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# Reinstatement of old taxa and publication of new genera for naming some lineages of the *Pezizaceae* (Ascomycota)

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**Abstract:** Based on both molecular data obtained from databases and from new studies of type collections of species of *Peziza* described by Donadini and morphological characters, taxonomical changes are proposed. Some names are given based on lineages of the *Pezizaceae* previously assigned to *Peziza*. A new multigene phylogeny (LSU, RPB2,  $\beta$ -tubulin) is provided. The following genera are reinstated: *Daleomyces* Setch., with *D. gardneri* (syn. *Peziza proteana* f. *sparassoides*) as type species, *Geoscypha* (Cooke) Lambotte, with *Peziza violacea* as type species, and *Phaeopezia* Sacc. ex Vido, with *Peziza apiculata* as type species. *Peziza* sect. *Purpureodiscus*, with *Peziza subisabellina* as type species, is raised to the generic rank. Six new genera are proposed: *Ionopezia*, with *Peziza gerardii* as type species, *Malvipezia*, with *Peziza howsei* as type species, *Elaiopezia*, with *Galactinia polaripapulata* as type species, *Paragalactinia*, with *Peziza succosa* as type species, *Phylloscypha*, with *Peziza phyllogena* as type species, and *Legaliana*, with *Peziza badia* as type species. The genera *Galactinia*, *Heteroplegma*, *Infundibulum*, *lotidea*, *Paramitra* and *Podaleuris* are also discussed. The amyloid reaction of asci is also discussed and characterised with three new categories inspired by those of HANSEN *et al.* (2001).

**Keywords:** amyloidity, *Pezizales*, *Peziza*, rDNA phylogeny, taxonomy, typification, 6 new genera.

## Introduction

The genus *Peziza* Fr. in a wide sense contains numerous epigeous and hypogeous species, 104 according to KIRK *et al.* (2008) but this number is probably underestimated. It is the type genus of *Pezizaceae* Dumort. of which one of the main characters is the amyloid reaction of asci (KORF, 1972), but other characters can also be cited: absence of carotenoid pigments in cells and uninucleate ascospores (BERTHET, 1964). For review of the history of the name *Peziza*, see RIFAI (1968) and DENNIS (1983).

With the general application of molecular analyses, the *Pezizaceae* have been studied using a wide sampling of species. A first work was published by NORMAN & EGGER (1999), but the first analysis which produced significant results was published by HANSEN *et al.* (2001). Based on the large subunit (LSU) of ribosomal DNA, this work strongly focused on the genus *Peziza*. Six lineages were highlighted. These results were confirmed by the works of HANSEN *et al.* (2002) focused on the core-group of *Peziza*, i.e. the lineage containing the type-species, *P. vesiculosa* Bull., and particularly by HANSEN *et al.* (2005) who produced a multigene phylogeny (LSU, RPB2,  $\beta$ -tubulin). The latter established the genus *Peziza* to be paraphyletic with a dozen possible lineages, some of them with uncertain robustness. *Plicaria* Fuckel, as typified by KORF (1960), characterised by spherical ascospores, was also confirmed as an independent genus.

The subsequent works on *Peziza* using molecular data, focused either on *Peziza* s. str. (MEDARDI *et al.*, 2012; LANTIERI *et al.*, 2016; PFISTER *et al.*, 2016; VIZZINI *et al.*, 2016; VIZZINI *et al.*, 2020) or on other groups (MEDARDI *et al.*, 2014b; LOIZIDES *et al.*, 2017; VAN VOOREN *et al.*, 2017; AGNELLO *et al.*, 2018; VAN VOOREN *et al.*, 2018) did not change significantly the results of HANSEN *et al.* (2001, 2005), but help us to better understand the affinities among some species or to identify new taxa. Despite this, few nomenclatural changes have been made in the clades that do not belong to *Peziza* s. str. We only noted the reinstatement of *Lepidotia* (VAN VOOREN *et al.*, 2015) or the publication of the new genus *Sarcopeziza* (AGNELLO *et al.*, 2018).

PFISTER (2015) declared: "In conclusion, I suggest that several names that trace to Boudier and Cooke can be reinstated in the *Pezizaceae*. Although phylogenetic studies are still incomplete, it is evident that the broad definition of *Peziza* that has been applied for many years is untenable. As ecological, morphological and molecular data accumulate, we will surely see more lineages defined and we should name them." We fully agree with this point of view. Although it is practical for many mycologists to unite all the pezizoid fungi having an amyloid ascus reaction into a large genus *Peziza*, numerous morphological and ecological differences can be easily

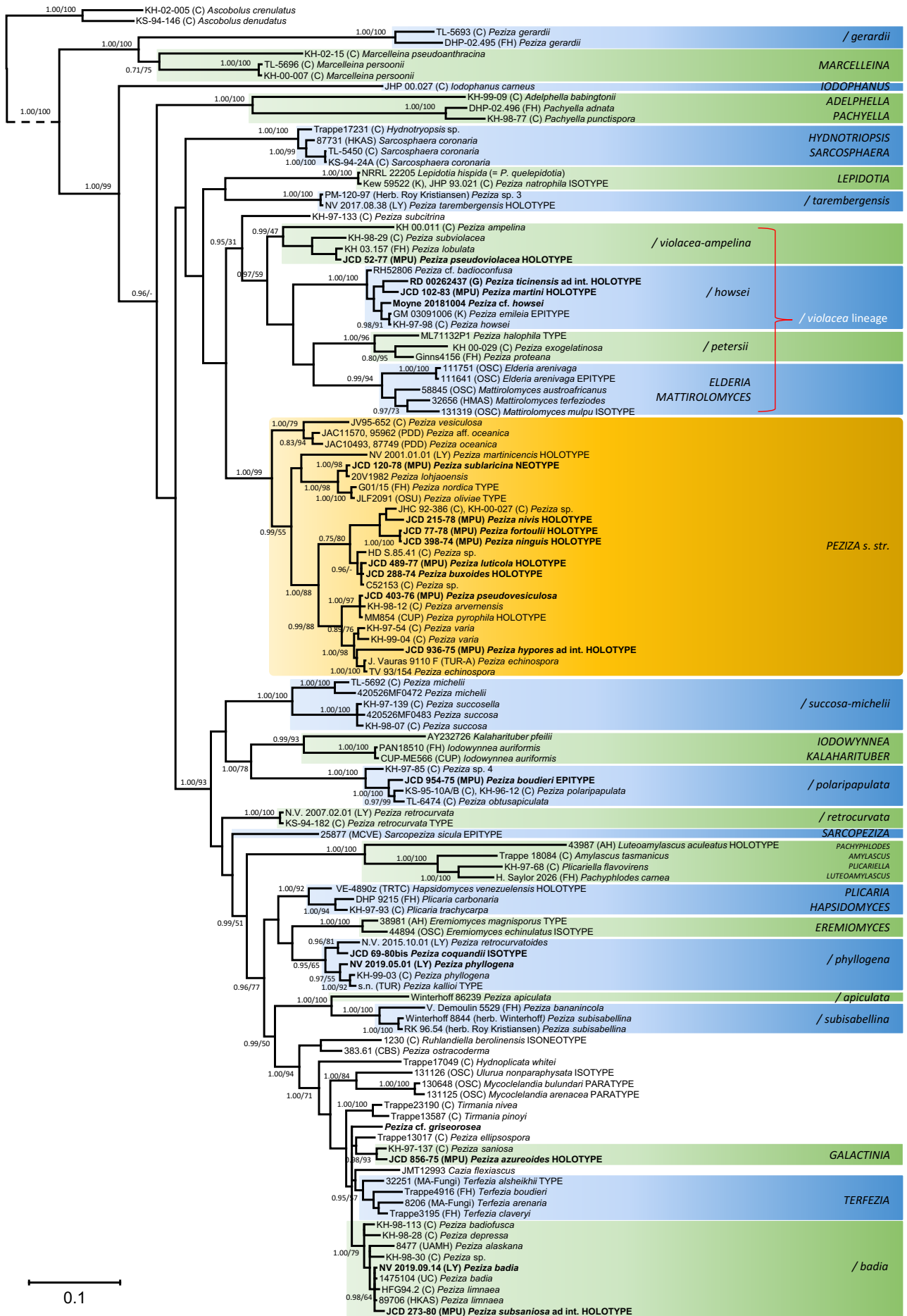
observed, i.e. fruitbody form, pigments, excipular structures, intensity and location of ascus amyloid reaction, ascospores shape and ornamentation, asexual morphs, trophic status, etc. These morphological and life history features, along with molecular evidences, enable classification of this species in a natural way. The challenge is to provide a taxonomy accessible to the whole community of mycologists.

The aim of this paper is to name some of these lineages in agreement with the current nomenclatural rules (TURLAND *et al.*, 2018), especially to account for previously published names and to clarify their typification. This is a preliminary work that is part of a larger project dedicated to the revision of pezizalean type collections from Donadini's herbarium (housed at MPU). Jean-Claude Donadini (1939-1987) was a French mycologist who published numerous articles dealing with pezizalean fungi, especially in the genus *Peziza* (NEVILLE, 2007). He described 55 new taxa, including 29 *Peziza* species or varieties, from the French Alps and from the Mediterranean area.

## Material and methods

**DNA extraction, amplification and sequencing.** — The methods are those described in VAN VOOREN *et al.* (2018).

**Phylogenetic analyses.** — A combined 28S rDNA (LSU) – RPB2 –  $\beta$ -tubulin alignment was built using sequences from O'DONNELL *et al.* (1997), HANSEN *et al.* (2001, 2005), CABERO *et al.* (2016), VAN VOOREN (2020) and VAN VOOREN *et al.* (2018) retrieved from the International Nucleotide Sequence Database Collaboration (INSDC) public database (COCHRANE *et al.*, 2011), and new sequences obtained during this study (Table 1). Sequences were first aligned in MEGA 5.0 (TAMURA *et al.*, 2011) software with its Clustal W application and then corrected manually. The final alignment included 399/935 bp (28S rDNA, 120 sequences), 894/1702 bp (RPB2, 73 sequences) and 276/772 bp ( $\beta$ -tubulin, 56 sequences) variable/total sites. The aligned loci were loaded in MrBayes 3.2.6 (RONQUIST *et al.*, 2012), where a Bayesian analysis was performed (data partitioned into LSU, RPB2 exons and  $\beta$ -tubulin exons, two simultaneous runs, four chains, temperature set to 0.2, sampling every 100<sup>th</sup> generation) until convergence parameters were met after 3.27 M generations, standard deviation having fallen below 0.01. Finally a full search for the best-scoring maximum likelihood tree was performed in RAxML 8.2.12 (STAMATAKIS, 2014) using the standard search algorithm (data partitioned, 2000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP).



