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Lichenicolous fungi from Florida growing on *Graphidales*

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Abstract. The lichenicolous fungi growing on *Graphidales* hosts in Florida are revised, mainly based on collections by the second author (R. C.). Twenty-one species are recognized. The new genus and species *Lawreya glyphidiphila* is described for a common asexual fungus growing on *Glyphis scyphulifera* and more rarely *Trypethelium eluteriae*, characterized by black stromatic conidiomata in which subspherical conidiogenous loculi develop, producing aseptate, subglobose, brown conidia. Nine additional new species are described: *Amerosporiopsis phaeographidis* (on *Phaeographis brasiliensis*), *Arthonia acanthotheciicola* (on *Acanthothecis floridensis*), *A. subgraphidicola* (on *Graphis assimilis*), *Hemigrapha graphidicola* (on *G. assimilis*), *Skyttea graphidicola* (on *Graphis* spp.), *Strigula graphidicola* (on *G. assimilis*), *S. perparvula* (on *Graphidales*), *Talpapellis graphidis* (on *Graphis caesiella*) and *Tremella wedinii* (on *Glyphis scyphulifera*). Phylogenetic placements of *Lawreya glyphidiphila*, *Skyttea graphidicola* and *Tremella wedinii* are presented. Identification keys are given for the species of *Cornutispora* and *Talpapellis*, and for the 66 species known to grow on *Graphidales* hosts worldwide.

Key words: lichen parasites, lichens, phylogeny, taxonomy, *Cornutispora*, *Lawreya*, *Talpapellis*

Introduction

The *Graphidales*, for a long time placed in *Ostropales* but recently proposed as a separate order by Kraichak et al. (2018), are known to harbour a large diversity of lichenicolous fungi, with 66 known species (Diederich et al. 2018). Some of these are opportunists, growing on a wide variety of lichens belonging to different orders, such as *Corynespora laevistipitata*, *Etayoa trypethelii*, *Lichenodiplis lecanorae*, *Marchandiomyces corallinus*, *Ovicuculispora parmeliae* or *Taeniolella delicata*. Two species appear to be specialized on a small number of hosts, including *Graphidales* but also species from other orders: *Lichenostigma chlaroterae* (mainly on *Lecanora* but also on *Buellia*, *Fuscidea* and *Graphis*) and *Taeniolella punctata* (mainly on *Graphis*, rarely on *Arthonia*, *Fissurina*, *Pertusaria* and *Phaeographis*). *Polycoccum arnoldii* has been reported from *Diploschistes* and *Rhizocarpon*, while *Sphinctrina leucopoda* is known from *Pertusaria* and *Diploschistes*; in both cases, further studies may reveal that populations from different hosts represent genetically distinct species. All other known species have been reported from a single *Graphidales* host genus. Amongst these, eight were known from *Diploschistes*, eight from *Graphis*, five from *Phaeographis* and 12 from *Thelotrema*. Each of the genera *Acanthothecis*, *Anomomorpha*, *Chapsa*, *Diorygma*, *Fissurina*, *Nitidochapsa*, *Pallidogramme*, *Reimnitzia* and *Sarcographa* were known to host one lichenicolous species.

Over many years, the second author has collected corticolous lichens in Florida and has carefully scrutinized the specimens for lichenicolous fungi. Several lichenicolous species have already been published in previous papers: *Etayoa trypethelii* (Ertz et al. 2014), *Taeniolella delicata* (Heuchert et al. 2018), *T. hawksworthiana* (Ertz et al. 2016), *Tremella graphidis*, *T. phaeographinae* and *T. pyrenulae* (Ariyawansa et al. 2015). The aim of this paper is to publish all species of lichenicolous fungi

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collected and identified on *Graphidales* hosts in Florida, to describe one new genus and 10 new species, and to present an identification key to all lichenicolous fungi known to inhabit *Graphidales* hosts.

General information on the lichen flora from Florida can be found in many papers, such as DeBolt et al. (2007), Harris (1990, 1995) or Seavey and Seavey (2019). More specific information on the lichens of Fakahatchee Strand Preserve State Park, one of the richest localities in Florida for 'graphidicolous' fungi, can be found in Lücking et al. (2011).

Material and methods

Morphological examination

Almost all specimens studied in this paper were collected by the second author (R. C.); these are kept in BR, MSC and/or in the private herbarium of P. Diederich (Luxembourg), with some duplicates in HAL and S. Additional specimens have been obtained on loan from NY and SBBG. Specimens collected by R. Common are abbreviated C, followed by the collection number. For all other specimens the collector is indicated.

Macroscopic photographs were obtained using a Canon 40D camera (Tokyo, Japan) with Nikon BD Plan 10 or Nikon M Plan 40 ELWD microscope objectives (Tokyo, Japan), StackShot (Cognisys, MI, USA) and Helicon Focus (HeliconSoft, Kharkiv, Ukraine) for increasing the depth of field (P. Diederich); or a Keyence VHX-5000 digital microscope and a VH-Z20R/W/T lens (Osaka, Japan) (D. Ertz); or a Wild Heerbrugg M400 Photomakroskop (Heerbrugg, Switzerland) fitted with an Apozoom objective and a Nikon D700 digital camera (Tokyo, Japan), using Zerene Stacker (Zerene Systems, WA, USA) for increasing the depth of field (R. Common). Hand-made sections of ascomata and thallus were studied in tap water, 5% KOH (K), Lugol's reagent (1% I_2) without (I) or with KOH pre-treatment (K/I), lactophenol-cotton blue (LCB), Congo Red or phloxine B. Measurements based on statistical data are indicated as (minimum–) X-sd – X+sd (–maximum), where X represents the arithmetic mean and sd the corresponding standard deviation, followed by the number of measurements (n); the length/breadth ratio is indicated as L/B and given in the same way. Microscopic photographs were prepared using a Leica DMLB microscope (Wetzlar, Germany) with interference contrast, fitted with a Leica EC3 camera (P. Diederich); or an Olympus BX51 microscope (Tokyo, Japan) with interference contrast, connected to an Olympus Color View I digital camera (D. Ertz); or a Nikon Microphot-FXA microscope with DIC optics (Tokyo, Japan), fitted with a Nikon D5000 digital camera, and using Zerene Stacker for increasing the depth of field (R. Common).

DNA extraction, amplification and sequencing

DNA extraction and polymerase chain reaction (PCR) amplification of *Tremella* specimens were performed following Millanes et al. (2012). Direct PCR of *Lawreya* was performed following Ertz et al. (2015). The PCR products were purified with Exosap in Macrogene Inc. (Amsterdam, the Netherlands). Genomic DNA from *Skyttea* specimens was extracted from ascomata of dried herbarium specimens, 3–4 ascomata per reaction, using a High Pure PCR Template Preparation Kit (Roche Applied Science, Penzberg, Germany) and following the protocol provided by the manufacturer. The internal transcribed spacer (ITS) was amplified using primers ITS0F (Tedersoo et al. 2008) or ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990). The PCR reaction mix (25 µL) consisted of 5 µL 5× HOT FIREPol Blend Master Mix (Solis BioDyne, Tartu, Estonia), 0.5 µL of both primers (both at a concentration of 20 µM), 3 µL of target DNA, and distilled water up to the total volume. The PCR cycle consisted of 36 cycles and annealing temperature was set at 57°C. For purification of PCR products, 1 µL of FastAP and 0.5 µL of exonuclease I (Thermo Scientific, Waltham, MA, USA) were added per 20 µL of the product, and the tubes were incubated at 37°C for 45 min; the enzymes were deactivated by heating at 85°C for 15 min.

DNA sequencing of both complementary strands was performed in Macrogen Inc. (Amsterdam, the Netherlands) with the same primer set as for amplifications to generate *Tremella* sequences; primers LIC15R (Miadlikowska et al. 2002), LR3 and LR6 (Vilgalys & Hester 1990) for *Lawreya* sequences; and primers ITS4 and ITS5 (White et al. 1990) for *Skyttea* sequences.

Sequence alignment and phylogenetic analyses

Twelve new *Tremella* sequences (6 ITS and 6 nLSU rDNA) were edited and assembled using Geneious ver. 6.1.2 (Biomatters Ltd., Auckland, NZ). Assembly of the nuclear rDNA included the whole ITS and a continued fragment of ~1000 bp in the nLSU region. Sequencher ver. 4.10.1 (GeneCodes Corp.®, Ann Arbor, MI, USA) was used to check, assemble and manually adjust the resulting sequence fragments of four new *Skyttea* sequences, and Sequencher ver. 5.3 of three new *Lawreya* sequences. The consensus sequences generated for this study are deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

The new *Tremella* sequences were aligned together with sequences already available in GenBank (Table 1). After a preliminary alignment including all regions, the ITS1, 5.8S, ITS2 and nLSU regions were identified and aligned separately using the Q-INS-I (for ITS1 and ITS2), and the G-INS-i (for 5.8S and nLSU) algorithms in MAFFT ver. 7 multiple sequence alignment software (Katoh & Toh 2008). The 5.8S region was considered unambiguously aligned, whereas ambiguous regions in ITS1, ITS2 and nLSU were identified and eliminated with Gblocks ver. 0.91b (Castresana 2000), adjusting the filtering parameters to relaxed settings as suggested by Tan et al. (2015). Dataset congruence was assessed manually by analysing the datasets separately by maximum likelihood bootstrapping. No incongruence was found, and the data were concatenated into a single dataset in Mesquite ver. 3.04 (Maddison & Maddison 2018).

Bayesian inference (BI) and maximum likelihood (ML) analyses were performed following Zamora et al.

Table 1. Voucher information and GenBank accession numbers (NCBI) for ITS and nLSU sequences of *Tremellales* used in this study. Newly generated sequences are in bold.

Species name	Country	Host	Collector and number	Herbarium	Culture reference	ITS	nLSU
Bulleribasidium oberjochense (Type)	–	–	–	–	CBS 9110	NR121467	NG042388
Bulleromyces albus (Type)	–	–	–	–	CBS 501	KY101819	KY106261
Carcinomyces effibulatus (Type)	Sweden	*Gymnopus ocior*	Santos	S F40014	–	JN053499	JN043605
Cryptococcus neoformans (Type)	–	–	–	–	CBS 8710	EF211144	FJ534909
Cuniculitrema polymorpha (Type)	–	–	–	–	CBS 8088	AF444320	NG042349
Naematelia encephala	Sweden	*Stereum sanguinolentum*	Hjortsberg 500	S F102416	–	JN053481	JN043587
Phaeotremella foliacea	Sweden	–	Wiklund 018	S F102409	–	JN053502	JN043609
Pseudotremella moriformis (Type)	–	–	–	–	CBS 7810	KY104686	AF075493
Rhynchogastrema coronatum (Type)	–	–	–	–	BBA 65155	MH168095	KJ170152
Sirobasidium magnum	–	–	–	–	CBS 8485	JN053497	JN043603
Tremella caloplacae	France	*Variospora dolomitica*	Sérusiaux	S F102489	–	JN053469	JN043574
Tremella cetrariicola	Finland	*Nephromopsis chlorophylla*	Suija	S F102413	–	JN053490	JN043596
Tremella christiansenii (Type)	Denmark	*Physcia tenella*	Christiansen 6846	MSC 607	–	–	JN043577
Tremella cladoniae	Estonia	*Cladonia* sp.	Suija 872	TU 45019	–	JN053477	JN043583
Tremella coppinsii	Estonia	*Platismatia glauca*	Suija 38a	TU 38637	–	JN053496	JN043602
Tremella diploschistina a (Type)	Sweden	*Diploschistes scruposus*	Westberg 09-400	S F211875	–	JN790586	N790588
Tremella diploschistina b	Sweden	*Diploschistes scruposus*	Westberg 09-452	S F211901	–	JN790587	JN790590
Tremella diploschistina c	Sweden	*Diploschistes scruposus*	Westberg	S F211910	–	**MN258553**	**MN243148**
Tremella diploschistina d	USA	*Diploschistes muscorum*	Rosentreter 6836	IMI 365462	–	JN790585	JN790589
Tremella fuciformis	–	–	–	–	CBS 6970	JN053466	JN043571
Tremella graphidis a (Type)	USA	*Graphis caesiella*	Common 9434B1	BR	–	**MN258557**	**MN243152**
Tremella graphidis b (Type)	USA	*Graphis assimilis*	Common 9434B2	BR	–	KR058781	KR058786
Tremella hypogymniae	Estonia	*Hypogymnia physodes*	Suija	TU 39402	–	JN053485	JN043591
Tremella lobariacearum	Portugal (Madeira)	*Lobaria pulmonaria*	Diederich 4935	S F102418	–	JN053473	JN043579
Tremella macrobasidiata (Type)	Spain	*Lecanora chlarotera*	Zamora & Zamora	MAF Lich.16877	–	KT334582	KT334594
Tremella mayrhoferi b (Type)	Sweden	*Lecanora allophana*	Zamora & Millanes	UPS 877384	–	MH168093	MH168097
Tremella mesenterica	Sweden	–	Ryman 9146	–	–	JN053463	JN043568
Tremella phaeographinae a	USA	*Phaeographis* sp.	Common 9481B	hb Diederich	–	KR058782	KR058787
Tremella phaeographinae b	USA	*Phaeographis* sp.	Common 9249C	hb Diederich	–	KR058783	KR058788
Tremella phaeographinae c	USA	*Phaeographis* sp.	Common 9425C	hb Diederich	–	**MN258558**	**MN243153**
Tremella phaeophysciae	Luxembourg	*Phaeophyscia orbicularis*	Diederich 12429	S F102505	–	JN053479	JN043585
Tremella pyrenulae	USA	*Pyrenula ochraceoflavens*	Common 9170B	BR	–	KR058784	KR058789
Tremella tuckerae a (Type)	Mexico	*Ramalina sinensis*	Tucker 37335	SBBG	–	JN053482	JN043588
Tremella wedinii a	USA	*Glyphis scyphulifera*	Common 9880B	hb Diederich	–	**MN258554**	**MN243149**
Tremella wedinii b (Type)	USA	*Glyphis scyphulifera*	Common 10067B	BR	–	**MN258555**	**MN243150**
Tremella wedinii c	USA	*Glyphis scyphulifera*	Common 10035C	hb Diederich	–	**MN258556**	**MN243151**
Trimorphomyces papilionaceus	–	–	–	–	CBS 443.92	AF444483	AF075491

Table 2. Voucher information and GenBank accession numbers (NCBI) for ITS sequences of *Helotiales* used in this study. Newly generated sequences are in bold.

Species name	Country	Host	Collector and number	Herbarium	NCBI
Diplolaeviopsis ranula (sexual stage)	Portugal (Azores)	*Lecanora strobilina*	Diederich 16988	BR	KJ559532
Diplolaeviopsis ranula (asexual stage)	Canada	*Lecanora strobilina*	Clayden 21924	NBM FL-14388	KP984782
Macroskyttea parmotrematis	Bolivia	*Parmotrema aberrans*	Kukwa 11316	UGDA	KP984784
Skyttea cismonicae	Canada	*Loxospora cismonica*	Clayden 21501	NBM FL-13271	KP984783
Skyttea cismonicae	Canada	*Loxospora cismonica*	Driscoll 502	NBM FL-13131	**MK282253**
Skyttea graphidicola (Type)	USA	*Graphis oshioi*	Common 9793B	BR	**MK282255**
Skyttea gregaria	USA	*Violella fucata*	Lendemer 22769	NY 0118113	KJ559537
Skyttea insignis	Canada	*Lecanora insignis*	Clayden 23187	NBM FL-14764	**MK282252**
Skyttea lecanorae	Canada	*Lecanora circumborealis*	Harris 57563	NY 1595972	KJ559539
Skyttea radiatilis	USA	*Loxospora pustulat*a	Lendemer 12949	NY 00977030	KJ559536
Skyttea tephromelarum	UK	*Tephromela atra*	Coppins 23703	E 00468345	**MK282254**

(2017). A GTR+Γ model was selected for the ITS1 and ITS2, a SYM+Γ for the 5.8S, and finally a GTR+I+ Γ for the nLSU rDNA. The combined matrix contained 1248 characters (ITS1: 1–79; 5.8S: 80–190; ITS2: 191–306; nLSU: 307–1248). The best tree obtained from the ML analysis had an ln-likelihood value of –8896.828285. BI was halted after 1 800 000 generations, at which time the average standard deviation of split frequencies across runs was below 0.01, which indicates that the three runs had converged. Moreover, the potential scale reduction factor (PSRF) for all models and parameters was below 1.002. A majority-rule consensus tree was constructed from the 27 500 trees of the stationary tree sample.

Prior to alignment of the *Skyttea* sequences, ITSx (Bengtsson-Palme et al. 2013) was used for exclusion of neighbouring conservative rDNA (nLSU, nSSU) regions. The newly generated sequences together with those downloaded from GenBank (Table 2) were aligned using MUSCLE (Edgar 2004); the alignments were then manually checked with SeaView ver. 4.6 (Gouy et al. 2010). The resulting alignment consisted of 631 characters, of which 122 were informative. ML implemented with RAxML ver. 8.1.10 (Stamatakis et al. 2008) at the CIPRES Science Gateway (Miller et al. 2010) and BI with MrBayes ver. 3.2.1. (Ronquist et al. 2012) were conducted to confirm the phylogenetic position of *Skyttea graphidicola*. The best-fit nucleotide substitution model according to the AICc criterion calculated with jModeltest ver. 2.1.6. (Darriba et al. 2012) was GTR+Γ and applied in both analyses. In ML, bootstrap support (BS) was calculated over 300 pseudoreplicates; the rest of the parameters were set at default value. In BI, two parallel simultaneous runs were applied with four-chain runs over 150 000 generations starting from a random tree until the average standard deviation of split frequencies was >0.01. Sampling was done after 100 steps; the first 25% of saved data was discarded as burn-in; the 50% majority-rule consensus tree and posterior probabilities (PP) were calculated from the rest.

The new *Lawreya* sequences were aligned together with sequences of *Capnodiales* already available in GenBank (Fig. 5), using MAFFT v6.814b (Katoh & Toh 2008) and improved manually using Mesquite 3.04 (Maddison & Maddison 2018). Terminal ends of sequences and ambiguously aligned regions were delimited manually and excluded from the datasets, resulting in an alignment of 1286 characters (including 469 unique site patterns) for 70 taxa. ML implemented with RAxML ver. 8.2.10 (Stamatakis et al. 2008) at the CIPRES Science Gateway (Miller et al. 2010) and BI with MrBayes ver. 3.2.6. (Ronquist et al. 2012) were conducted to place the genus *Lawreya* in a phylogeny of the *Capnodiales*. The best-fit nucleotide substitution model according to the AICc criterion calculated with jModeltest ver. 2.1.6. (Darriba et al. 2012) was TIM2+I+Γ and applied in both analyses. In ML, the bootstrap support (BS) was calculated over 1000 pseudoreplicates. In BI, two parallel simultaneous runs were applied with four-chain runs and 80 million generations, sampling trees every 1000th generation. Posterior probabilities (PP) were determined by calculating a majority-rule consensus tree generated from the 120 002 post-burn-in trees of the 160 002 trees sampled by the two MCMCMC runs using the 'sumt' command of MrBayes.

Since the topologies of the ML and the BI trees were congruent in the *Lawreya*, *Skyttea* and *Tremella* analyses, only the best trees from the ML analysis are shown in Figures 5, 9 and 16, with ML bootstrap values (BS) and Bayesian posterior probabilities (PP) indicated. The phylogenetic trees were visualized with FigTree ver. 1.4.2 (Rambaut 2014). Adobe Illustrator CS3® was used for artwork.

Results and discussion

Amerosporiopsis phaeographidis Diederich & Common, sp. nov. (Fig. 1)

MycoBank MB 831995

Diagnosis: Distinguished from *Amerosporiopsis gaubae* by its narrower, almost bacilliform conidia (7.7–)8.8–11.1(–12.3) × (1.0–)1.3–1.6(–1.8) µm, the presence of conidiophores, conidiomata often surrounded by a clypeus-like structure, and the lichenicolous habitat, growing on *Phaeographis brasiliensis*.

Type: USA, Florida, Collier Co., Fakahatchee Strand State Preserve, trail north of Boardwalk (25.94183°N, 81.47405°W), on *Phaeographis brasiliensis*, 11 Nov. 2011, Common 9435I (BR 5030086834775 – holotype).

