# A Reexamination of the Fungal Genera *Cryphonectria* and *Endothia*

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## ABSTRACT

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The morphology of nine species of *Cryphonectria* and three species of *Endothia* was examined by light microscopy to determine if the separation of *Endothia* from *Cryphonectria* proposed by Barr is warranted. Barr's descriptions of the fungi were accurate. Those species retained in *Endothia* produced diatrypoid stromata and nonseptate, allantoid ascospores; those species transferred to *Cryphonectria* formed valsoid stromata and monoseptate, ovoid to ellipsoid ascospores. The adoption of Barr's classification system is recommended because it attempts to organize relationships within the Diaporthales in a consistent manner.

The fungal genus *Endothia* Fr. is well known because *Endothia parasitica* (Murr.) P. J. & H. W. And., sensu priori, is the causal agent of chestnut blight. Since its introduction to the United States in the early 1900s, *E. parasitica* has virtually destroyed the American chestnut, *Castanea dentata* Borkh., and vastly changed the composition of the eastern hardwood forest. *E. parasitica* is perhaps the only plant pathogen that has brought a host species close to extinction (6). *E. parasitica* is not the only species of *Endothia*; 13 species are traditionally recognized (9,16,17,18,20). Individual species are differentiated by the size and color of the stromata, and the size, shape, and degree of septation of the ascospore (9,16,17,18).

Barr's monograph on the Diaporthales (4) dramatically altered the taxonomy of the genus *Endothia*, including the classification of *E. parasitica*. The genus was divided into two separate genera of two different families based on the configuration and texture of the stromata and the septation and shape of the ascospores. The genus *Endothia* was reassigned from the Diaporthaceae (14) to the Gnomoniaceae; this change is part of a reorganization at the ordinal level because the Diaporthaceae *sensu* Müller & von Arx is represented by the four families of the Diaporthales *sensu* Barr. The genus was also restricted to those species with diatrypoid stromata, predominantly pseudoparenchymatous tissue, and nonseptate, allantoid ascospores. Those species retained in *Endothia* were: *E. gyrosa* (Schw.) Fr., *E. viridistroma* Weymeyer, and *E. singularis* (H. & B. Syd.) Shear & Stevens. The remaining species were transferred to the genus *Cryphonectria* of the Valsaceae (which includes the Diaporthaceae) due to their valsoid stromata, predominantly prosenchymatous tissue, and monoseptate, ovoid to ellipsoid ascospores. The new species designations are presented in Table 1. Several species were not mentioned by Barr (4) but are presumably placed in *Cryphonectria* because of their morphology; these include *E. longirostris* and *E. coccolobii*.

The terminology used by Barr (4) needs to be defined. Snell and Dick (19) described a valsoid stroma as having its perithecia "clustered in a group of limited extent and with the perithecial necks convergent and erumpent . . . in a stromatic disc of limited area." The disk was described as being "less strongly developed and less widely erumpent than in the diatrypoid type" and was usually "ectostromatic"; this latter term was employed by Wehmeyer (22) to describe the uppermost portion of the stroma, which is composed primarily of fungal tissue with few host cells. A diatrypoid stroma was subsequently defined (19) as having a "somewhat widely erumpent stroma, in which the perithecia are clustered in limited or widely effuse areas and with perithecial necks erumpent separately over the entire stromatic surface. The stroma is usually more strongly developed and more widely erumpent . . . than in the valsoid type, and the disk is usually 'entostromatic' ", a term used to define the lower portion of the stroma, which is composed of both fungal tissue and host bark cells (22). Two other terms employed by Barr are "prosenchyma" and "pseudoparenchyma," which described the texture of the stroma. Prosenchyma refers to fungal tissue that is composed of loosely woven cells that retain their hyphal appearance, whereas pseudoparenchyma has differentiated into "closely packed, more or less isodiametric or oval cells resembling the parenchyma cells of higher plants" (1).

The discovery of hypovirulent forms of *C. parasitica* as potential biological control agents for chestnut blight (2) has renewed interest in these organisms. Other pathogens, including *E. gyrosa*, the causal agent of pin oak blight (3) and *C. cubensis*, the causal agent of eucalyptus canker (15) and "acute dieback" of clove (*Syzygium aromaticum* (L.) Murr. & Perry) (7,8), also belong to the *Endothia*-*Cryphonectria* complex. The taxonomic position of this group of fungi needs to be resolved. For this reason, the criteria used by Barr were reexamined to determine if the separation of *Cryphonectria* from *Endothia* is warranted. Preliminary results (12) validated Barr's separation; her nomenclature will therefore be used (Table 1).