**Fig. 1** – 50% majority rule consensus 28S rDNA–RPB2– $\beta$ -tubulin phylogram of the family Pezizaceae obtained in MrBayes. Nodes supported by >0.95 Bayesian posterior probability (PP) or >70% maximum likelihood (ML) bootstrap proportion (BP) are shown annotated. Terminals in **bold** are newly generated sequences. *Ascobolus* species served as the outgroup.

**Table 1** – List of collections sequenced during this study. Species marked with a \* come from a type collection.

Species	Country	Voucher #	GenBank Accession number		
			ITS	LSU	RPB2
<i>Peziza azureoides</i> *	France	MPU:JCD 856-75	MT278876	MT273592	MT274698
<i>Peziza badia</i>	France	LY:NV 2019.09.14	MT278877	MT273593	MT274699
<i>Peziza badioides</i> *	France	MPU:JCD 210-78	MT278878	MT273594	–
<i>Peziza boudieri</i> *	France	MPU:JCD 954-75	MT278879	MT273595	MT274700
<i>Peziza buxoides</i> *	France	MPU:JCD 288-74	MT278880	MT273596	–
<i>Peziza coquandii</i> *	France	MPU:JCD 69-80bis	MT278881	MT273597	–
<i>Peziza echinophora</i> *	France	MPU:JCD 202-81	–	MT273598	–
<i>Peziza fortoulia</i> *	France	MPU:JCD 77-78	MT278882	MT273599	MT274701
<i>Peziza heimii</i> (as <i>P. flos-nivium</i> )	France	MPU:JCD 174-78	MT635329	MT635332	MT635814
<i>Peziza hypores</i> ad int.*	France	MPU:JCD 936-75	MT278883	MT273600	–
<i>Peziza lilacinoalba</i> *	France	MPU:JCD 293-76	MT278884	–	–
<i>Peziza lundellii</i> *	Sweden	MPU:JCD 402-75	MT635331	MT635334	MT635815
<i>Peziza luticola</i> *	France	MPU:JCD 489-77	MT278885	MT273601	–
<i>Peziza martini</i> *	France	MPU:JCD 102-83	–	MT273602	MT274703
<i>Peziza muscicola</i>	France	MPU:JCD 121-78	MT635330	MT635333	–
<i>Peziza ninguis</i> *	France	MPU:JCD 398-74	MT278886	MT273603	MT274704
<i>Peziza nivis</i> *	France	MPU:JCD 215-78	MT278887	MT273604	MT274705
<i>Peziza phyllogena</i>	France	LY:NV 2019.05.01	MT278888	MT273605	MT274706
<i>Peziza pseudoampelina</i> *	France	MPU:JCD 275-78	MT278889	–	MT274707
<i>Peziza pseudovesiculosa</i>	France	MPU:JCD 403-76	MT278890	MT273606	–
<i>Peziza pseudoviolacea</i> *	France	MPU:JCD 52-77	MT278891	MT273607	–
<i>Peziza sublaricina</i> *	France	MPU:JCD 120-78	MT278892	MT273608	MT274707
<i>Peziza subsaniosa</i> ad int.*	Italy	MPU:JCD 273-80	MT278893	MT273609	–
<i>Peziza subuliginosa</i> *	France	MPU:JCD 185-78	MT278894	–	–
<i>Peziza violacea</i> (as <i>P. lobulata</i> )*	France	LY:NV 2010.05.34	MT495253	MT476965	–
<i>Peziza violacea</i> f. <i>terricola</i> *	France	MPU:JCD 466-77	MT278895	MT273610	–

**Nomenclature.** — The taxonomic novelties were registered in the MycoBank database ([www.mycobank.org](http://www.mycobank.org)), including typifications (MBT number). With some exceptions (due to historical context), the new genera proposed in this article are feminine following the recommendation 62A of Shenzhen ICN (TURLAND *et al.*, 2018). The herbarium codes are in conformity with the Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>).

## Available names

We explored ancient literature, especially the work of ECKBLAD (1968) to find names that could be applied to genera of *Pezizaceae* in the light of known molecular results. These names are listed below, and their circumscription is explained.

### *Daleomyces*

This genus was published as a member of the *Tuberales* by SETCHELL (1924) for the new species *Daelomyces gardneri* Setch. which was finally identified as *Peziza proteana* f. *sparassoides* (Boud.) Korf (SEEVER, 1942; KORF, 1956). In this context, this name should be used for the clade IVb in HANSEN *et al.* (2001). Phylogenetically, *P. proteana* f. *sparassoides* belongs to a clade with *Peziza petersii* Berk. and some other violet species, like *P. halophila* Loizides, Agnello & P. Alvarado and *P. exogelatinosa* K. Hansen & Sandal. The recent publication by VIZZINI *et al.* (2020) confirms that *Peziza proteana* (Boud.) Seaver represents a later synonym of *P. petersii* and *P. proteana* f. *sparassoides* deserves the rank of species. Based on the ICN Art. 11,

the oldest legitimate species-rank name for this taxon is *Gyromitra phillipsii* Masee (1895). Since *G. phillipsii* is a synonym of *Daelomyces gardneri* then *Durandiomyces* published by SEEVER (1928), with *Gyromitra phillipsii* as type species, is considered as a later synonym. Based on our multigene phylogeny of *Pezizaceae* (Fig. 1) and morphological characters, we disagree with the choice of VIZZINI *et al.* (2020) to maintain this group of species in the genus *Peziza*.

### *Galactinia*

First published as a subgenus of *Peziza* by COOKE (1879), with only two species, *P. succosa* Berk. and *P. saniosa* Schrad., BOUDIER (1885) raised it at the rank of genus, although the definition of the genus — by Boudier's own admission — was still unclear. The etymology of this name remains that the flesh of these species produces a latex (from the ancient Greek, γάλακτος, *galactos*, meaning milk).

As mentioned by ECKBLAD (1968), among the two species listed by COOKE (1879), only *Peziza succosa* was cited by SACCARDO (1884) and BOUDIER (1885) with some additional taxa. The designation of the type species was first made by CLEMENTS & SHEAR (1931) who selected *P. saniosa* and must be followed (ICN Art. 10.5) contrary to Eckblad's opinion. Thus, the typification proposed by LE GAL (1953), designating *P. succosa*, is not retained.

The widened concept of *Galactinia* by BOUDIER (1907) and subsequent authors is not followed here, based on molecular data. This concept applied by various authors including LE GAL (1953, 1962), GAMUNDÍ (1960, 1975), SVRČEK & KUBICKA (1961) or SVRČEK (1962) was largely based on a rejection of the name *Peziza* as ill-defined and ambiguous. Based on molecular results (Fig. 1), *Galactinia* applies



**Table 2** – Correspondence between current names of violet *Peziza* growing on burnt soils and older names in literature

Current name	Older names
<i>Peziza lobulata</i> (Velen.) Svrček (1976)	<i>Aleuria violacea</i> s. BOUDIER (1905-1910)
	<i>Peziza violacea</i> s. DENNIS (1978)
	<i>Peziza pseudoviolacea</i> Donadini (1978)
	<i>Plicaria adusta</i> Velen. (1934)
<i>Peziza tenacella</i> W. Phillips (1886), <i>nom. illeg.</i>	<i>Galactinia praetervisa</i> s. BOUDIER (1905-1910)
	<i>Peziza praetervisa</i> s. DENNIS (1978), BREITENBACH & KRÄNZLIN (1981)
	<i>Peziza subviolacea</i> SVRČEK (1976)
	<i>Peziza violacea</i> "f. <i>typica</i> " s. DONADINI (1978)
<i>Peziza moseri</i> Aviz.-Hersh. & Nemlich (1974)	<i>Peziza violacea</i> s. BREITENBACH & KRÄNZLIN (1981)
	<i>Aleuria lilacina</i> Boudier (1907)
	<i>Peziza sublilacina</i> Svrček (1976)

to a small clade that requires a larger sampling to define its characters.

As a consequence, the species included in the "*P. succosa* – *P. michelii*" clade (HANSEN *et al.*, 2005) or in the group *V.p.p.* (HANSEN *et al.*, 2001) need a new genus and we propose the name *Paragalactinia*. All the species in this clade form ectomycorrhizas (SMITH, 2014; JABEEN *et al.*, 2015). GAROFOLI & BAIANO (1996) treat and illustrate this group in detail. One of the species, *P. sesiana* Garofoli & Baiano (GAROFOLI & BAIANO, 1994) seems however likely related to *P. phyllogena* according to its characters (especially spore shape, ornamentation and spore content). A molecular phylogenetic evaluation of this species is required to determine its correct position.

### Geoscypha

It is again COOKE (1879) who published this name as a subgenus of *Peziza*, which contained many diverse species and forming a heterogeneous assemblage that is difficult to circumscribe. SACCARDO (1884) cited *P. violacea* Pers. for *Peziza* subgen. *Aleuria* "unranked" c. *Geoscypha*. LAMBOTTE (1888) raised it to generic rank, and included in this group a small number of discomycetes sharing the following characters: sessile or subsessile, glabrous ascomata, and hyaline spores. *Peziza violacea* is included and cited as "*Geo. violacea*, Pers.", but no type species was designated for the genus. This designation was made by ECKBLAD (1968) and must be followed (ICN Art. 10.5). In this context, would it be possible to apply this name to one of the pezizalean lineages? For that, a non-ambiguous definition of *P. violacea* would be required; this is far from obvious.

