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Cryptic speciation in *Reticularia*: two hardly distinguishable new species from Japan and Tasmania

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Abstract: We report the results of a revision of the genus *Reticularia* sensu stricto (*Amoebozoa, Myxomycetes*) from specimens collected in Europe, Asia, the Americas, and Australia. A two-gene phylogeny revealed at least four near-cryptic species, two of which are described here. *Reticularia lucidula*, discovered in Japan, is characterized by a shiny cortex, rigid pseudocapillitium and coarsely reticulate spores bearing large warts and ridges on the reticulation-free area. *Reticularia tasmanica*, found in Tasmania, is distinguished by a thin membranous cortex, a delicate pseudocapillitium, and finely reticulated spores with isolated polygonal meshes in the reticulation-free area. Both species are difficult to distinguish from *R. jurana*, although the phylogeny indicates that *R. lucidula* is more closely related to *R. splendens*.

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INTRODUCTION

The genus *Reticularia*, established in 1787, comprises bright-spored myxomycetes forming aethalia, defined as compound fructifications resulting from the fusion of sporocarps (Poulain *et al.* 2011). Within these aethalia, the remnants of the individual peridia (sporothecal walls) form the pseudocapillitium, a system of plates or strands constituting the internal skeleton of the fruiting body (Martin & Alexopoulos 1969). These structures serve the same purpose as the true capillitium of solitary sporocarps: preventing the spores to be blown out at once. Initially, *Reticularia* included only species with a dichotomous type of pseudocapillitium (Lister 1925), but was later expanded to forms with other structural organizations (Farr 1976); the current name was stabilized for this genus only in 2001 (Lado *et al.* 1998, Lado & Pando 1998, Gams 2001).

The formation of aethalia is a common evolutionary trend in myxomycetes, occurring across nearly all major lineages (Rojas & Stephenson 2022). Thus, it was not surprising when molecular phylogenetic studies showed that the olive-spored species *R. olivacea* belongs to a different family (Leontyev *et al.* 2019b, Zamora *et al.* 2025). At present, two olive-spored species formerly placed in *Reticularia* have been transferred to the resurrected genus *Enteridium*, whose circumscription has changed multiple times. Three additional species with warted, but non-olivaceous spores (*R. aurea*, *R. rubiginosa* and *R. liceoides*), though not yet formally excluded from the genus *Reticularia*, are no longer regarded as related to it (Leontyev & Ronikier 2024). As a result, only five species now remain within the more narrowly circumscribed *Reticularia*, all having reticulated rusty-brown spores: *R. jurana*, *R. lycoperdon*, *R. splendens*, *R. intermedia*, and *R. lobata*, with the last two being extremely rare and poorly studied.

Among the three common species of "true" *Reticularia*, only *R. lycoperdon* has a relatively straightforward nomenclatural history. Its large size, silvery cortex, and wide, dichotomously branched pseudocapillitial threads allow a reliable identification even in the field (Poulain *et al.* 2011). In contrast, *R. jurana* and *R. splendens* are morphologically similar, and attempts to distinguish them often lead to difficulties. *Reticularia splendens* was originally described as a strictly American species (Morgan 1893), contrasted with the European *R. rozeana,* a doubtful taxon, representing a synonym of *R. jurana* or other taxa (Lister 1925, Krzemieniewska 1960, Martin & Alexopoulos 1969). *Reticularia jurana* itself was often treated as a variety of *R. lycoperdon* (Lister 1925) or *R. splendens* (Kowalski 1975) rather than a separate species. The latter interpretation gained wide acceptance: *R. splendens var. jurana* was considered the European counterpart of the American *R. splendens*, with the nominotypical variety absent in European identification keys (Nannenga-Bremekamp 1991, Neubert *et al.* 1993). However, this hypothesis was later refuted by molecular genetic data. Our previous study demonstrated that both *R. jurana* and *R. splendens* occur in Eurasia and North America, and represent independent evolutionary branches (Leontyev *et al.* 2015). These data, however, were obtained as a secondary outcome of

a study on the genus *Tubifera,* and this line of investigation was not continued.

Recently, we examined notable collections of *Reticularia* resembling *R. jurana* and *R. splendens*: Japanese material collected by various authors and housed at the National Museum of Nature and Science, Tsukuba, Japan (TNS); and a Tasmanian collection gathered by Sarah J. Lloyd (SJL) and preserved in the National Herbarium of Victoria, Australia (MEL). This study also incorporated several specimens collected by co-authors of this paper in Belarus, Norway, and Kamchatka, as well as a number of DNA sequences published by other researchers. Using this broader geographic sampling, we attempted to reassess the morphological and genetic diversity of the "true" *Reticularia*.

MATERIALS AND METHODS

The research material consists of 48 myxomycete specimens (Fig. 1), collected from 12 countries in Europe (15 specimens), Asia (9), North America (8), South America (4), and Australia (12). Of these, 42 were available for direct investigation, while the remaining five were represented by sequences obtained by other authors (Table S1).

The morphological study and photographing of myxomycete specimens were carried out with a Keyence VHX 7000 digital microscope and a Leica DM2500 microscope in conjunction with a Flexacam C1 camera. The range of variation in size is given in the descriptions as (minimum) 25 % quartile – 75 % quartile (maximum) for aethalia, and as (minimum) Mean-SD – Mean+SD (maximum) for spores (Table S2). Spore size values are rounded to two significant digits, down if closer to the lower bound, up if closer to the upper bound, and the last digit is adjusted to 0 or 5.

In an attempt to provide a unique molecular signature for every specimen, we sequenced two independently inherited markers: partial sequences of the nuclear (nucSSU) and mitochondrial (mtSSU) genes of the small subunit ribosome RNA (Leontyev & Schnittler 2022). Genomic DNA extraction was done using the Mag-Bind Plant DNA DS 96 Kit and laboratory robot KingFisher Flex (Thermo Fisher Scientific, US). Amplification by PCR was performed using the protocols, described earlier for nucSSU (Leontyev *et al.* 2024) and mtSSU (García-Cunchillos *et al.* 2022). For the nucSSU we used the primer pairs S1/SR4Bright and S1/SR6 (annealing temperatures 58.2 °C and 60.2 °C, respectively), for mtSSU the pair KmitF/KmitR (52.0 °C). The PCR product, purified by exonuclease and alkaline phosphatase (1:5), was sent to Macrogen Europe (Amsterdam, the Netherlands) for Sanger sequencing. Obtained chromatograms were visually checked and edited in Chromas v. 2.6.6 (Technelysium 1998) and collected in fasta files using BioEdit v. 7.2 (Hall 1999). For 48 specimens, we analysed 45 nucSSU and 28 mtSSU sequences, of which 32 and 25, respectively, were newly obtained in this study. Twenty-six specimens were barcoded for both genes, 19 were barcoded for nucSSU and two for mtSSU only. Six specimens were barcoded by a third gene, *TEF1-α* (Leontyev *et al.* 2019a), but these data were not included in further phylogenetic analysis. Sequences were deposited in NCBI GenBank under the accession numbers PX377275–PX377306 and PX377326–PX377350 (Table S1).

