Podospora bullata, a new homothallic ascomycete from kangaroo dung in Australia

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Abstract: *Podospora bullata* sp. nov. is described and illustrated based on five kangaroo dung collections from Australia. The species is placed in the genus *Podospora* based on its teleomorph morphology and its ITS sequence from a fertile homothallic axenic culture. Perithecial necks are adorned with prominent simple unswollen filiform flexuous and non-agglutinated greyish hairs. Ascospores are characterized by minute pedicels, lack of caudae and an enveloping frothy gelatinous material with bubble-like structures both in the amorphous gel and attached to the ascospore dark cell. No anamorph was observed.
Keywords: coprophilous fungi, *Lasiosphaeriaceae*, *Podospora*, ribosomal DNA, taxonomy.

Résumé : *Podospora bullata* sp. nov. est une nouvelle espèce qui a été trouvée sur cinq isolats provenant d'Australie et obtenus à partir de déjections de kangourou. Cette nouvelle espèce est décrite ici avec des illustrations. Cet ascomycète est placé dans le genre *Podospora* en se basant sur la séquence des ITS et sur l'aspect de son téléomorphe, en l'occurrence un individu homothallique fertile en culture axénique. Les cols des périthèces sont ornés par une touffe de longs poils grisâtres fins, flexueux, en majorité sans ramification et non agglutinés. Les ascospores sont caractérisées par de courts pédicelles et une absence d'appendices. Les ascospores matures sont noires et entourées par un mucilage contenant des inclusions ayant l'aspect de bulles, adjacentes à la paroi de l'ascospore. Nous n'avons pas observé d'anamorphe.
Mots-clés : champignon coprophile, ITS, *Lasiosphaeriaceae*, phylogramme, *Podospora*, taxinomie.

Introduction

Podospora Ces. is one of the genera most frequently found on dung, a substrate from which most of its species are described. Even excluding those species now included in *Schizothecium* Corda (Lundqvist, 1972, 1997; Cai *et al*., 2005; Chang *et al*., 2010) or in other genera, *Podospora* has well over 100 species (http://www.indexfungorum.org/names/names.asp). No world monograph exists although historical records and keys are available in Cain (1934), Mirza & Cain (1969), Lundqvist (1972) and Doveri (2004, 2008). The species described herein is an undescribed species recorded as "*Podospora* n. sp." by the senior author in her publication on coprophilous ascomycetes of Australia (Bell, 2005).

Materials and Methods

Dung collection, incubation and examination

Four of the five collections were made by volunteer naturalists who were taking part in the Australian Fungimap Project centered at the National Herbarium in the Melbourne Botanic Gardens. The fifth collection was made by the Englishman Mike Richardson during his visit to Australia. Details of the collection sites (dung type, date of collection, geographic location and description of vegetation) were provided by the collectors and sent along with a paper bag containing the dried dung to Pat Grey and Katy Sommerville at the Botanic Gardens. They recorded the samples and sent them to the senior author in New Zealand who examined them as part of her project on coprophilous fungi of Australia (Bell, 2005). In New Zealand the samples were refrigerated at 5°C until later when they were incubated in moist chambers under ambient temperatures and diurnal lighting (Bell, 1983; Lundqvist, 1972). Records were kept of perithecial appearance on the dung and morphological features were examined in water, aniline blue lactic acid (0.05 g aniline blue in 100 ml lactic acid), Melzer's reagent and Shear's mounting fluid (SMF), see Bell (2005) for formulae of the latter two. SMF and aniline blue lactic acid mounts sealed with nail polish accompany the dried herbarium specimens. At least 50 ascospores were measured from each collection.

Axenic culture

Nutrient agar media used were Difco™ corn meal agar made up to 2% agar (CMA), CMA to which 100 units/ml penicillin G and 30 µg/ml streptomycin sulfate were added just prior to solidification in Petri dishes, CMA to which several whole autoclave-sterilized wild rabbit (*Oryctolagus cuniculus*) droppings were added just prior to solidification in Petri dishes and potato carrot agar (PCA) = 20 g potatoes, 20 g carrots, 20 g agar, 1.0 l distilled water (finely grated unpeeled organic potatoes and carrots, boiled 30 min in distilled water, agar added and water topped up to 1.0 l), sterilized at 120°C for 15 min. Incubation was at 25°C on a diurnal 12 h light – 12 h dark cycle.

