

AN ABSTRACT OF THE THESIS OF

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Title: THE GENUS *OPHIONECTRIA* (ASCOMYCETES, HYPOCREALES)

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A taxonomic study of the genus *Ophionectria* Saccardo is presented. The genus is described and the only remaining species, the type species, *Ophionectria trichospora*, is described and figured. *Ophionectria trichospora* is compared with *Nectria haematococca* to define relationships between the two genera.

All other species formerly placed in *Ophionectria* are reviewed and found to belong in other genera. A key to these species is presented. The disposition of excluded *Ophionectria* species is based on an examination of the type specimen of each species. One new species is described: *Barya byssicola*. Twelve new combinations are proposed: *Calonectria hendrickxii*, *C. muscivora*, *C. vernoniae*, *Torrubiella lloydii*, *Lasiosphaeria glabra*, *L. rufula*, *Podonectria coccorum*, *P. larvaespora*, *Tubeufia hidakaeana*, *T. palmarum* and *T. paludosa*. Several species excluded from the genus *Ophionectria* could not be placed in existing genera.

The Genus Ophionectria (Ascomycetes, Hypocreales)

by

Amy Yarnell Rossman

A THESIS

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## THE GENUS OPHIONECTRIA (ASCOMYCETES, HYPOCREALES)

### I. INTRODUCTION

The genus Ophionectria was erected by Saccardo in 1878 to accommodate the long-spored species of Nectria. The type species is Ophionectria trichospora. The genus has never been adequately described according to modern taxonomic criteria. As a result, Ophionectria has been the repository for an assortment of unrelated species with light- to bright-colored, fleshy perithecia and spores, without regard to other characters of the Hypocreales, particularly centrum structure and ascus type.

This thesis is a study of the species which have been referred to Ophionectria. The genus contains many species whose type specimens have not been examined since they were described. Fifty-seven valid species have been placed in the genus, in addition to twelve invalidly named species. I examined the type collections of 41 species to determine their correct taxonomic positions; the remainder could not be located. All Calonectria species were reviewed in order to include all the long-spored species that might be synonyms of species described as Ophionectria.

After revision, the genus Ophionectria contains only the type species, which is described and illustrated. The excluded species are discussed and taxonomic revision made where appropriate.

The type species of Ophionectria, O. trichospora, is related to some Calonectria and Nectria species on the basis of characters other than spore length and septation. Some of these, especially those formerly placed in Ophionectria, have very long, multiseptate spores whereas those placed in Nectria have short, uniseptate spores. Although the genera Nectria, Calonectria and Ophionectria are traditionally separated on differences in spore length:width ratios and septation, graphic analyses of these characters show that genera do not differ discretely in spore length. Thus, each of these traditional genera, when based on spore size and septation, is heterogeneous.

A detailed comparison reveals the close relationship of Ophionectria trichospora and Nectria haematococca.

Four species previously placed in Ophionectria are not related to the type species Ophionectria trichospora but belong in the Nectria-complex of the Hypocreales. These species are provisionally transferred to the genus Calonectria.

Many long-spored species which had been assigned to Ophionectria do not have nectrioid perithecia and do not belong in the Hypocreales. Rather, they belong to four other orders of the two subclasses of Ascomycetes. Each taxon in which an excluded Ophionectria species is provisionally placed is discussed.

## II. MATERIALS AND METHODS

### Collection of Fresh Specimens

This project was initiated by two collecting trips to the tropics; the first in June, 1970 to Puerto Rico and Dominica; the second in January, 1971 to Jamaica. Both trips were under the direction of Dr. Richard P. Korf, Cornell University, Ithaca, New York. Collections of Ophionectria trichospora were air-dried and mailed to Oregon State University, Corvallis, Oregon where they were packeted, fumigated and stored for subsequent study.

### Culture

A culture of Ophionectria trichospora, derived by single ascospore isolation from one of the Jamaican collections, was obtained from Dr. Gary Samuels, New York Botanical Gardens, Bronx, New York.

### Source of Type Specimens

The literature was thoroughly searched for all descriptions and references to Ophionectria species. All Ophionectria collections, particularly types, were requested from the following herbaria: B, BC, BO, BPI, BR, BRSL, C, CBS, DAOM, FH, G, H, HBG, IARI, IMI, K, KIEL, KRA, L, LD, LISE, LPS, MA, NY, PAD, PADA, PC, PO, RO, S, SAP, SCB, TAI, W, YAM, and ZT (abbreviations according to Lanjouw and Stafleu, 1964). Major herbaria in the United States were visited and searched for relevant collections. In several instances specimens were found under names not reported as synonyms in the literature.

Type specimens were obtained and examined for 41 of the 57 described species. Disappearance of the remaining type specimens may be due to misfiling or filing under unlikely names, deposit in minor or personal herbaria not listed in the Index Herbariorum, loss in the wars, disintegration due to repeated use by mycologists.

### Macroscopic Examination

Dried specimens were examined to determine the collapsed perithecial shape. Specimens were rehydrated by soaking in water or setting in a moist chamber from five minutes to overnight. These fungi are generally small (less than 0.5 mm diam) and fleshy so that rehydration was not difficult and in some cases aided location of the fruiting bodies on the substrate. Macroscopic observations of specimens on their natural substrate were made using a stereomicroscope. Fruiting bodies were picked off with a microscalpel and mounted in water for preliminary observations. Measurements of entire fruiting bodies were made with an ocular micrometer either on the substrate with a stereomicroscope or individually on a slide without a coverslip under the low power objective of a compound microscope. These methods proved to provide comparable measurements.

### Microscopic Examination

A Zeiss compound microscope with standard brightfield (Köhler) illumination and ocular micrometer was employed for study of material mounted in water. After preliminary observations in water mounts,

other media were gradually introduced for staining and preservation of the material. Cotton blue in lactophenol (Ainsworth, 1971) was used routinely to define spore sculpturing and to make semipermanent mounts. Melzer's reagent (Dennis, 1968) was used on unitunicate asci to determine whether the apical ring blued in iodine. Dehiscence of bitunicate asci was observed by mounting asci in ammoniacal Congo Red (Richardson and Morgan-Jones, 1964). This stimulates the rupture of the outer wall and extension of the inner wall of the bitunicate ascus. When necessary, rupture was encouraged by pressing the coverslip down on the fungal material on the slide. Longer-lasting semipermanent mounts were made by gradually replacing the medium with 50% glycerol and finally 100% glycerol. Coverslips were sealed with porcelain cement, nail polish or ZUT sealing agent.

Tissue types of perithecial surfaces were observed on squash mounts in water. Perithecial wall characters were determined from median free-hand sections mounted in water or from paraffin sections. Perithecia fixed in formalin-propiono-alcohol were dehydrated by a tertiary-butyl-alcohol series and embedded in paraplast (Johansen, 1940). Sections of 10-12  $\mu\text{m}$  were made with a Jung rotary microtome, stained with saffranin and fast green, and mounted permanently in balsam.

## Photography

External anatomy was photographed with a Zanza Bronica Model S2A camera using a 25 mm lens and diaphragm. The 6 x 6 cm Kodak Plus-X film was developed for 5-7 minutes in Microdol and fixed in Rapid Fix for 5 minutes at 29°C. Photomicrographs were made with a Ihagee Exa camera mounted on the compound microscope with a Vivitar adapter. An external shutter minimized vibration from the camera mirror slap. Kodak Panatomic-X 35 mm film was developed for 5-7 minutes in HC 110 and fixed in Rapid Fix for 5 minutes at 29°C.

### III. DEFINITION AND EVALUATION OF TAXONOMIC CHARACTERS

Separation of the Ascomycetes into two subclasses, the Euascomycetidae and the Loculoascomycetidae (Nannfeldt, 1932; Luttrell, 1951, 1955), has necessitated a reexamination of older type specimens. The Hypocreales belong to the subclass Euascomycetidae. Many taxa formerly placed in the Hypocreales are now placed in the subclass Loculoascomycetidae. Some species incorrectly assigned to the genus Ophionectria were among these taxa.

I have evaluated the criteria used to delimit families, genera and species within the Hypocreales to determine to what extent these characters are valid and consistent at various taxonomic levels. Recent taxonomic works on the Hypocreales (Booth, 1959, 1964; Dingley, 1951, 1953, 1954; Doi, 1969; Hanlin, 1961, 1963, 1971; Müller and von Arx, 1973; Quereshi and Page, 1972; Rogerson, 1970; Samuels, 1973a, 1973b, 1973c) provide the bases for evaluating these characters. In the other orders to which excluded Ophionectria species have been reassigned, I have accepted the familial and generic concepts embodied in major ascomycete works (Dennis, 1968; Müller and von Arx, 1973).

#### Fruiting Body Terminology

In this study the term perithecium is used for the fruiting bodies of members of the euascomycete orders Hypocreales, Clavicipitales and Sphaeriales (figure 1a - 1c). The term pseudothecium has been used for one-loculed, ostiolate ascostromata found in the loculoascomycete

order Pleosporales (figures 1d - 1f) but the developmental differences which this term implies, have not been clarified. Therefore, the term ascocarp is used in describing the one-loculed fruiting bodies of members of the Loculoascomycetidae.

With the recognition of two subclasses of Ascomycetes, the terminology used for one-loculed, ostiolate fruiting structures has become confused. The term perithecium is defined by some authors (Alexopoulos, 1962; Dennis, 1968) strictly as closed structures with a true peridial wall and an ostiolate opening surrounding the centrum contents of a member of the Euascomycetidae. This excludes species of the Loculoascomycetidae with one-loculed ascostromata which superficially resemble true perithecia. The one-loculed ascostromata are considered to be developmentally different and have been called pseudothecia (Luttrell, 1973). In mature specimens a pseudothecium is recognized by the presence of bitunicate asci. Macroscopically the ostiolate fruiting bodies of euascomycetes and loculoascomycetes are indistinguishable (figure 1a - 1f).

#### Perithecial Structure

The order Hypocreales includes fungi with soft-textured, light- to bright-colored perithecia (figure 1a, 6a, 6b, 11a and 11b). Until recently characteristics of the perithecium were used only at the ordinal level. Dingley (1951) and Booth (1959) use perithecial characters in defining relationships among hypocreaceous species. The perithecial characters used as taxonomic criteria in delimiting

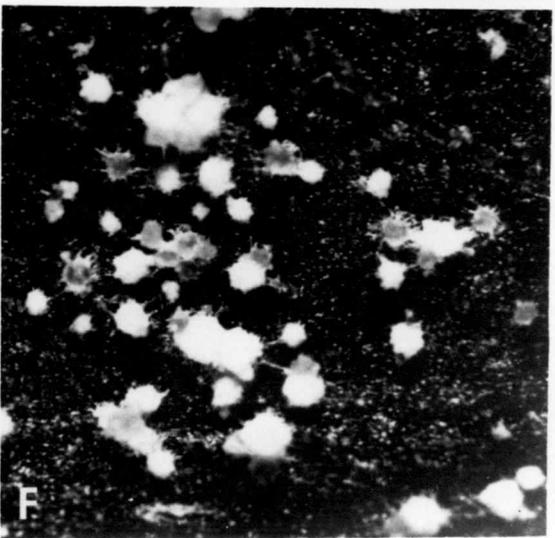
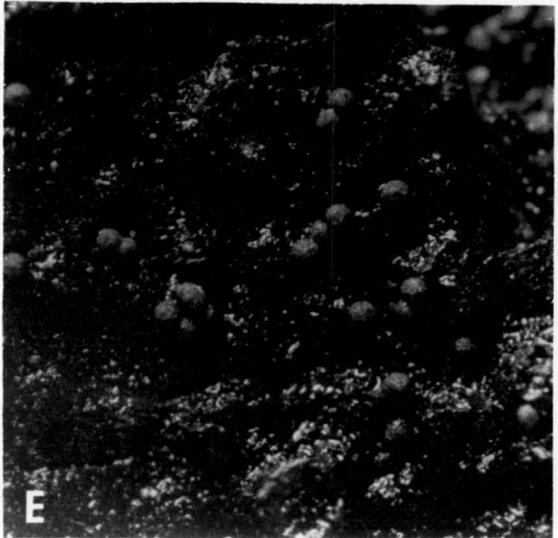
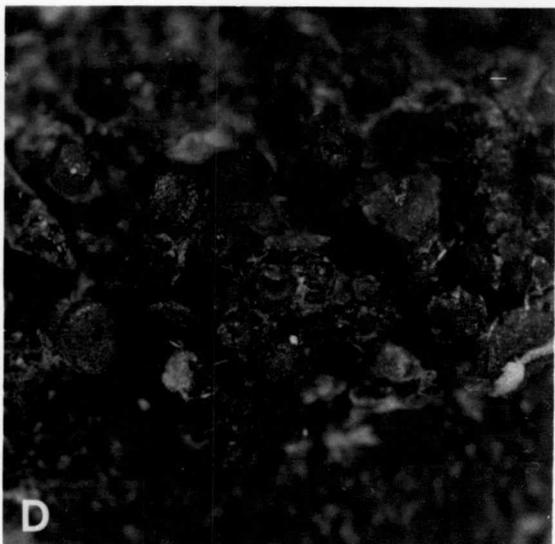
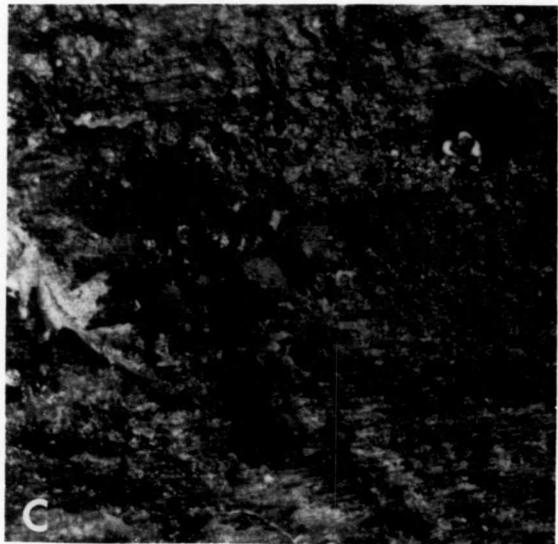
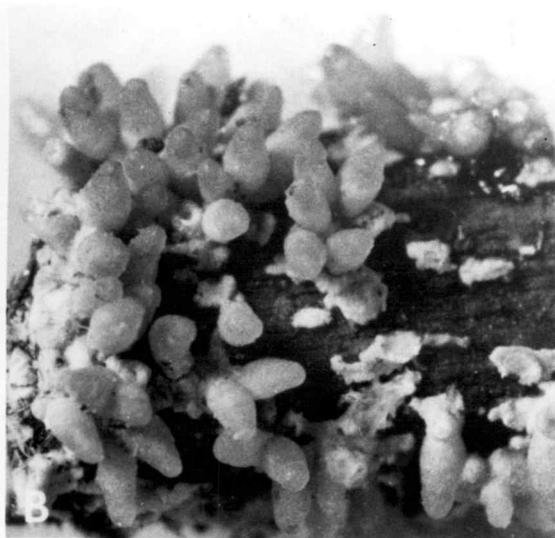
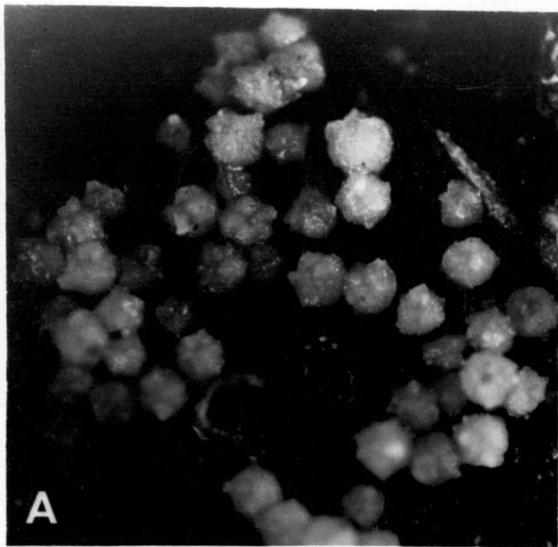
orders, families, genera and specific relationships include color, texture, wall structure, and wall cell characteristics.

Although perithecia of most species of the Hypocreales are light- to bright-colored, some are dark-blue to purple, as in Gibberella species, or dark-yellow to brown or black with age. The Clavicipitales are also characterized by light- to bright-colored perithecia (figure 1b) but the extremely slender asci with specialized apices and thread-like ascospores (figure 2c, 13c, 13d and 14a) easily distinguish this order. Some members of the Sphaeriales have light-colored perithecia, e.g., Mycomedusiospora flavida, or are bright-colored when young but dark at maturity, as in the Melanosporaceae. However, most members of the Sphaeriales have dark, carbonaceous perithecia (figure 1c). The order Pleosporales in the Loculoascomycetidae includes species with bright-colored fruiting bodies, e.g. the genera Podonectria and Tubeufia (figure 1d and 1e), and this group is being expanded as more "hypocreaceous" species are found to have bitunicate asci. Hyalocrea, Byssocallis, Puttemansia, Oomyces and Thaxteriella, all formerly placed in the Hypocreales, have been found to belong in the Loculoascomycetidae (Pirozynski, pers. comm., 1974). In characterizing the order Hypocreales, the light- to bright-color of the perithecium should be used as a correlative character, not a definitive one.

The texture of the perithecium of members of the Hypocreales and Clavicipitales is also a correlative, not definitive, character. The texture of the perithecia in these orders ranges from membranaceous,

FIGURE 1. Representative ascocarps including species described as Ophionectria, now placed in four different orders. All 20 X.

- A. Calonectria sp. (Euascomycetidae, Hypocreales)
- B. Torrubiella lloydii (Euascomycetidae, Clavicipitales)
- C. Lasiosphaeria depilata (Euascomycetidae, Sphaeriales)
- D. Podonectria coccicola (Loculoascomycetidae, Pleosporales)
- E. Tubeufia cerea (Loculoascomycetidae, Pleosporales)
- F. "Ophionectria" tropicalis (Loculoascomycetidae, Pleosporales)



fleshy, cartilagenous to leathery but is never brittle or carbonaceous, as in most species in the Sphaeriales and related orders. There are a few sphaeriaceous fungi with fleshy perithecia which are distinguished from the Hypocreales by other characters. Fruiting body texture is related to color and to a more fundamental character, perithecial wall structure.

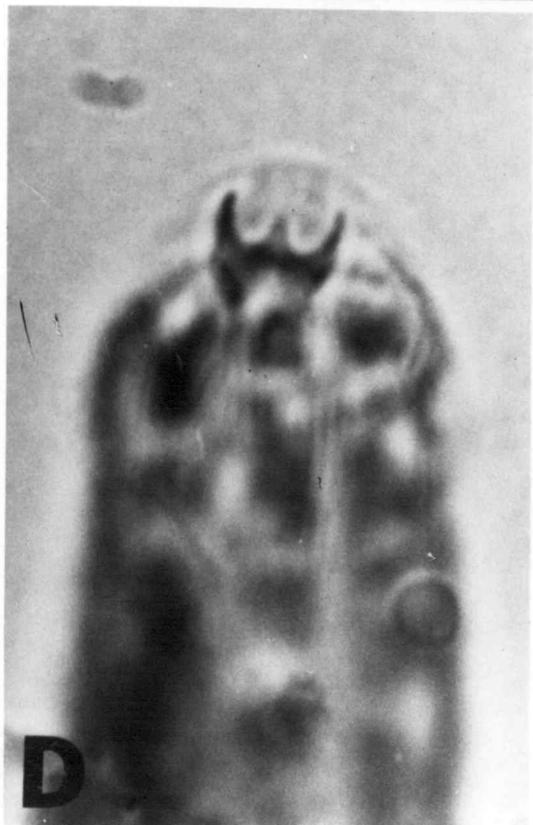
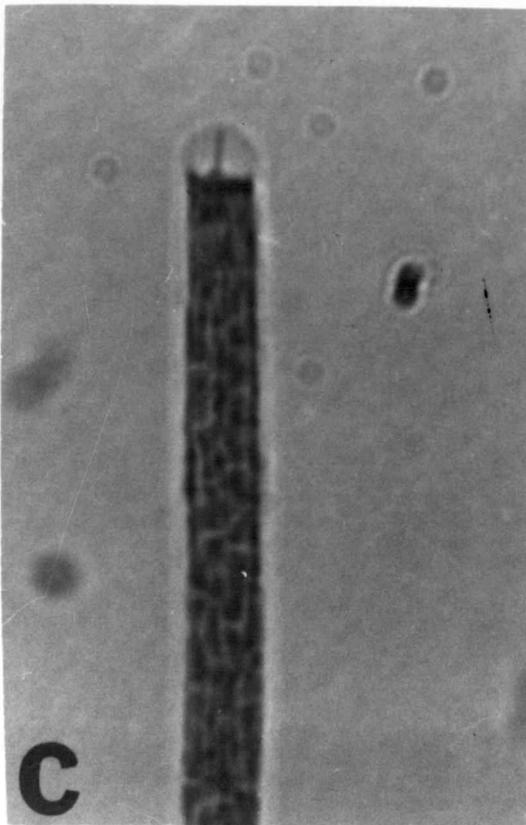
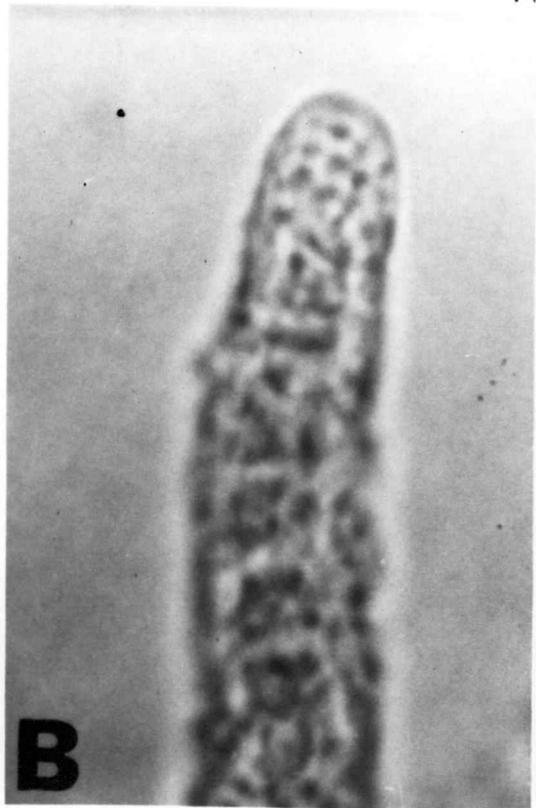
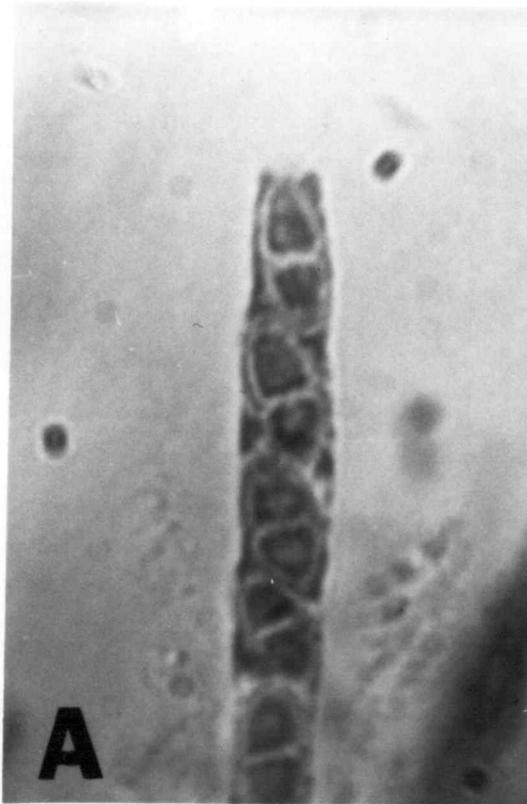
In this study perithecial wall structure is considered taxonomically important below the family level. Perithecial wall characters rather than spore length are used to define the genus Ophionectria. Eventually the relationship of Ophionectria trichospora with other species in the Nectria-complex can be defined at the generic level. Perithecial wall structure, including all the characters used by Dingley (1951) and Booth (1959) to indicate relationships among species in the Nectria-complex, are described in detail for each species.

Tissue type of the perithecial wall surface is noted for each species. The tissues are defined according to van Brummeln (1967) based on Korf (1958). Doi (1969) proposed the use of tissue terminology in describing stromal characters of Hypocrea species. However, his suggestion has not been followed for any perithecial ascomycetes nor have tissue types been defined independently for this group.

The cell characteristics of various perithecial wall layers are included in the species descriptions, whenever possible. Dingley (1951) used the following perithecial wall characters to differentiate sections of Nectria species: tissue structure, i.e. pseudo-

FIGURE 2. Apices of unitunicate asci.

- A. Nectria polyporina
- B. Thyronectria balsamea
- C. Torrubiella lloydii
- D. Lasiosphaeria glabra



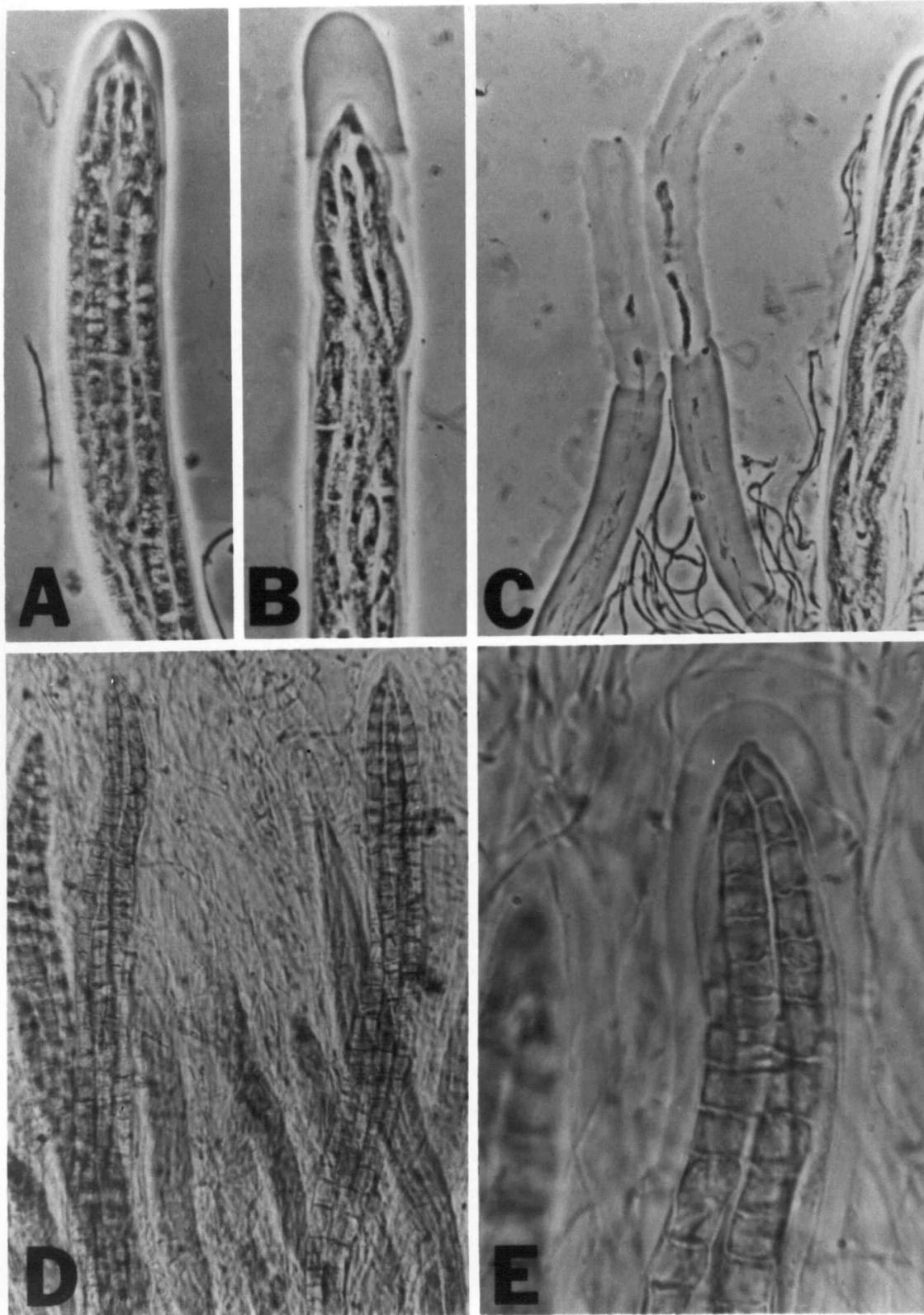
parenchymatous or not; location and degree of pigmentation, i.e. location of pigments within cell walls or as globules within the cytoplasm of perithecial wall cells; thickening of walls of perithecial cells. Booth (1959) divides the British species in the Nectria-complex into "groups", later called sections (Booth, 1960). These are based on stromal and perithecial wall characters, including external wall features and surface anatomy, shape after drying, determined by perithecial wall structure, wall layers as seen in cross-section, and characteristics of the cells forming the wall layers, i.e. location of pigments within the cells and wall thickness. The sections into which Dingley separates Nectria species and those of Booth are in agreement. Studies of their imperfect states (Booth, 1960, 1971; Dingley, 1957) confirm the relationships of these sections based on perithecial wall structure, suggesting that these morphological characters should be emphasized taxonomically above the species level.

#### Sterile Interascal Filaments

In this study the term paraphysis is used for any sterile, interascal filaments found in the perithecial Euscomycetidae and pseudoparaphysis for the analogous structures in the Loculoascomycetidae (figure 3d). The term apical paraphysis is used for the characteristic sterile, interascal filaments occurring in the Hypocreales. Although Luttrell (1965a) attempted to clarify the terms, others have ignored his terminology by referring to these structures as "sterile filaments

FIGURE 3. Bitunicate asci.