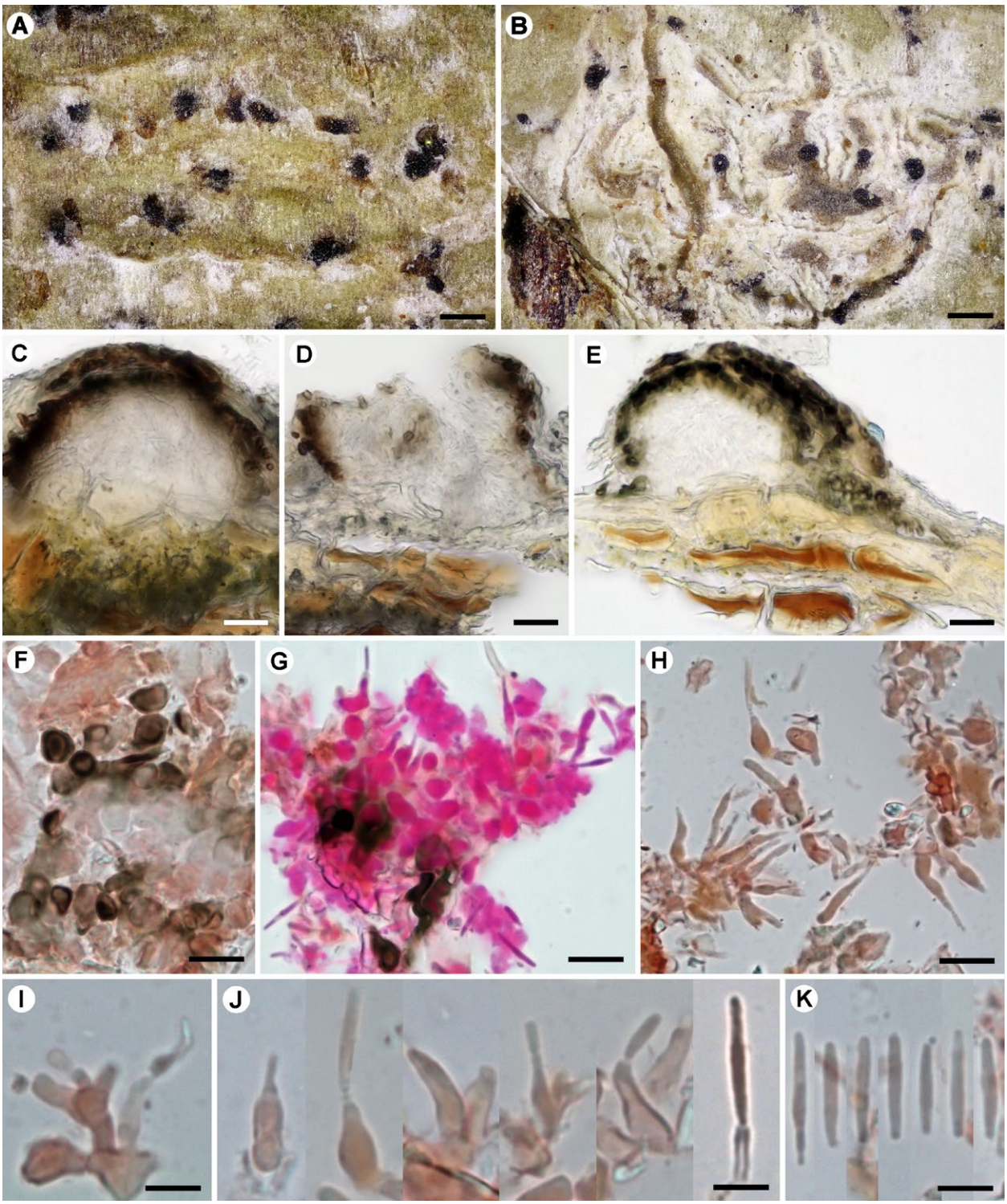

Figure 1. *Amerosporiopsis phaeographidis* (holotype). A – conidiomata on host thallus; B – conidiomata on host apothecia; C – section through closed pycnidium, in water; D – section through opened, cupulate conidioma, in water; E – section through conidioma with clypeus-like structure at right, in 5% KOH, showing olivaceous reaction; F – dark cells of outer conidiomatal wall in squash preparation; G – conidiogenous layer in squash preparation, in phloxine; H – conidiogenous cells with young conidia; I – conidiophore; J – conidiogenous cells; K – conidia (H–K in Congo Red). Scales: A–B = 200 µm; C–E = 20 µm; F–H = 10 µm; I–K = 5 µm. Photos: P. Diederich.

Description. Mycelium immersed, hyaline. Ascomata unknown. Conidiomata pycnidial, separate, subglobose, black, immersed, later erumpent, unilocular, thick-walled, 60–100 µm diam., often surrounded by a clypeus-like structure, giving the conidioma an irregular form in surface view, up to 200 µm diam. Conidiomatal wall present only in upper and lateral parts, several cells thick, external layers dark brown, K+ dark olivaceous, inner layers hyaline; outer layer covered by subspherical to elongate darker cells, well visible in microscopic squash preparations, giving the conidiomata a somewhat rugose appearance; wall basally hyaline or indistinct; when mature, occasionally opening irregularly and becoming cupulate; ostiole indistinct or absent. Conidiophores arising basally or laterally from the conidiomatal wall, irregularly catenate and branched, of short and irregularly

formed cells. Conidiogenous cells enteroblastic, phialidic, discrete, ellipsoid to elongate ampulliform, straight, hyaline, smooth, abruptly tapered at the apex to a minute aperture, (7.5–)8.5–12.3(–12.7) × (2.3–)2.5–3.2(–3.5) µm (n = 11). Conidia hyaline, aseptate, bacilliform to narrowly fusiform, apex rounded, base indistinctly truncate, thin-walled, smooth, (7.7–)8.8–11.1(–12.3) × (1.0–)1.3–1.6(–1.8) µm, L/B (4.6–)5.7–8.3(–10) (n = 38).

Etymology. Named after the host *Phaeographis*.

Notes. Although this species is known only from a single specimen, it is clearly distinguished by: the half-immersed pycnidial conidiomata, with a dark conidiomatal wall missing or indistinct in the lower part, with a clypeus-like structure giving the conidiomata an irregular outline macroscopically, and by the long and narrow conidia, often slightly broader in the middle or lower half, arising from elongate phialides. Most conidiomata in the type specimen are flat, irregular in outline, and do not present a visible opening, but some conidiomata are cupulate, with an irregular, enlarged opening, often not surrounded by a clypeus-like structure. These two conidiomatal types appear distinct but microscopically are indistinguishable except for the conidiomatal opening. Cupulate conidiomata grow mostly on the host hymenium, rarely on the surrounding thallus, while flattened conidiomata grow exclusively on the host thallus.

The new species does not perfectly fit any known coelomycetous genus. Without molecular data, we prefer not to describe a new genus for a species known only from the holotype. We searched for a known genus that shares most characters. Amongst the genera of pycnidial fungi with an enteroblastic conidiogenesis and aseptate, hyaline conidia keyed out by Sutton (1980), the genus *Amerosporiopsis* resembles our new fungus most; we choose therefore to describe it as the second known species of that genus. The single previously known species, *A. gaubae*, seems to be known only from the holotype, collected on dead leaves of *Sesleria* in Iran (Sutton 1980). That species differs from *A. phaeographidis* by having broader, fusiform conidia, 8–10.5 × 2.5–3.5 µm, by the absence of conidiophores, by the absence of a clypeus, and by a different habitat.

Host and distribution. Lichenicolous on the thallus of *Phaeographis brasiliensis*, the host not visibly damaged. Known only from the type locality, Fakahatchee Strand State Preserve in Florida. Obviously a rare species in Florida.

Ampullifera foliicola Deighton

Ampullifera species typically grow on foliicolous lichens. In one Florida locality we collected specimens on several corticolous lichen species. Hyphopodia in this material are not abundant but are typical for *A. foliicola*. Aseptate conidia also fit the dimension range of that species.

Specimens examined. USA Florida. Hillsborough Co.: Hillsborough River State Park, Florida Trail (28.149°N, 82.235°W), on *Fissurina mexicana*, 2011, C9479C; on cf. *Pyrenula*, C9479D; on *Astrothelium variolosum*, C9479E (all in hb Diederich).

Arthonia acanthotheciicola Ertz & Common, sp. nov. (Fig. 2)

MycoBank MB 831996

Diagnosis: Similar to *Arthonia graphidicola*, but having ±rounded, rarely elongate, wider ascomata, an I+ reddish subhymenium, subspherical asci, 3–4-septate ascospores and a different host, *Acanthothecis floridensis*.

Type: USA, Florida, Pasco Co., 38439 5th Ave., Zephyrhills (28°14.89′N, 82°11.18′W), on ornamental *Lagerstroemia* twigs, on *Acanthothecis floridensis*, 14 Apr. 2015, Common 9887A (BR 5030086833747 – holotype; MSC – isotype).

Description. Thallus absent, lichenicolous. Apothecia in groups or scattered, immersed in the host thallus, fleck-like, ±rounded with an irregular outline, rarely elongate, not branched, emarginate, black, bursting through the host thallus, 0.13–0.46 mm when ±rounded, 0.19–0.42 × 0.11–0.14 mm when elongate; hymenial disc black, flat, level with surface of host thallus, rarely slightly convex, not pruinose. Hymenium 45–55(–65) µm tall, hyaline, not inspersed, I+ pale blue, some parts turning reddish, K/I+ blue; epihymenium pale to dark brown; brownish pigment K+ olivaceous. Subhymenium ~4–6 µm tall, hyaline or pale brown, I+ reddish. Paraphysoids rather scanty, sparingly branched, 1–1.5 µm wide, apices branched, brown-walled, elongate, 1.5–2 µm wide. Asci subspherical, with a short foot, with a thick wall in the upper part, 25–33 × 20–25 µm, (4–)8-spored, with an I+ reddish thin outer layer, without K/I+ blue apical ring. Ascospores (13–)14.5–17(–18) × (5–)6–6.5(–7) µm (n = 50), 3–4-septate, upper cell distinctly enlarged, lower cell often slightly enlarged, middle cells usually much wider than long, oblong to clavate, at first colourless and smooth, when overmature covered by brownish, granular warts; perispore sometimes visible, 0.5 µm thick. Conidiomata not seen.

Notes. *Arthonia acanthotheciicola* is the first lichenicolous *Arthonia* species known to grow on the host lichen genus *Acanthothecis*. Several other lichenicolous *Arthonia* species are known from *Graphidales* hosts, most of them also having ascospores with an enlarged upper cell, but they differ from the new species in several aspects. *Arthonia graphidicola* and *A. subgraphidicola* differ from the new species by having narrower ascomata, an I+ blue hypothecium, broadly clavate asci, less septate (2–3-septate) ascospores and a different host selection (*Graphis* spp.) (Coppins 1989, Coppins & Aptroot 2009, this paper). *Synarthonia hodgesii*, also growing on *Graphis*, differs greatly by the elongate ascomata having a brownish orange, K+ magenta epihymenium (Lendemer et al. 2016). *Arthonia thelotrematis* differs by having clavate asci, smaller (11–14 × 4.5–5 µm), less septate (2–3-septate) ascospores, a reddish brown hypothecium, and *Thelotrema lepadinum* as host (Coppins 1989). *Arthonia diorygmae* differs greatly from the new species by having a notably thick hypothecioid layer, clavate asci

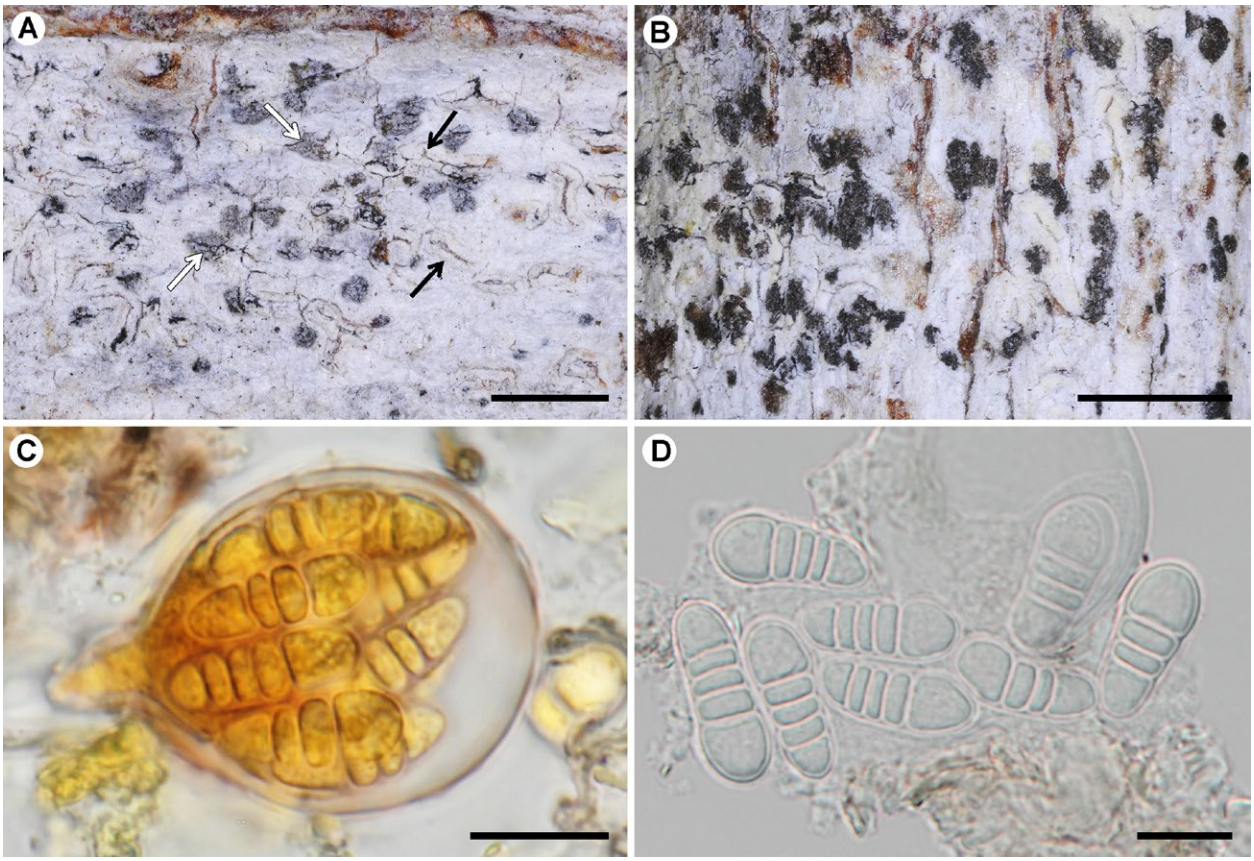

Figure 2. *Arthonia acanthotheciicola* (holotype). A, B – ascomata on host (white arrows: ascomata of *A. acanthotheciicola*; black arrows: ascomata of host); C – ascus, in Lugol; D – ascospores, in water. Scales: A–B = 1 mm; C–D = 10 µm. Photos: R. Common (A–C) and D. Ertz (D).

and 1-septate ascospores, and by growing on *Diorygma* (Joshi et al. 2013).

Etymology. Growing on *Acanthothecis*.

Host and distribution. On *Acanthothecis floridensis*, producing necrotic areas at a late stage, when ascomata are numerous. Known from three localities in Florida.

Additional specimens examined (all on *Acanthothecis floridensis*). USA Florida. Citrus Co.: Citrus Wildlife Mgmt. Area, Withlacoochee State Forest, on Trail 13, 1.8 mi. N of CR 480 (28.723°N, 82.426°W), 1992, C5500G (MSC). Dade Co.: SW 388th St., 1.2 mi. E of Old Dixie Hwy., near Homestead (25.405°N, 80.560°W), 1992, C5889z13 (MSC). Pasco Co.: same locality and year as type, C9902E (MSC).

Arthonia subgraphidicola Ertz, Common & Diederich, sp. nov. (Fig. 3)

MycoBank MB 831997

Diagnosis: Similar to *Arthonia graphidicola* but having more elongate, longer ascomata, an I+ persistently blue hymenial gel and a different host species, *Graphis assimilis*.

Type: USA, Florida, Sumter Co., Green Swamp Wilderness Preserve near FL471 (28.347°N, 82.055°W), dead branches of oak, on *Graphis assimilis*, 30 July 2016, Common 10171B (BR 5030086832719 – holotype).

Description. Thallus absent, lichenicolous. Apothecia in groups or scattered, immersed in the host thallus, fleck-like, usually elongate, oblong to ±lirelliform, emarginate, 0.15–0.6 × 0.04–0.1 mm; hymenial disc pale brown to dark brown or blackish, not pruinose, level with the surface of the thallus. Hymenium 40–50 µm tall, hyaline to pale brown, not inspersed; brownish pigment K+ pale olivaceous; hymenial gel I+ persistently blue, K/I+ blue; epihymenium indistinct or pale brown, K+ pale olivaceous. Hypothecium ~7–15 µm tall, hyaline to pale brown, I+ blue. Paraphysoids rather scanty and difficult to observe, branched, ~1.5 µm wide, not distinctly enlarged at the apex. Asci broadly clavate, wall apically thickened, ~28–35 × 13–16 µm, 8-spored, with an I+ reddish thin outer layer, with a tiny K/I+ blue apical ring. Ascospores (11–)13–15(–17) × 4–5.5 µm, 2–3-septate, upper cell enlarged, oblong-ovoid, at first colourless and smooth but often with a thin perispore; when overmature covered by dark brown, granular warts. Conidiomata not seen.

Notes. *Arthonia graphidicola* is the closest species and differs by having less elongate, reddish brown ascomata, an I+ reddish brown to vinose (or blue, turning quickly reddish) hymenium (but I+ blue hypothecium) and a different host species (*Graphis scripta*) (Coppins 1989, Coppins & Aptroot 2009). *A. graphidicola* is known from oceanic woodlands in Europe (Luxembourg, Diederich et al. 1991; France, Coste 1993; Spain, Etayo & Diederich 1998; Great Britain and Ireland, Coppins & Aptroot 2009; the Netherlands, www.verspreidingsatlas.nl/7288) and was also reported from Japan (Frisch et al. 2014), while the new species inhabits subtropical forests in North America (Florida). *Arthonia agelastica* is also known from Florida

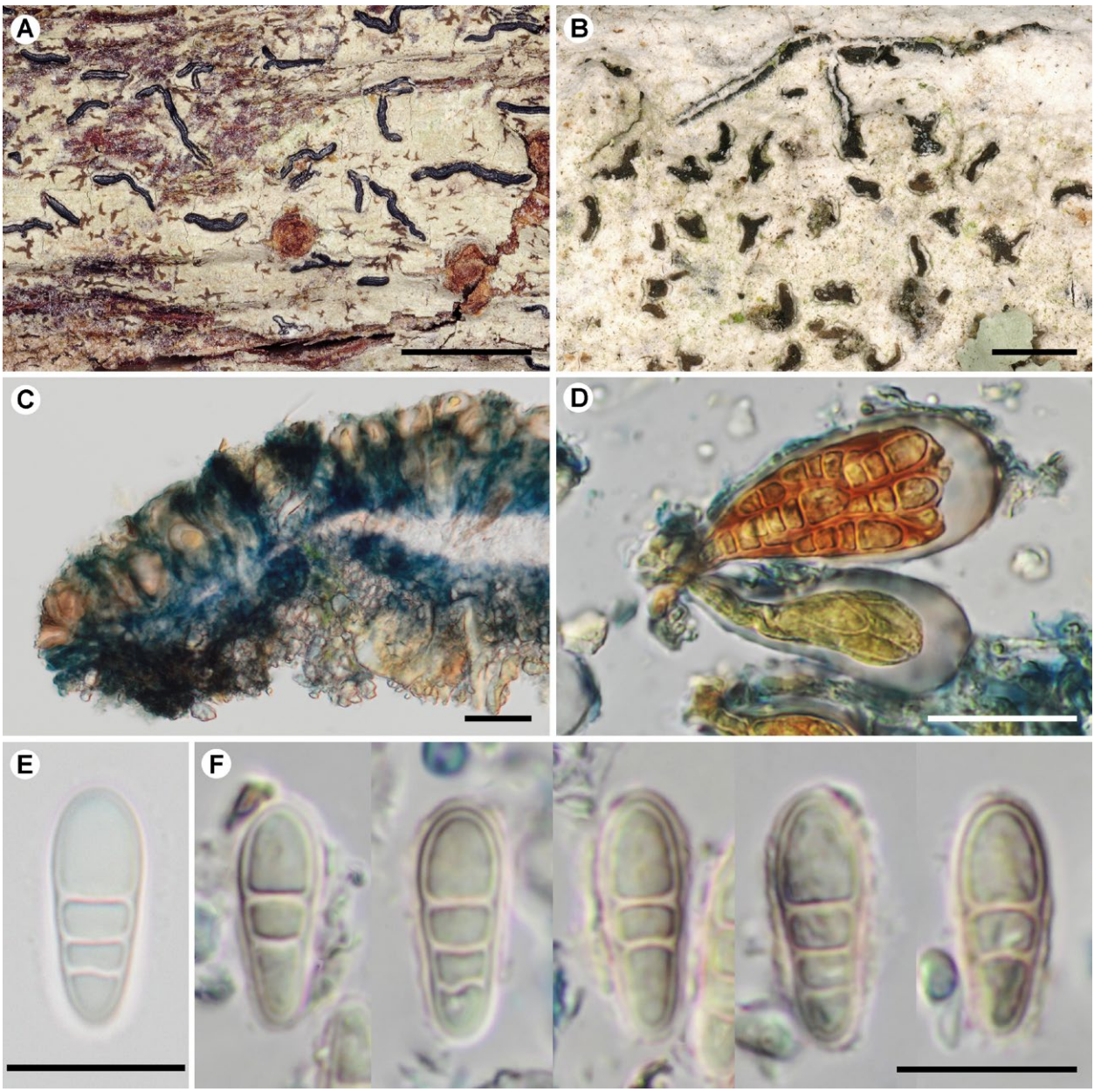

Figure 3. *Arthonia subgraphidicola* [A, F: C9434F; B, C, E: holotype; D: C6905C]. A, B – ascomata on host thallus; C – section of hymenium, in Lugol (reagent still entering towards centre of hymenium in right part of photo); D – asci, in Lugol; E – ascospore, in water; F – ascospores, in Lugol. Scales: A = 2 mm; B = 500 µm; C–D = 20 µm; E–F = 10 µm. Photos: R. Common (A, D, F) and D. Ertz (B–C, E).

and has ascospores similar to *A. subgraphidicola*, though being mainly 2-septate. It differs from *A. subgraphidicola* by having rounded ascomata, a colourless hypothecium, an I+ orange hymenial gel and a different host (*Lecanora louisianae*) (Lendemer et al. 2016). *Arthonia subgraphidicola* belongs to a group of lichenicolous fungi (with notably *A. graphidicola*, *A. thelotrematis*, *A. agelastica*) having macrocephalic ascospores and brownish to reddish, flat ascomata, that are closely related to the genera *Coniocarpon*, *Reichlingia* and *Synarthonia* within the *Arthoniaceae*.

