

An Evaluation of the Fungal Genus *Endothia*

Martha K. Roane and R. J. Stipes

Department of Plant Pathology and Physiology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

ABSTRACT.— Of the several species ascribed to the genus *Endothia* or its imperfect state, *Endothiella*, four, *Endothia sordida*, *Endothia parryi*, *Endothia nitschkei* and *Endothiella robiniae*, have been removed from the genus. Since materials of *Endothia tetraspora* and *Endothiella simoniani* have not been examined, the status of these taxa is uncertain. The synonymy of *E. longirostris* with *E. radicalis* and of *E. tropicalis* with *E. havanensis* is being studied. The position of *E. eugeniae* is doubtful because of the atypical stromata, the absence of bisanthraquinone pigments and the ovoid rather than bacillioid conidia. *Endothia coccolobii*, *E. gyrosa*, *E. havanensis*, *E. japonica*, *E. macrospora*, *E. parasitica*, *E. radicalis*, *E. singularis*, and *E. viridistroma* are retained as discrete species.

Endothia Fries

The genus *Endothia*, described by Fries (1849) from specimens of *Sphaeria gyrosa* Schw. (Schweinitz, 1822), and its imperfect state, *Endothiella* Sacc. (Saccardo, 1906), today contain 18 species aside from the synonyms listed in Shear *et al.* (1917). *Endothia* is characterized by stromata subcortical in origin, variable in size and shape, pustular to subspherical, subcoriaceous to friable, sometimes confluent, surface light auburn or chestnut to mahogany red (dark olive green in one species), capucine yellow or cadmium orange to scarlet within (dark olive green in one species); pycnidial and perithecial stromata the same or similar; pycnidia few to numerous, consisting of simple cavities or complex and irregular chambers; conidia minute, simple, bacilliiform to oblong, yellowish to reddish in mass; perithecia deeply immersed, in one or more irregular layers, usually black when mature, with long necks, black within, colored like the stroma without; asci clavate to oblong-fusoid, 8-spored, usually without paraphyses; ascospores oblong-fusoid or subellipsoid to cylindrical or allantoid-cylindric, one-celled or two-celled, hyaline to pale yellow. There are two sections in the genus, the first of which is made up of species having one-celled ascospores and the second having species with two-celled ascospores.

Section 1. Ascospores one-celled

Endothia gyrosa (Schw.) Fr.

As we know the type of the genus today, it is

characterized by bright orange to chestnut pulvinate stromata, 1.5-3 mm diameter by 1.5-2 mm high; one-celled, oblong, hyaline conidia, 3-4 x 1.5-2 μ m, formed in labyrinthiform chambers in the stromata and exuded in droplets; dark brown to black membranous, slender-necked perithecia, 150-300 μ m diameter, embedded in the stromata; oblong-fusoid or subclavate asci, 25-30 x 6-7 μ m, containing eight cylindrical to allantoid, one-celled, hyaline ascospores, 7-11 x 2-3 μ m.

Endothia singularis (H. & P. Syd.) Shear & Stevens

The second member of the section was described as *Calopactis singularis* by H. & P. Sydow (1912) and was removed to *Endothia* in Shear *et al.* (1917). Characteristics of this species are the very large (3-5 mm diameter by 2-4 mm high) scarlet stromata; one-celled oblong hyaline conidia, 6-8 x 1 μ m, formed in nearly spherical cavities, 25-35 μ m diameter, embedded in the stromata and set free in a powdery mass by the disintegration of the stroma wall; dark brown to black membranous, slender-necked perithecia, 200-350 μ m diameter, embedded in the stromata; oblong-cylindric to fusoid or subclavate asci, 25-35 x 4.5-5.5 μ m, containing eight cylindrical to allantoid, hyaline, one-celled ascospores, 6-11 x 1.5-3 μ m.

Endothia viridistroma Weh.

The third member of the section, described by Wehmeyer (1936) has dark olive-green tuberculate stromata, 2-5 mm diameter by 1-1.5 mm high; one-celled, hyaline, cylindrical to allantoid conidia, 2.5-3.5 x 0.5-1 μ m, formed in irregular locules surrounded by a greenish-black pseudo-parenchymatous wall in the stromata and set free by formation of yellow spore tendrils; dark brown to black membranous, slender-necked perithecia, 200-350 x 150-250 μ m, embedded in the stromata; clavate asci, 15-20 x 3-4 μ m, containing eight allantoid, hyaline, one-celled ascospores, 5-6 x 1-1.5 μ m.