- A. Podonectria coccicola ascus before rupture of outer wall.
- B. P. coccicola ascus after rupture of outer wall and extension of inner wall.
- C. P. coccicola ascus after rupture of outer wall, extension of inner wall and discharge of spores.
- D. P. larvaespora centrum showing asci before dehiscence and branched, filiform pseudoparaphyses.
- E. P. larvaespora ascus apex before dehiscence showing an indentation in the inner wall, characteristic of bitunicate asci.



associated with the asci" followed by a detailed description. The Hypocreales are characterized by apical paraphyses which are described by Luttrell (1965a) as "the downward-growing palisade of hyphae with free tips which often disintegrate at maturity, leaving nothing or only fragments of sterile threads". Developmental studies of members of the Hypocreales substantiate Luttrell's definition (Hanlin, 1961, 1963, 1971; Samuels, 1973c).

The mature hypocreaceous specimens examined in this study either had no sterile hyphae associated with the asci or had only scanty, irregularly-branched remnants of interascal filaments. Members of the Sphaeriales may or may not have true, generally unbranched, paraphyses arising from the base of the perithecium and growing upward with the asci. The Clavicipitales seem to lack sterile elements associated with mature asci. In the Pleosporales, Loculoascomycetidae, the sterile hyphae associated with the asci have been termed pseudoparaphyses (Luttrell, 1951, 1965a) which develop as outgrowths of the stroma into the locule. Unlike apical paraphyses they are ultimately attached at both ends and are usually branched and filiform.

### Asci

Although the functional ascus type, unitunicate or bitunicate, is now accepted as the most easily determined distinction between the two subclasses of Ascomycetes (Alexopoulos, 1962; Dennis, 1968; Luttrell, 1965b; Müller and von Arx, 1973), many type collections

have not been reexamined since their initial description. Their ascus type is unknown and their assignment to a subclass is in question. In this study I have determined the ascus type of the collections examined and have used this character to determine the subclass to which each species should belong.

The unitunicate ascus characterizes the subclass Euascomycetidae (figure 2a - 2d). It is "an ascus in which both the inner and outer wall are more or less rigid and do not separate during spore ejection" (Alexopoulos, 1962). The apical discharge apparatus of unitunicate asci is a modification of a more or less developed ring and pore-plug mechanism. The type of mechanism is used as a distinguishing character at the family and order level. An ascus with an enlarged, thickened, apical cap penetrated by a narrow, threadlike pore in a perithecium is characteristic of the pyrenomycete order Clavicipitales. (figure 2c and 13c). A thickened apex is often found in species of Ascomycetes with filiform spores and, presumably, aids discharge. The violent discharge of filiform ascospores could only be accomplished through a narrow canal. As the osmotic pressure within the ascus builds up, the thin spore plugs the narrow canal formed by the thickened walls of the ascus apex. When enough pressure forces the spore through the pore, the spore is shot through the canal as the thickened apex constricts around the spore (Ingold, 1971). The ascus apex with a distinct ring and plug with or without a refractile sphere below the apex is characteristic of the asci in the Sphaeriales (figure 2d). The absence or presence and characteristics of any visible apical

mechanism is generally used in delimiting orders and families of Euascomycetidae.

Within the Hypocreales the unitunicate asci may (figure 2a) or may not (figure 2b) have an apical ring. This character is used only at the species level. Many species have an undifferentiated ascus apex. The asci are apparently evanescent at maturity, leaving the mass of spores loose within the centrum. They ooze out through the ostiole as a cirrhus or coiled mass of spores, and may eventually become airborne as the mass dries.

The bitunicate ascus characterizes the subclass Loculoascomycetidae. It is one in which "the inner wall is elastic and expands greatly beyond the outer wall at the time of spore liberation" (Alexopoulos, 1962). The bitunicate ascus is recognized by stimulating the rupture of the outer wall and noting the extension of the inner wall as described in the Materials and Methods section. Before rupture bitunicate asci have an indentation or "dimple" in the thick inner wall (figure 3e). The inner tunic often has a ring in the apex which aides in violent spore discharge after it has extended. Figures 3a and 3b show a bitunicate ascus before and after the outer wall has ruptured with the extension of the inner wall. Eventually the spores are discharged leaving the inner ascus empty (figure 3c).

### Ascospores

Spore characters have been used as important taxonomic criteria in the Ascomycetes, probably due to the ease with which they are

observed. Within the Hypocreales ascospore characters that have been assigned taxonomic value include length, width, length:width ratio, shape, septation, ornamentation and color.

Traditionally the length or length:width ratio and septation of ascospores has been an overriding basis for generic delimitation in the Hypocreales, as shown in Table 1. Often genera cannot be clearly differentiated by differences in spore length (figure 5).

TABLE 1. Some genera of Hypocreales based solely on spore length and septation and presence or absence of a stroma.

|   | <u>Well-developed<br/>stroma</u>     | <u>Poorly developed<br/>or no stroma</u>                                 |
|---|--------------------------------------|--|
| Short, uniseptate<br>spores                   | <u>Creonectria</u><br><u>Nectria</u> | <u>Nectria</u> (Seaver,<br>1909)<br><u>Dialonectria</u><br>(Petch, 1938) |
| Medium length,<br>2-to multiseptate<br>spores | <u>Puttemansia</u>                   | <u>Calonectria</u>   |
| Long, multiseptate<br>spores                  | <u>Scoleconectria</u>                | <u>Ophionectria</u>  |
| Muriform spores                               | <u>Pleonectria</u>                   | <u>Thyronectria</u>  |

Scoleconectria and Ophionectria were defined as having filiform to subfiliform spores by Seaver (1909) or spores with a length:width ratio greater than 20:1 (Rogerson, 1970). Some species of Scoleconectria and hypocreaceous species described as Ophionectria have spore lengths in the range of Calonectria species. Calonectria is delimited by ellipsoid to fusiform ascospores (Seaver, 1909) or spores with a length:width ratio greater than 10:1 but less

than 20:1 (Rogerson, 1970). The distinction between these genera based on spore length is unsatisfactory (figure 4a - 4k). The eight hypocreaceous species which have been placed in Ophionectria because of their very long spores, are not related except in this one feature (figure 4h - 4k). Spore length, width, length:width ratio and shape as a function of length are not characters which should be used to differentiate genera.

Spore septation has been used to differentiate genera in the Nectria-complex. The number of septa is generally correlated with spore length. For example, the genus Nectria is characterized by uniseptate spores (figure 4a, b, c, and g), but in Nectria cinnabarina, the type species, the ascospores may vary in size within a single ascus (Booth, 1959) with the longest spores 2-3 septate (Samuels, pers. comm, 1974). Calonectria has multiseptate spores which typically are correspondingly longer than spores of Nectria species. However, in some Calonectria species the spores are as short as those of some Nectria species (figure 4a, b, c, d, g, and 5). The range of spore length of multiseptate Calonectria species overlaps that of the usually uniseptate Nectria species. Scoleconectria and Ophionectria which contain species with spores more than triseptate, also overlap some Calonectria and Nectria species in range of spore length. The presence of longitudinal septa, that is, muriform spores, is used to distinguish the genus Thyronectria from Ophionectria, Scoleconectria and Calonectria. Some scolecosporous species have oblique transverse septa while in some muriform-spored

FIGURE 4. Ascospores of species in the Nectria-complex  
A-G 1000 X. H-K 500 X.

- A. Nectria sp., punctate, uniseptate
- B. Nectria haematococca, striate, uniseptate
- C. Scoleconectria polythalama, multiseptate
- D. Nectria sp., striate, uniseptate
- E. Calonectria sp., multiseptate
- F. Thyronectria pseudotrichia, muriform
- G. Nectria subfalcata, uniseptate
- H. Calonectria puiggarii, multiseptate
- I. C. vernoniae, multiseptate
- J. C. muscivora, multiseptate
- K. Ophionectria trichospora, multiseptate

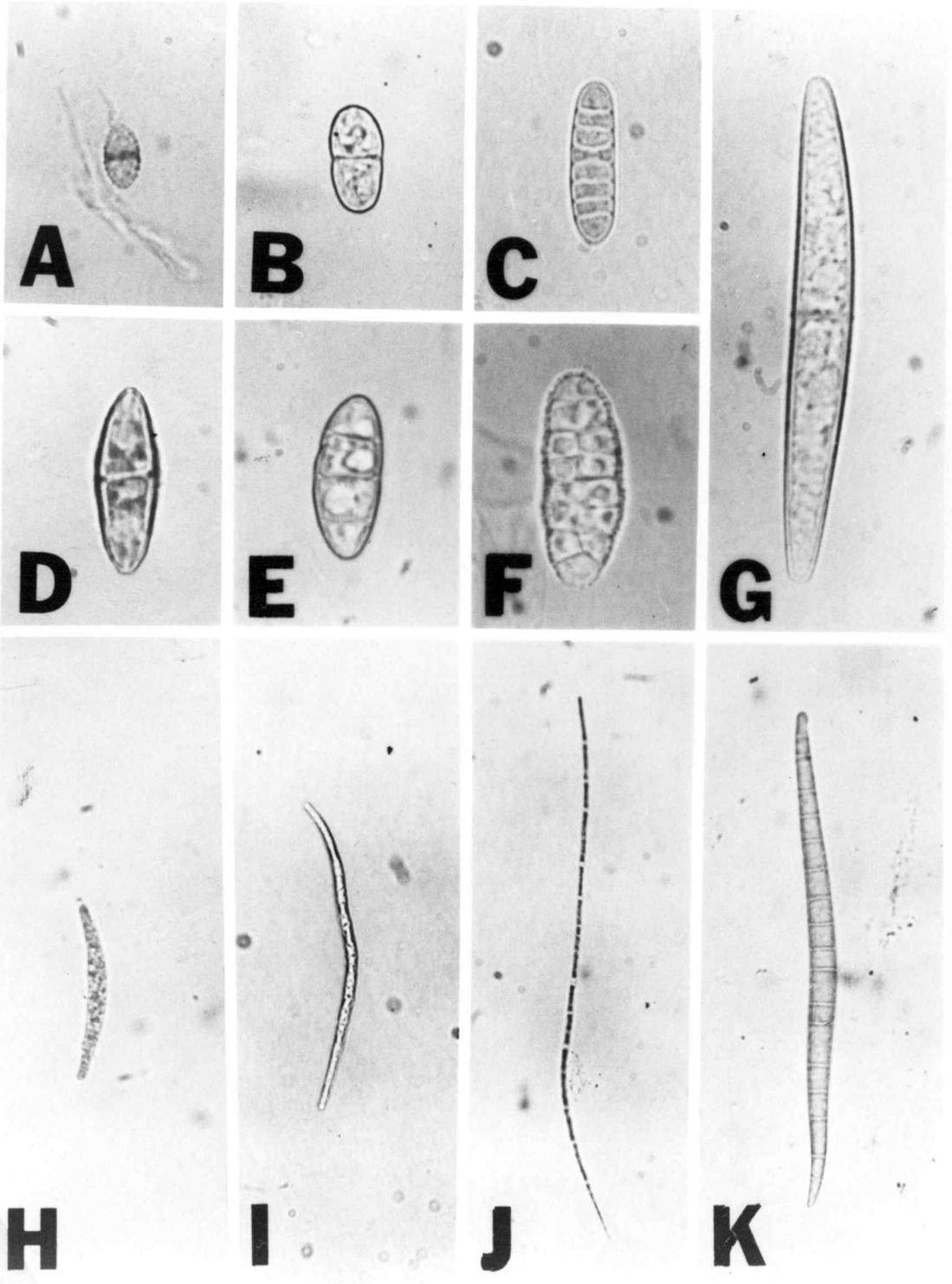
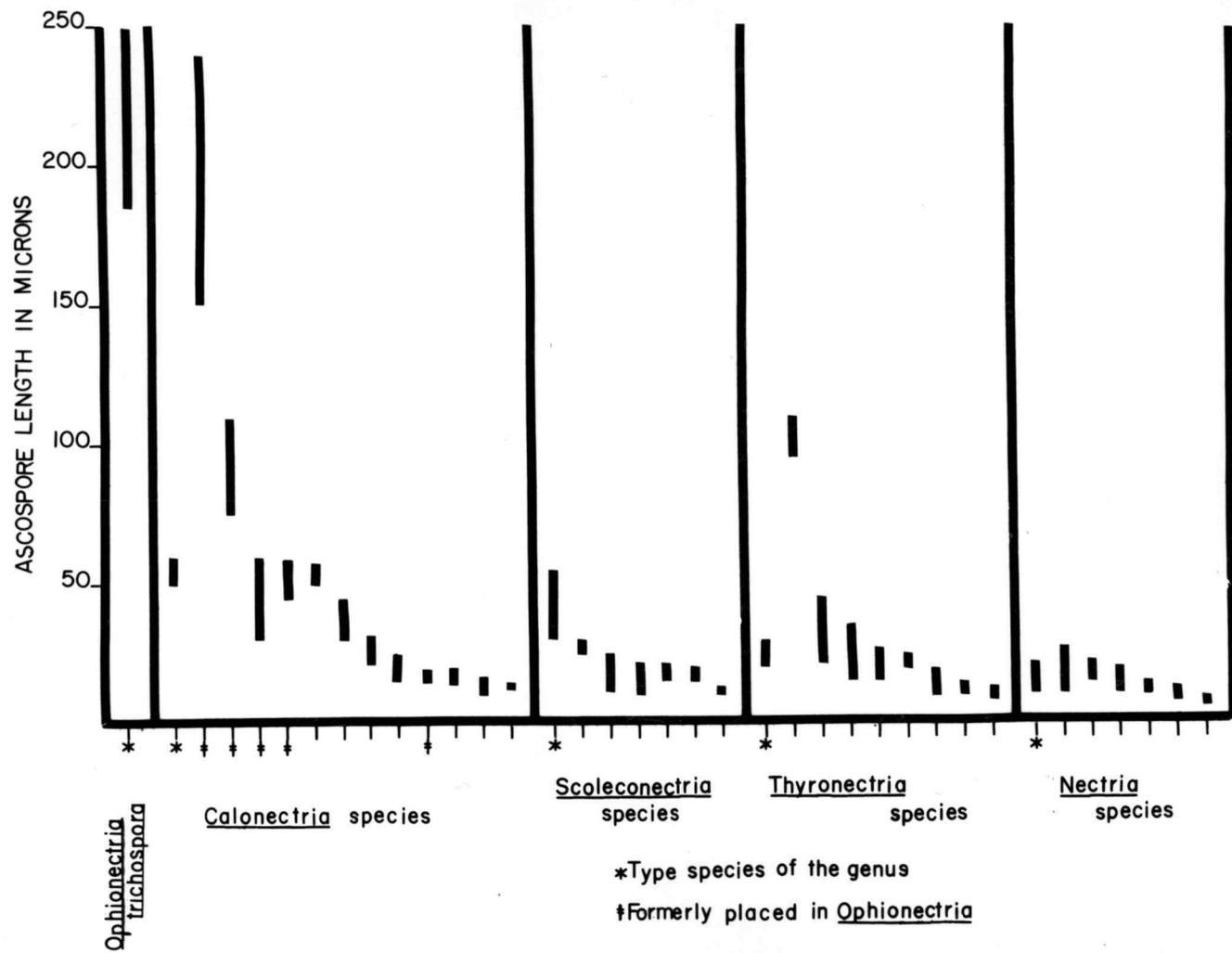


FIGURE 5. Ascospore length of representative species in genera of the Nectria-complex. Genera do not differ discretely in spore length. Species were selected to represent the range of variation within each genus.



ASCOSPORE LENGTHS WITHIN THE NECTRIA-COMPLEX

species, the longitudinal septa are somewhat transverse. This problem is particularly difficult in distinguishing Thyronectria balsamea from Scoleconectria cucurbitula, where in both species the primary ascospores are obscured by the presence of ascoconidia within the ascus (figure 11 a-d). Spore septation therefore does not serve as an important taxonomic criterion at the generic level.

Spore ornamentation may be a useful character in the Hypocreales at the species level. In the Nectria-complex it is limited to longitudinal striations and warts. Striate spores were the basis of the genus Neuronectria erected for Nectria peziza, a temperate species. However, striate spores proved to be common in tropical species of Nectria and the genus Neuronectria is no longer recognized (figure 4a, b and c).

Spore color is a definitive character only at the species level. Samuels (1973a) reviewed the genus Macbridiella, described by Seaver (1909) for stromatic, brown-spored species of Nectria, and other genera based on Nectria species with brown spores. He concluded that brown coloration of the ascospores is insufficient for generic delimitation. None of the long-spored species described as Ophionectria have colored spores.

### Stroma

I consider any mass or matrix of vegetative tissue in or on which reproductive structures are formed to be stromatic. A subiculum is a stroma subtending or surrounding fruiting bodies. A byssus is a sub-

iculum composed of cottony, loosely-associated hyphae (figure 6b, 12a and 12b). Presence or absence of a stroma may depend on environmental and substrate conditions and should not be used as a definitive taxonomic criterion.

The presence or absence of a stroma and the extent of its development has been used as a taxonomic character at the generic and specific level in the Hypocreales (table 1, page 20). The type specimen of Ophionectria trichospora has some basal hyphae and within the species the stroma varies from absent to a conspicuous byssus. Seaver (1909) erected the genus Scoleconectria for those Nectria-like species with long spores and a well-developed stroma. He transferred two species of Ophionectria and four species of Calonectria into Scoleconectria. Seaver did not define a stroma and the term has come to have a very broad meaning. Any tissue at the base or around the fruiting body may be regarded as a stroma.

Seaver (1909) divided the family Nectriaceae into tribes on the basis of the presence (Creonectrieae) or absence (Nectrieae) of a "stromata or stromatic base". He placed nectrioid species with uniseptate spores without a stroma in Nectria and those with a stroma in Creonectria. Petch (1938) placed nectrioid species with uniseptate spores with a stroma in Nectria and those without a stroma in Dialonectria.

The genus Nectriopsis was described for species of Hypomyces having uniseptate, rounded to subacute ascospores and perithecia formed in a subiculum. Through a study of perithecial ontogeny and morphology,

Samuels (1973b) determined that the species included in Nectriopsis should be placed in Nectria. The subiculum of N. violacea and N. candicans was found to originate vegetatively, not comparable to the sexually-stimulated subiculum of Hypomyces species. Samuels does not consider the presence of a subiculum a sufficient criterion for delimiting genera.

At present the genus Nectria includes species with and without a well-developed basal stroma. Booth (1959) uses this character for the first dichotomy in keying his sections of Nectria species. The "coccinea" section must be included under both dichotomies as specimens of Nectria coccinea, which typically have a well-developed, basal stroma, do not have a stroma when the perithecia develop on bare wood. In the "ochroleuca" section Booth includes species with "perithecia aggregated on a stroma" while two of the three species listed are "seated on a byssus or scattered". The presence or absence of a stroma is not a consistent character and should not be used above the species level and perhaps not even at that level, as in Nectria coccinea.

Within the order Clavicipitales, the genus Cordyceps is characterized by a well-developed stroma but in C. tuberculata (= Ophionectria cockerellii), the development of the stroma is variable, ranging from an effuse subiculum to a clavate stroma over one cm high (Dingley, 1953). Torrubiella lloydii (figure 1b) has pseudoparenchymatous plates subtending the fruiting bodies. Barya byssicola has a byssoid subiculum surrounding and subtending the perithecia (figure 12a and b).

In the Pleosporales the genus Podonectria includes species with the ascocarps superficial on scale insects, others with the fruiting body seated on a byssoid subiculum and some species in which each locule is surrounded or immersed in a well-developed stroma. Within the species Podonectria coccicola ( $\equiv$ Ophionectria coccicola), the thin-walled ascocarps may be superficial on scale insects with only a scant byssoid subiculum, to immersed in a thick-walled stroma completely covering the scale insect.

#### Imperfect States

As the imperfect states of hypocreaceous species become known, they are assuming increasing importance in determining taxonomic relationships. All the conidial states known for Nectria-like species are phialosporic. The phialospores may be simple or multiseptate, hyaline or colored. The conidiophores may be variously branched, aggregated into a sporodochium, forming a stalked synemma or enclosed in a pycnidium. The imperfect state of Ophionectria trichospora has recently been described as Antipodium spectabile Pirozynski. It is phialosporic with hyaline, multiseptate, fusiform conidia (figure 9). It is like the form-genus Fusarium, the imperfect state of many Nectria species, except that the foot cell of the conidium is located at the apex, forming a beak. The imperfect states of the Calonectria species previously placed in Ophionectria are unknown. Scoleconectria cucurbitula and Thyronectria balsamea, both previously placed in Ophionectria, have phialosporic pycnidia

belonging to the form-genus Zythiostroma (figure 11b). Despite the placement of S. cucurbitula and T. balsamea in different perfect genera because of different spore septations, their similar imperfect states suggest that they are closely related. For more details of their relationship see page 84.

Webster (1964) correlated subtle differences in perfect states of three Hypocrea species by careful observation of the imperfect states. Doi (1969) reviews the characteristics of the conidial states of Hypocrea and allied genera, noting genetically constant characters. Such studies would be useful in the Nectria-complex.

IV. THE GENUS OPHIONECTRIAHistorical Review

The genus Ophionectria was erected by Saccardo in 1878 to accommodate species of Nectria with very long spores. The original description is brief. "Perithecia Nectriae - Asci octospori. Sporidia filiformia multiseptata v. multiguttulata" (Michelia 1:323). (Translated: Perithecia as in Nectria - Asci eight-spored. Spores filiform, multiseptate or multiguttulate.) Thus by the original definition Ophionectria has Nectria-like perithecia and long slender spores. To Saccardo and his contemporaries "Nectria-like perithecia" meant brightly colored perithecia with soft, fleshy walls. Saccardo differentiated Ophionectria from Nectria solely on the basis of spore shape and septation. Although he described the spores as filiform, none of his species have filiform spores in the literal sense of being threadlike. They are long-fusiform.

In his original description Saccardo included three species, all of which he transferred from the genus Nectria: Ophionectria trichospora, O. mellina and O. paludosa. Twenty-three more Ophionectria species were subsequently described by several authors, before Seaver (1909) designated Ophionectria trichospora the type species. O. mellina was later transferred to Calonectria, where it belongs. The type specimen of O. paludosa does not have a nectrioid perithecium and belongs in the loculoascomycete genus Tubeufia.

Ellis and Everhardt (1886) described the genus Ophionectria as "Perithecia globose-conical, superficial, papillate, subcarnose,

bright-colored (red, yellow & c). Asci 8-spored. Sporidia filiform, multiseptate or multinucleate." They include Ophionectria cerea ( $\equiv$ Tubeufia cerea) and O. coccicola ( $\equiv$ Podonectria coccicola) both of which have bitunicate asci and belong in the Pleosporales, Loculoascomycetidae.

Seaver (1910) considered the genus Tubeufia Penz. & Sacc. 1898 (Pleosporales, Loculoascomycetidae) a synonym of Ophionectria. He included I. cylindrothecia as a synonym of O. cylindrothecia. Seaver lists O. cerea and O. cylindrothecia as the North American species of Ophionectria. However, both of these species have bitunicate asci and thus belong in the Loculoascomycetidae. They have subsequently been transferred to the pleosporaceous genus Tubeufia. In his description of O. cylindrothecia Seaver recognized the bitunicate nature of the asci by the description: "Spores apparently enclosed in a separate membrane within the ascus, so that the outer wall of the ascus stretches 10-20 u beyond the apex of the spore cluster." The significance of this criterion was not recognized at that time. Seaver lists O. theobromae (= O. trichospora) and Torrubiella rubra (Clavicipitales) as doubtful species. At the same time, Seaver erected the genus Scoleconectria for species of Ophionectria with a well-developed stroma. The type species of Scoleconectria is Ophionectria scolecospora (= Scoleconectria cucurbitula).

Petch (1912) placed O. trichospora in Tubeufia and therefore, considered the two genera synonymous.

Höhnel (1919) separated Ophionectria from Tubeufia on the basis of the absence or presence of paraphyses. At maturity O. trichospora lacks any sterile filaments associated with the asci while Tubeufia javanica, the type species of Tubeufia, has branched, filiform sterile hyphae associated with the asci. These are regarded as pseudoparaphyses. Most hypocreaceous species have apical paraphyses at some stage of development (Rogerson, 1970) but in O. trichospora they are not present in mature specimens.

Petch (1921) stated that the type species of Ophionectria, O. trichospora, had perithecia seated on a thin, byssoid layer and for this reason did not accept Seaver's separation of Scoleconectria from Ophionectria on the basis of the presence of a stroma.

Clements and Shear (1931) list Scoleconectria as a synonym of Ophionectria.

Dingley (1952) considered Ophionectria to include species with "operculate" asci and placed the genus in the Clavicipitaceae. The "operculate" asci in this case refer to asci with thickened, capitate apices characteristic of the Clavicipitales. In discussing the Clavicipitaceae, Ophionectria species are mentioned only as synonyms of Cordyceps tuberculata, Torrubiella "cordyceps" ( $\equiv$  T. lloydii) and Barya agaricicola (Dingley, 1953, 1954). No valid species of Ophionectria are mentioned. Dingley (1952) placed in the genus Calonectria all species of Hypocreales with multiseptate spores divided by transverse septa only and "inoperculate" asci.

In Volume IV A of The Fungi, the genus Ophionectria is included in both the euascomycetes and loculoascomycetes. Müller and von Arx (1973) place it in the Sphaeriales, Hypocreaceae. They separate Ophionectria from Scoleconectria by the well-developed stroma and ascospores budding in the ascus as in S. cucurbitula, the type species of that genus. At the same time Luttrell (1973) includes Ophionectria in the loculoascomycetes. He states that "Ophionectria may be maintained as a separate genus distinguished by lack of the ring of apical appendages around the ostiole that is typical of Tubeufia." This statement is based on species with bitunicate asci which have been mistakenly placed in Ophionectria. Ophionectria, as typified by O. trichospora and characterized by the original description can only contain species with unitunicate asci and light- to bright-colored perithecia. It is therefore only superficially similar to Tubeufia.

Booth (1959), discussing the genera Ophionectria and Scoleconectria, notes that Ophionectria "has become a depository for unrelated species which have merely filiform ascospores in common". My study confirms this statement. After studying most of the type specimens of the species which have been included in Ophionectria, only one species, the type species, remains. All others are excluded; they belong in five orders of the two subclasses of Ascomycetes.

Ophionectria Saccardo, *Michelia* 1:323. 1 July 1878.

= Calonectria de Notaris, p.p., *Comment. Soc. Crittogam. Ital.*  
2:477. 1867.

Fruiting bodies superficial on substrate, solitary to gregarious, with or without a byssoid subiculum.

Perithecia bright-colored, fleshy to membranaceous, ovoid to cylindrical, papilla present or indistinct from perithecia, ostiole lined with periphyses. Perithecia covered with conspicuous, concolorous tubercles extending from the outer perithecial wall. Perithecial wall of two layers: the outer composed of irregularly globose cells with thickened, pigmented cell walls; the inner of hyaline, thin-walled, elongate cells paralleling the centrum axis.

Apical paraphyses, presumably present during development, not visible in mature perithecia.

Asci unitunicate, thin-walled, clavate to cylindric, without a well-developed apical apparatus.

Ascospores long-fusiform, multiseptate, hyaline.

Habitat: On dead bark, decorticated wood and other rotting, woody substrates.

Etymology: Greek, ophio-, pertaining to snakes, snake-like, and nect-, a swimmer, in reference to the long, undulating spores of the type species.

Type: Ophionectria trichospora (Berkeley & Broome) Saccardo.

Ophionectria trichospora (Berkeley & Broome) Saccardo, *Michelia* 1:323.

1878. Figures 6, 7, and 8.

≡Nectria trichospora Berkeley & Broome, *Journal of the Linnean Society*, London 14:115. 1875.

≡Tubeufia trichospora (Berkeley & Broome) Petch, *Annals of the Royal Botanic Gardens, Peradeniya* 5:285. 1912.

=Calonectria cinnabarina P. Henn., *Hedwigia* 36:220. 1897.

≡Ophionectria cinnabarina (P. Henn.) P. Henn., *Hedwigia* 41:7. 1902.

=Calonectria ornata A. L. Smith, *Journal of the Linnean Society*, London 35:18. 1901.

=Calonectria theobromae Pat. in Duss, *Enumeration methodique de champignons recueillis a la Guadeloupe et a la Martinique*, p. 81. 1903.

=Ophionectria portoricensis Chardon, *Mycologia* 13:285. 1921.

=Ophionectria anomala Petch, nom. illeg., *Trans. Brit. Myc. Soc.* 27:143. 1944. (Later homonym of Ophionectria anomala Raciborskii, 1907.)

Fruiting bodies gregarious to scattered, sometimes seated on a white to bright-yellow subiculum; mycelium of subiculum 5-7.5  $\mu\text{m}$  diam, thick-walled with small warts, septate, each cell swollen at one end, as in Antipodium spectabile Pirozynski, the imperfect state.

Perithecia bright red-orange, "Brazil-Red"<sup>1</sup> or lighter when young, ovoid to cylindrical; apex truncate, 250-350 x 400-600  $\mu\text{m}$ ; fleshy

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<sup>1</sup>Color names in quotations are those of Ridgeway (1912).

to membranaceous, sometimes collapsing laterally when dried; covered with conspicuous, concolorous tubercles 25-100  $\mu\text{m}$  tall that extend from the outer perithecial wall layer; composed of loosely-compacted, irregularly-globose cells, 10-25  $\mu\text{m}$  diam with thickened, pigmented cell walls; perithecia may be naked toward apex, papillae indistinct from perithecia, ostiole 45-50  $\mu\text{m}$  diam lined with periphyses.

Perithecial wall of two layers: outer layer 15-90  $\mu\text{m}$  thick, pseudoparenchymatous, composed of large, globose cells 10-25  $\mu\text{m}$  diam with thickened, pigmented walls, textura globulosa in surface view; inner layer 7-10  $\mu\text{m}$  thick, composed of hyaline, thin-walled elongate, cells paralleling the centrum axis.

Asci unitunicate 180-260 x 25-30  $\mu\text{m}$ , clavate, with a long narrow stipe when young; immature spores short and narrow in the ascus apex, extending into the stipe as they mature so the ascus becomes long-clavate with a short stipe; ascus wall closely appressed to spores at maturity; specialized apical discharge mechanism lacking; asci evanescent; spores spirally twisted within the ascus.

