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First records of bryophilous myxomycetes in the lowlands of Ukraine reveal an undescribed species of *Lamproderma*

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Bryophilous myxomycetes are found mainly in humid mountainous regions, particularly in the Ukrainian Carpathians. Over the last three seasons, three species from this group (*Colloderma oculatum*, *Diderma tigrinum*, and *Lamproderma* sp.) have been discovered in Slobozhanskyi National Nature Park, a lowland region in the forest-steppe zone of north-eastern Ukraine. These finds indicate an expansion of the distribution range of bryophilous myxomycetes beyond their typical montane and boreal habitats. The unidentified species of the genus *Lamproderma*, related to *L. muscicola*, exhibits distinct morphological and molecular characteristics sufficient to consider it a separate species.

Key words: 18S rDNA, *Bryophyta*, Carpathians, *Dicranum montanum*, forest-steppe, hidden biodiversity, molecular barcoding.

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Viunnyk V.O., Leontyev D.V., López-Villalba Á. (2023): První nálezy bryofilních hlenek z ukrajiských nížin s odhalením dosud nepopsaného druhu rodu *Lamproderma*. – Czech Mycol. 75(2): 191–206.

Bryofilní hlenky jsou nacházeny převážně ve vlhkých horských oblastech, zvláště v Ukrajinských Karpatech. Během posledních tří sezón však byli objeveni tři zástupci této skupiny (*Colloderma oculatum*, *Diderma tigrinum* a *Lamproderma* sp.) ve Slobožanském národním přírodním parku, tedy v nížinné oblasti v lesostepním pásmu severovýchodní Ukrajiny. Tyto objevy naznačují rozšíření areálů bryofilních hlenek mimo jejich typická horská a boreální stanoviště. Neurčený druh rodu *Lamproderma*, příbuzný *L. muscicola*, vykazuje zřetelné odlišnosti v morfologické a molekulární charakteristice, dostatečné pro úvahu o tom, že jde o samostatný druh.

INTRODUCTION

Bryophilous myxomycetes are an ecological guild closely associated with mosses and liverworts. Unlike species which produce fruitbodies on living herbaceous plants, bryophilous myxomycetes not only sporulate, but complete their entire life cycle on mosses (Novozhilov et al. 2022a). It is currently unknown what exactly they feed on, but algae biofilms formed on the bryophyte shoots may play a significant role in their nutrition (Ing 1994). Bryophilous myxomycetes require special conditions for their development, primarily a dense moss cover which develops either on large logs of mainly coniferous trees (Ing 1994) or on the surface of limestone rocks (Schnittler et al. 2010). A distinct group of species is found on bryophytes growing on soil (Ing 1994), but in this case a soil, not a moss, may serve as feeding substrate.

The number of myxomycete species that have a stable association with bryophytes is quite limited. This group includes *Barbeyella minutissima* Meyl., *Colloderma oculatum* (C. Lippert) G. Lister, *C. robustum* (G. Lister ex Meyl.) Meyl., *Dianema corticatum* Lister, *Diderma lucidum* Berk. et Broome, *D. ochraceum* Hoffm., *D. tigrinum* (Schrad.) Prikhodko, Shchepin, Novozh., López-Vill., G. Moreno et Schnittler, *D. umbilicatum* Pers., *Elaeomyxa cerifera* (G. Lister) Hagelst., *Lamproderma columbinum* (Pers.) Rostaf., *L. puncticulatum* Härk., and several species of *Licea* (Schnittler et Novozhilov 1998, Schnittler et al. 2000, 2010, Rojas et al. 2015, Lloyd 2022, Novozhilov et al. 2022a).

Most discoveries of typical bryophilous species have been made in humid mountainous regions (Schnittler et al. 2000, 2010, Rojas et al. 2015). In Ukraine, such conditions are only found in the Carpathians, so it is not surprising that all known records of the group originate from this area. Currently, *B. minutissima*, *C. oculatum*, *D. tigrinum*, and *L. columbinum* are known to occur in the Ukrainian Carpathians. However, all findings date back to the late 19th and early 20th centuries (Krupa 1889, Jarocki 1931, Krzeminiewska 1934). Despite a notable upswing in myxomycetological research in Ukraine over the past two decades (Dudka et Kryvomaz 1996, Romanenko 2001, Kryvomaz 2004, Leontyev et al., 2012, 2020, 2021, Kochergina et Markina 2021), no recent records of bryophilous species have been made so far.

In 2021, 2022, and 2023, the first author of this paper discovered representatives of three bryophilous myxomycete species within the borders of Slobozhanskyi National Nature Park, a protected area situated in the lowlands of northeastern Ukraine. This area lacks rocky outcrops and is dominated by deciduous forests, thus broadening our understanding of the distribution of bryophilous myxomycetes. In this publication we describe these remarkable findings, which also include a putative new species.