Etymology. Resembling *Arthonia graphidicola*.

Host and distribution. On *Graphis assimilis* growing on branches of *Quercus*, known from several localities in Florida.

Additional specimens examined (all on *Graphis assimilis*). USA Florida. Collier Co.: Fakahatchee Strand State Preserve, trail E of Big Cypress Boardwalk, US 41 (25°56.51′N, 81°28.16′W), 2011, C9434F (MSC, hb Diederich), C9916E (BR); ibid., trail from Gate 7 (25º58.78′N, 81º24.61′W), 2011, C9370B (MSC); ibid., canoe launch site along US 41, mangrove area (25.931°N, 81.444°W), 2014, C9682G (MSC); ibid., first bend of Janes Scenic Drive (25°58.74′W, 81°22.26′W), 2014, C9736P (BR). Hillsborough Co.: Hillsborough River State Park, 1990, C4789B (MSC); ibid., along CR. 581, 3.2 mi. S of junction with I-75, NW of bridge (28.095°N, 82.399°W), 1995, C6788C (MSC); ibid., SE of bridge, 1996, C6905C (MSC). Pasco Co.: Zephyrhills, near Henry Ave. (28°14.74′N, 82°11.21′W), on oak twigs, 2015, C9916E (MSC).

Coniambigua phaeographidis Etayo & Diederich

This species has been described from northern Spain on *Leiorreuma lyellii* (Etayo & Diederich 1995) and later

Table 3. Variability of conidial size and septation in *Coniambigua phaeographidis*, based on the measurements of 10 conidia from each of nine specimens.

Specimen	Conidial length in µm (X±sd)	Conidial breadth in µm (X±sd)	Average number of cells per conidium
C3693S	7.6–9.7	6.0–6.9	1.6
C3865I	8.4–11.4	5.4–7.2	1.4
C3918I	9.1–12.6	5.3–6.5	1.0
C4374K	8.4–11.8	5.1–6.3	1.1
C5320V	7.8–12.0	5.3–6.9	1.3
C5321F	7.7–16.2	5.1–6.8	1.2
C5323R	8.3–11.7	5.3–6.3	1.4
C5567N	7.6–10.2	5.6–7.0	1.2
C10143E	7.3–9.5	5.3–7.2	1.0
Original description	'8–13'	'5–8'	1.0

was reported from the USA (Delaware, South Carolina) by Diederich (2003), always on the thallus of *Phaeographis* s.lat. species. It is here newly reported from Florida and Mississippi, and the host in North America seems to be mostly *Leiorreuma sericeum*.

It is interesting to note that 2-celled conidia have been observed in several specimens, unlike in the original description, in which conidia were described as exclusively aseptate. Also, conidial size is much more variable than initially believed (Table 3).

Specimens examined (all on *Leiorreuma sericeum*). USA Florida. Hillsborough Co.: On US-301, 5 mi. S of Hillsborough River, 1977, C4374K (MSC). Pasco Co.: Withlacoochee State Forest, on Clay Sink Rd., ~1 mi. from W boundary of forest (28.482°N, 82.075°W), 1975, C3693S (MSC). Sumter Co.: Richloam Wildlife Management Area (28.526°N, 82.054°W), 2016, C10143E (hb Diederich); Withlacoochee River, at boundary with Polk Co., 1992, C5320V, C5321F, C5323R (MSC); 2.4 mi. N of county boundary on SR 471, Green Swamp Wildlife Management Area, 1992, C5567 (MSC). Mississippi. Franklin Co.: on US-84, 2.5 mi. E of Kirby Rd., E of Roxie, 1976, C3865I (MSC). Madison Co.: Natchez Trace, S of Farmhaven, 1976, C3918I (MSC).

Cornutispora ciliata Kalb

Specimen examined. USA Florida. Collier Co.: Fakahatchee Strand State Preserve, Janes Scenic Drive (25°58.74′N, 81°22.26′W), on *Graphis cupei*, 2014, C9736C (hb Diederich, kept under *Spirographa fusisporella*, also present in the specimen).

Cornutispora intermedia Punith. & D. Hawksw.

Conidia of *Cornutispora* are typically Y-shaped, with a more or less linear 'main body' and two divergent 'arms'. Narrow appendages are usually present at the base of the main body and at the apex of each arm. Identification of *Cornutispora* species became complicated by the question of whether or not conidial length should include the basal appendage.

When Hawksworth (1976) described *Cornutispora lichenicola* he gave the conidial length 'from the truncate base to the point at which appendages diverge'. From this it was not clear if the basal appendage was included in his measurements. Later in the same paper he described the conidial base as 'truncate with a tapered, unbranched, cellular appendage 2.5–3 µm long', clarifying that his measurements did not include the appendage.

Punithalingham (2003) revised the known *Cornutispora* species and described two new species. Under *C. intermedia* he explained that conidial length is considered 'from the truncate base to a point on the apex', and he referred to the 'Basal conidial extension or basal appendage arising at the truncate base'. Thus, Punithalingham (2003) also measured conidia without appendages.

This has been wrongly understood by most subsequent authors, and it seems that at least Brackel (2008, 2010), Etayo (2017) and Knoph (2004) included the basal appendage in conidial length. This has led to much confusion and certainly to some misidentifications.

In species with a narrow main body the distinction between the lower part of the conidium and the basal appendage is often not obvious, so it is best to always include the basal appendage in conidial length. We have therefore re-estimated the conidial dimensions from Punithalingham (2003) by adding to the conidial length the average length of the basal appendage. We present here a new identification key in which the length of the main body always includes the basal appendage.

Specimens examined. USA Florida. Citrus Co.: Citrus Wildlife Mgmt. Area, Withlacoochee State Forest at intersection of CR 480 and Trail 13 (sect. 33), on *Phaeographis* cf. *leiogrammodes* (thallus), 1992, C5523U (MSC). Pasco Co.: Zephyrhills, Samuel W. Pasco Recreation Area (28.213°N, 82.048°W), on oak, on *P. major*, 2019, C10220B (hb Diederich). Sumter Co.: 7.3 mi. N of county boundary on SR 471, Green Swamp Wildlife Management Area, on sterile cf. *Phaeographis* (thallus), 1992, C5573Y (MSC).

Updated key to the species of *Cornutispora*

1 Conidial segments distinctly triangular, arranged in a circle, 11–17 µm diam. . . . . ***C. triangularis***

Conidia Y-shaped 2

2(1) Main body of conidia 4–5.2 µm long (basal appendage included); main body and arms swollen, of almost equal length 3

Conidia longer 4

3(2) Main body of conidia and arms slightly swollen, 1–1.5 µm wide; main body 4.2–4.6 µm long (basal appendage included) . . . . . ***C. pittii***

Main body of conidia and arms strongly swollen, 2.5–3 µm wide; main body 4–5.2 µm long . . . . . ***C. tricupalata***

4(2) Main body of conidia over 20 µm long, not or indistinctly swollen 5

Conidia shorter 6

5(4) Main body of conidia 20–24 × 2–3 µm; arms distinctly shorter than main body. . . . . ***C. limaciformis***

Main body of conidia 20–26 × 1.5–2 µm; arms almost as long as main body . . . . . ***C. ophiurospora***

6(4) Main body of conidia (2–2.5 µm wide) and arms (2.5–3 µm wide) strongly swollen; main body 9.5–11.5 µm long (basal appendage included) . . . ***C. ciliata***

Conidia not or slightly swollen 7

7(6) Main body of conidia 1.5(–2.0) µm broad, 10.5–12 µm long . . . . . ***C. lichenicola***

Main body of conidia 2–3 µm broad, 10.5–15.5 µm long [incl. *C. herteliana*] . . . . . ***C. intermedia***

Etayoa trypethelii (Flakus & Kukwa) Diederich & Ertz

This species has been reported by Ertz et al. (2014) from Florida, Collier Co. (Fakahatchee Strand State Preserve), Hernando Co., Hillsborough Co. (Hillsborough River State Park), Marion Co. (Ocala National Forest), Sarasota Co. (Myakka River State Park) and Taylor Co. (Big Blend Wildlife Management Area) on *Dyplolabia afzelii*, *Fissurina columbina*, *F. mexicana*, *Graphis caesiella*, *G. cupei*, *G. lucifuga*, *Graphis* sp., *Ocellularia americana*, *Phaeographis inconspicua*, *P. major*, *P. schizoloma* and *Phaeographis* sp.

Specimens examined. USA Florida. Pasco Co.: Zephyrhills, Henry Ave. (28.246°N, 82.177°W, alt. 30 m), on *Sarcographa tricosa*, 2015, C9918B (hb Diederich). Sumter Co.: Richloam Wildlife Management Area (28.526°N, 82.054°W), on *Coniarthonia pyrrhula*, *Graphis cupei*, *G. lucifuga* and *Leiorreuma sericeum*, 2016, C10143B (hb Diederich).

Hemigrapha graphidicola Diederich & Common, sp. nov. (Fig. 4)

MycoBank MB 831998

Diagnosis: Distinguished from other *Hemigrapha* species by the absence of ascomata, the presence of small, roundish to irregular conidiomata 70–130(–200) µm in diameter, the ellipsoid macroconidia with almost parallel sides (6.2–7.8 × 2.7–3.6 µm), and a different host species, *Graphis assimilis*.

Type: USA, Florida, Collier Co., Fakahatchee Strand State Preserve, trail north of Boardwalk (25.94183°N, 81.47405°W), on *Graphis assimilis*, 11 Nov. 2011, Common 9434L (BR 5030086831682 – holotype; hb Diederich – isotype).

Description. Ascomata unknown. Conidiomata pycnothyria, black, superficial, flat, roundish to elongate or irregular in form, often with a ±lobed margin, 70–130(–200) µm diam. Upper conidiomatal wall entirely covering the conidiogenous layer, 6–10 µm thick, composed of a single layer of ±parallel, radiating rows of dark brown, shortly rectangular or polygonal cells, 3–6.5 µm diam.; lower plate missing, although the border between the host cortex and the conidiogenous layer may become brownish; ostiole present, central, best visible when examining a whole conidioma by microscopy. Conidiophores absent. Conidiogenous cells arising from the upper conidiomatal wall, difficult to observe, subspherical, hyaline, ~3–4 µm diam. Macroconidia hyaline, aseptate, smooth, base rounded or indistinctly truncate, oblong, i.e. ellipsoid with almost parallel sides, (5–)6.2–7.8(–10) × (2.2–)2.7–3.6(–4) µm, L/B (1.5–)2.0–2.5(–3) (n = 105). Microconidia unknown.

Notes. The currently known species of *Hemigrapha* grow either on *Peltigerales* (Diederich & Wedin 2000) or on foliicolous *Byssoloma*, *Porina* or *Strigula* (Matzer 1996; Cáceres & Lücking 2000). This is the first known species on *Graphidaceae* and also the first one on a corticolous lichen.

Ascomata and conidiomata in *Hemigrapha* species are macroscopically similar and cannot be distinguished without microscopic examination. Two asexual stages have been observed, one producing macroconidia, previously known from *H. asteriscus* and *H. pseudocyphellariae*, and one producing microconidia, known from *H. asteriscus* and *H. atlantica* (Diederich & Wedin 2000).

The new species is known only from the macroconidial stage. *Hemigrapha asteriscus* differs by much larger conidiomata, up to 800 µm diam. and distinctly longer and narrower macroconidia, (8–)8.5–10(–10.5) × 2.5–2.7(–3) µm; *H. pseudocyphellariae* by smaller macroconidia, 5–6.5 × 2.5–3(–3.5) µm, that are almost rhomboid in form, always distinctly broader in the median part; *H. atlantica* by the larger conidiomata, 150–600 µm diam., in which only the microconidial morph is known; from *H. nephromatis*, no asexual stage is known, but ascomata are up to 500 µm diam.; as ascomata and conidiomata are of a similar size and thus macroscopically indistinguishable in all known *Hemigrapha* species, this suggests that conidiomata in *H. nephromatis* should also be up to 500 µm diam., and thus much larger than in the new *H. graphidicola* (Diederich & Wedin 2000). In the four *Hemigrapha* species known from foliicolous lichens (Matzer 1996; Cáceres & Lücking 2000), conidiomata are unknown, and ascomata are elongate, up to 700 µm long in *H. pilocarpacearum* and up to 1400–1600 µm long in the other three species, and less than 150 µm wide.

Etymology. Growing on *Graphis*.

Host and distribution. Lichenicolous on the thallus of *Graphis assimilis*, the host not visibly damaged. Known only from the Fakahatchee Strand State Preserve in Florida, where it appears to be rather common. Although 26 species of *Graphis* are known from the type locality and surroundings (Lücking et al. 2011), no other *Graphis* species has been found to host the new *Hemigrapha*.

Additional specimens examined (all on *Graphis assimilis*). USA Florida. Collier Co.: Fakahatchee Strand State Preserve, trail from Gate 7 (25.9796°N, 81.4101°E), 2011, C9370L (hb Diederich); ibid., K2 trail (26.010°N, 81.416°W), 1997, C7356R, C7368S (MSC); ibid., Big Cypress Bend Boardwalk on U.S. 41 (25.944°N, 81.468°W), 1997, C7425K (MSC); ibid. (25.925°N, 81.470°W), 2014, C9827M (MSC).

Lawreya Ertz, Common, Diederich & U. Braun, gen. nov.

MycoBank MB 831999

Diagnosis: Differs from *Sclerococcum* in its distant phylogenetic position and in having well-developed stromata in which simple, medium to dark brown, smooth conidia are formed within bulbil-like conidiogenous loculi, the mode of conidiogenesis being unclear.

Type: *Lawreya glyphidiphila* U. Braun, Common, Diederich & Ertz.

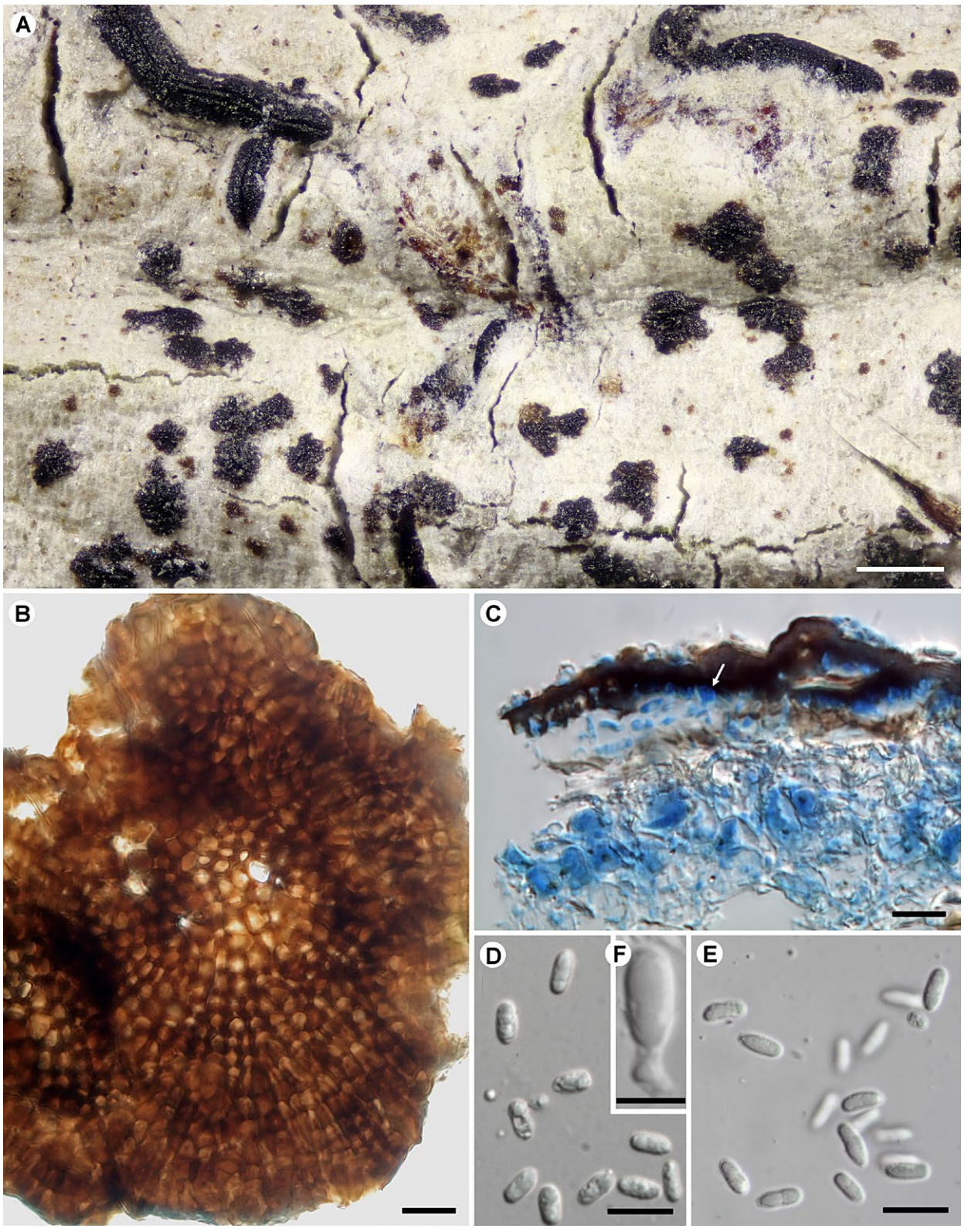

Figure 4. *Hemigrapha graphidicola* [A–D: holotype; E: C9827M; F: C7356R]. A – conidiomata on the thallus of *Graphis assimilis*; B – conidioma (pycnothyrium) in surface view, in water; C – section through conidioma showing conidiogenous cell (arrow) arising from upper conidiomatal wall, in LCB; D, E – conidia in water; F – conidiogenous cell (upper part) and conidium in water. Scales: A = 200 µm; B–E = 10 µm; F = 5 µm. Photos: P. Diederich (A–D) and R. Common (E–F).

Description. Mycelium immersed; hyphae sparse, septate, subhyaline to pigmented, wall smooth. Conidiomata initially small, internal, flattened, sporodochioid, pulvinate, colourless; later turning brown, becoming stromatic, immersed to erumpent, compact, macroscopically black, size and shape variable, subglobose, hemispherical, applanate to irregularly shaped; stromatic cells subcircular to angular-irregular in outline; during maturation, with few or numerous subspherical, almost superficial conidiogenous loculi, giving the upper surface a moriform appearance,

made of bulbil-like structures; when fully mature, these bulbil-like loculi open irregularly, the conidioma surface being macroscopically sometimes centrally dented but without a deep cavity, i.e., not distinctly cupulate. Conidiogenous cells not evident, conidia formed from colourless or pale swollen hyphal cells arranged within conidiogenous loculi; conidiogenesis thallic, possibly meristem thallic. Conidia solitary, reminiscent of chlamydospores, subglobose to mostly angular-irregular, simple, brown, wall rather thick and ±smooth.

Notes. After examination of the lichenicolous fungus on *Glyphis scyphulifera* it quickly became clear that we were dealing with an undescribed species, but in the context of lichenicolous genera, the generic allocation of the new species was challenging and complicated. At first glance the new species was reminiscent of *Coniambigua phaeographidis* (Etayo & Diederich 1995). In the original publication, the conidiomata of *Coniambigua* were referred to as 'pycnidia' but this classification is not appropriate and has to be corrected. True pycnidia are characterized by being globose to lageniform, usually with a thin brown wall, closed or usually provided with a distinct ±circular apical ostiolum (Sutton 1980; Kiffer & Morelet 2000). The conidiomata of *Coniambigua* are stromatic in the sense of Sutton (1980) and range from being sporodochial to pseudopycnidial. The apical opening, when present, is not preformed but is caused by fissures and rupturing. The stromata and wall structures of the pseudopycnidia are colourless. This is quite unusual for stromatic conidiomata, which are usually distinctly pigmented. Distinct conidiogenous cells are not evident. The conidiogenesis is thallic, i.e., swollen hyphal cells transform into conidia which are reminiscent of chlamydospores (details of the thallic conidial formation are not discernible on the host and require observations in culture). The general habit of the conidiomata and the conidiogenesis of the new species on *Glyphis scyphulifera* resemble *Coniambigua phaeographidis*, but the lack of pigmented stromatic structures and conidiomata that finally may become pseudopycnidial impede its allocation to this genus.

