



Four new Arthoniomycetes from Bwindi Impenetrable National Park, Uganda – supported by molecular data

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With 3 figures and 1 table

Abstract: *Arthonia physcidiicola* Frisch & G.Thor, *Chiodecton soledatum* G.Thor & Frisch, *Herpothallon kigeziense* Frisch & G.Thor and *Reichlingia syncesioides* Frisch & G.Thor are described as new to science. All species have been collected in the montane rainforests of Bwindi Impenetrable National Park in south western Uganda. The earlier monotypic genus *Reichlingia* with one anamorphic species is emended to include three fertile species and is newly reported to Africa. The combinations *Reichlingia virginea* (Müll.Arg.) Frisch for *Arthothelium virgineum* Müll. Arg. from the Usambara Mts. in north eastern Tanzania, and *Reichlingia zwackhii* (Sandst.) Frisch & G.Thor for the European *Arthonia zwackhii* Sandst. are made. A phylogenetic tree based on Bayesian and ML analyses of combined mtSSU, nLSU and RPB2 data showing the position of the new species in Arthoniomycetes is presented.

Key words: *Arthonia*, *Chiodecton*, *Herpothallon*, *Reichlingia*, tropical Africa, phylogeny.

Introduction

Bwindi Impenetrable National Park ("Bwindi"), a UNESCO world heritage site famous for its population of about 340 mountain gorillas, is one of the most biologically diverse regions in eastern Africa. Covering an area of 331 km² at the intersection of Kabale, Kanungu and Kisoro districts in south western Uganda, Bwindi's tropical rainforests

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form an isolated island in a densely populated agricultural landscape. The park with its rugged and steeply incised terrain lies within the Kigezi Highlands that were formed through up-warping of the Albertine Rift Valley. The underlying geology of precambrian shale phyllite, with some quartzite, schist and localised granite (Howard 1991) has weathered to well differentiated humic ferralsols with abundant organic matter and moderate to high acidity (Twongyirwe et al. 2011; Twongyirwe et al. 2013). The local climate has two rainfall peaks, from March to May and September to November. Available data show annual precipitation within the range of 1236–1826 mm and mean annual temperatures of 16.4 to 21.7°C – with mean temperature highly dependent on elevation (Institute of Tropical Forest Conservation (ITFC) [http:// www.itfc.org](http://www.itfc.org), 22/7/2013).

With elevations of 1190–2560 m above sea level, Bwindi is one of the few regions in eastern Africa where lowland and montane rainforests meet. Due to its geographical position at the intersection of the Albertine, Congo Basin and Eastern Africa ecological zones, biogeographic elements of western and eastern Africa contribute to the rich species diversity. More than 1000 flowering plant species, 324 tree and shrub species, and over 104 fern species have been reported (ITFC herbarium, unpublished data), and the wider Albertine Rift region is likewise the most species rich area of comparable size in Africa for vertebrates (Plumptre et al. 2007). Detailed pollen studies in local swamps show that the highland region remained relatively wet and forested during and since the extensive desiccation of the last Pleistocene glaciation (Jolly et al. 1997; Morrison & Hamilton 1974; Taylor 1990), explaining the region's many restricted species (Hamilton 1981).

However, only few data exist on the rich lichen mycota of Bwindi and only ten species of macrolichens have been reported so far: *Coccocarpia erythroxyli* (Sprengel) Swinscow & Krog (Swinscow & Krog 1976), *Everniopsis trulla* (Ach.) Nyl. (Dodge 1959), *Hypotrachyna endochlora* (Leight.) Hale and *Parmelinopsis minarum* (Vain.) Elix & Hale (Krog & Swinscow 1979), *Parmotrema permutatum* (Stirt.) Hale and *P. reticulatum* (Taylor) M. Choisy (Krog & Swinscow 1981), *Ramalina hoehneliana* Müll.Arg. (Dodge 1971) as well as *Usnea cristata* Mot., *U. pulvinata* Fr. and *U. rubicunda* Stirton (Swinscow & Krog 1974, 1979). The present publication is part of ongoing efforts to improve our knowledge on the lichens of Bwindi and the lichen mycota of tropical Africa. Epiphytic lichens are sensitive indicators of the environment with value for monitoring continuity, disturbance, air pollution and microclimatic conditions (e.g., Nimis et al. 2002; Rivas Plata et al. 2008). Knowledge of species and their distributions and ecology is a prerequisite for developing further studies in biodiversity and clarifying conservation requirements in African forests.

In the course of an ecological study on epiphytic lichens in Bwindi in 2011, conducted as a collaboration between the Institute of Tropical Forest Ecology (ITFC), Kabale, Uganda and The Uganda Wildlife Authority (UWA, the agency responsible for managing Uganda's National Parks), and the Department of Ecology, Swedish University of Agricultural Sciences in Uppsala, a large number of lichens were collected for further identification. In the present publication we report on four new species of Arthoniomycetes and make two additional new combinations in *Reichlingia*.

Material and methods

INVESTIGATION OF LICHEN SPECIMENS: Holotype specimens of the new species are located in UPS, with duplicates in EA and M when selected. Morphology was studied on hand sections in water and lactic blue, and on squash-preparations. For investigation Olympus BX40 and Leica MZ8 microscopes were used.

Secondary lichen compounds were identified by TLC (Orange et al. 2010) and HPTLC (Arup et al. 1993), using solvents B' and C. The amyloidity of thallus and ascomata was examined using 1% (I) and 0.2% (I_{dl}) aqueous iodine solution without and with pretreatment with 10% aqueous potassium hydroxide (KI). The colour reaction of the thallus was tested using 10% aqueous potassium hydroxide (K), sodium hypochloride (C), 10% aqueous potassium hydroxide followed by sodium hypochloride (KC), 1,4-phenyldiamine in 96% ethanol (PD) and short wave UV₂₅₄ light. Calcium oxalate crystals were identified by formation of gypsum needles in squash-preparations of thallus samples after applying 10% sulfuric acid.

DNA EXTRACTION: For DNA extraction, variable amounts of clean lichen samples were extracted with 1ml acetone, frosted in liquid nitrogen and finely ground with pellet pestles in 1.5 ml microtubes. Genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen) following the manufacturers instructions. The extracts were kept in a refrigerator for at least 1 hour and then used undiluted or in 1:10 dilutions depending on the DNA concentration in the extracts.

For lichen parasites, minute species or were contamination with parasitic fungi or molds was a problem, hand cuttings of the hymenium about 20–50 × 50–100 µm in size were used for a direct PCR approach. Pigmented, carbonized or crystal encrusted portions were removed from the cuttings as far as possible. Hymenial pigments were removed with acetone or 1% aqueous KOH solution. In sterile species, clean growing portions of the thallus (e.g., prothallus hyphae, soredia, isidia) were extracted thrice with acetone and potential calcium oxalate crystals rinsed out with water. Such lichen preparations were then placed directly in 0.2 ml microtubes for DNA amplification.

PCR AND SEQUENCING: 20 µl (DNA extractions) and 30 µl (direct PCR) PCR reactions were used. Each 10 µl of PCR mix contained 0.5–1 µl genomic DNA extraction (or the lichen sample), 0.4 µl of each primer (20pmol/µl) and 5 µl HotStarTaq Plus Mastermix Kit (Qiagen). The following primers were used for PCR amplification: mtSSU (mtSSU1 and mtSSU3R; Zoller et al. 1999), nLSU (LIC24R and LR7; Miadlikowska & Lutzoni 2000, Vilgalys & Hester 1990) and RPB2 (RPB2-7cF and RPB2-11aR; Liu et al. 1999). PCR cycling conditions were 95°C for 15 minutes, followed by 45 cycles of 95°C for 45 sec., 53°C for 45 sec., and 72°C for 1 min., followed by a final extension of 72°C for 7 minutes. The PCR products were visualized on a 0.5× GelRed (Biotium, Inc)-stained agarose gel under UV light. PCR products were purified either using the QIAquick PCR Purification kit (Qiagen) or gel extracted and purified using the QIAquick Gel Extraction Kit (Qiagen).

Sequencing of the amplicons was done at the Uppsala Genome Centre, Uppsala, Sweden. The sequences obtained were assembled in BioEdit v7.1.3 (Hall 1999) and their identity checked with Blast search in GenBank and the local Blast functionality implemented in the BioEdit v7.1.3 package.