Ascospore germination

Eight whole fertile perithecia from dung collection MR1999.045 were immersed in 3% hydrogen peroxide for 20 minutes. Six of these were subsequently transferred, three each, to two different solutions of 10% buffered (pH 7 and pH 8) pancreatin (porcine pancreas, Sigma Chemical Company) and these incubated in the dark for 3 h at 37°C. Similar treatments for germinating ascospores of *Podospora austrohemisphaerica* (Lundqvist *et al*., 1999) had earlier proved successful. The remaining two perithecia were transferred to sterile distilled water only and incubated in the same manner. Dishes bearing each different treatment were placed in larger Petri dishes to avoid evaporation. In all cases evaporation did occur and only dried perithecia resulted. Nonetheless, perithecia from each treatment were transferred to CMA containing antibiotics. Ascospores were then dispersed over the agar surface and the plates incubated at 25°C on a diurnal 12 h light – 12 h dark cycle.

ITS sequencing

In order to sequence the ITS, one of us (Robert Debuchy), grew *Podospora bullata* on M2 media (Esser, 1974) covered with a cellophane membrane. After three days, a tiny bit of *P. bullata* mycelium was taken from the cellophane membrane and transferred to a 0.2 ml tube filled with 100 µl of a Taq PCR mixture according to Q-BIOgen instructions (Strasbourg, France) with primers PN3 (5'-ttggtgaaccagcggaggatc-3') and PN10 (5'- tccgcttattgatatgcttaag-3') (Neuvéglise *et al*., 1994). The tube containing the mycelium and the PCR reaction was then frozen at -20°C to disrupt the mycelium. After freezing, the PCR reaction tube was directly submitted to an initial denaturation for 2 min at 94°C, and then to 40 cycles of amplification (1 min at 94°C, 1 min at 60°C, 1 min at 72°C). The reaction ended with a final elongation step of 5 min at 72°C. The success of amplification was checked by depositing 5 µl of the PCR reaction on an agarose gel. The PCR reaction was sent for sequencing with primers PN3 and

PN10 to Genome Express (Meylan, France). Sequence files were compared with the electrophoregrams to correct any nucleotide miscalling and the 532 base pairs of the *P. bullata* ITS were assembled with CAP3 (Huang & Madan, 1999).

Phylogeny analysis

Species included in the phylogenic analyses are listed in Table 1. Phylogenic analyses were performed at http://www.phylogeny.fr/ (Dereeper *et al.*, 2008; Dereeper *et al.*, 2010). The phylogram is presented in Figure 3.

Taxonomy

Podospora bullata A. Bell & D. Mahoney, *sp. nov.* — Mycobank MB 492868, Figs 1–2.

Holotype: (dried dung and slides): AUSTRALIA. Victoria. Little Desert National Park, 27 km S of Nhill along McDonald Highway, Mallee heathland with *Eucalyptus incrassata* and *Leptospermum continentale.* Eastern grey kangaroo dung (*Macropus giganteus*), 9 Jun. 1997, R.J. Fletcher dung collection A35, PDD 77984 (= Bell & Mahoney 825).

Culture and GenBank deposits: A single-ascospore culture from the MR1999.045 collection was deposited as CBS 115576. ITS from CBS 115576 was deposited in GenBank with accession number DQ166960.

Etymology: From the Latin '*bulla*' (=bubble), referring to small bubble-like vacuoles in gelatinous sheaths of the ascospores, especially visible on the pigmented spore surface.

