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The phylogenetic relationships of *Torrendiella* and *Hymenotorrendiella* gen. nov. within the Leotiomycetes

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Abstract

Morphological and phylogenetic data are used to revise the genus *Torrendiella*. The type species, described from Europe, is retained within the *Rutstroemiaceae*. However, *Torrendiella* species reported from Australasia, southern South America and China were found to be phylogenetically distinct and have been recombined in the newly proposed genus *Hymenotorrendiella*. The *Hymenotorrendiella* species are distinguished morphologically from *Rutstroemia* in having a *Hymenoscyphus*-type rather than *Sclerotinia*-type ascus apex. *Zoellneria*, linked taxonomically to *Torrendiella* in the past, is genetically distinct and a synonym of *Chaetomella*.

Keywords: ascus apex, phylogeny, taxonomy, *Hymenoscyphus*, *Rutstroemiaceae*, *Sclerotiniaceae*, *Zoellneria, Chaetomella*

Introduction

Torrendiella was described by Boudier and Torrend (1911), based on *T. ciliata* Boudier in Boudier and Torrend (1911: 133), a species reported from leaves, and more rarely twigs, of *Rubus*, *Quercus* and *Laurus* from Spain, Portugal and the United Kingdom (Graddon 1979; Spooner 1987; Galán *et al.* 1993). Boudier & Torrend compared the fungus with *Dasyscypha* because of very long, brown, pointed setae at the apothecial margin. Later placed in the *Rutstroemiaceae*, the anatomical similarity of *T. ciliata* to *Rutstroemia* spp. was discussed by Galán *et al.* (1993) who argued that the presence of brown setae was likely to be of little phylogenetic significance and that *Torrendiella* should perhaps be placed in synonymy with *Rutstroemia*.

Dennis (1959b, 1978) suggested a possible relationship between *Rutstroemia hirsuta* Dennis (1959b: 460), or *Torrendiella ciliata*, respectively, and the type species of *Zoellneria*, *Z. rosarum* Velenovsky (1934: 298) (typified by Dennis 1959a), with both fungi characterised in part by brown setae on the apothecia and stromatic development on host tissue. Dennis (1958, 1963) and Beaton and Weste (1977) transferred four species with setose apothecia to *Zoellneria*. These species were later assigned to *Torrendiella* by Spooner (1987) who discussed differences between the type species of the two genera, differences he considered to be significant at the generic level. Johnston and Gamundí (2000) noted that although the outer part of the excipulum of *Z. rosarum* was gelatinised, it lacked the characteristic 3-layered excipulum structure of *Torrendiella* described by Galán *et al.* (1993), had nonamyloid asci, and an apparently consistent association with its putative anamorph, *Chaetomella oblonga* Fuckel (1870: 402) (Clark 1980, as *Amerosporium patellarioides* Smith & Ramsbottom (1918: 52), a synonym of *C. oblonga*, fide Rossman *et al.* 2004). Kirk *et al.* (2008) list *Amerosporium* as the anamorph of *Zoellneria*, based on the reported link between *A. patellarioides* and *Z. rosarum* (Clark 1980, Spooner 1987). Based on the synonymy of Rossman *et al.* (2004) the *Zoellneria* anamorph should in fact be recorded as *Chaetomella*.

From the Southern Hemisphere, *Torrendiella* was first reported by Spooner (1987), including three species previously treated by Dennis (1958) and Beaton and Weste (1977) as *Zoellneria*. Of these species, *T. madsenii* and *T.*

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clelandii were reportedly found on dead wood, twigs and/or bark of *Nothofagus* and *Eucalyptus*, respectively, while *T. eucalypti* was reported from the fallen leaves and phyllodes of five different host genera (Spooner 1987). Of these hosts, *Acacia*, *Banksia*, and *Metrosideros* were reported from Australasia, *Eucalyptus* from the UK, while *Myrica* was the host of *Zoellneria callochaetes* (Ellis & Everh.) Dennis (1963: 333), described from North America and placed in synonymy with *T. eucalypti* by Spooner (1987). *Torrendiella eucalypti* had been reported also by Gamundí (1962, as *Zoellneria eucalypti*) on fallen leaves and wood of *Nothofagus* from Argentina. In contrast, Beaton and Weste (1977) and Johnston and Gamundí (2000) regarded *T. eucalypti* as an *Acacia*-specialised species. Despite its epithet, the type specimen of *T. eucalypti* is on *Acacia* phyllodes (Dennis 1958).

Later reports of *Torrendiella* from the Southern Hemisphere include Gamundí and Romero (1998: 104), who mention in passing the regular occurrence of unidentified *Torrendiella* apothecia in association with *Hymenoscyphus gregarius* (Boud.) Gamundí & Giaiotti (1977: 18) on fallen leaves of *Nothofagus* and *Drimys* in Argentina, and Johnston and Gamundí (2000) who described several new, *Nothofagus*-specialised species from Argentina and New Zealand. Argentine collections cited as *Zoellneria eucalypti* by Gamundí (1962) were variously redetermined by Johnston and Gamundí (2000) as *Torrendiella andina*, *T. grisea*, and *T. madsenii*. Johnston and Gamundí (2000) and Johnston (2006, 2010) discussed the occurrence of many host-specialised, genetically distinct species of *Torrendiella* in Australasia. Most of these species remain undescribed.

Spooner (1987) and Johnston and Gamundí (2000) accepted the Southern Hemisphere species of *Torrendiella* as members of the *Rutstroemiaceae* (as *Sclerotiniaceae*). Recent DNA sequencing has shown that the Southern Hemisphere species are genetically distinct from the *Rutstroemiaceae* (Johnston *et al.* 2010), the family to which the type species of *Torrendiella* belongs. The genetic distinctness between the Southern Hemisphere *Torrendiella* spp. and the type species of *Torrendiella* is reflected morphologically by differences in microanatomical features of the ascus apex and cytoplasmic features of the living paraphyses. This paper provides a taxonomic revision of the genus *Torrendiella* sensu Spooner (1987).

Materials and methods

Details of specimens and cultures for which sequences have been generated as part of this study are listed in Table 1. Cultures, when available, were derived from germinated ascospores shot onto agar plates from fresh collections, except for AH 7636 (*Hymenotorrendiella eucalypti*), which was grown from fresh apothecial tissues. All cultures have been stored in the International Collection of Microorganisms from Plants (ICMP), Landcare Research, Auckland and the Fundación Medina Microbial Collection (F, www.medinadiscovery.com/microbial-collection).

For micromorphological documentation, fresh specimens were examined in tap water while avoiding pressure on the cover slip in order to maintain their vital state (Baral 1992). In contrast, the study of the apical apparatus of the asci was made with dead asci, either by rehydrating a dried specimen in water, or by applying stronger pressure to the cover slip. A high concentration of Lugol's solution (IKI, ca. 1% iodine, 3% KI in tap water) without KOH-pretreatment was used for staining the apical ring (Baral 1987a, 1987b, 2009), or sometimes Melzer's Reagent (MLZ). For median sections, fresh specimens were sectioned freehand with a razor blade, with sections mounted in water, whereas dried specimens were rehydrated in 3% KOH, sectioned at about 10 µm using a freezing microtome, with sections mounted in lactic acid.

Abbreviations used in the descriptions include LBs = lipid bodies (oil drops) in living spores and paraphyses, VBs = refractive vacuolar bodies (in living paraphyses), * = living state, † = dead state. A number in curly brackets {} indicates the number specimens studied, or the number of collection sites for which a host was recorded. An arrow → indicates the development from immature to mature.

DNA extraction, PCR amplification and sequencing

DNA was extracted from mycelia of agar cultures or from dried apothecia taken from herbarium specimens. DNA was extracted and amplified using PCR following the methods of Peláez *et al.* (1996) or Johnston and Park (2013). Amplification primers used for the ITS1-5.8S-ITS2 region were ITS1F, ITS5, ITS4, or ITS4a (White *et al.* 1990; Gardes and Bruns 1993; Larena *et al.* 1999), for the LSU region were LROR and LR5 (Bunyard *et al.* 1994; Vilgalys and Hester 1990), and for the SSU region were NS1 and NS4 (White *et al.* 1990). Purified PCR products were directly sequenced using the same primer pairs as in the PCR reactions. Partial sequences obtained in sequencing reactions were assembled with Genestudio 2.1.1.5 (Genestudio, Inc., Suwanee, GA, USA), or Sequencher 4.10.1 (Genecodes Corporation, Ann Arbor, MI, USA). All sequences were deposited in GenBank (Table 1).

TABLE 1. Specimens sequenced for this study.

Species	Specimen voucher or culture number[a]	Country and province collected	Host	GenBank SSU	GenBank ITS	GenBank LSU
Coccomyces lauraceus	ICMP 17399	New Zealand	*Beilschmiedia tarairi* leaf	KJ606671	KJ606678	KJ606672
Cyclaneusma minus	ICMP 17358	New Zealand	*Pinus radiata* needles	KJ606669	KJ606680	KJ606674
Hymenoscyphus subferrugineus	F 267859	Spain, Burgos	*Genista hispanica* branch	-	KF588380	-
Hymenotorrendiella andina	ICMP 17994	Argentina	*Nothofagus dombeyi* leaves	-	KJ606682	-
Hymenotorrendiella eucalypti	AH 7636	Spain, Asturias	*Acacia melanoxylon* phyllode	-	KF588379	-
Hymenotorrendiella madsenii	ICMP 15648	New Zealand	*Nothofagus* sp. wood	KJ606666	AY755336	KJ606676
Hymenotorrendiella eucalypti	ICMP 15651	Australia, Victoria	*Acacia* sp. phyllode	KJ606667	AY755335	KJ606677
Marthamyces desmoschoeni	ICMP 17350	New Zealand	*Desmoschoenus spiralis* leaves	KJ606670	KJ606679	KJ606673
Propolis farinosa	ICMP 17380	New Zealand	wood	KJ606668	KJ606681	KJ606675
Rutstroemia calopus	F 148155	Spain, Madrid	*Festuca indigesta* stems	-	KF588373	-
Rutstroemia calopus	CBS 854.97	Netherlands, Noord-Brabant	culms of grass	-	KF588374	-
Rutstroemia cuniculi	CBS 465.73	England	rabbit dung	-	KF588375	-
Rutstroemia echinophila	F 132998	Spain, Mallorca	*Quercus ilex* fruits	-	KF588371	-
Rutstroemia firma	F 162343	Spain, Alava	*Quercus robur* branch	-	KF588368	-
Rutstroemia firma	CBS 341.62	France, Ain	*Alnus glutinosa* twigs	DQ471010	KF588369	DQ470963
Rutstroemia fruticeti	F 163001	Spain, Burgos	*Rubus* sp. canes	-	KF588370	-
Rutstroemia maritima	F 118839	Spain, Asturias	*Ammophila arenaria* stems	-	KF588372	-
Rutstroemia paludosa	CBS 464.73	USA, New York	*Symplocarpus foetidus* culms	-	KF588377	-
Rutstroemia paludosa	H.B. 6912	Luxembourg, L'Oesling	*Juncus effusus* culms	-	KF588376	-
Torrendiella setulata	NBM# F-04646 (= H.B. 9775)	Canada, Prince Edward Island	*Acer spicatum* twigs	-	KF588367	-
Torrendiella ciliata	F132996 (AH 7538)	Spain, Mallorca	*Quercus ilex* leaves	-	KC412008	KJ627220
Zoellneria rosarum	PDD 102789 (= H.B. 7919)	Germany, Baden Württemberg	*Rosa* leaves	KF661534	KF661532	KF661533

[a] PDD, New Zealand Collection of Fungi and Plant Diseases. ICMP, International Collection of Fungi from Plants. H.B., private herbarium of H.O. Baral. AH, Herbarium of the University of Alcalá. F, Fundación Medina Microbial Collection.CBS, Centraalbureau voor Schimmelcultures. NBM, New Brunswick Museum.

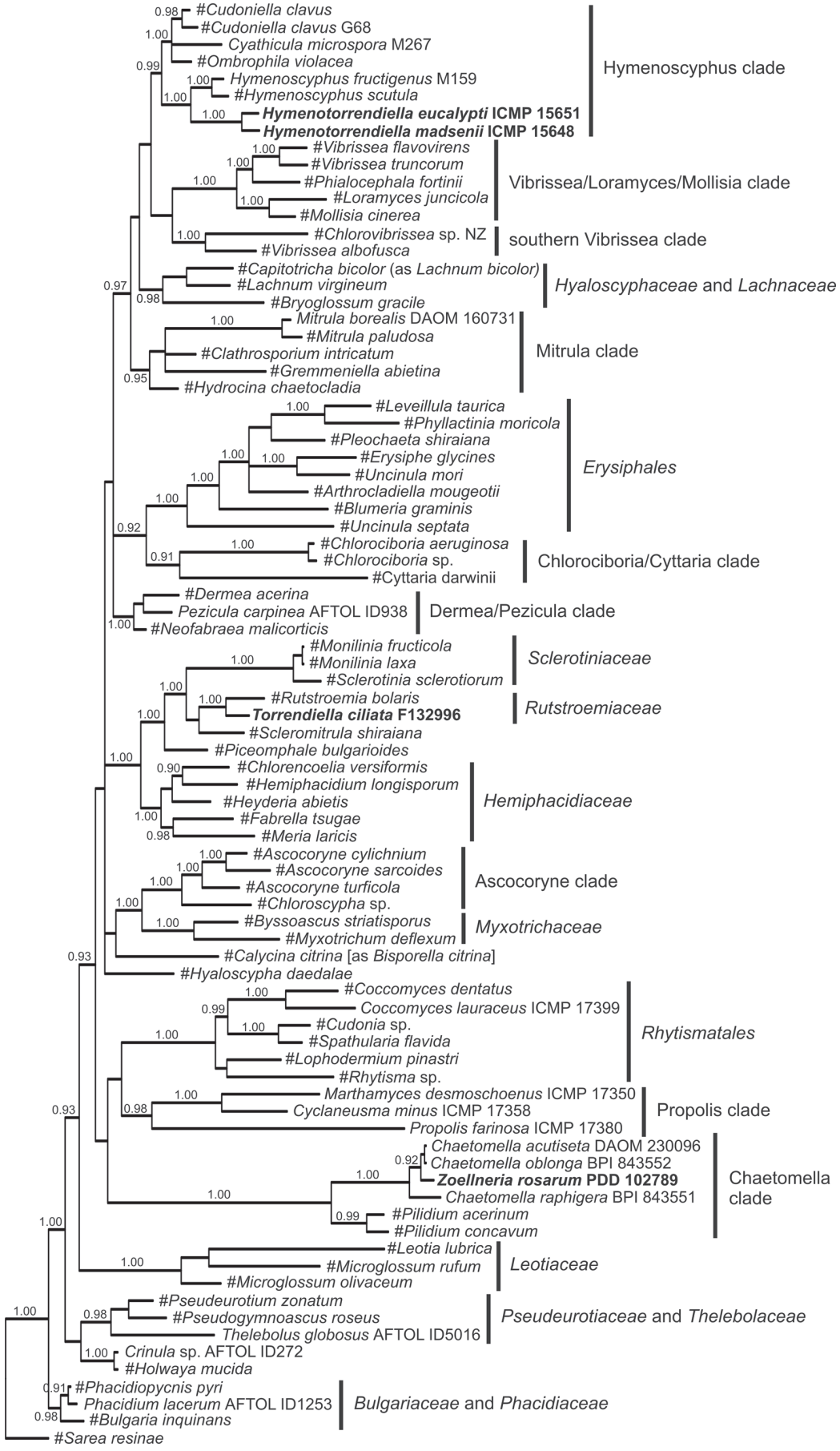

FIGURE 1. 50% majority-rule consensus tree based on a Bayesian analysis of SSU, 5.8S rRNA, and LSU gene sequences. Bayesian posterior probabilities greater than 90% are shown above the edges. Sequences for taxa marked # from Wang *et al.* (2006), the *Chaetomella* and *Pilidium* sequences are from Rossman *et al.* (2004), the remaining taxa sequenced as part of this study are listed in Table 1.

