

REFERENCES

- Alami, M., Luke, I., Deitermann, S., Eisner, G., Koch, H.G., Brunner, J., and Muller, M. (2003) Differential interactions between a twin-arginine signal peptide and its translocase in *Escherichia coli*. *Mol Cell* 12: 937-946.
- Allen, S.C., Barrett, C.M., Ray, N., and Robinson, C. (2002) Essential cytoplasmic domains in the *Escherichia coli* TatC protein. *J Biol Chem* 277: 10362-10366.
- Baneyx, F., and Mujacic, M. (2004) Recombinant protein folding and misfolding in *Escherichia coli*. *Nat Biotechnol* 22: 1399-1408.
- Barbas, C.F., 3rd, Kang, A.S., Lerner, R.A., and Benkovic, S.J. (1991) Assembly of combinatorial antibody libraries on phage surfaces: the gene III site. *Proc Natl Acad Sci U S A* 88: 7978-7982.
- Bardwell, J.C., McGovern, K., and Beckwith, J. (1991) Identification of a protein required for disulfide bond formation *in vivo*. *Cell* 67: 581-589.
- Bass, S., Greene, R., and Wells, J.A. (1990) Hormone phage: an enrichment method for variant proteins with altered binding properties. *Proteins* 8: 309-314.
- Berks, B.C. (1996) A common export pathway for proteins binding complex redox cofactors? *Mol Microbiol* 22: 393-404.
- Berks, B.C., Sargent, F., and Palmer, T. (2000) The Tat protein export pathway. *Mol Microbiol* 35: 260-274.
- Biswas, C., Zhang, Y., DeCastro, R., Guo, H., Nakamura, T., Kataoka, H., and Nabeshima, K. (1995) The human tumor cell-derived collagenase stimulatory

factor (renamed EMMPRIN) is a member of the immunoglobulin superfamily. *Cancer Res* 55: 434-439.

Bitto, E., and McKay, D.B. (2002) Crystallographic structure of SurA, a molecular chaperone that facilitates folding of outer membrane porins. *Structure (Camb)* 10: 1489-1498.

Bitto, E., and McKay, D.B. (2003) The periplasmic molecular chaperone protein SurA binds a peptide motif that is characteristic of integral outer membrane proteins. *J Biol Chem* 278: 49316-49322.

Blaudeck, N., Sprenger, G.A., Freudl, R., and Wiegert, T. (2001) Specificity of signal peptide recognition in tat-dependent bacterial protein translocation. *J Bacteriol* 183: 604-610.

Blaudeck, N., Kreutzenbeck, P., Freudl, R., and Sprenger, G.A. (2003) Genetic analysis of pathway specificity during posttranslational protein translocation across the *Escherichia coli* plasma membrane. *J Bacteriol* 185: 2811-2819.

Bolhuis, A., Mathers, J.E., Thomas, J.D., Barrett, C.M., and Robinson, C. (2001) TatB and TatC form a functional and structural unit of the twin-arginine translocase from *Escherichia coli*. *J Biol Chem* 276: 20213-20219.

Bordador, L.C., Li, X., Toole, B., Chen, B., Regezi, J., Zardi, L., Hu, Y., and Ramos, D.M. (2000) Expression of emmprin by oral squamous cell carcinoma. *Int J Cancer* 85: 347-352.

Bothmann, H., and Pluckthun, A. (1998) Selection for a periplasmic factor improving phage display and functional periplasmic expression. *Nat Biotechnol* 16: 376-380.

- Bruser, T., Deutzmann, R., and Dahl, C. (1998) Evidence against the double-arginine motif as the only determinant for protein translocation by a novel Sec-independent pathway in *Escherichia coli*. *FEMS Microbiol Lett* 164: 329-336.
- Bruser, T., and Sanders, C. (2003) An alternative model of the twin arginine translocation system. *Microbiol Res* 158: 7-17.
- Buchanan, G., Leeuw, E., Stanley, N.R., Wexler, M., Berks, B.C., Sargent, F., and Palmer, T. (2002) Functional complexity of the twin-arginine translocase TatC component revealed by site-directed mutagenesis. *Mol Microbiol* 43: 1457-1470.
- Bukau, B. (1993) Regulation of the *Escherichia coli* heat-shock response. *Mol Microbiol* 9: 671-680.
- Bukau, B., and Horwich, A.L. (1998) The Hsp70 and Hsp60 chaperone machines. *Cell* 92: 351-366.
- Caudroy, S., Polette, M., Tournier, J.M., Burlet, H., Toole, B., Zucker, S., and Birembaut, P. (1999) Expression of the extracellular matrix metalloproteinase inducer (EMMPRIN) and the matrix metalloproteinase-2 in bronchopulmonary and breast lesions. *J Histochem Cytochem* 47: 1575-1580.
- Caudroy, S., Polette, M., Nawrocki-Raby, B., Cao, J., Toole, B.P., Zucker, S., and Birembaut, P. (2002) EMMPRIN-mediated MMP regulation in tumor and endothelial cells. *Clin Exp Metastasis* 19: 697-702.
- Cesareni, G. (1992) Peptide display on filamentous phage capsids. A new powerful tool to study protein-ligand interaction. *FEBS Lett* 307: 66-70.
- Chaddock, A.M., Mant, A., Karnauchov, I., Brink, S., Herrmann, R.G., Klosgen, R.B., and Robinson, C. (1995) A new type of signal peptide: central role of a

