The *Lecythophora-Coniochaeta* complex

II. Molecular studies based on sequences of the large subunit of ribosomal DNA

by

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With 2 figures and 1 table


**Abstract:** Phylogenetic analyses of LSU rDNA confirm the association of *Lecythophora* species with teleomorphs of *Coniochaeta*. The *Lecythophora* states described until now, including the type species, *L. lignicola*, as well as *L. hoffmannii*, *L. mutabilis*, *L. luteoviridis*, *L. fasciculata*, and *L. decumbens*, cluster together with *Coniochaeta* species. In neighbour-joining analysis, the *Lecythophora-Coniochaeta* group was found to be situated with strong support in a cluster consisting of unitunicate pyrenomycetes. It was not possible to clarify relationships at ordinal level. The *Lecythophora* states of *Coniochaeta ligniarii*, *C. malacotricha*, *C. velutina*, and *C. pulveracea*, differing from each other in both morphological and cultural characteristics, were also distinguishable by LSU rDNA analysis, but proved not to be identical with any of the described *Lecythophora* species. *Lecythophora lignicola*, *L. luteoviridis*, and *L. fasciculata* clustered together with *C. velutina*, and are therefore regarded as closely related to this species, while *L. mutabilis* was close to *C. ligniarii*, and *L. decumbens* close to *C. pulveracea*. The tested species of other genera with adelophialides were found to cluster at a relatively great distance from the *Lecythophora-Coniochaeta* group within the groups of unitunicate pyrenomycetes, as well as the Helotiales, Chaetothyriales, and Dothideales.

**Key words:** ascomycete systematics, LSU rDNA, phylogeny.

**Introduction**

In the anamorph genus *Lecythophora* Nannf., six species have been described so far, including three transferred to the genus by Weber et al. (Weber 2002): *L. lignicola* Nannf. as type species, *L. mutabilis* (van Beyma) W. Gams & McGinnis, *L. hoffmannii*
(van Beyma) W. Gams & McGinnis, *L. luteoviridis* (van Beyma) E. Weber et al., *L. fasciculata* (van Beyma) E. Weber et al., and *L. decumbens* (van Beyma) E. Weber et al. None of these species can definitely be assigned to a known teleomorph. However, the genus *Coniochaeta* appears generally to be the teleomorph of *Lecythophora*. Lecythophora-like states are known in 16 *Coniochaeta* species (an overview is given in Weber 2002). In general, the similarity of the anamorphs to one another is problematic. According to Gams & McGinnis (1983), ‘they cannot be distinguished from each other in culture without the appropriate teleomorph being present’. Weber (2002) described *Lecythophora* states of four species of *Coniochaeta, C. ligniaria* (Grev.) Cooke, *C. velutina* (Fuckel) Munk, *C. pulveracea* (Ehrh.) Munk, and *C. malacotricha* (Niessl) Traverso. The first three were isolated from dead stems of *Picea abies* (L.) Karst., while *C. malacotricha* was isolated from bark beetles. These *Lecythophora* states are morphologically distinct from each other.

Additional genera form adelphialides similar to those of *Lecythophora*. These genera differ relatively strongly from *Lecythophora*, but a clear delimitation is difficult in some cases. For example, the genus *Phialemonium* W. Gams & McGinnis (1983), has cylindrical adelphialides with collarettes lacking or very inconspicuous and without visible periclinal wall thickening. Its adelphialides are always very narrow (0.5–1 μm wide), and its vegetative hyphae are also often less than 1 μm wide. *Phialemonium* species have often been found to be human and animal pathogens (de Hoog et al. 2000). None of the species has ever been isolated from wood, and teleomorphs are unknown. Wang & Zabel (1990), in their work on fungi from utility poles, included two *Phialemonium* species; however, the placement of these isolates in this genus is questionable. Gams (in Wang & Zabel 1990) considered the species to belong in *Lecythophora*.

