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## PRODROMUS TO NONLICHENIZED, PYRENOMYCETOUS MEMBERS OF CLASS HYMENOSCOMYCETES

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### SUMMARY

The orders and families of nonlichenized, pyrenomycetous fungi in class Hymeniascomycetes are classified in four supraorders, based upon characteristics of the centrum and certain features of the peridium in ascomata. Morphological features of value are discussed generally and numerous variations are illustrated. A dichotomous key separates the orders. Five orders: Eurotiales, Onygenales, Coryneliales, Spathulosporales and Halosphaeriales, are treated briefly and references are made to recent detailed studies. Nine orders: Erysiphales, Meliolales, Diaporthales, Sordariales, Microascales, Hypocreales, Clavicipitales, Xylariales and Calosphaeriales, are treated in more detail. Keys are provided to families and genera for these orders. Anamorphs are discussed briefly, as are recent studies in the literature. The family Catabotrydaceae Petrak ex Barr is newly described; new combinations include *Valsonectria hypoxylodes* (Ellis & Everh.) Barr and *Phylleutypa kalmiae* (Peck) Barr.

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## INTRODUCTION

Preparation of diagnoses and keys to orders and families of Class Loculoascomycetes and disposition of a number of genera within that framework (Barr 1987b) provided some understanding of the importance of variations in certain characteristics among those taxa. A companion Prodomus is presented here for a classification of certain taxa in Class Hymenoascomycetes. Discomycetous and lichenized fungi, so numerous and so important within the class, are not included. The assimilation and incorporation of available information on these taxa pose many problems and would not provide a satisfactory disposition at this time. Thus, only pyrenomycetous fungi, both perithecioid and cleistothecioid, are outlined in the following pages. Considerable diversity is evident among these fungi. Some deviation of genera and families from the positions assigned to them by O. Eriksson and Hawksworth (1988b, 1990) will be seen in the following pages, ample evidence that much remains to be understood about these fungi, their relationships, and the importance of various characteristics. The present classification does not yet accommodate all described genera, e.g., some marine genera (Kohlmeyer 1986) and numbers of tropical and southern hemispheric pyrenomycetes.

The introductory remarks on Loculoascomycetes hold also for the Hymenoascomycetes. Most nonparasitic forms are rather poorly known. Modern comprehensive keys are few; Müller and von Arx (1973) presented one in volume IVA of *The Fungi*. Certain orders have modern treatments, e.g., the Eurotiales (Malloch and Cain 1972b, Fennell 1973, Benny and Kimbrough 1980), Onygenales (Benny and Kimbrough 1980, Currah 1985, 1988), Coryneliales (Benny et al. 1985a-d), Spathulosporales (Kohlmeyer 1973, Kohlmeyer and E. Kohlmeyer 1975), Halosphaeriales (Kohlmeyer and E. Kohlmeyer 1979, Jones and Moss 1987). These orders are incorporated in the key, otherwise they are mentioned only briefly. Two other orders that have received considerable attention, the Erysiphales and Meliolales, are sketched out here because of their economic importance and because they have been regarded by some as members of Loculoascomycetes (see Barr 1987b).

## ACKNOWLEDGMENTS

As in the work on Loculoascomycetes, my indebtedness to mycologists of both past and present is obvious by the citations of their studies or personal communications. In particular, my appreciation goes to Clark Rogerson and Gary Samuels for their suggestions on a number of issues; Gary Samuels provided extensive comments when he reviewed the manuscript. This study is dedicated to the memory of E. S. Luttrell, whose impressive review of the taxonomy of the pyrenomycetes (Luttrell 1951) provided a firm basis for my

studies, and whose thought-provoking questions and detailed presentations of data serve as superb models to follow.

Progress in this study was facilitated by a Faculty Fellowship Award that provided a year free from instructional duties; for this I am grateful to the University of Massachusetts. I thank the curators of herbaria (BPI, DAOM, FH, IMI, NY, NYS, UBC, UPS) for permission to study fungi in their keeping. I thank too colleagues who sent many specimens for identification, fungi that posed problems, but that enlightened also.

## BASES OF CLASSIFICATION

Supraordinal classification of the ascomycetous fungi follows that of Barr (1983a) emended (1987b) and again here. Limitations in this study to nonlichenized, pyrenomycetous taxa result in the following sequence of orders within subclasses (Table I). The comparable arrangement of subclasses and orders within Loculoascomycetes is included; the parallel arrangement of orders does not necessarily indicate correspondence between the two classes. The orders that are listed are those included by Barr (1983a) with some exceptions. The Halosphaeriales is recognized as a separate order (Kohlmeyer in Hawksworth and O. Eriksson 1986), whereas the Coronophorales is reduced to a family in the Sordariales, as Nannfeldt (1975a, b) and others have suggested. The Phyllachorales and Trichosphaeriales, proposed by Barr (1983a), do not deviate in general centrum characteristics from the Xylariales and are reduced to family status in that order. The orders correspond otherwise to those accepted by O. Eriksson and Hawksworth (1988b, 1990) except that the Ophiostomatales is included under the Microascales and the Diatrypales under the Xylariales. The Ceratostomatales (Vasilyeva 1987) includes taxa that are referred here to the Sordariales or the Diaporthales.

The subclasses (Table I) are separated on characteristics of the centrum, the absence or presence and type of hamathelial tissues. In addition, peridium structure differs among the subclasses. Parguey-Leduc and Janex-Favre (1981) provided a detailed and important review of variations in primordia and the parts of ascomata in the Hymenoascomycetes. Their references permit continuity of citation beyond those in Luttrell (1951).

The members of the Plectomycetidae, whose cleistothecioid ascomata may exhibit indeterminate growth, whose peridia are rather soft and thin, and whose asci are not arranged in a hymenium, comprise two orders. Within each of the other major subclasses, one or two orders contain the great majority of taxa. Other orders within a subclass are separated by combinations of specialized features.

In the Parenchymatomycetidae the pseudoparenchymatous centrum tissues disintegrate as asci mature. Short chains of cells or paraphyses may develop into the cavity, as in

TABLE I

HYMENOASCOMYCETES	LOCULOASCOMYCETES
Plectoascomycetidae:	Loculoplectoascomycetidae:
Onygenales	Myriangiales
Eurotiales	Arthoniales
Parenchymatomycetidae:	Loculoparenchymatomycetidae:
Erysiphales	Asterinales
Meliolales	Capnodiales
Coryneliales	Dothideales
Spathulosporales	
Diaporthales	
Halosphaeriales	
Sordariales	
Microascales	
Anoteromycetidae:	Loculoanoteromycetidae:
Hypocreales	Chaetothyriales
Edaphomycetidae:	Loculoedaphomycetidae:
Clavicipitales	Opegraphales
Xylariales	Patellariales
Calosphaeriales	Pleosporales
	Melanommatales

species of *Sordaria* (Huang 1976, Uecker 1976, Read and Beckett 1985), or in species of *Diaporthe* (Jensen 1983, Uecker 1989). Such structures have been termed catenophyses in members of the Halosphaeriales (Kohlmeyer and E. Kohlmeyer 1971). While the sterile cells often deliquesce as the asci develop, they may persist until ascospores are mature. The peridia in members of the subclass are often composed of few rows of pseudoparenchymatous cells. The largest orders are the Diaporthales, whose ascomata typically are immersed erumpent, often hemibiotrophic or biotrophic, and whose asci loosen at their bases to float freely in the centrum, and the Sordariales, whose ascomata are usually superficial and saprobic, and whose asci do not float freely in the centrum, although ascus walls may deliquesce and free the ascospores into the centrum. The other orders are superficial biotrophs, as in the typically temperate-zone Erysiphales and the mostly tropical Meliolales and Coryneliales, or marine biotrophs as in the Spathulosporales, marine saprobes as in the Halosphaeriales or terrestrial saprobes as in the Microascales.

The Anoteromycetidae includes only the one order, Hypocreales. Apical paraphyses (periphysoids), develop into the centrum and are usually deliquescent at maturity or may be visible as a fringe in the upper centrum at times. Additionally, ascomata typically have soft-textured and often brightly pigmented peridia.

In the Edaphomycetidae, centrum tissues are prosenchymatous at first; apically free paraphyses, either interspersed among the asci or lateral in position, develop into the space formed by the enlarging peridium. Peridia are typically composed of two layers of compressed cells. The

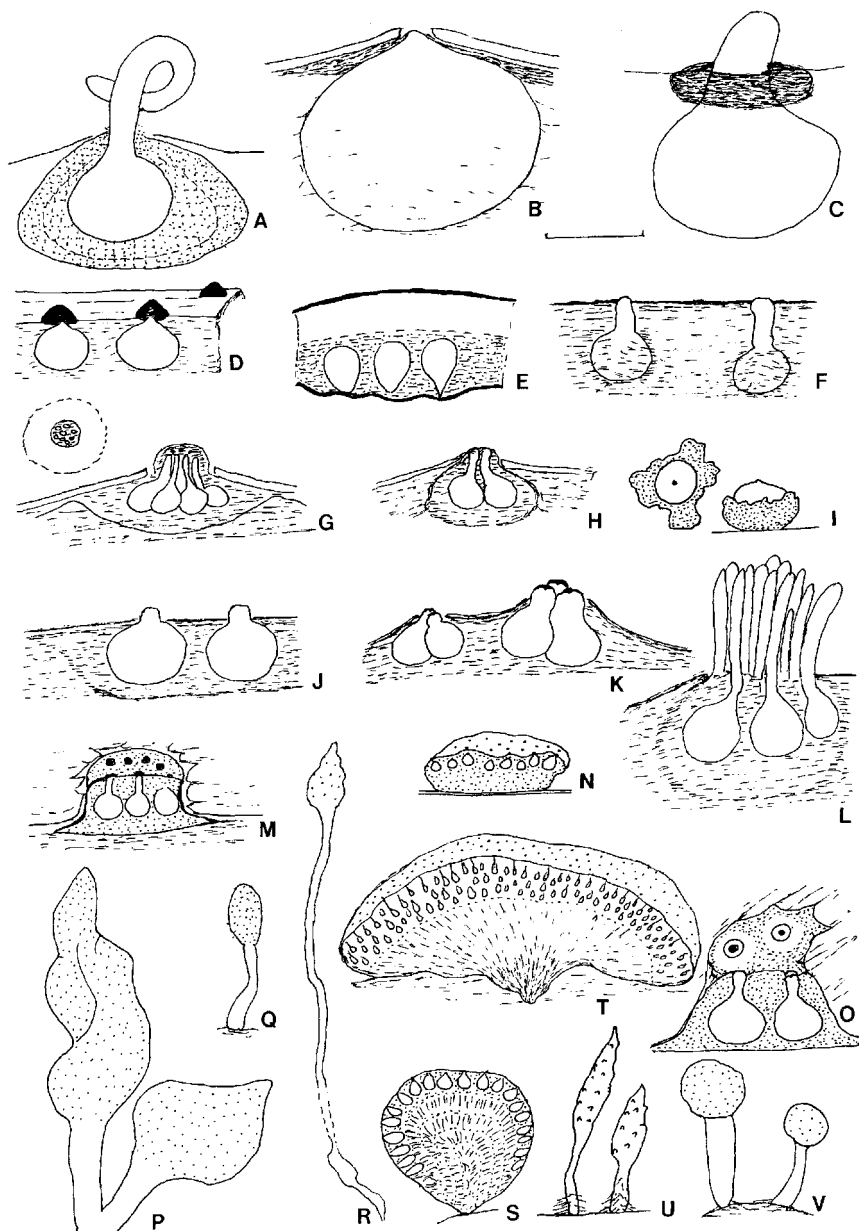
largest order is the Xylariales, whose members show considerable variability in a number of characteristics, including position of ascomata, presence and type of sterile tissues, and habit. A centrum containing lateral paraphyses and a biotrophic habit are typical of the Clavicipitales; the ascomata are often brightly pigmented and develop in stromatic tissues, and the asci are long cylindric. In the saprobic Calosphaeriales the paraphyses are few, often only one or two elongate, tapered paraphyses forming part of each fascicle of asci.

## MORPHOLOGICAL AND OTHER IMPORTANT FEATURES

### Vegetative stromatic tissues:

Some differences in character states between Hymenoascomycetes and Loculoascomycetes become apparent promptly. First of all, stromatic tissues are much more developed and appear to be quite useful at several levels of classification in the Hymenoascomycetes (Plate 1). In several

Plate 1. Variations in stromatic tissues and configuration of ascomata: A. *Mamianiella coryli* (Batsch: Fr.) von Höhnelt var. *spiralis* (Peck) Barr, single ascoma in pseudo-parenchymatous stroma. B. *Pestalosphaeria concentrica* Barr, ascoma immersed beneath clypeus. C. *Linocarpon palmetto* (Ellis & Everh.) Barr, ascoma immersed, short beak protruding through clypeus. D. *Melomastia mastoidea* (Fr.) Schröter, conspicuous carbonaceous ascoma apex. E. *Phyllachora fusicarpa* Seaver, stromatic tissues surrounding ascoma, epidermal clypeus. F. *Endoxyla parallela* (Fr.) Fuckel, effuse stroma, blackened crust. G. *Valsa melanodiscus* Otth, valsoid configuration, blackened marginal zone. H. *Valsaria insitiva* (Tode: Fr.) Ces. & de Not., valsoid configuration. I. *Astrocystis mirabilis* Berk. & Broome, stroma surrounding single erumpent ascoma. J. *Cryptosphaeria lignyota* (Fr.: Fr.) Auersw. in Rabenh., eutypoid configuration. K. *Eutypella goniostoma* (Schwein.) Sacc., eutypelloid configuration, sulcate apices. L. *E. scoparia* (Schwein.: Fr.) Ellis & Everh., eutypelloid configuration, elongate beaks. M. *Diatrype virescens* (Schwein.) Curtis, diatrypoid configuration. N. *Hypocrea gelatinosa* (Tode) Fr., ascomata peripheral in pulvinate stroma. O. *Hypoxydon sassafras* (Schwein.: Fr.) Curtis, ascomata basal in pulvinate, erumpent stroma, annulate apices. P. *Xylaria grandis* Peck, stipitate clavate stroma. Q. *Podostroma alutaceum* (Pers.: Fr.) Karsten, stipitate clavate stroma. R. *Podosordaria pedunculata* (S.F. Gray) Dennis, long stipitate stroma from sclerotial base. S. *Daldinia concentrica* (Bolt.: Fr.) Ces. & de Not., globose, zonate stroma. T. *Camarops petersii* (Berk. & Curtis) Mannfeldt, ascomata polystichous in pulvinate stroma. U. *Xylaria acuta* Peck, hispid stipitate stroma. V. *Cordyceps capitata* (Fr.) Link, stipitate capitate stroma. Standard line = 150  $\mu$ m for A-C. D-O not to scale. P-V x ca. 1.



orders there is a tendency to a 'developmental' series that runs from superficial, stromatic to nonstromatic, to immersed, stromatic to nonstromatic. Most conspicuous are the massive stromatic structures found in numbers of xylariaceous, clavicipitaceous and hypocreaceous fungi. These are composed of fungus hyphae and are usually differentiated into a firm, compact, external region and an inner region composed of loosely interwoven hyphae or of pseudo-parenchymatous cells. The stroma may be fleshy, brittle and carbonaceous or tough and woody in texture. Some stromata are differentiated into sterile stalk and fertile upper region, for example in some species of *Xylaria* or *Cordyceps*. Others are sessile and subglobose or globose: in species of *Daldinia* internal tissues are in zonate layers; in other xylariaceous or clavicipitaceous fungi internal tissues not layered or zonate, in *Entonaema* gelatinous fleshy, collapsing when dry. Stromatic tissues containing numbers of ascomata may be erumpent from the substrate or superficial, in the form of crustose, applanate or pulvinate structures, sometimes effused for several cm. Stromatic tissues, developed within the substrate and remaining immersed or becoming slightly or strongly erumpent, show considerable variation in size, pigmentation and shape of the final structure, in delimitation as recognizable ectostroma and entostroma, or in incorporation of substrate cells to form a pseudostroma. Some immersed stromatic tissues are effuse within a small or large area of substrate and may only be evident at the surface by a slight change in texture or color, or may be obvious by a darkening of the surface. A pigmented clypeus may develop over the surface of one or several ascomata. In some cases several stromata are contained within a region of the substrate that is delimited from noninfected tissues by a blackened ventral and sometimes also a dorsal zone or line, utilized to recognize species of *Diaporthe* especially (Wehmeyer 1933). Stromatic tissues that are superficial on the substrate may be reduced to a thin crust or may form a subiculum on and in which the superficial ascomata are seated. Because stromatic tissues are vegetative tissues, there may be considerable variation in amount and extent of their development within a taxon. Their characteristics should be considered in conjunction with more stable ones such as those of asci and ascospores.

The disposition of ascomata in stromatic tissues provides useful features for identification. Within well-developed, erumpent-superficial stromata, ascomata are usually peripheral and apices reach the surface. These may protrude slightly or strongly, so that the surface is roughened by obvious outlines of the ascomata. The apex is often rounded and protruding, but it may be sunken, or the papilla surrounded by an annular depression. Within immersed-erumpent stromata, the configuration of ascomata varies, as well as the apical papilla or beak, and the



combination of configuration and amount or kind of stromatic tissues permits a special terminology. Definitions have been proposed recently by Rappaz (1987) and Vasilyeva (1988). Diatrypoid and diatrypelloid configuration has ascomata seated at about the same level in a well-developed stroma, usually subperidermal, that is mostly composed of fungus hyphae; short or elongate beaks reach the surface separately. In a lesser number of taxa, the ascomata are polystichous, developed and seated in several layers within a stroma. Valsoid and eutypelloid configuration has ascomata seated at about the same level in a stroma, within the periderm, that may be composed of fungus hyphae only or may be of mixed hyphae and substrate cells; converging beaks reach the surface. The beaks may be separate but closely grouped at the surface or may fuse to form a common ostiole. Eutypoid configuration has ascomata seated in an effuse stroma, within the wood layer, that is composed of fungus hyphae and substrate cells, each ascoma separately reaching the surface by papilla or beak, depending on the depth of the ascoma. Ascomata in effuse stromata are usually upright, but in some taxa they are tilted or horizontal and the papilla or beak then is eccentric in position.

#### Ascomata:

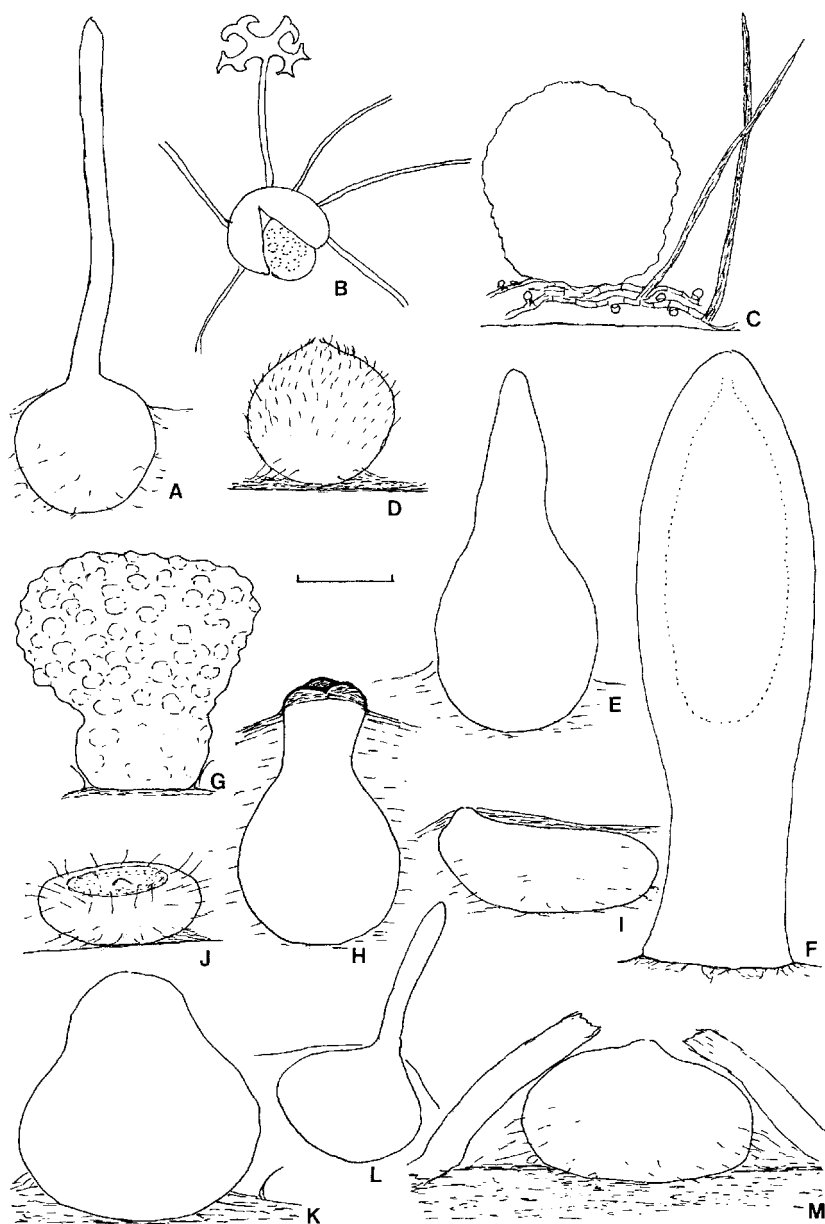
The shape, size and position of ascomata provide useful criteria (Plate 2). Ascomata in members of the Hymenoascomycetes vary considerably in size from minute to large. They are most frequently globose or slightly to strongly sphaeroid in shape, but may be ovoid, obpyriform, turbinate or vertically elongate to ligulate. Ascomata may be separate beneath a small clypeus, or gregarious and covered at the surface by an enlarged clypeus or by fused clypei that form a blackened area on the substrate. Some erumpent ascomata may split the clypeal or surrounding stromatic covering and emerge through a lacerated region of tissue. Other ascomata may be widened in the upper region by closely adhering tissues, sometimes of different consistency than the rest of the peridium, or the stromatic tissues may surround an individual ascoma closely. Ascomata may be immersed in the substrate or be widely erumpent or superficial, whereupon stromatic tissues may be reduced to a crust or a hyphal subiculum, or lacking.

The apex of perithecioid ascomata may be bluntly rounded or form a papilla or beak, the former usually small and tapering or blunt, the latter extending for a short or long distance. Most beaks taper gently in width toward the tip but some are cylindric. Some are narrow, others wide. Beaks may elongate under alternating humid and dry conditions; this elongation is often visible as one or more flangelike thickenings which denote cessation and resumption of growth. A papilla is often formed of cells similar to those in the peridium but smaller; occasionally short setae form a short, sharp papilla. A beak may also have

constituent cells as in the peridium or it may be composed of vertically oriented, parallel rows of cells. Some stout and elongate beaks, or even some vertically elongate ascogmata, may have reinforcing rows of cells that run obliquely or in two directions so that they cross. The tips of papillae or beaks are usually rounded. Some may be enlarged and flared outward, others thickened with ridges, designated as sulcate, appearing X or Y shaped from above. The ostiole or ostiolar canal is frequently but not always periphysate. In some taxa the rounded ascogmata open by a pore at the apex, without a noticeable papilla, and often lack periphyses. Periphyses may be found in crush mounts but sometimes sections are necessary. Cleistothecioid ascogmata do not have a preformed apical opening. They may open by weathering and disintegration of the peridium. Those whose peridia are cephalothecioid open along weak lines between plates. The unique Quellungskörper of some coronophoraceous fungi is a mass of small cells in a gel matrix that imbibes water and expands, finally rupturing the peridium (Nannfeldt 1975b, Fig. 1, c-f).

The peridium is typically two layered, in lateral view composed of rows of pseudoparenchymatous or prosenchymatous, compressed cells that are normally pigmented externally, pallid internally. A third layer is found in a number of taxa and this tends to be more pseudoparenchymatous, at times having cells or groups of cells or short hyphal appendages or setae that project and produce a distinctive surface. Such a layer probably originated as a thin vegetative stroma, but it is convenient to term and describe it as an extra layer of the peridium. A bombardoid peridium is known in some of the Sordariales. Lundqvist (1972) has detailed its complexity. The arrangement of cells at the surface of the peridium varies:

Plate 2. Variations in ascogmata: A. *Ophiostoma microsporum* (Davidson) von Arx, globose, erumpent, beaked. B. *Podosphaera myrtilina* (Schub.: Fr.) Kunze, globose, cleistothecioid, superficial, appendaged. C. *Meliola niessleana* Winter, ovoid, superficial on hyphae with setae and hyphopodia. D. *Trichosphaeria pilosa* (Pers.) Fuckel, globose, superficial, short setose. E. *Acrospermoides subulata* Miller & Thompson, erumpent superficial, beaked. F. *Acrospermum compressum* Tode: Fr., superficial, vertically elongate. G. *Nitschkia parasitans* (Schwein.) Nannfeldt, turbinate, sterile base, tuberculate surface. H. *Diatrype disciformis* (Hoffm.: Fr.) Fr., obpyriform, immersed in stroma, apex sulcate. I. *Oxydothis sabalensis* (Cooke) Petrak, horizontal, immersed under thin clypeus. J. *Niesslia exilis* (Alb. & Schwein.: Fr.) Winter, collabent, setose, superficial. K. *Nectria episphaeria* (Tode) Fr., obpyriform, erumpent from pulvinate stroma. L. *Gnomonia similisetacea* Barr, globose, immersed, erumpent beak. M. *Pseudomassaria chondrospora* (Ces.) Jacz., sphaeroid, immersed, raising periderm. Standard line = 150  $\mu$ m.

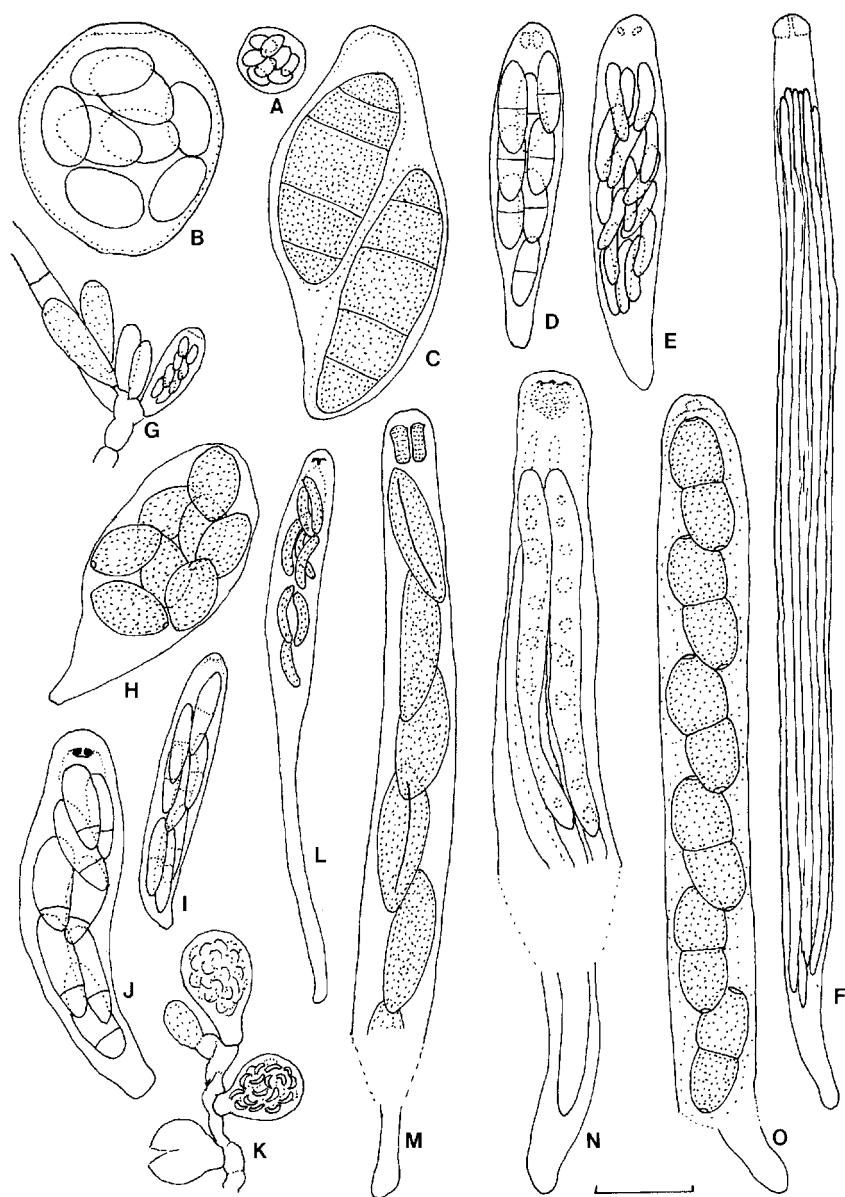


prosenchymatous or pseudoparenchymatous, forming *textura intricata*, *textura porrecta*, *textura epidermoidea*, *textura prismatica*, *textura angularis*, or combinations thereof (Jensen 1985; Korf 1973, Fig. 3, reproduced in Hawksworth et al. 1983 as Fig. 13). Septal pores, so-called "Munk pores," (Nannfeldt 1975b, Fig. 2e) are found in cell walls of some taxa. The peridium of plectomycetous taxa in the Eurotiales and Onygenales may be scanty, of interwoven hyphae, or pseudoparenchymatous or sclerotial. Pigmentation may be lacking (white ascomata) or bright -- shades of yellow, orange, red, green or blue -- or dark -- reddish brown or dull brown -- giving a black appearance to many of the **pyrenomycetes**. The texture of a peridium varies also: soft and fleshy, membranous, leathery, firm, woody, carbonaceous or brittle. By definition, the peridium and centrum in the Hymenoascomycetes are formed after the dicaryon is established, whether on hyphae or in a vegetative stroma. This is one of the basic differences between Hymenoascomycetes and Loculoascomycetes, where the dicaryon is established within stromatic tissues that develop into peridium and centrum.

#### Centrum: Hamathecium and asci:

The centrum of asci and any sterile tissues is utilized in classification at the level of subclass in the Hymenoascomycetes as it was in the Loculoascomycetes. Scattered asci not arranged in a hymenium, usually lacking

Plate 3. Variations in asci and arrangements of ascospores: A. *Ophiostoma microsporum*, globose, ascospores crowded. B. *Sphaerotheca fuliginea* (Schlecht.: Fr.) Poll., globose, ascospores crowded. C. *Irenopsis quercifolia* Hansford, oblong inflated, two-spored. D. *Diaporthe medusaea* Nits., oblong, apical ring refractive, ascospores biseriate. E. *Valsella nigro-annulata* Fuckel, polysporous. F. *Neobarya parasitica* (Fuckel) Lowen, cylindric, enlarged refractive apex, ascospores filiform, in fascicle. G. *Erostella minima* (Tul. & C. Tul.) Trav., spicate cluster, base of paraphysis, ascospores biseriate. H. *Chaetomium globosum* Kunze: Fr., clavate, ascospores crowded. I. *Niesslia exilis*, oblong, shallow refractive apical ring, ascospores overlapping biseriate. J. *Pseudomassaria corni* (Sowerby) von Arx, oblong inflated, amyloid apical ring, ascospores biseriate. K. *Pleurostoma ootheca* (Berk. & Curtis) Barr, catenate, polysporous. L. *Eutypella quadrifida* (Schwein.) Ellis & Everh., clavate, stipitate, amyloid apical ring, ascospores biseriate. M. *Xylaria polymorpha* (Pers.: Fr.) Grev., cylindric, amyloid apical ring, ascospores uniseriate. N. *Lasiosphaeria chrysentera* Carroll & Munk, oblong cylindric, apical globule below refractive apical ring, ascospores in fascicles. O. *Trichodelitschia bisporula* (Crouan & H. Crouan) Munk, cylindric, refractive pulvillus, ascospores uniseriate. Standard line = 15  $\mu$ m.



sterile tissues, are typical of the Plectoascomycetidae, the taxa arranged in Eurotiales and Onygenales. The other three subclasses have asci arranged basally or peripherally in a hymenium, sometimes in fascicles or tufts. The Parenchymatomycetidae includes taxa whose asci develop into space which is formed by disintegration of thin-walled, pseudoparenchymatous cells. Some of these cells may persist as short chains, or wide paraphyses may develop (Kohlmeyer and E. Kohlmeyer 1971, Huang 1976, Jensen 1982). The Anoteromycetidae includes taxa in which apical paraphyses (periphysoids), grow downward, reaching the hymenium, usually deliquescent as the asci develop but persisting at times among the asci or as a short fringe that lines the upper part of the centrum. The Edaphomycetidae includes taxa whose paraphyses develop from the subhymenial region or from lateral walls or from the basal cells that support a fascicle of asci. These paraphyses, with free apical ends, are often narrow, thin walled and delicate; some are relatively wide throughout their length, others are wide at the base and taper upward. Again, the paraphyses may deliquesce as the centrum matures.

The functionally unitunicate asci of Hymenoascomycetes show considerable variability throughout the class (Plate 3). They are usually thin walled at maturity except for the apical region. They do not have the footlike base so prevalent in the Loculoascomycetes but are more truncate or rounded at the base. They vary in shape (globose, ovoid, oblong, ellipsoid, clavate, cylindric) and in the presence and length of a stipe. Most representatives of the Diaporthales have asci that become loose at the base, float free in the centrum and may be forced up the ostiole to ooze out from the tip of the beak. A number of taxa, e.g., in the Halosphaeriaceae and Chaetomiaceae, have deliquescent asci and at maturity the ascospores lie free in the centrum. As noted earlier, asci may arise in a hymenium that is restricted to the base or that forms over the entire periphery of the centrum, or they may arise in basal tufts or fascicles, or in chains. In cleistothecioid taxa they are catenate, or are scattered irregularly throughout the centrum.

The ascus apex may be simple or may contain an apical apparatus of varying complexity. The apical ring at the tip of the cytoplasm is usually refractive in water. It may form a shallow or elongate to tubular ring or may be composed of stacked plates. Above the apical ring a pulvillus or dome, shallow or deep and conspicuous, is evident in a number of taxa. Staining properties vary: the apical ring may be amyloid (euamyloid) (direct blueing) in iodine solutions (IKI or Melzer's reagent), or after pretreatment with KOH (provoked blueing) (O. Eriksson 1966, Kohn and Korf 1975, Baral 1987); the apical ring or the pulvillus may be chitinous in 1% nigrosin or in blue-black ink, or the apparatus may show both reactions or no reaction. A dextrinoid (hemiamyloid) reaction is useful in

a few pyrenomycetous fungi, e.g., in ascospores of members of the Microascaceae, where in iodine solution young ascospores are dark orange to reddish violet (Malloch 1970), and in *Valettoniella crucipila* von Höhnelt where ascospores are red in Melzer's solution (Samuels 1983). Additional stains have been tested but not consistently, and have not as yet provided any useful diagnostic features. Fluorescence microscopy is providing more information about ascus apices (Romero and Minter 1988).

Most asci in the class are octosporous. Some families, e.g., Valsaceae, Diatrypaceae, Calosphaeriaceae, contain taxa with polysporous asci, the numbers usually multiples of eight. This feature seems to be valid at the generic level within these families, although not necessarily so in the Sordariaceae, Nitschkiaceae or Hypocreaceae. A lesser number of genera, or species in typically octosporous genera, have less than eight ascospores at maturity. Members of the Meliolales typically produce two, sometimes three or four ascospores per ascus. In the Erysiphales the numbers of ascospores per ascus vary from two to eight; the number is quite consistent within a species.