- twin-arginine motif in transfer signals for the delta pH-dependent thylakoidal protein translocase. *Embo J* 14: 2715-2722.
- Chappel, J.A., He, M., and Kang, A.S. (1998) Modulation of antibody display on M13 filamentous phage. *J Immunol Methods* 221: 25-34.
- Click, E.M., and Webster, R.E. (1998) The TolQRA proteins are required for membrane insertion of the major capsid protein of the filamentous phage f1 during infection. *J Bacteriol* 180: 1723-1728.
- Cristobal, S., de Gier, J.W., Nielsen, H., and von Heijne, G. (1999) Competition between Sec- and TAT-dependent protein translocation in *Escherichia coli*. *Embo J* 18: 2982-2990.
- Dalberg, K., Eriksson, E., Enberg, U., Kjellman, M., and Backdahl, M. (2000) Gelatinase A, membrane type 1 matrix metalloproteinase, and extracellular matrix metalloproteinase inducer mRNA expression: correlation with invasive growth of breast cancer. *World J Surg* 24: 334-340.
- Danese, P.N., and Silhavy, T.J. (1997) The sigma(E) and the Cpx signal transduction systems control the synthesis of periplasmic protein-folding enzymes in *Escherichia coli*. *Genes Dev* 11: 1183-1193.
- Danese, P.N., and Silhavy, T.J. (1998) Targeting and assembly of periplasmic and outer-membrane proteins in *Escherichia coli*. *Annu Rev Genet* 32: 59-94.
- Darby, N.J., and Creighton, T.E. (1995) Catalytic mechanism of DsbA and its comparison with that of protein disulfide isomerase. *Biochemistry* 34: 3576-3587.
- de Keyzer, J., van der Does, C., and Driessen, A.J. (2003) The bacterial translocase: a dynamic protein channel complex. *Cell Mol Life Sci* 60: 2034-2052.

- De Las Penas, A., Connolly, L., and Gross, C.A. (1997) The sigmaE-mediated response to extracytoplasmic stress in *Escherichia coli* is transduced by RseA and RseB, two negative regulators of sigmaE. *Mol Microbiol* 24: 373-385.
- de Leeuw, E., Granjon, T., Porcelli, I., Alami, M., Carr, S.B., Muller, M., Sargent, F., Palmer, T., and Berks, B.C. (2002) Oligomeric properties and signal peptide binding by *Escherichia coli* Tat protein transport complexes. *J Mol Biol* 322: 1135-1146.
- DeCastro, R., Zhang, Y., Guo, H., Kataoka, H., Gordon, M.K., Toole, B., and Biswas, G. (1996) Human keratinocytes express EMMPRIN, an extracellular matrix metalloproteinase inducer. *J Invest Dermatol* 106: 1260-1265.
- DeLisa, M.P., Lee, P., Palmer, T., and Georgiou, G. (2004) Phage shock protein PspA of *Escherichia coli* relieves saturation of protein export via the Tat pathway. *J Bacteriol* 186: 366-373.
- Deng, L.W., Malik, P., and Perham, R.N. (1999) Interaction of the globular domains of pIII protein of filamentous bacteriophage fd with the F-pilus of *Escherichia coli*. *Virology* 253: 271-277.
- Duong, F., and Wickner, W. (1997) The SecDFyajC domain of preprotein translocase controls preprotein movement by regulating SecA membrane cycling. *Embo J* 16: 4871-4879.
- Endemann, H., and Model, P. (1995) Location of filamentous phage minor coat proteins in phage and in infected cells. *J Mol Biol* 250: 496-506.
- Erickson, J.W., and Gross, C.A. (1989) Identification of the sigma E subunit of *Escherichia coli* RNA polymerase: a second alternate sigma factor involved in high-temperature gene expression. *Genes Dev* 3: 1462-1471.

