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A Synopsis of the Taxonomic Revisions in the Genus *Ceratocystis* Including a Review of Blue-Staining Species Associated with *Dendroctonus* Bark Beetles

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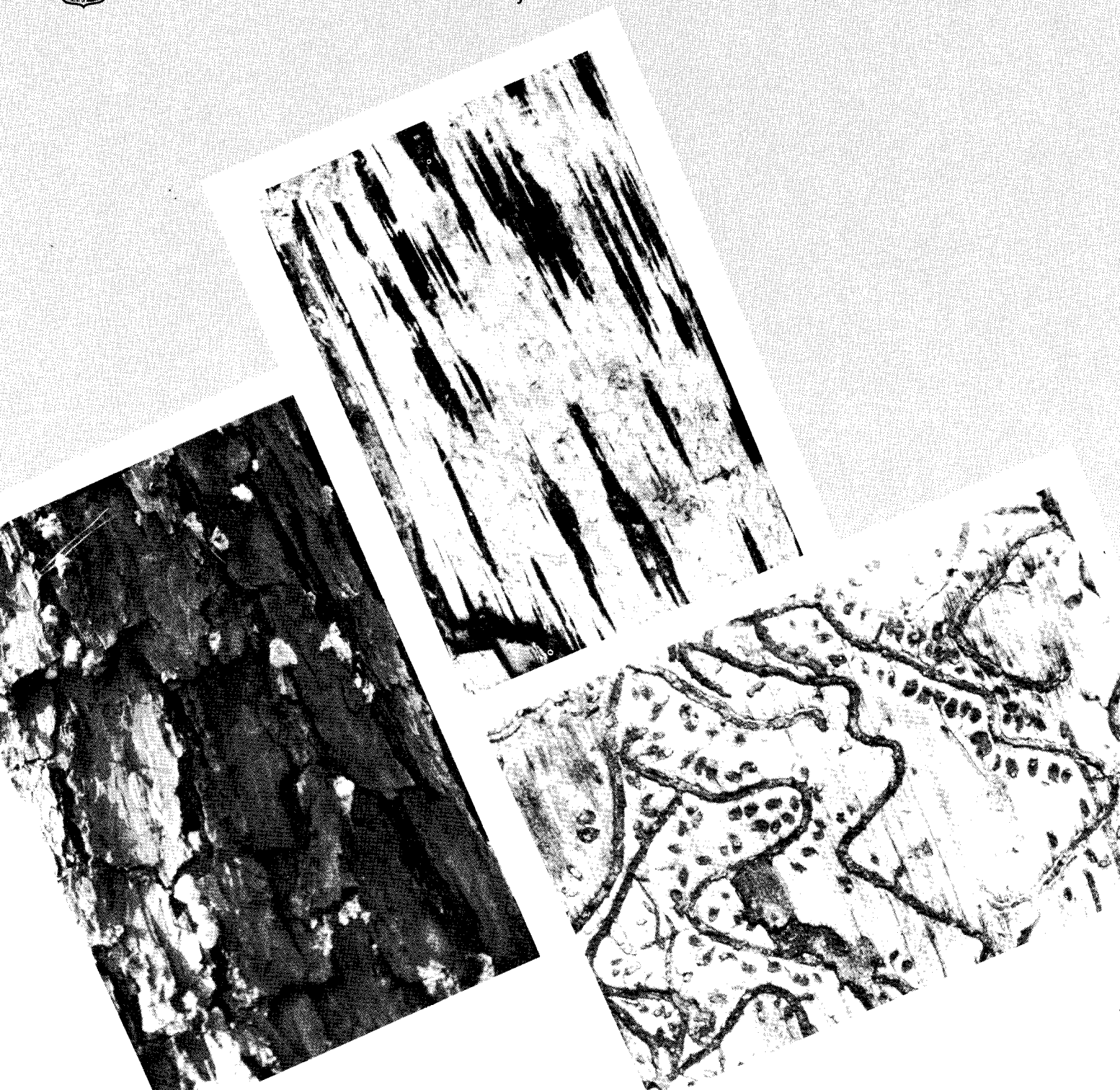

SUMMARY

Taxonomic revisions in both the teleomorphic (sexual) and anamorphic (asexual) forms of the genus *Ceratocystis* Ellis & Halstead are chronicled in this review. Recognized species associated with *Dendroctonus* Erichson bark beetles are summarized, and several species that have been published as recombinations, species that were previously described as *Ophiostoma*, and species that have not yet been recombined are listed.

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INTRODUCTION

Because the fungi of the genera *Ceratocystis* Ellis & Halstead (1890) and *Ophiostoma* H. & P. Sydow (1919) are wood stainers and plant pathogens, they are economically important. Among the best known are the blue stain fungus *Ophiostoma minus* (Hedgc.) H. & P. Sydow (≡ *Ceratocystis minor* [Hedgc.] Hunt), the oak wilt fungus *Ceratocystis fagacearum* (Bretz) Hunt, the Dutch elm disease fungus *Ophiostoma ulmi* (Buism.) Nannfeldt (≡ *Ceratocystis ulmi* [Buism.] C. Moreau), the sweet potato rot fungus *Ceratocystis fimbriata* Ellis & Halstead, and the root pathogen *Leptographium wageneri* (Kendr.) Wingfield (≡ Verticicladiella Wageneri: Kendrick).

Insects disperse these fungi's spores that are produced in a sticky substance by both the teleomorphs (sexual form) and the anamorphs (asexual form) (table 1) and readily adhere to beetle body parts. Most Scolytidae (bark beetles) transport one or more *Ceratocystis* species. These fungi are found in or near bark beetle galleries. Some species may assist the beetles as tree drying agents (Bramble and Holst 1940; Nelson 1934) or may elicit tree defensive reactions (Mattson and others, 1988). Some *Ceratocystis* species are ambrosia fungi, which serve as food for developing beetle larvae (Whitney 1971, 1982). Other species compete with immature beetles for space and nutrients in the phloem (Barras 1970; Bridges and Perry 1985; Franklin 1970).

The fungal–bark-beetle–host associations have been listed in publications such as Barras and Perry (1975), Upadhyay (1981), Whitney (1982), and Beaver (1989). Because of recent taxonomic revisions of the genus *Ceratocystis* in both the anamorphic and teleomorphic forms, there is a need for an updated bibliography of fungal–insect–host interactions. Harrington (1988) lists 34 *Leptographium* Lagerberg & Melin species, 20 of which have a known *Ophiostoma* teleomorph, and 30 species of bark beetles that vector these *Ophiostoma / Leptographium* fungi. Literature searches for bark beetle-fungal associations should not be limited to the keyword *Ceratocystis* but should also include the fungi *Ophiostoma* and *Ceratocystiopsis* Upadhyay & Kendrick.

Because of the disagreements about the taxonomic status of the genus *Ceratocystis,* various reclassifications have contributed to the use of incorrect names in the fungal-bark beetle literature. My objectives are (1) to chronicle the events that led to revisions in both the teleomorphic genera and the anamorphic form-genera that make up the genus *Ceratocystis* and (2) to provide a quick and easy guide to the accepted taxonomic names of these fungi.

