# 5 Basidiomycota: Homobasidiomycetes

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## I. Introduction

Homobasidiomycetes include the mushroom-forming fungi and related taxa. Over 13000 species of homobasidiomycetes have been described, which is equal to approximately 23% of all known species of eumycota (Hawksworth et al. 1995). Homobasidiomycetes occur in all terrestrial ecosystems, including deserts, and there are also a few aquatic species, in both marine and freshwater habitats (Kohlmeyer and Kohlmeyer 1979; Desjardin et al. 1995). The oldest unambiguous homobasidiomycete fossils are from the mid-Cretaceous, but indirect evidence, including molecular clock dating, suggests that the group may have been in existence by the late Triassic (ca. 200 ma; Berbee and Taylor 1993; Hibbett et al. 1997a). In contemporary ecosystems, homobasidiomycetes function as saprotrophs, plant pathogens, and partners in diverse symbioses, including ectomycorrhizae. Thus, homobasidiomycetes play a significant role in the carbon cycle, and they have a profound economic impact on agricultural industries, especially forestry. Finally, homobasidiomycetes are culturally significant, having served as food, drugs, and spiritual symbols in diverse human societies.

Homobasidiomycetes have been studied extensively, but there is still no comprehensive phylogenetic classification of the group. In this chapter, we synthesize results of recent phylogenetic studies in homobasidiomycetes and provide a preliminary phylogenetic outline for the group as a whole. We also discuss selected characters that appear to be phylogenetically informative or that have particular ecological or functional signifi-

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cance. Our goal is to provide an overview of current knowledge regarding homobasidiomycete phylogeny as well as a framework for further studies.

## II. Phylogeny

### A. Higher-Level Relationships of Homobasidiomycetes

Molecular and ultrastructural evidence suggests that the homobasidiomycetes are nested in a clade of Basidiomycota that have biglobular spindle pole bodies, complex dolipore septa, and (usually) membrane-bound parenthesomes (Wells 1978; Moore 1980; McLaughlin 1981; Swann and Taylor 1993, 1995a,b). This group has been termed the hymenomycete lineage by Swann and Taylor (1993). In addition to homobasidiomycetes, the hymenomycete lineage includes the heterobasidiomycete orders Auriculariales sensu stricto, Dacrymycetales, Tremellales, Ceratobasidiales, and Tulasnellales (Oberwinkler 1972; Bandoni 1984; Tehler 1988; Wells 1994; Sjamsuridzal et al. 1997). Major characters that have been used to distinguish homobasidiomycetes from heterobasidiomycetes include basidial morphology, parenthesome ultrastructure, mode of spore germination, and gelatinization of fruiting bodies (Talbot 1973a; Tu and Kimbrough 1978; Jülich 1981; Ingold 1985, 1992; Oberwinkler 1985; Wells 1994; see Wells et al., Chap. 4, this Vol.). In this chapter, we generally follow the classification of heterobasidiomycetes proposed by Wells (1994).

The homobasidiomycetes have generally been accepted as monophyletic (e.g., Savile 1955; Schaffer 1975; Oberwinkler 1982). However, in a morphological cladistic analysis of fungal phylogeny, Tehler (1988) was unable to find any uncontradicted synapomorphies supporting the monophyly of the homobasidiomycetes. Higher-level relationships of homobasidiomycetes have been investigated in molecular studies using sequences of nuclear small-subunit ribosomal DNA (nuc-ssu rDNA; Swann and Taylor 1993, 1995a,b; Gargas et al. 1995; Fig. 3 in Sjamsuridzal et al. 1997), and nuclear large-subunit rDNA (nuc-lsu rDNA; Begerow et al. 1997). These studies support the monophyly of Auriculariales, Dacrymycetales, and Tremellales, but they give mixed results regarding the monophyly of the homobasidiomycetes (Fig. 1). In some analyses the Auriculariales and Ceratobasidiales appear to be nested within the homobasidiomycetes, whereas in others they are outside the homobasidiomycetes (Fig. 1). The nuc rDNA studies all support or are consistent with the view that the homobasidiomycetes plus Auriculariales and Ceratobasidiales form a monophyletic group, and that the Tremellales and Dacrymycetales are near the base of the hymenomycete lineage (their positions are interchangeable, however; Fig. 1). Tulasnellales have not been included in the studies just cited. Analyses of nuc-ssu rDNA and partial mitochondrial small-subunit (mt-ssu) rDNA sequences (Hibbett et al. 1997b, D.S. Hibbett, unpubl.; Lee and Jung 1997) suggest that the Tulasnellales and Ceratobasidiales are nested within the homobasidiomycetes, and that the Auriculariales is the sister group to this clade (Fig. 1). This is consistent with results of analyses of mt-lsu rDNA sequences (Bruns et al. 1998), which suggest that *Tulasnella* (Tulasnellales) and *Waitea* (Ceratobasidiales) are in the homobasidiomycetes.

### B. Overview of Homobasidiomycete Taxonomy

Classification of homobasidiomycetes is in a period of major revision. One of the earliest broad classifications for homobasidiomycetes (and other macrofungi) was the Friesian system (Fries 1874), which grouped taxa based on gross morphology of the hymenophore, as follows (emphasizing Hymenomycetes, after Donk 1971):

| | |
|---|---|
| Gasteromycetes | (enclosed hymenophore) |
| Hymenomycetes | (exposed hymenophore) |
| Agaricales | (lamellate hymenophore) |
| Agaricaceae | |
| Aphyllophorales | (nonlamellate hymenophore) |
| Cantharellaceae | (wrinkled hymenophore, erect, pileate) |
| Clavariaceae | (smooth hymenophore, erect, branched or unbranched) |
| Hydnaceae | (toothed hymenophore) |
| Meruliacae | (wrinkled hymenophore, resupinate or pileate) |
| Polyporaceae | (poroid hymenophore) |
| Thelephoraceae | (smooth hymenophore, resupinate or erect) |

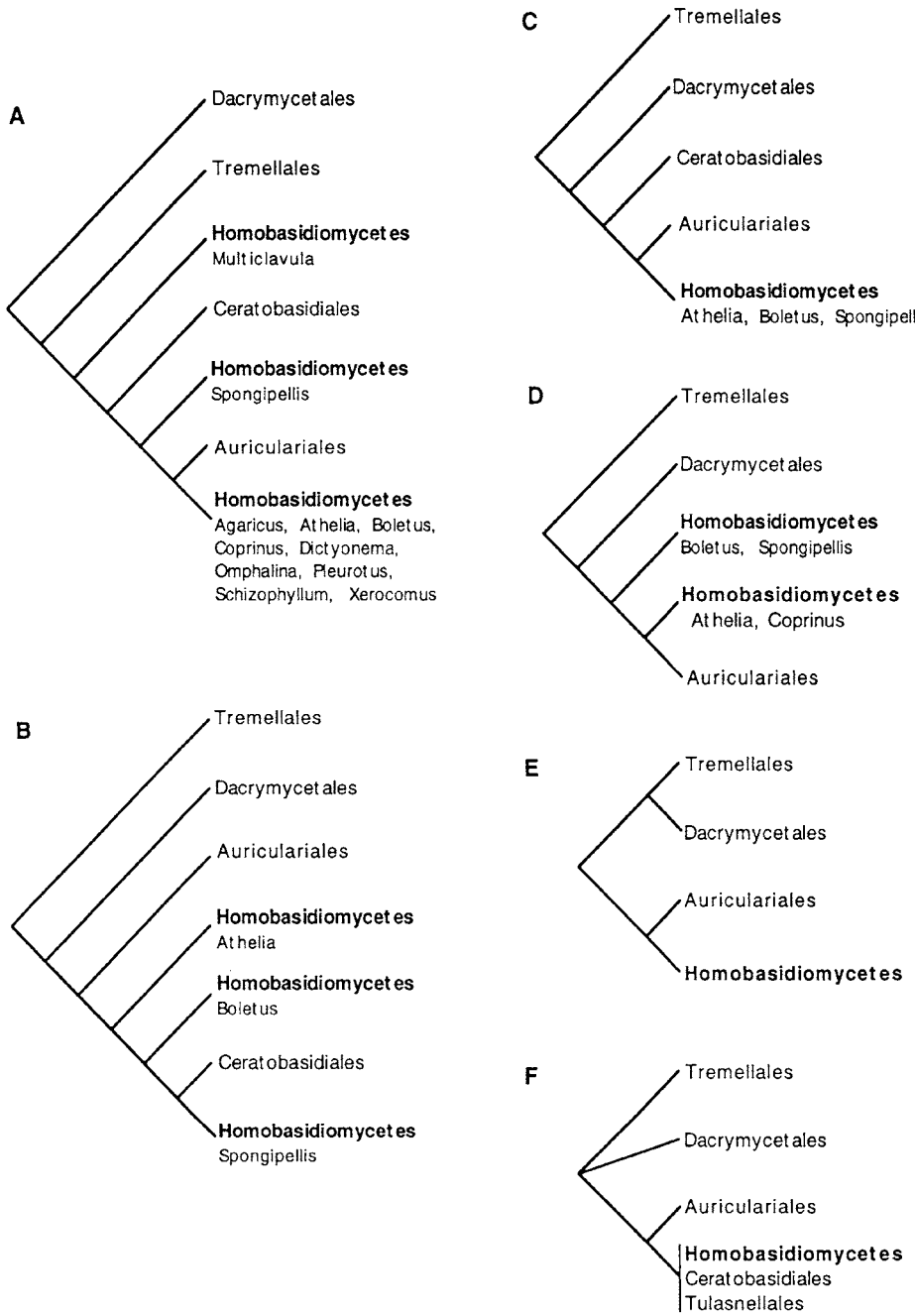


**Fig. 1A–F.** Higher-level phylogenetic relationships of homobasidiomycetes. **A–E** Simplified cladograms based on prior studies using nuc rDNA sequences (**A–D** nuc-ssu rDNA, **E** nuc-lsu rDNA). Note that studies disagree about the monophyly of homobasidiomycetes and the relative positions of heterobasidiomycete orders. **A** (Gargas et al. 1995, Fig. 1). **B** (Swann and Taylor 1993, Fig. 2; neighbor-joining analysis). **C** (Swann and Taylor 1993, Fig. 1; parsimony analysis). **D** (Swann and Taylor 1995a, Fig. 1). **E** (Begerow et al. 1997). **F** Summary cladogram incorporating results of Bruns et al. (1998), Hibbett et al. (1997b), and D.S. Hibbett (unpubl.; see text)

The Friesian system is intuitively accessible, but it is artificial (see Table 2). Anatomical studies since the turn of the century (Fayod 1889; Patouillard 1900) have resulted in major reclassifications of the Friesian higher taxa (for reviews, see Jülich 1981; Walker 1996). Among the most influential modern treatments are those of Donk (1964, 1971), who divided the 6 Friesian families of the Aphyllophorales into 23 families, Singer (1986), who divided the Agaricales into 17 families, and Dring (1973), who divided the Gasteromycetes into 9 orders with 23 families. In general, the taxonomic names used here are based on these works.

The classifications of Donk, Singer, and Dring each include a number of putatively monophyletic groups that have distinguishing morphological features (e.g., Ganodermataceae, Coprinaceae, Phallales), and therefore represent major advances toward a phylogenetic classification of homobasidiomycetes. Nevertheless, these classifications also include large residual taxa that lack synapomorphies and that are presumably polyphyletic (e.g., Clavariaceae, Corticiaceae, Polyporaceae, Tricholomataceae, Hymenogastrales). Moreover, they maintain the Friesian division of macrofungi into Aphyllophorales, Agaricales, and Gasteromycetes (with some modifications, such as the inclusion of boletes in Agaricales), in spite of strong evidence that these taxa are artificial.

The Friesian higher taxa must be integrated if a natural classification of the homobasidiomycetes is to be achieved. This was attempted by Jülich (1981), who based his phylogenetic hypothesis and classification on anatomy and morphology. Jülich's system was a bold attempt to unify homobasidiomycete classification, but it was widely criticized (e.g., Nuss 1983; Redhead and Ginns 1983) and has not been generally adopted. Alternative higher-level classifications of homobasidiomycetes were proposed by Kreisl (1969), Oberwinker (1977), Pegler (in Hawksworth et al. 1995), and Walker (1996), but there is still no consensus about the broad outlines of homobasidiomycete phylogeny.

## C. Phylogeny Within Homobasidiomycetes

In recent years, there have been many phylogenetic studies centered on specific groups of homobasidiomycetes, but there has been no comprehensive analysis of the entire group. The most taxonomically inclusive phylogenetic study in homobasidiomycetes so far is that of Hibbett et al. (1997b), which was based on nuc-ssu and mt-ssu rDNA sequences. The analysis of Hibbett et al. (1997b) included 81 species of homobasidiomycetes, which represent 10 families of Agaricales sensu Singer (1986), 18 families of Aphyllophorales sensu Donk (1964), and 7 families of Gasteromycetes sensu Dring (1973). In this chapter, we have used the results of Hibbett et al. (1997b) as a framework for developing a preliminary phylogenetic outline of the homobasidiomycetes (Table 1).

The strict consensus of the shortest trees found by Hibbett et al. (1997b) is shown in Fig. 2. The data matrix used to infer the tree included about 2400 base pairs of sequence data per terminal taxon. Nevertheless, many nodes in the tree were weakly supported (as measured by bootstrapping), especially those near the base of the tree (Fig. 2). Consequently, the higher-order relationships and the position of the root of the homobasidiomycetes remain unclear. To resolve these issues, it will be necessary to perform phylogenetic analyses that include additional rDNA and protein-coding gene sequences, or morphological characters (see Sect. III).

We have tentatively divided the homobasidiomycetes into eight major clades (Fig. 2, Table 1). By referring to the results of other molecular studies (see Table 1 for references), we have increased the number of taxa that can be assigned to these clades to 246 genera (from a total of 79 genera sampled by Hibbett et al. 1997b). The genera in Table 1 represent most of the major groups of homobasidiomycetes recognized in current taxonomy. However, many small, taxonomically controversial groups have yet to be studied, such as *Astraeus*, *Cantharocybe*, *Horakia*, *Pachykytospora*, and cyphelloid forms. In addition, sampling is still limited in certain large polyphyletic groups, such as Hymenogastrales, Tricholomataceae, Polyporaceae, and especially Corticiaceae. With that caveat, we present crude estimates of the numbers of described species in each clade based on species counts for higher taxa of homobasidiomycetes in *The Dictionary of the Fungi*, 8th ed. (Hawksworth et al. 1995; Fig. 2). Exemplars of the eight major clades are shown in Figs. 3–14.

### 1. Polyporoid Clade

This group includes members of Corticiaceae, Ganodermataceae, Polyporaceae, and Sparassidaceae (Fig. 2, Table 1). The polyporoid clade is

**Table 1.** Preliminary phylogenetic outline of homobasidiomycetes based on molecular characters

| Clade | Exemplar genera sampled in molecular studies, and references[1] |
|---|---|
| 1. **Polyporoid clade** | |
| Hymenomycetes | |
| Aphyllophorales | |
| **Corticiaceae** | *Candelabrochaete*[26], *Cotylidia*[26], *Crustoderma*[26], *Dendrocorticium*[26], *Dentocorticium*[2], *Epithele*[26], *Galzinia*[26], *Hyphoderma*[26], *Lopharia*[26], *Mycoacia*[26], *Phanerochaete*[2,3,16,26], *Phlebia*[2,3,26], *Phlebiopsis*[25,26], *Porogramme*[26], *Pulcherricium*[3,25,26], *Punctularia*[26], *Scopuloides*[26], *Sistotrema*[2], *Vuilleminia*[26], symbionts of *Xyleborus* and *Dendroctonus* bark beetles[25] |
| **Ganodermataceae** | *Ganoderma*[2,3,4,6,26] |
| **Hydnaceae ("residual")** | *Climacodon*[26], *Steccherinum*[26] |
| **Polyporaceae** | *Abortiporus*[4], *Albatrellus*[2,11], *Antrodia*[2,3,4,25,26], *Antrodiella*[4,26], *Aurantioporus*[4], *Bjerkandera*[2,3,4,26], *Ceriporia*[2,3,26], *Ceriporiopsis*[4,26], *Climacocystis*[4], *Cryptoporus*[3], *Daedalea*[2,3], *Daedaleopsis*[3], *Datronia*[3], *Faerberia*[16], *Fomes*[2,3], *Fomitopsis*[2,3,26], *Gloeophyllum*[16,26], *Gloeoporus*[4], *Irpex*[16], *Juhnghunia*[26], *Laetiporus*[2,3], *Lentinus*[2,3,24], *Lenzites*[3,26], *Leptoporus*[4,26], *Meripilus*[2,25,26], *Oligoporus* (= *Postia*)[4,16,26], *Panus*[2,4,11,24], *Perenniporia*[2,26], *Phaeolus*[2,3], *Physisporinus*[26], *Piptoporus*[3], *Polyporoletus*[11], *Polyporus*[2,3,24], *Pycnoporus*[3], *Rigidoporus*[26], *Skeletocutis*[4], *Spongipellis*[4,9,26], *Trametes*[2,3,26], *Tyromyces*[4], *Wolfiporia*[2] |
| **Sparassidaceae** | *Sparassis*[2,3] |
| 2. **Euagarics clade** | |
| Hymenomycetes | |
| Agaricales | |
| **Agaricaceae** | *Agaricus*[2,6,7,9,11,12,16,22], *Chlorophyllum*[6], *Cystoderma*[6,22], *Lepiota*[2,6,7,12,22], *Leucoagaricus*[6,7,12], *Leucocoprinus*[6,7,16,22], G1 and G3 attine ant symbionts[6,7] |
| **Amanitaceae** | *Amanita*[2,6,11,12,17], *Limacella*[6] |
| **Bolbitiaceae** | *Agrocybe*[6,8,16], *Bolbitius*[6,7,8,11,12,16,17], *Conocybe*[6] |
| **Coprinaceae** | *Annellaria*[6], *Coprinus*[2,6,8,9,16], *Lacrymaria*[6,16], *Paneolina*[6,7], *Paneolus*[6,8], *Psathyrella*[6,8] |
| **Cortinariaceae** | *Cortinarius*[2,6,7,11,12,17,22], *Dermocybe*[6], *Inocybe*[6,11], *Hebeloma*[6,7,11,12,22] |
| **Entolomataceae** | *Clitopilus*[6,16], *Entoloma*[6,12,17] |
| **Hygrophoraceae** | *Hygrocybe*[5,6,11,12,17,23], *Hygrophorus*[5,6,11,12,17] |
| **Paxillaceae** | *Lampteromyces*[6,16,22], *Omphalotus*[6,22], *Ripartites*[22] |
| **Pluteaceae** | *Pluteus*[2,6,17] |
| **Strophariaceae** | *Hypholoma*[6], *Kuhneromyces*[6], *Pholiota*[6], *Psilocybe*[6,16], *Stropharia*[2,6,16] |
| **Tricholomataceae** | *Armillaria*[6,11,12,16], *Arrhenia*[6,23], *Asterophora*[6,11], *Clitocybe*[6,16,22,23], *Collybia*[6,16], *Crinipellis*[6,7,12], *Flammulina*[6], *Gerronema*[5,6,23], *Hohenbuehelia*[6,16], *Laccaria*[6,11,13], *Lentinula*[2,3,6,24,25], *Lepista*[16], *Lyophyllum*[6,16], *Marasmiellus*[6], *Marasmius*[6,7,12], *Melanoleuca*[16], *Mycena*[6], *Omphalina* pro parte[6,9,23], *Panellus*[2,3], *Phaeotellus*[6,23], *Resupinatus*[6], *Termitomyces*[6], *Tricholoma*[6,11,12,17,22], *Xeromphalina*[6], G2 attine ant symbionts[7] |
| Aphyllophorales | |
| **Clavariaceae** | *Clavaria*[5], *Clavulinopsis*[5], *Macrotyphula*[5], *Pterula*[5], *Typhula*[2,5] |
| **Corticiaceae** | *Athelia*[9], *Piloderma*[11,17], *Gloeocystidium ipidophilum*[25] |
| **Dictyonemataceae** | *Dictyonema*[9] |
| **Fistulinaceae** | *Fistulina*[2,3] |
| **Polyporaceae** | *Phyllotopsis*[6,24], *Pleurotus*[2,3,6,9,12,16,22,24,25] |
| **Schizophyllaceae** | *Schizophyllum* (incl. *Auriculariopsis* pro parte)[2,9,18] |
| Gasteromycetes | |
| Hymenogastrales | |
| **Coprinaceae** | *Montagnea*[8] |
| **Tricholomataceae** | *Hydnangium*[13], *Podohydnangium*[13] |
| **Strophariaceae** | *Weraroa*[22] |
| **unplaced** | *Leratia*[22] |
| Lycoperdales | |
| **Lycoperdaceae** | *Calvatia*[2], *Lycoperdon*[2] |
| Nidulariales | |
| **Nidulariaceae** | *Crucibulum*[2,12,16,20], *Cyathus*[2,12,16,20] |
| Podaxales | |
| **Podaxaceae** | *Podaxis*[8] |
| Tulostomatales | |
| **Tulostomataceae** | *Tulostoma*[2] |
| Heterobasidiomycetes | |
| Ceratobasidiales | |
| **Ceratobasidiaceae** | *Ceratobasidium*[2], *Waitea*[11] |