In *Phialophora* Medlar discrete phialides predominate. They possess a basal septum and normally also a distinct collarette, which is generally cup- or beaker-shaped. The phialides are frequently flask-shaped and are borne singly or on conidiophores. Gams (2000) considers the genus to be ‘poorly defined, little differentiated and highly polyphyletic’. Teleomorphs are found in many ascomycetous orders, for example Chaetothyriales, Helotiales, Sordariales, Diaporthales, and Hypocreales. Also the ‘*Phialophora hoffmannii* group’ was placed here until Gams & McGinnis (1983) reintroduced the genus *Lecythophora* to accommodate it.

In *Coryne* Nees, the anamorph of the discomycetous genus *Ascocoryne* J. W. Groves & D.E. Wilson (Helotiales), adelphialides can occur below discrete phialides in pure culture. The colonies are slimy and have cream to purple or lilac tinges. Weber (2002) very frequently isolated an anamorph of *Ascocoryne* sp. from stems of *Picea abies*. This *Coryne* state does not seem to be conspecific with the known anamorphs of *Ascocoryne* mainly because of differences in conidial morphology. Especially in young cultures, adelphialides were abundant.

*Acremonium* Link : Fr. and *Phaeoacremonium* W. Gams, Crous & M.J. Wingf. (in Crous et al. 1996) usually have relatively long, discrete phialides predominating; these phialides are slender and never ventricose. If adelphialides are present in *Acremonium*, e.g. in *A. strictum* W. Gams, they are formed on submerged hyphae.
(Gams & McGinnis 1983), whereas in *Lecythophora* they are regularly found on aerial hyphae or hyphal strands.

The genus *Cladorrhinum* Sacc. & Marchal is characterized by pustular conidiophore complexes consisting of fertile hyphae with lateral phialidic openings and flaring collarettes (‘pleurophialides’ per Gams 1971). Conidia are usually daecryoid to clavate. Teleomorphs have been found to be within the genera *Apiosordaria* Arx & W. Gams and *Cercophora* Fuckel (Lasiosphaeriaceae). The five known species have mainly been isolated from soil and dung (Mouchacca & Gams 1993).

In certain genera, conidiogenesis is not phialidic but the conidiogenous cells can easily be mistaken for small adelphialides. In *Exophiala* J.W. Carmich. (de Hoog 1977) colonies are olivaceous-brown and slow-growing, and conidiogenesis is annellidic. No collarettes or periclinal wall thickenings are recognizable, but the annellated zones are also not clearly visible under the light microscope. *Exophiala* species are associated with teleomorphs in *Capronia* Sacc. (Untereiner et al. 1995, Untereiner 2000).

*Hyphozyma* de Hoog & M.Th. Smith (1981) includes yeast-like hyphomycetes with pink colonies and short conidiogenous pegs. These species have been isolated from various substrata such as meat, fresh water plants (*H. variabilis* de Hoog & M.Th. Smith), and galls and cankers of *Populus tremuloides* Michx. (*H. lignicola* L.J. Hutchison et al. 1993). De Hoog & Smith (1981, 1986) recognized these anamorphs as ascomycetes because they were shown in electron-microscopy to have ascomycete-type cell walls and Woronin-bodies close to the septal pores. The authors suggested a possible relationship to *L. hoffmannii* because of similar colony characteristics, conidial production from lateral openings, and budding.

Another similar anamorph is that of *Tromeropsis microtheca* (P. Karsten) Sherwood, a species growing on dead stems of *P. abies*. In both *Hyphozyma* and the anamorph of *Tromeropsis*, the conidiogenous cells appear to be small holoblastic pegs (Weber 2002).

