



Pseudoplectania africana (Sarcosomataceae, Pezizales), a new species from South Africa

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Background: An undescribed species of *Pseudoplectania* was found during an excursion in Mpumalanga.

Objectives: To describe *Pseudoplectania africana* M.Carbone & Sochorová as a new species and to evaluate presence of crystals as a diagnostic character in *Pseudoplectania*.

Methods: The description was based on standard macro- and microscopical methods. Presence of crystals was tested for in UV light. Phylogeny was inferred using sequencing of the LSU and ITS loci.

Results: *Pseudoplectania africana* is characterised by shortly stipitate to sessile apothecia up to 18 mm broad, richly developed basal tomentum, ascospores with an eccentrically positioned, relatively small sheath, straight, sometimes bifurcate paraphyses, wavy to coiled external hairs and presence of large yellow crystals mainly in the hymenium and ectal excipulum. It was found on a decaying coniferous trunk. The species forms a distinct lineage in the clade with *P. tasmanica* and *P. ericae*. All of these three species exhibited presence of the large yellow crystals (sulphur yellow in UV light). No or only small hyaline crystals (whole mount blue in UV light) were found in *P. nigrella*, *P. lignicola*, *P. epispagnum* and *P. melaena*.

Conclusion: The new species represents the first report of *Pseudoplectania* in South Africa and probably also in the whole of continental Africa. Crystals in hymenium and excipulum appear to be an important trait in *Pseudoplectania* taxonomy.

Keywords: Ascomycota; crystals; fungal diversity; phylogeny; taxonomy.

Introduction

Pseudoplectania Fuckel, typified by *Pseudoplectania nigrella* (Pers.) Fuckel, is a genus of ascomycetes belonging to the family Sarcosomataceae Kobayasi. It includes species with hemispherical, cupulate to plane apothecia, which are sessile or stipitate, coloured in shades of black or brown, having the outer surface covered by brown to black hairs and reaching a size between ca. 0.5 and 6.0 cm in diameter. Typical microscopical characters of the species of *Pseudoplectania* are globose, hyaline, usually smooth, thick-walled ascospores, operculate, inamyloid, octosporic asci arising from simple septa, presence of two types of paraphyses (common ones and so called hymenial hairs), medulla organised as a *textura intricata*, ectal excipulum with a *t. globulosa* or *t. angularis* and thick-walled, septate but unbranched hairs with blunt apex (Eckblad 1968; Donadini 1987). Fruit bodies of *Pseudoplectania* occur on dead wood, in litter, on soil or *Sphagnum*.

Nine species have been accepted by Carbone et al. (2014), namely *Pseudoplectania nigrella*, *P. episphagnum* (J.Favre) M.Carbone, Agnello & P.Alvarado, *P. melaena* (Fr.) Sacc., *P. ericae* Donadini, *P. affinis* M.Carbone, Agnello & P.Alvarado, *P. tasmanica* M.Carbone, Agnello & P.Alvarado, *P. stygia* (Berk. & M.A.Curtis) Sacc., *P. carranzae* (Calonge & M.Mata) M.Carbone, Agnello & P.Alvarado and *P. ryvardeenii* Iturr., M.Mardones & H.Urbina. In 2015, *P. lignicola* Glejdura, Kučera, Lizoň & Kunca was described (Glejduara et al. 2015), and in 2020 *P. sinica* Qiao Zhang & Jie Zhang (Zhang & Zhang 2020). The first six species and *P. sinica* have already been characterised by molecular methods (Carbone et al. 2014; Zhang & Zhang 2020) whilst the other four have been described only by their morphology and ecology (Calonge & Mata 2002; Iturriaga et al. 2012; Carbone 2013; Glejdura et al. 2015). One more species belonging to this genus, *Pseudoplectania kumaonensis* Sanwal is regarded to be doubtful (Sanwal 1953; Carbone et al. 2014).

Many reports of *Pseudoplectania* have been published from different regions of the northern hemisphere (e.g. Seaver 1913; Otani 1973; Breitenbach & Kränzlin 1981; Donadini 1987; Kristiansen 1990; Lincoff 1997; Calonge & Mata 2002; Medardi 2006; Barseghyan & Wasser 2008; Pant & Prasad 2008; Iturriaga et al. 2012; Van Vooren et al. 2013; Deckerová & Šuhaj 2014; Glejdura et al. 2015; Uzun & Kaya 2018), while data from the southern hemisphere are much rarer (Le Gal 1953; Sandoval 2012; Carbone et al. 2014; Gates & Ratkowsky 2016). No literature reports documenting *Pseudoplectania* spp. from continental Africa are known to us, with only a single report from the island of Madagascar (Le Gal 1953). In March 2018, a rich population of *Pseudoplectania* was discovered in Mpumalanga, South Africa, which did not match phenotypic descriptions of any of the currently known species. Especially striking were large yellow crystals found during microscopical examination in hymenium and ectal excipulum, which had been reported so far only in *P. tasmanica* (Carbone et al. 2014).

The aim of the present article is to introduce *Pseudoplectania africana* sp. nov., compare it with other species of the genus and evaluate presence of crystals in available *Pseudoplectania* spp. collections.

Material and methods

Sample collection and observation

Description of macroscopical characters is based on fresh apothecia. Microscopical characters were studied in living (*) cells and tissues and rehydrated material (†) at magnifications up to 1000×, using light microscopes Olympus CX41 and CX21. The following media were

used: tap water (H₂O), 3% potassium hydroxide (KOH), Lugol's solution (IKI), Brilliant Cresyl Blue (CRB) and Lactic Acid Cotton Blue (LACB). Nuclei were visualised in rehydrated apothecia upon staining with DAPI (4',6-diamidino-2-phenylindole; 10 µg/mL, 10 min, room temperature, dark) and fluorescence signal excited by a mercury lamp was combined with transmission light channel (50:50) (Olympus BX60 with attached DP73 camera). Measurements of microscopical characters were made in tap water (if not otherwise stated) directly with an ocular micrometre scale or in photographs with the PIXIMÈTRE 5.10 software (Henriot & Cheype 2020). Diameter of ascospores is given as minimal measured value – arithmetic mean – maximal measured value; Q = length/width ratio; n = sample size. Crystals were studied in exsiccates. Their solubility in *P. africana* was tested in Melzer's reagent (MLZ), 60% ethanol, 9% hydrochloric acid (HCl) and 40% KOH. Their autofluorescence was tested using excitation by Jaxman U1C UV flashlight (3W UV LED Nichia, 365 nm), which radiation was applied to mounts obliquely from above.

DNA extraction, PCR amplification and sequencing

DNA was extracted from dried apothecia using the CTAB method (Doyle & Doyle 1987). Sequence data were generated for two loci – internal transcribed spacers (ITS) of ribosomal DNA (ITS1–5.8S rDNA–ITS2 region) using primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990), and the large subunit of ribosomal DNA (LSU) using primers LR0R and LR6 (Vilgalys & Hester 1990). PCR was performed with Kapa polymerase (Kapa Biosystems), following a standard protocol with 37 cycles and annealing temperature of 56°C. The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25M NaCl in the precipitation mixture) and sequenced in both directions using the Sanger method (Macrogen Europe, The Netherlands).

Phylogenetic analysis

Sequences of *Pseudoplectania africana* and all other available *Pseudoplectania* species were included in molecular analysis (Table 1), *Urnula craterium* (Schwein.) Fr. served as an outgroup. Sequences were assembled, edited and aligned in GENEIOUS 8.1.9 (Biomatters, New Zealand) using the MAFFT plugin (ver. 1.3.3), manually checked and corrected. Bayesian phylogeny inference for concatenated data was computed in MRBAYES (ver. 3.2.4; Ronquist et al. 2012) with 5×10⁶ generations, sampling every 1000th tree, in two independent runs, each with 4 chains, first 50% (2.5×10⁶) generations were excluded as burn-in. The most suitable substitution model for each locus was determined in PARTITION-FINDER 2.1.1 (Lanfear et al. 2017) using the corrected AIC (AICc) and a greedy search. SYM+I+G was selected for ITS and GTR+I+G for LSU. Single-locus phylogenies

Table 1. List of collections used in the phylogenetic study together with their GenBank accession numbers. Sequences newly generated for this study in bold font.

