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Synopsis of genera of Erysiphales (powdery mildew fungi) occurring in the Pacific Northwest

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Abstract: The Erysiphales (powdery mildew fungi) are Ascomycetes of major economic significance. Recent taxonomic research, mostly in Asia and Europe, has produced major changes in genus concepts complicating identification of powdery mildew fungi and communication about the diseases they cause. This paper provides a summary of genus concepts applicable to powdery mildew fungi known in the Pacific Northwest, as well as dichotomous keys based on both anamorphic and teleomorphic features, and brief summaries of diagnostic features. Salient morphological features are illustrated with photographs made from recent collections from the region. The following genera are included: *Arthrocladiella*, *Blumeria*, *Erysiphe*, *Golovinomyces*, *Leveillula*, *Neoerysiphe*, *Phyllactinia*, *Podosphaera*, and *Sawadaea*. Consistent with modern systems of classification, *Microsphaera*, *Uncinula*, and *Uncinuliella* are subsumed within the modern concept of *Erysiphe*, and *Sphaerotheca* species are included in *Podosphaera*.

Key Words: Erysiphales, powdery mildew, *Arthrocladiella*, *Blumeria*, *Erysiphe*, G*olovinomyces*, *Leveillula*, *Microsphaera, Neoerysiphe*, *Phyllactinia*, *Podosphaera*, *Sawadaea, Sphaerotheca, Uncinula, Uncinuliella,* biodiversity, fungal taxonomy, fungal morphology.

Introduction

The Erysiphales (powdery mildew fungi) are Ascomycetes obligately parasitic on angiosperms (Braun, 1987). They are among the most economically important plant pathogenic fungi and because of their significance there is a long history of research on their taxonomy and biology. In North America, taxonomic research on Erysiphales has lagged behind other parts of the world (Braun et al., 2002). Consequently it can be difficult to determine the modern names to apply to Erysiphales occurring on this continent.

This paper is intended to be a practical aid to determining the genus names to apply to Erysiphales in the North American Pacific Northwest. The paper briefly summarizes and illustrates diagnostic features for modern genera applicable to these fungi. Diagnostic features are illustrated with photographs made from recent collections of Pacific Northwest species.

Morphological features used in distinguishing genera of Erysiphales

Determination of Erysiphales is based on a variety of morphological structures produced throughout their life cycles (Braun, 1987; Braun et al., 2002). Erysiphales are pleomorphic fungi, with life cycles typically involving both sexual (teleomorphic) and asexual (anamorphic) states. Erysiphales ascocarps, termed chasmothecia, usually range from about 80 µm to 450 µm in diameter and vary from nearly spherical to more or less hemispherical, rarely turbinate. Chasmothecia form various kinds of appendages including ones that can be acicular, dichotomously-branched, uncinate, subulate, or mycelioid. Chasmothecia with mycelioid appendages typically overwinter on the substrate on which they formed. Chasmothecia with other kinds of appendages typically dehisce from the site of origin and disperse to new locations before overwintering. Appendages can play roles in detaching chasmothecia from substrates, providing aerodynamic qualities enhancing dispersal, or attaching them to new substrates (Webster, 1979). After overwintering, asci protrude or are discharged through ruptured chasmothecial walls to eject ascospores which then infect new host material (Salmon, 1907).

Ascospores germinate to form hyphae that generally produce differentiated outgrowths termed appressoria. Appressoria in turn form infection structures to penetrate walls of epidermal cells, forming haustoria within them. In most taxa, hyphae primarily are formed superficially on host tissue, although in some, perhaps most notably species of *Phyllactinia* and *Leveillula*, extensive amounts of hyphae grow within host tissue. Conidiophores are formed from superficial mycelia, or in taxa with internal mycelia can arise inside host tissue and emerge through stomata to produce conidia. Multiple conidia are produced in succession from each conidiophore. Two basic kinds of conidiophores are recognized (Braun et al., 2002): in one kind, conidia mature singly, dehiscing upon maturation at which time a new conidium develops (Fig. 10); in the other kind, a series of conidia mature more gradually, resulting in a chain of conidia exhibiting increasing maturity distal to the conidiogenous cell (Fig. 8). In the absence of disturbance, conidia formed singly may accrue in false chains (Fig. 29). In most taxa, conidia produced from a single conidiophore are morphologically similar. However, in *Leveillula* two kinds of conidia are produced. The first-formed conidium, sometimes termed the primary or lanceolate conidium, exhibits a narrowed apex. The other kind of conidium, termed the secondary or cylindrical conidium, is formed following production of the primary conidium and lacks the narrowed apex. In species of *Sawadaea* both macroconidia and microconidia are formed, distinguished on the basis of relative size. An additional conidial feature with taxonomic significance is the fibrosin body. Fibrosin bodies are refractive, cytoplasmic structures that occur within conidia and exhibit varied shapes including comma's, cones, or rods (Braun et al., 2002).

Life cycles may lack either the teleomorph or the anamorph, and this feature may vary within the same species. In regions with climates including cold winters the entire life cycle, involving both teleomorphs and anamorphs, commonly operates. In regions with mild winters, such as the coastal Pacific Northwest, teleomorphs can be difficult to find, suggesting that they may occur either infrequently or perhaps have been lost (e.g., Glawe, 2003). At least one species of Erysiphales, *Parauncinula septata* (E. S. Salmon) S. Takam. & U. Braun, appears to form only the teleomorph (Takamatsu et al., 2005), but it has not been found in the Pacific Northwest.

In practice, a rather small number of morphologic features distinguishable with light microscopy are sufficient to determine genera of Erysiphales. With respect to species known to occur in the Pacific Northwest, examples of taxonomically useful features of the anamorph include morphology of: appressoria (usually either nipple-shaped [Fig. 1] or lobed [Fig. 9]); conidiophore foot cells (with inflated base [Fig. 7] or cylindrical base [Fig. 37]); conidiophores (forming conidia singly [Fig. 10]or in chains [Fig. 53]); fibrosin bodies (present [Fig. 54] or absent [Fig. 4]) and conidia (monomorphic [Fig. 3], or dimorphic [Fig. 32], or with both macroconidia and microconidia [Figs. 65, 66]). Teleomorph features include: number of asci contained in a single ascocarp (one ascus [Fig. 56] or multiple asci [Fig. 14]); and ascocarp appendages. At the genus level significant distinctions are made between two groups of taxa: those with both acicular appendages and penicillate cells (Figs. 42-44) and those that produce mycelioid (Fig. 11), dichotomously branched (Fig. 15), or uncinate appendages (Fig. 17). In some cases, such as *Arthrocladiella*, host information can also be useful in determining the genus of powdery mildew. *Arthrocladiella* has been found only on the solanaceous genus *Lycium* (Braun, 1987). However, most genera include species with varied host ranges.

Genus names used for Erysiphales

The nomenclatural history of Erysiphales dates to 1753 when the first binomial for a powdery mildew was published by Linnaeus (Braun, 1987). Far from being a mere historical curiosity, early work continues to be influential. Léveillé's (1851) genus concepts for Erysiphales marked a significant advance over previous approaches and continue to influence classification systems. Names applied to North American species of Erysiphales traditionally followed an approach that can be traced to work of Burrill (Burrill and Earle, 1887; Ellis and Everhart, 1892) and Salmon (1900). A conspicuous feature of those taxonomic systems is the emphasis on teleomorphic features to the point that anamorphic features are nearly ignored. Interestingly enough, Burrill's treatment of Erysiphales in Ellis and Everhart's (1892) *North American Pyrenomycetes* includes little information on anamorphs, while the accompanying drawings by F. W. Anderson clearly illustrate features such as whether conidia formed either singly or in chains—characteristics emphasized heavily in modern approaches. Anamorphic characters in most named species remain to be described (Braun et al., 2002).

Shaw's (1973a, b) compilation of fungi in the Pacific Northwest reflected taxonomic approaches typical of North American mycologists (e.g., Yarwood, 1973; Alexopoulos, 1962) of the 20th century, and included the following genera of Erysiphales: *Erysiphe, Microsphaera, Uncinula, Podosphaera, Sphaerotheca,* and *Phyllactinia.*

A typical artificial key in that era for genera of Pacific Northwest Erysiphales likely would have resembled the following:

1. Ascocarps containing single asci……………………………………………………………2
1.' Ascocarps containing multiple asci…………………………………………………………3
    2. Ascocarp appendages dichotomously-branched…………………………. *Podosphaera*
    2.' Ascocarp appendages mycelioid………………………………………………*Sphaerotheca*
3. Ascocarp appendages acicular……………………………………………………… *Phyllactinia*
3.' Ascocarp appendages mycelioid……………………………………………………….. *Erysiphe*
3.'' Ascocarp appendages uncinate……………………………………………………………*Uncinula*
3.''' Ascocarp appendages dichotomously branched…………………………………..*Microsphaera*

Because of the heavy emphasis on sexual state features in such systems, they are difficult to use during the growing season when conidial states are the predominant forms encountered.

Since the time of Shaw's work our knowledge of Pacific Northwest Erysiphales has changed markedly. Braun's (1987) world monograph of Erysiphales helped stimulate an explosion of taxonomic research, resulting in regional monographs for Erysiphales in many countries outside of North America (Braun et al., 2002). Recent collecting work in the Pacific Northwest revealed the existence of many previously unrecognized species of Erysiphales in the region. It is now estimated that 150-200 species of Erysiphales occur in the Pacific Northwest, rather than the several dozen recognized in Shaw's era (Glawe, 2004b). Genus concepts for Erysiphales have undergone marked changes because of analysis of nucleic acid sequences (Braun and Takamatsu, 2000; Braun et al., 2002; Takamatsu, 2004 and references therein). A surprising finding was that evolutionary lineages within Erysiphales are more clearly reflected in differences in anamorphic states than in teleomorphic features such as ascocarp appendages (Saenz and Taylor, 1999; Mori et al., 2000a, b; Takamatsu, 2004). Such work is consistent with morphological studies involving both light and scanning electron microscopy that reinforced the view that species of Erysiphales can be determined using anamorphic features (Bosewinkel, 1980b; Cook et al., 1997). The realization that anamorphic features are sufficient to determine most powdery mildew species is of great importance to plant pathologists and others who need to diagnose and control plant diseases caused by Erysiphales.

Following is a key with synopses of diagnostic features for genera of Erysiphales currently known to occur in the Pacific Northwest. Features not seen by the author or illustrated herein are enclosed by brackets. Genus names used are consistent with recent taxonomic innovations (Braun et al., 2002). To provide some assistance for readers who also need to use older North American phytopathological and mycological literature, significant synonyms are also listed.

Artificial key to genera, based on current taxonomy

1. Conidiophores emerging through stomata; conidia borne singly, dimorphic, both lanceolate and cylindrical; ascocarp appendages mycelioid ……………………………………………*Leveillula*

1.' Conidiophores not emerging through stomata, not forming both lanceolate and cylindrical conidia; ascocarps with or without differentiated appendages……………………………..……..2

  2. Conidia obclavate, borne singly; appressoria unlobed to moderately lobed; ascocarps with two kinds of appendages: conspicuous equatorial appendages acicular, dorsal surfaces with digitate cells deliquescing to form gelatinous mass…………………………………………………………………………..*Phyllactinia*

  2.' Combination of features otherwise; conidia ovoid, barrel-shaped, ellipsoidal or cylindrical but not obclavate; appressoria variously absent, nipple-shaped, or lobed; ascocarp appendages mycelioid, uncinate, dichotomously branched or bi- or trifurcate but not acicular……..……………………………………..…………………3

3. Host is a member of the Poaceae; base of conidiophore foot cell inflated; forming ellipsoid conidia in chains………….....…………………………………………………..……*Blumeria*

3.' Host not a member of the Poaceae; conidiophore foot cell not inflated; conidia ranging from ovoid to cylindrical; conidia formed singly or in chains……………………………...…………4

  4. Appressoria nipple-shaped; both macroconidia and microconidia formed in chains and containing fibrosin bodies; ascocarp appendages bi- or trifurcate; on *Acer* spp. ………...…………………………………………...…………………………*Sawadaea*

  4.' Combination of features otherwise; appressoria various, conidia monomorphic; conidia with or without fibrosin bodies; conidia formed singly or in chains.……………………………..……………….…………………………………5

5. Appressoria lobed; conidia lacking fibrosin bodies; conidia formed singly; ascocarps with multiple asci and appendages that may be mycelioid, dichotomously branched, or uncinate………………………………………..……………..………………………*Erysiphe* emend.