Sequences were aligned using Genestudio 2.1.1.5 or with MAFFT as implemented in Geneious 5.6 (Drummond *et al.* 2012), and modified manually to improve the quality of the alignments. Phylogenetic analyses were performed using Bayesian inference in MrBayes 3.01 or MrBayes 3.2.1 (Ronquist and Huelsenbeck 2003; Ronquist *et al.* 2012), with separate partitions created for each gene with their own model of nucleotide substitution. Models selected, using the AIC method in MrModelTest (Posada and Crandall 1998; Nylander 2004; Posada and Buckley 2004), were GTR+I+G for SSU, LSU and ITS, and SYM+I+G for 5.8S. The 18S-5.8S-28S, analyses used a concatenated alignment of the partial SSU, partial LSU and 5.8S rDNA, with separate partitions created for each gene. The analysis included our newly generated sequences (Table 1) together with taxa and data from Wang *et al.* (2006), and the *Chaetomella* and *Pilidium* sequences reported by Rossman *et al.* (2004). The analysis was run with two chains for 5 M generations, trees sampled every 500 generations. Convergence of all parameters was checked using the internal diagnostics of the standard deviation of split frequencies and performance scale reduction factors (PSRF), and then externally with Tracer 1.5 (Rambaut and Drummond 2007); the first 25% of generations being discarded as burn-in. The ITS1-5.8S-ITS2 analysis ran four incrementally heated simultaneous chains over 2M generations with a sampling frequency of 100, the first 1000 trees discarded as burn-in.

Alignments and phylogenetic trees have been deposited in TreeBase, study S15697.

Results

Phylogeny

The major clades resolved in Figure 1 are similar to those reported by Wang *et al.* (2006). *Zoellneria rosarum* belongs in a clade with *Chaetomella*, distant from the type species of *Torrendiella*, *T. ciliata*. This confirms the opinion of Spooner (1987) that these are different genera, despite both having distinctive, setose apothecia. The molecular phylogeny confirms the anamorph-teleomorph relationship between *Zoellneria* and *Chaetomella*, suggested by Clark (1980, the anamorph referred to *Amerosporium patellarioides*) on the basis of the two states being consistently found together, and because both bear the same type of setae. The *Z. rosarum* sequences reported here were from DNA extracted from dried fruiting bodies morphologically typical of the teleomorph.

Torrendiella as it has been applied is polyphyletic. *T. ciliata*, the type species, and *T. setulata* belong in the *Rutstroemiaceae*. Both species are morphologically very close to species we accept as *Rutstroemia.* The similarity between the ITS1–5.8S–ITS2 gene sequences of both species is 94%. The phylogenetic analysis of the ITS1–5.8S–ITS2 region (Figure 2) showed that these two *Torrendiella* species clustered within a well supported clade including both *Sclerotiniaceae* and *Rutstroemiaceae*. The generic relationships within the latter family remain unresolved, awaiting more intensive taxon sampling and data from additional genes.

The Southern Hemisphere *Torrendiella* spp. are phylogenetically distinct, belonging in the core *Hymenoscyphus* clade of Wang *et al.* (2006). On the basis of this result, we propose a new genus *Hymenotorrendiella*, with *H. eucalypti* (basionym *Peziza eucalypti*) selected as the type species. Morphologically, *Hymenotorrendiella* matches *Hymenoscyphus* Gray and *Phaeohelotium* Kanouse with respect to ascus apex structure, as discussed below. It differs from those genera in the presence of brown setae, from *Hymenoscyphus* also in the consistent absence of heteropolar (scutuloid) ascospores, and from *Phaeohelotium* in the consistent absence of *textura globulosa-angularis* in the ectal excipulum.

Based on the analysis of the ITS1-5.8S-ITS2 gene sequences (Figure 3), the six *Hymenotorendiella* species included in this study clustered in a well supported clade that also includes other undetermined *Hymenotorrendiella* species (Crous *et al.* 2006; Sánchez-Márquez *et al.* 2011; Johnston *et al.* 2012). The overall similarity between these sequences ranges from the 92 to 100%. The *Hymenotorrendiella* species have a strongly supported sister relationship to *Dicephalospora rufocornea*. The tropical genus *Dicephalospora* Spooner differs from *Hymenotorrendiella* in the absence of setae, but otherwise the spores are morphologically similar, with the polar gelatinous ascospore caps characteristic of *Dicephalospora* occurring also in some *Hymenotorrendiella* species. The *Dicephalospora*/*Hymenotorrendiella* clade is phylogenetically distinct from other genera in the broader core *Hymenoscyphus* clade, including clades containing the type species of *Cyathicula* (*C. coronata*), *Hymenoscyphus* (*H. fructigenus*), and *Phaeohelotium* in the emended sense of Baral *et al.* (2013) (the type species *P. monticola* belongs in the clade with *P. undulatum*).

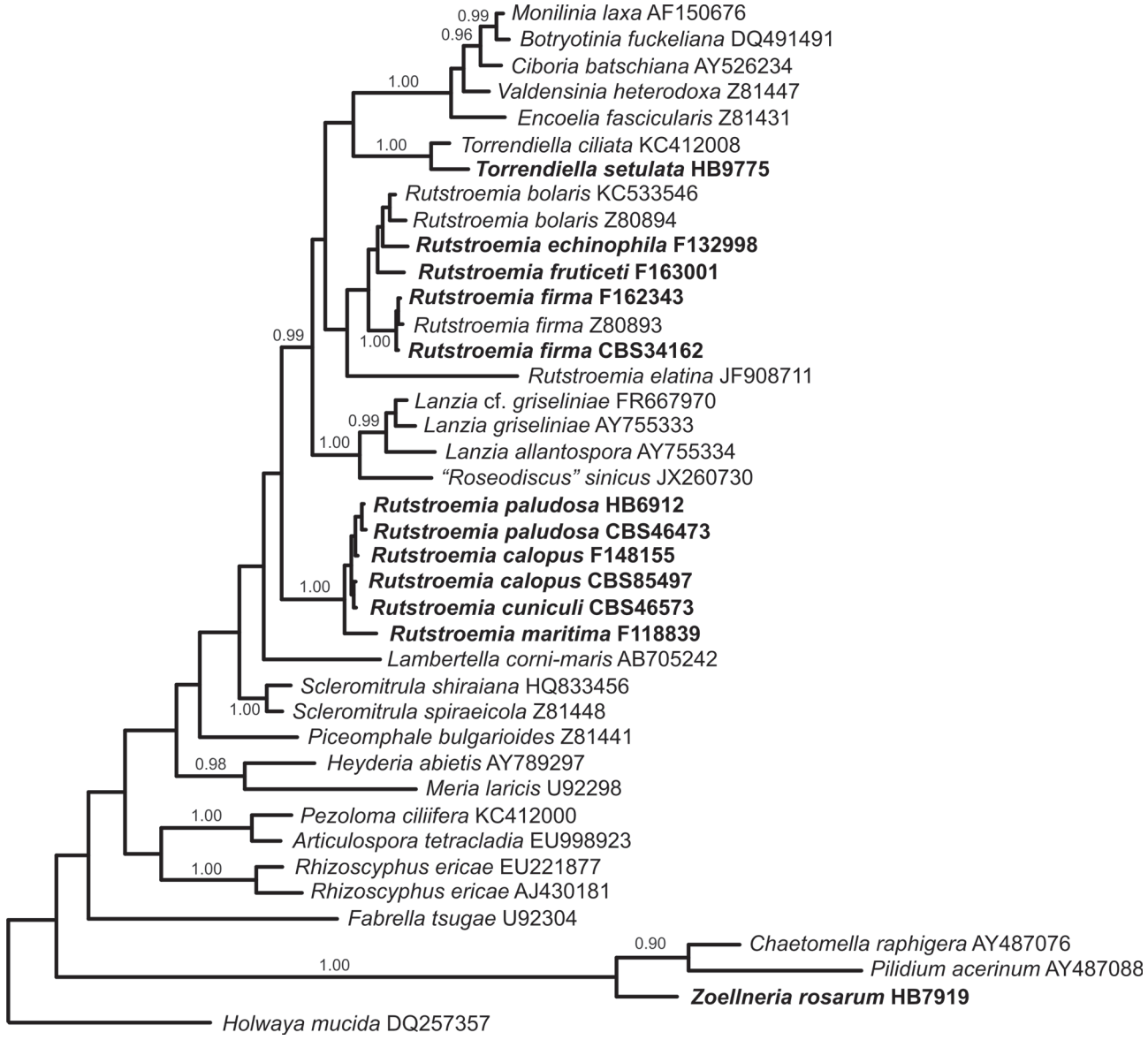

FIGURE 2. Bayesian analysis of ITS gene sequences, showing detailed species-level relationships of *Torrendiella* and *Rutstroemia* within the *Sclerotiniaceae* plus *Rutstroemiaceae*. Bayesian posterior probabilities greater than 90% are shown above the edges. Sequences marked with voucher numbers (CBS, F, H.B.) were newly generated for this study (see Table 1), the others were downloaded from GenBank.

Taxonomy

Torrendiella Boud. in Boudier & Torrend, Bull. Soc. Mycol. Fr. 27: 133 (1911).

Type: *T. ciliata* Boud.

Apothecia 0.3–2 mm diam., with short to long stalk erumpent from host tissue, disc whitish to cream or grey, exterior concolorous or light to black-brown, receptacle and partly also stalk with dark brown setae. *Asci* 8-spored, apex hemispherical to slightly conical, apical ring staining blue in IKI (without KOH, type bb, euamyloid), of the *Sclerotinia*-type: forming a thick-walled tube extending through the entire apical thickening, at the apex laterally widened, basally distinctly projecting to form an apical chamber; base arising from simple septa (often with a basal protuberance). *Ascospores* non-septate when mature, hyaline, straight or slightly to strongly curved, narrowly to broadly ellipsoid (-subclavate) or ovoid (slightly heteropolar), containing in the living state some large and many small oil drops (high

lipid content), with a thin sheath around the entire spore that separates after discharge, without polar gelatinous caps, overmature 1–3-septate, budding narrowly tear-shaped microconidia. *Paraphyses* cylindrical, straight, not or slightly enlarged at the apex, containing a few large, short to very long, strongly refractive, hyaline vacuolar bodies (living state), mainly in the terminal cell. *Ectal excipulum* comprising three layers, outer layer (ec1) of meandering hyphae encrusted with light brown wall pigment (banded aspect); central layer (ec2) hyaline, at flanks of non-gelatinized, horizontal *textura prismatica* (*T. ciliata*) or strongly gelatinized, ± vertical *textura oblita* (*T. setulata*), towards margin of narrow, long-cylindrical cells immersed in abundant gel (t*extura oblita*) oriented at a low angle to the surface; inner layer (ec3) of non-gelatinized *textura prismatica-porrecta*, pale brown, smooth-walled to slightly encrusted. *Setae* with dark brown, thick, smooth wall, base unbranched, rooting.

Habitat:—developing on fallen leaves and corticated twigs of angiosperm trees and *Rubus*.

Further included species:—*T. quintocentenaria* R. Galán & J.T. Palmer in Galán *et al.* (1993: 230), *T. setulata* (Dearn. & House) R. Galán & J.T. Palmer in Galán *et al.* (1993: 236).

