

Towards monophyletic genera in the holomorphic *Hypocreales*

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Abstract: Within the hypocrealean lineages, monophyletic genera are emerging that encompass both sexual and asexual fungi. A recent monograph of three of the major families of the Ascomycete order *Hypocreales* included 56 teleomorph genera, many of which correlate with anamorph genera. Within the *Nectriaceae*, most of the 20 genera exhibit an equivalence in sexual and asexual generic concepts. In the *Bionectriaceae*, many of the associated anamorphs of the 30 genera are relatively nondescript, acremonium-like and are not useful for defining genera. The *Hypocreaceae* consist primarily of the genus *Hypocrea* with *Trichoderma* anamorphs and *Hypomyces* with a diverse array of anamorphs. A few anomalous species allied with *Hypocrea* have gliocladium-like or verticillium-like anamorphs; in these cases, both the teleomorph and the anamorph are often atypical for their respective genera. Groups of species within *Hypomyces* correspond to a limited degree with anamorph and biological characteristics, particularly host.

Key words: anamorph–teleomorph correlation, genus concept, phylogeny, *Bionectriaceae*, *Hypocreaceae*, *Nectriaceae*.

Introduction

The *Hypocreales* is an order of *Euascomyces* that includes over one thousand described species and related asexual fungi. Until recently, the *Hypocreales* included only sexually reproducing ascomycetes, but increasingly they are considered to include species that reproduce only asexually, apparently having evolved from sexually reproducing ancestors. Rossman (1996) provided an overview of the hypocrealean fungi and their economic importance as plant pathogens, agents of biological control, and producers of powerful antibiotics and mycotoxins. A monograph of three of the major families of the *Hypocreales*, specifically the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae*, was subsequently published by Rossman *et al.* (1999) and concentrated primarily on the teleomorphs of these fungi. The fourth major family, the *Clavicipitaceae*, is reviewed by White *et al.* (this volume).

Most plant-associated fungi are asexually reproducing, as evidenced by Farr *et al.* (1989), in which 78% of the listed species are either ascomycetes or deuteromycetes, 90% of these deuteromycetes lacking known teleomorphs (Rossman, 1993). In the United States, 5,644 species, or almost half of the 13,000

species of fungi reported on plants, do not have a known teleomorph. Thus, the asexually reproducing fungi traditionally classified in the deuteromycetes have by far the highest number of species of all fungal groups associated with plants. Although teleomorphs for these fungi are unknown and thus these species are thought to reproduce only asexually, there is increasing evidence that the genetic structure for some asexual fungi is that of sexually reproducing populations. This suggests that at least some of these fungi are not clonal, in the sense of remaining genetically identical over time (Taylor *et al.*, 1999; see also Seifert & Samuels, this volume). How else could these fungi be so successful, apparently out-competing their sexually reproducing counterparts?

Traditionally, deuteromycetes were classified using what appeared to be scientific names but, in reality, they were considered form-taxa. Because deuteromycetes apparently lack sexuality, they cannot be classified in natural groups defined using teleomorph characters. The concept of form-taxa originated with Saccardo for all groups of fungi and his “pigeon-hole” philosophy of fungal classification has influenced taxonomic mycology for the past one-hundred years. Saccardo’s classification system em-

phasized easily recognized characteristics such as spore shape, colour and septation, and presence or absence of a stroma. These characters do not necessarily reflect evolutionary relationships. Among the sexually reproducing fungi, these concepts have gradually been abandoned but, for the deuteromycetes, they have lingered. This is possibly because the concept of form-taxa is thought to be more applicable for fungi that lack a teleomorph. The deuteromycetes are becoming integrated into an ascomycete-taxonomic framework, either through increased discovery of teleomorph-anamorph connections or through phylogenetic analysis of DNA sequence data. The nomenclature of this very large and important group of fungi should eventually reflect evolutionary concepts that incorporate fundamental biology and thus increase the probability of accurately predicting their 'behavior'.

