Studies in Mycology, No. 45: 141–149 *May 2000*

Capronia and its anamorphs: exploring the value of morphological and molecular characters in the systematics of the *Herpotrichiellaceae*

Wendy A. Untereiner

Botany Department, Brandon University, Brandon Manitoba R7A 6A9, Canada

Correspondence: <untereiner@brandonu.ca>

Abstract: Characters employed in the taxonomy of *Capronia* are discussed in light of results of recent investigations of the systematics of this genus. *Capronia* is an anamorph-rich taxon and asexual spore states are important in the identification of members of this genus. However, the complete life-histories of the majority of *Capronia* species are unknown and the construction of a comprehensive taxonomy is hampered by the scarcity of specimens and cultures. Molecular phylogenies based on analyses of rDNA sequences demarcate these fungi from ascomycetes with morphologically similar anamorphs, but often fail to clearly resolve species and genera within the *Herpotrichiellaceae*. The stromatic *Capronia* species and species with fusoid or elongate ascospores in particular warrant further taxonomic study.

Key words: ascomycetes, black yeast, *Exophiala*, *Phialophora*, ribosomal RNA genes, taxonomy.

Introduction

Capronia Sacc. (*Herpotrichiellaceae*) is a poorly understood ascomycete genus that includes species described from rotting wood as well as decaying leaves and stems of herbaceous plants (Barr 1991; Müller *et al.*, 1987). Many species of *Capronia* known from plant material also occur in association with or on other lignicolous Ascomycota and Basidiomycota, and a significant number of the members of this genus have been described from the thalli of lichens and other fungi. The genus has been characterized as saprobic or hypersaprobic (Barr, 1987; Müller *et al.*, 1987; Munk 1957a) but the trophic relationships of these species have yet to be elucidated experimentally (Untereiner & Malloch, 1999). Species of *Capronia* are common and may in fact be ubiquitous, but their diminutive ascomata are ephemeral and are seldom produced in abundance *in situ*. They are also extremely difficult to observe on darkened substrata that are often colonized by other microfungi. Eriksson (1981) remarked that species of *Capronia* are typically found only when mycologists search collections for other fungi. I would stress that the problem lies not in finding the members of this genus but in recognizing these ecologically and morphologically distinctive microfungi.

Species of *Capronia* have attracted considerable attention despite their relative obscurity. Members of the genus were first studied critically by Munk (1953, 1957a, 1957b), who was intrigued by the relationship between ecology and taxonomy in this and other ascomycete taxa. Interest in these fungi increased when the anamorphs of a number of *Capronia* were discovered to belong to the genus *Exophiala* Carmichael, a member of a medically important group of fungi known as the 'black yeasts' (Müller *et al.*, 1987; Samuels & Müller, 1978; Scholl-Schwarz, 1968). Subsequent investigations have demonstrated both the prevalence of these anamorphs within *Capronia* and their predictive value for inferring the close phylogenetic relationship between *Capronia* and species of *Exophiala* for which teleomorphs have not been observed (Untereiner, 1995, 1997; Untereiner *et al.*, 1995). The latter conclusion has been confirmed by a number of molecular studies aimed at clarifying both the position of the black yeasts within the Ascomycota and the phylogeny of the anamorphic *Herpotrichiellaceae* (Haase *et al.*, 1999; Masclaux *et al.*, 1995; Spatafora *et al.*, 1995; Untereiner & Naveau, 1999; Untereiner *et al.*, 1995).

Although a significant body of morphological and DNA sequence data is available, a unified taxonomy of *Capronia* and its anamorphs has not been forthcom-

Table 1. Anamorphs of *Capronia*.