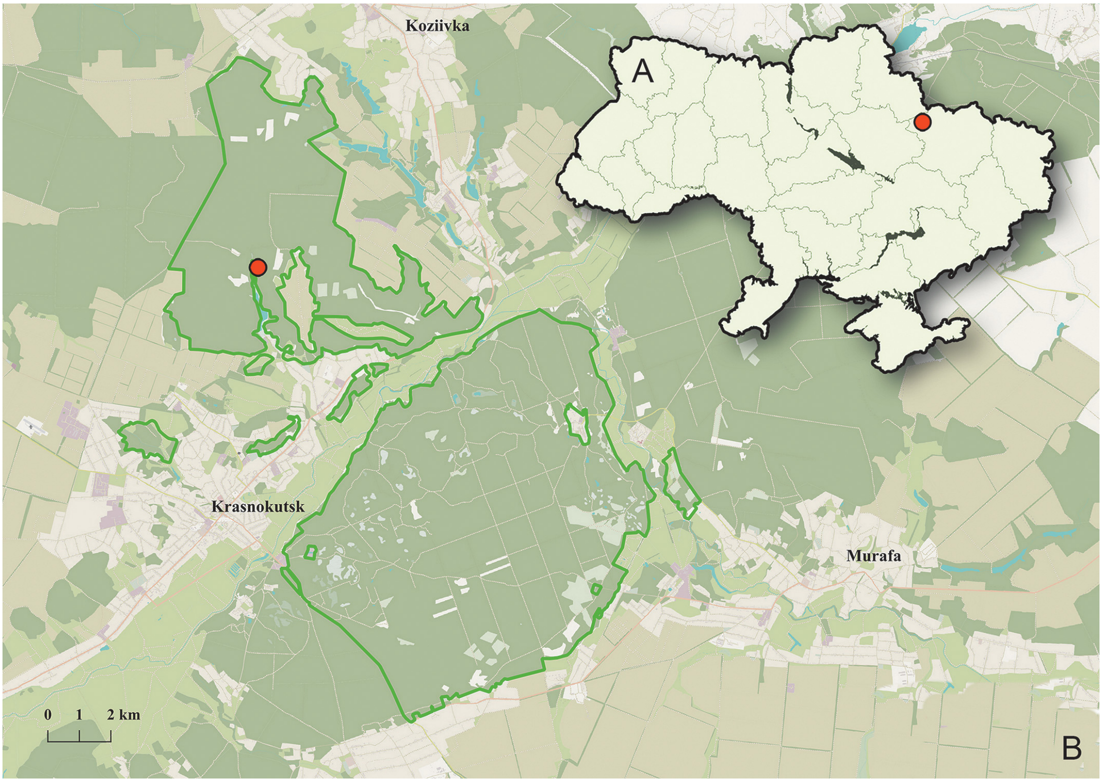


Fig. 1. Study area. **A** – Slobozhanskyi National Nature Park (red dot) on the map of Ukraine; **B** – border of Slobozhanskyi National Nature Park (green line) and sampling point (red dot). Map B was created in QGIS using the Humanitarian OpenStreetMap layer set (https://www.hotosm.org/).

MATERIAL AND METHODS

The material was collected in Slobozhanskyi National Nature Park, situated in the north-western part of the Kharkiv Region, north-eastern Ukraine, on the southwestern spurs of the Central Russian Upland. The Park is located alongside the Merla River and its tributary, Merchyk (Fig. 1). On the right bank of the Merla, an oak forest is situated where *Quercus robur* dominates in the first layer, with admixed *Fraxinus excelsior*. The second layer comprises mainly *Tilia cordata*, *Acer platanoides*, *A. campestre*, and *Ulmus glabra*. The understory typically includes *Corylus avellana*, *Acer tataricum*, *Euonymus europaea*, and *E. verrucosa* (Filatova et al. 2012). The terrain of the Central Russian Upland is generally characterised by folding. This also applies to the landscape within the oak-dominated area of Slobozhanskyi Park, where deep ravines covered with forest vegetation are widespread. All our discoveries of bryophilous species were made in the same wet gully with a significant amount of dead oak logs covered with mosses and liverworts (Fig. 2).

All specimens are deposited in the herbarium of the H.S. Skovoroda Kharkiv National Pedagogical University (CWP). The occurrence dataset including all studied collections was published in biodiversity data platform PlutoF (Viunnyk et Leontyev 2023). Microscopic analysis was conducted

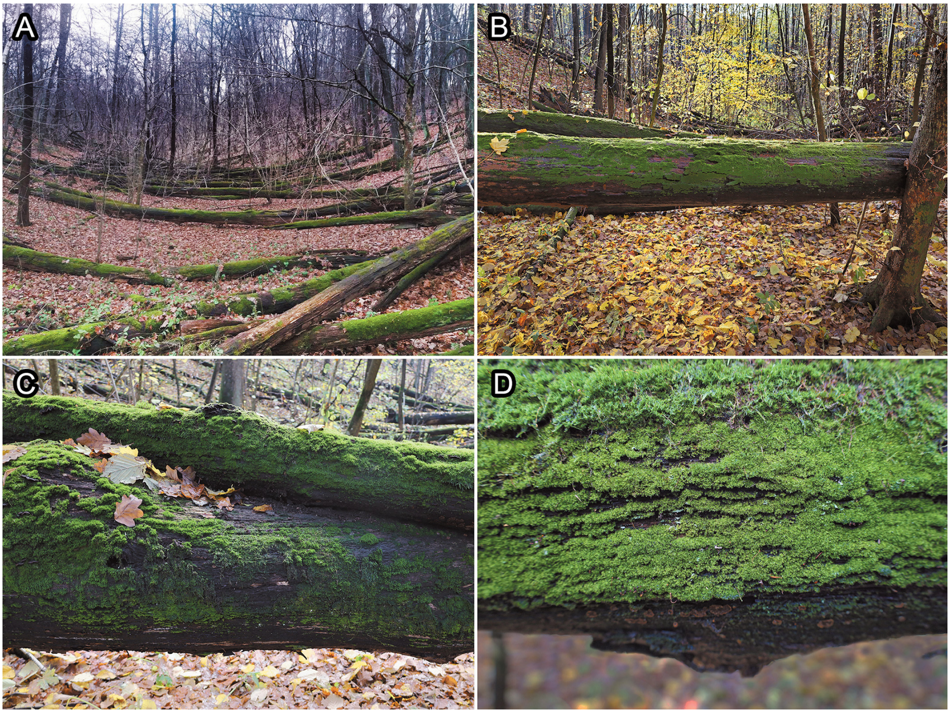


Fig. 2. Studied habitat in the Slobozhanskyi National Nature Park. **A** – general view of the gully where all bryophilous species were found; **B** – log of *Quercus robur* on which *Colloderma oculatum* and *Lamproderma* sp. were found; **C** – log of *Quercus robur* on which *Diderma tigrinum* was found; **D** – detail of the wood surface covered by the moss *Dicranum montanum*. Photographs by V.O. Viunnyk.

using the following equipment: Optima Biofinder Trino 40×–1000× compound microscope (Optima Technology, China), MICROmed XS-6320 stereoscopic microscope (MICROmed, China), and Keyence VHX 7000 digital dissecting microscope (Keyence Corporation, Japan). Microphotographs were taken using the Delta Optical DLT-Cam Pro 5MP (Delta Optical, Eiterfeld, Germany) and the built-in Keyence VHX 7000 digital camera. Measurements of microscopic structures were carried out using the ToupView software (ToupTek, China). Spore diameter was measured including ornamentation.

