# Phylogenetic and morphological studies in the genus Pseudoplectania (Ascomycota, Pezizales)

#### Matteo CARBONE Carlo AGNELLO Pablo ALVARADO

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**Summary:** New phylogenetic studies focused on the genus *Pseudoplectania* confirm the independence of the already known species *Pseudoplectania nigrella*, *P. melaena*, and *P. ericae*, although there seems to exist a species complex around both *P. nigrella* and *P. melaena*. The status of *Peziza spongiosa* is discussed. In addition, molecular results support the independence of *P. sphagnophila* in the sense of European authors. However, the original diagnosis of the latter does not fit the modern concept of this species, and so *P. episphagnum* is proposed as a substitute for the species growing in bogs on *Sphagnum* spp. Finally, the new species *P. affinis* and *P. tasmanica* are proposed to accomodate material from New Zealand and Tasmania, respectively. A review on the remaining known species of the genus is also discussed.

Keywords: ITS, 28S LSU, phylogeny, type study, Sarcosomataceae, Pseudoplectania, Plectania.

# Introduction

The genus Pseudoplectania was proposed by FUCKEL (1870) for the European species Pseudoplectania nigrella (Pers.) Fuckel (= Peziza nigrella Pers.). Recently, this species has been neotypified by CARBONE & AGNELLO (2012). The genus is discriminated from other members of the family Sarcosomataceae Kobayasi mainly by the spherical smooth spores. In the past, it was thought to be independent by many authors (Seaver, 1928; NANNFELDT, 1949; LE GAL, 1953; SANWAL, 1953; Berthet, 1964; Kreisel, 1962; Eckblad, 1968; Rifai, 1968; Korf, 1972, 1973). However, other researchers such as KORF (1982) and PADEN (1983) considered it to be a synonym of Plectania sect. Sphaerosporae Paden mainly due to the discovery of a Conoplea Pers. conidial state in Pseudoplectania melaena (Fr. : Fr.) Sacc., and because of the rounded spores in the early development of *Plecta*nia. From that time on, Paden's wide concept of *Plectania* was largely adopted (Korf & Zhuang, 1991; Medel & Chacòn, 2000; Calonge & Mata, 2002; CALONGE et al. 2003; BENKERT, 2005; PERÉZ-DE-GREGORIO et al., 2009). Still other authors (DONADINI, 1987; BELLEMÈRE et al., 1990) argued that Pseudoplectania was different on the basis of its ultrastructure and so they decided to preserve it as a separate genus. As shown by CAR-BONE et al. (2013), phylogenetic inference based on the neotype of the type species Pseudoplectania nigrella, showed that the genus Pseudoplectania is well supported as a sister clade to Plectania Fuckel.

Until now, about ten species have been described in *Pseudo-plectania*: *P. nigrella*, *P. kumaonensis* Sanwal, *P. melaena* (Fr.) Sacc. [= *P. vogesiaca* (Moug. & Nestl.) Seaver], *P. ericae* Donadini, *P. sphagnophila* (Pers.) Kreisel, *P. stygia* (Berk. & M.A. Curtis) Sacc., *P. carranzae* (Calonge & M. Mata) M. Carbone, Agnello & P. Alvarado, recently from Venezuela, *P. ryvardenii* Iturr., M. Mardones & H. Urbina (ITURRIAGA et al., 2012), and from Slovakia and Czech Republic, a new *Pseudoplectania* species belonging to the *P. nigrella* group (GLEJDURA et al., in press).

*Pseudoplectania fulgens* (Pers.) Fuckel has been excluded from this genus and combined into *Caloscypha* Boud. (BOUDIER, 1885). Subsequently this genus was placed into the new family *Caloscyphaceae* Harmaja (HARMAJA, 2002). This later move was supported by further phylogenetic studies (HANSEN & PFISTER, 2006; PERRY *et al.*, 2007; PFISTER *et al.*, 2012).

The present work aims to delimit the molecular and morphological species concepts of *Pseudoplectania nigrella*, *P. melaena*, *P. ericae* and *P. sphagnophila*.

## **Materials and methods**

**Morphological study.** — The microscopic studies were based on both fresh and dried specimens. Two optical microscopes were used: Olympus CX41 trinocular and Optika B353 trinocular with plan-achromatic objectives 4×, 10×, 40×, 60×, 100× in oil immersion. The following main reagents were used: Melzer's reagent, cotton blue, Congo red, KOH. Water mounts were used for the observation of the pigmentation and measurements. At least 30 spores were measured from each apothecium. Species concepts have been based on the original descriptions, and in some cases, on the type revisions.

**DNA extraction, amplification and sequencing.** — DNA was extracted and amplified from dried specimens following the methods published before (ALVARADO *et al.*, 2010, ALVARADO *et al.*, 2012). The primers LR1 or LR0R and LR5 or LR7 (VILGALYS & HESTER, 1990; VAN TUINEN *et al.*, 1998) were used to amplify and sequence the 28S nuclear large ribosomal region (nrLSU), while ITS1F and ITS4 (WHITE *et al.*, 1990; GARDES & BRUNS, 1993) were used to amplify the internal transcribed spacer region. Sequences were visually inspected searching for reading errors in MEGA5.0 (TAMURA *et al.*, 2011). Validated sequences were stored in GenBank under the accession numbers listed in table I.

Phylogenetic analyses. — ITS and 28S LSU sequences produced were aligned with their relatives and the closest matches obtained in BLAST searches. Sequences were first aligned in MEGA 5.0 software using its ClustalW application and then corrected manually. Two independent alignments were constructed: one including only ITS sequences, and another made of combined ITS-LSU data. A third alignment narrowed to the ITS2 region of some species in Pseudoplectania was also constructed to show the position of some partial sequences obtained. Aligned loci were subjected to MrModeltest 2.3 (NyLander, 2004) in PAUP\* 4.0b10 (Swofford, 2001). The best models were implemented in MrBayes 3.1 (RONQUIST & HUELSENBECK, 2003), where a Bayesian analysis was performed (ITS1-5.8S-ITS2-LSU data partitioned, 2 simultaneous runs, 6 chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after about 170K (ITS-only), 320K (ITS-LSU) and 10K (ITS2) generations. Significance thresholds were above 70% for bootstrap (BP) and 90% for posterior probability (PP).