Sclerococcum is another lichenicolous genus that has to be taken into consideration. Diederich (2015) published a survey of asexual *Sclerococcum* spp., including a key to the species, and described two new species assigned to this genus. One of them, *S. aptrootii* (on *Fissurina dumastii*, Puerto Rico), is morphologically rather similar to the new species on *Glyphis*, above all due to its smooth, one-celled conidia. *Sclerococcum crassitunicatum* (on *Cladonia* spp. in North America: USA, Alaska; Zhurbenko & Pino-Bodas 2017) is an additional comparable species. Amongst lichenicolous ascomycete genera, the asexual stage of *Sclerococcum* (s.lat.), characterized by having sporodochial-stromatic conidiomata with inconspicuous conidiogenous cells and pigmented conidia, seemed to be suitable to accommodate the new species on *Glyphis*, at least at first glance. The conidiogenesis of *Sclerococcum* spp. is little examined and poorly comprehended. It is usually classified as blastic (mono- or polyblastic or possibly meristem thallic, according to Seifert et al. 2011). Hawksworth & Jones (1981) examined *S. sphaerale*, the type species of *Sclerococcum*, in vitro, and described and illustrated the conidial development but nevertheless avoided a specific classification of the conidiogenesis. However, in culture they found hyphae giving rise to chains of cells forming more deeply pigmented conidia, with a basipetal arrangement. They emphasised that these details were not visible in vivo. Diederich (2015) described the conidiogenesis of *S. aptrootii* to be 'mono-, rarely polyblastic' and conidia in basipetal chains, which is contradictory. Conidia formed in basipetal chains agree with observations in Hawksworth & Jones (1981) for *S. sphaerale*. However, basipetal conidial formation is characteristic for meristem arthric (meristem thallic) conidiogenesis (Kiffer & Morelet 2000; Seifert et al. 2011). In the type material of *L. glyphidiphila*, distinct conidiogenous cells are not evident, and blastic conidiogenesis has not been observed. Swollen hyphal cells turn into conidia which are reminiscent of chlamydospores. The conidiogenesis in *Sclerococcum* can in general be classified as thallic, probably meristem thallic (meristem arthric), i.e., the conidia result from the basipetal transformation of the conidiogenous hyphae into conidia (Kiffer & Morelet 2000). Descriptions of (micronematous) conidiophores in *Sclerococcum* species seem to refer to such 'conidiogenous hyphae'. Another problem regards the pronounced stromatic structure of the conidiomata in the new species on *Glyphis*, which is lacking or less evident in species of *Sclerococcum*. Ellis (1976) described the stromata in *Sclerococcum* as lacking or rudimentary, but stromatic cells may occur to a certain extent in *S. sphaerale* (Diederich et al. 2013: 68, fig. 3B, C) and *S. aptrootii* (Diederich 2015: 36–37, figs 1D, E, 2A). Basal stromatic layers have also been described in *S. gelidarium* (Berger 2000, termed 'paraplectenchyma'), but less pronounced than in the fungus on *Glyphis*. Mature conidiomata of the species on *Glyphis* may be centrally dented with age, imitating young pseudopycnidia. This phenomenon was also described for *Sclerococcum tephromelarum* (Etayo & Calatayud 1998), which is characterized by having conidiomata that finally become concave (crateriform). Attempts to find an appropriate genus for the new lichenicolous species on *Glyphis scyphulifera* using Diederich's (in Seifert et al. 2011) key to lichenicolous hyphomycete genera led straight to *Sclerococcum*. The asexual members of this genus undoubtedly represent a heterogeneous assemblage. The new species on *Glyphis* and other species with one-celled smooth conidia, including *S. aptrootii*, probably are not congeneric with *S. sphaerale*, the type species of *Sclerococcum*, and other species with multi-celled conidia. Diederich et al. (2013) clarified the phylogenetic position of *S. sphaerale*, and hence the phylogenetic affinity of *Sclerococcum* s.str., which clustered within the Eurotiomycetes, close to *Dactylospora*. Diederich et al. (2018) synonymized *Dactylospora* under *Sclerococcum* and showed that the genus belongs to the *Dactylosporaceae* in the recently described *Sclerococcales*. The proper generic affiliation of the new species on *Glyphis* required phylogenetic analyses. First results clearly show that the nLSU sequences (viz. GenBank

accessions MK693147 for specimen C9506N, MK693148 for specimen C10000B and MK693149 for specimen C10035B) retrieved from this species form a distinct clade of its own within the *Teratosphaeriaceae* (*Capnodiales*) (Fig. 5), thus far distant from *Sclerococcum* s.str. as determined by its type species, *S. sphaerale.* Hence, the new species on *Glyphis* needs to be assigned to a new genus, *Lawreya* gen. nov. The new genus differs from *Sclerococcum* s.str. in having well-developed stromata and one-celled smooth conidia, and its introduction is supported by results of phylogenetic analyses.

Etymology. The new genus is named in honour of our friend James D. Lawrey (Virginia, USA), in recognition of his important contribution to lichenology, especially in the fields of lichen biology (specifically the ecological role of metabolites and monitoring), lichenicolous fungi and basidiolichens.

Lawreya glyphidiphila U. Braun, Common, Diederich & Ertz, sp. nov. (Figs 5–8)

MycoBank MB 832000

Diagnosis: Resembling *Sclerococcum aptrootii* and *S. crassitunicatum*, but stromatic portions of conidiomata more strongly developed, conidia smaller, (2.7–)3.5–4.5(–5.3) × (2–)2.6–3.5 (–4.5) µm, formed in bulbil-like loculi, and lichenicolous on other hosts, *Glyphis scyphulifera* and rarely *Trypethelium eluteriae*.

Type: USA, Florida, Pasco Co., Zephyrhills, Fairlawns Ave. (28.248°N, 82.192°W, alt. 30 m), on *Glyphis scyphulifera* growing on *Lagerstroemia* twigs, 29 Jan. 2014, Common 9642 (BR 5030086830654 – holotype; HAL 3277 F, MSC, hb Diederich – isotypes).

Description. Mycelium of sparingly developed hyphae, ~3–4 µm wide, septate, subhyaline to pigmented, wall smooth. Conidiomata lichenicolous, scattered to

Figure 5. Maximum likelihood (ML) best tree including *Lawreya glyphidiphila* (in bold; clade highlighted). ML bootstrap values (BS) are indicated over branches. Internal branches supported by Bayesian posterior probability values (BPP) ≥ 0.95 are represented by thicker lines.

gregarious, occasionally seriate, separate to confluent, immersed to superficial, compact, stromatic, black, subglobose, hemispherical, applanate to irregularly shaped, 0.1–1.2 mm diam.; stromatic cells subcircular to angular-irregular in outline, 3–7 µm diam., brown, wall to 1 µm wide; during maturation, with few or numerous subspherical, almost superficial conidiogenous loculi, giving the upper surface a moriform appearance, covered by bulbil-like structures 30–90 µm diam.; when fully mature, these bulbil-like loculi open irregularly, releasing conidia. Conidiogenous cells not evident, conidia formed from colourless or pale swollen hyphal cells arranged within conidiogenous loculi, 3–6 µm diam. Conidia simple, medium to dark brown, (2.7–)3.5–4.5(–5.3) × (2–)2.6–3.5(–4.5) µm, L/B (1–)1.1–1.5(–2.2) (n = 165), wall 0.2–0.8 µm wide, ±smooth.

Etymology. Growing preferentially on *Glyphis*.

Hosts and distribution. Lichenicolous on the thallus of *Glyphis scyphulifera*, more rarely on *Trypethelium*

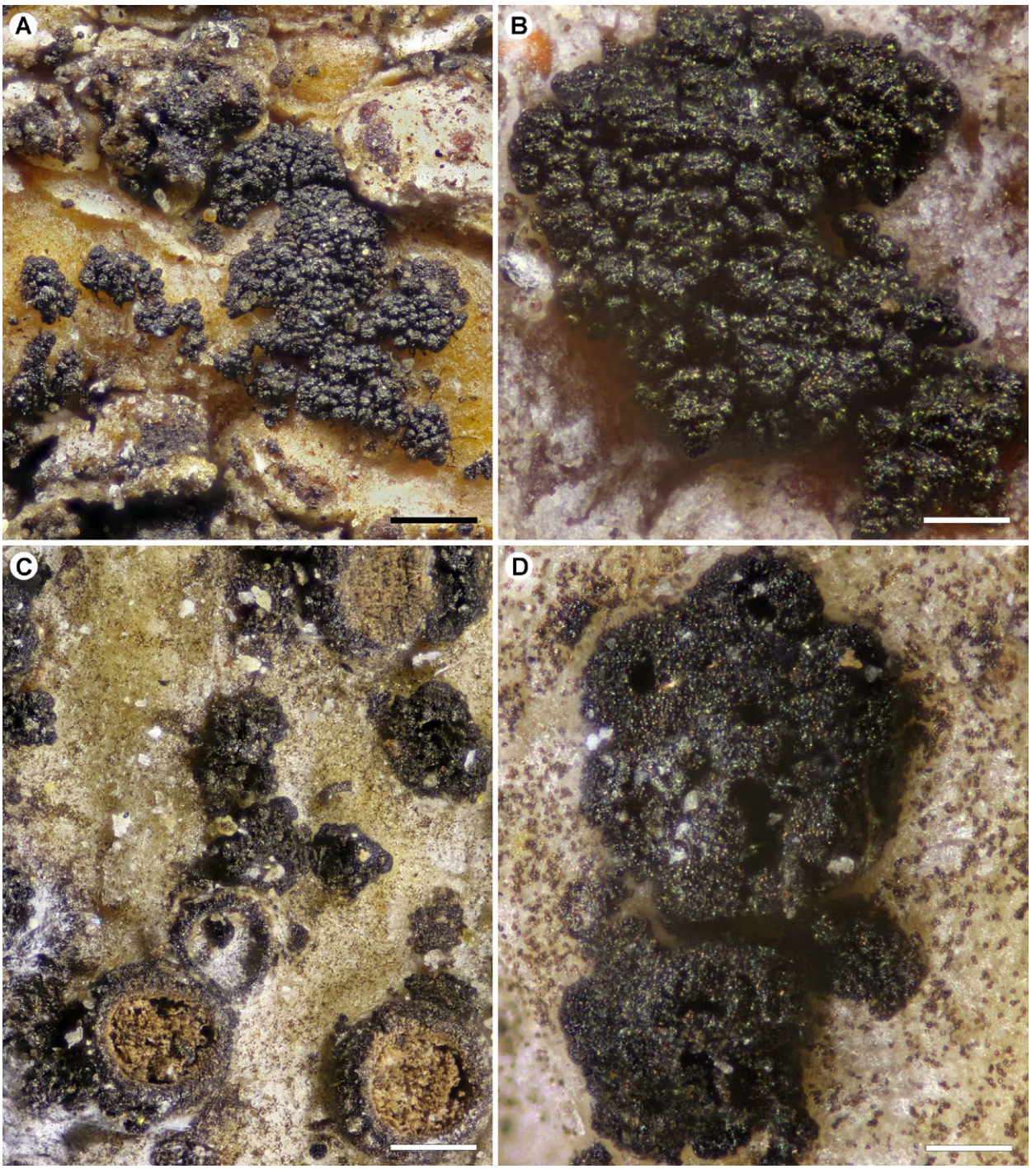

Figure 6. *Lawreya glyphidiphila* [A–B: C9510B; C–D: holotype]. A – maturating stromata with moriform surface on *Trypethelium eluteriae*, each 'bulbil' representing a conidiogenous loculus; B – the same at higher magnification; C – mature stromata on *Glyphis scyphulifera*; D – the same at higher magnification, showing irregular openings of mature conidiogenous loculi; note the numerous brown conidia covering the host thallus and the black stromata (on which they are visible through the reflective surface). Scales: A, C = 200 µm; B, D = 50 µm. Photos: P. Diederich.

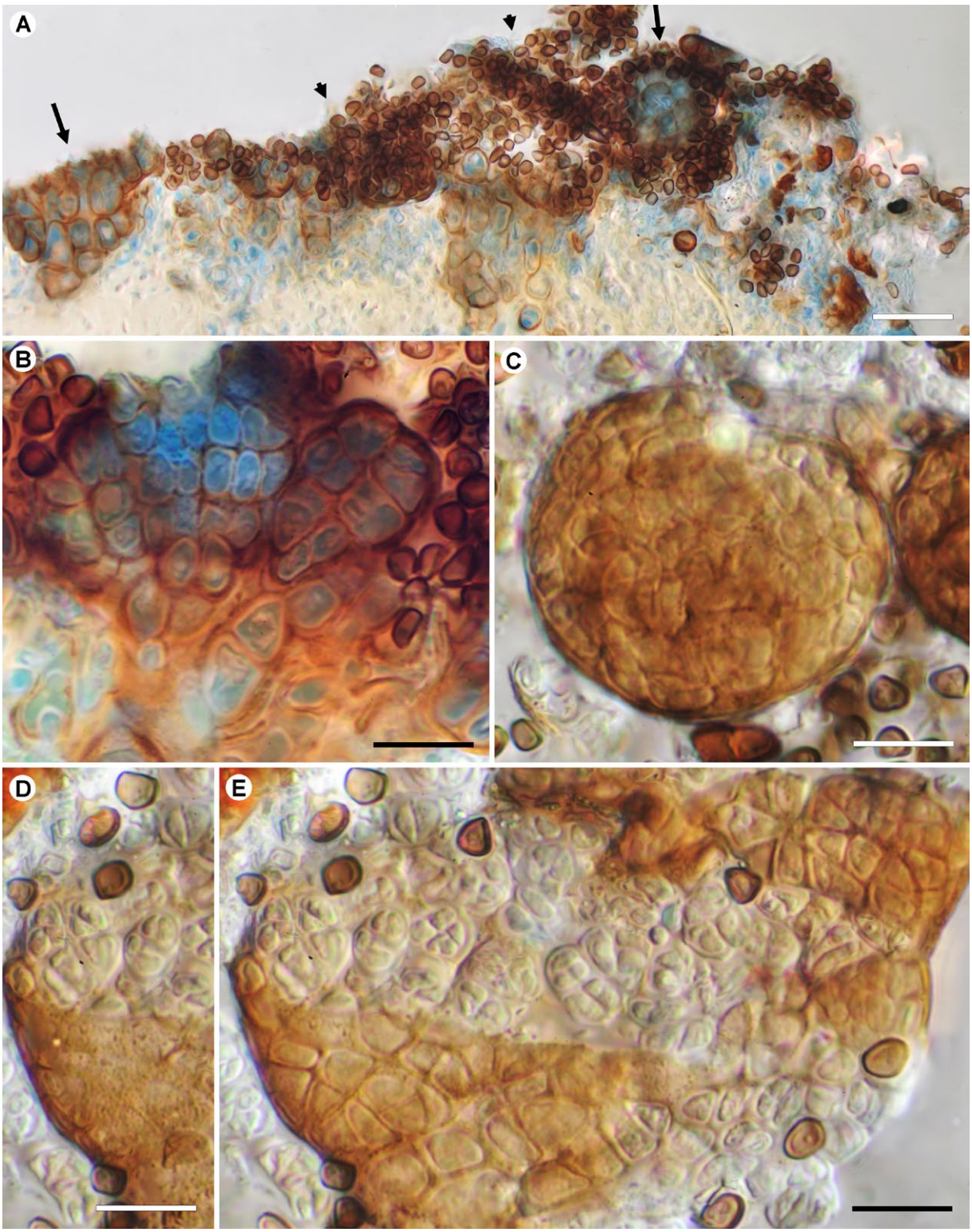

Figure 7. *Lawreya glyphidiphila* [C9510B]. A – section through a young stroma on *Trypethelium eluteriae*, with young developing (arrows) and mature (arrow heads) conidiogenous loculi, the mature ones producing conidia; B – section through young developing conidiogenous loculus; C – section through immature subspherical conidiogenous loculus; D – immature subspherical conidiogenous loculus broken and opened after pressure on cover glass, showing verruculose ornamentation of outer wall; E – same at a different focus level, showing cells of outer wall and interior cells. Photos A–B in LCB, the others in water. Scales: A = 20 µm; B–E = 10 µm. Photos: R. Common.

eluteriae, not gall-inducing, not causing any visible damage to the hosts. Known only from Florida, where it seems to be very common and abundant.

Additional specimens examined (all on *Glyphis scyphulifera*, unless otherwise mentioned). USA Florida. Citrus Co.: Chassahowtzka Springs, near boat ramp, 1992, C5489K (MSC). Collier Co.: Everglades City, near Everglades City Motel on FL 29 (25.862°N, 81.386°W), 1997, C7346D (MSC). Hillsborough Co.: Along CR. 581, 3.2 mi. S of junction with I-75, SE of bridge (28.087º N, 82.407º W), 1995, C6625B (MSC); ibid. (28.095°N, 82.399°W), 1996, C6892H (MSC). Pasco Co.:

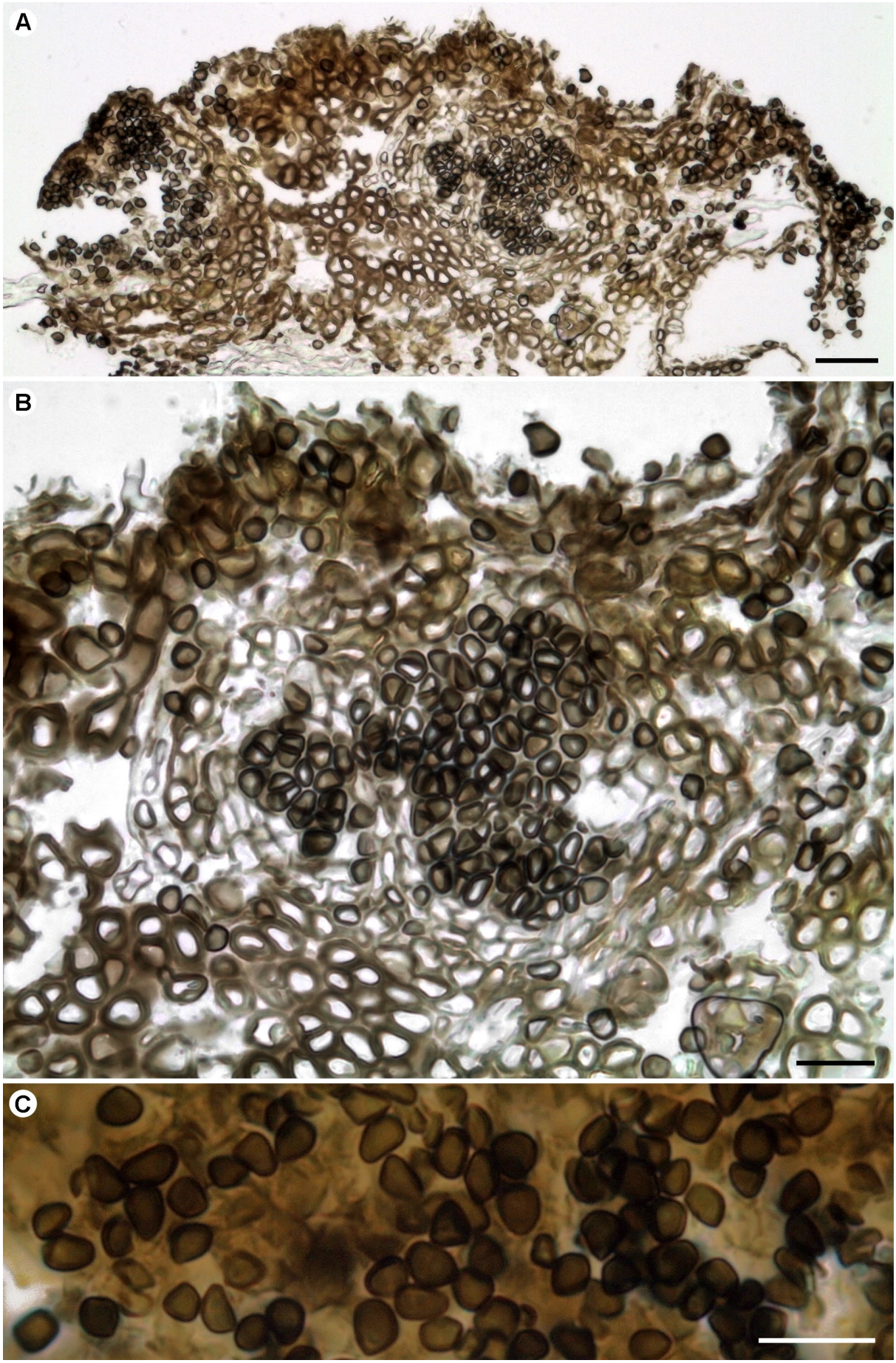

Figure 8. *Lawreya glyphidiphila* [holotype]. A, B – section through mature stroma, showing subglobose conidiogenous loculi filled with conidia, in water; C – conidia, in water. Scales: A = 20 µm; B–C = 10 µm. Photos: P. Diederich.

Zephyrhills, Henry Ave. (28.248°N, 82.179°W, alt. 25 m), 2013, C9578A (MSC, hb Diederich); ibid., on *Trypethelium eluteriae*, C9578B (hb Diederich); ibid., 2015, C9903P (MSC, hb Diederich), C9929B (hb Diederich); ibid., 2009, C9018B (MSC); ibid., 2010, C9052B (MSC); ibid., at intersection of Fort King Rd. and Gall Blvd. (28.249°N, 82.19°W, alt. 35 m), 2015, C9961B (HAL 3278 F, MSC, hb Diederich); ibid., 38439 5th Ave. (28.248°N, 82.186°W, alt. 30 m), 2015, C9902D (MSC, hb Diederich); ibid., C9881 (BR, MSC); ibid., Woodfern Ave., 2012, C9506N (BR, hb Diederich), C9509A (MSC, hb Diederich); ibid., on *T. eluteriae*, C9510B (MSC, hb Diederich); ibid., at intersection of US 301 and CR 54 (28.213°N, 82.156°W), 2016, C10000B (BR); ibid., Zephyr Park (28.231°N, 82.186°W), 2016, C10035B (BR, MSC).

Skyttea graphidicola Diederich, Common & Suija, sp. nov. (Figs 9–10)

MycoBank MB 832001

Diagnosis: Characterized by small apothecia, 80–100 µm diam., a brown, K– exciple, narrowly ellipsoid, straight, nonsigmoid ascospores, ~11–14 × 2.5–3 µm in diameter, and the host selection (*Graphis* spp.).

Type: USA, Florida, Collier Co., Fakahatchee Strand State Preserve, Janes Scenic Drive (25°58.74′N, 81°22.26′W), on *Graphis oshioi*, 2014, Common 9793B (BR 5030086829917 – holotype). GenBank ITS: MK282255.

Description. Ascomata initially immersed, later erumpent, brown to blackish, (60–)80–100(–120) µm diam.; margin in opened ascomata 30–40 µm thick (surface view), smooth when young, becoming striate; pore reaching 35% of the ascomatal diameter in mature ascomata. Exciple laterally brown, K–, up to 35 µm thick; basal exciple brown, up to 25 µm thick; excipular hairs hyaline to brownish, not distinctly curved, 8–12 × 3–4 µm. Subhymenium hyaline, ~5 µm thick. Hymenium 30–52 µm thick. Epihymenium brownish. Paraphyses filiform, simple or rarely branched, 1.5–2.5 µm thick. Asci cylindrical to clavate, 8-spored, wall apically thicker, biconvex, I–, K/I–, (30–)33.6–43.3(–46) × (5.5–)5.8–7.5(–8) µm (n = 15). Ascospores hyaline, narrowly ellipsoid, straight, not sigmoid, aseptate, (9–)10.9–14.1(–16) × (2.3–)2.6–3.1(–3.5) µm, L/B (3.2–)3.7–5.2(–5.9) (n = 76).

