

SEM-studies on nivicolous *Myxomycetes*. The *Diderma niveum* complex in Europe

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Abstract – A SEM study of the nivicolous taxa belonging to the *Diderma niveum* complex including the six previously described taxa *D. alpinum*, *D. cristatosporum*, *D. microcarpum*, *D. niveum*, *D. niveum* var. *ferrugineum* and *D. niveum* var. *macrosporum* is presented. Type collections of Rostafinski and Meylan were examined. New lectotypes for *Diderma alpinum* and *D. microcarpum* are proposed. Spore ornamentation of 95 specimens was studied with the scanning electron microscope. *Diderma niveum* var. *ferrugineum* is considered to be synonym of *D. niveum*. Two new combinations, *D. niveum* var. *cristatosporum* and *D. alpinum* f. *microcarpum*, are proposed and one new species, *D. meyerae*, is described.

Austria / *Diderma* / France / new combinations / new species / Physarales / SEM / Spain / Switzerland

Résumé – On réalise une étude au microscope électronique à balayage d'un complexe de taxons nivicoles comprenant six taxons décrits *D. alpinum*, *D. cristatosporum*, *D. microcarpum*, *D. niveum*, *D. niveum* var. *ferrugineum* et *D. niveum* var. *macrosporum*. Les spécimens-types de Rostafinski et Meylan ont été examinés. Des lectotypes de *Diderma alpinum* et *Diderma microcarpum* sont proposés. Suite à l'étude de l'ornementation sporale de 95 spécimens *Diderma niveum* var. *ferrugineum* est considérée un synonyme de *D. niveum*, et deux nouvelles combinaisons sont proposées: *Diderma niveum* var. *cristatosporum*, *D. alpinum* f. *microcarpum*. Les auteurs décrivent *Diderma meyerae* comme une nouvelle espèce.

Autriche / *Diderma* / France / nouvelles combinaisons / nouvelle espèce / Physarales / MEB / Espagne / Suisse

INTRODUCTION

Nivicolous *Myxomycetes* represent a distinct ecological group of organisms found in spring and early summer at high elevations in the mountains of the temperate zone. Fruiting takes place along the margins of melting snowbanks, where special microenvironmental conditions required for their growth and fruiting exist. Fruiting bodies develop on plant debris (*Cirsium*, *Gentiana*, *Festuca*), on living twigs of shrubs and other woody plants (*Cytisus*, *Vaccinium*, *Juniperus*), on branches of living trees (*Pinus*, *Alnus*), or simply like lignicolous *Myxomycetes* on decaying trunks or dead twigs.

* Correspondence and reprints.

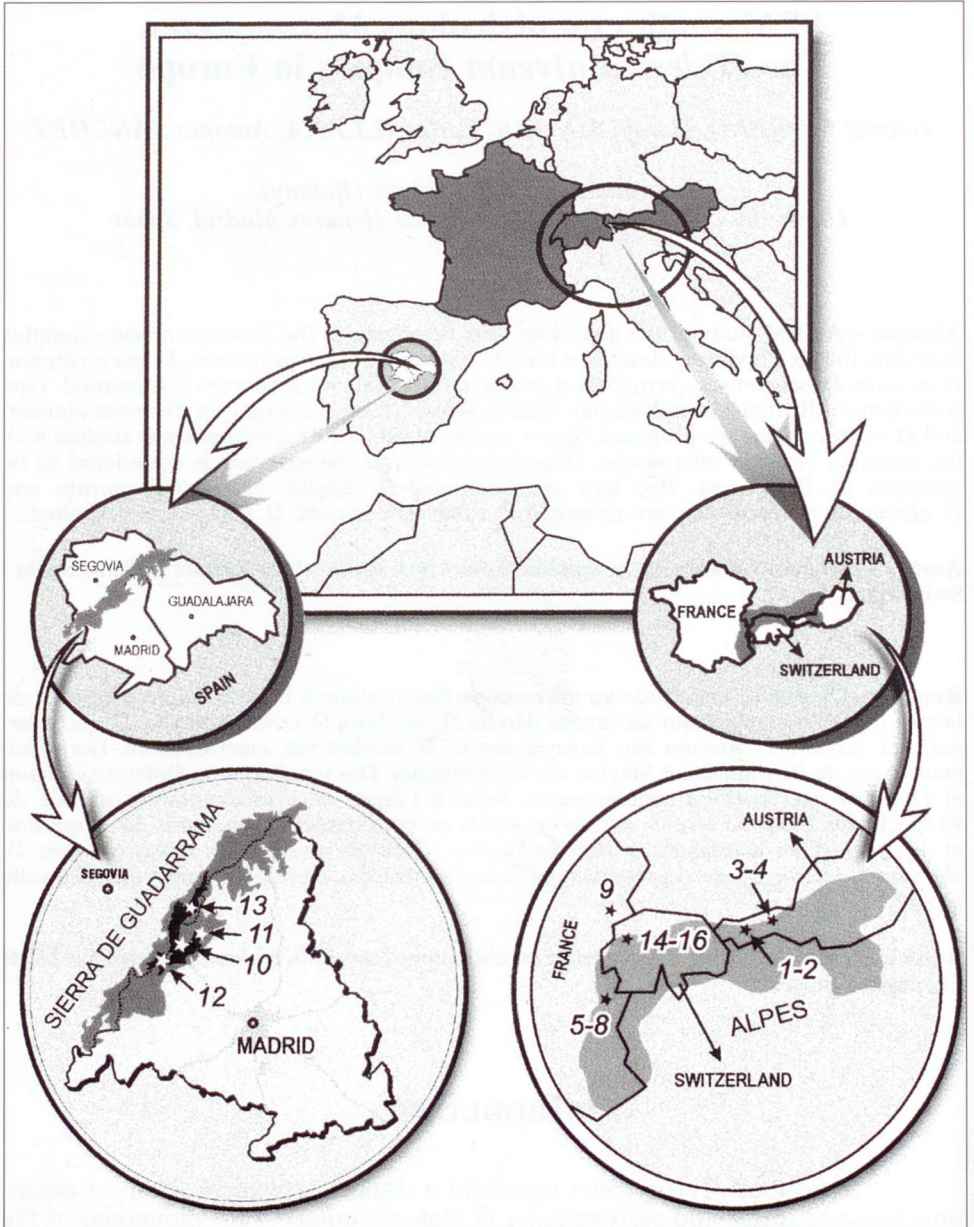


Fig. 1. Map showing the localities from where material has been studied.

The Swiss myxomycologist Charles Meylan studied nivicolous *Myxomycetes* intensively in the Swiss Alps during the years 1905-1937. In his papers he described five new genera, 36 species, 49 varieties, and numerous forms (Meylan, 1913, 1914, 1924, 1931, 1932).

Table I. Descriptions of *Diderma niveum* according to different authors.

