

## Generic delimitation of the fungicolous *Hypocreaceae*

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**Abstract:** The fungicolous species of the *Hypocreaceae* are distributed among six genera. *Hypocrea* and *Hypomyces* are distinguished by several unique teleomorph and anamorph characters. *Arachnocrea*, *Protocrea* and *Sphaerostilbella* share combinations of characters found in *Hypocrea* and *Hypomyces*. The phylogenetic relationships of species of these genera are assessed by analyses of large subunit rDNA sequences. Informal groups are outlined in *Hypomyces*, as well as ideas on developing more reliable generic concepts for this complex.

**Key words:** *Hypocrea*, *Hypomyces*, *Arachnocrea*, *Protocrea*, *Sphaerostilbella*, 28S rDNA, phylogeny

### Introduction

The ascomycete order *Hypocreales* encompasses the highest number of fungicolous ascomycete species. While many members of the *Bionectriaceae* and *Nectriaceae* are mycoparasitic or mycosaprobic, most species that grow on fruit-bodies of other fungi belong to the *Hypocreaceae* (Rossman *et al.*, 1999). Traditionally, species with light or brightly-coloured perithecia produced in a subiculum and growing on carposomata of fungi have been described in *Hypomyces* (Fr.) Tul. The first segregates at the generic level were *Apiocrea* Syd. & P. Syd. and *Peckiella* (Sacc.) Sacc., both distinguished solely by ascospore septation. Later, a few species were transferred to *Sphaerostilbella* (Henn.) Sacc. & D. Sacc., *Arachnocrea* Z. Moravec and *Protocrea* Petch, which were erected for deviating members of *Hypocrea* or *Hypomyces*. While these genera (except for *Protocrea*) comprise exclusively fungicolous species, *Hypocrea* Fr. and *Hypocreopsis* P. Karst. contain, in addition to their lignicolous members, species that are frequently or exclusively found on fruit-bodies of other fungi (Table 1). These, however, are of secondary concern in this paper.

The complex of fungicolous fungi considered here is a good illustration of problems encountered in understanding the taxonomy of a group of species with different life cycle patterns. The majority of these species are pleomorphic, having both teleomorph and anamorph, the latter often comprising

two distinct forms (= synanamorphs) in species of *Hypomyces*. Fewer than ten species of *Hypomyces* lack a known anamorph, but the number of species lacking a known teleomorph is much larger, though more difficult to estimate (Table 1). The anamorph genera *Cladobotryum* Nees, *Mycogone* Link, *Sepedonium* Link and *Stephanoma* Wallr. have not been linked to teleomorphs other than *Hypomyces*. The other known anamorphs of the fungicolous *Hypocreaceae* considered have been placed in the species-rich genera *Acremonium* Link, *Gliocladium* Corda and *Verticillium* Nees, suggesting that more asexual fungi may belong to this complex than is presently known.

The first detailed taxonomic treatment of these fungicolous fungi was presented by Arnold (1971a). He distinguished the genera *Arachnocrea*, *Hypomyces*, *Apiocrea* and *Peckiella* and introduced an intricate infrageneric classification for *Hypomyces*. For the accompanying anamorphs, he recognized several anamorph genera and described new ones for the anamorphs of *Hypomyces* species growing on aphyllaphores (Arnold, 1969, 1970). Rogerson & Samuels (1985, 1989, 1993, 1994), in contrast, adopted broader generic concepts for *Hypomyces* and the anamorph genera involved. They recognized *Apiocrea* and *Peckiella* as synonyms of *Hypomyces*, within which they distinguished four informal groups based on host range and anamorphs. They merged most of the anamorphs of *Hypomyces* species that

occur on aphyllaphores into *Cladobotryum*. These monographic treatments deal only with the sexually-reproducing members of *Hypomyces*, and the descriptions of asexually reproducing species are scattered in numerous papers (e.g. recently Helfer 1991; Pöldmaa, 1998; Pöldmaa & Samuels, 1999; Sahr *et al.*, 1999, for *Sphaerostilbella* Seifert, 1985). A few species that share characters of *Hypocrea* and *Hypomyces* have been transferred between these genera but are currently mostly accepted in *Arachnocrea* and *Protocrea* (Doi, 1972; Moravec, 1956; Rossman *et al.*, 1999).

The results of molecular analyses (Rehner & Samuels 1994, 1995; Spatafora & Blackwell 1993, 1994; Pöldmaa *et al.*, 1999) suggest that *Hypocrea* and the fungicolous species of the *Hypocreaceae* form a monophyletic group. While in the well-supported *Hypocrea/Trichoderma* clade the main problem is species delimitation, the low support for the clades of fungicolous fungi presents a challenge to generic delimitation. This situation is paralleled in morphology, where in contrast to the supposedly lignicolous species of *Hypocrea*, with mainly *Trichoderma* anamorphs, the fungicolous species encompass a broader range of morphological variation, especially in the anamorphs. To establish phylogeny-based generic concepts in this complex, more detailed studies are underway (Pöldmaa, 1998; Pöldmaa *et al.*, 1999). These indicate that different types of characters, i.e. the morphology of teleomorphs and anamorphs, the taxonomy of hosts, and molecular data, often provide contradictory signals for generic delimitation, as is discussed below.

## Teleomorph characters

The main morphological characters traditionally used in delimitation of teleomorph genera in the fungicolous *Hypocreaceae* are the presence and characteristics of a subiculum or stroma, presence or absence of an apical thickening at the top of asci, septation and disarticulation of ascospores, and the presence or absence of apiculi at the ends of ascospores. There is a trend for species producing a stroma to form nonapiculate ascospores that disarticulate inside asci (*Hypocrea*) while species with a subiculum are characterized by intact apiculate ascospores (*Hypomyces*). However, there are several exceptions (Fig. 1). In *Arachnocrea*, the *Hc.*<sup>1</sup> *pallida*-complex, *Protocrea* and *Sphaerostilbella* species, perithecia are produced in a subiculum. In *Arachnocrea* species, the ascospores bear minute apiculi and disarticulate. In *Protocrea*

species and the *Hc. pallida*-complex, they are non-apiculate and disarticulating and in *Sphaerostilbella* species, the non-apiculate ascospores remain intact. In a few species of *Hypomyces*, the ascospores lack apiculi and may disarticulate after being discharged from the asci.

