Redefining Ellisembia sensu stricto with a reassessment of related taxa in Sordariomycetes

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Abstract

The generic limits of the large and polyphyletic genus *Ellisembia* are redefined in a strict sense based on a recent collection of its type species, *E. coronata*, on the original host at the type locality in Germany. Multigene phylogenetic analyses revealed that the fungus belongs to *Sporidesmiaceae* (*Sordariomycetes*) where it groups together with other morphologically similar ellisembia-like taxa in a distinct monophyletic lineage distant from *Sporidesmium*. *Ellisembia* is therefore restricted to those members of this novel group having distoseptate conidia and producing none or a few percurrent extensions. Its previous synonymy under *Sporidesmium* is rejected and four novel combinations are proposed including *E. pseudobambusae* comb. nov., recently collected on a dead branch of *Arundinaria* sp. (*Poaceae*) in Texas, USA. To further stabilize the application of this generic name, *Ellisembia* is lectotypified with an authentic specimen of *S. coronatum*, the basionym of *E. coronata*, preserved at G. Additionally, the genus *Lomaantha*, typified by *L. pooga*, is expanded and emended to include *E. brachypus* and related ellisembia-like taxa grouping together in a distinct lineage within *Chaetosphaeriaceae* (*Sordariomycetes*) distant from *Sporidesmiaceae*. A reassessed taxonomy for members of this monophyletic clade is proposed including six new combinations. The presence of distinct pores in the conidial distosepta was assessed for this group of species and their developmental processes are described for *L. brachypus* and *L. folliculata* based on fresh and herbarium specimens. *Sporidesmiella angustobasilaris*, which typifies the genus *Anasporidesmiella*, is reduced to synonymy of *L. folliculata* upon examination of its type material.

Introduction

The taxonomy of *Sporidesmium* Link has long been a contentious issue especially since Subramanian (1992) rearranged its many taxa in different genera based on type of conidial septation, presence or absence of conidiophores and whether they extend percurrently or not including certain characteristics of these extensions. These features have been repeatedly shown to be phylogenetically irrelevant for generic separation, and morphology-based delimitation of these genera has proved to be problematic in the absence of molecular data (Shenoy et al. 2006; Su et al. 2016; Yang et al. 2018; Wu and Diao 2022). One of these segregated genera is *Ellisembia* Subram., with its type species based on *Sporidesmium coronatum* Fuckel. The genus was originally defined as having distoseptate conidia and conidiophores lacking or with rare percurrent extensions. *Ellisembia* is presently known to be polyphyletic and species with available molecular data are currently placed in four separate clades in *Sordariomycetes* including the families *Chaetosphaeriaceae, Distoseptisporaceae, Sporidesmiaceae* and the order *Xylariales* (Hyde et al. 2019).

The family *Sporidesmiaceae* was resurrected to accommodate some taxa with available molecular data and morphology similar to that of *S. ehrenbergii* M.B. Ellis, the lectotype species of *Sporidesmium* (Su et al. 2016). The clade they formed was regarded as the genus sensu stricto, but ultimately this designation is a working hypothesis in the absence of DNA sequence data for the lectotype (Delgado et al. 2018). Some ellisembia-like species with distoseptate conidia were revealed to belong to this lineage and
therefore Su et al. (2016) synonymized *Ellisembia* under *Sporidesmium*. Subramanian's concept of *Sporidesmium*, originally restricted to euseptate taxa, was expanded to include distoseptate species such as *E. bambusicola* (M.B. Ellis) J. Mena & G. Delgado and *E. minigelatinosa* (Matsush.) W.P. Wu which were retained in *Sporidesmium*. However, authors such as Hyde et al. (2019), Yang et al. (2021) and Wu and Diao (2022) preferred to keep *Ellisembia* as a separate genus until molecular data become available for the type species of both genera.

The family *Chaetosphaeriaceae*, on the other hand, comprises an array of morphologically diverse anamorphs, mostly phialidic but also ellisembia-like hyphomycetes (Réblová and Winka 2000; Réblová et al. 2020; Wu and Diao 2022). Members of this group are characterized by pigmented, distoseptate conidia, macronematous conidiophores with or without percurrent extensions and telemorphs with multiseptate, versicolorous ascopores in asci with a non-amyloid apical annulus, persistent paraphyses and immersed ascomata (Hyde et al. 2019). Réblová and Winka (2001) first described the teleomorphic ascomycete *Lecythothecium duriligni* Réblová & Winka with a *Sporidesmium folliculatum* (Corda) E.W. Mason & S. Hughes anamorph and placed it within *Chaetosphaeriales* using LSU sequence data. Later, Shenoy et al. (2006) revealed that *E. brachypus* (Ellis & Everh.) Subram. clustered with *Le. duriligni* in a strongly supported clade within *Chaetosphaeriales* following a comprehensive phylogenetic assessment of sporidesmium-like fungi using nuclear ribosomal and *RPB2* sequence data. Magyar et al. (2011) described a distinct anamorph isolated from grapevine and tree bark in Hungary that was placed sister to *Le. duriligni* based on analysis of LSU sequences. They introduced the monotypic genus *Pyrigemmula* D. Magyar & Shoemaker, with *P. aurantiaca* D. Magyar & Shoemaker as the type species, to accommodate it. Subsequent phylogenetic studies dealing with novelties or peripheral genera belonging to *Chaetosphaeriales* have consistently shown the monophyly and strong support for this *E. brachypus–Lecythothecium–Pyrigemmula* clade. Hyde et al. (2019) recently described a second holomorphic member of this lineage, *E. aurea* Réblová & J. Fourn., also with an ellisembia-like anamorph. They recommended using the name *Ellisembia* for species placed in this clade until the systematic position of *E. coronata* is revealed, an approach that has been followed by some authors (Wu and Diao 2022; Yang et al. 2023) but not others (Réblová and Nekvindová 2023). Hyde et al. (2019) also suggested that members of this clade are congeneric and could be accommodated into the morphologically similar *Pyrigemmula* once the distant position of the type species of *Ellisembia* is confirmed. Following the above-mentioned criteria, the monotypic *Le. duriligni* has been treated under the name of its anamorph *E. folliculata* (Corda) Subram. in recent phylogenetic studies (Réblová et al. 2021b, d; Zhang et al. 2022). Other authors, however, continue using its original name of *Le. duriligni* (Yan et al. 2023; Zheng et al. 2020, 2021). Similarly, Su et al. (2016) treated *Ellisembia* as a synonym of *Sporidesmium* followed by Luo et al. (2019) who collected *E. brachypus* on submerged decaying wood in China and retained its name in *Sporidesmium*. In the case of novelties described or reported without molecular data and phylogenetic position, they continue to be placed in *Ellisembia* following the traditional morphological concept (Kuo and Goh, 2019; Ma et al. 2020; Pereira et al. 2022; Qiao et al. 2017, 2018; Xia et al. 2016, 2017), whereas ellisembia-like taxa mostly resembling *E. adscendens* (Berk.) Subram. are placed in *Distoseptisporaceae* (Afshari et al. 2023; Luo et al. 2018, 2019; Su et al. 2016; Yang et al. 2018, 2021; Zhang et al. 2022).
These different approaches in naming ellisembia-like taxa, particularly in *Chaetosphaeriaceae*, are rather confusing and reflect the need for a consensus on the taxonomy of these lineages with a relatively stable molecular phylogeny. At the center of this counterproductive situation is the absence of molecular data for the generic type, *E. coronata*, and the lack of information on its phylogenetic placement in Pezizomycotina. A first attempt in this direction was recently implemented by Wu and Diao (2022) who further expanded *Ellisembia* to include *Lecythothecium* and *Pyrigemmula* as its synonyms following the recommendation in Hyde et al. (2019) mentioned above. Wu and Diao also placed *Lomaantha* Subram. (Subramanian 1954) for the first time in *Chaetosphaeriaceae* based on specimens collected in China and suggested that this genus could be adopted as a potential generic name for ellisembia-like fungi in *Chaetosphaeriaceae*. However, two novelties recently described in this clade, *E. reblovae* W.P. Wu & Y.Z. Diao and *E. aquirostrata* J. Yang, Jian K. Liu & K.D. Hyde, were still retained in *Ellisembia* (Wu and Diao 2022; Yang et al. 2023).

During mycological surveys carried out in central Europe and subtropical Texas, USA, some ellisembia-like hyphomycetous anamorphs inhabiting dead plant debris were collected. Emphasis was made on targeting the type species of the genus in its type locality of west-central Germany as well as other poorly collected species still lacking DNA sequence data. The aims of this paper are twofold: first, to characterize these collections and isolates in detail using morphological, cultural and molecular data and, second, to provide a more effective taxonomic approach towards the problematics surrounding members of *Ellisembia* in *Chaetosphaeriaceae* and *Sporidesmiaceae*. Morphological and molecular evidence presented in this study support the proposal of new combinations in both *Ellisembia* and *Lomaantha* following the recommendations and data provided by Hyde et al. (2019) and Wu and Diao (2022).

**Materials and methods**

**Morphological and cultural studies**

Fresh specimens were collected on plant debris obtained in the vicinity of Wiesbaden, Germany, and southeastern Texas, USA, between the years 2020 and 2022. Materials were briefly washed off under running tap water and incubated in moist chambers at room temperature (23–25°C) for a few days. Sporulating structures were located under the stereoscope and single conidia were picked-up directly using a sterile needle for isolation. They were transferred to 2% Malt Extract Agar with 0.01% chloramphenicol (MEA), Potato dextrose agar (PDA) and potato carrot agar (PCA) plates followed by incubation at 25°C. Once conidia germinated in around 24 h they were further transferred aseptically to clean MEA or PDA plates and re-incubated under similar conditions. Colony features were recorded after time periods of 2–3 weeks or longer. Fungal structures were mounted in Melzer’s reagent, lacto-cotton blue or lactic acid, heated to remove bubbles, and examined under an Olympus BX45 microscope or using differential interference contrast (DIC) on an Olympus BX-51 microscope with an Olympus DP72 digital camera (Olympus, Tokyo, Japan). Minimum, maximum, 5th and 95th percentile values were calculated based on 50 measurements of each structure at 1000× magnification with outliers given in parenthesis. Air dried pieces of specimen BPI 911246 containing colonies of *E. pseudobambusae* were observed under
a JEOL JSM IT-200 (Jeol Ltd., Tokyo, Japan) scanning electron microscope (SEM). They were mounted on an aluminum stud and observed at 3–5 kV, with a working distance of approximately 14 mm, a probe current of 30 nA, and a pressure of 10 Pa at 23°C after the chamber achieved local thermodynamic equilibrium. Voucher specimens are deposited in BPI or PRC and living strains in CBS or CCF. Fungaria and culture collection acronyms throughout the text follow Index Herbariorum (http://sweetgum.nybg.org/science/ih/) and the Culture Collections Information Worldwide of the WFCC-MIRCEN World Data Center for Microorganisms (http://www.wfcc.info/ccinfo/), respectively. Fungal names follow Index Fungorum (http://www.indexfungorum.org/) and host plant names are shown according to the International Plant Names Index (https://www.ipni.org).

