

#### 4 Literaturverzeichnis

- Adam, E.J. and Adam, S.A. (1994) Identification of cytosolic factors required for nuclear location sequence-mediated binding to the nuclear envelope. *J Cell Biol*, **125**, 547-555.
- Andrade, M.A., Petosa, C., O'Donoghue, S.I., Muller, C.W. and Bork, P. (2001) Comparison of ARM and HEAT protein repeats. *J Mol Biol*, **309**, 1-18.
- Aouida, M., Page, N., Leduc, A., Peter, M. and Ramotar, D. (2004) A genome-wide screen in *Saccharomyces cerevisiae* reveals altered transport as a mechanism of resistance to the anticancer drug bleomycin. *Cancer Res*, **64**, 1102-1109.
- Bajorek, M., Finley, D. and Glickman, M.H. (2003) Proteasome disassembly and downregulation is correlated with viability during stationary phase. *Curr Biol*, **13**, 1140-1144.
- Baumeister, W., Walz, J., Zuhl, F. and Seemuller, E. (1998) The proteasome: paradigm of a self-compartmentalizing protease. *Cell*, **92**, 367-380.
- B Blobel, G. (1985) Gene gating: a hypothesis. *Proc Natl Acad Sci U S A*, **82**, 8527-8529.
- Braun, B.C., Glickman, M., Kraft, R., Dahlmann, B., Kloetzel, P.M., Finley, D. and Schmidt, M. (1999) The base of the proteasome regulatory particle exhibits chaperone-like activity. *Nat Cell Biol*, **1**, 221-226.
- Casolari, J.M., Brown, C.R., Komili, S., West, J., Hieronymus, H. and Silver, P.A. (2004) Genome-wide localization of the nuclear transport machinery couples transcriptional status and nuclear organization. *Cell*, **117**, 427-439.
- Chen, P. and Hochstrasser, M. (1996) Autocatalytic subunit processing couples active site formation in the 20S proteasome to completion of assembly. *Cell*, **86**, 961-972.
- Chook, Y.M. and Blobel, G. (1999) Structure of the nuclear transport complex karyopherin-beta2-Ran x GppNHp. *Nature*, **399**, 230-237.
- Chook, Y.M. and Blobel, G. (2001) Karyopherins and nuclear import. *Curr Opin Struct Biol*, **11**, 703-715.
- Cingolani, G., Petosa, C., Weis, K. and Muller, C.W. (1999) Structure of importin-beta bound to the IBB domain of importin-alpha. *Nature*, **399**, 221-229.
- Conti, E., Uy, M., Leighton, L., Blobel, G. and Kuriyan, J. (1998) Crystallographic analysis of the recognition of a nuclear localization signal by the nuclear import factor karyopherin alpha. *Cell*, **94**, 193-204.
- Ditzel, L., Huber, R., Mann, K., Heinemeyer, W., Wolf, D.H. and Groll, M. (1998) Conformational constraints for protein self-cleavage in the proteasome. *J Mol Biol*, **279**, 1187-1191.
- Enenkel, C. (2003) Wer reguliert das 26S Proteasom, ein Schlüsselenzym regulierter Proteolyse? *Bioforum*, **7-8**, 448-449.
- Enenkel, C., Blobel, G. and Rexach, M. (1995) Identification of a yeast karyopherin heterodimer that targets import substrate to mammalian nuclear pore complexes. *J Biol Chem*, **270**, 16499-16502.
- Enenkel, C., Lehmann, A. and Kloetzel, P.M. (1998) Subcellular distribution of

