- Berlin, V. et al. (1990) BIK1, a protein required for microtubule function during mating and mitosis in Saccharomyces cerevisiae, colocalizes with tubulin. *J Cell Biol* 111 (6 Pt 1), 2573-2586
- Matsuura, K. et al. (2004) Bld10p, a novel protein essential for basal body assembly in Chlamydomonas: localization to the cartwheel, the first ninefold symmetrical structure appearing during assembly. *J Cell Biol* 165 (5), 663-671
- Kellogg, D.R. et al. (1995) CP60: a microtubule-associated protein that is localized to the centrosome in a cell cycle-specific manner. *Mol Biol Cell* 6 (12), 1673-1684
- Oegema, K. et al. (1995) The cell cycle-dependent localization of the CP190 centrosomal protein is determined by the coordinate action of two separable domains. *J Cell Biol* 131 (5), 1261-1273
- Hung, L.Y. et al. (2004) Identification of a novel microtubule-destabilizing motif in CPAP that binds to tubulin heterodimers and inhibits microtubule assembly. *Mol Biol Cell* 15 (6), 2697-2706
- Rehberg, M. and Graf, R. (2002) Dictyostelium EB1 is a genuine centrosomal component required for proper spindle formation. *Mol Biol Cell* 13 (7), 2301-2310
- Berrueta, L. et al. (1998) The adenomatous polyposis coli-binding protein EB1 is associated with cytoplasmic and spindle microtubules. *Proc Natl Acad Sci U S A* 95 (18), 10596-10601
- Oakley, B.R. et al. (1990) Gamma-tubulin is a component of the spindle pole body that is essential for microtubule function in Aspergillus nidulans. *Cell* 61 (7), 1289-1301
- Stearns, T. et al. (1991) Gamma-tubulin is a highly conserved component of the centrosome. *Cell* 65 (5), 825-836
- Knop, M. and Schiebel, E. (1997) Spc98p and Spc97p of the yeast gamma-tubulin complex mediate binding to the spindle pole body via their interaction with Spc110p. *Embo J* 16 (23), 6985-6995
- Murphy, S.M. et al. (1998) The mammalian gamma-tubulin complex contains homologues of the yeast spindle pole body components spc97p and spc98p. *J Cell Biol* 141 (3), 663-674
- Geissler, S. et al. (1996) The spindle pole body component Spc98p interacts with the gamma-tubulin-like Tub4p of Saccharomyces cerevisiae at the sites of microtubule attachment. *Embo J* 15 (15), 3899-3911
- Murphy, S.M. et al. (2001) GCP5 and GCP6: two new members of the human gamma-tubulin complex. *Mol Biol Cell* 12 (11), 3340-3352
- Martin, O.C. et al. (1998) Xgrip109: a gamma tubulin-associated protein with an essential role in gamma tubulin ring complex (gammaTuRC) assembly and centrosome function. *J Cell Biol* 141 (3), 675-687
- Zhang, L. et al. (2000) The role of Xgrip210 in gamma-tubulin ring complex assembly and centrosome recruitment. *J Cell Biol* 151 (7), 1525-1536
- Hoffner, G. et al. (2002) Perinuclear localization of huntingtin as a consequence of its binding to microtubules through an interaction with beta-tubulin: relevance to Huntington's disease. *J Cell Sci* 115 (Pt 5), 941-948
- Mascardo, R.N. et al. (1982) Localization of high molecular weight microtubule-associated proteins (MAP1 and MAP2) in a HeLa microtubule-organizing centre. *Cytobios* 35 (138), 113-127
- Sato, C. et al. (1985) Localization of 350K molecular weight and related proteins in both the cytoskeleton and nuclear flecks that increase during G1 phase. *Exp Cell Res* 160 (1), 206-220
- Dominguez, J.E. et al. (1994) A protein related to brain microtubule-associated protein MAP1B is a component of the mammalian centrosome. *J Cell Sci* 107 (Pt 2), 601-611
- Popov, A.V. et al. (2001) XMAP215 regulates microtubule dynamics through two distinct domains. *Embo J* 20 (3), 397-410
- Graf, R. et al. (2003) Regulated expression of the centrosomal protein DdCP224 affects microtubule dynamics and reveals mechanisms for the control of supernumerary centrosome number. *Mol Biol Cell* 14 (10), 4067-4074
- Lemos, C.L. et al. (2000) Mast, a conserved microtubule-associated protein required for bipolar mitotic spindle organization. *Embo J* 19 (14), 3668-3682

- Stein, P.A. et al. (2002) A novel centrosome-associated protein with affinity for microtubules. *J Cell Sci* 115 (Pt 17), 3389-3402