- Fadool, J.M., and Linser, P.J. (1993) 5A11 antigen is a cell recognition molecule which is involved in neuronal-glia interactions in avian neural retina. *Dev Dyn* 196: 252-262.
- Felzmann, T., Gadd, S., Majdic, O., Maurer, D., Petera, P., Smolen, J. and Knapp, W. (1991) Analysis of function-associated receptor molecules on peripheral blood and synovial fluid granulocytes from patients with rheumatoid and reactive arthritis. *Journal of Clinical Immunology*; 11: 205-212.
- Fossum, S., Mallett, S., and Barclay, A.N. (1991) The MRC OX-47 antigen is a member of the immunoglobulin superfamily with an unusual transmembrane sequence. *Eur J Immunol* 21: 671-679.
- Frech, C., Wunderlich, M., Glockshuber, R., and Schmid, F.X. (1996) Preferential binding of an unfolded protein to DsbA. *Embo J* 15: 392-398.
- Fulford, W., and Model, P. (1984) Gene X of bacteriophage f1 is required for phage DNA synthesis. Mutagenesis of in-frame overlapping genes. *J Mol Biol* 178: 137-153.
- Gamer, J., Multhaup, G., Tomoyasu, T., McCarty, J.S., Rudiger, S., Schonfeld, H.J., Schirra, C., Bujard, H., and Bukau, B. (1996) A cycle of binding and release of the DnaK, DnaJ and GrpE chaperones regulates activity of the *Escherichia coli* heat shock transcription factor sigma32. *Embo J* 15: 607-617.
- Gao, C., Mao, S., Lo, C.H., Wirsching, P., Lerner, R.A., and Janda, K.D. (1999) Making artificial antibodies: a format for phage display of combinatorial heterodimeric arrays. *Proc Natl Acad Sci U S A* 96: 6025-6030.

- Goloubinoff, P., Mogk, A., Zvi, A.P., Tomoyasu, T., and Bukau, B. (1999) Sequential mechanism of solubilization and refolding of stable protein aggregates by a bichaperone network. *Proc Natl Acad Sci U S A* 96: 13732-13737.
- Graf, P.C., and Jakob, U. (2002) Redox-regulated molecular chaperones. *Cell Mol Life Sci* 59: 1624-1631.
- Green, N.M. (1991) Biological membranes. The semiotics of charge. *Nature* 351: 349-350.
- Greenwood, J., Hunter, G.J., and Perham, R.N. (1991) Regulation of filamentous bacteriophage length by modification of electrostatic interactions between coat protein and DNA. *J Mol Biol* 217: 223-227.
- Grossman, A.D., Erickson, J.W., and Gross, C.A. (1984) The *htpR* gene product of *E. coli* is a sigma factor for heat-shock promoters. *Cell* 38: 383-390.
- Guo, H., Zucker, S., Gordon, M.K., Toole, B.P., and Biswas, C. (1997) Stimulation of matrix metalloproteinase production by recombinant extracellular matrix metalloproteinase inducer from transfected Chinese hamster ovary cells. *J Biol Chem* 272: 24-27.
- Halbig, D., Wiegert, T., Blaudeck, N., Freudl, R., and Sprenger, G.A. (1999) The efficient export of NADP-containing glucose-fructose oxidoreductase to the periplasm of *Zymomonas mobilis* depends both on an intact twin-arginine motif in the signal peptide and on the generation of a structural export signal induced by cofactor binding. *Eur J Biochem* 263: 543-551.
- Harms, N., Koningstein, G., Dontje, W., Muller, M., Oudega, B., Luirink, J., and de Cock, H. (2001) The early interaction of the outer membrane protein phoe

- with the periplasmic chaperone Skp occurs at the cytoplasmic membrane. *J Biol Chem* 276: 18804-18811.
- Hartl, F.U., and Hayer-Hartl, M. (2002) Molecular chaperones in the cytosol: from nascent chain to folded protein. *Science* 295: 1852-1858.
- Hatzixanthis, K., Palmer, T., and Sargent, F. (2003) A subset of bacterial inner membrane proteins integrated by the twin-arginine translocase. *Mol Microbiol* 49: 1377-1390.
- Hesterkamp, T., Deuerling, E., and Bukau, B. (1997) The amino-terminal 118 amino acids of *Escherichia coli* trigger factor constitute a domain that is necessary and sufficient for binding to ribosomes. *J Biol Chem* 272: 21865-21871.
- Hiniker, A., and Bardwell, J.C. (2003) Disulfide bond isomerization in prokaryotes. *Biochemistry* 42: 1179-1185.
- Holmgren, A. (1989) Thioredoxin and glutaredoxin systems. *J Biol Chem* 264: 13963-13966.
- Hoogenboom, H.R., Griffiths, A.D., Johnson, K.S., Chiswell, D.J., Hudson, P., and Winter, G. (1991) Multi-subunit proteins on the surface of filamentous phage: methodologies for displaying antibody (Fab) heavy and light chains. *Nucleic Acids Res* 19: 4133-4137.
- Hori, K., Katayama, N., Kachi, S., Kondo, M., Kadomatsu, K., Usukura, J., Muramatsu, T., Mori, S., and Miyake, Y. (2000) Retinal dysfunction in basigin deficiency. *Invest Ophthalmol Vis Sci* 41: 3128-3133.
- Iannolo, G., Minenkova, O., Petruzzelli, R., and Cesareni, G. (1995) Modifying filamentous phage capsid: limits in the size of the major capsid protein. *J Mol Biol* 248: 835-844.