#### Ascospores:

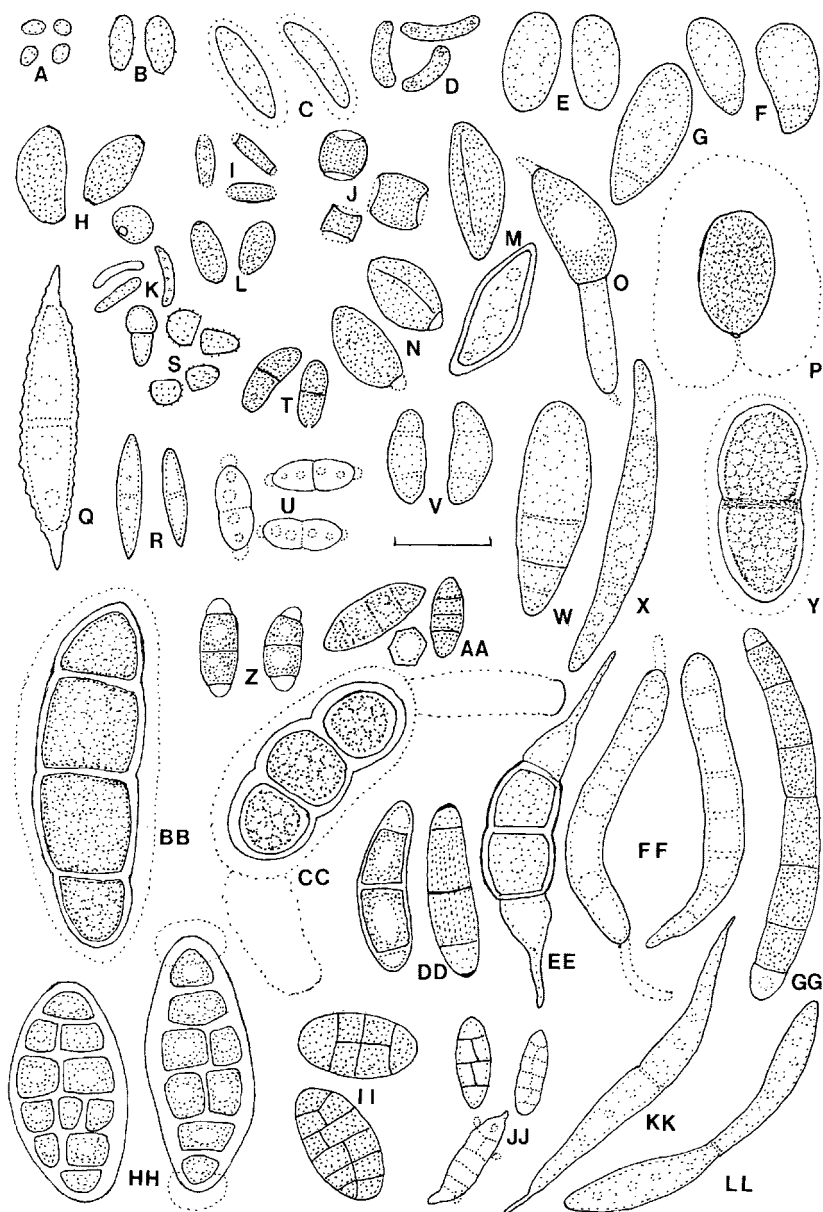
Ascospores in pyrenomycetous Hymenoascomycetes provide a number of criteria that are used in classification (Plate 4). Pigmentation may be lacking, i.e., hyaline, or slight as yellowish, pinkish, bluish, greenish, or light brown, or of varying shades and densities of brown to nearly black and opaque. Shapes and bipolar symmetry vary: symmetric and globose, ellipsoid, fusoid, oblong, allantoid or filiform, or asymmetric and ovoid, clavate or elongate, tapered more strongly to one end. Ascospores in many species are straight and radially symmetric, but more are radially asymmetric, some inequilateral, others slightly or strongly curved (allantoid is a special case and is treated as a shape). One-celled ascospores are common in the Hymenoascomycetes in contrast to the situation in the Loculoascomycetes. One-septate ascospores, whether the septum is median or supra- or submedian, or near one end with the small cell less than one-third length of ascospore (apio-sporous, obapio-sporous), or cuts off a small "dwarf" cell of different pigmentation, are also frequent. Two- to multi-septate ascospores are less common, and muriform ascospores quite infrequent. Those taxa with additional septa in the ascospores are thus more readily determinable. In general, septa are eusepta and only rarely are distosepta recognizable, as in species of *Pseudovalsa* and *Dictyophorthe*.

The ascospore wall may be thin or thickened as an obvious double wall. The wall is frequently smooth but may be ornamented by longitudinal ridges or by verruculae, reticulations or foveolae that appear punctate in surface view. A number of brown-spored taxa have a short or

elongate, straight or spiral germ slit in the wall, rarely more than one; this appears to be a family characteristic. Others have one or more germ pores in the wall, or short terminal slits. Few lightly pigmented ascospores show these mechanisms, nor would they be so essential for germination. Gel coatings or appendages are conspicuous in certain taxa, notably in the Halosphaeriales and in some

Plate 4. Variations in ascospores: A. *Ophiostoma microsporum*, ovoid to subglobose. B. *Trichosphaeria pilosa*, ellipsoid, verruculose. C. *Iodosphaeria* sp., fusoid, gel coating. D. *Diatrype disciformis*, allantoid. E. *Phyllachora ambrosiae* (Berk. & Curtis) Sacc., wide oblong. F. *Apiospora montagnei* Sacc., obovoid, apiosporous. G. *Pseudomassaria chondrospora*, obovoid, apiosporous. H. *Melanospora brevirostris* (Fuckel) Tulasne, ellipsoid, terminal germ pores. I. *Syspastospora parasitica* (Tulasne) Cannon & Hawksworth, oblong, terminal germ pores. J. *Scopinella sphaerophila* (Peck) Malloch, cubical, terminal germ pores. K. *Coronophora gregaria* (Lib.) Fuckel, allantoid. L. *Camarops petersii*, single germ pore. M. *Xylaria grandis* Peck, fusoid naviculate, germ slit. N. *Anthostomella formosa* Kirschst., ellipsoid, dwarf cell, germ slit. O. *Bombardia bombardia* (Batsch: Fr.) Schröter, dark upper, hyaline basal cell, short appendages. P. *Sordaria fimicola* (Rob.) Ces. & de Not., terminal germ pore, gel coating. Q. *Hypomyces lactifluorum* (Schwein.) Tulasne, fusoid, apiculate, verruculose. R. *Niesslia exilis*, fusoid. S. *Hypocrea gelatinosa*, separating into two partspores, one globose, the other oblong. T. *Pseudovalsaria foedans* (Karst.) Spooner, oblong, germ pore. U. *Diaporthe medusaea*, ellipsoid, short pulvinate appendages. V. *Telimenella gangraena* (Fr.) Petrak, ellipsoid, two septate. W. *Buergenerula spartinae* Kohlmeyer & Gessner, obovoid, apiosporous with additional septa. X. *Melogramma campylosporum* Fr., elongate fusoid. Y. *Massariovalsa sudans* (Berk. & Curtis) Sacc., wide oblong, gel coating. Z. *Litschaueria corticiorum* (von Höhnelt) Petrak, ellipsoid, pallid end cells. AA. *Lepteutypa fuckelii* (Nits.) Petrak, hexagonal. BB. *Meliola niessleana*, ellipsoid, inequilateral, gel coating. CC. *Hapalocystis berkeleyi* Auersw. ex Fuckel, gel coating, straplike appendages. DD. *Chaetosphaerella fusca* (Fuckel) Müller & Booth, oblong, pallid end cells. EE. *Broomella montaniensis* (Ellis & Everh.) Müller & Ahmad, fusoid, setose appendages. FF. *Lasiosphaeria ovina* (Pers.: Fr.) Ces. & de Not., geniculate, appendaged young, septate mature. GG. *Melanamphora spinifera* (Wallr.) LaFlamme, narrowly oblong, multiseptate. HH. *Dictyoportha acerophila* Barr, distoseptate, muriform, pulvinate appendages. II. *Thyridium vestitum* (Fr.) Fuckel, ellipsoid, muriform. JJ. *Nectria balsamea* Cooke & Peck, fusoid, muriform, budding. KK. *Oxydothis sabalensis*, elongate fusoid. LL. *Vialaea insculpta* (Fr.) Sacc., isthmoid. Standard line = 15  $\mu$ m.





genera of the Diaporthales and Sordariales and occasionally in other orders. The contents of ascospores are usually guttulate when immature and may remain so, or are granular or form one or more conspicuous, rounded, refractive globules; refringent septumlike bands are found in species of *Linocarpon* (Hyde 1988). The arrangement of ascospores within the ascus is dependent upon the shape of both, e.g., short ellipsoid ascospores are uniseriate, often obliquely, in cylindric asci, allantoid ascospores are biseriate in clavate asci, filiform ascospores form a fascicle in an elongate ascus.

#### Anamorphs:

Anamorphs known in the Hymenoascomycetes are varied and their presence is noted in the characterization of orders and families. Anamorphs may be hyphomycetous, with conidiophores scattered on the substrate or over the peridium of ascomata, or arranged in a layer on sporodochia or synnemata; they may be coelomycetous, forming pycnidial or acervular conidiomata or locules in a stroma. Conidiogenesis also varies from thallic to blastic, thallic with rhexolytic or schizolytic separation, or meristematic, holoblastic with sympodial or percurrent proliferation, enteroblastic with phialidic production of conidia. The conidia may be hyaline or pigmented, are variable in shape, size and septation, and at times are versicolarous, the mid cells pigmented and end cells hyaline. They may bear appendages; walls are often smooth, but may be variously ornamented. Many recent studies and interpretations of anamorphs are cited under the appropriate orders and families. Samuels (personal communication) has pointed out some generalizations on anamorphs. Often ascomata succeed conidia on a stroma, less commonly in Loculoascomycetes. Phialidic hyphomycetes are rare in Loculoascomycetes, but prevalent in many Hymenoascomycetes.

#### Habit:

Certain orders of Hymenoascomycetes contain only biotrophic taxa. Others include biotrophic, hemibiotrophic and saprobic taxa, whereas a few orders contain saprobes or hypersaprobes predominantly. The substrates vary widely: animal tissues, insects and spiders, other fungi, algae, mosses and liverworts, and all the groups of vascular plants. As much as possible, the substrate is characterized as part of the description of orders and families.

## KEY TO ORDERS

1. Asci irregularly scattered in centrum, small, without discharge mechanism, deliquescent; ascomata cleistothecoid, many light pigmented; ascospores hyaline or lightly pigmented, one celled, small.....2
1. Asci arranged in hymenial layer or fascicle in centrum, variable in size, shape and persistence; ascomata perithecoid or cleistothecoid, light or dark pigmented; ascospores variable in pigmentation, septation and size.....3
  2. Peridium hyphal, membranous, occasionally lacking or pseudoparenchymatous, not appendaged; anamorphs enteroblastic phialidic.....Eurotiales\*
  2. Peridium hyphal, membranous or netlike or lacking, appendaged at times; anamorphs thallic.....Onygenales\*
3. Ascomata superficial on substrate or stromatic tissues, biotrophic.....4
3. Ascomata immersed becoming erumpent from substrate or stromatic tissues when biotrophic, variable in position when saprobic.....7
  4. Ascomata cleistothecoid, opening by splitting or disintegration of peridium; ascospores one celled....5
  4. Ascomata perithecoid, opening by apical ostiole; ascospores one or several celled.....6
5. Ascomata globose or sphaeroid, appendaged, on pallid hyphae, usually on leaves; asci sessile; ascospores hyaline or pallid.....Erysiphales
5. Ascomata urceolate or nearly columnar, not appendaged, on dark stromatic base, erumpent from leaves, fruits or branches; asci stipitate; ascospores brown....Coryneliales\*
  6. Ascospores hyaline, one celled; ascomata on crustose stromatic base on marine red algae.....Spathulosporales\*
  6. Ascospores brown, several celled; ascomata on dark hyphopodiate hyphae, usually on leaves of land plants.....Meliolales
7. Ascomata and stromatic tissues mostly brightly pigmented, to blue, brown or blackish, fleshy or soft textured; paraphyses or apical paraphyses inconspicuous or lacking among mature asci; ascospores hyaline or lightly pigmented, rarely dark.....8
7. Ascomata and stromatic tissues typically dark pigmented, soft to firm and carbonaceous; paraphyses conspicuous or not among mature asci; ascospores hyaline or dark.....9
  8. Asci forming basal or peripheral layer, oblong, cylindric or inflated, apical ring lacking or shallow to distinct; ascospores variable in shape and septation; saprobic, hypersaprobic, hemibiotrophic or biotrophic on various substrates.....Hypocreales
  8. Asci forming basal fascicle, long cylindric, apex usually conspicuous, refractive, penetrated by narrow canal; ascospores filiform or elongate fusoid, multi-septate; biotrophic on insects, arachnids, hypogeous fungi, or monocots.....Clavicipitales

9. Ascomata saprobic, marine; asci deliquescent; ascospores typically surrounded by gel coating and/or bearing appendages.....Halosphaeriales\*
9. Ascomata biotrophic to saprobic, typically not marine; asci deliquescent or persistent; ascospores with or lacking gel coating and/or appendages.....10
10. Ascomata small, perithecioid and often with long narrow beak or cleistothecioid; asci small, deliquescent; ascospores one celled, rarely one septate, hyaline or shades of brown, often dextrinoid when young.....Microascales
10. Ascomata small to large, perithecioid and apex papillate to beaked, or cleistothecioid; asci variable in size and persistence; ascospores variable in septation, pigmentation, not or rarely dextrinoid when young.....11
11. Ascomata typically immersed in substrate or stroma, beaked; asci usually loosening from subhymenium, floating freely in centrum, apical ring nonamyloid.....Diaporthales
11. Ascomata immersed in substrate or stroma or superficial, beaked or not; asci not loosening from subhymenium nor floating freely in centrum, apical ring amyloid or nonamyloid.....12
12. Ascomata typically superficial on substrate, usually lacking stroma, saprobic or hypersaprobic, perithecioid or cleistothecioid; peridium of pseudoparenchymatous cells; apical ring of ascus mostly nonamyloid or lacking.....Sordariales
12. Ascomata immersed erumpent from substrate or stromatic tissues, or superficial, saprobic, hemibiotrophic or biotrophic, mostly perithecioid; peridium of compressed rows of cells; apical ring of ascus amyloid or nonamyloid.....13
13. Asci in small fascicles or in spicate clusters lining centrum, apical ring shallow, nonamyloid; ascospores hyaline, allantoid or oblong.....Calosphaeriales
13. Asci forming basal or peripheral layer, apical ring shallow or complex, many amyloid; ascospores variable in pigmentation and shape but brownish when allantoid.....Xylariales

#### \*ORDERS BRIEFLY NOTED

**Eurotiales** Martin ex Benny & Kimbrough, Mycotaxon 12: 23. 1980.

A single family Trichocomaceae E. Fischer 1897 includes the Eurotiaceae Clements & Shear 1931 and accommodates cleistothecioid genera whose asci are irregularly scattered, ascospores are frequently oblate, and anamorphs are enteroblastic phialidic, often forming aggregations of phialides that produce one-celled conidia. Because of the importance of the *Aspergillus* and *Penicillium* anamorphs, literature on this order is voluminous. Some of the

background citations may be found in the book edited by Samson and Pitt (1985). Malloch and Cain (1972b) presented an approach to separation of genera that utilizes anamorphs in conjunction with peridium structure of the ascomata; the key provided by Benny and Kimbrough (1980) is similar in concept. The Eurotiales has many similarities to the Onygenales in types of ascomata, asci and ascospores and the two orders have been united as one (Fennell 1973, von Arx 1987a). The latter author recognized four families: Eurotiaceae, Gymnoascaceae, Onygenaceae and Amauroascoaceae, in his arrangement, which reduced the importance of anamorphs (see also von Arx and van der Walt 1986).

The Cephalothecaceae von Höhnelt (Chesters 1934), enlarged to include the Pseudeurotiaceae Malloch & Cain with dark ascomata having cephalothecoid peridium, was assigned to the Eurotiales (Benny and Kimbrough 1980). Malloch (1979) arranged the Pseudeurotiaceae in the Diaporthales (in his sense comprising pyrenomycetes exclusive of the Hypocreales). The anamorphs are mostly enteroblastic phialidic, but in some taxa are holoblastic sympodial. O. Eriksson and Hawksworth (1987c, 1990) did not assign either family to order. Von Arx (1987a) included the Cephalothecaceae under the Onygenaceae.

**Onygenales** Ciferri ex Benny & Kimbrough, Mycotaxon 12: 8. 1980.

The order includes taxa having cleistothecioid, often small ascomata with membranous or netlike peridium or lacking peridium, small and irregularly scattered asci, small, one-celled, smooth or ornamented ascospores, one or several-celled thallic conidia having rhexolytic dehiscence. Benny and Kimbrough (1980) reviewed the genera belonging to the order and separated them into three families: Dendrosphaeraceae, Gymnoascaceae and Onygenaceae. Currah (1985) provided a detailed revision of genera and species in the order, utilizing four families: Arthrodermataceae, Gymnoascaceae, Myxotrichaceae and Onygenaceae. He recently (Currah 1988) presented an annotated dichotomous key to the genera. Numbers of taxa are keratinolytic and consequently some are known animal pathogens; others are cellulolytic.

**Coryneliales** Seaver & Chardón, Sci. Surv. Porto Rico Virgin Isl. 8(1): 40. 1926.

A single family Coryneliaceae comprises the order. The majority of taxa are tropical or southern hemispheric in distribution. Only one genus *Caliciopsis* is represented in temperate North America. Detailed studies were conducted by Fitzpatrick (1920) who recognized four genera; in 1942a, b he added another genus so that *Corynelia*, *Tripospora*, *Corynelospora*, *Lagenulopsis*, *Caliciopsis* were

included. These were separated on ascospore shape and wall features. Butin (1972) described *Coryneliopsis* from *Cyttaria stromata* parasitic on *Nothofagus*. Benny et al. (1985a-d) recognized these genera and added one more, *Fitzpatrickella*. Disposition of the order in the Hymenozascomycetes follows Luttrell (1951, 1955). The developmental study made by McCormack (1936) was suggestive of a dothideaceous centrum, but a differing interpretation, that of a columnar stroma that contains ascogenous tissues that in turn form a thin peridium around an ascoma, is feasible. Photographs by Kuijt (1969) of *Wallrothiella arceuthobii* (Peck) Sacc. [= *Caliciopsis arceuthobii* (Peck) Barr] reinforce this interpretation. The asci are said to be bitunicate but with early breaking of the ectotunica (O. Eriksson and Hawksworth 1987a), however, the aspect of asci is quite unlike that of any bitunicate ascus that I know. In a recent study on ascus structure, Johnston and Minter (1989) described and illustrated asci from all genera ascribed to the Coryneliaceae. The asci have more than one functional wall layer, but the outer layer breaks at an early stage, before ascospores are delimited. Release of mature ascospores is through irregular breaks in the remaining wall and no specialized apical structures were observed. Johnston and Minter support the separation of the order from all others on the bases of ascus structure and development. They questioned the position of *Coryneliopsis*, where habit, morphology, and in the case of one species at least, asci having only one wall layer, make it suspect in the order.

**Spathulosporales** Kohlmeyer, Mycologia 65: 615. 1973.

One family Spathulosporaceae contains the sole genus *Spathulospora*. These unique superficial parasites on marine red algae (*Ballia* spp.) in southern hemispheric waters were first described by Cavaliere and Johnson (1965). Kholmeier (1973) provided many more details and suggested that the order might be a "possible missing link between Laboulbeniales and pyrenomycetes." Kholmeier and E. Kholmeier (1975) added more information on development and distribution. Ascomata develop on a crustose stromatic base, have a firm peridium of several rows of cells, periphysate ostiole, pseudoparenchymatous centrum, numerous deliquescent asci in a peripheral layer, and hyaline, one-celled ascospores with a lateral appendage. Walker et al. (1979) reported on germination of ascospores to form infection pegs into algal cells and the production of an internal (intramural) crust of filaments preceding emergence of hyphae to produce the external crust and ascomata. This sequence of development is similar to that in other biotrophs.

**Halosphaeriales** Kohlmeyer in Hawksworth & O. Eriksson, Syst. Ascomyc. 5: 179. 1986.

The order includes one family Halosphaeriaceae of marine, saprobic fungi, whose ascomata and peridia are variable and asci are deliquescent. Many of the species have some sort of sheathing material or appendages on the ascospores. Kihlmeyer (1972) formally established the family and provided a key to genera. Many additional studies have added numerous taxa and more information about members of the order. Jones et al. (1986) reviewed characteristics of value for taxonomy and Kirk (1986) wrote on evolutionary trends in the family. Jones and Moss (1987) provided a key to 21 genera, where ascospores of species had been studied under the electron microscope. The key utilizes the variations of position, numbers and manner of formation of appendages. Other marine taxa are assigned to different orders of Hymenoascomycetes or of Loculoascomycetes, for example, see Kihlmeyer and E. Kihlmeyer (1979), Schatz (1980, 1983), Kihlmeyer and Volkmann-Kihlmeyer (1987).

#### ORDERS TREATED IN DETAIL

**Erysiphales** Gwynne-Vaughan, Fungi 78. 1922.

Ascomata superficial on superficial, hyaline or lightly pigmented mycelium (some taxa with endophytic as well as superficial mycelium), globose or sphaeroid, cleistothecoid, minute to small or medium; peridium relatively narrow, externally of brown somewhat compressed cells, internally of hyaline cells, at times outermost layer separating, typically bearing hyaline or lightly pigmented appendages of some kind: irregularly placed and mycelial, or in ring and bristlelike, uncinatc to circinate, or dichotomously branched at tips or occasionally as clavate gelatinizing cells in upper region; forming haustoria in epidermal cells of host plant. Asci unitunicate, basal, ovoid, oblong or subglobose, one or two to many per ascus, often less than octosporous; wall evenly thickened, apical ring lacking. Paraphyses lacking, some pseudoparenchymatous remnants of centrum tissues present at times. Ascospores hyaline to yellowish, oblong, ovoid or ellipsoid, one celled; wall smooth; guttulate; crowded in the ascus.

Anamorphs hyphomycetous; conidia one celled, hyaline, meristem arthrospores maturing in basipetal succession, originating by meristematic growth of conidiophore apex. Described as *Oidium*, *Oidiopsis*, *Ovulariopsis*, *Streptopodium* (Hammett 1977, Bosewinkel 1980, Braun 1987).

Biotrophic on numerous angiosperms, cosmopolitan, frequently as anamorph only in south temperate and in tropical regions.

One family:

Erysiphaceae Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 22. 1885.

The family names Erysibaceae Schröter 1893 and Cystothecaceae Hennings 1900 are included. The monographic study of Salmon (1900) recognized six genera in the family: *Erysiphe*, *Microsphaera*, *Phyllactinia*, *Podosphaera*, *Sphaerotheca*, *Uncinula*. Five of these genera contain the majority of the species, whereas *Phyllactinia guttata* (Wallr.: Fr.) Lév. is the sole representative in North America of that genus. Parmelee's (1977) study of powdery mildews in Ontario and adjacent regions is based upon this conservative taxonomy. A number of genera have been segregated in modern studies, the most recent of which is the exhaustive monograph by Braun (1987), wherein 18 genera were accepted. The following key, which presents 13 genera recognized in temperate North America, follows Braun's treatment.

In addition to *Phyllactinia guttata*, mentioned above, seven other genera are each represented by one species in temperate North America: *Blumeria graminis* (DC.) Speer, cosmopolitan on grasses, *Brasiliomyces trina* (Harkn.) Zheng on *Quercus* and *Lithocarpus* in California, *Cystotheca lanestris* (Harkn.) Miyake on *Quercus* in California, *Leveillula taurica* (Lév.) Arn. on *Heliopsis* and *Prosopis* in southern regions, *Pleochaeta polychaeta* (Berk. & Curtis) Kimbrough & Korf on *Celtis* in southern USA, *Typhulochaeta couchii* (Solheim, Eboh & McHenry) U. Braun on *Quercus* in Arizona, *Uncinuliella flexuosa* (Peck) U. Braun on *Aesculus* in eastern North America. In addition, *Arthrocladiella mougeotii* (Lév.) Vassilkov, on *Lycium* species, has been introduced into North America (Braun 1987); *Sawadaea bicornis* (Wallr.: Fr.) Homma is known on *Acer macrophyllum* Pursh from coastal British Columbia (e.g., collections UBC 827, 1488, 1885, 1888).

#### Key to Genera of Erysiphaceae

1. Mycelium partly endophytic; anamorphs belonging to *Oidiopsis*, *Ovulariopsis* or *Streptopodium*; ascomata over 150  $\mu$ m diam, containing two to several asci.....2
1. Mycelium external only; anamorphs belonging to *Oidium*; ascomata varied in size, containing one or two to several asci.....4
2. Appendages mycelial; anamorph *Oidiopsis*.....*Leveillula*
2. Appendages not mycelial.....3
3. Appendages bristlelike with bulbous base, equatorial; anamorph *Streptopodium*.....*Phyllactinia*
3. Appendages uncinulate at apex, lacking bulbous base, in ring toward apex; anamorph *Ovulariopsis*.....*Pleochaeta*
4. Ascomata bearing clavate gelatinizing cells but not true appendages.....*Typhulochaeta*
4. Ascomata bearing appendages.....5



5. Ascomata minute or small, containing single ascus; conidia catenate, containing fibrosin bodies.....6
5. Ascomata small to medium sized, containing two to several asci; conidia neither catenate nor containing fibrosin bodies.....8
  6. Peridium composed of two layers, the outer peeling away; appendages mycelial.....*Cystotheca*
  6. Peridium not composed of separable layers; appendages mycelial or dichotomously branched at tips.....7
7. Appendages mycelial.....*Sphaerotheca*
7. Appendages dichotomously branched at tips....*Podosphaera*
  8. Appendages mycelial, sparse, lacking at times.....
  8. Appendages mycelial or dichotomously branched or uncinulate at apex.....9
9. Appendages mycelial.....10
9. Appendages dichotomously branched or uncinulate at apex.11
  10. Ascomata over 150  $\mu$ m diam; primary mycelium white, secondary mycelium pigmented; haustoria digitate in epidermal cells of grasses.....*Blumeria*
  10. Ascomata minute, small or medium; primary mycelium only; haustoria neither digitate nor in grasses.....
  - .....*Erysiphe*
11. Appendages dichotomously branched at apex..*Microsphaera*
11. Appendages not branched but uncinulate or circinate at apex.....12
  12. Ascomata bearing both uncinulate median and apical short bristlelike appendages.....*Uncinuliella*
  12. Ascomata bearing only uncinulate appendages.....
  - .....*Uncinula*

*Meliolales* Gumann ex Hawksworth & O. Eriksson, Syst. Ascomyc. 5: 180. 1986; Gumann, Die Pilze, Ed. 2: 158. 1964, nom. inval., ICBN, Art. 36.

Ascomata superficial on dark mycelium, globose or sphaeroid, small or medium; apex rounded, pore minute, at times composed of short setae, ostiole periphysate; peridium narrow, externally of dark, pseudoparenchymatous cells, internally of pallid rows of compressed cells, surface roughened by protruding cells or setae at times; mycelium relatively coarse, brown, forming a network, bearing setae at times, producing hyphopodia: capitate appressed to substrate and forming a narrow hypha producing an haustorium within host cell, mucronate directed upward, opening as phialides at times. Asci unitunicate, basal, oblong, ellipsoid or subglobose, mostly two (three or four) spored at maturity; wall thin, lacking apical ring, deliquescent. Paraphyses lateral, few, wide, deliquescent. Ascospores brown, ellipsoid, subfusoid or oblong, often inequilateral, three or four septate, usually constricted at septa; wall smooth, often surrounded by narrow gel coating; one globule per cell; in fascicle in the ascus.

Anamorphs not known beyond ephemeral phialoconidia.

Biotrophic on leaves, stalks, twigs, mostly tropical in distribution.

One family:

**Meliolaceae** Martin ex Hansford, Mycol. Pap. 15: 23. 1946.

In North America four genera of Meliolaceae are recognizable and are separated in the following key. Most taxa of the "black mildews" develop in tropical regions. Hansford's (1961) monograph is a detailed study in which five genera (including the extralimital *Amazonia*) are recognized and a multitude of species (1,800) is arranged by host family and genus. Additional taxa have since been added to the family. Hughes (1981) observed that the mucronate hyphopodia in a number of species serve as phialides, the conidia probably functioning as spermatia.

The genus *Diporotheca* (Gordon and Shaw 1960) does not belong in the Meliolaceae (Luttrell 1989). The mature ascoma differs in shape from that of meliolaceous fungi, ascospores are two septate with a large central cell and two smaller terminal cells; the subterranean habit is another deviation from meliolaceous fungi. The developmental study of *D. rhizophila* Gordon & Shaw (Gordon and Shaw 1964) shows a number of features that are similar to development in members of the Ceratostomataceae (e.g., *Melanospora zamiae* Corda, Doguet 1955), although phialides are lacking and the initial is not coiled. According to the thick-walled septate ascospores with terminal germ pores, this genus could be a member of the Lasiosphaeriaceae in the Sordariales.

The precisely detailed study by Luttrell (1989) of morphology in *Meliola floridensis* Hansford leaves no doubt that the asci are indeed unitunicate and that meliolaceous fungi are quite different from the Erysiphaceae and from any Loculoascomycetes to which they have been compared.

#### Key to Genera of Meliolaceae

1. Mycelial setae present.....*Meliola*
1. Mycelial setae lacking.....2
  2. Ascomata bearing setae.....*Irenopsis*
  2. Ascomata lacking setae.....3
3. Ascomata bearing larviform appendages.....*Appendiculella*
3. Ascomata lacking larviform appendages.....*Asteridiella*

**Diaporthales** Nannfeldt, Nova Acta Regiae Soc. Sci. Upsal. ser. 4, 8(2): 53. 1932.

Valsales Nannfeldt, Nova Acta Regiae Soc. Sci. Upsal. ser. 4, 8(2): 54. 1932.

Stromatic tissues lacking or present, when present prosenchymatous and at times with included substrate cells (pseudostroma) or pseudoparenchymatous, forming clypeus,

surrounding and thickening beak or compact, containing several ascomata, at times forming blackened ventral and/or dorsal marginal zones, at times forming ectostromatic disc. Ascomata immersed to erumpent, rarely superficial, in various configurations in stromata or substrate, separate or gregarious, globose or sphaeroid, perithecioid, small to large; apex central or lateral to eccentric, usually beaked, papillate at times, ostiole periphysate; peridium narrow, two layered, externally of thin-walled, brown, somewhat compressed cells, often appearing as *textura epidermoidea* in surface view, internally of few rows of pallid, compressed cells. Asci unitunicate, peripheral or basal, ellipsoid, oblong, inflated, clavate or cylindric, loosening from subhymenium and floating freely in centrum, rarely remaining attached, mostly octosporous, some polysporous or with fewer than eight ascospores; apical ring refractive, shallow or deep, chitinous, nonamyloid. Paraphyses lacking at maturity, remnants of short rows of cells, filaments or centrum cells remaining at times. Ascospores hyaline, yellowish or brown, variable in shape and septation, symmetric or asymmetric.

Anamorphs mostly coelomycetous; conidiomata acervular, pycnidial or stromatic; conidiogenous cells enteroblastic phialidic or holoblastic determinate or proliferating percurrently, rarely hyphomycetous with phialidic conidiogenous cells; conidia variable in pigmentation, shape and septation.

Hemibiotrophic or biotrophic, at times saprobic, in tissues of vascular plants.

Several authors have segregated families in the Diaporthales to utilize various criteria: stromatic tissues, arrangement of ascomata in the stroma or substrate, ascospore characteristics, for example allantoid and nonallantoid. Nannfeldt (1932) in fact placed so much importance on the latter characteristic that he proposed two orders, Diaporthales and Valsales, an extension of von Höhnelt's (1917) subfamilies Eu-Diaportheen and Valseen in the Diaporthaceae. The Diaporthaceae and Valsaceae were recognized in the Diaporthales by von Arx and Müller (1954) and Gümman (1964). Later, Müller and von Arx (1962, 1973) united these families as the Diaporthaceae in the Sphaeriales, as did Munk (1957), Dennis (1968), Kobayashi (1970). Wehmeyer (1975) separated three families in the Diaporthales: the allantoid-spored Valsaceae, the non-allantoid-spored Gnomoniaceae for nonstromatic and Diaporthaceae for stromatic taxa. Barr (1978) utilized as well as ascoma and beak position thin or firm wall of ascospores, and arranged the genera in four families, without special emphasis on allantoid ascospores. O. Eriksson and Hawksworth (1988b) accepted these families and included the Melogrammataceae, which is here referred to the Xylariales. More recently (O. Eriksson and Hawksworth 1990) they accepted only the Melanconidaceae and Valsaceae, following

Cannon (1988). Monod (1983) accepted the allantoid-spored Valsaceae and the Gnomoniaceae and Diaporthaceae, separating the latter two by substrate and absence or presence of stromatic tissues. He also included the Endoxylaceae, where asci remain in a hymenium, following von Arx (1951, as Phomatosporaceae). Vasilyeva (1987) recognized the Gnomoniaceae and Valsaceae, for nonstromatic or slightly stromatic and stromatic taxa respectively. In addition, she separated the Sydowiellaceae as a family of the Ceratostomatales; she, like Monod, did not believe that *Sydowiella*, because of more persistent attachment of ascus bases, could be retained in the Diaporthales.

Cannon (1988) proposed merging the Phyllachorales with the Diaporthales, and recognized three families: Valsaceae (including Gnomoniaceae), Melanconidaceae (including Pseudovalsaceae and Melogrammataceae), and Phyllachoraceae. Cannon argued that details of the centrum are not well known, which is indeed true in many taxa throughout the pyrenomycetes, and that the differences that have been described between diaporthaceous and phyllachoraceous taxa may not be significant. I must disagree, for despite lack of information in development in many, the aspects of mature centra differ. The members of the Phyllachoraceae exhibit free-ended paraphyses, narrow or wide, that are at times deliquescent, as do other taxa in the Xylariales, where this family once again finds a home. The asci are thin walled and often deliquesce at maturity, but they do not separate from the subhymenium to float freely in the centrum as do those of the majority of Diaporthales. The studies on development in *Diaporthe phaseolorum* (Cooke & Ellis) Sacc. by Jensen (1983) and Uecker (1989), who used a timed sequence, show the presence of short paraphyses in early stages. These disappear at maturity and the asci become freed into the centrum.

The arrangement of families followed here accepts the Valsaceae for taxa whose ascospores are allantoid, thin walled and hyaline. Additional separating characteristics are the consistent formation of stromatic tissues (except in the recently described *Paravalisa indica* Ananthapadmanaban, 1990) and the *Cytospora* or related anamorphs, where the conidiomata are stromatic, conidiogenous cells are phialidic and conidia are hyaline, minute, one celled or one septate. Two families having nonallantoid ascospores each show a range in formation of stromatic tissues and in positions of ascomata. The taxa whose ascospores are hyaline or yellowish and thin walled, amerosporous, apiosporous, didymosporous or scolecosporous, in numerous readily detached asci, are grouped in the Gnomoniaceae which again includes the Diaporthaceae. Some of the genera are nonstromatic, others stromatic. Their anamorphs are coelomycetous, acervular or stromatic, rarely hyphomycetous, conidiogenous cells are enteroblastic phialidic or less often holoblastic proliferating percurrently and conidia are hyaline, one celled or few septate. The taxa

whose ascospores are hyaline or brown and firm walled, amerosporous, didymosporous, phragmosporous or dictyosporous, in relatively fewer asci that may detach late from the subhymenium, are grouped in the Melanconidaceae including the Pseudovalsaceae. Some sort of stromatic tissues are formed in all of the taxa in this family. Their anamorphs are coelomycetous also, conidiogenous cells may be enteroblastic phialidic or holoblastic determinate or proliferating percurrently and conidia vary more in pigmentation and septation.

#### Key to Families of Diaporthales

1. Ascospores allantoid, hyaline, thin walled, one celled; ascomata in various configurations in stromatic tissues; anamorphs coelomycetous, stromatic, conidiogenous cells enteroblastic phialidic, conidia hyaline, one celled or one septate.....Valsaceae
1. Ascospores nonallantoid, hyaline or pigmented, thin or firm walled, one celled or septate; ascomata in various configurations, separate in substrate or in stromatic tissues; anamorphs coelomycetous (rarely hyphomycetous), acervular, pycnidial or stromatic, conidiogenous cells enteroblastic phialidic or holoblastic determinate or proliferating percurrently, conidia hyaline or pigmented, one celled or septate.....2
2. Ascospores hyaline or nearly so, thin walled, amerosporous, apiosporous, didymosporous or scolecosporous; conidia hyaline or nearly so, one celled or one or few septate.....Gnomoniaceae
2. Ascospores hyaline or pigmented, firm walled, amerosporous, didymosporous, phragmosporous or dictyosporous; conidia hyaline or pigmented, one celled or one or several septate.....Melanconidaceae

**Gnomoniaceae** Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 570. 1886.

Diaporthaceae von Höhnelt, Ber. Deutsch. Bot. Ges. 35: 631. 1917.