Notes. The new species is distinguished from most hitherto known species of *Skyttea* by its entirely brown, K– exciple. Most other species have a greenish, K+ olivaceous excipular pigment, and some, including the generic type *S. nitschkei*, have a dark reddish black, K+ bright aeruginose green pigment, and/or a brownish, K+ purple to violet pigment.

According to our phylogenetic analysis, the new species belongs to a well-defined *Skyttea* clade (BS = 100, PP = 1.0), being sister to *S. insignis* and *S. lecanorae* (BS = 75; PP = 0.98). Morphologically, it strongly resembles both by the very small apothecia and similar elongate and narrow ascospores. The new species is distinguished mainly by the ascospore size, ~11–14 × 2.5–3 µm, vs. mainly 7–9 µm long in *S. lecanorae* (Diederich & Etayo 2000) and 16.5–21.5 µm long in *S. insignis* (Driscoll et al. 2016). Although specimen Common 9370C is by far the richest and best developed, we nevertheless chose specimen Common 9793B as the holotype, as it is the only specimen from which DNA sequences could be obtained.

Etymology. Growing on *Graphis*.

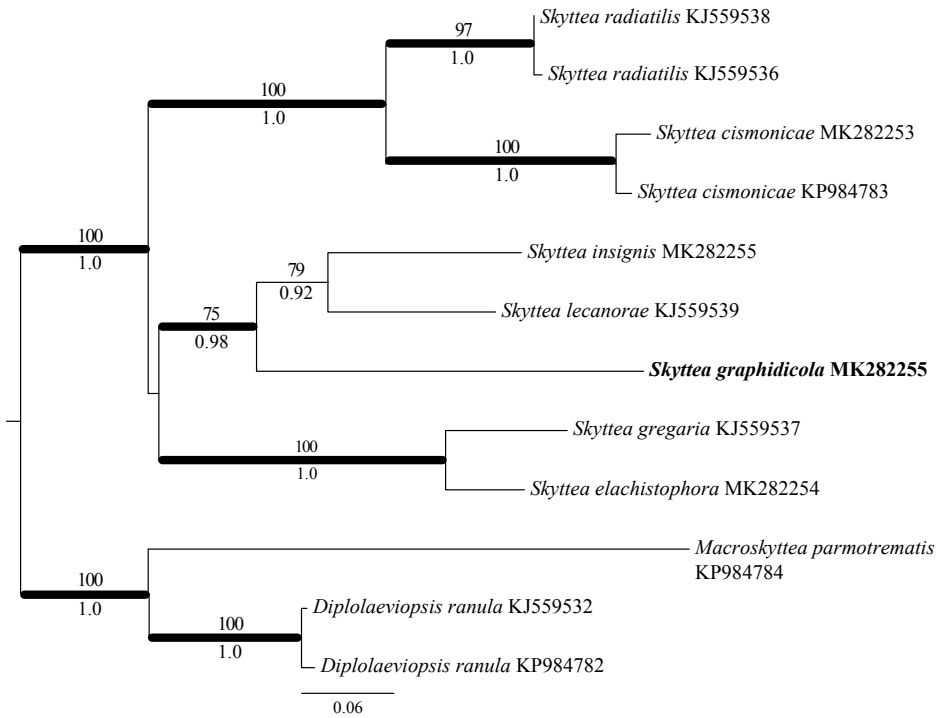

Figure 9. Maximum likelihood phylogeny based on 12 ITS sequences, showing position of *Skyttea graphidicola* (in bold) within the *Skyttea* clade. Branches with bootstrap values (BS) ≥ 70 (indicated above branches) and posterior probabilities (PP) ≥ 0.95 (indicated below branches) are considered as supported.

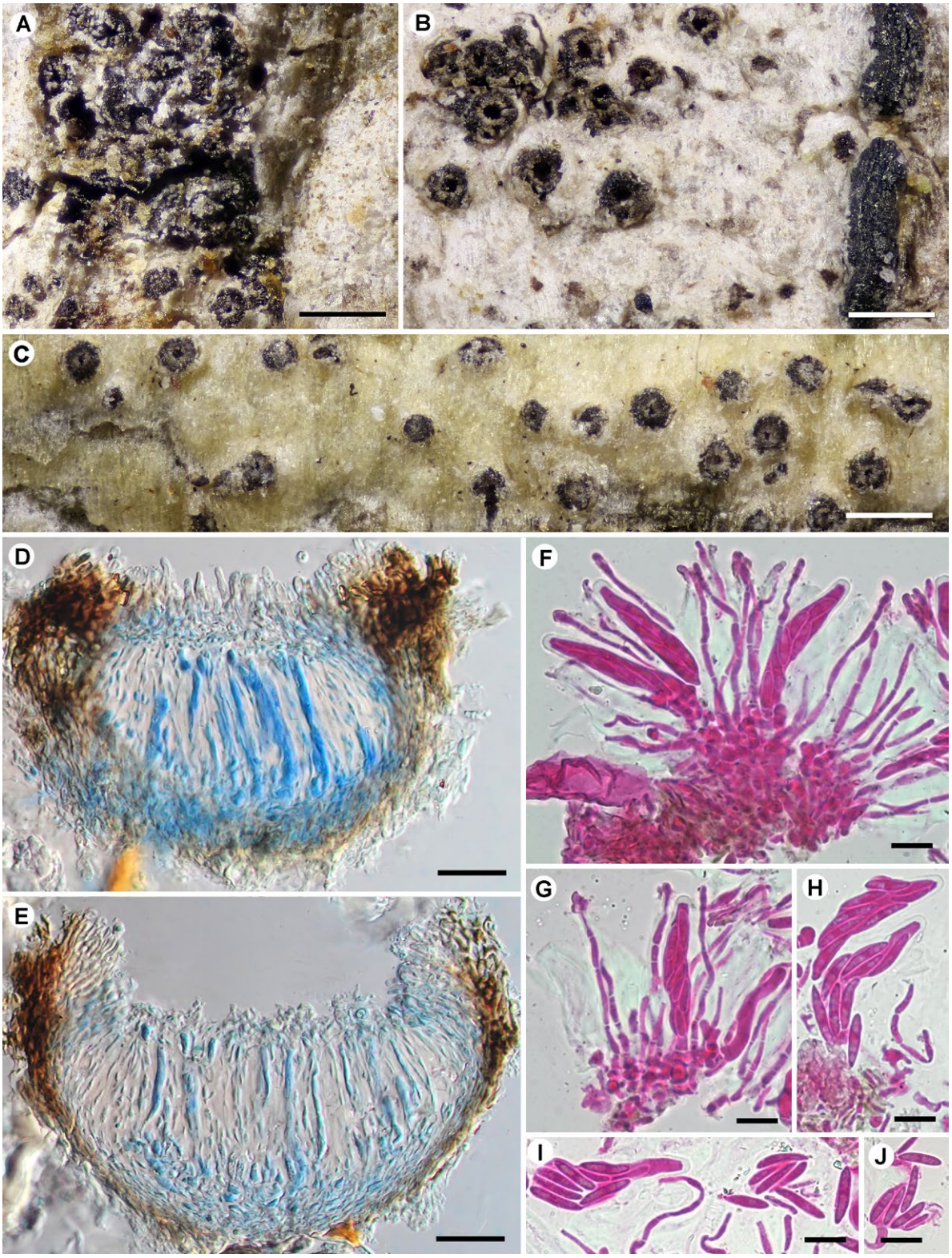

Figure 10. *Skyttea graphidicola* [A: holotype; B: C9409E; C–J: C9370C]. A–C – ascomata partly immersed in the thallus of *Graphis oshioi* (A, C) or of *Melaspilea* sp. (B; host apothecia visible on the right); D, E – sections through ascomata, showing excipular hairs (D, through lateral part of ascoma; E, through central part), in LCB; F–J – hymenium, paraphyses, asci and ascospores, in 5% KOH + phloxine. Scales: A–C = 200 µm; D–E = 20 µm; F–J = 10 µm. Photos: P. Diederich (A–C, F–J) and R. Common (D–E).

Hosts and distribution. Known only from the Fakahatchee Strand State Preserve in Florida, where it grows on the thallus of several *Graphis* species, including *G. caesiella* and *G. oshioi*. In one locality the fungus is also present in a specimen of an unidentified lichenized *Melaspilea* s.lat. species, although it is not excluded that it grows on a sterile *Graphis* thallus adjacent to the *Melaspilea* thallus. It does not visibly damage the host thallus.

Additional specimens examined. USA Florida. Collier Co.: Fakahatchee Strand State Preserve, near lake by Ranger Station (25.9796°N, 81.4101°W), on *Graphis caesiella*, 2011, C9409F (hb Diederich); ibid., possibly on a corticolous,

lichenized *Melaspilea* s.lat., C9409E (hb Diederich); Fakahatchee Strand State Preserve, trail from Gate 7 (25.9796°N, 81.4101°E), on *G. oshioi*, 2011, C9370C (MSC, hb Diederich); Fakahatchee Strand State Preserve, Janes Scenic Drive, just past bend near gate 14 (26.020°N, 81.414°W), on *G. oshioi*, 1997, C7313I (MSC).

Spirographa fusisporella (Nyl.) Zahlbr.

≡ *Graphis fusisporella* Nyl.

= *Opegrapha spiralis* Müll.Arg., ≡ *Spirographa spiralis* (Müll. Arg.) Zahlbr.

Both *Graphis fusisporella* and *Opegrapha spiralis* were originally described as lichens, distinguished from related species by the polysporous asci and the unusual ascospores. Santesson (1993) recognized that they represent lichenicolous fungi developing in the host hymenium, and he lectotypified both on the lichenicolous fungus.

When Nylander (1866) described *Graphis fusisporella*, he wrote that externally the species resembles *Fissurina nitida*, suggesting that the host may be a species of *Fissurina*. Müller (1880) wrote that *Opegrapha spiralis* is macroscopically similar to *O. bonplandii*, *O. interalbicans*, etc. As some *Graphis* species, such as *G. brittoniae* (see below), have *Opegrapha*-like lirellae (Seavey & Seavey 2011), the host of *O. spiralis* may as well be a species of *Graphis*. We refrained from studying the two type specimens, as this should be done within the framework of a taxonomic revision of the genus *Spirographa*.

In Florida we collected what obviously represents the same species in the hymenium of *Graphis cupei*. We also have examined a specimen collected by R. Harris on a *Graphis* containing norstictic acid; additional material of the host is kept in NY as Harris 23509 and may belong to *Graphis brittoniae* (Seavey & Seavey 2011).

Specimens examined. USA Florida. Collier Co.: Fakahatchee Strand State Preserve, Janes Scenic Drive (25°58.74′N, 81°22.26′W), on *Graphis cupei*, 2014, C9736C (with *Cornutispora ciliata*), C9755I, C9763K (hb Diederich). Franklin Co.: *Taxodium* swamp W of Florida Hwy. 65, 4.8 mi. N of Sumatra, Apalachicola National Forest, on *Graphis*, 1990, Harris 25021 (NY).

Strigula graphidicola Diederich & Common, sp. nov. (Fig. 11–12)

MycoBank MB 832002

Diagnosis: Distinguished from most *Strigula* species by being non-lichenized and lichenicolous, by the host selection, *Graphis assimilis*, the particularly small ascomata (29–36 µm diam.) and conidiomata (33–41 µm diam.), the mucronate to subrostrate pycnidia, and the presence of two (instead of one) basal conidial appendages.

Type: USA, Florida, Sumter Co. (28.347°N, 82.055°W), on dead branches of oak, on *Graphis assimilis*, 30 July 2016, Common 10171A (BR 5030086828880 – holotype; hb Diederich – isotype).

Description. Lichenized thallus absent. Ascomata perithecia, half immersed to almost superficial, subspherical, with a flattened or slightly convex ostiolar region, reddish brown to dark brown, (26–)29–36(–39) µm diam. (n = 22, from holotype). Perithecial wall medium to dark brown in the upper part, paler below, of isodiametric cells, 6–11 µm diam.; involucrellum absent. Paraphysoids sparse, 1.8–3 µm diam. Asci fissitunicate, broadly ellipsoid, basal narrow 'foot' present or absent, wall apically thickened, I–, (20–)23–27(–33) × (9–)11–13 µm, 8-spored. Ascospores 2–3-seriate, 1-septate, not breaking in semi-spores, hyaline, (8.8–)10.0–12.5(–13.8) × (2.5–)2.8–3.7(–4.0) µm, L/B (2.8–)3.0–4.1(–4.5) (n = 24, from 3 specimens, incl. type). Conidiomata pycnidia, subspherical, partly immersed to almost superficial, distinctly ostiolate, mucronate to subrostrate, dark brown to black, (29–)33–41(–47) µm diam. (n = 45, from holotype). Conidiomatal wall medium brown in lower half, dark brown in upper half, of isodiametric cells ~4–7.5 µm diam. Conidiogenous cells elongate, subcylindrical. Macroconidia hyaline, 1-septate, not constricted at the septum, smooth, without halo, subcylindrical, apically rounded, basally truncate, (9.0–)11.6–14.2(–16.3) × (2.0–)2.5–3.0(–3.4) µm, L/B (3.0–)4.0–5.5(–6.5) (n = 90, from nine specimens, incl. type), with one straight apical mucoid appendage 3.5–5.5 µm long and two parallel or divergent basal appendages 4.5–7 µm long. Microconidia not observed.

Notes. Roux & Sérusiaux (2004) presented a remarkable revision of the genus *Strigula* in Europe and Macaronesia. The 23 species studied and recognized by these authors are all lichenized, and none of them are known to grow on lichens. Similarly, Lücking (2008) revised the foliicolous *Strigula* species from the Neotropics (26 species), and none of them are lichenicolous. Etayo (2002) described the first lichenicolous, non-lichenized species, *S. dichosporidii* Etayo, collected on *Dichosporidium nigrocinctum* in Colombia. He further reported a probably undescribed specimen on *Dictyonema*, known only from the asexual stage, and two additional morphologically similar specimens were discovered by Etayo & Sancho (2008) on *Nephroma* and *Pseudocyphellaria*.

The new *Strigula graphidicola* is the second described lichenicolous species of the genus. It is distinguished from all hitherto known species by the extremely small ascomata and conidiomata, the mucronate to subrostrate pycnidia, and the presence of two (instead of one) basal conidial appendages. Conidiomata are present and abundant in each known specimen and are easily recognizable under strong magnification by the blackish beaked pycnidia. Ascomata are often absent, but if present are always intermixed with conidiomata. They can be distinguished macroscopically from the conidiomata by being subspherical, not subrostrate, and by the colour: medium to dark brown, not blackish.

Etymology. Growing on *Graphis*.

Host and distribution. The new species seems to be confined to *Graphis assimilis*. It is known only from Florida, where it appears not to be rare, including in residential areas. Although the host thalli are not obviously damaged, many of them are sterile; the identification of some was based on fertile thalli in the same collection.

Additional specimens examined (all on *Graphis assimilis*). USA Florida. Pasco Co.: Zephyrhills (28.2458°N, 82.1867°W), on oak twigs, 2015, C9928B (MSC, hb Diederich); ibid., along Henry Ave. (28.24°N, 82.18°W), on *Eriobotrya*, 2015, C9921B (hb Diederich); ibid., Samuel W. Pasco Recreation Area (28.213°N, 82.048°W), on oak, 2019, C10216B (hb Diederich). Hillsborough Co.: Hillsborough River State Park (28.15°N, 82.24°W), 1990, C4891C, C4927A (MSC); ibid., Florida Trail (28.15°N, 82.24°W), 2011, C9482A (MSC, hb Diederich); ibid., C9255B (hb Diederich); ibid., Parking Area 1, north along 301, C9270E (hb Diederich); ibid., trail from Parking Area 2, 2011, C9218F (MSC); along CR. 581, 3.2 mi. S of junction with I-75, 1995, C6660B (MSC); along Morris Bridge Rd., near Morris Bridge, 1995, C6864E (MSC).

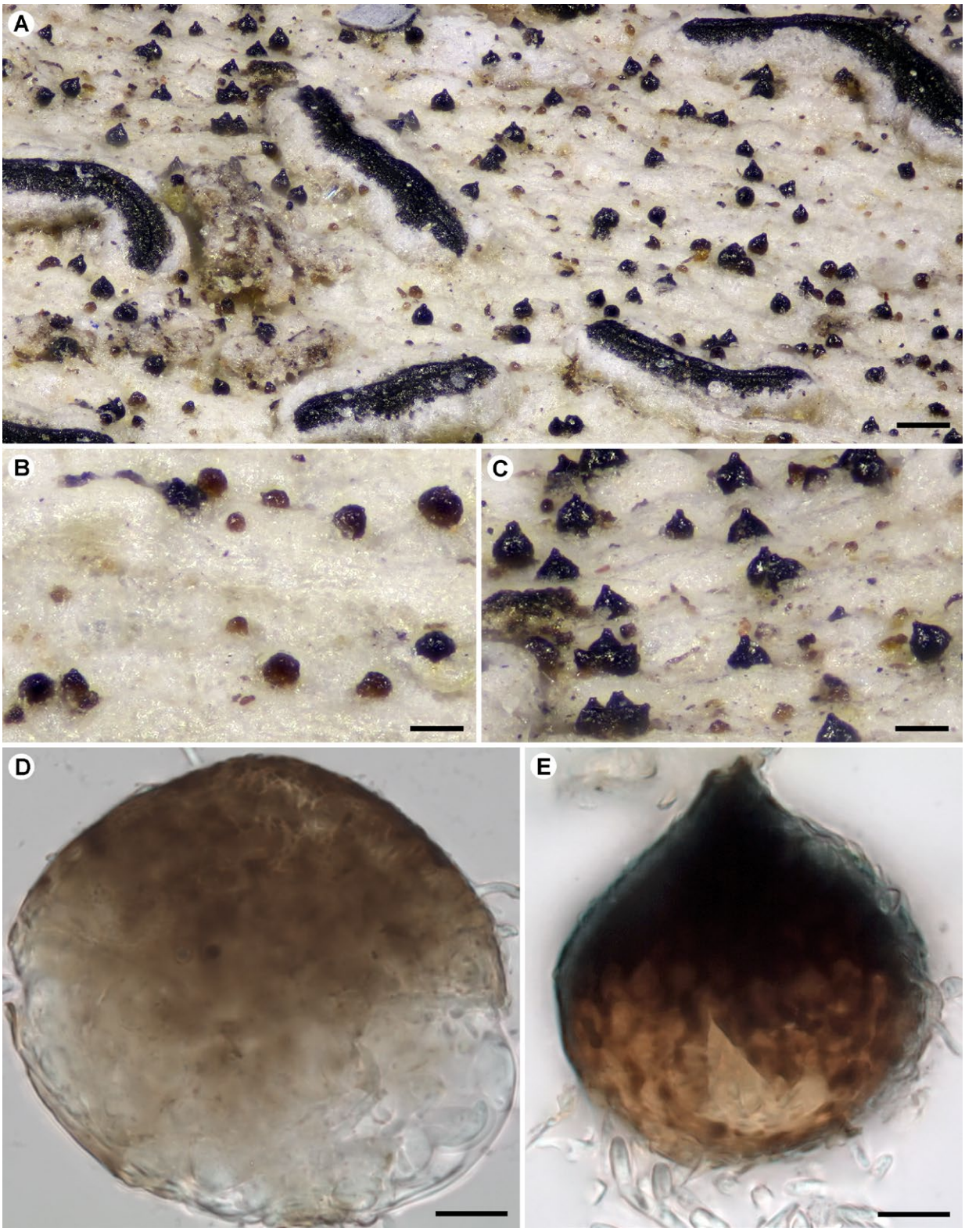

Figure 11. *Strigula graphidicola* [A–D: holotype; E: C9842B]. A – conidiomata (and a few intermixed ascomata) on the thallus of *Graphis assimilis*; B – ascomata; C – conidiomata; D – ascoma, in water; E – conidioma, in water. Scales: A = 100 µm; B–C = 50 µm; D–E = 10 µm. Photos: P. Diederich.

