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Evolution of complex fruiting-body morphologies in homobasidiomycetes

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The fruiting bodies of homobasidiomycetes include some of the most complex forms that have evolved in the fungi, such as gilled mushrooms, bracket fungi and puffballs ('pileate-erect') forms. Homobasidiomycetes also include relatively simple crust-like 'resupinate' forms, however, which account for *ca.* 13–15% of the described species in the group. Resupinate homobasidiomycetes have been interpreted either as a paraphyletic grade of plesiomorphic forms or a polyphyletic assemblage of reduced forms. The former view suggests that morphological evolution in homobasidiomycetes has been marked by independent elaboration in many clades, whereas the latter view suggests that parallel simplification has been a common mode of evolution. To infer patterns of morphological evolution in homobasidiomycetes, we constructed phylogenetic trees from a dataset of 481 species and performed ancestral state reconstruction (ASR) using parsimony and maximum likelihood (ML) methods. ASR with both parsimony and ML implies that the ancestor of the homobasidiomycetes was resupinate, and that there have been multiple gains and losses of complex forms in the homobasidiomycetes. We also used ML to address whether there is an asymmetry in the rate of transformations between simple and complex forms. Models of morphological evolution inferred with ML indicate that the rate of transformations from simple to complex forms is about three to six times greater than the rate of transformations in the reverse direction. A null model of morphological evolution, in which there is no asymmetry in transformation rates, was rejected. These results suggest that there is a 'driven' trend towards the evolution of complex forms in homobasidiomycetes.

Keywords: comparative methods; corticioid fungi; molecular phylogeny

1. INTRODUCTION

Complex multicellular forms have arisen independently in several clades of eukaryotes, including fungi, plants, animals and stramenopiles. The repeated evolution of complex forms has been taken as evidence that natural selection tends to favour morphological elaboration (Bonner 1988). Alternatively, it has been suggested that the overall increase in the complexity of biological forms has occurred simply because there is a lower limit of allowable complexity, represented by unicellular forms, but no upper limit on complexity. If so, an overall increase in complexity could occur by a 'passive' process, which can be conceptualized as diffusion through morphospace (McShea 1994, 1996). Much of the debate concerning trends in the evolution of organismal complexity resides in the palaeontological literature and concerns morphological evolution in animals (e.g. Gould 1988; Wagner 1996; Sidor 2001).

Within the fungi, some of the most conspicuous and elaborate forms that have evolved are the fruiting bodies of homobasidiomycetes. Familiar examples include gilled mushrooms, polypores, coral fungi, puffballs and stinkhorns (hereafter, 'pileate-erect' forms). Nevertheless, homobasidiomycetes also produce relatively simple 'resupinate' forms, which lie flat on their substrates. Resupinate fruiting bodies range from 'athelioid' forms, which consist only of sparse networks of fertile hyphae, to more robust, crust-like or fleshy forms that have smooth, ridged, toothed or poroid spore-bearing surfaces. Resupinate fruiting bodies are often produced on the underside of woody substrates, where they are easily overlooked.

There is general agreement among mycologists that resupinate homobasidiomycetes are not monophyletic (Donk 1964, 1971; Jülich 1981; Parmasto 1986), but their precise relationships are not well resolved. Some authors have suggested that resupinate forms represent a polyphyletic assemblage of species that have been derived by reduction from pileate-erect forms (Jülich 1981; Corner 1991), but others have suggested that resupinate forms constitute a paraphyletic grade, from which pileate-erect forms have repeatedly arisen (Oberwinkler 1985; Parmasto 1995). Recent phylogenetic studies have confirmed that resupinate taxa are intermingled with pileate-erect taxa in a number of clades of homobasidiomycetes (Hibbett *et al.* 1997; Hibbett & Thorn 2001; Langer 2002), but so far there has not, to our knowledge, been an analysis with sufficiently broad sampling to resolve the overall pattern of evolution of fruiting-body forms.

