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REGULAR PAPER

Phylogenetic position of *Synarthonia* (lichenized Ascomycota, Arthoniaceae), with the description of six new species

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Background and aims – The Arthoniaceae form a species-rich family of lichenized, lichenicolous and saprophytic fungi in the order Arthoniales. As part of taxonomic revisions of the African Arthoniaceae, a number of species assignable to the genus *Synarthonia* were collected and sequenced. The present study aims at placing the genus in a phylogeny for the first time and at clarifying its circumscription.
Methods – Nuclear (*RPB*2) and mitochondrial (mtSSU) DNA sequences from freshly collected specimens were obtained and analysed with phylogenetic Bayesian and maximum likelihood (ML) methods.
Key results – *Synarthonia* is closely related to the genera *Reichlingia* and *Coniocarpon* in the Arthoniaceae. Six *Synarthonia* species are described as new to science and ten new combinations into this genus are made. A worldwide identification key to the genus *Synarthonia* is provided. Lectotypes are chosen for *Arthonia elegans*, *A. inconspicua*, *A. lopingensis*, *A. ochracea*, *A. subcaesia* and *A. translucens*. *Arthonia thamnocarpa* is synonymized with *Sclerophyton elegans*, and *Arthonia elegans* with *Coniocarpon fallax*. *Synarthonia ochracea* is shown to be a misunderstood species in the past and recent literature, since it was erroneously synonymized with *Coniocarpon elegans*. *Synarthonia ochracea* appears to start its life cycle as a non-lichenized lichenicolous fungus on *Graphis* before developing a lichenized thallus or it might be a facultatively lichenicolous fungus. It belongs to a complex of closely related species whose biology and circumscription are still in need of further studies.
Conclusions – *Synarthonia* forms a monophyletic but somewhat heterogeneous lineage closely related to *Coniocarpon* and *Reichlingia*. As delimited here, *Synarthonia* includes corticolous lichens with a trentepohlioid photobiont as well as non-lichenized lichenicolous fungi. The core group is characterized by white pruinose ascomata, but species producing orange pruinose or non-pruinose ascomata are also included. Ascospores are transversely septate with an enlarged apical cell or are muriform. Future molecular and morphological studies are needed for a better circumscription and definition of the genus.

Key words – Arthoniales, macrocephalic ascospores, mtSSU, phylogeny, synascomata, *RPB*2, tropics.

INTRODUCTION

The cosmopolitan family Arthoniaceae is the largest family in the order Arthoniales, which includes about 1500 species of mainly lichenized, more rarely lichenicolous and saprophytic fungi (Ertz et al. 2009, Sundin et al. 2012, Frisch et al. 2014a). The family, first described by Reichenbach (1841), is characterized by a reduction of the ascomatal borders and by globose to clavate asci of the *Arthonia*-, *Arthothelium*- and *Cryptothecia*-types (Grube 1998, Frisch et al. 2014a). The family Arthoniaceae is a major component of the lichen flora of many forest types, especially in the tropics where many corticolous and foliicolous species occur (Tehler 1983, Tehler 1990, Follmann & Werner 2003, Frisch et al. 2014a).

During the past decades, several genera were described or reinstated in the Arthoniaceae in order to circumscribe smaller, monophyletic groups such as *Coniarthonia* Grube (Grube

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2001a), *Sporostigma* Grube (Grube 2001b), *Synarthothelium* Sparrius (Sparrius 2009), *Herpothallon* Tobler (Aptroot et al. 2009), *Crypthonia* Frisch & G.Thor (Frisch & Thor 2010), *Coniocarpon* DC. (Frisch et al. 2014a), *Myriostigma* Kremp. (Frisch et al. 2014a), *Pachnolepia* A.Massal. (Frisch et al. 2014a), *Inoderma* (Ach.) Gray (Frisch et al. 2015), *Glomerulophoron* Frisch, Ertz & G.Thor (Frisch et al. 2015), *Sporodophoron* Frisch, Y.Ohmura, Ertz & G.Thor (Frisch et al. 2015), *Cryptophaea* Van den Broeck & Ertz (Van den Broeck & Ertz 2015), *Snippocia* Ertz, Kukwa & Sanderson (Ertz et al. 2018) and *Leprantha* Dufour ex Körb. (Ertz et al. 2018). Using molecular data, several genera of uncertain family affiliation were placed in the Arthoniaceae, such as *Reichlingia* Diederich & Scheid. (Ertz & Tehler 2011, Frisch et al. 2014a, 2014b) and *Tylophoron* Nyl. ex Stizenb. (Lumbsch et al. 2009, Ertz et al. 2011). Several phenotypically distinct genera currently accepted in Arthoniaceae have still not been treated in phylogenetic studies, including *Synarthonia* Müll. Arg. The phylogenetic position of this genus was unclear, and the synonymy with *Reichlingia* has been suggested recently (Joseph & Sinha 2015).

Synarthonia is a small genus originally described from Costa Rica based on the type species *S. bicolor*. It encompasses only five species accepted so far: *S. bicolor* Müll. Arg. (= *Arthonia inconspicua* Stirt.), *S. psoromica* S.Joseph & G.P.Sinha, *S. sarcographoides* Aptroot et al., *S. sikkimensis* S.Joseph & G.P.Sinha and *S. stigmatidialis* Müll. Arg. (Joseph & Sinha 2015). According to Joseph & Sinha (2015), the genus is characterized by solitary ascomata becoming mono- to pluri-carpocentral synascomata embedded in a slightly elevated to immersed pseudostroma, with a thin white thalline margin, and *Arthonia*-type asci producing transversely septate ascospores with enlarged apical cell or muriform ascospores.

All *Synarthonia* species seem to have a rather restricted distribution. *Synarthonia bicolor* has been mentioned only from Costa Rica (Müller 1891). *Synarthonia psoromica* and *S. sikkimensis* are currently known only from India (Joseph & Sinha 2015), while *S. sarcographoides* has been reported only once from north-east Brazil (Menezes et al. 2013) and *S. stigmatidialis* once from Mexico (Müller 1895). Most species are probably overlooked as they are rather inconspicuous in the field. Often only limited material is available, but additional specimens are possibly stored in herbaria under other names such as *Arthonia* sp.

During our ongoing studies on the biodiversity of lichens in tropical Africa, several specimens of the type species of *Synarthonia* were collected and sequenced, allowing for placing the genus in a phylogeny for the first time. Moreover, six species new to science and ten species currently placed in *Arthonia* could be assigned to or combined into this genus based on anatomical, chemical, morphological, ecological and/or molecular data. The new species are described below along with the new combinations. A world key to all known species is provided. A phylogenetic tree showing the position of the genus in the family Arthoniaceae is presented.

MATERIAL AND METHODS

Morphological study

Specimens for this study collected by the authors in Belgium, D.R. Congo, France, Madagascar, Rwanda, Tanzania and Uganda are deposited in the herbaria of the Meise Botanic Garden (BR), the Museum of Evolution in Uppsala (UPS) and the private herbaria of R. Common and A. Frisch. Other specimens were borrowed from the following herbaria: B, BM, BR, BSA, FH, G, H, M, S, TUR, UPS, US and WU. Morphological characters were studied using an Olympus SZ61 stereomicroscope and a Leica MS5 dissecting microscope. The anatomy was studied using an Olympus CHR-TR45 and an Olympus BX51 microscope. Microscopic photographs were taken with an Olympus BX51 microscope fitted with an Olympus UC30 camera. Macroscopic photographs were taken using a Keyence VHX-5000 digital microscope. For species identification, hand sections and squash preparations of specimens were studied in water, methyl blue, 5% KOH (K), and Lugol's reagent (1% I_2) either without (I) or with KOH pre-treatment (K/I). Measurements of ascospores refer to material examined in water, those of asci to material examined in K/I. For measurements of asci, ascospores and conidia, the minimum and maximum values are given, all values except those of the conidia rounded to the nearest multiple of 0.5 µm, followed by the number of measurements (N). When more than 50 ascospores were measured, ascospore measurements are presented as (minimum) $\bar{X}$-σ_x – $\bar{X}$+σ_x (maximum). Microchemical reactions and spot tests were performed using 10% KOH (K), a sodium hypochlorite solution (C), *para*-phenylenediamine (PD) and short wave UV_{254} light according to Orange et al. (2010). Secondary lichen compounds were identified by TLC in solvents A and B. Calcium oxalate crystals were identified by applying 25% sulfuric acid to squash preparations of thallus and/or ascomata.

Type specimens and non-type material of corticolous *Arthonia* species described from or mentioned to occur in Africa were studied. The original descriptions of all *Arthonia* species occurring in tropical Africa were consulted. The following types of (sub)tropical corticolous species of *Arthonia* which according to the protologues have ascospores with at least one enlarged apical cell and between two and five septa were requested on loan and examined to ensure that no older names were available for the new species (types not received are indicated): *A. angulosa* Müll.Arg. (G, type not available for our study), *A. berberina* Zahlbr. (WU), *A. borbonica* Ertz, Elix & Grube (BR), *A. carneoumbrina* Zahlbr. (WU), *A. compensata* Nyl. (G), *A. costaricensis* Müll.Arg. (BR), *A. dichotoma* Vain. (TUR), *A. dispartibilis* Müll.Arg. (G), *A. elegans* (Ach.) Almq. (S), *A. ferruginea* Vain. (M, BM web), *A. gracilior* Müll.Arg. (G), *A. inconspicua* Stirt. (BM), *A. lecideoides* Zahlbr. (=*A. knightii* Zahlbr., BM; not *A. lecideoides* C.Knight), *A. leptographidea* Vain. (TUR), *A. linearis* Kremp. (M), *A. lopingensis* Zahlbr. (WU), *A. modesta* C.W.Dodge (BM), *A. nigrorufa* Müll.Arg. (G), *A. obscurella* Müll.Arg. (G), *A. ochracea* Dufour (PC, type not available for our study but scan received), *A. ochraceella* Nyl. (G), *A. ochrodes* Nyl. ex Willey (H), *A. picea* Vain. (TUR), *A. phymatodes* C.Knight (WELT, type not available for our

Table 1 – **Specimens and their GenBank accession numbers.**
Newly generated sequences are indicated by an asterisk; en-dash indicates missing data.

Specimens	Voucher	mtSSU	*RPB2*
Arthonia anglica	Rwanda; *Ertz* 7775 (BR)	EU704049	EU704012
Arthonia apotheciorum	Sweden; *Frisch* 11/Se23 (UPS)	KJ850970	KJ851148
Arthonia calcarea	France; *Ertz* 7539 (BR)	EU704064	EU704028
Arthonia didyma	Belgium; *Ertz* 7587 (BR)	EU704047	EU704010
Arthonia granithophila	Sweden; *Frisch* 10/Se74 (UPS)	KJ850981	KJ851107
Arthonia physcidiicola	Uganda; *Frisch* 11/Ug318 (UPS)	KF707646	KF707657
Arthonia punctiformis	Sweden; *Thor* 26158 (UPS)	KJ850973	KJ851113
Arthonia radiata	Sweden; *Frisch* 11/Se25 (UPS)	KJ850969	KJ851109
Arthonia sp. 9090	Florida; *Ertz* 9090 (BR)	EU704050	EU704013
Arthonia subfuscicola	Sweden; *Frisch* 11/Se15 (UPS)	KJ850972	KJ851111
Arthothelium norvegicum	USA; *McCune* 31061 (UPS)	KJ851003	KJ851114
Arthothelium sp. Gy10	Guyana; *Jönsson* s.n. (Guyana 10, UPS)	KJ850957	KJ851095
Arthothelium sp. Gy8	Guyana; *Jönsson* s.n. (Guyana 8, UPS)	KJ850958	KJ851094
Coniocarpon aff. *cinnabarinum*	Uganda; *Frisch* 11/Ug3 (UPS)	KJ850978	KJ851102
Coniocarpon cinnabarinum 1	Norway; *Johnsen* 111003 (UPS)	KJ850976	KJ851103
Coniocarpon cinnabarinum 2	Uganda; *Frisch* 11/Ug297 (UPS)	KJ850977	KJ851104
Coniocarpon cinnabarinum 3	Uganda; *Frisch* 11/Ug296 (UPS)	KP870158	KP870170
Coniocarpon cinnabarinum 4	Rwanda; *Ertz* 8730 (BR)	EU704046	EU704009
Coniocarpon fallax	Great Britain (L10175)	KJ850979	KJ851101
Crypthonia aff. *vandenboomii*	Uganda; *Frisch* 11/Ug21 (UPS)	KJ850960	KJ851085
Crypthonia palaeotropica	Uganda; *Frisch* 11/Ug457 (UPS)	KJ850961	KJ851084
Cryptothecia sp. Ug1	Uganda; 11/Ug194 (UPS)	KJ850956	KJ851093
Cryptothecia sp. Ug2	Uganda; 11/Ug18 (UPS)	KJ850955	KJ851092
Cryptothecia sp. Ug3	Uganda; 11/Ug39 (UPS)	KJ850954	KJ851086
Cryptothecia subnidulans	Reunion; *v.d.Boom* 40613 (hb Boom)	KJ850952	KJ851087
Herpothallon inopinatum	Mexico; *Rudolphi* 12 (UPS)	KJ850964	KJ851099
Herpothallon kigeziense	Uganda; *Frisch* 11/Ug26 (UPS)	KF707644	KF707654
Herpothallon rubrocinctum	Mexico; *Rudolphi* 5 (UPS)	KF707643	KF707655
Inoderma afromontanum	Uganda; *Frisch* 11/Ug164 (UPS)	KJ850963	KJ851090
Inoderma byssaceum	Japan; *Thor* 25952 (UPS)	KJ850962	KJ851089
Myriostigma candidum 1	Uganda; *Frisch* 11/Ug125 (UPS)	KJ850959	KJ851096
Myriostigma candidum 2	Gabon; *Ertz* 9260 (BR)	EU704052	EU704015
Pachnolepia pruinata	Sweden; *Frisch* 11/Se34 (UPS)	KJ850967	KJ851098
Reichlingia leopoldii	Belgium; *Ertz* 13294 (BR)	JF830774	HQ454723
Reichlingia syncesioides	Uganda; *Frisch* 11/Ug14 (UPS)	KF707651	KF707656

Table 1 (continued) – Specimens and their GenBank accession numbers.
Newly generated sequences are indicated by an asterisk; en-dash indicates missing data.