Species	Identification code in GenBank	Country, collection date	Herbarium code	GenBank accession numbers	
				ITS	LSU
<i>Pseudoplectania affinis</i>	PDD 81842 (holotype)	New Zealand, 24 Nov. 2004	PDD 81842	JX669826	JX669865
<i>Pseudoplectania africana</i>	ZE59/18 (holotype)	South Africa, 5 Mar. 2018	PRM 954013	MT496892	MT496884
<i>Pseudoplectania episphagnum</i>	ERD 6456	Spain, 30 May 2015	PRM 954123	MT502112	MT500571
<i>Pseudoplectania episphagnum</i>	TUR 064171	Finland, 30 May 1948	TUR 064171	KF305712	-----
<i>Pseudoplectania episphagnum</i>	TUR 064173	Finland, 26 Jun. 1943	TUR 064173	KF305711	KF305724
<i>Pseudoplectania episphagnum</i>	G00566257 (isolectotype)	Switzerland, 20 May 1945	G00566257	-----	MT782281
<i>Pseudoplectania ericae</i>	MCVE 27581	Italy, 23 Dec. 2012	MCVE 27581	KF305721	KF305731
<i>Pseudoplectania ericae</i>	TUR-A 195789	Spain, 16 Jan. 2007	TUR-A 195789	JX669822	JX669862
<i>Pseudoplectania ericae</i>	TUR-A 195790	Spain, 17 Feb. 2010	TUR-A 195790	JX669823	JX669863
<i>Pseudoplectania ericae</i>	ZE1228/18	France, 28 Dec. 2015	PRM 954131	MT476910	MT476900
<i>Pseudoplectania ericae</i>	CA1/18	Greece, 17 Mar. 2018	PRM 954125	MT476909	MT496885
<i>Pseudoplectania ericae</i>	MCVE 31255	France, 2 Dec. 2019	MCVE 31255	MT498082	MT491442
<i>Pseudoplectania ericae</i>	MCVE 30339	Italy, 2 Jan. 2020	MCVE 30339	MT226749	-----
<i>Pseudoplectania ericae</i>	Sousa	Portugal, 9 Feb. 2019	pers. herb. E. Sousa	MT498083	-----
<i>Pseudoplectania lignicola</i>	HR89756 (paratype)	Czech Republic, 1 Apr. 2011	HR 89756	MT496886	MT496882
<i>Pseudoplectania lignicola</i>	SAV 105/17	Slovakia, 21 Apr. 2010	SAV 105/17	MT496881	MT496883
<i>Pseudoplectania lignicola</i>	MCVE 27580	Canada, 17 Jul. 2011	MCVE 27580	KF305713	KF305726
<i>Pseudoplectania lignicola</i>	TUR 172564	Finland, 06 Nov. 2004	TUR 172564	-----	JX669860
<i>Pseudoplectania melaena</i>	MCVE 27579	France, 07 Apr. 2008	MCVE 27579	KF305717	KF305728
<i>Pseudoplectania melaena</i>	TUR-A 198588	USA, 21 Apr. 2006	TUR-A 198588	KF305719	KF305729
<i>Pseudoplectania melaena</i>	NY 54130	USA, 5 Apr. 2008	NY 54130	KF305718	KF305730
<i>Pseudoplectania melaena</i>	NY 96459	USA, 12 May 1947	NY 96459	KF305720	-----
<i>Pseudoplectania nigrella</i>	MCVE 27396	Italy, 1 May 2009	MCVE 27396	KF305715	KF305725
<i>Pseudoplectania nigrella</i>	MCVE 27397	Italy, 31 May 2009	MCVE 27397	-----	MT491441
<i>Pseudoplectania nigrella</i>	MCVE 27582	Italy, 13 Apr. 2013	MCVE 27582	KF305716	KF305727
<i>Pseudoplectania nigrella</i>	TUR-A 198587	USA, 30 Apr. 1999	TUR-A 198587	KF305714	-----
<i>Pseudoplectania nigrella</i>	Fan & Guo 1500201	China, 15 Aug. 2015		KX394804	-----
<i>Pseudoplectania sinica</i>	LYS02 (holotype)	China, 13 May 2017	CGMCC 3.19892	MN396767	MN396768
<i>Pseudoplectania tasmanica</i>	MCVE 27583 (holotype)	Australia, 22 Dec. 2012	MCVE 27583	KF305722	KF305732
<i>Pseudoplectania tasmanica</i>	MCVE 27584	Australia, 22 Dec. 2012	MCVE 27584	KF305723	KF305733
<i>Urnula craterium</i>	30.15.291.11	France, 13 Jan. 2011	pers. herb. R. Dougoud 30.15.291.11	KF311230	KF305734

were computed with similar settings, only the temp parameter was set to 0.01 for ITS to improve chain mixing.

Phylogenetic results

P. africana forms a distinct lineage in the clade with *P. tasmanica* and *P. ericae* (Figure 1). Although it clearly appears to be the closest (known) relative of the former species according to the ITS locus (Bayesian posterior probability, PP=0.93; Sup. Figure 1), LSU provided an ambiguous signal due to a lack of shared apomorphic SNP's in the clade, which resulted in clustering of *P. africana* and *P. ericae* with very low support (PP=0.8; Sup. Figure 2). Subsequently, the concatenated dataset did not provide a well-supported phylogeny in this clade either (Figure 1). However, branch lengths indicate relatively large divergence between the three species (sequence divergence \pm 20% and 1.8% at ITS and LSU, respectively, between *P. africana* and *P. ericae*, and 21% and 1.7% between *P. africana* and *P. tasmanica*).

Taxonomy

Pseudoplectania africana M. Carbone & Sochorová, sp. nov. (Figures 2, 3, 4 A, B).

Mycobank MB 838266.

TYPE: SOUTH AFRICA, Mpumalanga: Ehlanzeni district,

8.3 km SSW of the NG Kerk in Sabie, 25°10'7.6"S / 30°45'49.2"E, 1480 m asl, on a decaying trunk (probably *Pinus* sp.), 5 Mar. 2018, Z. Egertová (Sochorová) & M. Sochor (PRM 954013 – holotype, TUR-A 208915 – isotype, PREM - isotype).

Diagnosis: Differs from other *Pseudoplectania* species in a combination of the following characters: shortly stipitate or sessile, brown to black, sometimes olive-tinged apothecia up to 18 mm in diameter, richly developed basal tomentum; smooth ascospores having an eccentrically positioned, relatively small sheath, straight, often bifurcate paraphyses, wavy to coiled external hairs and presence of large yellow crystals mainly in hymenium and ectal excipulum.

Etymology: From the Latin adjective '*Africanus-a-um*', referring to the African continent.

Description: *Apothecia* up to 18 mm in diameter, hemispherical or cup-shaped, becoming flattened, often irregularly deformed by a mutual pressure, shortly stipitate or sessile. *Hymenium* smooth, shiny, brown to brownish black, in some apothecia with an olivaceous tinge. *External surface* tomentose, brownish black, darker than the hymenium, base with a richly developed black tomentum. *Stipe* short or lacking, up to 3 mm long and 2 mm wide, black. *Flesh* pale greyish, rubbery. Occurring in groups or clusters.