(Former segregates of *Erysiphe* in modern sense)

Ascocarp appendages uncinate…………….……………….…………*Uncinula*

Ascocarp appendages both uncinate and subulate………………...*Uncinuliella*

Ascocarp appendages mycelioid……………………...*Erysiphe* sect. *Erysiphe*

Ascocarp appendages dichotomously branched………….……...*Microsphaera*

5.' Combination of features otherwise; conidia with or without fibrosin bodies; conidia formed in chains; appressoria absent, nipple-shaped or lobed; ascocarp appendages mycelioid or dichotomously branched …..……………………………………………………………………6

  6. Appressoria lobed; conidia lacking fibrosin bodies, formed in chains; [ascocarps with multiple asci and mycelioid appendages, ascospores formed after overwintering] ……………….……………………………………………………………*Neoerysiphe*

  6.' Combination of features otherwise; appressoria nipple-shaped or absent; conidia with or without fibrosin bodies; ascocarps with single or multiple asci; ascocarp appendages mycelioid or dichotomously branched; ascospores typically formed during the current growing season……………….…………………......…………7

7. Host genus is *Lycium*; appressoria nipple-shaped; conidia lacking fibrosin bodies, formed in chains; [ascocarps with multiple asci and dichotomously-branched appendages] …………………………………………………………………………………..…*Arthrocladiella*

7.' Combination of features otherwise; host genus is not *Lycium*; appressoria are nipple shaped; conidia with or without fibrosin bodies; ascocarps with single or multiple asci; ascocarp appendages mycelioid or dichotomously branched…………………..……..…………...8

8. Appressoria nipple-shaped; conidia lacking fibrosin bodies, formed in chains; ascocarps with multiple asci and mycelioid appendages; asci usually 2-spored ………………………………………………..……………………………*Golovinomyces*
8.' Appressoria nipple shaped; conidia with fibrosin bodies, formed in chains, asci with single asci and mycelioid or dichotomously-branched appendages; asci usually 8-spored.…………………………………………………………….…..………..*Podosphaera*
   (Former segregates of *Podosphaera* in modern sense)
   Ascocarp appendages dichotomously branched………….………..*Podosphaera*
   Ascocarp appendages mycelioid……………………………….……*Sphaerotheca*

Genus names applicable to known species of Erysiphales in the Pacific Northwest

Genus concepts reflect those presented in Braun et al. (2002). Summaries of diagnostic features are made for each. For detailed taxonomic information and full descriptions of genera, readers are referred to accounts of Zheng (1985), Braun (1987; 1995), Braun and Takamatsu (2000), Braun et al. (2002), and Takamatsu (2004) which further reference a large body of pertinent literature. Photographs illustrate features of species collected in the Pacific Northwest.

Arthrocladiella **Vassilkov**

Diagnostic features: Appressoria nipple-shaped. Conidia lacking fibrosin bodies, formed in chains. Ascocarp appendages dichotomously branched. Asci multiple. Figs. 1-4.

Species illustrated: Arthrocladiella mougeotii (Lév.) Vassilkov (Figs. 1-4).

Comments: Braun (1987) regards *Arthrocladiella* as monotypic. The only species, *A. mougeotii*, is known in the Pacific Northwest from a single location in Seattle where it occurs on *Lycium chinense* Mill. (Glawe, 2004a). The teleomorph has not yet been observed here; according to Bosewinkel (1980a) and Braun (1987) it can be rare. Features of the anamorph resemble those of *Golovinomyces* but this species appears confined to *Lycium*. The conidia also are rather unusual in their shape, having nearly parallel sides, with ends that are convex.

Blumeria **(DC.) Speer**

Diagnostic features: Conidiophore foot cell conspicuously inflated. Conidia lacking fibrosin bodies, formed in chains. Ascocarp appendages mycelioid. Asci multiple. Figs. 5-8.

Significant synonym: Erysiphe p.p.

Species illustrated: Blumeria graminis (DC.) Speer (Figs. 5-8).

Comments: *Blumeria* is monotypic and the only genus of Erysiphales recorded from Poaceae (Braun, 1987). The sole species, *B graminis*, formerly was designated *Erysiphe graminis* DC. Host-specific strains exist and are of major significance in efforts to develop powdery mildew-resistant cultivars of small grains (Agrios, 2004).

Erysiphe **R. Hedw. ex DC. (emend. Braun & Takamatsu 2000)**

Diagnostic features: Appressoria lobed. Conidia lacking fibrosin bodies, formed singly. Ascocarp appendages variously mycelioid, uncinate, or dichotomously branched. Asci multiple, 3- to 8-spored. Figs. 9- 22.

Significant synonyms:

Microsphaera Lév. for species with dichotomously branched ascocarp appendages (now *Erysiphe* sect. *Microsphaera*)

Uncinula Lév. for species with uncinate ascocarp appendages (now *Erysiphe* sect. *Uncinula*)
Uncinuliella R.Y. Zheng & G.Q. Chen for species with both uncinate and subulate ascocarp appendages (now *Erysiphe* sect. *Uncinula* p.p.)

Species illustrated: Erysiphe knautiae Duby (Figs. 9, 10); *Erysiphe aquilegiae* DC. (Figs. 11, 12); *Erysiphe azaleae* (U. Braun) U. Braun & S. Takam**.** (Figs. 13, 15); *Erysiphe penicillata* (Wallr.) Fr. (Fig. 14); *Erysiphe adunca* (Wallr.) Fr. (Figs. 16-19); *Erysiphe flexuosa* (Peck) U. Braun & S. Takam. (Figs. 20-22).

Comments: Rationale for including *Microsphaera*, *Uncinula*, and *Uncinuliella* in *Erysiphe* is discussed in Braun and Takamatsu (2000) and Braun et al. (2002). The ascocarp appendage features formerly used to differentiate genera are now regarded as species-level characters. Glawe and Dugan (2006) recently described appendage development in Pacific Northwest collections of *E. flexuosa*, formerly classified in *Uncinuliella*. If appressoria or conidiogenous structures are not seen, species of *Erysiphe* with mycelioid ascocarp appendages might be confused with species of *Golovinomyces* (but in that genus asci usually are 2-spored) and *Neoerysiphe* (but in that genus ascospores do not develop before overwintering).

Golovinomyces (U. Braun) V.P. Gelyuta

Diagnostic features: Appressoria nipple-shaped. Conidia lacking fibrosin bodies, formed in chains. Ascocarp appendages mycelioid. Asci multiple, usually 2-spored. Figs. 23-27.

Significant synonym: Erysiphe p.p., *Erysiphe* sect. *Golovinomyces*.

Species illustrated: Golovinomyces cynoglossi **(**Wallr.) V.P. Heluta (Fig. 23); *Golovinomyces cichoracearum* (DC.) V.P. Heluta (Figs. 24-27.

Comments: Species of *Golovinomyces* formerly were classified in *Erysiphe*. One of the most commonly used powdery mildew binomials in the older phytopathological literature, *Erysiphe cichoracearum* DC., refers to the fungus now known as *Golovinomyces cichoracearum* (DC.) V.P. Heluta. In the absence of appressoria or conidiogenous structures, species of this genus can be easily confused with species of *Erysiphe* (but in that genus asci are 3- to 8-spored) and *Neoerysiphe* (but ascospores in that genus are not formed before overwintering). The anamorph of *Arthrocladiella mougeotii* (Lév.) Vassilkov also exhibits the diagnostic features listed here for *Golovinomyces*. At present, the only known host for *A. mougeotii* is *Lycium* (Solanaceae). See also comments for *Arthrocladiella*.

Leveillula G. Arnaud

Diagnostic features: Conidia lacking fibrosin bodies, dimorphic (the two kinds of conidia either lanceolate or cylindrical), formed singly. Ascocarp appendages mycelioid. Asci multiple, usually 2-spored. Figs. 28-34.

Species illustrated: Leveillula taurica (Lév.) G. Arnaud (Figs. 28-34).

Comments: The only species known in the Pacific Northwest is *L. taurica*. Unknown in the region until the late 1980's (Forster, 1989), it now has been reported from *Allium cepa* L. (onion) (du Toit et al., 2004; Mohan and Molenaar, 2005), *Capsicum annuum* L. (pepper) (Cerkauskas and Buonassisi, 2003), *Cucumis sativus* L. (cucumber) and *Lycopersicon esculentum* P. Mill. **(**tomato) (Forster, 1989), *Gaillardia* × *grandiflora* (Glawe et al., 2006), *Solanum tuberosum* L. (potato) (Glawe et al., 2004), and the salt marsh plant *Triglochin maritima* L. (Glawe et al., 2005). With a known host range encompassing both dicots and monocots and more than 50 plant families (Braun, 1987), it seems likely that additional hosts will be found in the future. *Leveillula taurica* recently was found co-infecting potato with *Golovinomyces orontii* (Castagne) V.P. Heluta (Glawe et al., 2004). The teleomorph has been found only on *T. maritima* (Glawe et al., 2005) but it would not be surprising to find it on other hosts. The dimorphic conidia and conidiophores can be used to distinguish the anamorph from those of *Phyllactinia* species. See also the comments for *Phyllactinia*.

Neoerysiphe **U. Braun**

Diagnostic features: Appressoria lobed. Conidia lacking fibrosin bodies, formed in chains. Ascocarp appendages mycelioid. Asci multiple, usually only developed after overwintering (i.e., asci immature in the current season). Figs. 35-38.

Significant synonym: Erysiphe p.p., *Erysiphe* sect. *Galeopsidis*.

Species illustrated: Neoerysiphe galeopsidis (DC.) U. Braun (Figs. 35-38).

Comments: *Neoerysiphe* is differentiated from *Erysiphe* by the chains of conidia and from *Golovinomyces* by the lobed appressoria. In the absence of these features it can be confused with either genus. However it is distinguished from those genera by production of ascospores after overwintering.

Phyllactinia **Lév.**

Diagnostic features: Appressoria unlobed to moderately lobed. Conidia lacking fibrosin bodies, formed singly, obclavate. Ascocarp appendages acicular; dorsal side of ascocarp forming penicillate cells. Asci multiple, usually 2-spored. Figs. 39-46.

Species illustrated: Phyllactinia guttata (Wallr.) Lév. (Figs. 39-46).

Comments: Collections generally include very sparse vegetative mycelium and the anamorph be difficult to find, especially by late summer. The distinctive appendages function in prying the maturing ascocarp from the leaf on which it was formed, while the penicillate cells form a gelatinous mass that attaches the ascocarp to a new substrate where it overwinters (Webster, 1979). If only the anamorph is present, the obclavate conidia could possibly be confused with the lanceolate conidia formed by species of *Leveillula*. Collections of *Leveillula taurica* (Lév.) G. Arnaud seen are distinguished from *Phyllactinia* by forming dimorphic conidia (lanceolate and cylindrical) and conidiophores from internal mycelia that emerge through host stomata. *Phyllactinia* species occur primarily (but not exclusively) on woody hosts with deciduous leaves. See also the comments for *Leveillula*.

Podosphaera **Kunze emend. Braun & Takamatsu (2000)**

Diagnostic features: Appressoria nipple-shaped. Conidia containing fibrosin bodies, formed in chains. Ascocarp appendages mycelioid or dichotomously branched. Ascus single, usually (6-)8-spored. Figs. 47-58.