Individual alignments were compiled with MAFFT v. 7 web service (Katoh *et al.* 2019) using Q-INS-i algorithm (Files S1 and S2). Preliminary species delimitation was carried out separately for each marker gene using the Assemble Species

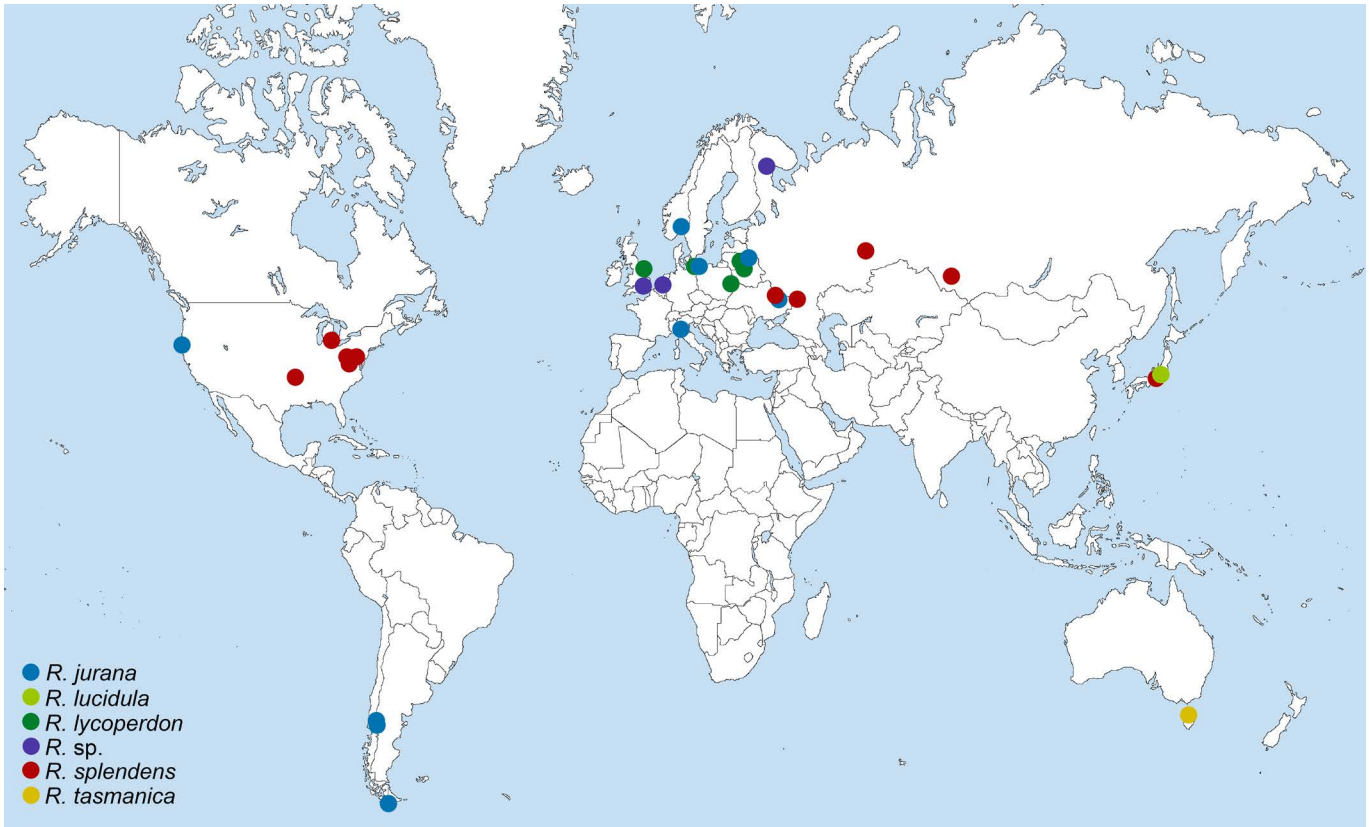

Fig. 1. Collection sites of studied specimens of *Reticularia*. Visualization was made in GPSVisualizer (https://www.gpsvisualizer.com/map_input?form=data).

by Automatic Partitioning algorithm (ASAP) at the platform iTaxoTools (Vences *et al.* 2021) employing the Kimura (K80) 2.0 distance model (Puillandre *et al.* 2021). Five best scores were calculated for each marker. Data from the two gene alignments were combined using the Concatenator software (Vences *et al.* 2022) with the following partition: nucSSU: 1–894; mtSSU: 895–1337. For the construction of the maximum likelihood tree based on the combined two-gene alignment the IQ-TREE webserver was used (Nguyen *et al.* 2015). The best evolutionary model chosen by the ModelFinder (Kalyaanamoorthy *et al.* 2017) as implemented in IQ-TREE, was TN+F+G4 for nucSSU and TIM2+F+G4 for mtSSU. The Shimodaira-Hasegawa approximate likelihood ratio test, the approximate Bayes test and a Bootstrap analysis with 1000 pseudo-replicates were used as criteria of the branch support.

RESULTS

The obtained 45 nucSSU and 28 mtSSU sequences were separately analysed by ASAP to provide a preliminary distance-based species delimitation scheme (Table S3). For both markers, the lowest (best) score partitions produced identical species hypotheses. For nucSSU we obtained six putative species, for mtSSU five, since one taxon, here named *Reticularia* sp., failed to give sequences for mtSSU. One of the species hypotheses supported by ASAP corresponds to *Reticularia lycoperdon*, while the remaining sequences belong to the *R. jurana* – *R. splendens* morphological complex. The two-gene phylogeny (Fig. 2) confirms that the ASAP-delimited groups form statistically supported branches. Among these, *R. lycoperdon* is represented by two ribotypes; *R. jurana* (Fig. 3) is fully uniform across both genes; while *R.*