Our study had three main objectives: (i) to infer broad phylogenetic relationships among resupinate and pileate-erect homobasidiomycetes; (ii) to estimate the ancestral fruiting-body morphology of the homobasidiomycetes; and (iii) to determine whether the rate of transformations from resupinate to pileate-erect forms is different from the rate of transformations in the reverse direction. Resupinate forms are morphologically simple relative to pileate-erect forms because they are not divided into a cap and stalk or other discrete parts, and they have simple ontogenies that do not include the production of veils or other protective tissues that are common among pileate-erect forms. We used maximum likelihood (ML) to estimate a simple model of evolution of homobasidiomycete

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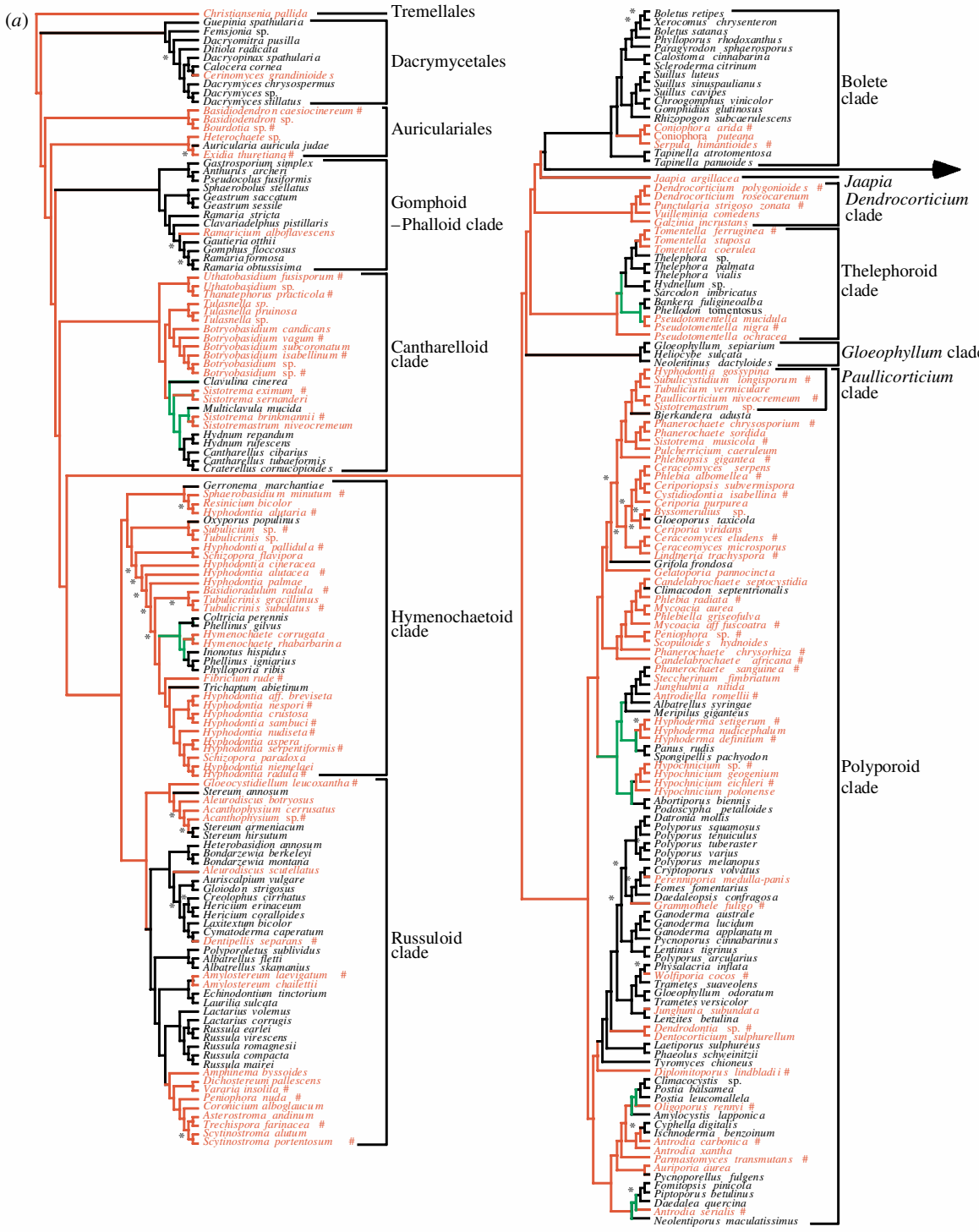

