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## Fungicolous pyrenomycetes 1. *Helminthosphaeria* and the new family Helminthosphaeriaceae

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**Abstract:** *Helminthosphaeria*, a genus of pyrenomycetes, is monographed. Its members occur on basidiomata of species of the Aphyllophorales. The following species are included: *H. clavariarum*, the type, *H. odontiae*, *H. corticiorum*, and the new species *H. hyphodermiae*. A new family, Helminthosphaeriaceae, is proposed for the genus. *Litschaueria* is found to be a synonym of *Helminthosphaeria*.

**Key Words:** Fungi, fungicolous fungi, *Litschaueria*, systematics

### INTRODUCTION

*Helminthosphaeria* is best known from its type species, *H. clavariarum* (L.-R. Tul.) Fuckel, the anamorph of which blackens the base of basidiomata of members of the Clavariaceae. *Helminthosphaeria clavariarum* is easily recognizable through its black, setose ascomata and dark unicellular ascospores that have an inconspicuous pore in each end, and *Diplococcium* Grove anamorph. In the present study we have found three additional species of *Helminthosphaeria* on old corticioid basidiomata. These differ from the type species in that their hosts are not clavariaceous, and in that the two of the species have septate ascospores.

Several additional species have been placed in the genus (Kirschstein, 1933), but these are now recognized to be species of *Coniochaeta* (Sacc.) Cooke or *Rosellinia* de Not. (Martin, 1967). Following is a discussion of taxonomy and systematics of *Helminthosphaeria*.

*Perithecial characters.*—Perithecia of *Helminthosphaeria* species are nonstromatic, black to gray (FIGS. 13, 41), pyriform to subglobose and nonpapillate. They do not, or rarely, collapse when dry and do not release any pigment when immersed in 3% KOH. The perithecial wall is firm. It is formed of several layers of, thick-walled, melanized cells (FIGS. 1, 2, 15, 27, 42). It was difficult to obtain good perithecial sections because of the tendency of the perithecial wall to fragment when sectioned following rehydration in 3% KOH. Cells at the surface of the perithecial wall are polyhedral and are arranged into low warts (14, 16, 17), from the surface of which setae often arise (FIGS. 1, 16). Setae are black, stiff, erect, acute, septate, thick-walled and unbranched (FIGS. 9, 16, 33, 37). Setae form from the entire surface of the perithecium, but may be more abundant from the ostiolar region. In all species but *H. clavariarum* setae are opaque, black. In *H. clavariarum* they are golden brown, consistent with the generally lighter melanization of the perithecial wall. Within an individual collection of a species, some perithecia may have more setae than others, and some perithecia may appear to lack setae.

The perithecial apex is characteristic. It is formed of more or less clavate, thick-walled hyphal elements (FIG. 9). This aspect is easily seen in crush mounts. The ostiolar canal is periphysate. Perithecial setae arise as outgrowths of the clavate elements as well as from cells at the surface of the perithecial wall.

Asci are unitunicate and form in a hymenium that lines the interior of the perithecial wall. The ascus apex is inamyloid; it may be simple, lacking an apical ring, and may be somewhat thinner than the lateral ascus wall (FIGS. 7, 29, 44), or thickened and appear to have a discharge mechanism (FIGS. 22, 31). Paraphyses persist among asci (FIGS. 3, 4, 10, 18, 20, 28, 34). Within the same perithecium they may be unbranched, infrequently branched, or—in *H. clavariarum*—frequently branched. They are attached to the ascogenous hyphae, apically free, cylindrical or slightly tapering from base to tip, and septate. Asci develop from apparently normal croziers.

Ascospores are ellipsoidal and basically unicellular (FIGS. 6, 21, 30), although one or more septa may form in spores of some species either while spores are still in the ascus, or following discharge (FIGS. 24,

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38, 45) Ascospores of *H. clavariarum* and *H. hyphodermiae* remain unicellular. Ascospores of *H. odontiae* become apiosporous while still in asci; there is no polarity to septum formation as the septum may be supra- or submedian in reference to orientation of the spore in the ascus. Ascospores of *H. corticiorum* may remain unicellular for a long time, but some—or many—spores develop from one to three or four septa.

A characteristic of *Helminthosphaeria* is that there is a pore at both ends of each ascospore (FIGS. 6, 11, 21, 24, 30, 35, 38). However, the pore is very fine and can be very difficult, or impossible, to see in spores that are still in asci. It is more easily seen, but often remaining obscure, in discharged spores.

Ascospores of *Helminthosphaeria* are pigmented, tending to be greyish, greenish or olivaceous rather than brown when viewed in 3% KOH. They are translucent rather than opaque. Discharged ascospores, in mass, are black.

*Anamorph characters.*—We have not observed ascospore germination in any species of *Helminthosphaeria*, and we are not aware of reports of any species of *Helminthosphaeria* having been cultured. However, the close and constant physical association of *Helminthosphaeria* with *Diplococcium* species leads us to conclude that the two spore stages represent a single fungus. It should be emphasized, though, that old aphylloporaceous basidiomata are home to many dematiaceous hyphomycetes and that mere juxtaposition is not proof of biological connection. Coarse black mycelium, and conidiophores of *Helminthosphaeria clavariarum* blacken the base of basidiomata of members of the Clavariaceae. The anamorphs of the other species of *Helminthosphaeria* are less conspicuous. Conidiophores are infrequently to frequently and irregularly branched, each branch bearing a single, terminal conidiogenous cell (FIGS. 25, 39, 47, 48). Conidiogenous cells are monotretic or polytretic, marked by one or minute pores through which conidia form. Conidia of *Diplococcium* species are translucent, dark brown, septate, and have a more or less conspicuous pore at one or both ends. Septa are very dark, and sometimes they are marked by a wide, dark band. Conidia are joined end-to-end in short, dry chains.

We have found *Diplococcium* conidia in association with half or more of the collections of *H. odontiae* and *H. corticiorum*. A dematiaceous hyphomycete that we were not able to identify to genus was associated with several collections of *H. hyphodermiae* (FIGS. 32, 36); it most closely resembles *Heteroconium* Petrak. It differs from the *Diplococcium* anamorphs in that the conidia are holoblastically formed or are

formed through fragmentation of the conidiophore rather than enteroblastically, as they are in *Diplococcium*. Given the differences between this anamorph and the *Diplococcium* anamorphs of closely related species of *Helminthosphaeria* we question whether this is a *Helminthosphaeria* anamorph, while noting its association with collections of one species.

*Host relationships.*—The four *Helminthosphaeria* species that we recognize all occur on basidiomata of members of the Aphylloporales. It is not clear, however, whether they are parasitic, as the hosts continue to produce spores. The hymenium of the hosts is not covered by mycelium that would prevent discharge of basidiospores. The clavariaceous basidiomata infected with *H. clavariarum* are not deformed. Perithecia of *H. corticiorum* are immersed in circular holes in the hymenium of the host. *Helminthosphaeria clavariarum* is found only on members of the Clavariaceae. The remaining members of the genus are found on corticioid basidiomycetes. Usually we have not been able to determine the hosts, but at least in the case of *H. hyphodermiae* the host when determinable has been *Hyphoderma puberum* (Fr.) Wallr. In many cases, probably old specimens, there is no obvious basidiomycete and then perithecia appear to arise from decorticated wood.

*Systematics of Helminthosphaeria.*—We have found only one generic synonym for *Helminthosphaeria*, *Litschaueria* Petrak. Petrak (1923) removed *H. corticiorum* from *Helminthosphaeria* to the new genus *Litschaueria*. He considered the absence of a copiously produced anamorph in *H. corticiorum*, and the formation of nonpapillate perithecia that are covered with conidiogenous hyphae in *H. clavariarum*, and leathery rather than carbonaceous perithecia in *H. clavariarum* to be important points in separating *Litschaueria* from *Helminthosphaeria*. As has been noted, we have found *Diplococcium* conidia associated with perithecia of *H. corticiorum*, but in no species of *Helminthosphaeria*—including *H. corticiorum*, have we found conidiogenous cells arising from the perithecial surface. Perithecia of *H. clavariarum* are less heavily melanized than are the walls of the other species in the genus but perithecia are not leathery; perithecial wall anatomy in *H. clavariarum* is the same as is found in other species of the genus. Petrak further noted that ascospores of *H. corticiorum* become septate after discharge whereas in *H. clavariarum* they remain unicellular. Given the overall similarity between the two species, we discount the significance of ascospore septation in generic delimitation and do not accept *Litschaueria* as distinct from *Helminthosphaeria*. Petrak considered that *Litschaueria* and *Hel-*

*minthosphaeria* were closely related to each other and to *Rosellinia*.

Barr (1976) accepted *Litschaueria corticiorum* in a different sense. She examined the type specimen of *H. corticiorum* and concluded that the unicellular ascospores in the asci were immature. She identified as *L. corticiorum* a fungicolous ascomycete that has setose perithecia and three-septate ascospores, the middle two cells of which are brown and the end cells hyaline; and a phialidic, *Codinaea* Maire anamorph. In our examination of the type specimen of *H. corticiorum* we found only one discharged ascospore; it had three septa, was uniformly olivaceous, and had a pore at each end. We could not see a pore in ascospores that were still held in asci, but this is not unusual in *Helminthosphaeria*. We also found a few conidia of *Diplococcium* on the type specimen of *H. corticiorum*. The name, *H. corticiorum*, is misapplied to this common fungicolous pyrenomycete, for which new generic and specific epithets have been proposed (Samuels et al., 1996).

