The Lichenologist (2021), **53**, 81–94
doi:10.1017/S0024282920000511

CAMBRIDGE UNIVERSITY PRESS

Standard Paper

Four new *Micarea* species from the montane cloud forests of Taita Hills, Kenya

Annina Kantelinen[1], Marko-Tapio Hyvärinen[1], Paul M. Kirika[2] and Leena Myllys[1]

[1]Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland and [2]East African Herbarium, National Museums of Kenya, P.O. Box 40658, 00100 Nairobi, Kenya

Abstract

The genus *Micarea* was studied for the first time in the Taita Hills, Kenya. Based on new collections and existing data, we reconstructed a phylogeny using ITS, mtSSU and *Mcm7* regions, and generated a total of 27 new sequences. Data were analyzed using maximum likelihood and maximum parsimony methods. Based mainly on new collections, we discovered four undescribed well-supported lineages, characterized by molecular and phenotypic features. These lineages are described here as *Micarea pumila*, *M. stellaris*, *M. taitensis* and *M. versicolor*. *Micarea pumila* is characterized by a minutely granular thallus, small cream-white or pale brownish apothecia, small ascospores and the production of prasinic acid. *Micarea stellaris* has a warted-areolate thallus, cream-white apothecia usually darker at the centre, a hymenium of light grey or brownish pigment that dissolves in K, and intense crystalline granules that appear as a belt-like continuum across the lower hymenium when studied in polarized light. *Micarea taitensis* is characterized by a warted-areolate thallus and cream-white or yellowish apothecia that sometimes produce the Sedifolia-grey pigment. *Micarea versicolor* is characterized by a warted-areolate, sometimes partly granular thallus and apothecia varying from cream-white to light grey to blackish in colour. This considerable variation in the coloration of its apothecia is caused by an occasional mixture of the Sedifolia-grey pigment in the epihymenium and another purplish brown pigment in the hymenium. *Micarea stellaris*, *M. taitensis* and *M. versicolor* produce methoxymicareic acid. The main distinguishing characters are presented in a species synopsis. Three of the new species are nested in the *M. prasina* group, and the fourth one (*M. taitensis*) resolves as a basal taxon to the *M. prasina* group. The new species inhabit montane cloud forests, which have fragmented dramatically throughout the Eastern Arc Mountains in recent decades.

Key words: biodiversity hotspot, Eastern Arc Mountains, endemism, lichens, molecular phylogenetics, taxonomy

(Accepted 6 October 2020)

Introduction

The Taita Hills are part of the Eastern Arc Mountains that range from south-eastern Kenya to eastern Tanzania. The montane cloud forests of this area are known for their high degree of biodiversity and endemism, and they are recognized as one of the biodiversity hotspots of the world (Rogo & Oguge 2000; Burgess *et al.* 2006; Lange 2006; Malonza *et al.* 2010). This rich and unique ecosystem is an outcome of long isolation as well as favourable climatic conditions. The mountains rise abruptly from the surrounding plain and native vegetation effectively captures precipitation from clouds and mist developed by the relatively cool air rising from the Indian Ocean.

The forests in the Taita Hills are influenced considerably by human action and have become highly fragmented. The remaining indigenous forests are mainly found on the hilltops and continue to shrink year by year. According to Pellikka *et al.* (2009), the total area of indigenous forest diminished by 50% between 1955 and 2004. Today, the largest remaining indigenous forests are on the mountains of Mbololo (220 ha), Ngangao (124 ha) and Chawia (50 ha) (Burgess *et al.* 2006; Rogers *et al.* 2008; Pellikka *et al.* 2009). The total forest area of the Taita Hills has, however, only reduced by 2%. This is due to exotic forest plantations that have replaced large areas of the indigenous forest comprising *Acacia mearnsii*, *Cupressus lusitanica*, *Eucalyptus saligna* and *Pinus patula* stands growing side by side, or even intermixed with natural forests. Planted forests are usually less efficient in capturing moisture and more susceptible to forest fires and, therefore, may permanently change the whole ecosystem towards a drier one (Pellikka *et al.* 2009).

Following on from several historical works (e.g. Zahlbruckner 1926; Cengia Sambo 1938; Santesson 1952; Maas Geesteranus 1955; Klement 1962), a critical and comprehensive study of lichens in East Africa including Kenya was conducted by Swinscow & Krog (1988), and their work has since been continued by several authors (e.g. Farkas 1987; Farkas & Vězda 1993; Jørgensen 1994; Kalb & Vězda 1994; Frisch & Hertel 1998; Frisch 1999; Marbach 2000; Lücking & Kalb 2002; Alstrup & Aptroot 2005; Alstrup & Christensen 2006; Yeshitela 2008; Yeshitela *et al.* 2009; Rikkinen 2010; Kirika *et al.* 2012; Farkas & Flakus 2015; Bjelland *et al.* 2017; Suija *et al.* 2018). However, the genus *Micarea* Fr., with over 100 species known worldwide (International Mycological Association 2019), is largely

Author for correspondence: Annina Kantelinen (formerly Launis).
E-mail: annina.kantelinen@helsinki.fi

Cite this article: Kantelinen A, Hyvärinen M-T, Kirika PM and Myllys L (2021) Four new *Micarea* species from the montane cloud forests of Taita Hills, Kenya. *Lichenologist* **53**, 81–94. https://doi.org/10.1017/S0024282920000511

overlooked in Africa (but see Coppins 1999; Brand *et al.* 2014) and its species have not been collected in the Taita Hills until now. In Australasia, Europe and the Russian Far East, the taxonomy and systematics of the genus has recently received much scientific interest (e.g. Czarnota 2007; van den Boom *et al.* 2017; Guzow-Krzemińska *et al.* 2019; Kantvilas & Coppins 2019; Konoreva *et al.* 2019; Launis *et al.* 2019*a*, *b*).

Recent molecular phylogenies show that *Micarea* is paraphyletic (Andersen & Ekman 2005; Sérusiaux *et al.* 2010), even after the introduction of the new genera *Brianaria* S. Ekman & M. Svensson for the *M. sylvicola* group (Ekman & Svensson 2014) and *Leimonis* Harris & Lendemer for the *M. erratica* group (Harris 2009). The *M. prasina* group, which includes the type species *M. prasina* Fr., forms a monophyletic core group in the genus. The group is characterized by a 'micareoid' photobiont (a coccoid green alga with cells of 4–7.5 µm diam.), immarginate small apothecia, a hyaline hypothecium, branched paraphyses, and an ascus of the *Micarea* type, with a K/I+ blue amyloid tholus and a more lightly staining axial body often with a darkly stained lining (Hafellner 1984; Czarnota 2007; Ekman *et al.* 2008). Many species develop effuse thalli composed of goniocysts and produce Sedifolia-grey pigment (K+ violet, C+ violet), which is typically present in the epihymenium of the apothecia as well as the pycnidia (Coppins 1983; Czarnota & Guzow-Krzemińska 2010).

In this study, we explored the diversity and systematics of *Micarea* species in the Taita Hills of Kenya. We used phenotypic characters and molecular DNA sequence data from three loci (nuclear rDNA internal transcribed spacer region (ITS1-5.8S-ITS2 = ITS), mitochondrial rDNA small subunit (mtSSU) and replication licensing factor *Mcm7*). We also continued to investigate the use of crystalline granules as a character for species delimitation (Guzow-Krzemińska *et al.* 2019; Launis *et al.* 2019*a*, *b*). The focus of this study was the epiphytic and epixylic *Micarea* species in indigenous and planted forests of the two mountains, Ngangao and Vuria. This study increases our knowledge of the diversity of lichens in the Taita Hills, and also reveals the suitability of plantation forest habitats for *Micarea* species.

Material and Methods

Taxon sampling

Fresh specimens were collected on the mountains of Ngangao (*c.* 1952 m) and Vuria (2228 m) in Kenya, during an expedition in 2017. According to Pellikka *et al.* (2009), the intensity of human disturbance in the Ngangao forests is moderate, whereas it is relatively higher in Vuria, where only 1 ha of indigenous forest remains (Wilder *et al.* 1998). Type material of related *Micarea* species from the herbaria H-NYL and UPS were studied for comparison. The samples used in phylogenetic analyses are listed in Table 1 and include a total of 52 specimens of 42 taxa.

DNA extraction, polymerase chain reaction and DNA sequencing

Genomic DNA was extracted from 1–3 apothecia of specimens stored for a maximum of 1 year, using the DNeasy Blood & Tissue Kit (Qiagen, Maryland, USA) following the protocol described by Myllys *et al.* (2011). Polymerase chain reactions (PCRs) were prepared using PuReTaq Ready-To-Go PCR Beads (GE Healthcare, Chicago, Illinois, USA). Each 25 µl reaction volume contained 19 µl distilled water (dH_2O), 1 µl of each primer (10 µM), and 4 µl extracted DNA. The primers listed below were used for PCR amplification and sequencing.

For the ITS region, PCR was run under the following conditions: initial denaturation for 5 min at 95 °C followed by five cycles of 30 s at 95 °C (denaturation), 30 s at 58 °C (annealing), and 1 min at 72 °C (extension); for the remaining 40 cycles, the annealing temperature was decreased to 56 °C; the PCR program ended with a final extension for 7 min at 72 °C. The primers used were ITS1-LM (Myllys *et al.* 1999) and ITS4 (White *et al.* 1990).

For the mtSSU gene, PCR was run under the following conditions: initial denaturation for 10 min at 95 °C followed by six cycles of 1 min at 95 °C (denaturation), 1 min at 62 °C (annealing), and 1 min 45 s at 72 °C (extension); for the remaining 35 cycles, the annealing temperature was decreased to 56 °C; the PCR program ended with a final extension of 10 min at 72 °C. The primers used were mrSSU1 and mrSSU3R (Zoller *et al.* 1999).