## MATERIALS AND METHODS

Fresh and dried material of *Endothia* and *Cryphonectria* species were examined using light microscopy; the sources of these materials are listed in Table 1. Small specimens, bearing one to several stromata, were fixed in ethanol: glacial acetic acid: formaldehyde: water (5.0: 0.5: 1.0: 3.5) for 48–72 hr. Trapped air was removed from the woody tissue by the application of a vacuum (10–20 psi) for 1–5 min during fixation. After fixation, the specimens were dehydrated at room temperature in a standard tert-butyl alcohol (TBA) series (5); solutions were changed every 3 hr. Specimens were transferred to TBA: paraffin oil: chloroform (6:3:1) before infiltration in Paraplast. Eight- to 12-$\mu$m sections were cut with a rotary microtome and stained in a safranin: fast green series.

Sections were examined for the type and distribution of tissues

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within the stroma, and the position and characteristics of perithecia, ascospores, pycnidia, and conidia.

## RESULTS

Sections were prepared from fresh and dried material of *Cryphonectria* and *Endothia* stromata. Pycnidial and perithecial stromata were located among specimens of *E. gyrosa, C. coccolobii, C. longirostris, C. cubensis, C. nitschkei, C. gyrosa, C. parasitica,* and *C. radicalis*. Perithecial stromata alone were observed in specimens of *C. macrospora, C. havanensis,* and *E. viridistroma*; pycnidial stromata were found in *E. singularis*. The organization of the stroma and distribution of stromatic tissues could be discerned in the absence of the perfect stage.

**Configuration of the stroma.** The distribution of host and fungal cells was easily observed by the differential staining of the safranin: fast green series; lignified host cells appeared red, whereas chitinous fungal tissue was green. Ecto- and entostroma were readily separable by their constitutive cells. Two stromatic configurations were observed. Specimens of *C. parasitica* (Fig. 1), *C. cubensis, C. havanensis, C. nitschkei* (Fig. 2), *C. longirostris, C. macrospora, C. radicalis* (Fig. 3), *C. coccolobii* (Fig. 5), and *C. gyrosa* contained sharply defined areas of ecto- and entostroma. In most cases, the ectostroma was erumpent and formed a narrow, confining disk. The entostromatic layer was immersed and extended beyond the boundaries of the ectostroma. Perithecial bases were frequently located in the entostroma, although exceptions were observed. Perithecia along the periphery of the stroma were usually oblique; the perithecial necks grew towards the center of the stroma and penetrated the confining ectostromatic disk. Perithecia in the center of the stroma were upright; these perithecial necks had unrestricted access to the top of the stroma and were not forced to bend. This description is consistent with the definition of a valsoid stroma and supports Barr's concept of the genus *Cryphonectria*. *E. coccolobii* and *E. longirostris* are therefore formally transferred to *Cryphonectria* (Table 1).

In some cases, the valsoid appearance of these stromata was difficult to discern. This was particularly common among small stromata that contained large numbers of pycnidia or perithecia (Figs. 6 and 7). Vegetative stromal tissue was limited in these stromata, and it was difficult to differentiate the layers of ecto- and entostroma. The nature of the host tissue also altered the appearance and the size of the stroma; this was observed on different specimens of *C. coccolobii* on *Coccolobis uvifera* (L.) Jacq. Stromata formed on exposed roots (Fig. 5) produced a typical valsoid configuration; those formed on the seed coat (Fig. 6) were unable to penetrate the host tissue and were confined to the seed surface. A much smaller stroma was subsequently formed on the seed, and the boundary between ecto- and entostromatic tissue was obscured. In some species, as in *C. nitschkei* (Fig. 2), the ectostromatic disk was very wide (as observed in cross section), and the majority of the perithecia appeared upright. Perithecia along the periphery of the stroma were oblique, and there was a sharp delineation of ecto- and entostroma; the configuration was considered valsoid.