<i>Author</i>	<i>Columella</i>	<i>Capillitium</i>	<i>Spores</i>
Rostafinski (1875) <i>English translation</i>	"Columella thick, easily visible due to notable size and bright, brownish-rusty colour, diverse with snow-white wall. It is covered by a robust, thick, dark brown membrane, the inside part of which has spongy structure, often fully calcified."	"Capillitium strongly developed, with thick threads, normally undilated, only seldom branched into two near the top, dark violet. Capillitium originating from the columella, primary threads solitary, then become two or three times branched towards the periphery. These threads are thick, with many bulges and nodules, dark brownish, 1.7 – 2.5 μm ."	"Spores dark-violet, verrucose, 10-11.6 μm in diam."
Macbride (1899)	"Columella well developed, globose or hemispherical, orange tinted or ochraceous."	"Capillitium abundant, made up of threads of two sorts, some purplish or dusky, with pale extremities, uneven, others more delicate and colorless, and with wartlike thickenings, all sparingly branched."	"Spores violet brown, minutely roughened, 9-10 μm ."
Lister (1925)	"Columella broad, convex, or hemispherical, orange or buff."	"Capillitium of branching and anastomosing rather stout purple threads with pale extremities, sometimes intermixed with more delicate threads, often beaded with wart-like thickenings."	"Spores purple brown, minutely spinulose, 9 to 13 μm in diam."
Macbride & Martin (1934)	"Columella well developed, globose or hemispherical, orange-tinted or ochraceous."	"Capillitium abundant, made of threads of two sorts, some purplish or dusky, with pale extremities, uneven, others more delicate and colorless, and with wart-like thickenings, all sparingly branched."	"Spores violet-brown, minutely roughened, 9-13 μm ."
Martin & Alexopoulos (1969)	"Columella large, globose or hemispheric, ochraceous to deep orange."	"Capillitium abundant, elastic, the threads of two sorts, some purplish or dusky, coarse, uneven, with pale extremities, others delicate and colorless, often beaded with wart-like thickenings, all rather sparsely branched and anastomosing."	"Spores black in mass, violet-brown by transmitted light, minutely roughened, (8-)-9-11(-12) μm in diam."
Buyck (1982)	"Columella hemispherical or conical, rusty orange."	"Capillitium threads straight, often dichotomously branched, 600-700 μm long, dark brown to black, with scattered, large, blunt warts; the extremities shortly branched and often with membranous expansions. Capillitium very abundant, dark purplish brown, loosely attached to the peridium."	"Spores circular to ovate in optical section, (11.3)-12-(12.7) μm diam, pale yellowish brown, sometimes paler on one side, densely and minutely warted, the warts often in lines so that in some specimens the spores appear subreticular."
Neubert et al. (1995) <i>English translation</i>	"Columella globose to hemispheric, rough, beige to light orangebrown, up to 1 mm in diam."	"Capillitium generally made of threads of two sorts, mainly robust, dark brown, up to 5 mm in diam, thinner and hyaline at the extremities, intermixed with delicate, hyaline threads about 1 mm in diam, with dark, wart-like thickenings. Capillitium altogether sparsely branched, seldom somewhat netted, sometimes with expansions up to 8 μm ."	"Spores in mass blackish brown, purple brown by transmitted light, densely and minutely spinulose to minutely warted, 9-12(13) μm in diam, sometimes distinctly paler on one side."

MATERIALS AND METHODS

High latitude mountain ranges located in Austria (Alps, Tyrol), in France (Alps, various localities) and in Spain (Central System, Madrid and Segovia) were studied as shown on the map (Fig 1):

Austria:

1. Gramais (2132 m)
2. Stanzach (939-1302 m)
3. Innsbruck (1905-1661 m)
4. Kolsassberg (1600 m)

France:

5. Bonneval, Lachat (1800-2000 m)
6. Col de la Madeleine (1800 m)
7. Les Arcs (2000-2300 m)
8. Méribel (1800 m)
9. Giromagny, Vosges (elevation not indicated by the collector)

Spain:

10. Pto. de Cotos (1850 m)
11. Pto. de la Morcuera (1600-1680 m)
12. Pto. de Navacerrada (2000-2100 m)
13. Pto. de Navafria (1950 m)

Switzerland:

14. La Gittaz (1250 m)
15. Joux de Baulmes (1950 m)
16. Côte-aux-Fées (1200 m)

Specimens were collected during the months of March to June, at elevations between approximately 900 m and 2200 m. Altogether, 95 different samples have been examined. The collector of the specimen is indicated only if the material was not collected by an author of the present work.

The lectotypes of *Diderma alpinum* var. *macrosporum* Meyl., *D. niveum* var. *ferrugineum* Meyl. (LAU, "Musée Botanique Cantonal, Lausanne, Switzerland"), designated by Kowalski (1975) after visiting the herbarium of Charles Meylan, were revised. Two other lectotypes chosen by Kowalski, those for *D. alpinum* (Meyl.) Meyl. and *D. microcarpum* Meyl., were not found in the herbarium LAU, nor in herbarium G ("Conservatoire et Jardin Botanique, Genève, Switzerland") and are according to the curators of both herbaria permanently lost. Therefore two new lectotypes were selected from the collections of Meylan from the same localities, differing only in the collecting date from those chosen by Kowalski.

The type species of *Chondrioderma niveum* Rostaf. (= *D. niveum*) was located in the herbarium STR ("Université Louis Pasteur, Institut Botanique de Strasbourg, France") and revised by us.

Specimens from Austria, France and Spain are deposited in the herbarium of the "Departamento de Biología Vegetal, Universidad de Alcalá, Alcalá de Henares" (AH), Spain, and in the herbarium of the "Institut für Mikrobiologie, Universität Innsbruck" (IB), Austria. Isotypes of *Diderma meyerae* have been deposited in the herbarium of Innsbruck (IB), the herbarium of M. Meyer, and the herbarium "Real Jardín Botánico de Madrid" (MAF-Fungi).

Specimens were mounted in Hoyer's medium and studied with a Nikon (Optiphot) microscope. Scanning electron microscopy (SEM) micrographs were taken at the University of Alcalá de Henares, using a Zeiss DSM-950. All the

material cited in the text was studied with SEM applying the critical point drying technique and micrographs of different spores from various specimens were selected to illustrate the ample variation of the spore ornamentation. Spore measurements were made under the oil immersion objective and include surface structures like spines or warts.

The terminology of the spore-producing stages follows Dörfelt *et al.* (1990) and Lado *et al.* (1997). The spore wall ornamentation as seen in the SEM is described according to the terminology proposed by Rammeloo (1975a, b).

LIST OF SPECIES

***Diderma alpinum* (Meyl.) Meyl., Bull. Soc. Vaud. Sci. Nat. 51: 261. 1917. (Figs 2-10)**
 ≡ *D. globosum* var. *alpinum* Meyl., Annuaire Conserv. Jard. Bot. Genève 15-16: 310. 1913.

Collections examined.

AUSTRIA: (2), 939 m, on fern, 21-IV-2000, AH 27351. *Ibidem*, on living conifer branch, 28-IV-2000, AH 27352. *Ibidem*, on grass, IB 2000/0253. (2), Fallerscheinalpe (1302 m), on conifer needles, 28-IV-2000, AH 27353. *Ibidem*, on twig of living bush (with *Lamproderma* sp.), IB 2000/0252. (4), near Studlalm, on living moss, 5-V-2000, M. Kirchmair, AH 27354. *Ibidem*, on conifer needles, AH 27355. *Ibidem*, on branches of living bush, AH 27356. (3), near Bodensteinalm (1661 m), on grass, 10-V-2000, IB 2000/0254.