For the *Mcm7* gene, PCR was run under two different conditions depending on the primers selected. For the first protocol, an initial denaturation for 10 min at 94 °C was followed by 38 cycles of 45 s at 94 °C (denaturation), 50 s at 55 °C (annealing), and 1 min at 72 °C (extension), with the PCR program ending with a final extension for 5 min at 72 °C. The primers used were MCM7_AL1r and MCM7_AL2f (Launis *et al.* 2019*a*). The second protocol used an initial denaturation for 10 min at 94 °C, followed by 38 cycles of 45 s at 94 °C (denaturation), 50 s at 56 °C (annealing), and 1 min at 72 °C (extension); the PCR program ended with a final extension for 5 min at 72 °C. The primers used were x.Mcm7.f (Leavitt *et al.* 2011) and Mcm7.1348R (Schmitt *et al.* 2009).

PCR products were cleaned and sequenced by Macrogen Inc. (Amsterdam, The Netherlands; www.macrogen.com).

Phylogenetic analyses

In order to examine the phylogenetic position of our study species within *Micarea* s. lat., we made a preliminary analysis of a combined mtSSU + *Mcm7* data set using *Psora decipiens* (Hedw.) Hoffm. from the family *Psoraceae* as an outgroup, based on a study by Andersen & Ekman (2005). ITS regions were too variable and could not be included in the analysis. In the phylogeny (tree not shown) our new samples fall within the *Micarea prasina* group as delimited by van den Boom *et al.* (2017), Launis & Myllys (2019), Launis *et al.* (2019*a*, *b*) and Guzow-Krzemińska *et al.* (2019), except for one specimen, *M. taitensis* sp. nov., which appears as basal to the *M. prasina* group.

The final phylogenies comprising 33 ITS, 52 mtSSU and 40 *Mcm7* sequences were first aligned separately with MUSCLE v.3.8.31 (Edgar 2004) using the European Molecular Biology Laboratory, European Bioinformatics Institute's (EMBL-EBI) freely available web server (http://www.ebi.ac.uk/Tools/msa/muscle/). Phylogenetic analyses for each gene region were performed as below for the concatenated data set. The single gene trees did not show any strongly supported conflicts according to the approach of Kauff & Lutzoni (2002) (with threshold bootstrap values ≥ 75%) and the three data sets were combined into a concatenated matrix in PhyDE® (Phylogenetic Data Editor, http://www.phyde.de/index.html). Based on our previous studies (Launis *et al.* 2019*a*, *b*) and our preliminary phylogenetic reconstruction, *Micarea peliocarpa* (Anzi) Coppins & R. Sant. was used as an outgroup. The hypervariable region at the end of the

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

Table 1. List of *Micarea* specimens used in the phylogenetic analyses with locality, voucher information and GenBank Accession numbers. New species and new sequences generated for the current study are marked in bold.

Taxon	Locality	Voucher information, sequence ID	ITS	mtSSU	*Mcm7*
M. adnata	Japan	*Andersen* 48 (BG)	AY756468	AY567751	—
M. aeruginoprasina	Portugal, Azores	*van den Boom* 51445 (LG), 3973	—	MK562024	MN105888
M. azorica	Portugal, Azores	*van den Boom* 51468 (LG), 3977	—	MK562026	MN105891
M. byssacea	Finland	*Launis* 289103 (H), A98	MG521562	MG707768	MG692527
M. czarnotae	Finland	*Launis* 1010133 (H), A455	MG521557	MG707760	MG692517
M. elachista	Finland	*Launis* 67113 (H), A340	MG521548	MG707745	—
M. endocyanea	USA, Maine	*Kantelinen* 4449 (H), A325	**MT981601**	**MT982135**	**MT981445**
M. eximia	Finland	*Kantelinen* 3785 (H), A785	**MT981600**	**MT982134**	**MT981444**
M. eximia	Finland	*Kantelinen* 3734 (H), A789	**MT981599**	**MT982133**	**MT981443**
M. fallax	Finland	*Launis* 59132 (H), A559	MK454942	MK454759	MK456617
M. fennica	Finland	*Launis* 3220 (H), A790	MK517712	MK517716	MK520931
M. fennica	Finland	*Launis* 68 (H), A117	MK517711	MK517715	MK520930
M. flavoleprosa	France	*Sérusiaux* s. n. (LG), 3841	—	MK454754	MK456613
M. flavoleprosa	Czech Republic	*Malíček* 5098 (H), A616	—	MK454756	MK456615
M. globulosella	Finland	*Launis* 67112 (H), A240	MG521546	MG707743	MG692507
M. hedlundii	Finland	*Launis* 67119 (H), A254	MG521551	MG707749	MG692512
M. herbarum	Netherlands	*P & G van den Boom* 52575 (hb. van den Boom), LG DNA 4236	—	KX459349	MG692513
M. incrassata	Finland	*Kantelinen* 90 (H), A90	**MT981598**	**MT982132**	**MT981442**
M. isidioprasina	France	*Sérusiaux* s. n. (LG), 3437	MN095788	KX459362	MN105894
M. isidioprasina	Poland	*Kukwa* 17367a & *Łubek* (UGDA)	MN095789	MK562016	MN105897
M. laeta	Finland	*Launis* 59153 (H), A825	MG521565	MG707771	MG692530
M. levicula	France, Réunion	*Sérusiaux* s. n. (LG), 3532	—	MK562019	MN105900
M. melanobola	Finland	*Launis* 27123 (H), A437	MK454946	MK454770	MK456625
M. melanobola	Finland	*Launis* 11014 (H), A424	MK454950	MK454774	MK456630
M. meridionalis	Portugal	*van den Boom* s. n. (LG), 4279	—	KX459353	MN105901
M. microareolata	Sweden	*Launis* 148131 (H), A393	MG521558	MG707762	MG692518
M. micrococca	Finland	*Launis* 299101 (H), A100	MG521552	MG707753	MG692514
M. microsorediata	Poland	*Kukwa* 17053 (UGDA)	MN095791	MK562012	MN105906
M. misella	Finland	*Launis* 108111 (H), A264	MG521545	MG707742	MG692506
M. neostipitata	USA, North Carolina	*Lendemer* 29572 (H), A347	—	**MT982136**	—
M. nowakii	Romania	*Sérusiaux* s. n. (LG), 4380	—	KX459359	MN105908
M. pauli	Poland	*Kukwa* 17544 & *Łubek* (UGDA)	MN095795	MK562010	MN105913
M. peliocarpa	USA, Maine	*Launis* 66123 (H), A324	MG521544	MG707741	MG692505
M. prasina s. str.	Finland	*Launis* 265101 (H), A92	MG521549	MG707747	MG692510
M. pseudomicrococca	Scotland	*Launis* 171141 (H), A645	MG521556	MG707758	MG692516
M. pumila	Kenya	*Kantelinen* 4630 (H, NAI), A836	—	**MT982140**	—
M. pusilla	Finland	*Launis* 1010137 (H), A460	MK454941	MK454752	MK456611
M. pusilla	Finland	*Launis* 101035 (H), A464	—	MK454753	MK456612
M. soralifera	Poland	*Kukwa* 13001 & *Łubek* (UGDA)	KT119887	KT119886	MN105917
M. stellaris	Kenya	*Kantelinen* 4625 (H, NAI), A831	—	**MT982139**	**MT981448**
M. subviridescens	Scotland	*Czarnota* 3599 (GPN)	—	EF453666	—

(*Continued*)

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

Table 1. (*Continued*)

Taxon	Locality	Voucher information, sequence ID	ITS	mtSSU	*Mcm7*
M. taitensis	Kenya	*Kantelinen* 4623 (H, NAI), A829	—	**MT982137**	**MT981446**
M. tomentosa	Finland	*Kantelinen* 2592 (H), A414	—	**MT982138**	**MT981447**
M. versicolor	Kenya	*Kantelinen* 4624 (H, NAI), A830	**MT981604**	**MT982143**	—
M. versicolor	Kenya	*Kantelinen* 4626 (H, NAI), A832	—	**MT982144**	—
M. versicolor	Kenya	*Kantelinen* 4627 (H, NAI), A833	**MT981603**	**MT982142**	—
M. versicolor	Kenya	*Kantelinen* 4647 (H, NAI), A834	**MT981602**	**MT982141**	—
M. viridileprosa	Poland	*Czarnota* 3436 (GPN)	—	EF453671	—
M. viridileprosa	Netherlands	*P. & B. van den Boom*, 50066 (hb. van den Boom), LG DNA 3493	—	KX459366	MN105918
M. xanthonica	USA	*Tønsberg* 25674 (BG)	—	AY756454	—
Micarea sp. (as *M. eximia* in GenBank)	not available	*Hermansson* 8866b (UPS)	AY756476	AY756447	—
Micarea sp. 'lineage A'	Scotland	*Launis* 171142 (H), A648	MG521571	MG707782	MG692542

mtSSU and the ambiguously aligned region at the end of the ITS2 were removed from the analyses. The concatenated data set, including 52 terminals, was subjected to maximum parsimony (MP) analysis as implemented in TNT v.1.1 (Goloboff *et al.* 2008) and to maximum likelihood (ML) analysis using RAxML 8.1.15 (Stamatakis 2014) on the CSC-IT Center for Science server (http://www.csc.fi/home). The MP analysis was performed using 'traditional search' with random addition of sequences with 100 replicates and the tree bisection reconnection (TBR) branch swapping algorithm. Ten trees were saved for each replicate and gaps were treated as missing data. Node support was estimated by bootstrapping (Felsenstein 1985) with 1000 replicates. Bootstrap values > 75% were considered significant. For the ML analysis, the combined data set was assigned to seven partitions: ITS1, 5.8S, ITS2, mtSSU, and each of three codon positions of *Mcm7*. An independent GTR + G model was used for each subset, and branch lengths were assumed to be proportional across subsets. Node support was estimated with 1000 bootstrap replicates using the rapid bootstrap algorithm. The alignments are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.vmcvdncqv).