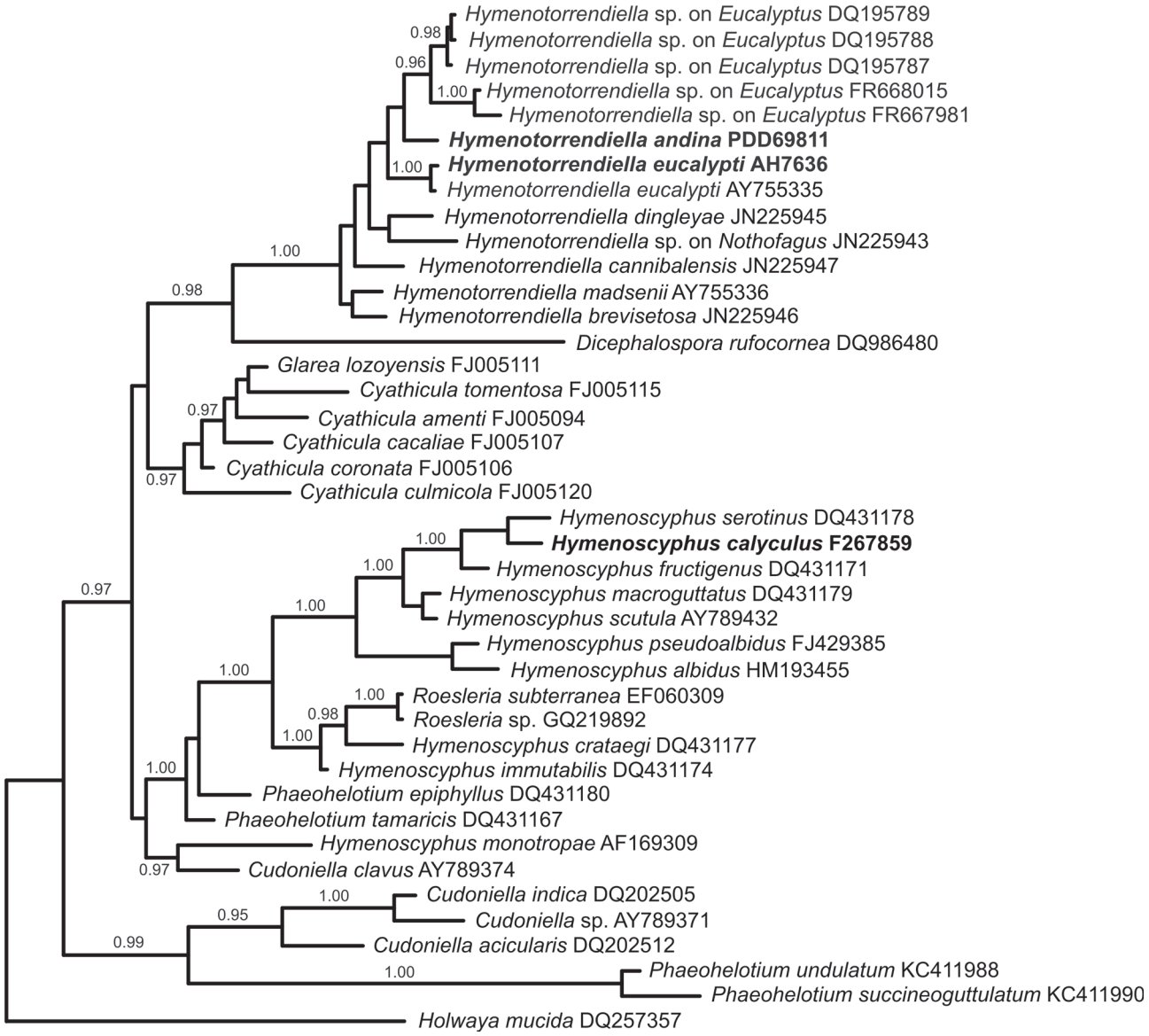

FIGURE 3. Bayesian analysis of ITS gene sequences, showing detailed species-level relationships of *Hymenotorrendiella* within the 'Hymenoscyphus clade' from Figure 1. Bayesian posterior probabilities greater than 90% are shown above the edges. Sequences marked with voucher numbers (AH, PDD, F) were newly generated for this study (see Table 1), the others were downloaded from GenBank.

Torrendiella ciliata Boud. in Boudier & Torrend, Bull. Soc. Mycol. Fr. 27: 133 (1911). (Figs. 4–6)

Synonyms: *Dasyscyphus ciliatus* (Boud.) Saccardo, Syll. fung. 24(2): 1205 (1928); ?= *Rutstroemia rubi* Velen., Monogr. Discom. Bohem. (Prague): 229 (1934); ?= *Rutstroemia hirsuta* Dennis, Kew Bull. 13(3): 460 (1959) [1958].

Apothecia formed on fallen leaves and corticated twigs, singly or scattered, indistinctly erumpent through epidermis or periderm, mature apothecia 0.5–1.7 mm diam. when fresh, disc greyish-white to light cream-ochraceous-brownish, slightly concave to flat, receptacle greyish-ochraceous, with medium dense, dark reddish-brown, straight setae, stipe 0.2–1 × 0.28–0.4 (–0.5) mm, non-translucent, greyish-ochraceous, dark brown at base, covered by ± scattered setae. *Asci* *(98–) 115–140 (–160) × (12–) 13–14 (–15) µm {3}, †(88–) 95–120 (–138) × (7–) 8–12 (–13) µm {10}, 8-spored, *pars sporifera* *50–63 µm long (spores obliquely biseriate), †60–85 µm (spores irregularly 1–2-seriate), living mature asci protruding ~0–3 µm beyond paraphyses; ascus apex conical, wall at apex †3.7–4.2(–4.8) → 2.8–3.2 µm thick, apical ring staining strongly blue (bb) in IKI, forming a thick-walled tube in lower 3/4 of wall, with distinct basal protrusion that surrounds a small apical chamber, apically strongly laterally widened (*Sclerotinia*-type); base with short, thick stalk arising from simple septa with basal protuberances {6}. *Ascospores* *(15–) 17–21.5 (–24) × (5–) 5.5–6.5 (–7) µm {4}, †(11.5–) 13–17.5 (–20.8) × (4–) 5–6 (–6.5) µm {10}, ellipsoid-fusoid, homo- or slightly heteropolar, both ends obtuse, medium to strongly curved (falcate), containing 1(–2) large lipid bodies 2.5–5 µm diam. in each half and many medium-sized and small ones, containing one central nucleus, with delicate sheath that slips off the spore; postmature spores 1-3 septate (as reported by Graddon 1979), not becoming pigmented. *Paraphyses* apically straight or slightly flexuous, undifferentiated, terminal cell *~40–52 × 3–4.7 µm, overmature sometimes capitate-spathulate and *4–6 µm wide; containing strongly refractive vacuolar bodies (VBs) at a length of (40–) 55–75 µm, hyaline, often divided into several bodies, individual VBs short to often very elongate, multiguttulate only at the base, staining bright turquoise-blue in aqueous Cresyl blue and deep red-brown in IKI, lower cells *13–27 µm long, often branched at lower septa. *Ectal excipulum* three-layered: outer zone (ec1) of flexuous, narrow, meandering hyphae with thin walls encrusted with light to bright, olive- to red-brown pigment (banded aspect), arranged parallel to the surface (*textura porrecta*); median layer (ec2) of hyaline, non-gelatinized *textura prismatica*, towards margin of strongly gelatinized *textura oblita*; inner zone (ec3) a non-gelatinized *t. porrecta* with light brown, slightly encrusted walls. *Medullary excipulum* hyaline, of a medium dense, hyaline *textura prismatica* to *t. porrecta*, upwards oriented in centre, obliquely horizontal at the flanks, individual cells *35–75 × 6–13 µm, much shorter below the hymenium. *Setae* arising from the central layer of the ectal excipulum, rooting at a length of up to 40–45 µm, (120–) 200–350 (–450) × 9–13 µm, 16–24 µm wide at the swollen base, 7–15-septate, septa (0.5–) 1–2.5 (–3.5) µm thick, wall in middle and lower part (1.5–) 2–3 (–3.5) µm thick, smooth, bright to dark red- to olive-brown, towards the strongly tapered apex pale olive-cream, terminal cell 4–6 µm wide, wall 0.5–1 µm thick.

Habitat:—on fallen, usually previous year's leaves of *Quercus coccifera* {2}, *Q. ilex* {3}, *Q. suber* {4}, *Cistus ladanifer* {1} lying in moist litter, on petioles or main veins at upper face of leaves, also on bark of a twig of ?*Quercus suber* {1}. Atlantic to Mediterranean Europe, Macaronesia.

Phenology:—(Oct.–)Nov.–May(–July).

Specimens examined:—Belgium. Flanders, Flemish-Brabant, 21 km ESE of Brussels, 1 km SE of Terlanen, Rodebos-Laanvallei, 95 m, cane of *Rubus fruticosus* agg., 3 March 2013, *R. Vandiest*, vid. *B. Declercq* (*B.D. 13/105*, photograph only examined). France: Poitou-Charentes, dépt. Charente-Maritime, Ile de Ré, 2 km SE of St.-Martin-de-Ré, 1.8 km W of La Flotte, Les Maraises, 19 m, *Quercus ilex* fallen leaves, 23 November 2008, *M. Hairaud* (*M.H. 71108*, photograph only examined). dépt. Charente, 7.5 km ESE of Cognac, 1.5 km WSW of Bourg-Charente, 55 m, *Quercus ilex* fallen leaves, 15 July 2012, *M. Hairaud* (*M.H. 70712*, photograph only examined). Great Britain. Workestershire : 5 km NW of Bromsgrove, Chaddesley Woods, 120 m, leaves of *Rubus fruticosus*, 10 November 1971, *M.C. Clark (J.T.P. 4486*, photograph only examined). Portugal. Norte (Viana do Castelo): Valença do Minho, *Quercus suber* fallen leaves, 10 March 1989, *J.T. Palmer* (fungarium of J.T. Palmer 4484). Spain. Galicia: Pontevedra, 25 km SE of Santiago de Compostela, route P-204 (between Bandeira and Merza) 240 m, *Quercus suber* fallen leaves, 26 Oct. 1987, *J.T. Palmer J.T.P. 4381, 4382* (AH 6762, CUP 061925). Asturias: 20 km NNE of Villablino, 2.4 km N of Pola de Somiedo, 703 m, *Quercus ilex* fallen leaves, 1 May 2008, *E. Rubio* (*E.R.D. 4435*, photograph only examined). Andalucía: Huelva, Sierra de Aracena, 7 km NW of Aracena, 0.2 km S of Cortelazor, Finca El Palancar, 655 m, *Quercus suber* and *Cistus ladanifer* fallen leaves, 15 November 1997, *J.T. Palmer & R. Galán* (AH 7127). 11 km WNW of Aracena, 2.5 km E of Galaroza, Área Recreativa de Valdelarco, 685 m, ?*Quercus suber* fallen twig, on bark, 16 January 2010, *J.F. Moreno, P. Siljeström, D. Estrada & D. Merino* (*D.M.A. 20100116*, photograph only examined). 20 km NW of Aracena, 2 km E El Repilado (route N-433, km 72), 450 m, *Quercus suber* fallen leaves, 23 November 1990, *R. Galán* (AH 6761). Extremadura: Cáceres, Monfragüe National Park, Villarreal de San Carlos, slope of the Monfragüe castle, 450 m, *Quercus suber* fallen leaves, 24 October 1988, *J.T. Palmer* (fungarium of J.T. Palmer 4488) Valenciana: Valencia, 14 km SSE of Valencia, El Saler, 0.5 km SSE of Les Gavines, Gola de Puçol, 6 m, *Quercus coccifera* fallen leaves, 5 January 2010, *R. Tena & J. Ormad* (*R.T.10010501*, photograph only examined). Comunidad Valenciana, Valencia, 14 km SSE of Valencia, El Saler, 0.3 km SE of Les Gavines, 5 m, *Quercus coccifera* fallen leaves, 12 Nov. 2011, *R. Tena* (*R.T. 11111202*, photograph only examined). Islas Baleares: Mallorca, s'Estret, 2 km E of Valldemossa, 340 m, *Quercus ilex* fallen leaves, 3 November 2001, *R. Galán et al.* (AH 7538, F 132996).

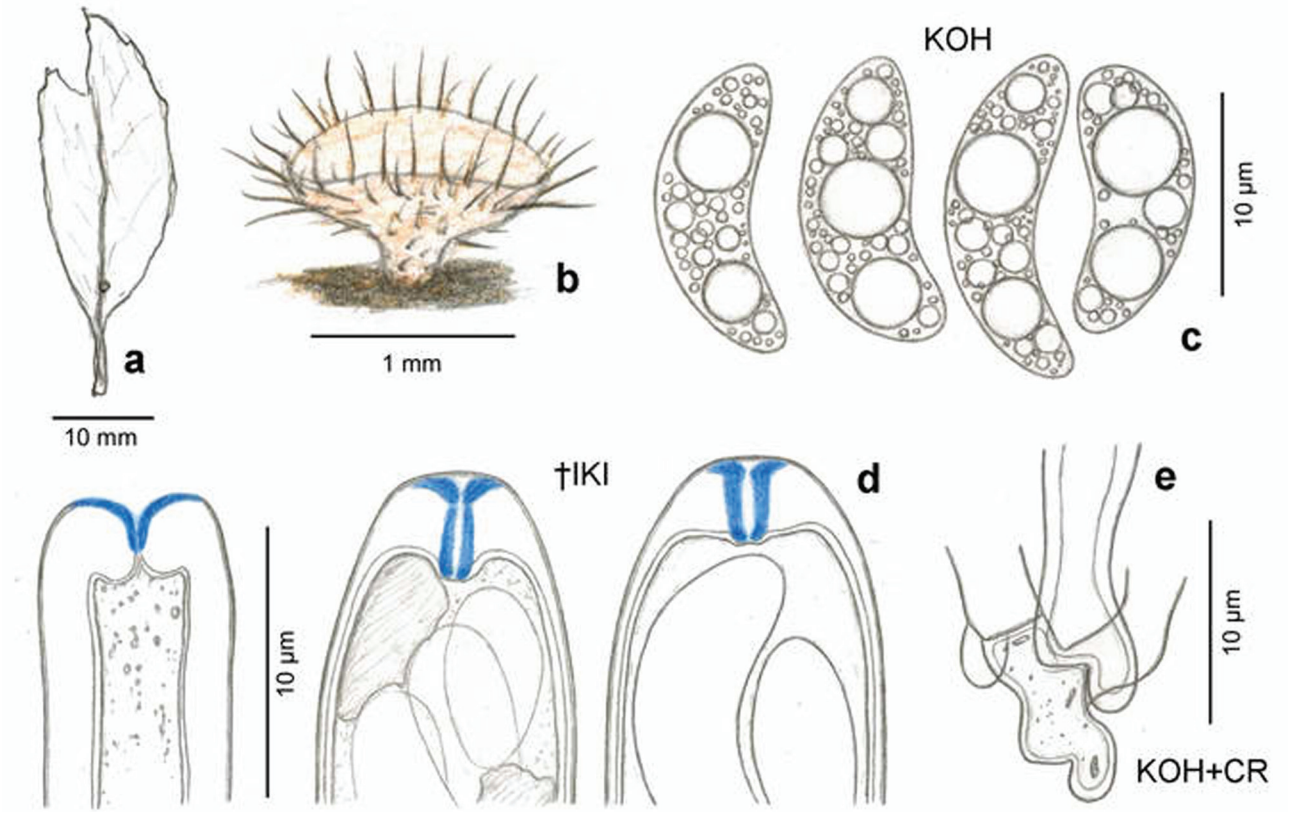

FIGURE 4. *Torrendiella ciliata*. **a**. Leaf of *Quercus suber* with apothecium on mid vein. **b**. Apothecium (rehydrated). **c**. Ascospores. **d**. Ascus apices in IKI (left: after ejection). **e**. Simple-septate ascus bases with a basal protuberance. All elements in dead state.—Spain, Andalucía, Huelva, Cortelazor (H.B. 7096, AH 7127).

Hymenotorrendiella P.R. Johnst., Baral & R. Galán, *gen. nov.*

Registration identifier: IF550522

Differs from *Torrendiella* by the *Hymenoscyphus*- or *Calycina*-type ascus apex structure and the contents of the living paraphyses comprising numerous globose vacuolar bodies.

Type:—*Hymenotorrendiella eucalypti* (Berk.) P.R. Johnst., Baral & R. Galán

Etymology:—refers to the phylogenetic position of this *Torrendiella*-like genus in a clade containing the type species of *Hymenoscyphus*.