A scientific name is intended to anchor any phylogenetic knowledge that might exist about the organism or group of organisms the name represents. In the case of deuteromycetes, scientific names are used despite the original recognition that the names represented only form-taxa rather than natural or phylogenetic taxa. As phylogenetic knowledge of deuteromycetes accumulated, the scientific names did not keep pace. Thus, there is considerable confusion among non-systematists about the classification of the anamorphs, because species differing in phylogeny, morphology, and biology are placed in the same genus. Two examples are encountered in the literature on fungi used as biological control agents. One involves two species both classified in the genus *Verticillium* Nees. Strains of *Verticillium lecanii* (Zimm.) Viégas and its relatives are being developed for the control of insects, nematodes, and rust fungi. Both morphological and molecular data suggest this species is a member of the *Clavicipitaceae* (Gams *et al.*, 1998). On the other hand, *Verticillium dahliae* Kleb. is encountered as a plant pathogen of numerous crops and has been shown to be a member of the *Phyllachorales* (Rehner & Samuels, 1995). Despite the fact that these two species can easily be differentiated based on morphology and are very different biologically, they are both formally classified in *Verticillium*. As a second example, *Fusarium larvarum* Fuckel occurs on scale insects and adelgids and is being investigated for their control. This fungus is the anamorph of *Cosmospora auranticola* (Berk. & Broome) Rossman & Samuels and is related to other species that generally occur on other fungi and insects (Rossman *et al.*, 1999). In contrast, many species of *Fusarium* Link such as *F. sambucinum* Fuckel are virulent plant pathogens. *Gibberella pulicaris*

(Fr.) Sacc. is the teleomorph of *F. sambucinum* and many of the fast-growing, plant-pathogenic fusaria have teleomorphs in or are allied with *Gibberella* (Rossman *et al.*, 1999). The distinctions that are summarized in scientific names should reflect the recognized differences in morphology, biology and phylogeny.

In moving toward phylogenetic generic concepts in the *Hypocreales*, it has been necessary to re-evaluate the generic names used for the teleomorphs starting with the type species of the described genera. The following synopsis is drawn primarily from Rossman *et al.* (1999). The purpose of this evaluation is to demonstrate that there is a trend toward equivalency among correlated teleomorph and anamorph genera in these families of the *Hypocreales*.

Nectriaceae

The *Nectriaceae* is a family of 20 genera in which there is a close equivalency between sexual and asexual generic concepts, as summarized in Table 1. These fungi exemplify a group in which knowledge of the complete life cycles of the holomorphs has contributed to an understanding of the relationships between species, particularly in the circumscription of genera. There is a tendency for conidia of the family to be phragmosporous, e.g. *Cylindrocarpon*, *Cylindrocladium*, and *Fusarium*, a condition that is relatively rare in other families of the order. In general, members of the *Nectriaceae* are weak to virulent plant pathogens, although some fungicolous and insecticolous species or saprobes are included.

The genus *Nectria* is now restricted to the type species, *N. cinnabarina* (Tode) Fr., and 27 related species that share many morphological and biological characteristics, as well as similar anamorphs. The anamorphs of *Nectria sensu stricto* are generally placed in the genus *Tubercularia*, despite fruiting structures that may be sporodochial, synnematosus or pycnidial on natural substrata (Seifert, 1985). In culture, these species sporulate as slimy, orange fungi, often with simple, irregularly aggregated conidiophores. The characteristics of species of *Nectria* are enumerated in Rossman (1989, 1993), Rossman *et al.* (1999), and Seifert (1985). Based on molecular data, three species in *Nectria sensu stricto* cluster together in a clade separated from many species previously placed in that genus (O'Donnell, 1993; Rehner & Samuels, 1995). However, relatively few species of *Nectria sensu stricto* have been included in these molecular studies and few exclusively anamorph species have been integrated into this group.

One of the most important groups of genera in the *Nectriaceae* includes *Albonectria*, *Gibberella* and

Table 1. Genera of the *Nectriaceae* with known anamorphs.

