

831

REFERENCES

- 832 Altschul, S.F., Madden, T.L., Schaffer, A.A., Zhang, J., Zhang, Z., Miller, W., and Lipman, D.J.
833 (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs.
834 *Nucleic Acids Res* **25**: 3389-3402.
- 835 Antonaru, L.A., and Nürnberg, D.J. (2017) Role of PatS and cell type on the heterocyst spacing
836 pattern in a filamentous branching cyanobacterium. *FEMS Microbiol Lett* **364**: fnx154.
- 837 Bauer, C.C., Ramaswamy, K.S., Endley, S., Scappino, L.A., Golden, J.W., and Haselkorn, R.
838 (1997) Suppression of heterocyst differentiation in *Anabaena* PCC 7120 by a cosmid carrying
839 wild-type genes encoding enzymes for fatty acid synthesis. *FEMS Microbiol Lett* **151**: 23-39.
- 840 Black, T.A., Cai, Y., and Wolk, C.P. (1993) Spatial expression and autoregulation of *hetR*, a
841 gene involved in the control of heterocyst development in *Anabaena*. *Mol Microbiol* **9**: 77-84.
- 842 Black, T.A., and Wolk, C.P. (1994) Analysis of a *Het⁻* mutation in *Anabaena* sp. strain
843 PCC 7120 implicates a secondary metabolite in the regulation of heterocyst spacing. *J Bacteriol*
844 **176**: 2282-2292.
- 845 Buikema, W.J., and Haselkorn, R. (1991a) Isolation and complementation of nitrogen fixation
846 mutants of the cyanobacterium *Anabaena* sp. strain PCC7120. *J Bacteriol* **173**: 1879-1885.
- 847 Buikema, W.J., and Haselkorn, R. (1991b) Characterization of a gene controlling heterocyst
848 differentiation in the cyanobacterium *Anabaena* 7120. *Genes Devel* **5**: 321-330.
- 849 Buikema, W.J., and Haselkorn, R. (2001) Expression of the *Anabaena hetR* gene from a copper-
850 regulated promoter leads to heterocyst differentiation under repressing conditions. *Proc Natl*
851 *Acad Sci USA* **98**: 2729-2734.
- 852 Cai, Y., and Wolk, C.P. (1997) *Anabaena* sp. strain PCC 7120 responds to nitrogen deprivation
853 with a cascade-like sequence of transcriptional activations. *J Bacteriol* **179**: 267-271.
- 854 Callahan, S.M., and Buikema, W.J. (2001) The role of HetN in maintenance of the heterocyst
855 pattern in *Anabaena* sp. PCC 7120. *Mol Microbiol* **40**: 941-950.
- 856 Chao, K.-M., and Zhang, L. (2009) Sequence comparison: theory and methods. In *Scoring*
857 *Matrices*, Chapter 8. Springer-Verlag, London. pp. 149-172.
- 858 Corrales-Guerrero, L., Mariscal, V., Flores, E., and Herrero, A. (2013) Functional dissection and
859 evidence for intercellular transfer of the heterocyst-differentiation PatS morphogen. *Mol*
860 *Microbiol* **88**: 1093-1105.
- 861 Corrales-Guerrero, L., Mariscal, V., Nürnberg, D.J., Elhai, J., Mullineaux, C.W., Flores, E., and
862 Herrero, A. (2014) Subcellular localization and clues for the function of the HetN factor
863 influencing heterocyst distribution in *Anabaena* sp. strain PCC 7120. *J Bacteriol* **196**: 3452-
864 3460.
- 865 Crooks, G.E., Hon, G., Chandonia, J.M., and Brenner, S.E. (2004) WebLogo: a sequence logo
866 generator, *Genome Res*, 14: 1188-1190.

867 Dawson, J.P., Weinger, J.S., and Engleman, D.M. (2002) Motifs of serine and threonine can
868 drive association of transmembrane helices. *J Mol Biol* **316**: 799-805.

869 Dong, Y., Huang, X., Wu, X.-Y., and Zhao, J. (2000) Identification of the active site of HetR
870 protease and its requirement for heterocyst differentiation in the cyanobacterium *Anabaena* sp.
871 strain PCC 7120. *J Bacteriol* **182**: 1575-1579.