Apothecia 0.2–5 mm diam., with short to long stalk, disc whitish to cream or grey, exterior concolorous or light to black-brown, receptacle and often also stalk with dark brown setae. *Asci* 8-spored, apex distinctly conical, apical ring staining blue in IKI (without KOH, type bb), either of the *Hymenoscyphus*-type: forming a thin-walled tube restricted to the lower part of the apical thickening or extending to the apex, or sometimes of the *Calycina*-type: tube apically thicker-walled and here laterally extending, ring basally not distinctly projecting, not forming an apical chamber; base arising from croziers or simple septa (without basal protuberance). *Ascospores* non-septate when mature, hyaline, straight or slightly, rarely medium curved, narrowly to broadly ellipsoid, fusoid, fusiform, or lemon-shaped (homopolar), containing in the living state some large and a few or many small oil drops (high lipid content), with a thin sheath around the entire spore that separates after discharge, sometimes with polar mucilaginous caps, overmature non-septate, spores sometimes budding ellipsoid microconidia (*H. madsenii*). *Paraphyses* cylindrical, straight, not or only slightly enlarged at the apex, containing many globose, small or large, strongly refractive, hyaline vacuolar bodies (living state), mainly in the terminal cell. *Ectal excipulum* comprising three layers: outer layer (ec1) one-layered, of meandering hyphae, encrusted with olivaceous to red-brown wall pigment, or hyaline and smooth; central layer (ec2) of prismatic or long-cylindrical cells, very slightly to strongly gelatinized, hyaline, rarely pale brown and encrusted; inner layer (ec3) of long-cylindrical hyphae, pale to bright brown, not or ± distinctly encrusted. *Setae* with dark brown, 1–3.5 µm thick wall, rooting or superficial, base unbranched or T- to L-shaped.

Habitat:—developing on fallen leaves or dead wood, or bark of angiosperms.

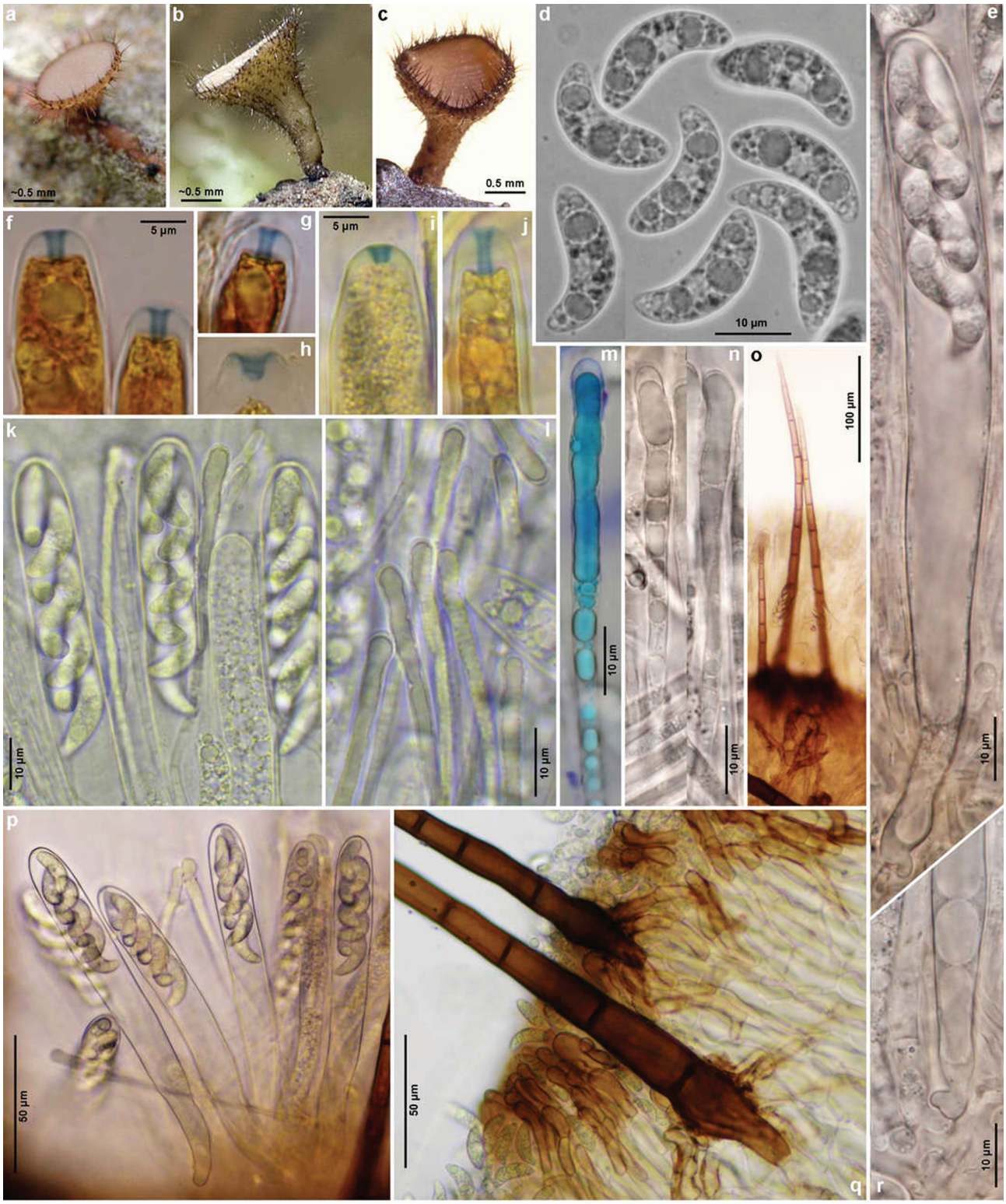

FIGURE 5. *Torrendiella ciliata*. **a–c**. Fresh apothecia. **d**. Ascospores**. e, k, p**. Mature asci. **f–j**. Ascus apices in IKI (**h**, after ejection). **l–n**. Paraphyses containing vacuolar bodies. **s, o, q**. Marginal setae. **e, r.** Simple-septate ascus bases with a basal protuberance. All elements in living state except for f–j (in IKI, unpretreated).—**a, i–l**. France, Charente-Maritime, Ile de Ré, les Maraises, *Quercus ilex* leaf (M.H. 71108, phot. M. Hairaud). **b**. Spain, Asturias, Somiedo, *Quercus ilex* leaf (E.R.D. 4435, phot. E. Rubio). **c**. Andalucía, Huelva, Galaroza, ?*Quercus suber* twig (D.M.A. 20100116, phot. D. Merino). **d–h, n–p, r**. Valencia, El Saler, *Quercus coccifera* leaves (R.T. 10010501). **m, q**. ibid. (R.T. 11111202).

Further included species:—*H. andina*, *H. brevisetosa*, *H. cannibalensis*, *H. clelandii*, *H. dingleyae*, *H. grisea*, *H. guangxiensis*, *H. madsenii*.

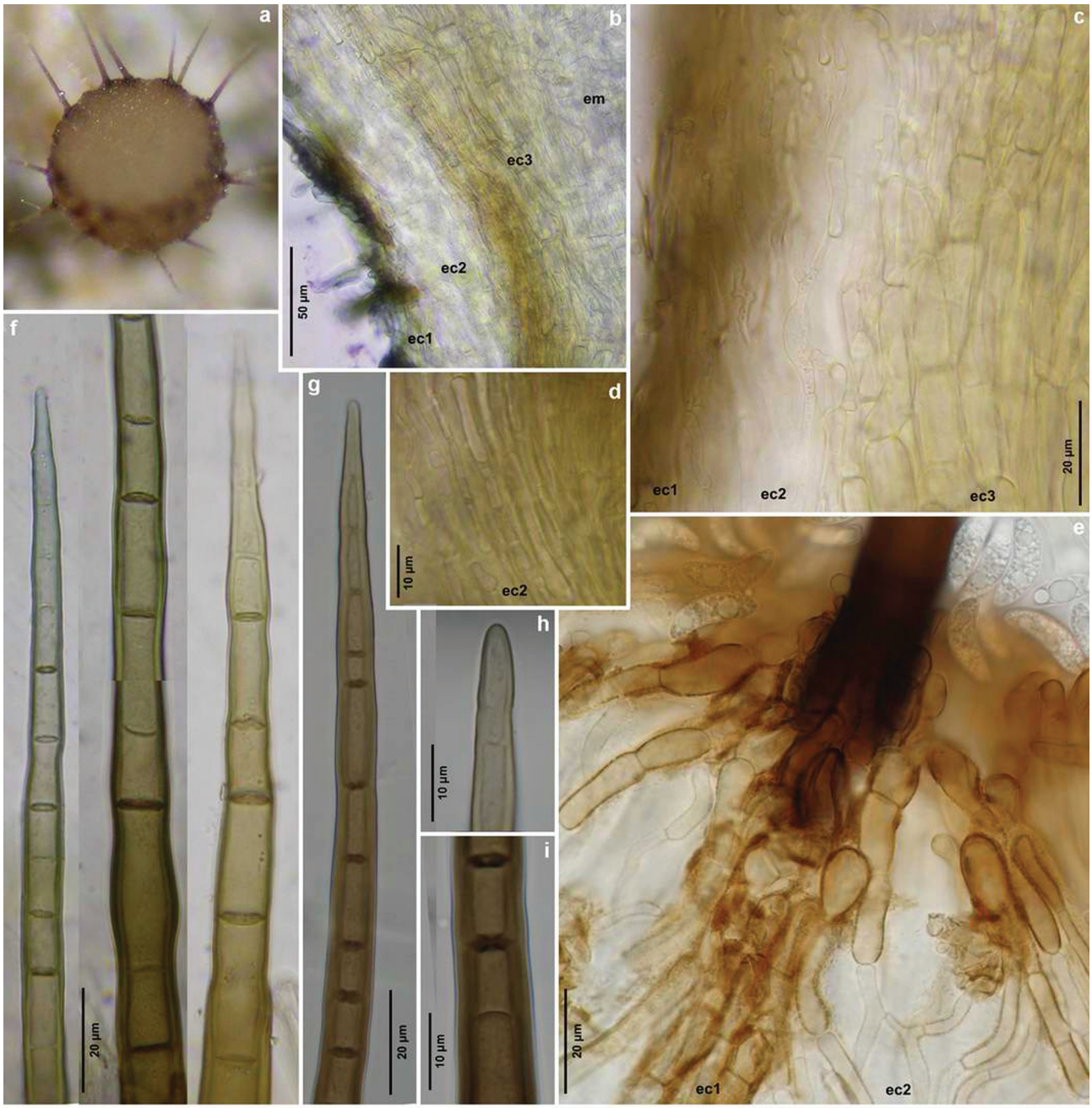

FIGURE 6. *Torrendiella ciliata*. **a**. Fresh apothecium. **b–c**. Median section of receptacle at lower flanks. **d**. Median section of receptacle at margin. **e**. Surface view on ectal excipulum at margin, brown undulating cortical hyphae surrounding base of seta. **f–i**. Marginal setae. All elements in living state. ec1 = cortical layer of ectal excipulum, ec2 = gelatinized outer layer of main part of ectal excipulum, ec3 = non-gelatinized inner layer of ectal excipulum, em = non-gelatinized medullary excipulum.—**a–d, f.** France, Charente, Bourg-Charente, *Quercus ilex* leaf (M.H. 70712, a: phot. M. Hairaud). **e, g–i**. Spain, Valencia, El Saler, *Quercus coccifera* leaves (R.T. 11111202).

Hymenotorrendiella eucalypti (Berk.) P.R. Johnst., Baral & R. Galán, *comb. nov.* (Figure 7–10)

Registration identifier: IF550523

Synonyms: *Peziza eucalypti* Berk. in Hooker, Flora Tasmaniae 2: 274, 1860; *Dasyscyphus eucalypti* (Berk.) Sacc., Sylloge Fungorum 8: 462, 1889; *Zoellneria eucalypti* (Berk.) Dennis, Kew Bulletin 13: 324, 1958; *Torrendiella eucalypti* (Berk.) Spooner, Bibliotheca Mycologica 116: 322, 1987.

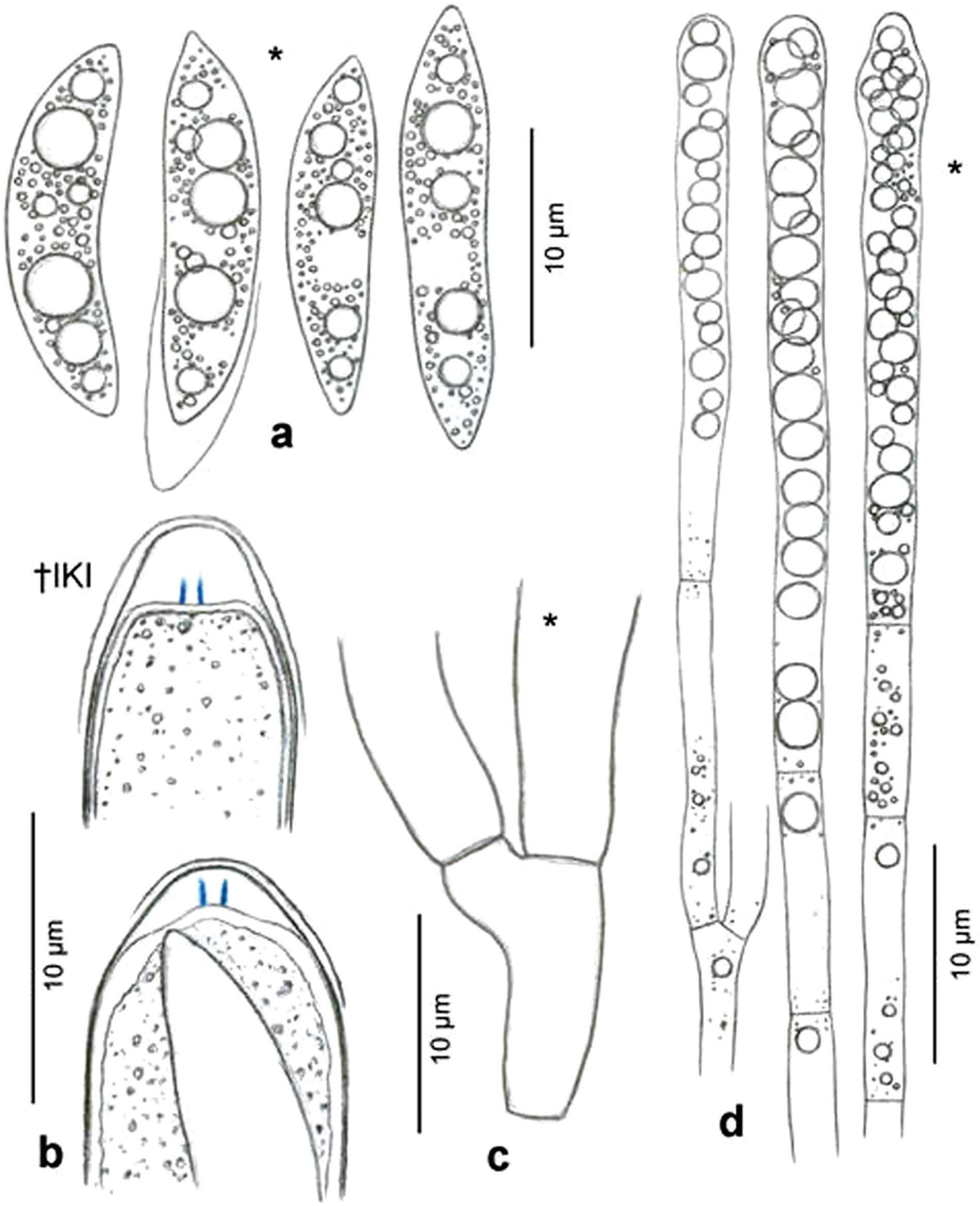

FIGURE 7. *Hymenotorrendiella eucalypti*. **a**. Ascospores. **b**. Ascus apices in IKI. **c**. Simple-septate ascus bases without a basal protuberance. **d**. Paraphyses. All elements in living state except for b.—Spain, Asturias, Grado, Las Ablanosas, on phyllodes of *Acacia melanoxylon* (H.B. 9664).