Teleomorph	Anamorph and accompanying synanamorph	Reference
Capronia spp. [1]	*Cladophialophora* sp.	*Ined.*
Capronia sp. [2]	*Exophiala* sp.	*Ined.*
Capronia sp.	*Phialophora* sp.	*Ined.*
Capronia spp.	*Ramichloridium* cf. *cerophilum*	*Ined.*
Capronia spp. [3]	*Ramichloridium* cf. *anceps*	*Ined.*
Capronia sp. [4]	*Exophiala calicioides* (Fr.) Okada *et al.*	Seifert & Okada, 1993; Okada *et al.*, 1998; Okada *et al.*, 2000;
C. acutiseta Samuels	*Exophiala* sp., phialidic syanamorph	Müller *et al.*, 1987; Untereiner *et al.*, 1995
C. coronata Samuels	*Exophiala* sp.	Müller *et al.*, 1987
C. dactylotricha Untereiner *et al.*	*Exophiala* sp., phialidic synanamorph	Untereiner, 1995
C. epimyces M.E. Barr	*Exophiala* sp., phialidic synanamorph	Untereiner *et al.*, 1995
C. fungicola (Samuels & E. Müller) Untereiner	*Ramichloridium* cf. *anceps*	Samuels & Müller, 1978
C. mansonii (Schol-Schwarz) E. Müller *et al.*	*Exophiala* sp.	Schol-Schwarz, 1968
C. montana M.E. Barr [5]	*Exophiala* sp.	Barr, 1991
C. munkii Untereiner [6]	*Exophiala* sp.	Untereiner, 1995
C. nigerrima (Bloxam) M.E. Barr	*Exophiala* sp.	Untereiner & Naveau, 1999
C. parasitica (Ellis & Everhart) E. Müller *et al.*	*Rhinocladiella* cf. *spinifera*, *Exophiala* sp.	Müller *et al.*, 1987; Untereiner *et al.*, 1995
C. pilosella (P. Karsten) E. Müller *et al.* [7]	*Exophiala* sp.	Untereiner *et al.*, 1995; Untereiner 1997
C. perpusilla Réblová [5]	*Rhinocladiella* sp.	Réblová, 1996
C. pleiospora (Mouton) Saccardo	Colonies not producing conidial anamorph	*Ined.*
C. pulcherrima (Munk) E. Müller *et al.* [8]	*Exophiala* sp.	Untereiner, 1997
C. semiimmersa (Candoussau & Sulmont) Untereiner & Naveau [9]	*Phialophora americana* (Nannf.) S.J. Hughes	Untereiner & Naveau, 1999
C. spinifera (Ellis & Everhart) E. Müller *et al.*	*Exophiala* sp.	Müller *et al.*, 1987
C. villosa Samuels	*Exophiala* sp.	Müller *et al.*, 1987

1. This species complex includes CBS 125.88 (listed as *Capronia* sp. 1 in Untereiner *et al.*, 1999, *C. pilosella* in Untereiner, 1994, and *Cladosporium* sp. in Untereiner & Malloch, 1999 and Untereiner & Naveau, 1999) and CBS 552.78 (listed as *Capronia* sp. 1 in Untereiner *et al.*, 1999, *C. moravica* (Petrak) E. Müller *et al.* in Untereiner, 1994, and *Cladosporium* sp. in Untereiner & Malloch, 1999 and Untereiner & Naveau, 1999).
2. Includes strains listed as *Capronia pulcherrima* (Untereiner *et al.*, 1995) and *Capronia 'pulcherrima'* (Untereiner & Naveau, 1999).
3. This species complex includes CBS 164.92 (listed as *Capronia* sp. in Untereiner & Naveau, 1999, and *Capronia* sp. 1 in Untereiner & Malloch, 1999, and *Capronia* sp. 2 in Untereiner *et al.*, 1999).
4. Anamorph observed *in situ*, association confirmed experimentally.
5. Anamorph observed *in situ*, association not confirmed experimentally.
6. Includes isolates listed as *Capronia* sp. 1 (Untereiner, 1994; Untereiner *et al.*, 1995).
7. Includes isolates (DAOM 208453, DAOM 216387) listed as *Capronia moravica* in Untereiner (1994) and Untereiner *et al.* (1995).
8. Includes one isolate (DAOM 216384) listed as *Capronia moravica* in Untereiner (1994).
9. Includes an isolate listed as *Capronia* sp. 2 in Untereiner & Malloch (1999).

ing. In this paper, I will examine the characters used in the systematics of the *Herpotrichiellaceae* and highlight a number of problems that warrant attention in producing a more comprehensive taxonomy of this group of fungi.