The aim of this paper is to study the homogeneity of the genus *Lecythophora* using a molecular biological technique, the analysis of the large subunit (LSU) of ribosomal DNA. We analyzed the relation of *Lecythophora* to *Coniochaeta* and the placement of both within the euascomycetes. We also investigated the *Lecythophora* states of *C. ligniaria*, *C. malacotricha*, *C. pulveracea* and *C. velutina*. A further goal of this study was the elucidation of relationships of *Lecythophora-Coniochaeta* with other genera forming adelphialides or similar conidiogenous cells.

**Material and methods**

Species studied in morphological and molecular analyses are listed in Table I. DNA from *Coniochaeta* specimens was isolated from cultures or herbarium material. The DNA of *Lecythophora* species was isolated only from culture. The cultures were cultured on Malt Extract Agar plates (MEA 2%).

DNA was isolated using a modified SDS protocol as described by Begerow et al. (1997). Partial LSU rDNA was amplified using the primer pairs NL1/NL4 (O’Donnell 1993) or NL1/LR6 (Vilgalys 2000) and a touchdown protocol with decreasing annealing temperature (60-50EC). Products were
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1 Isolates obtained in one of the following ways:
- F: DNA isolated from fruitbodies
- A1: DNA isolated from anamorph culture obtained from fruitbodies
- A2: DNA isolated from anamorph culture obtained from wood of *Picea abies* (*' or bark beetles*
- A3: DNA isolated from anamorph culture from CBS
- C: DNA isolated from culture

(The collection data of own material can be found in Weber (2002), with the exception of *A. cylichnium* Ro.Ki. 85, *C. pulvacea* E.W. 92/1, *N. pura* E.W. 98/2, *P. inouei* F289, and *T. amentorum* F.O. 35624)


**Species from Genbank:**

purified on Qiaquick™ columns following the manufacturer’s protocol. The ABI Prism™ dye terminator cycle sequencing kit and an automated ABI 373A sequencer were used for sequencing.

The sequences were analysed in two sets to answer two questions. A first set of 52 sequences, each 532 bp long, was used to place Coniochaeta and their Lecythophora anamorphs into a broader ascomycetous context, and a second set of 23 sequences 470 bp long was used for a more detailed analysis of the species concerned. The sets were aligned with Megalign (Lasergene, DNASTAR Inc.) and optimized visually. The phylogenetic analysis was carried out using PAUP (Swofford 2000). For comparison of substitution models, the model test 3.0 for PowerPC (Posada & Crandall 1998) was used. The alignments are available from the third author.

Morphological work was done with a Zeiss microscope Standard 20, using tap water as medium. Measurements are based on living cells.

Results

The likelihood ratio test as well as the Akaike information criterion from the model test resulted in TIMIG as substitution model for the first dataset. Therefore, neighbour-joining analysis was performed with this substitution model. Fig. 1 shows the results of this analysis. The different groups are clearly separated, mostly with a high bootstrap support. Maximum likelihood analysis (ML) resulted in 122975 rearrangements in three nearly identical topologies with a ln likelihood of 7383.09147 each. The position of Sphaeronaemella fimicola seemed to be problematic due to its short sequence, and therefore the trees of the ML analysis are not reproduced. For the second dataset we used the Kimura two-parameter model, as there were only about 50 informative sites and only 22 strains of the Coniochaeta/Lecythophora complex. The resulting neighbour-joining tree is illustrated in Fig. 2. The more complicated models resulted in nearly the same topology and had lower support in bootstrap analysis than the basic model had.

Phylogeny of the first set

Fig. 1

The neighbour-joining tree of 52 species (Fig. 1) shows a well-supported basal trifurcation: the basal ascomycetes (with Taphrina and Protomyces), the true yeasts (with Lipomyces and Saccharomyces), and the higher ascomycetes.

Within the higher ascomycetes, the following groups are well supported: unitunicate pyrenomycetes, Eurotiales, Chaetothyriales, Dothideales, and Pezizales.

