

INTRODUCTION

The *Hypocreales* is an order of *Euascomycetes* that includes over one thousand described species and related asexual fungi. An overview of the hypocrealean fungi by Rossman (1996) provided a synopsis of their economic importance as plant pathogens, agents of biological control, and producers of powerful antibiotics and mycotoxins. Although the group referred to as hypocrealean fungi now includes many asexually reproducing fungi, the order *Hypocreales* is herein dealt with in the traditional sense referring only to those fungi that reproduce sexually. For the past 100 years the *Hypocreales* have been a repository for light to bright-colored, soft-texture, perithecial ascomycetes. Rogerson (1970) presented a detailed history of the *Hypocreales* and reviewed changes in the circumscription of the order up to that time. His publication included useful keys to the genera of both the *Hypocreales* and *Clavicipitales*, followed by a list of genera, each with the literature citation of the original descriptions and type species. These keys were based on a review of the literature rather than on first-hand knowledge of most genera. Rogerson (1970) accepted 115 genera in the *Hypocreales* and listed 26 generic synonyms. Since 1970, 58 additional genera

have been included in the *Hypocreales*. For the present work all available type specimens were examined of the type species in the 199 genera considered to belong in the *Hypocreales* (Rogerson, 1970; Hawksworth *et al.*, 1995). Based on these studies, 56 genera including six newly described genera with 43 generic synonyms are accepted in three families, *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae*, of the *Hypocreales*. Fourteen genera with two generic synonyms are included in the *Niessliaceae* and six genera with one generic synonym are placed in the *Clavicipitaceae*. Both the *Niessliaceae* and the *Clavicipitaceae* are now considered either part of or closely related to the *Hypocreales*, however, neither of these families are considered further in this study except as genera to be excluded from the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae*. The remaining 83 genera are excluded from the *Hypocreales* and redispersed in their appropriate family and order, see Table I (page 12) and Checklist (page 171). For 16 genera previously placed in the *Hypocreales* the type specimen was either not located or not sufficient to make a modern taxonomic evaluation of the type species. These genera are listed in the excluded genera with notes on their status.

MATERIALS AND METHODS

Herbarium specimens were rehydrated by placing a drop of water directly on the ascomata for a few minutes. Ascomata were routinely mounted in cotton blue in lactic acid or in water that was later replaced with 50% aqueous glycerol. Other stains were used such as cotton blue, acid fuchsin, Melzer's reagent and ammoniacal Congo Red. The test for color reaction of the ascomata was made with 3% KOH and 100% lactic acid. If a color change occurs other than the normal change from rehydration, this is indicated as KOH+. Longitudinal median sections were made using a freezing microtome. To make sections, ascomata were picked off the substratum, rehydrated briefly in water, placed on a freezing stage, and mounted in Tissue-Tek (Miles, Inc., Elkhart, IN). Sections of ascomata and stromata were approximately 15 μ m thick. Ascomatal wall structure is described based on longitudinal median sections.

Cultures of fresh specimens were obtained by the isolation of single and mass ascospores in the laboratory. Recently collected fresh or air-dried specimens were rehydrated with water. Several ascomata were placed in a drop of sterile water in the well of a hanging drop slide. The ascomata were smashed with a needle, releasing asci and ascospores into the water that was stirred vigorously in order to distribute the centrum

contents evenly. The drop of water with asci, ascospores and remnants of the ascomata was placed on a plate of agar using a sterile micropipette. Firm cornmeal-dextrose agar with antibiotics (Difco Corn Meal Dextrose agar plus 2% Difco agar with about 2 mg/L each of streptomycin, tetracyclin and neomycin) was used for primary isolation. The drop was spread over the surface of the agar plate using a sterile blunt glass rod. Plates were incubated overnight at room temperature. The next day the agar surface was examined using a 50 \times binocular dissecting microscope with transmitted light. Germinated single or mass ascospores with subtending agar were picked out of the agar with a fine insect pin and transferred to agar plates and tubes. Several ascospores were placed in a drop of cotton blue in lactic acid for observation of germination and to check the identity of the isolated ascospores. Alternatively, some cultures were isolated using a micromanipulator as described in Samuels (1976a).

Cultures were grown for two weeks under alternating near-UV light (12 h on, 12 h off) at room temperature (about 25° C) on the following media: cornmeal agar (CMA) (Difco Corn Meal Agar), V-8 juice agar (V-8) (200 ml V-8 juice, 3 g CaCO₃, 20 g Difco agar, 800 ml distilled water), potato-dextrose agar (PDA) (Difco Potato Dextrose Agar), potato-sucrose agar (PSA), and

potato-carrot agar (PCA). At that time detailed observations of colony characteristics and sporulation were noted. Plates were returned to the light and further events were observed as they occurred, e.g., formation of ascomata. Cultures derived from mass and single ascospores were placed on CMA slants in screw top tubes and placed in a cold room (10°C) for future reference. Specimens from which cultures were obtained, dried cultures and living cultures were deposited at NY or BPI. Abbreviations used for herbaria are those of Holmgren *et al.* (1990). All specimens cited have been examined unless otherwise noted.

