

Diversity and distribution of coprophilous *Saccobolus* species in Ukraine

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Abstract: This study provides the first comprehensive account of the genus *Saccobolus* in Ukraine. Fourteen species are listed and discussed, with data on their distribution and substrate preferences. Detailed morphological descriptions and photomicrographs of Ukrainian collections of *Saccobolus diffusus*, *S. dilutellus*, and *S. succineus* are presented here for the first time. The most frequently recorded taxa in Ukraine were *S. citrinus*, *S. depauperatus*, *S. minimus*, *S. saccoboloides* and *S. truncatus*. In contrast, *S. caesariatus*, *S. diffusus*, *S. dilutellus*, *S. obscurus*, *S. succineus* and *S. thaxteri* appear to be rare in Ukraine, several of which are also globally uncommon. *Saccobolus glaber*, *S. verrucisporus* and *S. versicolor* are widespread but infrequently recorded in Ukraine. An updated identification key to all coprophilous species of *Saccobolus* recorded in Ukraine is presented.

Key words: coprophilous fungi, distribution, Eastern Europe, identification key, new records, Pezizales, taxonomy

INTRODUCTION

In the family Ascobolaceae, the genus *Saccobolus* is the second most species-rich, after *Ascobolus*. Both genera are globally distributed dung-inhabiting ascomycetes (Richardson, 2007). Despite morphological and ecological similarities, they differ diagnostically: *Saccobolus* has densely clustered ascospores and usually shorter, broadly clavate asci, unlike *Ascobolus* (van Brummelen, 1967; Doveri, 2004; Melo et al., 2014). The pattern of spore aggregation within clusters is an important taxonomic feature of the genus. Van Brummelen (1967) recognized six main patterns of aggregation, some with additional subtypes.

Saccobolus comprises saprotrophs mostly developing on animal dung; however, several species, including *S. obscurus* and *S. saccoboloides*, have also been reported from soil, decaying textiles, and other plant-derived materials (van Brummelen, 1967; Wijayawardene et al., 2017; Van Vooren & Meyer, 2010). Some species are homothallic, likely as an adaptation to this specialized substrate, resulting in sexual isolation (Ranalli, 1974; Ramos et al., 2011).

The only comprehensive monograph on *Saccobolus* and *Ascobolus* is that of van Brummelen (1967), describing 18 *Saccobolus* species. He

divided the genus into two sections: *Saccobolus* sect. *Saccobolus*, with yellow or amber receptacles and hymenial discs containing pigmented paraphyses, and *Saccobolus* sect. *Eriobolus*, with white, pale purple, purple, or brown receptacles and hyaline paraphyses. Several new species were added in the following decades (van Brummelen, 1969; Aas, 1978; O'Donnell, 1978; Kaushal & Viridi, 1986; Dissing, 1987, 1989; Prokhorov & Raitviir, 1991), gradually expanding the genus concept. Recent publications indicate that approximately 45 species of *Saccobolus* are currently recognized worldwide (Hyde et al., 2024).

Since the 2000s, biochemical and molecular methods have complemented classical morphological approaches in *Saccobolus* taxonomy, helping to clarify species boundaries and intra-specific variation (Ramos et al., 2000, 2011). AFLP markers have been applied to assess genetic diversity and delimit several species within the genus (Ramos et al., 2011). However, molecular data for *Saccobolus* remain very limited, and available phylogenetic studies based on DNA sequence data are still insufficient.

In the broader context of coprophilous fungi, molecular approaches are increasingly employed. Yet traditional taxonomy remains predominant, with most studies relying on

morphology, and only a few incorporating phylogenetic data to describe or revise species (Calaça et al., 2023). Over the past decades, studies focusing on the taxonomy or revision of *Saccobolus* species diversity have been published worldwide: in European countries (van Brummelen, 1967; Larsen, 1970; Moravec, 1970; Caillet & Moyne 1982; Prokhorov, 1989; De Sloover, 2002; Doveri, 2014); in Asia (Kaushal & Viridi, 1986; Abdullah & Alutbi, 1993; Yattoo et al., 2021); in Africa (Mungai et al., 2012; Calaça et al., 2023); in North America, including Greenland (O'Donnell, 1978; Dissing, 1987, 1989); in South America (Ranalli & Mercuri, 1995; Melo et al., 2014); and in Australia and New Zealand (Bell, 1983, 2005).

Published information on *Saccobolus* in Ukraine is sparse and not consolidated. The first records appeared in the late 1930s, with only *S. versicolor* (P. Karst.) P. Karst. reported (Milovtsova, 1937). A significant contribution was made by Prokhorov (1991), who recorded 37 coprophilous discomycetes for Ukraine, including eight *Saccobolus* species. Since the early 2000s, the authors of this article and other researchers have continued studying coprophilous fungi in Ukraine, reporting new records of *Saccobolus* species (Golubtsova, 2009; Golubtsova et al., 2010; Yatsiuk, 2017; Lytvynenko et al., 2018). Despite these efforts, published data remain fragmentary, and current taxonomic guides do not allow reliable species-level identification of *Saccobolus*. Earlier identification keys, include only two species (Smitska, 1980). Therefore, revising the diversity and distribution of *Saccobolus* in Ukraine and providing an updated dichotomous key are essential for improving taxonomic knowledge of the genus.

MATERIAL AND METHODS

The study was based on herbivore dung samples collected during field studies conducted between 2005 and 2023, from which apothecia were subsequently obtained in moist-chamber culture under laboratory conditions. In addition, published records of *Saccobolus* species from Ukraine were critically analyzed (Milovtsova, 1937; Prokhorov, 1991; Yatsiuk, 2017).

Apothecia were obtained using the moist-chamber incubation method (Richardson, 2001, 2007). Previously collected dung samples were

placed in Petri dishes on moistened filter paper and incubated at room temperature (18–22 °C) under natural light. Humidity was maintained by adding water when necessary. Samples were examined regularly using a stereomicroscope during the incubation period.

The examined material is deposited in the National Herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (KW), the Herbarium of V.N. Karazin Kharkiv National University (CWU(Myc)), and the Herbarium of Taras Shevchenko National University of Kyiv (KWU). The species localities in the text are organized according to the map of the physiographic regions of Ukraine proposed in the Flora of Fungi of Ukraine by Heluta (2022). Geographic coordinates together with information on collectors and identifiers have been published as open-access occurrence records in GBIF datasets (Govorun et al., 2024; Lytvynenko et al., 2025). In addition, several historical records not represented in GBIF datasets were included based on literature sources. The fungal species names and author citations follow the nomenclature used in the Index Fungorum database (<https://www.indexfungorum.org/>).

To observe the surface of the dung and the morphology of the apothecia, a stereomicroscope SM-6630 ZOOM (MICROmed, China) was used. Apothecial structures were studied using light microscopes MB-302 LED Trino (Sigeta, Ukraine) and XSM-40 (Ningbo Sunni Instruments Co., China). Measurements of microstructures were performed using the modular software Tsview7 (Fuzhou Tucsen Imaging Technology Co., China). Photomicrographs were taken with a 3.0 MP digital microscope camera (Fuzhou Tucsen Imaging Technology Co., China).

The fungal specimens were studied following standard mycological methods (Senanayake et al., 2020). Microscopic features were studied from fresh squash mounts prepared from apothecia. Microstructures mounted in distilled water were examined at magnifications up to 600×. Thirty spores and twenty asci per specimen were measured. The following abbreviations are used for spore sizes: Q = quotient of spore length to width (L/W), Qav = average quotient. The amyloid reaction of the apical

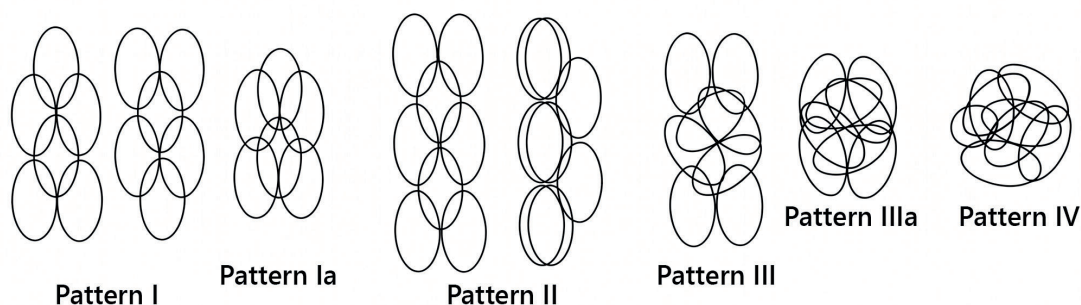


Fig. 1. Patterns of ascospore arrangement in Ukrainian species of *Saccobolus* according to van Brummelen (1967).

apparatus and ascus walls was tested using Meltzer's reagent (MLZ). To highlight the hyaline gelatinous sheath of the spores, Lactophenol Cotton Blue (LPCB) was used. The patterns of ascospore arrangement within the clusters are presented according to van Brummelen (1967) (Fig. 1).