Significant synonym: Sphaerotheca Lév.

Species illustrated: Podosphaera clandestina (Wallr.) Lév. (Figs. 47-50); *Podosphaera aphanis* (Wallr.) U. Braun & S. Takam. (Figs. 51, 53); *Podosphaera fusca* (Fr.) U. Braun & Shishkoff (2000) (Figs. 52, 54-58).

Comments: In the older literature *Podosphaera* refers to species with dichotomously branched ascocarp appendages, and *Sphaerotheca* to species with mycelioid appendages. If fibrosin bodies are not observed or are incorrectly interpreted it would be possible to confuse species of *Podosphaera* and species of *Golovinomyces* and possibly *Arthrocladiella*. Unlike those genera, chasmothecia of *Podosphaera* contain a single ascus.

Sawadaea Miyabe

Diagnostic features: Appressoria nipple-shaped. Conidia containing fibrosin bodies; dimorphic, with both macroconidia and microconidia. Ascocarp appendages dichotomously or trichotomously branched. Asci multiple. Figs. 59-66.

Species illustrated: Sawadaea bicornis (Wallr:Fr.) Homma (figs. 59-66).

Comments: The species known from the Pacific Northwest is *S. bicornis* (Nischwitz and Newcombe, 2003), reported on *Acer platanoides* L. The anamorph is distinctive in producing microconidia that resemble the macroconidia except for the much smaller size. Ascocarp appendages are also distinctive, with rather short stalks, dichotomous or trichotomous branching and recurved apices. Superficial examination of the anamorph might result in confusion with an anamorphic *Podosphaera* because of the fibrosin bodies common to conidia of both. However, the dimorphic conidia readily distinguish *Sawadaea* from other anamorphic Erysiphales. The dichotomously branched ascocarp appendages could cause confusion with *Erysiphe* species of section *Microsphaera*, but the fibrosin bodies in conidia and nipple-shaped appressoria would be useful in distinguishing *Sawadaea*.

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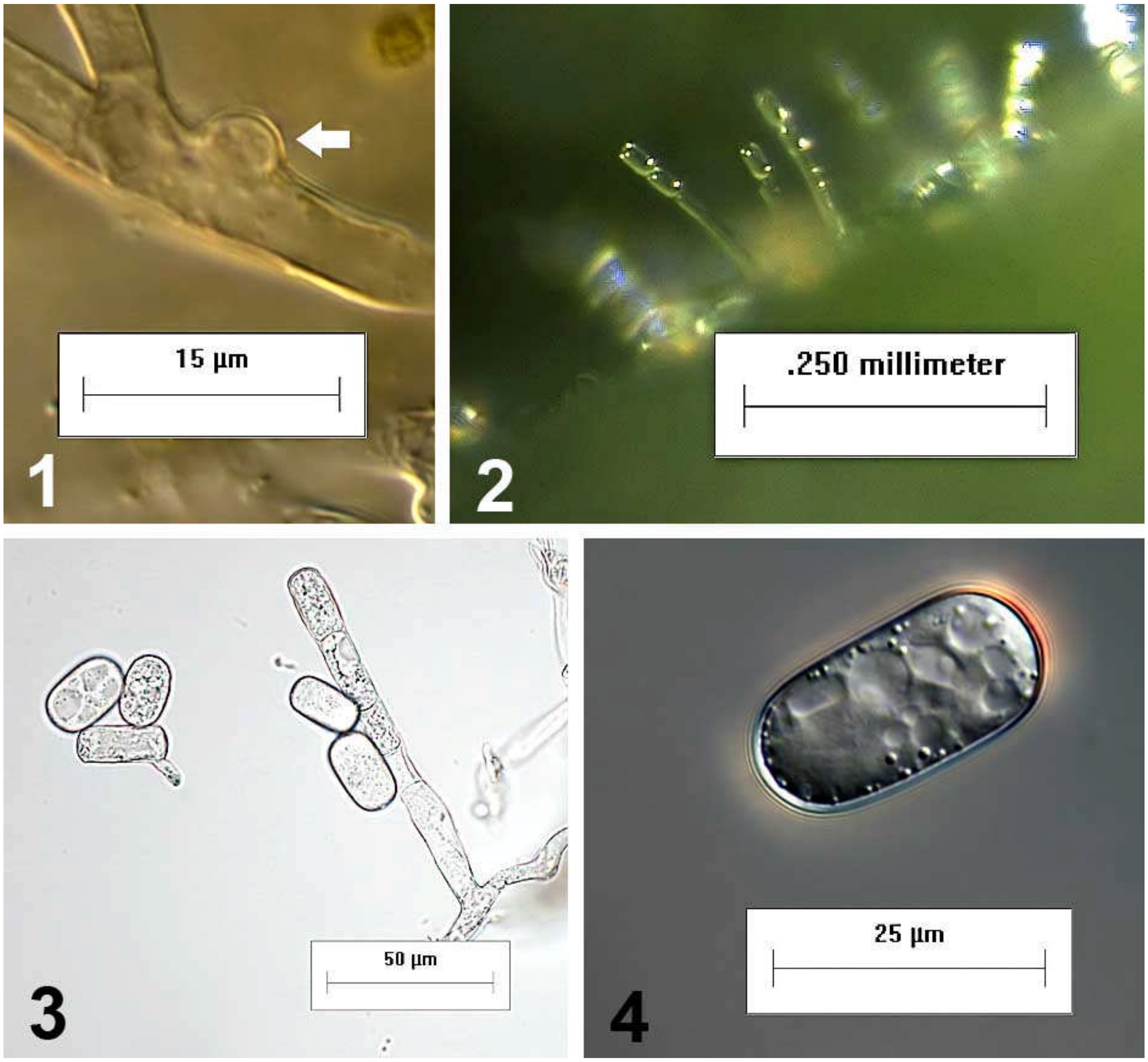
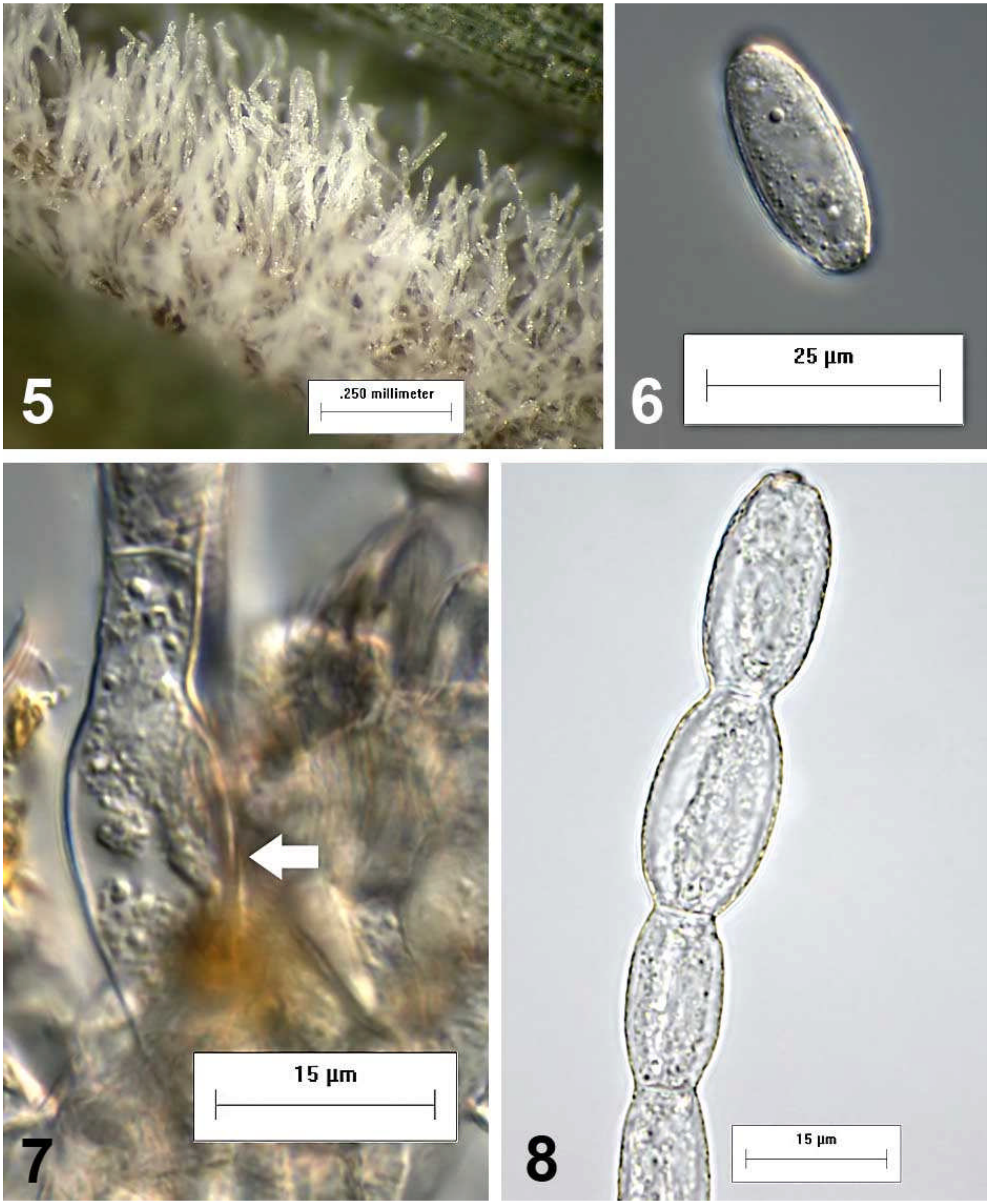
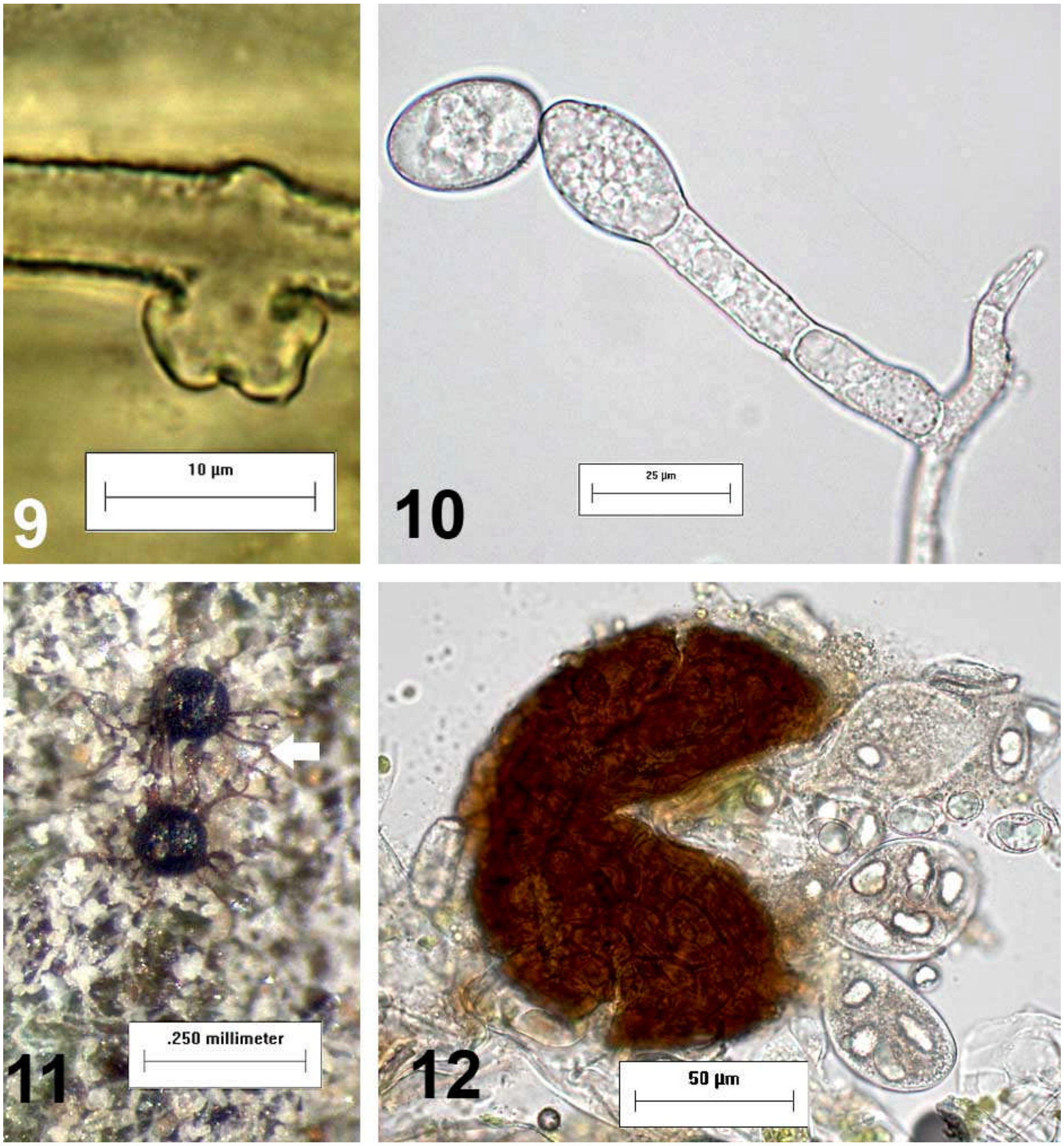


