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NOTES ON PHIBALIS, TYPE GENUS OF THE ENCOELIOIDEAE (DISCOMYCETES)

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I. CLASSICAL DELIMITATION OF THE ENCOELIOIDEAE (CENANGIACEAE) AND PRESUMED RELATIONSHIP TO THE CIBORIOIDEAE (SCLEROTINIACEAE)

The Encoelioideae was erected as a subfamily of the Helotiaceae (= Leotiaceae) by Nannfeldt (1932) to include the majority of genera and species that had previously been assigned to an autonomous family, the Cenangiaceae. Though Nannfeldt excluded the genus *Cenangium* Fr. ex Fr. 1822 from the subfamily, indicating he had not studied it in sufficient detail to assign it a position in his classification, later authors (e.g., Dennis, 1960, 1968; Korf, 1973) have placed that genus in its restricted sense also in the Encoelioideae.

An examination of the keys to subfamilies and genera given by Nannfeldt (1932), Dennis (1956), and Korf (1973) demonstrates that the key characters which allow one to assign a species to the Encoelioideae are the presence of globose, brown-walled excipular cells that disarticulate to become a powdery mass of loosely adherent cells lacking hyphal orientation. This mealiness is very pronounced in the type species of *Encoelia, E. furfuracea* (Roth ex Fr.) Karst., and in *Velutarina rufo-olivacea* (Alb. & Schw. ex Fr.) Korf. In some species, such as *E. heteromera* (Mont.) Nannf., the excipular cells are aggregated into conical pustules. Throughout the subfamily the apothecia tend to be large (for an inoperculate discomycete), leathery to horny (when dry), and often on drying inroll, becoming hysteriform or triangular in shape. On rehydrating the apothecia revive to a cupulate form, and discharge their ascospores over a long period of time, apparently dessicating and reviving many times during their life span. This is an unusual feature among true discomycetes (the Hyaloscyphaceae subf. Trichoscyphelloideae being one of the few other groups similarly adapted for long life and periodic spore discharge). Some species of the Encoelioideae are even perennial, and overwinter their apothecia.

The great emphasis on microanatomy as a basis for classification of the inoperculate discomycetes begun by Starbäck (1895) and Durand (1900), carried much further by von Höhnel in a long series of papers beginning about 1906 and continuing in posthumous papers until the mid 1920's, reached codification in the monumental work by Nannfeldt (1932) that has served as the basis for all more recent major inoperculate discomycete classifications. The presence of brown-walled, globose excipular cells in stalked apothecia occurs not only in the Encoelioideae, but is also characteristic of many genera assigned by Nannfeldt to the Helotiaceae subf. Ciborioideae [=Sclerotiniaceae of Whetzel (1945) and more recent authors]. Members of the Sclerotiniaceae have short-lived apothecia. Normally these have much thinner-walled excipular cells, but this varies greatly among species; they normally also produce a stroma, either immersed in the host tissue or completely of fungal origin (and then termed a sclerotium). No stromata have been associated with any members of the Encoelioideae. Not

unexpectedly, some species have been referred to both the Sclerotiniaceae and to the Encoelioideae [e.g., species of *Chlorencoelia* Dixon (1975), placed by Ramamurthi et al. (1958) in *Chlorociboria* in the Sclerotiniaceae, correctly reassigned to the Encoelioideae by Dixon]. Nannfeldt (1932) was strongly of the opinion that the two subfamilies are close: "Diese Unterfamilie [Encoelioideae] ist zweifelsohne mit *Ciborioideae* am nächsten verwandt, unterscheidet sich aber von ihr durch die lederiche Konsistenz der Apothecien und ihre grössere Lebenslänge. Inbesondere nähert sich der Bau der Gattung *Encoelia* dem der Ciborioideen."

In the light of our studies reported here, the Encoelioideae seem to have little in common with the Sclerotiniaceae. Indeed, the presence of loose excipular cells and rhomboidal crystals in some species of *Pezicula* leads us to postulate that the Encoelioideae may find its closest relatives in the Dermateaceae subf. Peziculoideae rather than in the Sclerotiniaceae.

II. PHIBALIS, AN OLDER NAME FOR ENCOELIA, AND ITS DISTINCTION FROM CENANGIUM

Fries (1822) erected a "tribe" *Encoelia* within *Peziza* sect. *Aleuria* in which he included 8 species, some of diverse relationships. This tribe was elevated to generic rank by Karsten (1871), who restricted the genus to include only three of Fries's species and two new species described there. Karsten's genus was accepted by Schroeter (1893), Boudier (1907), von Höhnel (1918, 1923), Petrak (1925, 1956), van Overeem and Weese (1926), Nannfeldt (1932, 1936, 1939), Kirschstein (1935, 1938), Dennis (1954, 1955, 1956, 1960, 1968, 1971), Gremmen (1956), Cash and Corner (1958), Korf (1973), and Svrček (1974), among others.