Figure 1. Phylogenetic relationships of homobasidiomycetes inferred with EP analysis. Tree 1/10 000. Branch shading indicates ASR with parsimony: red, resupinate; black, pileate-erect; green, uncertain. Nodes that collapse in the strict consensus tree are marked with asterisks. Resupinate taxa that were deleted from the 'pruned' trees are indicated by a hash sign. Bracketed groups are discussed in the text.

fruiting-body forms, in which there are two character states (resupinate and pileate-erect) and two parameters that specify the rates of forward and backward transformations between the states (Pagel 1997). If the values of these parameters could be shown to be significantly different, then this would indicate the existence of a 'driven' trend in the evolution of complex forms in fungi.

2. METHODS

(a) *Taxon sampling and sequence data*

We assembled a dataset that contains 464 species of homobasidiomycetes and 17 species of 'jelly fungi' (heterobasidiomycetes *pro parte*), including six species of Auriculariales, 10 species of Dacrymycetales and one species of Tremellales,

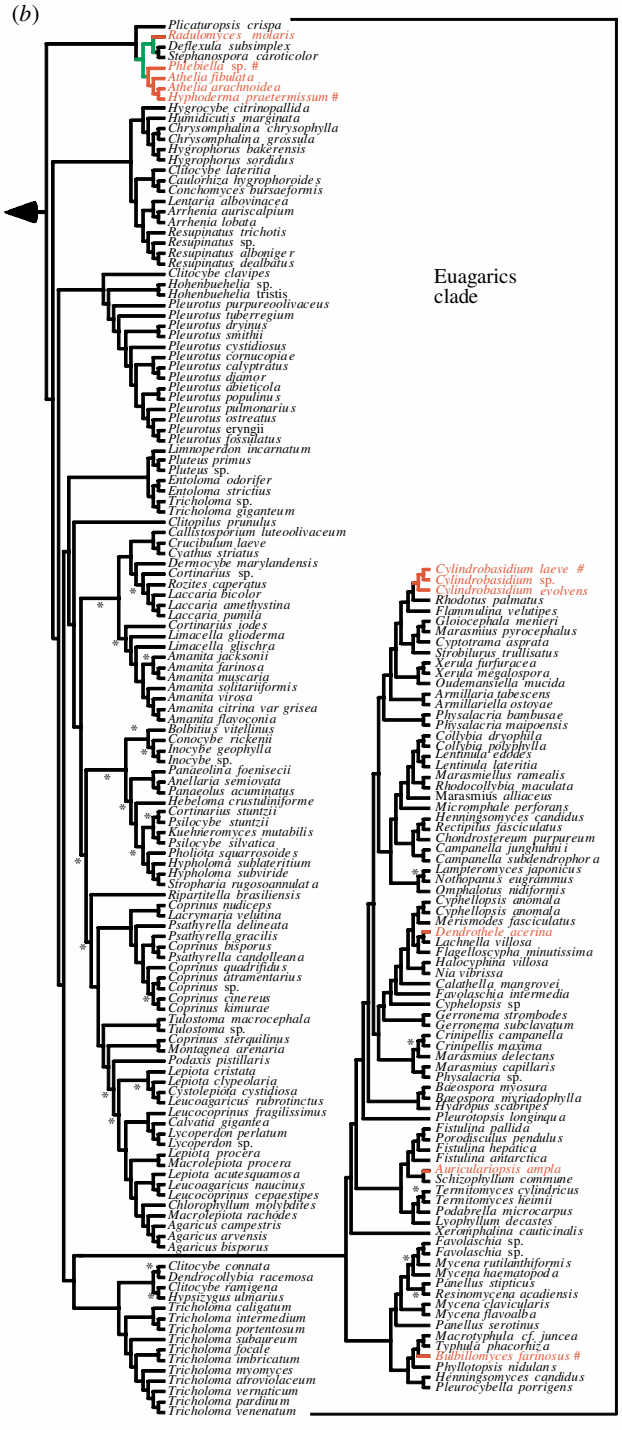

Figure 1. (*Continued.*)

Christiansenia pallida, which was used for rooting purposes. The jelly fungi plus homobasidiomycetes make up a monophyletic group that has been termed the Hymenomycetes (Swann & Taylor 1995). Homobasidiomycetes include 96% of the species in our dataset, which is comparable with the proportion of described species of homobasidiomycetes in the Hymenomycetes (98%) (Hawksworth *et al.* 1995).