**DNA extraction, PCR amplification and sequencing**

In the case of strains belonging to *E. brachypus*, genomic DNA was extracted from two weeks old cultures grown on MEA using a custom protocol outlined in Maciá-Vicente et al. (2022). DNA from the strains of *E. coronata* and *S. pseudobambusae* was extracted using a Zymo Research Fungal/Bacterial Kit (Zymo Research, Orange, USA). Nuclear ribosomal DNA including the complete internal transcribed spacer (ITS nrDNA) region and the first 900 bp of the 5' end of the large subunit (LSU nrDNA) together with fragments of the translation elongation factor 1α (*TEF1*) and RNA polymerase II second largest subunit (*RPB2*) were amplified with the primer sets ITS1F/ITS4, LR0R/LR7, 983F/2218R and RPB2-5f/fRPB2-7cR, respectively (Hopple and Vilgalys 1994; Liu et al. 1999; Rehner and Buckley 2005; White et al. 1990). The PCR products were purified and sequenced at Eurofins Genomics (Cologne, Germany) with the same primers used for amplification. Contig sequences were assembled using EMBOSS v6.6.0.0 (Rice et al. 2000) and deposited in GenBank.

**Taxon sampling and phylogenetic analyses**

Newly generated sequences and their closest hits in GenBank were selected and downloaded to build two separate datasets, one for *Sporidesmiaceae* and another one for *Chaetosphaeriaceae*. An unpublished ITS-LSU sequence of *E. brachypus* was retrieved from the NBRC website (http://www.nite.go.jp/en/nbrc/cultures/index.html), whereas an unpublished ITS sequence belonging to *E. folliculata* was downloaded from the NARO Genebank database (https://www.gene.affrc.go.jp/databases_en.php) and both added to the *Chaetosphaeriaceae* dataset. Additional sequences from recent phylogenetic studies of *Chaetosphaeriaceae* (Réblová et al. 2020, 2021a, c) and *Sporidesmiaceae* (Bao et al. 2021) were also included (Table 1). Sequences from strains *Buergenerula spartinae* ATCC 22848 and *Magnaporthe salvinii* M21 were used as outgroups for the *Sporidesmiaceae* phylogeny, whereas those of *Gelasinospora tetrasperma* CBS 178.33 and *Lasiosphaeria ovina* SMH 4605 were outgroups for the *Chaetosphaeriaceae* phylogeny. The novel *TEF1* sequences obtained from the Texas specimens of *E. brachypus* were used only for pairwise comparisons with those of available strains due to missing data for this marker among ellisembia-like chaetosphaeriaceous taxa. Sequences were aligned separately with MAFFT v.7.487 on the online server (https://mafft.cbrc.jp/alignment/server/index.html) (Katoh and Standley 2013; Katoh et al. 2019). Phylogenetic relationships were first inferred for individual datasets using Maximum Likelihood (ML) in
RaxML v.8.2.12 (Stamatakis 2014) on the CIPRES Science Gateway server (Miller et al. 2010) and Bayesian inference (BI) using MrBayes 3.2.7a (Ronquist et al. 2012). Analyses were run following the settings outlined in Delgado et al. (2022). Separate phylogenies were topologically compatible for the most part (not shown) and therefore alignments were concatenated in MEGA6 (Tamura et al. 2013) and run using similar settings. Best fit-substitution models were obtained also in MEGA using the corrected Akaike Information Criterion with the GTR + G + I selected for all datasets. Trees were visualized and edited in MEGA and Inkscape (https://inkscape.org). They are deposited together with alignments used for pairwise and phylogenetic analyses at figshare.com (10.6084/m9.figshare.24612297).

Results

Pairwise comparison of sequences

A total of four strains of ellisembia-like hyphomycetes were obtained as a result of fieldwork. Three of them belonging to *E. brachypus* or *E. pseudobambusae* were isolated from materials collected in Texas, USA, whereas one strain was isolated from a specimen of *E. coronata* collected in Germany. Intraspecific pairwise comparisons between the available ITS sequences of *E. brachypus* showed that the Texas strains were identical to strain NN 076460 from China. However, they differ by one C-T transition from strains MFLUCC 18-1573, NBRC 104942 and NN 050658 at position 104 along the length of their 431 aligned positions. In the case of the LSU, all new and available sequences were identical except for another C-T transition at position 353 for strain MFLUCC 18-1573 along the length of their 474 aligned positions. Interestingly, the *TEF1* sequences of the Texas strains, OK383438 for CBS 147395 and OK383439 for CBS 147396, showed more variation and differed in one G-T transversion at position 306, one C-G transversion at position 336 and one C-T transition at position 703 along a length of 766 aligned positions. The only *TEF1* sequence of *E. brachypus* available in GenBank belongs to strain MFLU 18-1615 from Thailand and differs from the *TEF1* sequences of the Texas strains in five positions. In the case of *E. folliculata*, the LSU sequence available in GenBank was considerably longer (1826 bp) compared with the one belonging to the type of *Le. duriligni* CBS 101317 with only 870 bp. However, they were almost identical and overlapped well for 873 bps except for a G-A transition at position 76 and gaps at positions 382, 453, 487 of the pairwise alignment.

Phylogenetic analyses

The concatenated ITS-LSU-*RPB2* alignment of the *Sporidesmiaceae* dataset consisted of 81 taxa and 2489 characters including the outgroups, 624 from the ITS alignment, 826 from the LSU and 1039 from the *RPB2*. The single best scoring RaxML tree with a final ML optimization likelihood = -28477.599526 is presented in Fig. 1. The tree is similar in topology to the 50% majority rule consensus tree of the 9978 sampled trees in the Bayesian analysis. *Sporidesmiaceae* was recovered as a strongly supported monophyletic clade (100% BS, 1 BPP) consisting of four distinct well supported lineages: the *Sporidesmium* clade (95% BS, 1 BPP), including sporidesmium-like taxa such as *S. aturbinatum* and *S. parvum* among others with obpyriform or obclavate conidia together with the teleomorphic *S.*
thailandense; the Lylea clade (99% BS, 1 BPP) containing strains of S. tetracoilum (formerly L. tetracoilum) and its teleomorph along with L. dalbergiae; the Ellisembia s. l. clade (81% BS, 0.99 BPP) including ellisembia-like species such as S. appendiculatum, E. minigelatinosa and S. chiangmaiense having distoseptate conidia ending in an elongated apical cell surrounded by a gelatinous sheath or cap; and the Ellisembia s. str. clade (100% BS, 1 BPP), including E. coronata, the type species of Ellisembia represented by a fresh collection obtained on its original host at the type locality in Germany, and morphologically similar taxa such as E. bambusicola and four other species currently placed within Sporidesmium e.g. S. cangshanense, S. melaleucae, S. spiraeae and S. pseudobambusae, the latter represented by a specimen recently collected in Texas.

The concatenated ITS-LSU alignment belonging to Chaetosphaeriaceae consisted of 54 taxa and 1405 characters including the outgroups, 545 from the ITS alignment and 860 from the LSU. The single best scoring RaxML tree with a final ML optimization likelihood = -9009.119585 (Fig. 6) was similar in topology to the 50% majority rule consensus tree of the 2933 sampled trees in the Bayesian analysis. The Lomaantha/Ellisembia clade formed a strongly supported monophyletic group (100% BS, 1 BPP). The Texas strains of E. brachypus grouped together with five other strains available in GenBank or retrieved from NBRC with maximum support (100% BS, 1 BPP). They were sister to the only strain available of the morphologically similar E. aequostrata GZCC 20-0503a and a strain named ‘Pyrigemmula’ sp. BCC 28210 with strong support (87% BS, 0.99 BPP). The available strains of Lomaantha pooga, E. aurea and P. aurantiaca each formed strongly supported groups (100% BS, 1 BPP). A strain belonging to E. folliculata CBS 147152 and an ex-type strain of Le. duriligni CBS 101317 having an E. folliculata anamorph clustered together as expected but only with moderate ML support (74% BS). The only strain available of E. reblavae NN 044776 grouped sister to the remaining six taxa. A strain named E. folliculata MAFF 240276 grouped distant from the Lomaantha/Ellisembia clade and clustered together with chloridium-like Gongromeriza and Chaetosphaeria species. It formed a highly supported clade (100% BS, 1 BPP) with Ch. guttulata MFLU 18-1617.

Taxonomy


Descriptions and illustrations

Ellis (1958); Subramanian (1992); Wu and Zhuang (2005); this study

Notes

In view of the results of our phylogenetic analyses together with their shared morphological features, Ellisembia is restricted here to the members of that novel lineage within Sporidesmiaceae which includes
E. coronata and some other morphologically similar species having distoseptate conidia and conidiophores producing none or a few percurrent extensions. This is in agreement with the original generic concept of Subramanian (1992) but different from Hyde et al. (2019) and Wu and Diao (2022) who recently adopted Ellisembia for those taxa within the distant family Chaetosphaeriaceae. Therefore, we propose the following four new combinations within the genus and amend the description of E. coronata based on the study of its freshly collected material.

**Ellisembia cangshanensis** (Z.L. Luo & K.D. Hyde) G. Delgado, comb. nov.

MycoBank: MB#851172


**Description and illustration**

Su et al. (2016)

**Notes**

This fungus was originally described as *S. aquaticum* on decaying wood submerged in a freshwater stream in China (Su et al. 2016). This name is a homonym of a previously described species, *S. aquaticum* Cabello, Mengasc. & Aramb. (Arambarri et al. 1989), and therefore invalid. Luo et al. (2019) replaced it with the name *S. cangshanense* but did not cite an identifier from a recognized repository in the protologue so a new one was issued in Index Fungorum. In all respects, this species matches well *Ellisembia* in having short conidiophores, 14–23 µm long, bearing determinate conidiogenous cells and narrowly obclavate or subcylindrical, long rostrate, 9–11-distoseptate, pale brown conidia with a pale brown to brown conico-truncate basal cell. Considering its placement and morphological similarity with related species within the *Ellisembia* s. str. clade, a new combination is proposed to accommodate this fungus.