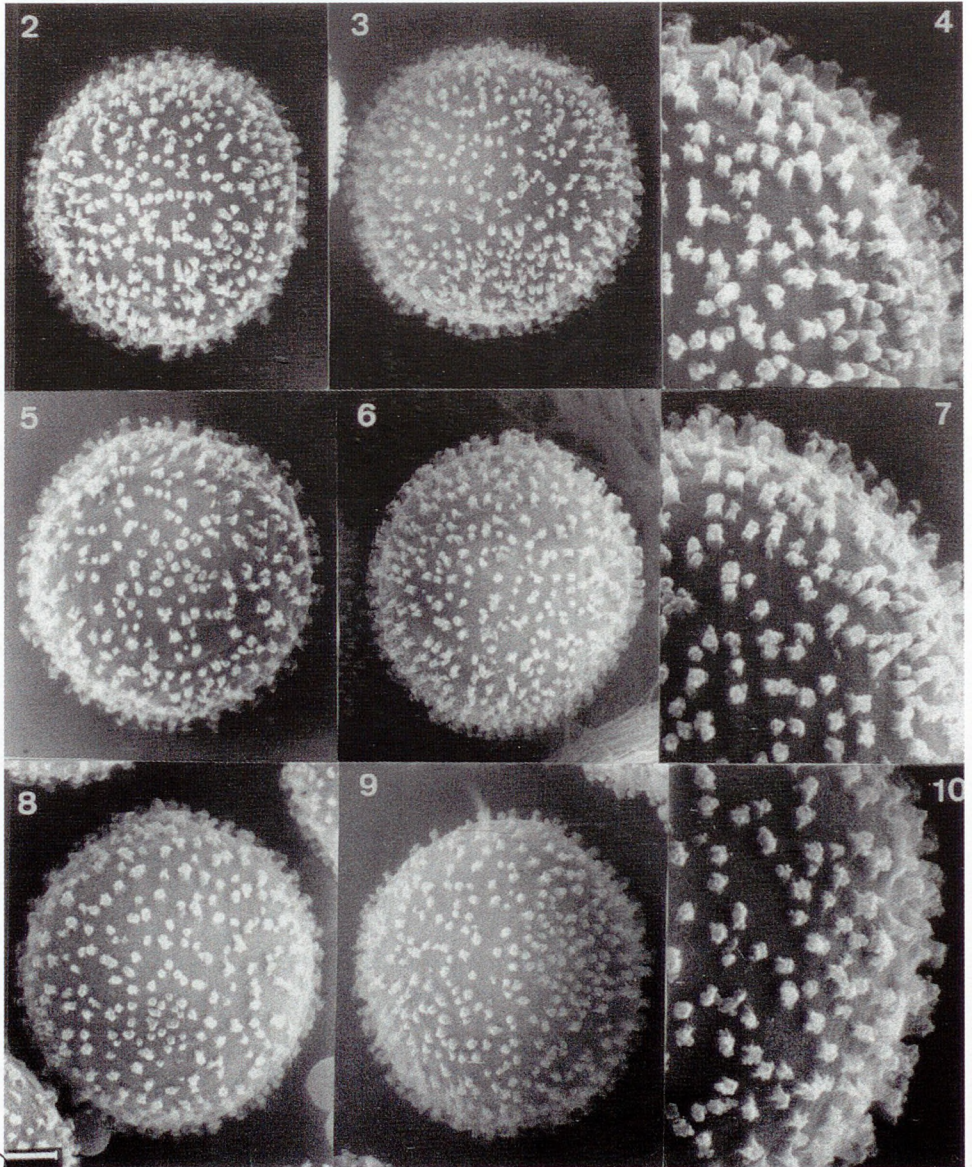
FRANCE: (5), on ligneous residues, 15-V-1996, M. Meyer, Meyer 16840. (7), 2000 m, on *Rhododendron ferrugineum*, 2-VI-2000, AH 27265. *Ibidem*, 2100 m, on *Epilobium* sp., AH 27318, 27340 and 27344 (with *Trichia alpina*). (6), on *Alnus viridis*, 3-VI-2000, AH 27297, 27298 and 27299 (with *Diderma niveum* var. *niveum*). *Ibidem*, 2000 m, on *Alnus viridis*, AH 27253 and 27314. *Ibidem*, on herbaceous plants, AH 27317. SPAIN: (10), Segovia, on *Rubus ulmifolius*, 4-V-1996, AH 19629. (13), Segovia, on branches and leaves of *Pinus sylvestris*, 9-III-1997, AH 19628.

SWITZERLAND: (14), near Sainte Croix, Canton de Vaud, leg. and det. Ch. Meylan, IV-1936, in LAU (new lectotype).

Diagnosis and original description.

"A *typo differt sporangiis plasmodiocarpiis, rarius subglobosis, columella et internaque cuticula semper carneo-bruneis.*

Répondue dans tout le Haut-Jura, de 1000 à 1500 m, au bord de la neige fondante en mai et juin, principalement sur les tiges de framboisier, cette nouvelle variété est peut-être complètement indépendante du D. globosum. Ce qui me fait plus ou moins croire à cette autonomie, c'est d'abord l'absence complète de formes intermédiaires, puis le fait que la variété est plus répandue que le type, enfin que tous deux croissent assez fréquemment ensemble sur la même tige et ne peuvent être considérés comme des formes stationnelles ou déterminées par les variations des conditions physiques qui influent si fréquemment sur le développement de certaines espèces. On ne peut pas parler non plus de formes successives, le type et la variété se développant au même moment et dans des conditions identiques. Si par plusieurs caractères importants cette nouvelle variété se sépare nettement du D. globosum, d'un autre côté elle s'y rattache par son capillitium, ses spores, son manque de columelle et ses grains de calcite de 2 µm."



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Figs 2-10. *Diderma alpinum* var. *alpinum* (Meyl.) Meyl. (2-4: lectotype, 5: IB 2000/0253, 6-7: IB 2000/0254, 8: AH 27317, 9-10: AH 27299). 2-3, 5-6, 8-9. Spores and variation in spore ornamentation, bar = 2 μ m. 4, 7, 10. Detail of spore ornamentation, bar = 1 μ m.

Description

Sporocarps globose, subglobose 0.7-1.7 mm in diam to plasmodiocarpous 1.6-2.0 × 0.5-0.7 mm, aggregated. Peridium double, the outer layer thick, coriaceous, irregularly dehiscent, snow-white, the inner layer tenuous, fragile, membranous, greyish. Columella variable, sometimes scarcely more than a thickened base, broad and flat, snow-white to pale flesh colored, sometimes globose to subglobose, up to 1 mm in diam, warted or papillate, greyish white to ochraceous-orange, continuing to the base of the inner peridial layer. Hypothallus white to ochraceous yellow, generally abundant, seldom poorly developed. Capillitium radiating, abundant, hyaline with violaceous zones to lightly violaceous.

Spores (10)11-13(14) µm in diam, globose, black in mass, violaceous by transmitted light, distinctly spinose. SEM shows the ornamentation to be formed by baculae with irregular apices, coralloid, observed vertically as having a more or less starlike appearance. Capillitium with a variable morphology, formed by delicate and sinuous threads approximately 1 µm diam, sometimes with a few darker nodes and with paler ramifications at the extremities.

Observations

Diderma alpinum is a species which in its typical expression differs from *D. niveum* by its plasmodiocarpous fructifications (Meylan, 1913; Neubert *et al.*, 1995). However, this character does not seem to be stable, as plasmodiocarps were observed in all the taxa examined. Furthermore, spore ornamentation of the two taxa is very similar (Figs 2-10, 22-37). The only differences are the tendency towards a more hyaline, flexuous capillitium and a generally well developed hypothallus in *D. alpinum* and dark violaceous, rigid capillitial threads and generally a poorly developed hypothallus in *D. niveum*. Both taxa are maintained as different species in accordance with Meyer and Nowotny (personal communication), until molecular studies are completed.

Diderma alpinum var. *macrosporum* Meyl., *Bull. Soc. Vaud. Sci. Nat.* 58: 319. 1935. (Figs 11-13)

Collections examined

SWITZERLAND: Canton Neuchâtel, Forêt des Baulmes, near (16), 2000 m, on living twigs, *Ch. Meylan*, V-1930, in LAU (lectotype).

Diagnosis and original description

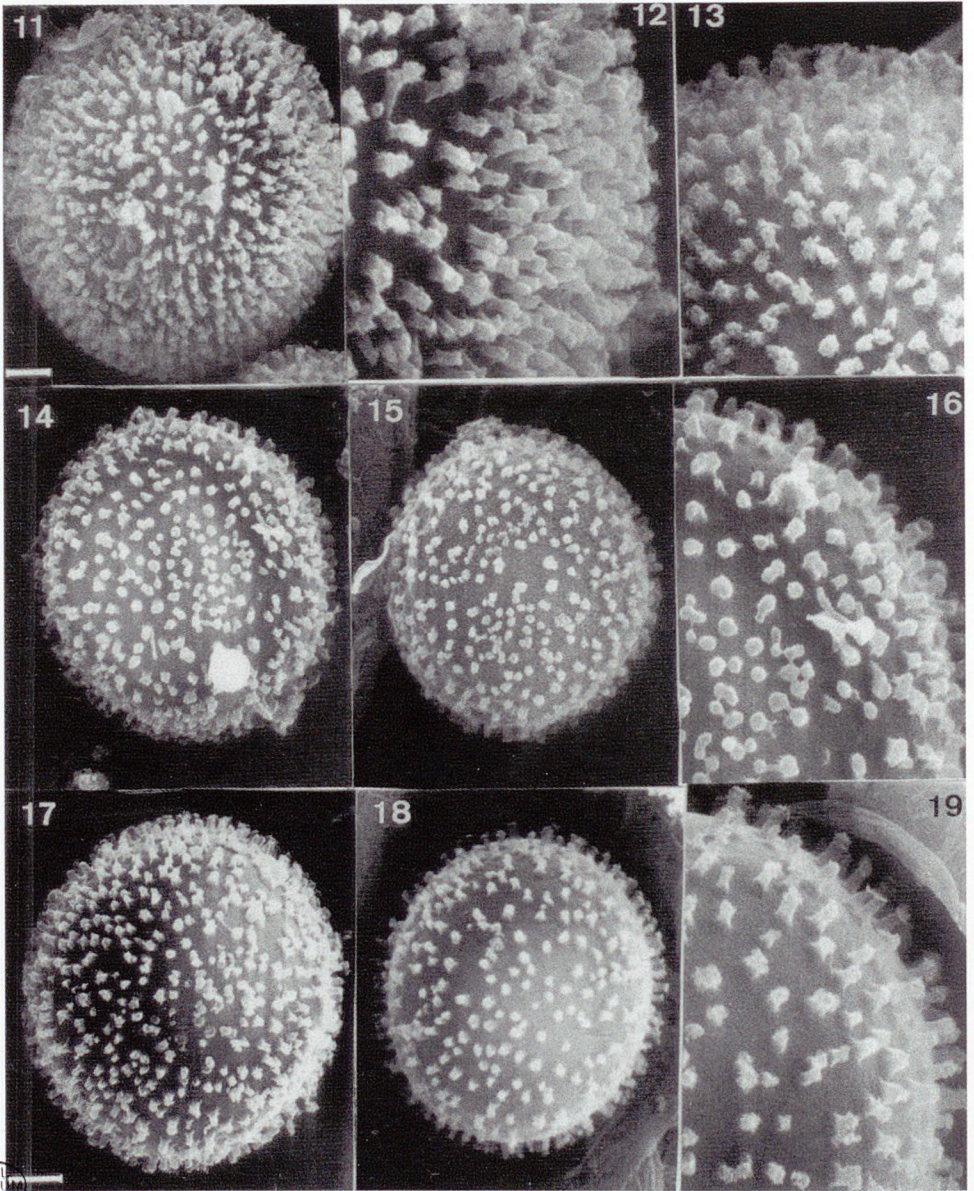
"A typo differt peridii interna parte ad externam adhaerenti, columella coloratiore, sporis 15-18 µm latis.

