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Fifteen new species from the myxomycete genus *Lycogala*

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ABSTRACT

Based on a study of 255 collections from four continents and four floristic kingdoms, we describe 15 new species of the genus *Lycogala*. The new species, all morphologically close to *L. epidendrum, L. exiguum*, and *L. confusum*, differ from each other by the structure of the peridium and, in some cases, also by the color of the fresh spore mass and the ornamentation of the capillitium and spores. Species delimitation is confirmed by two independently inherited molecular markers, as well as previously performed tests of reproductive isolation and genetic distances. We studied authentic material of *L. exiguum* and *L. confusum* and found fresh specimens of these species, which allowed us to obtain molecular barcodes and substantiate the separation of new species from these taxa. We propose to retain the name *L. epidendrum* for the globally most abundant species, for which we provide a more precise description and a neotypification. Two formerly described species, *L. leiosporum* and *L. fuscoviolaceum*, we consider to be dubious. We do not recognize the species *L. terrestre*.

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INTRODUCTION

The genus *Lycogala* Adans. was introduced in mid-18th century, based on a pre-Linnean name provided by Micheli (1729). During the same century, several species were described within *Lycogala*, but only one of these, *L. epidendrum* (L.) Fr., is currently recognized. Subsequently, six more species of this genus were described, differing from each other by eye-catching macroscopic characters: conical shape of sporocarps (*L. conicum* Pers.), large size and silvery coloration of sporocarps (*L. flavofuscum* (Ehrenb.) Rostaf.), or clustered vesicles covering the peridium (*L. exiguum* Morgan and *L. confusum* Nann.-Bremek. ex Ing). Two other species, until today known only from the original descriptions, are distinguished by a dark brown spore mass (*L. fuscoviolaceum* Onsberg) or smooth spores (*L. leiosporum* Reichardt).

The morphological variability of the most common species of the genus, *L. epidendrum*, as well as its vague differences from related taxa, let researchers assume that *L. epidendrum* represents a complex of species (Nannenga-Bremekamp 1991). In order to define some frequently occurring morphotypes, Ing (1999) suggested using the old name *L. terrestre* Fr. & Lindgr. for particularly large, crowded specimens of *L. epidendrum*. This author published as well the diagnosis of L. *confusum*, previously proposed by Nannenga-Bremekamp for specimens that combine the habit of *L. epidendrum* with the peridial structure the *L. exiguum*.

Previous molecular studies (Leontyev et al. 2015, 2022b) demonstrated that herbarium collections identified as *L. epidendrum* (and, occasionally, as *L. exiguum*) combine at least 60 phylogenetic groups. Testing for gaps in genetic distances revealed significant differences between these groups, and a reproductive test performed for 18 of them revealed reproductive isolation (Leontyev et al. 2022b). A morphological study showed that the structure of the peridium in representatives of the genus *Lycogala* is extremely variable and includes previously unknown features (Leontyev et al. 2022a). Vesicles, which cover the peridium, may include single crystals and druses of Ca-containing compounds, oil droplets, granular accumulations, or orange pigment deposits. These vesicles can be covered by uni- or multilayered walls and arranged in several different ways, which are much more variable than described for *L. exiguum* and *L. confusum* (Leontyev et al. 2022a). All this led us to the conclusion that dozens of undescribed species exist within the *L. epidendrum* complex. From the material available to us, we selected 15 species for which we have sufficient information for a taxonomic description, including (i) at least three well-preserved specimens from different places

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For political reasons, Yury Ishchenko does not indicate his country of origin.
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of origin (with one exception, *L. oncoides*, where three specimens came from one locality); (ii) molecular barcodes, differing from each other by at least 10%; and (iii) comprehensible morphological differences. These species are described in this paper.

MATERIALS AND METHODS

The material examined in this study consisted of 255 specimens of *Lycogala: L. epidendrum* s. str. (116 specimens), new species of *Lycogala* (117 specimens), *L. confusum* (15 specimens), and *L. exiguum* s. str. (7 specimens). In addition, we included in the study three DNA sequences retrieved from the National Center for biotechnology Information (NCBI) GenBank (SUPPLEMENTARY FILE 1). Analyzed specimens and sequences originate from four continents: Europe (196 specimens), Asia (17), North America (34), and Australia (11). A number of specimens, kept in the Komarov Botanical Institute (LE), including presumable vouchers of new species, were excluded from this study due to the interruption of our cooperation with state organizations of the Russian Federation. Information on these materials is available in our previous publication on the subject (see supplementary file 1 in Leontyev et al. 2022b). Authentic material of *L. exiguum*, which includes two lectotypes (five specimens kept in herbarium BPI, Beltsville, Maryland, USA), and of *L. confusum* (five specimens kept in the herbarium BR, Meise, Belgium) was included in the study.

Type collections of the species, described here, are kept in following collections: CWP (Herbarium of the H.S. Skovoroda Kharkiv National Pedagogical University, Kharkiv, Ukraine), EJ (private collection of Edvin Johannesen, Oslo, Norway), PFb (Herbarium of the University of Santo Tomas, Philippines), sc and IY (myxomycete section of the Herbarium of the University of Greifswald, Greifswald, Germany [GFW]), and USJ (Herbarium of the University of San Jose, San Jose, Costa Rica).

Microscopic characters were studied with a Keyence VHX 7000 digital microscope (view in reflected light [RL]) (Keyence Deutschland GmbH, Neu-Isenburg, Germany) and a Leica DM2500 microscope (Leica Camera AG, Wetzlar, Germany) in conjunction with a Flexacam C1 camera (view in natural [TL] and polarized [PL] transmitted light) (Leica Camera AG, Wetzlar, Germany). Measurements of microscopic structures were carried out with the application Leica LAS X. Scanning electron microscopy (SEM) was carried out a Zeiss Evo LS10 device (Carl Zeiss AG, Oberkochen, Germany) in the Institute of Microbiology, University of Greifswald.

To study variation in sporocarp size, nearly all available sporocarps were measured, including their length and width. Between 30 and 90 spores and 5–10 capillitium threads were measured for specimens that contain these structures. Measurements included spore ornamentation. The range of variation in size for sporocarps and spores is given in descriptions as (minimum–)25% quartile–75% quartile(–maximum). Spore size was rounded to 0.5 µm.

Microscopic slides with peridium pieces were prepared using pure lactic acid as a mounting medium, since polyvinyl lactophenol (Aman's medium), often used in myxomycete studies (Rojas Alvarado and Stephenson 2022), appeared too viscous to allow air bubbles to escape from the peridium. If bubbles were too numerous, a slide was left for several days, until the specimen became completely free of air. Microscopy of spores and capillitium was carried out in lactic acid mixed with methyl blue (0.1 mg in 60 g). This mixture allows visualizing the ornamentation, which otherwise remains nearly invisible, since both spores and capillitium of *Lycogala* are almost hyaline. Microphotographs of capillitium and spores (sections H and M of each color plate) were processed with the program Sharpen AI (Topaz Labs, Dallas, Texas) to enhance visibility of the spore ornamentation.

Molecular data involved in this study were published earlier (Leontyev et al. 2022a, 2022b). Here we cite NCBI GenBank codes of DNA sequences for at least one of two marker genes, 18S rDNA (for all new species) and *COI* (cytochrome *c* oxidase subunit 1; for 10 of the new species; see SUPPLEMENTARY TABLE 1), that may serve as molecular barcodes to recognize species of *Lycogala*.

RESULTS

As a result of this study, 15 new species of the genus *Lycogala* were described (FIGS. 1–15), a neotype was proposed for the *L. epidendrum* (FIG. 16), and emended diagnoses of *L. exiguum* (FIG. 17) and L. *confusum* (FIG. 18) were provided with an emphasis on the structure of peridial vesicles. Macromorphological differences between new and previously described species, including the overall colony habit and sporocarp size, are shown in FIG. 19. The position of the species described here on the 18S rDNA phylogeny is shown in SUPPLEMENTARY FILE 2.

TAXONOMY

Lycogala roseosporum Leontyev, Schnittler, Ishchenko & P. Vetlesen, sp. nov. FIG. 1
MycoBank MB848143

Typification: RUSSIA. MOSKOVSKAYA OBLAST: Moscow, North-Eastern Administrative District, Severnyi (55.92831 37.55656), on decaying deciduous tree stump, directly on the surface of the wood, 13

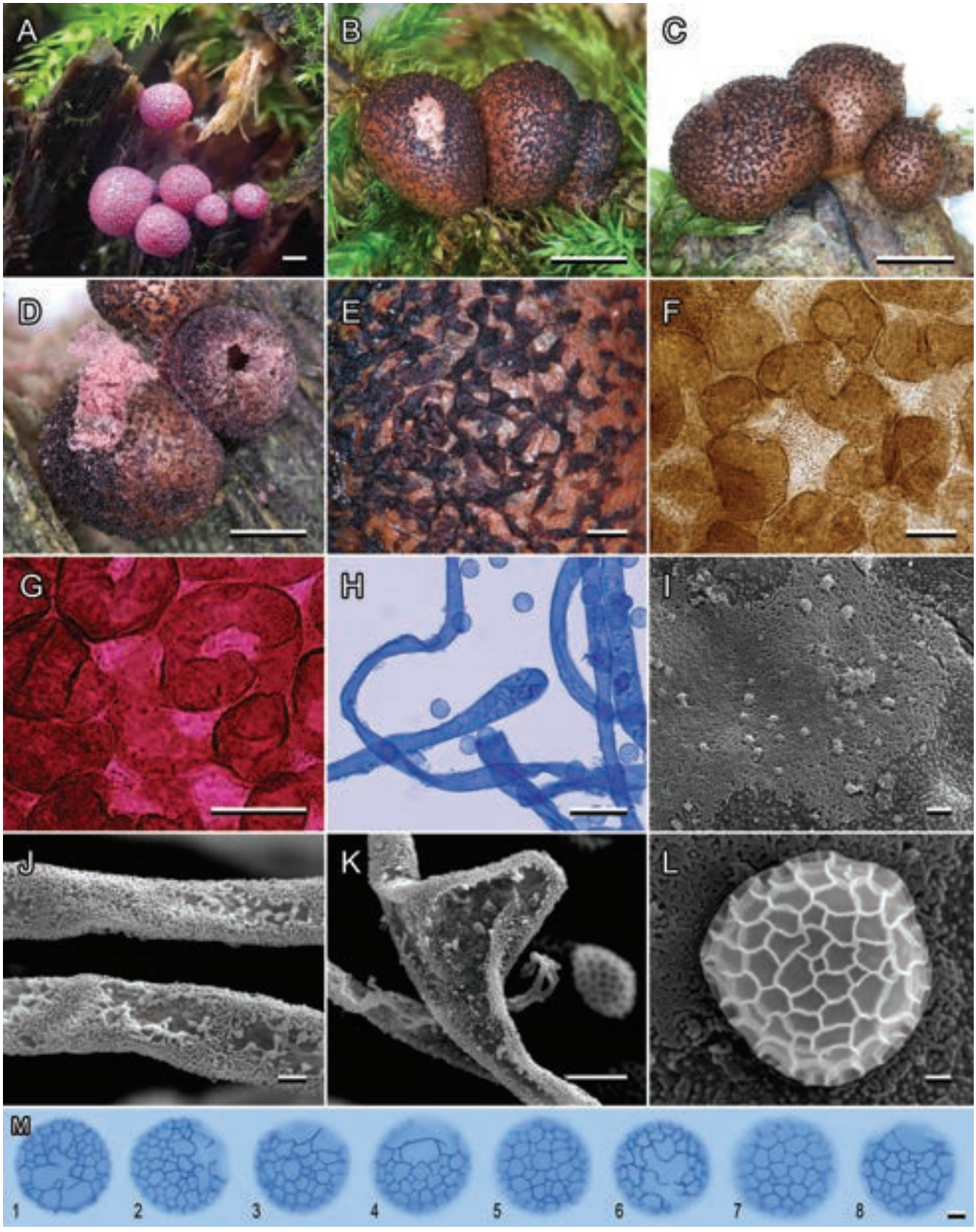

Figure 1. *Lycogala roseosporum*, sp. nov. A. Immature fructifications. B–D. Sporocarps. E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A–E. IY05 (holotype). F, G, I–L. EJ14908701. H, M. sc10973. Bars: A–C = 1 mm; D = 200 µm; E–G = 100 µm; H = 20 µm; I, J, M = 1 µm; K = 5 µm; L = 0.5 µm.

Jun 2020, *Y. Ishchenko* (**holotype** IY05). GenBank: 18S rDNA = ON920572.

Diagnosis: Sporocarps small, reddish-brown, with black spots. Peridial vesicles densely and unevenly distributed, solitary, dark brown in TL. Spore mass bright pink.

Etymology: rosa (Latin), rose, and *spora* (Greek), seed, referring to the color of the fresh spore mass.

Sporocarps in small groups, spherical to short horizontally ovoid, often deformed by mutual pressure, (1–)1.5–3.5(–4) mm diam (FIG. 1B, C). Peridium membranous, pinkish- to reddish-brown, in old collections ochraceous-brown, densely covered by vesicles, which are concentrated in the upper part of a sporocarp. Peridial vesicles 90–320 µm diam, in RL looking like dried droplets, almost black, tightly distributed, forming a small-meshed reticulum or an entire mass (FIG. 1E), in TL solitary, rounded with a wavy border, sometimes ring-like or C-like, dark brown (FIG. 1F). Vesicle walls dark brown, thick (3 µm), smooth. Crystals and large oil droplets absent (FIG. 1G). Granular deposits hardly visible. Inner surface of the peridium smooth or covered by scattered warts, sometimes fused forming an entirely knobby surface (FIG. 1I). Capillitium tubular, 4–20 µm diam, with smooth contours, surface fine pitted-warty, with ring-shaped islets (FIG. 1H, J, K). Spore mass light pink (FIG. 1D), in old specimens ochraceous-yellow. Spores 5.5–7(–7.5) µm diam, hyaline, reticulate, with 7–10(–12) meshes across diameter, the unornamented area small, occupies ¼ of the spore surface (FIG. 1L, M). Immature fructifications bright pink (FIG. 1A).

Distribution: Europe.

Comments: Pink spore mass, much brighter than in other species, as well as the pinkish color of the unusually small fruiting bodies, caused by the spore mass, allows this species to be distinguished even in the field. Large, mainly solitary peridial vesicles distinguish *L. roseosporum* from other species with small gregarious sporocarps (*L. aggregatum, L. exiguum*). The peridial morphotype in *L. roseosporum* was previously referred to as "solanum" (Leontyev et al. 2022a).

Lycogala maculatum Leontyev, Schnittler & Ishchenko, sp. nov. FIG. 2
MycoBank MB848144

Typification: UKRAINE. KHMELNYTSKYI REGION: Medobory Nature Reserve, Kremenetski Hory District (50.1132 25.8044), on dead wood of *Carpinus betulus*, 15 Aug 2009, *D.V. Leontyev* (**holotype** CWP2348). GenBank: 18S rDNA = OM423818.

Diagnosis: Sporocarps medium-sized, dark brown to almost black. Peridial vesicles densely and unevenly distributed, solitary, ovoid, dark brown in TL. Spore mass gray, warm gray.

Etymology: macula (Latin), spot, referring to the spotty appearance of the peridium.

Sporocarps grouped, spherical to short horizontally ovoid, often deformed by mutual pressure, (1.5–)2.5–5.5(–7) mm diam (FIG. 2B, C). Peridium membranous, dark brown, ochraceous-brown, almost black, densely covered by vesicles, and sometimes by fine whitish strands of dried slime. Peridial vesicles 100–230 µm, in RL looking like dried droplets, dark brown to black, densely distributed, forming small groups or a loose net (FIG. 2D, E), in TL solitary, ovoid, polygonal or lobular, dark brown (FIG. 2F). Vesicle walls under TL dark brown, rather thick (2–3 µm). Crystals and large oil droplets absent (FIG. 2G). Granular deposits abundant, irregularly distributed (FIG. 2F). Inner surface of the peridium smooth or covered by scattered warts (FIG. 2I). Capillitium tubular, 5–20 µm diam, with wavy contours, ornamented by regular warty bracelet-like thickenings (FIG. 2H, J, K). Spore mass gray(?), later warm gray, in old specimens yellowish-gray. Spores (6–)6.5–8.5(–9.5) µm diam, hyaline, reticulate, with 5–7 meshes across diameter, unornamented area occupying nearly ¼ of the spore surface (FIG. 2L–M). Immature fructifications yellow to dull orange (FIG. 2A).

Distribution: Europe, Southeast Asia.

Comments: The most eye-catching character of this species is the dark, often black pigmentation of peridium. However, this character is not sufficiently reliable: in some collections, the peridium of *L. maculatum* is ochraceous- or cinnamon-brown and only the vesicles remain dark. Large, solitary, dark brown vesicles seem to represent a more stable character of this species. Similar vesicles also occur in *L. roseosporum* and *L. alisaulianovae*, but these species have a peculiar spore mass color, bright pink and bluish, respectively. The peridial morphotype in *L. maculatum* was previously referred to as "maculatum" (Leontyev et al. 2022a).

Lycogala alisaulianovae Leontyev, Ishchenko, Schnittler & Sarzhevskyi, sp. nov. FIG. 3
MycoBank MB848145

Typification: UKRAINE. DONETSK REGION: Environs of Liman (49.0021 37.7129), on dead wood, Aug 2019, *S.V. Sarzhevskyi* (**holotype** CWP3656). GenBank: 18S rDNA = OM423852; *COI* = ON931544.

Diagnosis: Sporocarps medium-sized, copper or umber brown. Peridial vesicles scattered, solitary, dark brown in TL. Spore mass bluish-gray.

Etymology: Ms Alisa Ulianova, the person who inspired Y.I. to study biology.

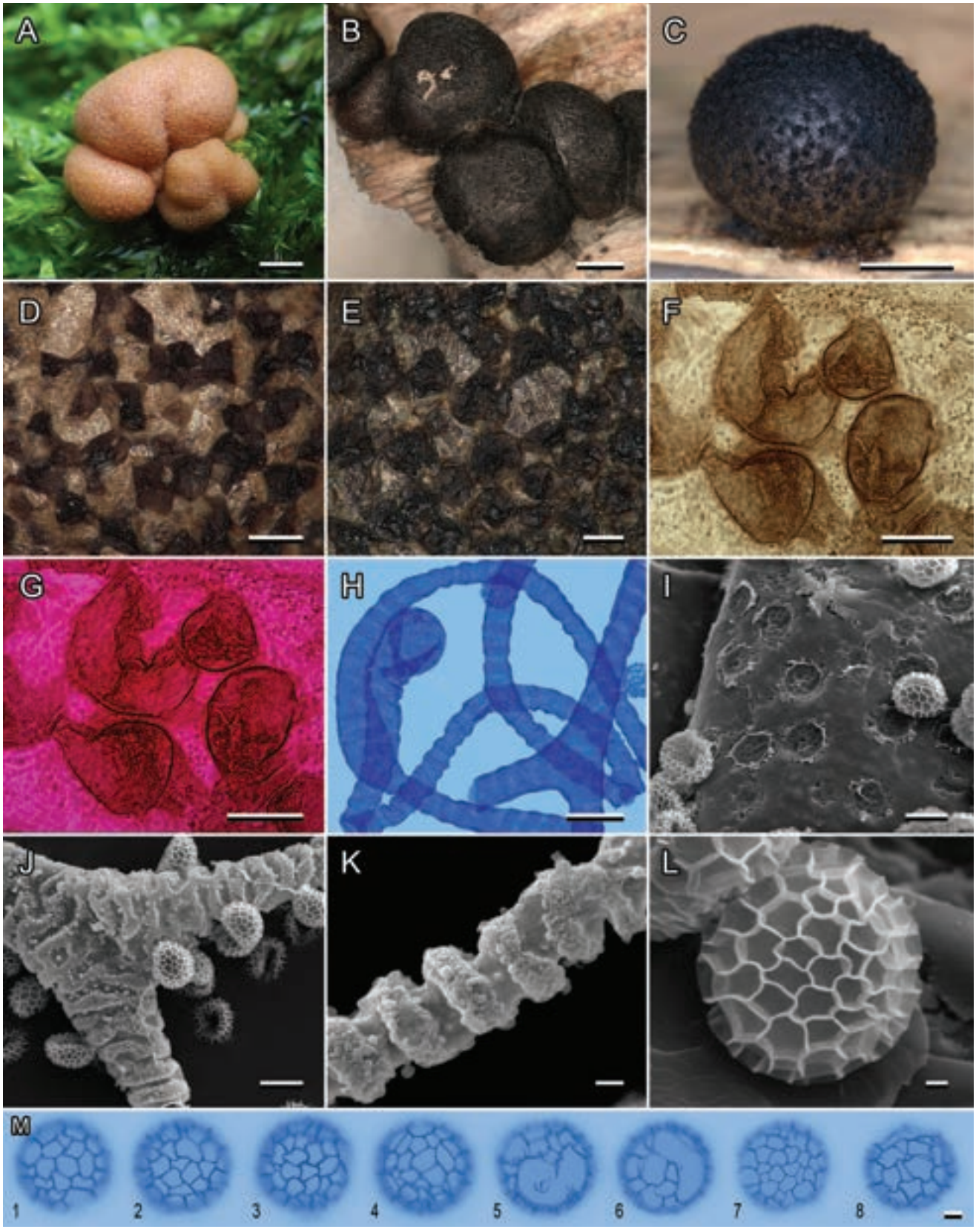

Figure 2. *Lycogala maculatum*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium, methyl blue in lactic acid. I. Inner surface of the peridium with spore "stamps," SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A. IY35. B, E. CWP2348 (holotype). C. sc27823. D, H, M. CWP2569. F, G. sc22096. I–L. sc22077. Bars: A–C = 1 mm; D = 200 µm; E–G = 100 µm; H = 10 µm; I, J = 5 µm; K, M = 1 µm; L = 0.5 µm.