- proteasomes implicates a major location of protein degradation in the nuclear envelope-ER network in yeast. *Embo J*, **17**, 6144-6154.
- Enenkel, C., Lehmann, A. and Kloetzel, P.M. (1999) GFP-labelling of 26S proteasomes in living yeast: insight into proteasomal functions at the nuclear envelope/rough ER. *Mol Biol Rep*, **26**, 131-135.
- Enenkel, C., Schulke, N. and Blobel, G. (1996) Expression in yeast of binding regions of karyopherins alpha and beta inhibits nuclear import and cell growth. *Proc Natl Acad Sci U S A*, **93**, 12986-12991.
- Febres, D.E., Pramanik, A., Caton, M., Doherty, K., McKoy, J., Garcia, E., Alejo, W. and Moore, C.W. (2001) The novel BLM3 gene encodes a protein that protects against lethal effects of oxidative damage. *Cell Mol Biol (Noisy-le-grand)*, **47**, 1149-1162.
- Fehlker, M., Wendler, P., Lehmann, A. and Enenkel, C. (2003) Blm3 is part of nascent proteasomes and is involved in a late stage of nuclear proteasome assembly. *EMBO Rep*, **4**, 959-963.
- Fontes, M.R., Teh, T., Jans, D., Brinkworth, R.I. and Kobe, B. (2003) Structural basis for the specificity of bipartite nuclear localization sequence binding by importin-alpha. *J Biol Chem*, **278**, 27981-27987.
- Frentzel, S., Pesold-Hurt, B., Seelig, A. and Kloetzel, P.M. (1994) 20 S proteasomes are assembled via distinct precursor complexes. Processing of LMP2 and LMP7 proproteins takes place in 13-16 S preproteasome complexes. *J Mol Biol*, **236**, 975-981.
- Fried, H. and Kutay, U. (2003) Nucleocytoplasmic transport: taking an inventory. *Cell Mol Life Sci*, **60**, 1659-1688.
- Gavin, A.C., Bosche, M., Krause, R., Grandi, P., Marzioch, M., Bauer, A., Schultz, J., Rick, J.M., Michon, A.M., Cruciat, C.M., Remor, M., Hofert, C., Schelder, M., Brajenovic, M., Ruffner, H., Merino, A., Klein, K., Hudak, M., Dickson, D., Rudi, T., Gnau, V., Bauch, A., Bastuck, S., Huhse, B., Leutwein, C., Heurtier, M.A., Copley, R.R., Edelmann, A., Querfurth, E., Rybin, V., Drewes, G., Raida, M., Bouwmeester, T., Bork, P., Seraphin, B., Kuster, B., Neubauer, G. and Superti-Furga, G. (2002) Functional organization of the yeast proteome by systematic analysis of protein complexes. *Nature*, **415**, 141-147.
- Ghaemmaghami, S., Huh, W.K., Bower, K., Howson, R.W., Belle, A., Dephoure, N., O'Shea, E.K. and Weissman, J.S. (2003) Global analysis of protein expression in yeast. *Nature*, **425**, 737-741.
- Gillette, T.G., Huang, W., Russell, S.J., Reed, S.H., Johnston, S.A. and Friedberg, E.C. (2001) The 19S complex of the proteasome regulates nucleotide excision repair in yeast. *Genes Dev*, **15**, 1528-1539.
- Glickman, M.H., Rubin, D.M., Fried, V.A. and Finley, D. (1998) The regulatory particle of the *Saccharomyces cerevisiae* proteasome. *Mol Cell Biol*, **18**, 3149-3162.
- Gonzalez, F., Delahodde, A., Kodadek, T. and Johnston, S.A. (2002) Recruitment of a 19S proteasome subcomplex to an activated promoter. *Science*, **296**, 548-550.