ALIGNMENT: The mtSSU and nLSU sequences were aligned in RNAsalsa (Stocsits et al. 2009) using the secondary structure of *Eremicella nidulans* (mtSSU) and *Saccharomyces cerevisiae* (nLSU; Kjer 1995) as template. RPB2 sequences were aligned in MAFFT as implemented in the Guidance Web Server (Penn et al. 2010). Confidence scores in Guidance were calculated and columns with confidence values < 0.95 were removed from the analysis. The alignments were further checked for obvious aligning errors and all remaining phylogeny uninformative insertions removed. The final alignments comprised 522 (mtSSU), 615 (nLSU) and 876 (RPB2) columns, resulting in a combined alignment of 2013 nucleotide positions.

PHYLOGENETIC ANALYSES: A general-time-reversible model with a proportion of invariable sites (GTR-I-Γ) was found to best explain the sequence evolution for the mtSSU, nLSU and RPB2 data set using the Akaike Information Criterion (AIC; Akaike 1973) implemented in MEGA5 (Tamura et al. 2011). Bayesian inference (Holder & Lewis 2003; Huelsenbeck et al. 2001) and Maximum Likelihood search (ML) were applied to estimate phylogenetic hypotheses. Prior to concatenation of the three

Table 1. Species of Arthoniomycetes included in the phylogenetic analyses and the GenBank accession numbers of the sequences. New sequences generated are indicated in bold.

Species	Voucher	mtSSU	nLSU	RPB2
<i>Alyxoria varia</i>	Sweden; Thor 11/Se50 (UPS)	KF707642	-	KF707664
<i>Arthonia anglica</i>	Rwanda; Ertz 7775 (BR)	EU704049	EU704084	EU704012
<i>Arthonia calcarea</i>	France; Ertz 7539 (BR)	EU704064	-	EU704028
<i>Arthonia didyma</i>	Belgium; Ertz 7587 (BR)	EU704047	EU704083	EU704010
<i>Arthonia dispersa</i>	Sweden; K. & L.Holm (UPS)	AY571383	AY571381	-
<i>Arthonia maculiformis</i>	New Zealand; Wedin 9393b(S)	-	KF707635	KF707658
<i>Arthonia physcidiicola</i>	Uganda; Frisch 11/Ug318 (UPS)	KF707646	-	KF707657
<i>Arthonia radiata</i>	Belgium; Ertz s.n. (BR)	EU704048	-	EU704011
<i>Arthothelium galapagoense</i>	Galapagos; Ertz 11790 (BR)	-	HQ454516	HQ454658
<i>Chiodecton natalense</i>	Uganda; Frisch 11/Ug324 (UPS)	KF707647	KF707641	KF707660
<i>Chiodecton natalense</i>	Zambia; Ertz 6576 (BR)	EU704051	EU704085	EU704014
<i>Chiodecton sorediatum</i>	Uganda; Frisch 11/Ug447 (UPS)	KF707648	KF707638	KF707661
<i>Chrysothrix caesia</i>	USA; Amtoft (AFTOL 775)	FJ469671	FJ469668	FJ469670
<i>Chrysothrix candelaris</i>	Sweden; Frisch 11/Se45 (UPS)	KF707649	KF707640	KF707663
<i>Chrysothrix chrysophthalma</i>	Canary Islands, Ertz 10927 (BR)	-	HQ454519	HQ454661
<i>Combea mollusca</i>	South Africa; Tehler 7725 (S)	AY571384	EF081383	DQ987626
<i>Coniocarpon cinnabarinum</i>	Rwanda; Ertz 8730 (BR)	EU704046	-	EU704009
<i>Cryptothecia candida</i>	Gabon; Ertz 9260 (BR)	EU704052	HQ454520	EU70415
<i>Dendrographa leucophaea</i>	Mexico; Tehler 9130 (S)	-	HQ454524	HQ454664
<i>Dichosporidium boschianum</i>	Fiji Islands; Lumbsch 19815a (F)	GU327692	GU327716	-
<i>Dimidiographa graphidiza</i>	Angola; Tehler 9731 (S)	-	HQ454572	HQ454712
<i>Dirina catalinariae</i>	Galapagos Islands; Tehler 8726 (S)	-	EF081387	DQ987630
<i>Dothidea sambuci</i>	AFTOL-ID274	AY544739	AY544681	DQ522854
<i>Enterographa crassa</i>	France; Ertz 5041 (BR)	EU704056	EU704088	EU704020
<i>Enterographa hutchinsiae</i>	Belgium; Ertz 10066 (BR)	EU704057	EU704089	EU704021
<i>Erythrodictyon granulatum</i>	Gabon; Ertz 9908 (BR)	EU704058	EU704090	EU704022
<i>Herpothallon kigeziense</i>	Uganda; Frisch 11/Ug26 (UPS)	KF707644	-	KF707654
<i>Herpothallon rubrocinctum</i>	Mexico; Rudolphi 5 (UPS)	KF707643	-	KF707655
<i>Herpothallon sp. Ug4</i>	Uganda; Frisch 11/Ug401 (UPS)	KF707645	-	KF707653
<i>Lecanactis abietina</i>	Belgium; Ertz 5068 (DUKE)	AY548813	AY548812	AY552018
<i>Lecanographa amylicata</i>	Sweden; Thor 26176 (UPS)	KF707650	KF707639	KF707659
<i>Lecanographa hypothallina</i>	Mexico; Tehler 9108 (S)	-	HQ454558	HQ454698

<i>Opegrapha lithyrga</i>	Belgium; Ertz 8784 (BR)	EU704068	EU704096	EU704032
<i>Opegrapha vulgata</i>	Belgium; Ertz 7564 (BR)	EU704080	EU704108	EU704044
<i>Pleospora herbarum</i>	AFTOL-ID 940	FJ190610	DQ247804	DQ247794
<i>Reichlingia leopoldi</i>	Belgium; Ertz 13294(BR)	JF830774	HQ454582	HQ454723
<i>Reichlingia syncesiooides</i>	Uganda; Frisch 11/Ug14 (UPS)	KF707651	KF707636	KF707656
<i>Reichlingia zwackhii</i>	Canary Islands; Ertz 10928 (BR)	-	HQ454514	HQ454655
<i>Reichlingia zwackhii</i>	Sweden; Thor 11/3 (UPS)	KF707652	KF707637	KF707662
<i>Roccella fuciformis</i>	Canary Islands; Tehler 8255 (S)	-	EF081406	DQ987649
<i>Roccella phycopsis</i>	Azores, Tehler 8221 (S)	-	EF081423	DQ987666
<i>Roccellina mahuiana</i>	Chile; Tehler 8459 (S)	-	HQ454596	HQ454736
<i>Roccellographa cretacea</i>	Socotra; Tehler 9341 (S)	-	HQ454601	HQ454741
<i>Sparria endlicheri</i>	Belgium; Ertz 12651 (BR)	-	HQ454511	HQ454652
<i>Syncesia intercedens</i>	Rwanda; Ertz 11059 (BR)	-	HQ454644	HQ454784
<i>Syncesia madagascariensis</i>	Madagascar; Ertz 12966 (BR)	-	HQ454645	HQ454785
<i>Tylophoron hibernicum</i>	France; Diederich 16335 (BR)	JF830779	JF295084	-
<i>Tylophoron moderatum</i>	DR Congo; Ertz 14504 (BR)	JF830780	JF295085	-

single-gene alignments, the alignments and all possible combinations were tested for conflicting tree topologies. Bayesian and ML analyses were performed for all resulting alignments using the same settings as for the concatenated three-gene alignment. Conflict was assumed when deviant tree topologies were supported by $\geq 70\%$ bootstrap values (BS) and $\geq 95\%$ posterior probabilities (PP). The RPB2 data set was further partitioned according to codon positions to allow for the higher evolutionary rates of the 3rd codon position.

Bayesian analysis was performed with MrBayes 3.2.1 (Ronquist & Huelsenbeck 2003) implemented in the CIPRES Science Gateway (Miller et al. 2010). A GTR-I- Γ model of sequence evolution was applied to the partitioned dataset, and the model parameters were estimated during the run for each gene partition separately starting from a default flat Dirichlet distribution. The analysis was run for 10.000.000 generations in 8 chains and every 500th generation was sampled. The first 50% of trees were discarded as burnin and a 50% majority rule consensus tree calculated with the sumt command in MrBayes 3.2.1.