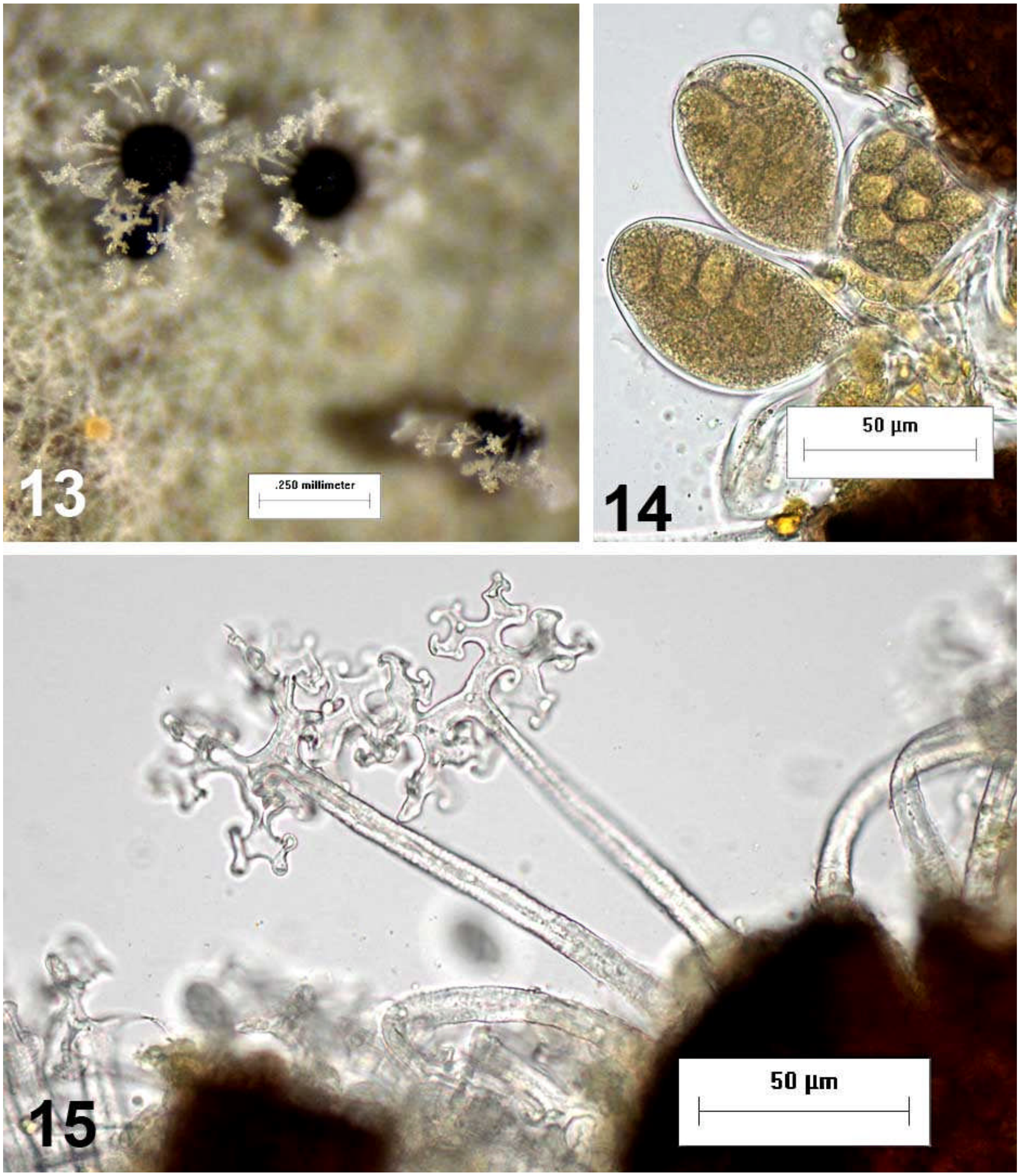
Figs. 1-4. Diagnostic features of *Arthrocladiella*, illustrated with *A. mougeotii*. 1. Appressorium (arrow). Scale bar = 15 µm. 2. Conidiophores with chains of conidia. Scale bar = 0.25 mm. 3. Conidiophore with chain of developing conidia and several nearby dehisced conidia. Scale bar = 50 µm. 4. Conidium. Scale bar = 25 µm.



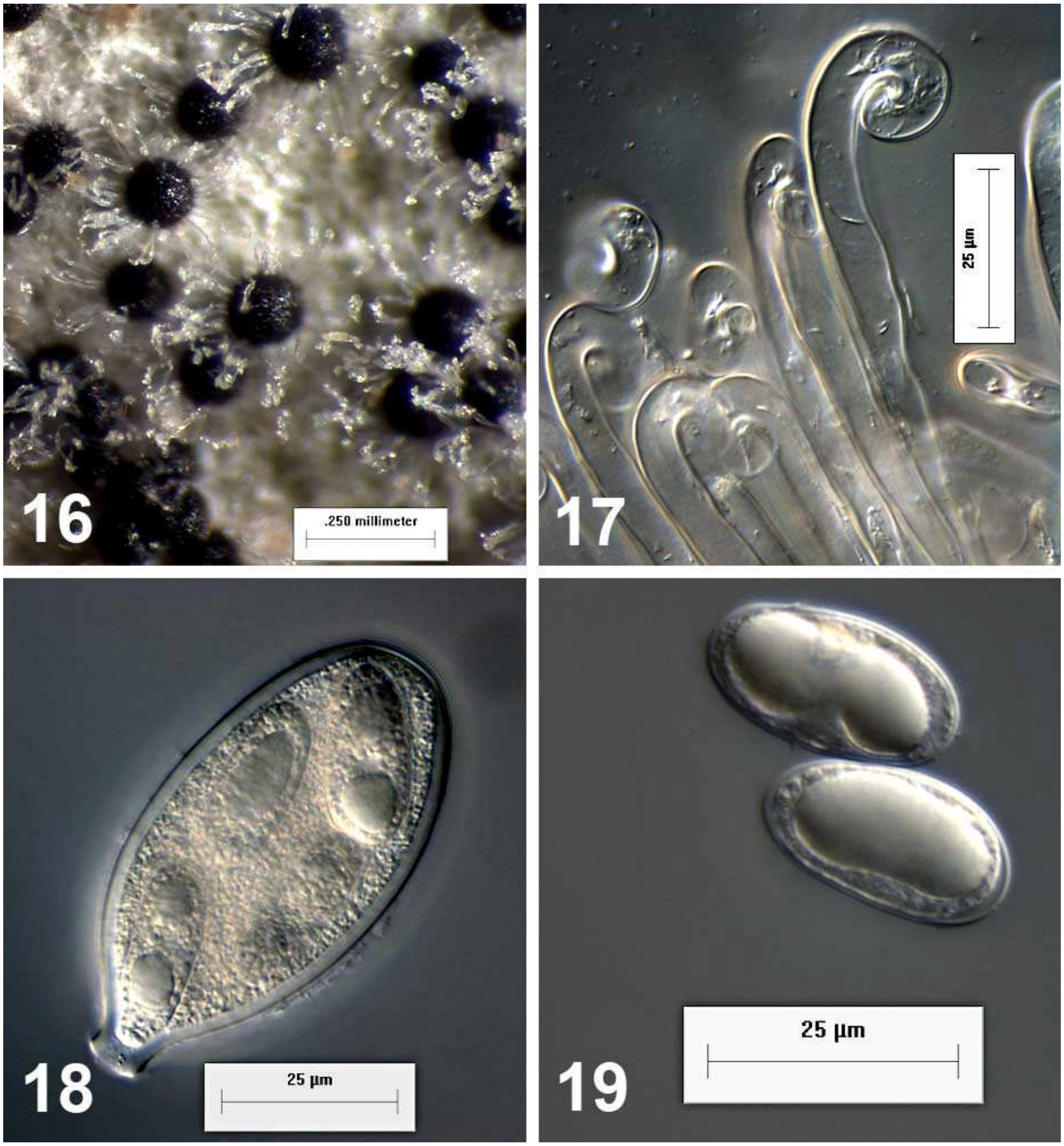
Figs. 5-8. Diagnostic features of *Blumeria*, illustrated with *B. graminis.* 5. Palisades of conidiophores with chains of conidia. Scale bar = 0.25 mm. 6. Ellipsoidal conidium. Scale bar = 25 µm. 7. Foot cell of conidiophore with inflated base (arrow) and narrowed distal region. Scale bar = 15 µm. 8. Chain of conidia adhering to conidiophore. Scale bar = 15 µm.