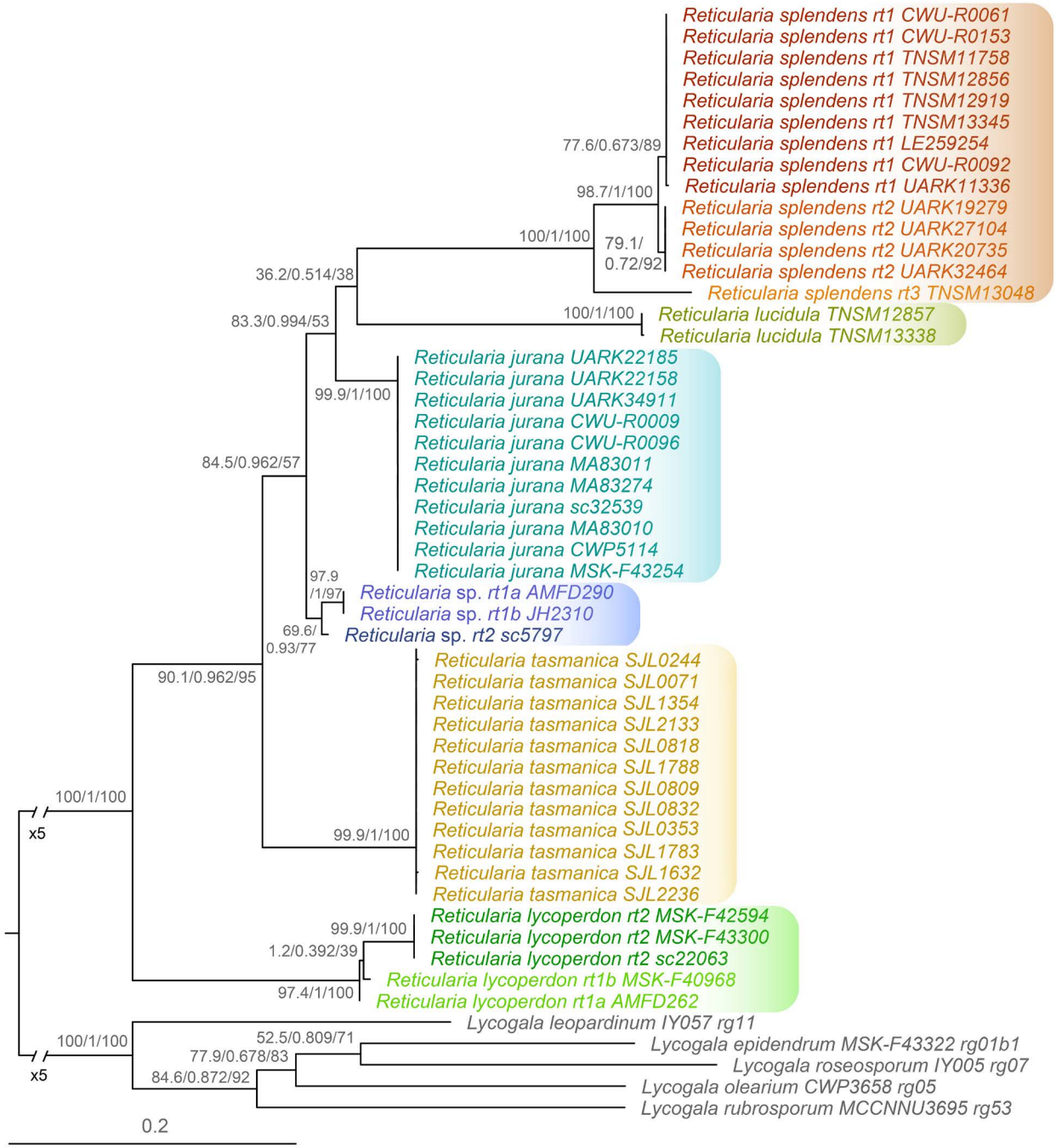

Fig. 2. Two-gene maximum likelihood phylogeny of the *Reticulara* species, based on 45 nucSSU and 28 mtSSU sequences. Branch support is shown as follows: Shimodara-Hasegawa SH-aLRT test / Approximate Bayes test / Ultrafast bootstrap test (1000 replicates).

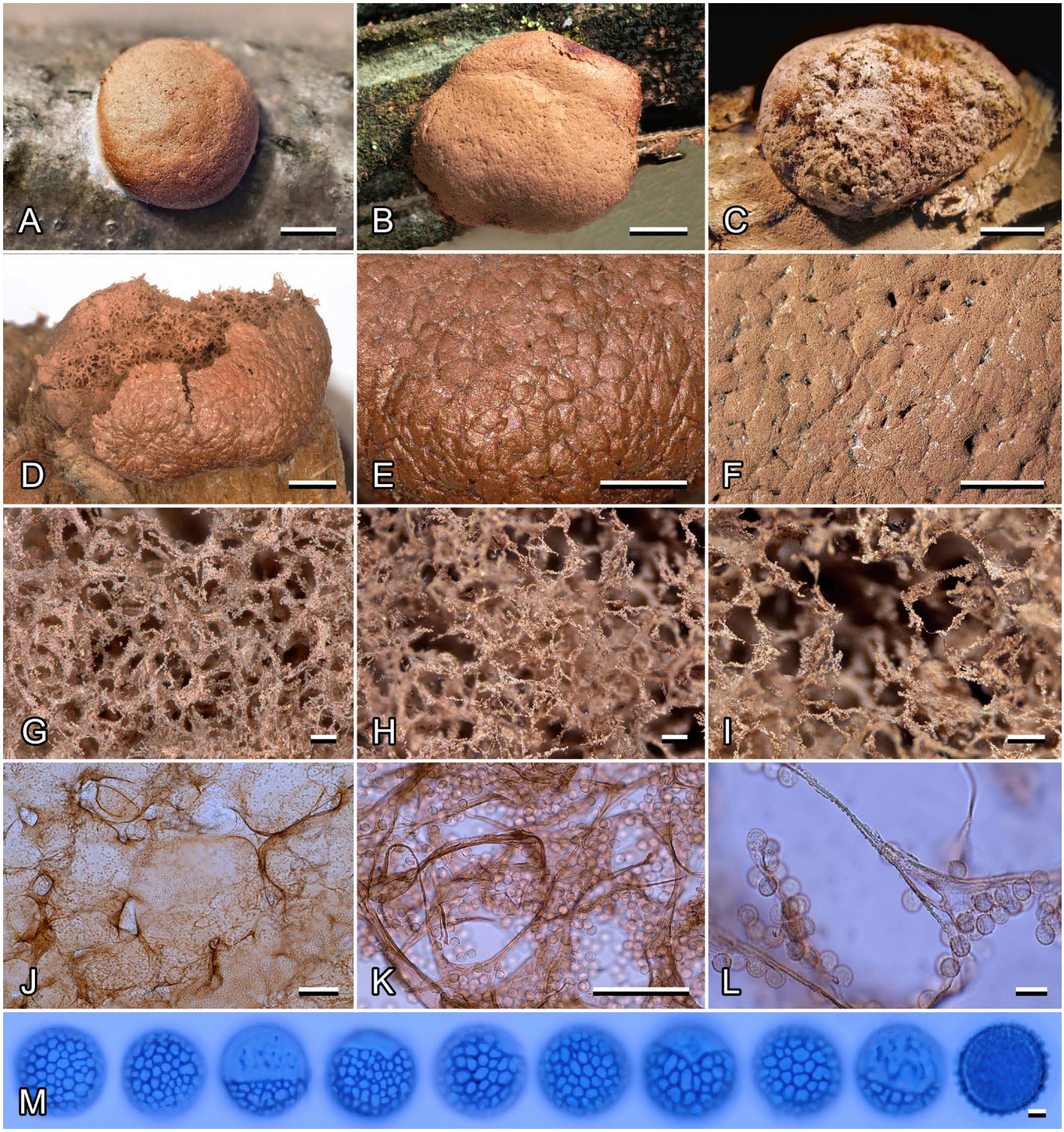

Fig. 3. *Reticularia jurana* [A. CWP-R0009. B, F. MSK-F43363. C, H, I. UARK22158. D, E. sc32530. G, J, L. MSK-F43245. K. CWP5114. M. CWP5114 (left half), MSK-F43254 (right half)]. **A–D.** Mature aethalia. **E, F.** Outer surface of the cortex. **G–I.** Pseudocapillitium. **J.** Cortex in transmitted light. **K, L.** Pseudocapillitium in transmitted light. **M.** Spores stained by methyl blue; the last picture shows optical section. Scale bars: A–C = 5 mm; D–F = 1 mm; G–J = 100 µm; K = 50 µm; L = 10 µm; M = 2 µm. Photo authorship: A, C–E, G–M: D. Leontyev; B, F: E. Moroz.

splendens (Fig. 4) includes three ribotypes, one of which, the ribotype (rt) 3, is recognized by ASAP as a separate species. Distinct branches were also formed by some Japanese collections and all specimens from Tasmania, which we describe here as two new species: *R. lucidula (Fig. 5) and R. tasmanica* (Fig. 6). The last branch, *Reticularia* sp., comprises three samples collected in the UK, the Netherlands, and Karelia. We refrain from formally describing this species at present, as we have only nucSSU sequences and only a single specimen available for the morphological study. Similarly, *R. jurana* rt3 is not described here as a separate taxon.