# **Studied and sequenced collections**

Pseudoplectania affinis: New ZEALAND, Auckland, Waitakere, Scenic Drive, Spraggs Bush, on wood and sticks among leaf litter under Leptospermum J.R. Forst. & G. Forst. and mixed indigenous scrub, 24.11.2004, leg. C. Shirley (PDD 81842, holotype). Pseudoplectania nigrella: CANADA, British Columbia, Fernie, Island Lake, on rotting and mossy wood of conifers, 17.07.2011, leg. J. Harnisch, det. M. Carbone & C. Agnello (MCVE 27580). ITALY, Lombardia, Bergamo, Gromo, loc. Spiazzi, on a mossy stump of probably Picea abies (L.) H. Karst., even if also Abies alba Mill. was present, 01.05.2009, leg. F. Calledda & M. Carbone, det. M. Carbone (MCVE 27396). ITALY, Friuli-Venezia-Giulia, Udine, Prato Carnico, loc. Val Pesarina, on buried and mossy wood and in the mossy ground under Picea abies, 900 m a.s.l., 13.04.2013, leg. et det. M. Carbone, E. Campo (MCVE 27582). U.S.A., Washington, Pend Oreille County, near hwy 31 on road NW of Slate Cr. Rd., on mossy soil under mixed conifers, 30.04.1999, leg. et det. A.D. Parker (TUR-A 198587). Pseudoplectania melaena: FRANCE, department of Doubs, in the village of Gevresin, into the forest of Levier, near the "Maison forestière du Rondé", LAT 46.95834, LNG 6.0694, on fallen mossy branch of Abies alba, 07.04.2008, leg. et det. J.-M. Moingeon & N. Van Vooren (MCVE 27579, duplicate of NV 2008.04.02 Van Vooren's pers. herb.). U.S.A., Vermont, Rutland County, Mount Tabor, Green Mt. National Forest, on fallen branch in wet moss under Abies balsamea (L.) Mill., 12.05.1947, leg. J. R. Hansbrough (NY 96459, as Pseudoplectania vogesiaca). U.S.A., Virginia, Smyth County, Jefferson National Forest, Whitetop Mountain, 36°38'17"N, 81°36'21"W, ca. 1675 m a.s.l., in humid hardwoodconifer forest on summit of mountain, 05.04.2008, leg. et det. R.C. Harris (NY 54130, as Pseudoplectania vogesiaca). U.S.A., Washington, Pend Oreille County, Boundary dam overlook Rd., on sticks among conifer litter under Abies, Tsuga and Thuja, 21.04.2006, leg. et det. A.D. Parker (TUR-A 198588). Pseudoplectania ericae: ITALY, Liguria, Genova, Sestri Levante, loc. Punta Baffe, in the ground on roots and buried sticks of Erica arborea L., 23.12.2012, leg. et det. M. Carbone & F. Boccardo (MCVE 27581). Pseudoplectania episphagnum: FINLAND, Perä-Pohjanmaa, Ranua, 6 km north of the church, in a bog, on Sphagnum fuscum (Schimp.) H. Klinggr., 26.06.1943, leg. A.V. Auer, det. T. Ulvinen (TUR 064173 as Pseudoplectania sphagnophila). FIN-LAND, Varsinais-Suomi, Masku, Karevanrahka, side of a bog among Sphagnum, 30.05.1948, leg. A. Vuorisalo, det. T. Ulvinen (TUR 064171 as Pseudoplectania sphagnophila). Pseudoplectania tasmanica: Australia, Tasmania, Duckhole Lake, on mossy wood, 22.12.2012, leg. G. Gates (MCVE 27583, holotype). Same place, along the same trail, 22.12.2012, leg. G. Gates (MCVE 27584).

### Other studied but not sequenced collections

Pseudoplectania nigrella: CANADA, Aurora, Ontario, on rotten stump, 02.05.1936, leg. et det. R.F. Cain (TUR 040065). East of Schefferville airport, Québec, on rotten stump, 08.07.1967, leg. E. Kankainen, det. S. Huhtinen (TUR 069195). Marble Lake, Newfoundland-Labrador, 13.07.1967, leg. E. Kankainen, det. S. Huhtinen (TUR 069196). Churchill Falls, Newfoundland-Labrador, on rotten stump, 28.07.1968, leg. P. Kallio, det. S. Huhtinen (TUR 069194). ITALY, Valle d'Aosta, Aosta, Morgex, Arpy, on rotten mossy wood of Picea abies, 31.05.2009, leg. et det. M. Carbone (MCVE 27397). Pseudoplectania episphagnum: FINLAND, Varsianis-Suomi, Masku, Karevanrahka, west side of a bog, among Sphagnum papillosum Lindb., 01.06.1941, leg. A.V. Auer, det. T. Ulvinen (TUR 064177 as Pseudoplectania sphagnophila). Inarin-Lappi, Inari, Inarinjärvi lake, south of Vironniemi, in a bog, among Sphagnum sp. 09.07.1962, leg. Y. Mäkinen, det. S. Huhtinen (TUR 187314 as Pseudoplectania sphagnophila). Varsianis-Suomi, Masku, Karevansuo, in a bog, among Sphagnum sp., 08.05.1990, leg. et det. T. Lindholm (TUR-A 149587 as Pseudoplectania sphagnophila). Pseudoplectania melaena: U.S.A., Maine, Oquossoc Camp., May 1916, leg. W.C. Sturgis (NY). Vermont, Mt. Mansfield, on decaying firs wood, 18.05.1880, leg. C.G. Pringle #791 as Peziza spongiosa Peck, named P. melaena by J.W. Paden (NY). No locality, no date, F.J. Seaver (NY 00914776, filed as the "type" of Peziza spongiosa). Vermont, Mt. Mansfield, no date, leg. C.G. Pringle, filed as Peziza spongiosa Peck, but named P. melaena by J.W. Paden (NY 00914777). Pseudoplectania affinis: New ZEALAND, Northland, Waipoua S.F., track between Yakas Kauri and Forest H.Q., on ground. 23.07.1981, leg. G.J. Samuels, E. Horak, A.P. Hawthorne, R.H. Petersen, det. J. Paden (PDD 42064, as Pseudoplectania nigrella). Northland, Waipoua Forest, on debris, 21.06.1981, leg. G.J. Samuels & E. Horak, det. G.J. Samuels (PDD 62464, as Pseudoplectania nigrella). Taupo, Wairakei, Craters of the Moon thermal area, on ground, 22.07.1996, leg. R.E. Beever, det. P.R. Johnston (PDD 66228, as Pseudoplectania nigrella). Pseudoplectania cf. affinis: New Zealand, Auckland, Hunua Ranges, Mangatangi Dam, July 1981, leg. G.J. Samuels & P.R. Johnston, det. J.W. Paden (PDD 41653, as Pseudoplectania nigrella). Auckland, Hunua Ranges, Mangatangi Dam, no date, leg. G.J. Samuels & P.R. Johnston, det. J.W. Paden (PDD 41476, as Pseudoplectania nigrella). Auckland, Waitakere Ranges, Cascade Kauri Park, on Agathis australis, 01.10.1980, leg. G.J. Samuels & P.R. Johnston, det. J.W. Paden (PDD 41652, as Pseudoplectania nigrella).

**TABLE I** – Samples sequenced for the present study,

 GenBank codes.

