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## A taxonomic evaluation of the stipitate *Licea* species

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A taxonomic study was made of the type specimens of 21 stipitate *Licea* species. Relevant characters were examined by light microscope and by SEM. Evidence of synonymy was found in five of the taxa, *Licea tropica* with *L. bulbosa*, *L. cristallifera* with *L. eleanorae*, *L. longa* and *L. capitata* with *L. floriformis* var. *aureospora*, and *L. tanzanica* with *L. scyphoides*. One taxon *Licea capitatoidea* var. *fujiokana* is recombined as a variety of a different species, *Licea rugosa* var. *fujiokana*. A new name *Licea verrucospora*, and a new status was given to *Licea scyphoides* var. *reticulata*. One species, *Licea takahashii* was excluded as it is an immature form of another genus. Detailed standardized descriptions are made of each species examined, with comments on the most relevant taxonomic characters. Light and scanning electron micrographs of relevant morphological details are included. Nomenclatural information is given for each taxon. A key to the stipitate *Licea* species is proposed.

**Key words:** distribution, *Liceales*, *Myxomycetes*, nomenclature, taxonomy, type collections.

### Introduction

The genus *Licea* (order *Liceales*, *Myxomycetes*) currently encompasses more than 65 species of worldwide distribution (Lado, 2001). The original description of the genus *Licea* was by Schrader at the end of the 18<sup>th</sup> century. In his *Nova Genera Plantarum*, Schrader (1797: 16) established the “character essentialis” and the “character generalis” of the genus and included descriptions of and comments on four species, *L. variabilis* Schrad. and *L. pusilla* Schrad., now accepted as autonomous species, and *L. tubulina* Schrad. and *L. clavata* Schrad., which are now considered synonyms of *Tubulifera arachnoidea* Jacq. [= *Tubifera ferruginosa* (Batsch) J.F. Gmel.] (Lado, 2001). Since then the genus has been maintained, although it is an unnatural genus (Gilert, 1994) since it is defined mainly by the lack of one of the most informative characters of myxomycetes, the capillitium.

The taxonomic treatment of the genus has been changed over the years. The type of dehiscence of the peridium and the presence or absence of a stalk

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have been used in the past as the most relevant characters, and served to segregate the genus *Orcadella* Wingate (1889), based on sporocarps which were stalked and dehiscent by a membranous lid (Lister, 1925), and the genus *Hymenobolina* Zúkal (1893), based on sessile sporocarps opening by a membranous lid (Lister, 1925). Even these characters, are of questionable taxonomic relevance, as Lado and Pando (1997: 109) recognized, and characters which are important at first glance, and used occasionally to distinguish species, can be unstable within taxa or even within fructifications.

Nannenga-Bremekamp (1965), in a revision of the genus also emphasized the type of dehiscence and recognized within the genus *Licea* three subgenera, the subgen. *Orcadella* (Wingate) Nann.-Bremek., which dehisces by means of a circular or almost circular lid. The subgen. *Pleiomorpha* Nann.-Bremek., cracks open irregularly or by a split, and the subgen. *Licea*, opens along ridges that divide the peridium in platelets. With the descriptions of recent new species, the limits between these subgenera are unclear, and the proposal of Nannenga-Bremekamp is now of doubtful application.

Martin and Alexopoulos (1969) recognized 19 species in the genus and this total was increased eight years later by Keller and Brooks (1977) to 30. In the latter classic contribution towards a monograph of the genus the authors established the bases for a more rational study of the group, and elaborated a detailed key of the species that the authors recognised. In this paper all the species were placed in a single genus *Licea*, the subgenera proposed by Nannenga-Bremekamp were not recognised, and only 5 truly stipitate species were included.

Since then Lakhanpal *et al.* (1990) added three new stipitate species in their paper “Notes on *Licea* (Myxomycetes) from India”, and at present, among the 67 recognized species belonging to this genus (Lado, 2001), a large number (27) of stipitate *Licea* have been described in the literature (Table 1).

The current concept of the genus (Lado and Pando, 1997) includes species with plasmodiocarpic to sporocarpic, sessile or stipitate minute sporophores, with a peridium that is membranous or coriaceous, consisting of one or two layers. A columella, capillitium and pseudocapillitium are always absent. On account of this, species and specimens that should be placed under the genus *Didymium* (order *Physarales*) or *Perichaena* (order *Trichiales*) are sometimes erroneously identified as belonging to *Licea*, if they lack capillitium when the specimens develop under unfavourable conditions.

The number of recent descriptions of stipitate taxa (Table 1), some of them practically simultaneously in press (Ing, 1999; Flatau, 2000), coupled with the simplicity of the sporophores and lack of taxonomic characters, made the systematics of these minute myxomycetes somewhat confused. The fact

**Table 1.** Stipitate *Licea* described in the literature in chronological order of their description.

Name	Reference
<i>Licea operculata</i> (Wingate) G.W. Martin, described as <i>Orcadella operculata</i> Wingate, 1889	Wingate (1889); Martin (1942)
<i>Licea pedicellata</i> (H.C. Gilbert) H.C. Gilbert, described as <i>Hymenobolina pedicellata</i> H.C. Gilbert, 1934	Gilbert (1934); Martin (1942)
<i>Licea erecta</i> K.S. Thind & Dhillon	Thind and Dhillon (1967)
<i>Licea scyphoides</i> T.E. Brooks & H.W. Keller	Keller and Brooks (1977)
<i>Licea perexigua</i> T.E. Brooks & H.W. Keller	Keller and Brooks (1977)
<i>Licea lucens</i> Nann.-Bremek.	Nannenga-Bremekamp (1981)
<i>Licea capitata</i> Ing & McHugh	Ing (1982)
<i>Licea atricapilla</i> Nann.-Bremek. & Y. Yamam.	Nannenga-Bremekamp and Yamamoto (1983)
<i>Licea erectoides</i> Nann.-Bremek. & Y. Yamam. = <i>Licea erecta</i> var. <i>erectoides</i> (Nann.-Bremek. & Y. Yamam.) Y. Yamam.	Nannenga-Bremekamp and Yamamoto (1983); Yamamoto (1998)
<i>Licea bulbosa</i> Nann.-Bremek. & Y. Yamam.	Nannenga-Bremekamp and Yamamoto (1987)
<i>Licea rugosa</i> Nann.-Bremek. & Y. Yamam.	Nannenga-Bremekamp and Yamamoto (1987)
<i>Licea capitatoides</i> Nann.-Bremek. & Y. Yamam.	Nannenga-Bremekamp and Yamamoto (1990)
<i>Licea lilacina</i> Nann.-Bremek., T.N. Lakh. & R.K. Chopra	Lakhanpal <i>et al.</i> (1990)
<i>Licea scyphoides</i> var. <i>reticulata</i> T.N. Lakh., Nann.-Bremek. & R.K. Chopra	Lakhanpal <i>et al.</i> (1990)
<i>Licea floriformis</i> T.N. Lakh. & R.K. Chopra	Lakhanpal <i>et al.</i> (1990)
<i>Licea floriformis</i> var. <i>aureospora</i> M.T.M. Willemse & Nann.-Bremek.	Willemse and Nannenga-Bremekamp (1994)
<i>Licea tropica</i> Chao H. Chung & C.H. Liu	Chung and Liu (1996)
<i>Licea tanzanica</i> Ukkola, Härk. & Gilert	Ukkola <i>et al.</i> (1996)
<i>Licea poculiformis</i> Ukkola	Ukkola (1998)
<i>Licea erddigensis</i> Ing	Ing (1999)
<i>Licea eleanorae</i> Ing	Ing (1999)
<i>Licea crateriformis</i> Ing	Ing (1999)
<i>Licea cristallifera</i> Flatau	Flatau (2000)
<i>Licea longa</i> Flatau	Flatau (2000)
<i>Licea capitatoides</i> var. <i>fujiokana</i> Y. Yamam.	Yamamoto (2000)
<i>Licea parvicapitata</i> Y. Yamam.	Yamamoto (2000)
<i>Licea takahashii</i> Y. Yamam.	Yamamoto (2000)

that the species of *Licea* are very small (about 0.1 to 1 mm in height) and mainly the result of moist chamber culture, which means that there are often few specimens to work with, and many aberrant forms, have further complicated the picture. Gilert (1994) did ultrastructure studies on some members of the genus, which clarified the relationships between some species, but she studied mainly sessile species. She commented on the heterogeneous nature of the genus as a whole and expressed doubt over the taxonomic significance of the presence or absence of a capillitium, concluding that a protoplasmodium with certain fructification morphotypes was more important. The only stipitate species in her study was *Licea operculata*.

No comparative study of type material of the stipitate species, had been done when this paper was begun, there were no keys to the numerous new species recently described, some of the descriptions did not allow for easy species identification, and so a taxonomic revision of these members of the genus was deemed necessary. The contribution of Keller and Brooks (1977) detailed most of the sessile species, of which 17 more have been described since. The present paper attempts to clarify the similarities and differences between the stipitate species, as a step towards further analysis of the genus *Licea* as a whole.

## Materials and methods

This revision is based on the study of almost 100 herbarium collections. Type specimens of all the stipitate species in the literature (Table 1) were requested, and 21 of the 27 listed in the table were examined simultaneously. The remainder were requested, but were not sent. Type material was loaned by the following herbaria BPI, BR, H, TNS and B, and material conserved in MA-Fungi, our own collections (dwb, Lado), and those kindly lent to us by Dr. L. Flatau (LF), Dr. B. Ing (Ing), Dr. F. Pando (Pando), Dr. M. Schnittler (sc), Ms. M. de Haan (MdH) and Mr. A. Varela-García (VGA), were all studied in the same manner. The same optical instruments, a Nikon SMZ-1000 stereomicroscope and a Nikon Eclipse E-600 microscope with a Nomarski system, were used to examine the specimens. The same magnifications and the same light intensity were used, to allow valid comparisons of such taxonomic characters as spore and peridial colour, and ornamentation by transmitted light, and in order to unify the terminology used for their description. Slides of most of the type material were not included in the samples sent from the different herbaria. Consequently slides were made by us in a standardized way by mounting a whole sporocarp in PVA (polyvinyl alcohol) and squashing it very gently with a cover slip, just sufficient to encourage dehiscence while

maintaining the sporocarp whole when possible. Other diagnostic techniques such as PCR were not possible due to the scant type material of some species and the regulations of some herbaria. Light micrographs were made with Nomarski optics, and SEM photographs were taken using the critical point technique. The age and treatment of some herbarium specimens meant they did not respond well to the critical point technique used for the SEM observations, leaving some spores collapsed (Fig. 32). Colour notations in parentheses are from the ISCC-NBS Color-Name Charts Illustrated with Centroid Colors (Anonymous, 1976). The terminology used follows Lado and Pando (1997).

## Results and discussion

As described by Martin and Alexopoulos (1969) and Martin *et al.* (1983: 41) the family *Liceaceae*, has a single genus, *Licea*. This genus includes species with plasmodiocarpic to sporocarpic, sessile or stipitate sporophores, with a peridium membranous or coriaceous, consisting of one or two layers, then the external layer gelatinous when wet, drying horny, the inner always membranous, the external surface frequently with deposits of granular material, the peridium dehiscence can be irregular, by platelets or by lids; the columella, the capillitium and the pseudocapillitium are always absent, and the spores are free, globose, subglobose or ovoid, of variable colour but usually pale, decorated or smooth, and with spore wall of uniform thickness or with a thinner area. The nomenclatural treatment of the genus in this paper is according to Lado (2001) and Hernández-Crespo and Lado (2005).

***Licea*** Schrad., Nov. Gen. Pl.: 16. 1797.- Lectotype, *Licea pusilla* Schrad. (designated by Martin, 1942: 700)

= *Cylichnium* Wallr., Fl. Crypt. Germ. 2: 267. 1833.- Type: *Cylichnium operculatum* Wallr.

= *Protoderma* Rostaf., Sluzowce Monogr.: 90. 1874 [Nom. illeg., non *Protoderma* Kütz., 1854]. *Protodermium* Rostaf. ex Berl. in Saccardo, Syll. Fung. 7: 328. 1888 [Nom. nov., based on *Protoderma* Rostaf.]. *Protodermodium* Kuntze, Revis. Gen. Pl. 2: 867. 1891 [Nom. nov., based on *Protoderma* Rostaf.].- Type: *Protoderma pusillum* (Schrad.) Rostaf. (= *Licea pusilla* Schrad.).

= *Orcadella* Wingate, Proc. Acad. Nat. Sci. Philadelphia 41: 280. 1889. *Licea* subgen. *Orcadella* (Wingate) Nann.-Bremek., Acta Bot. Neerl. 14: 132. 1965.- Type: *Orcadella operculata* Wingate.

= *Hymenobolus* Zukal, Oesterr. Bot. 43: 73. 1893 [Nom. illeg., non *Hymenobolus* Durieu & Mont., 1845]. *Hymenobolina* Zukal, Oesterr. Bot. 43: 133. 1893 [Nom. subst., based on *Hymenobolus* Zukal].- Type: *Hymenobolus parasiticus* Zukal.

= *Kleistobolus* C. Lippert, Verh. Zool.-Bot. Ges. Wien 44: Abh. 70. 1894.- Type: *Kleistobolus pusillus* C. Lippert.

= *Licea* subgen. *Pleiomorpha* Nann.-Bremek., Acta Bot. Neerl. 14: 132. 1965 [as "Pleismorpha"].- Type: *Licea variabilis* Schrad.

The genus *Licea* has a worldwide distribution, and a total of 67 species are now recognised (Lado, 2001). The species described in this genus as stipitate were studied and are treated here in alphabetical order.

**1. *Licea bulbosa*** Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 90(3): 324. 1987. TYPE: JAPAN, Kochi Pref., Aki-shi, Nabika, developed on the bark of a living tree in a moist chamber, 28 VI – 16 V 1986, Y.Y. 3919 (holotype: TNS; isotype NENB 15.055 now at BR!). (Figs. 1-7)

= *Licea tropica* Chao H. Chung & C.H. Liu, Proc. Natl. Sci. Council Republ. China, B 20(4): 140. 1996, **syn. nov.** TYPE: TAIWAN, Pingtung, Manchou Hsiang, Wan-li-te-shan, about 120°50'E 22°2'N, tropical rain forest, on unidentified dead leaves of angiosperms collected in 2 II 1996, cultured in a moist chamber from 4 II 1996-25 III 1996, fruiting bodies appeared since 18 III 1996, C.-h. Chung M1000 (holotype: TAI).

Sporocarps scattered, stipitate, 150-280(-340) µm in height. Sporotheca brown, subglobose, up to 160 µm diam. Hypothallus inconspicuous. Stalk up to 180 µm in height, straight, subcylindrical, tapering slightly towards the apex, opaque, nearly black by reflected light, especially at the base, mid-width less than one third of the height, by transmitted light (TL) pale brown and filled with granular material. Peridium double, except for the equatorial area where it is single, in this area a clear ring of dehiscence is visible by reflected light (Figs. 1-2), the top half to two thirds of the peridium lifts off as a lid with very prominent protuberances on the inner edge, the outer layer gelatinous continuous with the stalk, transparent in the lower half showing the spores inside, brown by reflected light in the upper half with granular refuse material, the inner layer membranous, smooth except for the area of dehiscence, where there are some warts; dehiscence circumcissile and more or less equatorial. Spores free, pale yellow or greyish green to almost hyaline (121. p. Y G-122. gy. Y G) by TL, globose, 10-11 µm diam., smooth; spore wall of uniform thickness (Fig. 6).

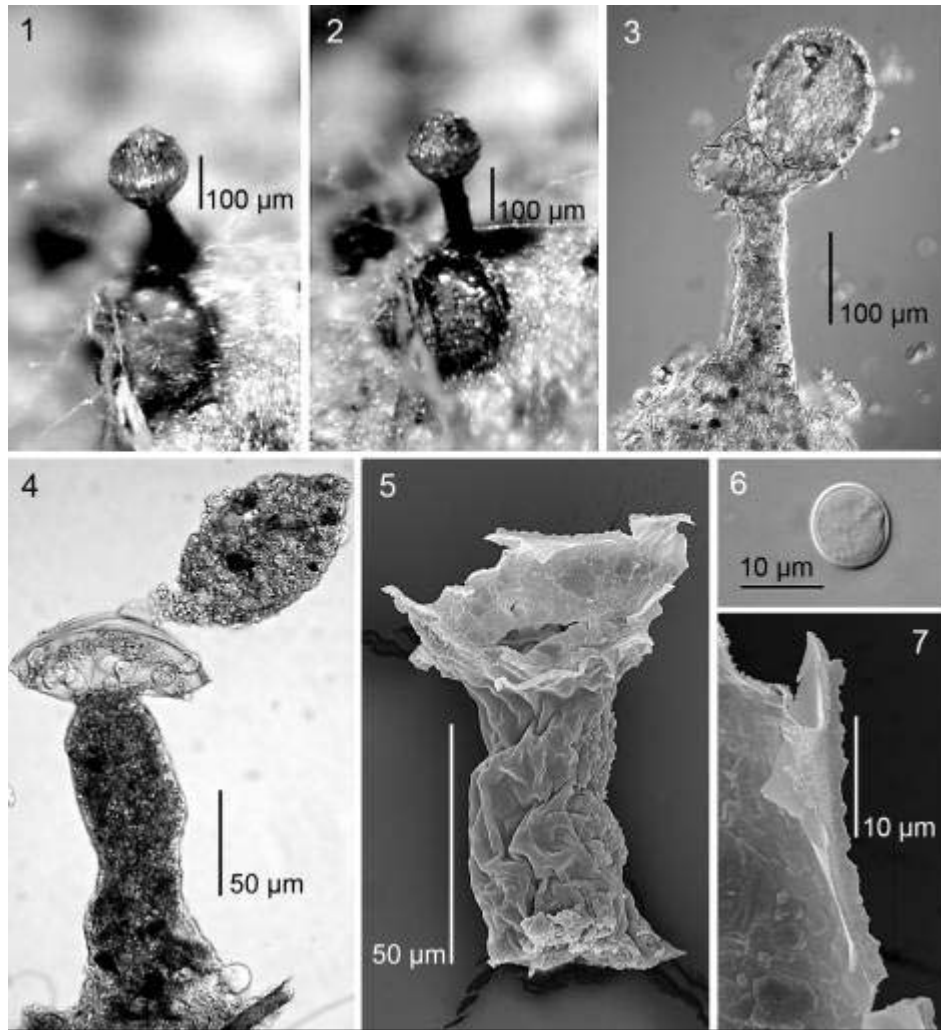
*Material examined:* JAPAN, Kochi Pref.: Aki-shi, Nabika, on bark of living tree in moist chamber, 28-IV to 19-V-1986, NENB 15.055 (BR, isotype). CUBA, Sancti Spiritus, Alturas de Banao, 21°52'39"N 79°36'03"W, on *Cyathea woodwardiodes* petioles in moist chamber, 8-II-2003, dwb 2256.