Most of the recent taxonomic disagreements occur at the level or order, family, and genus (fig. 1). In 1980, Benny and Kimbrough described the accepted order as Ophiostomatales with four genera: *Ophiostoma, Ceratocystis, Ceratocystiopsis,* and *Sphaeronaemella* Karsten. In 1932, Nannfeldt had erected the family Ophiostomataceae for the genus *Ophiostoma.* This is the traditionally accepted family for the genus *Ceratocystis* and the synonomized genera *Europhium* Parker and *Ophiostoma.* Von Arx and van der Walt (1988) accepted the order Ophiostomatales with the family Ophiostomataceae representing the genera *Ceratocystiopsis, Europhium,* and *Ophiostoma.* They accepted the anamorphic form-genus *Raffaelea* v. Arx & Hennebert and 16 other form-genera that are described in Upadhyay (1981) (table 2), with the exception of *Verticicladiella* S. Hughes, which is synonomized as *Leptographium* (Wingfield 1985). In 1988, Wingfield and others described *Knoxdaviesia,* a new anamorph of the genus *Ceratocystiopsis.* Von Arx and van der Walt (1988) established the family Pyxidiophoraceae for species with the anamorph *Chalara* (Corda) Rabenhorst, representing the genera *Ceratocystis* Ellis & Halstead, *Cryptendoxyla* Malloch & Cain, *Mycorhynchidium* Malloch & Cain, and *Pyxidiophora* Brefeld & Tavel.

At the generic level, three genera are currently accepted: (1) *Ceratocystis* Ellis & Halstead, containing only those species with the form-genus *Chalara* (Corda), Rabenhorst; (2) *Ophiostoma* H. & P. Sydow;

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Table 1.—Dendroctonus *species (Wood 1982) and associated blue-staining fungi*

Dendroctonus sp.	Fungal associate	Publication
Dendroctonus adjunctus Blandford =*D.convexifrons* Hopkins	*Ophiostoma stenoceras* (Robak) Melin & Nannfeldt	
	≡ *Ceratocystis stenoceras* (Robak) C. Moreau	
	= *Ceratocystis gossypina* var. *robusta* Davidson	Davidson 1971
	≡ *Ceratostomella stenoceras* Robak	
	= *Ceratocystis gossypina* Davidson	
	Ophiostoma adjuncti (Davids.) Harrington	
	≡ *Ceratocystis adjuncti* Davidson	Davidson 1978
	Leptographium pyrinum Davidson	Davidson 1978
	Leptographium sp. Lagerberg & Melin	Harrington 1988
Dendroctonus brevicomis Le Conte	*Ophiostoma minus* H. & P. Sydow	
	≡ *Ceratocystis minor* (Hedgc.) Hunt	Mathre 1964
	≡ *Ceratostomella minor* Hedgcock	
	= *Ceratostomella pini* Munch	Rumbold 1931
	= *Ceratostomella exigua* Hedgcock	
	= *Ceratostomella pseudotsugae* Rumbold	Rumbold 1936
	Ophiostoma nigrocarpum (Davids.) de Hoog	
	≡ *Ceratocystis nigrocarpa* Davidson	Davidson 1966
Dendroctonus frontalis Zimmermann	*Ophiostoma minus* H. & P. Sydow	
	≡ *Ceratocystis minor* (Hedgc.) Hunt	
	≡ *Ceratostomella minor* Hedgcock	
	= *Ceratostomella pini* Munch	Rumbold 1931
	= *Ceratostomella exigua* Hedgcock	
	= *Ceratostomella pseudotsugae* Rumbold	Rumbold 1936
	Ophiostoma nigrocarpum (Davids.) de Hoog	
	≡ *Ceratocystis nigrocarpa* Davidson	Davidson 1966
	Ceratocystiopsis ranaculosus Perry & Bridges	Bridges & Perry 1987
Dendroctonus jeffreyi Hopkins	*Ophiostoma ips* (Rumb.) Nannfeldt	
	≡ *Ceratocystis ips* (Rumb.) C. Moreau	Mathre 1964
	= *Ceratostomella montia* Rumbold	Rumbold 1941
Dendroctonus ponderosae Hopkins =*D.monticolae* Hopkins	*Ophiostoma huntii* (Robins.-Jeff.) de Hoog & Scheffer	
	≡ *Ceratocystis huntii* Robinson-Jeffrey & Grinchenko	Robinson-Jeffrey & Grinchenko 1964
	Ophiostoma minus H. & P. Sydow	
	≡ *Ceratocystis minor* (Hedgc.) Hunt	
	≡ *Ceratostomella minor* Hedgcock	
	= *Ceratostomella pini* munch	Rumbold 1931
	= *Ceratostomella exigua* Hedgcock	
	= *Ceratostomella pseudotsugae* Rumbold	Rumbold 1936
	Ophiostoma ips (Rumb.) Nannfeldt	
	≡ *Ceratocystis ips* (Rumb.) C. Moreau	Mathre 1964
	= *Ceratostomella montia* Rumbold	Rumbold 1941
	Ophiostoma piliferum (Fries) H. & P. Sydow	
	≡ *Ceratocystis pilifera* (Fries) C. Moreau	
	= *Sphaeria pilifera* Fries	
	= *Ceratocystis shrenkiana* (Hedgc.) C. Moreau	Mathre 1964
	Ophiostoma clavigerum (Robins.-Jeff. & Davids.) Harrington	
	≡ *Ceratocystis clavigera* (Robins.-Jeff. & Davids.) Upadhyay	
	≡ *Europhium clavigerum* Robinson-Jeffrey & Davidson	Robinson-Jeffrey & Davidson 1964
	Ceratocystiopsis minuta (Siem.) Upadhyay & Kendrick	
	≡ *Ceratocystis minuta* (Siem.) Hunt	Mathre 1964
	≡ *Ophiostoma minutum* Siemaszko	
	Leptographium Lagerberg & Melin	Harrington 1988, Robinson 1962

Table 1.—Dendroctonus *species (Wood 1982) and associated blue-staining fungi—Continued*