Characteristics on moist-chamber dung from field collections

Perithecia 590–760 × 340–470 µm, few to moderate in number, scattered or in small groups of 2–5, dark, obpyriform, with venters variously immersed and necks emergent, inconspicuously clothed with long flexuous hairs on the venter and with similar but shorter and stouter more obvious hairs on the neck (Figs 1A; 2A–C). **Necks** prominent, darker than the venters, brown to blackish, broadly cylindrical or conical and truncate apically, mostly 200–300 × 160–200 µm but variable. **Ostiole** prominent (Figs 1A; 2A) and lined with hyaline periphyses. **Neck hairs** varying from short to 160 µm in length but mostly 50–100 × 2(–3) µm, sparse to numerous, evenly scattered or more numerous on one side, simple to sparingly branched, usually separate but sometimes in loose aggregates, straight to flexuous, moderately thin-walled, smooth, with widely spaced septa more easily observed in lower portions of the hair, smoky-grey in mass, of uniform width with only slight tapering near the rounded apex (Fig. 2C). Closer observations reveal that these separate to loosely aggregated hairs are actually occasional extensions from a uniform palisade of short crowded anticlinal hyphae ca 20–40 × 2 µm that cover the entire neck - the more extensions, the hairier the neck. On the more lightly pigmented lower neck, patches of small single-celled sparsely verrucose dark tubercles are visible among the anticlinal hyphae (Fig. 1B). **Venter peridium** relatively thin, consisting of several layers of pseudoparenchyma (*textura angularis*) whose cells are mostly 4–8 µm in long axis, thin-walled and grey to greyish-brown. Cells of the outer venter smaller and darker than those of the flatter-celled inner peridium. **Peridium of the upper venter - just beneath the neck** consisting of several rows of horizontally aligned elongate rectangular cells which encircle the base of the neck. **Peridium of the neck** consisting of dark vertically aligned, tightly compacted hyphae which originate just above the rows of encircling cells. Near the neck surface these hyphae branch and diverge as a uniform palisade layer of short anticlinal hyphae that cover the neck surface, their uppermost portions slightly curving toward the neck apex. **Paraphyses** crowded among the asci (most easily seen where squashed free of the asci), branching, septate, smooth; basally composed of swollen cells strongly indented at their septa, these gradually less swollen and apically becoming narrower, attenuated and lacking septal indentations. **Asci** cylindrical to cylindrically clavate, with rounded unspecialized non-amyloid apices and long narrow stipes, containing 8 ascospores (consistently located in the uppermost portion of the asci), initially uniseriate and either remaining so or becoming partially biseriate; ascospore-bearing portions 155–235 × 25–40 µm with stipe lengths to ca ½ of this (Figs 1C; 2F). **Ascospores** two-celled (Figs 1C,D; 2D,F,H), consisting of a large pigmented apical cell (body cell) and a small hyaline basal cell (pedicel); **body cells** smooth, dark brown to black, broadly ellipsoid to ellipsoid-fusoid, symmetrical to slightly asymmetrical, with an apical germ pore 3 µm in diam. (Figs 1D; 2E) and containing a large de Bary bubble when mounted in SMF or aniline blue lactic acid, (27–)32–40(–43) × (17–)20–25(–29) µm; **pedicels** smooth, narrow, cylindrical although tapering very slightly from transverse septum with body cell to rounded extremity, normally directed obliquely downwards in the asci (Fig. 1C) but in squash mounts many ascospores come to lie with their pedicels directed at right angles to the long axis of the ascus (Fig. 2F), 5–8(–10) × (1.5–)2(–3) µm. Pedicels of all ages and immature ascospores most easily observed when stained in aniline blue lactic acid (Fig. 2D,F,H); **gelatinous sheath** amorphous, highly vacuolated, surrounding the spores inside the ascus (Figs 1C; 2E,F) and after their release in squash mounts (Fig. 2G), the bubble-like vacuoles especially obvious where they cling to the body cell wall (Figs 1D; 2H); **no gelatinous caudae**.

Although asci with fewer than 8 ascospores were occasionally seen in all collections, collection A266 warrants a short comment. Typical asci and ascospores still predominated but here asci with <8 ascospores were common and in these asci (and even in some of the 8-spored asci) ascospore body cells tended to be more broadly ellipsoid and often subglobose to globose, 26–38 × 26–36.5 µm. Also the body cell was sometimes slightly extended at the base of the pedicel; the slight extension being dark brown and truncate. Pedicels were typical. We attribute these aberrations to the unusually long dung incubation period of over 4 months for this collection. In other collections, mature perithecia were observed and described after 1–2 months of incubation. Extended periods of incubation require repeated drying and rewetting and ambient temperatures and lighting tend to be more variable.

Not included under 'Characteristics on moist-chamber dung from field collections' above, but characteristic of all collections, is the possible presence of jacket paraphyses (Bell & Mahoney, 1995). These were originally described among the *Schizothecium* group of *Podospora* species and are characterized as sterile elements surrounding the asci of the centrum but not appearing among them. Squash mounts often result in the squeezing out of the entire centrum. Such a feature was occasionally observed as water squash mounts were prepared for the presently described collections, jacket paraphyses appearing as a hyaline sheet of swollen vertically elongate cells surrounding the centrum and differing considerably from cells of the inner peridium.

Ascospore germination and axenic growth (MR1999.045 specimen)

Unlike the success achieved with ascospore germination in *Podospora austrohemisphaerica* (Lundqvist *et al.*, 1999), none of the many ascospores from the buffered pancreatin treatments germinated. Surprisingly, however, roughly 50% of the ascospores from the same treatment with 3% hydrogen peroxide for 20 min followed instead by a treatment in distilled water at 37°C for 3 h did. This occurred despite the perithecia drying down during their treatment at 37°C. Ascospores germinated in roughly 24 h. In each case a large germination vesicle (12–16 µm in diam) formed at the apical germ pore and from this grew 4–4+ arms in irregular sequence (Fig. 2I). Although at first simple, the arms soon began to branch. Pedicels

