

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 ascial 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 ascomatal 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