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***Cover image* —** Sporocarps of *Lamproderma andinum* from the Malalcahuello-Nalca National Reserve, Chile. Photo: Carlos de Mier. See article by Ronikier and Lado in this issue.

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Nivicolous Stemonitales from the Austral Andes: analysis of morphological variability, distribution and phenology as a first step toward testing the large-scale coherence of species and biogeographical properties

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Abstract: Nivicolous myxomycetes occur at the edge of spring-melting snow in mountainous areas. They are mostly considered cosmopolitan species morphologically and ecologically uniform across their entire distribution ranges. Thus, long-distance dispersal has been suggested to be the main mechanism shaping their ranges and geographical variability patterns. To test this hypothesis we conducted the first detailed analysis of morphological variability, occurrence frequency and phenology of nivicolous myxomycetes collected in the hitherto unexplored Austral Andes of South America (southern hemisphere = SH) in the comparative context of data from the northern hemisphere (NH). We used Stemonitales, the most representative and numerous taxonomic order in nivicolous myxomycetes, as a model. A total of 131 South American collections represented 13 species or morphotypes. One of them, *Lamproderma andinum,* is new to science and described here. Several others, *L. aeneum, L. album, L. pulveratum,* ''*Meriderma* aff. *aggregatum* ad. int.'', *M. carestiae* and ''*M. spinulosporum* ad. int.'', were previously unknown from the SH. *Lamproderma ovoideum* is reported for the first time from South America and *Collaria nigricapillitia* is new for Argentina. The fine-scale morphological analysis of all species from the study area and reference NH material demonstrated a high intraspecific variability in most of them. This suggests isolation and independent evolutionary processes among remote populations. On the other hand, the uniform morphology of a few species indicates that long-distance dispersal is also an effective mechanism, although not as universal as usually assumed, in some nivicolous myxomycetes. Analysis of nivicolous species assemblages also showed significant differences among major geographic regions in that the Stemonitales were significantly less common in the SH than in the NH. Furthermore, the occurrence of nivicolous species in summer and autumn, out of the typical phenological season, is recognized as a possible distinctive phenomenon for the SH populations.

Key words: Amoebozoa, Argentina, Chile, Eumycetozoa, Myxogastria, SEM, species distribution, taxonomy

INTRODUCTION

Taxonomy of myxomycetes (slime molds) is essentially based on the morphological species concept (e.g. Clark 2000, Schnittler and Mitchell 2000, Clark and Haskins 2014). Thus understanding of morphological variability of a given taxon is a basic prerequisite to assessing species diversity and defining delimitation of species.

Nivicolous myxomycetes form a particular ecological group of slime molds that occur at the edge of spring-melting snow in mountainous areas of the world (Meylan 1932, Bozonnet et al. 1991, Lado 2004, Ronikier and Ronikier 2009). Due to the specific ecology and occurrence in areas with often difficult access, the general diversity and taxonomic assessment of nivicolous myxomycetes are still incipient and often problematic. The moist-chamber culture technique and cultures on defined media became helpful tools to test intraspecific variability and stability of morphological and micromorphological characters of species. However, these techniques are rarely employed for nivicolous myxomycetes, because they are rarely successful due to specific ecological constraints of this group (Ronikier et al. 2010, Shchepin et al. 2014). Phylogenetic methods and barcoding, based on sequencing of DNA, have been applied to some nivicolous species (e.g. Fiore-Donno et al. 2012, Novozhilov et al. 2013), but these data are scarce and knowledge on genetic variability of species is still rudimentary. Therefore a thorough analysis of morphological characters based on wide sampling from various geographical areas remains the basis for the taxonomy of the group. Gathering data on worlwide diversity and biogeography of nivicolous myxomycetes is a recently developing field and data from various previously unexplored areas have become available recently (e.g. Tamayama 2000; Moreno et al. 2003; Lado et al. 2005; Lado and Ronikier 2008, 2009; Ronikier et al. 2008; Meyer 2010;

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Novozhilov et al. 2013). In spite of this progress, the biogeography of myxomycetes remains poorly understood.

As a whole, slime molds have been considered to be widely distributed and devoid of barriers, thanks to extremely efficient dispersal through spores (e.g. Martin and Alexopoulos 1969). Analysis of distribution of some species (Aguilar et al. 2014) or species assemblages (Stephenson et al. 2008, Estrada-Torres et al. 2013) revealed that recognizable distribution patterns can be found and that distant geographic areas may differ considerably in species composition. In the case of nivicolous myxomycetes, species are known to occur in mountains of the northern hemisphere (NH), such as the Alps, the Pyrenees, the Caucasus and the Carpathians in Europe, the Rocky Mountains or the Sierra Nevada in USA, the Atlas in Africa, the Himalaya and mountains of Hokkaido and Honsiu in Asia. As a whole, they were classified as a widely distributed mountain element (Ronikier and Ronikier 2009), but no detailed analysis of species assemblages or single species distribution has been undertaken to date. Data on nivicolous myxomycetes from the southern hemisphere (SH) originated so far mostly from Australia and New Zealand (Mitchell 1992; Stephenson 2003; Stephenson and Johnston 2003; Stephenson et al. 1992, 2007a, b, 2009; Stephenson and Shadwick 2009). Some records from the Antarctic region (Ing and Smith 1980, 1983) are available on nivicolous myxomycetes, but records from South America are scarce, and only 13 nivicolous species, including three nivicolous representatives of the order Stemonitales, *Collaria nigricapillitia, Lamproderma echinosporum* and *L. maculatum*, have been reported from the continent to date (Lado and Wrigley de Basanta 2008, Wrigley de Basanta et al. 2010, Lado et al. 2013, Ronikier and Lado 2013, Ronikier et al. 2013).

At present, nearly 80 species of nivicolous myxomycetes are described worldwide (Lado 2005–2014). More than 55% (45 species) represent the order Stemonitales and most (33 species) have been described based on type material from Europe. Because most data concerning nivicolous myxomycetes are known from the European mountains, the species concept of most taxa is inherently based on the morphological variability of European material. Studies of nivicolous myxomycetes from hitherto unexplored SH areas usually result either in lists of species without information on morphology (e.g. Stephenson and Johnston 2003) or the description of new species (e.g. Stephenson et al. 2007b). Intraspecific morphological variation is discussed rarely and in only a few cases, such as *Lamproderma maculatum, L. ovoideum* and *Collaria nigricapillitia*, small discrepancies are noticed (Stephenson et al. 2007b) or morphological uniformity is confirmed (Lado et al. 2013).

South America, despite harboring the longest mountain chain of the world, the Andean Cordillera, is almost unexplored for nivicolous myxomycetes and this is the first study focused on this ecological group from that continent. Our first objective is to present the diversity and occurrence of nivicolous Stemonitales collected at several sampling sites in the Austral Andes. Because Stemonitales constitute the largest group of all nivicolous taxa, we consider it an appropriate model to address morphological variability, phenology and biogeography of nivicolous myxomycetes in a comparative context. Based on a detailed comparative analysis of the South American collections with the reference data from populations sampled in the best explored areas, we attempt to address these questions: (i) does the morphological variability of collections from remote and unexplored areas of South America fit the current morphological concept of the species? (ii) in relation to the previous point, do the patterns of morphological variability support unlimited dispersal and thus lack of the morphological differentiation or, on the other hand, could the presence of morphological differentiation be found suggesting isolation and independent evolutionary processes among remote populations? We also discuss: (iii) whether any differences in species assemblages between the SH and the NH can be detected and (iv) are there any differences in phenology and frequency of nivicolous myxomycetes between the SH and the NH?

MATERIAL AND METHODS

Material was collected in the framework of the Myxotropic Project (www.myxotropic.org) during four expeditions to South America carried out over 4 y (2006–2009). In total 37 localities where nivicolous mycomycetes occurred in Argentina were surveyed. All localities were geo-referenced with a GPS (Garmin, eTrex Vista HCx, Datum WGS84). In total 120 collections representing the order *Stemonitales* were found at 12 sites. Thirty-five collections were damaged, molded, too scanty or not well developed, so they were excluded from the taxonomic part of the present study. The remaining 85 collections came from eight localities (TABLE I; FIGS. 1, 2). In addition, 11 specimens of *Lamproderma maculatum* reported from two localities in Chile (Lado et al. 2013) were re-examined. The morphological characters of each Andean collection were compared to published descriptions and illustrations of a given species, including some type material. A list of source literature is given with each species in *Comparison with descriptions of NH material.* The authors' experience based on observations of numerous collections from various areas also was used in morphological analysis. For direct

TABLE I. Localities studied

Locality No.	Details
ARG-07-26	Argentina: Mendoza, Malargüe, Bardas Blancas, Paso del Maule, route RN −145, 37 km West of Las Loicas, 35°57′57″S, 70°21′38″W, 2407 m, 3 Mar 2007, *A. Estrada-Torres* & *C. Lado*, low shrubs and Andean cushion vegetation (FIG. 2B).
ARG-07-37	Argentina: Mendoza, Malargüe, Los Molles, Las Leñas, Portezuelo Ancho, 12 km by the track to Valle Hermoso, 35°05′49″S, 70°08′20″W, 2805 m, 5 Mar 2007, *A. Estrada-Torres, C. Lado* & *D. Wrigley de Basanta*, Andean grassland (FIG. 2A).
ARG-08-40	Argentina: Mendoza, Las Heras, Uspallata, Los Penitentes, route RN-7, 1211 km, 32°50′30″S, 69°49′54″W, 2594 m, 1 Mar 2008, *A. Estrada-Torres, E. García, C. Lado* & *D. Wrigley de Basanta*, low shrubs and Andean cushion vegetation (FIG. 2C).
AGR-09-16	Argentina: Neuquén, Ñorquin, Andacoyo, Moncol, Puerto Pichachén, route 57, 17 km Southwest of police station, 37°26′51″S, 71°05′57″W, 1930 m, 8 Nov 2009, *A. Estrada-Torres, E. García, C. Lado, A. Ronikier* & *D. Wrigley de Basanta*, shrubby and ''krummholz'' forms of *Nothofagus* sp. (FIG. 2E).
AGR-09-17	Argentina: Neuquén, Ñorquin, Andacoyo, Moncol, Puerto Pichachén, route 57, 16 km Southwest of police station, 37°26′49″S, 71°06′18″W, 1880 m, 8 Nov 2009, *A. Estrada-Torres, E. García, C. Lado, A. Ronikier* & *D. Wrigley de Basanta*, shrubby and ''krummholz'' forms of *Nothofagus* sp. (FIG. 2D).
AGR-09-62	Argentina: Río Negro, Bariloche, San Carlos de Bariloche, Nahuel Huapi NP, Villa Cerro Catedral ski centre, 41°09′49″S, 71°27′34″W, 1364 m, 21 Nov 2009, *A. Estrada-Torres, E. García, C. Lado, A. Ronikier* & *D. Wrigley de Basanta*, forest of *Nothofagus pumilio* (FIG. 2G).
AGR-09-63	Argentina: Río Negro, Bariloche, San Carlos de Bariloche, Nahuel Huapi NP, Challhuaco valley, Neumeyer refuge, 41°15′33″S, 71°17′31″W, 1438 m, 22 Nov 2009, *A. Estrada-Torres, E. García, C. Lado, A. Ronikier* & *D. Wrigley de Basanta*. Forest of *Nothofagus pumilio* (FIG. 2H).
ARG-06	Argentina: Río Negro, Bariloche, San Carlos de Bariloche, Nahuel Huapi NP, Cerro Tronador valley, 41°12′00″S, 71°49′33″W, 1020 m, 5 Dec 2006, *C. Lado*, forest of *Nothofagus pumilio* (FIG. 2F).

comparisons (e.g. measurements) of characters with the NH collections, additional herbarium specimens from Europe and North America served as comparative material. Twenty-seven NH collections were compared directly, and they are listed in *Specimens examined* under a given species.

Observations and measurements of morphological characters were conducted under stereoscopic microscopes Nikon SMZ 1000 and SMZ1500. The total height of the sporocarps as well as the height and the width of the sporothecae of most mature individuals were measured. The number of measured sporocarps (n) is provided with each species description or comment on the species. Observations and measurements of microscopic characters were made on material mounted in Hoyer's medium, under a light microscope (LM) Nikon Eclipse E-600, with Nomarski interference contrast, with a digital Nikon DS-Fi1 camera head for photographs. Collections and permanent slides of examined collections are deposited in MA-Fungi and KRAM. Spore measurements of mature specimens were made under an oil-immersion objective and include ornamentation. The number of measured spores (S) is provided for each spore range. Values present in fewer than 3% measurements are in parentheses.

Critical-point drying was used for scanning electron microscopy (SEM) preparations, and specimens were examined with a Hitachi S-3000N and Hitachi S-4700 scanning electron microscopes at 10–15 kV. SEM studies of the collections were made at the Royal Botanic Garden of Madrid, Spain, and in the Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis, at the Institute of Geological Sciences of the Jagiellonian University, Kraków, Poland. Terminology of spore ornamentation observed by SEM is according to Rammeloo (1975) and Kirk et al. (2008).

TAXONOMY

Ten species and three undescribed morphotypes of nivicolous members of the Stemonitales were recognized in the material from South America. One of the undescribed morphotypes is proposed here as a new species, *Lamproderma andinum*.

Six species/morphotypes from the list are reported for the first time from the SH, one more is recorded as new for South America and another one for Argentina. The list includes species and undescribed morphotypes arranged in alphabetical order, with detailed descriptions and comparison with the NH data.

Collaria nigricapillitia (Nann.-Bremek. & Bozonnet) Lado

Specimens examined: Loc. ARG-09-63: near patches of melting snow, on wood of *Nothofagus pumilio, Lado 20831* (MA-Fungi 86920).

Comparison with descriptions of NH material: Europe (Nannenga-Bremekamp 1989, Lado 1992, Neubert et al. 2000, Lado et al. 2005, Poulain et al. 2011), North America (Moreno et al. 2004).

Comments: The collection represents a typical form of the species, characterized by the evanescent

FIG. 1. The study area. Black circles = Argentinian localities on which identified collections of the order Stemonitales were found, gray circles = Argentinian localities with not identified Stemonitales specimens.

peridium and the black, rough capillitium. The spores are almost black in mass, 8.8–10.4 μm diam, av. 9.83 μm diam (S = 21). All these characters agree with the original description based on specimens from the French Alps (Nannenga-Bremekamp 1989), with the description of Lado (1992) based on specimens from the Sierra de Guadarrama (Spain) and with the North American specimens (Moreno et al. 2004). *Collaria nigricapillitia*, a species with presumed preference for higher elevations (Ronikier and Ronikier 2009), was found in the Andes at 1438 m (this study) and 1536 m (Lado et al. 2013), at localities with *Nothofagus pumilio* and mixed *Araucaria araucana/Nothofagus* sp. forests. The Andean sites are among the lowest localities known for the species (Nannenga-Bremekamp 1989, Lado 1992, Moreno et al. 2004). Thus data from the Andes do not confirm the possible preferences for higher elevations for *Collaria nigricapillitia*.