**Table 1.** *Continued*

| Clade | Exemplar genera sampled in molecular studies, and references[1] |
|---|---|
| 3. **Bolete clade** | |
| Hymenomycetes | |
| Agaricales | |
| **Boletaceae** | *Austroboletus*[11,17], *Boletus*[2,3,6,7,9,10,11,12,17,22], *Gyroporus*[11,17], *Paragyrodon*[10,11,17], *Phylloporus*[6,7,10,11,12], *Strobilomyces*[11,12], *Suillus*[3,6,10,11,12,26], *Tylopilus*[11], *Xerocomus*[9,10,11] |
| **Gomphidiaceae** | *Chroogomphus*[10,11,14], *Gomphidius*[10,11,12,14] |
| **Paxillaceae** | *Hygrophoropsis*[11,12,22], *Paxillus* (including *Tapinella*)[2,10,11,12,22] |
| Aphyllophorales | |
| **Coniophoraceae** | *Coniophora*[11,12,17], *Serpula*[11,12,16] |
| Gasteromycetes | |
| Hymenogastrales | |
| **Cortinariaceae** | *Chamonixia*[11] |
| **Gomphidiaceae** | *Brauniellula*[11] |
| **Hymenogastraceae** | *Hymenogaster*[11] |
| **Rhizopogonaceae** | *Gastrosuillus*[14,26], *Rhizopogon*[10,11,12,14,26], *Truncocolumella*[11,14] |
| Melanogastrales | |
| **Melanogastraceae** | *Alpova*[11,17], *Melanogaster*[11] |
| Sclerodermatales | |
| **Sclerodermataceae** | *Pisolithus*[11], *Scleroderma*[2] |
| Tulostomatales | |
| **Calostomataceae** | *Calostoma*[19] |
| 4. **Thelephoroid clade** | |
| Hymenomycetes | |
| Aphyllophorales | |
| **Thelephoraceae** | *Boletopsis*[17], *Hydnellum*[2,12], *Pseudotomentella*[11], *Sarcodon*[11], *Thelephora*[2,11,12,17], *Tomentella*[11,17] |
| 5. **Russuloid clade** | |
| Hymenomycetes | |
| Agaricales | |
| **Russulaceae** | *Lactarius*[6,11,12,17,21,22], *Russula*[2,3,6,11,12,17,21,22,25,26] |
| Aphyllophorales | |
| **Auriscalpiaceae** | *Auriscalpium*[2,3,21,26], *Gloeodontia*[21,26], *Gloiodon*[26], *Lentinellus*[2,3,11] |
| **Bondarzewiaceae** | *Bondarzewia*[2,3,6,11,17,21] |
| **Corticiaceae** | *Acanthophysium*[2,26], *Aleurodiscus*[2,26], *Boidinia*[21,26], *Byssoporia*[11], *Conferticium*[21], *Entomocorticium*[25], *Peniophora* (incl. *Dendrophora, Duportella*)[2,3,25,26], *Pseudoxenasma*[21], *Vesiculomyces*[21] |
| **Echinodontiaceae** | Echinodontium[2,3,21,26] |
| **Hericiaceae** | *Clavicorona*[2,5,21], *Creolophus*[21], *Dentipellis*[21,26], *Gloeocystidiellum*[2,21,26], *Hericium*[2,3,21], *Laxitextum*[2,21,26] |
| **Lachnocladiaceae** | *Dichostereum*[21,26], *Scytinostroma*[2,26], *Vararia*[21,26] |
| **Polyporaceae** | *Albatrellus*[11,17], *Heterobasidion*[2,3,11,16,21,25,26] |
| **Stereaceae** | *Amylostereum*[2,25,26], *Stereum* (incl. *Xylobolus*)[2,3,25,26] |
| Gasteromycetes | |
| Hymenogastrales | |
| **Astrogastraceae** | *Cystangium*[21], *Gymnomyces*[21], *Macowanites*[21], *Martellia*[21], *Zelleromyces*[21] |
| 6. **Hymenochaetoid clade** | |
| Hymenomycetes | |
| Aphyllophorales | |
| **Corticiaceae** | *Basidioradulum*[2], *Hyphodontia*[2] |
| **Hymenochaetaceae** | *Coltricia*[2,3,15], *Hymenochaete*[26], *Inonotus*[2,3,15,26], *Phellinus*[2,3,26], *Phylloporia*[3] |
| **Polyporaceae** | *Oxyporus*[2,3], *Schizopora*[2], *Trichaptum*[2,3,15] |
| 7. **Cantharelloid clade** | |
| Hymenomycetes | |
| Aphyllophorales | |
| **Cantharellaceae** | *Cantharellus*[2,5,11], *Craterellus*[5] |
| **Clavariaceae** | *Multiclavula*[2,5,9,23] |
| **Clavulinaceae** | *Clavulina*[2,5] |
| **Corticiaceae** | *Botryobasidium*[2,5] |
| **Hydnaceae** | *Hydnum*[2,5] |
| Heterobasidiomycetes | |
| Tulasnellales | |
| **Tulasnellaceae** | *Tulasnella*[2,11] |

**Table 1.** *Continued*

| Clade | Exemplar genera sampled in molecular studies, and references[1] |
|---|---|
| 8. **Gomphoid-phalloid clade** | |
| Hymenomycetes | |
| Aphyllophorales | |
| **Clavariaceae** | *Clavariadelphus*[2,5,12] |
| **Gomphaceae** | *Gloeocantharellus*[5], *Gomphus*[2,5,11,12,17], *Kavinia*[11], *Lentaria*[5], *Ramaria*[2,5,11,12,16,17] |
| Gasteromycetes | |
| Gauticriales | |
| **Gautieriaceae** | *Gautieria*[11,12] |
| Hymenogastrales | |
| **Cortinariaceae** | *Kjeldsenia*[12] |
| **Hymenogastraceae** | *Chondrogaster*[12] |
| Lycoperdales | |
| **Geastraceae** | *Geastrum*[2,5] |
| Phallales | |
| **Clathraceae** | *Aseroe*[12,16], *Clathrus*[12], *Lysurus*[12], *Pseudocolus*[2,5] |
| **Hysterangiaceae** | *Hysterangium*[12], *Trappea*[12] |
| **Phallaceae** | *Phallus*[12] |
| **Protophallaceae** | *Protubera*[12] |
| Nidulariales | |
| **Sphaerobolaceae** | *Sphaerobolus*[2,5,16] |

[1] List does not include all taxa sampled in studies of Gardes and Bruns (1996), Moncalvo et al. (2000, and unpubl.), Bruns et al. (1998), Colgan et al. (1997), J. Spatafora (unpubl.), R.E. Thorn (unpubl.), D.S. Hibbett (unpubl.), and Boidin et al. (1998).
[2] Hibbett et al. (1997 and unpubl.).
[3] Hibbett and Donoghue (1995).
[4] Y.-J. Yao and D.S. Hibbett (unpubl.).
[5] Pine et al. (1999).
[6] Moncalvo et al. (2000, and unpubl.).
[7] Chapela et al. (1994).
[8] Hopple and Vilgalys (1994).
[9] Gargas et al. (1995).
[10] Bruns and Szaro (1992).
[11] Bruns et al. (1998; see also Cullings et al. 1996).
[12] Colgan et al. (1997) and J. Spatafora (unpubl.).
[13] Mueller and Pine (1994).
[14] Kretzer and Bruns (1997).
[15] Ko et al. (1997).
[16] Thorn et al. (2000, and unpubl.).
[17] Gardes and Bruns (1996).
[18] Nakasone (1996).
[19] Hughey et al. (2000).
[20] A. Gargas (unpubl.).
[21] S. Miller and E. Larsson (unpubl.).
[22] Binder et al. (1997).
[23] Lutzoni (1997) and Lutzoni and Pagel (1997).
[24] Neda and Nakai (1995).
[25] Hsiau (1996).
[26] Boidin et al. (1998).

primarily composed of polypores and corticioid fungi, but also includes the gilled mushrooms *Lentinus*, *Panus*, and *Faerberia* (= *Geopetalum*), as well as the "cauliflower fungus" *Sparassis* (which appears to be closely related to the polypores *Laetiporus* and *Phaeolus*; Fig. 2). The tree in Fig. 2 suggests that the poroid habit is plesiomorphic in the polyporoid clade and has given rise to gilled, toothed, and corticioid forms. Monophyly of the polyporoid clade is only weakly supported by bootstrapping, and in certain analyses of mt-ssu rDNA (Hibbett and Donoghue 1995) or mt-ssu rDNA and nuc-ssu rDNA (Hibbett 1996) it appears to be polyphyletic (but see Ko et al. 1997).

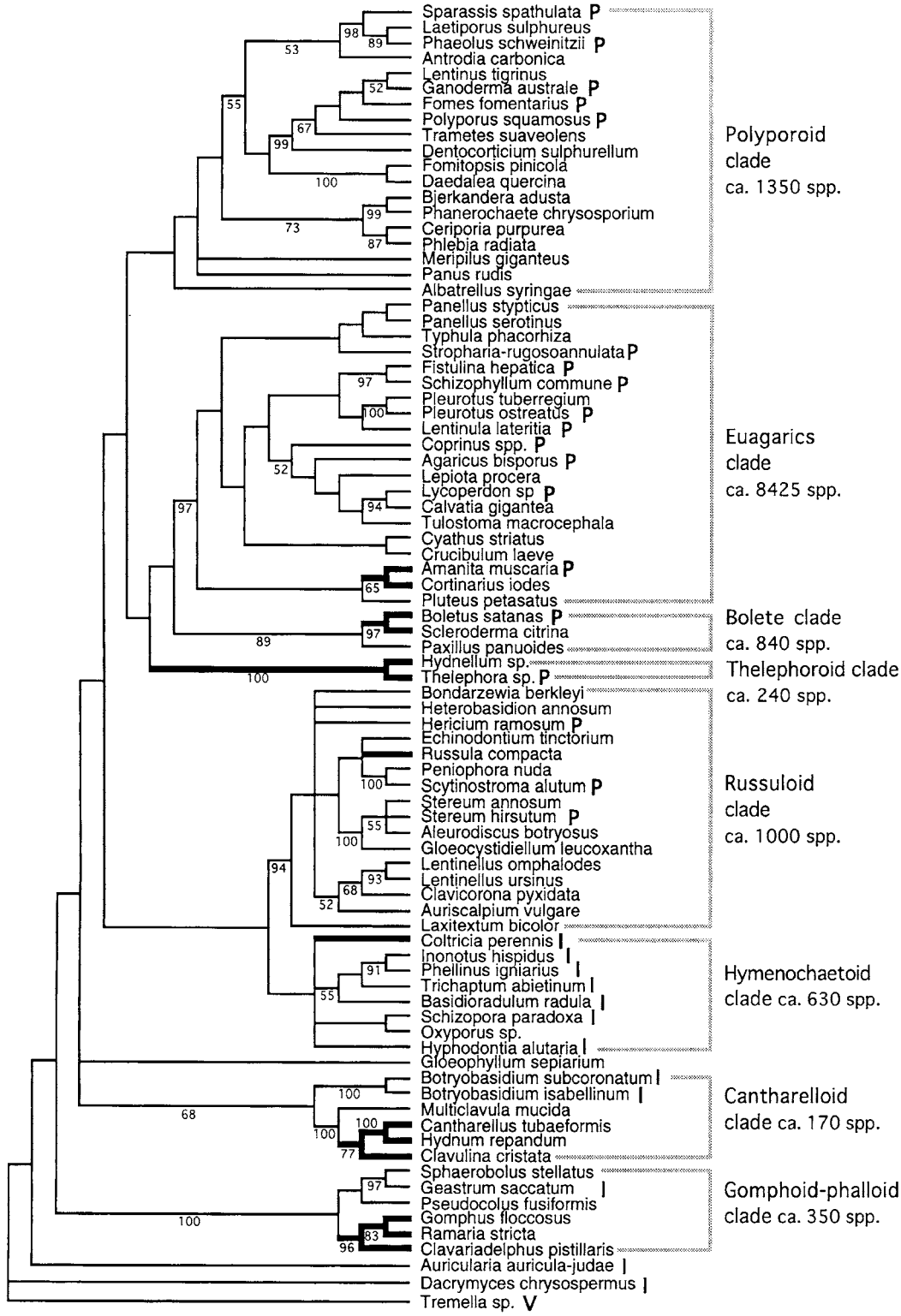


**Fig. 2.** Phylogenetic relationships of homobasidiomycetes. Strict consensus of 52 equally parsimonious trees found in analysis of nuc-ssu and mt-ssu rDNA sequences (Hibbett et al. 1997b). *Heavy lines* indicate ectomycorrhizal lineages. *Capital letters after taxon names* indicate parenthesome morphology, if known (*P* perforate; *I* imperforate; *V* vesiculate; see Table 4 for references). *Numbers by branches* are frequencies (%) of occurrence out of 100 bootstrap replicates (values <50% are not shown). Branch lengths do *not* correspond to numbers of nucleotide substitutions. *Bracketed groups to right of tree* are discussed in text. Estimates of diversity refer to described species only, based on Hawksworth et al. (1995)

An especially problematic result concerns *Gloeophyllum*; analyses of nuc-ssu and mt-ssu rDNA sequences have placed *Gloeophyllum* outside the polyporoid clade (Hibbett et al. 1997b; Fig. 2), but analyses of nuc-lsu rDNA sequences have placed it inside the polyporoid clade (Thorn et al. 2000). The latter placement is consistent with morphology, and it is accepted here. Despite the weak or conflicting results of molecular analyses, many members of the polyporoid clade have similar morphology and anatomy (i.e., the polypore habit, dimitic hyphal construction) and nutritional modes (wood decay). Thus, we tentatively conclude that the polyporoid clade is monophyletic, but this hypothesis should be tested in additional studies. Although the polyporoid clade as a whole is weakly supported, there are four groups within the polyporoid clade that are strongly supported and that have corroborating anatomical and physiological characters. Examples include the *Fomitopsis-Daedalea-Piptoporus* group (brown rot, bipolar mating system), and the *Polyporus-Lentinus-Ganoderma* group (white rot, tetrapolar mating systems, binding hyphae). For discussion of these and other lineages in the polyporoid clade, see Hibbett and Donoghue (1995).

The study of Hibbett et al. (1997b) included 19 genera in the polyporoid clade. An additional 27 genera of this group were sampled in studies by Bruns et al. (1998), Hibbett and Donoghue (1995), D.S. Hibbett (unpubl.), and Y.-J. Yao et al. (unpubl.; Table 1). In addition, Boidin et al. (1998) sampled approximately 37 genera in the polyporoid clade, including 19 that have not been examined elsewhere.[1] These additional genera represent the Corticiaceae, "residual" Hydnaceae (Donk 1964), and Polyporaceae. The latter includes *Faerberia* (Singer 1986; Thorn et al. 2000), and *Polyporoletus*, which is a terrestrial polypore that resembles *Albatrellus* (Singer et al. 1945; Gilbertson and Ryvarden 1986). Analyses of mt-lsu rDNA by Bruns et al. (1998; see also Gardes and Bruns 1996) suggest that *Polyporoletus* and some species of *Albatrellus* form a lineage in the polyporoid clade. However, these studies also suggests that *Albatrellus* is polyphyletic, with some species in the polyporoid clade and others in the russuloid clade (see below). *Albatrellus* has been interpreted as entirely mycorrhizal (Gilbertson and Ryvarden 1986), but Ginns (1997) suggested that *A. syringae* (polyporoid clade) is lignicolous.

The main families represented in the polyporoid clade, Polyporaceae and Corticiaceae, are polyphyletic, which makes it difficult to estimate the number of described species that can be assigned to this group. Ryvarden (1991) listed 11 groups of "related genera" in the Polyporaceae. Eight of these groups are represented in Table 1, and each of these has at least one member in the polyporoid clade (several of the groups appear to be polyphyletic). Parmasto (1986) divvided the Corticiaceae into 11 subfamilies. Eight of Parmasto's subfamilies are represented in Table 1, and three of these have species in the polyporoid clade (again, some subfamilies appear to be polyphyletic). Taking Ryvarden and Parmasto's divisions of the Polyporaceae and Corticiaceae into account, we estimate that the polyporoid clade contains roughly 1350 described species of homobasidiomycetes, including 90% of known Polyporaceae and 25% of Corticiaceae, as well as all Ganodermataceae and Sparassidaceae.

## 2. Euagarics Clade

This large clade is composed mostly of Agaricales (gilled mushrooms), but it also includes Aphyllophorales, Gasteromycetes, and possibly certain Ceratobasidiales (see below). In the study of Hibbett et al. (1997b), the euagarics clade was found to include exemplars of seven families of gilled Agaricales (Agaricaceae, Amanitaceae, Coprinaceae, Cortinariaceae, Pluteaceae, Strophariaceae, Tricholomataceae), four families of Aphyllophorales (Clavariaceae, Fistulinaceae, Polyporaceae, Schizophyllaceae), and three families of Gasteromycetes (Lycoperdaceae, Nidulariaceae, Tulostomataceae; Fig. 2, Table 1). It appears that the agaricoid habit is plesiomorphic in the euagarics clade and has given rise to multiple lineages of nongilled hymenomycetes and gasteroid forms (Hibbett et al. 1997b).

Members of the euagarics clade have been investigated in numerous phylogenetic studies, most notably the studies of Moncalvo et al. (2000, and unpubl.), who have sampled over 300 species in this group. The studies of Moncalvo et al., and others (see Table 1), have included many exem-

[1] Boidin et al. (1998) analyzed rDNA internal transcribed spacer (ITS) sequences from 360 species of basidiomycetes, mostly Aphyllophorales. The use of such a highly variable gene for broad phylogenetic analyses is questionable, and there were no bootstrap values reported. Taxonomic conclusions based solely on Boidin et al.'s study should be interpreted with caution.

plars of the families sampled by Hibbett et al. (1997b; Table 1), as well as five families of Agaricales (Bolbitiaceae, Crepidotaceae, Entolomataceae, Hygrophoraceae, Paxillaceae pro parte), two famillies of Aphyllophorales (Corticiaceae, Dictyonemataceae), and several secotioid Gasteromycetes that were not sampled by Hibbett et al.

The Paxillaceae are represented in the euagarics clade by *Lampteromyces*, *Omphalotus*, and *Ripartites* (Binder et al. 1997; Moncalvo et al. 2000, and unpubl.; Thorn et al. 2000). However, *Hygrophoropsis* and *Paxillus* (including *Tapinella*) occur in the bolete clade (see below), which indicates that the Paxillaceae is polyphyetic. There are no published reports on the relationships of Crepidotaceae, but preliminary analyses of nuc-lsu rDNA sequences suggest that *Crepidotus crocophyllus* is closely related to the euagarics clade or bolete clade (Thorn et al. 2000).

Monophyly of the euagarics clade was strongly supported in the analysis of Hibbett et al. (1997b), but other studies, with different samples of taxa, have found weak support for the group, or have suggested that it is polyphyletic. For example, analyses by Bruns et al. (1998) and Gardes and Bruns (1996) suggested that the Hygrophoraceae is outside the euagarics clade, contrary to the results of Pine et al. (1999) and Moncalvo et al. (2000). Even without the Hygrophoraceae, the euagarics clade would contain the majority of the gilled mushrooms in the Agaricales sensu Singer (1986). The largest groups of gilled mushrooms that are not in the euagarics clade are the Russulaceae (russuloid clade), and Gomphidiaceae and Paxillaceae pro parte (bolete clade, see below).

Aphyllophorales make up a relatively small part of the euagarics clade (Table 1). Several small, morphologically distinctive families are represented, including the Fistulinaceae, Schizophyllaceae, and Dictyonemataceae (Fig. 2, Table 1), as well as the large, polyphyletic families Corticiaceae and Clavariaceae (Table 1). In the analysis of Hibbett et al. (1997b), the euagarics clade contains a single species of the Clavariaceae, *Typhula phacorhiza* (Donk 1964, 1971). The analysis of Pine et al. (1999) suggested that the euagarics clade may contain four additional genera of Clavariaceae (Table 1), including *Clavaria* and *Clavulinopsis*, but bootstrap support was weak. The Corticiaceae is represented by *Athelia bombacina* (Gargas et al. 1995) and possibly *Piloderma fallax* (as *P. croceum*; Bruns et al. 1998; Gardes and Bruns 1996; see below). In addition, the corticioid bark beetle symbiont *Gloeocystidium ipidophilum* appears to be in the euagarics clade (Hsiau 1996).

Heterobasidiomycetes are represented in the euagarics clade by two members of Ceratobasidiales, *Ceratobasidium sp.* (D.S. Hibbett, unpubl.) and *Waitea circinata* (Bruns et al. 1998). *Ceratobasidium* has "ceratobasidioid" basidia (with large, fingerlike sterigmata) and parenthesomes with large perforations (Wells 1994). *Waitea* has typical homobasidia, but it also has parenthesomes with large perforations and has therefore been classified in the Ceratobasidiales (Tu and Kimbrough 1978) or Botryobasidiales (e.g., Müller et al. 1998). In the study of Bruns et al. (1998), *Waitea* and *Piloderma* (Corticiaceae) form a monophyletic group that is weakly supported as the sister group of the rest of the euagarics clade (excluding Hygrophoraceae). Analyses of mt-ssu and nuc-ssu rDNA sequences (D.S. Hibbett, unpubl.) suggest that *Ceratobasidium* is nested in the euagarics clade, although the exact placement is uncertain. Surprisingly, analyses including *Thanatephorus*, which is also classified in the Ceratobasidiales, have repeatedly placed this taxon outside of the euagarics clade (Swann and Taylor 1993; Gargas et al. 1995; Lee and Jung 1997; D.S. Hibbett, unpubl.). Taken at face value, these results suggest that the Ceratobasidiales is polyphyletic. However, Lee and Jung (1997) observed that two isolates identified as *Thanatephorus cucumeris* (= *T. praticola*) did not form a monophyletic group in analyses of nuc-ssu rDNA sequences, which suggests that some cultures or DNA preparations of *Thanatephorus* have been misidentified or mislableled. Clearly, additional studies are needed to resolve the relationships between Ceratobasidiales, corticioid members of the euagarics clade, and other homobasidiomycetes.