Specimens	Voucher	mtSSU	*RPB2*
Reichlingia zwackhii	Sweden; *Thor* 26800 (UPS)	KF707652	HQ454655
Synarthonia albopruinosa	DR Congo; *Van den Broeck* 6086 (BR)	*MH251873	*MH271696
Synarthonia aurantiacopruinosa	DR Congo; *Van den Broeck* 5764 (BR)	*MH251874	*MH271697
Synarthonia fuscata	DR Congo; *Van den Broeck* 6101 (BR)	*MH251875	*MH271706
Synarthonia inconspicua	Florida; *Common* 10048 (hb Common)	*MH251878	–
Synarthonia inconspicua 1	Madagascar; *Ertz* 19739A (BR)	*MH251879	*MH271700
Synarthonia inconspicua 2	Uganda; *Van den Broeck* 6325 (BR)	*MH251880	*MH271701
Synarthonia inconspicua 3	Tanzania; *Van den Broeck* 7013B (BR)	*MH251881	*MH271702
Synarthonia inconspicua 4	Tanzania; *Van den Broeck* 7034 (BR)	*MH251882	*MH271703
Synarthonia josephiana	Madagascar; *Ertz* 19739B (BR)	*MH251876	*MH271698
Synarthonia muriformis 1	Uganda; *Frisch* 11/Ug41 (UPS)	KJ851025	KJ851100
Synarthonia muriformis 2	Madagascar; *Ertz* 19344 (BR)	*MH251877	*MH271699
Synarthonia ochracea	France; *Van den Broeck* 6653 (BR)	*MH251884	*MH271705
Synarthonia pilosella	Rwanda; *Ertz* 7808 (BR)	*MH251883	*MH271704
Tylophoron hibernicum	Uganda; *Frisch* 11/Ug220 (UPS)	KJ850966	KJ851097

study), *A. polygramma* Nyl. (M), *A. polygrammodes* Vain. (TUR), *A. polystigmatea* Vain. (BM), *A. pruinosula* Nyl. (G, BR), *A. puiggarii* Müll.Arg. (G, type not available for our study), *A. pulveracea* Müll.Arg. (G), *A. radians* Müll.Arg. (G), *A. rubiginella* Nyl. (H), *A. serialis* Müll.Arg. (G), *A. ramulosa* C.Knight (WELT, type not available for our study), *A. somaliensis* Müll.Arg. (G), *A. subcaesia* C.W.Dodge (FH), *A. subgracilis* Müll.Arg. (G), *A. subnovella* Müll.Arg. (G), *A. subtecta* Müll.Arg. (BR), *A. subtilissima* Müll.Arg. (G), *A. symmicta* Müll.Arg. (G), *A. thamnocarpa* Vain. (TUR), *A. translucens* Stirt. (BM), *A. tuckermaniana* Willey (US), *A. viridicans* Willey (H). *Synarthonia psoromica* (BSA) was checked for the presence of psoromic acid. Specimens not seen are indicated by "n.v.", while specimens only seen as digital images available on the internet are indicated by "web". Specimens from private herbaria are indicated by "hb" followed by the name of the owner.

Molecular techniques

Well-preserved and freshly collected specimens lacking any visible symptoms of fungal infection were used for DNA isolation. Hand-made sections of ascomata or thallus were used for direct PCR as described in Ertz et al. (2014). The lichen material was washed with a 1% KOH solution or acetone, and then rinsed with water to remove remnants of pigments. The material was placed directly in microtubes with 20 µl H_2O. Amplification reactions were prepared for a 50 µl final volume containing 5 µl 10× DreamTaq Buffer (Thermo Fisher Scientific, Waltham, MA), 1.25 µl of each of the 20 µM primers, 5 µl of 2.5 mg ml^{-1} bovin serum albumin (Thermo Fisher Scientific, Waltham, MA), 4µl of 2.5mM each dNTPs (Thermo Fisher Scientific, Waltham, MA), 1.25 U DreamTaq DNA polymerase (Thermo Fisher Scientific, Waltham, MA) and the tiny fragments of lichen material. A targeted fragment of about 0.8 kb of the mtSSU rDNA was amplified using primers mrSSU1 and mrSSU3R (Zoller et al. 1999). A fragment of about 1 kb of the *RPB2* protein-coding gene was amplified using primers *fRPB2*-7cF and *fRPB2*-11aR (Liu et al. 1999). The yield of the PCR reactions was verified by running the products on a 1% agarose gel using ethidium bromide. Both strands were sequenced by Macrogen® using amplification primers. A BLAST search in GenBank was performed for a preliminary taxonomic assignment of the sequences. They were assembled and edited with Geneious ver. 5.1.7 (Kearse et al. 2012).

Taxon selection and phylogenetic analyses

Twenty-three new sequences were obtained for this study and 76 additional sequences were retrieved from GenBank (table 1). For the phylogenetic analyses a set of 49 OTUs was used, consisting of taxa representing all major clades currently accepted in the Arthoniaceae except for the more distantly related *Bryostigma* clade (Frisch et al. 2014a) and for which the mtSSU and the *RPB2* were available (table 1). *Arthothelium norvegicum* Coppins & Tønsberg was chosen as outgroup species. One mtSSU sequence of *Synarthonia inconspicua* (= *S. bicolor*) from the USA (*Common* 10048, hb Common) was not used in the final phylogenetic analysis since the *RPB2* sequence was not available for the specimen. Morphologically, this specimen fits well with other material

of *S. inconspicua* and it was placed within *S. inconspicua* in a preliminary phylogenetic analysis (results not shown).

The sequences were aligned using MAFFT v6.814b (Katoh et al. 2002) within Geneious 5.1.7 and manually corrected for errors using Mesquite 3.04 (Maddison & Maddison 2015). Ambiguously aligned regions according to Lutzoni et al. (2000) and introns were manually removed and excluded from subsequent analyses. All new sequences were deposited in GenBank (table 1) and the alignments uploaded to TreeBASE (study accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S22136).

To examine topological incongruence among data sets, Bayesian and maximum likelihood (ML) analyses were carried out on each of the single-locus data sets. We used MrBayes ver. 3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003), and RAxML ver. 7.2.7 (Stamatakis 2006) with 1000 replicates of ML bootstrapping (ML BS) under the GTRGAMMA model of sequence evolution. In both cases, analyses were run on the CIPRES Web Portal (Miller et al. 2010). All topological bipartitions were compared for the two loci. A conflict was assumed to be significant when differing topologies for the same set of taxa (one being monophyletic and the other being non-monophyletic) were each supported with PP values ≥ 0.95 and/or bootstrap values ≥ 70 (Mason-Gamer & Kellogg 1996). Based on this criterion, one conflict was detected regarding the sister-group relationship of *Synarthonia* with either *Coniocarpon* or *Reichlingia*, see discussion section below. As this conflict had no impact on the monophyly of *Synarthonia* or our general conclusions on this genus, the mtSSU and *RPB*2 data sets were concatenated.

The combined two-locus data set of 49 samples consisted of 1503 unambiguously aligned sites, 639 for mtSSU and 864 for *RPB*2.

Phylogenetic relationship and confidence were inferred for the concatenated two-locus data set using Bayesian inference and maximum likelihood (ML) as optimization criteria. For the Bayesian analyses, best-fit evolutionary models for each partition were estimated using the Akaike Information Criterion (AIC) as implemented in jModelTest2 (Darriba et al. 2012). The TVM+I+G model was selected for the mtSSU data set as well as for the *RPB*2/2nd position, while the GTR+I+G model was selected for the *RPB*2/1st and *RPB*2/3rd positions.

Two Bayesian MCMC runs were executed in parallel, each using four independent chains and 120 million generations, sampling trees every 1000th generation. TRACER ver. 1.6.0 (Rambaut et al. 2013) was used to ensure that convergence was reached by plotting the log-likelihood values of the sample points against generation time. Convergence between runs was also verified using PSRF (Potential Scale Reduction Factor), confirming that values for all parameters were equal to 1.000. A tree was generated from 180002 post-burnin trees out of 240002 trees for each MCMC runs using the sumt option of MrBayes. Posterior probabilities (PP) were determined by calculating majority-rule consensus trees. For the ML analyses, RAxML was used under a GTRGAMMA model of molecular evolution. Bootstrap support (ML BS) was obtained from 1000 replicates of ML bootstrapping conducted with the same settings and program. Internodes with bootstrap proportions ≥70 and Bayesian posterior probabilities ≥0.95 were considered strongly supported (Alfaro et al. 2003, Lutzoni et al. 2004). Phylogenetic trees were visualized using FigTree ver. 1.3.1 (Rambaut 2012).

RESULTS

Phylogenetic analysis

The Bayesian tree obtained from the combined two-locus analysis of 49 OTUs is shown in fig. 1. The main well-supported lineages of Arthoniaceae are in accordance with the results obtained by Frisch et al. (2014a). The genus *Synarthonia* is placed in a well-supported lineage (ML BS = 99 and PP = 1) with the genus *Coniocarpon* and the *Reichlingia* group, both also being well-supported monophyletic groups (ML BS = 99–100 and PP = 1) (fig. 1).

The relationships between the species of *Synarthonia* are usually well supported (fig. 1). *Synarthonia albopruinosa*, *S. inconspicua*, *S. muriformis* and *S. pilosella* are closely related (ML BS = 98 and PP = 1). These four species are characterized by white pruinose ascomata which react PD+ yellow to orange. *Synarthonia aurantiacopruinosa*, *S. fuscata* and *S. ochracea* form the sister clade to the core group of *Synarthonia*, this sister relationship being strongly supported (ML BS = 86 and PP = 0.99). These three species have small ascomata lacking white pruina (two having an orange pruina and one being epruinose) and predominantly 3-septate ascospores. *Synarthonia josephiana* is the most distantly related species, characterized by black epruinose ascomata and 4-septate ascospores.

Independent Bayesian analysis of the mtSSU and *RPB*2 alignments for the 49 OTUs revealed a phylogenetic conflict between the nuclear and the mitochondrial gene. Based on the mtSSU, *Reichlingia* (including *Arthonia* sp. 9090 and *A. anglica*) forms a poorly supported sister group to *Coniocarpon* (ML BS = 69 and PP = 0.95; figs not shown), while *Synarthonia* forms a well-supported sister group to the *Coniocarpon-Reichlingia* clade (ML BS = 93 and PP = 1; figs not shown). In the phylogenetic tree based on the *RPB*2, *Synarthonia* is the well-supported (ML BS = 95 and PP = 1) sister group to *Reichlingia*, while *Coniocarpon* is the well-supported sister taxon to the *Reichlingia-Synarthonia* clade (ML BS = 90 and PP = 1; figs not shown). This phylogenetic conflict between the nuclear and the mitochondrial genes is difficult to explain. It does not seem to be due to our delimitation of excluded ambiguous regions in mtSSU because the conflict persisted with different analyses performed using a narrow or large concept of excluded ambiguous regions in this alignment. Phylogenetic conflicts among closely related and recently diverged species have been reported as a signature of hybridization (Mallet 2005). However, we do not think that this might be responsible for the different sister relationships observed for the genera *Coniocarpon*, *Reichlingia* and *Synarthonia*. Whatever the cause of this conflict, both genes recover *Synarthonia* as a strongly supported monophyletic genus (ML BS = 95 and PP = 1) closely related to but distinct from *Coniocarpon* and *Reichlingia*.

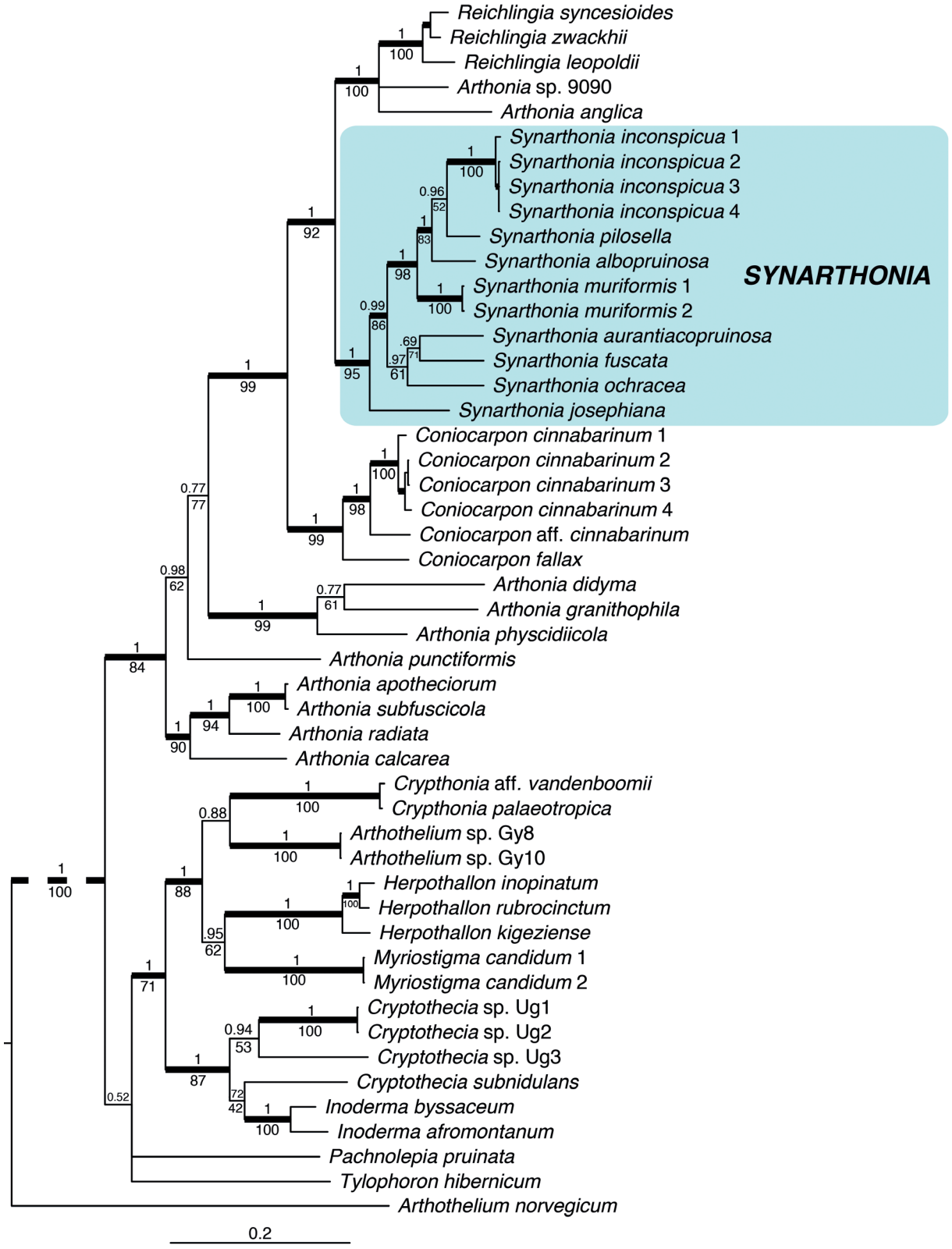

Figure 1 – Phylogenetic relationships among a selected group of Arthoniaceae resulting from a Bayesian analysis based on a data set of 49 samples of mtSSU and *RPB*2 sequences. *Arthothelium norvegicum* was chosen as outgroup. MrBayes posterior probabilities are shown above branches, and RAxML bootstrap values are shown below branches. Thicker lines highlight internodes considered strongly supported by both analyses. *Synarthonia* is indicated in bold and highlighted with a blue coloured box.

Taxonomic treatment

Synarthonia Müll.Arg. (Müller 1891: 85). – Type species: *Synarthonia bicolor* Müll.Arg. (= *Synarthonia inconspicua*).

Thallus corticolous, rarely absent when young or throughout the life cycle (non-lichenized lichenicolous fungus), crustose, endophloeodal to epiphloeodal, whitish to greenish-grey to green, with or without white striae or spots, continuous to cracked, smooth to verrucose or farinose, sorediate or esorediate, ecorticate; thallus hyphae hyaline. Prothallus not observed, or forming a black to brown compact line in contact with other lichens, sometimes fibrous-like (*S. psoromica* and *S. stigmatidialis*) or rhizomorph-like (*S. sikkimensis*). Photobiont trentepohlioid, in short chains or single-celled, the cells globose to ellipsoid, absent in the non-lichenized lichenicolous species. Ascomata solitary or forming irregular clusters in most of the species, immersed to slightly elevated above thallus level to ± sessile; disc white, greyish or orange pruinose (brown to orange when pruina removed), light brown and almost translucent or blackish-brown with remnants of thallus. Excipulum hyaline to pale brownish to straw-coloured, composed of brown pigmented or hyaline hyphae, non-carbonized. Epihymenium pale brownish, formed by branched and anastomosing brown-walled (K+ olivaceous or K-) or hyaline (K-), 1.3–2.3 µm wide paraphysoids with tips thickened or not, inspersed with hyaline, red-brown to orange granular crystals. Hymenium hyaline, not inspersed or rarely inspersed with hyaline or orange granular crystals, I+ directly red, I+ blue rapidly turning into red or I+ persistently blue, K/I+ blue. Paraphysoids hyaline, branched and anastomosing, ± parallel between the asci and forming a dense or loose mesh around the asci. Hypothecium hyaline, yellowish or brownish. Asci broadly clavate, obovoid to ellipsoid or (sub-)globose, 8-spored, with or without K/I+ blue ring like structures in the tholus, occasionally with a distinct or indistinct ocular chamber. Ascospores persistently hyaline, or brownish and ornamented with small brown (K+ olivaceous) warts at late maturity, ellipsoid to oblong-ovoid, transversely septate with an enlarged apical cell or muriform, with or without a gelatinous sheath. Pycnidia black, walls brown. Conidia hyaline, bacilliform, non-septate, straight to slightly curved.