Ascospores in H₂O* globose, 10.5–11.4–13 μ m (n = 100); in H₂O⁺ globose or rarely subglobose, 9–10.7–13

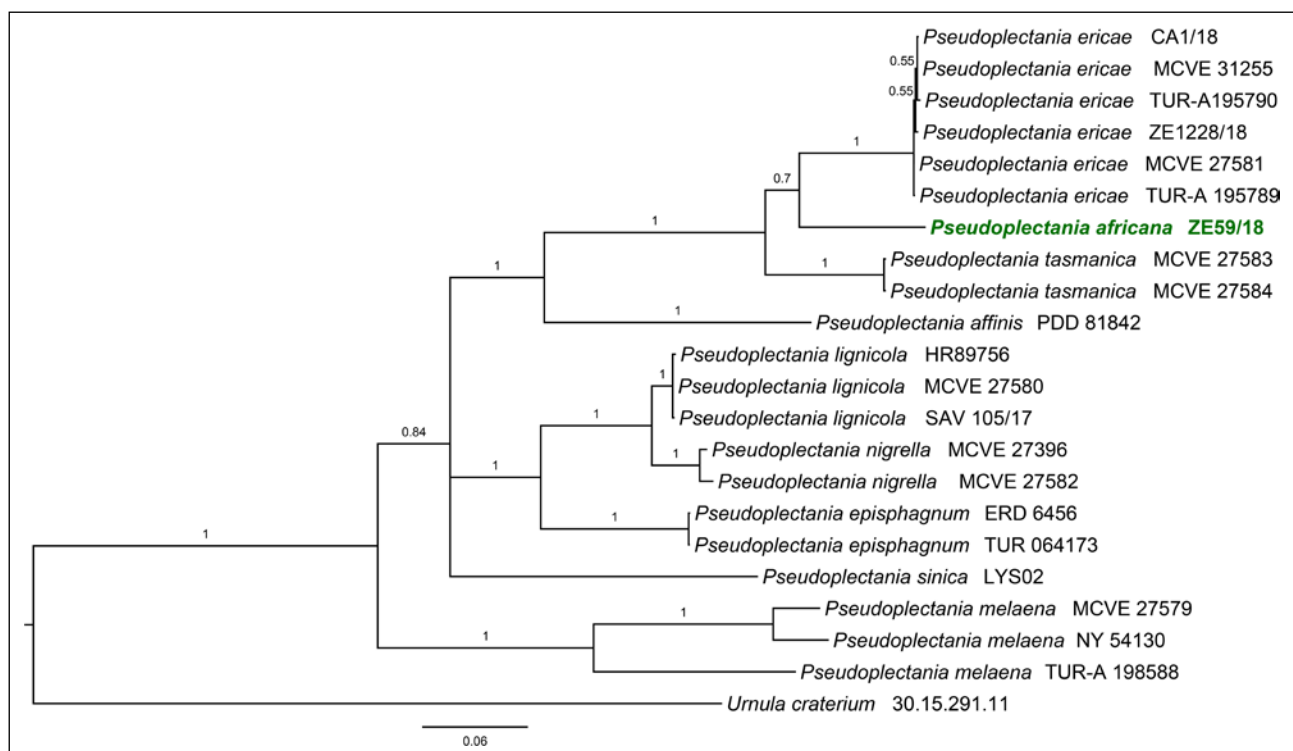


Figure 1. Bayesian phylogeny inference based on concatenated alignment of LSU and ITS sequences. Bayesian posterior probabilities are shown above branches; *Urula craterium* serves as an outgroup.

μm ($n = 100$), $Q = 1.00\text{--}1.06$; in heated LACB⁺ globose or less often subglobose, $9\text{--}10.7\text{--}13\ \mu\text{m}$ ($n = 100$), $Q = 1.00\text{--}1.08$; hyaline, smooth, thick-walled, with vacuolar content, 1–4 nucleate, surrounded by an eccentrically arranged globose membranous sheath, which in its most convex part exceeds the sporal wall for up to $2\ \mu\text{m}$; de Bary bubbles induced in heated LACB; ascospores germinating with one hypha. *Asci* narrowly cylindrical, $^{\dagger}250\text{--}340 \times 11\text{--}14\ \mu\text{m}$, operculate, operculum $^{\dagger}4.5\text{--}6\ \mu\text{m}$ broad; inamyloid, 8-spored, *pars sporifera* $^{\dagger}75\text{--}83\ \mu\text{m}$ when all 8 ascospores are fully developed, base flexuous, tapered, arising from simple septa. *Paraphyses* of two types: 1) cylindrical, apical cell $^{\dagger}12\text{--}29 \times 2\text{--}3.5\ \mu\text{m}$, lower cells $^{\dagger}1\text{--}2.5\ \mu\text{m}$ in diam., septate, branched, sometimes anastomosing with paraphyses of the same type or with the hymenial hairs, light brownish in the upper half; apex slightly enlarged, simple, bifurcate or less often diverticulate to lobed; some paraphyses showing short diverticula growing from the lower elements; 2) so called hymenial hairs cylindrical, measuring $^{\dagger}2\text{--}3\ \mu\text{m}$ in diam., very light brownish, with a single septum at the base; apex straight, hooked or bent in right or obtuse angle, $^{\dagger}2\text{--}3\ \mu\text{m}$ broad; cytoplasm in both types cyanophilic, walls cyanophobic. *Crystals* in hymenium very abundant, yellow, angular, cracked, sometimes very long (to over the whole thickness of hymenium), up to $60\ \mu\text{m}$ wide, oriented with their long axis like the hymenium, not dissolving in KOH (40%), HCl (9%), ethanol (60%) and MLZ. *Subhymenium* $^{\dagger}25\text{--}55\ \mu\text{m}$ thick, structured as a dense *textura intricata* with cylindrical septate hyphae. *Medullary excipulum* $^{\dagger}200\text{--}380\ \mu\text{m}$ thick at flanks, formed by a slightly gelified *textura intricata*, hyphae cylindrical, septate, subhyaline, $^{\dagger}2\text{--}12\ \mu\text{m}$ wide, $^{\dagger}1.5\text{--}6.5\ \mu\text{m}$ wide, walls up to $0.8\ \mu\text{m}$ thick; cytoplasm cyanophilic, walls cyanophobic. *Ectal excipulum* $^{\dagger}40\text{--}120\ \mu\text{m}$ thick, composed of a *textura globulosa-angularis*, cells thick-walled, in the inner layer subhyaline, $^{\dagger}(7)12\text{--}24 \times (5)12\text{--}21\ \mu\text{m}$, in the 2–4 most external rows with blackish-brown walls, $^{\dagger}5\text{--}15 \times 4\text{--}12\ \mu\text{m}$, walls cyanophobic; containing crystals of the same character like in hymenium, but smaller. *External hairs* emerging from the external layer of the ectal excipulum, cylindrical, † ca. $500\text{--}3000\ \mu\text{m}$ long, $5\text{--}8\text{--}(10)\ \mu\text{m}$ diam., with walls up to $1.5\ \mu\text{m}$ thick, septate, wavy or coiled; brown, unbranched, with blunt apex. Many very small hairs, up to $^{\dagger}30\ \mu\text{m}$ long, are present among the longer ones. *Basal tomentum* composed of very long cylindrical hairs looking similar to the external hairs, $^{\dagger}5\text{--}7\ \mu\text{m}$ diam., walls up to $1.1\ \mu\text{m}$ thick. Section in UV light – most of structures blue (subhymenium paler than hymenium, medulla and ectal excipulum), outline of ascospores whitish, external hairs and basal tomentum black, crystals sulphur yellow.

Habitat and distribution: The apothecia grew in a forest patch surrounded by logged pine plantations, on a decaying mossy trunk. Microscopical examination of the substrate showed a typical structure of a conifer

wood. Resin canals further indicated the substrate was most likely *Pinus* sp. (alien in South Africa; van Wyk & van Wyk 2013).