- Cullen, C.F. et al. (1999) mini spindles: A gene encoding a conserved microtubule-associated protein required for the integrity of the mitotic spindle in Drosophila. *J Cell Biol* 146 (5), 1005-1018
- Price, C.M. et al. (1984) NuMA protein is a human autoantigen. Arthritis Rheum 27 (7), 774-779
- Maekawa, T. and Kuriyama, R. (1993) Primary structure and microtubule-interacting domain of the SP-H antigen: a mitotic MAP located at the spindle pole and characterized as a homologous protein to NuMA. *J Cell Sci* 105 (Pt 2), 589-600
- Nakaseko, Y. et al. (1996) Dissection of fission yeast microtubule associating protein p93Dis1: regions implicated in regulated localization and microtubule interaction. *Genes Cells* 1 (7), 633-644
- Zhou, R.P. et al. (1991) In vitro and in vivo characterization of pp39mos association with tubulin. *Cell Growth Differ* 2 (5), 257-265
- Wang, P.J. and Huffaker, T.C. (1997) Stu2p: A microtubule-binding protein that is an essential component of the yeast spindle pole body. *J Cell Biol* 139 (5), 1271-1280
- Cross, D. et al. (1996) Tau-like proteins associated with centrosomes in cultured cells. *Exp Cell Res* 229 (2), 378-387
- Wittmann, T. et al. (1998) Localization of the kinesin-like protein Xklp2 to spindle poles requires a leucine zipper, a microtubule-associated protein, and dynein. *J Cell Biol* 143 (3), 673-685
- Wittmann, T. et al. (2000) TPX2, A novel xenopus MAP involved in spindle pole organization. *J Cell Biol* 149 (7), 1405-1418
- Maxwell, C.A. et al. (2003) RHAMM is a centrosomal protein that interacts with dynein and maintains spindle pole stability. *Mol Biol Cell* 14 (6), 2262-2276
- Errico, A. et al. (2004) Spastin interacts with the centrosomal protein NA14, and is enriched in the spindle pole, the midbody and the distal axon. *Hum Mol Genet* 13 (18), 2121-2132
- Clark, S.W. and Meyer, D.I. (1992) Centractin is an actin homologue associated with the centrosome. *Nature* 359 (6392), 246-250
- Purohit, A. et al. (1999) Direct interaction of pericentrin with cytoplasmic dynein light intermediate chain contributes to mitotic spindle organization. *J Cell Biol* 147 (3), 481-492
- Blangy, A. et al. (1995) Phosphorylation by p34cdc2 regulates spindle association of human Eg5, a kinesin-related motor essential for bipolar spindle formation in vivo. *Cell* 83 (7), 1159-1169
- Vashishtha, M. et al. (1996) The kinesin-homologous protein encoded by the Chlamydomonas FLA10 gene is associated with basal bodies and centrioles. *J Cell Sci* 109 (Pt 3), 541-549
- Kuriyama, R. et al. (1995) Characterization of a minus end-directed kinesin-like motor protein from cultured mammalian cells. *J Cell Biol* 129 (4), 1049-1059
- Page, B.D. et al. (1994) Localization of the Kar3 kinesin heavy chain-related protein requires the Cik1 interacting protein. *J Cell Biol* 124 (4), 507-519
- 249 Neighbors, B.W. et al. (1988) Localization of kinesin in cultured cells. J Cell Biol 106 (4), 1193-1204
- Boleti, H. et al. (1996) Xklp2, a novel Xenopus centrosomal kinesin-like protein required for centrosome separation during mitosis. *Cell* 84 (1), 49-59
- Tanaka, T. et al. (2004) Lis1 and doublecortin function with dynein to mediate coupling of the nucleus to the centrosome in neuronal migration. *J Cell Biol* 165 (5), 709-721
- Espreafico, E.M. et al. (1998) Localization of myosin-V in the centrosome. *Proc Natl Acad Sci U S A* 95 (15), 8636-8641
- Endow, S.A. et al. (1994) Mutants of the Drosophila ncd microtubule motor protein cause centrosomal and spindle pole defects in mitosis. *J Cell Sci* 107 (Pt 4), 859-867
- Yan, X. et al. (2003) Human Nudel and NudE as regulators of cytoplasmic dynein in poleward protein transport along the mitotic spindle. *Mol Cell Biol* 23 (4), 1239-1250
- Karki, S. et al. (1998) Characterization of the p22 subunit of dynactin reveals the localization of cytoplasmic dynein and dynactin to the midbody of dividing cells. *J Cell Biol* 142 (4), 1023-1034
- Quintyne, N.J. et al. (1999) Dynactin is required for microtubule anchoring at centrosomes. *J Cell Biol* 147 (2), 321-334
