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RESEARCH ARTICLE

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Finding the missing link: Resolving the *Coryneliomycetidae* within *Eurotiomycetes*

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Key words

Corynelia
DNA phylogeny
Lagenulopsis
phytopathogenic fungi
Sordariomycetes
systematics
Tripospora

Abstract Species belonging to the *Coryneliaceae* and parasitizing *Podocarpaceae* hosts were collected from different locations in South Africa and studied morphologically by light microscopy and molecularly by obtaining partial nrDNA (ITS-1/5.8S/ITS-2, 18S and 28S) gene sequences. The position of the *Coryneliaceae* within the *Eurotiomycetidae* was not confirmed and a new subclass, *Coryneliomycetidae*, was introduced. While *Eurotiomycetidae* usually form cleistothecia/gymnothecia with evanescent, unitunicate asci, and *Chaetothyriomycetidae* mostly perithecia with bitunicate/fissitunicate to evanescent asci, *Coryneliomycetidae* form pseudothecial mazaedial ascomata, initially with double-walled asci with the outer layer deliquescing, resulting in passive ascospore release. The *Coryneliomycetidae* thus occupies a unique position in the *Eurotiomycetes*. Furthermore, epitypes were designated for *Corynelia uberata*, the type species of *Corynelia* (type genus of the family, order and subclass), *Lagenulopsis bispora*, the type species of *Lagenulopsis*, and *Tripospora tripos* the type species of *Tripospora*, with *Lagenulopsis* and *Tripospora* confirmed as belonging to the *Coryneliaceae. Corynelia uberata* resolved into three clades, one on *Afrocarpus* (= *Podocarpus*) *falcatus* and *A. gracilior*, and two clades occurring on *P. latifolius*, herein described as *C. africana* and *C. fructigena*. Morphologically these three species are not readily distinguishable, although they differ in spore dimensions, ascomata shape, ornamentation and DNA phylogeny. It is likely that several more species from other parts of the world are currently erroneously placed in *C. uberata*.

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INTRODUCTION

Recent molecular phylogenic evidence places the *Coryneliales* (sole family *Coryneliaceae*) as basal within the *Euryotiomycetidae* (Geiser et al. 2006). This order has a unique set of morphological characters including ascolocular ascomata, spermogonia, initially bitunicate asci with an outer wall layer that breaks away early in their development so that they appear unitunicate at maturity, and ascospores that are liberated passively by the eventual degradation of the inner ascus wall (Johnston & Minter 1989, Geiser et al. 2006). These characters distinguish the *Coryneliales* from all other members of the *Euryotiomycetidae* (*Eurotiales*, *Onygenales*). The *Coryneliaceae* currently contains seven genera: *Corynelia* (7 species), *Lagenulopsis* (1), *Tripospora* (4) (Catania & Romero 2001), *Caliciopsis* (29) (Garrido-Benavent & Pérez-Oriega 2015), *Coryneliopsis* (2), *Coryneliospora* (2), and *Fitzpatrickella* (1) (www.indexfungorum.org, www.mycobank.org), of which the first three mentioned are obligate parasites only recorded on members of the *Podocarpaceae*. Johnston & Minter (1989) suggested that *Coryneliopsis* (on *Cyttaria* galls on *Nothofagus*) does not belong to this family, and Benny et al. (1985b) excluded *Corynelia sydowii*. Checa et al. (1996) assigned their new species *Bicornispora exophiala* to the *Coryneliales*, but this species has recently been placed within the *Helotiales* (Galán et al. 2015).

The *Podocarpaceae*, with approximately 173 species, is morphologically and ecologically the most diverse family of conifers and largely restricted to the Southern Hemisphere (Kelch 1998). The majority of species occur in angiosperm-dominated humid forests, unusual amongst conifers (Biffin et al. 2011). The family possibly first evolved during the upper Triassic to Jurassic, though the majority of extant species are of recent evolutionary origin. A major shift in diversification rates is estimated to have occurred in the mid to late Cretaceous, possibly in response to the radiation and expansion of angiosperm-dominated forests (Biffin et al. 2011). Pirozynski & Weresub (1979) postulated that the *Coryneliaceae* had evolved by the early Cretaceous, being long co-evolved with their podocarp hosts and characterised by conserved characters and stability within species. *Podocarpus*, by far the largest extant genus in its family with approximately 105 species, is widespread occurring on all continents except Antarctica and Europe (Biffin et al. 2011). Recently it has been split into a number of genera (Kelch 1998, Biffin et al. 2011, Knopf et al. 2012). Africa and Madagascar have a low diversity of *Podocarpaceae* compared to the rest of the Southern Hemisphere, with only 13 to 17 species (depending on species limits accepted). They all belong to either the segregate genus *Afrocarpus* or the African subclade of the subgenus *Podocarpus* (Biffin et al. 2011, Knopf et al. 2012). These species predominantly follow a discontinuous distribution, being associated with temperate mountainous regions (Adie & Lawes 2011).

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Table 1 Details of specimens/strains included in the molecular analyses.

Species	Specimen number[1]	Substrate	Collector	Collection date	Location	GenBank accession numbers[2]		
						ITS	LSU	SSU
Caliciopsis orientalis	CBS 138.64 (ex-type culture)	*Tsuga canadensis*	A. Funk	26 Nov. 1960	Canada: Ontario	KP881690	DQ470987	DQ471039
Caliciopsis pinea	CBS 139.64	*Pinus strobus*	–	–	Canada: Ontario	KP881691	DQ678097	DQ678043
Corynelia africana	PREM 57242 (holotype) = ARW 247	*Podocarpus latifolius*	A.R. Wood	20 Nov. 2000	South Africa: Western Cape	KP881693	KP881714	KP881719
	PREM 59200 = ARW 656	*Podocarpus latifolius*, leaves	A.R. Wood	17 Oct. 2004	South Africa: Western Cape	KP881694	–	–
	PREM 61194 = ARW 671	*Podocarpus latifolius*, leaves	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881695	–	–
	PREM 61196 = ARW 673	*Podocarpus latifolius*, leaves	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881696	–	–
	PREM 61198 = ARW 675	*Podocarpus latifolius*, leaves	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881697	–	–
	PREM 61201 = ARW 678	*Podocarpus latifolius*, leaves	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881698	KP881715	–
	PREM 61204 = ARW 688	*Podocarpus latifolius*, leaves	A.R. Wood	18 July 2006	South Africa: Eastern Cape	KP881699	–	–
	PREM 61205 = ARW 682	*Podocarpus latifolius*, leaves	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881700	–	–
	PREM 61206 = ARW 683	*Podocarpus latifolius*, leaves	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881701	–	–
	ARW 681	*Podocarpus latifolius*	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881692	–	–
	UD 259	*Podocarpus* cf. *latifolius*, leaves	U. Damm	1 July 2007	South Africa: Western Cape	KP881702	–	–
Corynelia fructigena	PREM 57240 (holotype) = ARW 250	*Podocarpus latifolius*, fruits	A.R. Wood	20 Nov. 2000	South Africa: Western Cape	KP881704	KP881716	KP881720
	PREM 59201 = ARW 657	*Podocarpus latifolius*, fruits	A.R. Wood	17 Oct. 2004	South Africa: Western Cape	KP881705	–	–
	ARW 684	*Podocarpus latifolius*, leaf	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881703	–	–
Corynelia uberata	PREM 61203 = ARW 680	*Afrocarpus falcatus*, leaves	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881706	–	–
	PREM 61207 (epitype) = ARW 686	*Afrocarpus falcatus*, leaves	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881707	–	–
Lagenulopsis bispora	PREM 57232 (epitype) = ARW 249	*Podocarpus latifolius*	A.R. Wood	20 Nov. 2000	South Africa: Western Cape	KP881709	KP881717	KP881721
	PREM 59202 = ARW 655	*Podocarpus latifolius*, leaves	A.R. Wood	17 Oct. 2004	South Africa: Western Cape	KP881710	–	–
	PREM 61197 = ARW 674	*Podocarpus latifolius*, leaves	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881711	–	–
	ARW 685	*Podocarpus latifolius*, leaves	A.R. Wood	15 July 2006	South Africa: Western Cape	KP881708	–	–
Tripospora tripos	PREM 61200 = ARW 677	*Afrocarpus falcatus*, leaves	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881712	KP881718	–
	PREM 61202 (epitype) = ARW 679	*Afrocarpus falcatus*	A.R. Wood	14 July 2006	South Africa: Western Cape	KP881713	–	–

[1] ARW: personal number of Alan Wood; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; PREM: South African National Collection of Fungi (NCF), Mycology Unit, Biosystematics Division, Plant Protection Research Institute, Agricultural Research Council, Roodeplaat, Pretoria, South Africa; UD: personal number of Ulrike Damm.

[2] ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S nrDNA; SSU: partial 18S nrDNA.

The yellowwoods (*Podocarpus*) are iconic trees of the Afromontane forests of South Africa, being long sought after for their valuable timber. Currently four species are recognised from South Africa (*Afrocarpus falcatus* (= *Podocarpus falcatus*), *Podocarpus elongatus*, *P. henkelii*, and *P. latifolius*) (Barker et al. 2004). Application of these names by early workers was highly confusing, in particular specimens of *A. falcatus* were frequently referred to as *P. elongatus* or *A. gracilior*, whereas *P. latifolius* was frequently referred to as *P. elongatus* or *P. thunbergii*. *Podocarpus elongatus* as currently understood has a limited distribution in the most south-westerly mountains of the Western Cape Province of South Africa.

Corynelia uberata and *Tripospora tripos* on *Podocarpus* spp. and *Coryneliospora fructicola* on fruit of *Rapanea melanophloes* (*Myrsinaceae*) are the only members of the *Coryneliaceae* recorded from South Africa (Doidge 1950, Crous et al. 2000). *Corynelia uberata* was one of the first South African plant parasitic fungi to be collected and described by European explorers, being collected in 1772 by Carl Peter Thunberg during his travels in this country (Doidge 1950). Thunberg made his collection in 'sylvis Houtniquas Cap.' (forests of the Outeniqua mountains) on *A. falcatus* (Juel 1918). This species has been recorded historically as being 'extremely common throughout southern Africa on leaves, twigs and fruit of Yellow-woods' (Doidge 1950: 58). Phillips (1927) noted that in the forests around the town of Knysna (on the southern slopes of the Outeniqua mountains) in some years *P. latifolius* 'bear scarcely a single podocarpium that is not diseased by *Corynelia*'. It has also been observed as very common on leaves and fruit, at times up to 100 % of fruit, of *A. gracilior* in Ethiopia (Assefa et al. 2014, 2015).

Lagenulopsis bispora was first described as a form of *Corynelia clavata*, namely as *C. clavata* f. *macrospora*. Fitzpatrick (1920) described it as the new species *C. bispora*, and later established the genus *Lagenulopsis* to accommodate it (Fitzpatrick 1942a). The species is easy to identify as it is the only one in the family with the character combination of two ascospores per mature ascus and ostiolate ascomata. Originally described from material collected near Ruwenzori (now in Uganda), *L. bispora* has also been recorded from Fiji, Jamaica, Malawi, and Mexico (Fitzpatrick 1942a, Benny et al. 1985c, Johnston & Minter 1989). Benny et al. (1985c) listed a specimen collected in South Africa in 1926, which was found amongst specimens of *C. uberata* received from K (K(M) 187631, pers. comm. Begoña Aguirre-Hudson). Recently a number of specimens of *L. bispora* have been collected on *P. latifolius* at several sites in the Western and Eastern Cape Provinces, South Africa. It is usually rare, and easily overlooked. The aim of the present paper is to morphologically re-evaluate the *Coryneliaceae* based on fresh material of *Corynelia*, *Lagenulopsis*, and *Tripospora*, and to study the phylogenetic placement of the family/order *Coryneliaceae*/*Coryneliales* and the three genera based on newly generated DNA sequence data.

MATERIALS AND METHODS

Specimens and isolates

Ascomata on *P. latifolius* and *A. falcatus* were collected at several sites in the Western and Eastern Cape Provinces of South Africa (Table 1). Type specimens (holo- and paratypes) of the species studied as well as additional specimens are located at the fungaria of the Royal Botanic Garden, Kew, UK (K(M)), the Swedish Museum of Natural History, Stockholm, Sweden (S), the Museum of Evolution, Uppsala University, Uppsala, Sweden (UPS), the University of Florida Herbarium, Gainesville, Florida, USA (FLAS) and of the Plant Pathology Herbarium, Cornell University, Ithaca, New York, USA (CUP). Specimens, or high resolution photos of specimens, were obtained from these herbaria. The newly collected specimens including holotype specimens of new species were deposited in the National Collection of Fungi, Pretoria, South Africa (PREM). Isolates of *Caliciopsis* spp. from the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, the Netherlands were included as well. All descriptions are based on holo- or epitypes. Features of additional specimens are included, if they deviate from the type specimens. Host plant nomenclature follows currently accepted names according to The Plant List (http://www.theplantlist.org) and the African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an).

