

---

## Reinstatement of *Coleonaema* for *Coleophoma oleae* and notes on *Coleophoma*

---

Junxin Duan<sup>1,2</sup>, Xinzhong Liu<sup>1</sup> and Wenping Wu<sup>2\*</sup>

<sup>1</sup>Institute of Microbiology, The Chinese Academy of Sciences, Beijing 100081, PR China

<sup>2</sup>Novozymes China, 14 Xin Xi Lu, Shangdi Zone, Haidian District, Beijing 100085, PR China

Duan, J.X., Wu, W.P. and Liu, X.Z. (2007). Reinstatement of *Coleonaema* for *Coleophoma oleae* and notes on *Coleophoma*. *Fungal Diversity* 26: 187-204.

The development of conidiomata and paraphyses in currently accepted species of *Coleophoma* is of two types. In both, initials are formed by aggregation of epidermal mycelium and then cells in the upper layer grow upward and become septate. Subsequently, development differs. In *C. crateriformis* (type species), *C. empetri*, *C. cylindrospora*, *C. aesculi*, *C. fusiformis* and *C. prunicola* sp. nov., some hyaline to very pale brown, upwardly growing hyphae with septa only at the base develop from the upper layer of the conidiomatal initials. The apical cells of these hyphae are hyaline, elongated, swollen and with free apices. They develop into paraphyses which persist for a long time and can be seen even in the mature conidiomata. In the second group, which only contains *C. oleae* and two unnamed collections, the upwardly growing hyphae are pale to dark brown, septate and branched, and anastomose at the apices. They collapse before conidiomata mature, so no paraphyses develop. Based on such differences *Coleophoma oleae* is reassigned to *Coleonaema*. *Coleophoma prunicola* sp. nov. is described and microconidiogenesis is first reported in this genus.

**Key words:** *Coleophoma prunicola* sp. nov., conidiomatal development, paraphyses.

### Introduction

*Coleophoma* Höhn. was redescribed by Nag Raj (1978) and Sutton (1980) and recently a brief review of the 22 published names in this genus was given by Wu *et al.* (1996). Only six species were accepted. During a study of endophytes and epiphytes from leaves of *Prunus lusitanica* L., several collections of *Coleophoma* were made around Royal Holloway, University of London, and two of these collections were identified as species similar to *C. oleae* (DC.) Petr. & Syd., but with minor differences. This fungus was also recovered as a leaf endophyte from the same plant. Studies on development of conidiomata and paraphyses show that the new collections are not *C. oleae* and

---

\*Corresponding author: W.P. Wu; e-mail: wuwp@novozymes.com

furthermore that *C. oleae* does not belong in *Coleophoma*. The placement of this species in *Coleonaema* Höhn. is reinstated.

## Materials and methods

*Coleophoma* species studied include *C. cylindrospora* (Desm.) Höhn., *C. empetri* (Rostr.) Petr., *C. oleae*, *C. fusiformis* W.P. Wu, B. Sutton & Gange and one unnamed species on leaves of *Prunus lusitanica*. Most specimens used for this study are from herb. IMI. The remainder were collected by the authors.

For developmental studies of conidiomata, infected leaves with fruitbodies were examined under the dissecting microscope and some portions with conidiomata in different stages of maturation were selected for sectioning. These were softened in 50% gum arabic solution for 24 hours before sectioning with a microtome with freezing attachment. The sectioned material was mounted in lactofuchsin or cotton blue and examined with compound microscope.

## Results and Discussion

### *Development of conidiomata, paraphyses and conidiophores in Coleophoma sensu stricto*

Bauke (1876) differentiated two types of pycnidium primordium formation and these were independently named meristogenous (formed from the division of one or more cells of a single hypha) and symphogenous (formed from the intermingling of several hyphal branches) by de Bary (1887). Later, a third type (formed from the repeated division and growth of a single conidium) was recognised by von Tavel (1886). However, later studies showed different types of primordium formation can occur in a single species (Mercer, 1913; Kempton, 1919; Calvert and Pound, 1949; Boerema, 1964; Boerema and van Kesteren, 1964; Sutton, 1973; Punithalingam, 1974, 1979; Maiello and Peterson, 1976; Maiello, 1978; Muthumary and Vanaja, 1986; Roux and van Warmelo, 1990; Muthumary *et al.*, 1993). In species of *Coleophoma* the pycnidial initial is formed from division of cells of epidermal hyphae and this is more likely to be meristogenous (Figs 1-5). The shape of the initial is flattened and composed of many dark brown, thick-walled cells in several layers (textura angularis). Continued hyphal growth breaks down the epidermis and externally gives the upper part of the epidermal a slightly swollen appearance.

Three different types of cavity formation within developing pycnidial conidiomata have been recognised: 1) schizogenous (by rupture of the inner

cells of the primordium); 2) lysigenous (by breaking down of the inner cells of the primordium); and 3) upward and inward growth of the conidiomatal wall (de Bary, 1887; Baccarini, 1890; Dodge, 1923, 1930; Archer, 1926; Sutton, 1973, 1980; Punithalingam, 1974, 1979; Maiello and Peterson, 1976; Maiello, 1978, 1988; Muthumary and Vanaja, 1986; Roux and van Warmelo, 1990; Muthumary *et al.*, 1993). However, different types have been found in the same fungus (Baccarini, 1890; Dodge, 1923; Harris, 1935; Punithalingam, 1966; Sutton, 1973). In species of *Coleophoma*, cavity formation can not be attributed to any one of these three types, but shows some similarities with the latter two. The third type was described for *Chaetomella raphigera* by Dodge (1930), where the slender upwardly growing hyphae develop from the upper layer of the basal stroma and form a pycnidial primordium. Further differentiation of these hyphae inside and outside produces the wall and cavity. The slender hyaline hyphae in the cavity develop into conidiophores. In this case neither lysis nor rupture of cells inside the conidiomatal initials is involved.

In different species of *Coleophoma*, cells in the upper layer of the stroma also grow upward and inward. However, these are hyaline, septate only at the base and remain sterile (or basal cells become fertile) and are interpreted as paraphyses. When they grow upward they mechanically force both the epidermis upward and the basal stroma downward to produce the conidiomatal cavity. In some cases the cells in the margin of the basal stroma also grow upward and inward and these form the lateral and upper walls of the conidioma (Figs 2-3).

The development of conidiophores and conidiogenous cells commences after cavity formation. They are formed either directly from the upper layer of cells of the basal wall or from the basal cells of paraphyses. The conidiogenous cells as shown by Sutton (1980) and Nag Raj (1978) are 'phialides' (*sensu* Sutton, 1980).