Morphological characters employed in the taxonomy of *Capronia*

Capronia presently includes 58 species that possess septate, hyaline or pigmented ascospores, 8-, 16- or 32-spored fissitunicate asci, and minute, often setose ascomata that are solitary, gregarious or grouped within a basal stroma (Barr, 1991; Müller *et al.*, 1987; Untereiner & Naveau, 1999). Members of the genus lack pseudoparaphyses but periphysoids have been reported in a number of species (Barr, 1972, 1991; Eriksson, 1981; Müller *et al.*, 1987; Samuels & Müller, 1978; Untereiner *et al.*, 1995). The history of the taxonomy of *Capronia* and its synonyms has been summarized by Barr (1991), Holm (1975) and Müller *et al.* (1987).

Identification of species of *Capronia* on the basis of teleomorph characters is problematic. Current keys to members of this genus rely on ascospore septation, shape, and size, the number of spores per ascus, the presence or absence of setae or protuberances on ascomata, ascomatal shape and depth of submersion, the degree of stromatal development, and substratum (Barr, 1991; Müller *et al.*, 1987). However, a number of these characters, including the presence, size and arrangement of setae, the degree of submersion of ascomata, and substratum, are known to vary among collections identified as the same taxon (Barr, 1991; Untereiner, 1997; Untereiner & Naveau, 1999). The taxonomy of stromatic members of the genus is particularly difficult because stromatal development can vary considerably within species (see discussion below). Ascospore colour, size and septation and the number of spores per ascus appear to be consistent within species, but considerable overlap with respect to these characters exists among the members of the genus.

Four species of *Capronia* possess ascospores that exhibit distinctive colour reactions in Melzer's reagent, but the diagnostic value of this character has yet to be evaluated in other members of the genus. Other potentially valuable taxonomic characters that warrant further investigation include the IKI+ blueing reaction of the centrum discussed by Rossman (1980) and reported for members of the *Herpotrichiellaceae* by Winka *et al.* (1998), and the yellowing of the apical rings of the asci of *C. mansonii* and *C. munkii* in Melzer's reagent discussed by Untereiner (1995, 1997). Examination of the hymenium employing fluorescence microscopy and optical brighteners such as calcofluor has permitted the observation of new structures in other ascomycetes (Romero & Minter, 1988) and may also prove useful in the taxonomy of species of *Capronia*.

As noted above, species of *Capronia* lack pseudoparaphyses and possess periphysoids. Confusion regarding the type of hamathecium found in members of the genus by previous workers (Untereiner *et al.*, 1995) has likely resulted from the observation of filaments resembling pseudoparaphyses among the asci. These structures are common in collections of species of *Capronia* and can be demonstrated to be germ tubes that originate from ascospores retained within mature asci or the remnants of discharged asci (Untereiner, unpublished).

In culture, species of *Capronia* produce dark, slow-growing colonies that range from moist to exceedingly slimy, and most species exhibit both filamentous and yeast-like growth. The transition from hyphal to yeast-like growth is thought to be mediated by changes in oxygen tension and water activity, but there have been few studies documenting the effects of these factors on form of growth in the black yeasts (de Hoog *et al.*, 1994). *Capronia* is an anamorph-rich taxon (Table 1) and the majority of its members form conidial anamorphs that are species of *Exophiala* (including the synonym *Wangiella* McGinnis), *Ramichloridium* Stahel ex de Hoog *pro parte* and *Rhinocladiella* Nannf. These anamorphs elaborate percurrently or sympodially proliferating conidiogenous cells, and the former often appear annellate. A limited number of species of *Capronia* possess anamorphs that produce either phialoconidia (*Phialophora* Medlar) or conidia in acropetally elongating chains (*Cladophialophora* Borelli). *Capronia pleiospora* forms a mycelium that does not produce conidia.