Teleomorph	Anamorph	Habitat
<i>Albonectria</i> Rossman & Samuels	<i>Fusarium decemcellulare</i> Brick, fast-growing fusaria	saprobic, plant pathogenic
<i>Calonectria</i> De Not.	<i>Cylindrocladium</i> Morgan	saprobic, plant pathogenic
<i>Calostilbe</i> Sacc. & P. Syd.	<i>Calostilbella</i> Höhn.	lignicolous
<i>Corallomycetella</i> Henn.	<i>Fusarium</i> Link, <i>Rhizostilbella</i> Wolk	lignicolous, plant pathogenic
<i>Cosmospora</i> Rabenh.	slow-growing fusaria, acremonium-like, <i>Volutella</i> Fr.	fungicolous, insecticolous and herbicolous
<i>Gibberella</i> Sacc.	<i>Fusarium sambucinum</i> Fuckel, fast-growing fusaria	saprobic, plant pathogenic
<i>Haematonectria</i> Samuels & Nirenberg	<i>Fusarium solani</i> (Martius) Sacc., fast-growing fusaria	saprobic, plant pathogenic
<i>Lanatonectria</i> Rossman, Samuels & Lowen	<i>Actinostilbe</i> Petch	herbicolous, lignicolous, rarely fungicolous
<i>Leuconectria</i> Samuels & Rossman	<i>Gliocephalotrichum</i> J.J. Ellis & Hesseltine	herbicolous, isolated from soil
<i>Nectria</i> (Fr.) Fr.	<i>Tubercularia</i> Tode	lignicolous, leaves of <i>Agavaceae</i>
<i>Neocosmospora</i> E.F. Sm.	acremonium-like	herbicolous, isolated from soil, plant-pathogenic
<i>Neonectria</i> Wollenw.	<i>Cylindrocarpon</i> Wollenw.	lignicolous, isolated from soil, plant-pathogenic
<i>Ophionectria</i> Sacc.	<i>Antipodium</i> Piroz.	lignicolous
<i>Pseudonectria</i> Seaver	<i>Volutella</i> , some with verticillium-like synanamorphs	herbicolous (<i>Buxaceae</i>), plant-pathogenic
<i>Rubrinectria</i> Rossman & Samuels	sporodochia with phialides and slimy ameroconidia	lignicolous
<i>Viridisporea</i> Samuels & Rossman	<i>Penicillifer</i> Emden	lignicolous, isolated from roots and soil

Haematonectria, plant pathogens with fast-growing *Fusarium* anamorphs. Although these teleomorph genera bear some morphological similarities and could be regarded as one genus, there are distinct morphological differences in both the teleomorphs and anamorphs. In addition, these genera have been shown to be separate monophyletic lineages based on DNA sequence analysis (O'Donnell, 1993). Based on molecular data, the type species of *Neocosmospora* appears to be closely related to *Haematonectria*. We can speculate that the acremonium-like anamorph of *N. vasinfecta* E.F. Sm. may be homologous with the

microconidial anamorph of a *Fusarium* (O'Donnell & Gray, 1995; Rehner & Samuels, 1995). This interpretation agrees with the biology of this genus, which consists of species that are weak plant pathogens.

Cosmospora includes species with anamorphs that are slow-growing, fusarium-like, as well as other anamorphs that are acremonium-like and verticillium-like. Different anamorphs often correlate with the biological differences, such as a habit that is fungicolous, insecticolous or herbicolous (Rossman *et al.*, 1999; Samuels *et al.*, 1991). The group of slow-growing fusaria that are anamorphs of *Cosmospora*

are a distinct monophyletic group within the currently recognized genus *Fusarium* (O'Donnell, 1993). However, the results presented by Rehner & Samuels (1995) suggest that they are a monophyletic group distinct from the major clade that includes the fast-growing *Fusarium* anamorphs. Based on morphological characteristics of the ascotal wall and ascospores that correlate with diverse anamorphs and biology, *Cosmospora* should probably be further subdivided into monophyletic genera.

