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## Molecular characterization of copper-dependent enzymes involved in Streptomyces morphology

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# References

- Alteri, CJ, Xicohténcatl-Cortes, J, Hess, S, Caballero-Olín, G, Girón, JA, and Friedman, RL (2007) *Mycobacterium tuberculosis* produces pili during human infection. *Proc Natl Acad Sci U S A* **104**: 5145–50.
- Anné, J, Maldonado, B, Van Impe, J, Van Mellaert, L, and Bernaerts, K (2012) Recombinant protein production and streptomycetes. *J Biotechnol* **158**: 159–67.
- Antholine, W (2005) Low frequency EPR of Cu<sup>2+</sup> in proteins. In *Biological Magnetic Resonance*. Eaton, SR, Eaton, GR, and Berliner, LJ (eds). Springer-Verlag, New York. pp. 417–454.
- Arends, IWCE, Gamez, P, and Sheldon, RA (2006) Green oxidation of alcohols using biomimetic Cu complexes and Cu enzymes as catalysts. *Adv Inorg Chem* **58**: 235–279.
- Avigad, G, Amaral, D, Asensio, C, and Horecker, BL (1962) The D-galactose oxidase of *Polyporus circinatus*. *J Biol Chem* **237**: 2736–43.
- Bagos, PG, Nikolaou, EP, Liakopoulos, TD, and Tsirigos, KD (2010) Combined prediction of Tat and Sec signal peptides with hidden Markov models. *Bioinformatics* **26**: 2811–7.
- Bagos, PG, Tsirigos, KD, Liakopoulos, TD, and Hamodrakas, SJ (2008) Prediction of lipoprotein signal peptides in Gram-positive bacteria with a Hidden Markov Model. *J Proteome Res* **7**: 5082–93.
- Banci, L, Bertini, I, Cavallaro, G, and Rosato, A (2007) The functions of Sco proteins from genome-based analysis. *J Proteome Res* **6**: 1568–1579.
- Barnes, AMT, Ballering, KS, and Leibman, RS (2012) *Enterococcus faecalis* produces abundant extracellular structures. *mBio* **3**: 1–9.
- Baron, AJ, Stevens, C, Wilmot, C, Seneviratne, KD, Blakeley, V, Dooley, DM, et al. (1994) Structure and mechanism of galactose oxidase. The free radical site. *J Biol Chem* **269**: 25095–105.
- Battye, TGG, Kontogiannis, L, Johnson, O, Powell, HR, and Leslie, AGW (2011) iMOSFLM: a new graphical interface for diffraction-image processing with MOSFLM. *Acta Crystallogr D Biol Crystallogr* **67**: 271–81.
- Bekker, C de, Veluw, GJ van, Vinck, A, Wiebenga, LA, and Wosten, HAB (2011) Heterogeneity of *Aspergillus niger* microcolonies in liquid shaken cultures. *Appl Environ Microbiol* **77**: 1263–7.
- Bendtsen, JD, Nielsen, H, Widdick, D, Palmer, T, and Brunak, S (2005) Prediction of twin-arginine signal peptides. *BMC Bioinformatics* **6**: 167.
- Bentley, SD, Chater, KF, Cerdeño-Tárraga, A-M, Challis, GL, Thomson, NR, James, KD, et al. (2002) Complete genome sequence of the model actinomycete *Streptomyces coelicolor* A3(2). *Nature* **417**: 141–147.
- Berardo, C Di, Capstick, DS, Bibb, MJ, Findlay, KC, Buttner, MJ, and Elliot, MA (2008) Function and redundancy of the chaplin cell surface proteins in aerial hypha formation, rodlet assembly, and viability in *Streptomyces coelicolor*. *J Bacteriol* **190**: 5879–5889.
- Bereman, RD, and Kosman, DJ (1977) Stereoelectronic properties of metalloenzymes. 5. Identification and assignment of ligand hyperfine splittings in the electron spin resonance spectrum of galactose oxidase. *J Am Chem Soc* **99**: 7322–5.

## References

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- Berliner, LJ, Khramtsov, V, Fujii, H, and Clanton, TL (2001) Unique *in vivo* applications of spin traps. *Free Radic Biol Med* **30**: 489–99.
- Berner, I, Konetschny-Rapp, S, Jung, G, and Winkelmann, G (1988) Characterization of ferrioxamine E as the principal siderophore of *Erwinia herbicola* (*Enterobacter agglomerans*). *Biol Met* **1**: 51–56.
- Bewick, MW, Williams, ST, and Veltkamp, C (1976) Growth and ultrastructure of *Streptomyces venezuelae* during chloramphenicol production. *Microbios* **16**: 191–9.
- Bibb, MJ, Domonkos, A, Chandra, G, and Buttner, MJ (2012) Expression of the chaplin and rodlin hydrophobic sheath proteins in *Streptomyces venezuelae* is controlled by  $\sigma^{BldN}$  and a cognate anti-sigma factor, RsbN. *Mol Microbiol* **84**: 1033–49.
- Bierman, M, Logan, R, O'Brien, K, Seno, ET, Rao, RN, and Schoner, BE (1992) Plasmid cloning vectors for the conjugal transfer of DNA from *Escherichia coli* to *Streptomyces* spp. *Gene* **116**: 43–9.
- Blake, C, and Serpell, L (1996) Synchrotron X-ray studies suggest that the core of the transthyretin amyloid fibril is a continuous beta-sheet helix. *Structure* **4**: 989–998.
- Blanco, LP, Evans, ML, Smith, DR, Badtke, MP, and Chapman, MR (2012) Diversity, biogenesis and function of microbial amyloids. *Trends Microbiol* **20**: 66–73.
- Blundell, KLIM, Hough, MA, Vijgenboom, E, and Worrall, JAR (2014) Structural and mechanistic insights into an extracytoplasmic copper trafficking pathway in *Streptomyces lividans*. *Biochem J* **459**: 525–38.
- Blundell, KLIM, Wilson, MT, Svistunenko, DA, Vijgenboom, E, and Worrall, JAR (2013) Morphological development and cytochrome c oxidase activity in *Streptomyces lividans* are dependent on the action of a copper bound Sco protein. *Open Biol* **3**: 120163.
- Boersema, PJ, Raijmakers, R, Lemeer, S, Mohammed, S, and Heck, AJR (2009) Multiplex peptide stable isotope dimethyl labeling for quantitative proteomics. *Nat Protoc* **4**: 484–494.
- Bokhove, M, Claessen, D, De Jong, W, Dijkhuizen, L, Boekema, EJ, and Oostergetel, GT (2013) Chaplins of *Streptomyces coelicolor* self-assemble into two distinct functional amyloids. *J Struct Biol* **184**: 301–9.
- Bougault, C, Hediger, S, and Simorre, J-P (2012) Solid-state NMR of the bacterial cell wall. In *Bacterial Glycomics: Current Research, Technology and Applications*. Horizon Scientific Press, p. 270.
- Breton, C, Snajdrová, L, Jeanneau, C, Koca, J, and Imbert, A (2006) Structures and mechanisms of glycosyltransferases. *Glycobiology* **16**: 29R–37R.
- Capstick, DS, Jomaa, A, Hanke, C, Ortega, J, and Elliot, MA (2011) Dual amyloid domains promote differential functioning of the chaplin proteins during *Streptomyces aerial* morphogenesis. *Proc Natl Acad Sci U S A* **108**: 9821–6.
- Capstick, DS, Willey, JM, Buttner, MJ, and Elliot, MA (2007) SapB and the chaplins: connections between morphogenetic proteins in *Streptomyces coelicolor*. *Mol Microbiol* **64**: 602–13.
- Celler, K, Picioreanu, C, Loosdrecht, MCM van, and Wezel, GP van (2012) Structured morphological modeling as a framework for rational strain design of *Streptomyces* species. *Antonie Van Leeuwenhoek* **102**: 409–23.
- Chao, JD, Papavinasasundaram, KG, Zheng, X, Chávez-Steenbock, A, Wang, X, Lee, GQ, and Av-Gay, Y (2010) Convergence of Ser/Thr and two-component signaling to coordinate expression of the dormancy regulon in *Mycobacterium tuberculosis*. *J Biol Chem* **285**: 29239–29246.
- Chaplin, AK, Petrus, MLC, Mangiameli, G, Hough, MA, Svistunenko, DA, Nicholls, P, et al. (2015) GlxA is a new structural member of the radical copper oxidase family and is required for glycan deposition at hyphal tips and morphogenesis of *Streptomyces lividans*. *Biochem J* **469**: 433–444.
- Charnock, SJ, and Davies, GJ (1999) Structure of the nucleotide-diphospho-sugar transferase, SpsA from *Bacillus subtilis*, in native and nucleotide-complexed forms. *Biochemistry* **38**: 6380–5.

