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New data on the distribution of hypogeous species *Leucogaster nudus* (Basidiomycota) in the Republic of North Macedonia with note on its taxonomy and morphology

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Abstract

A field work organized in 2020 and 2022 revealed new data on distribution and habitat types for *Leuco-gaster nudus* in North Macedonia. While examining the newly collected materials and comparing it with the original description of *Hydnangium nudum* a suspicion on the taxonomic position of *L. nudus* arose, since in the original description the species is defined by having warty ornamentation of the spores instead of reticulate. Therefore, we made an extensive literature review on the characteristics of *L. nudus* and its proposed synonyms and provide an in-detail morphological examination of the observed materials with illustrations. In order to clarify the taxonomic position of *L. nudus* and the diversity of this genus in Europe along with morphological, phylogenetic approach is needed.

Key words: hypogeous fungi, diversity, ecology, *Leucogaster fragrans, L. tozzianus, L. badius, L. floccosus, Leucophleps*.

Introduction

The interest on hypogeous fungi is continuously increasing with an aim to get acquainted with the biodiversity of this ecological group of organisms. Until now, a total of 22 hypogeous species within the phylum Basidiomycota are known from North Macedonia (Pilat & Lindthner, 1938; Chavdarova et al., 2011; Karadelev et al., 2018; Tofilovska et al., 2019). The latest article containing data on this topic was a contribution to the checklist of Basidiomycota for North Macedonia where 10 hypogeous species belonging to the genera *Gautieria*, *Hymenogaster*, *Leucogaster*, *Melanogaster* and *Russula* were reported for the first time for the country (Tofilovska et al., 2019).

Genus *Leucogaster* R. Hesse was described based on the characteristics of *L. liosporus* R. Hesse (1882) as the type species and at the moment it comprises 24 valid species according to Index Fungorum database (Index Fungorum, 2023). Species within this genus produce hypogeous to emergent false-truffles and have gleba with characteristic cavities filled with gelatinous mass. They are mostly distributed in the Northern Hemisphere (Zeller & Dodge, 1924; Fogel, 1975) and

only one is reported from Australia (Beaton et al., 1985). Most of the species are described from Noth America where this genus has been under revision by Zeller & Dodge (1924) and Fogel (1975) while the European taxa have not been subject of revision and are not clearly delimitated (Fogel, 1975; Montecchi and Sarasini, 2000). By most authors it is regarded that in Europe only the species *L. nudus* (Hazsl.) Hollós is present while other *Leucogaster* taxa as *L. badius* Mattir., *L. fragrans* Mattir., *L. tozzianus* (Cavara & Sacc.) Mattir. ex Zeller & C.W. Dodge, *L. floccosus* R. Hesse are regarded as synonyms (Szemere, 1965; Montecchi and Sarasini, 2000) and here in we follow this concept.

L. nudus is widespread species throughout Europe, known from at least 20 countries. In GBIF 55 occurrences are listed from 12 countries, Austria, Belgium, France, Georgia, Germany, Hungary, Italy, Poland, Slovakia, Spain, Switzerland and United Kingdom, mostly from preserved specimens (GBIF, 2023). It is included in the check list of gasteroid and secotioid fungi of Europe where additionally the Czech Republic, Lithuania, Sweden, Turkey and Ukraine are listed (Kreisel, 2001). Concerning the type of habitat, it is mainly found in decidu-