Morphology and chemistry

Hand-cut apothecial sections and squashed thallus preparations were examined with a dissecting and compound microscope. Ascospores and other anatomical details were studied, and measurements made on material mounted in water or in 10% potassium hydroxide (K) to relax features. Measurements are given in the format of minimum and maximum values. Rare minimum or maximum measurements of ascospores are given in parentheses. Chemical spot tests were performed under a compound microscope using sodium hypochlorite (C) and K (Orange *et al.* 2010). Pigments were defined following Coppins (1983), Meyer & Printzen (2000) and Czarnota (2007). The chemistry of the samples was further studied using thin-layer chromatography (TLC) in solvent system 'C', following Culberson & Kristinsson (1970) and Orange *et al.* (2010). The crystalline granules were investigated using a compound microscope with polarization filters.

Results

The multilocus data matrix from sequences of 52 specimens included 1793 aligned nucleotide characters, with 776 positions in the mtSSU, 592 positions in the *Mcm7* gene and 425 positions in the ITS regions. Since the topologies of the ML and MP analyses did not have any strongly supported conflicts, only the tree obtained from the ML analysis is shown (Fig. 1).

The highly resolved phylogeny agrees with that already presented in earlier studies (Guzow-Krzemińska *et al.* 2016; van den Boom *et al.* 2017; Launis & Myllys 2019; Launis *et al.* 2019*a*, *b*). However, it should be noted that our new accessions of *Micarea eximia* Hedl. form a basal clade in the phylogeny after *M. incrassata* Hedl., and the *M. eximia* sequence obtained from GenBank groups instead with *M. misella* (Nyl.) Hedl. Our sequences of *M. eximia* are extracted from reliably identified specimens collected in 2015 from central Finland, and the species has been collected several times since. *Micarea eximia* is a rarely collected species and most of the specimens are from Fennoscandia and northern Scotland. The GenBank accession is most probably obtained from an undescribed species or is a sequence of *M. misella*. A North American species, *M. endocyanea* (Tuck. ex Willey) R. C. Harris, is analyzed here for the first time and is closely related to *M. elachista* (Körb.) Coppins & R. Sant. The species has a darkly pigmented hypothecium, which is a rare exception amongst its relatives.

The *Micarea prasina* group is strongly supported (97%) and a clade including *M. tomentosa* Czarnota & Coppins and *M. pusilla* Launis *et al.* appears as basal. The remaining taxa of the *M. prasina* group are divided into two clades: the first, strongly supported clade (99%) includes *M. hedlundii* Coppins, *M. xanthonica* Coppins & Tønsberg and species referred to the *M. byssacea* and *M. micrococca* complexes (see Czarnota & Guzow-Krzemińska 2010; Launis *et al.* 2019*a*); the second clade remains unsupported and consists of species from the *M. prasina* complex (see Launis *et al.* 2019*b*).

Our new material was found in four separate lineages and is supported by unique molecular and phenotypic characters. The main distinguishing morphological characters are presented in a species synopsis (Table 2). *Micarea stellaris* sp. nov., represented by one specimen in our phylogeny, is nested in the *M. micrococca*

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

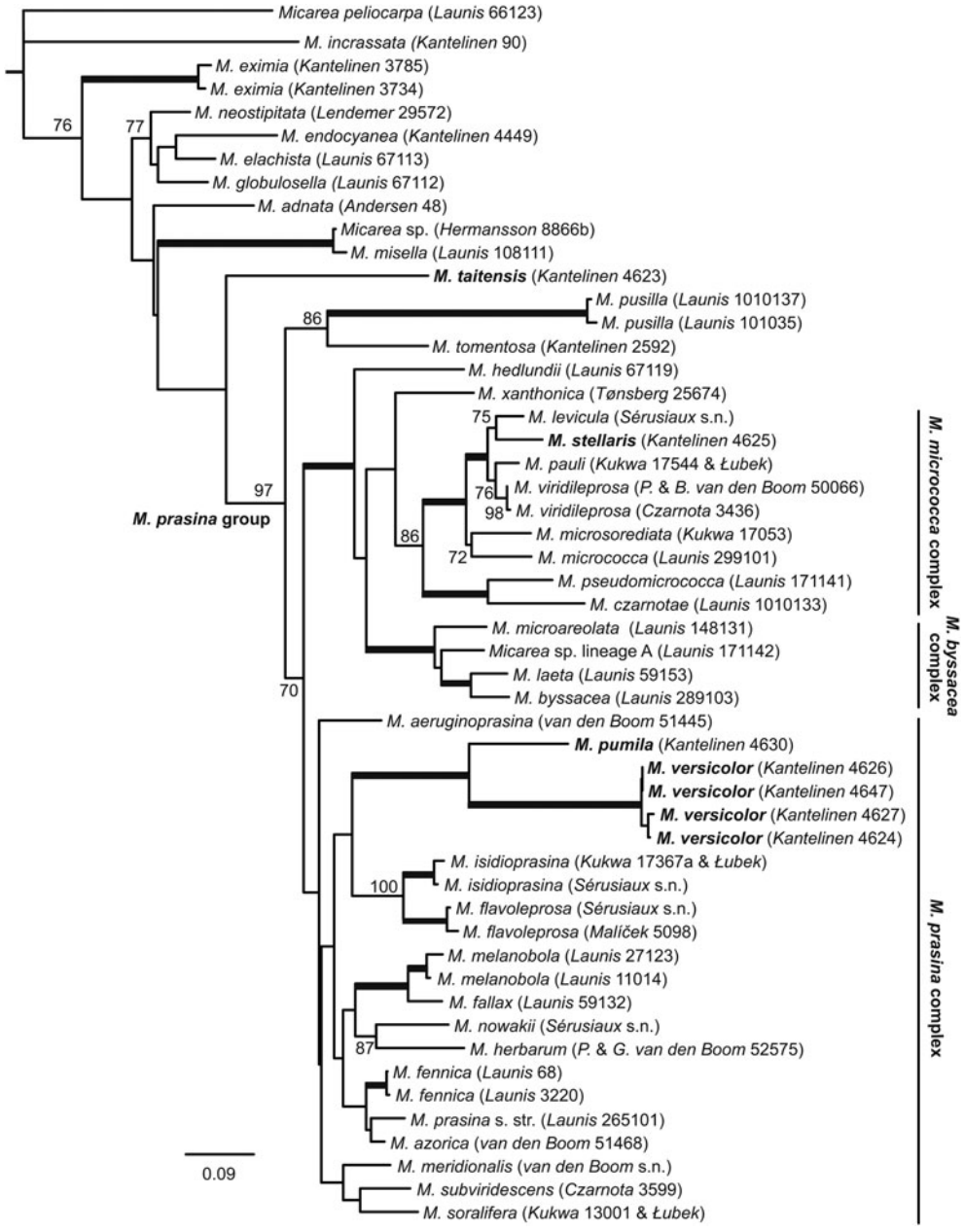

Fig. 1. Phylogenetic positions of *Micarea pumila* sp. nov., *M. stellaris* sp. nov., *M. taitensis* sp. nov. and *M. versicolor* sp. nov. (shown in bold) in a maximum likelihood phylogram obtained from the RAxML analysis (Stamatakis 2014) based on the combined ITS, mtSSU and *Mcm7* data set. Branches supported with bootstrap values ≥ 70% in both analyses (RAxML and TNT (Goloboff *et al.* 2008)) are indicated in bold. Bootstrap values ≥ 70% supported only in the maximum likelihood analysis are shown above nodes.

complex and forms a strongly supported clade with *M. levicula* (Nyl.) Coppins (a specimen collected from the island of Réunion by Brand *et al.* (2014)). *Micarea versicolor* sp. nov., including four specimens, and *M. pumila* sp. nov. with one specimen are both members of the *M. prasina* complex. The two species form a strongly supported group but are separated from each other by rather long branches and also from other members of the complex. The fourth new species discovered in our study, *M. taitensis* sp. nov., appears as a basal taxon to the *M. prasina* group.

Small crystalline granules, soluble in K, were studied in polarized light and are shown in detail in Fig. 3. The granules were detected in the hymenium of all four new species. In *M. stellaris*, the granules appear as an intense belt-like continuum across the lower hymenium. In *M. pumila*, *M. taitensis* and *M. versicolor*, the granules are scattered across the hymenium, sometimes clustered (*M. taitensis*) or occasionally not visible at all (*M. pumila*).

Discussion

Based on new collections from the Taita Hills, Kenya, we describe four species: *M. pumila* sp. nov., *M. stellaris* sp. nov., *M. taitensis* sp. nov. and *M. versicolor* sp. nov. Three of the new species are nested in the *M. prasina* group, and the fourth (*M. taitensis*) resolves as a basal taxon to this group. The phylogenetic placement of our new species is also supported by their phenotypic characters.

We continued to investigate the use of crystalline granules as a character for species delimitation (Guzow-Krzemińska *et al.* 2019; Launis *et al.* 2019*a*, *b*). The granules were found to be highly informative for the description of *M. stellaris*, in which they appear as an intense belt-like continuum across the lower hymenium. However, they were not found to be particularly useful for the delimitations of *M. pumila*, *M. taitensis* and *M. versicolor*. In those species, the granules are either occasionally absent

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

Table 2. A species synopsis representing the main distinguishing morphological characters for the new *Micarea* species and for their closest relatives or morphologically similar species.

