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ORIGINAL RESEARCH PAPER

Meriderma species (Myxomycetes) from the Polish Carpathians: a taxonomic revision using SEM-visualized spore ornamentation

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Abstract

Meriderma represents a recently described genus of nivicolous myxomycetes with high morphological variability. Due to many complications in its taxonomy and species recognition in the past, the group was considered a morphologically variable complex. Recent clarifications and recognition of morphological boundaries into species and morphotypes has fostered a classification revision of specimens found in the Carpathians. Material used in this study was systematically collected in the Polish part of the Carpathians from 2004 to 2009. As a result of micro- and macroscopic observations of 54 collections, we recorded nine taxa of *Meriderma*. Seven of these (all but *M. carestiae* and *M. cribrarioides*) are the first records for Poland and for the Carpathians overall. Our observations based on analysis of spore ornamentation by SEM are in accordance with recently proposed classification and confirm segregation of taxa based on spore ornamentation pattern.

Keywords

Mycetozoa; *Meriderma*; the Carpathians; taxonomy; morphological variability; SEM

Introduction

The genus *Meriderma* Mar. Mey & Poulain is a relatively new taxon described by Poulain et al. [1] that accommodate species of *Lamproderma* characterized by evanescent peridium and funnel-shaped capillitium ends. Initially, one species, *Lamproderma atrosporum* Meyl. described by Meylan in 1910 [2] belonged to the group. Later, Meylan [3] distinguished a few varieties and forms of *Lamproderma atrosporum* Meyl. and described *L. fuscatum* Meyl. as a separate species differing from black *L. atrosporum* by ferruginous brown sporocarps. American myxomycetologist Donald T. Kowalski [4] recognized *L. cribrarioides* as a species with evanescent peridium, closely related to *Lamproderma atrosporum*, but differing by featuring completely reticulate spores ornamentation. However, his interpretation was not supported by European researchers, who interpreted *L. cribrarioides* as a taxon with persistent peridium. On the other hand, Kowalski [4] misinterpreted *L. fuscatum* and considered it as a species with persistent peridium (see Ronikier et al. [5]). Due to high variability of general habit, spore size and ornamentation pattern observed already by Meylan [2,3], Neubert et al. [6] recognized *L. atrosporum* to be a species complex and this view was followed by other researchers (e.g., [7]).

Taxonomic revision of the type collection of *Stemonitis carestiae* [8], published in 2003, revealed that it also belongs to the group of *Lamproderma* species that feature an evanescent peridium. Thus the name *Lamproderma carestiae* became an older synonym of *L. atrosporum*. The typical collection of *Stemonitis cribrarioides* also turned out to be a *Lamprodema* from *atrosporum* group [7], in accordance with Kowalski's [4] interpretation of *Lamproderma cribrarioides*. Thus, after 2003 the names *Lamproderma carestiae* and *L. cribrarioides* has been used for morphotypes of *L. atrosprum*

with subreticulate and reticulate spores, respectively. Additionally, in 2003, Martìn et al. [9], suggested that *Lamproderma atrosporum* with spore ornamentation of complete reticulum (= *Lamproderma cribrarioides*), represent a separate, genetically distinct taxon from other *L. atrosporum* specimens. Simultaneously, in 2002 Poulain et al. [10] proposed a new generic name *Meriderma* (from greek: *meris* – a morsel, fragment; *derma* – skin), for the whole *L. atrosporum* complex, and was later (2011) officially confirmed by Poulain et al. [1]. The key to species of *Meriderma* written by Poulain et al. [1] shed a new light on the taxonomy and diversity of species and morphotypes belonging to this genus. Namely, there are four valid species currently assigned in this genus: *Meriderma fuscatum* (= *L. fuscatum*), *M. echinulatum* (= *L. atrosporum* var. *echinulatum*), *M. carestiae* (= *L. carestiae*), *M. cribrarioides* (= *L. cribrarioides*) [11] and four temporarily delimited morphotypes at species rank (*Meriderma atrofuscatum*, *M. verrucosporum*, *M. aggregatum*, and *M. spinulosporum*) [1].

Recent molecular analysis, based on 18S SSU rRNA sequences, confirmed that *Meriderma* represents a separate clade clearly divergent from *Lamproderma* group [12].

From ecological point of view, *Meriderma* is a strictly nivicolous myxomycete genus [1–3,6,10], forming sporocarps during relatively short periods of time (late spring and early summer) at the margins of melting snow patches [13]. Sporocarps can be found on almost all accessible organic substrates [6]. They have been recorded at many mountain ranges from around the world [6,14] (as *L. carestiae*, *L. cribrarioides*, *L. fuscatum*), but only a few records have been noted from the Carpathians [15–19].

This study represents the analysis of *Meriderma* diversity in the Polish part of the Carpathians. Description and illustration of macro- and micromorphological characteristics, including scanning electron microscopy (SEM) images of spores showing every morphotype are provided as part of this research. At the same time, because of complicated taxonomic interpretations and nomenclatural changes made by different authors, detailed descriptions for each species and morphotypes are also presented.

Material and methods

The Carpathians are relatively a low but vast central European mountain range (the highest peak 2655 m). The northernmost part of this mountain range, studied within a framework of the present project, is situated in southern Poland and includes the Tatra Mts (the highest Carpathian massif) and several lower mountain massifs to the north of the Tatra Mts. The material for this study was collected in lower elevational belts (montane zone) of several Carpathian massifs (Fig. 1) from 2004 to 2009, in spring (April to June), in forests and also in open areas such as glades and meadows (Tab. 1).

Included in the examined material there are specimens from the Gorce Mts reported previously by Ronikier et al. [18] as being *Lamproderma carestiae* and *L. cribrarioides*. Due to recent changes in taxonomy of this group these collections required revision. In order to include all Carpathian collections we have previously collected, the material from the Gorce Mts was re-examined. All specimens have been identified using the key by Poulain et al. [1].