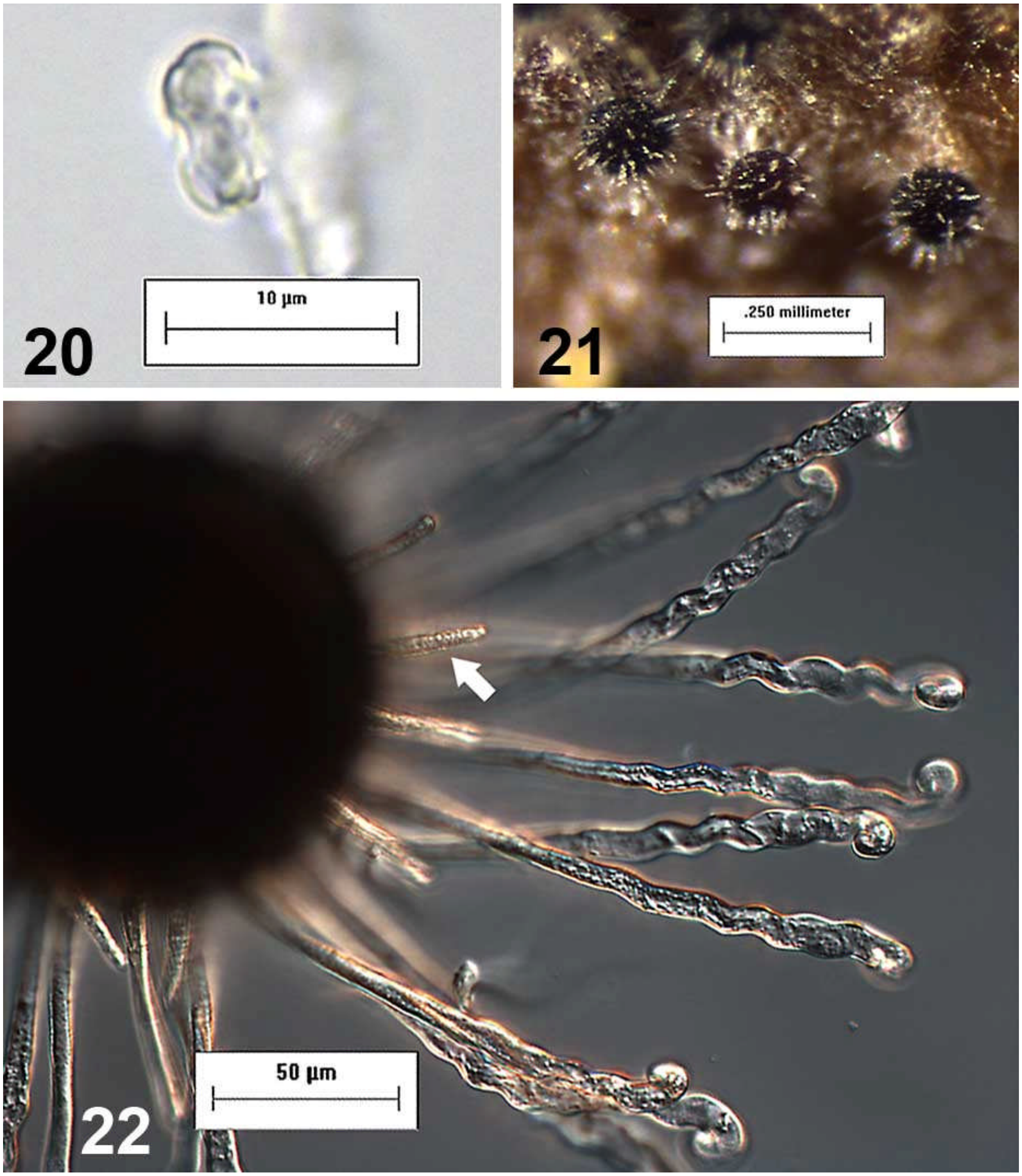
Figs. 9-12. Diagnostic features of *Erysiphe* (section *Erysiphe*). 9, 10, *E. knautiae*. 11, 12. *E. aquilegiae*. 9. Lobed appressorium. Scale bar = 10 µm. 10. Conidiophore with single conidium and nearby dehisced conidium. Scale bar = 25 µm. 11. Ascocarps (chasmothecia) with melanized, myceliod appendages (arrow). Scale bar = 0.25 mm. 12. Ascocarp (chasmothecium) crushed beneath microscope slide cover slip to expel group of asci. Scale bar = 50 µm.



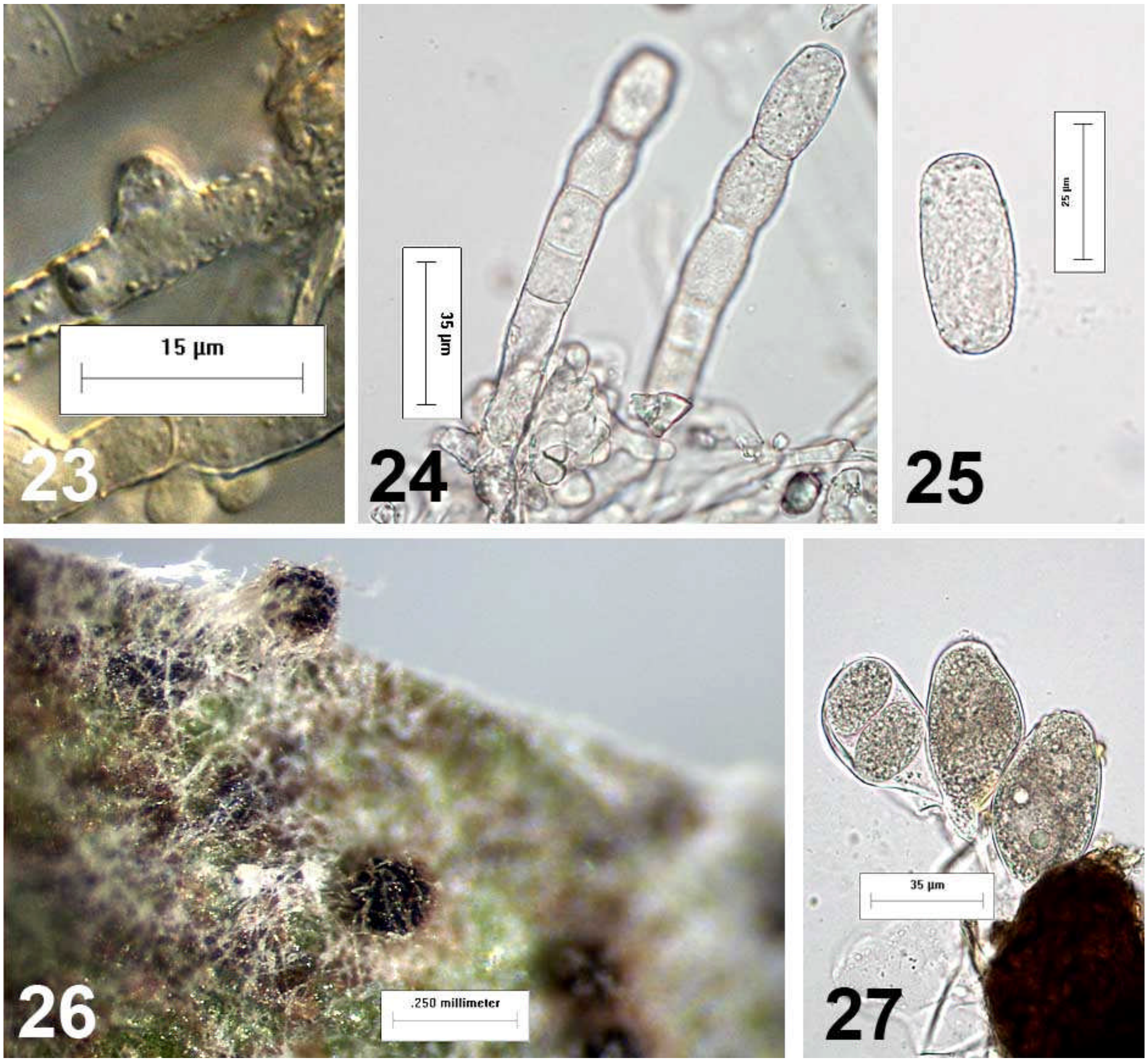
Figs. 13-15. Diagnostic features of *Erysiphe* (section *Microsphaera*). 13, 15. *E. azaleae*. 14. *E. penicillata*. 13. Three ascocarps (chasmothecia), one on lower right has detached from substrate. Note equatorial band of appendages. Scale bar = 0.25 mm.14. Group of asci emerging from ascocarp crushed beneath a microscope slide cover slip. Scale bar = 50 µm. 15. Ascocarp appendages displaying dichotomously branched apices. Scale bar = 50 µm.



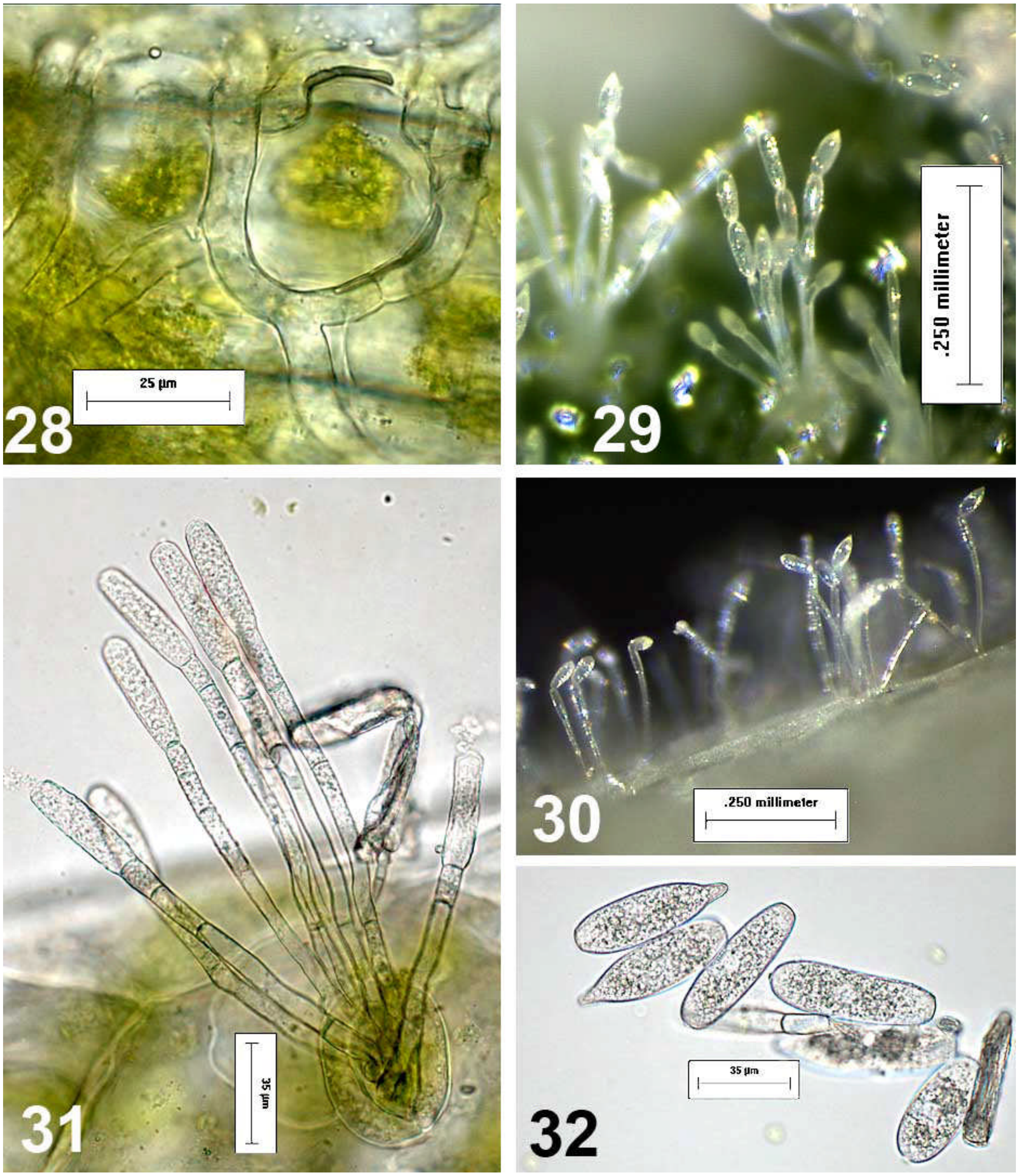
Figs. 16-19. Diagnostic features of *Erysiphe* (section *Uncinula*) illustrated with *Erysiphe adunca*. 16. Ascocarps (chasmothecia) with characteristic appendages. Scale bar = 0.25 mm. 17. Uncinate (recurved) apices of appendages. Scale bar = 25 µm. 18. Clavate, short-stipitate ascus containing ascospores. Scale bar = 25 µm. 19. Ascospores. Scale bar = 25 µm.