872 Elhai, J., Vepritskiy, A., Muro-Pastor, A.M., Flores, E. and Wolk, C.P. (1997) Reduction of
873 conjugal transfer efficiency by three restriction activities of *Anabaena* sp. strain PCC 7120. *J*
874 *Bacteriol* **179**: 1998–2005.

875 Elhai, J., Taton, A., Massar, J.P., Myers, J.K., Travers, M., Casey, J., *et al.* (2009) BioBIKE: A
876 web-based, programmable, integrated biological knowledge base. *Nucleic Acids Res* **37**: W28-
877 W32.

878 Feldmann, E.A., Ni, S., Sahu, I.D., Mishler, C.H., Risser, D.D., Murakami, J.L., *et al.* (2011)
879 Evidence for direct binding between HetR from *Anabaena* sp. PCC 7120 and PatS-5.
880 *Biochemistry* **50**: 9212-9224.

881 Feldmann, E.A., Ni, S., Sahu, I.D., Mishler, C.H., Levengood, J.D., Kushnir, Y., *et al.* (2012)
882 Differential binding between PatS C-terminal peptide fragments and HetR from *Anabaena* sp.
883 PCC 7120. *Biochemistry* **51**: 2436-2442.

884 Flaherty, B.L., Van Nieuwerburgh, F., Head, S.R., and Golden, J.W. (2011) Directional RNA
885 deep sequencing sheds new light on the transcriptional response of *Anabaena* sp. strain
886 PCC 7120 to combined-nitrogen deprivation. *BMC Genomics* **12**: 332.

887 Flaherty, B.L., Johnson, D.B.F., and Golden, J.W. (2014) Deep sequencing of HetR-bound DNA
888 reveals novel HetR targets in *Anabaena* sp. strain PCC7120. *BMC Microbiol* **13**: 255.

889 Flores, E., and Herrero, A. (1994). Assimilatory nitrogen metabolism and its regulation, In *The*
890 *Molecular Biology of Cyanobacteria*. Bryant, D.A. (ed.). Kluwer Academic Publishers, Boston,
891 Mass. p. 487-517.

892 Gerdtzen, Z.P., Salgado, J.C., Osses, A., Asenjo, J.A., Rapaport, I., and Andrews, B.A. (2009)
893 Modeling heterocyst pattern formation in cyanobacteria. *BMC Bioinform* **10 (Suppl 6)**: 516.

894 Gierer, A., and Meinhardt, H. (1972) A theory of biological pattern formation. *Kybernetik* **12**:
895 30-39.

896 Gugger, M.F., and Hoffmann, L. (2004) Polyphyly of true branching cyanobacteria
897 (Stigonematales). *Intl J Syst Evol Microbiol* **54**: 349-357.

898 Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. (2010)
899 New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the
900 performance of PhyML 3.0. *Syst Biol* **59**: 307-321,

901 Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. (2017)
902 PhyML 3.0: new algorithms, methods and utilities. [WWW document] URL [http://www.atgc-](http://www.atgc-montpellier.fr/phyml/)
903 [montpellier.fr/phyml/](http://www.atgc-montpellier.fr/phyml/)

904 Henikoff, S., and Henikoff, J.G. (1992) Amino acid substitution matrices from protein blocks.
905 *Proc Natl Acad Sci USA* **89**: 10915-10919.

906 Herrero, A., Stavans, J., and Flores, E. (2016) The multicellular nature of filamentous heterocyst-
907 forming cyanobacteria. *FEMS Microbiol Rev* **40**: 831-854.

908 Higa, K.C., Rajagopalen, R., Risser, D.D., Rivers, O.S., Tom, S.K., Videau, P., and Callahan,
909 S.M. (2012) The RGSGR amino acid motif of the intercellular signalling protein, HetN, is
910 required for patterning of heterocysts in *Anabaena* sp. strain PCC 7120. *Mol Microbiol* **83**: 682-
911 693.

912 Higgs PG, and Attwood TK (2005). Bioinformatics and Molecular Evolution. Malden MA,
913 Blackwell Publishing.

914 Holczyk, E., and Hansel, A. (2000) Cyanobacterial cell walls: news from an unusual prokaryotic
915 envelope. *J Bacteriol* **182**: 1191-1199.