This species was first laconically defined by PERSOON (1797) as "*subsessilis, dilatata, purpureo-caerulea. (Ad truncos putridos passim.)*". PERSOON (1801) described it as "*subsessilis demum depressa orbicularis purpureo-caerulea [...] Rarius ad terram et in truncis cariosis ineunte autumno.*" Later, PERSOON (1822) was not significantly more explicit: "*subsessilis orbicularis depressa purpureo-caerulea. Syn. Fung. p. 629. Consp. Page. 312. Ad terram et interdum in truncis cariosis nascitur. Primo subcampanulata, dein dilate, margine subinvoluta, latitudine semiuncialis.*" Since the name is sanctioned by FRIES (1822), we must follow the Friesian interpretation and choose among the references cited by the Swedish author (ICN Art. F.3.9) to typify this name. Unfortunately, none of the cited references (FRIES, 1822: 69) are illustrated. One of the important characters given by Fries concerns the development on burnt soil ("*Ad terram praecipue adustam*"). Following this reference to ecology, all subsequent authors have used *P. violacea* for violet cup-fungi growing on burnt sites. There is no material of *P. violacea* in Persoon's herbarium in Leiden (L) nor in Fries' herbarium in Uppsala (UPS). SVRČEK (1976: 130) pointed out the

impossibility of providing a modern interpretation of this name because three violet species grow on this substrate: *P. lobulata* (Velen.) Svrček, *P. tenacella* W. Phillips *illeg.*, and *P. moseri* Aviz.-Hersh. & Nemlich (Table 1). In the 19<sup>th</sup> century and at the beginning of the 20<sup>th</sup>, authors like FÜCKEL (1869), KARSTEN (1871)<sup>1</sup>, COOKE (1877), GILLET (1879-1887), PHILLIPS (1887), MASSEE (1895), REHM (1895), BOUDIER (1905-1910) and BRESADOLA (1933) all described *P. violacea* as having smooth ascospores. This concept was followed by subsequent authors like LE GAL (1941), MOSER (1963), MAAS GEESTERANUS (1967), AVIZOHAR-HERSHENZON & NEMLICH (1974), DENNIS (1978) or CETTO (1982). SEAYER (1917, 1928) used the name *P. violacea* for a species with ornamented ascospores, but PFISTER (1982) who revised Seayer's collections concluded this was a misinterpretation of "*P. praetervisa*". DONADINI (1979) also considered *P. violacea* as an ornamented-spore species and asserted: "Il se peut que Persoon ait ensuite confondu les deux espèces<sup>2</sup> mais le taxon a été créé (1801) pour l'espèce à spores ornées (il dit "*purpureo caerulea*", p. 639 : on ne trouve pas de purpurin chez *P. pseudoviolacea*)" that is "It is possible that Persoon may have confused the two species but the taxon was created (1801) for the species with ornamented spores (he says "*purpureo caerulea*", p. 639:

**Table 3** – Spore size of *Peziza violacea*, with supposed smooth ascospores, in selected literature

Author	Spore size (in µm)
FÜCKEL (1870)	11 × 6
KARSTEN (1871)	11–14 × 7–8.5
COOKE (1877)	12–14 × 7–9
PHILLIPS (1887)	12–14 × 7–9
LAMBOTTE (1888)	11 × 6
REHM (1895)	10–12 × 5–6
MASSEE (1895)	12–14 × 7–8
BOUDIER (1905-1910)	15–17 × 8–9
BRESADOLA (1933)	12–14 × 7–9
LE GAL (1941)	13–15 × 7–9
MOSER (1963)	(11) 13–15 × (6) 7–9
MAAS GEESTERANUS (1967)	11–15.7 × (6) 8–9.8
AVIZOHAR-HERSHENZON & NEMLICH (1974)	13.7–15.7 × 7.3–9.8
DENNIS (1978)	13–15 × 7–9
CETTO (1982)	13–15 × 7–8

<sup>1</sup> Karsten's description of *P. violacea* does not explicitly indicate that the spores are smooth, but for other species he mentions the ornamentations when present.

<sup>2</sup> *Peziza pseudoviolacea* and *P. violacea*.

we do not see purplish on *P. pseudoviolacea*”. He was followed by HOHMEYER (1986) and ROUX (2006).

**Table 4** – Spore size of *Peziza lobulata*, *Plicaria adusta* or its synonym *P. pseudoviolacea* in literature

Author	Species	Spore size (in µm)
SVRČEK (1976)	<i>P. lobulata</i>	13–14 × 7–8
SVRČEK (1976)	<i>Pl. adusta</i>	13–14 × 7–8
DONADINI (1978)	<i>P. pseudoviolacea</i>	13–16 × 7–9
HOHMEYER (1986)	<i>P. pseudoviolacea</i>	13–16 × 7–9
MONTI <i>et al.</i> (1992)	<i>P. lobulata</i>	13–16 × 7–9
MEDARDI (2006)	<i>P. lobulata</i>	12–13 × 6–7
VAN VOOREN (2014)	<i>P. lobulata</i>	12.5–14 (15) × 7.8–8.5

Finally, although it cannot be proved at 100% that the original *Peziza violacea* corresponds to a species with smooth ascospores, the Friesian tradition goes to this direction. This also agrees with this important remark of MASSEE (1895: 418): “Specimen named by Fries examined.” A neotype of *P. violacea* is provided in the present paper to fix this choice. This solution also offers the advantage of disposing many posterior synonyms.

This group of violet species is kept in the genus *Peziza* s. str. by HANSEN *et al.* (2001, 2005) and VIZZINI *et al.* (2020) although HANSEN *et al.* (2005) demonstrated that the “*Peziza* s. str.” lineage does not form a monophyletic group. Two clades are identified: the first one is the *Peziza*-core group as defined by HANSEN *et al.* (2002), with *Peziza vesiculosa*, *P. varia*, etc., and the second one with the *Peziza violacea* group. These share the same type of amyloid ascus ring (HANSEN *et al.*, 2001), but they diverge in other features. For example, the spore content is different: in the *Peziza*-core species, ascospores are eguttulate<sup>3</sup>, but in *P. violacea* group ascospores are mainly biguttulate except in *P. violacea* (= *P. lobulata*) in which the ascospores can be considered as eguttulate although young spores show two small polar drops. In *Peziza*-core species, paraphyses when mature do not show any pigment or if pigmented only a yellow vacuolar pigment (*P. vesiculosa*, *P. sublaricina*, *P. monterivicola*...), but in the *P. violacea* group, paraphyses possess a brown or brown purple vacuolar pigment when mature. Given these differences, it seems difficult to keep these two groups in the same genus. In our multigene phylogeny (Fig. 1), the /violacea lineage contains four distinct clades, including the /elderia-mattirolomyces clade represented by hypogeous species which lost their ascus amyloidity.

### Heteroplegma

The name was proposed by CLEMENTS (1903) for a single species, *Heteroplegma caeruleum*, characterised by large apothecia reaching 8 cm diam., blue-coloured at the base, an olivaceous hymenium, exuding a bluing latex. The ascospores are finely warted; nothing is said about their content but PFISTER (1978) who revised the type collection indicated “obscurely biguttulate”. Based on these characters, this species may be related to *Peziza saniosa* or *P. badiofusca* (Boud.) Dennis as suggested by PFISTER (1978), but except the bluing juice, they also remain *Peziza phyllogena* Cooke. These three species belong to three different clades (Fig. 1). The genus *Heteroplegma* is not retained waiting for modern collections of *H. caeruleum* to evaluate its taxonomic position.

### Infundibulum

This genus was published by VELENOVSKÝ (1934) and typified with *Peziza linteicola* W. Phillips & Plowr. The protologue indicates “As. [...] *jodo coerulei* [...] *Sp. monostichae, ellipticae, eguttulatae, hyalinae*.” This suggests the genus *Peziza* s. str. The original description of *P. lin-*

*teicola* (PHILLIPS, 1887), revision of ECKBLAD (1968: 76), and comments of DENNIS (1978: 20) agree with its position within *Peziza* s. str. Thus *Infundibulum* is considered as a later synonym of *Peziza*.

### lotidea

This genus was published by CLEMENTS (1909) and typified with *Peziza pleurota* W. Phillips (COOKE, 1878; PHILLIPS, 1887). *Peziza pleurota* is synonymised with *P. badiofusca* (Boud.) Dennis by SPOONER (2001). ECKBLAD (1968: 76) revised the type collection of *P. pleurota* and said “Asci [...] strongly amyloid in Melzer’s reagent, with a distinct dark blue ring around the ascostome.” Such a reaction characterises the species of *Peziza* s. str. or the apothecial species of the /violacea lineage. Although the brownish colours of apothecia (as drawn by COOKE, 1878, fig. 351) and its growth on cow dung point to a *Peziza* species, some of the microscopical characters, i.e. paraphyses containing a brown pigment, guttulate and warted ascospores, agree with features of some species in the /violacea lineage; brown-coloured apothecia are also common in old specimens in the latter group. It seems difficult to correctly fix the taxonomic position of *P. pleurota* without molecular data. The genus *lotidea* is not retained here.

### Paramitra

This genus was published by BENEDIX (1962) and typified with *Paramitra ochreoides*, described as a new species. The microscopical features, i.e. amyloid asci and smooth eguttulate ascospores, clearly point to the genus *Peziza* s. str. as already suggested by ECKBLAD (1968). NANNFELDT (1966) considered *Paramitra ochreoides* to be a later synonym of *Peziza tectoria* Cooke.

### Phaeopezia

This name was invalidly proposed by SACCARDO (1877: 71) when he listed a collection of *Peziza apiculata* Cooke from Italy. It was validated by VIDO (1879). See RIFAI (1968: 225–226) for more details.

This group corresponds to the section *Aleurodiscina* Malençon of *Aleuria* s. Boudier (MALENÇON, 1939) or section *Apiculatae* Donadini of *Peziza* (DONADINI, 1977). The taxonomic position of *Peziza apiculata* and some of its possible allies (see HÄFFNER, 1995) is far from clear. Based on the current data this species belongs to the same lineage of *P. subisabellina* but into another clade. These species are morphologically very different and only share a tendency to grow on woody substrates.

Based on the description of type-collection (PFISTER, 1979) and modern illustration of WANG (1996), *Peziza elachroa* Berk. & M.A. Curtis may belong to *Phaeopezia*.

