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 firsthand 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 redisposed 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 µm 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 × 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

A. Y. Rossman et al.

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, HYPOCREA-CEAE, 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. 41, 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-