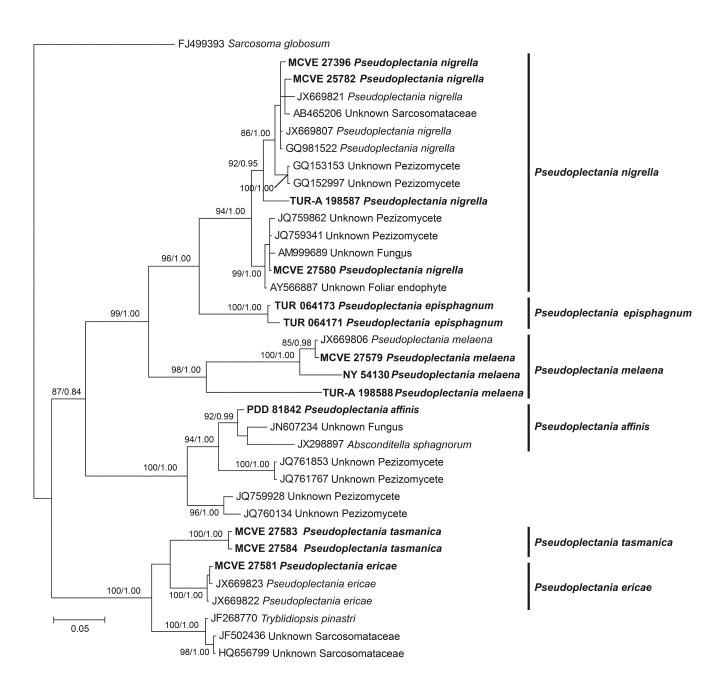
Taxon	Voucher Strain	ITS	28S nrLSU
Pseudoplectania ericae	MCVE 27581	KF305721	KF305731
Pseudoplectania melaena	MCVE 27579	KF305717	KF305728
Pseudoplectania melaena	TUR-A 198588	KF305719	KF305729
Pseudoplectania melaena	NY 54130	KF305718	KF305730
Pseudoplectania melaena	NY 96459	KF305720	-
Pseudoplectania nigrella	MCVE 27396	KF305715	KF305725
Pseudoplectania nigrella	MCVE 27580	KF305713	KF305726
Pseudoplectania nigrella	MCVE 27582	KF305716	KF305727
Pseudoplectania nigrella	TUR-A 198587	KF305714	-
Pseudoplectania affinis	PDD 81842	JX669826	X669865
Pseudoplectania tasmanica	MCVE 27583	KF305722	KF305732
Pseudoplectania tasmanica	MCVE 27584	KF305723	KF305733
Pseudoplectania episphagnum	TUR 064171	KF305712	-
Pseudoplectania episphagnum	TUR 064173	KF305711	KF305724
Urnula craterium	30.15.291.11	KF311230	KF305734

# Results

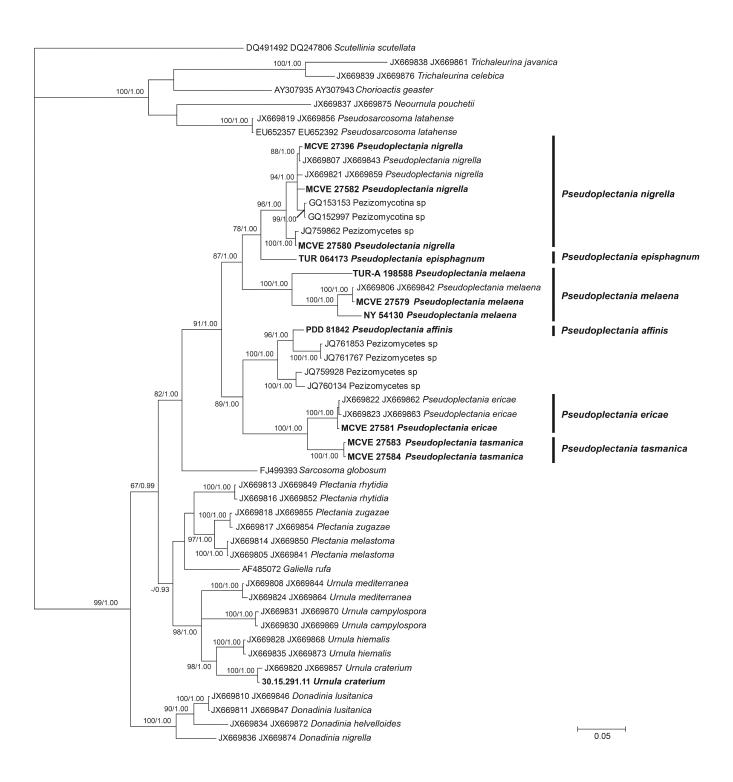
### **Phylogenetic results**

The alignment of ITS region included 282 of 562 variable sites, while the one combining ITS-LSU regions was composed of 593 variable sites among 1147 total bases. In turn, ITS2 alignment included 129 bases in 315 sites. The results of all analyses were consistent with each other with regards to the overall topology of the genus Pseudoplectania. A major clade formed by P. nigrella, P. melaena and P. episphagnum was recognized (Figs. 1, 2), while P. ericae and P. tasmanica seemed themselves to be closely related. Pseudoplectania affinis was suggested to be a close relative of these species (ITS-LSU inference), or else, to represent an independent clade (ITS alone phylogeny). This species is related to some unidentified sequences in public databases which could represent sister species (Figs. 1, 2), while some others are close enough to be considered conspecific. One of these, identified as Absconditella sphagnorum, is probably misidentified, since it seems clearly different from all other sequences of this genus stored in public databases.

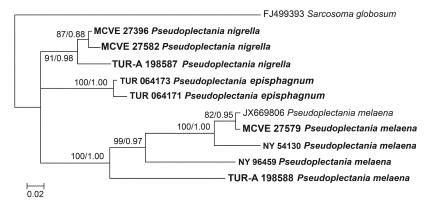
Some degree of genetic variability was detected between the different samples of *P. nigrella* as well as among those of *P. melaena*, al-



**Fig. 1** — Bayesian consensus tree obtained from the ITS sequence alignment of genus *Pseudoplectania*. Values next to nodes represent maximum likelihood bootstrap proportions (BP) and bayesian posterior probabilities (PP), respectively. Only nodes supported or almost supported by both analyses were annotated. Values higher than 70 BP and 90 PP were considered significant. Names highlighted in **bold** represent those sequences obtained *de novo* for the present study.



**Fig. 2**— Bayesian consensus tree obtained from the combined ITS-LSU sequence alignment of genus *Pseudoplectania* and related genera in the families *Sarcosomataceae* and *Chorioactidaceae*. Values next to nodes represent maximum likelihood bootstrap proportions (BP) and bayesian posterior probabilities (PP), respectively. Values higher than 70 BP and 90 PP were considered significant. Names highlighted in **bold** represent those sequences obtained *de novo* for the present study.



**Fig. 3** — Bayesian consensus tree obtained from the ITS2 sequence alignment of *Pseudoplectania melaena* and other related species in the genus *Pseudoplectania*. Values next to nodes represent maximum likelihood bootstrap proportions (BP) and bayesian posterior probabilities (PP), respectively. Only nodes supported or almost supported by both analyses were annotated. Values higher than 70 BP and 90 PP were considered significant. Names highlighted in **bold** represent those sequences obtained *de novo* for the present study.

though it was not related to any relevant morphological or ecological feature, and hence, the differences were considered by now to represent intraspecific variability. In accordance with this view, the partial ITS sequence of the specimen of *P. spongiosa* from Vermont suggest this collection should be accepted as a *P. melaena*.

### **Taxonomic results**

Pseudoplectania nigrella (Pers. : Fr.) Fuckel, Jahrb. Nassau. Ver. Naturk., 23-24: 324 (1870).

Basionym: Peziza nigrella Pers., Syn. meth. fung.: 648 (1801).

#### Synonyms:

≡ Lachnea nigrella (Pers.: Fr.) Gillet, Champ. Fr., Discom.: 78 (1879); Plectania nigrella (Pers.: Fr.) P. Karst., Acta Soc. fauna fl. Fenn., 2 (6): 119 (1885); Crouania nigrella (Pers.: Fr.) Hazslinszky, Math. Term.-Tud. Közlem., 21: 261(1886); Sepultaria nigrella (Pers.: Fr.) Lambotte, Mém. Soc. Roy. Sci. Liège, sér. 2, 14: 301 (1887); Sphaerospora nigrella (Pers.: Fr.) Massee, Brit. Fung.-Fl., 4: 296 (1895); Otidella nigrella (Pers.: Fr.) J. Schröt., Kryptog.-Fl. Schlesien; Namen Schles. Gesells. vaterländ. Cultur, 3 (2): 48 (1908).