The genus *Podaleuris* Clem. was published as a member of *Pezizaceae* for species with “spores dark, 1-celled” and “apothecia stalked” (CLEMENTS, 1909). *Aleuria reperta* Boud. was designated as type-species. This species, published by BOUDIER (1894), differs from *P. apiculata* by its short-stipitate apothecia, olive-coloured, and its growth on rotten wood. Such characters can occur in *P. apiculata* (see VAN VOOREN, 2014, under *P. obtusapiculata*) or in *P. obtusapiculata* J. Moravec as suggested by DONADINI (1977, under *P. apiculata* var. *flavobrunnea*). The correct identity of this fungus cannot be revised because no type specimen is preserved in Boudier’s herbarium (PC) according to DONADINI (1977). However *Podaleuris* is considered as a later synonym of *Phaeopezia*.

### Purpureodiscus

This section of *Peziza* was published by HIRSCH (1992) with *P. subisabellina* as type species. For more information about this species, see for example VAN VOOREN & VALADE (2006). The morphology of this species, including the diffusely amyloid reaction of ascus wall, sometimes led authors to place it in the genus *Pachyella* (e.g.

<sup>3</sup> *Peziza arvernensis* has ascospores containing polar granules that can merge on rehydrated material, looking like guttulate spores. The same thing occurs with *P. domiciliana*.

TRIMBACH, 1999). The works of HANSEN *et al.* (2001, 2005) demonstrated that it was not the case and the species is placed in an isolated clade, accompanied by *Peziza bananincola* (Rehm) Sacc. (PFISTER, 1991). We propose to combine *Purpureodiscus* at the rank of genus to accommodate *P. subisabellina* and allies. Based on its characters (LE GAL, 1959, 1960) and following the opinion of PFISTER (*op. cit.*), *P. luteorosella* (Le Gal) Pfister is considered to belong to this group.

## Unnamed lineages and clades

### /Marcelleina–*Peziza gerardii* lineage

A lineage /Marcelleina–*Peziza gerardii* was clearly identified by HANSEN *et al.* (2005) and confirmed in the subsequent phylogenetic works. It contains the species of *Marcelleina* Brumm., Korf & Rifai — characterised by spherical ascospores and inamyloid asci —, a clade containing some genera of hypogeous fungi (*Temperantia*, *Stouffera* and *Hydnobolites*), and *Peziza gerardii*. The latter is characterised by fusoid ascospores, ornamented by fine ridges, and appears isolated in a distinct clade that deserves its own genus. We do not find any available name in literature, therefore a new genus *Ionopezia* is herein proposed. *Peziza gerardii* appears to be a species complex with 4–5 different species based on the LSU analyses available. Since *Peziza gerardii* originally applied to an American species, we reinstate Quélet's *Peziza ionella* (QUÉLET, 1878) based on a collection from Jura (France). More investigations are required to circumscribe the taxa of this complex, including the designation of an epitype for *P. ionella*. This will be done in a forthcoming paper.

### /howsei clade

As a part of the /*Peziza violacea* lineage, this clade contains a series of species with pale violet to violet tinges, i.e. *Peziza howsei*, *P. lividula*, *P. pauli* ( $\equiv$  *P. martini* Donadini *illeg.*), etc. Based on the morphological characters and phylogenetic data, a new genus *Malvipezia* is proposed.

### /polaripapulata clade

This clade was already appearing in the phylogeny by HANSEN *et al.* (2005, Fig. 4). It includes a group of species with small apothecia showing yellowish to olive colours due to yellowish vacuolar oil drops in the paraphyses (MORAVEC, 1969; HUTH & HUTH, 1998; BAIANO *et al.*, 2000; DOUGOUD, 2002). Their ascospores are eguttulate, smooth, warty or finely reticulate. The ascus tips are diffusely amyloid. The presence of *Peziza obtusapiculata* in this clade is surprising because of its close morphology to *P. apiculata* nested in another clade. As a consequence, the presence of ascospore apiculi is not a synapomorphic character in *Pezizaceae*. We think that this point should be clarified with a larger sampling. However we propose to name this clade as *Elaiopezia* gen. nov.

Note that the genus *Podaleuris*, typified by *Aleuria reperta*, a possible synonym of *Peziza obtusapiculata*, is not retained for naming this clade. See our comments under *Phaeopezia*.

### /retrocurvata clade

This clade contains only one known species, *Peziza retrocurvata* K. Hansen & Sandal mainly characterised by its *Discina*-like habit and pluriguttulate, verrucose ascospores (HANSEN *et al.*, 1998; VAN VOOREN *et al.*, 2018). Although this clade deserves its own genus, we are waiting for new molecular data integrating new species in this group and fix its main characters. For practical reasons, we name it provisionally *Discinopsis*.

### /phylogena lineage

This lineage was also distinguished in HANSEN *et al.* (2005) and VAN VOOREN *et al.* (2018) and contains several species mainly characterised by ascospores containing small polar granules, ornamented with warts, and asci bluing at the top in an iodine solution but with-

out forming a ring (as exemplified by *Peziza s. str.*). The taxa currently identified as members of this clade are *Peziza phylogena* (including *P. kallioi* Harmaja which is a later synonym), *P. coquandii* Donadini, *P. boltonii* Quél., *P. labessiana* (Boud.) Sacc. & Traverso and *P. retrocurvatooides* Van Vooren. For a description of some of these species see VAN VOOREN (2014) and VAN VOOREN *et al.* (2017). Based on their morphological characters and phylogenetic data, a new genus *Phylloscypha* is proposed.

### /badia clade

This clade belongs to a large lineage partly corresponding to the /*Peziza depressa*-*Ruhlandiella* lineage established by HANSEN *et al.* (2005), including also the genera *Tirmania* and *Ruhlandiella*. This lineage needs more species analyses to understand the relationships among the taxa and to increase the robustness of the support for some clades. There is too many morphological and microscopical differences among the genera belonging to this lineage to unite them in a single genus.

The /badia clade appears robust and contains species that share the following microscopical characters: ascospores biguttulate, or sometimes uniguttulate, ornamented by warts, often elongated in small crests,  $\pm$  reticulate, or isolated, asci with crozier, strongly bluing at the top in an iodine solution but not forming a ring, i.e. WT type, see next paragraph), paraphyses often with an external encrusting brown pigment and ectal excipulum of *textura globulosa/angularis*, of large cells. A new genus *Legaliana* is proposed to accommodate this group of species.

## Amyloid reaction, a neglected character?

The amyloid reaction of asci, i.e. staining in blue in contact with an iodine reagent, is not identical in the *Pezizaceae*. Species of some genera have lost this character (HANSEN *et al.*, 2001), species of some other genera have species show an inconsistent reaction, e.g. *Marcelleina* with *M. pseudoanthracina* (DOUGOUD, 2002), and some species show a distinct amyloid reaction but the reaction pattern is variable. It is important to note that this reaction is sometimes difficult to observe when the reaction is faint or not concentrated at the top of asci. In many cases, examination of dehiscent asci allow observation of the reaction on the walls. In some rather rare samples, the reaction seems to be missing, probably because of external factors.

PFISTER (1973) discussed the amyloid reaction of *Pachyella* species: "In *Pachyella* species, the amyloid material is present either as an external layer on the ascus wall (which may separate from the ascus wall proper), or occurs in the gel which surrounds the asci and paraphyses and is not restricted to the wall. Since the reaction is not restricted to the apex of the ascus, nor is it in the form of a J+ ring at the apex of the ascus as in *Peziza*, the reaction in *Pachyella* is said to be diffuse." This character was evaluated by HANSEN *et al.* (2001) who identified four different types of known amyloid reaction:

1) A faint reaction over the entire length of asci, more intense at the top but diffuse (i); this applies to the /*succosa*-*michelii* clade.

2) A faint reaction of the wall but very strong at the top, showing a distinct ring (ii); this applies to the *Peziza s. str.* and to clades /*howsei*, /*violacea*-*ampelina*, etc.

3) An even reaction of the wall, more or less intense, sometimes stronger but diffuse at the top (type iii<sub>a</sub>), or strongly amyloid (type iii<sub>b</sub>) in other cases. The (iii<sub>a</sub>) type applies for example to *Plicaria*, the /*gerardii* clade, etc. The (iii<sub>b</sub>) type applies for example to *Iodowynnea*, *Sarcosphaera*, *Peziza retrocurvata*, etc.

4) A lack of reaction; this applies for example to *Cazia* or *Marcelleina*.

The distinction between (i) type and (iii<sub>a</sub>) type is not easy for some species, because the intensity of the reaction may change during the life of the ascus or sometimes with the iodine concentration. This is why we propose a slightly different classification to categorise



the amyloid reaction, again with three types of reaction, completed if necessary with the symbol “+” for quantifying the intensity. No category is given for the absence of reaction, the term “inamyloid” being sufficiently explicit. Here is the list of categories:

- WTR: weak reaction on wall, only intense at the top with a distinct ring.
- WT: weak reaction on wall, more intense at the top but with no obvious distinct ring.
- W: homogeneous reaction on wall, over the entire length of ascus.

**Table 5** – Correspondence between our categories of amyloid reaction and those of HANSEN *et al.* (2001)

HANSEN <i>et al.</i> (2001)	Our categories
(i)	WT
(ii)	WTR
(iii a)	W or WT
(iii b)	WT
(iv)	inamyloid

Fig. 2 and 3 present some examples of the amyloid reaction, with the corresponding category.

We encourage the mycologists to use these categories and describe precisely this reaction in their description of *Pezizaceae* species to include the amyloid reaction as a useful character to identify some of the genera, combined with other traditional features.

## Taxonomy

The following taxonomy is proposed in accordance with the clades of *Pezizaceae* that appear robust on our multigene phylogeny, combined with morphological characters. The genera are given in alphabetical order. Some of the new combinations concern species that are not represented in the multigene phylogeny (Fig. 1) but we obtained ITS or LSU sequences which prove their relationship with these genera. They will be treated in detail in a further work. The trophic status of the genera is based on HEALY *et al.* (2013).

***Daleomyces*** Setch., *Mycologia*, 16 (5): 240 (1924) – MB 1409.

Type-species: *Daleomyces gardneri* Setch. = *Daleomyces phillipsii* (Masse) Seaver.

