

Pézizomycètes d'Europe

Nicolas Van Vooren



Pezizaceae



History

According to ECKBLAD (1968), *Pezizaceae* family was introduced by FRIES (1822) under the name *Pezizeae*, directly derived from the genus *Peziza* Dill. ex Fr., its type. One may also choose to refer to DUMORTIER (1829), who was the first to use the term *Pezizaceae*. In both cases, the typification of this family is based on the genus *Peziza* as defined by Fries in his *Systema Mycologicum* and therefore sanctioned (FRIES, 1822). The Linnaean definition of the genus *Peziza* (LINNAEUS, 1753) is therefore not retained in the current taxonomy. In Fries' definition of *Pezizaceae*, the main characters retained concern the cup-shaped apothecia, the smooth hymenium, the fleshy and membranous nature of the receptacle, and the dehiscence of the asci by spore ejection ('*sporidia, elasticè ejienda*'). This definition therefore encompasses most of what are commonly referred to as discomycetes.

BOUDIER (1885) treated the *Pezizaceae* family ('Pezizés') in a more restricted sense, within the operculate fungi, in a systematics of discomycetes based on the mode of dehiscence of asci, placing on one side the species whose spores are ejected through the opening of a summit operculum and those whose expulsion passes through a canal formed by dilation, also located at the ascus summit. It includes five groups, including the *Aleuriaceae*, which comprises genera with amyloid asci: *Lepidotia* Boud., *Aleuria* Fr., *Galactinia* (Cooke) Boud., *Sarcosphaera* Auersw., *Sphaerosoma* Klotzsch. and *Plicaria* Fuckel. This classification evolved somewhat thereafter, as the *Aleuriaceae* became a tribe to which the genus *Pachyella* Boud. was added and from which *Sphaerosoma* was excluded (BOUDIER, 1907). REHM (1896) used an alternative classification in which he expanded the genus *Plicaria* to include all pezizalean fungi with amyloid asci. This position was followed by VELENOVSKÝ (1934) who proposed the family *Plicariaceae* for this group of species, including the genera *Plicariella* (Sacc.) Rehm, *Ur-nula* Fr., *Infundibulum* Velen., *Pustularia* Fuckel, and *Otidea* in the sense of Persoon.

ECKBLAD (1968) adopted Fries' definition, particularly the cup-shaped nature of the apothecia ('the non-helvelloid character of the apothecium'), but also in a more restricted sense, emphasising the globular texture of the excipulum and the absence of carotenoid pigments. He accepted genera with amyloid asci (*Peziza*, *Plicaria*) and non-amyloid asci (*Psilopezia*, *Marcelleina*, *Discomycetella*). RIFAI (1968) includes only genera with amyloid asci in the *Pezizaceae*, i.e. *Aleuria* in the sense of Boudier, to which he adds the genera *Iodo-*

phanus Korf, *Gelatinodiscus* Kanouse & A.H. Sm., *Boudiera* Cooke and *Sphaerosoma*. RIFAI (1968) proposed numerous synonyms for the genus *Peziza*, such as *Phaeopezia* (Sacc. ex Vido) Vido, *Daleomyces* Setch., *Aleuria* in the sense of Boudier, *Plicaria*, etc.

KORF (1972) partly followed Rifai's classification but adopted a more restricted sense and retained only the genera *Peziza* (including the genus *Plicaria*), *Sarcosphaera*, *Pachyella* and *Gelatinodiscus*. This definition was followed, with a few minor differences, by most authors until the mid-1990s. The early molecular biology work of NORMAN & EGGER (1996) led to the emergence of significant new data and confirmations concerning the systematics of the *Pezizaceae*. Thus, the autonomy of the genus *Plicaria* was demonstrated. These two Canadian authors laid the first bricks of a phylogeny centred on the *Pezizaceae* (NORMAN & EGGER, 1999), work that was more successfully continued with the publication of a new phylogeny by HANSEN *et al.* (2001), in which several dozen evolutionary lineages appear within this family. This publication was consolidated four years later by multigene analyses (HANSEN *et al.*, 2005), laying the foundations on which all future works will be based to build the modern taxonomy of the *Pezizaceae*. Among the initial findings of this research, in addition to the paraphyletic nature of the genus *Peziza* — i.e. the absence of a common ancestor for all species known by this name — the presence of hypogeous species previously classified among the *Tuberales*, as well as species that do not exhibit an amyloid reaction in the asci (e.g. *Marcelleina*).

Although monophyletic lineages were highlighted in the aforementioned studies, these were not followed by nomenclatural changes, or only marginally, probably in anticipation of the sequencing of new species to improve the robustness of phylogenetic reconstructions. New multigene analyses conducted by VAN VOOREN (2020) established new genera within the *Pezizaceae* or rehabilitated others to better integrate the phylogeny of this family. Other studies focusing on a few critical species have since been conducted to confirm or complete the outline of the latter (ALBANESE *et al.*, 2022; PAZ *et al.*, 2022; VAN VOOREN *et al.*, 2021a, 2021b, 2022a, 2022b, 2023).

Current definition

Pezizaceae family now comprises 55 genera and approximately 235 listed species. Beyond their genetic profile, species in this family are characterised by:

- Ascomata forming apothecia or cleistothecia for hypogeous species.
- Apothecia cup- or disc-shaped, rarely stipitate.
- Asci operculate, exhibiting an amyloid reaction of their wall in the presence of an iodine reagent, more rarely without reaction, normally containing eight spores.
- Ascospores uninucleate, most often hyaline, guttulate or not, with a thin wall, smooth or ornamented surface.
- Absence of carotenoid pigments (except for the genus *Iodophanus*).
- Presence of at least one layer of rounded cells in the excipulum (*textura globulosa*).

It is important to note that the amyloid reaction of asci, when present, occurs in three distinct configurations, as codified by VAN VOOREN (2020). This particular character is generally consistent within each genus and is therefore very useful for taxonomic purposes.

