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Studies on three rare coprophilous plectomycetes from Italy

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Abstract — The concept of plectomycetes is discussed and their heterogeneity emphasised. Three ascohymenial cleistothecial ascomycetes, collected or isolated from herbivore or omnivore dung in damp chamber cultures, are described. *Emericella quadrilineata* and *Lasiobolidium orbiculoides* are discussed and compared morphologically with similar taxa. A key to *Lasiobolidium* and the related *Orbicula* is provided. The importance of the second worldwide isolation of *Cleistothelebolus nipigonensis* and the difficulties of distinguishing it from *Pseudeurotium* species are stressed. The Italian collection of *C. nipigonensis* from canid dung is compared with the original strain from wolf, and its epidermoid peridial tissue is regarded as one of the main morphological differentiating features from *Pseudeurotium ovale*. The morphological characteristics of the monospecific genus *Cleistothelebolus* are discussed and compared with those of *Pseudeurotiaceae* and *Thelebolaceae*, particularly with *Pseudeurotium* and *Thelebolus*. ITS and LSU rDNA sequences of the *Cleistothelebolus* isolate support its placement in *Thelebolaceae*.

Key words — coprophily, phylogeny, *Pyronemataceae*, *Thelebolales*, *Trichocomaceae*

Introduction

Our twenty-year study on fungi growing on faecal material (Doveri 2004), both in the natural state and in damp chamber cultures, has allowed us to record from Italy several species of plectomycetes, which must be regarded as an assemblage of heterogeneous *Ascomycota* characterised by small, globose or subglobose, prototunicate asci, irregularly disposed in a centrum of cleistothecial or gymnothecial ascomata (Ulloa & Hanlin 2000, Geiser et al. 2006, Stchigel & Guarro 2007, Kirk et al. 2008). Most are pleomorphic, often with a hyphomycetous asexual state, whose features have a primary taxonomic value in separating genera and families and in establishing their phylogenetic relationships. Many are saprotrophic, growing on decaying wood or vegetables, soil, and dung, while some are parasites of human and mammal tissues (Udagawa 1987).

Plectomycetes are found in different orders and families of discomycetes, pyrenomycetes, and loculoascomycetes (Cain 1956, Benny & Kimbrough 1980). Phylogenetic studies resulting from gene sequencing combined with cladistics (Sugiyama et al. 1999, Suh & Blackwell 1999) have confirmed their great heterogeneity.

The aim of this work is to provide a detailed morphological description of *Emericella quadrilineata* and *Lasiobolidium orbiculoides*, two plectomycetous fungi recently isolated by us from dung, and to analyse their relationships with similar taxa. We also include an extensive study of the second collection worldwide of the very rare *Cleistothelebolus nipigonensis*, attempting to determine, by morphological, physiological and preliminary molecular data (ITS and LSU rDNA sequences), its connection with *Thelebolaceae* Eckblad and other families with an uncertain position in *Leotiomycetes* O.E. Erikss. & Winka.

Material & methods

Collection of *Emericella quadrilineata* and *Lasiobolidium orbiculoides*

Specimens of *E. quadrilineata* (on dried sheep dung) and *L. orbiculoides* (on dried goat dung) were collected in the Tuscan archipelago (North Tirreno sea) and placed in a non-sterilised damp chamber according to Richardson & Watling (1997) and Richardson (2001) as slightly modified by Doveri (2004). Cultured material, incubated at room temperature (20–25°C) under natural light but not exposed to direct sunlight, was examined every day under a stereomicroscope. Ascomata of both species grew fast, maturing after 7 days incubation, those of *E. quadrilineata* directly on dung, while those of *L. orbiculoides* on blotting paper at the dung base, partly obscured by the thick meshes of an aerial mycelium. Only three specimens of *E. quadrilineata* were produced, which were picked up from dung by a sterile needle, utilised for the microscopic study, preserved later in a luted slide. Specimens of *L. orbiculoides* were produced in a large quantity; however, all the attempts to isolate this fungus in axenic culture were unsuccessful. Part of the material was utilised for the microscopic study and for preservation as dried material.

Isolation of *Cleistothelebolus nipigonensis*

Cleistothelebolus nipigonensis was obtained from dried canid dung collected in northern Italy, placed in a non-sterilised damp chamber, and cultured following the same methods utilised for the other two species. Mature ascomata were hardly noticed after 20 days incubation but, owing to their smallness and staying in hiding, they may have appeared a few days earlier. Ascomata were picked up from dung by a sterile needle and crushed on PDA (Potato Dextrose Agar, Difco Lab.) amended by 2 mg L^{-1} streptomycin, for primary isolation. Plates were incubated for 14–15 days at room temperature (20–25°C) under natural light. After incubation, plates were observed at the stereomicroscope (up to 100×) and germinating groups of ascospores were selected,

picked out of the agar and transferred to PDA plates using a glass needle. Pure cultures on PDA were used to obtain single-spore isolates.

100 µl of a water suspension of ascospores were placed on WA (Water Agar, 15 g dissolved in 1 L of distilled water) plates by a sterile micropipette and incubated at 25 ± 2°C 12h/12h light/darkness. Monoascosporic isolations were transferred to PDA.

Morphological studies

Emericella quadrilineata, *L. orbiculoides* and *C. nipigonensis* were examined microscopically in mounts of water, Congo red, and methyl blue or cotton blue in lactic acid. Fifty ascospores discharged from mature asci derived from at least two ascomata were measured in water.

Cultural studies

To assess the effect of different substrates on the growth of *C. nipigonensis*, a 6 mm diameter agar disk, collected from the actively growing margin of PDA colonies, was placed in the centre of 90 mm Petri dishes containing CMA (Corn Meal Agar, Difco Lab.), MA (Malt Agar, Difco Lab.), NA (Nutrient Agar, Difco Lab.), PDA, V8 agar (Gams et al. 1998), and Emerson YpSs agar (Yeast protein Soluble starch Agar) (Gams et al. 1998). Five plates of each medium were incubated at 24 ± 2°C 12h/12h light/darkness. Radial growth of the colonies was recorded at different times from the second day of incubation. Regression and variance analysis of growth curves were performed by using SigmaPlot package (SPSS Inc., Chicago, IL) and Graphpad Prism 5.02 Software. $P \leq 0.05$ was assumed as significant level.

