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A taxonomic revision of the species of *Licea* subg. *Licea* (Myxomycetes)

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Abstract

A taxonomic revision of the genus *Licea*, subgenus *Licea*, using type collections and SEM imaging of the type material is presented. The type specimens of 20 species were obtained and studied simultaneously, and detailed comparisons of morphological features by light microscope and SEM were made. In four other species only published information was analized. The SEM imaging of the type material has enabled clarification of some taxonomic characters, such as the number of peridial layers, ornamentation of the inner surface of the peridium, and the ornamentation of the epispore. As a result of this study a new species from Mexico, *Licea ampullliformis,* has been formally described, and synonymy has been found in the case of two species, *L. castanea* and the recently described *L. bryocorticola*. As no type material was found for *L. minima*, a neotype has been designated here. In the case of *L. pusilla* an epitype has been selected in addition to the illustration, published in 18th century, which was chosen as a lectotype. A dichotomous key of the species examined is proposed to facilitate their identification.

Key words: Distribution, nomenclature, SEM, taxonomy, type material

Introduction

The genus *Licea* was proposed by Schrader (1797: 16) in *Nova Genera Plantarum*, and is one of the oldest genera recognized in the myxomycetes. Schrader (l.c.) included descriptions and comments on four species, *L. pusilla* Schrad., considered the type species of the genus, and provided with a good description, for its time (Martin & Alexopoulos 1969), *L. variabilis* Schrad., now also accepted as a separate species, and *L. tubulina* Schrad. and *L. clavata* Schrad., which are now considered synonyms of *Tubifera ferruginosa* (Batsch) J.F. Gmel. (Lado 2005-2023). Since then, although considered a catchall for the myxomycetes that did not appear to fit elsewhere, the genus has been maintained. Martin (1942) emended the genus to include all myxomycete species lacking a massive hypothallus and capillitium. Due to the lack of capillitium the taxonomy of *Licea* remained controversial. Several authors considered the genus as unnatural (Eliasson 1977, 2017, Gilert 1987, Lado & Eliasson 2021), since other genera of the orders Trichiales, Reticulariales and even Physarales also include capillitium-lacking species.

Nannenga-Bremekamp (1965), in her review of the genus, used the type of dehiscence of the peridium to separate the genus into three subgenera. The subgenus *Licea* Schrad. includes the species with the peridium dehiscing into platelets, like in the type species of the genus, *L. pusilla* Schrad. The subgenus *Pleiomorpha* Nann.-Bremek. shows irregular or longitudinal dehiscence by a crack. The subgenus *Orcadella* (Wingate) Nann.-Bremek. has dehiscence by means of a lid. Currently the limits between these subgenera are unclear, and the proposal of Nannenga-Bremekamp is now of doubtful taxonomic application, however it remains a convenient way to divide the genus into smaller groups for study.

The current concept of the genus (Lado & Pando 1997, Lado & Eliasson 2021, Nannenga-Bremekamp 2022) includes species with sporocarpic to plasmodiocarpic, sessile or stipitate minute sporophores, with a peridium that is membranous or coriaceous, consisting of one or two layers, and without a capillitium or pseudocapillitium.

Several authors such as Nannenga-Bremekamp (1965), Keller & Brooks (1977), Gilert (1996), Wrigley de Basanta & Lado (2005), Ronikier *et al.* (2017) or Bortnikov *et al.* (2022), have carried out detailed taxonomic studies

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of *Licea* species, and, in some cases, have applied analytical techniques such as scanning electron microscope (SEM), transmission electron microscope (TEM) or Energy dispersive X-ray spectrometry to clarify the structure and concept of some species. But the taxonomy of the genus is complex, due to the absence of capillitium, and the fact that the only differential diagnostic characters, available in *Licea*, are the peridium and spores. Most of the species have very small fruiting bodies (0.1–0.5 mm diam) and produce a limited number of spores, thus complicating the extraction of DNA and phylogenetic analysis. Currently only partial sequences of 4 species are available in GenBank. In addition, the species of *Licea* usually have a scattered habit and the moist chamber technique, together with a powerful stereoscope (magnification over 20x) is necessary to detect them.

Despite this, there are now 80 accepted species of the genus *Licea* (Lado 2005-2023). Of these, 21 stipitate species were the subject of a taxonomic evaluation treated previously by the authors (Wrigley de Basanta & Lado 2005). Although the presence or absence of a stalk is also of questionable taxonomic relevance (in certain species and even in some collections of the same species, there are stalked and sessile sporocarps), it provides a useful grouping for detailed study. During our study of the stipitate *Licea*, several species (e.g. *L. erecta, L. verrucispora*), considered by some authors (Thind & Dhillon 1967, Lakhanpal *et al.* 1990, etc.) to dehisce by means of platelets, were shown to have peridia that break into irregular fragments, not platelets with a defined, often ornamented, margin, and so excluded from the subg. *Licea*.

With the exception of the work of Wrigley de Basanta & Lado (2005), there has been no comparative study of type material of the *Licea* species to date, and many new species have been added to the genus in recent years. Therefore, for the sake of dealing with a manageable number of species, the authors decided to continue the comparative taxonomic investigation of the genus *Licea* with the species with peridial dehiscence into clearly defined platelets that Nannenga-Bremekamp (1965) grouped in the subgenus *Licea*.

The rationale for using type material as far as possible, was to avoid erroneous interpretations of a species by researchers other than its authors. Nowadays, obtaining type material on loan from many herbaria remains very difficult. However, it seems to be the only possible approach, since many species were described two or three centuries ago, with the tools available at the time, and the interpretation of the original descriptions is sometimes difficult.

Thus, the objective of this study is to carry out a taxonomic review of the subgenus *Licea*, analyze and standardize the descriptions of the types, provide new taxonomic information on the distinctive characters revealed by SEM images, and elaborate a dichotomous key to help to identify the species.

Material and Methods

Type material was requested and loaned by the following herbaria: AH, B, BR, M, MA-Fungi, LAU, MYX. Other specimens from MA-Fungi and private collection of Diana Wrigley de Basanta (dwb) were used to compare and corroborate descriptive characters. If type collections were unavailable for study, iconography from the original publication is used to compare them with the rest of the species.

The descriptive information on each species was taken from the original publication and from observations of type material by the authors, unless otherwise stated. The descriptive data and light micrographs of the characters of each species were obtained using microscopes Nikon Eclipse 600 and Nikon 80i with differential interference contrast (DIC), as well as a steremicroscope Leica M205 C, and a stereomicroscope Nikon AZ100, provided with a Jenoptik Gryphax Naos digital camera.

To confirm the number of peridial layers, a feature sometimes difficult to see, specimens were mounted in polyvynil alcohol and before drying completely, the cover glass was moved over the peridium separating closely adhered layers.

For the available species, preparations for scanning electron microscope (SEM) using critical-point drying (Meek 1976) and the analyses and photomicrographs of specimens were made by the Scanning Electron Microscopy Department of the Royal Botanic Garden of Madrid, employing a Hitachi S-3000N scanning electron microscope at 10–15 kV. Other diagnostic techniques such as PCR were not possible due to the scanty amount of the type material and the restrictive regulations of most herbaria.

New micrographs of the fruiting bodies and their details made under transmitted light (TL) and SEM are included for each species. The terminology of Rammeloo (1974, 1975) for the epispore ornamentation is used. Colour notations are made according to the ISCC-NBS Color-Name Charts Illustrated with Centroid Colors (Kelly & Judd 1976).

The nomenclature of the taxa is according to Lado (2005-2023). The information on the distribution of the species

was obtained from recent specialized literature on the biodiversity of Myxomycetes (e.g. Schnittler & Novozhilov 1996, Yamamoto 1998, 2006, 2021, Novozhilov *et al.* 1999, 2006, 2017, Lado *et al.* 2003, 2007, 2011, 2013, 2014, 2016, 2017, 2019, Estrada-Torres *et al.* 2009, Wrigley de Basanta *et al.* 2010, 2013, Kylin *et al.* 2013, Rojas *et al.* 2018, Stephenson *et al.* 2019), as well as from checklists (e.g. Drozdowicz *et al.* 2003, McHugh & Ing 2012, Yatsiuk *et al.* 2020, Kryvomaz *et al.* 2020, Zemlyankaya *et al.* 2020, Johannesen & Vetlesen 2020), catalogues (e.g. Keller & Braun 1999, Flatau 2000, Lado & Wrigley de Basanta 2008, Ronikier *et al.* 2017, Bortnikov *et al.* 2020, Kuhnt 2021), monographs (e.g. Nannenga-Bremekamp 1991, 2022, Neubert *et al.* 1993, Lado & Pando 1997, Poulain *et al.* 2011, Yamamoto 2021) and the species distribution database GBIF (https://www.gbif.org), but in latter case, we considered only records of specimens preserved in public herbaria.

Results

The studied species are presented below in alphabetical order. The new species *Licea ampullliformis* is formally described here. The data of each species includes the author(s), reference to the original publication, figure references, followed by a description of the macro and microscopic characters of the species by light microscope, and the characters seen under SEM. Additionally, the material examined, habitat, distribution, iconography references, and notes are included.

Due to different geographical reference systems, the coordinates for type specimens are from the original labels of the specimens or publications and therefore cannot be standardized.

1. *Licea alpina* A. Sánchez, G. Moreno, & D. W. Mitch., in Moreno, Sánchez & Mitchell, Bol. Soc. Micol. Madrid 34: 156 (2010) Figs. 1A–F

Sporophores sporocarpic, dispersed or in groups. Sporocarps stalked, sometimes sub-sessile, 0.25–0.8 mm in total height. Hypothallus inconspicuous. Stalk thick and black (0.1–0.3 mm long, 0.05–0.1 mm wide). Sporotheca 0.15–0.4(–0.5) mm diam., dark brown to black, shining, with distinct pale lines of dehiscence that form a cross at the apex. Peridium double, outer layer of refuse material and the inner layer membranous, closely adhering together; dehiscence by fragmenting into polygonal plates leaving a basal calyculus at the union with the stalk. Spores free, dark brown in mass, olivaceous to olive brown by TL, with a thinner area by TL, subglobose, (14–)15–17 µm diam., smooth. By SEM the inner peridium is densely warted, the platelet margins are warted and paler with fewer inclusions; the epispore is verrucate with small dense warts and larger warts.

Material examined: Holotypus. SPAIN. Madrid, Puerto de Navacerrada, UTM 30T-04164516, 2075 m, on stems of Cytisus *oromediterraneus,* 26-V-2001, AH 28531!.

Habitat: nivicolous areas, on stems of shrubs.

Distribution: Known only from type locality (Spain).

Icon.: Moreno *et al.* (2010: 157, Figs. 1–16).

Notes. The reason to include this normally stipitate species is that it dehisces into platelets, and sub-sessile sporocarps may be confused with sessile species. In addition it was not included in our study of the stalked *Licea* species (Wrigley de Basanta & Lado 2005). The edges of the platelets in this species have many small warts and less refuse material on the outer surface. The pale dehiscence lines were not as obvious in some sporocarps. Because of its habitat, with its host plant covered in winter and spring by snow, this is a nivicolous species and in fact it looks like a really minute *Lamproderma* under the stereoscope. The nivicolous habitat, clear silvery dehiscence lines and large spores easily distinguish this species. All these are different from its nearest stipitate species *L. pedicellata* (H. C. Gilbert) H. C. Gilbert. It is clearly distinguished from *L. eremophila* D. Wrigley, Lado & Estrada by the larger globose vs. angular spores. The excellent SEM images in the original publication (Moreno *et al.* 2010) obviated the need to repeat them.

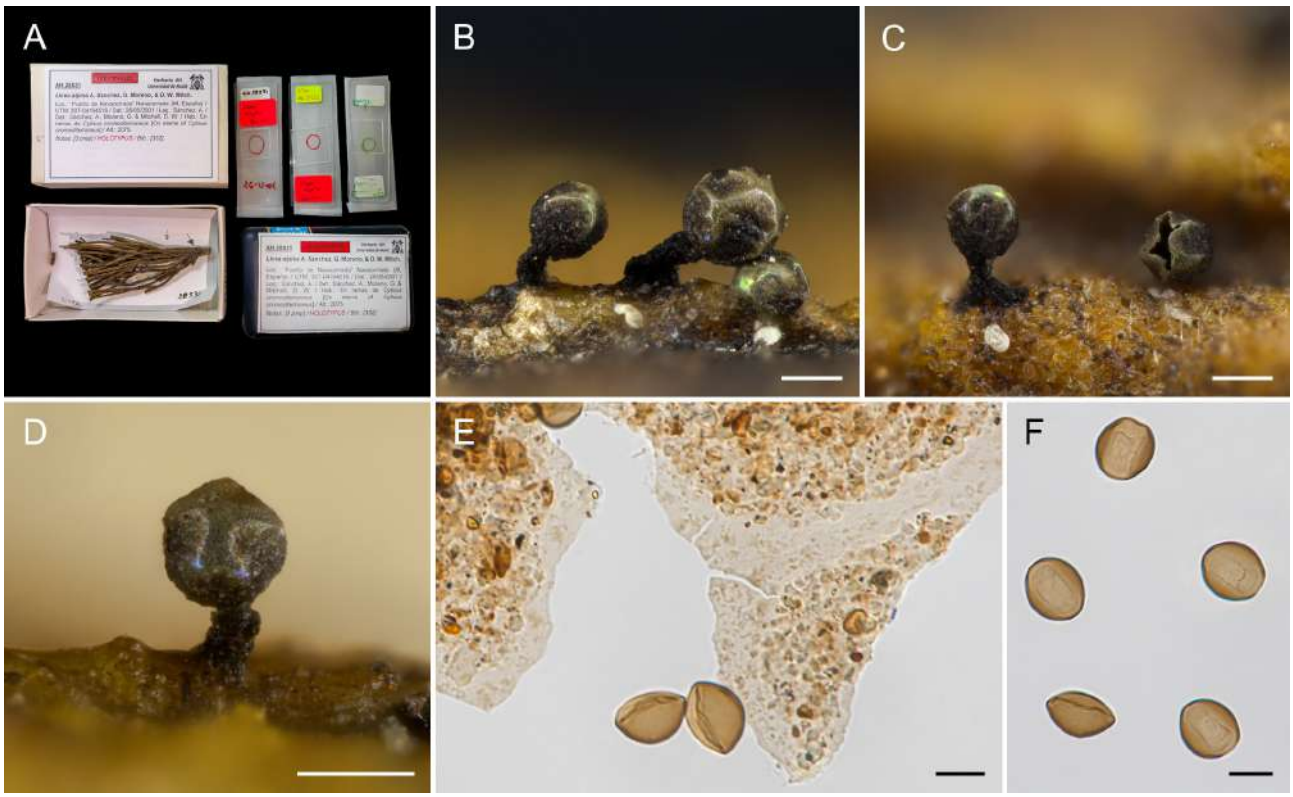

FIGURE 1. *Licea alpina.* A–F (AH 28531, Holotype). A. Herbarium boxes and slides. B–D. Stalked and subsessile sporocarps. E. Spores and peridial platelets by TL. F. Spores by TL. Scale bars: B–D = 0.1 mm, E–F = 10 µm.

2. *Licea ampulliformis* D. Wrigley & Lado ***sp. nov.*** Figs. 2A–M

HOLOTYPUS: MEXICO. Puebla, Emilio Portes Gil, 19°17'40.1''N 97°30'21.9''W, 2430 m, 3-III-2001, in moist chamber of *Yucca filifera* bark (pH 7.0), leg. *D. Wrigley de Basanta,* dwb 1988 (MA-Fungi 98835)!.

Mycobank: MB 850897.

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglobose, (0.05–) 0.1–0.3 mm diam., yellowish brown (74. s y Br-78. d. y Br). Hypothallus inconspicuous. Peridium single, membranous, thin, with lighter lines marking small peridial platelets (Figs. 2B–D), light orange-yellow (70. l. OY) by LM, inner surface slightly roughened by LM, warted by SEM (Fig. 2J), outer surface roughened or covered with granular material, except in lighter areas edging the platelets (Fig. 2E arrows); dehiscence into small irregular platelets with smooth clear margins (Fig. 2I arrow). Columella absent. Capillitium absent. Spores free, dark yellowish brown (78. d. y Br) in mass, yellowish-brown (76. l. y Br) to orange-yellow (71. m. OY) by LM, subglobose, (11.5–)12–14(–14.5) µm diam., minutely punctate by LM, with dispersed baculae by SEM (Fig. 2M), spore wall uniform thickness, except for the germination area one side that is thinner and lighter. Protoplasmodium colourless.

Etymology: Latin (*ampulla*) or blister from the macroscopic appearance of the fresh sporophore.

Habitat: On the bark of living *Yucca filifera* and *Yucca periculosa*

Distribution: At the moment known from the States of Hidalgo, Puebla and Queretaro (Mexico). Probably occurring in other regions of the world where *Yucca* spp. are present.

Other material examined: *Licea ampulliformis*. MEXICO. PUEBLA: Emilio Portes Gil, 19°17'40.1''N 97°30'21.9''W, 2430 m, 3-III-2001, in moist chamber culture (mc) of *Yucca filifera* bark, (pH 7.0), dwb 1973. Esperanza, Cañada Morelos, 18°51'14"N;97°28'47"W, 2420 m, 2-III-2005, *Yucca periculosa* bark (mc, pH 7.1), dwb 253. San Luis las minas, Santiago Miahuatlan, 18°33'52"N 97°23'27"W, 2020 m, 7-VII-2005, on *Yucca* sp. bark, (mc, pH 7.0), dwb 2614. HIDALGO: Tlanalapa, route Mex 130, Km 37, 19°50'15"N 98°37'03" W, 2457 m, 12-IV-2002, on *Yucca periculosa* bark, (mc, pH 6.8), dwb 2182; idem 11-V-2002, (mc, pH 7.1), dwb 2189. QUERETARO: Vizarrón, Cadereyta, 20°48'32"N 99°43'20"W, 2120 m, 28-V-2005, on *Yucca filifera bark,* (mc, pH 6.8), dwb 2613 (slide only). *Licea nannengae* Pando & Lado. *Holotypus:* SPAIN. Soria, Cubillos, 30TWM0421, 1090 m, on bark of *Juniperus thurifera,* 24-II-1986, 246 Pando (MA-Fungi 16056).

Notes. While studying the myxomycetes associated with plants in semi-arid lands and deserts in Mexico as part of the Myxotropic project (www.myxotropic.org) a *Licea* subg. *Licea* that presents some differences from currently described species was found. It is described here as a new species. The group of characters that distinguish it from other species of the genus are the wrinkled, yellowish brown sporocarps, that break into small irregular platelets with clear margins lacking any ornamentation, the single peridium and the spore ornamentation as seen by SEM. Germination of spores on water agar, transferred to WMY (Haskins & Wrigley de Basanta 2008) with the mélange of bacteria carried from the spore surface, produced hyaline protoplasmodia from both collection dwb 1988 and dwb 2614, but these never developed fully into sporocarps on agar in spite of enriching the medium with sterile *Yucca* sp. bark extract. This species may appear somewhat similar to the recently described *L. aurea* D. Wrigley, Lado & Estrada, but its wrinkled yellow-brown sporocarps, with thin lighter lines marking the numerous platelets with smooth clear margins, differ from the golden sporocarps dehiscing into very few platelets with the margins showing no differentiation from the rest of the peridium in *L. aurea*. It also resembles *L. nannengae* Pando & Lado from which it differs in its single vs. double peridium and warted vs. smooth spores.