Synonyms: *Durandiomyces* Seaver, *N. Amer. Cup-Fungi (Operc.)*: 242 (1928); *Napomyces* Setch ex Clem. & Shear, *Gen. Fungi*: 333 (1931).

**Amended description:** Ascomata epigeous, cupulate, discoid or sparassoid (cabbage-head), of various colours: whitish with pinkish tinges, becoming more or less brownish with age, purplish brown, olivaceous brown or distinctly violet. Flesh without latex. Asci operculate, 8-spored, with the top strongly bluing in an iodine solution (WTR type), with or without crozier. Paraphyses containing a vacuolar pigment, brown, purple brown or yellowish becoming brown with maturity. Ectal excipulum of *textura globulosa*, with large cells, sometimes partly gelatinised in the outer part (e.g. *D. exogelatinosus*). Ascospores biguttulate, ornamented with isolate warts, punctiform or irregular, often more dense at the poles. Species saprobic, preferentially growing on basic substrates (burned soil, sandy soil, soil with a high pH).

Containing the following species:

• ***Daleomyces phillipsii*** (Masse) Seaver, *N. Amer. Cup-fungi (Operc.)*, suppl.: 337 (1942).

Basionym: *Gyromitra phillipsii* Masse, *Brit. Fungus-fl.*, 4: 479 (1895).

Homotypic synonym: *Durandiomyces phillipsii* (Masse) Seaver, *N. Amer. Cup-fungi (Operc.)*: 337 (1928).

Other synonyms: *Aleuria proteana* var. *sparassoides* Boud., *Bull. Soc. mycol. France*, 15: 51 (1899); *Galactinia proteana* var. *sparassoides* (Boud.) Sacc. & P. Syd., *Syll. fung.*, 16: 709 (1902); *Underwoodia sparassoides* (Boud.) Bánhegyi, *Index Horti bot. univ. Budapest*, 3: 167 (1938);

*Peziza proteana* f. *sparassoides* (Boud.) Korf, *Mycologia*, 48 (5): 714 (1956).

*Underwoodia campbellii* Sacc., *Ann. Mycol.*, 7 (5): 433 (1909); *Peziza proteana* f. *campbellii* (Sacc.) Korf, *Rep. Tottori Mycol. Inst.*, 10: 392 (1973); *Daleomyces campbellii* (Sacc.) J. Moravec, *Česká Mykol.*, 36 (2): 112 (1982); *Peziza campbellii* (Sacc.) Vizzini, Medardi & Forin, *Mycol. Progress*, 19: 515 (2020).

*Daleomyces gardneri* Setch., *Mycologia*, 16 (5): 241 (1924); *Napomyces gardneri* (Setch.) Clem. & Shear, *Gen. Fungi*: 333 (1931).

*Aleuria proteana* var. *slavkoviensis* F. Neuwirth, *Stud. Bot. Čechoslav.*, 7: 172 (1946).

• ***Daleomyces petersii*** (Berk.) Van Vooren, *comb. nov.* – MB 835804.

Basionym: *Peziza petersii* Berk., *Grevillea*, 3 (28): 150 (1875).

Homotypic synonym: *Galactinia petersii* (Berk.) Le Gal, *Discomycètes de Madagascar*: 51 (1953).

Synonym: *Peziza proteana* (Boud.) Seaver; For other synonyms, see VIZZINI *et al.* (2020).

• ***Daleomyces exogelatinosus*** (K. Hansen & Sandal) Van Vooren, *comb. nov.* – MB 835805.

Basionym: *Peziza exogelatinosa* K. Hansen & Sandal, in Hansen *et al.*, *Nord. J. Bot.*, 18 (5): 612 (1998).

• ***Daleomyces halophilus*** (Loizides, Agnello & P. Alvarado) Van Vooren, *comb. nov.* – MB 835806.

Basionym: *Peziza halophila* Loizides, Agnello & P. Alvarado, *Persoonia*, 39: 337 (2017).

• ***Daleomyces badioides*** (Donadini) Van Vooren, *comb. nov.* – MB 835807.

Basionym: *Peziza badioides* Donadini, *Bull. Soc. linn. Provence*, 31: 20 (1979).

***Elaiopezia*** Van Vooren, *gen. nov.* – MB 835808.

Type-species: *Galactinia polaripapulata* J. Moravec.

Etymology: From the ancient Greek ἐλαία (*elaía*) meaning “olive” and πέζις (*pezis*) meaning “fungus without stipe”.

**Description:** Ascomata epigeous, discoid or slightly cupulate, small-sized, olive, yellowish or brown with distinct olivaceous tinges. Flesh without latex. Asci operculate, 8-spored; ascus wall diffusely amyloid (W type). Paraphyses containing a yellow, yellow-ochre or olivaceous pigment, sometimes also with an external pigment at the top. Ectal excipulum of *textura globulosa* with small to medium-sized cells. Ascospores eguttulate, sometimes containing small granules or drops in young state, smooth or ornamented. Species saprobic.

Containing the following species:

• ***Elaiopezia polaripapulata*** (J. Moravec) Van Vooren, *comb. nov.* – MB 835809.

Basionym: *Galactinia polaripapulata* J. Moravec, *Česká Mykol.*, 23 (1): 33 (1969).

Homotypic synonym: *Peziza polaripapulata* (J. Moravec) K. Hansen, *Nordic J. Bot.*, 18 (5): 619 (1998).

• ***Elaiopezia boudieri*** (Cooke) Van Vooren, *stat. et comb. nov.* – MB 835810.

Basionym: *Peziza granulosa* var. *boudieri* Cooke, *Mycographia*, 6: 232 (1879).

• ***Elaiopezia luteola*** (Velen.) Van Vooren, *comb. nov.* – MB 835924.

Basionym: *Plicaria luteola* Velen., *Novit. Mycol. Novissim.*: 150 (1947).

Homotypic synonym: *Peziza luteoloflavida* Svrček, *Česká Mykol.*, 30 (3-4): 137 (1976).

***Geoscypha*** (Cooke) Lambotte, *Mém. Soc. roy. sci. Liège, 2<sup>e</sup> sér.*, XIV: 320 (1888) – MB 2054.

Basionym: *Peziza* subgen. *Geoscypha* Cooke, *Mycographia*: 254 (1879) – MB 700365.

Type-species: *Peziza violacea* Pers., *nom. sanct.* (FRIES, 1822).



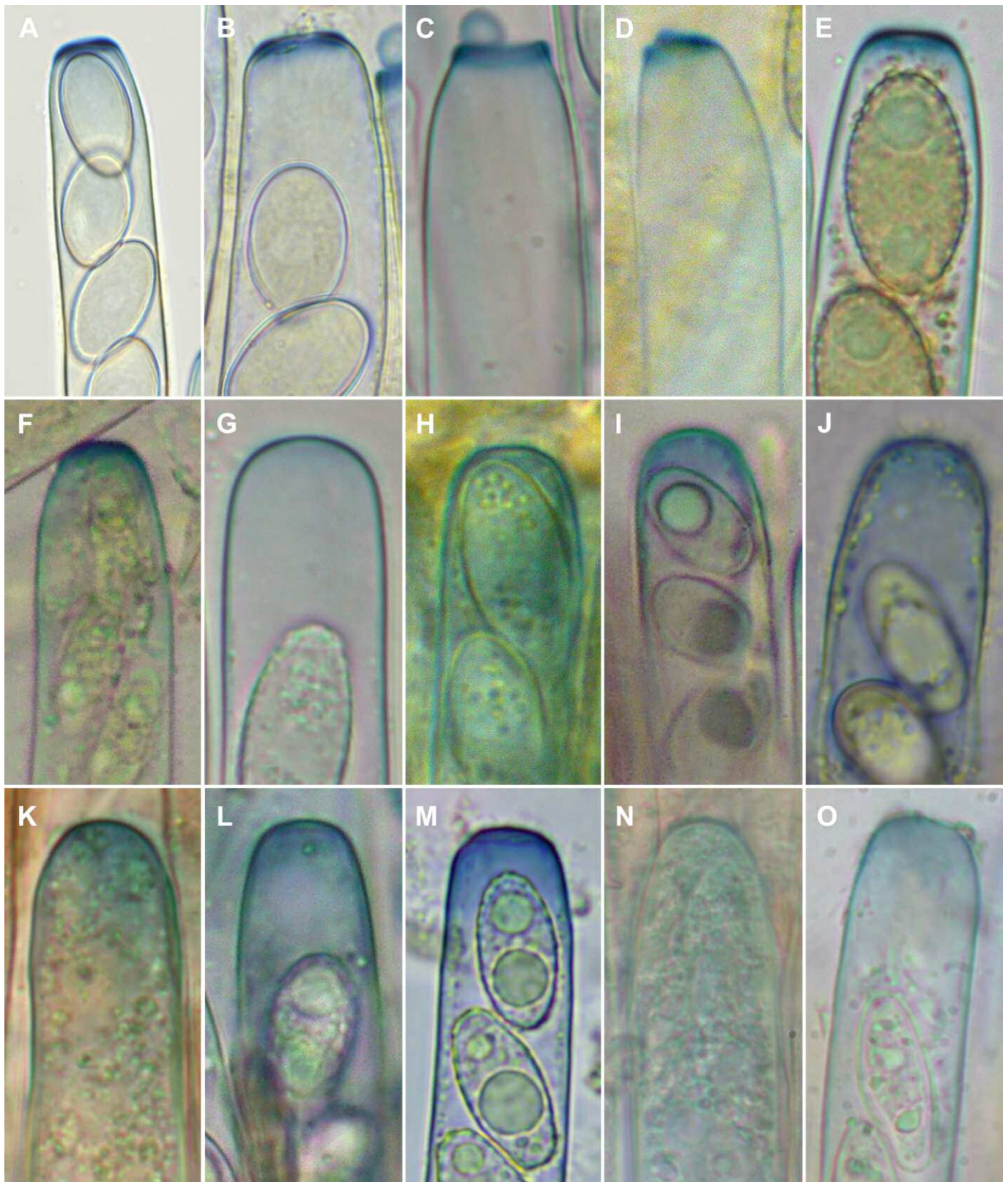
**Amended description:** Ascum epigeous, cupulate or discoid, violet-coloured. Asci operculate, 8-spored, with the top intensely bluing in iodine solution (WTR or WT type in *G. ampelina*), with crozier. Paraphyses containing a brown or purple brown vacuolar pigment. Ectal excipulum of *textura globulosa*, with large cells. Ascospores smooth or ornamented with isolated warts, biguttulate, except in *G. violacea* where the drops may be visible only in young

spores. Species saprobic, often growing on burnt soil.