Maximum likelihood was performed on the partitioned dataset with the RAxML-HPC black box implemented in the CIPRES Science Gateway (Miller et al. 2010) using rapid bootstrapping and full ML analysis under the GTR+GAMMA approximation. The analysis was stopped after 814 bootstraps using the bootstopping option implemented in RAxML 3.2.7 (Pattengale et al. 2009).

Results

Phylogenetic analysis We generated 30 new sequences for 12 species of Arthoniomycetes. 81 additional sequences for 34 species were obtained from GenBank (Table 1). A total of 46 species of Arthoniomycetes is included in the analysis. *Pleospora herbarum* and *Dothidea sambuci* in Dothideomycetes are used as outgroup. The

structure of the phylogenetic tree (Fig. 1) confirms recent results by Ertz & Tehler (2011) showing Arthoniaceae, Chrysothrichaceae, 'Lecanographaceae', Opegraphaceae, Roccellaceae, and Roccellographaceae as distinct families in Arthoniomycetes. The position of the new taxa is indicated in bold: *Herpothallon kigeziense* is the sister taxon to *Herpothallon rubrocinctum* (Ehrenb:Fr.) Aptroot, Lücking & G.Thor, the type of the genus. *Herpothallon* is the closest relative to *Cryptothecia candida* (Kremp.) R.Sant. in our phylogeny. The genus *Reichlingia* with three species is included in Arthoniaceae in a clade with *Arthonia anglica* Coppins and *Coniocarpon cinnabarinum* DC. *Arthonia physcidiicola* groups with *A. maculiformans* Wedin & Haf., another parasitic *Arthonia* species collected from *Pseudocyphellaria glabra* and *P. homoeophylla* in New Zealand (Wedin & Hafellner 1998), and with the lichenized *A. didyma* Körb. *Chiodecton sorediferum* is placed in a clade with *Chiodecton natalense* Nyl. in Roccellaceae close to *Lecanactis abietina* (Ach.) Körb., the type of *Lecanactis*.

The species

Arthonia physcidiicola Frisch & G.Thor, **sp. nov.**

Figs 2a, 3a–d

MycoBank [MB 805573]

A. physcidiicola is characterized by the orange, maculate ascomata produced on raised galls on the thallus of *Physcidia wrightii*; the orange, K+ purple pigments in the hymenium; paraphysoids tips with pale walls; the hyaline narrowly elliptical to slipper-shaped, 1-septate spores, 10–15 × 3.5–4.5 µm large, which get brown and minutely warty at late maturity; and the I+ wine red, KI+ blue reaction of the ascomatal gels.

TYPE: Uganda, Kanungu District, Bwindi Impenetrable National Park, Eastern Sector, Ihihizo River, on *Physcidia wrightii* on the trunk of a large unidentified tree in mixed montane rainforest close to river crossing, 01°01'26.5"S, 029°41'43.5"E, elev. 1900 m, A.Frisch 11/Ug318, 27 May 2011 (UPS holotype; EA, M).

GALLS INDUCING on thallus and isidia of *Physcidia wrightii* (Tuck.) Tuck.; galls numerous and crowded, about 0.5–1.0 mm in diameter, strongly convex, usually ± constricted at base, somewhat irregular in shape, of thallus colour; medulla of galls solid, white. ASCOMATA usually aggregated 3–15 on each gall, developing in the uppermost parts of the photobiont layer but soon erumpent, orange, maculate, level with the galls' surface to weakly convex and elevated, irregularly rounded to elliptical in outline, 0.10–0.35 × 0.10–0.30 mm. PROPER EXCIPLE indistinct. EPITHECIUM deep orange, 5–12 µm thick. HYMENIUM strongly conglutinated, with diffuse orange pigmentation, 30–45 µm thick. HYPOTHECIUM deep orange, 20–45 µm thick, strongly conglutinated, comprising a dense mesh of c.1 µm wide branched and netted prosoplectenchymatic hyphae; pigments amorphous in the gelatinous matrix. PARAPHYSOIDS loosely branched and netted, slightly wavy, c.1 µm wide; tips up to 1.5 µm wide, densely branched and anastomosing, with pale walls. ASCI loosely spaced, clavate, of *Arthonia*-type, 35–48 × 12–15 µm, lateral walls 1–2 µm thick, apically thickened up to 4 µm with a broadly triangular to rounded ocular chamber, 8-spored (spores in 2 irregular rows). Spores narrowly elliptical to slipper shaped, 10–15 × 3.5–4.5 µm, hyaline, becoming pale brownish with minutely warty ornamentation at late maturity, 1-septate, occasionally slightly constricted at the septa, with enlarged apical cell; perispore thin, I–. PYCNIDIA not seen.

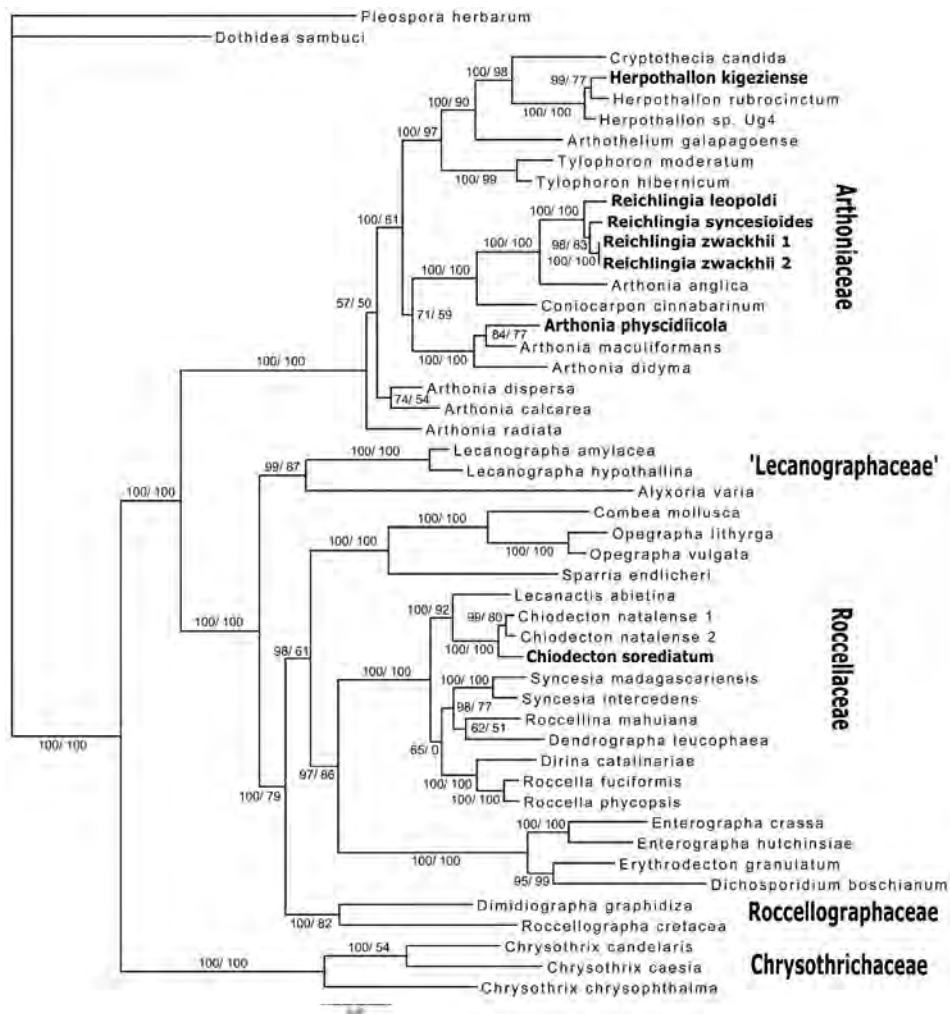


Fig. 1. Bayesian 50% majority rule tree showing the position of the new species within the Arthoniomycetes. Bayesian and ML support values are indicated. Bayesian support is presented first.

CHEMISTRY: Divaricatic acid (major), sekikaic acid (major) and alectorialic acid (minor) detected by TLC in the host thallus. Ascotal gels I_{dil} – (with blue patches in the outer epithecium), I+ deep wine red (with patches of blue in the outer epithecium; hypothecium deeper orange brown), KI+ deep blue. Asci without KI+ blue tholus structures. The orange pigment dissolves in K with purplish solution in which purple granules precipitate.