Chemistry – Parietin, evernic acid, psoromic acid, unidentified xanthones, unknown secondary compounds or secondary compounds absent. Calcium oxalate crystals absent in most of the species (occasionally present in the ascomata of *S. muriformis*).

Distribution and ecology – Lichenized species of *Synarthonia* occur mainly in the tropics, more rarely in temperate regions, and are corticolous with a preference for smooth barked trees and rather exposed conditions (branches, free standing trees). The (facultatively) lichenicolous species of the *S. ochracea* complex appear to be restricted to corticolous species of *Graphis* early in their development, while *S. rimeliicola* is living on species of Parmeliaceae.

Notes –The genus *Synarthonia* is characterized by a combination of the following characters: ascomata often aggregated in clusters, ascospores transversely septate with an enlarged apical cell or muriform, and a secondary chemistry including evernic acid, psoromic acid, xanthones, unknown secondary compounds, or compounds absent.

According to Joseph & Sinha (2015) the genus *Synarthonia* is characterized by solitary ascomata becoming mono- to pluri-carpocentral synascomata embedded in a slightly elevated to immersed pseudostroma, with a thin white thalline margin. Cross sections of ascomata in some of our specimens showed two or three loculi of hymenium separated by thin interhymenial strands suggesting synascomata (fig. 2C). However, these interhymenial strands may also be caused by ascoma branching or grouped ascomata and cannot be differentiated from excipular hyphae. Moreover, this character is not always easy to observe. Therefore, we decided not to use the terminology of Joseph & Sinha (2015) pending further studies on the ascoma ontogeny of *Synarthonia*.

According to Joseph & Sinha (2015), the asci in the genus *Synarthonia* belong to the *Arthonia*-type. This is one of the four main ascus types in Arthoniales (Grube 1998), characterized by an obovoid (clavate) shape in combination with a thin lateral ascus wall and a large apical dome pierced by a distinct ocular chamber. To our observations, the shape of the asci in *Synarthonia* is rather variable and varies between broadly clavate, obovoid to ellipsoid or (sub-)globose. A distinct ocular chamber is only occasionally present in some of the species.

Type species

Synarthonia inconspicua (Stirt.) Van den Broeck & Ertz, **comb. nov.**

Arthonia inconspicua Stirt., Proceedings of the Philosophical Society of Glasgow 11: 319. 1879 (Stirton 1879). – Type: India, Nilgiri Hills, 1876, *Watt* s.n. (lecto-: BM, barcode BM001107381, **designated here**, see notes).

Arthonia translucens Stirt. (Stirton 1881: 188). – Type: India, Assam, *Watt* s.n. (lecto-: BM, barcode BM001107493, **designated here**, see notes).

Synarthonia bicolor Müll.Arg. (Müller 1891: 86). – *Synarthoniomyces bicoloris* Cif. & Tomas., nomen illeg. (Ciferri & Tomaselli 1953: 79; see Lücking & Hawskworth 2007). – Type: Costa Rica, San José, 1890, *Pittier* 5292 (holo-: G web; iso-: BR, barcode BR5030011732923).

Arthonia subcaesia C.W.Dodge (Dodge 1953: 307). – Type: Sierra Leone, Njala (Kori), on twigs of *Bauhinia tomentosa*, *Deighton* M4307H (lecto-: FH, **designated here** on the species of *Synarthonia*, see notes).

MycoBank No.: MB 825152. GenBank accession numbers: MH251878 (mtSSU, *Common* 10048); MH251879 (mtSSU, *Ertz* 19739A); MH251880 (mtSSU, *Van den Broeck* 6325); MH251881(mtSSU, *Van den Broeck* 7013B); MH251882 (mtSSU, *Van den Broeck* 7034); MH271700 (*RPB*2, *Ertz* 19739A); MH271701 (*RPB*2, *Van den Broeck* 6325); MH271702 (*RPB*2, *Van den Broeck* 7013B); MH271703 (*RPB*2, *Van den Broeck* 7034).

Thallus c. 32–46 µm thick, inconspicuous to whitish to greenish-grey, smooth, continuous to cracked; thallus hyphae hyaline, 1.3–1.7 µm wide. Prothallus a black to brown

compact line in contact with other lichens. Photobiont trentepohlioid, forming an algal layer of c. 15 µm, cells 10–13 × 9.0–9.5 µm, rounded, solitary or in chains. Ascomata solitary, 0.1–0.5 × 0.1–0.5 mm, rounded, often forming irregular clusters of 0.5–1.2 × 0.4–0.9 mm, numerous, slightly elevated above thallus level, scattered more or less evenly over the thallus; disc heavily white pruinose, light brown when pruina removed, flat to convex. Excipulum 10–15 µm wide, composed of hyaline, loosely intricate hyphae 1.5–2.5 µm wide, orientated in all directions, inspersed with orange brown granules, K+ completely dissolving. Epihymenium 10–20 µm tall, composed of loosely intricate hyaline tips of the paraphysoids, the tips 1.3–2.3 µm wide, occasionally slightly swollen up to 2.5 µm, and adspersed with orange-brown granules which are K+ completely dissolving. Hymenium 40–75 µm tall, hyaline, not inspersed, I+ blue rapidly turning into red, K/I+ blue. Paraphysoids 1.6–1.7 µm wide, loosely intricate around the asci. Hypothecium 5–15 µm thick, hyaline to yellowish, composed of loosely intricate hyphae, inspersed with orange granules which are K+ completely dissolving, I+ red, K/I+ blue. Asci 40–70 × 15–25 µm (N = 12), clavate, obovoid to ellipsoid, or (sub-) globose, stipitate, occasionally with a distinct ocular chamber; no K/I+ blue ring structure in the tholus observed. Ascospores (15–)16.5–21.3(–24.5) × (5.3–)6.2–7.7(–8.5) µm (N = 60), hyaline, becoming brown (K+ olivaceous) and ornamented with small brown warts at late maturity sometimes already in the asci, with enlarged apical cell, oblong-ovoid, (1–)3–4(–5)-septate; lumina of enlarged apical cell 5.5–7.4 × 4.9–5.6 µm, other lumina 1.5–2.6 × 2.2–5.0 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath distinct, c. 1.5 µm wide. Pycnidia black, more or less immersed or slightly elevated above thallus level, with a wide brown ostiole, walls brown, composed of hyphae of 2.1–2.4 µm wide, K+ olivaceous. Conidia 4.7–6.4 × 0.8–1.3 µm (N = 20), hyaline, bacilliform, non-septate, straight to slightly curved to sigmoid. Fig. 2 A–E.

Chemistry – Thallus K-, C-, KC-, PD-, UV+ (often patchily) bright yellow-orange to ± whitish yellow. Pruina PD+ yellow, K-, KC-. Calcium oxalate crystals absent in ascomata and thallus. TLC (solvent A) revealed two major UV+ secondary compounds after spraying and heating. The colour of the first spot, situated a little above that of psoromic acid is dull orange. The other spot is UV+ turquoise just after heating, but the UV intensity is decreasing after one night. This spot is situated a little below that of parietin and represents an unidentified xanthone.

Distribution and ecology – *Synarthonia inconspicua* is widely distributed in the tropics being known from Costa Rica, Cuba, D.R. Congo, India, Madagascar, Netherlands Antilles, Rwanda, Sierra Leone, Tanzania, Uganda and USA. The species seems to prefer exposed smooth barked trees close to human settlements (gardens, parks, plantations, roads) or other rather dry conditions. To our knowledge, it has never been found within dense tropical rain forests. In India, it is mentioned from the town Haldibari and from Sundarbans National Park without further specifications (Joseph & Sinha 2015). Many of the species described from India by Stirton (1881) were collected on or in the neighbourhood of tea plantations.

Notes – The type specimens of *Synarthonia bicolor* Müll. Arg., *Arthonia inconspicua* Stirt., *A. subcaesia* C.W.Dodge and *A. translucens* Stirt. agree well in the morphology of thallus, ascomata and ascospores. *S. inconspicua* is the correct name due to its nomenclatural priority (oldest name).

Types specimens of *Arthonia inconspicua* and *A. translucens* bear labels added by Patwardhan & Makhija in 1977 indicating "lectotype", but to our knowledge the lectotypifications have not been effectively published. Therefore, lectotypes are designated here. The examined *Deighton* type specimen of *Arthonia subcaesia* contains two twigs, each with a different species of Arthoniaceae. On one of the twigs a specimen of *Synarthonia* is present, and on the other twig a specimen of *Coniocarpon*. The description by Dodge fits best the species of *Synarthonia* (disc densely white pruinose and ascospores of 18.0–22.0 × 5.5–6.0 µm), which is therefore selected here as lectotype. The species of *Coniocarpon* is characterized by purplish spots on the ascomata, a character not mentioned by Dodge, and larger ascospores of 23.0–23.5 × 8.0–8.5 µm.

Synarthonia inconspicua is characterized by rounded to elongate ascomata, soon lobed or forming irregular stellate-radiating clusters, heavily white pruinose when young but becoming less pruinose and with a brownish disc in later stages, and by 3–4(–5)-septate ascospores. The thallus is UV+ bright yellow-orange (often patchily) or ± whitish yellow, and the pruina is PD+ yellow. According to Joseph & Sinha (2015) and our own observations, the UV+ bright yellow-orange reaction is caused by the presence of an unidentified xanthone. The authors do not mention the PD+ yellow reaction of the pruina. The width of the ascospores in the protologue is, according to Sparrius (2009), only 4.0–5.0 µm, whilst the study of Joseph & Sinha (2015) shows the width to be 5.0–9.0 µm, close to the width found in the present study, 5.5–9.0 µm.

Additional specimens examined – **Cuba**: small thallus of *S. inconspicua* present in the holotype specimen (*Wright* s.n., H-NYL 5455–holo-: H) of *Arthonia ochrolutea* Nyl. (in Willey 1890).
D.R. Congo: Oriental Province, Tshopo District, Kisangani, Lubunga, garden in village, on *Manihot* sp., 0°30′04.33″N 25°10′57.9″E, elev. c. 400 m, 3 Jun. 2014, *Van den Broeck* 6261 (BR, barcode BR5030076983797).
Madagascar: Province Diego Suarez, Antsiranana, W of Sambava from village of Manentenina to entrance to Marojejy National Park, through agricultural landscape with rice fields and coffee and vanilla plantations, on *Cocos nucifera*, from ± 14°28′21″S 49°48′31″E, elev. 100 m to 14°27′44.7″S 49°47′46.6″E, elev. 180 m, 17 Oct. 2014, *Ertz* 19739A (BR, barcode BR5030076980703).
Netherlands Antilles: Saba, Wells Bay end of North Coast Trail, in ravine near the road, low secondary forest on bottom of ravine, 17°38′21.76″N 63°15′02.27″W, elev. c. 50 m, 10 Mar. 2007, *Sipman* 54892 (B, barcode B600200326).
Rwanda: Kibungo Province, Akagera National Park, dry forest on the border of Lake Ihema, on trunk of *Haplocoelum gallaense*, 01°55′17.8″S 30°42′33.1″E, elev. 1312 m, 11 Apr. 2005, *Ertz* 8623A (BR, barcode BR5040372222490V).
Tanzania: Morogoro, Pest Management Center, on exposed tree with smooth bark in the garden of the Center,

06°50′46.7″S 37°39′28.4″E, elev. 541 m, 10 Jul. 2016, *Van den Broeck* 6885 (BR, barcode BR5030076513604; TAWIRI); Udzungwa, Twiga hotel, along the road between Kidatu and Kiberege, on small trees in a plantation close to the hotel, 07°50′53.5″S 36°53′20.6″E, elev. 345 m, 20 Jul. 2016, *Van den Broeck* 7013B (BR, barcode BR5030076613632; TAWIRI); Saadani National Park, on exposed small trees near Tourist Info Center, 06°02′30.6″S 38°46′29.8″E, elev. 10 m, 25 Jul. 2016, *Van den Broeck* 7034 (BR, barcode BR5030076634682; TAWIRI); ibid., coastal rain forest, 85 m

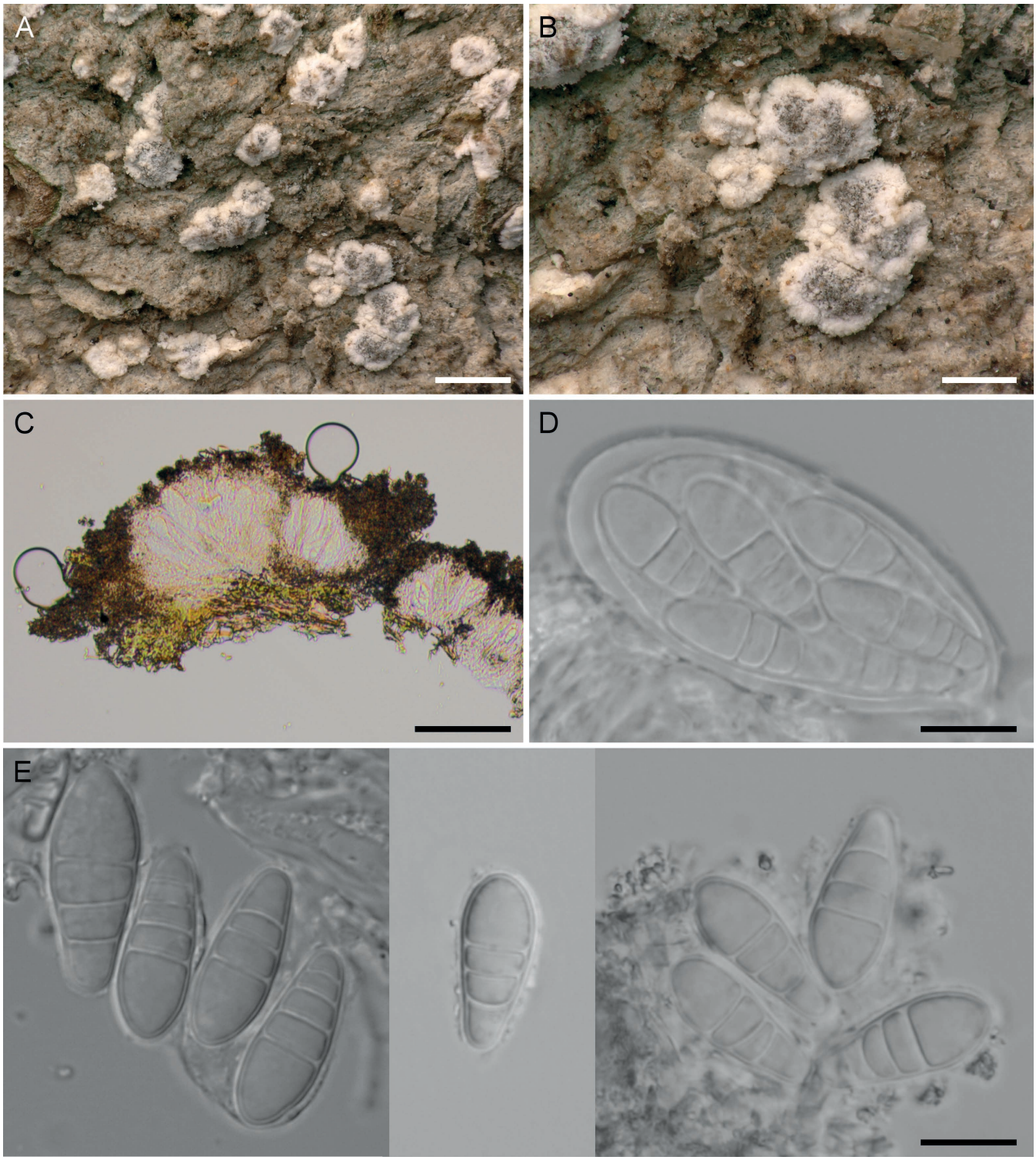

Figure 2 – Morphological and anatomical characters of *Synarthonia inconspicua*: A–B, thallus with ascomata; C, section through ascoma; D, ascus; E, ascospores. A–E from *Van den Broeck* 6325 (BR). Scale bars: A = 500 µm; B = 250 µm; C = 50 µm; D–E = 10 µm.