Taxonomy

Reticularia lucidula Leontyev, J. Matsumoto, M. Kobayashi, Schnittler, ***sp. nov.*** MB 860707.

Etymology: *lucidula* (Lat.), somewhat shiny; referring to the character of the cortex.

Diagnosis: Differs from *R. splendens* by its membranous, semitranslucent cortex, and by the large warts and ridges covering the reticulation-free area of the spore.

Aethalia solitary, pulvinate on narrowed base, irregularly ovoid as seen from above, 7–17 × 4–11 mm in diam. (Fig. 5A–C). *Cortex* persistent, membranous, shiny, translucent, yellow-brown under transmitted light, formed by confluent tips of the sporothecae, which are visible as rounded lids of variable size, sometimes overlapping or hardly defined (Fig. 5D–F, J). *Hypothallus* inconspicuous. *Pseudocapillitium* formed by three-dimensional net of thin, relatively rigid strands, often densely covered with adhering spores (Fig. 5G–I). Under transmitted light the pseudocapillitium strands are brown, mostly smooth, but occasionally ornamented with large warts; the strands often form membranous extensions at the branching points (Fig. 5K, L). *Spores* (7–)7.5–8.5(–9) µm diam., rusty-brown in mass, light yellowish in transmitted light. Around half of the spore surface is covered by a regular reticulum with 4–6 meshes across the diameter, the other half is free of reticulation and ornamented with large warts and ridges forming an intricate pattern (Fig. 5M). *Immature fructifications* not observed.

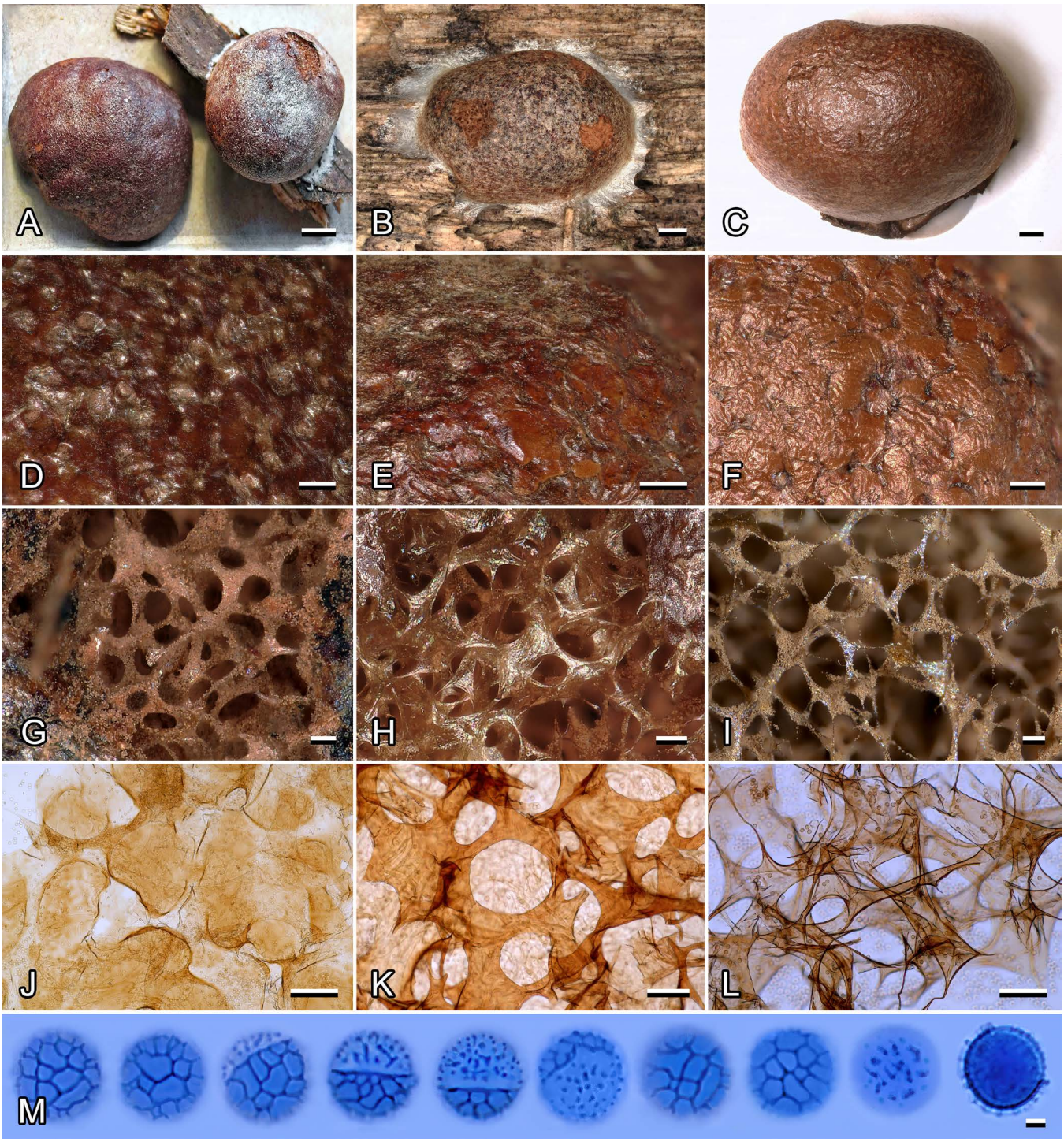

Fig. 4. *Reticularia splendens* [A. CWU-R0061. B, G. TNSM11758. C, D, H, J. TNSM13345. E. TNSM12919. F. TNSM12856. I. UARK20735. K. sc11333. L. sc11333. M. sc11336 (left half), TNSM11758 (right half)]. **A–C.** Mature aethalia. **D–F.** Outer surface of the cortex. **G–I.** Pseudocapillitium. **J.** Cortex in transmitted light. **K, L.** Pseudocapillitium in transmitted light. **M.** Spores stained by methyl blue; the last picture shows optical section. Scale bars: A = 5 mm; B, C = 1 mm; D–F = 200 µm; G–L = 100 µm; M = 2 µm. Photo authorship: D. Leontyev.