Taxonomic placement of *Helminthosphaeria* has been problematic. Parguey-Leduc (1960) found perithecial ontogeny and the ascal ascal apex in *H. clavariarum* to be of the *Sordaria*-type. Because of this, and because the unicellular ascospores have a pore at each end, she concluded that the genus was a primitive member of the Sordariales, allied to the Melanosporaceae (nom. inval. = Ceratostomaceae fide Barr, 1990). Lundqvist (1972) adopted a strict interpretation of the Sordariaceae within which filiform paraphyses are lacking and ascospores often have a gelatinous sheath. Most of the genera that he included in the Sordariaceae comprise mainly coprophilous species. *Helminthosphaeria* species have filamentous paraphyses, their asci are not ensheathed, and they are not coprophilous. Following Parguey-Leduc (1960), Lundqvist placed *Helminthosphaeria* in an uncertain position in the "vicinity of the sordariaceous genera." He thought that *Helminthosphaeria* ultimately should be placed in its own subfamily or family. Under Barr's (1990) circumscription of the Sordariaceae, paraphyses are described as being as wide and delicate, or chains of cells. Barr (1990) included *Helminthosphaeria* in the Sordariaceae with reservations because of its hypersaprobic habit on fleshy fungi. Dennis (1978) included the genus in the Sordariaceae but considered that it was transitional to the Sphaeriaceae, from which it was separated by the superficial, scattered, setose perithecia. Eriksson and Hawksworth (1993), without comment, placed the genus in the Sordariales but did not assign it to any family.

On the basis of anatomical characters of perithecia, and because of ascal characters *Helminthosphaeria*

can be placed in the order Sordariales (sensu Barr, 1990). In its fungicolous habit and in the filamentous paraphyses the genus is not consistent with the Sordariaceae. Ascospores of *Helminthosphaeria* species are further distinctive in the Sordariales in being translucent and gray-brown or olivaceous rather than opaque and black.

The tetric conidia of the *Diplococcium* anamorphs consistently associated with perithecia of *H. clavariarum*, *H. corticiorum*, and *H. hyphodermiae* are not known elsewhere in the unitunicate pyrenomycetes. Tetric conidia are found among members of the loculoascomycete family Pleosporaceae (e.g. *Drechslera* Ito anamorphs of *Setosphaeria* Leonard & Suggs and *Cochliobolus* Drechsler).

Porate ascospores are found in representatives of apparently unrelated pyrenomycetous ascomycetes. As was discussed by Parguey-Leduc (1960), the formation of a single pore in ascospores is common in the Sordariaceae (Lundqvist, 1972). She considered that the formation of polar germ-pores in unicellular ascospores was a primitive condition shared by *Melanospora* Cda. (Ceratostomaceae) and *Helminthosphaeria*. However, there are considerable differences separating the two genera. Asci of *Melanospora* are clavate; deliquescing early they lack any differentiated apical apparatus, and no paraphyses form in the centrum (Goh and Hanlin, 1994). The perithecial wall of *Melanospora* species is translucent, thin and fleshy whereas the perithecial wall of *Helminthosphaeria* species is firm, opaque black (sometimes tending to be greenish in 3% KOH). The genus can be excluded from the Ceratostomaceae because of its paraphysate hamathecium, and cylindrical asci that have a chitinous apical ring (Parguey-Leduc, 1960), in addition to differences in perithecial wall anatomy.

Ascospores of *Scotiosphaeria endoxylinae* Sivan., type of the monotypic genus (Sivanesan, 1977), have a conspicuous pore at each end. This species shares important anatomical characters with *Helminthosphaeria* species in addition to porate ascospores, including black, carbonous (not leathery) perithecia that have a wall formed of distinct pseudoparenchymatous cells, and a hamathecium of unbranched paraphyses. Asci of *S. endoxylinae* lack a differentiated apical ring. *Scotiosphaeria endoxylinae* occurs on ascomata of an *Endoxyla* species. Unfortunately, *S. endoxylinae* has not been linked to an anamorph, making it difficult to determine its higher taxonomic affinities. Sivanesan (1977) originally referred this genus to the Sphaeriales. Eriksson and Hawksworth (1993) did not specify an order for it. *Scotiosphaeria* may be related to *Helminthosphaeria* at the familial level.

*Porosphaerella* Müller & Samuels (Müller and Sam-

uels, 1982) and *Porosphaerellopsis* Samuels & Müller (Samuels and Müller, 1978, as *Porosphaeria*; Müller and Samuels, 1982) are also characterized in part by having a pore at each end of each ascospore. Unlike *Helminthosphaeria*, where the pores in the ascospores are extremely difficult to see, pores in ascospores of *Porosphaerella* and *Porosphaerellopsis* are conspicuous. Ascospores of *Porosphaerella* are brown, bicellular and have a pore at each end. The anamorph of *P. codanophora* is *Cordana pauciseptata* Preuss. Ascospores of *Porosphaerellopsis sporoschismophora* (Samuels & Müller) Müller & Samuels, the only known species, are three septate from an early stage in their development. The perithecial wall is formed of many layers of nondescript small cells, and the paraphyses are repeatedly branched. The anamorph of *P. sporoschismophora* is a *Sporoschisma* Berk. & Broome. The affinities of *Porosphaerella* and *Porosphaerellopsis* lie with *Chaetosphaeria* L.-R. & C. Tulasne (Lasiosphaeriaceae) and we do not see a close relationship between *Helminthosphaeria* and any of the Lasiosphaeriaceae.

Perithecia of *Helminthosphaeria*, *Melanospora*, *Porosphaerella*, *Porosphaerellopsis*, and *Scotiosphaeria* are nonstromatic. Among the stromatic pyrenomycetes, we only know members of the Boliniaceae (*Camarops* Karsten, *Apiocamarops* Samuels & J.D. Rogers; Nannfeldt, 1972; Samuels and Rogers, 1987; Rogers and Samuels, 1988) to have porate ascospores. Ascospores of most species of *Camarops* have a pore at only one end, but ascospores of *C. biporosa* J.D. Rogers & Samuels (Rogers and Samuels, 1987) have a pore at both ends. Perithecia of most members of the Boliniaceae are immersed in a hard, black, conspicuous stroma although perithecia of *Apiocamarops alba* Samuels & J.D. Rogers are completely immersed in a white subiculum. Moreover, members of the Boliniaceae are generally easy to culture, frequently produce teleomorphs, and never produce anamorphs (Callan and Rogers, 1989). *Helminthosphaeria* and members of the Boliniaceae share the apparently unusual features of ascospores that are more grey or green than brown and that have minute pores in one or both ends. No species of the Boliniaceae has been unequivocally linked to an anamorph. Barr (1990) included the Boliniaceae in the Xylariales whereas Eriksson and Hawksworth (1993) did not place the family in any order. We do not see a familial relationship for *Helminthosphaeria* and the Boliniaceae.

*Helminthosphaeria* is anomalous. The four species that we include in the genus are remarkably similar to each other and cannot be accommodated in any previously described family. Therefore we propose a new family for *Helminthosphaeria*. On the basis of perithecial characters, for now we place the Helminthosphaeriaceae in the Sordariales (*sensu* Barr, 1990)

while recognizing that that order is probably polyphyletic.

### **Helminthosphaeriaceae** Samuels, Candoussau et Magni, fam. nov.

Mycelium non manifestum. Perithecia nigra, ostiolata, canale ostiolarum periphysato. Parietes peritheciae carbonaceae, pseudoparenchymatosae. Asci in hymenio formati. Ascospores cinereo-brunneae vel olivaceae, translucidae, poro inconspicuo minuto uno vel utroque apice praedito. Hamathecium non ramosis, apicaliter discretis paraphysis compositum. Status anamorphosis partim *Diplococcii* pertinens, conidia e minutis poris orientia.

Genus typicum: *Helminthosphaeria* Fuckel emend.

Mycelium not visible. Perithecia black, ostiolate; ostiolar canal periphysate. Perithecial wall carbonaceous, of pseudoparenchyma. Asci forming in a hymenium. Ascospores grey-brown or olivaceous, translucent, with an inconspicuous, minute pore at one or both ends. Hamathecium of unbranched, apically free paraphyses. Anamorph in part *Diplococcium*, conidia forming through minute pores.