916 Howard-Azzeh, M., Shamseer, L., Schellhorn, H.E., and Gupta, R.S. (2014) Phylogenetic
917 analysis and molecular signatures defining a monophyletic clade of heterocystous cyanobacteria
918 and identifying its closest relatives. *Photosynth Res* **122**: 171-185.

919 Hu, H.-X., Jiang, Y.-L., Zhao, M.-X., Cai, K., Liu, S., Wen, B., *et al.* (2015) Structural insights
920 into HetR-PatS interaction involved in cyanobacterial pattern formation. *Sci Reports* **5**: 16470.

921 Huang X., Dong Y., and Zhao J. (2004) HetR homodimer is a DNA-binding protein required for
922 heterocyst differentiation, and the DNA-binding activity is inhibited by PatS. *Proc Natl Acad Sci*
923 *U S A* **101**: 4848-4853.

924 Hug, L.A., Baker, B.B., Anantharaman, K, Brown, C.T., Probst, A.J., Castelle, C.J. *et al.* (2016)
925 A new view of the tree of life. *Nature Microbiol* **1**: 1-6.

926 Janson, S., Wouters, J., Bergman, B., and Carpenter, E.J. (1999). Host specificity in the *Richelia*-
927 diatom symbiosis revealed by *hetR* gene sequence analysis. *Environ Microbiol* **1**: 431-438.

928 Kaneko, T., Nakamura, Y., Wolk, C.P., Kuritz, T., Sasamoto, S., Watanabe, A., *et al.* (2001)
929 Complete genomic sequence of the filamentous nitrogen-fixing cyanobacterium *Anabaena* sp.
930 strain PCC 7120. *DNA Res* **8**: 205–213; 227-53.

931 Khudyakov, I.Y., and Golden, J.W. (2004) Different functions of HetR, a master regulator of
932 heterocyst differentiation in *Anabaena* sp. PCC7120, can be separated by mutation. *Proc Natl*
933 *Acad Sci USA* **101**: 16040-16045.

934 Kim, Y., Joachimiak, G., Ye, Z., Binkowski, T.A., Zhang, R., Gornicki, P., *et al.* (2011)
935 Structure of transcription factor HetR required for heterocyst differentiation in cyanobacteria.
936 *Proc Natl Acad Sci USA* **108**: 10109-10114.

937 Kim, Y., Ye, Z., Joachimiak, G., Videau, P., Young, J., Hurd, K., *et al.* (2013) Structures of
938 complexes comprised of *Fischerella* transcription factor HetR with *Anabaena* DNA targets. *Proc*
939 *Natl Acad Sci USA* **110**: E1716-E1723.

940 Koch, R., and Kupczok, A., Stucken, K., Ilhan, J., Hammerschmidt, K., Dagan, T. (2017)
941 Plasticity first: molecular signatures of a complex morphological trait in filamentous
942 cyanobacteria. *BMC Evol Biol* **17**: 209.

943 Krogh, A., Larsson, B., von Heijne G., and Sonnhammer, E.L.L. (2001) Predicting
944 transmembrane protein topology with a hidden Markov model: Application to complete
945 genomes. *J Mol Biol* **305**: 567-580.

946 Kumar, K., Mella-Herrera, R.A., and Golden, J.W. (2010) Cyanobacterial heterocysts. *Cold*
947 *Spring Harb Perspect Biol* **2**: a000315.

948 Lamont, H.C. (1969) Sacrificial cell death and trichome breakage in an Oscillatorian blue-green
949 alga: the role of murein. *Arch Mikrobiol* **69**: 237-259.

950 Li, B., Huang, X., and Zhao, J. (2002) Expression of *hetN* during heterocyst differentiation and
951 its inhibition of *hetR* up-regulation in the cyanobacterium *Anabaena* sp. PCC 7120. *FEBS Lett*
952 **517**: 87-91.

953 Li, X., Sandh, G., Nenninger, A., Muro-Pastor, A.M., and Stensjö, K. (2015) Differential
954 transcriptional regulation of orthologous *dps* genes from two closely related heterocyst-forming
955 cyanobacteria. *FEMS Microbiol Lett* **362**: fnv017.