Dendroctonus sp.	Fungal associate	Publication
Dendroctonus pseudotsugae Hopkins	*Ophiostoma minus* H. & P. Sydow	
	≡ *Ceratocystis minor* (Hedgc.) Hunt	Mathre 1964
	≡ *Ceratostomella minor* Hedgcock	
	= *Ceratostomella exigua* Hedgcock	
	= *Ceratostomella pini* Munch	Rumbold 1936
	= *Ceratostomella pseudotsugae* Rumbold	Rumbold 1936
	Leptographium abietinum (Peck) Wingfield	Wingfield 1983
	≡ *Verticicladiella abietina* (Peck) S. Hughes	
	= *Sporocybe abietina* Peck	
	Leptographium sp. A	Harrington 1988
Dendroctonus rufipennis (Kirby) =*D.engelmanni* Hopkins =*D.piceaperda* Hopkins	*Ophiostoma bicolor* Davidson & Wells	Davidson 1955
	≡ *Ceratocystis bicolor* (Davids. & Wells) Davidson	Davidson 1958
	Ophiostoma piceaperda (Rumb.) von Arx	
	≡ *Ceratocystis piceaperda* (Rumb.) C. Moreau	Mathre 1964
	≡ *Ceratostomella piceaperda* Rumbold	Rumbold 1936
	= *Ceratocystis europhioides* Wright & Cain	Wright & Cain 1961
	Ophiostoma penicillatum (Grosm.) Siemaszko	
	≡ *Ceratocystis penicillata* (Grosm.) C. Moreau	
	≡ *Ceratostomella penicillata* Grossmann	
	= *Ophiostoma truncicola* Davidson	Davidson 1955
	Ophiostoma coerulescens (Munch) Nannfeldt	
	≡ *Ceratocystis coerulescens* (Munch) Bakshi	
	≡ *Endoconidiophora coerulescens* Munch	Davidson, 1955
	Leptographium abietinum (Peck) Wingfield	Wingfield 1983, Harrington 1988
	≡ *Verticicladiella abietina* (Peck) S. Hughes	
	= *Sporocybe abietina* Peck	
	Leptographium engelmanni Davidson	Davidson 1955
Dendroctonus terebrans (Olivier)	*Ophiostoma ips* (Rumb.) Nannfeldt	
	≡ *Ceratocystis ips* (Rumb.) C. Moreau	Rane & Tatter 1987
	= *Ceratostomella montia* Rumbold	
	Leptographium procerum (Kendr.) Wingfield	Wingfield 1983, Harrington 1988
	≡ *Verticicladiella procera* Kendrick	
	Leptographium terebrantis Barras & Perry	Barras & Perry 1971
Dendroctonus valens Le Conte	*Ophiostoma piliferum* (Fries) H. & P. Sydow	
	≡ *Ceratocystis pilifera* (Fries) C. Moreau	
	= *Sphaeria pilifera* Fries	
	Ophiostoma wageneri (Goheen & Cobb) Harrington	
	≡ *Ceratocystis wageneri* Goheen & Cobb	Goheen & Cobb 1978
	Ophiostoma ips (Rumb.) Nannfeldt	
	≡ *Ceratocystis ips* (Rumb.) C. Moreau	
	= *Ceratostomella montia* Rumbold	Rumbold 1931
	Leptographium terebrantis Barras & Perry	Wingfield 1983
	Ophiostoma piceaperdum (Rumb.) von Arx	
	≡ *Ceratocystis piceaperda* (Rumb.) C. Moreau	
	≡ *Ceratostomella piceaperda* Rumbold	Rumbold 1931
	= *Ceratocystis europhioides* Wright & Cain	Wright & Cain 1961
Dendroctonus Erichson	*Ceratocystis leucocarpa* Davidson*	Davidson 1966
	Ophiostoma aureum (Robins.-Jeff. & Davids.) Harrington	
	≡ *Ceratocystis aurea* (Robins.-Jeff. & Davids.) Upadhyay	
	≡ *Europhium aureum* Robinson-Jeffrey & Davidson	Robinson-Jeffrey & Davidson 1968
	Ophiostoma robustum (Robins.-Jeff. & Davids.) Harrington	
	≡ *Ceratocystis robusta* (Robins.-Jeff. & Davids.) Upadhyay	
	≡ *Europhium robustum* Robinson-Jeffrey & Davidson	Robinson & Davidson 1968

*This species has not been examined or published as *Ophiostoma*.

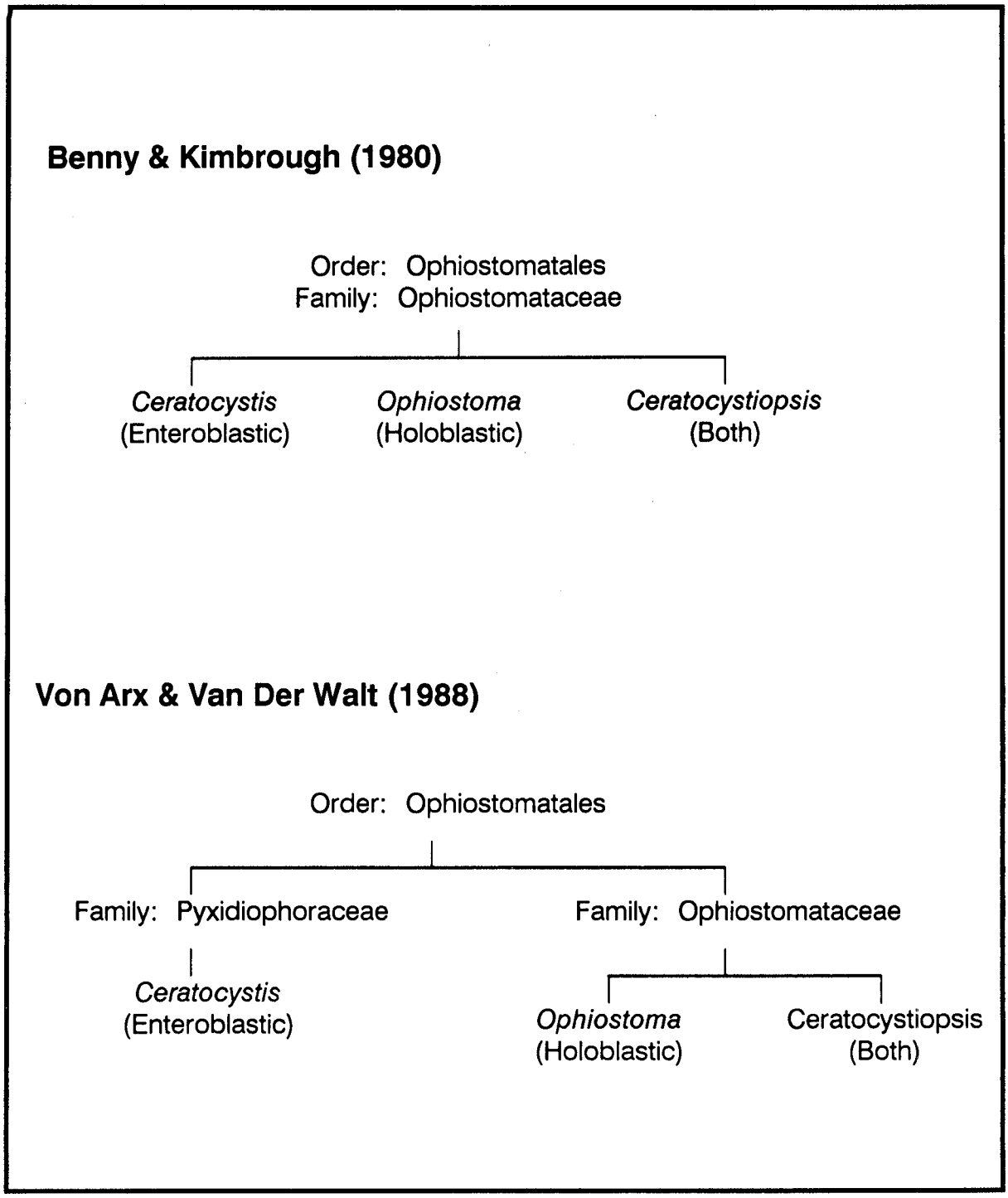

Figure 1 — *Synopsis of the most recent classification schemes of these genera.*

Table 2.—*Form-genera with asexual conidiation, Nag Raj and Kendrick (1975), Upadhyay (1981), Upadhyay and Kendrick (1975), Wingfield (1985)*