For each genus of the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae*, the accepted generic name and synonymous generic names with their respective types are listed. This is followed by a generic description and a discussion of the origin and current state of knowledge about that genus, along with an account of each generic synonym. Next is presented the nomenclator and description of the type species as well as a description of each type species of the generic synonyms based on our examination of the type specimen. If the genus is relatively small, all additional species are described along with a key to species. For relatively large genera that have not been recently monographed, or those for which the generic concept is not yet well-delineated, the included species are listed along with relevant references. For genera that have been recently monographed, reference is made to that publication. Species that are excluded from an accepted genus are cited in the excluded genera if their status is known, however, not all described species are considered here, particularly those of very large genera. For genera excluded from the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae* (see also Table I), a generic description and a description of the type species are presented, based on an examination of the type specimen, along with a discussion of the placement of the genus.

CHARACTERISTICS OF THE *BIONECTRIACEAE*, *HYPOCREACEAE*, AND *NECTRIACEAE*

Following is an explanation and evaluation of the morphological and biological characteristics of the three families of hypocrealean fungi. The discussion includes definitions of the characteristics and the range of variability that occurs within the three families.

Stroma.— A stroma is any vegetative tissue that subtends or surrounds the ascomata. The stroma may be pseudoparenchymatous, composed of hyphae that have

lost their hypha-like structure, prosenchymatous, consisting of cells that form a tissue but retain their hyphal integrity, or reduced to a hyphal subiculum. Pseudoparenchymatous tissues are described using the terminology defined and illustrated in Hawksworth *et al.* (1995). Characteristics of the stroma are considered to have importance at both the generic and species levels. The structure of an individual stroma may vary from prosenchymatous to pseudoparenchymatous forming distinct regions. Surface structures such as free hyphal ends and setae in the stroma are noted. Placement of the ascomata within the stroma and location of the stroma within the substratum are characteristic of certain genera. Within the *Bionectriaceae*, the ascomata of *Valsonectria* (Fig. 15 b–c) are immersed in a stroma that is itself immersed in host tissue, and in *Clibanites* (Fig. 1 g–h) the ascomata are immersed in a thin, poorly developed stroma that is differentiated into regions. The stroma is often lacking or reduced to a subiculum as in *Dimerosporiella* (Fig. 4a) and *Nectriopsis* (Fig. 9 a, b). A striking exception of a genus with a well-developed stroma in the *Bionectriaceae* is *Mycocitrus* that has a very large stroma surrounding the stem of living bamboo with ascomata developing at the surface. Within the *Hypocreaceae*, most genera have ascomata embedded in a more or less extensive pseudoparenchymatous stroma. The stroma may be large and expansive as in *Hypocreopsis* (Fig. 4 h–i), in which the stromata are lobed and spreading up to 20 cm diam across the substratum. In *Hypocrea* (Figs. 4 f, g, 17 e–h) the stroma may range from 1 mm to 3 cm or more in diameter; it may or may not be stipitate as in *Podostroma* (Figs. 4 l, 20 a), in which the stromata are often clavate extending up to 6 cm high. In the related genera *Arachnocrea* (Figs. 4 e, 16 a), *Protocrea* (Fig. 4 m, n) and *Sphaerostilbella* (Fig. 22c), the stroma is weakly developed existing only as a subiculum. In some species of *Hypomyces* (Figs. 4 j, k, 18 a–h) the stroma may completely cover and obliterate the hymenium of the host, particularly those occurring on members of the *Agaricales*, or the stroma may be a thin subiculum beneath which the host fungus can still produce viable basidiospores. Within the *Nectriaceae* the stroma may be inconspicuous or absent as in most species of *Cosmospora* (Figs. 22 f, 26 b, c), or it may be basal, consisting of a pseudoparenchymatous pad of tissue giving rise to two or more ascomata. The pseudoparenchymatous basal stroma is often continuous with the outer region of the ascomatal wall and is frequently associated with the anamorph, as in *Nectria sensu stricto*, in which the basal stroma is initially associated with a sporodochial, synnematal or pycnidial anamorph.

Ascomata and ascomatal wall structure.— Ascoma-

ta of the *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* are generally light- to bright-colored, soft-textured, uniloculate perithecia, rarely cleistothecia. Unless stated otherwise, the described ascomata are perithecia. The six genera with cleistothecia lack a distinct hymenium and often have globose, deliquescent asci with globose to ellipsoid, non-septate or one-septate ascospores. Hypocrealean fungi in the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae* have hyaline, white, pale yellow, orange, red, to purple, brown and even dark brown ascomata. The genus *Gibberella* (Fig. 29 c) and its allies, *Stalagmites* and *Pleogibberella*, have ascomata that appear black macroscopically but are bluish-purple microscopically. Another genus having relatively dark ascomata is *Allonectella* (Fig. 25 k) with dark pigments in the ascomatal cell walls that dissolve in KOH but do not change color. For all genera the ascomatal color is slightly darker in dried specimens; descriptions are based on the color of fresh or rehydrated ascomata. The nature of the ascomatal pigmentation, specifically the reaction in KOH or lactic acid, correlates with other characteristics useful in defining relationships within genera and families. The occurrence of KOH+ ascomata is often correlated with thickened walls of the ascomatal wall cells as well as the presence of pores between the cells (Samuels & Brayford, 1993). Within the *Hypocreaceae*, some species of *Hypomyces* and *Hypocrea* have ascomata and/or stromal tissues that become red in KOH, e.g. *Hypomyces lactifluorum* and *Hypocrea pallida*. The significance of this color reaction does not, however, seem to extend above the species level in these genera.