Mechanisms of dehiscence vary in this genus and depend on the degree of development of lateral and upper walls of the conidiomata. Some conidiomata have typical ostioles, while in other cases no ostiole is developed. In the latter case the conidiomata have minimal lateral or upper wall tissue and so the epidermis of the host is ruptured mechanically by the force produced by paraphyses or conidial masses. In the former case, the formation of an ostiole is due to lysis of the upper wall combined with mechanical rupture and possibly biochemical break down of the epidermis. Circular ostioles with regular margins can be seen in this case. In both types the paraphyses may play some role in dehiscence of conidiomata. In some collections of different species of *Coleophoma*, especially *C. empetri* and *C. cylindrospora*, circular ostioles are

well-developed, while in others the ostioles have not been seen and appear to open like acervular conidiomata, i.e. by splitting of the overlying host tissues (Sutton, 1973, 1980). The formation of ostioles and lateral and upper walls are probably related to host leaf structure. Leaves of *Rhododendron ponticum* have a thick cuticular layer and dark epidermis but the hypodermis is comparatively soft and with thin cell walls. Conidiomata formed in the hypodermis usually have well-developed lateral and upper walls and also an ostiole, while those formed in the epidermis have poorly developed lateral walls and normally no ostioles. The conidiomata formed on dead *Rhododendron* leaves (with a high water content) usually have well-developed walls and also ostioles.

Conidiomata in most species of *Coleophoma* are typically pycnidial, with well-developed walls. However, others are intermediate between acervular and pycnidial with only the basal wall well-developed and poorly developed lateral walls. The final form of conidiomata at least to some extent depends on leaf structure, especially the hardness of the cuticle and epidermis because these affect the upward and inward growth of cells in the margin of stromata in the pycnidial primordium.

Conidiomatal ontogeny in *C. cylindrospora* in pure culture (on oat meal agar) was described by Masilamani and Muthumary (1995) as typically pycnidial, the pycnidial initial formed by a simple meristogenous method and the cavity formed by dissolution of some of the smaller thin-walled cells in the centre of initial. These were clearly illustrated. However, identification of the fungus as *C. cylindrospora* or another species must be tentative because no paraphyses developed and the conidia were much smaller than is usual ( $10-15 \times 2-3.5 \mu\text{m}$  from the illustration). We also studied the conidiomatal ontogeny in *C. fusiformis*, *C. prunicola* and *C. empetri* in pure culture. The conidiomata are rarely formed on agar and not typically pycnidial but are in agreement with those formed on host tissues with the paraphyses always seen in pure culture.

Of the examined species of *Coleophoma*, *C. cylindrospora*, *C. empetri*, *C. fusiformis* and *C. prunicola* sp. nov. fall into this developmental type. Although the type species, *C. crateriformis* (Dur. & Mont.) Höhn., was not examined here, Nag Raj (1978) did see this material of the species from Höhnel's herbarium in FH. He described and illustrated the same morphological characters shown for *C. empetri* and *C. cylindrospora* by Sutton (1980). Thus all of these species including a new described species on *Prunus lusitanica* from the UK are considered to be congeneric. However, *C. oleae* (DC.) Petr. & Syd. does not develop in this way and is thus excluded from the genus (see below).

***Coleophoma*** Höhn., *Sber. Akad. Wiss. Wien* 116: 637 (1907).

*Bactropycnis* Höhn., *Hedwigia* **62**: 65 (1920).

*Basilocula* Bubák, *Annl. mycol.* **12**: 210 (1914).

*Ceuthosira* Petr., *Annl. mycol.* **22**: 265 (1924).

*Rhabdostromina* Died., *Annl. mycol.* **19**: 297 (1921).

*Xenodomus* Petr., *Annl. mycol.* **20**: 206 (1922).

*Sp. typ.*: *C. crateriformis* (Dur. & Mont.) Höhn., *Sber. Akad. Wiss. Wien* 116: 637 (1907).

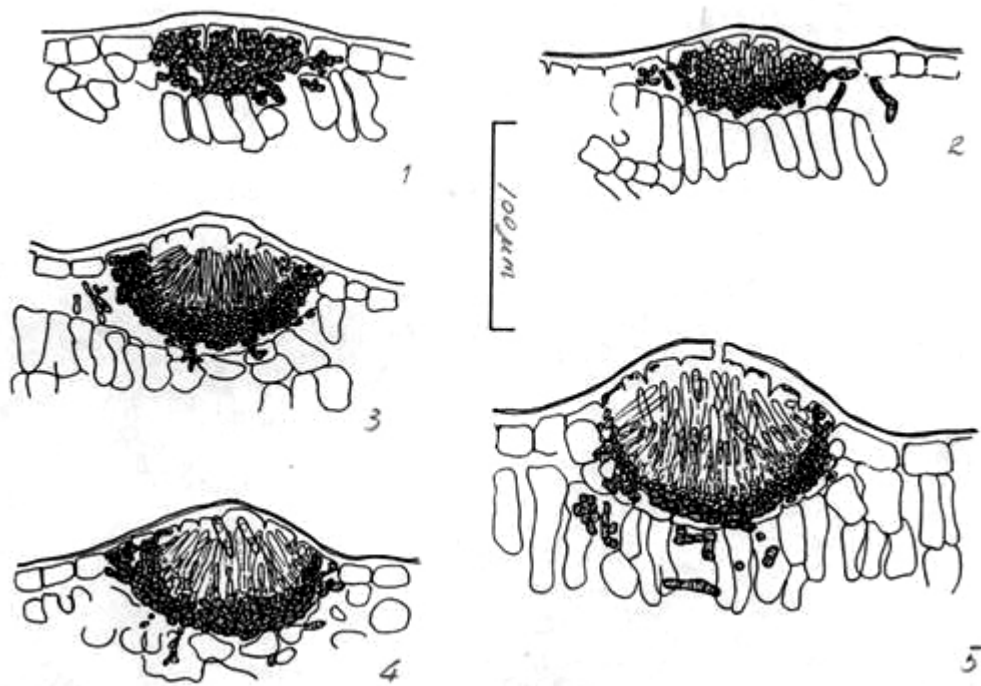
*Description and illustration*: Nag Raj (1978); Sutton (1980).

**Key to accepted species of *Coleophoma***

- 1. Conidia 3-5.5 µm wide ..... 2
- 1. Conidia up to 3 µm wide ..... 3
- 2. Conidia cylindrical, 4.5-5.5 µm wide..... *C. prunicola*
- 2. Conidia fusiform, 3-4.5 µm wide..... *C. fusiformis*
- 3. Conidia 1.5-2 µm wide..... *C. aesculi*
- 3. Conidia 2-3 µm wide ..... 4
- 4. Conidia 11-20 µm long, with small guttules ..... *C. empetri* & *C. crateriformis*
- 4. Conidia 16.5-28 µm long, with a few large guttules ..... *C. cylindrospora*