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ous forest of Fagus and Quercus, in mixed woods with conifers, as well as in Abies forests on calcareous and sandy soils, at altitude between 400-1000 m.a.s.l. where the sporocarps are produced from late spring to autumn (Montecchi & Sarasini, 2000; Kreisel, 2001). In Turkey it has been found in mixed forest of Abies nordmanniana var. bornmulleriana (Mattf.) Coode & Cullen and Fagus orientalis Lipsky (Türkoğlu at al., 2015), as well as in mixed forest of F. orientalis, Castanea sativa Mill., Rhododendron ponticum L. and Alnus sp., and in mixed forest of F. orientalis with Picea orientalis (L.) Link and R. ponticum (Kaya and Uzun, 2020). In Poland, one of the localities is in Abies forest with scattered trees of Fagus, Quercus and Salix on clay soil (Snowarski, 2023). It has also been confirmed on Pieniny Mountains, a limestone mountain range in the Western Carpathians of Poland, where it was proved to be part of the diet of small mammals (Komur et al., 2021). From the neighboring countries it has been recorded in Bulgaria in Fagus forest, Picea forest and Abies forest (Nedelin et al., 2018; Nedelev, 2019), as well as in Serbia (Ivančević, 2016) and Greece (Kauonas, 2015).

Methodology

The examined material was collected in autumn seasons of 2020 and 2022 during fieldwork organized with truffle hunter with trained dogs. Material was collected in the biogeographical region Skopska Crna Gora, a middle altitude mountain range, mostly covered by grasslands, oak and beech forests (Melovski et al., 2013). During the fieldwork data on locality, altitude and type of habitat were noted. The collected basidiocarps were photographed in the field or in the lab with Canon EOS 2000D and Samsung A7. After examination the specimens were dried on air dehydrator at 50°C and deposited in the Macedonian Collection of Fungi (MCF), Mycological laboratory, Institute of Biology, Faculty of Natural Sciences and Mathematics, Skopje. The microscopic analyses were performed on fresh and dried sporocarps, the slides were prepared by cross-section of the peridium and gleba mounted in Meltzer's reagent and 3% KOH. LW Scientific i4 microscope was used for observation of the material prepared in Meltzer's reagent while the photos were taken with MiniVID USB 1MP camera. For the material observed in 3% KOH, microscope ZEISS Primostar 3 was used, photos were taken on ZEISS Axiocam 208 color microscope camera with the Software ZEN 3.0 blue edition for obtaining of the measurements. The photos presented on the figures were arranged in Photoshop CC 2018. Randomly selected mature basidiospores (nu. 60) were measured with included perisporium. The minimum and maximum values of length, width and quotient (Q), along with the average values are presented. Average thickness of the peridium was analyzed by cross section of five basidiocarps and a total number of 25 measurements of the peridium were taken. SEM images were taken using a Phenom G2-Pro desktop scanning electron microscope with accelerator voltage 5 kV and emission current 1.2 nA at the Bialystok University of Technology, Institute of Forest Sciences, Scientific Research Centre in Hajnowka, Poland. The spores were mounted on the SEM sample tip by pressing onto the carbon disk. All samples were coated with gold using a vacuum sputtering machine.

Results and discussion

Leucogaster nudus (Hazslinsky) Hollós (Russulales, Albatrellaceae) was reported for the first time in North Macedonia, as part of a contribution to the check list of Basidiomycota, on only one locality in mixed forest of Fagus and Abies (Tofilovska et al., 2019). Here in, we report a new data on the distribution of this species in North Macedonia with detailed morphological examination of its characters and critical note on its taxonomy.

Taxonomy

Leucogaster nudus (Hazsl.) Hollós, Annls hist.-nat. Mus. natn. hung. 6: 319 (1908)

Basionym: Hydnangium nudum Hazsl., Verh. Kaiserl. -Königl. zool.-bot. Ges. Wien 25: 64 (1875). Synonym: Leucogaster floccosus R. Hesse, Botan. Centralbl. 40: 1 (1889); Octaviania pityophila L. Becker, Schlesiens unterirdische pilz-flora 35: 356 (1886); Octaviania silesiaca L. Becker, Schlesiens unterirdische pilz-flora 35: 356 (1886).