Within the *Bionectriaceae* and *Nectriaceae* ascomatal wall structure is useful in defining genera, and this structure correlates with other morphological characteristics of both the teleomorph and anamorph. Characteristics of the ascomatal wall include surface cells, ascomatal wall anatomy, specifically the thickness of the wall itself measured in longitudinal section, the recognizable regions within the ascomatal wall and the characteristics of the cells in each region including their size, shape, and wall pigmentation and thickness. The ascomatal wall of hypocrealean fungi generally consists of one to three regions of cells with each region composed of two to four cell layers. The outer region is usually composed of angular to globose cells with walls that may or may not be thickened. The inner region is almost always composed of thin-walled, hyaline cells elongated parallel to the centrum. The walls of the ascomatal wall cells are described as thickened, about 1 μm thick, or thin, less than 1 μm thick. If extraordinary, the characteristics of the ascomatal wall are described in detail.

In the *Hypocreaceae*, the ascomatal wall features are

generally the same in all genera and are thus not used as defining characters. In the *Bionectriaceae* and *Nectriaceae* the structure of the wall may be characteristic of the genus; e.g., the ascomatal wall of *Hydropisphaera* consists of large, thin-walled, globose cells; it can become extremely thick, over 100 μm in *H. pachyderma*. In *Neonectria* (Fig. 33 d–f), particularly in species having a distinctive ‘mammoidea-type’ ascomatal wall structure, the cells near the ascomatal surface are thick-walled and flattened, forming a *textura epidermoidea* that results in a varnished appearance. In some species of this group an additional outer layer of loose cells obscures the *textura epidermoidea*, yet the distinctive structure is evident in longitudinal section. Some genera have characteristic features on the surface of the ascomata. In *Albonectria rigidiuscula* (Fig. 25 c, d) and *Bionectria byssicola*, the ascomata have large wart-like projections on the surface, and the outermost walls of the outer wall cells are greatly thickened, a characteristic described as capitate. Most species of *Ijuhya* have fasciculate, triangular hairs around the ostiole, while species of *Trichonectria* have long, solitary, hyaline, thick-walled hairs on the surface of the ascomata. The presence or absence of hairs is generally not considered a definitive generic character, unless it correlates with other characters such as ascomatal wall structure and anamorph. For example, all species of *Lanatonectria* (Fig. 22 g) have bright yellow, spinulose hairs on the red, KOH+ ascomata as do the conidiomata of their anamorphs. Most genera have more subtle ascomatal structures such as the large, loose, globose outer wall cells of *Haematonectria* and *Calonectria*.

Centrum characters, such as the presence/absence of the apical paraphyses and the paraphyses lining the ostiole, are similar for all hypocrealean fungi. The ostiole canal is always paraphysate in perithecial members of the *Hypocreales* and the characteristics of the paraphyses are described only if they are unusual or distinctive. Interthecial elements in hypocrealean fungi are, by definition, apical paraphyses; these may often appear as deliquescent strands in mature ascomata, although they may be present as thin-walled, inflated cells as they go through the process of deliquescent. The non-hypocrealean nature of certain soft-textured, light- to bright-colored, uniloculate perithecial fungi is often indicated by the presence of true paraphyses, a characteristic not found in the *Hypocreales*.

Asci.— The asci of hypocrealean fungi are unitunicate. They may or may not have a ring at the apex. The presence of an apical ring generally correlates with ascospore size and shape and is useful only in defining species. In hypocrealean species having relatively short ascospores, i.e. less than 20 μm , the asci have an apical

ring; species having elongate or large ascospores generally lack an apical apparatus. For example, *Ophionectria trichospora* has long fusiform ascospores and asci that deliquesce at maturity and lack any form of ascular apical apparatus. In many hypocrealean species the relatively short ascospores are forcibly discharged. In others the asci deliquesce, releasing the ascospores into the centrum. As the soft-textured ascomata periodically dry out, and swell up again when rehydrated, aided by the gelatinous, deliquescing apical paraphyses, the ascospores are extruded *en masse* through the ostiole and appear as a cirrus or column emerging from the ascumatal apex. Neither the apex nor any other part of the ascus or centrum reacts with iodine.

Ascospores.— Within the *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae*, the ascospores are typically ellipsoid to fusiform with rounded apices, although there is some variability. Ascospores may be allantoid as in *Nectria miltina* (Fig. 31 f), globose, non-septate as in *Neocosmospora* (Fig. 33 b), or appear as globose part-ascospores, the result of disarticulating, naviculate ascospores in *Hypocrea* (Fig. 17 g, h). The longest ascospores are produced by *Ophionectria trichospora* (Fig. 34 b) that has long fusiform ascospores over 180 μm long. Within these families, ascospores are never narrowly cylindrical and filiform, a characteristic of the *Clavicipitaceae*. The ascospore apices of many species of *Hypomyces* (Fig. 18 d–h) are apiculate, and in the genus *Paranectria* the ascospores are characteristically attenuated. Ascospore color is generally hyaline to golden-yellow or golden-brown, as in *Calostilbe*, *Cosmospora*, and *Rubrispora* (Fig. 35 d–e) in the *Nectriaceae*. However, there are some amazing exceptions. An undescribed species of *Nectria sensu lato* from Madeira has translucent red ascospores, while in *Viridisporea* the ascospores may be green, particularly when grown on a culture medium rich in simple carbohydrates (Polishook *et al.*, 1991). Species in the *Hypocrea gelatinosa*-complex of the *Hypocreaceae* typically have green ascospores. Neither germ slits nor germ pores are known in the *Hypocreales*. Ascospore ornamentation in the hypocrealean fungi is variable, ranging from smooth to verrucose or striate, and is sometimes characteristic of a genus. For example, ascospores of species of *Hypomyces* are often verrucose to tuberculate; in *Cosmospora* and *Xenonectriella* ascospores tend to be verrucose and golden-brown; in *Hydropisphaera*, *Ijuhya*, and *Protocreopsis* (Figs. 11 f, h–i, 12 f, g) the ascospores are generally striate.