Material collected in the field was put into carton boxes and air-dried for further examination in the laboratory. Observations and measurements of morphological characters were conducted under a stereoscopic microscope Nikon SMZ 1500. The total height of the sporocarps, the height and the width of the sporothecae and length of the stalk of most mature individuals were measured, usually up to 10 sporocarps per collection. Collections and permanent slides of examined specimens are deposited at KRAM. Analysis of microscopic characters and all microscopic measurements were performed on permanent preparations fixed in Hoyer's medium and observed under a light microscope (LM) Nikon Eclipse E-600, with Nomarski interference contrast, equipped with a digital Nikon DSFi1 camera head for photography. Measurements were made under the oil immersion ×100 objective. For each collection 30 spores

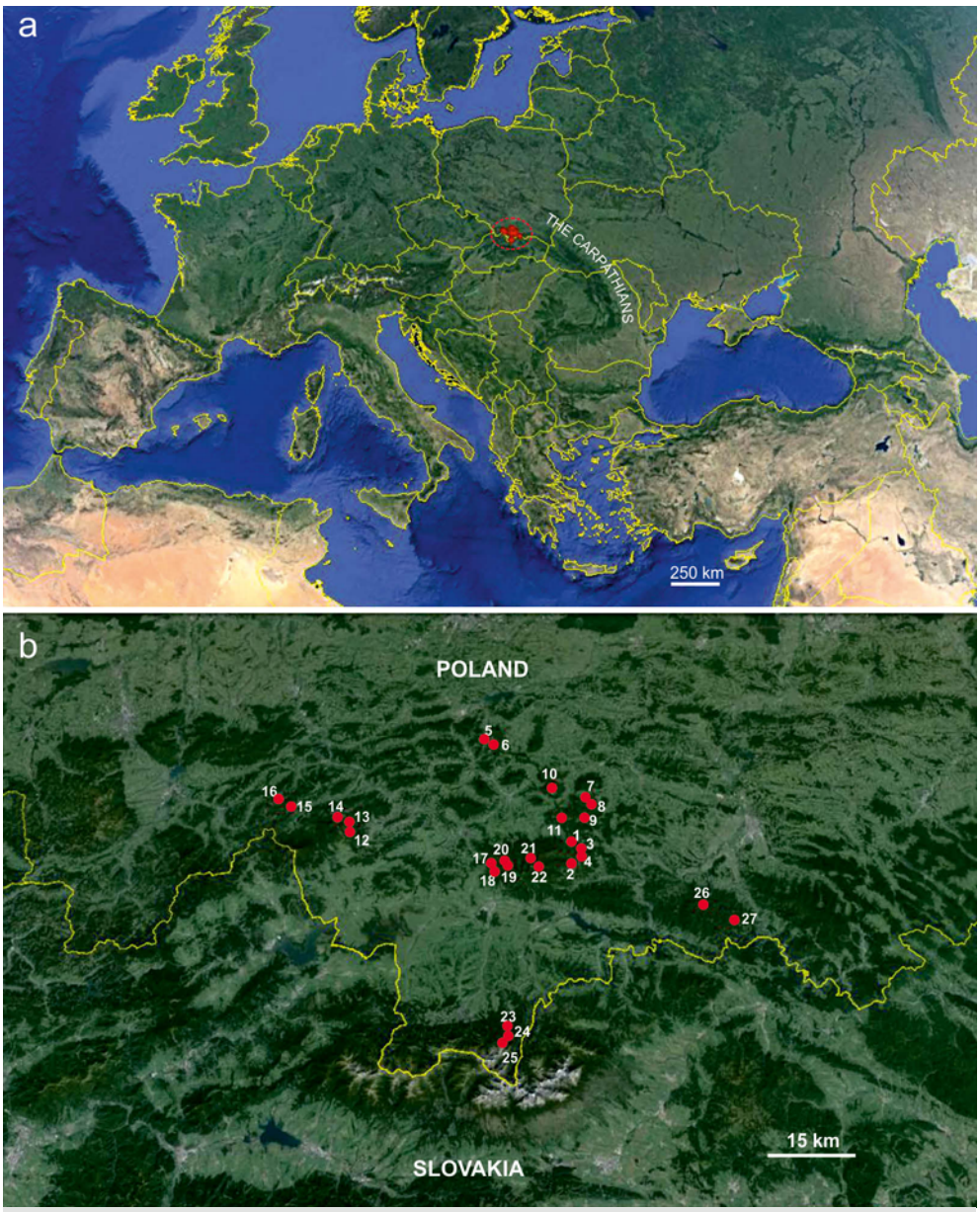

Fig. 1 Study area and localities of collection sites. **a** Location of study area within main massif of the Carpathians. **b** Sampling sites of specimens of *Meriderma*; numbers of localities refer to those from Tab. 1 and are cited for each species/morphotypes.

were measured. The reported spore sizes include spore ornamentation. Values noted in less than 1% of all measurements are given in parentheses. The scanning electron microscopy (SEM) observations were carried out with a Hitachi S-4700 microscope, using 10 kV voltage and working distance of about 12 mm. The material was prepared in a sequence of acetone dilutions (50–100%) followed by the critical point drying procedure and coating with gold. SEM studies were made in the Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis, at the Institute of Geological Sciences of the Jagiellonian University, Cracow. Spore ornamentation by SEM is given according to terminology of Rammeloo [20,21] with some modifications.

Results

In this study a total of 54 collections yielded nine taxa of *Meriderma* (two species, two varieties, and five forms). One species, *Meriderma fuscatum* is new for Poland. Other species or morphotypes are also reported here for the first time in Poland under

Tab. 1 List of localities of studied collections.