Fries (1822) also accepted the genus *Cenangium*, and Fries (1849) subsequently treated *Encoelia* as an infrageneric taxon under *Dermatea* Fr. in another family than that in which he placed *Cenangium*. Karsten (1871), however, ranged *Encoelia* and *Cenangium* as immediately adjacent genera, a position adopted by many subsequent authors. Rehm (1887–1896) and Saccardo (1889) treated *Encoelia* as an infrageneric taxon under *Cenangium*, and Lindau (1897) gave *Encoelia* definite subgeneric rank there. Seaver (1951) did not accept *Encoelia*, but placed some of its species in *Cenangium*.

Von Höhnel (1923) clearly pointed out the carbonaceous nature of the excipular cells in *Cenangium ferruginosum* Fr. ex Fr., the lectotype species of the genus. He referred *Cenangium* to the Tryblidiaceae, a family that still remains very doubtful and in need of further study. It was this treatment by von Höhnel that led Nannfeldt (1932) to exclude *Cenangium* from the Encoelioideae, and thus to coin a new subfamilial name for the majority of genera and species previously referred to the Cenangiaceae.

Von Höhnel (1923) apparently overlooked the earlier name, *Phibalis* Wallroth 1833, much older than *Encoelia* (Fr.) Karst. 1871. Though *Phibalis* was often listed in the synonymies of *Cenangium* and of *Encoelia* by later authors, it was not until very recently that this name was correctly adopted instead of *Encoelia* by Groves and Elliott (1971). The synonymy appears to be obligate, since Wallroth (1833) specifically noted "Pezizae tribus Encoelia Fr. syst. P. erumpentes corticolae sicciores Wallenb. suec." in his generic diagnosis. Korf (1973) noted that "*Phibalis* may be an older generic name" for *Encoelia*, which our nomenclatural studies have now confirmed. We hereby designate *Phibalis furfuracea* (Roth ex Fr.) Wallr. as the LECTOTYPE species of Wallroth's genus. This same species has also been called *Cenangium furfuraceum* (Roth ex Fr.) Gill. and *Encoelia furfuracea*. It is also the lectotype species of *Encoelia* (Fr.) Karsten (1871), and hence of *Peziza* trib. *Encoelia* Fries (1822), selected by Clements and

Shear (1931). Nannfeldt's (1932) designation of *Peziza fascicularis* Alb. & Schw. ex Fr. as the "pseudotypus" of *Encoelia* (Fr.) Karst. merely reflects Karsten listing that species first among those he included; Clements and Shear's designation of lectotype for the genus appears to be the first. It should be noted that Clements and Shear also designated this same species as lectotype for *Cenangium* Fr. ex Fr., but this is not acceptable since the species was not included in *Cenangium* when erected, and furthermore it was not the first designation of a type species for that genus.

III. STUDIES ON PHIBALIS PRUINOSA (=CENANGIUM SINGULARE)

Recently an unusual fungus, the apparent cause of a sooty-bark canker disease on *Populus deltoides* Marsh., was brought to our attention by Mr. Thomas Stasz. The abundant collection, made in May, 1975 near Ithaca, New York, appeared to be distinctly encoelioid, yet was so anomalous microanatomically that we could find no satisfactory niche for it in recent keys. Macroscopically, the dark brown, leathery apothecia bore a granular, external hoar frost of white crystals and dried in a distinctive hysteriform or triangular shape, reviving in water to a cupulate form. While these characters suggested *Encoelia* (=*Phibalis*), keys of recent authors (Nannfeldt, 1932; Dennis, 1956; Korf, 1973) stress that the external mealiness in *Encoelia* is derived specifically from the disarticulation of thick-walled, globose, brown excipular cells; in our collection these excipular cells remained embedded in gel and did not disarticulate, and the mealiness was due instead to a thick incrustation of rhomboidal crystals. Equally confounding were the allantoid, one-septate spores in our collection, many of which produced polar, spermatium-like buds while still within the ascus. Although Dennis (1956) illustrates similar polar buds in *E. tiliacea* (Fr.) Karst., he delimits the genus as one having strictly nonseptate ascospores.