- Igakura, T., Kadomatsu, K., Kaname, T., Muramatsu, H., Fan, Q.W., Miyauchi, T., Toyama, Y., Kuno, N., Yuasa, S., Takahashi, M., Senda, T., Taguchi, O., Yamamura, K., Arimura, K., and Muramatsu, T. (1998) A null mutation in basigin, an immunoglobulin superfamily member, indicates its important roles in peri-implantation development and spermatogenesis. *Dev Biol* 194: 152-165.
- Intasai, N., Arooncharus, P., Kasinrerak, W., and Tayapiwatana, C. (2003) Construction of high-density display of CD147 ectodomain on VCSM13 phage via gpVIII: effects of temperature, IPTG, and helper phage infection-period. *Protein Expr Purif* 32: 323-331.
- Izard, J.W., and Kendall, D.A. (1994) Signal peptides: exquisitely designed transport promoters. *Mol Microbiol* 13: 765-773.
- Ize, B., Stanley, N.R., Buchanan, G., and Palmer, T. (2003) Role of the *Escherichia coli* Tat pathway in outer membrane integrity. *Mol Microbiol* 48: 1183-1193.
- Jack, R.L., Sargent, F., Berks, B.C., Sawers, G., and Palmer, T. (2001) Constitutive expression of *Escherichia coli* tat genes indicates an important role for the twin-arginine translocase during aerobic and anaerobic growth. *J Bacteriol* 183: 1801-1804.
- Jespers, L.S., Messens, J.H., De Keyser, A., Eeckhout, D., Van den Brande, I., Gansemans, Y.G., Lauwereys, M.J., Vlasuk, G.P., and Stanssens, P.E. (1995) Surface expression and ligand-based selection of cDNAs fused to filamentous phage gene VI. *Biotechnology (NY)* 13: 378-382.

- Jiang, J.L., Zhou, Q., Yu, M.K., Ho, L.S., Chen, Z.N., and Chan, H.C. (2001) The involvement of HAb18G/CD147 in regulation of store-operated calcium entry and metastasis of human hepatoma cells. *J Biol Chem* 276: 46870-46877.
- Jones, C.H., Danese, P.N., Pinkner, J.S., Silhavy, T.J., and Hultgren, S.J. (1997) The chaperone-assisted membrane release and folding pathway is sensed by two signal transduction systems. *Embo J* 16: 6394-6406.
- Kanekura, T., Chen, X., and Kanzaki, T. (2002) Basigin (CD147) is expressed on melanoma cells and induces tumor cell invasion by stimulating production of matrix metalloproteinases by fibroblasts. *Int J Cancer* 99: 520-528.
- Kasinrerk, W., Fiebiger, E., Stefanova, I., Baumruker, T., Knapp, W., and Stockinger, H. (1992) Human leukocyte activation antigen M6, a member of the Ig superfamily, is the species homologue of rat OX-47, mouse basigin, and chicken HT7 molecule. *J Immunol* 149: 847-854.
- Kasinrerk, W., Tokrasinwit, N., and Phunpae, P. (1999) CD147 monoclonal antibodies induce homotypic cell aggregation of monocytic cell line U937 via LFA1/ICAM-1 pathway. *Immunology* 96: 184.
- Kataoka, H., DeCastro, R., Zucker, S., and Biswas, C. (1993) Tumor cell-derived collagenase-stimulatory factor increases expression of interstitial collagenase, stromelysin, and 72-kDa gelatinase. *Cancer Res* 53: 3154-3158.
- Keiler, K.C., Silber, K.R., Downard, K.M., Papayannopoulos, I.A., Biemann, K., and Sauer, R.T. (1995) C-terminal specific protein degradation: activity and substrate specificity of the Tsp protease. *Protein Sci* 4: 1507-1515.