= Helvella hemisphaerica Wulfen (ut "Elvela hemisphaerica"), Schrift. Berl. Ges. naturf. Freunde, 8: 141 (1788).

This species has been typified and treated in detail by CARBONE & AGNELLO (2012), although these authors studied exclusively Euro-

pean collections. In the present study additional collections coming from North America were also included. The macro-morphological and microscopic characters did not show any striking difference from the European material examined. Some degree of genetic variability was already detected by the authors among European samples (CARBONE *et al.*, 2013). However, samples coming from the American continent do not seem to constitute a monophyletic clade. In absence of any morphological, physiological, ecological or geographical feature explaining the observed genetical diversity, this is here interpreted *ad interim* as intraspecific variability of a single taxon, *P. nigrella*. This could be regarded as a complex of species or lineages, with different genotypes representing partially (or recently) isolated populations. Further studies involving more samples are required to solve this question.

Pseudoplectania episphagnum (J. Favre) M. Carbone, Agnello & P. Alvarado, comb. nov. — MB 807894

**Basionym:** *Pseudoplectania nigrella* var. *episphagnum* J. Favre, *Beitr. Kryptfl. Schweiz*, 10 (3): 212 (1948).

**Misapplications:** *Pseudoplectania sphagnophila* (Pers.) Kreisel *sensu* KREISEL (1962) *et auct. plur. non Peziza melania* var. *sphagnophila* Pers., *Mycol. Eur.*, 1: 240 (1822) *et Peziza melaena* var. *sphagnophila* Fr., *Syst. mycol.*, 2: 61 (1822) = ? *Pseudoplectania melaena* (Fr. : Fr.) Sacc. (see discussion below).



Plate 1. — *Pseudoplectania nigrella* (MCVE 25782). Moist specimens *in situ*. Photo: M. Carbone

**Plate 2.** — *Pseudoplectania nigrella* (MCVE 25782). Fresh (less moist) specimens *in situ*. Photo: M. Carbone



Plate 3. — *Pseudoplectania episphagnum*. Dried specimens from TUR-A 064171. Photo: M. Carbone

PERSOON (1822) described Peziza melania var. sphagnophila to accomodate Ehrenberg's material, with the following diagnosis: "Submagna, stipitata, cupula campanulata intus atra, extus rugosa subumbrina, stipite subcrasso, fibrillis radicato. Hab. in Germaniae paludosis. Ehrenb. Cupula in specimine transmisso, farinacea et valde plicata, ultra unc. lata. Stip. 2 lin. altus, fibrillis muscos obtegit". FRIES (1822) sanctioned this taxon as Peziza melaena var. sphagnophila in the following terms: "campanulata, rugosa, subpruinosa, umbrina, intus atra, stipite brevi crasso fibrillis radicato. Pers. I. c. Cupula unciam lata, subplicata. Stipes 2 lin. altus. In paludosis Germaniae. Ehrenberg. (v.s.)". Both authors seem to have studied dried material, collected and sent to them by Ehrenberg, and they reported a cup size measuring 2.5–3 cm in diameter, and a stipe length of about 4 mm. These measures definitely contrast with the modern concept of this species, based mainly on the work by KREISEL (1962) and other authors (Dennis, 1969; Ulvinen, 1976; Breitenbach & Kränzlin, 1981; Kris-TIANSEN, 1990; BAUER, 1999; DISSING & ECKBLAD, 2000). We have done extensive research to find out if the original material still exists. According to the Index Herbariorum, Ehrenberg's collections are housed in CWU, HAL, JE, MPU and VT, even though some samples (or duplicates) of this author are known to be present also among Persoon's and Fries' collections. Regarding the five herbaria mentioned, we unfortunately were informed by the respective curators that no samples of this taxon were present. They were also absent from Persoon's collections in L, LG, CWU and Fries' in LD, GH and UPS-Fries, although in the latter some of Ehrenberg's samples were present. According to STAFLEU & COWAN (1976: 727), many other herbaria possibly house Ehrenberg's duplicates, and so at present we cannot exclude that, sooner or later, the original material could turn up.

FAVRE (1948) described *Pseudoplectania nigrella* var. *episphagnum* with the following diagnosis: "A typo differt minore statura; stipite curto, crasso; receptaculo minus expanso frequenter urceolato. Inter *Sphagna*". This taxon was synonymized with *P. sphagnophila* by KREISEL (1962), who based his opinion on personal collections but cited no original material of the latter species. The species known as *P. sphagnophila* after Kreisel's article, is small (10–12 mm diam., in fresh state), with very similar (if not identical) microscopic characters to those of *P. nigrella*, but differing from it mainly because of its ecology and a very short and stout pseudostipe. This species seems to be exclusively associated with *Sphagnum* spp. in bogs (FAVRE, 1948; KREISEL, 1962; DENNIS, 1969; ULVINEN, 1976; BREITENBACH & KRÄNZLIN, 1981; KRISTIANSEN, 1990; BAUER, 1999; DISSING & ECKBLAD, 2000; SPOONER, 2002; SANDOVAL, 2012). Our macro- and micro-morphological observations are in agreement with those available in literature.

Thus we claim that this *Sphagnum*-inhabiting taxon does not match the original *P. sphagnophila* species concept, which represents — according to the diagnosis — very probably *P. melaena*. In

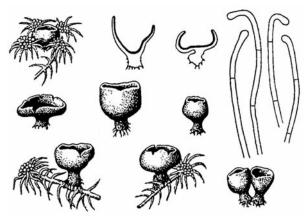


Plate 4. — Favre's original plate (adapted) of Pseudoplectania nigrella var. episphagnum

fact, the presence of a real stipe and the size of the dried apothecia (according to our results size is a good taxonomical character in the genus *Pseudoplectania*) fit very well with this taxon. For these reasons, and at least until the original material of *P. sphagnophila* is located, we propose to abandon the use of the epithet *sphagnophila* for Favre's taxon.

As mentioned above, the *Sphagnum*-inhabiting taxon producing small apothecia and without a true stipe, currently known as *P. sphagnophila*, could be accommodated under the epithet *episphagnum* created by FAVRE (1948). The ITS and LSU genetic data obtained from two Finnish collections perfectly matching the *episphagnum* concept, suggest that this species should be considered as an independent sister taxon to *P. nigrella*.

**Pseudoplectania melaena** (Fr. : Fr.) Sacc., *Syll. fung.*, VIII : 165 (1889).

Basionym: Peziza melaena Fr., Syst. mycol., II: 60 (1822).

#### Synonyms:

 $\equiv$  Melascypha melaena (Fr. : Fr.) Boud., Icon. mycol., liste prélim.: 3 (1904);  $\equiv$  Plectania melaena (Fr. : Fr.) Paden, in Korf, Mycotaxon, 14 (1): 1 (1982).

= Peziza melanea Pers., Mycol. Europ., 1: 239 (1822), p.p.; Aleuria melanea (Pers.) Gillet, Champ. Fr. Discom.: 37 (1879) ["melania"].

= *Pseudoplectania vogesiaca* (Moug. & Nestl.) Seaver, *Mycologia*, 5 (6): 300 (1913); *Peziza vogesiaca* Moug. & Nestl., *Stirp. Crypt. Vog.-Rhen.*, 6, no. 584 (1818); *Peziza melanea* var. *vogesiaca* (Moug. & Nestl.) Pers., *Mycol. Europ.*, 1: 239 (1822) ["melania"].