Molecular studies

DNA extraction, amplification and sequencing — Mycelium for DNA extraction, produced on PDA plates overlaid with a cellophane membrane at 25°C, was scraped from the plates with a sterile scalpel, placed in a 1.5 ml tube (0.15 g) and extracted using the DNeasy® Plant Mini Kit (QIAGEN) according to the manufacturer's instructions. Polymerase Chain Reaction (PCR) was used to amplify the LSU and the ITS regions of the nuclear ribosomal DNA, employing the following primers: LROR and LR3 for the first 650 kb of the LSU gene and ITS1 and ITS4 for the ITS region (Gardes & Bruns 1993, White et al. 1990). Amplification reaction mixtures contained 25–50 ng of template DNA, GoTaq®Green Master Mix (Promega) 1X and 0.5 mM of each primer in a volume of 50 µL (Doveri et al. 2010). Amplification was performed in a GeneAmp® PCR System 2400 (Perkin Elmer) using the following parameters: for LSU initial denaturation step at 94°C for 5 min, 35 cycles consisting of denaturation at 94°C for 1 min, annealing at 52°C for 1 min and extension at 72°C for 2 min, final extension of 72°C for 7 min; for ITS initial denaturation step at 94°C for 1 min, 30 cycles consisting of denaturation at 94°C for 30 s, annealing at 54°C for 1 min and extension at 72°C for 1 min, final extension of 72°C for 4 min. After the final extension of 72°C, reactions were held at 4°C. PCR products were purified by the QIAquick PCR Purification Kit (Qiagen) according to the manufacturer's protocol and submitted to sequencing. Samples to be sequenced were processed by the DNA Sequence Facility at the Bio Molecular Research (BMR), Servizio di Sequenziamento – CRIBI, University of Padova (Italy).

Results

Cultural studies

Equations resulting from regression analysis obtained for each medium were all highly significant ($R^2 \geq 0.880$, $P<0.001$). From slopes comparison, growth rate of *Cleistothelebolus nipigonensis* on YpSs ($a=1.7$ mm d^{-1}) was statistically higher than on all the other media ($P \leq 0.001$) (data not shown).

Molecular study

Amplifications produced sequence lengths of about 600 bp (ITS) and 650 bp (LSU). Comparison of our ITS sequence (KC492060) with those deposited in GenBank resulted in high similarity percentages (96%) with *Antarctomyces* Stchigel & Guarro and other uncultured thelebolaceous fungi. Comparison of the LSU sequence (KC492061) within the same database confirmed the close relationship between *C. nipigonensis* and two species of *Thelebolus* (*T. ellipsoideus* and *T. globosus*, 97% similarity).

Taxonomy and discussion

Emericella quadrilineata (Thom & Raper) C.R. Benj., Mycologia 47: 680, 1955 Pl. 1

Ascomata cleistothecioid, 300–350 µm diam., globose, non-ostiolate, smooth, purple-red but appearing straw coloured and slightly granulose-reticulate at first sight, as surrounded and obscured by dense yellowish masses of Hülle cells and sparse hyphae.

Hülle cells terminal, globose, exceptionally ellipsoidal, 15–25 µm diam., hyaline in the middle, with yellowish, up to 5 µm thick walls, arising out of hyaline, branched, septate, slightly encrusted hyphae, not forming a pseudostalk at the peridial base; Peridium thin-walled, purple-red, a layer of firmly pressed, narrow (about 1 µm diam.), purple-red hyphae; paraphyses absent; asci irregularly disposed, 8-spored, globose to broadly ellipsoidal, 8.5–11 × 8–9 µm, thin-walled, lacking an apical apparatus, evanescent; ascospores oblate, globose in frontal view, ellipsoidal in side view, 4–5(–5.5) × 3–3.5 µm, bivalved, hyaline at first, becoming purple-red, smooth, with four slightly raised equatorial crests, less than 0.5 µm wide, seemingly with an entire margin; asexual state only some hyaline, globose, echinulate conidia, about 3 µm diam., observed in association with ascomata.

Ecology & Distribution — Three specimens collected from sheep (*Ovis aries*) dung in a damp chamber culture. April. Rare. Known from one island coastal site in Italy, possibly cosmopolitan. Usually isolated from soil.

Specimen examined — **ITALY**, **Tuscany**, **Livorno**, Capraia island, 9°49′13″N 43°01′29″E, 50 m a.s.l., 11.IV.2011, leg. L. Levorato (Herbarium F. Doveri 007.12).

Most plectomycetes are distributed in *Eurotiomycetidae* Doweld, particularly in *Eurotiales* G.W. Martin ex Benny & Kimbr. and *Onygenales* Cif. ex Benny

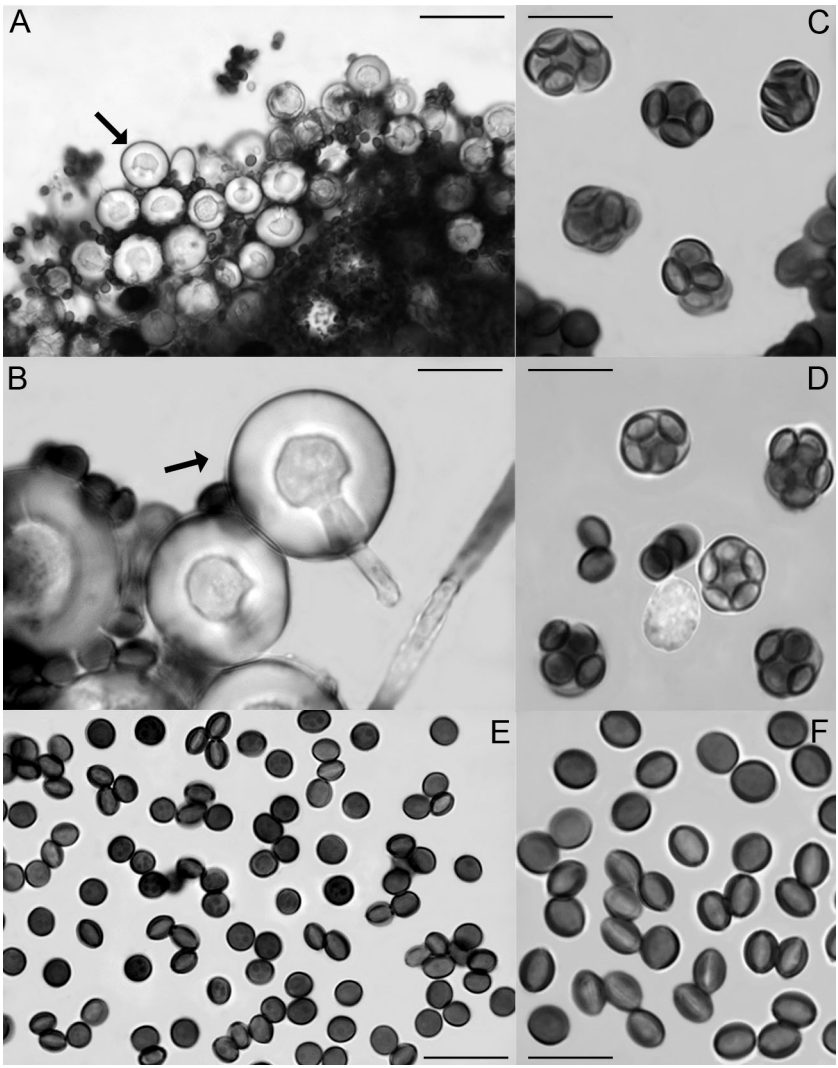


Plate 1. *Emericella quadrilineata* (Herbarium F. Doveri 007.12): A–B, clusters of Hülle cells (arrows) around the peridial wall; C, asci with conglobate ascospores; D, asci in different stages of maturity and some free ascospores; E–F, ascospores. Scale bars: A = 40 µm; B–D = 10 µm; E = 12 µm; F = 8 µm.