Endothia tetraspora Kobayashi

Material of the last member of the section described by Kobayashi (1965) was not available for study. As Kobayashi (1970) noted, it has an atypical, small, compact, yellow-orange ectostroma and scanty entostroma; no conidia were reported; dark brown to black walled perithecia, 420-520 μ m diameter, embedded beneath the disc-like ectostroma, with confluent black necks erumpent through the stroma as in *Valsa*; clavate to oblong-clavate asci, 70-88 x 10-18 μ m, containing four one-celled, hy-

aline, fusoid or elliptic ascospores, 21-31 x 7.5-10 μm . Kobayashi found some characteristics common to this species and certain members of *Cryptosporella*. Further work is necessary to determine whether this species belongs in *Endothia* or in another genus.

Section 2. Ascospores two-celled

***Endothia radicalis* (Schw.) Ces. & DeNot.**

Endothia fluens (Sow.) Shear and Stevens is properly placed in synonymy with *E. radicalis* since the former was based upon *Sphaeria fluens* Sow. described by Sowerby (1814) in its pycnidial condition. The name *E. fluens* was quite correct for Shear *et al.* (1917) since they were observing the American Rules of Nomenclature. However, under the International Rules of Nomenclature now being observed, the name first applied to the sexual state of a fungal taxon takes priority. Therefore, the name *E. radicalis* (Schw.) Ces. & DeNot. takes precedence since it is based on the description of an ascosporic specimen. This species was first described as *Sphaeria radicalis* by Schweinitz (1832) and was removed to *Endothia* by Cesati and DeNotaris (1863). It is characterized by pulvinate, light auburn to chestnut stromata, 0.75-3 mm diameter by 0.5-2.5 mm high, containing irregular pycnidial chambers with oblong, hyaline, one-celled conidia, 3-5 x 1.5 x 2 μm ; dark brown to black perithecia, 300-400 μm diameter, with long slender black necks, containing oblong-fusoid or subclavate asci, 30-40 x 6-8 μm , with eight hyaline, 2-celled, oblong-fusoid or subellipsoid ascospores, not constricted at the septum, 6-10 x 3-4.5 μm .

***Endothia sordida* Fuckel**

The material of this species described by Fuckel (1866) that we examined (*E. sordida* Fuckel. Fungi Rhenani #1586. Type. National Fungus Collection) had stromata that were sandy brown to dark brown on the outside, chocolate brown within; black necks of perithecia forming papillae on the surface of the stromata, erumpent through the bark and scarcely distinguishable from the color of the bark, asci 8-spored, cylindrical, 118 x 13 μm ; 2-celled, brown, ellipsoid ascospores, 20 x 10 μm , with conspicuous globules. Because of the color of the stromata and the quite large, ellipsoid, brown ascospores with conspicuous globules, this species is removed from the genus *Endothia*.

***Endothia nitschkei* Otth**

Otth (1868) in describing this species said that the base of the tawny-rusty brown tubercle-like stroma was covered with dark brown to black membranous sacs of hyaline, cylindrical, one-celled conidia, 5 x 1 μm , that were expelled as a coarse white tendril. The perithecia were immersed in the bark with erect, converging necks piercing through the stroma with few black exerted ostioles. The 2-celled, oblong, blunt, faintly colored ascospores, 12-16 x 4-5 μm , were constricted at the septum. When the perithecia mature in the spring following the fall maturation of

the conidia, the stromata become whitish due to weathering on the outer surface.

We were unable to find stromal tissue near the perithecia which we examined in material from the National Fungus Collection (*E. nitschkei* Otth. Herbarium Fuckel 1894. #739). No pigments from tissue of this specimen dissolved in absolute ethanol in contrast to the almost immediate solution of pigments of *E. gyrosa*, *E. radicalis*, etc. Because of the perithecia immersed in the bark rather than in stromata, with converging necks like *Valsa*, and the absence of pigments soluble in absolute ethanol, this species is removed from the genus *Endothia*.

***Endothia parryi* Earle.**

The description of this species is included by Cooke (1885) in his Synopsis Pyrenomyceten. However, Theissen and Sydow (1915) removed the taxon to the genus *Dothidella*. We concur with this disposition after examination of specimens from the National Fungus Collection and the Farlow Herbarium.

