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

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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 ephymenium and another purplish brown pigment in the hymenium. *Micarea stellaris*, *M. taitensis* and *M. versicolor* produce methoxyemicareic 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

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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 caps ultra 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 & Aptonoot 2005; Alstrup & Christensen 2006; Yeshitela et al. 2008; Yeshitela et al. 2009; Rikkinen et al. 2012; Kfir & 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
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. 2019a, 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. sylibica 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 gonocysts and produce Sedifolia–grey pigment (K+ violet, C+ violet), which is typically present in the epiphymenium 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. 2019a, b). The focus of this study was the epiphytic and epixylic Micarea species in indigenous and planted forests of the two mountains, Ngango 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 Ngango (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 Ngango 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 (dH2O), 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 mtSSU1 and mtSSU3R (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. 2019a). 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.l (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. (2019a, 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. 2019a, b) and our preliminary phylogenetic reconstruction, Micarea peliocarpa (Anzii) Coppins & R. Sant. was used as an outgroup. The hypervariable region at the end of the
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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>Voucher information, sequence ID</th>
<th>ITS</th>
<th>mtSSU</th>
<th>Mcm7</th>
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<td>Japan</td>
<td>Andersen 48 (BG)</td>
<td>AY756468</td>
<td>AY567751</td>
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<td><em>M. aeruginoprasina</em></td>
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<td><em>van den Boom</em> 51445 (LG), 3973</td>
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<td>MN105888</td>
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<td>MG707768</td>
<td>MG692527</td>
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<td>USA, Maine</td>
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<td><em>P &amp; G van den Boom</em> 52575 (hb. van den Boom), LG DNA 4236</td>
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<td><em>M. incrassata</em></td>
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<td>MN95788</td>
<td>XK459362</td>
<td>MN105894</td>
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<td>MN95789</td>
<td>MK562016</td>
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<td>MG707771</td>
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<td><em>M. melanobola</em></td>
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<td>MK454770</td>
<td>MK456625</td>
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<td><em>M. nowakii</em></td>
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<td><em>M. subviridescens</em></td>
<td>Scotland</td>
<td>Czarnota 3599 (GPN)</td>
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<td>EF453666</td>
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</tbody>
</table>

(Continued)
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 2008) and to maximum likelihood (ML) analysis using RAxML (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 1000 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.vmcvdncqy).

**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. 2019a, b). However, it should be noted that our new accesses 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. endocyanaea (Tuck. ex Willey) R. C. Harris, is analyzed here for the first time and is closely related to M. elachista (Körb.) Coppens & 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 & Coppens 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 Coppens, M. xanthonica Coppens & Tønsberg and species referred to the M. byssacea and M. micrococca complexes (see Czarnota & Guzow-Krzemińska 2010; Launis et al. 2019a); the second clade remains unsupported and consists of species from the M. prasina complex (see Launis et al. 2019b).

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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>Voucher information, sequence ID</th>
<th>ITS</th>
<th>mtSSU</th>
<th>Mcm7</th>
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<tbody>
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<td>Kenya</td>
<td>Kantelinen 4623 (H, NAI), A829</td>
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<td>Finland</td>
<td>Kantelinen 2592 (H), A414</td>
<td>—</td>
<td>MT982138</td>
<td>MT981447</td>
</tr>
<tr>
<td>M. versicolor</td>
<td>Kenya</td>
<td>Kantelinen 4624 (H, NAI), A830</td>
<td>MT981604</td>
<td>MT982143</td>
<td>—</td>
</tr>
<tr>
<td>M. versicolor</td>
<td>Kenya</td>
<td>Kantelinen 4626 (H, NAI), A832</td>
<td>—</td>
<td>MT982144</td>
<td>—</td>
</tr>
<tr>
<td>M. versicolor</td>
<td>Kenya</td>
<td>Kantelinen 4627 (H, NAI), A833</td>
<td>MT981603</td>
<td>MT982142</td>
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</tr>
<tr>
<td>M. versicolor</td>
<td>Kenya</td>
<td>Kantelinen 4647 (H, NAI), A834</td>
<td>MT981602</td>
<td>MT982141</td>
<td>—</td>
</tr>
<tr>
<td>M. viridileprosa</td>
<td>Poland</td>
<td>Czarnota 3436 (GPN)</td>
<td>—</td>
<td>EF453671</td>
<td>—</td>
</tr>
<tr>
<td>M. viridileprosa</td>
<td>Netherlands</td>
<td>P. &amp; B. van den Boom, 50066 (hb. van den Boom), LG DNA 3493</td>
<td>—</td>
<td>KX459366</td>
<td>MN105918</td>
</tr>
<tr>
<td>M. xanthonica</td>
<td>USA</td>
<td>Tønsberg 25674 (BG)</td>
<td>—</td>
<td>AV756454</td>
<td>—</td>
</tr>
<tr>
<td>Micarea sp. (as M. eximia in GenBank)</td>
<td>not available</td>
<td>Hermansson 8866b (UPS)</td>
<td>AY756476</td>
<td>AY756447</td>
<td>—</td>
</tr>
<tr>
<td>Micarea sp. ‘lineage A’</td>
<td>Scotland</td>
<td>Lounis 171142 (H), A648</td>
<td>MG521571</td>
<td>MG707782</td>
<td>MG692542</td>
</tr>
</tbody>
</table>

**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 Coppens (1983), Meyer & Pritzen (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.