ETYMOLOGY: The name of the new taxon refers to its host species, *Physcidia wrightii*.

HABITAT AND DISTRIBUTION: The species was found on the thallus of *Physcidia wrightii* in a humid mixed montane rainforest at 1900 m elevation. *A. physcidiicola* is only known from the type collection.

NOTES: *Arthonia physcidiicola* is easily identified by the small fleck-like orange ascomata aggregated on distinctly raised galls on the thallus of *Physcidia wrightii*, the small hyaline 1-septate ascospores turning brownish with warty epispore at late maturity, tips of the paraphysoids with pale walls, and the K+ purple ascomatal pigments. *A. plectocarpoides* (S.Y.Kondr. & D.J.Galloway) Wedin & S.Y.Kondr., the only other gall-inducing *Arthonia* species known so far, differs by possessing much larger (0.5–2.0 mm in diameter) dark brown to black ascomata, the hyaline I+ blue ascomatal gel, paraphysoids with dark-caped capitate tips, the I+ red perispore, and the absence of K+ purple pigments. This species parasitizes *Pseudocyphellaria scabrosa* and is only reported from the Valdivian rainforests of southern Chile (Wedin & Kondratyuk 1997). Only two additional parasitic *Arthonia* species with characters similar to *A. physcidiicola* are described in literature: *A. pseudocyphellariae* Wedin (Wedin 1993) from *Pseudocyphellaria* in New Zealand, Australia and Chile (Juan Fernandez Islands), and *A. cinnabarinula* Müll.Arg., reported from foliicolous *Porina* and *Trichothelium* species in Costa Rica and Brazil (Grube et al. 1995). Both species share with *A. physcidiicola* the fleck-like K+ purple ascomata and hyaline, 1-septate ascospores of similar size, but differ in not being gall inducing and the different host species and distribution.

A. physcidiicola is included in the phylogeny in a clade with *A. maculiformans* and *A. didyma*, which accommodates both parasitic and lichenized taxa. *A. maculiformans* shares with *A. physcidiicola* the maculate ascomata and 1-septate ascospores, but is not gall inducing and differs further in the dark brown to black ascomata, the dark epithecium formed by the brown-walled paraphysoid tips, and the hyaline hymenium lacking an orange, K+ purple pigment. *A. physcidiicola* is placed separate from *Arthonia radiata* (Pers.) Ach., the type of *Arthonia*, on the phylogenetic tree, but the species is here included in *Arthonia* following the established concepts of the genus until the taxonomy of parasitic *Arthonia* species is better understood.

***Chiodecton sorediatum* G.Thor & Frisch, sp. nov.**

Fig. 2d–e

Mycobank [MB 805574]

C. sorediatum is distinguished from all other species of *Chiodecton* by possessing a sorediate thallus with soralia not originating from pustules.

TYPE: Uganda, Kabale District, Bwindi Impenetrable National Park, Eastern Sector, Ruhija, Kasone, on bark of *Drypetes ugandensis* in mixed montane rainforest dominated by *Olinia usambarensis*, *Podocarpus milanjanus*, *Xymalos monospora*, *Psychotria mahoni*, *Syzygium guineense* and *Tecllea nobilis* (plot 2200, T3), 01°03'01.8"S, 29°45'52.6"E, elev. 2200 m, 04 May 2011, A.Frisch 11/Ug774 (UPS holotype).

THALLUS to 10 cm in diameter, tightly attached to the substrate, smooth to minutely granular, cracked, greenish grey with sometimes a brownish tinge, not pruinose, 0.1–0.3 mm thick. PROTHALLUS indistinct to distinct, brown. MEDULLA whitish, with few calcium oxalate crystals; thallus hyphae with many crystals on the walls, 1–2 µm

in diameter. HYPOTHALLUS not developed. PHOTOBIONT trentepohlioid, in short chains or single-celled, the cells globose to ellipsoid, $5\text{--}12 \times 4\text{--}10 \mu\text{m}$. SORALIA frequent, irregularly shaped, to 0.6 mm in diameter, plane to slightly convex, whitish to whitish grey, often confluent and then almost completely covering areas of at least 1 cm in diameter, though the margins of individual soralia may still be visible by their darker colour; soredia to $25 \mu\text{m}$ in diameter, consisting of 1–3 algal cells surrounded partly by tightly adnate hyphae (2–)3 μm wide. ASCOMATA not seen. PYCNIDIA not seen.

CHEMISTRY: Roccellic acid detected by HPTLC. Thallus C–, K–, PD–, UV+ white; medulla KI+ blue.

ETYMOLOGY: The name of the new taxon refers to the sorediate thallus.

HABITAT AND DISTRIBUTION: *Chiodecton sorediatum* is a relatively common species in more open montane rainforest communities in Bwindi Impenetrable National Park at 1600–2400 m elevation. The species has been collected from a variety of tree species including *Drypetes ugandensis*, *Ficalhoa laurifolia*, *Lansonia lucida*, *Podocarpus milanjanus*, *Polyscias fulva*, *Psychotria mahonii*, *Rapaenia rhododendroides* and *Teclea nobilis* with smooth, fissured or flaky bark. *C. sorediatum* is so far only known from Bwindi Impenetrable National Park.

NOTES: The taxonomic placement of this sterile new species in *Chiodecton* is indicated by the similarities in thallus structure with other *Chiodecton* species including the brownish prothallus hyphae, and roccellic acid as the only thallus compound. The results of the phylogenetic study confirm this placement. *C. sorediatum* is included as sister taxon of *C. natalense* on the phylogenetic tree (Fig. 1), the only other *Chiodecton* species found in Bwindi. No sorediate *Chiodecton* species was reported by Thor (1990). Aptroot (in Lumbsch et al. 2011) described *C. pustulatum* Aptroot from Madagascar, which differs from *C. sorediatum* in the soralia which are formed from pustules and the distinct brown hypothallus.

SELECTED SPECIMENS EXAMINED: Uganda, Kabale District, Bwindi Impenetrable National Park, Eastern Sector, Ruhija, Katonve, on bark of *Psychotria mahonii* in open montane rainforest dominated by *Syzygium guineensis*, *Chrysophyllum albidum*, *Drypetes ugandensis*, *Ficus natalensis* and *Mimulopsis* undergrowth (plot 2100, T1), $01^{\circ}02'59.5''\text{S}$, $029^{\circ}45'35.8''\text{E}$, elev. 2120 m, 05 May 2011, A.Frisch 11/Ug775 (UPS); Kanungu District, Bwindi Impenetrable National Park, Eastern Sector, Ihihizo River, on bark of *Strombosia scheffleri* in mixed montane forest with *Leptonichia mildbraedii*, *Carapa grandiflora*, *Xymalos monospora*, *Sapium ellipticum*, *Newtonia buchananii* and *Drypetes gerrardii*, $01^{\circ}01'34.4''\text{S}$, $029^{\circ}42'24.7''\text{E}$, elev. 1970 m, 26 May 2011, A.Frisch 11/Ug447 (UPS).