Gasteromycetes that have been sampled in the euagarics clade include bird's nest fungi, puffballs, false truffles, and secotioid fungi (Table 1). *Lycoperdon* and *Calvatia* (Lycoperdales) and *Tulostoma* (Tulostomatales pro parte) form a weakly supported monophyletic group that is nested in the Agaricaceae (Fig. 2; Hibbett et al. 1997b). The exact placement of the bird's nest fungi (Nidulariales) is not resolved with confidence. Secotioid fungi and false truffles in the euagarics clade that have been studied using molecular techniques include *Hydnangium*, which is closely related to *Laccaria* (Tricholomataceae),

*Podaxis* and *Montagnea*, which are closely related to Coprinaceae, *Weraroa*, which is thought to be related to Strophariaceae, and *Leratia*, which is of uncertain placement (Heim 1971; Hopple and Vilgalys 1994; Mueller and Pine 1994; Binder et al. 1997). Based on anatomical characters, at least five additional families of euagarics are thought to contain secotioid fungi and false truffles, including Agaricaceae (these secotioid forms may be related to Lycoperdales and Tulostomatales), Amanitaceae, Bolbitiaceae, Cortinariaceae, and Entolomataceae (Dring 1973; Smith 1973; Thiers 1984; Miller and Miller 1988; Castellano et al. 1989).

We estimate that the euagarics clade contains approximately 7400 species of Agaricales and 1025 species of Aphyllophorales and Gasteromycetes. This represents over half of all known homobasidiomycetes, including approximately 87% of all known gilled mushrooms (Hawksworth et al. 1995). The euagarics clade includes saprotrophs, pathogens, and symbionts of both plants and animals (see Sect. III F).

### 3. Bolete Clade

Hibbett et al. (1997b) sampled only three species in the bolete clade, representing the Boletaceae, Paxillaceae (which appears to be polyphyletic, see above), and Sclerodermataceae (Fig. 2, Table 1). However, the bolete clade has been sampled extensively by Bruns and colleagues, and others (see Table 1), who have demonstrated that the bolete clade also includes members of the Gomphidiaceae, Coniophoraceae, Hymenogastrales, Melanogastraceae, and Calostomataceae, as well as many additional exemplars of the groups studied by Hibbett et al. (1997; Table 1).

The bolete clade contains poroid forms, gilled mushrooms, resupinate fungi, false truffles, secotioid fungi, and puffballs, including the unusual stalked, gelationous puffball *Calostoma* (Hughey et al. 2000). Analyses by Bruns et al. (1998) show a basal trichotomy in the bolete clade, including one mostly agaricoid lineage that includes *Paxillus*, *Hygrophoropsis*, and *Serpula*. The bolete clade is weakly supported as the sister group of the euagarics clade in the analysis of Hibbett et al. (1997b), as well as the analysis of Begerow et al. (1997). Taken together, these results suggest that the ancestor of the bolete clade may have been a gilled mushroom.

Monophyly of the bolete clade has been moderately to strongly supported in analyses based on nuclear and mitochondrial rDNAs (Colgan et al. 1997; Hibbett et al. 1997b; Bruns et al. 1998). In many cases, close relationships have been suspected between the poroid boletes (e.g., *Boletus* and *Suillus*) and certain gilled (e.g., *Phylloporus*), resupinate (e.g., *Coniophora*), and gasteroid (e.g., *Rhizopogon* and *Melanogaster*) forms based on anatomy, spore morphology, wood decay chemistry, susceptibility to certain fungal pathogens, and pigments (e.g., Nilsson and Ginns 1979; Singer 1986; Gill and Steglich 1987; Besl et al. 1996). The Boletaceae, Paxillaceae, and Gomphidiaceae were placed in the suborder Boletineae of the Agaricales by Singer (1986).

The majority of the taxa in the bolete clade occur in two main ectomycorrhizal lineages that were termed the boletoid group and the suilloid group by Bruns et al. (1998). In both groups there are secotioid fungi and false truffles along with pileate poroid and gilled forms. Outside the boletoid and suilloid groups, there are several lineages that contain resupinate and pileate brown-rotting saprotrophs as well as ectomycorrhizal poroid forms and puffballs (Fig. 2 in Bruns et al. 1998). We estimate that the bolete clade includes about 840 described species.

### 4. Thelephoroid Clade

In the study of Hibbett et al. (1997b), the thelephoroid clade was represented by *Hydnellum* and *Thelephora*, which were strongly supported as monophyletic. Based on studies by Bruns et al. (1998) and Gardes and Bruns (1996), *Boletopsis*, *Sarcodon*, *Thelephora*, *Tomentella*, and *Pseudotomentella* are also in the thelephoroid clade. These taxa represent the majority of the Thelephoraceae sensu Donk (1964). Characters used by Donk to support the Thelephoraceae include dark, ornamented spores with an angular outline (in addition to the ornamentations), pigmentation of the fruiting body, and presence of thelephoric acid (see Sect. III.E).

The Thelephoraceae has been generally accepted as monophyletic, but its relationship to the Bankeraceae (which includes *Bankera* and *Phellodon*) is controversial. *Bankera* and *Phellodon* strongly resemble *Hydnellum*, but they have subglobose, spinose spores and often have light-colored fruiting bodies. Donk (1964, p. 247) suggested that the similarity of the Bankeraceae to certain Thelephoraceae is "an example of extreme convergence", but other authors have suggested

that the Bankeraceae and Thelephoraceae are closely related (e.g., Jülich 1981; Stalpers 1993). As far as we are aware, *Bankera* and *Phellodon* have yet to be included in molecular studies.

With or without the Bankeraceae, the thelephoroid clade is a morphologically diverse group that includes corticioid fungi (*Tomentella*), clavarioid forms (*Thelephora*), and pileate forms with poroid (*Boletopsis*), toothed (*Hydnellum*, *Sarcodon*), smooth to wrinkled or tuberculate (*Thelephora*), or lamellate hymenophores (*Lenzitopsis*). In addition, Oberwinkler (1975) suggested that the agaricoid fungus *Horakia* (= *Verrucospora*) is related to Thelephoraceae based on spore morphology. Nevertheless, Singer (1986) placed *Horakia* in the Agaricaceae. Except for *Lenzitopsis*, which is apparently lignicolous (and has not been included in molecular studies), all members of this group are thought to be ectomycorrhizal or orchid symbionts (Cullings et al. 1996; Taylor and Bruns 1997; Bruns et al. 1998). Assuming that the Bankeraceae and Thelephoraceae form a monophyletic group, we estimate that the thelephoroid clade includes about 240 described species of homobasidiomycetes.

## 5. Russuloid Clade

In the analysis of Hibbett et al. (1997b), the russuloid clade is a strongly supported group that contains representatives of Russulaceae (Agaricales), and eight families of Aphyllophorales: Auriscalpiaceae, Bondarzewiaceae, Corticiaceae, Echinodontiaceace, Hericiaceae, Lachnocladiaceae, Polyporaceae, and Stereaceae (Fig. 2, Table 1). Analyses of mt-ssu rDNA sequences alone (Hibbett and Donoghue 1995) placed the Stereaceae outside of this group (with low bootstrap support), but otherwise supported monophyly of the russuloid clade (not all of the same taxa were sampled, however). The russuloid clade has been intensively sampled by Boidin et al. (1998), who examined ITS sequences, and S. Miller and E. Larsson (unpubl.), who examined nuc-lsu rDNA sequences. Miller and Larsson have investigated over 80 species of the russuloid clade, including every family that was studied by Hibbett et al. (197b), except Stereaceae sensu stricto. In addition, Miller and Larsson sampled five gasteroid genera in the Astrogastraceae (Hymenogastrales sensu Smith 1973), which their results show to be scattered throughout a clade that is otherwise composed of *Russula* and *Lactarius* species. The russuloid clade has also been examined using mt-lsu rDNA sequences by Bruns et al. (1998) and Gardes and Bruns (1996), who have demonstrated relationships between Russulaceae, Bondarzewiaceae, and Polyporaceae, the latter being represented by *Albatrellus* pro parte, *Heterobasidion*, and *Byssoporia*. Taken together, the studies of Bruns et al. (1988), Gardes and Bruns (1996), and Hibbett et al. (1997b) suggest that *Albatrellus* consists of two separate lineages: one group of species in the polyporoid clade, along with *Polyporoletus*, and another in the russuloid clade, with *Byssoporia* (which is a resupinate, mycorrhizal polypore with broadly elliptic to subglobose spores, similar to those of *Albatrellus*; Ryvarden and Gilbertson 1993).

The russuloid clade has a remarkable diversity of fruiting body morphologies (Table 2). The hymenomycetous forms are resupinate, pileate, or coralloid, with smooth, toothed, lamellate, or poroid hymenophores; the gasteroid forms include false truffles and secotioid fungi. The russuloid clade is also ecologically variable, having ectomycorrhizal, pathogenic, saprotrophic, and possibly lichenized species (see Sect. III.F; Singer 1984). There is no obvious morphological synapomorphy for the russuloid clade. As discussed by Donk (1964), many members of the russuloid clade have spores with amyloid ornamentations and gloeoplerous cystidia or hyphae, but these characters are variable within the group (consequently, they might be useful for resolving phylogenetic relationships within the russuloid clade). Based on anatomical characters, close relationships have been proposed to exist between certain subsets of the russuloid clade, such as Bondarzewiaceae and Russulaceae (Singer 1984), Stereaceae, *Peniophora*, and Echinodontiaceae (Jülich 1981), *Lentinellus* and Auriscalpiaceae (Maas Geesteranus 1963), *Albatrellus* and Hericiaceae (Stalpers 1992), and various gasteroid taxa (e.g., *Arcangeliella*, *Macowanites*) and Russulaceae (Smith 1973; Pegler and Young 1979; Castellano et al. 1989).

Most of the families in the russuloid clade have distinctive characters and are probably monophyletic, or at least restricted to the russuloid clade (e.g., Russulaceae, Bondarzewiaceae, Hericiaceae). However, the Corticiaceae is certainly polyphyletic. We estimate that the russuloid clade contains approximately 1000 described species of homobasidiomycetes, including roughly 20% of Corticiaceae.

**Table 2.** Distribution of fruiting body morphotypes over the major clades of homobasidiomycetes

| Major clades | Fruiting body types | | | | | | |
|---|---|---|---|---|---|---|---|
| | Agaricoid | Poroid | Toothed | Club-shaped or coralloid | Corticioid | Epigeous gasteroid-secotioid | Hypogeous gasteroid |
| Polyporoid clade | ✓ | ✓ | ✓ | ✓[a] | ✓ | ✓[b] | |
| Euagarics clade | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ |
| Bolete clade | ✓ | ✓ | ✓[c] | | ✓ | ✓ | ✓ |
| Thelephoroid clade | ✓[d] | ✓ | ✓ | ✓ | ✓ | | |
| Russuloid clade | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Hymenochaetoid clade | ✓[e] | ✓ | ✓ | ✓[f] | ✓ | | |
| Cantharelloid clade | ✓[g] | | ✓ | ✓ | ✓ | | |
| Gomphoid-phalloid clade | ✓ | | ✓ | ✓ | ✓[h] | ✓ | ✓ |

[a] Environmentally induced coralloid forms of *Neolentinus lepideus*.
[b] Secotioid form of *Lentinus tigrinus*.
[c] *Gyrodontium*.
[d] *Horakia*? *Lenzitopsis*.
[e] *Cyclomyces*.
[f] *Clavariachaete*?
[g] *Cantharellus spp*.
[h] *Ramaricium*.

## 6. Hymenochaetoid Clade

The hymenochaetoid clade includes the Hymenochaetaceae, as well as certain members of the Corticiaceae (*Basidioradulum*, *Hyphodontia*) and Polyporaceae (*Trichaptum*, *Oxyporus*, *Schizopora*; Fig. 2, Table 1). Thus, the hymenochaetoid clade includes poroid, toothed, and corticoid forms (Tables 1, 2). In addition, the clavarioid *Clavariachaete* and the stipitate-sterioid *Stipitochaete* are probably in the hymenochaetoid clade, based on anatomical features (Corner 1991).

In analyses of mt-ssu rDNA sequences alone (Hibbett and Donoghue 1995), the hymenochaetoid clade was moderately supported (bootstrap = 75%), but with the inclusion of nuc-ssu rDNA sequences support dropped below 50% (Hibbett et al. 1997b; Fig. 2). An analysis of nuc-ssu rDNA sequences alone (Ko et al. 1997) supported monophyly of *Trichaptum* and *Inonotus*, but excluded *Coltricia* (no other members of the hymenochaetoid clade were sampled in the study).

The Hymenochaetaceae has been generally regarded as monophyletic based on the following suite of characters: clampless generative hyphae, fruiting bodies darkening in KOH, production of white rot, and presence of setae (in some species). The inclusion in the hymenochaetoid clade of Corticiaceae and Polyporaceae, which lack this combination of characters, conflicts with the generally accepted delimitation of the Hymenochaetaceae. Nevertheless, members of the hymenochaetoid clade appear to be united by the possession of an imperforate parenthosome, which has been observed in *Basidioradulum*, *Coltricia* (W. Müller, pers. comm., contra Moore 1980), *Hyphodontia*, *Inonotus*, *Phellinus*, *Schizopora*, and *Trichaptum* (Traquair and McKeen 1978; Moore 1980, 1985; E. Langer 1994; Hibbett and Donoghue 1995; see Sect. III.B.5).

The hymenochaetoid clade is primarily composed of lignicolous species. However, *Coltricia* is ectomycorrhizal (Danielson 1984) and a number of lignicolous hymenochaetoid fungi have been shown to form orchid mycorrhizae (Umata 1995). It is likely that all the Hymenochaetaceae are in the hymenochaetoid clade, but it is difficult to estimate how many Corticiaceae and Polyporaceae are in this group. We conservatively estimate that the hymenochaetoid clade includes about 630 described species of homobasidiomycetes, which includes Hymenochaetaceae and the genera of the Corticiaceae and Polyporaceae discussed above.

## 7. Cantharelloid Clade

The analysis of Hibbett et al. (1997b) suggested that the cantharelloid clade contains Cantharellaceae (*Cantharellus*), Hydnaceae (*Hydnum*), Clavariaceae (*Multiclavula*), Clavulinaceae (*Clavulina*), and Corticiaceae (*Botryobasidium*).

These results are consistent with the findings of Pine et al. (1999), who performed analyses focused on the cantharelloid and clavarioid homobasidiomycetes. Pine et al's study also included *Craterellus* and additional species of *Cantharellus* and *Clavulina* that were not sampled in the study of Hibbett et al. (1997b).

Analyses of mt-rDNA sequences suggest that the heterobasidiomycete order Tulasnellales is in the cantharelloid clade (Bruns et al. 1998; D.S. Hibbett, unpubl.). Based on mt-ssu rDNA sequences (D.S. Hibbett unpubl.), *Tulasnella* is the sister group of *Botryobasidium*. *Tulasnella* and *Botryobasidium* are both corticioid fungi that have imperforate parenthesomes (G. Langer 1994; Wells 1994). The major difference between the two is in basidial morphology; *Tulasnella* has tulasnelloid basidia with inflated epibasidia Wells 1994), whereas *Botryobasidium* has rounded to subcylindrical homobasidia. In addition, analyses of mt-lsu rDNA sequences (Bruns et al. 1998) suggest that the sister group of *Cantharellus* is a clade composed of *Tulasnella* and an isolate that was tentatively identified as "*Sebacina* sp." (Auriculariales sensu Wells). Ignoring the questionable *Sebacina* isolate, the mt-rDNA studies collectively suggest that a lineage that contains *Tulasnella* and *Botryobasidium* is the sister group of the rest of the cantharelloid clade.

The analysis of Hibbett et al. (1997b) placed *Multiclavula* within the cantharelloid clade. However, the nuc-ssu rDNA analysis of Gargas et al. (1995) suggested that *Multiclavula* is the sister group of all other homobasidiomycetes plus Auriculariales and Ceratobasidiales. As discussed by Pine et al. (1999), the rate of sequence evolution of nuc-ssu rDNA appears to be greater in the cantharelloid clade than in most other homobasidiomycetes. Thus, it is possible that the phylogenetic artifact known as long branch attraction (Felsenstein 1978) is responsible for the placement of *Multiclavula* in the analysis of Gargas et al. (1995).

The cantharelloid clade includes cantharelloid to agaricoid, hydnoid, coralloid, clavarioid, and corticioid fungi. A distinctive feature of the cantharelloid clade is the possession of stichic basidia (see Sect. III.B.4), which have been observed in *Cantharellus*, *Clavulina*, *Craterellus*, *Hydnum*, and *Multiclavula* (Donk 1964; Restivo and Petersen 1976; Hubbard and Petersen 1979; Juel 1898; Pine et al. 1999). Most members of the cantharelloid clade are known or presumed to be mycorrhizal, but *Multiclavula* is a basidiolichen (see Sect. III.F.5). *Botryobasidium* produces fruiting bodies on wood or soil, but it is not known whether it is saprotrophic or mycorrhizal. We estimate that the cantharelloid clade contains about 170 described species of homobasidiomycetes.

### 8. Gomphoid-Phalloid Clade

In the study of Hibbett et al. (1997b; Fig. 2), the gomphoid-phalloid clade included club- and coral-shaped hymenomycetes in Clavariaceae (*Clavariadelphus*) and Gomphaceae (*Gomphus* and *Ramaria*), and morphologically diverse Gasteromycetes in Lycoperdales (*Geastrum*), Nidulariales (*Sphaerobolus*), and Phallales (*Pseudocolus*). The gomphoid-phalloid clade has also been studied by Bruns et al. (1998), Colgan et al. (1997), Pine et al. (1999), Spatafora (unpubl.), and Thorn et al. (2000; see Table 1). These studies suggest that the gomphoid-phalloid clade includes additional Gomphaceae (*Gloeocantharellus*, *Kavinia*, *Lentaria*), as well as epigeous and hypogeous Gasteromycetes in Gautieriales, Hymenogastrales, and Phallales (Table 1).

The internal topology of the gomphoid-phalloid clade varies from study to study. Nevertheless, the results of Hibbett et al. (1997b) and most of the studies cited above, suggest that there are two groups. One group contains the Gomphaceae sensu Donk (1964; *Gomphus*, *Gloeocantharellus*, *Kavinia*, *Lentaria*, *Ramaria*), *Clavariadelphus*, and the Gautieriales. This clade includes club-shaped fungi (*Gomphus*, *Clavariadelphus*), coralloid fungi (*Lentaria*, *Ramaria*), hydnoid resupinate fungi (*Kavinia*), gilled mushrooms (*Gloeocantharellus*), and false truffles (*Gautieria*). The corticioid fungus *Ramaricium* is also in this group, based on spore morphology and staining reactions to iron salts (Eriksson 1954; Eriksson and Ryvarden 1976; Ginns 1979). The Gomphaceae are united by cyanophilic, ornamented (occasionally smooth) spores and green staining reactions to iron salts (Donk 1964; Petersen 1967). *Clavariadelphus* has smooth, non-cyanophilic spores, and *Gautieria* has ridged, non-cyanophilic spores, but both stain green or red in response to iron salts (Donk 1964; Stewart 1974). The other group in the gomphoid-phalloid clade contains the earthstar *Geastrum*, the cannon-ball fungus *Sphaerobolus*, stinkhorns (Clathraceae and Phallaceae), and various hypogeous Phallales and Hymenogastrales (see Table 1). Other than the

lack of ballistospory, and certain pigments (see Sect. III.E), there are no obvious characters that unite these taxa or that suggest a relationship to the Gomphaceae-*Clavariadelphus-Gautieria* lineage. However, Colgan et al. (1997) noted similarities in the ectomycorrhizal mats formed by *Gautieria* and Hysterangiaceae. We estimate that the gomphoid-phalloid clade includes about 350 described species.

## III. Characters

Most recent phylogenetic studies in homobasidiomycetes have used molecular characters, especially those derived from rDNA (Bruns et al. 1991; Hibbett 1992; Hibbett and Donoghue 1998). In this section, we present an overview of selected "morphological" (= nonmolecular) characters that may be phylogenetically informative at high taxonomic levels in homobasidiomycetes, or that provide insight into the evolution of ecological strategies. For additional general discussions of taxonomic characters in homobasidiomycetes, including many characters that are not discussed here (e.g., cystidia, tramal anatomy, fruiting body development, etc.), see Clémençon (1997), Donk (1964), Singer (1986), Jülich (1981), Kühner (1980, 1984), Oberwinkler (1985), Petersen (1971), and Reijnders and Stalpers (1992).

### A. Fruiting Body Macromorphology

The major fruiting body morphotypes of homobasidiomycetes include gilled mushrooms, polypores, toothed fungi, club and coral fungi, corticioid fungi, and epigeous and hypogeous gasteroid fungi (Figs. 3–14). For taxonomic overviews of these morphologically defined groups, see Kühner (1980), Singer (1986), Smith (1973), and Moser (1978) for agarics and boletes; Gilbertson and Ryvarden (1986), Ryvarden (1991), and Pegler (1973) for polypores (excluding boletes and poroid Agaricales); Harrison (1971, 1973) and Gilbertson (1971) for toothed fungi; Petersen (1971, 1973) and Corner (1950, 1966, 1970) for club and coral fungi; Parmasto (1986), Hjortstam et al. (1988, and subsequent volumes), Talbot (1973b), Christiansen (1960), Ginns and Lefebvre (1993), and Jülich and Stalpers (1980) for resupinate fungi; and Coker and Couch (1928), Smith (1973), Dring (1973), Castellano et al. (1989), and Miller and Miller (1988) for gasteroid fungi.