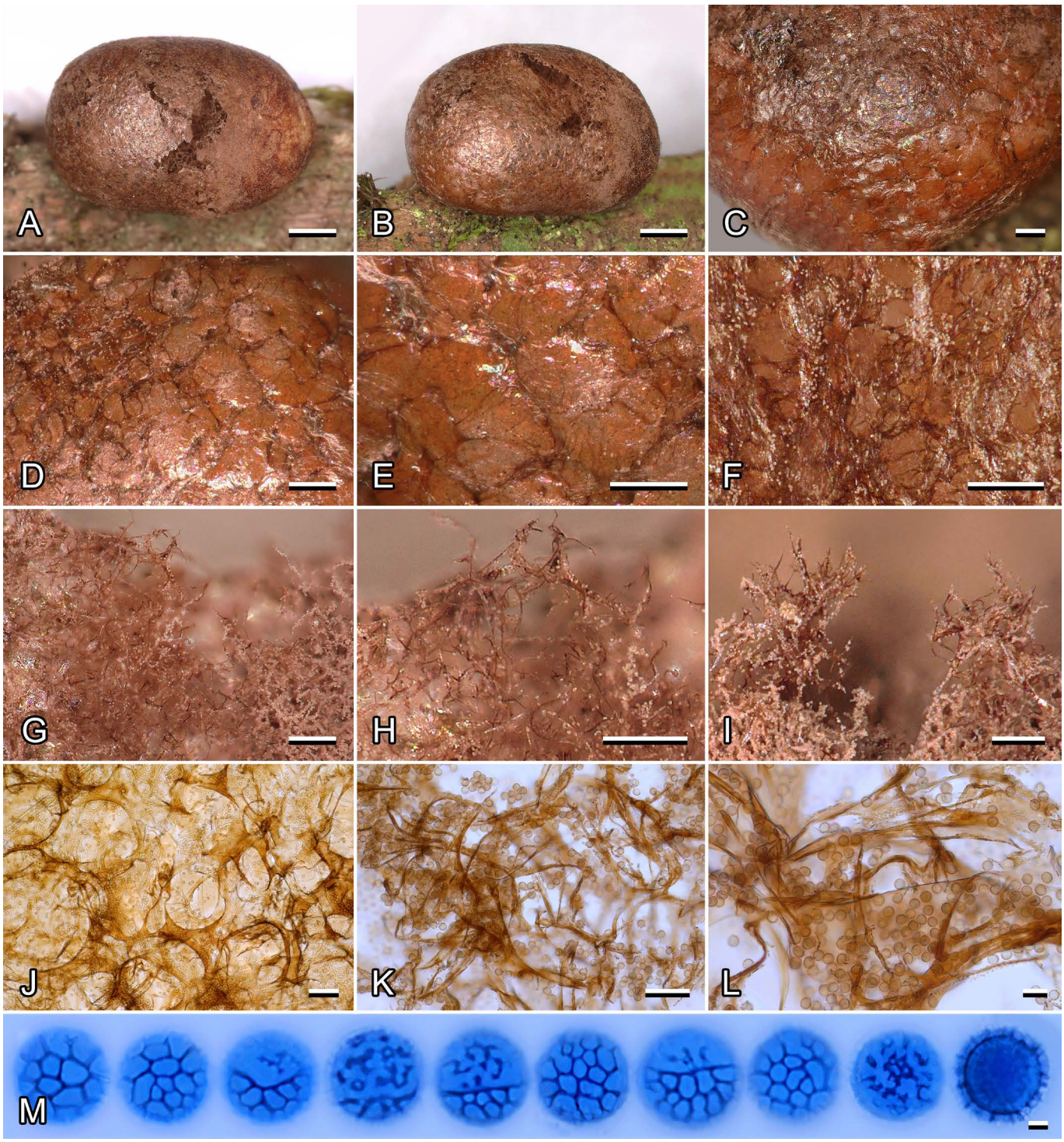

Fig. 5. *Reticularia lucidula sp. nov.* [A–E, F, G, H, K. TNSM12857 (holotype). F, I, J, L, M. TNSM13338]. **A, B.** Mature aethalia. **C–F.** Outer surface of the cortex. **G–I.** Pseudocapillitium. **J.** Cortex in transmitted light. **K, L.** Pseudocapillitium in transmitted light. **M.** Spores stained by methyl blue; the last picture shows optical section. Scale bars: A, B = 1 mm; C–H = 200 µm; I, J = 100 µm; K = 50 µm; L = 20 µm; M = 2 µm. Photo authorship: D. Leontyev.