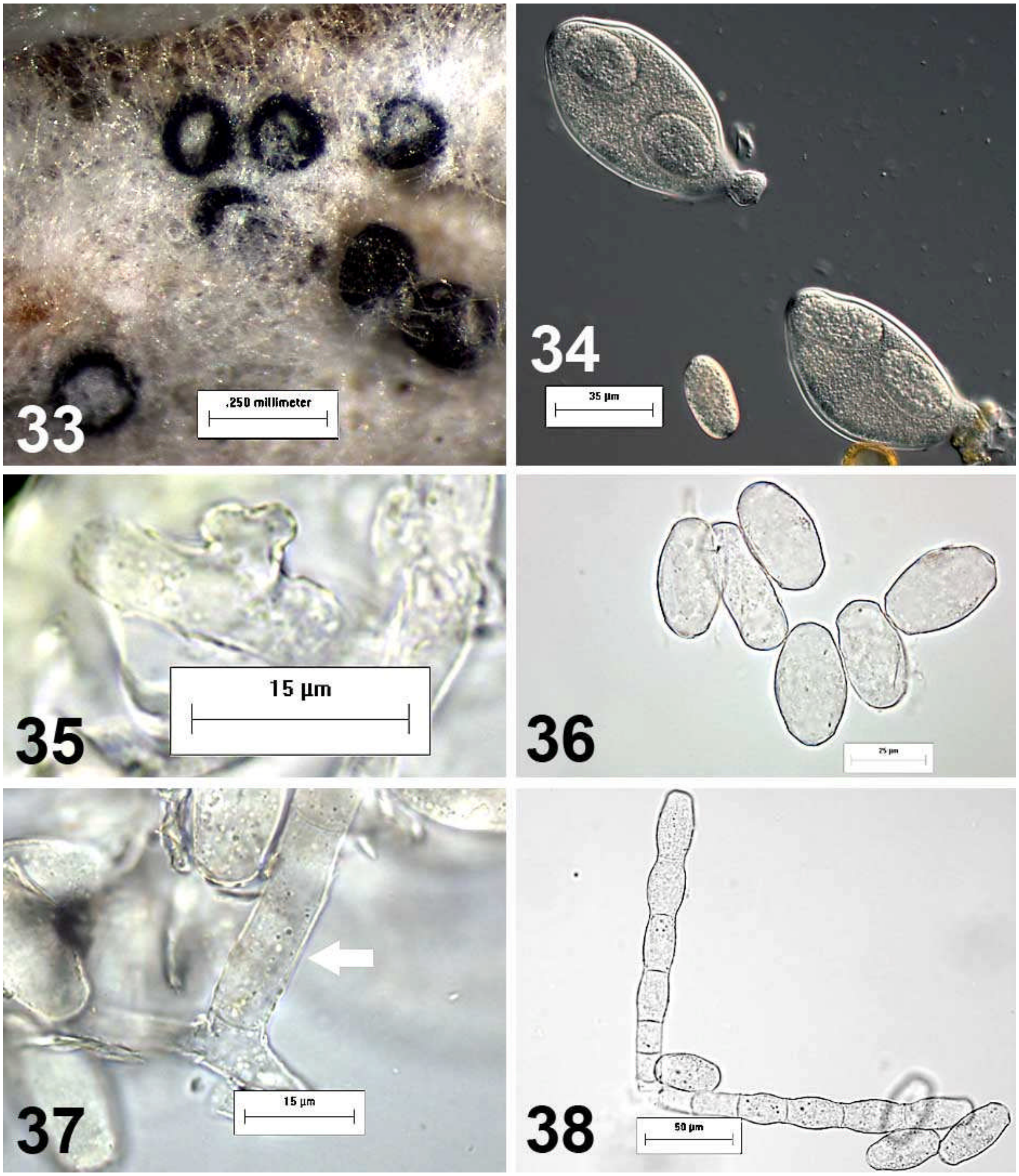
Figs. 20-22. Diagnostic features of *Erysiphe* (obsolete *Uncinuliella*, section *Uncinula*) illustrated with *E. flexuosa*. 20. Lobed appressorium. Scale bar = 10 µm. 21. Immature ascocarps (chasmothecia) displaying spike-shaped, subulate appendages. Scale bar = 0.25 mm. 22. Mature ascocarp displaying long uncinate appendages and shorter subulate appendages (arrow). Scale bar = 50 µm.



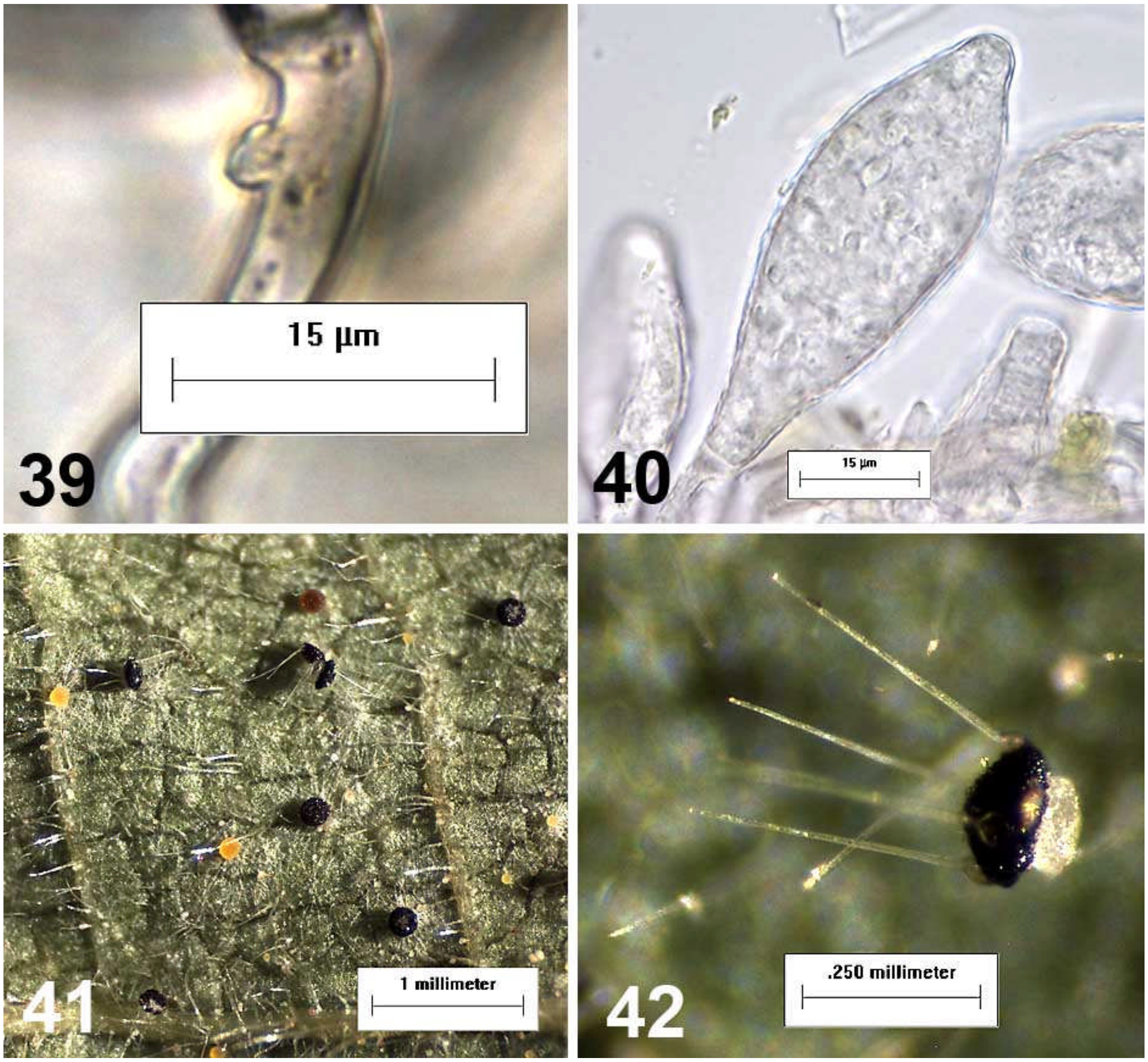
Figs. 23-27. Diagnostic features of *Golovinomyces*. 23. *G. cynoglossi*. 24-27. *G. cichoracearum*. 23. Nipple-shaped appressorium. Scale bar = 15 µm. 24. Conidiophores with chains of developing conidia. Scale bar = 35 µm. 25. Conidium. Scale bar = 25 µm. 26. Ascocarps (chasmothecia) displaying mycelioid appendages. Scale bar = 0.25 mm. 27. Three asci extruded from crushed ascocarp. Scale bar = 35 µm.



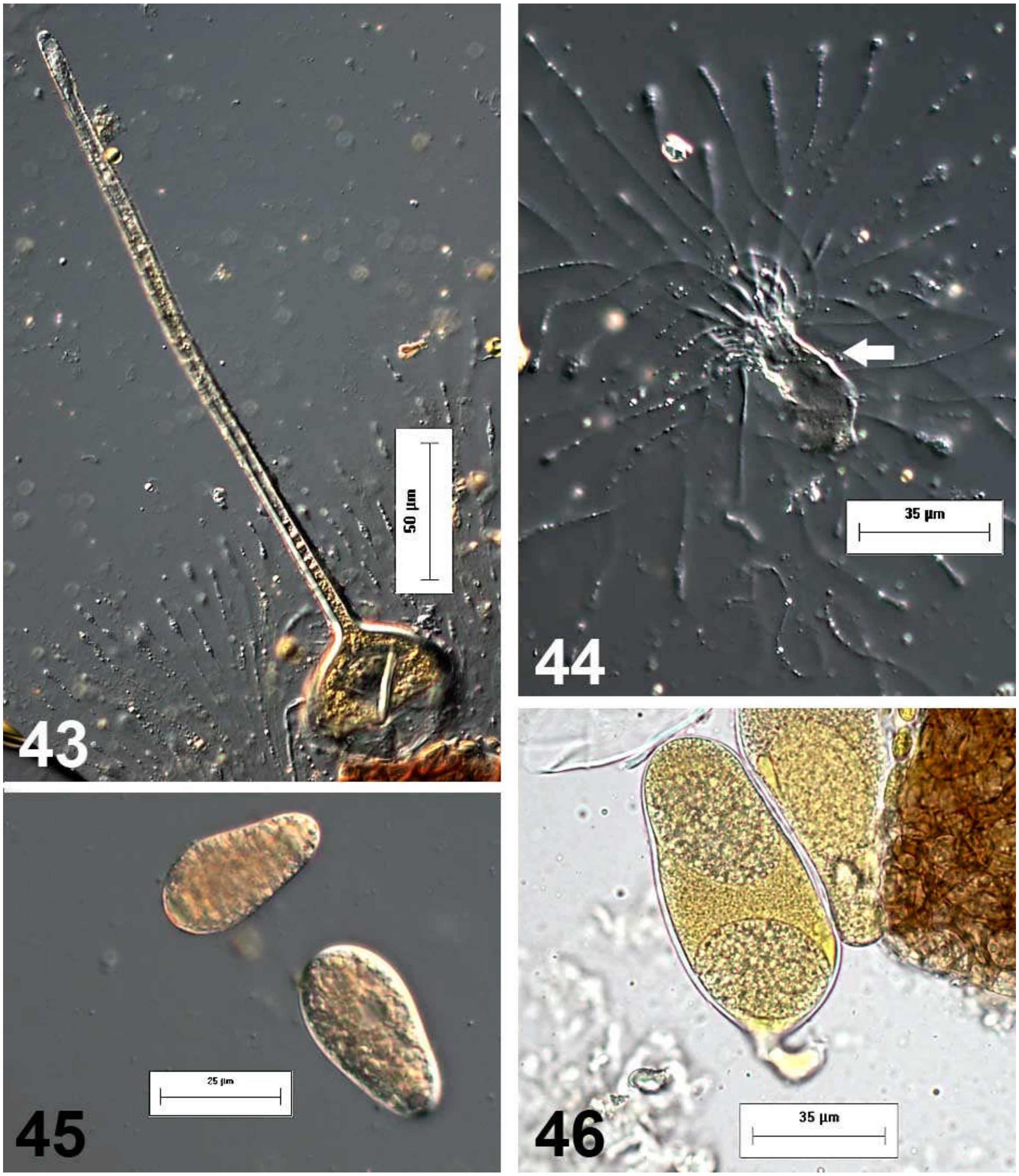
Figs. 28-32. Diagnostic features of *Leveillula*, illustrated with *L. taurica*. 28. Hyphae of internal mycelium encircling host mesophyll cells. Scale bar = 25 µm. 29. Conidia adhering in false chains. Scale bar = 0.25 µm. 30. Conidiophores producing single conidia. Scale bar = 0.25 mm. 31. Group of conidiophores emerging from host stoma, bearing single developing conidia. Scale bar = 35 µm. 32. Dimorphic conidia typical of *Leveillula*, some lanceolate (with narrowed apex), others cylindrical (lacking narrowed apex). Scale bar = 35 µm.