NE of Beach campsite, on bark, 06°01′34.0″S 38°46′44.2″E, elev. 7 m, 26 Jul. 2016, *Van den Broeck* 7080 (BR, barcode BR5030076680610; TAWIRI).
Uganda: Mbrarara, small *Eucalyptus* plantation along the road between Mwizi and Isingiri, on *Eucalyptus*, 00°37′18.9″S 30°38′46.3″E, elev. 1406 m, 14 Jun. 2014, *Van den Broeck* 6325 (BR, barcode BR5030076977901).
USA: Florida, Pasco Co, windfall oak twigs, Zephyr Park, Zephyrhills, 28°13′51.7″N, 82°11′09.46″W, 15 Mar. 2016, *Common* 10048 (hb Common).

New species

Synarthonia albopruinosa Van den Broeck & Ertz, **sp. nov.**

The new species differs from all other *Synarthonia* species by heavily white pruinose elongated ascomata in combination with 2–3-septate ascospores and its distinctive chemistry. – Type: D.R. Congo, Oriental Province, Tshopo District, Yangambi, Man Biosphere Reserve, old-growth mixed rain forest, on moss-covered canopy branch of *Scorodophloeus zenkeri*, 00°46′50.1″N 24°31′13.6″E, elev. 452 m, 16 Nov. 2013, *Van den Broeck* 6086 (holo-: BR, barcode BR5030076972753).

MycoBank No.: MB 825146. GenBank accession numbers: MH251873 (mtSSU, *Van den Broeck* 6086); MH271696 (*RPB*2, *Van den Broeck* 6086).

Thallus c. 10–20 µm thick, green, smooth to farinose, the brown colour of the bark often visible through the thallus; thallus hyphae hyaline, 0.9–2.5 µm wide. Prothallus a brown compact line in contact with other lichens. Photobiont trentepohlioid, forming an algal layer of 10–15 µm, cells 3.5–12.0 × 3.0–8.5 µm, rounded to angular, solitary or in short chains. Ascomata solitary, 0.1–0.4 × 0.1–0.2 mm, often more or less grouped in elongated clusters with individual ascomata arranged in lines, 1.0–1.6 × 0.1–0.2 mm, numerous, slightly elevated above thallus level, scattered more or less evenly over the thallus; disc heavily white pruinose, especially at the margins, brown when pruina removed, flat to concave. Excipulum 30–35 µm wide, composed of hyaline hyphae, orientated in all directions. Epihymenium 30–35 µm tall, brown (K-), composed of branched hyaline hyphae of 2.0–2.5 µm, orientated in all directions, inspersed with hyaline granular crystals. Hymenium 30–65 µm tall, hyaline, not inspersed, I+ blue rapidly turning into red, K/I+ blue. Paraphysoids 1.1–2.5 µm wide, forming a loose mesh around the asci, the tips with hyaline walls. Hypothecium 15–20 µm thick, brownish, inspersed with granular crystals, I+ red, K/I+ blue. Asci 24–60 × 13–25 µm (N = 9), obovoid to ellipsoid, stipitate; ocular chamber inconspicuous; no K/I+ blue ring structure in the tholus observed. Ascospores 12.5–17.5 × 5.0–6.5 µm (N = 36), hyaline, becoming brown (K+ olivaceous) and ornamented with small brown warts at late maturity, with enlarged apical cell, oblong-ovoid, (1–)2–3-septate; lumina of enlarged apical cell 6.3–6.8 × 4.6–5.4 µm, other lumina 1.8–3.6 × 3.7–5.1 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath granular, c. 0.7 µm wide. Pycnidia not observed. Fig. 3A & B.

Chemistry – Thallus K-, C-, KC-, PD+ orange (pruina and thallus), UV± pale yellowish to white. Ascomata UV± pale yellowish to white. Calcium oxalate crystals absent in ascomata and thallus. TLC (solvents A and B) revealed an unknown substance (R_f52 in B and R_f41 in A) with the same R_f values as perlatolic acid but UV+ green after acid spray and heating.

Distribution and ecology – *Synarthonia albopruinosa* was found only in D.R. Congo in an old-growth mixed rain forest, on a moss-covered canopy branch of *Scorodophloeus zenkeri*.

Etymology – The epithet *albopruinosa* refers to the white pruina on the ascomata.

Notes – *Synarthonia albopruinosa* is characterized by white pruinose ascomata with a light brown disc below the pruina and 2–3-septate ascospores of 12.5–17.5 × 5.0–6.5 µm. The similar *S. astroidestera* and *S. inconspicua* differ by larger ascospores (18–24 × 6–7 µm and 15.0–24.5 × 5.3–8.5 µm respectively) with more septa and a different chemistry (xanthone). *Synarthonia psoromica* differs by the presence of psoromic acid, and less elongated, more immersed, slightly cerebriform, thinly grey pruinose ascomata; *S. stigmatidialis* by thinly pruinose ascomata, I+ blue hymenium and (3–)4(–5)-septate ascospores; and *S. pilosella* by UV+ bright orange-yellow ascomata (xanthone) contrasting on the UV- thallus and by the presence of hair like hyaline extensions on the ascomata.

Additional specimen examined – **D.R. Congo**: Oriental Province, Tshopo District, Yangambi, Man Biosphere Reserve, old-growth mixed rain forest, on moss-covered canopy branch of *Scorodophloeus zenkeri*, 00°46′50.1″N 24°31′13.6″E, elev. 452 m, 16 Nov. 2013, *Van den Broeck* 6069, 6191 (BR, barcodes BR5030076986880 and BR5030076987917).

Synarthonia aurantiacopruinosa Van den Broeck & Ertz, **sp. nov.**

The new species differs from all other species of *Synarthonia* by orange pruinose ascomata in combination with (2–)3(–4)-septate ascospores and an I+ blue hymenium turning rapidly into red. – Type: D.R. Congo, Oriental Province, Tshopo District, Yangambi, Man Biosphere Reserve, tropical rain forest, branch of *Displasia* sp. in river Mooni, 00°49′13.8″N 24°31′46.43″E, elev. 404 m, 8 Nov. 2013, *Van den Broeck* 5764 (holo-: BR, barcode BR5030076978939).

MycoBank No.: MB 825147. GenBank accession numbers: MH251874 (mtSSU, *Van den Broeck* 5764); MH271697 (*RPB*2, *Van den Broeck* 5764).

Thallus c. 5–20 µm thick, inconspicuous; thallus hyphae not observed. Prothallus a black compact line in contact with other lichens. Photobiont trentepohlioid, forming an algal layer of 15–20 µm, cells 4.9–9.0 × 4.7–7.4 µm, rounded, solitary or in chains. Ascomata solitary, 0.2–0.3 × 0.1–0.3 mm, rounded to elongate, often in clusters of 0.2–0.7 × 0.2–0.3 mm, sparse, slightly elevated above thallus level, scattered more or less evenly over the thallus; disc black, matt, orange pruinose, K+ purplish, rough, flat to concave. Excipulum 18–25 µm wide, composed of hyaline hyphae, inspersed with red-brown to orange granular crystals. Epihymenium 6–12 µm tall, inspersed with red-brown to orange granular

crystals, with hyaline-walled hyphae. Hymenium 40–50 µm tall, hyaline, not inspersed, I+ blue rapidly turning into red, K/I+ blue. Paraphysoids 1.0–1.3 µm wide, the tips hyaline. Hypothecium 13–18 µm thick, hyaline, I+ red, K/I+ blue. Asci 30–41 × 12–24 µm (N = 4), (sub)globose to obovoid, stipitate; no K/I+ blue ring structure observed. Ascospores 15.0–19.0 × 5.5–6.5 µm (N = 20), hyaline, becoming brown (K+ olivaceous) and finely warted at late maturity, with enlarged apical cell, oblong-ovoid, (2–)3(–4)-septate; lumina of enlarged apical cell 7.2–7.8 × 5.0–6.5 µm, other lumina

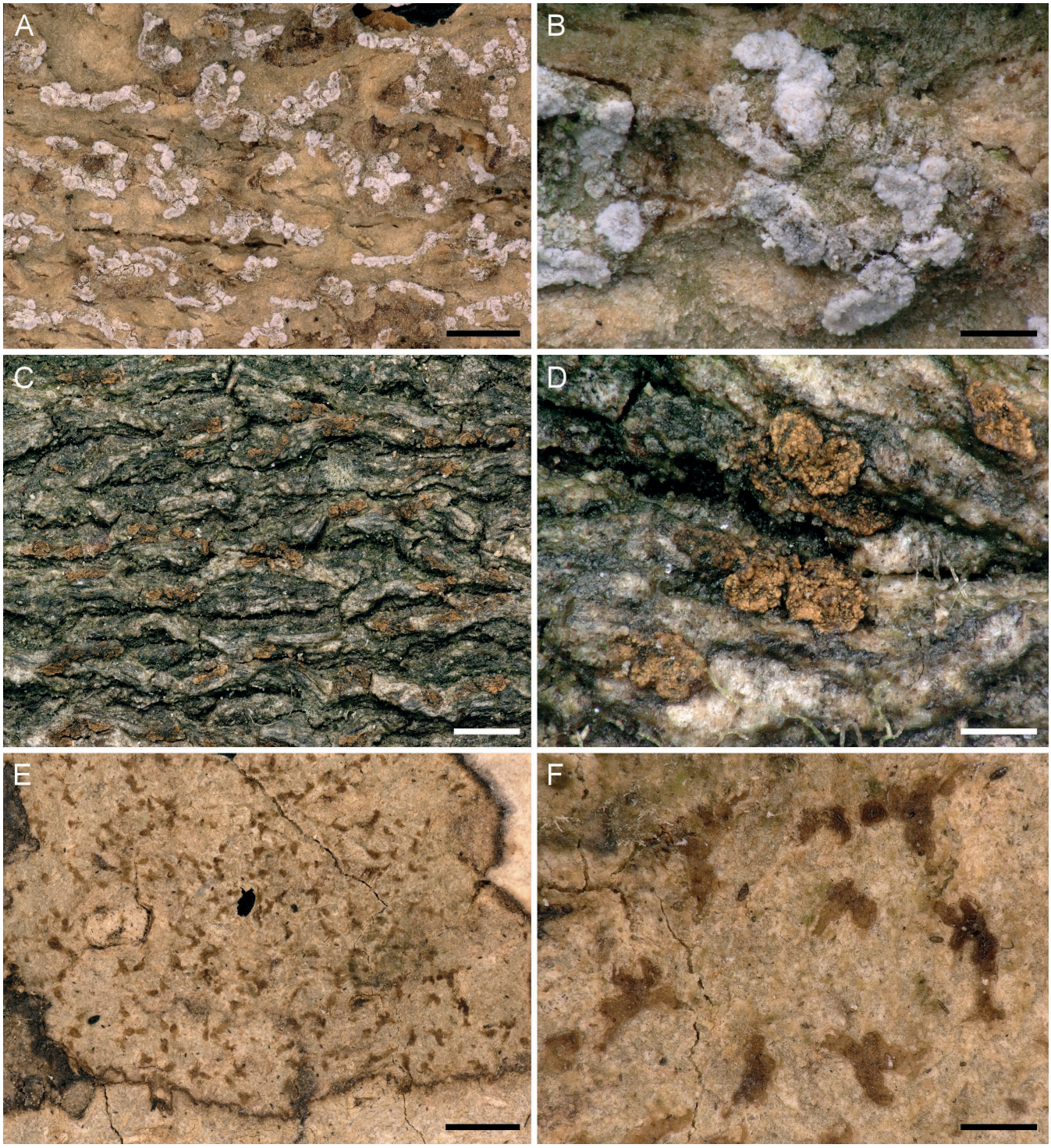

Figure 3 – Thallus with ascomata of *Synarthonia* species: A–B, *S. albopruinosa*; C–D, *S. aurantiacopruinosa*; E–F, *S. fuscata*. A–B from *Van den Broeck* 6086 (holo-: BR); C–D from *Van den Broeck* 5764 (holo-: BR); E–F from *Van den Broeck* 6101 (holo-: BR). Scale bars: A, C & E = 1000 µm; B, D & F = 250 µm.

3.2–5.0 × 1.7–3.6 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath distinct, granular, 0.4–0.5 µm wide. Pycnidia not observed. Fig. 3C & D.

Chemistry – Thallus K-, KC-, C-, PD-, UV-. Pruina K+ purplish. TLC not performed (specimen to small). Calcium oxalate crystals absent in thallus and ascomata.

Distribution and ecology – The corticolous *Synarthonia aurantiacopruinosa* was found only once on a branch arching over a river, in very exposed and humid conditions in a tropical rain forest.

Etymology – The epithet *aurantiacopruinosa* refers to the orange pruina on the ascomata.

Notes – *Synarthonia aurantiacopruinosa* is similar to *S. borbonica*, *S. ferruginea*, *S. karunaratnei*, *S. lopingensis*, *S. ochracea* and *S. ochrodes* in the presence of an orange pruina (K+ purplish) on the ascomata and transversely septate ascospores with an enlarged apical cell. The new species is similar to *S. borbonica* from Reunion in having hyaline 3-septate ascospores of 14.0–20.0 × 5.0–7.5 µm, becoming brown and finely warted at late maturity (Ertz et al. 2010). *Synarthonia borbonica* differs from *S. aurantiacopruinosa* by a white, UV+ orange thallus with more numerous and larger ascomata, slightly broader ascospores (7.0–8.0 µm instead of 5.5–6.5 µm broad) and the presence of a K/I+ blue ring like structure in the tholus (Ertz et al. 2010); and *S. ferruginea* by an I+ persistently blue hymenium and larger, persistently hyaline ascospores (19.5–27.0 µm) with consistently 5 septa (Vainio 1890). The ascomata of the recently described *S. karunaratnei* Weerakoon & Aptroot also have an orange pigment surrounding the ascomata, but the ascospores are consistently 2-septate and distinctly smaller (9.0–10.5 × 3.5–5.0 µm) than those of *S. aurantiacopruinosa* (Weerakoon et al. 2016). *Synarthonia lopingensis* and *S. ochracea* appear to start as non-lichenized lichenicolous fungi on *Graphis* species before developing their own thalli or they might be facultatively lichenicolous fungi. Both species differ also from *S. aurantiacopruinosa* by more stellate ascomata and a persistently I+ blue hymenium. *Synarthonia hodgesii* and *S. ochrodes* are non-lichenized lichenicolous fungi on *Graphis* species.

Synarthonia fuscata Van den Broeck & Ertz, **sp. nov.**

The new species differs from all other species of *Synarthonia* by brown, epruinose, lirellate ascomata in combination with 3-septate ascospores. – Type: D.R. Congo, Oriental Province, Tshopo District, Yangambi, Man Biosphere Reserve, old-growth mixed rain forest, on moss-covered canopy branch of *Scorodophloeus zenkeri*, 00°46′50.1″N 24°31′13.6″E, elev. 452 m, 16 Nov. 2013, *Van den Broeck* 6101 (holo-: BR, barcode BR5030076979967).