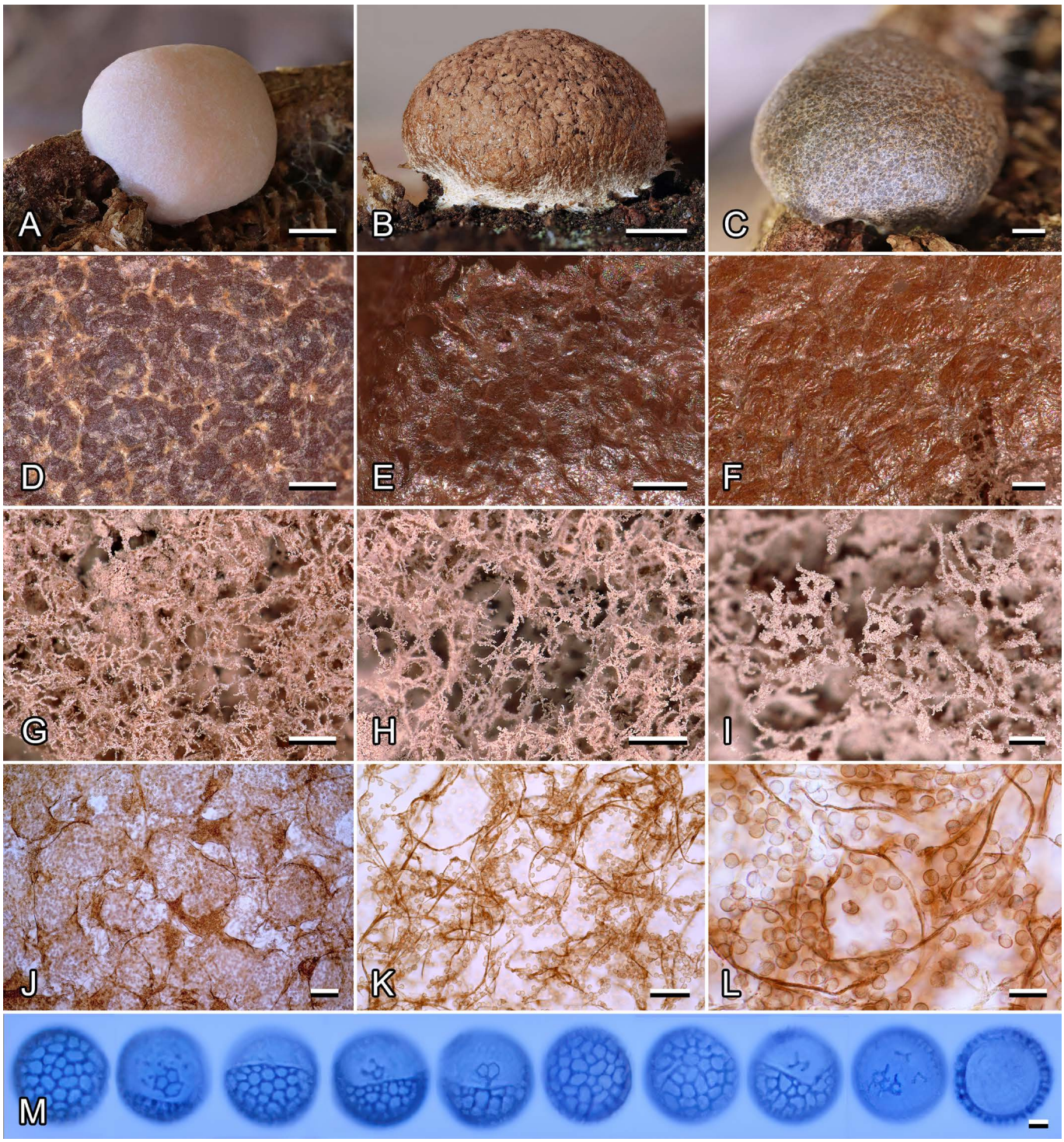

Fig. 6. *Reticularia tasmanica sp. nov.* [A, C. Not collected. B. SJL2451. D, L. SJL1783. E, M (left half). SJL818 (holotype). F, G. SJL1632. H. SJL2236. I. SJL832. J. SJL2133. K. SJL244. M (right half). SJL1632]. **A.** Immature aethalium. **B, C.** Mature aethalia. **D–F.** Outer surface of the cortex. **G–I.** Pseudocapillitium. **J.** Cortex in transmitted light. **K, L.** Pseudocapillitium in transmitted light. **M.** Spores stained by methyl blue; the last picture shows optical section. Scale bars: A, B = 5 mm; C = 1 mm; D, E, G, H = 500 µm; F = 200 µm; I–K = 100 µm; L = 20 µm; M = 2 µm. Photo authorship: A–C: S.J. Lloyd; D–M: D. Leontyev.

Typus: **Japan**, Nagano, Kitayatsugatake Mts, Minami-Sakugun, 35.9531N, 138.4244E, on dead wood, 30 Oct. 2005, *M. Kobayashi & M. Kobayashi* (**holotype** TNSM12857). GenBank: nucSSU = PX377283, mtSSU = PX377330.

Distribution: Asia (so far known from Japan).

Reticularia tasmanica Leontyev, S.J. Lloyd, Schnittler, ***sp. nov.*** MB 860708.

Etymology: *tasmanica* (Lat.) originating from Tasmania; referring to the type locality.

Diagnosis: Differs from *R. jurana* by isolated, solitary or grouped polygonal meshes covering the reticulation-free area of the spore.

Aethalia usually solitary, flat pulvinate, irregularly ovoid as seen from above, (7–)15–18(–43) × (6–)8–13(–15) mm diam. (Fig. 6A–C). *Cortex* membranous, dull and evanescent (Fig. 6B), or shiny and more stable (Fig. 6E, F); both types may be observed on the same aethalium (Fig. 6B); translucent, almost hyaline under transmitted light, formed by confluent tips of sporothecae, which are visible as rounded lids of variable size (Fig. 6D–F, J). If partially sclerified, the cortex becomes durable, dark purple (Fig. 6D) or greyish (Fig. 6C). *Hypothallus*, if conspicuous, forming a white ring around the base of aethalium (Fig. 6B). *Pseudocapillitium* formed by three-dimensional net of very thin and lax strands, densely covered with adhering spores (Fig. 6G–I). Under transmitted light the pseudocapillitium strands are brown, smooth; they are almost thread-like, but may form membranous extensions at branching points (Fig. 6K, L). *Spores* (6.5–)7–9(–9.5) µm diam., rusty-brown in mass, light yellowish in transmitted light. Around half of the spore surface is covered by regular reticulum with 7–10 meshes across the diameter, the other half is free of regular reticulation and ornamented with isolated, solitary or grouped polygonal meshes, along with fragmentary ridges and warts (Fig. 6M). *Immature fructifications* light flesh pinkish (Fig. 6A), later dark greyish brown.

Typus: **Australia**, Tasmania, Black Sugarloaf, Birralee, big tree track, 41.393S, 146.809E, on the stump of a large eucalypt tree, 4 Jan. 2017, *S.J. Lloyd*, SJL818 (**holotype** MEL2533241). GenBank: nucSSU = PX377299, mtSSU = PX377346.

Distribution: Australia (so far known from Tasmania, but can be expected on the southeastern Australian mainland).

DISCUSSION

The problem of cryptic species in myxomycetes has been repeatedly discussed in literature (Feng & Schnittler 2015, Dagamac *et al.* 2017). Many authors conducting molecular barcoding of collections have revealed that morphologically defined species often consist of several genetically distinct, and even reproductively isolated lineages that nevertheless lack obvious morphological differences (Shchepin *et al.* 2022, Gøtzsche *et al.* 2025). The question of whether such lineages should be formally described as separate taxa remains unresolved (Leontyev *et al.* 2023b). For practical reasons (recognizability with morphological methods, assignment of older specimens with degraded DNA), recently published recommendations advise against the description of myxomycete species without morphological differences (Schnittler *et al.* 2025). However, careful analyses often reveal minute characters that correspond to lineages identified by molecular methods (Leontyev *et al.* 2022, 2023a). These findings suggest that species first appearing to be cryptic may in fact be distinguishable, although their separation requires greater effort. For myxomycetes, a group in which sporulation is strongly influenced by weather conditions (Schnittler *et al.* 2025), there is however a significant risk of misinterpreting developmental anomalies for diagnostic traits (Lloyd *et al.* 2024a). In cases like this, the taxonomic challenge is not just to discover morphological differences, but to determine how reliable they are. This holds true as well for our new *Reticularia* species.

Although well separated from *R. lycoperdon*, the four species of the studied complex (*R. jurana*, *R. lucidula*, *R. splendens*, and *R. tasmanica*) show considerable similarity in habit. However, several distinguishing features separate them from each other. The classical species *R. splendens* has stiff aethalia that retain their shape when pressed gently with a finger. The pseudocapillitium in this species is dense and forms a rigid labyrinth of plates (Fig. 4G–I). The aethalia of *R. jurana* and *R. tasmanica* are so soft, that they sway when the sample is shaken or blown on. The pseudocapillitium in these species is formed by lax, flexible strands, forming a three-dimensional net (Figs 3G–I, 6G–I); it also sways under minimal shaking. The fourth species, *R. lucidula*, shows intermediate characters: its aethalia are relatively stiff, but the pseudocapillitium is formed by flexible strands.

More variable, but also more problematic, are characteristics of the cortex. In *R. splendens* it is thick and non-translucent, often silvery and glossy (Fig. 4A). However, in some cases the silvery coat is totally absent (Fig. 4C, F). *Reticularia jurana* has a fugacious cortex, appearing as a faint, matt membrane before disappearing (Fig. 3B, F). Nonetheless, specimens with a denser, shiny, partially persistent cortex also occur (Fig. 3D, E). Interestingly, this second type of cortex resembles that of *R. lucidula*, which is also membranous, shiny and persistent (Fig. 5D–F). Some specimens of *R. tasmanica* possess a fully developed membranous cortex, either glossy (Fig. 6E–F) or matt and in this case very similar to that of *R. jurana* (Fig. 6B). Others exhibit a dense, cartilaginous cortex reminiscent of the peridium of *Siphoptychium* (Fig. 6D). Finally, some specimens of *R. tasmanica* show a silvery cortex apparently formed from sclerified plasmodial material (Fig. 6D). The observed within-species variability of the cortex structure probably arises from the varying weather conditions at aethalia maturation (Schnittler *et al.* 2025). Field observations by S.J. Lloyd show that specimens with a partially sclerified cortex developed on elevated parts of logs and were exposed to direct sunlight.