No.	Locality, habitat, date of collection, collectors	Coordinates	Elevation (m)
1	The Gorce Mts; upper part of the valley of Głębieniec River, E slope of N-NNW ridge running from Gorc Mt, about 200 m N from the glade Polana Świnkówka; steep slope in beech forest; 18 April 2004; leg. AR, MR	20°14′24″ E 49°34′32″ N	1060
2	The Gorce Mts; the ridge between the Gorc Mt and the Przysłop Mt, the glade on S slopes (the Chyżniocka glade), W from Skałka and the glade Polana Przysłop Dolny; a glade; 18 April 2004; leg. AR, MR	20°13′19″ E 49°33′13″ N	1080–1090
3	The Gorce Mts; N-W part of the glade hala Gorc Kamienicki (N ridge of the Gorc Mt); a glade; 18 April 2004; leg. AR, MR	20°14′56″ E 49°34′17″ N	1130–1150
4	The Gorce Mts; S part of the glade hala Gorc Kamienicki (N ridge of the Gorc Mt); a glade; 18 April 2004; leg. AR, MR	20°15′07″ E 49°34′03″ N	1150
5	The Beskidy Zachodnie Mts; Lubomir and Łysina massif, ridge between Kudłacze mountain hostel and summit of Łysina Mt; mixed forest; 24 April 2005; leg. AR, MR	20°02′45″ E 49°46′48″ N	850–980
6	The Beskidy Zachodnie Mts; ridge between Lubomir Mt and Łysina Mt; mixed forest; 24 April 2005; leg. AR, MR	20°03′20″ E 49°46′30″ N	870
7	The Beskid Wyspowy Mts; N ridge of Mogielica Mt, towards Chyszówki pass; beech forest with spruce; 17 April 2005; leg. AR, MR	20°16′40″ E 49°39′42″ N	990–1030
8	The Beskid Wyspowy Mts; N ridge of Mogielica Mt, towards Chyszówki pass; meadow; 17 April 2005; leg. AR, MR	20°16′40″ E 49°39′16″ N	1080
9	The Beskid Wyspowy Mts; Mogielica Mt, summit area; 17 April 2005; leg. AR, MR	20°16′44″ E 49°39′12″ N	1165
10	The Beskid Wyspowy Mts; Ćwilin massif, vicinity of Jurków town; 8 April 2006; leg. AR, MR	20°11′26″ E 49°41′17″ N	1000
11	The Beskid Wyspowy Mts; vicinity of Półrzeczki village (S from Jurków), Kobylica Mt, summit area, S-W slopes; meadows; 9 April 2006; leg. AR, MR	20°12′18″ E 49°38′05″ N	900
12	The Beskid Żywiecki Mts; range of Polica, above the village Sidzina Wielka Polana, the Dolina Zakulawki (Psia Dolina) valley, S-W slopes of the Okrąglica Mt; along the black tourist trail; 23 April 2006; leg. AR, MR	19°39′32″ E 49°36′44″ N	950
13	The Beskid Żywiecki Mts; range of Polica, above the village Sidzina Wielka Polana, the Dolina Zakulawki (Psia Dolina) valley, S-W slopes of the Okrąglica Mt; 23 April 2006; leg. AR, MR	19°39′19″ E 49°37′12″ N	1050
14	The Beskid Żywiecki Mts; range of Polica, above the village Sidzina Wielka Polana, Hala Kucałowa meadow, on the ridge between Okrąglica Mt and Polica Mt, exposed to S-E; 24 April 2006; leg. AR, MR	19°38′37″ E 49°37′35″ N	1150
15	The Beskid Sądecki Mts; range of Jałowiec, E ridge of the Jałowiec Mt, towards Zawoja-Wełcza; shrubs in mixed forest with *Sorbus*; 2 May 2006; leg. AR, MR	19°30′16″ E 49°39′23″ N	850
16	The Beskid Żywiecki Mts; range of Jałowiec, the Jałowiec Mt, the Hala Trzebińska meadow, S-SW slopes; meadow; 2 May 2006; leg. AR, MR	19°28′39″ E 49°39′37″ N	1100
17	The Gorce Mts; the Turbacz range, ridge of the Średni Wierch Mt, above the village Obidowa, below the glade Polana Stusy; degraded beech forest with spruce; 13 May 2006; leg. AR, MR	20°02′32″ E 49°32′52″ N	880
18	The Gorce Mts; the Turbacz range, ridge of the Średni Wierch Mt, above the village Obidowa, surroundings of the glade Polana Stusy; on *Vaccinium myrtillus* stems; 13 May 2006; leg. AR, MR	20°02′40″ E 49°32′48″ N	950
19	The Gorce Mts; the Turbacz range, ridge of the Średni Wierch Mt, above the village Obidowa, sourroundings of the glade Polana Tynowe; stems of *Rubus* sp.; 13 May 2006; leg. AR, MR	20°03′19″ E 49°32′49″ N	1020

Tab. 1 Continued

No.	Locality, habitat, date of collection, collectors	Coordinates	Elevation (m)
20	The Gorce Mts; the Turbacz range, ridge of the Średni Wierch Mt, above the village Obidowa, small glades close to the Średni Wierch Mt; 13 May 2006; leg. AR, MR	20°03′19″ E 49°32′49″ N	1090
21	The Gorce Mts; the Turbacz range, the Rozdziele Mt, at the red tourist trail; edge of spruce forest; 13 May 2006; leg. AR, MR	20°05′52″ E 49°32′57″ N	1190
22	The Gorce Mts; top area of the Turbacz Mt; spruce forest (upper montane belt); 13 May 2006; leg. AR, MR	20°06′41″ E 49°32′34″ N	1310
23	The Tatra Mts, High Tatra Mts; mouth of a gully descending from Koszysta Mt to the Waksmundzka Polana; spruce forest; 1 June 2008; leg. AR, MR	20°03′31″ E 49°15′17″ N	1430
24	The Tatra Mts, High Tatra Mts; gully descending from Koszysta Mt to the Waksmundzka Polana; scrub of *Salix silesiaca*; 1 June 2008; leg. AR, MR	20°03′28″ E 49°15′03″ N	1630
25	The Tatra Mts, High Tatra Mts; upper part of a gully descending from Koszysta Mt to the Waksmundzka Polana; grass near the fence; 1 June 2008; leg. AR, MR	20°03′28″ E 49°14′56″ N	1780
26	The Beskid Sądecki Mts; the Radziejowa range, Mała Prehyba Mt; edge of a spruce forest, at the road, at snow patch; 3 May 2009; leg. AR, MR	20°33′32″ E 49°27′48″ N	1156
27	The Beskid Sądecki Mts; the Radziejowa range, summit of the Radziejowa Mt; edge of a spruce forest, at snow patch; 3 May 2009; leg. AR, MR	20°36′15″ E 49°26′58″ N	1264

Collector initials: AR – Anna Ronikier; MR – Michał Ronikier.

currently used names. They were previously identified as *Lamproderma carestiae* or *L. cribrarioides* (currently *Meriderma carestiae* and *M. cribrarioides*, respectively). Thus all but *M. carestiae* and *M. cribrarioides* are the first records for Poland and for the Carpathians overall. The list below contains all taxa (species, varieties, and forms) that could be distinguished using the key by Poulain et al. [1].