With the exception of *C. montana* (Barr, 1991), *C. perpusilla* (Réblová, 1996) and an unnamed species of *Capronia* (Seifert & Okada, 1993; Okada *et al.*, this volume), anamorphs are not found in association with ascomata on natural substrata. Demonstrating anamorph–teleomorph connections in the *Herpotrichiellaceae* has depended, therefore, on obtaining mass- and single-ascospore isolates from specimens bearing ascomata (Müller *et al.*, 1987; Samuels & Müller, 1978; Untereiner 1995, 1997). Ascospores from air-dried specimens germinate on standard laboratory media for up to one year following collection; older specimens generally do not yield viable ascospores (Untereiner, unpublished). The culture of species of *Capronia* from the direct plating of substrata or ascomata is usually unsuccessful; the

isolates obtained, although also frequently anamorphic *Herpotrichiellaceae*, rarely correspond to cultures derived from ascospores obtained from ascomata present on the same specimen.

Considerable emphasis has been placed on anamorphs in recent taxonomic treatments of the *Herpotrichiellaceae* and the prevalence of black yeast anamorphs in this group figured prominently in the recircumscription of the genus *Capronia* (Müller *et al.*, 1987; Samuels & Müller, 1978). Anamorphs are also significant in the recognition of species of *Capronia* and are useful particularly in the separation of morphologically similar taxa found on the same substratum (Müller *et al.*, 1987; Untereiner, 1997; Untereiner & Naveau, 1999). The importance of anamorphs in the systematics of *Capronia* will likely increase as greater numbers of species are characterized in axenic culture. In fact, given the overlap and variation in key characters utilized to separate members of the genus *Capronia*, it may prove increasingly difficult to apply older epithets to collections for which anamorph data are not available.

A second aspect concerning the *in vitro* characterization and study of *Capronia* is an awareness of the potential for these species to complete their life cycles in axenic culture. The *in vitro* production of ascomata has been documented in only six members of the genus (Schol-Schwarz, 1968; Untereiner, 1994, 1995, 1997) but other species form ascomatal initials and immature ascomata in axenic culture (Untereiner, 1994, data not provided). The development of ascomata is dependent on the presence of compatible mating types in three members of the genus (Untereiner, 1995, 1997), but factors such as lighting, characteristics of the growth medium, and temperature of incubation are important in the maturation of ascomata of both heterothallic and homothallic species (Untereiner, unpublished).

Methods used to promote the *in vitro* production of teleomorphs in *Capronia* have not proven successful in the anamorphic *Herpotrichiellaceae*, but ascomatal initials and developmentally arrested ascomata have been reported for isolates of *Exophiala*, including strains of *E. dermatitidis* (Kano) de Hoog (de Hoog *et al.*, 1994; Untereiner, 1994, Untereiner *et al.*, 1995) and *Phialophora* sp. (Ajello & Runyon, 1953; Schol-Schwarz, 1970). These structures are extremely small and are typically observed in cultures only after prolonged periods (months) of incubation (neglect). The formation of ascomatal initials in anamorphic *Herpotrichiellaceae* is enhanced in isolates grown on natural, low-nutrient media such as sterile plant material or agars containing oatmeal (Untereiner, 1994; unpublished). The occurrence of ascomatal initials in the anamorphic *Herpotrichiellaceae* is likely under-reported because short periods of incubation (normally only 2–4 weeks) and media containing relatively high sugar concentrations (2–4%) are generally employed in the characterization of strains.