*Basionym: Sporidesmium coronatum* Fuckel, Jb. nassau. Ver. Naturk. 27–28: 77 (1874) [1873-74]

≡ Clasterosporium coronatum (Fuckel) Sacc., Syll. fung. (Abellini) 4: 385 (1886)

*Colonies* effuse, hairy. Mycelium mostly immersed in the substratum, composed of branched, septate, pale brown, smooth hyphae, 2–4 µm wide, with swollen, brown to dark brown, 5–10 µm wide cells around the base of conidiophores. *Stromata* absent or rudimentary and composed of a few swollen cells at the
base of groups of conidiophores, brown to dark brown or blackish brown. **Conidiophores**
macronematous, mononematous, solitary or aggregated in small groups of 2–3 which may be loosely to
somewhat densely grouped, arising from rudimentary stromata when in groups, erect, simple, straight or
slightly flexuose, brown to dark reddish brown, (1−)2−5(−6)-septate, up to 66 µm long, 5–7 µm wide, 7−9
µm wide at base, with 0−2 ampulliform, lageniform or subcylindrical percurrent extensions, 0−1-septate,
pale brown to brown, sometimes dark brown at the proximal end, 7–18 × 5–7 µm. **Conidiogenous cells**
monoblastic, integrated, terminal, percurrent, brown, apex truncated. **Conidia** narrowly obclavate, less
often subcylindrical or subfusiform, sometimes short rostrate, straight or slightly flexuose, pale brown,
smooth, 7−14-distoseptate, with small pores in distosepta slightly darkened in DIC, (40−)52−89(−101) ×
8−11 µm, occasionally bearing wall remnants around the basal and proximal cells as a result of aborted
conidia initials which continue growing at a later time; apical cell subhyaline, rounded or tapered toward a
rounded tip, with or without a mucilaginous cap; basal cell conico-truncate or less often short-cylindrical,
brown to dark brown, 4−6 (−7) × 4.5−5.5 µm.

**Colonies** on PCA slow growing reaching 8−10 mm diam. after 30 days at 25°C, velvety, flat, white, pale
cream and slightly raised at the center, margin somewhat undulose, reverse dull white. **Colonies** on PDA
similar to PCA but reaching 13−15 mm diam after 30 days at 25°C, whitish cream to cream, yellow and
slightly raised at the center, margin entire, reverse dull cream. **Cultures** sterile.

**Typification**

Germany, Hesse, Niederwalluf, on dried twigs of *Philadelphus coronarius* L., s.d., leg. K.W.G.L. Fuckel
(G00266276, lectotype designated here).

**Other specimens examined**

Germany, Hesse, Niederwalluf, by the northwest side of Sankt Johannes der Täufer Catholic church,
50°02′03.7″N, 8°09′38.4″E, 86 m a.s.l., on dead twig of *P. coronarius*, 28 Sep 2022, leg. G. Delgado & M.
Piepenbring (PRC 9257, CCF 6699); Germany, Hesse, Niederwalluf, on dried twigs of *P. coronarius*, s.d.,
leg. K.W.G.L. Fuckel (IMI 11864, slides).

**Notes**

The original material deposited in G, designated here as the lectotype, consists of several twigs of *P.
coronarius* having effuse colonies of *E. coronata* in some of them. The other specimen examined,
originally deposited in IMI and now in K, consists of two permanent slides in poor condition but structures
are still rather visible. A comparison between them and the fresh specimen described above shows they
are morphologically similar although a few minor differences were noticed. Conidia in G00266276 were
reddish brown, probably due to the age of the material, paler toward the apex and often long obclavate-
rostrate, 8−14(−18)-distoseptate and (45−)52−92(−113) × 8−10 µm in size, the longer ones having more
distosepta. The basal cells were more often short-cylindrical, less often conico-truncate, brown but rarely
dark brown and 3−5(−6) × 4−4.5 µm in size. This is consistent with the drawing in the protologue (Fuckel
1874) which depicts a single long obclavate-rostrate conidium with a short-cylindrical basal cell. Conidiophores matched well and measured up to 49 µm long, 5–6 µm wide, and bear 0–2 lageniform, 0–1-septate percurrent extensions. Conidia in the IMI slides were mostly obclavate or subfusciform as reflected in the standardized description of Ellis (1958). He did not properly depicted the brown colored conidal basal cells but they were confirmed in both the G and IMI specimens. Moreover, Ellis (1958) described shorter conidia, 35–70 µm long, whereas the original description mentioned a length of 96 µm in agreement with our specimen which possesses similarly longer conidia, probably as an effect of incubation in a moist chamber previous to isolation. Gelatinous caps were not detected in the original specimen or the IMI slides and most likely they are now missing due to their age and condition. Ellis (1958) did not mention this feature either, but he never referred to or depicted gelatinous caps in his descriptions of sporidesmium-like fungi. A rudimentary stroma composed of a few swollen cells was found at the base of groups of conidiophores in agreement with Ellis (1958) who reported 'swollen, rather dark hyphal cells at the point of origin of the conidiophores'. In general, the three specimens overlap well and, therefore, we consider our material, collected on the original host plant species at the type locality, as a good representative of the fungus.

Ellisembia melaleucae (Crous) G. Delgado, comb. nov.

MycoBank: MB#851174


Description and illustration

Crous et al. (2018)

Notes

Crous et al. (2018) described this species based on two specimens collected on Melaleuca sp. (Myrtaceae) in Australia. The fungus is characterized by short, 1–4-septate conidiophores, apparently lacking percurrent extensions, and obclavate, mid brown conidia, with conico-truncate basal cells and 5–21 distosepta having small pores in them. Morphologically, it fits well the remaining members of the Ellisembia s. str. clade in having similarly shaped distoseptate conidia and conidiophores lacking percurrent extensions. Based on its phylogenetic placement distant from the putative Sporidesmium s. str. clade, the fungus is transferred here to Ellisembia.

Ellisembia pseudobambusae (P.M. Kirk) G. Delgado & Koukol, comb. nov. (Figs. 4a–l, 5)

MycoBank: MB#851176


Colonies effuse, hairy, black. Mycelium mostly immersed in the substratum, composed of branched, septate, smooth, pale brown to brown hyphae, 1.5–4 µm wide. Conidiophores macronematous, mononematous, solitary or aggregated in loose groups, simple, straight or flexuous, sometimes curved at the base, 3–7(–10)-septate, cylindrical, smooth, brown to dark brown, thick-walled, (39–)46–105(–117) × 4–7 µm, often swollen at their base and 6–8 µm wide, with 0–4 mostly lageniform or subcylindrical, rarely narrowly doliiform, 0–1-septate percurrent extensions, pale brown to brown or sometimes dark brown at the proximal end, (8–)10–22(–25) × 3–7 µm. Conidiogenous cells monoblastic, integrated, terminal, percurrent, brown to dark brown, apex truncated, sporadically bearing funnel-shape wall remnants of aborted conidia associated or not with extensions. Conidia narrowly obclavate, sometimes subfusiform or subcylindrical, often rostrate, golden brown to brown, paler toward the apex, smooth, straight or slightly flexuous, sometimes bent, 9–17-distoseptate, occasionally constricted at one septum, 61–117(–131) × 8–10 µm in the broadest part; basal cell conico-truncate, short conico-truncate or short cylindrical, brown to dark brown, 3–7 × 3–4(–5) µm, apex sometimes rounded or more often gradually tapering into an euseptate, subhyaline, subacute beak 2–3 µm wide at the tip in older, longer conidia.

Colonies on MEA very slow growing reaching 6–8 mm diam. after 2 mo at 25°C, velvety, irregular, somewhat cerebriform, convex and raised 3–4 mm, yellowish orange at the center, creamy toward the edges, margin irregular, reverse yellowish to pale amber, cracking the medium and sterile after 3 months incubation. Colonies on PCA similar to those on MEA but sporulation was obtained after 1 mo. Conidiophores solitary or aggregated in small groups of up to 3, cylindrical, straight or slightly flexuous, smooth, 1–3-septate, pale brown to brown, 29–51 × 4–5 µm. Conidiogenous cells cylindrical or subcylindrical, determinate, apex truncate, 14–18.5(–21) × 4–5 µm. Conidia similar to those on natural substrate, obclavate, often rostrate to long obclavate rostrate, brown, paler brown to subhyaline toward the apex, smooth, straight or flexuous, 9–16-distoseptate, (80–)89–120(–136) × 7.5–10 µm, with small pores in distosepta, darkened and thickened in DIC; basal cell conico-truncate, brown.

Specimen examined

United States, Texas, Montgomery County, The Woodlands, George Mitchell Nature Preserve, along the Main Trail, 30°08'49.3"N, 95°30'46.9"W, 38 m a.s.l., on dead branch of Arundinaria sp., 8 May 2022, leg. G. Delgado (BPI 911246; CCF 6709).

Other specimen examined


Notes: The Texas specimen described above agrees well with the redescription of the holotype of S. pseudobambusae from United Kingdom made by Hernandez and Sutton (1997). They share conidia almost identical in size and shape: 65–118 × 8–10 µm and 8–18 distosepta, but percurrent extensions in
the protologue were described as cylindrical to narrowly doliiform whereas those of the Texas material are more often lageniform. In culture, the fungus behaves like on natural substrate but conidiophores were shorter and conidiogenous cells were determinate, cylindrical or subcylindrical and distinctly truncate at the apex. Kirk (1981) mentioned a hyaline gelatinous cap that occasionally appeared on the conidial apices. However, this feature was not detected in our specimen on natural substrate or in culture in which conidia are gradually tapered toward an elongated apex likely formed as an effect of incubation in moist chamber previous to isolation or due to growth on synthetic media. The illustration of Hernandez and Sutton (1997) based on the holotype shows mostly rounded but sometimes elongated conidial apices. *Sporidesmium carrii*, a rarely collected species, was originally considered an appropriate name for our collection and the holotype of this species was examined during this study. However, numerous subtle differences were found that are discussed in detail in the Discussion.