- Vancoillie, G. et al. (2000) Colocalization of dynactin subunits P150Glued and P50 with melanosomes in normal human melanocytes. *Pigment Cell Res* 13 (6), 449-457
- Adams, R.R. et al. (1998) pavarotti encodes a kinesin-like protein required to organize the central spindle and contractile ring for cytokinesis. *Genes Dev* 12 (10), 1483-1494

- Stirling, D.A. et al. (1994) Interaction with calmodulin is required for the function of Spc110p, an essential component of the yeast spindle pole body. *Embo J* 13 (18), 4329-4342
- Stemple, D.L. et al. (1988) Dynamics of a fluorescent calmodulin analog in the mammalian mitotic spindle at metaphase. *Cell Motil Cytoskeleton* 9 (3), 231-242
- 261 Lee, V.D. and Huang, B. (1993) Molecular cloning and centrosomal localization of human caltractin. *Proc Natl Acad Sci U S A* 90 (23), 11039-11043
- Huang, B. et al. (1988) Molecular cloning of cDNA for caltractin, a basal body-associated Ca2+-binding protein: homology in its protein sequence with calmodulin and the yeast CDC31 gene product. *J Cell Biol* 107 (1), 133-140
- Spang, A. et al. (1993) The calcium-binding protein cell division cycle 31 of Saccharomyces cerevisiae is a component of the half bridge of the spindle pole body. *J Cell Biol* 123 (2), 405-416
- Paoletti, A. et al. (1996) Most of centrin in animal cells is not centrosome-associated and centrosomal centrin is confined to the distal lumen of centrioles. *J Cell Sci* 109 (Pt 13), 3089-3102
- Errabolu, R. et al. (1994) Cloning of a cDNA encoding human centrin, an EF-hand protein of centrosomes and mitotic spindle poles. *J Cell Sci* 107 (Pt 1), 9-16
- Moudjou, M. et al. (1991) A human centrosomal protein is immunologically related to basal body-associated proteins from lower eucaryotes and is involved in the nucleation of microtubules. *J Cell Biol* 115 (1), 129-140
- Eng, K. et al. (1998) Rng2p, a protein required for cytokinesis in fission yeast, is a component of the actomyosin ring and the spindle pole body. *Curr Biol* 8 (11), 611-621
- Inaguma, Y. et al. (2001) AlphaB-crystallin phosphorylated at Ser-59 is localized in centrosomes and midbodies during mitosis. *Eur J Cell Biol* 80 (12), 741-748
- Yang, Z. et al. (1997) An unexpected localization of basonuclin in the centrosome, mitochondria, and acrosome of developing spermatids. *J Cell Biol* 137 (3), 657-669
- Kim, J.C. et al. (2004) The Bardet-Biedl protein BBS4 targets cargo to the pericentriolar region and is required for microtubule anchoring and cell cycle progression. *nature genetics* 36 (5), 462-470
- Trimbur, G.M. et al. (1999) Cloning, sequencing, and nucleolar targeting of the basal-body-binding nucleolar protein BN46/51. *J Cell Sci* 112 (Pt 8), 1159-1168
- Wang, Z. et al. (2004) Characterization of Ceap-11 and Ceap-16, two novel splicing-variant-proteins, associated with centrosome, microtubule aggregation and cell proliferation. *J Mol Biol* 343 (1), 71-82
- Berryman, M.A. and Goldenring, J.R. (2003) CLIC4 is enriched at cell-cell junctions and colocalizes with AKAP350 at the centrosome and midbody of cultured mammalian cells. *Cell Motil Cytoskeleton* 56 (3), 159-172
- Zhang, R. et al. (2004) Dynamic association of the mammalian insulator protein CTCF with centrosomes and the midbody. *Exp Cell Res* 294 (1), 86-93
- Quaroni, A. and Paul, E.C. (1999) Cytocentrin is a Ral-binding protein involved in the assembly and function of the mitotic apparatus. *J Cell Sci* 112 ( Pt 5), 707-718
- Miyoshi, K. et al. (2004) DISC1 localizes to the centrosome by binding to kendrin. *Biochem Biophys Res Commun* 317 (4), 1195-1199
- Hori, T. et al. (2003) Dynamic behavior of Nuf2-Hec1 complex that localizes to the centrosome and centromere and is essential for mitotic progression in vertebrate cells. *J Cell Sci* 116 (Pt 16), 3347-3362
- Rasmussen, T.P. et al. (2000) Dynamic relocalization of histone MacroH2A1 from centrosomes to inactive X chromosomes during X inactivation. *J Cell Biol* 150 (5), 1189-1198
- Rothwell, W.F. et al. (1999) The Drosophila centrosomal protein Nuf is required for recruiting Dah, a membrane associated protein, to furrows in the early embryo. *J Cell Sci* 112 ( Pt 17), 2885-2893