Cette variété diffère du type par la paroi externe moins fragile, adhérente; enfin par ses spores plus grosses, de 15 à 18 µm, et sa columelle d'un roux plus foncé."

Observations

The spore size of 15-17 µm is the only characteristic in which this variety differs from *Diderma alpinum* (spores generally 11-13 µm in diam). Nevertheless, it seems reasonable to separate this variety from *D. alpinum*, as nivicolous macrosporic varieties are common and generally accepted. Therefore, we maintain this taxon as a variety of *D. alpinum*.

Kowalski (1975) measured spore diameters of around 14 µm and did not recognize this taxon. He interpreted it to fall within the variability of *Diderma alpinum*.



Figs 11-13. *Diderma alpinum* var. *macrosporum* Meyl. (lectotype). 11. Spore, bar = 2 µm. 12, 13. Detail of spore ornamentation, bar (Fig. 17) = 1 µm. Figs 14-19. *D. microcarpum* Meyl. (14-16: lectotype, 17: AH 27358, 18-19: AH 27315). 14-15, 17-18. Spores and variation in spore ornamentation, bar (Fig. 17) = 2 µm. 16, 19. Detail of spore ornamentation, bar (Fig. 17) = 1 µm.

***Diderma microcarpum* Meyl., Bull. Soc. Vaud. Sci. Nat. 55: 240. 1924. (Figs 14-19)**

Collections examined

AUSTRIA: (2), 939 m, on living grass shoot, 28-IV-2000, AH 27357. *Ibidem*, on living woody plant, IB 2000/0255. (4), near Studlalm, on grass, 5-V-2000, M. Kirchmair, AH 27358.

FRANCE: (6), on branch of *Alnus viridis*, 3-VI-2000, AH 27315.

SWITZERLAND: (15), Canton de Vaud, *leg.* and *det.* Ch. Meylan, IV-1914, in LAU (new lectotype).

Diagnosis and original description

Meylan (1924) does not include a Latin diagnosis and gives the following description: "*Plasmodium* ? *Sporanges subglobuleux, lisses, d'un blanc éclatant, tous petits, et n'atteignant que 0,3 à 1 mm. de diamètre. Paroi externe du péridium formée de granules de 1 µm en moyenne, adhérente à l'interne, plus rarement plus ou moins séparée. Face interne du péridium et columelle d'un fauve clair légèrement carné ou roussâtre. Columelle de même forme que celle de D. niveum. Capillitium d'un violet pâle et assez semblable à celui de D. globosum. Spores de 10-11 µm, d'un pourpre violet, finement échinulées. Dans de nombreuses localités du Jura central au bord des névés, en compagnie des Diderma niveum, Physarum venum et autres espèces nivales, de 1150 à 1400 m.*

Cette nouvelle espèce que j'observe depuis le printemps 1908 est très constante. Elle diffère de D. niveum par ses sporanges de très petite taille, d'un blanc éclatant, la couleur de son capillitium et de sa columelle: des D. globosum et alpinum par ses granules de calcite de 1 µm et la couleur de la face interne du péridium. Elle se distingue en outre des trois espèces ci-dessus par l'adhérence des parois de son péridium et la manière radiale dont se fait la déhiscence de ses sporanges. Le D. alpinum a, d'autre part, toujours des sporanges de forme irrégulière et un peu plasmodiocarpes."

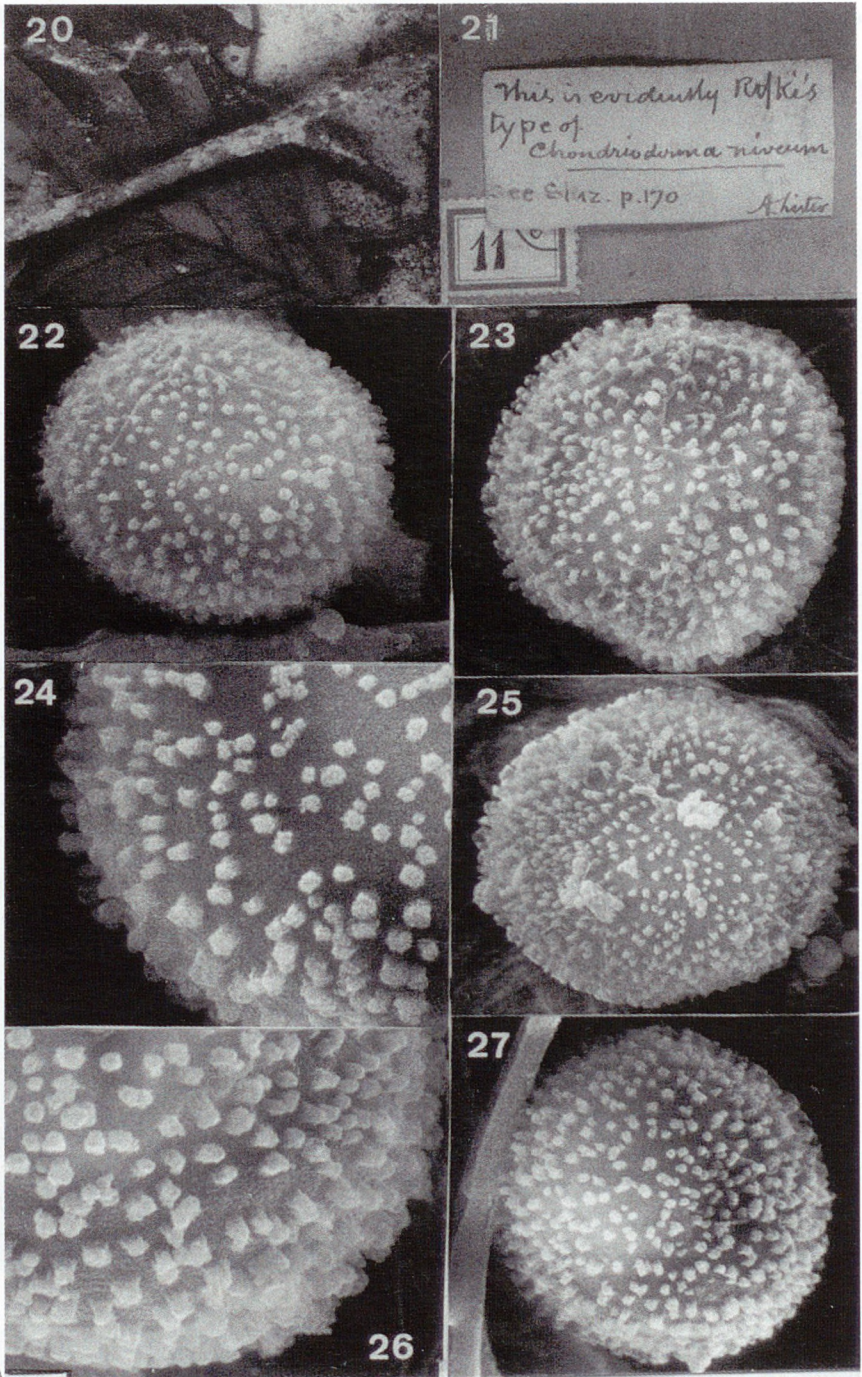
Description

Sporocarps globose, subglobose to plasmodiocarpous, aggregated, 0.5-1.1 mm in diam. Peridium double, the outer layer thick, coriaceous, irregularly dehiscent, snow-white, the inner layer tenuous, fragile, membranous, greyish white. Columella globose to subglobose, up to 0.3-0.5 mm in diam, white to yellowish ochre, warted or papillate. Hypothallus white to yellowish ochre, generally poorly developed. Capillitium radiating, abundant, hyaline to greyish violet.