For scanning electron microscopy (SEM), small dried pieces of dung with apothecia were mounted directly on metal stubs. The samples were coated with an ultrathin layer of silver using a vacuum coater VUP-5M (OJSC "Selmi", Ukraine) and examined with a scanning electron microscope SEO-SEM Inspect S50-B (Sumy Electron Optics, Ukraine). SEM studies were conducted at the Center for Collective Use of Scientific Equipment, Laboratory of Materials Science for Helium Energy, Sensory, and Nanoelectronic Systems, Sumy State University, Ukraine.

RESULTS AND DISCUSSION

Currently, 14 species of *Saccobolus* are known from Ukraine, 12 of which have been confirmed through the authors' own research. Two additional species, *S. obscurus* (Cooke) W. Phillips and *S. thaxteri* Brumm., are included based on previously published records (Prokhorov, 1991; Yatsiuk, 2017). Since detailed morphological descriptions and photomicrographs of Ukrainian collections of *S. diffusus* S.C. Kaushal & Virdi, *S. dilutellus* (Fuckel) Sacc., and *S. succineus* Brumm. have not been published previously, they are presented here. In addition, this study provides the first consoli-

dated identification key to the genus *Saccobolus* in Ukraine.

1. Taxonomy

Saccobolus caesariatus Renny

Distribution in Ukraine. Left Bank Grass Steppe, Left Bank Polissya; on dung of horse and hare (Prokhorov, 1991; Lytvynenko et al., 2025).

Specimen examined. SUMY REGION – Shostka District, Ochkyne village, on hare dung, 15 Jun 2005, Yu. Lytvynenko, KWU 63918.

Notes. Published data indicate considerable variation in the ascospore dimensions of *Saccobolus caesariatus*. Prokhorov (1991) reported relatively smaller spores from Ukrainian material, whereas van Brummelen (1967), Doveri (2004), and Prokhorov (2004) reported somewhat larger values. Measurements obtained from the Ukrainian specimen examined in the present study ($17\text{--}18.5 \times 7.5\text{--}8.5 \mu\text{m}$) generally agree with the latter reports.

Saccobolus citrinus Boud. & Torrend.

Distribution in Ukraine. Carpathian Forests, Crimean Steppe, South Coast of Crimea, Kharkiv Forest-Steppe, Left Bank Forest-Steppe, Left Bank Polissya; on dung of sheep, cattle, goat, horse and rabbit (Lytvynenko et al., 2025).

Selected specimens examined. CRIMEA – Alushta city council, Luchyste village, on horse dung, 2 Jul 2008, O. Akulov, CWU(Myc) 2873. SUMY REGION – Konotop District, Buryn town, on goat dung, 7 Aug 2019, T. Khandiuk, KWU 67918; on cattle dung, 20 Jul 2019, T. Khandiuk, KWU 68918; Vyrivka village, on rabbit

dung, 27 Jul 2019, N. Velychko, KWU 69918. Okhtyrka District, Kuzemyn village, on goat dung, 23 Jul 2023, Yu. Lytvynenko, KWU 64918; Lutyshche village, on horse dung, 21 May 2015, Yu. Lytvynenko, KWU 65918; Striletska Pushkarka village, on cattle dung, 28 Jun 2015, Yu. Lytvynenko, KWU 66918. Shostka District, Znob-Novhorodske settlement, on rabbit dung, 16 Jul 2015, Yu. Lytvynenko, KWU 70918. Sumy District, Nyzhna Syrovatka village, on cattle dung, 16 Jun 2015, A. Butsyk, KWU 71918; Stets'kivka village, on cattle dung, 6 Sep 2010, S. Kravtsov, KWU 72918; Markivka village, on rabbit dung, 28 Aug 2013, V. Stepanovska, KWU 73918.

Notes. *Saccobolus citrinus* shows considerable variability in ascospore dimensions. Van Brummelen (1967) reported a broad range of $16\text{--}22\text{--}(23) \times 7.5\text{--}9\text{--}(9.5) \mu\text{m}$. Smaller spores were recorded in New Zealand material ($13\text{--}15 \times 6\text{--}7 \mu\text{m}$; Bell, 1983), while collections from Australia ($17\text{--}20 \times 8\text{--}10 \mu\text{m}$; Bell, 2005) and Kenya ($17\text{--}21 \times 8\text{--}9 \mu\text{m}$; Mungai et al., 2012) fall near the lower limits of this range. Conversely, Italian ($20\text{--}22 \times 9\text{--}9.5 \mu\text{m}$; Doveri, 2014) and Brazilian specimens ($20\text{--}23 \times 7.5\text{--}11 \mu\text{m}$; Melo et al., 2014) tend to be larger, in line with data from Prokhorov (2004) – $19.4 \times 8.9\text{--}9.2 \mu\text{m}$. Our own material also shows spores exceeding $20 \mu\text{m}$ ($20\text{--}22 \times 8.5\text{--}9.0 \mu\text{m}$), whereas two Ukrainian collections described by Prokhorov (1991) yielded smaller values ($16.5\text{--}18.5 \times 6.0\text{--}8.0 \mu\text{m}$), suggesting intraspecific variability.

Saccobolus depauperatus (Berk. & Broome) E.C. Hansen

Distribution in Ukraine. Carpathian Forests, Central (Right Bank) Polissya, Kharkiv Forest-Steppe, Left Bank Forest-Steppe, Left Bank Grass Steppe, Left Bank Polissya, Mountain Crimea, Polynovyi (Artemisia) Steppe, Right Bank Forest-Steppe, South Coast of Crimea; on dung of cattle, elk, goat, hare, horse, roe deer and sheep (Lytvynenko et al., 2025).

Selected specimens examined. CRIMEA – Alushta city council, Demerdzhy Mountain, on horse dung, 2 Jul 2008, O. Akulov, CWU(Myc) 2846; Yalta city council, Ai-Petri Mountain, on horse dung, 1 Jul 2008, O. Akulov, CWU(Myc) 2867. KHERSON REGION – Skadovsk District, on hare dung, 7 Jul 2020, K. Orlova-Hudim, KWU 74918; Dzharylhach Island, on roe deer dung,

23 Jul 2020, K. Orlova-Hudim, KWU 75918; Tendra Spit, on horse dung, 23 May 2007, V. Hayova, KW 50610; Tendra Spit, Cape Bili Kuchuhury, on horse dung, 25 May 2007, V. Hayova, KW 50651. SUMY REGION – Sumy District, Nyzy village, on goat dung, 5 Sep 2014, A. Butsyk, KWU 76918; on horse dung, 11 Jul 2014, A. Butsyk, KWU 77918; Myrne village, on roe deer dung, 6 Jun 2019, Yu. Lytvynenko, KWU 78918. Shostka District, Ochkyne village, on elk dung, 15 Jun 2005, Yu. Lytvynenko, KWU 79918; Stara Huta village, on horse dung, 24 May 2005, Yu. Lytvynenko, KWU 80918; on roe deer dung, 22 Jun 2017, Yu. Lytvynenko, KWU 81918. TRANSCARPATHIAN REGION – Rakhiv District, Petros Mountain, on goat dung, 27 Aug 2015, Yu. Shcherbakova, KWU 45918; on horse dung, 27 Aug 2015, Yu. Shcherbakova, KWU 01918; on sheep dung, 27 Aug 2015, Yu. Shcherbakova, KWU 07918.

Notes. *Saccobolus depauperatus* resembles *S. versicolor* but the latter has larger apothecia, asci, ascospores, and spore clusters (van Brummelen, 1967; Doveri, 2004). The excipulum in *S. depauperatus* is mainly *textura globulosa*, unlike the *t. intricata* of *S. versicolor*. Its paraphyses and excipular cells lack intercellular pigment, producing a whitish hymenium rather than the pale purple typical of *S. versicolor* (van Brummelen, 1967; De Sloover, 2002; Doveri, 2004), though van Brummelen (1967) noted that pigmentation may sometimes be faint.