MycoBank No.: MB 825148. GenBank accession numbers: MH251875 (mtSSU, *Van den Broeck* 6101); MH271706 (*RPB*2, *Van den Broeck* 6101).

Thallus c. 5–60 µm thick, slightly greenish with white striae or spots, smooth, continuous; thallus hyphae not observed. Prothallus a brown to black compact line in contact with other lichens. Photobiont trentepohlioid, forming an algal layer of c. 10 µm between the ascomata and the host, cells 5–11 × 4–10 µm, rounded, cells solitary or in chains. Ascomata solitary, not in clusters, 0.2–0.5 × 0.1–0.3 mm, elongate to irregularly lobed, numerous, slightly elevated above thallus level, scattered more or less evenly over the thallus; disc light brown, epruinose, semi-translucent when dry, translucent when wet, flat. Excipulum c. 11 µm wide, composed of brown rounded to elongate, hyaline to yellowish hyphae of 7–5 × 3–4 µm wide, orientated in all directions. Epihymenium 6–15 µm tall, hyaline to brown, composed of tips of the paraphysoids with dark brown walls and caps, orientated in all directions, not inspersed, composed of two layers: an I+ deep blue layer covered by an I+ yellowish layer. Hymenium 24–40 µm tall, hyaline, not inspersed, I+ sordid blue rapidly turning into red, K/I+ blue. Paraphysoids 1.0–1.4 µm wide. Hypothecium 5–8 µm thick, composed of rounded hyaline to orange hyphae, 2–3 µm wide, I+ blue, K/I+ blue. Asci 32–38 × 13–17 µm (N = 4), obovoid, stipitate; no ocular chamber observed; some asci with a K/I+ blue ring like structure in the tholus. Ascospores 13.5–17.0 × 4.5–6.5 µm (N = 16), hyaline, becoming brown (K+ olivaceous) and ornamented with brown warts at late maturity, with enlarged apical cell, oblong-ovoid, (1–)3(–4)-septate; lumina of enlarged apical cell 5.2–6.8 × 4.0–6.1 µm, other lumina 1.6–3.7 × 2.4–4.5 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath distinct, 0.7–0.9 µm wide. Pycnidia not observed. Fig. 3E & F.

Chemistry – Thallus K-, KC-, C-, PD-, UV-. TLC not performed (specimen to small). Calcium oxalate crystals absent in thallus and ascomata.

Distribution and ecology – *Synarthonia fuscata* was found only once in the D.R. Congo in an old-growth mixed rain forest on a moss-covered canopy branch of *Scorodophloeus zenkeri.*

Etymology – The epithet *fuscata* refers to the brownish colour of the ascomata.

Notes – *Synarthonia fuscata* is characterized by epruinose, light brown, almost translucent, lirellate ascomata and the presence of a K/I+ blue ring like structure in the asci. *Synarthonia albopruinosa*, *S. aurantiacopruinosa*, *S. inconspicua*, *S. ochracea* and *S. pilosella* differ by the presence of pruina on the ascomata and the absence of a K/I+ blue ring like structure in the asci. *Synarthonia fuscata* shares with *S. josephiana* the presence of a K/I+ blue ring like structure in the tholus, but differs by larger black (only brown when wet) ascomata and predominantely 4-septate ascospores. *Arthonia ochraceella* and *A. linearis* are two other species with brown epruinose ascomata, but their hymenium reacts I+ blue and the ascospores are larger with more septa (4-septate and 29.0–34.0 µm in length in *A. ochraceella*, 5-septate and 36.0–40.0 µm in *A. linearis*).

Synarthonia josephiana Van den Broeck & Ertz, **sp. nov.**

The new species differs from all other *Synarthonia* species by brownish-black epruinose ascomata in combination with 4-septate ascospores. – Type: Madagascar, Province Diego Suarez, Antsiranana, W of Sambava, from village Manentenina to entrance to Marojejy National Park, through agricultural landscape with rice fields and coffee and vanilla plantations, on *Cocos nucifera*, from ± 14°28′21″S

49°48′31″E, elev. 100 m to 14°27′44.7″S 49°47′46.6″E, elev. 180 m, 17 Oct. 2014, *Ertz* 19739B (holo-: BR, barcode BR5030076981731).

MycoBank No.: MB 825149. GenBank accession numbers: MH251876 (mtSSU, *Ertz* 19739B); MH271698 (*RPB*2, *Ertz* 19739B).

Thallus c. 11 µm thick, whitish, smooth, continuous to cracked; thallus hyphae not observed. Prothallus a brown to black compact line in contact with other lichens. Photobiont trentepohlioid, forming a discontinuous algal layer of 5–10 µm, cells 6–10 × 4–8 µm, rounded to very irregular, cells solitary or in chains. Ascomata rounded, 0.1–0.4 × 0.1–0.3 mm, solitary or mostly forming irregular clusters of 0.3–1 × 0.3–0.8 mm, occasionally with a thin margin, numerous, first ± immersed in the thallus, bursting through it to become more or less sessile, scattered more or less evenly over the thallus; disc black, epruinose but with remnants of thallus, brown and ± translucent when wet, sometimes with a darker margin, rough, flat. Excipulum 10–14 µm wide, composed of brown-walled hyphae of 1.9–2.9 µm wide, orientated in all directions, with brown amorphous pigment in the gelatinous matrix. Epihymenium 5–15 µm tall, brown, composed of brown-walled (K-) tips of paraphysoids 2.3–2.8 µm wide, covered by a hyaline layer of 4–5 µm, inspersed with dark granular crystals not dissolving in K. Hymenium 60–70 µm tall, hyaline, densely inspersed with hyaline granular crystals not dissolving in K, I+ blue rapidly turning into red, K/I+ blue. Paraphysoids 1.7–1.9 µm wide, forming a dense mesh around the asci. Hypothecium 10–15 µm thick, hyaline to yellowish, I+ red, K/I+ blue. Asci 40–50 × 18–25 µm (N = 5), obovoid, stipitate, with a distinct ocular chamber; a K/I+ blue ring structure observed surrounding the top of the ocular chamber. Ascospores 15.5–21.5 × 5.5–8.0 µm (N = 20), persistently hyaline, with an enlarged apical cell, oblong-ovoid, (2–3–)4-septate; lumina of enlarged apical cell 6.2–6.5 × 3.7–4.3 µm, other lumina 1.9–3.0 × 3.2–4.2 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath distinct, 0.6–0.9 µm wide, somewhat granular. Pycnidia numerous, black, almost completely immersed in the thallus, walls brown. Conidia 4.4–6.3 × 1.1–1.4 µm, hyaline, non-septate, bacilliform, straight to slightly curved; conidiogenous cells hyaline, growing out of a circular cell of 2.7–3.6 × 2.4–2.7 µm. Fig. 4A & B.

Chemistry – Thallus K-, C-, KC-, PD-, UV-. Calcium oxalate crystals absent in ascomata and thallus. TLC not performed (specimen to small).

Distribution and ecology – *Synarthonia josephiana* is at present known only from the type location in northern Madagascar from trees in an agricultural landscape with rice fields and coffee and vanilla plantations.

Etymology – This new species is dedicated to Siljo Joseph for his contributions to the genus *Synarthonia*.

Notes – Measuring the asci was very difficult since the asci are surrounded by a dense mesh of strongly gelatinized paraphysoids and the hymenium is densely inspersed with hyaline insoluble (in K) granular crystals.

Synarthonia josephiana is characterized by epruinose blackish-brown ascomata with remnants of thallus on the disc and a K/I+ blue ring structure surrounding the top of the ocular chamber. *Synarthonia fuscata* differs by smaller, light-brown, almost translucent, epruinose ascomata (0.2–0.5 × 0.1–0.3 mm against clusters of 0.3–1 × 0.3–0.8 mm in *S. josephiana*) and 3-septate ascospores becoming brown at late maturity. The other species of *Synarthonia* are clearly orange, greyish or white pruinose.

Synarthonia muriformis Van den Broeck, Frisch & Ertz, **sp. nov.**

The new species differs from all other *Synarthonia* species by muriform ascospores of 22.0–36.5 × 10.0–14.5 µm. – Type: Madagascar, Province Diego Suarez, Antsiranana, Region Diana, District Diego II, commune Joffreville, Forontany, Morafeu, Parc National de la Montagne d'Ambre, along trail from Gîte des Roussettes, across stream at small dam to dirt road, moist but not wet lower mountain forest, with tall tree and tree ferns, on trunk of 30 cm diameter on the edge of a trail, 12°31′55″S 49°10′33″E, elev. 1119 m, 7 Oct. 2014, *Ertz* 19344 (holo-: BR, barcode BR5030072407648).

MycoBank No.: MB 825150. GenBank accession numbers: MH251877 (mtSSU, *Ertz* 19344); MH271699 (*RPB*2, *Ertz* 19344); KJ851025 (mtSSU, *Frisch* 11/Ug41); KJ851100 (*RPB*2, *Frisch* 11/Ug41).

Thallus c. 10–19 µm thick, whitish to greenish-grey, smooth to granular, discontinuous, slightly patchily byssoid in some of the specimens; thallus hyphae not observed. Prothallus a brown to black compact line in contact with other lichens. Photobiont trentepohlioid, forming a distinct algal layer, cells 3–8 × 3–8 µm, irregular, rounded to angular, solitary or in chains. Ascomata solitary, 0.1–0.4 × 0.08–0.2 mm, rounded to slightly elongate, never stellate or lirellate, often in clusters of 0.2–0.5 × 0.1–0.4 mm, with a byssoid margin, numerous, sessile, scattered more or less evenly over the thallus or more or less grouped; disc heavily white pruinose, black to brown when pruina removed, speckled with heaps of overmature and released dark brown ascospores, flat to convex. Excipulum 8–24 µm wide, composed of hyaline to yellowish hyphae 0.8–2.8 µm wide, orientated in all directions, inspersed with granular crystals. Epihymenium 9–28 µm tall, brown, inspersed with angular orange and hyaline granular crystals which are partly dissolving in K. Hymenium 58–100 µm tall, hyaline to orange, not inspersed, I+ blue rapidly turning into red, K/I+ blue. Paraphysoids 1.9–2.4 µm wide, forming a dense mesh around the asci, the tips often with dark brown walls and caps. Hypothecium 12–27 µm thick, yellowish to brown, inspersed with granular crystals dissolving in K, I+ red, K/I+ blue. Asci 52–102 × 27–32 µm (N = 4), obovoid to ellipsoid, stipitate; a K/I + blue ring like structure in the tholus not observed. Ascospores 22.0–36.5 × 10.0–14.5 µm (N = 24), hyaline becoming brown (K+ olivaceous) with ornamentation of brown warts at late maturity, muriform, without enlarged apical cells, oblong-ovoid with 5–8 transverse septa and 1–3 longitudinal septa per segment, 12–25 loculate in surface view; lumina 2.8–7.5 × 2.1–4.4 µm; gelatinous sheath not observed. Pycnidia not observed. Fig. 4C & D.

Chemistry – Thallus K-, C-, KC-, PD+ orange, UV-. Pruina PD+ orange. Calcium oxalate crystals occasionally present in the ascomata, not observed in the thallus. TLC (solvent A)

revealed the presence of evernic acid, psoromic acid and two unknown UV+ white secondary compounds (R_f 13 and 67).

Distribution and ecology – *Synarthonia muriformis* is at present known from Madagascar, where it was found on a small tree in a lower mountain forest, and from Uganda, where it grows in mixed mountain forests on smooth as well as on fissured bark.

Etymology –The epithet *muriformis* refers to the muriform ascospores.

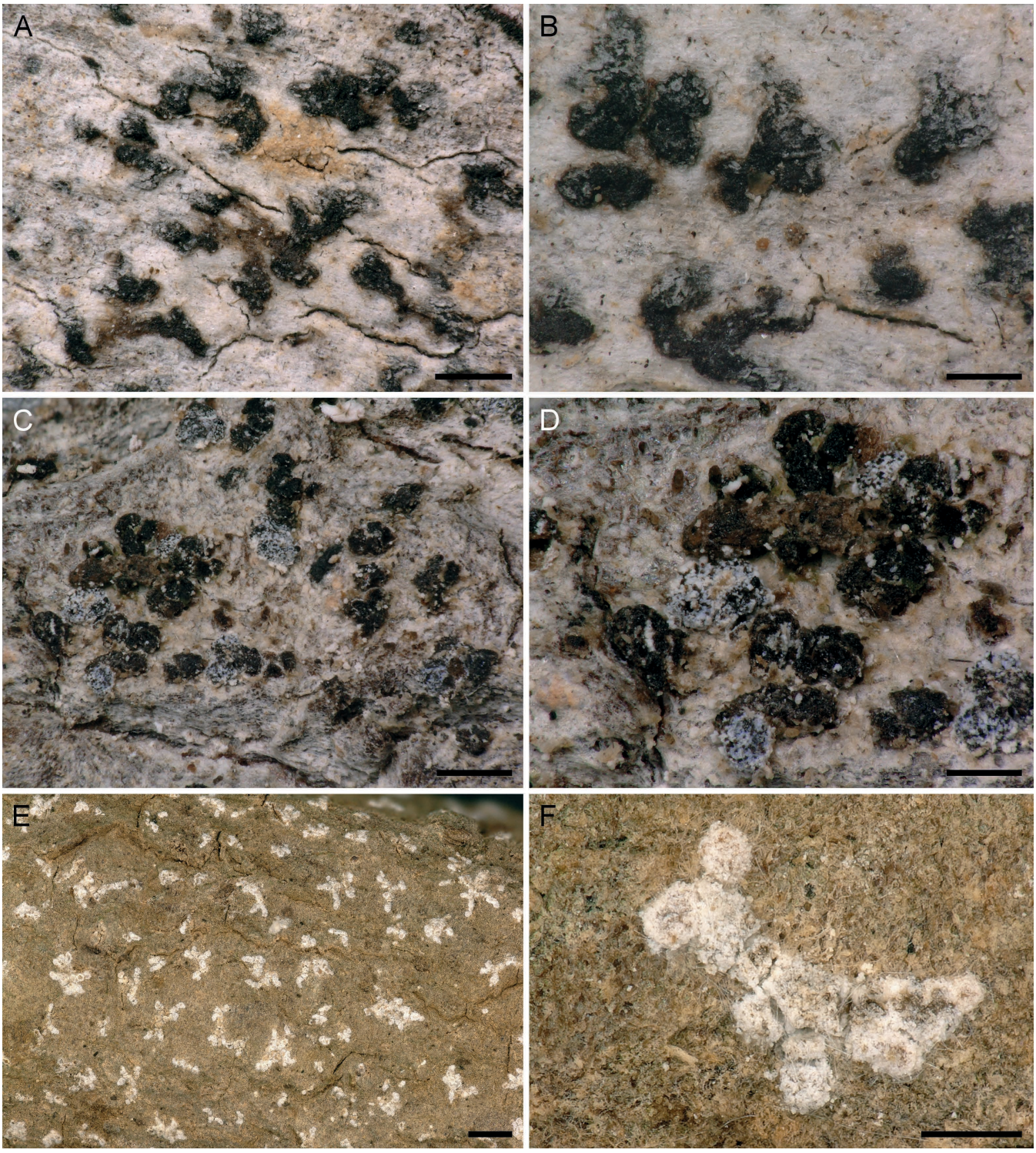

Figure 4 – Thallus with ascomata of *Synarthonia* species: A–B, *S. josephiana*; C–D, *S. muriformis*; E–F, *S. pilosella*. A–B from *Ertz* 19739B (holo-: BR); C–D from *Ertz* 19344 (holo-: BR); E–F from *Ertz* 7808 (holo-: BR). Scale bars: A & C = 500 µm; B, D & F = 250 µm; E = 1000 µm.