The aptness of the epithet "pruinosa" to describe the hoar frost of crystals led us to a consideration of *Cenangium pruinosum* (Ell. & Everh.) Seaver, described on *Populus*. Seaver (1951) does not, however, describe the distinctive excipular layer and illustrates the ascospores as nonseptate and ellipsoid. Subsequent examination of an isotype collection of Ellis and Everhart's species, originally described as *Dermatea pruinosa* Ell. & Everh., substantiated our early identification. Although allantoid, septate, budding spores were sparse in the type material, their presence there indicated that the abundance of such spores in our material might be due to time of collection, and not a matter of particular taxonomic significance. Davidson and Cash (1956) describe sooty-bark canker of aspen caused by this fungus, which, because Seaver's combination was a later homonym, they renamed *Cenangium singulare* (Rehm in Starb.) Davidson & Cash. We propose a new combination in *Phibalis* for this fungus, which has a rather complicated synonymy:

Phibalis pruinosa (Ellis & Everhart) Kohn & Korf, comb. nov.

≡*Dermatea pruinosa* Ell. & Everh., Jour. Mycol. **4:** 100. 1888, *non D. pruinosa* (Farl.) Petr., Ann. Mycol. **20:** 196. 1922 (later homonym).

≡*Cenangium pruinosum* (Ell. & Everh.) Seaver, N. Am. Cup-fungi (Inop.), p. 300. 1951 (later homonym), *non C. pruinosum* Ces., Hedwigia **1:** 43. 1854.

≡[*Peziza pruinosa* (Ell. & Everh.) Seaver *pro synon.*, N. Am. Cup-fungi (Inop.), p. 300. 1951 (*lapsus calmi*)], *non P. pruinosa* Wallr., Fl. Crypt. Germ. **2:** 487. 1833.

=*Cenangium populneum* (Pers. ex Pers.) Rehm var. *singulare* Rehm in Starb., Bih. Kongl. Svenska Vetensk.-Akad. Handl., Afd. 3, **21**(5): 19. 1895.

≡[*Cenangium populneum* (Pers. ex Pers.) Rehm var. *solaris* Rehm in Farlow, Rel. Farl. No. 104. 1922 (*lapsus calami*)].

≡*Cenangium singulare* (Rehm in Starb.) Davidson & Cash, Phytopathology **46:** 36. 1956.

Apothecia erumpent under bark, from blackened, stringy wood, single, gregarious, leathery, outer surface thickly encrusted with a hoar frost of crystals, drying to an angular or hysteriform shape but easily rehydrating to assume a cupulate form as when fresh. *In section*: medullary excipulum composed of light brown, roughened hyphae immersed in gel, oriented parallel to the hymenial surface; ectal excipulum composed of hyaline hyphae which turn out to form a layer of dark brown, thick-walled, globose cells in rows perpendicular to the apothecial surface, and immersed in a gel; encrusting this layer are rhomboidal and diamond-shaped crystals (which soon disappear in glycerine mounts). *Asci* clavate, 8-spored, apex J-, arising from croziers. *Paraphyses* filiform, slender, with enlarged apices immersed in gel and forming a pale brown pseudoepithecium. *Ascospores* allantoid to ellipsoid, non-septate, but in some collections a few, in other collections the majority, becoming one-septate, 8–11 × 1.5–2.9 μm, sometimes elongating and producing polar, spermatia-like buds (phialospores?) while still within the ascus or after discharge.

Critical Specimens Examined: COLORADO: Cockerell s.n., 1888, CUP-D 7398 (35–235), isotype of *Dermatea pruinosa*. NEW HAMPSHIRE: Reliquiae Farlowianae 104, on bark of *Populus grandidentata*, Chocurea, 18 May 1908, sub. *Cenangium populneum* var. *solaris*, CUP. NEW YORK: Smith, Phelps & Rogerson (3971), on dead *Populus*, Franklin County, Oct. 8, 1960, R.P.K. 3120; Stasz s.n., on *Populus deltoides*, Lower Creek Road at Ithaca-Etna line, Tompkins County, 5 May 1975, R.P.K. 4261; Kohn, Korf & Stasz s.n., same locality, 7 May 1975, to be issued in Discomycetae Exsiccatae. SWEDEN: Sernander s.n., Närke, Lerbäck, Klockarhyttan, on an old *Populus tremula*, Aug. 1891, holotype of *Cenangium populneum* var. *singulare*, S; Starbäck 29, Nerike, Lerbäck, Klockarhyttan, Juli [18]94, authentic material of *C. populneum* var. *singulare*, S-Rehm.

IV. COMPARATIVE STRUCTURE OF OTHER SPECIES OF ENCOELIA

The decision to place *Cenangium pruinosum* in *Phibalis* (=*Encoelia*) necessitated a redefinition of the range of excipular types acceptable within the generic concept. We proceeded to examine allied species to determine if any of these were also characterized by a failure of globose, brown-walled excipular cells to disarticulate and form the mealiness long accepted as a key character in delimiting the genus *Encoelia*. Such mealiness, perhaps best exemplified by the type species, *E. furfuracea*, is lacking in nearly all of the other species we examined.