Several additional examples exist in which species originally described as *Nectria sensu lato* are now recognized in segregate monophyletic genera that correlate with distinct anamorphs. The sexual and asexual morphs of these genera have distinct morphological characteristics that suggest an equivalency that has been confirmed for a limited number of species using sequence data (Rehner & Samuels, 1995). The species of *Calonectria* have anamorphs in *Cylindrocladium*. The number of species in *Calonectria* has increased over the years and many of the anamorphs placed in *Cylindrocladium* lack known teleomorphs. However, the equivalency between these genera has remained consistent (Crous *et al.*, 1997). A closely related monotypic genus, *Leuconectria*, with the distinctive anamorph *Gliocephalotrichum*, was initially suggested to be closely related to *Calonectria*. Although *Leuconectria* remains distinct within the group, recent molecular data place this genus near *Neonectria* species having *Cylindrocarpon* anamorphs (Schoch *et al.*, this volume). *Ophionectria* represents another example of a distinctive teleomorphic genus with an unusual anamorphic genus, *Antipodium*. Finally, the three species of *Lanatonectria* are distinguished by ascomata with bright yellow, curled, spiny hairs. These hairs are also present in the sporodochial to synnematus anamorphs, classified in *Actinostilbe* (Rossman *et al.*, 1999).

Bionectriaceae

The anamorphs of the 26 genera currently accepted in the *Bionectriaceae* are predominantly placed in the relatively nondescript genus *Acremonium* (Table 2). The anamorphs are not particularly useful for defining genera or species in this family; however, there are some exceptions. The genus *Acremonium* is defined primarily by mostly simple, erect, aculeate phialides and non-septate, hyaline conidia. However, species have been ascribed to *Acremonium* based on a relatively simple morphology in culture that may be the reduced form of a more complicated morph occurring in nature. Thus, the concept of the genus *Acremonium* appears to be phylogenetically diverse.

The *Acremonium* anamorphs of members of the *Bionectriaceae* are often known only in cultures derived from single ascospores of the teleomorph; they are not commonly encountered on natural substrata, and they are distinct from the common saprotrophic anamorph-species of *Acremonium* (Gams, 1971). Most members of the *Bionectriaceae* are generally fungicolous or hypersaprobic, although at least one plant pathogen is known, namely, *Nectriella pironii* Alfieri & Samuels.

Following are three examples from the *Bionectriaceae* in which careful examination of both sexual and asexual morphs of a group of related species reveals an equivalency in generic concepts of the alternate morphs.

The first example concerns the genus *Bionectria* and its anamorph *Clonostachys*. Because the type of the genus, *B. tonduzii* Speg., is known only from the type specimen and lacks an ascertained anamorph (Schroers & Samuels, 1997), the genus is essentially characterized by the relatively common species *Bionectria ochroleuca* (Schw.) Schroers & Samuels. *Bionectria ochroleuca* and its anamorph *Clonostachys rosea* (Link) Schroers *et al.* was studied in detail by Schroers *et al.* (1999). Used as a biocontrol agent for wilt diseases in greenhouses in Europe, *C. rosea* is a morphologically distinctive fungus that forms sporodochia on natural substrata. In culture, as well as in nature, it produces two distinct kinds of conidiophores, one with verticillate branches producing conidia in a moist head and the other with penicillate branches bearing conidia in imbricate chains. Three additional species of *Bionectria*, *B. apocyni* (Peck) Schroers & Samuels, *B. aureofulva* (Cooke & Ellis) Schroers & Samuels, and *B. byssicola* (Berk. & Broome) Schroers & Samuels, are similar to *B. ochroleuca* in ascotal wall structure and anamorph. Each species produces a sporodochial anamorph on natural substrata; they form loose to compact penicillately branching conidiophores, described as verticillium-like or gliocladium-like (Samuels, 1976; Samuels *et al.*, 1990; Schroers, this volume).