*Habitat:* bark of living trees, angiosperm leaf litter, tree-fern petioles, ground litter.

*Distribution:* Australia, Cuba, Japan, Taiwan, Tanzania.

*Illustrations:* Nannenga-Bremekamp and Yamamoto (1987: Fig. 9); Chung and Liu (1996: 141, Figs. 2-4) as *L. tropica*; Ukkola *et al.* (1996: 56, Figs. 2-4); Yamamoto (1998: 149); McHugh *et al.* (2003: 492, Fig. 2)

The sporocarps of the isotype of this species had a height and diam. somewhat larger than the original description. The height was up to 280 µm vs.



**Figs. 1-7.** *Licea bulbosa*. **1-2.** Habit. Note line of circumcissile dehiscence (isotype NENB 15055 BR). **3.** Dehiscent sporocarp with transparent base to sporotheca and upper half lifting as a lid (NENB 15055). **4.** Whole sporocarp with transparent base to sporotheca containing spores and band of refuse below the line of dehiscence (dwb 2256). **5.** Dehiscent sporocarp by SEM (NENB 15055). **6.** Spore by TL (NENB 15055). **7.** Detail of outer edge of base of sporotheca with warted edge (NENB 15055).

150-200 µm in the original description, and the diam. of the sporotheca was up to 160 µm in the largest specimens (40-60 µm in the original description). The stalk was light brown by TL with refuse deposits inside (Figs. 3-4). There was a definite separation between the stalk and the sporotheca. The inner peridium was smooth and transparent with an adhering outer layer containing refuse particles, some of which can be crystals visible with Nomarski. It is difficult to

distinguish the two layers. The upper part of the peridium lifts off in one piece almost like a lid (Figs. 3-4) with very prominent protuberances on the edge (Fig. 7). The cup that is left has few refuse particles included (Fig. 5) and appeared totally transparent.

We were not able to examine the type of *Licea tropica*, which was found on unidentified dead angiosperm leaves in Wan-li-te-shan, Manchou Hsiang, Pingtung, Taiwan (Chung and Liu, 1996). The material was requested, but not sent. However according to the description, comments and illustrations by Chung and Liu (1996: 141), the constant and very clear characters of the transparent base to the sporotheca and the darkened brownish band below the area of dehiscence (Fig. 4), were observed in material recently isolated from moist chamber cultures of tree fern petioles from Cuba. The separation between the outer peridial layer of the top half and the bottom half of the sporotheca are other clear features. All these characters, except the brown stalk, concur with the isotype of *L. bulbosa*, and so we agree with McHugh *et al.* (2003: 491) and believe these to be the same species. These authors made no comments in their synonymy of the species, but their photograph of Australian material shows all the above-mentioned characters. In the description of *L. tropica*, Chung and Liu (1996: 142) recognized the similarity of their species with *L. bulbosa*, but found height and diam. differences of the sporocarps. We found, in our examination of the isotype of *L. bulbosa*, that there is an overlap in the measurements.

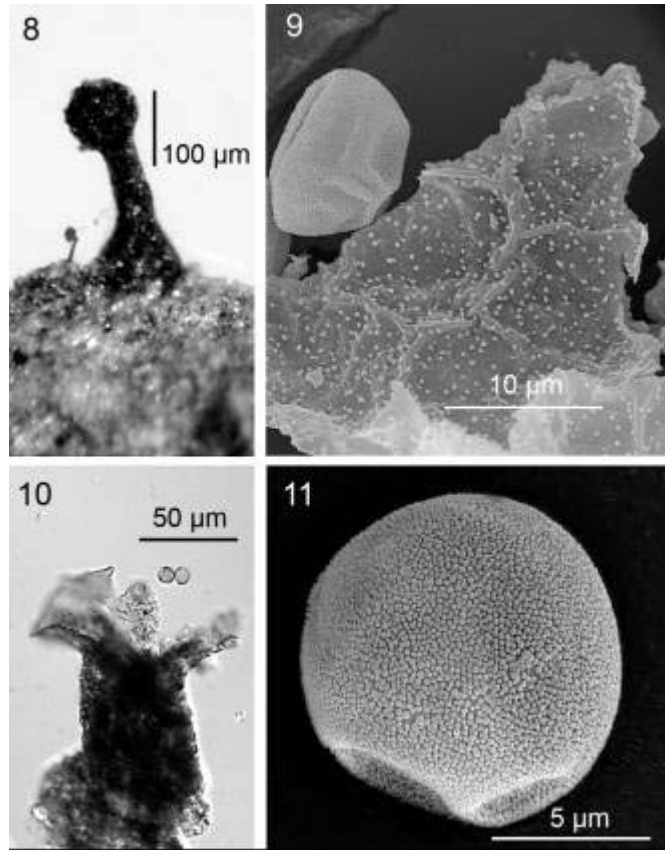
In the Cuban material in moist chamber, the equatorial thinner band was observed as a light line in developing sporocarps as soon as the sporotheca formed as a transparent bulb at the top of the stalk, before spore formation and darkening of the upper half. It was as if the developing outer peridium is stretched forming two halves, which are separated in the middle.

This species is also like *L. scyphoides* and *L. eleanorae* in its circumcissile dehiscence, but differs from the former in its almost hyaline smaller spores (10-11  $\mu\text{m}$  vs. 11-14  $\mu\text{m}$  in *L. scyphoides*), and from both in the smooth spores, smooth inner peridium, and smooth transparent base to the sporotheca.

**2. *Licea capitatoidea*** Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch. 93(3): 269. 1990. TYPE: JAPAN, Tokushima Pref., Tokushima-shi, Kamo, developed in a moist chamber on bark of a living *Aphananthe aspera*, 11-28 V 1988, Y. Yamamoto 6387 (holotype: TNS!, isotype NENB 16.136, now at BR!). (Figs. 8-11)

Sporocarps scattered, stipitate, 200-400  $\mu\text{m}$  in height. Sporothecae dark grey-brown, globose or subglobose, 100-120  $\mu\text{m}$  diam. Stalk 100-200(-280)





**Figs. 8-11.** *Licea capitatooides* (NENB 16.136). **8.** Habit. **9.** Inner surface of peridium stippled with dispersed warts. **10.** Dehiscent sporocarp with v-shaped calyculus. **11.** Spore by SEM with dense even warts.

µm in height, concolourous and continuous with sporotheca, cylindrical, expanded at the base, full of refuse, mid-width less than half the height. Peridium double, outer gelatinous layer with granular refuse in patches, the inner layer membranous yellowish grey (93. y. Gray) by TL, inner surface stippled with very obvious warts; dehiscence by irregular fracture, into “wavy-edged” fragments of the upper sporotheca, leaving a calyculus with a clear inner separation from stalk (Fig. 10). Spores free, greyish yellow to pale yellow (90. gy. Y-89. p. Y) by TL, 8-10 µm diam., smooth by TL, closely warted by SEM (Fig. 11); spore wall with an obvious paler area.

*Material examined:* JAPAN, Tokushima Pref.: Tokushima-shi, Kamo, on bark of living *Aphananthe aspera* in moist chamber, 11 to 28-V-1988, Y. Yamamoto 6387 (TNS, holotype) as *Licea capitatooides*; also NENB 16.136 (BR, isotype)

*Habitat:* bark of living *Aphananthe aspera*.

*Distribution:* Known only from the type locality.

*Illustrations:* Nannenga-Bremekamp and Yamamoto (1990: 269, Figs. 3A-C); Yamamoto (1998: 139).

This species is known only from the type locality. It is most similar in habit to *L. pedicellata*, but differs from it in the ornamentation and smaller size of the spores. By transmitted light the spores appear to be smooth, but by SEM (Fig. 11) very dense close warts are visible which are smaller and denser than the warts in *L. pedicellata*. The *L. capitatooides* also has paler spores which are slightly smaller than those of *L. pedicellata* (8-10 vs. 11-13 µm diam.). Another difference is that in *L. capitatooides* only the top part of the sporotheca, not the whole sporotheca, breaks into platelets on dehiscence. This leaves a large v-shaped calyculus showing the separation of the inner peridium from the stalk. The separation visible in the *L. pedicellata* is a small flat disc shape. The densely stippled inner surface of the peridium however, is very similar by SEM (Fig. 9) in the two species (Fig. 68).

*Licea capitatooides* can be distinguished from *L. scyphoides* and *L. tanzanica* on the basis of the mode of dehiscence (platelets vs. circumcissile), the different spore ornamentation and darker smaller spores of *L. capitatooides*.

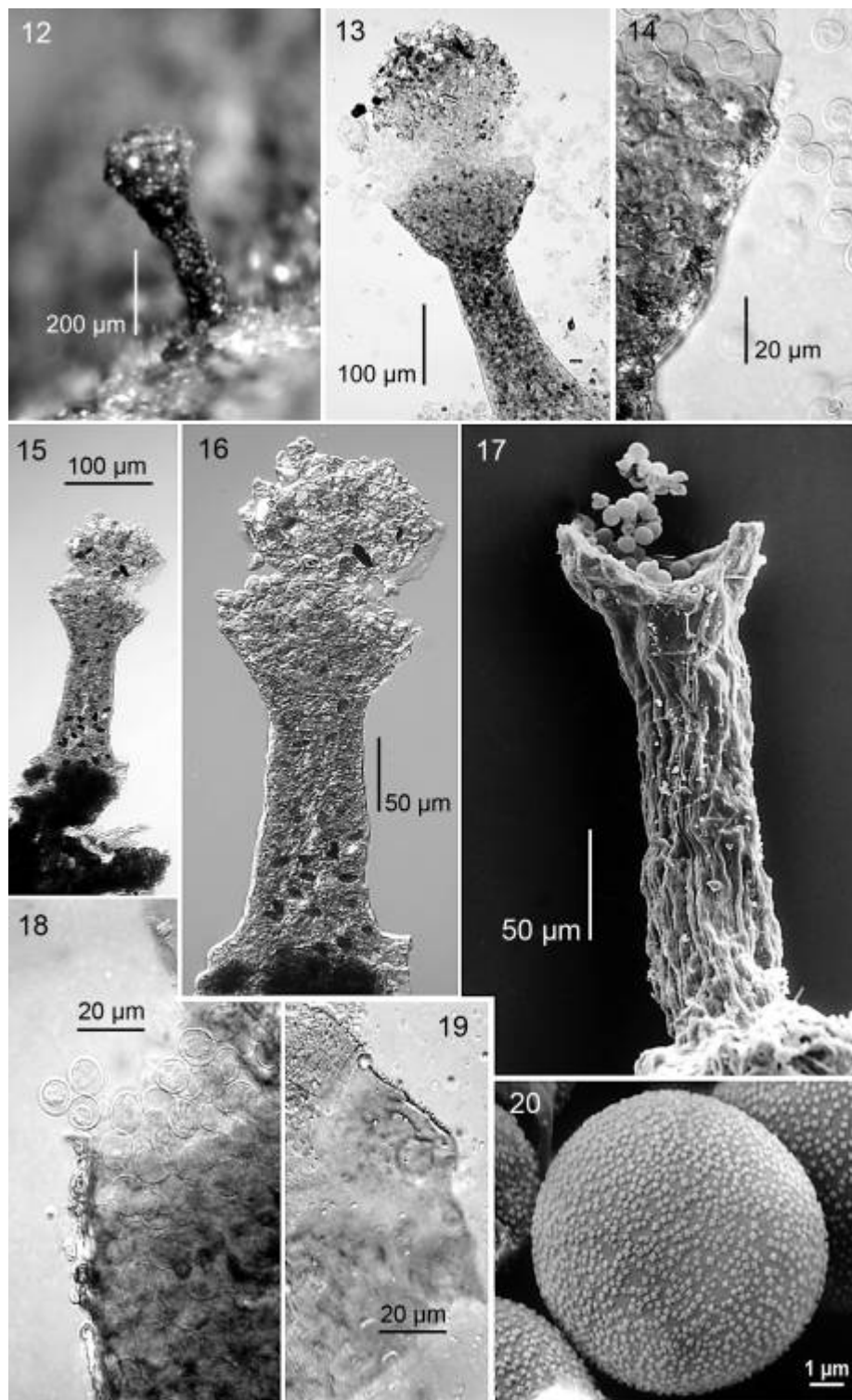
**3. *Licea eleanorae*** Ing, Myxomycetes Britain and Ireland: 50. 1999. TYPE: SWITZERLAND, Ticino, Lugano, Cantine di Gandria, in cortice vivo *Platanus* × *hispanicae* in camera humida, September 1997, B. Ing (holotype: Hb. Ing No. 97097!) (Figs. 12-20)

= *Licea cristallifera* Flatau, Stapfia 73: 65. 2000., **syn. nov.** TYPE: GERMANY, Hessen, Kassel, Borke, liegender *Fagus*-Stamm (*F. sylvatica*), (2), 170 m über NN., 3.-27.7 1998, LF 3148 (holotype: B!).

Sporocarps scattered, solitary stipitate, 360-480 µm in height. Sporotheca shiny golden, 175-220 µm diam. Stalk 185-260 µm in height, dark brown by reflected light, straight, sub-cylindrical, full of crystals and refuse matter, continuous with outer layer of sporotheca, mid-width one third of the height. Peridium double, outer layer dark and full of refuse, birefringent crystals on the outer upper surface (Fig. 13), inner layer translucent and finely warted (Fig. 19); dehiscence by means of a circular apical split (Figs. 15-16). Spores free, pale yellow (89. p. Y) by TL, subglobose 8-11 µm diam., smooth by TL (Fig. 14), with square or rhomboid ornamentation by SEM (Fig. 20); spore wall of uniform thickness (Fig. 18).

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**Figs. 12-20. *Licea eleanorae*.** 12. Habit (B. Ing 98136). 13. Dehiscing sporocarp showing crystals on upper surface of sporotheca (B. Ing 97097). 14. Spores by TL with wall of uniform diam. (B. Ing 97097). 15. Whole sporocarp (LF 3148 as *Licea cristallifera* Flatau). 16. Dehiscing sporocarp showing inner peridium separate from stalk (LF 3148). 17. Dehiscid sporocarp and spores by SEM (LF 3148). 18. Spores by TL with wall of uniform diam. (LF 3242 *Licea cristallifera* Flatau). 19. Inner surface of peridium (LF 3148). 20. Spore ornamentation by SEM showing rhomboid granules (LF 3148).



*Material examined:* SWITZERLAND, Ticino: Lugano, Cantine di Gandria, on bark of living *Platanus* × *hispanicae* in moist chamber, IX-1997, Ing 97097 (slide of the holotype). ENGLAND, London: Holland Park, bark of *Tilia* in moist chamber, XII-1998, Ing 98136. GERMANY, Hessen, Kassel, Fuldata, Nähe Kragenhofbrücke, on bark of *Fagus sylvatica*, 3 to 27-VII-1998, LF 3148 (1) (B, isotype of *L. cristallifera*); LF 3148 (18) (isotype of *L. cristallifera*); 8 to 20-VII-1999 LF 3242 (all specimens as *L. cristallifera*).

*Habitat:* bark of living trees.

*Distribution:* England, Germany, Scotland, Switzerland.

*Illustrations:* Ing (1999: 49, Fig. 24); Flatau (2000: 65, Fig. 1A-E as *L. cristallifera*)

The type material shows shiny sporocarps somewhat vase shaped with a slightly flattened top to the sporotheca (Fig. 12). The most distinguishing character apart from the crystals in the peridium and stalk is the inner peridium holding the spores. By TL this looks like a clear bubble full of spores (Figs. 13, 16), surrounded by the outer crystalline layer which is continuous with the stalk (Fig. 17). The appearance and characters of the type material of *Licea cristallifera*, as well as the abundant material kindly sent to us by L. Flatau, are identical to those of *L. eleanorae*. A range of sizes was seen in the sporocarps of *L. cristallifera*. The former species was being described while the description of *L. eleanorae* was in press which may account for the double description. We synonymize these two species here.

*Licea eleanorae* is similar in its method of dehiscence to *L. bulbosa*, *L. tanzanica* and *L. scyphoides*. It differs from them and from all the other stipitate *Licea* species in having the upper half of the peridium covered with birefringent crystals and the tiny rhomboid or square ornamentation of the spores by SEM (Fig. 20).

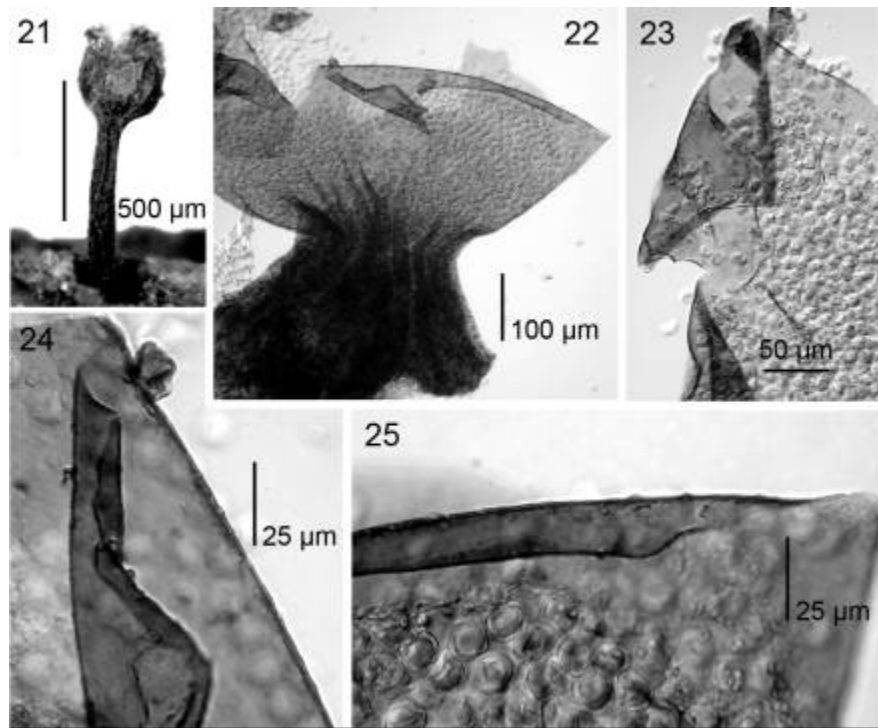
**4. *Licea erddigensis*** Ing, Myxomycetes Britain and Ireland: 48. 1999. TYPE: UNITED KINGDOM, Gallia septentrionalis, Wrexham, Erddig Park, in cortice vivo *Aceris pseudoplatanis* in camera humida, March 1999, B. Ing (holotype: Hb. B. Ing No. 99006). (Figs. 21-25)

Sporocarps solitary scattered, stipitate, 500-800 µm in height. Sporotheca subglobose, brown, 250-500 µm diam. Hypothallus inconspicuous. Stalk black by reflected light, furrowed, straight, cylindrical but narrower at the apex, full of debris, mid-width one third of height, continuous with the sporotheca. Peridium single, dark greyish yellow to mid yellow brown (91. d. gy. Y-77. m. y Br), stippled with very faint flattened warts on the inner surface (Fig. 24); dehiscence by irregular apical split. Spores free, very pale yellow to almost colourless (89. p. Y-92. y White) by TL, subglobose, smooth, 10-12 µm diam.; spore wall of uniform thickness (Fig. 25).