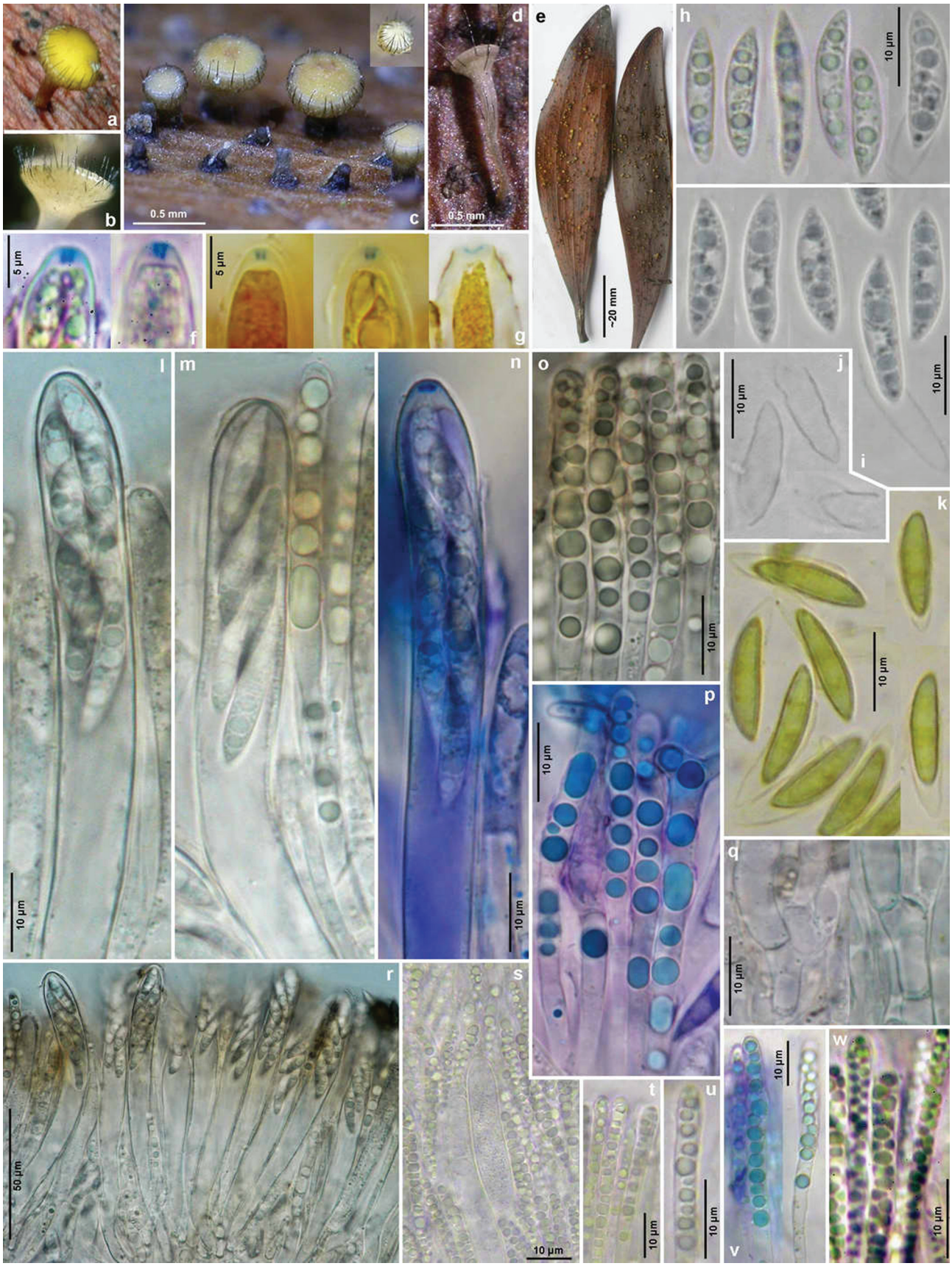

FIGURE 8. *Hymenotorrendiella eucalypti*. **a–d**. Fresh apothecia. **e**. Phyllodes with apothecia. **f–g**. Ascus apices (g, right, after ejection). **h–i, k**. Ascospores. **j**. Detached sheaths of ascospores. **l–n, r**. Mature asci. **o–p, s–w**. Paraphyses containing refractive vacuolar bodies. **q**. Simple-septate ascus bases without a basal protuberance. All elements in living state (**n, p, v** in CRB) except for **f–g, k** (in IKI, unpretreated except for two left in **g**, KOH-pretreated).—a–w. Spain: **a–b, f, w**. Asturias, Pravia, Los Cabos (E.R.D. 3285, phot. E. Rubio). **c–e, g-h, k, s–v**. Asturias, Grado, Las Ablanosas (H.B. 9664). **g, i–j, l–r**. País Vasco, Vizcaya, Rebortun (J.F. 2012021201).

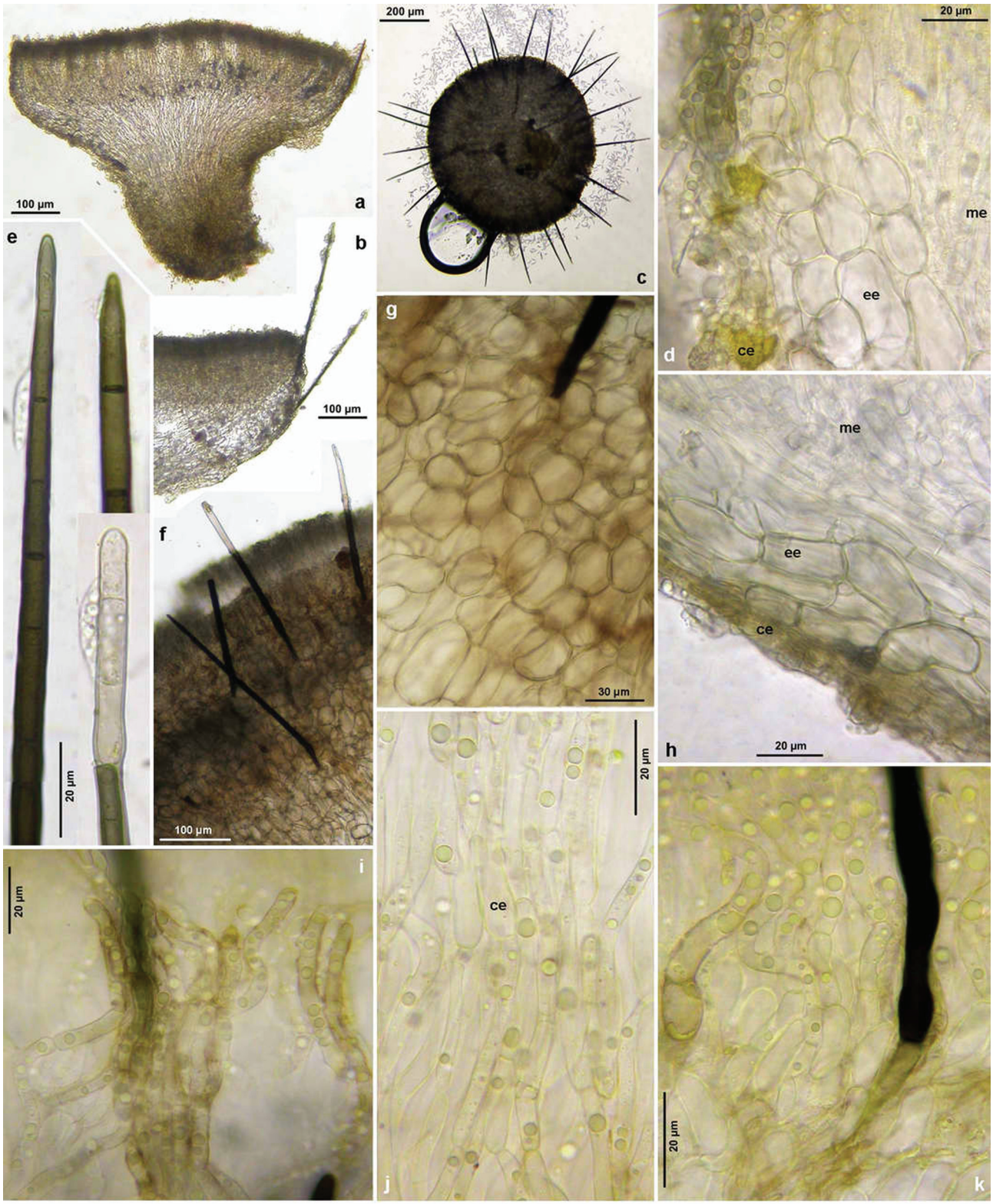

FIGURE 9. *Hymenotorrendiella eucalypti*. **a–b**. Apothecium in median section. **c, f.** Apothecium in bottom view, with projecting setae. **d, h**. Margin and flanks in median section showing ectal excipulum of *textura prismatica* (ec2) covered by a thin cortical layer (ec1), an inner layer of *t. porrecta* (ec3), and medullary excipulum (me). **e**. Upper part of setae. **g, i–k**. External view on ectal excipulum showing base of setae and in **i–k**, hyaline to pale brown, undulating cortical hyphae with included refractive vacuolar bodies. All elements in living state.—**a–e, h–k**. Asturias, Grado, Las Ablanosas (H.B. 9664). **f–g**. País Vasco, Vizcaya, Rebortun (J.F. 2012021201).

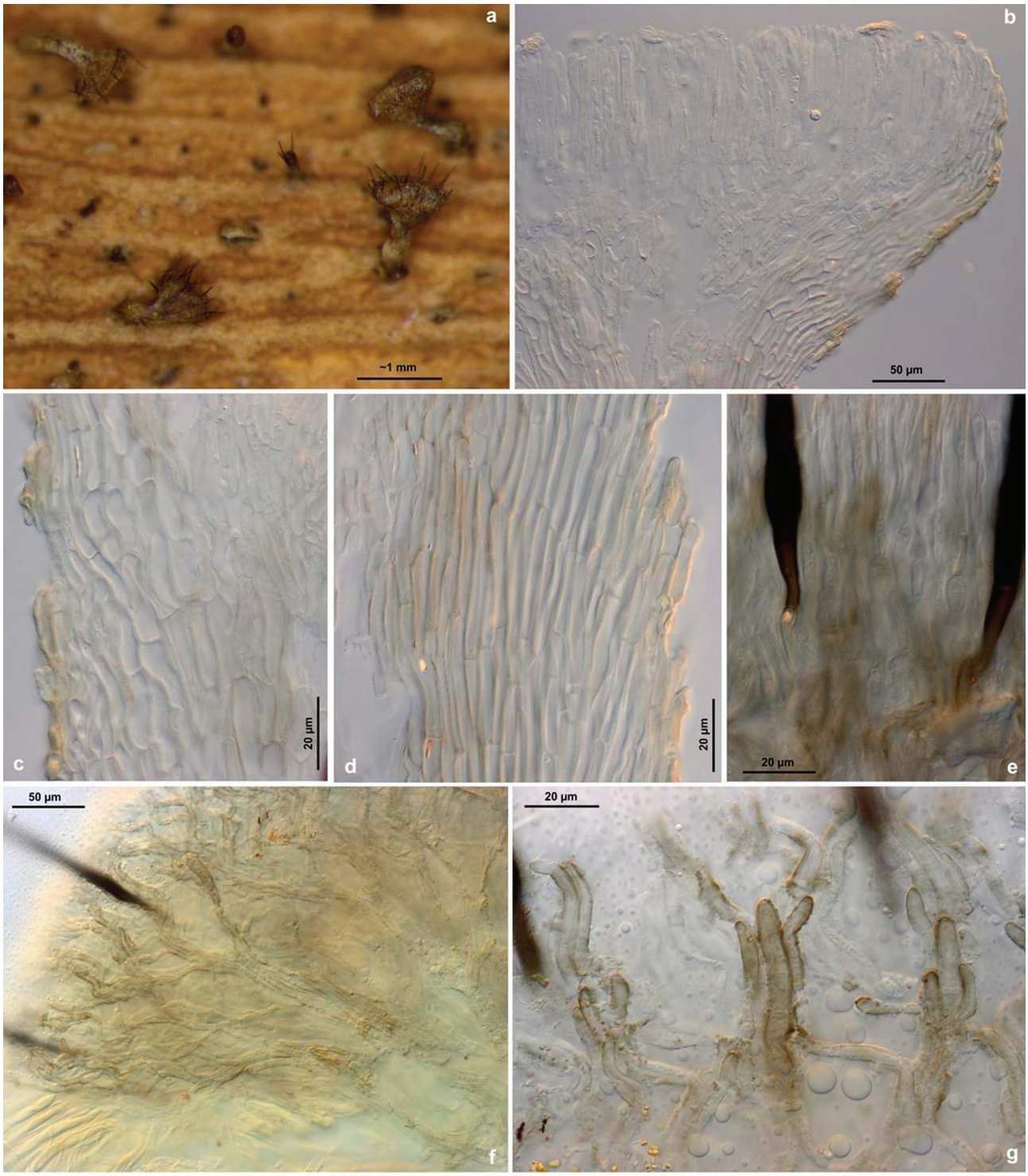

FIGURE 10. *Hymenotorrendiella eucalypti*. **a**. Dry apothecia on leaf surface. **b**. Median section of receptacle. **c**. Detail of ectal excipulum near margin. **d**. Detail of ectal excipulum on stipe. **e**. Base of setae. **f**. Surface view on receptacle near margin, showing brownish rough cortical hyphae (squash mount). **g**. Detail of f. All elements in dead state (in 3% KOH).—**a–d**. Australia, Wilsons Promontory National Park (PDD 70279). **e–g**. Australia, Errinundra National Park (PDD 77802).