Notes – In most of the examined ascomata no asci or ascospores could be found. *Synarthonia muriformis* is most similar to *S. sarcographoides* in having muriform ascospores and heavily white pruinose ascomata, but *S. sarcographoides* differs by larger ascomata (up to 2 mm), smaller ascospores (20–22 µm long) and in lacking psoromic and evernic acids (thallus and ascomata PD-).

A survey of all protologues and the study of all types of the African *Arthothelium* species failed to identify any species with the same characteristics as *S. muriformis*.

Additional specimens examined – **Uganda**: Kabale District, Bwindi Impenetrable National Park, Eastern sector, Ruhija, Katonve, on fissured bark of *Chrysophyllum albidum* in mixed mountain forest dominated by *C. albidum* and *Cassipourea* sp. (plot 2200-1, T1), 01°04′31.8″S 29°46′13.6″E, elev. 2200 m, 5 May 2011, *Frisch* 11/Ug482 (hb Frisch); ibid. Ihihizo, on bark of tree in mixed mountain forest after crossing of Ihihizo, elev. 1900 m, 27 May 2011, *Frisch* 11/Ug41 (UPS); ibid. Rushaga, Kijumwa, on smooth bark of *Teclea nobilis* (dbh 0.57 m) in mixed mountain forest of *Chrysophyllum albidum*, *Xanthozyllum gileti*, *Cassipourea* sp. and *Strombosia schefflerii* (Kijumwa, plot 2100-1, T3), 01°06′17″S 29°44′19″E, elev. 2140 m, 1 Jun. 2011, *Frisch* 11/Ug1893 (hb Frisch).

Synarthonia pilosella Van den Broeck, Eb.Fisch., Killmann & Ertz, **sp. nov**.

The new species differs from all other *Synarthonia* species by hair like hyaline extensions on the ascomata that are UV+ bright orange-yellow, an I+ directly red hymenium, and mostly 3-septate ascospores of 14.5–19.0 × 5.0–7.0 µm. – Type: Rwanda, Province of Cyangugu, forest of Oyamudongo [as 'Cyamudongo' on voucher], on smooth shadowed trunk of 20 cm diameter of *Alangium chinense*, 02°33′50.6″S 28°58′49.9″E, elev. 2000 m, 30 Mar. 2005, *Ertz* 7808 (holo-: BR, barcode BR50403722223527V).

MycoBank No.: MB 825151. GenBank accession numbers: MH251883 (mtSSU, *Ertz* 7808); MH271704 (*RPB2*, *Ertz* 7808).

Thallus c. 22–33 thick, green, granular, continuous; thallus hyphae hyaline, 2.7–3.0 µm wide. Prothallus not observed. Photobiont trentepohlioid, cells 4–9 × 3–7 µm, rounded, solitary or in chains. Ascomata solitary, rounded, 0.06–0.2 × 0.04–0.2 mm, mostly aggregated in clusters of up to 8 ascomata of 0.4–1 × 0.1–0.6 mm, numerous, sessile; disc heavily white pruinose, orange below the pruina, flat, with distinct hyaline hair like extensions 1.2–2.9 µm wide. Excipulum 20–40 µm wide, composed of hyaline, loosely intricate hyphae 1.5–2.5 µm wide, orientated in all directions, inspersed with orange brown to hyaline granules, the granules K+ completely dissolving. Epihymenium 7–11 µm tall, composed of loosely intricate hyaline tips of the paraphysoids, 1.3–2.3 µm wide, not swollen, inspersed with orange-brown to hyaline granules which are K+ completely dissolving. Hymenium 46–75 µm tall, not inspersed, I+ directly red, K/I+ blue. Paraphysoids 0.9–1.4 µm wide. Hypothecium 29–32 µm thick, hyaline to yellowish, composed of loosely intricate hyphae, inspersed with orange granules which are K+ completely dissolving, I+ red, K/I+ blue. Asci 44–71 × 17–22 µm (N = 4), clavate, stipitate; a K/I blue ring like structure in the tholus or an ocular chamber not observed. Ascospores 14.5–19.0 × 5.0–7.0 µm (N = 25), (2–)3(–4)-septate, persistently hyaline, with enlarged apical cell, oblong-ovoid; lumina of enlarged apical cell 6.4–7.0 × 5.1–6.5 µm, other lumina 2.6–6.1 × 1.7–3.9 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath 0.3–0.7 µm wide. Pycnidia not observed. Fig. 4E & F.

Chemistry – Thallus K-, C-, KC-, PD+ yellow, UV-. Pruina PD+ yellow. Ascomata UV+ bright orange-yellow contrasting with the dark UV- thallus. Calcium oxalate crystals absent in ascomata and thallus. TLC (solvents A and B) revealed the presence of the same unidentified xanthone (major) as in *S. inconspicua* and traces of some other unknown secondary compounds.

Distribution and ecology – The corticolous *Synarthonia pilosella* was found only once on a shadowed smooth trunk in a tropical rain forest.

Etymology – The epithet *pilosella* refers to the hair like hyaline extensions on the ascomata.

Notes – *Synarthonia pilosella* is characterized by white pruinose, minute (0.06–0.2 × 0.04–0.2 mm) ascomata which are mostly grouped in clusters of 0.4–1.6 × 0.1–0.6 mm, with hyaline hair like extensions, in combination with mostly 3-septate, persistently hyaline ascospores (14.5–19.0 × 5.0–7.0 µm), an I+ directly red hymenium and an unidentified xanthone as secondary metabolite rending the ascomata UV+ bright orange-yellow. The similar *S. albopruinosa* differs by the absence of hyaline extensions on the ascomata, smaller 2–3-septate ascospores (12.5–17.5 × 5.0–6.5 µm) becoming brown and ornamented with brown warts at late maturity, and a different chemistry (xanthone absent). *Synarthonia inconspicua* differs by larger ascospores (15.0–24.5 × 5.3–8.5 µm) with 3–4(–5) septa, becoming brown and ornamented with brown warts at late maturity, and an I+ blue hymenium rapidly turning into red. *Synarthonia psoromica* differs by larger ascomata (0.4–1.4 × 0.2–0.9 mm) without hyaline hair like extensions and by psoromic acid as a secondary metabolite.

New combinations in *Synarthonia*

We here place some species of *Arthonia* with an orange pruina on the ascomata (K+ purplish) and transversely septate ascospores with enlarged apical cell in *Synarthonia*, even though molecular data are missing for these species. We did not include the orange pruinose *A. leucographella* Müll.Arg. since this species, according to the protologue, is characterized by elliptic-fusiform, 7–9-septate ascospores with narrowed obtuse ends and larger median cells (Willey 1890). We also did not include *A. rubiginella* Nyl. since this species has ascospores with two larger apical cells (Nylander 1900). Two of the newly combined species are starting growth as a non-lichenized lichenicolous fungus on species of *Graphis*, sometimes subsequently developing an independent thallus, while two others are presistently non-lichenized lichenicolous fungi on species of *Graphis*. Morphologically, these species are highly similar in sharing orange pruinose/pigmented ascomata with small (< 20 µm long), (2–)3(–4)-septate hyaline ascospores becoming brown and ornamented with small

brown warts at late maturity and an I+ blue hymenium (*Synarthonia ochracea* complex). They differ by the external appearance of the ascomata and distribution (cf. identification key). ITS sequences were obtained from a specimen of *S. ochracea* from France (*Van den Broeck* 6674, BR; GenBank accession number MH298880) and two specimens of *S. lopingensis* from Japan (Frisch 12/Jp4, UPS and Frisch 12/Jp5D2, UPS; GenBank accession numbers MH298878 and MH298879). The sequence of *S. ochracea* differs significantly from those of *S. lopingensis*. We also include the lichenized *A. astroidestera* Nyl. and the non-lichenized lichenicolous *A. rimeliicola* Diederich which judged by their morphology seem to be typical *Synarthonia*.

Synarthonia astroidestera (Nyl.) Ertz & Van den Broeck, **comb. nov.**

Mycobank No.: MB 827636.

Arthonia astroidestera Nyl., Flora, Regensburg 57: 13. 1874 (Nylander 1874). – Type: England [V.C.11, South Hants], New Forest, on *Ilex*, 15 Jul. 1873, *Crombie* & *Larbalestier* s.n. (H-NYL 5447 – lecto-: H, designated in Coppins 1989; isolecto-: BM).

A description is given in the protologue and in Smith et al. (2009).

Synarthonia borbonica (Ertz, Elix & Grube) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825158.

Arthonia borbonica Ertz, Elix & Grube, Plant Ecology and Evolution 143: 222. 2010 (Ertz et al. 2010). – Type: Reunion Island, Cilaos Cirque, Grand Matarum forest, road of the village of Cilaos to Piton des Neiges, elev. c. 1900 m, on large exposed trunk of *Acacia heterophylla*, 21°07′S 55°29′E, Jun. 2003, *Ertz* 4666 (holo-: BR, barcode BR5030008181338).

A description and illustrations are given in the protologue.

Synarthonia ferruginea (Vain.) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825163.

Arthonia ferruginea Vain., Acta Societas pro Fauna et Flora Fennica 7(2): 165. 1890 (Vainio 1890). – Type: Brazil, Rio de Janeiro, 1885, *Vainio* s.n. (BM web; iso-: M, barcode M0204989).

Thallus white, smooth, ± continuous. Prothallus a compact black line in contact with other lichens. Photobiont trentepohlioid, cells 7–15 × 6–11 µm, rounded to angular, solitary or in short chains. Ascomata solitary, 0.6–1.9 × 0.4–0.7 mm, punctiform, becoming lobate, immersed, erumpent, closely spaced; disc black with marginal orange pruina, orange brown when wet, flat. Excipulum 23–28 µm wide, inspersed with clusters of orange brown granular crystals. Epihymenium 12–16 µm tall, inspersed with clusters of orange brown granular crystals. Hymenium 25–43 µm tall, hyaline to orange, inspersed with some orange granular crystals, I+ blue, K/I+ blue. Paraphysoids 0.6–1.5 µm wide, the tips swollen up to 1.7 µm. Hypothecium 14–20 µm thick, inspersed with clusters of orange brown granular crystals. Asci subglobose, 21–37 × 22–28 µm (N = 6); a K/I + blue ring like structure not observed in the tholus. Ascospores 19.5–27.0 × 7.0–9.5 µm (N = 7), oblong-ovoid with enlarged apical cell, hyaline, 5-septate; gelatinous sheath 0.7–1.0 µm wide. Pycnidia not observed.

Chemistry – Thallus UV+ orange. Calcium oxalate crystals absent in ascomata and thallus. TLC and spot tests not performed (type specimen).

Synarthonia hodgesii (Lendemer & R.C. Harris) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825164.

Arthonia hodgesii Lendemer & R.C.Harris, Castanea 81(1): 33. 2016 (Lendemer et al. 2016). – Type: USA, Georgia, Doughtery Co., Chickasawhatchee Wildlife Management Area, 31°29′25″N 84°25′7″W, pond cypress swamp forest, 10 Nov. 2012, on *Graphis lineola* on branch of *Morella cyrifera*, *Hodges* 9228 (holo-: NY, n.v.).

Arthonia hodgesii, a species with orange ascomata, has recently been described as a lichenicolous fungus on *Graphis lineola* from North America (Lendemer et al. 2016).

Arthonia hodgesii is morphologically similar in most aspects to *Synarthonia ochracea*, *S. ochrodes* and *S. lopingensis*, but the ascomata are evenly orange, with a non-granular pigmentation.

A description and illustrations are given in the protologue.

Synarthonia karunaratnei (Weerakoon & Aptroot) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825178.

Arthonia karunaratnei Weerakoon & Aptroot, The Bryologist 119(2): 133. 2016 (Weerakoon et al. 2016). – Type: Sri Lanka, Imbulpitiya, on bark of tree, Jan. 2015, *Weerakoon & Arachchige* Im33 (holo-: PD, n.v.; iso-: F, n.v.).

A description and illustrations are given in the protologue.

Synarthonia lopingensis (Zahlbr.) Van den Broeck, Frisch & Ertz, **comb. nov.**

Mycobank No.: MB 825165.

Arthonia lopingensis Zahlbr., Symbolae Sinicae 3: 36. 1930 (Zahlbruckner 1930). – Type: China, Yunnan province, prope vicum Tjintjischan ditionis oppida Loping, in silva frondosa Collins, elev. c. 1600 m, corticolous on *Schoepfia jasminodora*, Jun. 1917, *Handel-Mazzetti* 1976 (herbarium Zahlbruckner 10107 – lecto-: WU, **designated here** on the *Synarthonia* species, see notes).

Starting as a lichenicolous fungus on species of *Graphis*, not changing the whitish thallus of the host, or facultatively lichenicolous. Prothallus not observed. Ascomata 0.04–0.9 × 0.04–0.5 mm, numerous, young minute and ± immersed to becoming semi-sessile, irregularly rounded to lirellate and aggregated in irregular star-shaped clusters of 0.5–1.0 mm, with marginal orange pruina; disc black, orange brown and partly translucent when wet, flat. Epihymenium 10–12 µm tall, densely inspersed with orange crystals which are K+

purple to red and partly dissolving, without amorphous pigment. Hymenium 34–53 µm tall, orange, not inspersed, I+ blue, K/I+ blue. Paraphysoids 0.7–0.9 µm wide, the tips with hyaline walls. Hypothecium orange brown, 20–25 µm thick, I+ blue, K/I+ blue. Asci broadly clavate to subglobose, 36–50 × 14–28 µm (N = 5), stipitate; a K/I blue ring like structure not observed; the asci occasionally filled with amorphous orange pigment. Ascospores 15.0–19.0 × 5.0–6.5 µm (N = 15), hyaline becoming brown with ornamentation of brown warts at late maturity, with enlarged apical cell, oblong-ovoid; lumina of apical cell 7.0–7.2 × 3.9–4.2 µm, lumina other cells 1.0–1.5 × 3.1–3.4 µm, (3–)4-septate; gelatinous sheath not observed. Pycnidia not observed.

Chemistry – Calcium oxalate crystals in ascomata and thallus not observed. Thallus UV+ pale orange, ascomata UV+ dark orange. TLC and spot tests not performed (type specimen).

Distribution and ecology – *Synarthonia lopingensis* appears to start as a juvenile parasite on the thallus of *Graphis* spp. in E Asia (China, Japan; Frisch et al. 2018) before developing its own thallus or it might be a facultatively lichenicolous fungus.

Notes – *Synarthonia lopingensis* belongs to the *S. ochracea* complex based on the orange pruinose ascomata, the ascospores type and the (facultatively) lichenicolous growth on species of *Graphis*. The type specimen consists of two pieces of bark. *Synarthonia lopingensis* is found only on one of the pieces while another species of *Arthonia* s. lat. is present on both. The latter differs from *S. lopingensis* by black ascomata with a purplish tinge, a purplish pigment in the ascomata, and 3-septate ascospores with an enlarged apical cell becoming brown at late maturity, 14.5–17.0 × 5.0–6.5 µm. Calcium oxalate crystals could not be observed for this species, which probably belongs to *Coniocarpon*. We lectotypify *S. lopingensis* based on the protologue on the specimen with substellate ochraceous ascomata as indicated by an arrow on the voucher.

Synarthonia lopingensis is morphologically similar in most aspects to *S. hodgesii*, *S. ochracea* and *S. ochrodes* but the ascomata are aggregated in irregular star-shaped clusters.