The stromal morphology of *E. gyrosa* (Fig. 4), *E. singularis* (Fig. 8), and *E. viridistroma* (Fig. 9) was quite different from that observed in the other species. A larger portion of the stroma was erumpent, and the perithecial bases of *E. gyrosa* and *E. viridistroma* were located in the erumpent region of the stroma. There was no sharp delineation of ecto- and entostroma; host cells were distributed uniformly throughout the erumpent area indicating that the stroma is primarily entostromatic. Perithecial necks grew unimpeded to the stromal surface or diverged slightly to the closest stromal edge; perithecia were generally upright. These characteristics are consistent with the definition of a diatrypoid stroma and support Barr's delineation of the genus *Endothia*.

**Distribution of pseudoparenchyma and prosenchyma.** The distribution of pseudoparenchyma and prosenchyma was observed among nine species of *Cryphonectria* and three of

TABLE 1. Sources of fresh and dried material used to prepare sections[a]

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*Cryphonectria coccolobii* (Vizioli) Micales & Stipes, comb. nov.
≡ *Endothia coccolobii* Vizioli. Mycologia 15:107-119. 1923.
Dried material:
Cornell #11899 (type)
Fresh material:
E. Barnard. 10/82. Fort Lauderdale, FL. *Coccolobis uvifera* (L.) Jacq.
R. Dow. 2/84. Grape Bay, Bermuda. *Coccolobis uvifera*

*C. cubensis* (Bruner) Hodges
≡ *E. eugeniae* (Nutman & Roberts) Reid & Booth
Dried material:
IMI 45440
IMI 401954 (type)

*C. gyrosa* (Berk. & Br.) Sacc.
≡ *E. tropicalis* (Berk. & Br.) Shear & Stevens
Dried material:
Dingley #18377

*C. havanensis* (Bruner) Barr
≡ *E. havanensis* Bruner
Dried material:
National Fungus Collection #740 (type)

*C. longirostris* (Earle) Micales & Stipes, comb. nov.
≡ *E. longirostris* Earle. Muhlenbergia 1:10-17. 1901.
Dried material:
Dingley #28477
National Fungus Collection #4340 (type)

*C. macrospora* (Kobayashi & Ito) Barr
≡ *E. macrospora* Kobayashi & Ito
Dried material:
Kobayashi isotype
Kobayashi #3662

*C. nitschkei* (Otth.) Barr
≡ *E. japonica* Kobayashi & Ito
Dried material:
National Fungus Collection #2486 (type)
R. J. Stipes, Dept. Plant Pathology, Physiology & Weed Science, Virginia Polytechnic Institute & State University #E59
Kobayashi #1048
Kobayashi #1049

*C. parasitica* (Murr.) Barr
≡ *E. parasitica* (Murr.) H. W. & P. J. And.
Fresh material:
J. A. Micales. 5/83. Blacksburg, VA. *Castanea dentata* Borkh.
J. A. Micales. 7/83. Blacksburg, VA. *Castanea dentata*
J. A. Micales. 5/83. Arlington, VA. *Castanea crenata* Sieb. & Zucc.
J. A. Micales. 10/82. Doylestown, PA. *Quercus velutina* Lam.
J. A. Micales. 9/82. Blacksburg, VA. *Castanea dentata*
J. A. Micales. 10/82. Buckingham, PA. *Castanea dentata*
J. A. Micales. 10/80. Matthew's Courthouse, VA. *Q. virginiana* Mill.

*C. radicalis* (Schw. ex Fries) Barr
≡ *E. radicalis* (Schw.) Ces. & DeNot.
Dried material:
Dingley #23586
National Fungus Collection

*E. gyrosa* (Schw.) Fr.
Fresh material:
B. Nash. 10/82. Durham, NC. *Q. palustris* Muenchh.
J. A. Micales. 3/82. Blacksburg, VA. *Q. palustris*
B. Harris. 11/82. Arlington, VA. *Q. palustris*
M. Mahoney. 8/82. Gulfport, MS. *Q. palustris*
R. J. Stipes. 5/81. Norfolk, VA. *Q. velutina*
R. J. Stipes. 5/81. Richmond, VA. *Q. palustris*
J. A. Micales. 11/80. Fairfax, VA. *Q. palustris*
J. A. Micales. 11/80. Fairfax, VA. *Q. phellos* L.