Encoelia fascicularis (Alb. & Schw. ex Fr.) Karst. (=*Cenangium populneum*) is most easily distinguished from *Phibalis pruinosa* by its caespitose apothecia with a comparatively less abundant superficial layer of crystals. Microscopically, markedly broader medullary hyphae in *E. fascicularis* differentiate the two, closely allied species, both of which occur on *Populus*. In addition, old collections of *E. fascicularis* frequently contain amorphous, amber bodies within the tissues of the apothecium which we interpret as remnants of gel or resin. As in *Phibalis pruinosa*, the globose excipular cells remain in a perpendicular, hyphal orientation and do not disarticulate.

Encoelia heteromera (Mont.) Nannf., like *Phibalis pruinosa*, develops one-septate spores, a brown pseudoepithecium, and an ectal excipulum composed of hyphal cells which turn outward to form a layer of globose brown cells perpendicular to the apothecial surface. In *E. heteromera*, however, these globose cells are amber colored and aggregate, bound in gel, in conical pustules, in which the hyphal orientation becomes impossible to discern, recalling in this respect *E. furfuracea*.

Encoelia acicolum (Fckl.) v. Höhn. closely resembles *Phibalis pruinosa* in excipular structure, with globose, brown cells bound, with crystals, in gel, and like it develops septate spores and has a light brown pseudoepithecium. Dennis (1960, 1968), and by implication Korf (1973), incorrectly assign this species to *Cenangium*, presumably because it occurs on coniferous needles and because its ascospores are more fusoid than allantoid.

In strong contrast, *Encoelia tiliacea* (Fr.) Karst. and *E. siparia* (Berk. & Br.) Nannf. have excipular tissues composed of loose hyphae, relatively unbound by gel, running parallel to the apothecial surface and not turning out to form a perpendicular layer of globose cells. Neither species fits within the defined boundaries of excipular types expected in *Encoelia* (=*Phibalis*).

V. TWO UNUSUAL CONCEPTS OF ENCOELIA (PHIBALIS)

Two authors who have accepted *Encoelia* at generic rank have proposed radically different concepts of the genus which deserve attention here.

The basis on which Schroeter (1893) differentiated *Encoelia* from *Cenangium* was that the apothecium remains closed by a membrane for a long period, eventually rupturing to give a lacerate margin, while in *Cenangium* the apothecium opens by a pore. The lacerate margin has not been used as a generic character for *Encoelia* by other authors. The torn margin of *E. furfuracea* is illustrated by Dennis (1956, 1960, 1968).

Kirschstein (1935) proposed a novel enlargement of *Encoelia*, finding that for him the genus *Ocellaria* (Tul. & Tul.) Karst. had sufficient similarities that the two genera should be merged. He then proposed dividing *Encoelia* into three subgenera: *Encoelia* subg. *Euencoelia* Kirschst., embracing *E. furfuracea, E. populnea* (Pers. ex Pers.) Boud., "usw.;" *Encoelia* subg. *Ocellaria* (Tul. & Tul.) Kirschst., to include *E. aurea* (Tul. & Tul.) Kirschst., *E. ulmi* (Tul. & Tul.) Kirschst., *E. carpini* (Rehm) Kirschst., "usw.;" *Encoelia* subg. *Encoeliopsis* Kirschst., to include *E. tiliacea, E. glaberrima* (Rehm) Kirschst., "usw."

The subgenus *Euencoelia* was characterized by large, clustered, strongly pulverulent apothecia opening by a lacerate margin; the subgenus *Ocellaria* by smaller, single or scattered, sessile, mealy apothecia with an entire margin; the subgenus *Encoeliopsis* by larger, more or less scattered, substipitate, smooth apothecia with an often wavy but never torn margin.

Three years later Kirschstein (1938) further enlarged his concept of *Encoelia* by adding a fourth subgenus, *Encoelia* subg. *Velutaria* (Fuckel) Kirschst., to accommodate *E. rufo-olivacea* (Alb. & Schw. ex Fr.) Kirschst., *E. cinereofusca* (Schw.) Kirschst., and a new species, *E. sitchensis* Kirschst. The first two species are currently referred to the genus *Velutarina* Korf (Dennis 1960, 1968; Korf, 1973), whereas the third is the subject of another study in progress by the authors of this paper. Whether *Velutarina* deserves generic rank or should be reduced to synonymy with *Phibalis*, as Kirschstein's proposal would imply, remains an as yet unresolved question for us.