The branch unifying the members of unitunicate pyrenomycetes (including Sordariales, Xylariales, Hypocreales, and Microascales) is well supported with a bootstrap value of 99%. The members of Lecythophora and Coniochaeta form a monophyletic clade with a bootstrap support of 81%. Five of the remaining Sordarialean species form a monophyletic branch at some distance to Coniochaeta/Lecythophora. Melanospora fallax (Ceratostomataceae) is situated within the cluster containing the Hypocreales. The cluster containing the Helotiales seems to be a sister group to the unitunicate pyrenomycetes. An additional group is composed of the orders Eurotiales and Oxygenales (bootstrap value 100%), and the Chaetothyriales. Other taxa forming adelophialides or similar conidiogenous cells are dispersed among the unitunicate pyrenomycetes, Helotiales, Chaetothyriales, and Dothideales.
Fig. 1. Topology obtained by neighbour-joining analysis of LSU rDNA sequences of 52 ascomycetes. The topology is rooted with *Taphrina amentorum* and *Protomyces inouei*. Percentage bootstrap values of 1000 replicates are given at each furcation. Values smaller than 50% are not shown.
Phylogeny of the second set

We used Chaetomium sp. to root the phylogeny of an extended set of Coniochaeta/Lecythophora sequences. Figure 2 shows the neighbour-joining tree of 22 species of Lecythophora and Coniochaeta. ‘Coniochaeta ligniaria’ (CBS 424.65) and the two unidentified ‘Lecythophora’ species (sp. 1 and sp. 2), which Weber (2002) recognized as deviating from the other Lecythophora species, were omitted from this set. The analysis of the first set had located these three species in the Helotiales (see Fig. 1).

Four species – C. ligniaria, C. malacotricha, C. pulveracea, and C. velutina – are situated in distinct clusters. The cluster of C. ligniaria strains, consisting of four Lecythophora strains isolated from Picea abies and one ascospore isolate from a C. ligniaria fruitbody (F 3331), is well supported by a bootstrap value of 95%. Lecythophora mutabilis (2 strains, including the ex-type culture) and CBS strain 178.75, designated C. ligniaria, seem to represent a sister taxon to the first cluster. Lecythophora lignicola (CBS 267.33) and L. luteoviridis on the one hand, and the Lecythophora anamorph of C. velutina, L. fasciculata, and a second L. lignicola strain (CBS 641.82) on the other, form a third cluster, also a sister taxon (bootstrap value 93%) to the clusters of C. ligniaria and L. mutabilis.

Two strains of L. hoffmannii form a fourth separate, well-supported group (bootstrap value 100%).

A fifth group is composed of L. decumbens, C. subcorticalis and C. pulveracea. A substituent cluster containing C. subcorticalis and C. pulveracea has a bootstrap support of 100%.

A sixth well-separated cluster contains two Lecythophora states and an ascospore isolate of C. malacotricha (bootstrap value 100%).

Discussion

Observations on the molecular classification of the Ascomycota

The partition of the phylum Ascomycota into three subphyla (Eriksson & Winka 1997): Taphrinomycotina (the basal ascomycetes), Saccharomycotina (budding yeasts and their relatives) and Pezizomycotina (euascomycetes), is confirmed by our LSU rDNA analysis of 52 ascomycetous species. Also, the classes of euascomycetes created by Eriksson & Winka (1997) are visible in our analysis: Sordariomycetes (containing Sordariales, Hypocreales, Xylariales, and Microascales), Leotiomycetes (with Helotiales, Erysiphales, and perhaps Patellariales), Eurotiomycetes (with Eurotales and Onygenales), Chaetothyriomycetes (with Chaetothyriales), Dothideomycetes (with Dothideales), and Pezizomycetes (with Pezizales).