The phylogenetic distribution of fruiting body forms in homobasidiomycetes is summarized in Table 2 (see also Table 1 in Donk 1971). Each of the eight major clades of homobasidiomycetes that we recognize contains at least four of the basic fruiting body types. Notable gaps in the Table include the absence of toothed forms from the euagarics clade, and gasteroid forms from the thelephoroid and cantharelloid clades. Only the russuloid clade contains all the morphotypes.

Phylogenetic uncertainty and limited taxon sampling make it difficult to infer the history of morphological transformations in homobasidiomycetes in detail. Nevertheless, on a coarse scale it appears that the nongilled hymenomycetes make up a paraphyletic assemblage from which gilled mushrooms and Gasteromycetes have been repeatedly derived (Hibbett et al. 1997b). This underscores the need to integrate the classification of the Agaricales, Aphyllophorales, and Gasteromycetes. Based on comparison to heterobasidiomycetes, the ancestor of the homobasidiomycetes may have been a resupinate or sessile pileate form. In the following sections, we discuss general patterns of morphological evolution in homobasidiomycetes, highlighting agarics, corticioid fungi, and gasteroid forms.

#### 1. Agarics

The Agaricales sensu Fries has long been recognized as an artificial taxon, but the number of independent lineages of gilled mushrooms, and their higher-order relationships, have remained controversial (Kühner 1980; Singer 1986). One of the most influential hypotheses regarding the origin of agarics is Corner's (1950) "*Clavaria* theory" (Jülich 1981; Miller and Watling 1987; Pine et al. 1999), which holds that simple club-shaped fruiting bodies are plesiomorphic in the homobasidiomycetes and were transformed in multiple lineages into cantharelloid and agaricoid forms (via hydnoid intermediates in some cases). Our present understanding of homobasidiomycete phylogeny is partially consistent with the *Clavaria* theory; agarics are polyphyletic, but there is no indication that they have all been derived from paraphyletic grades of club and coral fungi.

Hibbett et al. (1997b) suggested that agaricoid forms evolved at least six times. However, their analysis omitted a number of gilled taxa that could


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represent additional independent origins of agaricoid fruiting bodies (e.g., *Phylloporus*, *Gomphidius*, *Faerberia*, *Gloeocantharellus*). As indicated in Table 2, taxa with some kind of lamellate hymenophore probably occur in all of the eight major clades that we recognize. The main concentrations of gilled mushrooms are in the euagarics, bolete, and russuloid clades.

Gilled mushrooms have probably been derived from morphologically diverse precursors. In a few cases, we have a good idea of what the ancestors of agarics may have looked like. For example, there is strong evidence that *Lentinus* sensu stricto was derived from stipitate polypores (Hibbett and Vilgalys 1993; Hibbett et al. 1997b). Developmental modifications involved in this pore-gill transformation were described by Hibbett et al. (1993b). Certain gilled taxa in the bolete clade are also probably derived from poroid forms. Examples include *Phylloporus*, which is nested in the boletoid group sensu Bruns, and *Gomphidius*, which is in the suilloid group (Bruns et al. 1998). Other lamellate taxa of the bolete clade are in lineages outside the boletoid and suilloid groups (e.g., *Paxillus*). As discussed previously (Sect. II.C.3), it is plausible that the plesiomorphic morphology of the bolete clade is lamellate. In the cantharelloid clade, corticioid, clavarioid, and coralloid taxa (*Botryobasidium*, *Tulasnella*, *Multiclavula*, *Clavulina*) form a paraphyletic assemblage from which agaricoid (*Cantharellus*) and other pileate forms (*Craterellus*, *Hydnum*) were derived (Fig. 2; Hibbett et al. 1997b; Pine et al. 1999). Thus, in the cantharelloid clade gills and teeth were probably derived by elaboration from smooth hymenophores. similar pattern may exist in the gomphoid-phalloid clade, where the agaricoid *Gloeocantharellus* is closely related to coralloid, clavarioid, and cantharelloid forms (*Ramaria*, *Clavariadelphus*, *Gomphus*; Pine et al. 1999). In both the cantharelloid and gomphoid-phalloid clade, the precise sequence of morphological transformations is unclear, however. Finally, in the russuloid clade, the agaricoid *Lentinellus* is closely related to coralloid and hydnoid forms (*Clavicorona*, *Auriscalpium*), but again the order of transformations is unresolved. To better understand the pathways of morphological evolution that have led to agarics, a combination of phylogenetic and comparative developmental approaches will be necessary.

## 2. Corticioid Fungi

Corticioid forms occur in each of the eight major clades that we recognize (Table 2). The morphological simplicity of corticioid fungi has led to contradictory views that they are either (1) a plesiomorphic, paraphyletic group that has given rise to multiple lineages of complex forms (e.g., Parmasto 1995), or (2) a polyphyletic group that has been repeatedly derived by reduction (e.g., Corner 1991). Molecular studies suggest that in many cases corticioid fungi have been derived from pileate and erect forms. Apparently derived corticioid forms include *Dentocorticium*, *Phanerochaete*, and *Phlebia* in the polyporoid clade (Fig. 2), *Athelia* in the euagarics clade (Gargas et al. 1995), *Serpula* and *Coniophora* in the bolete clade (Bruns et al. 1998), and possibly *Tomentella* in the thelephoroid clade (Bruns et al. 1998). In addition, the minute, cupulate *Schizophyllum ampla* (= *Auriculariopsis ampla*) appears to be in the euagarics clade (Nakasone 1996), which supports the view that certain cyphelloid fungi (with minute, pendent cups lacking lamellae) are reduced agarics (Donk 1959, 1962, 1964; Reid 1963; Singer 1962, 1986). The contrasting view that the cyphelloid habit is primitive (Agerer 1986) seems unlikely.

Despite these examples, it would be premature to conclude that corticioid forms have never given rise to pileate or erect forms. There are three clades within the homobasidiomycetes in which the polarity of corticioid-erect transformations are particularly ambiguous: (1) The hymenochaetoid

**Figs. 3–14.** Examples of major fruiting body forms in the eight major clades of homobasidiomycetes. **Fig. 3.** *Daedaleopsis confragosa*. Poroid, polyporoid clade. **Fig. 4.** *Hyphodontia sambuci*. Corticioid, hymenochaetoid clade. **Fig. 5.** *Hydnellum* sp. Hydnoid, thelephoroid clade. **Fig. 6.** *Geastrum saccatum*. Epigeous gasteroid (puffball), gomphoid-phalloid clade. **Fig. 7.** *Rhizopogon* sp. Hypogeous gasteroid (false truffle), bolete clade. **Fig. 8.** *Heimiomyces* sp. Agaricoid, euagarics clade. **Fig. 9.** *Clavulinopsis fusiformis*. Coralloid, euagarics clade. **Fig. 10.** *Boletus* sp. Poroid, bolete clade. **Fig. 11.** *Auriscalpium vulgare*. Hydnoid, russuloid clade. **Fig. 12.** *Clavariadelphus truncatus*. Clavarioid, gomphoid-phalloid clade. **Fig. 13.** *Phallus* cf. *tenuis*. Epigeous gasteroid (stinkhorn), gomphoid-phalloid clade. **Fig. 14.** *Cantharellus cibarius*. Agaricoid, cantharelloid clade. Photo credits: **Figs. 4, 14** R.G. Thorn; **Figs. 7, 9** R.G. Thorn and G.L. Barron; others: D. Hibbett

clade contains a mix of corticioid and erect forms, but the topology of the clade is too poorly resolved (and the sampling of the corticioid taxa is too limited) to infer the pattern of morphological transformations (Fig. 2; Hibbett et al. 1997b). (2) In the russuloid clade, the work of S.L. Miller and E. Larsson (unpubl.) demonstrates that there is a complex pattern of relationships between corticioid and pileate-erect forms, which may include derivation of pileate-erect forms from corticioid forms. (3) In the cantharelloid clade, the basal split is between a corticioid lineage (containing *Botryobasidium* and *Tulasnella*) and a pileate-erect lineage, but the ancestral morphology of the cantharelloid clade is unresolved. Finally, because of uncertainty about higher-level relationships, and limited sampling of corticioid taxa, it is not clear whether the plesiomorphic morphology of the homobasidiomycetes as a whole is corticioid or pileate-erect.

### 3. Gasteroid Forms

Gasteromycetes produce spores internally and lack forcible spore discharge (see Sect. III.B.2). Some Gasteromycetes, including most false truffles and secotioid fungi, have strong anatomical similarities to certain taxa of Hymenomycetes (Smith 1973; Thiers 1984; Castellano et al. 1989), but many others, such as stinkhorns and other "true" Gasteromycetes, have no obvious morphological resemblance to any group of Hymenomycetes. Gasteromycetes have been interpreted as (1) a paraphyletic assemblage from which the Agaricales were derived (Singer 1986), or (2) a polyphyletic group that was derived from Hymenomycetes (e.g., Savile 1955; Schaffer 1975; Thiers 1984; Oberwinkler 1985; Miller and Watling 1987). Molecular studies indicate that there have been multiple origins of Gasteromycetes in the euagarics, bolete, russuloid, and gomphoid-phalloid clades (Fig. 2, Table 1). The genetic and developmental bases of transformations from Hymenomycetes and Gasteromycetes, and the ecological forces that may have selected for gasteroid fruiting bodies, have been discussed by Baura et al. (1992), Bruns et al. (1989), Hibbett et al. (1994b, 1997b), Miller et al. (1994), and Thiers (1984).

Diverse fruiting body morphologies and spore-dispersal mechanisms have evolved in Gasteromycetes (Ingold 1971). Some gasteroid forms have evolved multiple times, including puffballs, false truffles, and secotioid fungi. In puffballs, spores are dispersed into air through cracks or pores in the peridium. Many puffballs have a "capillitium" of sterile hyphae in the gleba, which is thought to aid dispersal by disrupting the spores or by supporting the structure of the fruiting body (Ingold 1971; Miller and Miller 1988; Pegler 1996). Most capillitial elements resemble skeletal or generative hyphae (see Sect. III.B.3), but others are highly modified, especially the elaters of *Battarrea*, which are sparingly branched cells that have spiral wall thickenings. Puffballs have evolved at least three times, in the euagarics clade (Lycoperdaceae, Tulostomataceae), bolete clade (Sclerodermataceae, Calostomataceae), and gomphoid-phalloid clade (Geastraceae, Fig. 2, Table 1). However, there are many puffballs that have yet to be included in molecular studies, such as *Astraeus*, which is an earthstar that has been classified in the Sclerodermatales (Dring 1973; see Sect. III.F.4).

In false truffles, spores are dispersed by rodents that consume the fruiting bodies, or are released directly into the soil as the fruiting body breaks down (Johnson 1996; Miller et al. 1994; Trappe and Maser 1977). The latter mode may facilitate the establishment of mycorrhizae (Miller et al. 1994). As far as we know, all false truffles are ectomycorrhizal (Trappe and Maser 1977). Thiers (1984) and others have suggested that false truffles were derived from agarics and boletes via secotioid intermediates. In addition, Oberwinkler and Horak (1979) suggested (on the basis of spore morphology) that the false truffle *Stephanospora* is closely related to the corticioid fungus *Lindtneria*. If so, this might represent a unique case of a corticioid-gasteroid transformation. Based on a combination of molecular and morphological evidence, false truffles and secotioid fungi have evolved repeatedly in the euagarics, bolete, russuloid, and gomphoid-phalloid clades (Table 1).

Puffballs, false truffles, and secotioid fungi are clearly polyphyletic, but certain other gasteroid forms have evolved only once. Uniquely derived gasteroid forms in the gomphoid-phalloid clade include the stinkhorns (epigeous Phallales), which disperse spores via flies and other insects that are attracted by the foul-smelling gleba and showy receptacle, and cannon ball fungi (*Sphaerobolus*), which forcibly eject a glebal mass by the sudden evagination of the endoperidium. The pathways of morphological evolution leading to these unusual forms are not well understood, but it seems likely

that they were derived from Hymenomycetes via puffball, false truffle, or secotioid intermediates. As mentioned previously, the work of Colgan et al. (1997) and J. Spatafora (unpubl.) suggests that stinkhorns were derived from false truffles (Hysterangiaceae), which suggests that in the Phallales olfactory attractants evolved before showy epigeous receptacles. *Sphaerobolus* and the earthstar *Geastrum* appear to be closely related to the Phallales, but the precise relationships between these taxa are not known.

Another uniquely derived gasteroid form is found in the bird's nest fungi (Nidulariaceae, euagarics clade), which disperse packets of spores (peridioles) by a splash-cup mechanism (e.g., *Cyathus*, *Crucibulum*; Brodie 1975). The Nidulariaceae also includes forms that lack splash cups (Brodie 1975). For example, the fruiting bodies of *Nidularia* resemble minute puffballs, except that the spores are contained in peridioles, which are passively released as the exoperidium breaks down. Brodie (1975) suggested that forms that lack splash cups are primitive in the Nidulariaceae, but this hypothesis has yet to be evaluated through phylogenetic studies.

## B. Anatomy, Cytology, and Ultrastructure

### 1. Basidia

The defining character of the homobasidiomycetes is the homobasidium. Typical homobasidia are nonseptate, clavate to cylindric, with four short, apically positioned sterigmata. However, there is considerable departure from this archetype in the homobasidiomycetes. For example, the stalked puffball *Tulostoma* has laterally attached basidiospores; basidia of *Pulcherricium* develop dendrohyphidial branches; *Tulasnella* has inflated epibasidia that develop adventitious septa at their bases; *Ceratobasidium* has subglobose basidia; and *Cantharellus*, *Sistotrema*, and others have up to eight sterigmata per basidium. Other variable characters of homobasidia include presence and form of a basal clamp, mode of attachment (i.e., whether terminal or *pleural*, as in *Xenasma*, Corticiaceae), and presence or absence of nested, or *repeating* basidia (as in *Repetobasidium*, Corticiaceae). For reviews of basidium morphology, see Oberwinkler (1982), Jülich (1981), and Talbot (1973a). Basidium morphology has been emphasized in the taxonomy of corticioid fungi and other Aphyllophorales (e.g., Hjortstam et al. 1988), but it has had relatively little impact on the taxonomy of Agaricales (Jülich 1981; Oberwinkler 1982). Basidial shape is a subtle, essentially quantitative character, and it is therefore difficult to code for phylogenetic analysis. As discussed by Oberwinkler (1982), there has been convergence in basidial form in unrelated taxa, such as *Sistotrema* and *Multiclavula* (which have urniform basidia), *Phlebia* and *Panellus* (meruliaceous basidia), and *Cantharellus* and *Hygrophorus* (elongate, slender basidia). In addition, there are several cases identified through molecular studies of closely related taxa that have strongly divergent basidial morphology. A prime example concerns *Tulasnella*; according to mt-ssu rDNA sequences (D.S. Hibbett, unpubl.), *Tulasnella* is closely related to *Botryobasidium*, which has nonseptate, urniform basidia, with up to eight sterigmata. These observations cast doubt on the utility of basidial morphology for resolving major clades of homobasidiomycetes, although it may be informative at lower taxonomic levels (e.g., Larsen and Gilbertson 1977).

### 2. Basidiospores

Basidiospores and an important source of characters for homobasidiomycete systematics. Variable aspects of basidiospore morphology include shape, size, color, staining reactions, ornamentation, wall structure, apical pores, hilar appendix morphology, presence and form of a suprahilar disk, and germination mode. For surveys of basidiospore morphology in homobasidiomycetes, see Singer (1986), Kühner (1972, 1980, 1984), Jülich (1981), Donk (1964), Castellano et al. (1989), Coker and Couch (1928), and Pegler and Young (1971). This section focuses on broad patterns of basidiospore evolution in homobasidiomycetes. The first part of this discussion considers only the basidiospores of Hymenomycetes.

Based on comparison to basidiospores of Auriculariales, Dacrymycetales, and Tremellales, it is likely that smooth, hyaline, inamyloid basidiospores are plesiomorphic in the homobasidiomycete. Spores with this combination of characters (with varying shapes) are typical of the polyporoid, cantharelloid, and hymenochaetoid clades, although other, presumably derived, morphologies also occur in these groups. For example, in the polyporoid clade there is strong evidence

that *Ganoderma*, which has brown, ornamented spores with multilayered walls, is nested in a lineage that also includes *Polyporus*, *Lentinus*, and *Fomes* (and others), which have smooth, hyaline spores (Hibbett and Donoghue 1995; Hibbett et al. 1997b). Similarly, the strongly warted spores of *Botryobasidium isabellinum* are probably a derived feature in the cantharelloid clade.

The euagarics clade has a wide range of spore morphologies, which were discussed at length by Pegler and Young (1971), Singer (1986), and Kühner (1980, 1984). A few examples of putatively monophyletic groups in the euagarics clade that are distinguished by spore morphology are the Cortinariaceae (brown, generally warted spores, without an apical pore), Entolomataceae (angular, pink, cyanophilic spores), and Coprinaceae (dark, thick-walled spores with an apical pore). It is beyond the scope of this chapter to comment in detail on spore morphology and phylogenetic relationships within the euagarics clade. Nevertheless, we note that there is an apparent, if imperfect, correlation between the possession of an "open pore" type hilum, apical pore, and dark spore print in the Agaricaceae, Bolbitiaceae, Coprinaceae, Crepidotaceae, and Strophariaceae (Pegler and Young 1971), suggesting that these taxa may be closely related. In addition, Kühner (1984) emphasized double wall layers as an important character supporting his concept of the Pluteales, which encompasses the Entolomataceae and Pluteaceae sensu Singer [as well as *Macrocystidia*, which Singer (1986) placed in the Tricholomataceae]. Whether these basidiospore characters are actually synapomorphies of major lineages within the euagarics clade will only be determined when the phylogeny of the euagarics clade is better understood.

Basidiospores in the bolete clade are quite variable, but typically they are smooth, some shade of brown or yellow-brown, and fusoid (elongate with rounded, tapering ends), but elliptic to subglobose spores also occur. Corner (1972) suggested that there is a functional correlation between elongate basidiospores and poroid hymenophores in boletes. Based on measurements of spore shape and positioning, Corner concluded that fusoid spores use space more efficiently in narrow poroid hymenophores than spores that are more globose. By this reasoning, he suggested that elongate spores are derived in the boletes. Pegler (1983, p. 10) noted that elongate, cylindric spores are also common in polypores, and suggested that: "Spore elongation may therefore be seen as a phyletic trend occurring in both the Aphyllophorales and the Boletales". Based on the work of Bruns et al. (1998), it seems plausible that the plesiomorphic condition in the bolete clade is to have smooth, elliptic to ovoid spores, which would be consistent with Corner's hypothesis. Elliptic-ovoid spores are found in *Serpula*, *Paxillus*, *Hygrophoropsis*, *Coniophora*, *Gyroporus*, and *Gyrodon*, which form two lineages outside the main "boletoid" and "suilloid" groups, in which fusoid spores prevail (Pegler and Young 1971; Bruns et al. 1998). Derived ornamented spores in the boletoid group include those of *Boletellus*, *Austroboletus*, and *Strobilomyces*. Corner (1972) suggested that the subglobose spores of *Strobilomyces* are primitive in the boletes, but the analysis of Bruns et al. (1998) suggests that *Strobilomyces* is nested in the boletoid group (indicating that its subglobose spores are derived in the bolete clade).

Basidiospores of the thelephoroid, russuloid, and gomphoid-phalloid clades were mentioned previously (see Sects. II. C. 4, 5, 8). Each clade is characterized by derived spore morphologies, including (1) angular or globose-elliptic, pigmented, ornamented spores in the thelephoroid clade, (2) hyaline spores with amyloid ornamentations in the russuloid clade, and (3) warted, cyanophilic spores in the gomphoid-phalloid clade (Donk 1964). Spore morphologies are not uniform in these clades, however. For example, in the russuloid clade, there are taxa with smooth, amyloid or inamyloid spores (e.g., *Albatrellus*, *Peniophora*, *Stereum*), and ornamented inamyloid spores (*Heterobasidion*; Redhead and Norvell 1993, but see Stalpers 1979). In the gomphoid-phalloid clade, *Clavariadelphus* has smooth, non-cyanophilic spores (which may represent the plesiomorphic state in this clade).

So far, we have mentioned only the ballistosporic (forcibly discharged) basidiospores of Hymenomycetes. Structural features associated with ballistospory include short, curved sterigmata, bilateral spore symmetry, heterotropy (excentric positioning of spores on the sterigmata), and formation of a droplet of liquid at the time of discharge (Buller 1922; Ingold 1971; Webster and Chien 1990). Ballistospory has been repeatedly lost with the evolution of gasteroid fruiting bodies (Thiers 1984). Gasteroid basidiospores are statismosporic (not forcibly discharged) and, with the exception of some Hymenogastrales, radially symmetric and orthotropic (positioned directly over

the apex of the sterigmata). Aside from these features, gasteroid basidiospores are morphologically variable. The spores of many false truffles and secotioid fungi resemble the spores of their putative Hymenomycete ancestors (e.g., fusoid spores in *Rhizopogon* and *Suillus*, angular, pink spores in *Richoniella* and *Entoloma*, and elliptic, ornamented spores in *Thaxterogaster* and *Cortinarius*; Castellano et al. 1989). In addition, there are certain recurring spore morphologies in Gasteromycetes that may be correlated with the mode of dispersal. For example, dark, globose to broadly elliptic, ornamented spores have evolved repeatedly in puffballs (e.g., *Lycoperdon*, *Scleroderma*, *Geastrum*), which have aerial spore dispersal, and smooth, elliptic, thick-walled spores have evolved independently in Nidulariaceae and Sphaerobolaceae, which have herbivore dispersal (Brodie 1975). For reviews of gasteroid basidiospore morphology, see Castellano et al. (1989), Coker and Couch (1928), Miller and Miller (1988), and Pegler et al. (1993, 1995). Besides terrestrial Gasteromycetes, the only statismosporic homobasidiomycetes are certain marine fungi (see below) and corticioid bark beetle symbionts (see Sect. III. F. 6).