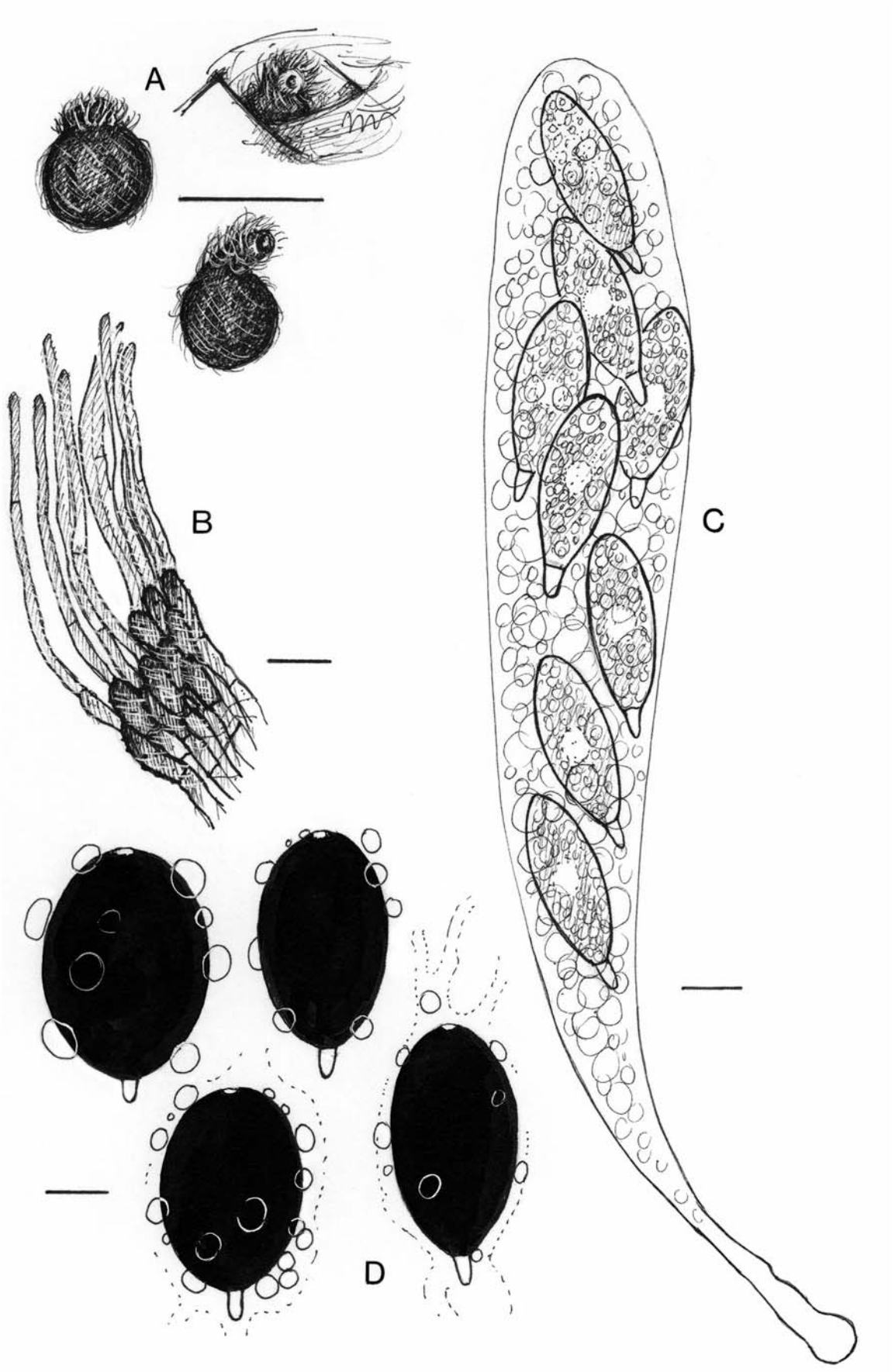

Fig. 1 – *Podospora bullata* from moist-chamber-incubated kangaroo dung. A. Perithecia shown free and sunken within the dung. B. Squash mount (from lower neck area) of crowded anticlinally oriented hyphae that cover the neck (not visible in low magnification view of A), showing also single-celled sparsely verrucose tubercles at their base. C. Ascus containing 8 immature ascospores. D. Mature ascospores, showing bubble-like vesicles in the gelatinous matrix at and near the spore surface. Scale bars: A = 1 mm; B = 5 µm; C, D = 10 µm.