= Peziza spongiosa Peck, Bot. Gaz., 5 (3): 35 (1880); Bulgaria spongiosa (Peck) Peck, Bot. Gaz., 6 (7): 240 (1881); Pulparia spongiosa (Peck) Sacc., Syll. fung., VIII: 612 (1889) (see discussion); non Rhizina spongiosa Berk. & M.A. Curtis, in Berkeley, J. Linn. Soc., Bot., 10 (46): 364 (1869).

This species has been recently studied in depth and lectotypified by VAN VOOREN *et al.* (2013), who reported *Peziza spongiosa* Peck as a synonym, in agreement with SEAVER (1913) and PADEN (1967). In fact, the original diagnosis and description of *Peziza spongiosa* (PECK, 1880) match perfectly with the species concept of *P. melaena* in its basic macro- and microscopic features. For an immediate comparison we here report the diagnosis: "Cups large, one inch or more broad, concave or infundibuliform, thin, soft, externally black, the hymenium blackish brown, becoming porous when old; stem short, slender, black; asci cylindrical; spores uniseriate, globose, smooth, granular within and often uninucleate, .0005 of an inch in diameter; paraphyses filiform, colored, circinate or uncinate-curved at the tips.



**Plate 5.** — *Pseudoplectania melaena*. Fresh specimens *in situ*. Photo: M. Carbone

Plate 6. — *Pseudoplectania melaena* (TUR-A 198588). Fresh specimens *in situ*. Photo: A. Parker

Ground under fir trees. Near the summit of Mt. Mansfield, Vermont. May. C.G. Pringle".

A topotype specimen of *P. spongiosa* (see frame below), as well as other material from both western and eastern USA were examined, and did not show any important or striking macro- and micro-morphological difference from *P. melaena*. Unfortunately, no molecular data could be recovered from the topotype specimen, while NY 96459 (also coming from Vermont) and NY 54130 (from Virginia), both matching the *P. spongiosa* concept, seem to be monophyletic with the European samples. The same can be said for TUR-A 198588, coming from the Pacific Northwest of USA and matching the *P. melaena*/spongiosa concept.

From the data in our hands, we suggest the acceptance of a broad phylogenetic species concept for the same reasons as described above for *P. nigrella*. American and European samples do not seem to constitute independent monophyletic clades so far, but a variation continuum.

### Revision of Peziza spongiosa (coll. NY 00914776)

#### **Macroscopic characters**

The collection is in a good state and composed of stipitate apothecia up to 3 cm in diam. and with a stipe up to 2 cm long. Hymenium is dark brownish with greenish tints. External surface is dark brown to blackish, and rugulose.

#### **Microscopic characters**

**Spores** globose, 11.5–13 µm, smooth, with granular content, wall 1–1.2 µm thick, on the external surface traces of a gelatinous matter are present. Asci cylindrical,  $250-300 \times 12-15 \mu m$ , inamyloid, operculate, 8-spored, with walls thickened up to 1  $\mu m$  and with a flexuous, tapered base. Paraphyses cylindrical, 1.5-2 µm in diam., septate, branched, sometimes anastomosed, more or less diverticulated or curved to hooked at the apex or with nodules; very slightly brownish in the upper half due to an extracellular amorphous pigment. **Hymenial hairs** cylindrical, 3 µm wide, with a single septum at the base, straight to curved at the apex; a little more brownish than the paraphyses. Subhymenium of thick textura intricata with hyphae cylindrical, septate; uniformly brown to brownish at low magnification. Medullary excipulum of textura intricata with hyphae cylindrical, hyaline, up to 8 µm wide, very slightly thick-walled (up to 0.4 µm). Ectal excipulum arranged as a textura globulosa-angularis to angularis with cells up to 20 µm long or wide, with thickened walls; dark brown mainly for an epimembranaceous and extracellular pigment. External hairs very inconspicuous and difficult to find, but those seen were cylindrical to slightly tapered upward, 7-8 µm diam., on average less than 100 µm long, smooth, walls up to 1 µm thick, septate, mostly straight or also very slightly curved; light brown for an epimembranaceous pigment.

#### **Brief note**

Regarding the discussion below on collection NY 00914776, it must be noted that our studies on that material did not highlight any macro- and microscopic morphological difference.

#### Notes on the type of Peziza spongiosa

When we started this study we were informed that a type specimen of *Peziza spongiosa* was present in the New York State Herbarium (NYS) under the access code NYS 2902 but it was not available for loan (Lorinda Leonardi, pers. comm., Collections Manager, Bryology and Mycology). Thanks to the courtesy of L. Leonardi, we have checked the labels of this collection (Plate 8), where it is stated it was collected by C.G. Pringle (#174) from Mt. Mansfield, Vt. on May 24, 1879, and so it must be regarded as the type specimen.

Due to that temporary unavailability, we then asked the New York Botanical Garden Herbarium (NY) if they had material under the names *melaena/spongiosa/vogesiaca* coming from Vermont or nearby States. We were informed that some collections matched our request and that they also had the type of *Peziza spongiosa*. When the loan arrived we saw that the collection NY 00914776 was in "type cover" due to a Seaver's note: "*Peziza spongiosa* Peck (part of type)" (Plate 7, fig. C). We could accept Seaver's note, but because we cannot be sure that these three apothecia come from Pringle's original material, we believe that this collection should not be regarded as a "type" (perhaps, at least, as a duplicate, i.e. an isotype).

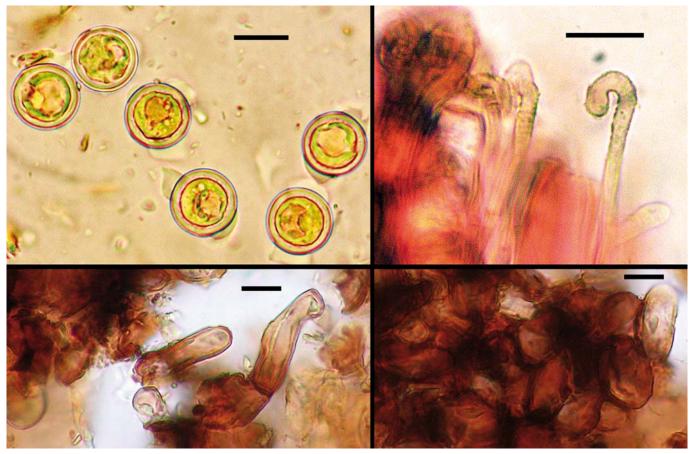
On the contrary, among the loaned collections there is one from Ellis' collection belonging to C.G. Pringle. The label of this collection reports : "*Peziza spongiosa* Peck, *n. sp.* On decaying fir wood. Mt. Mansfield, Vt. May, 18. 1880". Since the protologue was published in March 1880, it seems quite obvious that this collection could not represent the type of *Peziza spongiosa*. However, the protologue reports "near the summit of Mt. Mansfield, Vermont. May. C.G. Pringle", and so we decided to study this topotype collection obtaining the above data.