Sporocarps solitary or in small loose groups, in large (>10) groups, spherical to short horizontally ovoid, sometimes deformed from mutual pressure, (2–)3–6(–7.5) mm diam (FIG. 3B, C). Peridium membranous, copper brown, umber brown, covered by vesicles and, sometimes, tender strands of dried slime. Peridial vesicles 100–300 µm, in RL looking like dried droplets or spots, dark brown to black, evenly distributed or forming small groups with the shape of broken lines, stars, fragmentary reticulum (FIG. 3D, E), in TL solitary, ovoid, polygonal or lobular, brown (FIG. 3F). Crystals and large oil droplets absent (FIG. 3G). Granular deposits brown, from scanty to rather numerous (FIG. 3F). Inner surface of the peridium smooth or covered by scattered warts (FIG. 3I). Capillitium tubular, 2–15 µm diam, with wavy contours, surface fine pitted-warty, with ring-shaped islets (FIG. 3H, J, K). Spore mass bluish-gray, later greenish-gray, in old specimens yellowish-gray (FIG. 3B). Spores 6.5–7.5 µm diam, hyaline, reticulate, with 5–7 meshes across diameter, unornamented area occupies nearly ⅓ of the spore surface (FIG. 3L, M). Immature fructifications dull pink (FIG. 3A).

Distribution: Europe.

Comments: The combination of bluish-gray spore mass with a copper-brown pigmentation of the peridium allows this species to be distinguished. *L. alisaulianovae* seems to be one of several species with such a color of the spore mass, but the only one described thus far.

Lycogala irregulare Leontyev, Schnittler, Ishchenko & G. Konstantinides, sp. nov. FIG. 4
MycoBank MB848146

Typification: GERMANY. MECKLENBURG-WESTERN POMERANIA: Greifswald, mixed forest near Weitenhagen (54.04811 13.41229), on strongly decayed trunk of *Pinus sylvestris*, 8 Jun 2013, *M. Schnittler* (**holotype** sc27520). GenBank: 18S rDNA = OM423981.

Diagnosis: Sporocarps medium-sized, ochraceous- or grayish-brown, irregular ovoid. Peridial vesicles inconspicuous, solitary, yellow-brown in TL. Spore mass light gray, warm gray.

Etymology: irregularis (Latin), irregular, referring to the shape of sporocarps.

Sporocarps solitary or in small groups, short horizontally ovoid, rather irregular in shape, often deformed from mutual pressure, (2–)3–6(–7) mm diam (FIG. 4B, C). Peridium membranous, ochraceous-brown, grayish-brown, covered by vesicles. Peridial vesicles 70–160(–250) µm, in RL looking like dried droplets, brown, solitary or loosely grouped (FIG. 4D, E), in TL solitary, irregular, angular, fusiform, blot-like, often touching each other by elongate projections, yellow-brown (FIG. 4F). Vesicle walls slightly brownish. Crystals occur in some vesicles as scanty solitary needles. Large oil droplets scanty or absent (FIG. 4G). Granular deposits present, but inconspicuous (FIG. 4F). Inner surface of the peridium covered by warts (FIG. 4I). Capillitium tubular, 4–12 µm diam, with smooth or wavy contours, ornamented by regular bracelet-like thickenings or almost smooth, with fine pitted-warty surface (FIG. 4H, J, K). Spore mass light gray(?), later light warm gray, in old specimens ochraceous-yellow. Spores (6.5–)7–7.5(–8) µm diam, hyaline, reticulate, with 7–9 meshes across diameter, unornamented area occupies nearly ⅓–½ of the spore surface (FIG. 4L, M). Immature fructifications pale pink to light salmon pink (FIG. 4A).

Distribution: Europe, Far East of Asia.

Comments: This species is a "twin" of *L. epidendrum*, and small fructifications of the latter species can easily be confused with *L. irregulare*. The irregular shape of sporocarps, small colonies, and nearly absent slime remnants on the peridium may help to distinguish this species, which seems to be one of the most difficult taxa to be recognized by morphology alone.

Lycogala olearium Leontyev, Schnittler & D. Panayotova, sp. nov. FIG. 5
MycoBank MB848147

Typification: GERMANY. THURINGIA: Rhön, Stedtlingen (50.533 10.289), on dead wood, Oct 2014, *E. Heinrich* (**holotype** sc32006). GenBank: 18S rDNA = OM424011; *COI* = ON931595.

Diagnosis: Sporocarps medium-sized to large, walnut brown or dark brown. Peridial vesicles inconspicuous, solitary, brownish in TL, contain large oil droplets. Spore mass light pinkish-gray, light reddish-gray.

Etymology: olearius (Latin), oily, referring to the presence of large oil droplets in peridial vesicles.

Sporocarps grouped, spherical to short horizontally ovoid, often deformed from mutual pressure, dull brown, (1–)2–5(–7.5) mm diam (FIG. 5B, C). Peridium membranous, walnut brown, dark brown, covered by vesicles. Peridial vesicles 50–150 µm, in RL looking like dried droplets, light to dark brown, solitary or loosely grouped (FIG. 5D), in TL solitary, ovoid, brownish (FIG. 5E, F). Vesicle walls under TL hyaline, very thin, inconspicuous. Crystals absent (FIG. 5G). Oil droplets numerous, dull yellowish, with several large (30–80 µm) and many small round droplets (FIG. 5E), or with only small ones that look like brownish granular deposits (FIG. 5F). Inner surface of the peridium smooth, covered by scattered warts or regular rings 1–5 µm diam (FIG. 5I). Capillitium tubular, 4–20(–100) µm diam, with smooth or wavy contours, ornamented

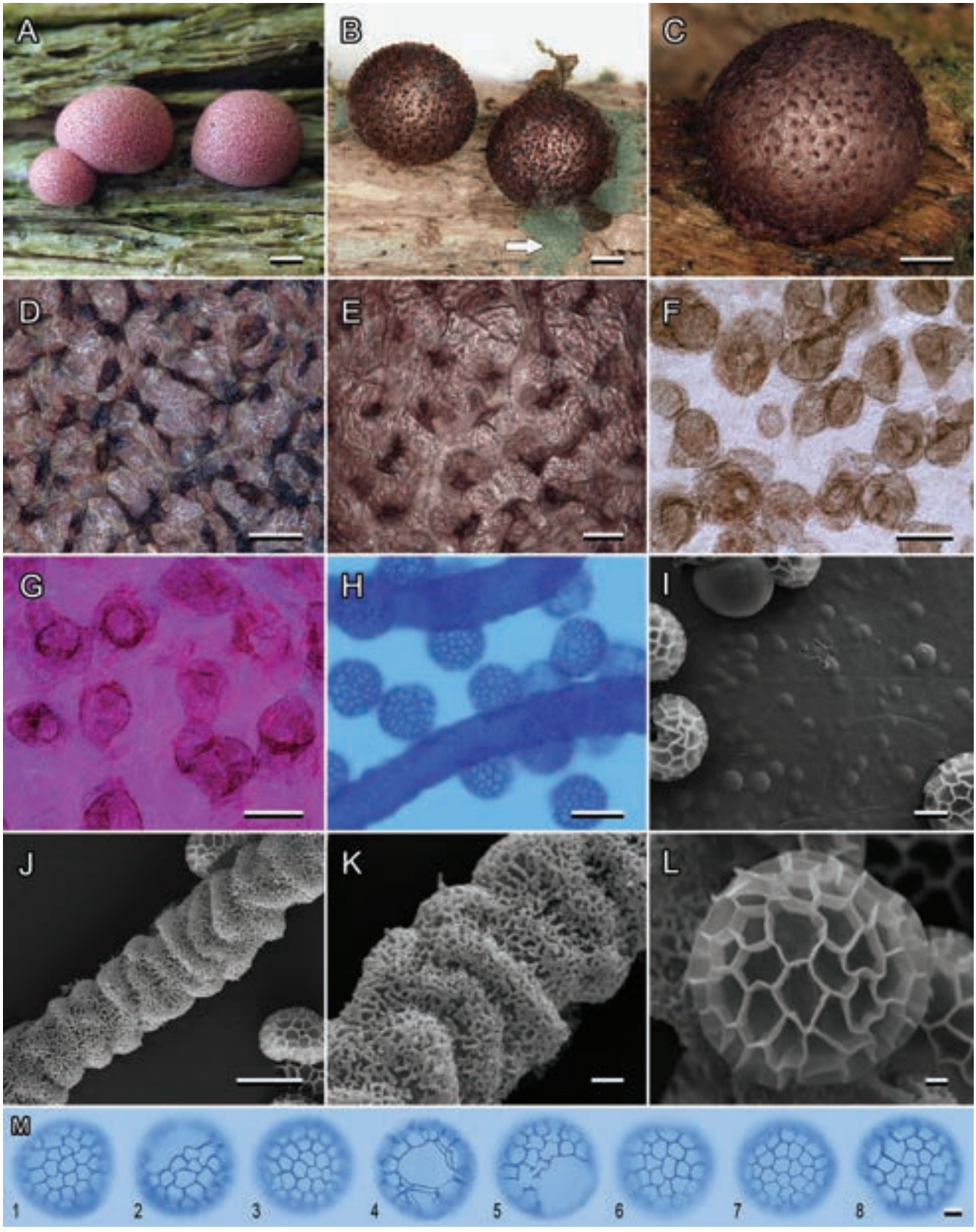

Figure 3. *Lycogala alisaulianovae*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, D, H. IY07. B. sc27822. C, E, I–M. CWP3656 (holotype). F, G. sc32540. Bars: A–C = 1 mm; D = 200 µm; E–G = 100 µm; H, J = 5 µm; I = 2 µm; K, M = 1 µm; L = 0.5 µm.

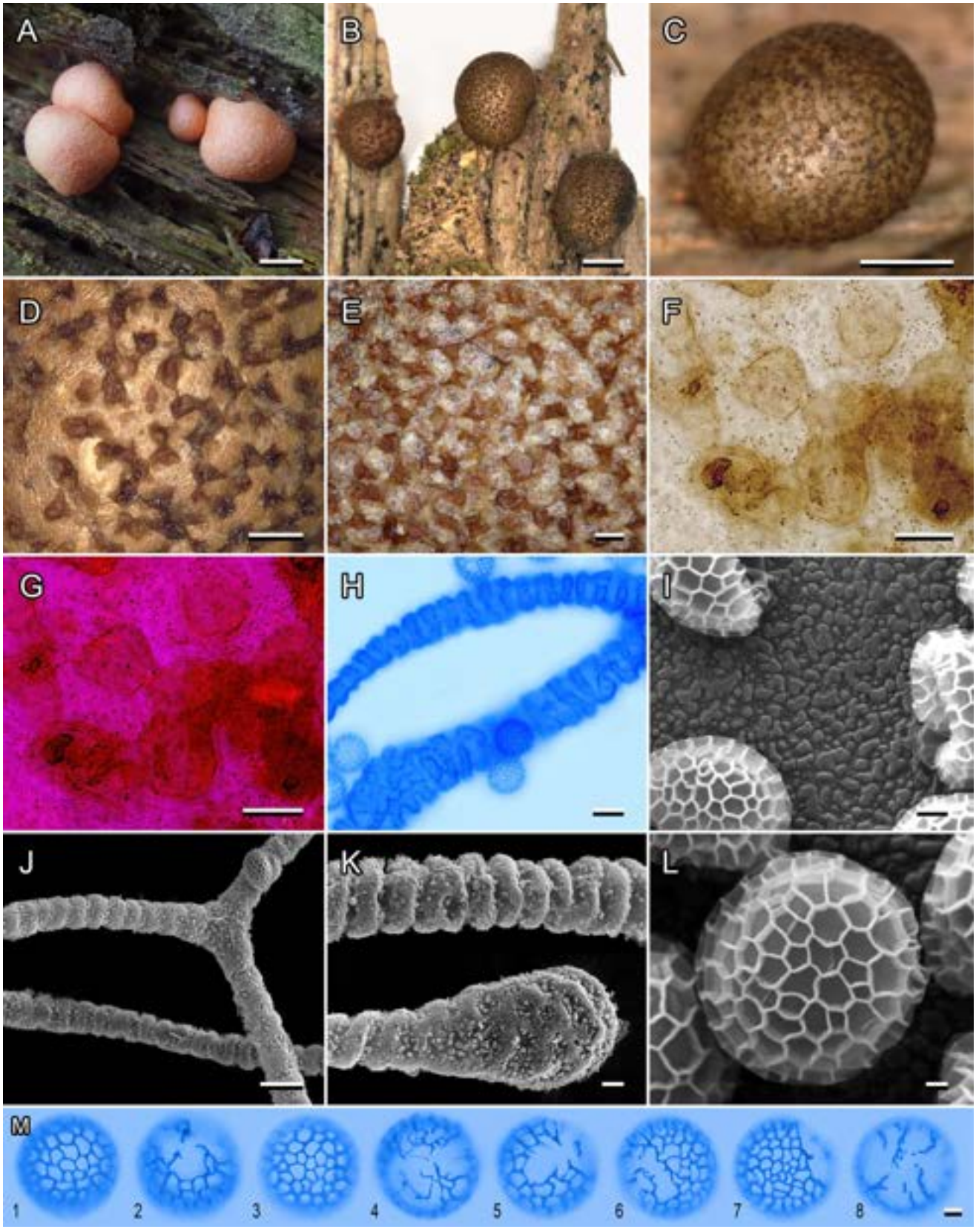

Figure 4. *Lycogala irregulare*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A. IY04. B, D, F, G. sc27520 (holotype). C. sc27507. E, H, M. CWP4226. I–L. sc27536. Bars: A–C = 1 mm; D = 200 µm; E–G = 100 µm; H, J = 5 µm; I, K, M = 1 µm; L = 0.5 µm.

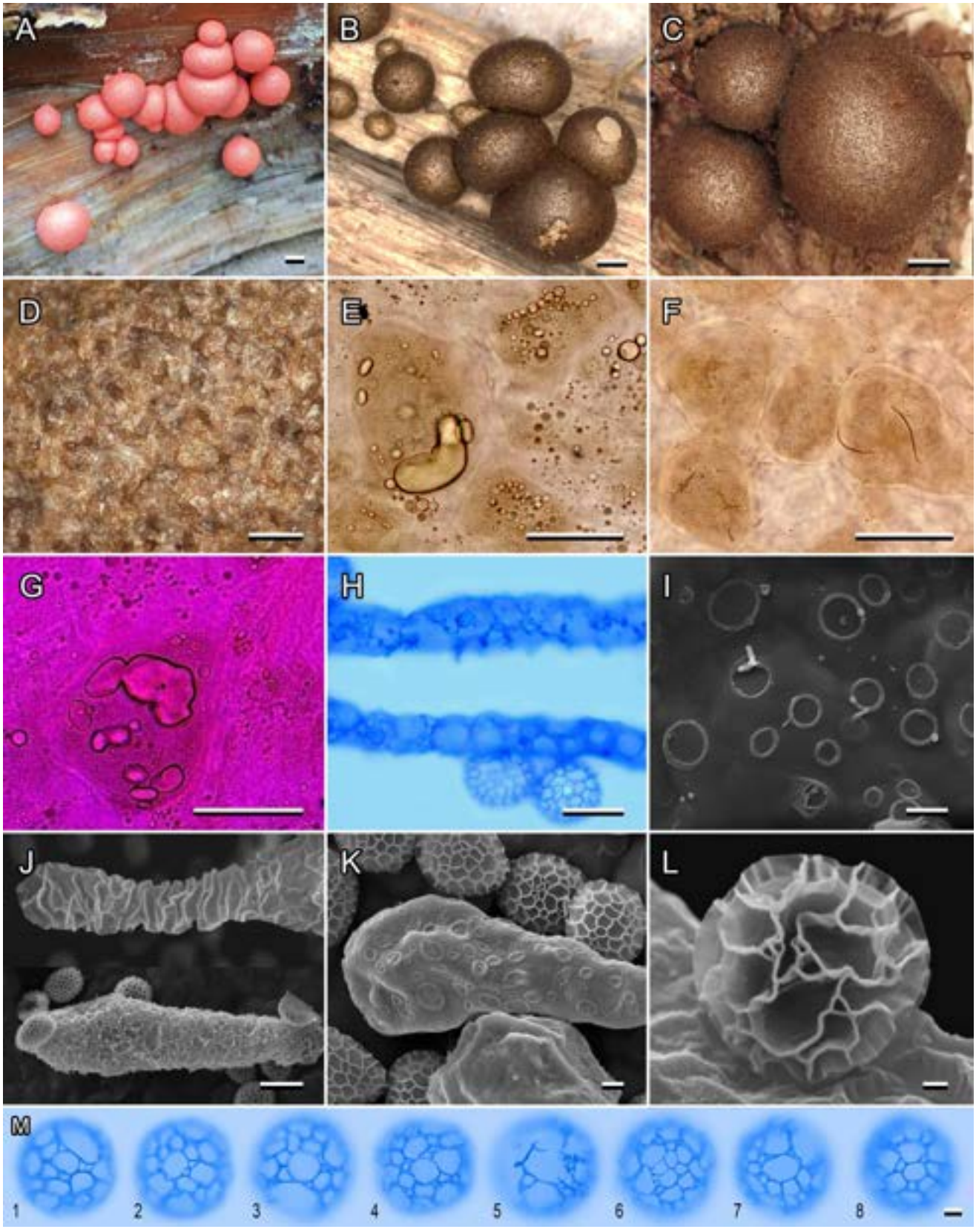

Figure 5. *Lycogala olearium*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D. Peridium in RL. E, F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A (courtesy of Mariko Creasman), E, G. CWP3658. B, I–K. sc27534. C, D, L, M. sc32006 (holotype). F. sc27531. H. CWP4225. Bars: A–C = 1 mm; D = 200 µm; E–G = 100 µm; H, J = 5 µm; I, K, M = 1 µm; L = 0.5 µm.

by rings, reticulum of irregular folds, warts, ridges, irregular bracelet-like thickenings (FIG. 5H, J, K). Spore mass light pinkish-gray(?), later light reddish-gray, in old specimens yellowish-gray. Spores (5.5–)6.5–7(–7.5) µm diam, hyaline, reticulate, with 3–7 meshes across diameter, very different in size, with small meshes tending to surround every large mesh; unornamented area unclear, if present, occupies nearly ⅓ of the spore surface (FIG. 5L, M). Immature fructifications orange-pink (FIG. 5A).