Meriderma carestiae (Ces. & de Not.) Mar. Mey. & Poulain var. *carestiae*

Material studied. Loc. 14, on stems of *Rubus* sp., Ron353 KRAM M-1640. Loc. 24, on small twigs, Ron635 KRAM M-1641.

Description. Sporocarps mostly gregarious, stalked (Fig. 2a), (1.26–)1.30–1.98(–2.06) mm total height. Sporotheca black, ovoid to broadly ovoid, with conical to obtuse base, occasionally globose to subglobose, 0.96–1.12(–1.18) mm high, 0.70–0.94(–1.20) mm wide. Stalk (0.26–)0.34–0.82(–0.88) mm long, broadened at the base, black, shining. Peridium evanescent with small pieces remaining attached to the tips of the capillitium, usually persistent at the base of the sporocyst, with silvery and golden reflections. Columella reaching the center of the sporotheca. Capillitium dense, uniformly dark brown by LM, originating from the whole length of the columella, threads mostly smooth, with funnel-shaped ends and occasionally with some irregularities. Hypothallus discoid, sometimes common for a group of sporocarps, ferruginous brown to dark brown. Spores black in mass, moderately to dark brown by LM, paler on one side, 10–13 µm in diameter, subreticulate (covered with incomplete reticulum composed of fused spines), reticulate with perforated muri under SEM (Fig. 2b,c).

Meriderma carestiae var. *retisporum* f. *retisporum* ad int.

Material studied. Loc. 1, on stems of *Rubus* sp., Ron155 KRAM M-1230 (as *Lamproderma carestiae* [18]). Loc. 2, on stems of *Rubus* sp., Ron178 KRAM M-1228 (as

Lamproderma carestiae [18]). Loc. 4, on stems of *Rubus* sp., Ron163b KRAM M-1216b (as *Lamproderma carestiae* [18]); on stems of *Rubus* sp., Ron166b KRAM M-1247b (as *Lamproderma carestiae* [18]). Loc. 19, on stems of *Rubus* sp., Ron401 KRAM M-1235 (as *Lamproderma carestiae* [18]). Loc. 22, on stems of *Rubus* sp., Ron433b KRAM M-1267b (as *Lamproderma carestiae* [18]).

Description. Differing from the typical variety by almost completely reticulate spores forming almost closed meshed reticulum; meshes small, ornamentation mostly 0.5 µm up to 1 µm high (Fig. 2d,e).

Meriderma carestiae var. *retisporum* f. *macrosporum* ad int.

Material studied. Loc. 3, on stems of *Rubus* sp., Ron160 KRAM M-1269 (as *Lamproderma carestiae* [18]).

Description. Differing from the typical form by larger spore size, 15–18 µm (Fig. 2 f,g).

Meriderma cribrarioides (Fr.) Mar. Mey. & Poulain

Material studied. Loc. 18, on *Vaccinium myrtillus* stems, Ron391 KRAM M-1214 (as *Lamproderma carestiae* [18]). Loc. 26, on *Vaccinium myrtillus* stems, Ron662b KRAM M-1642; on *Vaccinium myrtillus* stems, Ron668 KRAM M-1643.

Description. Sporocarps gregarious, sometimes scattered, stalked (Fig. 3a), (0.60–)1.00–1.34(–1.44) mm total height. Sporotheca black, mostly globose to subglobose, occasionally broadly ovoid or pyriform, with umbilicate base(0.64–)0.90–1.04 mm high, (0.60–)0.80–1.00(–1.10) mm wide. Stalk rather short, (0.14–)0.20–0.44(–0.46) mm long, black, slightly shining. Peridium evanescent with small pieces remaining attached to the tips of the capillitium, usually persistent at the base of the