Distribution in the SH: After the specimen reported from Chile (Lado et al. 2013), the present collection represents the second record for the SH and the first for Argentina. Also it has been reported from North America (Moreno et al. 2004), but it seems to be more frequent only in Europe especially in the Alps and the Spanish mountains.

Comatricha laxa Rostaf.

Specimens examined: Loc. ARG-09-17: near patches of melting snow, on branches of *Nothofagus* sp., *Lado 20345* (MA-Fungi 86921), *Lado 20350* (MA-Fungi 86922), *Lado 20354* (MA-Fungi 86923). *Other species*: *Comatricha calderaensis* P. Price, G. Moreno & A. Castillo, USA: New Mexico: Sandoval County, Jemez Mts., Valles Caldera Nacional Preserve, 2800 m, on decomposing spruce-fir branches, UTM: 13S 0358595 3973557, 22 May 2005, *leg. R. Price*, (AH 31974, holotype).

Comparison with descriptions of NH material: Europe (Rostafiński 1874, Castillo et al. 1997, Neubert et al. 2000, Poulain et al. 2011), North America (Martin and Alexopoulos 1969).

Comments: Comatricha laxa is variable, so we provide a more detailed description of the Andean specimens: They are characterized by scattered, stipitate sporocarps, 1.25–1.88 mm (n = 16) total height, with almost round sporotheca, 0.58–1.10 mm high, 0.63–1.05 mm wide, the peridium is evanescent, the stalk reaches 0.58–0.98 mm long, attaining two-fifth–five-eights (the most often one-half) of the total sporocarp height, the columella reaches almost the top of sporotheca, and it is divided at the apex into 2–3 not well distinguished branches, the capillitium is moderately dense, dark brown when the spores are blown out, uniformely dark brown by LM, the primary branches are ± perpendicular and merging from the whole columella length, 5–8 μm thick, the rest of the capillitial threads are 3–4 μm thick, and 1.5–3 μm thick at the peripheries, with scattered, short, pointed spines and with many free ends without a distinct surface net. The spores are dark brown in mass, moderately brown by LM, with a small, paler germ pore area on one side, globose, (8–)8.5–10(–10.5) μm diam, av. 9.21 μm diam (S = 70), densely and regularly warted (FIG. 3), baculate by SEM.

We identified our specimens based on the following characters that are in agreement with the original description of the species provided by Rostafiński (1874): columella reaching almost the top of the sporotheca, where it divides into 2–3 threads and merges into the capillitium; the capillitium is composed of thick, dark brown threads almost of uniform

FIG. 2. Landscapes and vegetation of the study area. A. Grassland in Portezuelo Ancho, Mendoza, Argentina (ARG-07-37). B. Andean cushion vegetation at Paso del Maule Mendoza, Argentina (ARG-07-26). C. Andean cushion vegetation in Aconcagua Nature Reserve, Mendoza, Argentina (ARG-08-40). D–E. Andean shrubland of *Nothofagus* sp. in Puerto Pichachen area, Neuquén, Argentina (ARG-09-16, ARG-09-17). F. Forest of *Nothofagus pumilio* in Cerro Tronador, Nahuel Huapi National Park, Río Negro, Argentina (ARG-06). G–H. Forest of *Nothofagus pumilio* in Nahuel Huapi National Park, Río Negro, Argentina (ARG-09-62, ARG-09-63).

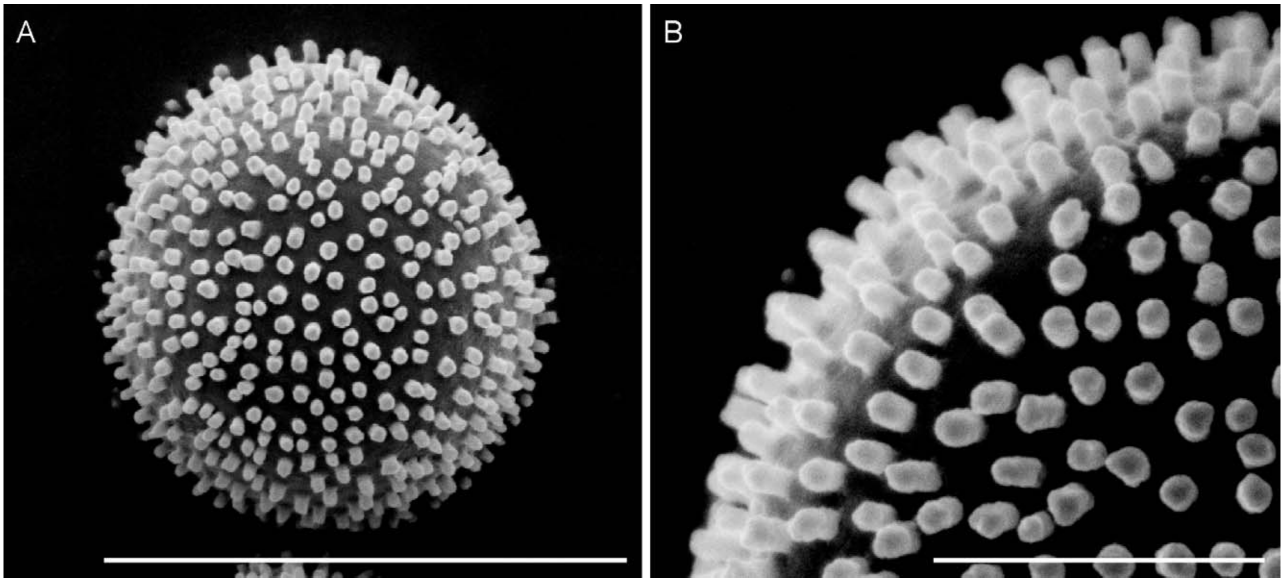

FIG. 3. *Comatricha laxa* (*Lado 20350*) by SEM. A. Spore. B. Details of spore ornamentation. Bars: A = 10 μm; B = 3 μm.

diameter from the columella to the peripheries, and the spores are small, 9.2–10.8 μm diam (according to Rostafiński 1874). Our specimens also are similar to the type specimens of *C. laxa* illustrated by Castillo et al. (1997) and to the specimens of that species illustrated by Martin and Alexopoulos (1969) and Poulain et al. (2011) with scattered spines on the capillitium.

Comatricha laxa is not a strictly nivicolous species. There is a nivicolous species of *Comatricha*, *C. calderaensis* R. Price, G. Moreno & A. Castillo (Moreno et al. 2008), that is similar to our specimens, in that it also has the dark brown capillitium covered with scattered spines, but after the examination of the holotype of *C. calderaensis* we noted these differences: denser and thinner capillitium that form a clear, almost complete, small-meshed outer net at sporotheca base, more interrupted in upper sporotheca part, and the slightly larger, 10.5–12 μm diam (S = 30), and darker spores (see Moreno et al. 2008).

Distribution in the SH: Comatricha laxa is known from Australia (Knight and Brims 2010), New Zealand (Mitchell 1992) and it has been reported from several South American countries: Argentina, Brazil, Chile, Venezuela (Lado and Wrigley de Basanta 2008, Lado et al. 2013). Our specimen represents the first nivicolous record of the species in the SH.

Comatricha nigra (Pers. ex J.F. Gmel.) J. Schröt.

Specimens examined: Loc. ARG-09-63: near patches of melting snow, on wood of *Nothofagus pumilio*, *Lado 20782* (MA-Fungi 86924, duplicate in KRAM M-1518). SPAIN: Guadalajara, Galve de Sorbe, carretera a Valdepinillos, 30TVL8461, 1500 m, en rama de *Pinus sylvestris*, 31 Oct 1986, *Lado 1888* (MA-Fungi 23657).

Comparison with descriptions of NH material: Europe (Neubert et al. 2000, Poulain et al. 2011), North America (Martin and Alexopoulos 1969).

Comments: The collection is typical for the species, forming tall sporocarps 1.84–2.88 mm (n = 6) total height, with long stalk, 1.42–2.24 mm, attaining five-sevenths to seven-ninths of the total sporocarp height, the sporotheca is slightly ovoid-fusiform, 0.42–0.76 mm diam, the inner capillitial net is dense. The ornamentation is typical in the Andean collection: spinulose, with a small germ pore by LM, covered with baculae that are not smooth but covered with tiny verrucae when observed by SEM (FIG. 4). But the spores are larger, (8.5–)11–12(–12.5) μm diam, av. 11.6 μm (S = 30), vs. (8–)9–10(–11) μm diam from the literature (Martin and Alexopoulos 1969, Neubert et al. 2000, Poulain et al. 2011). These differences might be caused by differences in the method of measuring spores, without ornamentation by Poulain et al. (2011), but if we excluded the ornamentation in the Andean material the dimensions are (8.5–)10.5–12 μm diam, av. 10.03 μm diam (S = 30). In addition, we measured spores of a typical European collection (MA-Fungi 23657) and the spores are slightly smaller, indeed, (8.75–)9–11 μm diam, av. 9.77 μm diam (S = 30).

Distribution in the SH: The species, considered cosmopolitan by many authors, is not strictly nivicolous, although often found near melting snow in spring. It has been reported from the SH from Australia, New Zealand and South America, including Argentina (Cheeseman and Lister 1915; Mitchell 1992; Farr 1968, 1976; Lado and Wrigley de Basanta

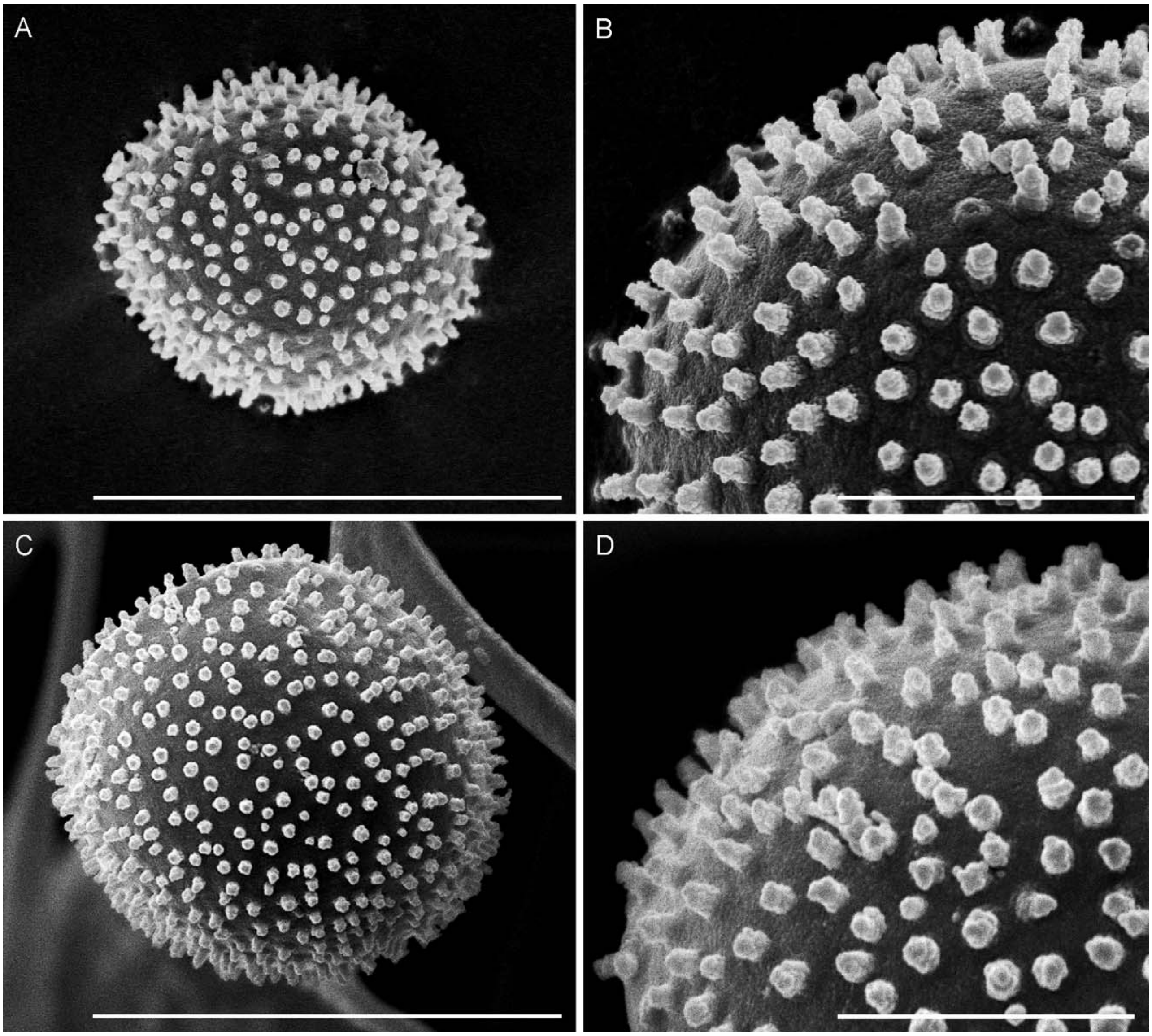

FIG. 4. Comparison of South American and European specimens of *Comatricha nigra* by SEM. A. Spore (*Lado 20782*). B. Details of spore ornamentation (*Lado 20782*). C. Spore (MA-Fungi 23657). D. Details of spore ornamentation (MA-Fungi 23657). Bars: A, C = 10 µm; B, D = 3 µm.

2008; Wrigley de Basanta et al. 2010; Lado et al. 2013; Moreno et al. 2013; Stephenson et al. 2014).

Lamproderma aeneum Mar. Mey. & Poulain

Specimen examined: Loc. ARG-09-63: near patches of melting snow, on branches of *Nothofagus pumilio*, *Lado 20852* (MA-Fungi 86925, duplicate in KRAM M-1596).

Comparison with descriptions of NH material: Europe, Asia, North America (Poulain et al. 2002, 2011; Poulain and Meyer 2005).

Comments: Our specimens fit the description provided by Poulain et al. (2011). The sporocarps are 0.88–1.38 mm (n = 6) total height, stipitate, the sporotheca is 0.54–0.98 mm high and 0.66–0.98 mm wide, round or slightly wider than high, with predominantly silver and golden peridium, the stalk is 0.20–0.50 mm long, the capillitium is dark brown, paler only at the extremities, not dense, arising from the upper part of columella. The spores are moderately brown, (10–)10.5–12 µm diam, av. 11.20 µm diam (S = 30), minutely warted. The Andean specimens have longer stipes than the type collection from the Frech Alps, up to two-fifths vs. up to one-fifth of the total height (see Poulain et al. 2002) and than NH material (Poulain et al. 2011).