Although many species in the *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* have one-septate ascospores, ascospore septation may be variable within genera. Traditionally the genus *Nectria sensu lato* has

included species with one-septate, non-apiculate ascospores that do not disarticulate at the septum. However, in *Nectria sensu stricto* ascospores are variable in size and septation, ranging from non-septate, allantoid, 5–7 μm long in *N. miltina* to large, muriform, up to 40 μm long in *N. pseudotrichia* (Rossman, 1989). Within *Ijuhya*, the ascomata appear remarkably similar; however, the ascospores range from one-septate, very small, to large, transversely septate or muriform, apparently increasing in size and septation with elevation (Rossman, 1983; Samuels, 1988). Within the three families of the *Hypocreales* considered here, disarticulating ascospores occur primarily among members of the *Hypocreaceae*. Both the *Niessliaceae* and *Clavicipitaceae* include species with disarticulating ascospores.

Anamorphs.— The anamorphs of the *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* are primarily phialidic, producing hyaline or bright-colored conidia, although there are some exceptions. They are diverse and have been assigned to numerous anamorph genera as enumerated by Samuels and his co-workers (Samuels & Rossman, 1979; Samuels & Seifert, 1987). Conidiomata range from non-existent to synnematos, sporodochial or pycnidial. Conidia may be aseptate or septate, ranging from having one or multiple transverse septa to being muriform, and are generally hyaline or slightly yellow to yellow-brown or green, but not brown or black. As in other ascomycetes, characteristics of the conidia, such as color and septation, often correlate with those of the ascospores. Anamorphs of hypocrealean fungi have been particularly useful in defining genera of teleomorphs; this trend has generally been corroborated using sequence data (O'Donnell, 1993; Rehner & Samuels, 1994, 1995; Spatafora & Blackwell, 1993, 1994). In addition to anamorph species that have known teleomorphs, a vast number of anamorphs exists without known teleomorphs, although they are undoubtedly allied with hypocrealean fungi. Many of these apparently asexual species are included in anamorph genera that have some species with known hypocrealean teleomorphs. Asexual states of most genera in the *Bionectriaceae* are reduced, often described as *Acremonium*-like, although there are exceptions such the anamorphs of *Bionectria* classified in *Clonostachys* (Fig. 1 e, f) (Schroers *et al.*, 1999). Species of *Stilbocrea* and *Peethambara* having synnematos anamorphs and multiseptate, ornamented conidia are placed in *Didymostilbe* (Seifert, 1985), related to *Albosynnema*, *Solheimia*, and *Virgatospora*. Increasing numbers of primarily anamorphic fungi are now placed in the *Hypocreales* (Gams *et al.*, 1998b; Glenn *et al.*, 1996; Ogawa *et al.*, 1997; Okada *et al.*, 1997; Seifert *et al.*, 1997). Major modern monographs of hypocrealean

anamorph fungi related to the *Hypocreales* include: *Acremonium* (Gams, 1971), *Cladobotryum* (Gams & Hoozemans, 1970; Rogerson & Samuels, 1994), *Cylindrocarpon* (Booth, 1966), *Cylindrocladium* (Crous & Wingfield, 1994; Peeraly, 1991); *Fusarium* (Booth, 1971; Gerlach & Nirenberg, 1982; Nelson *et al.*, 1983), *Gliocladium* (Seifert, 1985), *Stilbella* (Seifert, 1985), *Trichoderma* (Bissett, 1984, 1991 a, b; Domsch *et al.*, 1980; Gams & Bissett, 1998; Rifai, 1969a; Samuels *et al.*, 1998b), and *Tubercularia* (Seifert, 1985). Except for the genus *Acremonium*, these large genera of anamorphic fungi are now sufficiently well-defined, and they have known teleomorphs only in the *Hypocreales*.

Geographic distribution.— Although members of the *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* occur worldwide, the greatest diversity of species in most genera appears to be in warm temperate and tropical regions. In general the teleomorphs of hypocrealean fungi are found more commonly in the tropics while the anamorphs are known from temperate regions, particularly as plant pathogens, for example, *Haematonectria haematococca* and its anamorph *Fusarium* sp. The few regional studies of the *Hypocreales* include outdated accounts of species in North America (Seaver 1909 a, b; 1910 a, b) and Sri Lanka as Ceylon (Petch, 1912, 1920), and more recently England (Booth, 1959; Petch, 1936, 1937, 1938, 1941), New Zealand (Dingley 1951 a, b; 1952 a, b), Venezuela and adjacent countries (Dennis, 1970), and North Sulawesi, Indonesia (Samuels *et al.*, 1990). Lists have been published of the *Hypocreales* found in the Guyana Highlands region of northern South America (Rogerson *et al.*, 1990) and French Guiana (Courtecuisse *et al.*, 1995). All of these treatments are incomplete because of the increased number of taxa, changed taxonomic concepts, or both. A model of geographic differentiation within a group of *Gibberella* species has been published by O'Donnell *et al.* (1998).