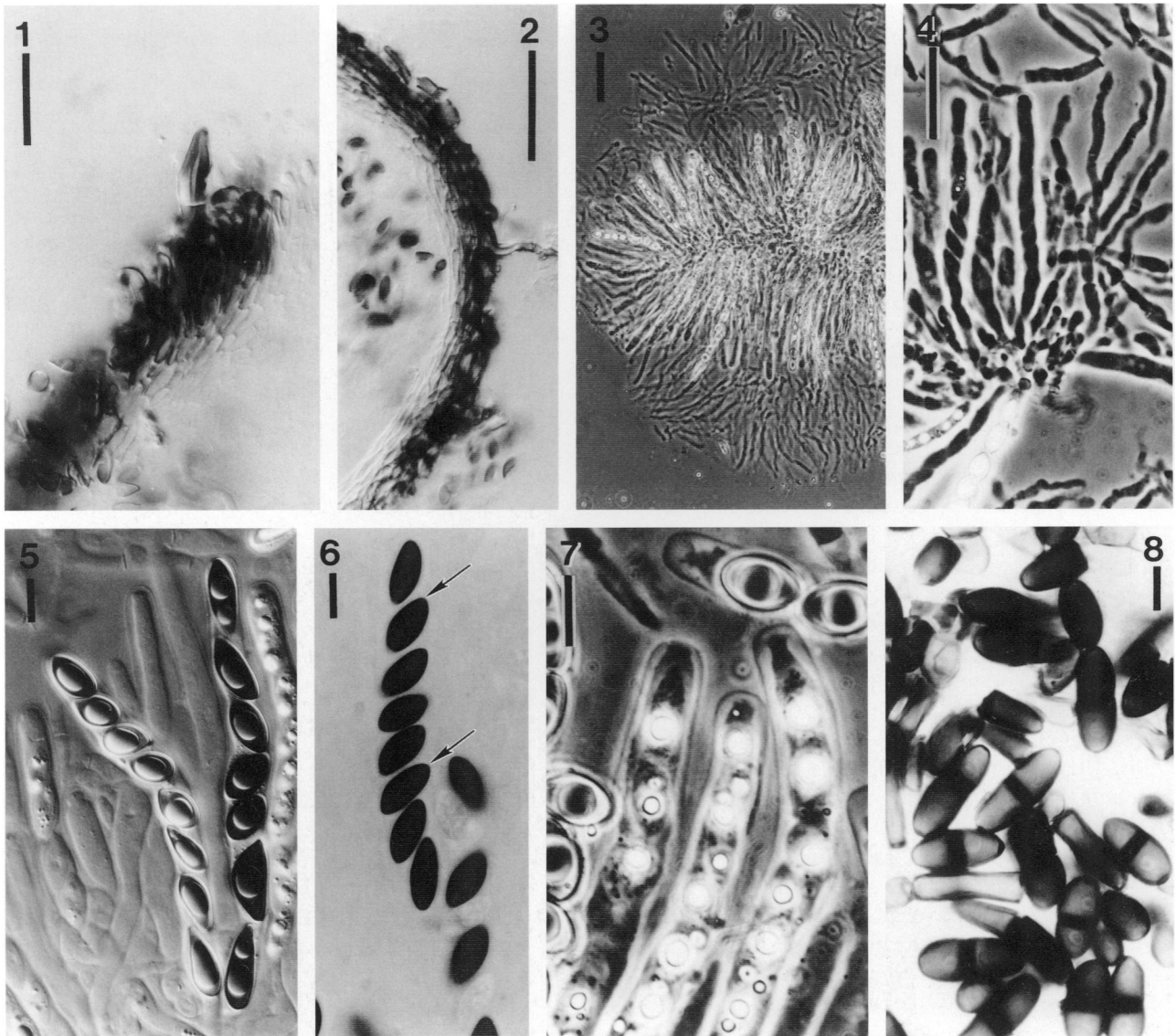
### *Helminthosphaeria* Fuckel emend Samuels, Candoussau et Magni

Perithecia superficial or basally immersed in host tissue, black, carbonaceous, not collapsing when dry, wall roughened, setae or modified cells arising from cells of the perithecial surface around the ostiolar area. Perithecial wall 25–50  $\mu\text{m}$  wide, of two regions of cells; cells of outer region angular, 10–25  $\mu\text{m}$  diam, walls to 2  $\mu\text{m}$  thick and pigmented, cells of inner region small, thin-walled and hyaline; cells of the perithecial wall angular, to 15  $\mu\text{m}$  diam. Paraphyses abundant among mature asci, apically free, cylindrical, unbranched or infrequently branched. Asci unitunicate, apex lacking a visible apical ring, J- (Melder's). Ascospores ellipsoidal to narrowly clavate, aseptate or tardily becoming 1–2-septate, with a frequently inconspicuous pore at one or both ends of discharged ascospores, greyish-brown, smooth.

### MATERIALS AND METHODS

Dry specimens were rehydrated briefly in 3% (aq.) KOH and the mounts were then flooded with water. Photographs were taken of ascospores and asci mounted in water mounts. Photographs were taken of perithecial sections mounted in 100% lactic acid.

Three types of microscopy were used in this study. These are indicated in the legends to the illustrations as bright field (BF), fluorescence (FL), interference contrast (IC), and phase contrast (PC).



FIGS. 1–8. *Helminthosphaeria clavariarum*. 1, 2. Median, longitudinal sections through mature perithecia. 1. showing perithecial apex, 2. showing lateral perithecial wall. 3–7. Asci, ascospores and paraphyses. Arrows indicate paraphyses in FIGS. 3, 4; pores in ascospores are indicated by arrows in FIG. 6. FIGS. 1, 2, 5: IC; 3, 4, 7: PC; 6, 8: BF. FIGS. 1, 2, 6 from Rehm: *Ascomyceten* 1559; 3–5, 7 from BPI 580732; 8 from BPI 580730. Scale bars: FIGS. 1–4 = 50  $\mu\text{m}$ ; 5–8 = 10  $\mu\text{m}$ .

Frequent collectors names are abbreviated as follows: F. Candoussau (FC) and J.-F. Magni (JFM).

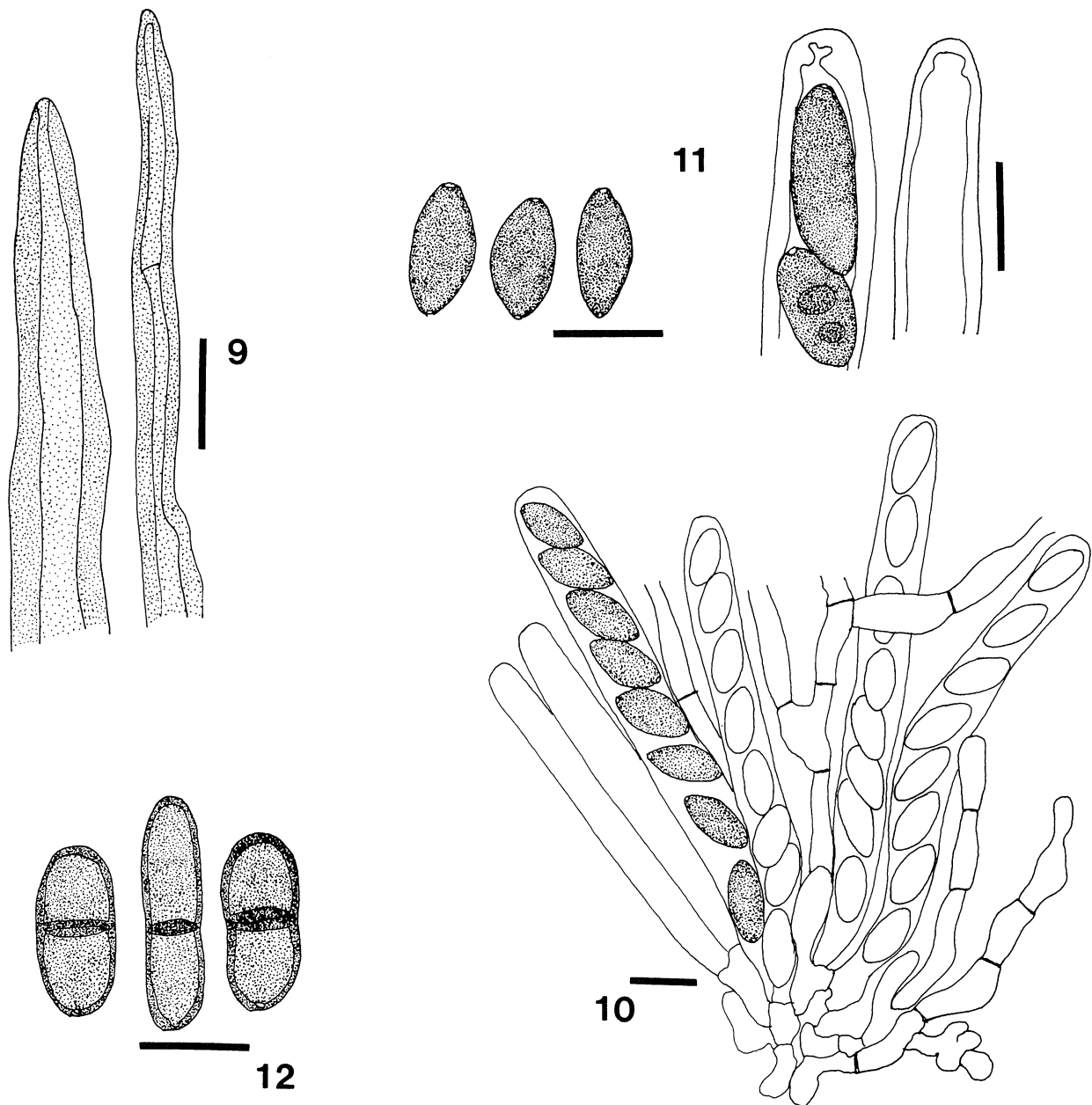
#### KEY TO SPECIES OF *HELMINTHOSPHAERIA*

1. Host a member of the Clavariaceae. . . . . 1. *H. clavariarum*
1. Host a resupinate basidiomycete . . . . . 2
2. Ascospores averaging longer than 12  $\mu\text{m}$ , often developing 2–3 septa . . . . . 2. *H. corticiorum*
2. Ascospores averaging shorter than 12  $\mu\text{m}$ , remaining aseptate or becoming apiosporous . . . . . 3
3. Ascospores (6.0–)7.9–10.7(–12.7)  $\times$  (2.9–)4.1–6.1(–7.5)  $\mu\text{m}$ , many spores apiosporous in asci . . . . . 4. *H. odontiae*
3. Ascospores (7.2–)8.9–12.1(–16.0)  $\times$  (3.3–)4.2–5.4(–6.9)  $\mu\text{m}$  remaining aseptate. . . . . 3. *H. hypodermiae*

#### DESCRIPTIONS OF THE SPECIES

1. *Helminthosphaeria clavariarum* (L.-R. Tul.) Fuckel, *Symb. bot.* 166. 1870. (as “*clavariae*”) FIGS. 1–12  
 = *Sphaeria clavariarum* L.-R. Tul., *Ann. Sci. Nat. Ser.* 4, 5: 113. 1856.  
 = *Pleospora clavariarum* (L.-R. Tul.) L.-R. & C. Tul., *Sel. Fung. Carp.* 2: 271. 1863.  
 = *Sphaeria (Byssisedae) clavariina* Peck, *Ann. Rep. New York State Mus.* 32: 51. (for 1878) 1880  
 [*vide* Barr et al., 1986].