Distribution in the SH: The species has not been reported previously from the SH. This record is also the first for Argentina.

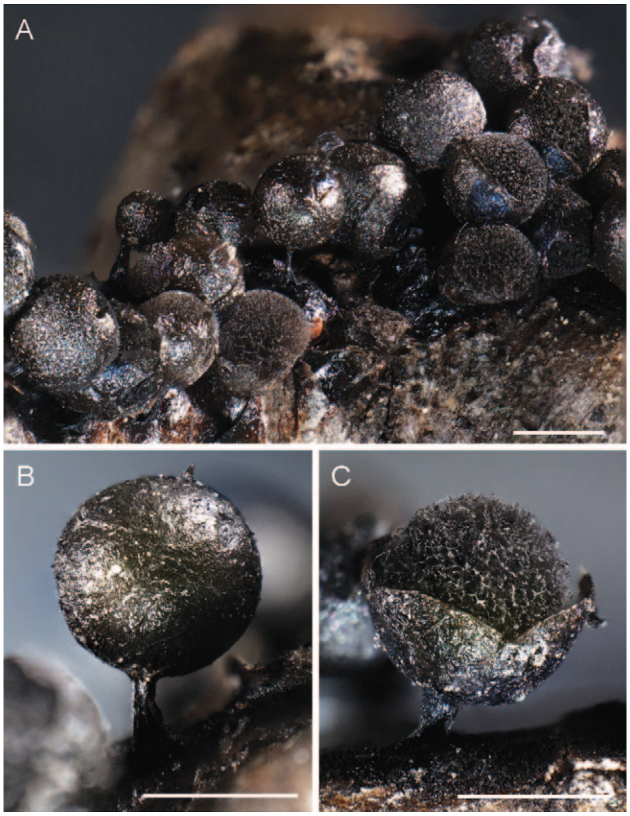

Fig. 5. *Lamproderma andinum* (*Lado 17773*, holotype). A. Group of sporocarps. B. Sporocarp with peridium. C. Sporocarp with peridium dehisced. Bars = 1 mm.

Lamproderma album H. Neubert, Nowotny & Baumann

Specimens examined: Loc. ARG-09-63: near patches of melting snow, on leaves of living *Berberis* sp., *Lado 20771* (MA-Fungi 86926, duplicate in KRAM M-1590); on bark of branches of *Nothofagus pumilio*, *Lado 20878* (MA-Fungi 86927, duplicate in KRAM M-1591), *Lado 20915* (MA-Fungi 86928, duplicate in KRAM M-1592).

Comparison with descriptions of NH material: Europe, Asia (Poulain et al. 2011).

Comments: The specimens are characterized by stalked, rarely sessile sporocarps. The stalk is up to 1.10 mm high, attaining up to three-fifths of the total sporocarp height, the sporothecea is broadly ovoid, always wider than high, 0.70–1.14 mm high, 0.85–1.22 mm (n = 15) wide, the peridium is smooth, with many color reflections (blue, violet, green, golden), without crystals on its surface, distinctly darker brown at the base under reflected light, and brown to dark brown at the base by LM. The capillitium is dense, totally white on the outer part and brown a short distance from the columella under reflected light, pale brown by LM, slightly darker at columella becoming progressively paler or almost hyaline toward the peripheries, the capillitial threads are slightly to strongly flattened, the spores are globose, (9.5–)10–11.5(–12) µm diam, av. 10.71 µm diam (S = 90), pale brown, uniformely colored and warted. The Andean specimens seem to represent the typical form of the species (see Poulain et al. 2011).

Distribution in the SH: This is the first record of the species for the SH, also the first record for the Americas.

Lamproderma andinum A. Ronikier & Lado, sp. nov.
MycoBank MB810404

Typification: CHILE. ARAUCANÍA: IX Region, Malleco, Lonquimay, Malalcahuello-Nalca National Reserve, Corralco ski center, Lonquimay volcano, 38°25′49″S, 71°32′16″W, 1368 m (Loc. CHI-06-40, see Lado et al. 2013), mixed forest with *Araucaria araucana* and *Nothofagus* sp., 28 Mar 2006, on wood of living *Nothofagus* sp., *Lado 17773* (holotype MA-Fungi 80613). Isotype (KRAM M-1569).

Etymology: From Latin: *andinum* = from the Andes. The epithet refers to the area of occurrence of the species.

Sporocarps grouped or scattered, stipitate, total height (0.88–)0.98–1.80 mm (n = 62) (Fig. 5A). Sporotheca globose to subglobose, 0.60–1.50 mm diam, dark blackish brown to black, surface shining, smooth or slightly wrinkled, without color reflections (Fig. 5B). Hypothallus membranous, thick, dark red-brown to dark brown, irregular and common for a group of sporocarps, more rarely discoid and individual. Stalk erect, 0.05–0.75(–0.80) mm long, short, up to one-half total sporocarp height, black, shining. Peridium single, persistent, thick, dark brown all over, without darker patches and without needle-like crystals, brown and rough from incrusting pigment all over by LM, usually also with darker areoles or points (Fig. 6B, C), inner surface delicately rough by SEM (Fig. 7B); dehiscence splitting irregularly and the peridium often persisting in the lower part of the sporotheca at some distance from the capillitium (Fig. 5C). Columella reaching about half the sporotheca height or less, cylindrical, blunt or even enlarged at apex. Capillitium dense (Figs. 6A, 7A), under reflected light blackish brown with pale ends (Fig. 5C), dark brown in major part by LM, abruptly paler only at ends (Fig. 6E), primary branches thick and with many anastomoses and frequent expansions at axils, surface of threads rough from incrusting pigment, especially in the peripheral part, forming zebra-like pattern (discontinuous) at the extremities (Fig. 6D), the threads slightly flattened (Fig. 7C). Spores black in mass, moderately brown by LM, of uniform color or only slightly paler at one side, globose, (11–)12–15.2(–17.2) µm diam, av. 13.17 µm diam (S = 950), spinulose, baculate by SEM (Figs. 6F, G; 7D; 8A, B). Plasmodium unknown.

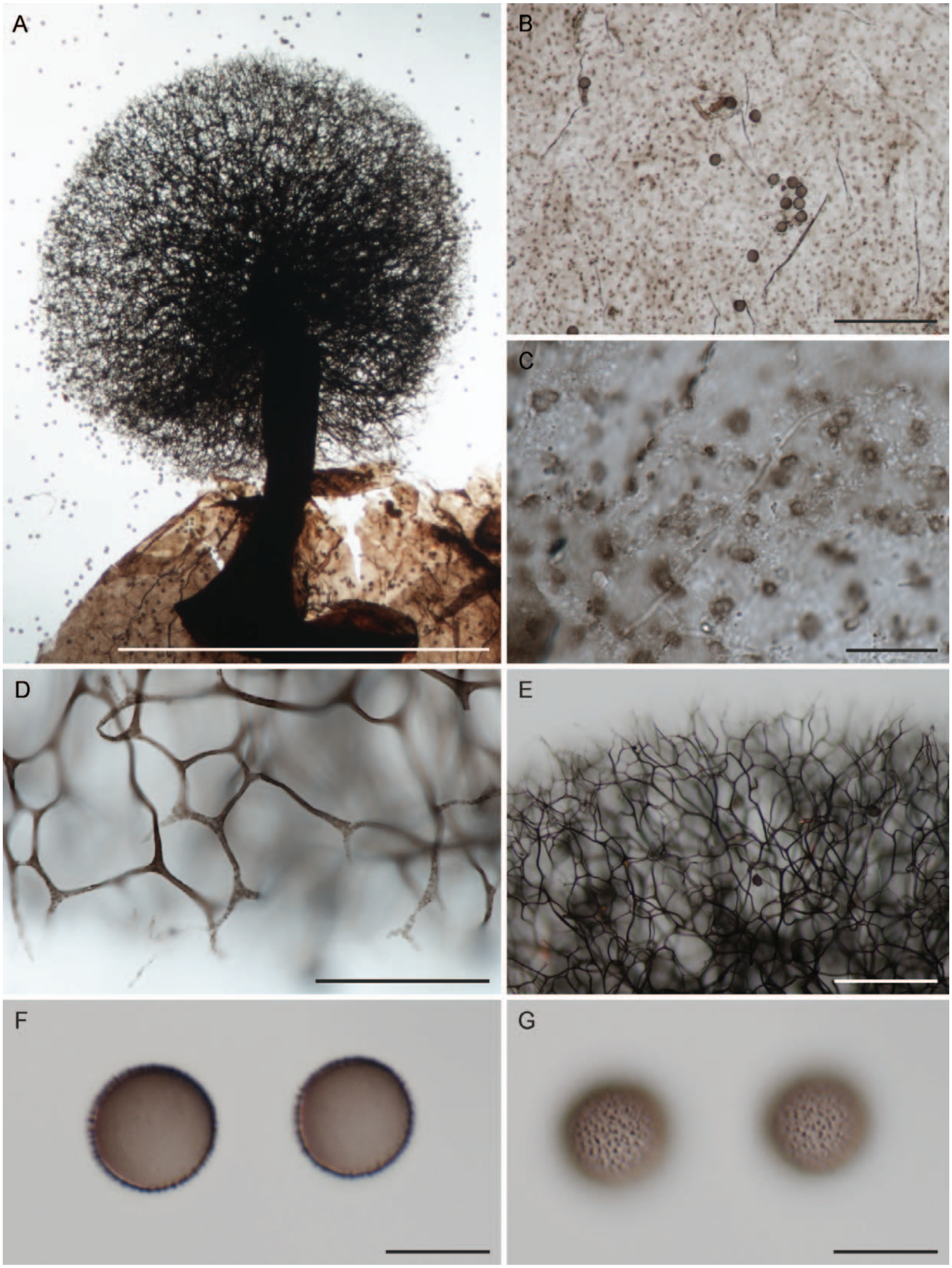

FIG. 6. *Lamproderma andinum* (*Lado 17773*, holotype) by LM. A. Sporocarp showing the columella and dense capillitium. B–C. Peridium inner surface with dark brown areoles. D. Capillitial extremities with discontinuous pigment. E. Peripheral part of capillitium. F–G Spores. Bars: A = 1 mm; B, D, E = 100 μm; C = 20 μm; F, G = 10 μm.

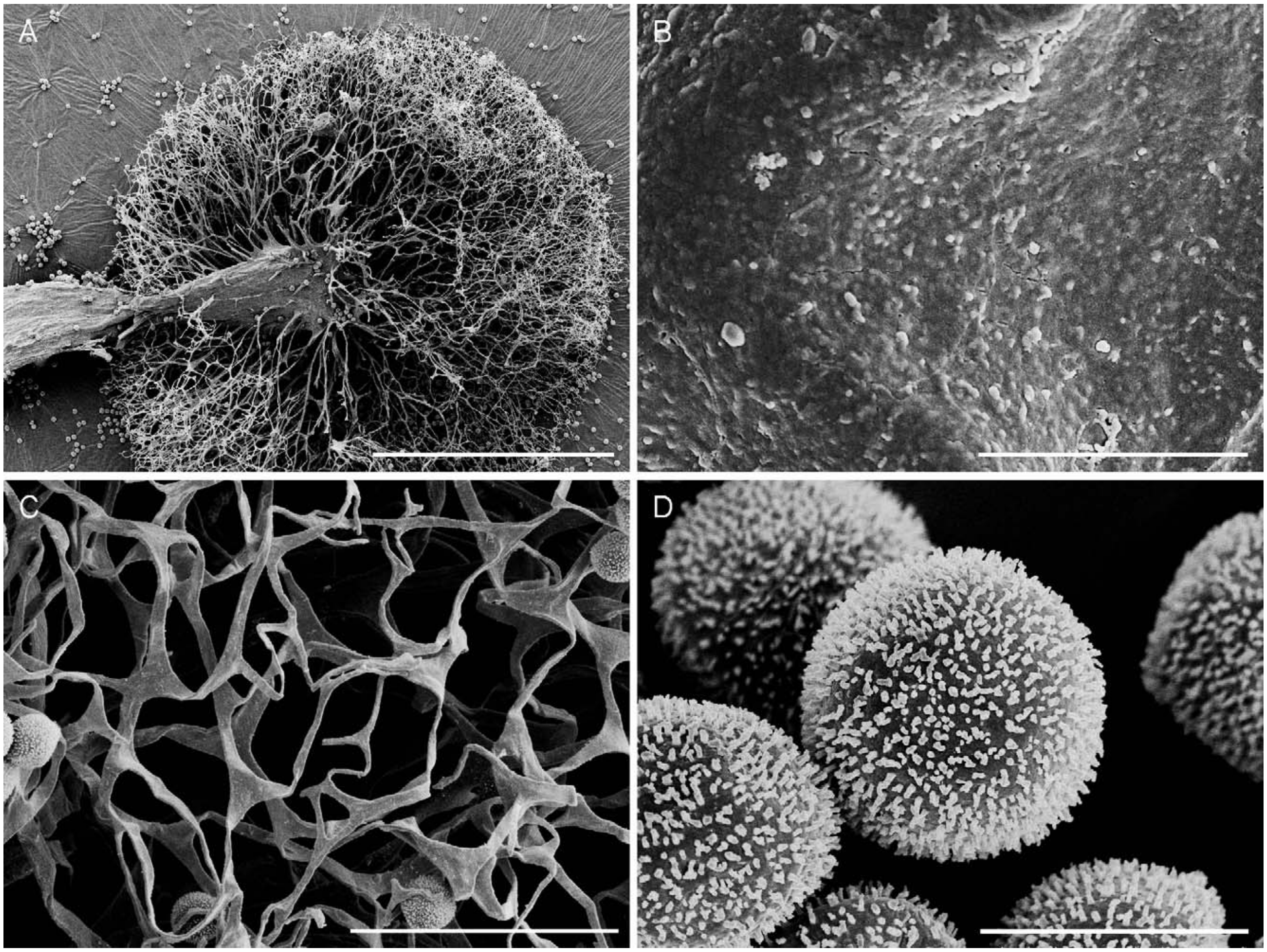

FIG. 7. *Lamproderma andinum* (*Lado 17773*, holotype) by SEM. A. Sporocarp. B. Inner peridium surface. C. Capillitial threads. D. Spores. Bars: A = 500 μm; B = 5 μm; C = 50 μm; D = 10 μm.

Habitat: The species was found at three localities, in two countries and in two separate years. The Argentinian locality was typically nivicolous (presence of many snow patches), while at the two Chilean localities no snow was recorded in the vicinity but the substrates had signs of a previous snow cover, the snow could have melted several days or weeks before. The Argentinian specimens, collected during austral spring, with most sporothecae closed, seemed to be younger than the Chilean specimens, collected during the end of austral summer or beginning of austral autumn, well developed and with many opened sporothecae. It seems that the species requires a period of melting snow at the beginning of sporophore development and it is possible that either it develops slowly or thanks to a relatively thick peridium it is persistent and it still looks freshly formed a relatively long time after snow melts.