The homobasidiomycetes include about 13 500 described species (Hawksworth *et al.* 1995), which are distributed across at least eight major clades (Hibbett & Thorn 2001). Our dataset includes less than 4% of the described species of homobasidiomycetes. Nevertheless, all of the major clades of homobasidiomycetes are represented, in proportions that are comparable with the estimated proportions of described species in each clade (table 1). Parmasto (1997) recognized 1733 described species of corticioid homobasidiomycetes, which include the majority of resupinate forms. Based on Parmasto's figures, we estimate that *ca.* 13–15% of described species of homobasidiomycetes are resupinate. Our dataset includes 144 resupinate species (27%), which means that these forms may be over-represented.

Taxa in our dataset are represented by one to four molecular regions, including nuclear and mitochondrial small- and large-subunit ribosomal DNA (rDNA) regions. The nuclear small subunit rDNA is a nearly full-length sequence (1.8 kb), whereas the other regions are represented by partial sequences that have been described elsewhere (White *et al.* 1990; Bruns & Szaro 1992; Moncalvo *et al.* 2000). One hundered and seventeen species are represented by all four regions, 78 species are represented by three regions and 12 species have two regions. All species in the dataset have the nuclear large-subunit (nuc-lsu) rDNA region (*ca.* 1.0 kb). Sequences were obtained in our laboratory using established protocols, or were downloaded from GenBank (http://www.ncbi.nih.gov/genbank/). The studies of Moncalvo *et al.* (2000) and Langer (2002) provided 174 (36%) of the nuc-lsu rDNA sequences. One hundred and fifty seven new sequences were generated in this study and have been deposited in GenBank (accession numbers AF518568–AF518724). A complete list of species and GenBank numbers of all sequences analysed are available on request from D.S.H.

(b) *Phylogenetic analyses*

Sequences were aligned by eye in MacClade v. 4.0 (Maddison & Maddison 2000) or Paup* v. 4.0 (Swofford 2001) and regions that were deemed too divergent to align were excluded from analysis. The data matrix is available on request from D.S.H. Phylogenetic analyses in Paup* used equally-weighted parsimony (EP) or differentially weighted parsimony (WP). The latter used a step-matrix of transformation costs that were estimated with ML (HKY85 model of evolution, with empirical base frequencies, transition–transversion bias 2, four rate classes modelled on discrete gamma distribution, shape parameter $\alpha = 0.5$) on a tree derived from EP analysis. Transformation probabilities were scaled to approximate integer values and adjusted in Paup* to avoid violation of the triangle inequality. Transformation costs in WP were as follows: A–G = 4, A–C = 10, A–T = 8, C–G = 12, C–T = 2, T–G = 10.

EP analysis used a two-step search protocol. The first step used 1000 heuristic searches with random taxon addition sequences and tree bisection and reconnection (TBR) branch swapping, keeping two trees per replicate. The second step used the shortest trees found in the first step as starting trees for TBR branch swapping, with MaxTrees set to 10 000. The WP analysis used the same protocol, except that only 100 searches were done in the first step and MaxTrees was set to 1000 in the second step.