Stromatic tissues lacking or present, prosenchymatous or pseudoparenchymatous, slightly developed as clypeus or blackened area over one or few ascomata, or as ectostromatic disc and/or immersed stroma, sometimes mixed with substrate cells (pseudostroma) or entirely fungal, at times delimited by dark ventral or dorsal marginal zones. Ascomata immersed, becoming erumpent at times, separate and upright or horizontal or in eutypelloid, valsoid or diatrypelloid configurations; sphaeroid or globose, small to medium; apex beaked or at times papillate, central, oblique or lateral, narrow or wide, ostiole periphysate; peridium narrow. Asci oblong, ellipsoid or cylindric, numerous, floating free in centrum at maturity, mostly octosporous; apical ring narrow or wide, refractive, usually chitinous.

Ascospores hyaline or yellowish, ellipsoid, fusoid, ob-ovoid, oblong or elongate to filiform, one celled, apiosporous, one septate or several delicate septa when elongate; wall thin, usually smooth, verruculose at times, at times bearing terminal appendages; two or three globules per cell; overlapping biserial or crowded or in one or two fascicle(s) in the ascus.

Anamorphs coelomycetous, acervular or stromatic, rarely hyphomycetous; conidiogenous cells enteroblastic phialidic or holoblastic proliferating percurrently; conidia hyaline, one celled or one or few septate. Described as: *Amphicytostroma*, *Asteroma*, *Chondroplea*, *Cryptosporium*, *Cylindrogloeum*, *Cylindrosporella*, *Depazea*, *Diplodina*, *Discella*, *Discosporium*, *Discula*, *Disculina*, *Endothiella*, *Fusicoccum*, *Gloeosporidium*, *Gloeosporium*, *Libertina*, *Marssoniiella*, *Marssonina*, *Mazzantiella*, *Monostichella*, *Neobarclayella*, *Paramazzantiella*, *Phialophora*, *Phomopsis*, *Polynema*, *Septogloeum*, *Septomyxa*, *Sporonema*, *Zythia*.

Hemibiotrophic or biotrophic, at times apparently saprobic, in leaves, petioles, herbaceous stems, monocot culms or woody branches.

Two scolecosporous genera are removed from Barr's (1978) concept, *Linocarpon* and *Plagiosphaera*. Representatives of both are saprobic, lack superficial hyphopodiate mycelium (Walker 1980), and asci remain attached to the subhymenium, in contrast to species of *Gaeumannomyces*. Species of *Linocarpon* usually develop in members of Palmae; the ascomata are separate beneath a clypeus and are surrounded by some stromatic tissues. The filiform ascospores contain numerous refringent septum-like bands and bear short terminal gelatinous appendages; a *Phialophora* anamorph is known (Hyde 1988, Samuels, personal communication). Monod (1983) pointed out that *Linocarpon* has many features in common with *Ophiodothella* in the Phyllachoraceae. The anamorph to Samuels (personal communication) suggests disposition in the Lasiosphaeriaceae (Sordariales), but teleomorph features are those of the Hyponectriaceae (Xylariales), where I now arrange *Linocarpon*. Some species or collections in *Plagiosphaera* have a subapical globule in the ascus, others show a distinctively tapered, geniculate base to the ascospores; both of these features occur in the Sordariales, especially in the Lasiosphaeriaceae, and redistribution to that family seems logical.

With the exception of allantoid-spored taxa, the majority of genera that Barr (1978) had in families Gnomoniaceae and Valsaceae are incorporated here under the Gnomoniaceae. Walker (1980) recognized two other species in *Gaeumannomyces* beyond *G. graminis* (Sacc.) von Arx & Olivier with three varieties: *G. caricis* Walker and *G. cylindrosporus* Hornby et al. He provided a detailed survey of the *Phialophora* anamorphs and a discussion on

hyphopodia. Another species on Poaceae, *G. incrustans* Landschoot & Jackson, is heterothallic (Landschoot and Jackson 1989a).

Monod (1983) did not recognize the presence of clypeal tissues as valid to separate genera, and under *Gnomoniella* included *Sphaerognomonia*, under *Gnomonia* included *Ditopella*, *Clypeoporthes*, *Ditopellopsis*, under *Plagiostoma* included *Plagiophiale*. He also chose to lectotypify *Plagiostoma* Fuckel by *P. devexum* (Desm.) Fuckel, because he questioned the position of the beak in *P. euphorbiae* (Fuckel) Fuckel, which is the lectotype species according to von Höhnelt (1917) and Farr et al. (1979). His detailed study of type specimens resulted in separation of a number of North American taxa that had been placed under some European names. Monod and Ziegler (1983) utilized numerical taxonomy for the rearrangement of genera and species in the Gnomoniaceae. Still other North American species await description. The study of *Gnomoniella fraxini* Redlin & Stack and its anamorph (Redlin and Stack 1988) provides an excellent example for investigators to follow.

The separation of *Cryphonectria* and *Endothia* (Barr 1978) is based upon characteristics of stroma and configuration of ascomata as well as those of ascospores. This separation is further confirmed by species responses to exposure to certain fungitoxicants (Micales and Stipes 1986), although Roane (1986) prefers to merge these names under *Endothia*. In addition to studies on morphology and cultural characteristics, Hodges et al. (1986) utilized protein and isoenzyme analysis to prove conspecificity of *Cryphonectria cubensis* (Bruner) Hodges on *Eucalyptus* and *Endothia eugeniae* (Nutman & Roberts) Reid & Booth on *Eugenia* and other plants, with a pantropical distribution for the species.

Vasilyeva (1987) erected *Apiothecium* for *A. vepris* (DeLacr.) Vasilyeva, an apiosporous taxon hitherto placed in *Cryptodiaporthe*, and earlier disposed in *Apioporthella*, once again in use. Reid and Booth (1987) monographed the species of *Winterella* Kuntze 1898 (non Berlese 1894), the earlier name for *Cryptospora* Tulasne & C. Tulasne 1863, non Kar. & Kiril. 1842 and for *Ophiovalsa* Petrak 1966. They assigned the known anamorphs to *Disculina*, whose conidia are elongate to falcate, produced in open layers in the ectostroma and whose conidiogenous cells under the light microscope appear to be enteroblastic phialidic. Reid and Booth (1989) determined too that *Cryptosporella hypodermia* (Fr.) Sacc., the type species of that genus, differs from other species assigned to *Cryptosporella* by dark or dull pigmented stromatic disc, by fusoid, thin-walled ascospores, and by the *Disculina* anamorph, and is more appropriate as a species of *Winterella*. As a consequence, *Cryptosporella* becomes another synonym of *Winterella*. Reid and Booth (1989) utilized *Wuestneia* and erected additional genera for other "*Cryptosporella*" species, placed here in the Melanconidaceae. One of the segregate genera,

*Kensinjinia* with *K. umbrina* (Jenkins) Reid & Booth, has thin-walled ascospores and is included under the Diaporthaceae. Uecker (1988) provided an extensive listing of names published in *Phomopsis*, with notes on nomenclature, morphology, biology, and on the connections made or suggested to various species of *Diaportha*.

#### Key to Genera of Gnomoniaceae

1. Ascospores one celled.....2
1. Ascospores septate or scolecosporous.....8
  2. Stromatic tissues lacking, in leaves....*Gnomoniella*
  2. Stromatic tissues present in some degree, in leaves, herbaceous stems, rarely woody branches.....3
3. Stromatic tissues prosenchymatous, forming clypeus over single ascoma or blackening surface over one or several ascomata.....4
3. Stromatic tissues pseudoparenchymatous, surrounding one or few ascomata.....6
  4. Clypei small, over apex of single ascoma, in leaves.....*Sphaerognomonia*
  4. Clypei larger, blackened over several ascomata, in herbaceous stems.....5
5. Ascomata upright, apex central, in herbaceous stems or fern rachises.....*Diaporthopsis*
5. Ascomata oblique or horizontal, apex oblique or lateral, in herbaceous stems.....*Clypeoporthella*
  6. Beaks relatively short or lacking; cells of stromatic tissues thick walled and sclerotial, in herbaceous stems.....*Mazzantia*
  6. Beaks narrow; cells of stromatic tissues thin walled, in leaves or woody branches.....7
7. Beaks elongate, narrow, erumpent from stromatic tissues around one or few ascomata, in leaves.....*Mamianiella*
7. Beaks barely erumpent from stromatic tissues, ascomata in diatrypelloid configuration, in woody branches.....*Kensinjinia*
8. Ascospores apiosporous (lower cell less than one third length of ascospore).....9
8. Ascospores not apiosporous (if septum submedian, lower cell one third or more length of ascospore)...15
9. Stromatic tissues lacking; in leaves.....10
9. Stromatic tissues present in some degree; in leaves or branches.....11
  10. Ascomata upright, apex central.....*Apiognomonina*
  10. Ascomata oblique or horizontal, apex oblique or lateral.....*Apioplagiostoma*
11. Stromatic tissues prosenchymatous.....12
11. Stromatic tissues pseudoparenchymatous.....14
  12. Stromatic tissues forming ectostromatic disc; ascomata in valsoid configuration, beaks converging, in woody branches.....*Apioporthella*



12. Stromatic tissues forming separate clypeus over single ascoma or blackening surface over one or several ascomata, in leaves.....13
13. Ascomata upright, apex central.....*Stegophora*
13. Ascomata oblique or horizontal, apex oblique or lateral.....*Hypospilina*
14. Ascomata solitary or few, upright in stromatic tissues, in leaves.....*Mamiania*
14. Ascomata in diatrypelloid configuration in stromatic tissues, in branches.....*Anisogramma*
15. Ascospores ellipsoid or fusoid, one (rarely more) septate (median or submedian or supramedian).....16
15. Ascospores elongate fusoid or cylindric, septate or not.....24
16. Stromatic tissues lacking, in leaves or herbaceous stems.....17
16. Stromatic tissues present in some degree, in monocot culms, stems, petioles, twigs or woody branches.....18
17. Ascomata upright, apex central.....*Gnomonia*
17. Ascomata oblique or horizontal, apex oblique or lateral.....*Plagiostoma*
18. Stromatic tissues prosenchymatous.....19
18. Stromatic tissues pseudoparenchymatous.....23
19. Ascomata in eutypelloid configuration, in monocot culms, herbaceous stems or woody branches.....20
19. Ascomata in valsoid configuration. in woody branches...21
20. Ascomata upright, apex central, usually separate beneath blackened surface, in monocot culms.....*Clypeoportha*
20. Ascomata upright or oblique, apex central, inclined or lateral, separate or grouped, in herbaceous stems or woody branches.....*Diaporthe*
21. Ectostromatic and entostromatic tissues well developed, brightly pigmented (yellowish, greenish, gray to light brown).....*Cryphonectria*
21. Entostromatic tissues dull brown.....22
22. Entostromatic tissues poorly developed, ectostromatic disc usually well developed.....*Cryptodiaporthe*
22. Entostromatic and ectostromatic tissues well developed.....*Amphiportha*
23. Ascomata separate, apices surrounded by stromatic tissues, in twigs or herbaceous stems.....*Ditopelopsis*
23. Ascomata in diatrypelloid configuration in well-developed stromatic tissues, in woody branches.....*Diaporthella*
24. Stromatic tissues lacking, in leaves.....25
24. Stromatic tissues present in some degree, in leaves, monocot culms or woody branches.....26
25. Ascomata upright, apex central.....*Ophiognomonina*
25. Ascomata oblique or horizontal, apex oblique or lateral.....*Pleuroceras*

26. Ascomata in diatrypelloid configuration in pseudoparenchymatous stromatic tissues, in woody branches.....*Sillia*
26. Ascomata separate or gregarious in prosenchymatous stromatic tissues, in monocot culms, leaves or woody branches.....27
27. Ascomata upright beneath blackened surface, in monocot culms.....*Gaeumannomyces*
27. Ascomata horizontal or inclined, in leaves or woody branches.....28
28. Ascomata single, horizontal with lateral beak, in leaves.....*Linospora*
28. Ascomata in valsoid configuration, beaks erumpent through ectostromatic disc, in woody branches.....*Winterella*
- Valsaceae Tulasne & C. Tulasne, Sel. Fung. Carp. 1: 180. 1861.

Stromatic tissues prosenchymatous or pseudoparenchymatous, forming ectostromatic disc and/or immersed stroma, at times delimited by blackened marginal zone. Ascomata in eutypelloid, valsoid or diatrypelloid configuration, sphaeroid or globose, small to medium; apex beaked, reaching or extending beyond surface, wide, ostiole periphysate; peridium narrow. Asci ellipsoid or oblong, octosporous or polysporous, occasionally less than eight; apical ring narrow, refractive, usually chitinous. Ascospores hyaline, allantoid or almost straight and oblong at times, one celled; wall thin, smooth; two or three globules or guttulate; overlapping biseriate or crowded in the ascus.

Anamorphs coelomycetous, stromatic; conidiogenous cells enteroblastic phialidic; conidia hyaline, one celled. Described as: *Calopactis*, *Cytophoma*, *Cytospora*, *Endothiella*, *Leucocytospora*.

Hemibiotrophic or biotrophic in woody branches.

Spielman (1985) monographed the species of *Valsa* that occur on woody angiosperms in North America. She recognized six species and reduced many names to synonymy. Their anamorphs in *Cytospora* develop in differing configurations in stromatic tissues. *Valseutypella* now has a second species, *V. multicolis* Checa et al. (Checa et al. 1986) and both species have *Cytospora* anamorphs (Checa and Martinez 1989).

#### Key to Genera of Valsaceae

1. Stromatic tissues prosenchymatous.....2
1. Stromatic tissues pseudoparenchymatous.....5
2. Ascomata in eutypelloid configuration, substrate cells often included, beaks erumpent separately or in small groups.....*Xenotypha*

2. Ascomata in valloid configuration, beaks converging and erumpent through ectostromatic disc.....3
3. Entostromatic tissues poorly developed, ectostromatic disc well developed.....*Valsa*
3. Entostromatic and ectostromatic tissues well developed.4
  4. Asci octosporous.....*Leucostoma*
  4. Asci polysporous.....*Valsella*
5. Stromatic tissues brightly pigmented.....*Endothia*
5. Stromatic tissues dark.....*Valseutypella*

**Melanconidaceae** Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 764. 1887.

**Massariovalsaceae** Hara, Bot. Mag. Tokyo 27: (474). 1913.

**Pseudovalsaceae** Barr, Mycol. Mem. 7: 151. 1978.

**Sydowiellaceae** Vasilyeva, Pirennonmitsety i Lokuloasko-mitsety severa Dalbnego Vostoka 210. 1987.

Stromatic tissues prosenchymatous or pseudoparenchymatous, slightly developed as clypeus over one or few ascomata or as blackened surface or well developed, at times mixed with substrate cells (pseudostroma) or delimited by dark ventral or dorsal marginal zone. Ascomata immersed or at times erumpent to superficial, separate and upright or horizontal or in eutypelloid, valloid or diatrypelloid configuration; sphaeroid or globose, medium to large; apex papillate or beaked, wide, central, oblique or lateral, ostiole periphysate; peridium narrow. Asci ellipsoid, oblong, clavate or wide cylindric, mostly octosporous, occasionally polysporous; apical ring wide or narrow, usually refractive and chitinous. Ascospores hyaline or brown, ellipsoid, fusoid or oblong, one celled, one septate or several septate, muriform in one genus; wall thickened and firm, smooth or verruculose, at times bearing appendages and/or surrounded by gel coating; two or three globules or guttulate; overlapping uniseriate, biseriate or crowded in the ascus.

Anamorphs coelomycetous, acervular, pycnidial or stromatic; conidiogenous cells holoblastic determinate or proliferating percurrently; conidia hyaline or brown, one celled or one or several septate, distoseptate in some; or conidiogenous cells enteroblastic phialidic; conidia typically hyaline, one celled. Described as: *Coryneum*, *Cytosporina*-like, *Harknessia*, *Hendersoniopsis*, *Hendersonula*, *Melanconiopsis*, *Melanconium*, *Phoma*-like, *Phomopsis*, *Rabenhorstia*, *Stegonsporium*, *Stilbospora*.

Hemibiotrophic or biotrophic in woody substrates or leaves or herbaceous stems.

A citation inadvertently missed by Barr (1978) is that of LaFlamme (1976), who erected *Melanamphora* to accommodate *M. spinifera* (Wallr.) LaFlamme, a species that differs from species of *Pseudovalsa* especially in elongate, oblong ascospores and in anamorph.

*Phragmoporthe* in the sense of Monod (1983) included the species of *Magnaporthe*, *M. salvinii* (Cattaneo) Krause & Webster and *M. grisea* (Hebert) Barr, that are more suitably assigned to the Hyponectriaceae of the Xylariales (Barr 1977). Rogers (1984b) recognized *Caudospora taleola* (Fr.) Starb. as representing a separate genus, related to *Diaporthe leiphaemia* (Fr.) Sacc. var. *raveneliana* (Thümen & Petrak) Wehm., which is assigned to *Amphiportha* (Barr 1978) in the Gnomoniaceae. Both species have verruculose ascospores, but *C. taleola* produces median as well as terminal appendages. Rogers also compared *Hercospora tiliiae* (Pers.: Fr.) Fr., whose ascospores are smooth walled and lack appendages. Glawe (1985b) described the anamorph of *Hapalocystis berkeleyi* Auersw. in Fuckel as *Phoma*-like with integrated phialidic conidiogenous cells.

Vasilyeva (1987) removed *Plagiophiale* to the Cainiaceae, which she assigned to the Sordariales, and *Sydowiella* to its own family Sydowiellaceae in the Ceratostomatales. The Cainiaceae, typified by *Cainia*, has many attributes of the Amphisphaeriaceae in the Xylariales. The Ceratostomatales is not recognized here, for *Ceratostoma* is a rejected name replaced by *Melanospora*, and that genus is a member of the Sordariales. (*Lentomita*, the only genus Vasilyeva listed in the Ceratostomataceae in her study, is a synonym of *Chaetosphaeria*, also in the Sordariales.) Monod (1983) had also excluded *Sydowiella* from his concept of the Gnomoniaceae, citing lack of stromatic tissues. These tissues are compact and surround single ascomata according to my interpretation. Neither species formed anamorphs in culture: *S. fenestrans* (Duby) Petrak produced ascomata and *S. depressula* (Karsten) Barr remained sterile (Monod 1983).

For the species formerly in *Cryptosporiella* that differ from *Winterella* in the Gnomoniaceae by brightly pigmented stromatic disc, ellipsoid, firm-walled ascospores and other anamorphs, *Wuestneia* is an available name (Holm 1975, Ananthapadmanaban 1988, Reid and Booth 1989). Reid and Booth (1989) provided a key and descriptions of the species that they accepted in *Wuestneia*. Further, they erected five new genera to accommodate five species that are clearly separable from *Wuestneia*. Four of these belong in the Melanconidaceae: *Wehmeyera acerina* (Wehm.) Reid & Booth and *Mebarria thujina* (Nag Raj & DiCosmo) Reid & Booth are North American, whereas *Keinstrichia megalosperma* (Kirschst.) Reid & Booth is known from Germany and *Kapooria musarum* (Kapoor) Reid & Booth from India. Some amero-sporous species that develop separately or few beneath a clypeus in leaves and petioles, foliicolous counterparts of *Wuestneia*, are to be separated (Reid, personal communication). For some tropical taxa whose ascomata are erumpent to superficial, separate, bearing scaly remnants of stromatic tissues, papillate rather than beaked, and ascospores one celled, another genus will be needed. *Gnomoniella destruens* Barr & Hodges is one of the species.

A new genus is not proposed here, for the species known are all extralimital.

# Key to Genera of Melanconidaceae

1. Ascospores one celled.....2
1. Ascospores septate.....5
  2. Stromatic tissues prosenchymatous, ascomata separate or in valsoid configuration, in woody branches...3
  2. Stromatic tissues pseudoparenchymatous, ascomata separate or grouped in valsoid configuration, in leaves or woody branches.....4
3. Ascospores hyaline, ellipsoid.....*Wuestneia*
3. Ascospores dark brown, globose or broadly ellipsoid....
  - .....*Mebarria*
  4. Ascomata separate or few, beaks thickened by stromatic tissues, in leaves.....*Dicarpella*
  4. Ascomata grouped beneath dark ectostromatic disc fused to beaks, in woody branches.....*Wehmeyera*
5. Ascospores one septate; in leaves, petioles, stems or woody branches.....6
5. Ascospores several septate; in woody branches.....16
  6. Stromatic tissues prosenchymatous.....7
  6. Stromatic tissues pseudoparenchymatous.....13
7. Ascomata separate beneath clypeus, in herbaceous stems.....*Plagiophiale*
7. Ascomata grouped, in woody branches.....8
  8. Ascomata in eutypelloid configuration.....
    - .....*Allantoportha*
    8. Ascomata in valsoid configuration.....9
9. Ectostromatic and entostromatic tissues brightly pigmented (yellowish, orange, greenish, gray brown).....10
9. Ectostromatic and entostromatic tissues dull brown....11
  10. Ascospore appendages short, narrow or pulvinate when formed.....*Melanconis*
  10. Ascospore appendages elongate, straplike.....
    - .....*Pseudovalsella*
11. Ascospores brown.....*Massariovalsa*
11. Ascospores hyaline or lightly pigmented.....12
  12. Ascospores smooth walled, lacking appendages; ostioles of ascomata fused into one.....*Hercospora*
  12. Ascospores verruculose, appendages terminal and median; ostioles of ascomata not fused into one.....
    - .....*Caudospora*
13. Ascomata separate, stromatic tissues surrounding beaks, in leaves, herbaceous stems or twigs.....14
13. Ascomata grouped in stromatic tissues, in woody branches.....15
  14. Asci octosporous.....*Sydowiella*
  14. Asci polysporous.....*Ditopella*
15. Ascospores brown, appendages short when formed.....
  - .....*Chapeckia*
15. Ascospores hyaline or lightly pigmented, appendages elongate, straplike.....*Macrodiaporthe*

16. Stromatic tissues prosenchymatous.....17  
 16. Stromatic tissues pseudoparenchymatous.....20  
 17. Ascomata in eutypelloid configuration; ascospores hyaline.....*Phragmodiaporthe*  
 17. Ascomata in valsoid configuration; ascospores brown..18  
 18. Ascospores muriform.....*Dictyoporthe*  
 18. Ascospores transversely septate.....19  
 19. Entostromatic tissues poorly developed; ascospore appendages elongate, straplike.....*Hapalocystis*  
 19. Entostromatic tissues well developed; ascospore appendages pulvinate or short and tapered.....*Prosthecium*  
 20. Ascomata separate or few, beaks thickened by stromatic tissues; ascospores hyaline....*Phragmoporthe*  
 20. Ascomata grouped in stromatic tissues; ascospores brown.....21  
 21. Ascospores ellipsoid or fusoid, often distoseptate....  
 .....*Pseudovalsa*  
 21. Ascospores elongate oblong, not distoseptate.....  
 .....*Melanamphora*

**Sordariales** Chadeffaud ex Hawksworth & O. Eriksson, Syst. Ascomyc. 5: 182, 183. 1986.

Stroma typically not produced, when formed soft pulvinate or upright stipitate or columnar, subiculum or crustose layer not infrequent, clypeal and/or stromatic tissues in some immersed taxa. Ascomata separate to gregarious, mostly superficial, bases immersed or seated beneath and erumpent from periderm, often in subiculum or on crustose layer, more rarely in stroma, small to large, perithecioid or cleistothecioid, globose, sphaeroid, ovoid, obpyriform, turbinate or dolabrate, some collabent or pinched laterally on drying; apex rounded or cleft, short papillate or beaked, tips of short setae or sulcate at times, ostiole rounded, periphysate or lined with small cells, lacking in cleistothecioid ascomata; surface glabrous or verrucose or warted, often bearing setae or hyphal appendages or conidiophores, setae short or elongate, pallid or dark, often thick walled, hyphal appendages usually septate, straight, coiled or uncinatate, smooth or roughened; peridium of two or three layers, dark or pallid, membranous or coriaceous, externally of relatively large pseudoparenchymatous cells, walls frequently containing pores (Munk pores; Nannfeldt 1975b, Fig. 2e), heavily encrusted and darkened at surface, or areolate, internally less pigmented, or peridium bombardoid, pseudobombardoid or cephalothecoid, narrow or wide, at times peridium thickened and dark above, extending outward in substrate as stromatic tissues or thickened basally and short stipitate. Asci unitunicate, basal in one or more fascicles, oblong, cylindric, inflated ellipsoid, ovoid, clavate or nearly globose, mostly octosporous, at times less than eight or polysporous; wall thin, apical ring narrow, refractive, nonamyloid or rarely amyloid, or apical ring lacking, at times subapical globule present below apical ring, at times deliquescing at maturity. Paraphyses lacking or as short

chains of cells or relatively wide, delicate, cellular structures, deliquescent in pseudoparenchymatous centrum. Ascospores hyaline, yellowish, light brown or brown to blackish, variable in shape and septation; wall smooth or variously ornamented, when pigmented often with one or more terminal germ pores or germ slit, appendaged at times, surrounded by gel coating at times; guttulate; uniseriate, biseriate, crowded or fasciculate in ascus.

Anamorphs hyphomycetous; conidiogenous cells variable, enteroblastic phialidic or tretic or holoblastic solitary or proliferating percurrently or sympodially, or basauxic and tretic; conidia various.

Mostly saprobic or hypersaprobic on plant materials, dung, moist wood, roots, in soil, etc., occasionally hyperparasitic on other fungi or hemibiotrophic on plants.

The order includes a somewhat diverse assemblage of taxa, mostly superficial saprobes whose peridium is relatively soft and composed of pseudoparenchymatous cells, whose centrum is pseudoparenchymatous at first, whose asci may be interspersed by rather broad cellular structures, or these reduced to short chains of cells or lacking. The various shapes of ascomata and their surface vestiture as well as the variations in ascospores throughout the families indicate relationships. A number of taxa in several families within the order have deliquescent asci that free ascospores within the centrum (von Arx et al. 1988, as Sphaeriales suborder Sordarinae).

The families included here are essentially those of recent classifications. I have chosen to separate the Tripterosporaceae from the Lasiosphaeriaceae, contrary to Lundqvist (1972) and O. Eriksson and Hawksworth (1987c, 1988b, 1990), for the taxa of the Tripterosporaceae typically lack an apical ring in the ascus, or the ring is nonfunctional, and the pigmented ascospores frequently possess complex appendages. I also agree that a sufficiently close relationship exists between members of the Nitschkiaceae (Coronophorales sensu Barr 1983a) and the Lasiosphaeriaceae to arrange both families in the Sordariales, following Nannfeldt (1975a, b) and others.

Species of *Camarops* (sensu lat., Nannfeldt 1972) in the Boliniaceae have small brownish, flattened ascospores with one germ pore. It has been suggested that the family is more closely allied to sordariaceous than to xylariaceous taxa. Characteristics such as immersed-erumpent stromata of various configurations, containing numerous ascomata with thin membranous peridia, numerous small, cylindrical, stipitate asci, and narrow paraphyses are not those encountered among sordariaceous taxa. The Boliniaceae does share a number of features with xylariaceous taxa, and is retained in the Xylariales in a somewhat isolated position.

The disposition of *Acanthotheciella* within the Sordariales should receive some consideration, according to the detailed study and excellent illustrations presented by

Nag Raj (1977b). The ovoid ascomata have a pseudoparenchymatous peridium, thickened below as a sterile base, the surface is tuberculate and sometimes setose, asci are basal, paraphyses are lacking, ascospores are hyaline to somewhat pigmented, scolecosporous, guttulate. Against this disposition, the anamorphs in *Ypsilonia* form urceolate to cupulate setose conidiomata, conidiogenous cells are holoblastic with percurrent proliferation, and conidia are staurosporous. The habit, forming colonies over scale insects on leaves and branches of tropical plants, would also be unusual in the Sordariales. Should *Acanthotheciella* find its home in this order, a separate family would be needed to accommodate the divergent character states that it embodies.

#### Key to Families of Sordariales

1. Asci deliquescent early, releasing one-celled, brown ascospores into centrum.....2
1. Asci typically present when ascospores mature, or ascospores hyaline when asci deliquescent.....4
  2. Ascomata cleistothecioid, globose, borne on elongate annellate base; peridium dark, carbonaceous, surface cephalothecoid; ascospores lacking germ pore .....Batistiaceae\*
  2. Ascomata perithecioid or cleistothecioid, not borne on elongate annellate base; peridium dark or light, surface cephalothecoid at times; ascospores with or lacking germ pore.....3
3. Ascomata bearing dark setae or appendages; ascospores usually with single germ pore.....Chaetomiaceae
3. Ascomata glabrous, or setae pallid; ascospores usually with two germ pores.....Ceratostomataceae
4. Ascomata immersed in soft, superficial, pulvinate stroma; ascospores hyaline to light yellowish, one celled.....Catabotrydaceae\*
4. Ascomata not immersed in soft, superficial, pulvinate stroma; ascospores variable in pigmentation and septation.....5
5. Ascospores allantoid, oblong or ellipsoid, less often elongate, fusoid or reniform, hyaline to light brown; ascomata globose, sphaeroid, turbinate or subcylindric, often with sterile base; nonostiolate, opening at times by pressure from internal cells, forming short, domelike mass or elongate (Quellkörper).....Nitschkiaceae
5. Ascospores variable in shape and pigmentation; ascomata perithecioid or cleistothecioid, variable in shape, usually lacking sterile base; lacking Quellkörper.....6
6. Ascospores brown, one celled, often compressed, with elongate germ slit, lacking germ pore.....Coniochaetaceae
6. Ascospores hyaline or brown, one celled or septate, not compressed, without germ slit, at times with germ pore(s).....7



7. Asci ellipsoid inflated, apical ring narrow and non-functional or lacking; ascospores one celled or one septate, entirely or mostly brown, often with complex appendages.....Tripterosporeaceae
7. Asci oblong or cylindric, apical ring refractive, functional, or asci subglobose and deliquescent; ascospores one celled or one or several septate, hyaline or brown, appendages when formed simple.....8
8. Ascospores brown, occasionally hyaline or yellowish, ellipsoid ovoid, one celled or one septate, with one or more germ pores, often surrounded by gel coating, not appendaged.....Sordariaceae
8. Ascospores hyaline, lightly pigmented or partially brown, shape and septation variable, lacking germ pore, gel coating when present surrounding hyaline ascospores, appendages simple when formed.....Lasiosphaeriaceae

\*Batistaceae Samuels & K. F. Rodrigues, Mycologia 81: 54. 1989.

This family was described to accommodate the neotropical *Batistia annulipes* (Mont.) Ciferri. This unique fungus forms a single, thick-walled ascoma on an annulate stipitate base. The anamorph was described recently as *Acrostroma annellosynnema* Seifert (Seifert 1987); phialidic conidiogenous cells develop from a palisade of conidiophores over the subulate-capitate synnemata. Samuels and Rodrigues (1989) obtained a *Phialophora*-like anamorph in culture from germinated ascospores prior to formation of synnemata.

\*Catabotrydaceae Petrak ex Barr, fam. nov.

Catabotrydaceae Petrak, Sydowia 8: 302. 1954, nom. inval. ICBN, Art. 36.

*Stromata superficialia mollia pulvinata; ascomata immersa globosa; rostra superficeae attingens, peridia cellulae compressae composita. Asci unitunicati oblongi, annuli apicali inamyloidei. Paraphyses cellulosae dilatatae et breviae. Ascospores hyalinae vel luteolae unicellularis ellipsoideae. Genus typicus: Catabotrys.*

*Catabotrys deciduum* (Berk. & Broome) Seaver & Waterston is a saprobe on dead leaves and stems of palms and other large monocots such as species of *Musa*. Its distribution is evidently pantropical, although records are scattered. Seaver and Waterston (1946) described and illustrated collections from Bermuda; a recent collection is from Florida (Mahogany Hammock, Everglades Nat'l Park, 16 Aug 1986, J. L. Crane and J. Schoknecht, part in MASS, now NY). The original material came from Sri Lanka (Ceylon) and the species is also known from southeast Asia (Borneo), New Caledonia [as *C. palmarum* (Patouill.) Theissen & H. Sydow], and New Zealand. Dingley (1977)

described some New Zealand collections and Samuels (personal communication) notes that the species is not uncommon in New Zealand, and that, although many attempts were made, ascospores did not germinate and no anamorph was found associated with stromata in nature. Petrak (1934) provided a detailed description and (Petrak 1954) proposed the family to accommodate the fungus. *Catabotrys* has not been assigned with any confidence to another family; validation of a separate family seems essential. The centrum appears to be similar to that in other taxa of the Sordariales.

**Sordariaceae** Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 161, 162. 1885.

Ascomata perithecioid or cleistothecioid, globose, ovoid, obpyriform or vertically elongate and dolabrate, small to medium; apex papillate, ostiole periphysate when present; surface glabrous or at times ornamented with setae or hyphal appendages, cells often protruding and surface roughened; peridium two layered, of pseudoparenchymatous cells, externally brown, internally hyaline compressed cells, at times bombardioid or forming cephalothecioid plates. Asci basal, cylindric, clavate in cleistothecioid taxa, octosporous or polysporous or less than eight; apical ring refractive, nonamyloid, chitinous, mostly functional. Paraphyses as wide, delicate structures when present, or as chains of cells. Ascospores mostly brown, at times hyaline to yellowish, ovoid, ellipsoid or subglobose, one celled or one septate, at times with hyaline basal cell; wall smooth or ornamented, often surrounded by gel coating, with one or two terminal germ pores, lacking appendages; guttulate or one globule per cell; uniseriate in cylindric asci, crowded in clavate asci.

Anamorphs hyphomycetous; conidiogenesis holoblastic, arthric or determinate, tretic, or enteroblastic phialidic. Described as *Chrysonilia*, *Cladorhinum*-like, *Diplococcium*, *Phialophora*-like, *Spadicoides*.

Saprobic in dung, seeds, branches and leaves of plants, on roots and in soil, or hyperbiotrophic on fleshy fungi.

The Sordariaceae in Lundqvist's (1972) delimitation included *Anixiella*, *Apodus*, *Boothiella*, *Copromyces*, *Diplogelasinospora*, *Gelasinospora*, *Neurospora*, *Sordaria*. Both the Fimetariaceae Griffiths & Seaver 1910 and Neurosporaaceae Cain 1961 (nom. nud.) are included in the Sordariaceae. Several genera -- *Apodospora*, *Bombardioides*, *Fimetariella*, *Jugulospora*, *Strattonia* -- are placed in this family rather than in Lundqvist's subfamily Podosporoidiae, i.e., Tripterosporaaceae, because their cylindric asci have a functional apical ring and ascospores lack elaborate appendages. Some of the genera listed above are not yet known from North America. Excellent studies have been provided by Cain (1934, 1950, 1961), Cain and Mirza (1970),

Lundqvist (1972), Guarro and von Arx (1987), von Arx et al. (1987).

The *Monilia sitophila* (Mont.) Sacc. anamorph of *Neurospora sitophila* Shear & Dodge was redescribed as the type species of *Chrysonilia* (von Arx 1981b). Conidia are arthric and separate by dehiscence of the wall around each septum and by excretion of protoplasmic strands. Similar anamorphs are known in *Diplogelasinospora* as well as in members of the Microascaceae and the Onygenales. Lodha (1987) reviewed the anamorphs reported in sordariaceous taxa.

A few of the taxa assigned to the Sordariaceae here require some explanation. *Helminthosphaeria* deviates in hyperbiotrophic habit on fleshy fungi, and as Lundqvist (1972) noted, could be separated into its own family. Parguey-Leduc (1961) studied development and ascus morphology of the type species, *H. clavarium* (Desm.) Fuckel [cited by Fuckel as *H. clavariae* (Tul. & C. Tul.) Fuckel]. The anamorph, *Spadicoides clavarium* (Desm.) Hughes, termed *Diplococcium* by Ellis (1971), forms dark, one-septate, solitary conidia terminally and laterally from polytretic, determinate conidiogenous cells that develop from conidiophores on the host fungus.

The species of *Trichodelitschia* have one-septate, brown ascospores with terminal germ pores, surrounded by a gel coating. This genus has been classified as a member of Loculoascomycetes by most mycologists (e.g., Munk 1953, Cain 1956a, Müller and von Arx 1962, Lundqvist 1964, O. Eriksson in O. Eriksson and Hawksworth 1988a), but Barr (1987b) argued against such a disposition. The asci in both *T. bisporula* (Crouan & H. Crouan) Munk and *T. munkii* Lundqvist are not bitunicate as far as I am able to determine from studies of fresh and dried examples over a number of years. The wall appears to be double, but a minute refractive apical ring is present in the apex. The wall breaks at the apex and often wrinkles down as ascospores are released; no endotunica is visible. The apical ring frequently remains attached to the gel coating surrounding the uppermost ascospore. The base of the ascus is blunt, rather than the typical footlike base seen in Loculoascomycetes. The peridium is similar to those of other taxa accepted in the Sordariaceae, and I assign *Trichodelitschia* to this family. Von Höhnelt (1920) had suggested a position in the Trichosphaeriaceae which I had tentatively accepted (Barr 1987b), but the differences in centrum and peridium do not permit such disposition.