- Kiefhaber, T., Rudolph, R., Kohler, H.H., and Buchner, J. (1991) Protein aggregation *in vitro* and *in vivo*: a quantitative model of the kinetic competition between folding and aggregation. *Biotechnology (N Y)* 9: 825-829.
- Kirk, P., Wilson, M.C., Heddle, C., Brown, M.H., Barclay, A.N., and Halestrap, A.P. (2000) CD147 is tightly associated with lactate transporters MCT1 and MCT4 and facilitates their cell surface expression. *Embo J* 19: 3896-3904.
- Kleerebezem, M., Crielaard, W., and Tommassen, J. (1996) Involvement of stress protein PspA (phage shock protein A) of *Escherichia coli* in maintenance of the protonmotive force under stress conditions. *Embo J* 15: 162-171.
- Kobayashi, T., Kishigami, S., Sone, M., Inokuchi, H., Mogi, T., and Ito, K. (1997) Respiratory chain is required to maintain oxidized states of the DsbA-DsbB disulfide bond formation system in aerobically growing *Escherichia coli* cells. *Proc Natl Acad Sci U S A* 94: 11857-11862.
- Kramer, G., Rauch, T., Rist, W., Vorderwulbecke, S., Patzelt, H., Schulze-Specking, A., Ban, N., Deuerling, E., and Bukau, B. (2002) L23 protein functions as a chaperone docking site on the ribosome. *Nature* 419: 171-174.
- Kuno, N., Kadomatsu, K., Fan, Q.W., Hagihara, M., Senda, T., Mizutani, S., and Muramatsu, T. (1998) Female sterility in mice lacking the basigin gene, which encodes a transmembrane glycoprotein belonging to the immunoglobulin superfamily. *FEBS Lett* 425: 191-194.
- Laskowska, E., Wawrzynow, A., and Taylor, A. (1996) IbpA and IbpB, the new heat-shock proteins, bind to endogenous *Escherichia coli* proteins aggregated intracellularly by heat shock. *Biochimie* 78: 117-122.

- Lee, S., Sowa, M.E., Watanabe, Y.H., Sigler, P.B., Chiu, W., Yoshida, M., and Tsai, F.T. (2003) The structure of ClpB: a molecular chaperone that rescues proteins from an aggregated state. *Cell* 115: 229-240.
- Li, R., Huang, L., Guo, H., and Toole, B.P. (2001) Basigin (murine EMMPRIN) stimulates matrix metalloproteinase production by fibroblasts. *J Cell Physiol* 186: 371-379.
- Li, W., Alfaidy, N., and Challis, J.R. (2004) Expression of extracellular matrix metalloproteinase inducer in human placenta and fetal membranes at term labor. *J Clin Endocrinol Metab* 89: 2897-2904.
- Liberek, K., Galitski, T.P., Zylicz, M., and Georgopoulos, C. (1992) The DnaK chaperone modulates the heat shock response of *Escherichia coli* by binding to the sigma 32 transcription factor. *Proc Natl Acad Sci U S A* 89: 3516-3520.
- Linderoth, N.A., Simon, M.N., and Russel, M. (1997) The filamentous phage pIV multimer visualized by scanning transmission electron microscopy. *Science* 278: 1635-1638.
- Lowman, H.B. (1997) Bacteriophage display and discovery of peptide leads for drug development. *Annu Rev Biophys Biomol Struct* 26: 401-424.
- Major, T.C., Liang, L., Lu, X., Rosebury, W., and Bocan, T.M. (2002) Extracellular matrix metalloproteinase inducer (EMMPRIN) is induced upon monocyte differentiation and is expressed in human atheroma. *Arterioscler Thromb Vasc Biol* 22: 1200-1207.
- Makrides, S.C. (1996) Strategies for achieving high-level expression of genes in *Escherichia coli*. *Microbiol Rev* 60: 512-538.

- Malik, P., Terry, T.D., Gowda, L.R., Langara, A., Petukhov, S.A., Symmons, M.F., Welsh, L.C., Marvin, D.A., and Perham, R.N. (1996) Role of capsid structure and membrane protein processing in determining the size and copy number of peptides displayed on the major coat protein of filamentous bacteriophage. *J Mol Biol* 260: 9-21.
- Manosroi, J., Tayapiwatana, C., Gotz, F., Werner, R.G., and Manosroi, A. (2001) Secretion of active recombinant human tissue plasminogen activator derivatives in *Escherichia coli*. *Appl Environ Microbiol* 67: 2657-2664.
- Manting, E.H., and Driessen, A.J. (2000) *Escherichia coli* translocase: the unravelling of a molecular machine. *Mol Microbiol* 37: 226-238.
- Marciano, D.K., Russel, M., and Simon, S.M. (1999) An aqueous channel for filamentous phage export. *Science* 284: 1516-1519.
- Marieb, E.A., Zoltan-Jones, A., Li, R., Misra, S., Ghatak, S., Cao, J., Zucker, S., and Toole, B.P. (2004) Emmprin promotes anchorage-independent growth in human mammary carcinoma cells by stimulating hyaluronan production. *Cancer Res* 64: 1229-1232.
- Marmorstein, A.D., Gan, Y.C., Bonilha, V.L., Finnemann, S.C., Csaky, K.G., and Rodriguez-Boulan, E. (1998) Apical polarity of N-CAM and EMMPRIN in retinal pigment epithelium resulting from suppression of basolateral signal recognition. *J Cell Biol* 142: 697-710.
- Martin, J.L., Bardwell, J.C., and Kuriyan, J. (1993) Crystal structure of the DsbA protein required for disulphide bond formation *in vivo*. *Nature* 365: 464-468.