One distinctive clade within the *Bionectriaceae* includes the type species of the genus *Acremonium*, *A. alternatum* Link, for which no teleomorph is known, as well as several additional species of true *Acremonium* and six cleistothecial, teleomorph genera. Two brightly-coloured, cleistothecial teleomorph genera, *Emericellopsis* and *Mycoarachis*, have *Acremonium* anamorphs and were included in the *Bionectriaceae* by Rossman *et al.* (1999). Three additional cleistothecial genera with *Acremonium* anamorphs have recently been shown to be related to *Emericellopsis* and *Mycoarachis*, namely *Bulbithecium*, *Hapsi-*

Table 2. Genera of the *Bionectriaceae* with known anamorphs

Teleomorph	Anamorph	Habitat
<i>Bionectria</i> Speg.	<i>Clonostachys</i> Corda	fungicolous
<i>Bulbithecium</i> Udagawa & T. Muroi	<i>Acremonium</i> Link	horse dung
<i>Dimerosporiella</i> Speg.	acremonium-like	<i>Meliola</i> and similar fungi
<i>Emericellopsis</i> J.F.H. Beyma	<i>Acremonium</i>	soil and organic debris
<i>Hapsidospora</i> Malloch & Cain	<i>Acremonium</i>	lawn grass compost heap
<i>Heleococcum</i> C.A. Jørg.	<i>Acremonium</i> /trichothecium-like	soil and organic debris
<i>Hydropisphaera</i> Dumort.	acremonium-like or homothallic	herbicolous
<i>Ijuhya</i> Starbäck	acremonium-like	herbicolous
<i>Lasionectria</i> (Sacc.) Cooke	acremonium-like	herbicolous and lignicolous, rarely fungicolous
<i>Leucosphaerina</i> Arx	<i>Acremonium</i> , sporothrix-like	neelgai dung
<i>Mycoarachis</i> Malloch & Cain	<i>Acremonium</i>	isolated from herbivore dung
<i>Mycocitrus</i> A. Möller	acremonium-like	on living stems of bamboo
<i>Nectriopsis</i> Maire	acremonium-like, rarely <i>Kutilakesa</i> Subram., <i>Rhopalocladium</i> Schroers, verticillium-like	fungicolous
<i>Nigrosabulum</i> Malloch & Cain	<i>Acremonium</i>	cow dung
<i>Ochronectria</i> Rossman & Samuels	acremonium-like	herbicolous
<i>Peethambara</i> Subram. & D.J. Bhat	<i>Didymostilbe</i> Henn. (= <i>Virgatospora</i> Finley)	lignicolous
<i>Pronectria</i> Clem.	acremonium-like	lichenicolous
<i>Protocreopsis</i> Y. Doi	acremonium-like	graminicolous
<i>Stilbocrea</i> Pat.	<i>Gracilistilbella</i> (Seifert, this volume), acremonium-like,	lignicolous
<i>Trichonectria</i> Kirschst.	acremonium-like	lichenicolous, herbicolous
<i>Valsonectria</i> Speg.	acremonium-like, stilbella-like	herbicolous

dospora and *Nigrosabulum* (Suh & Blackwell, 1999). The fourth genus, *Leucosphaerina*, has species with either *Acremonium* or sporothrix-like anamorphs. Thus, one might expect the teleomorph of the type species of *Acremonium* to be cleistothecial. Two genera of strictly anamorphic fungi have also recently been shown to belong to this clade. One of these, *Stanjemonium* W.

Gams, O'Donnell, Schroers, & M. Christensen is similar to *Acremonium* in having hyaline, non-septate conidia but, unlike *Acremonium*, the conidia are borne singly on conidiogenous cells borne singly or in pseudowhirls on the subtending hyphae (Gams *et al.*, 1999). A second anamorphic genus in this clade, *Geosmithia* J. Pitt, includes species with penicillate

branching (Ogawa *et al.*, 1997). In this example, the monophyletic group is predominantly composed of anamorphic species with only a few teleomorphic connections.

Another distinctive clade within the *Bionectriaceae* consists of the teleomorph genus *Peethambara*, and several related anamorph genera. The genus *Peethambara* was originally described with one species, *P. sundara* Subram. & D.J. Bhat, having a distinctive synnematous, golden-spored anamorph placed in a monotypic anamorph genus. The anamorph species was transferred to *Didymostilbe* by Seifert (1985). Meanwhile, the distinctive species, *Nectria spirostriata* Rossman was described and linked to the anamorph, *Virgatospora echinofibrosa* E.F. Morris (Rossman, 1983). A recent morphological evaluation of these species revealed that *N. spirostriata* has the distinctive ascomatal wall structure of *P. sundara* and that the anamorph is similar to *Didymostilbe* (Rossman *et al.*, 1999). Molecular evidence suggests that this group includes the two teleomorph species of *Peethambara* with anamorphs in *Didymo-*

stilbe as well as the morphologically similar *Albosynnema elegans* E.F. Morris and, surprisingly, the type species of *Myrothecium* Tode, *M. inundatum* Tode (Rossman *et al.*, 2000).