To provide a molecular barcoding of our myxomycete collections, we obtained partial sequences of the nuclear 18S rDNA. DNA extraction was performed using the King Fisher Flex robot (Thermo Fisher Scientific, USA) following the previously described procedure (Leontyev et al. 2023). PCR was conducted using the S2/SU19R primer pair (Fiore-Donno et al. 2012) with the following protocol: initial denaturation at 94 °C for 2 minutes, 35 cycles including denaturation at 94 °C for 30 seconds, annealing at 56.5 °C for 30 seconds, and elongation at 72 °C for 2 minutes, followed by a final elongation at 72 °C for 5 minutes. PCR products were assessed through gel electrophoresis and then purified by adding 1.3 µl of Exonuclease with Alkaline Phosphatase at a 1:2 ratio, followed by incubation in a thermocycler at 37 °C for 1 hour and 85 °C for 15 minutes. The purified products were sent to Macrogen Europe (Amsterdam, Netherlands) for Sanger sequencing. The obtained chromatograms were visually inspected and edited using Chromas 2.6.6 (https://technelysium.com.au/wp/chromas/)

and compiled into FASTA files using BioEdit 7.2 (https://bioedit.software.informer.com/7.2/). The sequences have been deposited in NCBI GenBank under accession numbers OR791422–OR791425. Phylogenetic analysis was conducted using additional 92 partial 18S rDNA sequences retrieved from the NCBI GenBank (Tab. 1), trimmed to obtain 707 positions. Sequence alignment was carried out in MAFFT 7 (https://mafft.cbrc.jp/alignment/server/index.html). A maximum likelihood phylogenetic tree was constructed using the IQtree webserver (http://iqtree.cibiv.univie.ac.at/). The evolutionary model TIM3e+I+G4, selected based on the BIC criterion, was used to construct phylogeny. Statistical support is shown using three criteria: the Shimodara-Hasegawa SH-aLRT test, the Approximate Bayes test and the Ultrafast bootstrap test with 1000 replicates.

Tab. 1. Sequences used for phylogenetic analyses.

Species	Herbarium voucher/isolate	GenBank accession number	Reference
Colloderma oculatum	HS2885	JQ031959	Fiore-Donno et al. 2012
Colloderma oculatum	**CWP4638**	**OR791422**	**This study**
Colloderma oculatum	**CWP4640a**	**OR791423**	**This study**
Colloderma oculatum	**CWP4641**	**OR791424**	**This study**
Colloderma robustum	AMFD270	JQ031960	Fiore-Donno et al. 2012
Lamproderma acanthosporum	MM36058	JQ031968	Fiore-Donno et al. 2012
Lamproderma aeneum	MM35162	JQ031969	Fiore-Donno et al. 2012
Lamproderma aeneum	AH50063	OR253735	Lloyd et al. 2023
Lamproderma aeneum	AH50826	OR253736	Lloyd et al. 2023
Lamproderma aeneum	AH55507	OR253737	Lloyd et al. 2023
Lamproderma aeneum	AH50704B	OP679828	Yatsiuk et al. 2023
Lamproderma aeneum	AH50718	OP679830	Yatsiuk et al. 2023
Lamproderma arcyrioides	sc22912	KT358693.1	Feng et Schnittle 2017
Lamproderma arcyrioides	MYX8864	MZ005912.2	NCBI GenBank
Lamproderma arcyrioides	LE317280	MZ005913.2	NCBI GenBank
Lamproderma arcyrioides	LE317258	MZ005914.2	NCBI GenBank
Lamproderma 'carpatiense'	MM UK14	JQ031994	Fiore-Donno et al. 2012
Lamproderma columbinum	isolate 63b	HQ687197	Fiore-Donno et al. 2011
Lamproderma columbinum	isolate 94	HQ687199	Fiore-Donno et al. 2011
Lamproderma columbinum	isolate 132	HQ687200	Fiore-Donno et al. 2011
Lamproderma columbinum	isolate F2	HQ687204	Fiore-Donno et al. 2011
Lamproderma columbinum	isolate 144	HQ687201	Fiore-Donno et al. 2011
Lamproderma columbinum	isolate 132	HQ692813	Fiore-Donno et al. 2011
Lamproderma columbinum	clone CS_33	JQ900809.1	Kamono et al. 2013
Lamproderma columbinum	LE325825	MZ005911.2	NCBI GenBank
Lamproderma cristatum	MM37003	JQ031977	Fiore-Donno et al. 2012
Lamproderma cucumer	AH50546	OR253718	Lloyd et al. 2023
Lamproderma cucumer	AH55638	OP679838	Yatsiuk et al. 2023
Lamproderma cucumer	AH55641	OP679840	Yatsiuk et al. 2023
Lamproderma echinosporum	AK06016	JQ031979	Fiore-Donno et al. 2012
Lamproderma echinosporum	AMFD136	JQ031980	Fiore-Donno et al. 2012