In addition to the unconstrained analyses described above, we performed three constrained EP analyses to explore alternative topologies suggested by a previous phylogenetic study (Binder & Hibbett 2002). The study from which the constraint topologies were drawn included 93 species that are a subset of the 481 species in the present analysis and that were represented by all four of the rDNA regions used in the present study (i.e. there were no missing data). Trees derived from EP and ML analyses of the 93-species dataset were loaded as backbone constraint trees (trees used as constraints 1–3 are shown in Binder & Hibbett (2002), figs 1, 3 and 5, respectively) and analyses were

Table 1. Taxa sampled.

clade	number of species sampled	estimated number of described species in clade[a]
homobasidiomycetes	464	13 497
Bolete clade	18 (4%)	840 (6%)
Cantharelloid clade	23 (5%)	170 (1%)
Euagarics clade	214 (46%)	8425 (62%)
Gomphoid–Phalloid clade	13 (3%)	350 (3%)
Hymenochaetoid clade	34 (7%)	630 (5%)
Polyporoid clade	98 (21%)	1350 (10%)
Russuloid clade	42 (9%)	1000 (7%)
Thelephoroid clade	13 (3%)	240 (2%)
other minor clades	9 (2%)	—

[a] Estimated numbers of species in each group based on figures from Hawksworth *et al.* (1995) and Hibbett & Thorn (2001).

performed using the same settings as in the unconstrained EP analyses.

(c) *Analyses of character evolution*

We scored fruiting-body morphology as resupinate (0) or pileate-erect (1) (effused-reflexed taxa, which have both resupinate and pileate parts of the fruiting body, were scored as pileate-erect) and performed ancestral state reconstruction (ASR) using EP optimization in MacClade, on all of the EP, WP and constrained EP trees. We also inferred the ancestral fruiting-body morphology of the homobasidiomycetes with ML, using the 'local' method of Pagel (1999), which was implemented in Discrete. To run the ML tests of ancestral states, we fixed the ancestral node of the homobasidiomycetes as resupinate and obtained the likelihood of the data; next, we fixed the ancestral node as pileate-erect and obtained the likelihood again. Following Pagel (1999) and others (Mooers & Schluter 1999), we used a difference of two units of log likelihood as the criterion for 'strong' support of one ancestral state over another. We performed ML tests of ancestral states using nine different trees that varied in topology, branch-length estimates and sampling regimes, including (i) one tree each from the EP, WP and constrained EP analyses, with branch lengths estimated with ML from the nuc-lsu rDNA only (which is shared by all species); (ii) 'punctuational' versions of the unconstrained EP and WP trees, in which all branch lengths were set to have the same value; and (iii) 'pruned' versions of the unconstrained EP and WP trees, in which the number of resupinate taxa was reduced by half, with the deletions spread across the tree (with ML branch lengths). The pruned trees include 72 (17%) resupinate species, which may be a more representative sample than that in the unpruned trees (Hawksworth *et al.* 1995; Parmasto 1997).

To test whether the rate of transformations from resupinate to pileate-erect forms is significantly different from the rate of transformations in the reverse direction (these transformations are hereafter called gains and losses, and their rate parameters are called α and β, respectively), we used ML analysis in Discrete, with the same nine trees as were used in ML tests of ancestral states. To run the test, we first estimated α and β without restriction on their values and obtained the likelihood; next, we restricted the values of α and β to be equal and repeated the analysis. The test statistic is equal to twice the difference in log likelihoods and is χ^2-distributed with one degree of freedom (Pagel 1997, 1999).

3. RESULTS

The dataset has 3977 bp of aligned sequence, of which 177 bp were too divergent to be included in our analyses. There are 2262 variable positions and 1605 parsimony-informative positions. The EP and WP analyses each recovered 10 000 trees (EP: 23 536 steps, consistency index (CI) = 0.174, retention index (RI) = 0.584; WP: 125 982 steps, CI = 0.175, RI = 0.592). The constrained EP analyses recovered trees that are 69–75 steps longer than the unconstrained trees (23 605–23 611 steps, CI = 0.173, RI = 0.583). Despite the large number of equally parsimonious trees, the strict consensus trees in each analysis are highly resolved (only the EP tree is shown in detail; figure 1).