956 Maldener, I., Summers, M.L., and Sukenik, A. (2014) Cellular differentiation in filamentous
957 cyanobacteria. In *The Cell Biology of Cyanobacteria*. Flores, E., and Herrero, A. (eds). Caister
958 Academic Press. pp. 263-291.

959 Marcon, L., and Sharpe, J. (2012) Turing patterns in development: What about the horse part?
960 *Curr Opin Genet Dev* **22**: 578-584.

961 Meeks, J.C., Elhai, J., Thiel, T., Potts, M., Larimer, F., Lamerdin, J., *et al.* (2002) An overview
962 of the genome of *Nostoc punctiforme*, a multicellular, symbiotic cyanobacterium. *Photosyn Res*
963 **70**: 85-106.

964 Meinhardt, H. (2008) Models of biological pattern formation: From elementary steps to the
965 organization of embryonic axes. *Curr Top Dev Biol* **81**: 1-63.

966 Mitschke, J., Vioque, A., Haas, F., Hess, W.R., and Muro-Pastor, A.M. (2011) Dynamics of
967 transcriptional start site selection during nitrogen stress-induced cell differentiation in *Anabaena*
968 sp. PCC7120. *Proc Natl Acad Sci USA* **108**: 20130-20135.

969 Monera, O. D., Sereda, T.J., Zhou, N.E., Kay, C.M., and Hodgesis, T.S. (1995) Relationship of
970 sidechain hydrophobicity and α -helical propensity on the stability of the single-stranded
971 amphipathic α -helix. *J Peptide Sci* **1**: 319-329.

972 Muñoz-Garcia, J., and Ares, S. (2016) Formation and maintenance of nitrogen-fixing cell
973 patterns in filamentous cyanobacteria. *Proc Natl Acad Sci USA* **113**: 6218-6223.

974 Muro-Pastor, A.M. (2014). The heterocyst-specific NsiR1 small RNA is an early marker of cell
975 differentiation in cyanobacterial filaments. *mBio* **5**:e01079-14.

976 Muro-Pastor, A.M., Brenes-Álvarez, and M., Vioque, A. (2017) A combinatorial strategy of
977 alternative promoter use during differentiation of a heterocystous cyanobacterium. *Environ*
978 *Microbiol Rep* **9**: 449-458.

979 Muro-Pastor, A.M., Valladares, A., Flores, E., and Herrero, A. (2002) Mutual dependence of the
980 expression of the cell differentiation regulatory protein HetR and the global nitrogen regulator
981 NtcA during heterocyst development. *Mol Microbiol* **44**: 1377-1385.

982 National Center for Biotechnology Information (2017) Prokaryotic RefSeq genome re-
983 annotation project. [WWW document] URL
984 <https://www.ncbi.nlm.nih.gov/refseq/about/prokaryotes/reannotation/>

985 Nayar, A.S., Yamaura, H., Rajagopalan, R., Risser, D.D., and Callahan, S.M. (2007) FraG is
986 necessary for filament integrity and heterocyst maturation in the cyanobacterium *Anabaena* sp.
987 strain PCC 7120. *Microbiol* **153**: 601-607.

988 Nürnberg, D.J., Mariscal, V., Parker, J., Mastroianni, G., Flores, E., Mullineaux, C.W. (2014)
989 Branching and intercellular communication in the Section V cyanobacterium *Mastigocladus*
990 *laminosus*, a complex multicellular prokaryote. *Mol Microbiol* **91**: 935-949.

991 Petersen, T. N., Brunak, S., von Heijne, G., and Nielsen, H. (2011) SignalP 4.0: discriminating
992 signal peptides from transmembrane regions. *Nature Methods* **8**: 785-786.

993 Picossi, S., Flores, E., and Herrero, A. (2014) ChIP analysis unravels an exceptionally wide
994 distribution of DNA binding sites for the NtcA transcription factor in a heterocyst-forming
995 cyanobacterium. *BMC Genomics* **15**: 22.

996 Rajagopalan, R., and Callahan, S.M. (2010) Temporal and spatial regulation of the four
997 transcription start sites of *hetR* from *Anabaena* sp. strain PCC 7120. *J Bacteriol* **192**: 1088-1096.