***Endothia longirostris* Earle**

Characteristics of the species described by Earle (1901) are the yellow to chestnut stromata, 1-3 mm diameter; with oblong-elliptic, hyaline, one-celled conidia 2-4 x 1-1.5 μm , produced in labyrinthiform cavities and expelled from a single large pore or irregular rupture at the apex of the stroma in a stout coral-red spore tendril; black, membranous, long-necked, up to 1 cm perithecia, 300-400 μm diameter, embedded in the stromata usually at the base of the pycnidial locules; oblong-cylindrical to fusiform asci, 25-35 x 5-7 μm , with eight 2-celled, hyaline, ovoid to ovoid-elliptical ascospores, 6-8.5 x 3-4 μm .

According to Kobayashi (1970), *E. longirostris* is a synonym of *E. radicalis*. However, we (1978) have found that stromal tissue of *E. longirostris* contains the bisanthraquinones, skyrin and rugulosin, while *E. radicalis* contains only skyrin. Also, in numerical analysis of percent similarity of *Endothia* spp., we (1976) found that *E. radicalis* (= *E. fluens*) and *E. longirostris* were 28 percent similar, a value that does not indicate a very close relationship. Until we obtain fresh material of both, we prefer to retain *E. radicalis* and *E. longirostris* as separate species.

***Endothia parasitica* (Murr.) P. J. & H. W. And.**

The fungus found associated with a serious canker of the American chestnut in the New York Zoological Park was described as *Diaporthe parasitica* (Murrill, 1906) and *Endothia gyrosa* var. *parasitica* (Clinton, 1912). It was removed from *Diaporthe* and placed in *Endothia* as *E. parasitica* by P. J. and H. W. Anderson (1912). However, in the early reports of work on the chestnut blight organism there is much confusion among *E. gyrosa*, *E. radicalis* (= *E. fluens*) and *E. parasitica* because of the close resemblance of the asexual states of these species (Roane and Stipes, 1978). Ascosporic voucher specimens remain the best way of separat-

ing these species at present, although certain cultural characteristics, pigment analysis and protein and enzyme analysis are also valuable.

Endothia parasitica is characterized by yellow to auburn, corticular, slightly erumpent to truncate conical, usually separate but frequently confluent stromata, 0.75-3 mm diameter by 0.5-2.5 mm high; hyaline, oblong to cylindrical, one-celled conidia, 3-5 x 1.5-2 µm, formed in irregular cavities in the stromal tissue and expelled in spore tendrils that are yellow when fresh and coral red when old; dark brown to black, membranous, globose to flask-shaped, black-necked perithecia, 300-400 µm diameter, embedded in the stromata; oblong-elliptical to subclavate asci, 30-60 x 7-9 µm, containing eight hyaline, ellipsoid, 2-celled ascospores, 7-11 x 3.5-5 µm, sometimes constricted at the septum, with a gelatinous envelope. In the cambium and bark of the host this fungus typically produced yellow or buff fan-shaped formations of mycelium. These are not produced by *E. gyrosa* or *E. radicalis*.

***Endothia havanensis* Bruner**

In his description of this fungus Bruner (1916) compared it with cultures and specimens of *E. longirostris* and *E. radicalis* and concluded that the three represented different species. *Endothia havanensis* is denoted by rounded, wart-shaped to subelongate, bright-yellow to orange to yellow-brown stromata, 2-15 by 2-4 mm, containing irregular pycnidial chambers with hyaline, rod-shaped, one-celled, conidia, 3-4 x 0.5-2 µm, discharged in yellow or orange-yellow spore tendrils; black, globose, long-necked perithecia, 275-400 µm diameter, deeply embedded in stromata; subclavate, 8-spored asci, 33-41 x 5-7.5 µm, with hyaline, fusoid 2-celled ascospores, 7.5 - 9.5 x 3-4.5 µm, constricted at the septum.

***Endothia tropicalis* (Berk. & Br.) Shear & Stevens**

In 1875, Berkeley and Broome described this fungus and named it *Diatrype gyrosa*. Shear and Stevens (Shear *et al.*, 1917) studied material collected by Petch in Ceylon in 1913 and removed it from *Diatrype* to *Endothia* but had to supply a new specific epithet, *tropicalis*, since *gyrosa* was pre-empted by the earlier *E. gyrosa* (Schw.) Fr.

Endothia tropicalis has orange chrome to sanford brown, pustular to pulvinate stromata, 1-5 mm diameter, with numerous irregular cavities containing the hyaline, oblong to cylindrical, one-celled conidia, 3.5-7 x 1.5-2.5 µm; black, membranous, slender-necked, globose perithecia, 250-500 µm diameter, with oblong or subclavate, 8-spored asci containing 2-celled, not constricted at the septum, hyaline, subelliptical ascospores, 7.5-10.5 x 3.5-5 µm, with a gelatinous envelope.