- Gorbea, C., Goellner, G.M., Teter, K., Holmes, R.K. and Rechsteiner, M. (2004) Characterization of mammalian Ecm29, a 26 S proteasome-associated protein that localizes to the nucleus and membrane vesicles. *J Biol Chem*, **279**, 54849-54861.
- Gorlich, D., Dabrowski, M., Bischoff, F.R., Kutay, U., Bork, P., Hartmann, E., Prehn, S. and Izaurrealde, E. (1997) A novel class of RanGTP binding proteins. *J Cell Biol*, **138**, 65-80.
- Gorlich, D., Henklein, P., Laskey, R.A. and Hartmann, E. (1996) A 41 amino acid motif in importin-alpha confers binding to importin-beta and hence transit into the nucleus. *Embo J*, **15**, 1810-1817.
- Gorlich, D., Kostka, S., Kraft, R., Dingwall, C., Laskey, R.A., Hartmann, E. and Prehn, S. (1995a) Two different subunits of importin cooperate to recognize nuclear localization signals and bind them to the nuclear envelope. *Curr Biol*, **5**, 383-392.
- Gorlich, D. and Kutay, U. (1999) Transport between the cell nucleus and the cytoplasm. *Annu Rev Cell Dev Biol*, **15**, 607-660.
- Gorlich, D., Prehn, S., Laskey, R.A. and Hartmann, E. (1994) Isolation of a protein that is essential for the first step of nuclear protein import. *Cell*, **79**, 767-778.
- Gorlich, D., Vogel, F., Mills, A.D., Hartmann, E. and Laskey, R.A. (1995b) Distinct functions for the two importin subunits in nuclear protein import. *Nature*, **377**, 246-248.
- Groll, M., Bajorek, M., Kohler, A., Moroder, L., Rubin, D.M., Huber, R., Glickman, M.H. and Finley, D. (2000) A gated channel into the proteasome core particle. *Nat Struct Biol*, **7**, 1062-1067.
- Groll, M., Bochtler, M., Brandstetter, H., Clausen, T. and Huber, R. (2005) Molecular Machines for Protein Degradation. *Chembiochem*, **6**, 222-256.
- Groll, M., Brandstetter, H., Bartunik, H., Bourenkov, G. and Huber, R. (2003) Investigations on the maturation and regulation of archaeabacterial proteasomes. *J Mol Biol*, **327**, 75-83.
- Groll, M., Ditzel, L., Lowe, J., Stock, D., Bochtler, M., Bartunik, H.D. and Huber, R. (1997) Structure of 20S proteasome from yeast at 2.4 Å resolution. *Nature*, **386**, 463-471.
- Groll, M., Heinemeyer, W., Jager, S., Ullrich, T., Bochtler, M., Wolf, D.H. and Huber, R. (1999) The catalytic sites of 20S proteasomes and their role in subunit maturation: a mutational and crystallographic study. *Proc Natl Acad Sci U S A*, **96**, 10976-10983.
- Gueckel, R., Enenkel, C., Wolf, D.H. and Hilt, W. (1998) Mutations in the yeast proteasome beta-type subunit Pre3 uncover position-dependent effects on proteasomal peptidase activity and in vivo function. *J Biol Chem*, **273**, 19443-19452.
- Harris, J.R. (1968) Release of a macromolecular protein component from human erythrocyte ghosts. *Biochim Biophys Acta*, **150**, 534-537.
- Hartmann-Petersen, R. and Gordon, C. (2004) Proteins interacting with the 26S proteasome. *Cell Mol Life Sci*, **61**, 1589-1595.
- Heinemeyer, W., Fischer, M., Krimmer, T., Stachon, U. and Wolf, D.H. (1997) The

- active sites of the eukaryotic 20 S proteasome and their involvement in subunit precursor processing. *J Biol Chem*, **272**, 25200-25209.
- Heinemeyer, W., Gruhler, A., Mohrle, V., Mahe, Y. and Wolf, D.H. (1993) PRE2, highly homologous to the human major histocompatibility complex-linked RING10 gene, codes for a yeast proteasome subunit necessary for chymotryptic activity and degradation of ubiquitinated proteins. *J Biol Chem*, **268**, 5115-5120.
- Heinemeyer, W., Kleinschmidt, J.A., Saidowsky, J., Escher, C. and Wolf, D.H. (1991) Proteinase yscE, the yeast proteasome/multicatalytic-multifunctional proteinase: mutants unravel its function in stress induced proteolysis and uncover its necessity for cell survival. *Embo J*, **10**, 555-562.
- Heinemeyer, W., Ramos, P.C. and Dohmen, R.J. (2004) The ultimate nanoscale mincer: assembly, structure and active sites of the 20S proteasome core. *Cell Mol Life Sci*, **61**, 1562-1578.
- Hendil, K.B., Hartmann-Petersen, R. and Tanaka, K. (2002) 26 S proteasomes function as stable entities. *J Mol Biol*, **315**, 627-636.
- Hershko, A. and Ciechanover, A. (1998) The ubiquitin system. *Annu Rev Biochem*, **67**, 425-479.
- Hilt, W., Ennenkel, C., Gruhler, A., Singer, T. and Wolf, D.H. (1993) The PRE4 gene codes for a subunit of the yeast proteasome necessary for peptidylglutamyl-peptide-hydrolyzing activity. Mutations link the proteasome to stress- and ubiquitin-dependent proteolysis. *J Biol Chem*, **268**, 3479-3486.
- Ho, Y., Gruhler, A., Heilbut, A., Bader, G.D., Moore, L., Adams, S.L., Millar, A., Taylor, P., Bennett, K., Boutilier, K., Yang, L., Wolting, C., Donaldson, I., Schandorff, S., Shewnarane, J., Vo, M., Taggart, J., Goudreault, M., Muskat, B., Alfarano, C., Dewar, D., Lin, Z., Michalickova, K., Willems, A.R., Sassi, H., Nielsen, P.A., Rasmussen, K.J., Andersen, J.R., Johansen, L.E., Hansen, L.H., Jespersen, H., Podtelejnikov, A., Nielsen, E., Crawford, J., Poulsen, V., Sorensen, B.D., Matthiesen, J., Hendrickson, R.C., Gleeson, F., Pawson, T., Moran, M.F., Durocher, D., Mann, M., Hogue, C.W., Figeys, D. and Tyers, M. (2002) Systematic identification of protein complexes in *Saccharomyces cerevisiae* by mass spectrometry. *Nature*, **415**, 180-183.
- Holmberg, C.I., Staniszewski, K.E., Mensah, K.N., Matouschek, A. and Morimoto, R.I. (2004) Inefficient degradation of truncated polyglutamine proteins by the proteasome. *Embo J*, **23**, 4307-4318.
- Holzhutter, H.G., Frommel, C. and Kloetzel, P.M. (1999) A theoretical approach towards the identification of cleavage-determining amino acid motifs of the 20 S proteasome. *J Mol Biol*, **286**, 1251-1265.
- Huh, W.K., Falvo, J.V., Gerke, L.C., Carroll, A.S., Howson, R.W., Weissman, J.S. and O'Shea, E.K. (2003) Global analysis of protein localization in budding yeast. *Nature*, **425**, 686-691.
- Jager, S., Groll, M., Huber, R., Wolf, D.H. and Heinemeyer, W. (1999) Proteasome beta-type subunits: unequal roles of propeptides in core particle maturation and a hierarchy of active site function. *J Mol Biol*, **291**, 997-1013.
- Jelinsky, S.A., Estep, P., Church, G.M. and Samson, L.D. (2000) Regulatory networks revealed by transcriptional profiling of damaged *Saccharomyces*

