(1984) *J. Biol. Chem.* 259, 14406–14412
21 CANDAU, R. *et al.* (1996) *Mol. Cell. Biol.* 16, 593–602
22 YANG, X., OGRYZKO, V., NISHIKAWA, J., HOWARD, B. and NAKATANI, Y. (1996) *Nature* 382, 319–324
23 CHICOINE, L. G., RICHMAN, R., COOK, R. G., GOROVSKY, M. A. and ALLIS, C. D. (1987) *J. Cell Biol.* 105, 127–135
24 KUO, M. H. *et al. Nature* (in press)
25 WOLFFE, A. P. and PRUSS, D. (1996) *Trends Genet.* 12, 58–62
26 WOLFFE, A. P. and PRUSS, D. (1996) *Cell* 84, 817–819
27 CARLSON, M. and LAURENT, B. C. (1994) *Curr. Opin. Cell Biol.* 6, 396–402
28 WINSTON, F. and CARLSON, M. (1992) *Trends Genet.* 8, 387–391
29 PETERSON, C. L. and TAMKUN J. W. (1995) *Trends Biochem. Sci.* 20, 143–146
30 OWEN-HUGHES, T. and WORKMAN, J. L. (1994) *Crit. Rev. Euk. Gene Expr.* 4, 403–441
31 KWOK, R. P. S. *et al.* (1994) *Nature* 370, 223–226
32 ARANY, Z., SELLERS, W. R., LIVINGSTON, D. M. and ECKNER, R. (1994) *Cell* 77, 799–800
33 ARIAS, J. *et al.* (1994) *Nature* 370, 226–229
34 DYSON, N. and HARLOW, E. (1992) *Cancer Surv.* 12, 161–195
35 KAMEI, Y. *et al.* (1996) *Cell* 85, 403–414
36 PARTHUN, M., WIDOM, J. and GOTTSCHLING, D. *Cell* (in press)
37 VERREAULT, A., KAUFMAN, P. D., KOBAYASHI, R. and STILLMAN, B. *Cell* (in press)
38 WOLFFE, A. P. (1996) *Science* 272, 371–372

Highly divergent *Caenorhabditis* and *Saccharomyces* tubulins evolved recently from genes encoding γ-tubulin

The tubulin gene family consists of three types, the well-known α- and β-tubulins and the more recently discovered γ-tubulin. However, genome-sequencing projects of *Caenorhabditis elegans* and *Saccharomyces cerevisiae* have revealed recently two tubulin genes each so divergent from any known tubulin that they prompted a proposal to classify these as representatives of new families, 'δ-' and 'ε-tubulin', respectively[1], a reclassification implicit in the analyses of tubulin structure and function published recently in this journal[2]. However, substantial evidence is accumulating from the distribution, function and phylogeny of these genes for a contrasting argument that really they are rapidly evolving orthologues of γ-tubulin[3,4].

If these genes are members of novel tubulin subfamilies, then representatives should be found in reasonably diverse genomes, yet, to date, 'δ-' and 'ε-' tubulins have only been found in the genera where they were first described. Moreover, neither the recently sequenced *S. cerevisiae* genome nor the *C. elegans* expressed-sequence tag database contains a gene specifically similar to that found in the other organism or a 'conventional' γ-tubulin; instead, they contain only homologues of α, β and either of the genes in question. Since the gene encoding γ-tubulin is essential where known in animals and fungi[5,6], there is a definite implication that these divergent genes may be functionally equivalent to γ-tubulin. Indeed, this is borne out by experimental observations in *S. cerevisiae* that show the localization of the 'novel' tubulin to the spindle pole body (as expected of a γ-tubulin orthologue), and reveal that disruption of the gene results in a phenotype very similar to that arising from γ-tubulin disruption in another ascomycete, *Aspergillus*[3,7,8].

Strong evidence that these genes indeed encode γ-tubulins also comes from their phylogenetic relationship to other tubulins. Although quite divergent, both the *C. elegans* and *S. cerevisiae* sequences branch with γ-tubulins in trees of all three types[3,4] and even show an affinity to orthologues from the animals and fungi, respectively, in trees containing only γ-tubulins[4].

In short, these genes seem to have evolved recently, albeit rapidly, from genes encoding γ-tubulin. Additional, testable, expectations of this conclusion based on phylogeny and the conservation of gene structure are also apparent. The *C. elegans* gene contains five introns, none of which is in a position shared with introns from any other tubulin gene[7]. Given the moderate conservation of intron positions between *C. elegans* and vertebrates, we predict, therefore, that determination and analysis of a vertebrate γ-tubulin genomic sequence will reveal one or more introns in identical locations to those in the *C. elegans* gene. Furthermore, the exact distribution of these rapidly evolving genes within their respective lineages ought to become more apparent with continued sequencing.

References

1 BURNS, R. G. (1995) *Cell Motil. Cytoskeleton* 31, 255–258
2 BURNS, R. G. (1996) *Trends Cell Biol.* 6, 297–303
3 SOBEL, S. G. and SNYDER, M. (1995) *J. Cell Biol.* 131, 1775–1788
4 KEELING, P. J. and DOOLITTLE, W. F. *Mol. Biol. Evol.* (in press)
5 ZHENG, Y. M., JUNG, K. and OAKLEY, B. (1991) *Cell* 65, 817–823
6 SUNKEL, C. E. *et al.* (1995) *EMBO J.* 14, 28–36
7 SPANG, A., GEISSLER, S., GREIN, K. and SCHEIBEL, E. (1996) *J. Cell Biol.* 134, 429–441
8 MARSCHALL, L. G., JENG, R. L., MULHOLLAND, J. and STEARNS, T. (1996) *J. Cell Biol.* 134, 443–454
9 LOGSDON, J. M., Jr (1995) *Origin and Evolution of Spliceosomal Introns*, PhD Thesis, Indiana University, IN, USA

Patrick J. Keeling and John M. Logsdon, Jr

Dept of Biochemistry, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4H7.
E-mail: pkeeling@is.dal.ca

This letter was sent in response to an article published in the August issue of *trends in* CELL BIOLOGY, by Roy Burns and Kevin Farrell, on the structure of the β-tubulin GTP-binding site.
Overleaf, Roy Burns replies with arguments in favour of retaining the γ-, δ- and ε-classification.

Copyright © 1996 Elsevier Science Ltd. All rights reserved.
0962-8924/96/$15.00
PII: S0962-8924(96)20033-9