*Material examined:* UNITED KINGDOM, Wales: Wrexham, Erddig Park, on bark of living *Acer pseudoplatanus* in moist chamber, II-1999, Ing 99005 (paratype).

*Habitat:* bark of living sycamore tree.

*Distribution:* Known only from the type locality.



**Figs. 21-25.** *Licea erddigensis* (B. Ing 99005). **21.** Habit (photo D.W. Mitchell with permission). **22.** Sporothecha by TL showing irregular dehiscence. **23.** Thin transparent peridium. **24.** Detail peridial surface with faint flat warts. **25.** Spores with uniform thick wall inside peridium.

*Illustrations:* Ing (1999: 49, Fig. 23)

This species has a very wide sporothecha and the stalk is gathered below it (Fig. 22). This, the membranous peridium (Fig. 23), which tends to roll back on itself, with very faint warts on the inner surface, and the large size of the sporocarp make it very easy to distinguish this taxon from the other stipitate species examined. The reddish-brown colour of the spores, described by Ing (1999: 49) was not visible in the paratype examined, which had pale yellow to colourless spores. The author suggests that this is a sign of immaturity.

This species looks very similar to the description of *L. floriformis* var. *floriformis* (see below), which we requested, but were not able to obtain. In comparison to the original description of the latter species (Lakhanpal *et al.*, 1990), it is different in its persistent dark peridium and mode of dehiscence. Ing (1999) also distinguishes it from other stipitate species by the orange colour of the sporocarp during development.

**5. *Licea erecta* var. *erectoides*** (Nann.-Bremek. & Y. Yamam.) Y. Yamam., Myxomycete Biota Japan: 130. 1998. *Licea erectoides* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 86(2): 209. 1983. TYPE: JAPAN, Kochi Pref., Motoyama-cho, cult. on bark of an unidentified tree, 1-19 VII 1980 (holotype: NENB 13.043 now at BR!, isotype Y.Y. 640 p.p.)

(Figs. 26-32)

Sporocarps scattered, stipitate, 800 -1300 µm in height. Sporothecae dark brown, ovoid 200-400 µm diam. Hypothallus inconspicuous. Stalk up to 700 µm long, concolourous with sporotheca, brownish orange (54. br O), straight, sub-cylindrical, tapering towards the top, furrowed, mid-width one tenth of the height. Peridium double, although appearing single, inner layer yellowish grey to colourless (93. y Gray) by TL, covered with a gelatinous layer with granular refuse material forming longitudinal striations continuous with the outer layer of the stalk, the inner surface prominently warted by TL (Fig. 29); dehiscence into elongated platelets in upper sporotheca leaving a short lobed calyculus. Spores free, whitish in mass, almost hyaline to pale yellow green (121. p. Y G) by TL, subglobose, 10-12 µm diam., smooth by TL, evenly and densely warted by SEM (Fig. 32); spore wall of uniform thickness.

*Material examined:* JAPAN, Kochi Pref.: Motoyama-cho, bark of unidentified tree, in moist chamber, 1 to 19-VII-1980, NENB 13.043 (BR, holotype). COSTA RICA, Puntarenas Prov: Monteverde, nr St. Elena village, 10°19'21"N 84°46'05"W, on a decayed frond of *Chamaedorea tepijote*, field collection. 11-VI-1999, M. Schnittler & Y. Novozhilov, sc 14529. CUBA, Sancti Spiritus: Alturas de Banao, 21°52'39"N 79°37'03"W, on dead liana in moist chamber, 6-II-2003, dwb 2258.

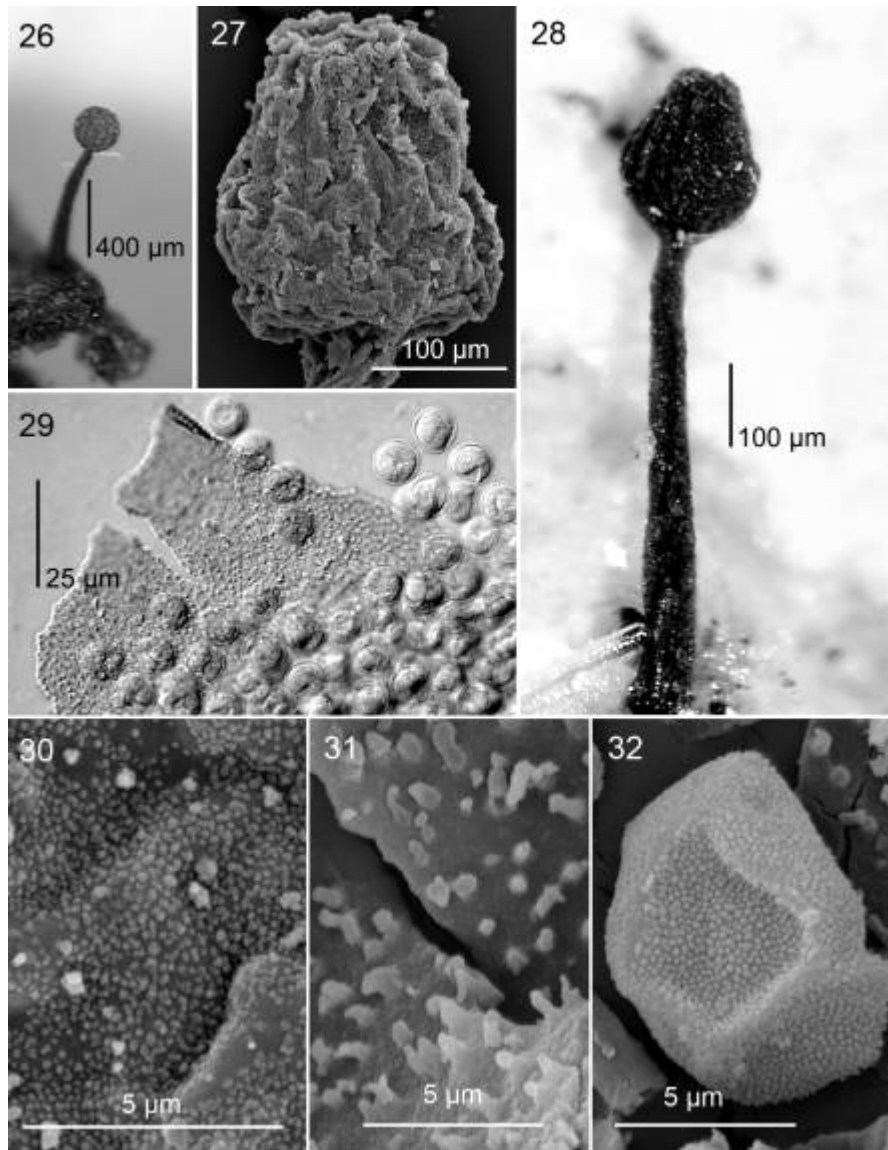
*Habitat:* bark of trees and vines.

*Distribution:* Costa Rica, Cuba, Japan,

*Illustrations:* Nannenga-Bremekamp and Yamamoto (1983: 210, Fig. 2a-d); Yamamoto (1998: 131).

The large closed tulip-shaped sporocarps (Figs. 26-28) were over 800 µm tall. When viewed with TL the sporotheca can be seen as almost transparent and distinct from the brown stalk. The stalk has longitudinal striations of granular material within an outer covering giving the appearance of a stalk within a stalk. The inner surface of the peridium is covered with large warts (Fig. 31) especially in the upper half. Between these warts or baculae by SEM, at very high magnification, smaller flatter warts are visible (Fig. 30). Dehiscence is by means of platelets which break away and open leaving a lobed cup. The spores are whitish in mass, almost hyaline by TL, smooth and thin-walled, 10-12 µm diam. (Fig. 29). The neotropical specimens (sc 14529 and dwb 2258) have shorter peridial warts.

This species was published as *Licea erectoides*, but later combined as a variety of *L. erecta* by one of the authors (Yamamoto, 1998), who stated that the only difference from *L. erecta* was the spore size. We requested the type of



**Figs. 26-32.** *Licea erecta* var. *erectoides*. **26.** Habit (dwb 2258). **27.** Tulip-shaped sporotheca by SEM with granular striations (NENB 13.043 as *Licea erectoides*). **28.** Habit (NENB 13.043). **29** Warted inner peridial surface and spores with wall of uniform diam. by TL (dwb 2258). **30.** Detail of inner peridial ornamentation with smallest surface warts x9000 by SEM. **31.** Larger warts of inner peridial surface x6000 by SEM. **32.** Detail of spore surface by SEM.

*L. erecta* var. *erecta* but had no reply and so have been unable to study it. De Haan (2002) SEM photographs shows a spore of *L. erecta* var. *erecta* from the collection of Nannenga- Bremekamp, showing it is smooth. We studied this material [BR-Myc 067670,61 from the collection Nannenga- Bremekamp

14807 (ex Yamamoto Y. 2912)] and doubt the rather small sporocarps belong to *L. erecta* var. *erecta*. The sporocarps measured 288 µm in height, and the diam. of the sporotheca was 115 µm. The box is labeled “*Licea erecta* Thind ? & Dhillon”. It did not fit the description of *L. erecta* var. *erecta* (see below), which exactly matches our observations of the holotype of *L. erecta* var. *erectoides*, with the exception of the spore size and ornamentation.

Our SEM and microscopic examination of *L. floriformis* var. *aureospora* (see below) shows similarities between these two species. The inner surface of the peridium is warted in both, they have almost colourless spores by TL of similar size range, and the ornamentation of the spores by SEM is also similar. They are different, however, when viewed by TL, as the inner layer of the peridium of *Licea erecta* var. *erectoides* appears as a flat base to the sporotheca and the outer layer of refuse appears as ribs outside along the length of the sporotheca, continuous with the ribbed stalk. The inner layer of the peridium of *L. floriformis* var. *aureospora* ends in a pointed calyculus, protruding down into the stalk and the outer refuse appears as a thin layer covering only the basal portion of the sporotheca. Macroscopically they are also different, with *L. floriformis* var. *aureospora* having a rounded sporotheca with a yellow spore mass showing through the top half, which fractures into small irregular platelets. The sporotheca of *Licea erecta* var. *erectoides* is tulip shaped, denser and all one colour, since none of the whitish spore mass shows through. The platelets are also slightly elongated.

Nannenga-Bremekamp and Yamamoto (1983) and de Haan (2002) both commented on specimen YY 101 (NENB 13044), as being different from the type of *L. erecta* var. *erectoides*. The spores by SEM are very similar to those of *L. floriformis* var. *aureospora*, and it seems probable that it belongs to that taxon.

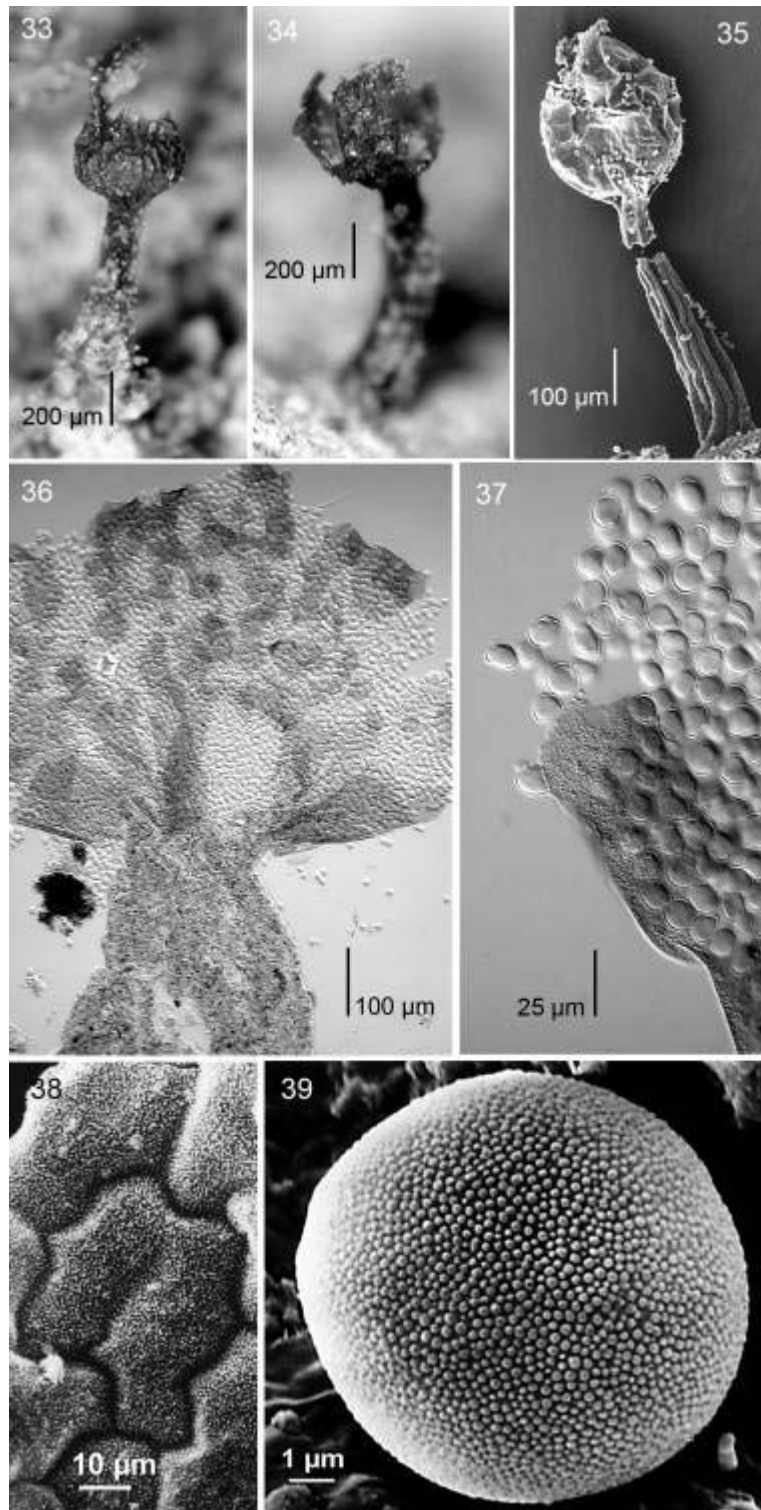
**6. *Licea floriformis* var. *aureospora*** M.T.M. Willemse & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. 97(1): 137. 1994. TYPE: THE NETHERLANDS, in the rural estate of Hoekelum near Ede, on bark of living *Sambucus nigra*, on 16 XII 1986 (holotype: 104 L in the collection of M.T.M. Willemse 104a, isotype NENB 16.075 now at BR!). (Figs. 33-46)

= *Licea longa* Flatau, Stapfia 73: 67. 2000, **syn. nov.** TYPE: GERMANY, Kassel, Borke von *Populus* spec., (1), 150 m über NN, 6.-26.10.1998, LF 3180 (holotype: B!).

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**Figs. 33-39.** *Licea floriformis* var. *aureospora*. **33-34.** Habit (NENB 16.705). **35.** Whole sporocarp by SEM. Dehiscing sporotheca and stalk with multiple strands (M. de Haan 001014). **36.** Dehiscing sporocarp by TL (M. de Haan 001014). **37.** Detail of spores by TL (M. de Haan 001014). **38.** Inner peridial surface with warts (M. de Haan 001014). **39.** Spore by SEM (Lado 11715).





= *Licea capitata* Ing & McHugh in Ing, Trans. Brit. Mycol. Soc. 78(3): 439. 1982, **syn. nov.** TYPE: UNITED KINGDOM, Scotia, Dumbarton, Balloch Park, reperta *in vitro* in cortice ablato ab arboris vivae *Aceris pseudoplatani*, 4 Oct. 1980, *B. Ing* (holotype: K!).

Sporocarps scattered, stipitate, 450 -1200  $\mu\text{m}$  in height. Sporotheca light olive brown, subglobose, 200-400(-700)  $\mu\text{m}$  diam. Stalk olive brown (94. l. Ol Br) concolourous with the sporotheca, 250-800  $\mu\text{m}$  long, straight, subcylindrical, tapering towards the top, plicate, filled with algae by TL, continuous with the sporotheca, mid-width a quarter of the height. Peridium double, covered below with gelatinous layer with granular refuse material forming patches or longitudinal striations continuous with the outer layer of the stalk, the inner layer membranous, greyish yellow (90. gy. Y- 91. d. gy. Y) with no inclusions, its inner surface warted to almost spiny by TL and by SEM (Fig. 38); dehiscence irregular in upper sporotheca into platelets, which are spiny at edge, leaving a short calyculus. Spores free, yellow gold in mass, pale yellow green (121. p. Y G) to colourless by TL, smooth, densely warted by SEM, 10-12,5  $\mu\text{m}$  diam.; spore wall of uniform thickness (Fig. 37).

*Material examined:* THE NETHERLANDS, Ede: Hoekelum, on bark of living *Sambucus nigra* in moist chamber, 16-XII-1986, NENB 16.705 (BR, isotype); BELGIUM, Zillebeke: Palingbeek, on logs of broad-leaved trees, 28-X-2001, MdH 001014; MEXICO, Veracruz: Catemaco, Los Tuxtlas Biological Reserve, 18°35'04"N 95°04'30"W, 200 m, on bark of living tree and bryophytes, 2-XII-1999, Lado11715. GERMANY, Hessen, Kassel-Wolfsanger, bark of living *Populus* sp. in moist chamber, 6 to 26-X-1998, LF 3180 (B, holotype of *Licea longa*); 7 to 26-X-1998, Hessen, Kassel, Fuldata, bark of living *Populus* sp. in moist chamber, 17-IX to 26-X-1998, LF 3169; 10-XII-1998, LF 3194 as *Licea longa*; Hessen, Kassel-Wolfsanger, bark of living *Populus* sp. in moist chamber, 21-XII-1999 to 3-II-2000, LF 3277 as *Licea longa*. UNITED KINGDOM, Scotland, Dumbartonshire, Dumbarton, Balloch Park, on bark of *Acer pseudoplatanus*, 4-X-1980, *B. Ing* [K(M): 129676 holotype of *Licea capitata*]. Wales, Coed Aber, SH665 718, on bark of *Quercus petraea* in moist chamber, 2-III-1993, dwb 1128.