Ecologically, *Pezizaceae* are found in many habitats, mainly in temperate and boreo-arctic environments, and are less common in tropical or subtropical areas. The species are mainly saprotrophs, but many also forms ectomycorrhizas, including hypogeous taxa (TEDERSOO *et al.*, 2006; LÆSSØE & HANSEN, 2007).

Key to the European epigeous genera of *Pezizaceae*

This key is based on characters observed on vital material. It is important to note that the term “guttule” concerns the oil bodies of large size present inside the ascospores and distinguished from the term “granule” which concerns the small bodies, often accumulated at the poles, abbreviated in BSG (bipolar small granules), but without distinguishing between lipidic granules or not. The codes W, WT and WTR used for the amyloid reaction of asci are defined in VAN VOOREN (2020).

- | | |
|--|-----------------------------------|
| 1. Asci amyloid, with reaction of WTR type | 2 |
| 1. Asci amyloid, with a different reaction, or inamyloid | 8 |
| 2. Ascospores eguttulate, sometimes with polar granules; apothecia most of the time with the following colours: beige, yellowish, tawny yellow, ochraceous brown | <i>Peziza</i> [p. 0] |
| 2. Ascospores guttulate, at least in asci; apothecia otherwise coloured | 3 |
| 3. Ascospores smooth | <i>Geoscypha</i> [p. 0] |
| 3. Ascospores ornamented | 4 |
| 4. Asci without croziers | <i>Daleomyces</i> [p. 0] |
| 4. Asci with croziers | 5 |
| 5. Apothecia whitish, becoming brownish, reddish brown, olivaceous brown | <i>Daleomyces</i> [p. 0] |
| 5. Apothecia lilac, bluish, violet, becoming brown with age | 6 |
| 6. Ectal excipulum with a thin gelatinous layer | <i>Daleomyces</i> [p. 0] |
| 6. Ectal excipulum not gelatinous | 7 |
| 7. Excipulum entirely of <i>textura globulosa</i> , with cells smaller in the ectal part, usually < 65 µm diam.; ascospores often heteromorphic | <i>Malvipezia</i> [p. 0] |
| 7. Excipulum more distinctly bilayered, with large cells in the ectal part, usually > 50 µm diam.; ascospores regular in shape and size | <i>Geoscypha</i> [p. 0] |
| 8. Ascospores fusoid | <i>Ionopezia</i> [p. 0] |
| 8. Ascospores globose | 9 |
| 8. Ascospores of different shape | 10 |
| 9. Ascospores eguttulate, sometimes with granules; apothecia shallowly cupuliform or discoid, flesh not milky | <i>Plicaria</i> [p. 0] |
| 9. Ascospores guttulate | 22 |
| 10. Apothecia first globose, semi-hypogeous | 11 |
| 10. Apothecia different | 12 |
| 11. Ascospores ellipsoid, eguttulate but containing BSG; amyloid reaction of WT type | <i>Sarcopeziza</i> [p. 0] |
| 11. Ascospores cylindrical, guttulate; amyloid reaction of W type | <i>Sarcosphaera</i> [p. 0] |
| 12. Apothecia distinctly stipitate (stipe sometimes buried) | 13 |
| 12. Apothecia sessile, turbinate or very shortly stipitate | 14 |
| 13. Ascospores eguttulate, smooth in water; asci with croziers, amyloid reaction of W type | <i>Lepidotia</i> [p. 0] |
| 13. Ascospores guttulate, ornamented with longitudinal crests; asci without croziers, amyloid reaction of WT type | <i>Iodowynnea</i> [p. 0] |

14. Ascospores eguttulate, sometimes with BSG	15
14. Ascospores uni- or biguttulate	17
14. Ascospores pluriguttulate	Hansenopezia [p. 0]
15. Ascospores ± brown when mature, apiculate	Phaeopezia [p. 0]
15. Ascospores hyaline, not apiculate	16
16. Apothecia very small, < 2 mm diam., ± pulvinate; ascospores without BSG, warted; ectal excipulum with small roundish cells	Iodophanus [p. 0]
16. Apothecia larger; ascospores with or without BSG.....	21
17. Milky flesh, with juice colouring in air	18
17. Non-milky flesh or with a colourless juice	19
18. Asci without crozier; juice becoming yellowish; paraphyses containing a brown pigment; ectal excipulum with roundish cells ≥ 45 µm diam. max.....	Paragalactinia , lineage <i>succosa</i> [p. 0]
18. Asci with croziers	29
19. Excipulum having a gelatinous layer; amyloid reaction of W or WT type	20
19. Excipulum without gelatinous layer; amyloid reaction of WT type	27
20. Ascospores smooth	Adelphella [p. 0]
20. Ascospores finely or strongly warted	25
21. Paraphyses containing yellow or yellow-olive coloured guttules.....	Elaiopezia [p. 0]
21. Paraphyses without guttules; ascospores without BSG	Lepidotia [p. 0]
21. Paraphyses without guttules; ascospores with BSG	26
22. Asci amyloid	23
22. Asci inamyloid or faintly amyloid	24
23. Ascospores pluriguttulate, smooth or ornamented	28
23. Ascospores uniguttulate, warted; apothecia deeply cupuliform, with a milky flesh . Plicariella (syn. <i>Scabropezia</i>) [p. 0]	
24. Apothecia deeply violet or brownish with purple tinges; asci inamyloid	Marcelleina [p. 0]
24. Apothecia dark brown to blackish; asci faintly amyloid (at least on young asci)	Scotopezia [p. 0]
25. Ascospores finely warted; amyloid or faintly amyloid reaction of W type	Pachyella [p. 0]
25. Ascospores strongly warted; amyloid reaction of WT type	Velenovskya [p. 0]
26. External surface often distinctly pustulate; flesh violet or greyish lilac.....	Phylloscypha [p. 0]
26. External surface different	Purpureodiscus [p. 0]
27. Ascospores smooth; paraphyses with small refractive vacuoles	Urinopezia [p. 0]
27. Ascospores ornamented; paraphyses without refractive vacuoles.....	31
28. Ascospores ornamented with spines	Boudiera [p. 0]
28. Ascospores smooth	Iodomarcelleina [p. 0]
29. Juice becoming yellowish, paraphyses containing a brown pigment; ascospores biguttulate; ectal excipulum with roundish cells > 45 µm diam.	Paragalactinia , lineage <i>michelii</i> [p. 0]
29. Juice of different colours	30
30. Juice ± deep blue; ascospores biguttulate; ectal excipulum with roundish cells < 45 µm diam. max. ..	Galactinia [p. 0]
30. Juice present or not, whitish, opalescent, more rarely pale blue; ascospores uni- or biguttulate; ectal excipulum with large roundish cells > 45 µm diam. in mean	Legaliana [p. 0]
31. Ascospores biguttulate, < 12 µm in length, ornamented with thick warts, forming short crests; ectal excipulum with roundish cells up to 50 µm diam.	Pyropezia [p. 0]
31. Ascospores uni- or biguttulate, ≥ 13 µm in length; ectal excipulum with large roundish cells > 45 µm diam. in mean ...	32
32. Ascospores biguttulate, rarely uniguttulate, ornamented with longitudinal crests, forming a complete network; paraphyses without vacuolar pigment	Chromelosporium (teleomorph) [p. 0]
32. Ascospores uni- or biguttulate, ornamented with warts or longitudinal crests, ± anastomosed; paraphyses containing a brown or olive brown vacuolar pigment	Legaliana [p. 0]