Saccobolus diffusus S.C. Kaushal & Virdi (Fig. 2). Description. Apothecia scattered or gregarious, semi-immersed to superficial, sessile, globose at first, becoming discoid at maturity, 0.8–2.0 mm diam. Hymenial disc greenish yellow, plane or concave, dark-dotted, with a few black protruding tips of asci at maturity; margin distinct, entire. Hypothecium thin, *textura globulosa*. Medullary excipulum not well delineated. Ectal excipulum of *t. globulosa-angularis*, $7.5\text{--}13.5 \times 7.0\text{--}9.5 \mu\text{m}$. Asci 8-spored, $121\text{--}175 \times 27.5\text{--}35.5 \mu\text{m}$, broadly clavate, operculate, somewhat flattened at the apex, with short stout and lobate stipe, rather long-stalked, weakly amyloid. Paraphyses numerous, exceeding the asci in length, cylindric-filiform, $2.5\text{--}3.5 \mu\text{m}$ diam. at the base, simple, septate, slightly inflated at the tips, containing greenish-yellow pigments. Spore clusters compact, with ascospores in four rows of two longi-

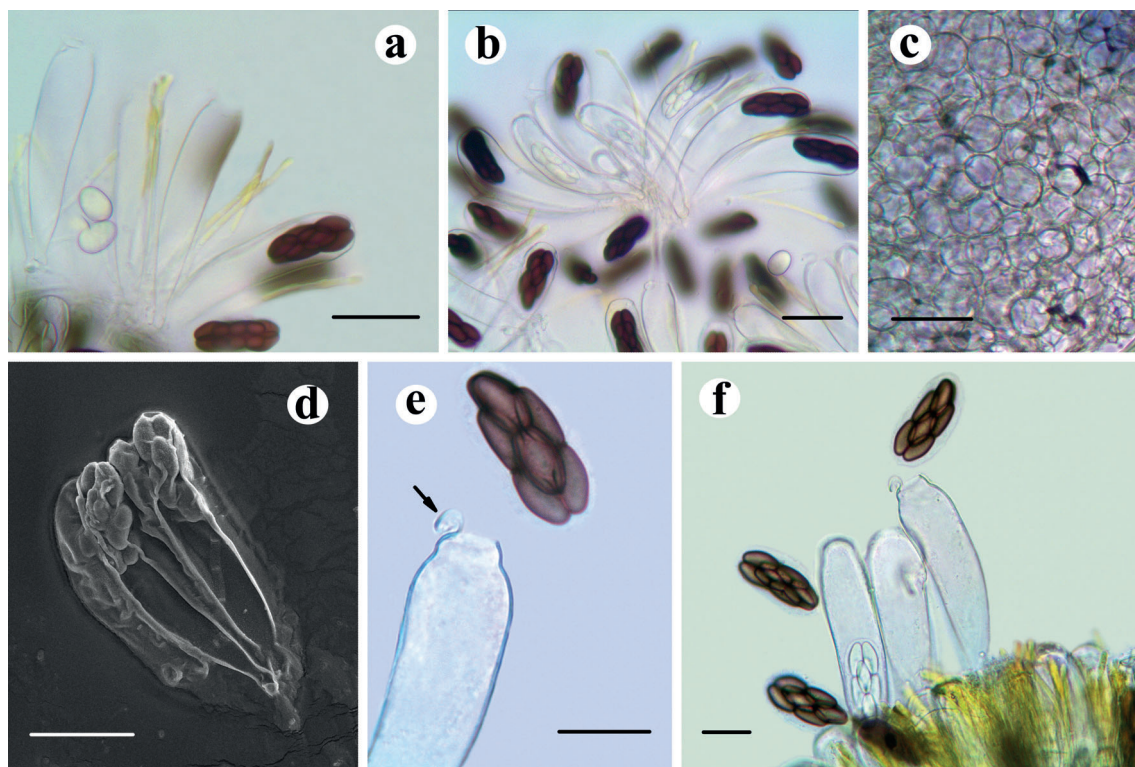


Fig. 2. *Saccobolus diffusus*: a – asci surrounded by paraphyses; b – asci containing spore clusters at various stages of maturity; c – excipular cells; d – asci with ascospores; e – apex of an empty ascus showing the operculum (arrow) and a mature spore cluster; f – asci, spore clusters, and paraphyses with pigmented apices; a–c, e–f from fresh material mounted in water; d under SEM. Scale bars: a, b, d = 50 μ m; c = 20 μ m; e, f = 25 μ m. Photos by Yulia Lytvynenko.

tudinally disposed spores and two longitudinal planes of symmetry (van Brummelen pattern I) (Fig. 1), $47.4\text{--}55.2 \times 15.4\text{--}18.6$ μ m, with a rather narrow gelatinous sheath of 2–5 μ m in the polar region and 4–8 μ m along the sides. Ascospores aseptate, $21.2\text{--}23.8 \times 8.4\text{--}9.8$ μ m, $Q=2.39\text{--}2.48$, $Q_{av}=1.42$; ellipsoidal, roundish at the ends, equilateral, smooth, sometimes with some irregular cracks, hyaline at first, purplish at maturity, turning brown with age.

Distribution in Ukraine. Left Bank Forest-Steppe; on cattle and goat dung (Lytvynenko et al., 2025).

Specimens examined. SUMY REGION – Konotop District, Mykhailivka village, on cattle dung, 18 Jul 2019, T. Khandiuk, KWU 82918; on goat dung, 7 Aug 2019, T. Khandiuk, KWU 83918.

Notes. *Saccobolus diffusus* is similar to *S. citrinus*, but differs in ascospore morphology: in *S. citrinus*, the ascospores are distinctly truncate at both ends and ornamented with isolated warts, whereas the ascospores of *S. diffusus* have rounded ends and are smooth or occasionally finely punctate (Kaushal & Virdi, 1986; Doveri, 2004) (Fig. 2e). Another similar species, *S. glaber*, has golden-yellow to amber apothecia, larger asci, spore clusters, and ascospores, and shows paraphyses-like hyphae in the upper excipulum (Kaushal & Virdi, 1986; Doveri, 2004). Doveri (2004) considered *S. diffusus* a morphotype, i.e., a depauperate form, of *S. glaber*.

Saccobolus dilutellus (Fuckel) Sacc. (Fig. 3). Description. Apothecia scattered to gregarious, superficial, sessile, subglobose in the early

stages, pulvinate to almost discoid at maturity, 0.5–1 mm diam. Hymenial disc convex or flat, at first white, then often pale violet, dark-dotted with a few black protruding tips of mature asci; margin not differentiated. Hypothecium and medullary excipulum thin, not well delineated; ectal excipulum of *textura globulosa-angularis*, cells $5.5\text{--}7.5 \times 4\text{--}6.5 \mu\text{m}$. Asci 8-spored, $71\text{--}88 \times 17.5\text{--}20.5 \mu\text{m}$, broadly clavate, operculate, somewhat flattened at the apex, with a short lobate stipe, weakly amyloid. Paraphyses numerous, exceeding the asci, cylindrical, $2.5\text{--}3.5 \mu\text{m}$ diam. at the base, simple, septate, slightly inflated at the tips, without pigmentation. Spore

clusters compact, subglobose to ellipsoidal, arranged according to van Brummelen pattern IV (Fig. 1), $23.5\text{--}26.3 \times 14.8\text{--}19.4 \mu\text{m}$; gelatinous sheath not observed. Ascospores aseptate, $12.6\text{--}14.7 \times 7.2\text{--}8.1 \mu\text{m}$, $Q=1.65\text{--}2.01$, $Q_{av}=1.81$; ellipsoidal, sometimes asymmetrical or even slightly triangular, hyaline at first, brownish-violet with age; ascospore surface ornamented with minute warts densely grouped along the line of contact between spores, while the free surface bears fine warts evenly distributed over the pigmented area; pigmentation is restricted to the exposed side of the spores.