VI. PHIBALIS AND THE ENCOELIOIDEAE REDEFINED

It is clear from our microanatomical studies that someone attempting to key out a species of *Encoelia* such as *E. siparia* (=*E. ulmi*) or *E. tiliacea* in the treatments by Nannfeldt (1932), Dennis (1956, 1960, 1968) or Korf (1973) could simply never arrive at the genus, much less at the Encoelioideae, since the key character of the subfamily in all these treatments—mealy, loose cells on the outside of

the apothecium—is simply not present. For other species lacking such loose cells but covered by loose crystals, such as *Phibalis pruinosa* or *E. fasciculatis*, the student will arrive at the genus or subfamily only by indirection.

An examination of the species diagnoses of *E. siparia* and *E. tiliacea* as presented by Dennis (1956) shows that he did know that the structure of these apothecia lacks loose excipular cells. Yet his key to reach the subfamily requires a conclusion that the apothecia are "externally mealy" and that the outer layers of the ectal excipulum "slough off to form the meal," this key being essentially a translation of that by Nannfeldt (1932). Korf's (1973) treatment is no improvement, for his key also requires a decision that the ectal excipulum has "the outermost cells globose, loose, forming a mealy or powdery surface," despite his inclusion in the subfamily of *Chlorencoelia*, one species of which he (Ramamurthi et al., 1958) was well aware bears no disarticulating or mealy excipular cells.

The presence of regularly septate ascospores in some collections of *Phibalis pruinosa* and their occasional occurrence in certain other species also requires a modification of the generic diagnosis of "*Encoelia*" to embrace such species. Nannfeldt (1932) distinguished the genus *Encoeliopsis* Nannf. from it in his key to genera on the basis of 1-septate spores; Korf (1973) transferred that genus out of the subfamily to the Dermateoideae. Dennis (1956) took up that generic name for another species which Korf (1971) made the type species of *Dencoeliopsis* Korf; it was referred (Korf, 1973) to the Encoelioideae and separated from other members of the subfamily on the basis of fusoid, one-septate ascospores. All keys obviously need rewriting to accommodate septate-spored specimens of *Phibalis*.

Another ascospore feature, turning brown at maturity, has been noted in the species of the poorly known genus *Phaeangella*. In regard to *P. ulicis* (Cooke) Massee, Nannfeldt (1939) stated that "this is a species of *Encoelia*," but provided no transfer. Dennis (1960, 1968), who included only that species in *Phaeangella*, called it "a genus of very doubtful value, possibly distinguished from *Encoelia* by its ascospores becoming brown and by the flesh yielding crimson colour in KOH solution." We have not examined this species, apparently known only from the type collection. We are also not certain which is the lectotype species: Clements and Shear (1931) designate *P. aceris* (Hazsl.) Sacc. in Clem. & Shear as the type, while Dennis (1960, 1968) states that *P. ulicis* is the type. The synonymy, though probable, needs confirmation.

The great diversity of apothecial structure now known in *Phibalis* requires revision of our concepts of the subfamily Encoelioideae to include that variation. The mealy excipulum, known only in some species, must be eliminated as our key character. Features which appear to need stressing are the leathery to horny consistency of the apothecia, their consequent long life, their ability to revive and dry down according to moisture conditions, the consequent intermittent spore discharge, the brown-walled excipular hyphae which may merely run parallel to the outer surface or may turn outward to give rise to globose cells, which in turn may or may not disarticulate and become mealy, and the pronounced tendency to form allantoid ascospores (a rare feature in any other subfamily) in at least three genera [*Phibalis, Chlorencoelia,* and *Phyllomyces* Lloyd (=*Ionomidotis* Durand, =*Cordierites* Mont. sensu Korf 1973)].

At this time we are unable to accept Kirschstein's (1935) conclusion that *Ocellaria* is close to *Encoelia*, and as noted above we reserve judgement on his conclusion (Kirschstein, 1938) that "*Velutaria*" (=*Velutarina*) should be merged. But Kirschstein (1935) did note the glabrous apothecia in *E. tiliacea*, and proposed

the (invalid) subgeneric epithet *Encoeliopsis* for that species and some others. We concur that *E. tiliacea*, with an ectal excipulum of hyphae running parallel to the outer surface, and lacking globose cells, must be separated from other species of *Encoelia*. We are torn as to whether to recognize for such species a separate genus, or to include these within *Phibalis* as a distinct subgenus, following Kirschstein's lead. Von Höhnel faced the same dilemma: "Vorbehaltlich einer genaueren Untersuchung der einzelnen Arten, die zeigen wird, dass nicht alle hieher gehören und vielleicht auch neue Gattungen ergeben wird, halte ich es für zweckmässigsten, bis auf weiteres alle *Cenangium*-Arten im Sinne Rehms zu *Encoelia* Fries emend. Höhn. zu stellen" (von Höhnel 1923).