Among the studied characters of the spores, it is their ornamentation rather than their size (Table S2) that seems to be the most reliable diagnostic feature. Our morphological study of *R. jurana* (8 specimens), *R. lucidula* (2), *R. splendens* (15), and *R. tasmanica* (12) revealed uniformity in this character within each species. Both large, grouped warts in

R. lucidula and isolated polygonal meshes in *R. tasmanica* seem to be species-specific characters. Another prominent feature is the number of meshes across spore diameter, which is much lower in *R. splendens* and *R. lucidula*, and higher in *R. jurana* and *R. tasmanica*. In general, spore ornamentation in *Reticulariaceae*, although not highly diverse, shows remarkable stability at the species and even at genus level (Leontyev *et al.* 2019a, b). Nevertheless, exceptions exist. For instance, in *Lycogala epidendrum* s. str. different genetic lineages vary in the density of the reticulum. In *L. olearium*, which is remarkably uniform in several marker genes (Leontyev *et al.* 2025), the typical ornamentation pattern of larger and smaller meshes is not present in all specimens (Leontyev *et al.* 2023a). Since our specimens of *R. tasmanica* and *R. lucidula* originate from a single region in Tasmania and Japan, respectively, we cannot reliably assess the stability of spore ornamentation at the species level.

Although the available dataset is limited to 48 specimens, the information on their localities (see Fig. 1) allows for some preliminary biogeographic conclusions. The two classical species, *R. splendens* and *R. jurana*, both occur in the Old and New Worlds, as it was already demonstrated in our earlier publication (Leontyev *et al.* 2015). At present, *R. jurana* and *R. splendens* appear to have similar distributions, although only *R. jurana* has been found in South America.

The existence of a unique myxomycete biota in Tasmania is receiving increasing support. In recent years, one new genus and six new species have been described from this region, and the true number of endemic taxa is likely to be much higher (Leontyev *et al.* 2014, Lloyd *et al.* 2024a, b, 2019). Myxomycete diversity is best studied at the Private Forest Reserve at Black Sugarloaf, Birralee in northern Tasmania, where Sarah J. Lloyd has been conducting long-term monitoring of these organisms (Lloyd 2022, Lloyd et al. 2024b). *Reticularia tasmanica* has also been collected there. However, at least two species originally described from Tasmania also occur in south-eastern Australia and New Zealand, within the relict Gondwanan forest zone (Lloyd *et al.* 2024a, b). It is therefore highly probable that *R. tasmanica* is also distributed throughout this broader region. At the same time, citizen science platforms contain data on the occurrence of the morphologically similar *R. jurana* in Gondwanan forests, and this necessitates a re-evaluation of all Australian records of this species, as they all may represent *R. tasmanica*.

The Japanese myxomycete biota is among the richest and best studied worldwide (e.g. Takahashi & Hada 2012, Takahashi *et al.* 2018, Yamamoto 2021), although data on its endemicity remain limited. Nevertheless, several *Reticulariaceae* species are known to occur only, or predominantly, in Japan (Leontyev *et al.* 2025, 2019a). The discovery of *R. lucidula*, not yet known from other regions, may represent a Japanese, or at least East Asian, endemic. Another example of possible endemism of Japanese myxomycetes is *R. splendens* rt 3, which may represent a separate species (see above).

Although none of our newly described species occur in Europe, there is still work to be done at this well-studied continent. The enigmatic *Reticularia* sp., reported from the UK, the Netherlands, and Karelia (Fig. 1), remains understudied. Molecular barcoding of specimens resembling *R. jurana* is needed to obtain more material required for the formal description of this species.

The taxonomy of myxomycetes is currently advancing, driven by the broad application of molecular barcoding and the practice of integrative taxonomy, which relies on the comparison of molecular and morphological data. Although many taxa revealed by DNA sequences exhibit no conspicuous morphological features, the example of our semi-cryptic *Reticularia* spp. demonstrates that, with sufficient persistence, minor diagnostic characters can still be found.

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Conflict of interest: The authors declare that there is no conflict of interest.

REFERENCES

Dagamac NHA, Rojas C, Novozhilov YK, *et al.* (2017). Speciation in progress? A phylogeographic study among populations of *Hemitrichia serpula* (*Myxomycetes*). *PLoS ONE* **12**: e0174825. https://doi.org/10.1371/journal.pone.0174825

Farr ML (1976). *Reticularia* Baumgarten (Lichenes) versus *Reticularia* Bulliard (*Myxomycetes*). *Taxon* **25**: 403–406.

Feng Y, Schnittler M (2015). Sex or no sex? Group I introns and independent marker genes reveal the existence of three sexual but reproductively isolated biospecies in *Trichia varia* (*Myxomycetes*). *Organisms Diversity & Evolution* **15**: 631–650. https://doi.org/10.1007/s13127-015-0230-x

Gams W (2001). Report of the Committee for *Fungi*: 9. *Taxon* **50**: 269–272. https://doi.org/10.2307/1224527

García-Cunchillos I, Zamora JC, Ryberg M, *et al.* (2022). Phylogeny and evolution of morphological structures in a highly diverse lineage of fruiting-body-forming amoebae, order *Trichiales* (*Myxomycetes*, *Amoebozoa*). *Molecular Phylogenetics and Evolution* **177**: 107609. https://doi.org/10.1016/j.ympev.2022.107609

Gøtzsche HF, Woerly B, Popa F, *et al.* (2025). A new species of *Diacheopsis* (*Myxomycetes*) and a new habitat for myxomycetes. *Mycologia* **117**: 183–200. https://doi.org/10.1080/00275514.2024.2413343

Hall TA (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.

Kalyaanamoorthy S, Minh BQ, Wong TKF, *et al.* (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**: 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Rozewicki J, Yamada KD (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**: 1160–1166. https://doi.org/10.1093/bib/bbx108

Kowalski DT (1975). The myxomycete taxa described by Charles Meylan. *Mycologia* **67**: 448–494. https://doi.org/10.1080/00275514.1975.12019774

Krzemieniewska H (1960). *Śluzowce Polski. Na tle flory śluzowców Europjskich*. Polska Akademia Nauk, Instytut Botaniki, Warsaw.

Lado C, Pando F (1998). Proposal to conserve the name *Reticularia* (*Myxomycetes*) with a conserved type. *Taxon* **47**: 453.

Lado C, Pando F, Rico VJ (1998). The nomenclatural status of *Reticularia* (*Myxomycetes*). *Taxon* **47**: 109.

Leontyev D, Ishchenko Y, Leontieva M, *et al.* (2025). Expanding *Lycogala*: twenty-four new species, their morphology and phylogenetic relationships. *Fungal Systematics and Evolution* **16**: 119–154. https://doi.org/10.3114/fuse.2025.16.7

Leontyev D, Ishchenko Y, Schnittler M (2023a). Fifteen new species from the myxomycete genus *Lycogala*. *Mycologia* **115**: 524–560. https://doi.org/10.1080/00275514.2023.2199109

Leontyev DV, Moroz E, Schnittler M (2024). Molecular barcoding of herbarium collections reveals diversity of *Reticulariaceae* (*Myxomycetes*) in Belarus. *Nova Hedwigia* **119**: 369–386. https://doi.org/10.1127/nova_hedwigia/2024/1029

Leontyev DV, Ronikier A (2024). Priority of the generic name *Enteridium* over *Licaethalium* in referring to *Cribrariaceae* species with aethalia. *Nova Hedwigia* **119**: 107–115. https://doi.org/10.1127/nova_hedwigia/2024/0955