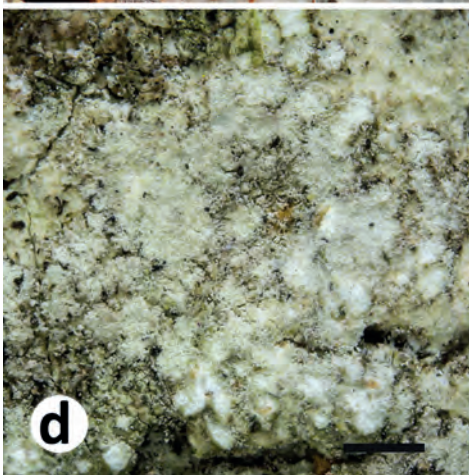
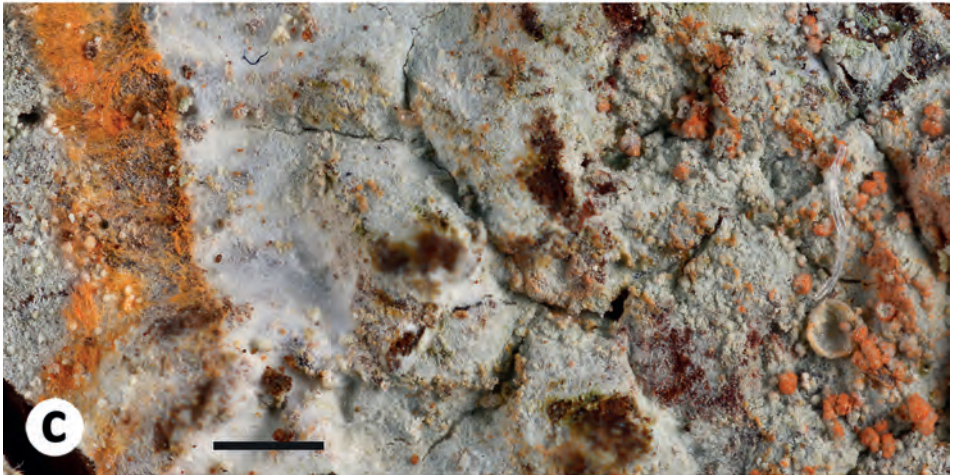
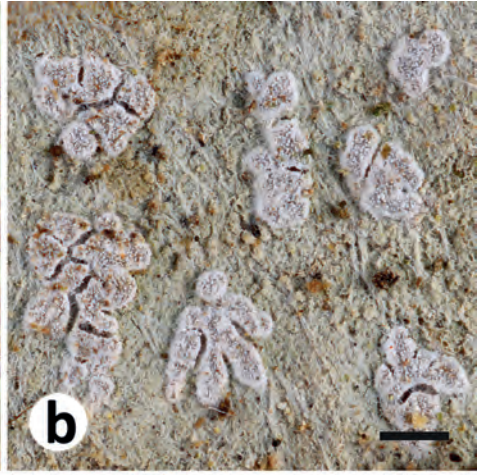
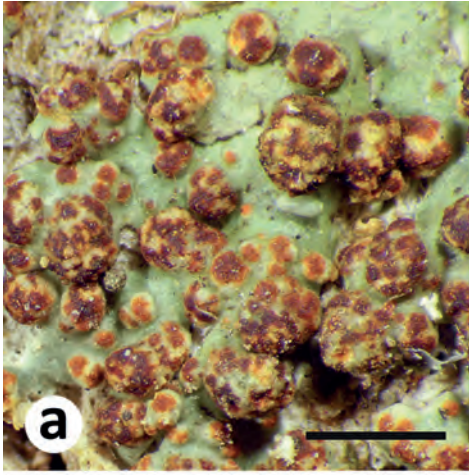
***Herpothallon kigeziense* Frisch & G.Thor, sp. nov.**

Fig. 2c

Mycobank [MB 805575]

H. kigeziense is characterized by the tightly attached thallus, the orange prothallus and orange globular to shortly clavate pseudoisidia $0.1\text{--}0.15 \times 0.1\text{--}0.2 \text{mm}$, the absence of calcium oxalate crystals, and confluent and chiodectonic acids as thallus compounds.

TYPE: Uganda, Kanungu District, Bwindi Impenetrable National Park, Western Sector, Buhoma, Pont Svamp trail, on bark of *Leptonichia mildbraedii* in dense mixed montane rainforest dominated by *Strombosia scheffleri*, *Entandrophragma cylindricum*, *Sapium ellipticum* and *Ficus capensis*, $00^{\circ}59'39''\text{S}$, $29^{\circ}37'23''\text{E}$, elev. 1580 m, 12 May 2011, A.Frisch 11/Ug26 (UPS holotype).



THALLUS corticolous, byssoid, to 8 cm in diameter, tightly attached to the substrate, ecorticate, minutely felty to subgranular in the thallus centre, pale grey-olive to almost whitish, heteromerous, up to 0.05 mm thick. PHOTOBIONT LAYER 20–50 μm thick; photobiont trentepohlioid, in short chains or single cells, the cells irregularly globular to ovoid, 8–15 \times 4–10 μm ; thallus hyphae 1.5–2.0 μm wide, densely branched and anastomosing, with numerous brownish granules attached; appressorial hyphae short, occasionally branched, slightly wavy, about 1 μm wide. MEDULLA not developed. CALCIUM OXALATE CRYSTALS absent, but hyaline crystals, 1–3(–5) μm in diameter, solving in acetone but not in K or H_2SO_4 , numerous. HYPOTHALLUS not developed. PROTHALLUS up to 1.5 mm wide, thin, byssoid, of loosely interwoven radiating hyphae, orange; hyphae c. 2 μm wide, with hyaline to pale orange walls with orange granules attached. PSEUDOISIDIA globular to shortly clavate, compact byssoid, pale to deep orange, 0.1–0.15 \times 0.1–0.2 mm. ASCI not seen. PYCNIDIA not seen.

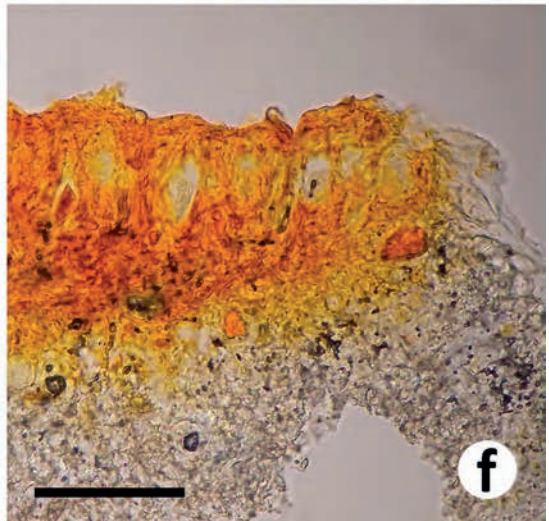
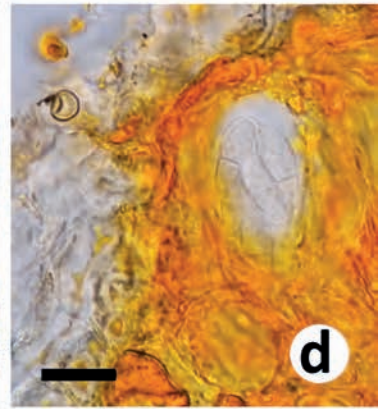
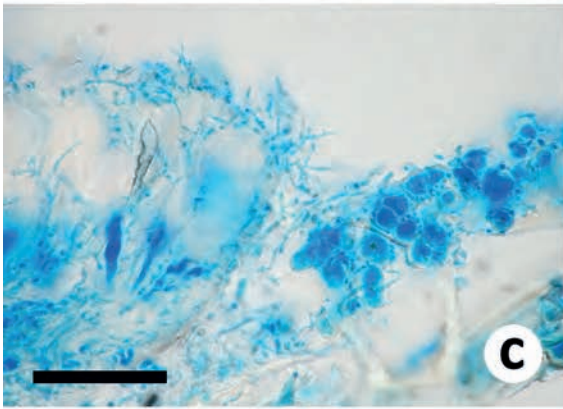
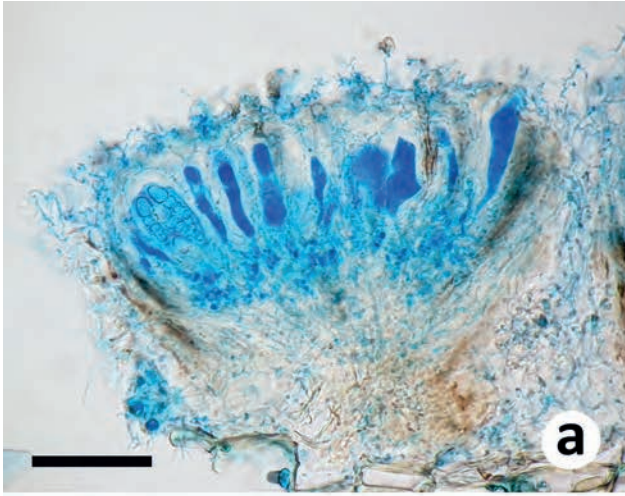
CHEMISTRY: Confluent acid (major) and chiodectonic acid (minor to trace) detected with TLC; thallus K–, C–, KC–, PD–, UV–, I–, KI–; orange pigment K+ purple.

ETYMOLOGY: The name is derived from the Kigezi Highlands of south western Uganda, where Bwindi is located.

HABITAT AND DISTRIBUTION: *Herpothallon kigeziense* is only known from Bwindi Impenetrable National Park where it is a rather common species in open montane rainforest communities at 1400 to 2330 m elevation. It has been collected from a large variety of trees including *Carapa grandiflora*, *Drypetes gerardii*, *Ficus natalensis*, *Leptonichia mildbraedii*, *Polyscias fulva*, *Psychotria mahonii*, *Sapiam ellipticum*, *Strombosia scheffleri*, *Symphonia globulifera* and *Syzygium guineensis*.