Finally, I am assigning *Cainiella* to the Sordariaceae. This genus has been placed in the Amphisphaeriaceae (Müller 1957, Barr 1959, Müller and von Arx 1962), but it deviates in several respects from other representatives of that family. Vasilyeva (1987) assigned it to the Cainiaceae, which is a family close to the Amphisphaeriaceae. The species develop in and are erumpent from branches and leaves of arctic-alpine plants. The ascomata have a stout,

short beaklike apex and the peridium is composed of pseudoparenchymatous cells. The asci, with a conspicuous refractive, nonamyloid apical ring, are basal among wide, striplike and deliquescent paraphysis-like structures. The ascospores are hyaline to yellowish, uniseptate, and at times contain terminal germ pores. Wall ornamentation is foveolate, small pits that under the light microscope appear similar to the pitted walls in species of *Gelasinospora*, although they are much smaller.

O. Eriksson and Hawksworth (1987c) followed Farr et al. (1979), who in turn followed Theissen and H. Sydow (1915) to typify *Lizoniella* (P. Henn.) Sacc. & D. Sacc. (Syll. Fung. 17: 661. 1905) by *L. johansonii* Rehm, which is the type species of *Cainiella*. *Lizonia* subgenus *Lizoniella* P. Henn. [Hedwigia 40: (96). 1901] did not include *L. johansonii*, however, and was instead erected for *L. gastrolobii* P. Henn. and *L. oxylobii* P. Henn. Müller and von Arx (1962) designated *L. gastrolobii* as the lectotype species of *Lizoniella*, then von Arx (in Müller and von Arx 1962) transferred both species to *Microcyclus* (Loculoascomycetes). I believe that one of the original species of the subgenus must be the type of the genus, and follow Müller and von Arx in their decision. *Lizoniella* then is a synonym of *Microcyclus*. *Lizoniella johansonii* was merely the first species described (although not the first mentioned) by Saccardo and D. Saccardo when they raised Hennings' taxon to generic rank.

#### Key to Genera of Sordariaceae

1. Ascospores hyaline to yellowish, one septate...*Cainiella*
1. Ascospores brown, one celled or one septate.....2
  2. Ascospore septum median, with two terminal germ pores; ascomata setose.....*Trichodelitschia*
  2. Ascospores one celled or with one minute, hyaline cell, with one or two or cluster of germ pores; ascomata not usually setose.....3
3. Ascospores with minute, hyaline cell; germ pore apical or subapical.....4
3. Ascospores lacking minute, hyaline cell; germ pore apical or basal or both.....5
  4. Ascospore wall smooth, surrounded by gel coating...  
.....*Strattonia*
  4. Ascospore wall thickened with dark internal spots, aspect reticulate, lacking gel coating....*Jugulospora*
5. Ascospore wall smooth, with terminal germ pore and/or cluster of minute pores, surrounded by gel coating.....6
5. Ascospore wall smooth or ornamented, with one or two germ pores, lacking cluster of minute pores.....7
  6. Ascomata ovoid; peridium pseudoparenchymatous, membranous.....*Fimetariella*
  6. Ascomata vertically elongate, dolabrate; peridium tough, bombardioid.....*Bombardioida*

- 7. Ascospore wall smooth.....8
- 7. Ascospore wall ornamented.....12
  - 8. Ascospores with two terminal germ pores; hyperbiotrophic on fleshy fungi.....*Helminthosphaeria*
  - 8. Ascospores with basal or apical germ pore; not hyperbiotrophic on fleshy fungi.....9
- 9. Ascospores with basal germ pore; gel coating indented and thin over germ pore.....*Sordaria*
- 9. Ascospores with apical germ pore; gel coating lacking or continuous over ascospore.....10
  - 10. Gel coating continuous over ascospores; ascomata perithecioid.....*Apodospora*
  - 10. Gel coating lacking over ascospores; ascomata cleistothecioid.....11
- 11. Asci nearly globose, lacking refractive apical ring; ascospores one celled.....*Melanocarpus*
- 11. Asci elongate, with refractive apical ring; ascospores developing septum at times.....*Apodus*
  - 12. Ascospores warted, with one germ pore; ascomata cleistothecioid.....*Copromyces*
  - 12. Ascospores differently ornamented, with one or two germ pores; ascomata cleistothecioid or perithecioid.....13
- 13. Ascospores with platelike ornamentation, areolate.....*Emblemospora*
- 13. Ascospores differently ornamented.....14
  - 14. Ascospores with longitudinal ridges, with two germ pores.....*Neurospora*
  - 14. Ascospores with pitted walls, with one or two germ pores.....15
- 15. Ascomata perithecioid.....*Gelasinospora*
- 15. Ascomata cleistothecioid.....16
  - 16. Ascospores one celled.....*Anixiella*
  - 16. Ascospores one septate, one cell hyaline, both pitted.....*Diplogelasinospora*

*Tripterosporaceae* Cain, *Canad. J. Bot.* 34: 699. 1956, emend.

Ascomata perithecioid or cleistothecioid, globose, ovoid or obpyriform, medium; surface glabrous, setose, or bearing septate, short to elongate, hyphal appendages, setae in tufts at times; peridium membranous or tough and pseudobombardioid, cephalothecioid in some cleistothecioid taxa. Asci inflated ellipsoid or short clavate, octosporous, polysporous or less than eight; apical annulus very narrow, nonfunctional, or lacking, deliquescent at times. Paraphyses when present as wide, septate, deliquescent bands longer than asci. Ascospores partly or entirely pigmented at maturity, ellipsoid, ovoid or triangular, never cylindric nor vermiform, one celled or one septate; wall smooth or sometimes ornamented, often bearing gelatinous, ornate appendages, with one to four germ pores.

Anamorphs little known; conidiogenous cells enteroblastic phialidic. Described as *Cladorhinum*, *Phialophora*-like.

Saprobic, mostly coprophilous, some on plant debris or in soil.

The name *Podosporaceae* Hochberzanke 1930 (nom. nud.) would convey more appropriately the sense of this family, but the name *Tripterosporeaceae* was the first validated name for taxa similar in some aspects to *Podospora*. The diagnosis must be enlarged to accommodate perithecioid taxa having other attributes, for Cain (1956b) described the family to include only *Tripterospora*, that is, cleistothecioid with deliquescent asci. For the most part, this family is outlined here in the sense of Lundqvist's *Lasiosphaeriaceae* subfamily *Podosporoideae* [Symb. Bot. Upsal. 20(1): 118. 1972], and much of the information presented here is derived from his detailed descriptions and superb illustrations. Mirza and Cain (1969) presented a revision of species in *Podospora*. A close link between the *Lasiosphaeriaceae* and *Tripterosporeaceae* is obvious in peridium structure and ornamentation. The mature ascospores in taxa of the *Tripterosporeaceae* always have one (or two) pigmented cell(s) and many form most elaborate appendages in addition to a hyaline pedicellate cell.

#### Key to Genera of *Tripterosporeaceae*

1. Ascospores composed of two pigmented, smooth-walled cells, with appendages.....2
1. Ascospores composed of one pigmented cell sometimes becoming septate, smooth or ornamented, with hyaline pedicel and/or appendages present at times.....3
  2. Pigmented cells separated by elongate, hyaline, intercalary cell.....*Zygopleura*
  2. Pigmented cells constricted at septum but not separated by elongate, intercalary cell.....*Zygospermella*
3. Ascospores composed of one pigmented cell, lacking hyaline pedicel, appendaged.....4
3. Ascospores composed of one pigmented cell, with hyaline pedicel, often appendaged.....5
  4. Ascospore wall smooth.....*Arnium*
  4. Ascospore wall pitted.....*Arniella*
5. Hyaline pedicel apical, appendages lacking.....*Anapodium*
5. Hyaline pedicel basal, appendages present or lacking...6
  6. Pedicel persistent, cytoplasmic; ascomatal appendages agglutinated, forming tufts.....*Schizothecium*
  6. Pedicel usually collapsing at maturity, devoid of cytoplasm; ascomatal appendages when present not agglutinated.....7
7. Ascospores nearly triangular, pedicel about as wide as pigmented cell.....8
7. Ascospores ellipsoid or obovoid, pedicel narrower than pigmented cell.....9

8. Ascomata perithecioid; ascospores with one pigmented cell.....*Triangularia*  
 8. Ascomata cleistothecioid; ascospores with two pigmented cells.....*Zopfiella*  
 9. Ascospore wall smooth.....10  
 9. Ascospore wall ornamented.....11  
 10. Ascomata perithecioid; ascospores often bearing conspicuous, complex appendages.....*Podospora*  
 10. Ascomata cleistothecioid; ascospores lacking appendages.....*Tripterospora*  
 11. Ascospore wall with thickened dots of pigment growing inward.....*Lacunospora*  
 11. Ascospore wall with spines over surface.....12  
 12. Ascomata perithecioid.....*Apiosordaria*  
 12. Ascomata cleistothecioid.....*Echinopodospora*

**Lasiosphaeriaceae** Nannfeldt, Nova Acta Regiae Soc. Sci. Upsal. ser. IV, 8(2): 50. 1932.

Ascomata globose, sphaeroid or ovoid, at times obpyriform or turbinate, superficial or immersed becoming erumpent, small to large, separate or often gregarious to crowded; apex rounded to papillate or with short or elongate beak, papilla smooth or sulcate ribbed, at times of short setae, ostiole usually periphysate, occasionally lacking opening; surface tuberculate or smooth, bearing short or long setae or hyphal appendages or appressed tomentum, at times in subiculum, pallid to dark; peridium narrow or wide, two layered or with additional external layer, of relatively large pseudoparenchymatous cells, walls at times containing Munk pores, brown externally, some bombardioid or pseudobombardioid, apex thickened with stromatic tissues in some, internally of compressed, pallid rows of cells. Asci basal, oblong, inflated, cylindric, clavate and stipitate or subglobose and deliquescent, usually octosporous; wall thin; apical ring narrow, refractive, nonamyloid, rarely amyloid, subapical globule present at times. Paraphyses when present relatively wide, narrowed toward tips or occasionally enlarged at tips, delicate, thin walled, deliquescent. Ascospores hyaline, yellowish, pinkish, light brown, or becoming dark brown in part, cylindric, oblong, allantoid, galeate, reniform, ellipsoid, fusoid, elongate to filiform, when elongate frequently geniculate and curved in lower third, ends obtuse or tapered to acute tip, one celled or one to several septate; wall thin, smooth or finely roughened or foveolate, with terminal appendages at times, appendages narrow, elongate or short conoid or pulvinate, at times surrounded by gel coating; frequently several globules; overlapping biseriate, crowded, or in fascicle(s) in the ascus.

Anamorphs hyphomycetous; conidiogenous cells enteroblastic phialidic, phialides developing from mature ascospores, germ tubes, hyphae or conidia, or from upright

conidiophores in various configurations; or conidiogenous cells holoblastic, solitary or percurrently or sympodially proliferating; synanamorphs basauxic. Described as *Arthrinium*, *Chalara*, *Chloridium*, *Codinaea*, *Phialophora*, *Pteroonium*, etc. (see discussion below).

Saprobic or hypersaprobic, frequently on moist rotting wood or stems, culms, leaves or dung, less often hemibiotrophic.

Carroll and Munk (1964) introduced some new species of *Lasiosphaeria* by stating "We conceive this genus in its very broadest sense, ranging in spore type from the typical cylindrical, geniculate, appendaged *Lasiosphaeria* spore to a long, filiform, multiseptate spore on one hand and to a broad, allantoid, nonseptate spore with a gelatinous covering on the other. Radically different spore types may occur together with one and the same peridium type; the genus shows a marked noncorrelation of characters." Not only do ascospore and peridium types vary within the family, but so do ascoma shapes and anamorphs. Although some taxa are now separated from *Lasiosphaeria*, that genus still remains as a diverse, large, central taxon, to which others may be linked by various characteristics. I conceive the family as comprising various series of taxa, separable at the generic level by combinations of certain characteristics. It is entirely likely that additional genera will be recognized.

On the one side, the Lasiosphaeriaceae shares characteristics with the Nitschkiaceae, on the other with the Tripterosporaceae (Lasiosphaeriaceae subfam. Podosporoideae, sensu Lundqvist 1972). The presence of rather delicate, but wide and septate paraphysis-like structures and frequent germination of allantoid ascospores by phialides separate the Lasiosphaeriaceae from the Nitschkiaceae; those members of the Lasiosphaeriaceae whose ascomata are turbinate with an inconspicuous ostiole also have septate ascospores. Separation of the Lasiosphaeriaceae from the Tripterosporaceae is a matter of degree as Lundqvist recognized. Asci in the Lasiosphaeriaceae typically have a refractive, functional apical ring, whereas in the Tripterosporaceae asci have no apical ring or a narrow, nonfunctional one. Another feature in some but not all species in the Lasiosphaeriaceae is the presence of a subapical globule in the cytoplasm just beneath the apical ring. Ascospores in the Lasiosphaeriaceae are hyaline or slightly pigmented, or may become brown in part, and often germinate by phialides in addition to germ tubes, whereas in the Tripterosporaceae the ascospores are brown when mature and germinate by germ tubes. Many taxa in the latter family have elaborate appendages of various types on the ascospores, but when appendages are formed on ascospores in the Lasiosphaeriaceae they are quite simple, elongate and tapered or pulvinate or short conoid. The peridia of ascomata in both families are varied in con-



struction, layering, surface roughening and vestiture (Munk 1957, Carroll and Munk 1964, Lundqvist 1972). These features appear to be mostly of specific value, although the bombardioid peridium in *Bombardia* serves to set apart that genus, as does that of *Bombardioidea* in the Tripterosporeaceae.

Differences that appear to be sufficient to recognize genera are mostly those of ascospore shape, although ascomatal variations are also utilized. Ascospores in species of *Lasiosphaeria* show considerable variety (R. Hilber and O. Hilber 1983). Frequently they germinate directly to produce small phialides. Typically, as in *L. ovina* (Pers.: Fr.) Ces. & de Not., they are hyaline to yellowish, cylindric, often tapered to a geniculate base. They may remain one celled or become septate. Taxa whose ascospores become enlarged and pigmented in part are segregated into *Bombardia*, *Cercophora* and *Tripterosporella*. The peridium in species of *Bombardia* is extremely complex as Lundqvist (1972) explained. That in the other two genera is simpler: species of *Cercophora* may have a pseudobombardioid or a two-layered peridium and ascomata are perithecioid (R. Hilber and O. Hilber 1979), whereas in *Tripterosporella* the peridium is composed of cephalothecoid plates and ascomata are cleistothecioid. In *Herminia dichroospora* (Ellis & Everh.) R. Hilber (R. Hilber and O. Hilber 1979), the ascospores do not become enlarged but the upper portion is pigmented and septate. The ascospores of species in *Camptosphaeria* (as *Cercophora* subgenus *Camptosphaeria*, Lundqvist 1972) are hyaline and clavate when young and darken above at maturity (Krug and Jeng 1977).

Another taxon with somewhat similarly shaped ascospores to those of *Camptosphaeria* is *Apiospora*. The ascospores remain hyaline and develop a basal septum. The species form long rows of ascomata in culms of large monocots, usually thickened above by stromatic tissues. They have been assigned to the Amphisphaeriaceae (Müller and von Arx 1962) or Hyponectriaceae (Barr 1976b). Samuels (personal communication) has advanced convincing arguments that the genus is better disposed in the Lasiosphaeriaceae. The anamorphs are species of *Arthrinium* (Samuels et al. 1981), described as *Papularia* (Hudson 1963, Hudson et al. 1976) and *Pteroconium* (Ellis 1971). Conidiophores are basauxic, the polyblastic conidiogenous cells are terminal and intercalary, and conidia are brown, one celled, with a pallid slit or rim. The unusual anamorph could be explained as a condensation of a life cycle that originally had phialoconidia and *Wardomyces* or *Mammaria* aleuriospores, dark, with an elongate germ slit, hypothesized in some detail by Minter (1985). If *Chalara*-like phialoconidia in chains did not disarticulate, but instead each segment produced an aleuriospore directly, *Arthrinium* would be the result. The extralimital *Lasiobertia africana* Sivanesan (Sivanesan 1978) has an associated anamorph described as *Melanographium*-like, whose dark conidia contain a hyaline

slit and are produced on denticles from sympodially proliferating conidiogenous cells. The ascomata in *L. africana* are tuberculate and approach those of the Nitschkiaceae, but the ascospores are elongate fusoid, and the apical ring of the ascus is amyloid. Samuels (personal communication) has obtained *Mammaria echinobotryoides* Cesati, as well as a *Phialophora* synanamorph, in culture from ascospores of *Cercophora solaris* (Ellis) R. Hilber & O. Hilber.

Ascospores of other species of *Lasiosphaeria* may be oblong and allantoid. These approach the septate ascospores of *Lasiosphaeriella* (Sivanesan 1975). The tropical *Thaxteria archeri* (Berk.) Hansford also has wide allantoid, septate ascospores; the ascomata are turbinate and approach those of the Nitschkiaceae. Still other species of *Lasiosphaeria* have elongate fusoid ascospores that taper to one or both ends and are multiseptate. The ascospores of these species approach the narrow, filiform ones found in *Acrospermoides*, *Mycomedusiospora*, *Ophioceras* and *Plagiosphaera*. The pale yellow, obpyriform ascomata with gently tapered apices in *Mycomedusiospora flavida* (Rick) Carroll & Munk (Carroll and Munk 1964) are similar in shape to the blackish ascomata of *Acrospermoides subulata* Miller & Thompson (Miller and Thompson 1940); the filiform ascospores of *M. flavida* disarticulate into partspores in the ascus whereas those of *A. subulata* do not. Species of *Ophioceras* have globose ascomata and elongate beaks (Conway and Barr 1977), and those of *Plagiosphaera* have short, stout beaks. The latter genus is relocated from the Diaporthales (Barr 1978). The central or eccentric position of the beak in species of *Plagiosphaera*, stressed by Barr (1978), is not a reliable characteristic in this genus (Dennis 1975).

Ascospores that are ellipsoid, oblong or short fusoid may be one celled or septate. Species of *Iodosphaeria*, with one-celled ascospores, have peridium and centrum similar to those of other taxa in the family. The apical ring of the ascus may be amyloid, an unusual reaction in the family, but otherwise the taxa accord well. The anamorphs described (Samuels, Müller and Petri 1987) are holoblastic with denticulate conidiogenous cells (*Selenosporella*) and solitary, two- or three-armed (*Ceratosporium*). Somewhat similar anamorphs are known in *Phaeotrichosphaeria* (Sivanesan 1983), whose ascospores are one celled or septate and become brown, and in several species of *Lasiosphaeria* (Munk 1957, Hughes 1979, Shoemaker and White 1986). These species have *Endophragmiella* or *Sporidesmium* states in addition to *Selenosporella* states. An unnamed anamorph described as having enteroblastic, percurrently proliferating conidiogenous cells is associated with yet another species of *Lasiosphaeria* (O. Hilber et al. 1987). Sivanesan (1983) also described and illustrated germination of the *Endophragmiella* state of *Phaeotrichosphaeria indica* Sivanesan by phialides. The

species of *Chaetosphaerella* produce *Oedemium* anamorphs, solitary or catenate conidia from percurrently proliferating conidiogenous cells and an enteroblastic-phialidic phase is known (Hughes and Hennebert 1963, Ellis 1971). The ascospores in *Chaetosphaerella* are one or three septate, brown with hyaline ends, and the ascomata approach those of the Nitschkiaceae (Müller and Booth 1972). *Spinulosphaeria thaxteri* (Pat.) Sivanesan (Sivanesan 1974) has one-septate, brown ascospores and similar but short setose ascomata. No anamorph is known for this taxon that Sivanesan placed in the Nitschkiaceae.

Another series of taxa produces upright conidiophores on the peridia of ascomata or closely associated with ascomata. These exhibit considerable diversity in the shape and arrangement of enteroblastic-phialidic conidiogenous cells and in shape and septation of conidia (Gams and Holubová-Jechová 1976 and others); as a consequence they have been assigned to various genera such as *Catenaria*, *Chloridium*, *Custingophora*, *Cylindrotrichum*, *Codinaea*, *Gonytrichum*, *Menispora*, *Sporoschisma*, *Zanclospora*. The species of *Chaetosphaeria* (including *Zignoella*) form one to several-septate, hyaline or pallid ascospores. *Melanopsammella inaequalis* (Grove) von Höhnelt was included under *Chaetosphaeria* by Gams and Holubová-Jechová (1976), but the genus may be recognized by the one-septate ascospores that disarticulate into partspores at maturity. *Litschaueria corticiorum* (von Höhnelt) Petrak (Barr 1976a) produces a *Codinaea* anamorph; both sympodial and percurrent proliferation of phialides occur on specimens and in culture (Hughes, Rogerson, personal communications). Several extralimital genera having similar anamorphs are known. The southern hemispheric species of *Melanochaeta*, with ascospores having brown mid cells and hyaline end cells much as in *Litschaueria*, produce *Sporoschisma* anamorphs (Hughes 1966, Müller et al. 1969) and a *Chalara* synanamorph (Müller and Samuels 1982c). *Striatosphaeria codinaeaphora* Samuels & Müller (Samuels and Müller 1979a), from Brazil, has a *Codinaea* anamorph and brown, uniseptate, longitudinally furrowed ascospores. *Porosphaerellopsis sporoschismophora* (Samuels & Müller) Müller & Samuels (Samuels and Müller 1979a, Müller and Samuels 1982b), also from Brazil, has brown, three-septate ascospores with terminal germ pores and also has a *Sporoschisma*-like anamorph, although the conidia are unique in producing pores within septa and at the tips. The paraphyses are branched and netlike above the asci, unlike those of other genera in the family.

*Ceratocystis* is also inserted in the Lasiosphaeriaceae, among the group of taxa that includes *Chaetosphaeria* and *Melanochaeta*. The small, long-beaked ascomata, deliquescent asci and typically galeate ascospores of the species are distinctive and probably represent a reduction. The anamorphs are species in *Chalara*, differing from the holoblastic, sympodially

proliferating anamorphs of taxa in the Ophiostomataceae. Separation of *Ceratocystis* from *Ophiostoma* has been supported by analyses of cell-wall constituents (Jewell 1974, de Hoog 1974, Weijman and de Hoog 1975) in combination with anamorphs. Samuels and Müller (1979b) proposed that the long tubular phialides in *Ceratocystis* were similar to those in *Melanochaeta*. Von Arx (1981a, b) suggested affinities of *Ceratocystis* with *Chaetosphaeria*, but von Arx and van der Walt (1988) retained *Ceratocystis* in the Ophiostomataceae.

In a recent study on *Phragmodiscus arundinariae* Hansford, O. Eriksson and Yue (1989b) proposed that this genus also is a member of the Lasiosphaeriaceae. The fungus, known from Uganda and the Congo on culms of bamboo, forms a large, spongy subiculum in which beaked ascomata are immersed. Asci are similar to those in species of *Lasiochaeta*, as are the elongate-fusoid, several-septate ascospores.

#### Key to Genera of Lasiosphaeriaceae

1. Ascospores cylindric, oblong, elongate fusoid or allantoid, often curved and geniculate, ends obtuse or acute and tapered below to narrow pointed base, at times bearing narrow elongate terminal appendages.....2
1. Ascospores differently shaped.....5
  2. Ascospores hyaline or faintly pigmented, upper region not becoming greatly enlarged and pigmented....*Lasiochaeta*
  2. Ascospores becoming enlarged and deeply pigmented in upper region.....3
3. Peridium bombardioid, of up to five layers of cells....*Bombardia*
3. Peridium not bombardioid, of fewer layers of cells....4
  4. Peridium pseudobombardioid or two layered, of pseudoparenchymatous cells; ascomata perithecioid....*Cercophora*
  4. Peridium of cephalothecoid plates; ascomata cleistothecioid.....*Tripterosporella*
5. Ascospores cylindric, upper portion pigmented, several septate; appendages short conoid.....*Herminia*
5. Ascospores differently shaped and pigmented; appendaged or not.....6
  6. Ascospores obovoid to clavate when young, tapered to obtuse base.....7
  6. Ascospores differently shaped.....8
7. Ascospores appendaged, upper cell becoming dark, lower cell remaining hyaline.....*Camptosphaeria*
7. Ascospores not appendaged, becoming septate near base, both cells remaining hyaline.....*Apiospora*
8. Ascospores broadly allantoid, septate.....9
8. Ascospores differently shaped, septate or not.....10

9. Ascospores becoming dictyosporous, surrounded by gel coating; ascomata ovoid, short papillate...*Lasiosphaeriella*
9. Ascospores becoming phragmosporous, not surrounded by gel coating; ascomata turbinate, apex not papillate, usually in small clusters.....*Thaxteria*
10. Ascospores ellipsoid, oblong, short fusoid or galeate, one celled or septate.....11
10. Ascospores elongate filiform, several septate.....18
11. Ascomata turbinate, apex not papillate.....12
11. Ascomata globose, sphaeroid or ovoid, apex papillate or beaked.....13
12. Peridium bearing short setae; ascospores one septate, evenly brownish.....*Spinulosphaeria*
12. Peridium tuberculate; ascospores one or three septate, ends pallid.....*Chaetosphaerella*
13. Ascomata small, long beaked; ascospores galeate.....*Ceratocystis*
13. Ascomata medium sized, papillate; ascospores not galeate.....14
14. Ascospores one celled, hyaline.....*Iodosphaeria*
14. Ascospores septate or brownish or both.....15
15. Ascospores brownish, one celled or one septate; associated anamorphs holoblastic.....*Phaeotrichosphaeria*
15. Ascospores hyaline or brown, one to several septate; associated anamorphs enteroblastic-phialidic on well-developed conidiophores.....16
16. Mid cells of ascospores brown, end cells pallid; ascomata bearing short setae as well as conidiophores.....*Litschaueria*
16. Ascospores hyaline or nearly so; ascomata bearing conidiophores or glabrous with conidiophores on nearby hyphae.....17
17. Ascospores disarticulating at septum into partspores.....*Melanopsammella*
17. Ascospores not disarticulating at septum into partspores.....*Chaetosphaeria*
18. Ascomata obpyriform with tapered apex.....19
18. Ascomata globose or sphaeroid with short stout or elongate beak.....20
19. Ascomata pale yellowish, peridium wide; ascospores disarticulating into partspores.....*Mycomedusiospora*
19. Ascomata blackish, peridium relatively narrow; ascospores not disarticulating into partspores..*Acrospermoides*
20. Ascomata with stout short beak (length up to diameter of ascoma).....*Plagiosphaera*
20. Ascomata with greatly elongate beak (longer than diameter of ascoma).....*Ophioceras*

Ascomata separate or gregarious to crowded, developing beneath periderm and becoming widely erumpent or superficial on decorticated substrates, in slight or well-developed dark subiculum composed of branched, at times short or long setose hyphae; ascomata sphaeroid, globose, turbinate or subcylindric, relatively small to large, often with sterile base, often collabent on drying; apex nonostiolate; apical region with short domelike or elongate (at times to base) Quellskörper, of concentrically arranged, thin-walled cells in gel matrix; peridium of two layers, pseudoparenchymatous, relatively soft, wide, externally of brown, large cells containing Munk pores, often thickened below as short sterile stipe, internally of hyaline, thin-walled, compressed cells; surface often roughened with protruding cells or short setae or tubercles. Asci basal or lateral in fascicles, oblong or obovate, rarely cylindric, usually stipitate, octosporous or polysporous, occasionally four or two spored, deliquescent; apex thickened at times, apical apparatus faintly visible in some but apparently nonfunctional. Paraphyses lacking, rarely a few short rows of cells among asci. Ascospores mostly hyaline, light brown or grayish brown, slightly or strongly allantoid, oblong, elongate, fusoid, ellipsoid or reniform, one celled or one to several septate; wall smooth, rarely ornamented, occasionally with terminal appendages; one or two or several globules; biseriate, rarely uniseriate or in rows, often obliquely in the ascus.

Anamorphs not known.

Saprobic or hypersaprobic on branches or decorticated wood, often over other fungi, or hyperparasitic on fungi.

The Coronophoreen von Höhnelt 1907, Coronophoraceae Nannfeldt 1932 is included under the Nitschkiaceae. Fitzpatrick (1923, 1924) studied a number of taxa in the Nitschkiaceae (as a subfamily related to the Cucurbitariaceae and the Sphaeriaceae of Lindau in Engler and Prantl 1897). The numbers of genera and criteria for their separation vary in recent studies. Müller and von Arx (1973) accepted the Coronophorales as a separate order, having one family that contained 11 genera (*Acanthonitschkea*, *Bertia*, *Biciliospora*, *Calculosphaeria*, *Coronophora*, *Fracchiacea*, *Gaillardielliella*, *Nitschkia*, *Scortechiniella*, *Thaxteria*, *Tympanopsis*). They separated these genera on the presence (and amount) of subiculum, shape and presence or absence of setae on ascomata, shape, septation and appendages of ascospores, and octosporous or polysporous asci. Within the family, as within the Sordariales, polyspory seems not to be a criterion sufficient in itself to separate genera. Sivanesan (1974) added two genera (*Spinulosphaeria*, *Scortechiniellopsis*) and provided a key to 14 genera [including *Cryptosphaerella*, a name submerged by Munk (1957) under *Coronophora*]. Nannfeldt (1975a, b), in his detailed morphological and taxonomic survey, recognized three groups of taxa in the Nitschkiaceae, and placed the family in the

Sordariales, stressing its close relationship to the Lasiosphaeriaceae: 1) *Nitschkia* (including several genera that were separated earlier) and *Acanthonitschkea* with turbinate ascomata, usually collabent, small to large, with or lacking sterile base, often tuberculate; 2) *Coronophora* with subglobose to ellipsoid (sphaeroid) ascomata, not collabent, large, not thickened at base, rarely tuberculate; 3) *Bertia* with subcylindric ascomata not collabent, large, with well-developed sterile base, coarsely tuberculate and *Gaillardielliella* with globose ascomata and the peridium strongly thickened in upper regions. Nannfeldt removed *Thaxteria* and *Spinulosphaeria* to the Lasiosphaeriaceae, both having paraphyses in the centrum as well as deviating from the family concept in other features. Corlett and Krug (1984) recognized three varieties of *Bertia moriformis* (Tode: Fr.) de Not. on the bases of ascospore shape and septation and noted that the isolated position of this genus was emphasized by proposal of the illegitimate family name Bertiaceae Smyk 1981.

Von Arx (1981b) also reviewed the family. He believed that *Nitschkia* in Nannfeldt's sense was heterogeneous, and would again accept *Fracchiacea*, *Tympanopsis* and *Bicilio-spora*, and would in addition separate *Sydowinula* from *Acanthonitschkea*. I agree that several genera are recognizable as segregates from *Nitschkia* and the salient features are utilized in the following key. I have also become convinced that similarities between these genera and several in the Lasiosphaeriaceae indicate two closely related families, and that the Coronophorales cannot be upheld. Nonostiolate genera of the Lasiosphaeriaceae do possess paraphysis-like structures in the centrum, thus *Thaxteria*, *Spinulosphaeria* and *Lasiobertia* must be arranged in that family. Two lichenicolous genera, *Rhagadostoma* and *Lasiosphaeriopsis*, have been assigned to the Coronophorales (Hawksworth 1980a). These are aparaphysate, have a verrucose peridium, subcylindric ascomata, and the two- or four-spored asci have respectively hyaline, one-celled or one-septate ascospores or brown, three- to four-septate ascospores. Both have minute ostioles lined with periphyses and are not representative of the Nitschkiaceae as that family is recognized here. Other genera assigned to the Nitschkiaceae by O. Eriksson and Hawksworth (1987c, 1990) include *Botryola* Bat. & Bez. and *Groenhiella* Koch et al., and of these two I have no knowledge.

#### Key to Genera of Nitschkiaceae

1. Ascomata large, sphaeroid, not collabent, sterile base lacking; asci mostly polysporous.....*Coronophora*
1. Ascomata small to large, turbinate, globose or subcylindric, often collabent on drying, usually with well-developed sterile base; asci mostly octosporous.....2
2. Ascomata large, subcylindric, collabent or not; Quellskörper short and dome-like.....3

2. Ascomata small to large, turbinate or globose, usually collabent; Quellkörper elongate or short and dome-like.....4
3. Ascomata coarsely tuberculate, not collabent, upper part of peridium not thickened in ring; ascospores elongate, one to several septate.....*Bertia*
3. Ascomata roughened, not coarsely tuberculate, collabent, upper part of peridium thickened in ring; ascospores ellipsoid, one septate.....*Gaillardielia*
4. Ascomata and/or hyphae of subiculum bearing well-developed elongate setae; Quellkörper elongate.....*Acanthonitschkea*
4. Setae of ascomata and/or hyphae of subiculum short when formed; Quellkörper elongate or short and dome-like.....5
5. Ascospores ellipsoid to reniform, ends appendaged; Quellkörper short and dome-like.....*Biciliospora*
5. Ascospores oblong, ellipsoid or allantoid, ends not appendaged; Quellkörper short and dome-like or elongate...6
6. Ascomata small to medium sized, lacking setae; Quellkörper short and dome-like.....*Nitschkia*
6. Ascomata medium to large sized, often bearing short setae on peridium or subiculum; Quellkörper short and dome-like or elongate.....7
7. Ascomata bearing short setose warts on peridium; Quellkörper short and dome-like; asci notably polysporous (to 200); ascospores allantoid.....*Fracchiacea*
7. Ascomata bearing setose warts on peridium or short setae on hyphae of subiculum; Quellkörper elongate; asci octosporous; ascospores ellipsoid oblong.....*Tympanopsis*

**Coniochaetaceae** Malloch & Cain, *Canad. J. Bot.* 49: 878. 1971.

Ascomata gregarious or separate, superficial on substrate or stromatic crust; perithecioid or cleistothecioid, small to medium, globose, ovoid or obpyriform; apex papillate, ostiole periphysate, or apex rounded and enclosed; surface smooth or roughened by verrucae, protruding cells or simple or branched setae, areolate at times; peridium dark or pallid, of two layers, externally of pseudoparenchymatous or somewhat compressed, brown cells, internally of compressed rows of pallid cells. Asci basal or lateral in fascicles, cylindric, oblong or subglobose, persistent or deliquescent, octosporous or less than eight or polysporous; apical ring narrow, nonamyloid, rarely amyloid. Paraphyses delicate, as narrow or wide, septate strips. Ascospores light to dark brown, discoid, ellipsoid, fusoid, somewhat compressed at times, one celled; wall thickened and firm, surface smooth or ornamented, with elongate germ slit, rarely surrounded by gel coating; usually one globule; uniseriate, biseriate or crowded in the ascus.

Anamorphs hyphomycetous; conidiogenesis enteroblastic-phialidic. Described as *Phialophora*-like, *Verticillium*.



Saprobic on woody and herbaceous plant parts, in dung, isolated from roots and soil.

When it was erected, the family included only *Coniochaeta* and the cleistothecioid *Coniochaetidium* (Malloch and Cain 1971c). The species of *Coniochaeta* that are known in culture were surveyed by Hawksworth and Yip (1981). Most of these produce phialidic conidia, but *C. nodulisporioides* Hawksworth forms holoblastic *Nodulisporium*-like conidia and the species probably does not belong in *Coniochaeta*. Mahoney and LaFavre (1981) summarized information on growth habit, ascoma and ascus morphology, ascospore size and shape in species of *Coniochaeta*. Checa et al. (1988) provided descriptions, illustrations, and a key to a number of Spanish taxa that should prove valuable for identification in other regions as well. Müller and von Arx (1973) included *Coniochaeta* in the Sordariaceae, and Dennis (1978) had both *Coniochaeta* and *Synaptospora* in that family. *Synaptospora* (Cain 1957) is tentatively placed in the Coniochaetaceae. *Synaptospora petrakii* Cain has smooth-walled ascospores, with a faint germ slit, that adhere together usually in two's or four's. The peridium of dark pseudoparenchymatous cells bears tuberculate protrusions on the surface. Cain (1957) at first suggested a position in the Xylariaceae, but later Jeng and Cain (1976) thought the genus better in the Trichosphaeriaceae. *Collematospora venezuelensis* Jeng & Cain (Jeng and Cain 1976) may be another taxon related to *Synaptospora*. The one-celled ascospores become fused in groups of two or four within the ascus and no germ slit is visible.