Spores 180-250 x 6-10  $\mu\text{m}$ , shorter when immature, hyaline, long-fusiform, often somewhat bent to vermiform; proximal end slightly inflated and bluntly rounded, distal end tapering to narrow, rounded base; walls thickened, spirally striate, 13-24 septa.

Imperfect state: Antipodium spectabile Pirozynski, Can. J. Bot. 52: 1142-1145. 1974. (Figure 9).

Colony growing at a mean of 2.2 mm per day (12 days at 26° C) with odor of decaying wood; pigments diffusing into media (corn meal agar) "Ochraceous-Orange" to "Cinnamon-Rufous"; mycelium sparse,

superficial or submerged with aerial conidiophores, white to yellow-orange with age; hyphae 5–7.5  $\mu\text{m}$  diam, younger hyphae hyaline with small warts forming a reticulate ornamentation on very young hyphae; older hyphae with pigmented, thickened walls covered with numerous warts.

Macroconidia 120–140 x 26–28  $\mu\text{m}$ , 3–5 septate, fusiform with beaked apex, beak variable in length, 3–11  $\mu\text{m}$  but always present, basal cell truncate, borne on phialides.

Type: Nectria trichospora Berkeley & Broome, Berkeley no. 1879, Ceylon, Nov. 1867. IMI #71785, ex herb. R.B.G. #490. (IMI).

Host: On rotting bark and wood.

Distribution: Probably pantropical but at present known from the Asian tropics, the Caribbean and South America.

Etymology: Greek, tricho, a hair, and spora, a seed, in reference to the long, slender, vermiform spores.

Specimens examined:

Brazil: St. Catharine pr. Blumenau, on dead bark, A. Möller No. 229, herb. Pat. #6786. (FH) (NY). The specimen at FH is the type specimen of Calonectria cinnabarina P. Henn.

Canal Zone: Barro Colorado Island, along Drayton Trail, on fallen branch, possibly of Tiliaceae, 9 July 1973, Roger D. Goos BCI #73. (NY).

Ceylon: Berkeley no. 1879, Nov. 1867. IMI #71785, ex herb. R.B.G. #490. Collected as Nectria trichospora Berkeley & Broome. HOLOTYPE. (IMI).

\_\_\_\_\_ T. Petch, Nuwara Eliya, 29 July 1928, on dead bamboo (Arundinaria sp.). (K). This is the type specimen of Ophionectria anomala Petch 1944, a later homonym of O. anomala Raciborskii 1907.

China: Tan-hsien, Hainan, on bark, 16 Oct. 1934, S.Q. Deng #5347, BPI #4925. (BPI).

Costa Rica: Above El Silencia near Tilaran, elev. 2500 ft., on bark 14 Sept. 1964, George Carroll #664. (Herb. George Carroll) (NY).

Dominica: River Douce Valley, on twigs, Feb. 1896, W. R. Elliott #1416. (K). This is the type specimen of Calonectria ornata A. L. Smith.

Guadelope: Coulee du Balisier (massif du Houelmont), on the core of a small pod of Theobroma cacao, 12 March 1903, Duss #749, herb Pat. #6841. (FH). This is the type collection of Ophionectria theobromae Pat.

Jamaica: Woodcutters Gap, elev. 1000 m, on rotten, moss-covered bark, 9 Jan 1971, coll. R. P. Korf, et al. (Herb. Amy Rossman #369) (Herb. Gary Samuels #31J) (NY).

\_\_\_\_\_ Dolphin Head near Askenish, Hanover Parish, elev. 545 m, on rotten bark, 19 Jan 1971. (Herb. Amy Rossman #512). (Herb. Gary Samuels #185J) (NY).

Puerto Rico: Mayaguez, Lajuga, on a log, 13 March 1916, Whetzel and Olive, CUP #11129. (CUP). This is the type collection of Ophionectria portoricensis Chardon.

United States: Hawaii, Waihole Ditch, Waihole, Oahu, elev. 800 ft., on dicot bark among moss, 23 March 1947, R. S. Cowan. (NY).

\_\_\_\_\_ Hawaii, on naked wood, 1923, H. Purdy. (NY).

Venezuela: In mountains north of Nirgua, Edo. Yaracuy, on unidentified wood, 4 July 1971, coll. Dumont, et al. Dumont-VE-1547. (NY).

\_\_\_\_\_ Caucagua, on Theobroma cacao, 7 Oct 1948, A. Coccaway, Herb. R. Ciferri #597. (BPI). This specimen is identified as Ophionectria theobroma forma major but no published description of this taxon has been located. It is Ophionectria trichospora.

FIGURE 6. Fruiting bodies of Ophionectria trichospora

- A. Without subiculum. 40 X.
  
- B. With byssoid subiculum of imperfect state,  
Antipodium spectabile, surrounding the  
perithecia. 30 X.

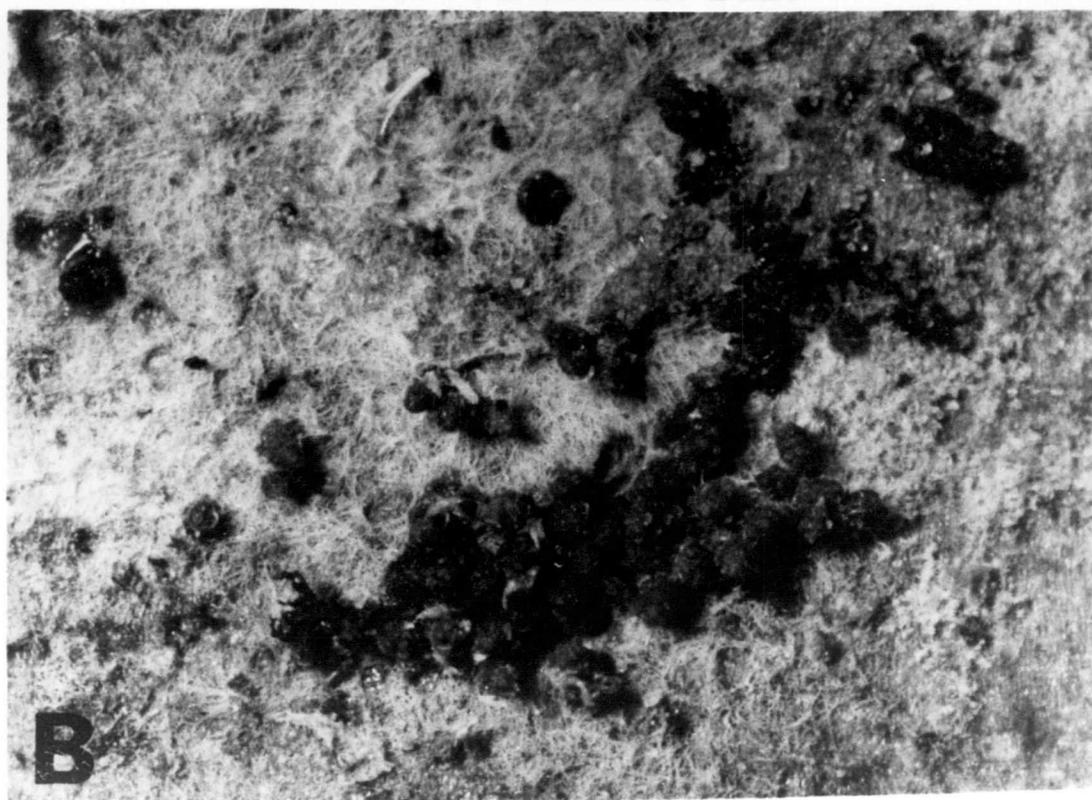
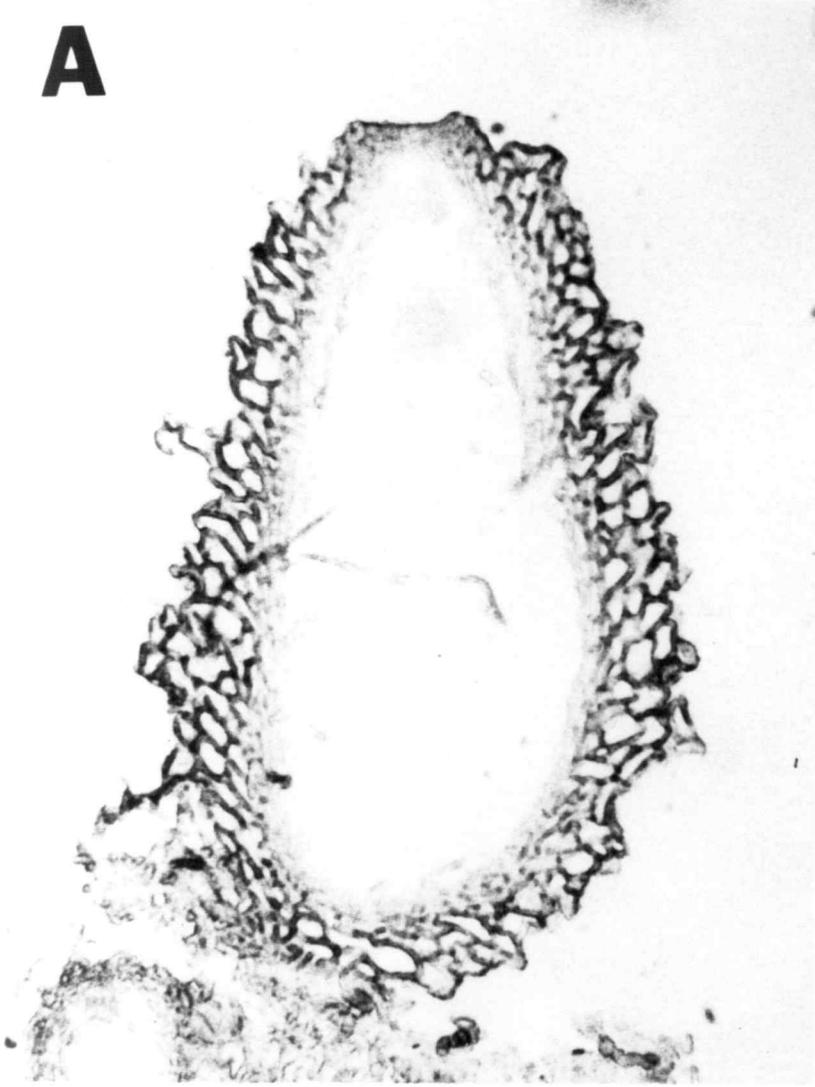


FIGURE 7. Type specimen of Ophionectria trichospora (IMI).

A. X-section. 300 X.

B. Close-up of the perithecial wall showing two-layered structure: inner wall of hyaline, thin-walled, elongate cells; outer wall of pigmented, thick-walled cells forming tubercles. 1500 X.

**A**



**B**

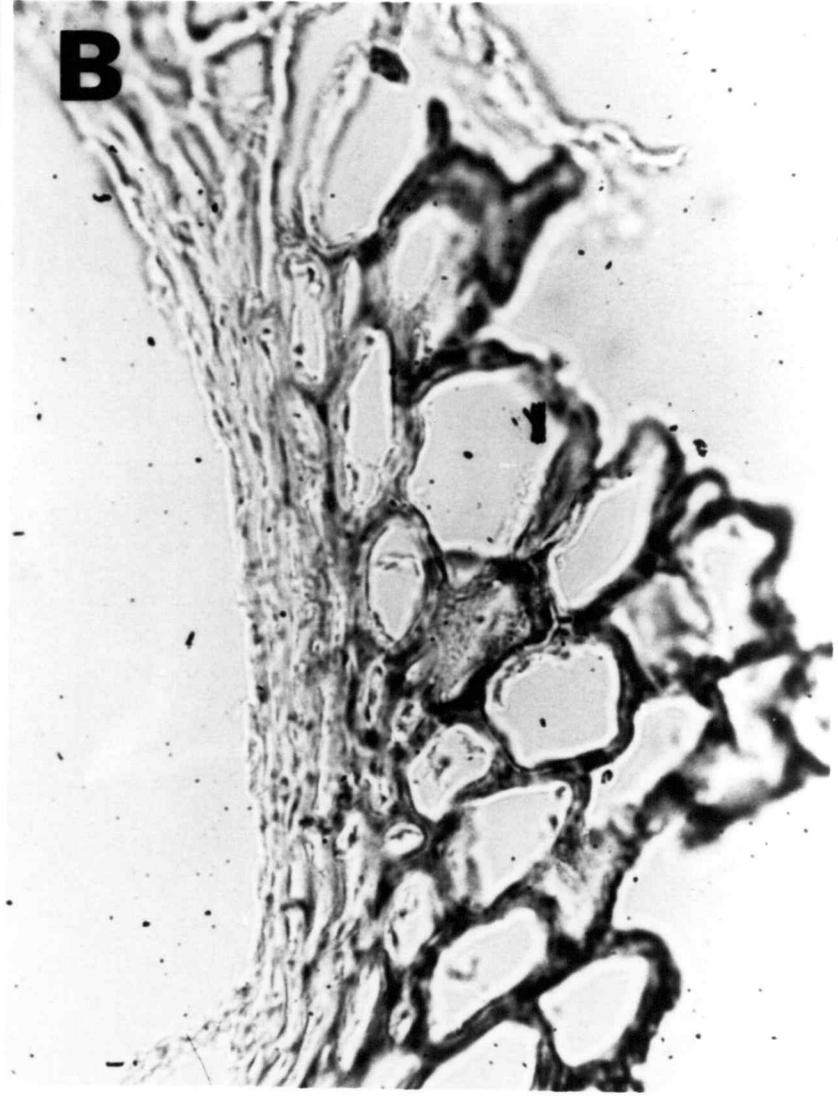


FIGURE 8. Asci and spores of Ophionectria trichospora.

A. Young ascus with immature spores. 1000 X.

B. Mature ascus with spores spirally arranged.  
450 X.

C. Spore. 500 X.

D. Close-up of spore showing spiral striae.  
2000 X.

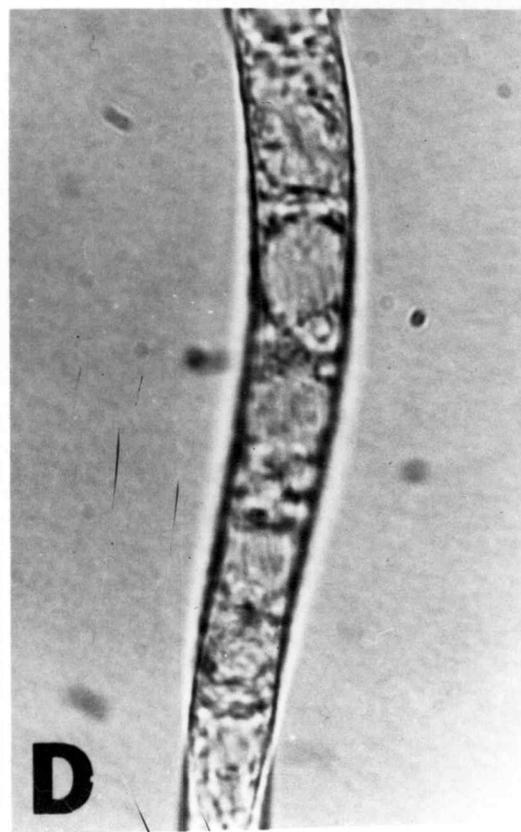
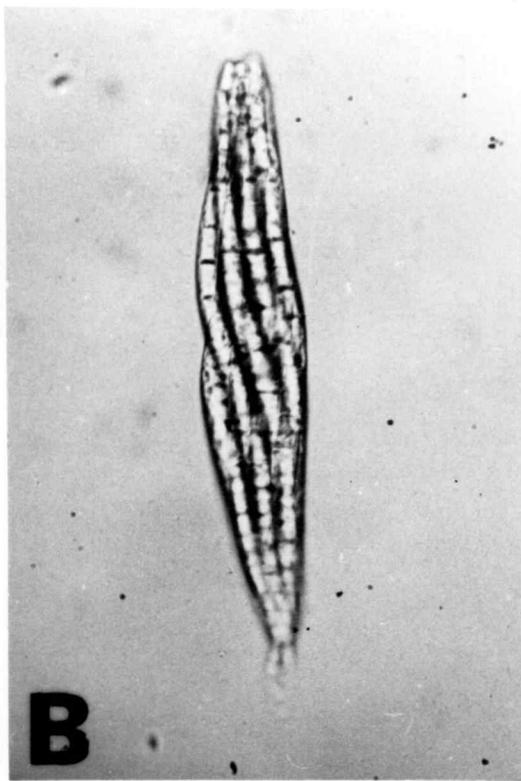
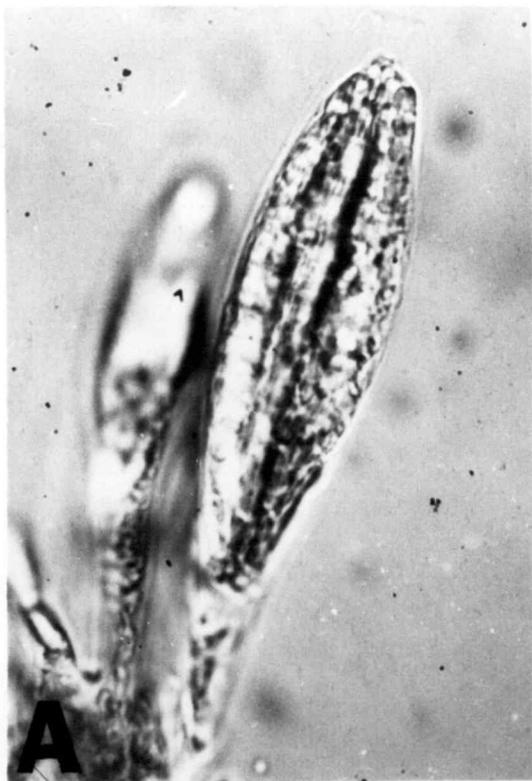
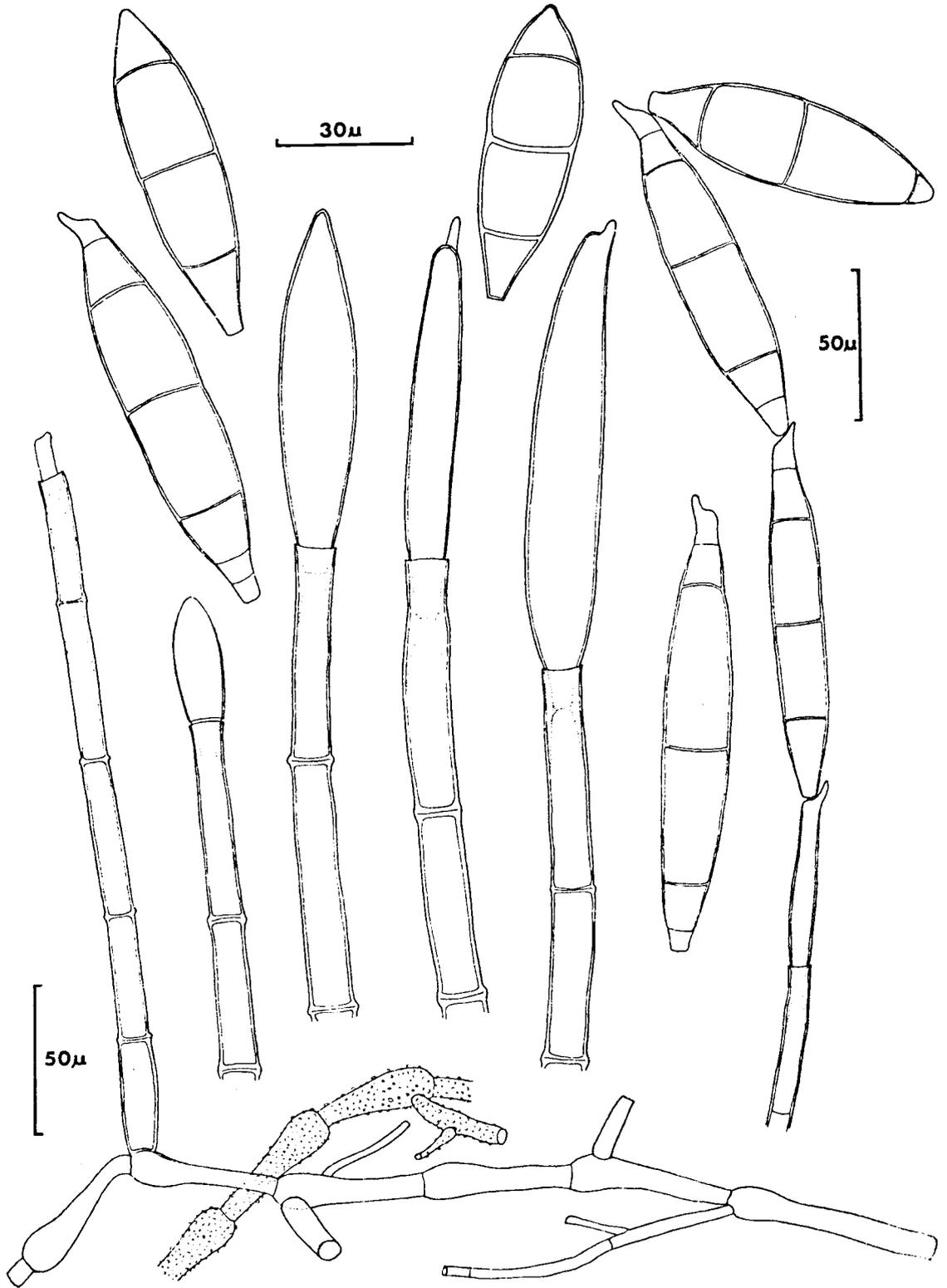


FIGURE 9. Antipodium spectabile: mycelium, conidiophores and conidia from holotype (Pirozynski, 1974).



A Comparison of Ophionectria trichospora and Nectria haematococca

Ophionectria trichospora is more closely related to Nectria haematococca than to the other hypocreaceous species previously placed in Ophionectria. These species are now provisionally transferred to Calonectria. Neither Ophionectria trichospora nor Nectria haematococca fit easily into any of the sections of the genus Nectria delimited by Booth (1959). Booth based his sections on temperate species while both Ophionectria trichospora and Nectria haematococca are tropical. There are many other tropical species of Nectria-like fungi and most are incompletely known. Further study of this group of fungi will undoubtedly clarify generic and subgeneric relationships. Some patterns have already emerged, including the similarity between Ophionectria trichospora and Nectria haematococca. The following paragraphs discuss this relationship in detail (table 2).

Ophionectria trichospora and Nectria haematococca are similar in habitat and distribution. Both are pantropical, although Ophionectria trichospora has not been reported from Africa. These species occur on dead organic matter, particularly well-rotted wood in a moist situation often in association with mosses and other organisms characteristic of such a habitat. Neither species is substrate specific. They have been found growing together on the same substrate.

The perithecia of Nectria haematococca are scattered to gregarious on natural substrates. They are superficial and may or may not be associated with a sparse white byssus. Similarly, the fruiting bodies of Ophionectria trichospora are scattered to gregarious on natural

Table 2. A comparison of Ophionectria trichospora and Nectria haematococca.

|                        | <u>Ophionectria trichospora</u>  | <u>Nectria haematococca</u>  |
|------------------------|--|--|
| Substrate              | on rotting, organic matter usually wood or bark  | on rotting, organic matter but isolated from various substrates  |
| Distribution           | probably pantropical but not reported from Africa  | pantropical and isolated from the temperature zone   |
| Stroma                 | byssus or absent   | sparse byssus or absent  |
| Perithecia arrangement | superficial, scattered to gregarious   | superficial, scattered to occasionally gregarious  |
| color                  | bright red-orange  | red-orange to brick-red  |
| shape                  | ovoid to cylindric   | globose to pyriform  |
| size                   | 250-350 x 400-600 $\mu\text{m}$  | 170-300 x 220-330 $\mu\text{m}$  |
| wall                   | 35-120 $\mu\text{m}$ thick, including warts, of two layers   | 35-120 $\mu\text{m}$ thick, including warts, of two layers   |
| outer layer            | <u>textura globulosa</u> , 15-90 $\mu\text{m}$ , of large, globose cells, 10-25 $\mu\text{m}$ diam, with thickened, pigmented cell walls, extended to form large tubercles | <u>textura globulosa</u> , 15-90 $\mu\text{m}$ , of large, globose cells, 10-25 $\mu\text{m}$ diam, with thickened, pigmented cell walls, extended to form large tubercles |
| inner layer            | <u>textura porrecta</u> , 5-10 $\mu\text{m}$ , of thin-walled, elongate cells, 2-3 layers lining centrum   | <u>textura porrecta</u> , 5-10 $\mu\text{m}$ , of thin-walled, elongate cells, 2-3 layers lining centrum   |
| Asci                   | unitunicate, wall very thin, evanescent at maturity  | unitunicate, thin-walled, may be evanescent at maturity  |
| Apical Mechanism       | no discharge mechanism   | ring present, but spores often found loose in perithecium  |

Table 2 - Continued

|                 | <u>Ophionectria trichospora</u>                      | <u>Nectria haematococca</u> |
|-----------------|--|-----------------------------|
| Spores          |  |                             |
| shape           | long-fusiform  | ellipsoid to obovate        |
| septation       | 13-24 transverse                                     | 1 transverse                |
| size            | 180-250 x 6-10 $\mu\text{m}$                         | 11-18 x 6-8 $\mu\text{m}$   |
| ornamentation   | longitudinally-spirally striate                      | longitudinally striate      |
| Imperfect State | <u>Fusarium-like</u><br><u>Antipodium spectabile</u> | <u>Fusarium solani</u>      |

substrates. They are superficial, occasionally formed on a byssoid stroma composed of the characteristic warty hyphae of Antipodium spectabile, the conidial state. The stroma is poorly developed or absent in both species. The stromal character and arrangement of perithecia on the substrate vary with environmental conditions. The extent of variation seems to be similar for both species, i.e. neither species is formed on a well-developed, basal stroma nor immersed in a byssoid stroma.

Perithecial wall structure is considered an important phylogenetic character. In external appearance the perithecia of Nectria haematococca and Ophionectria trichospora are similar. Both have tubercles, up to 100  $\mu\text{m}$  high, formed by the extension of the outer layer of the perithecial wall (figure 10). The wall consists of two layers in both species. The outer layer varies from 25-100  $\mu\text{m}$  thick, composed of textura globulosa, in which the cells are irregularly globose, 10-25  $\mu\text{m}$  diam with thickened, pigmented walls. The inner layer of the perithecial wall lining the centrum is 10-12  $\mu\text{m}$  thick and is composed of thin-walled, colorless cells which are elongate along the axis of the fruiting body. Within the ostiole these cells extend upwards to form the periphyses.

The perithecia of Nectria haematococca and Ophionectria trichospora are orange to scarlet, presumably depending on the exposure to light during development. The shape of the perithecia of Nectria haematococca is globose to pyriform, 170-300 x 220-330  $\mu\text{m}$ , while Ophionectria trichospora is more elongate, ovoid to cylindrical, 250-350 x 400-600  $\mu\text{m}$ . Neither species has a distinct papilla. Around

FIGURE 10. Comparison of perithecia of Nectria haematococca and Ophionectria trichospora.

A. Nectria haematococca

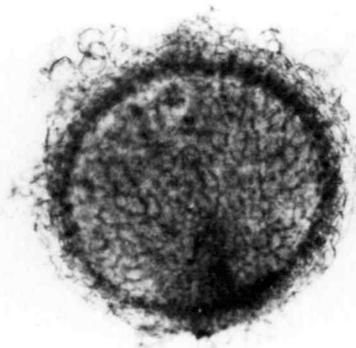
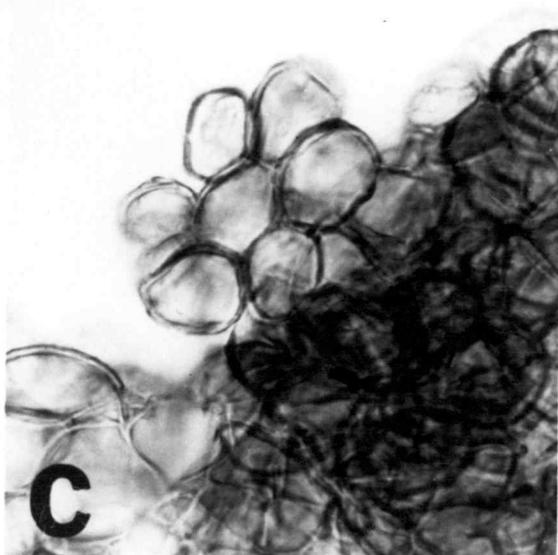
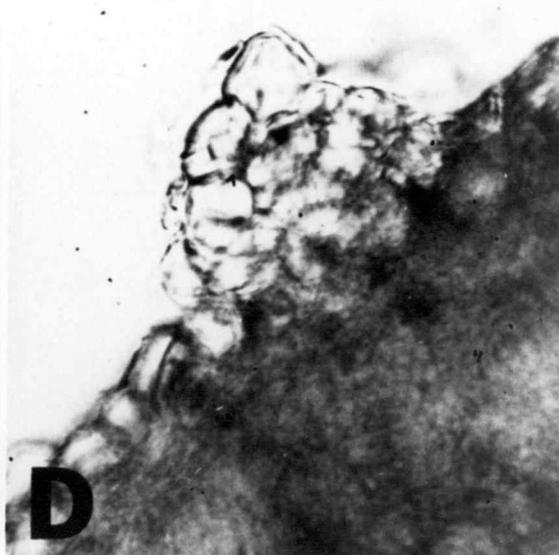
B. Ophionectria trichospora

A and B 125 x.

C. Tubercle of Nectria haematococca formed by the extension of outer perithecial wall of thick-walled, pigmented cells.

D. Tubercle of Ophionectria trichospora formed as in Nectria haematococca.

C and D 750 X.

**A****B****C****D**

the ostiole the outer layer becomes thinner and the inner layer extends to the apex.