**Ellisembia spiraeae** (Crous) G. Delgado, comb. nov.

MycoBank: MB#851177

*Basionym: Sporidesmium spiraeae* Crous, in Crous et al., Persoonia 47: 217 (2021)

**Description and illustration**

Crous et al. (2021)

**Notes**

This species was originally described from *Spiraea japonica* (*Rosaceae*) in The Netherlands (Crous et al. 2021). Morphologically, it is similar to our specimen of *E. coronata* from Germany in having obclavate, sometimes short-rostrate, pale brown conidia, (4−)6−10 distosepta bearing small pores in them and similar in size, (45−)70−85(−100) × (8−)9(−10) µm, with a dark brown, conico-truncate basal cell and short, 15−40 × 5−7 µm, 1−4-septate conidiophores, solitary or aggregated in clusters. However, conidiogenous cells were described as subcylindrical but percurrent extensions were not mentioned originally and are not visible in the illustration of the protologue. Phylogenetically, both species grouped distantly within the *Ellisembia* s. str. clade despite their strong morphological resemblance. Considering its placement and morphological similarity with related species in *Sporidesmiaceae*, the fungus is transferred here to *Ellisembia*.


Illustrations

Subramanian (1954), Ma et al. (2011), Wu and Diao (2022)

*Emended description:* Colonies effuse, black to brown, hairy. Mycelium mostly immersed in the substratum and composed of branched, septate, smooth, brown hyphae. Anamorph: Conidiophores macronematous, mononematous, simple, erect, cylindrical, brown, septate, or reduced to a conidiogenous cell. Conidiogenous cells monoblastic, integrated, terminal, determinate or extending percurrently a few times. Conidia acrogenous, cylindrical, obclavate or narrowly fusiform, distoseptate with cell lumina often reduced, simple, rostrate or not, with or without a filiform, simple or branched apical appendage and having distinct pores often associated with darkened and thickened distosepta. Teleomorph: Ascomata perithecial, immersed with protruding necks or becoming superficial, flask-shaped, glabrous, ostiolate. Perithecial wall leathery, consisting of two distinct layers. Ostiolar canal periphysate. Paraphyses persistent, hyaline, branched, anastomosing, septate. Asci unitunicate, 8-spored, cylindrical to clavate; ascal apex with nonamyloid, refractive apical annulus. Ascospores ellipsoidal to fusiform, transversely septate, versicolorous, central cells brown, end-cells hyaline, smooth-walled, without mucilaginous sheath or appendages.

*Notes:* Lomaantha as previously defined (Ma et al. 2011; Subramanian 1954; Wu and Zhuang 2005; Wu and Diao 2022) was characterized by sporidesmium-like anamorphs having conidia with hyaline, aseptate and branched apical appendages. A broader generic concept is here proposed after Wu and Diao (2022) who synonymized Pyrigemmula with those anamorphic or holomorphic Ellisembia species placed in a distinct clade in Chaetosphaeriaceae. The expanded Lomaantha now contains novel morphological features such as the presence of a teleomorph and conidiophores reduced to conidiogenous cells as well as conidia with or without simple or branched apical appendages and mostly bearing distinct pores in the distosepta. This latter character of septal pores has been neglected in most descriptions of ellisembia-like chaetosphaeriaceous anamorphs but it is present in most species within this lineage as shown below. With the recent placement of Lomaantha within the ellisembia-like chaetosphaeriaceous clade (Wu and Diao 2022), the genus is considered here to better accommodate this group of taxa and the following six new combinations are proposed:

Lomaantha aquirostrata (J. Yang, Jian K. Liu & K.D. Hyde) G. Delgado & Koukol, comb. nov.

MycoBank: MB#851178


*Description and illustration*

Yang et al. (2023)
Notes

Yang et al. (2023) recently described this species based on a single specimen collected on a decaying twig submerged in a freshwater stream in China. The fungus strongly resembles *E. brachypus* in all respects including the presence of distinct pores in distosepta. Its cultural features, however, are different from those reported for *E. brachypus*. Colonies of *L. aquirostrata* on PDA are yellowish white, raised and pale brown in the center, with concentric rings and somewhat sulcate. They also lack the red diffuse pigment seen in the Texas isolates and other strains of *E. brachypus*.

*Lomaantha aurantiaca* (D. Magyar & Shoemaker) G. Delgado & Koukol, comb. nov. (Fig. 7g–i)

MycoBank: MB#851179


Description and illustrations

Magyar et al. (2011), this study

Specimens examined

Hungary, Pest County, Gőd, 47°42′58.46″N, 19°08′03.18″E, on bark of *Platanus hybridus* Brot., 27 Oct 2009, leg. D. Magyar (BP 100757); idem, Visegrád, on bark of *Elaeagnus angustifolia* L., 12 May 2010, leg. idem (Tk1005/1).

Notes

Compared with other members of this chaetosphaeriaceous lineage, *L. aurantiaca* morphologically deviates in many respects from the remaining taxa. Its conidiophores when present are micronematous, short and branched bifurcately but they are usually reduced to ovoid, pyriform, ampulliform or rarely spherical conidiogenous cells arising directly from the hyphae and ending up in a solitary pore, 2 µm in diam. They produce ellipsoidal, thin-walled, 0–5(–7)-distoseptate conidia lacking apical appendages or distinct pores in the distosepta. An examination of two representative specimens of the fungus confirmed the absence of this latter character. The inner lateral wall is thin in early stages of development but it becomes moderately thick in older conidia. Its width was found to vary somewhat depending on the conidia width, with cell lumen not distinctly reduced and squarish shaped in wider conidia or distinctly reduced and narrowly cylindrical in narrower conidia. They often show a single pore at the base which is sometimes inconspicuous as a slight depression of the outer basal wall or some other times distinct, slightly thickened and darkened or rarely somewhat protruding. These basal pores are a continuation of the solitary channel visible at the tips of the conidiogenous cells.
**Lomaantha aurea** (Réblová & J. Fourn.) G. Delgado, comb. nov.

MycoBank: MB#851180


**Description and illustration**

Hyde et al. (2019)

**Notes**

This is one of the two holomorphic members of this chaetosphaeriaceous lineage linked with an ellisembia-like anamorph, the other one is *L. folliculata*. The fungus produces obclavate to fusiform or lanceolate, 11–13(–15)-distoseptate, brown to reddish brown conidia in natural substrate, ending in an apical extension up to 26 µm long and having a darker conico-truncate basal cell. The cell lumina are visibly reduced, distinct and cylindrical as seen in the illustrations of the protologue, and most distosepta are darkened and thickened in a fashion similar to the darkening surrounding septal pores in other species of the group. In culture, conidia are longer and present more distosepta, cell lumina are not distinctly reduced and distosepta are darkened but not as thickened as in vivo with a few visible septal pores that confirm the presence of this character in *L. aurea*. Wu and Diao (2022) recently reported a second specimen from China but the anamorph was not observed for comparison with the type material from France.

**Lomaantha brachypus** (Ellis & Everh.) G. Delgado, Koukol & Maciá-Vicente, comb. nov. (Fig. 7a–f)

MycoBank: MB#851181


≡ *Sporidesmium brachypus* (Ellis & Everh.) S. Hughes, Can. J. Bot. 36: 807 (1958)

≡ *Sporidesmium deightonii* M.B. Ellis, Mycol. Pap. 70: 26 (1958)


*Colonies* on natural substrate effuse, hairy, black. *Mycelium* mostly immersed in the substratum, composed of brown, septate, smooth, branched hyphae, 2–3 µm wide. *Conidiophores* macronematous, mononematous, single or aggregated in groups of 2–3 at the base, simple, cylindrical, erect, straight or flexuous, smooth, 3–10-septate, brown to dark brown or dark reddish brown, 45–162(–185) × 6–9 µm, rarely with 1 percurrent extension, sometimes with 1–2- enteroblastic regenerative extensions unrelated to conidiation, base often blackish brown and bulbous, 8–15 µm wide. *Conidiogenous cells* integrated,
terminal, cylindrical, determinate, smooth, brown, attenuated to a truncate apex, 3–4 µm wide, rarely percurrent and lageniform or doliiform, 6–19 × 6–7 µm. Conidia narrowly obclavate, fusiform, ellipsoidal to broadly ellipsoidal, rostrate, smooth, brown, (4–)5(–6)-distoseptate, rarely constricted at one eccentric septum, 31–48(–53) × (9–)10–15(–17) µm, with 4–6(–7) cylindrical to barrel-shaped septal pores per conidia, 2–3.5 mm wide and ending in a hyaline, aseptate, filiform appendage, up to 56 µm long, 2–3.5(–5) wide at the base, often collapsing and tapering to 1–2 µm wide at the distal end; basal cell conico-truncate, dark brown, (5–)6–8(–9) × (5.5–)6–8 µm, 3–5 µm wide at base; total length of conidial body and appendage 47–95 µm long.

Colonies on MEA moderately slow growing reaching 27–30 mm diam. after 3 weeks at 25°C, flat, somewhat convolute, pinkish whitish in color due to diffusible exudate, with gray areas of sparse to moderately dense sporulation around the center, margin irregular, reverse reddish brown, surrounded by a red soluble pigment diffused into the medium, sporulation developing around second week. Mycelium composed of hyaline, septate, smooth, branched hyphae, 1.5–4 µm wide, brown to dark brown in mass, chains or clumps of swollen cells 4–14 mm diam. present around the colony center. Conidiophores semimacronematous, rarely macronematous, terminal or intercalary in the hyphae, mostly single but sometimes aggregated in groups of 2–4 at the base, cylindrical or subcylindrical, often reduced to the conidiogenous cell and lageniform, ampulliform or obconical, rarely bifurcating at the apex in two conidiogenous cells, smooth or verruculose, 0–3-septate, hyaline or subhyaline to brown, partly or fully pigmented, up to 38 mm long, 4–8 (~10) µm wide, attenuated to a truncate apex, 2–3.5 µm at the tip, rarely with 1–2 percurrent extensions. Conidia ellipsoidal to broadly ellipsoidal, rarely narrowly obclavate, fusiform or subcylindrical, rostrate, sometimes Y-shaped, mostly smooth, rarely verrucose, straight or curved, less often flexuous or sinuous, hyaline or subhyaline to pale brown or brown, partly or fully pigmented, with 2–6 transverse distosepta, sometimes with 1- oblique distoseptum, 2–6 pores per conidia ranging from distinct and similar to those on natural substrate to inconspicuous and not darkened or thickened, 24–52(–65) × (7–)9–12(–13) µm, ending in a hyaline or pale brown apical appendage up to 49 µm long and tapering to 1–2.5 µm at the apex, often with apical or subapical spherical cells 5–13 µm diam. and 0–3 eusepta, sometimes missing or reduced to a swollen cell, total length of conidial body and appendage 36–84 µm long.