Distribution: Europe, North America.

Comments: Presence of numerous oil deposits, typically including large round droplets, within vesicles distinguishes this species from the similar *L. epidendrum* and *L. irregulare*. The additional characters are large meshes of the spore ornamentation, often with small meshes surrounding one large one, and ornamentation of capillitium and peridium by rings. The peridial morphotype in *L. olearium* was previously referred to as "olearium" (Leontyev et al. 2022a).

Lycogala palianytsia Leontyev, Schnittler & Ishchenko, sp. nov. FIG. 6
MycoBank MB848148

Typification: GERMANY. MECKLENBURG-WESTERN POMERANIA: Greifswald (54.02530 13.25070), on a small, well-decayed trunk of *Fagus sylvatica*, near the ground, 17 Jul 2011, *M. Schnittler* (**holotype** sc22074). GenBank: 18S rDNA = OM423963; *COI* = ON931578.

Diagnosis: Sporocarps medium-sized, yellowish- or dull brown. Peridial vesicles scattered, solitary, brown in TL, contain birefringent crystals. Spore mass gray, warm gray.

Etymology: palianytsia (Ukrainian), round bread, referring to the appearance of sporocarps.

Sporocarps in small loose groups, spherical to short horizontally ovoid, more-or-less regular in shape, (2–)2.5–5.5(–6.5) mm diam (FIG. 6B, C). Peridium membranous, yellowish-brown, dull brown, covered by vesicles. Peridial vesicles 70–240 µm, in RL looking like dried droplets, light yellow-brown, mainly solitary, loosely and evenly distributed, distant from each other on 1–2 times their diameter (FIG. 6D, E), in TL solitary, ovoid or angular, brown (FIG. 6F). Vesicle walls light brownish. Crystals present, forming fine irregular aggregates (FIG. 6G). Oil droplets absent. Pigment accumulations, if present, dull orange-brown. Inner surface of the peridium smooth or covered by warts (FIG. 6I). Capillitium tubular, 5–15 µm diam, with faintly wavy contours, surface fine pitted-warty, with ring-shaped fossae (FIG. 6H, J, K). Spore mass gray(?), later warm gray, in old collections yellowish-gray (FIG. 6B). Spores 6–7.5(–7.5) µm diam, hyaline, reticulate, with 5–7 meshes across diameter, unornamented area occupies ½–⅓ of the spore surface (FIG. 6L, M). Immature fructifications orange (FIG. 6A).

Distribution: Europe.

Comments: Among other "crystalliferous" species, *L. palianytsia* differs by scattered sporocarps and by rather irregular and inconspicuous peridial vesicles. The peridial morphotype in *L. palianytsia* was previously referred to as "punctulatum" (Leontyev et al. 2022a).

Lycogala caviaroides Leontyev, Schnittler, S.L. Stephenson & G. Konstantinides, sp. nov. FIG. 7
MycoBank MB848149

Typification: GERMANY. MECKLENBURG-WESTERN POMERANIA: Greifswald (54.0241 13.2532), on strongly decayed log of *Pinus sylvestris*, 13 Sep 2011, *P. Lamkowski* (**holotype** sc22165). GenBank: 18S rDNA = KM262640.

Diagnosis: Sporocarps medium-sized, beige, with orange spots. Peridial vesicles densely and evenly distributed, solitary, bright orange in TL, contain pigment accumulations and birefringent crystals. Spore mass pinkish-white, light warm gray.

Etymology: caviarum (Latin), roe, referring to the appearance of peridium vesicles, similar to dried salmon roe ("red caviar").

Sporocarps grouped, mainly horizontally ovoid, often deformed from mutual pressure, (1.5–)2–4.5(–10) mm diam (FIG. 7A–C). Peridium membranous, beige, light grayish-brown, covered by vesicles. Peridial vesicles 140–220 µm, in RL looking like dried droplets, orange to dark red, similar to dried red caviar, solitary, rather densely and evenly distributed, distant from each other on length of their diameter (FIG. 7d, E), in TL solitary, rounded, bright orange (FIG. 7F). Vesicle walls almost hyaline. Crystals rather numerous, forming large irregular aggregates (FIG. 7G). Oil droplets absent. Pigment accumulations abundant, bright orange (FIG. 7G). Inner surface of the peridium smooth or covered by scattered warts (FIG. 7I). Capillitium tubular, 5–15 µm diam, with wavy contours, ornamented by regular bracelet-like thickenings, or less regular, with pitted-warty surface, interrupted by rounded fossae (FIG. 7H, J, K). Spore mass pinkish-white, in old specimens light warm gray. Spores (5.5–)6–7(–7.5) µm diam, hyaline, reticulate, with 6–9 meshes across diameter, unornamented area wide, occupying nearly ⅓ of the spore surface (FIG. 7L, M). Immature fructifications probably orange.

Distribution: Europe, Southeast Asia, North America.

Comments: In many species, peridial vesicles may occasionally dry at the "red" stage under suboptimal

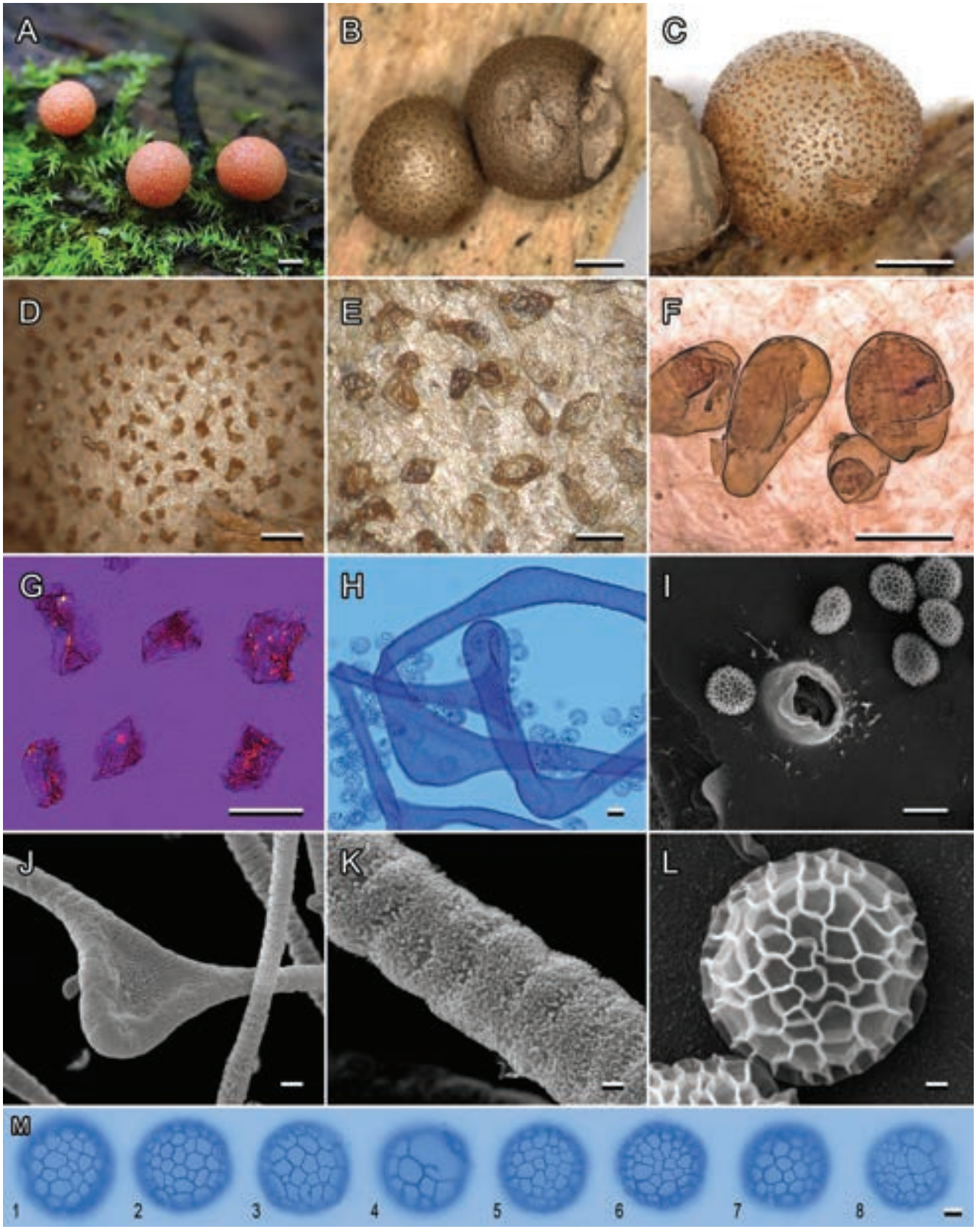

Figure 6. *Lycogala palianytsia*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium with the basis of the capillitial tubule, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A. IY28. B, G. sc22074 (holotype). C, D, F. sc22100. E, M. EJ22295263. H–L. sc27508. Bars: A, B = 1 mm; C = 0.5 mm; D = 200 µm; E–G = 100 µm; H–J = 5 µm; K, M = 1 µm; L = 0.5 µm.

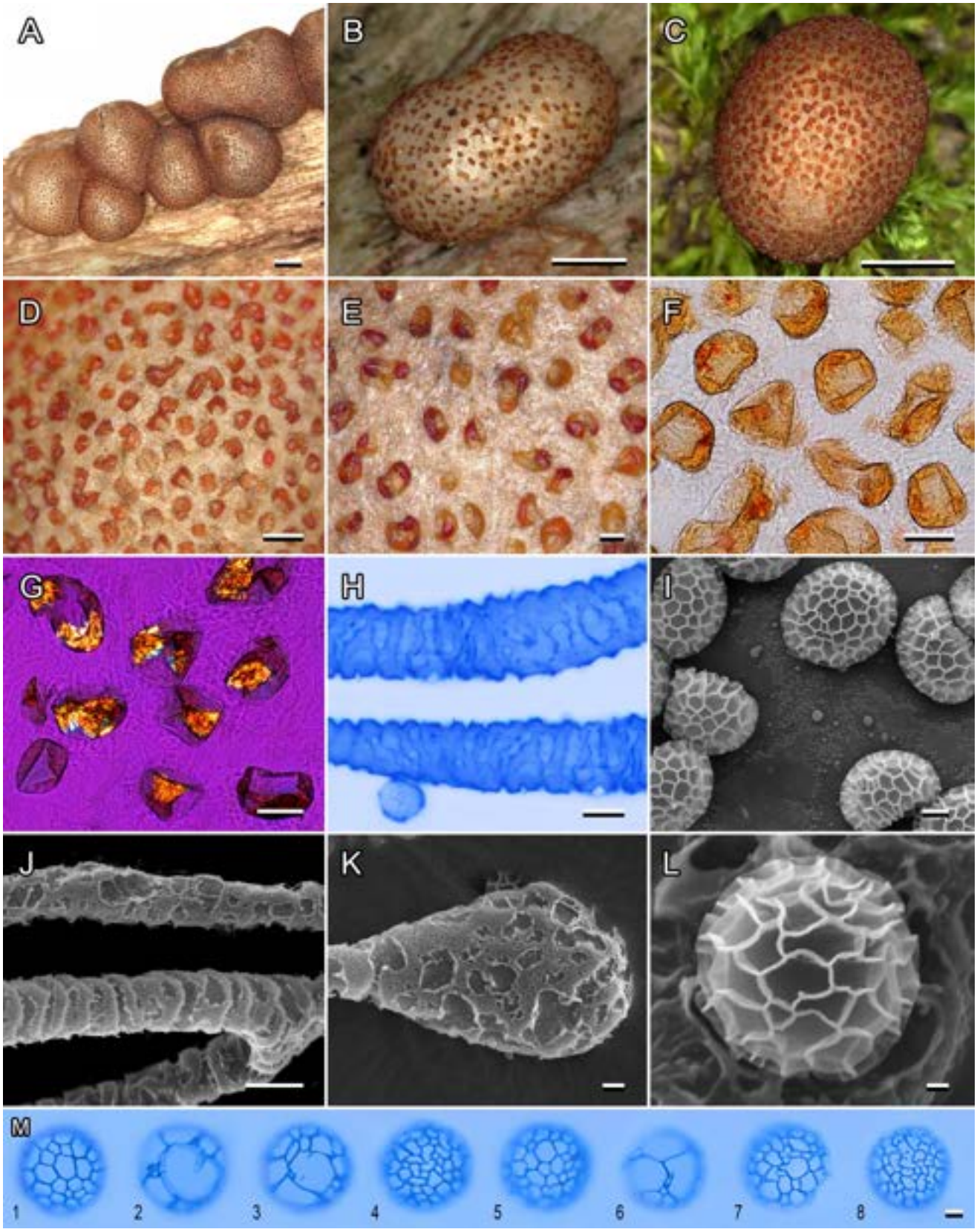

Figure 7. *Lycogala caviaroides*, sp. nov. A–C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spore, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, E, G. UARK26963. B, H, M. sc32018. C, D, F, I–L. sc22165 (holotype). Bars: A–C = 1 mm; D = 200 µm; E–G = 100 µm; H, J = 5 µm; I, K, M = 1 µm; L = 0.5 µm.

conditions and may look similar to those of *L. caviaroides*. Therefore, to be sure that your specimen belongs to *L. caviaroides*, it is necessary to note that the red vesicles are evenly developed on the entire surface of the sporocarp, and not only in zones with signs of impaired development, as well as to observe crystals in the vesicles. The peridial morphotype in *L. caviaroides* was previously referred to as "caviaroides" (Leontyev et al. 2022a).

Lycogala acinonychum Leontyev, Schnittler, T.E. dela Cruz, M.F.B. Eloreta & T. van der Heul, sp. nov. FIG. 8
MycoBank MB848150

Typification: PHILIPPINES. BICOL REGION: Brgy Digdigon, Goa, Camarines Sur (13.70558 123.40032), on fallen log, 1 Nov 2018, *T.E.E. dela Cruz* (**holotype** PFb75). GenBank: 18S rDNA = OM423955; *COI* = ON931577.

Diagnosis: Sporocarps medium-sized, beige with brown spots. Peridial vesicles very densely and evenly distributed, solitary, rounded, ovoid, brown in TL, include birefringent crystals. Spore mass light gray when fresh.

Etymology: acinonyx (Latin), cheetah (*Acinonyx jubatus*), referring to the appearance of the peridium, tightly covered with rounded brown spots.

Sporocarps in small groups, spherical, more-or-less regular in shape, (1.5–)2–4.5(–5.5) mm diam (FIG. 8A, B). *Peridium* membranous, beige, light grayish-brown, densely covered by vesicles. Peridial vesicles 70–350 µm, in RL looking like dried droplets, brown, solitary, densely and evenly distributed, distant from each other on ⅓–½ their diameter (FIG. 8C, D), in TL solitary, rounded, brown (FIG. 8F). Vesicle walls hyaline. Crystals present, rather numerous, forming irregular aggregates (FIG. 8G). Granular deposits with small oil droplets, brown, abundant. Inner surface of the peridium smooth (FIG. 8I), or with scanty warts. Capillitium tubular, 5–20 µm diam, with wavy contours, ornamented by regular bracelet-like thickenings (FIG. 8H, J, K). Spore mass light gray(?), later light warm gray, in old specimens yellowish-gray. Spores 6–6.5(–7) µm diam, hyaline, reticulate, with 6–8 meshes across diameter, unornamented area occupies ⅓–½ of the spore surface (FIG. 8L, M). Immature fructifications unknown.

Distribution: Southeast Asia, Australia.

Comments: This species is a "twin" of *L. leopardinum* but differs from the latter by smaller sporocarps and denser arrangement of peridial vesicles. The distribution areas of *L. acinonychum* and *L. leopardinum* probably do not overlap.

Lycogala leopardinum Leontyev, Ishchenko, Schnittler & E. Johannesen, sp. nov. FIG. 9
MycoBank MB848151

Typification: GERMANY. MECKLENBURG-WESTERN POMERANIA: Greifswald, mixed forest near Steffenshagen (54.12776 13.34837), on strongly decayed wood of *Betula pendula*, 6 Jun 2013, *M. Schnittler* (**holotype** sc27504). GenBank: 18S rDNA = OM423974.

Diagnosis: Sporocarps large, beige with brown spots. Peridial vesicles densely and evenly distributed, solitary, rounded, brown in TL, contain numerous birefringent crystals, which often form one durse. Spore mass dull pink, light salmon-colored.

Etymology: leopardus (Latin), leopard (*Panthera pardus*), referring to the appearance of the peridium, tightly covered with rounded brown spots, sometimes with a bright center.

Sporocarps in small to rather large groups (>10), spherical to short horizontally ovoid, regular in shape or slightly deformed from mutual pressure, (1.5–)2.5–6 (–9.5) mm diam (FIG. 9B, C). *Peridium* membranous, beige, light grayish-brown, covered by vesicles. Peridial vesicles 90–200 µm, in RL looking like dried droplets, brown, solitary, densely and evenly distributed, distant from each other on ½–1 times their diameter (FIG. 9D, E), in TL solitary, rounded, brown (FIG. 9F). Vesicle walls hyaline. Crystals numerous, forming radial druses or irregular aggregates, filling up to all the inner space of the vesicle (FIG. 9G). Granular accumulations with small oil droplets present, mainly brown. Inner surface of the peridium smooth or covered by scattered warts (FIG. 9I). Capillitium tubular, 5–20 µm diam, with wavy or smooth contours, ornamented by regular bracelet-like thickenings, or less regular, with pitted-warty surface (FIG. 9H, J, K). Spore mass dull pink(?), later light salmon-colored, in old specimens yellowish-gray. Spores (5.5–)6–7.5 µm diam, hyaline, reticulate, with 5–8 meshes across diameter, unornamented area occupies ⅓–½ of the spore surface (FIG. 9L, M). Immature fructifications bright orange, pinkish-orange, dull pinkish (FIG. 9A).

Distribution: Europe.

Comments: After *L. epidendrum*, this is the second-most abundant species in the temperate zone. From other "crystalliferous" species, it differs by largest sporocarps and biggest colonies. From other species with large fructifications, it can be distinguished by light pigmentation of the peridium and uniformly rounded vesicles, densely and evenly distributed over the entire peridial surface. The peridial morphotype in *L. leopardinum* was previously referred to as "crystalliferum" (Leontyev et al. 2022a).