Species	Thallus colour	Thallus structure	Apothecial pigmentation	Ascospore size (μm)	Crystalline granules	Secondary chemistry
M. fallax	vivid green or pale to dark olive green	granular, goniocysts usually aggregated or form ±thick almost continuous and cracked thallus, if less developed warted or partly membranous and ±shiny	cream-white, pale brownish, honey brown to brown, sometimes with greyish tinge, K± violet, C± violet	8–11 × (3–) 3.2–4.0	across hymenium	micareic acid
M. levicula	vivid green	goniocysts delicately coralloid	cream-white, K–, C–	10.3–10.8 × 3.7–4.1	not studied	gyrophoric acid
M. micrococca	bright green to pale olive green	minutely granular, goniocysts usually aggregated	cream-white, K–, C–	10–12 (–16) × 3–4.5	across hymenium	methoxymicareic acid
M. pumila sp. nov.	olive green to bright green	minutely granular	cream-white or pale brownish, K–, C–	7.0–10.5 × 2.5–3.2 (–3.5)	across hymenium, often weak or not visible	prasinic acid
M. stellaris sp. nov.	whitish green to bright green	warted-areolate	cream-white, usually darker at the center, hymenium with light grey or brownish pigment dissolving in K	10.0–14.0 × 3.8–5.0	intense, appearing as a belt-like continuum across lower hymenium	methoxymicareic acid
M. sublithinella	green	continuous or areolate	light brownish, dull	12.5–15.0 × 5.0– 5.8	not studied	protolichesterinic acid
M. taitensis sp. nov.	whitish green to bright green	warted-areolate or sometimes membranate	cream white or yellowish, often with a greyish tinge K± violet, C± violet	10.0–14.0 × 4.0–4.7 (–5.0), often slightly constricted at the septum	in hymenium, sometimes clustered	methoxymicareic acid
M. versicolor sp. nov.	whitish green to bright green	warted-areolate or continuous crust, sometimes partly granular and then composed of goniocysts	cream-white to light grey to dark brownish-grey or blackish, if pigmented K+ intensifying purple and K+ violet	9.5–13.0 × 3.2–4.0 (–4.5)	in hymenium and upper part of hypothecium	methoxymicareic acid

(*M. pumila*) or simply scattered across the hymenium, sometimes clustered (*M. taitensis*). The chemical composition of the crystalline granules remains unclear.

Half (50%) of the indigenous forests of the Taita Hills were replaced with exotic tree plantations between 1955 and 2004 (Pellikka *et al.* 2009), and it is estimated that the natural forest coverage in the region has diminished by up to 90% within the last 200 years (Rodgers 1993). Therefore, it is important to understand how well epiphytic lichen diversity could survive in the exotic forest plantations. Concerning *Micarea*, examples of such translocations between natural and planted forests have already been observed in the Azores and Réunion (Purvis & James 1993; Brand *et al.* 2014). In Tasmania, however, *Micarea* species were found to be sensitive to ecological change, such as logging, silvicultural treatments and fire. Interestingly, the Tasmanian examples vividly demonstrate how species in this genus are adapted to a wide range of ecological niches: almost all the species of *Micarea* from unlogged forest were replaced by other *Micarea* species that proliferated in just 3–5 years after the logging (Jarman & Kantvilas 2001*a*, *b*; Kantvilas & Jarman 2006; Kantvilas *et al.* 2015).

Our results from Ngangao and Vuria show that at least some *Micarea* species have found favourable habitats in the *Pinus patula* plantations. In these locations, the species were encountered frequently, especially on dead wood. This result is not particularly surprising, since the *Pinus* plantations are quite similar to the environments epiphytic *Micarea* species inhabit elsewhere in the world, that is habitats with medium to high precipitation and substrata of low pH such as bark and wood of coniferous trees (e.g. Coppins 1983; Czarnota 2007). *Micarea* is also recognized as one of the major lichen groups on dead wood in North America and Fennoscandia (Spribille *et al.* 2008), which is in line with our discoveries from the Taita Hills.

Since the majority of our collections are from *Pinus* plantations, the question arises: are the new species in fact native or unintentionally transported together with the exotic central American tree species? Unfortunately, we cannot answer this question conclusively. However, a native origin is suggested for the following reasons: 1) *Micarea stellaris* and *M. taitensis* appear to share close relationships with two species collected from Réunion, an island in the Indian Ocean east of Madagascar; 2) three specimens of *M. versicolor* were indeed collected from indigenous forests that had low human disturbance; 3) our survey effort was limited by time and resources, which particularly impacted the exploration of the indigenous forests. In these localities, finding the specific tree species with favourable pH and bark structure among the rich tropical biodiversity was challenging. Hence, it is possible that we just did not find the suitable tree species and that they do exist and host the source populations for the *Micarea* species found in the *Pinus* plantations.

Based on this study, and that of Brand *et al.* (2014), the diversity of the genus *Micarea* in eastern Africa and the islands in the Indian Ocean is rich, though understudied. Broader phylogeographical investigations are needed to understand the distribution, endemism and speciation of the group in this unique geographical region.

The Species

Micarea pumila Kantelinen & Myllys sp. nov.

MycoBank No.: MB 836919

Thallus olive green to bright green, minutely granular; apothecia numerous, cream-white or pale brownish, 0.2–0.4 mm diam., plane, convex or hemispherical, simple or tuberculate, K− and C−; ascospores oblong-ellipsoid or obovoid, 0–1-septate, 7.0–10.5 × 2.5–3.2(–3.5) µm; prasinic acid.

Type: Kenya, Taita Taveta, Taita Hills, Ngangao forest, near top of the mountain, *Pinus patula* plantation, on wood of dead standing *Pinus patula* (*c.* 180 cm tall), 3.355015°S, 38.338873°E, 1868 m a.s.l., 23 November 2017, *Annina Kantelinen* 4630 (H—holotype; NAI—isotype). GenBank Accession number: MT982140 (mtSSU).

(Fig. 2A & B)

Thallus effuse, olive green to bright green, minutely granular, composed of goniocysts, 12–30 µm diam., usually coalescing to form larger granules; *photobiont* micareoid, algal cells 4.5–7.5 µm diam.

Apothecia numerous, cream-white or pale brownish, 0.2–0.4 mm diam., plane, convex or hemispherical, simple or sometimes tuberculate, K− and C−; *hypothecium* hyaline; *hymenium* hyaline, *c.* 40–52 µm high; *epihymenium* hyaline; *paraphyses* numerous, 1.2–2.0 µm wide with apices not wider or increasing up to 2.7 µm, mostly branched, sometimes branched 1–2 times from the apices resulting in a fork-like appearance; *asci* clavate, *Micarea*-type, 8-spored, 25–35 × 8–10 µm; *ascospores* oblong-ellipsoid or obovoid, 0–1-septate, 7.0–10.5 × 2.5–3.2(–3.5) µm.

Pycnidia of one type; mesopycnidia, sessile or immersed within goniocysts, whitish, K− and C−, globose or barrel-shaped, up to 90 µm wide; *mesoconidia* cylindrical or cylindrical-fusiform, 4.0–5.2 × 1.0–1.5 µm.

Crystals (studied in polarized light) spread across the hymenium, often rather weakly polarizing, or not visible at all. Soluble in K (Fig. 3A).

Chemistry. Prasinic acid.

Etymology. 'Pumila' (Latin) meaning small/dwarf, referring to the small size and inconspicuous appearance of the species.

Habitat and distribution. *Micarea pumila* is known from a *Pinus patula* plantation near the top of Ngangao Mountain. The species was collected from two trunks of fallen decaying *Pinus patula* (Fig. 4C & D).

Notes. *Micarea pumila* is characterized by a minutely granular thallus, small cream-white or pale brownish apothecia and small ascospores. It resembles species in the *M. prasina* complex, especially *M. fallax* Launis & Myllys and *M. prasinastra* Coppins & Kantvilas. The small whitish apothecia are also similar to *M. micrococca* and *M. pseudomicrococca*. The main morphological characters separating *M. pumila* from the other species are the smaller ascospore size and wider paraphyses, with the exception of *M. prasinastra* which has a similar ascospore size but the thallus contains gyrophoric acid. In addition, the geographical distribution of these species is not known to overlap.

In the phylogenetic analysis, *M. pumila* is nested within the *M. prasina* complex. The species forms a well-supported group with another new species from the Taita Hills, *M. versicolor*. The close relationship probably reflects a geographical and evolutionary isolation that these two species have encountered in the mountains. However, *M. pumila* and *M. versicolor* are