The species is so far known and confirmed only from the type locality. Although no *Pseudoplectania* species have been reported in the checklist of macrofungi of South Africa (Kinge et al. 2020), we are aware of the existence of four collections identified as *Pseudoplectania nigrella* housed in the PREM fungarium (R. Venter-Jacobs pers. comm.). Unfortunately, our attempts to loan these specimens for verification of their identification have not been successful.

Evaluation of presence of the crystals and appearance in UV light

Beside *P. africana* (Figures 3A–C, Figures 4A, B), large yellow crystals have been confirmed in *P. tasmanica* (Figures 4D, F, G) and newly found in *P. ericae* (Figures 4C, E, H), i.e. the three closely related species. The crystals are located mostly in the hymenium and ectal excipulum, less so in the medullary excipulum or subhymenium, and appear sulphur yellow in UV light. Hymenium, subhymenium, medullary and ectal excipulum are in shades of blue, outline of ascospores whitish and hairs and basal tomentum black. All other species available for our study (*P. episphagnum*, *P. lignicola*, *P. melaena* and *P. nigrella*) lack these crystals; they contain only small hyaline crystals, which are most abundant in the medulla, but occur also in the hymenium, subhymenium and ectal excipulum. Therefore, the whole slide has shades of blue in UV light, only the outline of the ascospores is whitish with hairs and tomentum black (Figure 5). The quantity of crystals varies strongly between collections. In some of them, including the neotype of *P. nigrella* (KL BK-4914), aggregates of the crystals can be found, which look pale blue in UV light. As already mentioned in the material and methods chapter, studies on crystals have been performed on dry material. Whether the crystals are also present in vital collections is yet to be verified. Collections of *P. affinis*, *P. carranzae*, *P. ryvardeenii*, *P. sinica* and *P. stygia* were not available.

Additional collections examined (collections studied for presence of crystals marked ☀):

Pseudoplectania episphagnum

FINLAND, Lapland: Ranua, 6 km N of the church, on



Figure 2. *Pseudoplectania africana* – apothecia *in situ* (PRM 954013). Photos: Z. Sochorová.

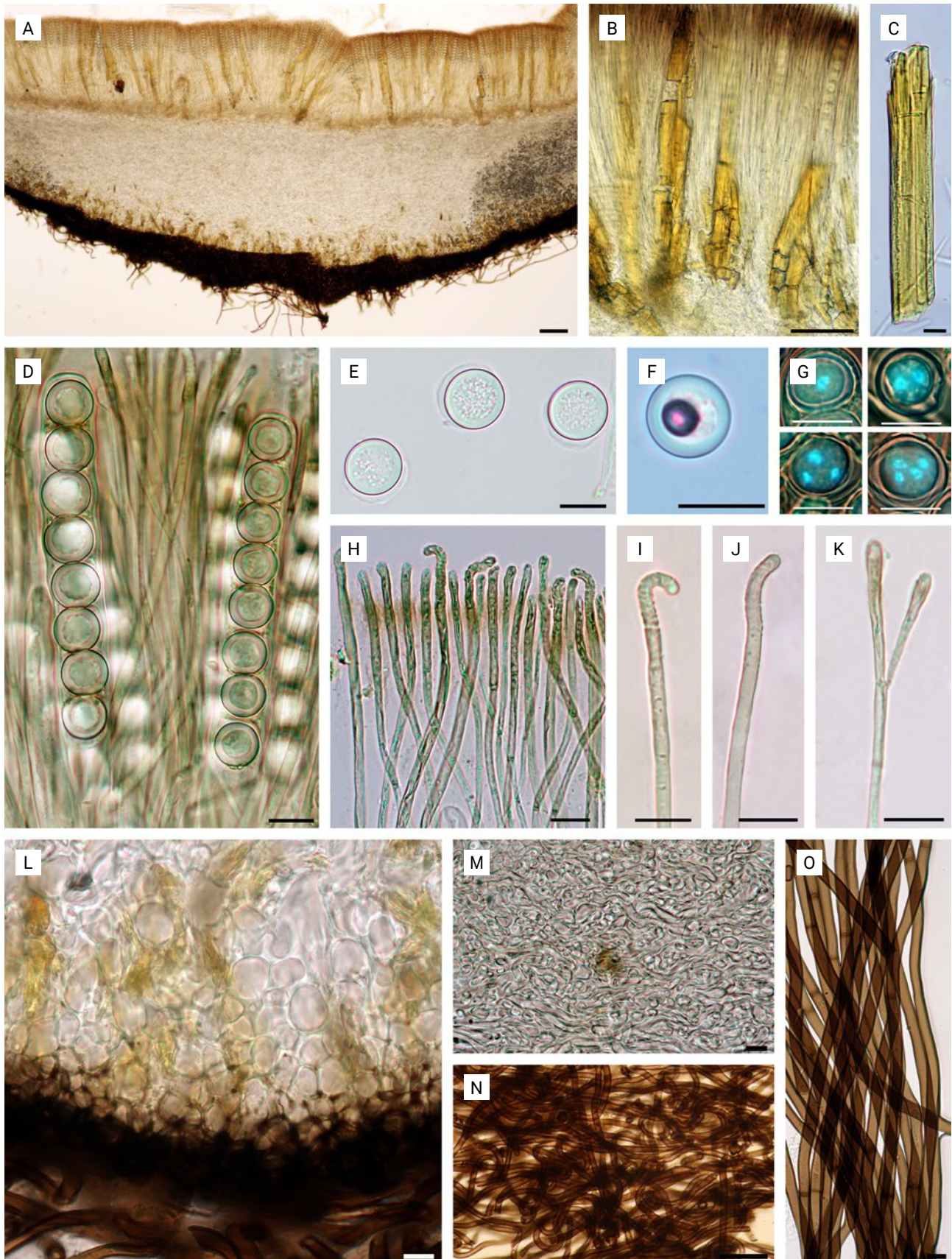


Figure 3. *Pseudoplectania africana* – microscopical characters (PRM 954013); A, section of an apothecium († in tap water); B, crystals in hymenium (in tap water); C, crystal freely floating in the mount (in tap water); D, asci with ascospores and paraphyses († in tap water); E, free ascospores († in tap water); F, ascospore with de Bary bubble († stained with LACB); G, nuclei in ascospores († stained with DAPI); H, two types of paraphyses († in tap water); I, J, hymental hairs († in tap water); K, bifurcate paraphyse († in tap water); L, ectal excipulum († in tap water); M, medullary excipulum († in tap water); N, external hairs († in tap water); O, basal tomentum († in tap water). Scale bars: A = 100 μm ; B, N = 50 μm , C–M, O = 10 μm . Photos: A–F, H–O, Z. Sochorová; G, M. Sedlářová.