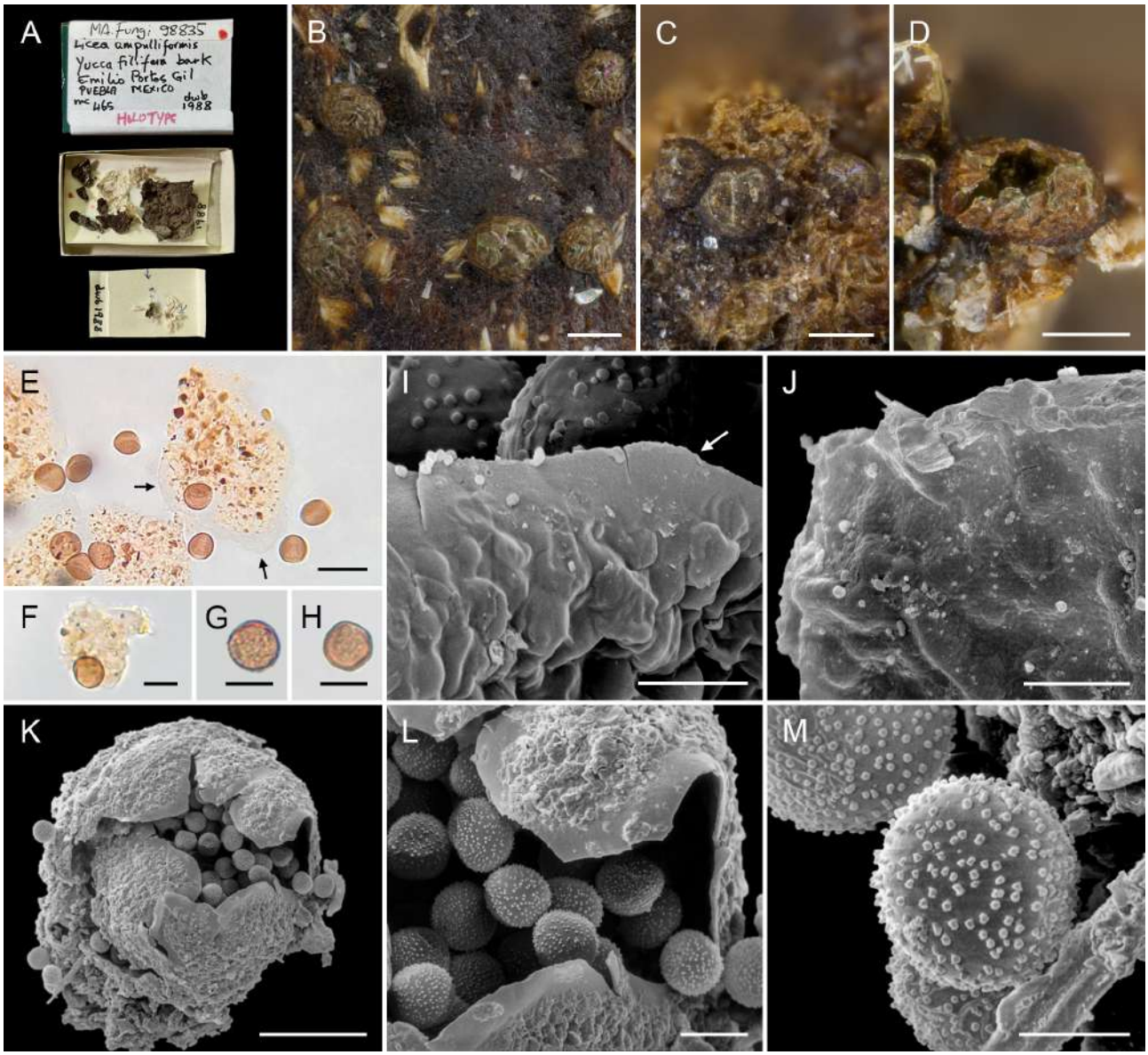

FIGURE 2. *Licea ampulliformis.* A–H, K–M (dwb 1988, MA-Fungi 98835, Holotype), I–J (dwb 2535). A. Herbarium box. B–D. Sessile sporocarps. E. Spores and peridial platelets by TL showing clear margins to the platelets (arrows). F–H. Spores by TL. I. detail of platelet margin showing clear area by SEM (arrow). J. Inner surface of a platelet showing warted surface. K–L Detail of open sporocarp showing platelets and spore by SEM. M. Spores by SEM. Scale bars: B–D = 0.1 mm, E = 20 µm, F–H, L = 10 µm, I–J, M = 5 µm, K = 50 µm.

3. *Licea aurea* D. Wrigley, Lado & Estrada, in Wrigley de Basanta, Estrada & Lado, Phytotaxa 391(3): 221 (2019) Figs. 3A–J

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglose, 0.05–0.15 mm diam., golden yellowish brown. Peridium single, membranous, translucent with a rough inner surface; dehiscence by fracture along preformed lines leaving 4–6 polygonal platelets with well-defined margins, no clear areas, pegs or larger ornamentation at the edges. Spores free, yellow in mass, pale yellow by TL, subglobose, (13.5–)14–15(–16) µm diam., smooth, spore wall thick with a large thinner area on one side. By SEM the inner peridial surface is roughened by an irregular reticulum of warts, the platelet margins are a continuum with no other ornamentation; the epispore is smooth with a wrinkled surface on the thinner area. Protoplasmodium colourless.

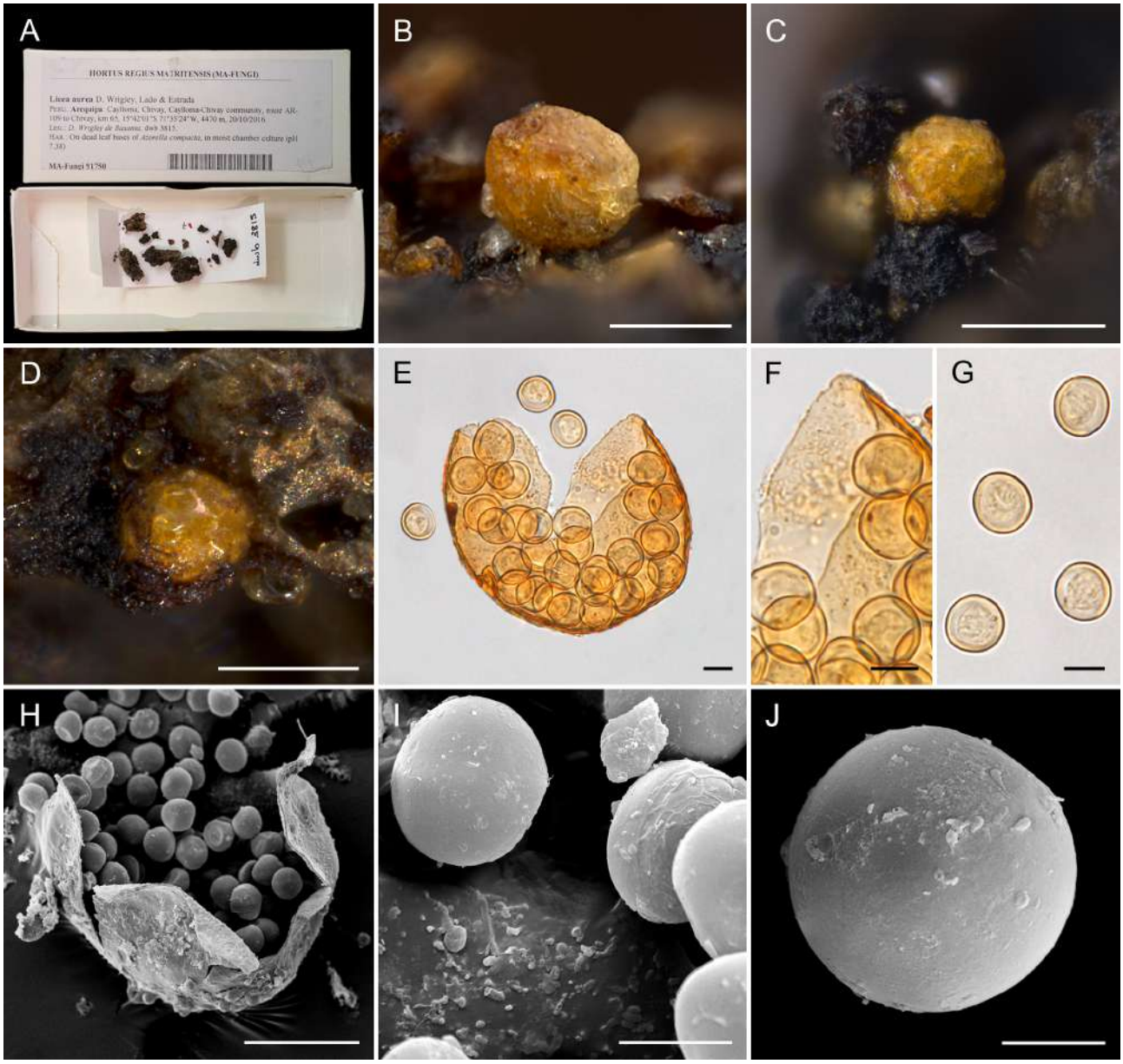

FIGURE 3. *Licea aurea.* A–G. (dwb 3815, MA-Fungi 91750, Holotype), H–J. (dwb 3533). A. Herbarium box. B–D. Sporocarps. E. Whole sporocarp and spores by TL. F. Fragment of the inner surface of the peridium and spores. G. Spores by TL with thick walls and thinner germination area. H. Whole open sporocarp showing spores by SEM. I. Group of spores by SEM. J. Spore by SEM. Scale bars: B–D = 0.1 mm, E–G, I = 10 µm, H = 50 µm, J = 5 µm.

Material examined: Holotypus. PERU. Arequipa, Caylloma, Chivay, Caylloma-Chivay community, route AR-109 to Chivay, km 65,15º42´01”S 71º35´24”W, 4470 m, on dead leaf bases of *Azorella compacta* in moist chamber culture (pH 7.4), 20-X-2016, dwb 3815 (MA-Fungi 91750)!. Arequipa: Chivay, Caylloma-Chivay community, route PE-1SE, km 60, 24 km S of Chivay, 15°42’41”S 71°36’22”W, 4747 m, on dead leaf bases of *Azorella compacta* in moist chamber culture (pH 7.4), 9-XI-2012, dwb 3533. Caylloma, Chivay, Caylloma-Chivay community, route AR-109 to Chivay, km 57, 15º44´00”S 71º35´45”W, 4823 m, on dead leaf bases of *Azorella compacta* in moist chamber culture (pH 6.6), 19-X-2016, dwb 3814.

Habitat: on dead leaves of *Azorella* spp.

Distribution: Known only from the Peruvian Andes.

Icon.: Wrigley de Basanta *et al.* (2019: 219, Figs. 1–11).

Notes. This species was found from leaf bases inside the compact cushion of the host plant *Azorella compacta* in the Peruvian Andes at almost 5000 m elevation. The unique combination of characters of this species includes its tiny, sessile, golden yellow sporocarps (Figs. 3B–E), the dehiscence of the peridium into a few polygonal platelets with no border ornamentation (Figs. 3E–H), and the large, yellow, smooth spores, with a conspicuous germination pore (Figs. 3F–G, I–J). This species differs from *L. ampulliformis* by its golden sporocarps with no ornamentation and no clear areas on the margins to the platelets vs. the wrinkled, yellowish brown sporocarps with clear margins to the platelets in *L. ampulliformis*. In addition, this species has smooth spores vs. warted spores in *L. ampulliformis*. *Licea aurea* differs from *L. belmontiana* Nann.-Bremek. by its larger spores, 14–15 µm diam. vs. 10–13(–14) µm diam. in the latter. In addition, *L. belmontiana* has a double peridium, not a single like in *L. aurea* and dark brown angular sporocarps.

4. *Licea belmontiana* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 69(3): 337 (1966). Figs. 4A–J

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglobose, angular, 0.05–0.2 mm diam., dark brown. Peridium apparently single, brown by TL with preformed dehiscence lines; dehiscence into polygonal plates that remain vertical like petals with smooth edges without outgrowths but minutely crenulate. Spores dark brown in mass, light brown with a slightly paler area by TL, subglose, 10–14 µm diam., apparently smooth. By SEM the peridium is double the inner surface of the peridium is ornamented with dense tiny warts (granular) that continue to the platelet margins, the margin is crenulated; the epispore is verrucate with irregularly sparsely spaced warts and some areas with no warts.

Material examined: Holotypus. NETHERLANDS. Wageningen, Belmonte Botanic Gardens, on bark from an *Acer* sp. stump in moist chamber culture, 2-4-1965. NENB-5879 (BR-MYC 5020057898868)!.

Habitat: on bark, trunks and stumps of angiosperms and gymnosperms.

Distribution: Norway, Sweden, Russian Federation, Ukraine, Ireland, Netherlands, France, Switzerland, Germany, Italy, Spain, Greece, Malta, Kazakhstan, Mongolia, China, India, USA, Canada, Mexico, Guatemala, Paraguay, Argentina, Chile.

Icon.: Nannenga-Bremekamp (1966: 337, Figs. 1A–C; 1975: 64; 1991: 43), Neubert *et al.* (1993: 282, Pl. V: 1), Novozhilov *et al.* (1999: 84, Figs. 3A–D), Yamamoto (2002b: 4, Figs. 2A–C; 2006: 13, Figs. 4A–C; 2021: 139, Figs. A–C), Novozhilov & Schnittler (2008: 108, Figs. 26–27), Schnittler *et al.* (2013: 101, Figs. 31–34 (as *L.* cf. *belmontiana*), Bortnikov *et al.* (2022: 25, Figs. 3a–k).

Notes. This species was described as having smooth spores on the basis of light microscope examination available to its author at that time. However, our examination of the holotype by SEM has shown that the spores are not entirely smooth, since the epispore has some widely-spaced warts of different size (Fig. 4I).

In the original description the species is characterized as having a single peridium with included granular matter, but our SEM micrographs show (Fig. 4H arrow), that the granular matter forms a complete layer, so the peridium is double. This fact was pointed out also by Novozhilov *et al.* (1999) for collections they ascribed to this species. The spore size in the original description was given as about 13 µm in diameter, but the author herself specified the wider range in her later expanded monographs (Nannenga-Bremekamp 1975, 1991, 2022). According to GBIF, there is a collection marked as isotypus in UPS BOT F 646101.

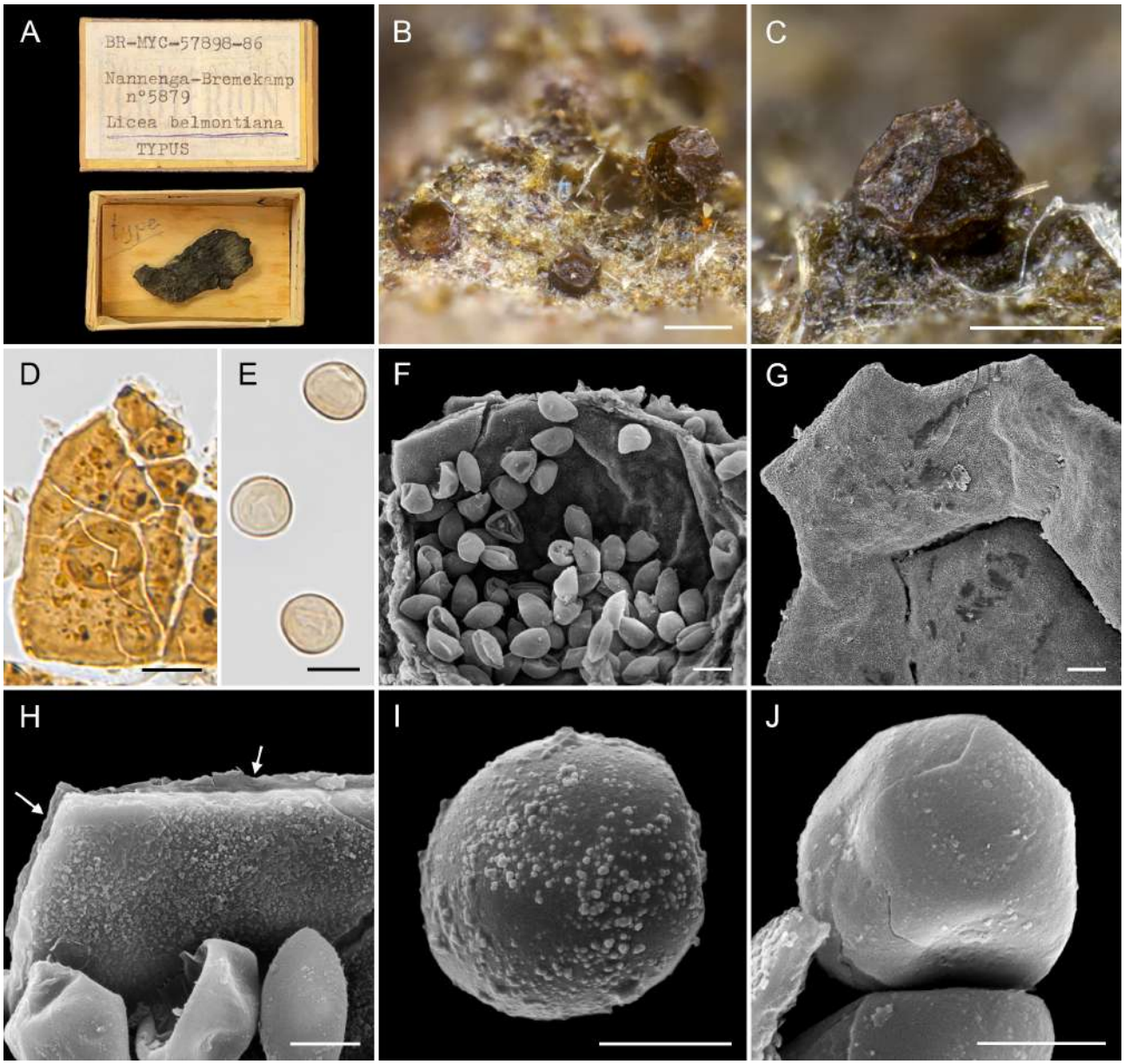

FIGURE 4. *Licea belmontiana.* A–J (NENB-5879, BR-MYC 5020057898868, Holotype). A. Herbarium box. B–C. Sessile sporocarps. D. Peridial platelets by TL. E. Spores by TL. F. Dehisced sporocarp by SEM. G–H. Peridial platelets by SEM showing margins without outgrowths (arrows). I–J. Warted spores by SEM. Scale bars: B–C = 0.1 mm, D–G = 10 µm, H–J = 5 µm.

5. *Licea capacia* Oltra & G. Moreno, in Moreno & Oltra, Bol. Soc. Micol. Madrid 38: 56 (2014) Figs. 5A–I

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps elongated, 0.05–0.15 mm length, 0.05 mm wide, 0.05 mm high, reddish brown to yellow brown. Peridium double, smooth, membranous, marked with dehiscence lines to make 4 platelets, two short and two long (Figs. 5C–D); peridial platelets pale reddish brown by TL, with smooth lighter margins; dehiscence along the upper longitudinal line. Spores pale reddish brown in mass, very pale yellow brown by transmitted light, subglobose to angular 10–11 µm diam., minutely verrucose. By SEM the inner peridium is granular with tiny sparsely distributed warts and the surface is uniform right to the margins of the platelets with no larger ornamentation; the epispore is densely verrucate with different sized warts and the spores appear to be polygonal.

Material examined: Holotypus. SPAIN. Valencia, Onteniente, Pontó de Marín, 30SYH0299, 456 m, on leaves of *Agave americana*, 22-I-2010, leg. *M. Oltra*, 12486.Oltra (AH 42711)!.