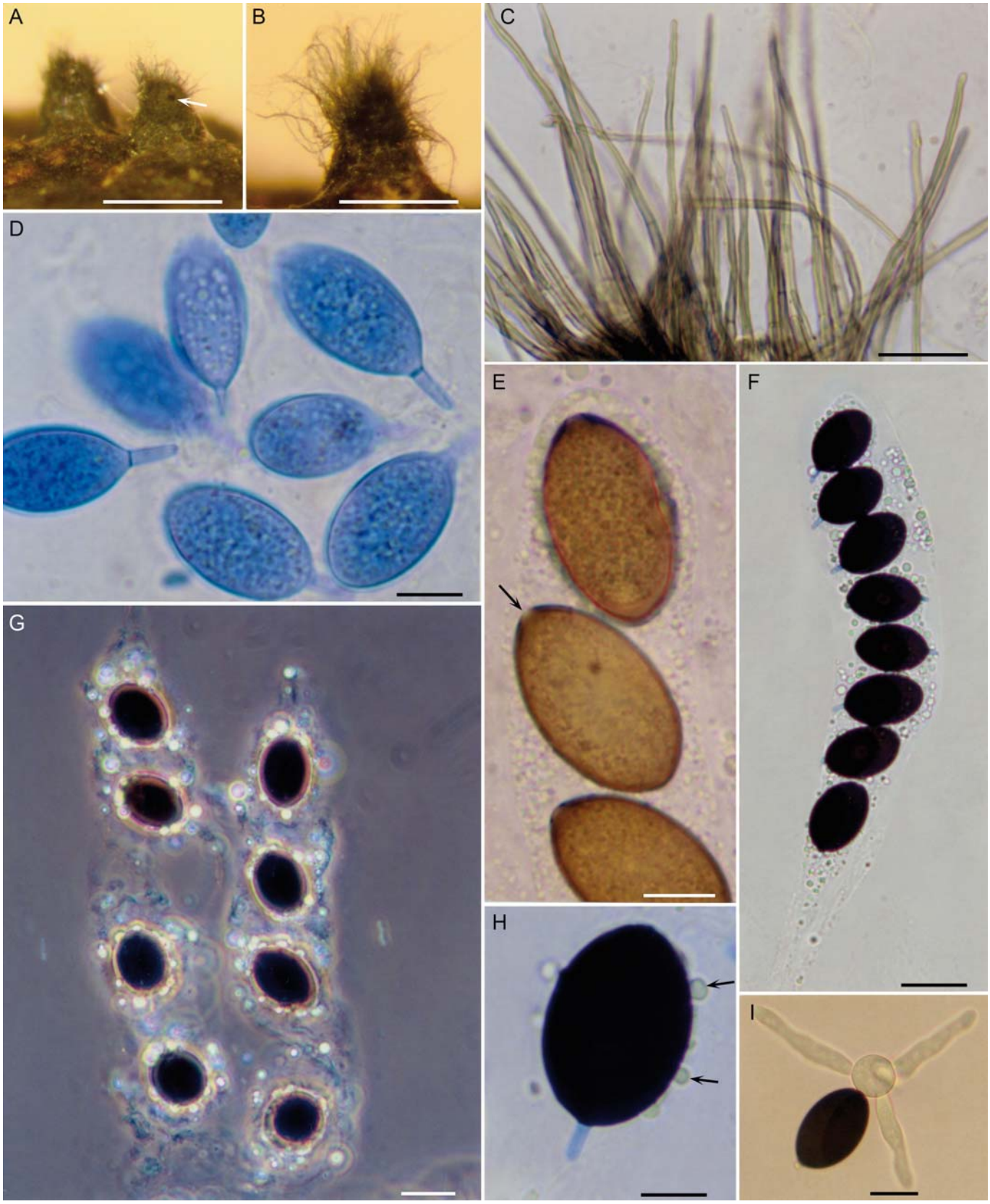

Fig. 2 – *Podospora bullata*. A, B. Perithecia, *in situ* on the dung, showing upper venters and hairy necks. Arrow indicates an ostiole. C. Hairs on the perithecial neck. D. Young ascospores. E. Ascospores, not fully pigmented. Arrow indicates an apical germ pore. F–H. Mature ascospores, showing bubble-like vesicles in the diffuse gelatinous material surrounding them. F. Single ascus. F, H. Ascospores with aniline blue stained pedicels. H. Arrows on bubble-like vesicles adjacent to the ascospore wall. I. Germinating ascospore with globose germination vesicle and four hyphae. A, B, D, F, H = dung collection A35; C, E, G, I = MR1999-045. Mounting media: C, E = SMF; D, F, H = aniline blue lactic acid; G = distilled water; I = coverslip directly on agar medium. Scale bars: A = 400 µm; B = 300 µm; C = 20 µm; D, E, H = 10 µm; F, G = 25 µm; I = 15 µm.