Paragalactinia

The genus *Paragalactinia* Van Vooren was proposed to accommodate species belonging to the '*Peziza succosa-michelii*' clade as defined by HANSEN *et al.* (2005) and VAN VOOREN (2020). It partly corresponds to the genus *Galactinia* (Cooke) Boud. as typified by LE GAL (1953), with *Peziza succosa* Berk. as the type. However, the first typification of this genus was proposed by CLEMENTS & SHEAR (1931), with *Peziza saniosa* Schrad. designated as the type. This typification must be followed according to Article 10.5 of the ICN (TURLAND *et al.*, 2025). The genus is phylogenetically well defined, but also morphologically by its species with succulent flesh, ornamented ascospores and pigmented paraphyses. Some species (those related to *P. succosa*) have asci without croziers, a feature that is quite rare in *Pezizaceae* (JAKLITSCH *et al.*, 2016). Finally, all known species are mycorrhizal (TEDER-SOO *et al.*, 2006, 2010; SMITH, 2014; VAN VOOREN, 2022).

Three lineages are clearly distinguishable within the genus *Paragalactinia*: The first lineage contains species related to the '*P. succosa*' complex, characterised by a dark grey-brown hymenium and juice that turns yellow; The second lineage includes taxa closely related to *P. michelii* (VAN VOOREN *et al.*, 2022a). Species in this group have a hymenium with purple or purplish-brown hues and asci arising from croziers, unlike the *succosa* lineage, whose asci have a simple septum at their base. The third lineage was recently highlighted by CAIAFA *et al.* (2025) for certain hypogeous taxa found in the southern hemisphere (South America and Australia).

There is considerable diversity within the *Paragalactinia succosa* lineage. This name encompasses numerous unpublished species, both in Europe and worldwide, which still require characterisation based on their morphology, host,

and biogeography. In Europe, the species *Paragalactinia hypoleuca* (Boud.) Van Vooren has recently been reinstated for the Mediterranean basin (VAN VOOREN, 2022). There we also found *Paragalactinia succosella* (Le Gal & Romagn.) Van Vooren (LE GAL, 1940), *P. infuscata* (Qué.) Van Vooren (GAROFOLI & BAIANO, 1996), as well as North American hypogeous taxa, *P. infossa* (Fogel & States) Van Vooren (FOGEL & STATES, 2002, under *Peziza quercicola*, *nom. illeg.*) and *P. erinia* (M.E. Sm.) M.E. Sm. & Van Vooren (SMITH, 2014).

The *Paragalactinia michelii* lineage, comprising species with generally more vividly coloured hymenia (at least initially), yellow or yellow-orange juice, and asci with croziers, includes *P. berthetiana* (Donadini) Van Vooren (DONADINI, 1985), and *P. pseudomichelii* Van Vooren, I. Khomenko, Lebeuf & Healy, a North American species (VAN VOOREN *et al.*, 2024).

Definition of *Paragalactinia*

Ascomata epigeous or hypogeous; species forming apothecia are sessile and cup-shaped; hypogeous species form ptychothecia. Flesh succulent, producing juice that turns yellowish, orange-yellow or greenish when exposed to air. Spore print white. Asci operculate, 8-spored, with walls diffusely turning blue in iodine solutions, but more intensely at the top (WT type), with or without croziers. Medullary excipulum containing laticiferous hyphae. Ectal excipulum with a globular texture composed of large cells. Ascospores uniseriate, uni- or biguttulate, ornamented with \pm coarse warts. Ectomycorrhizal species.

Type: *Peziza succosa* Berk. 1841, designated by VAN VOOREN (2020).

Key to the European species of *Paragalactinia*

1. Asci with croziers 2
1. Asci without croziers 4
2. Hymenium dark chestnut brown to blackish brown ***P. benatii***
2. Hymenium violet \pm dark to purplish brown 3
3. Hymenium first violet, soon becoming purplish brown. Ascospores 14.6–17.2(–19.8) \times 7.9–9.2(–10) μm , Qm=1.8, ornamented by irregular, angular warts, often coalescent, forming short ridges ***P. michelii*** [p. 12]
3. Hymenium vinaceous brown to dark violet, becoming purplish brown at maturity. Ascospores 15.2–18.5(–20) \times 8–9(–10) μm , Qm=2.0, ornamented with small warts, more or less elongated, sometimes forming ridges. Mediterranean basin ***P. berthetiana*** [p. 8]

4. Ascospores mainly uniguttulate. Apothecia rather small, often < 20 mm diam. *P. succosella* [p. 16]
 4. Ascospores mainly biguttulate. Apothecia larger 5
 5. Ascospores narrowly ellipsoid, $Q_m \geq 2.0$, $18-22(-23) \times 9-10.5 \mu m$ *P. hypoleuca* [p. 10]
 5. Ascospores with $Q_m < 2.0$ 6
 6. Hymenium grey to grey-brown. Ascospores $17-20(-21) \times 9.5-11(-12) \mu m$, with irregular and coarse warts, up to $2 \mu m$ high *P. succosa* [p. 14]
 6. Hymenium fuliginous dark brown. Ascospores $15-19 \times 8.5-10 \mu m$, with smaller and lower warts, up to $1 \mu m$ high.....
 *P. infusata*



Pl. 1 – Overview of *Paragalactinia* spp.