Habitat: on leaves of succulent plants (*Agave americana*) and leaves of scrubs (*Pistacea lentiscus*).

Distribution: Known only from Spain.

Icon.: Moreno & Oltra (2014: 57, Figs. 1–14).

Notes. The curious almost cuboid sporocarps, are easy to recognize; and give the appearance of an historical doctors medical bag. The species was described as having a single peridium, but as can be seen in the SEM micrograph (Fig. 5G, arrow) the peridium is double. The occurrence on succulent plants and longitudinal dehiscence bring the species close to *L. succulenticola* Mosquera, Lado, Estrada & Beltrán-Tej., but it is quite different, since the spores are smaller and subglobose in that species, not angular to polygonal, and dehiscence is into two flat halves by a split, not four platelets.

FIGURE 5. *Licea capacia.* A–I (12486.Oltra, AH 42711, Holotype). A. Herbarium box. B–D. Sessile sporocarps. E. Peridial platelets by TL. F. Angular spores by TL. G. Peridial platelet margins by SEM showing double peridium (arrow) and no outgrowths. H–I. Spores by SEM. Scale bars: B–D = 0.1 mm, E–F = 10 µm, G–I = 5 µm.

6. *Licea castanea* G. Lister, J. Bot. 49: 61 (1911) Figs. 6A–S

= *Licea bryocorticola* A. Kuhnt, Ber. Bayer. Bot. Ges. 91: 181 (2021), ***syn. nov.*** (Holotype see below).

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglobose, 0.13–0.25 mm diam., to elongated, 0.3–0.7 mm × 0.2–0.25 mm broad, chestnut brown with definite lighter lines of dehiscence. Peridium somewhat cartilaginous, colourless to pale purplish by TL, overlaid with layer of minute bright brown granules (Fig. 6E); dehiscence into platelets along lighter lines with slightly thickened minutely toothed margins. Spores free, pale olive in mass, almost colourless to yellow brown by TL, smooth, 8–10(–12) µm diam., spore wall thinner on one side. By SEM the inner layer of the peridium is smooth with dispersed tiny granules, and the platelet margins have a single row

of outgrowths of up to 1 µm diam. (Fig. 6I); the epispore is smooth with fine stippling of irregularly spaced flat warts visible only at very high (5000×) magnification (Figs. 6 H, J).

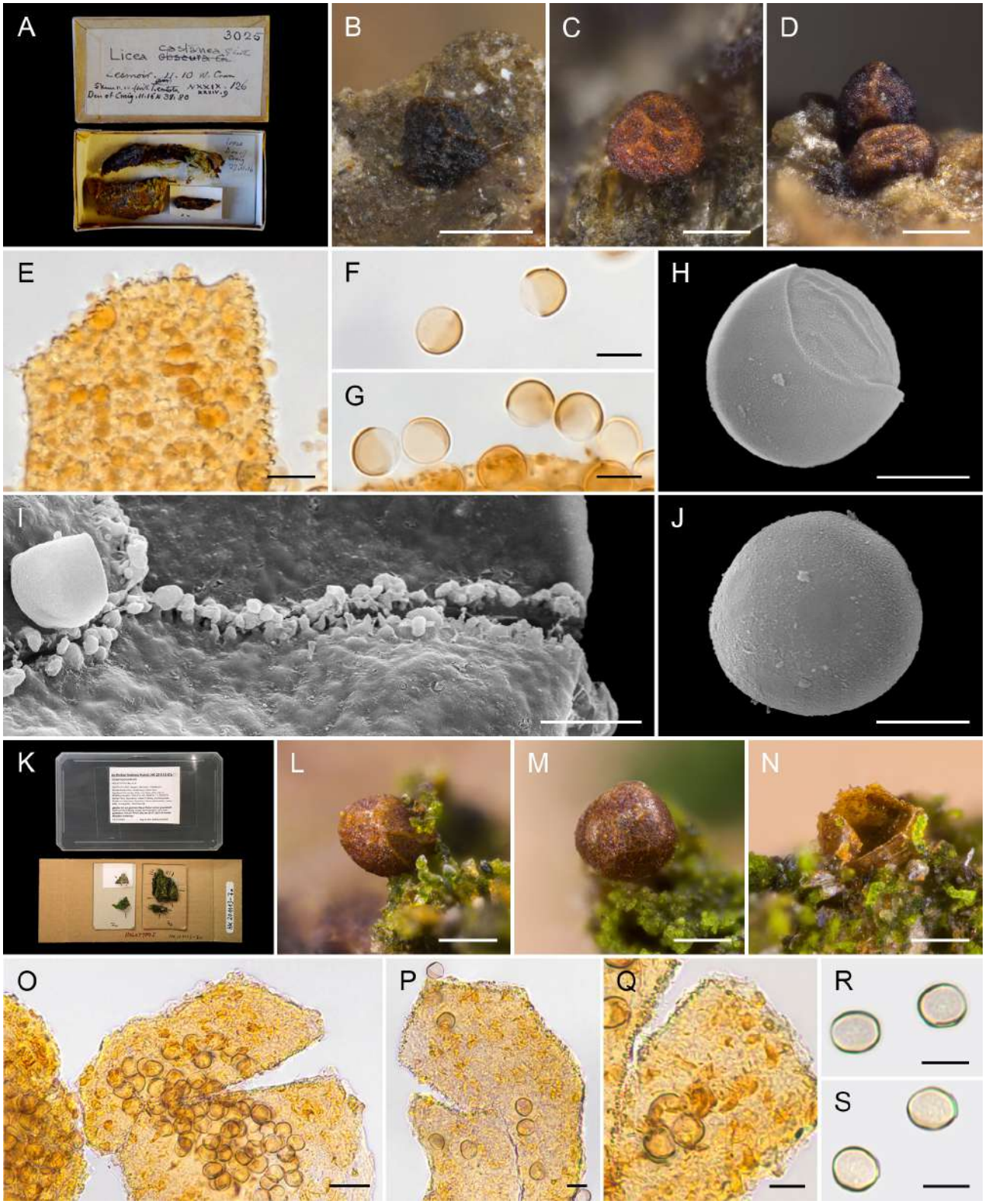

FIGURE 6. *Licea castanea.* A (BM 3025, BM001089212, Lectotype); B–G (MA-Fungi 16013)*;* H, J (MA-Fungi 29564); I (MA-Fungi 15932); K–S (Holotype of *L. bryocorticola*, HK 201113-07a, M-0313079). A. Herbarium box. B–D. Sessile sporocarps. E. Spores and peridial platelets by TL showing outgrowths on the edges. F–G. Spores by TL. H. Spore by SEM. I. Peridial platelets by SEM, showing outgrowths along the margins. J. Spore by SEM. K. Herbarium specimen. L–N sessile sporocarps. O–Q. Peridial platelets by TL showing outgrowths on the edges. R–S. Spores by TL. Scale bars: B–D, L–N = 0.1 mm, E–G, P–S = 10 µm, H–J = 5 µm, O = 20 µm.

Material examined: Lectotypus. UNITED KINGDOM. Scotland, Aberdeen, Lesmoir, 57.1526ºN 2.1100ºW, on bark of *Pyrus aucuparia,* Nov 1911, leg. *W. Cran*, BM 3025 (BM001089212!, see Lado & Wrigley de Basanta 2018). SPAIN. Guadalajara, Tamajón, ermita de la Virgen del Enebral, 30TVL7941, corteza de *Juniperus thurifera* vivo, cultivado, leg. *F. Pando*, 203 Pando, 17-II-1986, MA-Fungi 16013. Guadalajara, carretera a Tamajón, km 29, 30TVL8326, 900 m, corteza de *Juniperus oxycedrus*, 15-V-1980, leg. *C. Lado*, 224 Lado, MA-Fungi 29564 (Rev. NENB 5-12-VII-1982). Guadalajara, Anchuela del Campo, 30TWL8343, corteza de *Juniperus thurifera*, 21-XI-1984, Leg. *C. Lado et al*., 123 Lado, MA-Fungi 15932. GERMANY. Bayern, München, Stadtbezirk, Schwanthalerhöhe, Gießerweg, neben dem Sportplatz/Spielplatz, 530 m, MTB 7835/314, kleiner Park, Baumallee, auf mit Algen und etwas Moos bewachsener Rinde von lebendem Spitzahorn (*Acer platanoides*), in ca. 150–180 cm Höhe,13-11-2020, HK 201113-07a (M-0313079)! (as holotypus of *Licea bryocorticola*).

Habitat: on bark of living and dead trees, trunks and stumps of angiosperms and gymnosperms, between mosses.

Distribution: Norway, Sweden, Finland, Russian Federation, Ukraine, Denmark, Netherlands, Belgium, Germany, Poland, United Kingdom, Ireland, France, Switzerland, Austria, Spain, Hungary, Greece, Türkiye, India, Thailand, Japan, Canada, USA, Mexico, Peru, Brazil, Paraguay, New Zealand.

Icon.: Lister (1925: pl. 219, Figs. e–g), Martin & Alexopoulos (1969: 481: Pl. I: 5a–f), Nannenga-Bremekamp (1965: 135, Figs. 3A–B; 1975: 62; 1991: 41), Neubert *et al.* (1993: 149, 282, Pl. V: 3), Lado & Pando (1997: 114, Figs. 27a–b), Yamamoto (1998: 130, Figs. A–B; 2021: 140, Figs. A–D), Härkönen & Sivonen (2011: 52, Fig. 63), Härkönen & Varis (2012: 146, Fig. 214), Poulain *et al.* (2011: 66), Ronikier *et al.* (2017: 248, Figs. 1E–H), Kuhnt (2021: 182: Figs. 47a–b; 183: Figs. 48a–d; 184: Figs. 49a–d; 185: Figs. 50a–d; 186: Fig. 51b, d, all as *L. bryocorticola*; 186: Fig. 51a–c; 187: Figs 52a–d, all as *L. castanea*), Bortnikov *et al.* (2022: 27, Figs. 5a–i).

Notes. *L. castanea* was found by the Rev. W. Cran at Lesmoir, Aberdeenshire, Scotland where it occurred on moss growing on the bark of *Pyrus aucuparia* and also on the bark itself, according to G. Lister (1911: 61). In the box of the type specimen (Fig. 6A) there is a plentiful collection of sporocarps of different sizes. This type material was examined and compared with the description and excellent iconography of *L. bryocorticola* A. Kuhnt (Kuhnt 2021) to check if they are conspecific. We repeated light micrographs of the latter (Figs. 6K–S), to compare the colours with the same instruments. Macroscopically the two species are very similar, and both appear on bryophytes and bark. Microscopically both species have a single line of outgrowths on the platelet edges visible by TL and by SEM. Both species have smooth spores with a large pale area, as seen under TL, and the epispore of both species is smooth, with fine stippling at very high magnification by SEM. The differences separating the two species, according to Kuhnt (2021), include slightly darker peridium, slightly darker spore mass and smaller outgrowths on the margins of the platelets. However, our examination of the two species did not corroborate these differences, and since the stated variations are very minor, our opinion is that they do not warrant the creation of a separate species. Therefore we synonymize them here.

The regulations of the BM herbarium discourage use of the sporocarps of the historic collection of *L. castanea* for SEM analysis, so for the micrographs we used a typical collection from our herbarium.

Licea castanea differs from *L. testudinacea* Nann.-Bremek. and *L.minima* Fr. by the chestnut colour of the sporocarps, not dark brown, and in the pale smooth spores, not warted, as in the above-mentioned two species, nor grey or red-brown as in *L. testudinacea* or *L. minima* respectively.

7. *Licea castaneoides* Y. Yamam. & Nann.-Bremek., in Nannenga-Bremekamp & Yamamoto, Proc. Kon. Ned. Akad. Wetensch., C. 93(3): 269 (1990) Figs. 7A–I

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglobose to pulvinate, 0.03–0.1mm diam., shiny, olivaceous. Peridium double (Fig. 7G), outer layer with minutely roughened outer surface, thin gelatinous with included particles, inner layer membranous, no preformed lines; dehiscence irregular from above. Spores free, olivaceous brown in mass, pale brown by TL, with a thinner paler area, subglobose, 9–10.5 µm diam., minutely warted. By SEM the inner surface of the inner peridium is smooth with a few scattered warts at high magnification (3000×) (Figs. 7F–G), the margins of the irregular peridial pieces are totally smooth to the edge with no larger outgrowths; the epispore is evenly covered with pila (Figs. 7H–I).

Material examined: Isotypus. JAPAN. Donari-cho, Tokushima Pref., bark of living tree in moist chamber, 3-VI-1988, NENB 16.135 (ex Y.Y. 6407) (BR5020070191601)!.

Habitat: bark of living trees.

Distribution: Known only from type territory (Japan).

Icon.: Nannenga-Bremekamp & Yamamoto (1990: 270, Figs. 4A–C), Yamamoto (2021: 159, Figs. A–C).

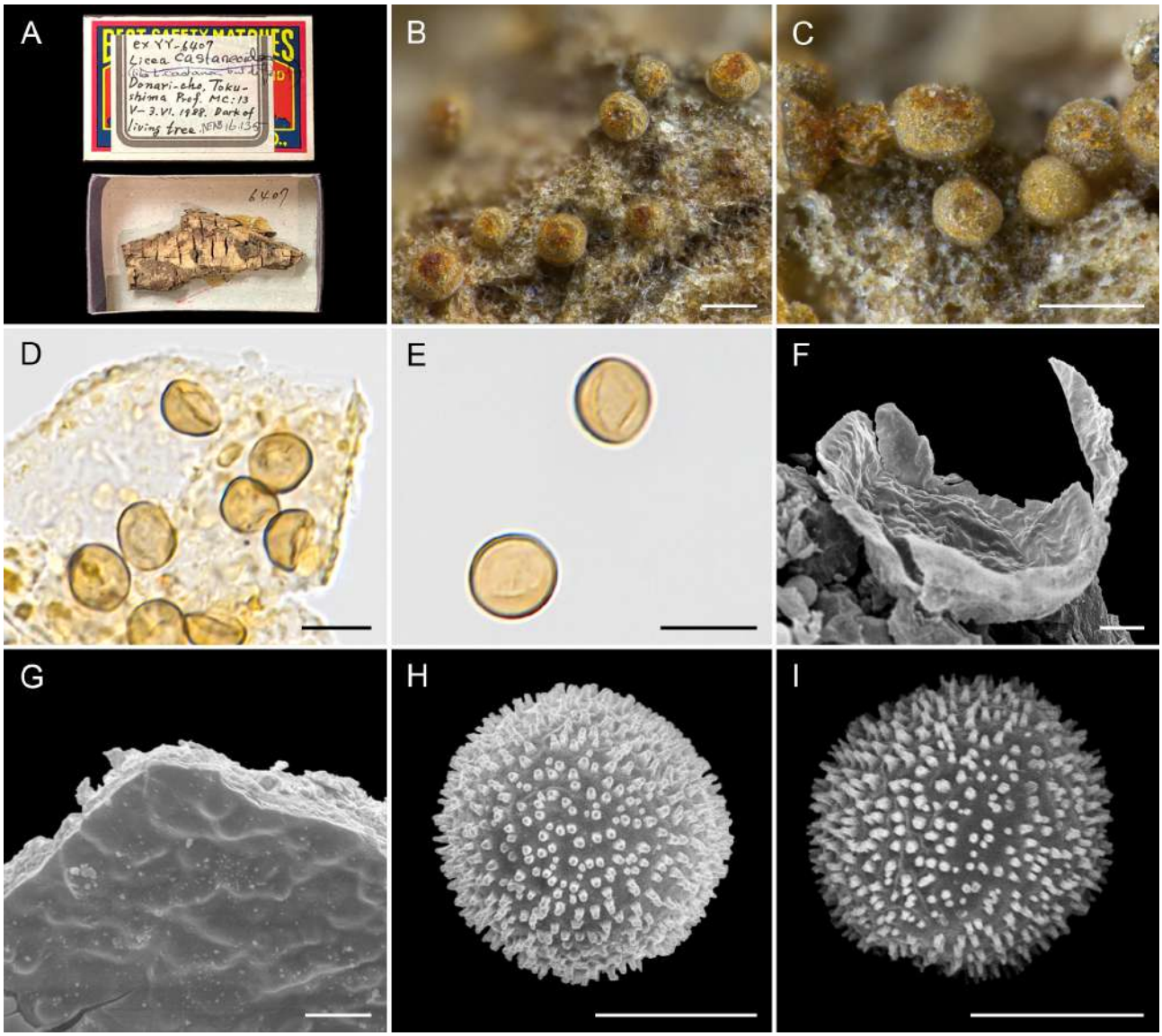

FIGURE 7. *Licea castaneoides.* A–I (NENB 16135, ex Y.Y. 6407, BR5020070191601, Holotype). A. Herbarium box. B–C. Sessile sporocarps. D. Peridial platelet and spores by TL. E. Spores by TL. F. Dehisced sporocarp by SEM. G. Platelet by SEM showing double peridium with no outgrowths on the edge. H–I. Spores by SEM. Scale bars: B–C = 0.1 mm, D–F = 10 µm, G–I = 5 µm.

Notes. This species does not have true defined peridial platelets and fits better into the subgenus *Pleiomorpha*, as Yamamoto comments (Yamamoto 2021), but it is included here since the wrinkled peridium can be interpreted as platelets, and macroscopically this species could be confused with a small *L. castanea*. The spore colour, dehiscence and spore ornamentation however all differ from *L. castanea* (see above).

8. *Licea chelonoides* Nann.-Bremek., Acta Bot. Neerl. 14: 136 (1965) Figs. 8A–J

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglobose to subhemisphaerical, variable in size, height up to 0.5 mm × 0.8 mm diameter, dull black. Peridium thick, double, layers adhering (Fig. 8I), outer layer granular, with minute ridges, inner layer orange to burnt sienna by TL (Fig. 8E); dehiscence along preformed lines edged with rows of interlacing outgrowths. Spores free, dark brown in mass (Fig. 8D), rosy brown by TL, with a pale area for germination, globose, (14–)15–18(–19) µm diam., densely unevenly warted. By SEM the inner peridium is minutely densely warted and the platelet margins have larger outgrowths; the epispore is densely covered with flattened verrucae.