- cerevisiae cells: Rpn4 links base excision repair with proteasomes. *Mol Cell Biol*, **20**, 8157-8167.
- Ju, D., Wang, L., Mao, X. and Xie, Y. (2004) Homeostatic regulation of the proteasome via an Rpn4-dependent feedback circuit. *Biochem Biophys Res Commun*, **321**, 51-57.
- Kajava, A.V., Gorbea, C., Ortega, J., Rechsteiner, M. and Steven, A.C. (2004) New HEAT-like repeat motifs in proteins regulating proteasome structure and function. *J Struct Biol*, **146**, 425-430.
- Kloetzel, P.M. (2004) Generation of major histocompatibility complex class I antigens: functional interplay between proteasomes and TPPII. *Nat Immunol*, **5**, 661-669.
- Knecht, E. and Rivett, J. (2000) *Intracellular Localization of Proteasomes*. Eurekah.com / Landes Bioscience, Georgetown, Texas, USA.
- Knuehl, C., Seelig, A., Brecht, B., Henklein, P. and Kloetzel, P.M. (1996) Functional analysis of eukaryotic 20S proteasome nuclear localization signal. *Exp Cell Res*, **225**, 67-74.
- Kohler, A., Cascio, P., Leggett, D.S., Woo, K.M., Goldberg, A.L. and Finley, D. (2001) The axial channel of the proteasome core particle is gated by the Rpt2 ATPase and controls both substrate entry and product release. *Mol Cell*, **7**, 1143-1152.
- Kohler, M., Speck, C., Christiansen, M., Bischoff, F.R., Prehn, S., Haller, H., Gorlich, D. and Hartmann, E. (1999) Evidence for distinct substrate specificities of importin alpha family members in nuclear protein import. *Mol Cell Biol*, **19**, 7782-7791.
- Kostova, Z. and Wolf, D.H. (2003) For whom the bell tolls: protein quality control of the endoplasmic reticulum and the ubiquitin-proteasome connection. *Embo J*, **22**, 2309-2317.
- Krüger, E., Kloetzel, P.M. and Enenkel, C. (2001) 20S proteasome biogenesis. *Biochimie*, **83**, 289-293.
- Kutay, U., Izaurralde, E., Bischoff, F.R., Mattaj, I.W. and Gorlich, D. (1997) Dominant-negative mutants of importin-beta block multiple pathways of import and export through the nuclear pore complex. *Embo J*, **16**, 1153-1163.
- Lam, Y.A., Lawson, T.G., Velayutham, M., Zweier, J.L. and Pickart, C.M. (2002) A proteasomal ATPase subunit recognizes the polyubiquitin degradation signal. *Nature*, **416**, 763-767.
- Leggett, D.S., Hanna, J., Borodovsky, A., Crosas, B., Schmidt, M., Baker, R.T., Walz, T., Ploegh, H. and Finley, D. (2002) Multiple associated proteins regulate proteasome structure and function. *Mol Cell*, **10**, 495-507.
- Lehmann, A., Janek, K., Braun, B., Kloetzel, P.M. and Enenkel, C. (2002) 20 S proteasomes are imported as precursor complexes into the nucleus of yeast. *J Mol Biol*, **317**, 401-413.
- Lipford, J.R. and Deshaies, R.J. (2003) Diverse roles for ubiquitin-dependent proteolysis in transcriptional activation. *Nat Cell Biol*, **5**, 845-850.
- Liu, C.W., Corboy, M.J., DeMartino, G.N. and Thomas, P.J. (2003) Endoproteolytic activity of the proteasome. *Science*, **299**, 408-411.