The centrum characters of both species are typical of Nectria species as described by Hanlin (1961, 1963, 1971). The paraphyses of both species are evanescent at maturity. Because the one isolate could not be induced to fruit in culture, the perithecial development of Ophionectria trichospora was not studied. Several workers have studied the perithecial development of Nectria haematococca (Hanlin, 1971; Quereshi & Page, 1972). The asci of Nectria haematococca are thin-walled, unitunicate, cylindrical becoming clavate with a rounded apex. An apical ring is reported but is not visible in tropical collections. The spores are monostichous at first but become distichous at maturity. The asci of Ophionectria trichospora are thin-walled, unitunicate, clavate when the spores are immature but become long-clavate as the spores develop, extending into the basal stalk of the ascus. At maturity the ascus wall becomes very thin and is finally evanescent. The ascus apex is rounded with no evidence of a ring. The spores are polystichous eventually becoming spirally intertwined.

The spores of Nectria haematococca are typical of the genus. They are two-celled, ellipsoid to obovate, hyaline, 11-18 x 4-8  $\mu\text{m}$  with longitudinal striations. Ophionectria trichospora spores are long-fusiform, 185-250 x 6-10  $\mu\text{m}$ , with 13-24 transverse septa, and longitudinal striations at maturity.

The imperfect state of Nectria haematococca is Fusarium solani (Mart.) Sacc., a common soil fungus and plant pathogen. According to Booth (1971), it has been isolated from an extremely wide range of plants and animals including ulcerated human tissue, and is considered a serious pathogen of members of the Solanaceae and other temperate and tropical plants. The macrospores of Fusarium solani are hyaline, fusiform with a characteristic foot-cell. There are two morphological strains based on the size of the macrospores, 35-55 x 4.5-6  $\mu\text{m}$  and 45-100 x 5-8  $\mu\text{m}$  (Booth, 1971). In addition Nectria haematococca has both homothallic and heterothallic strains which under proper conditions readily develop fruiting bodies in culture. Ophionectria trichospora has never been found to fruit in culture. It may be heterothallic and compatible strains have not been cultured. The imperfect state of Ophionectria trichospora is Antipodium spectabile Pirozynski 1974. The Fusarium-like macrospores have the "foot-cell" at the apex and the conidia are borne in chains. They develop from an unusual type of phialide. A complete description of this state is given under the description of Ophionectria trichospora.

The differences between Nectria haematococca and Ophionectria trichospora are not considered phylogenetically important. Study of more species in this section may indicate the significance of these differences. The shape of the perithecium is dissimilar, however, Ophionectria trichospora could be considered a taller version of the globose to pyriform shape of Nectria haematococca. This may be correlated with

spore length. Secondly, although the ascus type is unitunicate, the ascus apex of Nectria haematococca is reported to have an apical ring while the entire ascus of Ophionectria trichospora is evanescent. This may also be correlated with spore length. Perithecia of Nectria haematococca are often seen with a cirrhus of ascospores emerging from the ostiole suggesting nonviolent spore discharge (pers. obs.; Samuels, 1973, pers. comm.). Thirdly, the difference in spore length and septation has been the basis for separating these species into different genera. The spores of both species are essentially fusiform with longitudinal striations. Finally, the imperfect state of Ophionectria trichospora is similar but not identical to that of Nectria haematococca. All known imperfect states of species of the Nectria-complex are variations of the simple, phialosporic Cephalosporium structure (Booth, 1959). Conidia of both Fusarium solani and Antipodium spectabile are septate, hyaline phialospores characteristic of several species of Nectria with Fusarium imperfect states. The presence of an apical "foot-cell" on the Antipodium spectabile conidium is a minor variation. In summary, these differences do not suggest unrelatedness, rather they may all be a result of the difference in ascospore length.

## V. EXCLUDED OPHIONECTRIA SPECIES

All species except the type species, Ophionectria trichospora, are excluded from the genus Ophionectria. The excluded species are placed in five orders of the two subclasses of Ascomycetes. A summary of the disposition of excluded Ophionectria species is given in Table 3. They are discussed briefly in the following section.

### Euascomycetidae

#### Hypocreales

The order Hypocreales contains seven species previously placed in Ophionectria. Four of these are here transferred to Calonectria: C. hendrickxii, C. muscivora, C. puiggarii, and C. vernoniae. One species, Calonectria mellina, was originally described as a Calonectria species and should remain in that genus. The remaining Ophionectria species in the Hypocreales have been synonymized with other species in that order by previous authors. Ophionectria cylindrospora and O. scolecospora are synonyms of Scoleconectria cucurbitula, and Ophionectria cylindrospora var. tetraspora is a synonym of Thyronectria balsamea.

#### Clavicipitales

Five species placed in Ophionectria belong to the order Clavicipitales. One new species of Barya, B. byssicola, based on an Ophionectria herbarium name, is here provisionally described. Another species, O. lloydii, is here transferred to Torrubiella. This transfer was suggested by a previous author who transferred the invalid name O. "cordyceps".

## Euascomycetidae

## Loculoascomycetidae

## Hypocreales

## Hypocreaceae

- Calonectria hendrickxii (Hansford) Rossman = Ophionectria hendrickxii  
C. mellina (Mont.) Höhnelt = Ophionectria mellina  
C. muscivora (Petch) Rossman = Ophionectria muscivora  
C. puiggarii (Speg.) Rossman = Ophionectria puiggarii  
C. vernoniae (Hansford) Rossman = Ophionectria vernoniae  
Scoleconectria cucurbitula (Fries) Booth = Ophionectria cylindrospora,  
= O. scolecospora  
Thyronectria balsamea (Cooke & Peck) Seeler = Ophionectria cylindrospora  
var. tetraspora

## Clavicipitales

## Clavicipitaceae

- Barya agaricola (Berk.) Höhnelt = Ophionectria agaricola  
Barya byssicola Rossman = Ophionectria "byssicola"  
Byssostilbe stilbiger (Berk. & Br.) Petch = Ophionectria trichia  
Cordyceps tuberculata (Libert) Maire = Ophionectria cockerellii  
Torrubiella lloydii (Mains) Rossman = Ophionectria lloydii, = O. "cordyceps"

## Sphaeriales

## Sordariaceae

- Lasiosphaeria glabra (Penz. & Sacc.) Rossman = Ophionectria conica  
L. depilata Fuckel = Ophionectria depilata, = O. ambigua  
L. rufula (Penz. & Sacc.) Rossman = Ophionectria trichospora var. rufula  
Mycomedusiospora flavida (Rick) Carroll & Munk = Ophionectria flavida

## Sphaeriaceae

- "Ophionectria" clerodendri Tilak & Kale

## Ostropales

## Ostropaceae

- Erinella cfr. bicolor = Ophionectria palicoureae

## Pleosporales

## Pleosporaceae

- Podonectria aurantii (P. Henn.) Petch = Ophionectria aurantii, = O. tetraspora  
P. coccicola (Ellis & Everh.) Petch = Ophionectria coccicola  
P. coccorum (Petch) Rossman = Ophionectria coccorum  
P. larvaespora (Cooke & Masee) Rossman = Ophionectria larvaespora  
Tubeufia anceps Penz. & Sacc. = Ophionectria anceps  
I. cerea (Berk. & Curt.) Höhnelt = Ophionectria cerea, = O. anonae,  
= O. belonospora, = O. belonospora var. unicadata, = O. briardi,  
= O. briardi var. longipila, = O. cupularem  
= O. episphaeria, = O. everhartii  
I. cylindrothecia (Seaver) Höhnelt = Ophionectria cylindrothecia  
I. hidakaeana (Hino & Katamoto) Rossman = Ophionectria hidakaeana  
T. palmarum (Torrend) Rossman = Ophionectria palmarum  
T. paludosa (Crouan) Rossman = Ophionectria paludosa  
"Ophionectria" erinacea Rehm  
"Ophionectria" tropicalis Speg.  
"Ophionectria" uredinicola Teng = "Ophionectria" uredinicola Petch  
"Ophionectria" luxurians (Rehm) Hansford  
"Ophionectria" balladynae Hansford

Table 3. Proposed Disposition of Excluded Ophionectria Species

The remaining species have been synonymized with members of the Clavicipitales by previous authors: Barya agaricicola ( $\equiv$ Ophionectria agaricicola), Byssozilbe stilbiger ( $\equiv$ O. trichia) and Cordyceps tuberculata ( $\equiv$ O. cockerellii).

#### Sphaeriales

The Sphaeriales contains six species previously placed in Ophionectria. Two taxonomic changes are made in the genus Lasio-sphaeria: L. glabra ( $\equiv$ Ophionectria conica) and L. rufula ( $\equiv$ O. trichospora var. rufula). Ophionectria ambigua is a synonym of Lasio-sphaeria depilata ( $\equiv$ Ophionectria depilata). One species was transferred to Mycomedusio-spora, M. flavida ( $\equiv$ O. flavida), a genus closely related to Lasio-sphaeria. Another species, Ophionectria clerodendri, belongs to the Sphaeriales but its generic disposition cannot be determined.

#### Ostropales

One species excluded from Ophionectria has an apothecial ascocarp and is placed in the Ostropales: Erinella cfr. bicolor ( $\equiv$ O. palicoureae).

#### Loculoascomycetidae

#### Pleosporales

Twenty-five species erroneously placed in Ophionectria have bitunicate asci and belong in the order Pleosporales of the subclass Loculoascomycetidae. Two species are here transferred to the genus Podonectria; P. coccorum ( $\equiv$ O. coccorum) and P. larvaespora ( $\equiv$ O.

larvaespora). Three other species were placed in Podonectria by earlier authors: P. aurantii ( $\equiv$ O. aurantii,  $\neq$ O. tetraspora) and P. coccicola ( $\equiv$ O. coccicola). The genus Tubeufia includes six species with Ophionectria synonyms. Three Ophionectria species are transferred here to Tubeufia: T. hidakaeana ( $\equiv$ O. hidakaeana), T. palmarum ( $\equiv$ O. palmarum) and T. paludosa ( $\equiv$ O. paludosa). Tubeufia cylindrothecia ( $\equiv$ O. cylindrothecia) and T. anceps ( $\equiv$ O. anceps) have already been correctly synonymized. Nine Ophionectria taxa which belong in Tubeufia are synonyms of T. cerea ( $\equiv$ O. cerea, = O. anonae,  $\neq$ O. belonospora,  $\neq$ O. belonospora var. unicaudata,  $\neq$ O. briardi,  $\neq$ O. briardi var. longipila,  $\neq$ O. cupularem,  $\neq$ O. episphaeria,  $\neq$ O. everhartii).

The remaining Ophionectria species which have bitunicate asci cannot be placed in any existing genera. Three of these species, Ophionectria erinacea, O. tropicalis and O. uredinicola, occur as parasites on rusts while the other two species, Ophionectria balladyna and O. luxurians, are found on the dark mycelium of superficial, leaf-surface fungi.

#### Doubtful and Invalid Species

The remaining eleven species of Ophionectria are doubtful because the type specimen is exhausted or could not be located. In addition twelve Ophionectria names are invalid ones which were either illegitimately, invalidly or never published.

Following is a detailed account of the excluded Ophionectria species. Each taxon is reviewed, new and transferred species are

described and illustrated, and a key to all species which have been assigned to the genus Ophionectria is included.

KEY TO THE SPECIES  
WHICH HAVE BEEN ASSIGNED TO THE GENUS OPHIONECTRIA

- |  |                     |    |
|--|---------------------|----|
| 1. Asci unitunicate, usually arranged in a hymenial layer;<br>unbranched paraphyses or apical paraphyses present or not.   | (Euascomycetidae)   | 2  |
| 1. Asci bitunicate, arranged in a hymenial layer or not;<br>branched pseudoparaphyses generally present.   | Loculoascomycetidae | 20 |
| 2. Ascocarp an apothecium. Discomycetes, Ostropales.<br><u>Erinella</u> cfr. <u>bicolor</u> (= <u>Ophionectria palicoureae</u> )                                 |                     |    |
| 2. Ascocarp a perithecium.   |                     | 3  |
| 3. Perithecia typically black to dark brown; texture<br>carbonaceous, cartilaginous, leathery or (rarely)<br>fleshy.   | Sphaeriales         | 16 |
| 3. Perithecia light- to bright-colored; texture soft,<br>fleshy to membranaceous.  |                     | 4  |
| 4. Asci with an enlarged, thickened apical cap penetrated<br>by a narrow, threadlike pore; spores filiform.  | Clavicipitales      | 12 |
| 4. Asci with or without a specialized apical ring; apex<br>without an enlarged, thickened apical cap; spores<br>short elliptical to long fusiform, not filiform. | Hypocreales         | 5  |

5. Primary ascospores budding in the ascus producing ascoconidia. 6
5. Primary ascospores not budding in the ascus. 7
6. Primary ascospores dictyosporous, 14-27 x 3.5-6  $\mu\text{m}$ .  
Thyronectria balsamea (= Ophionectria cylindrospora var. tetraspora)
6. Primary ascospores scolecosporous, 37-77 x 2.5-4  $\mu\text{m}$ .  
Scoleconectria cucurbitula (= Ophionectria cylindrospora, = O. scolecospora)
7. Perithecia brown, fleshy, small, 100-130 x 80-100  $\mu\text{m}$ , spores acicular, 18-20 x 1-1.5  $\mu\text{m}$ . Calonectria hendrickxii (= O. hendrickxii)
7. Perithecia light- to bright-colored, not brown, larger than 130  $\mu\text{m}$ ; spores long-fusiform, longer than 20  $\mu\text{m}$ . 8
8. Perithecia not smooth, with some external thickening of the outer wall. 9
8. Perithecia with smooth walls, no irregular thickening of the outer perithecial wall. 10
9. Outer perithecial cells, with thin, hyaline walls, forming a ring of tubercles around the ostiole; spores 40-60 x 4-7  $\mu\text{m}$ . Calonectria puiggarii (= Ophionectria puiggarii)
9. Outer perithecial cells with thickened, pigmented walls; outer perithecial cells extended to form large tubercles covering the entire fruiting body; spores 180-250 x 6-10  $\mu\text{m}$ . Ophionectria trichospora.

10. Perithecia without a byssoid subiculum, superficial on rotten wood; spores 50-60 x 4.5-6  $\mu\text{m}$ . Calonectria mellina ( $\equiv$  Ophionectria mellina)
10. Perithecia with a byssoid subiculum, superficial or partially immersed, on moss or leaves; spores greater than 60  $\mu\text{m}$  long, less than 4  $\mu\text{m}$  wide. 11
11. Perithecia immersed in a white byssoid subiculum, on moss; spores 180-240 x 2-3  $\mu\text{m}$ . Calonectria muscivora ( $\equiv$  O. muscivora)
11. Perithecia superficial on a thin, byssoid subiculum, on leaves; spores 80-111 x 2  $\mu\text{m}$ . Calonectria vernoniae ( $\equiv$  O. vernoniae)
12. Stroma pseudoparenchymatous, usually well-developed, erect, stipitate, but in some specimens reduced to a basal tissue; on insects and spiders. Cordyceps tuberculata ( $\equiv$  Ophionectria cockerellii,  $\equiv$  Cordyceps cockerellii).
12. Stroma generally hyphal, poorly developed, present as a byssoid subiculum or absent (Torrubiella lloydii has pseudoparenchymatous basal tissue forming flattened plates.); on other fungi or dung. 13
13. Spores not separating at each septum into partspores within the ascus. 14
13. Spores separating at each septum into partspores within the ascus. 15

14. On decaying fructification of fleshy Agaricales. Barya agaricicola (≡Ophionectria agaricicola)
14. On wild guinea pig dung. Barya byssicola
15. On myxomycetes; partspores cuboidal or spherical, associated with a stilbaceous imperfect stage; stroma a byssoid subiculum. Byssostilbe stilbiger (≡Ophionectria trichia)
15. On Cordyceps spp.; partspores rectangular; no known imperfect state; stroma pseudoparenchymatous forming flattened, basal plates bearing perithecia superficially. Torrubiella lloydii (≡Ophionectria lloydii)
16. Perithecia fleshy, pale yellow; spores vermiform, coiled in the ascus, breaking into numerous small fragments at maturity.  
Mycomedusiospora flavida (≡Ophionectria flavida)
16. Perithecia leathery to cartilaginous, dark-brown to black; spores fusiform, not breaking up in the ascus. 17
17. Asci without a distinct apical ring; spores short-fusiform with thickened septa; perithecia on very rotten bark. "Ophionectria" clerodendri
17. Asci with a distinct apical ring; spores generally long-fusiform with thin septa; perithecia on rotten wood.  
Lasiosphaeria spp. 18
18. Spores 130-160 x 7-8  $\mu\text{m}$ , septa generally more than 12; perithecia 200-250  $\mu\text{m}$  diam. Lasiosphaeria rufula (≡Ophionectria trichospora var. rufula)

- 67
18. Spores less than 130  $\mu\text{m}$ , septa generally 12 or less;  
perithecia greater than 250  $\mu\text{m}$  diam. 19
19. Spores 90-125 x 5-5.5  $\mu\text{m}$ , 8-12 septate. Lasiosphaeria  
glabra ( $\equiv$ Ophionectria conica)
19. Spores 65-80 x 5-6  $\mu\text{m}$ , 5-8 septate; perithecia covered  
with closely-appressed, brown hyphae. Lasiosphaeria  
depilata ( $\equiv$ L. fuckelii,  $\equiv$ Ophionectria depilata,  $\equiv$ O.  
ambigua)
20. On scale insects. Podonectria 21
20. On other fungi or rotten plant material. 24
21. Ascocarps brown; spores 50-55 x 1.5-2.5  $\mu\text{m}$ , 7-septate; no  
known imperfect state. Podonectria coccorum ( $\equiv$ Ophio-  
nectria coccorum)
21. Ascocarps dirty-white to bright-colored; spores 6-12  $\mu\text{m}$   
wide; imperfect state Tetracrium or Melanconium, if  
known. 22
22. Ascocarps dull-orange, covered with bright-yellow  
scurf; spores 145-190 x 7.5-11  $\mu\text{m}$ ; imperfect state  
reported to be Melanconium luteocinctum. Podonectria  
larvaespora ( $\equiv$ Ophionectria larvaespora,  $\equiv$ Lasiosphaeria  
larvaespora)
22. Ascocarps dirty-white to brown; imperfect state  
Tetracrium with distinct 3 or 4-armed stauroconidia. 23
23. Spores 50-75 x 7.5-12  $\mu\text{m}$ , 9-13 septate. Podonectria  
aurantii ( $\equiv$ Ophionectria aurantii)

23. Spores 110-180 x 6-8  $\mu\text{m}$ , 15-23 septate. Podonectria  
coccicola ( $\equiv$ Ophionectria coccicola)
24. On old stromatic pyrenomycetes and rotten plant  
material; ascocarps dirty-white, bright-colored,  
ochraceous-yellow to almost black. Tubeufia spp. 25
24. On rusts or dark, leaf-surface fungi; ascocarps  
translucent, white to light-colored. 30
25. Ascocarps cylindric; spores 60-80 x 4-5  $\mu\text{m}$ . Tubeufia  
cylindrothecia ( $\equiv$ Ophionectria cylindrothecia)
25. Ascocarps globose, subglobose to ellipsoid. 26
26. Ascocarps dull-orange, covered with bright-yellow  
scurf; spores 40-50 x 2.5-5  $\mu\text{m}$ , 4-5 septate.  
Tubeufia palmarum ( $\equiv$ Ophionectria palmarum)
26. Ascocarps dirty-white to brown, not covered with  
scurf. 27
27. Ascocarps ochraceous-yellow to brown or black with  
age; spores 30-50 x 2.5-4  $\mu\text{m}$ . Tubeufia cerea  
( $\equiv$ Ophionectria cerea,  $\equiv$ O. belonospora,  $\equiv$ O. belonospora  
var. unicaudata,  $\equiv$ O. cupularem,  $\equiv$ O. anonae,  $\equiv$ O. briardi,  
 $\equiv$ O. briardi var. longipila,  $\equiv$ O. episphaeria,  $\equiv$ O. everhartii)
27. Ascocarps dirty-white to yellow; spores generally longer  
than 50  $\mu\text{m}$ . 28
28. Ascocarps 80-100  $\mu\text{m}$  diam.; spores 50-60 x 3.5  $\mu\text{m}$ .  
Tubeufia anceps ( $\equiv$ Ophionectria anceps)
28. Ascocarps larger than 100  $\mu\text{m}$  diam, spores longer than  
60  $\mu\text{m}$ . 29

29. Ascocarps 260-295  $\mu\text{m}$  diam; spores 75-100 x 3-4  $\mu\text{m}$ . Tubeufia paludosa ( $\equiv$ Ophionectria paludosa)
29. Ascocarps 200-450  $\mu\text{m}$  diam; spores 100-120 x 2.5-3  $\mu\text{m}$ .  
Tubeufia hidakaeana ( $\equiv$ Ophionectria hidakaeana)
30. On uredosori of rusts. 31
30. On dark hyphae of leaf-surface fungi. 33
31. Ascocarps bright yellow-orange, covered with hyphae developing from a byssoid stroma. "Ophionectria" uredinicola
31. Ascocarps white to pale-yellow, not covered with hyphae; no stroma present. 32
32. Ascocarps with straight, hyaline hairs surrounding the ostiole. "Ophionectria" erinacea
32. Ascocarps lacking hairs but with flexuous hyphal projections surrounding the ostiole; hyphae radiating from the base of the ascocarp. "Ophionectria" tropicalis
33. Ascocarps on Balladyna sp. (Englerulaceae); spores narrow, 0.5-1  $\mu\text{m}$  wide, spirally coiled in the ascus. "Ophionectria" balladyna.
33. Ascocarps on Meliola spp. (Meliolaceae); spores greater than 1  $\mu\text{m}$  wide. 34
34. Spores long-fusiform without appendages, hyaline, 75 x 2  $\mu\text{m}$ . "Ophionectria" luxurians ( $\equiv$ Paranectria luxurians)

34. Spores short-fusiform with terminal appendages, becoming dark with age, 30-40 x 3  $\mu\text{m}$ . Malacaria entebbeensis (Specimens labelled Paranectria luxurians issued as C. F. Baker #171, Fungi Malayana, are M. entebbeensis.)

## EUASCOMYCETIDAE

The subclass Euascomycetidae contains those Ascomycetes in which the asci are functionally unitunicate. The asci typically develop from ascogenous hyphae and are enclosed in an ascocarp. The ascogonia, whether free or in a stroma, become surrounded by an envelope of hyphae which develops into the peridium of the ascocarp. The Euascomycetidae includes all the ascomycetous yeasts, the plectomycetes, the laboulbeniomyces, the pyrenomycetes and the discomycetes. (For a complete historical review, see subclass Loculoascomycetidae.) The species excluded from Ophionectria that belong to the Euascomycetidae are placed in the Hypocreales, Clavicipitales, Sphaeriales and Ostropales.

## HYPOCREALES

The Hypocreales includes those Euascomycetidae with perithecia which are soft, fleshy or membranous, and are typically white to bright-colored. The unitunicate asci form a single layer lining the base and sides of the perithecial cavity and grow upward among the apical paraphyses. The ascus apex may or may not contain a ring with a pore through which the spores are discharged. The Hypocreales have been placed in the Sphaeriales (Dennis, 1968; Müller & von Arx, 1973). Following Rogerson (1970) one family, the Hypocreaceae, is recognized.

## HYPOCREACEAE

The Hypocreaceae includes three major sections of genera which have been recognized at the family level by some authors. These families are reviewed by Rogerson (1970). The Hypomyces-complex includes those genera which generally occur on other fungi. Perithecia typically form within a byssoid to well-developed stroma which is not pseudoparenchymatous. The asci are unitunicate and the ascospores are fusiform, often apiculate and warty. The Hypocrea-complex includes those genera in which the perithecia are typically immersed in a well-developed pseudoparenchymatous stroma and generally have two-celled spores which break into partspores at maturity. The remaining genera belong to the large Nectria-complex. It typically includes those genera with perithecia not immersed in a stroma and having hyaline, uniseptate to multiseptate ascospores. There are many genera which do not fall into any of these complexes as Rogerson suggests by recognizing only one family.

Several species excluded from Ophionectria belong to the Hypocreales, Hypocreaceae. They belong to Calonectria, Scoleconectria and Thyronectria, which are members of the Nectria-complex. These genera include species which are essentially like Nectria but are placed in related genera on the basis of spore length and septation. The correct position and relationship of these species and genera within the Nectria-complex can only be determined by an extensive overview of all the species. The number of species involved is enormous; a study of them is beyond the limits of one person. Some

sections of species within the complex have been defined (Dingley, 1953; Booth, 1959). A study of the tropical members of the Nectria-complex, including the hypocreaceous species formerly placed in Ophionectria, will help in determining these relationships.

CALONECTRIA de Notaris, Comment. Soc. Crittogam. Ital. 2:477. Feb. 1867.

The genus Calonectria de Notaris was described in 1867 to include those Nectria-like species with two- to multiseptate ascospores. The type description is as follows: "Perithecia discreta v. caespitosa, erumpenti-superficialia, molliuscula, laeticoloria, globosa, papillata subinde byssiseda v. pilosula. Sporidia oblonga v. fusoida, 2- pluriseptata, hyalina, subinde (immatura?) continua nucleata. -- Status secundarii in nonnullis cogniti." (Sacc. II:540). Only one species is described, the type species, Calonectria daldiniana. The asci are described as evanescent and are probably unitunicate. The genus Calonectria belongs in the Hypocreales (Pirozynski, 1974, pers. comm.). Calonectria, like Ophionectria, has been the repository of unrelated species which have in common, bright-colored perithecia and multiseptate spores. Several hundred species of Calonectria have been described. Like Ophionectria many may have bitunicate asci and belong in the subclass Loculoascomycetidae. No one has attempted a monographic treatment of this genus.

Ellis & Everhardt (1892) include Calonectria in their suborder Hypocreaceae. The genus is described as "Perithecia scattered or caespitose, superficial or erumpent, soft (carnose-membranaceous),

bright-colored. Sporidia oblong or fusoid, 2- or more-septate, hyaline" (p. 112). This description is similar to that of Ophionectria and Nectria except in spore shape and septation. Ellis & Everhardt include seven species, four of which were later transferred to Scoleconectria.

Seaver (1909) placed all Nectria-like species without a well-developed stroma and multiseptate spores in either Ophionectria or Calonectria on the basis of spore shape and septation. Seaver erected Scoleconectria for multiseptate-spored Nectria-like species with a well-developed stroma without regard to the extent of septation and shape of the spores. At the same time Höhnelt (1910b) used the genus Puttemansia to accommodate Calonectria species with a well-developed stroma.

The difference between Calonectria and Ophionectria has never been well-defined. Rogerson (1970) separated Calonectria from Ophionectria on the basis of ascospore length:width ratio less or greater than 20:1. After examining length:width ratios for most species (figure 1) described in these genera, I can find no difference in spore length:width ratio between the two genera.

Unlike Ophionectria, there are several common temperate species of Calonectria which are truly hypocreaceous. As a result the taxonomic position of Calonectria has not been confused as in Ophionectria which has been placed in the Loculoascomycetidae. Calonectria is used as a repository for hypocreaceous species which have been excluded from Ophionectria. Eventually Calonectria will be studied and natural relationships within the entire Nectria-complex will be determined.

Calonectria hendrickxii (Hansford) comb. nov. Figure 14d.

≡Ophionectria hendrickxii Hansford, Syd. Bei. 2:122. 1957.

Fruiting bodies superficial on hyphae of Englerula macaranga.

Perithecia brown, globose to subglobose with a broadly-rounded papilla, small 80-120 x 90-110  $\mu\text{m}$  diam, surface smooth, solitary to scattered. Perithecial wall composed of thin-walled, small cells forming textura angularis, pigment globules located within cytoplasm.

Sterile hyphae associated with asci scant, filiform, unbranched.

Asci unitunicate, clavate, no apical mechanism, 23-30 x 5-6  $\mu\text{m}$ , tapering to base, polystichous, somewhat fasciculate.

Spores acicular, 18-21 x 1-1.5  $\mu\text{m}$ , curved, pointed at both ends, indistinctly septate.

Type: Congo. Mt. Biega, Kiva, parasitic on superficial mycelium of Englerula macaranga P. Henn., on leaves of Macaranga ?schweinfurthii, June, 1946, F. L. Hendrickx #3400, Holotype (IMI). Isotype (BR).

The type collections have brown, fleshy perithecia and unitunicate asci. The small fruiting bodies are smooth with thin, transparent perithecial walls. This species lacks the thick-walled cells of the outer perithecial wall layer characteristic of the genus Ophionectria, rather the perithecial wall is composed of hyaline, thin-walled cells. The centrum contains some sterile hyphae and numerous, persistent asci. This species belongs in the Hypocreales and is probably related to other tropical hypocreaceous species parasitic on superficial, leaf-surface fungi. Dennis (1970) cites

FIGURE 14. Asci of species of Euscomycetidae which have been transferred to new genera. All 1000 X.