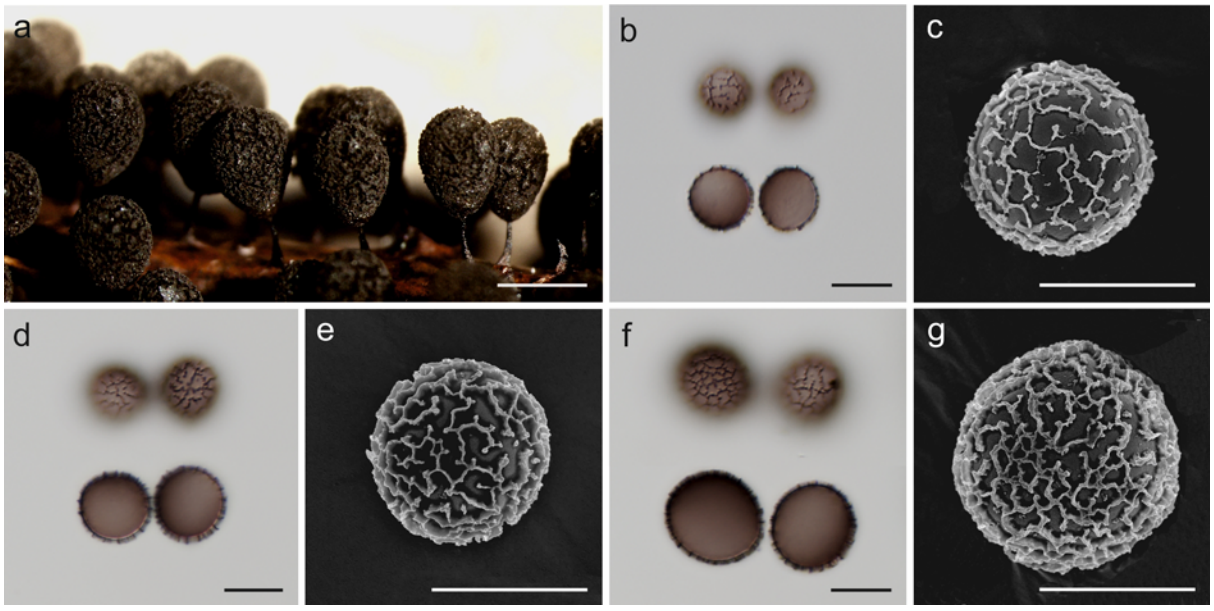

Fig. 2 Morphological features of *Meriderma carestiae*. **a** Sporocarps of *Meriderma carestiae* var. *retisporum* (Ron178). **b** Spores of *M. carestiae* var. *carestiae* (Ron353) observed in light microscope. **c** Spore ornamentation of *M. carestiae* var. *carestiae* (Ron353) visualized by SEM. **d** Spores of *M. carestiae* var. *retisporum* f. *retisporum* (Ron401). **e** Spore ornamentation of *M. carestiae* var. *retisporum* f. *retisporum* (Ron401) under SEM. **f** Spore of *M. carestiae* var. *retisporum* f. *macrosporum* (Ron160). **g** Spore ornamentation of *M. carestiae* var. *retisporum* f. *macrosporum* (Ron160) under SEM. Bars: **a** 1 mm; **b–g** 10 µm.

sporocyst, with silvery and golden reflections Columella reaching the center of the sporotheca. Capillitium uniformly dark brown by LM, originating from the whole length of the columella, threads mostly smooth, with funnel-shaped ends and occasionally with some irregularities. Hypothallus discoid, sometimes common for a group of sporocarps, brown to very dark brown. Spores black in mass, moderately to dark brown by LM, paler on one side, (11–)12–17(–18) µm in diameter, with complete, large-meshed reticulum, ornamentation about 1–2 µm high, reticulate with non-perforated and perforated muri under SEM (Fig. 3b,c).

Meriderma echinulatum (Meyl.) Mar. Mey. & Poulain var. *echinulatum*

Material studied. Loc. 4, on stems of *Rubus* sp., Ron174 KRAM M-1218 (as *Lamproderma carestiae* [18]); Ron175 KRAM M-1248 (as *Lamproderma carestiae* [18]). Loc. 5, on leaves of *Rubus* sp., Ron267 KRAM M-1644. Loc. 6, on small twigs, Ron272b KRAM M-1645. Loc. 7, on leaves of *Rubus* sp., Ron244 KRAM M-1646. Loc. 8, on stems of *Rubus* sp., Ron252a KRAM M-1647. Loc. 9, on *Vaccinium myrtillus* stems, Ron256 KRAM M-1648; on stems of *Rubus* sp., Ron 257a KRAM M-1649. Loc. 10, on stems of *Rubus* sp., Ron298a KRAM M-1650. Loc. 11, on grasses, Ron304 KRAM M-1651; on plant remnants and mosses, Ron310 KRAM M-1652. Loc. 12, on stems of *Rubus* sp., Ron318 KRAM M-1653. Loc. 16, on plant remnants and *Vaccinium* sp. shoots, Ron362b KRAM M-1654; on plant remnants and *Vaccinium* sp. shoots, Ron364 KRAM M-1655. Loc. 18, on plant remnants, Ron390 KRAM M-1238 (as *Lamproderma carestiae* [18]). Loc. 20, on stems of *Rubus* sp., Ronikier 411a KRAM M-1241 (as *Lamproderma carestiae* [18]). Loc. 23, on *Vaccinium myrtillus* stems Ron621 KRAM M-1656.

Description. Sporocarps aggregated, in compacted groups, sessile or very short-stalked (Fig. 4a), 0.84–1.32(–1.50) mm total height. Sporotheca black, mostly obovoid, sometimes oblong, with obtuse to flattened base, 0.80–1.40 mm high, (0.68–)0.76–0.90(–1.36) mm wide. Stalk, if present, (0.06–)0.08–0.22 mm long, black. Peridium evanescent with small pieces remaining attached to the tips of the capillitium, mostly silvery, sometimes with golden reflections. Columella reaching the center of the

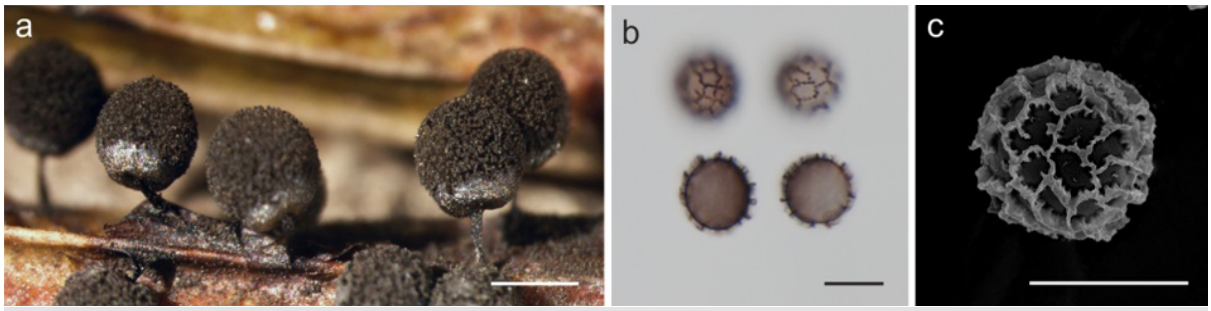

Fig. 3 Morphological features of *Meriderma cribrarioides*. **a** Sporocarps (Ron668). **b** Spores in light microscope. **c** Spore ornamentation by SEM. Bars: **a** 1 mm; **b,c** 10 µm.