Exogenous, Holoblastic	
Acremonium Link ex Fries	Simple, reduced conidiophores
Allescheriella Henn.	Nonspecific, hyaline
Hyalodendron Diddens	Acropetal chains, simple, hyaline
Hyalopesotum Upadhyay & Kendrick	Annellidic, synnematous, hyaline
Hyalorhinocladiella Upadhyay & Kendrick	Mononematous, sympodial, hyaline
Gabarnaudia Samson & W. Gams	Mononematous, phialidic, hyaline
Graphilbum Upadhyay & Kendrick	Synnematous, sympodial, hyaline
Graphium Corda	Synnematous, annellidic, pigmented
Graphiocladiella Upadhyay	Mononematous, annellidic, hyaline
Knoxdaviesia Wingfield, Van Wyk & Marassas	Mononematous, phialidic, hyaline
Leptographium Lagerb. & Melin	Mononematous, annellidic, pigmented
Pachnodium Upadhyay & Kendrick	Nonspecific
Pesotum Crane & Schoknecht	Synnematous, sympodial, pigmented
Sporothrix Hekt. & Perkins ex. Nicot & Mariat	Simple, sympodial, hyaline
Verticiladiella S. Hughes = *Leptographium*, Wingfield	Mononematous, sympodial and annellidic, pigmented
Endogenous, Enteroblastic	
Chalara (Corda) Rabenh.	Phialidic, simple, hyaline
Chalaropsis Peyronel = *Chalara*	
Phialocephala Kendrick	Phialidic, mononematous, hyaline
Phialographium Upadhyay & Kendrick	Phialidic, synnematous, pigmented
Thielaviopsis Went = *Chalara*	

and (3) *Ceratocystiopsis* Upadhyay & Kendrick for the other form-genera (table 2).

DISCUSSION

When both the teleomorph and the anamorph are known, the fungus is called a holomorph (the whole fungus). The teleomorph, which reproduces with ascospores, is the sexual form of the fungus. It may have one (mono-anamorphic) or many (pleo-anamorphic) asexual stages. The anamorph, or asexual form, is placed into a form-genus. Form-genera, formerly known as fungi imperfecti, are the asexual, conidial-producing forms of a fungus. Form-genera are classified according to the method of conidia formation and conidiophore morphology (conidiogenesis) and may or may not be associated with a teleomorph. In the Ophiostomataceae, conidiogenesis may be holoblastic (when both inner and outer walls contribute to the formation of conidia) or enteroblastic (when the inner wall or neither wall contributes to the formation of conidia). Older terms for holoblastic conidiogenesis are exoconidial and exogenous; for enteroblastic, endoconidial and endogenous. These terms are defined in Kendrick (1971), Hennebert and Weresub (1977), and Ainsworth and Bisby's *Dictionary of the Fungi* (Hawksworth and others 1983). In *The Whole Fungus* (Kendrick 1979), noteworthy scientists have written stimulating discussions of the history, conidial formation, terms, and relative importance of anamorphs as taxonomic features.

Scientists have made taxonomic revisions in both the teleomorphs and the anamorphs of the genus *Ceratocystis*. Since cultural and microscopic analyses alone are not always sufficient to delineate genus and species characteristics, new methods of ultrastructural, chemical, biochemical, immunological, and genetic analyses are being used to realign the genus *Ceratocystis* and its anamorphs.

More complete historical data on this genus can be found in Bakshi (1951), Hunt (1956), and Upadhyay (1981). Over the years, several genera have been synonomized and placed in the genus *Ceratocystis*. Bakshi (1951) synonomized six genera and the species *Endoconidiophora coerulescens* Munch and *Ophiostoma coerulescens* (Munch) Nannfeldt as *Ceratocystis coerulescens* (Munch) Bakshi. In this enteroblastic species, spores (conidia) are produced within the spore-bearing structure (conidiophore). He also described *Ceratocystis galeiformis*, a holoblastic species where spores were formed at the "end of hypha" or conidiophore (*Cephalosporium* Corda) or at the "ends of the collection of hyphae" or conidiophores

(*Graphium* Corda and *Leptographium*). Ellis and Halstead's (1890) generic concept of *Ceratocystis* was then changed to accommodate species that produced both enteroblastic and holoblastic spores. Hunt (1956) accepted Bakshi's (1951) changes, synonomized two more genera, redescribed the genus *Ceratocystis*, completed the transfer of synonomized species, made new combinations, and described new species.

In 1974, de Hoog proposed the resurrection of the genus *Ophiostoma* with the type species *O. piliferum* for species producing holoblastic conidia. Von Hohnel (1918) originally described the genus as *Linostoma*, an invalid name, which Sydow and Sydow (1919) renamed *Ophiostoma*, and Bakshi (1951) synonomized with the genus *Ceratocystis*.

Melin and Nannfeldt (1934) divided the genus *Ophiostoma* into sections to accommodate species that produced their spores inside the conidial bearing structure (enteroblastic) and to accommodate the holoblastic species. De Hoog used Nannfeldt's sections in Melin and Nannfeldt (1934) to divide the two genera based on the type of conidia formed, either enteroblastic or holoblastic. In 1975, Weijman and de Hoog divided the genus *Ceratocystis* as *Ceratocystis sensu stricto* (in the strict sense) to contain all species with enteroblastic conidiogenesis and *Ceratocystis sensu lato* (in the wide sense) as the *Ophiostoma* group for holoblastic species. In 1975, Upadhyay and Kendrick proposed to split the genus *Ceratocystis* and to establish the genus *Ceratocystiopsis* for those species with falcate ascospores and ascoma (perithecia) with short necks.

In 1981, Upadhyay published a monograph of the *Ceratocystis* species, synonomized *Ophiostoma* and *Europhium*, and transferred 13 of 15 *Ceratocystis* species to *Ceratocystiopsis*. In 1984, de Hoog and Scheffer established *Ophiostoma* as a valid genus characterized by having cellulose, lignin, and rhamnose in their cell walls; growing on cycloheximide media; and producing holoblastic conidia. The genus *Ceratocystis* was limited to species with enteroblastic *Chalara* anamorphs and those that were cellulose negative and sensitive to cycloheximide. De Hoog and Scheffer accepted Upadhyay and Kendrick's genus *Ceratocystiopsis*.

The genus *Ceratocystis* now contains only those species having the enteroblastic form-genus *Chalara*, with the type species *C. fimbriata* Ellis & Halstead (table 3). *Ceratocystiopsis*, with the type species *C. minuta* (Siem.) Upadhyay & Kendrick, is an exception in that it does have an enteroblastic *Chalara* anamorph as well as holoblastic anamorphs. The holoblastic *Ophiostoma*, type species *O. piliferum*, has several form-genera of which two or more anamorphs may develop in culture. *Ophiostoma clavigerum* (Robins.-Jeff. & Davids.) Harrington (1987), when continually subcultured, has produced as many as six forms: *Graphiocladiella* Upadhyay, *Verticicladiella*, *Hyalorhinocladiella* Upadhyay & Kendrick, *Leptographium*, an annellidic yeast, and a holoblastic yeast (Tsuneda and Hiratsuka 1984).