Morphology

Macroscopic features. Basidiocarp hypogeous, gasteroid type, subglobose, ovoid to irregularly lobbed, 5 – 18 mm long and 3 – 13 mm wide (Fig. 1), solitary to gregarious. Peridium yellow-ochre (Fig. 1a) soon becoming ocher, later when drying is darkening to brownreddish color, not separable from the gleba, when completely dried at some spots it looks like having warts. Gleba compact, white, gelatinous and very bright, when drying becoming dark yellow-olive, denser and





Fig. 1. Leucogaster nudus, fresh basidiocarp. a. yellow color of peridium. b. gleba, gelatinous and very bright, chambers can be noticed. Scale bar: a-b. 5 mm.

(MCF17818)

powdery (Fig. 1b), it is composed of round to polygonal chambers 0.3–1.2 mm broad (Fig. 2a), when the fruit-body is cut and fresh the chambers exudates liquid. Odor very pleasant, intensive, fruity, cherry like. Taste is very sweet and also pleasant.

Microscopic features. Peridium is composed of two layers (Figs 3a-b, 4a), external and internal, total thickness varies between 90 µm and 350 µm, on the average is 215 µm (measured on 5 basidiocarps at randomly chosen 25 places in total). External peridium is brown, composed of hyphae that are hard to be observed since they are covered with brown crystal mass, width varies between 50 μm and 215 μm, on average 110 μ m, hyphae are ±5 μ m wide and cell wall is ±0.5 µm thick. Sometimes in one basidiocarp the color of external peridium can be red-brown or yellow at places in 3% KOH. Internal peridium width varies between 40 μm and 175 μm, on average 105 μm, hyphae are parallel, 2.5 - 5 μ m wide and cell wall is ±1 μ m thick, at some places hyphae are swollen and look like pseudoparenhymatic tissue, forming more elongated or rounded

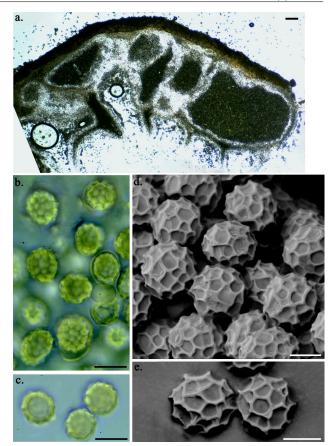


Fig. 2. *Leucogaster nudus*. a. cross section of basidiocarp, peridium and gleba with chambers filled with spores. b-c. basidiospores, focus on reticulate ornamentation (b) and focus on shape (c), also the perisporium can be observed. d-e. basidiospores viewed with SEM, reticulate ornamentation at the conjunction places is taller, spine-like. Scale bar: a. 100 μm, b-c. 10 μm, d-e. 5 μm. Light microscope slides prepared in Meltser's reagent. (a, d-e. MCF17818, b-c MCF17051)

elements (5.2×7 ; 10×12 ; 5.7×15 ; 9×14 µm). Sometimes, especially if the cross-section is thicker the color of internal peridium might become pink at some places in 3% KOH. Tramal plate (Figs. 3a, 4b) composed of elongated, thin hyphae 2.5-4 µm wide, at places swollen, somewhere swollen elements look dominant (inflated cells), found in different sizes, smaller or larger, cell wall is ± 0.5 µm thick. Basidiospores (Fig. 2b-e, 4c-d) mainly globose, some subglobose, sometimes variable in form due to perisporium formation, size (10) $11-14(15) \times (10)10.5-13.5(14)$ µm, 12.3×11.6 µm on average, Q = 1.00-1.20, Qav = 1.05 (n = 60), including the perisporium which might be more adherent to the cell wall or more loosely attached (1-1.7 µm), reticulate ornamentation with 3-4 (5) openings, 1 µm tall.