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

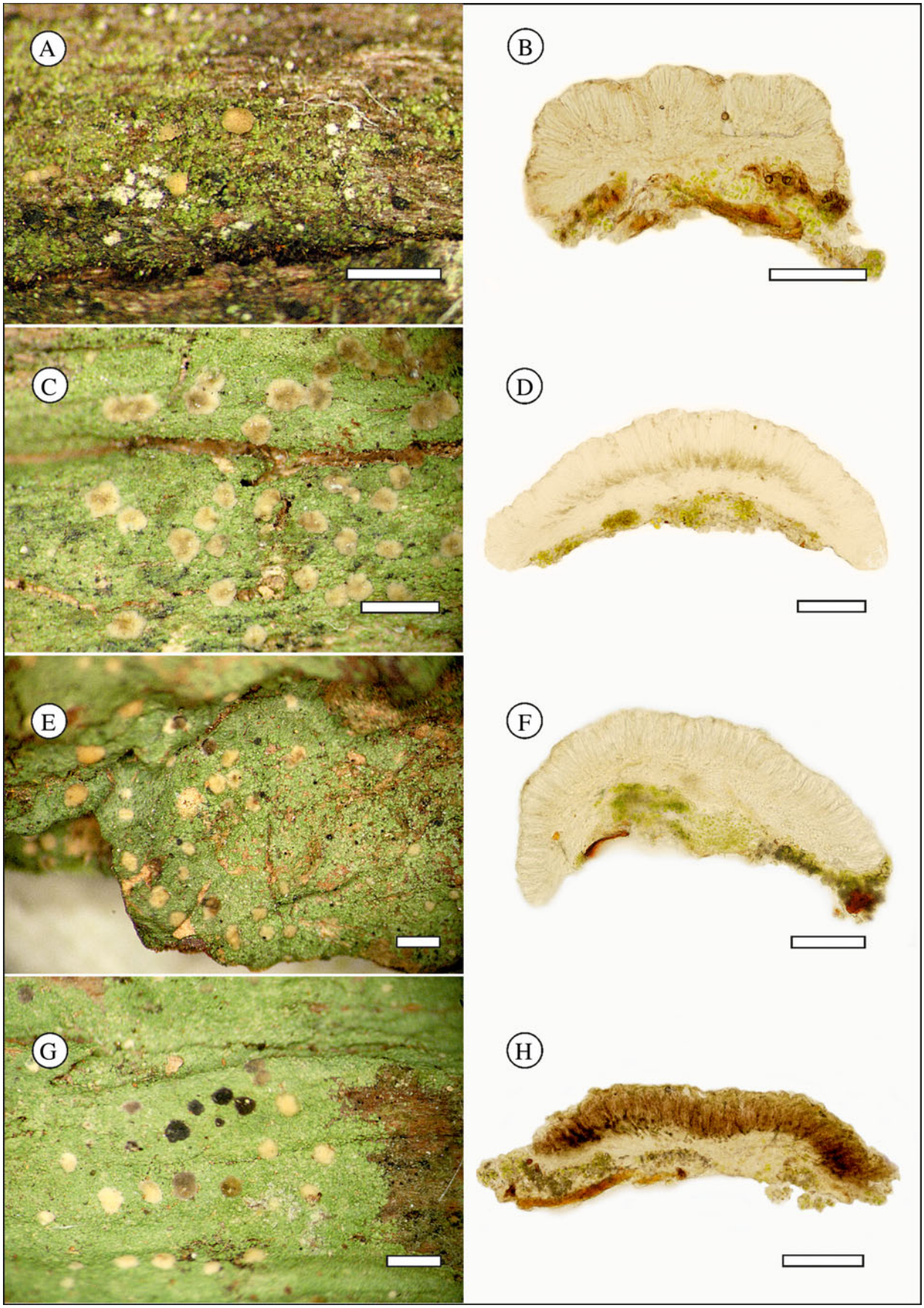

Fig. 2. Morphological and anatomical features. *Micarea pumila* (*Kantelinen* 4630, holotype, H): A, habit; B, apothecial section. *Micarea stellaris* (*Kantelinen* 4625, holotype, H): C, habit; D, apothecial section. *Micarea taitensis* (*Kantelinen* 4623, holotype, H): E, habit; F, apothecial section. *Micarea versicolor* (*Kantelinen* 4626, holotype, H): G, habit; H, apothecial section. Scales: A, C, E & G = 1 mm; B, D, F & H = 100 μm.

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

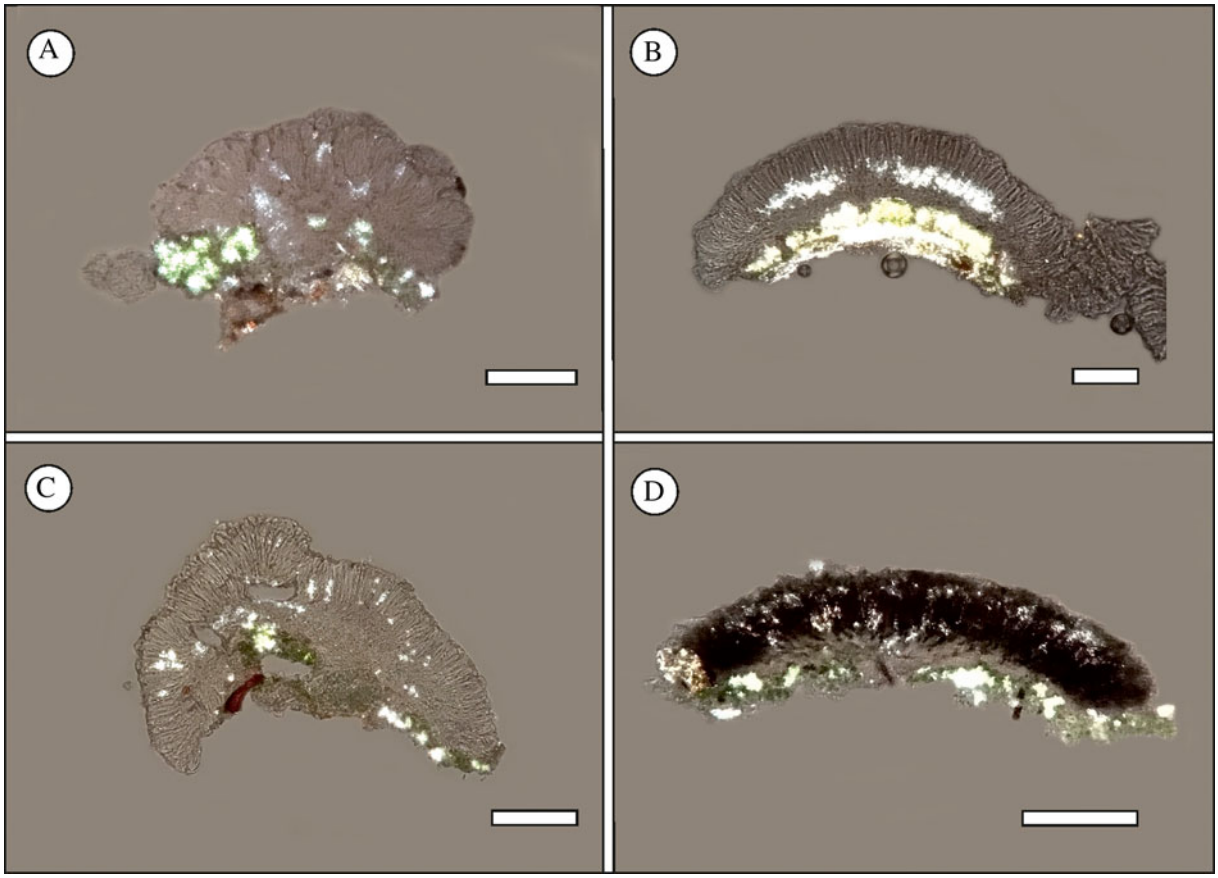

Fig. 3. Crystalline granules detected in apothecial sections in polarized light. A, *Micarea pumila* (*Kantelinen* 4630, holotype, H). B, *Micarea stellaris* (*Kantelinen* 4625, holotype, H). C, *Micarea taitensis* (*Kantelinen* 4623, holotype, H). D, *Micarea versicolor* (*Kantelinen* 4626, holotype, H). Scales = 100 µm. In colour online.

morphologically quite distinct. They can be separated by the structure of the thalli (minutely granular vs warted-areolate, respectively), size and pigmentation of the apothecia (bigger and K+ violet when pigmented in *M. versicolor*), ascospore size (7.0–10.5 × 2.5–3.2(–3.5) µm vs 9.5–13.0 × 3.2–4.0 µm, respectively) and secondary metabolites (prasinic acid vs methoxymicareic acid).

Additional specimen examined. **Kenya:** *Taita Taveta*: Taita Hills, Ngangao forest, west side, near top of the mountain, *Pinus* plantation, by a forest path, on wood of fallen decaying *Pinus patula* trunk, 3.366105°S, 38.341582°E, 1850 m a.s.l., 2017, *Annina Kantelinen* 4632 (H, NAI).

Micarea stellaris Kantelinen & Myllys sp. nov.

MycoBank No.: MB 836920

Thallus whitish green to bright green, warted-areolate; apothecia numerous, cream-white, usually darker at the centre, 0.3–0.5 (–0.6) mm diam., adnate, convex, simple; hymenium light grey or brownish, pigment dissolving in K; crystalline granules intense, appearing as a belt-like continuum across lower hymenium; ascospores, oblong-ellipsoid or obovoid, 0–1-septate, 10.0–14.0 × 3.8–5.0 µm; methoxymicareic acid.

Type: Kenya, Taita Taveta, Taita Hills, Ngangao forest, east side, near road, by a path in the indigenous forest, on wood of decaying fallen tree trunk, 3.370467°S, 38.340808°E, 1808 m a.s.l., 24 November 2017, *Annina Kantelinen* 4625 (H—holotype; NAI—isotype). GenBank Accession numbers: MT981448 (*Mcm7*), MT982139 (mtSSU).

(Fig. 2C & D)

Thallus effuse, whitish green to bright green, warted-areolate; *photobiont* micareoid, algal cells 4.5–7.5 µm diam.

Apothecia numerous, cream-white, usually darker at the centre, 0.3–0.5(–0.6)mm diam., adnate, convex, simple; *hypothecium* hyaline or slightly pigmented near hymenium; *hymenium* light grey or brownish, pigment K− and dissolving (possibly Elachista-brown pigment), 50–60 µm high; *epihymenium* hyaline; *paraphyses* numerous, mostly branched, 0.8–1.2 (–1.5) µm wide, sometimes slightly wider at the apices; *asci* clavate, *Micarea*-type, 8-spored, 42–50 × 10–13 µm; *ascospores* oblong-ellipsoid or obovoid, 0–1-septate, 10.0–14.0 × 3.8–5.0 µm.

Pycnidia of one type; micropycnidia immersed in thallus, small and inconspicuous, whitish, K− and C−, globose, up to 80 µm wide; *microconidia* filiform to narrowly fusiform, straight or slightly curved, 6.5–8.0 × 0.8–1.0 µm.

Crystals (studied in polarized light) intense, appearing as a belt-like continuum across lower hymenium. Soluble in K (Fig. 3B).

Chemistry. Methoxymicareic acid.