The five phylogenetic analyses that we performed indicate different patterns of higher-order relationships among the major clades of homobasidiomycetes (figure 2). Nevertheless, the eight major clades of homobasidiomycetes recognized by Hibbett & Thorn (2001) were resolved in all trees, as well as several independent minor clades, including the *Gloeophyllum* clade (three species), *Dendrocorticium* clade (five species) and *Jaapia argillacea* (figures 1 and 2). A clade of five species including *Paullicorticium niveocremeum* (the *Paullicorticium* clade) jumped between the Polyporoid clade (EP, constrained EP analysis 2), Russuloid clade (WP) and positions close to the Auriculariales (constrained EP analyses 1 and 3), but the composition of major clades in the homobasidiomycetes was otherwise stable across the different analyses (figure 2). Resupinate forms occur in each of the eight major clades of homobasidiomycetes, as well as the *Dendrocorticium* clade, *Jaapia argillacea*, and the *Paullicorticium* clade (figure 1).

Parsimony-based ASRs on the EP, WP and constrained EP trees indicate that there have been 50–54 transformations between resupinate and pileate-erect forms (figure 1; table 2). On average, the ASRs on the EP trees indicate a slight preponderance of gains relative to losses (29.3 gains versus 24.7 losses), but WP trees indicate a roughly equal number of gains and losses, and constrained EP trees indicate a preponderance of losses (table 2).

We examined parsimony-based ASRs in detail on one tree each from the EP, WP and constrained EP analyses. The various topologies imply different patterns of changes,