Specimens examined

United States, Texas, Harris County, Spring, Meyer Park, 30°00’15.9” N, 95°31’35.7” W, 33 m a.s.l., on leaflets of dead leaf of Sabal minor (Jacq.) Pers., 10 Oct 2020, leg. G. Delgado (BPI 926340; CBS 147395); Houston, Bear Creek Pioneers Park, by Langham Creek, 29°50’04.8” N, 95°37’29.0” W, 30 m. a.s.l., on petiole and leaflets of dead leaf of S. minor, 22 Oct 2020, leg. idem. (BPI 926341; CBS 147396); Humble, Jesse H. Jones Park & Nature Center, around the Turtle Pond, 30°01’35.4” N, 95°17’43.0”W, 41 m a.s.l., on dead hanging vine stem, 21 May 2021, leg. idem. (BPI 911245).

Notes: Two of the specimens described above, BPI 926340 and BPI 926341, have conidia mostly ellipsoidal to broadly ellipsoidal, (11–)12–16(–17) µm wide, and closer to some specimens in the
literature with broader, similarly shaped conidia up to 17–20 µm wide and having 5–6 distosepta (Kirk 1985; Luo et al. 2019). Conidia in specimen BPI 911245, on the other hand, are narrowly obclavate or fusiform, (9–)10–13.5(–14) µm wide and closer to some other collections with narrower conidia, up to 12 µm wide and slightly more, up to 8 distosepta (Hughes and Illman 1974a; Matsushima 1975; Révay 1988). The pores associated with conidial distosepta are conspicuous but their darkening and thickening in our materials are not as distinct as those of the Canadian specimens described by Hughes and Illman (1974a) with narrower conidia and cell lumina. In our specimens, these features seem to concentrate around the pore between cells with wider cell lumina (Fig. 7f), similar to the specimens depicted by Luo et al. (2019) and Wu and Diao (2022). A gradual process of pore formation and darkening was detected and will be explained in more detail in the Discussion. In culture, our strains on MEA produced a diffusible red pigment into the medium similar to the one described by Wu and Diao (2022) on PDA and the strain BCC 3466 depicted in the BIOTEC Culture Collection online catalogue (http://www1a.biotec.or.th/TNCC/dbstore/BCC_search.asp).

**Lomaantha folliculata** (Corda) Koukol & G. Delgado, comb. nov. (Fig. 7j–v)

MycoBank: MB#851182

*Basionym*: *Helminthosporium folliculatum* Corda [as 'Helmisporium'], Icon. fung. (Prague) 1: 12 (1837)

≡ *Sporidesmium folliculatum* (Corda) E.W. Mason & S. Hughes, in Hughes, Can. J. Bot. 31(5): 609 (1953)


= *Helminthosporium brachytrichum* Cooke & Ellis, Grevillea 6(no. 37): 6 (1877)

= *Lecythothecium duriligni* Réblová & Winka, Mycologia 93(3): 482 (2001)


**Descriptions and illustrations**

Ellis (1958); Hughes and Illman (1974b); Réblová and Winka (2001)

*Specimens examined*: *Lecythothecium duriligni*. Czech Republic, Moravia, Újezd near Moravský Krumlov, valley of the brook Rokytná, on decayed wood of *Quercus* sp., 3 Jul 1990, leg. V. Holubová-Jechová (PRM 842977, holotype); *Sporidesmiella angustobasilaris*. Cuba, Havana, Jaruco, Loma de la Coca (142 m s. m.), south-east from Campo Florido, on dead branch, 13 Feb 1981, leg. V. Holubová-Jechová (PRM 842728, holotype); *Sporidesmium folliculatum*. France, Massif Central, Cantal Mts., Mt. Puy Mary, on decorticated branch of *Salix* sp., 11 Jul 1997, leg. M. Réblová, (PRM 893047); Slovak Republic, Central Slovakia, Velká Fatra Mt., Gadierská dolina valley, on decaying wood of *Fagus sylvatica* L., 13 Jul 1976,
leg. V. Holubová-Jechová (PRM 893049); Southern Slovakia, Pokoradz near Rimavska Sobota, on decaying wood of *Quercus* sp., 9 Jul 1983, leg. idem (PRM 893052). Unknown (PRM 815967).

**Notes**

When Réblová and Winka (2001) first connected *E. folliculata* with its teleomorph *Le. duriligni*, no mention of pores in the conidial distosepta was made. This was similar to previous reports of the fungus (Ellis 1958; Sinclair et al. 1990) although septal darkening was illustrated. However, examination of the holotype specimen of *Le. duriligni* PRM 842977 confirmed their presence in mature conidia and their absence in recently formed septa (Fig. 7n–p). Moreover, the dark brown, barrel-shaped septal pores associated with thickened and darkened distosepta were as conspicuous as those in the remaining collections of *L. folliculata* here studied. A gradual process of pore formation and darkening was also detected in these collections. This is similar to the one observed in *L. brachypus* but somewhat different as conidia of *L. folliculata* possess more distosepta, ranging mostly from 8–10 but up to 15, and lack an apical appendage (Hughes and Illman 1974b). Examination of the type material of *Sporidesmiella angustobasilaris* Hol.-Jech. from Cuba, on the other hand, confirmed its similarities with *L. folliculata* (Fig. 7j–m) but the fungus was apparently in an immature state (see Discussion). Therefore, *S. angustobasilaris*, which is the type species of the genus *Anasporidesmiella* (Zhang et al. 2020), is reduced here to a synonym of *L. folliculata*.

**Lomaantha reblovae** (W.P. Wu & Y.Z. Diao), G. Delgado, comb. nov.

MycoBank: MB#851183


**Description and illustration**

Wu and Diao (2022)

**Notes**

Wu and Diao (2022) recently described this fungus from a dead culm of bamboo in China and considered it distinct from related species based in the absence of an apical appendage. Its conidia are obclavate or obclavate-rostrate, brown to dark brown with a pale brown apical cell, conical or rounded at the apex and with 11–14 distosepta. No comment on the presence of septal pores was made but the illustration in the protologue shows reduced cell lumina, often long cylindrical in shape or slightly wider around the center, and distinct darkening and thickening every two distosepta, some of them with a visible pore. Colonies on PDA are apparently sterile and no mention of sporulation was made.

**Discussion**

**Phylogeny and lectotypification of E. coronata**
The recollection and sequencing of the generic type *E. coronata*, on its original host and type locality in Germany, offered the possibility to refine the taxonomy of *Ellisembia* and circumscribe this large genus in a strict sense on the basis of combined morphological and molecular evidence. The German mycologist Karl Wilhelm Gottlieb Leopold Fuckel (1821–1876) originally collected this fungus around hundred fifty years ago on dry, but still standing twigs or branches of *P. coronarius* in Niederwalluf. This is a small town west of the city of Wiesbaden and near Oestrich where Fuckel owned a vineyard. Unfortunately, we do not know the exact collection date of the lectotype specimen of *E. coronata* designated here. The original description (Fuckel 1874) lacks dates as Fuckel usually did not add exact dates to his collections and even years are missing (U. Braun, pers. comm.). The packet is labeled “Herbier Fuckel 1894” but this is obviously not a collection year as Fuckel died by 1876. The specimen was overlabeled as such probably with the year when Fuckel’s Herbarium was incorporated into the Herbier Barbey-Boissier (Hennebert 2017), nowadays Herbarium of the Conservatoire et Jardin botaniques de la Ville de Genève (G), along with several other specimens having the same label.

Fuckel (1874) described *Sporidesmium coronatum*, the basionym of *E. coronata*, without designating any type specimen but cited an illustration in the protologue as Fig. 26. This is a somewhat ambiguous drawing consisting only of a single conidium upside down (Ellis 1958), narrow, long obclavate in shape and with 12 eusepta instead of distosepta, most cells having an associated guttule and a distinct short cylindrical basal cell. Interestingly, Index Fungorum includes Fig. 26 as the Typification for this name. However, if lectotype designation was the intention behind this IF statement, this is erroneous according to article 9.12 of the ICN as syntypes such as the one cited in the protologue of *S. coronatum* always have precedence over illustrations (Turland et al. 2018). Ellis (1958), in his revision of the genus *Sporidesmium* based on specimens at IMI, provided a standardized description of the fungus and indicated that IMI 11864 was the type of *S. coronatum*, probably unaware of authentic material deposited in G. Coincidentally that same year, Hughes (1958) indicated that the type of the fungus was housed in G. The IMI online database, on the other hand, cites IMI 11864 as an ex-type collection. An examination of specimen G00266276 confirmed that it corresponds to the original material described by Fuckel (1874). It even contains a drawing of the original picture Fig. 26 depicted in this work with the numbers 8 and 96 written on it (Fig. 2f) and matching the measurements in the original description and our examination. An online search in MycoPortal (MycoPortal 2023) shows that there are several specimens under the name *Clasterosporium coronatum* (Fuckel) Sacc. mostly deposited in North American herbaria such as BPI, CUP, DAOM, MICH, MU, S and WSP. Based on their labels, they are probably duplicates of the specimen in G. The “N.-Walluf” from their description should be Niederwalluf and not Neu-Walluf as written in several of these packets. The designation of specimen G00266276 as a lectotype of *S. coronatum* is made here in the hope that this will further stabilize the application of the generic name *Ellisembia* and clarify any ambiguity surrounding its usage. Specimen IMI 11864 (Fig. 2a–c) was not designated as an isolectotype based on the depauperated state of the slides.

**Ellisembia pseudobambusae, E. carrii and related ellisembia-like fungi**
Another member of the *Ellisembia* s. str. clade thoroughly characterized in this study was *E. pseudobambusae* which was isolated and sequenced for the first time based on a fresh specimen collected in Texas (Figs. 4–5). Interestingly, our specimen and the holotype from United Kingdom share the same *Arundinaria* sp. host. This is a north-temperate genus of bamboos native to North America (Clark and Triplett, 2023) which was probably planted and naturalized at the type locality of the fungus in the United Kingdom. A tentative identification of our material as *E. carrii* (Morgan-Jones) W.P. Wu was considered based on the striking morphologically similarity between the two species and therefore its holotype was examined for comparison (Fig. 4m–s). Morgan-Jones (1977) first described *E. carrii* under *Sporidesmium* from dead twigs of *Buxus sempervirens* var. *subfruticosa* in Alabama, USA. A rare species, it was subsequently recollected on dead branches of a woody plant in China by Wu and Zhuang (2005) who transferred it to *Ellisembia*. The original description provided a conidial length of 50–120 × 9–10 µm and 8–16-distoseptate conidia. However, a reexamination of the type material deposited in AUA showed longer (76–)82–187(–206) µm, more septate conidia with 12–30-distosepta, and small pores in them. Morgan-Jones (1977) noted that once the material on natural substrate was incubated in moist chambers, the conidia became distinctly rostrate but apparently these longer conidia were not included in the original description. *Ellisembia carrii* can be separated from *E. pseudobambusae* by subtle differences such as the presence of shorter conidiophores, 28–71(–81) µm long in our reexamination of the holotype, and sparsely, less septate with only 1–3 septa, mostly 1-septate in the protologue but predominantly 2-septate in our reexamination. Percurrent extensions when present in *E. carrii* are also 0–1 septate, non-septate in the protologue, but mostly ampulliform or sometimes doliiform with their apices as well as those of the subcylindrical conidiogenous cells attenuated to a 2.5–3(–4) µm wide tip and different from the truncated, slightly wider apices of *E. pseudobambusae*. Conidia in *E. carrii* are longer and more septate whereas the conidia of the Texas specimen of *E. pseudobambusae* reached only up to 131 µm long and 9–17 distosepta after incubation. The conidial basal cells of *E. carrii* are brown and slightly long conico-truncate in the holotype whereas they are consistently dark brown, short conico-truncate but also short-cylindrical in *E. pseudobambusae* (Fig. 4j–l, q–s).