Ballistospory has been lost in the lignicolous marine homobasidiomycetes *Nia vibrissa*, which is gasteroid, and *Digitatispora marina*, which is corticioid (Douget 1962, 1967; Kohlmeyer and Kohlmeyer 1979). In addition to being statismosporic, the basidiospores of *Nia* and *Digitatispora* have elongate processes (appendages) that probably function in anchoring the spores to substrates (Ingold 1971). Similarly appendaged conidia are found in aero-aquatic basidiomycetous hyphomycetes, such as *Ingoldiella* (see Sect. III. C), as well as the spores of many aquatic ascomycetes (Ingold 1971; Shaw 1972; Kohlmeyer and Kohlmeyer 1979). (see Seifert and Gams, Chap. 14, Vol. VII Part A). Ballistospory has also been lost in the gasteroid marine homobasidiomycete *Mycaureola dilseae*, which is a parasite of red algae that produces sigmoid, sessile basidiospores (Porter and Farnham 1986). The only other homobasidiomycetes known to produce basidiomata underwater are *Gloiocephala aquatica*, which is a minute agaric that grows in freshwater on *Scirpus* culms (Desjardin et al. 1995), and *Halocyphina villosa*, which is a cyphelloid fungus that grows on mangrove roots and other woody marine substrates (Ginns and Malloch 1977; Kohlmeyer and Kohlmeyer 1979). The clavate-cylindric basidia and smooth, asymmetric spores of *G. aquatica* and *H. villosa* are anatomically indistinguishable from those of ballistosporic homobasidiomycetes, which may indicate that they were recently derived from terrestrial ancestors (Ginns and Malloch 1977; Desjardin et al. 1995).

Basidiospores of homobasidiomycetes sensu stricto germinate to form hyphae directly. In contrast, basidiospores of many heterobasidiomycetes produce secondary ballistospores or conidia prior to the production of mycelium (Ingold 1985, 1992). "Germination by repetition" occurs in every order of heterobasidiomycetes, including Tulasnellales and Ceratobasidiales, but not all species of heterobasidiomycetes demonstrate this capability (Donk 1964; Tu and Kimbrough 1978; Jülich 1981; Oberwinkler 1982; Ingold 1985, 1992; Wells 1994). Diverse germination modes and secondary spore types occur in heterobasidiomycetes, and these may or may not be homologous. Nevertheless, it is plausible that germination by repetition is plesiomorphic for the hymenomycete lineage (it is also present in Uredinomycetes and Ustilaginomycetes *sensu* Swann and Taylor 1993) (see Swann and Frieders, Chap. 2, and Bauer et al., Chap. 3, this Vol.). If so, then it may have been lost in the lineage leading to the homobasidiomycetes (as well as certain heterobasidiomycetes), and secondarily derived in the Tulasnellales and Ceratobasidiales.

### 3. Hyphal Systems of Fruiting Bodies

Techniques for studying the micromorphology of hyphae that make up fruiting bodies were developed by Corner [1932, and later; see Pegler (1996) for a historical review of hyphal analysis], who described three main types of hyphae: skeletal hyphae (unbranched, thick-walled), binding hyphae (thick-walled, branched, and twining), and generative hyphae (thin-walled, branched, septate). Based on the presence or absence of these hyphal forms, context tissues were called monomitic (only generative hyphae), dimitic (generative hyphae and skeletal or binding hyphae), or trimitic (all three types present). Corner's early work centered on the polypores *Phellinus* (hymenochaetoid clade) and *Microporus* (unplaced, possibly polyporoid clade). As other homobasidiomycetes were examined, numerous intergrading hyphal types were described, which resulted in a proliferation of terms such as skeleto-ligative hyphae or sclerified generative hyphae. In 1966, Corner described sar-

codimitic and sarcotrimitic hyphae, in which there are inflated and thick-walled cells, combined with intertwining generative hyphae. Pegler (1996) recognized seven principle forms of hyphal systems in homobasidiomycetes (monomitic, sarcomitic, intermediate dimitic, dimitic with mostly unbranched skeletal hyphae, dimitic with skeletoligative elements, sarcotrimitic, and trimitic), which he divided into 32 subcategories. For descriptions of the morphology and taxonomic distribution of hyphal forms, see Donk (1964), Gilbertson and Ryvarden (1986), Largent et al. (1977), Lentz (1971), Pegler (1996), and Singer (1986). The following discussion highlights patterns of evolution in hyphal systems and their potential phylogenetic utility.

Hyphal anatomy has been overemphasized in some classifications, which has led to taxonomic errors. Polyphyletic taxa that are strongly based on hyphal characters include *Lentinus* sensu Pegler (1983; dimitic), *Trogia* sensu Corner (1966; sarcodimitic), and Xerulaceae sensu Redhead (1986; sarcodimitic). Nevertheless, molecular studies suggest that variation in hyphal morphology can be phylogenetically informative at some levels see Hibbett and Donoghue 1995 for examples in polypores. For example, analyses of rDNA sequences support the division of *Lentinus* sensu Pegler into three groups that can be differentiated by their hyphal anatomy: *Lentinus* sensu stricto (dimitic with binding hyphae), *Panus* (dimitic with strongly developed skeletals), and *Neolentinus* (dimitic with weakly developed skeletals; Corner 1981; Hibbett and Vilgalys 1993; Pegler 1975, 1983; Redhead and Ginns 1985). Similarly, *Hydropus* and *Baeospora* (Xerulaceae sensu Redhead, with sarcodimitic stipe trama) appear to be closely related, based on molecular and morphological evidence (Bas et al. 1990; Moncalvo et al. 2000). Taken together, molecular and morphological studies indicate that hyphal characters are taxonomically informative, but that their use is limited by homoplasy and the difficulty of delimiting character states.

Based on comparison to outgroups (Auriculariales, Dacrymycetales, Tremellales), the plesiomorphic condition of the homobasidiomycetes is probably monomitic. Monomitic context construction occurs in each of the eight major clades that we recognize, and it is apparently the sole form of construction in the bolete, thelephoroid, cantharelloid, and gomphoid-phalloid clades. The majority of species with dimitic and trimitic construction are in the polyporoid, hymenochaetoid, and russuloid clades. Each of these clades includes dimitic and trimitic perennial forms, such as *Fomes*, *Fomitopsis*, and *Ganoderma* (trimitic) in the polyporoid clade, *Phellinus* (dimitic) in the hymenochaetoid clade, and *Echinodontium* and *Heterobasidion* (dimitic; Gilbertson and Ryvarden 1986) in the russuloid clade. The repeated evolution of perennial fruiting bodies in these groups appears to be correlated with decay of large wood substrates. The euagarics clade is mostly monomitic, but some species of *Pleurotus* (e.g., *P. tuberregium*) are dimitic, as is the clavarioid *Pterula* (Corner 1970; Pine et al. 1999). In addition, certain desert-adapted Gasteromycetes in the euagarics clade have tough, woody stipes, and these may also be interpreted as dimitic (e.g., Tulostomataceae, *Podaxis*, *Montagnea*; Miller and Miller 1988). Sarcodimitic construction occurs in diverse agarics (Xerulaceae sensu Redhead, euagarics clade), as well as in *Meripilus* (polyporoid clade; Corner 1984), and the stereoid and cantharelloid species of *Trogia* sensu Corner (1966), which are of uncertain taxonomic placement. Overall, dimitic, trimitic, and sarcodimitic construction appears to have evolved repeatedly as a mechanism for toughening fruiting bodies in diverse ecological circumstances.

*Conducting elements* are hyphae with refractive or oily-looking contents (often with characteristic staining reactions) that are presumed to transport or sequester substances of unknown function (Largent et al. 1977; Singer 1986; Pegler 1996). Some are of rather limited taxonomic distribution, such as laticiferous hyphae (e.g., *Lactarius*, *Bondarzewia*; Redhead and Norvell 1993), chryso-vessels (Strophariaceae), and oleiferous hyphae (*Russula*, *Amanita*; Largent et al. 1977; Singer 1986). In contrast, gloeoplerous hyphae (including gloeocystidia; Larsen and Burdsall 1976) are broadly distributed. Gloeoplerous hyphae are common in the russuloid clade (e.g., *Auriscalpium*, *Bondarzewia*, *Clavicorona*, *Gloeocystidiellum*, *Lentinellus*, *Russula*), but they are also reported in *Fistulina*, *Laetiporus*, *Albatrellus*, and others. The taxonomic distribution of conducting elements suggests that they are phylogenetically informative, although they also display homoplasy. Other specialized hyphae of limited taxonomic distribution include sphaerocysts of Russulales, dichohyphae and asterosetae of

Lachnocladiaceae (Reid 1965), and "pressure cells" of *Amanita* (Bas 1969).

## 4. Nuclear Behaviour in Meiosis and Basidiosporogenesis

Taxonomic characters for homobasidiomycetes can be drawn from the orientation of first-division meiotic spindles and patterns of postmeiotic mitosis and nuclear migration during basidiosporogenesis. Beginning with the work of Juel (1898, 1916) and Maire (1902), two main patterns of meiosis have been recognized, with two corresponding types of basidia: chiastic basidia and stichic basidia. In chiastic basidia, the first meiotic division takes place in the apex of the basidium, with the spindle transverse to the long axis of the basdium, whereas in stichic basidia the first division takes place in the middle of the basidium, with the spindle parallel to the long axis of the basidium. Intermediate forms are known, which may complicate efforts to code this character for phylogenetic analysis. For example, Boidin (Fig. 14 in 1958) observed both transverse and longitudinal spindles in *Sistotrema*, which he nevertheless interpreted as stichic. Boidin also described "hemichiastic" basidia that have variable orientation of the spindles, but Donk (1964, p. 221) concluded that hemichiastic basidia "may be subordinated as a subtype to the chiastic".

Among the heterobasidiomycetes, *Auricularia*, *Dacrymyces*, and *Dacryopinax* are reportedly stichic, and *Exidia*, *Sebacina*, and *Phlogiotis* are chiastic (Juel 1898; Maire 1902; Bodman 1938; Furtado 1968). Most of the homobasidiomycetes that have been examined have chiastic basidia, including all species of the euagarics, bolete, thelephoroid, russuloid, gomphoid-phalloid, and polyporoid clades (Juel 1898, 1916; Maire 1902; Ehrlich and McDonough 1949; Boidin 1958; Penancier 1961; Donk 1964; Restivo and Petersen 1976; Hubbard and Petersen 1979; Hibbett et al. 1994a), except for *Sistotrema*, which is stichic and is supported as a member of the polyporoid clade by mt-ssu rDNA sequences (D.S. Hibbett, unpubl.). Other stichic homobasidiomycetes include *Cantharellus*, *Clavulina*, *Craterellus*, *Hydnum*, and *Multiclavula*, which are all in the cantharelloid clade (Pine et al. 1999), and *Clavulicium* (Clavulinaceae; Parmasto 1986), which is a corticioid fungus that has yet to be included in phylogenetic studies. Possession of stichic basidia would appear to be a synapomorphy of the cantharelloid clade (Pine et al. 1999) except that *Tulasnella* has chiastic basidia (Figs. 12–15 in Rogers 1932). Based on the taxonomic distribution of stichic and chiastic basidia, and the tree in Fig. 2, we tentatively conclude that chiastic basidia are plesiomorphic in the homobasidiomycetes, including the cantharelloid clade, and were transformed into stichic basidia on the branches leading to *Multiclavula* and *Cantharellus*, and *Sistotrema*.

Between meiosis and basidiospore discharge, the haploid nuclei usually undergo a mitotic division, which may be completed in the basidia, sterigmata, or basidiospores. If postmeiotic mitosis is completed outside of the basidium, there is often a back-migration of one daughter nucleus into the basidium. Duncan and Galbraith (1972) described four kinds of postmeiotic nuclear behavior, which they termed patterns A, B, C, and D. Mueller et al. (1993) designated two additional patterns, E and F, based on observations by Arita (1979) and Tommerup et al. (1991). Briefly, the postmeiotic nuclear behavior patterns are defined as follows: Pattern A: postmeiotic mitosis occurs in the basidium, one nucleus enters each basidiospore; Pattern B: postmeiotic mitosis occurs in sterigmata, one daughter nucleus backmigrates to the basidium; Pattern C: postmeiotic mitosis occurs in basidiospores, one nucleus backmigrates to the basidium; Pattern D: postmeiotic mitosis occurs in basidiospores, backmigration does not occur; Pattern E: postmeiotic mitosis does not occur; Pattern F: postmeiotic mitosis occurs in the basidium, multiple nuclei enter each basidiospore. Typically, patterns A, B, C, and E result in uninucleate basidiospores, whereas patterns D and F result in binucleate basidiospores. The number of nuclei per spore is also affected by the number of spores per basidium (e.g., Petersen 1995a).

There are few reports of postmeiotic nuclear behavior in heterobasidiomycetes, Urediniomycetes, or Ustilaginomycetes. In *Exidia nucleata* (Auriculariales) postmeiotic mitosis is completed in the elongate sterigmata, with backmigration of one daughter nucleus into the basidium (Furtado 1968). In *Auricularia fuscosuccinea* postmeiotic mitosis is completed in the basidiospores, but it is not known whether backmigration occurs (McLaughlin 1981). In *Dacryopinax* (Dacrymycetales) there appears to be no postmeiotic mitosis, and spores are uninucleate

**Table 3.** Patterns of postmeiotic nuclear behavior in homobasidiomycetes. The number of genera reported to have each pattern is indicated

| Major clades | Nuclear behavior patterns[a] | | | | | |
|---|---|---|---|---|---|---|
| | A | B | C | D | E | F |
| Polyporoid clade | | | 4 | | | |
| Euagarics clade | 40+ | 1 | 4 | 23+ | 3 | 3 |
| Bolete clade | | | 4 | | | |
| Thelephoroid clade | | 3?[b] | 3?[b] | | | |
| Russuloid clade | | | 3 (+1?[c]) | 1 (+1?[c]) | | |
| Hymenochaetoid clade | | | | | | |
| Cantharelloid clade | 2 | | | | 3[d] | 1[d] |
| Gomphoid-phalloid clade | 1?[e] | 1?[e] | | | | |

[a] A: postmeiotic mitosis occurs in the basidium; one nucleus enters each basidiospore. B: postmeiotic mitosis occurs in sterigmata; one daughter nucleus backmigrates to the basidium. C: postmeiotic mitosis occurs in basidiospores; one nucleus backmigrates to the basidium. D: postmeiotic mitosis occurs in basidiospores; backmigration does not occur. E: postmeiotic mitosis does not occur. F: postmeiotic mitosis occurs in the basidium; multiple nuclei enter each basidiospore.

[b] *Boletopsis*, *Hydnellum*, and *Sarcodon* are probably B or C, but not D, E, or F (Penancier 1961).

[c] *Clavicorona* could be C or D (Berbee and Wells 1989; Wilson et al. 1967).

[d] Including *Tulasnella* (Rogers 1932).

[e] *Ramaria* (Penancier 1961).

(Bodman 1938). In *Ustilago maydis* (Ustilaginomycetes sensu Swann and Taylor 1993) and *Eocronartium musicola* (Urediniomycetes sensu Swann and Taylor 1993), postmeiotic mitosis is completed in the basidiospores, followed by backmigration of one daughter nucleus into the basidium or sterigmata (O'Donnell and McLaughlin 1984; Boehm and McLaughlin 1989). Taken together, these observations suggest that postmeiotic mitosis with backmigration of daughter nuclei (pattern C, or possibly B) is plesiomorphic in the homobasidiomycetes, and possibly the entire hymenomycete lineage (if so, it may have been lost in the Dacrymycetales).

Mueller and Ammirati (1993) reviewed the literature on postmeiotic nuclear behavior in Agaricales. Additional information on Aphyllophorales, Gasteromycetes, and heterobasidiomycetes was presented by Berbee and Wells (1989), Brodie (1975), Ehrlich and McDonough (1949), Hibbett et al. (1994a), Hubbard and Petersen (1979), Penancier (1961), Restivo and Petersen (1976), Rogers (1932), and Wilson et al. (1967). A summary of the distribution of postmeiotic nuclear behavior patterns among the eight major clades of homobasidiomycetes that we recognize is shown in Table 3. Pattern C occurs in four or five of the eight clades, and it is the only pattern reported in the polyporoid and bolete clades (Table 3). As noted by Mueller and Ammirati (1993), there is considerable homoplasy in the evolution of postmeiotic nuclear behavior (Table 3). For example, there appears to have been a parallel loss of postmeiotic mitosis in the euagarics clade (e.g., *Pholiota*; Arita 1979) and cantharelloid clade (e.g., *Multiclavula*; Hubbard and Petersen 1979). Nevertheless, there is also some congruence between groupings based on nuclear behavior and those based on molecular characters, which suggests that this character could be phylogenetically informative. At present, it is difficult to assess broad patterns of evolution in postmeiotic nuclear behavior patterns, owing to inadequate sampling outside of the euagarics clade. In particular, there are no reports of which we are aware from the hymenochaetoid clade, and only a single genus (*Ramaria*) has been examined in the gomphoid-phalloid clade.

## 5. Parenthesome Ultrastructure

Parenthesomes are membrane-bound organelles that flank dolipore septa. Among the heterobasidiomycetes, Auriculariales and Dacrymycetales have imperforate (continuous) parenthesomes, Ceratobasidiales have parenthesomes with a few

**Table 4.** Parenthesome structure in representative homobasidiomycetes

| Perforate | Imperforate |
|---|---|
| 1. Polyporoid clade | |
| *Fomes* (Moore 1980) | *Phanerochaete* (Keller 1997) |
| *Ganoderma* (Mims and Seabury 1989) | |
| *Phaeolus* (Moore 1980) | |
| *Polyporus* (Moore 1980) | |
| *Sparassis* (Patrignani and Pellgrini 1986) | |
| 2. Euagarics clade | |
| *Agaricus* (Thielke 1972) | |
| *Amanita* (Flegler et al. 1976) | |
| *Ceratobasidium* (Tu and Kimbrough 1978) | |
| *Coprinus* (Oberwinkler 1985) | |
| *Dictyonema* (Slocum 1980) | |
| *Fistulina* (Patrignani and Pellgrini 1986) | |
| *Lentinula* (Tsuneda 1983) | |
| *Lycoperdon* (Flegler et al. 1976) | |
| *Pleurotus* (Moore and Patton 1975) | |
| *Schizophyllum* (Moore and Patton 1975) | |
| *Stropharia* (Thielke 1972) | |
| *Waitea* (Tu and Kimbrough 1978) | |
| 3. Bolete clade | |
| *Boletus* (Patrignani and Pellgrini 1986) | |
| *Coniophora* (Langvad 1971) | |
| *Pulveroboletus* (Keller 1997) | |
| *Serpula* (Keller 1997) | |
| 4. Thelephoroid clade | |
| *Bankera* (Keller 1997) | |
| *Hydnellum* (Keller 1997) | |
| *Thelephora* (G. Langer 1994) | |
| *Tomentella* (Calonge 1969) | |
| 5. Russuloid clade | |
| *Auriscalpium* (Keller 1997) | |
| *Hericium* (Flegler et al. 1976) | |
| *Laxitextum* (Keller 1997) | |
| *Scytinostroma* (Besson and Froment 1968) | |
| *Stereum* (Patrignani and Pellgrini 1986) | |
| *Zelleromyces* (Keller 1997) | |
| 6. Hymenochaetoid clade | |
| *Basidioradulum* (Langer and Oberwinkler 1993) | |
| *Coltricia* (W. Müller, pers. comm.) | |
| *Hymenochaete* (Oberwinkler 1985) | |
| *Hyphodontia* (E. Langer 1994) | |
| *Onnia* (Moore 1980) | |
| *Phellinus* (Moore 1985) | |
| *Schizopora* (Langer and Oberwinkler 1993) | |
| *Trichaptum* (Traquair and Mckeen 1978) | |
| 7. Cantharelloid clade | |
| *Botryobasidium* (G. Langer 1994) | |
| *Cantharellus* (Keller 1997) | |
| *Clavulicium*? (Oberwinkler 1985) | |
| *Tulasnella* (Khan and Talbot 1976) | |
| [*Stilbotulasnella* = missing (Bandoni and Oberwinkler 1982)] | |
| 8. Gomphoid-phalloid clade | |
| *Clathrus* (Eyme and Parriaud 1970) | *Geastrum* (E. Langer, pers. comm.) |
| | *Ramaria*? (Patrignani and Pellegrini 1986) |

large perforations, Tulasnellales have parenthesomes that are imperforate or absent, and Tremellales have parenthesomes that are vesiculate, absent, or reticulate (Adams et al. 1995; Bandoni and Oberwinkler 1982; Keller 1997; Moore 1985). Homobasidiomycetes have parenthesomes that have numerous small perforations or that are imperforate (Table 4).