Substrata and pathogenicity.— Members of the *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* are associated with a variety of substrata, ranging from living and decaying plant material, dung, and soil to fungi, insects, and, occasionally, animals and humans. Aggregations of ascospores of species in the *Nectriaceae* are often found in quantity erupting through the bark of recently killed woody substrata, especially in tropical regions. Some species appear to function as endophytes residing harmlessly in the healthy plant but sporulating profusely following the death of the host. Despite their primarily saprobic nature, many hypocrealean fungi, especially members of the *Nectriaceae*, are facultative, sometimes virulent plant pathogens, causing serious problems on crop plants, often encountered in the

anamorph. These include the *Fusarium decemcellulare* anamorph of *Albonectria rigidiuscula*, cause of cushion and green point gall of cacao; *Cylindrocladium* anamorphs of species of *Calonectria*, cause of *Eucalyptus* dieback, twig dieback of *Ilex*, potato tuber rot, and other diseases; the *Fusarium sambucinum* anamorph of *Gibberella pulicaris*, cause of hop canker, potato storage rot, and root rot of many crops, and many other species of *Gibberella* and their anamorphs, including *F. oxysporum*, cause of root rots, foot rots, and wilt diseases of numerous crop plants; *Nectria cinnabarina*, often seen as the *Tubercularia* anamorph, coral spot of fruit and hardwood trees; and *Neonectria coccinea*, cause of beech bark disease. In the *Bionectriaceae* the few plant-pathogenic species include *Nectriella pironii* causing galls on stems and leaves of woody plants in Florida, and *Mycocitrus aurantium*, a species that appears to exist as an endophyte in living bamboo.

Although often unrecognized as such, a majority of hypocrealean fungi are mycoparasitic or mycosaprobic, and are extremely versatile in their abilities to exploit fungal substrata (Gams *et al.*, 1999). In some species the fungicolous nature is conspicuous with ascospores developing on other fungi, as, for example, *Cosmospora episphaeria* on old carbonous black pyrenomycetes, *Dimerosporiella* on *Meliola* and related tropical leaf surface fungi, species of *Hypomyces* parasitizing mushrooms, and *Nectriopsis violacea* growing on myxomycetes. Less conspicuous are the hypocrealean fungi that appear to occur on old rotting wood, but actually are necrotrophic on the fungal hyphae in the wood. These include many of the biocontrol fungi in the *Hypocrea-Trichoderma* complex, such as *T. virens* and *T. harzianum*, and *Bionectria ochroleuca* often encountered as its anamorph, *Clonostachys rosea*. A number of hypocrealean species occur on lichens such as species of *Pronectria* and *Xenonectriella*. Although primarily fungicolous, the genus *Cosmospora* also includes insecticolous species such as *C. flammea* and *C. aurantiicola*, having in common the ability to degrade chitin as a substrate. Several genera occur on dung, including *Mycoarachis*, *Roumegueriella* and *Selinia* in the *Bionectriaceae* and *Aphysiostroma* in the *Hypocreaceae*. Two hypocrealean genera, *Halonectria* and *Kallichroma*, are considered marine fungi.

Definition of the order and families of the *Hypocreales*

The *Hypocreales* as a taxonomic entity was originally recognized as a family, the *Hypocreaceae* in the order *Sphaeriales*, and later elevated to the ordinal level as

the *Hypocreales* (Lindau, 1897). The most significant advance in circumscribing the *Hypocreales* was Luttrell's (1951) recognition of the distinctive *Nectria*-type centrum. This centrum type is characterized by apical paraphyses, developing from meristematic tissues in the upper part of the centrum, extending downwards to the base of the fruiting body, and dissolving at maturity. The *Nectria*-type centrum is correlated with other characteristics, the most conspicuous of which are generally light- to bright-colored, soft-textured, uniloculate, perithecial, rarely cleistothecial, ascomata, lack of interthecial elements at maturity, unitunicate asci, and phialidic anamorphs that have light- to bright-colored conidia, conidiophores, and cultures. In longitudinal sections of young ascomata the *Nectria*-type centrum is observed as apical paraphyses developing from an apical meristem. In mature *Nectria*-type ascomata, remnants of dissolving apical paraphyses may be evident in crush mounts but often the interthecial elements are lacking. The *Nectria*-type centrum development has been confirmed for numerous species in the *Hypocreales* including: *Bionectria ochroleuca* (as *Nectria gliocladioides*, Hanlin, 1961) and *Hydropisphaera peziza* (as *Neuronectria peziza*, Hanlin, 1963a) in the *Bionectriaceae*; *Hypocrea avellanea*, *H. citrina*, and *H. spinulosa* (Canham, 1969; Carey & Rogerson, 1977; Doguet, 1957), *Hypomyces aurantius*, *H. lactifluorum*, *H. polyporinus*, and *H. trichothecoides* (Carey & Rogerson, 1981; Hanlin, 1963b, 1964; Samuels, 1973c), and *Sarawakus lycogaloides* (Rifai, 1969b) in the *Hypocreaceae*; and *Cosmospora episphaeria* (as *Nectria episphaeria*, Strikmann, 1961), *Gibberella pulicaris* (Parguey-Leduc, 1964), *Nectria aurantiicola* (as *Sphaerostilbe aurantiicola*), and *N. austroamericana* (as *Thyronectria austroamericana*, Luttrell, 1944; Seeler, 1940), and *Neocosmospora vasinfecta* (Doguet, 1956) in the *Nectriaceae*.