- Loeb, J.D., Schlenstedt, G., Pellman, D., Kornitzer, D., Silver, P.A. and Fink, G.R. (1995) The yeast nuclear import receptor is required for mitosis. *Proc Natl Acad Sci U S A*, **92**, 7647-7651.
- Lommel, L., Ortolan, T., Chen, L., Madura, K. and Sweder, K.S. (2002) Proteolysis of a nucleotide excision repair protein by the 26 S proteasome. *Curr Genet*, **42**, 9-20.
- London, M.K., Keck, B.I., Ramos, P.C. and Dohmen, R.J. (2004) Regulatory mechanisms controlling biogenesis of ubiquitin and the proteasome. *FEBS Lett*, **567**, 259-264.
- Mannhaupt, G., Schnall, R., Karpov, V., Vetter, I. and Feldmann, H. (1999) Rpn4p acts as a transcription factor by binding to PACE, a nonamer box found upstream of 26S proteasomal and other genes in yeast. *FEBS Lett*, **450**, 27-34.
- Mayr, J., Wang, H.R., Nederlof, P. and Baumeister, W. (1999) The import pathway of human and Thermoplasma 20S proteasomes into HeLa cell nuclei is different from that of classical NLS-bearing proteins. *Biol Chem*, **380**, 1183-1192.
- McDonald, H.B. and Byers, B. (1997) A proteasome cap subunit required for spindle pole body duplication in yeast. *J Cell Biol*, **137**, 539-553.
- Moroianu, J., Blobel, G. and Radu, A. (1995) Previously identified protein of uncertain function is karyopherin alpha and together with karyopherin beta docks import substrate at nuclear pore complexes. *Proc Natl Acad Sci U S A*, **92**, 2008-2011.
- Moroianu, J., Blobel, G. and Radu, A. (1996) Nuclear protein import: Ran-GTP dissociates the karyopherin alphabeta heterodimer by displacing alpha from an overlapping binding site on beta. *Proc Natl Acad Sci U S A*, **93**, 7059-7062.
- Mullapudi, S., Pullan, L., Bishop, O.T., Khalil, H., Stoops, J.K., Beckmann, R., Kloetzel, P.M., Kruger, E. and Penczek, P.A. (2004) Rearrangement of the 16S precursor subunits is essential for the formation of the active 20S proteasome. *Biophys J*, **87**, 4098-4105.
- Muratani, M. and Tansey, W.P. (2003) How the ubiquitin-proteasome system controls transcription. *Nat Rev Mol Cell Biol*, **4**, 192-201.
- Nandi, D., Woodward, E., Ginsburg, D.B. and Monaco, J.J. (1997) Intermediates in the formation of mouse 20S proteasomes: implications for the assembly of precursor beta subunits. *Embo J*, **16**, 5363-5375.
- Nederlof, P.M., Wang, H.R. and Baumeister, W. (1995) Nuclear localization signals of human and Thermoplasma proteasomal alpha subunits are functional in vitro. *Proc Natl Acad Sci U S A*, **92**, 12060-12064.
- Nurse, P., Masui, Y. and Hartwell, L. (1998) Understanding the cell cycle. *Nat Med*, **4**, 1103-1106.
- Orlowski, M. and Wilk, S. (2000) Catalytic activities of the 20 S proteasome, a multicatalytic proteinase complex. *Arch Biochem Biophys*, **383**, 1-16.
- Ortega, J., Bernard Heymann, J., Kajava, A.V., Ustrell, V., Rechsteiner, M. and Steven, A.C. (2005) The Axial Channel of the 20S Proteasome Opens Upon