& Kimbr. Besides the cleistothecial ascomata and evanescent asci, these two orders share a thin, variously structured, usually brightly coloured or pale peridium, absence of an hamathecium, and small, usually brightly coloured,

one-celled, oblate ascospores often with equatorial ornamentations (Kirk et al. 2008). Blastic phialoconidiogenesis distinguishes *Eurotiales* (von Arx 1987) from *Onygenales*, where a thallic conidiogenesis produces both arthro- and aleurioconidia (Benny & Kimbrough 1980, Kirk et al. 2008).

In *Eurotiales, Trichocomaceae* E. Fisch. (= *Eurotiaceae* Clem. & Shear) encompasses several genera (including *Emericella* Berk.) characterised by brightly coloured ascomata with a cellular or hyphal peridium, often catenulate asci, usually saturnine (with equatorial crests) ascospores (Benny & Kimbrough 1980, Malloch 1985), and *Aspergillus* P. Micheli ex Link, *Paecilomyces* Bainier, or *Penicillium* Link asexual states (Malloch & Cain 1972, Kirk et al. 2008). They are cosmopolitan and usually soil inhabitants or saprotrophs on decaying plants; some are medically or industrially important as producers of antibiotics or toxins, sometimes behaving as opportunistic pathogens (Cannon & Kirk 2007) or agents of food spoilage (Geiser et al. 2006). Molecular phylogenetic studies (Berbee et al. 1995, Ogawa et al. 1997, Sugiyama 1998) have demonstrated that *Trichocomaceae* is monophyletic.

Berkeley (1857) erected *Emericella* for *E. variecolor* Berk. & Broome, a species with purplish long-spiny bordered ascospores and small cleistothecial ascomata supported by a spongy column, from which numerous threads extend, terminating in large globose cells. These stromatic (Malloch & Cain 1972), thick-walled, intercalary or end cells surrounding cleistothecia (Ulloa & Hanlin 2000, Geiser et al. 2006, Kirk et al. 2008) are called "Hülle cells" (Malloch 1985). In *Trichocomaceae* they are typical of *Fennellia* B.J. Wiley & E.G. Simmons and *Emericella*; *Fennellia* has yellow or green, often confluent ascomata, hyaline or pale ascospores, and often elongated Hülle cells (Wiley & Simmons 1973, Locquin-Linard 1990, Guarro et al. 2012), and *Emericella* has usually discrete, red or purplish to dark brown cleistothecia with a peridium of compressed hyphae, and oblate, purple-red, orange or violet, rarely pale ascospores usually ornamented with equatorial ridges. *Emericella* also has globose Hülle cells and an *Aspergillus* asexual state (von Arx 1974, Hanlin 1998, Guarro et al. 2012) of the so called "*A. nidulans* group" (Benjamin 1955, Christensen & Raper 1978, Christensen and States 1982, Pitt & Samson 2007), which is the equivalent of *Aspergillus* sect. *Nidulantes* (Gams et al. 1985). About forty species are recognised at the present (Guarro et al. 2012) in *Emericella;* they are airborne soil inhabitants (Stchigel & Guarro 1997, Samson et al. 2002), rarely growing elsewhere (Pitt and Samson 2007), thermotolerant, but not thermophilic (Zalar et al. 2008), and prefer warm climates and dry substrata (Samson & Mouchacca 1974). Some are opportunistic pathogens, uncommon agents of animal and human infections (Balajee et al. 2007, Verweij et al. 2008).

Emericella quadrilineata is characterised by rapid growth in culture, comparatively large ascomata, 8-spored asci, and smooth purple-red ascospores

with four low equatorial crests (Thom & Raper 1939). According to Balajee et al. (2007) and Verweij et al. (2008) the number of these inconspicuous crests can be detected only by electron microscopy, but we think it can be detected also by careful focusing under a light microscope.

Emericella acristata (Fennell & Raper) Y. Horie, *E. miyajii* Y. Horie, and *E. parvathecia* (Raper & Fennell) Malloch & Cain are morphologically indistinguishable from *E. quadrilineata* (Guarro et al. 2012) and possibly the same species: *E. acristata* was originally described without equatorial crests (Fennell & Raper 1955) but others have cited two (Ismail et al. 1995) or four low crests (Horie et al. 1996, Guarro et al. 2012); *E. miyajii* has four inconspicuous crests, and *E. parvathecia* has two (Raper & Fennel 1965).

The closely related *E. nidulans* (Eidam) Vuill. var. *nidulans* is also morphologically indistinguishable from *E. quadrilineata* except for having ascospores with two equatorial crests. Molecular studies that support microscopic examinations have helped separate the two species (Verweij et al. 2008, Matsuzawa et al. 2012). *Emericella quadrilineata,* usually isolated from soil (Thom & Raper 1939), has been also isolated sometimes from herbal drugs (Horie 1979), once from white wine (Stchigel et al. 1999), and now from dung. It is an opportunistic pathogen (Balajee et al. 2007), agent of onychomycosis (Gugnani et al. 2004) and rarely causes invasive aspergillosis (Drakos et al. 1993, Verweij et al. 2008). *Emericella nidulans*, which is thermotolerant (Chen and Chen 1991), cellulolytic (Reese & Downing 1951), possibly ligninolytic (Bull & Carter 1973), and opportunistically pathogenic (Balajee et al. 2007, Verweij et al. 2008) has been isolated not only from plants (Benjamin 1955), rotting wood (Eidam, 1883, Lumley et. al. 2000), and soil (Chen & Chen 1991) but also from rabbit (Benjamin 1955) and barking deer (Piasai & Manoch 2009) dung, goat droppings, pellets of free-living birds, and fresh human faeces (Domsch et al. 1993).

We know very few records of other *Emericella* species from dung, apart from *E. foveolata* Y. Horie from armadillo (Horie et al. 1996) and *E. rugulosa* (Thom & Raper) C.R. Benj. from rat (Jeamjitt et al. 2007). *Aspergillus recurvatus* Raper & Fennell, lacking a sexual state but related to *Emericella* as belonging to the *nidulans*-group (Raper & Fennell 1965), was isolated from lizard dung.