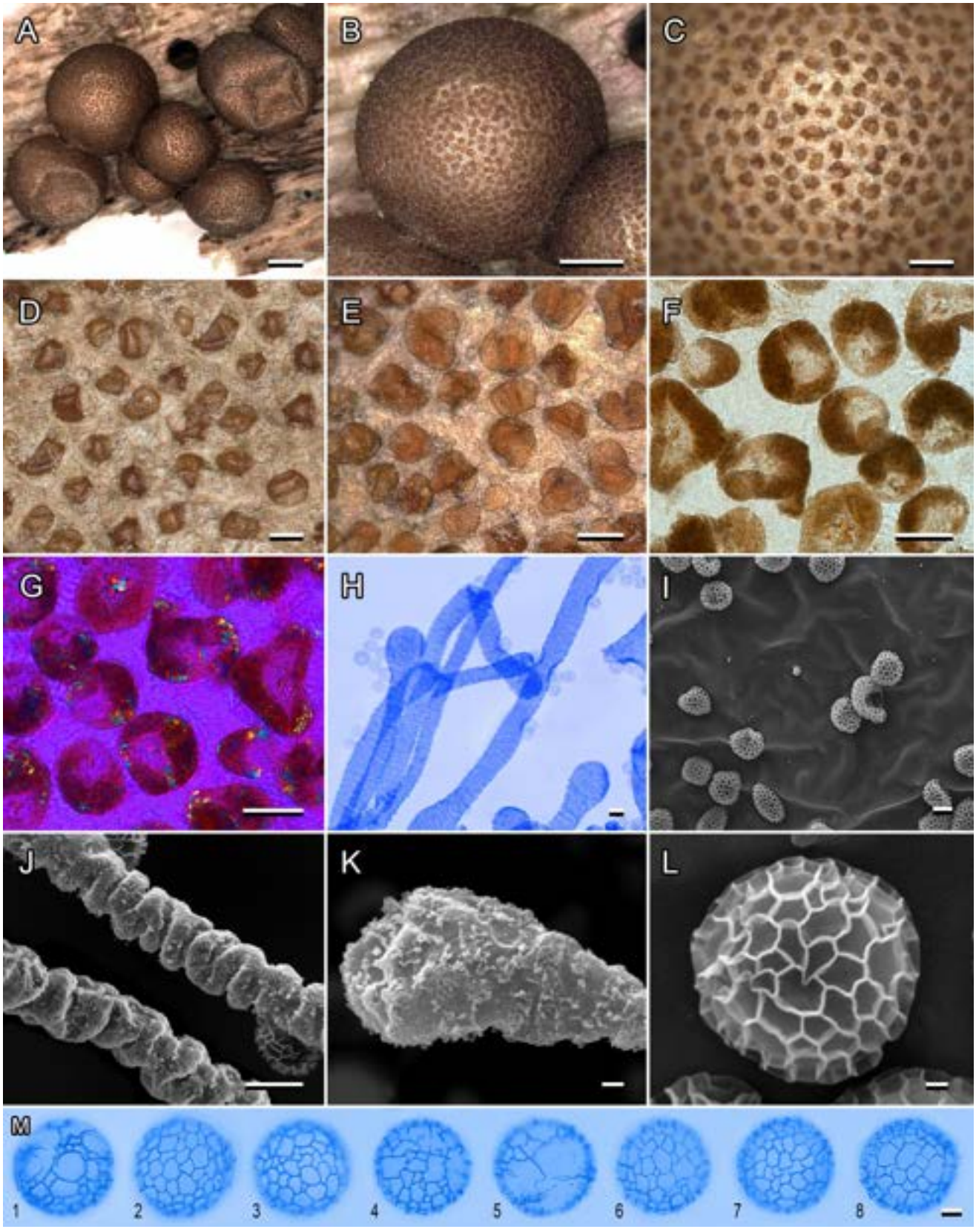

Figure 8. *Lycogala acinonychum*, sp. nov. A, B. Sporocarps. C–E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, B, E–M. DFb75 (holotype). C. DFb57. D. TVDH560. Bars: A, B = 1 mm; C = 0.5 mm; D–G = 100 µm; H, J = 5 µm; I = 2 µm; K, M = 1 µm; L = 0.5 µm.

Lycogala succineum Leontyev & Schnittler, sp. nov. FIG. 10

MycoBank MB848152

Typification: GERMANY. MECKLENBURG-WESTERN POMERANIA: Greifswald, mixed forest near Weitenhagen (54.04399 13.41806), on strongly decayed trunk of *Picea abies*, 8 Jun 2013, *M. Schnittler* (**holotype** sc27545). GenBank: 18S rDNA = OM423994; *COI* = ON931592.

Diagnosis: Sporocarps medium-sized, rufous beige. Peridial vesicles loosely and evenly distributed, solitary, rounded, amber yellow in RL, brown in TL, contain numerous birefringent crystals. Spore mass light pinkish-gray, light salmon-gray.

Etymology: succinum (Latin), amber, referring to the color of peridial vesicles.

Sporocarps in small groups, spherical to horizontally ovoid, regular in shape or slightly deformed from mutual pressure, (1.5–)2–5(–7.5) mm diam (FIG. 10A, B). *Peridium* membranous, rufous beige, light rufous brown, covered by vesicles. Peridial vesicles 50–300 µm, in RL looking like dried droplets, light amber-yellow, light-brownish, solitary, rather densely and evenly distributed, distant from each other on length of their diameter or more (FIG. 10C, D), in TL nonclustered, rounded, brown (FIG. 10E). Vesicle walls almost hyaline. Crystals numerous, forming irregular aggregates, often completely filling the inner space of the vesicle (FIG. 10F, G). Granular accumulations and oil droplets present, brown. Inner surface of the peridium smooth or covered by scattered warts (FIG. 10I). Capillitium tubular, 3–10 µm diam, with wavy or smooth contours, ornamented by warts or regular bracelet-like thickenings (FIG. 10H, J, K). Spore mass light pinkish-gray(?), later light salmon-gray, in old specimens light yellowish. Spores (5.5–)6–7.5(–8) µm diam, hyaline, reticulate, with 5–9 meshes across diameter, variable in size, unornamented area wide, occupying ⅓–½ of the spore surface (FIG. 10L, M). Immature fructifications probably orange.

Distribution: Europe.

Comments: Among other "crystalliferous" species, *L. succineum* differs by very light peridial vesicles, which are only slightly darker than the peridium. Crystal deposits in this species are especially numerous.

Lycogala aggregatum Leontyev, Kochergina, Schnittler & C. Rojas, sp. nov. FIG. 11

MycoBank MB848153

Typification: COSTA RICA. CARTAGO: Turrialba, FEIMA Experimental Forest near the village of La Suiza (9.86189 83.63401), strongly decayed log, 22 Feb 2020, *M. Schnittler* (**holotype** sc32100). GenBank: 18S rDNA = OM424025; *COI* = ON931601.

Diagnosis: Sporocarps small, dark brown to black. Peridial vesicles accreted, forming rosette-like groups with 1–3 vesicles across the group, dark brown in TL, with the granular contents. Capillitium with smooth contours, with fine pitted-warty surface and scattered large rings. Spore mass light pinkish-gray, light reddish-gray.

Etymology: aggrego (Latin), to attach, to append, referring to the aggregation of peridial vesicles.

Sporocarps in large groups (>100 of sporocarps), spherical to short horizontally ovoid, regular in shape, (1.5–)2–4(–5) mm diam (FIG. 11B, C). Peridium membranous, dull ochraceous-brown, covered by vesicles so densely that sporocarp looks almost black, at least in the upper part. Peridial vesicles 10–100 µm, in RL looking like merged dried droplets, convex, glossy, very dark brown to almost black, entirely covering the surface of the peridium or forming large spots (FIG. 11D), in TL merged into a very dense network of rosette-like groups with 1–3 vesicles across the group, angular from mutual pressure, brown to dark brown (FIG. 11E, F). Vesicle walls brown, mainly multilayered, with outer layers covering the whole group, or absent. Crystals absent. Oil droplets numerous, from rather large (FIG. 11E) to small, forming a granular mass, colorless, irregular in shape (FIG. 11F), sometimes birefringent (FIG. 11G). Inner surface of the peridium smooth or covered by scattered warts and inconspicuous rings 0.5–1 µm diam (FIG. 11I). Capillitium tubular, 2–10 µm diam, with smooth or uneven contours, ornamented by large (1–3 µm) rings or pitted-warty cover. Spore mass light pinkish-gray, later light reddish-gray (FIG. 11H, J, K). Spores 5.5–7 µm diam, hyaline, reticulate, with 7–9 meshes across diameter, unornamented area small, occupies nearly ¼ of the spore surface (FIG. 11L, M). Immature fructifications light pink (FIG. 11A).

Distribution: Central America.

Comments: Large, dense colonies of small sporocarps, densely covered by a dark vesicular mass, cause this species to resemble *L. exiguum*. However, the latter species has vesicles 2 times smaller, accreted in groups of 3–6 units across the group. In *L. exiguum*, vesicles cover nearly all surface of sporocarp, whereas in *L. aggregatum* they tend to concentrate in upper half of the fruiting body. From *L. oncoides*, which also occurs in Central America, *L. aggregatum* can be distinguished by its large colonies, a thin capillitium with wavy contours, and smaller meshes of the spore ornamentation. The peridial morphotype in *L. aggregatum* was previously referred to as "crystalloaggregatum" (Leontyev et al. 2022a).

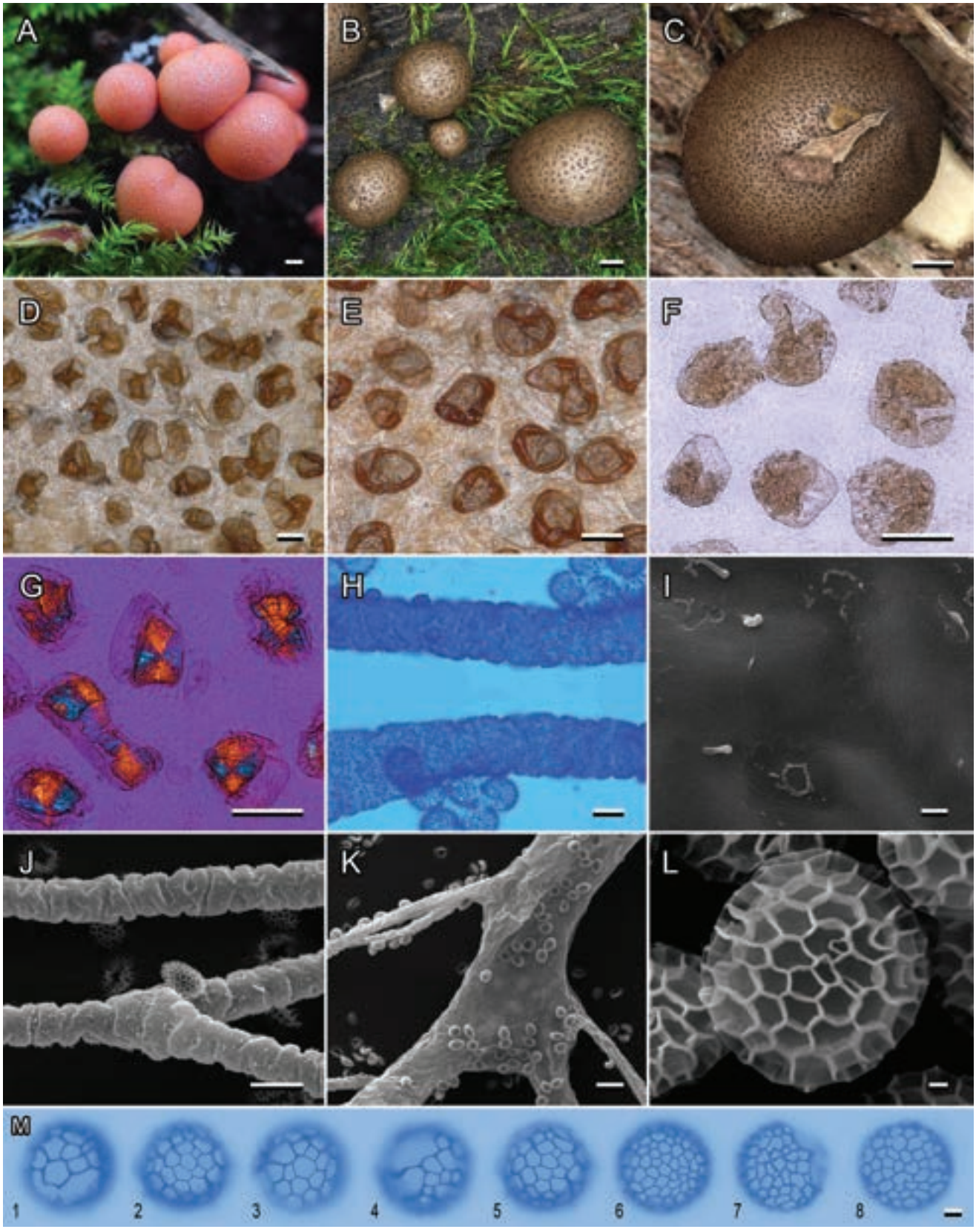

Figure 9. *Lycogala leopardinum*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A. IY09. B. IY03. C, F–L. sc27504 (holotype). D. IY12. E. IY18. M. sc27513 (1–4), sc27504 (5–8). Bars: A–C = 1 mm; D–G = 100 µm; H, J = 5 µm; I, M = 1 µm; K = 10 µm; L = 0.5 µm.

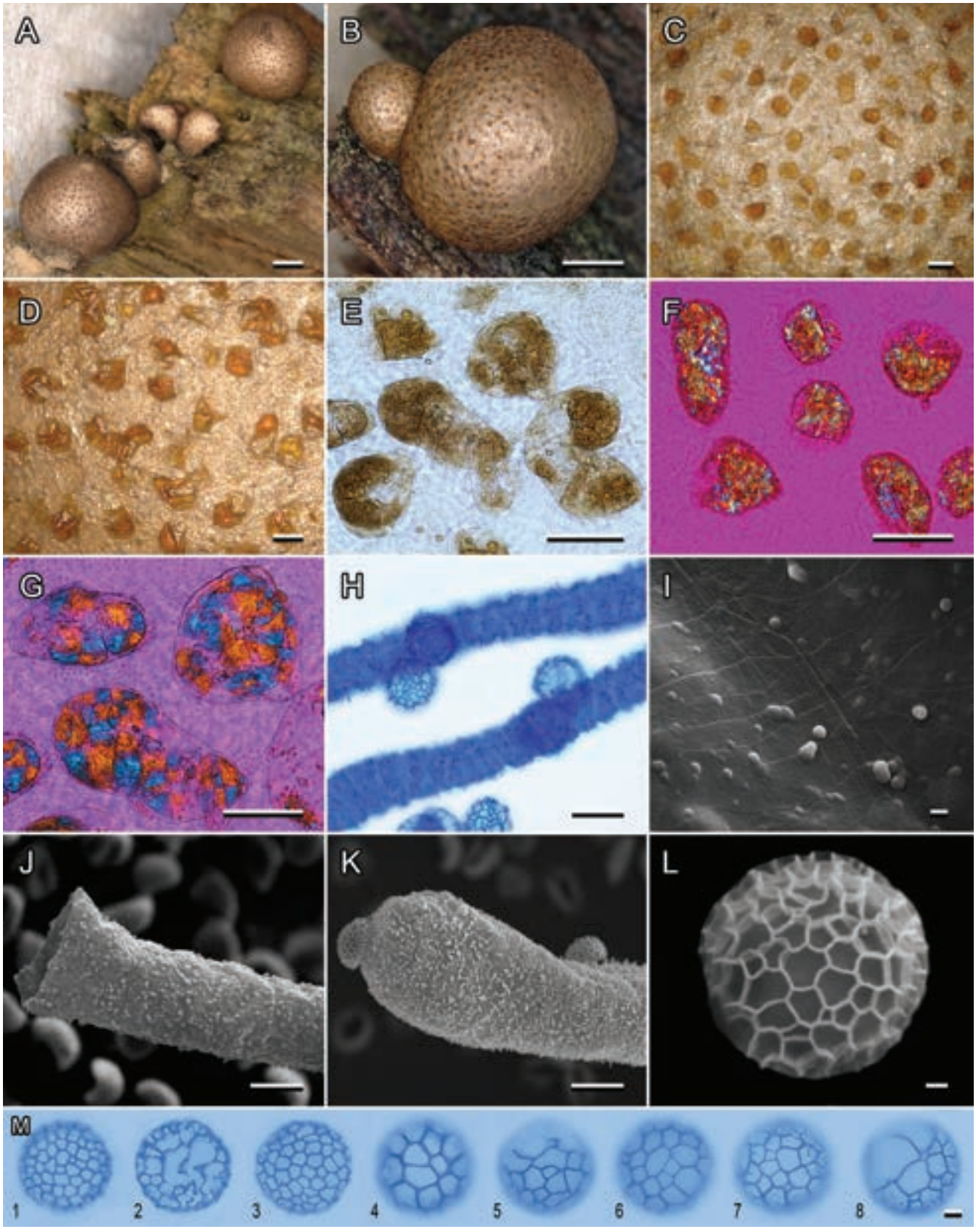

Figure 10. *Lycogala succineum*, sp. nov. A, B. Sporocarps. C, D. Peridium in RL. E. Peridial vesicles in TL. F, G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, D, F, I–L. sc27545 (holotype). B. CWP3093. C. CWP3092. E, G. sc27512. H. CWP4216. M. CWP4216 (1–3), CWP3092 (3–8). Bars: A, B = 1 mm; C–G = 100 µm; H, J = 5 µm; I, K, M = 1 µm; L = 0.5 µm.

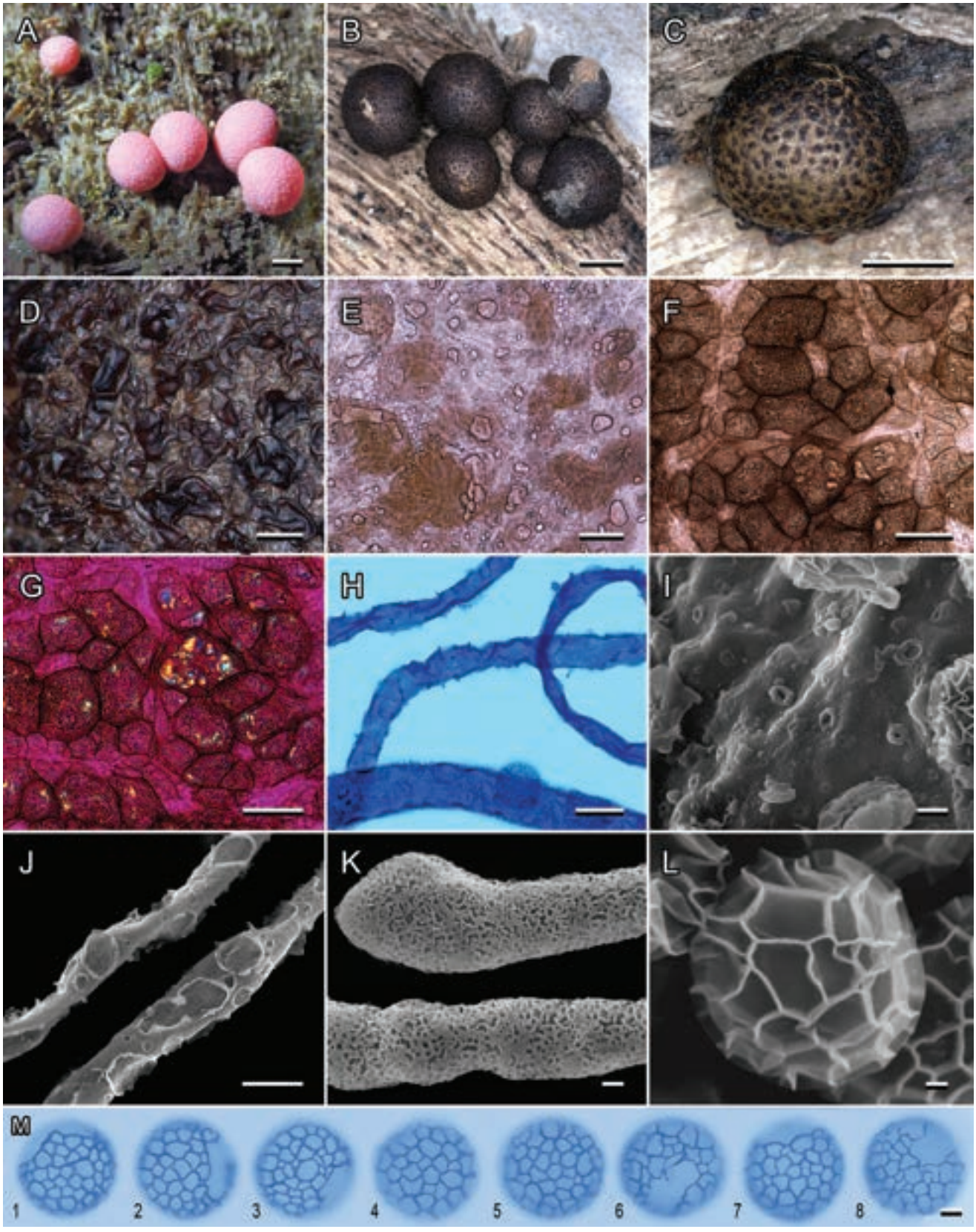

Figure 11. *Lycogala aggregatum*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D. Peridium in RL. E, F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spore, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A. CWP4000. B–H, M. sc32100 (holotype). I–L. CWP4006. Bars: A, B = 1 mm; C = 0.5 mm; D = 200 µm; E–G = 100 µm; H, J = 5 µm; I, K, M = 1 µm; L = 0.5 µm.