The three families of hypocrealean fungi considered here, namely the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae*, correspond to the three major phylogenetic clades revealed by Rehner & Samuels (1994, 1995) based on analyses of 28S rDNA gene sequences, and Ogawa *et al.* (1997) based on analyses of both 18S and 28S rDNA gene sequences. These major clades also correlate with morphological characteristics of both the sexual and asexual states. The clade referred to as the *Hypocrea* clade is herein regarded as the *Hypocreaceae*, and includes *Hypocrea*, *Hypomyces*, and related genera. Another clade referred to as the *Bionectria* clade is herein regarded as the *Bionectriaceae* and includes most of the nectrioid genera that have pallid, KOH-, superficial or immersed ascomata and non-, one- or multiseptate, non-apiculate, non-disarticulating ascospores. The third clade or *Nectria* clade encom-

passes the *Nectriaceae* and includes primarily genera having red to dark purple, KOH+ ascomata and non-, one-, multiseptate or muriform, non-apiculate, non-disarticulating ascospores.

One of the two remaining families in the *Hypocreales* is the *Niessliaceae* or black hypocrealean fungi. This family consists of genera that have small, soft-textured, brown to black ascomata and phialidic anamorphs. The dark pigments in the peridium neither change color nor diffuse in KOH or lactic acid, thus differentiating the *Niessliaceae* from members of the *Bionectriaceae* and *Nectriaceae* having brown ascomata. Although none of the members of the *Niessliaceae* have been critically studied to determine their centrum development, the structure of immature and mature ascomata indicates a *Nectria*-type centrum. The phialidic anamorphs of members of the *Niessliaceae* suggest hypocrealean affinities for these fungi as discussed by Samuels & Barr (1998). The other family, the *Clavicipitaceae*, recognized as the order *Clavicipitales* by Rogerson (1970) and others, has historically been placed near the *Hypocreales* based on the light- to bright-colored ascomata and unitunicate asci. Recent molecular data suggest that the *Clavicipitales* represent one or more lineages sharing a close common ancestor with or derived from the *Hypocreales* and should be recognized as a family within the *Hypocreales* (Gams *et al.*, 1998b; Glenn *et al.*, 1996; Spatafora & Blackwell, 1993, 1994). A fundamental incongruence exists between the molecular data and morphological studies concerning the type of centrum development of the *Clavicipitales* and *Hypocreales* as discussed by Rossman (1996). In the *Clavicipitaceae* (\equiv *Clavicipitales*) asci develop from a pseudoparenchymatous basal pad (White, 1997), while in the *Hypocreales* exclusive of the *Clavicipitaceae* asci develop from a broad region of ascogenous hyphae lining the centrum. Ascumatal wall structure and texture, ascal and ascospore characteristics, and habitat preferences all suggest that the *Clavicipitaceae* are distinct from other families in the *Hypocreales*. Definitive studies of clavicipitalean fungi are needed to reconcile the differences between the *Nectria*-type centrum development characteristic of the *Hypocreales* and that occurring in the clavicipitalean lineage.

Excluded Genera

A number of genera initially placed in the *Hypocreales* because of their bright-colored, soft-textured ascomata have been previously or are herein removed from the order (Gams & Müller, 1980; Palm *et al.*, 1996; Rossman, 1987; Samuels & Hallett, 1983; Samuels & Ross-

man, 1992; Samuels *et al.*, 1993). Such misplaced genera are accounted for in the section on excluded genera. The genera excluded from the *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae* in this study are placed among 19 families in 12 orders of ascomycetes as well as one basidiomycetous genus, *Mycaureola* (Porter & Farnham, 1986). Two genera are uniloculate, discomycetous loculoascomycetes (Rossman, 1987), while a number of excluded genera have true apothecia and belong in the *Helotiales* and *Pezizales* or are lichenized fungi and placed in the *Lecanorales*. Many pyrenomycetes confused with hypocrealean fungi are herein placed in the *Diaporthales* and *Xylariales*, often in the *Hyponectriaceae* and *Thyridiaceae*. Genera for

which ordinal placement is most difficult are those having immersed ascomata. The immersed habit often results in a simplification of ascomatal morphology, thus careful observations must be made of centrum characteristics. Immersed non-hypocrealean genera include: *Charonectria* and *Hyponectria*, differentiated from the *Hypocreales* by the presence of apically free paraphyses, now placed in the *Hyponectriaceae*, *Xylariales*; and *Cryptoleptosphaeria*, *Cryptonectriella* and *Schizoparme* also having apically free paraphyses and asci with a conspicuous ascal ring, now placed in the *Diaporthales*. Several genera are placed in the *Niessliaceae* and *Clavicipitaceae* of the *Hypocreales*.

