



Fig. 1 A possible phylogeny for the genera of basidiomycetes studied by Walker and Doolittle¹. The phylogeny incorporates the basic split between doliporous and adoliporous fungi as suggested by Walker and Doolittle, but all other details of the phylogeny are constructed so as to allow all the morphological traits considered by Walker and Doolittle¹ and additional taxonomic distinctions⁵⁻⁸ to evolve only once. Broken lines indicate the phylogenetic segment in which the derived characters first evolved. It cannot be inferred from this analysis whether having a dolipore is primitive or derived.

I next applied the same non-parametric tests to the alternative phylogenies in each cluster. The strongest discrimination occurred in the adoliporous cluster, with the most likely phylogeny grouping *Ustilago* and *Aessosporon* together, with *Rhodosporeidium* being more divergent. However, this phylogeny is not significantly better at the 5% level than any alternatives. Hence, as long as the adoliporous/doliporous dichotomy is maintained, the species within the clusters can be arranged in any fashion and still be compatible with the rRNA sequence data.

Since the rRNA data are inadequate to discriminate phylogenetic relationships within a cluster, other data must be used to reconstruct these within-cluster phylogenies. Figure 1 illustrates such a proposed phylogeny, using classical morphological and taxonomic distinctions. Clearly, all the morphological traits and class or subclass distinctions arise only once in this phylogeny. All the traits fit well into a scheme of monophyletic origin that is consistent with the rRNA sequence data. Walker and Doolittle¹ may ultimately be right, but their morphological conclusions are not justified from the published data on the 5S rRNA genes.

I thank Dr James Maniotis for help in preparing the manuscript. The work was supported by NIH grants GM27021 and GM31571.

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WALKER AND DOOLITTLE REPLY— We agree with Templeton that the nucleotide differences between the 5S rRNA sequences within each of the two sequence clusters are generally well below the optimal range for reconstructing accurate phylogenies. However, the strikingly few dissimilarities in the sequences from *Filobasidium* and the homobasidiomycetes led us to suggest that the haploid yeast phases in *Filobasidium* and *Tremella* may have evolved independently. We hope that further molecular comparisons will clarify whether convergence in the budding character or in 5S rRNA sequences has occurred. It should be said that *Filobasidium* has holobasidia (non-septate basidia)¹ as do all homobasidiomycetes (and some other heterobasidiomycetes)² whereas *Tremella* has longitudinally septate basidia². In fact, as detailed by Moore³, none of the other organisms listed in Templeton's Teliomycetes (Fig. 1) has true teliospores, such as are found in the rusts (Uredinales). Thus, we still believe that our sequence data add further support to Shaffer's⁴ assessment of the class Heterobasidiomycetes as "a group in search of meaningful definition and circumscription".

We now have 5S rRNA sequences from more than 20 basidiomycetes, including representatives of most higher taxa. In

general, the recent sequence data support our point that the dichotomy in septal pore ultrastructure matches a primary dichotomy in our sequence data. However, it is now evident that sequences from those taxa with simple septal pores represent a more diverse group than our more limited data set suggested. In fact, the (unpublished) sequence from *Exobasidium vaccinii* clearly is more closely allied with sequences from doliporous taxa. The ultrastructure of the simple septal pores of this organism closely resembles that of the rusts (Uredinales), Septobasidiales and parasitic Auriculariales^{5,6}. However, our (unpublished) sequence from one of the latter (*Rhizoctonia crocorum*) clearly indicates a more recent common ancestral sequence with those from other adoliporous species rather than those from *Exobasidium* and the doliporous species. Hence, our present sequence data set clearly suggests that the common ancestor of the two primary basidiomycete lineages so far identified possessed simple septal pores and that doliporous septa evolved once in one of these lineages. Furthermore, as most adoliporous basidiomycetes, including *Exobasidium*, are plant parasites², our present data set supports the proposal⁷ that the early basidiomycetes were plant parasites or were pre-adapted to evolve into such. Most, but not all, groups of heterobasidiomycetes have a budding haploid stage⁴. Thus, we agree that the common ancestral basidiomycete probably possessed this trait. However, our sequence data do not clearly suggest that these organisms probably resembled those present basidiomycetes usually described as being yeasts (saprophytic, with a diminutive mycelial stage and capable of prolonged budding in culture). It is still unclear from our data whether the common ancestral basidiomycete had septate or nonseptate basidia, an important character in basidiomycete systematics. The most isolated sequence in each of our present primary sequence lineages is from organisms with transversely septate and non-septate basidia respectively².

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