Six of the eight major clades that we recognize are apparently monomorphic for parenthosome type: as far as we know, all members of the euagarics, bolete, thelephoroid, and russuloid clades have perforate parenthosomes, whereas the hymenochaetoid clade and the few members of the cantharelloid clade that have been examined have imperforate parenthosomes (Table 4). *Coltricia*, in the hymenochaetoid clade, has been reported to have a perforate parenthosome (Moore 1980). However, reanalysis of this taxon has shown that it has an imperforate parenthosome (W. Müller, pers. comm.), as do all other members of the hymenochaetoid clade that have been examined (Traquair and McKeen 1978; Moore 1980, 1985; E. Langer 1994). Only the polyporoid and gomphoid-phalloid clades are reported to have both perforate and imperforate parenthosomes (Table 4). In the polyporoid clade, all taxa that have been examined have perforate parenthesomes, except *Phanerochaete sordida*, which is reported to have an imperforate parenthesome (Keller 1997). In the gomphoid-phalloid clade, imperforate parenthesomes are reported from *Geastrum* (E. Langer unpubl.) and *Ramaria ignicolor* (as *Clavaria ignicolor*; Patrignani and Pellegrini 1986), but *Clathrus* is reported to have perforate parenthesomes (Eyme and Parriaud 1970). Unplaced homobasidiomycetes with imperforate parenthesomes include the corticioid fungi *Paullicorticium pearsonii*, *Radulomyces confluens*, and *Subulicystidium longisporum*, and the clavarioid fungus *Typhula uncialis* (which may be related to *Multiclavula*; Oberwinkler 1985; Patrignani and Pellegrini 1986; Keller 1997).

The tree in Fig. 2 suggests that imperforate parenthosomes are plesiomorphic in the homobasidiomycetes and are homologous with the parenthosomes of Auriculariales and Dacrymycetales. Nevertheless, the position of the hymenochaetoid clade (as sister taxon of the russuloid clade) and the apparent co-occurrence of perforate and imperforate parenthosome types in the polyporoid and gomphoid-phalloid clades suggest that there has been some homplasy in the evolution of this character. In addition, the probable placement of *Ceratobasidium* and *Waitea* (which have parenthosomes with a few large perforations) in the eugarics clade suggests that there can be considerable variation in the size and number of parenthosome perforations among closely related taxa. Finally, the apparent loss of parenthosomes in *Stilbotulasnella* of the Tulasnellales (Bandoni and Oberwinkler 1982) seems to parellel their loss in the Tremellales.

Parenthosome ultrastructure may contain clues to the deepest splits in the homobasidiomycetes. However, inferences about the evolution of parenthosome types are limited by the weak support for nodes deep in the homobasidiomycete tree (Fig. 2) and poor sampling in many taxa (Table 4). To assess the phylogenetic significance of parenthosome ultrastructure in homobasidiomycetes, it will be necessary to improve resolution of higher-order relationships, confirm certain reports (i.e., *Phanerochaete* and *Clathrus*), and increase the number of observations of parenthosome types, especially in the cantharelloid and gomphoid-phalloid clades.

## C. Asexual Reproduction and Somatic Morphology

Asexual reproductive forms have received considerably less attention in homobasidiomycetes than in ascomycetes. Nevertheless, there is a diversity of anamorphic forms in homobasidiomycetes, including an abundance of simply arthroconidial forms in soil- and wood-inhabiting species (see Seifert and Gams, Chap. 14, Vol. VII, Part A). Much of the information on asexual reproductive structures in homobasidiomycetes comes from cultural studies (Nobles 1965, 1971; e.g., Miller 1971; Stalpers 1978; Nakasone 1990). Many saprotrophic homobasidiomyceetes produce abundant mitospores in culture, especially on nutrient-poor media or when confronted by other organisms (bacteria, nematodes, other fungi; e.g., Tsuneda et al. 1992). In contrast, it appears that ectomycorrhizal homobasidiomycetes (and ascomycetes) lack the ability to form mitrospores in culture (Hutchison 1989, 1991a). The functional significance (if any) of this apparent correlation between nutritional mode and asexual reproduction is unclear. As in ascomycetes, many basidiomycete anamorphs have no known teleomorph, but with the application of molecular techniques their relationships to sexual forms should be resolved. In the following sections, we discuss selected asexual reproductive structures of homobasidiomycetes, emphasizing their morphological variability and potential phylogenetic utility. An excellent review of this topic was provided by Stalpers (1987), which should be consulted for many taxa that

could not be included here (also see Kendrick and Watling 1979).

As far as we know, asexual reproductive structures occur in each of the eight major clades of homobasidiomycetes that we recognize, with the possible exceptions of the thelephoroid and gomphoid-phalloid clades. Nevertheless, the possession of particular kinds of asexual reproductive structures may be phylogenetically informative within the homobasidiomycetes. For example, the formation of *Sporotrichum* anamorphs (Stalpers 1984) in *Laetiporus* and *Pycnoporellus* suggests that they are closely related, which is consistent with the morphology of basidiomata (Ryvarden 1991). However, *Phanerochaete* also has a *Sporotrichum* anamorph, which suggests that there has been homoplasy in the evolution of this form (Fig. 2). Similarly, the presence of *Spiniger* and *Spiniger*-like anamorphs in *Bondarzewia*, *Dichostereum*, *Heterobasidion*, and *Laurilia* is consistent with rDNA analyses and morphology, which suggest that these taxa are all in the russuloid clade (similar anamorphs are also formed by *Mutatoderma* (*Hyphoderma*), and *Resinicium*, which are of uncertain taxonomic placement). As a final example, cylindric to barrel-shaped arthroconidia with schizolytic dehiscence are frequent in *Hypholoma*, *Pholiota*, and *Psilocybe* (Jacobsson 1989; Klán et al. 1989; R.G. Thorn, unpubl.), which are all placed in Strophariaceae (euagarics clade), but similar arthroconidia have also been recorded in *Phlebia* (polyporoid clade; Sigler and Carmichael 1976), and in cultures isolated from human specimens and pupal chambers of the mountain pine beetle *Dendroctonus ponderosae* (Tsuneda et al. 1993). Taken together, these observations indicate that asexual reproductive structures may be phylogenetically informative, but that certain anamorphic form-taxa are polyphyletic.

The simplest anamorphic forms are sterile mycelia, which lack conidia or multicellular structures for reproduction or dispersal. Among these are *Rhizoctonia* sensu lato and *Ozonium*. *Rhizoctonia* has been subdivided on the basis of nuclear states and associated teleomorphs into *Rhizoctonia* (typonym *Thanatophyton*; multinucleate anamorphs of *Helicobasidium*, with simple septal pores, Urediniomycetes), *Moniliopsis* (multinucleate anamorphs of *Thanatephorus*, parenthesomes with few, regular pores, Ceratobasidiales), *Ceratorhiza* (binucleate anamorphs of *Ceratobasidium*, parenthesomes with few, regular pores, Ceratobasidiales), *Chrysorhiza* (multinucleate anamorphs of *Waitea*, parenthesomes with few, irregular pores, Botryobasidiales or Ceratobasidiales), *Epulorhiza* (binucleate anamorphs of *Tulasnella*, parenthesomes imperforate, Tulasnellales), and *Opadorhiza* (binucleate anamorphs of *Sebacina*, parenthesomes imperforate, Auriculariales, Exidiaceae: Moore 1987; Müller et al. 1998; Stalpers and Andersen 1996). As mentioned previously, molecular studies tentatively suggest that *Ceratobasidium*, *Thanatephorus*, and *Waitea* (all with variously perforated parenthesomes) are in the euagarics clade, and that *Botryobasidium* and *Tulasnella* (imperforate parenthesomes) are in the cantharelloid clade (Table 1). However, *Waitea* has also been classified in the Botryobasidiales (e.g., Müller et al. 1998). *Moniliopsis* includes the economically important plant pathogen *M. solani* (teleomorph *Thanatephorus cucumeris*). *Ozonium* is now restricted in use to anamorphs of the *Coprinus domesticus* group (Watling 1979, euagarics clade).

Complex condiomata are found in relatively few homobasidiomycetes. Examples include the acervular *Necator* anamorph of *Phanerochaete salmonicolor*, unnamed sporodochial anamorphs formed in combs of *Termitomyces*, and the coremioid or synnematous *Antromycopsis* (teleomorph *Pleurotus*) and *Tilachlidiopsis* (= *Sclerostilbum*; teleomorph *Collybia*). Some basidiomycetes with complex conidiomata have no known teleomorph, including the pycnidial *Ellula*, the sporodochial *Glutinoagger*, and the coremioid or synnematous *Gloeosynnema* and *Riessia* (Botha and Eicker 1991; Seifert and Okada 1988).

Splash-cup anamorphs are formed by a number of polyporoid and corticioid basidiomycetes (Brodie 1951a,b). In the *Michenera* anamorph of *Licrostroma*, the *Matula* anamorph of *Aleurocystis*, and unnamed anamorphs of *Trametes conchifer* and *Phaeotrametes decipiens* the splash cups disperse arthroconidia; in contrast, the splash-cup anamorphs of *Corticium minnsiae* contain single hyphal bodies (Brodie 1951a; Jackson 1950; Wright 1966; all polyporoid clade, or unplaced). In all of these, the splash-cup dispersal of mitotic diaspores occurs during the summer or fall and is followed by the development of the basidiomata and meiospores. The splash-cup dispersal of mitospores in these fungi is a remarkable parallel to the splash-cup dispersal of basidiospores in the birds' nest fungi *Cyathus* and *Crucibulum* (euagarics clade; Fig. 2).

Many species of homobasidiomycetes produce mitospores within or on the surface of basidiomata. Examples include *Nyctalis* (anamorph *Asterophora*), *Mycena* Sect. Sacchariferae, and *Pleurotus* (anamorphs unnamed, euagarics clade), *Inonotus* (anamorph *Ptychogaster*, hymenochaetoid clade), *Abortiporus*, *Antrodia*, *Fomitopsis*, *Oligoporus*, *Phlebia*, and *Punctularia* (*Ptychogaster* and similar anamorph forms, polyporoid clade or unplaced), *Botryobasidium* (anamorphs *Haplotrichum* and *Allescheriella*, cantharelloid clade), and *Arthrosporella* (*Nothoclavulina*, anamorph unnamed, unplaced; Desjardin 1995; G. Langer 1994; Ryvarden 1991; Stalpers 1987). In addition, the mycoparasite *Squamanita* produces chlamydospores on the remains of its host's basidiomata (Redhead et al. 1994).

Several taxa of aero-aquatic hyphomycetes have clamp connections or dolipore septa, which indicates that they are basidiomycetes, but not all are necessarily homobasidiomycetes (Nawawi 1985; Webster 1992). For example, *Tricladiomyces* and *Dendrosporomyces* have branched conidia and dolipore septa with perforate parenthesomes (Nawawi 1985) and *Fibulotaeniella* has sigmoid, one- or two-celled conidia with clamp connections (Marvanová and Bärlocher 1988). The teleomorphs of these taxa are unknown. Teleomorphs of *Taeniospora* and *Ingoldiella*, which have clamped, tetraradiate conidia, are found in the corticioid genera *Fibulomyces*, *Leptosporomyces*, and *Sistotrema* (polyporoid clade or unplaced; Nawawi et al. 1977; Nawawi and Webster 1982; Marvanova and Stalpers 1987). *Cyrenella*, isolated from the stipe base of the arenicolous-maritime agaric *Laccaria trullisata*, forms mycelia with clamp connections and simple, obovate conidia with four apical appendages and one basal appendage, which superficially resemble conidia of some aeroaquatic hyphomycetes (Gochenauer 1981). However, monokaryons of *Cyrenella* form a *Rhodotorula*-like yeast phase with budding balastospores, which suggests that *Cyrenella* is a member of the Tremellales, not homobasidiomycetes.

In addition to asexual spores, many homobasidiomycetes produce aggregates of somatic hyphae that function in dispersal, colonization, and persistence. Examples include sclerotia (compact hyphal aggregates with a differentiated rind of thick-walled cells), bulbils (usually small hyphal aggregates without a differentiated rind), and pseudosclerotia (hyphal masses including nonfungal tissues), as well as rhizomorphs and mycelial cords (not discussed here). Selected examples of these forms, each of which has evolved repeatedly, are discussed below.

Teleomorphs of the form-genus *Sclerotium* are found in the euagarics clade (*Agrocybe*, *Athelia*, *Ceratobasidium*, *Clitopilus*, *Collybia* (= *Microcollybia*), *Coprinus*, *Hypholoma*, *Leucocoprinus*, *Panaeolus*, *Stropharia*, and *Typhula*) and bolete clade (*Boletinellus*, *Hygrophoropsis*, *Leucogyrophana*, *Paxillus*, and *Pisolithus*), as well as in *Thanatephorus*, which is of uncertain placement (Cotter and Miller 1985; Grenville et al. 1985a, b; Redhead and Kroeger 1987; Stalpers 1987; Hutchison 1991b; Ginns and Lefebvre 1993; Lee and Jung 1997; R.G., Thorn, unpubl.). Bulbils are found in a number of anamorph genera with corticioid teleomorphs, including *Aegerita* (teleomorphs *Bulbilomyces* and *Subulicystidium*), *Burgoa* (*Sistotrema*, polyporoid clade), *Hyphelia* (*Corticium*), and *Myriococcum* (*Athelia*), as well as the corticioid homobasidiomycetes *Ceraceomyces*, *Crustoderma*, *Dendrothele*, and *Limonomyces* (Eriksson and Ryvarden 1976; Ginns and Lefebvre 1993). Large sclerotia and pseudosclerotia are formed in the polyporoid clade by *Polyporus*, such as *P. tuberaster* (with anamorphs *Mylitta* and *Pietraia*), *Wolfiporia* (*Pachyma* anamorph), and *Panus*, and in the euagarics clade by *Psilocybe* and *Pleurotus*, including *P. tuberregium* (Petch 1915; Corner 1981; Pegler 1983; Stamets and Chilton 1983; Hibbett et al. 1993a; Hibbett and Thorn 1994). Sclerotia and pseudosclerotia of some wood-decaying homobasidiomycetes are massive, and these have often been utilized in various ways by indigenous peoples. For example, the *Pachyma* anamorph of *Wolfiporia*, known as a tuckahoe, was eaten by native Americans (Weber 1929), and pseudosclerotia of the pantropical *Pleurotus tuberregium* have been used as food or medicine in Africa and elsewhere (Walleyn and Rammeloo 1994). In Papua New Guinea, sclerotia identified as *P. tuberregium* (but perhaps actually *Panus fulvus*?) have been used to make club heads (Price et al. 1978).

Finally, yeastlike forms are reported from only two homobasidiomycetes, although they are widespread in other groups of Basidiomycota (Swann and Taylor 1995b). Both homobasidiomycete yeasts are insect symbionts. Symbionts of the leafcutter ant *Cyphomyrmex* (euagarics clade) are dimorphic, existing in both a yeast and hyphal form (Weber 1979). Similarly, an unnamed sym-

biont of the bark beetle *Dendroctonus frontalis* (russuloid clade) exists as a yeast in the beetle mycangia, but becomes mycelial when free-living (Happ et al. 1976). Reports that the parasitic agaric *Asterophora lycoperdoides* has a yeast phase (Koller and Jahrmann 1985) have been shown to be in error (Laaser et al. 1989).

## D. Mating Genetics

Sexual compatibility in heterothallic (outcrossing) homobasidiomycetes is regulated by multiallelic factors that occur at a single locus in bipolar (unifactorial) species, or at two loci (the A and B factors) in tetrapolar (bifactorial) species. Based on figures from Esser (1967), about 65% of homobasidiomycetes are tetrapolar, 25% are bipolar, and 10% are homothallic. Nobles (1971) and Ryvarden (1991) suggested that bipolarity is the primitive condition in the homobasidiomycetes, which implies that there have been multiple derivations of tetrapolar systems from bipolar systems. However, as noted by Raper and Flexer (1971), the functional similarity of tetrapolar mating systems in diverse homobasidiomycetes suggests that they are homologous. Bipolar mating systems could be derived from tetrapolar mating systems by two mechanisms: (1) self-compatible mutations in either the A or B factors could lead to effectively bipolar mating systems (or homothallism if both the A and B factors are affected), as has been demonstrated in *Coprinus* (Casselton and Kües 1994; Raper and Flexer 1971); (2) close linkage of A and B loci resulting from chromosome rearrangements could result in cosegregation of A and B loci, thus creating bipolarity (Bakkeren et al. 1992). Evidence for derivation of bipolar mating systems from tetrapolar systems is found in *Marasmius*, which contains both bipolar and tetrapolar species; molecular phylogenies suggest that the bipolar species form a clade that is derived from a paraphyletic assemblage of tetrapolar species (Owings and Desjardin 1997). Many other genera of homobasidiomycetes have been shown to contain both bipolar and tetrapolar mating species (as well as homothallic and heterothallic forms), such as *Sistotrema*, *Marasmius*, *Collybia*, and *Coprinus* (Lange 1952; Raper and Flexer 1971; Murphy and Miller 1993; Petersen 1995b). These observations indicate that the presence of tetrapolarity or bipolarity per se (ignoring the fact that bipolarity may arise by at least three different mechanisms) is not useful for delimiting major clades within homobasidiomycetes (it may be informative at low taxonomic levels, however, as in *Marasmius*). Nevertheless, the genetic architecture of mating systems may be informative for resolving higher-level relationships of homobasidiomycetes and heterobasidiomycetes. Among the heterobasidiomycetes, only the Auriculariales is known to have a bifactorial mating system with multiallelic loci such as that found in homobasidiomycetes, which supports the view that the Auriculariales is the sister group of the homobasidiomycetes. Tremellales (as well as Ustilaginales) have bipolar mating or "modified bifactorial compatibility" in which one locus is multiallelic and the other is biallelic (Wells 1994). In the Dacrymycetales, *Cerinomyces* has been shown to be tetrapolar (Maekawa 1987), but it is not known whether both the A and B factors are multiallelic.

## E. Pigments and Bioluminescence

Pigments of macrofungi, including compounds responsible for bluing and other color reactions, have drawn the attention of organic chemists for more than a century (see reviews by Arpin and Fiasson 1971; Gill and Steglich 1987; Gill 1996; Johnson and Schroeder 1996; see also Tyler 1971 for a general review of chemotaxonomy in homobasidiomycetes). Nevertheless, only a small proportion of the species of homobasidiomycetes have been examined and, until recently, the findings were not widely used for taxonomic purposes (Kühner 1980, 1984; Singer 1986). The available data suggest that pigment compounds may be phylogenetically informative in some groups, but that they also display considerable homoplasy. The following discussion of selected pigments follows the outlines of Gill (1996) and Gill and Steglich (1987), who sort pigments into those derived from the shikimate-chorismate pathway, the acetate-malonate pathway, the mevalonate pathway, nitrogen-heterocycles (not discussed here), and other nitrogen-containing compounds.

### 1. Shikimate-Chorismate Pathway Derivatives

The shikimate-chorismate pathway produces a number of compounds that are characteristic of the bolete clade, including atrotomentin, pulvinic acid derivatives, cyclopentanoids, and polyprenylquinones. These compounds have been found

in diverse poroid, lamellate, corticioid, and gasteroid-secotioid taxa, including *Boletus*, *Chamonixia*, *Chroogomphus*, *Coniophora*, *Gomphidius*, *Gyrodon*, *Hygrophoropsis*, *Leucogyrophana*, *Paxillus*, *Phylloporus*, *Pisolithus*, *Rhizopogon*, *Scleroderma*, *Serpula*, *Suillus*, and others (for details, see Gill and Steglich 1987).

Atrotomentin, pulvinic acid derivatives, and cyclopentanoids have also been found in the lignicolous agarics *Omphalotus* and *Lampteromyces*. Singer (1986) placed *Omphalotus* and *Lampteromyces* in the Paxillaceae (suborder Boletineae), largely on the basis of the presence of these pigments (see also Moser 1978; Kühner 1980). However, analyses of rDNA sequences suggest that *Omphalotus* and *Lampteromyces* are in the euagarics clade (Binder et al. 1997; Moncalvo et al. 2000; Thorn et al. 2000). This supports Jülich (1981), who placed *Omphalotus* and *Lampteromyces* in the Tricholomatales. In addition, atrotomentin and cyclopentanoids are found outside the bolete clade in *Albatrellus* (russuloid clade or polyporoid clade) and *Hydnellum* (thelephoroid clade). These observations imply that the production of atrotomentin, pulvinic acid derivatives, and cyclopentanoids has evolved repeatedly.

Thelephoric acid (which is a terphenylquinone, similar to atrotomentin) is found in *Bankera*, *Boletopsis*, *Hydnellum*, *Phellodon*, *Polyozellus*, *Pseudotomentella*, *Sarcodon*, and *Thelephora*. Thelephoric acid has been used as a defining character of the Thelephoraceae (including Bankeraceae; Bresinsky and Rennschmid 1971). This is consistent with molecular characters, which strongly support monophyly of the Thelephoraceae (Table 1). Nevertheless, thelephoric acid also occurs in *Suillus* and *Rhizopogon* (bolete clade), *Omphalotus* and *Lampteromyces* (euagarics clade), *Trametes* (polyporoid clade), and *Punctularia* (probably polyporoid clade).

Derivatives of cinnamic acids, the styrylpyrone pigments bisnoryangonin and hispidin, occur in *Hymenochaete*, *Inonotus*, *Onnia*, and *Phellinus* (Hymenochaetaceae, hymenochaetoid clade). These compounds also occur in *Phaeolus*, which has been classified in both the Hymenochaetaceae and Polyporaceae. According to molecular studies, *Phaeolus* is closely related to the polypore *Laetiporus* (polyporoid clade), which suggests that the presence of bisnoryangonin and hispidin in Hymenochaetaceae and *Phaeolus* is due to convergence. Furthermore, bisnoryangonin and hispidin also occur in *Gymnopilus*, *Hypholoma*, and *Pholiota* of the Strophariaceae (euagarics clade). In this context, it is worth noting that the xanthochroic reaction (tissues becoming dark on exposure to alkali), which has been an important character in delimiting the Hymenochaetaceae, is found in numerous Aphyllophorales (Parmasto and Parmasto 1979). A number of chemically dissimilar compounds darken in alkali, which may account for the occurrence of the xanthochroic reaction in diverse lineages of Aphyllophorales (Parmasto and Parmasto 1979).