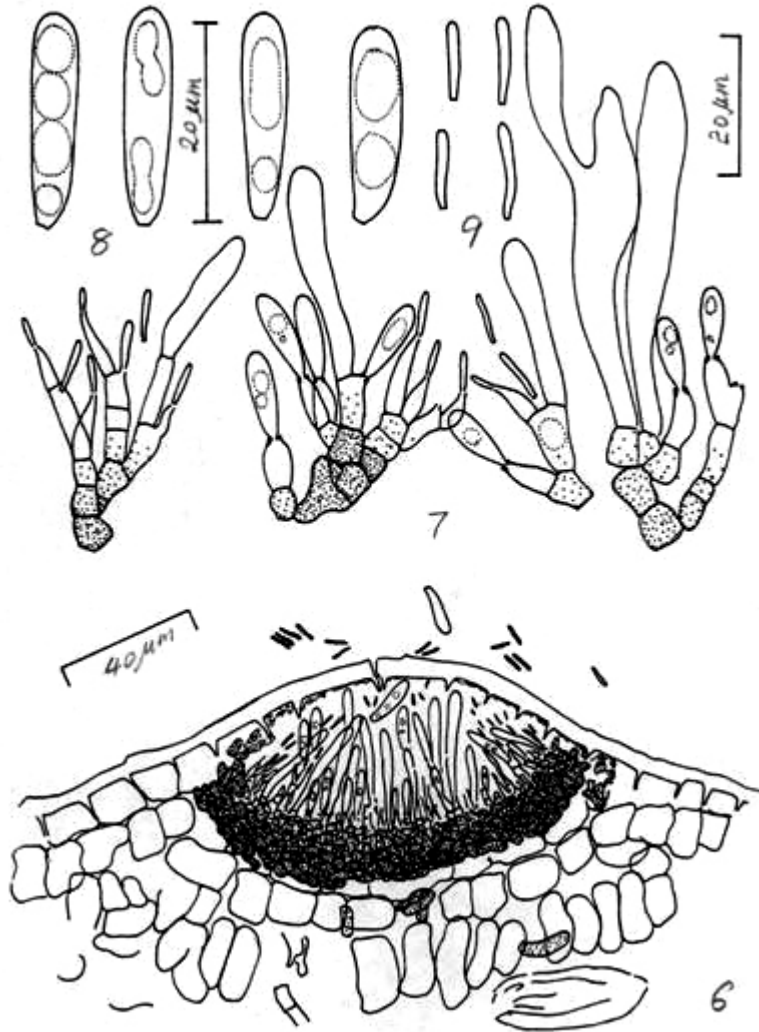
***Coleophoma prunicola*** J.X. Duan, W.P. Wu & X.Z. Liu, **sp. nov.** (Figs 1-12)  
 MycoBank: 510845

*Conidiomata* simplicia, eustromatica vel pycnidialia, subcuticularia, dispersa vel raro aggregata, brunnea, circularia, conica, unilocularia; paries basalis bene evolutus, ex textura angulari, ex cellulis brunneis vel atro brunneis, tenui- vel crassi-tunicatis irregularibus, 3-6 cellulis crassis; paries lateralis parce evolutus, ex 1-2 cellulis crassis, interdum absens. *Paraphyses* hyalinae vel palle brunnea, 0-1-septatae, clavatae, rectae vel curvatae, demum collapsae, inter conidiophora formatae, 65-70 µm longae et apicem versus 13 µm latae, basim versus 2.5-3 µm latae. *Conidiophora* ad basim pallide brunnea, apicem versus hyalina, ramosa vel non-ramosa, 0-3-septata, ex cellulis interioribus conidiomatum formata. *Cellulae conidiogenae* discretae vel in conidiophoris vel paraphyses incorporatae, ‘phialidicae’, determinatae, terminales vel laterales, hyalinae, laeves, ampulliformes vel lageniformes, 5-8 × 2.5-3.5 µm. *Conidia* holoblastica, hyalina, aseptata, subcylindrica, clavata, apicem obtusa et basim versus truncata, deminuta, irregulariter guttulata, laevia, tenuitunicata, 20-28 × 4.5-5.5 µm. *Microconidiophora* subcylindrica, hyalina vel ad basim pallide brunnea, laevia, 1-3-septata. *Cellulae microconidiogenae* discretae vel in conidiophoris vel paraphyses incorporatae, ‘phialidicae’, determinatae, terminales vel laterales, intercalaries, hyalinae, laeves, lageniformes, subcylindricae, 5-10 × 2.5-3 µm. *Microconidia* holoblastica, hyalina, aseptata, subcylindrica vel clavata, apicem versus obtusa et basim versus truncata, laevia tenuitunicata, 8-12 × 1-1.5 µm.



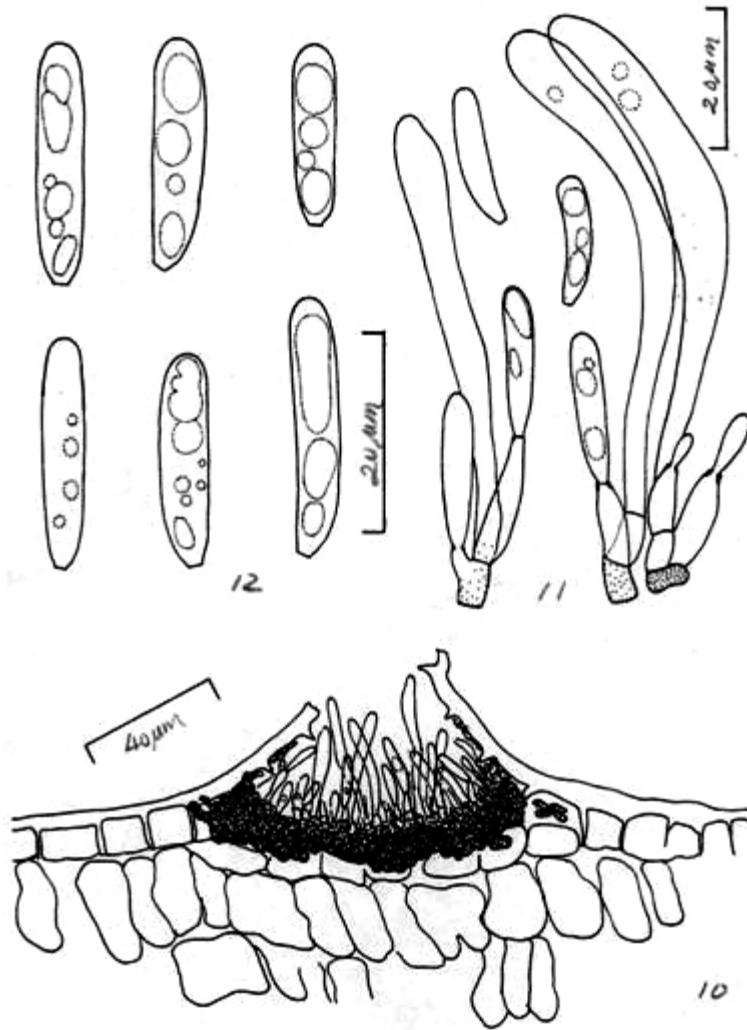
**Figs 1-5.** Development of conidiomata in *Coleophoma prunicola* within *Prunus* leaf. **1.** Conidiomatal initial composed of dark brown, thick-walled cells within the epidermis. **2.** Paraphyses start to form from the upper layer of conidiomatal initial, note the slightly swollen epidermis due to the growth of fungal tissue. **3.** Hyaline aseptate paraphyses have formed with the development of both basal and lateral walls, the conidiomatal cavity also form in this stage. **4.** Conidiogenous cells and conidia develop among paraphyses. **5.** Mature conidioma with hyaline, apex-swollen paraphyses, conidiogenous cells and conidia.