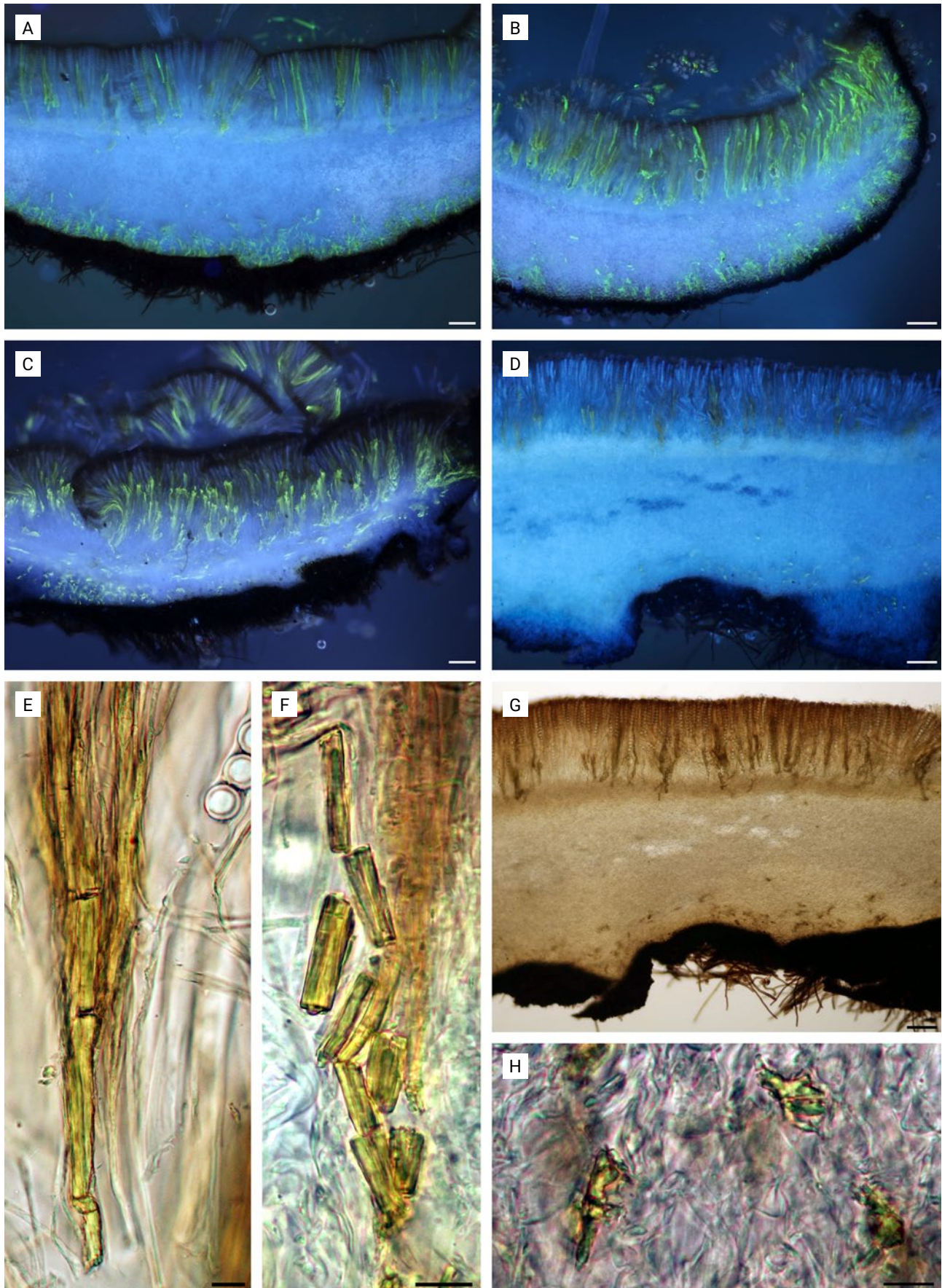


Figure 4. *Pseudoplectania* spp. – crystals and appearance in UV light; A,B, *P. africana* (PRM 954013) – sections in UV light; C,E,H, *P. ericae* – C, section in UV light (PRM 954125); E, crystals in hymenium (PRM 954124, in tap water); H, crystals in ectal excipulum (PRM 954124, in tap water); D, F, G, *P. tasmanica* (MCVE 27583); D, section in UV light; F, crystals in hymenium (in tap water); G, section of the apothecium (in tap water). Scale bars: A–D, G = 100 μm ; E, F, H = 10 μm

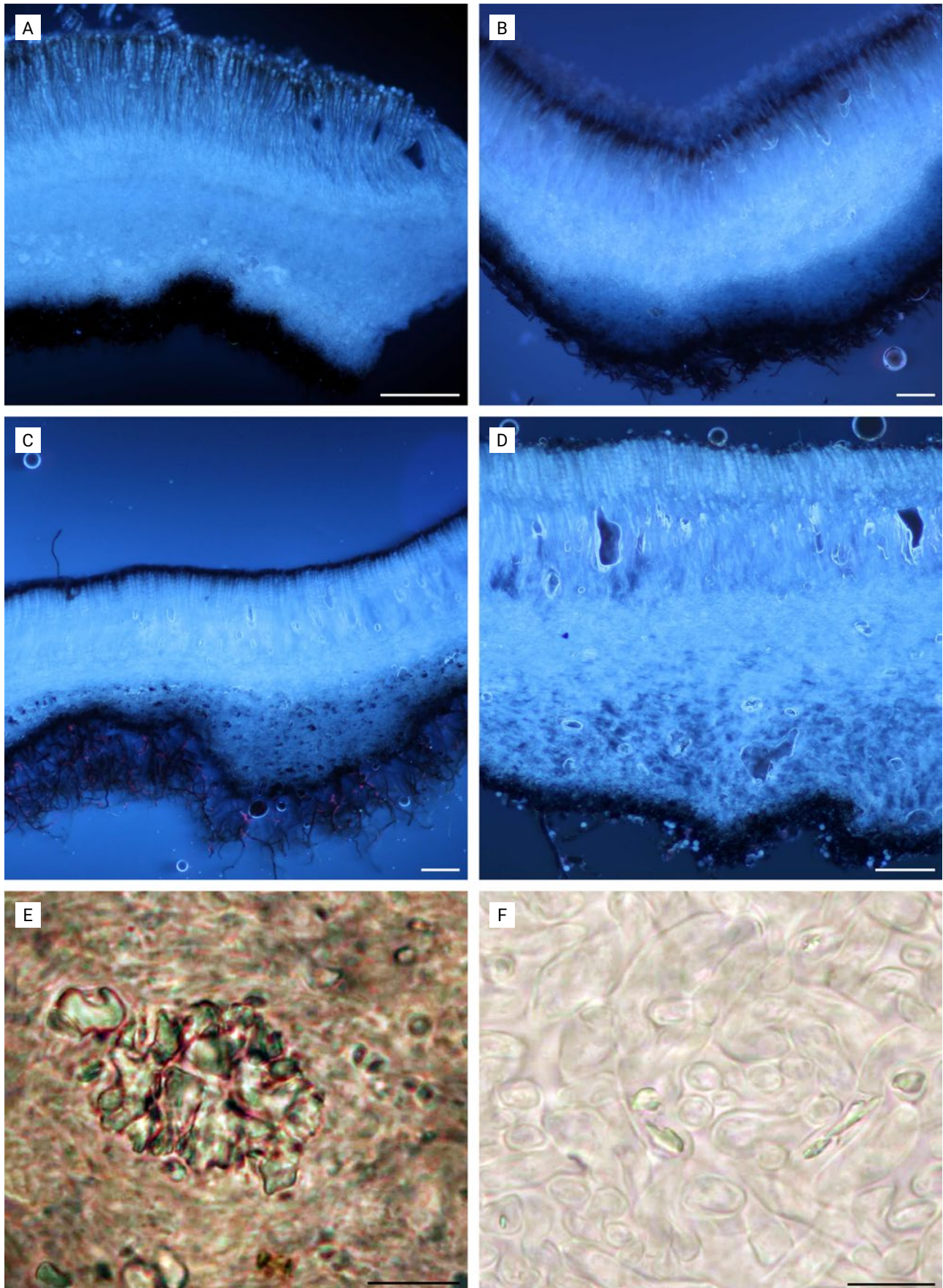


Figure 5. *Pseudoplectania* spp. – crystals and appearance in UV light; A,E,F, *P. nigrella*; A, section in UV light (KL BK-4914); E, aggregate of crystals in excipulum (KL BK-4914, in tap water); F, crystals in excipulum (BRNM 728214, in tap water); B, *P. lignicola* (PRM 954130) – section in UV light; C, *P. episphagnum* (PRM 954123) – section in UV light; D, *P. melaena* (BRNM 705053) – section in UV light. Scale bars: A = 200 μm; B–D = 100 μm, E, F = 10 μm

Sphagnum fuscum in a bog, 26 Jun. 1943, leg. A.V. Auer, det. T. Ulvinen (TUR 064173 – as *Pseudoplectania sphagnophila*, PRM 954134);

SPAIN, Asturias: Santa María del Puerto, Vega Címera, on *Sphagnum* sp., 30 May 2015, leg. P. Zapico, det. E. Rubio (PRM 954123 ☼).