Lasiobolidium orbiculoides Malloch & Benny, Mycologia 65: 655, 1973 Pl. 2–3

Ascomata cleistothecioid, 200–500 µm diam., globose to broadly ellipsoidal, semi-membranous, yellowish at first, becoming yellow-ochraceous, finally brownish, granulose due to protruding groups of peridial cells, fully covered by dense flexuous, ≤4 mm long hairs.

Peridium two-layered, pseudoparenchymatous: endostratum with textura angularis composed of pale, thin-walled, polygonal cells, 5–8 µm diam.,

exostratum thin, weakly dextrinoid, with textura globulosa–angularis composed of thick-walled, yellowish brown cells, 12–28 × 11–22 µm, interspaced with some irregularly lobed cells; HAIRS arising from the outermost exoperidial cells, 6–7.5 µm diam., yellowish, smooth, thick-walled (up to 3 µm), wavy, sometimes slightly coiled, sparsely septate, more densely septate at their base, with rounded tips and an usually swollen, bulbous, sometimes lobed base, 10–20 µm diam; PARAPHYSES apparently scarce and short, soon vanishing, mixed with asci, 2–3 µm diam., not enlarged at the apex, septate, often branched in the lower portion, filled with a few pigments; ASCI irregularly disposed, ephemeral, unitunicate, non-amyloid, inoperculate, 8-spored, cylindrical, 80–90 × 10–11 µm, thin-walled, rounded at the apex, without an apical apparatus, with a very short, slightly lobate stalk; ASCOSPORES regularly uniseriate, oblate, 11–12.5 × 9.5–11 × (7.5)8.5–10 µm, globose to subglobose in frontal view, broadly ellipsoidal in side view, hyaline to pale yellowish, smooth, thick-walled, uninucleate, with a de Bary bubble in aqueous media, forming a powdery mass at maturity, when asci disintegrate; ASEXUAL STATE unknown.

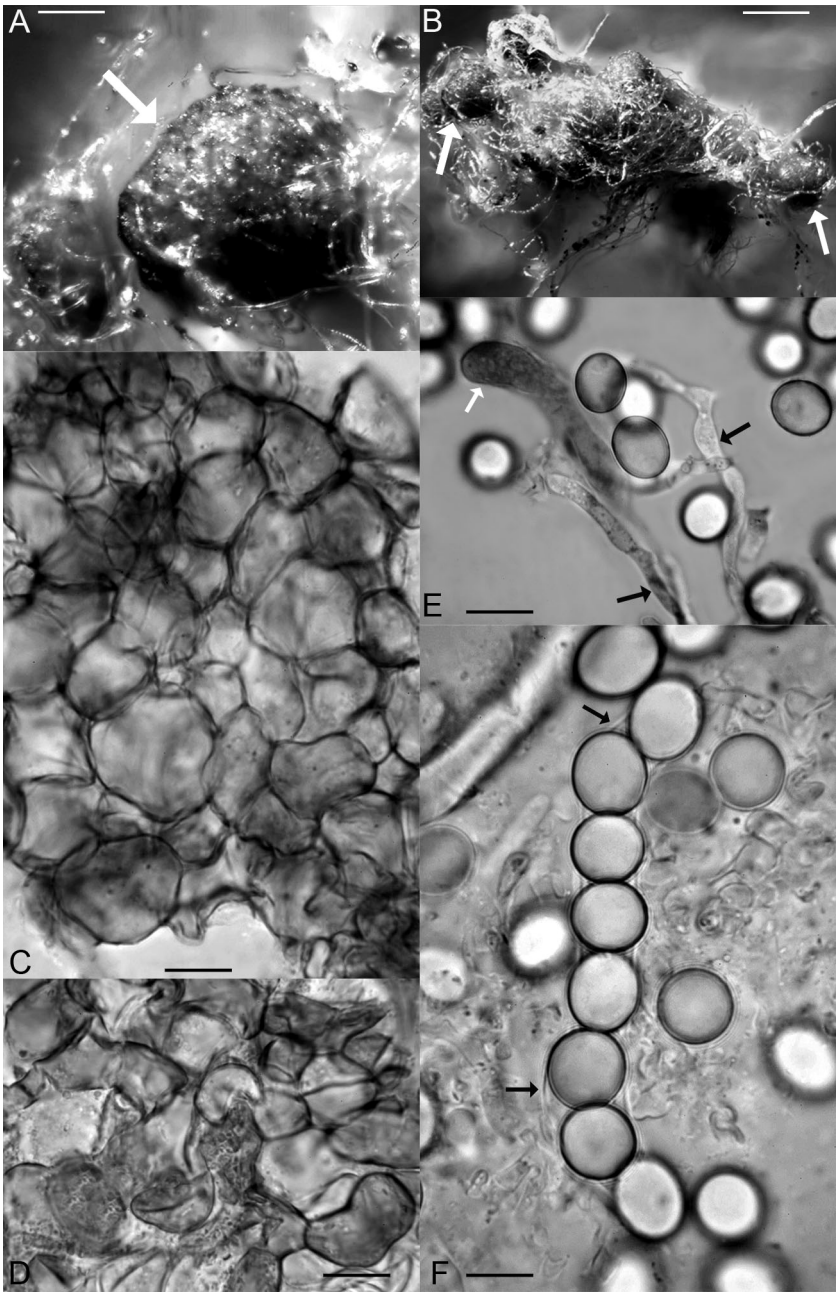
ECOLOGY & DISTRIBUTION — Hundreds of gregarious, superficial specimens collected from blotting paper at the base of goat (*Capra hircus*) dung in a damp chamber culture. April. Rare. Known from one island coastal site in Italy, possibly cosmopolitan, also known from other herbivore dung, exceptionally from soil.

SPECIMEN EXAMINED — **ITALY**, **TUSCANY**, **Livorno**, Capraia island, 9°49′13″N 43°01′29″E, 50 m a.s.l., 11.IV.2011, leg. L. Levorato (Herbarium F. Doveri 006.12).

Malloch & Cain (1971) erected the monospecific genus *Lasiobolidium*, describing *L. spirale* as a non-stromatic plectomycete with cleistothecial ascomata, a differentiated peridium with helically coiled appendages, ephemeral clavate asci, and hyaline, ellipsoidal ascospores. Malloch & Benny (1973) later described a second species, *L. orbiculoides*, so called for its strong resemblance to the monospecific genus *Orbicula* Cooke.