Foliicolous. *Mycelium* immersed, composed of branched, septate, hyaline to pale brown, thin-or thick-walled, smooth hyphae. *Conidiomata* pycnidial, separate or occasionally aggregated, globose, or flattened at the base, black, immersed, unilocular, wall thick at the base and thin or completely absent at the upper part, composed of brown, thick-walled *textura angularis*. *Conidiophores* absent or present, pale brown at the base but becoming hyaline towards the apices, branched or unbranched, septate or aseptate, cylindrical, smooth, formed from the inner cells of lower part of conidiomata and mixed with paraphyses. *Conidiogenous cells* integrated or discrete, determinate, terminal or intercalary within conidiophores or paraphyses, 'phialidic', ampulliform to lageniform or subcylindrical, hyaline, smooth, thin-walled, channel and collarete minute, occasionally with a percurrent proliferation,  $5-8 \times 2.5-3.5 \mu\text{m}$ . *Conidia* holoblastic, hyaline, aseptate, cylindrical, apex obtuse,



**Figs 6-9.** *Coleophoma prunicola* within dead leaves of *Prunus lusitanica*. **6.** Vertical section of a conidioma, note paraphyses, both macroconidiogenesis and microconidiogenesis occur in the cavity. **7.** Paraphyses, conidiophores, conidiogenous cells and conidia, note conidia and microconidia can form from the same conidiophores. **8.** Conidia. **9.** Microconidia.

base truncate, thin-walled, smooth, guttulate with several large guttules, 20-28 × 4.5-5.5 μm. *Microconidiophores* hyaline, branched and septate, thin-walled, smooth, lageniform, cylindrical, tapering towards the apices. *Microconidiogenous cells* integrated or discrete, determinate, lageniform,



**Figs 10-12.** *Coleophoma prunicola* on living leaves of *Prunus lusitanica*. **10.** Vertical section of a conidioma. **11.** Paraphyses, conidiogenous cells and developing conidia. **12.** Conidia.

subcylindrical, hyaline, thin-walled, smooth, with minute channels and collarettes,  $5-10 \times 2.5-3 \mu\text{m}$ . *Microconidia* holoblastic, solitary, hyaline, aseptate, thin-walled, smooth, rod-shaped, with obtuse apices and truncate bases,  $8-12 \times 1-1.5 \mu\text{m}$ . *Paraphyses* hyaline or pale brown at the base, aseptate or with 1 septum at the base, formed amongst and on conidiophores, clavate, persistent for a long time before collapsing,  $65-70 \mu\text{m}$  long, up to  $13 \mu\text{m}$  wide at the apices,  $2.5-3 \mu\text{m}$  wide at the base.



*Habitat:* On living and dead leaves of *Prunus lusitanica*.

*Known distribution:* UK.

*Material examined:* UK: UK: Surrey, Egham, Royal Holloway, University of London, on living leaves of *Prunus lusitanica*, 8 July 1996, Wenping Wu (IMI 372462 (**holotypus**); IMI 372461).

*Notes:* The above description for *C. prunicola* is based on the holotype collection (IMI 372461) on *Prunus lusitanica* where it grows on dead but still attached leaves. Both conidia and microconidia were observed from this collection. A second collection on living leaves shows the fungus associated with lesions, but whether these spots are caused by *C. prunicola* is not clear and from this collection, only conidia but not microconidia were observed. In addition several isolates were obtained from living leaves as endophytes of the same plant. The fungus on PDA grows slowly and produces white, circular colonies. Only a few conidiomata were produced from incubated leaf pieces or on agar. Except for slightly smaller conidia other characters are in agreement with those in the holotype collection. The cultural characters of this fungus on PDA are similar to those for *C. fusiformis* which was also recovered as an endophyte from *Rhododendron ponticum*, i.e. grows very slowly and produces white colonies with few aerial hyphae.

The conidia of *C. prunicola* are similar in size to those of *C. fusiformis*. However, *C. fusiformis* a pathogenic fungus causing leaf lesions of *Rhododendron ponticum* in the UK, has fusiform conidia, although they are cylindrical or fusiform when they are still developing on the conidiogenous cells. The conidia in *C. prunicola* are cylindrical or clavate, and taper only towards the base, and young conidia on conidiogenous cells are clavate or ovoid.

All other species of *Coleophoma* have smaller, cylindrical conidia (Nag Raj, 1978; Sutton, 1980; Wu, Sutton & Gange, 1996). *Coleophoma prunicola* differs from these species in that its conidia are much wider (4.5-5.5  $\mu\text{m}$  wide compared with less than 3  $\mu\text{m}$  wide in all other species). In conidial shape and size *C. prunicola* is most similar to *C. oleae*, which also has cylindrical conidia with obtuse apices and truncate bases. However, several characters are different from *C. oleae* as redescribed and illustrated by Sutton (1980) and these include: 1), development of conidiomata and paraphyses; 2), poorly developed upper walls of conidiomata; 3), longer, clavate and persistent paraphyses with swollen apices comparatively large in size; 4), microconidiogenesis; and 5), slightly larger conidia. Although the conidial size of *C. fusiformis*, a typical pathogenic fungus causing leaf lesions of *Rhododendron ponticum* in the UK, is similar to the fungus on leaves of *Prunus lusitanica*, the conidial shape and also their initials from conidiogenous cells are different. In *C. fusiformis* the conidia are fusiform and tapered

towards both ends, but they are cylindrical or fusiform when they are still developing on conidiogenous cells. The conidia in *C. prunicola* are cylindrical or clavate, and taper only towards the base, and young conidia on conidiogenous cells are clavate or ovoid.

Microconidiogenesis is reported for the first time in *Coleophoma*. The morphologies of microconidiophores, microconidiogenous cells and microconidia are similar to those in *Cryptosporiopsis* (Sutton, 1980), and can occur together in the same conidiomata with the macroconidia (Figs 6-9).

*Coleophoma prunicola* can be compared with several other coelomycetes described from *Prunus* spp. *Coleophoma collabens* (Cooke) Petr. & Syd. (based on *Phoma collabens* Cooke on *Prunus lusitanica* from England, Petrak & Sydow (1927)) has conidia that are cylindrical to subcylindrical,  $18-25 \times 2-3 \mu\text{m}$ . Petrak and Sydow (1927) noted this species is very similar to *C. cylindrospora* but differs from the latter by its host plant.