SWITZERLAND, Vaud: Le Chenit, Le Sentier, vallée de Joux, among *Sphagnum* sp., 20 May 1945, leg. et det. J. Favre (G00566257 – isolectotype ☼).

Pseudoplectania ericae

FRANCE, Var: Hyères, Porquerolles island, under *Erica arborea* and *Cistus* sp., 28 Dec. 2015, leg. J.-M. Moingeon, det. G. Moyne (PRM 954131 ☼); Pyrénées-Orientales: Argelès-sur-Mer, close to Château de Valmy, under *Erica arborea*, 2 Dec. 2019, leg. et det. M. Gomez (MCVE 31255);

GREECE, Chalkidiki: Ierissos, Gavriadia, under *Erica* cf. *manipuliflora*, 17 Mar. 2018, leg. et det. C. Agnello (PRM 954125 ☼).

ITALY, Liguria: Genova, Sestri Levante, Punta Baffe, in the ground on roots and buried sticks of *Erica arborea*, 23 Dec. 2012, leg. et det. M. Carbone & F. Boccardo (MCVE 27581, PRM 954132 ☼).

PORTUGAL, Norte Region: Oleiros, Vila Verde, under *Erica* sp., 9 Feb. 2019, E. Sousa (pers. herb.).

SPAIN, Cáceres: Talayueta, 8 Feb. 2013, on sandy soil, leg. et det. E. Rubio (PRM 954124 ☼).

Pseudoplectania lignicola

CANADA, British Columbia: Fernie, Island Lake, on rotting and mossy wood of conifers, 17 Jul. 2011, leg. J. Harnisch, det. M. Carbone & C. Agnello (MCVE 27580 as *P. nigrella*).

CZECH REPUBLIC, Hradec Králové Region: Nový Hradec Králové, 50°10'45"N / 15°54'15"E, 260 m asl, among *Leucobryum glaucum* in a mixed forest of *Picea abies* and *Pinus sylvestris*, 1 Apr. 2011, leg. Z. Egertová & M. Sochor, det. S. Glejdura (HR 89756 - paratype ☼); Karlovy Vary Region: Vysoká u Staré Vody, 49°59'10"N / 12°31'51"E, 680 m asl, on an old twig and on needles among twigs, in a *Picea* monoculture, 6 May 2017, leg. M. Tauš, det. L. Zibarová (HR B000901 ☼); ibid., 29 Mar. 2018, leg. M. Tauš, det. V. Halasů (PRM 954130 ☼); Liberec Region: Hamr na Jezeře, 50°40'58.5"N / 14°51'35.9"E, 360 m asl, in a relict *Pinus* forest, 20 Mar. 2020, leg. J. Šťastný, det. V. Halasů (PRM 954129 ☼).

FINLAND, Varsinais-Suomi: Perniö, Mutainen, on a mossy stump of *Picea abies*, 6 Nov. 2004, leg. S. Tuominen, det. S. Huhtinen (TUR 172564, as *P. nigrella*).

SLOVAKIA, Banská Bystrica Region: Nízke Tatry Mts., ca 3 km N of Hiadel' village, 48°50'7.38"N / 19°18'39.84"E, 700 m asl, in a mixed forest (*Picea abies*, *Abies alba*, *Larix decidua*), on wood of *Abies alba*, 21 Apr. 2010, leg. et det. V. Kučera (SAV 105/17); Žilina Region: Zuberec – 1.9 km E of the St. Vendelín church, on the ground, in moss, on strongly rotten *Picea abies* trunk and immersed branches in moss, 49°15'34.4"N / 19°38'20.7"E, 825 m asl, 1 Apr. 2017, leg. M. Krivuš, det. A. Polhorský (pers. herb. A. Polhorský, AP17109 ☼).

Pseudoplectania melaena

CZECH REPUBLIC, Moravian-Silesian Region: Bílá, Salajka, 850 m asl, on a dead *Abies* trunk covered with mosses, 30 Jun. 1971, leg. et det. J. Kuthan (BRA CR33022 ☼); South Bohemian Region: Pivonice u Pohorské Vsi, Žofínský prales NNR, on a decaying stem of *Abies alba*, in a mixed forest with *Picea abies*, *Abies alba* and *Fagus sylvatica*, 9 Apr. 2008, leg. J. Hlásek, det. P. Špinar (CB 17686 ☼, BRNM 739398 ☼); South Moravian Region: Adamov, Křtinský potok valley, on a decaying trunk of *Abies alba*, 15 Apr. 1951, leg. F. Valkoun, det. F. Šmarda, rev. J. Moravec (BRNM 705053 ☼).

ITALY, Veneto: Belluno, Bosco del Cansiglio, on mossy dead wood of *Abies alba*, 25 Mar. 2012, leg. et det. E. Campo & M. Carbone (MCVE 27433, PRM 954133).

Pseudoplectania nigrella

AUSTRIA, Carinthia: Bodental, in *Picea abies* forest, 1050 m asl, 18 May 1976, leg. et det. H. Engel (KL BK-4914 – neotype ☼, PRM 954135 ☼).

CZECH REPUBLIC, Central Bohemian Region: Borovsko, 49°41'8.3"N / 15°6'42.9"E, 410 m asl, on the ground among moss, 28 Mar. 2016, leg. P. Včelička, det. V. Halasů (PRM 954128 ☼); Nová Ves pod Pleší, 750 m NNE of the Dolní Jezberná hill, 49°48'55.4"N / 14°14'27.2"E, 360 m asl, in a coniferous forest with *Picea*, *Pinus* and *Abies*, 2 Apr. 2018, leg. P. Včelička, det. V. Halasů (PRM 954126 ☼); Region of Vysočina: Jívoví, Šebeň, 49°24'32"N / 16°03'47"E, 560–626 m asl, under *Picea* and *Corylus*, 25 Mar. 2015, leg. V. Antonín et al., det. H. Ševčíková (BRNM 766905 ☼); South Bohemian Region: Třitím, Hněvkovický les, 49°10'49"N / 14°28'23"E, 445 m asl, on *Picea* needles among moss, 21 Mar. 2018, leg. M. Kofroňová, det. V. Halasů (PRM 954127 ☼); South Moravian Region: Borotín u Boskovic, Borotínské čihadlo, NW of the village, 400–480 m asl, in moss and needles on the ground, 18 May 1996, leg. et det. J. Vágner (BRNM 603997 ☼); Brumov u Lomnice, 600 m asl, in moss under *Alnus* sp. and *Picea abies*, 15 Apr. 2000, leg. et det. Z. Bieberová (BRNM 728142 ☼); Rudice, Seč quarry, 49°20'22"N / 16°43'33"E, on the ground under *Picea abies* and *Pinus sylvatica*, 4 Apr. 2019, leg. et det. V. Antonín & H. Ševčíková (BRNM 815866 ☼); Žďárec, 2000 m SE of the church, 460 m

asl, in moss under *Picea*, 17 Apr. 2005, leg. et det. Z. Bieberová (BRNM 728214 ☼).

ITALY, Valle d'Aosta: Morgex (AO), Arpy, on rotten mossy wood of *Picea abies*, 31 May 2009, M. Carbone (MCVE 27397).