A. Torrubiella lloydii

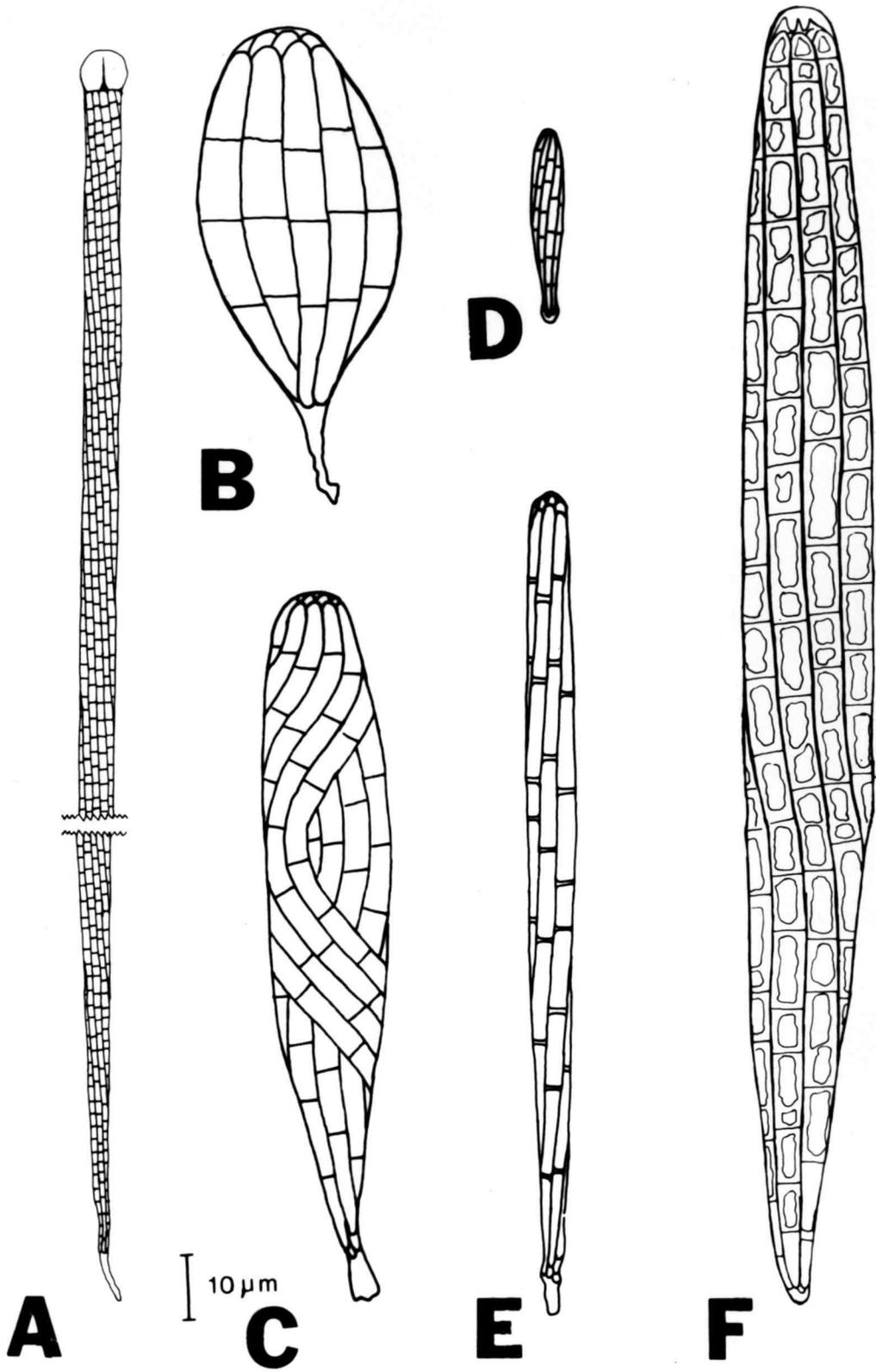
B. Calonectria puiggarii

C. C. vernoniae

D. C. hendrickxii

E. C. muscivora

F. Lasiosphaeria glabra



a group of Calonectria species on Meliolaceae and this seems to be the best genus for this species at present. These species, growing on the dark hyphae of superficial, leaf-surface fungi, may prove distinctive as a section within the Hypocreales.

Calonectria mellina (Mont.) Höhnelt, Ann. Myc. 8:467. 1910.

≡Nectria mellina Mont., Syll. Generum Spec. Plantarum Cryptogam. p. 225. 1856.

≡Ophionectria mellina (Mont.) Sacc., Michelia 1:323. 1878.

The type specimen has unitunicate asci. The smooth, honey-colored perithecia have small, pointed papillae surrounded by a darker ring indicating a relationship with the "mammoidea" section of the short-spored species of Nectria (Booth, 1959). It does not have the characteristic perithecial wall structure of Ophionectria and belongs in another hypocreaceous genus. Höhnelt's transfer is accepted.

Type: Algeria. Durieu, near Mustapha, on detached branch. (PC).

Calonectria muscivora (Petch) comb. nov. Figure 5j and 14e.

≡Ophionectria muscivora Petch, Trans. Brit. Myc. Soc. 27:142. 1945.

Fruiting bodies scattered or in clusters of two or three, superficial on living moss.

Perithecia light orange to pale red, translucent, globose to conoid, 250-350  $\mu\text{m}$  diam, surrounded and immersed in a white byssus of hyphae, 3  $\mu\text{m}$  diam, upper perithecium with short hyphoid hairs,

20-50  $\mu\text{m}$  long, 3-5  $\mu\text{m}$  diam at base. Perithecial wall composed of small, thin-walled cells, 3-6  $\mu\text{m}$  diam, forming textura angularis to textura epidermoidea.

No sterile hyphae associated with asci in mature specimens.

Asci unitunicate, very thin to evanescent at maturity, long-clavate, 175-275 x 10-12  $\mu\text{m}$ , no apical mechanism, spores parallel in the ascus.

Spores very long-fusiform, 140-240 x 2-2.5  $\mu\text{m}$ , 12-21 septate, sometimes curved or slightly sigmoid, apical end rounded, basal and narrowly rounded.

Type: Ceylon. Nuwara Eliya, on moss on tree trunk, 19 June 1927. (K).

The type specimen has unitunicate asci and fleshy perithecia; this species is a member of the Hypocreales. The lack of the characteristic outer perithecial wall layer composed of thick-walled, pigmented cells extended to form tubercles indicates that this species is not related to the genus Ophionectria. The light-colored perithecial wall is constructed of small, 3-6  $\mu\text{m}$  diam, thin-walled cells. The perithecia are partially immersed in a white, mycelial byssus as in the genus Nectriopsis Maire. The type species of this genus, N. violacea, was recently studied (Samuels, 1973b) and transferred to Nectria because "the features of perithecial ontogeny and morphology, asci and ascospores of Nectria violacea and N. candicans are not enough to distinguish these two species from other species of Nectria in a genus of their own." As in Nectria

violacea and N. hirsuta the upper perithecium has short hairs, hyphal extensions of the surface cells. The perithecial morphology of Calonectria muscivora shows a relationship to the myxomyceticolous species formerly grouped in the genus Nectropsis, i.e. Nectria violacea, N. hirsuta and N. candicans. Until the genera of the Nectria-complex are redefined, this species should be transferred to the genus Calonectria. Although the spores are long, Calonectria muscivora has a closer relationship to the medium- and short-spored species in the Nectria-complex than to Ophionectria trichospora.

Calonectria puiggarii (Speg.) comb. nov. Figures 5h and 14b.

=Ophionectria puiggarii Speg., Boletin Acad. Nacion. Cordoba, Buenos Aires 11:532. 1889.

=Nectria abnormis P. Henn., Hedwigia 36:219. 1897. Fide Höhnelt & Weese, 1910.

=Nectria leguminosum Rehm, Hedwigia 39:221. 1900.

Fruiting bodies solitary, superficial on the undersurface of dead leaves.

Perithecia dull orange to brown, "Pinkish-Cinnamon," globose to ovate, smooth or with a ring of hyaline cells irregularly around the ostiole, 250-350  $\mu\text{m}$  diam, papilla slightly darker than venter, small pointed. Perithecial wall two-layered: outer layer of large, thin-walled, globose cells, 18-20  $\mu\text{m}$  diam, forming textura globulosa becoming textura angularis toward the centrum.

No sterile hyphae associated with the asci.

Asci unitunicate, very thin to evanescent at maturity, no apical apparatus, clavate, 75-90 x 20-35  $\mu\text{m}$ , with a broadly rounded apex, sessile, spores polystichous.

Spores fusiform, curved, hyaline, 30-60 x 5-8  $\mu\text{m}$ , septation indistinct 0-5, walls covered with small granules.

Type: Brazil. In a forest near Apiahy, on the undersurface of fallen, rotting leaves of Laurineae, March 1888, Puiggarii #2562. (LPS).

Other Specimens:

Brazil. H. P. Rio de Papageio, on leguminous plant, 12 February 1896, Ule #2282. (S). Type specimen of Nectria leguminosum.

\_\_\_\_\_ St. Catharine near Blumenau, on bark, A. Möller #52c. This is the citation of the type specimen of Nectria abnormis which could not be located.

The type specimen of Calonectria puiggarii shows this species to be a member of the Nectria-complex in the Hypocreales. Unlike the true Ophionectria species, the outer perithecial wall consists of thin-walled cells without pigments in the cell walls. These cells form a ring of white tubercles around the ostiole. This species is placed in the genus Calonectria because it is not an Ophionectria as defined herein but is a member of the Hypocreales. C. puiggarii is related to the "coccinea" section (Booth, 1959) of short- and medium-spored members of the Nectria-complex.

Höhnel and Weese (1910) suggest that Nectria leguminosum is a synonym of Ophionectria puiggarii. The type collection of Nectria leguminosum was examined and their synonymy is confirmed. The type of Nectria abnormis has not been studied.

Calonectria vernoniae(Hansford) comb. nov. Figures 5i and 14d.

≡Ophionectria vernoniaeHansford, Proc. Linn. Soc. Lond.

158:39. 1945.

Fruiting bodies superficial on lower surface of dead leaf, loosely scattered in small groups of two to five on a byssoid stroma.

Perithecia light amber to yellowish-brown, globose to ovoid, 100-180 x 150-240  $\mu\text{m}$ , smooth, papilla short, broadly rounded, slightly darker, 40  $\mu\text{m}$  diam, small ostiole. Perithecial wall of two layers: outer 20  $\mu\text{m}$  wide, of irregularly-oriented hyphae forming prosenchyma; inner 14-16  $\mu\text{m}$  wide, pseudoparenchymatous, composed of thin-walled, nonpigmented, elongate cells.

No sterile hyphae associated with the asci.

Asci unitunicate, thin-walled, evanescent at maturity, no apical mechanism, long-clavate, 85-110 x 15-20  $\mu\text{m}$ , spores parallel and spirally arranged within the ascus.

Spores long-fusiform, vermiform, hyaline, 70-110 x 2-3  $\mu\text{m}$ , indistinctly 7-11 septate.

Type: Uganda. Entebbe Road, on lower surface of decaying leaf of Vernonia campanea May 1944, C. G. Hansford #3502 Holotype (IMI).  
Isotype (IARI).

The type specimen of Calonectria vernoniae is a member of the Hypocreales. The small, smooth perithecia have two-layered, transparent walls about 34-36  $\mu\text{m}$  thick. The outer layer consists of irregularly-oriented hyphae forming a prosenchymatous tissue 20  $\mu\text{m}$  thick while the inner layer is pseudoparenchymatous and is composed of thin-walled, non-pigmented cells. The perithecial wall structure and habit indicate that it is not related to the genus Ophionectria. Although the spores are long, it has a closer relationship to medium- and short-spored species in the Nectria-complex. It is related to a group of Calonectria species with similar morphology and habitat, i.e. small, light-colored perithecia on dead leaves.

SCOLECONNECTRIA Seaver, Myc. 1:197. Sept. 1909.

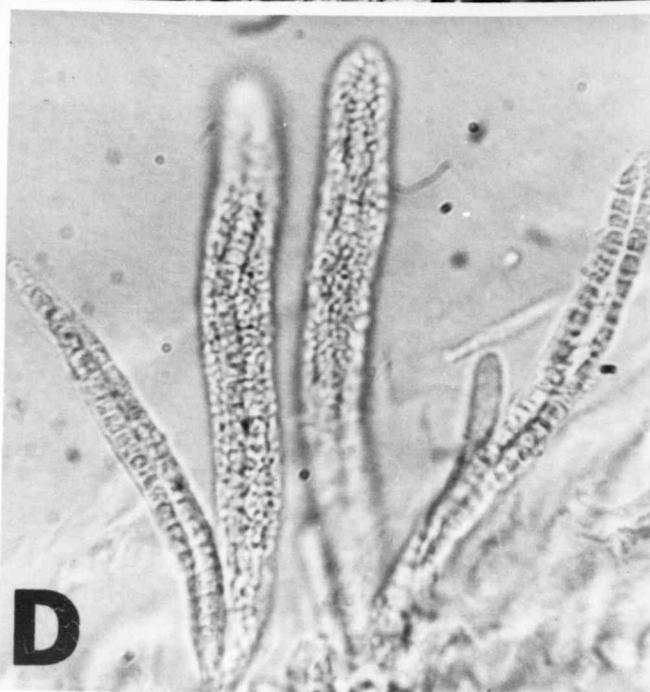
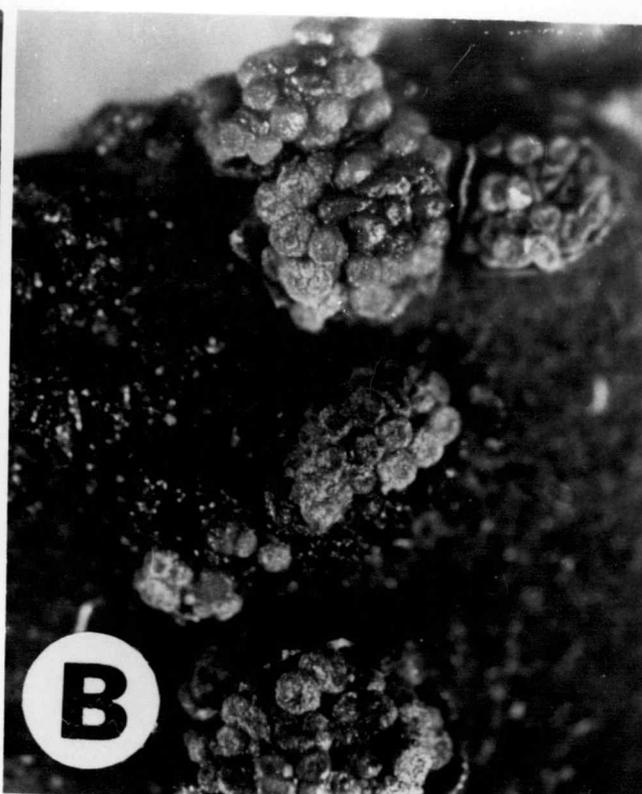
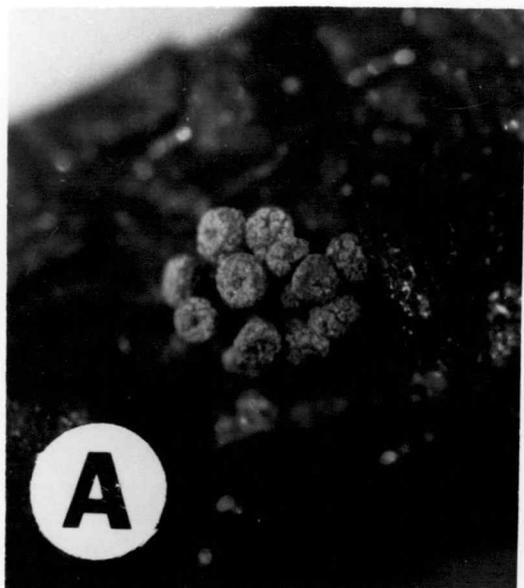
The genus Scoleconectria was erected in 1909 by Seaver for the species of Ophionectria and Calonectria with a well-developed basal stroma. The type species is Ophionectria scolecospora Bref. and Travel. Booth (1959) listed the synonyms of this species and determined the correct name to be Scoleconectria cucurbitula (Tode ex Fries) Booth (= Ophionectria cylindrospora, = O. scolecospora). Booth described S. cucurbitula and suggested that this species is related to Thyronectria balsamea, T. berolinensis, T. lamyi and some Nectria species forming his "aquifolii" section. These species are characterized by having the perithecial wall not differentiated into regions but slightly roughened and covered with a furfuraceous layer and having primary spores which usually bud in the ascus. The remaining species of Scoleconectria are ignored by Booth because they are unlike the type

species in all characters except spore length and septation, and stromal characters. By including species of Scolecnectria and Thyronectria with muriform spores in his group of related Nectria species, Booth suggests a closer relationship among Nectria-like species with spores of various lengths and septation than species related only by spore characters.

Although placed in different genera, Scolecnectria cucurbitula (= Ophionectria cylindrospora, = O. scolecospora) and Thyronectria balsamea (= O. cylindrospora var. tetraspora) are closely related. These species are almost indistinguishable except upon careful microscopic examination (figure 11). Both are found in the temperate zone erumpent through the needle scars and bark of Abies and Pinus species. A pycnidial imperfect stage is formed first on the well-developed basal stroma as in figure 11b. The perithecia develop on the same stroma. They are crowded, dark red to black when over-mature, globose and covered with a yellow furfuraceous layer which may wear off with age. The spores bud within the ascus forming numerous small ascoconidia which obscure the septation of the primary ascospores, the character on which these species are placed in different genera. Only after careful examination can one find a young ascus in which the septation of the primary ascospores is visible. The primary ascospores of Scolecnectria cucurbitula are transversely septate but the septa are often oblique and irregular (figure 11d). Those of Thyronectria balsamea are transversely and longitudinally septate but the longitudinal septa are sparse and indistinct (figure 11c).

FIGURE 11. Comparison of Thyronectria balsamea and Scoleconectria cucurbitula.

- A. Perithecia of Thyronectria balsamea.
- B. Perithecia of Scoleconectria cucurbitula and darker pycnidia of Zythia pinastri imperfect state. A and B 20 X.
- C. Thyronectria balsamea: asci with muriform spores and ascoconidia budding from primary spores.
- D. Scoleconectria cucurbitula: asci with scolecosporous spores and ascoconidia budding from primary spores. C and D 1350 X.



But the spores of S. cucurbitula are long, narrow and vermiform while those of T. balsamea are broader and shorter. These species are closely related and should not be separated at the generic level.

The species which have been placed in Scoleconectria are reviewed below. Scoleconectria coccicola is based on Nectria coccicola, a species which has also been included in Ophionectria and Dialonectria. Nectria coccicola is also the type species on which the genus Podonectria is based. Podonectria coccicola and, therefore the genus Podonectria, has bitunicate asci and belongs in the subclass Loculoascomycetidae.

Most species of Scoleconectria were transferred from Calonectria by Seaver (1909). Scoleconectria balsamea has muriform ascospores and belongs in Thyronectria, as T. balsamea, related to Scoleconectria cucurbitula in Booth's "aquifolii" section (1959). Scoleconectria polythalama also belongs to this section. The globose perithecia are covered with a greenish, furfuraceous layer and the spores are broadly fusiform but do not bud in the ascus. The remaining three Scoleconectria species are unrelated to the type species, S. cucurbitula. Like some species of Nectria, Scoleconectria atkinsonii is variably 1-3 septate. It is a later synonym of Calonectria chlorinella which is now placed in Thyronectria (Seeler, 1940). Scoleconectria tetraspora was found to be a synonym of a common Calonectria species, C. rigiduscula. Scoleconectria canadensis has a Tubercularia imperfect stage. The brick-red, globose perithecia are rough-warted, crowded on a well-developed basal stroma. S. canadensis

is related to the Nectria species in Booth's "cinnabarina" section (1959). It is very closely related to Nectria aurantiaca which, like S. canadensis, occurs on dead wood of Ulmus sp. After the original author no one has contributed additional species to Scoleconectria.

The genus Scoleconectria is like Ophionectria in that it includes unrelated hypocreaceous species and is not well differentiated from Calonectria. The type species, S. cucurbitula, is distinctive and provides a narrow concept for the genus. S. cucurbitula and Thyronectria balsamea are closely related as explained previously. Eventually Scoleconectria may include the species in the "aquifolii" section of Nectria, encompassing species with spores of various lengths and septation.

Scoleconectria cucurbitula (Tode ex Fries) Booth, CMI Myc. Pap. 73:

15-19. 1959. Figures 11b and d.

≡Nectria cucurbitula (Tode ex Fries) Fries, Summa Veg. Scand., 2:388. 1849.

=Nectria cylindrospora Sollm., Bot. Zeit. 22:264. 1864.

≡Ophionectria cylindrospora (Sollm.) Berl. & Vogl. in Saccardo, Syll. Fung. 9:995. 1891.

=Ophionectria scolecospora Bref. & Tavel, Unters, Myk. 10:178. 1891.

≡Scoleconectria scolecospora (Bref. & Tavel) Seaver, Myc. 1:198. 1909.

See Booth (1959) for additional synonyms.

Although the type specimen of Ophionectria cylindrospora could not be located and may no longer exist, an examination of many specimens identified as O. cylindrospora agreed with Sollman's description. They were identical with the detailed description of Scoleconectria cucurbitula given by Booth (1959). In the original description Sollman suggested that his species was related to Nectria cucurbitula Tode ex Fries. Seaver (1909) placed Nectria cylindrospora in synonymy with his species Scoleconectria scoleospora. Booth's comprehensive study (1959) suggests that this species is correctly placed in synonymy with Scoleconectria cucurbitula.

I examined the type specimen of Ophionectria scoleospora and found it agrees with the detailed description of Scoleconectria cucurbitula given by Booth (1959). Brefeld and Tavel noted that their species was very similar to Nectria cucurbitula ( $\equiv$  Scoleconectria cucurbitula). This interesting fungus is common on conifer needles and twigs in the temperate region.

Type: Lectotype designated by Booth (1959). Fries, Scler. Suc. #263 exsiccatum (1822). (K).

Other specimens (selected):

Austria. Lugenheim, on fallen twigs of conifer, Sept. 1865, H. Rehm #25, as Chilonectria rosellini Carest. (S).

Canada. Ontario, Oakland, May 1915, J. Dearness, Fungi Columbiana, Elam Bartholomew #4769, as Scoleconectria balsamea. (NY).

Germany. Near Herbartsdorf, "1½ Stunde von Coburg" (?by horseback), in a garden hedge, on dried twigs of Pinus silvestris L., mostly

erumpent through needle scars. This is the citation of the type specimen of Ophionectria cylindrospora which could not be located.

\_\_\_\_\_ Münster, Westfallen, Davers, on branches buds and fallen needles of pine, Autumn 1887, F. Tavel. Holotype of Ophionectria scolecospora ex Herb. F. v. Tavel. (ZT). Isotype Herb. A. Volkart. (ZT).

\_\_\_\_\_ Prignitz, Triglitz, on conifer needles, 31 Dec. 1895, O. Jaap, ex Herb. Rehm #147, as Ophionectria scolecospora form acicola. This form was never validly published. (B).

\_\_\_\_\_ Park Grossbehnitz, on dead twigs of Pinus strobus, 1 March 1901, W. Kirschstein, as Ophionectria sp. (B).

\_\_\_\_\_ München, on twigs of Pinus strobus, 1902, H. Rehm, as Chilonectria cucurbitula, Ex Herb. Rehm. (S).

\_\_\_\_\_ Havelland, Rathenow Forest, on rotting conifer branches, erumpent through needle scars, Oct. 1905, W. Kirschstein, as Ophionectria cylindrospora. (B).

\_\_\_\_\_ Bernauer Forest, on rotting twigs of Pinus silvestris, 14 July 1916, W. Kirschstein, as Ophionectria scolecospora. (B).

\_\_\_\_\_ Prignitz, Triglitz, on twigs of Pinus silvestris, March 1910, O. Jaap, as Ophionectria scolecospora. Rehm Ascomycetes #1921. (CUP) HBG) (S).

\_\_\_\_\_ Park Grossbehnitz, on rotting twigs and needles of Pinus silvestris, Nov. 1930, W. Kirschstein, as Ophionectria scolecospora. (B).

\_\_\_\_\_ Brandenburg, in a forest near Beelitz and Seddin, on fallen twigs of Pinus silvestris, 28 Feb. 1931, W. Kirschstein, as Pleonectria pinicola. (B).

\_\_\_\_\_ East Havelland, Finkenrug, on fallen branches of Pinus silvestris, 24 April 1937, W. Kirschstein, as Pleonectria pinicola. (B).

\_\_\_\_\_ Munchen, on Pinus peuce, Aug. 1939, W. Kirschstein, as Ophionectria scolecospora. (B).

Sweden. Stockholm, Horti Bergiana, on Abies sp., 27 March 1920, T. Vestergren, as Ophionectria cylindrospora. (S).

Switzerland. Zürich-Koferberg, on rotting conifer twigs, 23 Nov. 1893, F. v. Tavel, as Ophionectria scolecospora. Herb. A. Volkart. (ZT).

United States. California, Santa Clara County, Stanford University, on dead twigs of Pinus radiata, 12 Oct. 1901, C. F. Baker, Pacific Slope Fungi #68, as Ophionectria scolecospora. (S).

\_\_\_\_\_ Maryland, Montgomery Co., Takoma Park, on branches that had been cut from Pinus sp., 1 April 1900, C. L. Shear, Ellis & Everhardt's Fungi Columbiana #1433. (S).

\_\_\_\_\_ Massachusetts, Franklin Co., elev. 1000 ft., downed branches of Larix europaeae, 3 Nov. 1927, J. R. Hansbrough, as Scoleconectria balsamea. Ex Herb. J. R. Hansbrough. (NY).

\_\_\_\_\_ Michigan, Branch Co., Gilead, on bark of downed Abies balsamea, 8 June 1933, J. R. Hansbrough, as Scoleconectria balsamea. Ex Herb. J. R. Hansbrough #241. (NY).

\_\_\_\_\_ Michigan, Isle Royale, Rock Harbor, on spruce, August 1904, as Ophionectria scolecospora. Ex Herb. E. T. & S. A. Harper #1027. (S).

\_\_\_\_\_ New Hampshire, Cherry Mt., Carroll, on Abies balsamea as "common saprophyte on leaf scars," 19 July 1932, J. R. Hansbrough, as Scoleconectria balsamea. Ex Herb. J. R. Hansbrough #237. (NY).

\_\_\_\_\_ New York, Tompkins Co., Cayuga Lake Basin, as Chilonectria cucurbitula. Cornell Univ. #8384. (S).

\_\_\_\_\_ New York, Albany Co., near Alcove, on bark of dead Picea nigra, Jan. 1894, C. L. Shear, as Chilonectria cucurbitula. New York Fungi #242 and #362. (NY).

\_\_\_\_\_ Ohio, Hamilton Co., Cincinnati, on Pinus strobus, 4 May 1936, J. R. Hansbrough, as Ophionectria scolecospora. F. Path. #81729. (B).

THYRONECTRIA Saccardo, Grevillea 4:21. Sept. 1875.

The genus Thyronectria was erected by Saccardo in 1875 to include Nectria species with muriform spores. The following year he split off the genus Pleonectria on the basis of differences in perithecial stroma. Thyronectria, typified by T. patavina, contained species with perithecia immersed in a stroma while species of Pleonectria, typified by P. lamyi, had perithecia discrete or caespitose and seated on a stroma. Seeler (1940) observed that the size of the stromata and the number of fruiting bodies on the stroma was variable on different substrates under different environmental conditions. He included all Nectria-like species with muriform spores in the genus Thyronectria. Seeler considered Mattirolia and Thyronectrioidea, both established for Nectria species with dark, muriform spores and a Stilbum conidial

state, to be synonyms of Thyronectria. He used the following criteria in determining species of Thyronectria: "1) the structure and size of ascospores and their arrangement in young and mature asci, 2) the general appearance of perithecia, such as their size, shape and color, and 3) the structure and color of the stromata, always allowing for relatively slight deviations caused by variation in substratum, in the weather of the growing season and the growth-age of the specimen at hand." Since Seeler's monograph (1940), which included sixteen Thyronectria species, one new species and one variety have been added to the genus. Booth (1959) includes three species of Thyronectria in the "aquifolii" section of Nectria species. More study may show that the other Thyronectria species are related to Nectria and Calonectria species. A discussion of the relationship of Scoleconectria cucurbitula and Thyronectria balsamea is presented in the section on Scoleconectria.

Thyronectria balsamea (Cooke & Peck) Seeler, Journal of the Arnold

Arboretum 21:442. 1940. Figures 11a and 11c.

=Ophionectria cylindrospora var. tetraspora Weese, Centralb.

f. Bakt. 45:598 and 602. 1914.

≡Pleonectria pinicola Kirschst. Verhandl. Bot. Ver. Prov.

1906.

Ophionectria cylindrospora var. tetraspora was based on the type specimen of Pleonectria pinicola. This specimen has been examined and is found to be a specimen of Thyronectria balsamea. In establishing

his variety, Weese was apparently unable to see the longitudinal septa and placed it in Ophionectria. He noted the difficulty in differentiating Calonectria from Ophionectria; "It is often a matter of taste into which genus the fungus should be placed." Seeler (1940) excluded Pleonectria pinicola from Thyronectria (=Pleonectria) presumably because he accepted the synonymy with Ophionectria cylindrospora var. tetraspora without examining the specimen. Booth (1959) lists O. cylindrospora var. tetraspora and Pleonectria pinicola as synonyms of Thyronectria balsamea "teste Ehrlich in litt.". This synonymy is confirmed.

Type: United States. New York, North Elba, on dead branches of Abies balsamea, August 1872, C. H. Peck, as Nectria balsamea. (NY).

Other Specimens:

Canada. Newfoundland, Waghorne, on fir, 13 Nov. 1897, F. J. Seaver #321a, as Calonectria balsamea. (NY).

Germany. Brandenburg, in Rathenower Stadtforst, on rotting branches of Pinus silvestris, 11 Dec. 1904, W. Kirschstein. This is the type specimen of Pleonectria pinicola on which Ophionectria cylindrospora var. tetraspora is based. (B).

\_\_\_\_\_. East Havelland, Forest near Fuckenkrug, on rotting pine branches, literally "Kiefer" which usually refers to Scotch pine, Pinus silvestris, lying on the ground, Spring 1925, W. Kirschstein, as Pleonectria pinicola. One of the twigs in the collection had Scoleconectria cucurbitula on it. Two other specimens identified by Kirschstein as Pleonectria pinicola were actually Scoleconectria cucurbitula. (B).

United States. Maine, Piscataquis Co., Duck Point Camp (No. 8) near Milo, "in low woods more or less a mixture of maple, alder, birch, balsam and white cedar or in a virgin balsam forest", 2-6 Sept. 1905, W. A. Murrill #2157, as Scoleconectria balsamea. (NY).

\_\_\_\_\_. Minnesota, Vermilion Lake, lat. 48°, on Abies sp., 22 July 1886, F. S. Earle #178N, as Chilonectria cucurbitula. (NY).