Specimens examined:

Mountain Bistra (10309), vicinity of Mavrovo Lake, 41°41'58.16"N 20°44'7.31"E, hypogeous, mixed forest of *Fagus sylvatica* L. and *Abies borisii-regis* Mattf., classified as Balkano-Pontic Abies forests (G3.17) according to EUNIS (European Nature Information System) Habitat Classification 2012, at altitude 1300 m.a.s.l., leg. Toni Mitrov, Mitko Karadelev, Tine Grebenc, MCF 17051 (01.11.2014). Specimen reported in Tofilovska et al. (2019).

New data

Mountain Skopska Crna Gora (62078), near village Pobozje, 42°07'13.2"N 21°25'39.7"E, hypogeous, *Quercus pubescens* forest, classified as Thermophilous deciduous woodland (G1.7) by EUNIS Habitat Classification 2012, at altitude 650 m.a.s.l., leg. Tome Jovanovski, MCF 17818 (07.11.2020).

Mountain Skopska Crna Gora (62078), near village Brodec, 42°08'59.6"N 21°27'11.0"E, hypogeous, monodominant forest stand of *Fagus sylvatica*, classified as Moesian beech forests (G1.69) by EUNIS Habitat Classification 2012, at altitude 1200 m.a.s.l., leg. Tome Jovanovski, Mitko Karadelev and Slavica Tofilovska, MCF 19486 (12.11.2022).

Habitat

Leucogaster nudus has been found in three types of habitats at an altitude range between 650-1300 m.a.s.l. (Fig. 5). One of the habitats is Balkano-Pontic Abies forests which is defined mainly as mixed forest of Fagus sylvatica and Abies borisii-regis, at the precise locality the edificatory species of the habitat A. borisii-regis occurs as a small group of stands in the beech forest. In this type of habitat, usually the shrub layer is not developed or it has a small vegetation cover, while the layer of herbaceous plants and half-shrubs could cover 50% to 90%, however sometimes only 15% of vegetation cover (Matevski et al., 2021). The geological substrate of this locality is diabase (Pendzerkovski & Hadzimitrova, 1977) while the soil type is chromic leptic luvisol on hard limestones according to World Reference Base for Soil Resources Classification System (MaSIS, 2015). The second type of habitat, Moesian beech forests, is characterized by the presence of Fagus sylvatica as edificatory species, it comprises pure or mixed broadleaf deciduous forests. This habitat is

mainly distributed between 1,100-1,650 m.a.s.l., however sometimes it is found bellow 1,000 m or it may spread up to 2,200 m which is the reason for its high variation of the ecological and flora features (Matevski et al., 2021). This locality is found on geological substrate of biotite-muscovite schist (Pendzerkovski & Hadzimitrova, 1977) while the soil is complex of cambisol, humic eutric and umbric regosol (umbrisol) (MaSIS, 2015). The last type of habitat, the Thermophilous deciduous woodland is a forest stand of *Quercus pubescens* Willd., that is located on a substrate of flysch formations (Pendzerkovski & Hadzimitrova, 1977) and the soil is classified as a complex of rendzic leptosol and chromic leptic luvisol on hard limestones (MaSIS, 2015).

Taxonomic note

The basidiocarp dimensions reported in this study (5-18 mm) corresponds to description of other authors, however the size of 5 mm is reported for the first time, in available publications up until now, the minimum size is 10 mm (Zeller & Dodge, 1924) and the maximum size is 50 mm (Pegler et al., 1993). Montecchi and Sarasini (2000) report size between 10-30 mm, Türkoğlu et al. (2015) between 15-30 mm and Kaya and Uzun (2020) between 20-45 mm.