SLOVAKIA, Trnava Region: Lakšárska Nová Ves - Bežniško military area, 200 m asl, in mosses on sandy soil, 25 Apr. 2008, leg. et det. V. Kučera (BRA CR14162 ☼); Žilina Region: Oravská Polhora – Slaná Voda, in a swampy *Picea* forest with *Sphagnum*, 200 m asl, 26 Apr. 2011, leg. I. Kautmanová, det. S. Glejdura (BRA CR17264 ☼); Pribylina, Podbanské, Hrdovo, behind the Kokavský bridge, in moss in a *Picea* forest, 27 Apr. 2011, leg. et det. I. Kautmanová (BRA CR17270 ☼).

Pseudoplectania tasmanica

AUSTRALIA, Tasmania: Duckhole Lake, on mossy wood, 22 Dec. 2012, leg. G. Gates (MCVE 27583 – holotype ☼).

Discussion

Apart from molecular analyses, delimitation of species within the genus *Pseudoplectania* is possible only through a combination of their ecology and morphological characters. The most recent key (Carbone et al. 2014) places emphasis mainly on the substrate, geography, size of apothecia, presence/absence of stipe and eventually its length, shape and furcation of paraphyses and the character of external hairs. Ascospores seem to be of a low importance being globose, hyaline, smooth (with an exception of *P. rywardenii*) and in the same size range (9.0–13.5 μm) in all known species. Glejdura et al. (2015) introduced the position of the membranous sheath surrounding the ascospores as a new diagnostic character. It seems that not only the position, but also the size of the sheath has a taxonomic value, although information on this character is lacking in some species. *Pseudoplectania africana* and the two phylogenetically closest species *P. tasmanica* and *P. ericae* share an eccentrically positioned sheath, which is distinctly smaller than in *P. nigrella*, *P. lignicola* and *P. melaena* [compare illustrations in Glejdura et al. (2015), Carbone et al. (2014), Rubio et al. (2013) and this paper]. Another important character shared by *P. africana*, *P. tasmanica* and *P. ericae* is the large yellow crystals located mainly in hymenium and ectal excipulum, appearing sulphur yellow in UV light.

Pseudoplectania africana, beside its genetic profile, can be characterised by the following main features: shortly stipitate or sessile apothecia, ascospores surrounded by a relatively small, eccentrically arranged membranous sheath and presence of large yellow crystals especially in the hymenium and ectal excipulum. So far, it is probably the only species of *Pseudoplectania* reported

from continental Africa. In the following, comparison of *P. africana* with other species of the genus is provided.

Pseudoplectania ericae differs in smaller apothecia, which do not exceed 1 cm in diameter, bi- to often trifurcate tips of paraphyses and wavy to straight external hairs (e.g. Donadini 1987; Pérez-De-Gregorio et al. 2009; Domergue 2012; Boccardo et al. 2014; Carbone et al. 2014; Uzun & Kaya 2018; Basso et al. 2019). It is a Mediterranean species typically growing on (or close to) roots of *Erica arborea*. It has been reported from France (Domergue 2012), Italy (Donadini 1987; Boccardo et al. 2014; Basso et al. 2019) including Sicily (Saitta 2020), Spain (Pérez-De-Gregorio et al. 2009; Rubio et al. 2013) including the Canary Islands (Ribes et al. 2015), and Turkey (Uzun & Kaya 2018), and molecular data have been available only for the Spanish and Italian collections. In the present study we have added French, Greek and Portuguese collections as well as a topotype collection from Porquerolles Island (France).

Pseudoplectania tasmanica, described from Tasmania (Australia), shares most of the microscopical features with *P. ericae*, but has apothecia up to 3 cm in diameter. Beside larger and darker apothecia it differs from *P. africana* in straight external hairs and sometimes trifurcate paraphyses (Carbone et al. 2014).

Pseudoplectania affinis, described from New Zealand, can be distinguished mainly due to the straight external hairs in combination with a very diverticulated apex of the paraphyses and lack of large yellow crystals (Carbone et al. 2014).

Pseudoplectania melaena (in its wide sense including the American *Peziza spongiosa* Peck) can be easily distinguished due to much larger apothecia (up to 6 cm in diameter), usually longer stipe, larger ascospore sheath (judging freshly ejected ascospores), often hooked paraphyses, straight external hairs, absence of large yellow crystals and growth on mossy decayed *Abies* trunks (Van Vooren et al. 2013, Carbone et al. 2014).

Pseudoplectania nigrella differs in somewhat darker apothecia, larger ascospore sheath and absence of large yellow crystals. It is a common vernal species in the northern hemisphere inhabiting mossy soil and trunks of conifers, mainly *Picea abies* (Carbone & Agnello 2012). As stressed by Carbone et al. (2014), *P. nigrella* most likely constitutes a complex of species, which are difficult to circumscribe at the current state of knowledge. At present we continue to follow Carbone et al. (2014) because a more detailed phylogenetic analysis conducted on this clade (data not shown here) seems to confirm the difficulty in separating the numerous lineages at species level.

Pseudoplectania lignicola differs from *P. africana* especially in its ascospores having a distinctly larger, centrally positioned sheath and by the absence of large

yellow crystals. The species was reported from Slovakia and Czechia and distinguished from *P. nigrella* based on morphology and ecology. Our phylogenetic analysis included a collection of *P. lignicola* from the type locality in Slovakia and the paratype collection from Czechia, and confirmed the species belongs to the intricate *nigrella*-clade. Two collections (TUR 172564 from Finland and MCV 27580 from Canada) previously sequenced and determined as *P. nigrella* (Carbone et al. 2014), fall into the *lignicola*-lineage as well. Re-examination of MCV 27580 has shown that a few ascospores (the most immature) were surrounded by a centrally arranged globose membranous sheath, which is a characteristic feature of *P. lignicola*.

Pseudoplectania stygia, reviewed by Carbone (2013), clearly belongs to the *P. nigrella* clade, but recent material collected from the type locality is needed to clarify its concept also from a phylogenetic point of view.

Pseudoplectania episphagnum is a sister species of *P. nigrella*, with which it shares many microscopical features (e.g. the coiled external hairs). It can be distinguished from *P. africana* by its ecology (growth in bogs on *Sphagnum* spp.), size of apothecia usually smaller than 1 cm, mostly bent paraphyses tips (Favre 1948; Kreisel 1962; Dennis 1969; Ulvinen 1976; Breitenbach & Kränzlin 1981; Kristiansen 1990; Bauer 1999; Dissing & Eckblad 2000; Spooner 2002; Carbone et al. 2014) and absence of large yellow crystals. In the tested specimens no or only very few hyaline crystals were found. In our study, LSU sequence of the isolectotype collection housed in the Conservatoire et Jardin botaniques de la Ville de Genève (G00566257; see Carbone & Agnello 2015) was obtained, and an additional specimen from Spain was analysed. The isolectotype collection is identical in LSU with the collections from Spain and Finland.

Pseudoplectania sinica has recently been described from China (Zhang & Zhang 2020) based on its asexual morph. Morphological comparison with *P. africana* is not possible, as the teleomorph of *P. sinica* is still unknown. Nevertheless, the genetic differences are distinct enough to be sure the species is not identical with *P. africana*.

Pseudoplectania carranzae is a species described from Costa Rica (Calonge & Mata 2002), as *Plectania carranzae*. Beside the geographical disjunction it differs from *P. africana* in shorter asci (170–200 × 10–14 μm), ectal excipulum formed by a *textura globulosa* and curved paraphyses. Unfortunately, the loan of the holotype collection, housed in CR, for morphological and sequencing studies was not possible due to Costa Rican restrictions. Presence of crystals is not mentioned by the authors.