It is probable that the use of inappropriate culture media has also contributed to the degeneration of stains and the loss of key micro-morphological characters, particularly in clinical and older, ex-type isolates. Malt extract agar (2–4% malt extract) seems particularly ill-suited for the characterization of isolates of members of the *Herpotrichiellaceae*. Sabouraud's dextrose agar (2–4% glucose) and potato-dextrose agar (2% glucose) are unsuitable for the short-term preservation of *Capronia*, and the conidia, conidiogenous cells and hyphae formed on these media are often morphologically aberrant when compared to the same structures produced by isolates maintained on natural and semi-synthetic media. Modified Leonian's agar (0.625% maltose / 0.625% malt extract) (Malloch, 1981) and oatmeal agars have proven to be most useful in studies of the cultural characteristics and micro-morphology of members of the *Herpotrichiellaceae*, and I prefer the former for cultures to be stored under sterile, heavy mineral oil.

The use of DNA sequence data in taxonomic studies of the *Herpotrichiellaceae*

Molecular phylogenetic studies aimed at positioning the *Herpotrichiellaceae* within the *Ascomycota* and identifying their closest relatives have relied on the comparison of highly conserved sequences such as the small subunit (18S) ribosomal RNA (rRNA) and chitin synthase (CHS) genes (Berbee 1996; Bowen *et al.*, 1992; Haase *et al.*, 1995; Karuppayil *et al.*, 1996; Okada *et al.*, 1998; Spatafora *et al.*, 1995; Untereiner *et al.*, 1995; Winka *et al.*, 1998). Although phylogenies derived from analyses of both genes are similar in topology, chitin synthase genes (CHS1 and CHS2) lack sufficient variation for confidently resolving relationships above the level of family. The majority of phylogenies inferred from 18S rDNA sequences place the *Herpotrichiellaceae* (*Chaetothyriales*) as sister to the clade that includes members of the *Eurotiales* and *Onygenales*, but the publication of phylograms that include representatives of a larger number of orders have demonstrated the difficulty of studying relationships within the *Ascomycota* employing this gene (Silva-Hanlin & Hanlin, 1999; Winka *et al.*, 1998). Comparison of sequences of a subunit of the more slowly evolving nuclear RNA polymerase II gene (RPB2) offers greater promise for inferring the

deeper branches within the *Ascomycota* (Lui & Hall, 1999) but the phylogenetic structure of the filamentous ascomycetes will likely be resolved only through the construction of multi-gene phylogenies that include lichenized and non-lichenized taxa (Lutzoni *et al.*, 1999).

Investigations of relationships within the *Herpotrichiellaceae* have employed sequences from the 18S rRNA gene (Haase *et al.*, 1999, data not provided) and the 5' portion of the large (28S) rRNA subunit (Masclaux *et al.*, 1995; Untereiner & Naveau, 1999). The latter is a region shown to be phylogenetically informative at the genus to family level in filamentous ascomycetes (Holst-Jensen *et al.*, 1997; Rehner & Samuels, 1995; Seifert *et al.*, 1995). Phylogenies inferred from 28S sequences clearly demarcate anamorphic *Herpotrichiellaceae* from morphologically similar *Dothideaceae* and *Mycosphaerellaceae* (*Dothideales*) and have proven useful in identifying well-supported clades comprising morphologically and ecologically similar species of *Capronia*. However, 28S phylogenies do not resolve anamorph genera or species of *Capronia* with similar conidium ontogeny, patterns of ascospore septation and degree of stromatal development. This finding indicates that anamorph genera in the *Herpotrichiellaceae* are not monophyletic as circumscribed currently and suggests that morphology in the black yeasts may be a more accurate reflection of ecology than of phylogeny. The 18S rRNA gene lacks sufficient variation to resolve relationships within the *Herpotrichiellaceae* and the majority of internal branches of phylogenies based on analyses of this portion of the ribosomal repeat are weakly supported.

