

produce these mycotoxins encoded in their genomes, and may need to be further examined with regard to their mycotoxin-production capability. The mycotoxin productivity of the species for which data are missing (Table 2) will be tested by both biochemical and molecular methods in future studies.

Phylogeny can therefore be regarded as a powerful tool for predicting the characteristics of living organisms and the phylogenetic information that we collected was helpful for predicting potential toxin production by *Fusarium* species. These “phylotoxigenic relationships” may be especially useful when a new species of microorganism contaminating food is discovered, or to assess microorganisms found in food for which there is only limited information available about their pathogenicity.

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References

- Akaike H. 1973. A new look at the statistical model identification. *IEEE Trans Autom Contr.* 19:716–723.
- Aoki T, O'Donnell K. 1998. *Fusarium kyushuense*, sp. nov. from Japan. *Mycoscience.* 39:1–6.
- Booth C. 1971. The genus *Fusarium*. Surrey: Commonwealth Mycological Institute.
- Bosch U, Mirocha CJ. 1992. Toxin production by *Fusarium* species from sugar beets and natural occurrence of zearalenone in beets and beet fibers. *Appl Environ Microbiol.* 58:3233–3239.
- Chelkowsk J, Zawadzki M, Zawadzki P, Logrieco A, Bottalico A. 1990. Moniliformin production by *Fusarium* species. *Mycotoxin Res.* 6:41–45.
- Desjardins AE, Proctor RH. 2007. Molecular biology of *Fusarium* mycotoxins. *Int J Food Microbiol.* 119:47–50.
- Felsenstein J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *J Mol Evol.* 17:368–376.
- Gerlach W, Nirenberg H. 1982. The genus *Fusarium*: a pictorial atlas. Berlin: P. Parey.
- Gilmore SR, Grafenhan T, Louis-Seize G, Seifert KA. 2009. Multiple copies of cytochrome oxidase 1 in species of the fungal genus *Fusarium*. *Mol Ecol Resour.* 9:90–98.
- Grafenhan T, Schroers HJ, Nirenberg HI, Seifert KA. 2011. An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in *Cosmospora*, *Acremonium*, *Fusarium*, *Stilbella*, and *Volutella*. *Stud Mycol.* 68:79–113.
- Gupta S, Krasnoff SB, Underwood NL, Renwick JA, Roberts DW. 1990. Isolation of beauvericin as an insect toxin from *Fusarium semitectum* and *Fusarium moniliforme* var. *subglutinans*. *Mycopathologia.* 115:185–189.
- Harrow SA, Farrokhi-Nejad R, Pitman AR, Scott IA, Bentley A, Hide C, Cromey MG. 2010. Characterisation of New Zealand *Fusarium* populations using a polyphasic approach differentiates the *F. avenaceum*/*F. acuminatum*/*F. tricinctum* species complex in cereal and grassland systems. *Fungal Biol.* 114:293–311.
- Hasegawa M, Kishino H, Yano T. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *J Mol Evol.* 22:160–174.
- Herrmann M, Zoicher R, Haese A. 1996. Enniatin production by *Fusarium* strains and its effect on potato tuber tissue. *Appl Environ Microbiol.* 62:393–398.
- Joffe AZ. 1974. A modern system of *Fusarium* taxonomy. *Mycopathol Mycol Appl.* 53:201–228.