Plate 7. — A-B : Pringle's topotype collection of *Peziza spongiosa*. C-D : Seaver's "type" collection of *Peziza spongiosa*. Scale bars = 1 cm, valid for samples only. Photo: M. Carbone

14 a fingues from 117. Inansfield which 1 thought might possible may COLL. N. Y. STATE. Nom. Pulparia spongiosa (9k.) Sacc. Loc. Mt. Mansfield, Vt. Leg. C. G. Pringle May 79 (Bulgaria spongiosa 9k.) 174 New York State Museum Herbarium (NYS) Holotype Peziza spongiosa Peck Mount Mansfield, Vermont May 1879 C. G. Pringle 174 Mycology Type Database NYS # 2902

Plate 8. — Annotations on holotype of *Peziza spongiosa* in NYS Herbarium. Photo: L. Leonardi.



**Plate 9.** — *Peziza spongiosa* Pringle's "topotype" collection. Clockwise : spores in water, paraphyses tips in Congo red, ectal excipulum in water, short external hairs in water. Scale bars = 10 μm. Photos: M. Carbone

#### Pseudoplectania ericae Donadini, Mycol. Helv., 2(2): 225 (1987)

#### Synonym:

≡ *Plectania ericae* (Donadini) Roqué, *Fungi non Delineati*, 44: 43 (2009).

Up to now this species has been rarely recorded, always found around the Mediterranean basin growing on *Erica arborea* (DONA-DINI, 1987; PÉREZ-DE-GREGORIO *et al.*, 2009; DOMERGUE, 2012), recently has been recorded a little far from the sea and (probably) without *Erica* sp. (RUBIO *et al.*, 2013). BENKERT (2005) was skeptical about its independence from *P. nigrella* considering the differences found by DONADINI (*op. cit.*) were not important enough for their discrimination at the species level. However, the collections studied in the present work seem to confirm the observations reported by Donadini and the other mentioned authors. We have even found that the presence of wavy to straight (not coiled) external hairs could be considered as another important diagnostic feature to discriminate *P. ericae* from the *P. nigrella*-complex and *P. episphagnum*. In addition, this hypothesis is supported by molecular data, which clearly suggest *P. ericae* is an independent species, sister to *P. tasmanica* and some unidentified sequences (JF268770 was removed from Gen-Bank because the source organism could not be confirmed).



Plate 10. — *Pseudoplectania ericae* (MCVE 27581). Fresh specimens *in situ*. Photo: M. Carbone

Plate 11. — *Pseudoplectania ericae* (MCVE 27581). Fresh specimens *in situ*. Photo: M. Carbone

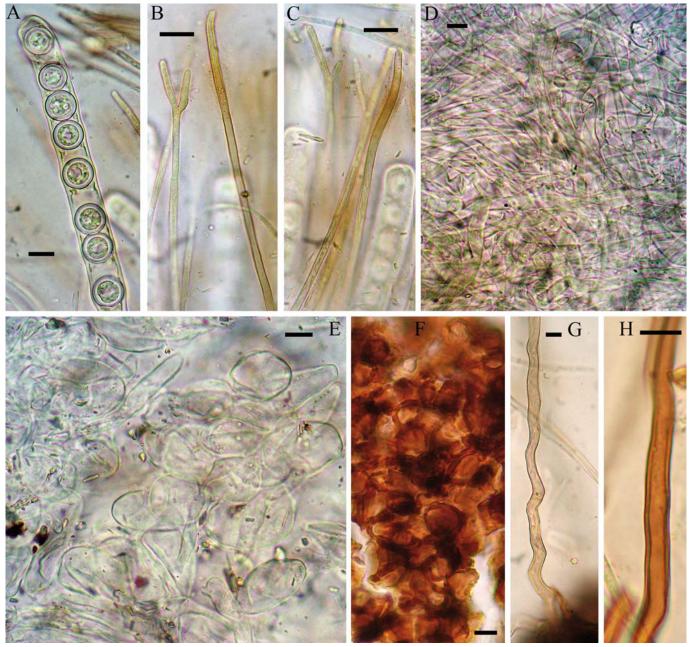


Plate 12. — Pseudoplectania ericae. Microscopic characters (all in water mounts).
A: ascus and spores; B-C: paraphyses and hymenial hairs; D: medullary excipulum; E: globose elements of the inner part of ectal excipulum; F: external layer of the ectal excipulum; G: waving external hair; H: external hair.
Scale bars = 10 µm. Photos: M. Carbone



The collections studied in the present work did not show any striking different macro- and micro-morphological features if compared to the detailed descriptions reported first by DONADINI (1987) and then by PÉREZ-DE-GREGORIO *et al.* (2009) and DOMERGUE (2012). Thus we publish here only a color plate summarizing the main microscopic features.

**Plate 13.** — *Pseudoplectania ericae* (MCVE 27581). Fresh specimens *in situ*. Photo: M. Carbone



Plate 14. — Pseudoplectania affinis (holotype). Fresh specimens. Photo: C. Shirley

**Pseudoplectania affinis** M. Carbone, Agnello & P. Alvarado, *sp. nov.* — MB 807952

**Etymology:** from latin *affinis* which means "relative", "related to", "kindred" due to its affinities with the other *Pseudoplectania* species.

**Diagnosis:** differs morphologically from *Pseudoplectania nigrella* and allied species mainly for the straight external hairs; from *P. melaena* for the smaller size of apothecia, the lack of a stipe, and not curved paraphyses tips.

Holotype: PDD 81842; New Zealand, Auckland, Waitakere, Scenic Drive, Spraggs Bush, 24.11.2004, *leg*. C. Shirley.

**Ascertained misapplications:** *Pseudoplectania nigrella sensu* PADEN (1983, *p.p.*, collections from New Zealand).

#### **Macroscopic characters**

**Apothecium** up to 2 cm in diameter, cup-shaped, becoming more flat with maturity. **Hymenium** smooth, polished, black. **External surface** rough, wrinkled, pubescent, mostly black. **Stipe** absent. **Flesh** dark grey to blackish, rubbery.

#### Microscopic characters

**Spores** globose,  $(9.5-)10-11.5(-12) \mu m$  in diam., smooth, with vacuolar content and thickened wall. **Asci** cylindrical,  $260-300 \times 12-13(-14) \mu m$ , inamyloid, operculate, 8-spored, with walls thickened up to 1 µm and with a flexuous, tapered base. **Paraphyses** cylindrical,  $1.5-2 \mu m$  in diam., septate, branched, sometimes anastomosed, light brownish in the upper half; apex slightly enlarged, frequently ramified and very diverticulated~lobed; in some cases the apex can be straight or slightly bent; some paraphyses show short diverticula growing from the lower elements. **Hymenial hairs** cylindrical, measuring  $2.5-3 \mu m$  in diam., light brownish, with a single septum at the base; apex only slightly inflated, straight or very slightly bent. **Sub-hymenium** structured as a thick *textura intricata* with cylindrical septate hyphae, uniformly brown to brownish at low magnification. **Medullary excipulum** slightly gelified and organized also as a *textura intricata* with cylindrical, septate, subhyaline hyphae, measur

ing 3–6 µm diam. on average, but sometimes more inflated, walls up to 0.5 µm thick. In the lower part of the medullary excipulum, the hyphae become a little more inflated, and arranged perpendicular to the external surface. **Ectal excipulum** appearing as a *textura subglobulosa-angularis* with cells up to 18 µm long and/or wide, presenting thickened walls, and looking mainly dark brown because of an epimembranaceous pigment. **External hairs** emerging from the external layer of the ectal excipulum, cylindrical in shape, 500 µm or more in length, 5–8 (–10) µm diam., with walls up to 1.5 µm thick, septate in their entire length but more frequently in the lower part, mostly straight or only slightly bent; brown due to an epimembranaceous pigment. Many very small hairs, up to 30 µm long, are present among the longest ones. **Basal tomentum** composed of very long cylindrical hairs looking similar to the external hairs.

