

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 The few regional studies of the *Hypocreales* include outdated accounts of species in North America (Seaver 1909 a, b; 1910 a, b) and Sri Lanka as Ceylon (Petch, 1912, 1920), and more recently England (Booth, 1959; Petch,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 ascocata 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 ascocata 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-