Indistinct forms in several characters and the resulting difficulties in distinguishing homologies complicate generic delimitation. For example, there are different patterns of formation and texture of the hyphal byssus (i.e. the subiculum) below the perithecia. In addition to species with typical stromata, in some species, e.g. *Hc. pallida*, the walls of perithecia embedded in the hyphal mat is surrounded by a stromatal layer. A clear distinction has been recognized between the hyphal vs. pseudoparenchymatous *textura* of the perithecial wall (Rogerson & Samuels, 1993), considered in segregating the new genus *Sporophagomyces* K. Pöldmaa & Samuels from *Hypomyces* (Pöldmaa *et al.*, 1999). The importance of the presence and location of the septum in ascospores, used for segregating *Apiocrea* and *Peckiella* from *Hypomyces*, has been overestimated (Pöldmaa *et al.*, 1997; Rogerson & Samuels, 1989; Sahr *et al.*, 1999). On the other hand, the irregular shape of ascospores and the not strictly median location of the septum are characteristic of species of *Sphaerostilbella*.

## Anamorph characters and genera

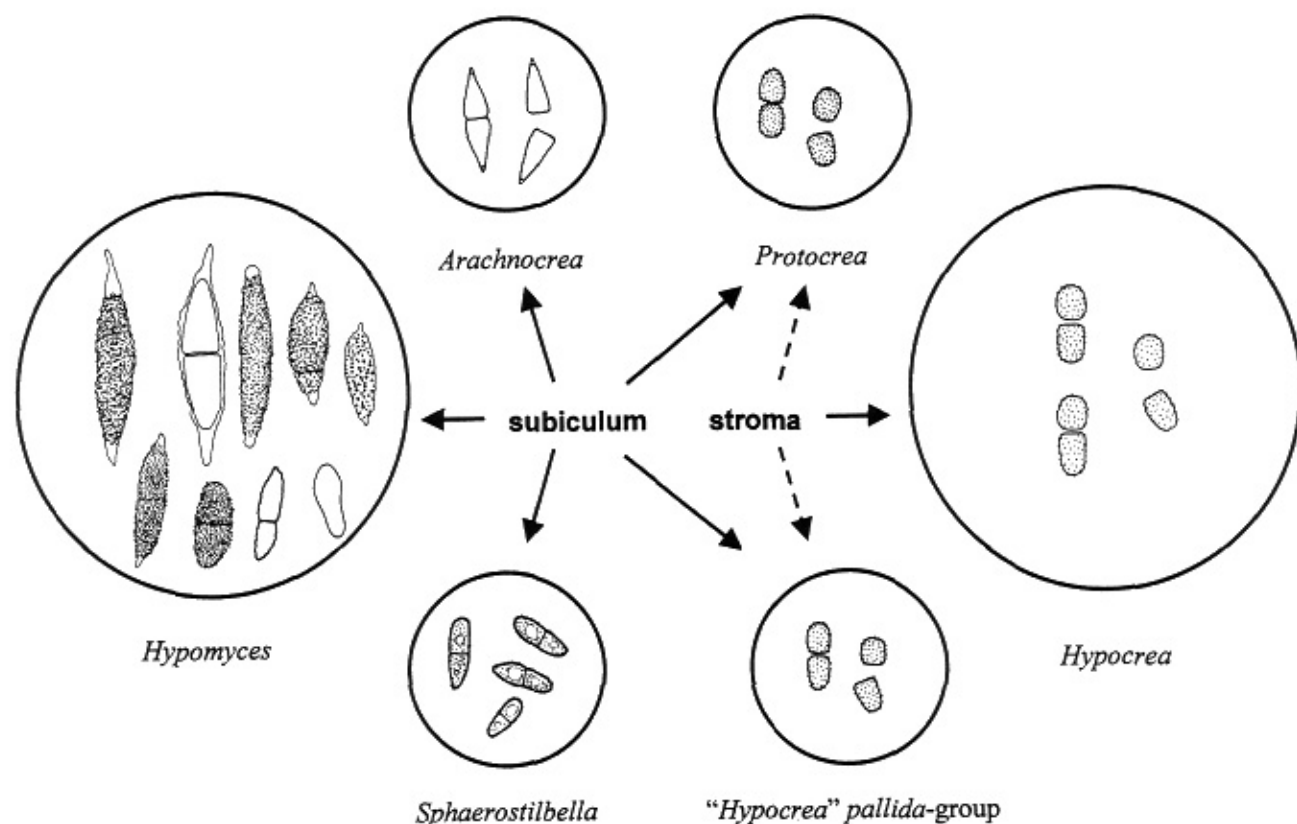
In most anamorphs of the *Hypocreaceae* as well as in the *Hypocreales*, conidia are formed from a single fixed locus at the apex of a phialide. Thick-walled resting spores, if present, are relatively small. Most species of *Hypomyces*, on the other hand, produce conspicuous thick-walled spores that are accompanied by various conidial synanamorphs. Generally, species with dehiscent thick-walled resting spores (aleuriocidia) also form conidia from phialides in drops of clear liquid. In contrast, species with nondehiscent thick-walled resting spores (chlamydospores) produce conidia that are held singly or in dry chains on one or multiple conidiogenous loci. In the following, I shall discuss the anamorphic genera recognized within these main types.