Table 1 – Species, GenBank accession numbers of sequences used in the phylogenetic analyses and information on the sequencing source, collection locality and substrate.

Species	GenBank accession number	Source	Collection locality	Substrate
Apodospora peruviana	EU573703	CBS 118394	Australia	wombat dung
Apodus deciduus	AY681199	CBS 506.70	U.S.A.	pack rat dung
Apodus oryzae	AY681200	CBS 376.74	Italy	sheaths of *Oryza sativa*
Arnium arizonense	KU955584	CBS 120289	Australia	camel dung
Cephalotheca foveolata	KJ573100	UTHSCSA DI 14-21	U.S.A.	blood of 59-year-old man
Cercophora ambigua	AY999137	CBS 215.60	Canada	decorticated twig
Cercophora caudata	AY999135	CBS 606.72	Netherlands	soil
Chaetomium globosum	KC146352	ATCC 6205		
Neurospora crassa	GU327630	ATCC MYA-4614		
Podospora anserina	AY278557	strain S (Rizet, 1952)		
Podospora anserina	DQ166956	CBS 112042	Australia	wallaroo? dung
Podospora appendiculata	AY999126	NBRC 8549	Japan	dung
Podospora austrohemisphaerica	AY026939	CBS 216.97	New Zealand	rabbit dung
Podospora bicolor	AF443848	CBS 248.71	Africa	hippopotamus dung
Podospora bullata	DQ166960	CBS 115576	Australia	kangaroo dung
Podospora cochleariformis	AY999123	CBS 249.71	Africa	*Redunca* sp. dung
Podospora comata	AF443849			
Podospora communis	EU621831	CBS 118393	New Zealand	horse dung
Podospora conica	AY515356	CBS 128.94	New Zealand	red deer dung
Podospora cupiformis	AY999125	CBS 246.71	C. African Republic	*Cobus defassa* dung
Podospora curvicolla	AY999122	NBRC 8548		rabbit dung
Podospora curvispora	AF443850			
Podospora curvuloides	AY515357	CBS 129.94	New Zealand	goat dung
Podospora dakotensis	AY515358	CBS 130.94	New Zealand	sheep dung
Podospora decidua	AF443851	CBS 254.71	C. African Republic	*Lepus aegyptiacus* dung
Podospora decipiens	AY515359	CBS 113104	New Zealand	sheep dung
Podospora dimorpha	DQ166963	CBS 115806	Australia	kangaroo dung
Podospora ellisiana	AY515360	CBS 112044	New Zealand	horse dung
Podospora excentrica	EU621832	CBS 118392	New Zealand	horse dung
Podospora fabiformis	DQ166958	CBS 112043	Australia	pademelon or wallaby dung
Podospora fimiseda	AY515361	CBS 990.96	New Zealand	horse dung
Podospora glutinans	AY615208	CBS 113105	Australia	brushtail opossum dung
Podospora intestinacea	AY515363	CBS 113106	New Zealand	horse dung
Podospora miniglutinans	AY515362	CBS 131.94	New Zealand	rabbit dung
Podospora myriaspora	DQ166961	CBS 115804	New Zealand	sheep or goat dung
Podospora petrogale	AY071831	CBS 109409	Australia	*Petrogale lateralis* dung
Podospora pleiospora	AY515364	CBS 113107	New Zealand	rabbit dung
Podospora prethopodalis	EF197085	BCRC 37816	Taiwan	ox dung
Podospora pyriformis	DQ166962	CBS 115805	New Zealand	pig dung
Podospora setosa	GU391421	CBS 118391	New Zealand	sheep or goat dung
Podospora setosa	AF443852			
Podospora tetraspora	DQ166957	CBS 132.94	New Zealand	rabbit dung
Podospora vesticola	AY515365	CBS 133.94	New Zealand	rabbit dung
Schizothecium glutinans	AY999116	CBS 134.83 as *P. glutinans*	Switzerland	*Arctostaphylos uva-ursi*
Sordaria macrospora	AF246293	CBS 957.73		
Strattonia insignis	AY277912	CBS 110351	Australia	wallaby dung
Strattonia oblecythiformis	DQ166959	CBS 110350	Australia	macropod dung
Zopfiella erostrata	AY999133	CBS 255.71	Africa	*Cobus defassa* dung
Zopfiella karachiensis	AY999128	NBRC 32902	India	garden soil
Zygopleurage zygospora	EF197088	BCRC 37729	Taiwan	ox dung