- McCafferty, J., Griffiths, A.D., Winter, G., and Chiswell, D.J. (1990) Phage antibodies: filamentous phage displaying antibody variable domains. *Nature* 348: 552-554.
- Missiakas, D., Georgopoulos, C., and Raina, S. (1993) Identification and characterization of the *Escherichia coli* gene *dsbB*, whose product is involved in the formation of disulfide bonds in vivo. *Proc Natl Acad Sci U S A* 90: 7084-7088.
- Missiakas, D., Betton, J.M., and Raina, S. (1996) New components of protein folding in extracytoplasmic compartments of *Escherichia coli* SurA, FkpA and Skp/OmpH. *Mol Microbiol* 21: 871-884.
- Missiakas, D., and Raina, S. (1997) Protein misfolding in the cell envelope of *Escherichia coli*: new signaling pathways. *Trends Biochem Sci* 22: 59-63.
- Miyauchi, T., Masuzawa, Y., and Muramatsu, T. (1991) The basigin group of the immunoglobulin superfamily: complete conservation of a segment in and around transmembrane domains of human and mouse basigin and chicken HT7 antigen. *J Biochem (Tokyo)* 110: 770-774.
- Mogk, A., Deuerling, E., Vorderwulbecke, S., Vierling, E., and Bukau, B. (2003) Small heat shock proteins, ClpB and the DnaK system form a functional triade in reversing protein aggregation. *Mol Microbiol* 50: 585-595.
- Mori, H., and Cline, K. (2002) A twin arginine signal peptide and the pH gradient trigger reversible assembly of the thylakoid Δ pH/Tat translocase. *J Cell Biol* 157: 205-210.

- Muramatsu, T., and Miyauchi, T. (2003) Basigin (CD147): a multifunctional transmembrane protein involved in reproduction, neural function, inflammation and tumor invasion. *Histol Histopathol* 18: 981-987.
- Musser, S.M., and Theg, S.M. (2000) Characterization of the early steps of OE17 precursor transport by the thylakoid DeltapH/Tat machinery. *Eur J Biochem* 267: 2588-2598.
- Nehme, C.L., Fayos, B.E., and Bartles, J.R. (1995) Distribution of the integral plasma membrane glycoprotein CE9 (MRC OX-47) among rat tissues and its induction by diverse stimuli of metabolic activation. *Biochem J* 310 (Pt 2): 693-698.
- Niviere, V., Wong, S.L., and Voordouw, G. (1992) Site-directed mutagenesis of the hydrogenase signal peptide consensus box prevents export of a beta-lactamase fusion protein. *J Gen Microbiol* 138: 2173-2183.
- Noguchi, Y., Sato, T., Hirata, M., Hara, T., Ohama, K., and Ito, A. (2003) Identification and characterization of extracellular matrix metalloproteinase inducer in human endometrium during the menstrual cycle *in vivo* and *in vitro*. *J Clin Endocrinol Metab* 88: 6063-6072.
- Palmer, T., and Berks, B.C. (2003) Moving folded proteins across the bacterial cell membrane. *Microbiology* 149: 547-556.
- Palmer, T., Sargent, F., and Berks, B.C. (2005) Export of complex cofactor-containing proteins by the bacterial Tat pathway. *Trends Microbiol* 13: 175-180.
- Paschke, M., and Hohne, W. (2005) A twin-arginine translocation (Tat)-mediated phage display system. *Gene* 350: 79-88.

- Petrenko, V.A., Smith, G.P., Gong, X., and Quinn, T. (1996) A library of organic landscapes on filamentous phage. *Protein Eng* 9: 797-801.
- Pengin, P. Role of CD147 molecule on regulation of cell proliferation and apoptosis. Thesis for Master of Science in Medical Technology, Chiang Mai University, 2003.
- Pogliano, J., Lynch, A.S., Belin, D., Lin, E.C., and Beckwith, J. (1997) Regulation of *Escherichia coli* cell envelope proteins involved in protein folding and degradation by the Cpx two-component system. *Genes Dev* 11: 1169-1182.
- Pop, O., Martin, U., Abel, C., and Muller, J.P. (2002) The twin-arginine signal peptide of PhoD and the TatAd/Cd proteins of *Bacillus subtilis* form an autonomous Tat translocation system. *J Biol Chem* 277: 3268-3273.
- Pugsley, A.P. (1993) The complete general secretory pathway in gram-negative bacteria. *Microbiol Rev* 57: 50-108.
- Raina, S., Missiakas, D., and Georgopoulos, C. (1995) The rpoE gene encoding the sigma E (sigma 24) heat shock sigma factor of *Escherichia coli*. *Embo J* 14: 1043-1055.
- Renno, T., Wilson, A., Dunkel, C., Coste, I., Maisnier-Patin, K., Benoit de Coignac, A., Aubry, J.P., Lees, R.K., Bonnefoy, J.Y., MacDonald, H.R., and Gauchat, J.F. (2002) A role for CD147 in thymic development. *J Immunol* 168: 4946-4950.
- Rietsch, A., Belin, D., Martin, N., and Beckwith, J. (1996) An *in vivo* pathway for disulfide bond isomerization in *Escherichia coli*. *Proc Natl Acad Sci U S A* 93: 13048-13053.