*Habitat:* bark of living trees.

*Distribution:* Belgium, Germany, Ireland, Japan, Mexico, The Netherlands, United Kingdom.

*Illustrations:* Willemse and Nannenga Bremekamp (1994: 138, 139, Figs. 1-2); Flatau (2000: 67, Fig. 3 as *Licea longa*); de Haan (2002: 30, Plate 1; 32, Figs. 3-4)

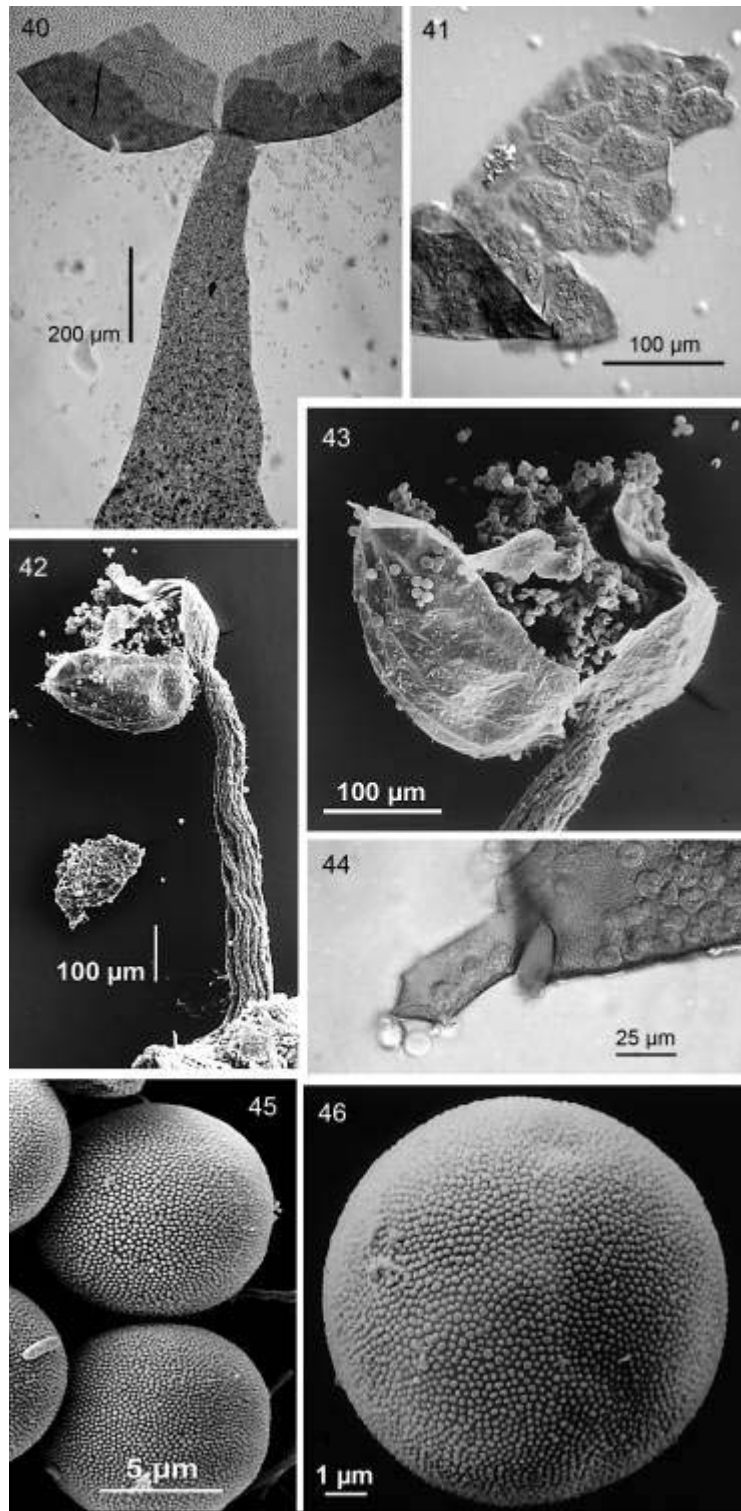
The type specimens were very big with a habit that is more like a *Trichia* than a *Licea* (Figs. 33-34) but without capillitium. The sporocarps were up to 1200  $\mu\text{m}$  in height with the largest sporotheca 700  $\mu\text{m}$  in diam. The peridium was dull pale brown by reflected light with a mottled appearance at the top with the yellow spore mass showing through the thinner outer peridial layer in places. The inner layer adhered to the outer layer and was densely warted on the inner surface (Fig. 38). The dark, obviously plicate stalk was made of overlapping strands visible by SEM (Figs. 35, 42) and filled with algae. The stalk was continuous with the sporotheca. Dehiscence was by platelets which had few patchy areas with refuse inclusions from the outer layer showing

through, and were warted to almost spiny and irregularly shaped (Figs. 35-36). An irregular very shallow calyculus was left. The spores were yellow gold in mass, hyaline to pale yellow green (121. p. Y G) and smooth by TL but evenly and densely warted with some fused warts by SEM (Fig. 39).

We also examined several collections of *L. longa* Flatau, kindly sent to us by the author, and the type material of this species (LF 3180). The habit, height (1000-1200  $\mu\text{m}$ ) and diam. (400-720  $\mu\text{m}$ ) of the specimens match those of the isotype of *L. floriformis* var. *aureospora* (Figs. 35, 42). The dehiscence was by irregular platelets which had plates with zip-like junctions and spines on the edge (Fig. 44) and similar patches of refuse to *L. floriformis* var. *aureospora* and which we think may be the remains of the outer peridium. The inner peridium surface has the same ornamentation of closely packed warts and the stalk was continuous with sporotheca SEM (Fig. 43). The spores were 10-12  $\mu\text{m}$  yellow gold and smooth by TL but evenly and densely warted with some fused warts by SEM (Figs. 45-46). In the description Flatau (2000) commented that these species were differentiated by the apparently single (*L. longa*) versus double peridium, and the opaque stalk of *L. floriformis* var. *aureospora*. We found the stalks and the peridium to be identical and we believe these to be the same species, on the basis of the detailed comparisons of the morphological features made of the type material of each and the SEM photographs. We therefore synonymize them here.

Comparison by SEM of this species with material from Mexico published under *Licea* sp. 1 by Lado *et al.* (2003) has allowed us to include this specimen in *L. floriformis* var. *aureospora*. De Haan (2002), in her SEM photographs shows the spores of the collection YY 101 (NENB 13044), tentatively identified as *L. erecta* var. *erectoides*, to be very similar to those of *L. floriformis* var. *aureospora*, and we agree that the specimen should be included in this species. Spore ornamentation viewed by SEM has been shown by Gilert (1994) to be a stable and important taxonomic character.

Ing (1999: 55) included under *Licea operculata* inoperculate forms previously described as *L. capitata* by Ing (1982), which he stated were the result of conditions of moisture during fructification. We requested the type specimen of *L. capitata* from Kew and compared it with the isotype of *L. floriformis* var. *aureospora*, and found that the size and ornamentation of the spores were the same, as were the characters of the stalk and the peridium. There were also comments on inoperculate sporocarps placed in *L. operculata* by Mitchell and McHugh (2000), but the photograph they publish with refuse material from the stalk continuing up the sides of the sporotheca to the middle, and the description of its irregular dehiscence at the apex, suggest that these specimens also belong to *L. floriformis* var. *aureospora*.



This variety was also recently reported from Asahi Town, Fukui Prefecture, Japan (Yamamoto *et al.*, 2004), extending its geographical distribution, previously limited to Europe and America.

The authors state that *L. floriformis* var. *aureospora* differs from *L. floriformis* var. *floriformis* in having a longer stalk and the colour of the spores in mass are yellow not black and colourless by TL not pale pink. As we were unable to study material of the latter variety we can not confirm this.

**7. *Licea lucens*** Nann-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 84(3): 285. 1981. TYPE: FRANCE, Dept. Doubs, near Gigot, on mosses and liverworts on bark taken from a living *Acer*, developed in a moist chamber: bark collected on 10 VI 1978, moistened 12 II 1979, the sporangia ripened from 15 III to 30 IV 1979 (holotype: NENB 11.194, now at BR!). (Figs. 47-51)

Sporocarps scattered or gregarious, stipitate, up to 150 µm in height. Sporotheca red brown when moist, rosy when dry, elliptical, 35-45 µm width, 70-100 µm height. Hypothallus inconspicuous. Stalk very short up to 30 µm long, hyaline by transmitted light, straight, cylindrical, with little included granular material, mid-width approximately equal to the height. Peridium single, transparent, hyaline, smooth and glossy on both sides; dehiscence by irregular fracture of the top, leaving a deep cup. Spores free, red brown to rosy in mass, pale yellow to light yellow by TL (89. p. Y-86. l. Y), subglobose, 8-10 µm diam., warted by TL, very prominent warts by SEM, spore wall uniformly thin.

*Material examined:* FRANCE, Dept. Doubs, Nr Gigot, on mosses and liverworts on bark of living *Acer* sp. in moist chamber, 15-III-1979 to 30-IV-1979, NENB 11.194 (BR, holotype)

*Habitat:* on mosses and liverworts on bark of living *Acer*.

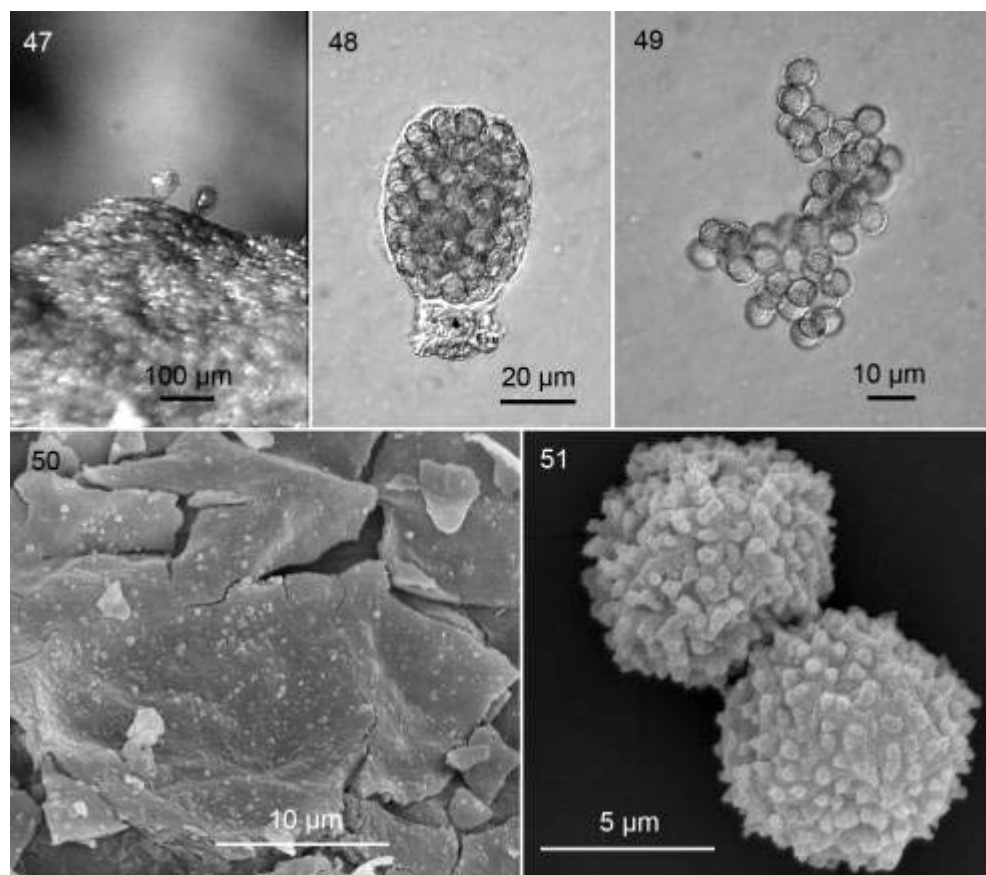
*Distribution:* Known only from the type locality.

*Illustrations:* Nannenga-Bremekamp (1981: 286, Fig. 1).

The type material shows many beautiful tiny sporocarps. They look like miniature glass beads full of rosy golden spores (Fig. 47). They appear to be sessile but close examination shows they are on a very short (30 µm) stalk which is just an extension of the peridium (Fig. 48). The peridium is completely hyaline and smooth outside and inside by transmitted light. By SEM however the inner surface is very sparsely and irregularly warted (Fig.

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**Figs. 40-46.** *Licea floriformis* var. *aureospora* (as *Licea longa* Flatau). **40.** Dehiscing sporocarp and spores by TL (LF 3169). **41.** Fragments of peridium by TL (LF 3180). **42.** Whole sporocarp by SEM. Dehiscing sporotheca and stalk with multiple strands (LF 3169). **43.** Detail of sporotheca by SEM (LF 3169). **44.** Detail of inner peridial surface and edge of platelet by TL (LF 3180). **45.** Group of spores by SEM (LF 3169). **46.** Surface detail of spore by SEM (LF 3169).



**Figs. 47-51.** *Licea lucens* (NENB 11.194). **47.** Habit. **48.** Intact sporocarp with spores by TL. **49.** Group of spores by TL. **50.** Smooth inner surface of peridium by SEM. **51.** Two spores showing verrucate ornamentation.

50). The spores show very clear dense ornamentation by TL (Fig. 49) which is prominent, and of the echinulate to verrucate type (Rammeloo, 1974, 1975) by SEM (Fig. 51).

This combination of characters is completely unique among the stipitate *Licea* species we have examined. The size and initial habit of shiny sporocarps is similar to *L. perexigua* (see below), but the shape, spore colour and ornamentation, and the mode of dehiscence are all different. This species is only known from the type locality, and its minute dimensions have probably caused it to be overlooked, or confused with algae or other bark epiphytes.

**8. *Licea operculata*** (Wingate) G.W. Martin, Mycologia 34(6): 702. 1942. *Orcadella operculata* Wingate, Proc. Acad. Nat. Sci. Philadelphia 41: 280. 1889. TYPE: U.S.A., Pennsylvania: Philadelphia, Fairmount Park or

Chestnut Hill, on trunks of living *Quercus rubra* L. (holotype: PH, now at BPI!). (Figs. 52-58)

Sporocarps scattered to loosely gregarious, stipitate, 500-1000 µm in total height. Sporotheca dull brown, usually urn-shaped, but rarely ovoid or almost globose, 200-500 µm diam. Stalk 300-640 µm in height, nearly black, slightly tapering towards the apex, furrowed, mid-width less than one fifth of height, filled with granular refuse material. Peridium single, thin, warted on the inner surface (Fig. 54) except for the lid, with ornamentation particularly visible at the edge of dehiscence (Fig. 55); dehiscence by a distinct shiny gold lid with a smooth inner surface by TL; the lid minutely punctate by SEM. Spores free, almost colourless to pale greenish yellow (104. p. g Y-121. p. Y G), smooth by TL (Fig. 54), 8-11µm diam., minutely punctate by SEM (Fig. 58); spore wall of uniform thickness.

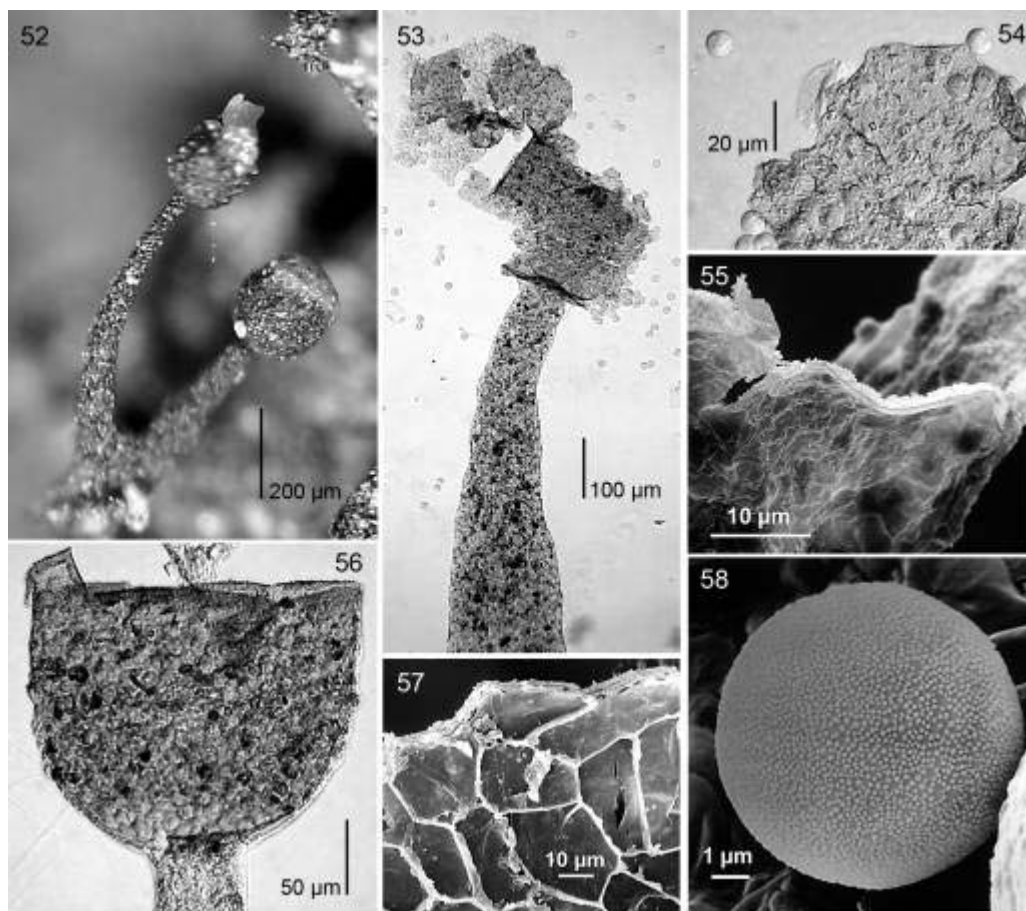
*Material examined:* USA, Philadelphia: Fairmount Park, [On bark living red-oak trees (*Quercus rubra*) Wingate 1889] (*Orcadella* Wingate 1275) ex state coll. (BPI 826296, type). ECUADOR, Prov. Orellana: Amazonian basin, Yasuni National Park, Lago Agrio, 0°40'30"S 76°23'45"W ± 600 m, bark of deciduous tree in moist chamber, sc17779; 0°40'09"S 76°24'03"W bark of *Cedrelinga catenaeformis* in moist chamber 28-V-2000, dwb 1833; 0°40'31"S 76°23'47"W, bark of deciduous tree in moist chamber, sc17808. Pichincha Prov.: Western Andean Slopes, Macquipucuna Reserve; Calacalí, 0°5'40"N 78°37'0"W, bark of dead liana in moist chamber, sc 13587. PERU, Mazan: 3°28'S 74°55'W, on dead liana in moist chamber, 22-VI-2002, dwb 2225. PUERTO RICO, Fajardo: El Verde, 18°20'30"N 65°49'30"W bark of living deciduous trees in moist chamber, sc 17091; sc 17336. Fajardo: on a ca. 1 km ESE San Vicente, 18°21'05"N 65°43'57"W, bark of a living deciduous tree in moist chamber, sc 17103. MEXICO, Veracruz: Catemaco, Los Tuxtlas Biological Reserve, 18°35'04"N 95°04'30"W, on bark of *Porteroni viridescens* in moist chamber, 31-V-2000, dwb 1836. Queretaro: Sta María del Mexicano, 20°49'25"N 100°03'24"W, on bark of *Yucca* sp. in moist chamber, 17-II-2004, dwb 2378.