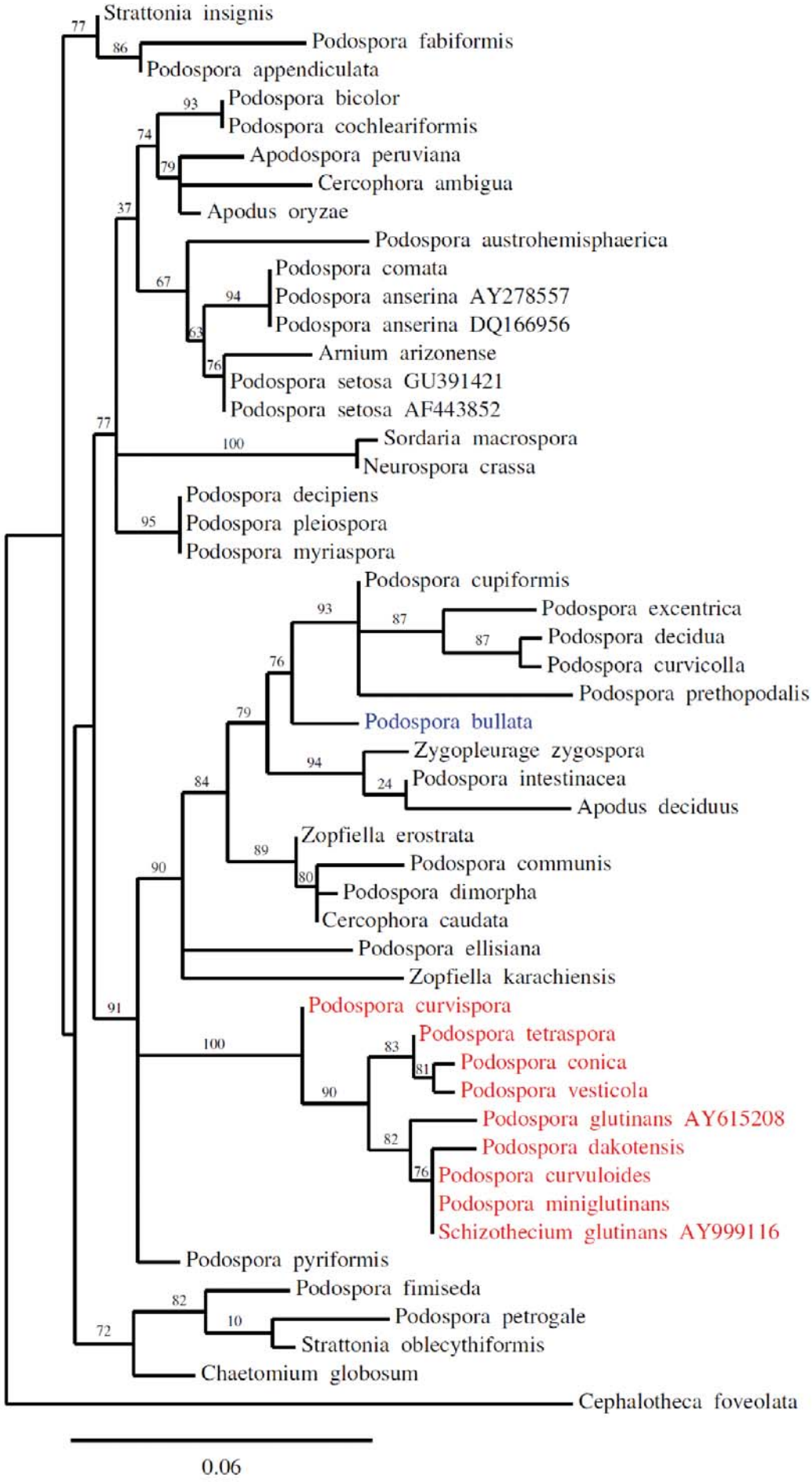

Fig. 3 – Phylogram based on ITS sequences. Numbers are branch support values in %. *Podospora bullata* is in blue. Species widely recognized in the genus *Schizothecium* (Lundqvist, 1972, 1997; Cai *et al.*, 2005) are in red. *Cephalotheca foveolata* was used as an outgroup.

were seen only as a tiny remnant at the opposite end of the spore. Remnants of the foamy gelatinous sheath were evident around ungerminated spores and some of the germinated ones. Single germinating ascospores were transferred to CMA Petri dishes augmented with sterile rabbit droppings and after pure culture was assured, to PCA slants.