A. *Paragalactinia berthetiana* (C. Agnello). **B.** *P. michelii* (M. Carbone). **C.** *P. benatii* (N. Van Vooren). **D.** *P. succosa* (N. Van Vooren). **E.** *P. succosella* (N. Van Vooren). **F.** *P. hypoleuca* (N. Van Vooren).

Paragalactinia berthetiana



Ascomata gregarious, more rarely isolated. **Apothecia** 10–34 mm diam., sessile, more or less deeply cup-shaped, spreading with age. **Receptacle** distinctly furfuraceous, even warty at the margin, orange-brown, yellow-brown, olive-brown, dark olive, dirty orangish to purple-brown in older specimens. **Disc** initially dark purple, wine-coloured, then brown with purplish tinges at maturity. **Margin** slightly incurved at first. **Flesh** thin, pale olive-coloured, brittle, producing a whitish or opalescent juice, turning yellowish or greenish-yellow when exposed to air, sometimes orangish yellow, within a few minutes.

Ascospores ellipsoid, sometimes slightly elongated, (15–)15.2–18.5(–20) × (7.5–)8–9(–10) μm, Md=17 × 8.5 μm {n=94}, Q=(1.7–)1.8–2.2(–2.4), Qm=2.0 [holotype †: (16.5–)17–19(–19.2) × (8–)8.5–10 μm, Md=18 × 9 μm {n=30}, Qm=2.0], hyaline, uni- or biguttulate, sometimes accompanied with a few droplets, ornamented with dense, irregular, low, cyanophilous warts, stretched, sometimes coalescent and forming some small crests (even subreticulate after DONADINI, 1985), 0.4–0.6 μm high, sometimes up to 1 μm at the poles. **Asci** 260–360 × 12–16 μm, cylindrical, narrowing toward base, with croziers, 8-spored, with wall bluing in iodine solutions, strongly at the top (WT type). **Paraphyses** cylindrical, 3–5 μm diam., widened at the top, 6–11 μm, containing a vacuolar pigment, yellow to brownish yellow, accompanied by brown granules, denser in the terminal cells. **Subhymenium** of *textura globulosa/angularis*, with cells 6–17 μm wide. **Medullary excipulum** yellowish to olivaceous yellow “en masse”, bi-layered: upper part of *textura intricata*, with hyphae 5–9 μm wide; lower part of *textura globulosa*, with cells 11–50 μm diam., mixed with clavate elements and laticiferous hyphae, 10–13 μm wide. **Ectal excipulum** rather thin (compared to the medullary part), of *textura angularis/globulosa*, with cells (10–)25–72 μm diam., mixed with clavate elements, 15–35 × 8–18 μm, containing a granular pigment, brownish yellow, often organised in pyramidal clusters, partly encrusted with a dark brown or olive-brown matter.

Distribution and ecology: Present in Europe, in the Mediterranean basin (Cyprus, France, Italy, and Spain), from the end of October to March, mainly on calcareous soil, under *Quercus* spp., sometimes mixed with *Pinus* spp. and other Mediterranean shrubs.

Iconography: AGNELLO (in VAN VOOREN & MAURUC, 2020: 84).

Comments: The species was described by DONADINI (1985) as very similar to *Paragalactinia michelii*, both sharing the same colours. *P. berthetiana* differs from the latter in its distinctly furfuraceous, even pustular outer surface, darker hymenium, finer spore ornamentation and a habitat that appears to be strictly Mediterranean, particularly in association with the holm oak (*Quercus ilex*). After revising the holotype, the aporynchous nature of the asci (DONADINI, 1985) was not confirmed by VAN VOOREN & MAURUC (2020), because the asci arise from croziers. This crucial information allows for a reassessment of this species, particularly regarding its distribution, because some other Mediterranean collections may have been misidentified due to Donadini's diagnostic error. As *P. michelii* is also present in the geographical area of *P. berthetiana*, careful examination is necessary — in the absence of molecular analysis — to distinguish between them. Based on the specimens studied, *P. berthetiana* has darker colours, with a hymenium that stays purple or wine-coloured for a long time, while in *P. michelii* the purple colour tends to disappear fairly quickly. Oldest specimens of *P. michelii* show a reddish light brown colour, while *P. berthetiana* is darker, brown with wine-coloured tinges. Microscopically, the spore ornamentation in *P. berthetiana* appears somewhat more delicate. This species also seems less common than its relative, being restricted to areas influenced by the Mediterranean climate.

Nomenclature: *Paragalactinia berthetiana* (Donadini) Van Vooren, *Ascomycete.org*, 12 (4): 189 (2020).

Basionym: *Peziza berthetiana* Donadini, *Doc. mycol.*, 14 (56): 47 (1985) – Type: Coll. MPU JCD 853-75 (holotype).