Distribution: Known only from South America (the Austral Andes of Argentina and Chile).

Additional specimens examined: Loc. ARG-09-63: near patches of melting snow, on branch of *Nothofagus pumilio*, *Lado 20756a* (MA-Fungi 86929), *Lado 20842* (MA-Fungi 86930), *Lado 20855* (MA-Fungi 86931, duplicate in KRAM M-1571), *Lado 20899* (MA-Fungi 86932, duplicate in KRAM M-1572), *Lado 20918* (MA-Fungi 86933, duplicate in KRAM M-1589); on leaves of *N. pumilio*, *Lado 20853* (MA-Fungi 86934), *Lado 20854* (MA-Fungi 86935); on branch of living *Berberis* sp., *Lado 20894* (MA-Fungi 86936). CHILE: Loc. CHI-06-37: on wood of living *N. pumilio*, *Lado 17743* (MA-Fungi 88239), *Lado 17745* (MA-Fungi 88241), *Lado 17756* (MA-Fungi 88245). Loc. CHI-06-40: on wood of living *Nothofagus* sp., *Lado 17763* (MA-Fungi 88243), *Lado 17767* (MA-Fungi 80607), *Lado 17768* (MA-Fungi 80608), *Lado 17771* (MA-Fungi 80611), *Lado* 17772 (MA-Fungi 80612); on wood of living *Berberis* sp., *Lado 17769* (MA-Fungi 80609); on branch of living bush, *Lado 17770* (MA-Fungi 80610) (for description of Chilean localities, see Lado et al. 2013). *Other species: Lamproderma nordica* Kuhnt, NORWEGEN: Fylke Nord-Trøndelag, Kommune Verran, Follafoss, zwischen Almi und Gotvassli, nahe dem See Kjåppån, Höhe 250 m, lichter Fichtenwald, Strassengraben mit Gebüschsaum, wenige Schneereste, nivicol, auf lebenden Ästchen (cf. *Salix* spec.), 25 May 2008, *leg. Andreas Kuhnt*, *HK 080525-1a* (M-0140863, holotype), *HK 080525-1b* (KRAM M-1594, isotype). Fylke Nordland, Kommune Sørfold, Mørsvikbotn, An der E6, nördlich vom Mørsvikbotn, oberhalb vom Tennvatnet, Richtung Tennvasshaugen, einige Restschneefelder, Höhe 380 m, lichter Birkenwald, Zwergsträucher, auf lebendem Ästchen, nivicol, 17 Jun 2008, *leg. Andreas Kuhnt*, *HK 080617-09* (KRAM M-1595). *Lamproderma puncticulatum* Härk., FINLAND: Uusimaa, Espoo, Myllykylä, on sporophores of *Cantharellus tubaeformis*, 3 Oct 1974, *leg. Mauri Korhonen*, (H 6025771, holotype). FRANCE: Savoie, St Paul/Isère, 1000 m, 4 Nov 1997, *herb. Meyer 18197* (H 7022213). Savoie, St Paul/Isère ''Les Rottes'', 1000 m, 27 Sep 1996, *herb. Meyer 16954* (H 7022224).

Comments: Lamproderma andinum can be characterized as a species forming dark blackish brown to black, shortly stipitate sporocarps, without color reflections and without dark patches on peridium (FIG. 5A, B), having dark brown capillitium threads with incrusting, brown pigment forming a zebra-like pattern at the extremities (FIG. 6D) and a dark brown peridium with a brown incrusted inner surface (FIG. 6B, C).

The only species from the genus that shares similar sporocarp colors is *Lamproderma nordica* Kuhnt (Kuhnt 2011). The two species share also sporotheca size and capillitium colors, dark brown with paler ends, but *L. nordica* is more robust; it has thicker, denser and darker capillitium with thicker extremities (measured at upper part of sporotheca, 1.5–3.0(–4.0) µm, av. 2.42, vs. 0.5–1.5 µm, av. 0.77 for *L. andinum*), firmly attached to the peridium, a thicker and darker peridium, with paler spots or lines, and darker and larger spores 13–23(–24) µm (S = 80, only globose spores measured), (see also Kuhnt 2011), vs. (11–)12–15.2(–17.2) µm diam in *L. andinum.* The spore ornamentation of *L. nordica* is also different, covered with thicker and more loosely arranged baculae that also may fuse into short irregularly branched crests when observed by SEM (FIG. 8C, D) vs. clearly baculate in *L. andinum* (FIG. 8A, B).

Lamproderma maculatum has the same capillitium characters as *L. andinum.* This species, however, has darker areas on peridium, often crystals on the peridium surface, and the spores are darker in the case of *L. maculatum* (dark purple-brown by LM vs. moderate brown in *L. andinum*), and the ornamentation is granulate to aculeate but not baculate (FIG. 11). The latter character is helpful in distinguishing the new species from atypical specimens of *L. maculatum,* which do not have darker areas under reflected light and become morphologically similar to *L. andinum.*

A non-nivicolous species, *L. puncticulatum* Härk., is microscopically similar to *L. andinum,* because its capillitium is brown-incrusted and mottled in the same way, but it is more delicate, paler, not rigid, mostly dichotomously branched and the threads are more flattened. The spores of *L. puncticulatum* are larger; an average value is higher, (13.0)13.5–15.0(17.0) µm, av. 14.33 (S = 150), and the ornamentation is more robust (thicker with more dispersed spines; FIG. 8E, F), while *L. andinum* have dense and more delicate baculae (FIG. 8A. B). *Lamproderma puncticulatum* also differs in sporocarp size, rarely exceeding 1 mm of the total height (up to 1.8 mm in *L. andinum*), and in the presence of clearly visible darker areas on the peridium surface. In addition, *L. puncticulatum* differs in ecology; it occurs on mosses and liverworts and has never been found at nivicolous localities (Härkönen 1978, Poulain et al. 2011).

Distribution in the SH: Only known from the Austral Andes (Argentina and Chile). The Chilean specimens reported by Lado et al. (2013) as *Lamproderma maculatum* belong to this new species.

Lamproderma echinosporum Meyl.

Specimens examined: Loc. ARG-09-16: near patches of melting snow, on branches of *Adesmia* sp., *Lado 20328* (MA-Fungi 86939), *Lado 20329* (MA-Fungi 86940). Loc. ARG-09-17: near patches of melting snow, on wood of *Nothofagus* sp., *Lado 20375* (MA-Fungi 86941). Loc. ARG-09-62, near patches of melting snow, on grasses, *Lado 20669* (MA-Fungi 86942), on branches of *Nothofagus* sp., *Lado 20680* (MA-Fungi 86943), *Lado 20681a* (MA-Fungi 86944), on herbaceous remnants, *Lado 20704* (MA-Fungi 86945), duplicate in KRAM M-1524), on branches of *Nothofagus pumilio*, *Lado 20714* (MA-Fungi 86946). Loc. ARG-09-63: near patches of melting snow, on branches of *N. pumilio*, *Lado 20748* (MA-Fungi 86947), *Lado 20758* (MA-Fungi 86948), *Lado 20775* (MA-Fungi 86949), *Lado 20857* (MA-Fungi 86950, duplicate in KRAM M-1525), *Lado 20865* (MA-Fungi 86951, duplicate in KRAM M-1526), *Lado 20882* (MA-Fungi 86952), *Lado 20906* (MA-Fungi 86953); on wood of *N. pumilio*, *Lado 20766* (MA-Fungi 86954); on branch of living *Berberis* sp., *Lado 20787* (MA-Fungi 86955), *Lado 20790* (MA-Fungi 86956); on branches of living *N. pumilio*, *Lado 20794* (MA-Fungi 86957), *Lado 20796* (MA-Fungi 86958); on leaves and branches of living *Berberis* sp., *Lado 20875a* (MA-Fungi 86959), *Lado 20879* (MA-Fungi 86960); on bark of branch of *N. pumilio*, *Lado 20910b* (MA-Fungi 86961), *Lado 20911* (MA-Fungi 86962); on trunk of *N. pumilio*, *Lado 20966* (MA-Fungi 86963). SPAIN: Lérida: Lladorre, Tavascan, road to Certascan, Naorte lake, 42°40′52″N, 01°18′08″E, 2000 m, on branch of *Rhododendron ferrugineum*, 4 Jun 1996, *Lado 8104* (MA-Fungi 75728, duplicate in KRAM M-1297). FRANCE: Savoie, the Alps, Massif de la Vanoise, Méribel, above le Raffort, 45°23′55″N, 06°33′34″E, 1480 m, among shrubs (*Alnus, Salix*), on plant remnants, at the melting snow patch, 28 Apr 2008, *leg. A. Ronikier, M. Ronikier* (KRAM M-1366). Savoie, the Alps, Massif de la Vanoise, Méribel, above le Raffort, 45°24′04″N, 06°33′22″E, 1490 m, mountain meadow, on plant remnants, at the melting snow

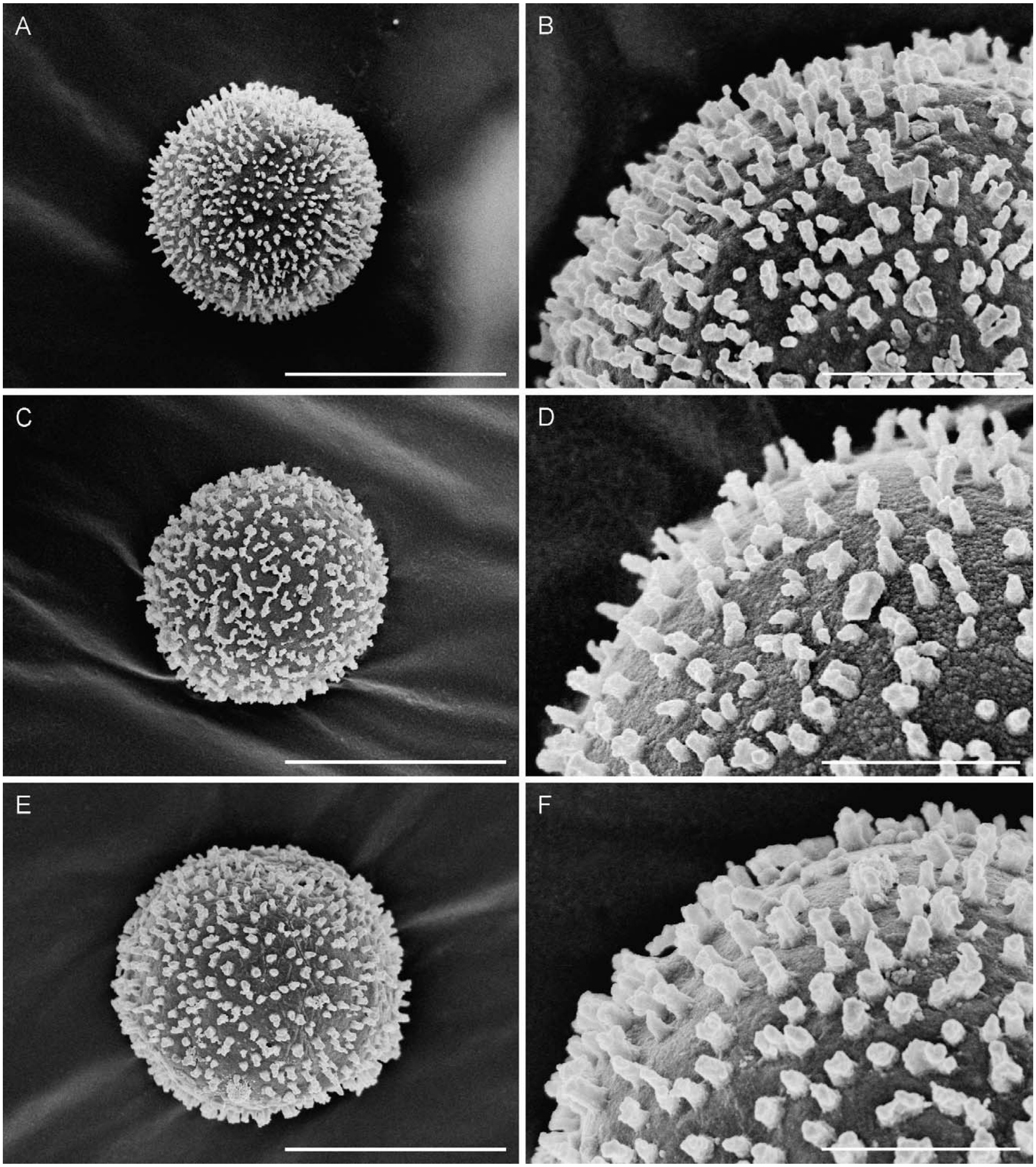

FIG. 8. Comparison by SEM of spore ornamentation of *Lamproderma andinum, L. nordica* and *L. puncticulatum*. A–B. Spore ornamentation of *L. andinum* (*Lado 17773*, holotype). C–D. Spore ornamentation of *L. nordica* (*HK080525-1b*, ISOTYPE). E–F. Spore ornamentation of *L. puncticulatum* (*H6025771*, holotype). Bars: A, C, E = 10 μm; B, D, F = 3 μm.

patch, 29 Apr 2008, *leg. A. Ronikier, M. Ronikier* (KRAM 1404). Savoie, The Alps, between Albertville and Moûtiers, Celliers (N from Col de la Madeleine), edge of a ski piste, 45°28′29″N, 06°24′57″E, 1385 m, at the melting snow patch, on *Alnus* shoots, 02 May 2008, *leg. A. Ronikier, M. Ronikier* (KRAM M-1447). Alpes Maritimes, Parc National du Mercantour, Belvedere, Vallon de Gordelasque, 1900 m, on dead grasses, at melting snow patches, 16 Apr 2001, *leg. A. Ronikier, M. Ronikier* (KRAM M-1012). POLAND: the Carpathians, the Beskid Śląski Mts, Wyrchczadeczka near

Jaworzynka, 635 m, on a meadow at a forest edge, on plant remnants, 30 Mar 2007, *leg. A. Bochynek*, (KRA MYXO 730, KRA MYXO 734).

Comparison with descriptions of NH material: Europe, North America, Asia (Meylan 1924; Kowalski 1970; Bozonnet et al. 1991, 1995; Neubert et al. 2000; Moreno et al. 2002; Poulain et al. 2011; Novozhilov et al. 2013).