- Binding of the PA200 Activator. *J Mol Biol*, **346**, 1221-1227.
- Ortolan, T.G., Chen, L., Tongaonkar, P. and Madura, K. (2004) Rad23 stabilizes Rad4 from degradation by the Ub/proteasome pathway. *Nucleic Acids Res*, **32**, 6490-6500.
- Plempner, R.K., Bohmler, S., Bordallo, J., Sommer, T. and Wolf, D.H. (1997) Mutant analysis links the translocon and BiP to retrograde protein transport for ER degradation. *Nature*, **388**, 891-895.
- Podlaska, A., McIntyre, J., Skoneczna, A. and Sledziewska-Gojska, E. (2003) The link between 20S proteasome activity and post-replication DNA repair in *Saccharomyces cerevisiae*. *Mol Microbiol*, **49**, 1321-1332.
- Princiotta, M.F., Finzi, D., Qian, S.B., Gibbs, J., Schuchmann, S., Buttgereit, F., Bennink, J.R. and Yewdell, J.W. (2003) Quantitating protein synthesis, degradation, and endogenous antigen processing. *Immunity*, **18**, 343-354.
- Quensel, C., Friedrich, B., Sommer, T., Hartmann, E. and Kohler, M. (2004) In vivo analysis of importin alpha proteins reveals cellular proliferation inhibition and substrate specificity. *Mol Cell Biol*, **24**, 10246-10255.
- Ramos, P.C., Hockendorff, J., Johnson, E.S., Varshavsky, A. and Dohmen, R.J. (1998) Ump1p is required for proper maturation of the 20S proteasome and becomes its substrate upon completion of the assembly. *Cell*, **92**, 489-499.
- Ramos, P.C., Marques, A.J., London, M.K. and Dohmen, R.J. (2004) Role of C-terminal extensions of subunits beta2 and beta7 in assembly and activity of eukaryotic proteasomes. *J Biol Chem*, **279**, 14323-14330.
- Rape, M. and Jentsch, S. (2002) Taking a bite: proteasomal protein processing. *Nat Cell Biol*, **4**, E113-116.
- Rechsteiner, M. and Hill, C.P. (2005) Mobilizing the proteolytic machine: cell biological roles of proteasome activators and inhibitors. *Trends Cell Biol*, **15**, 27-33.
- Reits, E.A., Benham, A.M., Plougastel, B., Neefjes, J. and Trowsdale, J. (1997) Dynamics of proteasome distribution in living cells. *Embo J*, **16**, 6087-6094.
- Rexach, M. and Blobel, G. (1995) Protein import into nuclei: association and dissociation reactions involving transport substrate, transport factors, and nucleoporins. *Cell*, **83**, 683-692.
- Ribbeck, K. and Gorlich, D. (2001) Kinetic analysis of translocation through nuclear pore complexes. *Embo J*, **20**, 1320-1330.
- Robben, J., Hertveldt, K. and Volckaert, G. (2002) Revisiting the yeast chromosome VI DNA sequence reveals a correction merging YFL007w and YFL006w to a single ORF. *Yeast*, **19**, 699-702.
- Rout, M.P., Aitchison, J.D., Suprapto, A., Hjertaas, K., Zhao, Y. and Chait, B.T. (2000) The yeast nuclear pore complex: composition, architecture, and transport mechanism. *J Cell Biol*, **148**, 635-651.
- Russell, S.J., Steger, K.A. and Johnston, S.A. (1999) Subcellular localization, stoichiometry, and protein levels of 26 S proteasome subunits in yeast. *J Biol Chem*, **274**, 21943-21952.
- Scherrer, K. (1990) Prosomes, subcomplexes of untranslated mRNP. *Mol Biol Rep*, **14**, 1-9.