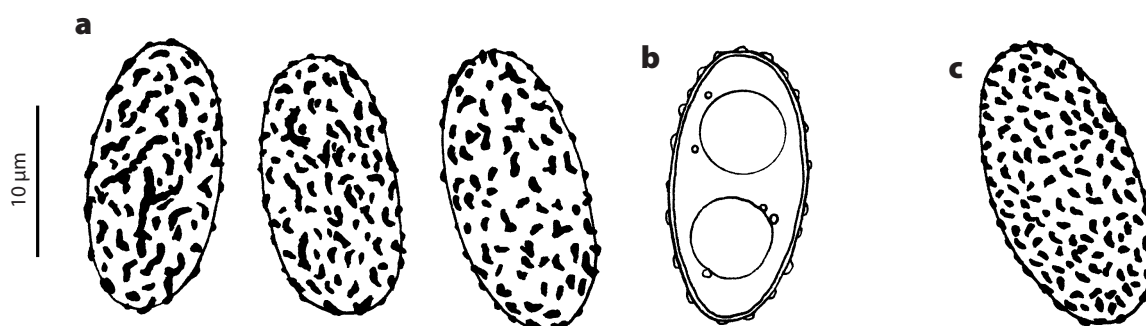


Fig. 1 – Ascospores. **a–b.** Coll. LY NV2021.11.01, (a) in CBL, (b) in water. **c.** Coll. MPU JCD 853-75 (holotype), in CBL.



Pl. 2 – *Paragalactinia berthetiana*. Various collections, *in situ*.

A. Coll. LY NV2021.11.01 (N. Van Vooren). **B.** Coll. MC-06-12-24 (M. Carbone). **C.** Coll. LY NV2024.11.13 (N. Van Vooren). **D.** Coll. GDOR 5074 (M. Carbone). **E.** Coll. CA12012013-15 (C. Agnello).

Paragalactinia hypoleuca



Ascomata gregarious or isolated. **Apothecia** 8–40 (–50) mm diam., 10–24 mm high, sessile, deeply cupuliform, spreading when mature. **Receptacle** paler than the hymenium or glaucous, or greyish, velvety, becoming rough with age, marked with some dark pustules at the margin, always with a pale grey to yellowish grey base. **Disc** dark grey-brown to blackish brown, sometimes with purplish tinges. **Margin** more or less incurved. **Flesh** soft, weakly succulent, with a whitish juice, becoming yellowish after several minutes.

Ascospores ellipsoid to narrow ellipsoid, (17–)20–23 (–25) × (8.8–)9–10.3(–11.5) μm, Md=21.5 × 9.9 μm {n=56}, Q=(1.9–)2.1–2.3(–2.5), Qm=2.2 [lectotype †: (17.2–)18–20 (–21) × (8.5–)9.2–10 μm, Md=19 × 9.8 μm, Qm=2.0], hyaline, containing two large oil drops (one drop often smaller), more rarely with one large drop, accompanied with smaller droplets; surface ornamented with low cyanophilous warts, up to 1 μm wide, angular or rounded, stretched or crest-like, more or less coalescent, but never forming a true network, sometimes mixed with tiny warts. **Asci** 320–350 × 14–19 μm, cylindrical, narrowing toward base, 8-spored, without croziers, with wall diffusely blue in iodine solutions, darker at the top (WT type). **Paraphyses** cylindrical, 5–7 μm diam., slightly broader at the top or subclavate, 8–16 μm diam., containing a dense brown vacuolar pigment. **Subhymenium** similar to the medullary excipulum, but with yellowish hyphae. **Medullary excipulum** of *textura intricata*, with hyaline hyphae, mixed with scattered globose cells. **Ectal excipulum** of *textura globulosa*, with globose hyaline cells, becoming pale brownish on the outside, 8–62 μm diam., some others clavate, mixed with laticiferous hyphae, intercellular brown pigment present in the outermost part.

Distribution and ecology: Originally discovered in Portugal, it is distributed in the Mediterranean basin, e.g. Southern France, Spain, etc. It grows on soil, under deciduous trees. Based on our ecological data and the presence

of environmental sequences from mycorrhizae in BLAST results, we suggest that *P. hypoleuca* may form ectomycorrhizae with Mediterranean oaks.

Iconography: BOUDIER & TORREND (1911, pl. IV, fig. I); VAN VOOREN (2022: 93).

Comments: The original Latin description for *Galactinia hypoleuca* given by BOUDIER & TORREND (1911) is sufficiently detailed to allow for a comprehensive morphological comparison with recent collections of *Paragalactinia succosa* complex, as well as the microscopical characters illustrated by BOUDIER & TORREND (1911). The authors did not mention the presence of succulent flesh, but this characteristic may vary depending on external conditions or the specimen's state (e.g., when drying).

Paragalactinia succosa is considered as a common species in temperate areas. It is characterised by cupuliform ascomata, a grey to grey-brown hymenium contrasting with a pale grey or grey-beige external surface, often marked by yellowish spots produced by the juice, and, microscopically, by biguttulate ascospores, ornamented with irregular and coarse warts, asci without croziers, brown pigment in paraphyses, and laticiferous hyphae in the excipulum (see under this name). *P. hypoleuca* presents a darker hymenium and larger ascospores with a different Q ratio, 20–23 × 9–10.5 μm and Qm ≥ 2.0 in *P. hypoleuca* vs. 16–20.5 × 8–12 μm and Qm=1.8, in *P. succosa*. The spore warts are also lower and less coarse in *P. hypoleuca*. The similar *P. succosella* (see under this name) differs by a smaller size, and mainly uniguttulate and slightly shorter ascospores.

Nomenclature: *Paragalactinia hypoleuca* (Boud. & Torrend) Van Vooren, *Fungi Iberici*, 2: 92 (2022).

Basionym: *Galactinia hypoleuca* Boud. & Torrend, *Bull. Soc. mycol. France*, 27 (2): 127 (1911) – Type: PC 0738326 (lectotype).