Eriksson & Winka (1997) proposed the class Sordariomycetes for the ‘unitunicate pyrenomycetes’. This classification is also confirmed in an analysis by Tehler et al. (2000) and by our analysis. All tested members of the Sordariales, Hypocreales, Xylariales, and Microascales are included in this clade, which is supported by a bootstrap value of 99%. However, the subclasses Sordariomycetidae, Hypocreomycetidae, and Xylariomycetidae were less sharply delimited.
Fig. 2. Topology obtained by neighbour-joining analysis of LSU rDNA sequences of 23 strains of ascomycetes. The topology is rooted with Chaetommium globosum. Percentage bootstrap values of 1000 replicates are given at each furcation. Values smaller than 50% are not shown. (T: ex-type culture; *: Lecythophora state, isolated from Picea abies or, in the case of C. malacotricha, from bark beetles)

In our analysis the Dothideales were distant from the Chaetothyriales, as in other molecular studies (Untereiner et al. 1995, Haase et al. 1999). The Chaetothyriales (Herpotrichiellaceae), together with the orders Eurotiales and Onygenales, form a monophyletic group (class Eurotiomycetes in Eriksson & Winka 1997) which has a bootstrap support of 68% in our study. Tehler et al. (2000) also considered species of these orders to form ‘a larger eurotialean clade’, a phrase suggesting a close relationship.
In our analysis, _Erysiphe aquilegiae_ clusters within the group of Helotiales, although this grouping lacks bootstrap support. This confirms the proposal of Eriksson & Winka (1997), who included the Erysiphales in their class Leotiomycetes.

_Evernia prunastri_ (Lecanorales) and _Stictis radiata_ (Ostropales) cluster together (Fig. 1), as in the analysis of Platt & Spatafora (2000) of LSU rDNA, but in another position.

**The Lecythophora-Coniochaeta complex**

In neighbour-joining analyses of LSU rDNA, the genus _Lecythophora_ appears as a monophyletic group and as an anamorph of _Coniochaeta_. _Lecythophora lignicola_, the type species, as well as _L. hoffmannii_, _L. mutabilis_, _L. luteoviridis_, _L. decumbens_, and _L. fasciculata_, form a single cluster together with the tested species of _Coniochaeta_, including the type species, _C. ligniaria_, and associated _Lecythophora_ anamorphs. The connection between _Coniochaeta_ and _Lecythophora_ has already been observed by several investigators who obtained lecythophora-like anamorphs in pure cultures of _Coniochaeta_ species (e.g. Schol-Schwarz 1970, Hawksworth & Yip 1981, Mahoney & LaFavre 1981).

The taxonomic position of the genus _Coniochaeta_ has until now not been quite clear. Earlier authors placed this genus in the Xylariaceae (e.g. von Arx & Müller 1954) because of similarity to _Rosellinia_, or in the Sordariaceae (e.g. Munk 1957). Malloch & Cain (1971) created the family Coniochaetaceae for _Coniochaeta_ and _Coniochaetidium_. The existence of this family and its placement in the Sordariales have been accepted by most recent authors (Cecha et al. 1988, Hawksworth et al. 1995, Eriksson & Winka 1997). According to Rogers (1994), on the other hand, the Coniochaetaceae are an isolated family whose relationship with other ascomycetes is obscure. Lee & Hanlin (1999) placed two species of _Coniochaeta_ in the Sordariales on the basis of small subunit rDNA analyses. The two species were separated from the Chaetomiaceae and Sordariaceae in a distinct cluster. Our analyses (Fig. 1) confirm the isolated position of _Coniochaeta_ and _Lecythophora_ species. The cluster containing these species is separated from that of the other Sordariales tested (including representatives of the families Sordariaceae, Lasiosphaeriaceae, and Chaetomiaceae), and is a sister group to the Xylariales and Hypocreales. Bootstrap support, however, is lacking for this conclusion. Likewise the relation of the Sordariales to the Xylariales and Hypocreales could not be resolved clearly. Further investigations with more species of these orders are necessary to clarify these matters prior to the possible introduction of a separate order for the Coniochaetaceae.