***Endothia coccolobii* Vizioli**

A fungus on sea grape collected by H. H. Whetzel in Bermuda was described and named *E. coccolobii* by Vizioli (1923), who concluded that *E. longirostris*

was closely related to but not the same as this species. Its characters are small, orange-rufous, hemispheric to conoid, erumpent stromata, 0.5-1 mm diameter, containing irregular pycnidial locules with hyaline, bacilliform conidia, 2-3 x 0.5-1 µm, discharged through a single black conoid papilla; leathery-membranous, coffee-black, long slender-necked, globose to subglobose perithecia, 290-420 µm diameter, containing oblong to subclavate 8-spored asci, 30-40 x 4-6 µm, with hyaline, 2-celled, not constricted at the septum, ovoid to fusoid ascospores, 5.5-8 x 1.5-3 µm.

***Endothia japonica* Kobayashi & Ito**

Endothia japonica Kobayashi & Ito (1956) was placed in synonymy with Otth's *E. nitschkei* by Kobayashi (1970). Since we have removed *E. nitschkei* sensu Otth from *Endothia*, we retain the original name of this species of Kobayashi & Ito. It is characterized by yellow-orange or brown-orange, erumpent, conic to truncate-conic stromata, 2-3 mm diameter by 1-2 mm high; dark brown to black, globose, long-necked perithecia, 280-610 µm diameter, with clavate to oblong-clavate, 8-spored asci, 40-68 x 5.5-11 µm, elliptic, 2-celled, constricted at the septum, hyaline to pale brown ascospores, 8.5-17 x 3-5.5 µm; conidial stromata smaller and paler than perithecial stromata, with multilocular cavities containing hyaline, one-celled, allantoid or rod-shaped conidia, 3-4 x 0.5-1 µm, discharged as sticky yellow tendrils.

***Endothia macrospora* Kobayashi & Ito**

This fungus, described by Kobayashi & Ito (1956), typically has orange, erumpent, pulvinate stromata, 1-3 mm diameter by 1-2 mm high, containing irregular pycnidial locules with hyaline, one-celled, allantoid or rod-shaped conidia, 4-6.5 x 0.5-1.5 µm, discharged through a central pore as sticky yellow tendrils; dark brown membranous, globular, long-necked perithecia, 340-580 µm diameter, embedded in lower part of stroma, containing clavate to oblong-clavate, 8-spored asci, 62-73 x 10-11 µm, with elliptic, 2-celled, slightly constricted at the septum, hyaline ascospores, 14-18 x 5-5.5 µm. As inferred by the specific epithet, *macrospora*, this species has the largest ascospores of this section of the genus.

***Endothia eugeniae* (Nutman & Roberts) Reid & Booth**

The causal agent of a die-back of clove was named *Cryptosporella eugeniae* by Nutman and Roberts (1952) and was later transferred to *Endothia* by Reid and Booth (1969). This species is typified by orange to rust brown, erumpent, conic stromata, 0.2-0.5 mm diameter by 0.5 mm high, containing one to several irregular pycnidial locules with one-celled, oval, hyaline conidia, 3.5-5 x 1.5-2 µm, extruded in yellow tendrils; dark brown to black, globose, long-necked perithecia, 500-900 µm diameter, containing clavate, 8-spored asci, 20-32 x 4-6.5 µm, with oblong to elliptical, 2-celled, not constricted at the septum,

hyaline ascospores, 6-8.5 x 2-3 μ m, widest in the upper cell.

Nutman and Roberts described the stromata as valsiform and noted that perithecia contained in the same stroma have converging necks. Reid and Booth considered this taxon typical of the genus *Endothia* because of the nature of the stroma, the nature of the pycnidia, the orange-brown coloration of the perithecial necks and papillae, the arrangement of the perithecia within the stroma, and the possession of two-celled ascospores. However, in our study of specimens of other species in the genus, we have found that these species have much more abundant stromal tissue that contains at least one bisanthraquinone (Roane and Stipes, 1978) and have not found this to be true of *E. eugeniae*. Cylindric or bacilliform conidia are typical of all members of the genus except this one which has oval conidia. Because of these deviations from the normal pattern in *Endothia* we regard this species as a doubtful member of the genus *Endothia*.