Single ascospore cultures on CMA spread slowly, 0.5 cm in 10 days and only 1.5 cm after two months, dark, low and with fertile perithecia (demonstrating homothallism) but no anamorph. Colonies on CMA with rabbit droppings and on PCA grew slightly better, the latter similar to those on CMA and approx. twice their diam – no anamorphs. The CMA culture with the best production of perithecia was selected for further growth on CMA with rabbit droppings. The resultant 2 month old cultures yielded numerous fertile perithecia both on the agar near the dung and on the dung itself. A PCA slant of this isolate was sent to CBS and to Robert Debuchy for sequencing. One of the 2 month old CMA rabbit dropping cultures was freeze-dried as a paratype. Ascospores, asci and other features of perithecia on this axenic culture were mostly as described from the moist chamber incubated dung. Larger, often less hairy, necks on the perithecia were a notable exception. Cylindrical, apically truncate necks, although variable, were up to 500 × 250 µm. Longer necks, especially, lacked hairs except near their bases. No anamorph was seen.

Additional specimens examined

AUSTRALIA. Victoria: Mt. Langi Ghiran, approx. 20 km SE of Ararat along the Western Highway, eucalypt woodland, 37°19´S, 143°06´E. Eastern grey kangaroo dung, 24 Apr. 1997, T. May dung collection A14, PDD 80314, slides only (= Bell & Mahoney 864); Little Desert National Park, 27 km S of Nhill, along McDonald Highway near Nhill-Harrow Road, *Eucalyptus leucoxylon* woodland, 36°35´S, 141°39´E. Eastern grey kangaroo dung, 9 Jun. 1997, R.J. Fletcher dung collection A36, PDD 90051 (= Bell & Mahoney 957). Western Australia: South Coast Highway 20 km W of Ravensthorpe at the Phillip's River crossing, open woodland with *Allocasuarina* and *Eucalyptus* species, 33°36´19´´S, 119°52´42´´E. Kangaroo dung, 12 Jun. 1998, K. Syme dung collection A266, PDD 82111 (= Bell & Mahoney 889); Two People's Bay Nature Reserve 20 km E of Albany, 34°58´26´´S, 118°10´02´´E. Western grey kangaroo? dung (*Macropus fuliginosus*), 1 Oct. 1999, M. Richardson dung collection MR1999.045, paratype PDD 80313 (= Bell & Mahoney 863) — the MR1999.045 specimen was deposited at PDD as a fully fertile, freeze-dried axenic culture (Difco™ corn meal agar/supplemented with whole sterilized rabbit dung incubated at 25°C, 12 h light/12 h dark for 2 mo) rather than as a dried dung specimen.

Other illustrations and a key

Podospora bullata, as *Podospora* n. sp., was previously illustrated and included in a key to coprophilous *Podospora* species of Australia (Bell, 2005).

Discussion

The relationship of *Podospora bullata* to other *Podospora* species or those in related genera remains unclear. Its cylindrical asci with uniseriately arranged ascospores and the lack of ascospore caudae are rarely seen among *Podospora* species (Doveri, 2008) and its amorphous frothy gelatinous ascospore sheathing is unique. Although Doveri (2008) provides a worldwide key to over 100 *Podospora* and *Schizothecium* species, none fit *P. bullata*. Our own work with *Podospora* species from New Zealand and Australia (Bell, 1983, 2005) also confirms its singularity. It was hoped that phylogenetic work would shed some light on possible relationships but species nesting near *P. bullata* in Fig. 3 (*P. cupiformis*, *P. decidua*, *P. excentrica*, *P. prethopodalis* and *P. curvicolla*) are dissimilar from a morphological perspective.

Worth emphasizing here are some of the problems bedevilling phylograms of large polyphyletic taxa like *Podospora*. First, most of the species have not been cultured or sequenced; second, GenBank and other depositories presently have only a limited number of sequences for most species; and third many new species probably remain undescribed. In addition to this, new DNA sequencing technologies and software programs constantly change our views of species relationships and the appearance of "family trees". Just as bedevilling as the sequence data in the identification of species relationships is the missing information on the species themselves – morphological description, illustrations, geographic location, substrate, culturing and more. These need to be as accurate and complete as possible. It is for this reason that details in this publication and those provided in Table 1 are essential. Thanks to R. Debuchy an ITS is now available for all but one of the New Zealand and Australian cultures provided by A. Bell and D. Mahoney from coprophilous substrates [Table 1 – *Podospora/Schizothecium* species, *Apodospora*, *Arnium* and *Strattonia* species (except *P. glutinans* AY615208; culture A.B. & D.M., sequencing John Krug)]. Most other Table 1 sequences were those used in Cai *et al.* (2005, 2006) and Chang *et al.* (2010) or provided from R. Debuchy's Paris lab.

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