Approximately 25 *Hypomyces* species and 25 related species lacking known teleomorphs are characterized by septate conidia, held singly or in dry, mostly imbricate chains at a locus on the conidiogenous cell, which often proliferates, either retrogressively or sympodially. The majority of these species produce comparatively large chlamydospores in a terminal position on lateral branches of vegetative hyphae or in sclerotium-like aggregations. Most of these features are uncommon in the *Hypocreales* (Samuels & Seifert,

<sup>1</sup> Abbreviations: *Hc.* = *Hypocrea*, *H.* = *Hypomyces*

**Table 1.** Numbers of fungicolous species in different genera of *Hypocreaceae*, their anamorphs and hosts.

Genus	Sexually reproducing species	Asexually reproducing species	Anamorphs	Hosts
<i>Hypomyces</i>	55	25	<i>Cladobotryum</i> , <i>Mycogone</i> , <i>Sepedonium</i> , <i>Stephanoma</i> , acremonium-, papulaspora-, verticillium-like	Ascomycetes ( <i>Leotiales</i> , <i>Pezizales</i> ), Homobasidiomycetes ( <i>Agaricales</i> , <i>Russulales</i> , <i>Boletales</i> , aphylllophores)
<i>Sphaerostilbella</i>	4	2	<i>Gliocladium</i>	aphylllophores
<i>Arachnocrea</i>	2	–	verticillium-like	aphylllophores
<i>Protocrea</i>	1	–	acremonium-like	aphylllophores
<i>Hypocreopsis</i>	1	–	<i>Stromatocrea</i>	aphylllophores
<i>Hypocrea</i>	5–10	–	acremonium-, verticillium-like	aphylllophores, <i>Marasmius</i> spp. ( <i>Agaricales</i> ), <i>Cyathus</i> spp. ( <i>Nidulariales</i> ), <i>Exidia</i> spp. ( <i>Ustilaginales</i> )
" <i>Hypocrea</i> " <i>pallida</i> complex	3	–	<i>Gliocladium</i>	aphylllophores

**Fig. 1.** The distribution of teleomorph characters among the genera of fungicolous *Hypocreaceae* [after Doi (1972); Rogerson & Samuels (1985, 1989, 1994); Moravec (1956); Seifert (1985)].

1987). Nevertheless, differences in conidiogenesis resulted in the description of several anamorph genera for different ontogenetic patterns. De-emphasizing differences in conidiogenesis, all the proven dry-conidial anamorphs of *Hypomyces* species that were previously classified in *Arnoldiomyces* Morgan-Jones, *Eurasina* G. Arnold, *Helminthophora* Bonord., *Pseudohansfordia* G. Arnold, *Sibirina* G. Arnold, *Sympodiophora* G. Arnold and *Trichothecium* Link (*pro parte*) were recently merged in *Cladobotryum* (Rogerson & Samuels, 1993).

Most of the other anamorphs of *Hypomyces* species are characterized by unique aleuriosporic anamorphs. Species with one-celled aleurioconidia (*Sepedonium*) also produce conidia from a single fixed locus at the top of the phialide, with the successively formed conidia left in a drop of liquid. These conidial synanamorphs have been described as *Verticillium* sp. Phialidic synanamorphs with solitary conidia ('*Sibirina*' spp.) have been described for four species with multicelled aleurioconidia (*Mycogone*, *Stephanoma*, papulaspora-like; Rogerson & Samuels, 1985). However, I have observed *H. cervinigenus* and *H. stephanomatis* forming more than one conidium from a conidiogenous locus, which is also the case in the anamorphic *M. calospora* and *M. rosea* Link.

Anamorphs of the remaining fungicolous members of the *Hypocreaceae* produce wet conidia from determinate conidiogenous cells and lack conspicuous thick-walled resting spores. These anamorphs are classified in three admittedly artificial genera, *Acremonium*, *Gliocladium* and *Verticillium*, which are distinguished primarily by the arrangement of their conidiophores, i.e. simple, penicillate or verticillate. Although common in the *Hypocreales*, such anamorphs occur only in a few *Hypomyces* species, the taxonomy of which has been the most problematic. Among these, *H. broomeanus* Tul. is the only one with a gliocladium-like anamorph. *Gliocladium* s. str., however, characterizes the genus *Sphaerostilbella* (Rehner & Samuels, 1994; Schroers *et al.*, 1999, this volume). Verticillium-like anamorphs have been described for *H. tremellicola* and two similar *Hypomyces* species (Gams & van Zaayen, 1982; Rogerson & Samuels, 1994), *Arachnocrea stipata* (Pöldmaa, 1999) and *Hypocrea avellanea* Rogerson & S. T. Carey (Carey & Rogerson, 1976). In addition, several anamorphic *Verticillium* species grow on fruit-bodies of fungi (Gams, 1971; Gams & van Zaayen, 1982). An associated acremonium-like anamorph has been reported for *H. lateritius* (Arnold, 1971b; Tulasne & Tulasne, 1865). Acremonium-like anamorphs are also produced by *H. chrysostomus* and the fungicolous species *Hc. pulvinata* Fuckel and its allies. For *Protocrea* species, both acremonium- and

verticillium-like anamorphs have been reported (Doi, 1972).

## The host interface

Most of the fungicolous species of the *Hypocreaceae* grow on the usually perennial basidiomata of polypores and other aphylliphorous basidiomycetes (Table 1). In addition to the fungicolous habit, the acremonium- or verticillium-like or *Gliocladium* anamorphs distinguish *Arachnocrea* species, *Protocrea* species, *Hc. pallida* and *Hc. pulvinata* and their allies from typical members of *Hypocrea* with *Trichoderma* anamorphs. Besides these aphylliphoricolous species, *Hc. avellanea* has been found only on basidiomata of *Marasmius subnudus* (Ellis) Peck (*Agaricales*), *Hc. latizonata* Peck only on *Cyathus* spp. (*Nidulariales*) and *Hc. sulphurea* only on species of *Exidia* s. l. (*Ustilaginales*; B. Overton, pers. comm.).