Comments: The Andean specimens are characterized by stalked sporocarps, the stalk is (0.15–)0.25–1.20(–1.75) mm (n = 80) long, up to two-thirds of the total sporocarp height (FIG. 9A), the sporotheca is globose to ovoid, often higher than wide, the peridium have darker areas, and the spores are large, (13.2–)14–17.6(–19.2) μm diam, av. 15.92 μm diam (S = 486), covered with isolated spines that usually are longer than 1 μm (1.5 μm), with long and irregularly distributed baculae by SEM (FIG. 9B–D).

Lamproderma echinosporum was described from the Swiss Alps (Meylan 1924) and in the original description, as well as in the European monographs and keys, it is described as a sessile or short-stalked species, with stalk up to 0.5 mm long, rarely exceeding half of the total height of sporocarp, and with spores covered by spines about or up to 1 μm long (Meylan 1924, Neubert et al. 2000, Moreno et al. 2002, Poulain et al. 2011). In the material described here, the sporocarps are usually long stalked, the stalk is usually longer than 0.5 mm and more than one-third of total sporocarp height (FIG. 10). Also the spores have longer spines, up to 2 μm, more loosely arranged than in the European specimens.

In the randomly selected comparative material from several European mountain massifs (n = 80, see *Specimens examined*) we also noticed mostly sessile to shortly stalked sporocarps (FIG. 9E) with stalk absent to up to 0.60 mm high (FIG. 10) and lower and denser spore ornamentation (FIG. 9F–H).

Distribution in the SH: The species has been reported from one locality in the Nahuel Huapi National Park in Argentina (Wrigley de Basanta et al. 2010). Based on these collections it can be said that the species is probably common in the Austral Andes.

Lamproderma maculatum Kowalski

Specimens examined: Loc. ARG-07-26: near partches of melting snow, on twigs, *Lado 18579* (MA-Fungi 86964). Loc. ARG-07-37: on twigs of Asteraceae, *Lado 18609* (MA-Fungi 86965). Loc. ARG-09-62: near patches of melting snow, on branches of *Nothofagus* sp., *Lado 20681b* (MA-Fungi 86966); on branches of *Nothofagus pumilio, Lado 20700b* (MA-Fungi 86967), *Lado 20702* (MA-Fungi 86968, duplicate in KRAM M-1563). Loc. ARG-09-63: near patches of melting snow, on twigs and leaves of living *Berberis* sp., *Lado 20747* (MA-Fungi 86969, duplicate in KRAM M-1565); on branches of *N. pumilio, Lado 20753* (MA-Fungi 86970), *Lado 20756b* (MA-Fungi 86971), *Lado 20761* (MA-Fungi 86972, duplicate in KRAM M-1564), *Lado 20808* (MA-Fungi 86973), *Lado 20846* (MA-Fungi 86974), *Lado 20869* (MA-Fungi 86975), *Lado 20920* (MA-Fungi 86976), *Lado 20921* (MA-Fungi 86977). SPAIN: Ávila: Sierra de Gredos, Zapardiel de la Ribera, central part of the Circo de Gredos, slopes to the South-West upwards from the Refugio Elola, 40°14′55″N, 05°17′14″W, 2020-2100 m, small patches of alpine meadows among granitic rocks, on old stem of *Eryngium bourgatii*, 31 May 2003, *leg. A. Ronikier, M. Ronikier*, KRAM M-1053. Lérida: the Pyrenees, Naut Aran, Arties, Coll de Pruedo, 42°39′23″N, 0°54′01″E, 2000 m, on branch of *Rhododendron ferrugineum*, 5 Jun 1996, *Lado 8176* (MA-Fungi 75744, duplicate in KRAM M-1307). FRANCE: Savoie, the Alps, Esserts-Blay, 1300 m, 20 May 1986, *MM1153* (KRAM M-1479). USA: Tehama Co., 3 miles W, of Child's Meadows, 5200 ft., on bark, 20 May 1967, *DTK 6200*, (UC 1408239, holotype). Tehama County, 3 miles E of Mineral, 5000 ft., on dead twig, 20 May 1967, *DTK 6100* (UC1408203). Butte County, 4 miles E of Inskip, 5500 ft., on decayed twig, 23 Apr 1966, *DTK 2813* (UC1408205).

Comparison with descriptions of NH material: Europe, North America, Asia (Kowalski 1970, Bozonnet et al. 1995, Neubert et al. 2000, Moreno et al. 2002, Poulain et al. 2011, Novozhilov et al. 2013).

Comments: Specimens are characterized by scattered, stalked sporocarps (1.02–)1.30–1.80(–2.00) mm (n = 48) total height, the stalk 0.25–0.90 mm long is one-fifth to one-half of the total sporocarp height. The sporotheca is dark brown to blackish brown, globose, 0.70–1.30(–1.45) mm diam, smooth and shining but with few color reflections. The peridium is dark brown in the lower half, usually with visible small darker patches in the upper half and needle-like crystals, thick, red-brown by LM, rough from incrusting pigment in the lower half, and usually thinner with visible darker patches in the upper half. The capillitium is blackish brown under reflected light, dark brown by LM, rough from incrusting pigment, forming a zebra-like pattern (discontinuous) at the extremities. The spores are (12–)12.8–17.6(–20) μm diam, av. 14.74 μm diam (S = 360), very dark brown to dark brown, paler at one side, minutely warted, granulate to aculeate by SEM (FIG. 11).

L. maculatum belongs to the group of species with brown patches on the peridium but differs from other species of the group by the minutely warted, dark brown spores and by the dark brown capillitium (Bozonnet et al. 1995, Neubert et al. 2000, Poulain et al. 2011). Most of the Andean specimens fit these characters. All have dark brown, minutely warted spores with an ornamentation similar to those of the type specimen (FIG. 11; Moreno et al. 2002: figs. 53, 54). However, some of them do not have clearly visible darker patches on peridium surface. Also under transmitted light the darker patches are not always visible. In many typical collections the perid-

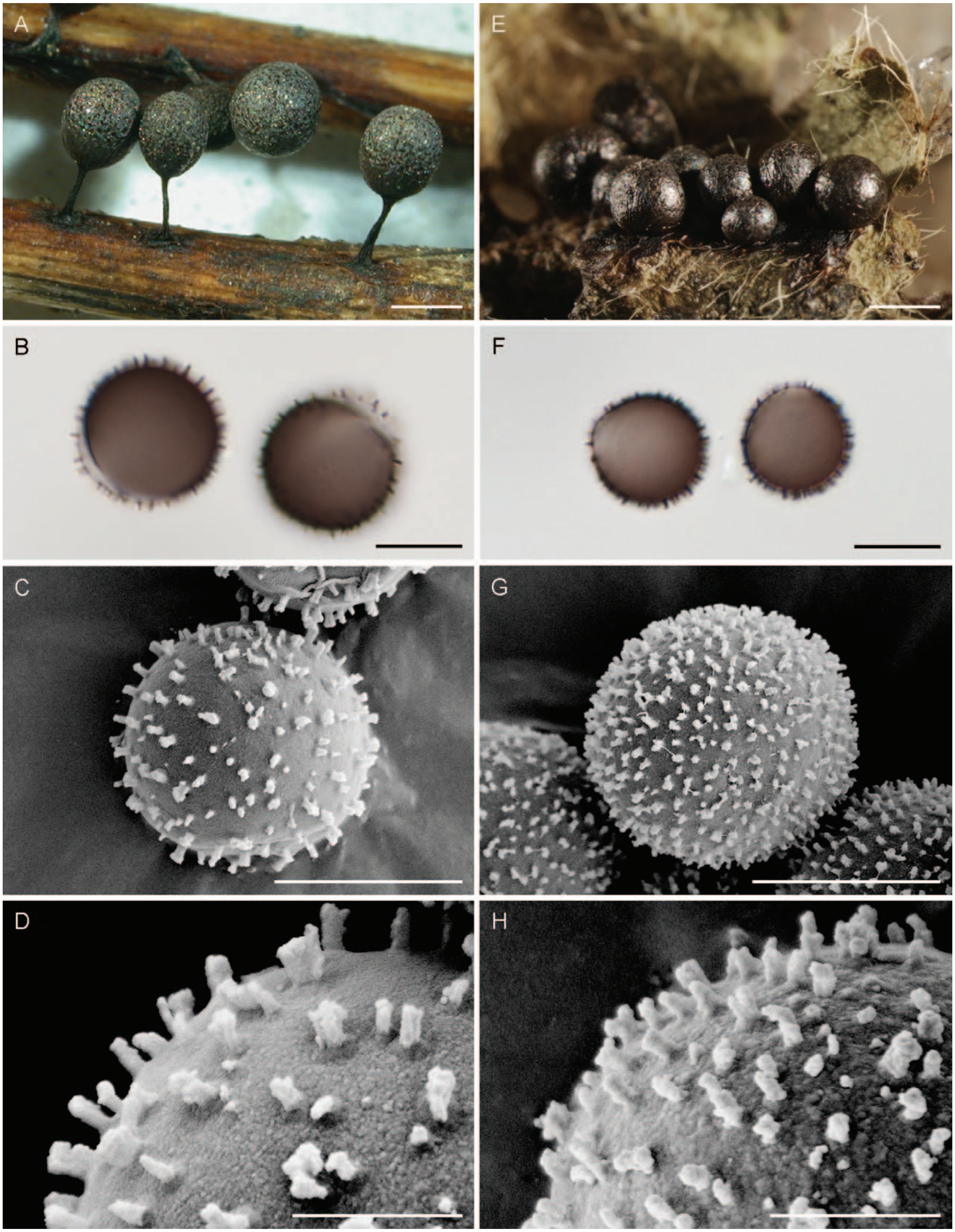

FIG. 9. Comparison of the South American and European specimens of *Lamproderma echinosporum*. A–D South American morphotype. A. Typical habit (*Lado 20704*). B. Spores (*Lado 20714*) by LM. C. Spore by SEM (*Lado 20857*). D. Detail of spore ornamentation by SEM (*Lado 20857*). E–H. European morphotype. E. Typical habit (KRAM M-1366). F. Spores (KRA-MYXO 730) by LM. G. Spore by SEM (KRAM M-1447). H. Detail of spore ornamentation by SEM (KRAM M-1366). Bars: A, E = 1 mm; B, C, F, G = 10 μm; D, H = 3 μm.

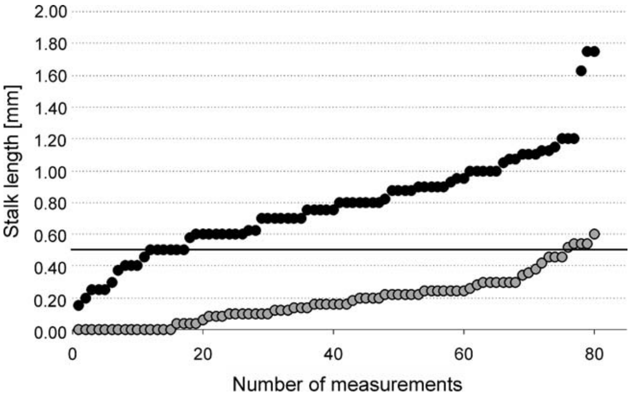

FIG. 10. Stalk length of *Lamproderma echinosporum*, black circle – South American specimens, grey circle – European specimens, horizontal line shows maximum stalk length for the species according to descriptions of European material (Neubert et al. 2000, Moreno et al. 2002).

ium has distinct brown patches and it is almost hyaline between the patches (FIG. 12A), while in other collections it is unevenly colored (FIG. 12B) or it is predominantly dark (FIG. 12C). The presence of the hyaline points of lines on the brown lower parts of peridum is shared by all specimens (FIG. 12). The spores of most of the collections are dark brown and minutely warted to almost smooth when observed by LM, but in two collections (*Lado 20753* and *Lado 20761*) they are slightly paler and the ornamentation is slightly higher when observed by SEM. The ornamentation is granulate to aculeate but not baculate (FIG. 11).

The brown capillitium with discontinuous pigmentation forming zebra-like pattern at extremities is characteristic for *Lamproderma maculatum*. This feature has never been mentioned in the literature, either in the original species description (Kowalski 1970) or when the type specimen was re-examined (Moreno et al. 2002). We checked specimens of *L.*

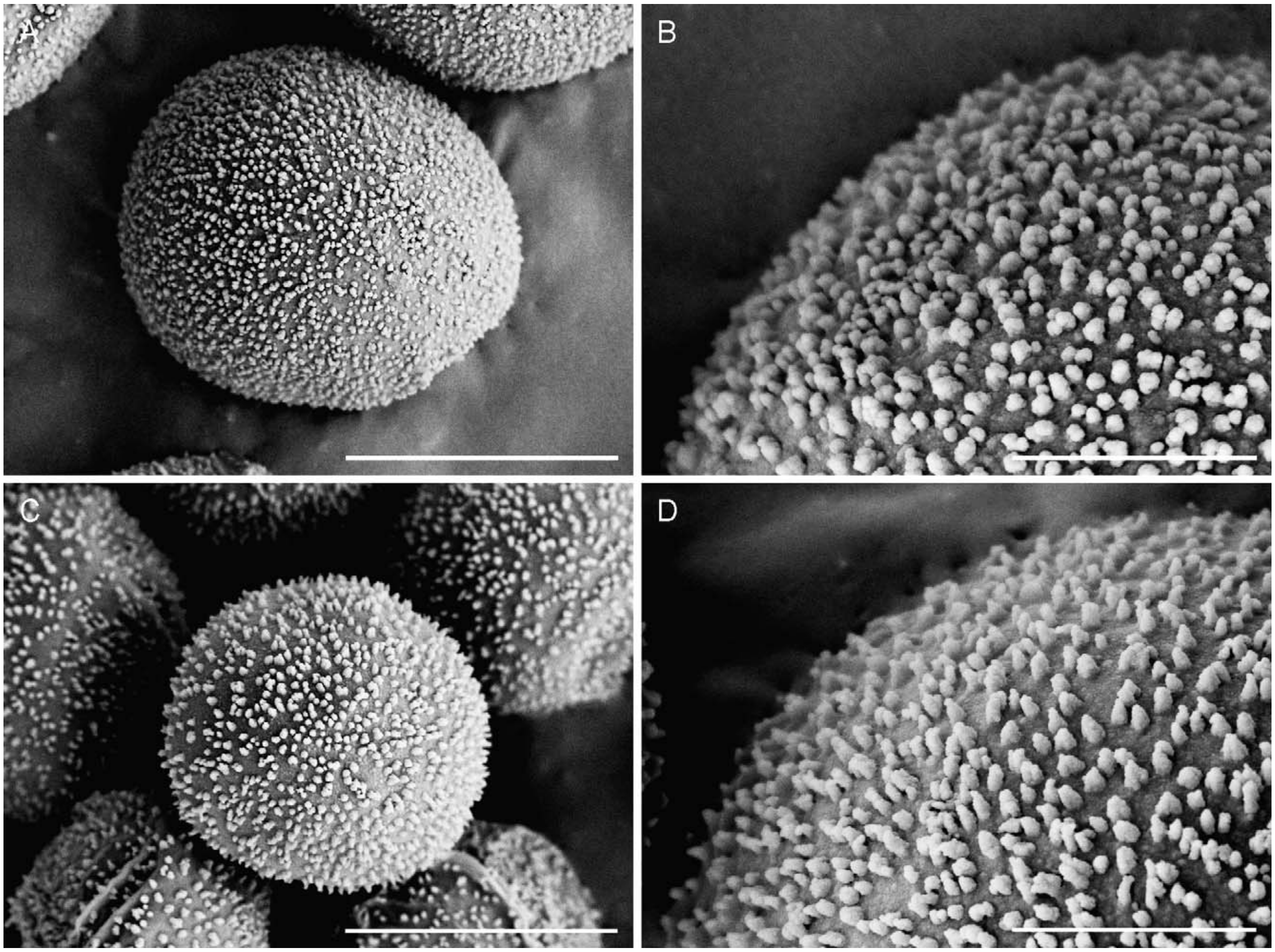

FIG. 11. Spore ornamentation by SEM of the South American specimens of *Lamproderma maculatum*. A. Spore (*Lado 20747*). B. Detail of spore ornamentation (*Lado 20747*), granulate according to Kirk et al. (2008). C. Spore (*Lado 20761*). D. Detail of spore ornamentation (*Lado 20702*), aculeate according to Kirk et al. (2008). Bars: A, C = 10 μm; B, D = 3 μm.