998 Ramaswamy, K.S., Carrasco, C.D., Fatma, T., and Golden, J.W. (1997) Cell-type specificity of
999 the *Anabaena fdxN*-element rearrangement requires *xisH* and *xisI*. *Mol Microbiol* **23**: 1241–
1000 1250.

1001 Rippka, R., Deruelles, J., Waterbury, J.B., Herdman, M., and Stanier, R.Y. (1979) Generic
1002 assignments, strain histories and properties of pure cultures of cyanobacteria. *J Gen Microbiol*
1003 **111**: 1-61.

1004 Risser, D.D., and Callahan, S.M. (2007) Mutagenesis of *hetR* reveals amino acids necessary for
1005 HetR function in the heterocystous cyanobacterium *Anabaena* sp. strain PCC7120. *J Bacteriol*
1006 **189**: 2460-2467.

1007 Risser, D.D., and Callahan, S.M. (2009) Genetic and cytological evidence that heterocyst
1008 patterning is regulated by inhibitor gradients that promote activator decay. *Proc Natl Acad Sci*
1009 *USA* **106**: 19884-19888.

1010 Rivers, O.S., Videau, P., and Callahan, S.M. (2014) Mutation of *sepJ* reduces the intercellular
1011 signal range of a *hetN*-dependent paracrine signal, but not of a *patS*-dependent signal, in the
1012 filamentous cyanobacterium *Anabaena* sp. strain PCC7120. *Mol Microbiol* **94**: 1260-1271.

1013 Sánchez-Baracaldo, P., Ridgwell, A., and Raven, J.A. (2014) A neoproterozoic transition in the
1014 marine nitrogen cycle. *Curr Biol* **24**: 6520657.

1015 Saw, J.H.W., Schatz, M., Brown, M.V., Kunkel, D.D., Foster, J.S., Shick, H., *et al.* (2013)
1016 Cultivation and complete genome sequencing of *Gloeobacter kilaueensis* sp. nov., from a lava
1017 cave in Kilauea Caldera, Hawai'i. *PloS ONE* **8**: e76376.

1018 Sazuka, T., Yamaguchi, M., and Ohara, O. (1999) Cyano2Dbase updated: Linkage of 234
1019 protein spots to corresponding genes through N-terminal microsequencing. *Electrophoresis* **20**:
1020 2160-2171.

1021 Schirrmeister, B.E., de Vos, J.M., Antonelli, A., and Bagheri, H.C. (2013) Evolution of
1022 multicellularity coincided with increased diversification of cyanobacteria and the Great
1023 Oxidation Event. *Proc Natl Acad Sci USA* **110**: 1791-1796.

1024 Schirrmeister, B.E., Gugger, M., and Donoghue, P.C.J. (2015) Cyanobacteria and the great
1025 oxidation event: evidence from genes and fossils. *Paleontol* **58**: 769-785.

1026 Shih, P.M., Wu, D., Latifi, A., Axen, S.D., Fewer, D.P., Talla, E., *et al.* (2014) Improving the
1027 coverage of the cyanobacterial phylum using diversity-driven genome sequencing. *Proc Natl*
1028 *Acad Sci USA* **110**: 1053-1058.

1029 Stucken, K., John, U., Cembella, A., Murillo, A.A., Soto-Liebe, K., Fuentes-Valdés, J.J., *et al.*
1030 (2010) The smallest known genomes of multicellular and toxic cyanobacteria: comparison,
1031 minimal gene sets for linked traits and the evolutionary implications. *PLoS One* **5**: e9235.

1032 Talavera, G., and Castresana, J. (2007) Improvement of phylogenies after removing divergent
1033 and ambiguously aligned blocks from protein sequence alignments. *Syst Biol* **56**: 564-577.

1034 Thompson, J.D., Higgins, D.G., and Gibson, T. J. (1994) CLUSTAL W: Improving the
1035 sensitivity of progressive multiple sequence alignment through sequence weighting, position-
1036 specific gap penalties and weight matrix choice. *Nucleic Acids Res* **22**: 4673-4680.

1037 Toyoshima, M., Sasaki, N.V., Fujiwara, M., Ehira, S., Ohmori, M., and Sato, N. (2010). Early
1038 candidacy for differentiation into heterocysts in the filamentous cyanobacterium *Anabaena* sp.
1039 PCC 7120. *Arch Microbiol* **192**: 23-31.