\_\_\_\_\_. New Hampshire, Bethlehem, Gale River Experimental Forest, on Abies balsamea, 20 July 1932, J. R. Hansbrough #238, as Scoleconectria balsamea. (NY).

\_\_\_\_\_. New York, Lake Placid, on Pinus strobus, July ?, C. H. Peck, as Scoleconectria balsamea. (NY).

\_\_\_\_\_. New York, Essex Co., Aidenhair, on Abies balsamea, July ?, C. H. Peck, as Scoleconectria balsamea. (NY).

## CLAVICIPITALES

The perithecia of the Clavicipitales are generally light- to bright-colored with a fleshy to membranaceous texture as in the Hypocreales (figures 1b, 12). They are differentiated from the Hypocreales by the asci which have an enlarged, thickened, apical cap penetrated by a narrow threadlike pore and filiform ascospores (figures 2c, 13c-d). Most species of Clavicipitales are entomogenous or fungicolous.

The Clavicipitales are considered a separate order by Rogerson (1970) and Dennis (1968), however, other recent works (Dennis, 1970; Müller & von Arx, 1973) have an enlarged concept of the order Sphaeriales which includes both the Hypocreales and Clavicipitales.

## CLAVICIPITACEAE

Following Rogerson (1970), one family is recognized within the Clavicipitales.

Several species which have been included in the genus Ophiognectria actually belong in four genera within the Clavicipitaceae: Barya, Byssostilbe, Cordyceps and Torrubiella. These genera are delimited by the extent of development of the stroma and whether or not the ascospores break into variously shaped partspores within the ascus.

BARYA Fuckel, Jahrb. Nassauischen Vereins Naturk. 23-24:93. 1869.

The genus Barya Fuckel was erected in 1869; the type species is Barya parasitica. This genus is differentiated from other genera in the Clavicipitaceae by the poorly developed stroma and continuous ascospores (Dingley, 1954; Rogerson, 1970). Five species and one variety have been previously included in the genus. One new species is added. Barya byssicola occurs on guinea pig dung while all other members of the genus occur on other fungi.

Barya agaricicola (Berk.) Höhnelt, Ann. Myc. 8:465. 1910.

≡ Nectria agaricicola Berk. in Hooker, Botany of the Antarct. Voyage, III. Flora Tasmaniae, p. 278. 1860.

≡ Ophionectria agaricicola (Berk.) Sacc., Syll. Fung. 2:563. 1883.

An examination of the type specimen shows that this species is a member of the Clavicipitales. The long asci have an enlarged, thickened apical cap penetrated by a narrow, threadlike pore and the ascospores are filiform. The texture of the smooth, light-colored fruiting bodies is rubbery to membranaceous with the small, thin-walled cells forming pseudoparenchyma. Barya is characterized by sessile perithecia and continuous ascospores not separating into partspores. Although the very long spores were originally described as continuous, this character is difficult to determine in the type specimen. Septa are not visible suggesting that the spores are continuous.

Höhnell (1921b; Höhnell and Weese, 1910) transferred this species to Barya. The transfer is accepted by Dingley (1954) and my examination of the type specimen suggests that this is correct.

Type: Tasmania. On putrid agaric. Herb. Berk. 1879. (K).

Other specimen reported (not seen): New Zealand. (K). (Dingley, 1954)

Barya byssicola Thaxter ex Rossman, sp. nov. Figures 12 and 13.

≡ Ophionectria byssicola Thaxter 1905. Unpublished herbarium name.

Fruiting bodies solitary to gregarious in small groups, partially immersed in cottony white, byssoid subiculum.

Perithecia light yellow, obpyriform with elongate neck tapering to rounded papilla, 585-640 x 290-390  $\mu\text{m}$ , perithecial wall smooth composed of small, thin-walled cells forming pseudoparenchyma.

Paraphyses simple, filiform, 2-2.5  $\mu\text{m}$  wide, densely packed, tips rounded.

Asci long-cylindric, tapering at base, 250-430 x 9-12  $\mu\text{m}$ , with enlarged, apical thickening penetrated by a narrow pore, spores parallel, twisting around each other within the ascus.

Spores filiform, 250-400 x 2.0-3.0  $\mu\text{m}$ , continuous, no evidence of septa.

Etymology: Byssos, from Greek, a fine, yellowish flax, fine thread, referring to the cottony, hyphal subiculum subtending and surrounding the perithecia, and -cola, Latin suffix meaning dweller.

Type: Argentina. Slavallob, on dung of wild guinea pig, 1905-1906, R. Thaxter #5262, Holotype (FH). Isotype slides at (NY).

FIGURE 12. A and B. Barya byssicola on guinea pig dung.  
Perithecia surrounded and partially immersed  
in byssoid subiculum. 15 X.

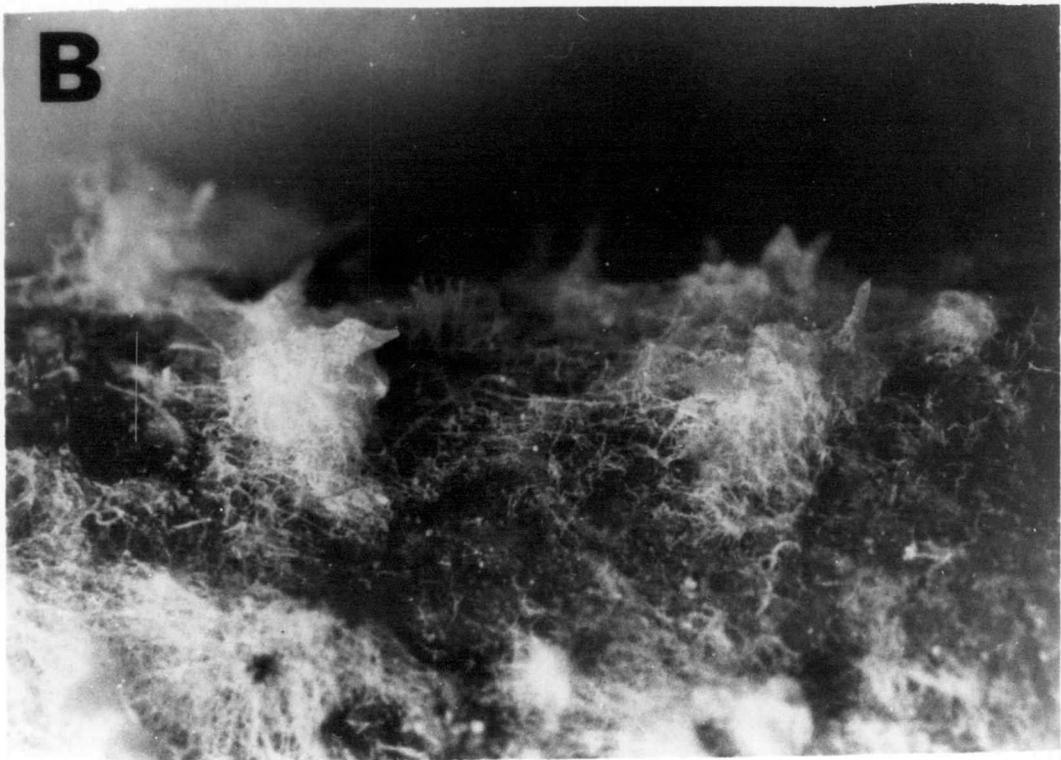
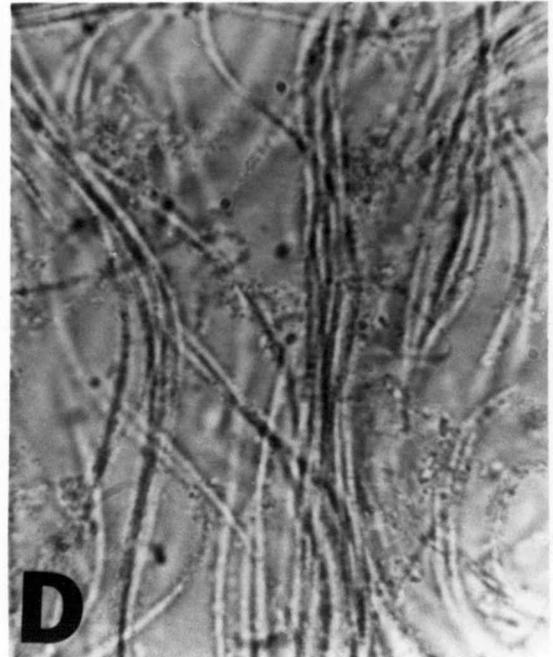
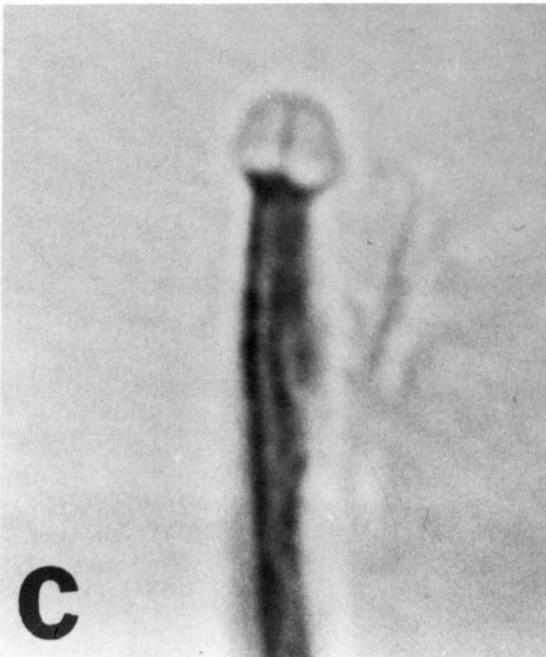
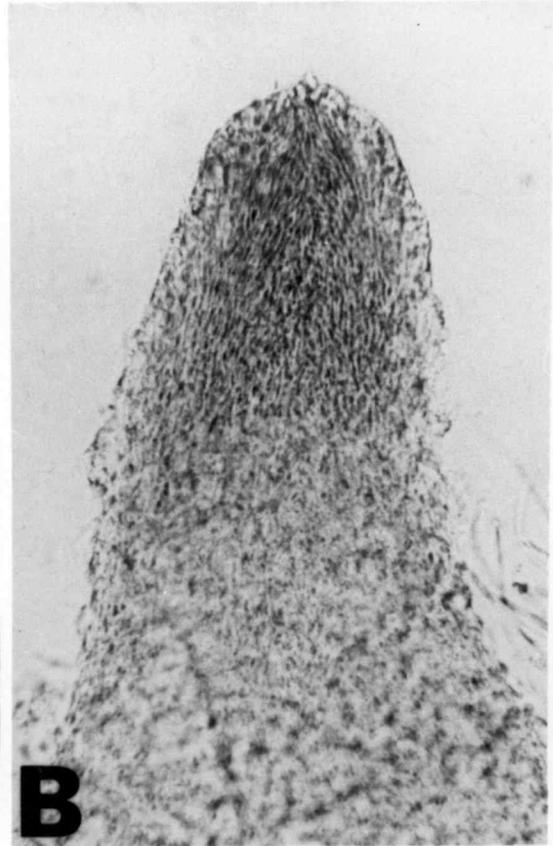
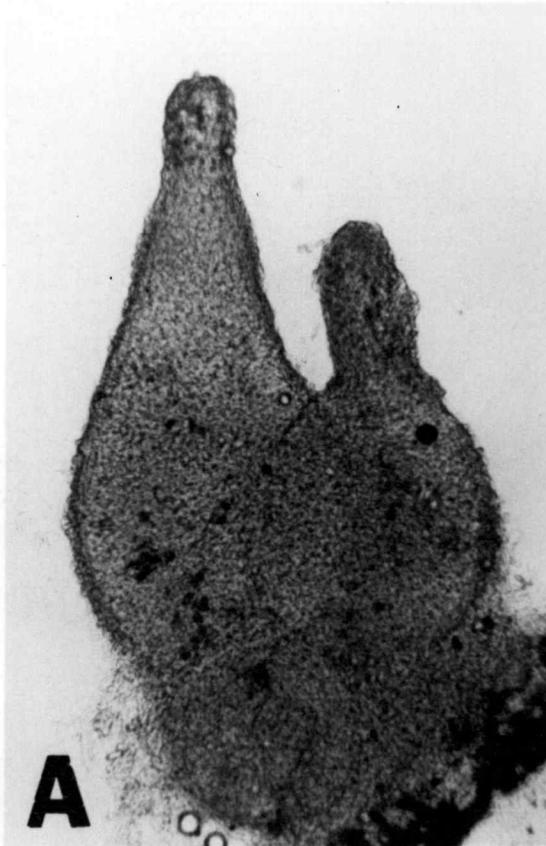


FIGURE 13. Barya byssicola.

- A. Whole perithecia with byssus around base.  
125 X.
- B. Neck of perithecia. 550 X.
- C. Ascus with enlarged, thickened apex penetrated  
by a narrow pore. 3000 X.
- D. Ascospores which are nonseptate and  
filiform. 1000 X.



The herbarium name, Ophionectria byssicola, was never validly published. The specimen has capitata asci with a narrow pore and filiform spores characteristic of the Clavicipitales (figure 13c). The stroma is poorly developed, consisting of a white byssoid subiculum in which the perithecia are partially immersed (figure 13c) and the filiform spores are continuous (figure 13d), characteristic of the genus Barya. This is the first coprophilous member of the Clavicipitales.

BYSSOSTILBE Petch, Ann. Roy. Bot. Gard. Peradeniya, Ceylon 5:296. Aug. 1912.

The genus Byssostilbe was erected by Petch in 1912 to accommodate the type species, B. stilbiger ( $\equiv$ Berkelella stilbigera,  $\equiv$ Hypomyces stilbiger). Berkelella Saccardo contained those Hypomyces species with multiseptate spores. Petch based his new genus Byssostilbe on the filiform spores of B. stilbigera. Later, Petch (1923) added two more species to Byssostilbe. All three species are fungicolous: B. stilbiger on myxomycetes in the Trichiales, B. tomentosa on Cordyceps dipterigera and B. fusca on Torrubiella luteorostrata. A study of the type specimen of the type species, B. stilbiger, indicates that the genus is correctly placed in the Clavicipitales, Clavicipitaceae. Byssostilbe is differentiated from the other genera in the family by the poorly-developed stroma and ascospores which break into cubodial part-spores within the ascus. Torrubiella also has a poorly developed stroma but the filiform

ascospores break into rectangular part-spores. After Petch (1923) no additional species have been added to the genus.

Byssostilbe stilbiger (Berk. & Br.) Petch, Ann. Roy. Bot. Gard.,  
Peradeniya, Ceylon 5:296-297. 1912.

≡ Hypomyces stilbiger Berk & Br., J. Linn. Soc. London, Botany  
14:113-114. 1875.

≡ Berkelella stilbigera (Berk. & Br.) Sacc., Syll. Fung. 9:998.  
1891.

= Ophionectria trichia Penz. & Sacc., Malpighia 11:516. 1897.

Ophionectria trichia was described as a member of the Hypocreales but the type collection reveals that this species belongs in the Clavicipitales. The asci have an enlarged, thickened apex penetrated by a narrow pore and very long, filiform spores which break up into cubodial part-spores. As suggested by Petch (1912), Ophionectria trichia is a synonym of Byssostilbe stilbiger.

Penzig and Saccardo (1897) suggested placing this species in a new genus, Ophiostilbe, because of the stilbaceous imperfect state. The genus was never validly published.

Byssostilbe stilbiger is associated with the imperfect species Stilbum tomentosum Schrad. var. tomentosum (Samuels, 1973b). S. tomentosum var. ovalispora (A. L. Smith) Rogerson is associated with perithecia of Nectria hirsuta Samuels which also occurs on myxomycetes. This does not indicate a relationship between the perfect species.

Type: Ceylon. Peradeniya, on Hemitrichia serpula, Dec. 1868, Thwaites #83, slides and notes ex Kew ex Herb. Berk. #1879, as Hypomyces stilbiger. (NY).

Other specimens:

Java. Tjibodas, on the peridium of Trichia verrucosa, 12 Feb. 1897, P. A. Saccardo #2380. This is the type specimen of Ophionectria trichia, also labelled Ophiostilbe trichia. (PAD)

United States. Tennessee, Burbank, on Hemitrichia serpula, Aug. 1887, R. Thaxter #1058, as Ophionectria with Stilbum. (FH).

CORDYCEPS Link, Handbuch 3:346. 1833.

The genus Cordyceps Link, typified by C. militaris, contains about 100 species (Ainsworth, 1971). It is characterized by a light- to bright-colored, well-developed stroma arising from the host in addition to the thickened ascus apex and filiform spores characteristic of the Clavicipitales. Cordyceps species are entomogenous or fungicolous.

Cordyceps tuberculata (Libert) Maire, Bull. Soc. d'Hist. Nat. de l'Afrique du Nord 7:165. 1917.

=Akrophyton tuberculatum Libert, Zeitschr. f. Wiss. Zool., 9:448.

=Cordyceps cockerellii (Ellis & Everh.) Ellis, Journal of the Institute of Jamaica 1:180. 1893. Fide Dingley, 1953 and Mains, 1958.

Ophionectria cockerellii Ellis & Everh., Journal of the  
Institute of Jamaica 1:141-142. 1892.

Although Ellis and Everhardt (Ellis, 1892) originally placed Cordyceps cockerellii in the hypocreaceous genus Ophionectria, Ellis soon recognized the error and transferred it to the Clavicipitales (Ellis, 1893). He suggested that this species may only be a variety of Cordyceps sphingum. Lloyd (1916) considered C. cockerellii to be identical with C. sphingum, a species in which the development of the stroma is variable. Dingley (1953) synonymized both Cordyceps cockerellii and C. sphingum with C. tuberculata and Mains (1958) confirmed this. He noted that the stroma of C. tuberculata varies with environmental conditions and suggested that this species is intermediate between the genera Cordyceps and Torrubiella. These genera are separated by the extent and form of their stromata. Cordyceps includes species with a typically well-developed, stipitate, light- to bright-colored stromata, not arising from a sclerotium but from a stromatized portion of the host. Torrubiella has a sessile stroma with superficial perithecia (Dingley, 1953). In fact, the type specimen of Ophionectria cockerellii has a very short, stalked to sessile stroma with superficial perithecia. Only a comparative study of Cordyceps and Torrubiella will determine the correct genus for this species within the Clavicipitales. Whatever the case, Cordyceps cockerellii does not belong in Ophionectria.

Type: Jamaica. Monteaque, on the body of a dead moth, Philampelus vitis, Jan. 1892, T. D. A. Cockerell #6, Holotype of Cordyceps cockerellii. (NY).

Other specimens examined:

Jamaica. Bath, on dead Coccytius antoews, Aug. 1892, coll. by Mrs. Swainson, comm. T. D. A. Cockerell. (NY). Seaver (1911) considered the collection from Bath, Jamaica to be the type specimen but the original description is based on the Monteaque specimen. Therefore, the Monteaque specimen is the holotype.

TORRUBIELLA Boudier, Revue Mycol. (Toulouse) 7:226. 1 Oct. 1885.

The genus Torrubiella was erected in 1885 by Boudier who described only one species, T. aranicida, occurring on dead spiders. Since then twenty species have been added to the genus, many of which occur on dead insects.

Höhnel (1909) considered Torrubiella to be related to Barya, Tubeufia, Ophionectria, Globulina and Acrospermum. He differentiated Torrubiella on the basis of the fleshy perithecia, paraphyses which are thickened above and asci like Cordyceps and Barya, both now placed in the Clavicipitales. Petch (1938) considered Torrubiella in the Nectriaceae because the perithecia are superficial with or without a basal stroma. He used the stromal character and position of the perithecium to define the families Nectriaceae and Hypocreaceae but did not recognize the clavicipitaceous ascus type as a family or order character. Dingley (1953) and Rogerson (1970) differentiate Torrubiella from other clavicipitaceous genera by the

ascospores dividing into rectangular partspores, and perithecia sessile on a subiculum or basal stroma. In the genus Byssostilbe the partspores are cuboidal and the conidial state is synnematosus.

Torrubiella lloydii (Mains) comb. nov. Figures 2c and 14a.

≡ Ophionectria lloydii Mains, *Lloydia* 20:226-227. 1957.

= Ophionectria "cordyceps" Lloyd, *Myc. Wri.* 5:692. 1917.

Not validly published.

≡ Torrubiella "cordyceps" (Lloyd) Dingley, *Trans. Roy. Soc. New Zealand* 81:340-341. 1953. New combination based on an invalid name.

Fruiting bodies caespitose to gregarious, superficial on a thin, basal stroma composed of pseudoparenchymatous tissue forming irregular plates, dirty white to cream.

Perithecia light-yellow to honey-yellow, "Cream-Buff", ovoid to elongate pyriform, with a rounded papilla, concolorous rim around ostiole, (450) 500-750 x 275-420  $\mu\text{m}$  diam. Perithecial wall 75-90  $\mu\text{m}$  thick, composed of three layers: inner 12-17.5  $\mu\text{m}$ , thin-walled cells, elongate, dense, parallel with sides of centrum; middle, 30-37  $\mu\text{m}$ , thin-walled cells, hyaline; outer 25-30  $\mu\text{m}$ , small cells with pigmented cell walls.

Paraphyses evanescent at maturity.

Asci 180-350 x 3.5-5  $\mu\text{m}$ , very-long cylindrical, distinctly capitate with a narrow canal through which partspores are expelled, spores parallel in asci.

Spores filiform 180-220 x 1-1.5  $\mu\text{m}$ , breaking into rectangular partspores 2.5-3.5 x 1-1.5  $\mu\text{m}$ .

The name Ophionectria cordyceps was given to an herbarium specimen by C. G. Lloyd but was never validly published. In the publication he merely chats about the specimen and states: "For convenience in our herbarium we have labelled it Ophionectria cordyceps." For this reason Dingley's new combination, Torrubiella cordyceps based in Lloyd's unpublished epithet, is not valid. Mains' epithet, O. lloydii, is the first valid name for Lloyd's specimen.

An examination of the type collection reveals that the asci have an enlarged, thickened apex penetrated by a narrow pore and very long, filiform spores which break up onto rectangular partspores (figure 3c). This species belongs in the Clavicipitales. The stroma is pseudoparenchymatous but poorly developed with superficial perithecia characteristic of the genus Torrubiella. Dingley (1953) suggests this by transferring the invalid species based on the Lloyd specimen to Torrubiella. The new combination Torrubiella lloydii is the correct name.

This species occurs on other clavicipitaceous fungi: Cordyceps robertsii Hook. ex Berk., C. hauturu Dingley fide Dingley (1953), and C. militaris (L. ex St. Amans) Link. fide Koval (1968). Other species of Torrubiella occur only on insects.

Type: New Zealand. Napier, on stromata of Cordyceps robertsii, H. Hill, Lloyd Herb. #42580. (BPI).

Other specimens:

New Zealand. Te Awamuta, on stromata of Cordyceps robertsii,  
1952, G. L. Miller, Lloyd Herb. #37145. (BPI).

Russia. Kuril Islands, Kunashir, on Mendeleev volcano, on stromata  
of Cordyceps militaris on pupae of Lepidoptera, 17 Sept. 1956,  
D. N. Vorobev (Reported in Koval, 1968).

## SPHAERIALES

The Sphaeriales includes those Euascomycetidae with typically brown to black perithecia which are carbonaceous, leathery or sometimes fleshy. The unitunicate asci typically form a single layer among true paraphyses. The ascus apex has a pore, often with a ring through which the spores are discharged. The Sphaeriales is defined in the narrow sense, following Rogerson (1970). Dennis (1968) and Müller & von Arx (1973) include all truly ostiolate, perithecial pyrenomycetes in the Sphaeriales treating the hypocreaceous fungi in the family Hypocreaceae. The species formerly placed in Ophionectria, belong to the families Sordariaceae and Sphaeriaceae.

## SORDARIACEAE

The Sordariaceae contains those members of the Sphaeriales with either dark, non-septate ascospores or hyaline to yellowish, vermiform ascospores. The genera have intergrading features such that the family is difficult to characterize. The Sordariaceae, as defined by Müller & von Arx (1973) and Carroll & Munk (1964), includes the Lasiosphaeriaceae sensu Dennis (1968). The closely related genera, Lasio-sphaeria and Mycomedusiospora, belong to the Sordariaceae. They contain species which were formerly placed in Ophionectria.

LASIOSPHAERIA Ces. & de Not., Comm. Soc. Critt. Ital. 1:229. 1863.

Five species formerly placed in Ophionectria belong in the genus Lasio-sphaeria. This genus has been broadly defined by Dennis (1968) and Carroll & Munk (1964) to include dark, tough-textured perithecia

and unitunicate asci with a refractile apical ring, often with a refractile apical globule. The hyaline, vermiform spores may vary in length and septation from elliptical, triseptate to long-fusiform, multiseptate. The Lasiosphaeria species which had been placed in Ophionectria lack the characteristic hairs of Lasiosphaeria but do have a roughened outer perithecial wall consisting of large, loose, globose cells which are analogous to hairs. Carroll & Munk (1964) describe two species, Lasiosphaeria raciborskii and L. lapaziana, whose outer perithecial wall also lack hairs but do have large, loose cells. These species and the species formerly placed in Ophionectria, Lasiosphaeria rufula, L. glabra and L. depilata, form a group of related species.

Lasiosphaeria depilata Fuckel, Symbol. Myc. II Nachtr. p. 27, 1873.

non L. depilata (Fries) Sacc., Syll. Fung. 2:205. 1883.

≡ Ophionectria depilata (Fuckel) Höhnelt, Sitzungsbei. Kaiserl.

Akad. Wiss., Math.-Naturwiss. Cl., Abt. I. 123:107-108. 1914.

≡ Lasiosphaeria fuckelii Sacc., Syll. Fung. 2:195. 1883.

= Ophionectria ambigua Höhnelt, Ann. Myc. 3:550-551. 1905.

Höhnelt (1914b) placed Lasiosphaeria depilata in the genus Ophionectria because of the lack of hairs on the perithecium. According to Dennis (1968) and Carroll & Munk (1964), Lasiosphaeria does include species with tuberculate to smooth fruiting bodies. The dark perithecia have a leathery rather than fleshy texture, and are covered with loose, globose cells. The unitunicate asci have a conspicuous apical ring. Höhnelt recognized that his species Ophionectria ambigua was identical

to Lasiosphaeria depilata Fuckel and made the combination O. depilata. My examination of the type specimen of L. depilata confirms that the two species are identical but the species belongs in the genus Lasiosphaeria. L. depilata is the earliest epithet. Saccardo mistakenly thought that L. depilata was an illegitimate homonym of the Friesian species, Sphaeria depilata, and erected the species Lasiosphaeria fuckelii based on L. depilata Fuckel. The Friesian epithet was not transferred to Lasiosphaeria until 1883 by Saccardo, so L. depilata is legitimate and the earliest epithet for this species.

The type collection of Ophionectria ambigua was issued as Rehm Ascomyceten Exsiccati Set 36, Number 1646 in 1906 (Rehm, 1906). Based on an examination of six specimens of Rehm Ascomyceten No. 1646, I conclude that the species belongs in the genus Lasiosphaeria. No single specimen had been designated as the type. The specimen located at CUP is hereby designated the lectotype; the other specimens in the exsiccati are isolectotypes.

Type: Switzerland. In upper Weisstannenthal near Ragaz, in autumn on rotten stems of Pinus abies. Herbarium Fuckel #1895. (G).

Other specimens:

Austria. Nordhänge des Hocheck bei Altenmarkt, on a rotten spruce stump, July 1905, Dr. von Höhnelt, Rehm Ascomyceten No. 1646, as Ophionectria ambigua. (CUP). Isolectotypes (B) (FH) (HBG) (PC) (ZT).

Lasiosphaeria glabra (Penz. & Sacc.) comb. nov. Figure 2 d & 14 f.

≡ Ophionectrica conica Penz. & Sacc., Malpighia 11:516. 1897.

Fruiting bodies gregarious, superficial on a rudimentary dark subiculum.

Perithecia black, leathery, globose, 360-500  $\mu\text{m}$  diam, ostiole 75  $\mu\text{m}$  diam, conic, formed by straight, thick-walled parallel hyphae with acute apices. Perithecial wall dark reddish-brown in transmitted light, composed of two layers: inner layer dense opaque, carbonaceous, 30-40  $\mu\text{m}$  thick; outer layer 50-60  $\mu\text{m}$  thick, of large, thin-walled cells, 15-25  $\mu\text{m}$  diam, forming textura globulosa. Perithecial wall surface roughened due to large loose cells of the outer wall layer.

Paraphyses scant, thin, 0.5  $\mu\text{m}$  diam.

Asci unitunicate, cylindric, 190-200 x 20-22  $\mu\text{m}$ , apex with a conspicuous refractile ring.

Spores parallel, twisted around each other, hyaline, 90-125 x 5-5.5  $\mu\text{m}$ , 8-12 septate, cylindric, slightly curved, tapering to rounded ends.

Type: Java. Tjibodas, on fragments of dead wood, 8 March 1897, Penzig and Saccardo no. 134. (PAD).

The type collection has black, leathery perithecia, asci with a distinct apical ring and hyaline, long-fusiform, vermiform ascospores; all characteristic of the genus Lasiosphaeria. It is transferred to that genus and given a new species epithet. Lasiosphaeria conica Hohnel (1904) has priority such that the new combination based on Ophionectrica conica is given the epithet glabra. Lasiosphaeria glabra and L. depilata

are indistinguishable except that the spores of L. glabra are longer and have more septa. In addition, L. glabra is known only from Java while L. depilata is reported from Austria and Switzerland.

Lasiosphaeria rufula (Penz. & Sacc.) stat. et comb. nov.

≡ Ophionectria trichospora var. rufula Penz. & Sacc., *Malpighia* 11:516. 1897.

Perithecia superficial, reddish-brown, leathery, smooth with loose globose cells extending from the outer wall, globose, 190-212  $\mu\text{m}$  diam.

Asci unitunicate, long clavate, 200-220 x 14-16  $\mu\text{m}$ .

Spores long-fusiform, vermiform, 130-160 x 7-8  $\mu\text{m}$ , hyaline, ends rounded, multiseptate.