*Habitat:* Bark of living trees.

*Distribution:* Ecuador, Mexico, Peru, Puerto Rico, Tanzania, USA.

*Illustrations:* Wingate (1889: 280); Lister (1925: pl. 149d-f, as *Orcadella operculata*); Nannenga-Bremekamp (1965: 134, 1974: 72); Martin and Alexopoulos (1969: Fig. 9); Emoto (1977: pl. 7, Figs. 5-8); Neubert *et al.* (1993: pl. 6, Figs. 3-4); Gilert (1994: Figs. 47-70); Lado and Pando (1997: 124, Fig. 24); Yamamoto (1998: 152).

The presence of variable morphotypes in this species was commented on by Wingate, in his original description (Wingate, 1889). He gave the range in height from 375-1250 µm. The sporocarps of the type material examined were > 800 µm in total height. The sporotheca were 300-500 µm in diam., urn-shaped, dull brown, and with a distinct shiny gold lid (Fig. 52) with a smooth inner surface by TL. The nearly black furrowed stipe had 3 or 4 intertwined strands inside it visible by TL. The type material had only a few (6) sporocarps left so we were not able to do SEMs of it. Our SEM pictures are of Schnittler's collection (sc17103) from Puerto Rico, and there are further SEM pictures in Gilert (1994).



**Figs. 52-58.** *Licea operculata*. **52.** Habit (BPI 826296). **53.** Urn-shaped sporotheca by TL (sc 17103). **54.** Inner peridial surface and spores by TL (sc 17103). **55.** Detail of rim of sporotheca by SEM (sc 17103). **56.** Urn-shaped sporotheca by TL (dwb 1833). **57.** Outer surface of sporotheca by SEM (sc 17103). **58.** Spore by SEM (sc 17103).

Typical large urn-shaped sporothecae with a distinct lid like the type specimens are unmistakable (Figs. 53, 56). Many of the smaller particularly tropical forms from moist chamber cultures we have examined are not as easily determined. They are variable in size from 500-700 µm in total height and the stalk is sometimes light brown and not furrowed. In addition in some collections the lid appears almost smooth on the inner surface, whereas in others some ornamentation (baculate processes see Gilert, 1994) is easily visible at 400x by TL. We have included in this taxon any specimens larger than 500 µm with a distinct lid, tapering stalk and smooth spores by TL within the size range and colour of this species.



This species is similar in habit and spore ornamentation to *L. floriformis* var. *aureospora* and *L. erecta* var. *erectoides* (see above), but it can be distinguished easily by its mode of dehiscence with a lid, and the edge of the sporotheca where the lid separates which has clear warts (Fig. 56). The spores of *L. operculata* are also smaller although there is overlap in the extremes of the sizes. The differences between this species and *L. poculiformis* Ukkola, the only other operculate stipitate *Licea*, are commented upon under that species below.

After comparing some specimens from Mexico published as *Licea* sp. 1 by Lado *et al.* (2003), with a visible lid, similar spores and peridium, we also include them in *L. operculata*, although the sporocarps are smaller. Ing (1999: 55) included inoperculate forms previously described as *L. capitata* but we have found that the type of *L. capitata* belongs to *L. floriformis* var. *aureospora* (see comments under this taxon). *Licea operculata* was also reported from Tanzania (Ukkola, 1998) on *Araucaria* bark in moist chamber culture. The author mentions that some specimens had poorly developed lids.

The brief description of *Orcadella operculata* var. *sessile* G. Lister (Monogr. Mycetozoa, ed. 3: 186. 1925) suggests a completely different sessile species.

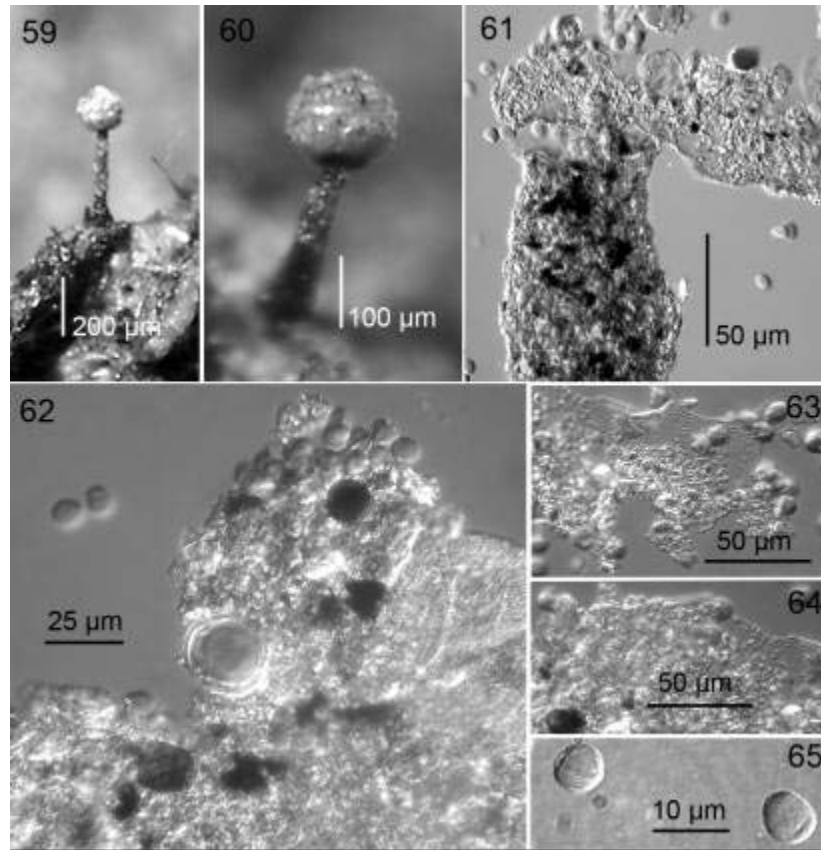
**9. *Licea parvicapitata*** Y. Yamam., Bull. Natl. Sci. Mus., Tokyo, B 26(3): 113. 2000. TYPE: JAPAN, Chiba Pref., Sawara-shi, Sawara-ho, Atago-jinja, on bark of living *Quercus acuta*, in culture, 18 V 1982, MT-2664 (holotype: TNS!). (Figs. 59-65)

Sporocarps scattered, solitary, stipitate, 480-700  $\mu\text{m}$  in height. Sporotheca golden, globose, 160  $\mu\text{m}$  diam., with large warts on the outer surface held up by a distinct thin darker stalk. Stalk 200-400  $\mu\text{m}$  in height, black (Fig. 59), straight, subcylindrical, tapering slightly towards the apex, filled with refuse matter (Fig. 61), opaque, mid-width up to a quarter of its height. Peridium single membranous, almost hyaline to pale grey, warted on its inner surface (Figs. 63-64), covered with refuse material discontinuous with the stalk, and irregular darker warts scattered on outer surface (Fig. 62); dehiscence circumcissile by a line very close to the base of the sporotheca leaving a very small calyculus, the remainder of the peridium breaks into small irregular platelets. Spores free, pale greenish yellow (121. p. Y G-104. p. g Y) to colourless, subglobose, smooth (Fig. 65), 7-8  $\mu\text{m}$  diam.; spore wall thin, with thickened area on one side.

*Material examined:* JAPAN, Chiba Pref.: Sawara-shi, Sawara-ho, Atago-jinja, on bark of living *Quercus acuta*, 18-V-1982, MT 2664 (TNS, holotype)

*Habitat:* bark of *Quercus acuta*.

*Distribution:* Known only from the type locality.



**Figs. 59-65.** *Licea parvicapitata* (MT 2664). **59.** Habit. **60.** Whole sporocarp showing line of dehiscence and spotted surface. **61.** dehiscid sporocarp by TL. **62.** Outer surface of peridium with refuse and darker irregular spots. **63-64.** Inner surface of hyaline peridium with warts. **65.** Spores by TL.

*Illustrations:* Yamamoto (2000: 113)

This species is only known from type material which showed stipitate sporocarps, most with a spotty appearance due to the peridial warts, although these were not evident on all sporocarps. The stalk was very thin and fragile and fractured on mounting. The combination of the dark thin stalk, the spotted golden brown sporotheca and the small spores make this species easily distinguished from the others. There were crystals among the refuse material of some specimens when viewed with Nomarski, but the longer thinner stalk, larger sporocarp size (480-700 µm vs. 360-480 in *L. eleanorae*), dehiscence near the base not the apex, and lighter spores (121. p. Y G-104. p. g Y vs. 89. p. Y) of *L. parvicapitata* differentiate it from *L. eleanorae*.

**10. *Licea pedicellata*** (H.C. Gilbert) H.C. Gilbert in Martin, Mycologia 34(6): 702. 1942. *Hymenobolina pedicellata* H.C. Gilbert, Stud. Nat. Hist. Iowa Univ. 16(2): 153. 1934. TYPE: U.S.A., Iowa, Milford, on bark of living *Ulmus*, 16 July, 1932, *H.C. Gilbert 2117* (holotype: BPI!). (Figs. 66-74)

Sporocarps scattered to gregarious, stipitate, 200-500  $\mu\text{m}$  in height. Sporotheca dark brown or black, subglobose, rounded even when dry, 75-175  $\mu\text{m}$  diam. Stalk 125-325  $\mu\text{m}$  in height, thick, straight, cylindrical, furrowed, continuous with outer peridium, filled with granular refuse material, mid-width less than half the height. Peridium double, but apparently single, with an adhering outer layer of refuse material, membranous, dull brown; dehiscence into irregular platelets 20-30  $\mu\text{m}$  wide, inner layer warted (Fig. 68). Spores free, dark brown in mass, medium yellow to greyish yellow (87. m. Y-90. gy. Y) by TL, subglobose, (10-)11-13(-14)  $\mu\text{m}$  diam., minutely warted by TL (Fig. 70) and densely warted by SEM (Fig. 72); spore wall with a paler thinner area.

*Material examined:* USA, Iowa, Milford [coll W. Okoboji acc. to Gilberts letter Dec. 7, 1934 on box] on bark of elm (in moist chamber), 16-VII-1932, H.C. Gilbert 2117 (BPI 826385, holotype) as *Hymenobolina pedicellata*; (BPI 657294, isotype) as *Licea pedicellata*. Iowa: Milford [on bark of living *Ulmus*, see Gilbert (1934: 154)], 16-VII-1932, coll. W. Okoboji [HC Gilbert 2117] (BPI 826368, isotype) as *Licea pedicellata*. Iowa city on dead *Ulmus* sp., 00-XII-1961, coll. G.W. Martin (BPI 805746). Virginia, Mt. Lake Biol. Station, on bark of *Quercus* sp. in moist chamber, 12-VIII-1969, leg. & det. C.J. Alexopoulos (BPI 826366). Texas: Austin, Hancock Center, on bark of living *Ulmus crassifolia* in moist chamber, 5-VIII-1974, leg. & det. C.J. Alexopoulos (BPI 737641).

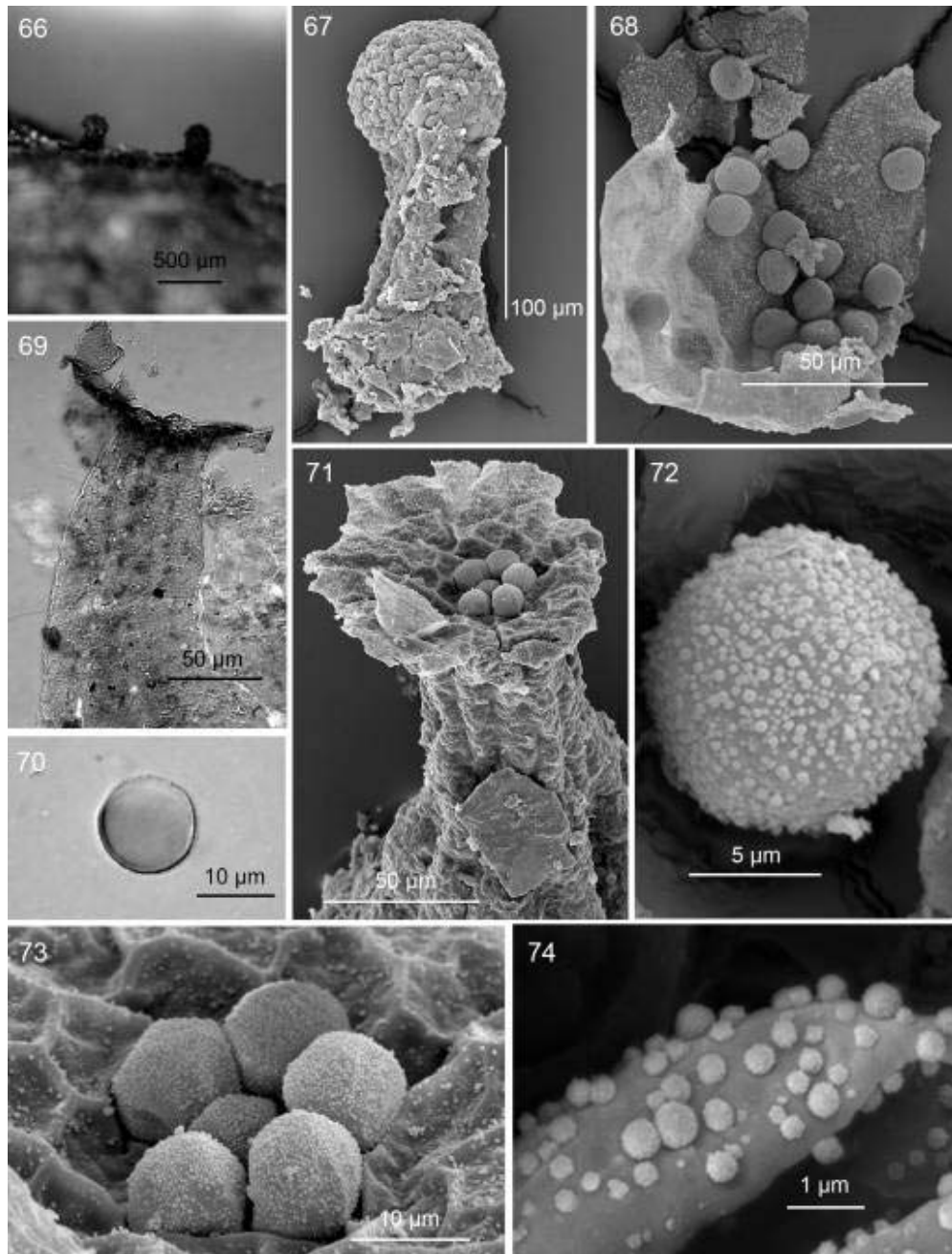
*Habitat:* Bark of living trees.

*Distribution:* Zaire?, USA.

*Illustrations:* Gilbert (1934: 154, Fig. 1); Martin and Alexopoulos (1969: 481, pl. 1 Fig. 11a-c); Gilert (1994: 17, Fig. 47); Yamamoto (1998: 142).

In the original description of the species, Gilbert (1934) states that the spores are “smooth or faintly and finely warted”. Examination of all the BPI collections of type material, both by TL and SEM, showed all the spores to be warted, and none were smooth as Gilbert suggested. This is the main distinguishing character of this species from other similar species like *L. rugosa* (Table 2). The faint warts are discernible by TL at 400x (Fig. 70), and SEM examination revealed dispersed warts (Fig. 72), which were irregular in size. At great magnification (Fig. 74) they were seen to have a warted surface themselves.