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

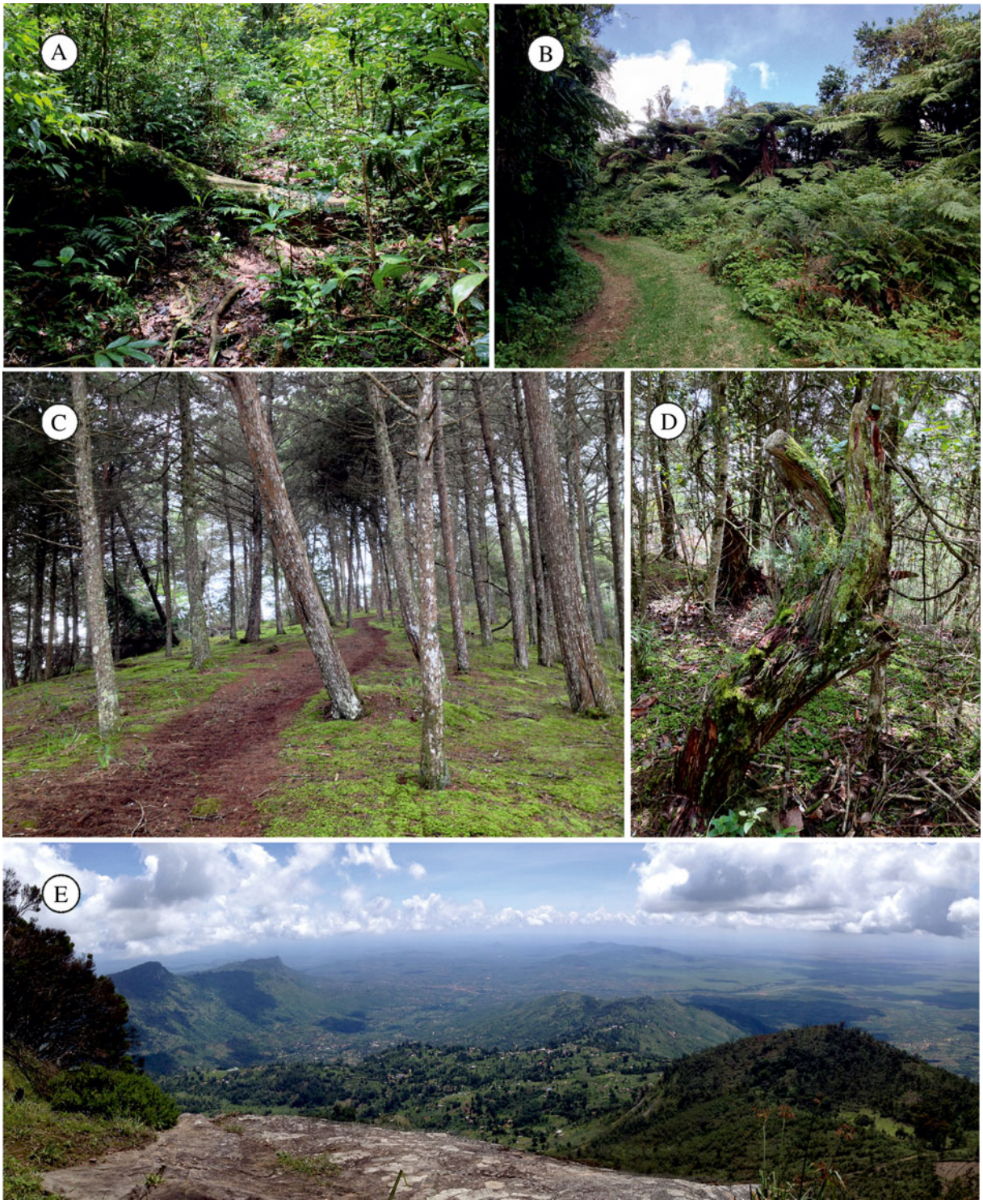

Fig. 4. Habitats. A, indigenous forest on Ngangao Mountain. B, indigenous forest on Vuria Mountain. C, *Pinus patula* plantation near top of Ngangao. D, collection site of *M. pumila* in the *Pinus patula* plantation. E, landscape seen from the top of Vuria (2228 m a.s.l.). In colour online.

Etymology. 'Stellaris' (Latin) meaning star, referring to the intensely shining crystalline granules.

Habitat and distribution. *Micarea stellaris* is known from two localities on Ngangao Mountain: an indigenous forest (Fig. 4A) and a *Pinus patula* plantation (Fig. 4C). In both localities the new species grew on wood of dead fallen tree trunks (*Pinus patula* and an unidentified, likely native tree species).

Notes. *Micarea stellaris* is characterized by a warted-areolate thallus, light grey or brownish (K−) pigment in the hymenium, and intensely polarizing crystals appearing as a belt-like continuum across the lower hymenium. It resembles *Micarea taitensis* and

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

M. versicolor but differs in the production of hymenial pigmentation and the intense crystals. Based on our phylogenetic analysis, the three species are not particularly closely related (Fig. 1).

In the phylogenetic analysis, *M. stellaris* resolves as a sister to *Micarea levicula,* and is nested within the *M. micrococca* complex. The specimen of *M. levicula* in our analysis was originally collected from a natural stand of *Acacia heterophylla* on the island of Réunion by Brand *et al.* (2014). However, we also collected a specimen of *M. levicula* from the Taita Hills, Vuria, and it is new to Kenya (specimen *Annina Kantelinen* 4648 & *Marko Hyvärinen*, see below for details). The two species resemble each other in many respects, such as the similar ecological preferences, and the shape and size of the apothecia. The main morphological features separating them are the structure of the thallus, ascospore size, pigmentation in the apothecia and secondary metabolites. *Micarea levicula* forms a thallus of delicately coralloid goniocysts which is distinctly different to the warted-areolate thallus of *M. stellaris*. The apothecia of *M. levicula* are non-pigmented throughout, the ascospores are thinner (3.7–4.1 µm vs 3.8–5.0 µm wide in *M. stellaris*) and it produces gyrophoric acid instead of methoxymicareic acid.

Selected specimens examined. **Kenya:** *Taita Taveta*: Taita Hills, Ngangao forest, west side, near Ngangao Forest Camp and by a forest path, indigenous forest, on wood of decaying fallen tree trunk, 3.370565°S, 38.346693°E, 1834 m a.s.l., 2017, *Annina Kantelinen* 4633 (H); *ibid*., near top of the mountain, indigenous forest, by a forest path, on wood of a small fallen decaying tree trunk, 3.368355°S, 38.343012°E, 1844 m a.s.l., 2017, *Annina Kantelinen* 4634 (H, NAI).

Micarea levicula *specimen examined.* **Kenya:** *Taita Taveta*: Taita Hills, Vuria, NE slope of the mountain, indigenous forest, near road to the hilltop, on wood of a decaying stump *c*. 1 m tall, in shade, together with *M. versicolor*, 3.39969444°S, 38.36472222°E, 2040 m a.s.l., 2017, *Annina Kantelinen* 4648 & *Marko Hyvärinen* (H).

Micarea taitensis Kantelinen & Myllys sp. nov.

MycoBank No.: MB 836921

Thallus whitish green to bright green, warted-areolate or sometimes membranate; apothecia numerous, cream-white or yellowish, often with a greyish tinge because of the Sedifolia-grey pigment (K± violet and C± violet), 0.4–0.6 mm diam., adnate, convex, simple; ascospores oblong-ellipsoid or obovoid, (0–)1(–2)-septate, when 1-septate often slightly constricted at the septum, 10.0–14.0 × 4.0–4.7(–5.0) µm; methoxymicareic acid.

Type: Kenya, Taita Taveta, Taita Hills, Ngangao forest, *Pinus* plantation near top of the mountain, on bark of fallen decaying *Pinus patula* trunk, 3.368355°S, 38.343012°E, 1850 m a.s.l., 24 November 2017, *Annina Kantelinen* 4623 (H—holotype; NAI—isotype). GenBank Accession numbers: MT981446 (*Mcm7*), MT982137 (mtSSU).

(Fig. 2E & F)

Thallus effuse, whitish green to bright green, warted-areolate or sometimes membranate, bright green especially in parts distinctly warted; *photobiont* micareoid, algal cells 4.5–7.5 µm diam.

Apothecia numerous, cream-white or yellowish, often with a greyish tinge because of the Sedifolia-grey pigment (K± violet and C± violet), 0.4–0.6 mm diam., adnate, convex, simple; *hypothecium* hyaline; *hymenium* hyaline, *c*. 45–60 µm high; *epihymenium* hyaline; *paraphyses* numerous, branched or straight, 0.8–1.2 µm wide, apices not widening; *asci* clavate, *Micarea*-type, 8-spored, 30–48 × 13–17 µm; *ascospores* oblong-ellipsoid or obovoid, (0–)1(–2)-septate, when 1-septate often slightly constricted at the septum, 10.0–14.0 × 4.0–4.7(–5.0) µm.

Pycnidia of one type; micropycnidia immersed in thallus, small and inconspicuous, whitish, K− and C−, globose, up to 80 µm wide; *microconidia* filiform to narrowly fusiform, straight or slightly curved, 6.5–8.0 × 0.8–1.0 µm.

Crystals (studied in polarized light) visible in hymenium, sometimes clustered. Soluble in K (Fig. 3C).

Chemistry. Methoxymicareic acid.

Etymology. The name *M. taitensis* refers to the type locality, the Taita Hills.

Habitat and distribution. Micarea taitensis was found on the bark of *Pinus patula* from Ngangao Mountain. The type locality is a mature *Pinus patula* plantation near the top of the mountain, and it is so far known only from that locality (Fig. 4C).

Notes. Micarea taitensis is characterized by a warted-areolate thallus and pale cream or yellowish apothecia that sometimes produce the Sedifolia-grey pigment. Macroscopically it resembles *Micarea stellaris* and *M. versicolor*, two other new species from the Taita Hills. However, the species differ in their microscopic features. *Micarea stellaris* produces a light grey or brownish pigment in the hymenium, and in polarized light it exhibits intense crystalline granules that appear as a belt-like continuum across the lower hymenium. *Micarea versicolor*, on the other hand, develops apothecia varying in colour from cream-white to blackish, and it has slightly thinner ascospores (3.2–4.0 µm vs 4.0–4.7 µm in *M. taitensis*). The phylogenetic relationship of these species is not particularly close, but instead *M. taitensis* resolves as a basal lineage to the *M. prasina* group (Fig. 1).

Micarea taitensis is possibly closely related to *M. sublithinella*, a species known from Madagascar and Réunion (Brand *et al.* 2014). These two species share morphological and ecological similarities. Both develop a warted thallus and grow in montane forests on acidic bark (*Acacia heterophylla* and *Pinus patula*). However, *M. taitensis* develops paler apothecia and thinner ascospores (4.0–4.7 µm vs 5.0–5.8 µm), and produces methoxymicareic acid, whereas *M. sublithinella* produces protolichesterinic acid. So far, their distribution is not known to overlap.

Micarea versicolor Kantelinen, Hyvärinen & Myllys sp. nov.