Lycogala skovorodaense Leontyev, Schnittler & Ishchenko, sp. nov. FIG. 12
MycoBank MB848154

Typification: UKRAINE. KHARKIV REGION: Homilsha Forests National Nature Park (49.6165 36.31402), on dead wood, 22 Jul 2020, *D.V. Leontyev* (**holotype** CWP4169). GenBank: 18S rDNA = OM423875; *COI* = ON931553.

Diagnosis: Sporocarps small, dark brown. Peridial vesicles accreted, forming dense, rounded, rosette-like clusters, brown in TL, with the oily contents. Capillitium ornamented by large warts and spines. Spores with 4–6 meshes across its diameter. Spore mass gray, warm gray.

Etymology: Hryhorii Skovoroda (1722–1794), Ukrainian philosopher, poet, teacher, and composer, referring to the affiliation of D.L. (Skovoroda University), 300th year anniversary of H. Skovoroda, and in memory of his house museum, ruined by a Russian bomb on 6 May 2022, as well as of the main building of the Skovoroda University, ruined on 6 Jun 2022.

Sporocarps solitary or in small groups, spherical to short horizontally ovoid, mostly regular in shape, (1–)2.5–5(–5.5) mm diam (FIG. 12B, C). Peridium membranous, beige, ochraceous, densely covered by vesicles. Peridial vesicles 50–140 µm, in RL looking like dried droplets, free or merged into isodiametric spots, dark grayish-brown, tightly and evenly distributed, not fused into entire mass (FIG. 12D, E), in TL grouped in dense, rounded, rosette-like clusters of 5–10, angular from mutual pressure, brown (FIG. 12F). Vesicle walls dull brown, thick (3 µm), single-layered, sometimes covered with a "chain mail" ornamentation. Crystals absent (FIG. 12G). Oil droplets numerous, from large to small, variable in shape, colorless (FIG. 12F). Granular deposits abundant, represented by small oil droplets. Inner surface of the peridium smooth (FIG. 12I). Capillitium tubular, 4–15 µm diam, with uneven contours, ornamented by prominent ridges and clustered warts (FIG. 12H, J, K). Spore mass gray(?), later warm gray, reddish-gray, in old specimens yellowish-gray. Spores (5–)5.5–6.5(–7) µm diam, hyaline, reticulate, with 4–6(–7) meshes across diameter, unornamented area ⅓–½ of the spore surface (FIG. 12L, M). Immature fructifications light pinkish (FIG. 12A).

Distribution: Europe.

Comments: A rather peculiar species, which can be preliminarily identified in the field by the contrasting appearance of the sporocarp with dark spots over a light peridial background. Dense, rounded clusters of vesicles, resembling spores of dematioid fungi (*Stemphylium* or *Alternaria*), are also very characteristic. The peridial morphotype in *L. skovorodaense* was previously referred to as "densum" (Leontyev et al. 2022a).

Lycogala fossiculatum Leontyev, C. Rojas, T. van der Heul, Kochergina & Schnittler, sp. nov. FIG. 13
MycoBank MB848155

Typification: UKRAINE. KHARKIV REGION: Homilsha Forests National Nature Park (49.6165 36.31831), on dead wood, 22 Jul 2020, *D.V. Leontyev* (**holotype** CWP4170). GenBank: 18S rDNA = OM423876.

Diagnosis: Sporocarps large, dark brown. Peridial vesicles accreted, 20–50 µm diam, rounded, light brownish in TL, filled with spherical oil droplets. Spore mass light pinkish-gray, light salmon-gray.

Etymology: fossicula (Latin), pit, small hole, referring to the appearance of the peridium.

Sporocarps in small groups, spherical to horizontally ovoid, often deformed from mutual pressure, (1–)2–6.5(–11) mm diam (FIG. 13A, B). *Peridium* membranous, light orange-brown, covered by vesicles so densely that sporocarp looks uniformly dark brown. Peridial vesicles 20–50 µm, in RL brown to black, forming vague marble-like or reticulate pattern, sometimes with pitted surface (FIG. 13C, D), in TL grouped in a dense network of polygonal clusters and rows, with 2–3 vesicles across the group, rounded-angular from mutual pressure, light brownish (FIG. 13E, F). Vesicle walls light brown to almost hyaline, often multilayered, with the outer layers covering the whole group or row. Crystals absent (FIG. 13G). Oil droplets numerous, from large (FIG. 13F) to small (FIG. 13E), variable in shape, colorless. Granular deposits, if present, represented by small oil droplets. Inner surface of the peridium smooth or covered by scattered warts (FIG. 13 I). Capillitium tubular, 5–15 µm diam, with wavy contours, ornamented by irregular bracelet-like thickenings, warts, and ring-shaped islets (FIG. 13H, J, K). Spore mass light pinkish-gray(?), later light salmon-gray, in old specimens yellowish-gray (FIG. 13B). Spores 5.5–7.5 µm diam, hyaline, reticulate, with 5–7 meshes across diameter, unornamented area occupies ⅓ of the spore surface (FIG. 13L, M). *Immature fructifications* unknown.

Distribution: Europe, Central America, Australia.

Comments: This species is a "twin" of *L. confusum*, sharing with the latter the rather large, irregular fructifications with a marble-like surface, on which individual vesicles or their aggregates are hardly distinguishable. However, *L. confusum* possesses angular, irregular vesicles, filled with pigmented granular mass, whereas in *L. aggregatum* they are small, rounded, nearly

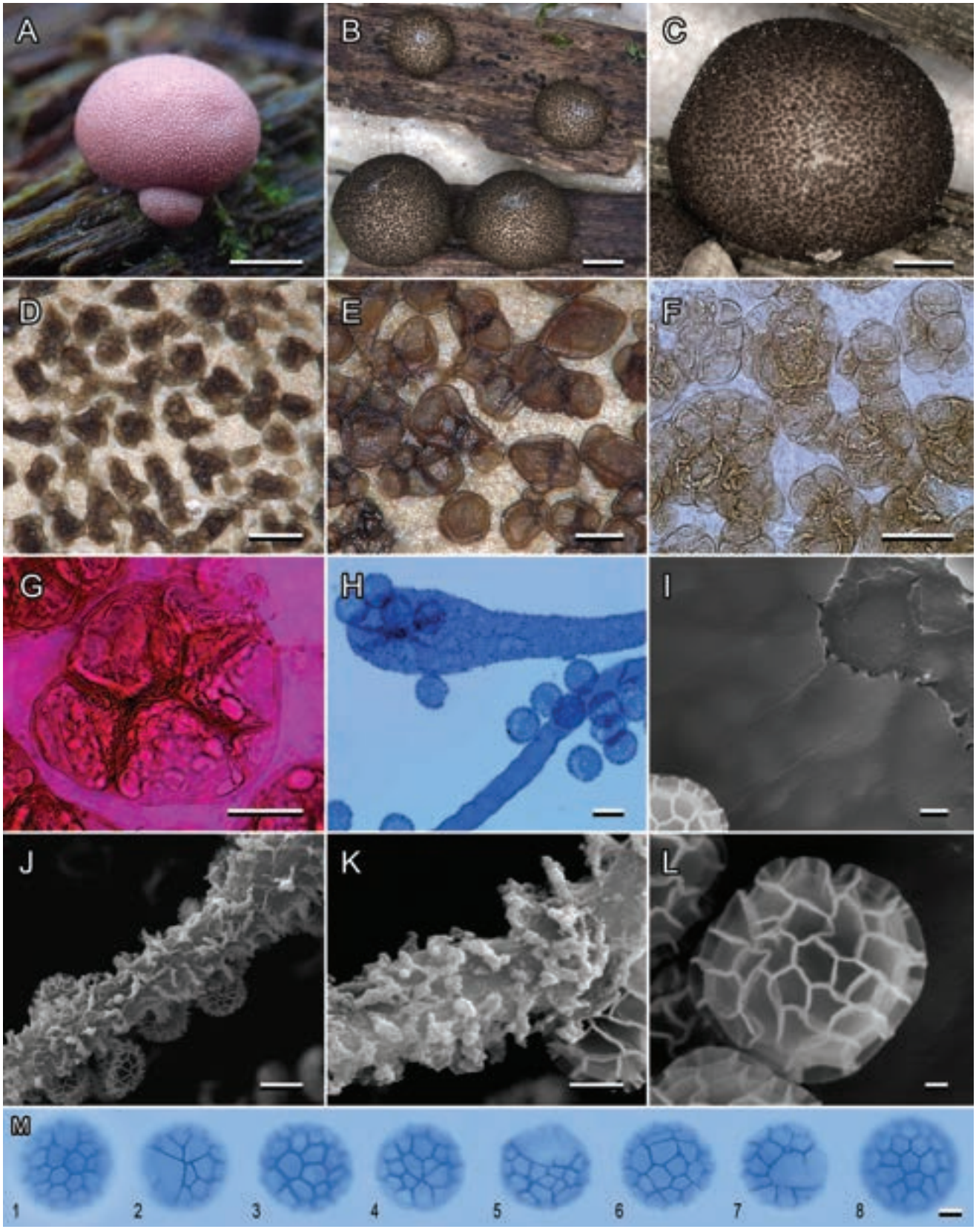

Figure 12. *Lycogala skovorodaense*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, E. IY15. B–D, I–M. CWP4169 (holotype). F–H. sc27535. Bars: A, B = 1 mm; C = 0.5 mm; D = 200 µm; E, F = 100 µm; G = 50 µm; H, J = 5 µm; I, M = 1 µm; K = 2 µm; L = 0.5 µm.

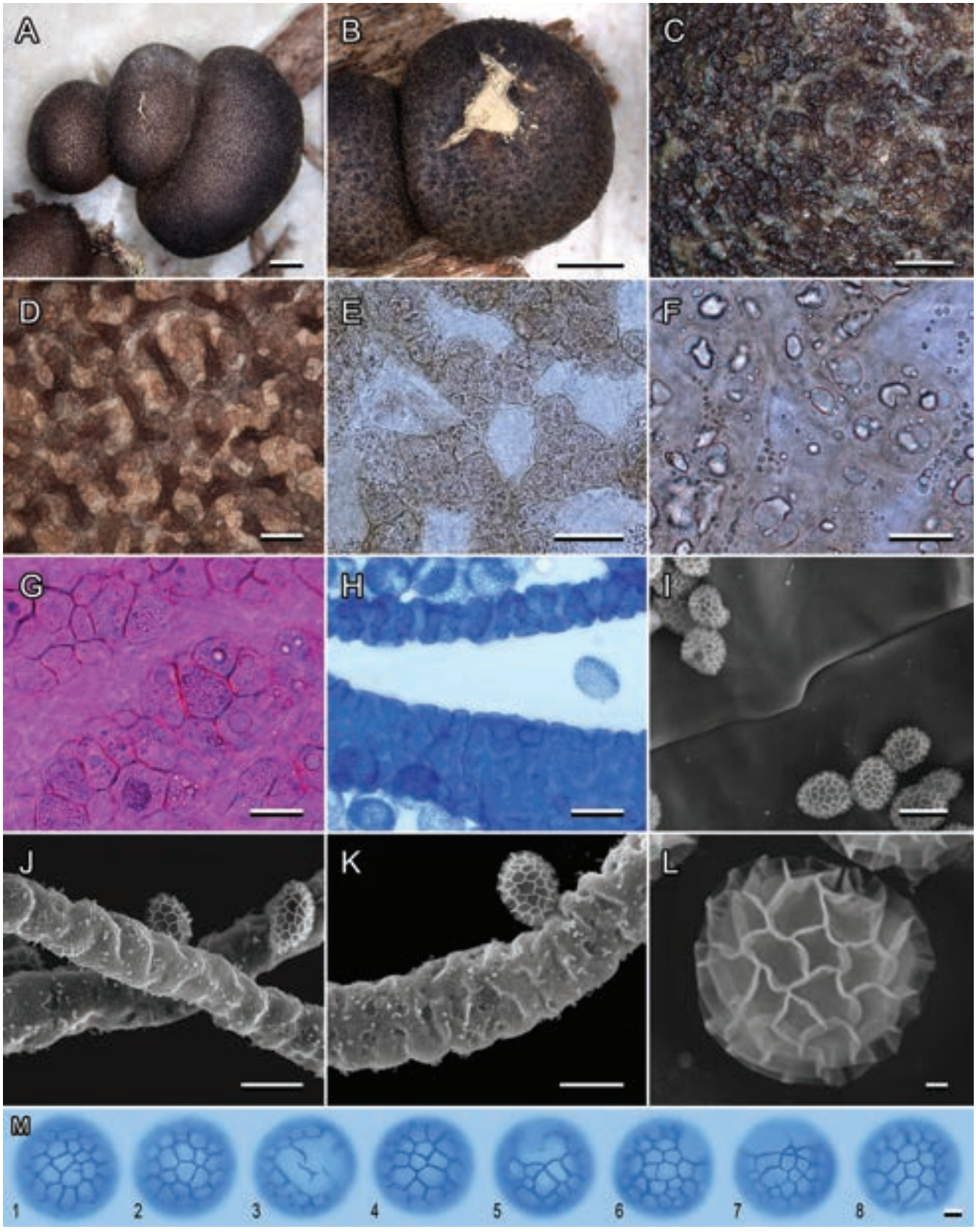

Figure 13. *Lycogala fossiculatum*, sp. nov. A, B. Sporocarps. C, D. Peridium in RL. E, F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, E, G, H. CWP4170 (holotype). B, I–M. USJ7513. C. USJ7502. D, F. TVDH552. Bars: A, B = 1 mm; C–E = 100 µm; F, G = 50 µm; H–K = 5 µm; L = 0.5 µm; M = 1 µm.

transparent, and filled with oil droplets. The peridial morphotype in *L. fossiculatum* was previously referred to as "fossiculatum" (Leontyev et al. 2022a).

Lycogala oncoides Leontyev, C. Rojas & Schnittler, sp. nov. FIG. 14

MycoBank MB848156

Typification: COSTA RICA. GUANACASTE: Nicoya, Diria National Park (10.16550 85.57890), on dead wood, 15 Jul 2016, *J.M. Zúñiga, D. Castillo* (**holotype** USJ7527). GenBank: 18S rDNA = ON920649.

Diagnosis: Sporocarps small, ochraceous-brown with black spots. Peridial vesicles accreted, grouped in small rosette-like clusters, irregularly lobate, dark brown in TL, with the granular contents. Capillitium with wavy contours, bearing bracelet-like thickenings or lobed folds. Spore mass pinkish-gray, light warm gray.

Etymology: Panthera onca (Latin), jaguar, referring to the appearance of peridial vesicles, which form complicate spots, and due to the distribution of the species in Central America.

Sporocarps solitary or in small groups, spherical to short horizontally ovoid, (2–)2.5–4(–5) mm diam (FIG. 14A, B). Peridium membranous, ochraceous-brown, densely covered by vesicles. Peridial vesicles 60–120 µm, in RL looking like grouped dried droplets, dark brown to almost black, in groups and rows, which form a reticulum (FIG. 14C, D), in TL grouped in small rosette-like clusters, irregularly lobate, dark brown (FIG. 14E, F). Vesicle walls thin (1 µm), light brown. Crystals scattered, in some vesicles forming aggregates and druses (FIG. 14G). Oil droplets numerous, from rather large to small, forming a granular mass, brownish or orange, irregular in shape (FIG. 14F). Inner surface of the peridium smooth or covered by inconspicuous rings 0.5–2 µm diam (FIG. 14I). Capillitium tubular, 4–15 µm diam, with wavy contours, surface fine pitted-warty, with ring-shaped islets, lobed folds, rings (FIG. 14H, J, K). Spore mass light pinkish-gray(?), later light warm gray. Spores (6–)6.5–7 µm diam, hyaline, reticulate, with 5–7 meshes across diameter, unornamented area occupies nearly ⅓ of the spore surface (FIG. 14L, M). Immature fructifications unknown.

Distribution: Central America.

Comments: This species is somewhat similar to *L. aggregatum* with its small sporocarps, covered with aggregated vesicles. However, *L. oncoides* forms mostly solitary or scattered sporocarps, its capillitium has wavy contours with prominent "bracelets," and the spores possess larger meshes of ornamentation. Small, compact clusters of peridial vesicles in *L. oncoides* resemble those in *L. skovorodaense*, but in the latter species they are not birefringent and often contain large oil droplets. The peridial morphotype in *L. oncoides* was previously referred to as "diversum" (Leontyev et al. 2022a).

Lycogala botrydium Leontyev, Ishchenko & Schnittler, sp. nov. FIG. 15

MycoBank MB848157

Typification: RUSSIA. MOSKOVSKAYA OBLAST: Moscow, North-Eastern Administrative District, Severnyi (55.92958 37.55156), on the log of a deciduous tree, covered with the liverwort *Lophocolea heterophylla*, 18 Jun 2020, *Y. Ishchenko* (**holotype** IY30). GenBank: 18S rDNA = OM423938.

Diagnosis: Sporocarps small, brown, irregularly ovoid. Peridial vesicles accreted, forming a dense network of ovoid, elongated, fusiform clusters, with 3–5 vesicles across the group, dark brown in TL, with the oily contents. Spore mass gray, warm gray.

Etymology: botrys (Latin), grape, referring to the appearance of peridial vesicles, which form large groups.

Sporocarps solitary, spherical, short horizontally ovoid or slightly irregular in shape, 1–3.5(–4) mm diam (FIG. 15B, C). Peridium membranous, ochraceous-brown, densely covered by vesicles. Peridial vesicles 10–40 µm, in RL dark brown to black, clustered in black spots, which form a reticulum (FIG. 15D), in TL grouped into a dense network of ovoid, elongated, fusiform clusters, with 3–5 vesicles across the group, angular by mutual pressure, brown (FIG. 15E, F). Vesicle walls hardly visible, thin (1 µm), 1–2-layered, with the smooth or granular layer covering the whole group. Crystals absent. Oil droplets small (FIG. 15E) or large (FIG. 15F), in the latter case one droplet fills the whole vesicle; sometimes birefringent (FIG. 15G). Inner surface of the peridium smooth (FIG. 15I). Capillitium tubular, 3–10 µm diam, with smooth contours, surface fine pitted-warty, with ring-shaped islets (FIG. 15H, J, K). Spore mass gray(?), later warm gray, in old specimens ochraceous-yellow (FIG. 15B). Spores (5.5–)6–6.5 µm diam, hyaline, reticulate, with 6–8 meshes across diameter, unornamented area small, occupies ¼ of the spore surface or even less (FIG. 15L, M). *Immature fructifications* bright orange-red (FIG. 15A).

Distribution: Europe.

Comments: The peridium of this species is easily recognizable by its regular network of elongated clusters, in which individual vesicles are hardly distinguishable. An especially characteristic pattern is formed when every vesicle is filled with one large oil droplet (FIG. 15F). *L. botrydium* is one of several species forming solitary sporocarps with a rather irregular shape. Another species with similar sporocarps, *L. irregulare*, possesses solitary peridial vesicles. The peridial morphotype in *L. botrydium* was previously referred to as "botrydium" (Leontyev et al. 2022a).