DNA extraction, amplification and analysis

Genomic DNA was isolated from fungal ascomata scraped from the surface of leaves or fruits and grinded with a mortar and pestle in liquid nitrogen, following the protocol of Lee & Taylor (1990). The 5.8S ribosomal gene with the two flanking internal transcribed spacers (ITS-1 and ITS-2), a partial sequence of the 28S rDNA gene (LSU) and of the 18S rDNA gene (SSU) were amplified and sequenced using the primer pairs ITS-1F (Gardes & Bruns 1993) + ITS-4 (White et al. 1990), NL1 + NL4 (O'Donnell 1993), and NS1 + NS8 (White et al. 1990), respectively, as well as NS4, NS5, NS2, and NS3 as internal sequence primers for SSU (White et al. 1990). The novel sequences were added to sequences obtained from GenBank (http://www.ncbi.nlm.nih.gov) using the megablast function, including the SSU sequence AF242262 which is derived from a specimen that had also been collected from South Africa (Winka 2000), and ITS and SSU sequences of *Corynelia uberata* from *Afrocarpus falcatus* from a recent study in Ethiopia (Assefa et al. 2014). Three alignments were made: SSU and LSU separately for higher order placement and ITS for species identification and placement. The alignments were assembled and manually adjusted using Sequence Alignment Editor v. 2.0a11 (Rambaut 2002). Phylogenetic analyses were performed using PAUP v. 4.0b10 (Swofford 2003). Alignment gaps were treated as 'fifth base' and all characters were unordered and of equal weight. Maximum parsimony analyses were performed using the heuristic search option with 100 random sequence additions and tree-bisection-reconstruction (TBR) as the branch-swapping algorithm. Branches of zero length were collapsed and all multiple, equally parsimonious trees were saved. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications with 100 random sequence additions (Hillis & Bull 1993). Other measures including tree length, consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were also calculated. Gaps in the SSU alignment longer than 10 bp were coded as single indels. Sequences derived in this study were lodged at GenBank (Table 1), and the alignments and derived trees in TreeBASE.

Morphology

Observations were made with a Zeiss V20 Discovery stereomicroscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and an AxioCam MRc5 camera and ZEN software. Measurements and photographs were made from structures mounted in clear lactic acid, derived from 30 observations (×1 000 magnification) unless otherwise stated, with the extremes given in parentheses. The terminology of Minter (2006a) was used for descriptions.

RESULTS

Phylogenetic analysis

The SSU sequence alignment contained 39 sequences (including the outgroup) and 1 257 characters (968 characters constant, 103 variable and parsimony-uninformative, 186 cha-

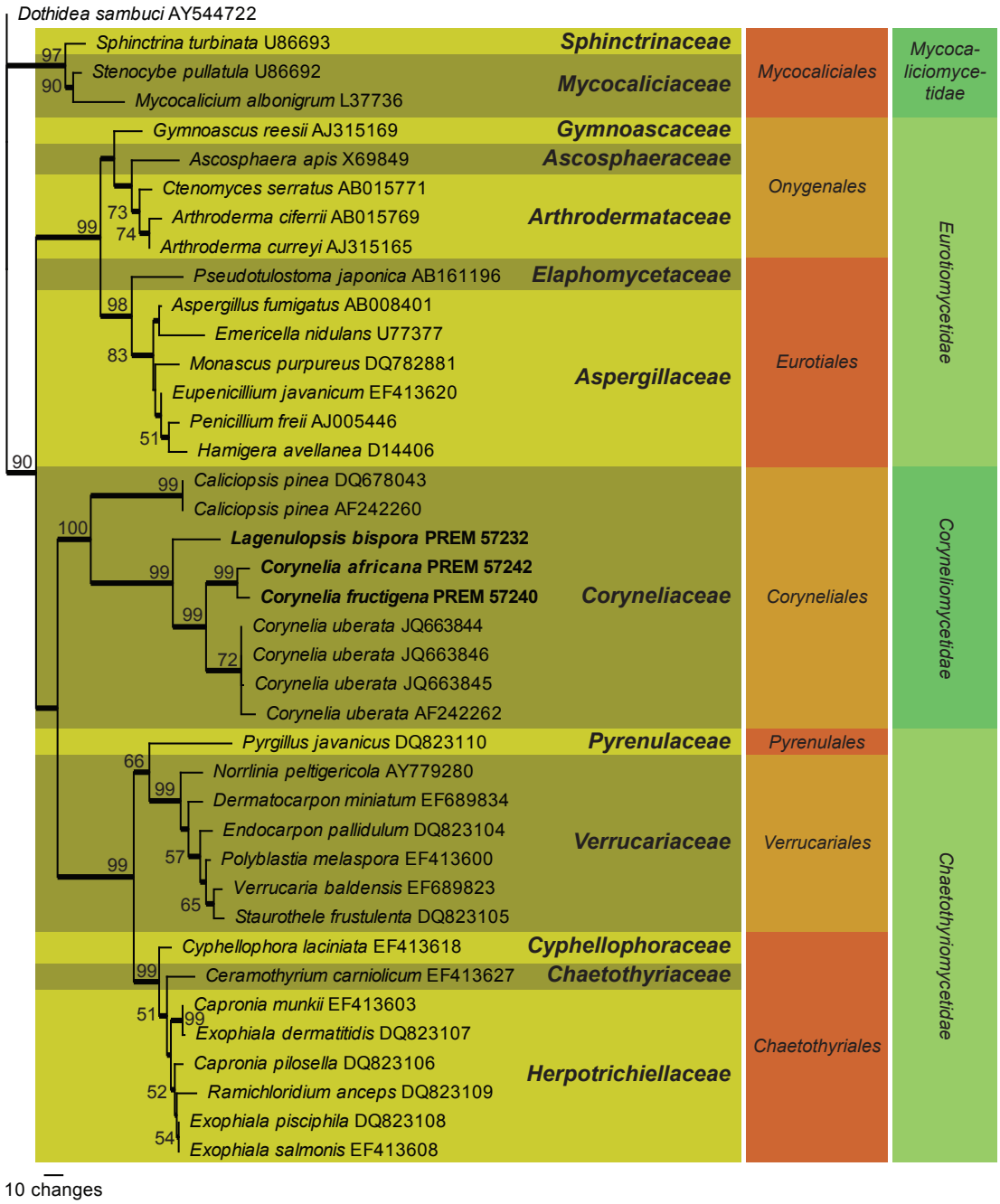

Fig. 1 The first of two equally most parsimonious trees obtained from the SSU sequence alignment. Branches present in the strict consensus tree are thickened and novel sequences generated in this study are shown in **bold** face. The subclass, order and family (from right to left) of the included species are shown to the right of the tree using blocks of different colours. Bootstrap support values > 50 % based on 1 000 replicates are shown at the nodes. The scale bar indicates 10 changes and the tree was rooted to *Dothidea sambuci* (GenBank AY544722).

racters parsimony-informative) and the heuristic search resulted in two equally most parsimonious trees (TL = 621 steps, CI = 0.604, RI = 0.861, RC = 0.520, HI = 0.396), of which one is shown in Fig. 1. The two trees differed only with regard to the position of *Monascus purpureus* (GenBank DQ782881) in the *Aspergillaceae*. Within the *Coryneliales* clade, the sequences of *C. uberata* group together (72 % bootstrap), with *C. africana* and *C. fructigena* (99 % bootstrap support) as sister lineages (99 % bootstrap support). *Lagenulopsis bispora* clustered basal to the *Corynelia* spp. (99 % bootstrap support). *Caliciopsis pinea* represents the most basal species in the *Coryneliales* (100 % bootstrap support). The *Coryneliales/Coryneliomycetidae* formed a strongly supported sister clade (100 % bootstrap support) to *Chaetothyriomycetidae* and *Eurotiomycetidae*, representing a separate subclass; not clustering (bootstrap support < 50 %) with either of them, but with closer affinities to *Chaetothyriomycetidae* than to *Eurotiomycetidae*.

Twelve equally most parsimonious trees (TL = 904 steps, CI = 0.446, RI = 0.686, RC = 0.306, HI = 0.554) (Fig. 2) were generated from the LSU alignment consisting of 35 sequences (including the outgroup) and 536 characters, of which 291 were constant, 47 variable and parsimony-uninformative, and 198 parsimony-informative. The trees differed mainly with regard to the position of genera in the *Chaetothyriomycetidae* and the *Aspergillaceae*. Species of *Corynelia* clustered together with high support (100 % bootstrap support) and had as more basal sister species *Tripospora tripos* and *Lagenulopsis bispora*. Similar to the SSU phylogeny, *Caliciopsis* represented the most basal lineages in the *Coryneliales/Coryneliomycetidae* (100 % bootstrap support). The *Coryneliomycetidae* clustered with the

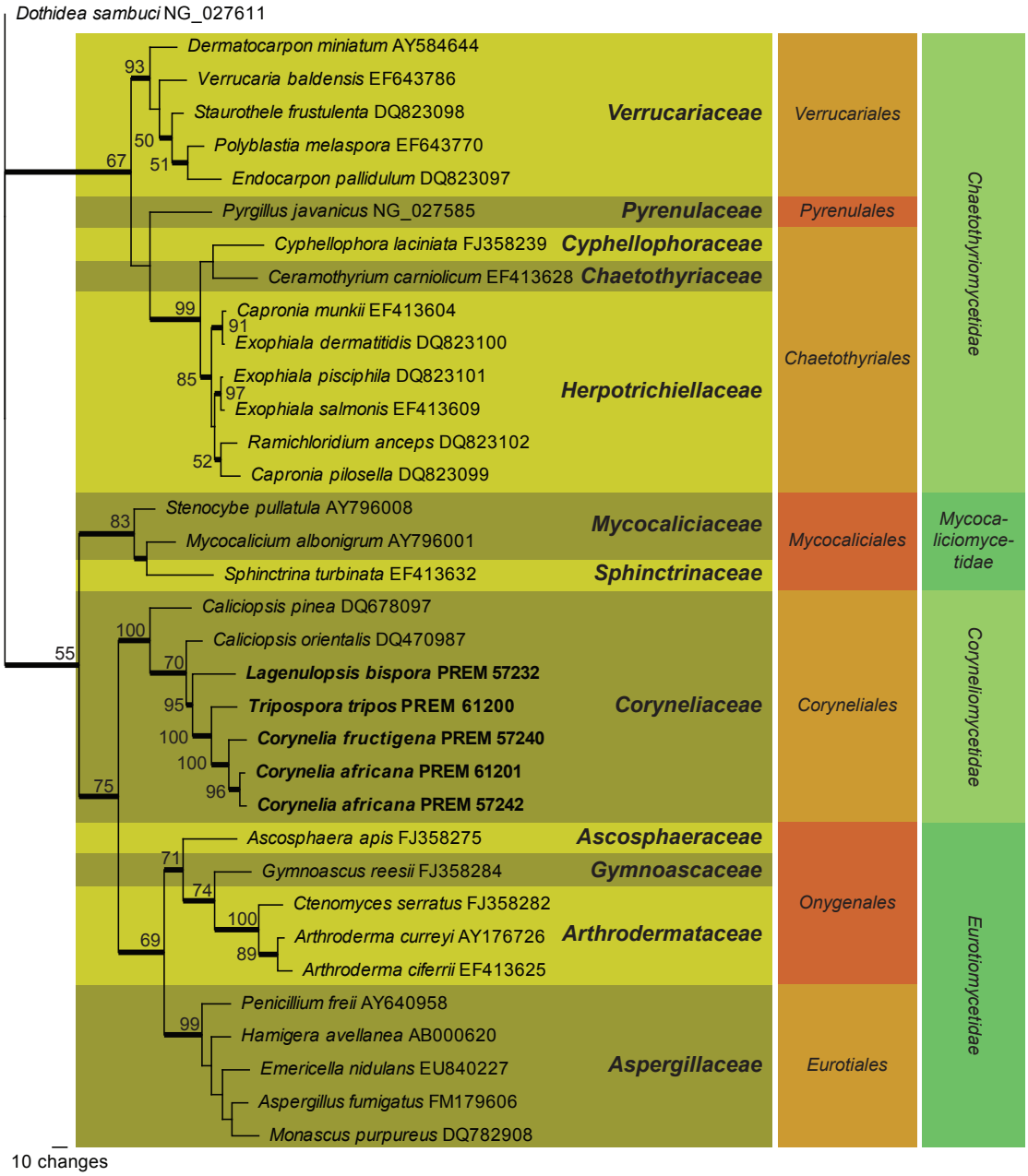

Fig. 2 The first of 12 equally most parsimonious trees obtained from the LSU sequence alignment. Branches present in the strict consensus tree are thickened and novel sequences generated in this study are shown in **bold** face. The subclass, order and family (from right to left) of the included species are shown to the right of the tree using blocks of different colours. Bootstrap support values > 50 % based on 1 000 replicates are shown at the nodes. The scale bar indicates 10 changes and the tree was rooted to *Dothidea sambuci* (GenBank NG_027611).

Eurotiomycetidae with low bootstrap support (75 %) forming a sister clade to the *Mycocaliciaceae*.

The ITS sequence alignment contained 42 sequences (including the outgroup) and 495 characters (239 constant, 56 variable and parsimony-uninformative, and 200 parsimony-informative characters) and the heuristic search resulted in three equally most parsimonious trees (TL = 549 steps, CI = 0.761, RI = 0.921, RC = 0.701, HI = 0.239), of which the first is shown in Fig. 3. The three trees differed mainly in the order of strains belonging to the same species. The *Corynelia* strains studied here clustered in three distinct clades, one of which is identified as *C. uberata* (100 % bootstrap support) and two clades for which the names *C. fructigena* (88 % bootstrap support) and *C. africana* (96 % bootstrap support) are proposed below. These latter two clades clustered with available sequences of *C. portoricensis* and *C. tropica*, all of which formed a sister clade to *C. uberata* s.str. The *C. africana* clade contained one sequence from GenBank (accession JX968551) which was deposited in the database as *C. uberata* from *P. latifolius* in South Africa. The *C. uberata* clade recognised in the present study contains several sequences from GenBank: JX968546, JF811342, JF811343, JF811344, and JN998125 from *A. gracilior* (as *P. falcatus*) trees in Ethiopia, JF895471 from *P. latifolius* in South Africa, and JX968544 and JX968545 from *Podocarpus* sp. in Kenya. The remaining isolates included in this study represented *Lagenulopsis bispora* (100 % bootstrap support) and *Tripospora tripos* (100 % bootstrap support).