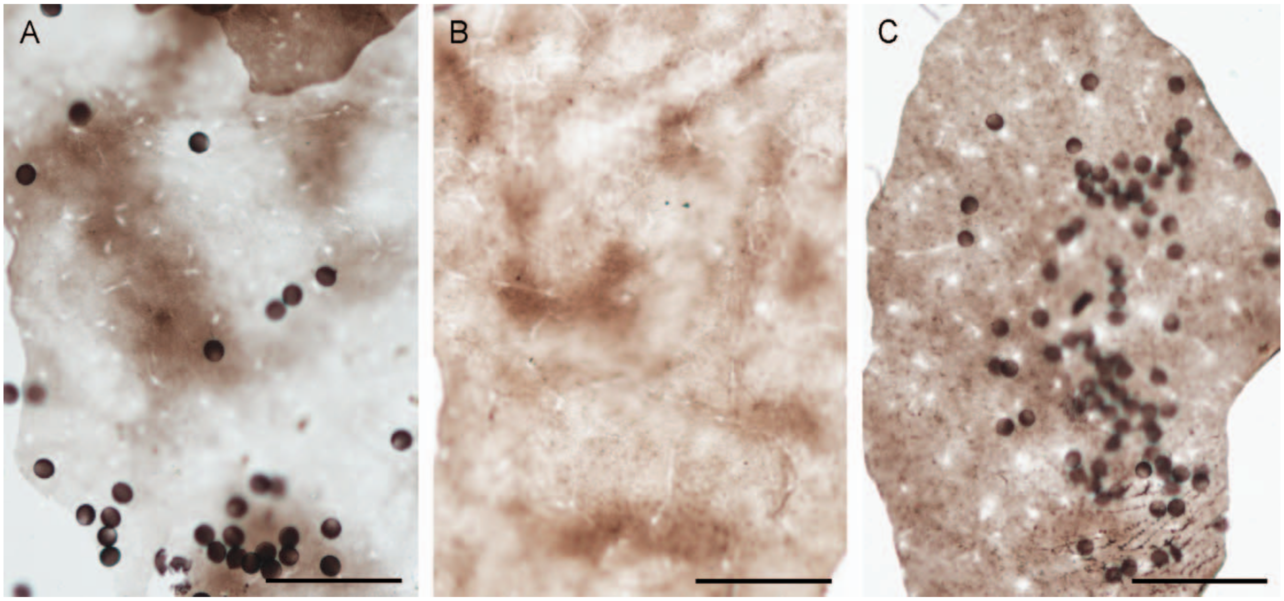

FIG. 12. Peridium coloration of the South American *Lamproderma maculatum* by LM. A. Typical with brown patches and with almost transparent fragments between the patches, as well as with small transparent dots and lines (*Lado 20747*). B. With darker brown patches and with pale brown fragments, also with small transparent dots and lines (*Lado 20846*). C. Entirely dark brown, without patches, but with small transparent dots and lines (*Lado 20761*). Bars = 100 μm.

maculatum from Europe and North America (see *Specimens examined*) and we found this character in all specimens, including the holotype. This capillitium character is shared by a few other *Lamproderma* species: *L. andinum*, *L. nordica* and *L. puncticulatum*.

Two varietes have been recognized in the species, var. *maculatum* and the var. *macrosporum* Mar. Mey. et Poulain (Bozonnet et al. 1995, Poulain et al. 2011). The first has longer stipes, smaller spores, 12–15 μm diam, and it usually has crystals on the peridium surface, while the variety *macrosporum* is subsessile, has larger spores, (15–)16–18(–21) μm diam, and has no crystals. According to the average spore size we can recognize two groups in the Andean material, one with an average varying 13.35–14.29 μm diam and the second with an average 15.37–16.89 μm diam, but this character is not correlated either with the stalk length or with the presence of crystals. All specimens with larger spores have crystals on the peridium surface. In addition, two Andean collections have spores covering the whole range for the two varietes. Therefore the Andean specimens seem to contradict the recognition of the two varietes.

Distribution in the SH: The species has been reported from Australia (Stephenson et al. 2007b, Stephenson and Shadwick 2009), and in South America. from the Nahuel Huapi National Park in Argentina (Wrigley de Basanta et al. 2010). The specimens from Chile (Lado et al. 2013) correspond with *L. andinum* as mentioned above.

Lamproderma ovoideum Meyl.

Specimens examined: Loc. ARG-06: near patches of melting snow, on twigs of *Lupinus* sp., *Lado 18475* (MA-Fungi 86978, duplicate in KRAM M-1533), *Lado 18476* (MA-Fungi 86979, duplicate in KRAM M-1534), *Lado 18477* (MA-Fungi 86980, duplicate in KRAM M-1535), *Lado 18481* (MA-Fungi 86981), *Lado 18482* (MA-Fungi 86982), *Lado 18483* (MA-Fungi 86983), *Lado 18484* (MA-Fungi 86984, duplicate in KRAM M-1537), *Lado 18485* (MA-Fungi 86985, duplicate in KRAM M-1538), *Lado 18487* (MA-Fungi 86986), *Lado 18486* (MA-Fungi 86987), *Lado 18489* (MA-Fungi 86988), *Lado 18490* (MA-Fungi 86989); on fruit of *Lupinus* sp. *Lado 18488* (MA-Fungi 86990, duplicate in KRAM M-1539). Loc. ARG-07-37: near patches of melting snow, on leaves and twigs of Asteraceae, *Lado 18642* (MA-Fungi 86991, duplicate in KRAM M-1540).

Comparison with descriptions of NH material: Europe, Asia, North America (Meylan 1932, Neubert et al. 2000, Moreno et al. 2002, Poulain et al. 2011, Lado et al. 2005, Poulain and Meyer 2005, Ronikier et al. 2008).

Comments: All the collections are characterized by ovoid sporocarps, stalked, with a dark brown peridium, with few reflections when observed in reflected light. The capillitium is rigid, originating from the whole columella length, dark brown, paler only at the extremities, and the spores are dark brown to very dark brown, paler at one side, densely warted, granulate (according to Kirk et al. 2008), minutely verrucate or minutely pilate (according to Rammeloo 1975) by SEM (FIG. 13A), and (12–)14–16.8(–20.8) μm diam, av. 15.46 diam (S = 410). All these

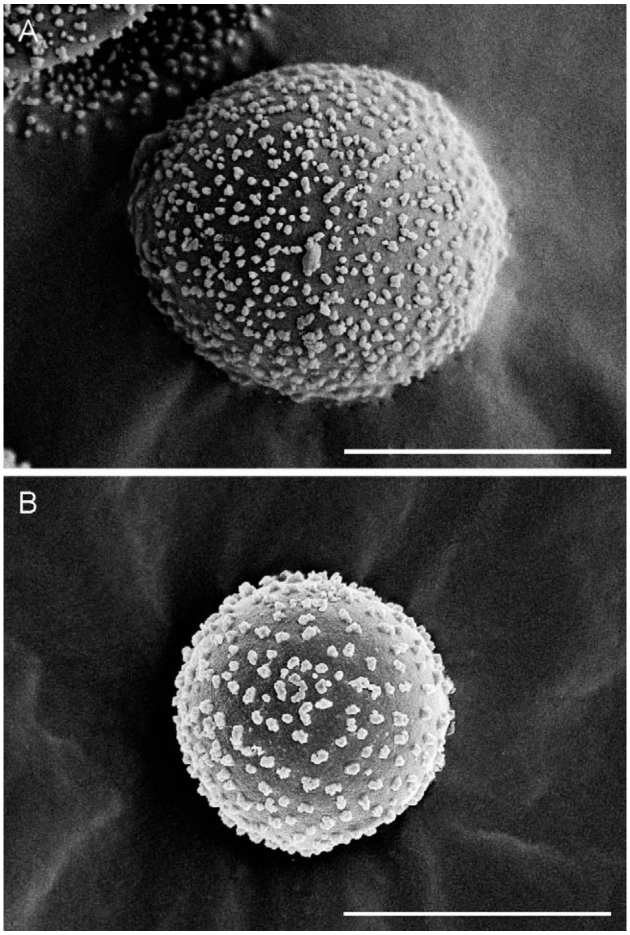

FIG. 13. Spores of *Lamproderma ovoideum* and *L. pulveratum* by SEM. A. Spore of *L. ovoideum* (*Lado 18642*). B. Spore of *L. pulveratum* (*Lado 20910a*). Bars = 10 μm.

characters agree with the description provided by Poulain et al. (2011).

Distribution in the SH: The species has been reported from Australia and New Zealand (Stephenson et al. 1992; Stephenson and Johnston 2003; Stephenson et al. 2007a, b; Stephenson and Shadwick 2009). This is the first record for South America.

Lamproderma pulveratum Mar. Mey. & Poulain

Specimens examined: Loc. ARG-09-63: near patches of melting snow, on bark of branch of *Nothofagus pumilio*, *Lado 20910a* (MA-Fungi 86992, duplicate in KRAM M-1593). POLAND: the Carpathians, the Gorce Mts., ridge between Gorc Mt. and the Przysłop Mt., S slopes, the glades Chyzniocka and Przysłop Dolny, meadow, 49°33′13″N, 20°13′19″E, 1080–1090 m, 18 Apr 2004, *leg. A. Ronikier, M. Ronikier*, on stems of *Rubus* sp., grass leaves and other plant remnants (KRAM M-1223, KRAM M-1224). FRANCE: Savoie, the Alps, Esserts-Blay, 45°37′16″N, 06°23′39″E, 1665 m, nivicole, on *Vaccinium myrtillus* shoots, *MM36571* (KRAM M-1315).

Comparison with descriptions of NH material: Europe, Asia (Bozonnet et al. 1991, Neubert et al. 2000, Poulain et al. 2011, Novozhilov et al. 2013).

Comments: The Andean specimens agree with the typical material from Europe (Bozonnet et al. 1991). Sporocarps are shortly stipitate, 1.35–1.55 mm (n = 3) total height, the stalk is 0.30–0.43 mm long, the sporotheca is slightly wider than high, 1.05–1.13 μm high, 1.13–1.25 μm wide, the peridium is rough, with blue-violet reflections and covered with small crystals, the capillitium is not dense, pale, with hyaline extremities when observed under reflected light, brown with paler extremities and with nodes filled with crystals, when observed with Nomarski interference contrast by LM. Spores are pale brown, (9.5–)10–12(–12.5) μm diam, av. 10.57 μm diam (S = 30), covered with robust warts, loosely arranged, punctate by SEM (FIG. 13B).

Distribution in the SH: This is the first report of *Lamproderma pulveratum* for the SH.

''*Meriderma* aff. *aggregatum* ad int.''

Specimens examined: Loc. ARG-09-63: near patches of melting snow, on branch of living *Berberis* sp., *Lado 20779* (MA-Fungi 86993). FRANCE: Savoie, the Alps, Massif de la Vanoise, Méribel-Mottaret, 45°22′03″N, 06°35′12″E, 1740 m, montane meadow, at the melting snow patch, on plant shoots, 29 Apr 2008, *leg. A. Ronikier, M. Ronikier*, KRAM M-1409. Savoie, the Alps, Massif de la Vanoise, Méribel, above le Raffort, 45°23′55″N, 06°33′34″E, 1480 m, shrubs (*Alnus, Salix*), at the melting snow patch, on *Alnus* shoots, 28 Apr 2008, *leg. A. Ronikier, M. Ronikier*, KRAM M-1378.

Comparison with descriptions of NH material: Europe (Poulain et al. 2011).

Comments: The one collection from the Argentinian Andes seems to correspond to an undescribed morphotype that is included under a provisional name ''*Meriderma aggregatum*'' (Poulain et al. 2011). The specimen from the Andes forms small groups of gregarious and sessile sporocarps, with sporothecae shortly cylindrical, 1.38–1.98 mm high and 0.88–1.25 mm wide (n = 8), with the columella about one-half sporotheca height. The capillitium is dark brown, dense, with funnel-shaped ends (FIG. 14A), a feature characteristic of the genus (FIG. 14D), and the spores are dark brown, paler on one side, with a small germ pore, 12.4–13.6(–14) μm in diam, av. 13.25 μm diam (S = 30), minutely warted, granulate-aculeate by SEM (FIG. 14B, C). The European ''*Meriderma aggregatum*'' differs in the conspicuously spinulose spores (FIG. 14E, F). Among species/morphotypes of *Meriderma* with warted spores Poulain et al. (2011) lists a collection (MM 1217) characterized by sessile sporothecae, but this specimen is keyed out in the group of globose to subglobose sporothecae, while the Andean specimen forms clearly elongate sporothecae, more than one and one-half times longer than wide.

Distribution in the SH: Not previously reported from the SH.