- Russel, M., Whirlow, H., Sun, T.P., and Webster, R.E. (1988) Low-frequency infection of F- bacteria by transducing particles of filamentous bacteriophages. *J Bacteriol* 170: 5312-5316.
- Saier, M.H., Jr. (1994) Computer-aided analyses of transport protein sequences: gleaned evidence concerning function, structure, biogenesis, and evolution. *Microbiol Rev* 58: 71-93.
- Sameshima, T., Nabeshima, K., Toole, B.P., Yokogami, K., Okada, Y., Goya, T., Kono, M., and Wakisaka, S. (2000) Expression of emmprin (CD147), a cell surface inducer of matrix metalloproteinases, in normal human brain and gliomas. *Int J Cancer* 88: 21-27.
- Santini, C.L., Bernadac, A., Zhang, M., Chanal, A., Ize, B., Blanco, C., and Wu, L.F. (2001) Translocation of jellyfish green fluorescent protein *via* the Tat system of *Escherichia coli* and change of its periplasmic localization in response to osmotic up-shock. *J Biol Chem* 276: 8159-8164.
- Sargent, F., Bogsch, E.G., Stanley, N.R., Wexler, M., Robinson, C., Berks, B.C., and Palmer, T. (1998) Overlapping functions of components of a bacterial Sec-independent protein export pathway. *Embo J* 17: 3640-3650.
- Sargent, F., Stanley, N.R., Berks, B.C., and Palmer, T. (1999) Sec-independent protein translocation in *Escherichia coli*. A distinct and pivotal role for the TatB protein. *J Biol Chem* 274: 36073-36082.
- Sargent, F., Gohlke, U., De Leeuw, E., Stanley, N.R., Palmer, T., Saibil, H.R., and Berks, B.C. (2001) Purified components of the *Escherichia coli* Tat protein transport system form a double-layered ring structure. *Eur J Biochem* 268: 3361-3367.

- Saul, F.A., Arie, J.P., Vulliez-le Normand, B., Kahn, R., Betton, J.M., and Bentley, G.A. (2004) Structural and functional studies of FkpA from *Escherichia coli*, a cis/trans peptidyl-prolyl isomerase with chaperone activity. *J Mol Biol* 335: 595-608.
- Schiebel, E., Driessen, A.J., Hartl, F.U., and Wickner, W. (1991) Delta mu H⁺ and ATP function at different steps of the catalytic cycle of preprotein translocase. *Cell* 64: 927-939.
- Saulberger, H., Unger, C.M., and Risau, W. (1992) HT7, Neurothelin, Basigin, gp42 and OX-47--many names for one developmentally regulated immunoglobulin-like surface glycoprotein on blood-brain barrier endothelium, epithelial tissue barriers and neurons. *Neurosci Lett* 140: 93-97.
- Sidhu, S.S., Weiss, G.A., and Wells, J.A. (2000) High copy display of large proteins on phage for functional selections. *J Mol Biol* 296: 487-495.
- Smith, G.P. (1985) Filamentous fusion phage: novel expression vectors that display cloned antigens on the virion surface. *Science* 228: 1315-1317.
- Soltes, G., Barker, H., Marmai, K., Pun, E., Yuen, A., and Wiersma, E.J. (2003) A new helper phage and phagemid vector system improves viral display of antibody Fab fragments and avoids propagation of insert-less virions. *J Immunol Methods* 274: 233-244.
- Specthrie, L., Bullitt, E., Horiuchi, K., Model, P., Russel, M., and Makowski, L. (1992) Construction of a microphage variant of filamentous bacteriophage. *J Mol Biol* 228: 720-724.
- Staffler, G., Szekeres, A., Schutz, G.J., Saemann, M.D., Prager, E., Zeyda, M., Drbal, K., Zlabinger, G.J., Stulnig, T.M., and Stockinger, H. (2003) Selective