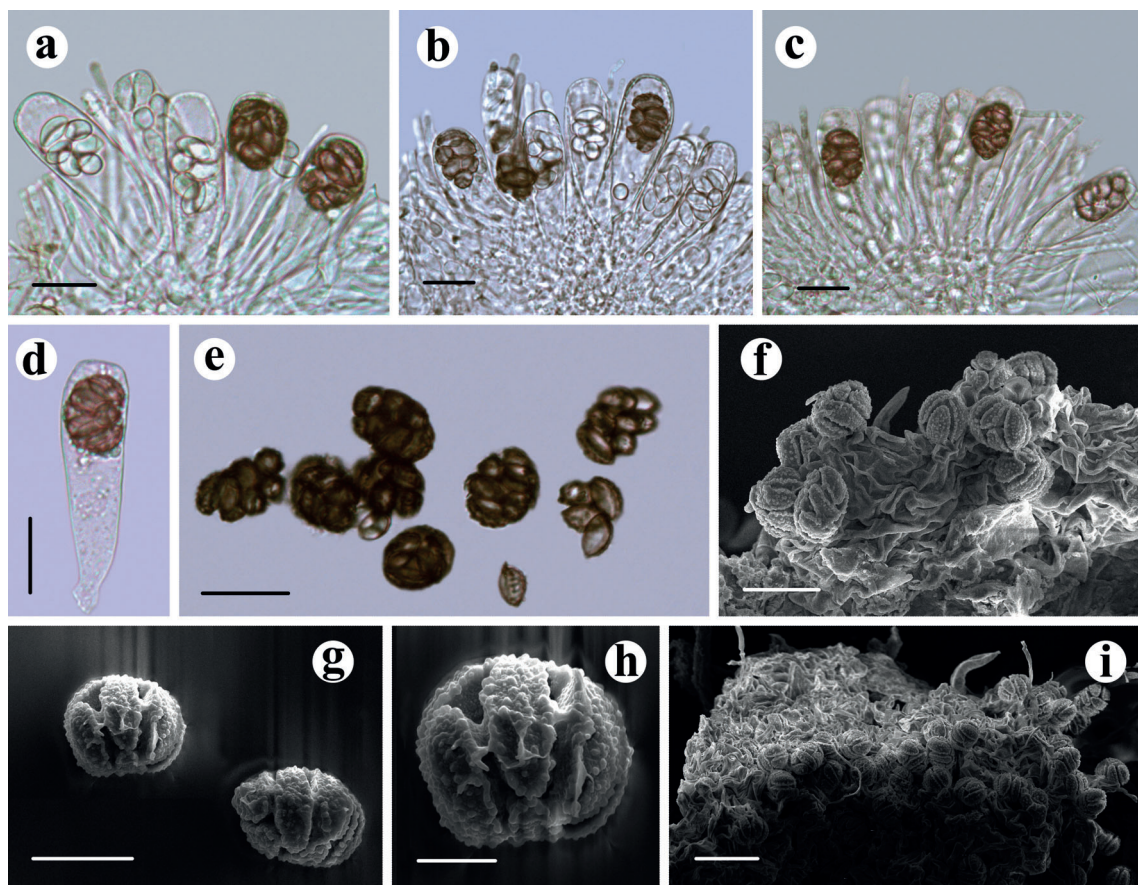


Fig. 3. *Saccobolus dilutellus*: a, b, c – asci containing spore clusters at different stages of maturity and paraphyses; d – ascus with a mature spore cluster; e – mature compact spore clusters with a separated ascospore; f – mature spore clusters; g, h – mature spore clusters showing the warty ornamentation of the ascospore walls; i – detail of the hymenial surface with released spore clusters; a–e from fresh material mounted in water; f–i under SEM. Scale bars: a–c, g = 20 μm ; d, e, f = 25 μm ; h = 10 μm ; i = 50 μm . Photos by Yulia Lytyvnenko.

Distribution in Ukraine. Left Bank Forest-Steppe; on goat and rabbit dung (Lytvynenko et al., 2025).

Specimens examined. SUMY REGION – Konotop District, Buryn town, on goat dung, 3 Apr 2019, T. Khandiuk, KWU 84918; on rabbit dung, 1 Oct 2019, T. Khandiuk, KWU 85918.

Notes. *Saccobolus dilutellus* is the only species in Ukraine with ascospores arranged in subglobose to ellipsoidal clusters (van Brummelen pattern IV). Morphologically, *S. dilutellus* is very similar to *S. globuliferellus*, and some authors consider these as conspecific (Doveri, 2004; Richardson, 2007). The main diagnostic trait of *S. dilutellus* is the compactness of spore clusters, with ascospores positioned more closely together. Van Brummelen (1967) considered these taxa extreme variants of a morphological continuum, where ascospore ornamentation correlates with cluster compactness. In *S. dilutellus*, episporium ornamentation is concentrated on the free surface of the ascospores: at the contact line, a band of large, closely appressed, darkly pigmented warts is formed (Fig. 3g–h), while the inner surface facing the cluster's interior remains smooth. By contrast, in *S. globuliferellus*, pigmentation and fine warts evenly cover the entire ascospore surface (van Brummelen, 1967; Doveri, 2004). Larsen (1970) also noted ascus shape as distinctive: in *S. dilutellus*, the asci are elongated, cylindric-clavate (Fig. 3d), whereas in *S. globuliferellus*, they are broader and subpyriform. Another difference is the stronger asymmetry of *S. dilutellus* ascospores, especially at maturity. Van Brummelen (1967) noted that although *S. dilutellus* ascospores form tightly aggregated subglobose clusters, they can be readily separated in preparations from fresh material (Fig. 3e). In immature asci, the ascospores are free (Fig. 3a–b), aggregating into compact clusters only during or after maturation, which then become progressively shortened and consolidated.

Saccobolus glaber (Pers.) Lambotte.

Distribution in Ukraine. Kharkiv Forest-Steppe, Left Bank Forest-Steppe; on dung of cattle, goat, horse and sheep (Lytvynenko et al., 2025).

Selected specimens examined. SUMY REGION – Konotop District, Buryn town, on cattle dung, 20 Jul 2018, T. Khandiuk, KWU 86918; on goat dung, 22 Jul 2019, T. Khandiuk, KWU 87918;

Vyryvka village, on horse dung, 17 Jul 2019, T. Khandiuk, KWU 88918. Okhtyrka District, Khukhra village, on horse dung, 21 Sep 2015, Yu. Lytvynenko, KWU 89918; on sheep dung, 20 Sep 2015, Yu. Lytvynenko, KWU 90918. Sumy District, Markivka village, on cattle dung, 27 Aug 2013, N. Stepanovska, KWU 91918; Verkhsulka village, on goat dung, 14 Jul 2013, N. Stepanovska, KWU 92918.

Notes. Specimens examined in the present study fully match the diagnostic features of *S. glaber*. This species was first reported in Ukraine by Prokhorov (1991) from the Left-Bank Forest-Steppe, based on material characterized by yellow-green apothecia and relatively small ascospores. These characters partially overlap with those reported for *S. diffusus*, a species also recorded in the present study. However, the original material examined by Prokhorov was not available for revision.

Saccobolus minimus Velen.

Distribution in Ukraine. Kharkiv Forest-Steppe, Left Bank Forest-Steppe, Left Bank Grass Steppe, Left Bank Polissya, Mountain Crimea, South Coast of Crimea, Polynovy (Artemisia) Steppe; on dung of cattle, donkey, European mouflon, goat, horse, roe deer, wild boar (Govorun et al., 2024; Lytvynenko et al., 2025).

Selected specimens examined. CRIMEA – Alushta city council, Demerdzhy Mountain, on cattle dung, 2 Jul 2008, O. Akulov, CWU(Myc) 2942; on horse dung, 2 Jul 2008, O. Akulov, CWU(Myc) 2846. KHERSON REGION – Skadovsk District, Tendra Spit, on horse dung, 23 May 2007, V. Hayova, KW 50632; Dzharlyhach Island, on European mouflon dung, 23 Jul 2020, K. Orlova-Hudim, KWU 93918. SUMY REGION – Konotop District, Buryn town, on goat dung, 21 Aug 2018, T. Khandiuk, KWU 94918; Konotop city, on horse dung, 9 Jul 2018, N. Velychko, KWU 95918. Shostka District, Stara Huta village, on roe deer dung, 23 Apr 2017, Yu. Lytvynenko, KWU 96918. Sumy District, Luhove village, on cattle dung, 26 Aug 2014, A. Butsyk, KWU 97918; Sad village, on donkey dung, 27 Jun 2020, Yu. Lytvynenko, KWU 98918; Verkhnia Syrovatka village, on goat dung, 16 Jul 2015, A. Butsyk, KWU 99918; Nyzy village, on roe deer dung, 12 Jan 2015, A. Butsyk, KWU 01919; on wild boar dung, 27 Jul 2015, A. Butsyk, KWU 02919.

Notes. *Saccobolus minimus* is readily identified by its small ascospores. Although *S. depauperatus* has ascospores of similar size, its fruiting bodies are white to pale violet, unlike the amber to ochre-yellow coloration of *S. minimus*. Moreover, these species also differ in ascospore aggregation: *S. depauperatus* forms spore clusters with pattern II or III, while *S. minimus* shows pattern I. Occasionally, *S. depauperatus* may also produce clusters with ascospores arranged according to pattern I, which can result in misidentification between the two species. Among Ukrainian species, *S. succineus* is morphologically closest, forming pattern I clusters with small, warted ascospores, yet smaller spores and more compact clusters distinguish *S. minimus*.

Saccobolus obscurus (Cooke) W. Phillips
Distribution in Ukraine. Central (Right Bank) Polissya, Left Bank Grass Steppe, Right Bank Forest-Steppe; on dung of hare and roe deer (Prokhorov, 1991).

Notes. *Saccobolus obscurus* belongs to the group of species with coarsely warted ascospores, including *S. thaxteri* and *S. verrucisporus*. According to the literature, *S. thaxteri* differs from *S. obscurus* by smaller ascospores and an unpigmented excipulum and hymenium (van Brummelen, 1967; Van Vooren & Meyer, 2010; Doveri, 2014). *Saccobolus verrucisporus* differs by coarser ascospore ornamentation, persistent uncontracted spore clusters at maturity, and paler excipular pigmentation.

Saccobolus saccoboloides (Seaver) Brumm.
Distribution in Ukraine. Carpathian Forests, Kharkiv Forest-Steppe, Left Bank Forest-Steppe, Left Bank Grass Steppe, Left Bank Polissya, Starobilsk Grass-Meadow Steppe; on dung of cattle, goat, horse, rabbit, red deer, roe deer, sheep (Govorun et al., 2024; Lytvynenko et al., 2025).