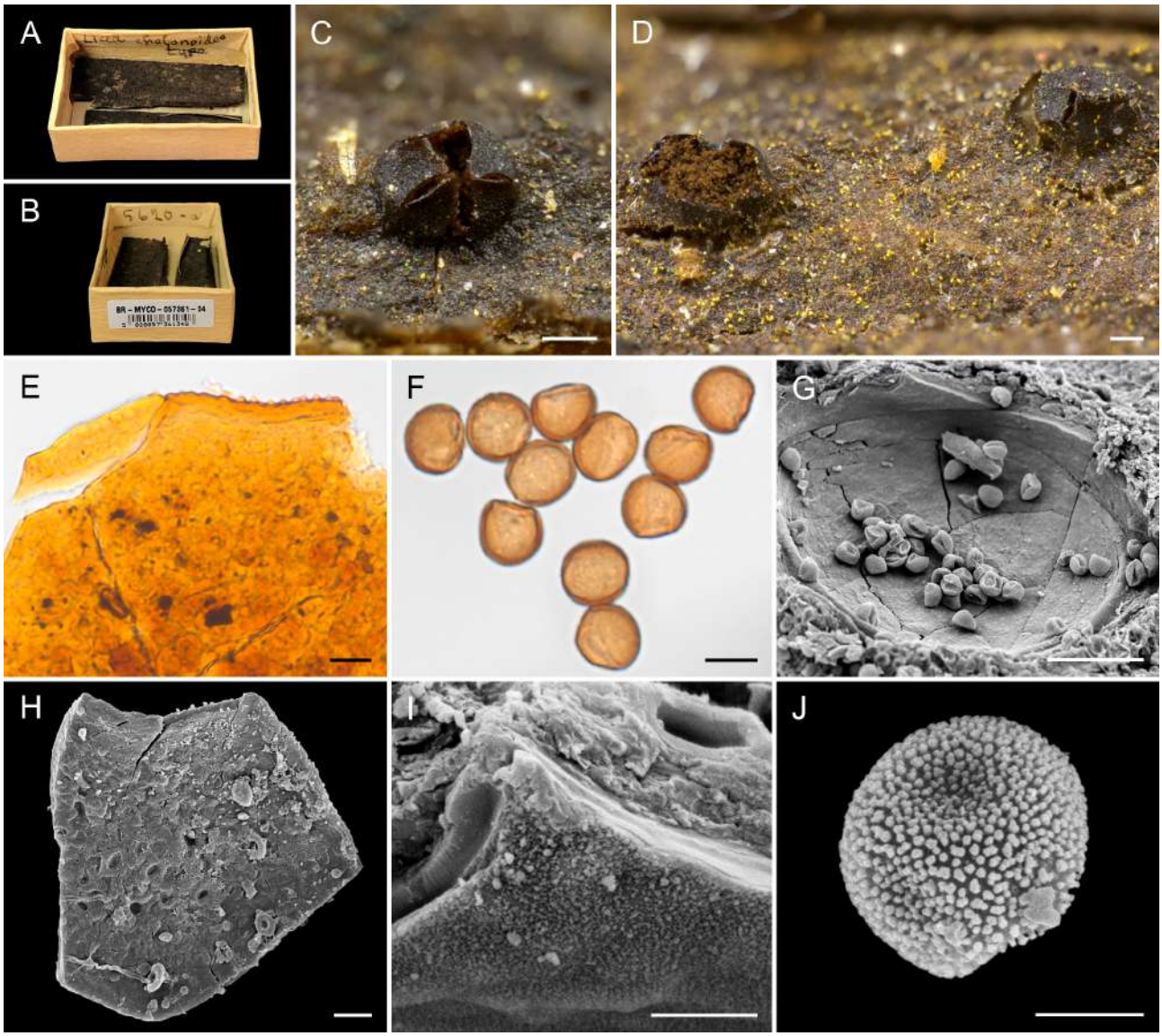

FIGURE 8. *Licea chelonoides.* A–J (NENB 5620, BR5020057361348, Isotype). A–B. Herbarium box. C–D. Sessile sporocarps. E. Peridial platelet and spores by TL. F. Spores by TL. G. Dehisced sporocarp base by SEM. H. Platelet outer surface by SEM. Whole platelet showing well-defined edges. I. Edge of a platelet by SEM showing double peridium and no outgrowths on the edge. J. Spore by SEM. Scale bars: C–D = 0.1 mm, E–F, H = 10 µm, G = 50 µm, I–J = 5 µm.

Material examined: Isotypus. NETHERLANDS. Doorwerth, on decaying pine wood, 9-I-1964, NENB 5620 (BR5020057361348)!.

Habitat: on decaying pine wood, also on bark of living and dead trees.

Distribution: Netherlands, Belgium, Germany, France, United Kingdom, Spain, Russian Federation, Japan.

Icon.: Nannenga-Bremekamp (1965: 137, Figs. 5A–D), Yamamoto (2006: 17, Figs. 6A–C; 2021: 142, Figs. A–C).

Notes. This species has dark sporocarps similar to *L. minima* Fr., but they are dull black in reflected light (Figs. 8C–D) and it has larger spores that are dark brown in mass, not reddish. In addition *L. minima* has more prominently ornamented spores by TL. In the description of *L. chelonoides* the author suggests the warts on the spores rub off, but in this was not observed in the type examined.

9. *Licea confundens* T.N. Lakh., Nann.-Bremek. & R.K. Chopra, Proc. Kon. Ned. Akad. Wetensch., C. 93(3): 253 (1990)

Sporophores sporocarpic, scattered, sessile. Sporocarps subglobose, 0.25–0.5 mm diam., dull ochraceous brown, ridged. Peridium double, outer layer gelatinous, with refuse inclusions, inner layer membranous, almost colourless;

dehiscence along ridges into platelets and lobes. Spores mostly adhering in pairs, or in large loose clusters of 3–12 in spores, very dark brown in mass, light lilac grey by TL, globose, 10–12 µm diam., or ovoid 10.5 × 12 µm, minutely warted or smooth in area attached to another spore.

Holotype: HPUB 13,135.

Habitat: on bark of living *Quercus incana*.

Distribution: Known only from type territory (India).

Icon: Lakhanpal *et al.* (1990: 254, Figs. 1A–B).

Notes. We were unable to study the type material of this species, it was requested by us, but not sent. Our comments are based on the original description and iconography by Lakhanpal *et al.* (1990). The paired to clustered spores suggest a similarity to *L. synsporos* Nann.-Bremek. and *L. synchrysospora* Bortnikov but it is distinguished by its lilac spore colour, not olivaceous.

10. *Licea deplanata* Kowalski, Madroño 21(7): 455 (1972)

[*Nom. nov.*, based on *L. applanata* Kowalski, Mycologia 62(5): 1058 (1970), non *L. applanata* Berk., 1845]

Sporophores sporocarpic, scattered, sessile. Sporocarps extremely depressed, 0.1–0.3 (–0.5) mm diam., dark brown to purplish to almost black with distinct ridges. Peridium single, thick, brittle, dehiscence usually whole peridium as a cap, rarely into lobes along 3–6 distinct glossy ridges; peridial platelet margins with rows of small papillae. Spores free, shiny golden brown in mass, very pale yellow by TL, with a paler area, globose, 11–13 µm diam., smooth.

Type: DTK 10000.

Habitat: on decayed leaves, especially those of *Eucalyptus* sp., also on bark of trees.

Distribution: Germany, Spain, USA, Mexico, Peru, Argentina.

Icon: Kowalski (1970: 1058, Figs. 1–3), Lado & Pando (1997: 117, Figs. 29a–b), Wrigley de Basanta (1988: 7, Figs. 3-4), Flatau (2000: 67, Fig 2A–C).

Notes. This species has flattened sporocarps that are almost flush with the substrate. We were unable to study the type material, which was requested, but not sent. However the original description (Kowalski 1972) is detailed and well-illustrated, and we base our comments on that in order to compare it with the other species.

11. *Licea eremophila* D. Wrigley, Lado & Estrada, Mycologia 102(5): 1186 (2010) Figs. 9A–L

Sporophores sporocarpic, dispersed or grouped. Sporocarps stipitate, occasionally subsessile, 0.1–0.35 mm high. Stalk cylindrical, dark brown to black, sometimes very short, 0.03–0.18 mm or absent. Sporotheca subglobose, angular where the peridial platelets meet 0.07–0.2 mm diam., angular, strong yellowish brown (Figs. 9B–E). Peridium single, light brown by TL, with refuse deposits like dark spots sometimes on the outer surface, inner surface smooth, entirely made up of platelets; dehiscence by 10–15 polygonal platelets (Fig. 9G). Spores free, strong yellow in mass, yellow by TL, often angular, (9–)10–12(–13) µm diam., roughened by TL (Figs. 9H–I). Protoplasmodium colourless, becoming milky then yellow. By SEM the inner peridium is smooth except for the margins of the platelets that have a line of warts; the epispore densely warted, except along slightly raised bands (Figs. 9K–L) with fewer or no warts (like a tennis ball).

Material examined: Holotypus. ARGENTINA. La Rioja, Independencia, Talampaya National Park, km 99 RN-26, 30º07’42’’S 67º44’19’’W, 1378 m, on dead leaf bases of *Puya* sp. in moist chamber culture,12-III-2007, dwb 2826 (MA-Fungi 79158)!. Catamarca, Tinogasta, 28º23’12’’S 67º39’44’’W,1647 m, on epidermis and internal tissue of *Trichocereus* sp.15-I-2008, dwb 3002. CHILE. III Region, Atacama: Chañaral, Pan de Azúcar National Park, mirador Pan de Azúcar, 26º06’40’’S 70º38’54’’W, 313 m, on dead leaf base of *Puya* sp., 6-VIII-2008, dwb 3092.

Habitat: on dead leaf base of the bromeliad *Puya* spp. and on dead remains of the cacti *Trichocereus* sp. and *Miqueliopuntia miqueli*.

Distribution: Peru, Argentina, Chile, Namibia.

Icon.: Wrigley de Basanta *et al.* (2010: 1187–1188, Figs. 1–22), Stephenson *et al.* (2019: 407, Figs 3B–C).

Notes. This species is included in this study because its sporocarps dehisce into platelets and, it sometimes has very short stalks, and may appear sessile. The species was published after our study of the stalked *Licea* (Wrigley de Basanta & Lado 2005) and therefore was not included there. The strong yellow-brown, subglobose sporotheca, the peridium that fragments into defined polygonal platelets, and the angular spores, distinguish even the sessile sporocarps of this species from others in the group. The closest species to *L. eremophila* is *L. verrucispora* D. Wrigley & Lado, but in the latter species the peridium dehisces into irregular fragments, not defined platelets, it has globose spores, not angular ones, and a densely warted inner surface to the peridium.

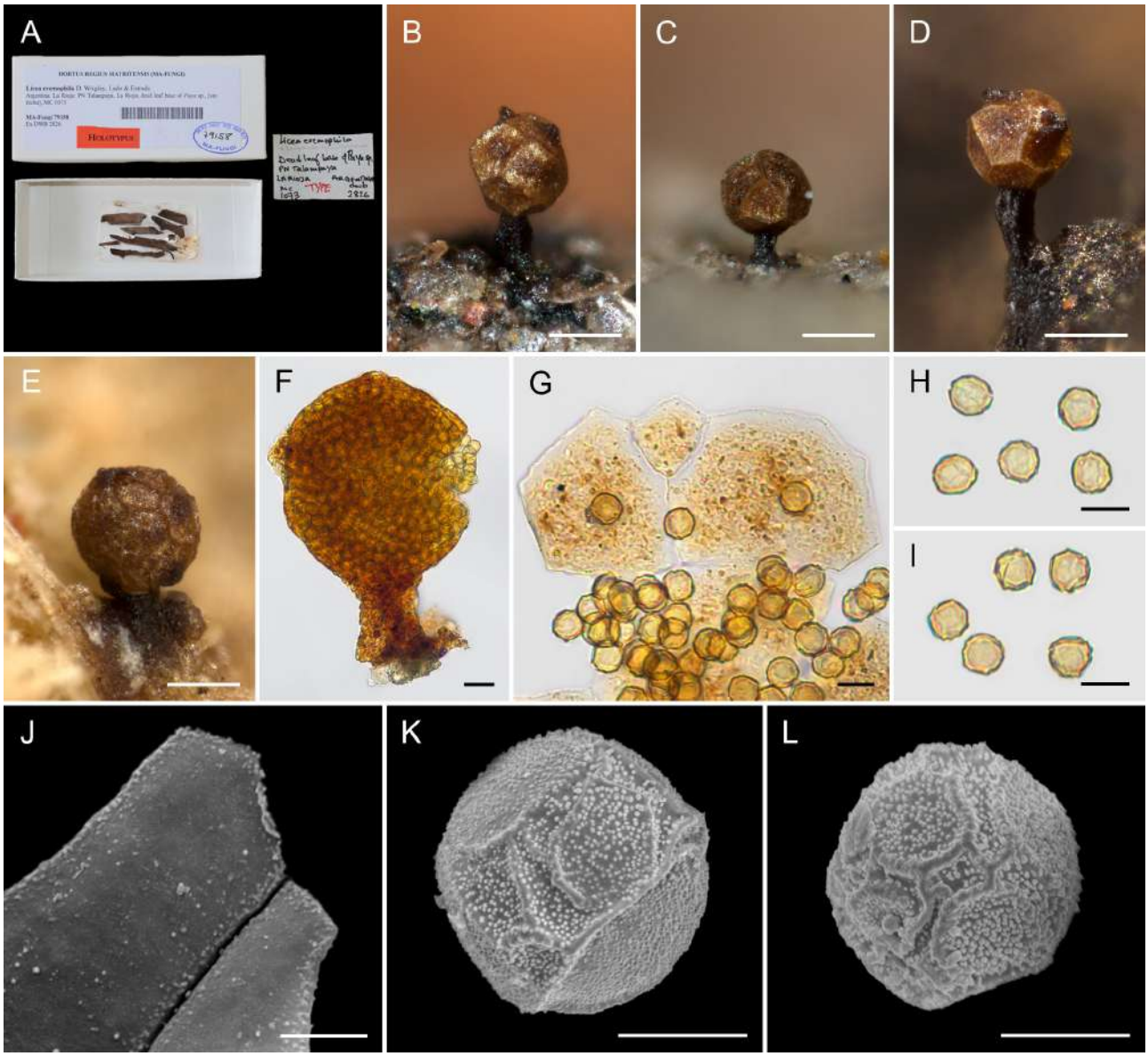

FIGURE 9. *Licea eremophila.* A–C, F–J, L (dwb 2826, MA-Fungi 79158, Holotype); D–E, K (dwb 3002). A. Herbarium box. B–C. Stipitate sporocarps. D. Sporocarps. F. Whole sporocarp and spores by TL. G. Platelets by TL with lighter edges (arrow). H–I. Polygonal spores by TL. J. Platelets by SEM showing well-defined margins. K. Spore by SEM. L. Spore by SEM. Scale bars: B–E = 0.1 mm, F = 20 µm, G–J = 10 µm, K–L = 5 µm.

12. *Licea hepatica* Kowalski, Mycologia 64(2): 359 (1972)

Sporophores sporocarpic, scattered, pulvinate to hemispherical, 100–120 µm diam. tan, copper coloured or bronze. Peridium thin, fragile, transparent iridescent, dehiscence into lobes or platelets along indistinct ridges. Spores shiny golden brown in mass, light brown by TL., globose, 8–9 µm diam., minutely ornamented but often appearing smooth.

Type: DTK 10910.

Habitat: in wet seepage areas on leafy liverworts growing over decorticated logs. Most frequently associated with *Anastrophyllum michaxii*.

Distribution: Known only from type territory (Washington, USA).

Icon: Kowalski (1972: 360, Figs. 1–3).

Notes. We were unable to study the type material, which was requested, but not sent to us. However the original description of Kowalski (1972) is detailed and we base our comments on that in order to compare it with the other species.

13. *Licea lignicola* A. Kuhnt, Ber. Bayer. Bot. Ges. 91: 187 (2021) Figs. 10A–I

Sporophores sporocarpic, dispersed or grouped, sessile. Sporocarps subglobose, 0.22–0.35 mm diam., orange brown or red brown. Peridium double, outer layer yellowish olive, marked with dark lines of dehiscence, inner layer orange with granular matter included (Fig. 10D); dehiscence into 3–4 lobes, having margins with lines of concentrated warts in a band. Spores free, medium brown in mass, light brown by TL, with paler germination pore, globose, 10.5–11.5 µm diam., densely warted. By SEM the peridium is 15–20 µm thick, the inner surface of the peridium is finely granular, and the platelet margins have linear concentrations of larger finger-like outgrowths (Fig. 10G); the epispore is densely covered with pila with a well-developed caput and short baculum (see Kuhnt, 2021: fig. 57b).

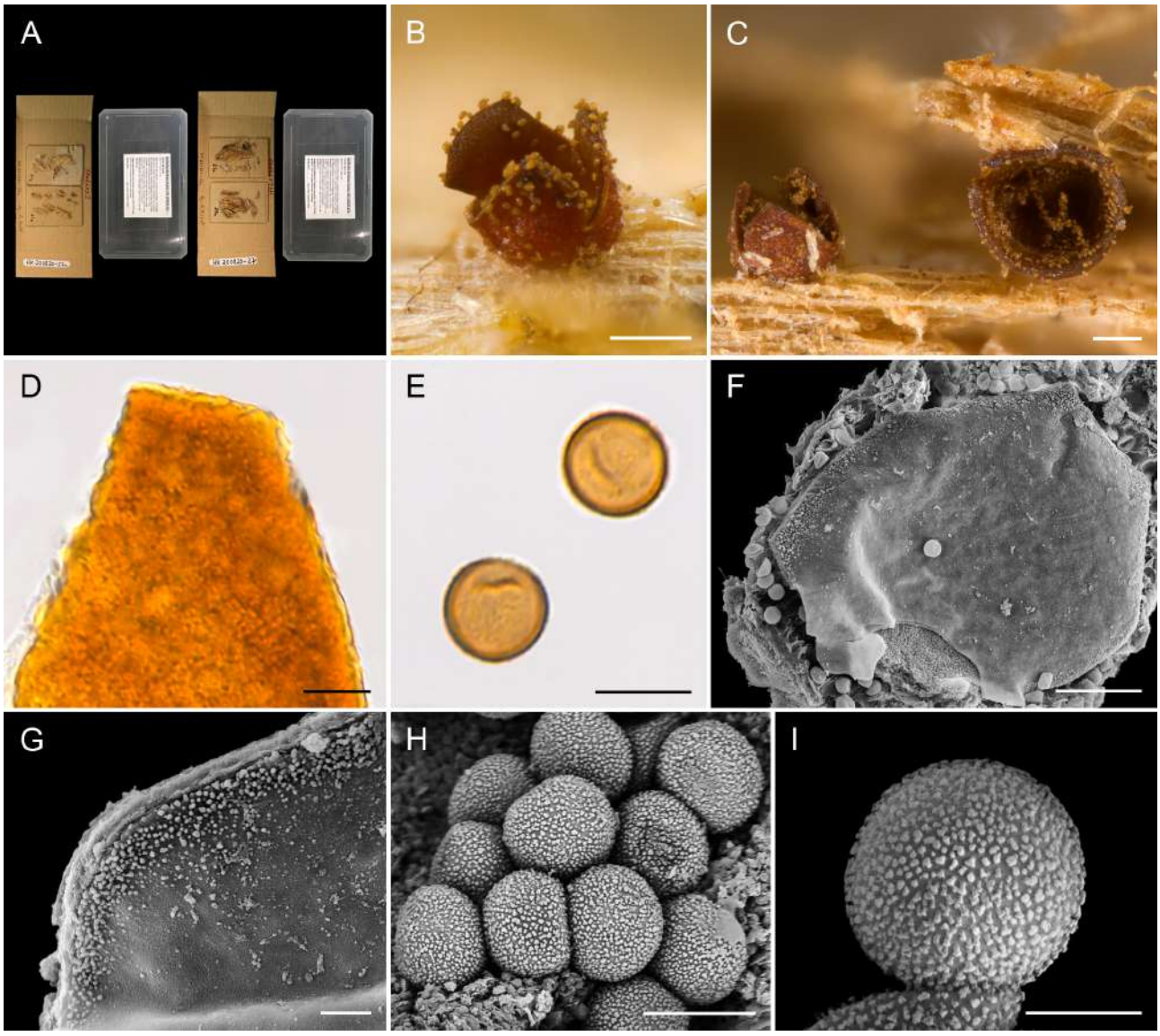

FIGURE 10. *Licea lignicola.* A–I (HK 200820-27a, M-0313080, Holotype). A. Herbarium specimen. B–C. Open sessile sporocarps. D. Peridial platelet by TL. E. Spores by TL. F. Dehisced sporocarp by SEM. G. Platelet margin by SEM showing lines of concentrated warts. H. Group of spores by SEM. I. Spore by SEM. Scale bars: B–C = 0.1 mm, D–E = 10 µm, F = 50 µm, G–H = 10 µm, I = 5 µm.