- inhibition of T cell activation via CD147 through novel modulation of lipid rafts. *J Immunol* 171: 1707-1714.
- Stanley, N.R., Findlay, K., Berks, B.C., and Palmer, T. (2001) *Escherichia coli* strains blocked in Tat-dependent protein export exhibit pleiotropic defects in the cell envelope. *J Bacteriol* 183: 139-144.
- Stanley, N.R., Sargent, F., Buchanan, G., Shi, J., Stewart, V., Palmer, T., and Berks, B.C. (2002) Behaviour of topological marker proteins targeted to the Tat protein transport pathway. *Mol Microbiol* 43: 1005-1021.
- Stengele, I., Bross, P., Garces, X., Giray, J., and Rasched, I. (1990) Dissection of functional domains in phage fd adsorption protein. Discrimination between attachment and penetration sites. *J Mol Biol* 212: 143-149.
- Stockinger H., Ebel T., Hansmann C., Koch C., Majdic O., Prager E., Patel D. D., Fox D. A., Horejsi V., Sagawa K., and Shen D. C. CD147 (neurothelin/basigin) workshop panel report. In Kishimoto T., Kikutani H., von dem Borne A. E. G.K., Goyert S. M., Mason D. Y., Miyasaka M., Moretta L., Okumura K., Shaw S., Springer T. A., Sugamura K. and Zola, H., eds, *Leukocyte Typing VI*. Garland Publishing, New York. 1997: 760.
- Stoller, G., Rucknagel, K.P., Nierhaus, K.H., Schmid, F.X., Fischer, G., and Rahfeld, J.U. (1995) A ribosome-associated peptidyl-prolyl cis/trans isomerase identified as the trigger factor. *Embo J* 14: 4939-4948.
- Summer, E.J., Mori, H., Settles, A.M., and Cline, K. (2000) The thylakoid delta pH-dependent pathway machinery facilitates RR-independent N-tail protein integration. *J Biol Chem* 275: 23483-23490.

- Sun, J., and Hemler, M.E. (2001) Regulation of MMP-1 and MMP-2 production through CD147/extracellular matrix metalloproteinase inducer interactions. *Cancer Res* 61: 2276-2281.
- Tamm, L.K., Hong, H., and Liang, B. (2004) Folding and assembly of beta-barrel membrane proteins. *Biochim Biophys Acta* 1666: 250-263.
- Thomas, J.D., Daniel, R.A., Errington, J., and Robinson, C. (2001) Export of active green fluorescent protein to the periplasm by the twin-arginine translocase (Tat) pathway in *Escherichia coli*. *Mol Microbiol* 39: 47-53.
- Thorns, C., Feller, A.C., and Merz, H. (2002) EMMPRIN (CD 174) is expressed in Hodgkin's lymphoma and anaplastic large cell lymphoma. An immunohistochemical study of 60 cases. *Anticancer Res* 22: 1983-1986.
- Veinger, L., Diamant, S., Buchner, J., and Goloubinoff, P. (1998) The small heat-shock protein IbpB from *Escherichia coli* stabilizes stress-denatured proteins for subsequent refolding by a multichaperone network. *J Biol Chem* 273: 11032-11037.
- Walton, T.A., and Sousa, M.C. (2004) Crystal structure of Skp, a prefoldin-like chaperone that protects soluble and membrane proteins from aggregation. *Mol Cell* 15: 367-374.
- Weiner, J.H., Bilous, P.T., Shaw, G.M., Lubitz, S.P., Frost, L., Thomas, G.H., Cole, J.A., and Turner, R.J. (1998) A novel and ubiquitous system for membrane targeting and secretion of cofactor-containing proteins. *Cell* 93: 93-101.
- Weiner, L., and Model, P. (1994) Role of an *Escherichia coli* stress-response operon in stationary-phase survival. *Proc Natl Acad Sci U S A* 91: 2191-2195.

- Weiss, G.A., and Sidhu, S.S. (2000) Design and evolution of artificial M13 coat proteins. *J Mol Biol* 300: 213-219.
- Wexler, M., Sargent, F., Jack, R.L., Stanley, N.R., Bogsch, E.G., Robinson, C., Berks, B.C., and Palmer, T. (2000) TatD is a cytoplasmic protein with DNase activity. No requirement for TatD family proteins in sec-independent protein export. *J Biol Chem* 275: 16717-16722.
- Wickner, W.T. (1994) How ATP drives proteins across membranes. *Science* 266: 1197-1198.
- Yoshida, S., Shibata, M., Yamamoto, S., Hagihara, M., Asai, N., Takahashi, M., Mizutani, S., Muramatsu, T., and Kadomatsu, K. (2000) Homo-oligomer formation by basigin, an immunoglobulin superfamily member, *via* its N-terminal immunoglobulin domain. *Eur J Biochem* 267: 4372-4380.
- Yurchenko, V., Zybarth, G., O'Connor, M., Dai, W.W., Franchin, G., Hao, T., Guo, H., Hung, H.C., Toole, B., Gally, P., Sherry, B., and Bukrinsky, M. (2002) Active site residues of cyclophilin A are crucial for its signaling activity *via* CD147. *J Biol Chem* 277: 22959-22965.
- Zucker, S., Hymowitz, M., Rollo, E.E., Mann, R., Conner, C.E., Cao, J., Foda, H.D., Tompkins, D.C., and Toole, B.P. (2001) Tumorigenic potential of extracellular matrix metalloproteinase inducer. *Am J Pathol* 158: 1921-1928.