Morphology

The ascomatal stromata and fertile extensions observed were as described previously (Fitzpatrick 1920, 1942a, Benny et al. 1985b, c, Minter 2006a, b). There were however small differences noticed in ascomatal shape and ascospore size between specimens initially identified as *C. uberata*. These differences

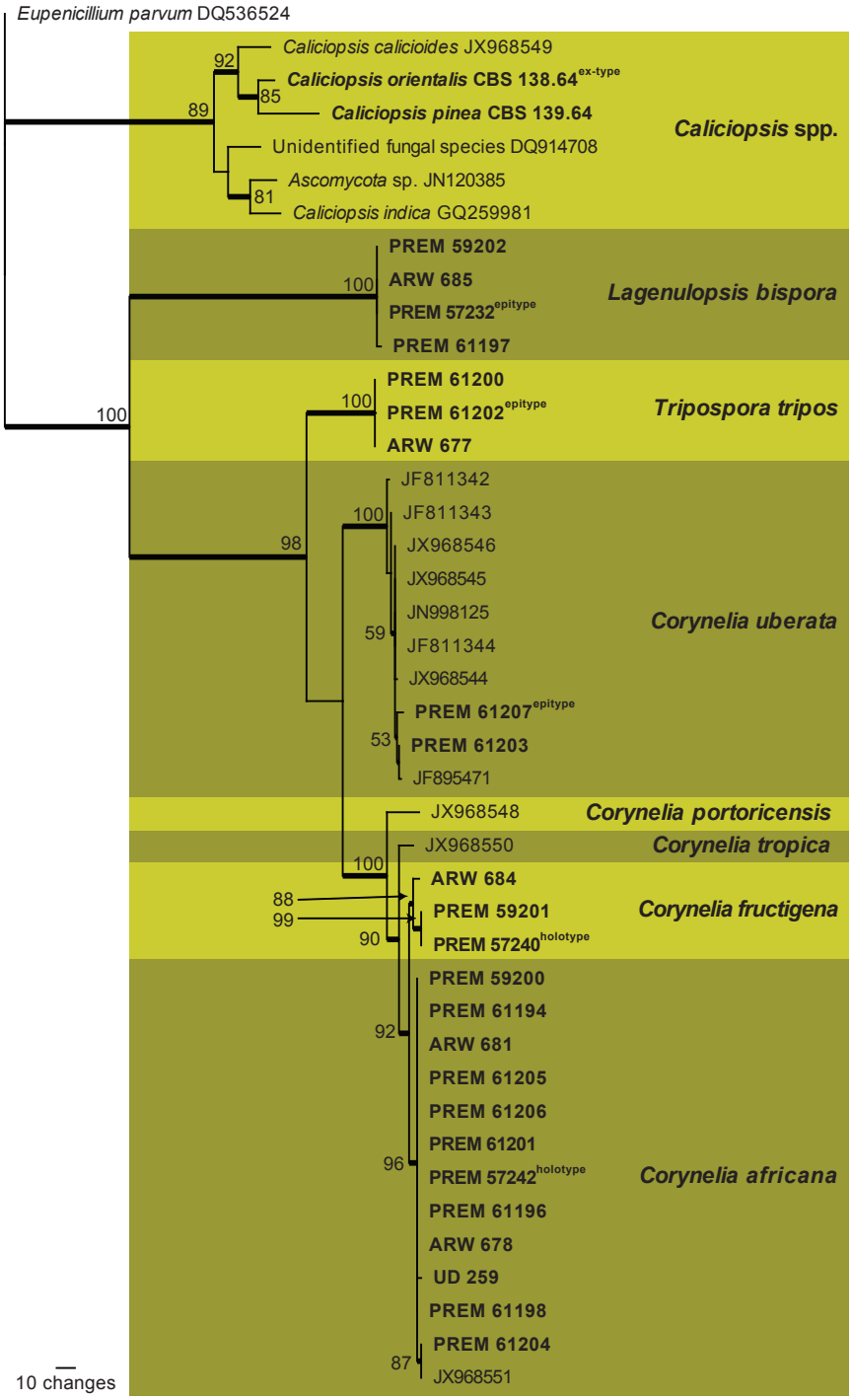

Fig. 3 The first of three equally most parsimonious trees obtained from the ITS sequence alignment. Branches present in the strict consensus tree are thickened and novel sequences generated in this study are shown in **bold** face. The species names are shown to the right of the tree and specimen or GenBank accession numbers are shown at the leaves. Bootstrap support values > 50 % based on 1 000 replicates are shown at the nodes. The scale bar indicates 10 changes and the tree was rooted to *Eupenicillium parvum* (GenBank DQ536524).

were consistent with the host species or organ on which the fungi were collected (Fig. 4) and corresponded to consistent differences in the molecular analysis using the rDNA ITS region (Fig. 3). Therefore, two new species are described below.

Fresh specimens of *C. uberata* and the two species here described were examined and found to have asci with uniformly thick walls when immature, which broke down with maturity, as described by Johnston & Minter (1989) and interpreted by them as bitunicate. The asci with developing spores were frequently observed to also have a thick wall structure surrounding them (Fig 5), which in progressively more developed asci was seen as breaking or thinner and eventually was not visible on asci ready to liberate the ascospores, as illustrated by Minter (2006a). Fully mature asci had only a thin wall. Young asci of *Lagenulopsis bispora* and *Tripos tripospora* were observed to also have a uniformly thick wall, presumably bitunicate, whereas mature asci were all thin-walled (Fig. 10).

Taxonomy

Coryneliomycetidae A.R. Wood, Damm, J.Z. Groenew., Cheew. & Crous, *subclass. nov.* — MycoBank MB814491

Type order. Coryneliales Seaver & Chardón (1926).

Mostly plant pathogenic and usually biotrophic, with internal mycelium that is early erumpent producing coriaceous to car-

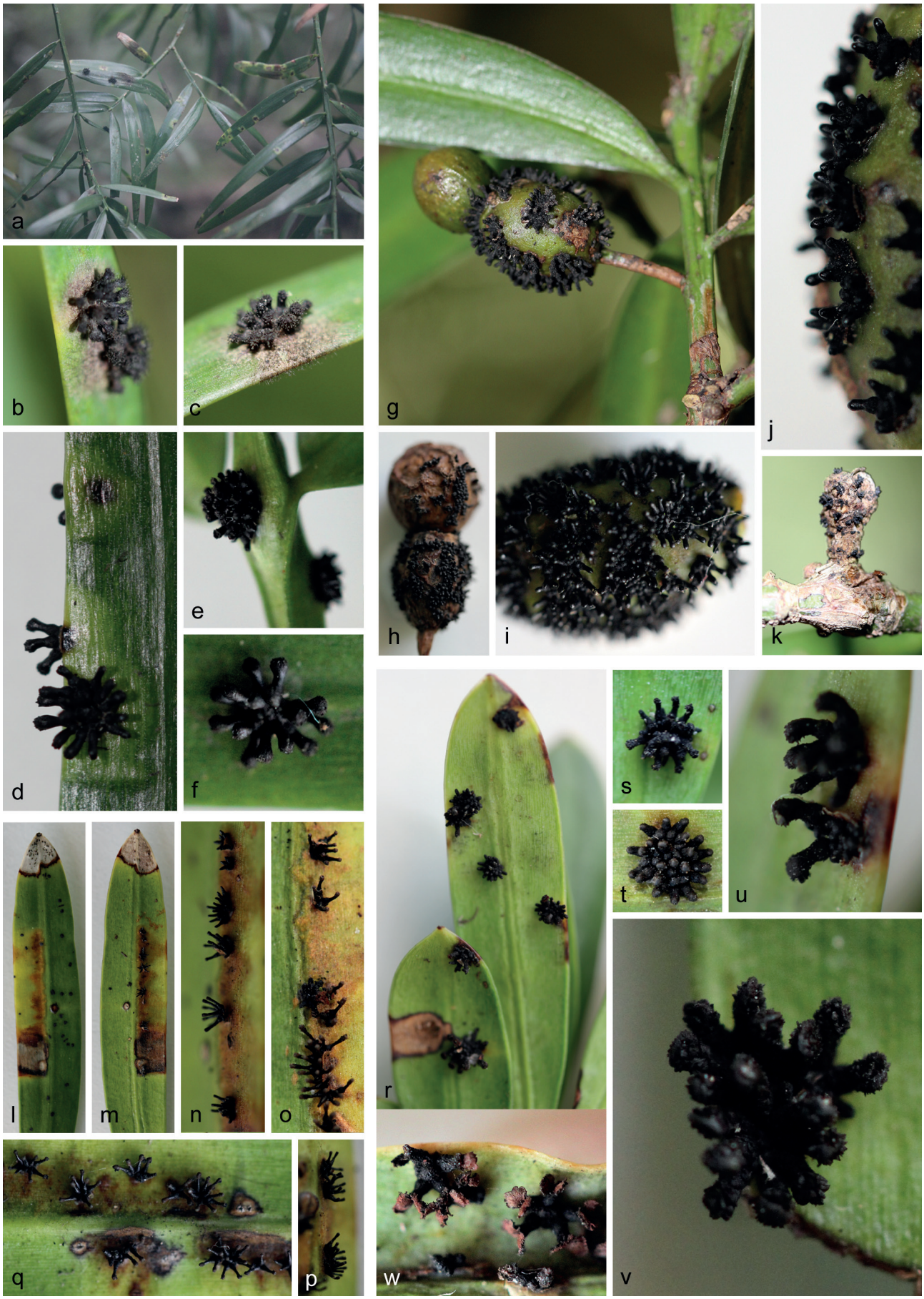

Fig. 4 a–f. *Corynelia uberata* on *Afrocarpus falcatus*. a. In habit; b, c. stromata with *Neodevriesia coryneliae*; d–f. stromata on leaves and stems showing dumbbell-shaped ascomata. — g–k. *Corynelia fructigena* on *Podocarpus latifolius* fruit. g. In habit, infected fruit persistent on trees; h. often only the podocarpium is infected, but the seed can also be infected; i, j. flask-shaped ascomata; k. occasional infected fruit several years old occur. — l–q. *Lagenulopsis bispora* on *Podocarpus latifolius* leaves. l. Adaxial surface showing chlorotic area associated with stromata; m. abaxial surface of same leaf showing stromata; n–q. smooth narrowly flask-shaped ascomata. — r–w. *Corynelia africana* on *Podocarpus latifolius* leaves. r. In habit; s, t. flask-shaped immature ascomata; u. mature ascomata with pronounced curvature; v. mature ascomata with shaggy appearance at dehiscence; w. fully opened ascomata showing wide clefts at tips.

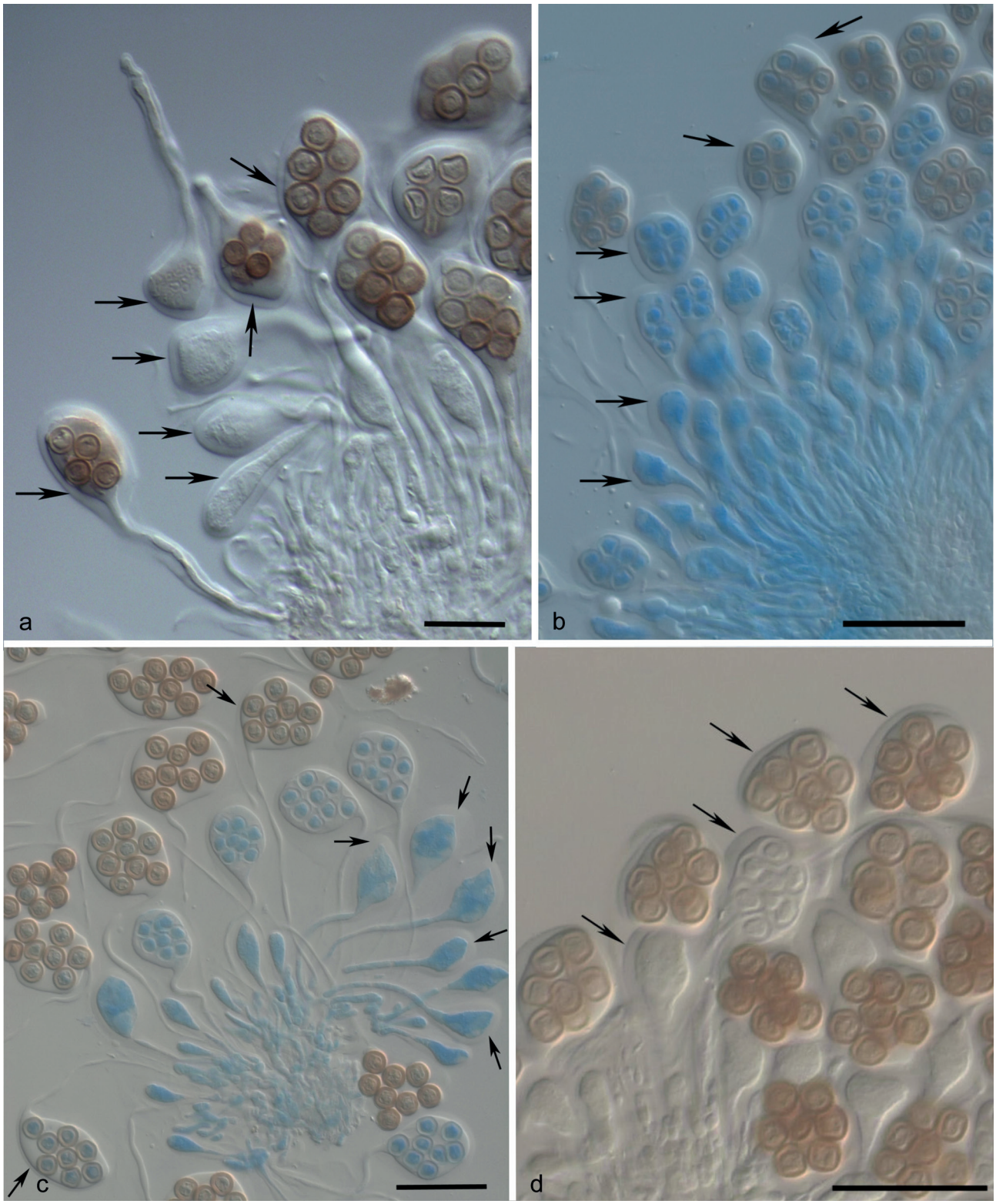

Fig. 5 Immature asci showing thick walls which are interpreted as bitunicate. a. *Corynelia uberata*; b. *Corynelia fructigena*; c, d. *Corynelia africana*. Arrows indicate thick-walled immature asci as well as more developed ones with remnants of the bitunicate wall still attached. — Scale bars = 50 µm.

bonaceous stromata. *Stromata* reduced or cushion-like, developing to variously shaped loculate fertile extensions that form ascomata or spermogonia. *Spermogonia* sessile, with minute ostiole, spermatia unicellular, elongate, hyaline. *Ascomata* clustered or individual, pseudothecial, with a mazaedial chamber above the ascus-bearing base, black, thick- and smooth or rough-walled, opening by an ostiole or dehiscence grooves. *Interascal tissue* absent. *Asci* clavate, spathulate to capitate, mostly 8-spored or 2–3-spored, initially thick double-walled, the outer layer breaking and sloughing away with elongation, becoming long-stalked and thin-walled, without apical release mechanism, evanescent. *Ascospores* aseptate, dark, variable, smooth-walled to prominently ornamented, aggregating in a mass above the ascus layer. Sexual propagules do not germinate in culture.