*E. singularis* (H. & B. Syd.) Shear & Stevens
Dried material:
R. J. Stipes. Dept. Plant Pathology, Physiology & Weed Science, Virginia Polytechnic Institute & State University #E58

*E. viridistroma* Wehmeyer
Dried material:
Cornell #3634 (type)

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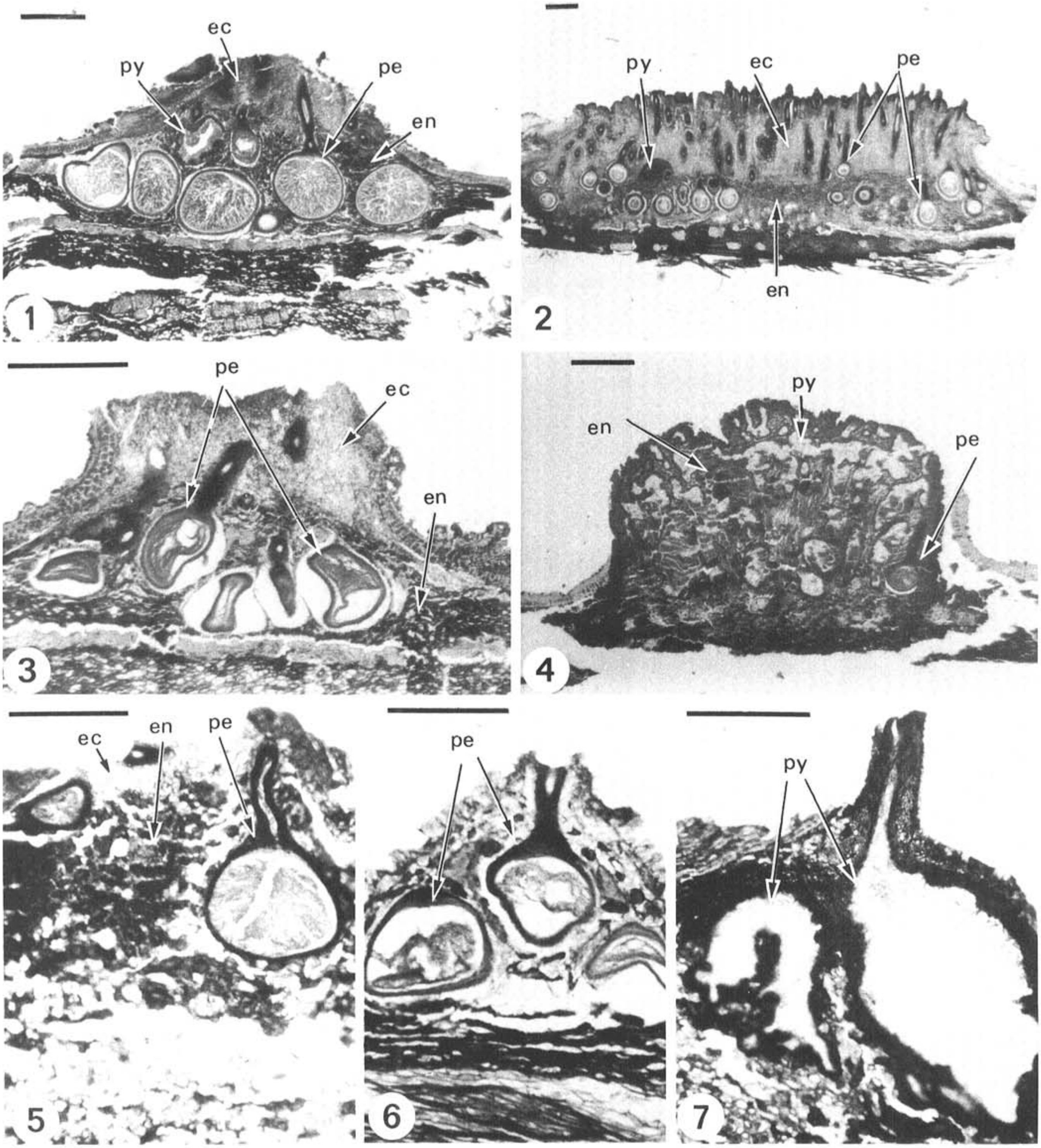
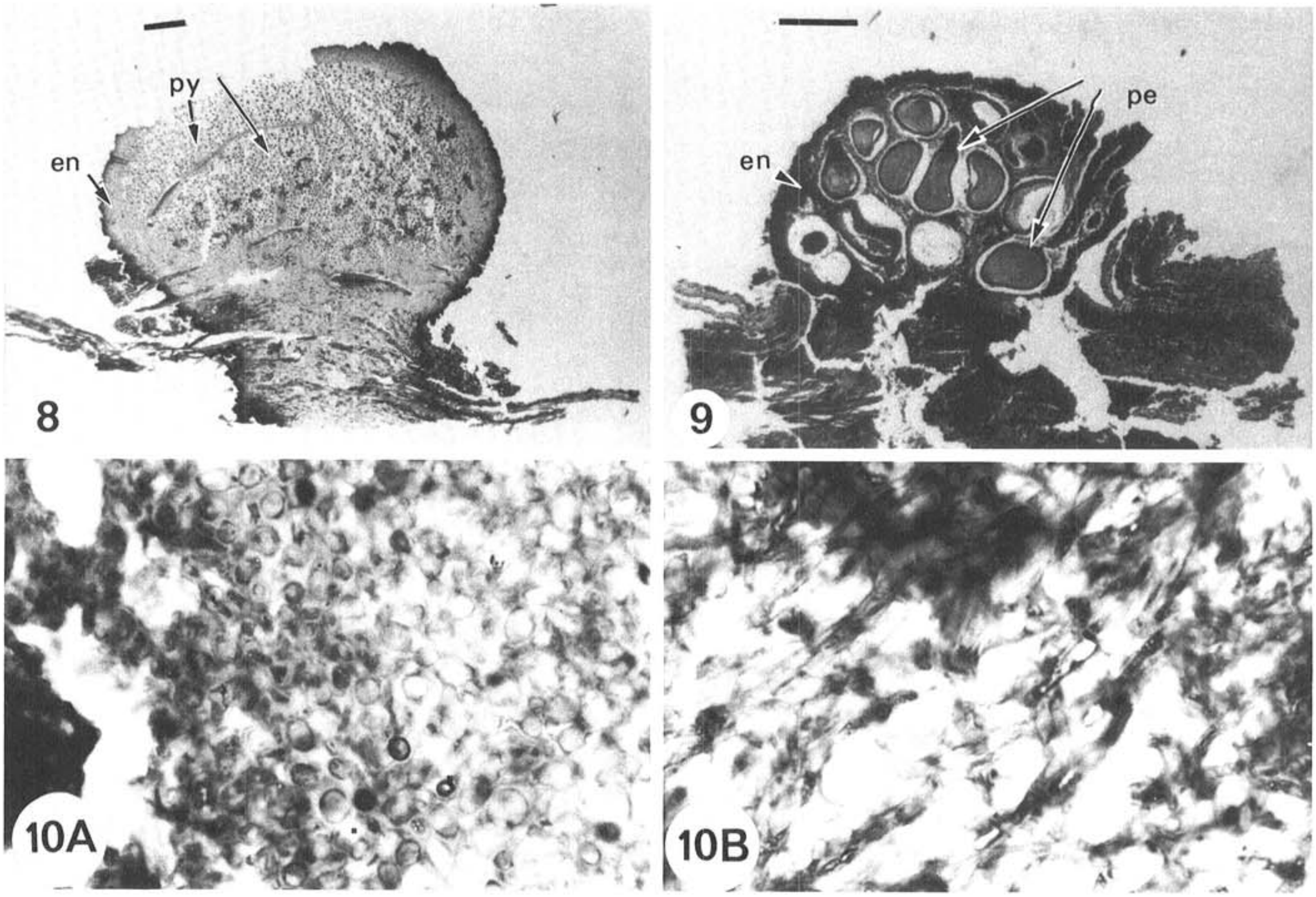
[a] Preserved specimens listed by herbarium location and number. Freshly collected material listed by collector, date, place of collection, and host.