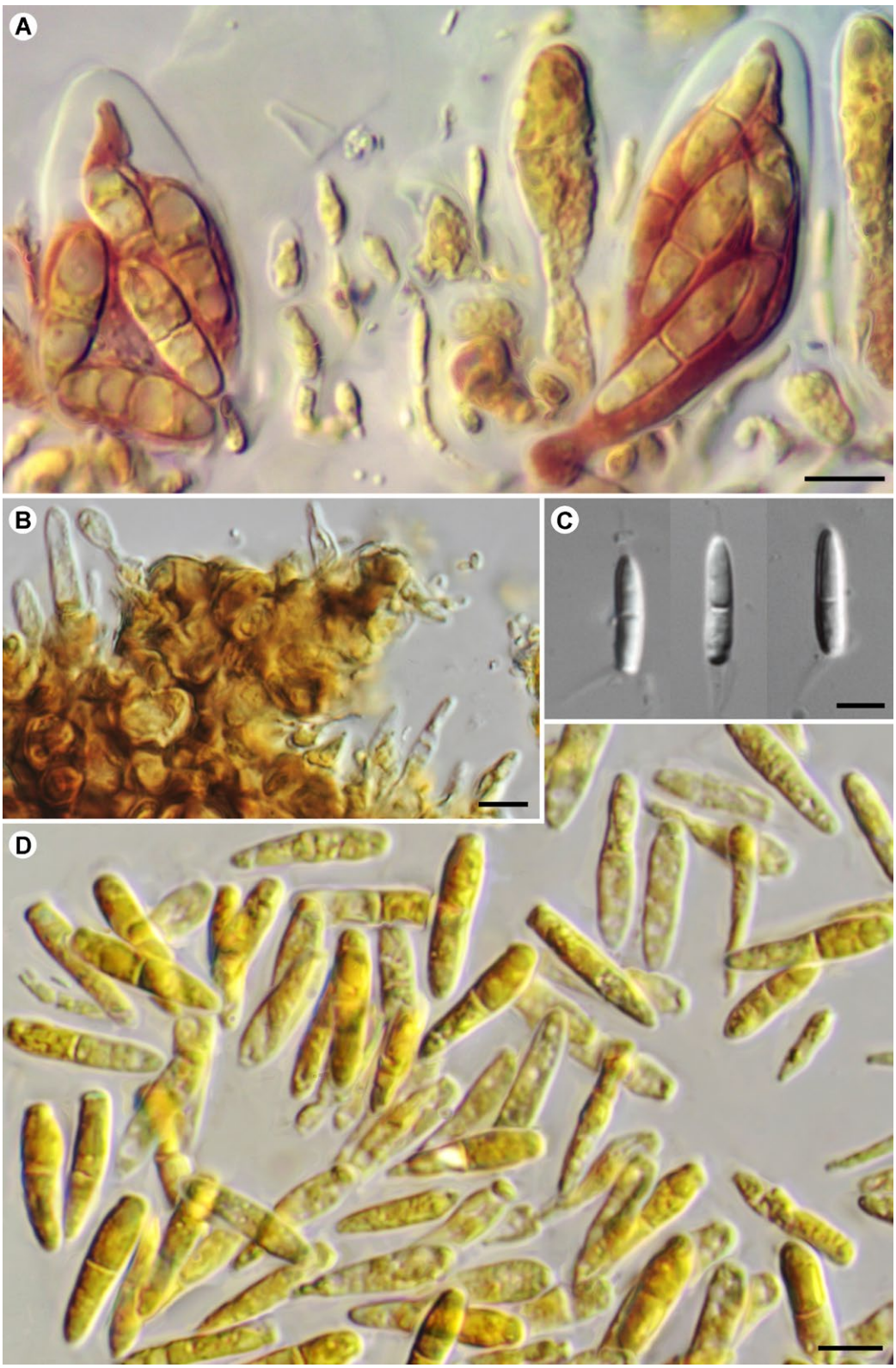

Figure 12. *Strigula graphidicola* [A: C10171A; B: C9918D; C: C9482B; D: C4891C]. A – hymenium with asci, ascospores and paraphyses, in Lugol; B – conidiomatal wall with conidiogenous cells, in Lugol; C – conidia with apical and basal appendages, observed in water using DIC optics; D – conidia, in Lugol. Scales: 5 µm. Photos: R. Common (A, B, D) and P. Diederich (C).

Strigula perparvula Diederich & Common, sp. nov. (Fig. 13)

MycoBank MB 832003

Diagnosis: Distinguished from other *Strigula* species, incl. *S. graphidicola*, by being non-lichenized and lichenicolous, by the host selection (species of *Graphidales*), the unknown sexual stage, the very small subrostrate pycnidia (53–78 µm diam.), the aseptate macroconidia lacking mucoid appendages, the presence of macro- and microconidia within the same conidioma, and the presence of paraphyses, especially in young conidiomata.

Type: USA, Florida, Hillsborough Co., Hillsborough River State Park, Florida Trail (28.149°N, 82.235°W), on the thallus

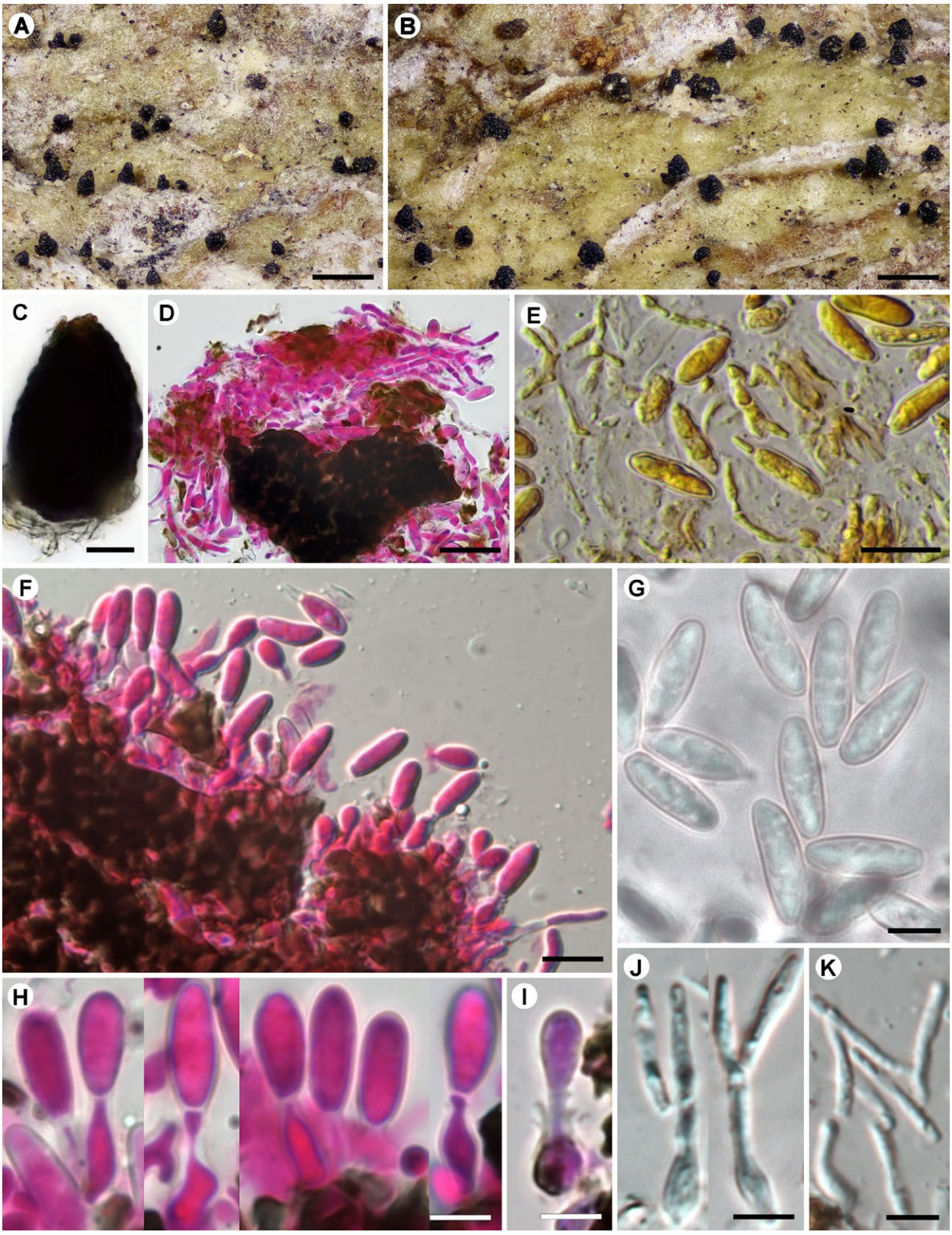

Figure 13. *Strigula perparvula* [holotype, except D: Harris 41580 and E: C4803]. A, B – conidiomata on the thallus of *Graphidales*; C – conidioma, in water; D – squash preparation of young conidioma, showing paraphyses, in 5% KOH + phloxine; E – evanescent paraphyses and macroconidia, in Lugol; F – conidiomatal wall and conidiogenous layer with macroconidia; bottom right: one conidiogenous cell with microconidium, in 5% KOH + phloxine; G – macroconidia, in water; H – conidiogenous cells with macroconidia, in 5% KOH + phloxine; I – idem, with three annellations; J – conidiogenous cells with microconidia, in water; K – microconidia, in water. Scales: A–B = 200 µm; C–D = 20 µm; E–F = 10 µm; G–K = 5 µm. Photos: P. Diederich, except R. Common (E).

of several *Graphidales*, incl. *Phaeographis* sp. and *Sarcographa* sp. [= *S. intricans* sensu Harris 1990, non (Nyl.) Müll. Arg.], 2012, Common 9481C (BR 5030086827852 – holotype; MSC, hb Diederich – isotypes).

Description. Lichenized thallus absent. Ascomata absent. Conidiomata pycnidia, ovoid, distinctly ostiolate, subrostrate, black, almost superficial, (45–)53–78(–95) µm diam. (n = 54, from holotype). Conidiomatal wall dark brown, of rather indistinct isodiametric cells ~6–8.5 µm diam. Paraphyses abundant in young pycnidia, elongate, branched, septate, cells 4–9 × 2–3.5 µm, evanescent at maturity. Conidiophores absent. Conidiogenesis holoblastic. Macroconidiogenous cells elongate ellipsoid to subcylindrical, percurrently profilerating with up to 3 annellations when old, 6–11 × 2.5–4.5 µm. Macroconidia hyaline, aseptate, elongate ellipsoid, apically rounded, basally truncate, (7.0–)10.4–13.1(–14.5) × (3.3–)3.7–4.2(–4.5) µm, L/B (2.0–)2.6–3.4(–4.0) (n = 100); wall ~0.7 µm thick; mucoid appendages not observed. Microconidiogenous cells elongate subcylindrical, swollen in the lower half, 9–13 × 2.5–3 µm, upper part 1–2 µm thick. Microconidia hyaline, aseptate, bacilliform, apically rounded, basally truncate, thin-walled, 10–15 × 1.5–2 µm; mucoid appendages not observed.

Notes. This species is rather unusual for the genus *Strigula*, as: (i) it is non-lichenized, lichenicolous, (ii) it is known only from the asexual stage, (iii) macroconidia are aseptate, (iv) mucoid appendages of macroconidia have not been observed, (v) the macroconidial and microconidial morphs are present within the same pycnidium, and (vi) distinct paraphyses are present and abundant in young pycnidia. No similar genus could be found in Sutton (1980). We describe it here in *Strigula*, as the overall aspect of the conidiomata, conidiogenous cells and conidia is reminiscent of the macro- and microconidial morphs of other *Strigula* species. Although macroconidia in many species of *Strigula* are 1-septate (rarely pluriseptate), a number of species with aseptate macroconidia are known, such as *S. concreta*, *S. maculata*, *S. nitidula* or *S. schizopora* (Lücking 2008). Mucoid appendages at both conidial extremities have been observed in all species of *Strigula* studied by Roux & Sérusiaux (2004), except in *S. smaragdula*, where the basal appendage is missing. To our knowledge, *S. perparvula* is the first species attributed to *Strigula* in which the basal and apical appendages have not been observed. It is also the first species in which the sexual stage is unknown. The new species probably does not belong to *Strigula* s.str., but we describe it provisionally here as long as no molecular data are available.

Etymology. Means 'very small', in reference to the very small ascomata.

Host and distribution. Lichenicolous on the thallus of *Graphidales*, including *Fissurina*, *Graphis*, *Phaeographis* and *Sarcographa*, the host thallus not visibly damaged. Currently known only from Florida, where it seems to be widespread and common, but much overlooked.

Additional specimens examined. USA Florida. Hillsborough Co.: same locality as type, on *Phaeographis concava*, 2011, C9249B (hb Diederich); Hillsborough River State Park (28.15°N 82.24°W), on sterile *Phaeographis*, 1977, C4385E (MSC); ibid., 1990, on sterile *Phaeographis*, 1990, C4803 (MSC); ibid., trail from Parking Area 2 (28°08.94′N, 82°13.61′W), on sterile *Graphis*, 2011, C9218J (MSC); along CR. 581, 3.2 mi. S of junction I-75 (28.087°N, 82.407°W), on *Sarcographa medusulina*, 1995, C6602F (MSC). Polk Co.: Green Swamp Wildlife Management Area, Strand Hammock, T.25S., R.23E., S14 (28°18′N, 81°59′W), hardwood-*Sabal* hammock, on *Carpinus*, on '*Graphina leuconephela*' (probably *Fissurina mexicana*, see Lücking et al. 2011), 1998, Harris 41580 (NY). Sumper Co.: SR 471 along river, just N of border with Hernando Co. (28°31′N, 82°03′W), on *Phaeographis* sp. [a species called 'Wilson 1259' in Harris 1990 and 1995, probably the same species called *P.* aff. *schizoloma* in Lücking et al. 2011], 1998, C7921C (MSC).

Synarthonia hodgesii (Lendemer & R. C. Harris) Van den Broeck & Ertz

The species was known only from two sites in the Coastal Plain of SE North America, where it was described recently (Lendemer et al. 2016). Our specimen fits well the original description, although the host lichen is different (*Graphis lineola* in the protologue). The species is very similar to *Synarthonia ochrodes* described from Cuba; further studies are needed to verify whether the two taxa are distinct (Van den Broeck et al. 2018).

Specimens examined. USA Florida. Collier Co.: Fakahatchee Strand State Preserve, first bend of Janes Scenic Drive (25°58.74′N, 81°22.26′W), on *Graphis cupei*, 2014, C9763C (BR), C9755K (MSC).

Taeniolella delicata M. S. Christ. & D. Hawksw.

This species has been reported by Heuchert et al. (2018) from Florida, Hillsborough Co., Hillsborough River State Park, on *Phaeographis inconspicua*.

Taeniolella hawksworthiana Heuchert, Ertz & Common

This species has been described by Ertz et al. (2016) from Florida, Hillsborough Co., Hillsborough River State Park, on *Phaeographis* cf. *brasiliensis* and *Phaeographis* sp.

Talpapellis graphidis Heuchert, Common, U. Braun & Diederich, sp. nov. (Figs 14–15)

MycoBank MB 832004

Diagnosis: Lichenicolous hyphomycete growing on *Graphis*, distinguished from all other species of *Talpapellis* in having conidia formed in long adhering chains, firm, not easily disarticulating, individual conidia usually 1–5-septate, rarely aseptate, 6–29 × 3–5 µm, or entire firm conidial chains breaking off, functioning as diaspores, 42–73 × 4–5 µm, 9–19-septate.

Type: USA, Florida, Collier Co., Fakahatchee Strand State Preserve, trail north of Boardwalk (25.94183°N, 81.47405°W), on *Graphis caesiella*, 11 Nov. 2011, Common 9425D (BR 5030086826824 – holotype; hb Diederich – isotype).

Description. Colonies on not or slightly discoloured host thalli, short caespitose with single long elements (evident when viewed under a stereomicroscope), effuse or aggregated in small tufts, punctiform, confluent, dark brown

to black. Mycelium sparse, immersed; hyphae flexuous, sparingly branched, 1.5–4 µm wide, septate, subhyaline to medium brown, smooth, thin-walled (wall up to 0.25 µm); stromata lacking. Conidiophores macronematous, mononematous, solitary or in small aggregations, arising from internal hyphae, erect, straight, subcylindrical or slightly tapering from base to top, non-geniculate, unbranched or once branched at the base, 10–46 × 3.5–5 µm, usually distinctly wider at the base, up to 7 µm, 1–10-septate, often somewhat constricted at the septa, medium brown to dark brown throughout or somewhat paler towards the tip and after rejuvenation, wall slightly thickened, about 0.5–0.75 µm, smooth to usually distinctly verruculose or verrucose, sometimes rimulose, at least in older portions of conidiophores and around rejuvenations; rejuvenation monopodial by enteroblastic proliferation, leaving conspicuous annellations. Conidiogenous cells directly formed by enteroblastic proliferation leaving several conspicuous, coarse, often flaring annellations, integrated, terminal, subcylindrical or somewhat conical, 4–6 µm long, determinate, with a single terminal conidiogenous locus, 3–3.5 µm wide, neither thickened nor darkened, at most somewhat refractive. Ramoconidia lacking. Conidia catenate, adhering in long, firm, unbranched chains, not easily disarticulating, chains disintegrating into fragments of different sizes and septation, short subcylindrical, doliiform, ellipsoid, straight, conidia rarely aseptate, 6 × 4–5 µm, 1-septate conidia 7–10 × 3–4 µm, 2-septate conidia 11–15 × 4 µm, and 3–5-septate conidia 20–29 × 4 µm, or entire conidial chains breaking off, 42–73 × 4–5 µm, 9–19-septate, conidial chain slightly constricted at the septa, shed conidial chains functioning as diaspores, conidia and shed conidial chains pale brown to brown, thin-walled, conidial wall usually up to 0.3 µm (conidia at the tips of the chains paler, sometimes even subhyaline, and wall usually unthickened), smooth or almost so to distinctly verruculose, often irregularly verruculose, sometimes rimulose, apex rounded in terminal (primary) conidia and truncate or subtruncate in catenate (secondary) conidia, base truncate, 2.5–4 µm wide, not darkened, occasionally slightly refractive.

Notes. Based on a *Taeniolella*-like general habit connected with conspicuous annellations caused by percurrent proliferations of the conidiophores, the new species can readily be assigned to the genus *Talpapellis* (Alstrup & Cole 1998) in its emended circumscription recently introduced by Heuchert et al. (2014).

Talpapellis graphidis is the only known species of the genus on a host belonging to the *Graphidaceae*. Most other *Talpapellis* species, including *T. beschiana* (Heuchert et al. 2018), occur on hosts pertaining to the order *Peltigerales* (various *Peltigera* species and *Solorina crocea*) or on *Cladonia* species (*Cladoniaceae*, *Lecanorales*). *Talpapellis graphidis* is easily distinguishable from all species hitherto assigned to *Talpapellis* by its conidia formed in firm, not easily disarticulating chains, (0–)1–5-septate conidia and firm conidial chains that may be shed and function as diaspores. There is no species in *Talpapellis* with comparable conidial traits. The conidial chains in all other species of this genus are easily disarticulating, conidial chains are not shed to serve as diaspores, and the conidia are either 0–1(–2)-septate [*T. solorinae* (Zhurbenko et al. 2015)] or usually aseptate [*T. beschiana* (Heuchert et al. 2018), *T. peltigerae* var. *peltigerae* and var. *rossica* (Heuchert et al. 2014)].

Talpapellis beschiana is the only other species in *Talpapellis* with similar conidiophores characterized by forming distinct, coarse, often flaring annellations, but besides the general differences in the characters of the conidial chains and conidia it differs from *T. graphidis* in having longer conidiophores (11–70 × 3–6 µm, (0–)1–8-septate, vs. 10–46 × 3.5–5 µm, 1–10-septate in *T. graphidis*), usually not distinctly wider at the base,

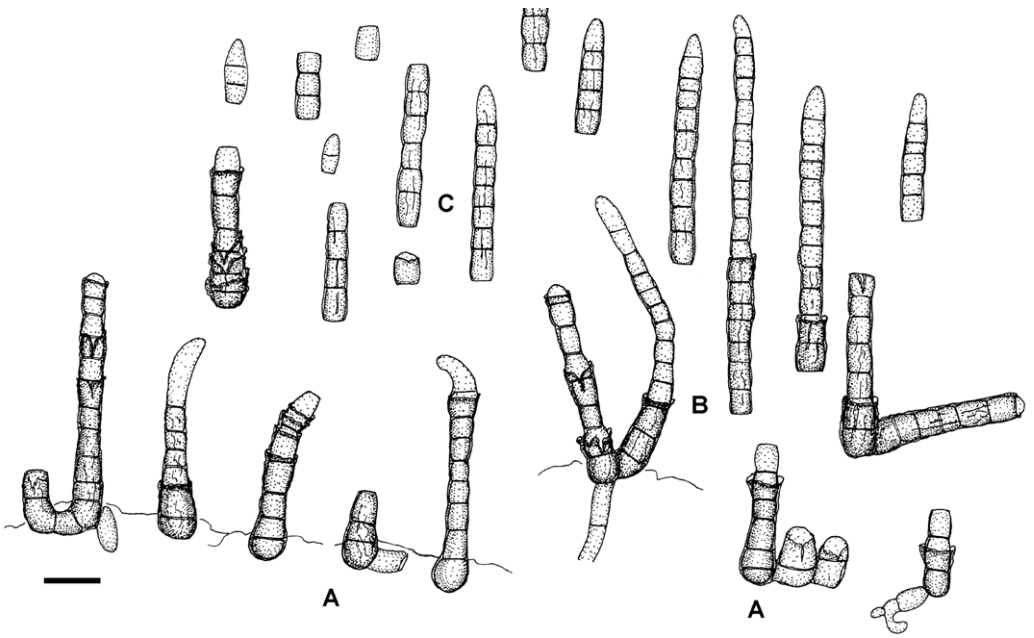

Figure 14. *Talpapellis graphidis* [holotype]. A – conidiophores with monopodial rejuvenation; B – conidiophore with adhering conidial chain; C – conidia and conidial chains. Scale: A–C = 10 µm. B. Heuchert del.