Lasiobolidium and *Orbicula* were initially placed (Malloch & Cain 1971, Malloch & Benny 1973, Benny & Kimbrough 1980) in *Eoterfeziaceae* G.F. Atk., now regarded as a plectomycete family with an uncertain position in *Pezizomycotina* O.E. Erikss. & Winka (Cannon & Kirk 2007, Kirk et al. 2008, Lumbsch & Huhndorf 2010). Jeng & Krug (1976) later transferred the genera to the tribe *Theleboleae* Korf (= *Thelebolaceae*) of *Pyronemataceae* Corda (*Pezizales* J. Schröt.), but phylogenetic studies (Hansen et al. 2005, Hansen

PLATE 2. *Lasiobolidium orbiculoides* (Herbarium F. Doveri 006.12): A–B, ascomata (arrows) in culture; C–D, details of exoperidium; E, free ascospores between paraphyses (black arrows) and an immature ascus (white arrow); F, uniseriate ascospores inside a thin-walled (arrows) 8-spored ascus. Scale bars: A = 100 µm; B = 500 µm; C, E = 10 µm; D = 15 µm; F = 8 µm.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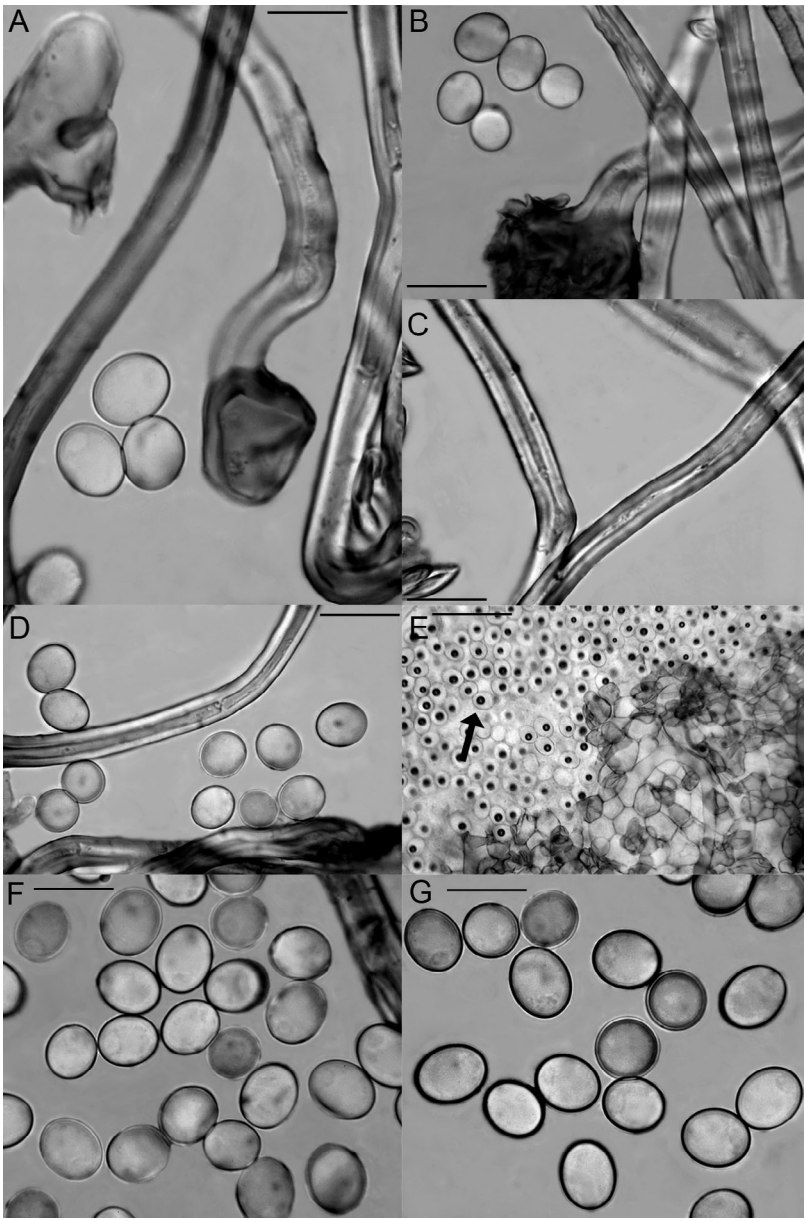


Plate 3. *Lasiobolidium orbiculoides* (Herbarium F. Doveri 006.12): A–D, details of hairs and some free ascospores; E, ascospores containing de Bary bubbles in aqueous medium; F–G, ascospores. Scale bars: A = 10 µm; B–D = 15 µm; E = 50 µm; F–G = 12 µm.

& Pfister 2006, Perry et al. 2007) place them in *Pyronemataceae*, a family of apothecioid discomycetes, with a minority of cleistothecial fungi evolved from an apothecial ancestor (Hansen et al. 2005).

Lasiobolidium orbiculoides is characterised by fast growth in culture, wavy peridial hairs, cylindrical short-stalked asci, and oblate medium-sized ascospores. The morphological characteristics of our collection fully match the protologue, and its ascospores contain a large de Bary bubble when mounted in aqueous media, a feature also reported by others (Janex-Favre & Locquin-Linard 1979, Bell 2005).

The main differences between *L. orbiculoides*, six other recognised *Lasiobolidium* species (Kirk et al. 2008), and *Orbicula parietina* (Schrad.) S. Hughes are reported in the following key, partly based on Yaguchi et al. (1996) and Guarro et al. (2012):

Worldwide key to *Lasiobolidium* and *Orbicula*

1a. Asci cylindrical. Ascospores uniseriate **2**
1b. Asci subglobose to claviform. Ascospores biseriate to conglobate, ellipsoidal **4**

2a. Ascospores broadly ellipsoidal, 11–12 × 8–9 µm (Moustafa & Ezz-Eldin 1989) . . . . . ***L. aegyptiacum***
2b. Ascospores oblate **3**

3a. Cleistothecia usually not flattened at their bases. Peridium thin, appearing one-layered, covered all over with hairy, wavy or sometimes irregularly coiled appendages. Asci short- or non-stalked. Ascospores 11–12.5 × 9.5–11 × 8.5–10 µm (9.8–14 × 9–12 µm; Malloch & Benny 1973). From dung, rarely from soil and vegetable material . . . . . ***L. orbiculoides***
3b. Cleistothecia often with a flattened base. Peridium thicker, two-layered. Hairy appendages hyphoid, present at the base only. Asci long-stalked. Ascospores 8–10.5 × 8–10.5 × 7–9 µm (7–13 × 8–10 µm; Hughes 1951). From several kinds of dung or vegetable material . . . . . ***O. parietina***

4a. Ascospores longer than 10 µm **5**
4b. Ascospores shorter **6**

5a. Hairs straight or somewhat flexuous, nodulose, septate, 2.5–3 µm diam. Asci subglobose or broadly clavate. Ascospores slightly warted, 18–24 × 12–18 µm (Yaguchi et al. 1996). From soil. . . . . ***L. gracile***
5b. Hairs helically coiled, non-septate, 5–10.5 µm diam. Asci clavate. Ascospores smooth, 12–17 × 9–12 µm (Malloch & Cain 1971). From dung, once from vegetables . . . . . ***L. spirale***