Finally, the colorless-red-black reactions found in species of *Agaricus*, *Hygrocybe*, and *Rhodocybe* (euagarics clade), *Daedaleopsis* (polyporoid clade), *Russula* (russuloid clade), and *Strobilomyces* (bolete clade) are a result of oxidation by tyrosinase of L-DOPA, which is derived from tyrosine or phenylalanine via the shikimate-chorismate pathway (Gill and Steglich 1987). It is perhaps not surprising that color reactions based on such physiologically fundamental compounds are phylogenetically uninformative at high taxonomic levels.

## 2. Acetate-Malonate Pathway Derivatives

Acetate-malonate pathway derivatives include ketides and anthraquinones. Anthraquinones have been much used in the specific- and generic-level taxonomies of *Cortinarius* and its subgenus or segregate *Dermocybe* (Høiland 1980, 1986; Keller 1982; Liu et al. 1997). Chemically similar pigments occur in *Claviceps* and *Hypomyces* (Ascomycota, Hypocreales) and in certain species of *Leucopaxillus* and *Tricholoma* (euagarics clade; Gill and Steglich 1987).

Fatty acid or higher polyketide pigments include merulic acids, which are found in *Phlebia* (= *Merulius*), ceriporiones, from *Ceriporia*, and sarcodontic acids, from *Sarcodontia* (a resupinate, hydnoid fungus that has yet to be included in molecular studies). Based on rDNA sequences, *Phlebia* and *Ceriporia* are part of a monophyletic group within the polyporoid clade that also includes *Bjerkandera*, other polypores, and corticioid fungi (Fig. 2; Y.-J. Yao et al., unpubl.).

## 3. Mevalonate Pathway Derivatives

The mevalonate pathway gives rise to carotenoid and sesquiterpenoid pigments. Too little is known of sesquiterpenoid distribution among homobasidiomycetes for phylogenetic comparisons, although

the search for antibiotics and other pharmaceuticals may gradually yield this information (Gill and Steglich 1987; Anke et al. 1995). Carotenoid pigments are widespread in the fungi, including operculate and inoperculate discomycetes (Ascomycota) and Dacrymycetales (Basidiomycota: Heterobasidiomycetes). Nevertheless, their distribution among the homobasidiomycetes suggests that they could be phylogenetically informative in some groups. Several groups of species that appear to be closely related based on rDNA sequences share similar carotenoids ($\psi$-$\psi$ carotenoids, $\beta$ carotenoids, and $\gamma$ carotenoids), including: (1) Phallales and *Sphaerobolus* (gomphoid-phalloid clade); (2) *Cantharellus* and *Craterellus* (cantharelloid clade); (3) *Peniophora* and *Stereum* (russuloid clade); (4) *Clavulinopsis*, *Chrysomphalina* (as *Gerronema*), *Haasiella*, and *Phyllotopsis* (euagarics clade; see Gill and Steglich 1987 for details).

### 4. Nitrogen-Containing Compounds

Among the diverse nitrogen-based pigments, an assortment of chemically similar quinone imines, phenyldiazonins, arylazoxycyanides and rubroflavins are found in *Agaricus* and *Calvatia*, which supports the view that they are closely related, as suggested by rDNA sequences (Fig. 2, Table 1).

Pistillarin, the compound responsible for colorless to dark green reactions with ferric chloride in fruiting bodies of *Ramaria*, is also found in *Clavariadelphus* and *Gomphus*, which supports the view that *Clavariadelphus* is closely related to the Gomphaceae (Fig. 2; Steglich et al. 1984; Gill and Steglich 1987). Similar staining reactions to iron salts are found in the false truffle *Gautieria* (Stewart 1974), supporting its placement in the gomphoid-ramarioid lineage, in contrast to the bolete lineage, where it has also been placed (Stewart 1974; Castellano et al. 1989; Pegler et al. 1993).

### 5. Bioluminescence

Bioluminescence has been reported in mycelia, fruiting bodies, and spores of *Armillaria*, *Dictyopanus*, *Favolaschia*, *Lampteromyces*, *Mycena*, *Omphalotus*, *Panellus*, and *Pleurocybella* (as *Pleurotus noctilucens*; Kobayasi 1952; Burdsall and Miller 1975; Wassink 1978; O'Kane et al. 1990). It has never been suggested that these taxa form a monophyletic group. Furthermore, there is variation for the presence or absence of bioluminescence within these taxa, even within single species (Petersen and Bermudes 1992). Nevertheless, all the taxa from which bioluminescence has been reported are white-spored saprotrophs in the euagarics clade. Bioluminescence in these fungi may result from modifications of a homologous metabolic pathway that is associated with saprotrophy.

## F. Nutritional Modes

Homobasidiomycetes have diverse mechanisms for obtaining nutrition. Although it is necessary to divide these mechanisms into discrete categories for the purpose of discussion, it has long been recognized that individual species may display more than one mode (Garrett 1981; Hudson 1972). For example, some wood-decaying fungi trap and consume animals, and certain ectomycorrhizal species can degrade components of plant tissues, or parasitize other fungi (e.g., Thorn and Barron 1984; Trojanowski et al. 1984; Zhao and Guo 1989; Durrall et al. 1994; Hutchison and Barron 1996). Clearly, simple definitions of homobasidiomycetes as mutualists, pathogens, or saprotrophs should be qualified by identifying the organisms involved in the interaction.

Among the heterobasidiomycetes, Tremellales may be exclusively mycoparasites, but the Auriculariales and Dacrymycetales are wood decayers (Bandoni 1987; Wells 1994). This supports the view that saprotrophy is the plesiomorphic nutritional mode of the homobasidiomycetes, and that pathogenic and mycorrhizal symbioses are derived (Hacskaylo 1971; Malloch 1987). The following discussion focuses on the evolution of different nutritional modes in homobasidiomycetes. For reviews of ecological and physiological aspects, see Ahmadjian (1993), Barron (1992), Cooke and Whipps (1993), Dix and Webster (1995), Jeffries and Young (1994), Rayner and Boddy (1988), Smith and Read (1997), and Thorn (1997).

### 1. Saprotrophs

Homobasidiomycetes include the major decomposers of plant tissues, which represent the vast majority of terrestrial biomass. (Decomposition of the remains of other organisms falls mostly to Eubacteria). Decomposition of wood is by the far the best-studied form of saprotrophy in homobasidiomycetes, owing in large part to its great eco-

nomic importance in forestry and its potential applications in biopulping and livestock forage treatment (Rayner and Boddy 1988; Eriksson et al. 1990; Blanchette 1991; Eaton and Hale 1993; Simpson 1996). Decay of leaf litter and other fine plant debris appears to occur through the same enzymatic mechanisms as wood decay (Orth et al. 1993; Tanesaka et al. 1993). Two main forms of wood decay are recognized: white rot and brown rot (also called cubical brown rot, or dry rot). In white rot, cellulose (50–70% of wood by weight), hemicellulose (10–20%), and lignin (10–20%) are all decayed, leaving a soft, white, often stringy residue, whereas in brown rot, only hemicellulose and cellulose are appreciably degraded, leaving a reddish brown, crumbly residue that may be almost pure lignin (Rayner and Boddy 1988; Preston et al. 1990; Green and Highley 1997; Worrall et al. 1997). Selective delignification (a form of white rot) also occurs, as in *Ceriporiopsis*, *Crucibulum*, and others (Blanchette et al. 1988; Worrall et al. 1997).

The primary lignin-modifying enzymes of white rot fungi are lignin peroxidases (LiPs), manganese peroxidases (MnPs), and laccases (Rayner and Boddy 1988; Hatakka 1994; Reddy and D'Souza 1994; Thurston 1994). Presence or absence of tyrosinase has been used as a taxonomic character in studies of cultures of wood-decaying fungi (Boidin 1951; Stalpers 1978), but this enzyme is not known to be directly related to the degradation of wood polymers.

Determination of rot type has traditionally been based on observations of natural substrates, or culture studies involving spot tests with reagents intended to detect wood-decaying enzymes (Davidson et al. 1942; Nobles 1965; Rayner and Boddy 1988). However, many colorimetric substrates used in such tests (e.g., gum guaiac and pyrocatechol) can be oxidized by any LiPs, MnPs, laccase, or tyrosinase, or nonbiological oxidants such as malt extract in culture media (Maehly and Chance 1954; Kratochvil et al. 1971). Consequently, older literature reporting "polyphenol oxidases" as physiological indicators or taxonomic characters must be interpreted with caution. On the basis of spot tests, it has been widely assumed that brown rot fungi and certain white rot fungi, such as *Phanerochaete chrysosporium*, do not produce laccases (Nobles 1965, 1971; Hatakka 1994). However, recent studies have shown that laccase-specific gene sequences and laccase activity occur in both brown rot fungi (D'Souza et al. 1996) and *P. chrysosporium* (Srinivasan et al. 1995).

Most wood- and litter-decaying homobasidiomycetes, including soil fungi that decay fine litter in and on soil, cause white rots. Based on species counts in Hawksworth et al. (1995) and Gilbertson (1980, 1981), homobasidiomycetes probably include about 8500 described white rot species, and 200 brown rot species. In North America, about 6% of wood decaying fungi are brown rot species (Gilbertson 1980, 1981), and approximately 85% of these occur on conifer substrates (Gilbertson 1980). Under controlled conditions, brown rot fungi remove biomass from wood more rapidly than white rot fungi (Gilbertson 1980). On this basis, it has been argued that production of a brown rot has adaptive value in the conifer-dominated forests of high latitudes and elevations, which have short growing seasons (Gilbertson 1980).

Brown rot has been interpreted as either a plesiomorphic (Nobles 1965, 1971) or derived condition in the homobasidiomycetes (Gilbertson 1981; Ryvarden 1991; Worrall et al. 1997). Among the heterobasidiomycetes, the Dacrymycetales contains species causing brown rots (and possibly white rots; Seifert 1983; Worrall et al. 1997), whereas the Auriculariales sensu stricto (the putative sister group of the homobasidiomycetes) contains only white rot species. Within the homobasidiomycetes, species with white rot activity occur in each of the eight major clades that we recognize, except the bolete clade (Ginns and Lefebvre 1993; Rayner and Boddy 1988). In contrast, brown rot species occur only in the euagarics, bolete, and polyporoid clades (as far as we know). This distribution suggests that white rot is the plesiomorphic form in the homobasidiomycetes.

In the euagarics clade, brown rot species are found in *Fistulina*, *Hypsizygus*, and, possibly, *Ossicaulis* (previous reports suggesting that *Coprinus* contains brown rot species have been shown to be erroneous; Redhead and Ginns 1985). The agaricoid genera *Neolentinus* and *Heliocybe* also produce brown rots, but their higher-level relationships are unclear (Hibbett and Vilgalys 1993). *Neolentinus* and *Heliocybe* were segregated from *Lentinus* largely because species of *Lentinus sensu stricto* (as well as *Lentinula* and *Panus*) produce a white rot (Redhead and Ginns 1985). Molecular

studies support the segregation of *Neolentinus* and *Heliocybe* from *Lentinus* and *Panus* (Hibbett and Vilgalys 1993).

In the bolete clade, brown rot species are found in *Hygrophoropsis*, *Paxillus* (including *Tapinella*), *Coniophora*, *Serpula*, and others. Brown rot fungi in the bolete clade are distinguished by their ability to degrade pure cellulose in culture (however, *Postia* and *Gloeophyllum* have been shown to degrade cellulose in soil-block tests; Nilsson 1974; Nilsson and Ginns 1979; Highley 1988; Green and Highley 1997). As discussed by Redhead and Ginns (1985), *Omphalotus* produces a white rot, which supports the view that it is not in the bolete clade (see Sect. II. C. 2). Phylogenetic studies suggest that production of a brown rot evolved once in the bolete clade, and several times in the euagarics clade, and that the production of brown rots in the euagarics and bolete clades are not homologous (Bruns et al. 1998; Moncalvo et al. 2000, and unpubl.).

The majority of brown rot species that have been studied using molecular characters occur in the polyporoid clade. However, brown rot fungi in this clade do not form a monophyletic group, suggesting that there is a complex pattern of transformations between decay types. Nevertheless, two strongly supported groups of genera are united by the production of a brown rot: (1) *Laetiporus-Phaeolus-Sparassis* (*Pycnoporellus* is probably in this group), and (2) *Fomitopsis-Daedalea-Piptoporus* (Hibbett and Donoghue 1995; Hibbett et al. 1997b). There are many other brown rot polypores that are of uncertain placement, however, such as *Antrodia*, *Postia* (= *Oligoporus*), *Wolfiporia*, and *Gloeophyllum* [as noted previously, the placement of *Gloeophyllum* outside of the polyporoid clade (Fig. 2) is contradicted by morphology and independent molecular studies]. In addition, there are several brown rot genera of Corticiaceae and Stereaceae that have yet to be investigated using molecular approaches, including *Chaetoderma* and *Crustoderma* (Corticiaceae), and *Columnocystis* (= *Veluticeps*, Stereaceae).

Taken together, the evidence discussed above suggests that the production of a brown rot has evolved multiple times in the homobasidiomycetes (Worrall et al. 1997), with most brown rot species occurring in the polyporoid clade. Although there is homoplasy in this character, it is nonetheless phylogenetically informative for some groups. As noted by Redhead and Ginns (1985), division of saproptrophic homobasidiomycetes into white rot and brown rot categories fails to represent the evolutionary diversity of decay systems. Detailed comparative studies of decay mechanisms (e.g., Vares and Hatakka 1997), especially analyses of the genes encoding decay enzymes, may provide many characters for homobasidiomycete systematics.

## 2. Mycorrhizae

Homobasidiomycetes include fungi that form ectomycorrhizae (including both arbutoid and monotropoid mycorrhizae), orchid mycorrhizae, and possibly ericoid mycorrhizae (Smith and Read 1997; Umata 1995). Historically, basic studies of mycorrhizae have been limited by the reliance of basidiomycete taxonomy on fruiting bodies, but molecular sequence databases are providing powerful new tools for identifying mycorrhizae in the absence of fruiting bodies, as well as for inferring evolution of mycorrhizae (Cullings et al. 1996; Gardes and Bruns 1996; Taylor and Bruns 1997; Bruns et al. 1998). The physiology, ecology, and morphology of mycorrhizae have been discussed at length elsewhere (e.g., Smith and Read 1997; Varma and Hock 1995). In this section, we consider the phylogenetic distribution of mycorrhizae in the homobasidiomycetes.

Ectomycorrhizae are the most widespread form of mycorrhizae in homobasidiomycetes. Ectomycorrhizae are also formed by certain ascomycetes, but they are absent from Auriculariales, Dacrymycetales, and Tremellales, which supports the view that the plesiomorphic condition of the homobasidiomycetes is saprotrophic (Hacskaylo 1971; Malloch 1987). Within the homobasidiomycetes, ectomycorrhizal species are concentrated in the bolete clade (Boletales, including Sclerodermataceae), thelephoroid clade (Thelephoraceae, Scutigeraceae), russuloid clade (*Albatrellus* pro parte, Russulaceae, including gasteroid forms), cantharelloid clade (Cantharellaceae, Hydnaceae sensu stricto), gomphoid-phalloid clade (Gomphaceae, *Gautieria*), and euagarics clade (*Amanita*, *Hygrophorus sensu stricto*, *Tricholoma*, *Inocybe*, *Cortinarius*, *Hebeloma*, and *Laccaria*; Trappe 1962). In addition, one ectomycorrhizal genus occurs in the predominantly saprotrophic hymenochaetoid clade (*Coltricia*). Within the euagarics clade, ectomycorrhizal

taxa are absent from the Agaricaceae-Lycoperdaceae clade, Coprinaceae, Strophariaceae, Pleurotaceae, and indeed most major groups of euagarics (Fig. 2). Most lineages containing ectomycorrhizal taxa also contain (and may be derived from) saprotrophic taxa (Malloch 1987). Based on species counts in Hawksworth et al. (1995), we estimate that approximately 4500 described species of homobasidiomycetes form ectomycorrhizae.

Phylogenetic studies (Hibbett et al. 1997b; Bruns et al. 1998; Moncalvo et al. 2000) indicate that there have been repeated transformations between ectomycorrhizal and saprotrophic forms in homobasidiomycetes, but the precise number of gains and losses is not resolved. We inferred the evolution of ectomycorrhizae in the homobasidiomycetes by mapping the distribution of ectomycorrhizae onto the tree from Hibbett et al. (1997b, Fig. 2) using parsimony, under the assumption that gains and losses of ectomycorrhizae are equally likely. The results suggest that there have been seven independent gains of ectomycorrhizae in the homobasidiomycetes, one in each of the eight major clades that we recognize, except the polyporoid clade (Fig. 2). However, this inference is sensitive to rearrangements in weakly supported parts of the tree topology, and might be affected by the addition of more ectomycorrhizal taxa (noteworthy ectomycorrhizal taxa that are missing from Fig. 2 include *Hygrophorus*, *Laccaria*, and *Tricholoma* in the euagarics clade, and *Albatrellus* pro parte in the russuloid clade). Furthermore, the optimization of character states on the tree is sensitive to changes in the relative weight given to gains vs. losses. It is surprising to find that a complex character such as ectomycorrhizae, which involves specialized physiological as well as morphological attributes, could have arisen as many as seven times. In contrast, the fact that some ectomycorrhizal species have apparently retained lignolytic or cellulolytic enzyme systems (Trojanowski et al. 1984; Durrall et al. 1994) suggests that transformations from ectomycorrhizal to saprotrophic habits might be easily reversible. Thus, it may be more appropriate to infer the evolution of ectomycorrhizae using a model that favors losses over gains rather than the "flat-weighted" model used in Fig. 2. To rigorously infer the evolution of ectomycorrhizae, it will be necessary to add more ectomycorrhizal lineages to the tree, resolve weakly supported nodes, and map character states under a range of realistic models.

Orchid associates are found in the euagarics clade (*Armillaria*, *Ceratobasidium*, and *Lentinula*), cantharelloid clade (*Tulasnella*), polypore clade (*Ganoderma*, *Loweporus*, *Microporus*), and hymenochaetoid clade (*Erythromyces* and *Phellinus*) (Currah and Zelmer 1992; Umata 1995, 1998), as well as in the Auriculariales (Umata 1997). However, it is not known whether *Lentinula* and the polypores and hymenochaetoid fungi listed form fully functional orchid mycorrhizae in nature, or only promote orchid seed germination (Umata 1995, 1998).

Early reports of clavarioid fruiting bodies associated with pot cultures of *Vaccinium* (Ericaceae) and of clamped hyphae in ericoid mycorrhizal roots (Seviour et al. 1973) have not, to our knowledge, been substantiated with synthesis of mycorrhizae between Ericaceae and *Clavaria argillacea*, the putative symbiont. With the exception of the study by Seviour et al. (1973), ericoid mycorrhizae appear to be predominantly formed by ascomycetous fungi (Read 1974; Currah et al. 1990).

## 3. Plant Pathogens

The ability to attack living plants has evolved repeatedly in the homobasidiomycetes. This section provides a very brief overview of the phylogenetic distribution of plant pathogens in the homobasidiomycetes (see also Sect. III.F.5, below, on bryophyte parasites). For much more comprehensive lists of plant pathogenic homobasidiomycetes, see Farr et al. (1989).

Plant pathogens occur in at least five of the eight major clades of homobasidiomycetes that we recognize, but (as far as we know) they are absent from the thelephoroid, cantharelloid, and gomphoid-phalloid clades. From a purely economic standpoint, the most important plant pathogens include *Thanatephorus cucumeris*, *Ceratobasidium* spp., and *Athelia rolfsii*, and their anamorphs, which cause damping off and root rot diseases of diverse crops. Phylogenetic placement of these taxa is controversial; some or all may be in the euagarics clade (see Sect. II.C.2). Other economically important pathogens that occur in the euagarics clade include *Typhula* spp. (which cause snow molds of turf and cereal crops), *Marasmius* and *Marasmiellus* spp. (leaf blights of maize), *Crinipellis perniciosa* (witches' broom of cacao), and *Mycena citricolor* (leaf blight of coffee). Similar plant diseases are caused by several corti-

cioid taxa of uncertain placement, including *Erythricium salmonicolor* (pink disease on various fruit trees), and *Laetisaria fuciformis*, *Limonomyces roseipellis*, and *Trechispora alnicola* (various turf diseases; Stalpers and Loerakker 1982; Ginns and Lefebvre 1993).

Ecologically similar timber pathogens have evolved repeatedly in the homobasidiomycetes. Forest pathogens that cause root and butt rots are primarily concentrated in the polyporoid clade (e.g., *Ganoderma*, *Phaeolus*, *Sparassis*), but also occur in the euagarics clade (*Armillaria*, *Coprinus*), russuloid clade (*Bondarzewia*, *Heterobasidion*), and hymenochaetoid clade (*Inonotus*, *Phellinus*). Similarly, pathogens that form cankers and heart rots of forest trees include members of the polyporoid clade (*Fomitopsis*, *Piptoporus*, *Polyporus*, *Postia*), euagarics clade (*Hypsizygus*, *Pholiota*, *Pleurotus*, *Volvariella*), russuloid clade (*Echinodontium*, *Hericium*), and hymenochaetoid clade (*Inonotus*, *Oxyporus*, *Phellinus*).

## 4. Mycoparasites, Bacteriovores, and Nematode-Trappers

Nitrogen is a limiting factor in many of the substrates occupied by homobasidiomycetes, especially wood (Cowling and Merrill 1966; Rayner and Boddy 1988). Consequently, microorganisms such as bacteria, nematodes, and other fungi are potentially important sources of nutrition for homobasidiomycetes. In this section, we discuss cases in which homobasidiomycetes appear to obtain nutrition by attacking and consuming fungi, bacteria, and nematodes.