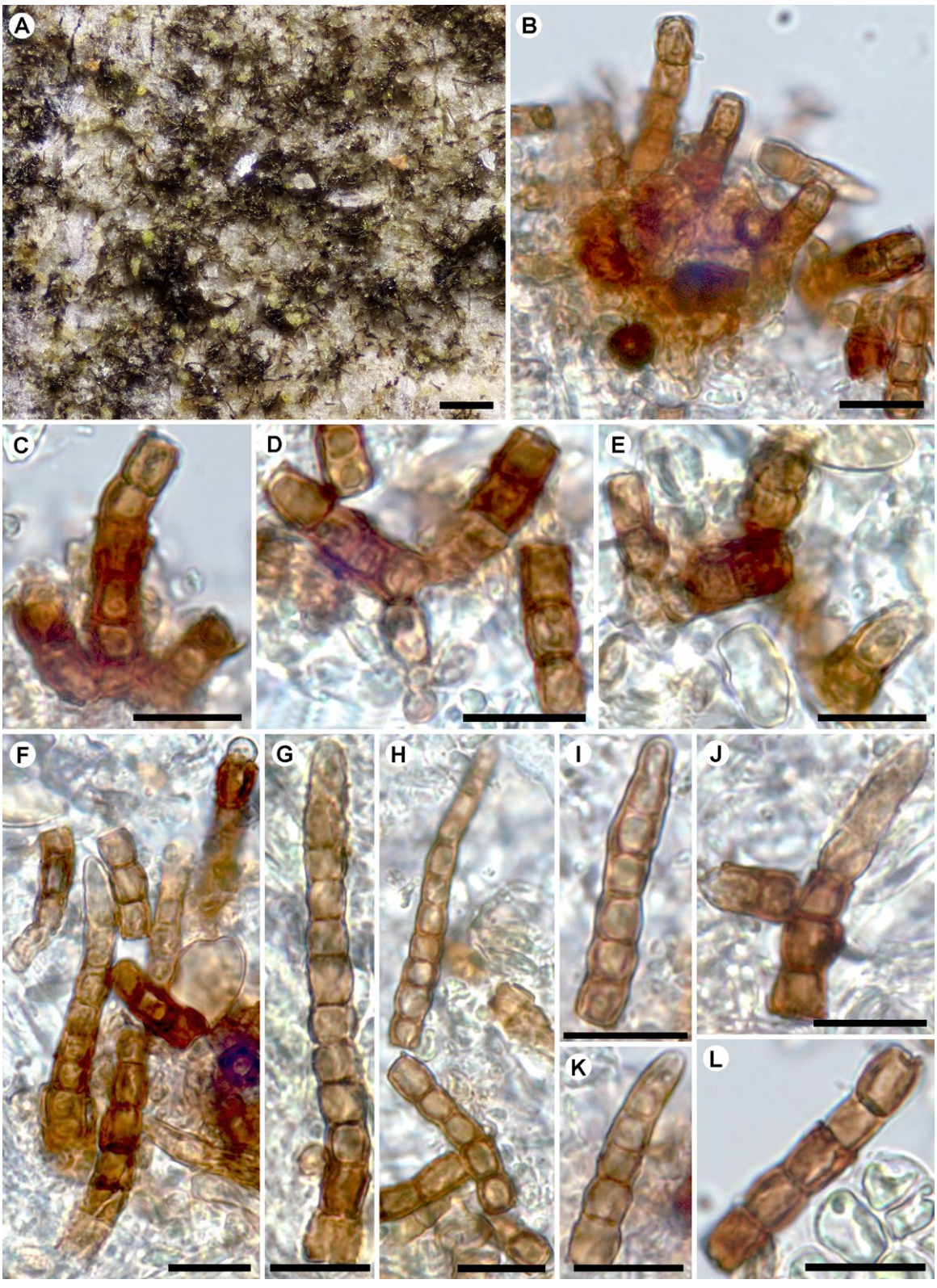

Figure 15. *Talpapellis graphidis* [holotype]. A – macroscopic overview of colonies on *Graphis caesiella*; B–E, J – conidiophores; F, G – conidiophores with adhering conidial chains; H, I, K – fragments of conidial chains; L – conidiophore with conspicuous flaring annellations. Scales: A = 200 µm; B–L = 10 µm. Photos: P. Diederich (A) and B. Heuchert (B–L).

and longer conidiogenous cells [(3.5–)4–18(–21) µm vs. 4–6 µm in *T. graphidis*].

Talpapellis mahensis (Diederich et al. 2017), recently described from the Seychelles on an unidentified crustose lichen, is only tentatively assigned to *Talpapellis* and is quite distinct from all other species, including *T. graphidis*, by its unusual conidiophores and conidia with unequally thickened and pigmented walls.

Etymology. Named after the host *Graphis*.

Host and distribution. Lichenicolous on *Graphis caesiella*. Known only from the type locality in Florida.

Updated key to the species of *Talpapellis*

1 Conidiophores arising from internal and external hyphae, erect, outline irregular, with swellings and constrictions, wall irregularly thickened and pigmented, with thicker and darker portions, to 1.5 µm wide; conidia catenate, 5–14 × 3–6 µm, 0–1-septate, wall not uniformly pigmented, with thicker and darker portions; on an unidentified crustose lichen, Seychelles . . . . . ***T. mahensis***

Conidiophores and conidia ±regular, width and pigmentation of conidia regular 2

2(1) Conidia in long adhering chains, firm, not easily disarticulating, individual conidia usually 1–5-septate, rarely aseptate, 6–29 × 3–5 µm, or entire firm conidial chains breaking off, functioning as diaspores, 42–73 × 4–5 µm, 9–19-septate; on *Graphis caesiella* . . . . . ***T. graphidis***

Conidia in easily disarticulating chains, not firm and adhering, 0–1(–2)-septate, conidial chains neither breaking off nor functioning as diaspores; on other hosts 3

3(2) Conidiophores relatively short, 8–40 × 3–5(–6) µm, sometimes branched; conidia 0–1(–2)-septate; on *Solorina crocea* . . . . . ***T. solorinae***

Conidiophores longer, 11–70(–80) × 3–6 µm, usually unbranched; conidia usually aseptate; on *Cladonia* spp. and *Peltigera venosa* 4

4(3) Conidiogenous cells with coarse, often flaring annellations; on *Cladonia* . . . . . ***T. beschiana***

Annellations more delicate, not or barely flaring; on *Peltigera venosa* 5

5(4) Conidiogenous cells with a single or up to four conidiogenous loci; ramoconidia present, 9–10.5 × 3–3.5 µm; conidia (3–)5.5–7(–8) × (2–)2.5–4(–4.5) µm, width on average < 4 µm. . . . . ***T. peltigerae*** var. ***peltigerae***

Conidiogenous cells with a single or occasionally two conidiogenous loci; ramoconidia lacking; conidia (4–)5.5–9.5(–13) × (3–)4–5.5(–6) µm, width on average > 4 µm . . . . . ***T. peltigerae*** var. ***rossica***

Tremella graphidis Diederich, Millanes, Wedin & Common

This species has been described from Florida, Collier Co. (Fakahatchee Strand State Preserve), on *Graphis assimilis*, *G. caesiella*, *G. cupei*, *G. desquamescens* and *Graphis* sp. (Ariyawansa et al. 2015).

Specimen examined. USA Florida. Hillsborough Co.: near Morris Bridge Road (28.115°N, 82.301°W), on *Graphis desquamescens*, 2016, C10107C (hb Diederich).

Tremella phaeographinae Diederich & Aptroot

This species has been described from Florida, Collier Co. (Big Cypress National Preserve), on '*Phaeographina* sp.' (Diederich 1996). Further specimens have been reported from Union Co. (Lake Butler Management Area) on *Leiorreuma explicans* (Diederich 2003) and from Hillsborough Co. (Hillsborough River State Park) on *Phaeographis* spp. (Ariyawansa et al. 2015).

Specimens examined. USA Florida. Collier Co.: Fakahatchee Strand State Preserve, trail E of Big Cypress Boardwalk area, on US 41 (25.9475°N, 81.4714°W), on *Phaeographis leiogrammoides*, 2014, C9844F (hb Diederich); on *Phaeographis*, C9837 (hb Diederich). Sumter Co.: Richloam Wildlife Management Area (28.526°N, 82.054°W), on *P. leiogrammodes*, 2016, C10143M (hb Diederich).

Tremella wedinii Diederich, Common & Millanes, sp. nov. (Figs 16–17)

MycoBank MB 832005

Diagnosis: Lichenicolous *Tremella* growing on *Glyphis scyphulifera* characterized by brownish, flat to convex, strongly gelatinous basidiomata and 1-transseptate basidia with a long attenuated stalk-like base.

Type: USA, Florida, Pasco Co., Zephyrhills, near US 301 (28.239°N, 82.184°W, alt. 30 m), windfall oak twigs, on *Glyphis scyphulifera*, 8 May 2016, Common 10067B (BR 5030086825797 – holotype; MSC, S, hb Diederich – isotypes). GenBank ITS: MN258555; nLSU: MN243150.

Description. Basidiomata pale brown, rarely becoming medium to dark brown when mature, pulvinate, strongly gelatinous, surface rather smooth, roundish, elongate or irregularly formed, up to 0.5(–0.8) mm diam., flat or slightly convex, rarely strongly convex, with a constricted base. Context hyphae thin-walled, 2–4 µm diam., clamp connections not observed; haustorial branches present, mother cell ~3.5–6 µm diam. Hymenium hyaline, containing numerous probasidia; hyphidia absent; probasidial initials ellipsoid to rarely clavate, proliferations occurring through the basal clamp. Basidia, when mature, 2-celled, with one transverse, rarely oblique or longitudinal septum, slightly constricted at the septum, often with a long attenuated stalk-like base, (16.5–)20.0–28.4(–31.5) × (8–)8.8–10.5(–11.3) µm, L/B (1.7–)2.0–3.1(–3.9) (n = 25); epibasidia subcylindrical, at least 45 µm long, 3–5 µm diam. Basidiospores ellipsoid to subspherical, with a distinct apiculus, (7.6–)7.7–9.5(–10) × (6.3–)6.7–8.6(–9) µm, L/B (0.9–)1.0–1.3(–1.5) (n = 10). Asexual morph not observed.

Notes. This species is distinguished from most lichenicolous *Tremella* species by the mainly 1-transseptate basidia with a long attenuated stalk-like base. *Tremella anaptychiae* also has such stalked basidia but they are much broader, 10–15 µm (Zamora et al. 2017). *Tremella harrisii* and *T. pertusariae* also have stalked basidia but these are frequently 4-celled (Diederich 1996).

The new species forms a distinct clade (BS = 100, PP = 1.0) and is the sister group of *Tremella phaeographinae*, with which it forms a strongly supported clade (BS = 100, PP = 1.0). Other species growing on *Graphidales*, such as *Tremella diploschistina* and *T. graphidis*, are not closely related to the new species according to our data and analyses (Fig. 16). The lichenicolous species groups I, II and III, distinguished by Millanes et al. (2011), are recovered with support (BS = 100, PP = 1.0 and BS = 80, PP = 0.98, respectively) and are not closely related to the new species either.

Etymology. *Tremella wedinii* is dedicated to our friend Mats Wedin (Stockholm) in recognition of his important contribution to the knowledge of lichenicolous heterobasidiomycetes.

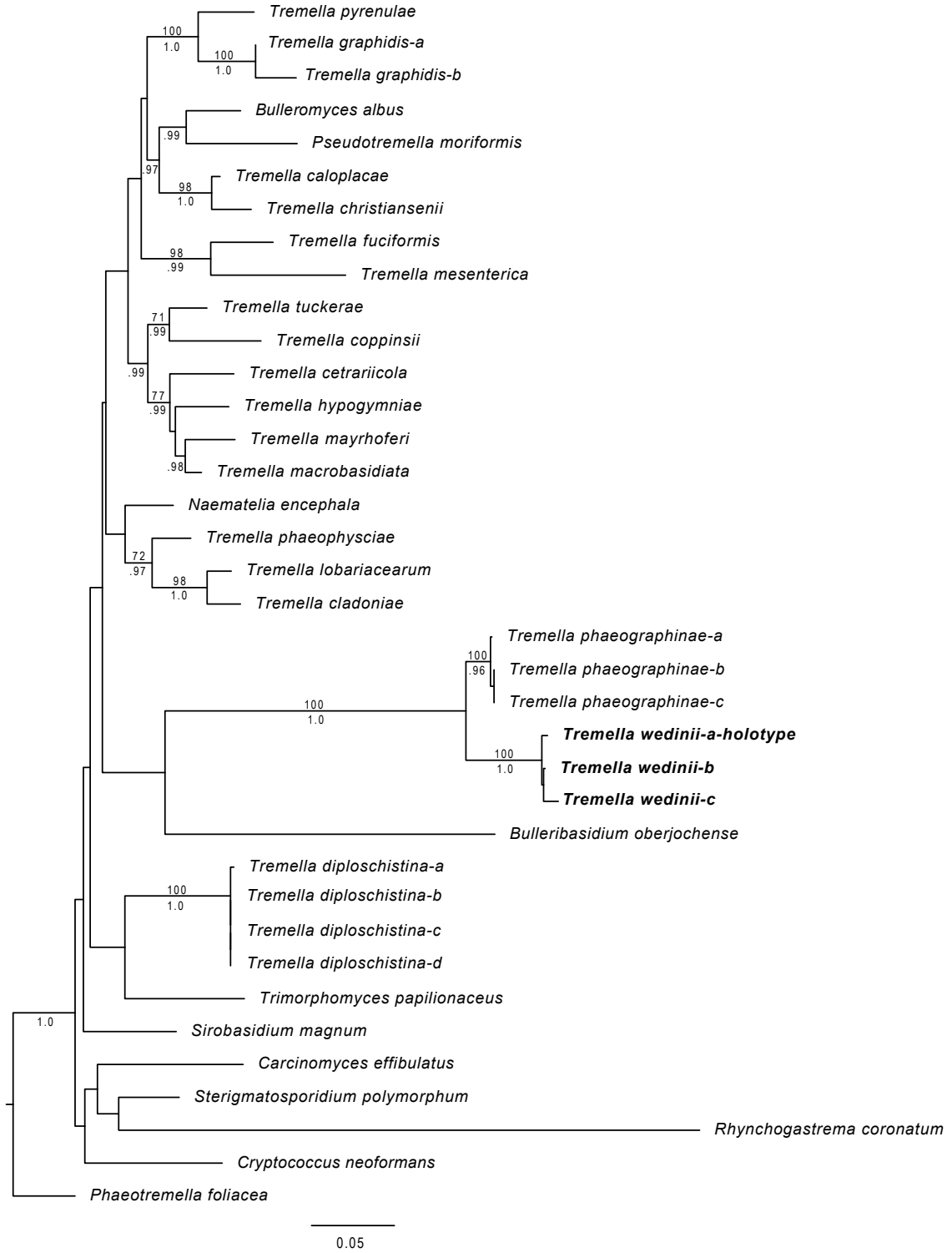

Figure 16. Maximum likelihood (ML) best tree including *Tremella wedinii* (in bold). ML bootstrap values (BS) ≥ 70 are indicated over branches and Bayesian posterior probability values (BPP) ≥ 0.95 below branches. Branch lengths are scaled to the expected number of nucleotide substitutions per site.

Host and distribution. Lichenicolous on the thallus, more rarely the apothecia, of *Glyphis scyphulifera*, not gall-inducing, not causing any visible damage to the host. Obviously very common in Florida, also known from Louisiana and Puerto Rico.

Additional specimens examined (all on *Glyphis scyphulifera*). PUERTO RICO. Bosque Estatal de Susua, along S edge of reserve (18°04′N, 66°53′W, alt. 275 m), 1992, Harris 27650 (NY). USA Florida. Citrus Co.: Citrus Wildlife Mgmt. Area, Withlacoochee State Forest, 1.8 mi. N of CR 480 on Trail 13 (28.723°N, 82.426°W), 1992, C5496L (MSC). Pasco Co.: Zephyrhills, Zephyr Park (28.231°N, 92.186°W, alt. 25 m), 2016, C10035C (hb Diederich); ibid., near post office (28.248°N, 82.186°W, alt. 45 m), 2015, C9880B (BR, hb Diederich); ibid., near intersection of US 301 and CR 54 (28.234°N, 82.182°W, alt. 30 m), 2016, C10000C (hb Diederich); ibid., along Henry Ave. (28.248°N, 82.179°W, alt. 25 m), 2013, C9566B-2

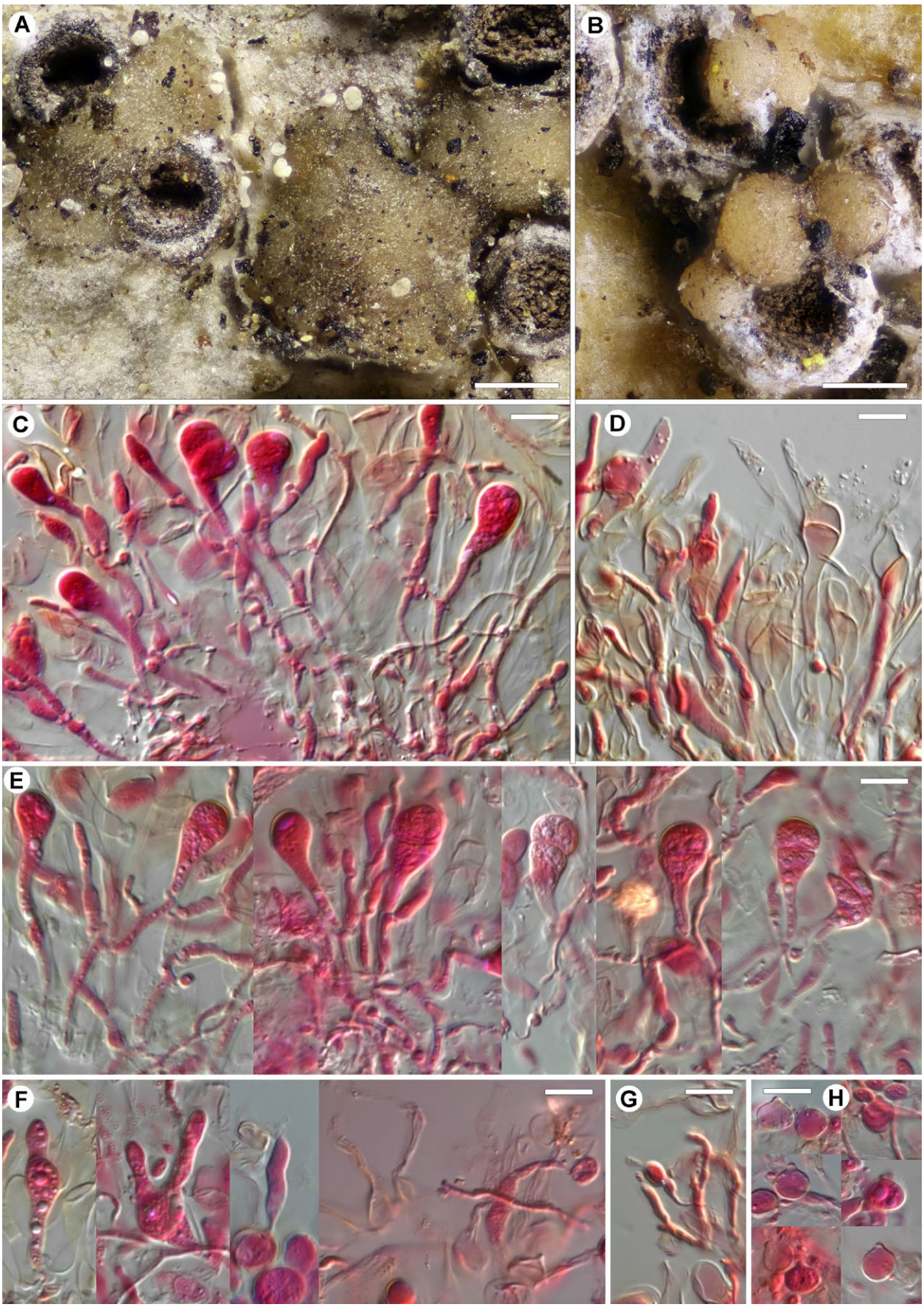

Figure 17. *Tremella wedinii* [holotype, except B: Harris 27650]. A – basidiomata on the host thallus; B – basidiomata on the host apothecia; C – hymenium with basidia; D – old basidia with epibasidia; E – transversely septate basidia; F – epibasidia, the one on the right with an attached basidiospore; G – haustorial branch; H – basidiospores. C–H in 5% KOH + Congo Red + phloxine. Scales: A–B = 200 µm: C–H = 10 µm. Photos: P. Diederich.

(hb Diederich); ibid., at intersection of Fort King Rd. and Gall Blvd. (28.249°N, 82.19°W, alt. 35 m), 2015, C9961C (hb Diederich). Pinellas Co.: Caladasi Island State Park (28.044°N, 82.828°W, alt. 1 m), shrubs near beach, 2013, C9616C (hb Diederich). Louisiana. East Baton Rouge Parish, south Baton Rouge, 1022 Baird Drive, on *Cornus florida* in garden, 1991, Tucker 31185 (SBBG).