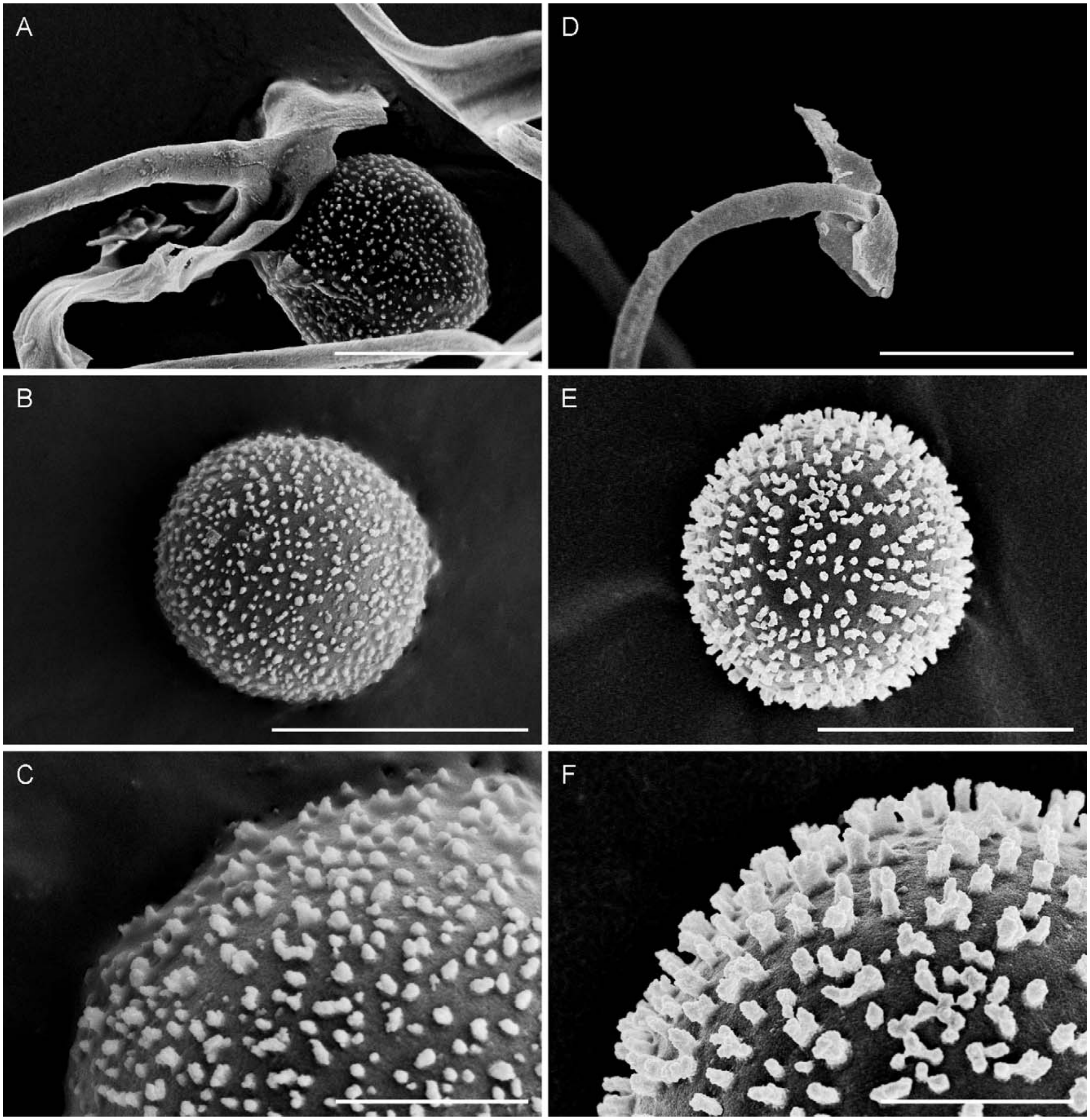

FIG. 14. Comparison of South American ''*Meriderma* aff. *aggregatum* ad. int.'' and European ''*Meriderma aggregatum* ad. int.'' by SEM. A–C. ''*Meriderma* aff. *aggregatum* ad. int.'' (*Lado 20779*). A. Funnel-shaped capillitial ends. B. Spore. C. Detail of spore ornamentation. D–F. ''*Meriderma aggregatum* ad. int.'' D. Funnel-shaped capillitial ends (KRAM M-1378). E. Spore (KRAM M-1409). F. Detail of spore ornamentation (KRAM M-1409). Bars: A, B, D, E = 10 μm; C, F = 3 μm.

Meriderma carestiae (Ces. & De Not.) Mar. Mey. & Poulain

Specimen examined: Loc. ARG-09-62: near patches of melting snow, branch of *Nothofagus* sp., *Lado 20678* (MA-Fungi 86994).

Comparison with descriptions of NH material: Europe, North America, Asia (Poulain et al. 2003, 2011).

Comments: The collection is characterized by stalked, broadly ovoid sporocarps with +/− conical base. The total height of the sporocarps is 1.83–2.25 mm (n = 6), and the stalk is short, 0.63–0.85 mm long, less than half the total height of the sporocarp. The spores are dark brown, paler at one side, (11.2–)12.8–15.2 μm in diam, av. 14.04 μm diam (S = 30), covered with spines of about 1 μm high, some free but others usually fused in a subreticulate pattern of branched ridges, without closed meshes. The morphotype from the Austral Andes agrees with the typical material from the NH (see Poulain et al. 2011).

Distribution in the SH: Not previously reported from the SH. There are a few records of *Lamrpoderma atrosporum* Meyl. from Australia and New Zealand (Mitchell 1992, Stephenson and Johnston 2003, Stephenson and Shadwick 2009) that may correspond to *M. carestiae.*

''***Meriderma spinulosporum*** ad int.''

Specimens examined: Loc. ARG-08-40: on branch of *Adesmia* sp., *Lado 19580* (MA-Fungi 86995). Loc. ARG-09-62: near patches of melting snow, on branch of *Nothofagus pumilio*, *Lado 20700a* (MA-Fungi 86996), *Lado 20720* (MA-Fungi 86997); on wood of *Nothofagus* sp., *Lado 20662* (MA-Fungi 86998). Loc. ARG-09-63: near patches of melting snow, on branch of *N. pumilio*, *Lado 20848* (MA-Fungi 86999), *Lado 20913* (MA-Fungi 87000), *Lado 20927* (MA-Fungi 87001), *Lado 20930a* (MA-Fungi 87002), *Lado 20934* (MA-Fungi 87003), *Lado 20935* (MA-Fungi 87004); on twigs and leaves of living *Berberis* sp., *Lado 20875b* (MA-Fungi 87005), *Lado 20892* (MA-Fungi 87006). FRANCE: Savoie, the Alps, Massif de la Vanoise, Méribel-Altiport, 45°24′10″N, 06°35′17″E, 1855 m, montane meadow, at the melting snow patch, on plant remnants, 27 Apr 2008, *leg. A. Ronikier, M. Ronikier*, KRAM M-1356.

Comparison with descriptions of NH material: Europe (Poulain et al. 2011).

Comments: All the Andean specimens are characterized by stalked sporocarps, (1.15–)1.43–2.53(–4.25) mm ($n = 76$) total height. The sporothecae are ovoid, with a rounded base, or obovoid, with a conical base, usually slightly higher than wide, (0.75–)0.88–1.50(–2.00) mm high, (0.75–)0.88–1.30(–1.63) mm wide, covered with a silvery peridium that is early fragmenting into small patches and persisting only at the sporotheca base. The stalk is long, usually one-third to one-half total sporocarp height, (0.25–)0.38–1.30(–2.25) mm long. The columella reaches about center of the sporotheca, and the capillitium is dark brown by LM, not smooth, usually covered with scattered nodes or spines, with funnel-shaped ends. The spores are very dark brown in mass, dark brown by LM, slightly paler on one side, (11.2–)12–13.6(–14.5) μm diam, av. 12.63 μm diam ($S = 290$), covered with irregularly distributed spinules, slightly irregularly baculate by SEM. The baculae are not cylindrical but irregularly enlarged at the apices and they sometimes are fused in short, sinuous ridges but not forming a subreticulate pattern (FIG. 15A, B). The Andean specimens seem to represent an undescribed morphotype of ''*Meriderma spinulosporum* ad. int.'' (Poulain et al. 2011), however, the baculae covering the spores seem to be more delicate, denser and have more connections than those in the European specimens (FIG. 15C, D).

Distribution in the SH: ''*Meriderma spinulosporum*'' had not been reported from the SH. It is possible that this morphotype was reported from Australia and New Zealand (Mitchell 1992, Stephenson and Johnston 2003, Stephenson and Shadwick 2009) under the name *Lamproderma atrosporum* Meyl.

DISCUSSION

Morphological variability of species.—The taxonomy of myxomycetes is based largely on morphological characters derived from their fruiting bodies (Martin and Alexopoulos 1969, Schnittler and Mitchell 2000, Clark and Haskins 2014), and an analysis of widely sampled collections from different geographical areas should be the basis for understanding the variability of species. Among the Andean representatives of the order Stemonitales we found (i) specimens that perfectly fit the current morphological species concept, (ii) specimens that have unique set of characters and could not be assigned to any described species and (iii) collections that fit known species concept but have slight to considerable deviations with respect to morphotypes known from Europe or the NH. The latter group was the most numerous and the Andean material in general was difficult to identify unequivocally.

Collaria nigricapillita is a good example of specimens displaying a morphological uniformity across its entire distribution range. The collections from the Austral Andes perfectly match the original description based on the material from the French Alps (Nannenga-Bremekamp 1989), as well as the characteristics of specimens from the mountains of Spain (Lado 1992) and the description of material from North America (Moreno et al. 2004). In a phylogenetic analysis of dark-spored myxomycetes (Fiore-Donno et al. 2008), specimens of *Collaria nigricapillitia* displayed two genotypes in SSU (rDNA) sequences, which correlated with a slight difference in one morphological character: color of sporotheca (dark brown vs. black). Because these results are based on a limited sampling (four specimens from one mountain range), it would be premature to suggest that the worldwide morphological uniformity has to be revised in a context of one morphological character. Until a more complex molecular analysis based on a larger sampling and more DNA regions is available, we suggest treating the slight morphological difference found in *C. nigricapillitia* as a possible intraspecific variability, because one character is not sufficient for recognition of a separate species (Schnittler and Mitchell 2000).

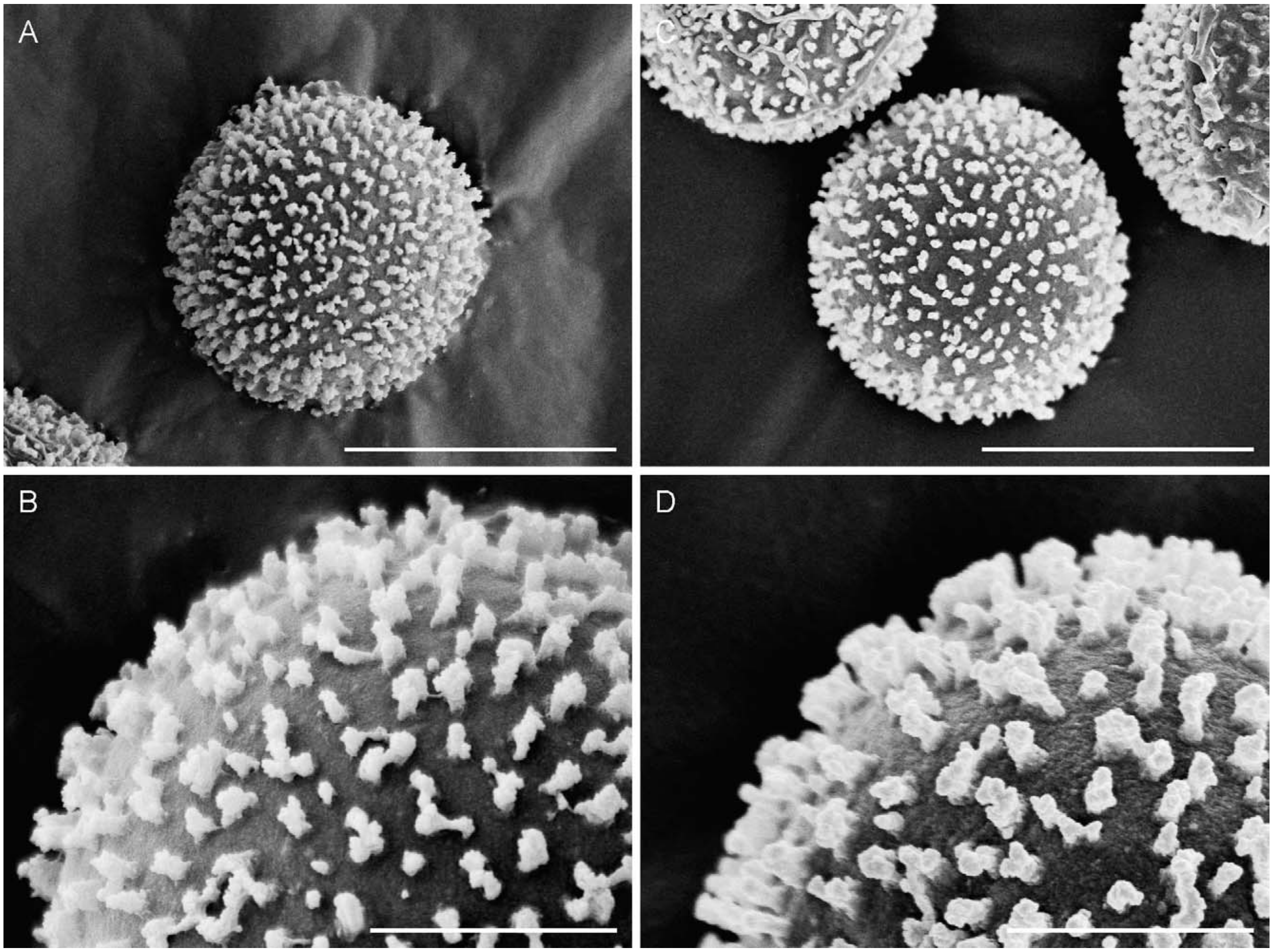

FIG. 15. Comparison of South American and European specimens of '*Meriderma spinulosporum*' by SEM. A. Spore of South American collection (*Lado 20720*). B. Detail of spore ornamentation (*Lado 20848*). C. Spore of European collection (KRAM M-1356). D. Detail of spore ornamentation (KRAM M-1356). Bars: A, C = 10 μm; B, D = 3 μm.

Among the nivicolous collections of Stemonitales from the Austral Andes that are different from any described species, *Lamproderma andinum,* proposed here as a new species, provides an excellent example. A total of nineteen morphologically coherent collections of this taxon were found in two separate seasons (eight from Argentina and 11 from Chile). It may be a SH species.