6a. Hairs helical, non-septate. Ascospores 8–9 × 5–6 µm (Locquin-Linard 1983). From goat and sheep dung . . . . . ***L. helicoideum***
6b. Hairs different in shape. **7**

7a. Hairs uncinate, not septate. Ascospores 8–10 × 5.5–7 µm (Locquin-Linard 1983). From gazelle dung. . . . . ***L. recurvatum***

7b. Hairs wavy, septate. Ascospores 9–10 × 5.5–7 µm (Locquin-Linard 1983). From camel and other ungulate dung . . . . . ***L. fallax***

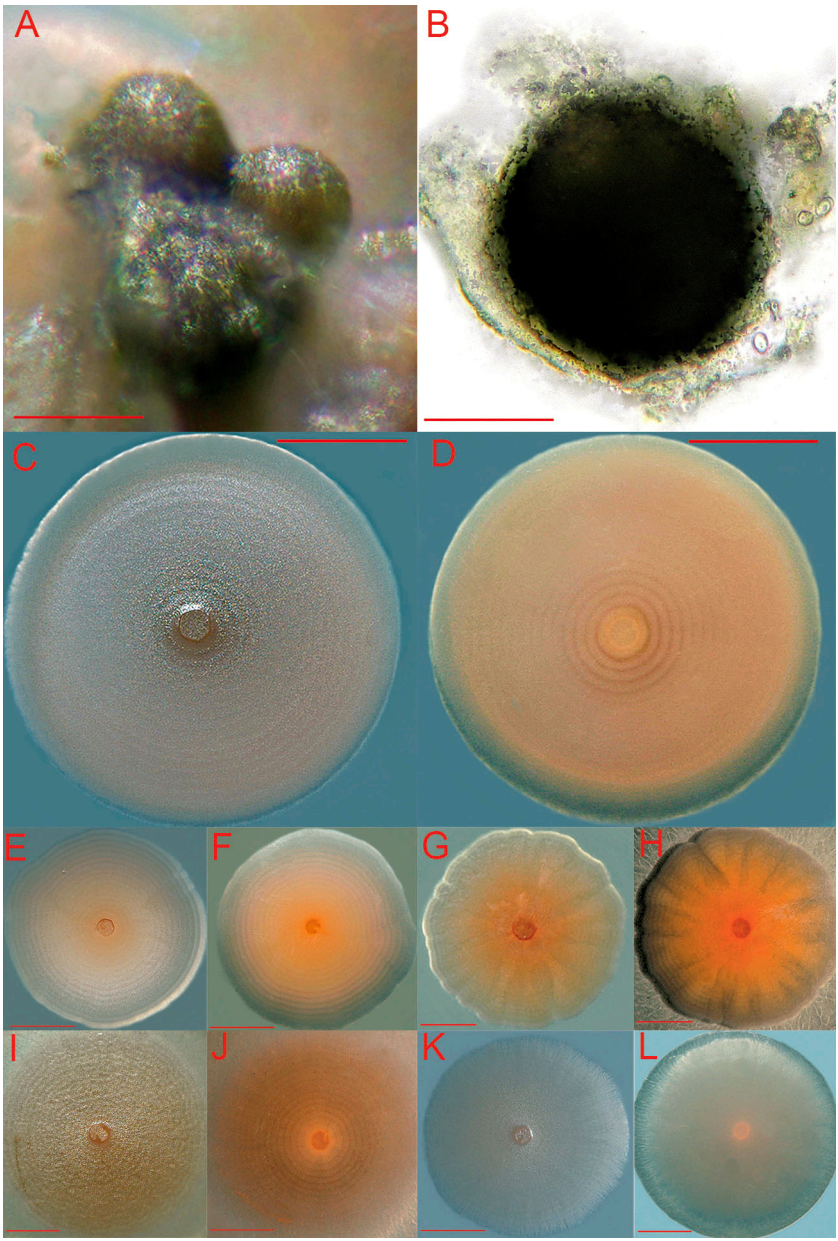
Guarro et al. (2012) regard *L. aegyptiacum* Mustafa & Ezz-Eldin is 'practically indistinguishable' from *L. orbiculoides*, but Mustafa & Ezz-Eldin (1989) originally described *L. aegyptiacum* with broadly ellipsoidal ascospores, quite different from the oblate ascospores of the latter.

Although *Lasiobolidium* is regarded as coprophilous (Kirk et al. 2008) only *L. fallax* Locq.-Lin., *L. helicoideum* Locq.-Lin., and *L. recurvatum* Locq.-Lin. have been isolated solely from dung (Locquin-Linard 1983, Abdullah & Alutby 1999). *Lasiobolidium orbiculoides* has been recorded from deer (Malloch & Benny 1973), gazelle (Janex-Favre & Locquin-Linard 1979), donkey (Abdullah & Alutby 1999), goat (Elshafie 2005), and possibly marsupial dung (Bell 2005) as well as from cultivated soil (Horie et al. 1992). Moustafa & Sharkas (1982) proved the cellulolytic activity of *L. orbiculoides* isolated from soil and grown in culture on filter paper. Its growth in our culture on blotting paper around the dung base confirms this activity. Simple or compound cellulose is found in plants and their derivatives, soil, and dung, so it is understandable that some cellulolytic fungi can develop on all these substrata without distinction, and it is possible that all other *Lasiobolidium* species are cellulolytic.

Cleistothelebolus nipigonensis Malloch & Cain, Can. J. Bot. 49: 851, 1971 Pl. 4–5

Colonies on Emerson YpSs medium attaining 60 mm diam. at 18 days, doughy-waxy, pink, with thin and soft concentric rings, which are more patent and brown shaded in the centre, margin even, reverse deeper pink, with clearly outlined central rings due to the presence of immersed, brown ascomata (YpSs medium resulted the best medium, suggesting complex nutrient requirements); Colonies on PDA and V8 juice morphologically similar to colonies on YpSs; Colonies on MA with radial soft grooves and with a wavy and sublobate margin, reverse deeper pink with more patent concentric rings and radial grooves; Colonies on NA very pale pink, with an indented margin; Ascomata cleistothecioid, globose, pale to dark brown at maturity, smooth, membranous, 60–80 µm diam.