While aphylliphores serve as hosts for the highest number of *Hypomyces* species, the hosts of other species are from various groups of asco- and basidiomycetes. In recent treatments of *Hypomyces* by Rogerson & Samuels (1985, 1989, 1993, 1994), host taxonomy in combination with anamorph type has been used for distinguishing four major groups. According to these authors, the species occurring on discomycetes (*Leotiales*, *Pezizales*) are characterized by *Mycogone*, *Stephanoma* or papulaspora-like and those on boletes by *Sepedonium* aleuriosporic anamorphs. While the majority of agaricolous species reportedly lack anamorphs, *Cladobotryum* anamorphs were described for some species and for most species growing on polypores. However, species with *Cladobotryum* anamorphs occur on members of various families across the homobasidiomycetes, including the *Russulales* and *Agaricales* but excluding the *Boletales*. Among the species lacking known anamorphs, the majority grow on members of the *Russulales*, including the type of *Hypomyces*, *H. lactifluorum* (Schw.) Tul., or on members of the *Agaricales* (*Amanita* spp., *Leptonia* spp.). A few species with verticillium-like anamorphs occur mostly on brown-spored members of the *Agaricales*.

The species of *Hypomyces* differ according to the mode of nutrition. A number of species that grow on representatives of the *Russulales* and other agaricoid basidiomycetes, are obligate parasites that have only been found causing systemic infections on their hosts. The species on discomycetes and boletes also occur only on their hosts but do not make the whole fruit-body of the host firm as happens with agarics. The *Hypomyces* species on aphylliphorous basidiomycetes can be considered facultative saprotrophs because many



also grow on decaying logs and litter. Host specificity appears to be more developed among obligate parasites, which attack only a few host species or genera.

### Molecular data

A few species of the *Hypocreaceae* were included in phylogenetic analyses of unitunicate perithecial ascomycetes based on the small subunit rDNA sequences (Spatafora & Blackwell, 1993, 1994). The ITS regions have been used for distinguishing between two *Hypomyces* species causing cobweb disease of the cultivated mushroom, *Agaricus bisporus* (J. Lange) Imbach (McKay *et al.*, 1999) and in delimiting species growing on members of the *Boletales* (Sahr *et al.*, 1999). However, when a broader range of fungicolous *Hypocreaceae* is considered, ITS sequences are highly heterogeneous, comprising several regions that cannot be unambiguously aligned (data unpublished). Considerations of phylogenetic relationships in this complex are based mainly on analyses of large subunit rDNA sequences (Pöldmaa *et al.*, 1999; Rehner & Samuels 1994, 1995).

For the current study, parsimony analyses of ca 1360 bp from the 5' end of the LSU rDNA were undertaken. The methods followed those of Pöldmaa *et al.* (1999). In addition to 29 sequences used in that study, eight new sequences were added (Table 2). The alignment was improved by applying a model of the secondary structure of the large subunit rRNA (Gutell *et al.*, 1993). The analyses involved 97 parsimony-informative characters, excluding 20 bp from variable regions that could not be unambiguously aligned. Two species of *Verticimonosporium* Matsush., which formed a sister group to the *Hypocreaceae* in an analysis of a larger set of different hypocrealean taxa (not shown), were used as the outgroup. The parsimony analysis, performed using PAUP 4.0b2a (Swofford, 1999), gave four most parsimonious trees (Fig. 2) and three trees of best fit (Fig. 3) when the Goloboff fit criterion ( $K = 2$ ) was applied. The latter method implies estimating character reliabilities and giving less weight to homoplasious characters during the analysis (Goloboff, 1993). The main clades mostly concur with those in the four most parsimonious trees but their relationships to each other are different.

The results of analyses from different studies suggest that *Arachnocrea*, *Aphysiostroma* Barrasa *et al.*, *Hypocrea*, *Hypomyces* and *Sphaerostilbella* form a monophyletic group. The delimitation of all these genera, except for *Hypomyces*, is supported by the LSU rDNA data. In the most parsimonious trees obtained in this study, all species with stromata and disarticulating ascospores, except for *Hc. pallida*, occur in one clade

that also includes *H. chrysostomus*. In the latter species, I have observed disarticulation of the nonapiculate ascospores after discharge. The sister group to this clade comprises *Sphaerostilbella* species and *H. broomeanus*, which have *Gliocladium* s. str. anamorphs (Fig. 3). The most tricky members of this complex, *Hc. pallida* and its allies with *Gliocladium* s. str. anamorphs, could be considered members of *Sphaerostilbella* on morphological grounds. However, in analyses of molecular data all alternative placements of *Hc. pallida* in the *Hypocreaceae* did not receive considerable support (Pöldmaa *et al.*, 1999) and there is no straightforward solution to the taxonomic placement of these species.

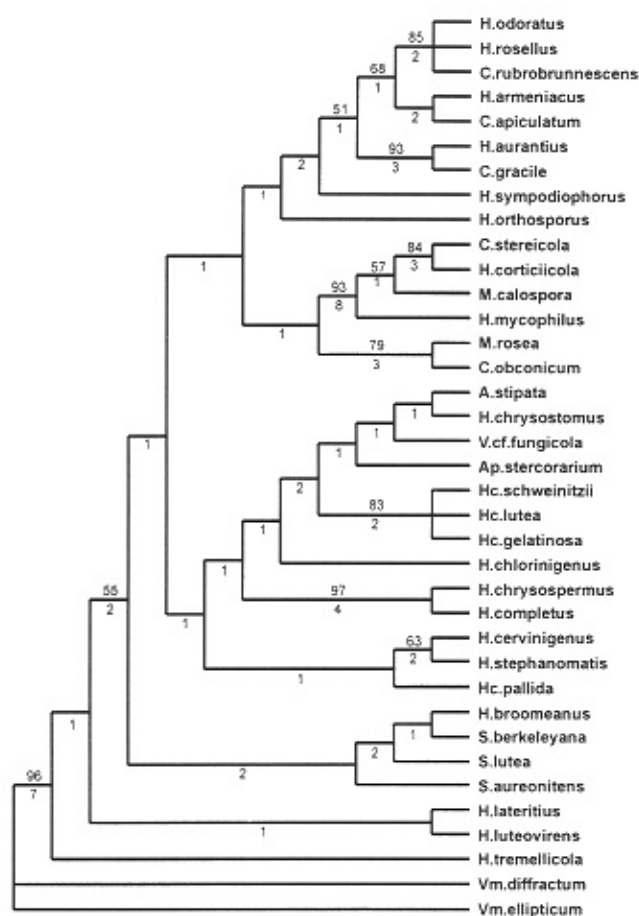


Fig. 2. The strict consensus tree of the four most parsimonious trees. Tree length = 426, CI = 0.38, HI = 0.62. Bootstrap values and decay indices are indicated above and below the branches, respectively.