Coryneliales Seaver & Chardón, Sci. Surv. Porto Rico & Virgin Islands 8: 40. 1926

Type family. *Coryneliaceae* Sacc. (1886).

Characters as for subclass.

Coryneliaceae Sacc., in Berl. & Voglino, Syll. Fung., Addit. I–IV (Abellini): 193. 1886

Type genus. *Corynelia* Ach. (1823).

Characters as for subclass.

Notes — The phylogenetic position of the *Coryneliales*, being variable and not closely associated with any of the three existing subclasses within the *Eurotiomycetes* (Fig. 1, 2) necessitated the establishment of the new subclass, *Coryneliomycetidae.* This new subclass is also supported by unique morphological features. While *Eurotiomycetidae* form cleistothecia/gymnothecia with usually evanescent, unitunicate asci and *Chaetothyriomycetidae* mostly perithecia with bitunicate/fissitunicate to evanescent asci (Geiser et al. 2006, Hibbett et al. 2007), *Coryneliomycetidae* form pseudothecial mazaedial ascomata with initially double-walled asci with the outer layer deliquescing, without an apical release mechanism resulting in passive ascospore release (Johnston & Minter 1989), and produce spermogonia (Geiser et al. 2006). The subclass *Coryneliomycetidae* consists of a single order with a single family only.

Corynelia Ach., in Fr., Syst. Mycol. (Lundae) 2: 534. 1823

Type species. *Corynelia uberata* Fr. (1818).

Phytopathogenic on *Podocarpaceae*. *Stromata* subcircular or elongated, coalescing, black, often crowded, bearing fertile extensions as ascomata or spermogonia. *Spermogonia* may or may not be present, if present globose, ovoid or irregularly compressed, sessile, loculate, with minute ostiole, spermatia unicellular, elongate, hyaline. *Ascomata* formed inside stromatic tissue then extending beyond the stromata as variously shaped cylindrical extensions, black, shiny, roughened, rather uniform, straight or slightly curved, rounded at base and tip, or constricted in the middle giving the ascomata a dumbbell shape, apex with a dehiscence zone splitting either along a single transverse groove or along several radiating grooves resulting in 2–several apical lobes, transverse groove may be indistinguishable; interior a locule, the lower portion containing the asci and the distal portion free ascospores. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled which is interpreted as a double wall (bitunicate) bounding an interior mucilaginous layer,

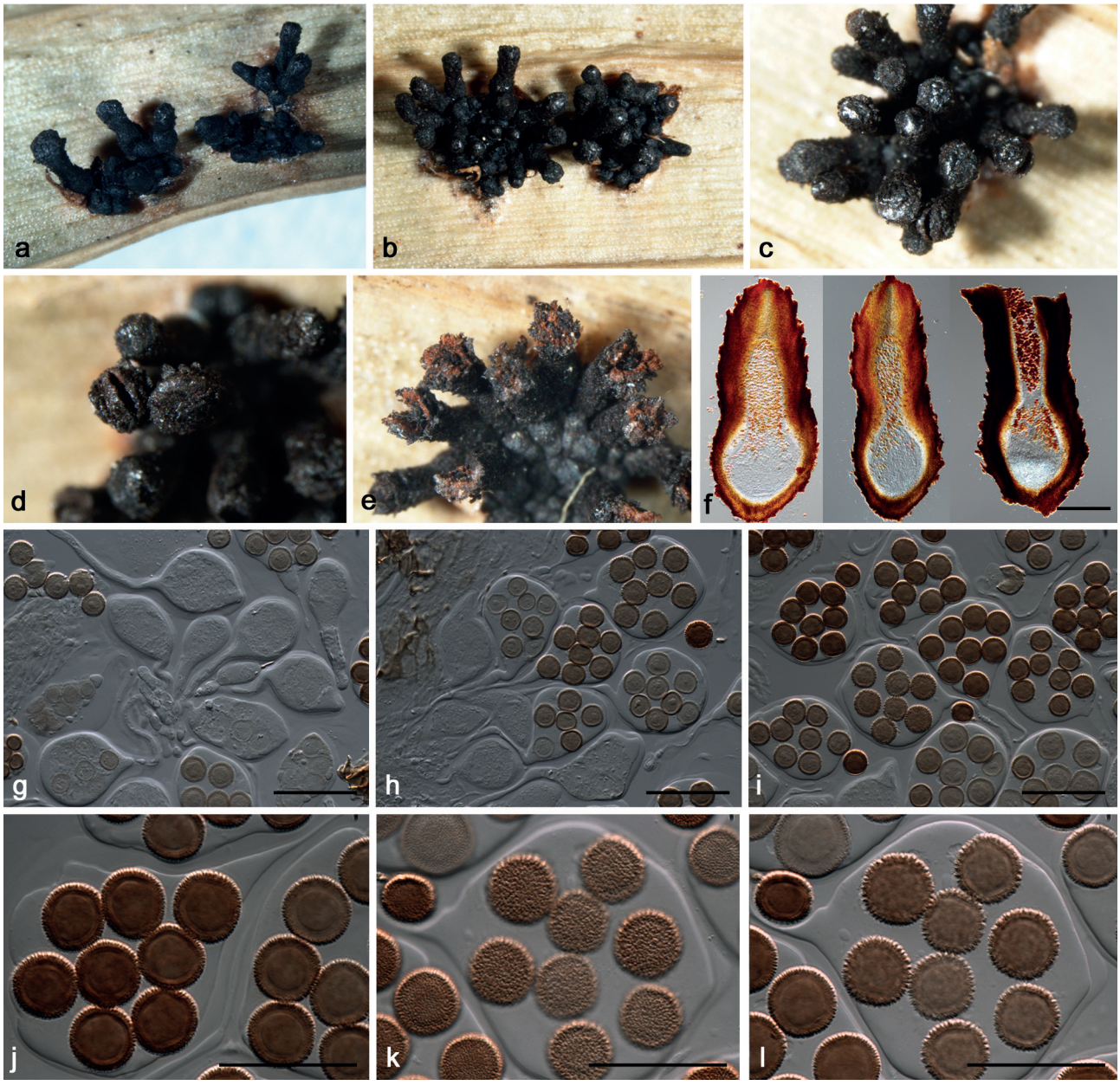

Fig. 6 Paratype of *Corynelia africana* (PREM 59200). a–e. Stomata with ascomata variously shaped and in different stages of dehiscence; f. mid-line transverse sections through ascomata; g–j. asci with eight ascospores; k. verrucose ascospores with focus on spore surface; l. verrucose ascospores with focus at the midline of the spores. — Scale bars: f = 1.5 mm; g–i = 50 µm; j–l = 30 µm.

clavate and short-stalked; as asci mature the stalk elongates, later spatulate to capitate, long-stalked, mature asci thin-walled which is interpreted as only the inner wall remaining after rupturing and passive loss of the outer wall and mucilaginous layer, mostly 8-spored or 3-spored, arranged in clusters. *Ascospores* at first hyaline, then becoming dark brown, unicellular, with thin outer wall and thick inner wall, smooth or warted.

Corynelia africana A.R. Wood, Van der Linde, Cheew. & Crous, *sp. nov.* — MycoBank MB814492; Fig. 4, 5, 6

Etymology. Named for the continent from where it has been collected.

Type. South Africa, Western Cape, Grootvadersbosch Nature Reserve, W of Heidelberg, on *Podocarpus latifolius*, 20 Nov. 2000, *A.R. Wood* 247 (holotype PREM 57242).

Diagnosis. Differs from *Corynelia uberata* by its larger (13–16(–18) µm) and prominently warted ascospores.

Colonies on attached green living leaves, occasionally stems, scattered, black, conspicuous, often on both sides of leaf, 1–13 colonies on each infected leaf; colonies breaking through leaf surface and producing erumpent stromata. *Stromata* subcircular or elongate, sometimes coalescing, black, few to more than 20 crowded fertile extensions mature to ascomata or spermogonia. *Spermogonia* usually preceding the ascomata, intermixed or developed on separate stromata. *Ascomata* vertical or, more often, irregularly arranged, pointing to sides from stromatic cushion, formed inside stromatic tissue and elongating as cylindrical extensions of the stromata, black, shiny, roughened, variable in shape, initially flask-shaped but tending to more or less distinctly dumbbell-shaped at maturity, rounded at base and apex, straight or slight constriction in middle, sometimes at maturity bending below the apex so that the apex is at an angle to the base and neck, 0.9–1.5 × 0.3–0.45 mm at base, 0.2–0.3 mm at neck and 0.23–0.45 mm at apex; immature ascomata present little indication of a dehiscence zone at the apex, not

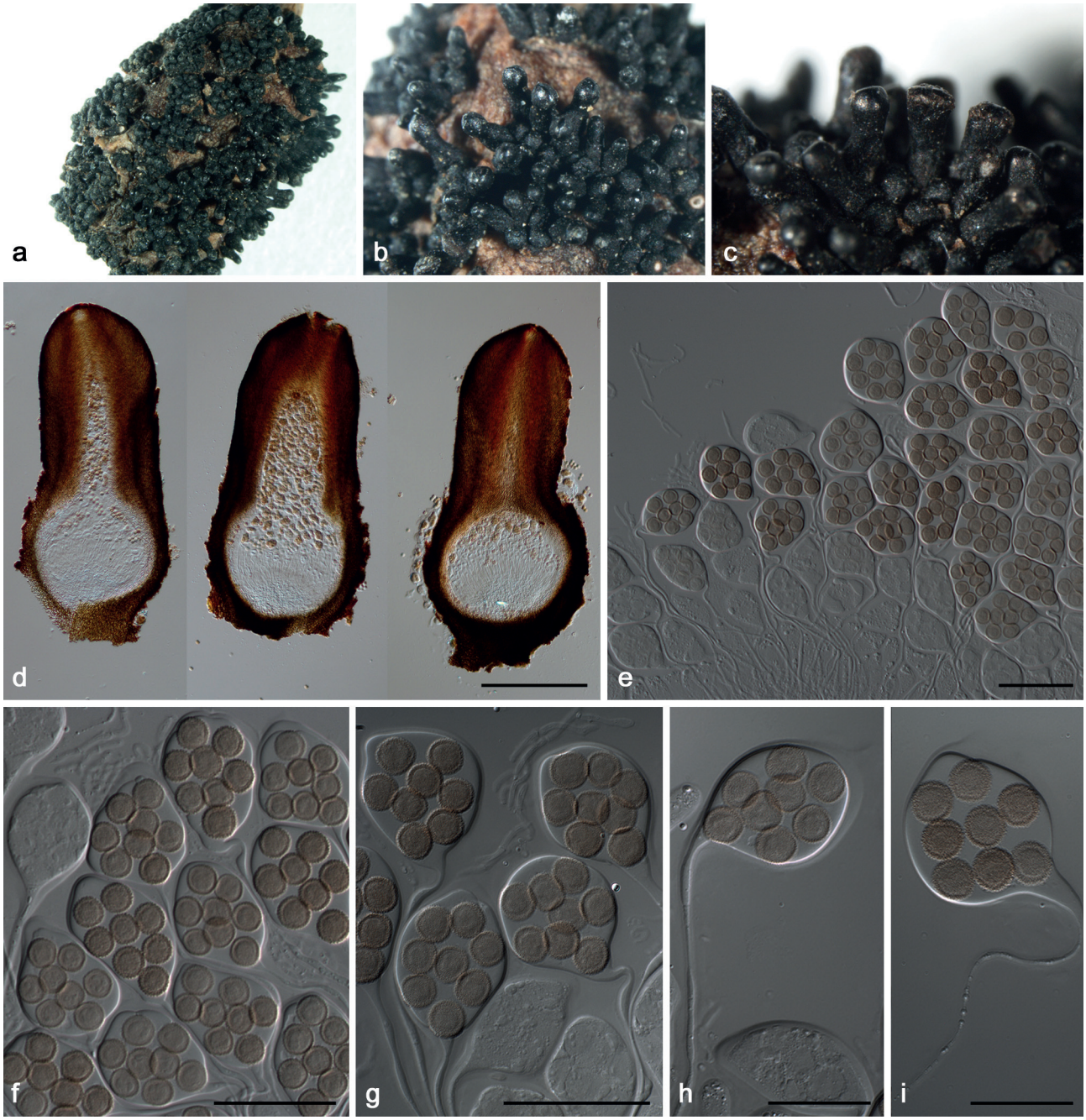

Fig. 7 Paratype of *Corynelia fructigena* (PREM 59201). a. Infected podocarpium; b, c. flask-shaped ascomata; d. mid-line transverse sections through ascomata; e–i. asci with eight ascospores. — Scale bars: d = 1.5 mm; e–g = 50 µm; h–i = 30 µm.

processing a true ostiolum, tip becomes shaggy in appearance at dehiscence, dehiscence via a wide, deep, single, transverse cleft which separates the tip of each ascoma into two broad sections, light brown on interior of sections; interior a locule, the lower portion globose containing the asci and the distal portion free ascospores; ascomatal wall composed chiefly of interwoven hyphae of *textura intricata*. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, then as ascus matures stalk elongates, mature ascus spatulate to capitate, pointed at the apex and long-stalked, the homogenous thick wall breaks and is lost during maturation of the asci so that mature asci are thin-walled, (38–)47–55(–67) × (45–)57–65(–75) µm, stalk up to 90 µm long, usually 8-spored, arranged in a cluster. *Ascospores* at first hyaline, then becoming dark brown, unicellular, globose, prominently warted, 13–16(–18) µm.