Table I. Disposition of genera previously included in the *Hypocreales** Included in Names in Current Use, List of Genera (Greuter *et al.*, 1993)

<i>Bionectriaceae</i>	* <i>Hypocrea</i>	<i>Chitinonectria</i>
* <i>Battarrina</i>	<i>Chromocrea</i>	* <i>Ophionectria</i>
<i>Bionectria</i>	* <i>Creopus</i>	* <i>Pleogibberella</i>
<i>Bryonectria</i>	* <i>Hypocreopsis</i>	* <i>Pseudonectria</i>
<i>Clibanites</i>	* <i>Hypomyces</i>	[<i>Nectriella</i> Sacc. 1877 non
<i>Dimerosporiella</i>	* <i>Apiocrea</i>	Nitschke 1870]
* <i>Epinectria</i>	<i>Bonordenia</i>	<i>Notarisiella</i>
* <i>Emericellopsis</i>	* <i>Chiariae</i>	<i>Rubrinectria</i>
* <i>Halonectria</i>	<i>Clintoniella</i>	<i>Stalagmites</i>
* <i>Heleococcum</i>	* <i>Peckiella</i>	<i>Viridispora</i>
* <i>Hydropisphaera</i>	* <i>Podostroma</i>	* <i>Xenonectriella</i>
<i>Hyphonectria</i>	<i>Podocrea</i>	
<i>Neohenningsia</i>	<i>Protocrea</i>	<i>Niessliaceae</i>
<i>Neuronectria</i>	* <i>Pseudohypocrea</i>	<i>Circinoniesslia</i>
<i>Perrotiella</i>	<i>Rogersonia</i>	<i>Cryptoniesslia</i>
<i>Ijuhya</i>	* <i>Sarawakus</i>	* <i>Malmeomyces</i>
<i>Lepidonectria</i>	* <i>Sphaerostilbella</i>	<i>Melanopsanma</i>
* <i>Peristomialis</i>		* <i>Melchioria</i>
<i>Kallichroma</i>	<i>Nectriaceae</i>	* <i>Miyakeomyces</i>
<i>Lasionectria</i>	<i>Albonectria</i>	<i>Myrmaeciella</i>
* <i>Mycoarachis</i>	* <i>Allonectella</i>	[<i>Myrmaecium</i> Sacc. 1880 non
* <i>Mycocitrus</i>	* <i>Calonectria</i>	Nitschke : Fr. 1870]
<i>Shiraiella</i>	* <i>Calostilbe</i>	* <i>Niesslia</i>
* <i>Nectriella</i>	* <i>Phaeonectria</i>	<i>Pseudonectriella</i>
* <i>Nectriopsis</i> 1911 nom. cons. prop.	* <i>Corallomycetella</i>	<i>Pseudorhynchia</i>
<i>Dasyphthora</i> 1909	[<i>Corallomyces</i> Berk. & M.A.	<i>Taiwanascus</i>
* <i>Peloronectriella</i>	Curtis 1853 non Fr. 1849]	* <i>Trichosphaerella</i>
<i>Ochronectria</i>	<i>Cosmospora</i>	<i>Bresadolella</i>
* <i>Paranectria</i>	<i>Chrysogluten</i>	* <i>Valetoniella</i>
<i>Ciliomyces</i>	<i>Dialonectria</i>	<i>Valetoniellopsis</i>
* <i>Peethambara</i>	<i>Stylonectria</i>	
* <i>Pronectria</i>	* <i>Gibberella</i>	<i>Clavicipitaceae</i>
* <i>Protocreopsis</i>	* <i>Lisea</i>	Only genera formerly classified in
[<i>Cryptothecium</i> Penz. & Sacc.	* <i>Lisiella</i>	the <i>Hypocreales</i>
1897 non Hübner 1851]	<i>Haematonectria</i>	* <i>Berkelella</i>
* <i>Roumegueriella</i>	<i>Lanatonectria</i>	* <i>Byssostilbe</i>
<i>Lilliputia</i>	<i>Leuconectria</i>	* <i>Cordycepioideus</i>
<i>Lysipenicillium</i>	* <i>Nectria</i>	* <i>Epicrea</i>
* <i>Selinia</i>	* <i>Allantonectria</i>	* <i>Hypocrella</i>
<i>Seliniana</i>	<i>Aponectria</i>	* <i>Neobarya</i>
<i>Winteria</i> Sacc. 1878	<i>Chilonectria</i>	<i>Barya</i>
* <i>Stilbocrea</i>	<i>Creonectria</i>	* <i>Podocrella</i>
* <i>Trichonectria</i>	<i>Ephedrosphaeria</i>	* <i>Stereocrea</i>
* <i>Valsonectria</i>	<i>Megalonectria</i>	* <i>Wakefieldiomyces</i>
* <i>Endocreas</i>	<i>Pleonectria</i>	
	* <i>Scoleconectria</i>	
<i>Hypocreaceae</i>	<i>Sphaerostilbe</i>	
* <i>Aphysiostroma</i>	* <i>Stilbonectria</i>	
* <i>Arachnocrea</i>	* <i>Neocosmospora</i>	
* <i>Dialhypocrea</i>	* <i>Neonectria</i>	

Genera excluded from the *Hypocreales***DIAPORTHALES**

- Cryptoleptosphaeria*
- * *Cryptonectriella*
- * *Schizoparme*

HALOSPHERIALES

- * *Trailia*

MICROASCALES

- * *Sphaeronaemella*
- * *Viennotidia*

LABOULBENIALES**Pyxidiophoraceae**

- Copranophilus*
- Ascolanthanus*
- * *Mycorhynchidium*
- * *Pyxidiophora*
- Mycorhynchus*
- Rhynchonectria*
- Eleutherosphaera*
- Treleasia*

SORDARIALES**Boliniaceae**

- * *Camarops*
- * *Chromendothia*

Lasiosphaeriaceae

- * *Phaeonectriella*

Nitschkiaceae

- * *Hydronectria*

Phyllachorales**Phyllachoraceae**

- * *Plectosphaerella*
- * *Phyllocrea*
- Stigmatula*
- * *Woronichina*
- * *Uropolystigma*