Anamorph. *Diplococcium* sp. (See Ellis, 1963 for synonymy).  
 FIGS. 8, 12



FIGS. 9–12. *Helminthosphaeria clavariarum*. 9. Perithecial setae. 10. Asci and paraphyses from hymenium. 11. Ascus apices and discharged ascospores. 12. Conidia. FIGS. 9, 11 (discharged ascospores) from Rehm: *Ascomyceten* 1559; 10, 11 (asci), 12 from BPI 579130. Scale bars = 10  $\mu$ m.

Anamorph forming a continuous black velutinous lawn of mononematous conidiophores and discoloring the host. Perithecia forming near the base of host, solitary to densely gregarious, superficial or partly immersed in host tissue, globose, subglobose to broadly pyriform, 200–600  $\mu$ m diam, nonpapillate, not collapsing or, less frequently, collapsing by lateral pinching when dry; with stiff, erect, unbranched, golden-brown setae arising as modified surface cells of the perithecia; setae robust, to 200  $\mu$ m long, to 12  $\mu$ m wide at base, wall 3–5  $\mu$ m thick. Perithecial wall

dark brown or greenish brown by transmitted light, cells at the surface *textura angularis*, tending to be built up as low warts from which setae arise, cells of warts tending to be brick like and longer than wide, walls to 2  $\mu$ m thick; lateral perithecial wall 25–35  $\mu$ m wide, of two regions. Outer region 15  $\mu$ m wide, cells angular to elliptic, 10–25  $\mu$ m diam, walls to 2  $\mu$ m thick and pigmented; inner region to 10  $\mu$ m wide, cells small, hyaline, thin-walled. Perithecial apex formed of conspicuously diverging hyphal elements with walls 1.5–2  $\mu$ m thick; short, blunt or acute setae

arising from around the ostiolar opening with walls to 5  $\mu\text{m}$  thick. Ostiolar canal periphysate. Paraphyses abundant among maturing asci, cylindrical, unbranched or infrequently branched, septate, 4–5  $\mu\text{m}$  wide, extending beyond asci by up to 100  $\mu\text{m}$ . Asci to 90  $\mu\text{m}$  long (Dennis, 1978), cylindrical, 8-spored; apex simple. Ascospores ellipsoidal, ( $n=132$ ) (10.0–)11.5–15.6(–19.0)  $\times$  (4.5–)5.2–7.2(–8.0)  $\mu\text{m}$ , unicellular, brown to gray-brown (transmitted light), a pore at each end visible after discharge, smooth.

*Presumed anamorph in nature.* See Ellis (1963, 1971). Conidia ellipsoidal, 13–23  $\times$  6–8.5  $\mu\text{m}$ , (0–)1-septate (Ellis, 1963, 1971).

*Habitat.* Basidiomata of the Clavariaceae, including *Clavaria cinerea*, *C. cristata* (Dennis, 1978).

*Known distribution.* Europe and North America.

*Illustrations.* Tulasne and Tulasne (1863, Pl. 30: 1–4). Müller and Arx (1954, Fig. 89). Ellis (1971, Fig. 271; anamorph). Dennis (1978, Fig. 11 G). Ellis and Ellis (1988, Fig. 63).

*Specimens examined.* FRANCE. Meaux, on *Clavaria* spp., Autunno 1896, *Signor P. Dumée* (Briosi e Cavara, I funghi parassiti delle piante coltivate od util. 293, BPI 580730). GERMANY. Holl. Limburg, on *Clavaria cristata*, Nov. 1900, *Rick, S. J.* (Rehm: Ascomyceten 1559, BPI 580733). UNITED STATES. CONNECTICUT: Montrose [?], on *Clavaria* ?, Sep. 1888, *R. Thaxter* (BPI 580735). NEW HAMPSHIRE: vic. Peterborough, Sargent Camp, on *Clavaria* sp., 24 Jul. 1956, *C. W. Emmons* (BPI 579130). NEW YORK: Dutchess County, Carey Arboretum, near Milbrook, on *Clavaria* sp., 19 Oct. 1979, *A. Y. Rossman, C. T. Rogerson & S. E. Carpenter* (BPI 580732); Saratoga County, trail to Lake Ann, Mt. McGregor, near Wilton, on *Clavaria* sp., 10 Oct. 1968, *C. T. Rogerson & S. J. Smith* (BPI 580734 ex NY).

2. *Helminthosphaeria corticiorum* Höhnelt, Sitzungsber. Kais. Akad. Wiss. Wien Math.-Naturw. Kl. Abt. 1, 116: 109. 1907. (Fragmente zur Mykologie 112). FIGS. 13–26

$\equiv$  *Litschaueria corticiorum* (Höhnelt) Petrak, Ann. Mycol. 21: 275. 1923 (non sensu Barr, 1976).

Anamorph. ? *Diplococcium* sp. (associated on host). FIGS. 25, 26

Perithecia scattered and solitary to gregarious, almost completely immersed in host hymenium, subglobose to pyriform 275–650  $\mu\text{m}$  high, 300–350  $\mu\text{m}$  wide, with an acute to broad apex, not collapsing, roughened by low warts; obtuse, black, setalike outgrowths (18–)33–67(–112)  $\mu\text{m}$  long, (4–)5–10(–15)  $\mu\text{m}$  wide at base, arising primarily from around the

perithecial apex, wall ca 1.5  $\mu\text{m}$  thick. Perithecial wall greenish by transmitted light (KOH), cells at the surface angular, built up as low warts in places and then bricklike, 10–15  $\mu\text{m}$  diam, wall 1  $\mu\text{m}$  thick; lateral perithecial wall to 65  $\mu\text{m}$  wide, of two regions. Outer region ca. 35  $\mu\text{m}$  wide, cells angular, 8–10  $\mu\text{m}$  diam, walls ca. 1  $\mu\text{m}$  thick, heavily pigmented; inner region ca. 30  $\mu\text{m}$  wide, cells thin-walled and nonpigmented, fusiform toward the locule. Perithecial apex of hyphal elements with blunt tips, ca. 10  $\mu\text{m}$  wide at the exterior, with thick tips and heavily pigmented, progressively narrower and unpigmented toward the ostiolar canal. Ostiolar canal periphysate. Paraphyses persisting among mature asci, cylindrical, unbranched, septate, 3–5  $\mu\text{m}$  wide, extending beyond asci 15–50  $\mu\text{m}$ . Asci cylindrical, (80–)90–118(–140)  $\times$  (4.8–)5.8–8.6(–10.0)  $\mu\text{m}$ , 4–8-spored; apex simple. Ascospores ellipsoidal to narrowly clavate, sometimes slightly geniculate, ( $n=283$ ) (10.0–)13.4–16.6(–20.0)  $\times$  (4.0–)5.0–6.4(–8.2)  $\mu\text{m}$ , 0–1–2(–3)-septate, a single septum often eccentric, gray-brown to olivaceous (in KOH), a pore at one or both ends, smooth.