Other material examined. South Africa, Western Cape, Grootvadersbosch Nature Reserve, W of Heidelberg, on *Podocarpus latifolius*, 17 Oct. 2004, *A.R. Wood* 656 (PREM 59200); Krisjan-se-Nek picnic site, Goudveld Forest, Garden Route National Park, N of Knysna, on *P. latifolius*, 15 July 2006, *A.R. Wood* 683 (PREM 61206); Jubilee Creek picnic site, Goudveld Forest, Garden Route National Park, N of Knysna, on *P. latifolius*, 15 July 2006, *A.R. Wood* 681 (whole specimen used for molecular analysis); same locality, on *P. latifolius*, 15 July 2006, *A.R. Wood* 682 (PREM 61205); Woodcutter trail, Millwood, Goudveld Forest, Garden Route National Park, N of Knysna, on *P. latifolius*, 5 June 2000, *A.R. Wood* 194 (PREM 57235); Terblans walk, Gouna Forest, Garden Route National Park, N of Knysna, on *P. latifolius*, 30 Aug. 2000, *A.R. Wood* 225 (PREM 57244); same locality, on *P. latifolius*, 14 July 2006, *A.R. Wood* 678 (PREM 61201); Kranshoek picnic site, Harkerville Forest, Garden Route National Park, E of Knysna, on *P. latifolius*, 14 July 2006, *A.R. Wood* 675 (PREM 61198); Perdekop walk, Harkerville Forest, Garden Route National Park, E of Knysna, on *P. latifolius*, 14 July 2006, *A.R. Wood* 673 (PREM 61196); Garden of Eden, Garden Route National Park, E of Knysna, on *P. latifolius*, 14 July 2006, *A.R. Wood* 671 (PREM 61194); Eastern Cape, approx. 4 km S of Grahamstown, on *P. latifolius*, 27 Jan. 2000, *A.R. Wood* 164 (PREM 57236); same locality, on *P. latifolius*, 18 July 2006, *A.R. Wood* 688 (PREM 61204).

Notes — *Corynelia africana* has the largest ascospores (13–16(–18) µm) of the three species considered here, as well as the most prominently warted ascospores. Its ascocarps are the most variable in shape, ranging from flask-shaped (especially when still immature) to prominently dumbbell-shaped (usually when the apices have dehisced). However, the width of the apex is never as broad as *C. uberata* can become. The apex tends to be the shaggiest in appearance, has the deepest dehiscence cleft, and in some specimens the opening ascomata curve over below their apices approximating a right angle. The majority of specimens collected on leaves and stems of *P. latifolius* and other species of African and Madagascan *Podocarpus* spp. (African subclade *fide* Knopf et al. 2012), and previously morphologically identified as *C. uberata*, likely belong to this species. These hosts include *P. elongatus*, *P. henkelii*, *P. madagascariensis*, and *P. milanjianus* (Minter 2006a).

Corynelia fructigena A.R. Wood, Van der Linde, Cheew. & Crous, *sp. nov.* — MycoBank MB814493; Fig. 4, 5, 7

Etymology. Named for its preference to infect the fruit of its hosts.

Type. South Africa, Western Cape Province, at information centre, Grootvadersbosch Nature Reserve, W of Heidelberg, on fruit of *Podocarpus latifolius*, 20 Nov. 2000, *A.R. Wood* 250 (holotype PREM 57240).

Diagnosis. Differs from *Corynelia uberata* by smooth flask-shaped ascomata and slightly larger ascospores (11.5–13.5 µm).

Colonies on attached fruits or sometimes leaves, scattered, black, conspicuous, not found on stems, colonies breaking through fruit surface and producing erumpent stromata. *Stromata* subcircular, coalescing to form longer colonies, often crowded, black, with fertile extensions which mature into ascomata that are vertical or irregularly arranged. *Spermogonia* not observed. *Ascomata* formed inside stromatic tissue and elongating as cylindrical extensions of the stromata, black, shiny, smooth, rather uniform and distinctly flask-shaped, only slightly constricted in the middle, straight or slightly curved, rounded at tip, 0.7–1.1 mm × 0.28–0.42 mm at base, 0.2–0.25 mm at neck and 0.16–0.3 mm at apex; immature ascomata present no indication of a dehiscence zone at the apex, not possessing a true ostiolum, ascomata remain closed for long periods, opening via an inconspicuous, shallow, single transverse cleft which separates into two sections; interior a locule, the lower portion globose containing the young asci and the distal portion free ascospores; ascomatal wall is composed mainly of interwoven hyphae of *textura intricata*. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, stalk elongates as asci mature, later spatulate to capitate, pointed at the apex and long-stalked; thin-walled in mature asci, 33–38(–44) × 50–58 µm, stalk up to 200 µm, mostly 8-spored, arranged in a cluster. *Ascospores* at first hyaline, then becoming dark brown, unicellular, with thin outer wall and thick inner wall, minutely warted, 11.5–13.5 µm.

Other material examined. South Africa, Western Cape Province, at information centre, Grootvadersbosch Nature Reserve, W of Heidelberg, on fruit of *Podocarpus latifolius*, 17 Oct. 2004, *A.R. Wood* 657 (PREM 59201); Krisjan-se-Nek picnic site, Goudveld Forest, Garden Route National Park, N of Knysna, on one leaf of *P. latifolius*, 14 July 2006, *A.R. Wood* 684 (whole specimen used for molecular analysis); Garden of Eden, Garden Route National Park, E of Knysna, on fruit of *P. latifolius*, 14 July 2006, *A.R. Wood* 672 (PREM 61195).

Notes — *Corynelia fructigena* differs from *C. uberata* (ascospores 9–12 µm, ascomata rough dumbbell-shaped) in having slightly larger ascospores (11.5–13.5 µm), and smooth flask-shaped ascomata. It differs from *C. africana* (ascospores 13–16(–18) µm, ascomata shaggy flask to dumbbell-shaped) in the slightly smaller ascospores and ascomata shape. It is possible that the majority of specimens collected on fruit of *P. latifolius* and other species of African and Madagascan *Podocarpus* species (African subclade *fide* Knopf et al. 2012), and previously identified morphologically as *C. uberata*, represent this species, though it may apparently also occasionally infect leaves. Unfortunately, specimens on fruit were infrequently observed and sequences were not obtained from some of the few specimens collected. This is in contrast to the observation by Phillips (1927) at the beginning of the 20th century that infection was, at least in some years, abundant and widespread.

H. Rehm distributed specimens under the name *C. clavata* f. *fructicola* (Ascomyceten no. 1326a) collected by P. MacOwan near Somerset East (South Africa, Eastern Cape; S F205134, S F205137/8/9) (Rehm 1900), however this name was never validly published. The name *C. fructicola* cannot be used as this binomial is pre-occupied by *C. fructicola* (Pat.) Höhn. (current name for this fungus is *Coryneliospora fructicola* (Pat.) Fitzp.).

Corynelia uberata Fr., Observ. Mycol. (Havniae) 2: 343. 1818. — Fig. 4, 5, 8, 9

(binomial sanctioned in Syst. Mycol. 2: 535. 1823)

non *Corynelia clavata* (L.f.) Sacc., in Berl. & Voglino, Syll. Fung., Addit. I–IV (Abellini): 193 (1886). Illegitimate name, the basionym used (*Mucor clavatus* L.f.) is a synonym of *Sphinctrina turbinata* (Pers.) De Not.

Type. South Africa, Western Cape Province, 'in Sylvis Houtniquas' (in forests on the Outeniqua mountains), on *Afrocarpus falcatus*, 1772, *C.P. Thunberg s.n.* (holotype UPS:BOT:F-005148 ex Herb E. Fries; consisting of one small piece of leaf with two stromata, which was taken from Thunberg's original collection UPS-Thunb 27440 & UPS:BOT:F-118557 (both numbers given to the same specimen); isotype S F38997); Krisjan-se-Nek picnic site, Goudveld forest, Garden Route National Park, N of Knysna, on *Afrocarpus falcatus*, 15 July 2006, *A.R. Wood* 686 (epitype PREM 61207, MBT202696).

Fig. 8 a. C.P. Thunberg's specimen of *Corynelia uberata* (UPS-Thunb 27440 & UPS:BOT:F-118557), the host is *Afrocapus falcatus*, inserts show the names the fungus was assigned by various people: *Sphaeria capitata* (now *Elaphocordyceps capitata*), *Calicium* (= *Lichen*) *helopherus* and *Mucor clavatus* (now *Sphinctrina turbinata*); b. locality recorded on the reverse of this specimen 'in Sylvis Houtniquas et Grootvadersbosch. Thunberg'; c. close up of this specimen showing stromata; d. holotype of *Corynelia uberata* (UPS:BOT:F-005148); e, f. close up of the holotype showing one immature and one mature stromata.

Colonies on green living leaves, scattered, black, conspicuous, often on only one side of leaf, sometimes on both sides, also often found on stems and fruit, 1–18 colonies on each infected leaf, colonies breaking through leaf surface and producing erumpent stromata. *Stromata* subcircular or elongated, black, with crowded fertile extensions which mature to ascomata or spermogonia, basal part of stroma composed of brown thick-walled cells. *Spermogonia* globose, usually preceding the ascomata. *Ascomata* formed inside stromatic tissue and elongating as cylindrical extensions of the stromata, distinctly dumbbell-shaped with upper and lower portions rounded and constricted in the middle, black, shiny, roughened, vertical or irregularly arranged, 0.7–1.1 × 0.3–0.36 mm at base, 0.19–0.23 mm at neck and 0.27–0.65 mm at apex; walls undifferentiated, composed of *textura angularis* or *prismatica* along the inner layer surrounding an internal locule in which asci are produced at the base and distal to which is a funnel-shaped chamber where released ascospores accumulate leading to the opening; lacking a true perithecial wall, immature ascomata present little indication of a dehiscence zone on the apex, a true ostiolum absent, dehiscence by a single transverse cleft which separates into two sections, the cleft deepening slowly and not opening outwards. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, then the stalk elongates so that the asci become spatulate to capitate, pointed at the apex and long-stalked, the apparently homogenous thick wall breaks and is lost during elongation and maturation so that mature asci are uniformly thin-walled, 33–36(–39) × 50–55(–57) µm, stalk up to 220 µm, usually 8-spored, occasionally fewer ascospores in asci, arranged in a cluster. *Ascospores* at first hyaline, then becoming dark brown, unicellular, with thin minutely warted outer wall and thick smooth inner wall, ascospores of specimen S F38997 (isotype) measure (8–)9–11 µm diam (Ibai Olariaga Ibarguren, Naturhistoriska Riksmuseet, Stockholm (S), pers. comm.; 10–11 µm diam *fide* Saccardo 1886), those of PREM 61207 (epitype) measure 11–12 µm diam.

Other material examined. South Africa, Western Cape Province, Grootvadersbosch Nature Reserve, W of Heidelberg, on *Afrocarpus falcatus*, 20 Nov. 2000, *A.R. Wood* 246 (PREM 57243); Jubilee creek picnic site, Goudveld forest, Garden Route National Park, N of Knysna, on *A. falcatus*, 15 July 2006, *A.R. Wood* 680 (PREM 61203); Ysterhoutrug picnic site, Diepwalle forest, Garden Route National Park, N of Knysna, on *A. falcatus*, 14 July 2006, *A.R. Wood* 676 (PREM 61199); Terblans trail, Gouna forest, Garden Route National Park, N of Knysna, on *A. falcatus*, 30 Aug. 2000, *A.R. Wood* 224 (PREM 57239); Woodcutter trail, Millwood, Goudveld Forest, Garden Route National Park, N of Knysna, on *A. falcatus*, 5 June 2000, *A.R. Wood* 187 (PREM 57237).