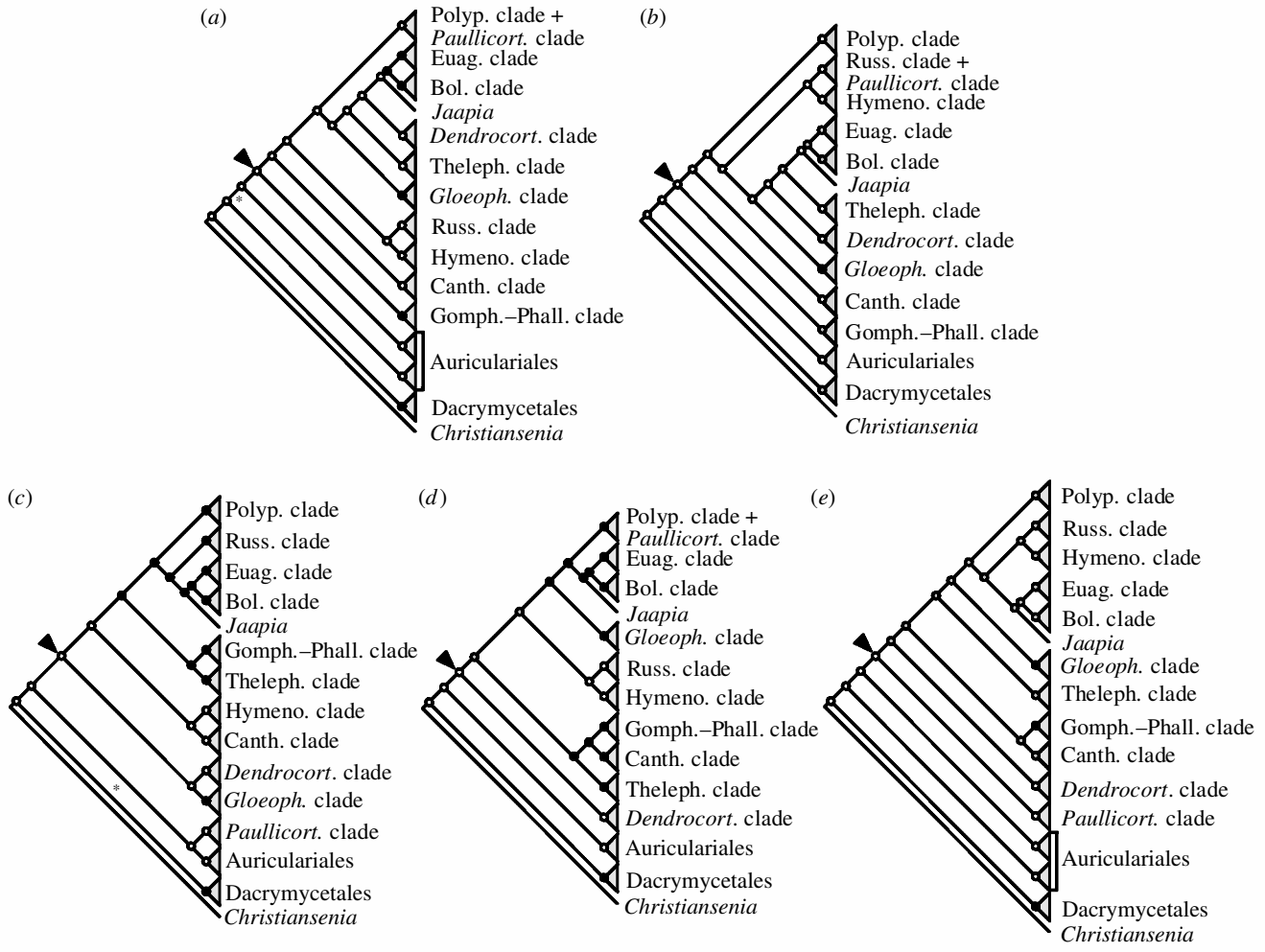

Figure 2. Higher-level relationships of homobasidiomycetes inferred with (*a*) EP, (*b*) WP and (*c–e*) constrained EP analyses ((*c*) constrained analysis 1; (*d*) constrained analysis 2; (*e*) constrained analysis 3). The ancestor of the homobasidiomycetes is indicated with an arrowhead. Ancestral states at nodes inferred with parsimony on one tree from each analysis are indicated by shaded circles: white, resupinate; black, pileate-erect; grey, uncertain. Labelled terminal groups are the same as in figure 1; asterisks denote nodes that collapse in the strict consensus tree.

Table 2. Numbers of transformations in fruiting-body form (0, resupinate; 1, pileate-erect) estimated with parsimony.

analysis	total steps	number of gains (0 → 1) minimum–maximum (average)	Number of losses (1 → 0) minimum–maximum (average)
EP	54	16–37 (29.3)	17–38 (24.7)
WP	50–51	20–30 (25.0)	20–31 (25.8)
EP constrained analysis 1	50–51	15–24 (19.4)	27–36 (31.6)
EP constrained analysis 2	53	19–24 (20.9)	29–34 (32.1)
EP constrained analysis 3	53–54	11–37 (25.7)	17–43 (28.2)

as optimized using parsimony (figure 2). For example, the ancestral state of the polyporoid clade is resolved as resupinate in the EP and WP trees, but it is resolved as pileate-erect in constrained EP analyses 1 and 2 and it is equivocal in constrained EP analysis 3 (figure 2). Nevertheless, in all the trees that we examined, the optimal ASR indicates that the ancestor of the homobasidiomycetes was resupinate (figure 2). Maximum likelihood analyses of ancestral states also indicate that the ancestor of the homobasidiomycetes was resupinate ($\Delta \log L > 2$ in all nine trees).

ML analyses indicate that the rate of transformations from resupinate forms to pileate-erect forms is greater than the rate of transformations in the reverse direction. In the trees with all 481 species included (seven trees tested), the unrestricted value of α is about three to four times greater than that of β (table 3). In the pruned trees, the asymmetry is even more pronounced, with α being about five to six times greater than β (table 3). In all trees, the restricted model, in which α and β are forced to take the same value, is significantly less likely than the unconstrained model ($p < 0.001$; table 3).

Table 3. ML tests of asymmetries in transformation rates.

	unrestricted ($\alpha \neq \beta$)			restricted ($\alpha = \beta$)			
analysis	α (0 → 1)	β (1 → 0)	−log$L$	α (0 → 1)	β (1 → 0)	−log$L$	2Δlog$L$*
EP	4.385	1.379	405.013	2.392	2.392	414.590	19.154
WP	4.063	1.242	397.893	2.142	2.142	407.738	19.690
EP constrained analysis 1	4.426	1.428	404.353	2.456	2.456	413.347	17.988
EP constrained analysis 2	4.296	1.559	410.438	2.450	2.450	418.114	15.352
EP constrained analysis 3	4.860	1.326	408.931	2.549	2.549	419.371	20.880
EP punctuational analysis	28.772	7.095	379.925	13.911	13.911	390.344	20.838
WP punctuational analysis	24.458	6.945	369.603	12.947	12.947	378.254	17.302
EP pruned	6.898	1.172	326.292	2.406	2.406	339.504	26.424
WP pruned	6.583	1.019	311.456	2.176	2.176	327.503	32.094

*$p < 0.001$.