Selected specimens examined. KHERSON REGION – Skadovsk District, Tendra Spit, Cape Bili Kuchuhury, on cattle dung, 22 May 2007, V. Hayova, KW 50609; Kinburn Peninsula, on horse dung, 12 Oct 2006, M. Prydiuk, KW 50659. SUMY REGION – Konotop District, Buryn town, on goat dung, 27 Feb 2019, T. Khandiuk, KWU 03919; Konotop city, on cattle dung, 12 Jul 2018, N. Velychko, KWU 04919; Popivka village, on cattle dung, 13 Jul 2018,

N. Velychko, KWU 05919. Shostka District, Stara Huta village, on roe deer dung, 22 Apr 2017, Yu. Lytvynenko, KWU 06919; Znob-Novhorodske settlement, on rabbit dung, 15 Jun 2015, Yu. Lytvynenko, KWU 07919. Sumy District, Lutsykvika village, on horse dung, 13 Aug 2013, N. Stepanovska, KWU 08919; Markivka village, on cattle dung, 27 Aug 2013, N. Stepanovska, KWU 09919; Nyzy village, on red deer dung, 11 Aug 2015, A. Butsyk, KWU 10919. TRANSCARPATHIAN REGION – Rakhiv District, Petros Mountain, on goat dung, 27 Aug 2015, Yu. Shcherbakova, KWU 11918; on sheep dung, 27 Aug 2015, Yu. Shcherbakova, KWU 07918; on goat dung, 28 Aug 2015, Yu. Shcherbakova, KWU 40918.

Notes. *Saccobolus saccoboloides* is characterized by delicate spore clusters that disperse at maturity, a feature shared only with *S. michiganensis* O'Donnell. In both species, ascospores are initially loosely aggregated but separate at maturity. *S. michiganensis* differs by smaller apothecia, asci, and smooth ascospores (O'Donnell, 1978; Wang, 1996), whereas *S. saccoboloides* may have a finely dotted episporium. Due to their morphological similarity, *S. saccoboloides* can be misidentified as *S. michiganensis*, which is known from North America and Taiwan (Wang, 1996).

Saccobolus succineus Brumm. (Fig. 4).

Description. Apothecia scattered or gregarious, sessile, superficial, globose at first, becoming discoid at maturity, 0.8–1.5 mm diam. Hymenial disc pale yellow to amber-coloured, plane or concave, dark-dotted with a few black protruding tips of mature asci; margin distinct, entire. Hypothecium and medullary excipulum thin, not well delineated; ectal excipulum of *t. globulosa-angularis*, cells 7.5–10.5 × 6.0–9.5 µm. Asci 8-spored, 108–146 × 25–40 µm, broadly clavate, operculate, somewhat flattened at the apex, with short stout and lobate stipe, weakly amyloid. Paraphyses numerous, exceeding the asci, cylindric-filiform, 3–3.5 µm diam. at the base, simple, septate, slightly inflated at the tips, containing amber-coloured substance. Spore clusters compact, with ascospores in four rows of two longitudinally disposed spores and two longitudinal planes of symmetry (van Brummelen pattern I) (Fig. 1), 46.5–52.7 × 15.3–18.7 µm, with a rather narrow gelatinous sheath of 3–4 µm in the polar region and 4–

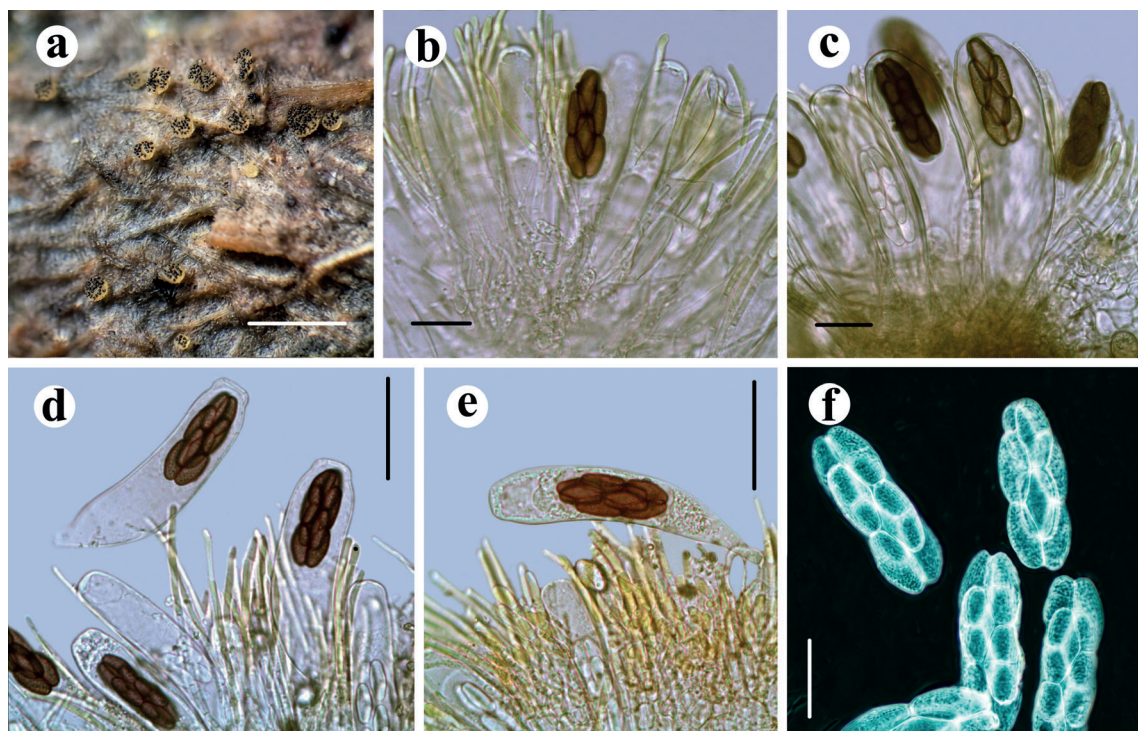


Fig. 4. *Saccobolus succineus*: a – apothecia on dung; b – immature asci surrounded by paraphyses with pigmented apices; c – asci containing spore clusters at different stages of maturity; d, e – asci with mature spore clusters and pigmented paraphyses; f – asci with spore clusters showing finely warted episporium ornamentation (photo negative); all photos from fresh material mounted in water. Scale bars: a = 5 mm; b–c = 25 μ m; d–e = 50 μ m; f = 20 μ m. Photos by Yulia Lytvynenko.

6 μ m along the sides. Ascospores aseptate, $18.8\text{--}20.4$ (-21.7) $\times$ $8.8\text{--}11.6$ (-12.3) μ m, $Q=2.00\text{--}2.29$, $Q_{av}=2.15$; ellipsoidal, roundish at the ends, equilateral, fine warted, sometimes with some irregular cracks, hyaline at first, purplish at maturity, turning brown with age.

Distribution in Ukraine. Left Bank Forest-Steppe; on cattle dung (Lytvynenko et al., 2025).

Selected specimens examined. SUMY REGION – Konotop District, Buryn town, on cattle dung, 22 Aug 2018, T. Khandiuk, KWU 11919; 18 Mar 2019, T. Khandiuk, KWU 12919.

Notes. *Saccobolus succineus* resembles several species with spore clusters of pattern I, notably *S. citrinus*, *S. minimus*, and *S. truncatus*, showing intermediate characteristics in ascospore and ascus dimensions. According to van Brummelen (1969), *S. citrinus* generally possesses narrower ascospores than *S. succineus*, al-

though ascospore size alone is considered unreliable for species delimitation (see *S. citrinus* notes). *S. citrinus* differs by lemon-yellow apothecia, distinctly truncated ascospores, and coarser warts, whereas *S. succineus* usually has finely warted or dotted ascospores (Fig. 4f). Doveri (2004) noted the difficulty in distinguishing fine warts from dots, underscoring the morphological overlap among these taxa. *S. succineus* differs from *S. minimus* by its larger ascospores and *S. truncatus* by smaller asci, less compact clusters, and darker apothecia.

Saccobolus thaxteri Brumm.

Distribution in Ukraine. Kharkiv Forest-Steppe; on elk dung (Yatsiuk, 2017).

Notes. *Saccobolus thaxteri* is morphologically similar to *S. verrucisporus* but differs by smaller asci and ascospores, as well as by looser ascospore clusters during maturation (van Brum-

melen, 1967). It also resembles *S. obscurus*, from which it differs by an unpigmented excipulum and hymenium (Doveri, 2014).

Saccobolus truncatus Velen.

Distribution in Ukraine. Carpathian Forests, Kharkiv Forest-Steppe, Left Bank Forest-Steppe, Left Bank Grass Steppe, Polynovyi (Artemisia) Steppe, South Coast of Crimea; on dung of cattle, donkey, goat, horse, marmot, rabbit, sheep, wild boar (Govorun et al., 2024; Lytvynenko et al., 2025).