Notes — The identity of the host plant of the Thunberg specimen is *A. falcatus* (Fig. 6), *C. uberata* is thus confirmed as occurring on *A. falcatus* in southern Africa and on *A. gracilior* in northern Africa (Assefa et al. 2014, 2015), but is likely to also occur on other species of *Afrocarpus* in Africa. Specimens previously identified as *C. uberata* but occurring on other host

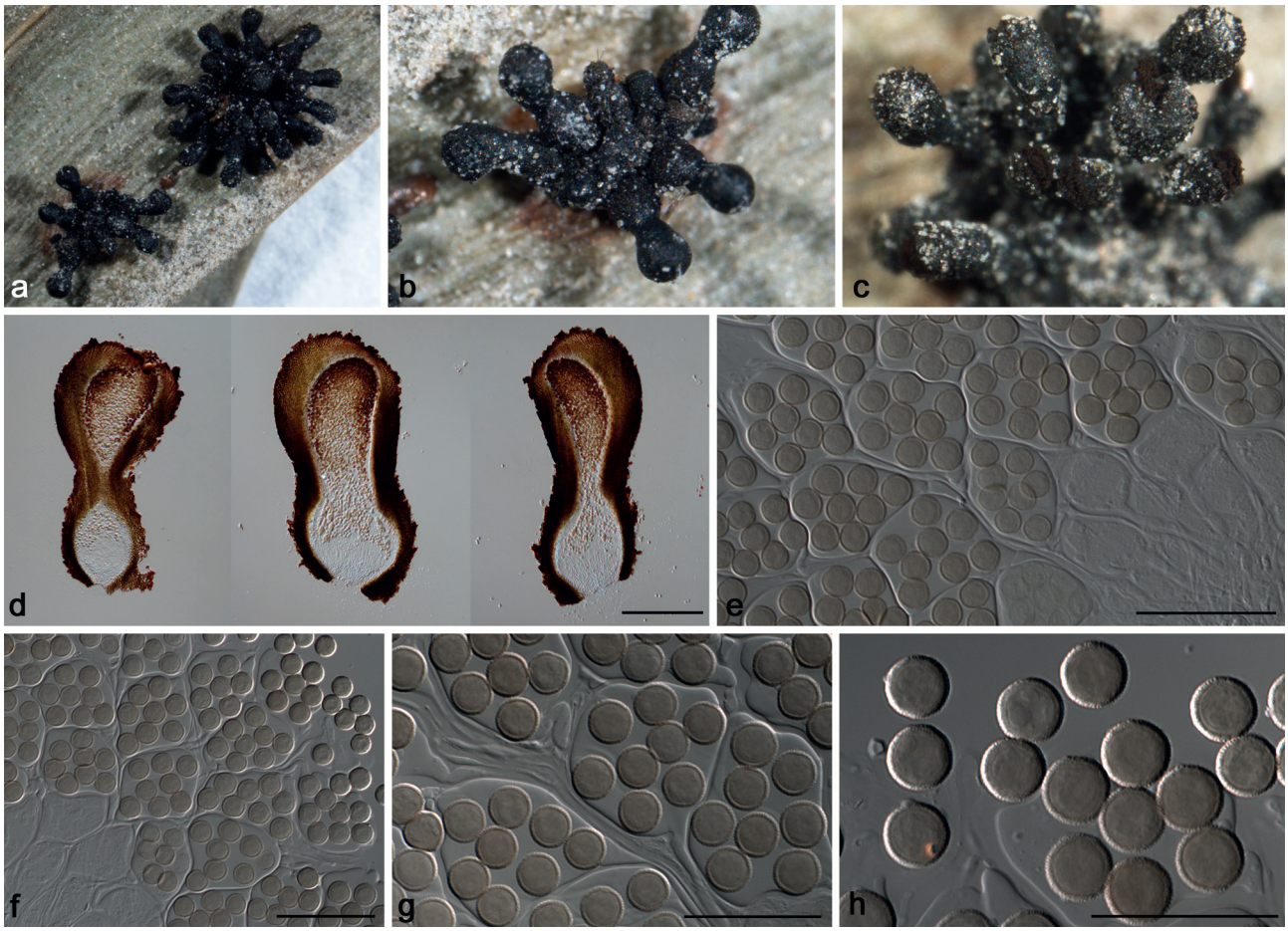

Fig. 9 Epitype of *Corynelia uberata* (PREM 61207). a–c. Stromata with dumbbell-shaped ascomata; d. mid-line transverse sections through ascomata; e–g. asci with 8 ascospores; h. minutely warted ascospores. — Scale bars: d = 2.5 mm; e–g = 50 µm; h = 30 µm.

genera and on continents other than Africa are likely to be other as yet undescribed species. The comprehensive description provided by Minter (2006a) refers to this species as well as the two described above. All three have similar morphology, the distinguishing characteristics are discussed under each.

Neodevriesia corynelia is frequently associated with stromata of this fungus (Fig. 4) (Crous et al. 2014), but has not yet been observed as occurring on stromata of the new species described above.

When establishing the family *Coryneliaceae*, Saccardo used the earliest epithet of the names associated with this fungus by various authors, namely *Mucor clavatus*. Thus this fungus was referred to as *C. clavata* for many years. However, *M. clavatus* is now recognised as a synonym of *Sphinctrina turbinata*, a lichen (www.mycobank.org). Thus the first epithet given which has both a valid description and a type specimen is *C. uberata*. Fitzpatrick (1920) gives a full account of the various names associated with this fungus. *Corynelia clavata* Mont. is a synonym of *Caliciopsis clavata* (Fitzpatrick 1942b).

Lagenulopsis Fitzp., Mycologia 34: 487. 1942

Type species: *Lagenulopsis bispora* (Fitzp.) Fitzp. (1942).

Phytopathogenic on *Podocarpus. Stromata* subcircular, sometimes coalescing, black, fertile extensions become ascomata or spermogonia. *Spermogonia* sessile, ovoid, loculate, with a minute apical perforation; spermatia unicellular, oblong to fusiform, hyaline. *Ascomata* formed inside stromatic tissue then extending beyond the stroma, black, smooth, shiny, crowded, narrowly flask-shaped, with a flat to slightly rounded tip, dehiscence by an apical pore through which ascospores are extruded appearing as a reddish brown knob, interior a locule, the lower rounded portion containing the developing asci and a distal long narrow neck with free ascospores; ascomatal wall composed mainly of interwoven hyphae of *textura intricata*. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, later spatulate to capitate and long-stalked, pointed at the apex and long-stalked, mature asci thin-walled, mostly 2-spored at maturity. *Ascospores* at first hyaline, then becoming dark brown, unicellular, with thin outer wall and thick inner wall.

Lagenulopsis bispora (Fitzp.) Fitzp., Mycologia 34: 488. 1942 — Fig. 10, 11

Basionym. *Corynelia bispora* Fitzp., Mycologia 12: 242. 1920.
≡ *Corynelia clavata* (L.f.) Sacc. f. *macrospora* Syd., Wiss. Ergebn. Deut. Zentr.-Afr.-Exped. (1907–1908), Bot. 2: 100. 1910.

Type. Uganda, Ruwenzori, west Butagu Thal., on *Podocarpus milanjianus*, Feb. 1908, *J. Mildbraed* 2547 (holotype S F51449). – South Africa, Western Cape Province, Grootvadersbosch Nature Reserve, Heidelberg, on *P. latifolius*, 20 Nov. 2000, *A.R. Wood* 249 (epitype PREM 57232, MBT202697).

Colonies on attached green living leaves, often associated with an angular chlorotic area of leaf, colonies breaking through leaf surface and producing an erumpent stroma, often on only one side of leaf, 1–10 colonies on each infected leaf, not found on stems. *Stromata* subcircular, small, several apparently originating from a single infection, sometimes coalescing, forming longer colonies aligned with the main axis of substratum, black, 2–5(–8) × (2–)5–12 mm, with few to crowded fertile exten-

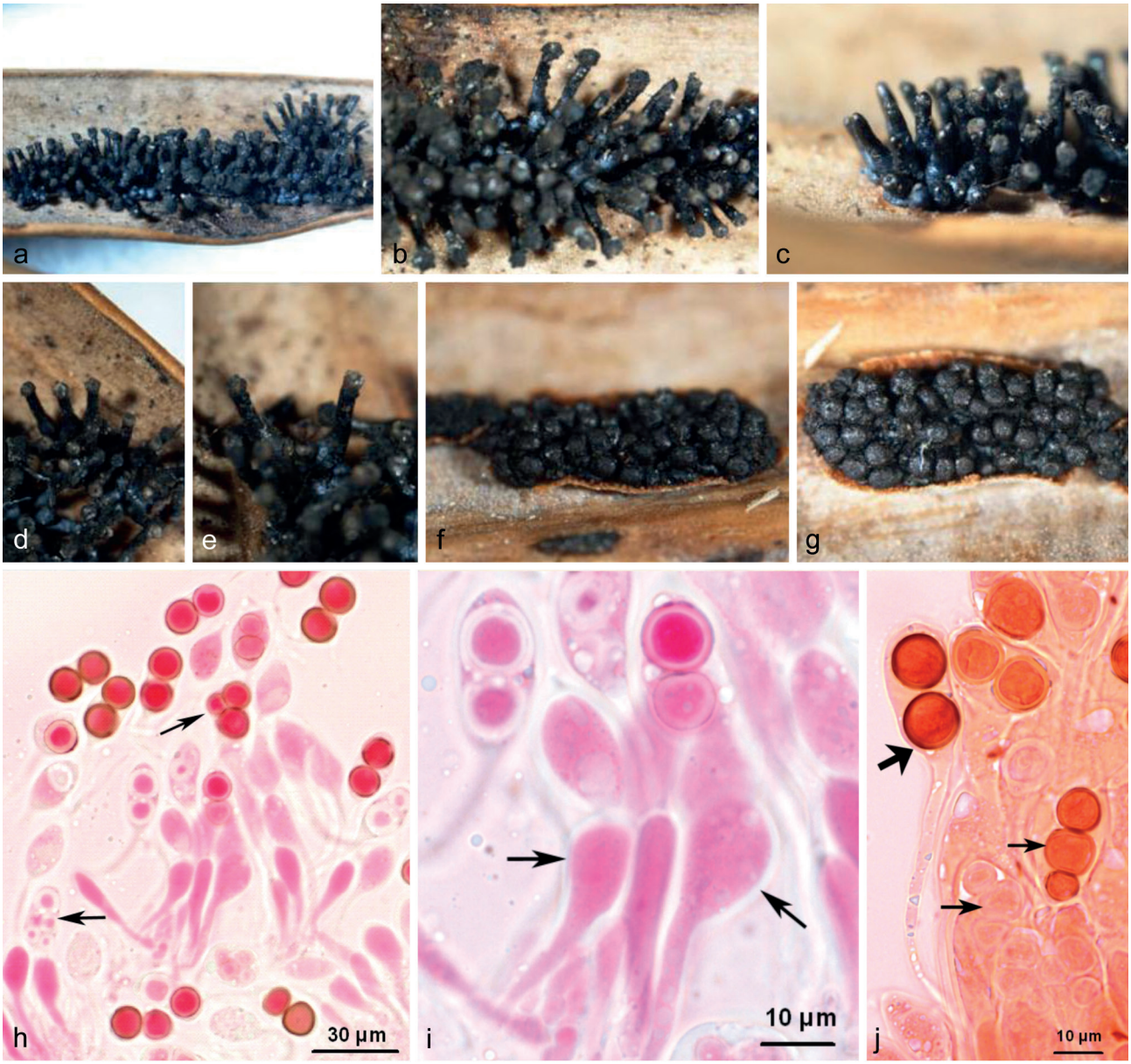

Fig. 10 *Lagenulopsis bispora*. — a–g. Holotype of *Lagenulopsis bispora* (S F51449). a. Stroma; b–e. narrow flask-shaped ascomata; f, g. immature stroma. — h–j. Epitype of *Lagenulopsis bispora* (PREM 57232). h. Asci, some with more than 2 ascospores (arrows); i. immature asci with thick bitunicate walls (arrows); j. asci, some with more than two ascospores (arrows) and a thin-walled mature ascus (thick arrow). — Scale bars: h = 30 µm; i–j = 10 µm.

sions which mature to ascomata or spermogonia. *Spermogonia* usually preceding the ascomata, intermixed, sessile, with a minute apical perforation; spermatia unicellular, minute, oblong to fusiform, hyaline. *Ascomata* formed inside stromatic tissue and elongating as cylindrical extensions of the stroma, 1–29 extensions per stromatum, black, smooth, shiny, flask-shaped with a glabrous, shiny, narrow neck, usually more than twice as long as it is wide, straight or slightly curved, with a flat to slightly rounded tip, 0.9–1.7 × 0.23–0.4 mm at base, 0.12–0.19 mm at middle of the neck and 0.17–0.24 mm at apex, dehiscence by a pore, the spore mass forming a powdery, reddish brown knob at the tip of the ascomata; interior a locule, the lower portion globose containing the asci and the long narrow distal portion the free ascospores; the ascomatal wall is composed mainly of interwoven hyphae of *textura intricata*. *Paraphyses* not observed. *Asci* arising from a basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, the stalk elongates, becoming spatulate to capitate, pointed at the apex and long-stalked, mature asci thin-walled, 15–19 × 35–55 µm, stalk up to 150 µm long, 2-spored when mature but sometimes up to 5-spored when immature. *Ascospores* at first hyaline, then becoming dark brown, unicellular, with thin outer wall and thick inner wall, minutely warted or smooth once released, 10–15 µm, wall 1–2.5 µm thick.

Other material examined. Cameroon, Western Province, Bafut-Ngem F.R., on *P. latifolius* (as *P. milanjiana*), no date, *M. Brunt* 827 (K(M) 154329). – Fiji, Nausori highlands, 2000 ft altitude, on *P. neriifolius*, together with *Corynelia braziliensis*, 3 July 1973, *de Laubenfels s.n.* (FLAS-F53225). – Jamaica, Newhaven Gap, Cinchona, on *P. urbanii*, 6 Mar. 1906, *W. Harris* 9199 (CUP 31753). – South Africa, Eastern Cape Province, ± 4 km SW of Grahamstown, on *P. latifolius*, 27 Jan. 2000, *A.R. Wood* 163 (PREM 57231); Western Cape Province, Terblans trail, Gouna forest station, Knysna, on *P. latifolius*, 30 Aug. 2000, *A.R. Wood* 223 (PREM 57230); Redwood trail, Grootvadersbosch nature reserve, Heidelberg, on *P. latifolius*, 17 Oct. 2004, *A.R. Wood* 655 (PREM 59202); Krisjan-se-Nek picnic site, Goudveld Forest, Garden Route National Park, N of Knysna, on *P. latifolius*, 15 July 2006, *A.R. Wood* 685 (whole specimen used for molecular analysis); Kranshoek picnic site, Harkerville Forest, on *P. latifolius*, 14 July 2006, *A.R. Wood* 674 (PREM 61197). – Tanzania, Mbulu, Masai District, on *P. latifolius* (as *P. milanjiana*), Jan. 1953, *Procter* 133 (K(M) 154330).