Another clear characteristic visible by TL is that the interior of the peridium is warted, but the warts are dispersed and separate (Fig. 73). In addition almost the entire peridium breaks into platelets leaving a very shallow structure attached to the stalk (Figs. 69, 71). We were not able to see clear ridges or lines of dehiscence in any of the specimens, and all the specimens retained their rounded shape even when dry (Fig. 67). Martin and Alexopoulos (1969: 48) also commented that they “rarely observed platelets in the



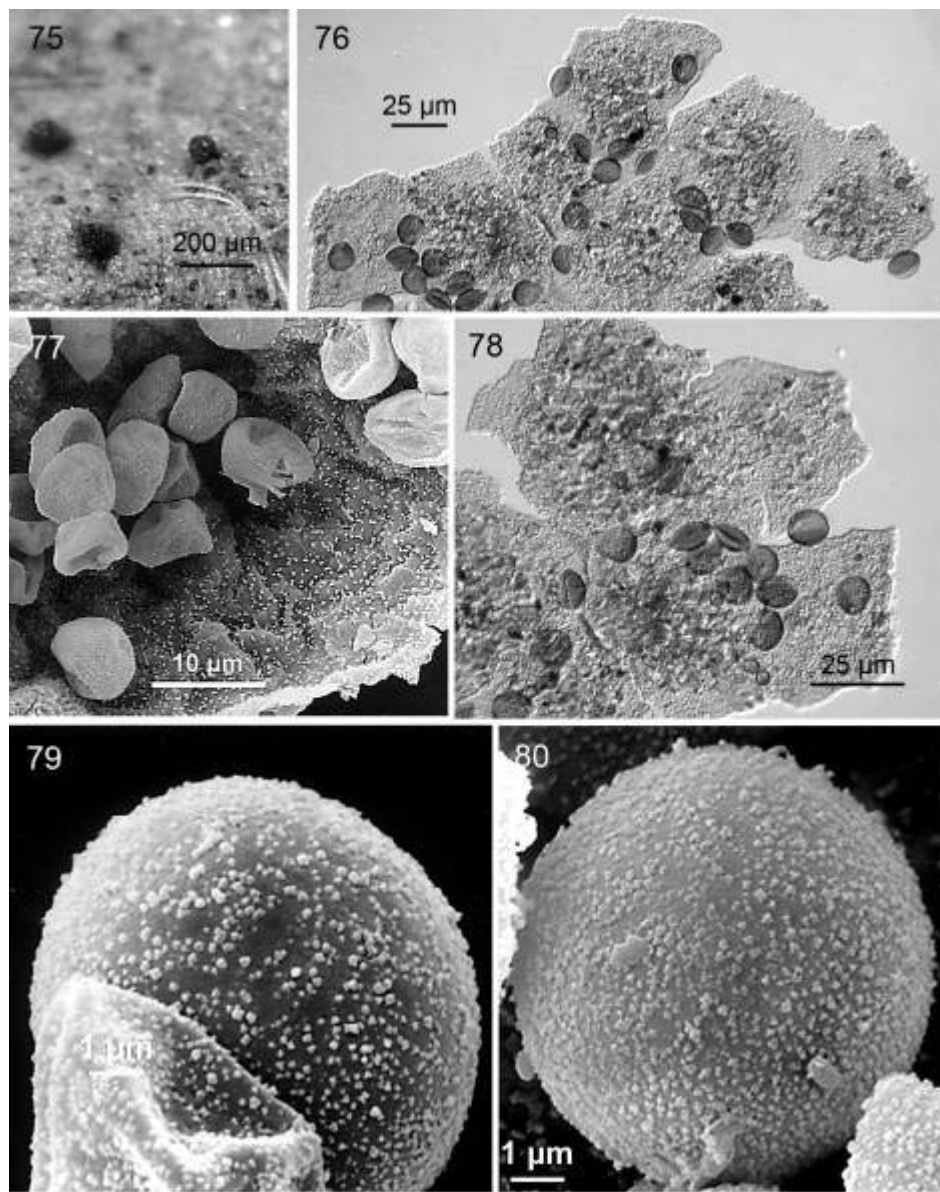
**Figs. 66-74.** *Licea pedicellata*. **66.** Habit (BPI 826368). **67.** Whole sporocarp by SEM (BPI 737641). **68.** Irregular platelets with warted inner surface (BPI 826385). **69.** Dehiscent sporocarp by TL with shallow flat remains of peridium (BPI 826385). **70.** Spore by TL (BPI 826385). **71.** Dehiscent sporocarp with flat remains of peridium by SEM (BPI 657294). **72.** Spore by SEM (BPI 657294). **73.** Group of spores and detail of inner peridial surface by SEM (BPI 657294). **74.** Highly magnified ( $\times 20,000$ ) detail of spore ornamentation by SEM (BPI 657294).

**Table 2.** Characters differentiating *L. pedicellata*, *L. rugosa* var. *rugosa* and *L. rugosa* var. *fujiokana*.

Name	Dehiscence	Peridium	Spore	Other
<i>L. pedicellata</i>	Irregular fragments; flat base of sporotheca left	Dispersed warts on inner surface	Yellowish brown; <b>warted</b> ; (10-)11-13(-14) $\mu\text{m}$ diam.	Sporotheca <b>round</b> when dry
<i>L. rugosa</i> var. <i>rugosa</i>	Irregular fragments	Prominent dense warts on inner surface	Olive-brown; <b>smooth</b> ; 14-16 $\mu\text{m}$ diam.	Sporotheca <b>wrinkled</b> when dry
<i>L. rugosa</i> var. <i>fujiokana</i>	Irregular fragments	Prominent dense warts on inner surface	Greyish yellow brown; <b>smooth</b> ; 10-12 $\mu\text{m}$ diam.	Sporotheca <b>wrinkled</b> when dry

peridium". We did a SEM study of material cited by Pando and Oltra (2001) from Mogente, Spain [MA-Fungi 40549 (Oltra 2519)] but found it to have smooth spores and a different ornamentation of the inner peridium and we conclude that it does not belong to this taxon. Of the other material examined in our herbarium that had been assigned to this species (DWM 3313 from Mexico on red cedar bark in moist chamber, and TEB 3704 from Virginia-Baskerville cemetery, USA, cedar tree #3, 28-VIII-1970), none had warted spores except another sample (DWM 4478) from Zaire, but the single slide of this was insufficient for us to positively confirm its identity. The SEM picture in Gilert (1994) shows a rugose sporocarp with apparent platelets, which casts doubt on its identity as *L. pedicellata*. It is possible that this species has been confused with *L. rugosa*, and that its distribution is not as widespread as Martin and Alexopoulos (1969: 48) and other authors (Yamamoto, 1998; Ing, 1999) believed, since they mention also Australia, Austria, Great Britain, Greece, India, Japan, Mexico, Tunisia and Turkey. The similarities between *L. pedicellata*, *L. rugosa* and the varieties of each are discussed below.

It is worth noting that the three boxes of dried type material lent to us by the BPI herbarium have slight differences in the labels. One of them (BPI 826385) lists the locality as Milford Iowa, as does Gilbert's description (1934), with a note "coll. W. Okoboji acc. to Gilberts letter Dec. 7, 1934", another (BPI 657294) lists Okoboji, Iowa, both in script. Collection BPI 826368 lists Milford and coll. W. Okaboji (sic). We note for clarification that West Okoboji is a town slightly West of Milford, both in Dickinson County Iowa. It seems that "coll." here refers to the place of collection, not who it was collected by, the accepted meaning of this abbreviation (Stearn, 1996).



**Figs. 75-80.** *Licea perexigua*. **75.** Habit (dwb 1936). **76.** Inner surface of peridium densely papillate by TL (HWK 1166). **77.** Inner surface of dehiscent sporotheca with spores by SEM (dwb 1936). **78.** Inner surface of peridium densely papillate by TL (HWK 1166). **79-80.** Detail of spore surface ornamentation by SEM (dwb1936).

**11. *Licea perexigua*** T.E. Brooks & H.W. Keller in Keller and Brooks, Mycologia 69(4): 674. 1977. TYPE: U.S.A., Arkansas, Crawford County, on the bark of living *Juniperus virginiana*, October 27, 1964, T.E. Brooks 2747 (holotype: BPI!). (Figs. 75-80)

Sporocarps scattered to gregarious, stipitate or sessile on a narrowed base, up to 100 µm in height. Sporotheca golden, iridescent, subglobose, 40-100 µm diam. Hypothallus inconspicuous. The stalk when present pale yellow by TL, less than half the total height of sporocarp, filled with granular refuse material. Peridium single, membranous, colourless by TL, with scant granular refuse matter evenly distributed over the surface, inner surface closely papillate; dehiscence circumcissile low down at the base of the sporotheca leaving a calyculus. Spores free, pale to greyish green yellow (121. p. Y G-122. gy. Y G), from 8.5-10.5 µm diam., smooth by TL, minutely ornamented with unevenly scattered warts by SEM (Fig. 79); spore wall thin, with a paler thinner area.

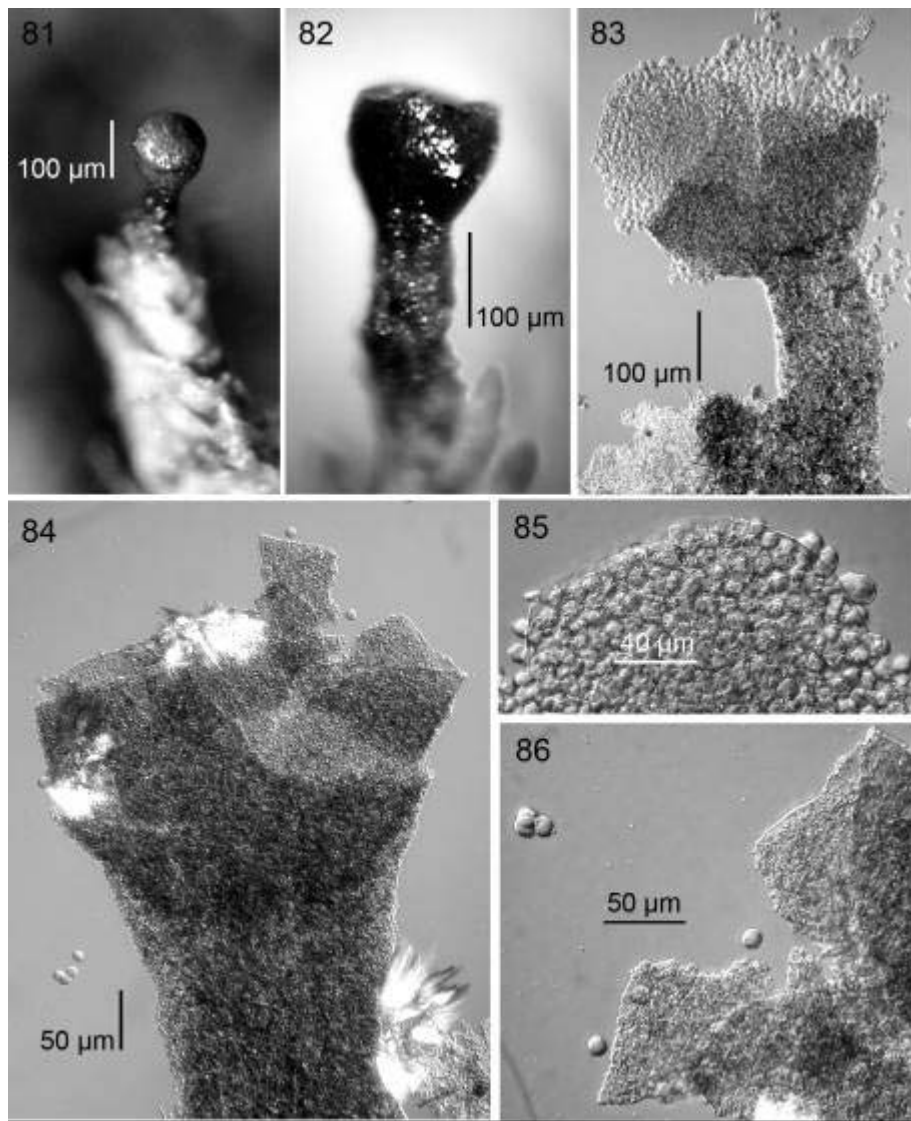
*Material examined:* USA, Arkansas: Crawford Co., [on bark of living *Juniperus virginiana* in moist chamber (Keller and Brooks, 1977)], 27-X-1964, coll. TEB 2747 (BPI 826404, holotype). Mississippi: Mississippi co., moist chamber, coll. HWK 1166 (slide). MEXICO, Tlaxcala: Cuapiaxtla, 19°19'40"N 97°41'44"W, on bark of living *Juniperus deppeana* in moist chamber, 18-I-2001, dwb 1936. Hidalgo: Progreso, La Cruz, 20°16'02"N 99°10'48"W, on bark of living tree *Opuntia* sp. in moist chamber, 26-III-2001, dwb 2021. SPAIN, Cuenca: Saceda-Trassierra, on bark of *Quercus ilex* in moist chamber, Pando 1185, 21-III-1990, MA-Fungi 31964.

*Habitat:* bark of living trees.

*Distribution:* Mexico, Spain, USA.

*Illustrations:* Keller and Brooks (1977: 675, Figs. 13-17); Lado and Pando (1997: 127, Fig. 35); Novozhilov *et al.* (2003) (as *L. cf. perexigua*).

The type material showed very tiny, almost sessile, golden iridescent sporocarps. The specific epithet gives the most obvious character of exceedingly small and with a stalk so short that even the stipitate sporocarps appear sessile. Many calyculi of dehiscent sporocarps were visible on the bark surface in the type specimen, the stalk remaining with a tiny cup-shaped sporothecal base on top. The single peridium in some specimens is completely hyaline, and refuse material is very sparse even when present. The ornamentation on the inner surface is visible at 400x (Figs. 76, 78), appearing to be in a reticulate pattern as described by the authors (Keller and Brooks, 1977), but by SEM (Fig. 77) it can be seen that this pattern is not a true reticulum but is the result of the uneven distribution of the papillae and there are some smooth areas without ornamentation. By TL the spores seem smooth and have thin walls with a paler thinner area at which they have a tendency to fold (Fig. 78), but by SEM irregularly distributed rhomboid warts are visible (Figs. 79-80) with some so close together as to appear fused, and others with spaces between them.



**Figs. 81-86.** *Licea poculiformis*. **81.** Habit (Ukkola 319A). **82.** Whole sporocarp showing goblet-shaped sporotheca and pale lid (Ukkola 319A). **83.** Dehiscent sporocarp (dwb 1759). **84.** Deep cup of dehiscent sporotheca by TL (dwb 1759). **85.** Spores by TL (dwb 1759). **86.** Inner surface of peridium by TL (dwb 1759).

The unique pattern of ornamentation on the spores distinguishes this species from the other stipitate species. In addition it is smaller than all of them except *L. lucens* (see above). The transparent peridium is another clear character. Keller and Brooks (1977) differentiate *L. perexigua* from *L. tenera* by the broad base of the sessile sporocarps in the latter species, its different



peridial colour and ornamentation, and its larger (12  $\mu\text{m}$  vs. 8.5-10.5  $\mu\text{m}$  diam.) spores. The authors also differentiate it from *L. scyphoides* by its almost sessile habit, its smaller [11-13.5(-14)  $\mu\text{m}$  diam. in the latter species] slightly darker spores (121. p. Y G-122. gy. Y G vs. 90. gy. Y-104. p. g Y), and its manner of dehiscence (irregular vs. circumcissile in *L. scyphoides*). Our observations concur with theirs.

**12. *Licea poculiformis*** Ukkola, Acta Bot. Fennica 160: 5. 1998. TYPE: TANZANIA, Tanga Province, Lushoto District, East Usambara Mts., on mosses growing on bark of *Cupressus* sp., in moist chamber culture, 12.XII.1995, Ukkola 319A (holotype: H!). (Figs. 81-86)

Sporocarps scattered, stipitate, 150-200(-400)  $\mu\text{m}$  in height. Sporotheca treacle-brown, goblet-shaped, 100-150  $\mu\text{m}$  diam., with a shiny pale lid (Fig. 81). Stalk 50-150  $\mu\text{m}$  in height, furrowed, mid-width half the stalk height. Peridium double, outer layer coriaceous, shiny, inner layer membranous; dehiscence by a pale shiny lid with a clear edge and warts on the margin, leaving a deep cup (Fig. 84). Spores free, pale greenish to greyish yellow (90. gy. Y - 104. p. g Y) by TL, 8.5-10  $\mu\text{m}$  diam., smooth by TL (Figs. 85-86) but warted by SEM (Ukkola, 1998: 6, Fig. 7); spore wall with a slightly thinner paler area.

*Material examined:* TANZANIA, Tanga Province, Lushoto District, East Usambara Mountains, Amani Forest Reserve, submontane forest, alt. 900 m, on mosses growing (sec. Ukkola, 1998) on bark of living *Cupressus* sp. in moist chamber culture, 13-IX-1995 (on the label), Ukkola 319A (H, holotype). MEXICO, Quintana Roo, El Eden, bark of living *Hematoxylon campechianum* in moist chamber, 10-II-2000, dwb 1759 [Lado *et al.*, 2003: 88].

*Habitat:* moss and bark of living trees.

*Distribution:* Mexico, Tanzania.

*Illustrations:* Ukkola (1998: 6, Figs. 2-7).

The sporotheca and stalk of this small species are concolourous, treacle-brown. The abundant sporocarps in the type specimen were mostly projecting from the tips of moss leaflets. The Mexican material is much larger (up to 400  $\mu\text{m}$  see Fig. 83) but otherwise agrees with the type. This species has been reported recently from Okayama Prefecture, Japan on the bark of living *Prunus* sp. (Yamamoto and Fujioka, 2004) and the Japanese specimens described are also larger than the type. This species is closest to *L. operculata*, and shows similarity in the habit, and also the inner surface of the peridium by SEM, but the type specimens are different in their deep brown colour, have a large difference in size (150-400  $\mu\text{m}$  in height vs. 500-1000  $\mu\text{m}$  in *L. operculata*), and a double peridium vs. single in *L. operculata*. The lid of *L. poculiformis* is at the broadest diam. of the sporotheca, and wider than that of *L. operculata*, has a clear edge and is distinctly papillose by TL, whereas the lid of the *L. operculata* appears smooth by TL and is at the narrowing top portion of its

more globose sporotheca. Finally, the ratio of stalk width to height is different with *L. poculiformis* much shorter and squatter and with a straight wide stalk (Fig. 82) and with the outer peridium continuous with the sporotheca, not long and tapered and separate from the sporotheca like *L. operculata*.

**13. *Licea rugosa*** Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 90(3): 326. 1987. **var. *rugosa***. TYPE: JAPAN, Kochi Pref., Agawa-mura, Mnt. Nakatsu, on the bark of a living *Aesculus turbinata* Blume, VII 1984, Y.Y. 2300 (holotype: TNS, isotype NENB 14.476 now at BR!).  
(Figs. 87-93)

Sporocarps scattered, stipitate, up to 150-500 µm in height. Sporotheca dark brown to almost black, subglobose up to 150 µm diam. Stalk up to 180 µm in height, straight, cylindrical, furrowed (Fig. 88), stout, continuous with the outer peridium, mid-width half of the stalk height. Peridium single, membranous, wrinkled with darkened ridges visible when dry, prominently warted on the inner surface; dehiscence irregular fracture into fragments in the upper part leaving a calyculus (Figs. 88, 92) Spores free, dark brown in mass, olive brown (94. l. Ol Br) by TL, subglobose, 14-16 µm diam., totally smooth; spore wall with a thinner area (Fig. 89).

*Material examined:* JAPAN, Kochi Pref.: Agawa-mura, Mnt. Nakatsu, bark of living *Aesculus turbinata*, VII 1984, coll. NENB 14.476 [ex YY 2300] (BR, isotype). MEXICO, Hidalgo: Progreso, La Cruz, 20°16'02"N 99°10'48"W, on bark of living *Prosopis laevigata* in moist chamber, 22-III-2001, dwb 2005; on bark of living *Schinus molle* in moist chamber, 16-III-2001, dwb 2006. Puebla: Emilio Portes Gil, 19°17'40"N 97°30'22"W, on bark of living *Yucca filifera* in moist chamber, 25-I-2001, dwb 1955. Zapotitlán de las Salinas, 18°20'00"N 97°27'45"W, on bark of living *Beaucarnea gracilis* in moist chamber, 11-IX-2003, dwb 2311; ibidem, 13-IX-2003, dwb 2319. Tehuacán, Santiago Nopala, 18°25'57"N 97°36'46"W, on bark of living *Yucca periculosa* in moist chamber, 11-XI-2003, dwb 2332; ibidem, bark of living *Beaucarnea gracilis* in moist chamber, 22-XI-2003, dwb 2335. Queretaro: Peña Miller, Camargo, 21°06'06"N 99°43'29"W, on bark of living *Prosopis laevigata* in moist chamber, 15-II-2002, dwb 2154.