Table 3.—Ceratocystis *species with* Chalara *anamorphs, de Hoog (1974) and von Arx (1987)*

de Hoog
Ceratocystis adiposa (Butler) C. Moreau
C. autographa Bakshi
C. coerulescens (Munch) Bakshi
C. fagacearum (Bretz) Hunt
C. fimbriata Ellis & Halstead
C. major (van Beyma) C. Moreau
C. moniliformis (Hedgcock) C. Moreau
C. musarum Riedl
C. paradoxa (Dade) C. Moreau
C. radicicola (Bliss) C. Moreau
C. variospora (Davidson) C. Moreau
C. virescens (Davidson) C. Moreau
von Arx
C. adiposum (Butler) C. Moreau
C. coerulescens (Munch) Bakshi
C. fagacearum (Bretz) Hunt
C. fimbriata Ellis & Halstead
C. paradoxa (Dade) C. Moreau

DeHoog in Malloch (1979) said of the *Verticicladiella-Phialographium* Upadhyay & Kendrick-*Leptographium* complex that older cultures degenerate and tend to form less well-structured, less complex, and less energy-consuming anamorphs.

Recognized form-genera now total 17 (table 2). Nag Raj and Kendrick (1975) synonomized *Chalaropsis* Peyronel and *Thielaviopsis* Went as *Chalara*. Upadhyay (1981) described 17 form-genera, but Wingfield (1985) reclassified *Verticicladiella* as *Leptographium*, and Wingfield and others (1988) described a new species, *Knoxdaviesia*. Harrington (1988) felt that most *Ophiostoma* anamorphs could probably be accommodated in the form-genera *Sporothrix* Hekt. & Perkins ex Nicot & Mariat, *Leptographium*, and *Graphium*. Form-genera of *Ceratocystis*, *Ceratocystiopsis*, and *Ophiostoma* need taxonomic study as recommended by the 1986 International Council of Botanical Names and by Kananaskis II, published as *The Whole Fungus* (Kendrick 1979).

Mycologists, plant pathologists, and botanists do not agree on the higher classifications of fungi. For instance, Ainsworth and Bisby's *Dictionary of the Fungi* (Hawksworth and others 1983) recognizes the Kingdom Fungi but does not recommend any one scheme for classes in the Subdivision Ascomycotina. Von Arx (197) advocated a limited number of orders and the omission of higher ranks. At an August 1990 meeting in Bad Windsheim, West Germany, specialists in the Ophiostomatales presented papers with startling opinions of this group of fungi (pers.

comm. Dr. M. Blackwell)[1]. Upadhyay would retain the family Ophiostomataceae in the order Microascales; Samuels would place *Ophiostoma* and *Ceratocystis* in the Order Sordariales and the Family Chaetosphaeriaceae; Wingfield would synonomize *Ceratocystiopsis* with *Ophiostoma*, except *Ceratocystiopsis falcata* (Wright & Cain) Upadhyay, which would reside in *Ceratocystis sensu stricto*.

Several authors discuss anamorphs; others discuss molecular methods, pathogenicity, vectors and dispersal, sapstain, tree response and host defense reactions, and chemistry. Kendrick[1] (Wingfield and others 1990) states that "since we do not yet have all this information (ultrastructure, development patterns, anamorph-teleomorph relationships, wall-chemistry, chemistry of slime, vectors and dispersal mechanisms, pathogenicity, and genetics) for any of the more than one-hundred members of the Ophiostomatales, it is clear that plenty of work remains to be done before we will properly understand this fascinating and important group of fungi."

Article 59 of the International Code of Botanical Nomenclature (Greuter and others 1983) states that the name of the holomorphic Ascomycete (the whole fungus, with both anamorph and teleomorph) takes precedence over the name of the anamorph. For example, one mycangial fungus of *Dendroctonus frontalis* Zimmermann, the southern pine beetle, is heterothallic (sexual reproduction requiring the union of two compatible mating types) and has been described as the anamorph *Sporothrix*[2], but since the anamorphic name was not validly described, the fungus must be cited by the name of the teleomorph, *Ceratocystiopsis ranaculosus* Perry & Bridges (Bridges and Perry 1987, Harrington and Zambino 1990). Mycologists have agreed that anamorphs that have been validly described and published may be cited separately, such as the anamorph *Sporothrix subannulata* Livingston & Davidson and its teleomorph *Ophiostoma subannulatum* Livingston & Davidson (Livingston and Davidson 1987).

A list of the *Ceratocystis* species that have been transferred (published as *Ophiostoma* species by new authors, table 4) can be found in this publication. If a described species of *Ceratocystis* having an anamorph other than *Chalara* is not listed as recombined in de Hoog and Scheffer (1984) and Harrington (1987, 1988) (examples 1, 2), then consult Upadhyay (1981) (example 3) for the original author of a *Ceratocystis* species that had been originally described as or tranferred to an *Ophiostoma* species (table 5). More than a hundred described species of *Ceratocystis* exist. Some species were originally described as *Ophiostoma*;

Table 4.—*New and recombined* Ophiostoma *species by other authors*

Ophiostoma ainoae Solheim (1986)
O. cucullulatum Solheim (1986)
O. davidsonii (Olchowecki & Reid) Solheim (1986)
O. europhioides (Wright & Cain) Solheim (1986)
O. flexuosum Solheim (1986)
O. longirostellatum (Bakshi) v. Arx & Muller (1954)
O. roboris Georgescu & Teodoru (1948)
O. sagmatospora (Wright & Cain) Solheim (1986)
O. subannulatum Livingston & Davidson (1987)

Table 5.—Ceratocystis *species that were originally described as, or transferred to* Ophiostoma, *de Hoog (1974) and Upadhyay (1981)*

Ophiostoma bicolor Davidson & Wells
O. brunneo-ciliatum Mathieson-Kaarik
O. ips (Rumb.) Nannfeldt
O. leptographioides (Davidson) v. Arx
O. microsporium (Davidson) v. Arx
O. minus (Hedgc.) H. & P. Sydow
O. multiannulatum (Hedgcock & Davidson) Hendrix
O. narcissi Limber
O. nigrocarpum (Davidson) de Hoog
O. olivaceum Mathieson
O. penicillatum Mathieson
O. perfectum (Davidson) de Hoog
O. piceae (Munch) H. & P. Sydow
O. piceaperdum (Rumbold) v. Arx
O. piliferum (Fries) H. & P. Sydow
O. polonicum Siemaszko
O. rostrocylindricum (Davidson) v. Arx
O. stenoceras (Robek) Melin & Nannfeldt
O. tetropii Matheison
O. triangulosporum Butin
O. ulmi (Buisman) Nannfeldt

[1]Blackwell, Meredith. 1990. Personal communication with Dr. Blackwell, Department of Botany, Louisiana State University, Baton Rouge, LA 70803, in Sept. 1990, regarding "The Biology and Taxonomy of the Ophiostomatales", an international symposium, held in Bad Windsheim, West Germany, on August 21-24, 1990. Program and Abstracts organized by Wingfield, M.J., Department of Microbiology, University of the Orange Free State, P.O. Box 339, Bloemfontein 9300, Republic of South Africa; Seifert, K., Biosystematics Research Institute, Central Experiment Farm, William Saunders Building, Ottawa, Ontario, KIA OC6, Canada; Webber, J.F., Forest Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, GU10 4LH, England. The proceedings will be published at a later date.