Plate 4. *Cleistothelebolus nipigonensis* (DS 26817): A, ascomata on dung in a damp chamber; B, ascoma in water; C–L, colonies at room temperature 18 days incubation in Petri dishes (C–D, in Emerson YpSs agar; E–F, in PDA; G–H, in MA; I–J, in V8 agar; K–L, in NA; D, F, H, J, L, reverses). Scale bars: A = 40 µm; B = 30 µm; C–F, K–L = 20 mm; G–J = 15 mm.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Peridium two–layered, pseudoparenchymatous, the inner layer hyaline, the outer brown, both a textura epidermoidea of irregularly lobed, thin-walled cells, 4–10 × 3–8 µm, sometimes interspaced with spots of textura angularis; interascal tissue absent; asci not born from croziers, irregularly disposed, evanescent, unitunicate, inoperculate, non–amyloid, 8-spored, 10–14 × 9.5–10 µm, globose or broadly ellipsoidal or even broadly clavate, then short–stipitate; ascospores conglobate, 5–5.5 × 3.5–4 µm, usually broadly ellipsoidal with rounded ends, but also broadly ovoidal (Q = 1.37–1.42; Q average = 1.39), sometimes hardly inequilateral, hyaline to pale yellow, thin-walled, lacking both germ pores and de Bary bubbles; asexual state filamentous, lacking phialides: hyphae 1–3 µm diam., thin-walled, hyaline, wavy, densely septate, splitting at septa into swollen arthrospore-like cells in older colonies, branched, with long or even short branches at right angles, sometimes diverticulate, often swollen at the septa up to 5 µm diam., abundantly vacuolate, with vacuoles particularly observable in Congo red; conidia 3.5–7 × 2–3 µm, 1–celled, smooth, hyaline, thin-walled, cylindrical to ellipsoidal, with a truncate pedicel, born from very small, cylindrical conidiophores along the upper hyphal side or at the apex of short branches, usually budding.

Ecology & Distribution — More than fifty, gregarious or often crowded and confluent, superficial specimens, collected from canid (possibly fox) dung in a damp chamber culture. July. Very rare, known from one mountain site (1300 m a.s.l.) in Italy, and from wolf (*Canis lupus*) dung of the type locality in Ontario (Canada).

Specimen examined — **ITALY**, **Veneto**, **Vicenza**, Roana, Cesuna, 11°27′29″N 45°50′21″E, 6.VII.2008, leg. R. Cerello and G. Robich (DS 26817; GenBank KC492060, KC492061).

The name *Cleistothelebolus* means '*Thelebolus* developing cleistothecia' and emphasises the resemblance between these two coprophilous genera, which usually share ascoma and ascospore shape, size, and colour. Sharp differences, however, are noticeable, such as the presence of blastoconidia, production of true cleistothecia, irregularly disposed ephemeral asci, lack of an interascal tissue, and mesophily in *Cleistothelebolus* Malloch & Cain (Malloch & Cain 1971) versus no or a simple asexual state with production of arthrospores, cleistohymenial apothecioid ascomata, persistent asci, presence of paraphyses, and psychrophily (de Hoog et al. 2005) in *Thelebolus* Tode.

Coprotiella Jeng & J.C. Krug (*Thelebolaceae*) is similar to *Cleistothelebolus* but differs in having larger and light coloured ascomata, a peridium of a textura

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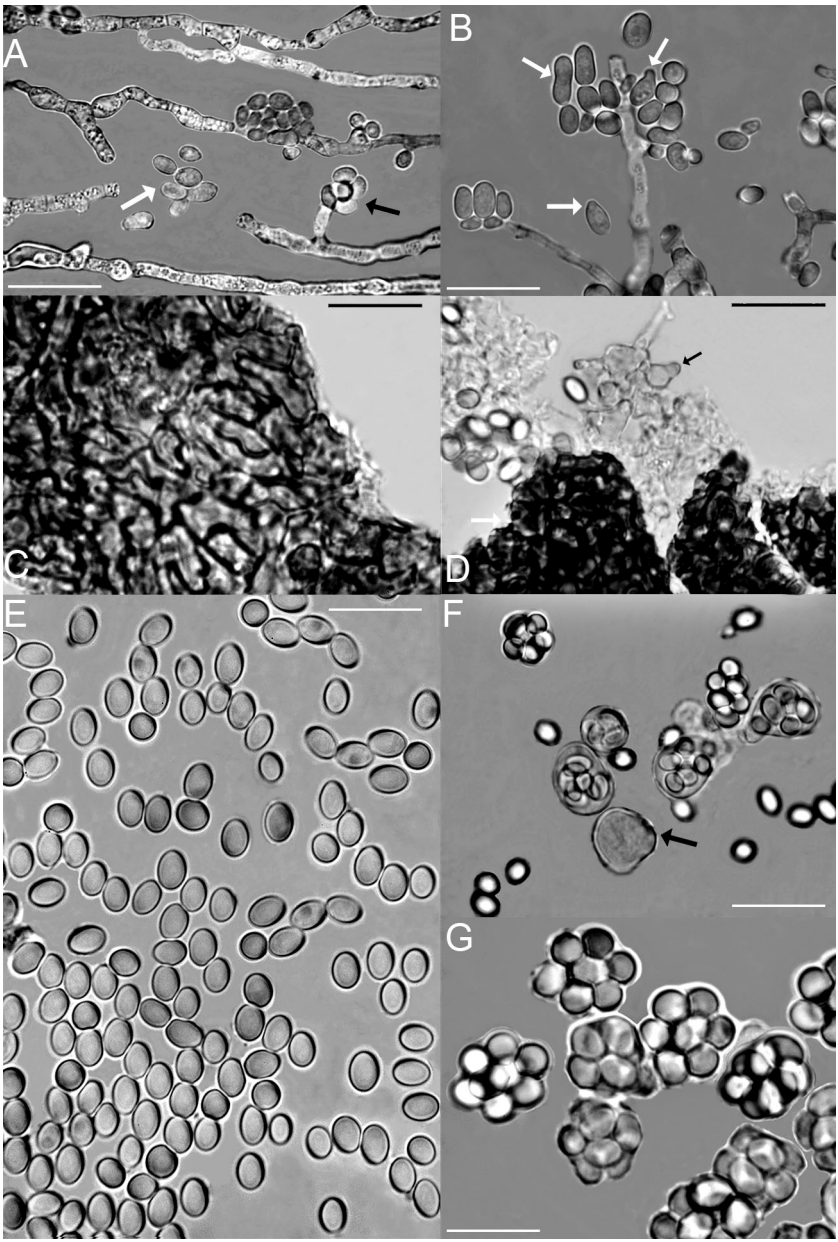
Plate 5 (right). *Cleistothelebolus nipigonensis* (DS 26817): A, free clustered conidia (white arrow) and anamorph hyphae with short conidiophores bearing conidia (black arrow); B, detail of the anamorph with some budding conidia (arrows); C, detail of exoperidial textura epidermoidea; D, exoperidial pocket of textura angularis (white arrow) beneath some free ascospores and pale



endoperidial cells (black arrow); E, ascospores; F, an empty ascus (arrow), asci with ascospores, and free ascospores; G, 8-spored asci. Scale bars: A = 25 µm; B, F = 15 µm; C, G = 10 µm; D = 20 µm; E = 12 µm.

angularis to globulosa, globose ascospores with a conspicuous de Bary bubble, and in lacking an asexual state (Jeng & Krug 1976).