- Chater, KF (1972) A morphological and genetic mapping study of white colony mutants of *Streptomyces coelicolor*. *J Gen Microbiol* **72**: 9–28.
- Chater, KF (1998) Taking a genetic scalpel to the *Streptomyces* colony. *Microbiology* **144**: 1465–1478.
- Chater, KF (2006) *Streptomyces* inside-out: a new perspective on the bacteria that provide us with antibiotics. *Philos Trans R Soc Lond B Biol Sci* **361**: 761–8.
- Chater, KF, Biró, S, Lee, KJ, Palmer, T, and Schrempp, H (2010) The complex extracellular biology of *Streptomyces*. *FEMS Microbiol Rev* **34**: 171–98.
- Chater, KF, and Losick, R (1997) Mycelial life style of *Streptomyces coelicolor* A3(2) and its relatives. In *Bacteria as multicellular organisms*. Shapiro, J.A., and Dworkin, M. (eds). Oxford University Press, New York. pp. 149–182.
- Chauhan, S, Sharma, D, Singh, A, Suriola, A, and Tyagi, JS (2011) Comprehensive insights into *Mycobacterium tuberculosis* DevR (DosR) regulon activation switch. *Nucleic Acids Res* **39**: 7400–7414.
- Cheah, IK, and Halliwell, B (2012) Ergothioneine; antioxidant potential, physiological function and role in disease. *Biochim Biophys Acta* **1822**: 784–93.
- Chen, C, Shrestha, R, Jia, K, Gao, PF, Geisbrecht, B V, Bossmann, SH, et al. (2015) Characterization of dye-decolorizing peroxidase (DyP) from *Thermomonospora curvata* reveals unique catalytic properties of A-type DyPs. *J Biol Chem* **290**: 23447–63.
- Chovancova, E, Pavelka, A, Benes, P, Strnad, O, Brezovsky, J, Kozlikova, B, et al. (2012) CAVER 3.0: a tool for the analysis of transport pathways in dynamic protein structures. *PLoS Comput Biol* **8**: e1002708.
- Claessen, D, Jong, W de, Dijkhuizen, L, and Wösten, HAB (2006) Regulation of *Streptomyces* development: reach for the sky! *Trends Microbiol* **14**: 313–9.
- Claessen, D, Rink, R, De Jong, W, Siebring, J, De Vreugd, P, Boersma, FGH, et al. (2003) A novel class of secreted hydrophobic proteins is involved in aerial hyphae formation in *Streptomyces coelicolor* by forming amyloid-like fibrils. *Genes Dev* **17**: 1714–1726.
- Claessen, D, Rozen, DE, Kuipers, OP, Søgaard-Andersen, L, and Van Wezel, GP (2014) Bacterial solutions to multicellularity: a tale of biofilms, filaments and fruiting bodies. *Nat Rev Microbiol* **12**: 115–24.
- Claessen, D, Stokroos, I, Deelstra, HJ, Penninga, NA, Bormann, C, Salas, JA, et al. (2004) The formation of the rodlet layer of streptomycetes is the result of the interplay between rodins and chaplins. *Mol Microbiol* **53**: 433–43.
- Claessen, D, Wösten, HAB, Van Keulen, G, Faber, OG, Alves, AMCR, Meijer, WG, and Dijkhuizen, L (2002) Two novel homologous proteins of *Streptomyces coelicolor* and *Streptomyces lividans* are involved in the formation of the rodlet layer and mediate attachment to a hydrophobic surface. *Mol Microbiol* **44**: 1483–1492.
- Cleveland, L, Coffman, RE, Coon, P, and Davis, L (1975) An investigation of the role of the copper in galactose oxidase. *Biochemistry* **14**: 1108–1115.
- Colpa, DI, Fraaije, MW, and Bloois, E van (2014) DyP-type peroxidases: a promising and versatile class of enzymes. *J Ind Microbiol Biotechnol* **41**: 1–7.
- Cornelis, P, and Andrews, SC (eds) (2010) *Iron uptake and homeostasis in microorganisms*. Caister Academic Press, Norfolk, UK.
- Cot, M, Ray, A, Gilleron, M, Vercellone, A, Larrouy-Maumus, G, Armau, E, et al. (2011) Lipoteichoic acid in *Streptomyces hygroscopicus*: structural model and immunomodulatory activities. *PLoS One* **6**: e26316.
- Coutinho, PM, Deleury, E, Davies, GJ, and Henrissat, B (2003) An evolving hierarchical family classification for glycosyltransferases. *J Mol Biol* **328**: 307–317.

## References

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- Cox, J, and Mann, M (2008) MaxQuant enables high peptide identification rates, individualized p.p.b.-range mass accuracies and proteome-wide protein quantification. *Nat Biotechnol* **26**: 1367–1372.
- Cox, J, Neuhauser, N, Michalski, A, Scheltema, RA, Olsen, J V., and Mann, M (2011) Andromeda: A peptide search engine integrated into the MaxQuant environment. *J Proteome Res* **10**: 1794–1805.
- Crick, DC, Mahapatra, S, and Brennan, PJ (2001) Biosynthesis of the arabinogalactan-peptidoglycan complex of *Mycobacterium tuberculosis*. *Glycobiology* **11**: 107R–118R.
- Cruz-Morales, P, Vijgenboom, E, Iruegas-Bocardo, F, Girard, G, Yáñez-Guerra, LA, Ramos-Aboites, HE, et al. (2013) The genome sequence of *Streptomyces lividans* 66 reveals a novel tRNA-dependent peptide biosynthetic system within a metal-related genomic island. *Genome Biol Evol* **5**: 1165–75.
- Cui, YQ, Okkerse, WJ, Lans, RGJM Van Der, and Luyben, KCAM (1998) Modeling and measurements of fungal growth and morphology in submerged fermentations. *Biotechnol Bioeng* **60**: 216–229.
- Cummings, RD, and Etzler, ME (2009) Antibodies and lectins in glycan analysis. In *Essentials of Glycobiology*. 2nd edition. Varki A, Cummings RD, Esko JD, et al. (ed.). Cold Spring Harbor Laboratory Press, New York.
- Davis, IW, Leaver-Fay, A, Chen, VB, Block, JN, Kapral, GJ, Wang, X, et al. (2007) MolProbity: all-atom contacts and structure validation for proteins and nucleic acids. *Nucleic Acids Res* **35**: W375–W383.
- Deacon, SE, and McPherson, MJ (2011) Enhanced expression and purification of fungal galactose oxidase in *Escherichia coli* and use for analysis of a saturation mutagenesis library. *Chembiochem* **12**: 593–601.
- Van Dissel, D, Claessen, D, Roth, M, and Van Wezel, GP (2015) A novel locus for mycelial aggregation forms a gateway to improved *Streptomyces* cell factories. *Microb Cell Fact* **14**: 44.
- Van Dissel, D, Claessen, D, and Van Wezel, GP (2014) Morphogenesis of *Streptomyces* in submerged cultures. *Adv Appl Microbiol* **89**: 1–45.
- Dueholm, MS, Petersen, S V., Sønderkær, M, Larsen, P, Christiansen, G, Hein, KL, et al. (2010) Functional amyloid in pseudomonas. *Mol Microbiol* **77**: 1009–1020.
- Duong, A, Capstick, DS, Berardo, C Di, Findlay, KC, Hesketh, A, Hong, H-J, and Elliot, MA (2012) Aerial development in *Streptomyces coelicolor* requires sortase activity. *Mol Microbiol* **83**: 992–1005.
- Ekkers, DM, Claessen, D, Galli, F, and Stadhuis, E (2014) Surface modification using interfacial assembly of the *Streptomyces* chaplin proteins. *Appl Microbiol Biotechnol* **98**: 4491–4501.
- Elliot, MA, and Talbot, NJ (2004) Building filaments in the air: Aerial morphogenesis in bacteria and fungi. *Curr Opin Microbiol* **7**: 594–601.
- Elliot, MA, Karoonuthaisiri, N, Huang, J, Bibb, MJ, Cohen, SN, Kao, CM, and Buttner, MJ (2003) The chaperins: A family of hydrophobic cell-surface proteins involved in aerial mycelium formation in *Streptomyces coelicolor*. *Genes Dev* **17**: 1727–1740.
- Emsley, P, and Cowtan, K (2004) Coot: model-building tools for molecular graphics. *Acta Crystallogr D Biol Crystallogr* **60**: 2126–32.
- Errington, J (2003) Regulation of endospore formation in *Bacillus subtilis*. *Nat Rev Microbiol* **1**: 117–126.
- Errington, J, Daniel, RA, and Scheffers, D-J (2003) Cytokinesis in bacteria. *Microbiol Mol Biol Rev* **67**: 52–65, table of contents.
- Evans, PR, and Murshudov, GN (2013) How good are my data and what is the resolution? *Acta Crystallogr D Biol Crystallogr* **69**: 1204–14.
- Fang, L, and Catchmark, JM (2015) Characterization of cellulose and other exopolysaccharides produced from *Gluconacetobacter* strains. *Carbohydr Polym* **115**: 663–9.