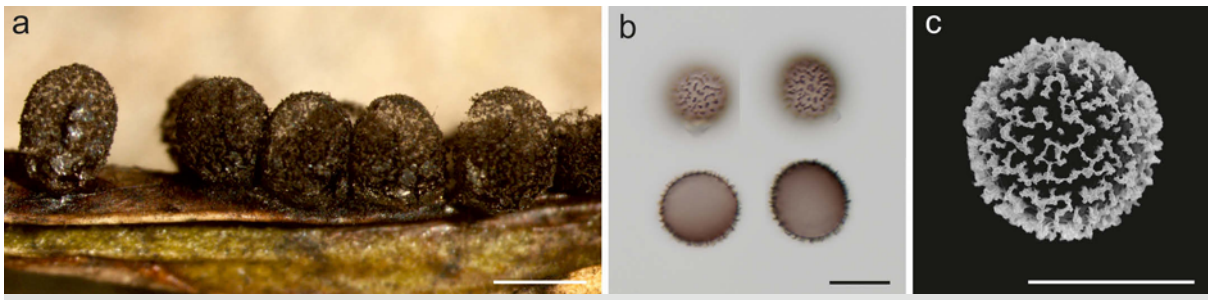

Fig. 4 Morphological features of *Meriderma echinulatum*. **a** Sporocarps (Ron256). **b** Spores in light microscope (Ron411). **c** Spore ornamentation by SEM (Ron257a). Bars: **a** 1 mm; **b,c** 10 µm.

sporotheca. Capillitium uniformly dark brown by LM, originating from the whole length of columella, threads mostly smooth sometimes widened at axils, with characteristic funnel-shaped ends and occasionally with some irregularities. Hypothallus usually common for a group of sporocarps, sometimes discoid, brown to very dark brown. Spores black in mass, dark brown by LM, paler on one side, 11–14(–15) µm in diameter, conspicuously echinulate (covered by long spines), spines usually connected by ridges and forming sinuous rows, sometimes even incomplete net, but never reticulate, simple subreticulate, cristate subreticulate and baculate under SEM (Fig. 4b,c).

Meriderma fuscatum (Meyl.) Mar. Mey. & Poulain

Material studied. Loc. 15, on stems of *Rubus* sp., Ron378a KRAM M-1657.

Description. Sporocarps gregarious, stalked (Fig. 5a), 1.32–1.50 mm total height. Sporotheca ferruginous brown, broadly ovoid, sometimes globose or subglobose with broadly conical to obtuse base, 0.92–1.10 mm high, 0.72–0.96 mm wide. Stalk 0.36–0.40 mm long, black, shining. Peridium evanescent with small pieces remaining attached to the tips of the capillitium, mostly with golden and silvery reflections. Columella reaching the center of the sporotheca. Capillitium ferrugineous brown by LM, with thin and paler ends, threads mostly smooth, with characteristic, but not numerous funnel-shaped ends and occasionally with some irregularities and nodules. Hypothallus discoid, brown, shining. Spores ferruginous-brown in mass, pale brown by LM, paler on one side, 9–10(–11) µm in diameter, irregularly warted, baculate (baculae short) under SEM (Fig. 5b,c).

Meriderma spinulosporum ad int. f. *spinulosporum*

Material studied. Loc. 6, on bark of fallen twigs, Ron272a KRAM M-1658. Loc. 7, on stems and leaves of *Rubus* sp., Ron235a KRAM M-1659. Loc. 9, on stems of *Rubus* sp., Ron255a KRAM M-1660; on small twigs, Ron257b KRAM M-1661. Loc. 12, on stems of *Rubus* sp., Ron316 KRAM M-1662; on stems and leaves of *Rubus* sp., Ron317 KRAM M-1663. Loc. 13, on stems of *Rubus* sp. and *Vaccinium myrtillus*, Ron322 KRAM M-1664; on *Vaccinium myrtillus* stems, Ron323 KRAM M-1665. Loc. 16, on plant remnants and *Vaccinium* shoots, Ron363 KRAM M-1666; on *Vaccinium myrtillus* stems, Ron365 KRAM M-1667; on *Vaccinium myrtillus* stems Ron367 KRAM M-1668. Loc. 17, on stems and leaves of *Rubus* sp., Ron386 KRAM M-1242 (as *Lamproderma carestiae* [18]). Loc. 19, on *Vaccinium myrtillus* stems, Ron400 KRAM M-1234 (as *Lamproderma carestiae* [18]). Loc. 20, on stems of *Rubus* sp., Ron411b KRAM M-1241 (as *Lamproderma carestiae* [18]). Loc. 25, on *Vaccinium myrtillus* stems, Ron642 KRAM M-1669.

Description. Sporocarps mainly gregarious, sometimes more or less scattered, occasionally grouped, stalked (Fig. 6a), (1.06–)1.34–2.20(–2.52) mm total height.

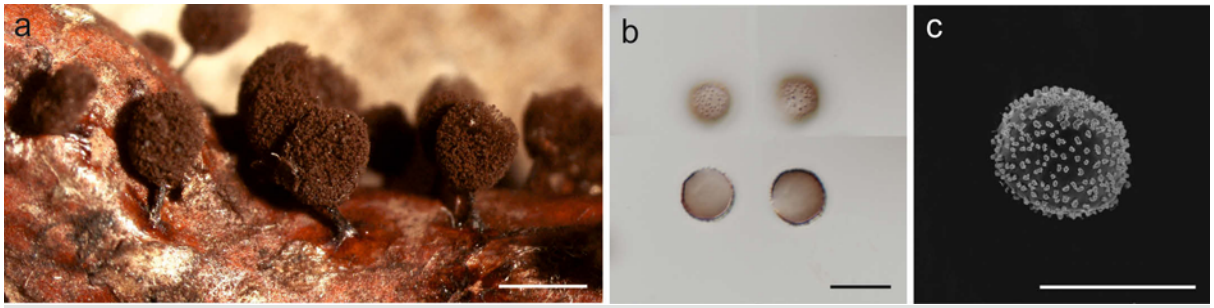

Fig. 5 Morphological features of *Meriderma fuscatum* (Ron378a). **a** Sporocarps. **b** Spores in light microscope. **c** Spore ornamentation by SEM. Bars: **a** 1 mm; **b,c** 10 µm.