The species with intact, apiculate ascospores, i.e. *Hypomyces*, fall into several clades that partially coincide with the host-based groups delineated by Rogerson and Samuels. *Hypomyces cervinigenus* and *H. stephanomatis*, which grow on members of the *Pezizales* and produce two- (*Mycogone*) or multicelled (*Stephanoma*) aleurioconidia, respectively, are closely related to each

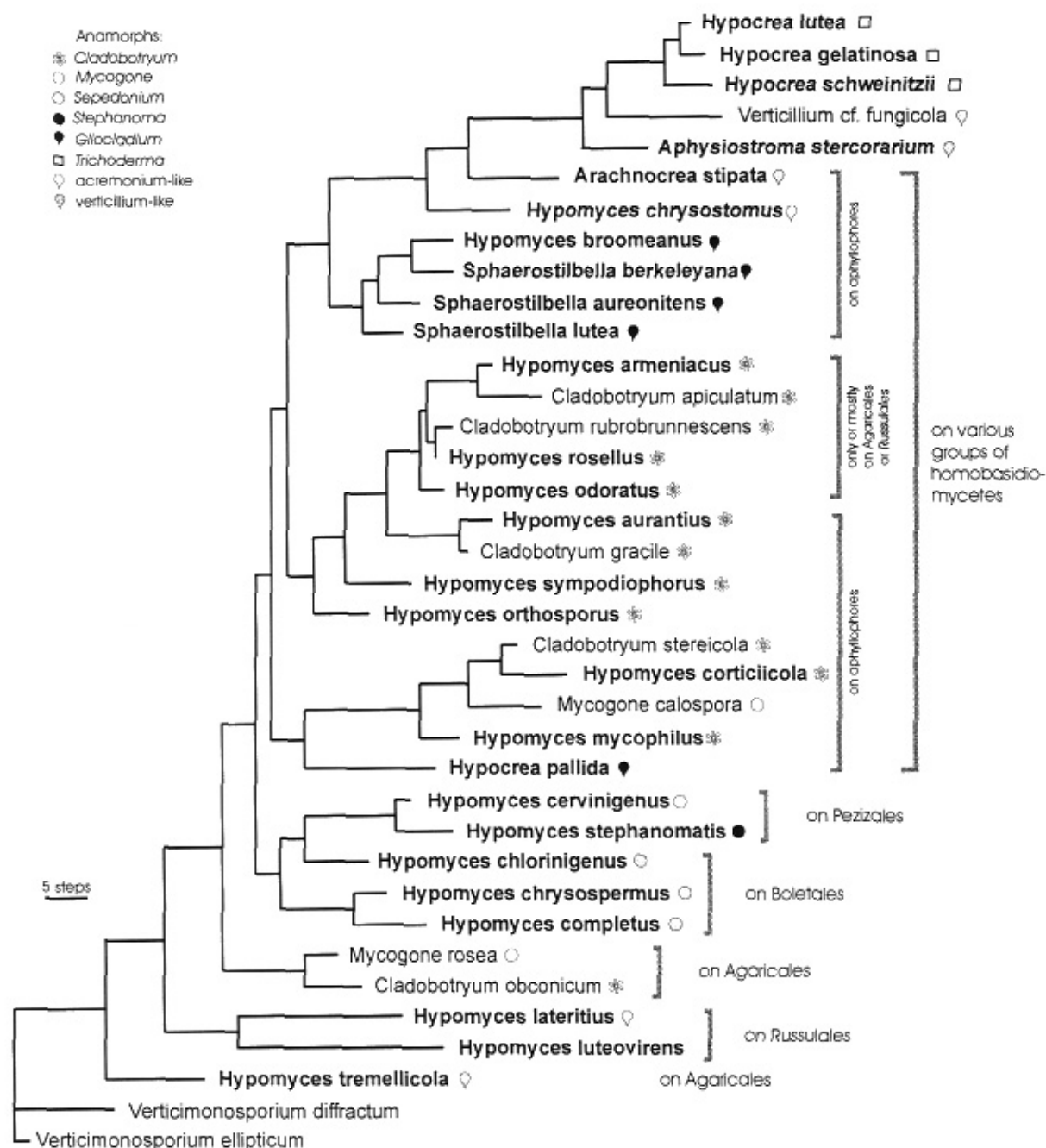


Fig. 3. One of the three most parsimonious trees obtained with PAUP 4.0b2a when applying Goloboff fit criterion. Tree fit = -63.687, length = 436, CI = 0.37, HI = 0.63. The names of species without a known teleomorph are not printed in bold.

other as well as to the boleticolous species with one-celled (*Sepedonium*) aleurioconidia (*H. chlorinigenus*, *H. chrysospermus*, *H. completus*). The obligate systemic parasites of the *Russulales*, *H. lateritius* and *H. luteovirens*, with acronium-like or unknown anamorphs, respectively, are distinct from the species of *Hypomyces* that occur on the *Russulales* or the *Agaricales* and have *Cladobotryum* or verticillium-like anamorphs.