#### Notes

Pseudoplectania affinis is macro- and micro-morphologically very similar to the other Pseudoplectania species. The holotype was housed as P. nigrella in PDD Herbarium, but it can be distinguished from this species mainly due to the presence of straight (not coiled) external hairs, more similar to those of P. ericae and P. tasmanica. The present genetic results based on ITS and LSU data, confirm this species should be considered independent from the P. nigrella complex and sister to both P. ericae and P. tasmanica, thus suggesting that the wavy to straight (not coiled) external hairs could be regarded as a good taxonomic character. Only the holotype collection was successfully analyzed since the other morphologically similar collection available (PDD 62464) could not be sequenced due to a persistent contamination. The first author examined other PDD New Zealand collections previously identified as P. nigrella, but they were mostly made up of scarce and very small apothecia so molecular analysis was discarded in order to preserve them (see above, studied collections). PDD 41652, 41653 and 41476 consisted in very young, small, mostly immature apothecia with some deviant microscopic features if compared to P. affinis, and so they are here reported as Pseudoplectania cf. affinis. PDD 41652 is probably the most mature of the three since some (but not many) asci contain spores. The external hairs in this collection are less straight but more

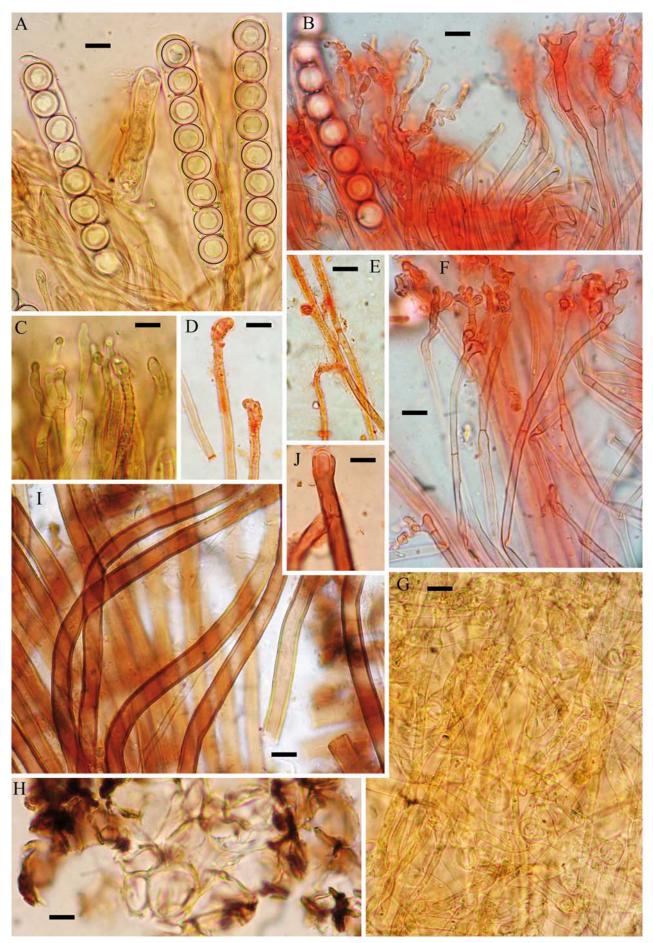


Plate 15. — *Pseudoplectania affinis* (holotype). Microscopic characters. A: Asci and spores in water; B-F: paraphyses in Congo red; C: paraphyses tips in water; D: hymenial hairs in Congo red; E: anastomosing of paraphyses in Congo red; G: medullary excipulum in water; H: Ectal excipulum in water; I: external hairs in water; J: external hairs tip in Congo red. Scale bars = 10 µm. Photos: M. Carbone

waving than in the typical collections of *P. affinis*; and the paraphyses tips are simple and not diverticulated. PDD 41653 (coming from the same site of the previous one) and PDD 41476 consist of few, very young and immature apothecia with waving and slightly coiled external hairs. Further studies on *Pseudoplectania* collections from New Zealand are required in order to determine the intraspecific variability of *P. affinis* and the development of paraphyses and external hairs during growth.

*Pseudoplectania affinis* differs from *P. ericae* by its chorology and larger apothecia, and also by the morphology of paraphyses, external hairs and ectal excipulum. The paraphyses tips of *P. affinis* seem to be more diverticulate, the external hairs are straighter, and globose elements in the ectal excipulum are less frequent.

Despite our genetic results, from a morphological point of view, *Pseudoplectania tasmanica* (see below) seems to be the most similar to *P. affinis*. The main characters distinguishing them are undoubtedly the simple, not diverticulated or lobed apex of the paraphyses (overmature sample examined), and the more abundant globose elements in the ectal excipulum in *P. tasmanica*. Besides we have also noticed an eccentric gelatinous spore sheath in *P. tasmanica*, not seen in *P. affinis*.

Pseudoplectania tasmanica M. Carbone, Agnello & P. Alvarado, sp. nov. — MB 807953

**Etymology:** referred to Tasmania, the island where the holotype was collected.

**Diagnosis:** genetically close to *Pseudoplectania ericae*, it differs from the latter mainly by its larger size, and the straighter and numerous external hairs.

Holotype: MCVE 27583; Australia, Tasmania, Duckhole lake, 22.12.2012, *leg*. G. Gates.

#### Macroscopic characters

**Apothecium** up to 3 cm in diameter, cup-shaped. **Hymenium** smooth, polished, blackish to dark brownish. **External surface** rough, pubescent, mostly black. **Stipe** absent. **Flesh** dark grey to blackish, rubbery.

#### **Microscopic characters**

Spores globose, (10-)11-12(-13) µm in diam., smooth, with vacuolar content and thickened wall up to 0.5 µm; an eccentric gelatinous sheath is present around the spores. Asci cylindrical, measuring up to  $300 \times 13(-14) \mu m$ , inamyloid, operculate, 8-spored, with walls thickened up to 1 µm and with a flexuous, tapered, apparently aporhynchous base. Paraphyses cylindrical, measuring 1.8-2.5 µm in diam., septate, very branched just from the lower part, anastomosed, light brownish; apex slightly enlarged up to 4 µm, mostly bi- to trifurcate with simple, slightly clavate, terminal cells; short diverticula growing from the lower elements definitely present in many paraphyses. Hymenial hairs cylindrical, measuring 3µm in diam., light brownish, with a single septum in the basal part; apex only slightly enlarged, straight or very slightly bent. Crystals present in the hymenium, yellowish. Subhymenium structured as a thick textura intricata with cylindrical, closely septate hyphae, 2-4 µm in diam., uniformly brown to brownish at low magnification. Medullary excipulum slightly gelified and organized also as a textura intricata with cylindrical, septate, subhyaline hyphae, measuring 3–6 µm diam. on average, some hyphae are more inflated measuring up to 10 µm, walls being up to 0.5 µm thick. Ectal excipulum appearing as a textura subglobulosa-angularis; internal part with subhyaline globose cells, up to 25 µm diam.; external part with cells up to 12–15 µm wide, presenting thickened walls, and looking mainly dark brown because of an epimembranaceous pigment. External hairs emerging from the external layer of the ectal excipulum, cylindrical in shape, up to 1000 µm in length, 5-8 µm diam., with walls up to 1  $\mu$ m thick, septate in their entire length but more frequently in the lower part, mostly straight; brown due to an epimembranaceous pigment. Basal tomentum composed of very long cylindrical hairs looking similar to the external hairs.