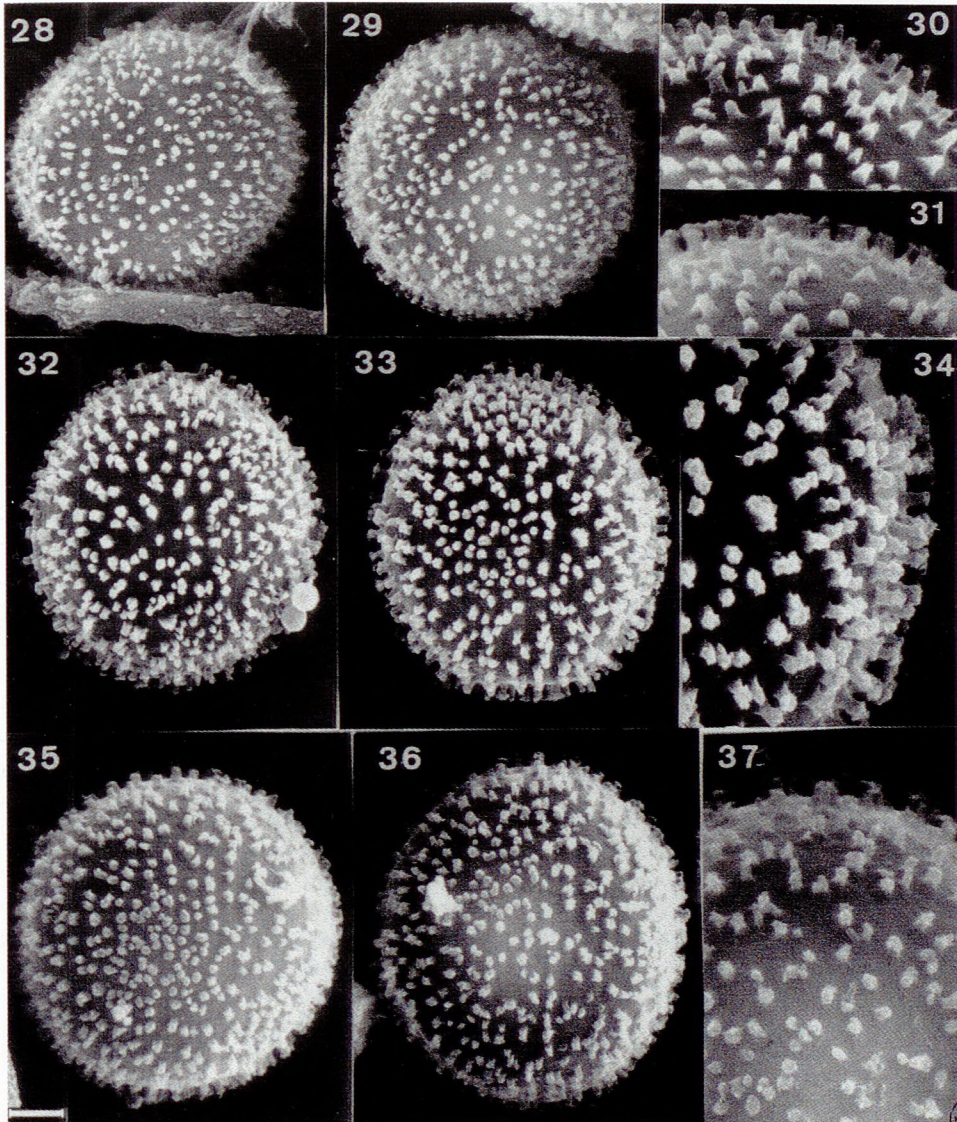
Spores 11-13 µm in diam, black in mass, violaceous by transmitted light, distinctly spinose. SEM shows the ornamentation to be similar to that of *Diderma alpinum* (Figs 2-10), formed by baculae with irregular apices, coralloid, observed from above as having a more or less stellate appearance. Capillitium with a variable morphology, formed by delicate threads approximately 1 µm diam, sometimes with a few darker nodes and with paler ramifications at the extremities.

Observations

As *Diderma microcarpum* displays no significant differences from either *D. niveum* or *D. alpinum*, we do not maintain *D. microcarpum* as an autonomous species. We recognize *D. microcarpum* as a form of *D. alpinum*, which can be distinguished only by its smaller sporocarps, possibly resulting from a response to environmental conditions.



Figs 20-27. *Diderma niveum* (Rostaf.) T. Macbr. (holotype). 20, 21. Type material and box lid of *Chondrioderma niveum* Rost. 22-23, 25, 27. Spores and variation in spore ornamentation, bar = 2 μ m. 24, 26. Detail of spore ornamentation, bar = 1 μ m.



Figs 28-37. *Diderma niveum* var. *ferrugineum* Meyl. (28-31: lectotype, 32-34: IB 2000/0259, 35: AH 27185, 36: AH 27182, 37: AH 21844). 28-29, 32-33, 35-36. Spores and variation in spore ornamentation, bar = 2 μ m. 30-31, 34, 37. Detail of spore ornamentation, bar = 1 μ m.

***Diderma niveum* (Rostaf.) T. Macbr., *N. Am. Slime-Moulds*: 100. 1899. (Figs 20-37)**

≡ *Chondrioderma niveum* Rostaf., *Sluzowce Monogr.*: 170. 1874.

= *Diderma niveum* var. *ferrugineum* Meyl., *Bull. Soc. Vaud. Sci. Nat.* 55: 240. 1924.

Collections examined

AUSTRIA: (4), near Studlalm, on branches of a living bush, 5-V-2000, *M. Kirchmair*, AH 27370 and IB 2000/0259.

FRANCE: (9), at the edge of snow, 16-IV-1873, *Prof. De Barego, det. J. Rostafinski* (type of *Chondrioderma niveum*), rev. A. Lister "this is evidently Rski's type of *Chondrioderma niveum*". (8), lenuous residues, 10-V-1997, AH 27176, 27180, 27182 and 27185. (7), 2100 m, on *Rhododendron ferrugineum*, 2-VI-2000, AH 27268, 27259, 27316, 27308 and 27309. *Ibidem*, on *Rhododendron ferrugineum* and *Vaccinium* sp., AH 27339. *Ibidem*, on *Rhododendron ferrugineum* and *Pinus uncinata*, AH 27319. *Ibidem*, 2150 m, on *Epilobium* and *Juniperus communis* subsp. *alpina*, AH 27310. (6), on *Vaccinium* sp., 3-VI-2000, AH 27328.

SPAIN: (10), Segovia, on branches of *Cytisus oromediterraneus*, 14-V-1996, AH 19534. *Ibidem*, on *Cytisus* sp., 21-V-1996, AH 19535. *Ibidem*, on branches and needles of *Pinus sylvestris*, 8-III-1997, AH 19539. *Ibidem*, 25-V-1996, AH 19536. (11), Madrid, on branches of *Cytisus oromediterraneus*, 21-IV-1996, AH 21771, 21772, 21776, 21774 and 21777. (12), Madrid, on *Juniperus communis* subsp. *alpina*, 18-IV-1996, AH 22224. (12), Segovia, on branches of *Pinus sylvestris*, 29-V-1996, AH 19537. *Ibidem*, on *Juniperus communis* subsp. *alpina* and *Cytisus oromediterraneus*, 29-V-1996, AH 19538. Crta. Navacerrada a Cotos km. 44, Segovia, on branches of *Juniperus communis* subsp. *alpina*, 4-VI-1996, AH 21844, 21771 and 21834. *Ibidem*, on branches of *Pinus sylvestris*, AH 21831. (13), Segovia, on bark of *Pinus sylvestris*, 15-III-1997, AH 19590.