- Flärdh, K (2003a) Growth polarity and cell division in *Streptomyces*. *Curr Opin Microbiol* **6**: 564–571.
- Flärdh, K (2003b) Essential role of DivIVA in polar growth and morphogenesis in *Streptomyces coelicolor* A3(2). *Mol Microbiol* **49**: 1523–36.
- Flärdh, K, and Buttner, MJ (2009) *Streptomyces* morphogenetics: dissecting differentiation in a filamentous bacterium. *Nat Rev Microbiol* **7**: 36–49.
- Flärdh, K, Richards, DM, Hempel, AM, Howard, M, and Buttner, MJ (2012) Regulation of apical growth and hyphal branching in *Streptomyces*. *Curr Opin Microbiol* **15**: 737–43.
- Fujimoto, M, Yamada, A, Kurosawa, J, Kawata, A, Beppu, T, Takano, H, and Ueda, K (2012) Pleiotropic role of the Sco1/SenC family copper chaperone in the physiology of *Streptomyces*. *Microb Biotechnol* **5**: 477–488.
- Gaskell, AA, Giovinazzo, JA, Fonte, V, and Willey, JM (2012) Multi-tier regulation of the streptomycete morphogenetic peptide SapB. *Mol Microbiol* **84**: 501–515.
- Gastebois, A, Mouyna, I, Simenel, C, Clavaud, C, Coddeville, B, Delepierre, M, et al. (2010) Characterization of a new beta-(1-3)-glucan branching activity of *Aspergillus fumigatus*. *J Biol Chem* **285**: 2386–96.
- Gebbink, MFBG, Claessen, D, Bouma, B, Dijkhuizen, L, and Wösten, HAB (2005) Amyloids - a functional coat for microorganisms. *Nat Rev Microbiol* **3**: 333–41.
- Gerasimova, A, Kazakov, AE, Arkin, AP, Dubchak, I, and Gelfand, MS (2011) Comparative genomics of the dormancy regulons in mycobacteria. *J Bacteriol* **193**: 3446–3452.
- Girard, G, Willemse, J, Zhu, H, Claessen, D, Bukarasam, K, Goodfellow, M, and Van Wezel, GP (2014) Analysis of novel kitasatosporae reveals significant evolutionary changes in conserved developmental genes between *Kitasatospora* and *Streptomyces*. *Antonie Van Leeuwenhoek* **106**: 365–80.
- Gloster, TM (2014) Advances in understanding glycosyltransferases from a structural perspective. *Curr Opin Struct Biol* **28**: 131–41.
- Goldman, E, and Green, LH (eds) (2008) *Practical Handbook of Microbiology, Second Edition*. CRC Press, Boca Raton.
- Goosens, VJ, Monteferrante, CG, and Van Dijl, JM (2014) The Tat system of Gram-positive bacteria. *Biochim Biophys Acta - Mol Cell Res* **1843**: 1698–1706.
- Goosens, VJ, Otto, A, Glasner, C, Monteferrante, CC, Van der Ploeg, R, Hecker, M, et al. (2013) Novel twin-arginine translocation pathway-dependent phenotypes of *Bacillus subtilis* unveiled by quantitative proteomics. *J Proteome Res* **12**: 796–807.
- Gras, SL, and Dennis, C (2014) Functional amyloid fibrils: lessons from microbes. In *Natural products analysis: instrumentation, methods, and applications*. Havlicek, V., and Spizek, J. (eds). Wiley, New York.
- Gubbens, J, Janus, M, Florea, BI, Overkleeft, HS, and Van Wezel, GP (2012) Identification of glucose kinase-dependent and -independent pathways for carbon control of primary metabolism, development and antibiotic production in *Streptomyces coelicolor* by quantitative proteomics. *Mol Microbiol* **86**: 1490–1507.
- Güssow, HT (1914) The systematic position of the organism of the common potato scab. *Science* **39**: 431–3.
- Hamilton, GA, Adolf, PK, Jersey, J De, DuBois, GC, Dyrkacz, GR, and Libby, RD (1978) Trivalent copper superoxide and galactose oxidase. *J Am Chem Soc* **100**: 1899–1912.
- Hammer, ND, Schmidt, JC, and Chapman, MR (2007) The curli nucleator protein, CsgB, contains an amyloidogenic domain that directs CsgA polymerization. *Proc Natl Acad Sci U S A* **104**: 12494–9.
- Hengge, R (2009) Principles of c-di-GMP signalling in bacteria. *Nat Rev Microbiol* **7**: 263–273.
- Hengst, CD den, Tran, NT, Bibb, MJ, Chandra, G, Leskiw, BK, and Buttner, MJ (2010) Genes essential for morphological development and antibiotic production in *Streptomyces coelicolor* are targets of BldD during vegetative

## References

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- growth. *Mol Microbiol* **78**: 361–379.
- Holmes, NA, Walshaw, J, Leggett, RM, Thibessard, A, Dalton, KA, Gillespie, MD, et al. (2013) Coiled-coil protein Scy is a key component of a multiprotein assembly controlling polarized growth in *Streptomyces*. *Proc Natl Acad Sci U S A* **110**: E397–406.
- Hong, H-J, Paget, MSB, and Buttner, MJ (2002) A signal transduction system in *Streptomyces coelicolor* that activates the expression of a putative cell wall glycan operon in response to vancomycin and other cell wall-specific antibiotics. *Mol Microbiol* **44**: 1199–1211.
- Hopwood, DA (2007) *Streptomyces in Nature and Medicine: The Antibiotic Makers*. Oxford University Press, New York.
- Hopwood, DA, Bibb, MJ, Chater, KF, Kieser, T, Lydiate, DJ, Smith, CP, et al. (1985) *Genetic manipulation of streptomyces – A laboratory manual*. The John Innes Foundation and Cold Spring Harbour Laboratory, Norwich, UK.
- Hopwood, DA, Kieser, T, Wright, HM, and Bibb, MJ (1983) Plasmids, recombination and chromosome mapping in *Streptomyces lividans* 66. *J Gen Microbiol* **129**: 2257–69.
- Hughes, AH, Hancock, IC, and Baddiley, J (1973) The function of teichoic acids in cation control in bacterial membranes. *Biochem J* **132**: 83–93.
- Hull, TD, Ryu, M-H, Sullivan, MJ, Johnson, RC, Klena, NT, Geiger, RM, et al. (2012) Cyclic-di-GMP phosphodiesterases RmdA and RmdB are involved in regulating colony morphology and development in *Streptomyces coelicolor*. *J Bacteriol* **194**: 4642–51.
- Hunt, AC, Servín-González, L, Kelemen, GH, and Buttner, MJ (2005) The *bldC* developmental locus of *Streptomyces coelicolor* encodes a member of a family of small DNA-binding proteins related to the DNA-binding domains of the MerR family. *J Bacteriol* **187**: 716–728.
- Hutter, KJ, and Eipel, HE (1979) Microbial determinations by flow cytometry. *J Gen Microbiol* **113**: 369–375.
- Innes, CMJ, and Allan, EJ (2001) Induction, growth and antibiotic production of *Streptomyces viridifaciens* L-form bacteria. *J Appl Microbiol* **90**: 301–308.
- Ito, N, Phillips, SE, Stevens, C, Ogel, ZB, McPherson, MJ, Keen, JN, et al. (1991) Novel thioether bond revealed by a 1.7 Å crystal structure of galactose oxidase. *Nature* **350**: 87–90.
- Ito, N, Phillips, SE, Yadav, KD, and Knowles, PF (1994) Crystal structure of a free radical enzyme, galactose oxidase. *J Mol Biol* **238**: 794–814.
- Jahn, CE, Selimi, DA, Barak, JD, and Charkowski, AO (2011) The *Dickeya dadantii* biofilm matrix consists of cellulose nanofibres, and is an emergent property dependent upon the type III secretion system and the cellulose synthesis operon. *Microbiology* **157**: 2733–44.
- Jakeman, DL, Graham, CL, Young, W, and Vining, LC (2006) Culture conditions improving the production of jadomycin B. *J Ind Microbiol Biotechnol* **33**: 767–772.
- Jakimowicz, D, and Van Wezel, GP (2012) Cell division and DNA segregation in *Streptomyces*: How to build a septum in the middle of nowhere? *Mol Microbiol* **85**: 393–404.
- De Jong, W, Manteca, A, Sanchez, J, Bucca, G, Smith, CP, Dijkhuizen, L, et al. (2009) NepA is a structural cell wall protein involved in maintenance of spore dormancy in *Streptomyces coelicolor*. *Mol Microbiol* **71**: 1591–603.
- De Jong, W, Vijgenboom, E, Dijkhuizen, L, Wösten, HAB, and Claessen, D (2012) SapB and the rodllins are required for development of *Streptomyces coelicolor* in high osmolarity media. *FEMS Microbiol Lett* **329**: 154–159.
- De Jong, W, Wösten, HAB, Dijkhuizen, L, and Claessen, D (2009) Attachment of *Streptomyces coelicolor* is mediated by amyloidal fimbriae that are anchored to the cell surface via cellulose. *Mol Microbiol* **73**: 1128–40.