MycoBank No.: MB 836922

Thallus whitish green to bright green, warted-areolate or continuous crust, sometimes partly granular and then composed of goniocysts; apothecia numerous, cream-white to light grey to dark brownish grey or almost black (Sedifolia-grey and a purplish brown pigment), K+ intensifying purple and K+ violet if pigmented, 0.3–0.6 mm diam., adnate, convex to slightly hemispherical, simple; ascospores oblong-ellipsoid or obovoid, 0–1-septate, 9.5–13.0 × 3.2–4.0(–4.5) µm; methoxymicareic acid.

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

Type: Kenya, Taita Taveta, Taita Hills, Ngangao forest, west side, near Ngangao Forest Camp and by a forest path, indigenous forest, on wood of decaying fallen tree trunk, 3.370565°S, 38.346693°E, 1834 m a.s.l., 24 November 2017, *Annina Kantelinen* 4626 (H—holotype; NAI—isotype). GenBank Accession number: MT982144 (mtSSU).

(Fig. 2G & H)

Thallus effuse, whitish green to bright green, quite thin, warted-areolate or continuous crust, sometimes partly granular and then composed of goniocysts of 18–40 µm diam; *photobiont* micareoid, algal cells 4.5–7.5 µm diam.

Apothecia numerous, cream-white or light grey to dark brownish grey to almost black (Sedifolia-grey and a purplish brown pigment), K+ intensifying purple and K+ violet when pigmented, 0.3–0.6 mm diam., adnate, convex to slightly hemispherical, simple; *hypothecium* hyaline; *hymenium* hyaline or purplish brown, K+ purple intensifying when pigmented, *c.* 42–50 µm high. *Epihymenium* hyaline to purplish brown or greenish grey, K+ violet; *paraphyses* numerous, branched, 1.2–2.0 µm wide, sometimes slightly wider from the apices; *asci* clavate, *Micarea*-type, 8-spored, 32–45 × 10–17 µm; *ascospores* oblong-ellipsoid or obovoid, 0–1-septate, 9.5–13.0 × 3.2–4.0(–4.5) µm.

Pycnidia of one type; micropycnidia numerous, sessile or immersed in thallus, cream-white, K− and C−, globose or barrel-like, sometimes with gaping ostiole, up to 100 µm wide; *microconidia* filiform to narrowly fusiform, straight or slightly curved, 7.0–9.0 × 0.8–1.0 µm.

Crystals (studied in polarized light) visible in hymenium and upper part of hypothecium. Soluble in K (Fig. 3D).

Chemistry. Methoxymicareic acid.

Etymology. The epithet *versicolor* refers to the coloration of the apothecia that vary considerably from cream-white to pale grey and to almost black.

Habitat and distribution. *Micarea versicolor* is known from four localities: two are in the indigenous forest on Ngangao Mountain, the third in a *Pinus patula* plantation near the top of Ngangao and the fourth in a small patch of indigenous forest on Vuria Mountain (Fig. 4B). In all localities the species grew on dead wood of fallen or standing tree species (*Pinus patula* and unidentified native trees).

Notes. *Micarea versicolor* is characterized by the warted-areolate, sometimes partly granular thallus and apothecia that vary in colour from cream-white to light grey to blackish. This considerable variation in the coloration of the apothecia is probably caused by a mixture of pigments that can occur independently of one another: 1) Sedifolia-grey pigment in the epihymenium (K+ violet, C+ violet), which is a common pigment in the *M. prasina* group and produced especially in response to sunlight; 2) a purplish brown pigment in the hymenium (K+ intensifying purple) that may either be the same as that known from the hypothecium of *M. melaena*, or an unknown pigment somewhat similar to that found in the hymenium of *Bacidia schweinitzii* s. str. (a species also known for having high variation in the coloration of its apothecia; see Ekman (1996) and Lendemer *et al.* (2016)). This mixture of pigments causes the apothecia of *M. versicolor* to appear as cream-white (no pigments), greyish (Sedifolia-grey pigment only), or dark brownish grey to blackish (purplish brown pigment + Sedifolia-grey pigment).

Macroscopically *M. versicolor* resembles two other new species from the Taita Hills, *M. stellaris* and *M. taitensis*. These species can be separated by microscopic features that include the pigmentation of the apothecia and hymenium, crystalline granules in polarized light and ascospore width (see more details under *M. taitensis*).

Based on our phylogenetic analysis, *M. versicolor* is not closely related to *M. stellaris* or *M. taitensis*. Instead it is sister to *M. pumila* and nested within the *M. prasina* complex, although with low support in the latter. Morphologically the sister species *M. versicolor* and *M. pumila* are quite distinct: *M. pumila* develops a minutely granular thallus composed of goniocysts, has smaller unpigmented apothecia (K− and C−) and smaller ascospores (7.0–10.5 × 2.5–3.2(–3.5) µm vs 9.5–13.0 × 3.2–4.0(–4.5) µm). They also produce different secondary metabolites: *M. versicolor* produces methoxymicareic acid, whereas *M. pumila* produces prasinic acid.

Selected specimens examined. **Kenya:** *Taita Taveta*: Taita Hills, Ngangao forest, west side, near top of the mountain, *Pinus* plantation, by a forest path, on wood of fallen decaying *Pinus patula* trunk, 3.366105°S, 38.341582°E, 1850 m a.s.l., 2017, *Annina Kantelinen* 4624 (H, NAI); *ibid.*, indigenous forest, by a forest path, on wood of a small fallen decaying tree truck, 3.368355°S, 38.343012°E, 1844 m a.s.l., 2017, *Annina Kantelinen* 4627 (H, NAI); *ibid.*, Vuria, NE slope of the mountain, indigenous forest, near road to the hilltop, on wood of a decaying stump *c.* 1 m tall, in shade, 3.39969444°S, 38.36472222°E, 2040 m a.s.l., 2017, *Annina Kantelinen* 4647 & *Marko Hyvärinen* (H, NAI).

Acknowledgements. Financial support for this study was provided by the Societas pro Fauna et Flora Fennica, the University of Helsinki LUOVA travel grants for doctoral candidates (personal grants for AK), and the Academy of Finland (Grant 323711). We thank the two anonymous reviewers for improving the manuscript. We would also like to acknowledge the organizers and participants of the expedition to the Taita Hills in 2017, namely Prof. Leif Schulman, head gardener Pertti Pehkonen and doctoral candidate Anton Savchenko. We also thank the Taita Research Station (University of Helsinki) for providing access to facilities and logistics during the stay. The staff and local people are warmly thanked for their helpfulness and hospitality.

Author ORCIDs. Annina Kantelinen, 0000-0001-8664-7662; Leena Myllys, 0000-0002-9566-9473.

References

Alstrup V and Aptroot A (2005) Pyrenocarpous lichens from Tanzania and Kenya. *Cryptogamie, Mycologie* **26**, 265–271.

Alstrup V and Christensen SN (2006) New records of lichens with cyanobacteria from Tanzania and Kenya. *Cryptogamie, Mycologie* **27**, 57–68.

Andersen HL and Ekman S (2005) Disintegration of the *Micareaceae* (lichenized Ascomycota): a molecular phylogeny based on mitochondrial rDNA sequences. *Mycological Research* **109**, 21–30.

Bjelland T, Bendiksby M and Frisch A (2017) Geographically disjunct phylogenetic lineages in *Leptogium hibernicum* reveal *Leptogium krogiae* sp. nov. from East Africa. *Lichenologist* **49**, 239–251.

Brand AM, van den Boom PPG and Sérusiaux E (2014) Unveiling a surprising diversity in the lichen genus *Micarea* (*Pilocarpaceae*) in Réunion (Mascarenes archipelago, Indian Ocean). *Lichenologist* **46**, 413–439.

Burgess ND, Butynski TM, Cordeiro NJ, Doggart NH, Fjeldså J, Howell KM, Kilahama FB, Loader SP, Lovett JC and Mbilinyi B (2006) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation* **134**, 209–231.

Cengia Sambo M (1938) Licheni del Kenia e del Tanganica raccolti dai Rev. Padri della Consolata. *Nouvo Giornale Botanico Italiano* **45**, 364–387.