SWITZERLAND: (16), Canton Neuchâtel, leg. and det. Ch. Meylan, V-1923, in LAU (lectotype of *Diderma niveum* var. *ferrugineum*).

Diagnosis and original description

Rostafinski (1875) does not include a Latin diagnosis and gives a description in Polish. We provide an English translation of this version: "Fruit bodies (sporangia) are usually semi-globose or, due to mutual pressure not so regular, 2-3 mm in diam, sessile, snow-white, with fragile walls. The lower part (hypothallus) extensive, normally somewhat flattened, rusty-brown. Capillitium strongly developed, with thick threads, normally undilated, only seldom branched into two near the top, dark violet. Spores dark-violet, verrucose, 10-11.6 µm in diam.

The species is very beautiful. Fruit bodies in relation to other species of the genus of big size, solitary normally semi-globose, somewhat flattened near the top. Growing in groups irregular due to mutual pressure. Wall (peridium) snow-white, very fragile, being slightly fissured. Calcification very strong, also small areas unite and fall away like plates, wall of ashy appearance. Being decalcified the wall is membranous, the upper part of the fruit body uncoloured, lower part with slight brownish tint. Columella thick, easily visible due to notable size and bright, brownish-rusty colour, diverse with snow-white wall. It is covered by a robust, thick, dark brown membrane, the inside part of which has spongy structure, often fully calcified. Capillitium originating from the columella, primary threads solitary, then become two or three times branched towards the periphery. These threads are thick, with many bulges and nodules, dark brownish, 1.7-2.5 µm. A rare species found by Prof. De Barego on mountain Vosges, near Giromagny, at the edge of snow."

Diagnosis and original description of Diderma niveum var. ferrugineum: Meylan (1924) does not include a Latin diagnosis and gives the following description: "J'ai rencontré dans le Jura une autre variété très intéressante caractérisée par des sporanges d'un blanc éclatant, exactement semblables à ceux du *D. globosum*, tandis que la paroi interne et la columelle sont d'un brun fauve rouillé très vif. Cette variété est si différente du *D. niveum* ordinaire que je préfère la distinguer sous le nom de *var. ferruginea var. nov.* Les granules calcaires ont 1 à 1,5 mm. de diamètre."

Description

Sporocarps globose, subglobose to sometimes plasmodiocarpous, aggregated, 1.0-2.0 mm in diam. Peridium double, the outer layer thick, coriaceous, irregularly dehiscent, snow-white, the inner layer tenuous, fragile, membranous, greyish. Columella globose to subglobose, 0.5-1.0 mm in diam, warted or papillate, ochraceous-orange to ferruginous, this colour sometimes continuing to the base of the inner peridial layer. Hypothallus white to ochraceous yellow or reddish, not present to poorly developed, seldom well developed. Capillitium radiating, abundant, reddish brown to violaceous brown and rigid, generally rough, after the dehiscence of the peridium a more or less parallel arrangement of threads can be observed.

Spores (10)11-13(14) μm in diam, black in mass, violaceous by transmitted light, distinctly spinose. When examined under SEM, the ornamentation is similar to that of *Diderma alpinum* (Figs 2-10) and *D. microcarpum* (Figs 14-19) and is formed by baculae with irregular apices, coralloid, with a more or less starlike appearance when observed perpendicularly. Capillitium with a variable morphology, formed by rigid threads 1-3 μm diam, with paler, sometimes dichotomous branches at the tips.

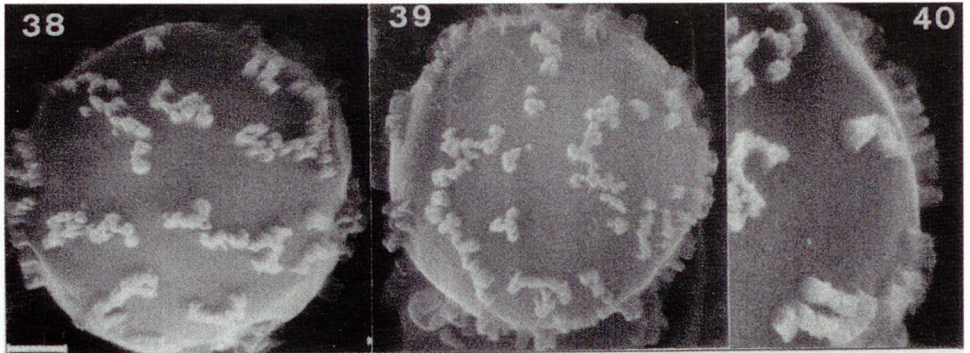
Observations

Diderma niveum is very variable in the morphology and size of the sporocarps and in the presence or absence of a columella, which is more or less orange or ferruginous, and the presence or absence of a hypothallus.

The type specimen of *Diderma niveum*, which is in very poor condition, was examined. The material was collected from leaves and branches of *Fagus sylvatica*. Numerous broken sporocarps were found, bearing orange tinted columellae, situated on a well developed hoary to yellowish white hypothallus; sometimes with a dark, rigid capillitium, "strongly developed, with thick threads, normally undilated, only seldom branched into two branches near the periphery, dark violet" (Rostafinski, 1874). Doubtless this material corresponds to what was later interpreted as *D. niveum var. ferrugineum*.

The type material of *Diderma niveum var. ferrugineum* has sporocarps with a well developed, ferruginous or ochraceous orange columella, and abundant, very dark capillitium (1-3 μm in diam), these two characters generally being constantly associated with a poorly developed hypothallus.

Meylan (1924) and Kowalski (1975) recognize two different species *Diderma niveum* and *D. alpinum*. However, the morphological variability of *D. niveum* and the presence of the same spore ornamentation in both taxa (Figs 2-10, 22-37) suggest they may be two varieties of the same species. We maintain the two species until molecular studies are realized.



Figs 38-40. *Diderma cristatosporum* A. Sánchez, G. Moreno & Illana (holotype). 38-39. Spores and variation in spore ornamentation, bar = 2 µm. 40. Detail of spore ornamentation, bar = 1 µm.

***Diderma niveum* var. *cristatosporum* (A. Sánchez, G. Moreno & Illana) H. Singer, G. Moreno, Illana & A. Sánchez stat. nov.**

≡ *Diderma cristatosporum* A. Sánchez, G. Moreno & Illana, *Persoonia* 17: 643. 2002. (Figs 38-40)

Collections examined

SPAIN: Puerto de Navafría 1800 m, Segovia, on bark of dead branches of *Pinus sylvestris* L., 15-V-1997, AH 18413 (holotype) and 19557.

Diagnosis and original description

Sánchez *et al.* (2001) indicate: "*Sporocarpia in gregibus, 0,7-1,6 mm diametro, globosae vel subglobosae, sessilia. Peridium duplex, stratum externum albidum, crustaceum, stratum internum membranaceum, hyalinum cinereum. Columella magna, convexa vel hemisphaerica, ferruginosa. Capillitium 2-5 µm diametro, abundans, fuscum, ramosum, apicibus distinctis. Sporae 12-15 µm, globosae, translucidae, irregulariter coloratae, griseae vel hyalino-griseae, cristis irregularibus sinuosis incrustatae.*"

Fructification formed by 15-30 sessile sporocarps, sporocarps globose to subglobose, some as small plasmodiocarps, 0.7-1.6 mm diam. Hypothallus membranous, continuous, whitish by lime incrustations, not present to poorly developed. Peridium clearly double; the outer layer very fragile, thick, smooth, irregularly dehiscent, white, the inner layer membranous, cinereous and closely applied to the spore mass. Columella hemispherical to elongated, rough, reddish brown. Capillitium abundant, branching and anastomosing, threads 2-5 µm diam, rigid, flexuous, often with many irregular swellings and membranous expansions, dark brown to violaceous and sometimes colourless at the extremities. Spores free, dark brown in mass, pale purple grey by LM, globose, 12-15 µm diam, with small, scattered ridges; when observed by SEM, the spore has a smooth surface and the ridges are formed by long baculae united to form sinuous lines."