- Käll, L, Krogh, A, and Sonnhammer, ELL (2004) A combined transmembrane topology and signal peptide prediction method. *J Mol Biol* **338**: 1027–36.
- De Keersmaeker, S, Van Mellaert, L, Lammertyn, E, Vrancken, K, Anné, J, and Geukens, N (2005) Functional analysis of TatA and TatB in *Streptomyces lividans*. *Biochem Biophys Res Commun* **335**: 973–982.
- De Keersmaeker, S, Vrancken, K, Van Mellaert, L, Anné, J, and Geukens, N (2007) The Tat pathway in *Streptomyces lividans*: interaction of Tat subunits and their role in translocation. *Microbiology* **153**: 1087–94.
- Keijser, BJ, Van Wezel, GP, Canters, GW, Kieser, T, and Vijgenboom, E (2000) The ram-dependence of *Streptomyces lividans* differentiation is bypassed by copper. *J Mol Microbiol Biotechnol* **2**: 565–74.
- Kelemen, GH, and Buttner, MJ (1998) Initiation of aerial mycelium formation in *Streptomyces*. *Curr Opin Microbiol* **1**: 656–662.
- Kelleher, FM, and Bhavanandan, VP (1986) Re-examination of the products of the action of galactose oxidase. Evidence for the conversion of raffinose to 6'-carboxyraffinose. *J Biol Chem* **261**: 11045–8.
- Kelley, LA, Mezulis, S, Yates, CM, Wass, MN, and Sternberg, MJE (2015) The Phyre2 web portal for protein modeling, prediction and analysis. *Nat Protoc* **10**: 845–858.
- Kelley, WL (2006) Lex marks the spot: The virulent side of SOS and a closer look at the LexA regulon. *Mol Microbiol* **62**: 1228–1238.
- Kendrick, KE, and Ensign, JC (1983) Sporulation of *Streptomyces griseus* in submerged culture. *J Bacteriol* **155**: 357–66.
- Kershaw, MJ, and Talbot, NJ (1998) Hydrophobins and repellents: proteins with fundamental roles in fungal morphogenesis. *Fungal Genet Biol* **23**: 18–33.
- Van Keulen, G, Jonkers, HM, Claessen, D, Dijkhuizen, L, and Wösten, HAB (2003) Differentiation and anaerobiosis in standing liquid cultures of *Streptomyces coelicolor*. *J Bacteriol* **185**: 1455–8.
- Khurana, R, Uversky, VN, Nielsen, L, and Fink, AL (2001) Is Congo red an amyloid-specific dye? *J Biol Chem* **276**: 22715–21.
- Kieser, T, Bibb, MJ, Buttner, MJ, Chater, KF, and Hopwood, DA (2000) *Practical Streptomyces Genetics*. The John Innes Foundation, Norwich.
- Kieser, T, and Hopwood, DA (1991) Genetic manipulation of *Streptomyces*: integrating vectors and gene replacement. *Methods Enzymol* **204**: 430–58.
- Kim, HJ, Graham, DW, DiSpirito, AA, Alterman, MA, Galeva, N, Larive, CK, et al. (2004) Methanobactin, a copper-acquisition compound from methane-oxidizing bacteria. *Science* **305**: 1612–5.
- Kim, SJ, and Shoda, M (1999) Purification and characterization of a novel peroxidase from *Geotrichum candidum* dec 1 involved in decolorization of dyes. *Appl Environ Microbiol* **65**: 1029–35.
- Kim, Y-M, and Kim, J (2004) Formation and dispersion of mycelial pellets of *Streptomyces coelicolor* A3(2). *J Microbiol* **42**: 64–7.
- Kirima, K, Tsuchiya, K, Sei, H, Hasegawa, T, Shikishima, M, Motobayashi, Y, et al. (2003) Evaluation of systemic blood NO dynamics by EPR spectroscopy: HbNO as an endogenous index of NO. *Am J Physiol Heart Circ Physiol* **285**: H589–96.
- Kirschner, DA, Abraham, C, and Selkoe, DJ (1986) X-ray diffraction from intraneuronal paired helical filaments and extraneuronal amyloid fibers in Alzheimer disease indicates cross-beta conformation. *Proc Natl Acad Sci U S A* **83**: 503–7.
- Kleinschmitz, E-M, Latus, A, Sigle, S, Maldener, I, Wohlleben, W, and Muth, G (2011) Genetic analysis of SCO2997, encoding a TagF homologue, indicates a role for wall teichoic acids in sporulation of *Streptomyces coelicolor*