Containing the following species:

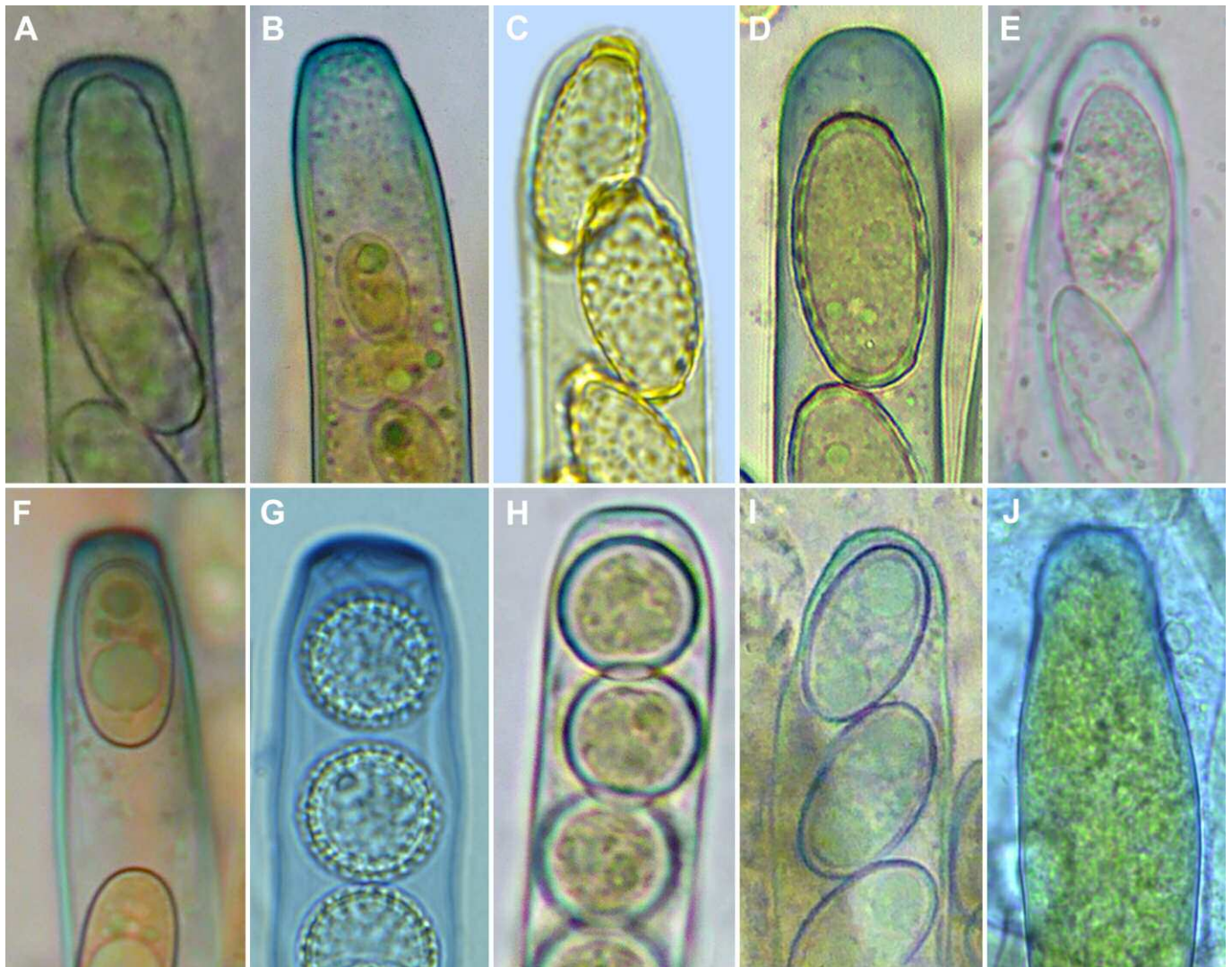
• ***Geoscypha violacea*** (Pers.) Lambotte, *Mém. Soc. roy. sci. Liège*, 2<sup>e</sup> sér., XIV: 320 (1888).

Basionym: *Peziza violacea* Pers., *Tentamen dispositionis methodicae Fungorum*: 33 (1797), *nom. sanct.*



**Fig. 2** – Amyloid reaction of some *Pezizaceae* species. A. *Peziza lilacinoalba* [WTR]. B. *P. granularis* [WTR]. C. *P. merdae* [WTR]. D. *P. petersii* [WTR]. E. *P. howsei* [WTR]. F. *P. lividula* [WTR]. G. *P. boltonii* [W]. H. *P. phyllogena* [W]. I. *P. michelii* [WT]. J. *P. infuscata* [WT]. K. *P. alaskana* [WT+]. L. *P. badiofusoides* [WT+]. M. *P. limnaea* [WT++]. N. *P. subisabellina* [W]. O. *P. apiculata* [WT]. Photos A by R. Dougoud; M by J.-L. Fasciotto; B, C, D, E, G, H, J, K, L, N by M. Hairaud; F, I by P. Tanchaud, O by N. Van Vooren.





**Fig. 3** – Amyloid reaction of some *Pezizaceae* species. A. *Peziza saniosa* [WT+]. B. *P. depressa* [WT+]. C. *P. obtusapiculata* [W]. D. *P. polaripapulata* [W]. E. *P. gerardii* [W]. F. *Sarcosphaera coronaria* [WT+]. G. *Plicariella scabrosa* [WT+]. H. *Plicaria endocarpoides* [W]. I. *Adelphella babingtonii* [W]. J. *Marcelleina pseudoanthracina* (young ascus) [W]. Photos C, G, J by R. Dougoud; B by M. Hairaud; D by R. Martínez; A, B, H, I by P. Tanchaud; E, F by N. Van Vooren.

Neotype designated here<sup>4</sup>: FRANCE, voucher LY:NV 2010.05.34, *leg.* N. Van Vooren, 23 May 2010 – MBT 392383. GenBank ITS MT495253, LSU MT476965.

Homotypic synonyms: *Aleuria violacea* (Pers.) Gillet, *Champ. France, Discom.*: 36 (1879); *Humaria violacea* (Pers.) Sacc., *Syll. fung.*, 8: 149 (1889); *Plicaria violacea* (Pers.) Fuckel, *Jahrb. nassau. Ver. Naturk.*, 23-24: 327 (1870); *Galactinia violacea* (Pers.) Svrček & Kubička, *Česká Mykol.*, 15 (2): 74 (1961).

Other synonyms: *Peziza lobulata* (Velen.) Svrček, *Česká Mykol.*, 30 (3-4): 130 (1976); *Plicaria lobulata* Velen., *Novit. mycol.*: 196 (1939).

*Plicaria adusta* Velen., *Monogr. Discom. Bohem.*: 348 (1934).

*Peziza pseudoviolacea* Donadini, *Bull. Soc. linn. Provence*, 31: 27 (1979).

• ***Geoscypha tenacella*** (Sacc.) Van Vooren, *comb. nov.* – MB 835811.

Basionym: *Humaria tenacella* W. Phillips ex Sacc., *Syll. fung.*, 8: 145 (1889)<sup>5</sup>.

Homotypic synonym: *Peziza tenacella* W. Phillips, in Cooke, *Grevillea*, 15: 100 (1887), *nom. illeg.*

• ***Geoscypha ampelina*** (Gillet) Van Vooren & Dougoud, *comb. nov.* – MB 835812.

Basionym: *Aleuria ampelina* Quél. ex Gillet, *Champ. France, Discom.*, livr. 8: 205 (1886)<sup>6</sup>.

Homotypic synonyms: *Galactinia ampelina* (Gillet) Boud., *Hist. classif. Discom. Eur.*: 47 (1907); *Plicaria ampelina* (Gillet) Rehm, *Rabenh. Kryptog.-Fl., Pilze – Ascom.*, 1 (3): 1003 (1894); *Peziza queletii* Medardi, Lantieri & Cacialli, *Mycotaxon*, 128: 204 (2014). See also MEDARDI *et al.* (2014a).

Note: this species has an important divergent character compared to the other taxa in this genus, i.e. an amyloid ascus reaction of WT type instead of WTR, maybe a first indication explaining its isolated position, with a rather long branch, in the /violacea-ampelina clade.

***Ionopezia*** Van Vooren, *gen. nov.* – MB 835813.

Type-species: *Peziza gerardii* Cooke

Etymology: From the ancient Greek "ἰων (ion) meaning "violet" and πέζις (pezis) meaning "fungus without stipe".

<sup>4</sup> Based on preliminary analyses from the LSU locus made on several collections, *P. violacea* seems to have a widespread distribution, present in Europe, Australia and North America. As Persoon's original location is unknown, we decided to choose a neotype among our own collections. This neotype is illustrated in VAN VOOREN (2014) under the name *P. lobulata*.

<sup>5</sup> *Peziza tenacella* W. Phillips (1887) is illegitimate as a later homonym of *P. tenacella* Weinm. (1828).

<sup>6</sup> *Peziza ampelina* Quél. (1880) is illegitimate as a later homonym of *P. ampelina* Pass. (1874).

**Description:** Ascomata epigeous, discoid or cupulate, sessile, violet-coloured. Flesh without latex. Asci operculate, 8-spored, with or without crozier, wall diffusely amyloid (W type). Paraphyses hyaline, with an external purplish brown to violet pigment located at the top. Ascospores fusoid, multiguttulate, ornamented with longitudinal striations (only seen with a high magnification). Ectal excipulum of *textura globulosa*, with medium-sized cells. Species forming ectomycorrhizas.

Containing the following taxa:

• ***Lonopezia gerardii*** (Cooke) Van Vooren, *comb. nov.* – MB 835814.