Pseudoplectania ryvardeenii is so far known only from Venezuela, and it is distinguished from other *Pseudoplectania* species, including *P. africana*, mainly by its ornamented ascospores and the absence of the so-called hymenial hairs (Iturriaga et al. 2012). Unfortunately,

due to Venezuelan restrictions, it has not been possible to obtain the holotype on loan for morphological and genetic studies (Neida Avendaño, curator of VEN, pers. comm.). The absence of hymenial hairs appears almost impossible to us, being a characteristic present in all the species of *Pseudoplectania* and *Sarcosomataceae* [apparently except *Galiella amurensis* (Lj.N.Vassiljeva) Raitv. (Popov & Carbone 2021)]. Either way, the species as described in Iturriaga et al. (2012) seems to be distinct enough from our new species and therefore of low importance in this study.

Conclusion

Pseudoplectania africana is a new species described from South Africa, where it was collected on a decaying coniferous trunk. Among species of *Pseudoplectania* with available molecular data, *P. ericae* known from Europe and *P. tasmanica* from Tasmania are phylogenetically the closest. In contrast to other known *Pseudoplectania* species, these three species are characterised by presence of large yellow crystals in the tissues. *Pseudoplectania africana* represents the first published record of the genus from South Africa and probably also from the whole of African continent.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

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Authors' contributions

ZS performed the fieldwork, studied microscopical characters in the new species and crystals in most

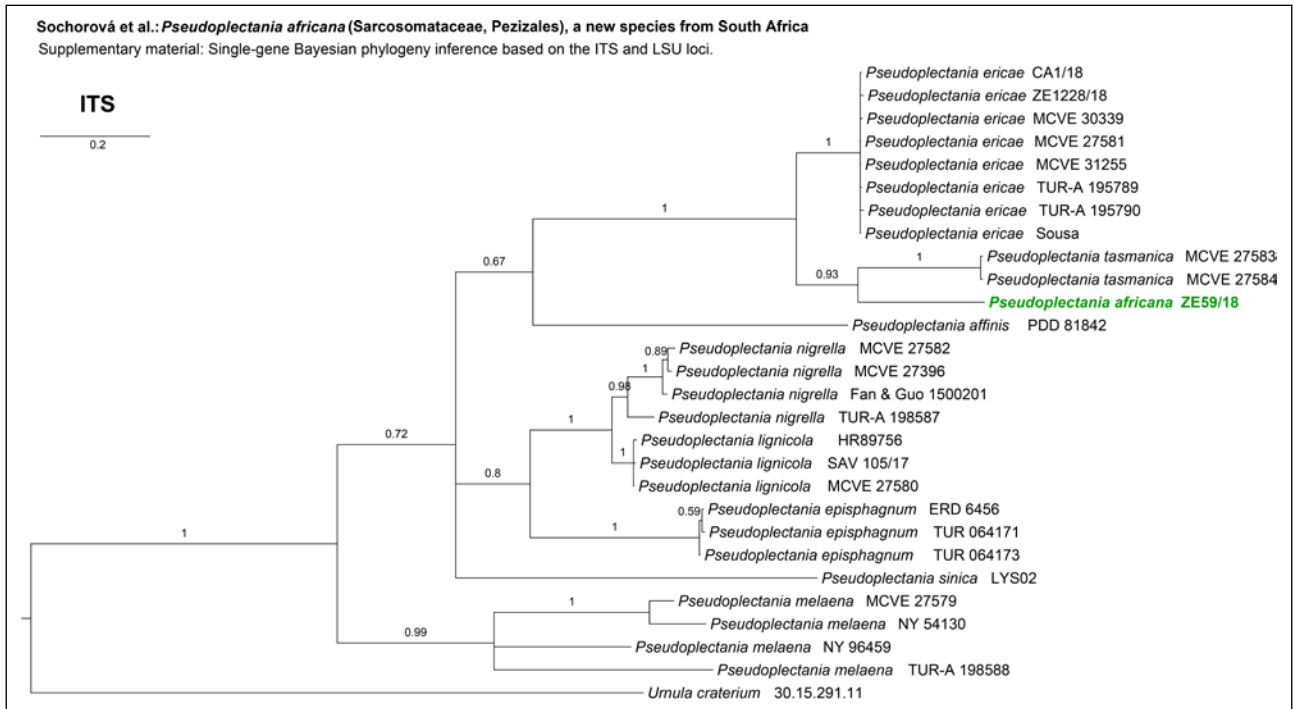
collections, wrote the article and took all of the photographs except those of nuclei, MC studied microscopical characters of the new species and wrote the first draft of manuscript, MSo performed phylogenetic analyses, MSe studied and documented nuclei in ascospores and AP studied crystals in five collections. All authors read and approved the final manuscript.

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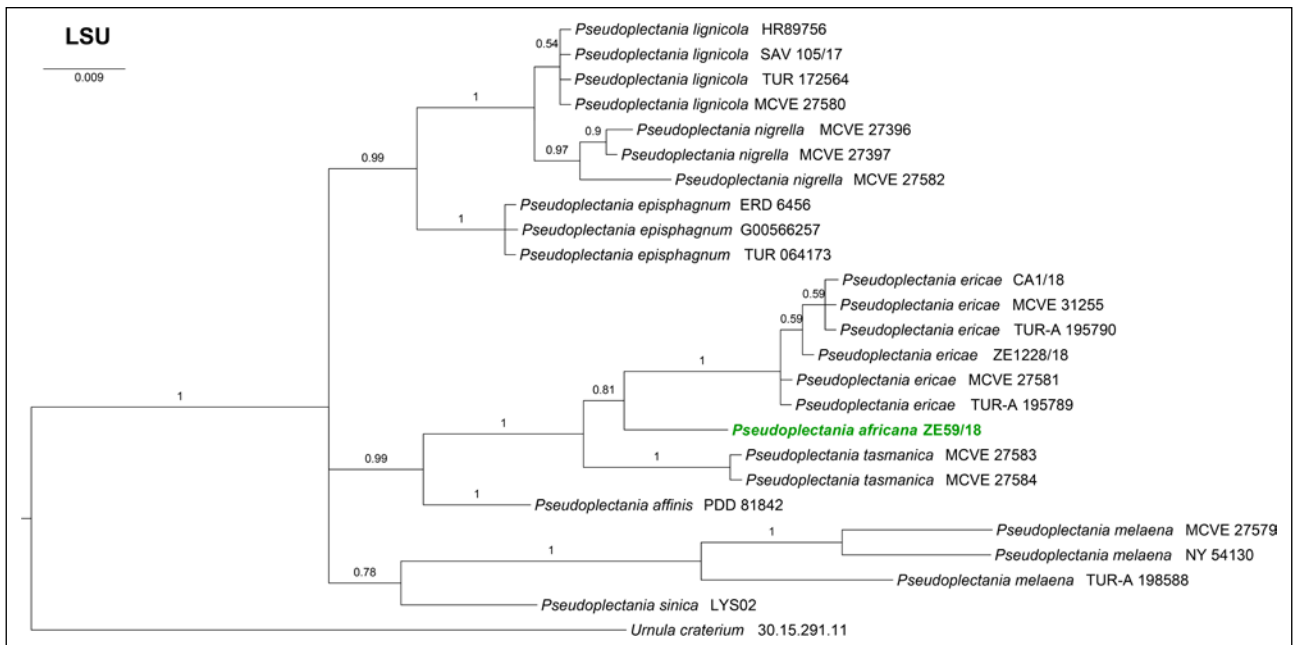
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Supplementary Material



Supplementary Figure 1. Bayesian phylogeny inference based on ITS sequences. Bayesian posterior probabilities are shown above branches; *Urnula craterium* serves as an outgroup.



Supplementary Figure 2. Bayesian phylogeny inference based on LSU sequences. Bayesian posterior probabilities are shown above branches; *Urnula craterium* serves as an outgroup.