Selected specimens examined. CRIMEA – Alushta city council, Demerdzhy Mountain, on horse dung, 2 Jul 2008, O. Akulov, CWU(Myc) 2913. KHERSON REGION – Skadovsk District, Tendra Spit, Cape Bili Kuchuhury, on cattle dung, 22 May 2007, V. Hayova, KW 50653; Tendra Spit, on horse dung, 23 May 2007, V. Hayova, KW 50631; Tendra Spit, on goat dung, 26 May 2007, V. Hayova, KW 50656. SUMY REGION – Konotop District, Buryn town, on cattle dung, 20 Jul 2018, T. Khandiuk, KWU 13919; on rabbit dung, 27 Jul 2019, T. Khandiuk, KWU 14919; Konotop city, on horse dung, 10 Aug 2018, N. Velychko, KWU 15919. Sumy District, Lutsykyivka village, on cattle dung, 15 Jul 2013, N. Stepanovska, KWU 16919; Sad village, on donkey dung, 27 Jun 2020, Yu. Lytvynenko, KWU 17919. TRANSCARPATHIAN REGION – Rakhiv District, Petros Mountain, on goat dung, 27 Aug 2015, Yu. Shcherbakova, KWU 13918; on horse dung, 27 Aug 2015, Yu. Shcherbakova, KWU 01918; on sheep dung, 27 Aug 2015, Yu. Shcherbakova, KWU 14918.

Notes. A distinctive feature of *S. truncatus* is the pronounced contraction of spore clusters at maturity (van Brummelen, 1967; Doveri, 2004). Among Ukrainian taxa, *S. truncatus* most closely resembles *S. citrinus* and *S. minimus*.

Saccobolus verrucisporus Brumm.

Distribution in Ukraine. Carpathian Forests, Crimean Steppe, Kharkiv Forest-Steppe, Left Bank Grass Steppe, Left Bank Polissya; on dung of hare, horse, red deer, roe deer, sheep (Govorun et al., 2024; Lytvynenko et al., 2025).

Selected specimens examined. KHERSON REGION – Skadovsk District, Tendra Spit, on horse dung, 26 May 2007, V. Hayova, KW 50641. SUMY REGION – Shostka District, Stara Huta village, on roe deer dung, 23 Apr 2017,

Yu. Lytvynenko, KWU 18919. Sumy District, Nyzy village, on red deer dung, 11 Aug 2015, A. Butsyk, KWU 19919.

Notes. *Saccobolus verrucisporus* belongs to a group of species characterized by more or less coarsely warted ascospores, including *S. thaxteri* and *S. obscurus*. Their distinctions from *S. verrucisporus* are described above.

Saccobolus versicolor (P. Karst.) P. Karst.

Distribution in Ukraine. Crimean Steppe, Kharkiv Forest-Steppe, Left Bank Forest-Steppe, Left Bank Grass Steppe, Left Bank Polissya, South Coast of Crimea; on dung of cattle, goat, hare, horse, roe deer, sheep (Milotsova, 1937; Prokhorov, 1991; Govorun et al., 2024; Lytvynenko et al., 2025).

Selected specimens examined. SUMY REGION – Okhtyrka District, Kuzemyn village, on deer dung, 23 Jul 2023, Yu. Lytvynenko, KWU 20919; Luhivka village, on goat dung, 30 Jun 2015, Yu. Lytvynenko, KWU 21919. Shostka District, Stara Huta village, on roe deer dung, 24 May 2005, Yu. Lytvynenko, KWU 22919.

Notes. *Saccobolus versicolor* is the most variable species, especially in apothecial size, pigmentation, excipulum thickness, spore size and ornamentation (van Brummelen, 1967; Doveri, 2004). It is morphologically similar to *S. caesariatus* but differs from it by tufts of cohering septate hyphae on the apothecial surface, present in the latter and absent in the former. *Saccobolus depauperatus* differs by smaller ascospores and an excipulum of *textura globulosa*, rarely with intercellular, amorphous pigment, whereas in *S. versicolor* the excipulum is predominantly of *t. intricata*, with intercellular pigment present both within the excipulum and among the tips of paraphyses.

2. Key to *Saccobolus* from Ukraine

1. Ascospores arranged in subglobose to ellipsoidal clusters (pattern IV of van Brummelen) *S. dilutellus*

1. Ascospores arranged otherwise 2

2. Spore clusters compact; ascospores remaining solidly cemented at maturity 3

2. Spore clusters loose, visible in young asci only; ascospores becoming free at maturity

S. saccoboloides

3. Ascospores arranged with four rows of two longitudinally disposed spores, and two longitudinal planes of symmetry (pattern I of van Brummelen) 4
3. Ascospores arranged otherwise 9
4. Receptacle lemon yellow; ascospores distinctly truncate, with small isolated warts, $16.5\text{--}22 \times 6.0\text{--}9.0 \mu\text{m}$ *S. citrinus*
4. Receptacle other shades of yellow; ascospores without truncate ends, finely warty, densely dotted, granular, or smooth 5
5. Ascospores more than $20 \mu\text{m}$ long 6
5. Ascospores up to $19 \mu\text{m}$ long 7
6. Receptacle golden yellow to amber; ascospores $23.5\text{--}28.5 \times 10\text{--}14 \mu\text{m}$, finely dotted or smooth, sometimes with 1–3 irregular cracks *S. glaber*
6. Receptacle greenish yellow; ascospores $21\text{--}24 \times 8.5\text{--}10 \mu\text{m}$, smooth *S. diffusus*
7. Spore clusters contracted at maturity; ascospores $14\text{--}18 \times 7\text{--}9 \mu\text{m}$, densely and finely dotted *S. truncatus*
7. Spore clusters not contracted at maturity; ascospores smooth, dotted, or finely warted, occasionally with 1–2 cracks 8
8. Ascospores $11.5\text{--}14.5 \times 5.5\text{--}7.5 \mu\text{m}$, finely dotted or smooth, sometimes with one transverse crack *S. minimus*
8. Ascospores $18.5\text{--}20.5 \times 9\text{--}10 \mu\text{m}$, densely dotted or very finely warted, sometimes with 1–2 thin irregular cracks *S. succineus*
9. Ascospores finely dotted, granular or smooth, sometimes with several irregular cracks 10
9. Ascospores with coarse, prominent warts 12
10. Apothecia tomentose, with thick hairs, sometimes fasciculate forming triangular scales; paraphyses simple or basally branched; ascospores $17\text{--}18.5 \times 7.5\text{--}8.5 \mu\text{m}$ *S. caesariatus*
10. Apothecia glabrous or without tufts of hair; paraphyses simple, usually once dichotomously branched at apex 11
11. Spore clusters $30\text{--}35 \times 10\text{--}13 \mu\text{m}$; ascospores $10.5\text{--}12.5 \times 5\text{--}7 \mu\text{m}$ *S. depauperatus*
11. Spore clusters $39\text{--}58 \times 15\text{--}20 \mu\text{m}$; ascospores $15.5\text{--}19.5 \times 7\text{--}10 \mu\text{m}$ *S. versicolor*
12. Spore clusters dense, compact; ascospores more than $14 \mu\text{m}$ long; excipulum with intercellular pigment 13
12. Spore clusters loose; ascospores $10.5\text{--}14 \times 7\text{--}9 \mu\text{m}$; excipulum without intercellular pigment *S. thaxteri*
13. Spore clusters not contracted at maturity; ascospores $13.5\text{--}16 \times 7.5\text{--}9 \mu\text{m}$, with large dense warts; excipulum with pale purple intercellular pigment *S. verrucisporus*
13. Spore clusters contracted at maturity; ascospores $16\text{--}18 \times 7.5\text{--}8.5 \mu\text{m}$, with angular warts; excipulum with purple-brown to brown intercellular pigment *S. obscurus*

3. Occurrence and substrate preferences

Within this study, 14 *Saccobolus* species were identified, ranging from common to rare taxa. Species richness and substrate preferences of *Saccobolus* in Ukraine are summarized in Table 1.

Common (more than 20 records in Ukraine) and widespread taxa *S. citrinus*, *S. depauperatus*, *S. minimus*, *S. saccoboloides*, and *S. truncatus* are consistent members of coprophilous fungal communities and occur on most examined dung samples. In some, fruit bodies aggregate into complexes or crusts of confluent apothecia (van Brummelen, 1967), making them conspicuous during substrate examination. The predominance of these species in Ukraine generally corresponds to observations from other countries, where they are likewise considered widespread coprophilous fungi.

Many published records of *S. citrinus* indicate that it is a widespread and cosmopolitan species (van Brummelen, 1967; Doveri, 2004). Richardson (2007) notes that it is the most common species within the section *Saccobolus*. According to van Brummelen (1967) and Doveri (2004), *S. minimus* and *S. truncatus* are also widespread worldwide, although they are probably underrecorded due to their tiny size. In Ukraine, all three species are widespread and were frequently observed in our material from various regions and different dung types.

Saccobolus saccoboloides is common in Ukraine, though not globally widespread. Most records of this species are from Europe, with a few reported in Asia and South America (Prokhorov & Raitviir, 1991; Melo et al., 2014). In certain countries, *S. saccoboloides* is considered rare (De Sloover, 2002; Melo et al., 2014) or is known from only a limited number of localities (Prokhorov & Raitviir, 1991; Doveri, 2014).