Material examined: Holotypus. GERMANY. Landkreis Oberallgäu, Gemeinde Oberstdorf, Stillachtal, Höhe 880 m, MTB 8627/23, Fichtenwald (überwiegend Fichten, wenige Laubbäume), schattiger Talgrund, an der Seitenfläche von stark vermorschtem, entrindetem Moderholzstumpf von *Picea abies*, überwiegend unter der Oberfläche im Holz, 20-08-2020, HK 200820-27a (M-0313080)!.

Habitat: On old, decayed, wood stumps of *Picea abies*, usually below the surface in the soft wood.

Distribution: Known only from type territory (Germany).

Icon.: Kuhnt (2021: 188, Figs. 53a–f; 189, Figs. 54a–c, Figs. 55a–d; 191, Figs.56a–d, 57a–b).

Notes. The orange to red-brown colour of sporocarps in this species, with dark lines of dehiscence make it easy to distinguish from others. *Licea rufocuprea* Nann.-Bremek. & Y. Yamam. has a similar, but darker, colour of the peridium in reflected light, and also differs in having a concolorous shiny circumcissile line at the base of a conical sporotheca. The illustrations in the original description are excellent.

14. *Licea mariae* Bortnikov, in Bortnikov, Gmoshinskiy & Novozhilov, Phytotaxa 541(1): 29 (2022) Figs. 11A–H

Sporophores sporocarpic, scattered or in small groups, sessile. Sporocarps subhemisphaeric to pulvinate, 0.42 × 0.3 mm diam., black. Peridium double, outer layer opaque, containing granular refuse material, ridged, marked with concolorous dehiscence lines, inner surface of inner layer smooth and glossy by TL; dehiscence along preformed lines, into 4–8 platelets, platelet margins with a clearly visible row of conical outgrowths (Figs. 11E–F arrow) that can make the edges appear dark. Spores free, brilliant yellow in mass, almost colourless by TL, thinner on one side, globose, (13–)14.5–16.5(–17.5) µm diam., smooth. By SEM the inner peridium is fibrous, roughened in a finely reticulate pattern; the platelet margins with conical outgrowths opposite each other on the junction of platelets like the teeth of a zip; the epispore is smooth.

Material examined: Holotypus. RUSSIAN FEDERATION. KPSNBR [Kedrovaya Pad State Nature Biosphere Reserve, Far East, Russia], 43°06’45.0’’N 131°26’48.9’’E, coniferous forest, on the bark of living *Abies holophylla*, in mcc, pH=5.31, bark sampling 13 August 2017, mcc starting 09 February 2018, sporocarps sampling 27 April 2018, leg. F.M. Bortnikov, MYX 11149!.

Habitat: on bark of living trees (*Quercus mongolica, Abies holophylla*) and rotten wood (in oak forest).

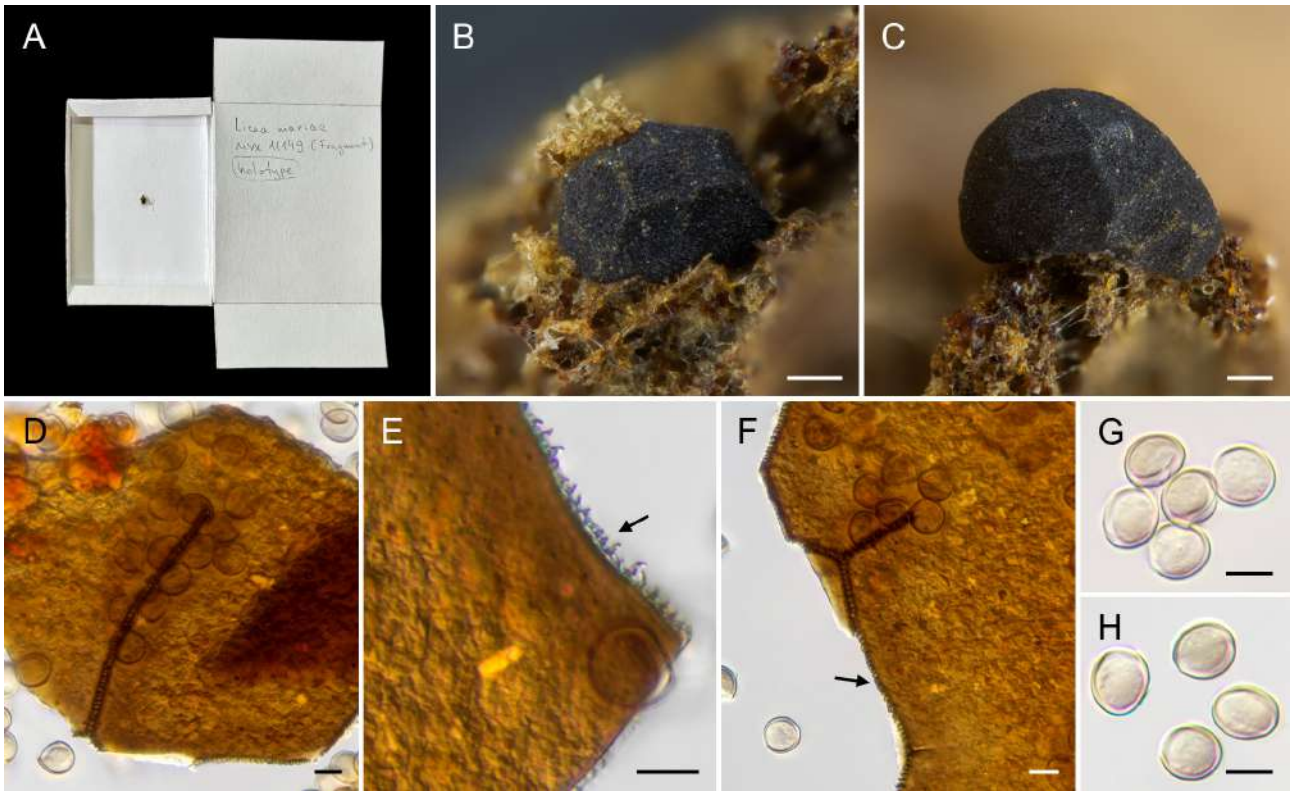

FIGURE 11. *Licea mariae.* A–H (MYX 11149, Holotype). A. Herbarium fragment. B–C. Sessile sporocarps. D. Peridial platelets by TL. E–F. Peridial platelets with row of conical outgrowths (arrows). G–H. Spores by TL. Scale bars: B–C = 0.1 mm, D–H = 10 µm.

Distribution: Known only from type territory (Russia).

Icon.: Bortnikov *et al.* (2022: 30, Figs. 8a–k).

Notes. This species is somewhat similar to *L. chelonoides* Nann.-Bremek., but has smooth spores not covered with flattened warts as in the latter. In addition, the platelet margins are black in *L. mariae*, not concolorous with the rest of the platelet as in *L. chelonoides,* and the spores in mass are bright yellow, not dark brown. The material we received for the study was a fragment of the holotype and we repeated light micrographs of it (Figs. 11B–H) to compare the colours with the other species, using the same instruments. However, in the case of SEM, the clear micrographs in the original paper obviated the need for repetition.

15. *Licea minima* Fr., Syst. mycol. 3(1): 199 (1829) Figs. 12A–K

Neotypus (designated here, see below)

Sporophores sporocarpic, scattered or in small groups, sessile. Sporocarps subglobose, 0.2–0.5 mm, to subhemisphaeric or elongated, 2–3 mm long blackish brown. Peridium double, outer layer cartilaginous, dark brown, opaque, inner layer membranous with an inner surface ornamented with warts; dehiscence into platelets following the shiny raised lines of dehiscence, down to the base of the sporocarps, platelet margins ornamented with large outgrowths clearly visible by TL. Spores free, red brown in mass, olivaceous to lilac brown by TL, thick walled, thinner and paler on one side, globose, 10–13 µm diam., warted. By SEM the inner peridium is granular, sometimes fusing in an irregular reticulum of granules the platelet margins ornamented in a range of outgrowths from simple rounded warts to finger-like warts 1–2 µm long; the epispore is pilate.

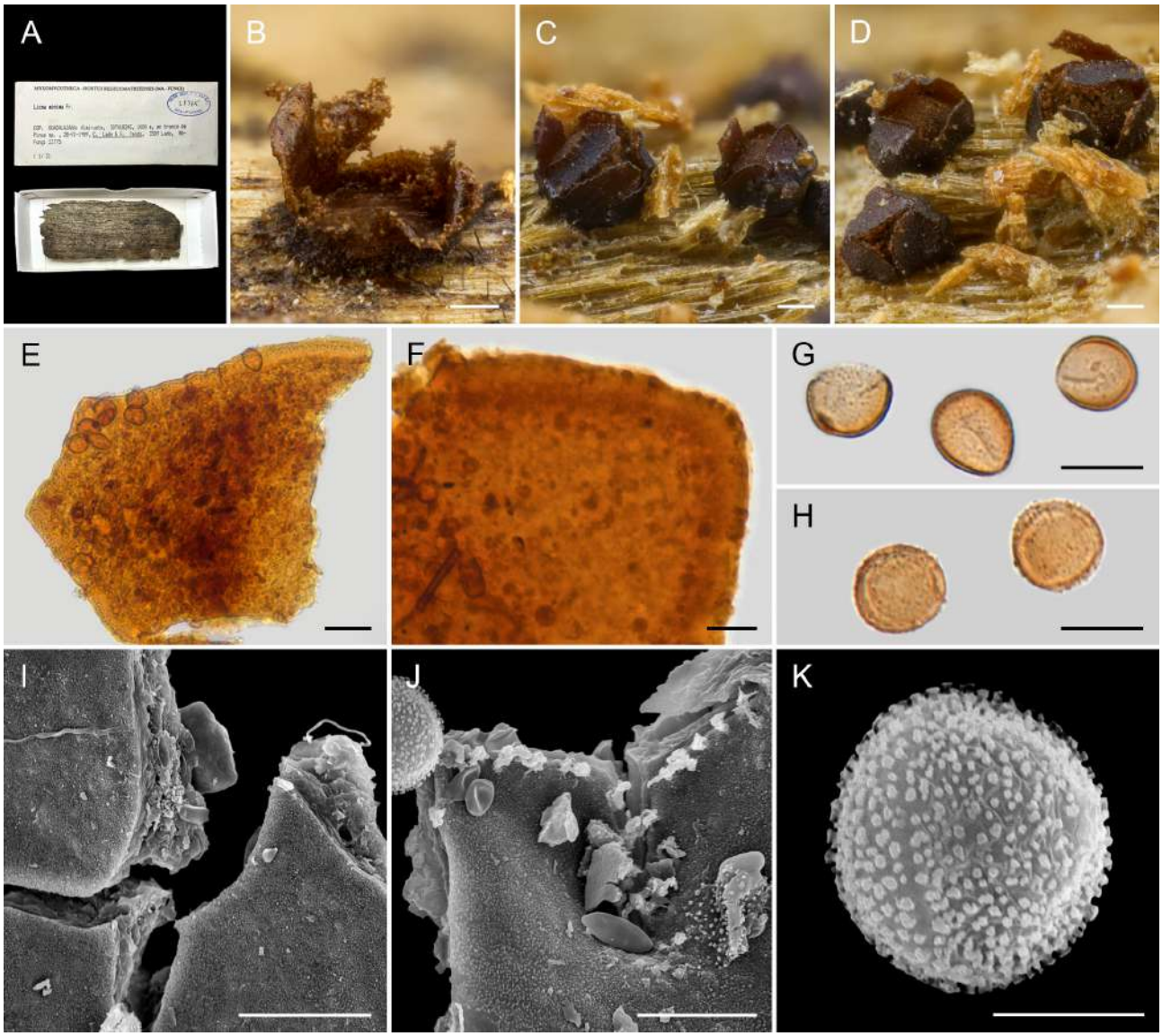

FIGURE 12. *Licea mínima.* A–B, E. G, I–K (MA-Fungi 23775, Neotype); C–D, F, H (MA-Fungi 17214). A. Herbarium box. B–D. Sessile sporocarps. E–F. Peridial platelets by TL. G–H. Spores by TL. I–J. Detail of inner peridium surface and platelet edges by SEM. K. Spore by SEM. Scale bars: B–D = 0.1 mm, E, I = 20 µm, F–H, J = 10 µm, K = 5 µm.

Material examined: Neotype (designated here). SPAIN: Guadalajara, Almiruete, 30TVL8243, 1000 m, en tronco de *Pinus* sp., 28-VI-1989, leg. *C. Lado & F. Pando*, 3589 Lado, MA-Fungi 23775!. Mycobank: MBT 10016507. SPAIN. Navarra, Articutza, 30TWN9788, 660 m, en madera descompuesta de *Abies excelsa*, 12-XI-1983, leg. *R. Galán*, 1548 Lado, MA-Fungi 17214.

Habitat: on bark of living and dead trees, on decaying trunks and stumps of angiosperms and gymnosperms, on old polypore.

Distribution: Largely distributed *(*Norway, Sweden, Finland, Estonia, Lithuania, Denmark, Netherlands, Belgium, Luxembourg, Germany, Poland, Belarus, Russian Federation, Ukraine, United Kingdom, Ireland, France, Andorra, Spain, Portugal, Switzerland, Austria, Greece, Turkey, Israel, Chine, India, Nepal, Vietnam, Seychelles Islands, Japan, Morocco, Madagascar, Canada, USA, Mexico, Guatemala, Costa Rica, Panama, Colombia, Brazil, Argentina, Uruguay, Chile, Australia, Papua New Guinea, New Zealand.

Icon.: Lister (1925: pl. 148d–f), Nannenga-Bremekamp (1965: 136: Figs. 4A–B; 1975: 63, 1991: 42), Martin & Alexopoulos (1969: 480, Pl. I: 8a–c), Gilert (1996: 521, Figs. 17–25; 522, Figs. 26–29), Neubert *et al.* (1993: 151, 283, Fig. VI: 2), Lado & Pando (1997: 120, Figs. 31a–b), Yamamoto (1998: 132, Figs. A–B; 2021: 145, Figs. A–C), Novozhilov *et al.* (1999: 85, Figs. 4A–D), Härkönen & Sivonen (2011: 54, Figs. 67–69), Poulain *et al.* (2011: 68), Härkönen & Varis (2012: 148, Figs. 218–220), Ronikier *et al.* (2017: 250, Figs. 2A–E), Lloyd (2020: 26).

Notes. *Licea minima* was described almost 200 years ago by Fries (1829). In the original description no precise collection was given as the type, as was the custom then. We tried to find original Fries material at the UPS herbarium, where his collection is preserved, but the curator said there was no original material kept there (Asa Kruys pers. comm.) and commented that Fries wrote v.v. (vidi vivam) meaning that material was not collected or preserved. Since no original material, neither specimens nor illustrations, exists, we have selected a typical specimen of *Licea minima* from MA-Fungi and neotypify it here.

The SEM image of the spore (Fig. 12J) shows the ornamentation on the epispore as T-shaped pila. A similar observation was made by Gilert (1996) who commented on T shaped rods by TEM.

This species is similar to *L. pusilla* Schrad. from which it differs by its reddish-brown spores and peridium, and its smaller spores. *Licea mariae* Bortnikov also has larger spores, than *L. minima* and they are smooth and almost colourless (Fig. 11H).

16. *Licea morchelloides* T.N. Lakh., Nann.-Bremek. & R.K. Chopra, Proc. Kon. Ned. Akad. Wetensch., C. 93(3): 258 (1990) Figs. 13A–D

Sporophores sporocarpic, subglobose, angular with a net of ridges, 90–170 µm diam. × 90–210 µm height, nearly black, shiny. Peridium triple, outer layer hyaline, membranous, middle layer gelatinous with granular matter, inner layer membranous, brown, papillose to the margins; dehiscence into irregular, angular lobes and platelets. Spores free, globose, nearly black in mass, very dark brown by TL (Figs. 13B–D), paler one side (12–)13–14 µm diam., smooth.

Material examined: Isotypus. INDIA. Himachal Pradesh, Shimla, Summer Hill, 27-VI-1981, in a moist chamber on bark from a living *Quercus incana*, 6 m above the ground, leg. *R.K. Chopra & T.N. Lakhanpal,* 310 CRK/TNL, NENB 13887 (BR5020071552630)! (only a slide).

Habitat: on bark of living *Quercus incana*, 0-9 m above the ground.

Distribution: Known only from type territory (India).

Icon: Lakhanpal *et al.* (1990: 258, Figs. 5A–C).

Notes. We were only able to study a slide of the type material. However the original description (Lakhanpal *et al.* 1990) and that provided by Nannenga-Bremekamp (2022) are detailed and we base our comments on our observations of the slide and the thorough description by the authors of the species.

17. *Licea nannengae* Pando & Lado, Mycotaxon 31(2): 299 (1988) Figs. 14A–I

Sporophores sporocarpic, scattered to gregarious, sessile. Sporocarps subglosose, 0.05–0.2 mm diam., ridged, dark brown to yellow ochraceous. Peridium double, outer layer gelatinous, covered with refuse material, inner translucent and iridescent very thin, pale olive, smooth; dehiscence along ridges into platelets and lobes leaving a shiny base. Spores free, dark brown in mass, olivaceous brown by TL (Fig. 14F), with a pale area, wall thick with thinner area, globose, 9.5–13.5 µm diam., smooth. By SEM the inner peridium surface is densely warted, with some warts joined in a loose reticulum, right up to the platelet margins (Figs. 14G–H), with no prominent outgrowths; the epispore is smooth with a thinner area appearing wrinkled (Fig. 14 I).