[2]Harrington, T.C. 1991. Personal communication with Dr. Harrington, Department of Plant Pathology, Iowa State University, Ames, IA 50011, who reviewed the manuscript in January, 1991, and disagreed with the taxonomic identification of this holomorph and stated that it needs further examination.

some species have been transferred to the genus *Ophiostoma*, and some have not yet been recombined (tables 6 & 7). Recombinations formed in the transfer of species must follow the rules of the International Code of Botanical Nomenclature, Article 33. The rules have been restated in the International Commission on the Taxonomy of Fungi (ICTF) Code of Practice for Systematic Mycologists (Sigler and Hawksworth 1987). Care must be taken to note the Latin or Greek endings of genera and species. For example, the genus *Ophiostoma* has a neuter ending, so the species ending must also be neuter.

Table 6.—Ceratocystis *species not recombined, Upadhyay (1981)*

Ceratocystis acericola Griffin
C. aequivaginata Olchowecki & Reid
C. allantospora Griffin
C. angusticollis Wright & Cain
C. arborea Olchowecki & Reid
C. brunneo-crinita Wright & Cain
C. california Devay, Davidson and Moller
C. columnaris Olchowecki & Reid
C. deltoideospora Olchewecki & Reid
**C. fimicola* (Marchal) Upadhyay
**C. helvellae* (Karsten) Upadhyay
C. hyalothecium Davidson
C. introcitrina Olchowecki & Reid
C. leucocarpa Davidson
C. magnifica Griffin
C. olivaceapini Davidson
C. populicola Olchowecki & Reid
C. pseudominor Olchowecki & Reid
C. stenospora Griffin
C. tenella Davidson
C. torticiliata Olchowecki & Reid
C. tubicollis Olchowecki & Reid

*Upadhyay synonomized these species, but Benny and Kimbrough (1980) and Cannon and Hawksworth (1982) recognize the genus *Sphaeronaemella* Karsten as valid.

Table 7.—Ceratocystis *species not recombined by other authors*

Ceratocystis grandicarpa Kowalski & Butin (1989)
C. kubanicum Scerbin-Parfenenko (1953)
C. nothofagi Butin (1984)
C. novae-zelandiae Hutchinson & Reid (1988)
C. prolifera Kowalski & Butin (1989)
C. valachium Georgescu, Teodoru & Badea (1948)

EXAMPLES

1. *Ophiostoma araucariae* (Butin) de Hoog & Scheffer ≡ *Ceratocystis araucariae* Butin.
2. *Ophiostoma abiocarpum* (Davids.) Harrington ≡ *Ceratocystis abiocarpa* Davidson
3. *Ophiostoma minus* (Hedgc.) H. & P. Sydow ≡ *Ceratocystis minor* (Hedgc.) Hunt.

The symbol "≡" designates an obligate synonym. Both names are based on the same type specimen. They are nomenclatural synonyms. The symbol "=" designates a facultative synonym—names based on different type specimens (Hawksworth and others 1983); See table 1.

SYNOPSIS OF RELEVANT PUBLICATIONS

1890 Ellis and Halstead, in Halstead (1890), established the genus *Ceratocystis* without a formal generic description.

1891 Halstead and Fairchild established the generic concept of the genus and provided the type species *C. fimbriata*, with an endogenous conidial form.

1919 Sydow and Sydow established the genus *Ophiostoma* for *Linostoma* von Hohnel, an invalid name. Von Hohnel (1918) characterized the genus *Linostoma* as having hyaline ascospores formed in evanescent asci and having fringes of ostiolar "cilia."

1932 Nannfeldt erected the family Ophiostomataeceae for the genus *Ophiostoma*.

1934 Melin and Nannfeldt divided *Ophiostoma* into two sections. The species of section *Brevirostrata* Nannfeldt have short, conical perithecial necks, and the species assigned to section *Longirostrata* were characterized by longer filiform necks; Longirostrata was further divided to contain species with both endogenous conidia, *Chalara*-type (synonomized *Endoconidiophora* Munch), and exogenous conidia.

1951 Bakshi revived the generic name *Ceratocystis* for species with both endogenous and exogenous conidia. He regarded *Ophiostoma*, *Endoconidiophora*, *Rostrella* Zimmermann, *Linostoma* von Hohnel, and *Grosmannia* G. Goidanich as synonyms. *Ceratostomella* Saccardo was retained as a separate genus. He described three new species and transferred the species *Endoconidiophora coerulescens* Munch (Munch 1907) and *Ophiostoma coerulescens* (Munch) Nannfeldt (Melin and

Nannfeldt 1934) to the genus *Ceratocystis*, as *Ceratocystis coerulescens* (Munch) Bakshi.

1956 Hunt published the first comprehensive monograph of *Ceratocystis* species, placed the genus in the order Plectascales, accepted Bakshi's emendations (that the genus contains species with both endogenous and exogenous conidia), and completed the transfer of species. He synonomized *Sphaeria* Haller ex Fries and *Sphaeronaemella* Karsten ex Seeler under *Ceratocystis*, and *Fugascus* Falck was listed as *nomen nudum* (a genus without adequate description). *Ceratostomella* was also excluded from synonomy. He presented a key to the species and sectioned them according to conidial development: section (1) species with an endoconidial imperfect stage, the Endoconidial Group; section (2) species with a *Leptographium* or *Graphium* imperfect state consisting of the *Grosmannia* Group and the *Ophiostoma* Group in part; and section (3) species with mycelial conidia only, the *Ophiostoma* Group in part.

1957 Parker established the genus *Europhium* with the type species *E. trinacriforme*. The species was distinguished from *Ceratocystis* by its neckless, closed ascocarps. Benny and Kimbrough (1980) and Upadhyay (1981) synonomized this genus with *Ceratocystis*; von Arx and van der Walt (1988) resurrected the genus and placed it in the family Ophiostomataceae.

1962 Kendrick redescribed the genus *Verticicladiella* S. Hughes, differentiated the genus *Leptographium* Lagerberg & Melin, placed three species in *Verticicladiella*, and described four new species, *V. procera*, *V. brachiata*, *V. antibiotica*, and *V. wagenerii*.

1964 Rosinski and Campana demonstrated both chitin and cellulose in the hyphal walls of Ceratocystis ulmi (Buisman) C. Moreau.

1965 Kendrick and Molnar described a new *Ceratocystis* with the first-described *Verticicladiella* anamorph.

1965 Rosinski confirmed the occurrence of cellulose in *C. ulmi*.

1967 Smith and others differentiated four species by their cell wall chemistry and divided them into two categories. The endoconidial (enteroblastic or endogenous) forms *Ceratocystis fagacearum* (Bretz) Hunt and *C. fimbriata* Ellis & Halstead have no cellulose in their cell walls, and the exoconidial (holoblastic or exogenous) forms of *C. olivacea* (Mathiesen) Hunt have both chitin and cellulose in their cell walls.

1968 Griffin published a monograph of 32 *Ceratocystis* species found in Ontario with descriptions, figures, distribution data, and a key to 60 species based on ascospore morphology. Eleven species were described as new.

1968 Robinson-Jeffrey and Davidson described three new species of *Europhium* (*clavigerum*, *aureum*, and *robustum*), which Upadhyay, in 1981, synonomized as *Ceratocystis* species including the type species *E. trinacriforme*. In 1987, Harrington recombined the four species as *Ophiostoma*.

1970 Von Arx urged revision of the form-genus *Graphium* because conidia of described species were formed exogenously as well as endogenously. He cited the genus as *Ceratocystis* Ellis & Halstead with 50 species and accepted Bakshi's synonyms but did not accepted Bakshi's (1951) or Hunt's (1956) emendations.