Our data indicate a high prevalence of *S. depauperatus* in Ukraine, recorded from numerous dung samples of domestic and wild herbivores. Similar findings were reported by Prokhorov (1991), confirming its relatively stable distribution across the country. Interestingly, Richardson (2007) noted that *S. depauperatus* is more common in samples from lower latitudes than temperate regions. However, our observations suggest that it occurs regularly under Ukraine’s climatic conditions, with a relative frequency surpassing that of *S. versicolor*, the most widespread species of the genus globally (van Brummelen, 1967; Richardson, 2007).

Following previous observations, *S. versicolor* is known for its widespread occurrence across

many countries (van Brummelen, 1967; Doveri, 2004; Richardson, 2007). In Ukraine, however, it, along with *S. glaber* and *S. verrucisporus*, is uncommon, with 10–15 recorded localities; *S. versicolor* has explicitly been documented at 12 sites across six physiographic regions. Globally, van Brummelen (1967) noted it as the most common *Saccobolus* species, a point reinforced by Richardson (2007), who reported that two-thirds of all *Saccobolus* records in his collections belong to *S. versicolor*. In contrast, *S. glaber* and *S. verrucisporus* are widespread but likely underrecorded, as their small, solitary apothecia do not aggregate and are often overlooked by researchers. In Ukraine, these species are widely distributed but infrequently reported.

The majority of the species treated here are rare in Ukraine and are known from only 1–5 localities: *S. caesariatus*, *S. diffusus*, *S. diluteillus*, *S. obscurus*, *S. succineus*, and *S. thaxteri*. Their global rarity remains debated; Richardson (2001) distinguishes “rarity” from “pseudorarity,” noting that absence of records may reflect either true rarity or insufficient observation,

Table 1. Number of records, species richness, and diversity of *Saccobolus* assemblages associated with different dung types in Ukraine.

Species	Cattle	Deer	Donkey	Elk	Goat	Hare	Horse	Marmot	Mouflon	Rabbit	Sheep	Wild boar	Total
<i>S. caesariatus</i>	0	0	0	0	0	1	1	0	0	0	0	0	2
<i>S. citrinus</i>	11	0	0	0	5	0	5	0	0	2	2	0	25
<i>S. depauperatus</i>	1	5	0	5	2	2	8	0	0	0	1	0	24
<i>S. diffusus</i>	1	0	0	0	1	0	0	0	0	0	0	0	2
<i>S. diluteillus</i>	0	0	0	0	1	0	0	0	0	1	0	0	2
<i>S. glaber</i>	8	0	0	0	3	0	2	0	0	0	2	0	15
<i>S. minimus</i>	5	6	1	0	2	0	4	0	1	0	0	1	20
<i>S. obscurus</i>	0	2	0	0	0	1	0	0	0	0	0	0	2
<i>S. saccoboloides</i>	9	2	0	0	6	0	3	0	0	2	1	0	23
<i>S. succineus</i>	5	0	0	0	0	0	0	0	0	0	0	0	5
<i>S. thaxteri</i>	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>S. truncatus</i>	11	0	1	0	4	0	5	1	0	1	1	1	25
<i>S. verrucisporus</i>	0	5	0	0	0	1	2	0	0	0	2	0	10
<i>S. versicolor</i>	1	1	0	0	2	2	4	0	0	0	2	0	12

particularly for inconspicuous species. The causes of pseudorarity among coprophilous fungi discussed by Richardson are also relevant to our study.

Saccobolus thaxteri is considered rare in Ukraine, Europe, and globally. Originally described from North America (USA), it has since been recorded from several locations including the Philippines, Thailand (van Brummelen, 1967), Japan (Otani & Kanzawa, 1970), New Zealand (Bell, 1983), India (Kaushal & Virdi, 1986), southwest Africa (Namibia), and Chile (Piontelli et al., 2004, 2006). In Ukraine, *S. thaxteri* is known from a single record collected in 2010 (Yatsiuk, 2017). Based on GBIF database (GBIF online 4), the species is rare, with only three records outside Ukraine (Australia, Pakistan, and Japan). The Ukrainian record is the only known site in Europe.

Doveri (2004) notes that *S. caesariatus* is a rare species recorded only from a few European countries. This view is shared by Richardson (2007), who analyzed the distribution and frequency of occurrence of particular Ascobolaceae species worldwide. The species is known from a limited number of localities in Germany (Jahn, 1997), Austria, the Netherlands, and the United Kingdom (Richardson, 2007), Italy (Doveri, 2014), Armenia, Azerbaijan, Uzbekistan, and Kyrgyzstan (Raitviir & Prokhorov, 1988; Prokhorov & Raitviir, 1991). In Ukraine, *S. caesariatus* is rare and known only from two localities.

Available data indicate that *S. succineus* is infrequent but widely distributed, with relatively few confirmed records worldwide. It was first reported from Thailand on elephant and horse dung, with later records from Argentina (Ranalli, 1974), Taiwan (Wang, 1996), Nepal, New Zealand (Jahn, 1997), and Sri Lanka (GBIF online 3). In Europe, it is known only from a few localities: Denmark (Larsen, 1970), Bosnia and Herzegovina (Jahn, 1997), Italy, and the Netherlands (GBIF online 3). The species occurs on dung of various herbivores, including large ungulates, but its records are scattered across the range. It may be more widespread than reported, yet it is often misidentified due to its similarity to globally common species.

Saccobolus obscurus and *S. diffusus* are rarely cited in the literature. *Saccobolus obscurus* is mainly known from Europe (GBIF online

2), with additional records from Asia, Africa, North and South America, and Greenland (Van Vooren & Meyer, 2010, GBIF online 2). In Ukraine, it has been reported only from three localities (Prokhorov, 1991). *Saccobolus diffusus* is documented in India (Kaushal & Virdi, 1986) and Kenya (Mungai et al., 2012) and may be more widespread than the available data suggests. However, Doveri (2004) questioned its taxonomic independence, proposing it as a morphotype of *S. glaber*, which may explain the few references to this species. Further study, especially with molecular methods, is needed to clarify its status and distribution.

Saccobolus dilutellus is relatively infrequent but widespread. The species is known from Europe and North and South America (Prokhorov & Raitviir, 1991; Jahn, 1997; Richardson, 2007), although it is generally represented by a limited number of records. The GBIF database (GBIF online 1) currently contains only 38 confirmed records of this species, mainly from Europe, with a few occurrences in South America and Asia. In Ukraine, the species is currently known from only two records at a single locality.

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REFERENCES

- Aas, O. 1978. Two new coprophilous species of *Saccobolus*. *Norwegian Journal of Botany* 25: 65–68.
- Abdullah, S. K. & Alutbi, S. D. 1993. Additions to coprophilous fungi of Iraq III. Ascobolaceae: Pezizales. *Basrah Journal of Sciences* 11: 33–34.
- Bell, A. 1983. *Dung fungi: an illustrated guide to coprophilous fungi in New Zealand*. 1st ed. Wellington, New Zealand: Victoria University Press. 88 pp.
- Bell, A. 2005. *An illustrated guide to the coprophilous Ascomycetes of Australia*. Utrecht, The Netherlands: CBS Diversity Series. 172 pp.
- Caillet, M. & Moyne, G. 1982. Contribution à l'étude des *Ascobolae* de Franche-Comté. *Bulletin de la Société d'Histoire Naturelle du Doubs* 80: 41–61 (in French).