Observations

Diderma cristatosporum has a snow-white peridium, a more or less well developed, reddish brown columella and a violaceous, rigid capillitium, similar to that of *D. niveum*. However, the spore ornamentation is less dense and formed by

baculae fusing to form large, more or less sinuous crests (Figs 38-40) and the spores are larger, 12-15 μm in diam. New collections from other areas are necessary for the study of the spore variations. We propose to recognize this taxon as a variety of *D. niveum* because of the similar capillitium and the presence of a baculate spore ornamentation.

***Diderma meyerae* H. Singer, G. Moreno, Illana & A. Sánchez, sp. nov. (Figs 41-49)**
= *D. niveum sensu auct. pluribus*

Collections examined

AUSTRIA: (3), Seegrube (1905 m), on grass, 21-V-2000, AH 27359, 27361, 27363, 27364 and IB 2000/0258. *Ibidem*, on living *Rhododendron* sp., AH 27360. *Ibidem*, on leaf and grass, IB 2000/0256. *Ibidem*, on living *Juniperus* sp., IB 2000/0257. *Ibidem*, on living grass, AH 27362. (1), near Gampenjoch, on grass, 12-VI-2000, AH 27365, 27366, 27367 and 27368. *Ibidem*, on plant, AH 27369.

FRANCE: (5), on lenuous residues, 15-V-1996, M. Meyer, Meyer 16841 (*det. as D. niveum*). (8), on lenuous residues, 10-V-1997, AH 27186 and 27188. (7), 2000 m, on herbs, 2-VI-2000, AH 27274, 27256 and 27311 (HOLOTYPUS). *Ibidem*, 2100 m, on *Epilobium* sp., AH 27326. (6), on *Alnus viridis*, 3-VI-2000, AH 27299 (with *Diderma niveum* var. *alpinum*.) and AH 27304. *Ibidem*, 2000 m, on herbs, AH 27323, 27322, 27336 and 27345. *Ibidem*, on *Vaccinium*, AH 27293. *Ibidem*, on *Rhododendrum ferrugineum* and *Poaceae*, AH 27303. *Ibidem*, on *Alnus viridis*, AH 27276.

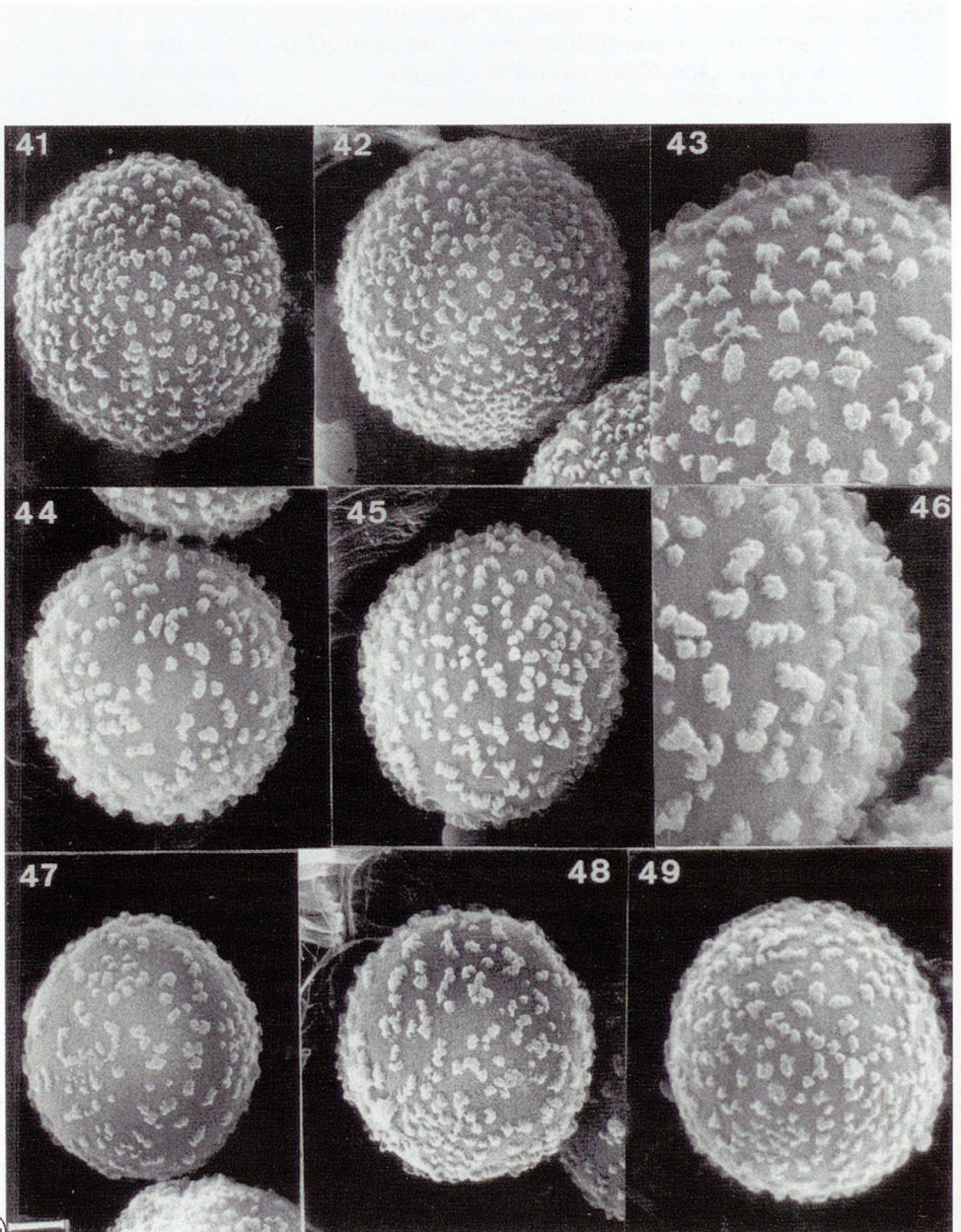
Sporocarpia globosa vel subglobosa, 1,0-2,0 mm latae; nonnunquam plasmodiocarpia, valde aggregata, 2-4 \times 0,6-1 mm. Peridium duplex, stratum externum album, crassum, coriaceum, stratum internum cinereum, tenue, membranaceum. Columella globosa vel subglobosa, 0,4-0,6 mm lata, verrucosa vel papillosa, albidolaurantiaca vel aurantiaco-ochracea vel ferruginea. Hypothallus albus vel ochraceolutes, sparsim vel valde evolutus. Capillitium asperum, radiale, abundans, cinereum vel violaceum. Sporae 10-13 (15) μm diam, globosae, violaceae, ornamentum verrucis in cristis coalescentibus constitutum. Capillitium 1-3 mm diam, violaceum, cum nodulis obscuris et ramificationibus extremis pallidioribus.

Holotypus: Gallia, Bourg-Saint-Maurice, "Les Arcs" (Sabaudia), 2100 m, in herbae, 2-VI-2000, AH 27311. Isotypus: in IB, herbarium M. Meyer et MAF-Fungi.

Description

Sporocarps globose, subglobose 1.0-2.0 mm in diam to sometimes plasmodiocarpous 2-4 \times 0.6-1 mm, strongly aggregated. Peridium double, the outer layer thick, coriaceous, irregularly dehiscent, snow-white, the inner layer tenuous, fragile, membranous, greyish. Columella well developed, globose to subglobose, 0.4-0.6 mm in diam, whitish grey, orange tinted to ochraceous orange or ferruginous. Hypothallus white to ochraceous yellow, poorly developed to abundant. Capillitium partly very rough, radiating, abundant, hoary to violaceous, emerging aggregated and stuck together after dehiscence.

Spores 10-13(15) μm in diam, globose, black in mass, violaceous by transmitted light, the ornamentation consisting of verrucae, fusing to form small crests. With SEM we observe the variability of the spore ornamentation and the shape of the crests (Figs 41-49). Capillitium 1-3 μm in diam, with dark nodules and paler branches at the extremities.