We agree with Malloch & Cain (1971) that *Cleistothelebolus* has a striking morphological resemblance to *Pseudeurotium* J.F.H. Beyma, the type genus of *Pseudeurotiaceae* Malloch & Cain. This family is characterised by non-stromatic, usually dark cleistothecial ascomata with a pseudoparenchymatous peridium, (sub)globose, thin-walled, ephemeral asci, lacking apical apparatus and irregularly arranged in the centrum, absence of interascal tissue, and small usually smooth one-celled ascospores lacking germ pores. *Pseudeurotiaceae,* which have a hyphomycetous, phialidic (*Acremonium*- or *Stilbella*-like) or sympodial (*Sporothrix*- or *Teberdinia*-like) asexual state, can be isolated from wood, soil, or dung (Malloch & Cain 1970, Kirk et al. 2001, Cannon & Kirk 2007, Stchigel & Guarro 2007). *Pseudeurotium*, with its superficial, dark, globose ascomata, a peridium with a textura angularis, brown ascospores at maturity, and a sympodial asexual state, differs from *Connersia* Malloch, *Leuconeurospora* Malloch & Cain, and *Pleuroascus* Massee & E.S. Salmon. *Connersia* has hyaline, ellipsoid-reniform, inaequilateral ascospores (Booth 1961, von Arx 1987) and lacks conidia (Malloch 1974); the psychrophilic, cephalothecoid *Leuconeurospora* has ridged to reticulate ascospores (Malloch & Cain 1970, von Arx et al. 1988), and *Pleuroascus* has ascomata with helical appendages and hyaline ascospores (Massee & Salmon 1901, Malloch & Benny 1973, Barrasa & Moreno 1984). *Pseudogymnoascus* Raillo, included in *Pseudeurotiaceae* by Wang et al. (2006), is easily differentiated from *Pseudeurotium* by its gymnothecial ascomata, fusoid ascospores, and a *Geomyces* Traaen asexual state (Rice & Currah 2006).

Pseudeurotium ovale, with ovoidal-broadly ellipsoidal ascospores (Stolk 1955), differs from the majority of recognised *Pseudeurotium* species (Sogonov et al. 2005) such as *P. bakeri* C. Booth, *P. desertorum* Mouch., *P. macroglobosum* Matsush., *P. luteolum* Matsush., and *P. zonatum* J.F.H. Beyma, which have spherical ascospores (Beyma 1937; Routien 1957; Booth 1961; Mouchacca 1971; Matsushima 1975, 1996). *Pseudeurotium ovale* differs also from *P. irregulare* Lodha and *P. jaipurense* Lodha, which have irregularly ovoidal or subglobose ascospores (Lodha 1971). The ascospore shape and size in *P. ovale* are similar to those of *Cleistothelebolus nipigonensis,* which, however, can be distinguished by a "lighter colored peridium, less complex ascogenous system, and lack of phialides" (Malloch & Cain 1971). Based on our collection *C. nipigonensis* and numerous reports on *P. ovale* (Stolk 1955, Booth 1961, Udagawa 1965, Ahmad & Sultana 1973, Dennis 1981, Eriksson 1992, de Hoog et al. 2000), we will note some additional differences between these two taxa. *Cleistothelebolus* ascomata are smaller (15–80 versus 90–250 µm diam.), asci are larger (9–14 × 8–10.5 versus 7–9 × 6.5–8 µm) and often short–stipitate (rather than globose to broadly

ovoid or ellipsoid), and the peridium is two- instead of one-layered. The nature of the *Cleistothelebolus* peridium is particularly noticeable: in our collection it is formed of a TEXTURA EPIDERMOIDEA, not unmentioned but clearly depicted in the protologue (Malloch and Cain 1971). A pseudoparenchymatous peridium was also described in *P. ovale* but depicted as a TEXTURA ANGULARIS (Stolk 1955, Udagawa 1965, de Hoog et al. 2000). The habitat of the two species also differs: originally isolated from nematode cysts (Stolk 1955), *P. ovale* has been isolated from soil (Udagawa 1965), grass, wood chips, and decaying algae (Richardson 2004), but only rarely from dung (Ahmad & Sultana 1973, Eriksson 1992), whereas the only two *C. nipigonensis* collections come from wolf (the holotype) and fox (ours) dung.

Based on morphological (Kimbrough & Korf 1967, Eckblad 1968) and ultrastructural studies (Brummelen 1998), the *Thelebolaceae* were accommodated in *Pezizales*, but the placement was later questioned by rDNA sequence data (Momol & Kimbrough 1994, Momol et al. 1996). *Thelebolus* and related genera were excluded from *Pezizales* based on morphological and ultrastructural (Samuelson & Kimbrough 1978, Kimbrough 1981) and molecular phylogenetic studies (Landvik et al. 1998, Mori et al. 2000, Gernandt et al. 2001, Hansen et al. 2005). Molecular analysis of the nuclear SSU rDNA gene (de Hoog et al. 2005) confirmed the placement of *Thelebolus*, *Caccobius* Kimbr., and *Ascozonus* (Renny) E.C. Hansen within the separate family *Thelebolaceae* (*Thelebolales* P.F. Cannon), near the leotialean fungi and far from those orders to which they were assigned previously. *Thelebolaceae* now are considered allied with the *Leotiomycetes*, as stated in a recent study by Hansen & Pfister (2006) on the molecular systematics of *Pezizomycetes* O.E. Erikss. & Winka.

Cleistothelebolus was originally placed with *Lasiobolidium*, *Orbicula,* and other cleistothecial fungi, in *Eoterfeziaceae* (Malloch & Cain 1971, Benny & Kimbrough 1980), a family with an uncertain position in *Ascomycota:* morphologically similar to *Pseudeurotiaceae*, but with an unknown asexual state (Kirk et al. 2001, Cannon & Kirk 2007).

Cleistothelebolus was later transferred (Jeng & Krug 1976) to *Pyronemataceae* trib. *Theleboleae*, which on the whole is the equivalent of the current *Thelebolaceae*.

Landvik et al. (1997) suggested that genera other than *Thelebolus* belonging to small pezizalean families with uncertain affinities (like *Cleistothelebolus*) might be related to *Leotiales* and noted that further phylogenetic analyses are needed to explain the relationships of *Cleistothelebolus*, which Malloch & Cain (1971) originally regarded as probably evolved from *Thelebolaceae*. Lumbsch & Huhndorf (2007, 2010) suggested placing *Cleistothelebolus* within *Pyronemataceae,* but further phylogenetic studies are needed there as well. Our ITS and LSU sequence analyses support *Cleistothelebolus nipigonensis* in *Thelebolaceae*.

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