Species	**Herbarium voucher/isolate**	**GenBank accession number**	**Reference**
Lamproderma echinosporum	AH50064	OR253725	Lloyd et al. 2023
Lamproderma echinosporum	AH50113	OR253726	Lloyd et al. 2023
Lamproderma echinosporum	AH50578	OR253727	Lloyd et al. 2023
Lamproderma echinosporum	M0180424	OP679842.1	NCBI GenBank
Lamproderma echinosporum	M0180429	OP679843.1	NCBI GenBank
Lamproderma echinosporum	AH55547	OP679835	Yatsiuk et al. 2023
Lamproderma echinosporum	AH55640	OP679839	Yatsiuk et al. 2023
Lamproderma lycopodiicola	AMFD309	JQ031981	Fiore-Donno et al. 2012
Lamproderma maculatum	MM37059	JQ031982	Fiore-Donno et al. 2012
Lamproderma maculatum	AH48792	OR253728	Lloyd et al. 2023
Lamproderma maculatum	AH50104	OR253729	Lloyd et al. 2023
Lamproderma maculatum	AH50253	OR253730	Lloyd et al. 2023
Lamproderma maculatum	AH55701	OR253731	Lloyd et al. 2023
Lamproderma maculatum	AH55715	OR253732	Lloyd et al. 2023
Lamproderma muscicola	MM37253	JQ031995	Fiore-Donno et al. 2012
Lamproderma ovoideoechinulatum	AMFD209	DQ903675	Fiore-Donno et al. 2008
Lamproderma ovoideoechinulatum	JMF527	JQ031983	Fiore-Donno et al. 2012
Lamproderma ovoideoechinulatum	AH30011	OR253717	Lloyd et al. 2023
Lamproderma ovoideoechinulatum	AH50437	OP679814	Yatsiuk et al. 2023
Lamproderma ovoideoechinulatum	AH50687	OP679825	Yatsiuk et al. 2023
Lamproderma ovoideoechinulatum	AH55511	OP679832	Yatsiuk et al. 2023
Lamproderma ovoideoechinulatum	AH55544	OP679833	Yatsiuk et al. 2023
Lamproderma ovoideoechinulatum	AH55546	OP679834	Yatsiuk et al. 2023
Lamproderma ovoideoechinulatum	AH55609	OP679837	Yatsiuk et al. 2023
Lamproderma ovoideum	AK06022	JQ031984	Fiore-Donno et al. 2012
Lamproderma ovoideum	AH50259A	OP679812	Yatsiuk et al. 2023
Lamproderma ovoideum	AH50693	OP679826	Yatsiuk et al. 2023
Lamproderma ovoideum	AH50694	OP679827	Yatsiuk et al. 2023
Lamproderma ovoideum	AH50711	OP679829	Yatsiuk et al. 2023
Lamproderma pseudomaculatum	MM37354	JQ031985	Fiore-Donno et al. 2012
Lamproderma pseudomaculatum	AH50046	OR253733	Lloyd et al. 2023
Lamproderma pseudomaculatum	AH50716	OR253734	Lloyd et al. 2023
Lamproderma pulchellum	MM36096	JQ031987	Fiore-Donno et al. 2012
Lamproderma pulveratum	MM37016	JQ031988	Fiore-Donno et al. 2012
Lamproderma pulveratum	AH50470	OP679815	Yatsiuk et al. 2023
Lamproderma pulveratum	AH50486	OP679817	Yatsiuk et al. 2023
Lamproderma pulveratum	AH50487	OP679818	Yatsiuk et al. 2023
Lamproderma pulveratum	AH50649	OP679824	Yatsiuk et al. 2023
Lamproderma pulveratum	AH55578	OP679836	Yatsiuk et al. 2023
Lamproderma puncticulatum	isolate 172	HQ687194	Fiore-Donno et al. 2011
Lamproderma puncticulatum	isolate 3	HQ687195	Fiore-Donno et al. 2011

Species	**Herbarium voucher/isolate**	**GenBank accession number**	**Reference**
Lamproderma puncticulatum	isolate 162	HQ687202	Fiore-Donno et al. 2011
Lamproderma retirugisporum	MM23831	JQ031989	Fiore-Donno et al. 2012
Lamproderma retirugisporum	AH50366	OR253719	Lloyd et al. 2023
Lamproderma sauteri	AMFD208	DQ903674	Fiore-Donno et al. 2008
Lamproderma sauteri	AH48832	OP679809.1	Yatsiuk et al. 2023
Lamproderma sauteri	AH48831	OP679808.1	Yatsiuk et al. 2023
Lamproderma sauteri	AH48833	OP679810	Yatsiuk et al. 2023
Lamproderma sauteri	AH50067	OP679811	Yatsiuk et al. 2023
Lamproderma sauteri	AH50587	OP679821	Yatsiuk et al. 2023
Lamproderma scintillans	JM3204	JQ031992	Fiore-Donno et al. 2012
Lamproderma scintillans	MA70223	JQ031993	Fiore-Donno et al. 2012
***Lamproderma* sp.**	**CWP4639**	**OR791425**	**This study**
Lamproderma spinulosporum	AH50582	OR253720	Lloyd et al. 2023
Lamproderma spinulosporum	AH50596	OR253721	Lloyd et al. 2023
Lamproderma spinulosporum	AH50429	OP679813	Yatsiuk et al. 2023
Lamproderma vietnamense	LE317740	MZ241460.1	Novozhilov et al. 2022b
Lamproderma vietnamense	LE326172a	MZ241461.1	Novozhilov et al. 2022b
Lamproderma zonatopulchellum	AH50597	OP679822.1	Yatsiuk et al. 2023
Lamproderma zonatopulchellum	AH50598	OP679823.1	Yatsiuk et al. 2023
Meriderma carestiae	MM35985	JQ031999.1	Fiore-Donno et al. 2012
Meriderma cribrarioides	MYX14644	MZ241444.1	Fiore-Donno et al. 2012
Meriderma fuscatum	MYX328	KM977877.1	Hoppe et Schnittler 2015
Meriderma fuscatum	MM20052	OP616399.1	Prikhodko et al. 2023a
Meriderma verrucosporum	MYX14637	OP621312.1	Prikhodko et al. 2023a

RESULTS

As a result of our study, three species of bryophilous myxomycetes, *Colloderma oculatum*, *Diderma tigrinum*, and *Lamproderma* sp., were revealed in Slobozhanskyi National Nature Park. These species had never been documented in Ukraine beyond the Carpathian Mountains and, to the best of our knowledge, have never been recorded in the forest-steppe zone.