#### Notes

*Pseudoplectania tasmanica* clearly belongs to the group of *P. ericae* and *P. affinis* which is thus composed of species characterized by sessile apothecia with wavy to straight (not coiled) external hairs. Our genetic results, based on ITS and LSU inference, confirm that *P. tasmanica* is significantly supported as a sister clade to *P. ericae*, and to a lesser extent, *P. affinis*. It displays a degree of genetic differentiation similar to that of other well supported species (Fig. 1, 2), and so it should be regarded as an independent taxon at the



Plate 16. — Pseudoplectania tasmanica. Fresh specimens in situ. Photo: G. Gates

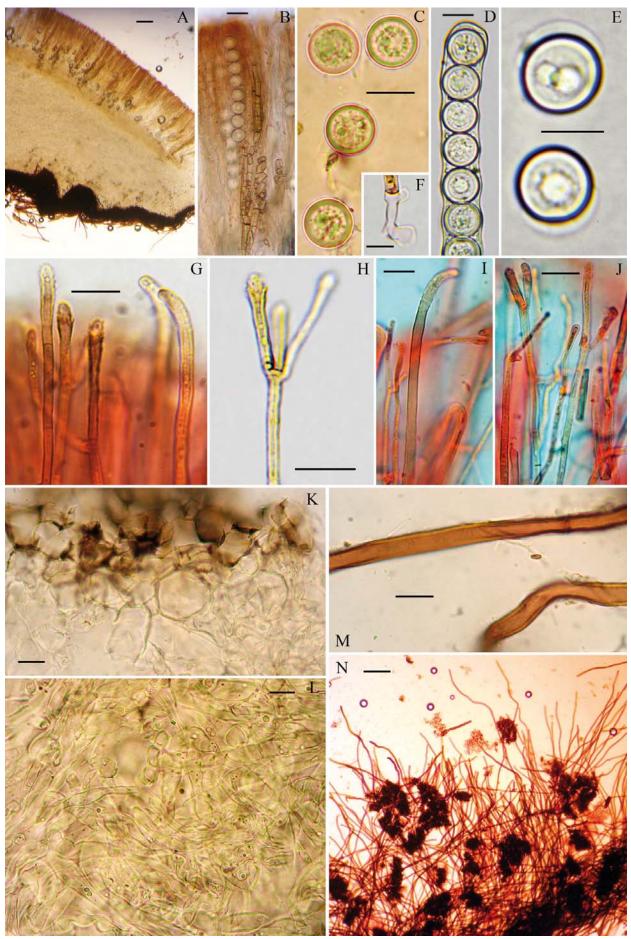


Plate 17. — Pseudoplectania tasmanica (holotype). Microscopic characters.
A: section; B: crystals in the hymenium; C: spores; D: ascus with spores; E: spores with gelatinous sheath; F: ascus base;
G-J: apical parts of paraphyses and hymenial hairs; K: ectal excipulum; L: medullary excipulum; M-N: external hairs.
Scale bars = 10 μm, except A and N = 100 μm, B = 20 μm. Photos: M. Carbone & C. Agnello

species level. At present, no significant intraspecific variability could be detected within this lineage. From a morphological point of view it differs from the *P. nigrella*-complex mainly because of the straight external hairs and from *P. melaena*, for the lack of a stipe, and the not-bent apex of paraphyses. It differs from *P. ericae* because of its larger size and the more abundant and straighter external hairs; ecology and chorology are also different.

Despite genetic results, *P. tasmanica* seems to be more similar in macro- and microscopic features to *P. affinis* (see discussion under this species).

# Discussion on the other known Pseudoplectania species

*Pseudoplectania stygia* (Berk. & M.A. Curtis) Sacc. has been studied by CARBONE (2013) who suggested to preserve its current generic placement and to keep it separated from the related species *P. nigrella* and *P. episphagnum*.

Pseudoplectania kumaonensis Sanwal was described from India (SANWAL, 1953) with the following diagnosis: "Apothecia aggregata vel dispersa, atra, sessilia vel subsessila, hyphis septatis, quasi rhizoideis, brunneis matrici affixa, in maturitate calyciformia, profunde concava, usque ad 0.7 cm diam., extus capillis minutissimis fere incospicuis obtecta; disco nigro; asci cylindracei vel subcylindracei, usque ad 120 imes12 μ; sporae omnino uniseriatae, hyalinae vel subhyalinae, leves, usque ad 12 µ diam. Paraphyses ascos multo superantes, filiformes, septatae, pallidae brunneae, usque ad 200  $\mu$  longae, 2.5  $\mu$  latae, superne subgelatinoso-conglutinatae". Unfortunately, SANWAL (op. cit.) did not cite any herbarium specimen, and no original material seems to have been stored in DUH (Prof. Arun Pandey, pers. comm.). Even though the protologue underlines some characters that could link this species to the genus Pseudoplectania, other features definitely are not so clear. The absence of hairs, or even their "inconspicuous" presence, as well as the use of the genus concept sensu SEAVER (1913, 1943) which included Caloscypha fulgens (Pers.) Boud. within Pseudoplectania, and above all, the lack of original material, suggest caution. We think that Pseudoplectania kumaonensis should be regarded as a doubtful species, at least until its identity is further clarified.

*Pseudoplectania carranzae* is a species described from Costa Rica and, according to CALONGE & MATA (2002), it is characterized by the length of asci, the excipular hairs, and the morphology of the paraphyses. We have not yet had the opportunity to study this species but the curved paraphyses are pretty common in this genus, as well as the presence of long excipular hairs.

*Pseudoplectania ryvardenii* has been recently described from Venezuela (ITURRIAGA *et al.*, 2012), and it seems to be distinguished from the other *Pseudoplectania* species mainly for its ornamented spores.

# Acknowledgements

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### Key of the *Pseudoplectania* species<sup>1</sup> based on morphological and ecological characters

2*. 3.	Spores slightly ornamented, known from Venezuela       P. ryvardenii         Spores smooth       2         Distinctly stipitate or hooked paraphyses tips are present       3         Sessile or subsessile, paraphyses tips straight, slightly bent, ramose-diverticulated, external hairs straight, wavy or coiled, on       4         Apothecia up to 6 cm wide, stipe up to 2 cm, hooked paraphyses tips, external hairs inconspicuous and mostly straight, on       P. melaena-complex (incl. P. spongiosa)         Apothecia up to 2 cm wide, stipe up to 5 mm, paraphyses tips bent, external hairs coiled, on wood, known from Costa Rica       P. melaena
4*. 5. 5*. 6. 6*.	P. carranzae         External hairs mostly coiled and bent
	Paraphyses tips mostly bi-trifurcate with the final elements slightly clavate, known from Tasmania

<sup>1</sup> The new species of GLEJDURA et al. (2014, in press) is not included; P. ryvardenii and P. carranzae are known only from their protologues.

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Matteo Carbone Via Don Luigi Sturzo 173 16148 Genova Italy matteocarb@hotmail.com



**Carlo Agnello** Via Antonio Gramsci 11 72023 Mesagne Italy agnellocarlo@libero.it



Pablo Alvarado ALVALAB, La Rochela 47 39012 Santander Spain pablo.alvarado@gmail.com