Finally, among those collections that have slight discrepancies in relation to morphotypes known from Europe or the NH, there are several examples. The collection of *Comatricha nigra* seems to be typical in all characters including general habit, but the Andean collection is characterized by larger spores. The collection of *Lamproderma aeneum* has a slightly longer stipe, while that of *L. pulveratum* has slightly darker capillitium than the NH specimens. Among the Andean collections of *L. maculatum* there are typical specimens with characteristic brown patches on the peridium and others having fewer visible patches. In addition, the spore sizes found in the Andean material of this species does not concur with the typical differences reported for the two recognized varietes of *L. maculatum* (Poulain et al. 2011). This observation is congruent with those based on material from another region of the SH, Australia (Stephenson et al. 2007b), where subsessile specimens (characteristic of the var. *macrosporum*) with a spore size of the var. *maculatum* were found. To further complicate this issue, two of the Andean collections have spores covering the whole range indicated for the two varietes. Taking into account the morphological variability of the material from the NH and the SH, it thus can be concluded that the recognition of two varietes is not justified.

The Andean specimens of *Lamproderma echinosporum*, with longer stalks and spores covered with longer spines, deviates considerably from the current concept of this species. However, morphological variability found in the material from Argentina

TABLE II. Comparison of the total number of identified collections of Stemonitales (S) versus the total number of collections (All) from various massifs of the northern (NH) and southern (SH) hemispheres

	Massif	All	S	%
NH	Gorce Mts., the Carpathians, Europe (Ronikier et al. 2008)	148	68	46
	Gredos Mts., Europe (Lado et al. 2005)	100	49	49
	Pyrenees, Europe (Lado and Ronikier 2008, 2009)	277	123	44
	Caucasus, Europe (Novozhilov et al. 2013)	397	168	42
	Sierra Nevada, Europe (Moreno et al. 2003)	168	69	41
SH	Austral Andes, South America (this paper)	790[a]	120[a]	15
	Snowy Mts. and Victorian Alps, Australia (Stephenson and Shadwick 2009)	295	51	17
	Sounhern Alps, New Zealand (Stephenson and Johnston 2003)	157	16	10

[a] These values correspond with all collections found, identified at least at order level.

overlaps that found in the European collections. We did not identify any clear morphological segregation between the South American and European specimens, thus recognition of a new taxon would not be justified. We consider a better option to enlarge the species concept of *L. echinosporum* so that it includes long stalked sporocarps and spores with spines up to 2 μm high (baculae by SEM).

Great morphological variability similar to that found in nivicolous Stemonitales from South America also has been discovered in non-nivicolous myxomycetes, such as *Badhamia melanospora* Speg. (Aguilar et al. 2014). The Chilean and Argentinian populations of *B. melanospora* slightly differ from the North American and European populations in spore diameter and ornamentation, but remaining morphological characters overlap in the two geographic groups. Lado et al. (2013) also found some morphological discrepancies in specimens of another common non-nivicolous myxomycete, *Didymium squamulosum* (Alb. and Schwein.) Fr. from central Chile, albeit too small to recognize the Chilean specimens among new species. Schnittler (2001) and Schnittler and Stephenson (2002) found deviating morphotype of *Arcyria cinerea* Fr. from Central America occurring on a specific substrate (inflorescence of tropical herbs).

Morphologically deviating populations are usually interpreted as ecotypes or morphologically distinct biotypes present in specific habitats or confined to particular regions (Schnittler 2001, Stephenson 2011, Lado et al. 2013). Morphological variability found in the South American collections may reflect the primary steps of speciation ongoing in the geographically isolated Andean populations and thus the presence of incipient morphological differentiation. On the other hand, the few cases of morphological uniformity across the distribution range suggest the effective long-distance dispersal, ensuring gene flow and counteracting the consequences of isolation. Further detailed morphological studies of material from various regions of the world are needed to better understand morphological limits of recognized morphospecies. Incorporation of DNA-based phylogenetic and population-genetic methods to the wide-scale morphological analysis of specimens from distant geographical areas should be a further step in unraveling gene flow, speciation and recognition of potential new cryptic species, for which morphological characters do not provide clear evidence.

Biogeography and frequency.—Nivicolous myxomycetes form a well defined ecological group of slime molds, linked to mountainous areas of the world, such as the Alps, Pyrenees, Carpathians, Caucasus, Rocky Mountains, New Zealand Alps or Himalaya, where they take advantage of the melting snow that accumulated during several months of the year. These particular ecological requirements result in highly fragmented geographical ranges, which makes this group an excellent model to study disjunct distributed microorganisms and their variability patterns.

Within the Myxotropic project (www.myxotropic.org) a total of 37 localities in the Argentinian Andes have been surveyed for nivicolous myxomycetes (C. Lado and A. Ronikier unpubl), but representatives of the Stemonitales appeared in only 12 of them. All collections of this order recorded and identified, at least, to order (120) constitute only 15% of all specimens found in these localities (TABLE II). This figure is similar to the values obtained from other regions of the SH such us Australia (17%) and New Zealand (10%) but significantly lower than proportions based on data from Europe (41–49%).

The total number of myxomycete collections found at each Andean nivicolous locality differs considerably (1–213). Also the number of Stemonitales collections was 0–57, but even at the locality most abundant in Stemonitales (ARG-09-63) the percentage of this group in the total number of collections (27%) is much lower than in the NH mountains. Also when counting the collections from only these localities where at least one collection of Stemonitales has been

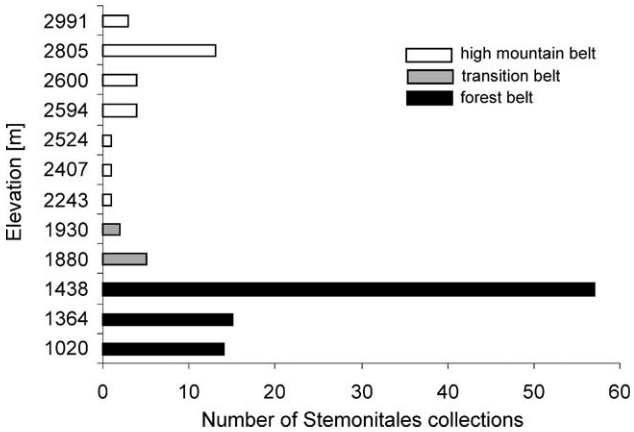

FIG. 16. Altitudinal distribution of the Stemonitales collections in the study area.

recorded (twelve localities with a total of 606 collections), the number of Stemonitales collections (120) is low and constitutes only 20% of all records.

It is probably premature to conclude that representatives of the order Stemonitales are much less abundant in the SH than in the NH, because our analysis is inherently based on limited data available so far. However, a significantly supported difference in the myxomycete assemblages has been demonstrated and this emerging tendency should be tested in further studies. Extending such investigations also to the North American mountains would be of prime importance as they are little studied. As no comprehensive regional lists of nivicolous myxomycetes are available from the Americas, it is not known whether differences in frequency of Stemonitales in the nivicolous myxomycete assemblages is a pattern differentiating the Hemispheres or the higher contribution of Stemonitales is specific for Europe.

Considerable differences in the number of Stemonitales collections among the Andean study sites may be explained by the availabilty of suitable substrates. Most Andean Stemonitales were collected either from *Nothofagus pumilio* forests or among shrubs of *Nothofagus* sp. and some sporophores were found on living twigs and branches of shrubs and trees (*Berberis* sp., *Nothofagus* spp., *Ribes* sp.) released from the snow. Most of the localities devoid of Stemonitales were characterized by other types of vegetation, like grassland or cryophilous vegetation, where shrubs were absent or had very reduced dimensions. The possible preference of Stemonitales to occur on shrubby and woody substrata is also reflected in the altitudinal distribution of the collections. Nivicolous localities were surveyed at elevations of the forest belt (regular canopy *Nothofagus pumilio* forest), the subalpine belt (shrubby and ''krummholz'' forms of *N. pumilio*) and the high mountain belt. Among all the localities with a presence of Stemonitales, three were located at the lowest elevations occupied by forest, two in the transition zone with shrub and ''krummholz'' forms of *Nothofagus* sp., and seven in the high mountain belt. Despite the prevalence of higher localities, quantitatively the Stemonitales dominated in the forest belt (86 collections, 72%) (FIG. 16). This picture matches previous observations on the altitudinal occurrence of *Physarum andinum* (Ronikier and Lado 2013) and demonstrates that, as previously postulated by Ronikier and Ronikier (2009) for other areas, also in the Andes nivicolous myxomycetes are not centered in the high-mountain (alpine) zone.

The sampling effort in the areas of nivicolous myxomycetes is very unevenly distributed. Some regions have been disregarded or surveyed for a short time only, and mostly without repeated observations at the same localities. This heterogeneity in data availability hampers discussion on the distribution patterns of nivicolous species. There is no regional (continental) uniformity of species frequency. *Lamproderma ovoideum* is the most common representative of nivicolous Stemonitales in the Polish and Spanish mountains, and also in the mountains of S-E Australia (Moreno et al. 2003, Lado et al. 2005, Ronikier et al. 2008, Lado and Ronikier 2009, Stephenson and Shadwick 2009). In turn, in another Spanish mountain range, *L. maculatum* is the most common (Sánchez et al. 2007), while *L. pulveratum* is the most common in the Caucasus in Russia (Novozhilov et al. 2013) and *L. splendens* – in the New Zealand Alps (Stephenson and Johnston 2003). In the Andean collections *L. echinosporum* was the most frequent. It is not known what factors could influence the regional species frequency. It may be either the constant characteristics of geographical situation (region/locality) or a set of microclimatic conditions present during the time of the year of collection or these two factors together. Apart from the previously mentioned significant difference in frequency of the Stemonitales at a macroscale, no clear frequency and diversity patterns can thus be addressed until more complex, long-term studies are undertaken in all key regions worldwide.

Phenology of nivicolous myxomycetes.—Nivicolous myxomycetes essentially require a long persisting snow cover period to ensure suitable conditions for sporophore development. They appear at the margins of snow patches and in places where the snow cover has just disappeared (Ronikier and Ronikier 2009), usually in spring or the beginning of summer when temperature and humidity of the substrates are the most suitable. Strictly nivicolous taxa are recognized, which form sporophores exclusively during the thawing period of snow cover. Several other species are not strictly nivicolous and may be found both near snow banks and also later during the season. Interestingly, there are reports of late occurrence of strictly nivicolous myxomycetes. *Trichia alpina* was incidentally found a few times to occur in autumn (October) in the European mountains (Meylan 1929, Ronikier et al. 2008), but more examples of the occurrence of strictly nivicolous myxomycetes in late summer or autumn (without the presence of snow cover), were recorded in the SH. Among the Stemonitales, Stephenson et al. (2009) reported a strictly nivicolous *Lamproderma retirugisporum* G. Moreno, H. Singer, Illana & A. Sánchez collected in May (austral autumn) from New Zealand. Stephenson et al. (2007a) found *Lamproderma ovoideum* in March (austral summer and beginning of autumn) in the subantarctic Macquarie Island. In the Austral Andes, Wrigley de Basanta et al. (2010) collected *L. echinosporum* and *L. maculatum* during mid austral summer (end of January), and Lado et al. (2013) reported *Collaria nigricapillitia* in autumn (end of March). The recently described *Perichaena megaspora* (Ronikier et al. 2013) was also collected during the austral summer (Feb–Mar), but at higher elevations (2257–3479 m), so at nivicolous or potentially nivicolous localities. This species, in turn, was successfully cultured at room temperature which suggests it may not be strictly nivicolous, or may be more tolerant to a range of environmental parameters.

The occurrence of nivicolus species in the absence of melting snow does not necessarily mean that the species are not strictly nivicolous, since nivicolous myxomycetes may also be found when the snow has disappeared and their sporophores can persist for some time after thawing until damaging factors appear. Therefore, a combination of several characters of a given locality has to be taken into account apart from the presence of snow: (i) elevation, (ii) latitude, (iii) collection time, (iv) local pluvial conditions (rain being among the main factors that can damage fructifications during or after formation). Lower elevated sites at lower latitude have to be surveyed for nivicolous species earlier, in spring, while at higher elevated places or those localised at higher latitude snow cover remains even until end of the summer.

Among the 37 localities surveyed for nivicolous myxomycetes in the Austral Andes, at many of them the presence of melting snow was not noted, but signs of a previous cover of snow were evident. In 2009 lower-elevation localities (1364–1930 m) were visited in November (austral spring) and snow patches were noticed at all of them. Similarly, in 2006 one locality (1020 m) with the presence of melting snow was studied in December. In 2007 and 2008 higher elevated areas (1965–3524 m) were surveyed in February and March (austral summer) and snow patches were still recorded at 2407 and 2805 m. Therefore we consider all 37 surveyed localities nivicolous although at most of them snow was not recorded during time of collection and although some of them were visited during austral summer (beginning of March).

The commonest explanation for the occurrence of some nivicolous species in the summer and autumn, supported by the fresh look of collected sporophores, is that they may not be obligate nivicolous (Stephenson et al. 2007a, Wrigley de Basanta et al. 2010, Ronikier et al. 2013). However, there is a striking regional discrepancy in such late records. Only one strictly nivicolous myxomycete, *Trichia alpina*, was recorded twice in autumn in the best explored area (Europe), while several (12) nivicolous species were found later in the season during sporadic observations in various regions of the much more poorely explored SH. This suggests that there are some specific climatic factors in the SH localities that allow the fructifications to be found in summer and autumn. Such factors could include: (i) conditions which allow persistence of sporophores for a long time after formation, or (ii) conditions interplay which allows development of nivicolous myxomycetes without the presence of melting snow layer [e.g. with low temperature and high substrate humidity as suggested by Wrigley de Basanta et al. (2010)], and thus some species that are strictly nivicolous in Europe may have a different development potential in the SH. The first explanation may be supported by observations of Lado et al. (2013) on *Lepidoderma chailletii* that was a little damaged when it was collected in the austral autumn. In turn, the second explanation may be supported by observation of Stephenson et al. (1992), who collected *Lamproderma ovoideum* during the austral spring, on a coast of the Macquarie Island (Subantarctic region), a place that would perhaps never or rarely be expected to receive direct snow deposition and only that from wind-blown drift. Irrespective of specific ecological explanations, it seems that the presence of nivicolous myxomycetes fructifications in non-nivicolous timespan (summer and autumn) is a phenomenon observed almost exclusively on the SH and thus differentiating myxomycete assemblages from this area.

Conclusions.—The present paper is the first attempt of a detailed analysis of morphological variability, occurrence frequency and phenology of widely distributed species of nivicolous myxomycetes characterised by disjunct distribution. Our study demonstrated that taxonomic concepts and delimitations mostly elaborated using the material from Europe often do not allow an efficient circumscription of taxa when material from another areas is incorporated. High intraspecific variability found in most species studied suggests isolation and independent evolutionary processes among remote populations. On the other hand, the uniform morphology of a few species indicates that long-distance dispersal is also an effective, although not as universal as usually assumed, mechanism of spread in some nivicolous myxomycetes. Biogeographical differentiation can be observed not only in the morphology but also in the species assemblages and also, presumably, influence of climatic differences on the sporophore persistence of nivicolous myxomycetes and their dependence on melting snow.

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