Hypocreaceae

The family *Hypocreaceae* consists primarily of the genus *Hypocrea*, with *Trichoderma* anamorphs, and *Hypomyces* having a diverse array of anamorphs (Table 3). The family includes species that are fungicolous, although their hyperparasitic nature is not always readily apparent. For the large genus *Hypocrea* and related genera such as *Podostroma*, i.e. stalked species of *Hypocrea*, and *Sarawakus*, i.e. species of *Hypocrea* having one-celled ascospores, most anamorphs are placed in *Trichoderma*. Species of *Hypocrea* having non-*Trichoderma* anamorphs, such as *H. pallida* Ellis & Everh. with a gliocladium-like anamorph and *H. avellanea* Rogerson & S.T. Carey with a verticillium-like anamorph, also tend to be atypical in their teleomorph characteristics, often having an effused stroma. Analysis of 28S rDNA

Table 3. Genera of the *Hypocreaceae* with known anamorphs.

Teleomorph	Anamorph	Habitat
<i>Aphysiostroma</i> Barrasa <i>et al.</i>	verticillium-like	coprophilous
<i>Arachnocrea</i> Z. Moravec	verticillium-like	lignicolous, herbicolous and fungicolous
<i>Hypocrea</i> Fr.	<i>Trichoderma</i> , acremonium-like, gliocladium-like, stilbella-like, verticillium-like	fungicolous, lignicolous
<i>Hypocreopsis</i> P. Karst.	<i>Stromatocrea</i>	lignicolous, fungicolous
<i>Hypomyces</i> (Fr.) Tul.	acremonium-like, <i>Cladobotryum</i> , <i>Mycogone</i> , papulaspora-like, <i>Stephanoma</i> , <i>Sepedonium</i> , verticillium-like	fungicolous
<i>Podostroma</i> P. Karst.	<i>Trichoderma</i>	lignicolous
<i>Protocrea</i> Petch	acremonium-like, verticillium-like	lignicolous, fungicolous
<i>Pseudohypocrea</i> Y. Doi	acremonium-like	corticolous
<i>Sarawakus</i> Lloyd	gliocladium-like, <i>Trichoderma</i> , verticillium-like	lignicolous
<i>Sphaerostilbella</i> (Henn.) Sacc. & D. Sacc.	<i>Gliocladium</i>	fungicolous, rarely lignicolous

sequences indicate that *H. pallida* can be excluded from *Hypocrea* (Rehner and Samuels, 1994).

Within the species of *Hypomyces*, diverging lines of evolution correlate with anamorphic and biological characteristics, primarily host. Rogerson & Samuels (1985, 1989, 1993, 1994) laid the monographic foundation for a closer examination of groups of related species within *Hypomyces* (Põldmaa, 1998, and this volume). Morphological and molecular data suggest a subdivision that could be recognized at the generic level and correlate teleomorphic and anamorphic concepts with biology (Põldmaa, this volume). At present, these groupings are an hypothesis with limited supporting evidence.

Conclusions

What can be concluded from this journey through three of the major families of the *Hypocreales*?

First, among plant-associated fungi there is a diversity of sexual and asexual species and a need to integrate knowledge of the anamorphic fungi into a phylogenetically based taxonomic framework.

Second, hypotheses of relationships among groups of species must consider the whole fungus, including evaluations of both teleomorphs and anamorphs, combining morphological observations with results of molecular studies.

Third, phylogenetic relationships often correlate with biological characteristics.

Finally, accurate scientific names are needed that reflect systematic knowledge about these fungi, not just for their identification, but so that a body of information can be structured on a meaningful taxonomic foundation.

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