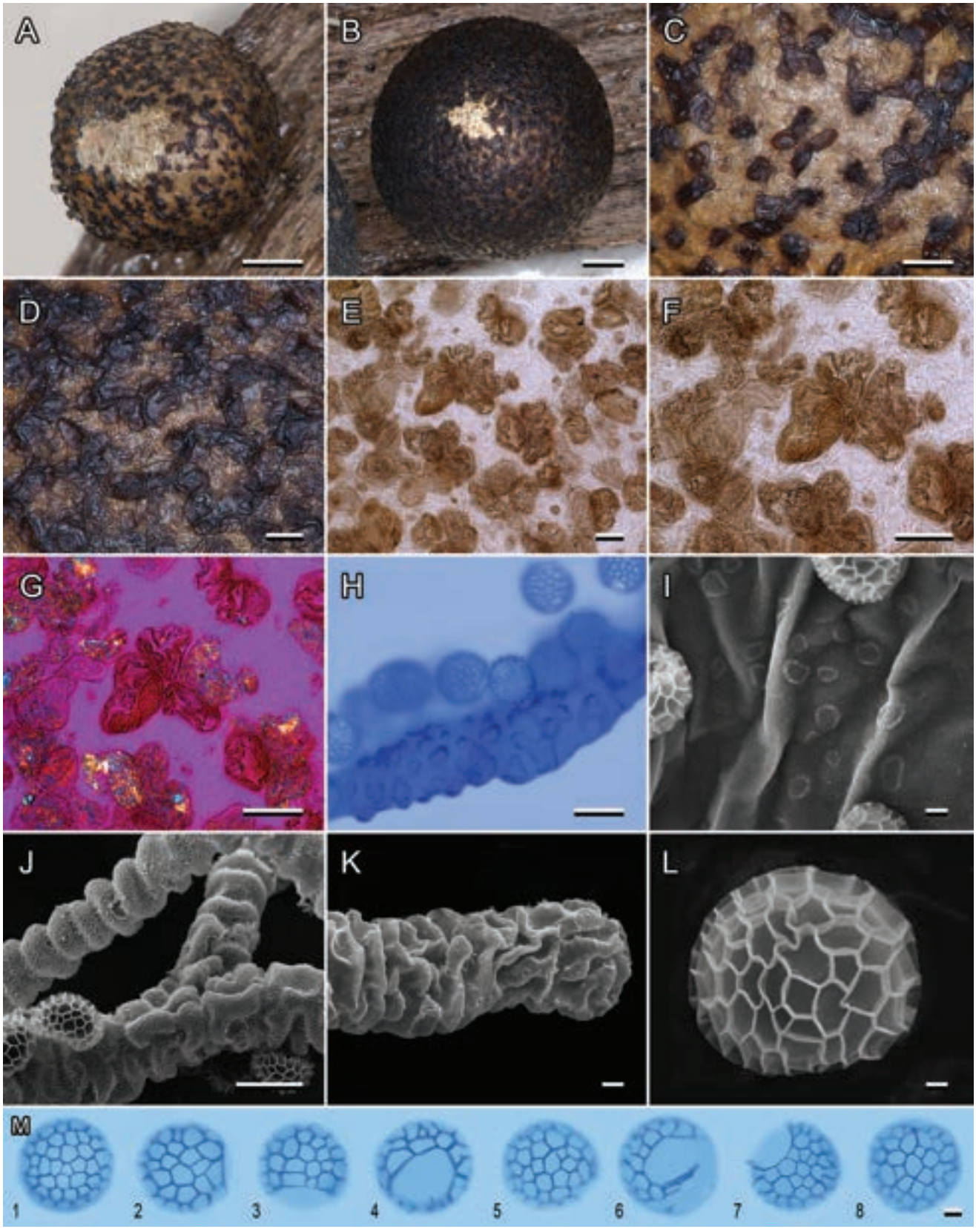

Figure 14. *Lycogala oncoides*, sp. nov. A, B. Sporocarps. C, D. Peridium in RL. E, F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, C, I–L. USJ7525. B, D–H, M. USJ7527 (holotype). Bars: A, B = 0.5 mm; C–F = 100 µm; G = 50 µm; H, J = 5 µm; I, K, M = 1 µm; L = 0.5 µm.

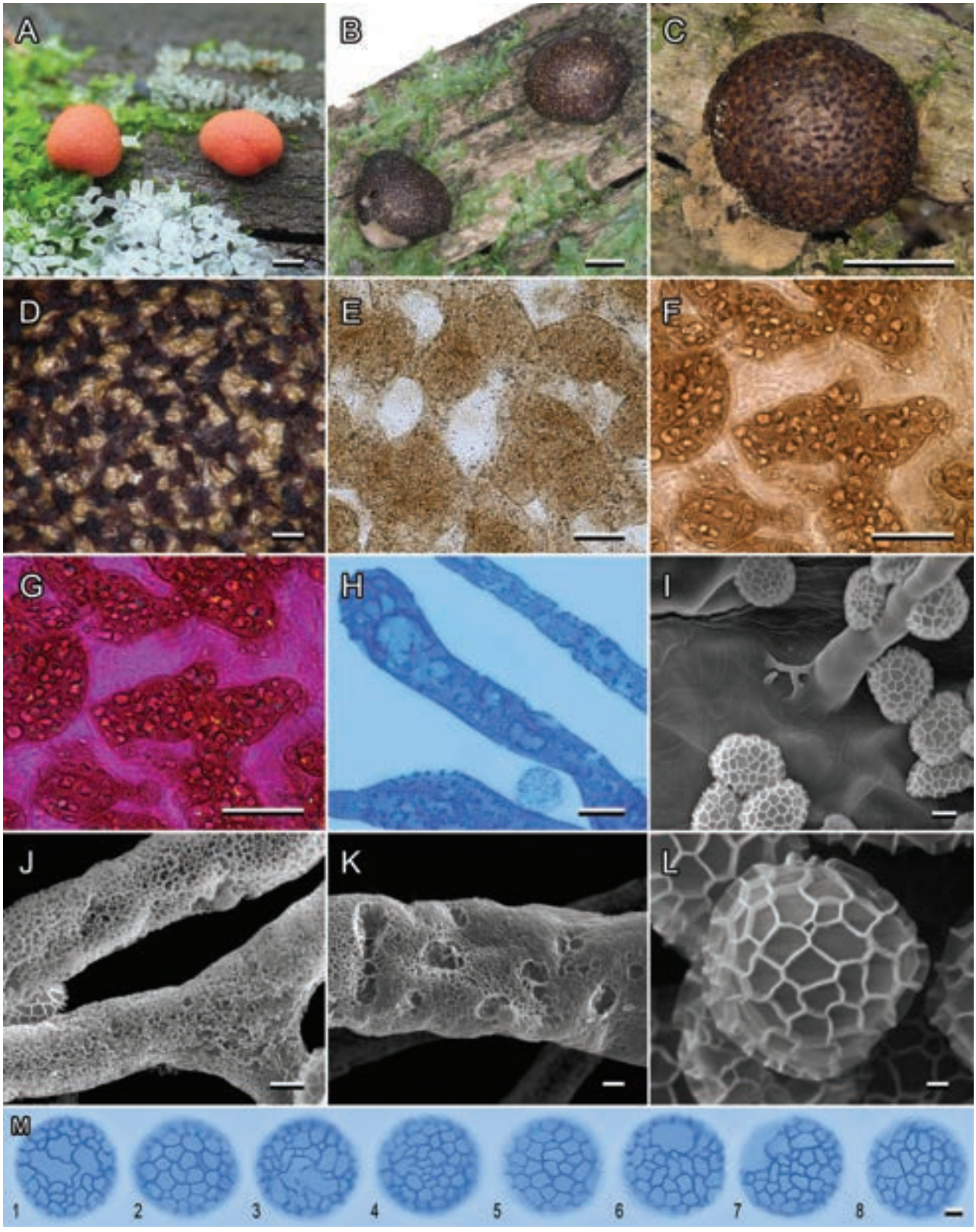

Figure 15. *Lycogala botrydium*, sp. nov. A. Immature fructifications. B, C. Sporocarps. D. Peridium in RL. E, F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, capillitium and spores, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, B, E, I–M. IY30 (holotype). C. CWP2236. D, F–H. sc10921. Bars: A–C = 1 mm; D–G = 100 µm; H = 5 µm; I, J = 2 µm; K, M = 1 µm; L = 0.5 µm.

Lycogala epidendrum (L.) Fr. emend. Leontyev, Ishchenko & Schnittler FIG. 16
MycoBank MB205910

Typification: NORWAY. INNLANDET: Stor-Elvdal, Bjørsjøåsen (61.70477 10.74966), log of *Picea abies*, 22 Sep 2019, *K.A. Mandal, E. Johannesen, K. Homble, I. Kristoffersen* (**neotype** selected here: EJ22747866, MB10012630). GenBank: 18S rDNA = OM423906.

Sporocarps in very large groups (>100), spherical to short horizontally ovoid, often deformed from mutual pressure, (0.5–)2–7.5(–15) mm diam (FIG. 16B, C). Peridium membranous, ochraceous-brown, grayish-brown, covered by whitish strands of dried slime, forming fine reticulum; peridium contains numerous air bubbles, which makes it slightly silvery. Peridial vesicles 35–150 µm, vesicles in RL hardly visible, intricate, light to dark brown, solitary or loosely grouped (FIG. 16D, E), in TL solitary, angular, fusiform, blot-like, often touching each other by elongate projections, brown, yellow-brown (FIG. 16F). Vesicle walls slightly brownish to almost hyaline. Crystals occur in come vesicles as scanty solitary needles (FIG. 16G). Large oil droplets scanty or absent. Granular deposits present (FIG. 16 F). Inner surface of the peridium smooth or covered by scattered warts (FIG. 16I). Capillitium tubular, 4–20 (~100) µm diam, with wavy contours, ornamented by regular bracelet-like or net-like thickenings and large, numerous warts, mainly concentrated on the surface of thickenings (FIG. 16H, J, K). Spore mass dull pink, later light warm gray, in old specimens ochraceous-yellow. Spores 6.5–8(–8.5) µm diam, hyaline, reticulate, with 7–10(–12) meshes across diameter, unornamented area small, occupies nearly ¼–⅓ of the spore surface (FIG. 16L, M). Immature fructifications pinkish-orange (FIG. 16A), sometimes dull pinkish or yellow.

Distribution: Europe, Asia, North and Central America, Australia.

Comments: Even with this narrowed delimitation, *L. epidendrum* s. str. remains the most widespread and abundant species, and the most polymorphous as well. Large (often exceeding 1 cm) sporocarps, rather irregular in shape (with prevalence of ovoid and bean-shaped), and very large colonies (>15 cm) help to distinguish the "real" *L. epidendrum* (rg01b) even in the field. However, some collections may consist of only several sporocarps much smaller in size. In such cases, the most characteristic feature of *L. epidendrum* is the presence of very pale, irregular vesicles, faintly visible in RL, as well as the whitish strands of dried slime between the vesicles. In some collections of *L. epidendrum*, vesicles may be rather dark and may resemble those in *L. maculatum*, in which, however, they are more regular in shape, more-or-less isodiametric, and peridium is darker. For the difference between *L. epidendrum* and *L. irregulare*, see the comments under the latter species. The peridial morphotype in *L. epidendrum* was previously referred to as "epidendrum" (Leontyev et al. 2022a).

Lycogala confusum Nann.-Bremek. ex Ing emend. Leontyev, Ishchenko & Schnittler FIG. 17
MycoBank MB450203

Typification: UNITED KINGDOM. Hb. B. Ing 92077, B. Ing. The specimen is inaccessible at the moment, but the authentic material, identified by N. E. Nannenga-Brmekamp, was studied by us. DNA barcodes of type collections are absent, but we received a number of 18S rDNA barcodes of this species (see SUPPLEMENTARY FILE 1).

Sporocarps in small groups, spherical to short horizontally ovoid, deformed by mutual pressure, (2–)2.5–6 (–8) mm diam (FIG. 17B, C). Peridium membranous, light orange-brown, covered by vesicles that are so dense that the sporocarp appears uniformly brown. Peridial vesicles 40–90(–100) µm, in RL looking like merged dried droplets, brown, dark brown, densely covering the surface of the peridium, forming vague marble-like or reticulate pattern (FIG. 17D, E), in TL grouped in irregular clusters and rows, rounded-angular from mutual pressure, isodiametric to somewhat elongate, light brown (FIG. 17F). Vesicle walls light brownish, thin (1–2 µm), single-layered. Crystals absent (FIG. 17G). Oil droplets numerous, different in size, with smallest forming granular mass, which may completely fill the inner surface of the vesicle (FIG. 17F). Inner surface of the peridium smooth or covered by scattered warts and inconspicuous rings 0.5–1 µm diam (FIG. 17I). Capillitium tubular, 5–20 µm diam, with wavy contours, ornamented by regular bracelet-like thickenings, or less regular, with scattered depressions, the surface of the tube fine pitted-warty, with ring-shaped islets (FIG. 17H, J, K). Spore mass very light pink (FIG. 17B), in old specimens yellowish-gray. Spores (5.5–)6–8 µm diam, hyaline, reticulate, with 5–7 meshes across diameter, unornamented area small, occupies nearly ¼ of the spore surface (FIG. 17L, M). Immature fructifications orange red, light pinkish-orange (FIG. 17A).

Distribution: Europe, North America.

Comments: The species seems to be rather common, and its relatively large size and dense colonies may increase its chances of being found. The hallmark of *L. confusum* is large polygonal vesicles, forming irregular clusters and rows and densely covering the surface of peridium, which therefore looks somewhat "marble-like" in RL. In contrast to the illustration published by Ing (1999), vesicle walls in *L. confusum* are not denticulate; instead, they are just somewhat wavy (see

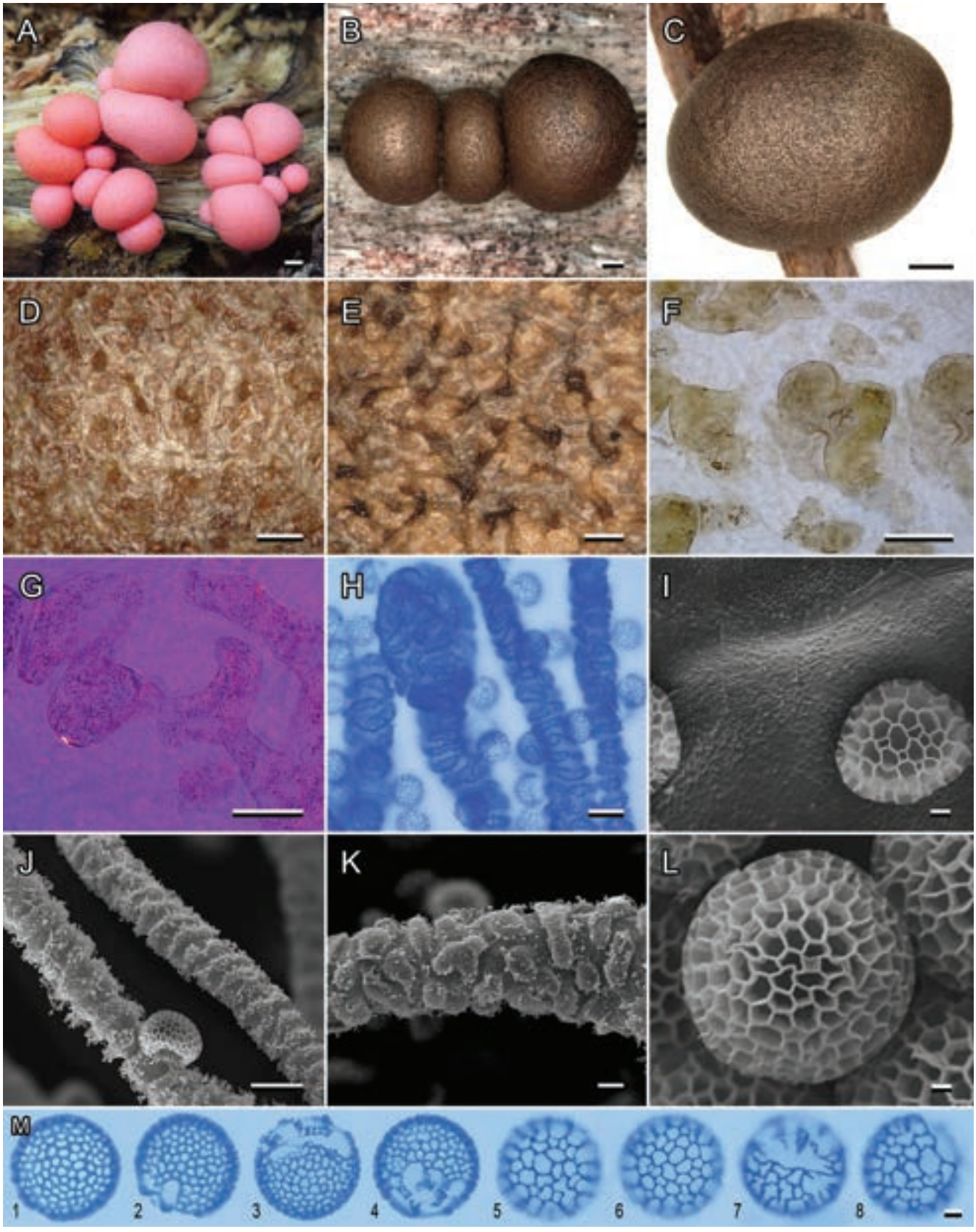

Figure 16. *Lycogala epidendrum*. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A. IY32. B, D. EJ22747866 (neotype). C. UARK17563. E. SJL1190. F. CWP2846. G. CWP2979. H. CWP4218. I. CWP4835. J, L. CWP3476. K. CWP2980. M. CWP4230 (1–4), CWP4218 (5–8). Bars: A–C = 1 mm; D–G = 100 µm; H, J = 5 µm; K, I, M = 1 µm; L = 0.5 µm.