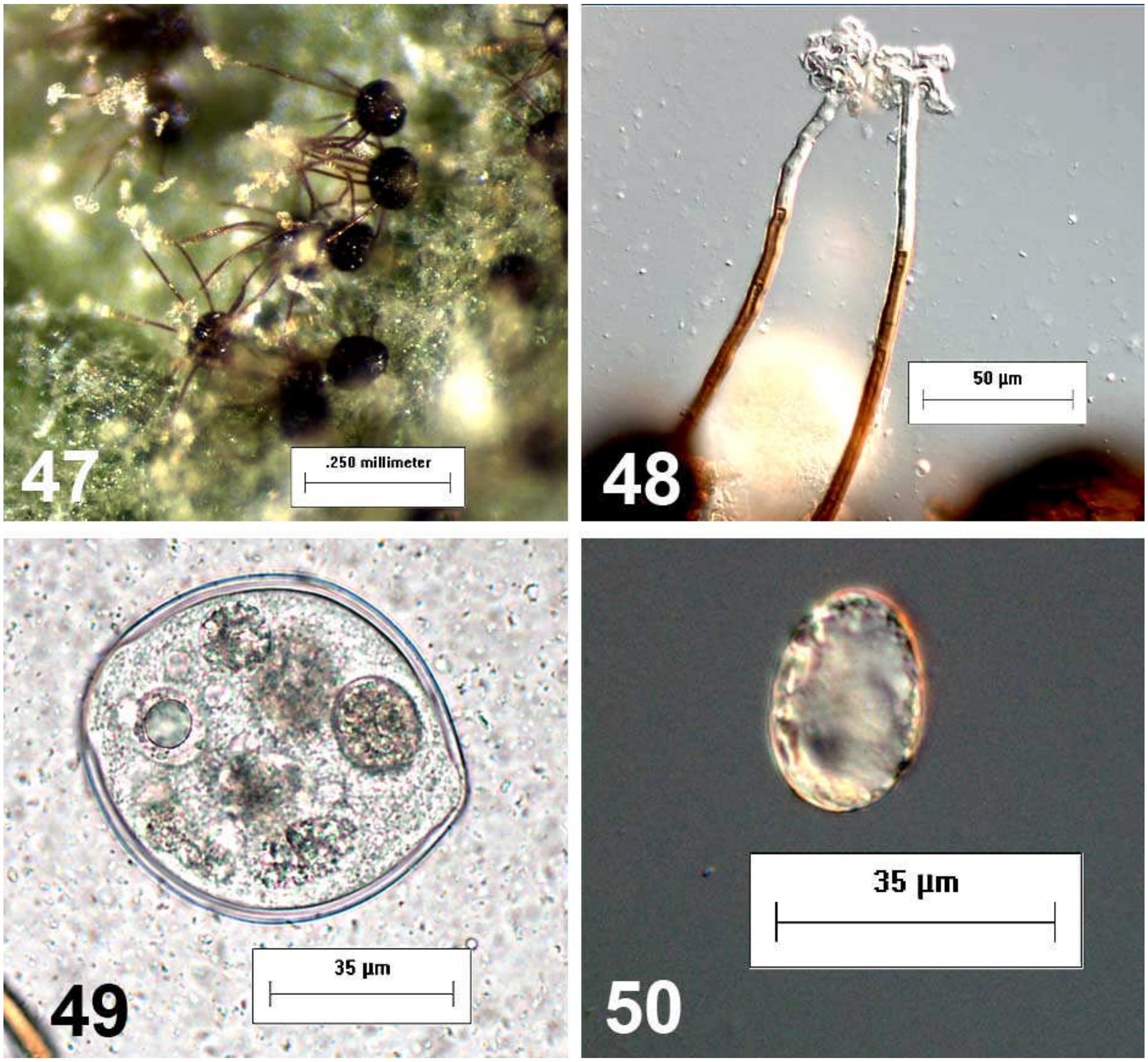
Figs. 33-38, Diagnostic features of *Leveillula* and *Neoerysiphe*. 33, 34. *L. taurica*. 33. Ascocarps (chasmothecia) and dense external mycelium. Scale bar = 0.25 mm. 34. Asci, each containing two ascospores; single ascospore in lower left. Scale bar = 35 µm. 35-38. *N. galeopsidis*. 35. Lobed appressorium. Scale bar = 15 µm. 36. Conidia. Scale bar = 25 µm. 37. Foot cell (arrow) of conidiophore. Scale bar = 15 µm. 38. Portions of two conidiophores displaying chains of developing conidia. Scale bar = 50 µm.



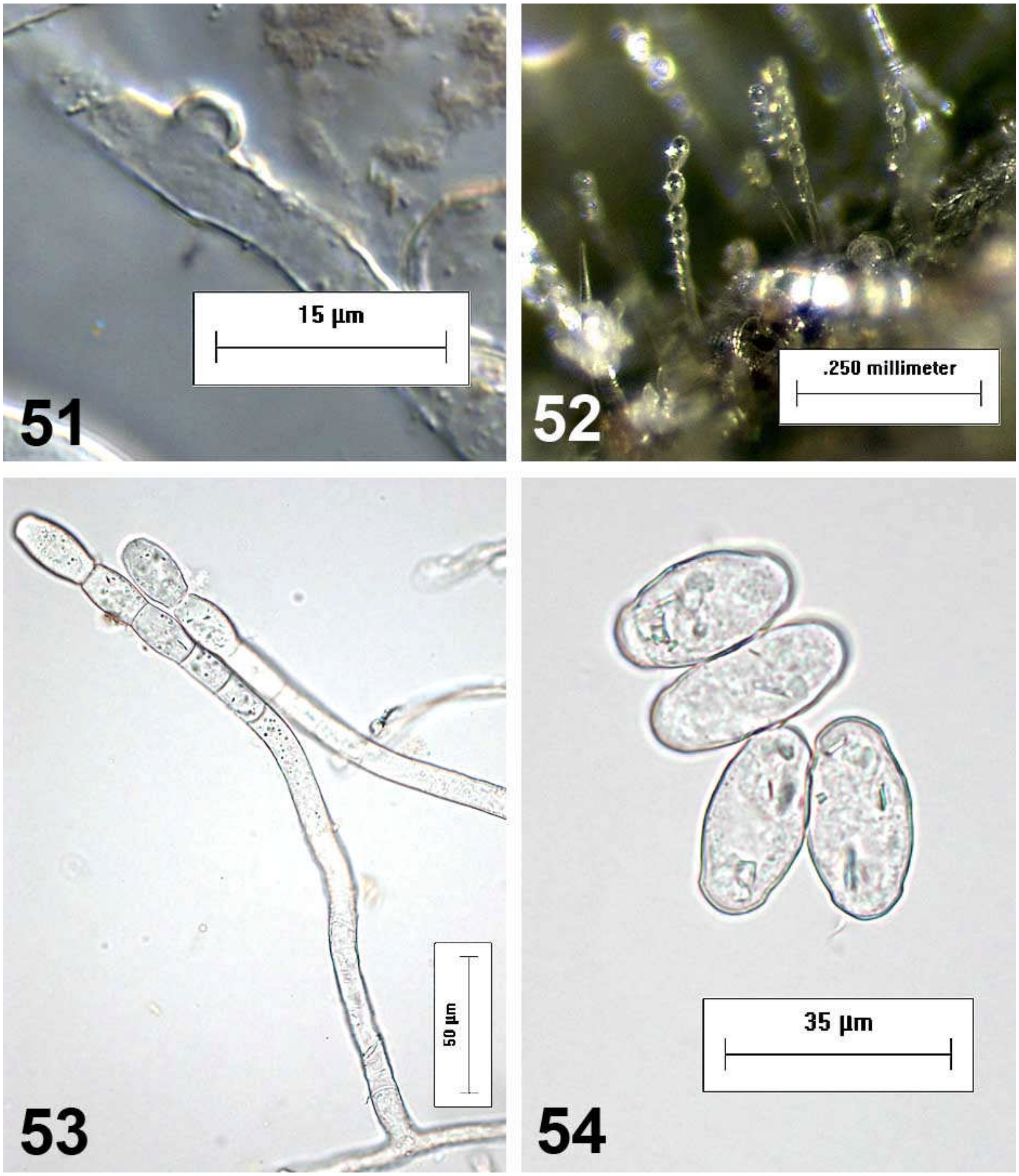
Figs. 39-42. Diagnostic features of *Phyllactinia*, illustrated with *P. guttata*. 39. Slightly lobed appressorium. Scale bar = 15 µm. 40. Obclavate conidium, formed singly on conidiophore. Scale bar = 15 µm. 41. Ascocarps (chasmothecia) on leaf surface. Amber-colored ones are immature, mature ones are nearly black. Note that conspicuous vegetative mycelium is lacking. Scale bar = 1 mm. 42. Dehisced ascocarp (chasmothecium), displaying acicular appendages. Note convex shape of ventral side of ascocarp. Gelatinous material on dorsal side is formed by penicillate cells. Scale bar = 0.25 mm.



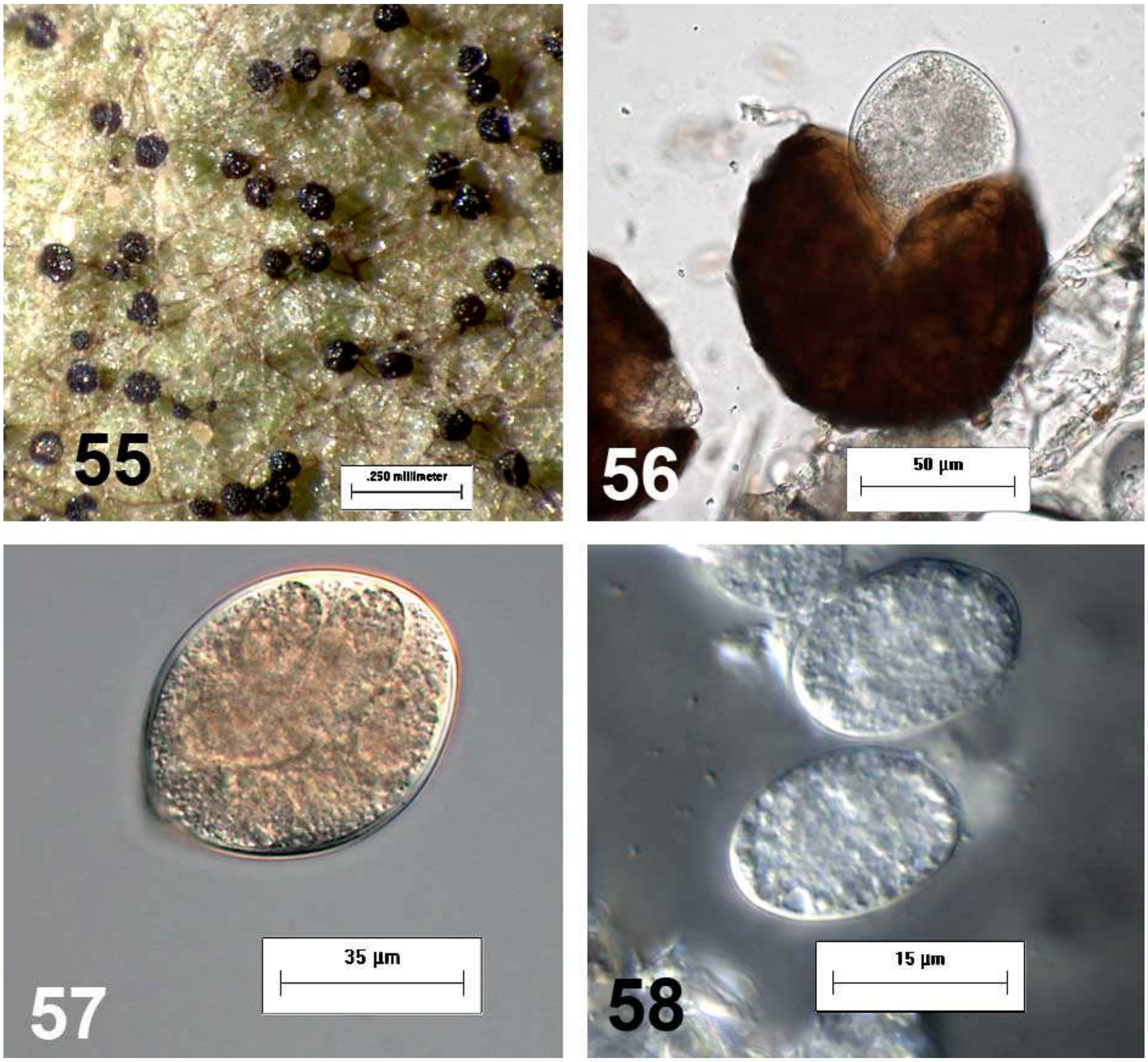
Figs. 43-46. Diagnostic features of *Phyllactinia*, illustrated with *P. guttata*. 43. Acicular appendage. Scale bar = 50 µm. 44. Penicillate cell. Numerous similar cells form the gelatinous material on the dorsal side of the ascocarp in Fig. 42. Arrow designates main body of cell; digitate processes radiate from apical portion of cell. Scale bar = 35 µm. 45. Ascospores. Scale bar = 25 µm. 46. Short-stipitate ascus containing two ascospores. Scale bar = 35 µm.