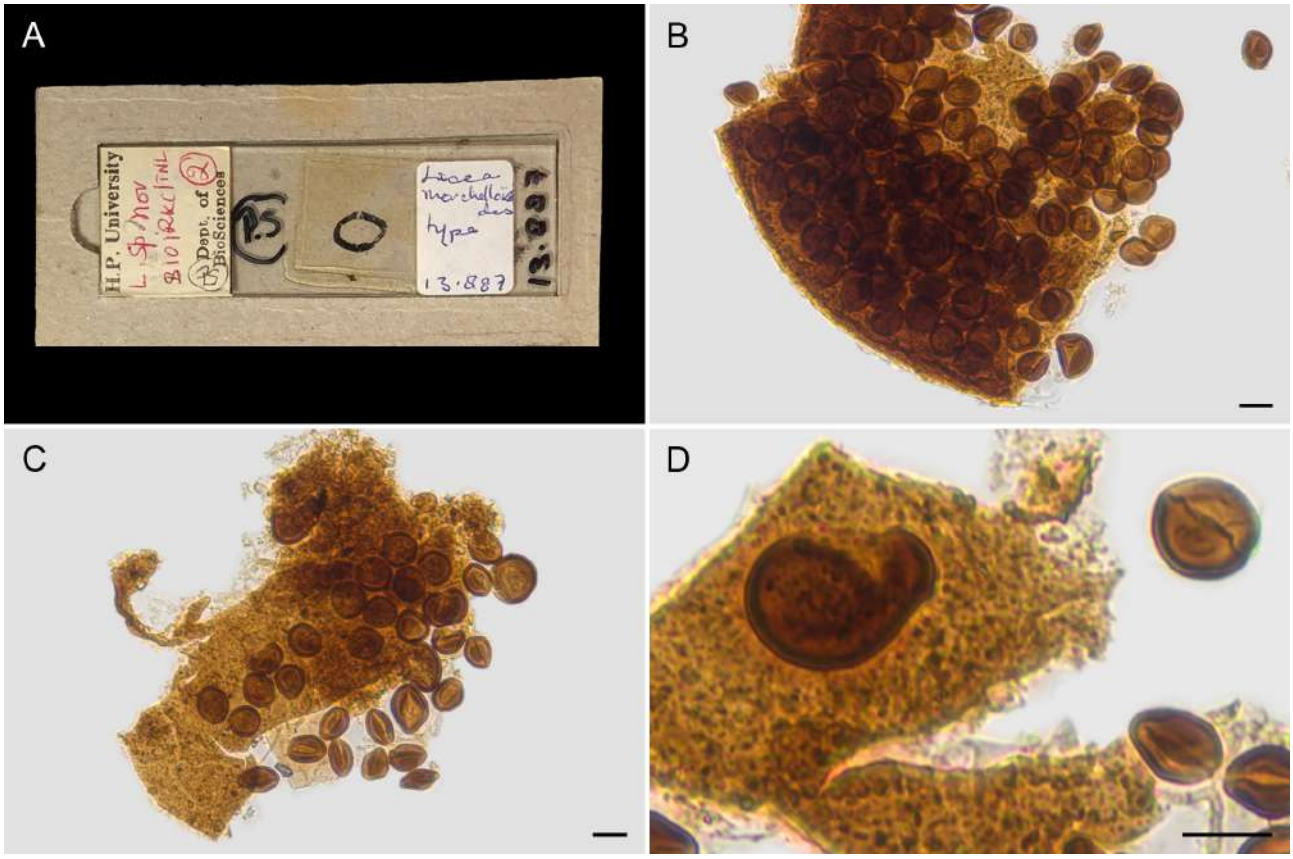

FIGURE 13. *Licea morchelloides.* A–D (NENB 13887, BR5020071552630, Isotype). A. Slide. B–D. platelets and spores by TL. Scale bars: B–D = 10 µm.

Material examined: Holotypus. SPAIN. Soria, Cubillos, 30TWM0421, 1080 m, corteza de *Juniperus thurifera* cultivado en cámara húmeda, 26-III-1986, 246 Pando (MA-Fungi 16056)!.

Habitat: bark of living trees.

Distribution: Norway (?), Lithuania, Russian Federation, Ireland, Germany, Spain, Kazakhstan, Mexico, Cuba, Argentina.

Icon.: Pando & Lado (1988: 300, Fig. 1), Lado & Pando (1997: 122, Figs. 32a–b), Johannesen & Vetlesen (2020: 77, Figs. 39A–C as *Licea* cf. *nannengae*), Nannenga-Bremekamp (2022: 533, Fig. 17).

Notes. This species was described as having a smooth inner surface of the inner peridium by TL. However, by SEM, which was not available at the time of the description, the inner peridium looks densely warted (Fig. 14H). In the collection of the holotype, that is marked with arrows (14A), we have found sporocarps of a different species mixed in with *L. nannengae* Pando & Lado, with an almost smooth peridium and spiny spores. This may have lead to misidentification, such as reports from Colorado (Novozhilov *et al.* 2003) and Madagascar (Wrigley de Basanta *et al.* 2013) with a SEM image showing ornamented spores, and could affect distribution data. *Licea nannengae* resembles *L. belmontiana* Nann.-Bremek., however that species has darker brown sporocarps, not yellowish brown (compare Fig. 4C with Fig. 14B taken with the same optical instruments). The spores of *L. belmontiana* are lighter brown and not olivaceous and the inner peridial markings, as seen by SEM, are different in each species. In addition, the spores of *L. belmontiana* are ornamented, as seen by SEM, whereas those of *L. nannengae* are entirely smooth. *L. denudescens* H.W. Keller & T.E. Brooks differs from *L. nannengae* by darker, larger sporocarps (0.2–0.4 mm diam. vs. 0.05–0.2 mm diam.), sporocarps lacking ridges, and by darker spores.

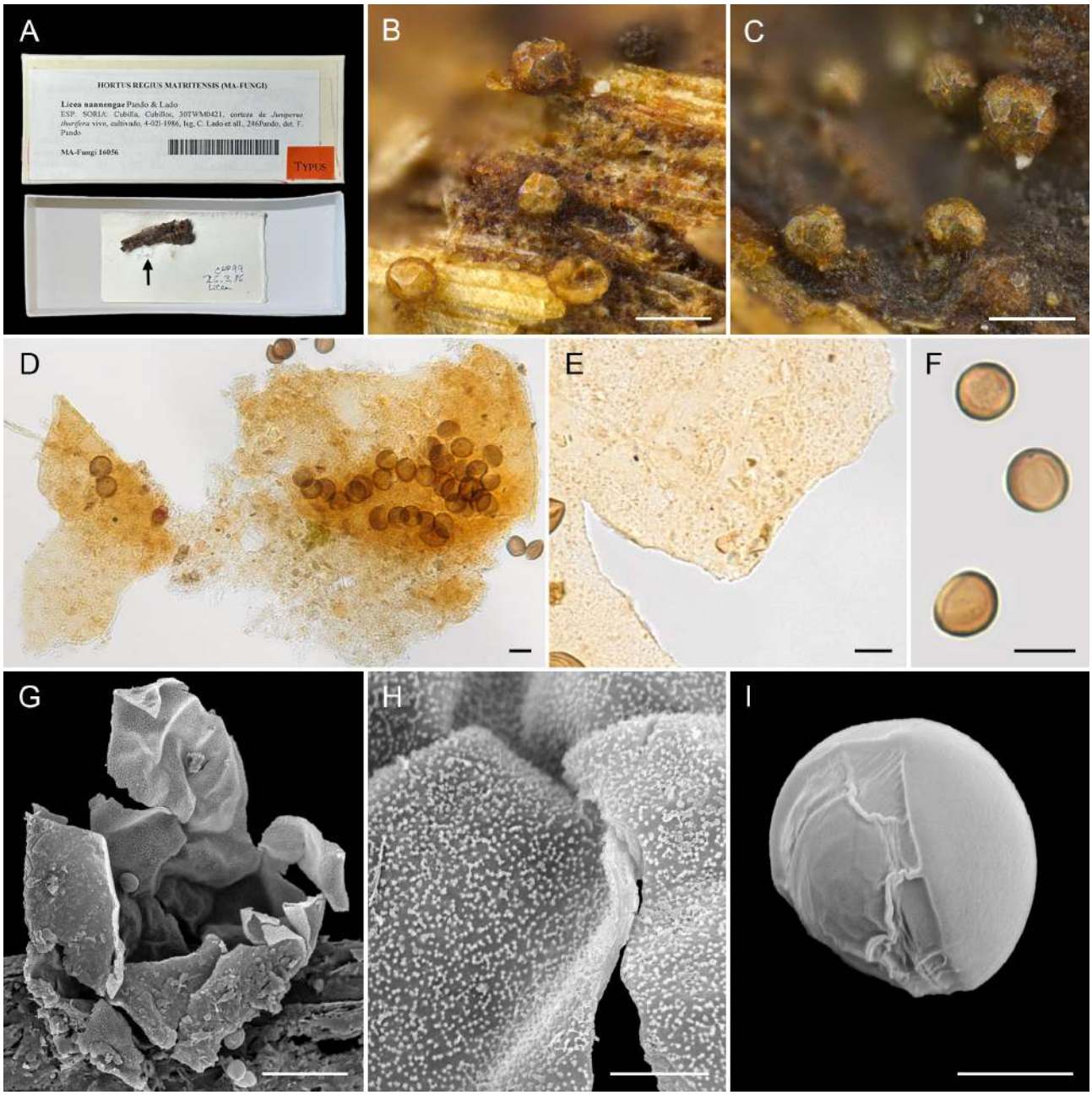

FIGURE 14. *Licea nannengae.* A–I (246 Pando, MA-Fungi 16056, Holotype). A. Herbarium box with holotype indicated with arrow. B–C. Sessile sporocarps. D–E. Peridial platelets by TL. F. spore by TL. G. Dehisced sporocarp by SEM. H. Detail of inner peridium surface at platelet edges by SEM. I. Spore by SEM. Scale bars: B–C = 0.1 mm, D–F, H = 10 µm, G = 50 µm, I = 5 µm.

18. ***Licea nigromarginata*** Nann.-Bremek., T.N. Lakh. & R.K. Chopra, in Lakhanpal, Nannenga-Bremekamp & Chopra, Proc. Kon. Ned. Akad. Wetensch., C. 93(3): 259 (1990) Figs. 15A–D

Sporophores sporocarpic, scattered, sessile. Sporocarps pulvinate, angular 0.3–0.6 mm diam. see from above, dull black. with a net of paler ridges. Peridium double, outer layer thick, gelatinous and pale, inner layer thick, membranous, smooth, brown; dehiscence into 5–12 platelets along preformed lines with dark perpendicular outgrowths (like sutures in Nannenga-Bremekamp´s drawing) in a darker zone at the margins (Figs. 15B–C). Spores free, pale brown in mass, pale ochraceous yellow by TL, thick walled with thin pale area, globose or subglobose, 13–15(–16) µm diam., smooth. Protoplasmodium greyish white, turning brown and very dark brown.

Material examined: Isotypus. INDIA. Himachal Pradesh, Shimla, Summer Hill, 6-VIII-1981, in a moist chamber on bark (6-9 m up the trunk) from living *Pinus wallichiana*, leg. *R.K. Chopra & T.N. Lakhanpal*, 2237 RKC/LTN (HPUB 13,237), NENB 13886 (BR5020071551626)! (only a slide).

Habitat: on bark (6–9 m up the trunk) from living *Pinus wallichiana*.

Distribution: Known only from type territory (India).

Icon: Lakhanpal *et al.* (1990: 259, Figs. 6A–C).

Notes. The holotype of this species is kept in HPUB under the number 13237, but although requested it was not sent to us. However, the slide of the isotype was found in the collection of Nannenga-Bremekamp in Meise (Fig. 15A), and we have used that for the images and description along with the detailed descriptions in Lakhanpal *et al.* (1990), and Nannenga-Bremekamp (2022).

The slide we examined is labelled "*L. morchelloides"* by hand, but on investigating the collection number and other details in the author's notes we can confirm that this is a slide of the isotype of *L. nigromarginata*.

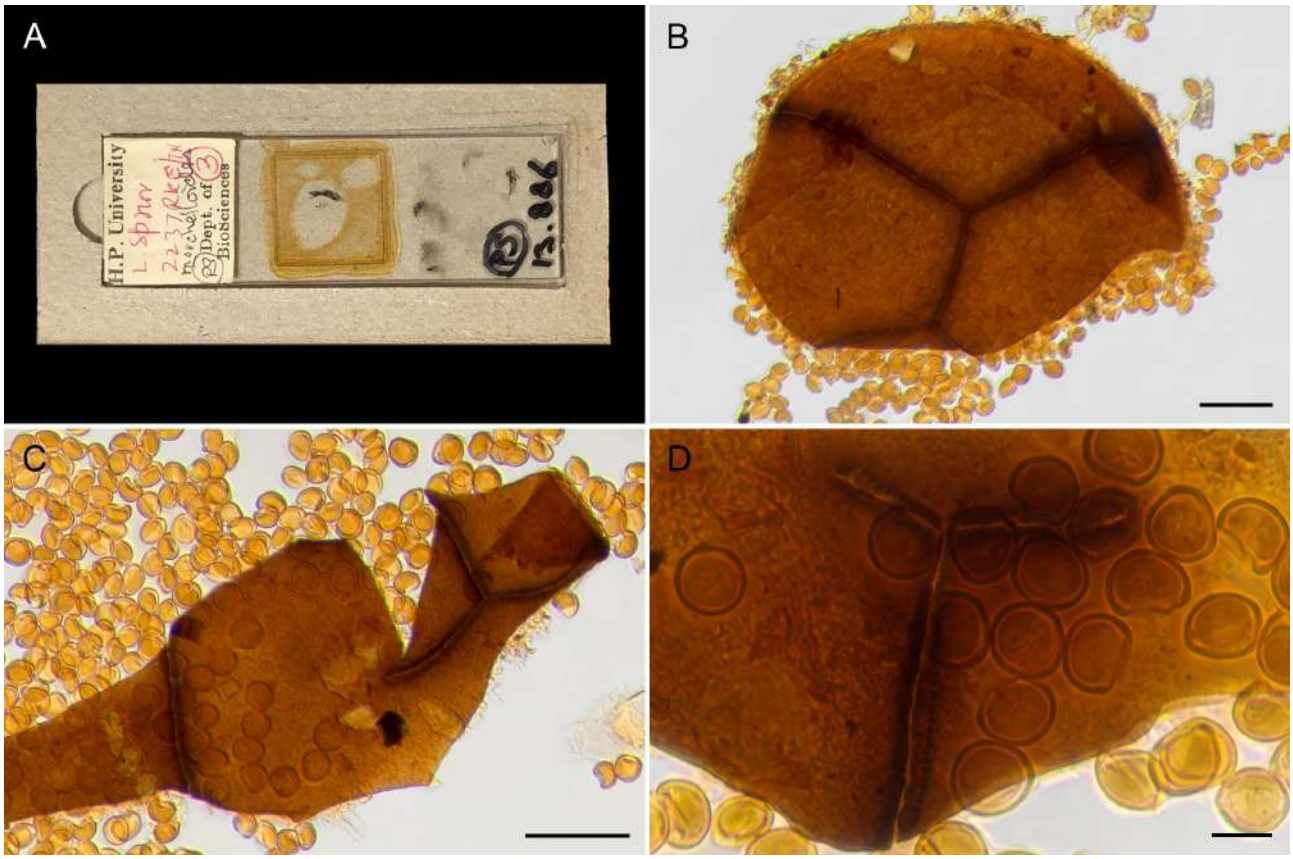

FIGURE 15. *Licea nigromarginata.* A–D (NENB 13886, BR5020071551626, Isotype). A. Isotype slide. B–D. Spores and peridial platelets by TL. Scale bars: B–C = 50 µm, D = 10 µm.

19. *Licea pusilla* Schrad., Nov. gen. pl. 19 (1797) Figs. 16A–P

Sporophores sporocarpic, gregarious, sessile. Sporocarp globose-pulvinate, 0.2–1.5 mm diam., ridged, purplish brown to blackish. Peridium double, outer layer gelatinous, dull, inner layer thin, translucent, shiny, the inner surface smooth; dehiscence into few lobes leaving a cup continuous at the base. Spores free, black to dark olive in mass, light olive brown by TL, with a paler area, globose, 15–17(–20) µm diam., densely warted. By SEM the inner peridium surface is densely and evenly warted (Figs. 16M–O), right up to the platelet margins, with prominent outgrowths (Fig. 16O) mostly in a single row, but several deep in places; the epispore is densely covered with bacula (Figs. 16N, P).

Material examined: Lectotype (designated here). Illustration of the Tab. 6, f.4 of the Schrader, Nova genera plantarum 19 (1797)!. Mycobank: MBT 10016510.

Epitype (designated here). SPAIN. Madrid, Puerto de Canencia, km 9,700, 30TVL3425, tronco de *Pinus sylvestris*, 26-VII-1980, leg. *C. Lado*, 331 Lado, MA-Fungi 20548!. Rev. NENB 13127 (BR5020065643719, Isoepitype). Mycobank: MBT 10016508.

Habitat: on bark of living and dead trees, trunks and stumps of angiosperms and gymnosperms.

Distribution: Norway, Sweden, Finland, Estonia, Lithuania, Russian Federation, Denmark, Netherlands, Belgium, Germany, Poland, United Kingdom, France, Spain, Switzerland, Austria, Ukraine, Turkey, Kazakhstan, India, Japan,

Congo Democratic Republic, Canada, USA, Mexico, Guatemala, El Salvador, Costa Rica, Panama, Jamaica, Colombia, Australia, New Caledonia, New Zealand.

Icon.: Schrader (1797: pl. VI: 4), Lister (1925: Pl. 149a–c), Nannenga-Bremekamp (1965: 139, Figs. 6A–B; 140, Fig. 7A; 1975: 65; 1991: 44), Martin & Alexopoulos (1969: 481, Figs. 12a–d), Neubert *et al.* (1993: 283, Fig. VI: 6), Mazelaitis (1995: 19, Figs. C1–2), Eliasson & Gilert (1982: 253, Figs. 4A–F), Gilert (1996: 517, Figs. 3–4; 519, Figs. 9–10; 520, Figs. 13, 15–16), Lado & Pando (1997: 129: Figs. 36a–b), Yamamoto (1998: 133, Figs. A–B; 2002c: 22, Figs. 3A–C; 2021: 147, Figs. A–C), Härkönen & Sivonen (2011: 56, Fig. 72), Poulain *et al.* (2011: 69), Härkönen & Varis (2012: 150, Fig. 223), Ronikier *et al.* (2017: 253, Figs. 4A–F), Bortnikov *et al.* (2022: 37, Figs. 14a–k).

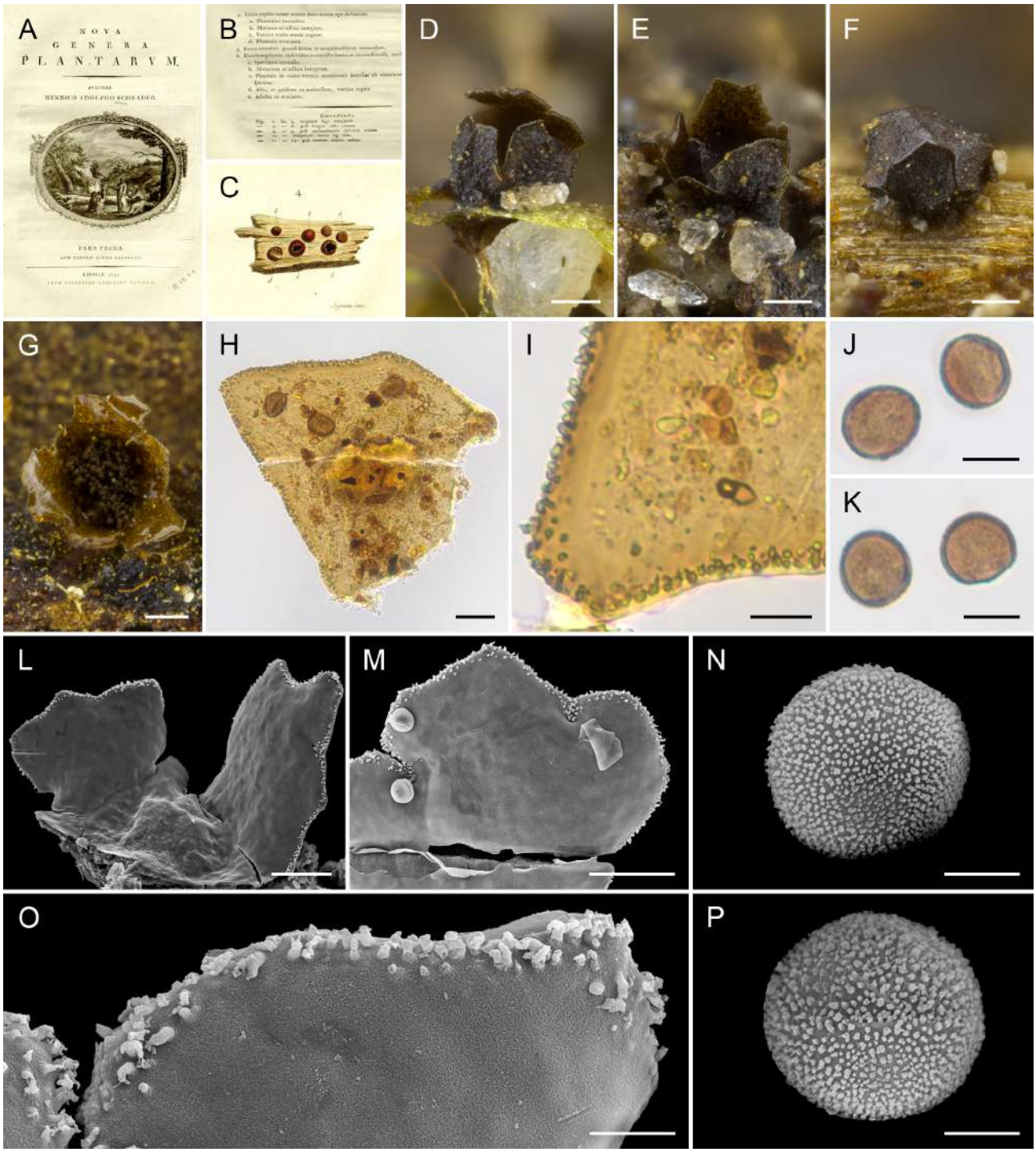

FIGURE 16. *Licea pusilla.* A–C. Original illustration of the Lectotype. D–P (MA-Fungi 20548, Epitype). D–G. Dehiscing sessile sporocarps. H–I peridial platelet showing ornamented margins by TL. J–K. Spores by TL. L. dehisced sporocarp by SEM. M. Peridial platelet by SEM. O. Detail of peridial ornamentation by SEM. N, P. Spores by SEM. Scale bars: D–G = 0.1 mm, H = 20 µm, I–K, O = 10 µm, L–M = 50 µm, N, P = 5 µm.