*Endothia*. In each case, pseudoparenchyma, textura angularis, was observed on the surface and along the upper edges of the stroma; prosenchyma, textura intricata, was found in the center of each stroma (Fig. 10). Each tissue type could be located at a magnification of 1,000× and was also distinguished at lower magnifications by differences in staining patterns; pseudoparenchyma was usually darker in appearance than prosenchyma because of its closely compacted cells. Specimens of *E. gyrosa, E. singularis,* and *E. viridistroma* differed in their staining and sectioning properties from those of the other species; they



**Figs. 1–7.** Light microscopy of stromata formed by species of *Endothia* and *Cryphonectria*. pe = Perithecium, py = pycnidium, ec = ectostoma, and en = entostroma. Bar represents 200 μm. **1,** Perithecial and pycnidial stroma of *C. parasitica* (50×). Stroma is valsoid with erumpent ectostromatic disk and immersed entostroma. Perithecial necks converge within the entostromatic disk. **2,** Perithecial and pycnidial stroma of *C. nitschkei* (25×). Stroma is valsoid with erumpent ectostromatic disk and immersed entostroma. Perithecia along periphery of stroma are convergent; those in the center are upright. **3,** Perithecial stroma of *C. radicalis* (100×). Morphology of stroma similar to that of *C. parasitica* (Fig. 1). **4,** Perithecial and pycnidial stroma of *E. gyrosa* (50×). Stroma is diatrypoid with a widely erumpent entostromatic disk. Perithecium is tilted toward stromal edge. **5,** Perithecial stroma of *C. coccolobii* on exposed root of *Coccolobis uvifera* (100×). Erumpent portion of ectostromatic disk partially lost; valsoid configuration still evident. **6,** Perithecial stroma of *C. coccolobii* (type specimen) on seed coat of *Coccolobis uvifera* (100×). Stroma restricted to surface of host tissue; typical valsoid appearance is obscured. **7,** Beaked pycnidial stroma of *C. coccolobii* on exposed root of *Coccolobis uvifera* (100×). Valsoid appearance of stroma obscured by large pycnidium and relative lack of vegetative tissue.



**Figs. 8–10.** Light microscopy of stromata formed by species of *Endothia*. pe = Perithecium, py = pycnidium, and en = entostroma. Bar represents 200 μm. **8,** Pycnidial stroma of *E. singularis* (25×) composed of sidely erumpent entostromatic disk. **9,** Perithecial stroma of *E. viridistroma* (type specimen) (50×). Stroma is diatrypoid with well-developed entostromatic disk. Perithecial necks diverge to stromal edge. **10A,** Pseudoparenchymatous and **10B,** prosenchymatous tissue within a single section of *E. gyrosa* (1,000×). The pseudoparenchyma is located along the periphery of the stroma, and the prosenchyma is found within the center of the stroma.

appeared much darker under the same staining regime and were subject to more sectioning damage. This may indicate a more tightly compressed texture. The ectostromatic disks of the species transferred to *Cryphonectria* were more filamentous and open in appearance than the entostromatic stromata of those species retained in *Endothia*.

**Ascospore shape and septation.** The shape and degree of septation of the ascospore are the most easily observed criteria used by Barr and those subject to the least interpretation. Specimens of *C. parasitica, C. coccolobii, C. radicalis, C. longirostris, C. nitschkei, C. macrospora, C. cubensis,* and *C. havanensis* produced ovoid to ellipsoid, two-celled ascospores, whereas those of *E. gyrosa* and *E. viridistroma* formed allantoid, one-celled ascospores (Fig. 11). This distribution is well documented (9,16,17,18) and corresponds to Barr's (4) separation of *Cryphonectria* from *Endothia*.

## DISCUSSION

Barr's (4) descriptions of these fungi were appropriate. Those species retained in *Endothia* produced nonseptate, allantoid ascospores in upright perithecia. The perithecia produced central beaks and were found within diatrypoid stromata. The species transferred to *Cryphonectria* formed two-celled, ellipsoid to ovoid ascospores. The perithecia along the periphery of these stromata were frequently tilted, and the oblique necks converged within the ectostromatic disk before growing to the stromal surface. The configuration of the stroma was valsoid with an immersed entostroma and an erumpent ectostroma.