Colloderma oculatum (C. Lippert) G. Lister, Journal of Botany, British and Foreign 48: 312, 1910 Fig. 3A–G

Specimens examined

Ukraine. Kharkiv Region, Slobozhanskyi National Nature Park, oak forest, in a wet gully (50°06'22.6" N, 35°10'42.6" E), on the moss *Dicranum montanum* Hedw. covering log of *Quercus robur*, 20 Nov 2021 (CWP4638), 14 Oct 2022 (CWP4640a), 2 Dec 2022 (CWP4641), leg. V.O. Viunnyk. GenBank, 18S rDNA: OR791422 (CWP4638), OR791423 (CWP4640a), OR791424 (CWP4641).

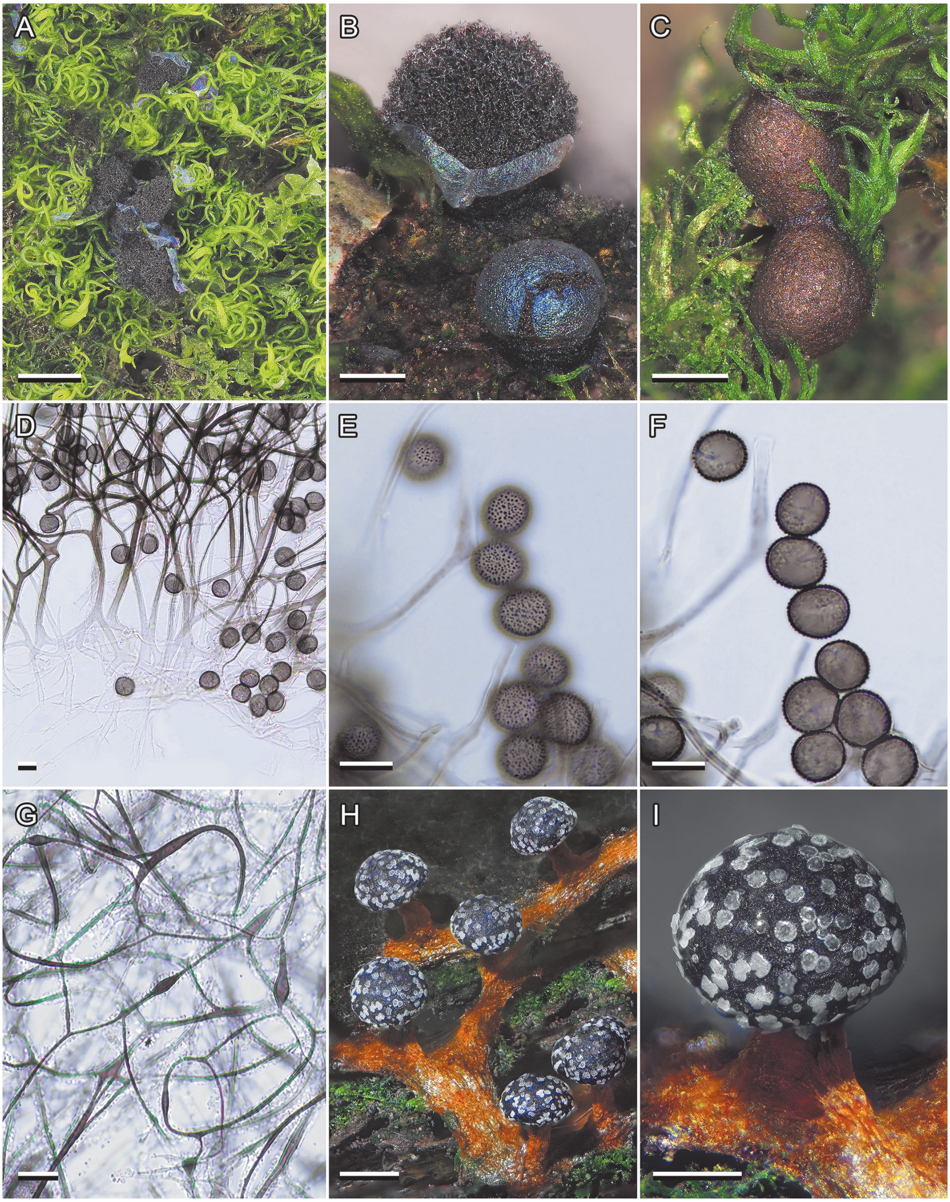


Fig. 3. *Colloderma oculatum* (A–G) and *Diderma tigrinum* (H–I). **A** – group of plasmodiocarps on the moss *Dicranum montanum*; **B** – plasmodiocarps lacking external slime sheath; **C** – plasmodiocarps with preserved external slime sheath; **D** – basal part of the capillitium; **E** – spores with visible ornamentation; **F** – spores in optical section; **G** – peripheral part of the capillitium; **H** – colony of sporocarps; **I** – individual sporocarp. Scale bars: 1 mm (A, H); 0.2 mm (B, C); 10 µm (D–G); 0.5 mm (I). Specimens: CWP4638 (A, B, D–F); CWP4640a (C); CWP4641 (G); CWP4643 (H, I). Photographs by D.V. Leontyev (A–G) and V.O. Viunnyk (H, I).

Other collections from Ukraine

Jarocki (1931) recorded *C. oculatum* during the autumn seasons of 1924–1925, on the Chornohora ridge of the Carpathians (nowadays Ivano-Frankivsk Region), at altitudes of 1100–1400 m, in shaded areas, on decaying wood of *Picea abies* covered with mosses, liverworts, and algae. Krzeminiewska (1934) recorded this species in September of 1929 and 1931, on the same mountain ridge, on wood covered with mosses and liverworts, rarely on bare wood.