Type: Java. Horto bogoriensi, on dead spathe of palm. Penzig and Saccardo no. 778. (PAD).

The type specimen has dark reddish-brown, leathery perithecia and unitunicate asci with a distinct apical ring. These characters exclude the species from the Hypocreales. The hyaline, vermiform spores and distinct ring in the ascus apex indicate that this species belongs in Lasiosphaeria. Despite the etymology of the generic name, the globose perithecia are covered with large, loose, globose cells rather than hairs. This is true of several species of Lasiosphaeria. The spores are longer than any previously described Lasiosphaeria species.

MYCOMEDUSIOSPORA Carroll & Munk, Myc. 56:91. 1964.

Carroll & Munk erected Mycomedusiospora for Ophionectria flavida. This genus is closely related to Lasiosphaeria, differentiated by the bright-colored, fleshy perithecia and spores coiled in the ascus. The presence of a refractile globule in the ascus apex establishes its close relationship to Lasiosphaeria.

Mycomedusiospora flavida (Rick) Carroll & Munk, Myc. 56:92. 1964.

≡Cyanocephalum flavidum Rick, Broteria 5:224. 1906.

≡Ophionectria flavida (Rick) Sacc. & Trotter, Syll. Fung. 22:498. 1913.

Although the perithecia are fleshy and light yellow, the unitunicate asci with a minute refractile globule in the apex and filamentous true paraphyses are the bases on which this species is placed in the Sphaeriales, not the Hypocreales. The apical refractile body in the ascus is characteristic of the genus Lasiosphaeria and indicates a relationship with this genus. Carroll & Munk characterize this species as "the logical extreme in the scolecosporous Lasiosphaeria line". The very long, septate, filiform spores are coiled within the ascus, breaking into numerous small fragments at maturity.

Type (only slides seen): Brazil. On very rotten wood. 1905. The specimen is apparently lost from the Rick Herbarium (PACA). Slides at (NY) (BPI) (IMI).

Other slides examined: Costa Rica. Near Vulcan Irazu, elev. 200 m, 22 June 1962, George Carroll #89. (Herb. George Carroll).

#### SPHAERIACEAE

The Sphaeriaceae includes those members of the Sphaeriales with superficial, brown to black perithecia. The unitunicate asci do not have distinct apical caps or rings and the spores are hyaline or bright without germ pores or germ slits. This family is defined by Müller & von Arx (1973) and Dennis (1968) to include those genera lacking the distinct characters of the other families in the Sphaeriales. One species described as Ophionectria, O. clerodendri, belongs in the Sphaeriaceae but its generic position could not be determined.

"Ophionectria" clerodendri Tilak & Kale, Sydowia 23:19-20. 1970.

The type specimen was studied. This species is not a member of the Hypocreales. Although the perithecia are described as being initially bright-colored, they are leathery to cartilagenous and become black at maturity. The sterile elements in the centrum are simple, filiform paraphyses, not apical paraphyses characteristic of the Hypocreales. The unitunicate asci are thick-walled when young. The hyaline spores have many, thickened septa as in the genera Zignoella and Saccardoella. These characters are indicative of the Sphaeriales. The generic placement could not be determined without a thorough study of the Sphaeriaceae.

Type: India. Nizambad and Amble wadi, on rotten bark of dead stem of Clerodendron inerme Goetn., October, 1967, S. B. Kale and M. Bhim Rao, No. 29414. (IARI).

## OSTROPALES

The order Ostropales contains ascomycetes with apothecial fruiting structures. If partially to wholly immersed in the substrate, they may appear discoid to perithecioid (Korf, 1973). Such was the case for one species described as Ophionectria, O. palicoureae.

The Ostropales are characterized by filiform spores developing in long, narrow asci which are strongly thickened but the filiform spores penetrate the apex, resulting in a V-shaped outline of the inner membrane. The apothecia do not develop within a stroma. There is only one family, the Ostropaceae.

Erinella Quel.

The genus Erinella belongs to a complex of genera related to Dasyscyphus (Korf, 1973), that is, apothecial fungi with inoperculate asci and hairs on the apothecium. Several species of Erinella have ostropalean affinities and should be considered in that group as suggested by Dennis (1954).

Erinella cfr. bicolor Pat. & Lagerh., Bull. Herb. Boissier 3:65. 1895.

=Ophionectria palicoureae Seaver & Whetzel, Sci. Survey Porto Rico and Virgin Islands 8, 1. Botany p. 45. 1926. Fide M. Sherwood & R. P. Korf, pers. comm., 1974.

=Tovariella pitteriana Syd., Ann. Myc. 28:172. 1930. Fide Ciferri, 1954.

The type specimen of Ophionectria palicoureae is an apothecial ascomycete belonging to the Ostropales. The dried apothecia are slightly immersed and resemble perithecia due to the inrolled margins. The ascus apex is thickened but not truly capitate penetrated by a narrow pore as in the Clavicipitales. The apothecia, non-capitate asci and long spores suggest the Ostropales. M. Sherwood & R. P. Korf (pers. comm., 1974) agree that this species is a member of the Ostropales having affinities with Erinella bicolor.

Without seeing either type specimen, Ciferri (1954) suggested that Ophionectria palicoureae was synonymous with Tovariella pitteriana indicating that the new name would be T. palicoureae. However, the new combination was not made. The type specimen of T. pitteriana must be examined before Ciferri's proposal can be evaluated.

Type: The type specimen of Erinella bicolor is not known.

Type of Ophionectria palicoureae: Puerto Rico. Guaynabo, on under-surface of living leaves of Palicourea sp., 25 June 1924, Whetzel, Kern & Toro, Puerto Rican Fungi no. 2682, CUP #14743. Holotype (CUP).

Isotype (NY).

Type of Tovariella pitteriana (not seen): Venezuela. Parasitic on living leaves of Psychotria (Palicourea) riparia Benth. Colonia Tovar #326.

## LOCULOASCOMYCETIDAE

The ascomycete subclass Loculoascomycetidae grew out of the order Dothideales proposed by Lindau in 1897 "for ascomycetes in which the fruiting bodies are 'without peridia, formed in a stroma'". Höhnelt (1907) expanded this order to include also the Myriangiaceae and Pseudo-sphaeriaceae which were elevated to ordinal rank by Theissen & Sydow (1918). Finally Nannfeldt (1932) proposed the series Ascoloculares to include these orders and the Hemisphaeriales and Hysteriales which form their asci in ascostromata. Nannfeldt noted additional correlative characters: bitunicate asci and the tendency to form parenchymatous tissues and dictyosporous ascospores and conidia (Luttrell, 1965b). Luttrell (1955) raised the series to subclass as the Loculoascomycetidae corresponding to the other subclass of Ascomycetes, the Euascomycetidae.

The subclass Loculoascomycetidae contains those ascomycete species with bitunicate asci and an ascostroma in which the asci are borne in locules. The mycelium cannot be distinguished from that of the Euascomycetidae. In the formation of the ascostroma, the ascogonia develop within a stroma. The growth and differentiation of the ascostroma forms the ascocarp which consists of stromatic tissue surrounding the asci and any sterile tissue.

The species with bitunicate asci, erroneously placed in Ophionectria, have uniloculate stromata and are, therefore, difficult to distinguish from members of the Euascomycetidae. The bitunicate asci

and pseudoparaphyses, generally branched, are used to indicate affinities with the Loculoascomycetidae. All species previously described in Ophionectria which belong in the Loculoascomycetidae are placed in the Pleosporales.

#### PLEOSPORALES

The Pleosporales is the largest order within the Loculoascomycetidae. It includes species with perithecioid ascocarps, relatively large locules and cylindrical, bitunicate asci among persistent pseudoparaphyses. They occur on a wide range of organic substrates, usually plant debris, although members of the genus Podonectria occur on scale insects.

#### PLEOSPORACEAE

Within the order, the large family Pleosporaceae is the least specialized, containing saprophytes. The ascocarps lack a compressed beak, as in the Lophiostomataceae, and the ascospores are generally multiseptate and do not have germ slits or pores, as in the Sporomniaceae (Müller & von Arx, 1973).

PODONECTRIA Petch, Trans. Brit. Myc. Soc. 7:146-149. 13 Dec. 1921.

The genus Podonectria was erected by Petch in 1921. The generic description is short: "Perithecia seated on a byssoid stroma, nectriaceous; asci thick-walled, spores biseriate; ascospores elongate fusiform, multiseptate, hyaline; conidial stage, Tetracrium." He included

three species: Podonectria coccicola, the type species, P. aurantii and P. echinata. Petch described the genus as "nectriaceous" implying bright-colored perithecia and unitunicate asci. However, the type species, Podonectria coccicola, has bitunicate asci and numerous pseudo-paraphyses. The genus belongs in the family Pleosporaceae. Podonectria aurantii also has bitunicate asci. P. echinata has not been examined. After Petch, three species have been added to the genus. Dingley (1954) described P. novae-zealandica and P. gahnia, both parasitic on scale insects. She included the genus in the Clavicipitaceae; these species must be examined to determine their functional ascus type. Podonectria tenuispora was described by Dennis (1958) as having biunicate asci. Podonectria is characterized by bright-colored perithecioid ascocarps containing bitunicate asci and occurring on scale insects.

Podonectria aurantii (P. Henn.) Petch, Trans. Brit. Myc. Soc. 7:149-151. 1921.

≡Tetracrium aurantii P. Henn., Hedwigia 41:116. 1902.

≡Puttemansia aurantii (P. Henn.) Höhnelt, Sitzungsbei, Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. I, 120:406. 1911.

≡Ophionectria aurantii (P. Henn.) Petch, Trans. Brit. Myc. Soc. 7:151. 1921.

=Ophionectria tetraspora Miyabe & Sawada, Jour. College Agric., Tohoku Imp. Univ., Sapporo, Japan 5:85-86. 1913.

The type specimen of Podonectria aurantii occurs on scale insects and has fleshy, light-colored ascocarps, bitunicate asci and scant

pseudoparaphyses. It is congeneric with the type species of the genus Podonectria. P. aurantii was described as an imperfect fungus, Tetracrium aurantii. The perfect stage was discovered and described later by Höhnel from the type collection.

Petch (1921) considered Ophionectria tetraspora synonymous with his new combination, Podonectria aurantii. Ophionectria tetraspora is identical with the type specimen of Podonectria aurantii. Both have the peculiar Tetracrium conidia and specialized habitat on scale insects of Citrus species. I accept Petch's synonymy. Miyabe & Sawada (1913) recognized the relationship of their species to Ophionectria coccicola ( $\equiv$ Podonectria coccicola). Hara (1954) lists O. tetraspora as a Podonectria.

Podonectria coccicola and P. aurantii are differentiated by the length of the ascospores and shape of the conidia. The spores of P. coccicola are considerably longer and the conidia generally have four "arms" instead of three.

Type: Brazil. Sao Paulo, Horto Botanico, on insect larvae covering the twigs and branches of Citrus aurantium L., 26 June 1901, coll.

A. Puttemans #282. (B).

Other specimen:

Taiwan. Tennaiho, Taihoku, on Parlatoria zizyphi (Lucas) Sign. infesting Citrus nobilis Lour., 11 March 1911, coll. Y. Fujikuro. This is the citation of the type specimen of Ophionectria tetraspora which could not be located.

Podonectria coccicola (Ellis & Everh.) Petch, Trans. Brit. Myc. Soc.

7:146-149. 1922. Figure 1 d, 3 a & 3 b.

≡Nectria coccicola Ellis & Everh., Journ. Myc. 2:39. 1886.

≡Ophionectria coccicola (Ellis & Everh.) Berl. & Vogl.,  
Add. Syll. Fung. p. 218. 1886.

≡Dialonectria coccicola (Ellis & Everh.) Ellis & Everh.,  
Journ. Myc. 2:137. 1886.

≡Scoleconectria coccicola (Ellis & Everh.) Seaver, Myc. 1:198.  
1909.

≡Tetracrium cocciculum (Ellis & Everh.) Höhnel, Sitzungsbei.  
Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1:408. 1911.

≡Puttemansia coccicola (Ellis & Everh.) Höhnel, Sitzungsbei.  
Kaiserl. Akad. Wiss., Math.-Naturwiss. C., Abt. 1:408. 1911.

=Scleroderris gigaspora Masee, Kew Bulletin p. 3, f. 1-5.  
1910. Fide Petch, 1921.

The type specimen of Nectria coccicola (≡Podonectria coccicola) has bitunicate asci and a pleosporaceous centrum; it belongs in the Pleosporaceae of the Loculoascomycetidae. It is the type species of the genus Podonectria. The stroma is a dirty white and may be more or less well-developed. The color of the ascocarps varies from white to dark brown, depending on the age of the specimen. The fleshy stroma and fruiting bodies, bitunicate asci, long ascospores, peculiar conidia and habit on scale insects makes this a distinctive genus. Podonectria coccicola is common in the tropics.

Type: United States. Florida, Brooksville, on scale lice on bark of living orange trees. Feb. 1886. (NY).

Other specimens:

New Zealand. Auckland, Turangi, on Leucapsis sp. on Brachyglottis repanda, Oct. 1949, coll. J. M. Dingley, Ex Herb. Plant Diseases Division #10947. (DAOM #46901).

Puerto Rico. On scale insects, 24 Jan.-4 Apr. 1923, coll. Fred J. Seaver & Carlos E. Chardon, #1064 as Scoleconectria coccicola. (NY).

Trinidad. In groups on the scutellum of Myctilaspidis citricolas on leaves of Citrus aurantii, coll. J. H. Hart. This is the citation of the type specimen of Scleroderris gigaspora. The specimen could not be located.

United States. Florida, City Point, Apr. 1904, coll. John Bentel, Exsiccati #1554, USDA-BPI #13632. (B) (CUP) (IARI) (MA) (NY). This set was issued as Ophionectria coccilola, a typographical variant of O. coccicola.

\_\_\_\_\_ Florida, Lake Helen, on grapefruit. 16 Feb. 1909. (HBG).

\_\_\_\_\_ Florida, Melbourne, on scale insects, 28 June 1937, coll. J. Young. Herb. Erdman West. (NY). This specimen was labelled Podonectria coccidicola, a typographical variant of P. coccicola.

\_\_\_\_\_ Florida, Monteverde, on orange leaves and twigs, Mar. 1890, coll. James Franklin. (NY).

Podonectria coccorum (Petch) comb. nov. Figure 15 b.

≡*Ophionectria coccorum* Petch, Trans. Brit. Myc. Soc. 12:49-50. 1927.

Fruiting bodies solitary to gregarious, superficial on a byssoid stroma covering the scale insects.

Ascocarps globose to conic, 250-300  $\mu\text{m}$  diam, brown, with small, pointed papilla, flexuous, thick-walled hairs around ostiole, 17-25 x 5  $\mu\text{m}$ , sparsely intermixed with straight setae, 110-125 x 9  $\mu\text{m}$ . Ascocarp wall composed of cells, 5-7.5  $\mu\text{m}$  diam with somewhat thickened walls forming textura globulosa to textura angularis.

Pseudoparaphyses branched, filiform.

Asci 87-105 x 7.5-9  $\mu\text{m}$ , cylindrical with short stipe, ascospores parallel.

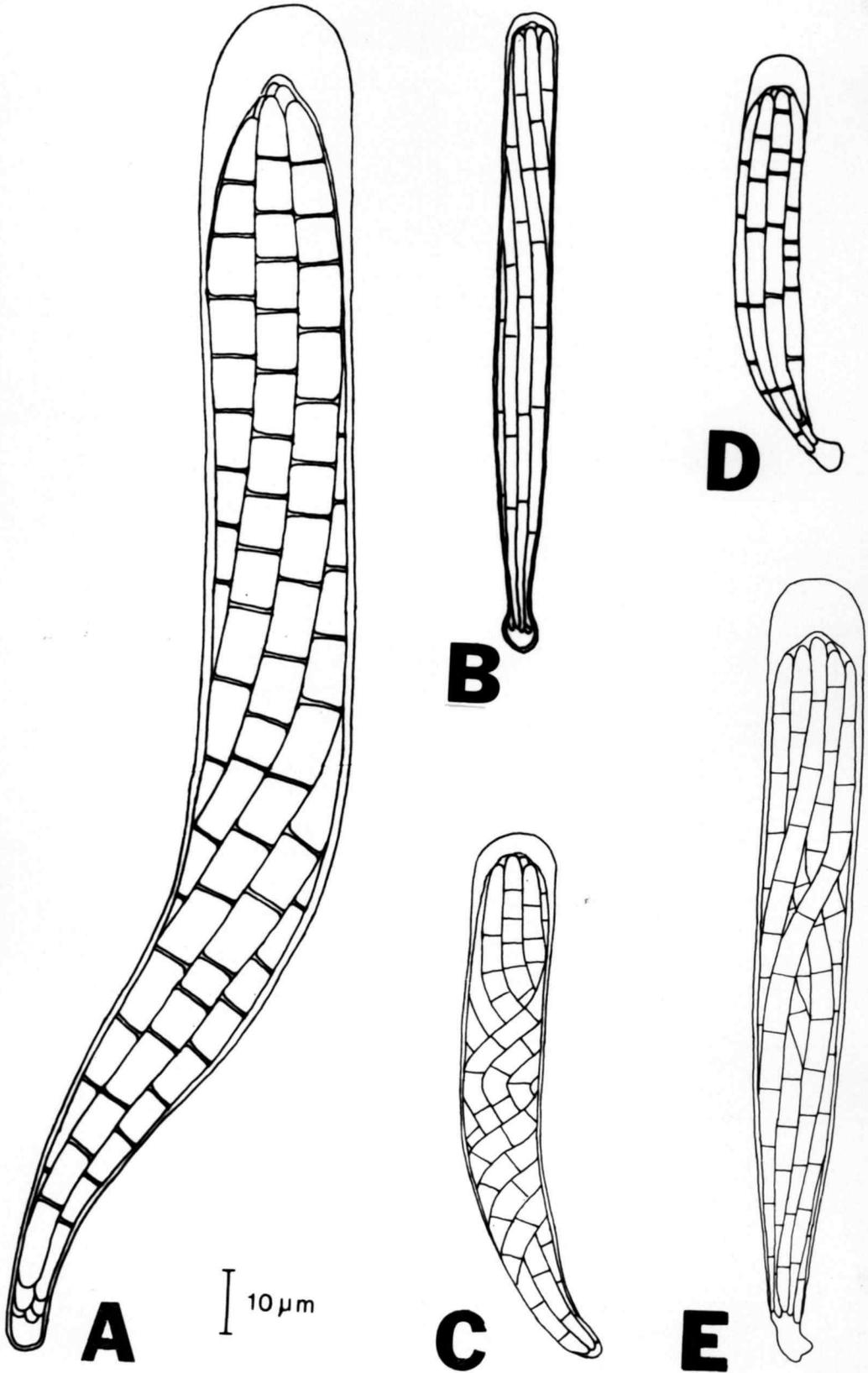
Spores 55-85 x 2-2.5  $\mu\text{m}$ , long-fusiform, slightly curved, hyaline, 7-9 septate.

Type: Ceylon. Royal Botanic Gardens, Peradeniya, on Fiorinia juniperi Green on Juniperus bermudiana, 1910, Herb. Petch #3172. (K).

The species has brown, translucent, firm-fleshy ascocarps. Although most species of Podonectria have light- or bright-colored fruiting bodies, this species is included because the ascocarps of the type species, P. coccicola, do become brown with age. The centrum of P. coccorum contains bitunicate asci and persistent pseudoparaphyses indicating that this species is a loculoascomycete in the genus Podonectria, rather than Ophionectria. It does not have the distinctive Tetracrium conidial state that the type species of Podonectria has. Petch differentiates this species from Podonectria "by the shape of the ascospores";

Figure 15. Asci of species of Loculoascomycetidae which have been transferred to new genera. All 1000 X.

- A. Podonectria larvaespora
- B. P. coccorum
- C. Tubeufia palmarum
- D. I. hidakaeana
- E. I. paludosa



this is a subtle difference. The ascospores of the Podonectria species are long-clavate, broadest at the upper end, rounded above, tapering to an obtuse end, while those of P. coccorum are not clavate but long-fusiform with the widest point toward the middle. I do not believe this difference is significant. In both species the spores are very long, so that the widest point is not readily determined. At the time Petch described this species the significance of bitunicate asci was not recognized.

Podonectria larvaespora (Cooke & Massee) comb. nov. Figures 3 e & 15 a.

≡ Lasiosphaeria larvaespora Cooke & Massee, Grevillea 19:83. 1891.

≡ Ophionectria larvaespora (Cooke & Massee) Hansford, Proc. Linn. Soc. N.S.W. 81:31. 1956.

Fruiting bodies scattered, partially immersed in a byssoid stroma of hyphae covered with bright-yellow granules.

Ascocarps dull-orange but appearing bright-yellow due to the covering of hyphae, globose to obpyriform, 600-750 x 375-650  $\mu\text{m}$  diam, papillae naked without byssoid covering. Ascocarp wall pseudoparenchymatous, composed of thick-walled, pigmented, polyhedral cells, 5-10  $\mu\text{m}$  diam forming textura globulosa approaching textura angularis.

Pseudoparaphyses abundant, branched, filiform.

Asci bitunicate, 240-295 x 16-25  $\mu\text{m}$ , cylindric tapering to the base, spores parallel within the asci.

Spores long-clavate tapering to a rounded apex and pointed base, curved, 135-190 x 7.5-10  $\mu\text{m}$ , 13-24 septate.

Type: Australia. Victoria, Mt. Macedon, on bark associated with scale insects and mosses, coll. Martin #566. Holotype (K). Isotype (NY).

The type specimen has bitunicate asci and numerous, filiform, racemose pseudoparaphyses in ostiolate uniloculate ascocarps characteristic of the Pleosporaceae, Pleosporales. The bitunicate asci exclude it from the Hypocreales. The bright-colored fruiting bodies associated with scale insects, bitunicate asci and very long spores place this species in the genus Podonectria. The spores are long-clavate with the widest point close to the apex as Petch (1921) suggests is characteristic of the genus. Most species with bitunicate asci have spores of this shape, even those with relatively short spores. It is different from the known Podonectria species in the presence of the bright-yellow, granular hyphae covering the fruiting bodies and forming a byssoid stroma. The spore size and shape is similar to that of P. coccicola, the type species, but P. coccicola usually has a well-developed, pseudoparenchymatous stroma and the ascocarps are dirty-white to cream in color.

Höhnelt (1914 a) suggested that Lasiosphaeria larvaespora ( $\equiv$  Podonectria larvaespora) did not belong in Lasiosphaeria but was related to the genus Acanthostigma without hairs but with a thin, bright-colored film on the fruiting body. Berlese (1886) noted that this species is "perpulchre", as, indeed, it is. Hansford (1956)

placed it in the genus Ophionectria on the basis of the bright-colored fruiting bodies.

TUBEUFIA Penz. & Sacc., Malpighia 11:517. 1897.

The genus Tubeufia was described by Penzig & Saccardo in 1897. They included three species: T. javanica, T. anceps and T. coronata. The type species, T. javanica, was designated by Höhnel (1919). The genus was originally placed in the Hypocreales but Booth (1964) determined that Tubeufia has bitunicate asci and ascocarps belonging to the Pleosporaceae. Tubeufia and Ophionectria have been confused. Höhnel (1912 a) and Petch (1912) suggested that Ophionectria trichospora belonged to the genus Tubeufia and, therefore, the genera were synonymous. This is certainly not true. O. trichospora has unitunicate asci and nectrioid ascocarps. It belongs in the Hypocreales.

Within the Pleosporaceae Tubeufia is characterized by light- to bright-colored ascocarps with long, multiseptate spores occurring as a saprophyte on rotten plant material usually in a moist habitat. The imperfect states, where known, are helicosporous. Podonectria is similar to Tubeufia but occurs on scale insects and has a Tetracrium imperfect state.

Tubeufia anceps Penz. & Sacc., Malpighia 11:518. 1897.

≡Ophionectria anceps (Penz. & Sacc.) Höhnel, Sitzungsbei.  
Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. I. 128:562.  
1919.

Höhnel transferred this species to Ophionectria because it "angeblich" (allegedly) lacked paraphyses. The type specimen has pseudoparaphyses and bitunicate asci which excluded it from the Hypocreales. This species belongs in the genus Tubeufia where it was described as one of the three species originally included in the genus. Tubeufia anceps is included in Booth's (1964) monograph. Type: Java On decorticated branch, 26 April 1895, Penzig & Saccardo #861. (PAD). The packet is labelled "n. 2396" and also "n. 1403 - Riva Vald 26 April '95. Foglis di Pteris aquilina. Ad Casestio. Typus." The collector and date are the same as those mentioned in the type description but the specimen number and substrate are different. The specimen fits the description. I believe this is the type specimen.

Tubeufia cerea (Berk. & Curt.) Höhnel, Sitzungsbei. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. I. 128:562. 1919.

≡Sphaeria cerea Berk. & Curt., Grevillea 4:108. 1876.

≡Calonectria cerea (Berk. & Curt.) Sacc., Syll. Fung. 2:551. 1883.

≡Ophionectria cerea (Berk. & Curt.) Ellis & Everh., North American Pyrenomycetes p. 118. 1892.

=Ophionectria anonae Rao, Sydowia 25:72,73. 1971.

=Calonectria belonospora Schroet., Krypt. Flora von Schlesien 3:261. 1894.

≡Ophionectria belonospora (Schroet.) Sacc., Syll. Fung. 11:366. 1895.

- =Ophionectria belonospora var. unicaudata Feltgen, Vorstud. Pilz. Luxem. Nachtr. 3:308. 1903.
- =Ophionectria briardi Boudier, Rev. Myc. p. 226. 1885.
- =Ophionectria briardi var. longipila Starbäck, Botaniska Notiser (Lund) p. 218-219. 1898.
- =Ophionectria cupularum Kirschst., Verhand. des Bot. Ver. der Provinz Brandenburg 48:60. 1906.
- =Ophionectria episphaeria Karsten, Hedwigia 28:26. 1889.
- =Ophionectria everhartii Ellis & Galloway, Journ. Myc. 6:32. 1890.
- =Nectria fulvida Ellis & Everh., Journ. Myc. 1:140. 1885. Fide Booth, 1959.
- ≡Calonectria fulvida (Ellis & Everh.) Berl. & Vogl., Add. Syll. Fung. p. 212. 1886.
- ≡Dialonectria fulvida (Ellis & Everh.) Ellis & Everh., Journ. Myc. 2:122. 1886.

Tubeufia cerea is common throughout the temperate and tropical zone, occurring on old fructifications of stromatic pyrenomycetes and very rotten deciduous wood. As the long synonymy implies, it has been described anew many times. The Ophionectria names which are synonyms of Tubeufia cerea are discussed individually. Booth (1964) describes Tubeufia cerea and reviews the synonyms. Several names are added to Booth's list: Calonectria fulvida, Dialonectria fulvida, Ophionectria briardi, O. briardi var. longipila, O. cupularem, O. episphaeria and O. everhartii.

An unfortunate consequence of the misplacement of this common temperate zone species in the genus Ophionectria is that many authors have accepted it as a characteristic member of the genus Ophionectria and have based their concept of the genus on this species rather than on the type Ophionectria trichospora which is tropical and thus less familiar.

The type collection of Tubeufia cerea ( $\equiv$ Ophionectria cerea) based on Sphaeria cerea is exhausted and can no longer be examined. Numerous specimens of this name have bitunicate asci and agree with Booth's comprehensive description based on the type material (Booth, 1964). Neither Booth (1964) nor Bigelow & Barr (1963) realized that the new combination with Tubeufia had already been made by Höhnel (1919).

Although the type specimen of Ophionectria anonae could not be obtained, this species is considered a synonym of Tubeufia cerea. The asci are described as bitunicate which excludes this species from the Hypocreales. The ochraceous-yellow ascocarps, pleosporaceous centrum and long spores suggest the genus Tubeufia. Although the spores of O. anonae are slightly longer and wider, 45-55 x 4-7  $\mu$ m, than those described by Booth for Tubeufia cerea, 40-50 x 3-5  $\mu$ m, there are collections of I. cerea with spores large enough to include the larger spores of O. anonae. Tubeufia cerea is commonly found on stromatic pyrenomycetes but several collections, particularly from the tropics, are found on rotten wood, as is this specimen. In all other characters, Ophionectria anonae is identical with Tubeufia cerea.

The type collection of Calonectria belonospora ( $\equiv$ Ophionectria belonospora) no longer exists but many early collections from northern Europe labelled O. belonospora have been examined and were found to be specimens of Tubeufia cerea. In the original description Schroeter suggested that his species may be identical to Calonectria cerea ( $\equiv$ Tubeufia cerea) but that Saccardo's description was too short and incomplete to determine if these species were identical. Upon transferring this species to Ophionectria, Saccardo noted that O. belonospora is not very different from O. everhartii, the American name for Tubeufia cerea. Rehm (1908) and Strasser (1911) recognized that Calonectria belonospora was identical to Ophionectria cerea ( $\equiv$ Tubeufia cerea), as did Petch (1941) and Booth (1964). Based on the type description, identified specimens and historical notes, this synonymy is accepted.

In describing Ophionectria belonospora var. unicaudata, Feltgen pointed out that his variety is different from the typical variety and O. Everhartii, both synonyms of Tubeufia cerea, "hauptsachlich durch die Form der Sporen (bei belonospora and Everhartii beidendig spitz), dann auch durch die Vielgestaltigkeit and variable Grössender Asci and die geringere Zahl der Querwände in den Sporen, sowie durch die ausschliesslich gelbbraunliche Farbe der Perithechien under Gehäusezellen" (Feltgen, 1903, p. 309). My examination of many specimens of Tubeufia cerea reveals variability in the species that

would include the differences on which this variety is based. Feltgen suggested that Calonectria fulvida (= Tubeufia cerea) is a closely related species. Feltgen's type specimen may have been immature which would account for the variable size of the asci and fewer septa in the spores. Although I have not seen the type specimen, it is another synonym of Tubeufia cerea.

The type specimen of Ophionectria briardi reveals that this species is synonymous with Tubeufia cerea. Rehm (1908), Strasser (1911) and more recently Petch (1941) have suggested that O. briardi is a synonym of Ophionectria cerea ( $\equiv$  Tubeufia cerea). My examination of the type specimen confirms this evaluation.