Several extralimital genera have been described. *Areolospora* (Jong and Davis 1974, Hawksworth 1980b) differs from *Coniochaeta* by warted ascospores, *Poroconiochaeta* (Udagawa and Furuya 1979) by pitted or punctate ascospores. *Germ slitospora* (Lodha 1978) with pitted ascospores and *Ephemerascus* (van Emden 1973) with ascomata aggregated into a stromatic crust, are both cleistothecioid; von Arx (1981b) believed that *Germ slitospora* was not separable from *Coniochaetidium*. *Wawelia* could perhaps be arranged in this family also, rather than in the Xylariaceae (O. Eriksson and Hawksworth 1987c, 1990), even though the formation of an upright stroma is unusual in the Sordariales. The peridium of the ascoma, the presence of short setae, and asci that lack apical structures and deliquesce early, are features found in several other taxa in the Sordariales. Müller (1959) described *W. regia* Namyslowsky in some detail. He suggested disposition in the Melanosporaceae (= Ceratostomataceae). Doguet (1961) described development and concluded also that the fungus belonged in the Melanosporaceae. The presence of germ slits in the brown ascospores leads instead to the related Coniochaetaceae.

#### Key to Genera of Coniochaetaceae

1. Ascomata cleistothecoid.....*Coniochaetidium*
1. Ascomata perithecioid.....2
  2. Ascomata tuberculate over surface; ascospores often adhering together in two's or four's.....*Synaptospora*
  2. Ascomata glabrous or short setose or with protruding cells over surface; ascospores not adhering together in two's or four's.....*Coniochaeta*

*Chaetomiaceae* Winter in Rabenhorst, *Kryptogamen-Fl.* 1(2): 153. 1885.

Ascomata separate or gregarious, superficial; perithecioid or cleistothecoid, globose, ovoid or obpyriform, small or medium; apex papillate or rounded and enclosed; surface glabrous or bearing setae or hyphal appendages; peridium dark or slightly pigmented, pseudoparenchymatous, narrow or wide at times, cephalothecoid at times. Asci basal in fascicles, clavate or subglobose and short stipitate or cylindric, usually octosporous, deliquescent; apical ring lacking. Paraphyses lacking or as short rows of cells. Ascospores brown, limoniform, ovoid, globose, fusoid or triangular, one celled; walls smooth or ornamented, with one or two terminal germ pores, lacking gel coating and appendages; at times dextrinoid when immature and unpigmented; often one globule; crowded or uniseriate in the ascus.

Anamorphs hyphomycetous; conidiogenous cells enteroblastic phialidic, simple, or holoblastic solitary (aleuric). Described as *Acremonium*, *Botryotrichum*, *Phialophora*-like, *Scopulariopsis*, *Sepedonium*.

Saprobic or hypersaprobic on vegetable debris, dung, in soil; often cellulolytic.

The family names *Thielaviaceae* von Arx 1967 (nom. inval.) and *Achaetomiaceae* Mukerji 1968 (nom. inval.), 1978, are included under the *Chaetomiaceae*.

Probably because of their ready growth and production of ascomata in culture, *Chaetomium* and related genera have received considerable attention. Monographic studies include those by Skolko and Groves (1953), Ames (1963), Seth (1971a), Cannon (1986) and von Arx et al. (1986, 1988). Several developmental studies have been made by, for example, Zopf (1881), Moreau and F. Moreau (1954), Corlett (1966b) and Cooke (1973). Electron-microscope studies have also been conducted, on ascomatal appendages (Hawksworth and Wells 1973), on ascospore surfaces (Millner et al. 1977, von Arx et al. 1986, 1988).

Von Arx et al. (1984) discussed and provided a key to many taxa in the family. They suggested that the simplest solution would be to accept only a single genus that showed considerable variation. Certain characteristics do allow separation of several genera quite precisely, although there exists a need for clarification of the limits of *Chaetomium* itself. *Thielavia* (including species with

vestiture, placed in *Chaetomidium*) apparently is the cleistothecioid counterpart of *Chaetomium*, and similarities are evident among the species of both genera in colony morphology, initials, vestiture, ascospores and anamorphs (Malloch and Cain 1973). Von Arx (1975a), however, included in *Thielavia* species of *Boothiella* and *Thielaviella*, and thought the genus to be nearer to the Sordariaceae. *Farrowia* was segregated from *Chaetomium* (Hawksworth 1975) on the bases of an elongate beak composed of vertically elongated cells, smooth appendages on the ascomata rather than the ornamented appendages in species of *Chaetomium* (Hawksworth and Wells 1973), and the presence of a pedestal-like tuft of basal hyphae. The anamorphs of *Farrowia* species are *Botryotrichum*-like. Several taxa in the family approach the Microascaceae in some features, for example in the dextrinoid reaction of young ascospores, but I limit the Microascaceae to those fungi whose asci are catenate, not stipitate nor borne from croziers. Thus *Emilmuelleria* (von Arx 1986), placed in the Microascaceae by O. Eriksson and Hawksworth (1987c, 1990), is instead assigned to the Chaetomiaceae in this study.

#### Key to Genera of Chaetomiaceae

1. Ascospores with one germ pore.....2
1. Ascospores with two germ pores.....10
  2. Ascomata perithecioid.....3
  2. Ascomata cleistothecioid.....7
3. Ascospores triangular; ascomata bearing ampulliform setae.....*Bommerella*
3. Ascospores limoniform, ovoid, globose, fusoid; ascoma ornamentation different.....4
  4. Ascomata glabrous, urn-shaped.....*Subramaniula*
  4. Ascomata bearing hyphae and/or appendages, not urn-shaped.....5
5. Ascomata attached to substrate by basal tuft of hyphae; appendages not ornamented, fused to form short or elongate, beaklike apex.....*Farrowia*
5. Ascomata not attached to substrate by basal tuft of hyphae; appendages ornamented, often coiled, not forming a beaklike apex.....6
  6. Ascomata bearing light spreading hyphae, peridium dark and wide beneath vestiture; asci cylindric.....*Achaetomium*
  6. Ascomata bearing simple or branched, coiled or undulate or uncinat appendages, usually ornamented, peridium brown or pallid and narrow beneath vestiture; asci clavate, rarely cylindric.....*Chaetomium*
7. Ascomata with pallid or light brown, translucent peridium lacking conspicuous appendages.....8
7. Ascomata with dark peridium, bearing appendages.....9
  8. Asci clavate; germ pore not protuberant...*Thielavia*
  8. Asci cylindric; germ pore protuberant....*Boothiella*

9. Ascomata bearing smooth, coiled appendages.....*Emilmuelleria*  
 9. Ascomata bearing verrucose and/or smooth, straight or undulate appendages, sometimes with circinate tips.....*Chaetomidium*  
 10. Ascomata perithecioid.....11  
 10. Ascomata cleistothecioid.....12  
 11. Ascomata bearing unbranched arcuate appendages.....*Achaetomiella*  
 11. Ascomata bearing setae or branched hyphae or circinate appendages.....*Chaetomium*  
 12. Ascospores with bordered germ pores...*Corynascella*  
 12. Ascospores lacking borders to germ pores.....*Corynascus*

*Ceratostomataceae* Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 247. 1885.

Ascomata separate or gregarious, immersed or superficial; perithecioid or cleistothecioid, globose or nearly so, small; apex papillate or beaked, at times composed of short setae, or rounded and enclosed; peridium lightly pigmented, yellowish or brownish, pseudoparenchymatous, thick-walled cells externally, at times containing Munk pores, narrow layer of compressed cells internally, at times cephalothecoid. Asci basal in fascicles, clavate, deliquescent, octosporous or less; apical ring lacking. Paraphyses lacking or as short chains of cells. Ascospores light to dark brown or nearly black, ellipsoid, fusoid, oblong, limoniform, broadly ovoid to cuboid or rectangular, one celled; wall smooth or ornamented, with (one) two germ pores, lacking gel coating and appendages; one globule; crowded in the ascus.

Anamorphs hyphomycetous; conidiogenous cells enteroblastic phialidic. Described as *Acremonium*, *Chlamydomyces*, *Gonatobotrys*, *Harzia*, *Paecilomyces*, *Protenphiala*.

Saprobic or hypersaprobic in vegetable debris, soil, dung, or hyperparasitic on other fungi.

*Ceratostomataceae* is the earlier name for the invalid but often used *Melanosporaceae* Bessey 1950. A few genera seem quite foreign to the family, and indeed to the Sordariales. *Sphaeronaemella* and *Viennotidia* are removed to the Hypocreales (Samson 1974). *Serenomyces* (and probably also *Phaeochora*), assigned to the *Melanosporaceae* by Müller and von Arx (1973), seem more related to the *Phyllachoraceae* of the Xylariales (Barr et al. 1989). *Arxiomyces* (*Phaeostoma*) *vitis* (Fuckel) Cannon & Hawksworth (Cannon and Hawksworth 1983) is out of place in the family. It must be assigned elsewhere, but I am not familiar with this fungus and cannot suggest disposition at this time. *Microthecium* is accepted as a synonym of *Melanospora*; studies on the species include those of Udagawa and Cain (1969) and

Hawksworth and Udagawa (1977). Cannon and Hawksworth (1982) surveyed many species of genera placed in the family and illustrated the variations in ascospore wall surfaces and types of pores that aid to separate genera.

#### Key to Genera of Ceratostomataceae

1. Ascospore wall smooth.....2
1. Ascospore wall ornamented.....4
  2. Ascospores ovoid to cuboid or rectangular, germ pores as wide slits.....*Scopinella*
  2. Ascospores ellipsoid, fusoid, limoniform or oblong, germ pores rounded.....3
3. Ascospores ellipsoid, fusoid or limoniform, germ pores depressed, lacking rim; ascomata mostly perithecioid.....*Melanospora*
3. Ascospores oblong, germ pores large, crateriform; ascomata perithecioid.....*Syspastospora*
4. Ascospores ornamented by winglike ridges, germ pores with rim; ascomata cleistothecioid.....*Pteridosperma*
4. Ascospores differently ornamented; ascomata cleistothecioid or perithecioid.....5
5. Ascospores wrinkled rugulose, germ pores small; ascomata cleistothecioid, peridium cephalothecioid.....*Rhytidospora*
5. Ascospores differently ornamented; ascomata perithecioid or cleistothecioid, peridium not cephalothecioid.....6
6. Ascospores finely pitted in longitudinal rows, germ pore small; ascomata perithecioid.....*Persiciopora*
6. Ascospores coarsely reticulate, ends strongly apiculate, germ pores protruding; ascomata mostly cleistothecioid.....*Sphaerodes*

**Microascales** Luttrell ex Benny & Kimbrough, Mycotaxon 12: 40. 1980.

**Ophiostomatales** Benny & Kimbrough, Mycotaxon 12: 48. 1980.

Stromatic tissues lacking or forming basal crust. Ascomata immersed erumpent or superficial, small, globose, perithecioid or cleistothecioid; apex papillate or beaked or rounded and enclosed, ostiole periphysate or not; surface frequently bearing hyphal appendages or setae; peridium two layered, few to several rows of cells, usually darkly pigmented externally, pallid internally. Asci unitunicate, small, globose or ovoid, terminal without croziers, often catenate, chains expanding laterally and basally into centrum, or in basal fascicles from croziers, thin walled, deliquescent; apical ring lacking. Paraphyses lacking, either centrum tissues of deliquescent pseudo-parenchymatous cells or short, ingrowing hyphae formed. Ascospores hyaline or yellowish or straw color, copper color, reddish brown, often dextrinoid when immature,

ovoid, ellipsoid, fusoid, triangular, reniform, galeate or elongate falcate, symmetric or asymmetric, one celled or rarely one septate; wall smooth or ornamented, with one or two germ pores often when pigmented, surrounded by gel coating at times; guttulate; crowded in the ascus.

Anamorphs hyphomycetous, at times sporodochial or synnematus; conidiogenous cells holoblastic, proliferating percurrently or sympodially; or thallic forming arthroconidia; more rarely enteroblastic phialidic.

Saprobic on dung, plant debris, in soil, wood, standing trees and lumber, often cellulolytic or keratinophilic.

Luttrell (1951) included both the Microascaceae and the Ophiostomataceae in his order Microascales (nom. inval. ICBN Art. 36), which he aligned under the Plectomycetes because of the small asci that appear to be scattered irregularly. He separated these families by features of centrum development: tapering filamentous hyphae that fill and enlarge the cavity in the Microascaceae and pseudoparenchymatous cells that collapse in the Ophiostomataceae. Benny and Kimbrough (1980) recognized two orders when they erected the Ophiostomatales. These were based in part upon centrum differences, in part upon the dextrinoid reaction of young ascospores and the presence of one or two germ pores in the Microascaceae and the lack of pigmentation, dextrinoid reaction and germ pores in the Ophiostomataceae.

The ascomata originate as coiled ascogonia that become surrounded by pseudoparenchymatous cells. In the young centrum of *Ophiostoma ulmi* Buisman (Rosinski 1961), thin-walled cells line a cavity in which the branched ascogenous system is basal. Successive branching and crozier formation lead to the formation of asci in a fan-shaped group where the uppermost asci are the earlier formed. In species of *Microascus* and *Petriella* (Corlett 1963, 1966a) and *Lophotrichus* (Whiteside 1962), the young centrum becomes occupied by sterile hyphae that protrude inward from the sides and base. The ascogenous system is pushed into the upper part of the centrum. Asci are borne terminally, often in catenate rows, on ascogenous hyphae that do not form croziers; they project downward into the centrum. In members of both families, the small, thin-walled asci deliquesce at maturity and ascospores are freed into the centrum. The similarities are such that one order should encompass both families. The variations in development and characteristics of ascospores separate the two families.

#### Key to Families of Microascales

1. Ascospores brown at maturity, often dextrinoid when immature, usually with one or two germ pores..Microascaceae
1. Ascospores hyaline at maturity, not dextrinoid when immature, lacking germ pores.....Ophiostomataceae

**Microascaceae** Luttrell<sup>1</sup> ex Malloch, *Mycologia* 62: 734. 1970.

Ascomata perithecioid or cleistothecioid, globose, small; apex papillate, ostiole periphysate, or apex rounded and enclosed; surface often appendaged; peridium narrow or wide. Asci terminal, often catenate, growing downward into centrum, becoming irregularly dispersed, ovoid to globose, wall thin, deliquescent. Paraphyses lacking, sterile hyphae developing from peridium inward, deliquescent. Ascospores yellowish, straw colored, copper colored or reddish brown, dextrinoid when immature, ellipsoid, fusoid, ovoid, triangular or reniform, asymmetric or symmetric, one celled; typically with one or two terminal germ pores; guttulate; crowded in the ascus.

Anamorphs hyphomycetous; conidiogenous cells holoblastic, proliferating percurrently or sympodially; or thallic. Described as *Graphium*, *Scedosporium*, *Scopulariopsis*, *Sporotrichum*, *Stysanus*, *Wardomyces*.

Saprobic or hypersaprobic in plant debris, dung, soil.

The concept of the family that is outlined above and in the key to genera is that of Malloch (1970) and Benny and Kimbrough (1980), with the addition of *Pithoascus* and the *Pithoascaceae* Benny & Kimbrough 1980. The pallid, fusoid ascospores in species of *Pithoascus* do not contain germ pores. The genus was erected and species were treated (von Arx 1973a, b). No anamorph is formed in *Pithoascus nidicola* (Massei & Salmon) von Arx, but *P. langeronii* von Arx was described with an *Arthrographis* anamorph (von Arx 1978). This latter species is the type of *Pithoascina* (Valmaseda et al. 1987), who also described the *Scopulariopsis* anamorph of *P. schumacheri* (Hansen) von Arx. *Pithoascus langeronii* has since been removed to the *Loculoascomycetes* as *Eremomyces langeronii* (von Arx) Malloch & Sigler (Malloch and Sigler 1988). *Pithoascus intermedius* (Emmons & Dodge) von Arx forms a *Scopulariopsis* anamorph and Roberts (1985) suggested that both genus and family were superfluous.

Illustrated monographic studies have been made of the species in the *Microascaceae*: *Microascus* was treated by Barron et al. (1961b) and added to by von Arx (1975b) and Udagawa and Furuya (1978), *Kernia* by Malloch and Cain (1971b), *Petriella* by Barron et al. (1961a). *Pseudallescheria* is the earlier name for *Petriellidium* (Malloch 1970, Malloch and Cain 1972a, von Arx 1973b) and several species were transferred by McGinnis et al. (1982). *Lophotrichus* was described for two species by Benjamin (1949), and was treated again by Seth (1971b), who erected the *Lophotrichaceae* to accommodate this genus.

Some other genera are known to me only from the literature. *Enterocarpus* (Locquin-Linard 1977) has cleistothecioid ascomata with spiral setae and relatively large ascospores, that separate *E. uniporus* Locquin-Linard

from species of *Kernia*. *Faurelina* (Locquin-Linard 1975) has been assigned to the Microascaceae or the Pithoascaceae. Ascomata are cleistothecioid, asci catenate on a basal cushion, ascospores fusoid, lacking germ pores and bearing distant longitudinal striations. Von Arx (1981b) and von Arx et al. (1981) suggested a relationship with *Neurospora*. *Chadefaudiella* (Faurel and Schotter 1966), the sole genus of the Chadefaudiellaceae Faurel & Schotter ex Benny & Kimbrough 1980, possesses elongate cleistothecioid ascomata, a capillitium above the basal layer of catenate asci, and fusoid, delicately longitudinally striate ascospores (Locquin-Linard 1973).

#### Key to Genera of Microascaceae

1. Ascospores fusoid, pale straw colored, lacking germ pores; ascomata perithecioid.....*Pithoascus*
1. Ascospores shades of brown, with one or two germ pores; ascomata perithecioid or cleistothecioid.....2
2. Ascospores asymmetric, with one or two germ pores.....3
2. Ascospores symmetric or ellipsoid, with two germ pores.....5
3. Ascomata cleistothecioid.....*Kernia*
3. Ascomata perithecioid.....4
4. Peridium narrow; ascospores reddish brown, with two germ pores.....*Petriella*
4. Peridium wide; ascospores yellowish to copper color, with one basal germ pore.....*Microascus*
5. Ascomata cleistothecioid.....*Pseudallescheria*
5. Ascomata perithecioid.....*Lophotrichus*

Ophiostomataceae Nannfeldt, Nova Acta Regiae Soc. Sci. Upsal., ser. 4, 8(2): 30. 1932.

Ascomata perithecioid or cleistothecioid, globose, small, beak often greatly elongate, ostiole not periphysate; peridium narrow, of compressed cells. Asci basal in fascicles, often catenate, globose or ovoid, thin walled, deliquescent. Paraphyses lacking. Ascospores hyaline, reniform, crescentic or elongate falcate, one celled, rarely one septate; wall smooth, at times surrounded by gel coating, lacking germ pore; guttulate; crowded in the ascus.

Anamorphs hyphomycetous, often sporodochial or synnematus; conidiogenous cells holoblastic, proliferating percurrently or sympodially, or enteroblastic phialidic. Described as *Graphium*, *Hyalorhinocladia*, *Leptographium*, *Pesotum*, *Sporothrix*, *Verticicladiella*.

Saprobic or hemibiotrophic, usually in wood, lumber, standing or fallen trees, often developing in beetle galleries; causing blue stain of lumber, Dutch elm disease.

The species of *Ophiostoma* have been included and illustrated under *Ceratocystis* in monographic studies by



Hunt (1956), Griffin (1968), and numerous accounts of new taxa. Olchowecki and Reid (1974) recognized several groups of species: *Ceratocystis* in the narrow sense would comprise the Fimbriata-group, *Ceratocystiopsis* the Minuta-group, and *Ophiostoma* the Ips- and Pilifera-groups. *Europhium* was established by Parker (1957) for cleistothecoid taxa, and enlarged by Robinson-Jeffrey and Davidson (1968); the genus has been submerged under *Ophiostoma* (de Hoog 1974). Upadhyay and Kendrick (1975) erected *Ceratocystiopsis* for species whose ascospores are elongate falcate and surrounded by a gel coating (Minuta-group of Olchowecki and Reid 1974).

*Ceratocystis* differs in several respects from *Ophiostoma* and is excluded from the family (von Arx 1974, de Hoog 1974). Samuels and Müller (1979b) remarked on similarities between the long tubular phialides of *Ceratocystis* and *Melanochaeta* species and von Arx (1981b) suggested affinities with *Chaetosphaeria*. The genus is assigned here to the Lasiosphaeriaceae (Sordariales) where *Chaetosphaeria* and related genera are also arranged. The species of *Ceratocystis*, having enteroblastic-phialidic anamorphs, lack rhamnose and cellulose in the cell walls (Weijman and de Hoog 1975), whereas taxa whose anamorphs are holoblastic with percurrent or sympodial proliferations, i.e., species of *Ophiostoma* and related genera, also contain rhamnose and cellulose in the cell walls of those tested. The presence of cellulose and chitin in cell walls was first described for *Ophiostoma ulmi* Buisman by Rosinski and Campana (1964) and was corroborated by others, for example, Jewell (1974). Weijman (1976) disposed of the suggestion that *Ophiostoma* and *Europhium* were related to *Cephaloascus*, a member of the Ascoideaceae (Cain 1972). De Hoog (1974) further clarified the separation of *Ophiostoma* from *Ceratocystis* and provided a key to species of *Ophiostoma* that have a *Sporothrix* anamorph. Samuels and Müller (1979b) gave additional information on the validity of the two genera. De Hoog and Scheffer (1984) re-evaluated the differences between *Ceratocystis* and *Ophiostoma*. They maintained *Ophiostoma* for species with anamorphs other than *Chalara*, that have rhamnose in the cell walls, and that are resistant to cycloheximide (Harrington 1981). They illustrated recent arrangements of *Ceratocystis*, *Ophiostoma* and *Ceratocystiopsis* and the features of each genus with emphasis on anamorphs. That these may cause confusion was shown by analysis of five types of propagulae in *O. araucariae* (Butin) de Hoog & Scheffer, which included phialidic conidiogenous cells forming small heads of conidia. De Hoog and Scheffer concluded that the separation of *Ceratocystis* with a limited number of species from *Ophiostoma* was warranted even though some exceptions occur. Von Arx and van der Walt (1988) accepted *Ceratocystis* in the Pyxidiophoraceae (here arranged under the Hypocreales), as one family in their polyphyletic interpretation of the Ophiostomatales.

Redhead and Malloch (1977) suggested that yeasts such as *Cephaloascus* and *Endomyces* and hyphal, ascoma-forming taxa in *Ceratocystis* (in the broad sense) be grouped together in an expanded concept of the Endomycetaceae. They utilized the presence of hyaline, galeate ascospores, holoblastic anamorphs, habit and dispersal by insects, and argued that variations in ascospore shape could be derived readily. They accepted without comment the presence of enteroblastic-phialidic anamorphs in the family, but expressly excluded taxa with arthric anamorphs. The grouping together of such diverse taxa has not been accepted by most others, and yeast-like taxa are excluded from this study. Von Arx and van der Walt (1988), however, included the Cephaloascaceae in their expanded version of the Ophiostomatales.

Benny and Kimbrough (1980) arranged both *Ceratocystis* and *Sphaeronaemella* in the Ophiostomataceae, a heterogeneous assembly as von Arx (1981b) pointed out. *Sphaeronaemella* seems best disposed in the Hypocreales (Cain and Weresub 1957, de Hoog and Scheffer 1984). *Klasteriskya acuum* (Mouton) Petrak was placed in the Ophiostomataceae by Petrak (1940b), removed to the Sphaeriaceae by Müller and von Arx (1962) and again (Minter 1983) redispersed to the Ophiostomataceae. Minter observed that germinating ascospores formed a conidiogenous cell and conidia that resemble a small *Hyalorhinocladiella*. The rather large, one-septate ascospores deviate from the family concept. *Subbaromyces splendens* Hesselstine (Hesselstine 1953) was also transferred to *Klasteriskya* (von Arx 1981a). Cole et al. (1974) described development of the fungus and of the *Scopulariopsis*-like anamorph. I am uncertain of the disposition of both these fungi at present.

#### Key to Genera of Ophiostomataceae

1. Ascospores elongate falcate, usually surrounded by gel sheath.....*Ceratocystiopsis*
1. Ascospores reniform or crescentic, lacking gel sheath..2
  2. Ascomata cleistothecoid.....*Europhium*
  2. Ascomata perithecioid.....*Ophiostoma*

Hypocreales Lindau in Engler & Prantl, Natürl. Pflanzenfam. 1(1): 343. 1897.

Nectriales Chadaud, Compt. Rend. Hebd. Séances Acad. Sci. 247: 1377. 1958.

Stromatic tissues when formed usually brightly pigmented, soft and fleshy, pseudoparenchymatous or prosenchymatous, immersed erumpent, effuse, pulvinate, tuberculate, or stipitate and clavate, at times as hyphal subiculum. Ascomata perithecioid or cleistothecoid, mostly globose, small to medium, collabent at times, superficial or immersed becoming erumpent from stromatic tissues,

subiculum or substrate; apex papillate or sometimes beaked, ostiole periphysate, or apex rounded and enclosed; peridium pallid to brightly pigmented or dark, two or three layered; surface glabrous, tuberculate or bearing setae or hyphal appendages. Asci unitunicate, basal or peripheral, thin walled, usually octosporous; apical ring lacking or shallow or elongate, nonamyloid, chitinous at times. Paraphyses apical (periphysoids), usually deliquescent, at times persistent or remaining as short fringe in the upper centrum. Ascospores hyaline or lightly pigmented, rarely dark, symmetric or asymmetric, ellipsoid, oblong, fusoid or elongate, one celled or one or several septate, disarticulating into partspores at times; wall smooth, verruculose or longitudinally striate.

Anamorphs usually hyphomycetous, sporodochial or synnematus at times, less often coelomycetous; conidiogenous cells enteroblastic phialidic, mononematous or branched penicillately or verticillately; conidia hyaline or greenish to dark green, one celled or septate; associated thick-walled structures present at times.

Biotrophic, hemibiotrophic, saprobic or hypersaprobic on various substrates, including other fungi and myxomycetes.

The order was monographed for North America early in this century (Seaver 1909a, b). Rogerson (1970) presented a detailed key to genera, arranged in the sole family Hypocreaceae. He also provided generic citations and notes on synonymy. A number of the taxa are extralimital to this synopsis and are not included in the following key. The ordinal name Hypomycetales has been used, for example O. Eriksson (1982a, b), Corlett (1986), but I have not determined that it was ever validly published.

The Pyxidiophoraceae is separated from the Hypocreaceae, following Lundqvist (1980). The Niessliaceae is newly inserted in the order, to accommodate taxa with dark, often short setose, collabent, superficial ascomata whose centra are identical to others in the order, i.e., with short apical paraphyses (periphysoids), and whose anamorphs may have green conidia.

Some taxa that Rogerson arranged in his key are now known not to belong to the Hypocreales. Several are Loculoascomycetes, e.g., *Macbridella* (Samuels 1973), *Podonectria* (Rossman 1978), *Shiraea* (Amano 1980). Articles by Pirozynski (1977), Barr (1980), and Rossman (1987) expanded on Petrak's (1931) "hypocreoid Dothideales" to remove genera to the Tubeufiaceae or other families of Pleosporales. Several taxa are placed in other orders of Hymenoascomycetes on the basis of centrum structure, even though brightly pigmented ascomata and/or stromata are produced, e.g., *Valsonectria*, *Cyanoderma* and *Thuemenella* in the Xylariales. The lichenized *Thelecarpon* (including *Ahlesia*) is now in the Lecanorales under family Acarosporaceae (O. Eriksson and Hawksworth 1987c, 1990). O.

Eriksson and Yue (1989a) suggested that *Thyridium* also belongs in the Hypocreales. Because of differences in centra, the Thyridiaceae is retained in the Xylariales in this study.

#### Key to Families of Hypocreales

1. Ascomata with awl-shaped beak; asci deliquescent; ascospores elongate fusoid, tapered to narrow base, wall often gelatinizing, finally with brown apical or lateral region.....Pyxidiophoraceae
1. Lacking above combination of characteristics.....2
2. Ascomata superficial, collabent, pallid to dark, bearing dark, thick-walled setae or glabrous.....Niessliaceae
2. Ascomata immersed or superficial, pallid or brightly pigmented, setae when present hyaline or pallid.....Hypocreaceae

Hypocreaceae de Notaris in Sacc. Syll. Fung. 2: 447. 1883.

Stromatic tissues present or lacking, when present soft and fleshy, pallid or brightly pigmented to light brownish, immersed erumpent, effuse, tuberculate or pulvinate, occasionally stipitate, then fertile region clavate, or subiculum of interwoven pallid or brightly pigmented hyphae. Ascomata separate or often gregarious, immersed in or erumpent from to superficial on stroma, subiculum or substrate, pallid, brightly pigmented, or shades of light brown or blue to violet (appearing black), rarely brown; globose, obpyriform, ovoid or sphaeroid, collabent at times; apex papillate, ostiole periphysate; surface glabrous or warted or bearing hyaline or pallid hyphal appendages or rarely thick-walled setae; peridium pallid to brightly pigmented or brown, blue or violet, externally of pseudoparenchymatous cells, sometimes with thick, sclerotial walls, internally of compressed rows of cells. Asci basal to peripheral, cylindric, oblong or inflated, mostly octosporous, occasionally polysporous or less than eight; apical annulus often lacking, when present shallow, refractive, nonamyloid. Paraphyses apical (periphysoids), usually deliquescent, occasionally visible at maturity, as cellular remnants among asci or as apical fringe. Ascospores hyaline, yellowish, pinkish to greenish or occasionally brown, ellipsoid, fusoid, allantoid, elongate or globose, one celled or one to several septate, occasionally with longitudinal septa, disarticulating into partspores at times or budding to form conidia within ascus; wall smooth, verruculose or longitudinally striate; usually one globule per cell; uniseriate, biseriate or in fascicle in the ascus.

Anamorphs hyphomycetous, grouped on sporodochia or synnemata at times, rarely coelomycetous; conidiogenous cells enteroblastic phialidic, thick-walled structures

present at times. Described as *Acremonium*, *Antipodium*, *Arnoldiomyces*, *Chaetopsina*, *Gladobotryum*, *Clonostachys*, *Cylindrocarpon*, *Cylindrocladium*, *Dactylium*, *Dactylaria*, *Dendrodochium*, *Dendrostilbella*, *Didymostilbe*, *Fusarium*, *Gliocladium*, *Kutilakesopsis*, *Mariannaea*, *Moeszia*, *Myrothecium*, *Pachybasium*, *Paecilomyces*, *Penicillifer*, *Sarcopodium*, *Sesquicillium*, *Stilbella*, *Stromatocrea*, *Tilachlidium*, *Trichoderma*, *Trichothecium*, *Tubercularia*, *Verticillium*, *Virgatospora*, *Volutella*, *Zythiostroma*; aleurioconidia as *Mycogone*, *Sepedonium*, *Sibirina*, *Stephanoma*; chlamydospores as *Blastotrichum*; papulospores as *Papulaspora*.

Biotrophic, hemibiotrophic, saprobic or hypersaprobic on various plants, other fungi, myxomycetes.

Rogerson (1970) cited the different family names that have been proposed and submerged the Nectriaceae and Hypomycetaceae under the Hypocreaceae. Samuels and Seifert (1987) reviewed a number of hypocrealean taxa with emphasis on anamorphs. They recognized three groups of genera within the family, based upon characteristics of ascospores, stromatic tissues and anamorphs. *Hypomyces* usually has one-septate, apiculate ascospores, ascomata that develop in a subiculum on fleshy fungi, and mononematous, nonaggregated conidiophores whose phialides are verticillate in arrangement. Additionally, indehiscent chlamydospores or dehiscent aleuriospores or papulospores may be present. Many of the species and their anamorphs are treated in detail by Rogerson and colleagues (Rogerson and Mazzer 1971, Rogerson and Simms 1971, Carey and Rogerson 1981, 1983, Rogerson and Samuels 1985, 1989).

*Hypocrea* and the related *Podostroma* have one-septate ascospores that disarticulate into partspores, ascomata immersed in stroma or subiculum, and loosely aggregated conidiophores whose phialides are penicillate in arrangement. Some species of *Hypocrea* in North America have been studied in nature and in culture (Canham 1969, Carey and Rogerson 1977, Doi and Yamatoya 1989). *Podostroma alutaceum* (Pers.) Atk. forms a conspicuous, clavate, stipitate stroma (Dennis 1978).

*Nectria* is a species-rich genus whose characteristics of stroma and ascomata are variable. The ascospores are ellipsoid or fusoid and one to several septate, ascomata may be seated on or in a stroma or subiculum, or may lack sterile tissues, and anamorphs may be loosely aggregated, may form on sporodochia or synnemata or within a pycnidium. The phialides may also vary from mononematous to grouped in verticillate or penicillate arrangement. Knowledge of the genus has been enhanced by developmental studies (Hanlin 1961, 1963, 1971), information on anamorphs (summarized by Samuels and Rossman 1979, Samuels and Seifert 1987), descriptions and keys to various groups of species (Booth 1959, Samuels 1973, 1976a, b, 1988a, 1989). Rossman (1983) accepted phragmo- and dictyosporous species in *Nectria*, and

restricted *Calonectria* to a few species with a particular set of characteristics (Rossman 1979, 1983). Both *Thyronectria* whose dictyospores frequently bud to produce conidia within the ascus (Seeler 1940), and *Scolecconectria* whose scolecospores also bud within the ascus (Booth 1959), are included under *Nectria* by Rossman (1983, 1989). *Calyptronectria ohiensis* (Ellis & Everh.) Barr (Barr 1983b) evidently has nonbudding dictyospores, in superficial, separate ascomata. *Ophionectria trichospora* (Berk. & Broome) Sacc. produces elongate fusoid, striate, multiseptate ascospores (Rossman 1977) and has as anamorph *Antipodium spectabile* Pirozynski. Its distribution is pantropical, known from Central America, the West Indies and elsewhere. Species of *Gibberella* have a blue to violet peridium and the ascospores are usually several septate. The didymosporous *Plectosphaerella cucumeris* Klebahn differs in forming dark brown ascomata, isolated from soil or rotting plant debris, and the anamorph is *Fusarium*-like (Gams and Gerlagh 1968).

Some of the other genera in the family differ by the formation of one-celled ascospores. Species of *Neocosmospora*, on roots and in soil, have brown, ornamented ascospores (Cannon and Hawksworth 1984), whereas those of other amerosporous genera are hyaline or faintly pigmented, and several taxa inhabit leaves. *Schizoparme straminea* Shear (Shear 1923) has the upper regions of immersed ascomata strongly thickened while *Pseudonectria rousseliana* (Mont.) Seaver, with ellipsoid ascospores, and *Allantonectria yuccae* Earle, with oblong, somewhat allantoid ascospores, have papillate apices on ascomata. *Sphaeronaemella* and *Viennotidia*, whose species have small, deliquescent asci, have been arranged near *Melanospora* in the Ceratostomataceae, Sordariales (Cannon and Hawksworth 1982) but are better disposed in the Hypocreaceae (Rogerson 1970, Samson 1974).

The other taxa separated from *Nectria*, didymosporous or phragmosporous, are based upon features of peridium or presence of stroma or particular anamorph. In *Hypocreopsis* the ascomata are immersed in stromatic tissues that at times are large and radially lobed as in *H. lichenoides* (Tode: Fr.) Seaver (Cauchon and Ouelette 1964). Species of *Sphaerostilbella* have ascomata on a thin subiculum over members of the Aphyllophorales and a *Gliocladium* anamorph (Seifert 1985). The species of *Nectriella* are immersed in and have apices erumpent from the substrate (Lowen 1989). Three typically fungicolous genera have pallid (white, yellowish, violaceous) ascomata whose peridia vary. Thick-walled hyaline setae characterize species of *Trichonectria*, a thickened apical disc sometimes bearing coronate points of matted hyphal appendages *Peristomialis*, and thin-walled ascomata that may bear cellular protrusions or thin-walled hyphal appendages *Nectriopsis* (Samuels 1988b).