According to our observations, the total thickness of the peridium is variable when compared between different collections, basidiocarps, as well as in different places in one basidiocarp. For example, in the collection MCF17818 which is consisted of five basidiocarps, in one the measurements varied between 90-240 µm (MCF17818B) and in other basidiocarp between 130-350 µm (MCF17818D). In the other two collections which ave only one basidiocarp the dimensions are 110-270 μm (MCF19486) and 155-330 μm (MCF17051). However, the total thickness of the peridium never reached 500 µm as reported by Montecchi and Sarasini (2000) and Pegler et al. (1993) who report thickness between 200-500 µm. Different size of peridium thickness is reported by other authors as well, 220-520 μm (Türkoğlu et al., 2015), 200-400 μm (Kaya & Uzun, 2020). Interestingly, Fogel (1975) reports smaller dimensions between 85-100 µm while Zeller and Dodge (1924) report only that the peridium is very thin. In the original description in one place is noted that it does not possess a proper peridium, however the author later describes composition of parallel hyphae that form almost pseudoparenchymatic-looking layer and

secrete a brown mucous-like mass which replaces the peridium (Hazslinsky, 1875). Compared with some of the synonymized species, for *Leucogaster badius* is reported size between 200-340 μ m (Zeller & Dodge, 1924) and 120-190 μ m (Fogel, 1975), for *L. fragrans* (syn. *L. tozzianus*) 140-220 μ m (Zeller & Dodge, 1924) and 100-170 μ m (35-70 μ m after drying) (Fogel, 1975). Türkoğlu et al. (2015) reports *L. tozzianus* as separate species and provides measurements of total peridium thickness of 150-220 μ m.

Concerning the spore size in our observations they vary between 10-14 µm and that fits in the reported dimensions by almost all authors, 10-14 µm (Montecchi & Sarasini, 2000), 11-18 μm (Pegler et al., 1993), 13-16 (Fogel, 1975). Though, in the original description a narrower range is given, 16-18 µm and a different ornamentation of the spores which are described as having warty ornamentation (Hazslinsky, 1875). Sizes of the spores, of L. badius are 12-16 µm (Zeller & Dodge, 1924), 11-14 μm (Fogel, 1975) and 12-15 μm in the original description (Mattirolo, 1903). For L. fragrans (syn. L. tozzianus) the size of spores is 12 µm (Zeller & Dodge, 1924), 10-12 μm (Fogel, 1975) and 12 μm in the original description (Mattirolo, 1900). Türkoğlu et al. (2015) reports spore size of 9.7-11.4 μm for L. tozzianus while in the original description is 10-12 μm (Saccardo & Cavara, 1900).

At the moment is accepted that in Europe only one species of *Leucogaster* genus is present, *L. nudus*, while the species *L. floccosus*, *L. badius*, *L. fragrans* and *L. tozzianus* are regarded as synonyms due to lack of differential characters that could justify the distinction (Szemere, 1965; Montecchi & Sarasini 2000). The materials that are examined in this study correspond to the description of *L. nudus* provided by Montecchi and Sarasini (2000), Pegler et al. (1993), Fogel (1975) but when looking at the original description of *Hydnangium nudum* (Hazslinsky, 1875) the differences rose a suspicion whether the material of *H. nudum* belongs to *Leucogaster*.

Leucogaster nudus (Hazsl.) Hollós was first described by Hazslinsky in 1875 as Hydnangium nudum Hazsl. and it was later transferred to Leucogaster by Hollós (1908). Hollós compared the type material with L. fragrans Mattir., L. badius Mattir. and L. bucholtzii Mattir. therefore, concluded that H. nudum Hazsl. with no doubt belongs to Leucogaster genus. Also, Hollós (1908) based only on the drawings and description of L.