I examined the type specimen of Ophionectria briardi var. longipila and found it to be a collection of Tubeufia cerea. Rehm (1908) and Strasser (1911) considered this variety to be a synonym of Ophionectria cerea ( $\equiv$  Tubeufia cerea), noting that it is differentiated only by the wider, indistinctly-septate spores. Starbäck (1898) described the spores of his variety as 4-5  $\mu\text{m}$  wide. Spores of the typical variety are described as 3-4  $\mu\text{m}$  wide. According to Booth's description and the specimens which I have examined, the spores of Tubeufia cerea may be 3-7  $\mu\text{m}$  wide. This variety is considered another synonym of Tubeufia cerea.

The type collection of Ophionectria cupularem has no fleshy fungal material left, only the carbonaceous stroma of a pyrenomycete in the base of the cupule. The collection was made simultaneously with Ophionectria

belonospora (= Tubeufia cerea), often found on the old carbonaceous stroma of various pyrenomycetes. The type description of O. cupularem strongly suggests Tubeufia cerea: yellow-brown fruiting bodies and asci with rounded, thickened apices which "durch Quellung der Verdickung schwellen die Schläuche oben oft kugelförmig an". Kirschstein is undoubtedly referring to the bitunicate asci in which the outer wall has ruptured and the inner wall has expanded previous to ascospore discharge or upon mounting in water for microscopic examination. Kirschstein thought this specimen different from the others he collected and identified as O. belonospora (= Tubeufia cerea). Perhaps this was the only specimen in which the bitunicate asci had "popped" and he thought this a new species. This may also account for the scanty type specimen.

An examination of the type collection of Ophionectria episphaeria reveals the presence of two species: Tubeufia cerea and Nectria episphaeria (Tode ex Fries) Fries. From the type description it is evident that Karsten was describing the specimen of T. cerea. Petch (1941) states that O. episphaeria was "apparently" identical to O. cerea ( $\equiv$  Tubeufia cerea). My examination confirms this synonymy. The label on the type collection says "Ophionectria episphaeria Karsten = Nectria episphaeria". However, Karsten's Ophionectria species is certainly not synonymous with Nectria episphaeria (Tode ex Fries) Fries. N. episphaeria is a short-spored Nectria which could not have been confused with a long-spored species.

Ophionectria everhartii was considered a synonym of Ophionectria cerea ( $\equiv$ Tubeufia cerea) by Ellis & Everhardt (1892), Rehm (1908) and Seaver (1909). My examination of the presumed type collection reveals that their conclusion was correct.

Type: United States. North Carolina, parasitic on Sphaeria stigma ( $\equiv$ Diatrype stigma), Car. Inf. #2315. (K). This is the type specimen of Sphaeria cerea but the specimen is almost exhausted such that it can no longer be examined.

Other specimens (partial list):

Austria. Schneeberg, Sept. 1902, Höhnel. (S). This specimen is labelled Ophionectria briardi var. ?pitrisfusers. The variety was apparently never published and is represented by this collection alone. The specimen is Tubeufia cerea on an old pyrenomycete stroma. The handwriting on the packet is almost illegible; no variety resembling the name has been found in the literature.

\_\_\_\_ Vorarlberg, Sonntagberg, on beech twigs, 1901, coll. P. Strasser, as Ophionectria episphaeria. (HBG) (S).

\_\_\_\_ Vorarlberg, Sonntagberg, on stroma of Diatrype stigma on rotting oak twigs, 1908, coll. P. Strasser, Rehm Ascomyceten #1783, as Ophionectria cerea. (CUP) (S) (HBG).

Canada. Ontario, Bear Island in Lake Temagami, on Diatrype stigma on Betula sp., 14 Aug. 1937, coll. R. F. Cain, Univ. of Toronto #12994 as Ophionectria cerea. (S).

Finland. Tammela, Mustiala, on Diatrype stigma, Oct. 1888, coll.

P. A. Karsten, Tavastia australis #856. (H). This is the holotype of Ophionectria episphaeria Karsten.

France. Near Montmarency, in Carnelle forest, on Eutypella and rotten wood, 23 April 1884, M. Boudier #1176. (PC). This is the type specimen of Ophionectria briardi.

Germany. Falkenberg, Wald bei Keuschnits, on stroma of Diatrype stigma, July-August 1894. This is the type citation of Calonectria belonospora ( $\equiv$ Ophionectria belonospora) but the collection no longer exists.

\_\_\_\_ Havelland, Rathenow Forest, on rotting hulls of oak acorns, 4 Nov. 1905, W. Kirschstein. (B). This is the type collection of Ophionectria cupularem.

\_\_\_\_ Havelland, Rathenow Forest, on the rotting hulls of acorns of Quercus sessiliflora, 4 Nov. 1905, W. Kirschstein, as Ophionectria belonospora. (B).

\_\_\_\_ Prignitz, Triglitz, on rotting, decorticated oak and birch twigs, 5 August. 1908, O. Jaap #595, labelled Belonidium tigrinum n.sp. (S).

\_\_\_\_ Prignitz, Triglitz, on old stroma of Eutypa hydnoidea on birch, 30 Oct. 1913, O. Jaap, as Ophionectria cerea. (HBG).

India. Chandreshwari, Maharastra, on dead stems and branches of Anona squamosa L. Sept. 1969. This is the citation of the type specimen of Ophionectria anonae which "was deposited in the herbarium of M.S.G. College, Malegaon, under number M.S.G. 104" but the institution has not responded to letters concerning this specimen.

Luxembourg (?Belgium). On withered limbs of Clematis vitalba, July 1902, W. F. Petrussthal, ad. nr. 1083 (H. 354). This is the type citation of Ophionectria belonospora var. unicaudata but the specimen could not be located.

Poland. Jaroslavl, Schedenewo, on stroma of Diatrype stigma, Sept. 1910, Tranzschel & Schestakow Mycotheca Rossica #120, as Ophionectria belonospora. (HBG).

Puerto Rico. Rosario, 9 km SE Mayaguez, elev. 140 m, on stroma and fibers of rotting wood, 17 June 1970, coll. R.P. Korf, et al., Amy Rossman #206. (CUP-PR #4178) (OSC).

Sweden. Knivsta near Ledinge, on Diatrype stigma. July 1895. (S). This is the type specimen of Ophionectria briardi var. longipila.

United States. Massachusetts, Conway State Forest, 24 Aug. 1963, coll. George Carroll, W. C. Denison #2873. (OSC #21257).

\_\_\_\_ New Hampshire, Waterville, on carbonous pyrenomycete on the bark of the prone Prunus pennsylvanica, 1 Sept. 1935, coll. J. R. Hansbrough #69515. (BPI). This specimen was labelled Ophionectria cerea var. miniata Dearness but this taxon was never validly published. The differences on which Dearness based his variety are within the limits of variation of Tubeufia cerea. "The perithecia are bright-red at first, instead of bees-wax color, turning sordid yellow and becoming dark and flat umbilicate instead of papillate or conic-papillate" (Dearness, notes in herbarium packet). There are bright-red perithecia of Nectria magnusiana on the type specimen in addition to perithecia of T. cerea which are dull greenish-yellow. Dearness

may have mistaken these for young perithecia of T. cerea. The color of the perithecia may have changed with time and the umbilicate shape could be due to the partial collapse upon drying. T. cerea typically shows a pomiform collapse upon drying.

\_\_\_\_ New Jersey, Cumberland Co., Newfield, on old Diatrype stigma and on the decaying bark of oak limbs, July 1890, coll. J. B. Ellis, Herb. W. G. Farlow. (FH). The original description of Ophionectria everhartii states that the type specimen was collected in January 1889 but the above collection is the only specimen in existence that could possibly be the type and, except for the date, matches the collection described in the original publication.

\_\_\_\_ New York, Tompkins Co., McLean Swamp, on Massaria canker, 22 Aug. 1925, coll. W. Whetzel & J. Miller #14874, as Ophionectria cerea. (CUP).

\_\_\_\_ New York, Onondaga Co., Apulia Station, on Fagus associated with Bertia moriformis, 5 Sept. 1925, coll. J. H. Miller #14984, as Ophionectria cerea. (CUP).

Tubeufia cylindrothecia (Seaver) Höhnel, Sitzungsbei. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl. 68:1479. Nov. 1909.

≡Ophionectria cylindrothecia Seaver, Myc. 1:70. Jan. 1909.

Seaver described this species in 1909 when he erected Scoleconectria for species of Ophionectria with a well-developed stroma. He considered O. cylindrothecia to be a true Ophionectria. Several months later, Höhnel (1909) transferred the species to Tubeufia based on the structure of the perithecium, and later (1919) on the presence of paraphyses.

Booth (1964) in reviewing the genus Tubeufia, mistakenly attributed the new combination to himself. The type specimen has dark-amber, cylindrical fruiting bodies, bitunicate asci and long-fusiform spores. It can be distinguished from Tubeufia cerea by the shape of the fruiting body, the larger asci and spores, and habit on dead herbaceous material.

Type: United States. Ohio, on old cornstalks of Zea mays L., Morgan #1007. (NY).

Other specimens:

Bermuda. Paget Marsh, on rotten petioles of Sabal blackburnianum, 16 Jan. 1922, coll. H. H. Whetzel, Bermuda Fungi #83. (CUP #11912).

\_\_\_\_\_ Paget Marsh, on Sabal bermudiana, 15 Jan. 1926, coll. Seaver & Whetzel #34607 & #34646. (CUP).

\_\_\_\_\_ Paget Marsh, on Sabal bermudiana, 6 Dec. 1940, #408. (NY).

\_\_\_\_\_ Paynter's Vale, on old wood, 20 Jan. 1926, Seaver, Whetzel & Ogilvie. (CUP #35077).

\_\_\_\_\_ Paynter's Vale, on Agave sp., 20 Jan. 1926, coll. Seaver & Whetzel (CUP #34677).

\_\_\_\_\_ Paynter's Vale, on old stalk of Agave sp., 21 Jan. 1926, coll. H. Whetzel. (CUP #34654).

Tubeufia hidakaeana (Hino & Katumoto) comb. nov. Figure 15 c.

≡ Ophionectria hidakaeana Hino & Katumoto, Bull. Fac. Agric. Yamaguti Univ. 6:41. 1955.

Fruiting bodies gregarious, superficial on substrate.

Ascocarps dirty-white, fleshy to membranaceous, globose to sub-globose, 200-450 x 130-160  $\mu\text{m}$ , papillae lacking but darker around the ostiole. Outer ascocarp wall of thin-walled, pigmented isodiametric cells, 7.5-10  $\mu\text{m}$  diam, forming pseudoparenchyma, inner wall of compact, thin-walled cells.

Pseudoparaphyses filiform, branching, abundant, dense, forming a network.

Asci 65-90 x 10-12  $\mu\text{m}$ , bitunicate, broadly cylindric, spores spirally twisted in the asci.

Spores 65-90 x 2.5-3  $\mu\text{m}$ , cylindric.

Type: Japan. Ooyama, Naka-gun, Kanagawa Pref., Prov. Sagami, 3 Sept., 1952, on stroma on culm of Pleioblastus vaginata Nakai, coll. Z. Hidaka. (YAM).

Tubeufia palmarum (Torrend) comb. nov. Figure 15 e.

$\equiv$ Ophionectria palmarum Torrend, Bull. Jard. Bot. Bruxelles 4:8. 1914.

Fruiting bodies scattered to gregarious in groups of two to four, seated on a thin byssus of pigmented hyphae.

Ascocarps dull-orange "Chamois", covered with bright-yellow hyphae, 3-4  $\mu\text{m}$  wide, except around ostiole, globose to ovoid, 130-200 x 150-275  $\mu\text{m}$ . Ascocarp walls of irregularly-shaped, pigmented cells, 10-17.5  $\mu\text{m}$  diam.

Pseudoparaphyses 1.5-2  $\mu\text{m}$  wide, distinctly septate, sparingly branched, extending beyond the asci.

Asci bitunicate, long-clavate, 65-70 x 8-10  $\mu\text{m}$ , spores parallel, spirally twisted toward the base of the asci.

Spores cylindrical, 55-65 x 2.5-3  $\mu\text{m}$ , multiseptate.

The type specimen was examined and found to have bitunicate asci. The habit, on stromatic pyrenomycetes covering rotting plant parts, the scurfy fruiting body and pleosporaceous centrum suggest the genus Tubeufia. It is differentiated from other members of the genus by the small ascocarps covered with bright-yellow scurf.

Type: Congo. Kisantu, on leaves and fragments of palm, 23 Dec. 1906, coll. H. Vanderyst. (BR).

Tubeufia paludosa (Crouan) comb. nov. Figure 15 f.

$\equiv$  Nectria paludosa Crouan, Florule du Finistere, no. 38. 1867.

$\equiv$  Ophionectria paludosa (Crouan) Saccardo, Michelia 1:323. 1878.

Fruiting bodies scattered to gregarious in small groups often with a scant subiculum extending upwards around base.

Ascocarps translucent yellow when moist, "Light Ochraceous-Buff", becoming dark amber to chestnut-brown upon drying, 165-210 x 260-295  $\mu\text{m}$ , rounded doliform to subglobose, irregularly collapsed upon drying, loose hyphae sometimes extending from outermost cells around base, ostiole

indistinct. Ascocarp wall composed of textura angularis, thin-walled cells, no pigments visible microscopically, loose cells forming an indistinct collar around apex and upper fruiting body.

Pseudoparaphyses scant in mature specimens, septate, 1  $\mu\text{m}$  wide.

Asci bitunicate, cylindric, 125-150 x 10-12  $\mu\text{m}$ , spores parallel, intertwined within asci.

Spores 75-100 x 3-4  $\mu\text{m}$ , hyaline, cylindric-fusiform, multiseptate.

Imperfect state Helicomyces roseus Link, associated with fruiting bodies. Conidia helicosporous, hyaline, filament 2.5-3  $\mu\text{m}$  wide, septate, 3.5-4.5 coils per conidia, coiled in two planes, whole conidia 24-28  $\mu\text{m}$  diam, apparently no differentiated conidiogenous cell, tip of hyphae coils and eventually conidium breaks off at septum.

The type specimen of Nectria paludosa suggests that this species belongs to the genus Tubeufia. The ascocarps are watery-yellow with diaphanous walls appearing brown when dried. The bitunicate asci contain long-fusiform spores characteristic of Tubeufia. In addition, conidia of Helicomyces roseus are associated with the fruiting bodies. Tubeufia cerea, I. helicomyces, I. helicoma (= I. rugosa) and I. cylinthrothecia have been shown to have helicosporous conidial states. Another genus closely related to Tubeufia, Thaxteriella, has some species with helicosporous conidial states but the fruiting bodies of Thaxteriella species are dark brown to black (Petraik, 1924) and the ascospores are generally shorter than those of Tubeufia species.

After Nectria paludosa was published and transferred to Ophionectria, no mention is made of this species until 1944 when Petch reported a specimen from Britain collected by E. A. Ellis. Although he labelled it O. paludosa, Petch suggested that it may be a Tubeufia and Booth (1959) found Ellis' specimen to be identical with Tubeufia helicomyces. The type material of T. helicomyces has not been studied so it is not known if these species are synonymous.

A specimen from (R0) labelled "O. paludosa Sacc." bore no resemblance to the species description; it was Nectriella diaphana Fuckel & Nitschke. A specimen from (S) labelled O. paludosa had no perithecial material.

Type: France. On the dead stem of a bramble, Rubus sp., in the bed of a stream, 22 June 1867. (PC).

#### Insertae Sedis

"Ophionectria" species parasitic on rusts

Three species described as Ophionectria are parasitic on uredosori of rusts: Ophionectria erinacea, O. tropicalis and O. uredinicola. The bitunicate asci and filiform, branching pseudoparaphyses place them in the Pleosporales, Pleosporaceae. They are related to each other and should belong to the same genus but no generic name is presently available for them. All three have been assigned to Ophionectria from which they are excluded by their bitunicate asci.

The Ophionectria species on rusts include synonyms in several different genera but none of these genera is an acceptable place for them. The type species of the genus Trichonectria, T. aculeata, has unitunicate asci (Pirozynski, pers. comm., 1973). Therefore, Ophionectria erinacea of which Trichonectria bambusicola is a later synonym, cannot be transferred to Trichonectria. Ophionectria erinacea has bitunicate asci and a pleosporaceous centrum. Another synonym of O. erinacea, Erinella setulosa, belongs to a genus of Ostroplaes. The other two species of Ophionectria parasitic on rusts have never been transferred out of Ophionectria but their bitunicate asci place them in the Pleosporales, not the Hypocreales.

The Ophionectria species of pleosporaceous parasites of rust have small, light-colored fruiting bodies with diaphanous walls such that the relatively few asci are visible through the walls in transmitted light. They are differentiated primarily on the basis of external fruiting body characteristics: Ophionectria erinacea has distinct, hyaline, seta-like hairs; O. tropicalis has flexuous, hyphal projections around the ostiole; and O. uredinicola is covered with irregular hyphae extending from the byssoid stroma.

Although these species are distinctive, I could not find a genus to which they belong. I hesitate to erect one because there are many little known tropical genera which were described without regard to the nature of the ascus. Several workers are studying type species and characterizing genera so that a genus may become available.

Ophionectria erinacea Rehm, Philippine Journal of Science 8:182. 1913.

=Trichonectria bambusicola Rehm, Leaflets of Philippine Botany  
6:2226. 1914.

=Erinella setulosa Sacc., Atti dell'Accad. Veneto-Trentino  
Istria 10:70. 1917. Fide Sydow, 1920.

The type specimens of Ophionectria erinacea and Trichonectria bambusicola are identical. The first time Rehm collected the fungus he apparently noticed the very long spores but the following year saw the hairs on the ascocarps as the prominent character. This species grows on rusts of living leaves of bamboo. It has translucent fruiting bodies with the ostiole surrounded by long, thick-walled, hyaline, septate hairs. It has a pleoporaceous centrum with bitunicate asci and long, septate spores which are spirally twisted in the ascus. Ophionectria erinacea is closely related to O. tropicalis and O. uredinicola. At present there is no genus to which these "hypocreaeous" loculoascomycetes on rusts belong.

Type: Philippines. Luzon, Prov. Laguna, Los Banos, on living leaves of Bambusa blumena, 12 Sept. 1912. C. F. Baker #36. Holotype (BPI). Isotype (S),

Other Specimens:

Philippines, Luzon, Prov. Laguna, Mt. Maquiling near Los Banos, on living leaves of Bambusa blumena. Sept. 1913. (BPI). This is the type collection of Trichonectria bambusicola. The type specimen is cited in the original publication as C. F. Baker #1655 but in all other details the data on this specimen match the citation of the type specimen. This specimen is regarded as the holotype.

Ophionectria tropicalis Speg., Anales de la Sociedad Cientifica Argentina 19:45. 1885. Figure 1 f.

The type specimen of this species has bitunicate asci with long spores spirally twisted in the ascus. It is related to Ophionectria erinacea and O. uredinicola, all occurring on rusts. The ring of flexuous hyphal projections around the ostiole distinguish this species. Type: Brazil. In a forest near a grove of Mbatobi, on living leaves of Blechnum sp. in association with a depauperate Uredinea, July 1883, Balansa #3882. Holotype (LPS #1686) Isotype (NY).

Other specimens:

Costa Rica. Los Angeles de San Ramon, parasitic on uredosori of Desmella superficialis Syd. on undersurface leaves of Blechnum volubilis, 30 Jan. 1925, H. Sydow, Fungi exotici exsiccati #655. (B) (CUP) (HBG) (NY) (S).

Trinidad. On uredosori on undersurface of living frond of a fern, before 1932, coll. R. Thaxter, det. L. W. Riddle, Herb. Roland Thaxter #2335, as Ophionectria tropica. (FH).

Venezuela. Caguita near Puerta La Cruz, parasitic on uredosori of Desmella superficialis Syd. on leaves of Dryopteridis tetragona, 27 Dec. 1927, H. Sydow, Fungi exotici exsiccati #840. (B) (CUP) (FH) (HBG) (NY) (PC) (S).

Ophionectria uredinicola Teng, Sinensia 4:277. 1934.

≡Ophionectria erinacea Teng, Contr. Biol. Lab. Soc. China, Bot. 8:271. 1933. A later homonym of Ophionectria erinacea Rehm, 1913.

=Ophionectria uredinicola Petch, Trans. Brit. Myc. Soc. 24:143. 1944. A later homonym of Ophionectria uredinicola Teng, 1934, but also a taxonomic synonym.

Although the type specimen of Ophionectria uredinicola, based on O. erinacea, was not located, the description and illustrations are sufficient to determine its affinities. Its relationship to Ophionectria tropicalis was recognized by Teng who considered his species to have "larger perithecia, longer asci and thicker spores". There is no difference in ascocarp, ascus or spore size between the description of O. uredinicola and the examined specimens of O. tropicalis. O. uredinicola Teng is differentiated by having bright-orange fruiting bodies which are covered with flexuous hyphae of the byssoid stroma. O. tropicalis has only sparse hyphae radiating from the base and a few short, hyphal projections around the ostiole of the white to pale-yellow fruiting bodies.

Type: China. Hangchow, Chekiang, on uredosori of Puccinia phyllostachydis Kus. on underside of leaves of Phyllostachys sp., Ling #125. This is the citation of the type specimen of Ophionectria erinacea Teng on which Ophionectria uredinicola is based. The specimen could not be located.

Other specimens:

Ceylon. Nuwara Eliya, on uredosori on Arundinaria debilis, 9 Aug. 1928. (K). This is the type specimen of Ophionectria uredinicola Petch. Although it is an invalid species, a later homonym of Ophionectria

uredinicola Teng, this species is synonymous with O. uredinicola Teng. Japan. Saga City, Kyusyu, on uredia of Puccinia kusanoi Dietel on Pleioblastus simoni Nakai, 3 June 1958, coll. I. Hino. (YAM).

"Ophionectria" species parasitic on dark, leaf-surface fungi

Two species described as Ophionectria occur as hyperparasites on dark, superficial, leaf-surface fungi: Ophionectria balladynae and O. luxurians. They have bitunicate asci and belong to the Pleosporales, Pleosporaceae. Both species have small, less than 130  $\mu\text{m}$  diam, reddish-brown fruiting bodies surrounded by scant, loose hyphae and a basal subiculum.

Specimens of these species have been placed in two genera in addition to Ophionectria: Malacaria and Paranectria. At present Malacaria is included in the Hypocreales (Rogerson, 1970) but the type species, M. meliolicola, must be examined to determine the ascus type. The description suggests that it is bitunicate: "asci numerosi, clavati, antice late rotundati, deorsum plus minus attenuate, ... firme et crassiuscule tunicati" (Sydow, 1930). The type specimen, of another species in Malacaria, M. entebbeensis, does have bitunicate asci. Malacaria is characterized by having multi-septate spores becoming dark at maturity. The type species of Paranectria, P. affinis, has unitunicate asci (Pirozynski, pers. comm., 1973) but P. luxurians ( $\equiv$ Ophionectria luxurians) has bitunicate asci. Ophionectria balladynae and O. luxurians must be transferred

to a bitunicate genus. At present such a genus is unknown but there are several genera of tropical "hypocreaceous" fungi with bitunicate asci which may accommodate them.

Ophionectria balladynae Hansford, CMI Myc. Pap. No. 15:134. 1946.

This species is hyperparasitic on Balladyna velutina. The type specimen has bitunicate asci and branching pseudoparaphyses, placing it in the Pleosporales, Pleosporaceae, related to Ophionectria luxurians. The ascocarps are small, 150-200  $\mu\text{m}$  diam, reddish-orange in color with flexuous hyphae at the base and growing from the outer wall. It is differentiated from O. luxurians by the very narrow, spirally-coiled ascospores.

Type: Uganda. Entebbe Road, on Balladyna velutina on undersurface of leaves of Pavetta oliveriana, Hansford #3452. (IMI).

Two specimens are mentioned in the type description. The first specimen listed is herein designated the lectotype.

Other specimen: Uganda. Entebbe Road, on Balladyna velutina on leaves of Canthii lacus-victoria, Hansford #3388. (IMI). Paratype of Ophionectria balladynae.

Ophionectria luxurians (Rehm) Hansford, CMI Myc. Pap. 15:135. 1946.

$\equiv$  Paranectria luxurians Rehm, Leaflets of Philippine Botany 8:2924. 1915.

Hansford transferred Paranectria luxurians to Ophionectria because the description did not mention terminal appendages on the

ascospores, as is characteristic of Paranectria species. The type specimen does not have appendaged spores but the asci are bitunicate with narrow, fusiform spores somewhat twisted around each other. This species is a loculoascomycete in the Pleosporales, Pleosporaceae.

The exsiccati issued as Paranectria luxurians C. F. Baker #171 is actually Malacaria entebbeensis Hansford, 1945, which has unitunicate asci and brownish, appendaged spores.

Type: Philippines. Luzon, Los Banos, parasitic on Meliola maesa on leaves of Maesa lax, Jan. 1913, coll. C. F. Baker #699, Rehm Ascomyceten #2116. (BPI).

#### Doubtful Species

Ophionectria anomala Racib., Anzuger der Akademie der Wissenschaften in Krakau. Mathematisch-Naturwissenschaftliche Classe 10:910-911. 1907.

Two packets which may have been part of the type collection were examined but no fungal material resembling the species was found. The identity of the species must remain in doubt.

Type: Java. Tjampea near Buitenzorg, on the underside of leaves of Hydnophytum, M. Raciborski. (KRA) (ZT).

Ophionectria calamicola P. Henn. & Nym. in O. Warburg, Monsunia 1:25. 1899. Non Nectria calamicola P. Henn. & Nym., 1899 = Nectria suffulta Berk. & Curt., 1876.

The type specimen apparently does not exist. No mention of this species is found in the literature after the original description. The identity of the species must remain in doubt.

Type citation: Java. Hort. Bogor., on rotting leaf petioles of Calamus sp., 31 Jan. 1898, E. Nyman.

Ophionectria conoidea Rehm, Hedwigia 37:199. 1898.

The type specimen of this species did not contain any material of the described fungus. The original description strongly suggests synonymy with Ophionectria trichospora (Berk. & Br.) Sacc. but until a good specimen becomes available, the identity of this species remains in doubt.

Type: Brazil. St. Catharine near Blumenau, June 1888, on bark of "Bugenbach", Ule #855 H.B. (HBG).

Ophionectria foliicola Zimm., Centralblatt für Bakt., Zweite Abteilung 8:182. 1902.

The type collection is not available and the description is inadequate to determine its affinities.

Type citation: Java. Buitenzorg Kulturgarten, on upper surface of living leaves of Coffea liberica.

Ophionectria globosa Sawada, Rep. Govt. Res. Inst. Formosa 85:24. 1943.

This type specimen had neither mature asci nor spores; the perithecia were empty. The very dark-brown fruiting bodies are superficial

on a stroma covering the scale insects. The dark perithecia and tough texture exclude this species from the Hypocreales. From the description of the centrum structure, the species may be related to Podonectria coccorum (Petch) comb. nov. ( $\equiv$  Ophionectria coccorum). O. globosa lacks setae arising from the stroma and the described asci and ascospores are larger than P. coccorum. The species is excluded from the Hypocreales and until good material becomes available, its affinities to other scale-inhabiting fungi remain in doubt.

Type: Taiwan. Sekijo, Taipei Province, parasitic on scale insects on Eurya japonica Thunberg, 6 Jan. 1927, coll. Kenkichi Sawada. (TAI).

Ophionectria hyphicola P. Henn., Hedwigia 41:7. 1902.

The type specimen apparently no longer exists, so the identity of this species remains in doubt.

Type citation: Brazil. St. Catharine near Blumenau, April 1891, on dead frond petiole of a tree fern, P. Henn. #521.

Ophionectria lagunensis Syd., Ann. Myc. 18:100. 1920.

The type collection could not be located; the identity of the species remains in doubt.

Type citation: Philippines. Mt. Maquiling, Laguna Province, on dead branch of Homonoia riparia (Euphorbiaceae). Nov. 1919, O. A. Reinking #6667.

Ophionectria sojae Hara, Pathologia Agriculturalis Plantarum p. 279. 1932.

No type collection of this species exists. From the description it seems doubtful that this could be an Ophionectria sensu stricto. Hara sites O. sojae as the cause of basal stem rot of soybean as in Neocosmospora vasinfecta and Kurata (1960) mistakenly identified an isolate of N. vasinfecta as O. sojae according to Udagawa (1963 a). The described O. sojae and N. vasinfecta are not at all similar; they could not be synonyms. Ophionectria sojae must remain in doubt until authentic material becomes available.

Type: The original description lacks any reference to a particular specimen and none could be located.

Ophionectria oubanghensis Saccas, Journal d'Agriculture Tropicale et de Botanique Appliquee, also called earlier Revue Internationale de Botanique Appliques et d'Agriculture Tropical 1:351. 1954.

From the description the dark perithecium suggest a member of the Sphaeriales but the type specimen could not be located. The identity of the species must remain in doubt.

Type citation: French Equatorial Africa (now called the Central African Republic). On dead branch of Hevea brasiliensis.

Ophionectria rubicola Pat., Bull. de la Societe Mycologique de France 9:154. 1893.

The type specimen contained no asci. The description of filiform branched paraphyses and subcapitate asci suggests that it may belong in the Pleosporales. Until good material becomes available, the identity of the species must remain in doubt.

Type: Ecuador. Lagerheim near Quito, on dead stems of Rubus sp. 31 Jan. 1892. (FH).

Ophionectria ulicis Unamuno, Asociacion Espanola Para ele Progreso de las Ciencias. Oporto: Seccion 4. Ciencias Naturales p. 88-89. 1921.

The type specimen is apparently lost. The identity of the species must remain in doubt.

Type: Spain. Asturias, at a place commonly called "El Bolao" near Llanes, on a spiny branch of Ulicis europaei, March, 1921. (MA).

The Instituto Botanico, Madrid, has an index card with collection data matching that mentioned by Unamuno in the type description. However, there is no specimen.

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