## References

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- A3(2). *J Bacteriol* **193**: 6080–5.
- Kodani, S, Hudson, ME, Durrant, MC, Buttner, MJ, Nodwell, JR, and Willey, JM (2004) The SapB morphogen is a lantibiotic-like peptide derived from the product of the developmental gene *ramS* in *Streptomyces coelicolor*. *Proc Natl Acad Sci U S A* **101**: 11448–53.
- Kodani, S, Lodato, MA, Durrant, MC, Picart, F, and Willey, JM (2005) SapT, a lanthionine-containing peptide involved in aerial hyphae formation in the streptomycetes. *Mol Microbiol* **58**: 1368–1380.
- Koepsch, I, Overbeck, J, Piepmeyer, S, Meschke, H, and Schrempf, H (2009) A molecular key for building hyphae aggregates: the role of the newly identified *Streptomyces* protein HyoS. *Microb Biotechnol* **2**: 343–360.
- Kozlikova, B, Sebestova, E, Sustr, V, Brezovsky, J, Strnad, O, Daniel, L, et al. (2014) CAVER Analyst 1.0: graphic tool for interactive visualization and analysis of tunnels and channels in protein structures. *Bioinformatics* **30**: 2684–5.
- Krogh, A, Larsson, B, Von Heijne, G, and Sonnhammer, EL (2001) Predicting transmembrane protein topology with a hidden Markov model: application to complete genomes. *J Mol Biol* **305**: 567–80.
- Kumar, N, and Borth, N (2012) Flow-cytometry and cell sorting: An efficient approach to investigate productivity and cell physiology in mammalian cell factories. *Methods* **56**: 366–374.
- Kumirska, J, Czerwcka, M, Kaczyński, Z, Bychowska, A, Brzozowski, K, Thöming, J, and Stepnowski, P (2010) Application of spectroscopic methods for structural analysis of chitin and chitosan. *Mar Drugs* **8**: 1567–636.
- Labeda, DP, Goodfellow, M, Brown, R, Ward, AC, Lanoot, B, Vannanneyt, M, et al. (2012) Phylogenetic study of the species within the family Streptomycetaceae. *Antonie Van Leeuwenhoek* **101**: 73–104.
- Lairson, LL, Henrissat, B, Davies, GJ, and Withers, SG (2008) Glycosyltransferases: structures, functions, and mechanisms. *Annu Rev Biochem* **77**: 521–55.
- Lambert, S, Traxler, MF, Craig, M, Maciejewska, M, Ongena, M, Van Wezel, GP, et al. (2014) Altered desferrioxamine-mediated iron utilization is a common trait of bald mutants of *Streptomyces coelicolor*. *Metallomics* **6**: 1390–9.
- Lee, JW, Deng, F, Yeomans, WG, Allen, AL, Gross, RA, and Kaplan, DL (2001) Direct incorporation of glucosamine and N-acetylglucosamine into exopolymers by *Gluconacetobacter xylinus* (= *Acetobacter xylinum*) ATCC 10245: Production of chitosan-cellulose and chitin-cellulose exopolymers. *Appl Environ Microbiol*.
- Lee, Y-K, Whittaker, MM, and Whittaker, JW (2008) The electronic structure of the Cys-Tyr(\*) free radical in galactose oxidase determined by EPR spectroscopy. *Biochemistry* **47**: 6637–49.
- Van Leeuwen, SS, Kralj, S, Van Geel-Schutten, IH, Gerwig, GJ, Dijkhuizen, L, and Kamerling, JP (2008) Structural analysis of the alpha-D-glucan (EPS180) produced by the *Lactobacillus reuteri* strain 180 glucansucrase GTF180 enzyme. *Carbohydr Res* **343**: 1237–50.
- Limam, R, Facey, PD, Van Keulen, G, Dyson, PJ, and Sol, R Del (2013) A laterally acquired galactose oxidase-like gene is required for aerial development during osmotic stress in *Streptomyces coelicolor*. *PLoS One* **8**: e54112.
- Lin, PJ, Grimm, LH, Wulkow, M, Hempel, DC, and Krull, R (2008) Population balance modeling of the conidial aggregation of *Aspergillus niger*. *Biotechnol Bioeng* **99**: 341–350.
- Lombard, V, Golaconda Ramulu, H, Drula, E, Coutinho, PM, and Henrissat, B (2014) The carbohydrate-active enzymes database (CAZy) in 2013. *Nucleic Acids Res* **42**: D490–5.
- López, D, Vlamakis, H, and Kolter, R (2010) Biofilms. *Cold Spring Harb Perspect Biol* **2**: a000398.
- Lugones, LG, Jong, JF De, Vries, OMH De, Jalving, R, Dijksterhuis, J, and Wösten, H a B (2004) The SC15 protein of *Schizophyllum commune* mediates formation of aerial hyphae and attachment in the absence of the SC3 hydrophobin. *Mol Microbiol* **53**: 707–716.

- MacNeil, DJ, Gewain, KM, Ruby, CL, Dezeny, G, Gibbons, PH, and MacNeil, T (1992) Analysis of *Streptomyces avermitilis* genes required for avermectin biosynthesis utilizing a novel integration vector. *Gene* **111**: 61–68.
- Manteca, A, Alvarez, R, Salazar, N, Yagüe, P, and Sanchez, J (2008) Mycelium differentiation and antibiotic production in submerged cultures of *Streptomyces coelicolor*. *Appl Environ Microbiol* **74**: 3877–86.
- Martin, SM, and Bushell, ME (1996) Effect of hyphal micromorphology on bioreactor performance of antibiotic-producing *Saccharopolyspora erythraea* cultures. *Microbiology* **142**: 1783–1788.
- Matthysse, AG (1986) Initial interactions of *Agrobacterium tumefaciens* with plant host cells. *Crit Rev Microbiol* **13**: 281–307.
- Matthysse, AG, White, S, and Lightfoot, R (1995) Genes required for cellulose synthesis in *Agrobacterium tumefaciens*. *J Bacteriol* **177**: 1069–75.
- May, JF, Levengood, MR, Splain, RA, Brown, CD, and Kiessling, LL (2012) A processive carbohydrate polymerase that mediates bifunctional catalysis using a single active site. *Biochemistry* **51**: 1148–59.
- McCoy, AJ, Grosse-Kunstleve, RW, Adams, PD, Winn, MD, Storoni, LC, and Read, RJ (2007) Phaser crystallographic software. *J Appl Crystallogr* **40**: 658–674.
- McNicholas, S, Potterton, E, Wilson, KS, and Noble, MEM (2011) Presenting your structures: the CCP4mg molecular-graphics software. *Acta Crystallogr D Biol Crystallogr* **67**: 386–94.
- Merrick, MJ (1976) A morphological and genetic mapping study of bald colony mutants of *Streptomyces coelicolor*. *J Gen Microbiol* **96**: 299–315.
- Messing, J, Crea, R, and Seburg, PH (1981) A system for shotgun DNA sequencing. *Nucleic Acids Res* **9**: 309–21.
- Miethke, M, Monteferante, CG, Marahiel, MA, and Van Dijl, JM (2013) The *Bacillus subtilis* EfeUOB transporter is essential for high-affinity acquisition of ferrous and ferric iron. *Biochim Biophys Acta - Mol Cell Res* **1833**: 2267–2278.
- Millard, WA (1922) Common scab of potatoes. *Ann Appl Biol* **v. 9** (1922): 70–88.
- Monteferante, CG, MacKichan, C, Marchadier, E, Prejean, M-V, Carballido-López, R, and Van Dijl, JM (2013) Mapping the twin-arginine protein translocation network of *Bacillus subtilis*. *Proteomics* **13**: 800–11.
- Morgan, JLW, McNamara, JT, and Zimmer, J (2014) Mechanism of activation of bacterial cellulose synthase by cyclic-di-GMP. *Nat Struct Mol Biol* **21**: 489–96.
- Morgan, JLW, Strumillo, J, and Zimmer, J (2013) Crystallographic snapshot of cellulose synthesis and membrane translocation. *Nature* **493**: 181–6.
- Mulloy, B, Hart, GW, and Stanley, P (2009) Structural analysis of glycans. In *Essentials of Glycobiology*. 2nd edition. Varki A, Cummings RD, Esko JD, et al. (ed.). Cold Spring Harbor Laboratory Press, New York.
- Van Munster, JM, Nitsche, BM, Krijgheld, P, Van Wijk, A, Dijkhuizen, L, Wösten, HAB, et al. (2013) Chitinases CtcB and CfCl modify the cell wall in sporulating aerial mycelium of *Aspergillus niger*. *Microbiology* **159**: 1853–1867.
- Murshudov, GN, Vagin, AA, and Dodson, EJ (1997) Refinement of macromolecular structures by the maximum-likelihood method. *Acta Crystallogr D Biol Crystallogr* **53**: 240–55.
- Nakagawa, YS, Kudo, M, Loose, JSM, Ishikawa, T, Totani, K, Eijsink, VGH, and Vaaje-Kolstad, G (2015) A small lytic polysaccharide monooxygenase from *Streptomyces griseus* targeting  $\alpha$ - and  $\beta$ -chitin. *FEBS J* **282**: 1065–79.
- Newcomb, WD, and Rimstidt, JD (2002) Trace element distribution in US groundwaters: a probabilistic assessment using public domain data. *Appl Geochemistry* **17**: 49–57.
- Nielsen, J (1996) Modelling the morphology of filamentous microorganisms. *Trends Biotechnol* **14**: 438–443.