*Hypomyces* species with *Cladobotryum* anamorphs, and the related asexual species, growing on a variety of basidiomycetes, fall into three subclades joined in one large clade in the four most parsimonious trees (Fig. 2). The largest subclade includes the type of *Cladobotryum*, *C. varium* (anamorph of *H. aurantius*), and all the included aurofusarin-producing species (*C. rubrobrunescens*, *H. odoratus*, *H. rosellus*). All species in this subclade (except for

*H. sympodiophorus*) have conidiogenous cells with one locus that proliferates retrogressively or remains of constant length during the production of successive conidia. The second subclade comprises aphyllorhizolous species with conidiogenous cells producing several loci (*C. stereicola*, *H. corticiicola* and *H. mycophilus*) and anamorphs previously placed in *Sympodiophora*. *Mycogone calospora*, which produces a few conidia from a single, apparently fixed locus, also belongs to this clade. The latter type characterizes *C. obclavatum* and *M. rosea*, which grow on members of the *Agaricales* and form the third clade.

### Integration of asexual fungicolous species and genera

Tulasne & Tulasne (1861) were among the first to introduce the concept of pleomorphism in fungi, based in part on their observations of *Hypomyces* species. For most of the *Hypomyces* species that they described based on only anamorphs, teleomorph connections have since been established. For the remaining *Cladobotryum*, *Mycogone*, *Sepedonium* and *Stephanoma* species, there is unequivocal morphological and molecular evidence that they belong to *Hypomyces*. We have either been unable to find teleomorphs for these species or there has been multiple loss of sexual reproduction, as described in other lineages of ascomycetes. Because of this and the fact that no species of *Cladobotryum*, *Mycogone* or *Sepedonium* has been linked to a teleomorph other than *Hypomyces*, these 'orphans' should be considered species of *Hypomyces* and could also be named as such. This is presently not permitted by International Code of Botanical Nomenclature (Greuter *et al.*, 1994), which does not allow teleomorph names for species lacking a known teleomorph. However, the practice of creating additional anamorphic binomials for species with a described teleomorph name should be discouraged, and a recommendation to this effect has been added to the St. Louis Code (W. Gams, pers. comm.).

When dealing with anamorph names, we cannot escape the issue of delimiting anamorph genera. In the phylogenetic analyses, the anamorph types unique for *Hypomyces* do not appear monophyletic. The results do not support the recognition of several anamorph genera that were distinguished by modes of proliferation of conidiogenous cells during conidiogenesis. Therefore, I advocate the continued use of the broad concept of *Cladobotryum* proposed by Rogerson and Samuels (1993). Sahr *et al.* (1999) provide evidence that confirms merging *Leiosepium*

Sacc. with *Sepedonium*. The suggestion to synonymize the aleuriosporic genera *Mycogone*, *Sepedonium* and *Stephanoma* (Samuels & Seifert, 1987), on the other hand, is not supported by the results of the present study.

In contrast, the data presented again show that the accurate phylogenetic placement of acremonium-like, gliocladium-like or verticillium-like anamorphic species in the system of Ascomycetes might not be possible without using molecular data. One would expect the fungicolous *Verticillium* species to belong to the *Hypocreaceae*. However, only *Verticillium cf. fungicola* has yet been shown to fall in the *Hypocrea-Hypomyces* clade (Fig. 2), although not close to *H. tremellicola*, which has a similar verticillium-like anamorph. Others, e.g. *V. lecanii* (Zimm.) Viégas and *V. psalliotae* Tresschew, are related to clavicipitalean fungi. *Cladobotryum gracile*, which I initially identified as a verticillium-like fungus because of its slender conidiophores and conidiogenous cells, and small, mostly one-celled conidia, is closely related to *H. aurantius*. While *Gliocladium s. str.* anamorphs are highly diagnostic for *Sphaerostilbella*, they are associated also with *Hc. pallida* and a few similar species that have an unknown position in the *Hypocrea-Hypomyces* clade. In order to achieve a more natural classification, splitting of anamorph genera that possibly represent plesiomorphic anamorph types has begun (Glenn *et al.*, 1996; Schroers *et al.*, 1999).

The fungicolous *Hypocreaceae* seem to support the idea presented by Seifert & Samuels (this volume) that anamorphs might not always be homologous and that we should start to reduce the nomenclatural significance given to them. This pertains mainly to phialidic anamorphs, e.g., the verticillium-like anamorphs of *H. tremellicola*, *Arachnocrea*, *Aphysiostroma* and those associated with *Sepedonium* synamorphs. For the acremonium- or verticillium-like anamorphs of the fungicolous *Hypocrea pulvinata* and related species, a spermatial role has been suggested (Samuels & Lodge, 1996). In the phylogenetic hypothesis presented here (Fig. 2), the species that produce aleurioconidia do not form a monophyletic group. Considering the rarity of aleurioconidia in fungi, it seems that these structures represent homoplasious plesiomorphic characters rather than being nonhomologous in this group of fungi. Furthermore, intermingling of the basidiomyceticolous *Mycogone* species with species of *Hypomyces* and *Cladobotryum* received strong support. This illustrates the confusion created by applying an anatomical system of naming anamorphs to the context of phylogeny-based monophyletic groups of organisms.

## Towards recognizing monophyletic genera

All the different kinds of characters discussed in this paper indicate that the fungicolous species of the *Hypocreaceae* can be divided among the species-rich, heterogeneous and paraphyletic genus *Hypomyces* and more narrowly defined satellite genera. The data suggest a radiation to have occurred according to major host groups with only limited host jumps. The parasites that grow only on short-lived fruit-bodies of apothecial ascomycetes (*Leotiales*, *Pezizales*), *Boletales* or *Agaricales* have developed similar morphological and life style patterns within each group. The fungi that occur mostly on the persistent basidiomata of aphyllophores, on the other hand, have undergone diversification to a much greater extent. This has led to the recognition of several small genera, among which *Arachnocrea* and *Sphaerostilbella* are distinguished by their unique combinations of teleomorph characters, the presence of verticillium-like or *Gliocladium* anamorphs, respectively, and LSU rDNA sequences. Molecular data show that *Hc. pulvinata* and its allies that have acromonium- or verticillium-like anamorphs form a monophyletic group within *Hypocrea* (B. Overton, pers. comm.). Regarding species with disarticulating ascospores and verticillium-like anamorphs, *Aphysiostroma* and *Arachnocrea* do not fall within *Hypocrea* (Fig. 2) but the position of *Protocrea* and *Hypocrea* species that have not been sequenced remains unresolved. On the other hand, *Hc. pallida* is definitely part of the *Hypocreaceae* but does not have close affinities to any other species according to the molecular data available.