Diderma tigrinum (Schrad.) Prikhodko, Shchepin, Novozh., López-Vill., G. Moreno et Schnittler, in Prikhodko, Shchepin, Bortnikova, Novozhilov, Gmoshinskiy, Moreno, López-Villalba, Stephenson et Schnittler, Mycological Progress 22(2), art. 11: 9, 2023 Fig. 3H, I

Specimens examined

Ukraine. Kharkiv Region, Slobozhanskyi National Nature Park, oak forest, in wet gully (50°06'22.6" N, 35°10'42.6" E), on the moss *Dicranum montanum* Hedw. covering log of *Quercus robur*, 4 Jan 2023 (CWP4642, CWP4643), leg. V.O. Viunnyk.

Other collections from Ukraine

Krupa (1889) found *D. tigrinum* near the village of Golovetsko (nowadays Lviv Region), on decaying stumps, alongside with *Cribraria vulgaris* Schrad. Jarocki (1931) found it in September of 1924 and 1925 on the Chornohora ridge, on logs of *Picea abies* covered with mosses, lichens, and algae. Krzeminiewska (1934) observed *D. tigrinum* in September and October time of 1929–1933, on Chornohora, on dead wood and bark of different tree species.

***Lamproderma* sp.** Fig. 4

Specimens examined

Ukraine. Kharkiv Region, Slobozhanskyi National Nature Park, oak forest, in wet gully (50°06'22.6" N, 35°10'42.6" E), on the moss *Dicranum montanum* Hedw. covering log of *Quercus robur*, accompanied by *Colloderma oculatum*, 11 Aug 2022 (CWP4639), 14 Oct 2022 (CWP4640b), leg. V.O. Viunnyk. GenBank, 18S rDNA: OR791425 (CWP4639).

Sporocarps scattered, short-stalked, 0.7–1.1 mm high. Sporotheca globose, 0.3–0.6 mm diam., iridescent, blue with cyan and purple tints. Stalk black, rigid, cylindrical, widening toward the base, 0.4–0.5 mm high, 50–150 µm diam., reaching from half to 2/3 of the overall height of the sporocarp. Hypothallus membranous, reddish brown to black. Peridium thin, membranous, wrinkly, pale brown in transmitted light. Columella black, rigid, tapering upwards, reaching half the height of the sporotheca. Capillitium dense, rigid, emerging radially from the tip of the columella, with threads 2.5 µm diam., moderately branched at acute angles, occasionally anastomosed; both central and peripheral threads dark brown, only the thinnest terminal tips nearly hyaline. Spore mass brown. Spores violet-brown in transmitted light, globose to subglobose, 12–14 µm diam., minutely warted with clusters of larger warts.

The partial sequence of the 18S rDNA gene of this specimen does not have a full match in the NCBI GenBank database. According to the BLAST search, it

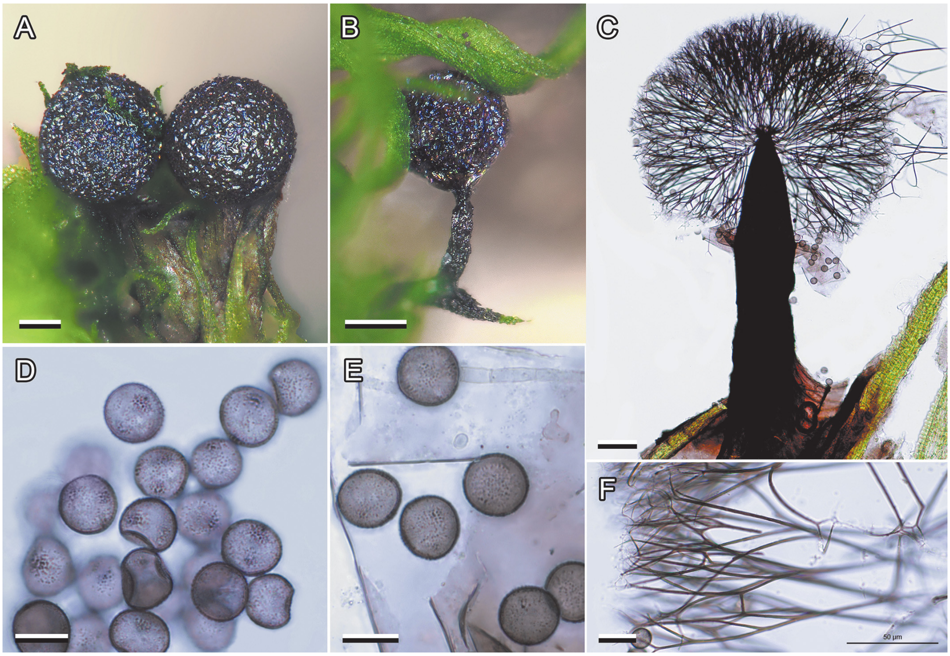
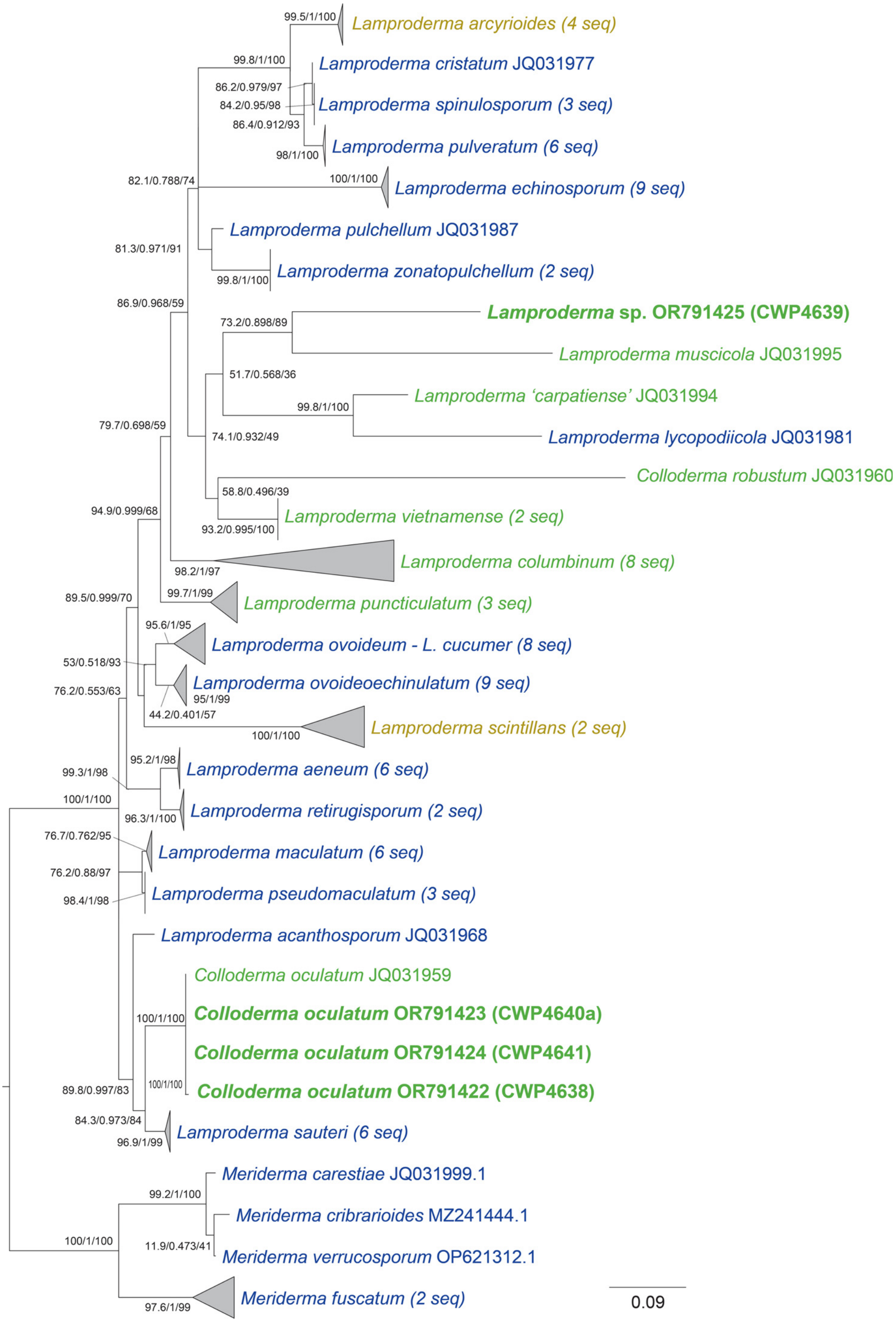