Other synonyms: MB 836309

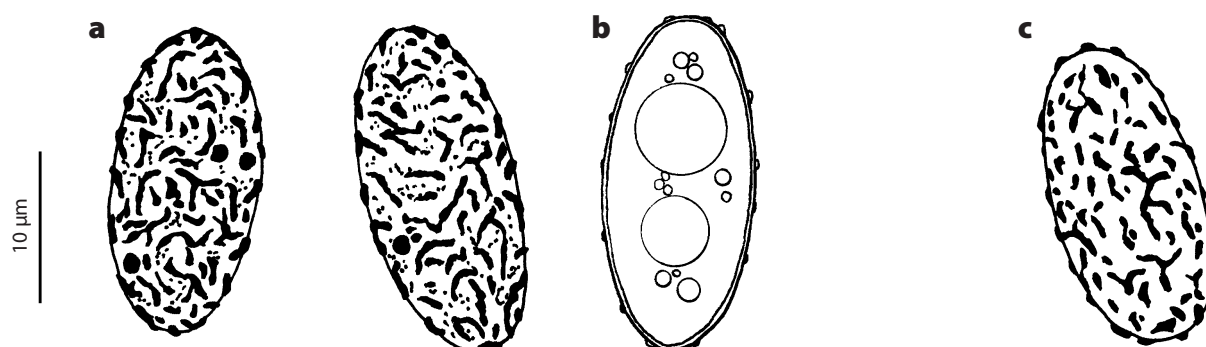


Fig. 2 – Ascospores. **a–b.** Coll. LY NV2020.02.01, (a) in CBL, (b) in water. **c.** Lectotype, in CBL.



Pl. 3 – *Paragalactinia hypoleuca*. Various collections, *in situ*.

A. Coll. LY NV2013.11.18 (N. Van Vooren). **B.** Coll. ERD-9745 (J. Mateos). **C.** Coll. Jr002 (J. Ruiz). **D.** Coll. MAR 081208 001 (M.A. Ribes). **E.** Coll. MAR 271219 305 (M.A. Ribes).



Ascomata gregarious or isolated. **Apothecia** 5–30 (–50) mm diam., 3–15 mm high, sessile, shallow cup-shaped, spreading with age. **Receptacle** subglabrous or slightly scaly, especially towards the margin, yellow-brown, reddish-brown, fawn-yellow, sometimes paler, greyish yellow, contrasting with the hymenium in young specimens. **Disc** initially deep purple or mauve, then becoming orange-brown, caramel or reddish-brown, with purplish tinges. **Margin** often slightly curved. **Flesh** brittle, releasing a milky white juice that becomes yellow when exposed to air.

Ascospores ellipsoid, $(13.2\text{--}14.6\text{--}17.2\text{--}19.8) \times (6.8\text{--}7.9\text{--}9.2\text{--}10) \mu\text{m}$, $Md=16 \times 8.7 \mu\text{m}$ { $n=263$ }, $Q=(1.5\text{--}1.6\text{--}2.0\text{--}2.2)$, $Qm=1.8$, hyaline, biguttulate, ornamented with irregular warts, cyanophilic, isolated or sometimes coalescent, up to $0.5 \mu\text{m}$ high. **Asci** $250\text{--}320 \times 11\text{--}15 \mu\text{m}$, cylindrical, narrowing toward base, with croziers, 8-spored, with wall turning blue in iodine solutions, slightly more intensely at the apex (WT type). **Paraphyses** not or very slightly widened at the apex, $4\text{--}8 \mu\text{m}$ diam., sometimes slightly curved, containing a brown or pale brown-yellow vacuolar pigment and darker brown granules. **Subhymenium** of *textura intricata*, with yellowish hyphae, oriented perpendicular to the hymenium, $6\text{--}10 \mu\text{m}$ wide. **Medullary** and **ectal excipulum** undifferentiated, of *textura globulosa*, with large cells, $10\text{--}75 \mu\text{m}$ diam., mixed with other more elongated or sausage-like, $7\text{--}10$ (15) μm wide, all embedded in a yellowish or olive-yellow context, presence of a sparse, intercellular, encrusting, brown pigment. In the outermost zone, some hair-like, hyaline, septate, obtuse hyphae, $30\text{--}47 \times 8\text{--}9 \mu\text{m}$, can sometimes be observed. **Marginal zone** composed of simple, elongated cells, swollen at the top, some forked at the base, the terminal article measuring $20\text{--}37 \times 4\text{--}8 \mu\text{m}$, the lower articles $10\text{--}30 \times 4\text{--}6 \mu\text{m}$.

Distribution and ecology: Widely distributed in Europe, from lowlands to mountainous areas, on soil, mainly in woodlands or parks, often along the paths or talus slopes, as well as on small banks along streams. In summer, sometimes until October.

Iconography: BOUDIER (1891, pl. XV, fig. II); BOUDIER (1905–1910, pl. 286); BREITENBACH & KRÄNZLIN (1981, n° 45); MEDARDI

(2006a: 180, under *P. berthetiana*); MEDARDI (2006b: 193); FRUND (2010: 66); VAN VOOREN (2014: 125).

Comments: *Paragalactinia michelii* is a relatively common species, growing from lowlands to mountainous areas, often on the edges of deciduous forests or mixed woodlands, and regularly along forest paths. Its distinctly purple hymenium when young, contrasting with the yellow-brown or fawn-yellow outer surface, characterizes this species, as well as the presence of a juice in the flesh that yellows when exposed to air. The colour variation between young and older specimens is significant, and the disappearance of the purple hues can easily lead to confusion (see, for example, DENNIS, 1960, about the colour). Apart from possible confusion with *P. berthetiana*, there is also a potential confusion with some collections of *Legaliana pudica* (Boud.) Van Vooren & Carbone, whose hymenium has more pronounced reddish hues. However, the latter produces blue-tinged juice (or no juice), which allows it to be distinguished. In the absence of juice, a microscopic examination will allow them to be separated, as *L. pudica* has wider, uniguttulate ascospores on average, i.e. a lower Q ratio than *P. michelii*, 1.6 vs. 1.8, according to our data; the spore ornamentation of *L. pudica* is also coarser.

Paragalactinia michelii is a mycorrhizal species, associated with various deciduous tree species, perhaps preferentially with *Betulaceae* (*Alnus* spp., *Betula* spp., *Carpinus* spp.) according to the literature consulted (TEDERSOO *et al.*, 2006; TEDERSOO *et al.*, 2008; ASHRAF *et al.*, 2012) and our data.