Worldwide key to the lichenicolous fungi growing on *Graphidales*

1 Sexual morph present . . . 2
Sexual morph absent, but asexual morph present . . . 41

2(1) Fruiting bodies ascomata; ascospores produced inside asci . . . 3
Fruiting bodies basidiomata; basidiospores produced at the apex of long epibasidia arising from septate basidia (*Tremella*) . . . 37

3(2) Ascomata stromatic . . . 4
Ascomata not stromatic . . . 6

4(3) Ascomata lirellate-labyrinthiform, with a distinct carbonized excipulum; ascospores (2-)3-septate; 16.5–20.0 × 4.5–5.5 µm; on *Sarcographa tricosa* s.lat. . . . ***Plectocarpon galapagoense***
Ascomata different, emarginate; ascospores 1-septate . . . 5

5(4) Ascomata composed of spherical yeast-like cells; ascospores hyaline, 1-septate, ellipsoid, 8.5–13 × 4.5–6 µm; on corticolous lichens, particularly common on *Graphidales* . . . ***Etayoa trypethelii***
Ascomata composed of cells separated by septa; ascospores dark brown, 1-septate, ellipsoid to obovate, 10–13 × 5–7 µm; on *Diploschistes* . . . ***Lichenothelia rugosa***

6(3) Ascomata perithecia, i.e. ±globose, surrounded by a pale or dark wall, opening by an ostiole; ascospores 1-septate . . . 7
Ascomata not perithecia; either stalked; or intrahymenial, subspherical, with an indistinct exciple; or urceolate, lirellate or arthonioid apothecia . . . 13

7(6) Ascospores hyaline . . . 8
Ascospores brown . . . 11

8(7) Perithecia translucent-orange, ~200 µm diam., with white hairs; ascospores of two kinds: macrospores 40–80 × 13–26 µm, and microspores 11–15 × 4.5–6 µm; on *Graphis* and many other hosts . . . ***Ovicuculispora parmeliae***
Perithecia brown to black, smaller; only on *Graphis* . . . 9

9(8) Perithecia immersed in dark necrotic spots (~5 mm diam.) of the host thallus, black, ~100 µm diam., wall cellular; ascospores 13–19 × 3–5 µm; on *Graphis scripta* . . . ***Stigmidium microspilum***
Perithecia superficial, not visibly damaging the host thallus, brown, less than 40 µm diam. . . . 10

10(9) Perithecia superficial, dark brown, 20–40 µm diam.; wall very thin, without a clear cell structure; asci claviform, 30–40 × 8–11 µm; ascospores 10–13 × 3.5–4.5 µm; pycnidia unknown; on *Graphis* cf. *angustata* . . . ***Pygmaeosphaera epigraphis***
Perithecia half immersed to superficial, reddish to dark brown, 29–36 µm diam.; wall of isodiametric cells, 6–11 µm diam.; asci broadly ellipsoid, 23–27 × 11–13 µm; ascospores 10–12.5 × 2.5–4 µm; pycnidia abundant, often dominant, mucronate to subrostrate; on *Graphis assimilis* . . . ***Strigula graphidicola***

11(7) Ostiole lateral; ascospores 12–15 × 5–6 µm, thick-walled with pentagonal lumina; perithecia 0.25–0.45 mm diam.; on *Graphis proserpens* . . . ***Distopyrenis japonica***
Ostiole apical; ascospores with thin, evenly thick cell wall . . . 12

12(11) Asci elongate clavate, 35–50 × 10–15 µm; ascospores distichous, 9–11.5(–13) × 4.5–6.5(–7) µm; on *Diploschistes scruposus* . . . ***Polycoccum arnoldii***
Asci narrowly cylindrical to slightly clavate, 65–85 × 8–10 µm; ascospores obliquely monostichous, sometimes half-overlapping, 10–12 × 5–6 µm; on *Pallidogramme* . . . ***Didymocyrtis graphidacearum***

13(6) Ascomata stalked, 0.2–0.3 mm tall, head 0.12–0.19 mm diam., dark brown to black, shiny; asci cylindrical, disintegrating; ascospores globose, simple, dark brown, ~4–6 µm diam.; on *Diploschistes scruposus* and corticolous *Pertusaria* . . . ***Sphinctrina leucopoda***
Ascomata not stalked; asci not disintegrating; ascospores septate . . . 14

14(13) Ascomata intrahymenial, subspherical, with an indistinct, hyaline exciple; asci multi-spored; ascospores hyaline, slightly helicoidal, 1-septate, ~23–40 × 2 µm; in the hymenium of *Graphidales*, incl. *Graphis* . . . ***Spirographa fusisporella***
Ascomata and ascospores different . . . 15

15(14) Ascomata urceolate, with short excipular hairs; hymenium K/I–; asci cylindrical to clavate, 8–spored, I–, K/I–; ascospores hyaline, aseptate, narrowly ellipsoid (*Skyttea*) . . . 16
Ascomata not urceolate, without excipular hairs . . . 18

16(15) Exciple with two main pigments, one of them often being dominant: a dark reddish pigment, most abundant in the upper exciple just below the hairs, reacting K+ bright aeruginose green, and a brownish pigment, occasionally also present in the epihymenium and subhymenium, reacting K+ purplish violet (strong reaction!); ascomata dark brown to black, 130–250 µm diam.; ascospores 8–13 × 2–3 µm; on *Thelotrema lepadinum* . . . ***Skyttea nitschkei***
These two pigments absent . . . 17

17(16) Ascomata blackish, but whitish around the pore, 125–250(–325) µm diam.; exciple greenish, K+ olivaceous; ascospores (7.5–)9–10(–11) × (1.7–)2.3–3 µm; on *Thelotrema lepadinum* . . . ***Skyttea thelotrematis***
Ascomata, blackish brown, 80–100 µm diam.; exciple and epihymenium brown, K–; ascospores 11–14 × 2.5–3 µm; on *Graphis* . . . ***Skyttea graphidicola***

18(15) Ascospores brown to dark brown from the beginning . . . 19
Ascospores hyaline or pale brown, sometimes brown when postmature . . . 21

19(18) Ascospores 3-septate, rarely submuriform, dark brown, surrounded by a thick halo, 15–22 × 5–10 µm; apothecia convex, margin absent or reduced, black; on *Diploschistes* . . . ***Rhizocarpon malenconianum***
Ascospores without a distinct halo . . . 20

20(19) Ascospores 3-septate, 8–13 × 4–5 µm; apothecia 50–100 µm diam., black, marginate; gel surrounding asci K/I+ blue; on *Thelotrema* . . . . . ***Sclerococcum thelotremicola***

Ascospores 1-septate, 11–17 × 6–8 µm; apothecia 300–600 µm diam., black; all parts K/I–; on *Diploschistes* . . . . . ***Karschia talcophila***

21(18) Ascomata black, roundish to ellipsoid, immersed in the host thallus, flat, 70–100 µm diam.; ascospores hyaline, 9–10-septate, 48–61 × 6–7 µm; on *Graphis sitiana* . . . . . ***Enterographa epigraphis***

Ascomata larger; ascospores smaller 22

22(21) Ascomata arthonioid; exciple absent or reduced; asci short ellipsoid; hymenium K/I+ blue 23

Ascomata not arthonioid, exciple present; asci more elongate 28

23(22) Ascomata orange; epihymenium K+ magenta; on *Graphis* . . . . . ***Synarthonia hodgesii***

Ascomata pale brown to black; epihymenium K+ olivaceous (*Arthonia*) 24

24(23) Ascospores 1-septate; on *Diorygma* . . . . . ***Arthonia diorygmatis***

Ascospores 2–4-septate 25

25(24) Ascospores 6–6.5 µm wide, 3–4-septate; subhymenium I+ reddish; on *Acanthothecis floridensis* . . . . . ***Arthonia acanthotheciicola***

Ascospores 4–5.5 µm wide, 2–3-septate; hypothecium I+ blue 26

26(25) Hypothecium red-brown; ascospores 11–14 µm long; on *Thelotrema lepadinum* . . . . . ***Arthonia thelotrematis***

Hypothecium hyaline to pale brown; ascospores 13–17 µm long 27

27(26) Hymenium I+ red; ascomata usually elongate, oblong to ±lirelliform, up to 0.6 mm long; on *Graphis scripta* agg. (in temperate regions) . . . ***Arthonia graphidicola***

Hymenium I+ persistently blue; ascomata fleck-like, rarely elongate up to 0.42 mm long; on *Graphis assimilis* (in tropical regions) . . . . . ***Arthonia subgraphidicola***

28(22) Ascospores 1-septate; ascus wall K/I–, without a K/I+ blue apical ring, but gelatinous coat in some species I+ bluish, resulting in a K/I+ pale blue hymenium (*Melaspilea* s.lat.) 29

Ascospores with more septa; ascus wall K/I–, except a K/I+ blue apical ring; hymenium I+ red or blue, K/I+ blue (strong reaction) (*Opegrapha*) 34

29(28) Ascospores 19.5–32 × 9.5–16 µm; ascomata 300–1500 × 200–500 µm; on *Graphis elegans* . . . . . ***Melaspileopsis*** cf. ***diplasiospora***

Ascospores and ascomata smaller 30

30(29) Ascospores up to 12 µm long 31

Ascospores longer 33

31(30) Ascomata 300–800 × 90–150 µm; disc slit-like, not exposed; ascospores 9–11 × 3.5–4.5 µm; on *Acanthothecis consocians* . . . . . ***Melaspilea epigraphella***

Ascomata shorter, up to 300 µm long 32

32(31) Ascomata up to 200 µm long; disc exposed, black; ascospores 10–12 × 5 µm; on *Reimnitzia santensis* . . . . . ***Melaspilea epigena***

Ascomata 180–300 × 100–110 µm; disc slit-like; ascospores 9.5–11.5 × 3–4 µm; on *Nitidochapsa leprieurii* . . . . . ***Melaspilea nitidochapsae***

33(30) Disc exposed, orange; ascomata 200–400 × 100–200 µm; ascospores 14–17 × 7–8 µm; on *Sarcographa* . . . . . ***Melaspilea lekae***

Disc slit-like; ascomata 300–500 × 100–200 µm; ascospores 10–16 × 5–7.5 µm; on *Phaeographis dendritica* . . . . . ***Stictographa lentiginosa***

34(28) Excipulum K–; on *Thelotrema glaucopallens* . . . . . ***Opegrapha pigozziana***

Excipulum K+ greenish (or greenish intensifying) . . 35

35(34) Asci 50–77 µm long; ascospores 5.5–7(–8) µm wide; on *Chapsa* . . . . . ***Opegrapha chapsae***

Asci 35–50 µm long; ascospores (4–)4.5–5.5(–6) µm wide 36

36(35) Asci 4-spored; on *Thelotrema petractoides* . . . . . ***Opegrapha brevis***

Asci (6–)8-spored; on *Thelotrema lepadinum* and *T. macrosporum* . . . . . ***Opegrapha thelotrematis***

37(2) Basidia intrahymenial, narrowly and elongate cylindrical, 2-celled, 30–38 × 4–5 µm; on *Graphis* . . . . . ***Tremella graphidis***

Basidia shorter and broader 38

38(37) Basidia 3–4-celled, with one transverse septum, the lower or upper half often with an additional longitudinal septum, not stalked, 22–32 × 9.5–11 µm; on *Leiorreuma* and *Phaeographis* . . . . . ***Tremella phaeographinae***

Basidia 2-celled, with one transverse, rarely oblique or longitudinal septum, often with a long, attenuated, stalk-like base 39

39(38) Basidiospores 5.5–7.5 × 5–6 µm; basidia 16–24 × 8–12 µm; basidiomata pale to dark brown, often reddish brown, gelatinous, 0.4–0.7 mm diam.; on *Phaeographis* . . . . . ***Tremella phaeographidis***

Basidiospores larger 40

40(39) Basidiomatal galls pale yellow, dark brown or black, at first regularly convex to subglobose, 0.3–0.9 mm diam., often forming groups measuring up to 3 mm diam.; basidia 14–30 × 8–14 µm; basidiospores 7–9 × 6–9 µm; on *Diploschistes*. . . . ***Tremella diploschistina***

Basidiomata pale brown, rarely medium to dark brown when mature, strongly gelatinous, up to 0.5 mm diam., not inducing the formation of galls; basidia 20–28.5 × 8.5–10.5 µm; basidiospores 7.5–9.5 × 6.5–8.5 µm; on *Glyphis scyphulifera* . . . . . ***Tremella wedinii***

41(1) Forming pastel to coral-red, often immersed bulbils, 100–200 µm diam.; on *Diploschistes* and many other host genera . . . . . ***Marchandiomyces corallinus***

Not forming bulbils 42

42(41) Conidiomata synnematous; conidia greenish, aseptate, in basipetal chains, truncate at both ends; conidiogenous cells phialidic; on *Diploschistes* . . . ***Arborillus llimonae***

Conidiomata not synnematous 43

43(42) Superficial mycelium with mucronate hyphopodia; conidia aseptate, ellipsoid, brown, smooth, 7–13 × 4–6 µm; on foliicolous, more rarely corticolous lichens, incl. *Fissurina* . . . . . ***Ampullifera foliicola***

Mycelium without hyphopodia 44

44(43) Conidiophores scattered or loosely grouped, always pigmented, brown to dark brown 45

Conidiophores aggregated in sporodochial, stromatic or pycnidial conidiomata, conidiophores various, colourless to pigmented, often small and reduced to conidiogenous cells or even inconspicuous or absent 52

45(44) Conidiophores well-differentiated, 60–230 × 5–10 µm, 4–10-septate; conidiogenous cells integrated, terminal, 13–40 µm long, proliferation percurrent with conspicuous annellations, with well-defined conidiogenous loci, visible as minute pores, sometimes surrounded by a pigmented halo; conidia solitary or occasionally in short chains, 1–4-distoseptate, basally truncate, 20–70 × 8–13 µm; on *Graphis* and many other hosts . . . . . ***Corynespora laevistipitata***

Conidiophores little differentiated, gradually developing from hyphae, differentiation between hyphae and conidiophores difficult; conidiogenous loci little differentiated, just visible as a ±truncate end of the conidiogenous cell, without porus; conidia aseptate to euseptate (*Taeniolella* and *Talpapellis*) 46

46(45) Conidiophores in sporodochial conidiomata, to 100 µm diam., base with stromatic hyphal aggregations; conidiophores 12–70 × 5–8 µm; conidia small, 6–16 × 5–7 µm, 0–3-septate, conidial septa conspicuously darkened, thickened and multi-layered; on *Thelotrema weberi* . . . . . ***Taeniolella weberi***

Sporodochia or sporodochioid aggregations of conidiophores not formed or, when formed, without stromatic hyphal base and/or much smaller; conidial septa not conspicuously darkened, thickened and multilayered 47

47(46) Conidiophores mostly verruculose-verrucose; conidiogenous cells with conspicuous terminal annellations, coarse, flaring (connected with the formation of conidiogenous cells); conidia in long firm chains, 6–29 × 3–5 µm, (0–)1–5-septate, smooth or almost to distinctly verruculose or even rimulose, sometimes conidial chains breaking off, functioning as 'propagules' 42–73 µm long, 9–17-septate; on *Graphis caesiella* . . . . . ***Talpapellis graphidis***

Conidiophores and conidiogenous cells without annellations, when present only few, distant, not strictly terminal, connected with the rejuvenation and monopodial growth of the conidiophores; conidia usually smooth (light microscopy), at most with some irregularly spread verrucae 48

48(47) Conidiophores mostly branched, usually at the base, sometimes with an additional branch in the upper part, 9–65 × 4–7 µm, 1–9-septate; conidia in easily disarticulating chains, 5–20 × 4–6(–7) µm, 0–2(–3)-septate; on *Thelotrema* . . . . . ***T. thelotrematis***

Conidiophores usually unbranched; conidia in firm, not easily disarticulating chains 49

49(48) Conidia in long, firm (persistent), toruloid chains (with numerous distinct constrictions), to 100 µm long; on *Thelotrema antoninii* and *T. lepadinum* . . . . . ***T. toruloides***

Conidia not in toruloid chains 50

50(49) Pathogenic, usually destroying infected apothecia and thalli, which are also discoloured; conidiophores 8–56(–90) × 3.5–7 µm; conidia 4–17 × 3–8 µm, (0–)1–2(–3)-septate, pale brown to brown; on a wide range of lichens, incl. *Graphis scripta* and *Phaeographis inconspicua* . . . . . ***T. delicata***

Not destroying infected apothecia and thalli; conidia darker brown 51

51(50) Conidiophores short, 8–15(–20) µm, often in tufts, wall smooth, 0.5 µm wide; conidia 5–13 × 4–5.5 µm, (0–)1–2(–3)-septate, hila narrow, 1–2 µm wide; on *Phaeographis* . . . . . ***T. hawskworthiana***

Conidiophores longer, 14–83(–)95 µm, wall thicker, 0.5–1.5 µm; conidia longer and wider, 7–28 × 5–8 µm, (0–)1–6-septate, hila much wider, 2–5 µm; on lichens of various genera, most often on *Graphis scripta*, also on *Fissurina* and *Phaeographis dendritica* . . . ***T. punctata***

52(44) Conidiomata consisting of an agglomeration of yeast-like cells; conidia multi-celled, moriform, brown 53

Conidiomata different; conidia 0–1-septate 54

53(52) Conidiomatal cells externally dark brown with a mosaic-like ornamentation, pale brown inside stroma; conidia with a mosaic-like ornamentation, 12–14.5 × 11–14 µm, composed of 20–31 cells mainly 3–4 µm diam.; on corticolous lichens, particularly common on *Graphidales* . . . . . ***Etayoa trypethelii***

Conidiomatal cells medium to dark brown, with a verrucose, rarely mosaic-like ornamentation; conidia smooth, becoming echinulate when overmature, 6–10 × 5.5–9 µm, composed of 4–9 cells mainly 3–4.5 µm diam.; on *Graphis* and other hosts . . . . . ***Lichenostigma chlaroterae***

54(52) Conidiomata sporodochioid, pulvinate, during maturation with few or numerous subspherical, almost superficial conidiogenous loculi opening at maturity and releasing subglobose to mostly angular, aseptate, dark brown, smooth-walled conidia, mostly 3.5–4.5 × 2.5–3.5 µm; on *Glyphis scyphulifera*, rarely on *Trypethelium eluteriae* . . . . . ***Lawreya glyphidiphila***

Conidia different; conidia produced superficially, not within subspherical conidiogenous loculi 55

55(54) Conidiomata pseudopycnidia with a colourless stromatic wall; conidiophores absent; conidiogenous cells not evident; conidia ellipsoid or irregular in form, dark brown, smooth-walled, 0(–1)-septate, 7.5–12.5(–16) × 5–8 µm; on *Phaeographis* s.lat., mostly on *Leiorreuma* . . . . . ***Coniambigua phaeographidis***

Conidiomata different 56

56(55) Conidiomata compact sporodochia; conidia medium to dark brown 57

Conidiomata pycnothyria or pycnidia; conidia hyaline or pale brown 59

57(56) Conidiogenous cells elongate, sympodial, smooth or unevenly warted; conidia coarsely warty, single, ellipsoid, mostly 1-septate, 9–11 × 6.5–8 µm; on *Diploschistes* . . . . . ***Deichmannia verrucosa***

Conidiogenous cells short; conidia aseptate (*Sclerococcum*) 58

58(57) Conidia smooth-walled, ellipsoid or angular, 5–6.5 × 4–5 µm; all parts K–; on *Fissurina dumastii* . . . . . ***Sclerococcum aptrootii***

Conidia with an ornamented wall, short to elongate ellipsoid, 10.5–13.5 × 5–6.5 µm; all parts K+ greenish olivaceous; on *Anomomorpha* cf. *roseola* . . . . . ***Sclerococcum sipmanii***

59(56) Conidiomata pycnothyria; upper wall composed of a single layer of radiating rows of dark brown polygonal cells; lower wall missing; conidiogenous cells arising from the upper wall, hyaline; conidia hyaline, aseptate, smooth, oblong, ~6–8 × 2.5–3.5 µm; on *Graphis assimilis* . . . . . ***Hemigrapha graphidicola***

Conidiomata pycnidia 60

60(59) Conidia pale brown, basally truncate, 1-septate, 4–7.5 × 2–3 µm; on *Diploschistes* and many other hosts. . . . . ***Lichenodiplis lecanorae***

Conidia hyaline 61

61(60) Conidia Y-shaped, with an elongate main body and two divergent arms; main body and arms may be swollen and may present narrow apical appendages; pycnidia pale to medium brown (*Cornutispora*) 62

Conidia different; pycnidia dark brown to black. . . . 63

62(61) Main body and arms strongly swollen; main body (incl. basal appendage) 9.5–11.5 × 2–2.5 µm; on various lichens, incl. *Graphis* . . . . . ***Cornutispora ciliata***

Main body and arms not or slightly swollen; main body (incl. basal appendage) 10.5–15.5 × 2–2.5(–3) µm; on various lichens, incl. *Phaeographis* . . . . . ***Cornutispora intermedia***

63(61) Conidia 3–6-septate, elongate and branched, 38–75 × 2–3 µm; conidiophores absent; conidiogenous cells hyaline, ampulliform, holoblastic, 6–9.5 × 4.5–7.5 µm; on *Diploschistes diacapsis* . . . . . ***Cladoniicola irregularis***

Conidia 0–1-septate 64

64(63) Conidia 1-septate; pycnidia mucronate to subrostrate, 33–41 µm diam.; conidia hyaline, 1-septate, smooth, subcylindrical, apically rounded, basally truncate, 11.5–14 × 2.5–3 µm, with one straight apical and two basal mucoid appendages; on *Graphis assimilis* . . . . . ***Strigula graphidicola***

Conidia aseptate, lacking mucoid appendages 65

65(64) Pycnidia ovoid, subrostrate, almost superficial, 53–78 µm diam.; paraphyses present in young pycnidia; conidiophores absent; conidiogenesis holoblastic; macroconidia hyaline, aseptate, elongate ellipsoid, apically rounded, basally truncate, 10.5–13 × 3.7–4.2 µm; microconidia hyaline, aseptate, bacilliform, 10–15 × 1.5–2 µm; on *Graphidales*, incl. *Fissurina*, *Graphis*, *Phaeographis* and *Sarcographa* . . . . . ***Strigula perparvula***

Pycnidia subglobose, immersed to erumpent, not subrostrate 66

66(65) Pycnidia 60–100 µm diam., immersed in the host thallus, often surrounded by a clypeus up to 200 µm diam.; wall basally hyaline or indistinct; conidiophores irregularly catenate and branched; conidiogenesis enteroblastic, phialidic; conidia bacilliform to narrowly fusiform, 8.8–11 × 1.3–1.6 µm; on *Phaeographis* . . . . . ***Amerosporiopsis phaeographidis***

Pycnidia 30–50 µm diam., immersed to superficial, without clypeus; wall entirely brown; conidiophores absent; conidiogenous cells obpyriform, phialidic; conidia narrowly ellipsoid to cylindrical, 3.5–5.5 × 1.5–2 µm; on *Diploschistes ocellatus* . . . . . ***Phoma aggregata***

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