NOTES: *Herpothallon* in the broad circumscription applied by Aptroot et al. (2009) was found polyphyletic by recent molecular studies and two of its species were transferred to *Diorygma* and the new genus *Heiomasia* in Graphidaceae (Nelsen et al. 2010, 2012), while *H. albidum* (Fée) Aptroot, Lücking & G.Thor and *H. mycelioides* (Vain.) Aptroot, Lücking & G. Thor were transferred to *Crypthonia* in Arthoniaceae on account of similarities in thallus structure with the fertile species of this genus (Frisch & Thor 2010). Based on characters of its thallus as the orange byssoid prothallus of interwoven radiating hyphae, contact between mycobiont and photobiont by means of short wavy and occasionally branched appressorial hyphae, the orange byssoid pseudoisidia similar in structure to those of *H. rubrocinctum*, and a chemistry including confluent and chiodectonic acids, *H. kigeziense* is placed in a group of species similar to *H. rubrocinctum*, the type of the genus *Herpothallon*. This is confirmed here by the phylogenetic analysis where *H. kigeziense* is placed as sister taxon of *H. rubrocinctum* on the phylogenetic tree. Among the species with a thallus morphology and chemistry similar to *H. rubrocinctum*, *H. kigeziense* compares only with the neotropical *H. roseocinctum* (Fr.) Aptroot, Lücking & G.Thor (Aptroot et al. 2009), from which

Fig. 2. a. *Arthonia physcidiicola*, ascomata on host thallus (Frisch 11/Ug318 – holotype). b. *Reichlingia syncesioides*, ascomata (Frisch 11/Ug14 – holotype). c. *Herpothallon kigeziense*, thallus with prothallus and pseudoisidia (Frisch 11/Ug26 – holotype). d–e. *Chiodecton soreliatum* (Frisch 11/Ug774 – holotype). d. soralia. e. prothallus. Scale bars: a, c = 2 mm, b, d, e = 1 mm.



it is separated by the thinner, tightly attached thallus, the absence of calcium oxalate crystals and smaller pseudoisidia (0.1–0.15 × 0.1–0.2 mm vs. c.0.4 × c.0.5 mm).

SELECTED SPECIMENS EXAMINED: Uganda, Kanungu District, Bwindi Impenetrable National Park, Eastern Sector, Ihihizo, on bark of *Strombosia scheffleri* in mixed montane rainforest, 01°01'34.4"S, 029°42'24.7"E, elev. 1970 m, 26 May 2022, A.Frisch 11/Ug449 (UPS); do, Northern Sector, Byumba, on bark of indet. tree in mixed montane rainforest, 00°54'04.9"S, 029°41'59.3"E, elev. 1400 m, 18 May 2011, A.Frisch 11/Ug243 (UPS).

Reichlingia Diederich & Scheid., **emend.**, Bull. Soc. Nat. Luxemb. 97: 4 (1996).

TYPE: *Reichlingia leopoldi* Diederich & Scheid., Bull. Soc. Nat. Luxemb. 97: 5 (1996).

THALLUS (pale) greyish green, loosely or tightly attached to the substrate, compact-felty to byssoid-granular, 1–10 cm in diam. or confluent into larger colonies. PROTHALLUS whitish fibrillose, thin, replaced by a dark brown prothallus line in contact with other lichens; whitish hypothallus hyphae present or absent. PHOTOBIONT trentepohlioid, in short chains or separate. ASCOMATA (known from three species) rounded to polygonal to short lirelliform, lobed or forming irregular stellate-radiating clusters up to 0.8–1.2 mm wide, with individual hymenia separated by deep but often incomplete fissures, immersed in the thallus or adnate, pale brown to brown below a thin whitish pruina, ± felty by the projecting tips paraphysoids and excipular hyphae; a thin patchy thallus margin may be occasionally developed. PROPER EXCIPLE usually constricted towards the base, parathecial, composed of ± parallel, woven, branched and netted prosoplectenchymatic hyphae with hyaline or dark brown walls; pale granular crystals present or absent. EPITHECIUM greyish by inspersions with pale granular crystals or dark brown, composed of the largely free, densely branched and intertwined tips of the paraphysoids. HYMENIUM 55–100 µm thick, hyaline, clear or sparsely inspersed with pale granular crystals. HYPOTHECIUM hyaline or pale brownish, up to 130 µm thick, conglutinated. PARAPHYSOIDS loosely branched and netted, 1–1.5 µm wide, embedded in dense gelatinous matrix; tips widened to 1.5–2.5 µm, without or with dark brown pigment in the walls. ASCI clavate, Arthonia-type, 45–65 × 14–25 µm, 8-spored, without KI+ tholus structures. ASCOSPORES persistently hyaline or getting pale brown with granular ornamentation in the epispore at late maturity, oblong-ovoid, 3–5 transversely septate with enlarged apical cells or submuriform (5 × 0–1 septate), with ca 0.7 µm thick walls and septa and a thin epispore. HYMENIAL GELATINE I+/ KI+ deep blue or I+ pale yellowish brown/ KI+ pale blue. PYCNIDIA unknown. SPOROCHOCIA (in *R. leopoldi*) reddish to dark chocolate brown, 0.1–0.4 mm diam. or confluent into large irregular patches up to 10 cm wide. CONIDIOPHORES dark brown, with thick verrucose walls. CONIDIAGENOUS CELLS not clearly defined. CONIDIA irregularly branched with one to several branches, 17–35 µm long, constricted at the septa, with cells subspherical to ellipsoid, 4–6 × 3.5–5.5 µm large, dark brown, strongly verrucose, with a dark brown granulose pigmentation (adapted from Diederich & Scheidegger 1996 and Diederich

Fig. 3. a–c. *Reichlingia syncesioides* (Frisch 11/Ug26 – holotype). a. Section through ascoma. b. Ascus with spores. c. Margin of young ascoma and thallus. d–e. *Arthonia physcidiicola* (Frisch 11/Ug14 – holotype). d. Margin of ascoma with ascus and spores. e. Hymenium with asci and paraphysoids. f. Ascomata. Scale bars: a, c, e, f = 50 µm, b = 20 µm, d = 10 µm.

& Coppins 2009). CHEMISTRY including 2'-*O*-methylperlatolic and perlatolic acids (+ indet. xanthone in *R. virginea*).

NOTES: The genus *Reichlingia* Diederich & Scheideg. was originally described for a lichenicolous fungus parasitizing an unidentified crustose lichen with trentepohlioid photobiont (Diederich & Scheidegger 1996), but its only species was later accepted as a hypohymetous lichen with reddish to chocolate brown sporodochia-like conidiomata and byssoid thallus (Diederich & Coppins 2009). In the phylogenetic analysis (Fig. 1), two fertile species lacking conidiomata are included in the same clade as *R. leopoldi*. *R. zwackhii* and *R. syncesioides* share with *R. leopoldi* the pale grey-olive byssoid to loosely felty thallus and a chemistry of 2'-*O*-methylperlatolic acid and perlatolic acid. Based on the morphological similarities with *R. syncesioides* and a thallus chemistry including perlatolic acid, *Arthothelium virgineum* Müll.Arg., for which molecular data are not available, is here included in *Reichlingia*. Fertile species of *Reichlingia* are characterized by the adnate, pruinose and often elongated to stellate-branched ascomata with a basally constricted exciple and a thin tomentum formed by the free tips of paraphysoids and excipular hyphae, a well-developed hyaline to pale brownish hypothecium, and the oblong-ovoid, hyaline, transversely septate or submuriform ascospores that may or may not get brownish with dark brown warty ornamentation in the epispore at late maturity. In ascoma and thallus morphology, *Reichlingia* shows similarities with species of *Coniocarpon* DC., represented by *C. cinnabarinum* DC. in Fig. 1. In addition to being separated from *Reichlingia* on the phylogenetic tree, *Coniocarpon* differs in its secondary chemistry including red anthraquinones in the ascomata but lacking perlatolic and 2'-*O*-methylperlatolic acids, and ascomata which are not divided by deep fissures. None of the other genera presently included in the synonymy of *Arthonia* can be compared with *Reichlingia* as here circumscribed.