Accepting several small genera and following the idea of strictly monophyletic taxa would imply the recognition of new genera within *Hypomyces* as presently delimited. Relying on teleomorph characters atypical of *Hypomyces* and the presence of acromonium-, *gliocladium*- or verticillium-like anamorphs, rare in *Hypomyces*, the process of segregation has been started. Two species (*H. broomeanus*, *H. tremelicola*) were transferred to *Nectriopsis* Maire (Gams & van Zaayen, 1982). However, molecular data show that *H. tremelicola* forms a basal branch in the *Hypocrea-Hypomyces* clade and the species is currently retained in *Hypomyces*. *Hypomyces broomeanus* was transferred to *Sphaerostilbella* and a new genus, *Sporophagomyces*, was erected for *H. chrysostomus* and two other deviating members of *Hypomyces* (Pöldmaa et al., 1999).

The remaining species of *Hypomyces* in the phylogenetic analyses fall into several modestly supported clades, which are generally correlated with host range and anamorph type. Ideally, each monophyletic

group, comprising species with different life-cycle patterns (i.e. pleomorphic, teleomorphic and anamorphic), would have one name at a certain taxonomic level. However, at present, it is not possible to apply such a concept in *Hypomyces* and the related anamorphic fungi because of the lack of robust phylogenetic hypotheses and the regulations of the ICBN (Greuter et al., 1994). Therefore, as a working hypothesis, I recognize the following informal groups in *Hypomyces*, admitting that some are probably not monophyletic:

1. Species growing on members of the *Pezizales* (and the *Leotiales*?); subiculum absent or poorly developed, ascospores naviculate, nonapiculate, mostly one-celled, smooth-walled; aleurioconidia two- or multicelled (*Mycogone*, *Stephanoma*, papulasporalike); phialidic conidia one-celled, held in groups of a few or singly (?) at the single locus on the conidiogenous cell; includes anamorphic species (*Stephanoma* spp.).

2. Species on members of the *Boletales*; subiculum formed on the host's tube layer, sometimes also on the pileus; ascospores fusiform or naviculate, apiculate or non-apiculate, one- or two-celled, smooth-walled or ornamented; aleurioconidia one-celled (*Sepedonium*); phialidic conidia one-celled, held in a drop of liquid at a single locus on the conidiogenous cell; conidiophores verticillium-like; includes anamorphic species (*Sepedonium* spp.).

3. Species on mostly brown-spored members of the *Agaricales* (*Crepidotus* spp., *Tubaria* spp.; *Pholiota* spp.); subiculum covering pileus, gills and stipe of the host, ascospores ellipsoidal or fusiform, apiculate or nonapiculate, two-celled, ornamented; phialidic conidia one-celled, held in a drop of liquid at a single locus on the conidiogenous cell; conidiophores verticillium-like; aleurioconidia or chlamydospores absent.

4. Species on representatives of the *Russulales* (and the *Agaricales*?), transforming the host's hymenophore into a subiculum; ascospores fusiform, apiculate, one- or two-celled, ornamented; anamorphs lacking in most species, or in some species forming one-celled conidia from phialides, held in groups of a few at a single locus on the conidiogenous cell; conidiophores acromonium-like; aleurioconidia or chlamydospores absent.

5. Hosts from various families of homobasidiomycetes (in some cases also heterobasidiomycetes); subiculum effused over the host's fruit-body, wood or litter; ascospores mostly fusiform and apiculate, one- or two-celled, ornamented; conidia septate, held in dry chains or singly at the single or several loci on the conidiogenous cell (*Cladobotryum*); terminal



multicelled chlamydospores formed on lateral branches of hyphae; includes anamorphic species (*Cladobotryum*); anamorphic *Mycogone* species involved produce aleurioconidia.

*Hypomyces* challenges the cladistic ideal of monophyletic genera. Despite the paraphyly suggested by the sequenced LSU rDNA region and the heterogeneity in some morphological characters, there are several synapomorphies (e.g. fungicolous habit, presence of a subiculum, apiculate fusiform ascospores, phialidic anamorphs accompanied by thick-walled spores) characterizing the genus as it is currently understood. If *Hypomyces* is to be split at the generic level, then these characters might be used at a higher taxonomic level. However, recognition of the family *Hypomycetaceae*, accepted earlier by some authors (Arnold, 1971a; Munk, 1957; Müller & von Arx, 1962), is not supported by the recent analyses of morphological or molecular data. Likewise, evidence has been added to support abandoning the genera *Apiocrea* and *Peckiella* (Sahr *et al.*, 1999; present study), distinguished only on the basis of ascospore septation.

For the time being, it seems best to retain a broad concept for *Hypomyces* and its satellite genera to avoid frequent taxonomic rearrangements within the *Hypocreaceae*. Combining hypotheses based on different types of data will certainly aid in piecing together the phylogenetic puzzle of these fungicolous species.

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**Table 2.** List of the LSU rDNA sequences included in the phylogenetic analyses.