*Ceuthospora lauri* (Grev.) Grev., *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc., and *Cryptocline phacidiella* (Grove) Arx have hyaline, aseptate, cylindrical conidia similar to those of *Coleophoma prunicola* (Sutton, 1980; Ellis and Ellis, 1985). Conidia in *Ceuthospora lauri* have apical appendages and are thus very different from *Coleophoma prunicola* which lack appendages. *Colletotrichum gloeosporioides* has typical acervular conidiomata with setae and lacks paraphyses and the conidia are somewhat shorter. *Cryptocline phacidiella* has typically acervular conidiomata without setae or paraphyses and conidia are much shorter and wider conidia ( $18-20 \times 7-8 \mu\text{m}$ ) and with a prominent tuberculate scars.

***Coleophoma cylindrospora* (Desm.) Höhn., *Ber. dtsh. Bot. Ges.* **37**: 14 (1919). (Figs 13-15)**

*Sphaeropsis cylindrospora* Desm., *Ann. Sci. nat.* 3 sér. 11:277, 1849

*Phoma collabens* Cooke, *Grevillea* **13**: 94 (1885).

*Macrophoma collabens* (Cooke) Berl. & Vogl., *Atti Soc. Venet.-trent. Sc. Nat.* **10**: 196 (1886).

*Coleophoma collabens* Petr. & Syd., *Beih. Repert. spec. nov. regni veg.* **42**: 516 (1927).

For other synonyms see Sutton (1980). The conidia of this species on *Prunus* spp. are  $22-28 \times 2-3 \mu\text{m}$ .

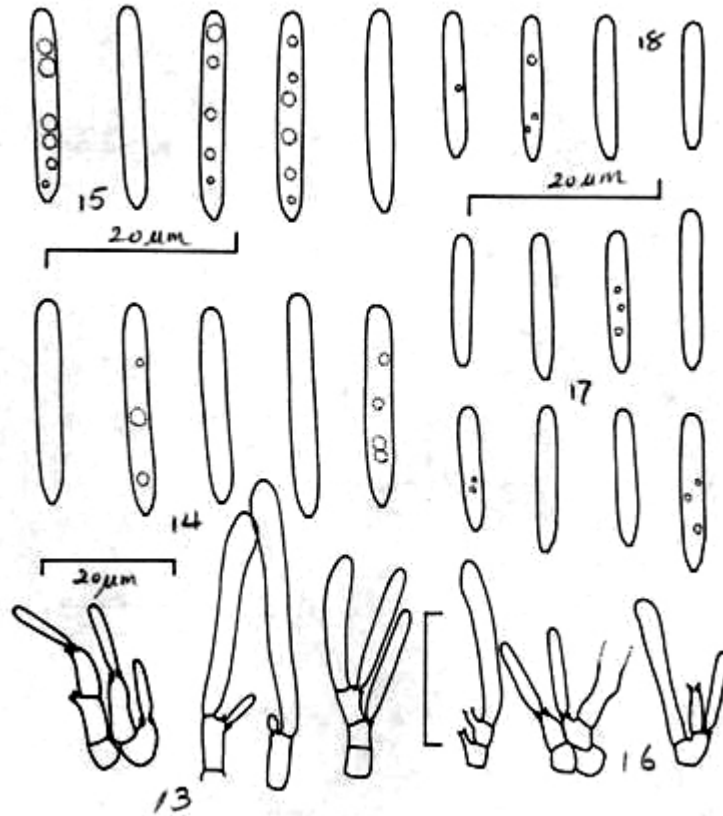
*Illustration and description*: Sutton (1980).

*Habitat*: On living and dead leaves of many different plants as reported by Sutton (1980) from material in herb. IMI.

*Known distribution*: Widely distributed (Sutton, 1980).

*Material examined*: UK: Surrey, Egham, Royal Holloway, University of London, On dead attached leaves of *Prunus lusitanica*, 8 July 1996, Wenping Wu (P003), IMI 372463; UK: Isle of Man, Riverside, Glen Mona, on dead attached leaves of *Prunus lusitanica*, 1 Feb. 1976, J.C. F. Hopkins, IMI 202697; UK: England, Devon, south Devon, Slapton, near Kingsbridge,

Slapton Ley National Nature Reserve, site J1, on dead leaves of *Prunus laurocerasus*, 11 May 1994, P.F. Cannon, IMI 362553.



**Figs 13-18.** *Coleophoma cylindrospora* and *Coleophoma empetri* on *Prunus* spp. **13-15.** *C. cylindrospora.*, paraphyses, conidiophores, conidiogenous cells and developing, and liberated conidia (**13-14** ex wu003; **15** ex IMI 202697). **16-18.** *C. empetri*, paraphyses, conidiophores, conidiogenous cells, developing and liberated conidia, and conidia (**16-17** ex IMI 250722; **18** ex IMI 202692).

*Notes:* IMI 202697 on *P. lusitanica*, also collected from the Isle of Man but from a different site (Riverside, Glen Mona) has guttulate conidia measuring 22-25 x 2-3  $\mu\text{m}$  and as such remain as *C. cylindrospora*.

***Coleophoma empetri*** (Rostr.) Petr., *Annals mycol.* 27: 331 (1929) (Figs 16-18)  
Synonyms have been listed by Sutton (1980).

Conidia of this species on *Prunus* spp. are 14-18 x 2-2.8  $\mu\text{m}$  and sparsely guttulate.

*Illustration and description:* Sutton (1980).

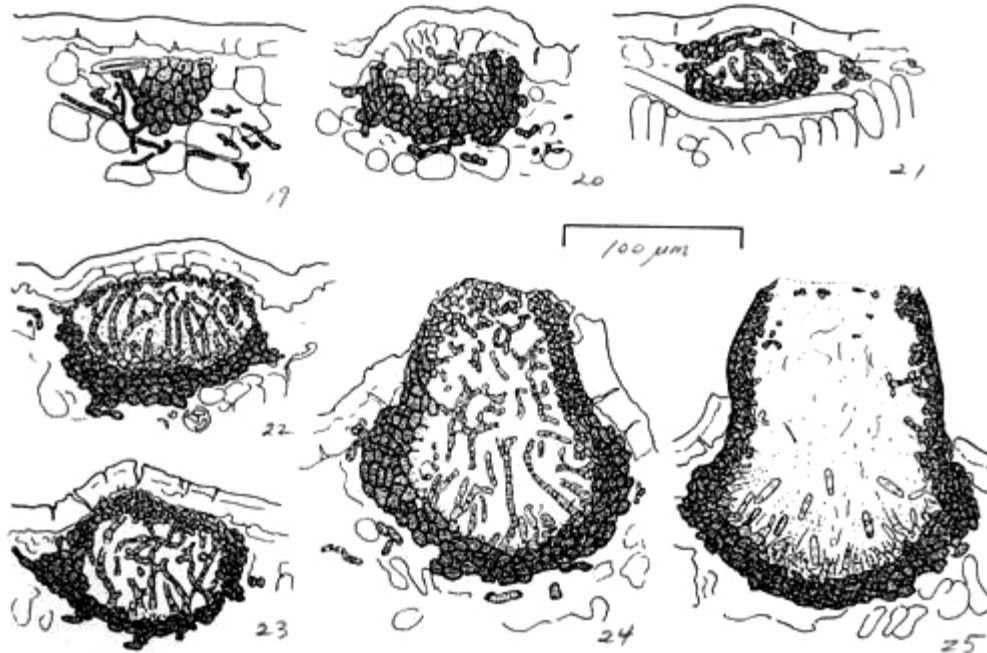
*Habitat:* On living and dead leaves of many different plants as reported by Sutton (1980) from material in herb. IMI.