- Prasanth, S.G. et al. (2004) Human Orc2 localizes to centrosomes, centromeres and heterochromatin during chromosome inheritance. *Embo J* 23 (13), 2651-2663
- Vinot, S. et al. (2004) Two PAR6 proteins become asymmetrically localized during establishment of polarity in mouse oocytes. *Curr Biol* 14 (6), 520-525
- Regnard, C. et al. (2003) Characterisation of PGs1, a subunit of a protein complex co-purifying with tubulin polyglutamylase. *J Cell Sci* 116 (Pt 20), 4181-4190
- Lachmann, M. et al. (2004) PIBF (progesterone induced blocking factor) is overexpressed in highly proliferating cells and associated with the centrosome. *Int J Cancer* 112 (1), 51-60
- Li, J. et al. (1997) Alzheimer presenilins in the nuclear membrane, interphase kinetochores, and centrosomes suggest a role in chromosome segregation. *Cell* 90 (5), 917-927

- 285 Rieder, C.L. (1979) Ribonucleoprotein staining of centrioles and kinetochores in newt lung cell spindles. *J Cell Biol* 80 (1), 1-9
- Kirkham, M. et al. (2003) SAS-4 is a C. elegans centriolar protein that controls centrosome size. *Cell* 112 (4), 575-587
- Guzzo, R.M. et al. (2004) A novel isoform of sarcolemmal membrane-associated protein (SLMAP) is a component of the microtubule organizing centre. *J Cell Sci* 117 (Pt 11), 2271-2281
- Pelletier, L. et al. (2004) The Caenorhabditis elegans centrosomal protein SPD-2 is required for both pericentriolar material recruitment and centriole duplication. *Curr Biol* 14 (10), 863-873
- Goto, M. and Eddy, E.M. (2004) Speriolin is a novel spermatogenic cell-specific centrosomal protein associated with the seventh WD motif of Cdc20. *J Biol Chem* 279 (40), 42128-42138
- Haberman, Y. et al. (2003) Synaptotagmin IX, a possible linker between the perinuclear endocytic recycling compartment and the microtubules. *J Cell Sci* 116 (Pt 21), 4307-4318
- Osmani, A.H. et al. (2003) TINA interacts with the NIMA kinase in Aspergillus nidulans and negatively regulates astral microtubules during metaphase arrest. *Mol Biol Cell* 14 (8), 3169-3179
- Xie, W. et al. (1998) Cell cycle-dependent subcellular localization of the TSG101 protein and mitotic and nuclear abnormalities associated with TSG101 deficiency. *Proc Natl Acad Sci U S A* 95 (4), 1595-1600
- Manning, B.D. et al. (1999) Differential regulation of the Kar3p kinesin-related protein by two associated proteins, Cik1p and Vik1p. *J Cell Biol* 144 (6), 1219-1233
- Bailey, C.J. et al. (2003) Association of adenovirus with the microtubule organizing center. *J Virol* 77 (24), 13275-13287
- Alonso, C. et al. (2001) African swine fever virus protein p54 interacts with the microtubular motor complex through direct binding to light-chain dynein. *J Virol* 75 (20), 9819-9827
- Grieshaber, S.S. et al. (2003) Chlamydia trachomatis uses host cell dynein to traffic to the microtubuleorganizing center in a p50 dynamitin-independent process. *J Cell Sci* 116 (Pt 18), 3793-3802
- Petit, C. et al. (2003) Targeting of incoming retroviral Gag to the centrosome involves a direct interaction with the dynein light chain 8. *J Cell Sci* 116 (Pt 16), 3433-3442
- **298** Lacaille, V.G. and Androlewicz, M.J. (2000) Targeting of HIV-1 Nef to the centrosome: implications for antigen processing. *Traffic* 1 (11), 884-891
- Nozawa, N. et al. (2004) Formation of aggresome-like structures in herpes simplex virus type 2-infected cells and a potential role in virus assembly. *Exp Cell Res* 299 (2), 486-497
- 300 Kim, S.W. et al. (2001) Microtubule- and dynein-mediated movement of Orientia tsutsugamushi to the microtubule organizing center. *Infect Immun* 69 (1), 494-500
- Kasamatsu, H. and Nehorayan, A. (1979) Intracellular localization of viral polypeptides during simian virus 40 infection. *J Virol* 32 (2), 648-660
- Ploubidou, A. et al. (2000) Vaccinia virus infection disrupts microtubule organization and centrosome function. *Embo J* 19 (15), 3932-3944
- 303 Kose, H. and Karr, T.L. (1995) Organization of Wolbachia pipientis in the Drosophila fertilized egg and embryo revealed by an anti-Wolbachia monoclonal antibody. *Mech Dev* 51 (2-3), 275-288