Studies of phylogenetic relationships of members of the *Herpotrichiellaceae* at or near the rank of species have focused on the comparison of sequences of the more rapidly-evolving internal transcribed spacers (ITS1 and ITS2). Investigations limited to comparisons of either the ITS1 or the ITS2 have not permitted the separation of species of anamorphic *Herpotrichiellaceae* (Attili et al, 1998; de Hoog *et al.*, 1999b; Uijthof, 1996; Uijthof *et al.*, 1997, 1998). Greater resolution has been achieved employing both spacer regions, particularly within species and species complexes. For example, analyses of ITS1–ITS2 sequences have resolved relationships among species of *Cladophialophora* (Gerrits van den Ende & de Hoog, 1999) and *Phialophora* (Yan *et al.*, 1995), and within the *Exophiala spinifera* (Nielson & Conant) McGinnis complex (de Hoog *et al.*, 1999a). A number of the well-supported clades revealed in these studies correlate with taxa defined on the basis of morphological and physiological criteria (de Hoog *et al.*, 1999a, 1999b; Gerrits van den Ende & de Hoog, 1999) as well as with phylogenies inferred from the comparison of ITS2 (de Hoog *et al.*, 1999b) and ITS1–ITS2-partial 28S sequences (Untereiner & Naveau, 1999).

Low levels of ITS variation have proven valuable in delimiting members of the *Herpotrichiellaceae*, particularly because clades resolved through ITS-sequencing often correspond to taxa defined on the basis of mating studies or morphological and physiological criteria. Variation in the ITS of well-defined species of *Capronia* (0–0.9%), anamorphic *Herpotrichiellaceae* including species of *Cladophialophora*, *Exophiala* and *Phialophora* (0.9–4.8%), and a complex of closely related *Capronia* possessing *Cladophialophora* anamorphs (0.9–6.6%) (Gerrits van den Ende & de Hoog, 1999; Uijthof *et al.*, 1998; Untereiner, unpublished; Untereiner & Naveau, 1999; Yan *et al.*, 1995) is low and falls within the range found in other species of ascomycetes (Seifert *et al.*, 1995). ITS sequence similarity has also been used to support anamorph–teleomorph connections within the *Herpotrichiellaceae*. For example, the level of ITS sequence variation between *Capronia semiimmersa* and *Phialophora americana* is comparable to the ranges observed within each taxon, and indicates that these species are teleomorph and anamorph of a single holomorph (Untereiner & Naveau, 1999). *Capronia acutiseta* has been connected to *Exophiala jeanselmei* (Langeron) McGinnis & Padhye on the basis of ITS sequence similarity (data not provided) (Rogers *et al.*, 1999) but additional, non-molecular evidence to support this suggestion is lacking.

The lack of resolution in phylogenies inferred from rDNA sequence data, particularly at the level of species and genus, argues strongly in favour of the use of combined data sets that include sequences from other regions of the nuclear ribosomal repeat or sequences from multiple loci. The former approach has been employed in species-level investigations using restriction profiles of the 18S or ITS in conjunction with ITS sequences (Attili *et al.*, 1998; de Hoog *et al.*, 1999b; Uijthof *et al.*, 1997; Yan *et al.*, 1995). Analyses of combined ITS–28S sequences have proven useful for improving the resolution within clades revealed in separate analyses of these regions (Untereiner & Naveau, 1999). Phylogenies inferred from the combined sequences of the 28S rRNA, mitochondrial small subunit rRNA, *rod*A hydrophobin, and β-tubulin genes have clarified species-level relationships in members of the *Hypocreales* (O'Donnell *et al.*, 1998) and *Eurotiales* (Geiser *et al.*, 1998), and it is likely that compilation and analyses of similar data sets will help to resolve

relationships of members of the *Herpotrichiellaceae* that demonstrate little or no ITS sequence variation.