*Known distribution:* Widely distributed (Sutton, 1980).

*Material examined:* UK: Isle of Man, Barouy Farm, on dead attached leaves of *Prunus lusitanica*, 21 Jan. 1976, J.C.F. Hopkins, IMI 202692 (sub *C. cylindrospora*); UK: Surrey, Esher Common, on dead attached leaves of *Prunus laurocerasus*, 9 Aug. 1980, P.M. Kirk, IMI 250722 (sub *C. cylindrospora*).

### ***Development of conidiomata and conidiophores in Coleophoma oleae within Olea leaf***

Conidiomatal initial formation in this species is the same as in other species of *Coleophoma*, as described above. Later events in development are very different. Some epidermal hyphae grow together and form the initial, the upper cells of which grow upward and inward to form a tissue structure of *textura porrecta* or *textura prismatica*, composed of pale to medium brown, septate, branched or unbranched hyphae. At the beginning these hyphae have free apices, but very soon they anastomose. At the periphery of this upward growth there are more deeply pigmented, thick-walled cells and these form the conidiomatal walls. On the inside of this wall the hyphae are also loosely aggregated, branched, septate and pale to medium brown. The outer cell walls of the inner hyphae are easily broken down and become mucilaginous shortly after, a feature seen in young conidiomata. Hyphal disintegration and lysis contributes to increasing the conidiomatal cavity. After cavity formation, the conidiophores and conidiogenous cells start to develop either from the bases of the inner hyphae or directly from cells lining the inner wall of the cavity. When the conidiomata mature the inner brown, septate hyphae totally disappear and leave some mucilaginous material in the cavity of the conidiomata (Figs 19-25). The shapes of conidiomata vary even within the collections. This type of cavity formation is difficult to place in any of the three developmental types hitherto recognised, but combines lysigenous activity and the upward and inward growth of the conidiomatal wall (Sutton, 1973). Again, they can be typically pycnidial with well-developed walls and ostioles, or intermediate between pycnidial and eustromatic but even in the latter case the lateral walls are also well-developed. The ostiole is formed by lysis of a restricted area of the upper wall. The upwardly growing hyphae at the periphery of the conidioma do not meet at the apices but the hyphae inside do meet and form a pale brown, loosely arranged hyphal structure, the lysis of which forms the ostioles and the swelling of mucilaginous material inside the cavity forces the epidermis to break open so that the conidiomata become erumpent through the leaf tissue. This type of conidiomatal development has been described from several different coelomycete fungi (Punithalingam, 1974, 1979; Maiello and

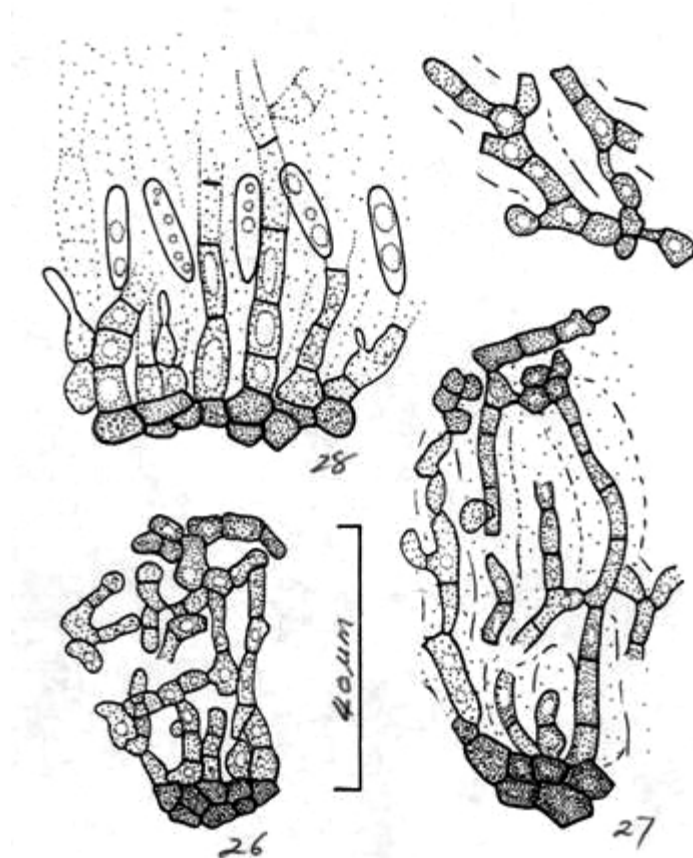


**Figs 19-25.** Conidiomatal development of *Coleonaema oleae* within *Olea* leaf. **19.** Subepidermal or intraepidermal conidiomatal initial composed of dark brown, thick-walled cells. **20-21.** Some pale brown, septate, and branched hyphae develop from the upper layer of conidiomatal initial. **22-24.** The upward and inward growth of hyphae form the lateral and upper walls and lysis of inside growing hyphae form the cavity within conidiomata. **25.** Vertical section of a mature conidioma with hyphal remains after lysis and conidiogenous cells and conidia.

Peterson, 1976; Maiello, 1978; Muthumary and Vanaja, 1986; Roux and van Warmelo, 1990; Muthumary *et al.*, 1993) and it is possibly the most common one.