- Schmidt, M., Haas, W., Crosas, B., Santamaria, P.G., Gygi, S.P., Walz, T. and Finley, D. (2005) The HEAT repeat protein Blm10 regulates the yeast proteasome by capping the core particle. *Nat Struct Mol Biol.*
- Schmidt, M., Lupas, A.N. and Finley, D. (1999) Structure and mechanism of ATP-dependent proteases. *Curr Opin Chem Biol.*, **3**, 584-591.
- Schmidtke, G., Kraft, R., Kostka, S., Henklein, P., Frommel, C., Lowe, J., Huber, R., Kloetzel, P.M. and Schmidt, M. (1996) Analysis of mammalian 20S proteasome biogenesis: the maturation of beta-subunits is an ordered two-step mechanism involving autocatalysis. *Embo J.*, **15**, 6887-6898.
- Schmidtke, G., Schmidt, M. and Kloetzel, P.M. (1997) Maturation of mammalian 20S proteasome: purification and characterization of 13 S and 16 S proteasome precursor complexes. *J Mol Biol.*, **268**, 95-106.
- Sommer, T. and Wolf, D.H. (1997) Endoplasmic reticulum degradation: reverse protein flow of no return. *Faseb J.*, **11**, 1227-1233.
- Tabb, M.M., Tongaonkar, P., Vu, L. and Nomura, M. (2000) Evidence for separable functions of Srp1p, the yeast homolog of importin alpha (Karyopherin alpha): role for Srp1p and Sts1p in protein degradation. *Mol Cell Biol.*, **20**, 6062-6073.
- Tanaka, K., Yoshimura, T., Tamura, T., Fujiwara, T., Kumatori, A. and Ichihara, A. (1990) Possible mechanism of nuclear translocation of proteasomes. *FEBS Lett.*, **271**, 41-46.
- Tatebe, H., Goshima, G., Takeda, K., Nakagawa, T., Kinoshita, K. and Yanagida, M. (2001) Fission yeast living mitosis visualized by GFP-tagged gene products. *Micron*, **32**, 67-74.
- Turner, G.C. and Varshavsky, A. (2000) Detecting and measuring cotranslational protein degradation in vivo. *Science*, **289**, 2117-2120.
- Ulrich, H.D. (2002) Degradation or maintenance: actions of the ubiquitin system on eukaryotic chromatin. *Eukaryot Cell*, **1**, 1-10.
- Ustrell, V., Hoffman, L., Pratt, G. and Rechsteiner, M. (2002) PA200, a nuclear proteasome activator involved in DNA repair. *Embo J.*, **21**, 3516-3525.
- Verma, R., Aravind, L., Oania, R., McDonald, W.H., Yates, J.R., 3rd, Koonin, E.V. and Deshaies, R.J. (2002) Role of Rpn11 metalloprotease in deubiquitination and degradation by the 26S proteasome. *Science*, **298**, 611-615.
- Vetter, I.R., Arndt, A., Kutay, U., Gorlich, D. and Wittinghofer, A. (1999) Structural view of the Ran-Importin beta interaction at 2.3 Å resolution. *Cell*, **97**, 635-646.
- Wang, H.R., Kania, M., Baumeister, W. and Nederlof, P.M. (1997) Import of human and Thermoplasma 20S proteasomes into nuclei of HeLa cells requires functional NLS sequences. *Eur J Cell Biol.*, **73**, 105-113.
- Warner, J.R. (1999) The economics of ribosome biosynthesis in yeast. *Trends Biochem Sci.*, **24**, 437-440.
- Weis, K., Mattaj, I.W. and Lamond, A.I. (1995) Identification of hSRP1 alpha as a functional receptor for nuclear localization sequences. *Science*, **268**, 1049-1053.
- Wendler, P., Lehmann, A., Janek, K., Baumgart, S. and Enenkel, C. (2004) The

- bipartite nuclear localization sequence of Rpn2 is required for nuclear import of proteasomal base complexes via karyopherin alphabeta and proteasome functions. *J Biol Chem*, **279**, 37751-37762.
- Wilkinson, C.R., Wallace, M., Morphew, M., Perry, P., Allshire, R., Javerzat, J.P., McIntosh, J.R. and Gordon, C. (1998) Localization of the 26S proteasome during mitosis and meiosis in fission yeast. *Embo J*, **17**, 6465-6476.
- Wolf, D.H. (2000) *Proteasomes: A Historical Retrospective*. Eurekah.com / Landes Bioscience, Georgetown, Texas, USA.
- Wozniak, R.W., Rout, M.P. and Aitchison, J.D. (1998) Karyopherins and kissing cousins. *Trends Cell Biol*, **8**, 184-188.
- Xie, Y. and Varshavsky, A. (2001) RPN4 is a ligand, substrate, and transcriptional regulator of the 26S proteasome: a negative feedback circuit. *Proc Natl Acad Sci U S A*, **98**, 3056-3061.
- Yang, Y., Fruh, K., Ahn, K. and Peterson, P.A. (1995) In vivo assembly of the proteasomal complexes, implications for antigen processing. *J Biol Chem*, **270**, 27687-27694.
- Yano, R., Oakes, M.L., Tabb, M.M. and Nomura, M. (1994) Yeast Srp1p has homology to armadillo/plakoglobin/beta-catenin and participates in apparently multiple nuclear functions including the maintenance of the nucleolar structure. *Proc Natl Acad Sci U S A*, **91**, 6880-6884.
- Yao, T. and Cohen, R.E. (2002) A cryptic protease couples deubiquitination and degradation by the proteasome. *Nature*, **419**, 403-407.
- Yen, H.C., Espiritu, C. and Chang, E.C. (2003a) Rpn5 is a conserved proteasome subunit and required for proper proteasome localization and assembly. *J Biol Chem*, **278**, 30669-30676.
- Yen, H.C., Gordon, C. and Chang, E.C. (2003b) Schizosaccharomyces pombe Int6 and Ras homologs regulate cell division and mitotic fidelity via the proteasome. *Cell*, **112**, 207-217.
- Yong, J., Wan, L. and Dreyfuss, G. (2004) Why do cells need an assembly machine for RNA-protein complexes? *Trends Cell Biol*, **14**, 226-232.
- Zwickl, P., Grziwa, A., Puhler, G., Dahlmann, B., Lottspeich, F. and Baumeister, W. (1992) Primary structure of the Thermoplasma proteasome and its implications for the structure, function, and evolution of the multicatalytic proteinase. *Biochemistry*, **31**, 964-972.