Notes. No type collection was mentioned in the original description. The illustration by Schrader (1797, Tab. 6, f.4) reproduced here Fig. 16A is the primary type of *L. pusilla,* and is selected as the lectotype. In addition, as no specimen exists, an epitype has been selected to facilitate future study and comparisons. We selected material from MA-Fungi and used it for the other images by TL and by SEM. On p. VIII of the book preface, Schrader states that the material sketched and described originated "in the lands near Goettinga, especially in Hercynia and some forests of the Duchy of Brunswick, well known by the names of Hils and Sollingerwald". *Licea pusilla* is a common species and is the type of the genus *Licea*.

In the SEM micrographs of the epitype, the inner surface of the peridial platelets are densely but evenly warted, not smooth as they have been described by other authors (Nannenga-Bremekamp 2022).

Ing (1982) raised Meylan's var. *pygmaea* Meyl. to the specific rank [see below *L. pygmaea* (Meyl.) Ing], but some authors still consider the differences between *L. pusilla* and *L. pygmaea* are insufficient to consider them as different species. Bortnikov *et al.* (2022) provided a detailed comparison of specimens collected by them of what they considered to be both *L. pusilla* and *L. pygmaea* and concluded that there is an overlap in the characters but stated the need for further study. We maintain these two taxa as separate species, pending further investigation, since the size and colour of the spores, as well as markings of the surface and margins of the inner peridium differ between specimens included in this study.

20. *Licea pygmaea* (Meyl.) Ing, Trans. Brit. Mycol. Soc. 78(3): 443 (1982) Figs. 17A–L

≡ *Licea pusilla* var. *pygmaea* Meyl., Bull. Soc. Vaud. Sci. Nat. 58: 89 (1933)

Sporophores sporocarpic, scattered to gregarious, sessile. Sporocarps subglobose to pulvinate, angular, 0.05–0.1 mm diam., brown. Peridium double, outer layer horny, inner layer membranous; dehiscence into platelets along shiny ridges, platelet margins with prominent outgrowths. Spores free, dark olive to dull dark brown in mass, greenish yellow by TL, globose, 12–13 µm diam., minutely evenly warted. By SEM the inner peridium inner surface is warted with different sized warts and some bare patches (Figs. 17I–J); the platelet margins have different sized outgrowths mostly in a single row but sometimes overlapping, fused and sausage-shaped (Figs. 17I–J); the epispore is covered with flattened bacula evenly dispersed, sometimes two or more fused (Figs. 17K–L).

Material examined: Lectotypus. SWITZERLAND. Vaud, nr. Ste Croix, La Gittaz, 1250 m, OCT 1930. Myxo 055 (LAU)!. (Designated by Kowlaski, Mycologia 67: 448-494. 1975).

Habitat: on bark of living and dead trees, trunks, stumps and debris of angiosperms and gymnosperms.

Distribution: Norway, Sweden, Lithuania, Russian Federation, Denmark, Netherlands, Belgium, Germany, Poland, Ireland, United Kingdom, France, Spain, Switzerland, Austria, India, Vietnam, Japan, Congo Democratic Republic, USA, Canada, Mexico, Brazil, Argentina, Paraguay, Australia, New Zealand.

Icon.: Nannenga-Bremekamp (1965: 140, Figs. 7B–C, as *L. pusilla* var. *pygmaea;* 1975: 66, as *L. pusilla* var. *pygmaea*; 1991: 45, as *L. pusilla* var. *pygmaea*), Gilert (1996: 517, Figs. 1–2, 5–6; 518, Figs. 7–8, 11–12; 520, Figs. 11–12, 14, all the images as *L. pusilla*), Lado & Pando (1997: 130, Figs. 37a–b), Yamamoto (2002a: 3. Figs. 1A–D; 2004: 23, Figs. 3A–C; 2006: 35, Figs. 15A–D; 2021: 148, Figs. A–D), Poulain *et al.* (2011: 70), Ronikier *et al.* (2017: 253, Figs. 4G–K), López-Villalba & Moreno (2020: 149, Figs. 3a–d), Johannesen & Vetlesen (2020: 79, Figs 40A), Bortnikov *et al.* (2022: 39, Figs. 15a–k).

Notes. This species was published by Meylan (1933), as a variety of *L. pusilla* Schrad. However based on the number of differences between these taxa, such as spore size, spore ornamentation and the peridium, Ing (1982) raised the variety to specific rank (see above). The minute size of sporocarps and the fact that it has been often included as a variety in the species *L. pusilla* makes the distribution of *L. pygmaea* unclear. As stated above, we agree with Ing (1982) and consider *L. pusilla* and *L. pygmaea* to be separate species based on the differences found by SEM in the ornamentation of the peridium and platelet edges, as well as spore colour and size.

21. *Licea rufocuprea* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C. 90(3): 325 (1987) Figs. 18A–K

Sporophores sporocarpic, scattered, sessile. Sporocarps subglososse to conical, up to 0.1 mm diam., red-coppery brown with a shiny circumcissile line near the base. Peridium double, the outer layer gelatinous, inner layer smooth with a minutely warted marginal area; dehiscence into irregularly sized lobes or platelets with a row of larger warts on the margins. Spores free, dark brown in mass, rosy brown by TL, globose, 9–11 µm diam., palely roughened. By SEM the inner peridium is minutely warted all over, with larger warts at the platelet margins; the epispore is densely covered with flat verrucae.

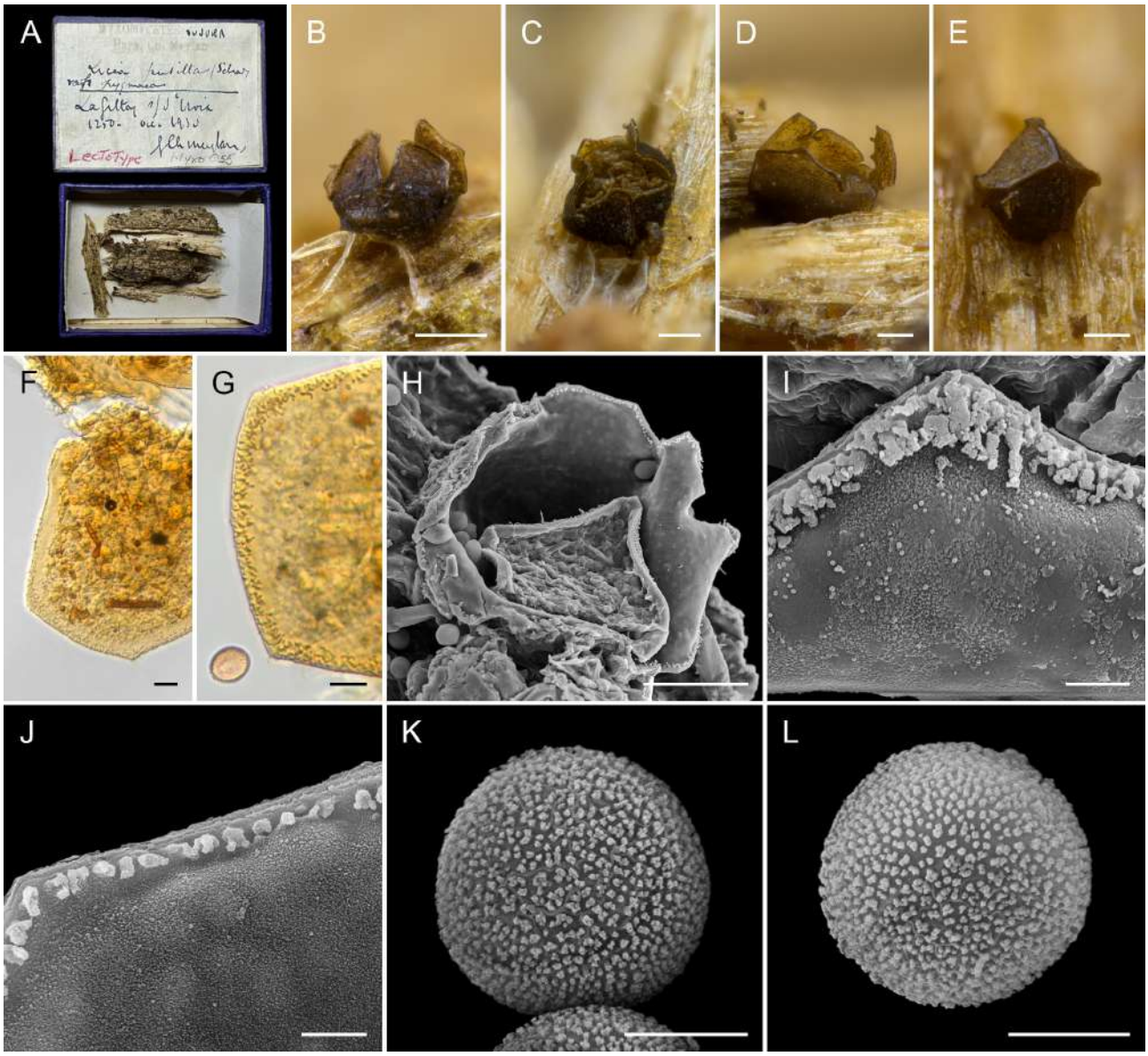

FIGURE 17. *Licea pygmaea.* A–L (Myxo 055, LAU, Lectotype). A. Herbarium box. B–E. Sessile sporocarps. F–G. Peridial platelets and spore by TL. H. Whole open sporocarp by SEM. I–J. Peridial platelet margins by SEM. K–L. Spores by SEM. Scale bars: B = 0.1 mm, C–E, H = 50 µm, F–G = 10 µm, I–L = 5 µm.

Material examined: Isotypus. JAPAN. Kochi Pref., Kitagowa-mura, Notomo, on bark from living *Chamaecyparis obtusa* in moist chamber culture, 22-XII-1984, NENB 14668 (BR5020067531199)!. MADAGASCAR. Fianarantsoa (Haute Matsiatra), Ambalavao, Andringitra NP, edge of the park, northern fringe of the Andringitra ridge, 22°07′36″S 46°53′35″E, 1622 m, on *Eucalyptus* sp. bark, in moist chamber culture, 3-V-2010, dwb 3291.

Habitat: on the bark of living and dead trees

Distribution: Japan, Singapore (?), La Réunion (?), Madagascar, USA, Puerto Rico, Brazil, Paraguay, Australia.

Icon.: Nannenga-Bremekamp & Y. Yamamoto (1987: 325, Figs. 10A–D), Yamamoto (1998: 134, Figs. A–B; 2021: 149, Figs. A–B), Wrigley de Basanta *et al.* (2013: 68, Figs. 31–36), Lima & Cavalcanti (2017: 284, Fig. 4E).

Notes. The species is easily recognisable by its coppery, conical sporocarps with a basal circumcissile ring. The whole peridium sometimes dehisces along this ring (Wrigley de Basanta *et al.* 2013, Figs. 26–32), but then it breaks up into irregular smaller platelets (Fig. 18H). For this reason Nannenga-Bremekamp & Yamamoto (1987) assigned the species to the subgenus *Licea*. Although apparently quite rare, the species has a wide distribution, since it is known from Japan (Nannenga-Bremekamp & Yamamoto 1987), Madagascar (Wrigley de Basanta *et al.* 2013), USA, Puerto Rico and Australia (GBIF), and Paraguay (as *Licea* sp., see McHugh 2009). There are also unconfirmed reports from La Réunion (Adamonyte *et al.* 2011) and Singapore (Rosing *et al.* 2011).

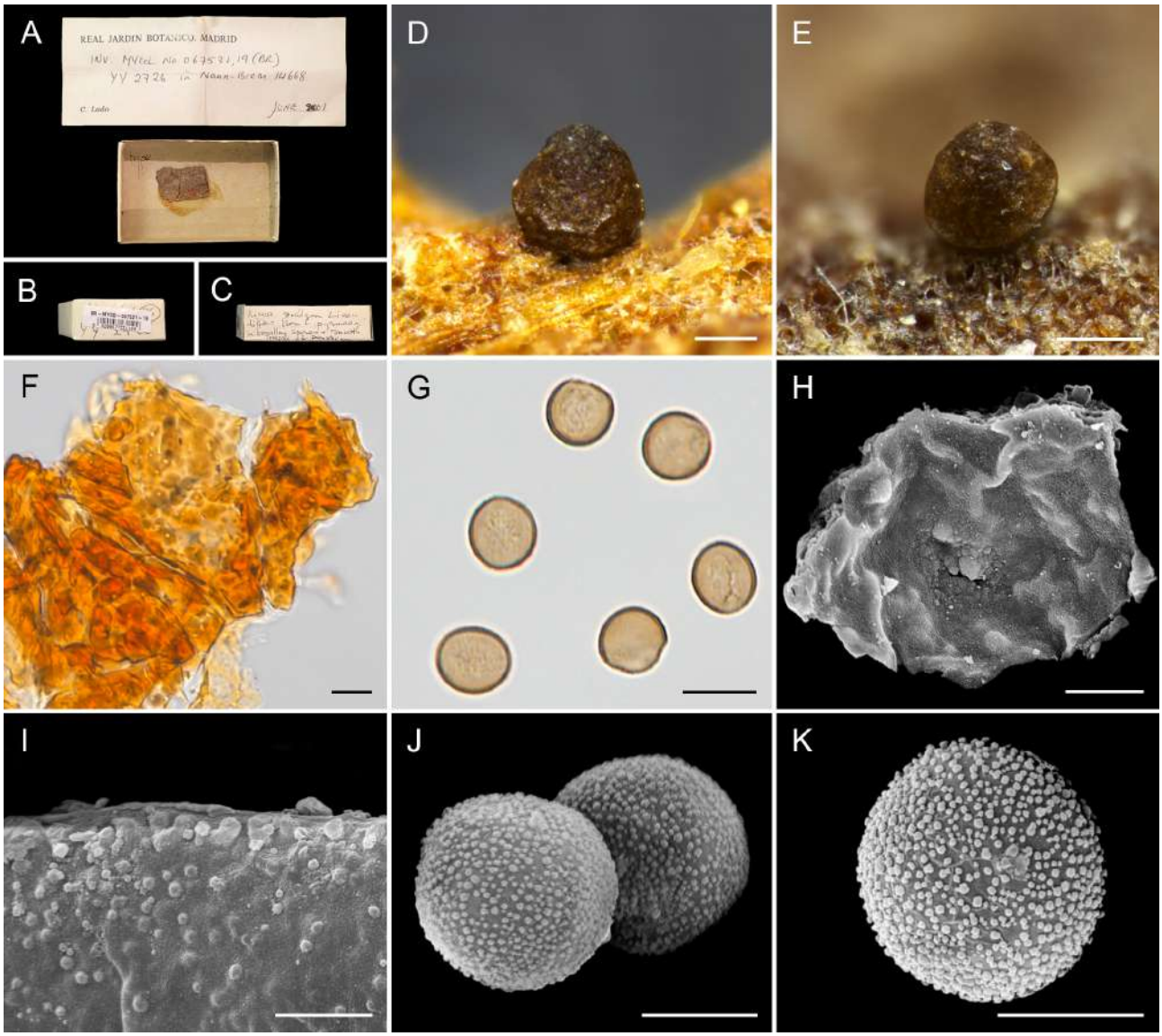

FIGURE 18. *Licea rufocuprea.* A–H, J (NENB 14668, BR5020067531199, Isotype); I, K. (dwb 3291). A–C. Herbarium box and labels. D–E. Sessile sporocarps. F. Peridial platelet by TL. G. Spores by TL. H. Peridial platelet by SEM. I. Detail of platelet margin by SEM. J–K. Spores by SEM. Scale bars: B–C = 0.1 mm, D–F, H = 10 µm, G = 50 µm, I = 5 µm.

22. *Licea synchrysospora* Bortnikov, in Bortnikov, Gmoshinskiy & Novozhilov, Phytotaxa 541(1): 29 (2022) Figs. 19A–G

Sporophores sporocarpic, scattered, sessile. Sporocarps pulvinate, slightly oval from above, 0.18–0.42 mm diam. black. Peridium brownish orange with granular deposits and black lines of dehiscence by TL (Figs. 19D–E arrows); dehiscence along preformed dark lines. Spores adhering in clusters of 5–15 spores, brilliant yellow to yellow brown in mass, greyish olive to almost colourless by TL (Figs. 18F–G), globose, (9.8–)10.2–11.2(–11.7) µm diam., smooth. By SEM the inner peridium is finely evenly warted; the platelet margins are smooth with small warts thickening along the edge (Bortnikov *et al.* 2022: Fig. 18h); the epispore densely ornamented with flattened verrucae, some joined in short lines.

Material examined: Holotypus. RUSSIA. Primorsky Krai, KPSNBR (Kedrovaya Pad State Nature Biosphere Reserve), 43°05’48.1’’N 131°33’30.9’’E, on the bark of living *Chosenia arbutifolia*, in mcc, pH=7.09, bark sampling 22 August 2017, mcc, starting 31 October 2017, sporocarps sampling January 2018, leg. *F.M. Bortnikov*, MYX11315!. RUSSIA. Primorsky Krai, KPSNBR (Kedrovaya Pad State Nature Biosphere Reserve), 43,1195°N 132,78986°E, on the bark of living *Populus maximowiczii*, in moist chamber, pH=6.63, 25-X-2021, leg. *F.M. Bortnikov,* s.n.

Habitat: on bark of living trees (*Chosenia arbutifolia, Kalopanas septemlobus, Populus maximowiczii*).

Distribution: Known only from type territory (Russia).

Icon.: Bortnikov *et al.* (2022: 42, Figs. 18a–j; 43, Figs. 20a–e).