liosporus R. Hesse proposed L. liosporus as synonym to H. nudum. However, since he did not make comparison with the original material this was not accepted (Zeller & Dodge, 1924). Two of the species which he compared H. nudum with to make the transfer, L. fragrans and L. badius are species with reticulate spore ornamentation which is noted in the original description and is confirmed after examination of other authors (Zeller & Dodge 1924, Fogel 1975). Contradictory, another of the species which Hollós compared H. nudum with, L. bucholtzii has aculeate ornamentation as noted in the original description (Mattirolo, 1900) and confirmed by Zeller and Dodge (1924) who suggest that this might be only due to phases in spore development. In their publication this is explained as Leucophleps stage (page 402), though they provide description of species that have spores with echinate ornamentation as a stable character, as the species Leucophleps magnata Harkn. For the type species of Leucogaster, L. liosporus in the original description the ornamentation of the spores is not mentioned, just the presence of characteristic exoand endo-sporium that develops depending on the stage of development of the spores and that the protoplasm is finely grained (Hesse, 1882). Zeller and Dodge (1924) did not have the chance to observe the original material, but as it is stated in the publication, they examined material they believed it corresponded to the description of L. liosporus (exsiccate 2605a von Hoehnel Herbarium). Afterwards, Fogel (1979) examined the same material (exsiccate 2605a von Hoehnel Herbarium) and described new species Leucophleps aculeatispora Fogel that have aculeate ornamentation. Also, Fogel (1975) gives description of L. liosporus based on literature and materials he was able to obtain from Europe (2705a von Hoehnel Herbarium and PR 485777) and described spores with aculate ornamentation in those specimens. Therefore, when Hollós made the transfer of H. nudum to Leucogaster he compared the type material with species that have aculeate (L. bucholtzii and L. liosporus) and reticulate ornamentation (L. fragrans and L. badius). Additionally, the accepted synonym L. floccosus R. Hesse in the work of Zeller and Dodge (1924) is described by having echinulate spores with total diameter of 7-10 μm and the authors note that is quite distinct from L. fragrans (page 390) expressing surprise why it is regarded as synonym by some authors. Interestingly, Pilát (1937) for L. floccosus explains that the mature spores possess a reticulum, while in a paper by Honrubia and Llimona

(1981) they present *L.* cf. *floccosus* with smooth spores expressing suspicion that the material might be too young. It should be examined whether it is really a development stage, or it is maybe a species of *Leucophleps*.

In the original description of Hydnangium nudum Hazsl. (Hazslinsky 1875) concerning the spores, their size is between 16-18 μm and the ornamentation is described as warty (Latin description, page 64: "... Sporis globosis in apicibus hypharum evolutis, demum cum articulo hypharum coniformi deciduis; maturis ochraceis episporio pellucido verrucoso tectis, diametro 0.016—0.018 Mm."; German description, page 65: "Die vollkommen entwickelten Sporen hingegen besitzen alle ein durchsichtiges grosswarziges Episporiurn, welches mich am meisten bewog diesen Pilz als selbstständige Species anzuführen."). Also, according to the drawing (Taf. III, Figs 12-14) it looks like the spores have warty ornamentation and the author specifies that this character is the main reason why he described this as a new species.

Fogel (1975) compared the illustrations for Leucogaster nudus made by Hollos (1911), Hazslinsky (1875), Pilát (1937), Svrček (1958) and also examined material from Europe. He reviewed two collections from Hungary, one of Hazlinsky and one of Bresadola, one collection from then Czechoslovakia from Pilát (PR 37908) which had been labeled as Hydnangium virescens Quél. and two collections from Germany probably borrowed from Soehner [1147 (M) and 1193 (M)]. Then he presents a description with different spore size than the one of H. nudum and ornamentation that he states is aleveolate with prominent reticulations, but also mentions "ornamentation of spines" where he presents the high of the spines, obviously meaning on the high of ornamentation, not mentioning warts anywhere as in concordance with the rest of the description (page 72: "Basidiospores 13-16(-17) x (12-)13-14(-15) μm, including alveolate ornamentation, globose, enclosed in a hyaline perisporal sac; ornamentation of spines 1 µm high, 3 µm apart, alveoli 5-6 sided, reticulations prominent, spore wall 1.5-2 µm thick, excluding ornamentation"). He proposes synonymy of L. tozzianus and L. fragrans, as previously proposed by Zeller and Dodge (1924). However, Fogel (1975) is not proposing synonymy of L. nudus with L. badius and L. tozzianus noting that the size of the spores of L. nudus are larger, though with the description he provides, he sets bigger spore range, therefore the sizes of spores of these spe-