## References

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- Nielsen, J, and Johansen, C (1995) Pellet formation and fragmentation in submerged cultures of *Penicillium chrysogenum* and its relation to penicillin production. *Biotechnol Prog* **11**: 93–98.
- Nieminen, L, Webb, S, Smith, MCM, and Hoskisson, PA (2013) A flexible mathematical model platform for studying branching networks: experimentally validated using the model actinomycete, *Streptomyces coelicolor*. *PLoS One* **8**: e54316.
- Noens, EE, Mersinias, V, Willemse, J, Traag, BA, Laing, E, Chater, KF, et al. (2007) Loss of the controlled localization of growth stage-specific cell-wall synthesis pleiotropically affects developmental gene expression in an *sgsA* mutant of *Streptomyces coelicolor*. *Mol Microbiol* **64**: 1244–1259.
- Oberto, J (2013) SyntTax: a web server linking synteny to prokaryotic taxonomy. *BMC Bioinformatics* **14**: 4.
- Ostash, B, Shashkov, A, Streshinskaya, G, Tul'skaya, E, Baryshnikova, L, Dmitrenok, A, et al. (2014) Identification of *Streptomyces coelicolor* M145 genomic region involved in biosynthesis of teichulosonic acid-cell wall glycopolymer. *Folia Microbiol (Praha)* **3**: 355–360.
- Palmer, T, and Berks, BC (2012) The twin-arginine translocation (Tat) protein export pathway. *Nat Rev Microbiol* **10**: 483–96.
- Pastor, MT, Esteras-Chopo, A, and Serrano, L (2007) Hacking the code of amyloid formation: the amyloid stretch hypothesis. *Prion* **1**: 9–14.
- Paul, GC, and Thomas, CR (1998) Characterisation of mycelial morphology using image analysis. *Adv Biochem Eng Biotechnol* **60**: 1–59.
- Peisach, J, and Blumberg, WE (1974) Structural implications derived from the analysis of electron paramagnetic resonance spectra of natural and artificial copper proteins. *Arch Biochem Biophys* **165**: 691–708.
- Perrakis, A, Morris, R, and Lamzin, VS (1999) Automated protein model building combined with iterative structure refinement. *Nat Struct Biol* **6**: 458–63.
- Petersen, TN, Brunak, S, Heijne, G von, and Nielsen, H (2011) SignalP 4.0: discriminating signal peptides from transmembrane regions. *Nat Methods* **8**: 785–6.
- Petrus, MLC, and Claessen, D (2014) Pivotal roles for *Streptomyces* cell surface polymers in morphological differentiation, attachment and mycelial architecture. *Antonie Van Leeuwenhoek* **106**: 127–139.
- Petrus, MLC, Van Veluw, GJ, Wösten, HAB, and Claessen, D (2014) Sorting of *Streptomyces* cell pellets using a complex object parametric analyzer and sorter. *J Vis Exp* e51178.
- Phillips, AP, and Martin, KL (1983) Immunofluorescence analysis of *Bacillus* spores and vegetative cells by flow cytometry. *Cytometry* **4**: 123–131.
- Piette, A, Derouaux, A, Gerkens, P, Noens, EEE, Mazzucchelli, G, Vion, S, et al. (2005) From dormant to germinating spores of *Streptomyces coelicolor* A3(2): New perspectives from the *crp* null mutant. *J Proteome Res* **4**: 1699–1708.
- Potekhina, NV, Streshinskaya, GM, Tul'skaya, EM, and Shashkov, AS (2011) Cell wall teichoic acids in the taxonomy and characterization of Gram-positive bacteria. In *Methods in Microbiology*. pp. 132–164.
- Prosser, JL, and Tough, AJ (1991) Growth mechanisms and growth kinetics of filamentous microorganisms. *Crit Rev Biotechnol* **10**: 253–274.
- Rahman, O, Cummings, SP, and Sutcliffe, IC (2009) Phenotypic variation in *Streptomyces* sp. DSM 40537, a lipoteichoic acid producing actinomycete. *Lett Appl Microbiol* **48**: 226–9.
- Rioseras, B, López-García, MT, Yagüe, P, Sánchez, J, and Manteca, A (2014) Mycelium differentiation and development of *Streptomyces coelicolor* in lab-scale bioreactors: Programmed cell death, differentiation, and lysis are closely linked to undecylprodigiosin and actinorhodin production. *Bioresour Technol* **151**: 191–8.

- Rogers, MS, Tyler, EM, Akyumani, N, Kurtis, CR, Spooner, RK, Deacon, SE, et al. (2007) The stacking tryptophan of galactose oxidase: a second-coordination sphere residue that has profound effects on tyrosyl radical behavior and enzyme catalysis. *Biochemistry* **46**: 4606–18.
- Romero, D, Aguilar, C, Losick, R, and Kolter, R (2010) Amyloid fibers provide structural integrity to *Bacillus subtilis* biofilms. *Proc Natl Acad Sci U S A* **107**: 2230–4.
- Römling, U (2002) Molecular biology of cellulose production in bacteria. *Res Microbiol* **153**: 205–12.
- Römling, U, and Galperin, MY (2015) Bacterial cellulose biosynthesis: diversity of operons, subunits, products, and functions. *Trends Microbiol* .
- Rose, RW, Brüser, T, Kissinger, JC, and Pohlschröder, M (2002) Adaptation of protein secretion to extremely high-salt conditions by extensive use of the twin-arginine translocation pathway. *Mol Microbiol* **45**: 943–50.
- Ross, P, Mayer, R, and Benziman, M (1991) Cellulose biosynthesis and function in bacteria. *Microbiol Rev* **55**: 35–58.
- Sambrook, J, Fritsch, EF, Maniatis, T, Fritsch, E.F and Maniatis, T, and J (1989) *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor Laboratory Press, New York.
- Sancar, A (1996) DNA excision repair. *Annu Rev Biochem* **65**: 43–81.
- Sánchez-Rodríguez, A, Tytgat, HLP, Winderickx, J, Vanderleyden, J, Lebeer, S, and Marchal, K (2014) A network-based approach to identify substrate classes of bacterial glycosyltransferases. *BMC Genomics* **15**: 349.
- Sarrà, M, Casas, C, Poch, M, and Gòdia, F (1999) A simple structured model for continuous production of a hybrid antibiotic by *Streptomyces lividans* pellets in a fluidized-bed bioreactor. *Appl Biochem Biotechnol* **80**: 39–50.
- Sawyer, EB, Claessen, D, Gras, SL, and Perrett, S (2012) Exploiting amyloid: how and why bacteria use cross- $\beta$  fibrils. *Biochem Soc Trans* **40**: 728–34.
- Sawyer, EB, Claessen, D, Haas, M, Hurgobin, B, and Gras, SL (2011) The assembly of individual chaplin peptides from *Streptomyces coelicolor* into functional amyloid fibrils. *PLoS One* **6**: e18839.
- Saxena, IM, Brown, RM, Fevre, M, Geremia, RA, and Henrissat, B (1995) Multidomain architecture of  $\beta$ -glycosyl transferases: Implications for mechanism of action. *J Bacteriol* **177**: 1419–1424.
- Saxena, IM, Lin, FC, and Brown, RM (1990) Cloning and sequencing of the cellulose synthase catalytic subunit gene of *Acetobacter xylinum*. *Plant Mol Biol* **15**: 673–83.
- Schaerlaekens, K, Van Mellaert, L, Lammertyn, E, Geukens, N, and Anné, J (2004) The importance of the Tat-dependent protein secretion pathway in *Streptomyces* as revealed by phenotypic changes in tat deletion mutants and genome analysis. *Microbiology* **150**: 21–31.
- Schaerlaekens, K, Schierová, M, Lammertyn, E, Geukens, N, Anné, J, and Van Mellaert, L (2001) Twin-arginine translocation pathway in *Streptomyces lividans*. *J Bacteriol* **183**: 6727–32.
- Schäffer, C, and Messner, P (2005) The structure of secondary cell wall polymers: how Gram-positive bacteria stick their cell walls together. *Microbiology* **151**: 643–51.
- Schatz, A, Bugle, E, and Waksman, SA (1944) Streptomycin, a substance exhibiting antibiotic activity against Gram-positive and Gram-negative bacteria. *Exp Biol Med* **55**: 66–69.
- Schiavone, M, Vax, A, Formosa, C, Martin-Yken, H, Dague, E, and François, JM (2014) A combined chemical and enzymatic method to determine quantitatively the polysaccharide components in the cell wall of yeasts. *FEMS Yeast Res* **14**: 933–47.
- Schneewind, O, and Missiakas, DM (2012) Protein secretion and surface display in Gram-positive bacteria. *Philos Trans R Soc Lond B Biol Sci* **367**: 1123–39.
- Schneider, CA, Rasband, WS, and Eliceiri, KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods*