Prospects for future research in the systematics of *Capronia*

Mycologists working to construct a comprehensive taxonomy of *Capronia* face a number of problems, the most significant of which is the paucity of specimens and cultures of the members of this genus. For example, 32 of the 58 species of *Capronia* described to date (including species of the synonymous genera *Berlesiella* Sacc., *Dictyotrichiella* Munk and *Herpotrichiella* Petrak) are known only from the type specimen or from three or fewer collections made by the describing author from the type locality. Cultures are available for 21 species of *Capronia* (Table 1) but only 11 members of the genus are represented by more than a single isolate.

The stromatic *Capronia* are species that warrant careful taxonomic study. This group, which includes *C. commonsii* (Ellis & Everhart) M.E. Barr, *C. episphaeria* (Peck) M.E. Barr, *C. fungicola* and *C. nigerrima*, is distinct in forming well-developed pulvinate or basal stromata on the ascomata of *Diatrypaceae*, *Melanommataceae* and *Xylariaceae*. These species tend to be more conspicuous than *Capronia* with smaller, solitary ascostromata, and are probably among the most frequently collected members of the genus. Species of stromatic *Capronia* are separated on the basis of differences in ascospore size and septation, and by the presence or absence of setae or ascomatal protuberances (Barr, 1991; Samuels & Müller, 1978). Collections of some species are reported to vary considerably with regard to the degree of stromatal development and the size of ascomata (Bigelow & Barr, 1969; Mathiassen, 1989, 1993). The relationships of *C. fungicola* and *C. nigerrima*, the only members of this group studied in axenic culture, to other *Capronia* species, have not been resolved clearly in phylogenies inferred from rDNA gene sequences (Untereiner & Naveau, 1999). The affinities of the stromatic *Capronia* to *Berlesiella hirtella* (Bacc. & Avetta) Sacc., a species with a well-developed stroma described from *Sambucus*, also require clarification.

Other *Capronia* species not represented in culture collections and molecular phylogenies are the members of the genus with fusoid or elongate ascospores. These species occur primarily on the leaves and stems of *Ericaceae* and herbaceous plants, and include taxa with polysporous asci (placed formerly in the genus *Polytrichiella* M.E. Barr) or 8-spored asci. A number of these species are unusual in possessing hyaline or light olivaceous ascospores (e.g., *C. albimontana* (M.E. Barr) E. Müller *et al.*, *C. fusispora* (M.E. Barr) E. Müller *et al.*, *C. longispora* (M.E. Barr) E. Müller *et al.*, *Herpotrichiella longispora* Remler) (Barr, 1959, 1972, 1991; Remler, 1979). Phylogenies inferred from rDNA sequences demonstrate that species of *Capronia* with ellipsoidal, dark brown, muriform ascospores and 8-spored asci form a well-supported lineage in the *Herpotrichiellaceae* (Untereiner & Naveau, 1999). It is reasonable to suggest that similarities in ascospore shape and pigmentation also reflect the close relationship of taxa with fusoid and/or lightly pigmented ascospores. Testing this hypothesis awaits the study of these species in axenic culture.

Substratum preference and specificity are recurring themes in the taxonomy of *Capronia* but we still have a limited understanding of the activities and host ranges of these fungi. The collection and culture of additional members of the genus *Capronia*, particularly species known only from the type specimen, are logical first steps in studies of the ecology and distribution of the *Herpotrichiellaceae*. Experimental evidence of their enzymatic capabilities is also required to answer questions related to host preference and the taxonomic importance of this character. Clearly, study of the life histories of members of the *Herpotrichiellaceae* will remain incomplete until we are able to elucidate the role(s) of these fungi in natural systems.

Acknowledgments

I am grateful to Gary McNeely and James Scott for providing suggestions for the improvement of this manuscript. Financial support to participate in the the IX International Congress of Mycology was provided by the Brandon University Research Account and an operating grant from the Natural Sciences and Engineering Research Council of Canada.

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