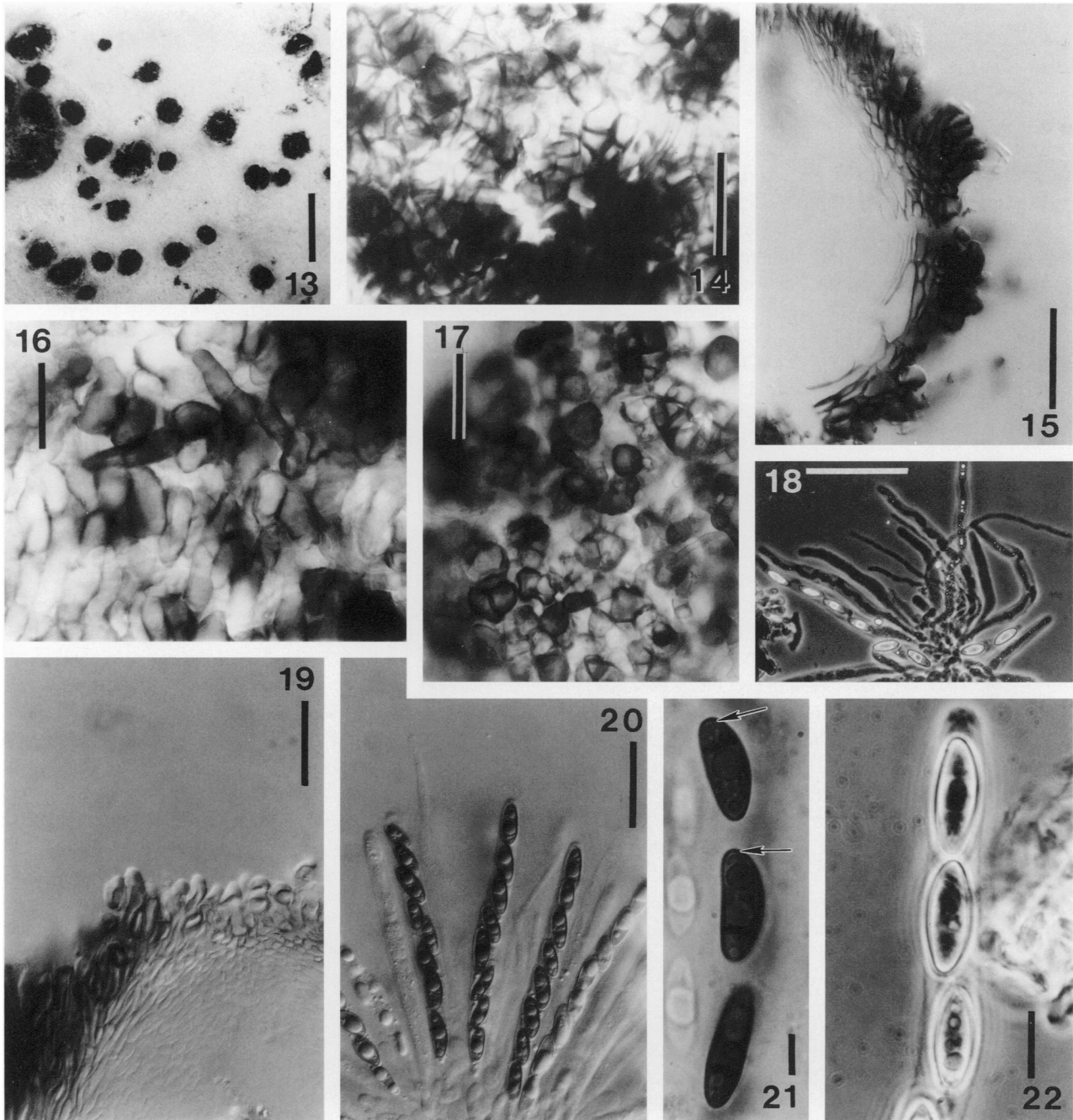
*Habitat.* On Corticiaceae.

*Known distribution.* Austria, France, Gabon, USA (Maine).

HOLOTYPE. AUSTRIA. Donau-Auen., Langenschönbiche-Tulln., on *Peniophora cremea* Bres. (det. Höhnelt) on *Salix* sp., 3/6 1905, Höhnelt (FH-Höhnelt)!

*Additional specimens examined.* FRANCE. ARIÈGE: 09410 Moulis, on *Hyphoderma* sp., 8 June 1995, *N. de Munnik 0806 comm. FC 370* (BPI). 09800 Lac de Bethmale, elev. 1300 m, on *Phanaerochaete sordida*, June 1995, *N. de Munnik 2702 comm. FC 371* (BPI). 09429 Rimont, “Las Muros,” on Corticiaceae on *Ulmus* sp., 5 June 1995, *J. Fournier comm. F. Candoussau 369* (BPI). HAUTE GARONNE: Ravin de Fonsegrive 31, on *Phanaerochaete sordida*, 5 Mar. 1994, *J. F. Magni A9446* (BPI); same locality, on Corticiaceae (?*P. sordida*) on branches, 18 Feb. 1996, *J. F. Magni A9619* (BPI). Fourquevaux 31, 20 km S of Toulouse, on Corticiaceae on *Ilex aquifolium*, 26 Mar 1995, *FC 352 & J.-F. Magni* (J.-F. Magni herbarium and BPI). HAUTES PYRÉNÉES: Capvern, Route du Moulin des Baronnies, Forêt de Tilhouse, on *Hyphoderma litschaueri* (Burt.) Eriks. & Strid, 11 Sep. 1994, *FC 305* (BPI). LANDES: Magescg (DAX) 40 Landes, on *Hyphodontia nespori* (Bres.) Erikss. & Hjortstam, 12 Feb 1995, *FC 345* (BPI). PYRÉNÉES ATLANTIQUES: Forêt Domaniale d’Oloron, on Corticiaceae on *Chamaecyparis lawsoniana*, 31 Feb. 1993, *FC 309* (BPI); Forêt Domaniale d’Oloron, on Corticiaceae, 28 Jan. 1996, *FC 423, 425* (BPI). 64 Bonnut, Bois de Feuillus, 60 km dela Côte Atlantique, on *Phanaerochaete sordida*,



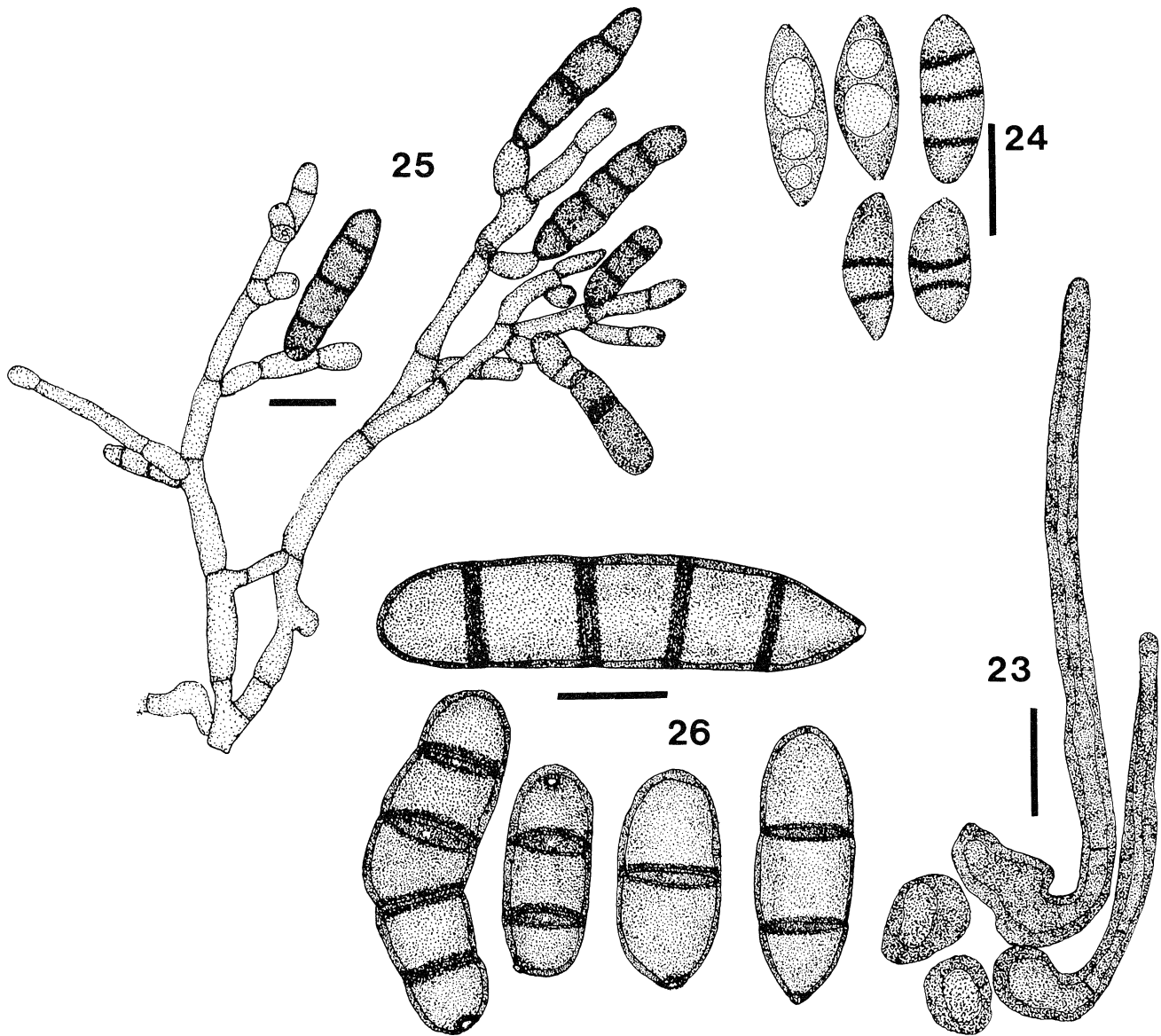


FIGS. 13–22. *Helminthosphaeria corticiorum*. 13. Habit of perithecia, immersed in host hymenium. 14, 16, 17. Cells at surface of perithecial wall. Two setae visible in FIG. 16. 15. Off-center section through a mature perithecialium showing warts and lateral paraphyses (arrow). 18, 20. Asci and paraphyses (arrow). 19. Median longitudinal section through a mature perithecialium showing perithecial apex. 21, 22. Ascospores in asci and ascus apex. A pore visible in two ascospores in FIG. 21 (arrows); ascus apex visible in FIG. 22. FIGS. 13, 14, 16, 21: BF; 15, 17, 19, 20: IC; 18, 22: PC. FIG. 13 from FC 371; 14, 19 from JFM 09446; 15, 16 from FC 357; 17, 18, 21 from FC 305; 20 from FC 352; 22 from Thaxter. Scale bars: FIG. 13 = 1 mm, 14–20 = 50  $\mu$ m; 21, 22 = 10  $\mu$ m.