Both, *E. carrii* and *E. pseudobambusae*, were transferred first to the genus *Imimyces* A. Hern.-Gut. & B. Sutton and later to *Imicles* Shoemaker & Hambl. after the type species of the former, *Im. densus* (Sacc. & Roum.) A. Hern.-Gut. & B. Sutton, was found to be conspecific with *Polydesmus elegans* Durieu & Mont. (Hernández and Sutton 1997, Shoemaker and Hambleton 2001). *Imicles* was proposed for the remaining five species of *Imimyces* except *Im. hollowayensis* A. Hern.-Gut. & B. Sutton which for some reason was missing. They are characterized by conidiogenous cells producing lageniform, doliiform or ovoid percurrent extensions and distoseptate conidia. However, Wu and Zhuang (2005) reduced *Imicles* to a synonym of *Ellisembia* considering that these features were not reliable for generic delimitation although Seifert et al. (2011) and Su et al. (2016) preferred to retain it as a separate genus. With the transfer of *I. pseudobambusae* to *Ellisembia* in order to reflect its placement within the *Ellisembia* s. str. clade, the other four species of *Imycles: I. aquatica* (Cabello, Mengasc. & Aramb.) Shoemaker & Hambl., *I. bambusae* (M.B. Ellis) Shoemaker & Hambl., *I. heterocateniformis* (Matsush.) Shoemaker & Hambl. and *I. leptospora* (Sacc. & Roum.) Shoemaker & Hambl., together with *Im. hollowayensis* and *E. carrii*, are still in
need of DNA sequence data and phylogenetic placement. Therefore, it would be premature to support the synonymy of *Imicles* under *Ellisembia* following Wu and Zhuang (2005) and more recently Wu and Diao (2022). Instead, it is recommended to wait until these species, especially the generic type *I. heterocateniformis*, are recollected and their systematic position using molecular data is revealed. This will also help to better separate morphologically close taxa such as *I. leptospora* and *Im. hollowayensis* from *E. carrii* and *E. pseudobambusae* and to achieve a more robust circumscription of this group of species.

**Ellisembia, Sporidesmium and Sporidesmiaceae**

The decision to synonymize *Ellisembia* under *Sporidesmium* (Su et al. 2016) is rejected here as *E. coronata*, along with other morphologically similar ellisembia-like taxa, forms a distinct lineage distant from the remaining sporidesmium-like members of the family (Fig. 1). The reason for this decision was the lack of phylogenetic significance of the type of conidial septum for generic delimitation after species with euseptate and distoseptate conidia, particularly *Ellisembia* species such as *E. bambusicola* and *E. minigelatinosa*, clustered together within the resurrected *Sporidesmiaceae*. This was quite arbitrary considering the evident polyphyletic status of the genus even with the poor representation of *Ellisembia* species available at the time for analysis and the absence of a well-defined *Sporidesmium* s. str. which is still pending definition. Similarly, the decision to resurrect *Sporidesmiaceae* based on the putative similarity of its members with *S. ehrenbergii*, the generic lectotype, seems quite odd in light of our results as none of the members of the recovered clades shows a close resemblance with this taxon. Ellis (1958) described *S. ehrenbergii* as having obclavate to subfusiform, sometimes short-rostrate, reddish brown, 7–10-euseptate conidia, with a tapered apex but rounded at the tip and a conico-truncate basal cell. In contrast, the most specious lineage within *Sporidesmiaceae* named here the *Sporidesmium* clade contained taxa with distinct obpyriform conidia having an inflated basal cell with a distinct scar and fewer eusepta. The *Lylea* clade, on the other hand, includes *L. dalbergiae* and *S. tetracoilum*, the latter recently transferred from *Lylea* to *Sporidesmium* based on its phylogenetic placement and remarkable morphological resemblance with the anamorph of *S. lignicola* (Koukol and Delgado 2021). Both species are characterized by 2–4-distoseptate, narrowly obclavate, long fusiform or subcylindrical conidia with tapering, truncate ends and forming long unbranched acropetal chains. The other two clades named *Ellisembia* sensu lato and *Ellisembia* sensu stricto include species with obclavate in shape but distoseptate conidia which may end or not in an elongated apical cell sometimes surrounded by a gelatinous sheath or cap. In a fashion similar to what was done during this study for *E. coronata*, a fresh specimen of *S. ehrenbergii* needs to be recollected and sequenced for a proper phylogenetic placement of this fungus and a better definition of *Sporidesmiaceae* and its lineages.

**Lomaantha and related chaetosphaeriaceous ellisembia-like fungi**

With the novel placement of *E. coronata* revealed in this study, the suggestion of Wu and Diao (2022) to adopt *Lomaantha* for those ellisembia-like taxa placed in *Chaetosphaeriaceae* was implemented here. Hyde et al (2019) previously suggested that this group of species were congeneric with *Pyrigemmula*
(Magyar et al. 2011, Fig. 7g–i) and recommended the use of this other generic name to accommodate them once the position of *E. coronata* was confirmed. However, *Lomaantha* is older than *Pyrigemmula* and its generic type, *L. pooga*, clustered within this clade and seems to better represent its members after sharing more morphological features in common with the remaining taxa in this group. Matsushima (1975) previously commented that *Sporidesmium brachypus* was congeneric with *Lomaantha* in what seems to be a far-reaching taxonomic statement later confirmed by molecular data and further evidence supporting the present taxonomic rearrangement. Moreover, the expanded concept of *Ellisembia* also proposed by Wu and Diao (2022), including *Lecythothecium* and *Pyrigemmula* as its synonyms, is no longer tenable as both genera are known members of the distant *Chaetosphaeriaceae*.

**Morphology, culturable features and molecular phylogenetics of *L. brachypus***

In the present study, the chaetosphaeriaceous anamorph *Ellisembia brachypus* here transferred to the genus *Lomaantha*, is shown to be a variable species based on morphological, cultural and molecular characters. The differences observed in conidial dimensions as well as the width and pigmentation of distosepta between the specimens collected in Texas and those from other latitudes, although representing the same species as shown from analysis of molecular data, suggest that these characters are influenced by the disparate environmental conditions they were exposed to. The specimens BPI 926340 and BPI 926341 were collected adjacent to a pond on the palm host *Sabal minor*, which tend to dominate the understory of shady and humid lowland floodplain forests near water bodies, whereas specimen BPI 911245 was collected on a dead hanging vine stem and therefore directly exposed to desiccation, wind and solar radiation among other environmental factors. Similarly, Wu and Zhuang (2005) commented on the wide range of conidial variation in their collections from China.

In culture, sporulation was abundant in our isolates and many conidia were morphologically similar to those of the fungus on natural substrate with visible pores in the distosepta (Fig. 7c). However, many aberrant conidia were also produced. They displayed abnormal conidial features such as partial or complete lack of pigmentation with fully developed conidia sometimes hyaline or subhyaline in color, long, slender, flexuous or sinuous subcylindrical conidia, swollen apical cells or apical appendages with swollen cells and aseptate or with 1–3-eusepta, pores missing or inconspicuous and not darkened or thickened or the well-distinct, obconical basal cell also missing. Curiously, aberrant Y-shaped-conidia with a more or less pentagonal or triangular central cells and two divergent arms were formed (Fig. 7d). They often end in subhyaline apical appendages with swollen cells at the tips and septal pores present along the arms or sometimes missing. Abnormalities also extended to conidiophores which produce hyaline or subhyaline, terminal or intercalary conidiophores reduced to a single conidiogenous cell (Fig. 7e) often with verrucose ornamented walls, and bearing brown, normal conidia or non-pigmented, aberrant ones. The presence of macronematous conidiophores on natural substrate in contrast with their relative absence in culture confirms the phenotypic plasticity of *L. brachypus* under different conditions. This feature together with the presence of conidia having both disto- and eusepta further supports the lack of taxonomic relevance of these characters in the phylogeny and classification of ellisembia-like fungi. Phenotypic plasticity in general is suspected to have an important role in colonization of new
environments and geographical range shifts (Bonamour et al. 2019) and among other factors it may help to explain the widespread distribution of L. brachypus. The fungus is quite common in the United States where it has been recorded in several states besides West Virginia, the type locality (Mycoportal 2023). It has been reported also in Asia, Africa, Europe, Australia and New Zealand (Ellis 1958; Kirk 1985; Révay 1988; Wu and Zhuang 2005) and it is probably the most widespread member of this clade. Strains represented by molecular data in GenBank originated only from Asia (China, Thailand). Our North American collections provide strains and sequence data from the geographical area of the type specimen, originally described as Helminthosporium brachypus Ellis & Everh. on wood in the state of West Virginia, southeastern USA, more than a century ago (Millspaugh and Nuttal 1896). Furthermore, the present specimens help to document its presence for the first time in subtropical Texas.

Phylogenetically, our strains from North America did not show significant molecular differences compared with the Asian ones, at least in the ITS and LSU markers, and only the TEF1 showed some apparent intra and interspecific variation. However, Yang et al. (2023) recently described Ellisembia aqirostrata, transferred here to Lomaantha, which is morphologically identical to L. brachypus except for its different cultural features and phylogenetic distinctiveness. This could be a first example of cryptic diversity hidden within this widespread fungus and reflects the need to use molecular data in the future for proper delimitation of L. brachypus s. str. and morphologically similar taxa. Species in the literature such as E. minibrachypus Subram., E. pruni (Jian Ma & X.G. Zhang) Santa Izabel, A.C. Cruz & Gusmão or E. phoebes (Ch.K. Shi & X.G. Zhang) Santa Izabel, A.C. Cruz & Gusmão (Ma and Zhang 2007; Santa Izabel et al. 2013; Shi and Zhang 2007; Subramanian 1994) are seemingly conspecific with L. brachypus based on morphological features. Whether they are phylogenetically distinct remains to be tested in the future as they were originally described without molecular data.