Peziza plebeia (Le Gal) Nannf. is considered a later synonym of *Paragalactinia michelii* based on the descriptions and illustrations of microscopic characters provided by LE GAL (1937, 1940). *Paragalactinia benatii* Van Vooren & Moyne seems to be also a synonym, based on molecular data, characterized by its darker colours and mountain habitat.

Nomenclature: *Paragalactinia michelii* (Boud.) Van Vooren, *Ascomycete.org*, 12 (4): 189 (2020).

Basionym: *Galactinia michelii* Boud., *Bull. Soc. mycol. France*, 7: 215 (1891) – Type: no collection in PC; Pl. XV, fig. II (lectotype), in BOUDIER (1891).

Other synonyms: MB 835932

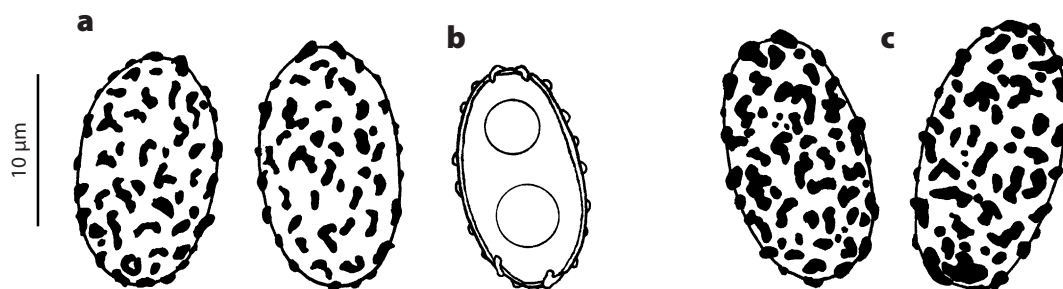


Fig. 3 – Ascospores. **a–b.** Coll. LY NV2011.08.09, (a) in CBL, (b) in water. **c.** Coll. LY NV2020.08.19, in CBL.



Pl. 4 – *Paragalactinia michelii*. Various collections, *in situ*.

A. Coll. MC-30-07-2023 (M. Carbone). **B.** Coll. MAR 051210 025 (M.A. Ribes). **C.** Coll. MAR 290809 025 (M.A. Ribes). **D.** Coll. LY NV2007.06.09 (N. Van Vooren). **E.** Coll. LY NV2011.08.09 (N. Van Vooren).



Ascomata mainly gregarious, rather robust. **Apothecia** 17–30(–50) mm diam., 10–25 mm high, cup-shaped, spreading slightly with age. **Receptacle** finely pustular, grey-beige, glaucous beige, often showing yellowish tinges, especially in wounds. **Disc** pale grey, grey-beige or deep hazelnut brown, sometimes with olivaceous tinges. **Flesh** soft, exuding a hyaline juice that turns greenish-yellow when exposed to air.

Ascospores ellipsoid, (15–)17–20(–21) × (8–)9.5–11 (–12) μm, Md=19 × 10 μm {n=207}, Q=(1.5–)1.7–2.0(–2.1), Qm=1.8, hyaline, biguttulate, more rarely uniguttulate, ornamented with cyanophilic warts, irregular, more or less coarse, 0.5–2 μm wide, up to 2 μm high, sometimes stretched into small, low, undulating ridges. **Asci** 290–360 (–410) × 15–19 μm, cylindrical, narrowing toward base, without croziers, 8-spored, with wall turning blue in iodine solutions, more intensely at the top (WT type). **Paraphyses** not or very slightly widened at the apex, 5–10 μm diam., containing a pale brown pigment concentrated in the terminal cells. **Medullary excipulum** of *textura intricata*, with more or less yellowish hyphae, mixed with larger, bulging cells. **Ectal excipulum** of *textura globulosa*, with hyaline cells, 9–50 μm diam.

Distribution and ecology: Originally described from Great Britain, it is widely distributed in Europe, except in the Mediterranean basin where it is probably replaced by *P. hypoleuca* and some other undescribed taxa. From lowlands to subalpine stage, under deciduous trees or in mixed woods, in mycorrhizal association mainly with *Fagaceae* (*Fagus* spp., *Quercus* spp.). From June to November.

Iconography: BOUDIER (1905–1910, pl. 284); BREITENBACH & KRÄNZLIN (1981, n° 52); GAROFOLI & BAIANO (1996: 250); MEDARDI (2006: 207); VAN VOOREN (2014: 132); EYSSARTIER & ROUX (2017: 1101).

Comments: This is a very common species, identifiable by its greyish beige hues, often yellowish stained by the presence of a juice that seeps from wounds. Some specimens have a darker hymenium, in shades of brown. Specimens with a dark brown hymenium are sometimes attributed to *Paragalactinia infuscata* (Quél.) Van Vooren, but this taxon requires a modern typification (see also our comments under *P. succosella*). Microscopically, the presence of asci without croziers is an uncommon feature in the *Pezizaceae*. The European collections of *P. succosa* are phylogenetically isolated, contrary to many other phyllospesies present in North America and identified under this name. The closest species is *P. hypoleuca*, which has a southern distribution and narrower ascospores (Qm ratio ≥ 2.0 vs. 1.7–1.8 in *P. succosa*). *Paragalactinia succosella* is also closely related, but its apothecia are smaller and its ascospores are mainly uniguttulate.

Nomenclature: *Paragalactinia succosa* (Berk.) Van Vooren, *Ascomycete.org*, 12(4): 189 (2020).

Basionym: *Peziza succosa* Berk., *Ann. Mag. Nat. Hist.*, 6: 358 (1841) – Type: Plate X, figs. 5–8 (lectotype), in BERKELEY (1841).