Fig. 4. Undescribed species of *Lamproderma*. **A, B** – sporocarps on the moss *Dicranum montanum*; **C** – sporocarp in transmitted light. **D, E** – spores. **F** – peripheral part of capillitium. Scale bars: 0.2 mm (A, B); 0.1 mm (C); 10 µm (D, E); 20 µm (F). Specimens: CWP4639 (A, D); CWP4640b (B, C, E, F). Photographs by D.V. Leontyev.

has the closest (82.5%) similarity to sequence JQ031995, annotated in GenBank as *Lamproderma* sp. and later identified as *Lamproderma muscicola* Poulain et Mar. Mey. (Poulain et Meyer 2015). The phylogenetic analysis of partial 18S rDNA sequences confirms the relatedness of these species (Fig. 5).

Fig. 5. 18S rDNA phylogeny of *Lamprodermataceae* (with *Meridermataceae* as an outgroup) showing the putative position of *Colloderma oculatum* (CWP4638, 4640a, 4641) and *Lamproderma* sp. (CWP4639) in the evolutionary tree. Newly obtained sequences are given in bold. Bryophilous species are shown in green, nivicolous species in blue, non-nivicolous species without clear substrate preferences in brown. Numbers in parentheses indicate the number of sequences from different accessions of the same species used to construct the phylogenetic tree. Branch support is shown as follows: Shimodara-Hasegawa SH-aLRT test / Approximate Bayes test / Ultrafast bootstrap test (1000 replicates). ▶


99.5/1/100
Lamproderma arcyrioides (4 seq)
99.8/1/100
Lamproderma cristatum JQ031977
86.2/0.979/97
84.2/0.95/98
Lamproderma spinulosporum (3 seq)
86.4/0.912/93
98/1/100
Lamproderma pulveratum (6 seq)
82.1/0.788/74
100/1/100
Lamproderma echinosporum (9 seq)
Lamproderma pulchellum JQ031987
81.3/0.971/91
99.8/1/100
Lamproderma zonatopulchellum (2 seq)
86.9/0.968/59
73.2/0.898/89
Lamproderma sp. OR791425 (CWP4639)
Lamproderma muscicola JQ031995
51.7/0.568/36
99.8/1/100
Lamproderma 'carpatiense' JQ031994
79.7/0.698/59
74.1/0.932/49
Lamproderma lycopodiicola JQ031981
Colloderma robustum JQ031960
58.8/0.496/39
94.9/0.999/68
93.2/0.995/100
Lamproderma vietnamense (2 seq)
98.2/1/97
Lamproderma columbinum (8 seq)
99.7/1/99
89.5/0.999/70
Lamproderma puncticulatum (3 seq)
95.6/1/95
Lamproderma ovoideum - L. cucumer (8 seq)
53/0.518/93
Lamproderma ovoideoechinulatum (9 seq)
76.2/0.553/63
95/1/99
44.2/0.401/57
100/1/100
Lamproderma scintillans (2 seq)
95.2/1/98
99.3/1/98
Lamproderma aeneum (6 seq)
100/1/100
96.3/1/100
Lamproderma retirugisporum (2 seq)
76.7/0.762/95
Lamproderma maculatum (6 seq)
76.2/0.88/97
98.4/1/98
Lamproderma pseudomaculatum (3 seq)
Lamproderma acanthosporum JQ031968
Colloderma oculatum JQ031959
100/1/100
Colloderma oculatum OR791423 (CWP4640a)
Colloderma oculatum OR791424 (CWP4641)
100/1/100
89.8/0.997/83
Colloderma oculatum OR791422 (CWP4638)
84.3/0.973/84
96.9/1/99
Lamproderma sauteri (6 seq)
Meriderma carestiae JQ031999.1
99.2/1/100
Meriderma cribrarioides MZ241444.1
100/1/100
11.9/0.473/41
Meriderma verrucosporum OP621312.1
97.6/1/99
Meriderma fuscatum (2 seq)
0.09