9 Apr. 1995, FC 360 (BPI, CUP 63,566). GABON. km 27.2 N of Libreville, Forêt La Mondah, on *Phanaerochaete* (*Phanericium* sp.) sp., 2 June 1979, G. Gilles comm. FC 357 (Gabon 77) (BPI). UNITED STATES.

MAINE: Kittery Point, on [Corticaceae], date unknown, Thaxter (herb. J.D. Rogers, BPI)

A *Diplococcium* anamorph was associated with perithecia of Magni A9446, Thaxter, FC 309, 357, 360,

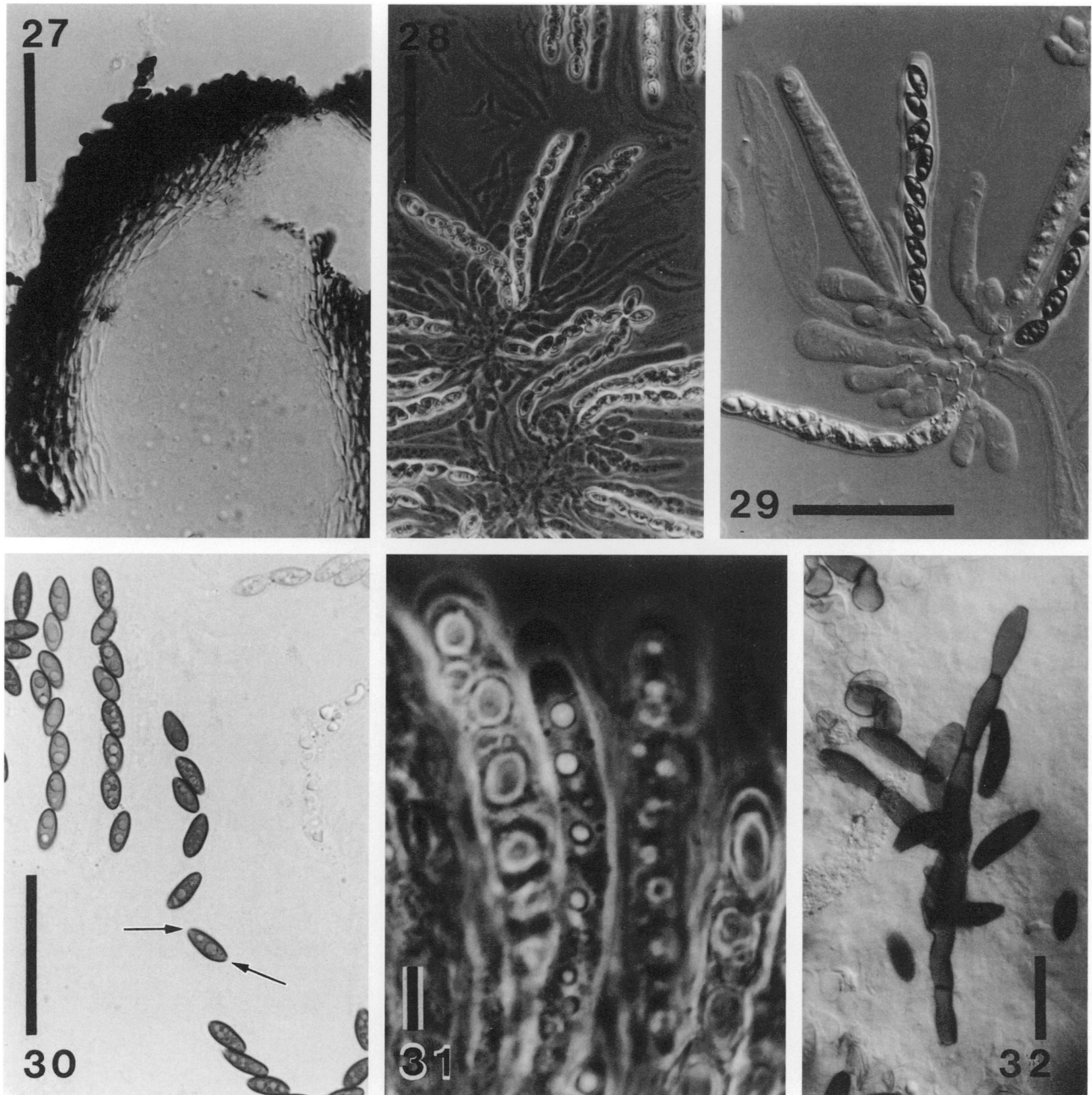


FIGS. 23–26. *Helminthosphaeria corticiorum*. 23. Perithecial setae. 24. Discharged ascospores. 25. Conidiophores with conidia. 26. Conidia. Scale bars = 10  $\mu\text{m}$ .

369, 370, and 371; no anamorph was found on the remaining cited specimens. The anamorph is described as follows: Conidiophores macronematous, mononematous, to 250  $\mu\text{m}$  long, cylindrical, 4–6  $\mu\text{m}$  wide, frequently septate and branched, smooth, gray-green, with at least one minute pore in terminal and some intercalary cells from which conidia are produced singly. Conidia cylindrical to ellipsoidal, (11–)19–42(–55)  $\times$  (5–)7–11(–15)  $\mu\text{m}$ , (1–)2–3(–4–5)-septate, with a minute pore at one or both ends, translucent brown but septa darker.

*Helminthosphaeria corticiorum* is characterized by its corticiaceous host and relatively long and narrow ascospores that often develop two septa after dis-

charge from the ascus. The associated anamorph, while distinctive because of its large conidia is consistent with anamorphs associated with *H. clavariarum* and *H. epimyces*. Perithecia of *H. corticiorum* are seated in a circular hole in the hymenium of the host, often half or more deeply immersed. Asci of *FC 305* contain four fully developed ascospores and four aborted ascospores, but asci of the other collections contain eight normal ascospores. Ascospores in this collection become apiosporous, developing a single submedian septum after discharge, and the perithecial setae are only bristles  $\leq 25 \mu\text{m}$  long. No anamorph was associated with perithecia in this collection.



FIGS. 27–32. *Helminthosphaeria hyphodermiae*. 27. Median longitudinal section through a mature perithecium showing part of perithecial apex and lateral wall. 28–31. Asci, ascospores and paraphyses. Paraphyses are indicated by an arrow in FIG. 28; two pores are visible in one ascospore in FIG. 30 (arrows); a thickened ascus apex is visible in a young ascus in FIG. 31. 32. Associated, unnamed anamorph. FIGS. 27, 29, 30, 32: IC; 28, 31: PC. FIGS. 27–31 from FC 306; 32 from Tranzschel et Serebrianiow, Mycotheca Rossica 318. Scale bars: 27–30, 32 = 50  $\mu\text{m}$ ; 31 = 10  $\mu\text{m}$ .

3. *Helminthosphaeria hyphodermiae* Samuels, Candoussau et Magni, sp. nov. FIGS. 27–36

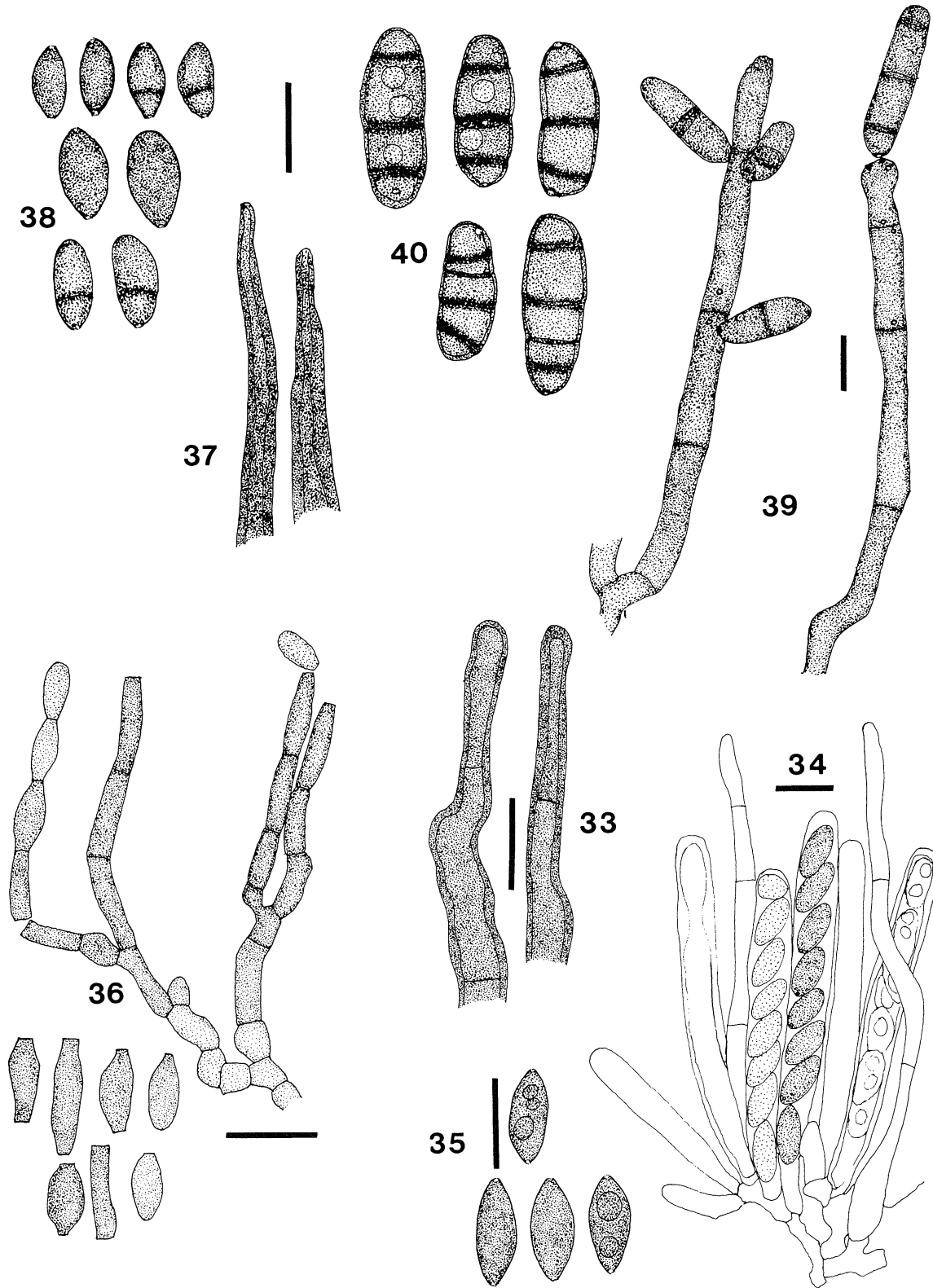
*Helminthosphaeria clavariarum* sed hospitis differt et ascosporae (7.2–)9.0–12.0(–8.8)  $\times$  (3.3–)4.2–5.4(–6.9)  $\mu\text{m}$ .