Despite a great difference in microanatomical structure, we are convinced that the similarities in biology, habit, ascospore shape and ascospore germination by budding all point to the true affinity that led Nannfeldt, Dennis and others to include these species in *Encoelia*. We therefore propose dividing *Phibalis* into two subgenera. Since Kirschstein's subgeneric epithet *Encoeliopsis* is invalid, and since there is also a generic name *Encoeliopsis* that has no relationship to Kirschstein's genus, we propose a new epithet for the second of the two subgenera we accept.

PHIBALIS Wallroth, Fl. Crypt. Germ. **2:** 445. 1833.

≡*Peziza* ser. *Aleuria* "trib." *Encoelia* Fries, Syst. Myc. **2**(1): 42, 74. 1822 (validly published, exception to Art. 33 of the International Code of Botanical Nomenclature).
≡*Dermatea* Fr. [subg. ?] a. *Encoelia* (Fr.) Fr., Summa veg. Scand., sect. post., 362. 1849.
≡*Encoelia* (Fr.) Karsten, Bidr. Känn. Finlands Natur Folk **19:** 18, 217. 1871.
≡*Cenangium* Fr. ex Fr. [subg. ?] A. *Encoelia* (Fr.) Rehm *in* Rabenh., Krypt.-Fl. Duetschl., Oesterr. Schweiz II **1**(3)[Lief. 31]: 219. 1889.
≡*Cenangium* Fr. ex Fr. [sect. ?] II. *Encoelia* (Fr.) Sacc., Syll. Fung. **8:** 565. 1889.
≡*Cenangium* Fr. ex Fr. subg. *Encoelia* (Fr.) Lindau in Engler & Prantl, Die natürl. Pflanzenf. I **1**(1): 232. 1897.
=? *Cenangella* Sacc. [sect. ?] II. *Phaeangella* Sacc., Syll. Fung. **8:** 592. 1889.
≡*Phaeangella* (Sacc.) Massee, Brit. Fungus-Fl. **4:** 136. 1895.
MISAPPLICATIONS: *Cenangium* Fr. ex Fr. sensu Auct., p. max. p.
Midotis Fries sensu Durand (1923), sensu Seaver (1951) p. min. p.

PHIBALIS Wallr. subg. PHIBALIS

≡[*Encoelia* (Fr.) Karst. subg. *Euencoelia* Kirschst., Ann. Mycol. **33:** 222. 1935 (not validly published: Art. 21).]

Apothecia with ectal excipular hyphae turning outward, perpendicular to the apothecial surface, to form chains of small, more or less isodiametric cells embedded in a gel, sometimes forming conical pustules, often producing massive amounts of crystals, the gel often disorganizing and the excipular cells then becoming disarticulated and not clearly arranged in rows, forming a powdery meal on the surface of the apothecium.

SPECIES LECTOTYPICA: *Phibalis furfuracea* (Roth ex Fr.) Wallr., Fl. Crypt. Germ. **2:** 447. 1833 (designated here).

SPECIES ALIAE: *Phibalis fasciculatis* (Alb. & Schw. ex Fr.) Wallr., Fl. Crypt. Germ. **2:** 446. 1833; **Phibalis heteromera** (Montagne) Korf & Kohn, comb. nov. (basionym: *Peziza heteromera* Mont., Ann. Sci. Nat. II **13:** 206. 1840); **Phibalis pinastri** (Cooke & Peck in Cooke) Korf & Kohn, comb. nov. [basionym: *Peziza pinastri* Cke. & Pk. in Cke., Bull. Buffalo Soc. Nat. Sci. **1:** 297. 1875, ≡*Cenangium acuum* Cke. & Pk. in Cke. & Ellis, Grevillea **7:** 40. 1878; a taxonomic synonym is *Cenangium acicolum* (Fuckel) Rehm]; *Phibalis pruinosa* (Ell. & Everh.) Kohn & Korf (see above, section III, for complete synonymy).

PHIBALIS Wallr. subg. **KIRSCHSTEINIA** Korf & Kohn, subg. nov.

≡[*Encoelia* (Fr.) Karst. subg. *Encoeliopsis* Kirschst., Ann. Mycol. **33:** 223. 1935 (not validly published: Arts. 21, 36).]

Sicut subgenus typicum, sed excipulum exterius e textura porrecta formatum, cellulae globosae nullae.

SPECIES HOLOTYPICA: **Phibalis tiliacea** (Fries) Korf & Kohn, comb. nov. [basionym: *Peziza tiliacea* Fr., Syst. Myc. **2**(1): 76. 1822.]

SPECIES ALIA: **Phibalis siparia** (Berk. & Br.) Korf & Kohn, comb. nov. (basionym: *Peziza siparia* Berk. & Br., Ann. Mag. Nat. Hist. II **13:** 465. 1854; a taxonomic synonym is *Cenangium ulmi* Tul. & Tul.).