- Calaça, F. J. S., Araújo, J. C., Silva-Neto, C. M. & Xavier-Santos, S. 2023. Overview of the global research on dung-inhabiting fungi: trends, gaps and biases. *Current Research in Environmental & Applied Mycology (Journal of Fungal Biology)* 13(1): 277–298. <https://doi.org/10.5943/cream/13/1/12>
- De Sloover, J. R. 2002. On four species of *Saccobolus* (Ascobolaceae, Pezizales) rarely collected or new to Belgium. *Systematics and Geography of Plants* 72: 211–224.
- Dissing, H. 1987. Three 4-spored *Saccobolus* species from northeast Greenland. In: Laursen, G. A., Ammirati, J. F. & Redhead, S. A. (eds). *Alpine and Arctic Mycology II. Environmental Science Research. Berlin, Germany: Springer-Verlag* 34: 79–86.
- Dissing, H. 1989. Four new coprophilous species of *Ascobolus* and *Saccobolus* from Greenland (Pezizales). *Opera Botanica* 100: 43–50.
- Doveri, F. 2004. *Fungi fimicoli Italiani: a guide to the recognition of Basidiomycetes and Ascomycetes living on faecal material*. Associazione Micologica Bresadola, Vicenza. 1104 pp.
- Doveri, F. 2014. An update on the genera *Ascobolus* and *Saccobolus* with keys and descriptions of three coprophilous species new to Italy. *Mycosphere* 5(1): 86–135. <https://doi.org/10.5943/mycosphere/5/1/4>
- GBIF (online 1). 2025. *Saccobolus dilutellus* (Fuckel) Sacc. Occurrence dataset. <https://doi.org/10.15468/dl.rycxx6> [Accessed via GBIF.org on 10 August 2025].
- GBIF (online 2). 2025. *Saccobolus obscurus* (Cooke) W. Phillips. Occurrence dataset. <https://doi.org/10.15468/dl.8dbvje> [Accessed via GBIF.org on 10 August 2025].
- GBIF (online 3). 2025. *Saccobolus succineus* Brumm. Occurrence dataset. <https://doi.org/10.15468/dl.tgm7g9> [Accessed via GBIF.org on 11 August 2025].
- GBIF (online 4). 2025. *Saccobolus thaxteri* Brumm. Occurrence dataset. <https://doi.org/10.15468/dl.2y8a2b> [Accessed via GBIF.org on 10 August 2025].
- Golubtsova, Yu. I. 2009. New records of coprophilous ascomycetes in Ukraine. II. Discomycetes. *Ukrainian Journal of Botany* 66(3): 384–393 (in Ukrainian, English summary).
- Golubtsova, Yu. I., Mikos, I. G. & Akulov, O. Yu. 2010. New records of coprophilous ascomycetes in the Crimea. *Chornomorski Botanical Journal* 6(1): 67–83 (in Ukrainian, English summary).
- Govorun, O., Lytvynenko, Y. & Orlova-Hudim, K. 2024. Coprophilous ascomycetes of the Left Bank grass steppe of Ukraine. Ukrainian Nature Conservation Group (NGO). Occurrence dataset. <https://doi.org/10.15468/esvcg9> [Accessed via GBIF.org on 23 July 2024].
- Heluta, V. P. 2022. A critical revision of the powdery mildew fungi (Erysiphaceae, Ascomycota) of Ukraine: *Arthrocladiella* and *Blumeria*. *Ukrainian Botanical Journal* 79(4): 205–220 (in Ukrainian, English summary). <https://doi.org/10.15407/ukrbotj79.04.205>
- Hyde, K. D., Noorabadi, M. T., Thiagaraja, V., He, M. Q., Johnston, P. R. et al. 2024. The 2024 outline of fungi and fungi-like taxa. *Mycosphere* 15(1): 5146–6239. <https://doi.org/10.5943/mycosphere/15/1/25>
- Jahn, E. 1997. Koprophile Pezizales von Dungkulturen aus dem norddeutschen Raum und aus verschiedenen Teilen der Erde. *Zeitschrift für Mykologie* 63(2): 133–148 (in German, English summary).
- Kaushal, S. C. & Virdi, S. S. 1986. Himalayan species of *Saccobolus*, a coprophilous genus of Pezizales. *Willdenowia* 16: 269–277.
- Larsen, K. 1970. The genus *Saccobolus* in Denmark. *Botanisk Tidsskrift* 65: 371–389.
- Lytvynenko, Y., Dzhanan, V. & Hayova, V. 2025. Coprophilous ascomycetes of the natural physiographic regions of Ukraine. Part 1. Ukrainian Nature Conservation Group (NGO). Occurrence dataset. <https://doi.org/10.15468/kned8e> [Accessed via GBIF.org on 04 July 2025].
- Lytvynenko, Yu. I., Dzhanan, V. V., Topchii, I. V. & Shcherbakova, Yu. V. 2018. Dung-inhabiting ascomycetes from the Ukrainian Carpathians. *Czech Mycology* 70(2): 145–167. <https://doi.org/10.33585/cmy.70204>
- Melo, R. F. R., Miller, A. N., Santiago, A. L. C. M. A. & Maia, L. C. 2014. The genera *Ascobolus* and *Saccobolus* (Ascobolaceae, Pezizales) in Brazil. *Mycosphere* 5: 790–804. <https://doi.org/10.5943/mycosphere/5/6/9>
- Milovtsova, M. O. 1937. Materials on the mycoflora of the Ukrainian SSR. *Works of the Research Institute of Botany at Kharkiv State University* 2: 17–22 (in Ukrainian).
- Mungai, P. G., Chukeatirote, E., Njogu, J. G., Hyde, K. D. 2012. Coprophilous ascomycetes in Kenya: *Saccobolus* species from wildlife dung. *Mycosphere* 3: 111–129. <https://doi.org/10.5943/mycosphere/3/2/2>
- O'Donnell, K. L. 1978. A new *Saccobolus* from Michigan. *Mycologia* 70(1): 189–192. <https://doi.org/10.2307/3758702>
- Otani, Y. & Kanzawa, S. 1970. Notes on coprophilous discomycetes in Japan I. *Transactions of the Mycological Society of Japan* 10: 117–126.
- Piontelli, E., Giusiano, G., Savino, E., Solari, N. & Caretta, G. 2004. Microfungi from different substrata in south west Africa (Namibia). *Boletín Micológico* 19: 63–69.
- Piontelli, E. L., Cruz, R. C. & Toro Santa Maria, M. A. 2006. Coprophilous fungal community of wild rabbit in a park of a hospital (Chile): a taxonomic approach. *Boletín Micológico* 21: 1–17.
- Prokhorov, V. & Raitviir, A. 1991. New or interesting species of *Ascobolus* and *Saccobolus* in the USSR. *Cryptogamic Botany* 2: 205–213.

- Prokhorov, V. P. 1989. The records of the discomycetes of the genera *Ascobolus* and *Saccobolus* from Estonia. *Proceedings of the Academy of Sciences of the Estonian SSR. Biology* 38: 24–32.
- Prokhorov, V. P. 1991. Coprophilous discomycetes from Ukraine and Moldova. *Ukrainian Journal of Botany* 48(1): 34–41 (in Ukrainian, English summary).
- Prokhorov, V. P. 2004. *Handbook of the fungi of Russia. Discomycetes. Iss. 1. Coprophilous species.* (in Russian). Tovarishestvo nauchnyh izdaniy, KMK, Moscow. 255 pp.
- Raitviir, A. & Prokhorov, V. 1988. Discomycetes of Middle Asia. IV. New data on Ascobolaceae and Thelebolaceae. *Proceedings of the Academy of Sciences of the Estonian SSR. Biology* 37: 215–222.
- Ramos, A. M., Cinto, I. E., Tadic, L. F. & Ranalli, M. E. 2011. AFLP molecular characterizations of some *Saccobolus* species (Ascomycota, Pezizales). *Mycotaxon* 116: 355–364. <https://doi.org/10.5248/116.355>
- Ramos, A. M., Forchiassin, F., Ranalli, M. E. & Saidman, B. 2000. Isozyme analysis of different species of the genus *Saccobolus* (Ascomycetes, Pezizales). *Mycotaxon* 74: 447–462.
- Ranalli, M. E. 1974. Estudio sistemático y biológico de las Ascobolaceas de Argentina. V. *Boletín de la Sociedad Argentina de Botánica* 15(4): 427–445 (in Spanish, English summary).
- Ranalli, M. E. & Mercuri, O. A. 1995. Taxonomy of some Argentine species of *Saccobolus*. *Mycotaxon* 54: 315–327.
- Richardson, M. J. 2001. Diversity and occurrence of coprophilous fungi. *Mycological Research* 105(4): 387–402.
- Richardson, M. J. 2007. The distribution and occurrence of coprophilous Ascobolaceae. *Mycologia Montenegrina* 10: 211–227.
- Senanayake, I. C., Rathnayaka, A. R., Marasinghe, D. S., Calabon, M. S., Gentekaki, E. et al. (2020). Morphological approaches in studying fungi: collection, examination, isolation, sporulation and preservation. *Mycosphere* 11(1): 2678–2754. <https://doi.org/10.5943/mycosphere/11/1/20>
- Smitska, M. F. 1980. *The flora of the fungi of Ukraine. Operculate discomycetes.* Naukova dumka, Kyiv (in Ukrainian).
- van Brummelen, J. 1967. A world monograph of the genera *Ascobolus* and *Saccobolus* (Ascomycetes, Pezizales). *Persoonia Supplement* 1: 1–260.
- van Brummelen, J. 1969. Studies on Discomycetes-III. *Persoonia* 5: 225–231.
- Van Vooren, N. & Meyer, M. 2010. *Saccobolus obscurus*, une curiosité au sein du genre coprophile *Saccobolus* (Ascomycota, Pezizales). *Cryptogamie, Mycologie* 31: 155–159 (in French, English summary).
- Wang, Y. Z. (1996). Notes of coprophilous discomycetes of Taiwan. III. *Bulletin of National Museum of Natural Science* 7: 131–136.
- Wijayawardene, N. N., Hyde, K. D., Rajeshkumar, K. C., Hawksworth, D. L., Madrid, H. et al. 2017. Notes for genera: Ascomycota. *Fungal Diversity* 86: 1–594. <https://doi.org/10.1007/s13225-017-0386-0>
- Yatoo, S. F., Phate, P. V. & Wani, T. A. 2021. Contributions to the family Ascobolaceae of India. *Studies in Fungi* 6(1): 263–272. <https://doi.org/10.5943/sif/6/1/17>
- Yatsiuk, I. I. 2017. Discomycetes of Kharkiv Forest-Steppe (Ukraine): the annotated checklist. *Chornomorski Botanical Journal* 13: 333–344. <https://doi.org/10.14255/2308-9628/17.133/8>