## Key to Genera of Hypocreaceae

1. Ascomata in subiculum, hyperbiotrophic on fleshy fungi; ascospores typically one septate and apiculate but apiosporous, one celled and/or nonapiculate in some...*Hypomyces*
1. Ascomata not in subiculum or if so not hyperbiotrophic on fleshy fungi; ascospores variable in septation, not apiculate.....2
  2. Ascospores disarticulating into partspores at maturity, oblong, one septate; ascomata immersed in stromatic tissues.....3
  2. Ascospores not disarticulating into partspores at maturity, variable in shape and septation; stromatic tissues present or lacking.....4
3. Stromata stipitate, with clavate fertile portion.....*Podostroma*
3. Stromata pulvinate or effuse.....*Hypocrea*
  4. Ascospores muriform, at times budding within ascus.....5
  4. Ascospores one celled or transversely septate....6
5. Ascomata superficial on substrate, lacking stromatic tissues.....*Calyptronectria*
5. Ascomata in or on tuberculate stroma.....*Nectria (Thyronectria)*
  6. Ascospores elongate filiform, several septate, in fascicle in the ascus.....7
  6. Ascospores ellipsoid, oblong or fusoid to elongate, one celled or one to several septate, uniseriate, biserial or in two fascicles in the ascus.....8
7. Ascospores budding to produce conidia in the ascus; ascomata gregarious, seated on stromatic tissues.....*Nectria (Scoleconectria)*
7. Ascospores not budding to produce conidia in the ascus; ascomata separate or gregarious on substrate...*Ophionectria*
  8. Ascospores fusoid elongate, (one) several septate; ascomata superficial on substrate.....9
  8. Ascospores ellipsoid, oblong or fusoid, one celled or one to several septate; ascomata immersed in substrate or stroma or on basal stroma or subiculum or superficial.....11
9. Ascomata blue or violet, appearing black; peridium smooth or warted.....*Gibberella*
9. Ascomata orange or red to umber or brown; peridium smooth, warted or scaly.....10
  10. Ascomata brown; peridium smooth...*Plectosphaerella*
  10. Ascomata orange or red to umber; peridium warted or scaly.....*Calonectria*
11. Ascospores one celled.....12
11. Ascospores one to several septate.....17
  12. Ascospores brown, globose, longitudinally striate; in soil and over roots.....*Neocosmospora*
  12. Ascospores hyaline or slightly pigmented; in plant parts or over fungi or myxomycetes.....13

13. Ascomata usually beaked, tip fimbriate; asci clavate, deliquescent.....14
13. Ascomata papillate, tip not fimbriate; asci oblong to cylindric.....15
  14. Ascospores ellipsoid, flattened, with narrow germ slit.....*Sphaeronaemella*
  14. Ascospores oblong, not flattened, with crateriform germ pore.....*Viennotidia*
15. Upper region of ascomata thickened, erumpent from substrate; ascospores ellipsoid.....*Schizoparme*
15. Upper region of ascomata not thickened, superficial; ascospores ellipsoid or oblong approaching allantoid.....16
  16. Ascomata seated on substrate; ascospores ellipsoid.....*Pseudonectria*
  16. Ascomata seated on basal stroma; ascospores oblong allantoid.....*Allantonectria*
17. Ascomata immersed in and partially erumpent from lichen thalli or woody or herbaceous substrates.....*Nectriella*
17. Ascomata superficial on substrate or basal stroma or subiculum, or immersed in stromatic tissues.....18
  18. Ascomata immersed in reddish brown or yellowish stromatic tissues.....*Hypocreopsis*
  18. Ascomata not immersed in stromatic tissues, often seated on stroma or subiculum.....19
19. Ascomata on thin subiculum over Aphyllophorales.....*Sphaerostilbella*
19. Ascomata on other substrates.....20
  20. Ascomata shades of red, orange or brownish to umber, seated on substrate or on basal stroma or subiculum, on various substrates.....*Nectria*
  20. Ascomata white to yellowish or violaceous, on scanty or well-developed subiculum, usually on other fungi or myxomycetes.....21
21. Ascomata thin walled, surface bearing thick-walled, hyaline setae.....*Trichonectria*
21. Ascomata not bearing thick-walled, hyaline setae.....22
  22. Ascomata thin walled, thickened above as apical disc, at times coronate with triangular fascicles of matted hyphae; ascospores one or several septate.....*Peristomialis*
  21. Ascomata thin walled, not forming apical disc nor coronate, surface smooth or with cellular protrusions or thin-walled hyphal appendages; ascospores one septate.....*Nectriopsis*

*Pyxidiophoraceae* G. Arnold, Z. Pilzk. 37: 191. 1972  
(1971), emend. Lundqvist, Bot. Not. 133: 133. 1980.

Basal stroma present or lacking, pallid, soft textured. Ascomata superficial or bases immersed in stroma or substrate, perithecioid or cleistothecioid, globose or ovoid; apex beaked or rounded and enclosed; peridium membranaceous, pallid to brownish, pseudoparenchymatous, cells in beak forming longitudinal rows, often protruding and



darkened. Asci clavate, deliquescent, usually less than octosporous; apex at times with refractive ring. Paraphyses not formed. Ascospores hyaline, at maturity with brown apical or lateral body, fusoid, often tapered below to narrow base, one or few septate, rarely one celled; wall smooth or verruculose, often gelatinized and thickened at maturity; guttulate; in fascicle in the ascus.

Anamorphs hyphomycetous; conidiogenous cells enteroblastic phialidic, *Thaxteriola* (Blackwell et al. 1986), or *Chalara*-like (Webster and Hawksworth 1986).

Saprobic, often coprophilous or on decomposing plant materials, or associated with mites in bark-beetle habitats (Blackwell et al. 1989), or biotrophic on other fungi.

As a genus of the Hypocreaceae (Rogerson 1970), species assigned to *Mycorhynchus* were revised by Breton and Faurel (1967) and Hawksworth and Webster (1977). Lundqvist (1980) analyzed the types of *Mycorhynchus*, *Pyxidiophora* and other genera, and included all under the oldest name *Pyxidiophora*. *Mycorhynchidium* is the cleistothecioid counterpart (Malloch and Cain 1971a) and the second genus in the family. Corlett (1986) described *Pyxidiophora lundqvistii* as a member of the Hypomycetales. Blackwell et al. (1986) observed similarities between *Pyxidiophora kimbroughii* and species of *Ceratocystis* and *Ceratocystiopsis*. The ascospores of species in the latter genus in particular present some similarities to those in *Pyxidiophora*, but ascomata differ in shape and peridium structure, and the centra differ in the two. *Ceratocystis* is disposed here in the Lasiosphaeriaceae of the Sordariales, and *Ceratocystiopsis* in the Ophiostomataceae of the Microascales. Blackwell et al. (1986) discovered that the ascospores of *Pyxidiophora kimbroughii* developed directly into thalli of the anamorph *Thaxteriola*; these form endoconidia with the terminal cell acting as a phialide. Blackwell and Malloch (1989) presented evidence, most notably of association with arthropods in dispersal, for a relationship of *Pyxidiophora* to laboulbenialean fungi. Of the various fungus orders that they compared: Ophiostomatales, Microascales, Xylariales, Sordariales, and Hypocreales, they believe that *Pyxidiophora* could be most closely related to the Hypocreales. Valldosera and Guarro (1989) separated *Pyxidiophora* from *Klasterskya* by the dark peridium and hyaline, ellipsoid to oblong ascospores of the latter. As noted earlier, *Klasterskya* has been arranged in the Ophiostomataceae.

#### Key to Genera of Pyxidiophoraceae

1. Ascomata perithecioid.....*Pyxidiophora*
1. Ascomata cleistothecioid.....*Mycorhynchidium*

Niessliaceae Kirschstein, Ann. Mycol. 37: 89. 1939.

Ascomata superficial on thin, pallid to brown hyphal subiculum or crustose stromatic layer, minute to small or medium, globose, usually becoming collabent, pallid to brown or shining blackish at maturity; apex short papillate, ostiole periphysate; surface bearing short, dark, thick-walled setae, pointed and simple or ornately branched at apex, or glabrous; peridium relatively thin, soft, of several rows of compressed cells, at times thickened and three layered, pigment (in walls of outermost cells, often presenting a netlike aspect (*textura epidermoidea*) at surface, pallid internally. Asci numerous, peripheral, oblong or inflated, mostly octosporous; apical ring shallow or elongate, refractive, nonamyloid. Paraphyses apical (periphysoids), short, usually deliquescent. Ascospores hyaline or slightly pigmented, fusoid to elongate or oblong ellipsoid, one celled or one septate, at times disarticulating into partspores; wall smooth or verruculose; homogeneous or one or two globules in each cell; uniseriate or partly biseriate in the ascus.

Anamorphs hyphomycetous where known; conidiogenous cells enteroblastic phialidic; conidia hyaline or greenish, one celled. Described as *Acremonium*, *Gliomastix*, *Monocillium*, *Stachybotrys*.

Saprobic on herbaceous and woody substrates, at times over and around other fungi.

*Niesslia* and related taxa are usually assigned to the Sphaeriaceae (Müller and von Arx 1962, 1973) or the Trichosphaeriaceae (Hawksworth et al. 1983, O. Eriksson and Hawksworth 1987c, 1990). *Trichosphaeria* differs in usually noncollabent ascomata, in peridium structure, and in the centrum that contains narrow, apically free paraphyses rather than short apical ones. The Trichosphaeriaceae is assigned to the Xylariales for these reasons. The Niessliaceae is assigned to the Hypocreales because of the formation of apical paraphyses and similarities in anamorphs. The family is readily separated from the Hypocreaceae by the peridium that usually appears brown or blackish when mature and often bears dark, short setae. No red pigment is released in KOH as it is in the dark blue or violet species of *Gibberella*. Those genera in the Hypocreaceae that have a setose peridium have hyaline or lightly pigmented setae, as is the peridium itself. The surface of the peridium in thin-walled species of the Niessliaceae usually is formed of *textura epidermoidea*, the cell walls darkened, and as Kirschstein (1939) emphasized on erecting the family is "contextu reticulato fabricatum." This feature, in combination with relatively small sizes, also helps set the family apart. Species of *Melanopsamma* have a three-layered, thickened peridium that is glabrous.

The Niessliaceae is treated in a restricted sense, for as Petrak (1940a) aptly remarked, some of the taxa included

by Kirschstein, for example, *Coleroa*, *Helminthosphaeria*, *Lizonia*, made it an unnatural one. Only a few genera are recognized at present in the family. Species of *Niesslia* are widely distributed on a number of substrates, have simple dark setae and usually uniseptate ascospores that vary in shape and size. *Trichosphaerella*, including *Bresadollella*, is represented by *T. decipiens* Bomm., Rouss. & Sacc. and differs from species of *Niesslia* by the ascospores that disarticulate into partspores at maturity. This is a feature that is utilized to characterize genera in the Hypocreaceae also. *Neorehmia* and the synonymous *Larseniella* are excluded from the synonymy of *Trichosphaerella*, for the ascomata in *N. ceratophora* von Höhnelt (synonym *Larseniella major* Munk) are not collabent and setae have branched apices; additionally conidiogenesis in the anamorph of this fungus is holoblastic sympodial and denticulate, rather than enteroblastic phialidic (Müller and Samuels 1982a). *Melanopsammella inaequalis* (Grove) von Höhnelt was also included under *Trichosphaerella* (Müller and von Arx 1962). The noncollabent ascomata bear conidiophores and the species has been placed in *Chaetosphaeria* (Gams and Holubová-Jechová 1976), but the ascospores that disarticulate into partspores could necessitate the retention of *Melanopsammella* as a separate genus in the Lasiosphaeriaceae. *Valettoniella* was considered to be a synonym of *Niesslia* by Müller and von Arx (1962) and is similar in many respects. The peridium in the southern-hemispheric type species *V. crucipila* von Höhnelt is only lightly pigmented and the setae are ornately branched at their apices. Samuels (1983) redescribed this species from New Zealand, parasitic on species of *Nectria*. He has discovered South American taxa that are also referable to the genus (personal communication).

*Melanopsamma pomiformis* (Pers.: Fr.) Sacc. has collabent ascomata with a dark brown, soft-textured, three-layered peridium that lacks setae. The short apical paraphyses, asci and ascospores are much like those of the Hypocreaceae, as von Höhnelt (1919b) and later Munk (1957) recognized. Booth (1957) provided details of the fungus and its cultural characteristics. He believed that the *Stachybotrys* anamorph was more sphaeriaceous than hypocreaceous. Müller in Müller and von Arx (1962) transferred *M. pomiformis* to *Chaetosphaeria*; centra and anamorphs differ in these two genera. *Wallrothiella* could be another taxon in the family. *Wallrothiella subiculosa* von Höhnelt has collabent but nonsetose ascomata and a *Gliomastix* anamorph (Hughes and Dickenson 1968), which is similar to *Acremonium* (Gams 1971). *Wallrothiella* is not yet known to me from North America.

#### Key to Genera of Niessliaceae

1. Ascomata setose.....2
1. Ascomata glabrous or bearing conidiophores.....4

2. Setae ornately branched at apices.....*Valettoniella*  
 2. Setae simple, tapering to pointed apices.....3  
 3. Ascospores disarticulating into partspores at maturity..  
 .....*Trichosphaerella*  
 3. Ascospores not disarticulating into partspores.....  
 .....*Niesslia*  
 4. Peridium three layered, relatively wide; ascospores  
 one septate.....*Melanopsamma*  
 4. Peridium two layered, narrow; ascospores one  
 celled.....*Wallrothiella*

*Clavicipitales* Nannfeldt, Nova Acta Regiae Soc. Sci. Upsal.  
 ser. 4, 8(2): 49. 1932.

Stromatic tissues fleshy, brightly pigmented or dark to blackish, sessile and effuse to pulvinate or globose, or stipitate with fertile region capitate or clavate, arising in substrate or from firm-walled sclerotium of compacted fungus hyphae, stroma lacking at times, or subiculum thin or well developed. Ascomata perithecioid, usually immersed in or erumpent from stromatic tissues, occasionally superficial on slight or well-developed subiculum, ovoid, medium, apex papillate, ostiole periphysate; peridium one or two layered, narrow, soft and fleshy or membranaceous, white or brightly pigmented or darkened, of rows of compressed cells. Asci unitunicate, arising as basal fascicle, long cylindric, at times inflated, usually octosporous; apical ring frequently as large, refractive, thickened region, penetrated by narrow canal, nonamyloid. Paraphyses short, arising from lateral walls, deliquescent. Ascospores hyaline or yellowish in mass, filiform or elongate fusoid, usually multiseptate, at times disarticulating into one- or few-celled partspores; wall smooth; guttulate; in fascicle in the ascus.

Anamorphs hyphomycetous, as effuse layer on stroma surface or forming sporodochia, cupulate structures or synnemata; conidiogenous cells enteroblastic phialidic; conidia hyaline, one celled, oblong or elongate, dry or glutinous. Termed, following Diehl (1950): ephelidial, waxy scolecosporous conidia borne in cupulate structures; sphacelial, glutinous ameroconidia borne on sporodochia; typhodial, dry ameroconidia borne on effuse layer. Described as *Akanthomyces*, *Aschersonia*, *Hirsutella*, *Hymenostilbe*, *Isaria*, *Paecilomyces*, *Sphacelia*, etc.

Biotrophic on monocots, arthropods or hypogeous fungi; often systemic when on monocot hosts.

One family:

*Clavicipitaceae* (Lindau) O. Eriksson, Mycotaxon 15: 224.  
 1982.

The Acrospormaceae and Hypomycetaceae were included in the order also (Hawksworth et al. 1983), but are excluded by O. Eriksson and Hawksworth (1987c, 1988b, 1990). The Clavicipitaceae has often been placed next to the Hypocreaceae; taxa in both families have fleshy and often brightly pigmented ascomata and stromatic tissues. The two families differ at the ordinal level in centrum development; elongate asci and ascospores, and the exclusively biotrophic nature aid to set the Clavicipitaceae apart.

The North American genera accepted in the following key are separated for the most part on the bases of stromatic tissues, host preferences and disarticulation of ascospores into partspores. The key owes much to that prepared by Rogerson (1970). *Podonectria*, once accepted in the Clavicipitaceae, is now recognized as a genus of Loculoascomycetes in the Pleosporales, Tubeufiaceae (Rossman 1978), whereas *Oomyces* is placed in the Acrospormaceae of the Xylariales (O. Eriksson 1981).

Species of *Torrubiella* and *Neobarya* (for *Barya* Fuckel 1864 non *Barya* Klotzsch 1854; Lowen in O. Eriksson and Hawksworth 1986a) do not form stromata but ascomata develop in a basal subiculum. Species of the other genera do form stromata. A number of the fungi that attack monocots were monographed by Diehl (1950). Doguet (1960) studied development of *Epichloë typhina* (Pers.) Tul. & C. Tul., and illustrated the centrum, in which lateral paraphyses develop prior to ascus formation. He observed that development was of the *Xylaria* type whereas the apical apparatus of the ascus was not greatly different from that in the Diaporthaceae. Luttrell and Bacon (1977) added *Myriogenospora* to the family. They provided details of development of the disease and the morphology of *M. acramentosa* (Berk. & Curtis) Diehl. Mains presented several accounts of species of *Cordyceps*, summarized (Mains 1957) for species on hypogeous ascomycetes and (Mains 1958) for species on insects and arachnids. *Claviceps*, another important genus in the family, has a voluminous literature. *Claviceps purpurea* (Fr.) Tul. is notorious for the production of alkaloids in sclerotia that replace the grains of rye and other grasses; these sclerotia cause ergotism in man and were the original source of LSD.

Several extralimital bambusicolous genera are known in the family, i.e., *Aciculosporium*, *Ascopolyporus*, *Konradia*, *Mycmalus*. Other extralimital genera include *Atricordyceps*, *Byssostilbe*, *Cavimalum*, *Helminthoascus*, *Hypocrella*, *Moelleriella*, *Phytocordyceps* and *Podocrella*.

#### Key to Genera of Clavicipitaceae

1. Ascomata in basal subiculum or on substrate; stromata not formed.....2
1. Ascomata developed on or in stromata.....3
  2. Ascospores disarticulating at maturity into partspores; on insects.....*Torrubiella*

2. Ascospores not disarticulating at maturity into partspores; on other fungi.....*Neobarya*
3. Stromata usually stipitate, fertile portion clavate or capitate; on insects or monocots.....4
3. Stromata sessile; on monocots.....7
  4. Stromata arising from firm, black sclerotium, on monocots; anamorph sphacelial.....*Claviceps*
  4. Stromata arising from stromatized areas of substrate; anamorphs ephelidial, typhodial or lacking...5
5. Stromata arising from insects, arachnids or hypogeous fungi; often stipitate, fertile portion clavate or capitate light to brightly pigmented or brown to blackish..*Cordyceps*
5. Stromata arising from parasitized monocots, short stipitate, fertile portion capitate, blackish.....6
  6. Hypothallus usually well developed, bearing ephelidial anamorph prior to formation of stromata....*Balansia*
  6. Hypothallus poorly developed, deliquescent, lacking anamorph prior to formation of stromata...*Balansiopsis*
7. Stromata pulvinate to globose, light colored, ascomata superficial and scattered on stroma; ascospores disarticulating at maturity into partspores.....*Dussiella*
7. Stromata effuse, ascomata immersed; ascospores disarticulating or not at maturity into partspores.....8
  8. Stromata white to brightly pigmented; ascospores not disarticulating into partspores.....*Epichloë*
  8. Stromata blackish; ascospores disarticulating or not into partspores.....9
9. Both typhodial and ephelidial anamorphs formed; ascospores not disarticulating into partspores....*Atkinsonella*
9. Fleeting anamorph formed on young stroma; ascospores separating at maturity into partspores, continuing development from rectangular to elongate fusoid partspores in asci that become distorted and enlarged.....*Myriogenospora*

Xylariales Nannfeldt, Nova Acta Regiae Soc. Sci. Upsal. ser. 4, 8(2): 66. 1932.

Stromatic tissues slight or well developed, at times massive and crustose, applanate, pulvinate, globose, threadlike or stipitate bearing branched or simple, clavate, pulvinate or turbinate fertile region, at times sparse over or around one or few ascomata, or forming clypeus over ascomata immersed in substrate, or variously shaped and constructed within substrate, or reduced to hyphal subiculum or blackened crustose layer. Ascomata perithecioid or at times cleistothecioid, immersed in stroma or substrate to erumpent or superficial, separate or gregarious to crowded, globose, ovoid, obpyriform, sphaeroid or vertically elongate, small to large; apex rounded with pore or papillate or beaked, surface plane or sulcate or sunken, ostiole usually periphysate; peridium narrow or wide, two layers of compressed rows of cells, soft to firm or

carbonaceous and brittle. Asci unitunicate, peripheral or basal, cylindric, clavate and stipitate, oblong, subglobose or inflated, mostly octosporous or polysporous or less than eight spored; apical ring shallow or elongate, sometimes elaborate as stacked platelike layers, occasionally lacking, often amyloid, at times nonamyloid, often surmounted by shallow or well-developed pulvillus, chitinous at times. Paraphyses apically free, relatively narrow or wide, usually numerous, thin walled, guttulate, sometimes deliquescent at maturity. Ascospores hyaline or shades of brown, ellipsoid, fusoid, oblong, allantoid, obovoid, isthmoid or filiform, symmetric or asymmetric, one celled or one or several septate, rarely muriform; wall thin or thick, smooth or ornamented, at times bearing elongate germ slit or one or more germ pores, at times surrounded by gel coating, occasionally bearing terminal appendages; uniseriate, biseriate or in fascicle in the ascus.

Anamorphs various, hyphomycetous or coelomycetous; conidiogenous cells mostly holoblastic, proliferating sympodially or percurrently, less frequently enteroblastic phialidic.

Biotrophic, hemibiotrophic, saprobic or hypersaprobic on diverse substrates.

This large order includes pyrenomycetous fungi with a *Xylaria*-type centrum (Luttrell 1951), that is, with apically free paraphyses that are interspersed among the unitunicate asci. The name *Sphaeriales* has often been used to designate the order. The orders *Phyllachorales* and *Trichosphaeriales*, separated by Barr (1983a) on the bases of habit or of position of ascomata, cannot be maintained and the taxa are again arranged in the *Xylariales*. The *Amphisphaeriales* and *Diatrypales*, evidently based on ascospore shape (Hawksworth and O. Eriksson 1986) are also incorporated within the *Xylariales*. Vasilyeva (1987, personal communication) accepts the *Diatrypales* for several families whose taxa have asci and paraphyses that emerge in fascicles when sections are crushed out, whereas her *Xylariales* have a hymenial arrangement that does not produce fascicles of asci and paraphyses when sections are crushed out. The *Loramyetaceae*, containing *Loramycetes*, a genus placed in the *Sphaeriales* by Müller and von Arx (1962), is excluded because ascomata are apothecioid (Digby and Goos 1987).

Several groups of related families are recognizable within the order. The *Xylariaceae* includes species whose ascospores are brown, one celled or septate with a dwarf cell that is often pallid, or rarely one septate, usually with an elongate germ slit in the wall; the ascomata typically develop within stromatic tissues, beneath a clypeus or in hyphal subiculum; the peridium is composed of compressed rows of cells; the apical ring of the ascus is typically amyloid. The taxa of the *Coniochaetaceae* also have brown, one-celled ascospores with a germ slit. Their

ascomata are superficial on the substrate, peridia are more pseudoparenchymatous, asci have a nonamyloid apical ring, and anamorphs are enteroblastic phialidic. This family is arranged in the Sordariales in the present study.

The Diatrypaceae, with oblong and allantoid, mostly light brown ascospores in clavate and stipitate asci, are readily set apart. They show variations in stromata and configuration of ascomata as well as amyloidity or non-amyloidity of the apical ring of the ascus. In members of the Boliniaceae stromata and arrangement of ascomata are also variable. Small brown, nonallantoid ascospores have a minute terminal germ pore and asci have a nonamyloid apical ring.

Another major group of taxa centers around the Amphisphaeriaceae, whose ascospores vary in pigmentation and septation and when dark pigmented frequently bear germ pores. Members of the Amphisphaeriaceae typically have sphaeroid ascomata immersed in the substrate beneath a clypeus; the apical ring of the ascus is often amyloid. Additionally, the anamorphs often produce versicolorous, several-septate, appendaged conidia. The Amphisphaerellaceae is not yet well understood, and was recognized by the presence of several germ pores in the ascospores, often ectorial in arrangement (Munk 1953). For the present, I retain *Amphisphaerella* under the Amphisphaeriaceae as do O. Eriksson and Hawksworth (1986b, 1987a, 1990). The Clypeosphaeriaceae is separated for taxa whose ascomata, usually beneath a clypeus, form a conspicuous papilla or beak, whose large apical ring in the ascus is usually nonamyloid, and whose anamorphs are not yet known. Members of the Thyridiaceae produce soft, often lightly pigmented, stromatic tissues, where the globose ascomata may be arranged in valsoid or diatrypoid configuration; the apical ring of the ascus is nonamyloid. Some of the species produce both holoblastic and enteroblastic-phialidic conidia. The Melogrammataceae is related to the Thyridiaceae by texture of stroma; the clavate asci and light brown ascospores differ in shape in *Melogramma* and the anamorph is holoblastic. The Cainiaceae, erected by Krug (1978) for the European *Cainia*, has immersed ascomata and asci that resemble those in the Amphisphaeriaceae. The uniseptate, brown ascospores are unique: conspicuous longitudinal ridges open as several elongate germ slits. Krug (1978) suggested that *Entosordaria* might belong in this family, but that genus is now relegated to synonymy with *Clypeosphaeria* in the Clypeosphaeriaceae (Barr 1989). *Stromatoneurospora* (Jong and Davis 1973) could be compared to *Cainia* because the ascospores bear longitudinal ridges, although ascomata are seated in the periphery of a fleshy pulvinate stroma.

The biotrophic species of the Phyllachoraceae typically have hyaline or slightly pigmented ascospores, a non-amyloid apical ring in the ascus, and stromatic development that causes hypertrophy of the host tissues. Related taxa



in the Hyponectriaceae are saprobic or hemibiotrophic, at times forming a clypeus but not causing noticeable hypertrophy; their asci frequently have an amyloid apical ring.

Finally, two families having superficial ascomata and hyaline or lightly pigmented ascospores are included in the order. Taxa of the Trichosphaeriaceae have globose, papillate, often setose ascomata, and small, one-celled or one- to few septate ascospores. (The Niessliaceae is separated from this family and is arranged under the Hypocreales.) The Acrospermaceae includes taxa whose ascomata are vertically elongate; both asci and ascospores are elongate. Although the position of the family has been debated, the presence of apically free paraphyses indicates that it is a somewhat aberrant member of the Xylariales.

#### Key to Families of the Xylariales

1. Ascospores brown, one celled or with small terminal cell, rarely one septate, with elongate germ slit.....Xylariaceae
1. Ascospores hyaline or brown, one celled or septate, lacking elongate germ slit.....2
2. Ascospores light brown (rarely dark), mostly one celled; ascomata immersed in stromatic tissues in or erupting from substrate in varying configurations....3
2. Ascospores variable in pigmentation and septation; ascomata variable in position and stromatic tissues..4
3. Ascospores allantoid; asci octo- or polysporous, apical ring amyloid or nonamyloid.....Diatrypaceae
3. Ascospores ellipsoid or ovoid, often compressed, with terminal germ pore; asci octosporous, apical ring non-amyloid.....Bolinaceae
4. Ascomata or small stromata superficial on substrate in subiculum or on thin stromatic crust at times....5
4. Ascomata immersed in substrate, under clypeus or in stromatic tissues.....6
5. Ascomata globose or ovoid, often setose over surface, solitary or gregarious; ascospores hyaline or light dull brown, one celled or one or few septate..Trichosphaeriaceae
5. Ascomata vertically elongate or ovoid, surface glabrous, solitary or few in reduced stroma; ascospores hyaline, filiform, usually multiseptate.....Acrospermaceae
6. Usually biotrophic, causing blotches or hypertrophy of substrate; ascomata typically immersed beneath clypeus in pseudostromatic tissues; apical ring of ascus typically nonamyloid.....Phyllachoraceae
6. Not usually biotrophic nor causing blotches or hypertrophy; ascomata immersed in stroma or beneath clypeus; apical ring of ascus amyloid or nonamyloid..7
7. Ascospores hyaline to light brown, usually thin walled, in oblong, cylindric or inflated asci, apical ring usually amyloid; ascomata often beneath clypeus.....Hyponectriaceae

7. Ascospores hyaline or brown, thickened and firm walled, in cylindric or clavate asci, apical ring nonamyloid or amyloid; ascomata in stromatic tissues or beneath clypeus.8
8. Stromatic tissues soft, ascomata globose in valloid or diatrypoid configuration; apical ring of ascus nonamyloid; ascospores brown, lacking germ pore.....9
8. Stromatic tissues firm when formed, ascomata sphaeroid, in various configurations or beneath conspicuous clypeus; apical ring of ascus amyloid or nonamyloid; ascospores hyaline or brown, germ pore(s) often present when brown.....10
9. Asci clavate; ascospores elongate fusoid, usually three septate.....Melogrammataceae
9. Asci oblong cylindric; ascospores ellipsoid, one septate or muriform.....Thyridiaceae
10. Apical ring of ascus usually nonamyloid; ascomata with stout, thick-walled papilla or beak.....Clypeosphaeriaceae
10. Apical ring of ascus usually amyloid; ascomata with short, inconspicuous papilla or short beak.....Amphisphaeriaceae

Xylariaceae Tulasne & C. Tulasne, Sel. Fung. Carp. 2: 3. 1861.

Stromatic tissues well developed, immersed, erumpent or superficial, firm, carbonaceous or fleshy, or small and tightly appressed to single or few ascomata, or forming clypeus above immersed ascomata, or reduced to basal hyphae or subiculum, hyphal or pseudoparenchymatous, brightly pigmented or black externally, white to dark internally, occasionally gelatinous, ectostromatic layer separable in some, forming crustose, applanate, cupulate, pulvinate, globose, cylindric, stipitate, clavate, turbinate or discoid structures. Ascomata immersed in or erumpent to superficial on stroma or in superficial subiculum, often in diatrypoid or valsoid configuration, globose, sphaeroid or ovoid, perithecioid or at times cleistothecioid, small to large; apex rounded, papillate or short beaked, ostiole periphysate, or nonostiolate; peridium of compressed rows of cells, darkened externally, pallid internally. Asci peripheral or sometimes basal, cylindric, oblong, clavate or subglobose and deliquescent, usually octosporous; apical ring rarely lacking, shallow or large and complex, refractive, typically amyloid, pulvillus small to large, often chitinous. Paraphyses usually numerous, narrow, at times lacking at maturity. Ascospores mostly brown, rarely lightly pigmented, ellipsoid, ovoid, fusoid, oblong or cuboid, symmetric or asymmetric, one celled, at times with terminal pallid dwarf cell, rarely one septate; wall firm, smooth or ornamented, typically with short to elongate, straight, curved or spiral germ slit, surrounded by gel coating at times or bearing terminal appendages; one or more globules; uniseriate, biseriate or crowded in the

ascus.

Anamorphs hyphomycetous, formed on young stromata or ascomata, on anamorph stromata or in synnemata; conidigenous cells holoblastic, proliferating sympodially, denticulate; conidiophores persistent or disarticulating; conidia small, hyaline or pallid, one celled. Described as *Acanthodochium*, *Basidiobotrys*, *Dematophora*, *Dicyma*, *Geniculosporium*, *Hadrotrichum*, *Nodulisporium*, *Periconiella*, *Rhinocladia*, *Virgariella*, *Xylocladium*, *Xylocoremium*.

Saprobic or hemibiotrophic, frequently on woody substrates, also fruits and strobili, leaves, culms and rachises of monocots, dung, plant debris.

The conspicuous, often massive and variable stromatic structures produced by many members of the family present difficulties in delimiting generic boundaries but they have engaged the attention of many investigators. Only a few of the investigations are cited below. Rogers (1979) produced a masterful summary of many taxonomic and biological aspects in members of the family. His "central core" of genera includes most of those listed in the key, as well as some extralimital ones. Numerous species of *Xylaria* in temperate North America have been studied by Rogers (1986a) who provided references to many articles concerning individual species or groups of species. *Hypoxylon* was treated in detail by Miller (1961). Martin (1967b, 1968a, b, 1969a) suggested different alignments of the taxa. L. Petrini and Müller (1986) treated both teleomorphs and anamorphs of *Hypoxylon* species in Europe, and discussed their ecology and occurrence as endophytes. *Ustulina*, treated as a species of *Hypoxylon* by Miller (1961), has features of *Xylaria* in the anamorph. *Daldinia* was monographed by Child (1932); the European species were described by L. Petrini and Müller (1986). *Biscogniauxia* O. Kuntze is utilized for species more familiarly known under the name *Nummularia* (Tulasne & C. Tulasne 1863, non Hill 1856). Pouzar (1979) described several taxa and enlarged the generic concept. *Camillea* has a few North American taxa and numerous Amazonian ones; the ascospores are lightly pigmented, lack a germ slit, and have ornamented walls; the anamorphs where known belong to *Xylocladium* (Laessle et al. 1989). *Pulveria* is cleistothecioid and the small, globose, deliquescent asci are borne in chains (Malloch and Rogerson 1977). The stromata are crustose and are similar to those of several species in *Hypoxylon*. *Entonaema*, having gelatinous-fleshy stromata, is represented in temperate North America by *E. liquescens* Moeller (Rogers 1981, 1982). Of the two genera having stipitate and fleshy stromata, *Poronia* was studied by Jong and Rogers (1969) and Paden (1978) and *Podosordaria* by Krug and Cain (1974a). After consultation with G. Samuels, who has observed a xylariaceous anamorphic state in nature and has grown it in culture, *Thuemenella* (*Chromocreopsis*) *cubispora* (Ellis & Holway) Boedijn is removed from the Hypocreales

and inserted in the Xylariaceae. Other species that have been placed in the genus differ from this, the type species (Corlett 1985). *Thuemenella cubispora* forms small yellowish pulvinate or lobed stromata, has no apical ring in the ascus, and has dark, smooth, cuboid ascospores that apparently lack a germ slit.

*Rosellinia*, whose stromata are small and surround one or few ascomata and often develop in a subiculum, was treated in part by Miller (1928), and with different delimitation by Martin (1967b) and L. Petrini and Müller (1986). *Astrocystis*, typified by *A. mirabilis* Berk. & Broome, is pantropical on bamboo culms. A carbonized stromatic layer surrounds one or few ascomata. During maturation the expanding ascomata break the stromatic tissues in a stellate fashion (pseudovolva, Diehl 1925), exposing the ascoma. A separate family Astrocystidaceae Hara 1913 has been proposed. The Japanese *Collodiscula japonica* Hino & Katumoto develops on bamboo culms in a similar fashion (Samuels, Rogers and Nagasawa 1987). Here the ascospores are one septate with an added, inconspicuous, hyaline basal cell. An unusual anamorph, *Acanthodochium collodisculae* Samuels et al. is connected and covers at first the developing ascomata. Conidiogenous cells are holoblastic, proliferate sympodially and are coarsely denticulate; conidia are hyaline, rather large, one celled. *Ascotricha* has been placed in the Chaetomiaceae (Ames 1963, Hawksworth 1971) or the Coniochaetaceae (Malloch and Cain 1971c, Hawksworth and Wells 1973). Khan and Cain (1977) described and illustrated asci with an amyloid apical ring in *A. erinacea* Zambett, although asci are deliquescent at maturity in many species of *Ascotricha* (Roberts et al. 1984). The one-celled, dark ascospores containing an elongate germ slit and the holoblastic *Dicyma* anamorph led Khan and Cain to arrange *Ascotricha* in the Xylariaceae, where O. Eriksson and Hawksworth (1987c, 1990) also placed the genus. A thin peridium and no well-developed stromatic tissues set the genus apart in the Xylariaceae.