4. DISCUSSION

Resupinate homobasidiomycetes have presented significant taxonomic challenges because of their morphological simplicity. The first objective of our study was to determine the phylogenetic distribution of resupinate homobasidiomycetes. Our analyses resolve the placements of many resupinate forms, confirming that they are scattered throughout the homobasidiomycetes, as has been suggested (Donk 1964, 1971; Jülich 1981; Parmasto 1986, 1995; Corner 1991). The taxonomic implications of these analyses will be presented elsewhere (M. Binder and D. S. Hibbett, unpublished data).

The second objective of our study was to infer the ancestral morphology of the homobasidiomycetes. Ancestral state reconstruction has many potential sources of error, including error in phylogenetic reconstruction and biased or incomplete taxon sampling (Cunningham 1999; Mooers & Schluter 1999; Omland 1999; Ree & Donoghue 1999; Salisbury & Kim 2001). The ML method of ASR is also sensitive to error in branch-length estimates (Ree & Donoghue 1999). Conversely, it is a strength of the ML method that it is able to incorporate information about branch lengths into estimates of ancestral states. We explored the sensitivity of our results to each of these factors by performing ASR using different tree topologies, sampling regimes and branch lengths. On all the trees that we tested, parsimony and ML analyses both indicate that the ancestor of the homobasidiomycetes had a resupinate fruiting body. These results are partially consistent with the view that resupinate homobasidiomycetes make up a paraphyletic grade of plesiomorphic forms, as suggested by Parmasto (1995) and Oberwinkler (1985). Nevertheless, parsimony analysis also implies that there have been multiple reversals from pileate-erect forms to resupinate forms (table 2). The precise number of transformations and the states of many internal nodes according to parsimony are, however, ambiguous (figure 2; table 2).

The final objective of our study was to address whether there is an asymmetry in the rate of transformations between resupinate and pileate-erect fruiting bodies in homobasidiomycetes. The same sources of error that affect ASR also affect estimation of evolutionary models, but again our results were consistent across all of the trees that we tested. The optimal models of morphological evolution indicate that the rate of transformations from resupinate to pileate-erect forms exceeds the rate of transformations in the reverse direction by a factor of at least three (table 3). In other words, resupinate forms appear to be evolutionarily more labile than pileate-erect forms, which may explain why pileate-erect forms have come to predominate in homobasidiomycetes.

At a first glance, it might appear that there is a conflict between the results of the ML analyses, which indicate a significant trend towards evolution of pileate-erect forms, and those of parsimony analyses, which reveal no consistent pattern of losses of resupinate forms outnumbering gains (tables 2 and 3). A major difference between these methods of analysis, however, is that under parsimony, a model of evolution in which the rates of losses and gains are equal is implicit, whereas under ML these parameters are estimated directly from the phylogeny and are allowed to vary. In this case, likelihood-ratio tests rejected models of evolution in which losses and gains have equal rates, indicating that ancestral state reconstructions based on equally weighted parsimony may not be reliable. One potential application of the ML analyses is to use the transformation rates inferred with ML to develop transformation costs (step-matrix values) for use in weighted parsimony analysis of fruiting-body morphology.

The analyses presented here employed a simple model of fruiting-body evolution, in which there are only two character states, and a uniform process of evolution is assumed to operate across the entire phylogeny. In future analyses, we will explore multi-state character codings, which may better reflect the diversity of fruiting-body forms, and we will test the assumption of process homogeneity, for example through analyses of character correlations (e.g. Hibbett & Donoghue 2001). Such analyses will involve models with many more parameters than the models used here, and may require larger, more densely

sampled phylogenetic trees to detect trends. In the meantime, our results indicate that there is an active, or 'driven', trend towards the evolution of complex forms in homobasidiomycetes, but they do not address the cause of this trend. Nevertheless, it seems probable that the driving force is related to selection for efficient spore dispersal, which is the sole function of fungal fruiting bodies.

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