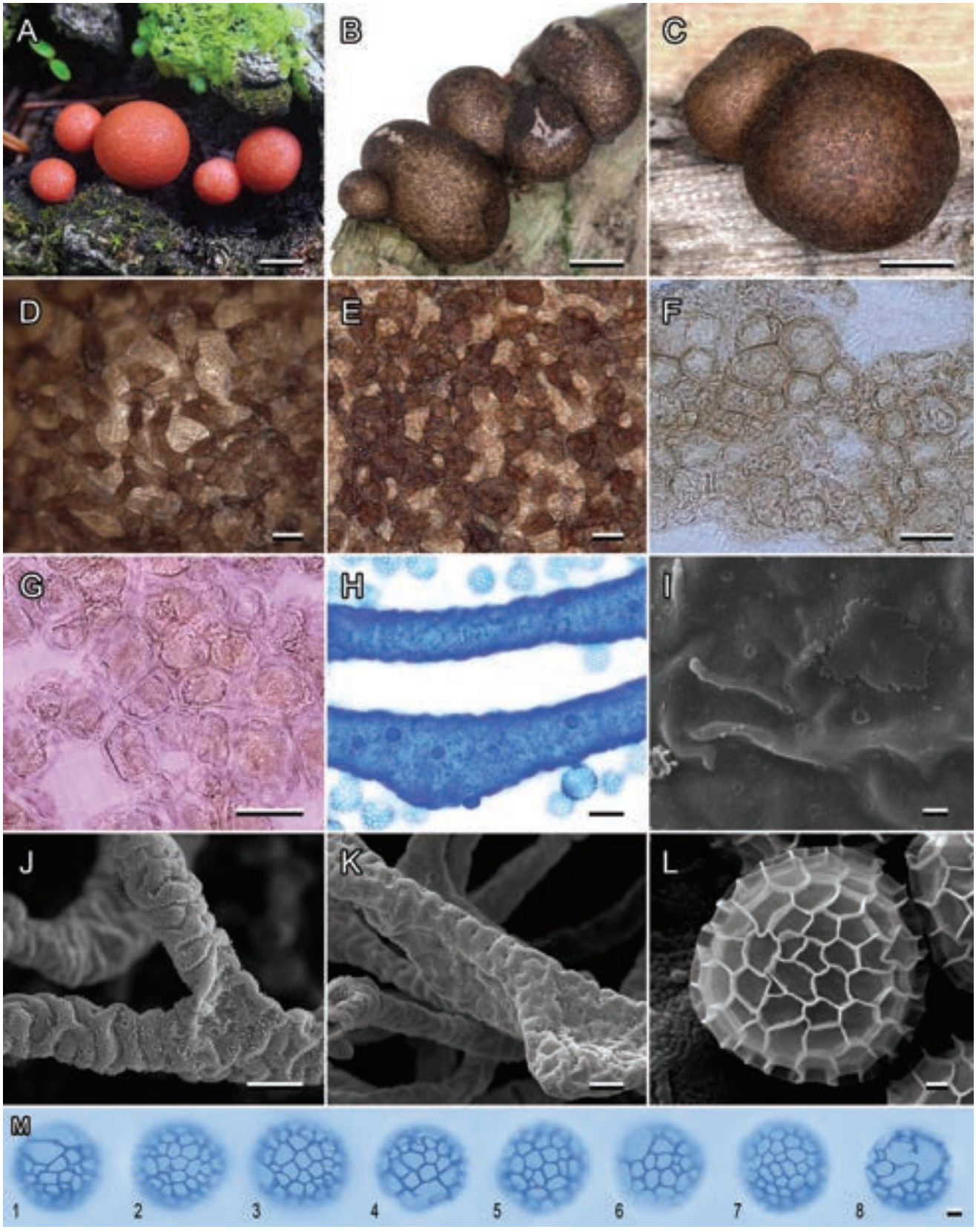

Figure 17. *Lycogala confusum*. A. Immature fructifications. B, C. Sporocarps. D, E. Peridium in RL. F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, F, I, K, M. IY20. B. IY11. C, E. NENB1869 (authentic collection). D. sc27523. G. NENB2010 (authentic collection). H, J, L. NENB4950 (authentic collection). Bars: A–C = 1 mm; D–G = 100 µm; H, J, K = 5 µm; I, M = 1 µm; L = 0.5 µm.

Discussion). From the "twin" species *L. fossiculatum*, which has a very similar appearance in RL, *L. confusum* differs by larger and darker vesicles. The peridial morphotype in *L. confusum* was previously referred to as "reticulatum" (Leontyev et al. 2022a). The morphotype, which we initially called "confusum," after examination of the authentic material of *L. confusum* was attributed to another, yet undescribed species.

Lycogala exiguum Morgan emend. Leontyev, Ishchenko & Schnittler FIG. 18
MycoBank MB212013

Typification: UNITED STATES. OHIO: Preston, on dead wood, 1893, *A.P. Morgan* (lectotype BPI834630 [specimen], BPI834633 [slide]). The type specimen is likely too old for successful molecular barcoding, but we obtained a number of 18S rDNA barcodes of this species (see SUPPLEMENTARY FILE 1).

Sporocarps in very large groups (>50), spherical to short horizontally ovoid, mostly regular in shape, (0.9–)1.5–3(–4.5) mm diam (FIG. 18A–C). Peridium membranous, ochraceous-yellow, ochraceous-brown, densely covered by vesicles. Peridial vesicles 20–40 µm, in RL black, forming a reticulum with pitted surface (FIG. 18D), in TL grouped to form rather accurate reticulum of rounded, ovoid and fusiform clusters, with 3–6 vesicles across the group, rounded-angular from mutual pressure, isodiametric, dark brown (FIG. 18E, F). Vesicle walls brown, rather thick (2 µm), multilayered, the outer layer covers the whole group. Crystals absent (FIG. 18G). Oil droplets large, one or few in central part of the vesicle (FIG. 18F), or small, forming granular deposits. Inner surface of the peridium smooth or covered by scattered warts (FIG. 18I). Capillitium tubular, 2–15 µm diam, with smooth contours, surface smooth or somewhat warty, with scanty rings 1–3 µm diam. Spore mass light pinkish-gray, in old specimens pale yellow (FIG. 18H, J, K). Spores (4.5–)5–6(–6.5) µm diam, hyaline, reticulate, with 8–10 meshes across diameter, unornamented area small, occupying nearly ¼ of the spore surface (FIG. 18L, M). Immature fructifications unknown.

Distribution: North and Central America.

Comments: Even with the 15 new taxa described herein, *L. exiguum* remains one of the species with the smallest sporocarps, having a very characteristic appearance with a nearly black reticulum of accreted vesicles on a contrastingly light peridium. Thick walls of individual vesicles, easily detectable under microscope, as well as the tuberous contours of vesicle aggregates, distinguish *L. exiguum* from the morphologically similar *L. botrydium*. Another American species with large colonies, *L. aggregatum*, has much smaller vesicle aggregates, typically 2–5 vesicles in one row, and its capillitium is ornamented by pits and rings, whereas in *L. exiguum* it is nearly smooth. The peridial morphotype in *L. exiguum* was previously referred to as "conidium" (Leontyev et al. 2022a). The morphotype, which we previously called "exiguum," after examination of the type material of *L. exiguum* was attributed to another, yet undescribed species.

DISCUSSION

Molecular features.—Molecular data we previously obtained indicate the possible existence of 60–108 entities (putative biospecies) within the *L. epidendrum* complex (Leontyev et al. 2022b). Only 15 of these species are described in the present work. Since the existing diversity of *Lycogala* is by no means limited to the species described here, the identification of field material, especially collected outside Europe, may still cause considerable difficulties, since the chances of finding a species not described in this paper are rather high.

For each new species, as well as for the morphologically similar *L. epidendrum, L. exiguum*, and *L. confusum*, we obtained molecular barcodes for one (18S rDNA: 6 species) or two (18S rDNA and *COI*: 12 species) marker genes (see Leontyev et al. 2022b for details). We recommend that such barcodes be obtained for accurate species identification in controversial cases, as well as in search of new species.

Size, shape, and mutual arrangement of sporocarps.—Within the *L. epidendrum* complex, size of the fruiting bodies varies within a fairly wide range. *L. confusum, L. epidendrum, L. irregulare, L. leopardinum*, and *L. palianytsia* possess large sporocarps (median 4–4.7 mm), whereas *L. aggregatum, L. botrydium, L. exiguum*, and *L. roseosporum* have small ones (median 2–2.9 mm). Sporocarp size can be used for species identification, for example, to distinguish the morphologically similar species pairs *L. roseosporum* and *L. maculatum* or *L. acinonychum* and *L. leopardinum*.

The shape of sporocarps in the *L. epidendrum* complex is not very diverse; they are all flattened-round or slightly horizontally elongated. Only *L. irregulare* and *L. botrydium* tend to form irregular, curved sporocarps even in single fruiting bodies; in the rest of species such a deformation is observed only in crowded fructifications.

The mutual arrangement of sporocarps is rather variable. In many cases, we observed both colonies and solitary sporocarps in the same species

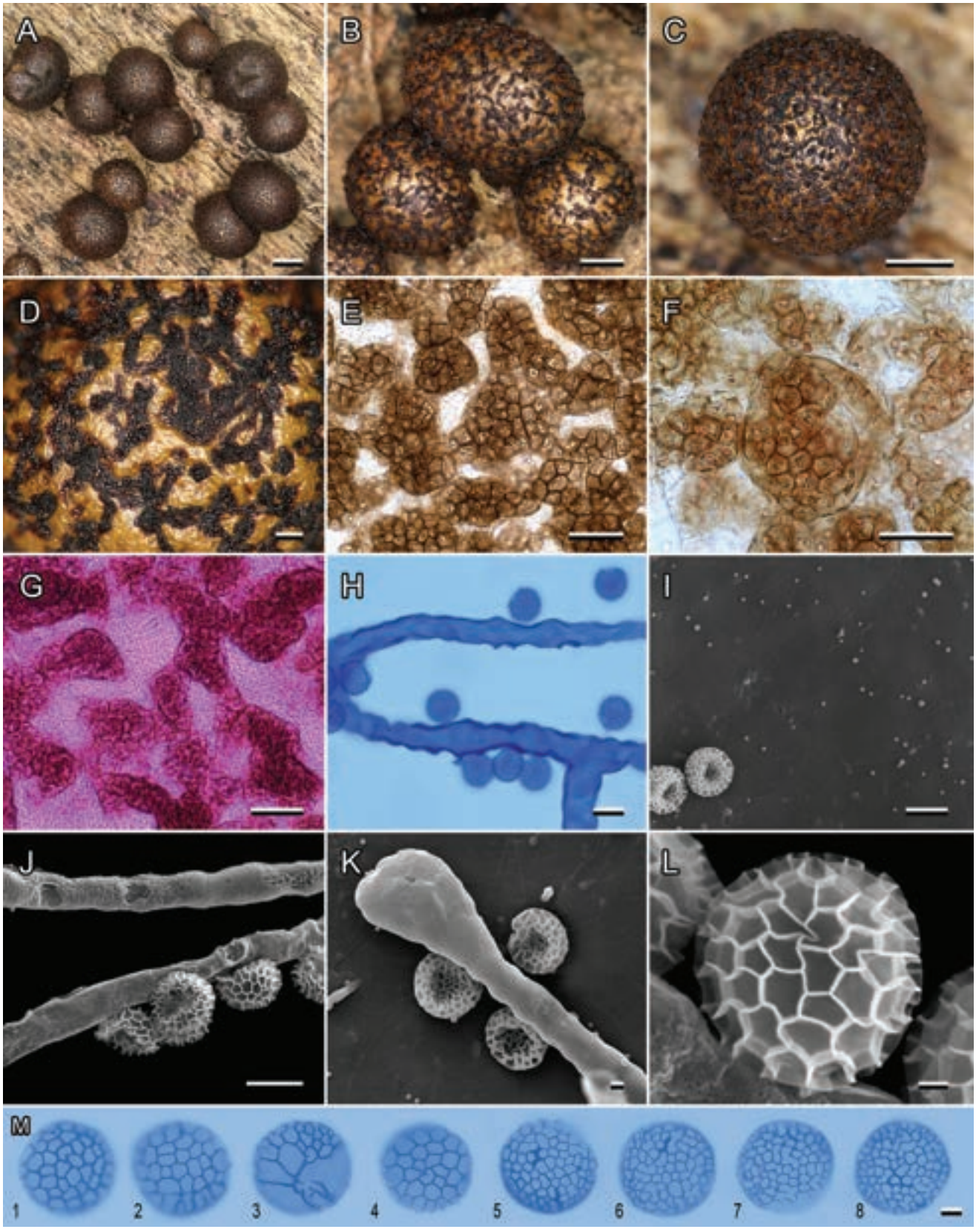

Figure 18. *Lycogala exiguum*. A–C. Sporocarps. D. Peridium in RL. E, F. Peridial vesicles in TL. G. Peridial vesicles in PL. H. Capillitium and spores, methyl blue in lactic acid. I. Inner surface of the peridium, SEM. J, K. Capillitial tubule, SEM. L. Spore, SEM. M. Spores, methyl blue in lactic acid. Specimens: A, C. BPI834632. B. BPI834612. D. BPI834700. E, H. USJ7523. F, G. BPI834630 (lectotype). I–L. USJ7524. M. USJ7523 (1–4), BPI834612 (5–8). Bars: A = 1 mm; B, C = 0.5 mm; D–G = 100 µm; H–K = 5 µm; L = 0.5 µm; M = 1 µm.

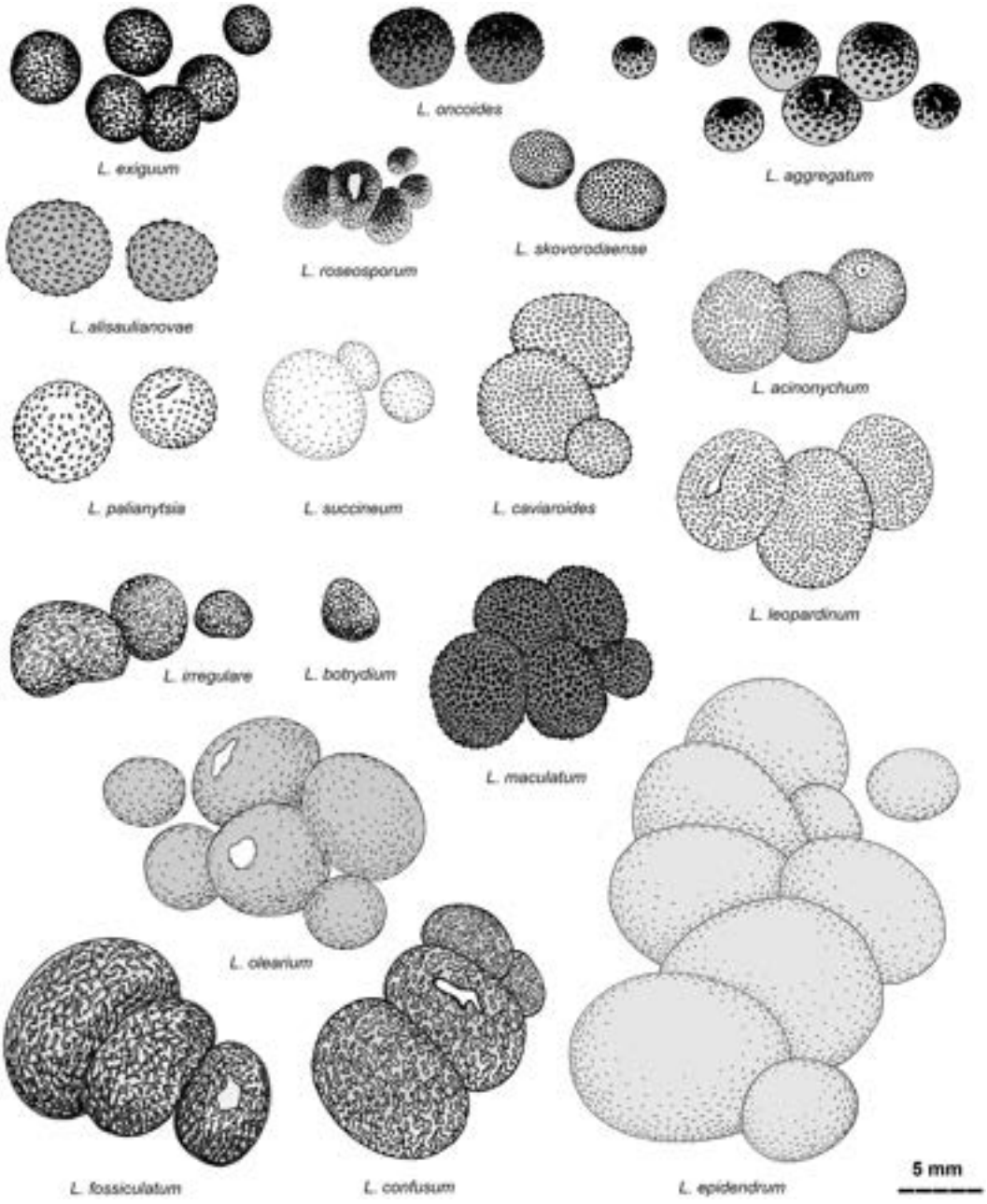

Figure 19. General appearance of sporocarps in *Lycogala* species (except for *L. conicum* and *L. flavofuscum*). Size is shown to scale.

(however, if a single sporocarp is present in a herbarium, it is impossible to know whether it was actually the only one). Nevertheless, some species clearly tend to form large, dense clusters (*L. aggregatum, L. epidendrum*, and *L. leopardinum*), whereas others mainly form solitary (*L. botrydium* and *L. skovorodaense*) or distantly scattered (*L. alisaulianovae, L. irregulare*, and *L. palianytsia*) fruiting bodies.

Peridial vesicles.—The morphology of *Lycogala* is rather poor: in fact, only the peridium, capillitium, and spores can be found within the fruiting bodies. Of these three structures, the most informative and most taxonomically reliable characters can be found within the peridium.

The peridial vesicles, the taxonomic significance of which was first pointed out by Morgan (1893), are exceptionally diverse in *Lycogala*. Most of the species described in this paper can be confidently identified by the shape, color, contents, and mutual arrangement of their peridial vesicles. The exceptions are, first, species with solitary thick-walled vesicles of irregular shape (*L. alisaulianovae, L. maculatum*, and *L. roseosporum*) and, second, species in which vesicles contain crystals (*L. leopardinum,*

L. acinonychum, L. palianytsia, and *L. succineum*). To recognize these species, additional characters such as spore mass coloration and sporocarp size can be used (see the key below).

The most unstable component of peridial vesicles seems to be oil droplets. Their number, size, and shape vary considerably within species (compare, e.g., FIG. 5E–F, FIG. 11E–F, and FIG. 13E–F). In the same species, or even specimen, vesicles may contain one large oil droplet, several large and small ones, or a solid mass of very small vesicles, perceived as granular material. Nevertheless, the accumulation of large amounts of oil itself seems to bear taxonomic significance (Leontyev et al. 2022a).

The presence of calcium-containing crystals in the vesicles is an important trait that allows us to distinguish several "crystalliferous" species (*L. acinonychum, L. caviaroides, L. leopardinum, L. palianytsia*, and *L. succineum*). Notably, these species form a monophyletic group in both the 18S rDNA and *COI* phylogenies (Leontyev et al. 2022b). The importance of this trait creates some difficulties in species identification because the crystals are only clearly visible in polarized light. The application of polarized light in myxomycete taxonomy is not new (Nannenga-Bremekamp 1982), but the use of this method for species identification seems to be proposed by us for the first time.

Spore mass coloration.—This character has not been widely used to identify species of *Lycogala*, although Ing (1999) and van Hoof (2013) mentioned it as an additional diagnostic feature. Our observations show that coloration of fresh spore mass in the *L. epidendrum* complex can be (i) pink (gray-pink, bright pink, very light pink), (ii) bluish, or (iii) warm or neutral gray to almost white. This diversity is enriched (and greatly complicated) by the fact that these colors significantly change during storage. All specimens collected 10 or more years ago have yellowish spore mass, from dull yellowish-gray to bright ochraceous-yellow. Specimens collected several months to several years ago show different stages of fading: the bluish color in *L. alisaulianovae* transforms into greenish, then yellow-green; the pink color quickly fades to salmon (only in *L. roseosporum* pink coloration remains rather stable for an unusually long time). In some cases, being unable to examine freshly collected material, we detected presumptively pink spores in salmon-colored or ochraceous-gray fading stages; in these cases the original color is listed with a question mark in the diagnoses.

We found that duplicates of the same collection, preserved in different countries, faded at different rates. This process is probably influenced by temperature, humidity, and other storage conditions. Thus, despite its potential informative value, the color of the spore mass can be confusing. It should be noted on fresh specimens as fast as possible (see recommendations below).

Spore size.—Spore size is widely used in myxomycete taxonomy as a diagnostic trait. Unfortunately, this is hardly distinctive for species of the genus *Lycogala*. Although spore size varies among species, ranging from (4.7–)5–6(–6.3) µm in *L. exiguum* to (6–)6.3–8.3 (–9.5) µm in *L. maculatum*, in closely related species spore sizes overlap greatly ("crystalliferous" species, *L. epidendrum* and *L. irregulare, L. confusum* and *L. fossiculatum, L. oncoides* and *L. aggregatum*). Therefore, we did not include information on spore size in the identification key below.