*Anthostomella* is a species-rich genus whose ascomata develop in the substrate beneath a clypeus. Considerable variability is seen in asci and in ascospore shapes and sizes, the presence of a dwarf cell, appendages or gel coating, as illustrated by Francis (1975). Martin (1969c) obtained *Nodulisporium*-like anamorphs in a few species but Francis was unable to confirm this from any of the species that she grew. The pantropical *Seynesia erumpens* (Berk. & Curtis) Petrak seems related and Samuels (personal communication) has suggested its inclusion in the family. The ascospores have a median septum, a germ slit in each cell, and a gel coating that extends as terminal appendages. *Helicogermis* was separated from *Anthostomella* for *H. celastri* (S. Kale & V. Kale) Lodha & Hawksworth from India (Hawksworth and Lodha 1983). Dargan et al. (1984) believed that *Helicogermis* probably could be placed in synonymy

under *Rosellinia* but they retained the genus separately. L. Petrini et al. (1987) redescribed and discussed the endophytic *Anthostomella calligoni* Frolov, which also has ascospores with a spiral germ slit, and opted to retain it and *A. celastri* S. Kale & V. Kale under *Anthostomella*. Hawksworth (in O. Eriksson and Hawksworth 1987b) urged that *Helicogermis* be upheld. Two North American entities, as yet unnamed, belong in the genus by the production of a small stroma around one or few ascomata and the presence of a spiral germ slit in the ascospore walls. *Hypocopra*, with the lectotype species *H. merdaria* (Fr.) Kickx (Lundqvist 1972), contains coprophilous species that have small stromata surrounding a single ascoma, clypeate at the surface; the brown ascospores with a germ slit are surrounded by a gel coating. The genus was monographed by Krug in his unpublished dissertation and numerous species were described by Krug and Cain (1974b). Species of *Lopadostoma* are wood inhabiting, have a few ascomata grouped in valsoid configuration in a small stroma that may be delimited by black margins. *Lopadostoma turgidum* (Pers.: Fr.) Trav. is the type species (O. Eriksson 1966), not *L. gastrinum* (Fr.) Traverso (Clements and Shear 1931, Shear 1938, von Arx and Müller 1954). Martin (1969c) provided a key to species that he included in *Lopadostoma*, none of which was cultured. His treatment includes several taxa that are now treated elsewhere. An associated anamorph that forms locules in stromata is described as *Cytospora*-like, with narrow conidia, but this goes back to Nitschke (1867) and Wehmeyer (1926) could not confirm the connection.

Many tropical or otherwise extralimital genera have been recognized. These include: *Camillea bacillum* (Mont.) Mont., with columnar stromata, dark ascospores, asci lacking an apical ring (Samuels and Müller 1980), now transferred as *Leprieuria bacillum* (Mont.) Laessle et al. (Laessle et al. 1989); *Kretzschmaria* with stipitate and convex stromata, often aggregated in crusts (Rogers et al. 1987); *Rhopalostroma* with stipitate, globose stromata, asci lacking apical ring, brown ascospores (Hawksworth 1977); *Phylacia* with stipitate, globose stromata, asci lacking apical ring and deliquescent early, amber ascospores (Martin 1969b, Rodrigues and Samuels 1989); *Thamnomycetes* with filamentous stromata, asci lacking apical ring (Martin 1969b, Samuels and Müller 1980); *Sarcoxydon* with solid, spongy, pulvinate to hemispheric stromata (Rogers 1981). *Penzigia* has white interior tissues as in *Xylaria* but is sessile as in *Hypoxydon*. Its standing is questioned, for example by Rogers et al. (1987) and Rogers (1990); Laessle (1989) opted to include the genus under *Xylaria*.

The variations in anamorphs range across genera. As examples of studies on these states, Jong and Rogers (1972) illustrated variations among species of *Hypoxydon*. Rogers (1984a, 1986b) utilized anamorphs to separate species of *Xylaria*, and Callen and Rogers (1986) treated anamorphs in species of *Biscogniauxia*. Other characteristics that have

taxonomic significance have been utilized in attempts to determine relationships among species or their disposition to genera. Martin (1967a) discussed such characteristics as pigmentation of stromatic tissues, shape and size of the apical ring in asci, pigmentation, shape, wall ornamentation, symmetry or asymmetry, presence of exospore as hyaline sheath, position of germ slit in the ascospores, in addition to anamorphs. Martin went on to provide details of his view of genera and species in a series of articles (Martin 1967b, 1968a, b, 1969a, b, c, 1970, 1976).

#### Key to Genera of Xylariaceae

1. Stromatic tissues well developed, often forming massive, erumpent-superficial structures containing numerous ascomata.....2
1. Stromatic tissues reduced or lacking, immersed or erumpent to superficial, containing one or few ascomata.....11
  2. Stromatic tissues fleshy or gelatinous, often brightly pigmented, not carbonaceous.....3
  2. Stromatic tissues carbonaceous or firm, tough or woody.....6
3. Stromata subglobose or pulvinate, gelatinous, surface gelatinous fleshy, yellow or white, drying hornlike, on woody substrates.....*Entonaema*
3. Stromata not subglobose nor gelatinous, dark or yellow..4
  4. Stromata sessile, pulvinate, yellow, on woody substrates; ascospores cuboid.....*Thuemenella*
  4. Stromata stipitate, fertile portion cupulate, discoid or pulvinate, dark, on dung or plant debris..5
5. Fertile portion cupulate or discoid, ascomata papillate over upper surface.....*Poronia*
5. Fertile portion pulvinate, ascomata papillate over upper and lateral surfaces.....*Podosordaria*
6. Ascospores lightly pigmented, lacking germ slits, wall ornamentation poroid, reticulate, ribbed or echinulate to verrucose.....*Camillea*
6. Ascospores brown to blackish, germ slits present, walls smooth or variously ornamented.....7
7. Stromata typically stipitate, fertile portion clavate or filiform, simple or branched; internal stromatic tissues white.....*Xylaria*
7. Stromata sessile; internal stromatic tissues dark.....8
  8. Stromata applanate, bipartite, ectostroma dehiscent; ascospores symmetric, lacking sheath.....*Biscogniauxia*
  8. Stromata variable in shape, not bipartite; ascospores asymmetric.....9
9. Stromata subglobose or hemispheric, zonate within.....*Daldinia*
9. Stromata crustose, applanate, effused, pulvinate or hemispheric, not zonate within.....10

10. Stromata crustose; ascomata cleistothecioid; asci subglobose, lacking apical ring, in chains, deliquescent.....*Pulveria*
10. Stromata variable in shape; ascomata perithecioid; asci cylindric, with apical ring, not in chains nor deliquescent.....*Hypoxylon*
11. Ascomata few, immersed in valsoid configuration in stromatic tissues, often delimited by blackened marginal line.....*Lopadostoma*
11. Ascomata usually solitary, upright in small compact stroma or beneath clypeus or superficial on subiculum....12
12. Ascomata immersed separately beneath darkened clypei.....*Anthostomella*
12. Ascomata immersed or erumpent to superficial, separate or few surrounded by pseudoparenchymatous tissues or on subiculum.....13
13. Germ slit spiral, encircling ascospores two to four times.....*Helicogerm slit*
13. Germ slit straight or oblique, visible in one face of ascospore only.....14
14. Stromatic tissues pallid except at surface; on dung.....*Hypocopra*
14. Stromatic tissues darkened, subiculum present when ascomata superficial.....15
15. Superficial ascomata on subiculum, lacking stromata, bearing *Dicyma* anamorph.....*Ascotricha*
15. Immersed or superficial ascomata each surrounded by stromatic tissue, not bearing *Dicyma* anamorph.....16
16. Stromatic tissues breaking stellately; on culms of bamboo.....*Astrocystis*
16. Stromatic tissues not breaking stellately; mostly on woody substrates.....*Rosellinia*

**Diatrypaceae** Nitschke, Verh. Naturhist. Vereines Preuss. Reinl. Westphalens 26(2): 62. 1869.

Stromatic tissues immersed to erumpent, compact, of fungus hyphae, or effuse and mixed with substrate cells, at times delimited by black marginal zone. Ascomata immersed, globose or ovoid, medium sized, in diatrypoid, valsoid, eutypoid or eutypelloid configuration in stromatic tissues; apex short to long beaked, tip often sulcate, ostiole periphysate; peridium of rows of compressed cells, darkened externally, pallid internally. Asci peripheral, clavate and stipitate, stipe elongate or short, octosporous or polysporous; apical ring shallow, amyloid or nonamyloid. Paraphyses numerous, narrow. Ascospores yellowish to light brown or at times dark brown, oblong and typically allantoid, slightly or strongly curved, one celled or less frequently septate; wall smooth, thin, firm, lacking germ pores or germ slit; two or three globules; biseriate or crowded in the ascus.

Anamorphs coelomycetous, pycnidia or open acervuli or

enclosed locules in stromatic tissues, or hyphomycetous on stroma surface or forming synnemata; conidiogeous cells holoblastic, proliferating percurrently or sympodially; conidia hyaline, one celled, allantoid, cylindric or filiform, often curved. Described as *Cytosporina*, *Harpographium*, *Libertella*, *Naemospora*, *Paracytospora*, *Phaeoisaria*.

Hemibiotrophic or saprobic, at times biotrophic, in woody substrates, including larger monocots.

The family is one that has been accepted by most mycologists, who place special emphasis upon stromatic tissues, configuration of ascomata, presence of sulcate tips to beaks, and allantoid ascospores in octosporous or polysporous asci. Species are frequently collected from woody branches in temperate North America. Studies on the Diatrypaceae by Tiffany and Gilman (1965), Glawe and Rogers (1984) and Rappaz (1987), recognize only a few genera. These are based upon classical separations that are utilized in the following key to genera. Associated anamorphs have been known for some time. Wehmeyer (1926) summarized much of the available early information in his review of species in the "Allantosphaeriaceae" and Diaporthaceae. Recent studies, such as those of Glawe and Rogers (1982a, b, 1984, 1986), Glawe (1983a, b, 1989) and Rappaz (1987) have shown some of the patterns of variation in conidogenesis.

The configurations of ascomata are defined, following Rappaz (1987) and Vasilyeva (1988), on page 51. Diatrypoid (Pl. 1, M) configuration of ascomata in well-developed stromatic tissues, mostly of fungus cells, is typical for the octosporous *Diatrype* and the polysporous *Diatrypella*. Valsoid (Pl. 1, G, H) or eutypelloid (Pl. 1, K, L) configuration of ascomata in less developed stromatic tissues, often incorporating substrate cells, is typical for the octosporous *Eutypella* and the polysporous *Cryptovalsa*. Rappaz (1989b) proposed to conserve *Eutypella* over the earlier names *Quaternaria* and *Scoptria*. Additionally, he (Rappaz 1987) submerged the taxa described under *Peroneutypa* and the illegitimate *Peroneutypella*, all with elongate beaks and in valsoid configuration, with small asci and ascospores, often causing necrosis of the substrate, as *Eutypella scoparia* (Schwein.: Fr.) Ellis & Everh., with a long list of synonyms. Barr (1985) had utilized *Scoptria* for a genus in the Calosphaeriales, but must instead use *Wegelia* for those species that have erumpent, elongate beaks and a calosphaeriaceous centrum.

Eutypoid (Pl. 1, F, J) configuration of ascomata in less developed stromatic tissues, often incorporating substrate cells, does not include a polysporous taxon to my knowledge. Two octosporous genera are recognized. The species of *Cryptosphaeria* develop in the periderm and often have a blackened marginal zone that dips into wood tissues. Rappaz (1989a) proposed that *Cryptosphaeria* Ces. & de Not.



be conserved against *Cryptosphaeria* Grev. in order to retain the name. He (Rappaz 1987) included in synonymy both *Cladosphaeria* and *Cryptosphaerina*; the type species of both genera fall under *Cryptosphaeria eunomia* (Fr.: Fr.) Fuckel var. *fraxini* (Richon) Rappaz. Species of *Eutypa* develop in wood and periderm and do not form a blackened marginal zone.

Rappaz (1987) recognized several small genera that are subtropical or tropical in distribution. The species of *Echinomyces* have diatrypoid configuration and small asci and ascospores. Those of *Leptoperidia* are related to *Eutypella scoparia*, but differ in their thin, pallid peridium. The species of *Dothideovalsa* are parasitic in branches, have eutypoid configuration, the stroma is composed of globose, heavily pigmented cells, and no peridium is recognizable. *Rostronitschkia nervincola* Fitzp. is widely erumpent from leaves of *Gesneria*. Stromatic tissues are similar to those of *Dothideovalsa* and no peridium is recognizable.

#### Key to Genera of Diatrypaceae

1. Stromatic tissues well developed, erumpent, composed mostly of fungus cells; ascomata in diatrypoid configuration, beaks separate, short, reaching surface of stroma..2
1. Stromatic tissues less developed, often mixed with cells of substrate; beaks separate or converging to or beyond surface of stroma, short or elongate.....3
2. Asci octosporous.....*Diatrype*
2. Asci polysporous.....*Diatrypella*
3. Ascomata typically in valsoid or eutypelloid configuration; asci octosporous or polysporous.....4
3. Ascomata typically in eutypoid configuration; asci octosporous.....5
4. Asci octosporous.....*Eutypella*
4. Asci polysporous.....*Cryptovalsa*
5. Stromatic tissues and ascomata in periderm, blackened marginal zones often present; beaks short, to surface.....
- .....*Cryptosphaeria*
5. Stromatic tissues and ascomata in wood or periderm, blackened marginal zones lacking; beaks short or elongate, to or beyond surface.....*Eutypa*

*Boliniaceae* Rick, Brotéria, Ser. Bot. 25: 65. 1931.

Stromatic tissues immersed or erumpent to superficial, slight as soft interwoven hyphae or thin crustose layer surrounding one or few ascomata, or well developed, small to large, firm, with compact ectostroma and loosely interwoven entostroma, crustose, applanate, pulvinate, clavate, subglobose, peltate, turbinate or pyriform. Ascomata immersed in stroma, globose, ovoid or vertically elongate, small to large, polystichous at times; apex papillate or

beaked, ostiole periphysate; peridium narrow, of compressed rows of cells, dark externally, pallid internally. Asci peripheral, cylindric or clavate, stipitate, octosporous; apical ring shallow or lacking, nonamyloid. Paraphyses narrow, numerous. Ascospores light smoky brown, reddish brown or dark brown, oblong or ellipsoid, laterally compressed at times, one celled or one septate, with small pallid cell at times; wall smooth or ornamented, minute germ pore at one end, rarely pore at each end; one or two globules; uniseriate or partially biseriate in the ascus.

Anamorphs scarcely known.

Saprobic or hemibiotrophic, in woody substrates.

*Camarops* has been the sole genus in the family according to the definitive treatment by Nannfeldt (1972), who set forth the diversities of stromatic development and configuration of ascmata in some detail. Shear (1938) had earlier concluded that *Camarops*, *Bolinia* and *Solenoplea* were not separable genera. Callan and Rogers (1989) synonymized *Peridoxylon* with *Camarops*. Nuss (personal communication) has evidence of the perennial nature of certain species of *Camarops*, an unusual characteristic for pyrenomycetous fungi. Samuels and Rogers (1987) described *Camarops flava*, whose globose, papillate ascmata are superficial and surrounded by a much reduced stroma. Samuels and Rogers (1987) also erected *Apiocamarops* for a South American species whose reduced stroma is soft, furfuraceous and white, surrounding several ascmata, and whose ascospores are one septate with a small hyaline cell. The larger brown cell contains a germ pore.

Nannfeldt (1972) doubted a relationship with the Xylariaceae, but Romero and Minter (1988) reported that four species of *Camarops* possessed a fluorescent apical ring in the asci, similar to those found in members of the Xylariaceae. O. Eriksson and Hawksworth (1988a) also noted that *C. microspora* Karsten at least has one-septate ascospores. *Rhynchostoma* is newly added to the family. The species do not have a well-developed stroma; instead it is reduced to a narrow, gelatinized outer layer over brownish, interwoven hyphae that cover the widely erumpent, beaked ascmata. As in most species of *Camarops*, asci in *Rhynchostoma minutum* Karsten (including *R. rubrocinctum* Karsten) and *R. rubefaciens* (Peck) Barr (Barr et al. 1986) are thin walled, stipitate, and lack an apical ring. The small brownish ascospores are one septate in *R. minutum*, one celled in *R. rubefaciens*. Both species have the ascospore wall ornamented by spiral, shallow ridges (Mathiassen 1989), somewhat similar to those in *Camarops flava* (Samuels and Rogers 1987). Mathiassen obtained an anamorph that is *Acremonium*-like from *R. minutum*.

1. Ascomata widely erumpent, beaked; stromatic tissues reduced to closely appressed layer surrounding each ascoma ..... *Rhynchostoma*  
 1. Ascomata immersed in stromatic tissues of diverse shapes and sizes, beaked, or papillate when stromatic tissues reduced..... *Camarops*

**Amphisphaeriaceae** Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 259. 1885.

Stromatic tissues usually forming blackened clypeus over one or several ascomata, at times as crustose layer over erumpent ascomata or compact stromata surrounding few ascomata, rarely stromatic tissues lacking. Ascomata perithecioid, immersed to erumpent, sphaeroid or globose, small to medium, separate or gregarious; apex rounded, papillate or short beaked, ostiole periphysate; peridium of rows of compressed cells, dark externally, hyaline internally. Asci peripheral or basal, cylindric or broadly oblong, mostly octosporous; apical ring shallow or enlarged, usually amyloid, pulvillus small, often chitinous. Paraphyses narrow, numerous. Ascospores hyaline to yellowish or shades of brown, ellipsoid, oblong or fusoid, one celled or one or several septate; wall smooth or ornamented, with inconspicuous terminal germ pore at times in pigmented ascospores, rarely in the form of short radiating slits, or with two to six germ pores in equatorial band or scattered; one or more globules in each cell; uniseriate or partially biseriate in the ascus.

Anamorphs coelomycetous, forming acervuli or pycnidia; conidiogenous cells enteroblastic phialidic, proliferating percurrently or holoblastic, determinate; conidia septate, often versicolorous, often appendaged; spermatia produced holoblastically on sympodially proliferating cells in same conidiomata at times (Swart 1973). Described as *Bleptosporium*, *Hyalotiopsis*, *Labridella*, *Pestalotia*, *Pestalotiopsis*, *Seimatosporium*, *Seiridium*, *Truncatella*.

Hemibiotrophic or saprobic in leaves, stems, branches of various plants.

*Amphisphaerella* has been separated into the *Amphisphaerellaceae* Munk (Dansk Bot. Ark. 15(2): 88. 1953, nom. inval.); the species have brown, one-celled ascospores with two to six germ pores arranged equatorially or scattered. Until more information is available, the genus is retained in the *Amphisphaeriaceae* (O. Eriksson 1966, O. Eriksson and Hawksworth 1987c, 1990).

Several of the genera (*Broomella*, *Discostroma*, *Lepteutypa*, *Pestalospaeria*) accepted in the restricted concept of the family have in common related anamorphic states belonging to *Pestalotiopsis*, *Seimatosporium*, *Seiridium* or *Truncatella* (Samuels, Müller and Petrini 1987, Shoemaker et al. 1989). Most are acervular, with enteroblastic-

phialidic conidiogenous cells, having percurrent proliferations, and conidia often versicolorous, septate, bearing one or more apical appendages and often a single basal appendage. *Labridella cornu-cervae* Brenckle, the anamorph of *Griphosphaerioma kansensis* (Ellis & Everh.) Shoemaker, is pycnidial; the conidiogenous cells are holoblastic, determinate, and the septate conidia have the pallid apical cell tapered into a branched appendage (Shoemaker 1963, Sutton 1969, 1980). No anamorphs have been reported for species of *Phomatospora* and *Amphisphaerella* to my knowledge; Samuels (personal communication) has grown *Phomatospora berkeleyi* Sacc. and obtained ascomata but no anamorph. For *Amphisphaeria* only an associated state in *Bleptosporium* (Nag Raj 1977a) continues the trend.

Shoemaker and Müller (1963) monographed species of *Broomella* with their *Pestalotia* (*Pestalotiopsis*) states, and reported on species now in *Discostroma* and their *Seimatosporium* or *Seiridium* states (Shoemaker and Müller 1964, Müller and Shoemaker 1965). Shoemaker et al. (1989) added another species to *Broomella*, recognized *Truncatella* as the correct genus for anamorphs in this genus, and provided keys to both teleomorph and anamorph species. Brockmann (1977) monographed the European species of *Discostroma*, including the didymosporous *Paradidymella*, several of which are also known from North America. Species of *Pestalosphaeria* with *Pestalotiopsis* anamorphs are widespread (Barr 1975, Shoemaker and Simpson 1981, Nag Raj 1985, van der Aa 1987, Samuels, Müller and Petrini 1987). In *Lepteutypa* the anamorphs are species of *Seiridium* (Shoemaker and Müller 1965, Swart 1973, Nag Raj and Kendrick 1986). Some extralimital genera belong in the *Amphisphaeriaceae* also. *Hymenoplella* (Shoemaker and Müller 1965) and *Blogiascospora* (Shoemaker et al. 1966) are both European taxa separated by ascospore characteristics and have *Seiridium* anamorphs. *Ellurema* was erected (Nag Raj and Kendrick 1986) for *Lepteutypa indica* Punithalingam, whose anamorph is pycnidial and conidiogenesis holoblastic, described as a species of *Hyalotiopsis*.

#### Key to Genera of *Amphisphaeriaceae*

1. Ascospores one celled.....2
1. Ascospores one or more septate.....3
  2. Ascospores hyaline to light brown, striate, germ pores lacking.....*Phomatospora*
  2. Ascospores brown, smooth, two to six germ pores in equatorial band or scattered.....*Amphisphaerella*
3. Ascospores elongate fusoid, three septate, bearing elongate appendages.....*Broomella*
3. Ascospores oblong, ellipsoid or short fusoid, one or several septate, not appendaged.....4
  4. Ascospores hyaline to light brownish.....5
  4. Ascospores clear brown or dark brown.....6

5. Ascomata grouped and surrounded by stromatic tissues; ascospores one (three) septate.....*Griphosphaerioma*  
 5. Ascomata separate or gregarious beneath clypeus or beneath thin stromatic crust when erumpent; ascospores one or several septate, at times with longitudinal septum.....*Discostroma*  
 6. Ascospores one septate, surface smooth or ornamented.....*Amphisphaeria*  
 6. Ascospores two or more septate.....7  
 7. Ascospores two septate, eusepta heavily pigmented, surface often longitudinally striate.....*Pestalosphaeria*  
 7. Ascospores three septate, distosepta often incomplete, surface smooth or verruculose.....*Lepteutypa*

**Melogrammataceae** Winter in Rabenhorst, Kryptogamen-Fl.

1(2): 797. 1886.

Stromata erumpent, pulvinate or somewhat irregular, soft textured, of reddish-brown, pseudoparenchymatous cells. Ascomata immersed, peripheral, globose, medium; apex papillate or short beaked to surface, ostiole periphysate; peridium of compressed rows of cells, brown externally, hyaline internally. Asci peripheral, clavate, short stipitate, octosporous; apical ring shallow, non-amyloid. Paraphyses narrow. Ascospores light brown, end cells often pallid, elongate fusoid, asymmetric, curved, several septate; wall thin, smooth; one or more globules per cell; in fascicle in upper part, biseriate in lower part of the ascus.

Anamorph coelomycetous; conidiogenous cells holoblastic, proliferating sympodially; conidia elongate falcate.

Hemibiotrophic in woody plants.

This family at present contains only one genus. *Melogramma campylosporium* Fr., the type and most common species, has a number of features in common with members of the Thyridiaceae, including erumpent, pulvinate, soft-textured stromata containing peripherally arranged ascomata. The anamorph was described by LaFlamme (1976), who separated *Melogramma* from *Melanamphora spinifera* (Wallr.) LaFlamme, a taxon that belongs in the Diaporthales. Pycnidia produced in culture formed holoblastic-sympodial conidiogenous cells from which developed elongate-falcate conidia. In short stipitate, clavate asci and elongate, fusoid ascospores, as well as in conidiogenesis, *Melogramma* differs from the taxa assigned to the Thyridiaceae so that two families are necessary.

Thyridiaceae Yue & O. Eriksson, Syst. Ascomyc. 6: 233. 1987.

Stromatic tissues immersed becoming erumpent to superficial, soft textured, brightly pigmented to reddish brown. Ascomata immersed in diatrypoid or valsoid configuration, globose, medium; apices short or long beaked to surface or extending beyond, ostiole periphysate, at times convergent beaks merging into single ostiole; peridium of compressed rows of cells, brown externally, hyaline internally. Asci peripheral, oblong cylindric, usually octosporous; apical ring shallow, nonamyloid. Paraphyses narrow. Ascospores shades of brown, ellipsoid or biconoid, symmetric, one septate or muriform; wall firm, thickened, smooth or ornamented, verruculose, foveolate or reticulate; one globule per cell; uniseriate in the ascus.

Anamorphs coelomycetous where known, forming multiloculate conidiomata in stroma; conidiogenous cells enteroblastic phialidic; conidia small, hyaline; holoblastic-sympodial conidia produced from hyphae and budding ascospores also reported. Described as *Cytosporella*-like, *Exophiala*-like, *Pleurocytospora*.

Saprobic or hemibiotrophic in woody substrates.

Yue and O. Eriksson (1987) erected this family to include *Thyridium* and their new genus *Sinosphaeria*, both dictyosporous genera that differ by configuration of ascomata in rather soft stromata. The asci have a nonamyloid, shallow apical ring and paraphyses are interspersed. They described periphysoids in *Sinosphaeria bambusicola* Yue & O. Eriksson, but I have not found such structures in *Thyridium vestitum* (Fr.) Fuckel (Barr 1983b). O. Eriksson and Yue (1989a) discovered that *Sinosphaeria bambusicola* had been described earlier as *Melanospora chrysomalla* Berk. & Broome, which is the type species of *Bivonella* (Sacc.) Sacc. In addition, *Thyridium flavum* Petch has yellowish stromatic tissues and ascomata in diatrypoid configuration, but darker ascospores. They concluded that *Thyridium* could accommodate the variations in stromata and ascomata that earlier separated *Sinosphaeria* and *Bivonella*. I prefer to accept two dictyosporous genera, *Thyridium* and now *Bivonella*. O. Eriksson and Yue (1989a) also believed that *Thyridium* in their sense is a member of the Hypocreales and would submerge the Thyridiaceae under the Hypocreaceae. They cited the bright pigmentation of stromatic tissues and presence of both paraphyses and periphysoids. The presence of a red pigment soluble in acetone, alcohol and 5% KOH solution in some collections of *Sinosphaeria bambusicola* they thought comparable to an orange pigment in *Nectria berolinensis* (Sacc.) Cooke that is soluble in KOH, alcohol and acetone. Bright pigments in stromata and/or ascomata do occur in taxa other than the Hypocreales, and KOH-induced red coloration in many unrelated taxa, including some Aphyllophorales. The centra of both *Bivonella*

(including *Sinosphaeria*, see Samuels and Rogerson 1989) and *Thyridium* are quite different from that in the Hypocreales. For these reasons, I accept the Thyridiaceae in the Xylariales and add two genera having uniseptate ascospores.

The ascomata, stromata and asci in species of *Valsaria* are comparable to those of *Thyridium*. *Valsonectria pulchella* Speg. forms brightly pigmented stromata similar to those of *Bivonella*. Another species, *Valsaria hypoxylodes* Ellis & Everh., (described also as *V. hypoxylodes* Rehm and *V. rehmana* Teng), forms a pulvinate, erumpent stroma as in *Valsonectria* or *Bivonella*. While the position of stromata differs somewhat from that in *Valsonectria pulchella*, other features do not, and *V. hypoxylodes* should be inserted in that genus as *Valsonectria hypoxylodes* (Ellis & Everh.) Barr, comb. nov. (basonym: *Valsaria hypoxylodes* Ellis & Everh. J. Mycol. 7: 131. 1892).

An associated anamorph, forming pycnidial locules in stromata similar to those that house ascomata of *Sinosphaeria bambusicola*, has branched conidiophores and phialidic conidiogenous cells that produce minute hyaline conidia (Yue and O. Eriksson 1987). This state is similar to the *Pleurocytospora vestita* Petrak anamorph of *Thyridium vestitum* (Leuchtmann and Müller 1986). These authors noted that the ascospores could germinate by hyphae or could bud directly to form conidia, that primary conidia were produced from holoblastic-sympodial conidiogenous cells on the mycelium and that eventually multiloculate conidiomata were formed and conidia were produced from phialides. *Valsaria insitiva* (Tode) Ces. & de Not. and *V. exasperans* (Gerard) Sacc. were noted by Wehmeyer (1923, 1926) to form locules in the same or separate stromata as those containing ascomata and to produce small allantoid conidia. Glawe (1985a) studied growth and development in a collection of *V. insitiva* and found pleomorphy also: ascospores germinated to form yeast-like cells that reproduced by budding, forming *Exophiala*-like proliferating loci, and eventually multiloculate conidiomata. The phialidic conidiogenous cells proliferated and produced small, hyaline, *Cytospora*-like conidia.

#### Key to Genera of Thyridiaceae

1. Ascospores muriform, walls smooth, uniformly pigmented or versicolorous.....2
1. Ascospores one septate, walls usually ornamented, uniformly pigmented.....3
2. Stromatic tissues yellowish, ascomata in diatrypoid configuration; ascospores pallid between pigmented septa and at tips.....*Bivonella*
2. Stromatic tissues reddish brown, ascomata in valsoid configuration; ascospores uniformly pigmented.....*Thyridium*

3. Stromatic tissues yellowish to reddish brown, ascomata in diatrypoid configuration.....*Valsonectria*  
 3. Stromatic tissues reddish brown, often compact and dark toward margins, ascomata in valsooid configuration..*Valsaria*

*Clypeosphaeriaceae* Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 554. 1886.

Stromatic tissues slight as hyphal layer around ascomata or forming darkened clypeus or compact or effused in substrate, at times forming blackened marginal zone. Ascomata immersed or erumpent, globose or sphaeroid, medium, separate, gregarious or in eutypoid or eutypelloid or valsooid to diatrypoid configuration; apex papillate or beaked, stout, thickened, central or eccentric, ostiole periphysate, tip rounded or sulcate at times; peridium firm, relatively wide, of compressed cells, externally brown, internally pallid; surface glabrous or roughened by clumps of cells and short hyphae. Asci peripheral, cylindrical or somewhat clavate and stipitate, usually octosporous; apical ring shallow or large, refractive, non-amyloid or occasionally amyloid, pulvillus chitinous at times. Paraphyses narrow, delicate, numerous. Ascospores hyaline or shades of brown, ellipsoid, fusoid or oblong, straight or inequilateral to slightly curved, appearing allantoid at times, one celled or one or several septate, pallid small cell formed at times; wall smooth or ornamented, verruculose, reticulate or longitudinally striate, at times surrounded by delicate gel coating or bearing terminal appendages, when brown often with terminal germ pore(s); one or several globules; uniseriate or partially biseriate in the ascus.

Anamorphs scarcely known.

Saprobic or hemibiotrophic in woody substrates or stout herbaceous stems and monocot culms.

This family is revived to accommodate some genera that are related to the *Amphisphaeriaceae*. They differ chiefly in the stout papillate or beaked apices of ascomata and in the typically large and nonamyloid apical ring of the ascus. Several taxa have ascomata whose apices are surrounded and thickened by clypeal tissues. *Clypeosphaeria* was reappraised by Barr (1989); *Apiorhynchostoma curreyi* (Rabenh.) Müller (Müller and von Arx 1962) is closely related. *Melomastia mastoidea* (Fr.) Schröter, with hyaline, two-septate ascospores, has similar ascomata whose apices are closely surrounded by a small clypeal structure. *Saccardoella* is added tentatively; the few collections that I have examined are also similar in ascomata and the hyaline ascospores may be elongate fusoid and multiseptate. Mathiassen (1989) believes that the asci are bitunicate in *Saccardoella transsylvanica* (Rehm) Berl., but that interpretation differs from mine.



Other taxa have ascomata surrounded by prosenchymatous stromatic tissues. Species whose ascomata develop in a valsooid or diatrypoid configuration and whose brown ascospores typically bear one or two terminal germ pores fit into *Pseudovalsaria* (Spooner 1986). *Diatrype moroides* Peck on *Alnus* appears to be conspecific with *P. foedans* (Karsten) Spooner, but has somewhat narrower ascospores. The statement in Barr et al. (1986) that Peck's species had been transferred to *Endoxylina* is incorrect. *Pseudovalsaria* could include the species described as *Endoxylina allantosporea* (Ellis & Everh.) Shoemaker & Egger on *Acer* (Shoemaker and Egger 1982). *Endoxylina* was reduced to synonymy under *Eutypa* (Rappaz 1987) and this taxon is not diatrypaceous. The two species assigned to *Urosporella* have separate or gregarious ascomata in somewhat valsooid configuration and one-celled, hyaline ascospores that bear elongate terminal appendages (Barr 1966). *Endoxyla* encompasses species whose ascomata are usually immersed in eutypoid or eutypelloid configuration beneath a slightly or strongly blackened surface; the ascospores are hyaline or light brown, one celled or delicately septate. *Endoxyla* has been placed in the Diaporthaceae (Müller and von Arx 1962), but asci do not float free within the centrum and free-ended paraphyses are present.

#### Key to Genera of Clypeosphaeriaceae

1. Ascomata immersed to erumpent separately, apices closely surrounded and thickened by clypeal tissues.....2
1. Ascomata immersed, gregarious, in prosenchymatous stromatic tissues.....5
  2. Ascospores brown, with small, pallid end cell.....3
  2. Ascospores hyaline, lacking small, pallid end cell.....4
3. Large portion of ascospore one celled....*Clypeosphaeria*
3. Large portion of ascospore one septate..*Apiorhynchostoma*
  4. Ascospores two septate, oblong.....*Melomastia*
  4. Ascospores several septate, elongate fusoid.....*Saccardoella*
5. Ascomata in eutypoid or eutypelloid configuration; ascospores hyaline to light brown, one celled or septate, germ pore present when brown.....*Endoxyla*
5. Ascomata in valsooid or diatrypoid configuration; ascospores hyaline or brown, one celled or one septate, lacking germ pore or with one or two germ pores.....6
  6. Ascospores hyaline, one celled, bearing elongate terminal appendages, lacking germ pore.....*Urosporella*
  6. Ascospores brown, one septate, lacking terminal appendages or appendages short when formed, with one or two terminal germ pores.....*Pseudovalsaria*

Phyllachoraceae Theissen & H. Sydow, Ann. Mycol. 13: 168, 176. 1915.

Stromatic tissues forming blackened clypeus at substrate surface or surrounding erumpent-superficial ascomata, often abundant and hyphal or compacted within plant tissues. Ascomata immersed, separate or gregarious, or at times erumpent to superficial, sphaeroid or globose, small to large; apex with low papilla or rounded at surface, ostiole periphysate; peridium usually narrow, of compressed rows of cells, darkened externally, pallid internally, cells of peridium or stromatic tissues blueing in iodine at times. Asci basal or peripheral, oblong, inflated, clavate or cylindric, usually octosporous; wall thin, apical ring narrow, nonamyloid, rarely amyloid. Paraphyses narrow or wide, thin walled, often deliquescent at maturity. Ascospores hyaline, yellowish or brown, symmetric and ellipsoid, fusoid, isthmoid or filiform or asymmetric and obvoid, one celled or one to several septate; wall narrow and thin when hyaline, wide and firm when brown, smooth or ornamented at times, at times surrounded by gel coating or bearing pulvinate appendages; guttulate or one or more globules; biseriolate or uniseriate in the ascus.

Anamorphs coelomycetous, forming locules in stroma or acervuli; conidiogenous cells enteroblastic phialidic, or holoblastic, proliferating sympodially; conidia hyaline, bacilloid, falcate, filiform, often spermatial. Described as *Acerviclypeatus*, *Colletotrichum*, *Polystigmina*, *Rhodosticta*.

Mostly biotrophic, often causing blotching and hypertrophy of infected tissues.

Holm (1975) reported on a problem with the type genus: *Phyllachora* Nits. ex Fuckel 1867, based on *P. agrostis* Fuckel [= *Scirrhia agrostis* (Fuckel) Winter] predates *Phyllachora* Nits. ex Fuckel 1870, whose lectotype is *P. graminis* (Pers.) Fuckel. Holm proposed rejection of the 1867 name to stabilize *Phyllachora* as it has been used and this was approved by the Special Committee for Fungi and Lichens (Petersen 1980).

The Phyllachoraceae was erected by Theissen and Sydow (1915) as part of their Dothideales and included a number of genera now recognized to belong in the Loculoascomycetes. Petrak (1924) provided a sound basis for the revised family by describing *Phyllachora graminis* in some detail and pointing out how it differed from dothideaceous taxa. Nannfeldt (1932) separated some of the pyrenomycetous genera and provided the replacement name of Polystigmataceae as a family in the Sphaeriales. Luttrell (1951) included the Phyllachoraceae, with a similar concept, in the Xylariales. A major assemblage of genera was set forth by von Arx and Müller (1954), where they included taxa now separated into the Hyponectriaceae, and under true Polystigmataceae, delimited 18 genera having amerospores.