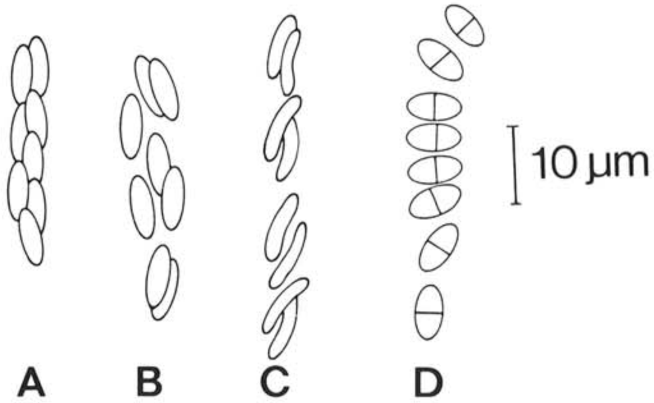


**Fig. 11.** Ascospores of *Endothia* and *Cryphonectria* species. **A,** *E. gyrosa* on *Quercus palustris* collected by P. M. Phipps, Gretna, VA, 1970. **B,** *E. singularis* on *Quercus* sp. collected by C. L. Shear, Palmer Lake, CO, 1913. **C,** *E. viridistroma* (type) on *Cercis canadensis* collected by J. H. Miller, Athens, GA, 1934, and determined by L. G. Wehmeyer (DAOM 120190). **D,** *C. parasitica* on *Castanea dentata* collected by C. L. Shear, Kennet Square, PA, 1913.

Barr (4) also reported the presence of pseudoparenchymatous tissue in *Endothia* and prosenchymatous tissue in *Cryphonectria*. These terms are meant to give an overall impression of stromal configuration and are not mutually exclusive. Barr has stated (M. E. Barr, *personal communication*) that the stromata of *Cryphonectria* are more condensed at the margins, especially in the ectostromatic disk, and may appear pseudoparenchymatous in these regions; the stromata of *Endothia* are more loosely arranged in the center and may appear prosenchymatous. This flexible interpretation corresponds with the descriptions of Kobayashi (9), Walker et al (21), and to the observations in this study. Pseudoparenchymatous cells were observed at 1,000× along the borders of the stromata of all 12 species, whereas prosenchyma was noted in the center of the same sections. Developmental studies would be necessary to determine the actual texture of the stroma before developmental pressures of expansion and eruption altered the appearance of the primordial tissue. The staining properties of the two groups were somewhat different; stromata of *E. gyrosa, E. viridistroma*, and *E. singularis* stained darker and were more difficult to section than those of species transferred to *Cryphonectria*. This indicates a difference in the texture or chemistry of the stromata and may reflect taxonomic differences.

One potential problem with any classification system is the influence of the host on stromal morphology. This effect was observed with specimens of *C. coccolobii* on the roots and seed coat of *Coccolobis uvifera*. Hodges et al (8) reported that stromal development was also extremely variable in *C. cubensis*. This fungus produced rudimentary to well-developed stromata on clove; stromal development was extremely limited on eucalyptus where perithecia and pycnidia were superficial and little or no stromal tissue was observed. The traditional taxonomic system did not recognize this variability; the clove fungus was designated *E. eugeniae*, whereas the eucalyptus pathogen was named *Diaporthe* (and later *Cryphonectria*) *cubensis*. Cross-inoculation studies with both hosts were needed to verify the identity of these organisms. The influence of host on stromal morphology could have a drastic impact on the taxonomy of the stromatic Ascomycetes; neither the traditional system nor Barr's classification allows this amount of variability. Further studies are needed to determine if such a large diversity in stromal configuration is frequent in nature.

The fundamental issue is whether differences in stromatic configuration and ascospore shape and septation are sufficient to redistribute these species into separate genera of different families. The trend in fungal taxonomy is to base classification on developmental parameters that reflect evolutionary relationships and to move away from groupings based on superficial characteristics. Barr included over 50 genera of the Diaporthales in her monograph and was able to organize the entire order with these criteria. A firm understanding of Barr's classification system would allow pathologists to distinguish among the different genera of the Diaporthales in an organized manner.

Barr's (4) descriptions of *Endothia* and *Cryphonectria* were accurate, and we believe that her classification system should be adopted because it organizes relationships within the entire order in a uniform manner. It would be beneficial for others to reexamine Barr's placement of additional genera to test further the usefulness of this system. Certain anamorphic forms of *Endothia* and *Cryphonectria* can be distinguished by isozyme analysis (11), polyacrylamide gel electrophoresis (10), and their differential sensitivities to cycloheximide (13). Additional chemotaxonomic procedures should be pursued to facilitate species identification and to evaluate further Barr's classification system.

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