Notes. The clear micrographs, provided in the original paper obviated the need for repetition of SEM, but light micrographs were repeated to compare colours. This species is very similar to *L. synsporos* Nann.-Bremek. The differences given in Bortnikov *et al.* (2022) are the shape of the sporocarp and slight difference in spore colour. The holotype of *L. synsporos* (NENB 6146) consists of only a few sporocarps mounted on slides (see below), so direct comparison of the two species was not possible. However from that publication, as far as we can judge, the main characters of two species are very similar. The sporocarps are dark, dehiscence is by preformed lines into platelets with thickened smooth margins, and the spores are clustered, 9–11(–12) µm diam., minutely warted, but the part of a spore turned to the center of the cluster or the contact areas of the adjacent spores are smooth. These similarities suggest that both species may be conspecific, but it is impossible to confirm this without detailed further study and, if possible, molecular information.

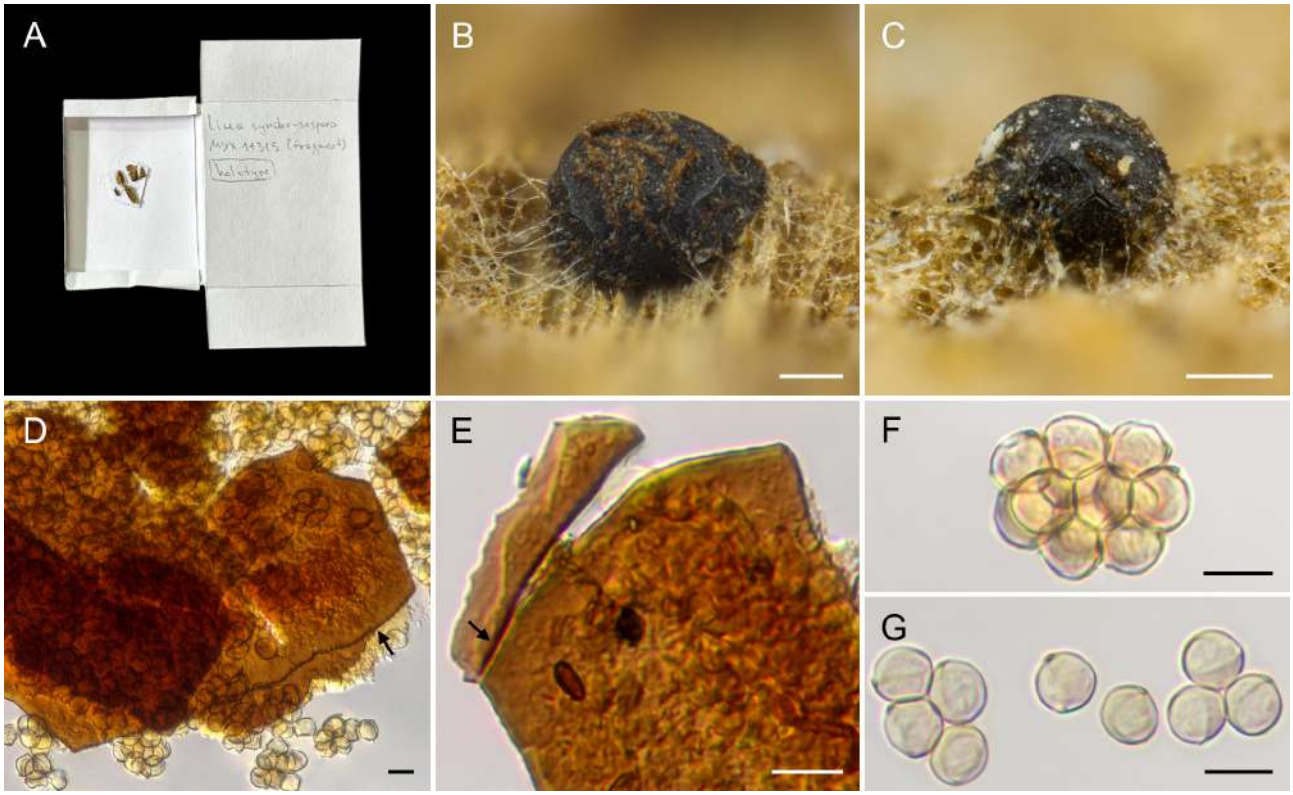

FIGURE 19. *Licea synchrysospora.* A–B, D, F (MYX11315, Holotype); C, E, G (s.n.). A. Herbarium box. B–C. Sessile sporocarp. D–E. Peridial platelets (arrows) and spores by TL. F–G. Spore in clusters by TL. Scale bars: B–C = 0.1 mm, D–G = 10 µm.

23. Licea synsporos Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 71(1):42 (1968)

Sporocarps scattered, globose to subglose, dark brown 0.1–0.2 mm diam. Peridium thin, translucent, ochraceous, partly smooth, partly minutely warted; dehiscence along preformed lines with thickened smooth margins. Spores dark brown in mass, yellow brown by TL, cohering in clusters, 9–11(–12) µm diam. with a thick pale wall, subglobose to turbinate, warted on the outer edge, smooth on the surface turned towards the centre of the cluster.

Type: NENB 6146.

Habitat: on moss growing on bark of *Acer pseudoplatanus.*

Distribution: United Kingdom.

Icon.: Nannenga-Bremekamp (1968: 43, Figs. 2A–C), Kuhnt (2019: 155, Abb. 9a–b), Johannesen & Wetlesen (2020: 79, Figs. 40G–H).

Notes. The holotype of *L. synsporos* (NENB 6146) only consists of a few sporocarps mounted on slides. These were not available for study so we base the description on the original publication. The illustrations in Kuhnt (2019) of the type slide were of insufficient quality to resolve any characters. The very similar characters of *L. synchrysospora* Bortnikov are discussed above.

24. *Licea testudinacea* Nann.-Bremek. Acta Bot. Neerl. 14: 141 (1965) Figs. 20A–K

Sporophores sporocarpic, grouped or scattered, sessile. Sporocarps suglobose, 0.1 mm diam., to pulvinate, angular, 0.15 mm high, 0.2–0.8 mm long, dark brown to black, with undulating glossy lighter ridges marking places of dehiscence (Fig. 19E). Peridium double, the outer layer closely appressed and covered with granular refuse material (Fig. 19F), the inner layer inner surface shiny, minutely warted, brownish yellow/orange by TL,; dehiscence along ridges into many small platelets with a band of interlacing outgrowths on platelet margins (Fig. 19F). Spores very dark brown in mass, grey by TL, with a conspicuous paler area, globose, (10–)12–13(–15) µm diam., warted. By SEM the inner peridial surface is densely and minutely warted, with different sized warts (Fig. 19I), the outer layer is covered with granular material; the platelet margins ornamented with a row of prominent different sized outgrowths and pegs, some interlacing (Figs. 19 H–I); the epispore is covered by flattened verrucae.

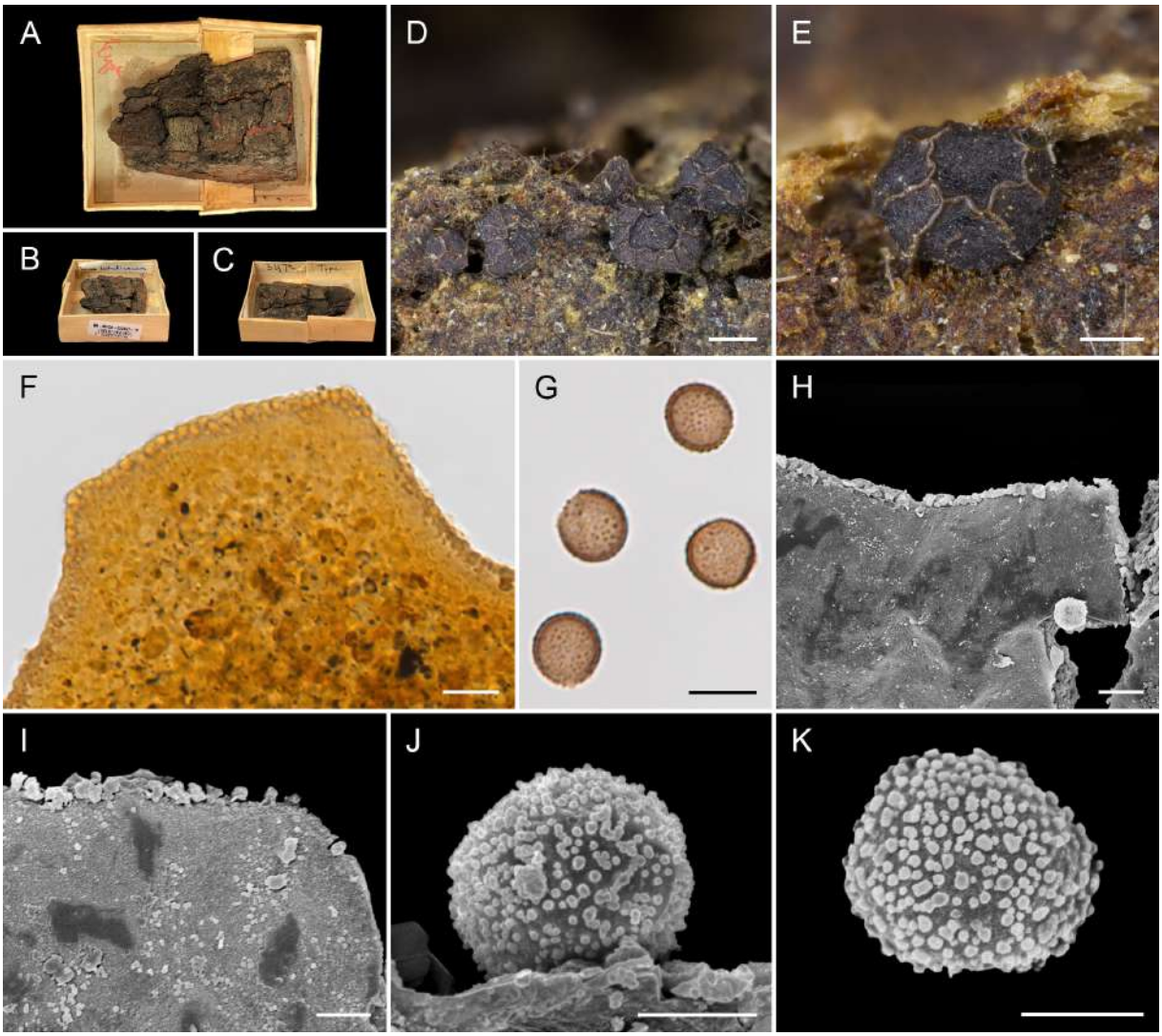

FIGURE 20. *Licea testudinacea.* A–K (NENB 3472, BR5020053457106, Holotype). A–C. Herbarium box. D-E. Sessile sporocarps. F. Peridial platelet with ornamented margin by TL. G. Spores by TL. H. Peridial platelet margin by SEM. I Detail of the inner surface of the peridium and ornamented margin by SEM. J–K. Spores by SEM. Scale bars: D = 0.2 mm, E = 0.1 mm, F–H = 10 µm, I–K = 5 µm.

Material examined: Holotypus. NETHERLANDS. Doorwerth, 10-October-1959, NENB 3472 (BR5020053457106)!.

Habitat: on bark of living and dead trees, dead trunks of angiosperms and gymnosperms.

Distribution: Norway, Sweden, Lithuania, Russian Federation, United Kingdom, Ireland, Denmark, Netherlands, Belgium, Germany, France, Portugal, India, Japan, USA, Mexico, Guatemala, Costa Rica, Brazil, Australia, New Caledonia.

Icon.: Nannenga-Bremekamp (1965: 141, Figs. 8A–B; 1975: 68; 1991: 46), Neubert *et al.* (1993: 283, Figs. VI: 7–8), Novozhilov *et al.* (1999: 85, Figs. 4E–H), Yamamoto (2006: 39, Figs. 17A–C; 2021: 150, Figs. A–C), Johannesen & Vetlesen (2020: 81, Figs. 41C–E), Barbosa & Cavalcanti (2020: 422, Figs. 3A–J).

Notes. This species has dark sporocarps with lighter dehiscence lines, small numerous platelets and dark warted spores with a pale area. It was described with a single peridium and by light microscope it appears single because the two layers are tightly appressed. The author indicates in her later keys (Nannenga-Bremekamp 2022) that the peridium is in fact double, and this can be seen in Fig. 19H herein. This combination of characters separates it from similar species like *L. pygmaea* (Meyl.) Ing, *L. castanea* G. Lister and *L. chelonoides* Nann.-Bremek.

Key to species in the subgenus *Licea.*

Species, critically studied within this publication, are marked in bold.

1. Sporophores stipitate 2
1'. Sporophores sessile 3

2. Peridium double. Spores globose, apparently smooth by TL ..... ***L. alpina***
2'. Peridium single. Spores angular, ornamented by TL ..... ***L. eremophila***

3. Spores in pairs or clusters 4
3'. Spores free 5

4. Spores grayish-olive to colourless by TL ..... ***L. synchrysospora***
4'. Spores yellow-brown by TL ..... *L. synsporos*
4''. Spores lilac-grey by TL ..... *L. confundens*

5. Peridium single 6
5'. Peridium double or triple 10

6. Peridium with multiple rows of fused outgrowths [pegs] on platelet edges ..... *L. deplanata*
6'. Peridium with a single row of outgrowths on platelet margins or no outgrowths 7

7. Peridium with a single row of outgrowths ..... ***L. castanea***
7'. Peridium without outgrowths 8

8. Spores 8–9 µm diam. ..... *L. hepatica*
8'. Spores larger than 9 µm diam. 9

9. Sporocarps pale brown. Peridial platelets with smooth clear margins. Spores warted, 12–14 µm diam. ..... ***L. ampulliformis***
9'. Sporocarps golden. Peridial platelets without smooth clear margins. Spores smooth, 14–15 µm diam. ..... ***L. aurea***

10. Peridium triple ..... ***L. morchelloides***
10'. Peridium double 11

11. Peridium platelet margins without prominent outgrowths 12
11'. Peridium with prominent warts or outgrowths at the margin of the platelets 15

12. Peridium without lines of dehiscence ..... ***L. castaneoides***
12'. Peridium with lines of dehiscence, or dehiscence along ridges 13

13. Spores angular to polygonal ..... ***Licea capacia***
[if stipitate with subglobose sporotheca see *L. eremophila* above]
13' Spores subglobose or globose 14

14. Sporocarps dark brown. Spores light brown, warted by SEM ..... ***L. belmontiana***
14' Sporocarps ochraceous. Spores olivaceous, smooth even by SEM ..... ***L. nannengae***
15. Sporocarps conical with a shiny basal ring ..... ***L. rufocuprea***
15'. Sporocarps pulvinate, or subglobose, not conical 16

16. Peridial platelets with lines of densely packed warts on the inner margins ..... ***L. lignicola***
16'. Peridial platelets with large outgrowths like pegs on the inner margins 17

17. Margins of platelets dark (see also *L. mariae*) ..... ***L. nigromarginata***
17'. Margins concolorous with the rest of the platelet 18

18. Spores in mass dark brown 19
18’. Spores in mass red, olive, yellow or almost colourless 20

19. Spores 15–18 µm diam ..... ***L. chelonoides***
19’. Spores 11–13 µm diam ..... ***L.testudinacea***
20. Spores pale red brown by TL ..... ***L. minima***
20’. Spores olive, greenish yellow or almost colourless by TL 21

21. Spores smooth, almost colourless by TL ..... ***L. mariae***
21’. Spores warted or spiny, olive to yellow by TL 22

22. Spores 16–20 µm diam, olive brown by TL ..... ***L. pusilla***
22’. Spores <15 µm diam, greenish yellow by TL ..... ***L. pygmaea***

Discussion

Twenty type specimens in the genus *Licea,* with sporocarps dehiscing into defined, preformed platelets (subgenus *Licea*) have been exmined using light and electron microscopy. Among these, a new species from Mexico, *Licea ampullliformis,* has been formally described, and synonymy has been found in the case of two species, *L. castanea* and the recently described *L. bryocortiola*. No type material was found for *Licea minima*, a species described almost 200 years ago, and so a neotype was designated. In the course of the study, the nomenclatural code was applied in the case of *Licea pusilla*, where the image in the original description of the species is the primary type. However as no original material exists, an epitype has been designated. Two species were represented only by a type slide. A further 4 species, that were requested, but not available for study, have been described using their original descriptions (Lado 2005–2023), and included in the dichotomous key to the subgenus elaborated using combinations of the similarities and differences of the characters.

The dehiscence of the sporocarp along preformed lines into defined platelets was a common character for all species of the subgenus *Licea*, studied by us. Most of the studied species have ornamented margins to the platelets. With the exception of two species, that are usually stipitate, most of the taxa have sessile sporocarps. Characters, that are important for distinguishing species, include the size of the sporocarp, the colour of the peridium and the spores (which are recommended to be compared with the same optical instruments), the number of layers of the peridium, the ornamentation of the inner surface of the peridium and of the epispore, as well as the ornamentation of the platelet margins. For the latter three characters, the use of scanning electron microscope has helped to resolve long-term uncertainties, such as spore ornamentation in *L. belmontiana* and *L.nannengae*, or the number of peridial layers in *L. capacia, L. belmontiana* and *L. testudinacea*.

The taxonomic complexity of the genus *Licea* is evidenced by the following facts: (1) there are only a few stable morphological characters, namely the structure of the peridium and spores; (2) nine species of the genus have been described in the last 20 years; (3) some of species are known only from the type locality; (4) little or no type material of older specimens exists *(L. minima*, *L. pusilla*). As a result of the small sporocarp size, species of *Licea* are virtually invisible in the field (Wrigley de Basanta & Lado 2005). Some can only be found in cultures, but moist chamber culture studies remain relatively rare, and have not been carried out in many areas. There may well be more synonymy in the group, and undoubtedly relationships between these taxa will further be clarified by molecular techniques, although this remains extremely difficult because of the small size of fructifications of *Licea*, and the small amount of material available for such studies.

As can be seen in the colour light micrographs made using the same optical instruments, some species such *as L. aurea, L. eremophila*, or *L. synchrysospora* have clearly light-spores but others such as *L. lignicola* or *L. morchelloides* have dark brown spores. In the absence of chemical analysis to indicate the presence or absence of melanin, and sufficient phylogenetic data on the genus *Licea*, to include this particular group into the Lucisporidia or Fuscisporidia grouping proposed by Cavalier-Smith (2013) and followed by Fiore-Donno *et al.* (2013) and Leontyev *et al.* (2019) is problematic.

The genus *Licea* may prove to be an unnatural genus as indicated by Eliasson (2017), since most of the existing information on the genus is based on morphology and only the lack of capillitium links them together. The emphasis on the importance of each taxonomic character, or its lack, in establishing relationships, is something that certainly needs to be further investigated.

Some of the morphological features of the subgenus *Licea* have been made clearer using type species and SEM

imaging in this paper. However, their relationships with other members of the genus, as well as with other genera, cannot be clearly understood using morphology alone. As it was stated above, only four members of the genus as a whole, and only one of these of the subg. *Licea* (*L. castanea*), have partial sequences currently available in GenBank, confirming the need for further examination using improved molecular techniques. Spore-to-spore cultivation may also provide more information about this group. This would allow the type of plasmodium to be confirmed, since the development from a protoplasmodium, where this has been observed (Wrigley de Basanta *et al.* 2010, 2019), is common in this subgenus and according to some authors is a characteristic of the genus as a whole. It does appear, however, from the observations herein, that this subgenus at least could be a natural taxonomic group.

As with so many other organisms of our diminishing biodiversity, but perhaps especially these visible microorganisms, that are so essential to soil and plant health, there is urgent need to accelerate and amplify research into vanishing plant substrates, and endangered and vulnerable habitats, before these and probably many undescribed species, are permanently lost.

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