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

Coppins BJ (1983) A taxonomic study of the lichen genus *Micarea* in Europe. *Bulletin of the British Museum* (*Natural History*), *Botany Series* **11**, 17–214.
Coppins BJ (1999) Two new species of *Micarea* from South Africa. *Lichenologist* **31**, 559–565.
Culberson CF and Kristinsson HD (1970) A standardized method for the identification of lichen products. *Journal of Chromatography A* **46**, 85–93.
Czarnota P (2007) The lichen genus *Micarea* (*Lecanorales*, Ascomycota) in Poland. *Polish Botanical Studies* **23**, 1–190.
Czarnota P and Guzow-Krzemińska B (2010) A phylogenetic study of the *Micarea prasina* group shows that *Micarea micrococca* includes three distinct lineages. *Lichenologist* **42**, 7–21.
Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**, 1792–1797.
Ekman S (1996) The corticolous and lignicolous species of *Bacidia* and *Bacidina* in North America. *Opera Botanica* **127**, 1–148.
Ekman S and Svensson M (2014) *Brianaria* (*Psoraceae*), a new genus to accommodate the *Micarea sylvicola* group. *Lichenologist* **46**, 285–294.
Ekman S, Andersen H and Wedin M (2008) The limitations of ancestral state reconstruction and the evolution of the ascus in the *Lecanorales* (lichenized Ascomycota). *Systematic Biology* **57**, 141–156.
Farkas E (1987) Foliicolous lichens of the Usambara Mountains, Tanzania I. *Lichenologist* **19**, 43–59.
Farkas E and Flakus A (2015) Rare or overlooked? Two species of *Lyromma* (*Lyrommataceae*, lichenized Ascomycota) are new for Africa. *Herzogia* **28**, 204–211.
Farkas E and Vězda A (1993) Five new foliicolous lichen species. *Folia Geobotanica et Phytotaxonomica* **28**, 321–330.
Felsenstein J (1985) Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.
Frisch A (1999) Afroalpine macrolichens of Mount Kenya (Kenya). *Bayreuther Forum Ökologie* **64**, 65–102.
Frisch A and Hertel H (1998) Flora of macrolichens in the alpine and subalpine zones of Mount Kenya (Kenya) [Die Flora der Blatt- und Strauchflechten in der alpinen und subalpinen Stufe des Mount Kenya (Kenia)]. *Sauteria* **9**, 363–370.
Goloboff P, Farris J and Nixon K (2008) TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786.
Guzow-Krzemińska B, Czarnota P, Łubek A and Kukwa M (2016) *Micarea soralifera* sp. nov., a new sorediate species in the *M. prasina* group. *Lichenologist* **48**, 161–169.
Guzow-Krzemińska B, Sérusiaux E, van den Boom PPG, Brand AM, Launis A, Łubek A and Kukwa M (2019) Understanding the evolution of phenotypical characters in the *Micarea prasina* group (*Pilocarpaceae*) and descriptions of six new species within the group. *MycoKeys* **57**, 1–30.
Hafellner J (1984) Studien in Richtung einer natürlicheren Gliederung der Sammelfamilien *Lecanoraceae* und *Lecideaceae*. *Beiheft zur Nova Hedwigia* **79**, 241–371.
Harris RC (2009) Four novel lichen taxa in the lichen biota of eastern North America. *Opuscula Philolichenum* **6**, 149–156.
International Mycological Association (2019) *MycoBank Database*. [WWW resource] URL www.mycobank.org. [Accessed May 2019].
Jarman SJ and Kantvilas G (2001*a*) Bryophytes and lichens at the Warra LTER Site. I. An inventory of species in *Eucalyptus obliqua* wet sclerophyll forest. *Tasforests* **13**, 193–216.
Jarman SJ and Kantvilas G (2001*b*) Bryophytes and lichens at the Warra LTER Site. II. Understorey habitats in *Eucalyptus obliqua* wet sclerophyll forest. *Tasforests* **13**, 217–243.
Jørgensen PM (1994) *Leptogium palustre*, a new lichen from East Africa. *Lichenologist* **26**, 213–215.
Kalb K and Vězda A (1994) Neue Arten der Flechtengattung *Gyalideopsis* Vězda (*Gomphillaceae*). *Nova Hedwigia* **58**, 511–528.
Kantvilas G and Coppins BJ (2019) Studies on *Micarea* in Australasia II. A synopsis of the genus in Tasmania, with the description of ten new species. *Lichenologist* **51**, 431–481.
Kantvilas G and Jarman SJ (2006) Recovery of lichens after logging: preliminary results from Tasmania's wet forests. *Lichenologist* **38**, 383–394.
Kantvilas G, Jarman SJ and Minchin PR (2015) Early impacts of disturbance on lichens, mosses and liverworts in Tasmania's wet eucalypt production forests. *Australian Forestry* **78**, 92–107.
Kauff F and Lutzoni F (2002) Phylogeny of the *Gyalectales* and *Ostropales* (Ascomycota, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. *Molecular Phylogenetics and Evolution* **25**, 138–156.
Kirika P, Mugambi G, Lücking R and Lumbsch HT (2012) New records of lichen-forming fungi from Kenya. *Journal of East African Natural History* **101**, 73–98.
Klement O (1962) Zur Flechten-Vegetation von Tanganjika. *Stuttgarter Beiträge zur Naturkunde* **85**, 1–8.
Konoreva L, Chesnokov S, Kuznetsova E and Stepanchikova I (2019) Remarkable records of *Micarea* from the Russian Far East and significant extension of *Micarea laeta* and *M. microareolata* range. *Botanica* **25**, 186–201.
Lange CD (2006) The endemic land snail *Gulella taitensis* of the Taita Hills forests, Kenya: on the brink of extinction. *Oryx* **40**, 362–364.
Launis A and Myllys L (2019) *Micarea fennica*, a new lignicolous lichen species from Finland. *Phytotaxa* **409**, 179–188.
Launis A, Pykälä J, van den Boom P, Sérusiaux E and Myllys L (2019*a*) Four new epiphytic species in the *Micarea prasina* group from Europe. *Lichenologist* **51**, 7–25.
Launis A, Malicek J, Svensson M, Tsurykau A, Sérusiaux E and Myllys L (2019*b*) Sharpening species boundaries in the *Micarea prasina* group, with a new circumscription of the type species *M. prasina*. *Mycologia* **111**, 574–592.
Leavitt SD, Johnson L, Goward T and St. Clair L (2011) Species delimitation in taxonomically difficult lichen-forming fungi: an example from morphologically and chemically diverse *Xanthoparmelia* (*Parmeliaceae*) in North America. *Molecular Phylogenetics and Evolution* **60**, 317–332.
Lendemer JC, Harris RC and Ladd D (2016) The faces of *Bacidia schweinitzii*: molecular and morphological data reveal three new species including a widespread sorediate morph. *Bryologist* **119**, 143–171.
Lücking R and Kalb K (2002) New species and further additions to the foliicolous lichen flora of Kenya (East Africa), including the first lichenicolous *Aulaxina* (*Ostropales*: *Gomphillaceae*). *Botanical Journal of the Linnean Society* **139**, 171–180.
Maas Geesteranus RA (1955) Some lichenological observations in Kenya. *Webbia* **11**, 519–523.
Malonza PK, Lötters S and Measey GJ (2010) The montane forest associated amphibian species of the Taita Hills, Kenya. *Journal of East African Natural History* **99**, 47–63.
Marbach B (2000) Corticole und lignicole Arten der Flechtengattung *Buellia* sensu lato in den Subtropen und Tropen. *Bibliotheca Lichenologica* **74**, 1–384.
Meyer B and Printzen C (2000) Proposal for a standardized nomenclature and characterization of insoluble lichen pigments. *Lichenologist* **32**, 571–583.
Myllys L, Lohtander K, Källersjö M and Tehler A (1999) Sequence insertion and ITS data provide congruent information in *Roccella canariensis* and *R. tuberculata* (*Arthoniales*, Euascomycetes) phylogeny. *Molecular Phylogenetics and Evolution* **12**, 295–309.
Myllys L, Velmala S, Holien H, Halonen P, Wang LS and Goward T (2011) Phylogeny of the genus *Bryoria*. *Lichenologist* **43**, 617–638.
Orange A, James PW and White FJ (2010) *Microchemical Methods for the Identification of Lichens*. London: British Lichen Society.
Pellikka PK, Lotjonen M, Siljander M and Lens L (2009) Airborne remote sensing of spatiotemporal change (1955–2004) in indigenous and exotic forest cover in the Taita Hills, Kenya. *International Journal of Applied Earth Observation and Geoinformation* **11**, 221–232.
Purvis OW and James PW (1993) Studies on the lichens of the Azores. Part 1: Caldeira Faial. *Arquipélago, Life and Marine Sciences* **11A**, 1–15.
Rikkinen J (2010) Cyanolichens of the Taita Hills and Mt. Kasigau. In Johansson T, Pellikka P and Sorvali J (eds), *Safari Njema – an Interdisciplinary Field Expedition to South-East Kenya*. Helsinki: Department of Geography, University of Helsinki, pp. 64–68.
Rodgers W (1993) The conservation of the forest resources of eastern Africa: past influences, present practices and future needs. In Lovett J and Wasser S (eds), *Biogeography and Ecology of the Rain Forests of Eastern Africa*. Cambridge: Cambridge University Press, pp. 283–332.

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press

Rogers PC, O'Connell B, Mwang'ombe J, Madoffe S and Hertel G (2008) Forest health in the Ngangao Forest, Taita Hills, Kenya: a five year assessment of change. *Journal of East African Natural History* **97**, 3–17.

Rogo L and Oguge N (2000) The Taita Hills forest remnants: a disappearing world heritage. *AMBIO*: *A Journal of the Human Environment* **29**, 522–523.

Santesson R (1952) Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsaliensis* **12**, 1–590.

Schmitt I, Crespo A, Divakar PK, Fankhauser JD, Herman-Sackett E, Kalb K, Nelsen MP, Nelson NA, Rivas-Plata E and Shimp AD (2009) New primers for promising single-copy genes in fungal phylogenetics and systematics. *Persoonia* **23**, 35–40.

Sérusiaux E, Brand AM, Motiejūnaitė J, Orange A and Coppins BJ (2010) *Lecidea doliiformis* belongs to *Micarea*, *Catillaria alba* to *Biatora* and *Biatora lignimollis* occurs in Western Europe. *Bryologist* **113**, 333–344.

Spribille T, Thor G, Bunnell FL, Goward T and Björk CR (2008) Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography* **31**, 741–750.

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**, 1312–1313.

Suija A, Kaasalainen U, Kirika P and Rikkinen J (2018) *Taitaia*, a novel lichenicolous fungus in tropical montane forests in Kenya (East Africa). *Lichenologist* **50**, 173–184.

Swinscow TDV and Krog H (1988) *Macrolichens of East Africa*. London: British Museum (Natural History).

van den Boom PPG, Brand AM, Coppins BJ and Sérusiaux E (2017) Two new species in the *Micarea prasina* group from Western Europe. *Lichenologist* **49**, 13–25.

White TJ, Bruns T, Lee S and Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In Innis MA, Gelfand DH, Sninsky JJ and White TJ (eds), *PCR Protocols: A Guide to Methods and Applications*. New York: Academic Press, pp. 315–322.

Wilder C, Brooks T and Lens L (1998) Vegetation structure and composition of the Taita Hills forests. *Journal of East African Natural History* **87**, 181–187.

Yeshitela K (2008) *Effects of anthropogenic disturbance on the diversity of foliicolous lichens of East Africa: Goder (Ethiopia), Budongo (Uganda) and Kakamega (Kenya)*. Ph.D. thesis, University of Koblenz-Landau.

Yeshitela K, Fischer E, Killmann D and Sérusiaux E (2009) Two new foliicolous species of *Enterographa* (*Roccellaceae*) from Kenya. *Lichenologist* **41**, 17–23.

Zahlbruckner A (1926) Afrikanische Flechten (Lichenes). *Engler's Botanische Jahrbücher* **60**, 468–552.

Zoller S, Scheidegger C and Sperisen C (1999) PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *Lichenologist* **31**, 511–516.

https://doi.org/10.1017/S0024282920000511 Published online by Cambridge University Press