XYLARIALES**Hyponectriaceae**

- * *Cesatiella*
- * *Charonectria*
- * *Hyponectria*
- * *Linocarpon*
- * *Micronectriopsis*

Thyridiaceae

- * *Balzanina*
- * *Leucocrea*
- Mattirolia*
- * *Thyridium*
- (*Calyptronectria ohiensis*)
- Thyronectrioidea*

Trichosphaeriaceae

- * *Neorehmia*
- Larseniella*

Xylariaceae

- * *Phomatospora*
- Cryptonectriopsis*
- * *Thuemenella*
- Chromocreopsis*

HELOTIALES**Amylocarpus**

Plectolitus

Loramycetes**PEZIZALES**

- * *Ascobolus*
- Seliniella*
- * *Orcardia*

LOCULOASCOMYCETES**CHAETOTHYRIALES**

- * *Treubiomyces*

MELANOMMATALES**Ascoporiaceae**

- Pseudosolidium*
- Ascoporia*

Melanommataceae

- * *Byssosphaeria*
- Macbridella*
- * *Calyptronectria*

PLEOSPORALES**Acrospermataceae**

- * *Cyanodermella*
- [*Cyanoderma* Höhn. 1919 non
Weber Bosse 1887]

Botryosphaeriaceae

- * *Botryosphaeria*
- Creomelanops*

Massariaceae

- * *Dubitatio*
- Spegazzinula*
- * *Passerinula*

Pleosporaceae

- * *Didymocrea*
- * *Valsaria*
- * *Phaeocreopsis*

Tubeufiaceae

- Borinquenia*
- * *Byssocallis*
- * *Chaetocrea*
- * *Malacaria*
- * *Melioliphila*
- Amphinectria*
- * *Puttemansia*
- Subcubicola*

DOTHIDEALES s.l.**Dothideaceae**

- * *Hyalocrea*
- * *Shiraia*

Mycosphaerellaceae

Micronectriella

PYRENULALES**Thelenellaceae**

- * *Aspidothelium*
- Patellonectria*

TRICHOTHELIALES**Trichotheliaceae**

- * *Trichothelium*
- Actiniopsis*

LECANORALES**Collemataceae**

- * *Leptogium*
- Pericoccis*

DISCOMYCETES WITH BITUNICATE ASCI

- * *Hyalosphaera*
- * *Dexteria*

Thelocarpaceae

- * *Thelocarpon*
- Ahlesia*
- Cyanocephalum*
- * *Metanectria*

BASIDIOMYCETES

Mycaureola

Unassigned genera

Type not available or not located

- Debarya* Schulzer
- * *Debaryella* Höhn.
- * *Erispora* Pat.
- Feracia* Rolland
- Lecythium* Zúkal
- Neoskofitzia* Schulzer
- Ochraceospora* Fiore
- Peloronectria* A. Möller
- * *Porphyrosoma* Pat.
- Weesea* Höhn.
- Zeta* Batista & Garnier

Type examined but material insufficient to evaluate:

- Gibberellulina*
- Loculistroma* (? *Clavicipitales*)
- Micronectria*
- * *Thyronectria*

KEY TO THE FAMILIES OF THE *HYPOCREALES*

1. Ascomata dark brown to black, soft-textured, generally solitary; anamorphs *Acremonium*, *Monocillium*, *Stachybotrys*, or unknown **Niessliaceae**
(see Samuels & Barr, 1997, and excluded genera)
1. Ascomata hyaline to light- or bright-colored, rarely brown or appearing black but internally bright-colored, soft-textured, solitary or aggregated; anamorphs generally phialidic, including *Acremonium* **2**
2. Ascospores filiform, multiseptate, usually disarticulating within the ascus, rarely dark-green and long-fusiform (*Cordycepioideus*); ascal apex usually thickened, penetrated by a narrow pore; on living grasses, insects or fungi **Clavicipitaceae**
(see excluded genera)
2. Ascospores globose, ellipsoid to long-fusiform, never truly filiform, disarticulating or not; ascal apex usually not distinctly thickened, rather with an apical ring or simple; on all kinds of substrata, rarely on living grasses **3**
3. Ascospores generally disarticulating; ascomata generally immersed in a stroma; if ascospores non-disarticulating, then ascal apex often thickened and ascomata immersed in a thin to cottony subiculum on fleshy, leathery, or woody basidiocarps; if ascomata superficial, then on a thin, compact stroma on *Aphylliphorales*, rarely subiculum absent and having a *Gliocladium* anamorph (*Sphaerostilbella*); or with transversely striate ascospores (*Rogersonia*) **Hypocreaceae**, page 80
3. Ascospores not disarticulating (except in two species of *Haematonectria*); ascomata superficial on substratum, subiculum or stroma, or ascomata immersed in substratum or in an immersed stroma **4**
4. Ascomata white, pale yellow to orange or brown, not reacting in KOH or lactic acid; ascomata superficial on the substratum or stroma, or immersed in a hyphal to well-developed stroma **Bionectriaceae**, page 15
4. Ascomata generally red to purple, reacting in KOH and lactic acid; if ascomata white to pale yellow, then having a *Fusarium* anamorph (*Albonectria*); ascomata superficial on the substratum or stroma, rarely immersed in lichen thalli (*Xenonectriella*) **Nectriaceae**, page 102