**Table 1. (Continued)**
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* complex, 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. 2019a, 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
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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Thallus colour</th>
<th>Thallus structure</th>
<th>Apothecial pigmentation</th>
<th>Ascospore size (μm)</th>
<th>Crystalline granules</th>
<th>Secondary chemistry</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. fallax</em></td>
<td>vivid green or pale to dark olive green</td>
<td>granular, goniocysts usually aggregated or form ±thick almost continuous and cracked thallus, if less developed warted or partly membranous and ±shiny</td>
<td>cream-white, pale brownish, honey brown to brown, sometimes with greyish tinge, K± violet, C± violet</td>
<td>8–11 × (3–) 3.2–4.0</td>
<td>across hymenium</td>
<td>micareic acid</td>
</tr>
<tr>
<td><em>M. levicula</em></td>
<td>vivid green</td>
<td>goniocysts delicately coralloid</td>
<td>cream-white, K−, C−</td>
<td>10.3–10.8 × 3.7–4.1</td>
<td>not studied</td>
<td>gyrophoric acid</td>
</tr>
<tr>
<td><em>M. micrococca</em></td>
<td>bright green to pale olive green</td>
<td>minutely granular, goniocysts usually aggregated</td>
<td>cream-white, K−, C−</td>
<td>10–12 (~16) × 3–4.5</td>
<td>across hymenium</td>
<td>methoxymicareic acid</td>
</tr>
<tr>
<td><em>M. pumila sp. nov.</em></td>
<td>olive green to bright green</td>
<td>minutely granular</td>
<td>cream-white or pale brownish, K−, C−</td>
<td>7.0–10.5 × 2.5–3.2</td>
<td>across hymenium, often weak or not visible</td>
<td>prasinic acid</td>
</tr>
<tr>
<td><em>M. stellaris sp. nov.</em></td>
<td>whitish green to bright green</td>
<td>warded-areolate</td>
<td>cream-white, usually darker at the center, hymenium with light grey or brownish pigment dissolving in K</td>
<td>10.0–14.0 × 3.8–5.0</td>
<td>intense, appearing as a belt-like continuum across lower hymenium</td>
<td>methoxymicareic acid</td>
</tr>
<tr>
<td><em>M. sublithinella</em></td>
<td>green</td>
<td>continuous or areolate</td>
<td>light brownish, dull</td>
<td>12.5–15.0 × 5.0–5.8</td>
<td>not studied</td>
<td>protolichesterinic acid</td>
</tr>
<tr>
<td><em>M. taitensis sp. nov.</em></td>
<td>whitish green to bright green</td>
<td>warded-areolate or sometimes membranate</td>
<td>cream-white or yellowish, often with a greyish tinge K± violet, C± violet</td>
<td>10.0–14.0 × 4.0–4.7 (~5.0), often slightly constricted at the septum</td>
<td>in hymenium, sometimes clustered</td>
<td>methoxymicareic acid</td>
</tr>
<tr>
<td><em>M. versicolor sp. nov.</em></td>
<td>whitish green to bright green</td>
<td>warded-areolate or continuous crust, sometimes partly granular and then composed of goniocysts</td>
<td>cream-white to light grey to dark brownish-grey or blackish, if pigmented K+ intensifying purple and K+ violet</td>
<td>9.5–13.0 × 3.2–4.0 (~4.5)</td>
<td>in hymenium and upper part of hypothecium</td>
<td>methoxymicareic acid</td>
</tr>
</tbody>
</table>
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, 1866 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 micaceous, 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; epithymenia 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 dying *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. prasinasta* Coppins & Kantelinas. The small whitish apothecia are also similar to *M. micrococcia* and *M. pseudomicrococcia*. The main morphological characters separating *M. pumila* from the other species are the smaller ascospore size and wider paraphyses, with the exception of *M. prasinasta* 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
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).


*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, 38.341582°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; hymenium light grey or brownish, pigment K– and dissolving (possibly Elachista-brown pigment), 50–60 μm high; 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.
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 warded-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...
**Micarea levicula** 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 coraloid 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 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 4646 & 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 obvoid, (0–)1(–2)-septate, when 1-septate often slightly constricted at the septum, 10.0–14.0 × 4.0–4.7(–5.0) μm.


(Fig. 2E & F)

Thallus effuse, whitish green to bright green, warted-areolate or sometimes membranate, bright green especially in parts distinctly warted; **photobiont** miccareid, 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 obvoid, (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 protolichisticericin 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 obvoid, 0–1-septate, 9.5–13.0 × 3.2–4.0(–4.5) μm; methoxymicareic acid.
Type: Kenya, Taita Taveta, Taita Hills, Ngangao forest, west side, near Ngangao Forest Camp and by a forest path, indigenous forest, on wood of falling 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. **Ephythymium** 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; **mucopycnidia** 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** liliform 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 Virua 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 ephythymium (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. meliensa* 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; seeEkman (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 falling *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 *Pinus patula* tree, 3.568355°S, 38.343012°E, 1844 m a.s.l., 2017, Annina Kantelinen 4627 (H, NAI); ibid., Virua, 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).

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