## 6 Publikationsverzeichnis

1. **Enenkel, C.** and Wolf, D.H. (1993) *BLHI* codes for a yeast thiol aminopeptidase, the equivalent of mammalian bleomycin hydrolase. *J. Biol. Chem.* **268**, 7038-7043.
2. **Enenkel, C.**, Lehmann, H., Kipper, J., Gückel, R., Hilt, W., and Wolf, D.H. (1994) *PRE3*, highly homologous to the human major histocompatibility complex-linked LMP2 (RING12) gene, codes for a yeast proteasome subunit necessary for peptidylglutamyl-peptide-hydrolyzing activity. *FEBS Lett.* **341**, 193-196.
3. Hilt, W., **Enenkel, C.**, Gruhler, A., Singer, T., and Wolf, D.H. (1994) The *PRE4* gene codes for a subunit of the yeast proteasome necessary for peptidylglutamylpeptide-hydrolyzing activity. Mutations link the proteasome to stress- and ubiquitin-dependent proteolysis. *J. Biol. Chem.* **268**, 3479-3486.
4. **Enenkel, C.**, Blobel, G., and Rexach, M. (1995) Identification of a yeast karyopherin heterodimer that targets import substrate to mammalian nuclear pore complexes. *J. Biol. Chem.* **270**, 16499-16502.
5. **Enenkel, C.**, Schülke, N., and Blobel, G. (1996) Expression in yeast of binding regions of karyopherin  $\alpha$  and  $\beta$  inhibits nuclear import and cell growth. *Proc. Natl. Acad. Sci. U.S.A.* **93**, 12986-12991.
6. Gückel, R., **Enenkel, C.**, Wolf, D.H., and Hilt, W. (1998) Mutations in the yeast proteasome beta-type subunit Pre3 uncover position-dependent effects on proteasomal peptidase activity and *in vivo* function. *J. Biol. Chem.* **273**, 9443-9452.
7. **Enenkel, C.**, Lehmann, A., and Kloetzel, P.-M. (1998) Subcellular distribution of proteasomes implicates a major location of protein degradation in the nuclear envelope-ER network in yeast. *EMBO J.* **17**, 6144-6154.
8. **Enenkel, C.**, Lehmann, A., and Kloetzel, P.-M. (1999) GFP-labelling of 26S proteasomes in living yeast: insight into proteasomal functions at the nuclear envelope / rough ER. *Mol. Biol. Rep.* **26**, 131-135.

- 9.** Krüger, E., Kloetzel, P.-M., and **Enenkel, C.** (2001) 20S proteasome biogenesis. *Biochimie* **83**, 289-293.
- 10.** Lehmann, A., Janek, K., Braun, B., Kloetzel, P.-M., and **Enenkel, C.** (2002) 20S proteasomes are imported as precursor complexes into the nucleus of yeast. *J. Mol. Biol.* **317**, 401-413.
- 11.** Fehlker, M., Wendler, P., Lehmann, A., and **Enenkel, C.** (2003) Blm3 is part of nascent proteasomes and is involved in a late stage of nuclear proteasome assembly. *EMBO rep.* **4**, 559-563.
- 12.** Wendler, P., Lehmann, A., Janek, K., Baumgart, S., and **Enenkel, C.** (2004) The bipartite nuclear localisation sequence of Rpn2 is required for nuclear import of proteasomal base complexes via karyopherin  $\alpha\beta$  and proteasome functions. *J. Biol. Chem.* **279**, 37751-37762.

### Übersichtsarbeiten:

- 1. Enenkel, C.** (2003) Wer kontrolliert das 26S Proteasom, ein Schlüsselenzym regulierter Proteolyse? *Bioforum* **7-8**, 448-449.
- 2. Enenkel, C.** (2005) Yeast Proteasome Structure and Biogenesis. Im Druck für Lehrbuch “Ubiquitin and the Proteasome in Neurodegeneration” (Eds. L. Stefanis and J. Keller, Kluwer Publisher).