Müller and von Arx (1962) added didymosporous genera and noted that *Ophiodothella* with filiform ascospores belonged in the family. O. Eriksson and Hawksworth (1987c) recognized 28 genera, and more recently (O. Eriksson and Hawksworth 1990) 31 genera, a number of these having septate ascospores. Many genera are tropical in distribution and only the temperate-zone genera with which I am familiar are keyed out here. The majority are holobiotrophic, but a few that mature in dead substrates also seem best disposed in the Phyllachoraceae.

Species of *Phyllachora*, the largest genus in the family, infect monocots and dicots. Orton (1944) published on North American species on grasses, and Parbery (1967) on Australian and other species. Parbery (1967) provided a detailed discussion of the characteristics of the species and concluded that ascospore shape and size and conidogenesis provided valid features for separation. He analyzed morphological variation in types of appressoria formed by germinating ascospores (Parbery 1963). The species on dicotyledonous hosts from temperate regions include, for example, *P. ambrosiae* (Berk. & Curtis) Sacc. on Asteraceae, *P. dalibardae* (Peck) Sacc. on Rosaceae, whereas many more are known in warmer regions.

*Trabutia* has been assigned as a bitunicate genus to the Botryosphaeriaceae (Petrak 1929, von Arx and Müller 1954). Barr (1987a) argued that the genus is unitunicate and closely related to *Phyllachora*, whereas von Arx (1987b) argued that it did in fact belong to the Botryosphaeriaceae. *Glomerella cingulata* (Stoneman) Spaulding & von Schrenk is somewhat anomalous: the *Colletotrichum* anamorph is parasitic (von Arx 1957) but the ascomata mature in dead infected material of many plants and hypertrophy is not obvious. *Isothea rhytismoides* (Babington ex Berk.) Fr. (von Arx and Müller 1954, Holm 1979) forms small black clypei over single ascomata in leaves of *Dryas* and is widely distributed in northern and arctic regions. *Phylleutypa wittrockii* (Erikss.) Petrak causes hypertrophy of shoot tips in *Linnaea*; in eastern North America at least infection occurs in one growing season and ascospores mature only after overwintering. *Phylleutypa kalmiae* (Peck) Barr, comb. nov. (basionym: *Dothidea kalmiae* Peck, Rep. New York State Mus. 25: 102. 1873), has a similar habit on *Kalmia* species, and for that reason is better disposed in *Phylleutypa* than in *Phyllachora*. The species of *Polystigma* have brightly pigmented hyphae and form reddish or yellowish areas in infected leaves. The infected tissues turn blue in iodine, a reaction that has been observed also in some species of *Phyllachora*. *Polystigma rubrum* (Pers.) DC. on *Prunus* is found in Europe and Asia but not yet in North America; *P. adenostomatis* Farlow on another member of the Rosaceae, and *P. astragali* (Lasch) von Höhnelt on legumes are both present in North America.

Three genera are known on large monocots in southern USA: *Apodothina pringlei* (Peck) Petrak, which produces

blackened clypei on species of *Yucca*, forms cylindric asci and large, brown ascospores with the thickened wall surrounded by a narrow gel coating that forms pulvinate appendages over each tip. *Serenomyces californica* Barr et al. (Barr et al. 1989) and *Sphaerodothis neowashingtoniae* Shear both develop in palms in California, each forming distinctive areas of infection. Cannon (1989b) defined *Sphaerodothis* precisely for species that have dark brown ascospores. *Serenomyces* was described for *S. sheari* Petrak, from Florida, as a member of the Ceratostomataceae with long beaks. Beak formation is not consistent in the type collection, and other characteristics place the genus in the Phyllachoraceae, even though the type species was described from dead leaves.

Taxa having septate ascospores are in the minority in the family. *Phycomelaina laminariae* (Rostrup) Kohlmeyer, a parasite on stipes of species of the marine alga *Laminaria* (Schatz 1983), has a median septum in the ascospores. The species of *Telimenella* have two septa, one near each end, leaving a long mid cell. Petrak (1947b), Müller and von Arx (1973) and Müller (1975) included *T. gangraena* (Fr.) Petrak in the Polystigmataceae. Barr (1977) placed the genus in the Physosporrellaceae (= Hyponectriaceae), chiefly because a second species *T. phacidioidea* Barr has an apical ring in the ascus that blues in iodine. In other respects, both species conform to the concept of the Phyllachoraceae, and I now accept that the apical ring of the ascus may occasionally be amyloid, as does Sivanesan (1987a). Two other genera have interesting, three-septate ascospores, *Telimenia* (Müller 1975) and *Telimenochora* (Sivanesan 1987a); both are tropical in distribution. Species of *Ophiodothella* produce filiform ascospores. Most are tropical, but *O. vaccinii* Boyd (Boyd 1934, Bigelow and Barr 1962) is found in eastern North America. The peridium blues in iodine and the asci are arranged equatorially, much as in *Diachora onobrychidis* (DC.: Fr.) J. Müller (Boyd 1934, von Arx and Müller 1954). Hanlin (1990) described the anamorph of *Ophiodothella vaccinii* as *Acerviclypeatus poriformans* Hanlin; the clypeate acervuli open by a pore, formed by growth of a vertical column of hyphae from the conidioma base. *Septoria angustissima* Peck (New York State Mus. Bull. 150: 62. 1911), although less apt as a specific epithet, is probably the earlier name. The host for this species was said to be osage orange [*Maclura pomifera* (Raf.) C. K. Schneider], but is instead *Vaccinium arboreum* Marsh, according to notes on the type collection at NYS.

Some other tropical taxa in the family include clypeate species with aseptate ascospores as in *Apiosphaeria guaranitica* (Speg.) von Höhnelt, *Stigmochora controversa* (Starb.) Theissen & H. Sydow, and *S. variegata* Barr & Hodges, or with isthmoid ascospores as in the species of *Diatractium* (Cannon 1989a). Erumpent-superficial ascomata and amero-spores are typical of species of *Coccoidella* (*Coccostroma*, *Bagnisiopsis* pro parte), and still other genera that were

redescribed by von Arx and Müller (1954).

The Leptopeltidaceae von Høhnelt has a number of features that suggest relationship with the Phyllachoraceae. Ascomata arise as subcuticular or superficial small stromata, the centrum contains unitunicate asci [demonstrated by Holm and K. Holm (1977) and seen in some North American collections since that time], among delicate paraphyses. The ascomata open by an irregular slit and are all saprobic as far as is known, a considerable deviation from the biotrophic, truly perithecioid habit of members of the Phyllachoraceae.

#### Key to Genera of Phyllachoraceae

1. Ascospores one celled or delicately one septate.....2
1. Ascospores conspicuously septate.....10
  2. Maturing in infected dead tissues, not causing noticeable hypertrophy, clypeus small, lacking well-developed stroma.....*Glomerella*
  2. Maturing in living tissues, usually causing hypertrophy, with well-developed stroma and usually clypeate at host surface.....3
3. Stromatic tissues forming reddish or yellowish areas in substrate, clypeus not blackened at surface.....*Polystigma*
3. Stromatic tissues yellowish to brown, clypeus blackened at surface.....4
  4. Clypeus and stroma surrounding single ascoma.....*Isothea*
  4. Clypeus and stroma surrounding several ascomata...5
5. Infecting and causing hypertrophy of branches.....*Phylleutypa*
5. Infecting leaves and culms.....6
  6. In large monocots (yuccas, bamboos, palms); ascospores light to dark brown.....7
  6. In smaller monocots or dicots; ascospores hyaline or yellowish.....9
7. Asci cylindric; ascospores large, thick walled, with pulvinate terminal appendages.....*Apodothina*
7. Asci short, ovoid or oblong; ascospores small to large, thin or thick walled, lacking terminal appendages.....8
  8. Ascospores dark brown, walls thickened, smooth or ornamented.....*Sphaerodothis*
  8. Ascospores light brown, walls not thickened, delicately ornamented.....*Serenomyces*
9. Clypeus and stromatic tissues subcuticular, on leaves of *Quercus*.....*Trabutia*
9. Clypeus and stromatic tissues variable in position; on monocots or other dicots.....*Phyllachora*
  10. Ascospores filiform, one or several septate.....*Ophiodothella*
  10. Ascospores shorter, fusoid or ellipsoid, one or two septate.....11

11. Infecting stipes of *Laminaria*; ascospores one septate..  
 .....*Phycomelaina*  
 11. Infecting monocots; ascospores two septate..*Telimenella*

**Hyponectriaceae** Petrak, Ann. Mycol. 21: 305. 1923.

Stromatic tissues forming clypei over immersed ascomata and/or surrounding and thickening apices of erumpent ascomata, slight within substrate. Ascomata immersed, erumpent or nearly superficial, sphaeroid, globose or ovoid, small or medium, upright or horizontal; apex setose at times, short papillate, ostiole periphysate; peridium narrow, of compressed rows of cells, dark externally, pallid internally or entirely pallid. Asci basal, oblong, cylindric or ellipsoid, usually octosporous; apical ring shallow, refractive, amyloid or nonamyloid, pulvillus chitinous. Paraphyses narrow or relatively wide, delicate, often deliquescing at maturity. Ascospores hyaline, yellow to pinkish or light brown, obovoid, oblong, fusoid, isthmoid or elongate filiform, asymmetric or symmetric, one celled or one to several septate; wall thin or thickened and firm, smooth or verruculose, surrounded by gel coating at times; guttulate; overlapping biseriate or in fascicle in the ascus.

Anamorphs hyphomycetous, forming sporodochia at times, little known; conidiogenesis holoblastic, proliferating sympodially or percurrently, denticulate; or enteroblastic phialidic [as *Phialophora* in *Magnaporthe* (Landschoot and Jackson 1989b) and in *Linocarpon* (Hyde 1988, Samuels, personal communication)]. Described as *Beltraniella*, *Gerlachia*, *Microdochium*, *Nakataea*, *Pyricularia*, *Selenosporella*.

Hemibiotrophic in leaves, stems, culms or saprobic in woody substrates.

The members of the Hyponectriaceae have been studied by several investigators. Von Höhnelt (1919c), who arranged the taxa under the invalid name *Physosporellaceae*, and Petrak (1923), were the first to recognize a family grouping. Von Arx and Müller (1954) included amerosporous genera under the *Polystigmataceae* (= *Phyllachoraceae*), but later (Müller and von Arx 1962) arranged them in the *Amphisphaeriaceae*, as did Dennis (1968) and Müller and von Arx (1973). Barr (1976b, 1977) reviewed some of the genera and separated the Hyponectriaceae (using the invalid name *Physosporellaceae*) from the *Amphisphaeriaceae*. The major differences between the two families are in ascospore symmetry and pigmentation, ascus shape and position in the centrum, and anamorphs. Barr also suggested that the family could be arranged with the *Phyllachoraceae* as order *Phyllachorales* (Barr 1976b, 1983a). The Hyponectriaceae appears to be most closely allied to the *Phyllachoraceae*, but both families are assigned again to the *Xylariales*.

Amerosporous (rarely didymosporous) taxa such as *Hyponectria* (Barr 1977) and *Physalospora* (von Arx and Müller 1954, Barr 1970) have ascomata that are immersed beneath a clypeus or erumpent with clypeal tissues forming a thickened apical region that is sometimes setose. Similar variations in position of ascomata and clypeus or thickened, sometimes setose apices are seen in the apiosporous *Pseudomassaria* (von Arx 1952, Barr 1964). *Apiothyrium* (Petrak 1947a) is another apiosporous genus, but the ascomata are horizontal in the substrate. This genus was monotypic with *A. arcticum* Petrak in leaves of *Diapensia* in arctic and alpine regions of the northern hemisphere (Barr 1959); now *A. tasmanicum* Swart joins it, in leaves of *Arthrotaxus*, endemic in Tasmania (Swart 1988). The species of *Buergenerula* (Kohlmeyer and Gessner 1976, Barr 1976b, von Arx 1977) could also be viewed as apiosporous with one or more added septa. *Apiospora* has some superficial similarities, but is here removed to the Lasiosphaeriaceae of the Sordariales.

The taxa having one- or several-septate, more symmetric, oblong or obovoid ascospores include *Arwidssonina* in leaves (B. Eriksson 1974) and *Exarmidium* in woody substrates (Barr and Boise 1985). *Induratia apiospora* Samuels et al. from New Zealand may also belong in the family; Samuels, Müller and Petrini (1987) compared it to *Exarmidium*. The anamorph in *I. apiospora* is a species of *Nodulisporium*, similar to anamorphs in the Xylariaceae. *Telimenella* (Barr 1977) is returned to the Phyllachoraceae, as Sivanesan (1987a) had proposed.

A number of taxa have fusoid to elongate, one- or several-septate ascospores. Those having upright ascomata include the European *Monographos* on ferns (Holm and K. Holm 1978), *Leiosphaerella*, in temperate regions on woody substrates (Müller and von Arx 1962, Bigelow and Barr 1966), *Monographella* (Müller 1977, Parkinson et al. 1981, Samuels and Hallet 1983) and *Magnaporthe* (Hebert 1971, Krause and Webster 1972, Barr 1977), both usually in monocot culms, and the European *Ceriospora* (Müller and von Arx 1962). *Oxydothis* species develop horizontal, clypeate ascomata in culms of large monocots (Müller and von Arx 1962, Samuels and Rossman 1987). *Linocarpon* is added to the family. The upright ascomata and ascospore shape separate *Linocarpon* from *Oxydothis* (see additional notes, page 72). *Vialaea insculpta* (Fr.) Sacc. (Redlin 1989) has isthmoid ascospores, narrowed to the septate median region and to the tips. Schrantz (1960) proposed the Vialaeaceae but did not publish a Latin diagnosis to validate the name.

Anamorphs are not well known within the family, but some trends can be noted. For *Pseudomassaria carolinensis* Barr & Hodges, a *Beltraniella* anamorph is known (Hodges and Barr 1971). The conidiogenous cells are holoblastic, proliferate sympodially and form denticles. The species of *Magnaporthe* (Hebert 1971, Krause and Webster 1972, Barr 1977) also have holoblastic, sympodially proliferating,

denticulate conidiogenous cells and septate brown conidia, described as *Nakataea* or *Pyricularia*. Taxa in *Monographella*, usually on monocots, form sporodochia from which holoblastic conidiogenous cells may proliferate either percurrently or sympodially within the same isolate (Gams and Müller 1980, Samuels and Hallett 1983). *Microdochium* is the accepted name and *Gerlachia* its later taxonomic synonym. The anamorph associated with *Buergenerula biseptata* (Rostrup) H. Sydow, at least the North American entity originally described as *Yukonia caricis* Sprague (Sprague 1962, Barr 1976b), is similar in appearance. At least one species of *Oxydothis* has an anamorph that is holoblastic and denticulate, described as *Selenosporella* (Samuels and Rossman 1987).

#### Key to Genera of Hyponectriaceae

1. Ascospores one celled, rarely one septate, oblong, obovoid or ellipsoid.....2
1. Ascospores usually septate, variable in shape.....3
  2. Ascomata sphaeroid; peridium soft and narrow, often pallid beneath clypeus, not setose.....*Hyponectria*
  2. Ascomata globose or ovoid; peridium firm, dark, setose over apex at times.....*Physalospora*
3. Ascospores apiosporous (lower cell less than one third length of ascospore).....4
3. Ascospores not apiosporous.....6
  4. Ascomata horizontal, papillae lateral...*Apiothyrium*
  4. Ascomata upright, papillae central.....5
5. Ascospores one septate; ascomata bearing setae over apex at times.....*Pseudomassaria*
5. Ascospores two to four septate; ascomata not setose over apex.....*Buergenerula*
  6. Ascospores oblong or obovoid.....7
  6. Ascospores fusoid, elongate or bifusoid.....8
7. Ascomata one or several beneath darkened clypeus, opening by papillate ostiole, in woody substrates...*Exarmidium*
7. Ascomata scattered, lacking conspicuous clypeus, opening by lacerations, in leaves.....*Arwidssonina*
  8. Ascospores isthmoid, narrowed toward mid regions; in woody branches.....*Vialaea*
  8. Ascospores fusoid to elongate, not narrowed toward mid region; in monocots or woody branches.....9
9. Ascospores elongate; in monocots.....10
9. Ascospores fusoid; in monocots or woody branches.....11
  10. Ascomata horizontal, papillae lateral; ascospores tapered sharply to ends, septate, contents guttulate...*Oxydothis*
  10. Ascomata upright, papillae central or eccentric; ascospores rounded above, often tapered and geniculate at base, contents with refringent septum-like bands...*Linocarpon*
11. Ascospores usually one septate, hyaline; in woody branches (at least temperate species).....*Leiosphaerella*



11. Ascospores usually several septate, hyaline to brown, mostly in monocot leaves and culms.....12  
 12. Peridium of ascomata narrow, yellowish becoming translucent brown; ascospores hyaline or yellowish....  
 .....*Monographella*  
 12. Peridium of ascomata narrow to relatively wide, dark; ascospores hyaline or versicolorous with mid cells brown and end cells hyaline.....*Magnaporthe*

*Trichosphaeriaceae* Winter in Rabenhorst, Kryptogamen-Fl. 1(2): 191. 1885.

Stromatic tissues reduced, as hyphal subiculum or crustose layer on substrate. Ascomata superficial, globose or ovoid, small; apical papilla short, ostiole periphysate; surface setose or glabrous, at times bearing protruding cells; peridium of compressed rows of cells, dark externally, pallid internally. Asci basal or peripheral, cylindrical or oblong, octosporous; apical ring shallow, non-amyloid. Paraphyses narrow, thin walled. Ascospores hyaline or lightly pigmented, ellipsoid, oblong or elongate fusoid, one celled or one or several septate, at times with longitudinal septa, at times disarticulating into part-spores; wall smooth or verruculose, at times surrounded by gel coating; guttulate; uniseriate or in fascicle in the ascus.

Anamorphs hyphomycetous, little known; conidiogenous cells holoblastic, proliferating sympodially, denticulate.

Saprobic or hypersaprobic on wood, bark or leaves, at times over other fungi.

The *Trichosphaeriales* was regarded as a separate order by Barr (1983a), but re-evaluation of character states has shown that the superficial position of ascomata is not sufficient to separate the taxon at ordinal rank. *Niesslia* and its allies had been included in the order; the presence of apical paraphyses (periphysoids) rather than basal, apically free paraphyses requires their removal to the *Hypocreales*. The remaining members of the *Trichosphaeriaceae* are taxa having small ascomata and a *Xylaria*-type centrum. *Trichosphaeria pilosa* (Pers.: Fr.) Fuckel has one-celled ascospores with scattered verruculae. *Eriospheria vermicularia* (Nees: Fr.) Sacc. is quite similar except for one-septate ascospores.

*Acanthostigma* is accepted to include species whose ascospores are narrow and elongate fusoid, usually arranged in a fascicle in the ascus. The type specimen of *A. perpusillum* de Not., the original species in the genus, could not be located (von Arx and Müller 1975). Müller and von Arx (1973) suggested that *Tonduzia* F. L. Stevens 1927 non Pittier 1908 (= *Dontuzia* Gómez) was identical with *Acanthostigma*, but *T. psychotriae* F. L. Stevens is a leaf parasite or epiphyte whose ascomata are nonsetose. Von Arx

and Müller (1975) thought *Acanthostigma* was perhaps similar to *Nematostoma*, but this too seems unlikely. *Nematostoma* includes superficial taxa of the Dimeriaceae (Loculoascomycetes), epiphytic on trichomes of herbaceous plants (Rossman 1987, Sivanesan 1987b), whereas *A. perpusillum* was described and illustrated from inner cortex of *Cerasus* (*Prunus*) associated with *Valsa pulchella* [*Calosphaeria pulchella* (Pers.: Fr.) Schröter]. The small, superficial, globose ascomata were short setose, and the thin-walled asci, that were illustrated by de Notaris (1863) differently from bitunicate taxa in the same article, contained elongate-fusoid, several-septate ascospores. Saccardo (1883) provided sizes for asci and ascospores as  $70 \times 15 \mu\text{m}$  and  $28-30 \times 4.5-5 \mu\text{m}$  respectively. De Notaris compared his fungus with *Sphaeria eres* (*Trichosphaeria*), *S. dickiei* (*Metacoleria*), and *S. chaetomium* (*Niesslia*). Later descriptions of species added to the genus have included diverse fungi (Saccardo 1883, Berlese 1894), such as some Loculoascomycetes now recognized in *Tubeufia* subgenus *Acanthostigmia* (Barr 1980). It seems reasonable to accept *Acanthostigma perpusillum* and to typify the genus and the type species from the de Notaris illustration (1863, Pl. XCIV) as a small, setose saprobe on decaying wood, having unitunicate asci and elongate ascospores borne in a fascicle.

*Rhamphoria* is also assigned to the family. The ascospores are variable in shape and septation (Sivanesan 1976). Müller and Samuels (1982a) described *R. pyriformis* (Fr.) von Höhnelt to encompass all of these variations. Ascospores may bud in the ascus to produce denticles and minute conidia; in culture vegetative hyphae may produce conidiogenous cells, and eventually brown, erect conidiophores with intercalary conidiogenous zones. In each case the minute conidia are borne on denticles and conidiogenesis is holoblastic, proliferating sympodially, assigned to *Phaeoisaria* (Müller and Samuels 1982a). *Neorehmia ceratophora* von Höhnelt is not yet known from North America. The setae are branched at the tips, one-septate ascospores disarticulate into partspores, and conidia are produced on denticles (Müller and Samuels 1982a, as *Trichosphaerella*). *Porosphaerella cordanophora* Müller & Samuels, with one-septate ascospores that finally become brown and have terminal germ pores, is known as yet only from Switzerland (Müller and Samuels 1982b); the anamorph *Cordana pauciseptata* Preuss is cosmopolitan (Ellis 1971). It is holoblastic, sympodial, and conidia arise from denticles on the apex of the terminal and intercalary conidiogenous cells. Samuels (personal communication) prefers to think of this as a modified phialide, where the whole locus is enteroblastic and conidia are budded from the tip, and to refer the fungus to a position close to *Chaetosphaeria* in the Sordariales. *Setocampanula* was described recently from Taiwan (Sivanesan and Hsieh 1989) as a member of the Trichosphaeriaceae. The collabent ascomata whose thickened

peridium is of pseudoparenchymatous cells suggests rather a position in the Sordariales, probably in the diverse family Lasiosphaeriaceae.

#### Key to Genera of Trichosphaeriaceae

1. Ascomata glabrous, at times roughened by protruding cells; ascospores becoming muriform, sometimes budding in the ascus.....*Rhamphoria*
1. Ascomata setose; ascospores one celled or one to three transversely septate, not budding in the ascus.....2
2. Ascospores elongate fusoid, one to three septate.....*Acanthostigma*
2. Ascospores oblong or ellipsoid, one celled or one septate.....3
3. Ascospores one celled.....*Trichosphaeria*
3. Ascospores one septate.....*Eriosphaeria*

**Acrospermaceae** Fuckel, Jahrb. Nassauischen Ver. Naturk. 23-24: 92. 1870.

Stromatic tissues erupt superficial, bases attached to substrate, white, pallid to yellowish, brownish or bluish green, soft fleshy or gelatinous, drying to hornlike consistency, upright columnar or pulvinate, ascomalike, of pseudoparenchymatous cells, sometimes walls thickened and sclerotial, surface at times reinforced by horizontal or oblique rows of cells or roughened by crystalline material. Ascomata single or few in stroma, vertically elongate or ovoid, medium to large; apex rounded, opening by pore surrounded by narrow converging cells, not periphysate; peridium narrow, pallid, of few rows of compressed cells. Asci basal, long cylindric, octosporous or tetrasporous; apex somewhat thickened and penetrated by narrow canal, or narrow apical ring visible at times, refractive, non-amyloid. Paraphyses narrow, free tips into ostiole. Ascospores hyaline, filiform, delicately septate; wall thin, smooth; guttulate; straight or spirally wound as fascicle in the ascus.

Anamorphs hyphomycetous where known; conidiogenous cells holoblastic, proliferating sympodially (Webster 1956).

Saprobic on mosses, fallen leaves and rachises, stems, culms, ferns, small branches, often in moist habitats.

The Acrospermaceae poses problems in disposition. The history of *AcrospERMUM* over the years has found the genus tentatively connected to various taxa. For example, Rehm in Engler and Prantl (1897) placed the family in the Hysteriineae, presumably because of its stature that suggests species of *Lophium*. Because of texture and pigmentation or lack of it, *AcrospERMUM* has been placed with hypocreaceous and clavicipitaceous fungi (Ellis and

Everhart 1892; von Höhnelt 1909, 1919a, Clements and Shear 1931, Müller and von Arx 1973, Sherwood 1977). Because of elongate asci having thickened apices, an ostropalean connection has been suggested (Dennis 1968, Korf 1973). A major point at issue has been to which class, Loculoascomycetes or Hymenoascomycetes, *Acrospermum* belongs. O. Eriksson (1967) arranged the Acrospermaceae among the Loculoascomycetes, and Samuels (personal communication) does also because of the nature of the anamorph. O. Eriksson and Hawksworth (1987c, 1988b, 1990) have the family, containing only *Acrospermum* and *Oomyces*, in an uncertain position. Pirozynski (1977) suggested that *Tubeufia* was closely related and could be included in the Acrospermaceae. This suggested relationship can be traced back to von Höhnelt (1919a) who provided a key to genera such as *Bombardiastrum*, *Acrospermum*, *Cyanoderma*, *Barya*, *Torrubiella*, *Ophionectria*, *Tubeufia*, a varied group of genera now arranged in at least four orders.

The only developmental study is that by Brandriff (1936) on *Acrospermum compressum* Tode. She described formation of a protruding lobe of pseudoparenchymatous stromatic tissues, the locule formed by disintegration of internal cells, apparently filled with ascogenous hyphae and later with asci and paraphyses. Her conclusion was that development was dothideaceous, but that the fungus was related to the Coryneliales by shape and "pseudo-ostiole." Luttrell (1955) was not convinced of dothideaceous development. He placed the family in the Coryneliales, and suggested that perhaps it could be a reduced perithecioid form of the Clavicipitaceae. Sherwood (1977) recognized that the outer layers of "ascomata" were actually stromatic tissues. I suggest that the members of the family are stromatic; solitary or few ascomata, each with a narrow peridium, are formed within a relatively small vegetative stroma. The simple, free-ended paraphyses are typical of a xylariaceous centrum.

Asci in species of *Acrospermum* have a thickened apex, occasionally seen with a shallow refractive, nonamyloid apical ring. The apex opens widely when ascospores are discharged, and no endoascus is visible. Savile (1968) observed that asci in *Acrospermum* were unitunicate. Sherwood (1977) observed that filiform ascospores tend to develop in cylindric asci having thickened apices. O. Eriksson (1981) illustrated and compared ascus apices in *Acrospermum*, *Oomyces*, *Cyanodermella*, *Claviceps* and *Cordyceps*. He reported that *Acrospermum* and *Oomyces* had morphologically bitunicate but nonfissitunicate asci, that those in *Cyanodermella* were similar to asci in the Stictidiaceae, and that all differed from asci in species of *Claviceps* and *Cordyceps*.

*Oomyces carneo-albus* (Lib.) Berk. & Broome is European and the stromatic tissues enclose two to five ascomata, whereas in the North American *O. langloisii* (Ellis & Everh.) Ellis & Everh. the stromata are more pulvinate and

contain numerous, ovoid-elongate ascomata. In specimens of both species a few narrow paraphyses are visible. *Cyanoderma viridula* (Berk. & Curtis) von Høhnelt, now *Cyanodermella viridula* (Berk. & Curtis) O. Eriksson, was excluded from the Acrospermaceae by O. Eriksson (1981), who determined that the thickened ascus apices were more those of the Stictidaceae. In centrum characteristics, this taxon is not a member of the Stictidaceae (Sherwood 1977), and for the present I retain it among the Acrospermaceae.

What may seem heretical is to suggest a parallel situation between *Acrospermum* and its relatives and *Vibrissea* (including *Apostemidium*). The sections of this genus were based upon morphological characteristics by Sánchez and Korf (1966). *Vibrissea* has usually been arranged in the Ostropales (Nannfeldt 1932, Dennis 1968, 1978, Sánchez and Korf 1966, Korf 1973), but was excluded from that order by Sherwood (1977) and has been tentatively referred to the Leotiaceae (O. Eriksson and Hawksworth 1987c, 1990). Both *Acrospermum* and *Vibrissea* have centra composed of paraphyses with free ends (forming an epithecium in some species of *Vibrissea*), elongate asci with a small apical pore in the thickened apex, and filiform ascospores. All are saprobic on fallen plant material and develop in moist, semiaquatic or aquatic regimes. Variations in apical opening of ascomata, in stipitate bases, in dextrinoid reaction of excipular cells, and in arrangement of excipulum or stromatic tissues are evident at the level of genus, section or species. *Obtectodiscus* (Müller et al. 1979) could be suggested as an intermediate, bridging taxon: the ascomata are perithecioid in immature condition but open to expose the hymenium at maturity. Needless to say, neither Korf nor Müller (personal communications) agree with the suggested relationships, but they are worth contemplation.

#### Key to Genera of Acrospermaceae

1. Stromata blueish green, darkest at base, surface powdered by whitish crystalline material; asci four spored.....*Cyanodermella*
1. Stromata pallid to yellowish brown, lacking crystalline material over surface; asci eight spored.....2
2. Stromata cylindric or pulvinate, containing one or several ascomata.....*Oomyces*
2. Stromata elongate ligulate, often compressed laterally when dry, containing one ascoma.....*Acrospermum*

*Calosphaeriales* Barr, *Mycologia* 75: 11. 1983.

Stromatic tissues slight or well developed as fungus stroma or intermixed with substrate cells or reduced to subiculum at times. Ascomata perithecioid, immersed,

separate, gregarious or grouped in valsoid, eutypoid or diatrypoid configuration, globose or sphaeroid, small to large; apex rounded, papillate or short to long beaked, ostiole periphysate; peridium two layered, of rows of compressed cells, externally dark, internally pallid. Asci unitunicate, peripheral in fascicles or spicate clusters, oblong or clavate and short or long stipitate, ovoid or subglobose and sessile, octosporous or polysporous, at times less than eight maturing; apex refractive, apical ring shallow, nonamyloid. Paraphyses few, one or two long tapering arising from basal cells of each fascicle of asci, or lacking when asci spicate. Ascospores hyaline or lightly pigmented, oblong and often allantoid or ellipsoid, one celled or one to few septate, occasionally budding within ascus; wall smooth; one or few globules; biseriate or crowded in the ascus.

Anamorphs hyphomycetous where known; conidiogenous cells holoblastic, proliferating sympodially, arising from beaks or surface of stroma (*Nodulisporium*-like); or conidiogenous cells enteroblastic phialidic (*Acremonium*-like). Coelomycetous locules in stroma associated at times (perhaps spermatial).

Saprobic or hypersaprobic in woody plants, often associated with stromata of other ascomycetous fungi.

One family:

*Calosphaeriaceae* Munk, Dansk Bot. Ark. 17(1): 278. 1957.

Little additional information has been presented on the fungi in the family since Barr (1985) provided a preliminary outline. One important paper is the study by Romero and Minter (1988) on the use of fluorescence microscopy to obtain more details of ascus structures. Unique features in *Pleurostoma ootheca* (Berk. & Curtis) Barr are a thickened, fluorescing, upper lateral region of the wall that makes the ascus asymmetrical, and asci seceding by the schizolytic splitting of a thick, basal septum. A thread-like structure appears between the two portions of the septum, remaining attached to the ascus base after secession.

Several taxonomic changes are necessary. It has been brought to my attention (J. Reid, personal communication) that *Togninia* may not be lectotypified by *T. minima* (Tulasne & C. Tulasne) Berl. as Clements and Shear (1931) had done, for Berlese (1900, p. 20), in disposing of species that he excluded from *Calosphaeria*, specified: "*C. ambigua* Berl. est novi generis *Togninia* typus." Because authentic material of *T. ambigua* seems no longer to exist, a careful comparison of Berlese's description and illustration of this species with those for *T. minima* indicates that two quite different fungi have been arranged in one genus. *Togninia minima* (and *Calosphaeria alnicola* Ellis & Everh. which I consider to be identical) has short oblong asci in spicate arrangement on hyphae ("ramose" according

to Berlese 1900). *Togninia ambigua*, on the other hand, has clavate asci that taper below to a stipe, similar to those in species of *Jattaea*. Incidentally, *Jattaea* was also typified by Berlese (1900 p. 20): "*Calosphaeria microtheca* et *C. microth.* var. *brevirostris* sunt novi generis *Jattaea* typus" so that lectotypification as *J. algeriensis* Berl. by Clements and Shear (1931) is invalid. This does not change the concept of *Jattaea* presented by Barr (1985). Separation of *Jattaea microtheca* and *Togninia ambigua* by perithecia sparse, immersed, short ostiolate vs. perithecia collected in valsoid groups, short ostiolate (Berlese 1900, p. 6 footnote) is not as these species are illustrated, which is separate or in small groups, not truly valsoid (Tab. VIII, f. 2 and Tab. XII, f. 2). Additionally, the isotype collection of *J. microtheca* bears ascomata separately, grouped or in rows, as do other collections from the type locality; the apices of ascomata vary from papillate to short beaked. The outcome of this preamble would submerge *Togninia*, type species *T. ambigua*, under *Jattaea*, type species *J. microtheca*.

*Calosphaeria minima* remains separate from *Togninia* and *Jattaea* because the small, oblong, sessile asci are borne in spicate arrangement from proliferating ascogenous hyphae. Material of *C. minima* no longer exists in Paris (J. Reid, personal communication), but the illustrations by Tulasne and C. Tulasne (1863, Tab. XIII, f. 23, 24) are clearly indicative of the characteristics of this fungus, as are those of Berlese (1900, Tab. XI, f. 2) and Traverso (1906, Fig. 27). As in *J. microtheca*, ascomata may be separate or grouped and the apices may vary from papillate to elongate and beaklike. The genus *Erostella* was based upon *Calosphaeria minima*, and this genus is revived to replace *Togninia* sensu Barr (1985).

Rappaz (1987) recognized *Eutypella scoparia* (Schwein.: Fr.) Ellis & Everh. to include the type species of *Scoptria*, *S. isariphora* Nits., of the illegitimate *Peroneutypella*, *P. isariphora* (Nits.) Berl., and of *Peroneutypa*, *P. bellula* (Desm.) Berl., as well as many other synonymous names. *Wegelia discreta* Berl., the type species of that genus, was transferred by Barr (1985) to *Scoptria*, but the species differs in several respects from *Eutypella scoparia*, and the name *Wegelia* is available for calosphaeriaceous fungi. Pirozynski (1974) described *Graphostroma* as a stromatic genus in the Xylariaceae; the anamorph is also considered to be a species of *Nodulisporium* (Glawe and Rogers 1986). The centrum in *Graphostroma platystoma* (Schwein.) Pirozynski is calosphaeriaceous rather than xylariaceous, so that I retain the genus in the Calosphaeriaceae.

#### Key to Genera of Calosphaeriaceae

1. Asci clavate or oblong and stipitate, grouped in small fascicles on short ascogenous hyphae.....2
1. Asci oblong, ovoid or subglobose and sessile, developing in spicate arrangement from proliferating ascogenous hyphae .....7
  2. Beaks of ascomata elongate (length equal to or greater than diameter of ascoma).....3
  2. Beaks of ascomata short or ascomata papillate.....4
3. Ascomata often circinate, radially disposed with beaks often lateral and emergent from a common point.....*Calosphaeria*
3. Ascomata solitary, upright, beaks central.....*Wegelia*
  4. Ascomata large (1-1.5 mm), sphaeroid, papillate, fringed with dark hyphae, seated in subiculum..*Enchnoa*
  4. Ascomata small to medium, globose, papillate or short beaked, without conspicuous subiculum.....4
5. Ascomata gregarious or separate, often in rows, lacking stroma, apex papillate or with a short and narrow, often eccentric beak.....*Jattaea*
5. Ascomata gregarious in slight or well-developed stroma, apex with wide, central beak.....6
  6. Stromatic tissues slight, of interwoven hyphae and included substrate cells; ascomata gregarious in eutypoid or valsoid configuration; beaks to or beyond substrate surface.....*Romellia*
  6. Stromatic tissues well developed as deciduous ectostroma and fungus entostroma; ascomata gregarious in diatrypoid configuration; beaks to surface of entostroma.....*Graphostroma*
7. Asci octosporous, oblong; papilla or beak of ascoma central.....*Erostella*
7. Asci polysporous, subglobose or ovoid; papilla of ascoma central or eccentric to lateral.....*Pleurostoma*

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