Pores in conidial distosepta and their development in L. brachypus and L. foliiculata

Members of this peculiar chaetosphaeriaceous clade possess inconspicuous or distinct pores in the conidial distosepta as shown in the Taxonomy section above and Fig. 7. This characteristic feature has been neglected in most descriptions of these anamorphs except by Hughes and Illman (1974a, b), who documented their presence in detail for L. brachypus and L. foliiculata, and more recently Yang et al. (2023) for L. aqirostrata. Ho and Hyde (2004) studied the ultrastructure of this type of septal pore in L. brachypus using transmission electron microscopy. They found out that the conidial periclinal wall is trilamellate and comprises a thin, electron-dense outer layer, a thick, electron-transparent middle layer and a thin, electron transparent inner layer. The middle layer in itself is bilamellate with an outer (M1) and an inner (M2) layer, which possess electron-dense granules and together with the conidial inner layer are continuous with the septal layers. Each septum at the pore region has an electron-dense, barrel-shaped structure with a hollow core embedded within the middle septal layers. Speculatively, other species within this clade may share a similar ultrastructure based on their protologues although confirmation is pending following further study. This type of septal pores could also be present in previously described Lomaantha species although neither Subramanian (1954) nor Ma et al. (2011) mentioned them in their treatments of the genus. When Matsushima (1975) introduced Sporidesmium magnibrachypus Matsush.,
he depicted up to ten septal pores per conidia associated or not with darkened distosepta. Except for having shorter conidia, this species could be considered conspecific or at least congeneric with *L. pooga*, the generic type (Wu and Zhuang 2005; Wu and Diao 2022). Ma et al. (2011), on the other hand, introduced a second species *L. phragmitis* also having this feature. In the case of the Chinese material on which Wu and Diao (2022) based the placement of *L. pooga* in *Chaetosphaeriaceae*, pores are not visible for most septa except for a few darkened and thickened ones, probably due to the low quality of the pictures presented.

Besides the presence of these septal pores, a non-random gradual process of pore formation was also detected in *L. brachypus* (Fig. 8) and consists of the following steps. A first septum is laid-down in the proximal area of the conidium initial which is going to delimit the conico-truncate basal cell of the conidium. The cell starts darkening and a first pore is then formed within this first septum at the distal wall of the basal cell. Next, a central septum is delimited around the median part of the conidium, first with a small invagination in the proximal side of the wall that eventually forms a second pore. Once these bottom and middle pores are well defined, third and fourth ones start forming more or less synchronously at the second and fifth distosepta, respectively, the third pore often developing earlier. Later, an opening is also seen at the apex of the conidium previous to the formation of the apical appendage together with the formation of a fifth pore at the fourth septum. The last pore to form is the apical one at the bottom of the apical appendage which emerges around this time as a short protrusion of the conidium apex.

Variations of this pattern were observed. Sometimes the fourth or fifth pores start forming before the third one or vice versa, with well-developed pores in one of them but still missing or barely developed in the other two septa. Sometimes both the third and fourth pores open up at the same time previous to the formation of the apical appendage. Once the apical pore is more or less formed with or without a septum fully laid down, the apical appendage starts developing, initially as an elongated, subhyaline cell that will eventually enlarge into a long, tapered appendage, filiform at its end. A fully developed conidium is then recognized by the presence of a dark brown, obconical basal cell with a pore at the distal wall, four pores at each remaining distosepta with the older pores often darkened or reinforced by the presence of a blackened line, and a well delimited apex with a pore visible or not and a subcylindrical appendage that become filiform toward its distal end (Fig. 8f).

Based on several collections from Central Europe, it was possible to observe a similar process of pore formation and septum maturation in *L. folliculata* but slightly different as conidia possess more distosepta and lack an apical appendage (Fig. 7l–v). In immature conidia, after the basal cell is well defined by a thickened and darkened distal wall, the darkening starts happening at the third septum followed by the fifth and then the seventh synchronous or not with the second one. By the time these latter septa are darkening, well distinct pores start to be visible at the distal wall of the basal cell or the third septum. Once conidia mature, darkening may also happen at the lateral walls of the cell lumina between the first and third septa or between the third and fifth ones determining the squarish fashion described by Hughes and Illman (1974b). Once they are fully mature, the squarish shape and darkened walls extend to the suprabasal two or four cells and even beyond if darkening and pore formation also
gradually happened at the remaining distal septa. Again, variations may happen in some conidia such as the darkening and pore formation may occur at the forth and second septa after the third one is well formed, or the second and fourth septa may darken at the same time, or darkening occurs instead at the fourth and six septa, or the distosepta adjacent to the apical cells of conidia are not darkened and only pores are visible depending of the stage of maturity of the conidia.

**Development of conidial septal pores in related fungi**

Besides *L. brachypus* and *L. folliculata*, this specific developmental process leading to the formation of distinct barrel-shaped septal pores could also be present in *L. aurea* or *L. reblovae*, suggesting this is a phylogenetically informative or unique feature of this clade. The only exception as already outlined is *L. aurantiaca* which morphologically deviates from the remaining members of the clade in its reduced morphology and lack of pores or darkening in its conidial distosepta. However, their moderately thick inner lateral walls and cell lumina reduced to a cylinder resemble the ones in other species. Its tretic conidiogenesis is also an exception compared with the remaining species of the group and the only pore visible at the conidia of *L. aurantiaca* was at their basal cells as a continuation of the pore at the tip of the conidiogenous cells (Fig. 7g–i). The conidiophores reduced to conidiogenous cells in natural substrate is reminiscence of a similar reduction observed in culture for species such as *L. brachypus* and *L. aurea* (Hyde et al. 2019, this study). Future phylogenomic studies may shed light on the reasons the fungus underwent morphological reduction probably influenced by its lifestyle on tree barks. Other *Ellisembia* or *Lomaantha* species with unknown phylogenetic placement but having also similarly darkened pores in the distosepta might be members of this chaetosphaeriaceous clade. Examples are *E. appendiculata* J.W. Xia, R.Y. Liu & X.G. Zhang, *E. henanensis* J.W. Xia & X.G. Zhang, *E. jinggangshanensis* Jian Ma, L. Qiu & X.G. Zhang, *E. minibrachypus*, *E. photinia*e Jian Ma & X.G. Zhang and *L. phragmitis* Jian Ma & X.G. Zhang (Liu et al. 2022; Ma et al. 2010, 2011, 2020; Subramanian 1994; Xia et al. 2016), but molecular data is needed to support this hypothesis. Small pores in distosepta were also observed in the fresh specimens of *E. coronata* and *E. pseudobambusae* (Figs. 3c, 4c–e), the lectotype of *E. coronata*, the holotype of *E. carrii*, and the protologues of *E. melaleucae* and *E. spiraeae*. They were slightly darkened or thickened but not distinctly barrel-shaped or together with reduced cell lumina. Whether their structure is somewhat similar to those in chaetosphaeriaceous *Lomaantha* anamorphs remains pending future ultrastructural studies. Similarly, several species of *Distoseptispora* such as *D. clematidis*, *D. crassispora*, *D. curvularia*, *D. dehongensis*, *D. nonrostrata*, *D. pachyconidia*, *D. rayongensis* or *D. tectonae* display relatively inconspicuous septal pores which were noticed by their authors as ‘gaps’ in their distosepta (Zhang et al. 2022). The presence of pores in the conidial distosepta is apparently widespread among ellisembia-like taxa but in general they have been poorly documented. Possibly, it could be a helpful character in establishing or confirming phylogenetic relationships between species in this group.

**Sporidesmiella angustobasilaris** is a synonym of *L. folliculata*

In this respect, we focused also on *Sporidesmiella angustobasilaris* described by Holubová-Jechová (1987) from a dead branch collected in Cuba. The fungus strongly resembles *L. folliculata* in having
rounded at the apex, cylindrical, slightly clavate or ellipsoidal, similar in size conidia, with inconspicuous, 3–10 distosepta but 1–2 darkened ones and distinct, dark brown basal cells. Examination of the type material from Cuba (Fig. 7j–m) confirmed these similarities and revealed a distinct darkening and thickening of the distal wall of the basal cells and a less marked darkening mostly at the third septum, rarely at the fifth and missing in the remaining ones, sometimes together with darkened lateral walls extended to the suprabasal two cells. A distinct pore was detected at the distal walls of the basal cells (not mentioned or depicted in the protologue) and another inconspicuous one at the third septa of several conidia. This is similar to the gradual developmental pattern described above for conidia of *L. folliculata* at their initial stages of maturity. Hughes and Illman (1974b), on the other hand, commented on a Canadian specimen of *L. folliculata* collected on wood under the bark of *Ulmus* sp. with shorter conidia, 25–45 µm long, fewer septa, 4 to 9 but mostly 4 to 6, and a characteristically darker basal cell. They described conidiophores in this specimen as faintly septate and paler than usual. Similarly, Holubová-Jechová (1987) mentioned the conidiophore septation of *S. angustobasilaris* as nearly inconspicuous, and both their conidiophores were attenuated apically to a truncate apex of 1–1.5 µm or 1.5–1.7 µm wide (Fig. 7j–k). Hughes and Illman (1974b) also hypothesized that this could be an aberrant collection due to its development beneath the bark of the host tree. In a similar fashion, this could be the case of *S. angustobasilaris* in which particular ecological conditions present at the type locality in tropical Cuba prevented its full conidial development at the moment of collection. Moreover, Ellis (1958) illustrated the type collection of *Helminthosporium brachytrichum* Cooke & Ellis, a synonym of *L. folliculata*, from New Jersey, USA. Its conidia are visibly in different developmental stages and the younger ones are lacking or having incomplete septation and a marked darkening at the distal wall of their basal cells or at a single septum. Therefore, the genus *Anasporidesmiella* (Zhang et al. 2020), which is typified by *S. angustobasilaris*, is reduced here to synonym of *Lomaantha* based on the available morphological and developmental evidence. Its second species, *A. manifesta* Heredia, J. Delgado, K. Zhang, R.F. Castañeda & Jian Ma, is morphologically close to *S. angustobasilaris* in having rounded at the apex, cylindrical to long oblong, 7–12-distoseptate conidia. Their cell lumen is strongly reduced and the distal wall of the conidial basal cell is distinctly darkened and thickened, bearing a small invagination that suggests the presence of a pore. However, in the absence of molecular data or clues about its conidial development, we refrain to transfer *A. manifesta* to *Lomaantha* and its generic position is momentarily left inconclusive.