HOLOTYPE. FRANCE. PYRÉNÉES ATLANTIQUES (64): Bois Bastard de Pau, on *Hyphoderma puberum*, 31 Oct. 1994, FC 306 (BPI).

*Etymology*. Refers to the host, where determined a species of *Hyphoderma*.

*Anamorph*. Unnamed, dematiaceous hyphomycete (associated) FIGS. 32, 36

Perithecia scattered and solitary to gregarious, im-



FIGS. 33–40. *Helminthosphaeria hyphodermiae*. 33. Perithecial setae. 34. Asci and paraphyses from the hymenium. 35. Discharged ascospores. 36. Associated anamorph showing conidiophores and conidia. 37–40. *H. odontiae*. 37. Perithecial setae. 38. Discharged ascospores. Top four spores from the type collection of *H. odontiae*, the middle two spores from the type collection of *L. epimyces*; the bottom two spores from *H. Vogelmayr*. 39. Conidiophores with conidia. 40. Conidia. FIGS. 33–36 from FC 306; 37–40 from the type of *L. epimyces*, except where noted. Scale bars = 10  $\mu$ m.

mersed only at base to almost completely immersed in host hymenium, subglobose to pyriform, 250–650  $\mu\text{m}$  high, 225–450  $\mu\text{m}$  wide, with an acute apex, not collapsing, roughened by low warts; acute, black, setae (15-)35–78(-109)  $\mu\text{m}$  long, (3.0-)4.5–9.2(-18.6)  $\mu\text{m}$  wide at base, arising from around perithecial apex, wall ca. 1.5  $\mu\text{m}$  thick. Perithecial wall greenish by transmitted light (in KOH), cells at the surface angular, built up as low warts in places, and then bricklike, 7–15  $\mu\text{m}$  diam, wall ca. 1  $\mu\text{m}$  thick; lateral perithecial wall to 50  $\mu\text{m}$  wide, of two regions. Outer region ca. 25  $\mu\text{m}$  wide, cells circular to elliptical, 5–7  $\mu\text{m}$  diam, walls ca. 1.5  $\mu\text{m}$  thick, heavily pigmented; inner region ca. 25  $\mu\text{m}$  wide, cells thin-walled and nonpigmented, fusiform toward the locule. Perithecial apex of hyphal elements with blunt tips; elements toward the exterior ca. 6  $\mu\text{m}$  wide and ca. 3  $\mu\text{m}$  wide toward the ostiolar canal. Ostiolar canal periphysate. Paraphyses persisting among mature asci, cylindrical, unbranched, septate, 3–4  $\mu\text{m}$  wide, extending beyond asci 40–80  $\mu\text{m}$ . Asci cylindrical, (48-)68–92(-125)  $\times$  (4.5-)5.6–9.2(-10.5)  $\mu\text{m}$ , 8-spored; apex with an obscure crown. Ascospores ellipsoidal, (n=195) (7.2-)9.0–12.0(-16.0)  $\times$  (3.3-)4.2–5.5(-7.0)  $\mu\text{m}$ , unicellular, brown to gray-brown (transmitted light), a pore at one or both ends visible after discharge, smooth.

*Known distribution.* France, Russia.

*Habitat.* On resupinate, corticioid basidiomycetes including *Hyphoderma puberum*; sometimes appearing to be on decorticated wood.

*Additional specimens examined.* FRANCE. ARIÈGE (09): Quérigut, ruisseau Le Rialet, Le Pla, elev. 1000, on *Hyphoderma puberum*, 24 Sep 1994, FC 391, 393 (BPI). PYRÉNÉES ATLANTIQUES (64): Bois Bastard de Pau, Bord Aygue Longue, on *Hyphoderma puberum* on *Fagus* sp., 20 Aug. 1995, FC 385 (BPI); Bois Bastard de Pau, Sentier Sportif, on decorticated wood of *Castanea sativa*, 6 Aug. 1995, FC 382 (BPI). RUSSIA. PROV. JAROSLAWL: Schedenewo, in corticio, Aug. 1911, *Serebrianikow & Schestakow* (Tranzschel et Serebrianikow, Mycotheca Rossica 318 as *Helminthosphaeria corticiorum*, BPI 580736)].

*Helminthosphaeria hyphodermiae* is distinguished from *H. corticiorum* by having somewhat shorter ascospores that remain unicellular, and in the putative anamorph.

We have not seen *Diplococcium* conidia associated with any of the specimens that we examined. A distinctive hyphomycetous anamorph was found associated with perithecia on four of the specimens cited above (FC 306, 385, 391 and *Tranzschel & Serebrianikow* 381). The anamorph is described as follows: Conidiophores macronematous, mononematous, to 125  $\mu\text{m}$  long, 5–7  $\mu\text{m}$  wide, frequently branched, the

ultimate branches fragmenting into chains of ellipsoidal to cylindrical conidia. Conidia (8.7-)12.6–18.0(-22.0)  $\times$  (4.0-)5.0–6.5(-7.3)  $\mu\text{m}$ , ellipsoidal (when terminal) to cylindrical (when intercalary), unicellular, with truncate ends and apparently held in chains. Conidia and conidiophores gray-brown (KOH).

We were not able to identify this fungus to any genera of dematiaceous hyphomycetes. Despite the association of this anamorph with collections from widely separated geographic areas, we are dubious of the link between the anamorph and the *Helminthosphaeria* because the other presumed anamorphs of *Helminthosphaeria* species are seemingly so different from this one.

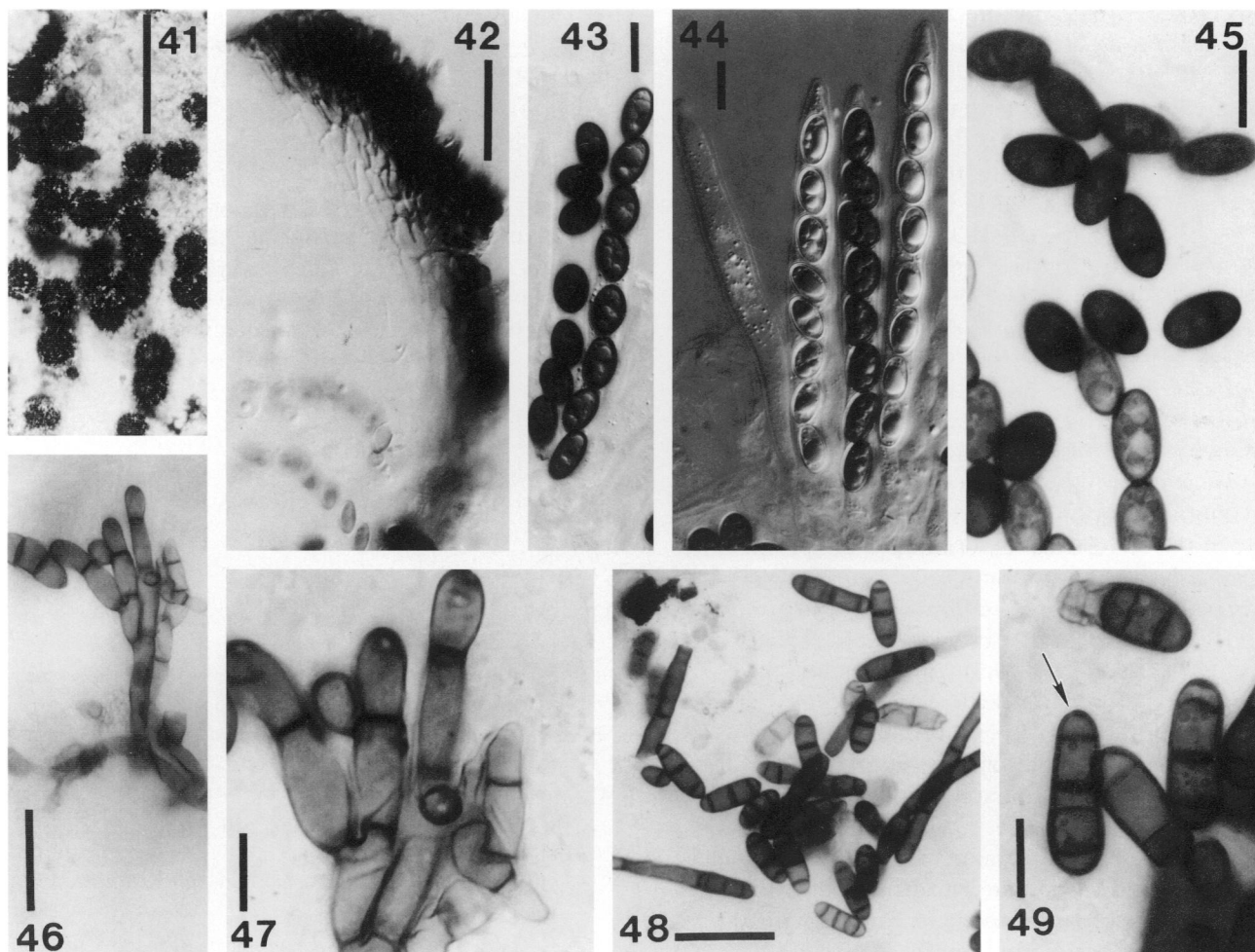
4. *Helminthosphaeria odontiae* Höhnelt, Sitzungsber. Akad. Wiss. Wien Math.-Naturwiss. Kl. Abt. I, 116: 109. 1907 (Fragmente zur Mykologie 111).