Much of what is known about mycoparasitism in homobasidiomycetes is based on culture studies. Although it is difficult to extrapolate to natural systems, some interactions in culture seem to correspond well with those in nature. For example, in culture *Lenzites betulina* parasitizes and grows through mycelia of *Trametes versicolor*, just as in nature *L. betulina* frequently colonizes hardwood substrates that are already inhabited by *T. versicolor*, replacing *T. versicolor* in the process (Rayner et al. 1987). In addition, *L. betulina* is apparently not an effective parasite of other common wood-decaying fungi, suggesting that it employs selective parasitism of *T. versicolor* as a resource capture strategy (Rayner et al. 1987). Facultative mycoparasitism of filamentous fungi and yeasts appears to be widespread among primarily saprotrophic species of homobasidiomycetes in the polyporoid, euagarics, and gomphoid-phalloid clades, and is also reported in certain ectomycorrhizal species in the bolete and thelephoroid clades (Griffith and Barnett 1967; Rayner et al. 1987; Zhao and Guo 1989; Jeffries and Young 1994; Owens et al. 1994; Hutchison and Barron 1996; R.G. Thorn, unpubl.).

A few homobasidiomycetes produce fruiting bodies directly on the fruiting bodies of other homobasidiomycetes. Examples are known in the bolete clade (*Boletus parasiticus* fruits on *Scleroderma*; *B. astraeicola* on *Astraeus*), but most occur in the euagarics clade (e.g., *Nyctalis*/*Asterophora* spp. on Russulaceae; *Entoloma parasitica* on *Polyporus*, *Coltricia*, or *Cantharellus*; *Psathyrella epimyces* on *Coprinus* spp.; *Volvariella surrecta* on various Tricholomataceae; *Squamanita* spp. on various agarics; Rayner et al. 1985; Spurr et al. 1985; Jeffries and Young 1994; Redhead et al. 1994). Such forms have generally been interpreted as necrotrophic parasites, which kill and then digest living tissue (Rayner et al. 1985). However, Rayner et al. (1985, p. 10) noted that *B. parasiticus* and *B. astraeicola* do not appear to be parasitic on *Scleroderma* and *Astraeus*, "but simply require the presence of the latter to stimulate fruiting." Another enigmatic interaction involves *Entoloma abortivum*, which forms irregular masses of tissue termed *carpophoroids* when infected by the mycelium of *Armillaria mellea* (Watling 1974). Many host-parasite (or host-necrotroph) relationships involving homobasidiomycetes have a high degree of taxon specificity. For this reason, the association of *B. parasiticus* and *B. astraeicola* with *Scleroderma* and *Astraeus*, respectively, may indicate that *Astraeus*, which has yet to be included in molecular studies, is closely related to *Scleroderma*.

Many species of saprotrophic homobasidiomycetes are capable of lysing bacterial cells in vitro (Barron 1988; Barron and Thorn 1987; Thorn and Tsuneda 1992). In *Agaricus* and other filamentous fungi, this is accomplished by muramidases, which degrade bacterial cell walls (Fermor 1983; Grant et al. 1986). Bacteriolytic ability has been found extensively in the polyporoid and euagarics clades, as well as in the Auriculariales and certain corticioid fungi of uncertain placement (e.g., *Dendrothele*; Thorn and Tsuneda 1992). Because of limited sampling, it is difficult to infer the pattern of evolution of bacteriolytic activity. The available data suggest that it is widespread, as is mycoparasitism, and may therefore be of limited

use for inferring higher-level phylogenetic relationships of homobasidiomycetes.

In contrast to mycoparasitism and bacteriolytic activity, the ability to attack and consume living nematodes has a limited taxonomic distribution among the homobasidiomycetes (nematode-trapping fungi also occur among ascomycetes; Barron 1977, 1988; Thorn and Barron 1984; Liou and Tzean 1992; Thorn and Tsuneda 1992). Species of *Pleurotus* and *Hohenbuehelia* capture and consume nematodes by immobilizing them with a toxin (*Pleurotus*; Barron and Thorn 1987) or adhering to them with adhesive knobs produced on hyphae or germinated spores (*Hohenbuehelia*; Barron and Dierkes 1977; Thorn and Barron 1986). This capability has been used as biological evidence for delimiting both *Pleurotus* and *Hohenbuehelia* (Hibbett and Thorn 1994; Redhead and Ginns 1985; Thorn and Barron 1986). Species of the dark-spored agarics *Conocybe* and *Panaeolina* produce droplets of nematotoxin of similar appearance to those in *Pleurotus*, but the nematodes are not colonized and consumed once immobilized (Hutchison et al. 1996). Toxin droplets in these taxa may serve a primarily defensive function. Droplets of similar appearance are also produced by species of *Psilocybe* (Heim and Wasson 1959), *Schizophyllum* (Parag 1965), *Resupinatus*, and *Stigmatolemma* (Thorn and Barron 1986), but their function in nature is as yet unknown. The taxa mentioned so far are all members of the euagarics clade, but there is no evidence that they form a monophyletic group. Thus, it seems likely that production of toxin droplets with nematode-trapping or antifeedant functions has evolved repeatedly within the euagarics clade. In addition, certain members of the corticioid genus *Hyphoderma* (which is unplaced) capture nematodes by production of specialized adhesive cells called stephanocysts, or by a toxin that apparently kills nematodes that have consumed hyphal cells (Tzean and Liou 1993).

## 5. Lichens, Algal Parasites, and Bryophyte Associates

A variety of fungi have independently formed symbioses with phototrophic green algae, cyanobacteria, and bryophytes (Hale 1983; Ahmadjian 1993; Gargas et al. 1995). Fungi in these associations form a continuum from necrotrophic parasites to mutualistic lichenized forms (Hawksworth 1988). This section discusses the diversity and evolution of symbioses involving homobasidiomycetes with algae and bryophytes.

More than 99% of the 20000 or more known species of lichens are formed by ascomycetes, but a few are formed by homobasidiomycetes (Oberwinkler 1970, 1984; Redhead and Kuyper 1987; Hawksworth et al. 1995). Basidiolichens have arisen at least twice in the euagarics clade, in the agaricoid *Omphalina* and the stereoid *Dictyonema* (Parmasto 1978). The lichenized forms of *Omphalina* are nested in a clade of saprotrophic *Omphalina* species (and other genera), but the precise placement of *Dictyonema* is not resolved with confidence (Gargas et al. 1995; Lutzoni 1997; Lutzoni and Pagel 1997). *Semiomphalina leptoglossoides* is another basidiolichen that is probably in the euagarics clade (Redhead 1984; Redhead and Kuyper 1987), but its phylogenetic relationships have yet to be investigated. In the cantharelloid clade, basidiolichens are formed by the minute clavarioid *Multiclavula*, which appears to be the sister group of an exclusively ectomycorrhizal clade that includes *Cantharellus*, *Hydnum*, and *Clavulina* (Hibbett et al. 1997; Fig. 2). In addition to these, Singer (1973, 1984) has suggested that *Marasmiellus affixus* (presumably euagarics clade) and *Lactarius* (= *Pleurogala*) *igapoensis* (a pleurotoid member of the russuloid clade; Redhead and Norvell 1993) are basidiolichens. However, Singer's conclusions were based only on the cooccurrence of the fungi and algae, not a rigorous demonstration of hyphal connections. Although the lichenized status of *M. affixus* and *L. igapoensis* is questionable, it is clear that there have been multiple derivations of lichenized forms in the homobasidiomycetes. Anatomical differences among fungus-alga interactions of basidiolichens support the view that they are polyphyletic (Oberwinkler 1984).

Lichen symbioses involve formation of a stable dual-organism thallus, but a range of less stable or morphologically differentiated associations is also possible (Hawksworth 1988; Hutchison and Barron 1997). Microscopic observations of complex substrates such as well-rotted wood frequently reveal clamped hyphae in close contact with or coiling around cells of green algae (Thorn and Barron 1986). For example, Oberwinkler (1970) has described parasitism of unicellular green algae by the corticioid fungi *Athelia epiphylla*, *Resinicium bicolor*, and *Sistotrema*

*brinkmanii* (the latter in culture). Recently, Hutchison and Barron (1997) found that 37 species of homobasidiomycetes (out of 74 species tested) were capable of attacking and parasitizing cells of the green alga *Protococcus* or the cyanobacterium *Synechococcus* in pure culture. Directional growth of hyphae toward algal or cyanobacterial colonies was followed by coralloid branching within the colonies, followed by cell death, lysis, and absorption of the cell contents by the invading fungi (Hutchison and Barron 1997). This pattern is similar to that seen in the attack of bacteria and yeasts by homobasidiomycetes (Barron 1988; Hutchison and Barron 1996). All of the species that attacked the algae or cyanobacteria were saprotrophs in the euagarics clade (e.g., *Crucibulum*, *Langermannia*, and *Typhula*), polyporoid clade (*Bjerkandera* and *Lenzites*), and russuloid clade (*Stereum*; the study did not include representatives of the thelephoroid, cantharelloid, or gomphoid-phalloid clades). Despite limited sampling, the observations cited above suggest that the ability to parasitize algae and cyanobacteria is widespread among saprotrophic homobasidiomycetes.

Homobasidiomycetes are often found growing among living bryophytes (Gulden et al. 1985; Gulden and Jenssen 1988; Redhead 1980, 1981, 1984). In some cases, necrotic zones have been described in the areas immediately adjacent to the fungi, but often the bryophytes have been described as healthy. Based on in vitro coculturing experiments with the moss *Sphagnum capillaceum*, Redhead (1981) demonstrated that *Lyophyllum* (*Tephrocybe*) *palustre* is capable of necrotrophic parasitism, which ultimately kills the host (Untiedt and Müller 1985), whereas *Galerina paludosa* forms a "balanced" parasitism, in which the moss is not killed. In addition to symbionts of mosses, homobasidiomycetes include symbionts of thallose liverworts, including *Rickenella pseudogrisella*, which is a symbiont of *Blasia*, and "*Gerronema*" *marchantiae*, which is a symbiont of *Marchantia* (Redhead 1980, 1981; Senn-Irlet et al. 1990). In cases of balanced parasitism of bryophytes, homobasidiomycetes form haustoria or appressoria on the rhizoids of the bryophytes (Redhead 1980, 1981). Redhead (1981) noted that the appressoria and haustoria formed by bryophyte parasites are similar to structures formed by homobasidiomycetous algal parasites and lichens, which suggests that they may be homologous. Based on the results of Moncalvo et al. (2000), *Rickenella, Lyophyllum*, and *Galerina* are in three separate lineages in the euagarics clade, which implies that bryophyte symbiosis has evolved repeatedly in the homobasidiomycetes.

## 6. Insect Symbionts

Homobasidiomycetes form ecological associations with diverse insects that feed on hyphae, spores, and fruiting bodies, or that colonize decayed wood (Batra 1979; Wheeler and Blackwell 1984; Wilding et al. 1989). In addition, there is a limited number of insect-homobasidiomycete symbioses, in which the life cycles of the fungi and insects appear to be tightly linked. The homobasidiomycetes in these symbioses make up a polyphyletic group of saprotrophs, each of which is closely related to (or perhaps conspecific with) free-living forms. Many have been successfully cultured, and some are probably able to complete their life cycles in the absence of the insect. As in the fungi, the insects involved are polyphyletic and are closely related to free-living forms. However, judged by their constant occurrence with fungi in nature, the insects appear to be obligate symbionts. In this section, we survey the phylogenetic distribution of homobasidiomycetes involved in symbioses with insects, which include (1) woodwasp symbionts, (2) bark and ambrosia beetle symbionts, (3) attine ant symbionts, and (4) termite symbionts.

Female woodwasps (Siricidae) have intersegmental pouches (mycetangia) that contain oidia or hyphal fragments of wood-rotting fungi, which are inoculated into trees at the time of oviposition (Stillwell 1966; Madden and Coutts 1979; Gilbertson 1984; Tabata and Abe 1995). Larvae feed on the mycelium that is produced by the oidia, and female larvae develop mycetangia, which house fungal inoculum for the next generation. Fungi involved in this symbiosis include species of *Amylostereum*, which are resupinate fungi that are associated with the wasp genera *Sirex* and *Urocerus*, and *Cerrena unicolor*, which is a polypore that is associated with the wasp *Tremex* (Gilbertson 1984; Tabata and Abe 1995). *Amylostereum* is in the russuloid clade (Table 1), but *Cerrena* is of uncertain placement. Ryvarden (1991) suggested that *Cerrena* is related to *Trametes*, which is in the polyporoid clade. If this is correct, then there must have been at least one switch of the fungal partner during the evolution

of the siricid-homobasidiomycete symbiosis. According to Stillwell (1966) and King (1966), *Amylostereum* fruiting bodies are apparently absent in certain areas where the siricid-fungus association is common (i.e., the fungus is found only as mycelium in association with wasps). Citing these observations, Gilbertson (1984, p. 144) suggested the possibility that *Amylostereum* species associated with wood wasps have become completely dependent on the insect for dissemination".

Bark and ambrosia beetles (Scolytidae and Platypodidae) inhabit dead tree trunks, where they form galleries in either phloem (bark beetles) or xylem (ambrosia beetles; Beaver 1989). The different taxa of beetles vary in the degree to which they feed on fungal tissue vs. wood, and in the anatomical locations of the mycangia by which they transmit fungi (Beaver 1989). Many homobasidiomycetes are found growing on trees colonized by bark and ambrosia beetles, and the work of Castello et al. (1976), among others, indicates that bark beetles can be effective vectors of wood-rotting homobasidiomycetes, such as *Cryptoporus volvatus* and *Fomitopsis pinicola* (polyporoid clade). However, only a few homobasidiomycetes have been directly isolated from beetle mycangia or galleries (most bark beetle symbionts are ascomycetes). One of these is the unusual corticioid fungus, *Entomocorticium dendroctoni*, which is apparently limited to the galleries of the bark beetle *Dendroctonus ponderosae* (Whitney et al. 1987). Whitney et al. (1987) suggested that the fungus is distributed exclusively by the insect, which seems plausible considering that its fruiting bodies are produced inside the galleries. Furthermore, the spores of *Entomocorticium* are symmetrically positioned over broad sterigmata, with no evidence of a hilar appendix, indicating that *Entomocorticium* is no longer ballistosporic.

Other unnamed bark-beetle symbionts have been recovered from mycangia of *Dendroctonus frontalis* (known only as SJB 122; Happ et al. 1976) and *D. brevicomis* (Whitney and Cobb 1972). Although no fruiting body is known, the presence of perforate parenthesomes strongly suggests that SJB 122 is a homobasidiomycete (Happ et al. 1976). Based on cultural studies, Whitney et al. (1987) concluded that SJB 122 and the fungus from *D. brevicomis* are similar, but that *E. dendroctoni* is a separate taxon.

Recent molecular and cultural studies of the fungal symbionts of Scolytidae suggest that there have been at least four independent origins of bark beetle symbionts in the homobasidiomycetes (Hsiau 1996). *Entomocorticium dendroctoni* and eight other unnamed taxa (including symbionts of *D. brevicomis*, *D. frontalis*, and other beetle species) form a monophyletic group that is nested in *Peniophora*, which is in the russuloid clade. The close relationship between these taxa is also supported by the presence of similar incrusted cystidia in *Peniophora* and *Entomocorticium*. Two other unnamed *Dendroctonus* symbionts are very closely related to the corticioid fungus *Phlebiopsis gigantea* (mt-ssu rDNA sequences of the beetle symbionts differ from that of *Phlebiopsis* by only three single base indels). In Hsiau's analysis, the sister group of the beetle symbiont-*Phlebiopsis* clade is *Pulcherricium*, suggesting that this group is in the polyporoid clade (also see Boidin et al. 1998). The fungal symbiont of the beetle *Xyleborus dispar* appears to be closely related to the brown rot polypores *Antrodia carbonica* and *Meripilus giganteus*, which are also in the polyporoid clade. The *X. dispar* associate is the only bark beetle symbiont that has a negative reaction on gallic and tannic acid agar, which supports the molecular phylogeny. Finally, *Gloeocystidium ipidophilum*, which is associated with the beetle *Ips typographus*, appears to be in the euagarics clade, which was represented in Hsiau's analysis by *Lentinula* and *Pleurotus*.

Attine leafcutter ants (Formicidae, Attini) of the Neotropics cultivate homobasidiomycetes on plant material inside large subterranean nests (Weber 1979; Cherrett et al. 1989). Occasional fruiting bodies produced on ant-fungus nests (e.g., Fisher et al. 1994) have indicated that some of the fungi involved in the symbiosis are members of the Agaricaceae sensu Singer (1986; euagarics clade). Recent molecular studies by Chapela et al. (1994) have shown that the attine ant fungi are composed of three groups: (1) The G1 group is nested in the Agaricaceae and is characterized by the production of modified hyphal tips termed gongylidia that are consumed by the ants. (2) The G2 group is a paraphyletic assemblage that is also nested in the Agaricaceae, and from which the G1 group was derived. Some ant symbionts in G2 are more closely related to free-living Agaricaceae (*Leucoagaricus*, *Leucocoprinus*) than they are to other ant symbionts. (3) The G3 group is unique among attine symbionts in being closely related to white-spored agarics in the Tricholomataceae (repre-

sented in their study by *Marasmius* and *Crinipellis*). The results of Chapela et al. (1994) indicate that there has been repeated acquisition of symbionts from free-living fungi in the Agaricaceae and Tricholomataceae.

Finally, termites (Macrotermitinae) of the Paleotropics exist in symbioses with the homobasidiomycete *Termitomyces* that in many ways parallel the association of attine ants and their fungi in the Neotropics (Batra and Batra 1979; Wood and Thomas 1989). Termite nests are large subterranean structures or mounds that include combs made up primarily of termite feces, on which *Termitomyces* produces "spherules" of conidiogenous hyphae that are eaten by the termites (Batra and Batra 1979; Wood and Thomas 1989). *Termitomyces* fruiting bodies are commonly produced on termite nests, and the elongate pseudorhizas can be traced to the combs. According to Singer (1986), there are about 13 species of *Termitomyces*, all of which are termite symbionts. Singer placed *Termitomyces* in the Termitomyceteae of the Tricholomataceae, along with *Podabrella*, which is found on dead organic matter, or occasionally on termite nests. Singer (1986) suggested that the Termitomyceteae is closely related to the Lyophylleae (*Lyophyllum*, etc.) based on their shared possession of siderophilous granules (which turn violet-black in acetocarmine) in the mature basidia. Recent molecular studies by Moncalvo et al. (2000) suggest that *Podabrella* is the sister group of *Termitomyces*, and that they are nested within *Lyophyllum*.

Summarizing the preceding discussion, insect symbionts have evolved repeatedly in the homobasidiomycetes, and occur in the euagarics clade (attine symbionts in Agaricaceae and Tricholomataceae, *Termitomyces*, *Gloeocystidium ipidophilum*), russuloid clade (*Amylostereum*, *Entomocorticium*), and polyporoid clade (*Cerrena*, *Xyleborus* symbionts, *Dendroctonus* symbionts). Each of these symbioses appears to be uniquely derived. Nevertheless, there are striking similarities between some systems: Symbioses with ants and termites occur in the tropics and involve cultivation of saprotrophic agarics inside massive communal nests, with fungal cells specialized for feeding insects. Symbioses with woodwasps and bark/ambrosia beetles occur primarily in temperate forests and involve insect-vectored transmission of wood-decaying corticioid fungi and polypores as oidia or mycelial fragments in mycangia, perhaps coupled with a loss of spore dispersal ability by the fungus (loss of ballistospory or fruiting body production).

## IV. Conclusions

In recent years there has been rapid progress in homobasidiomycete phylogenetics, which has been brought about largely through the analysis of molecular characters (Table 1). Molecular studies have supported many morphology-based taxonomic hypotheses, such as the placement of *Rhizopogon* in the Boletales (Bruns et al. 1989), or *Lentinus* sensu stricto among the polypores (Hibbett and Vilgalys 1993). Other hypotheses have been refuted, however, such as the inclusion of *Omphalotus* and *Lampteromyces* in the Boletales (Binder et al. 1997; Moncalvo et al. 2000). In addition to resolving preexisting controversies, molecular studies have also provided novel insights, such as the realization that the Gomphaceae and Phallales are closely related (Colgan et al. 1997; Hibbett et al. 1997b), or that bark beetle associates have evolved four times in the homobasidiomycetes (Hsiau 1996). Most importantly, molecular characters derived from universal genes such as rDNA provide comparative data that will eventually form the basis of a phylogenetic classification for all homobasidiomycetes, including asexual forms.

Summarizing current research, we have divided the homobasidiomycetes into eight mutually exclusive clades. Not all clades are equally well supported, however, and there is considerable danger in extrapolating from exemplar-based phylogenetic studies to a classification for over 13000 described species. Much more work will be needed to attain a comprehensive phylogenetic classification of the homobasidiomycetes. Specific challenges that remain include evaluating the monophyly, higher-order relationships, and internal structure of the eight major clades that we recognize, identifying the root and sister group of the homobasidiomycetes, and resolving relationships of certain controversial taxa, such as *Thanatephorus*. Molecular data will be essential for resolving homobasidiomycete phylogeny, but there are also numerous potentially informative morphological characters, many of which have never been included in phylogenetic analyses. We have highlighted selected characters that appear to be phylogenetically informative or ecologically significant.

However, many of our conclusions about character evolution are speculative, and we have often been limited by the number of published observations. We hope that the work presented here will provide a phylogenetic framework for studies of many non-molecular attributes of homobasidiomycetes, such as cytology and ultrastructure, developmental morphology, and mechanisms of symbiosis.

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