A recently reported specimen from Vietnam, published under the name *Arthonia elegans* (Joshi et al. 2018), is similar to *S. lopingensis*. It is lichenized and characterized by marginally reddish-brown pruinose ascomata aggregated in irregular star-shaped clusters. But the hyaline ascospores, which are not becoming brown at late maturity, are much smaller (10–12 µm long) with more septa (4–5). Additional collections are required to establish if these differences merit formal taxonomic recognition.

Synarthonia ochracea (Dufour) Van den Broeck & Ertz, **comb. nov.**

Arthonia ochracea Dufour, Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts 87: 205. 1818 (Dufour 1818). – *Opegrapha ochracea* (Dufour) Hepp (Hepp 1824: 76). – *Conangium ochraceum* (Dufour) Fr. (Fries 1825: 288). – *Arthonia cinnabarina* var. *ochracea* (Dufour) Nyl. (Nylander 1853: 159). – *Coniocarpon ochraceum* (Dufour) Fr. (Fries 1860: 380). – Type: [France], St-Sever, s.d., s. coll. s.n. (lecto-: PC0786154, **designated here** on the thalli with substellate ochraceous ascomata, see notes).

MycoBank No.: MB 825161. GenBank accession numbers: MH251884 (mtSSU, *Van den Broeck* 6653); MH271705 (*RPB2*, *Van den Broeck* 6653).

Starting as a non-lichenized lichenicolous fungus on *Graphis scripta* s. lat. but becoming independent with age or facultatively lichenicolous. Thallus c. 12–18 µm thick, whitish, smooth to cracked; thallus hyphae not observed. Prothallus not observed. Photobiont trentepohlioid, cells rounded, 9.5–13.5 × 9.5–12 µm, solitary or in chains. Ascomata solitary, 0.1–0.5 × 0.1–0.5 mm, or in clusters of 2–4 ascomata of 0.6–0.8 × 0.3–0.5 mm, lirellate, often stellate to lobed, numerous, first immersed, becoming semi-sessile, scattered more or less evenly over the thallus; disc heavily orange pruinose, blackish below the pruina when dry, reddish when wet, flat. In ascomatal sections, all layers more or less inspersed with clusters of granular, orange-brown crystals which are K+ purplish to reddish and partly dissolving. Excipulum 10–25 µm wide, brownish. Epihymenium 20–25 µm tall, orange-brown. Hymenium 40–60 µm tall, brownish to slightly reddish, I+ deep blue, K/I+ deep blue with purplish patches. Paraphysoids 1.5–2.2 µm wide, the tips hyaline. Hypothecium c. 30 µm thick, orange-brown. Asci 30–54 × 14–21 µm (N = 20), ellipsoid to obovoid, stipitate; a KI+ ring like structure in the tholus and an ocular chamber observed in young asci. Ascospores 11.5–17.0 × 4.0–7.5 µm (N = 50), hyaline, becoming brown and ornamented with brown warts at late maturity, slightly constricted at septa, with enlarged apical cell, oblong-ovoid, (2–)3(–4)-septate; lumina of enlarged apical cell 5.1–6.2 × 3.6–4.5 µm, other lumina 1.0–3.2 × 2.0–3.5 µm; spore ontogeny macrocephalic, unidirectional; gelatinous sheath distinct, granular, c. 0.7 µm wide. Pycnidia immersed to erumpent, pale, round, concentrated on some small patches of the thallus; the wall composed of brown-walled hyphae of 1.6–2.6 µm. Conidia 4.2–5.3 × 0.8–1.3 µm (N = 10), bacilliform, hyaline, simple. Fig. 5 A–C.

Chemistry – Thallus K+ yellowish, C-, KC-, PD-, UV+ pale orange. Ascomata UV+ dark orange, K+ purplish. Calcium oxalate crystals absent in ascomata and thallus. TLC (solvent B) revealed the presence of parietin (*Van den Broeck* 6653 tested).

Distribution and ecology – *Synarthonia ochracea* is a European species that seems to grow as a juvenile parasite on the thallus of *Graphis scripta* s. lat.

Notes – The holotype specimen (PC0786154) is a mixture of two species of Arthoniaceae: *Synarthonia ochracea* and *Coniocarpon cinnabarinum*. Therefore, we lectotypify *S. ochracea* on the thalli having the typical ochraceous pruinose ascomata as described in the protologue.

A species of the *Graphis scripta* species complex is present on most of the examinated specimens of *S. ochracea*. For instance, on specimens from Italy [in sylva le riane supra Trobasco in valle Intrasca ad Verbanum, ad corticem Tiliae, 1875, *De Notaris* s.n. (BR, barcode BR5030006284765)] and France [Vogesis, ad corticem abietit, circa bruyerium, Nov. 1825, *Prevost* s.n. (BR, barcode BR5030006285779)] no obvious line or prothallus is visible between the *Synar-*

thonia and the *Graphis* suggesting that *S. ochracea* starts as a lichenicolous fungus on *Graphis* before developing its own thallus. However, it is sometimes difficult to establish if *S. ochracea* is clearly parasitic or just marginally confluent with or overgrowing the *Graphis* species. On specimens from Saint-Sever (G, barcodes G00295952 and G00295953) no species of *Graphis* could be observed. More studies are necessary to understand the biology of *S. ochracea* and to investigate if more than one species is involved, in particular with respect to the possibly lichenicolous versus the lichenized specimens.

Synarthonia ochracea is part of a complex of closely related species whose biology and circumscription are still in need of further studies. It is morphologically similar in most aspects to *S. lopingensis* and *S. ochrodes*, but the ascomata are aggregated in irregular lobed clusters. In *S. hodgesii*, the ascomata are not aggregated in clusters and evenly orange, with a non-granular pigmentation.

In past and recent literature, *Synarthonia ochracea* has been incorrectly synomized with *Arthonia elegans* (e.g. Schaerer 1823, Almquist 1880, Zahlbruckner 1923–1924, Roux et al. 2014), a species characterized by a red, not orange, pruina and the presence of a purplish pigment in the ascomata, especially at the perihymenial margins (see below).

Additional specimens examined – **France**: Marne Department, Belval-en-Argonne, forest close to the lake of "La Dame", on smooth bark of *Sorbus torminalis*, 48°57′25.4″N 4°58′47.9″E, 6 Sep. 2015, *Van den Broeck* 6653 (BR, barcode BR5030076968923); ibid., on *Fagus sylvatica*, *Van den Broeck* 6674 (BR, barcode BR5030076285648); ibid., on *Sorbus torminalis*, 28 Dec. 2017, *Verhoeyen* (hb Verhoeyen); Vogesis, ad corticem abietit, circa bruyerium, Nov. 1825, *Leprévost* s.n. (BR, barcode BR503006285779); [as *Coniocarpon elegans*] Landes, Saint-Sever, s.n. (G, barcode G00295952); Landes, Saint-Sever, s.n. (G, barcode G00295953).
Germany: s. loc., s.d., *Körber* s.n. (BR, barcode BR5030006283751).
Italy: in sylva le riane supra Trobasco in valle Intrasca ad Verbanum, ad corticem *Tiliae*, 1875, *De Notaris* s.n. (BR,

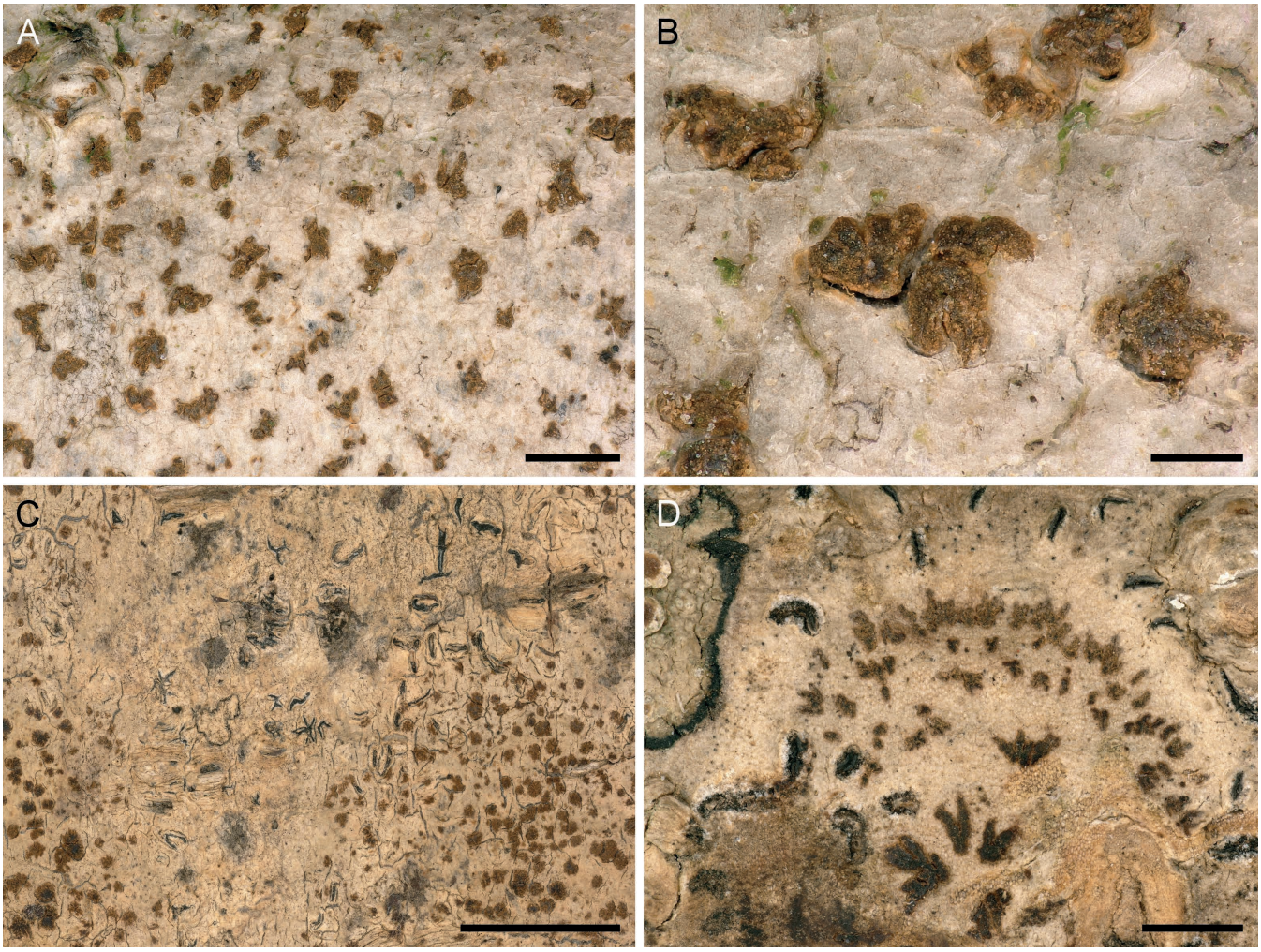

Figure 5 – Thallus with ascomata of *Synarthonia* species (*S. ochracea* complex): A–C, *S. ochracea*; D, *S. lopingensis*; A–B from *Van den Broeck* 6653 (BR); C from *De Notaris* s.n. (BR, barcode BR5030006284765); D from *Handel-Mazzetti* 1976 (holo-: WU). Scale bars: A & D = 1000 µm; B = 250 µm; C = 0.5 cm.

World key to the species of *Synarthonia*

1. Thallus sorediate ..... ***Synarthonia sikkimensis***
1'. Thallus esorediate or absent 2

2. Ascospores muriform 3
2'. Ascospores transversely septate 4

3. Ascospores 22.0–36.5 × 10.0–14.5 µm; psoromic and evernic acid present ..... ***S. muriformis***
3'. Ascospores 20.0–22.0 × 11.0–12.5 µm; psoromic and evernic acid absent, unidentified xanthones present ..... ***S. sarcographoides***

4. Ascomata epruinose or with remnants of thallus, appearing black or dull brown 5
4'. Ascomata distinctly orange or white pruinose, or appearing bright orange 6

5. Disc of ascomata brown; without remnants of thallus ..... ***S. fuscata***
5'. Disc of ascomata black; with remnants of thallus ..... ***S. josephiana***

6. Ascomata with orange pruina or pigmentation 7
6'. Ascomata white or greyish pruinose 14

7. Ascospores consistently 2-septate; 9.0–10.5 × 3.5–4.5 µm ..... ***S. karunaratnei***
7'. Ascospores with more septa; exceeding 10.5 µm in length 8

8. Ascospores consistently 5-septate; 19.5–27.0 µm ..... ***S. ferruginea***
8'. Ascospores (2–)3(–4)-septate; not exceeding 20 µm in length 9

9'. Hymenium I+ blue, rapidly turning into red 10
9'. Hymenium persistently I+ blue [*S. ochracea* complex] 11

10. Ascospores 7.0–8.0 µm broad; asci with a K/I+ blue ring like structure in the tholus ..... ***S. borbonica***
10'. Ascospores 5.5–6.5 µm broad; asci without a K/I+ blue ring like structure in the tholus ..... ***S. aurantiacopruinosa***

11. Ascomata evenly orange, with a non-granulose pigmentation; lichenicolous on *Graphis lineola* in southeastern North America ..... ***S. hodgesii***
11'. Ascomata brown to brownish black, with orange pruina; lichenized or lichenicolous on *Graphis* species in Cuba, E Asia or Europe 12

12. Ascomata not aggregated in clusters; lichenicolous on unknown *Graphis* species in Cuba ..... ***S. ochrodes***
12'. Ascomata aggregated in irregular clusters; lichenized or lichenicolous on *Graphis* species in E Asia or Europe 13

13. Ascomata in irregular star-shaped clusters; lichenized or lichenicolous on different species of *Graphis* (including *G. handelii*, *G. intricata* and *G. mikuraensis*) in E Asia (China, Japan) ..... ***S. lopingensis***
13'. Ascomata in irregular lobed clusters; lichenized or lichenicolous on *Graphis scripta* s. lat. in Europe ..... ***S. ochracea***

14. Lichenicolous, independent thallus absent, on thallus of Parmeliaceae ..... ***S. rimeliicola***
14'. Not lichenicolous, independent thallus present 15

15. Psoromic acid present ..... ***S. psoromica***
15'. Psoromic acid absent 16

16. Hymenium I+ blue; ascomata thinly white pruinose; thallus thick, cream-coloured ..... ***S. stigmatidialis***
16'. Hymenium I+ red or I+ blue turning red; ascomata densely white pruinose or greyish pruinose; thallus thin, whitish, cream or green 17

17. Clusters of ascomata not elongated with individual ascomata arranged in lines and usually not star-shaped ..... ***S. inconspicua***
17'. Clusters of ascomata mainly elongated with individual ascomata arranged in lines or ascomata star-shaped 18

18. Thallus and ascomata UV- or UV+ pale yellowish (xanthone absent) ..... ***S. albopruinosa***
18'. Thallus and/or ascomata UV+ brightly orange-yellow (xanthone present, at least patchily)..... 19

19. Ascomata without hyaline hair like extensions; ascospores 18–24 µm long, (3–)4-septate; hypothecium I+ blue; hymenial disc often thinly pruinose appearing then greyish to dark brown-almost blackish; Europe ..... ***S. astroidestera***
19'. Ascomata with hyaline hair like extensions; ascospores 14.5–19.0 µm long, (2–)3(–4)-septate; hypothecium I+ red; hymenial disc heavily white pruinose and pale brown-orange when pruina removed; tropical Africa ..... ***S. pilosella***

barcode BR5030006284765; Rabenhorst, Lich. Eur. Exs. 337).
Switzerland: an der Rinde junger Buchen, s.d., *Schaer. & Hepp* 882 (BR, barcode BR5030006282747).

Synarthonia ochrodes (Nyl.) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825166.