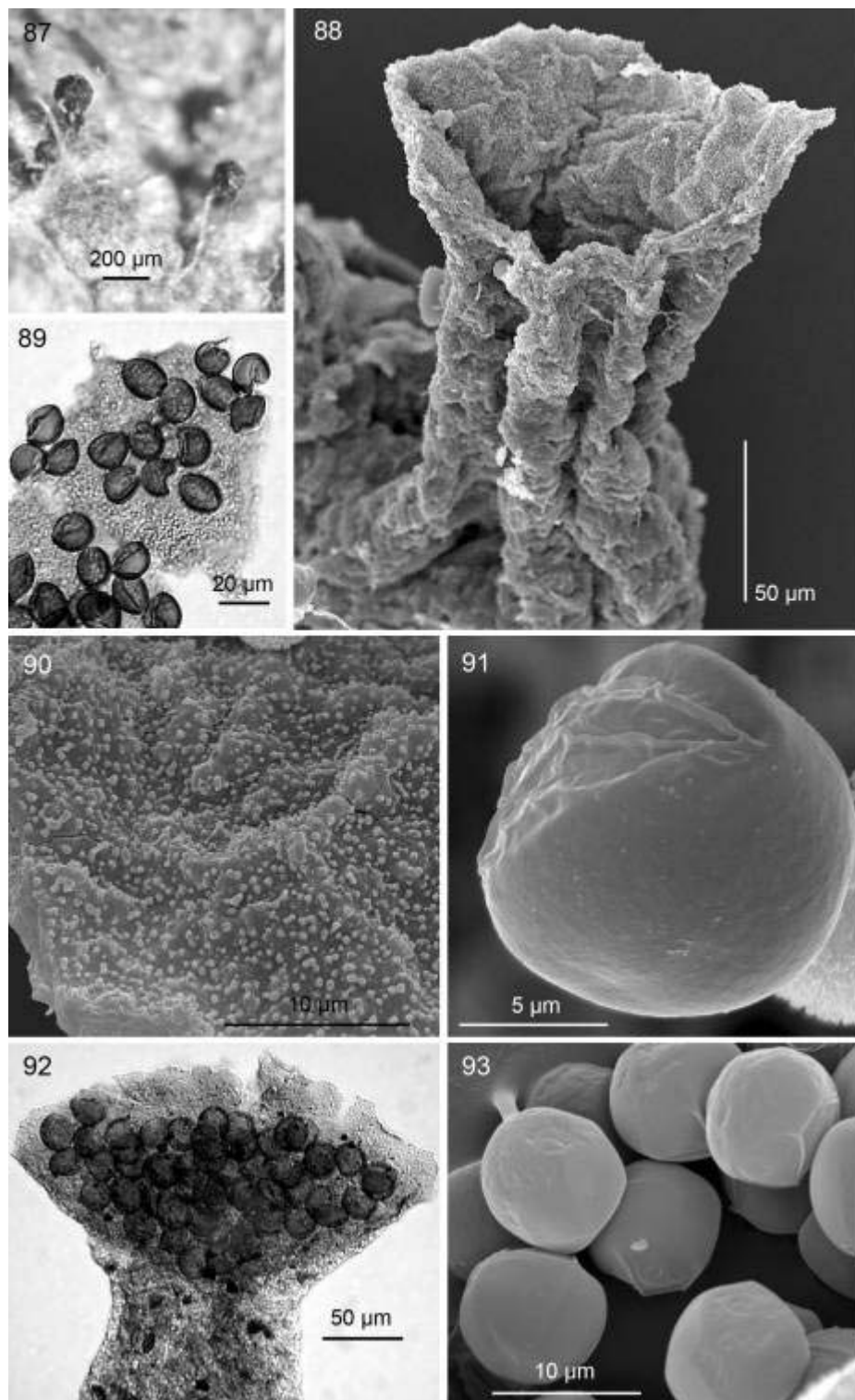
*Habitat:* bark of living trees.

*Distribution:* Japan, Mexico.

*Illustrations:* Nannenga-Bremekamp and Yamamoto (1987: 326); Yamamoto (1998: 144).

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**Figs. 87-93.** *Licea rugosa* var. *rugosa*. **87.** Habit (NENB 14.476). **88.** Dehisced sporocarp by SEM showing calyculus and furrowed stalk (NENB 14.476). **89.** Dark spores with wall thinner in one area by TL (dwb 2006). **90.** Inner surface of peridium with prominent dense warts (NENB 14.476). **91.** Smooth spore by SEM (NENB 14.476). **92.** Calyculus of dehisced sporocarp containing spores (dwb 2006). **93.** Group of smooth spores by SEM (dwb 2319).



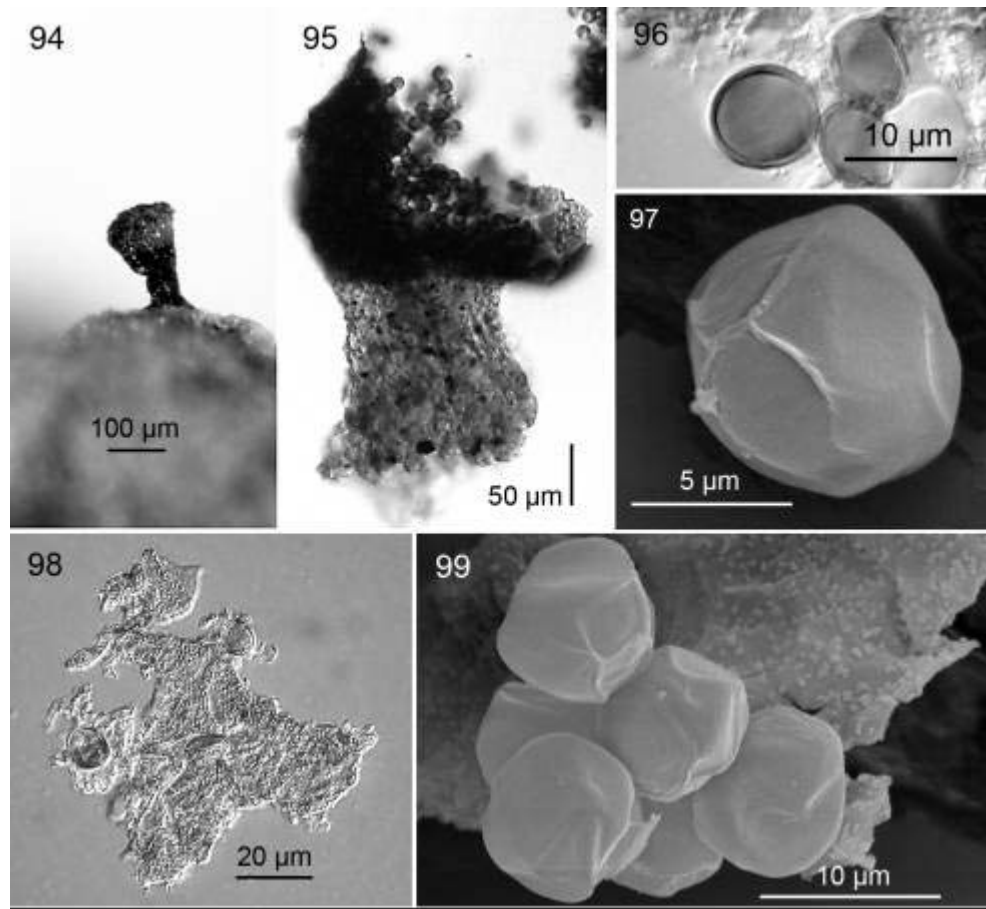
The abundant Mexican material was identical to the type both by microscopic examination and by SEM. The most obvious differentiating features of this species are the size and rather dark colour of the spores. The sporocarps examined were of varied height from almost sessile to 500 µm. The sporotheca are globose when wet but very wrinkled when dry, with prominent ridges. The spores by TL look like the spores of *L. parasitica* (Zukal) Martin [11-13(-16) µm diam.], but the thinner area is less pronounced, and the spores were completely smooth even by SEM (Figs. 91, 93). The wrinkled sporotheca breaking into platelets instead of the lid of *L. parasitica* easily avoids any confusion even with the sessile specimens. The plasmodium, visible in moist chamber cultures, is thick dull brown and appears as a continuous sludge on the bark surface like many large protoplasmodia combined.

In the original description of *L. rugosa* Nannenga Bremekamp & Yamamoto (1987) differentiated it from *L. pedicellata* on the basis of the spore colour being dark brown and the smooth spores. The spores are also slightly bigger in *L. rugosa* and the smooth surface vs. the warted surface of *L. pedicellata* spores (Figs. 68-70) is confirmed by SEM. The peridial ornamentation is also different in density and distribution (Figs. 64, 90) as revealed by SEM examination, and some of the warts are fused in *L. rugosa* (Fig. 90). However, *L. rugosa* and its var. *fujiokana* (see below) are very like *L. pedicellata* but with the definable differences listed (Table 2). DNA sequencing techniques may demonstrate that they are in fact a continuum of the same species, but at present pending further studies, we prefer to maintain them as separate taxa.

**14. *Licea rugosa* var. *fujiokana* (Y. Yamam.) D. Wrigley & Lado, **comb. nov.****  
(Figs. 94-99)

≡ *Licea capitatoidea* var. *fujiokana* Y. Yamam., Bull. Natl. Sci. Mus., Tokyo, B 26(3): 112. 2000. TYPE: JAPAN, Tokyo Pref., Chiyoda-ku, on the premises of Imperial Palace, on bark of living *Acer buergerianum*, 3 VI 1999, Y. Yamamoto, 99TK-29 (holotype: TNS!; isotype 99TK-26 in TNS).

Sporocarps scattered, stipitate, 150-320 µm in height. Sporothecae dark brown, globose or subglobose, 80-200 µm diam. Stalk 70-160 µm in height, slightly tapering towards the top, filled with refuse material, mid-width half the height. Peridium double, wrinkled, outer layer gelatinous with granular refuse material, inner layer membranous, yellow-grey (93. y Gray) with a densely warted surface; dehiscence by irregular fracture into fragments in upper peridium leaving a calyculus. Spores free, greyish yellow brown (80. gy. Y Br), subglobose, (9-)10-11 µm diam., smooth by TL and SEM; spore wall with an obvious paler area about half the diam. of the spore (Figs. 96-97).



**Figs. 94-99.** *Licea rugosa* var. *fujiokana* (99TK29 as *Licea capitatooides* var. *fujiokana* Y. Yamam.). **94.** Habit. **95.** Dehiscing sporocarp by TL. **96.** Spores by TL with paler area. **97.** Spore by SEM. **98.** Inner surface of peridium by TL. **99.** Group of spores and inner surface of peridium by SEM.

*Material examined:* JAPAN, Tokyo Pref.: Chiyoda-ku, bark of living *Acer buergerianum* in moist chamber, 3-VI-1999, leg. Y. Yamamoto, 99TK-29 (TNS, holotype). MEXICO, Tlaxcala: Calpulalpan, El Peñón, on *Abies religiosa* in moist chamber, 19-II-1998, VGA 671. Hidalgo: El Cardonal, 20°38'56"N 99°00'11"W, on bark of *Prosopis juliflora* in moist chamber, 9-XI-2000, dwb 1851. Metzquititlan, 20°29'48"N 98°40'03"W, on bark of *Acacia* sp. in moist chamber, 5-X-2001, dwb 2076, idem, 23-XI-2001, dwb 2067. Puebla: Emilio Portes Gil, 19°17'40"N 97°30'22"W, on bark of living *Nolina parviflora* in moist chamber, 18-I-2001, dwb 1932; on bark of living *Yucca filifera* in moist chamber, 25-I-2001, dwb 1955; 3-II-2001, dwb 1979. Zapotitlán de las Salinas, 18°19'22"N 97°29'57"W, on bark of living *Beaucarnea gracilis* in moist chamber, 1-X-2001, dwb 2077. S. Martin Esperilla, 18°44'45"N 97°31'44"W, on bark of living *Yucca periculosa* in moist chamber, 22-XI-2003, dwb 2348; idem, 29-XI-2003, dwb 2344. Veracruz: Totalco, 19°28'56"N 97°22'00"W, on bark of living *Juniperus deppeana* in moist chamber, 18-I-2001, dwb 1966. San Luis Potosi:

Xilitla, Reten, 21°18'04"N 99°05'07"W, on bark of living *Liquidamber styraciflua* in moist chamber, 26-XI-2001, dwb 2104. Oaxaca: Tepelmeme, La Unión, 18°06'33"N 97°20'31"W, on bark of living *Prosopis laevigata* in moist chamber, 15-XI-2003, dwb 2316; Tepelmeme, Mex-135 highway, Km. 109, 18°00'35"N 97°21'19"W, on bark of living *Yucca periculosa* in moist chamber, 29-XI-2003, dwb 2349.

*Habitat*: bark of living trees.

*Distribution*: Japan, Mexico.

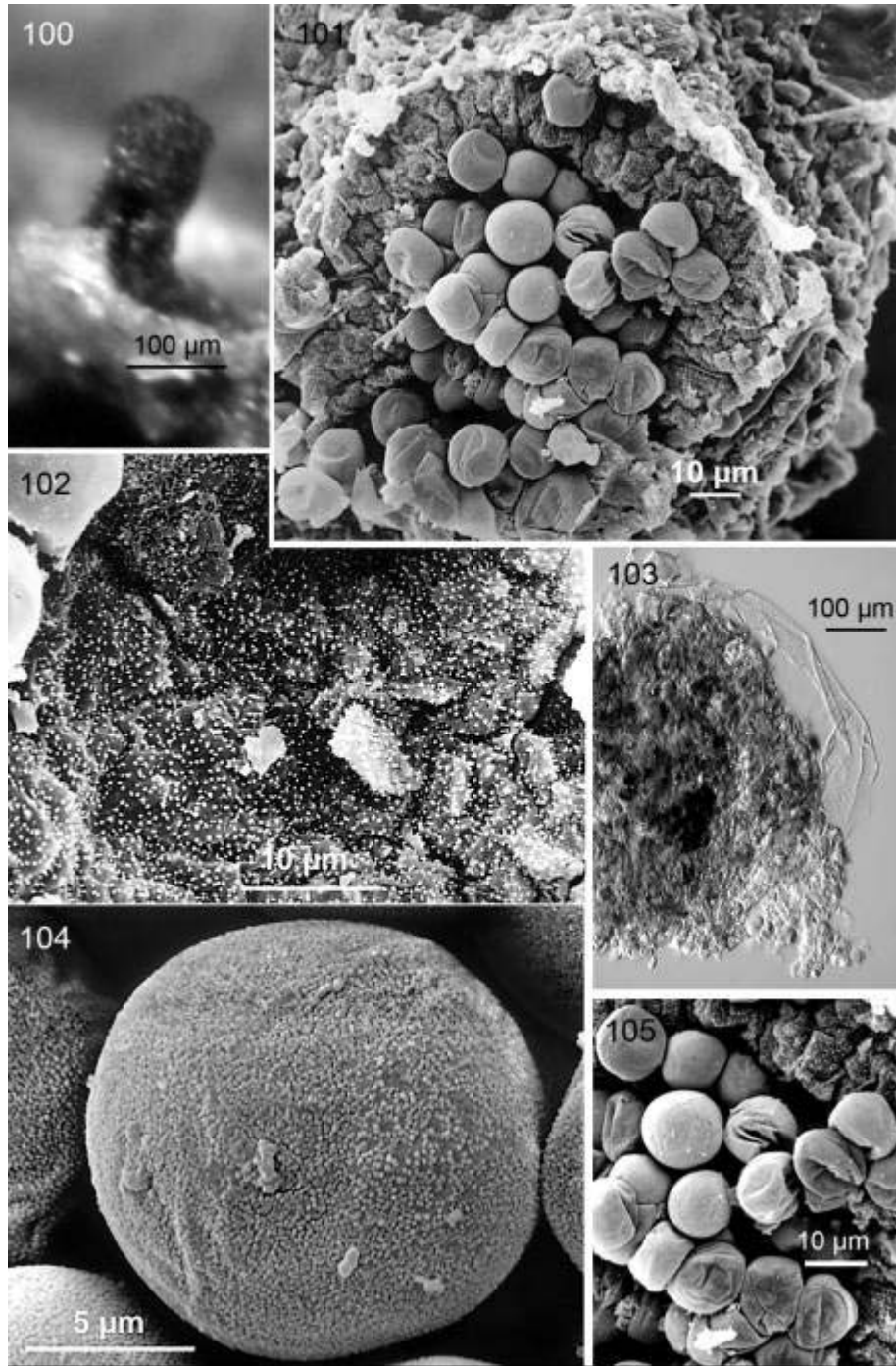
*Illustrations*: Yamamoto (2000: 112, Fig. 6).

When this species was originally described by Yamamoto as *L. capitatoides* var. *fujiokana* he stated that it differed from *L. capitatoides* by the colour and size of the spores (greyish yellow and 10-12 µm diam. in the former, and pale yellow, 8-10 µm diam. in the latter). However comparison of the types showed additional differences. *Licea rugosa* var. *fujiokana* has a roughened sporotheca when dry, a lighter stalk by TL and darker spores (Fig. 95). SEM examination showed the spores to be totally smooth (Fig. 97) like *L. rugosa* var. *rugosa*, although smaller. The peridium fractured into fragments of approximately 30 µm in diam. (Fig. 98), and the inner peridium by SEM (Fig. 99) was covered with warts with some fused warts. This ornamentation is the same as that of the inner peridium of *L. rugosa* var. *rugosa*, and different in both density and distribution from *L. capitatoides*. There are also patches of refuse material on the outer surface of the peridium, which suggest the remains of a gelatinous layer. The Mexican material was examined by SEM, and is identical to the type.