- Katoh K, Asiminos G, Toh H. 2009. Multiple alignment of DNA sequences with MAFFT. *Methods Mol Biol.* 537:39–64.
- Khaldi N, Wolfe KH. 2011. Evolutionary origins of the fumonisin secondary metabolite gene cluster in *Fusarium verticillioides* and *Aspergillus niger*. *Int J Evol Biol.* 2011:423821.
- Knutsen AK, Torp M, Holst-Jensen A. 2004. Phylogenetic analyses of the *Fusarium poae*, *Fusarium sporotrichioides* and *Fusarium langsethiae* species complex based on partial sequences of the translation elongation factor-1 alpha gene. *Int J Food Microbiol.* 95:287–295.
- Kristensen R, Torp M, Kosiak B, Holst-Jensen A. 2005. Phylogeny and toxigenic potential is correlated in *Fusarium* species as revealed by partial translation elongation factor 1 alpha gene sequences. *Mycol Res.* 109:173–186.
- Lee US, Jang HS, Tanaka T, Toyasaki N, Sugiura Y, Oh YJ, Cho CM, Ueno Y. 1986. Mycological survey of Korean cereals and production of mycotoxins by *Fusarium* isolates. *Appl Environ Microbiol.* 52:1258–1260.
- Leslie JF, Summerell BA, Bullock S. 2006. The *Fusarium* laboratory manual. 1st ed. Oxford: Blackwell.
- Logrieco A, Moretti A, Castella G, Kostecki M, Golinski P, Ritieni A, Chelkowsk J. 1998. Beauvericin production by *Fusarium* species. *Appl Environ Microbiol.* 64:3084–3088.
- Logrieco A, Rizzo A, Ferracane R, Ritieni A. 2002. Occurrence of beauvericin and enniatins in wheat affected by *Fusarium avenaceum* head blight. *Appl Environ Microbiol.* 68:82–85.
- Marasas WFO, Nelson PE, Toussoun TA. 1984. Toxigenic *Fusarium* species. University Park (PA): The Pennsylvania State University Press.
- Miyata T, Miyazawa S, Yasunaga T. 1979. Two types of amino acid substitutions in protein evolution. *J Mol Evol.* 12:219–236.
- Nelson PE, Toussoun TA, Marasas WFO. 1983. *Fusarium* species: an illustrated manual for identification. University Park (PA): The Pennsylvania State University Press.
- Nicholson P, Simpson DR, Wilson AH, Chandler E, Thomsett M. 2004. Detection and differentiation of trichothecene and enniatin-producing *Fusarium* species on small-grain cereals. *Eur J Plant Pathol.* 110:503–514.
- Nishihara H, Maruyama S, Okada N. 2009. Retroposon analysis and recent geological data suggest near-simultaneous divergence of the three superorders of mammals. *Proc Natl Acad Sci U S A.* 106:5235–5240.
- O'Donnell K. 1993. *Fusarium* and its near relatives. In: Reynolds DR, Taylor JW, editors. The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematics. Wallingford: CAB International; p. 225–233.
- O'Donnell K, Cigelnik E, Nirenberg HI. 1998. Molecular systematics and phylogeography of the *Gibberella fujikuroi* species complex of *Fusarium*. *Mycologia.* 90:465–493.
- O'Donnell K, Sarver BA, Brandt M, Chang DC, Noble-Wang J, Park BJ, Sutton DA, Benjamin L, Lindsley M, Padhye A, et al. 2007. Phylogenetic diversity and microsphere array-based genotyping of human pathogenic *Fusaria*, including isolates from the multistate contact lens-associated U.S.