1971 Spencer and Gorin, to aid classification, grouped species of *Ceratocystis* and *Graphium* according to their polysaccharide components. The endoconidial (endogenous) group formed glucomannans or galactoglucomannans rather than rhamnose- and mannose-containing polysaccharides as in the exoconidial (exogenous) group.

1972 Cain suggested a relationship to filamentous yeastlike taxa as *Cephaloascus* Hanawa and said that *Verticicladiella* may be more closely related to hyphal yeast genera with hat-shaped ascospores than to phialidic *Chalara*-like anamorphs.

1973 Muller and von Arx placed the genus *Ceratocystis* in the order Sphaeriales of the Pyrenomycetes and the family Ophiosomataceae Nannfeldt, removing it from the orders Plectascales (Nannfeldt 1932, Hunt 1956), the Microascales of the Plectomycetes (Luttrell 1951, 1955; Kendrick and Molnar 1965) and the Ophiostomatales (Rosinski 1961). The order Sphaeriales contains four genera: *Europhium* Parker, *Sphaeronaemella* Karsten ex Seeler, *Chadefaudia* Feldman, and *Ceratocystis* (Ellis & Halstead) Bakshi.

1974 De Hoog concluded that the genus *Ceratocystis* should be separated into 2 separate genera based on the morphology of the conidial states: *Ceratocystis* Ellis and Halstead with the anamorphs *Chalara*, *Chalaropsis* Peyronel, and *Thielaviopsis* Went accepting 11 species (see table 2), and the genus *Ophiostoma* H. & P. Sydow containing the anamorphs *Sporothrix* Hektoen & Perkins ex Nicot & Mariat, *Verticicladiella* S. Hughes, *Leptographium* Lagerberg & Melin, and *Graphium* Corda. He proposed four new *Ophiostoma* combinations, enlarged the concept of the form-genus *Sporothrix*, and described new species.

1974 Jewell studies cellulose distribution in cell walls of 47 species of *Ceratocystis* and 4 species of *Europhium* cytochemically and using x-ray diffraction analysis. Thirty-one species of *Ceratocystis* and all of the *Europhium* species contained cellulose.

1974 Olchowecki and Reid published a monograph of 50 *Ceratocystis* species found in Manitoba with a key to 70 species of which 25 were described as new. They provided a first-time conidial description for three species. They subdivided the genus into four groups based on ascospore morphology; (1) the Minuta Group, (2) the Ips Group, (3) the Fimbriata Group, and (4) the Pilifera Group.

1974 Von Arx urged revision of the genus *Ceratocystis* and suggested that species with *Chalara*-like anamorphs be retained within the genus, but those species having holoblastic conidia be transferred to *Ophiostoma*. He maintained *Europhium* as a distinct genus.

1975 Nag Raj and Kendrick placed the form-genera *Chalaropsis* and *Thielaviopsis* in synonomy with *Chalara*.

1975 Upadhyay and Kendrick proposed dividing the genus Ceratocystis and establishing a new genus *Ceratocystiopsis* based on Olchowecki and Reid's Minuta group that included 19 species with falcate ascospores and ascoma with short necks. The new genus was classed as Ascomycotina, Plectomycetes, Microascales, Ophiostomataceae. They listed 13 anamorphs of *Ceratocystis* and *Ceratocystiopsis*, 4 of which were described as new: *Hyalorhinocladiella*, *Graphilbum*, *Hyalopesotum*, and *Pachnodium*. *Europhium* was considered a synonym of *Ceratocystis*, and *Ophiostoma* was not accepted as a valid genus. Olchowecki and Reid's three other groups—Ips, Fimbriata, and Pilifera—were accepted.

1975 Weijman and de Hoog discussed the results of cell wall cellulose (Smith and others 1967) and the presence of rhamnose (Spencer & Gorin 1971) as an aid in the classification of teleomorphs and anamorphs. They divided the genus *Ceratocystis* into two groups: (1) the phialidic endogenous conidial forms— *Chalara* and allied genera—and (2) the exogenous conidial forms of the *Ophiostoma* group (Graphium-like states). *Ceratocystis sensu stricto* for the *Chalara* type was used where rhamnose and cellulose were absent.

1977 Redhead and Malloch placed the genus *Ceratocystis* in the order Endomycetales and the family Endomycetaceae as a yeast-related genus. The family Ophiostomataceae was synonomized with the family Endomycetaceae.

1978 Upadhyay dropped emendation of the genus *Ceratocystis* by Bakshi (1951) and Hunt (1956) to conserve the original description by Ellis and Halstead.

1979 The Proceedings of the Second International Mycological Congress (Kananaskas II) was published in two volumes as *The Whole Fungus* (Kendrick 1979). Included were discussions of fungal morphology, classification, ecology, evolution, and techniques. New terms such as holomorph, teleomorph, and anamorph were defined. Malloch, von Arx, de Hoog, and Luttrell presented divergent views of *Ceratocystis* classification. Kendrick and DiCosmo's paper of teleomorph-anamorph connections listed 70 species of *Ceratocystis* and 2 species of *Ceratocystiopsis*.

1980 Benny and Kimbrough proposed a new order, Ophiostomatales, having only one family Ophiostomataceae (Nannfeldt 1932) that included the genera *Ophiostoma*, *Ceratocystis*, *Ceratocystiopsis*, and *Sphaeronaemella*. *Europhium* was synonomized, and *Chadefaudia* Feldman was rejected from the family. They resurrected the genus *Sphaeronaemella*, which Hunt (1956) had placed in synonomy with the genus *Ceratocystis*.

1981 Harrington published on cycloheximide as an aid to classification of the species. *Ceratocystis sensu stricto* (*Chalara* anamorphs) is sensitive to cycloheximide, but *Certocystis sensu lato* (*Ophiostoma* spp.) is not sensitive.

1981 Upadhyay published a monograph on the genera *Ceratocystis* Ellis & Halstead and *Ceratocystiopsis* Upadhyay & Kendrick. He placed the two genera in the order Microascales of the Plectomycetes. *Ophiostoma*, *Rostrella*, *Endoconidiophora*, *Grosmannia*, *Sphaeronaemella*, and *Europhium* were rejected as valid genera and were reduced to synonomy with the genus *Ceratocystis*. He divided the genus *Ceratocystis* into four sections: (1) *Ophiostoma*, ascospores lacking a hyaline gelatinous sheath; (2) *Ips*, ascospores always surrounded by a hyaline gelatinous sheath, rectangular, never curved; (3) *Ceratocystis*, ascospores sheathed, partly curved; and, (4) *Endoconidiophora*, sheath elongated, inequilateral.

1983 Ainsworth and Bisby's *Dictionary of the Fungi* (Hawksworth and others 1983) listed the order Ophiostomatales and the family Ophiostomataceae as having 2 or 3 genera, 13 synonyms, and 85 species.

1983 Urosevic redescribed five *Ceratocystis* species that cause tracheomycoses of oak as *Ophiostoma* species.

1984 De Hoog and Scheffer published a historical reappraisal of the genera *Ceratocystis* and *Ophiostoma*. They concluded that all species with *Chalara* anamorphs are *Ceratocystis sensu strictu* and distinct from *Ceratocystiopsis*. All others having conidial anamorphs are *Ophiostoma* (other than *Chalara*, which has cell walls with rhamnose and is resistant to cycloheximide). The latter included *Europhium*. They recombined 14 *Ceratocystis* species as *Ophiostoma* species (table 8).