DISCUSSION

Distribution and ecology of *Colloderma oculatum* and *Diderma tigrinum*

The myxomycete diversity of Ukraine has been extensively studied in the past decades and a number of new species have been described for the country (Leontyev et al. 2015, 2019a, 2023, Yatsiuk et al. 2023). Species diversity in protected natural areas has obtained considerable attention during this period. As an example, in Homilsha Forests National Park, located 50 km from Slobozhanskyi Park, a total of 168 species have been documented (Prylutskyi et al. 2017). In the Slobozhanskyi Park, myxomycete studies have not been as extensive but revealed 77 species (Yatsiuk et al. 2018). For this reason, the lack of data on the distribution of *Diderma tigrinum* and *Colloderma oculatum* in the whole country since the 1930s is quite surprising, especially considering that both species are widely distributed in the Holarctic realm. There could be two factors explaining the lack of recent collections of the abovementioned species in Ukraine. Firstly, their ecology is quite distinctive, requiring a targeted search for specific substrates. Secondly, their phenology is also peculiar: both *D. tigrinum* and *C. oculatum* typically fructify during the cold autumn and winter months (Schnittler et Novozhilov 1998, Takahashi et Harakon 2012), as was also confirmed by our finds in November, December, and January. Field studies of myxomycetes in Ukraine are rarely conducted during this period due to the harsh winter conditions and heavy snowfall (Leontyev 2006, Khokhlov et al. 2016). However, our finds demonstrate that a search for myxomycetes in winter, at least during thaws, is indeed expedient.

Diderma tigrinum and *Colloderma oculatum* are primarily found in mountainous areas, where specific landscape and microclimate features occur, such as (1) narrow, shady gorges, protected from sun and wind, and (2) water condensation in calcareous mineral outcrops. Both factors contribute to an increased humidity of substrates (Schnittler et al. 2000, 2010). According to GBIF.org (Shadwick et Cooper 2018, British Mycological Society 2022, Prikhodko et al. 2023b), these species commonly occur in the Alps, Saxon Switzerland (Germany), and rocky regions of Scandinavia and Britain. Our finds have been made in a lowland, yet rugged landscape with numerous ravines and gullies. These environmental conditions coincide with those described by Schnittler et al. (2010) as typical of the bryophilous guild, except for the rocky outcrops, which are completely absent in our study area.

Putative new species of *Lamproderma*

Bryophilous myxomycetes occur in particular habitats which do not form a vast vegetation zone but occur as isolated spots distant from each other. Such isolation may promote allopatric speciation (Baum et al. 2013) with a formation of endemic species. This hypothesis is supported by the find of *Lamproderma* sp., which is likely to represent an undescribed species.

In terms of morphology, ecology, and the nucleotide sequence of the 18S rDNA marker gene, the *Lamproderma* species we discovered bears similarities to *Lamproderma muscicola*. This recently described bryophilous organism also features small stalked sporocarps with sparsely branched, radiating, heavily melanised capillitium threads and small purple-brown spores (Poulain et Meyer 2015). However, the genetic distance between *L. muscicola* and *Lamproderma* sp. (17.5%) is much greater than the minimum barcode gap of 0.9% established for dark-spored myxomycete species (Borg Dahl et al. 2018) and corresponds to the upper limit of the barcode gap range obtained for the genus *Lamproderma* (0.7–19.0%) when comparing partial 18S rDNA sequences (Yatsiuk et al. 2023). Importantly, these two species are clearly distinguishable based on their morphology as well. Specifically, stalks in *L. muscicola* are very short, not reaching 1/4 of the overall sporocarp height, sporothecae are larger, 0.6–0.9 mm diam., the capillitium is poorly branched, and spores are ornamented with widely and evenly distributed spines. The last feature seems to be the most crucial, since spore ornamentation in *Lamproderma* is considered to be a reliable species-delimiting character (Poulain et al. 2011, López-Villalba 2022). However, we currently refrain from describing this find as a new taxon. The existing material consists of two collections gathered at the same location with a 2-month interval and thus representing a single population. This provides limited information about the variation of morphological characters within a species. However, obtaining more collections and/or more molecular data, including sequences of the second marker gene, may render enough data to support the formal description of a new species.

There are other species closely related to *Lamproderma* sp. and *L. muscicola* which tend to develop on bryophytes. This fits to the recently described *L. vietnamense* Novozh., Prikhodko, Fedorova, Shchepin et Schnittler (Novozhilov et al. 2022b), but also to *Colloderma robustum* (G. Lister ex Meyl.) Meyl., a species of the polyphyletic genus *Colloderma*, which was proposed to be included into the genus *Lamproderma* (Leontyev et al. 2019b). Two other bryophilous species, *L. columbinum* (Pers.) Rostaf. and *L. puncticulatum* Härk., form a paraphyletic complex with the clade "*L. muscicola*, *L.* sp., *L. 'carpatiense'*, *L. vietnamense*". It seems that bryophilous taxa constitute a series of basal clades within a relatively large species group (ranging from *L. arcyrioides* to *L. puncticulatum* in Fig. 5). It can be inferred that, for this clade, the association with mosses is an ancestral trait, while nivicolous ecology is a derived one. However, since the single-gene phylogeny does not offer enough resolution to precisely determine the order of deep branching (Leontyev et Schnittler 2022), we cannot yet detect the exact position of bryophilous species in the phylogeny of the group.

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