Species	Anamorph	Host range	GenBank
<i>Arachnocrea stipata</i> (Fuckel) Z. Moravec	verticillium-like	aphyllophores, wood	AF160227
<i>Aphysiostroma stercorarium</i> Barrasa, A.T. Martínez & G. Moreno	verticillium-like	dung	U47820
<i>Cladobotryum apiculatum</i> (Tubaki) W. Gams & Hoozem.	–	<i>Russulales</i> ( <i>Agaricales</i> ) <sup>1</sup>	AF213025 <sup>2</sup>
<i>Cladobotryum gracile</i> K. Pöldmaa	–	aphyllophores	AF213026 <sup>2</sup>
<i>Cladobotryum obconicum</i> W. Gams & Schroers	–	<i>Entoloma</i> sp.	AF049165
<i>Cladobotryum rubrobrunnescens</i> W. Helfer	–	<i>Inocybe</i> sp.	AF160228
<i>Cladobotryum stereicola</i> G. Arnold	–	<i>Chondrostereum</i> , <i>Stereum</i> spp. (aphyllophores)	AF160229
<i>Hypocrea gelatinosa</i> (Tode : Fr.) Fr.	<i>Trichoderma</i> cf. <i>virens</i>	decorticated wood	U00738
<i>Hc. lutea</i> (Tode) Petch	<i>Gliocladium viride</i> Matr.	decorticated wood	U00739
<i>Hc. pallida</i> Ellis & Everh.	<i>Gliocladium</i> sp.	aphyllophores	U00740
<i>Hc. schweinitzii</i> (Fr.) Sacc.	<i>Trichoderma citrinoviride</i> Bissett	decorticated wood	U47833
<i>Hypomyces armeniacus</i> Tul.	<i>Cladobotryum verticillatum</i> (Link) S. Hughes	<i>Russulales</i> (decaying wood, litter, ground) <sup>3</sup>	AF160239
<i>H. aurantius</i> (Pers. : Fr.) Tul.	<i>Cladobotryum varium</i> Nees	aphyllophores, <i>Agaricales</i> <sup>4</sup>	AF160230
<i>H. broomeanus</i> Tul.	<i>Gliocladium microspermum</i> (Sacc.) W. Gams	<i>Heterobasidion anosum</i> (Fr.) Bref.	AF160231
<i>H. cervinigenus</i> Rogerson & Simms	<i>Mycogone cervina</i> Ditmar	<i>Helvella</i> spp.	AF160232
<i>H. chlorinigenus</i> Rogerson & Samuels	<i>Sepedonium chlorinum</i> (Tulasne) Damon	<i>Boletales</i>	AF213027 <sup>2</sup>
<i>H. chrysospermus</i> Tul.	<i>Sepedonium chrysospermum</i> Link	<i>Boletales</i>	AF160233
<i>H. chrysostomus</i> Berk. & Broome	<i>Acremonium lindtneri</i> (Kirschst.) Rogerson & Samuels	<i>Ganodermataceae</i>	AF160235
<i>H. completus</i> (G. Arnold) Rogerson & Samuels	<i>Sepedonium brunneum</i> Peck	<i>Suillus pictus</i> (Peck) A. Smith & Thiers	AF213028 <sup>2</sup>
<i>H. corticiicola</i> K. Pöldmaa	<i>Cladobotryum</i> sp.	aphyllophores	AF213029 <sup>2</sup>
<i>H. lateritius</i> (Fr. : Fr.) Tul.	acremonium-like	<i>Lactarius</i> spp.	AF160236
<i>H. luteovirens</i> (Fr. : Fr.) Tul.	Unknown	<i>Russula</i> spp.	AF160237

<i>H. mycophilus</i> Rogerson & Samuels	<i>Cladobotryum polypori</i> (Dearn. & House) Rogerson & Samuels	aphyllophores, (Agaricales) <sup>4</sup>	AF160238
<i>H. odoratus</i> G. Arnold	<i>Cladobotryum mycophilum</i> (Oudem.) W. Gams & Hoozem.	aphyllophores, Agaricales <sup>4</sup>	AF160240
<i>H. orthosporus</i> K. Pöldmaa	<i>Cladobotryum orthosporum</i> (W. Gams) K. Pöldmaa	aphyllophores	AF160241
<i>H. rosellus</i> (Alb. & Schw. : Fr.) Tul.	<i>Cladobotryum dendroides</i> (Bull.) W. Gams & Hoozem.	aphyllophores, Agaricales, (Russulales) <sup>4</sup>	AF160242
<i>H. stephanomatis</i> Rogerson & Samuels	<i>Stephanoma strigosum</i> Wallr.	<i>Humaria</i> spp.	AF160243
<i>H. sympodiophorus</i> Rogerson & Samuels	<i>Cladobotryum uniseptatum</i> (Castañeda) K. Pöldmaa	<i>Stereum</i> spp.	AF160244
<i>H. tremellicola</i> (Ellis & Everh.) Rogerson	verticillium-like	<i>Crepidotus</i> spp.	U17427
<i>Mycogone calospora</i> (P. Karst.) Höhn.	–	<i>Ramaria</i> spp.	AF213030 <sup>2</sup>
<i>M. rosea</i> Link	–	Agaricales	AF213031 <sup>2</sup>
<i>Sphaerostilbella aureonitens</i> (Tul. & C. Tul.) Seifert <i>et al.</i>	<i>Gliocladium penicillioides</i> Corda	<i>Stereum</i> spp. (aphyllophores)	U00755
<i>S. berkeleyana</i> (Plowr.) Samuels & Cand.	<i>Gliocladium</i> sp.	<i>Stereum</i> spp. (aphyllophores)	U00756
<i>S. lutea</i> (Henn.) Sacc. & D. Sacc.	<i>Gliocladium aurifilum</i> (W. R. Gerard) Seifert <i>et al.</i>	aphyllophores	U00757
<i>Verticillium</i> cf. <i>fungicola</i> (Preuss) Hassebr.	–	Agaricales, Russulales, aphyllophores,	AF213032 <sup>2</sup>
<i>Verticimonosporium diffractum</i> Matsush.	–	decaying leaves, twigs	AF049179
<i>Verticimonosporium ellipticum</i> Matsush.	–	decaying petioles of palmae	AF049181

<sup>1</sup> Groups of fungi that are only infrequently found as host of respective species are in brackets

<sup>2</sup> New sequences obtained for this study

<sup>3</sup> Teleomorph forming only on decaying wood, litter or on ground

<sup>4</sup> Teleomorph forming only on fruit-bodies of aphyllophores