1985 Kendrick recognized the order Ophiostomatales having 15 genera and 130 species.

1985 Wingfield reclassified *Verticicladiella* as *Leptographium*. He noted that the annellidic as well as the sympodial type of growth occurs in the *Leptographium* species.

1986 Solheim presented a key to genera of the family Ophiostomataceae and a key to ten Norwegian *Ophiostoma* species and one *Ceratocystiopsis* species; *O. ainoae*, *O. cucullatum*, and *O. flexuosum* were described as new.

1987 Bridges and Perry described a new species: *Ceratocystiopsis ranaculosus* Perry & Bridges, having a *Sporothrix* anamorph.

Table 8.—*Recombined* Ceratocystis *species by de Hoog and Scheffer (1974)*

Ophiostoma araucariae (Butin) de Hoog & Scheffer.
≡ *Ceratocystis araucariae* Butin

Ophiostoma bacillisporum (Butin & Zimmermann) de Hoog & Scheffer
≡ *Ceratocystis bacillispora* Butin & Zimmermann

Ophiostoma brevicolla (Davidson) de Hoog & Scheffer
≡ *Ceratocystis brevicollis* Davidson

Ophiostoma distortum (Davidson) de Hoog & Scheffer
≡ *Ceratocystis distorta* Davidson

Ophiostoma dryocoetidis (Kendrick & Molnar) de Hoog & Scheffer
≡ *Ceratocystis dryocoetidis* Kendrick & Molnar

Ophiostoma francke-grosmanniae (Davidson) de Hoog & Scheffer
≡ *Ceratocystis francke-grosmanniae* Davidson

Ophiostoma huntii (Robinson-Jeffrey) de Hoog & Scheffer
≡ *Ceratocystis huntii* Robinson-Jeffery

Ophiostoma megalobrunneum (Davidson & Toole) de Hoog & Scheffer
≡ *Ceratocystis megalobrunnea* Davidson & Tools

Ophiostoma nigrum (Davidson) de Hoog & Scheffer
≡ *Ceratocystis nigra* Davidson

Ophiostoma populinum (Hinds & Davidson) de Hoog & Scheffer
≡ *Ceratocystis populina* Hinds & Davidson

Ophiostoma rostrocoronatum (Davidson & Eslyn) de Hoog & Scheffer
≡ *Ceratocystis rostrocoronata* Davidson & Eslyn

Ophiostoma seticolle (Davidson) de Hoog & Scheffer
≡ *Ceratocystis seticollis Davidson*

Ophiostoma sparsum (Davidson) de Hoog & Scheffer
≡ *Ceratocystis sparsa* Davidson

Ophiostoma tremulo-aureum (Davidson & Hinds) de Hoog & Scheffer
≡ *Ceratocystis tremulo-aurea* Davidson & Hinds

1987 Von Arx accepted five species in the genus *Ceratocystis*. All have *Chalara* anamorphs, but only *C. fimbriata* has hat-shaped ascospores.

1987 Harrington recombined 11 *Ceratocystis* species as *Ophiostoma* (table 9).

1988 Hutchinson and Reid presented a key to seven potential wood-staining *Ceratocystis*. *Ceratocystis novae-zelandiae* was described as new. They listed one species of *Ceratocystiopsis* and a *Sphaeronaemella* species.

1988 Von Arx and van der Walt accepted the order Ophiostomatales by Benny and Kimbrough for the three genera *Ceratocystis*, *Ceratocystiopsis*, and *Ophiostoma* and the family Ophiostomataceae for *Ceratocystiopsis* and *Ophiostoma*. However, they proposed a new family, Pyxidiophoraceae, for *Ceratocystis* because of their *Chalara* anamorphs and the lack of cellulose in their cell walls (fig. 1).

1988 Wingfield and others described a new species *Ceratocystiopsis proteae* with a new anamorph genus *Knoxdaviesia*.

1989 Kowalski and Butin redescribed four species of *Ceratocystis* from oak in Poland and described two new species. *Ceratostomella quercus* Georgev. and *Ophiostoma roboris* were synonomized as *Ceratocystis piceae* (Munch) Bakshi.

1990 Harrington and Zambino rejected Ceratocystis minor var. *barrasi* J. Taylor as the mycangial fungus of *Dendroctonus frontalis* and established *Ceratocystiopsis ranaculosus* as the correct fungus based on isozyme analysis and mating studies.

Table 9.—*Recombined* Ceratocystis *species by Harrington (1987)*

Ophiostoma abiocarpum (Davidson) Harrington
≡ *Ceratocystis abiocarpa* Davidson

Ophiostoma adjuncti (Davidson) Harrington
≡ *Ceratocystis adjuncti* Davidson

Ophiostoma aureum (Robinson-Jeffrey & Davidson) Harrington
≡ *Europhium aureum* Robinson-Jeffrey & Davidson
≡ *Ceratocystis aurea* (Robinson-Jeffrey & Davidson) Upadhyay

Ophiostoma cainii (Olchowecki & Reid) Harrington
≡ *Ceratocystis cainii* Olchowecki & Reid

Ophiostoma clavigerum (Robinson-Jeffrey & Davidson) Harrington
≡ *Europhium clavigerum* Robinson-Jeffrey & Davidson
≡ *Ceratocystis clavigera* (Robinson-Jeffrey & Davidson) Upadhyay

Ophiostoma crassivaginatum (Griffin) Harrington
≡ *Ceratocystis crassivaginata* Griffin
≡ *Ceratocystiopsis crassivaginata* (Griffin) Upadhyay

Ophiostoma grandifoliae (Davidson) Harrington
≡ *Ceratocystis grandifoliae* Davidson

Ophiostoma robustum (Robinson-Jeffrey & Davidson) Harrington
≡ *Europhium robustum* Robinson-Jeffrey & Davidson
≡ *Ceratocystis robusta* (Robinson-Jeffrey & Davidson) Upadhyay

Ophiostoma trinacriforme (Parker) Harrington
≡ *Europhium trinacriforme* Parker
≡ *Ceratocystis trinacriforme* (Parker) Upadhyay

Ophiostoma valdivianum (Butin) Harrington
≡ *Ceratocystis valdiviana* Butin

Ophiostoma wageneri (Goheen & Cobb) Harrington
≡ *Ceratocystis wageneri* Goheen & Cobb

1990 Malloch and Blackwell proposed the genus *Kathistes* and presented a key to the genera likely to be confused with *Ceratocystiopsis* — *Gabarnaudia, Sphaeronaemella, Ceratocystis, Ophiostoma, Pyxidiophora, Rhynchonectria, Treleasia, Subbaromyces, Spumatoria,* and *Klasterskya.*

1990 Van Wyk and Wingfield reviewed the controversial taxonomic status of *Ceratocystis,* Ceratocystiopsis, and *Ophiostoma* regarding the development of asci, ascospores, and centrum structure. They suggested that additional ultrastructural studies are required to clarify these relationships.

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Lists *Ophiostoma* species previously described as *Ceratocystis* and summarizes events that led to revisions in the genera.

Keywords: *Ceratocystiopsis*, *Ophiostoma*

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