FIGS. 37–49

= *Litschaueria epimyces* Malençon & Bertault, Acta Phytotaxonomica Barcinonensia 11: 19. 1972.

Anamorph. *Diplococcium* sp. (? = *Helminthosporium conviviva* Malençon & Bertault, Acta Phytotaxonomica Barcinonensia 11: 19. 1972.) (associated on host) FIGS. 39, 40, 46–49

Perithecia scattered to gregarious, basally to 3/4 immersed in host tissue or seated in or on decorticated wood in older specimens, subglobose to pyriform and then with an acute papilla, 210–350  $\mu\text{m}$  diam, not collapsing, roughened by low warts; stiff, erect, unbranched, black setae (12-)38–86(-111)  $\mu\text{m}$  long, 4.5–8.0  $\mu\text{m}$  wide at base, wall 1  $\mu\text{m}$  thick, arising as modified cells of the surface of the perithecial surface. Perithecial wall reddish brown (type) by transmitted light (KOH), cells at the surface angular, built up as low warts in places, 10  $\mu\text{m}$  diam, walls to 1  $\mu\text{m}$  thick; lateral perithecial wall to 25  $\mu\text{m}$  wide, of two regions. Outer region ca. 10  $\mu\text{m}$  wide, cells nearly circular, ca. 7  $\mu\text{m}$  diam, walls 1.0–1.5  $\mu\text{m}$  thick, pigmented; inner region 7–10  $\mu\text{m}$  wide, cells nonpigmented, small. Perithecial apex of conspicuously diverging hyphal elements protruding slightly and crowded around the ostiolar opening, ca. 6  $\mu\text{m}$  wide with walls 1.5  $\mu\text{m}$  thick and pigmented, becoming progressively narrower and unpigmented toward the ostiolar canal. Ostiolar canal periphysate. Paraphyses persisting among mature asci, cylindrical, unbranched, septate, 2.5–3.0  $\mu\text{m}$  wide, extending beyond asci. Asci cylindrical, (48-)90–118(-140)  $\times$  (5.2-)5.5–8.5(-10.0)  $\mu\text{m}$ , 8-spored; apex simple. As-



FIGS. 41–49. *Helminthosphaeria odontiae*. 41. Habit of perithecia, immersed in host hymenium. 41. Median longitudinal section of a mature perithecium showing perithecial apex and lateral wall. 43–45. Asci and ascospores. Septa visible in ascospores in FIG. 45. 46–49. Associated *Diplococcium* anamorph. 46, 47. Conidiophores; pores visible at conidiogenous loci in FIG. 47. 48, 49. Conidia, a pore visible in one conidium in FIG. 49 (arrow). FIGS. 41, 45–49: BF; 42–44: IC. FIG. 41 from FC 384; 42–49 from FC 300. Scale bars: 41, 42, 46, 48 = 50  $\mu$ m; 43–45, 47, 49 = 10  $\mu$ m.

cospores ellipsoidal, ( $n=291$ ) (6.0–)8.0–10.7(–12.7)  $\times$  (3.0–)4.0–6.0(–7.5)  $\mu$ m, 0(–1–2)–septate, septum eccentric when single, gray-brown to olivaceous (transmitted light, KOH), a pore at one or both ends (most commonly seen in the smaller cell), smooth.

Presumed anamorph in nature. Conidiophores macronematous, mononematous, cylindrical, 50–112  $\mu$ m long, 5  $\mu$ m wide, unbranched or sparingly branched, septate, smooth, conidia formed through minute pores from the end cell as well as from intercalary cells. Conidia cylindrical to ellipsoidal, (7.5–)11.0–22.0(–36.0)  $\times$  (4.0–)5.0–7.5(–10.5)  $\mu$ m, 1–3(–4)–septate, olivaceous to brown but septa darker, with a minute pore at each end.

*Habitat.* On ‘corticoid’ basidiomycetes, including *Grandinia setigeriae* and *Hyphoderma calyciferum*

(Litsch.) Malencon & Bert. and *H. tenue* (Pat.) Donk (Doll, 1973).

*Known distribution.* Austria, France, Spain (Majorca).

**HOLOTYPE.** [AUSTRIA]. Sattelberg bei Pressbaum, Wiener Wald, ‘auf morschen *Fagus*-st.,’ 21 Aug. 1906, Höhnel (FH-Höhnel)!

*Additional specimens examined.* AUSTRIA. Bundesland, Kärnten, St. Margareten im Rosental, MTB 5452/3 (“Wograda”), elev. ca. 550 m, 31 Oct. 1995, W. Jagtlicht (BPI). FRANCE. HAUTES PYRÉNÉES (65): Capvern, on Corticiaceae, 4 Sep. 1994, F. Candoussau 300 (BPI); Bois de Lourdes, on Corticiaceae on *Quercus pedunculata*, 14 Nov. 1984, FC 351 (BPI). LANDES (40): Bois d’Amou, on Corticiaceae on *Alnus* sp., 25 Aug. 1986, FC 350 (BPI). PYRÉNÉES AT-

LANTIQUES (64): Bois de Pau, on Corticiaceae, 30 Jul. 1995, *FC 381* (BPI); on *Quercus rubra* L., 22 Oct. 1995, *FC 400* (BPI); Bois Bastard de Pau, ruisseau "Aygue Longue," on Corticiaceae on *Quercus* sp., 13 Aug. 1995, *FC 384* (BPI); Bois Bastard de Pau, Sentier Sportif, on wood, 6 Aug. 1995, *FC 383* (BPI); Forêt Domaniale d'Oloron, on *Quercus rubra*, 22 Oct 1995, *FC 400* (BPI). SPAIN. MAJORCA: Serra dels Pinetells, on *Hyphoderma calyciferum*, 18 Nov. [?1970], collector unknown (MPU, HOLOTYPE of *Litschaueria epimyces*). SWITZERLAND. KT. THURGAU: vic. Wangi, on decorticated wood of *Alnus glutinosa*, 23 Jun 1974, *W. Matheis comm. F. Candoussau 376* (BPI).

Our concept of *H. odontiae* includes the *Helminthosphaeria* collections that have small ascospores that become apiosporous. Often there is no basidiomycete in evidence and perithecia appear to be growing directly on decorticated wood. The type collection of *H. odontiae* is in poor condition, but clearly includes a resupinate, corticioid basidiomycete. Most of the perithecia on the collection were broken and thus could not be characterized. No asci were seen, but several apiosporous ascospores were found in the slide that had apparently been prepared by Höhnelt and preserved with the specimen. The similarity of these ascospores to those of other collections has led us to conclude that the correct name for these collections is *H. odontiae*. The type collection of *Litschaueria epimyces* is in excellent condition, but there is no evident basidiomycete. There is considerable variation in the presence of perithecial setae. Often none are visible whereas in other collections (e.g. the Austrian collection) the perithecia are densely setose. We presume that the absence of setae is a reflection of advanced age of the perithecia.

A *Diplococcium* anamorph is associated with several of the collections, including the types of *L. epimyces* and *H. odontiae*. The associated anamorph resembles *Diplococcium clarkii* M.B. Ellis (1976), as well as *Helminthosporium conviva* Malençon & Bertault, which was found associated with the type specimen of *Litschaueria epimyces* (Malençon and Bertault, 1972).

#### ACKNOWLEDGMENTS

We are indebted to Prof. Jean Boidin and Mr. G. Gilles for identification of the basidiomycete hosts. The authors express appreciation to H. Voglmyer and W. Jagtlicht for providing us with collections and for calling our attention to the Doll (1973) article. Dr. Margaret Barr kindly read an early draft of this work. Comments offered by two unindentifiable reviewers considerably improved this work. We also appreciate the loan of type material of *Helminthosphaeria* and *Litschaueria* species from FH. We are appreciative of

Dr. Orlando Petrini for preparing the Latin description. Mr. James Plaskowitz prepared the photographs and plates of illustrations.

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