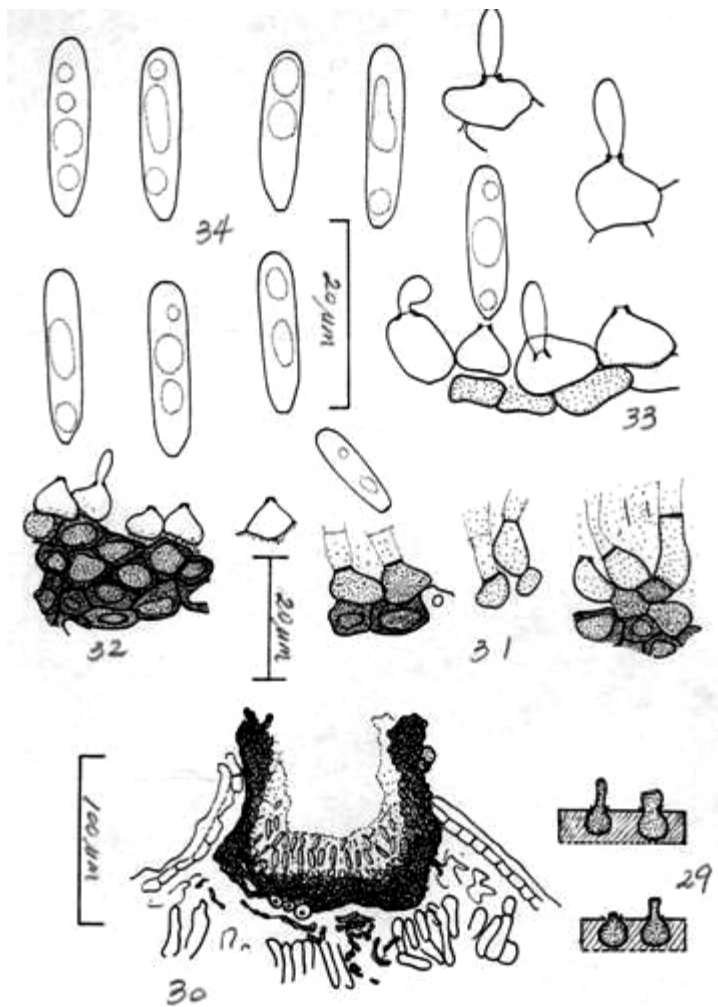
Differing from other species of *Coleophoma* in the development of both the conidiomatal cavity and ostiole, and in having no paraphyses, this species must be excluded from *Coleophoma*. However the morphology and development of conidiophores, conidiogenous cells and conidia are similar to those described in *Coleophoma* and *C. oleae* should be treated in a related genus.

This fungus was originally described as *Sphaeria oleae* DC., but subsequently the name was transferred to seven different genera: *Ascospora* Mont., *Coleonaema* Höhn., *Coleophoma* Höhn., *Diplodia* Fr., *Macrophoma* (Sacc.) Berl. & Vogl., *Phoma* Westend., and *Septoria* Sacc. (Petrak and



**Figs 26-28.** Hyphal structure, development of conidiophores and conidiogenous cells in *Coleonaema oleae*. **26.** Pale brown, septate and branched hyphae form from the upper layer of conidiomatal initial. **27.** Hyphae in developing conidiomata. **28.** Remains of hyphae after lysis and conidiophores, conidiogenous cells and conidia in mature conidiomata.

Sydow, 1927; Sutton, 1980). Among these genera and also other coelomycete genera documented by Sutton (1980), only *Phoma*, *Macrophoma* and *Coleonaema* seem to be possible placements for the species, based on morphology of conidiomata, conidiogenesis and conidia. In *Phoma*, cavity formation of conidiomata is either lysigenous or both lysigenous and schizogenous and the conidia are small (less than 10 µm long) (Boerema, 1964; Monte *et al.*, 1989). Species of *Macrophoma* have large conidia but this is a rather heterogeneous genus and although many species have been described, no modern treatments are available. Placement of this fungus in *Macrophoma* can only make the genus more heterogeneous, and in any event Sutton (1977, 1980) considers it a synonym of *Sphaeropsis*. *Coleonaema* was established for a single species, *Coleonaema oleae* by Höhnelt (1924). Petrak and Sydow (1927) transferred the name to *Coleophoma* and thus the generic name *Coleonaema* became a synonym of *Coleophoma*. However, because of



**Figs 29-34.**  
*Coleonaema oleae*.  
**29.** Conidiomata of different shape formed within *Olea* leaves. **30.** Vertical section of a conidioma. **31.** Remains of hyphae within the mature conidiomata. **32-33.** Conidiogenous cells formed from the inner layer of conidiomata. **34.** Conidia.

the differences between *C. oleae* and other species of *Coleophoma*, the two genera are distinct and *Coleonaema* is therefore reinstated for *C. oleae*.

*Coleonaema* Höhn., *Mitt. bot. Inst. tech. Hochsch. Wien* 1: 95 (1924).

Foliicolous. *Mycelium* immersed, composed of branched, septate, pale brown to dark brown, thin- or thick-walled, smooth hyphae. *Conidiomata* pycnidial, separate or occasionally aggregated, globose, or flattened at the base, black, immersed, unilocular, both basal and lateral walls well-developed, composed of brown, thick-walled textura angularis. *Paraphyses* absent. *Conidiophores* absent or poorly developed. *Conidiogenous cells* discrete, determinate, terminal or intercalary within conidiophores, 'phialidic',

ampulliform to lageniform or subcylindrical, hyaline, smooth, thin-walled, channel and collarete minute, occasionally with a percurrent proliferation. *Conidial ontogeny* holoblastic, wall hogenous, delimited by one septum from conidiogenous cells, secession schizolytic. *Conidia* hyaline, aseptate, cylindrical, apex obtuse, base truncate, thin-walled, smooth, guttulate.

*Sp. typ.*: *Coleonaema oleae* (DC.) Höhn., *Mitt. bot. Inst. tech. Hochsch. Wien* 1: 95 (1924).

***Coleonaema oleae* (DC.) Höhn., *Mitt. bot. Inst. Techn. Hochsch. Wien* 1: 95 (1924) (Figs 20-34)**

*Sphaeria oleae* DC., *Fl. Franc.* 6: 136, 1815.

*Coleophoma olivae* (DC.) Petr. & Syd., *Beih. Rep. spec. nov. regn. Veg.* 42: 469, 1927.

A list of synonyms was provided by Sutton (1980).

Foliicolous. *Mycelium* immersed, composed of branched, septate, pale brown to dark brown, thin- or thick-walled, smooth hyphae. *Conidiomata* pycnidial, separate or occasionally aggregated, globose, subcylindrical, or flattened at the base, dark brown, black, immersed, unilocular, both basal and lateral walls well-developed, of *textura angularis* composed of brown, thick-walled cells, 100-250 µm diam., up to 350 µm high. *Ostiole* single, central, circular, often becoming wide late in development. *Conidiophores* absent or poorly developed. *Paraphyses* absent. *Conidiogenous cells* discrete, determinate, terminal or intercalary within conidiophores or paraphyses, 'phialidic', ampulliform to lageniform or subcylindrical, hyaline, smooth, thin-walled, channel and collarete minute, occasionally with a percurrent proliferation, formed from the cells in the inner layer of pycnidial cavity, 8-15 × 3-5 µm. *Conidia* hyaline, aseptate, cylindrical, apex obtuse, base truncate, thin-walled, smooth, with several large guttules, 15-23 × 3-5 µm.

*Illustration and description*: Sutton (1980).

*Habitat*: On living and dead leaves of *Olea europaea*, *O. cuspidata*, *Olea* sp.

*Known distribution*: Israel, India, Pakistan, USA, Turkey, Greece (Sutton, 1980).