Leontyev DV, Schnittler M (2022). The phylogeny and phylogenetically based classification of myxomycetes. In: *Myxomycetes: Biology, Systematics, Biogeography and Ecology (*Rojas C, Stephenson SL, eds), 2nd edn. Elsevier, London: 97–124. https://doi.org/10.1016/B978-0-12-824281-0.00008-7

Leontyev DV, Schnittler M, Ishchenko Y, *et al.* (2022). Another species complex in myxomycetes: diversity of peridial structures in *Lycogala epidendrum*. *Nova Hedwigia* **114**: 413–434. https://doi.org/10.1127/nova_hedwigia/2022/0690

Leontyev DV, Schnittler M, Moreno G, *et al.* (2014). The genus *Alwisia* (*Myxomycetes*) revalidated, with two species new to science. *Mycologia* **106**: 936–948. https://doi.org/10.3852/13-314

Leontyev DV, Schnittler M, Stephenson SL (2015). A critical revision of the *Tubifera ferruginosa* complex. *Mycologia* **107**: 959–985. https://doi.org/10.3852/14-271

Leontyev DV, Schnittler M, Stephenson SL, *et al.* (2019a). Systematic revision of the *Tubifera casparyi–T. dictyoderma* complex: Resurrection of the genus *Siphoptychium* and introduction of the new genus *Thecotubifera*. *Mycologia* **111**: 981–997. https://doi.org/10.1080/00275514.2019.1660842

Leontyev DV, Schnittler M, Stephenson SL, *et al.* (2019b). Towards a phylogenetic classification of the *Myxomycetes*. *Phytotaxa* **399**: 209–238. https://doi.org/10.11646/phytotaxa.399.3.5

Leontyev DV, Schnittler M, Yatsiuk I (2023b). Should we describe cryptic species of myxomycetes? *Proceedings of the 11th International Congress on the Systematics and Ecology of Myxomycetes*, 28–31 August 2023. Tartu: University of Tartu: 17–18. https://doi.org/10.5281/zenodo.8252604

Lister A (1925). *A monograph of the Mycetozoa being a descriptive catalogue of the species in the Herbarium of the British Museum*. Revised by G. Lister. British Museum (Natural History), London.

Lloyd SJ (2022). *Where the slime mould creeps*, 4th edn. Tympanocryptis Press, Birralee.

Lloyd SJ, Leontyev D, Vigus P, *et al.* (2024a). Repent for *Alwisia repens*: emended descriptions of two species of *Alwisia* (*Myxomycetes*) thought to lack a capillitium. *Phytotaxa* **634**: 289–300. https://doi.org/10.11646/phytotaxa.634.3.7

Lloyd SJ, Leontyev DV, Dagamac NHA (2019). Three new species of *Tubifera* from Tasmania and New South Wales. *Phytotaxa* **414**: 240–252. https://doi.org/10.11646/phytotaxa.414.5.2

Lloyd SJ, Leontyev DV, Moreno G, *et al.* (2024b). *Tasmaniomyxa umbilicata*, a new genus and new species of myxomycete from Tasmania. *Mycologia* **116**: 170–183. https://doi.org/10.1080/00275514.2023.2274252

Martin GW, Alexopoulos CJ (1969). *The Myxomycetes*. University of Iowa Press, Iowa City.

Morgan AP (1893). The myxomycetes of the Miami Valley, Ohio. I. *Journal of the Cincinnati Society of Natural History* **15**: 127–144.

Nannenga-Bremekamp NE (1991). *A guide to temperate myxomycetes*. Biopress, Bristol.

Neubert H, Nowotny W, Baumann K (1993). *Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs: Band 1. Ceratiomyxales, Echinosteliales, Liceales, Trichales*. Baumann Verlag, Gomaringen.

Nguyen LT, Schmidt HA, von Haeseler A, *et al.* (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**: 268–274. https://doi.org/10.1093/molbev/msu300

Poulain M, Meyer M, Bozonnet J (2011). *Les Myxomycetes: 1. Guide de Détermination*. Fédération Mycologique et Botanique Dauphiné-Savoie, Delémont.

Puillandre N, Brouillet S, Achaz G (2021). ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources* **21**: 609–620. https://doi.org/10.1111/1755-0998.13281

Rojas C, Stephenson SL (eds) (2022). *Myxomycetes: Biology, Systematics, Biogeography and Ecology*, 2nd edn. Academic Press (Elsevier), London and Oxford (UK), San Diego and Cambridge (US).

Schnittler M, Leontyev D, Yatsiuk I, *et al.* (2025). Species descriptions in myxomycetes – can we settle on rules for good taxonomic practice? *IMA Fungus* **16**: e141199. https://doi.org/10.3897/imafungus.16.141199

Shchepin ON, Novozhilov YK, Woyzichovski J, *et al.* (2022). Genetic structure of the protist *Physarum albescens* (*Amoebozoa*) revealed by multiple markers and genotyping by sequencing. *Molecular Ecology* **31**: 372–390. https://doi.org/10.1111/mec.16239

Takahashi K, Hada Y (2012). Seasonal occurrence and distribution of myxomycetes on different types of leaf litter in a warm temperate forest of western Japan. *Mycoscience* **53**: 245–255. https://doi.org/10.1007/s10267-011-0158-8

Takahashi K, Harakon Y, Fukasawa Y (2018). Geographical distribution of myxomycetes living on *Cryptomeria japonica* bark in Japan. *Mycoscience* **59**: 379–385. https://doi.org/10.1016/j.myc.2018.02.005

Technelysium Pty Ltd (1998). Chromas Lite. http://technelysium.com.au/wp/chromas/ (accessed 8 Aug. 2025).

Vences M, Miralles A, Brouillet S, *et al.* (2021). iTaxoTools 0.1: Kickstarting a specimen-based software toolkit for taxonomists. *Megataxa* **6**: 1–28. https://doi.org/10.11646/megataxa.6.2.1

Vences M, Patmanidis S, Kharchev V, *et al.* (2022). Concatenator, a user-friendly program to concatenate DNA sequences, implementing graphical user interfaces for MAFFT and FastTree. *Bioinformatics Advances* **2**: vbac050. https://doi.org/10.1093/bioadv/vbac050

Yamamoto Y (2021). *Biota of Japanese Myxomycetes*. Committee for the Publication of Biota of Japanese Myxomycetes, Ibaraki.

Zamora JC, Rodrigues D, García-Cunchillos I, *et al.* (2025). First insights into the phylogeny of the order *Cribrariales* (*Amoebozoa*, *Myxomycetes*), with the definite exclusion of the genus *Enteridium*. *Fungal Systematics and Evolution* **16**: e159960. https://doi.org/10.3897/imafungus.16.159960

Supplementary Material: http://fuse-journal.org/

The supplementary files for this paper are also available on Zenodo: 10.5281/zenodo.17385715.

File S1. MAFFT alignment of partial *nucSSU* sequences of 45 specimens of *Reticularia* (*fasta* file).

File S2. MAFFT alignment of partial *mtSSU* sequences of 28 specimens of *Reticularia* (*fasta* file).

Table S1. Collection and barcoding data for all studied specimens of *Reticularia*.

Table S2. Spore measurement of for the studied specimens of *Reticularia*.

Table S3. Preliminary species delimitation based on ASAP analysis of nucSSU and mtSSU alignments. The five best score partitions are shown for both genes.