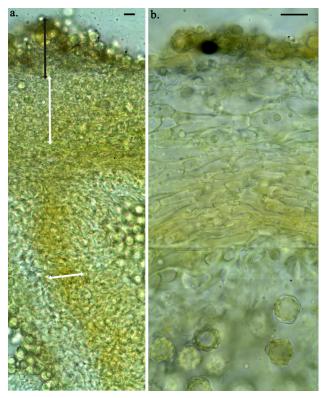


Fig. 3. *Leucogaster nudus*. a. cross-section, external peridium (black arrow), internal peridium (white arrow vertical), tramal plate between chambers (white arrow horizontal). b. details of the structure of peridium, composed of parallel hyphae, swollen and elongated at places resembling to pseudoparenchymatous tissue. Scale bar: a-b. 10 μm. Slides are prepared in Meltser's reagent. (MCF17818)

cies are overlapping. There is also overlapping between these species in another important characters as the peridium width. It is worth to mention that in the original description, Hazslinsky (1875) reports that the basidiocarp does not possess proper peridium which is probably the reason for the name of the species "nudum – naked", though in the same description later he describes peridium of parallel hyphae, as mentioned above.

Based on the comparison of the descriptions of *L. nudus* and the taxa regarded as its synonyms from the available literature, we suspect that it is possible the collection Hazslinsky (1875) described under the name *Hydnangium nudum* has different characteristics compared to the collections that have been examined by subsequent researchers. It is necessary to make a revision of the holotype of *H. nudum* and to compare it with *L. fragrans*, *L. tozzianus* and *L. badius* which, according to the authors mentioned above, have reticu-

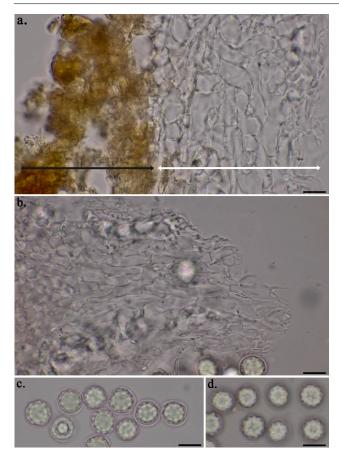


Fig. 4. *Leucogaster nudus*. a. external peridium brown, hyphae covered with crystal mass (black arrow), internal peridium of parallel hyphae looking like pseudoparenchym (white arrow). b. hyphae of tramal plate, elongated and swollen at places. c-d. basidiospores, focus on shape where the perisporium is easily observed (c), focus on reticulate ornamentation (d). Scale bar: a-d. 10 μm. Slides prepared in 3% KOH. (a-b. MCF19486, c-d. MCF17818)

late ornamentation. Comparison is also necessary with *L. floccossus* that might have warty ornamentation, as well as with *L. bucholtzii*. An in-depth revision on genus *Leucogaster* along with *Leucophles* in Europe is needed with an aim to precisely determine the morphological characters and their phylogeny. In the NCBI data base only 44 sequences are annotated as *Leucogaster* (Accessed date: 18 September 2023), most of them determined only to genus level, while for *L. nudus* only one sequence from Italy is available.

With this detail overview of the characteristics of *Leucogaster nudus* form literature, and the presented results from the observed material we hope to contribute and encourage a further in detail research on this species and the genus.

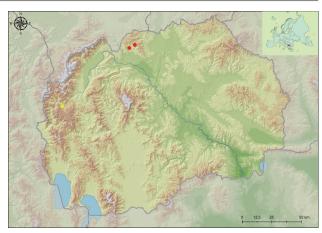


Fig. 5. Distribution of *Leucogaster nudus* (Hazsl.) Hollós.

• - New location • - Previously known location.

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