- keratitis outbreaks of 2005 and 2006. *J Clin Microbiol.* 45:2235–2248.
- O'Donnell K, Sutton DA, Rinaldi MG, Sarver BA, Balajee SA, Schroers HJ, Summerbell RC, Robert VA, Crous PW, Zhang N, et al. 2010. Internet-accessible DNA sequence database for identifying fusaria from human and animal infections. *J Clin Microbiol.* 48:3708–3718.
- Pagel M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biol.* 48:612–622.
- Pitt JI, Hocking AD. 2009. *Fungi and food spoilage.* 3rd ed. Berlin: Springer.
- Pupko T, Huchon D, Cao Y, Okada N, Hasegawa M. 2002. Combining multiple data sets in a likelihood analysis: which models are the best?. *Mol Biol Evol.* 19:2294–2307.
- Rabie CJ, Marasas WF, Thiel PG, Lubben A, Vleggaar R. 1982. Moniliformin production and toxicity of different *Fusarium* species from Southern Africa. *Appl Environ Microbiol.* 43:517–521.
- Reverberi M, Ricelli A, Zjalic S, Fabbri AA, Fanelli C. 2010. Natural functions of mycotoxins and control of their biosynthesis in fungi. *Appl Microbiol Biotechnol.* 87:899–911.
- Scott PM, Abbas HK, Mirocha CJ, Lawrence GA, Weber D. 1987. Formation of moniliformin by *Fusarium sporotrichioides* and *Fusarium culmorum*. *Appl Environ Microbiol.* 53:196–197.
- Seifert KA, Levesque CA. 2004. Phylogeny and molecular diagnosis of mycotoxicogenic fungi. *Eur J Plant Pathol.* 110:449–471.
- Shimodaira H, Hasegawa M. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Mol phylogeny Evol.* 16:1114–1116.
- Shimodaira H, Hasegawa M. 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. *J Mol Evol.* 12:219–236.
- Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biol.* 57:758–771.
- Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC. 2000. Phylogenetic species recognition and species concepts in fungi. *Fungal Genet Biol.* 31:21–32.
- Thrane U, Adler A, Clasen PE, Galvano F, Langseth W, Lew H, Logrieco A, Nielsen KF, Ritieni A. 2004. Diversity in metabolite production by *Fusarium langsethiae*, *Fusarium poae*, and *Fusarium sporotrichioides*. *Int J Food Microbiol.* 95:257–266.
- Torp M, Nirenberg HI. 2004. *Fusarium langsethiae* sp. nov. on cereals in Europe. *Int J Food Microbiol.* 95:247–256.
- Turner AS, Lees AK, Rezanoor HN, Nicholson P. 1998. Refinement of PCR-detection of *Fusarium avenaceum* and evidence from DNA marker studies for phenetic relatedness to *Fusarium tricinctum*. *Plant Pathol.* 47:278–288.
- Ward TJ, Bielawski JP, Kistler HC, Sullivan E, O'Donnell K. 2002. Ancestral polymorphism and adaptive evolution in the trichothecene mycotoxin gene cluster of phytopathogenic *Fusarium*. *Proc Natl Acad Sci USA.* 99:9278–9283.
- Watanabe M, Yonezawa T, Lee KI, Kumagai S, Sugita-Konishi Y, Goto K, Hara-Kudo Y. 2011. Molecular phylogeny of the higher and lower taxonomy of the *Fusarium* genus and differences in the evolutionary histories of multiple genes. *BMC Evol Biol.* 11:322.
- Wing N, Bryden WL, Lauren DR, Burgess LW. 1993. Toxicogenicity of *Fusarium* species and subspecies in section *Gibbosum* from different regions of Australia. *Mycol. Res.* 97:1441–1446.
- Wollenweber HW, Reinking OA. 1935. *Fusarien, Ihre Beschreibung, Schadwirkung Und Bekämpfung.* Berlin: Paul Parey.
- Yang Z. 1996. Maximum-likelihood models for combined analyses of multiple sequence data. *J Mol Evol.* 42:587–596.
- Yang Z. 2007. PAML 4: phylogenetic analysis by maximum likelihood. *Mol Biol Evol.* 24:1586–1591.
- Yang Z, Nielsen R, Hasegawa M. 1998. Models of amino acid substitution and applications to mitochondrial protein evolution. *Mol Biol Evol.* 15:1600–1611.
- Yli-Mattila T. 2010. Ecology and evolution of toxigenic *Fusarium* species in cereals in northern Europe and Asia. *J Plant Pathol.* 92:7–18.
- Yonezawa T, Kohno N, Hasegawa M. 2008. The origin and phylogenetic evolution of *Pinnipedia*. *Proc Inst Stat Math.* 56:81–99.