Basionym: *Peziza gerardii* Cooke, *Hedwigia*, 14: 81 (1875).

Homotypic synonyms: *Humaria gerardii* (Cooke) Sacc., *Syll. fung.*, 8: 150 (1889); *Leucoloma gerardii* (Cooke) House, *Bull. N.Y. St. Mus.*, 243-244: 86 (1923); *Humarina gerardii* (Cooke) Seaver, *N. Amer. Cup-Fungi (Operc.)*: 138 (1928); *Galactinia gerardii* (Cooke) Bánhegyi, *Borbásia*, 2: 105 (1940); *Plicaria gerardii* (Cooke) Bánhegyi, *Borbásia*, 2: 106 (1940).

• ***Lonopezia ionella*** (Quél.) Van Vooren, *comb. nov.* – MB 835815.

Basionym: *Peziza ionella* Quél., *Bull. Soc. bot. France*, 24: 328 (1878).

Lectotype here designated: Pl. VI, fig. 4, in QUÉLET (1878) – MBT392385.

Homotypic synonyms: *Aleuria ionella* (Quél.) Gillet, *Champ. France, Discom.*: 51 (1879); *Galactinia ionella* (Quél.) Boud., *Icon. mycol.; liste prélim.*: 3 (1904).

Note: *Plicaria pedicellata* Velen. (1940), considered by SVRČEK (1976) as a synonym of *P. gerardii*, needs to be revised to evaluate its taxonomic position within *Lonopezia*.

***Legaliana*** Van Vooren, *gen. nov.* – MB 835839.

Type-species: *Peziza badia* Pers.

Etymology: From Marcelle Le Gal, French mycologist, for her important contributions to the knowledge of *Pezizomycetes*, especially her work on spore ornamentation published in 1947.

**Description:** Ascomata epigeous, cupulate or discoid, sessile, dark coloured (brown, reddish brown, olivaceous brown, purplish brown, blackish purple). Flesh without coloured latex, but sometimes with a watery juice. Asci operculate, 8-spored, with crozier, wall diffusely bluing in an iodine solution, more or less intensely at the top (WT type). Paraphyses containing a brownish or olive-brown vacuolar pigment, and often showing an external brown pigment at the top. Ascospores biguttulate, sometimes with an oil drop larger than the other, more rarely uniguttulate, ornamented with irregular warts, but often with elongated warts or crests, sometimes forming a network or an incomplete reticulum. Ectal excipulum of *textura globulosa/angularis*, with large cells. Species saprobic or ectomycorrhizal.

Containing the following taxa:

• ***Legaliana badia*** (Pers.) Van Vooren, *comb. nov.* – MB 835840.

Basionym: *Peziza badia* Pers., *Observ. mycol.*, 2: 78 (1800).

Homotypic synonyms: *Scodellina badia* (Pers.) Gray, *Nat. Arr. Brit. Pl.*, 1: 669 (1821); *Plicaria badia* (Pers.) Fuckel, *Jahrb. nassau. Ver. Naturk.*, 23-24: 327 (1870); *Aleuria badia* (Quél.) Gillet, *Champ. France, Discom.*, livr. 2: 43 (1879); *Pustularia badia* (Pers.) Lambotte, *Mém. Soc. roy. Sci. Liège, 2<sup>e</sup> sér.*, 14: 322 (1887); *Galactinia badia* (Pers.) Arnould, *Bull. Soc. mycol. France*, 9 (2): 111 (1893).

• ***Legaliana limnaea*** (Maas Geest.) Van Vooren, *comb. nov.* – MB 835841.

Basionym: *Peziza limnaea* Maas Geest., *Persoonia*, 4 (4): 422 (1967).

Other synonyms: *Galactinia castanea* var. *limosa* Grelet, *Bull. Soc. bot. Centre-Ouest*, 1936: 8 (1936), *nom. inval.*; *Galactinia limosa* (Grelet) Le Gal & Romagn., *Rev. Mycol. (Paris)*, 4: 176 (1939), *nom. inval.*; *Peziza limosa* (Grelet) Nannf., *Fungi Exsiccati Suecici*, no. 373 (1941), *nom. inval.*

• ***Legaliana alaskana*** (E.K. Cash) Van Vooren, *comb. nov.* – MB 835842.

Basionym: *Peziza alaskana* E.K. Cash, *J. Wash. Acad. Sci.*, 44 (2): 44 (1954).

• ***Legaliana badiofuscooides*** (Donadini) Van Vooren, *comb. nov.* – MB 835843.

Basionym: *Peziza badiofuscooides* Donadini, *Bull. Soc. linn. Provence*, 31: 21 (1979).

• ***Legaliana muscicola*** (Donadini) Van Vooren, *comb. nov.* – MB 835844.

Basionym: *Peziza muscicola* Donadini, *Bull. Soc. mycol. France*, 93 (2): 186 (1977).

Note: *Peziza depressa* Pers. has been differently interpreted in the mycological literature, so we hesitate to combine this name in the genus *Legaliana* on the base of a single collection (C:KH 98-28).

***Malvipezia*** Van Vooren, *gen. nov.* – MB 835816.

**Description:** Ascomata epigeous, cupulate or discoid, sessile, with pale mauve, purple or violet colours. Flesh without latex. Asci operculate, 8-spored, with crozier, wall diffusely amyloid in an iodine solution except at the top where the reaction is intense and forms a ring (WTR type). Paraphyses containing a brown vacuolar pigment. Ascospores biguttulate, ornamented with isolated, rounded warts, more rarely with irregular and coalescent warts. Ectal excipulum of *textura globulosa* with medium-sized to large cells. Species saprobic.

Type-species: *Peziza howsei* Roze & Boud.

Etymology: Referring to the plant genus *Malva* for its mauve-purple colours, and from Greek πέζις (*pezis*) meaning “fungus without stipe”.

Containing the following taxa:

• ***Malvipezia howsei*** (Roze & Boud) Van Vooren, *comb. nov.* – MB 835817

Basionym: *Peziza howsei* Roze & Boud., *Bull. Soc. bot. France*, 26 (suppl.): 75 (1879).

Homotypic synonyms: *Aleuria howsei* (Roze & Boud.) Gillet, *Champ. France, Discom.*, livr. 8: 206 (1886); *Plicaria howsei* (Roze & Boud.) Rehm, *Rabenh. Kryptog.-Fl., Pilze – Ascom.*, 1 (3): 1015 (1894); *Galactinia howsei* (Roze & Boud.) Boud., *Hist. class. Discom. Eur.*: 48 (1907).

• ***Malvipezia emileia*** (Cooke) Van Vooren, *comb. nov.* – MB 835818

Basionym: *Peziza emileia* Cooke, *Mycographia*, 6: 226 (1879).

Homotypic synonyms: *Aleuria emileia* (Cooke) Gillet, *Champ. France, Discom.*, livr. 2: 43 (1879); *Galactinia emileia* (Cooke) Le Gal, *Rev. mycol. (Paris)*, 2: 197 (1937).

• ***Malvipezia pauli*** (Medardi, Lantieri & Cacialli) Van Vooren, *comb. nov.* – MB 835819.

Basionym: *Peziza pauli* Medardi, Lantieri & Cacialli, *Mycotaxon*, 128: 204 (2014), based on *Peziza martini* Donadini, *Bull. Soc. linn. Provence*, 35: 171 (1985), *nom. illeg.*

• ***Malvipezia lividula*** (W. Phillips) Van Vooren & Dougoud, *comb. nov.* – MB 835820.

Basionym: *Peziza lividula* W. Phillips, in Cooke, *Mycographia*, 4: 161 (1877).

Homotypic synonym: *Galactinia lividula* (W. Phillips) Boud., *Hist. class. Discom. Eur.*: 48 (1907).

***Paragalactinia*** Van Vooren, *gen. nov.* – MB 835925.

Type-species: *Peziza succosa* Berk.

Etymology: From ancient Greek παρά (*pará*), “close to”, and *Galactinia*, a close genus.

**Description:** Ascomata hypogeous or epigeous; apothecial species sessile and cupulate. Flesh producing watery latex, becoming yellowish, greenish or bluish in air. Asci operculate, 8-spored, mainly without crozier, wall weakly bluing in contact with an iodine solution, a little more intensely at the top (WT type). Paraphyses containing a brownish vacuolar pigment. Medullary excipulum containing laticiferous hyphae. Ectal excipulum of *textura globulosa*, with large cells. Ascospores uni- or biguttulate, warted. Species forming ectomycorrhizas.



Containing the following species:

• ***Paragalactinia succosa*** (Berk.) Van Vooren, *comb. nov.* – MB 835926.

Basionym: *Peziza succosa* Berk., *Ann. Mag. Nat. Hist.*, 6: 358 (1841).

Homotypic synonyms: *Aleuria succosa* (Berk.) Gillet, *Champ. France, Discom.*, livr. 2: 45 (1879); *Otidea succosa* (Berk.) Thüm., *Mycoth. Univ.*, cent. 15: no. 1411 (1879); *Galactinia succosa* (Berk.) Sacc., *Syll. fung.*, 8: 106 (1889); *Plicaria succosa* (Berk.) Rehm, *Rabenh. Kryptog.-Fl., Pilze – Ascom.*, 1 (3): 1016 (1894).

• ***Paragalactinia succosella*** (Le Gal & Romagn.) Van Vooren, *comb. nov.* – MB 835927.

Basionym: *Galactinia succosella* Le Gal & Romagn., *Rev. Mycol. (Paris)*, 5: 113 (1940).

Homotypic synonym: *Peziza succosella* (Le Gal & Romagn.) Aviz.-Hersh. & Nemlich, *Israel J. Bot.*, 23 (3): 156 (1974).

• ***Paragalactinia infusata*** (Quél.) Van Vooren, *comb. nov.* – MB 835928.

Basionym: *Peziza infusata* Quél., *C.R. Assoc. Fr. avanc. sci.*, 20 (2): 465 (1892).

Homotypic synonym: *Galactinia succosa* var. *infusata* (Quél.) Boud., *Hist. classif. discom. Eur.*: 48 (1907).