_Coniochaeta ligniaria_, _C. velutina_, _C. pulveracea_, and _C. malacotricha_ are clearly separated from each other by LSU rDNA analysis. This is in accordance with morphological observations made by Weber (2002).

An ascospore isolate of _C. ligniaria_ as well as four _Lecythophora_ strains isolated from stems of _Picea abies_ and referred to this species, have identical sequences. The sister group to this _C. ligniaria_ clade contains _L. mutabilis_ and CBS 178.75 catalogued as _C. ligniaria_. _Lecythophora mutabilis_ clearly belongs to the _Coniochaeta_/
Lecythophora group, even though no teleomorph has ever been observed. Our analysis shows that it is closely related to C. ligniaria. It is, however, clearly distinguishable from C. ligniaria by its differently coloured colonies and its chlamydospores (Weber 2002). C. ‘ligniaria’ CBS 178.75 shows a close relationship to L. mutabilis. After microscopical observation of its Lecythophora state and of the fertile perithecia formed in culture, we are convinced that this isolate represents an unidentified, perhaps undescribed species. Its main distinguishing character is the shape and size of spores, which are ellipsoid and measure 8.5-12 × 5.5-6 × 4.5-5.5 μm. In C. ligniaria, ascospores are broadly spindle- or lemon-shaped and somewhat larger (Weber 2002).

Strain CBS 424.65 (‘C. ligniaria’) clusters within the Helotiales. According to the culture label, this should be the strain Rogers (1965) mainly used in his work about cytology and morphology of the anamorph of C. ligniaria. It differs from Rogers’s description by lacking chlamydospores and by showing more uniform conidial sizes. Its main difference from C. ligniaria, however, is that it forms no adelophialides but only discrete phialides, making it a typical Philophora. Rogers clearly figured adelophialides, however, so it is doubtful that this strain truly represents the isolate he studied.

C. velutina clusters together with L. lignicola (two strains), L. luteoviridis, and L. fasciculata, supported by a bootstrap value of only 63%. This arrangement shows these three Lecythophora species as very closely related to C. velutina, matching the morphological findings of Weber (2002). No teleomorph, however, has so far been obtained in culture. LSU rDNA analysis does not support the previously suggested possible identity of L. fasciculata with L. lignicola. Therefore the new combination L. fasciculata is proposed in Weber (2002).

The low bootstrap values within this group entail uncertainty concerning species delimitation. Additional studies encompassing more isolates and other genes are needed to clarify this problematic group.

A second strain labelled L. lignicola (CBS 641.82, from Eucalyptus poles, Australia) is, according to the DNA analysis, not conspecific with the ex-type strain from Sweden, although we found no morphological differences between the isolates.

Although no teleomorph is known for L. hoffmannii s.str. (formerly Philophora hoffmannii), the species is obviously related to Coniochaeta. Apart from the ex-type culture (CBS 245.38) we used a second strain (CBS 140.41), which was originally described as Margarinomyces aurantiacus van Beyma and was synonymized later with P. hoffmannii (van Beyma 1943). This synonymy is here confirmed by molecular methods (Fig. 2). Lecythophora hoffmannii, however, is not identical with any of the Lecythophora or Coniochaeta species treated here.

The group including Coniochaeta pulveracea and C. subcorticalis is well supported by a bootstrap value of 100% (Fig. 2). The weak support for C. pulveracea itself (83%, Fig. 2) results from ambiguities in the sequence obtained from fruitbodies on Picea (E.W. 92/1).

According to Checa et al. (1988), C. subcorticalis is closely related to C. pulveracea. A culture of C. subcorticalis (CBS 551.75) differs from our isolate of C. pulveracea
by its darkening colonies, its chains of chlamydospores, and its ellipsoidal to cylindrical conidia, 3.5 × 1.3 μm, which are smaller than the 4.8–9.9 × 1.5–2.5 μm conidia of C. pulveracea (Weber 2002). In C. pulveracea perithecia initials occur after some weeks, and produce obtuse, clavate, 10–30 μm long setae. Setae from immature fruitbodies of the CBS strain of C. subcorticalis, however, were rather long (up to 50–60 μm), and more or less pointed, covering the whole perithecium. According to Checa et al. (1988), C. subcorticalis has only short pointed setae around the ostiolum. It is therefore not clear whether or not CBS 551.85 is a true C. subcorticalis. Further studies about the delimitation of these species are needed.