## References

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- 9: 671–675.
- Scholtmeijer, K, Vocht, ML de, Rink, R, Robillard, GT, and Wösten, HAB (2009) Assembly of the fungal SC3 hydrophobin into functional amyloid fibrils depends on its concentration and is promoted by cell wall polysaccharides. *J Biol Chem* **284**: 26309–14.
- Seebeck, FP (2010) In vitro reconstitution of mycobacterial ergothioneine biosynthesis. *J Am Chem Soc* **132**: 6632–6633.
- Serra, DO, Richter, AM, and Hengge, R (2013) Cellulose as an architectural element in spatially structured *Escherichia coli* biofilms. *J Bacteriol* **195**: 5540–54.
- Sezer, M, Genebra, T, Mendes, S, Martins, LO, and Todorovic, S (2012) A DyP-type peroxidase at a bio-compatible interface: structural and mechanistic insights. *Soft Matter* **8**: 10314.
- Shashkov, AS, Kosmachevskaya, LN, Streshinskaya, GM, Evtushenko, LI, Bueva, O V, Denisenko, VA, et al. (2002) A polymer with a backbone of 3-deoxy-D-glycero-D-galacto-non-2-ulopyranosonic acid, a teichuronic acid, and a beta-glucosylated ribitol teichoic acid in the cell wall of plant pathogenic *Streptomyces* sp. VKM Ac-2124. *Eur J Biochem* **269**: 6020–5.
- Shimon, LJ, Bayer, EA, Morag, E, Lamed, R, Yaron, S, Shoham, Y, and Frolov, F (1997) A cohesin domain from *Clostridium thermocellum*: the crystal structure provides new insights into cellulosome assembly. *Structure* **5**: 381–390.
- Sievers, F, Wilm, A, Dineen, D, Gibson, TJ, Karplus, K, Li, W, et al. (2011) Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Mol Syst Biol* **7**: 539.
- Silakowski, B, Ehret, H, and Schairer, HU (1998) *fbbB*, a gene encoding a putative galactose oxidase, is involved in *Stigmatella aurantiaca* fruiting body formation. *J Bacteriol* **180**: 1241–1247.
- Silakowski, B, Pospiech, A, Neumann, B, and Schairer, HU (1996) *Stigmatella aurantiaca* fruiting body formation is dependent on the *fbbA* gene encoding a polypeptide homologous to chitin synthases. *J Bacteriol* **178**: 6706–13.
- Sillitoe, I, Cuff, AL, Dessailly, BH, Dawson, NL, Furnham, N, Lee, D, et al. (2013) New functional families (FunFams) in CATH to improve the mapping of conserved functional sites to 3D-structures. *Nucleic Acids Res* **41**: D490–8.
- Simm, R, Morr, M, Kader, A, Nimtz, M, and Römling, U (2004) GGDEF and EAL domains inversely regulate cyclic di-GMP levels and transition from sessility to motility. *Mol Microbiol* **53**: 1123–1134.
- Singh, R, and Eltis, LD (2015) The multihued palette of dye-decolorizing peroxidases. *Arch Biochem Biophys* **574**: 56–65.
- Smits, WK, Kuipers, OP, and Veening, J-W (2006) Phenotypic variation in bacteria: the role of feedback regulation. *Nat Rev Microbiol* **4**: 259–271.
- Soliveri, J, Vijgenboom, E, Granozzi, C, Plaskitt, KA, and Chater, KF (1993) Functional and evolutionary implications of a survey of various actinomycetes for homologues of two *Streptomyces coelicolor* sporulation genes. *J Gen Microbiol* **139**: 2569–78.
- Stein, N (2008) CHAINSAW : a program for mutating pdb files used as templates in molecular replacement. *J Appl Crystallogr* **41**: 641–643.
- Studier, FW (2005) Protein production by auto-induction in high density shaking cultures. *Protein Expr Purif* **41**: 207–34.
- Sugano, Y, Sasaki, K, and Shoda, M (1999) cDNA cloning and genetic analysis of a novel decolorizing enzyme, peroxidase gene dyp from *Geotrichum candidum* Dec 1. *J Biosci Bioeng* **87**: 411–417.
- Sugano, Y, Muramatsu, R, Ichiyangai, A, Sato, T, and Shoda, M (2007) DyP, a unique dye-decolorizing peroxidase, represents a novel heme peroxidase family: ASP171 replaces the distal histidine of classical peroxidases. *J*

- Biol Chem 282: 36652–8.
- Sun, L, Bulter, T, Alcalde, M, Petrounia, IP, and Arnold, FH (2002) Modification of galactose oxidase to introduce glucose 6-oxidase activity. *Chembiochem* **3**: 781–3.
- Sunde, M, Serpell, LC, Bartlam, M, Fraser, PE, Pepys, MB, and Blake, CC (1997) Common core structure of amyloid fibrils by synchrotron X-ray diffraction. *J Mol Biol* **273**: 729–739.
- Świątek, MA, Tenconi, E, Rigali, S, and Van Wezel, GP (2012) Functional analysis of the *N*-acetylglucosamine metabolic genes of *Streptomyces coelicolor* and role in control of development and antibiotic production. *J Bacteriol* **194**: 1136–44.
- Takano, M, Nakamura, M, and Yamaguchi, M (2010) Glyoxal oxidase supplies hydrogen peroxide at hyphal tips and on hyphal wall to manganese peroxidase of white-rot fungus *Phanerochaete crassa* WD1694. *J Wood Sci* **56**: 307–313.
- Takano, M, Hayashi, N, Nakamura, M, Yamaguchi, M (2009) Extracellular peroxidase reaction at hyphal tips of white-rot fungus *Phanerochaete crassa* WD1694 and in fungal slime. *J. Wood Sci.* **55**, 302–307.
- Talbot, NJ (1997) Growing into the air. *Curr Biol* **7**: R78–R81.
- Talbot, NJ, Ebbole, DJ, and Hamer, JE (1993) Identification and characterization of MPG1, a gene involved in pathogenicity from the rice blast fungus *Magnaporthe grisea*. *Plant Cell* **5**: 1575–90.
- Talbot, NJ, Kershaw, MJ, Wakley, GE, De Vries, O, Wessels, J, and Hamer, JE (1996) MPG1 encodes a fungal hydrophobin involved in surface interactions during infection-related development of *Magnaporthe grisea*. *Plant Cell* **8**: 985–999.
- Tillotson, RD, Wösten, HA, Richter, M, and Willey, JM (1998) A surface active protein involved in aerial hyphae formation in the filamentous fungus *Schizophyllum commune* restores the capacity of a bald mutant of the filamentous bacterium *Streptomyces coelicolor* to erect aerial structures. *Mol Microbiol* **30**: 595–602.
- Tough, AJ, and Prosser, JI (1996) Experimental verification of a mathematical model for pelleted growth of *Streptomyces coelicolor* A3(2) in submerged batch culture. *Microbiology* **142**: 639–648.
- Tran, NT, Hengst, CD Den, Gomez-Escribano, JP, and Buttner, MJ (2011) Identification and characterization of CdgB, a diguanylate cyclase involved in developmental processes in *Streptomyces coelicolor*. *J Bacteriol* **193**: 3100–8.
- Tremblay, LW, Dunaway-Mariano, D, and Allen, KN (2006) Structure and activity analyses of *Escherichia coli* K-12 NagD provide insight into the evolution of biochemical function in the haloalkanoic acid dehalogenase superfamily. *Biochemistry* **45**: 1183–93.
- Tresner, HD, Hayes, JA, and Backus, EJ (1967) Morphology of submerged growth of streptomycetes as a taxonomic aid. I. Morphological development of *Streptomyces aureofaciens* in agitated liquid media. *Appl Microbiol* **15**: 1185–91.
- Tul'skaya, EM, Shashkov, AS, Streshinskaya, GM, Senchenkova, SN, Potekhina, N V, Kozlova, YI, and Evtushenko, LI (2011) Teichuronic and teichulosonic acids of actinomycetes. *Biochem Biokhimiia* **76**: 736–44.
- Ueda, K, Oinuma, K-I, Ikeda, G, Hosono, K, Ohnishi, Y, Horinouchi, S, and Beppu, T (2002) AmfS, an extracellular peptidic morphogen in *Streptomyces griseus*. *J Bacteriol* **184**: 1488–92.
- Ueda, K, Tomaru, Y, Endoh, K, Beppu, T (1997) Stimulatory effect of copper on antibiotic production and morphological differentiation in *Streptomyces tanashiensis*. *J. Antibiot. (Tokyo)* **50**, 693–5.
- Vara, J, Lewandowska-Skarbek, M, Wang, YG, Donadio, S, and Hutchinson, CR (1989) Cloning of genes governing the deoxysugar portion of the erythromycin biosynthesis pathway in *Saccharopolyspora erythraea* (*Streptomyces erythreus*). *J Bacteriol* **171**: 5872–81.
- Vecht-Lifshitz, SE, Magdassi, S, and Braun, S (1990) Pellet formation and cellular aggregation in *Streptomyces*