Apothecia developing on fallen phyllodes, scattered to gregarious, erumpent through small cracks in darkened epidermis, mature apothecia 0.4–1.7 (–2.5) mm diam. when fresh, disc whitish-cream to pale yellow, flat, receptacle greyish-ochraceous to olivaceous with scattered, blackish-brown, straight setae, stipe 0.2–1 × 0.2–0.4 mm, translucent whitish-grey or brownish-olivaceous, sometimes darker towards base, setae sparse to absent. *Asci* *100–130 (–140) × (9–) 9.7–10.8 µm, †90–100 (–106) × (7–) 7.5–8.5 (–9.5) µm, 8-spored, *pars sporifera* *40–50 µm long, †72–80 µm, spores obliquely biseriate, living mature asci protruding 0–7 µm beyond paraphyses; ascus apex conical, wall at

apex †1.3–2.7 µm thick, apical ring staining strongly blue (bb) in IKI, forming a thin-walled tube in lower 1/3–3/4 of wall, without apical chamber (*Hymenoscyphus*-type); base of ascus with short, thick stalk arising from simple septa without basal protuberances {2}. *Ascospores* *16–19 (–21) × 4–4.7 µm, †13.5–17.5 (–18.5) × 3–3.8 µm, fusiform with ± cylindrical middle part, homopolar, both ends subacute to acute, slightly inequilateral, straight to slightly (rarely medium) curved, containing 2–4 large lipid bodies (1–) 1.7–3.3 µm diam. in each half and many smaller ones, containing one central nucleus, with delicate sheath that slips off the spore; postmature spores sometimes 1-septate, not becoming pigmented. *Paraphyses* apically undifferentiated or slightly capitate-spathulate, terminal cell *(26–) 46–57 × (3–) 3.5–4.5 (–6) µm, containing strongly refractive hyaline vacuolar bodies (very pale yellowish with age), (1–) 2–4 µm wide globose to shortly-elongate, these staining bright turquoise-blue in aqueous Cresyl blue and deep red-brown in IKI, lower cells *13–27 µm long, often branched at lower septa. *Ectal excipulum* indistinctly 3-layered: outer layer (ec1) thin, of *2.7–6 µm wide hyphae that contain strongly refractive, globose vacuolar bodies and form an undulating network in surface view, encrusted by a rough, yellowish to olive-brown exudate 0.2–0.5 µm thick; central layer (ec2) at flanks of non- or slightly gelatinized, hyaline to very pale yellowish *textura prismatica* oriented at a 0–30° angle to the surface, 40–45 µm thick, cells *20–40 × 9–15 µm, more short-celled to isodiametric at upper flanks (*13–20 × 10–16 µm), layer at margin very thin and of *t. porrecta*; inner layer (ec3) of hyaline to pale brown *t. porrecta*, not encrusted; in stipe of similar texture, near base covered by larger amounts of red-brown exudate; complete tissue not staining in IKI, without crystals. *Medullary excipulum* of a rather dense, hyaline *textura prismatica* to *textura porrecta*, upwards oriented in centre, obliquely horizontal at the flanks, individual cells *35-75 × 6-13 µm, much shorter below the hymenium. *Setae* arising from the central layer of the ectal excipulum, rooting at a length of up to 30–40 µm, 220–307 × 7–8.5 µm, 7.5–10 µm wide at the swollen base, 7–10-septate, septa 0.4–1.5 µm thick, wall in middle and lower part 1–1.5 (–2) µm thick, smooth, blackish olive-brown, towards the tapered apex pale to medium olive-brown, terminal cell 4–6 (–7) µm wide, wall 0.5–0.8 µm thick.

Habitat:—on dead, fallen phyllodes of *Acacia* sp. {1}, *A.* ? *frigescens* {1}, *A. melanoxylon* {7}, lying in moist litter. Subtropical to Mediterranean, indigenous in Australia, but introduced with its host to Europe, South America, and New Zealand.

Phenology:—Northern Hemisphere November–February, Southern Hemisphere May.

Specimens examined:—Australia. Tasmania: unlocalized, on phyllode of *Acacia* sp., undated, *W. Archer* (K—Holotype). Victoria: Errinundra National Park, Result Creek Falls Tr., on *Acacia* ?*frigescens* fallen phyllodes, 24 May 1996, *P.R. Johnston AU96-125* (PDD 77802, ICMP 15651). Wilsons Promontory National Park, Lilly Pilly Tr., on *A. melanoxylon* fallen phyllodes, 19 May 1996, *P.R. Johnston AU96-37 & T.W. May* (PDD 70279). Chile. Fundo Las Palmas of the Universidad Austral de Chile, 18 km N of Valdivia, on *A. melanoxylon* fallen phyllodes, 10 May 1994, *M. Heykoop* (AH 6895). New Zealand. Wellington, Rimutaka Forest Park, Catchpool, near park entrance, on *A. melanoxylon* fallen phyllodes, 7 May 1997, *P.R. Johnston D1283* (PDD 70105). Spain. Asturias: 5.5 km NE of Grado, 1.6 km SE of Villar, S of Las Ablanosas, 325 m, on *A. melanoxylon* fallen phyllodes, 3 February 2012, *J. Linde & E. Rubio* (H.B. 9664). Avilés, naval harbour area, 10 m, on *A. melanoxylon* fallen phyllodes, 18 February 2006, *A. Suárez* (AH 7636). País Vasco: Vizcaya, 17 km WNW of Bilbao, 2.2 km S of Muskiz, Rebortun, 92 m, *A. melanoxylon* fallen phyllodes, 12 February 2012, *J. Fernández Vicente (J.F. 2012021201*, photograph only examined). Galicia: A Coruña, Fragas do Eume Natural Park, surroundings of the Caaveiro Monastery, 62 m, *A. melanoxylon* fallen phyllodes, 1 November 2000, *M. Castro* (AH 7649).

Based on both morphological and genetic results, the following additional new combinations are proposed. Six out of the nine *Hymenotorrendiella* species are included in the phylogenetic analysis presented here, but all of the *Nothofagus*-inhabiting species described in *Torrendiella* by Johnston and Gamundí (2000), along with the undescribed species discussed by Johnston (2006, 2010), are genetically typical of *Hymenotorrendiella* (P.R.J., unpubl. data). Since sequences are not available for *Torrendiella grisea* or *T. guangxiensis*, their recombinations are based on morphological evidence alone:

Hymenotorrendiella andina (P.R. Johnst. & Gamundí) P.R. Johnst., *comb. nov.*

Registration identifier: IF550524

Synonym: *Torrendiella andina* P.R. Johnst. & Gamundí, New Zealand Journal of Botany 38: 496 (2000).

Hymenotorrendiella brevisetosa (P.R. Johnst. & Gamundí) P.R. Johnst., *comb. nov.*

Registration identifier: IF550525

Synonym: *Torrendiella brevisetosa* P.R. Johnst. & Gamundí, New Zealand Journal of Botany 38: 499 (2000).

Hymenotorrendiella cannibalensis (P.R. Johnst. & Gamundí) P.R. Johnst., *comb. nov.*

Registration identifier: IF550526

Synonym: *Torrendiella cannibalensis* P.R. Johnst. & Gamundí, New Zealand Journal of Botany 38: 503 (2000).

Hymenotorrendiella clelandii (Hansf.) P.R. Johnst., *comb. nov.*

Registration identifier: IF550527

Synonyms: *Lachnella clelandii* Hansf., Proceedings of the Linnean Society of New South Wales 79: 126 (1954); *Zoellneria clelandii* (Hansf.) Dennis, Kew Bulletin 13: 324 (1958); *Torrendiella clelandii* (Hansf.) Spooner, Bibliotheca Mycologica 116: 327 (1987).

Hymenotorrendiella dingleyae (P.R. Johnst. & Gamundí) P.R. Johnst., *comb. nov.*

Registration identifier: IF550528

Synonym: *Torrendiella dingleyae* P.R. Johnst. & Gamundí, New Zealand Journal of Botany 38: 505 (2000).

Hymenotorrendiella grisea (P.R. Johnst. & Gamundí) P.R. Johnst*., comb. nov.*

Registration identifier: IF550529

Synonym: *Torrendiella grisea* P.R. Johnst. & Gamundí, New Zealand Journal of Botany 38: 510 (2000).

Hymenotorrendiella guangxiensis (W.Y. Zhuang) Baral & W.Y. Zhuang, *comb. nov.*

Registration identifier: IF550530

Synonym: *Torrendiella guangxiensis* W.Y. Zhuang, Mycotaxon 72: 331 (1999).

Hymenotorrendiella madsenii (G.W. Beaton & Weste) P.R. Johnst., *comb. nov.*

Registration identifier: IF550531

Synonyms: *Zoellneria madsenii* G.W.Beaton & Weste, Transactions of the British Mycological Society 68: 82 (1977); *Torrendiella madsenii* (G.W. Beaton & Weste) Spooner, Bibliotheca Mycologica 116: 330 (1987).

Discussion

The revised generic concept

The molecular results of the present study show that most *Torrendiella* s.l. species are genetically distant from the type species *T. ciliata*, belonging in the core *Hymenoscyphus* clade of Wang *et al.* (2006), rather than the *Rutstroemiaceae*. To accommodate them, the new genus *Hymenotorrendiella* is erected. Despite their genetic distance, *Hymenotorrendiella* is macromorphologically and anatomically very similar to *Torrendiella*. Species in both genera have usually stipitate apothecia with prominent dark brown-walled setae and a 3-layered ectal excipulum reminiscent of *Rutstroemia* (White 1941). The two genera can be distinguished micromorphologically by the ascus apex structure and the contents of the living paraphyses, whereas other features vary within each genus.

Several authors have noted the morphological similarity between *Torrendiella ciliata* and the genus *Rutstroemia*, and Galán *et al.* (1993) debated whether the presence or absence of setae should be considered diagnostic at the level of genus. Dennis (1959b) saw a close resemblance between *R. hirsuta* and members of *Rutstroemia*, except for the presence of scattered setae which closely resembled those of *Zoellneria*. He was apparently unaware of the genus *Torrendiella* at that time, but saw a difference to another setose species, *Rutstroemia setulata*, in which the setae occur only on the margin. In a similar manner, Velenovský placed *Rutstroemia rubi* Velenovský (1934: 229) in a genus with *R. firma*, the type species of *Rutstroemia*, and also White (1941) transferred *Ombrophila setulata* Dearness & House (1925: 60) to *Rutstroemia* despite the presence of setae. For a discussion on the generic limits around *Rutstroemia* see Baral (1994).

For now we retain *Torrendiella* s.str. as taxonomically distinct from *Rutstroemia*, despite the morphological similarity of the respective type species. In our genetic analysis (Figure 2), sequence data of the ITS rDNA region were available for nine species of *Rutstroemia* and two of *Torrendiella*. The analysis places *Rutstroemia* into two distinct clades, while *Torrendiella* constitutes with high support a further clade. The family *Rutstroemiaceae* appears paraphyletic in this analysis, with *Torrendiella* forming with medium support a sister clade to genera of *Sclerotiniaceae*, while the *Rutstroemia* clade which contains *R. firma* forms in turn with low support a sister clade to those.

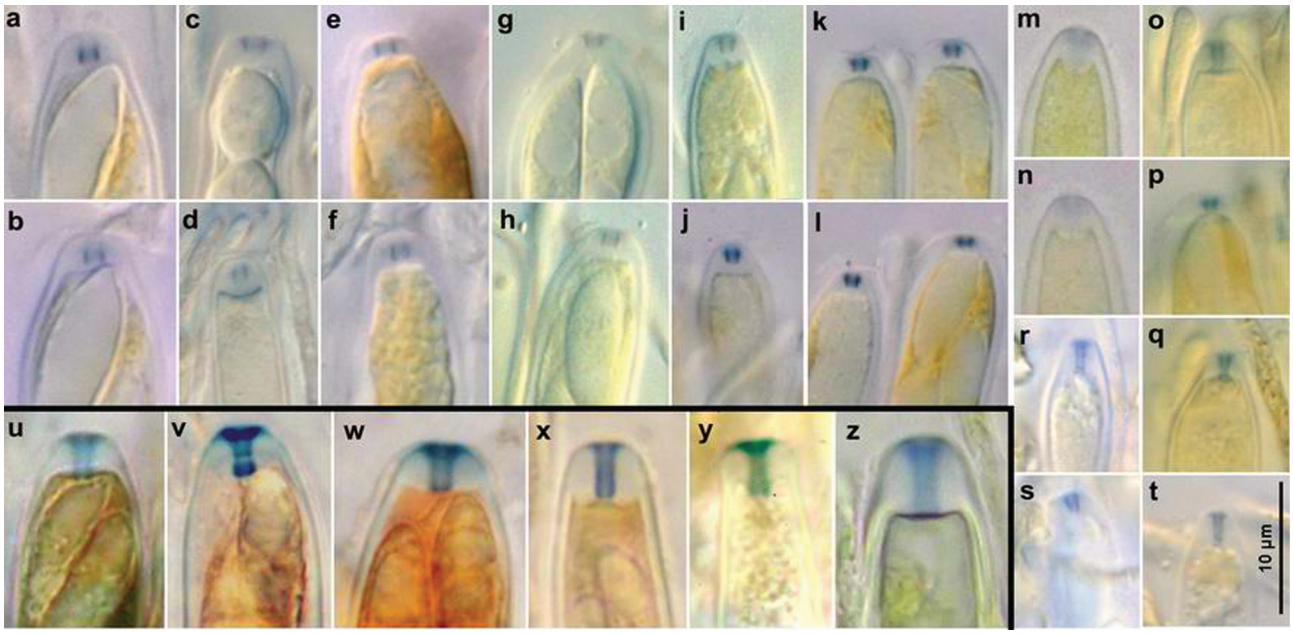

FIGURE 11. Morphology of dead ascus apices in *Hymenotorrendiella* (**a–t**) and *Rutstroemia* (**u–z**), comprising the *Hymenoscyphus*-type (**a–l**), *Calycina*-type (**m–t**), and *Sclerotinia*-type (**u–z**). **a–b**. *Hymenotorrendiella* sp. (on *Metrosideros*, PDD 102797). **c–d.** *H. dingleyae* (PDD 64828). **e–f**. *H. andina* (PDD 69808). **g–i.** *H. andina* (PDD 68405). **j–l**. *H. andina* (PDD 69811a). **m–n**. *H. brevisetosa* (PDD 64665). **o–q**. *H. andina* (PDD 69811b). **r–t**. *H. andina* (PDD 70295). **u**. *Rutstroemia* sp. (H.B. 8092). **v–w**. *R.* aff. *firma* (B.S.I. 11.65). **x**. *R. firma* (XI.2012). **y**. *R. fruticeti* (E.R.D. 5764). **z**. *Torrendiella setulata* (NBM# F-04646). **a–t** in KOH+MLZ, **u–z** in IKI. (phot. **v–w**: B. Senn-Irlet; **x**: P. Duboc; **y**: E. Rubio).