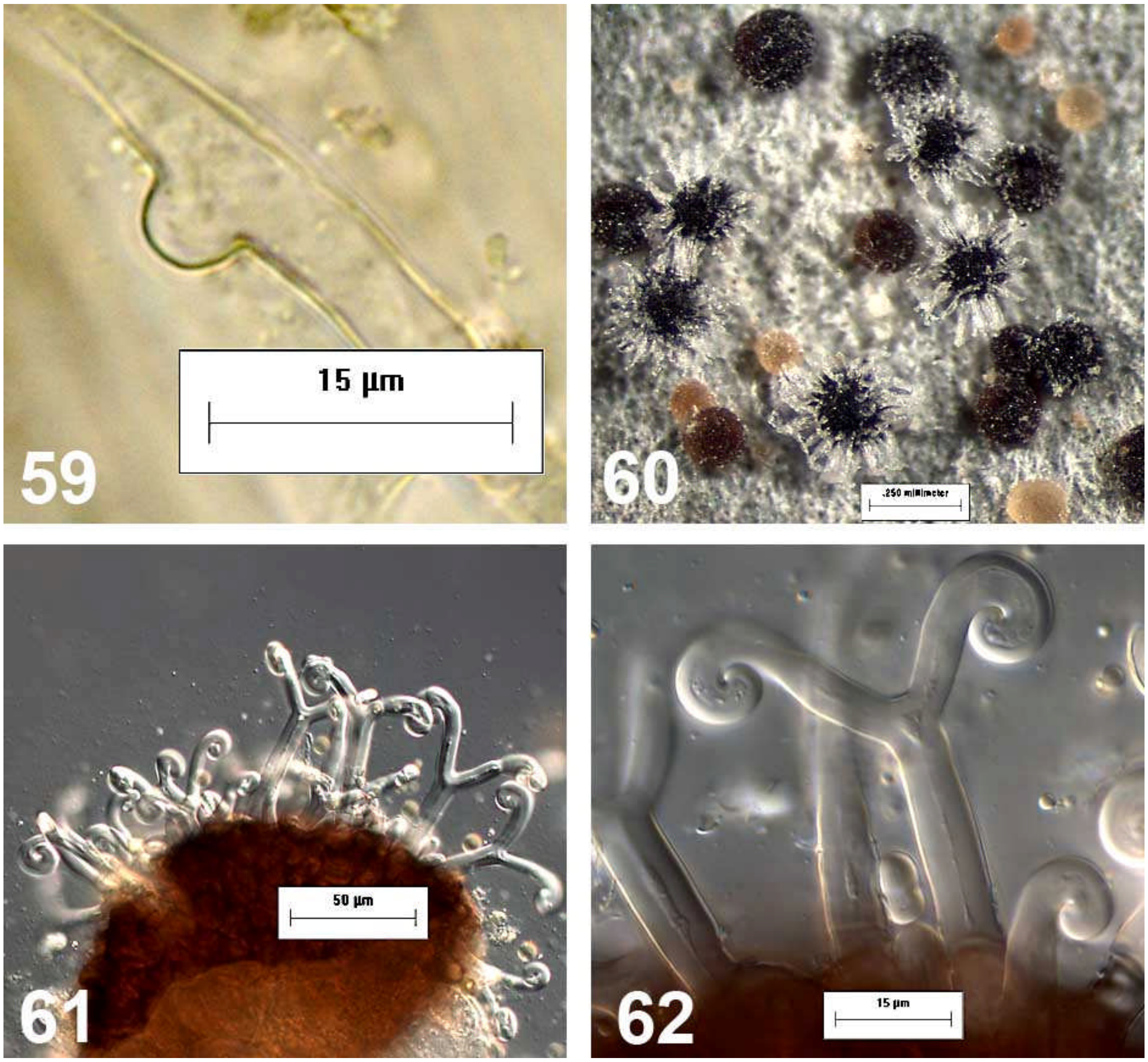
Figs. 47-50. Diagnostic features of *Podosphaera*, illustrated with *P. clandestina*. 47. Group of ascocarps (chasmothecia) with appendages. Scale bar = 0.25 mm. 48. Dichotomously branched apices of appendages. Scale bar = 50 µm. 49. Globose ascus containing ascospores. Scale bar = 35 µm. 50. Ascospore. Scale bar = 35 µm.



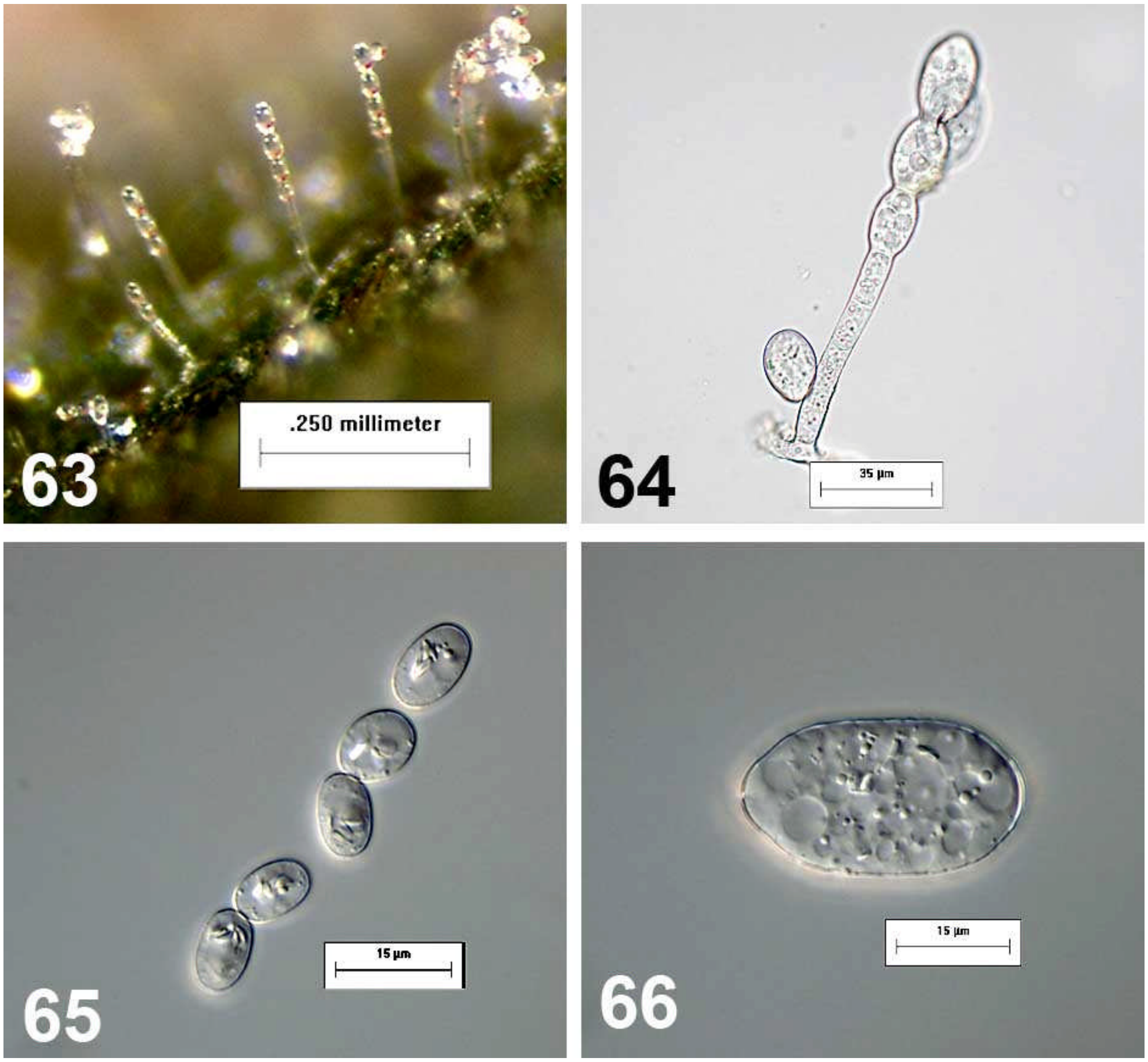
Figs. 51-54. Diagnostic features of *Podosphaera* (obsolete *Sphaerotheca*). 51, 53. *P. aphanis*. 52, 54. *P. fusca*. 51. Nipple-shaped appressorium. Scale bar = 15 µm. 52. Conidiophores bearing chains of developing conidia. Scale bar = 0.25 mm. 53. Conidiophore with chain of developing conidia. Scale bar = 50 µm. 54. Conidia containing fibrosin bodies. Scale bar = 35 µm.



Figs. 55-58. Diagnostic features of *Podosphaera* (obsolete *Sphaerotheca*), illustrated with *P. fusca*. 55. Group of ascocarps (chasmothecia) with mycelioid appendages. Scale bar = 0.25 mm. 56. Ascocarp crushed beneath microscope slide coverslip to release the single ascus. Scale bar = 50 µm. 57. Ascus containing ascospores. Scale bar = 35 µm. 58. Ascospores. Scale bar = 15 µm.



Figs. 59-62. Diagnostic features of *Sawadaea*, illustrated with *S. bicornis*. 59. Nipple-shaped appressorium. 60. Ascocarps (chasmothecia) exhibiting varying degrees of maturity; as they develop they change from amber-colored to black. Scale bar = 0.25 mm. 61. Ascocarp displaying characteristic birfurcating appendages. Scale bar = 50 µm. 62. Close up view of appendage apex showing recurved ends of bifurcations. Scale bar = 15 µm.



Figs. 63-66. Diagnostic features of *Sawadaea*, illustrated with *S. bicornis*. 63. Conidiophores with chains of developing conidia. Scale bar = 0.25 mm. 64. Conidiophore with chain of three developing conidia. Scale bar = 35 µm. 65. Microconidia containing fibrosin bodies. Scale bar = 15 µm. 66. Macroconidium; note rod-like fibrosin bodies interspersed among vacuoles. Scale bar = 15 µm.