Arthonia ochrodes Nyl., in Willey: Synopsis of the genus Arthonia: 10. 1890 (Willey 1890). – Type: Cuba, s.d., *Wright* 135 (H-NYL 5597– holo-: H, barcode H9507637).

Supposedly starting as a lichenicolous fungus on species of *Graphis*, not changing the whitish thallus of the host. Prothallus not observed. Ascomata 0.04–0.9 × 0.04–0.5 mm, numerous, young minute, becoming elongated-oblong and branched, not aggregated in clusters, ± sessile, scattered more or less evenly over the thallus, closely spaced; disc reddish brown to black, mostly entirely covered by an orange pruina, convex. Epihymenium 10–20 µm tall, dark reddish brown, I+ blue, K/I+ blue, inspersed by orange to brown crystals which are K+ partly dissolving with violet-red solution. Hymenium 37–42 µm tall, hyaline or pale brownish, sparsely inspersed by orange to brown crystals which are K+ partly dissolving with violet-red solution, I+ blue, K/I+ blue. Hypothecium 15–25 µm thick, pale brown, I+ blue, K/I + blue. Paraphysoids 1.0–2.5 µm wide, not distinctly swollen in the tips, hyaline. Asci 23–41 × 12–17 µm (N = 6), obovoid, with a K/I+ blue apical ring in the tholus. Ascospores 13.5–16.5 × 4–6.5 µm (N = 13), hyaline, becoming brown (K+ olivaceous) and ornamented with small brown warts at late maturity, with enlarged apical cell, oblong-ovoid, (2–)3-septate; gelatinous sheath c. 1–2 µm wide. Pycnidia not observed. Fig. 5D.

Chemistry – Thallus UV+ orange. Calcium oxalate absent in ascomata and thallus. TLC and spot tests not performed (type specimen).

Distribution and ecology – *Synarthonia ochrodes* has been described from Cuba. The specimen reported from Thailand by Vainio (1909) does not fit our concept of *S. ochrodes* since the hymenium of this species reacts I+ blue rapidly turning into red (persistently blue in *S. ochrodes*).

Notes – The ascomata of the type of *S. ochrodes* are strongly orange pruinose, a character not mentioned in the protologue (Willey 1890). They grow on the thallus of a species of *Graphis* without any visible own thallus. This suggests that *S. ochrodes* is a lichenicolous fungus.

Synarthonia ochrodes is morphologically similar in most aspects to *S. lopingensis* and *S. ochracea*, but the ascomata are not aggregated in clusters. In contrast to *S. hodgesii*, the disc of the ascomata is reddish brown to black and not evenly orange, but otherwise the two taxa are very similar.

Synarthonia rimeliicola (Diederich) Van den Broeck, Diederich & Ertz, **comb. nov.**

Mycobank No.: MB 825168.

Arthonia rimeliicola Diederich, Bibliotheca Lichenologica 64: 19. 1997 (Aptroot et al. 1997). – Type: Papua New Guinea, Madang prov., Huon Peninsula, Finisterre range, Yupna valley, Teptep village, 146°33′E 5°57′S, on decaying thalli of *Parmotrema crinitum*, 30 Jul. 1992, *Aptroot* 32323 (holo-: B, n.v.; iso-: hb Aptroot n.v., hb Diederich).

The host of the type specimen is in poor condition and was published as *Rimelia reticulata* (Aptroot et al. 1997). However, a re-examination of the isotype in hb Diederich revealed the presence of ciliate isidia, the absence of soralia, a K+ yellow-orange cortex and a PD+ orange medulla. These characters relate to *Parmotrema crinitum*, a species that had been reported from the type locality by Louwhoff & Elix (1999).

A description and illustrations can be found in the protologue. *Synarthonia rimeliicola* is morphologically similar to other species of *Synarthonia* by whitish pruinose, PD+ yellow ascomata and ascospores with an enlarged apical cell.

Notes on the related genus *Coniocarpon*

Coniocarpon differs from *Synarthonia* mainly in its secondary chemistry including anthraquinones and isofuranonaphtoquinones (Yamamoto et al. 2002, Frisch et al. 2014a). Red-purple pigments, K+ red or purple and partly to completely dissolving and calcium oxalate crystals are often present in the ascomata of species of *Coniocarpon*.

Coniocarpon elegans (Ach.) Duby (Duby 1830: 675). – *Spiloma elegans* Ach. (Acharius 1810: 135). – *Lichen elegans* (Ach.) Lam. (Lamarck & Poiret 1813: 352). – *Arthonia elegans* (Ach.) Almq. (Almquist 1880: 19). – Type:

Schleicher Pl. Cr. Helv. Centur. 5 n 54 (lecto-: S, **designated here**).

Notes – The typification of the name *Spiloma elegans* Ach. requires some discussion. In the protologue, Acharius (1810) noted that the original material of Schleicher, on which the name is based, consisted of a species with red coloured ascomata ("apotheciis punctiformibus substellatisque coccineis"). The colour drawing in the protologue shows two colours, red and a paler central part for some ascomata. Thus, it is clear from the protologue that the name applies to a taxon with red (or reddish pruinose) ascomata. A specimen of *S. elegans* with the annotation 'Helvetia' is preserved in H, labelled as 'syntype', the only specimen of *S. elegans* in H (according to the curator L. Myllys). This specimen has ochraceous ascomata and represents *Arthonia ochracea* Dufour, described in 1818. That species was considered a variety of *Coniocarpon cinnabarinum* by various authors (e.g. Nylander 1853, 1856, Zahlbruckner 1923–1924) or placed in synonymy with *A. elegans* (e.g. Schaerer 1823, Almquist 1880). However, this synonymysation probably was not based on the original material of *A. elegans* as there is no reference to the material of Schleicher Pl. Cr. Helv. Centur. 5 n 54 in the cited literature. Another syntype specimen in S bears the number 5 n 54 corresponding to Schleicher's Pl. Cr. Helv. and is labelled "*Arthonia elegans*". This is the name given by Schleicher in his exsiccate, cited as synonym of *Spiloma elegans* in the original description by Acharius. This specimen bears the number (5 n 54) cited in the protologue by Acharius and the red ascomata have the colour ("coccinea") described in the protologue. For this reason, we lectotypify the name *Spiloma elegans* on the syntype in S. The selected lectotype is characterized by ascomata having an exposed hymenial disc covered by a pale greyish pruina, and margins covered by an orange-reddish pruina; asci 45 × 24 µm, 8-spored; ascospores 14.0–18.0 × 6.0–7.0 µm (N = 11, from two different ascomata), hyaline becoming dark brown at late maturity, oblong-ovoid, with enlarged apical cell, 3–4-septate. Therefore, according to the ascospores, it fits with the current concept of *Coniocarpon fallax* (Ach.) Grube. As a consequence, *Spiloma elegans* becomes a synonym of *C. fallax* since this is the older name. A request to other herbaria (BM, BM, BPI, CAN, E, G, GOET, H, KIEL, L, LD, M, PC, W, WRSL) to obtain additional material of Schleicher Pl. Cr. Helv. Centur. 5 n 54 of *Spiloma elegans* to find out if this number of the exsiccate is homogeneous, was not successful. In selecting the type specimen from S with the number "5 n 54" of Schleicher Pl. Cr. Helv. and labelled "*Arthonia elegans*" as lectotype, we follow recommendation 9A.2. of the Botanical Code (Mcneill et al. 2012) that in choosing a lectotype all aspects of the protologue should be considered as a basic guide.

Coniocarpon fallax is newly recorded for Belgium (Gochenée, 1.5-2 km au N du centre du village, rive gauche de l'Hermeton, 50°12′05″N 4°45′23″E, elev. 143 m, frênaie marécageuse et claire en fond de vallée, tronc de jeunes *Fraxinus excelsior*, 20 Sep. 2015, *Ertz* 20399, barcode BR5030052292097), a locality that was first published for a specimen erroneously identified as *Arthonia cinnabarina* (Ertz & Duvivier 2006).

Coniocarpon carneoumbrinum (Zahlbr.) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825169.

Arthonia carneoumbrina Zahlbr., Annales de cryptogamie exotique 5: 206. 1932 (Zahlbruckner 1932). – Type: [Tanzania], Ostusambara, Amani, in valle Dodwe, elev. c. 750 m, ad corticem *Cyatheae usambarensis*, Aug. 1909, *Brunnthaler* s.n. (holo-: WU).

Notes – This species is characterized by rounded, convex, sessile and heavily white to pink pruinose ascomata, and (4–)5-septate, persistently hyaline ascospores of 24.0–28.5 × 8.0–10.0 µm with enlarged apical cell. The thallus is grey. Internally, a purplish pigment (K+ dissolving) is present at the perihymenial margins. Calcium oxalate crystals have been observed in the ascomata. This species is a typical member of *Coniocarpon*. It differs from the other species of this genus by a grey thallus, the absence of a reddish pruina and regularly rounded, sessile and convex ascomata.

Coniocarpon tuckermanianum (Willey) Van den Broeck & Ertz, **comb. nov.**

Mycobank No.: MB 825170.

Arthonia tuckermaniana Willey, Synopsis of the genus *Arthonia:* 20. 1890 (Willey 1890). – Type: USA, Florida, Auction, ex herbarium Tuck, s.d., *Custin* s.n. (iso-: US).

Notes – This species is characterized by a white, continuous thallus with numerous, semi-immersed, reddish brown to black ascomata, occasionally with some white pruina. The ascospores are (3–)4–5(–7)-septate, 17.0–23.5 × 6.0–8.0 µm and have an enlarged apical cell. Internally, a purplish pigment (K+ dissolving) is present at the perihymenial margins. Abundant calcium oxalate crystals have been observed in the ascomata. This species is a typical member of *Coniocarpon*. It differs from the other species of this genus by the absence of a reddish pruina, reddish brown to black ascomata and up to 7-septate ascospores.

Note on *Arthonia thamnocarpa*

Sclerophyton elegans Eschw. (Eschweiler 1824: 25). – Type: Brazil, near Pará, corticolous, s.d., *Von Martius* s.n. (holo-: M n.v.; iso-: M n.v.).

Arthonia thamnocarpa Vain. (Vainio 1923: 143), **synon. nov.** – Type: West-Indian, Trinidad, Sangre Grande, ad corticem arboris, 1912–1913, *Thaxter* 89 (Herbarium Vainio 28747 – holo-: TUR).

Notes – *Arthonia thamnocarpa* is characterized by a continuous to cracked, smooth to slightly pustulate, white thallus with immersed to erumpent, black, when wet dark brown but not translucent, epruinose ascomata which are lirellate when young but becoming distinctly dendroid, occasionally surrounded by a paler thalline margin, 0.08–7.6 × 0.04–0.06 mm. Ascospores are 3(–4)-septate, hyaline, 15.5–16.0 × 4.0–4.5 µm, with two enlarged apical cells. TLC (solvent B) revealed the presence of psoromic acid (major). *Arthonia thamnocarpa* is similar in almost all aspects to *Sclerophyton elegans* and is therefore synonymized with the latter.

Contrary to the key and description in Sparrius (2004), the ascospores of *S. elegans* are sometimes 4-septate as in *S. extenuatum* (Nyl.) Sparrius, but the latter species clearly differs by the presence of protocetraric acid.

DISCUSSION

Considerable progress has recently been made in the phylogeny of the Arthoniales, but much remains to be done in the family Arthoniaceae, where most species of the large and heterogeneous genus *Arthonia* still cannot be reallocated to other genera due to the lack of molecular data for several genera. Our study provides a further step in this process by resolving the phylogenetic placement of the genus *Synarthonia*, thanks to the sequencing of its type species and a few other related species.

Synarthonia is quite heterogeneous in morphology, particularly in the structure of the ascomata. The core group of *Synarthonia* is represented by the type species *S. inconspicua* and other species having notably white pruinose, PD+ yellow to orange ascomata that are often clustered, viz. *S. albopruinosa*, *S. muriformis* and *S. pilosella*. This group is phylogenetically well supported (fig. 1). *S. astroidestera* obviously also belongs to the core group of *Synarthonia* as judged by its morphology and chemistry, despite the species was not included in the phylogeny. The sister clade to the core group contains two orange pruinose species (*S. aurantiacopruinosa* and *S. ochracea*) and the epruinose *S. fuscata* (fig. 1). The more distantly related *S. josephiana* has also epruinose ascomata, but they are covered with remnants of thallus.

At present it is not fully clear which are the main morphological characteristics that distinguish *Synarthonia* from other genera in the family Arthoniaceae. The presence or absence of clustered ascomata is not sufficient because in the phylogenetic tree, species clearly lacking such ascomata are included in the genus (e.g. *S. fuscata*, fig. 3F). Already *S. sarcographoides* was assigned only with hesitation to the genus as the organisation of several ascomata in a pseudostroma makes it difficult to ascertain whether or not the pale marginal areas of the ascomata should be seen as ascomatal tissue (Menezes et al. 2013). Other characteristics, such as the transversely septate ascospores with enlarged apical cell can also be found in genetically distantly related species, such as *Arthonia ilicina* (Frisch et al. 2014a). *Arthonia ilicina* shares further characteristics with some species of *Synarthonia*, such as brown-walled (K+ olivaceous) paraphysoids in the epihymenium and ascospores becoming brown and warted at late maturity.

Our phylogenetic analysis clearly demonstrates that the morphologically and phylogenetically closely related genus *Reichlingia* is not a synonym of *Synarthonia* as was suggested by Joseph & Sinha (2015). Fertile species of *Reichlingia* are characterized by adnate, pruinose and often elongate to stellate-branched ascomata; epithecium greyish by inspersion with pale granular crystals or dark brown; hymenium hyaline, clear or sparsely inspersed with pale granular crystals, I+ blue or pale yellowish brown; a well-developed hyaline to pale brownish hypothecium; tips of paraphysoids with or without dark brown pigmented walls; oblong-ovoid, hyaline, transversely septate with enlarged apical cell or submuriform ascospores that may or may not get brownish with dark brown warty ornamentation at late maturity (Diederich & Scheidegger 1996). *Reichlingia* differs from *Synarthonia* by a compact-felty to byssoid-granular thallus, ascomata with individual hymenia separated by deep but often incomplete fissures and a secondary chemistry including 2'-*O*-methylperlatolic acid and perlatolic acid (Diederich & Scheidegger 1996, Frisch et al. 2014a). An unidentified xanthone has been found in *R. virginea* (Müll.Arg.) Frisch, but that species has not been sequenced yet (Frisch et al. 2014b). *Synarthonia* is also closely related to *Coniocarpon* in our phylogenetic tree (fig. 1), and the ascomata and thallus morphology of *Synarthonia* shows many similarities with *Coniocarpon*. The species of both genera are characterized by adnate, often pruinose and rounded, elongated to stellate to lobbed ascomata with a well-developed hyaline, brownish to yellowish hypothecium, and oblong-ovoid, hyaline, transversely septate with an enlarged apical cell ascospores that may or may not get brownish with dark brown warty ornamentation in the epispore at late maturity. *Coniocarpon* differs from *Reichlingia* and *Synarthonia* mainly in its secondary chemistry including anthraquinones and isofuranonaphtoquinones (Yamamoto et al. 2002; Frisch et al. 2014a). Red-purple pigments, K+ red or purple, partly or completely dissolving, and calcium oxalate crystals are often present in the ascomata of species of *Coniocarpon*. White pruinose ascomata can be observed in some species of the genus *Coniocarpon* but, to our observations, in such ascomata purplish pigments (K+ dissolving) are always discernible. The genus *Synarthothelium* Sparrius differs from *Synarthonia* mainly by muriform ascospores that are > 40 µm long and an *Arthothelium* type of asci (Sparrius 2009).

The current study is a further step in our understanding of the phylogenetic relationship of the taxa within Arthoniaceae, but much remains to be done since a lot of species currently placed in *Arthonia* s. lat. have not been sequenced yet.

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