The genus *Lanzia* was placed by Baral (1994) in synonymy with *Rutstroemia*. Three sequences from GenBank assigned to the genus *Lanzia* form in our analysis with "*Roseodiscus*" *sinicus* a highly supported clade situated between the two *Rutstroemia* clades. Although no sequence of the type species of *Lanzia* is available for comparison, the species of this clade might be representative of the genus and support its autonomy. The morphology of "*Roseodiscus*" *sinicus* as described by Zheng and Zhuang (2013) resembles that of *L. allantospora* and *L. griseliniae* as described by Spooner (1987), except for the prismatic cells of the ectal excipulum that tend towards a textura angularis in *R. sinicus* but towards a textura porrecta in the two *Lanzia* species. The authors of "*R.*" *sinicus* reported a *Calycina*-type of apical ring (Zheng and Zhuang 2013) but their drawing could well fit the *Sclerotiniaceae*-type. Based on ITS sequences, *R. sinicus* is genetically distant from the only available sequence of the type species of *Roseodiscus*, *R. rhodoleucus* (AJ430395).

Further studies need to be undertaken in this group of fungi before proposing formal transfer of *R. sinicus* to the genus *Lanzia*. Also we leave a taxonomic reconsideration of the genera *Rutstroemia* and *Torrendiella* open until additional genetic data is available.

Taxonomy and ecology of the species

Torrendiella. *Torrendiella* in its restricted sense is known from tropical America (Kohn 1982, as *Poculum* sp.), North America, and Europe (Galán *et al.* 1993). Although genetic data are available for only *T. ciliata* and *T. setulata*, the type of ascus apex allows most of the species to be recognised as sclerotiniaceous.

Descriptions and illustrations of *Torrendiella ciliata* are found in Boudier and Torrend (1911), Graddon (1979), Spooner (1987), Galán *et al.* (1993), Malaval (2005) and Ormad *et al.* (2010). These include some variation in ascus size and appearance of setae. Boudier figured dead asci, and his measurement (†130–140 × 8–10 µm) shows that they are longer and narrower in the type material (on unidentified twigs) compared to our samples on *Quercus* spp. leaves. Spooner (1987) examined two British specimens on *Rubus fruticosus* leaves and stems, with asci of a similar size [†(110–)118–132 × 10.5–13 µm] to those we found on *Quercus* leaves. One of them (on stems, W.D. Graddon 3023) was identified by Graddon (1979) as *Rutstroemia rubi*, while specimens on *Rubus* leaves were recorded by him under

the name *Torrendiella ciliata* in the same paper. Surprisingly, Graddon (1979) described and figured the setae of his *R. rubi* as pale, and those of *T. ciliata* as brown. Spooner stated for both substrates (leaves and stems of *Rubus*) the setae to be dark brown below, becoming paler upwards, and regarded *R. rubi* as a possible synonym of *T. ciliata*. Galán (1991) and Galán *et al.* (1993) reported *T. ciliata* mainly on *Quercus* leaves on the Iberian Peninsula, but also on *Laurus* leaves on the Canary Islands. Malaval's sample was on leaves of *Q. ilex* in Mediterranean regions of southern France.

Since no clear information on the ascus base is given in any of these reports (Malaval's statement of "rather long croziers" probably refers to the basal protuberances), it cannot be excluded that different species are hidden behind *T. ciliata*. Regrettably, the type material of *R. rubi* appears not to have survived (Johnston and Gamundí 2000). However, a record on *Rubus* stems from Belgium examined by B. Declercq (pers. comm.) is apparently simple-septate as he noted protuberances at the ascus base in concordance with the here reported specimens on *Quercus* leaves. *R. hirsuta*, on unidentified petioles from tropical Bolivia, was described by Dennis (1959b) as having shorter spores than *T. ciliata* but confirmation that it is a distinct species requires reexamination of the ascus base, also of its setae (as "hairs") which were drawn by Dennis more thin-walled.

Of the other *Torrendiella* spp., *T. quintocentenaria* (from Mexico, on leaves of *Quercus agrifolia*) clearly belongs in the *Rutstroemiaceae*, according to the typical sclerotiniaceous shape of apical ring as illustrated in Galán *et al.* (1993, Figure 5). This species differs from *T. ciliata* in much shorter, not curved, ovoid ascospores, and in slightly narrower setae (basally 9–16 µm) which are restricted to the margin of the apothecium. Simple-septate ascus bases with very occasional basal protuberances occur also in this species, according to a reexamination of the isotype material (*J.T.P. 4694*, CUP) by two of us (R.G., R.T.).

Torrendiella setulata, described from Vermont, USA, on twigs of *Acer spicatum*, differs from the above taxa in much shorter and also narrower setae (60–120 × 9.5–12 µm). The almost straight spores resemble *T. quintocentenaria* in shape, but are much longer, almost approaching *T. ciliata* in length but exceeding that species in width. In an unpublished reexamination of type material by J.T. Palmer, the spores were drawn with one medium-sized oil drop at each end, very different from the other included species. The protologue describes the spore contents as "with a nucleus filling each end and leaving a granulated zone that simulates a septum" (Dearness and House 1925). According to a reexamination of a slide of the type kept at AH, the asci arise also here from simple septa, partly with basal protuberances, and show the typical *Sclerotinia*-type of apical ring, staining strongly blue in MLZ (KOH-pretreated). A specimen from Canada (Prince Edward Island, NBM# F-04646) that grew on the type substrate was examined by one of us (H.O.B.) and found to fit the type of *T. setulata* very well, including the apex (Figure 11z, blue in IKI without KOH) and base of the asci. The spores show a high lipid content similar to *T. ciliata* and in concordance with the protologue of *T. setulata*.

Dennis (1959b) noted that the setae in *R. hirsuta* occur scattered over the whole exterior of the apothecium, in contrast to *T. setulata* where they "are said to occur only in fascicles on the margin". The restriction of the rather short and sparse setae to the apothecial margin is also obvious from White's (1941) redescription and J.T. Palmer's unpublished drawing of the type of *T. setulata*, and it is confirmed in the present study of a recent specimen.

Kohn's (1982) illustration of the apical ring of a further setose taxon, referred to as *Poculum* sp. 1385 (from Macaronesia, on stems of *Rubus*), is somewhat schematic but appears sclerotiniaceous despite not clearly showing the typical basal and apical parts of the sclerotiniaceous ring. This collection resembles *T. ciliata* in its microscopic characters but was said to have "asci arising from repeating croziers", also the spores are drawn straight. Kohn also noted morphologically similar species in the Neotropics and Paleotropics, though without any description. It is possible that she was referring to species of both *Torrendiella* and *Hymenotorrendiella* in the sense that we use these names.

Hymenotorrendiella. Based on known specimens, *Hymenotorrendiella* appears to be restricted to the Southern Hemisphere and tropical Asia, when disregarding artificial introduction of host trees and their associated fungi to countries of the Northern Hemisphere by humans.

The type species of *Hymenotorrendiella*, *H. eucalypti*, is *Acacia*-specialised and very common on the recently fallen phyllodes of *Acacia* in native forests of Australia. It has been found also on *Acacia* in Spain, New Zealand and Chile where it is exotic, having been imported along with its host. This fungus is likely to be an endophyte in the living phyllodes of *Acacia*. Reports of "*Zoellneria*" or "*Torrendiella*" *eucalypti* on *Eucalyptus* leaves (e.g. Dennis 1978; Graddon 1979; Cabral and Bertoni 1984) probably represent an undescribed species of *Hymenotorrendiella* that is widespread on *Eucalyptus* leaves in Australia (P.R.J., unpubl. data). The collections from *Eucalyptus* in Spain (Sánchez-Márquez *et al.* 2011) and in Indonesia (Crous *et al.* 2006), for which DNA sequences were provided, definitely do represent either this undescribed species or a close sister species (P.R.J., unpubl. data).

Misidentifications of the host substrate further complicate the situation. *Peziza eucalypti* was originally described on *Eucalyptus* leaves, but it grew in fact on *Acacia* phyllodes (Spooner 1987). A specimen on leaves of "*Eucalyptus*"

revised by Dennis (1958, Mt. Lofty, 21 May 1954, leg. C.G. Hansford) was reexamined by Spooner (1987), who reidentified the host substrate as "phyllodes of *Acacia*". Likewise, Graddon (1979) stated "*Eucalyptus* phyllodes" for *Zoellneria eucalypti* from the north of Spain (Viveiro, as "Viviero") and Scotland (Isle of Mull), following data by the collector M.C. Clark, which is either an improper word for leaves, or a misidentification for *Acacia*.

Most of the collections reported in the papers cited in this paragraph were found on leaves fallen to the ground, but Cabral and Bertoni (1984) reported the fungus isolated as an endophyte from living leaves of *Eucalyptus*. These authors noted the development of apothecia in culture, a feature also of the undescribed *Eucalyptus* specialised species (Johnston and Gamundí 2000). Johnston *et al.* (2012) reported several of the species originally described from fallen *Nothofagus* leaves in New Zealand, as endophytes present within symptomless, living leaves.

Spooner (1987) had a morphologically and biologically wide concept of *Hymenotorrendiella eucalypti*. Besides collections on phyllodes of *Acacia* from Australia he included those on leaves of *Banksia* (Australia), *Eucalyptus* (Scotland), *Metrosideros* (New Zealand, single apothecium as mixtum in the type of *Helotium metrosideri* Dennis), and *Myrica* (North America, isotype of *Zoellneria callochaetes* (Ellis & Everh.) Dennis). The *Metrosideros*-inhabiting species, although still undescribed, is distinct from *H. eucalypti* and there are many undescribed, host specialised species in both New Zealand and Australia (Johnston 2010). Spooner's redescription of *Zoellneria callochaetes* matches very well the holotype of *Torrendiella eucalypti*, nevertheless the host and geographic differences suggest that it is likely to be a distinct species.

Notes on morphological characters

Apical ring of asci. The apical rings of *Torrendiella ciliata*, *T. quintocentenaria* and *T. setulata* are of the *Sclerotinia*-type (Baral 1987a (Figs 9, 15–16); Verkley 1993a, 1995), which is characterised by a rather thick-walled euamyloid ring that always extends through the entire apical wall thickening. It is apically thickest by forming a lateral extension, and protrudes basally into the ascoplasm by forming a small apical chamber (Figures 4d, 5f–j). The apical chamber is better seen with the TEM or in immature living asci with the LM (Baral 1987a, Figure 9). The surface shape of the ascus apex is only slightly conical, almost hemispherical, or more or less distinctly truncate. The illustration by Dennis (1959b, Figure 2) shows that *R. hirsuta* also possesses this type of apical ring. This ascus type is very common within the *Sclerotiniaceae*, matching perfectly the apical rings of members of *Rutstroemia* spp. without setae (see Figures 11u–z).

The apical rings of *Hymenotorrendiella* spp. are of the *Hymenoscyphus*-type, i.e., the iodine-reactive part of the wall forms a more or less thin-walled cylinder that appears as two parallel lines in side view (Baral 1987a; Verkley 1993b, 1995). The ring is typically restricted to the lower part of the apical wall thickening, but in *Hymenotorrendiella* it often extends also through the upper part (Figures 7b, 8f–g, 11a–l), similar as in the Southern Hemisphere "*Discinella terrestris* aggregate" recently transferred to *Phaeohelotium* (Baral *et al.* 2013). Below, it does not clearly protrude into the ascoplasm. The surface shape of the ascus apex is distinctly conical, in both living and dead asci. This ascus type is very common in *Hymenoscyphus* s.l. (including *Phaeohelotium* and *Cyathicula*), but occurs also in *Dicephalospora* (H.O.B., unpubl. data). *Torrendiella guangxiensis* was described without information on the apical ring type, but a re-examination kindly performed by W.Y. Zhuang (pers. comm.) revealed it to match that of *H. andina* (Figures 11g–i). The holotype of *Hymenotorrendiella andina* (BCRU 1187) shows a deviating type of apical ring, reminiscent of the *Calycina*-type (Johnston and Gamundí 2000, Figure 1K). This is also the case in two specimens studied here (Figures 11o–t), whereas three further specimens show a *Hymenoscyphus*-type of apical ring (Figures 11e–l). Also in *Hymenotorrendiella brevisetosa* the apical ring resembles the *Calycina*-type, but differs in being rather faintly reactive (Figures 11m–n). Despite this deviating ring type, sequences taken from *H. andina* (PDD 69811) and *H. brevisetosa* fall in the *Hymenotorrendiella* clade.

Croziers. Although the ascus bases in the type species of both *Torrendiella* (*T. ciliata*) and *Hymenotorrendiella* (*H. eucalypti*) arise from simple septa, they differ in the two species. A basal protuberance is regularly present in *T. ciliata* (Figures 4e, 5e, 5r), *T. quintocentenaria* and *T. setulata*, whereas in *H. eucalypti* no such protuberance was ever seen (Figures 7c, 8q). No information on the ascus base is available for *R. hirsuta.* Species of *Rutstroemia* without setae usually possess croziers, while *R. elatina*, *R. paludosa* (on *Cyperaceae*), and an undescribed species on *Daphne* show simple-septate asci (H.O.B., unpubl. data). In *R. paludosa* basal protuberances as in *T. ciliata* were often seen. Species of *Hymenotorrendiella* associated with *Nothofagus* (*H. andina*, *H. brevisetosa*, *H. cannibalensi*s, *H. dingleyae*, and *H. madsenii*) share simple septa with *H. eucalypti*, and likewise never show basal protuberances (Figure 12g). *Eucalyptus* inhabiting species (*H. clelandii* and that reported by Crous *et al.* 2006 as *T. eucalypti*) have croziers at the ascus base, as do two undescribed species on *Kunzea* and *Metrosideros* (Figures 12d–f, P.R.J., unpubl. data).