The unusual strain *E. folliculata* MAFF 240276

Surprisingly, a strain named *E. folliculata* MAFF 240276 with only an available ITS sequence clustered with *Chaetosphaeria guttulata* MFLU 18-1617 outside the clade of ellisembia-like chaetosphariaceous fungi (Fig. 6). The specimen source of this strain was originally collected on dead culms of *Sasa senanensis* Rehder (*Poaceae*) in Japan (Shirouzu and Harada 2008). Based on its description, it agrees well in conidial dimensions (45–70 × 10–11 µm) and number of distosepta (6–11) with *L. folliculata*. In the drawing, cell lumina are reduced and some distosepta are darkened and thickened with pores depicted for some of them. Conidial morphology, however, somewhat differ from the usual cylindrical shape of this species and Fig. 3 shows subcylindrical, fusiform to ellipsoidal and narrowly obclavate conidia, although these variations have been previously documented for other specimens of *L. folliculata*. 
(Sinclair et al. 1990). On the other hand, *C. guttulata* (Luo et al. 2019) is an atypical anamorphic member of the family having a unique conidial apparatus among *Chaetosphaeriaceae* (Wu and Diao 2022). It consists of non-phaialidic, polyblastic, sympodially extending conidiogenous cells bearing numerous darkened and protuberant conidiogenous loci and hyaline, ovoid or fusiform, 3-septate conidia with a darkened scar at the slightly fimbriate base. The fungus was described from a single specimen collected on submerged decaying wood in a freshwater stream in China. Morphologically, it resembles species of *Minimelanolocus* R.F. Castañeda & Heredia in *Chaetothyriales* (*Eurotiomycetes*) which are often collected from freshwater habitats (Dong et al. 2018; Liu et al. 2015; Wan et al. 2021). This may suggest contamination during isolation in pure culture and a mismatched phylogenetic placement. More collections and data are needed to confirm the status of both *C. guttulata* and strain MAFF 240276, and whether other ellisembia-like fungi unrelated to the *Lomaantha* lineage may be present in *Chaetosphaeriaceae*.

In conclusion, the taxonomy of ellisembia-like fungi is in a state of flux and, although phylogenetic analyses of molecular data are helping nowadays to clarify relationships among *Ellisembia* and related taxa, there is still a long way before a more natural, less schematic classification of these fungi is finally developed. Special emphasis should be made on the recollection, isolation and sequencing of the many rare or poorly collected ellisembia-like taxa in order to systematically achieve this goal in the near future.

**Abbreviations**

**ATCC**
American Type Culture Collection, Manassas, United States

**BCC**
National Center for Genetic Engineering and Biotechnology (BIOTEC) Culture Collection, Khlong Luang, Thailand

**CBS**
Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands

**CPC**
Working collection of Pedro Crous housed at CBS

**DLUCC**
Dali University Culture Collection, Yunnan, China

**GZCC**
Guizhou University Culture Collection, Guiyang, China

**HKAS**
Herbarium of Cryptogams, Kunming Institute of Botany Academia Sinica, Kunming, China

**HKUCC**
The University of Hong Kong Culture Collection, Hong Kong, China

**ICMP**
International Collection of Micro-organisms from Plants, Manaaki Whenua Landcare Research, Auckland, New Zealand
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Author Contributions Conceived and designed the experiments: G.D., O.K. Field work, morphological and cultural studies: G.D., M.P., O.K., SEM microscopy: W.C. Molecular work: O.K., J.M.V. Phylogenetic analyses: G.D., O.K. Writing and reviewing the paper: G.D., O.K. Editing the draft: G.D., O.K., J.M.V., M.P., W.C. All authors read and approved the final version of the manuscript.

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Data availability All specimens are deposited in herbaria BPI or PRC, and strains in culture collections CBS or CCF; all sequence data are available in GenBank (https://www.ncbi.nlm.nih.gov) under the accession numbers given in Table 1; sequence alignments are available in figshare.
and new combinations were registered in MycoBank.

Ethics approval Not applicable.

Consent for publication All authors have approved and agreed with the submission of the final manuscript.

Competing interests The authors declare no competing interest.

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Tables

Table 1. Strains included in this study and their GenBank accession numbers.
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Abbreviations: **ATCC**: American Type Culture Collection, Manassas, United States; **BCC**: National Center for Genetic Engineering and Biotechnology (BIOTEC) Culture Collection, Khlong Luang, Thailand; **CBS**: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; **CPC**: Working collection of Pedro Crous housed at CBS; **DLUCC**: Dali University Culture Collection, Yunnan, China; **GZCC**: Guizhou University Culture Collection, Guiyang, China; **HKAS**: Herbarium of Cryptogams, Kunming Institute of Botany
Academia Sinica, Kunming, China; **HKUCC: The University of Hong Kong Culture Collection, Hong Kong, China; ICMP: International Collection of Micro-organisms from Plants, Manaaki Whenua Landcare Research, Auckland, New Zealand; KUMCC: Kunming Institute of Botany Culture Collection, Yunnan, China; MAFF: Microorganisms Section of the Ministry of Agriculture, Forestry and Fisheries Genebank, Tsukuba, Japan; MFLU/MFLUCC: Mae Fah Luang University Herbarium/Culture Collection, Chiang Rai, Thailand; MR: Working collection of Martina Reblova; NBRC: Biological Resource Center, National Institute of Technology and Evaluation, Kisarazu, Japan; NN: Working Collection of Wenping Wu stored at Novozymes, Beijing, China; PRA: Herbarium of the Institute of Botany, Průhonice, Czech Republic; PRC: Herbarium of the Charles University, Prague, Czech Republic; SH/SMH: Working collection of Sabine M. Huhndorf.


Figures
Figure 1

The best scoring RaxML phylogenetic tree obtained from a concatenated ITS-LSU-RPB2 dataset showing the *Ellisembia* s. str. clade within *Sporidesmiaceae* (*Sordariomycetes*) and the placement of *E. coronata* and *E. pseudobambusae* among related taxa. New strains are in bold and color boxes in the tree represent the four different lineages belonging to this family: *Sporidesmium* (blue); *Lylea* (yellow);
Ellisembia sensu lato (green) and Ellisembia sensu stricto (red). Bootstrap support values $\geq 70\%$ are indicated at the nodes and thickened branches correspond to Bayesian posterior probabilities $\geq 0.95$

Figure 2

Ellisembia coronata. IMI 11864. a Packet and slides. b Conidium. c Conidiophore with conidium. G00266276 (lectotype). d Packet. e Herbarium material. f Original label found inside the packet with drawing. g–j Conidia. h Conidiophore with conidium. i Conidiophore with percurrent extensions. Scale bars: b, g–j = 10 $\mu$m; c = 20 $\mu$m
**Figure 3**

*Ellisembia coronata.* **a** Host plant of *Philadelphus coronarius* at the type locality in Niederwalluf, Germany. **b** CCF 6699. Colonies on PCA and PDA after 30 days at 25 °C, surface view. PRC 9257. **c, g** Conidia. **d** Conidiophore with conidium. **e–f** Conidiophores. Scale bars: **c, e** = 20 μm; **d, f–g** = 10 μm
Figure 4

_Ellisembia pseudobambusae_. CCF 6709. **a–b** Colonies on MEA after 2 mo at 25 °C, surface and reverse views. **c–d** Conidiophores and conidia in culture. **e** Conidiophore with young conidium. **f** Conidiophores. BPI 911246. **g** Conidiophore. **h–i** Conidiophores with percurrent extensions and young conidium. **j–l** Conidia. _Ellisembia carrii_. AUA 1953 (holotype). **m** Packet. **n** Colonies on natural substrate. **o–**
Conidiophores with percurrent extensions and young conidium. q–s Conidia. Scale bars: a–b = 1 mm; c–l, o–s = 10 µm; n = 100 µm

Figure 5

SEM micrographs of *Ellisembia pseudobambusae*. BPI 911246. **a** Conidiophore with conidium. **b** Detail of the basal scar of a conidium. **c** Apical scars of conidiogenous cells. **d–e** Conidiophores with young conidia. Note the doliiform percurrent extension in e. Scale bars: a, e = 10 µm; b = 2 µm; c = 5 µm; d = 20 µm
Figure 6

The best scoring RaxML phylogenetic tree inferred from a concatenated ITS-LSU dataset showing the expanded *Lomaantha* and related genera in *Chaetosphaeriaceae* (*Sordariomycetes*). The *Lomaantha* clade is highlighted in a red colored box and the Texas strains of *L. brachypus* are in bold. The clade containing the strain *Ellisembia folliculata* MAFF 240276 is highlighted in a blue colored box. Bootstrap
support values ≥ 70% are shown at the nodes and Bayesian posterior probabilities ≥ 0.95 are indicated by thickened branches.

**Figure 7**

*Lomaantha brachypus.* CBS 147395. **a–b** Colonies on MEA after 3 wks at 25 °C, surface and reverse views. **c** Conidia. **d** Aberrant conidia showing septal pores. **e** Conidiogenous cells. BPI 926340. **f**
Conidiophore and conidium on natural substrate. *Lomaantha aurantiaca*. BP 100757. g Conidia. h Conidium showing darkened basal pore. i Conidiogenous cells. Arrow indicates apical pores. *Lomaantha folliculata*. PRM 842728 (holotype of *Sporidesmiella angustobasilaris*). j–k Conidiophores. l–m Conidia. Arrow indicates a pore at the distal wall of the basal cell. PRM 842977 (holotype of *Lecythothecium duriligni*). n–o Conidiophores and conidia. p Conidium showing septal pores. PRM 893047. q–r Conidiophores and conidia. s Conidium. PRM 893052. t–u Conidiophore and conidia showing septal pores. PRM 893049. v Conidium. Scale bars = 10 μm; c, f, g, u = 20 μm

**Figure 8**

*Lomaantha brachypus*. BPI 926340. Drawing of the gradual process of septal pore formation and maturation in conidia. a Conidium initial. b Conidium initial once basal septum is laid down. c Young conidium with basal pore and middle septum. d Young conidium with septa laid down and well-developed pores at basal and third septa, the fourth pore starting to form e Idem after fourth pore is formed and fifth and apical pores start forming. f Fully developed conidium showing a well-distinct basal cell, six pores and the apical appendage. Scale bar = 10 μm