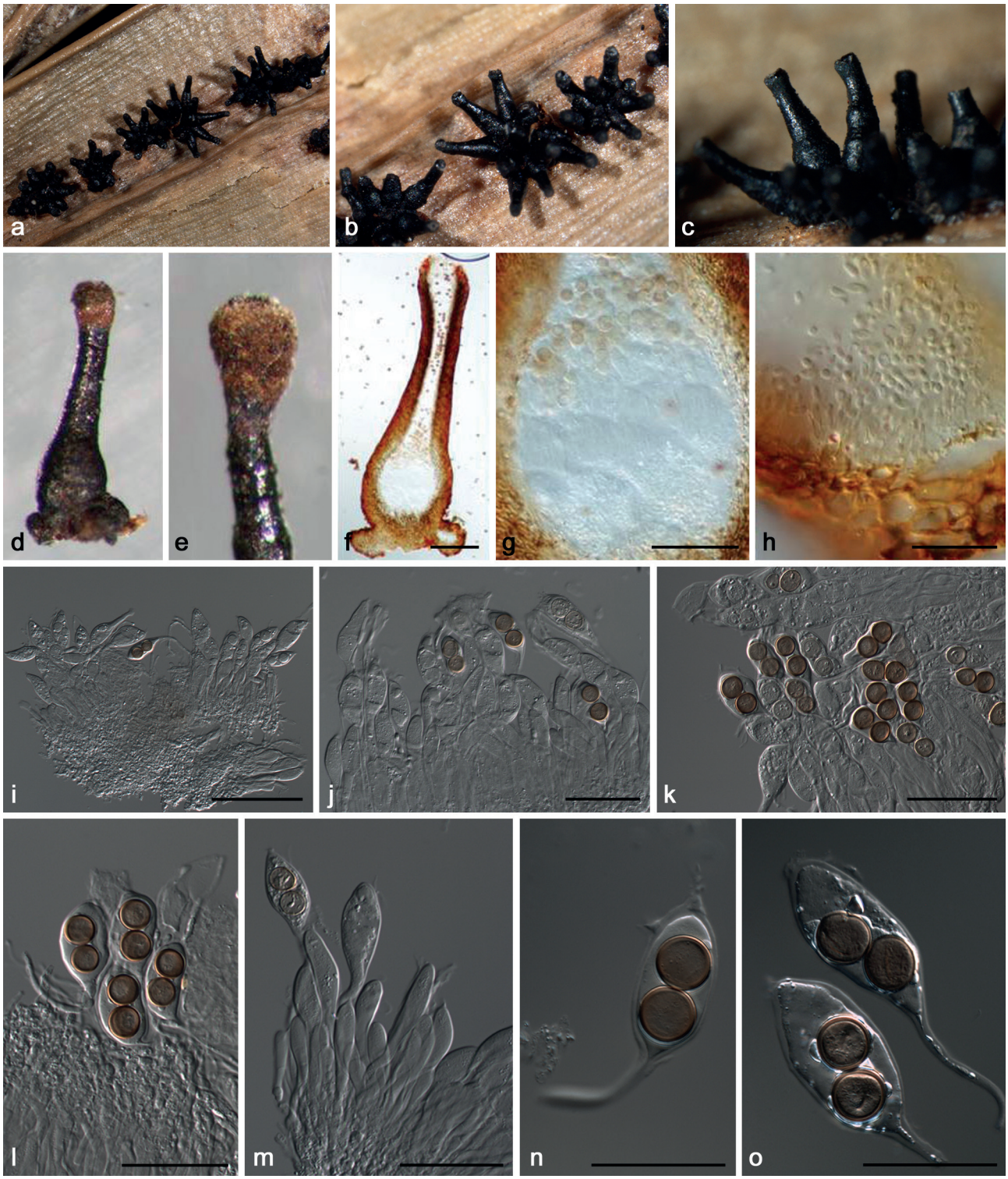

Fig. 11 *Lagenulopsis bispora*. — a–c, i–o. *Lagenulopsis bispora* (PREM 59202); d–h. epitype of *Lagenulopsis bispora* (PREM 61192). a. Stromata; b, c. ascomata; d. ascoma; e. head of an ascoma; f. mid-line transverse sections through an ascoma; g. transverse section through base of an ascoma; h. transverse section through a spermogonium; i–m. asci; n, o. ascospores in asci. — Scale bars: f = 2 mm; g = 1 mm; h = 200 µm; i = 100 µm; j–m = 50 µm; n–o = 30 µm.

Notes — The above description is based on South African material. However, Jamaican material differed from all the African specimens in the dimensions of the spores observed being slightly larger, broadly ellipsoidal to subspherical and slightly thicker-walled. Ascospores of the Jamaican specimen (CUP 31753) were 14–(mean 16.5)–19 × 11–(mean 13.3)–14(–16) µm, length : width ratio 1 : 1–(mean 1.3)–1.6 and wall 2–(mean 2.2)–3 µm thick (n = 20), whereas the equivalent measurements for the African specimens were 10–(mean 13)–15 × 10–(mean 12.5)–14 µm, length : width ratio 1 : 1–(mean 1.1)–1.3 and wall 1–(mean 1.6)–2.5 µm thick (n = 60).

A collection from Fiji was also examined (FLAS-F53225); however, on this specimen an unidentified conidial fungus was also present with flask-shaped pycnidia which was similar looking to the ascomata of *L. bispora*, though smaller. Ascospores observed on the apex of the ascomata of the *L. bispora* present were significantly smaller than all other specimens examined, being 8–10 × 6–8 µm and with 1 µm thick walls (n = 10) which were more prominently warted (verrucose). Benny et al. (1985c: f. 7) illustrated this specimen as having encrusted walls. The identity of this specimen is therefore uncertain. Based on these observations, we suspect that the genus *Lagenulopsis* is not

monotypic, but additional specimens and sequences from the Americas and Melanesia are required to resolve this issue.

Young asci typically had two ascospores developing within, though one or three to five ascospores were occasionally observed. Mature asci observed only had two ascospores, or very occasionally one ascospore.

Some released ascospores appeared to have a bilaminate wall, and on others the outer thinner wall was observed to be breaking away from the inner wall and disintegrating. Most released ascospores appeared as having a single smooth wall. On the other hand a bilaminate wall was readily visible on ascospores still within the asci in the ascomatal locules.

Tripospora Sacc., Syll. Fung., Addit. I–IV (Abellini): 194. 1886

Type species. *Tripospora tripos* (Cooke) Lindau (1897).

Phytopathogenic on *Podocarpaceae*. *Stromata* subcircular to elongate, coalescing to form longer colonies parallel to the main axis of substratum, black, often crowded, bearing fertile extensions as ascomata or spermogonia. *Spermogonia* sessile, semi-

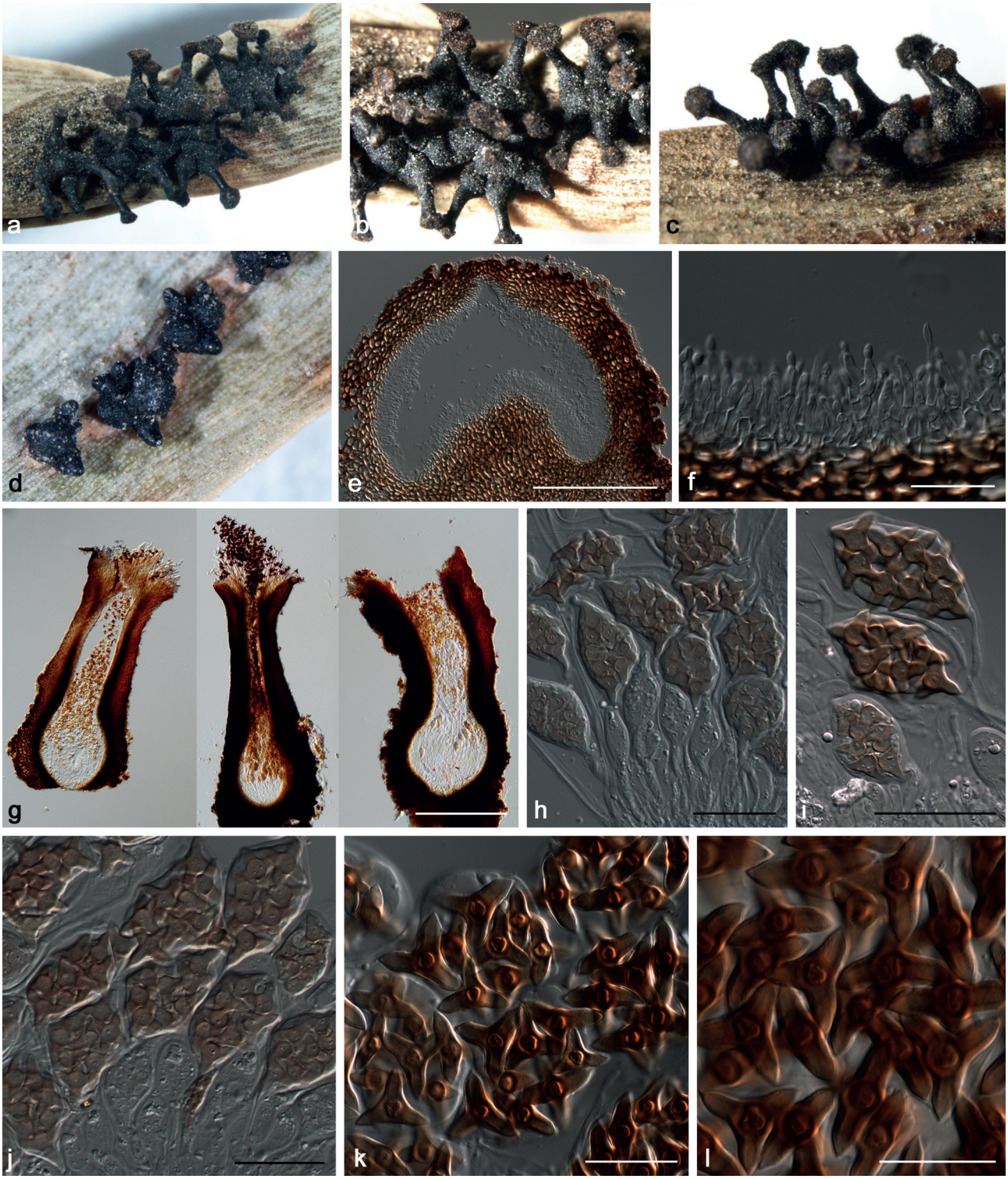

Fig. 12 Epitype of *Tripospora tripos* (PREM 61202). a. Stromata; b, c. ascomata; d. immature stromata; e, f. transverse section through a spermogonium; g. mid-line transverse sections through ascomata; h–k. asci with ascospores at various stages of maturity; n. ascospores. — Scale bars: e = 1 mm; f, h–j = 50 µm; g = 2 mm; k–l = 30 µm.

globose, with a minute, apical perforation; spermatia unicellular, minute, oblong to fusiform, hyaline. *Ascomata* formed inside stromatic tissue then extending beyond the stromata, black, shiny, roughened below, rather uniform, long slender flask or short dumbbell shaped, with glabrous shiny necks, apex rounded before dehiscence, dehiscence by an apical pore, the apex opening widely to become shallow funnel-shaped; interior a locule, the lower portion containing the asci and the distal portion free ascospores; the ascomatal wall is composed mainly of interwoven hyphae of *textura intricata*. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, stalk elongates as ascus matures, becoming subglobose, pointed at the apex and long-stalked, mature asci thin-walled, usually 8-spored, arranged in cluster. *Ascospores* at first hyaline, then becoming dark brown, unicellular, characteristically star-shaped, thick-walled, with 4 short or long conical sharp-pointed projections radiating from a rounded central portion.

Tripospora tripos (Cooke) Lindau in Engler & Prantl., Nat. Pflanzenfam., Teil. I (Leipzig) 1: 413. 1897 — Fig. 12

Basionym. *Corynelia tripos* Cooke, Grevillea 8: 34. 1879.

≡ *Tripospora cookei* Sacc. in Berl. & Voglino, Syll. Fung., Addit. I–IV (Abellini): 194. 1886.

Type. South Africa, Eastern Cape Province, near Somerset East, Cape of Good Hope, on leaves of *Afrocarpus falcatus* (as *Podocarpus elongatus*), *P. Mac-Owan* 1253 (holotype K(M) 137581 ex. herb. M.C. Cooke; syntypes K(M) 137582, K(M) 198323/4/5, S-F14549, S-F14550, S-F61022, BPI 629688, PREM 20983 all ex. Rabenh. Wint. Fung. Eur. 3150); Western Cape Province, at Gouna forest station, Garden Route National Park, N of Knysna, on *Afrocarpus falcatus*, 14 July 2006, *A.R. Wood* 679 (epitype PREM 61202, MBT202698).

Colonies on attached green living leaves and occasionally stems, scattered, black, conspicuous, often on only one side of leaf, sometimes on both sides, 1–15 colonies on each infected leaf, colonies producing erumpent stromata. *Stromata* subcircular when bearing 1–3 fertile extensions, otherwise undergoing further vertical elongation, coalescing to form longer colonies aligned with the main axis of substratum, black, 2–5(–8) × (2–)5–10(–18) mm, with crowded fertile extensions which mature into ascomata or spermogonia, *Spermogonia* usually preceding the ascomata, some lying among them or developed on separate stromata, ovoid. *Ascomata* formed inside stromatic tissue and elongating as cylindrical extensions of the stromata, vertical or more often regularly arranged in two lines pointing in opposite directions from the stromatic cushion on either side of spermogonia, black, shiny, roughened below, rather uniform and flask-shaped, lengthening into slender, long cylindrical columns with glabrous shiny necks, constricted in the central portion and usually twice as long as it is wide, straight or slightly curved, 0.5–1.2 × 0.2–0.35 mm; containing an internal locule in which asci are produced in the basal rounded portion and distal to which is a funnel-shaped chamber leading to the apex in which released ascospores accumulate; internal wall of *textura angularis* or *prismatica*, apex rounded before dehiscence, dehiscence by an apical pore, the apex then opening wide forming a convex disc, slightly narrower than ascoma below, disc becoming fimbriate-lacerate, reddish brown, margin recurving to expose paler inner wall of neck, and resulting in formation of broad, funnel-shaped cavity filled with reddish black mass of ascospores. *Paraphyses* not observed. *Asci* arising from basal cushion, maturing sequentially, young asci uniformly thick-walled, clavate and short-stalked, stalk elongates as ascus matures, later subglobose, thin-walled, pointed at the apex and long-stalked, (30–)35–45(–48) × (50–)55–65(–73) µm, stalk up to 230 µm long, usually 8-spored, arranged in a cluster. *Ascospores* at first hyaline, then becoming dark brown, unicellular, characteristically star-shaped, thick-walled, consisting of 4 conical sharp-pointed projections radiating from rounded central portion, (16–)20–27(–31) µm, (measured from tip to tip of adjacent portions), with each spore lobe slightly constricted near the base.