VII. EXCLUDED AND DOUBTFUL SPECIES OF PHIBALIS

1. *Phibalis ampliata* (Persoon ex Fries) Wallroth, Fl. Crypt. Germ. **2:** 447. 1833.

This species is generally considered today to be an operculate discomycete referable to the genus *Peziza*.

2. *Phibalis bicolor* Wallroth, Fl. Crypt. Germ. **2:** 446. 1833.

There are four specimens in Wallroth's herbarium, in two covers, associated with the name *Phibalis bicolor*. Three of the four are ample collections of *Pezicula frangulae* (Pers.) Fuckel. The fourth is a badly preserved fragment, also of a *Pezicula*, and very possibly also of *P. frangulae*. While none of the collections can be definitely associated with the description enough to qualify as holotype, it seems quite safe to assign *Phibalis bicolor* Wallr. to synonymy under *Pezicula frangulae*.

3. *Phibalis farinacea* (Persoon) Wallroth, Fl. Crypt. Germ. **2:** 446. 1833.

Groves (1952) examined a Persoon specimen at Leiden (910. 261.960) and determined it to be *Cenangium ferruginosum* Fr. ex Fr.

4. *Phibalis fissa* (Fries) Wallroth, Fl. Crypt. Germ. **2:** 447. 1833.

We have been unable to locate any type material either in the Fries or the Persoon herbarium, and there appears to be no current consensus as to the identity of this species.

5. *Phibalis glabra* Wallroth, Fl. Crypt. Germ. **2:** 447. 1833.

No material referable to this name was discovered by the curators of the Wallroth herbarium at Strasbourg; it may now be a lost species.

6. *Phibalis pulveracea* (Albertini & Schweinitz ex Fries) Wallroth, Fl. Crypt. Germ. **2:** 446. 1833.

This species is generally considered to be a *Dasyscyphus* (see von Höhnel, 1923).

SUMMARY

Studies of species of *Phibalis* Wallroth 1833 [the correct name for *Encoelia* (Fries) Karsten 1871] demonstrate that a structural definition of the Leotiaceae subf. Encoelioideae (=Cenangiaceae) based upon loose, mealy excipular cells is an oversimplification. *Phibalis* is here divided into two subgenera: *Phibalis* subg. **Phibalis** is characterized by species with ectal excipular hyphae turning outwards to become perpedicular to the outer surface where they form globose cells, at first immersed in a gel, in some species with these cells disarticulating to form a mealy surface, and often producing large, easily visible crystals; *Phibalis* subg. **Kirschsteinia** subg. nov. is distinguished by excipular hyphae also immersed in a gel, but remaining parallel to the outer surface of the apothecium and not giving rise to a scurfy layer of loose cells. Ascospores in both subgenera

are cylindrical to ellipsoid, often suballantoid, unicellular or sometimes distinctly one-septate, and may germinate even within the ascus by producing polar, spherical, spermatia-like bodies. New combinations proposed are **P. heteromera**, **P. pinastri**, **P. pruinosa**, **P. siparia**, and **P. tiliacea**.

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LITERATURE CITED

Boudier, E. J. 1907. Histoire et classification des Discomycètes d'Europe. 221 p. Paris.

Cash, E. K., and E. J. H. Corner. 1958. Malayan and Sumatran Discomycetes. Trans. Brit. Mycol. Soc. **41:** 273–282.

Clements, F. E., and C. L. Shear. 1931. The genera of fungi. vii + 496 p. Minneapolis.

Davidson, R. W., and E. K. Cash. 1956. A *Cenangium* associated with sooty-bark canker of aspen. Phytopathology **46:** 34–36.

Dennis, R. W. G. 1954. Some inoperculate Discomycetes of tropical America. Kew Bull. **1954:** 289–348.

———. 1955. Fungi from Sierra Leone: Pezizales and Helotiales. Kew Bull. **1955:** 363–368.

———. 1956. A revision of the British Helotiaceae in the Herbarium of the Royal Botanic Gardens, Kew, with notes on related European species. Mycol. Pap. **62:** 1–216.

———. 1960. British cup-fungi and their allies. An introduction to the Ascomycetes. 280 p. London.

———. 1968. British Ascomycetes. 455 p. Lehre.

———. 1971. New or interesting British microfungi. Kew Bull. **25:** 335–374.

Dixon, J. R. 1975. *Chlorosplenium* and its segregates. II. The genera *Chlorociboria* and *Chlorencoelia*. Mycotaxon **1:** 193–237.

Durand, E. J. 1900. The classification of the fleshy Pezizineae with reference to the structural characters illustrating the bases of their division into families. Bull. Torry Club **27:** 463–495, pl. 27–32.