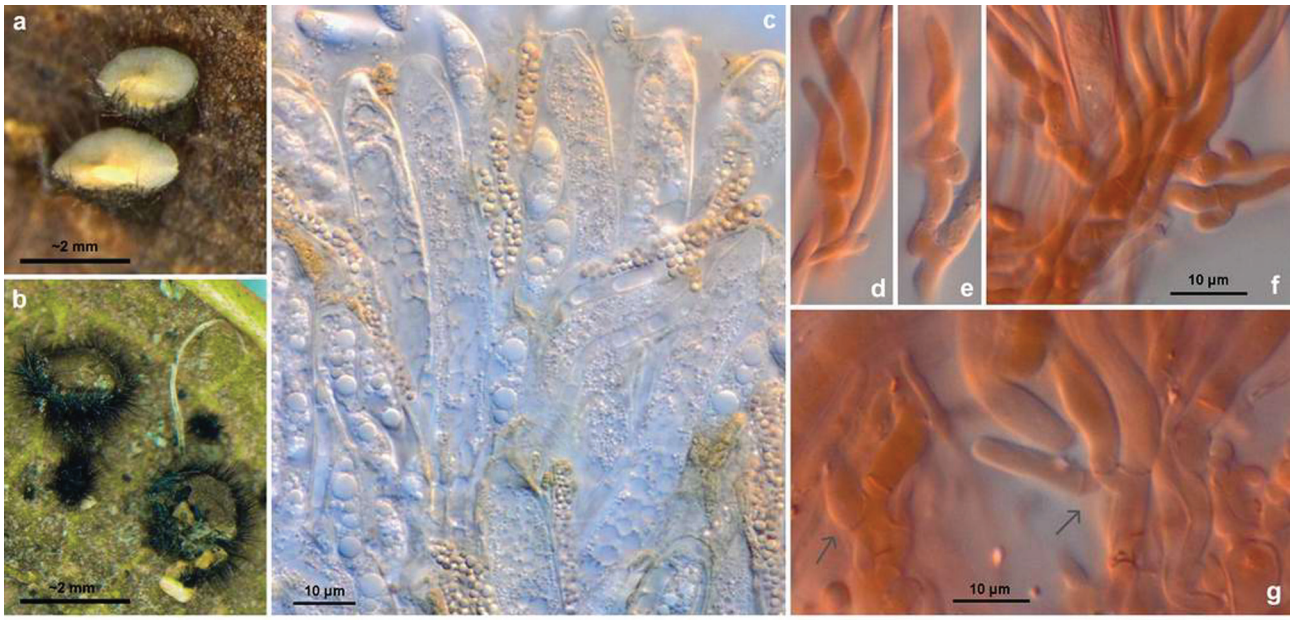

FIGURE 12. *Hymenotorrendiella* from New Zealand. **a**. Apothecia on leaf surface, fresh. **b.** Apothecia on leaf surface, dry. **c**. Squash mount of hymenial elements, showing ascospores that contain large lipid bodies, and paraphyses that include many small refractive vacuolar bodies. **d–f**. Squash mounts showing ascus bases arising from croziers. **g**. Ascus bases arising from simple septa. **c**: living state, **d–g**: dead state (in KOH+CR).—**a–f.** *Hymenotorrendiella* sp. (on *Metrosideros*). **a**, **c**. PDD 102797, **b, d–f**. PDD 43948. **g**. *H. cannibalensis*, PDD 64242.

Ascospores. Spore shape in *Rutstroemia* and *Torrendiella* is generally ellipsoid, showing rounded to obtuse, rarely subacute ends, and strong curvature is typical of some of the species. Spore shape in *Hymenotorrendiella* is frequently fusoid, with subacute to acuminate ends, and curvature is never strong. Differences between the two genera in the lipid content were not observed.

For a species on leaves of *Eucalyptus* misidentified as *Torrendiella eucalypti*, Crous *et al.* (2006) figured living ascospores with a gelatinous cap at both ends, a feature not seen in either *T. ciliata* or *H. eucalypti* as here redescribed in the living state. The species is closely related to *H. eucalypti* but represents a different species according to both morphological and genetic data. Such polar caps are typical of *Dicephalospora*, however, a small genus considered sclerotiniaceous by Spooner (1987) while in fact being closely related to *Hymenotorrendiella*.

Ascospores that formed ellipsoid to narrowly tear-shaped microconidia were illustrated by Graddon (1979) for *T. ciliata* and by Johnston and Gamundí (2000) for *H. madsenii*. In *T. ciliata* these were directly on the 1–3-septate spores, in *H. madsenii* on short germ tubes emerging from the non-septate spores. The shape of the microconidia deserves further observation, because microconidia of *Sclerotiniaceae* (including *Rutstroemia*) are usually broadly ellipsoidal to subglobose (Whetzel 1945, as "spermatia").

Refractive vacuolar bodies (VBs). The long terminal cells of the paraphyses in *Hymenotorrendiella eucalypti* contain abundant, globose or sometimes shortly elongate, refractive vacuolar bodies (Figures 7d, 8m, 8o–p, 8s–w), whereas those of *T. ciliata* contain very elongate VBs which are divided into roundish vacuoles only in the lower part of the terminal cells (Figures 5k–n). While other setose *Rutstroemia* spp. have not so far been studied in the living state, multiguttulate VBs are known from two undescribed species of *Hymenotorrendiella*: on leaves of *Eucalyptus* (Crous *et al.* 2006, as *T. eucalypti*), on leaves of *Metrosideros* (Figure 11c). The multiguttulate contents of the paraphyses are still recognizable in herbarium material. They were illustrated by Spooner (1987, Figures 56J, 57E) for *H. clelandii* and *H. madsenii*, and as large, globose, non-refractive contents for *H. eucalypti* (Spooner 1987, Figure 55C). Also Dennis (1958, 1978) figured multiguttulate paraphyses in *H. clelandii* and *H.* aff. *eucalypti* (as *Zoellneria clelandii* and *Z. eucalypti*). However, the VBs are not visible in reagents such as KOH or MLZ.

Setae. In both *Hymenotorrendiella* and *Torrendiella* the brown setae frequently root more or less deeply by arising from the central layer of the ectal excipulum. For *Torrendiella*, rooting setae were reported or illustrated by Graddon (1979, *T. ciliata*), Kohn (1982, "*Poculum* sp. 1385"), Spooner (1987, *T. ciliata*), Galán *et al.* (1993, *T. ciliata* and *T. quintocentenaria*), and in the present study (*T. ciliata* and *T. setulata*). For *Hymenotorrendiella*, rooting setae were reported or illustrated under the name *Torrendiella* by Spooner (1987, *T. eucalypti*, *T. clelandii*, and *T.*

madsenii), Johnston and Gamundí (2000, *T. andina*, *T. cannibalensis*, more or less also in *T. brevisetosa*, "*Torrendiella* sp. Johnston AU96-2", and *T. dingleyae*), Zhuang (1999, *T. guangxiensis*), and in the present paper (*H. eucalypti*). In *H. grisea* and *H. madsenii*, however, they arise superficially from the outer layer of the ectal excipulum (Johnston and Gamundí 2000: figure 10C). In *H. andina*, *H. dingleyae* and *H. grisea* the setae on the stipe are found to arise superficially while those at the receptacle are rooting (Johnston and Gamundí 2000, figures 1D, 2G, 7M, R).

Superficially inserted setae of *Hymenotorrendiella* often arise from a short, brown, horizontal hypha (Y-, L- or T-shaped), a feature typical of *H. madsenii* (Beaton and Weste 1977; Spooner 1987; Johnston and Gamundí 2000) and *H. andina* (Johnston and Gamundí 2000), though in the latter species such setae are restricted to the stipe. In *Torrendiella*, only unbranched seta bases are known. The wall of the setae is thicker in *T. ciliata* (1.5–3.5 µm) compared to *Hymenotorrendiella* (1–2 µm). *H. clelandii* and *H. madsenii* (1–1.8 µm according to Spooner's 1987 drawings) concur with *H. eucalypti*, but in *H. grisea* the wall also attains 3.5 µm in thickness (Johnston and Gamundí 2000, Figure 7L), and in the sparse hairs of *T. setulata* it is about 1–2 µm. *H. grisea* further deviates from all the other species in paler brown setae with a swollen apex.

TABLE 2. Differential characters between the type species and other species of *Torrendiella* and *Hymenotorrendiella* (features that are considered characteristic at the generic level are highlighted in bold).

	Torrendiella ciliata	***Torrendiella* remaining spp.**	***Hymenotorrendiella eucalypti***	***Hymenotorrendiella* remaining spp.**
Ascus apex	*Sclerotinia*-type	*Sclerotinia*-type	*Hymenoscyphus*-type	*Hymenoscyphus*-type (rarely *Calycina*-type)
protuberance on croziers	often present	often present	absent	absent
Ascospores	*(15–)17–21(–24) × (5–)5.5–6.5(–7) µm	9.5–20 × 5.2–8.8 µm	*16–19(–21) × 4–4.7 µm	11–30 × 3–8.5 µm
Ascospore shape	cylindric-ellipsoid, medium to strongly curved	ellipsoid-ovoid, ± straight	fusiform, straight to slightly (medium) curved	(cylindric-)ellipsoid, ellipsoid-fusoid to fusiform, ± straight
Ascospores during germination	1–3-septate, budding directly conidia	germination not observed	germination not observed	non-septate, budding conidia on short germ tubes
VBs in living paraphyses	mainly elongate	unknown	mainly globose	globose (often unknown)
VBs in living excipular cells	absent	unknown	globose	unknown
Ectal excipulum outer layer (ec1)	*textura porrecta*, light to bright brown, encrusted	*textura porrecta*, light to bright brown, encrusted	*textura porrecta*, pale brown, encrusted	*textura porrecta,* hyaline to bright brown, encrusted or not
Ectal excipulum medial layer (ec2)	*textrura prismatica*, near margin *textura oblita*, hyaline, not encrusted	*textrura oblita*, hyaline, not encrusted	*textrura prismatica-porrecta*, hyaline, not encrusted	*textrura prismatica-porrecta* to *textura oblita*, hyaline, not encrusted, rarely pale brown, finely encrusted
Ectal excipulum inner layer (ec3)	*textrura prismatica-porrecta*, light brown, slightly encrusted	*textrura porrecta*, light brown, ± encrusted	*textrura porrecta*, hyaline to pale brown, slightly encrusted	*textrura porrecta*, pale to bright brown, not or ± distinctly encrusted
Setae	(120–)200–350(–450) × 16–24 µm	60–310 × 9–16 µm	(150–)200–300(–400) × 7.5–10(–12) µm	100–600(–1000) × (4–)5–15(–20) µm
Setae, wall thickness	(0.5–)1–2.5(–3.5) µm	1–2.5 µm	1–1.5(–2) µm	1–3.5 µm
Setae base	unbranched, rooting	unbranched, rooting	unbranched, rooting	unbranched or T- to L-shaped, rooting or often superficial
Apothecial diam.	0.5–1.7 mm	0.3–2 mm	0.4–1.7(–2.5) mm	(0.2–)0.5–2(–6) mm

Ectal excipulum. The absence of a gelatinization of the ectal excipulum noted for *Torrendiella* s.l. (Spooner, 1987) was not confirmed for *Torrendiella ciliata* by Galán *et al.* (1993) or for *Hymenotorrendiella* by Johnston and Gamundí (2000). Also Graddon (1979) described the ectal excipulum of *T. ciliata* as "phialioid", while he stated it to be thin-walled in the material he referred to *Rutstroemia rubi*. Although the genus *Hymenotorrendiella* is characterised in part by its three-layered ectal excipulum, the extent to which the various layers develop, and the extent of the gelatinisation of the central layer, varies markedly between species (Johnston and Gamundí 2000).

There is some discrepancy in the naming of the different excipular layers. Galán *et al.* (1993) referred to the three layers of the ectal excipulum as outer layer (oe), middle layer (me), and inner layer (ie). Johnston and Gamundí (2000) followed this terminology by naming the middle layer as "central layer", and by using different acronyms (ec1, ec2, ec3) which are adopted in the present paper. Also Spooner (1987) described the ectal excipulum of *Poculum* as three-layered. Alternatively, the inner layer could be interpreted as an outer layer of the medullary excipulum. This alternative is supported when comparing the excipular anatomy of other members of sclerotiniaceous and helotiaceous fungi. The medullary excipulum is generally made up of a more or less loose *textura intricata*, while towards the ectal excipulum a *textura porrecta* is often found which is composed of similar hyphae. In sclerotiniaceous fungi these hyphae are often more pigmented and encrusted and also wider, whereas in helotiaceous taxa the difference to the inner layer lies mainly in a more compact and parallel orientation of the hyphae.

Stroma (pseudosclerotium). The leaf-inhabiting *Hymenotorrendiella* spp. are sometimes associated with stromatic lines on their host leaves, but not consistently so, and many specimens have no zone lines or other kinds of stromatic development. Many of the *Hymenotorrendiella* hosts are also associated with several other inoperculate discomycete species. It is possible that these latter species form stroma-like demarcation lines when they are present in adjacent areas on the same leaf. The wood and bark inhabiting species of *Hymenotorrendiella* are commonly associated with darkened tissue near the base of the apothecia, or more generally across the surrounding substrate. Within *Torrendiella*, a substratal stroma consisting of fine black lines that delimit irregular areas of the leaves is typical of *T. ciliata* (Graddon 1979, Spooner 1987) and *T. quintocentenaria* (Galán *et al.* 1993). The late J.T. Palmer (unpubl. data) obtained stromata also in pure culture of *T. ciliata*.

The dark stroma was previously considered as characteristic of the *Sclerotiniaceae* s.l., but its taxonomic value at the family level is questioned through species today placed in *Hymenoscyphus* but previously in *Lanzia* or *Lambertella*, such as *Hymenoscyphus albidus* (Roberge ex Gillet) Phillips (1887: 138), *H. pseudoalbidus* Queloz *et al.* (2011: 140), *H. vacini* (Velen.) Baral & Weber in Weber (1992: 121), *H. serotinus* (Pers.) Phillips (1887: 125), and *H. berggrenii* (Cooke & W. Phillips) Kuntze (1898: 485), which form a black pseudosclerotial tissue on their host substrate and belong in the core *Hymenoscyphus* clade sensu Wang *et al.* (2006) (Zhao *et al.* 2013, Baral and Bemmann 2013, Johnston and Park 2013).

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