Other materials examined. South Africa, Western Cape Province, at Gouna forest station, Garden Route National Park, N of Knysna, on *A. falcatus*, 30 Aug. 2000, *A.R. Wood* 222 (PREM 57233); Ysterhoutbrug picnic site, Diepwalle forest, Garden Route National Park, on *A. falcatus*, 14 July 2006, *A.R. Wood* 677 (PREM 61200); KwaZulu-Natal, Natal National Botanical Garden, Pietermaritzburg, on *A. falcatus*, 21 Jan. 1999, *A.R. Wood* s.n. (PREM 57234); Natal National Botanical Garden, Pietermaritzburg, on *A. falcatus*, 24 June 2006, *F.H.J. Rijkenberg* s.n. (PREM 61190).

Notes — The only host on which this species was observed in South Africa during the course of this study was *Afrocarpus falcatus* as well as all specimens examined in K, S, and PREM. Therefore records on *P. latifolius* and *P. elongatus* are based on misidentification of the host plant, for example in Doidge (1950), Benny et al. (1985c), and Minter (2006b). This is due to P. MacOwan, the original collector of this species, having incorrectly identified the host of the type specimen as *P. elongatus*, whereas the host plant was in fact *A. falcatus* as determined by examining original specimens (K(M) 137581/2, K(M) 198323/4/5). For some time *P. elongatus* was considered to be a synonym of *P. latifolius*. This fungus has also been recorded on *A. gracilior* and *A. usambariensis* (Minter 2006b), and therefore is restricted to members of *Afrocarpus*. Minter (2006b) and Tim (1971) provide comprehensive descriptions.

In erecting the genus *Tripospora*, P.A. Saccardo renamed *Corynelia tripos* as *T. cookei* (Saccardo 1886), however the epithet published earlier by M.C. Cooke (Cooke 1879) remains valid, and therefore G. Lindau's recombination is retained.

DISCUSSION

There have been several studies that have focused on monographic or morphological studies of the *Coryneliaceae* (Fitzpatrick 1920, 1942a, b, Funk 1963, Tim 1971, Benny et al. 1985a–d, Johnston & Minter 1989). In spite of this, however, the correct taxonomic placement of the *Coryneliales* remains debatable, due to the contradictory characters of having apparently unitunicate asci but ascolocular development (Johnston & Minter 1989). The latter type of ascocarp formation was considered characteristic for fungi with bitunicate asci, whereas fungi with unitunicate asci typically have ascohymenial development. This prompted Tim (1971) to propose a new centrum type, the Corynelioid type, to contrast this group from other fungi within the then recognised pyrenomycetes. This situation was resolved when it was shown that the asci of the *Coryneliales* are in fact bitunicate, but differ from all other types of bitunicate asci in that no modification of the ascus apex is present as a release mechanism, and that the outer wall layer usually breaks during ascus elongation. Between the two wall layers is a thick mucilaginous layer (Johnston & Minter 1989). The unmodified ascus apex results in passive ascospore release typical of the *Coryneliales*. Thus Johnston & Minter (1989) placed the family in the *Loculoascomycetes*. This class is now no longer recognised and the order was subsequently placed in the *Dothideomycetes* (Kirk et al. 2001). Sequence analyses of the SSU gene, however, revealed the *Coryneliales* to belong to the *Eurotiomycetes* where they clustered with the *Chaetothyriales* (now *Chaetothyriomycetidae*) (Winka 2000). While the SSU phylogeny in the present study corresponds to this analysis, the LSU phylogeny supports recent multi-gene-analyses that place the *Coryneliales* as a basal clade within, or alternatively interpreted as a sister clade to, the *Eurotiomycetidae* (Geiser et al. 2006, Gueidan et al. 2014, Chen et al. 2015), where the

Table 2 Historical sequence of the taxonomic placement of the *Coryneliaceae*.

Date	Event	References
1886	*Coryneliaceae* Sacc. ex Berl. & Voglino [as '*Corynelieae*']	Saccardo (1886)
1891	Family established, first spelt correctly; placed close to *Cucurbitariaceae*, *Sphaeriales*; including *Corynelia* and *Tripospora*	Saccardo (1891)
1892	*Corynelia* placed in *Perisporiaceae* with *Capnodium* and *Antennaria*; ostiole absent, irregularly split	Cooke (1892)
1895	*Coryneliella* (*Co. consimilis*) added, family related to *Cucurbitariaceae*, *Sphaeriales*	Saccardo (1895)
1897	Acknowledged monotypic genera (*C. uberata*, *T. cookei*, *Coryneliella consilimis*); related to *Cucurbitariaceae*	Lindau (1897)
1920	Typical *Sphaeriales* ostiolum lacking, not supporting placement either in *Sphaeriales* or in *Perisporiales*	Fitzpatrick (1920)
1926	Include the family in an order of its own, *Coryneliales*	Seaver & Chardon (1926)
1931	Included *Coryneliaceae* in the *Erysiphales*	Clements & Shear (1931)
1936	Ascocarp a loculoascomycetous pseudothecium, centrum aparaphysate, asci long stipitate, deliquescent	McCormack (1936)
1942	Established *Lagenulopsis* (type species *L. bispora*), as well as a detailed study of *Caliciopsis*	Fitzpatrick (1942a, b)
1946	Included the *Coryneliaceae* in the *Sphaeriales*	Hansford (1946)
1951	Centrum not typical *Dothideales*; placed in *Pyrenomycetes* even though the ascocarp is ascostromatic	Luttrell (1951)
1963	*Coryneliales* pseudoprototunicate, uncertain position; single-layered asci lacking apical pore, deliquescent	Funk (1963)
1969	Fourth genus, *Caliciopsis* (*C. podocarpi*) on two species of *Podocarpus*	Huguenin (1969)
1971	Corynelioid type of centrum proposed, unique to *Coryneliaceae*	Tim (1971)
1971	*Coryneliopsis* described	Butin (1971)
1973	*Coryneliopsis* and *Coryneliospora* either *textura angularis* or *textura prismatica*; *Acrospermum* in *Ostropales*	Korf (1973)
1973	Included the *Coryneliaceae* in the *Sphaeriales*	Muller & Von Arx (1973)
1976	Included the *Coryneliaceae* in the *Edaphomycetidae*	Barr (1976)
1982	*Coryneliales* similar to *Loculoascomycetes* but lacking of bitunicate asci; centrum aparaphysate, resembling capnodiaceous fungi and *Hysteriales*	Bezerra & Kimbrough (1982)
1982–1983	*Coryneliales* pseudoprototunicate, producing an ascostromatic ascocarp; of uncertain position	Eriksson (1982a, b, 1983)
1983	Included the *Coryneliaceae* in the *Parenchymaomycetidae*	Barr (1983)
1985	*Fitzpatrickella* described	Benny et al. (1985a)
1985	Centrum of *Caliciopsis*, *Coryneliopsis*, and *Coryneliospora* similar to other *Coryneliales*	Benny et al. (1985d)
1989	Asci different from other *Loculoascomycetes*, ascus apex elongation resulting in passive ascospore release	Johnston & Minter (1989)
2000	SSU sequence analyses placing *Coryneales* in *Eurotiomycetes*, clustering with the *Chaetothyriales*	Winka (2000)
2001	Class *Loculoascomycetes* no longer recognized; family placed in the *Dothideomycetes*	Kirk et al. (2001)
2004	Positioned in *Eurotiomycetes* based on SSU evidence, sister group *Chaetothyriomycetes*	Inderbitzin et al. (2004)
2006	Multigene phylogeny supporting placement of *Coryneliales*, basal clade within *Eurotiomycetidae*	Geiser et al. (2006)
2016	*Coryneliaceae* placed in new sub-class, *Coryneliomycetidae*	This publication

Coryneliales form a transition stage between the prototunicate *Eurotiomycetidae* and the bitunicate *Chaetothyriomycetidae*. Based on the results obtained in this study we placed the *Coryneliaceae*/*Coryneliales* in a separate subclass, the *Coryneliomycetidae*. Because of their unique morphology, the early nomenclatural history of the *Coryneliaceae* was complicated, a summary of which is presented in Table 2.

Benny et al. (1985b) noted that immature asci of *C. uberata* s.l. had a uniform thick wall. Johnston & Minter (1989) observed that this was the case for immature asci of most species in the *Coryneliaceae*, the only exception being *Coryneliopsis*. SEM observations of asci of *C. uberata* s.l. and *C. tropica* revealed an inner wall surrounded by a layer they interpreted as composed of mucilage, although this differentiation into wall layers could not be observed using a light microscope. As the asci matured the thick wall broke and sloughed off in sections, so that fully mature asci were thin-walled. A basal frill, the remnant of the bitunicate wall, may occur at the base of mature asci (Johnston & Minter 1989). This same ascus morphological development was observed for all species examined in this study, and was also observed in the recently described *Caliciopsis beckhausii* and *C. valentina* (Garrido-Benavent & Pérez-Ortega 2015). In some genera of the *Sordariales* (*Jattaea*, *Pleurostoma*, and *Togninia*) that are not closely related to typical bitunicate fungi, so-called remnant bases remain on the ascogenous hyphae after detachment of mature, undamaged asci, or hair-like structures were observed at the bases of asci that are reminiscent of the frills at the ascus base of *Coryneliomycetidae* (Réblová et al. 2004, Mostert et al. 2006, Damm et al. 2008a, b). This suggests the existence of additional outer wall layers in earlier stages of the ascus development as well. In *Calosphaeria africana* (*Calosphaeriaceae*, *Sordariomycetes*) two wall layers detach from each other during ascus development and are involved in changes of the ascus shape (Damm et al. 2008b) similar to those observed in *Coryneliomycetidae*.

Corynelia uberata is the type species of the *Coryneliaceae*, and before this study it was considered to be a wide-ranging species with a distribution through Africa to Asia and Australasia, occurring on many different species of *Podocarpus* (Minter 2006a). However, here we consider it to be restricted to Africa only, on members of the segregate genus *Afrocarpus*, e.g. *A. falcatus* and *A. gracilior* (Assefa et al. 2014), and most likely also *A. usambarensis* (Minter 2006a). To stabilise the application of the name, an epitype was selected for this taxon. Furthermore, two new species of *Corynelia* are newly described from *P. latifolius* in South Africa, and are likely to be the species present on other members of the African subclade of the subgenus *Podocarpus* (*fide* Knopf et al. 2012), from which *C. uberata* has been recorded (*P. elongatus*, *P. henkelii*, *P. madagascarensis*, and *P. milanjianus* (usually considered a synonym of *P. latifolius*), Minter 2006a). *Corynelia africana* was a common species typically occurring on leaves, whereas *Corynelia fructigena* was infrequently found and then usually on fruit. Although previously considered as belonging to *Corynelia uberata* by all previous workers (Fitzpatrick 1920, 1942a, Benny et al. 1985b, Minter 2006a), the two new species described herein could be distinguished from *C. uberata* s.str. by consistent differences in host preference, morphology, and nrDNA

sequences. Collections from other parts of the world on other host species identified as *C. uberata* need to be re-examined as it is likely that they belong to as yet undescribed species. Their hosts (Minter 2006a) belong to various subclades within *Podocarpus* and the segregate genus *Nageia* from Asia, which is a sister clade to *Afrocarpus*, and the distantly related genus *Falcatifolium* (Biffin et al. 2011, Knopf et al. 2012).

Lagenulopsis bispora is assumed to be rare in South Africa, though its presence may be masked by the more abundant *C. africana*. Previously only a single specimen of *L. bispora* from South Africa was known (Benny et al. 1985c, K(M) 187631). In this study, the presence of *L. bispora* in South Africa is confirmed. Some young asci were observed to have more than two, or sometimes only one developing ascospore, although mature asci observed appeared to have only two spores. *Corynelia jamaicensis* and *C. portoricensis* are typically 3-spored (Fitzpatrick 1942a), suggesting that programmed spore death (Raju & Perkins 2000) may occur in these species. *Lagenulopsis bispora* as currently delimited has a disjunct distribution, being recorded from Africa (on *P. latifolius*), the Neotropics (Jamaica and Mexico) and Micronesia (Fiji). Considering the differences in spore dimensions noted, as well as the hosts in this latter region belonging to the Tropical American subclade of the subgenus *Podocarpus* (*P. matudai* and *P. urbanii*; Benny et al. 1985c) and the Fijian subclade of the subgenus *Foliolatus* (*P. degenerii*; Benny et al. 1985c) of Knopf et al. (2012), it is possible that one or more segregate species await discovery.

The *Coryneliales* make ideal subjects for studies of the evolution of the *Ascomycetes*, biogeography of fungi, and co-evolution with their hosts. *Corynelia uberata* and *T. tripos* were only recorded on *Afrocarpus*, whereas *C. africana*, *C. fructigena*, and *L. bispora* were only recorded on African *Podocarpus* in this study. The present investigation indicates that more diversity within this group awaits discovery, particularly following molecular analyses. Increased knowledge of the true diversity of this group will allow a more detailed analysis of their co-evolution with the *Podocarpaceae*. Unfortunately this group of plants is under threat from over exploitation, which therefore also raises concerns about the continued existence of these associated obligate pathogens.

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