• ***Paragalactinia berthetiana*** (Donadini) Van Vooren, *comb. nov.* – MB 835929.

Basionym: *Peziza berthetiana* Donadini, *Doc. mycol.*, 14 (56): 47 (1985).

• ***Paragalactinia infossa*** (Fogel & States) Van Vooren, *comb. nov.* – MB 835930.

Basionym: *Peziza infossa* Fogel & States, *Mycotaxon*, 88: 155 (2003). First published as *Peziza quercicola* Fogel & States (2002), *nom. illeg.*

• ***Paragalactinia erinae*** (M.E. Sm.) M.E. Sm. & Van Vooren, *comb. nov.* – MB 835931.

Basionym: *Peziza erinae* M.E. Sm., *N. Amer. Fungi*, 9 (4): 3 (2014) [as “erini”].

• ***Paragalactinia michelii*** (Boud.) Van Vooren, *comb. nov.* – MB 835932.

Basionym: *Galactinia michelii* Boud., *Bull. Soc. mycol. France*, 7: 215 (1891).

Homotypic synonym: *Peziza michelii* (Boud.) Dennis, *Brit. Cup Fungi*: 15 (1960).

***Phaeopezia*** (Vido) Vido, *Michelia*, 1 (5): 595 (1879) – MB 3933.

Basionym: *Peziza* subgen. *Phaeopezia* Sacc. ex Vido, *Michelia*, 1 (5): 594 (1879) – MB 700367.

Type-species: *Peziza apiculata* Cooke

Etymology: From ancient Greek φαειος (*phaeos*), meaning “dusky, dark”, and πέζις (*pezis*) meaning “fungus without stipe”.

Synonyms: *Phaeopezia* subgen. *Geoscyphula* Sacc., *Bot. Centralbl.*, 18: 218 (1884); *Podaleuris* Clem., *Gen. fung.*: 89 (1909).

**Amended description:** Ascomata epigeous or hypogeous; apothecial species sessile and discoid. Asci operculate, 8-spored, with crozier, wall diffusely bluing in an iodine solution (WT type). Paraphyses diffusely coloured (olivaceous brown), with also a brownish external pigment on the top article. Ascospores containing numerous small polar granules, ornamented with warts and sometimes with polar apiculi, hyaline becoming brown with age. Excipulum of *textura globulosa*, with small to medium-sized cells. Species forming ectomycorrhizas.

Containing the following taxa:

• ***Phaeopezia apiculata*** (Cooke) Vido, *Michelia*, 1 (5): 595 (1879).

Basionym: *Peziza apiculata* Cooke, *Mycographia*: 175 (1877).

Homotypic synonyms: *Aleurina apiculata* (Cooke) Sacc. & P. Syd., *Syll. fung.*, 16: 739 (1902); *Aleuria apiculata* (Cooke) Boud., *Hist. class. Discom. Eur.*: 47 (1907); *Discina apiculata* (Cooke) Seaver, *Mycologia*, 13 (2): 70 (1921); *Galactinia apiculata* (Cooke) Le Gal, *Bull. Soc. mycol. France*, 78: 208 (1962).

• ***Phaeopezia apiculata* f. *alba*** (Van Vooren & Moyne) Van Vooren, *comb. nov.* – MB 835821.

Basionym: *Peziza apiculata* f. *alba* Van Vooren & Moyne, *Bull. Soc. mycol. France*, 119 (3–4): 247 (2004).

***Phylloscypha*** Van Vooren, *gen. nov.* – MB 835822.

Type-species: *Peziza phyllogena* Cooke

Etymology: From ancient Greek σκύφος (*skúphos*) meaning “cup” and φύλλον (*phýllon*) meaning “leaf”, referring to the type-species *P. phyllogena*.

**Description:** Ascomata epigeous, cupulate, sessile, external surface distinctly furfureous or pustulate. Flesh without latex, purplish-coloured. Asci operculate, 8-spored, with crozier, wall diffusely bluing in an iodine solution (W type). Paraphyses hyaline, with an external pigment at the top, pale brown, olivaceous brown or dark brown. Ascospores eguttulate but containing small polar granules, ornamented with warts. Excipulum of *textura globulosa*, with medium-sized to large cells. Species saprobic.

Containing the following species:

• ***Phylloscypha phyllogena*** (Cooke) Van Vooren, *comb. nov.* – MB 835823.

Basionym: *Peziza phyllogena* Cooke, *Mycographia*: 148 (1877).

Other synonyms: *Aleuria olivacea* Boud., *Bull. Soc. mycol. France*, 13 (1): 14 (1897), *nom. illeg.*; *Peziza olivacea* Boud. ex Sacc. & P. Syd., *Syll. fung.*, 14 (2): 745 (1899), *nom. illeg.*; *Galactinia olivacea* Boud. ex Boud., *Icon. Mycol.*, 2: pl. 282 (1907); *Peziza badioconfusa* Korf, *Mycologia*, 46: 838 (1954); *Galactinia badioconfusa* (Korf) Svrček & Kubicka, *Česká Mykol.*, 17 (2): 68 (1963); *Peziza kallioi* Harmaja, *Karstenia*, 26: 46 (1986).

• ***Phylloscypha coquandii*** (Donadini) Van Vooren, *comb. nov.* – MB 835824.

Basionym: *Peziza coquandii* Donadini, *Bull. trim. Féd. mycol. Dauphiné-Savoie*, 97: 11 (1985).

• ***Phylloscypha retrocurvatoides*** (Van Vooren) Van Vooren, *comb. nov.* – MB 835825.

Basionym: *Peziza retrocurvatoides* Van Vooren, *Mycol. Progress*, 17 (1–2): 73 (2017).

• ***Phylloscypha boltonii*** (Quél.) Van Vooren & Hairaud, *comb. nov.* – MB 835826.

Basionym: *Peziza boltonii* Quél., *Bull. Soc. bot. France*, 25 (4): 290 (1879).

Homotypic synonyms: *Aleuria boltonii* (Quél.) Gillet, *Champ. France, Discom.*, livr. 8: 206 (1886); *Galactinia boltonii* (Quél.) Boud., *Bull. Soc. mycol. France*, 15: 20 (1899).

• ***Phylloscypha labessiana*** (Boud.) Van Vooren, T. Richter & M. Vega, *comb. nov.* – MB 835827.

Basionym: *Aleuria labessiana* Boud., *Hist. classif. discom. Eur.*: 46 (1907).

Homotypic synonym: *Peziza labessiana* (Boud.) Sacc. & Traverso, *Syll. fung.*, 20: 315 (1911).

***Purpureodiscus*** (Hirsch) Van Vooren, *stat. et comb. nov.* – MB 835833.

Basionym: *Peziza* sect. *Purpureodiscus* Hirsch, *Boletus*, 16 (1): 4 (1992) – MB 538932.

Type-species: *Galactinia subisabellina* Le Gal

Etymology: From Latin *purpura*, purple, and *discus*, disk.

**Amended description:** Ascomata discoid or pulvinate, sessile, fleshy, whitish, pinkish to reddish-colored or purplish brown. Flesh without latex. Asci operculate, 8-spored, with crozier, with wall diffusely bluing in an iodine solution (W type). Paraphyses containing small vacuolar bodies. Ascospores eguttulate, but often with small granules at young stage, smooth or ornamented by isolated warts, in some species germinating to directly produce conidia. Ectal excipulum of *textura globulosa/angularis*, with large cells. Species saprobic.



Containing the following taxa:

• ***Purpureodiscus subisabellinus*** (Le Gal) Van Vooren, *comb. nov.* – MB 835834.

Basionym: *Galactinia subisabellina* Le Gal ex Le Gal, *Bull. Soc. mycol. France*, 83: 357 (1967).

Homotypic synonyms: *Peziza subisabellina* (Le Gal) Hohmeyer, Ludwig & Schmid, *Hoppea*, 47: 23 (1989); *Pachyella subisabellina* (Le Gal) Trimbach, *Doc. mycol.*, 29 (113): 8 (1999).

• ***Purpureodiscus subisabellinus f. ianthinus*** (Le Gal) Van Vooren, *comb. et stat. nov.* – MB 835835.

Basionym: *Galactinia subisabellina* var. *ianthina* Grelet ex Le Gal, *Bull. Soc. mycol. France*, 83: 358 (1967).

Homotypic synonyms: *Pachyella subisabellina* var. *ianthina* (Le Gal) Trimbach, *Doc. mycol.*, 29 (113): 8 (1999); *Peziza subisabellina* var. *ianthina* (Le Gal) Trimbach, *Micologia 2000*: 512 (2000).

• ***Purpureodiscus bananincola*** (Rehm) Van Vooren, *comb. nov.* – MB 835836.

Basionym: *Plicaria bananincola* Rehm, *Leaf. Philip. Bot.*, 6: 2234 (1914).

Homotypic synonym: *Peziza bananincola* (Rehm) Sacc., *Syll. fung.*, 24 (2): 1160 (1928).

• ***Purpureodiscus luteorosellus*** (Le Gal) Van Vooren, *comb. nov.* – MB 835837.

Basionym: *Galactinia luteorosella* Le Gal, *Bull. Jard. Bot. Etat*, 29: 82 (1959).

Homotypic synonym: *Peziza luteorosella* (Le Gal) Pfister, *Mycotaxon*, 41 (2): 507 (1991).

• ***Purpureodiscus kreiselii*** (Hirsch) Van Vooren, *comb. nov.* – MB 835838.

Basionym: *Peziza kreiselii* Hirsch, *Boletus*, 16 (1): 8 (1992).

## Conclusion

Thanks to new molecular data related to *Peziza s. lato* species produced these last years and through this study, the multigene phylogeny of *Pezizaceae* can be improved. The results of works done by HANSEN *et al.* (2005) have been consolidated by successive works on this genus (see introduction) for some lineages but new clades emerged which can be specified with morphological characters, a necessary condition to propose a useful taxonomy. The genera reinstated or newly published herein partially resolved the issue of *Peziza* paraphyly, using molecular data and morphology. Our contribution is a new step towards a more natural classification of *Pezizaceae*. Further studies including a larger sampling are needed to explore some species complexes (e.g. *Ionopezia gerardii*) or some clades with a low robustness.

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