Spore ornamentation.—The family Reticulariaceae is characterized by a rather uniform spore ornamentation, which is rare for myxomycetes. Without exception, all representatives of this group have reticulate spores (Leontyev et al. 2019b). Previously attributed to Reticulariaceae, species of the genus *Dictydiaethalium* and olive-spore species of *Reticularia* are now placed outside the family (García-Cunchillos et al. 2022; Leontyev et al. 2019b; Wijayawardene et al. 2022). Perhaps the only species of Reticulariaceae with a more distinctive spore ornamentation is *Thecotubifera dictyoderma*, in which the meshes of the reticulum are particularly large, and the bands forming it are very wide (Leontyev et al. 2019a).

The study of spore ornamentation in the *L. epidendrum* complex showed that spores in this group have share all the features characteristic of Reticulariaceae: ½ to ¾ of the spore surface is covered by a regular network; in the remaining part, the unornamented area is situated where the network is broken and smooth surface with occasional individual ridges and meshes are found instead. Interspecific differences of spore ornamentation have also been found. The spores in *L. olearium* (FIG. 5L, M) are very characteristically ornamented: large meshes are surrounded by smaller ones, which resembles the ornamentation of spores in *Oligonema* (García-Cunchillos et al. 2022). Unusually large meshes are characteristic of *L. skovorodaense* and *L. fossiculatum*, and unusually small meshes are typical of *L. epidendrum* and *L. exiguum*. Unfortunately, the taxonomic reliability of spore ornamentation remains doubtful at this stage of study. In some cases, we found high variability in mesh diameter within the same species (FIGS. 10M, 16M).

Capillitium.—Although capillitium ornamentation is widely used to identify species of bright-spored myxomycetes, this trait has not yet been employed in the taxonomy of the genus *Lycogala*. In classical monographs the tubes of *L. epidendrum* are usually shown with wavy contours, which form characteristic bracelets (FIGS. 4K, 8J, 16H). However, in many species, the tubes have smooth contours and no bracelets (FIGS. 1J, 10J, K, 11J, K, 15J, K, 18J, K) or remain wavy by forming irregular folds (FIGS. 13K, 14J, K). The surface of these tubes can be ornamented by large, often merging warts (FIG. 10J, K). These warts sometimes emphasize the shape of bracelets, being concentrated on their surface and almost absent in the interstices between them (FIG. 2K). On smooth tubes, they form a characteristic pitted-warty surface, sometimes interrupted by broad gaps (FIGS. 1J, K, 6J, K, 7K, 11K). In addition to warts, capillitium may be ornamented by rings with shaft-like (FIG. 5K) or filmy, torn (FIG. 11J) border and also by large ridges and spines (FIG. 12J, K). Finally, capillitium can be practically smooth (FIG. 18J, K).

Ultrastructure of the peridium.—In representatives of the genus *Tubifera*, the ornamentation of the inner surface of the peridium is an important diagnostic feature (Leontyev et al. 2015). Four main variants of ornamentation are known for this genus: smooth, scattered-warty, wavy-folded, and ring-bearing. In *Lycogala*, we observed similar patterns of ornamentation. The inner surface of the peridium may be smooth (FIGS. 6I, 8I), scattered-warty (FIGS. 4I, 10I), covered with wavy folds, which are much less pronounced than in *Tubifera* (FIG. 17I), or, finally, it may be covered by rings (FIGS. 5I, 14I). The latter type of ornamentation, as far as we know, has not been previously recorded for *Lycogala*.

The ornamentation of the peridium may be informative for the identification of *L. olearium* and *L. aggregatum*. In the first species, rings can also cover the capillitium, and this indicates an ontogenetic relationship between these two structures: the capillitium of bright-spored myxomycetes is considered to be derived from the peridium (Leontyev 2020).

Lycogala epidendrum.—Most of the species described here were previously included into *L. epidendrum*. Therefore, a classical question arose: which of the numerous taxa within the morphological species should retain the initial epithet? The information published by the taxon's authors was of little use here. The species was described by Linnaeus (1753); its first description is very superficial and does not include microscopic characters. Neither the author of the species, Linnaeus, nor the author of the current combination *L. epidendrum*, Fries (1829), published any illustrations. Therefore, among numerous biospecies we have found, we chose the one that, in our opinion, most probably corresponds to the taxon described by Linnaeus, assigned the epithet "epidendrum" to it, and chose a neotype (see Taxonomy).

When selecting the species for which the epithet "epidendrum" is preserved, we let ourselves be guided by the following considerations. Among the specimens we studied (Leontyev et al. 2022b), 44.3% belonged to one of the 60 ribogroups, rg01. This group is characterized by the largest sporocarps (up to 15 mm) and the largest colonies (at least 100 sporocarps). It is the only phylogroup found in all the macroregions we studied: Europe (where *L. epidendrum* was described), Siberia, Far East, Southeast Asia, North and Central America, and even Australia. All these factors increase the chances that representatives of this phylogroup were among the first to be discovered by naturalists. Available classical (yet not iconotypic) illustrations support this idea. Rg01 is characterized by dense and large colonies of smooth sporocarps strongly deformed by mutual pressure, devoid of dark vesicles. Similar traits are shown in the illustrations of Pankovius (1654:pl. A, fig. 1), Micheli (1729:pl. 95, fig. 5), and Rostafiński (1875:table 1, fig. 8). The image in Lister's monograph (Lister 1894:pl. LXXV; Lister 1925:pl. 156) does not show the general habit of the colonies, but the peridial vesicles shown on the figure are elongated and branched, which is characteristic of rg01. This evidence suggests that the epithet "*epidendrum*" is best preserved for rg01.

Rg01 shows significant polymorphism both in the appearance of sporocarps and in the structure of the molecular markers studied. We identified 12 subgroups, rg01a–rg01l, within it. Genetic data allow us to characterize this species as a taxon in the process of speciation (Leontyev 2022b). It cannot be excluded that rg01 also represents not a single species, but a complex of cryptic, closely related species (which leads us to a potentially second level of species fragmentation within the *L. epidendrum* complex). Therefore, the choice of a neotype should take into account not only the ribogroup but also the subgroup within it. We settled on the subgroup rg01b as the most numerous in Europe (39.8% of all rg01 specimens and 36.4% of European rg01 specimens). It is characterized by large colonies and weakly pronounced vesicle ornamentation on the peridium, which is typical for the classical images of *L. epidendrum*. Taking into account that the species was described from Scandinavia (both Linneus and

Fries worked mostly in Sweden), we have chosen the neotype among collections from southern Norway.

Lycogala exiguum.—This taxon was the first, and for a long time the only, species of *Lycogala* described on the basis of microscopic characters of the peridium. Additional features, such as small size and pronounced spotting, potentially allow attributing to *L. exiguum* any of the small species with such characters. Indeed, specimens identified as *L. exiguum* were sporadically found in the collections we studied. Most of them turned out to be representatives of other species, among which *L. roseosporum* was found most often (although in this species vesicles do not form the complexes characteristic of *L. exiguum* but are only located rather densely). At the same time, accreted vesicles are a feature of many species of *Lycogala*, including those with rather small sporocarps (*L. aggegatum* and *L. botrydium*). Therefore, only the study of type material allowed us to determine which of them was described by Morgan (1893) under the name *L. exiguum*.

Lycogala confusum.—In contrast to *L. exiguum*, this species is "unpopular" in biodiversity studies. For example, the Global Biodiversity Information Facility (GBIF) database contains 962 occurrences of *L. exiguum* and only 47 of *L. confusum*. However, this species does not seem to be overly rare: we have at our disposal 15 specimens of it, collected in Germany, Norway, France, the Netherlands, Russia, and the United States. *L. confusum* has fairly large sporocarps (median 4.0 mm) and forms medium-sized colonies, so it is definitely not difficult to find. The ignorance of this species may be explained by the low quality of its iconotype. Ing, publishing the description of this species, previously proposed by Nannenga-Bremekamp, accompanied it with a sketch, showing only one feature: the wrinkled edges of the vesicles (Ing 1999:fig. 77). Having studied the material of this species, collected by Nannenga-Bremekamp (1991, 58) and described in her publication under the name *L. epidendrum* var. *tesselatum* Lister (an early synonym for *L. confusum*), we concluded that the unevenness of vesicle contours is depicted in Ing's figure in a highly exaggerated way. In Nannenga-Bremekamp's collections and figure, the edges of vesicles are smooth or slightly wavy and have no traces of denticulation, which can be seen in Ing's figure. Unfortunately, at this stage, we do not know whether Ing described a structure that was not seen by Nannenga-Bremekamp and us or whether his figure was just imprecise. The holotype of the species is deposited in his private herbarium, which is currently unavailable for further studies. However, Ing mentioned Nannenga-Bremekamp as the author of the taxon, and himself as a publisher ("Nann.-Bremek. ex Ing") and explained this as follows: "it was Nannenga-Bremekamp's intention to publish this species, but her untimely death intervened." Therefore, we tend to consider Nannenga-Bremekamp's collections NENB1869, NENB2010, and NENB4950, identified by her as *L. epidendrum* var. *tesselatum*, as reliable reference materials for *L. confusum*, and we use this name for those of our collections that morphologically correspond to these specimens.

Several new species described herein appear similar to *L. confusum*, sharing accreted vesicles (*L. skovorodaense, L. fossiculatum*, and *L. oncoides*). Therefore, this trait can no longer be considered to be a reliable character of *L. confusum*. The most characteristic features of this species are large sporocarps with a "marbled" appearance, thing light brown walls of vesicles and their rather large size (40–100 µm). The latter feature distinguishes *L. confusum* from the morphologically similar *L. fossiculatum*.

Lycogala leiosporum.—This species, described by Reinhard (1866), is known only from the author's description, which is extremely brief and includes essentially only two features: (i) the smooth surface of the spores and (ii) their size given in an unusual unit—lines (1/600‴). The value of one line (1‴) used in botanical publications of the 18th and 19th centuries is 2.1–2.3 mm (Stearn 1992). Accordingly, 1/600‴ = 3.5–3.8 µm. This small size, together with the missing ornamentation of the spores, casts doubt about the reliability of the description of *L. leiosporum*. Species with smooth spores are currently unknown in the family Reticulariaceae (see above). The spore size indicated in the protolog is too small and inferior even to that of *Stemonitopsis microspora* (Lister) Nann.-Bremek., which is currently considered to have the smallest spores among myxomycetes (Poulain et al. 2011). Thus, we propose to consider *L. leiosporum* to be a doubtful taxon.

Lycogala fuscoviolaceum.—This species, known as well only from the original description, was found in the mountains of Nepal in 1968. The author provided a habit sketch, a microscopic photo of the peridium, and even SEM images of spores (Onsberg 1972). On the drawing we can see a large cluster of heaped fruiting bodies, seated on a thin branch. Such an arrangement of sporocarps is typical of litter myxomycetes, in which plasmodia are formed in the soil and climb on elevated plant branches. Fructifications of this type are completely unknown in *Lycogala* and are generally unusual for bright-spored myxomycetes. Other characters of

L. fuscoviolaceum, atypical for the genus *Lycogala*, are dark brown, thick-walled spores and the "cylindrical clusters" formed by the pseudocapillitium threads. Thus, despite the qualitative description of *L. fuscoviolaceum*, we believe that this species needs careful further study before we can assign it to the genus *Lycogala*, and to myxomycetes in general. The type collection of *L. fuscoviolaceum* is available for further studies; the results will be reported in a separate paper.

Lycogala terrestre.—This species is considered by most monographs to be synonymous with *L. epidendrum* (Lado 2005–2022). However, Ing (1999) interprets it to be an independent taxon and states that *L. terrestre* differs from *L. epidendrum* in its larger fruiting bodies, broader capillitium tubes, and pink spore mass (*L. epidendrum* in his interpretation has gray spores). However, it is difficult to find an explanation for such an attribution. The original diagnosis of *L. terrestre* is very concise and consists of a single phrase: "[fruiting bodies] in groups, projecting, globular and ovoid, finely pointed; spores pink" (Fries 1817, 10–11). The size of the fructification and diameter of capillitium are not mentioned in the protolog. As for the spore color, *L. terrestre* indeed possesses pink spores, but the problem is that *L. epidendrum* does not have only gray ones. Linnaeus (1753), the author of the species, does not mention the spore color at all, whereas Fries (1829), the author of the current taxonomic combination, states that spores of *L. epidendrum* are "pink, grey, pale, whitish, yellowish, etc."

Analysis of the available collections allowed us to conclude that particularly large sporocarps (10–15 mm diam) with wider tubes are often found in *L. epidendrum* s. str., but along with much smaller fructifications (4–5 mm), which belong to the same species, and even to the same ribosomal subgroup. Thus, we assume *L. terrestre* to be synonymous with *L. epidendrum* s. str. As for Ings "*L. epidendrum*" with gray spores, it may represent a complex of other species (*L. palianytsia, L. maculatum*, etc.) that possess such a spore color.

Recommendations for collection and study of Lycogala.—Compared with its abundance in nature, the whole genus *Lycogala* seems to be understudied. To obtain reliable data on distribution and ecology of its species, collectors should record some characters already in the field and then use a number of special approaches in microscopic studies. The following recommendations may help to collect and identify species of the genus *Lycogala*.

(i) Pay attention to fructifications with small (2–4 mm), solitary sporocarps. These include a large proportion of new (described herein) and yet undescribed species. (ii) Photograph immature specimens to document their coloration and return to them as they mature. (iii) Collecting immature specimens is impractical; *Lycogala* does not mature well in room conditions. However, the chances of maturation will increase if you place the immature specimen in a spacious lunchbox along with a large piece of substrate and a few tufts of moss. The lunchbox should remain closed until the specimen is fully mature, with only occasional air exchange to maintain a humid atmosphere. (iv) For mature, completely dry specimens, document the color of the spore mass immediately; it can fade rather quickly. If possible, document the process of fading as well. (v) Document in the field the number and mutual arrangement of sporocarps, since only a part of the colony is normally collected. If possible, always include sporocarps with an unbroken peridium in the collection. (vi) To examine the peridium, carefully clean its fragment from spores and capillitium and place it in a drop of lactic acid with the outer surface facing upward. If hollow cavities occur within the peridium (they look black in transmitted light), set the slide aside for several days to allow the air to vanish. (vii) A microscope with a polarization filter is necessary for the detection of peridial crystals. (viii) Use lactic acid mixed with methyl blue (standard formula is 0.1 mg in 60 g) to study spore and capillitium ornamentation. It is recommended to experiment with the concentration of methyl blue to achieve a saturation at which the spore wall is stained but the cytoplasm is not yet. The optimal concentration may be different for different specimens. Note that the intensity of staining depends on the number of spores: the more spores there are in the preparation, the weaker they will be stained. (ix) Examine the ornamentation of the spores with the condenser as high as possible to narrow the range of sharpness, so that the ornamentation does not visually merge with the contents of the spore.

CONCLUSION

This paper describes only a small fraction of the species diversity of the genus *Lycogala*, which we were able to disclose using a combination of morphological, histochemical, optical, ultrastructural, and genetic methods. We were fortunate to find that at least some of the species previously hiding under the general name *L. epidendrum* have clearly defined diagnostic traits. However, identification of these species is not easy, and it will become even more difficult as more new *Lycogala* species are

described. Species determination within this genus has become impossible without careful microscopic examination; in the future, this task is likely to become as difficult as identifying species in genera *Lamproderma, Cribraria*, or *Stemonitis*.

As not uncommon for many protistean groups poor in morphological characters, the taxonomy of myxomycetes is becoming more and more complex, and this shows that our knowledge about the diversity of these organisms is far from being complete. Studies involving large collections from different regions and using a set of complementary methods can help to make progress in this field.

KEY TO SPECIES OF *LYCOGALA*

1. Sporocarps conical, wide spindle-like, rarely ovoid, but taller than wide ..... *L. conicum*
1′. Sporocarps globose or ovoid, usually broader than tall 2

2. Sporocarps 2–5 cm diam, silvery gray, usually on living trees well above ground ..... *L. flavofuscum*
2′. Sporocarps <2 cm diam, brown, grayish-brown, ochraceous-yellow, black, on dead wood, wooden debris or moss 3

3. Spots on the peridium simple, consisting of one vesicle (visible under transmitted light) 4
3′. Spots on the peridium compound, consisting of several to numerous tightly accreted vesicles (visible under transmitted light; in reflected light the spot may look pitted) 14

4. Crystals inside vesicles absent or very scanty. Vesicles very irregular in shape, spot-like, star-like, scattered or densely spaced at the peridium, coalescing to an irregular net 5
4′. Crystals inside vesicles numerous (visible in polarized light). Vesicles rounded or short ovate, evenly distributed on the peridial surface, never forming a net 10

5. Vesicles thin-walled, light brownish to almost hyaline as seen in transmitted light 6
5′. Vesicles thick-walled, dark brown as seen in transmitted light 8

6. Vesicles filled with numerous oil droplets, small and/or large, capillitium ornamented by rings, folds, ridges, spores with 3–7 meshes across diameter, with small meshes tending to surround every large mesh ..... *L. olearium*
6′. Oil droplets scanty or absent, capillitium ornamented by regular bracelet-like thickenings, spores with 7–10(–12) meshes across diameter, meshes uniform in size 7

7. Sporocarps in large groups, up to 15 mm diam, rounded, wide- to narrow-ovoid from mutual pressure. Peridium covered with fine whitish strands of dried slime, which may cover and hide vesicles and make the peridium look uniformly smooth .... *L. epidendrum* s. str.
7′. Sporocarps solitary or in small groups, up to 7 mm diam, rather irregular in shape even without mutual pressure. Strands of dried slime scanty, not hiding vesicles ..... *L. irregulare*

8. Spore mass bright pink, sporocarps 1–3 mm diam ..... *L. roseosporum*
8′. Spore mass not pink, sporocarps 2–6 mm diam 9

9. Spore mass bluish-gray, later greenish-gray, sporocarps umber-brown ..... *L. alisaulianovae*
9′. Spore mass beige, sporocarps dark brown to black (if vesicles contain oil droplets; see also *L. aggregatum*) ..... *L. maculatum*

10. Vesicles orange-red, dark red, looking like dried red caviar ..... *L. caviaroides*
10′. Vesicles amber yellow or brown 11

11. Vesicles mostly elongated, distance between them exceeds their diameter ..... *L. palianytsia*
11′. Vesicles mostly isodiametric, distances between them smaller or equal to their diameter..... 12

12. Vesicles amber yellow, light brown, distant from each other by 1 times their diameter .... *L. succineum*
12′. Vesicles dark brown, distant from each other by ⅓–½ their diameter 13

13. Sporocarps up to 10 mm diam, holarctic distribution ..... *L. leopardinum*
13′. Sporocarps up to 6 mm diam, paleotropic distribution ..... *L. acinonychum*

14. Vesicles thin-walled, light brownish to almost hyaline under transmitted light 15
14′. Vesicles thick-walled, medium or dark brown under transmitted light 16

15. Vesicles 40–100 µm diam, rounded-angular, filled with granular mass. Spore mass pink .... *L. confusum*
15′. Vesicles 20–50 µm, rounded, filled with spherical oil droplets. Spore mass dull pinkish-gray .... *L. fossiculatum*

16. Capillitium ornamented by large warts and spines, sometimes fusing in transversal ridges. Spores with 4–6 meshes across its diameter .... *L. skovorodaense*
16′. Capillitium with fine pitted-warty surface. Spores with 5–10 meshes across diameter 17

17. Aggregates of vesicles large, with >10 vesicles in one row 18
17′. Aggregates of vesicles small, typically with 2–5 vesicles in one row 19

18. Sporocarps gregarious, in large groups. Aggregates of vesicles with tuberous, uneven contour. Capillitium almost smooth ..... *L. exiguum*
18′. Sporocarps solitary. Aggregates of vesicles with smooth contour. Capillitium with fine pitted-warty surface and scattered large rings .... *L. botrydium*

19. Capillitium with wavy contours, bearing bracelet-like thickenings or lobed folds. Spores with 5–7 meshes across its diameter..... *L. oncoides*
19′. Capillitium with smooth contours, fine pitted-warty surface and scattered large rings. Spores with 7–9 meshes across diameter .... *L. aggregatum*

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