1040 Tumer, N.E., Robinson, S.J., and Haselkorn, R. (1983) Different promoters for the *Anabaena*
1041 glutamine synthetase gene during growth using molecular or fixed nitrogen. *Nature* **306**: 337-
1042 342.

- 1043 Turing, A.M. (1952) The chemical basis of morphogenesis. *Phil Trans Royal Soc B* **237**: 37-72.
- 1044 Uyeda, J.C., Harmon, L.J., and Blank, C.E. (2016) A comprehensive study of cyanobacterial
1045 morphological and ecological evolutionary dynamics through deep geologic time. *PLoS ONE* **11**:
1046 e0162539.
- 1047 Valladares, A., Flores, E., and Herrero, A. (2016) The heterocyst differentiation transcriptional
1048 regulator HetR of the filamentous cyanobacterium *Anabaena* forms tetramers and can be
1049 regulated by phosphorylation. *Mol Microbiol* **99**: 808-819.
- 1050 Videau, P., Ni, S., Rivers, O.S., Ushijima, B., Feldmann, E.A., Cozy, L.M., *et al.* (2014a)
1051 Expanding the direct HetR regulon in *Anabaena* sp. strain PCC 7120. *J Bacteriol* **196**: 1113-
1052 1121.
- 1053 Videau, P., Oshiro, R.T., Cozy, L.M., and Callahan, S.M. (2014b) Transcriptional dynamics of
1054 developmental genes assessed with an FMN-dependent fluorophore in mature heterocysts of
1055 *Anabaena* sp. strain PCC 7120. *Microbiol* **160**: 1874-1881.
- 1056 Voß, B., Bolhuis, H., Fewer, D.P., Kopf, M., Möke, F., Haas, F., *et al.* (2013) Insights into the
1057 physiology and ecology of the brackish-water-adapted cyanobacterium *Nodularia spumigena*
1058 CCY9414 based on a genome-transcriptome analysis. *PLoS ONE* **8**: e60224.
- 1059 Wang, H., Sivonen, K., Rouhiainen, L., Fewer, D.P., Lyra, C., Rantala-Ylinen, A., *et al.* (2012)
1060 Genome-derived insights into the biology of the hepatotoxic bloom-forming cyanobacterium
1061 *Anabaena* sp. strain 90. *BMC Genomics* **13**: 613.
- 1062 Waterbury, J.B. (2006) The cyanobacteria -- isolation, purification, and identification. In *The*
1063 *Prokaryotes: Bacteria: Firmicutes, Cyanobacteria*, 3rd edition, Vol. 4. Dworkin, M., Falkow, S.,
1064 Rosenberg, E., Schleifer, K-H, Stackebrandt, E. (eds). Springer-Verlag, New York. pp. 1053-
1065 1073.
- 1066 Wei, T.F., Ramasubramanian, T.S., and Golden J.W. (1994) *Anabaena* sp. strain PCC 7120 *ntcA*
1067 gene required for growth on nitrate and heterocyst development. *J Bacteriol* **176**: 4473-82.
- 1068 Wu, X. Liu, D., Lee, M.H., and Golden, J.W. (2004) *patS* minigenes inhibit heterocyst
1069 development of *Anabaena* sp. strain PCC 7120. *J Bacteriol* **186**: 6422-6429.
- 1070 Yoon, H.- S., and Golden, J. W. (1998) Heterocyst pattern formation controlled by a diffusible
1071 peptide. *Science* **282**: 935-938.
- 1072 Yoon, H.-S., and Golden, J.W. (2001) PatS and products of nitrogen fixation control heterocyst
1073 pattern. *J Bacteriol* **183**: 2605-2613.
- 1074 Yoon, H.-S., Lee, M.H., Xiong, J., and Golden, J.W. (2003) *Anabaena* sp. strain PCC 7120 *hetY*
1075 gene influences heterocyst development. *J Bacteriol* **185**: 6995-7000.
- 1076 Zhang, J.-Y., Chen, W.-L., and Zhang, C.-C. (2009) *hetR* and *patS*, two genes necessary for
1077 heterocyst pattern formation, are widespread in filamentous nonheterocyst-forming
1078 cyanobacteria. *Microbiol* **155**: 1418-1426.