***Reichlingia syncesioides* Frisch & G.Thor, sp. nov.**

Figs 2b, 3a–c

Mycobank [MB805576]

R. syncesioides is characterized by the thin, pale grey-olive, compact-felty thallus with perlatolic acid, the white pruinose, adnate apothecia aggregated into lobed to lirelliforme to stellate clusters, and the hyaline, oblong-ovoid, 4–5-septate spores, 19–23 × 7–8 µm large, turning brown and minutely warty at late maturity.

TYPE: Uganda, Kabale District, Bwindi Impenetrable National Park, Eastern Sector, Ruhija, Nyaiguru, on bark of indet. tree in mixed montane rainforest dominated by *Xymalos monospora*, *Strombosia scheffleri* and *Entandrophragma excelsior*, 01°03'43"S, 029°47'33"E, elev. 2100 m, 08 May 2011, A.Frisch 11/Ug14 (UPS holotype).

THALLUS pale grey-olive, effuse, in section up to 0.07 mm thick, compact-felty with a minutely granular-warty surface with granules 0.05–0.08 mm in diameter, partly endophloeodal; PROTHALLUS indistinct, composed of strands of whitish fibrous hyphae or a dark brown line when in contact with other lichens. PHOTOBIONT LAYER 20–50 µm thick; photobiont trentepohlioid, in short chains or single-celled, the cells globose to ellipsoid, 5–14 × 4–10 µm; thallus hyphae hyaline, 1.5–2.0 mm wide, thinly adspersed with colourless to brownish granular crystals. MEDULLA not developed. CALCIUM OXALATE CRYSTALS absent. ASCOMATA rounded to polygonal to short lirelliform, but soon lobed or forming irregular stellate-radiating clusters up to 2 × 1 mm (exceptionally 3.5 × 2 mm), with individual hymenia separated by deep but often incomplete fissures,

developed in the outermost bark layers, soon erumpent and adnate, in section 170–220 μm thick, flat to weakly convex, densely covered by a coarse white pruina; ascomatal flanks white or with a thin and incomplete thallus margin, steep to slightly constricted at base. PROPER EXCIPIE 10–15 μm wide, composed of \pm parallel, woven, branched and netted prosoplectenchymatic hyphae with pale brown conglutinated walls. EPITHECIUM greyish, 12–25 μm thick, densely interspersed with hyaline crystals 1(–2) μm in diameter. HYMENIUM conglutinated, hyaline, 60–90 μm thick. HYPOTHECIUM hyaline to yellowish or pale brown, up to 40–100 μm thick, moderately conglutinated, composed of a loose mesh of c.1 μm wide branched and netted prosoplectenchymatic hyphae, often intermixed with empty, 1–3 μm wide, irregular, rounded to elliptical to forged cell lumina embedded in dense gelatinous matrix; pale brown pigment mainly amorphous in the gelatinous matrix. PARAPHYSOIDS forming a loose mesh of branched and netted, slightly wavy, c.1 μm wide; tips densely branched and intertwined, up to 1.5 μm wide, not pigmented, free in the apical parts to form a thin tomentum. ASCI loosely spaced, clavate to broadly clavate, Arthonia-type, 55–65 \times 20–25 μm , the lateral walls 1–2 μm thick and apically widened to 5 μm with a broadly triangular to rounded ocular chamber, 8-spored (spores in 2 irregular rows). SPORES oblong-ovoid, 19–23 \times 7–8 μm , hyaline first, becoming pale brownish with strong warty ornamentation at late maturity, 4–5-septate, not constricted at the septa, with enlarged apical cell; septation proceeding from the upper third downwards. PYCNIDIA or sporodochia not seen.

CHEMISTRY: 2'-O-methylperlatolic acid identified with HPTLC; thallus K–, C–, KC–, PD–, UV–, I–, KI–. Ascomatal gels I_{dil}–, I+ deep blue, KI+ deep blue. Asci without KI+ blue tholus structures; all parts K–.

ETYMOLOGY: The name of the new taxon refers to its superficial similarity with species of the genus *Syncesia*.

HABITAT AND DISTRIBUTION: The species was collected in rather dry mixed montane rainforest at 2100 m elevation. *Reichlingia syncesioides* is only known from the type collection.

NOTES: *R. syncesioides* is morphologically close to *R. virginea* (Usambara Mts., Tanzania (Holst 3542, G!)), see below), but that species differs in the submuriform spores (14–16 \times 6–7 μm , 5 \times 0–1-septate) and perlatolic acid plus an unidentified xanthone as thallus compounds. *Reichlingia zwackhii* (Sandst.) Frisch & G.Thor, a species from temperate regions of Europe, shares with *R. syncesioides* the transversely septate spores with enlarged apical cells and 2'-O-methylperlatolic acid (as unidentified substance 'A' in Coppins & James 1978; Coppins & Aptroot 2009), but the spores are 3–4-septate and slightly smaller (16–24 \times 5–7 μm), and the tips of the paraphysoids have dark brown pigmented walls.

Reichlingia virginea* (Müll.Arg.) Frisch, *comb. nov.

Mycobank [MB 805579]

BASIONYM: *Arthothelium virgineum* Müll.Arg., 1894, Bot. Jahrb. 20: 288 (= *Arthonia virginea* (Müll. Arg.) Stiz., 1895, Ber. Thätigk. St. Gallischen naturw. Ges. 1893–1894: 257).

NOTE: *A. virgineum* Müll.Arg. is here transferred to *Reichlingia* based on the similarities in morphology and thallus chemistry with *R. syncesioides* and *R. zwackhii*.

Reichlingia zwackhii (Sandst.) Frisch & G.Thor, **comb. nov.**

MycoBank [MB 805580]

BASIONYM: *Arthonia zwackhii* Sandst., 1903, Abh. naturw. Ver. Bremen 17: 604.

NOTE: *Arthonia zwackhii* Sandst. is here transferred to *Reichlingia* based on the results of the phylogenetic study (Fig. 1) and the similarities in morphology and thallus chemistry with other species of the genus.

Acknowledgements

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References

- KAKAIKE, H. 1973: Information theory and an extension of the maximum likelihood principle. – In: PETROV, B.N. & F. CASAKI (eds.): Second international symposium on information theory, pp. 267–281. – Acad. Kiado, Budapest.
- APTROOT, A., G. THOR, R. LÜCKING, J.A. ELIX. & J.L. CHAVES 2009: The lichen genus *Herpothallon* reinstated. – *Biblioth. Lichenol.* **99**: 19–66.
- ARUP, U., S. EKMAN, L. LINDBLOM & J.-E. MATTSSON 1993: High performance thin layer chromatography (HPTLC), an improved technique for screening lichen substances. – *Lichenologist* **25**: 61–71.
- COPPINS, B.J. & A. APTROOT 2009: *Arthonia* Ach. – In: SMITH, C.W., A. APTROOT, B.J. COPPINS, A. FLETCHER, O.L. GILBERT et al. (eds.): *The Lichens of Great Britain and Ireland*, pp. 153–171. – Brit. Lichen Soc., London.
- COPPINS, B.J. & P.W. JAMES 1978: New or interesting British lichens II. – *Lichenologist* **10**: 179–207.
- DIEDERICH, P. & B. COPPINS 2009: *Reichlingia* Diederich. & Scheid. – In: SMITH, C.W., A. APTROOT, B.J. COPPINS, A. FLETCHER, O.L. GILBERT et al. (eds.), *The Lichens of Great Britain and Ireland*, pp. 790–791. – Brit. Lichen Soc., London.
- DIEDERICH, P. & C. SCHEIDEGGER 1996: *Reichlingia leopoldii* gen. et sp. nov., a new lichenicolous hyphomycete from Central Europe. – *Bull. Soc. Nat. Luxemb.* **97**: 3–8.
- DODGE, C.W. 1959: Some lichens of tropical Africa. III. Parmeliaceae. – *Ann. Missouri Bot. Gard.* **46**: 39–193.
- DODGE, C.W. 1971: Some lichens of tropical Africa. V. Lecanoraceae to Physciaceae. – *Beih. Nova Hedwigia* **38**: 1–225.
- FRISCH, A. & G. THOR 2010: *Crypthonia*, a new genus of byssoid Arthoniaceae (lichenised Ascomycota). – *Mycol. Prog.* **9**: 281–303.
- GRUBE, M., M. MATZER. & J.HAFELLNER 1995: A preliminary account of the lichenicolous *Arthonia* species with reddish, K⁺ reactive pigments. – *Lichenologist* **27**: 25–42.
- HALL, T.A. 1999: BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucleic Acids Symp. Ser.* **41**: 95–98.