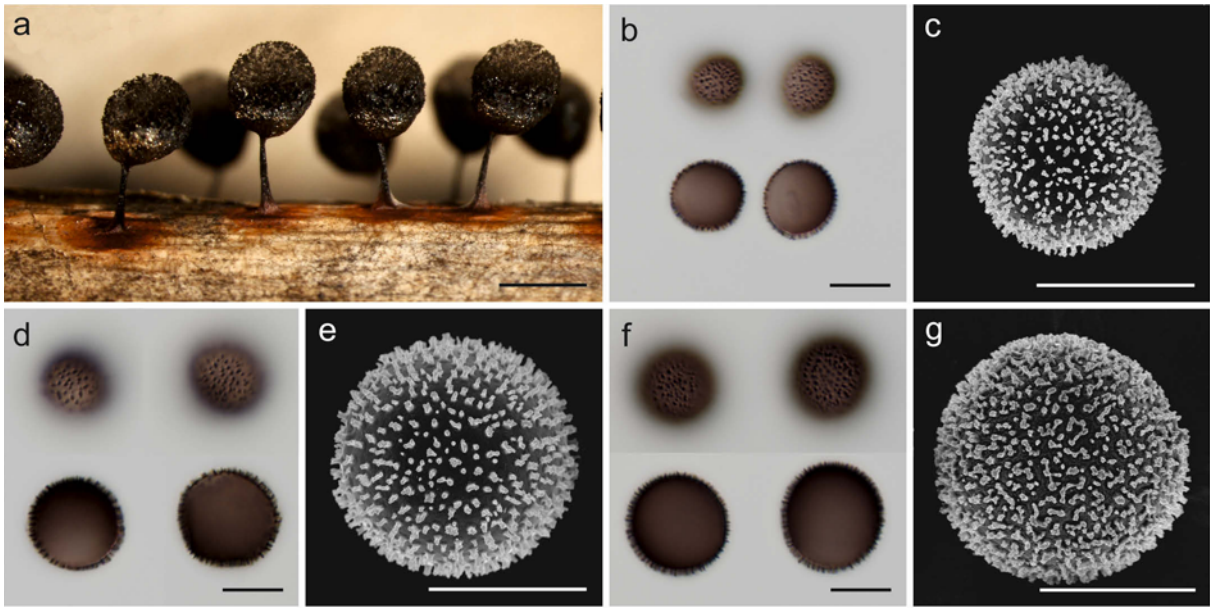

Fig. 6 Morphological features of *Meriderma spinulosporum*. **a** Sporocarps (Ron316). **b** Spores of *M. spinulosporum* f. *spinulosporum* (Ron257b) in light microscope. **c** Spore ornamentation by SEM (Ron316). **d** Spore of *M. spinulosporum* f. *intermedium* (Ron680). **e** *Meriderma spinulosporum* f. *intermedium* by SEM (Ron680). **f** *Meriderma spinulosporum* f. *gigasporum* (Ron177). **g** *Meriderma spinulosporum* f. *gigasporum* (Ron177) by SEM. Bars: **a** 1 mm; **b–g** 10 µm.

Sporotheca black, usually obovoid, broadly ovoid, occasionally subglobose, with conical or rounded base (0.66–)0.80–1.40 mm high and (0.60–)0.74–1.20(–1.24) mm wide. Stalk (0.30–)0.40–1.00(–1.12) mm long, usually broadened at the base, black, shining. Peridium evanescent with small pieces remaining attached to the tips of the capillitium, usually persistent at the base of the sporotheca, with silvery and golden reflections. Columella reaching the center of sporocyst, sometimes expanded at apex. Capillitium uniformly dark fuscous brown, originating from the whole length of the columella, threads mostly smooth, occasionally with some irregularities and nodular thickenings, with characteristic funnel-shaped ends. Hypothallus discoid, sometimes common for a group of sporocarps, usually ferruginous brown or pinkish brown, occasionally dark brown. Spores black in mass, dark brown by LM, paler on one side, 11–14 µm in diameter, spinulose, spines more or less irregularly distributed, occasionally fusing into very short, sinuous rows, baculate under SEM (Fig. 6b,c).

Meriderma spinulosporum f. *intermedium* ad int.

Material studied. Loc. 2, on stems of *Rubus* sp., Ron176 KRAM M-1226 (as *Lamproderma carestiae* [18]). Loc. 8, on stems and leaves of *Rubus* sp., Ron251a KRAM M-1670. Loc. 14, on stems of *Rubus* sp., Ron336 KRAM M-1671. Loc. 16, on plant remnants and *Vaccinium* shoots, Ron362a KRAM M-1672. Loc. 21, on *Vaccinium myrtillus* stems, Ron418 KRAM M-1232 (as *Lamproderma carestiae* [18]). Loc. 26, on *Vaccinium myrtillus* stems, Ron662a KRAM M-1673; on *Vaccinium myrtillus* stems, Ron671 KRAM M-1674. Loc. 27, on *Vaccinium myrtillus* stems, Ron680 KRAM M-1675.

Description. Differing from the typical form by more conspicuously spinulose ornamentation and larger spores (13.5–)14–17 µm in diam (Fig. 6d,e).

Meriderma spinulosporum f. *gigasporum* ad int.

Material studied. Loc. 2, on stems of *Rubus* sp., Ron177 KRAM M-1227 (as *Lamproderma carestiae* [18]).

Description. Differing from the typical form by much larger spore size, 18–21 μm in diam (Fig. 6f,g).

Discussion

The genus *Meriderma* is one of the most significant nivicolous myxomycetes, because all species occur during snowmelt, and secondly because they are very common at such sites. However, because the taxonomic clarification in the species complex of *Lamproderma atrosporum* was proposed very recently [1,7], all older records of *Lamproderma atrosporum*, *L. carestiae*, and *L. cribrarioides* available in the literature need to be revised. Here we provide a re-examination of collections reported by Ronikier et al. [18] from the Gorce Mts. Additionally, the new records from other Carpathian massifs resulted in recognition of nine taxa (including varieties and forms).