*Material examined*: Greece: Crete, Chania, on dead leaves of *Olea europaea*, Apr. 1942, K.H. Rechinger (F. Petrak, *Mycotheca generalis* 1721. *Coleophoma oleae* (DC.) Petr. & Syd.), IMI 33462; Turkey: Mersin (Ayas), 5 May 1948, G. Karel, IMI 248671 (*Reliquiae Petrakianae* 562 *Coleophoma oleae*); Greece: Crete: Sitia, Toplou Monastery, on dead leaves of *Olea europaea*, 10 July 1992, B.C. Sutton & A.V. Sutton, IMI 354113; USA: South California, on dead leaves of *Olea europaea*, 10 Nov. 1931, O.A. Plunkett, IMI 154335; Turkey: Kas, on dead leaves of *Olea europaea*, 3 Sept. 1991, B.C. Sutton, IMI 349854; Palestine: Ben Shemea, on dead leaves of *Olea europaea*, 27 Feb. 1924, J. Reichen, IMI 22109; Pakistan: Bahrain (Swat), on *Olea cuspidata*, 18 July 1969, M.A. Quraishi, IMI 171849; Pakistan: Bahrain (Swat), on *Olea cuspidata*, 17 July 1969, M.A. Quraishi, IMI 171851,142028; Pakistan: Bahrain, on *Olea cuspidata*, 22 July 1969, T. Mahmood, IMI 151753,142455; 24 July 1969, T. Mahmood, IMI 142010; Pakistan, Kohat, on *Olea cuspidata*, 2 Aug. 1967, S. Ahmad, IMI 133457; Greece, on *Olea* sp., 23 March 1988, J.E.M. Mordue, IMI 325782.



## Acknowledgements

We are indebted to Dr. Eric H.C. McKenzie (New Zealand Fungal Herbarium (PDD), Landcare Research, Auckland) for kindly reviewing the manuscript. Part of this work was conducted in CAB International. We thank the curators of herbarium IMI for allowing us to examine their specimens cited in this paper.

## References

- Archer, W.A. (1926). Morphological characters of some Sphaeriopsidales in culture. *Annales Mycologici* 24: 1-84.
- Baccarini, P. (1890). Sullo sviluppo dei picnidii. *Nuovo Giornale Italiano Botanico* 22: 150-151.
- de Bary, A. (1887). *Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria*. English Translation. Oxford: Clarendon press, London & New York.
- Bauke, H. (1876). Beiträge zur Kenntnis der Pycnidien. I. *Novo Acta Leopoldino-Carolinae Deutschen Akademie der Naturforscher* 38: 443-512.
- Boerema, G.H. (1964). *Phoma herbarum* Westend., the type species of the form-genus *Phoma* Sacc. *Persoonia* 3: 9-16.
- Boerema, G.H. and van Kesteren, H.A. (1964). The nomenclature of two fungi parasitizing *Brassica*. *Persoonia* 3: 17-28.
- Calvert, O.H. and Pound, G.S. (1949). Stimulated pycnidium production and symphogenous pycnidia in *Phoma lingam*. *Phytopathology* 39: 848-857.
- Dodge, B.O. (1923). Origin of the central and ostiolar cavities in pycnidia of certain fungous parasites of fruits. *Journal of Agricultural Research* 23: 743-759.
- Dodge, B.O. (1930). Development of the asexual fruitifications of *Chaetomella raphigera* and *Pezizella lythri*. *Mycologia* 22: 169-174.
- Ellis, M.B. and Ellis, J.P. (1985). *Microfungi on Land Plants. An Identification Handbook*. Croom Helm, London & Sydney.
- Harris, H.A. (1935). Morphologic studies of *Septoria lycopersici*. *Phytopathology* 25: 790-799.
- von Höhnelt, F. (1924). Über die Gattung *Rhabdospora*. *Mitteilungen aus dem botanischen Laboratorium der Technischen Hochschule Wien* 3: 94-98.
- Kempton, F.E. (1919). Origin and development of the pycnidium. *Botanical Gazette* 68: 233-261.
- Maiello, J.M. (1978). The origin of the pycnidium in *Macrophomina phaseolina*. *Mycologia* 70: 176-179.
- Maiello, J.M. (1988). Acervulus initiation in *Colletotrichum capsici*. *Mycologia* 80: 410-413.
- Maiello, J.M. and Peterson, J.L. (1976). Pycnidium ontogeny in *Phyllosticta antirrhini*. *Mycologia* 68: 1121-1125.
- Masilamani, S. and Muthumary, J. (1995). Pycnidium ontogeny in *Coleophoma cylindrospora*. *Mycological Research* 99: 693-696.
- Mercer, W.B. (1913). On the morphology and development of *Phoma richardsiae* n.sp. *Mycologisches Centralblatt* 2: 244-253.
- Monte, E., Martin, P.M. and Garcia-Acha, I. (1989). Pycnidial development in *Phoma betae*. *Mycological Research* 92: 369-372.
- Muthumary, J., Jayachandra, J.A. and Preetha, M.B. (1993). Development of conidiomata in the *Phyllosticta* state of *Guignardia mangiferae* Roy and observations on the fine structure of the conidium. *Mycotaxon* 47: 147-155.

- Muthumary, J. and Vanaja, R. (1986). Development of conidiomata in *Coniella fragariae*. Transactions of the British Mycological Society 87: 109-113.
- Nag Raj, T.R. (1978). Genera coleomycetum. XIV. *Alleohaeta*, *Basilocula*, *Ceuthosira*, *Microgloeum*, *Neobarclaya*, *Polynema*, *Pycnidiochaeta*, and *Xenodomus*. Canadian Journal of Botany 56: 686-707.
- Petrak, F. & Sydow, H. (1927). Die Gattungen der Pyrenomyzeten, Sphaeropsideen und Melanconieen. Beihefte Repertorium specierum novarum regni vegetabilis 42: 1-551.
- Punithalingam, E. (1966). Development of the pycnidium in *Septoria*. Transactions of the British Mycological Society 49: 19-25.
- Punithalingam, E. (1974). Studies on Sphaeriopsidales in culture II. Mycological Papers 136: 1-63.
- Punithalingam, E. (1979). Graminicolous *Ascochyta* species. Mycological Papers 142: 1-214.
- Roux, C. & van Warmelo, K.T. (1990). Conidiomata in *Bartalinia robillardoides*. Mycological Research 94: 109-116.
- Sutton, B.C. (1973). Coelomycetes. In *The Fungi IV A* (ed. Ainsworth, G.C., Sparrow, F.K and Sussman, A.S.), pp.513-582. Academic Press, New York and London,.
- Sutton, B.C. (1977). Coelomycetes VI. Nomenclature of generic names proposed for Coelomycetes. Mycological Papers 141: 1-253.
- Sutton, B.C. (1980). *The Coelomycetes*. CMI., Kew.
- von Tavel, F. (1886). Beiträge zur Entwicklungsgeschichte der Pyrenomyceten. Botanisches Centralblatt 44: 825.
- Wu, W.P., Sutton, B.C. & Gange, A.C. (1996). *Coleophoma fusiformis* sp. nov. from leaves of *Rhododendron*, with notes on the genus *Coleophoma*. Mycological Research 100: 943-947.

(Received 9 September 2006; accepted 28 March 2007)