- HAMILTON, A. 1981: The quaternary history of African forests: its relevance to conservation. – Afr. J. Ecol. **19**: 1–6.
- HOLDER, M. & P.O. LEWIS 2003: Phylogeny estimation: Traditional and Bayesian approaches. – Nat. Rev. Genet. **4**: 275–284.
- HOWARD, P.C. 1991: Nature conservation in Uganda's tropical forest reserves. – IUCN Trop. Forest Progr. Gland, Switzerland.
- HUELSENBECK, J.P., F. RONQUIST, R. NIELSEN & J.P. BOLLBACK 2001: Bayesian inference of phylogeny and its impact on evolutionary biology. – Science **294**: 2310–2314.
- JOLLY, D., D. TAYLOR, R. MARCHANT, A. HAMILTON, R. BONNEFILLE et al. 1997: Vegetation dynamics in central Africa since 18,000 yr BP: pollen records from the interlacustrine highlands of Burundi, Rwanda and western Uganda. – J. Biogeogr. **24**: 492–512.
- KJER, K.M. 1995: Use of ribosomal-RNA secondary structure in phylogenetic studies to identify homologous positions – an example of alignment and data presentation from the frogs. – Mol. Phyl. Evol. **4**: 314–330.
- KROG, H. & T.D.V. SWINSCOW 1979: *Parmelia* subgen. *Hypotrachyna* in East Africa. – Norw. J. Bot. **26**: 11–43.
- KROG, H. & T.D.V. SWINSCOW 1981: *Parmelia* subgen. *Amphigymnia* (lichens) in East Africa. – Bull. Brit. Mus. Nat. Hist. (Bot.) **9**: 143–231.
- LIU, Y.J., S. WHELEN & B.D. HALL 1999: Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. – Mol. Biol. Evol. **16**: 1799–1808.
- LUMBSCH, H.T., T. AHTI, S. ALTERMANN, G. AMO DE PAZ, A. APTROOT et al. 2011: One hundred new species of lichenized fungi: a signature of undiscovered global diversity. – Phytotaxa **18**: 1–127.
- MIADLIKOWSKA, J. & F. LUTZONI 2000: Phylogenetic revision of the genus *Peltigera* (lichen-forming ascomycetes) based on morphological, chemical and large subunit nuclear ribosomal DNA data. – Int. J. Plant Sci. **161**: 925–958.
- MILLER, M.A., W. PFEIFFER & T. SCHWARTZ 2010: Creating the CIPRES Science Gateway for inference of large phylogenetic trees. – Proc. Gateway Comp. Environ. Workshop (GCE), pp. 1–8. – New Orleans, LA.
- MORRISON, M.E.S. & A.C. HAMILTON 1974: Vegetation and climate in the uplands of south-western Uganda during the later Pleistocene period: II. Forest clearance and other vegetational changes in the Rukiga Highlands during the past 8000 years. – J. Ecol. **62**: 1–31.
- MÜLLER, J. 1894: Lichenes usambarenses. – Bot. Jahrb. **20**: 238–272.
- NELSEN, M.P., R. LÜCKING, E. RIVAS PLATA & J.S. MBATCHOU 2010: *Heiomasia*, a new genus in the lichen-forming family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales) with disjunct distribution in Southeastern North America and Southeast Asia. – Bryologist **113**: 742–751.
- NELSEN, M.P., R. LÜCKING, C.J. ANDREW, E. RIVAS PLATA, J.L. CHAVES et al. 2012: Dismantling *Herpothallon*: *Herpothallon antillarum* (Arthoniomycetes: Arthoniaceae) is a member of the genus *Diorygma* (Lecanoromycetes: Graphidaceae). – Bryologist **115**: 313–321.
- NIMIS, P.L., C. SCHEIDEGGER & P.A. WOLSELEY (eds.) 2002: Monitoring with Lichens – Monitoring Lichens. – NATO Sci. Ser. IV. Earth and Environm. Sci. 7. Kluwer Acad. Publ., Dordrecht.
- ORANGE, A., P.W. JAMES & F.J. WHITE 2010: Microchemical methods for the identification of lichens, 2nd ed. — Brit. Lichen Soc. London.
- PATTENGAL, N., M. ALIPOUR, O.R.P. BININDA-EMONDS, B.M.E. MORET & A. STAMATAKIS 2009: How many bootstrap replicates are necessary? – In: BATZOGLOU, S. (ed.): RECOMB 2009. – Lect. Notes Comput. Sci. **5541**: 184–200.

- PENN, O., E. PRIVMAN, G. LANDAN, D. GRAUR & T. PUPKO 2010: An alignment confidence score capturing robustness to guide-tree uncertainty. – *Mol. Biol. Evol.* **27**: 1759–1767.
- PLUMPTRE, A.J., T.R.B. DAVENPORT, M. BEHANYANA, R. KITYO, G. EILU et al. 2007: The biodiversity of the Albertine Rift. – *Biol. Conserv.* **134**: 178–194.
- RIVAS PLATA, E., R. LÜCKING & H.T. LUMBSCH 2008: When family matters: an analysis of Thelotremataceae (lichenized Ascomycota: Ostropales) as bioindicators of ecological continuity in tropical forests. – *Biodivers. Conserv.* **17**: 1319–1351.
- RONQUIST, F. & J.P. HUELSENBECK 2003: MrBayes 3: Bayesian phylogenetic inference under mixed models. – *Bioinformatics* **19**: 1572–1574.
- STIZENBERGER, E. 1895: Supplementa ad Lichenaem africanam. II. Addenda et corrigenda ex annis 1893/94. – *Ber. Thätigk. St. Gallischen Naturw. Ges.* **1893–1894**: 215–264.
- STOCSITS, R.R., H. LETSCH, J. HERTEL, B. MISOF & P.F. STADLER 2009: Accurate and efficient reconstruction of deep phylogenies from structured RNAs. – *Nucleic Acids Res.* **37**: 6184–6193.
- SWINSCOW, T.D.V. & H. KROG 1974: *Usnea* subgen. *Eumitria* in East Africa. – *Norw. J. Bot.* **21**: 165–185.
- SWINSCOW, T.D.V. & H. KROG 1976: The *Usnea articulata* aggregate in East Africa. – *Norw. J. Bot.* **23**: 261–268.
- TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI et al. 2011: MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. – *Mol. Biol. Evol.* **28**: 2731–2739.
- TAYLOR, D. 1990: Late quaternary pollen records from two Ugandan mires: evidence for environmental changes in the Rukiga Highlands of southwest Uganda. – *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **80**: 283–300.
- THOR, G. 1990: The lichen genus *Chiodecton* and five allied genera. – *Opera Bot.* **103**: 1–92.
- TWONGYIRWE, R., J. MAJALIWA, P. EBANYAT, M. TENYWA, D. SHEIL et al. 2011: Dynamics of forest cover conversion in and around Bwindi impenetrable forest, Southwestern Uganda. – *J. Appl. Sci. Environ. Manag.* **15**: 189–195.
- TWONGYIRWE, R., D. SHEIL, J.G.M. MAJALIWA, P. EBANYAT, M.M. TENYWA et al. 2013: Variability of soil organic carbon stocks under different land uses: A study in an afro-montane landscape in southwestern Uganda. – *Geoderma* **193–194**: 282–289.
- VILGALYS, R. & M. HESTER 1990: Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. – *J. Bact.* **172**: 4238–4246.
- WEDIN, M. 1993: *Arthonia pseudocyphellariae*, a new lichenicolous fungus from the southern hemisphere. – *Lichenologist* **25**: 301–303.
- WEDIN, M. & J. HAFELLNER 1998: Lichenicolous species of *Arthonia* on Lobariaceae with notes on excluded taxa. – *Lichenologist* **30**: 59–91.
- WEDIN M. & S.Y. KONDRATYUK 1997: *Dactylospora plectocarpoides*, a gall-forming species of *Arthonia* on *Pseudocyphellaria*. – *Lichenologist* **29**: 97–102.
- ZOLLER, S., C. SCHEIDEGGER & C. SPERISEN 1999: PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. – *Lichenologist* **31**: 511–516.