———. 1923. The genera *Midotis, Ionomidotis* and *Cordierites*. Proc. Amer. Acad. Sci. **59:** 1–18.

Fries, E. M. 1822. Systema mycologicum **2**(1): 1–274. Lund.

———. 1849. Summa vegetabilium Scandinaviae. Sectio posterior. p. 259–572. Holmiae & Lipsiae.

Gremmen, J. 1956. Further notes on discomycetous fungi on coniferous leaves. Sydowia Beih. **1:** 179–182.

Groves, J. W. 1952. The genus *Tympanus*. Canad. Jour. Bot. **30:** 571–651.

———, **and M. E. Elliott.** 1971. Notes on fungi from northern Canada VI. Additional records of Discomycetes. Rept. Kevo Subarctic Res. Stat. **8:** 22–30.

Höhnel, F. von. 1918. Fragmente zur Mykologie. 1118. Über *Coryne foliacea* Bresadola. Sitz.-ber. Akad. Wiss. Wien, Math.-nat. Kl. I **127:** 584–587.

———. 1923. Fragmente zur Mykologie. 1221. Über *Cenangium Abietis* (P.) Rehm, *Cenangium acicolum* (Fuck.) Rehm und die Gattung *Cenangium* Fries. Sitz.-ber. Akad. Wiss. Wien, Math.-nat. Kl. I **132:** 104–106.

Karsten, P. A. 1871. Mycologia fennica. Pars prima. Discomycetes. Bidr. Känn. Finlands Natur Folk **19:** viii + 263 p.

Kirschstein, W. 1935. Neue und seltene Ascomyceten. Ann. Mycol. **33:** 202–229.

———. 1938. Über neue, seltene und kritische Ascomyceten und Fungi imperfecti. Ann. Mycol. **36:** 367–400.

Korf, R. P. 1971. Some new discomycete names. Phytologia **21:** 201–207.

———. 1973. Chapter 9. Discomycetes and Tuberales. *In*: Ainsworth, Sparrow and Sussman, eds., The Fungi: An advanced treatise, vol. **4A:** 249–319. New York & London.

Lindau, G. 1897. Pezizineae. *In*: Engler und Prantl, eds., Die natürlichen Pflanzenfamilien I **1**(1): 178–243.

Nannfeldt, J. A. 1932. Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten. Nova Acta Regiae Soc. Sci. Upsal. IV **8**(2): 1–368.

———. 1936. Notes on type specimens of British inoperculate Discomycetes. (First part, notes 1–50). Trans. Brit. Mycol. Soc. **20:** 191–206.

———. 1939. Notes on type specimens of British inoperculate Discomycetes (second part, notes 51–100). Trans. Brit. Mycol. Soc. **23:** 239–252.

Overeem, C. van, and J. Weese. 1926. Icones fungorum Malayensium **13:** 1–3, pl. 13.

Petrak, F. 1925. Beiträge zur Pilzflora Südost-Galiziens und der Zentralkarpathen. Hedwigia **65:** 179–330.

———. 1956. Zwei neue Kleinpilze der schwedischen Flora. Sydowia **10:** 255–257.

Ramamurthi, C. S., R. P. Korf, and L. R. Batra. 1958. A revision of the North American species of *Chlorociboria*. Mycologia **49:** 854–863. '1957.'

Rehm, H. 1887–1896. Ascomyceten: Hysteriaceen und Discomyceten. *In*: Winter and Rehm, eds., Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz II **1**(3): 1–1275.

Saccardo, P. A. 1889. Sylloge Fungorum **8:** 1–1143. Patavii.

Schroeter, J. 1893. Die Pilze Schlesiens. *In*: Cohn, F., Kryptogamen-Flora von Schlesien **3**(2)[Lief. 1–2]: 1–256.

Seaver, F. J. 1951. The North American cup-fungi (Inoperculates). pp. 1–428. New York.

Starbäck, K. 1895. Discomyceten-Studien. Bih. Kongl. Svenska Vetensk.-Akad. Handl., Afd. 3, **21**(5): 1–42, 2 pl.

Svrček, M. 1974. New or less known Discomycetes. I. Nové nebo méně známé diskomycety. I. Česká Mykol. **28:** 129–137.

Wallroth, F. G. 1833. Flora Cryptogamica Germaniae. Pars posterior. *In*: Bluff and Fingerhuth, eds., Compendium Florae Germanicae Sect. II, Plantae Cryptogamicae S. Cellulosae **4:** 1vi + 923 p. Norimbergae.

Whetzel, H. H. 1945. A synopsis of the genera and species of the Sclerotiniaceae, a family of stromatic inoperculate Discomycetes. Mycologia **37:** 648–714.

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