Currently, the species delimitation of *Meriderma* is based on a morphological species concept. Characteristics such as general habit (stipitate vs. sessile sporocarps) and spore features (color, ornamentation pattern, size) are key characters in species delimitation. Poulain et al. [1] provide the key to identification of all recognized morphotypes with short descriptions, color images of sporocarps and drawings of spore ornamentation. Our studies based on specimens collected in the area of the Carpathians are in agreement with segregation of morphotypes proposed by these authors. Application of SEM images provide a highly precise and detailed characterization of spore ornamentation, which undoubtedly increase proper species determination. Thus, we provide results of observations of spore ornamentation under scanning electron microscope that supplement spore description given by Poulain et al. [1]. Among species with warted spores we found that *M. fuscatum* (Fig. 5) spore ornamentation under SEM can be described as composed of irregularly distributed, isolated, cylindrical short baculae (Fig. 5c), according to the terminology of Rammeloo [20]. *Meriderma fuscatum* is the only species in the genus forming ferruginous-brown sporophores (Fig. 5a), as described by Poulain et al., Meylan, Moreno et al. [1,3,22] and thus it is easy to distinguish from other morphotypes. All other species are black [1]. Among them there are two sessile or subsessile forms: *M. echinulatum* (Fig. 4a) and *M. aggregatum*, the latter not yet found in the study area. The two species are easily distinguished from one another by spore ornamentation: of spines (baculae under SEM) isolated or fused into very short ridges composed of a few spines in the case of *M. aggregatum* [1], for SEM image of spore see Ronikier and Lado [23], and covered by dense labyrinth of fused spines (forming complex cristate subreticulate with some isolated baculae type of ornamentation) in the case of *M. echinulatum* (Fig. 4b,c). All remaining species are stipitate, with short or long stalk, and macroscopically very similar to one another. *Meriderma spinulosporum* has spiny spores and spines (baculae) are isolated or fused into very short rows composed of a few spines (Fig. 6b–g; as in the case of a sessile *M. aggregatum*), *M. carestiae* has subreticulate spores (or reticulate with small meshes, in the case of var. *retisporum*), ornamentation is usually up to 1 μm high (Fig. 2b–g), and *M. cribrarioides* has spores covered with complete reticulum of larger meshes (reticulate with non-perforated and perforated muri under SEM), which often exceed 1 μm and sometimes even reach 2 μm height (Fig. 3b,c).

Macroscopic distinction between sessile morphotypes (*M. echinulatum* and *M. aggregatum*) and stalked ones (*M. spinulosporum*, *M. carestiae*, and *M. cribrarioides*) is quite obvious, whereas segregation within group of stiptate specimens appeared to be problematic. Although spore ornamentation is the most reliable characteristic to distinguish morphotypes, we found that shape of sporotheca can be another macroscopic feature (apart from stalk length) helpful in species identification. In the Carpathian specimens *Meriderma carestiae* has mostly broadly ovoid sporothecae with conical base (Fig. 2a) whereas sporothecae of *M. cribrarioides* is globose to subglobose, only occasionally broadly ovoid and with umbilicate base (Fig. 3a). *Meriderma spinulosporum* has obovoid sporothecae with conical or rounded base. Poulain et al. [1] do not describe differences in sporotheca shape for stalked morphotypes, so this character has to be verified based on observations on specimens from other areas.

Apart from *M. aggregatum*, we have not found in the Polish Carpathians *M. verrucosporum* and *M. atrofuscatum*. They are stipitate and have spores covered with warts [1].

Poulain et al. [1] recognize forms of four species according to spore dimensions. Among the Carpathian collections, we found a considerable variability of spore size in *M. spinulosporum* (Fig. 6b–g) so that three forms recognized by Poulain et al. [1] could be quite clearly distinguished based on this characteristic. On the other hand, the Carpathian specimens of *M. cribrarioides* have larger spores (up to 18 μm) than provided by these authors [1] for that species. Two from the three identified specimens have spore diameter fully overlapping with those indicated by Poulain [1]. Only one specimen has spore size exceeding indicated ranges, nevertheless one collection is not sufficient to distinguish a new form.

Worldwide distribution of *Meriderma* species is not yet fully known. As a whole, the genus is cosmopolitan and present in the many studied areas; about 553 records could be found for *Meriderma* at GBIF webpage [24], but many of them are still registered under the former name (*Lamproderma atrosporum*). All so far recognized *Meriderma* species are present mainly in Europe, the Alps [1,14]. Six of them have recently been reported from the Caucasus [13] and five from the Khibiny Mountains [25]. Three species, *M. aggregatum*, *M. carestiae*, and *M. spinulosporum* are known from the Andes in South America [23], however, the first and the last slightly deviating in spore ornamentation. *Meriderma carestiae* and *M. fuscatum* are also known from Japan and the first, additionally from the USA [1]. *Meriderma cribrarioides* was also reported from the North American mountains, as *L. cribrarioides* by Kowalski [4], who correctly interpreted this species (see explanation in the "Introduction"). Other species and morphotypes currently recognized in *Meriderma* are certainly present in many mountain massifs from which *L. atrosporum* s. l. was reported.

Nivicolous myxomycetes are widely known from their high morphological plasticity, which is often reflected in minor differences between morphotypes. This constantly challenges accurate determination of species, and during last years have led to increased number of newly described taxa [26]. Moreover, there are still some doubts, which of morphological characters could be used for reliable distinction between different species. *Meriderma* genus is an example of taxonomically difficult group of species with high morphological diversity, reflected mainly in the continuum of spore size and ornamentation pattern, the latter character was considered as one of the most important traits. Research of Fiore-Donno et al. [12], supported this idea, indicating that delimitation of *M. carestiae*, *M. cribrarioides*, and *M. aggregatum* seems to correlate with phylogenetic analysis based on the SSU sequences. As well established, molecular analysis provides a promising methodology to clarify as well as verify taxonomic positions of many genera and species [12,13]. This combinational approach could successfully resolve taxonomic problems and properly indicate inter- and intraspecific variability within this group.

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