***Endothiella* Saccardo. Imperfect state of *Endothia* *Endothiella robiniae* Chona & Munjal**

The slate-black, erumpent, pulvinate, stalked stromata, 0.75-1.5 mm diameter, are dark brown within and produce conidiophores and conidia on the outer surface rather than in pycnidial locules submerged in the stromal tissue (Chona & Munjal, 1950). The hyaline, cylindric-fusoid to allantoid, one-celled, very variable conidia, 8 μ m or more long, with papillae at both ends, are born on very long conidiophores, 92-185 μ m. When we placed stromal tissue of this taxon in lactophenol, no yellow to orange coloration appeared. We find from our examination of the fungus (Specimen 19759, Herb. Crypt. Ind. Orient. Fungi Indian Agricultural Research Institute, New Delhi) that it is not a species of *Endothiella* because of the black, stalked stroma with an external conidial layer, the atypical characters of the conidia and conidiophores, and the absence of the yellow and orange bisanthraquinone stromal pigments. It is probably the imperfect state of a species of *Hypoxylon*.

***Endothiella simoniani* Negru and Mozes**

We reserve judgment on this fungus described by Negru and Mozes (1965) since we have not seen it, although from the Latin description it seems to have characters similar to those of *Endothiella*. Negru and Mozes did not compare it with other members of the genus.

DISCUSSION

In 1951, Orsenigo divided *Endothia* into two subgenera, the first of which he called *Proendothia* and the second, *Euendothia*. He placed *E. gyrosa* and *E. singularis* in subgenus *Proendothia* and *E. radicalis*, *E. longirostris*, and *E. tropicalis* in subgenus *Euendothia*. He regarded *E. radicalis* as made up of two subspecies, ssp. *aflabellata* (= *E. fluens*

[Sow.] Shear and Stevens) and ssp. *parasitica* (= *E. parasitica* [Murr.] P. J. and H. W. And.). However, we (Roane and Stipes, 1978; Stipes *et al.*, 1978) have found that *E. parasitica* and *E. radicalis* can be differentiated by both pigment analysis and enzyme analysis and with the addition of these two characters to others previously known we consider these to be distinct species. Whether or not *Endothia* should be subdivided into the two subgenera as proposed by Orsenigo, divided into two genera, or left intact has not been considered by us at this time.

Kobayashi (1970) proposed that *E. fluens* and *E. longirostris* be placed in synonymy with *E. radicalis*, that *E. japonica* be placed in synonymy with *E. nitschkei* and that *E. tropicalis* be placed in synonymy with *E. havanensis*. We have already discussed the status of the first two synonymies. However, the situation regarding *E. tropicalis* and *E. havanensis* needs further clarification since, at present, there is insufficient material of *E. havanensis* available for comparison with *E. tropicalis*.

Two aids for the identification of an isolate obtained from a specimen containing only conidial stromata and presumed to be *E. gyrosa*, *E. parasitica*, or *E. radicalis* are 1) checking for the production of perilla purple by the culture when grown on white cornmeal medium and 2) analyzing the bisanthraquinone content by thin-layer chromatography. *Endothia gyrosa* and *E. parasitica* contain skyrin, oxyskyrin and rugulosin while *E. radicalis* contains only skyrin. Both *E. gyrosa* and *E. radicalis* produce perilla purple on white cornmeal but *E. parasitica* does not. In addition, we (Stipes *et al.*, 1978) have found that these three species have different electrophoretic enzyme and protein patterns.

We conclude that the genus *Endothia* contains the following species: *E. coccolobii*, *E. gyrosa*, *E. havanensis*, *E. macrospora*, *E. parasitica*, *E. radicalis*, *E. singularis* and *E. viridistroma*. We prefer not to consider *E. longirostris* as a synonym of *E. radicalis* and wish to obtain for study more fresh material of both species before making a final judgment. The same situation applies to the case of *E. havanensis* and *E. tropicalis*. As previously stated, we conclude that the original *E. nitschkei* Fuckel should be removed from the genus. Therefore, Kobayashi's species originally described as *E. japonica* is removed from synonymy with *E. nitschkei* and retains its first name. We reserve judgment on the status of *E. eugeniae* until further material can be obtained for study. The status of *Endothia tetraspora* and *Endothiella simoniani* is uncertain since we were unable to examine specimens of these species.

ACKNOWLEDGMENTS

The assistance of R. W. Davidson, J. Dingley, F. Hawksworth, T. Kobayashi, G. Samuels, Centraalbureau voor Schimmelcultures, Commonwealth

Mycological Institute, Cornell University Plant Pathology Herbarium, Farlow Herbarium, Indian Agricultural Research Institute Herbarium, National Fungus Collection, New York Botanical Garden, National Mycological Herbarium-Ottawa in obtaining cultures and specimens is gratefully acknowledged.

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