## References

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- tendae. *Biotechnol Bioeng* **35**: 890–6.
- Veenking, J-W, Smits, WK, and Kuipers, OP (2008) Bistability, epigenetics, and bet-hedging in bacteria. *Annu Rev Microbiol* **62**: 193–210.
- Van Veluw, GJ, Petrus, MLC, Gubbens, J, De Graaf, R, De Jong, IP, Van Wezel, GP, et al. (2012) Analysis of two distinct mycelial populations in liquid-grown *Streptomyces* cultures using a flow cytometry-based proteomics approach. *Appl Microbiol Biotechnol* **96**: 1301–12.
- Van Veluw, GJ, Teertstra, WR, De Bekker, C, Vinck, A, Van Beek, N, Muller, WH, et al. (2013) Heterogeneity in liquid shaken cultures of *Aspergillus niger* inoculated with melanised conidia or conidia of pigmentation mutants. *Stud Mycol* **74**: 47–57.
- Vrijenboom, E, Woudt, LP, Heinstra, PW, Rietveld, K, Van Haarlem, J, Van Wezel, GP, et al. (1994) Three *tuf*-like genes in the kirromycin producer *Streptomyces ramocissimus*. *Microbiology* **140** ( Pt 4): 983–98.
- Vinck, A, Terlouw, M, Pestman, WR, Martens, EP, Ram, AF, Van Den Hondel, CAMJJ, and Wösten, HAB (2005) Hyphal differentiation in the exploring mycelium of *Aspergillus niger*. *Mol Microbiol* **58**: 693–699.
- De Vocht, ML, Reviakine, I, Ulrich, W-P, Bergsma-Schutter, W, Wösten, HAB, Vogel, H, et al. (2002) Self-assembly of the hydrophobin SC3 proceeds via two structural intermediates. *Protein Sci* **11**: 1199–1205.
- Vrancken, K, and Anné, J (2009) Secretory production of recombinant proteins by *Streptomyces*. *Future Microbiol* **4**: 181–188.
- Wardell, JN, Stocks, SM, Thomas, CR, and Bushell, ME (2002) Decreasing the hyphal branching rate of *Saccharopolyspora erythraea* NRRL 2338 leads to increased resistance to breakage and increased antibiotic production. *Biotechnol Bioeng* **78**: 141–146.
- Weerapana, E, and Imperiali, B (2006) Asparagine-linked protein glycosylation: from eukaryotic to prokaryotic systems. *Glycobiology* **16**: 91R–101R.
- Weidenmaier, C, and Peschel, A (2008) Teichoic acids and related cell-wall glycopolymers in Gram-positive physiology and host interactions. *Nat Rev Microbiol* **6**: 276–87.
- Wessel, D, and Flügge, UI (1984) A method for the quantitative recovery of protein in dilute solution in the presence of detergents and lipids. *Anal Biochem* **138**: 141–143.
- Van Wezel, GP, Krabben, P, Traag, BA, Keijser, BJF, Kerste, R, Vrijenboom, E, et al. (2006) Unlocking *Streptomyces* spp. for use as sustainable industrial production platforms by morphological engineering. *Appl Environ Microbiol* **72**: 5283–5288.
- Van Wezel, GP, and McDowall, KJ (2011) The regulation of the secondary metabolism of *Streptomyces*: new links and experimental advances. *Nat Prod Rep* **28**: 1311–1333.
- Whitchurch, CB, Tolker-Nielsen, T, Ragas, PC, and Mattick, JS (2002) Extracellular DNA required for bacterial biofilm formation. *Science* **295**: 1487.
- White, AP, Gibson, DL, Collinson, SK, Banser, PA, and Kay, WW (2003) Extracellular polysaccharides associated with thin aggregative fimbriae of *Salmonella enterica* serovar enteritidis. *J Bacteriol* **185**: 5398–407.
- Whittaker, MM, Kersten, PJ, Cullen, D, and Whittaker, JW (1999) Identification of catalytic residues in glyoxal oxidase by targeted mutagenesis. *J Biol Chem* **274**: 36226–32.
- Whittaker, MM, and Whittaker, JW (1988) The active site of galactose oxidase. *J Biol Chem* **263**: 6074–80.
- Whittaker, MM, and Whittaker, JW (1990) A tyrosine-derived free radical in apogalactose oxidase. *J Biol Chem* **265**: 9610–3.
- Whittaker, MM, and Whittaker, JW (1993) Ligand interactions with galactose oxidase: mechanistic insights. *Biophys J* **64**: 762–72.

- Whittaker, MM, and Whittaker, JW (2003) Cu(I)-dependent biogenesis of the galactose oxidase redox cofactor. *J Biol Chem* **278**: 22090–101.
- Whittaker, MM, and Whittaker, JW (2006) *Streptomyces coelicolor* oxidase (SCO2837p): a new free radical metalloenzyme secreted by *Streptomyces coelicolor* A3(2). *Arch Biochem Biophys* **452**: 108–18.
- Widdick, DA, Dilks, K, Chandra, G, Bottrill, A, Naldrett, M, Pohlschröder, M, and Palmer, T (2006) The twin-arginine translocation pathway is a major route of protein export in *Streptomyces coelicolor*. *Proc Natl Acad Sci U S A* **103**: 17927–32.
- Widdick, DA, Eijlander, RT, Van Dijl, JM, Kuipers, OP, and Palmer, T (2008) A facile reporter system for the experimental identification of twin-arginine translocation (Tat) signal peptides from all kingdoms of life. *J Mol Biol* **375**: 595–603.
- Wildermuth, H, Wehrli, E, and Horne, RW (1971) The surface structure of spores and aerial mycelium in *Streptomyces coelicolor*. *J Ultrastruct Res* **35**: 168–80.
- Willemse, J, Borst, JW, Waal, E De, Bisseling, T, and Van Wezel, GP (2011) Positive control of cell division: FtsZ is recruited by SsgB during sporulation of *Streptomyces*. *Genes Dev* **25**: 89–99.
- Willemse, J, Ruban-Ośmialowska, B, Widdick, D, Celler, K, Hutchings, MI, Van Wezel, GP, and Palmer, T (2012) Dynamic localization of Tat protein transport machinery components in *Streptomyces coelicolor*. *J Bacteriol* **194**: 6272–81.
- Willey, J, Santamaria, R, Guijarro, J, Geistlich, M, and Losick, R (1991) Extracellular complementation of a developmental mutation implicates a small sporulation protein in aerial mycelium formation by *S. coelicolor*. *Cell* **65**: 641–50.
- Willey, JM, Willems, A, Kodani, S, and Nodwell, JR (2006) Morphogenetic surfactants and their role in the formation of aerial hyphae in *Streptomyces coelicolor*. *Mol Microbiol* **59**: 731–742.
- Wood, PJ (1980) Specificity in the interaction of direct dyes with polysaccharides. *Carbohydr Res* **85**: 271–287.
- Worrall, JAR, and Vijgenboom, E (2010) Copper mining in *Streptomyces*: enzymes, natural products and development. *Nat Prod Rep* **27**: 742–56.
- Wösten, H, De Vries, O, and Wessels, J (1993) Interfacial self-assembly of a fungal hydrophobin into a hydrophobic rodlet layer. *Plant Cell* **5**: 1567–1574.
- Wösten, HAB, Schuren, FH, and Wessels, JG (1994) Interfacial self-assembly of a hydrophobin into an amphipathic protein membrane mediates fungal attachment to hydrophobic surfaces. *EMBO J* **13**: 5848–54.
- Wösten, HAB, Van Wetter, M-A, Lugones, LG, Van der Mei, HC, Busscher, HJ, and Wessels, JGH (1999) How a fungus escapes the water to grow into the air. *Curr Biol* **9**: 85–88.
- Xu, H, Chater, KF, Deng, Z, and Tao, M (2008) A cellulose synthase-like protein involved in hyphal tip growth and morphological differentiation in *Streptomyces*. *J Bacteriol* **190**: 4971–8.
- Yamanaka, K, Oikawa, H, Ogawa, HO, Hosono, K, Shimmachi, F, Takano, H, et al. (2005) Desferrioxamine E produced by *Streptomyces griseus* stimulates growth and development of *Streptomyces tanashiensis*. *Microbiology* **151**: 2899–2905.
- Yeats, C, Bentley, S, and Bateman, A (2003) New knowledge from old: In silico discovery of novel protein domains in *Streptomyces coelicolor*. *BMC Microbiol* **3**: 3.
- Zogaj, X, Nimtz, M, Rohde, M, Bokranz, W, Römling, U, and Romling, U (2001) The multicellular morphotypes of *Salmonella typhimurium* and *Escherichia coli* produce cellulose as the second component of the extracellular matrix. *Mol Microbiol* **39**: 1452–1463.