Figs 41-49. *Diderma meyeri* H. Singer, G. Moreno, Illana & A. Sánchez, sp. nov. (41-43: holotype, 44-46: AH 27361, 47: AH 27364, 48-49: AH 27274). 41-42, 44-45, 47-48. Spores and variation in spore ornamentation, bar = 2 μ m. 43, 46, 49. Detail of spore ornamentation, bar = 1 μ m.

Etymology

The Latin *meyerae* is dedicated to Marianne Meyer, in recognition of her devotion to the study of nivicolous *Myxomycetes*.

Observations

This new species clearly differs from *Diderma alpinum* in its spore ornamentation of verrucae and small crests without baculae. *Diderma meyerae* is easily recognised under the light microscope (LM) by its scarcely projecting and non-spinose ornamentation. Type material of the *D. niveum* complex examined with SEM confirmed the differences in spore ornamentation. Differences of spore ornamentation as seen with SEM can also be recognized with LM without great difficulty with some experience in microscopic observation. *D. meyerae* generally appears to have been confused with *D. niveum*.

Different species and varieties were proposed within the nivicolous *Diderma niveum* complex by various authors, but the type material of the whole group has never been compared and studied in detail. Several taxa have not previously been separated on the basis of spore ornamentation, which we consider to be a constant character.

GENERAL DISCUSSION

The interpretations of *Diderma niveum* differ depending on the authors. In Table I we indicate the most important original descriptions.

The original description by Rostafinski (1875) of *Chondrioderma niveum* indicates a species with a columella of "brownish-rusty colour" and a capillitium dark violet "with many bulges and nodules, dark brownish, 1.7-2.5 μm ". His description corresponds well with *Diderma niveum* var. *ferrugineum* except for the "verrucose" spore ornamentation, which is typical for *D. meyerae*. However, in the type material spores are distinctly spinose with LM. Macbride (1899) states: "Columella orange tinted or ochraceous. Capillitium abundant, made up of threads of two sorts, some purplish or dusky, with pale extremities, uneven, others more delicate and colorless, and with wartlike thickenings, all sparingly branched". In our opinion, it is possible that he was confusing the varieties which we here regard as falling within the *D. niveum* complex. Lister (1925) indicates the following: "Columella orange or buff. Capillitium of branching and anastomosing rather stout purple threads with pale extremities, sometimes intermixed with more delicate threads, often beaded with wart-like thickenings". It also seems probable that Lister confused the taxa, having spores "minutely spinulose", or refers her description to *D. niveum* var. *ferrugineum*, as she points out the typical columella and the stout capillitium threads.

Buyck (1982) is the only author who, in his description, mentions "Spores densely and minutely warted, the warts often in lines so that in some specimens the spores appear subreticular". However, according to this author, *Diderma niveum* is not a strictly alpine species and belongs to the complex of *D. globosum*, which he considers to be a nivicolous species. Buyck's description (1988) of *D. globosum* var. *europaeum* is close to our *D. meyerae*.

Previous myxomycete monographers described spore ornamentation as verrucose (Rostafinski, 1875), minutely roughened (Macbride, 1899; Macbride &

Martin, 1934; Martin & Alexopoulos, 1969), densely and minutely warted (Buyck, 1982), minutely spinulose (Lister, 1925), and densely and minutely spinulose to minutely warted (Nowotny *et al.*, 1995). These authors all mention a combination of different spore ornamentation and none distinguishes another related species with a different spore ornamentation. Since *Diderma niveum* and *D. meyerae* are very common species, it can be assumed that they were confused under the concept of *D. niveum*. We favour this interpretation, because Meylan (1913, 1917, 1924), when creating *D. alpinum*, *D. microcarpum* and *D. niveum* var. *ferrugineum*, did not indicate differences from *D. niveum* in regard to spore ornamentation.

Various authors have utilized the morphology of the sporocarp, its size, the presence and colour of the columella, the presence or absence of a hypothallus, and the colour and morphology of the capillitium to distinguish between *Diderma niveum*, *D. niveum* var. *ferrugineum*, *D. microcarpum* and *D. alpinum*. These characters, except for the colour and morphology of the capillitium, are neither constant nor reliable for the separation of these taxa. Possibly the variability of these characters and the lack of detailed observations of differences in spore ornamentation led Farr (1976) to the conclusion that there was but one variable species, using *D. niveum* as the original name for the taxon.

Kowalski (1975) distinguishes only two species: *Diderma niveum* and *D. alpinum*, and considers *D. microcarpum*, *D. niveum* var. *ferrugineum* and *D. alpinum* var. *macrosporum* as synonyms of *D. alpinum*.

Study of the type material of *Chondrioderma niveum* Rostaf. has allowed us to solve the problematic nature of this abundant group of nivicolous *Diderma* spp. Finally, we recognize only three species: *D. niveum*, with spores bearing an ornamentation formed by baculae with SEM, appearing spinose by LM, and a rigid, rough, dark capillitium up to 3 µm in diam (Figs 22-37); *D. alpinum* with spores in dimension and ornamentation similar to *D. niveum*, but with a flexuous, generally brighter capillitium, about 1 µm diam (Figs 2-10); and *D. meyerae*, which is characterized by its spore ornamentation formed by verrucae and short crests (Figs 41-49).

The possibility that *Diderma niveum* might be a not strictly nivicolous species is left open. In order to solve these problems, further studies are necessary of other white non-nivicolous *Diderma* spp. which fructify in lowlands.

In conclusion from the above, the following species concepts are proposed:

***Diderma meyerae* H. Singer, G. Moreno, Illana & A. Sánchez, sp. nov.**
= *D. niveum sensu auct. pluribus*

***Diderma niveum* (Rostaf.) T. Macbr., N. Am. Slime-Moulds: 100. 1899.**
Basionym *Chondrioderma niveum* Rostaf., *Sluzowce Monogr.*: 170. 1874.
= *D. niveum* var. *ferrugineum* Mey., *Bull. Soc. Vaud. Sci. Nat.* 55: 240. 1924.

***D. niveum* var. *crystalloporum* (A. Sánchez, G. Moreno & Illana) G. Moreno, H. Singer & Illana, comb. et status nov.**
Basionym *D. crystalloporum* A. Sánchez, G. Moreno & Illana, *Persoonia* 17: 201. 2001.

***Diderma alpinum* var. *alpinum* (Meyl.) Meyl., *Bull. Soc. Vaud. Sci. Nat.* 51: 261. 1917.**
Basionym *D. globosum* var. *alpinum* Meyl., *Annuaire Conserv. Jard. Bot. Genève* 15-16: 310. 1913.

***Diderma alpinum* var. *macrosporum* Meyl., *Bull. Soc. Vaud. Sci. Nat.* 58: 319. 1935.**

***Diderma alpinum* f. *microcarpum* (Meyl.) G. Moreno, H. Singer & Illana, comb. et status nov.**Basionym *D. microcarpum* Meyl., *Bull. Soc. Vaud. Sci. Nat.* 55: 240. 1924.**KEY OF THE NIVICOLOUS TAXA WITH SESSILE, WHITE SPOROCARPS AND CORIACEOUS PERIDIUM, WHICH WE RECOGNIZE WITHIN THE *DIDERMA NIVEUM* COMPLEX**

Spore ornamentation and morphology of the capillitium help to separate different species in the *Diderma niveum* complex, whereas size of the sporocarps and the spore diameters distinguish infraspecific categories. Due to these facts we propose the following key:

1. Spores verrucose-crested with LM; SEM showing an ornamentation formed by verrucae that fuse into short, more or less sinuous crests . . . *Diderma meyeriae*
1. Spores spinose with LM; SEM showing an ornamentation formed by baculae 2
2. Capillitium rigid, rough, dark, 1-3 μm diam 3
2. Capillitium flexuous, hyaline to somewhat dark, about 1 μm diam 4
3. Spores without large crests, densely ornamented *D. niveum* var. *niveum*
3. Spores with large crests, sparsely ornamented, 12-15 μm in diam . . . *D. niveum* var. *crystalloporum*
4. Sporocarps < 1 mm in diam *D. alpinum* f. *microcarpum*
4. Sporocarps > 1 mm in diam 5
5. Spores 11-13 μm in diam *D. alpinum* var. *alpinum*
5. Spores 15-17 μm in diam *D. alpinum* var. *macrosporum*

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