Other synonyms: MB 835926

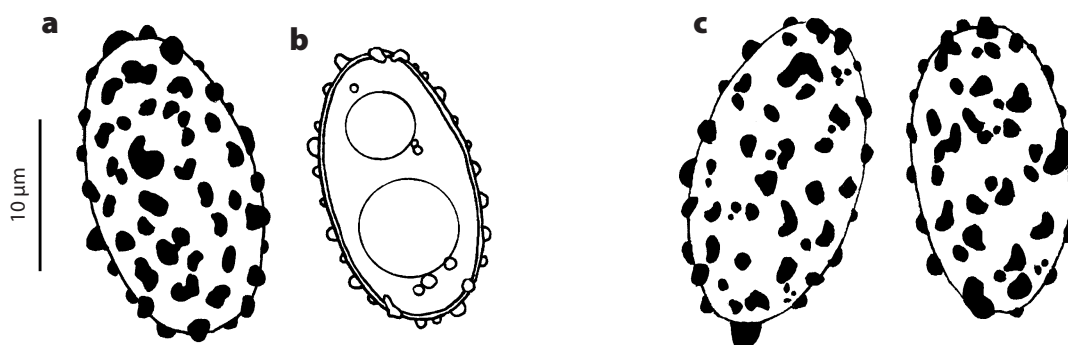


Fig. 4 – Ascospores. **a–b.** Coll. LY NV2025.09.09, (a) in CBL, (b) in water. **c.** Coll. LY NV2022.10.16, in CBL.



Pl. 5 – *Paragalactinia succosa*. Various collections, *in situ*.

A. Coll. MAR 240808 070 (M.A. Ribes). **B.** Coll. LY NV2025.10.17 (N. Van Vooren). **C.** Coll. LY NV2007.06.08 (N. Van Vooren). **D.** Coll. MAR 220808 121 (M.A. Ribes). **E.** Coll. BW 220816 (B. Wergen).

Paragalactinia succosella



Ascomata mainly gregarious. **Apothecia** 6–15 mm diam., sessile, shallow cup-shaped, soon spreading. **Receptacle** glabrous or finely furfuraceous, sometimes with yellowish tinges. **Disc** more or less wrinkled, dull grey, grey-brown, glaucous, often with subtle olivaceous tinges, blackening with age. **Flesh** soft, succulent, exuding an opalescent juice, yellowing when exposed to air or greenish yellow, sometimes not very abundant.

Ascospores ellipsoid, $(15-16-18(-19.5) \times (8-9.2-11(-11.5)) \mu\text{m}$, $Md=17 \times 10 \mu\text{m}$ { $n=149$ }, $Q=(1.4-1.5-1.8(-2.1))$, $Qm=1.7$, hyaline, uniguttulate, more rarely biguttulate (the second guttule being smaller), ornamented with cyanophilic, irregular, pustular warts, $0.5-2 \mu\text{m}$ wide, or stretched into small low ridges, up to $1 \mu\text{m}$ high. **Asci** $240-310 \times 13-17 \mu\text{m}$, cylindrical, narrowing toward base, without croziers, 8-spored, with wall turning blue in iodine solutions, more intensely at the apex (WT type). **Paraphyses** widened at the apex or subcapitate, $7.5-13(-15) \mu\text{m}$ diam., having a vacuolar brown pigment, more concentrated in the terminal cells. **Medullary excipulum** of *textura intricata*, with yellowish hyphae. **Ectal excipulum** of *textura globulosa/subglobulosa*, with hyaline cells, $16-55 \mu\text{m}$ diam., mixed with laticiferous hyphae, the whole embedded in a greenish-yellow context.

Distribution and ecology: It is probably widely distributed in Europe, but confusion with *Paragalactinia succosa*, *P. hypoleuca*, or undescribed species in southern countries (see comments) makes it difficult to accurately determine its distribution. From lowlands to submountainous areas, in cool or wet woodlands, mainly under deciduous trees or in mixed woods, along paths or talus slopes, sometimes also on burnt places. It often grows early, from April to October. Also confirmed in Pakistan and New Zealand.

Iconography: MEDARDI (2006a: 208); VAN VOOREN (2014: 132).

Comments: Although similar to *Paragalactinia succosa*, this species is distinguished by its slightly smaller and less cup-shaped apothecia, as well as its duller colours. Microscopically, the differences between these two taxa are small, except for the different guttulation of the ascospores, as well as the spore ornamentation (thinner in *P. succosella*). The carbonicolous habitat noted for some collections has not been reported for *P. succosa*. Note also that collections identified as *P. succosella* from southern countries of Europe are not always easy to separate from *P. hypoleuca* because of their low spore ornamentation, though the latter should have larger and narrower ascospores (Qm ratio ≥ 2.0). It is possible that *Peziza infusata* Quél. — often considered as a simple form of *P. succosa* — reported with a brown hymenium contrasting with the white outer surface, as described by QUÉLET (1880), might represent some of these “mediterranean” taxa named *P. succosella* because *P. infusata* was published based on collections made in Southern France, except for one collection — the latter being revised by LE GAL (1940) and considered to not be different from *P. succosa*. Another example of confusion can be found in ÇOLAK & KAYGUSUZ (2017) who described and illustrated a Turkish collection of *P. succosella* that clearly represents one of these species found in Mediterranean basin. Further investigations are required to improve the taxonomy of this group.

Interestingly, *P. succosella* is reported from Pakistan, in Himalayan moist temperate forests, in mycorrhizal association with *Cedrus deodora* (JABEEN *et al.*, 2015).

Nomenclature: *Paragalactinia succosella* (Le Gal & Romagn.) Van Vooren, *Ascomycete.org*, 12(4): 189 (2020).

Basionym: *Galactinia succosella* Le Gal & Romagn., *Rev. mycol. (Paris)*, 5: 113 (1940) – Type: Coll. PC0798348 (holotype).

Other synonyms: MB 835927



Fig. 5 – Ascospores. **a.** Coll. LY NV2012.05.51, in CBL. **b–c.** Coll. LY NV2025.09.10 (a) in CBL, (b) in water.



Pl. 6 – *Paragalactinia succosella*. Various collections, *in situ*.

A. Coll. LY NV2012.05.51 (N. Van Vooren). **B.** Coll. LY NV2025.09.10 (N. Van Vooren). **C.** Coll. BW 130622 (B. Wergen). **D.** Coll. MC-09-06-2018 (E. Campo). **E.** Coll. LY NV2024.11.11 - *succosella* cf. (N. Van Vooren).