Lecythophora decumbens, a further species previously included in the ‘P. hoffmannii group’ of Schol-Schwarz, can be found in the neighbourhood of C. pulveracea and C. subcorticalis, with a bootstrap support of 69%. This species also belongs to the Coniochaeta-Lecythophora complex and is more closely related to C. pulveracea and C. subcorticalis than to the remaining species of the complex. Weber et al. (in Weber 2002) formally combined Phialophora decumbens into Lecythophora.

The ascospore isolate of C. malacotricha and two Lecythophora isolates, all from bark beetles or their galleries in spruce and pine, form another well-supported group.

Other genera with adelphialides or similar conidiogenous cells

All tested species of miscellaneous genera with adelphialides or similar conidiogenous cells cluster outside the Coniochaeta/Lecythophora group. Phialemonium dimorphosporum is placed in the neighbourhood of Xylariales and Hypocreales (Fig. 1). Its teleomorph, if it has one, can be expected to belong to the unitunicate pyrenomycetes. Similarly, species of Acremonium, Cladorrhinum, and part of Phialophora, not dealt with in this study, can be found in the Sordariomycetes (Acremonium in the Hypocreales, Glenn et al. 1996, Cladorrhinum in the Sordariales, Mouchacca & Gams 1993).

All the other genera we tested fall outside of the unitunicate pyrenomycetes. The affinity of Phaeoacremonium chlamydosporum with the Herpotrichiellaceae (Chaetothyriales) was previously detected by Dupont et al. (1998) using molecular methods. This species is now classified in Phaeomoniella Crous & W. Gams (2001). Phialophora americana, the anamorph of Capronia semiimpressa (Candoussau & Sulmont) Untereiner & Naveau (1999), appears amongst the Chaetothyriales, as does Exophiala pisciphila with annelidic conidiogenesis.

The two species of Hypozyuma treated, H. variabilis and H. lignicola, clustered in different groups. The genus Hypozyuma is thus polyphyletic: H. variabilis, the type species of the genus, clusters within the Helotiales, while H. lignicola clusters within the Dothideales (bootstrap value 67%, Fig. 1). The morphological studies revealed small conidia-bearing pegs and masses of budding conidia for H. variabilis and more distinct conidiogenous pegs in H. lignicola. The pegs are similar to those seen in the anamorph of Tromeropsis microtheca in that they are holoblastic, lacking a collarette and periclinal wall thickening. In neither species was phialidic conidiogenesis observed.
The two lecythophora-like species 1 and 2, the CBS strain 424.65 of 'Coniochaeta ligniaria', and Tromeropsis microtheca cluster together with Ascocoryne cylindrium, Cudonia circinans and Neobulgaria pura in the Helotiales, suggesting a close relationship. However, further investigations are still necessary within this group.

Lecythophora is a genus with only few readily discernible morphological characteristics. Reduced phialides similar to adelophialides occur in many other genera in different orders, so it is necessary to carefully adhere to the description of Lecythophora given by Gams & McGinnis (1983) (see also Weber 2002). Above and beyond the characters mentioned in that description, it must be said that Lecythophora has colonies with colours ranging from nearly colourless to dark brown, but with pink to salmon tinged very often present (see Weber 2002). Colonies may be partially covered with hyphal strands, so the slimy appearance caused by the masses of conidia is not always clearly visible. The most reliable characteristic for ascertaining that a strain is a Lecythophora is the presence of fruitbodies of Coniochaeta. Often, however, these are not formed.

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