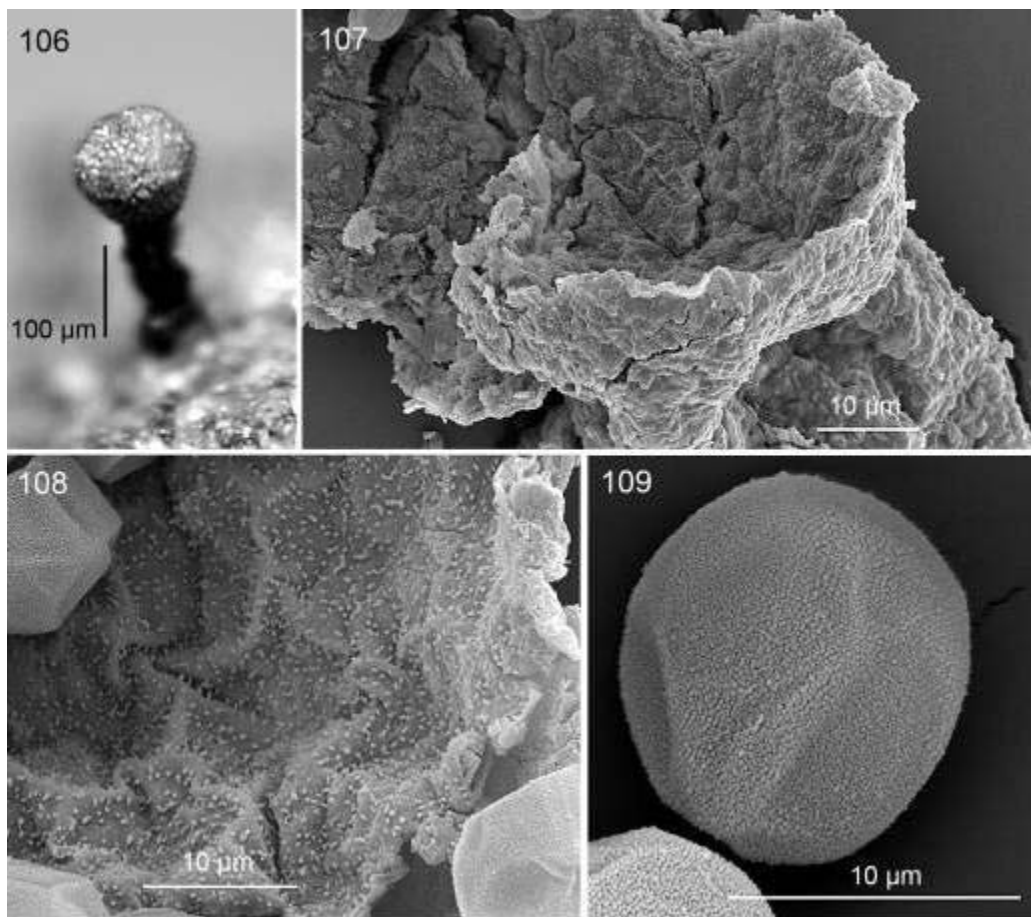
The type of var. *fujiokana* is therefore exactly the same as the type of var. *rugosa* in all other characters except its double peridium, spore size (10-12 µm diam. in var. *fujiokana* and 14-16 µm diam. in var. *rugosa*) and the yellowish brown spore colour of var. *fujiokana* (80. gy. y Br) instead of olive brown in var. *rugosa* (94. l. Ol Br). For this reason the new combination as a variety of *L. rugosa* is justifiable. The two taxa can be separated under the light microscope on the basis of the darker, larger spores of *L. rugosa* var. *rugosa* (Table 2).

**15. *Licea scyphoides*** T.E. Brooks & H.W. Keller in Keller & Brooks, Mycologia 69(4): 679. 1977. TYPE: U.S.A., Ohio, Greene County, next to the swimming pool at John Bryan State Park, from the bark of living *Juniperus virginiana*, August 18, 1976, *H.W. Keller 1945* (holotype: BPI!). (Figs. 100-109)  
= *Licea tanzanica* Ukkola, Härk. & Gilert in Ukkola, Härkönen & Saarimäki, Karstenia 36(2): 57. 1996, **syn. nov.** TYPE: TANZANIA, Tanga Prov., Lushoto Distr., W Usambara Mts., on *Azadirachta indica* in moist chamber cultura, 12.XII.1988, *Härkönen 3693* (holotype: H!).

Sporocarps scattered to gregarious, stipitate, 150-280(-400) µm in height. Sporotheca globose, golden brown, shiny, 80-160(-220) µm diam. Stalk 70-



**Figs. 100-105.** *Licea scyphoides* (HWK 1945). **100.** Habit. **101.** Base of sporotheca from above containing spores by SEM. **102.** Inner surface of peridium by SEM. **103.** Upper half of sporotheca showing clear area of dehiscence by TL. **104.** Spore with closely punctate ornamentation by SEM. **105.** Group of spores appearing roughened.



**Figs. 106-109.** *Licea scyphoides* (MH 3693 as *Licea tanzanica*). **106.** Habit. **107.** Dehiscent sporocarp leaving calyculus. **108.** Inner surface of peridium. **109.** Spore by SEM with closely punctate ornamentation.

180 µm in height, dark brown by reflected light, 150 µm in height, thick, erect, furrowed, straight, cylindrical, mid-width half of the height. Peridium single, membranous, with refuse matter on outside, inner surface of the peridium clearly punctate (Fig. 102); dehiscence circumcissile at a transparent equatorial band, visible by TL, leaving a basal calyculus (Fig. 101). Spores free, yellowish (90. gy. Y-104. p. g Y) by TL, globose, 11-13.5(-14) µm diam., roughened to smooth by TL and low magnification SEM (Figs. 101, 105), and closely punctate by at higher magnification SEM (Fig. 104); spore wall with a paler thinner area.

*Material examined:* USA, Ohio: Greene county, John Bryan State Park near swimming pool, on bark surface of red cedar, 18-XIII-1976, coll. Keller 1945 (BPI 826487, holotype). CUBA, Sancti Spiritus: Alturas de Banao, 21°52'39"N 79°37'03"W, on dead liana in moist



chamber, 6-II-2003, dwb 2255. MEXICO, Hidalgo: El Cardonal, 20°38'57"N 99°00'11"W, bark of living *Prosopis juliflora* in moist chamber, 9-XI-2000, dwb 1865. Progreso, La Cruz, 20°16'02"N 99°10'48"W, bark of living *Schinus molle* in moist chamber, 13-III-2001, dwb 1989; ibidem, bark of living *Prosopis laevigata* in moist chamber, 13-III-2001, dwb 1992, dwb 1993; ibidem, bark of living *Opuntia* sp., 16-III-2001, dwb 2004. PERU. Mazan: 3°28'S 74°55'W, dead liana in moist chamber, 27-V-2002, dwb 2193; ibidem, 4-VI-2002, dwb 2198; ibidem, 3-VI-2002, dwb 2232. PUERTO RICO, Fajardo, Dry Coastal Forest on rocks, Las Cabezas de San Juan Nature Reserve, near 'lands end', 18°23'13"N 65°37'29"W, bark of living *Tamarindus indica* in moist chamber, sc 16930. SPAIN. Cuenca: Saceda-Trasierra, bark of living *Quercus ilex*, in moist chamber, 21-III-1990, 1184-1 Pando, MA-Fungi 31963. UNITED KINGDOM, Wales: Aber, bark of living *Quercus petraea*, in moist chamber, 31-I-1993, dwb 1130a. TANZANIA, Tanga Province: Lusocho District, West Usambara Mts., Mombo, town centre, yard of the restaurant, 0438CD, on *Azadirachta indica* in moist chamber, 12-XII-1988, MH 3693 (H holotype); idem, MH 3591, MH 3592. Arusha (Northern) Province: Moshi District. Moshi International school park, 0337AD, on *Jacaranda* in moist chamber, 23-V-1988, MH 3576 as *Licea tanzanica*.

*Habitat*: Bark of living trees and living and dead vines.

*Distribution*: Mexico, Peru, Spain, Tanzania, USA, Wales.

*Illustrations*: Keller and Brooks (1977: 680, Figs. 23-28); Ukkola *et al.* (1996: 56, 58); Lado and Pando (1997: 132, Fig. 38); Flatau (2000: 70, Fig. 5); Yamamoto (1998: 145); de Haan (2001: 16, pl. 1).

The sporocarps examined were from 150-280(-450)  $\mu\text{m}$  in total height and 84-160(-200)  $\mu\text{m}$  diam., with globose, golden brown shiny sporotheca. The peridium contained refuse matter which thins towards the middle of the sporotheca leaving a transparent equatorial band, very obvious on both sides of the line of dehiscence when specimens are mounted and viewed by TL (Fig. 103). The warts of the inner surface of the peridium are visible in the transparent area of dehiscence by TL at 400x. In this species as with several other stipitate *Licea*, some sporocarps in dry material appear sessile if they are fallen against the substrate and the stalk blends with the substrate refuse material.

We examined the type material and several other specimens of *L. tanzanica*, which we found to be very similar to this species. The SEM examination showed the spore ornamentation (Figs. 104, 109) and the ornamentation of the inner peridium (Figs. 102, 108) of the two species to be identical. There are no differences in the spore sizes (*L. scyphoides* 11-14  $\mu\text{m}$  diam. and *L. tanzanica* 12-13  $\mu\text{m}$  diam.). The types show *L. tanzanica* somewhat larger, reaching 400  $\mu\text{m}$  in height and 200  $\mu\text{m}$  in diam., but the sizes overlap. The ratio of stalk width to height is also different with *L. scyphoides* shorter and squatter. In *L. scyphoides* a cup is left after dehiscence but *L. tanzanica* dehisces lower down and leaves only the base of the sporotheca. The spore colour is also subtly different. *Licea tanzanica* spores are olivaceous and *L. scyphoides* are pale yellow without the darker tints. The transparent border visible at the area of circumcissile dehiscence is a constant feature of both and

measures up to 70  $\mu\text{m}$ . The authors of each species recognized that they are very close, but believed them to be different (Ukkola *et al.*, 1996). We feel the combination of small differences may represent geographic differences, but are not sufficient to maintain these as separate species, and we synonymize them here. Perhaps these small differences indicate a continuum of a variable species.

*Licea bulbosa* (see above) is similar to *L. scyphoides* in habit, but its smaller (10-11  $\mu\text{m}$  diam.) almost hyaline smooth spores, its longer thinner stalk, and the smooth inner peridium with a totally transparent basal half differentiate it.

**16. *Licea verrucospora*** (T.N. Lakh., Nann.-Bremek. & R.K. Chopra) D. Wrigley & Lado, **nom. nov. et status nov.** (Figs. 110-115)

$\equiv$  *Licea scyphoides* var. *reticulata* T.N. Lakh., Nann.-Bremek. & R.K. Chopra, Proc. Kon. Ned. Akad. Wetensch. 93(3): 261. 1990 [basion.], non. *L. reticulata* Berk. & Broome, 1873. TYPE: INDIA, Himachal Pradesh, North Western Himalaya mountains, Shimla, Summer Hill area, 2067 m, developed in a moist chamber on bark of *Quercus incana* from 0-9 m above the ground, 6 IV 1981 (holotype HPUB 15405, paratype NENB 13.877 now at BR!).

Sporocarps scattered to gregarious, stipitate, 250-500(-700)  $\mu\text{m}$  in height. Sporothecae dark ochraceous-brown, shiny, subglobose, 100-200  $\mu\text{m}$  diam. Stalk 150-350(-500)  $\mu\text{m}$  in height, long, dark, straight, subcylindrical, rugose with several strands visible by TL within the main stalk (Fig. 110), mid-width a quarter of stalk height. Peridium single, membranous, covered with refuse matter, smoky grey, densely and prominently warted; dehiscence irregular into platelets formed by fragmentation of the whole peridium. Spores free, pale yellow to greyish yellow (89. p. Y - 90. gy. Y) by TL, globose, 10-12(-13)  $\mu\text{m}$  diam., very minutely warted but warts in irregular patches on the spore surface, visible by TL and also by SEM (Fig. 115); spore wall with a pale thinner area (Fig. 111).

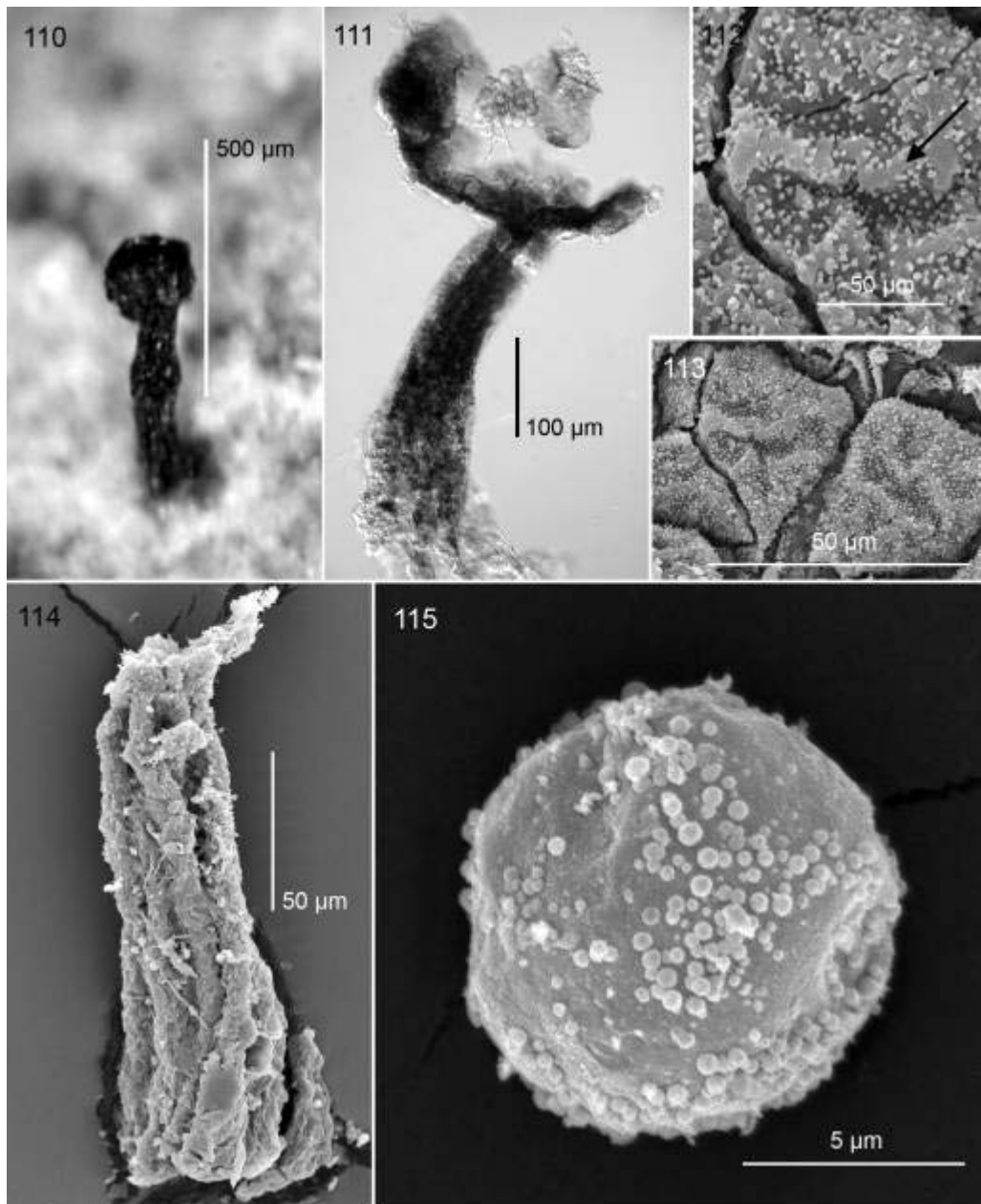
*Material examined*: INDIA, Himachal Pradesh: Shimla, Summer Hill, on bark of living *Quercus incana* in moist chamber, 14-IV-1981, NENB 13.877 (BR, paratype of *Licea scyphoides* var. *reticulata*)

*Habitat*: bark of living *Quercus incana*.

*Distribution*: Known only from the type locality.

*Illustrations*: Lakhanpal *et al.* (1990: 261, Fig. 7).

We raise its rank here to species level because on comparison of the material with *L. scyphoides* we noticed many differences, sufficient to consider it to be a totally different species. The original description of *L. scyphoides* var. *reticulata* notes that dehiscence takes place above an equatorial line to leave a cup with a smooth margin. We found no such line, and in fact the platelet margins are visible extending to the base of the sporotheca (Figs. 110, 113). The base, when remaining after dehiscence, is a thin vestige of peridium more



**Figs. 110-115.** *Licea verrucospora* (NENB 13.877 as *L. scyphoides* var. *reticulata*). **110.** Habit. **111.** Dehiscent sporocarp by TL. **112.** Detail of inner surface of peridium by SEM with flattened reticulate markings (arrow). **113.** Fragmented peridium by SEM. **114.** Stalk and fragmented remains of sporotheca. **115.** Spore showing irregular verrucose ornamentation.

like a collar than a cup (Fig. 114), whereas in *L. scyphoides* a clear cup is left after dehiscence. *Licea scyphoides* has a transparent equatorial band at the area of dehiscence which is not present in *L. verrucospora*. The inner surface of the peridium in *L. scyphoides* is minutely warted (Fig. 102), but the inner surface of *L. verrucospora* is densely marked with protruding warts of various sizes, and the lines of the outer reticulate pattern show through (Fig. 112). The spores in *L. verrucospora* have a unique ornamentation of rounded raised warts of different sizes, dispersed irregularly over the spore surface, different from *L. scyphoides* even by TL, and more so by SEM (Fig. 115). This pattern is also different from any other stipitate *Licea* described so far. These differences are in addition to those noted by the authors of this species which were the larger size of the sporocarps but they overlap, and its reticulately-ridged peridium. The surface of the sporothecae of the type material is crossed with a network of shiny lines on ridges, marking the surface, but not the platelets by which it dehisces (Fig. 112).

The epithet *verrucospora* was chosen to denote the character of the spore surface, since the variety name has already been used for a different species (Lado, 2001).

*Licea verrucospora* is different from *L. tanzanica* in spore size (10-12 µm diam. vs. 12-15 µm diam.), ornamentation, and in its mode of dehiscence (platelets vs. circumscissile). Its yellowish, irregularly ornamented spores, also separate it from *L. pedicellata* with regular ornamentation and *L. rugosa* which has completely smooth spores.

### Excluded species: (6)

*Licea atricapilla* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 86(2): 208. 1983. TYPE: JAPAN, Kochi Pref., Susaki-shi, Hachimangu, cult. on bark of living *Cinnamomum camphora* (L.) Presl, 7-31 X 1981 (holotype: Y.Y. 1277, isotype NENB 12.984).

We were unable to examine this species. The following description is adapted from Nannenga-Bremekamp and Yamamoto (1983).

Sporocarps scattered, stipitate, 260 µm in total height. Sporotheca silvery iridescent with a dark apical operculum, subglobose, 160 µm diam. Stalk nearly black, furrowed, filled with granular refuse material. Peridium membranous, separate from the stalk, densely and minutely warted on the inner surface. Dehiscence circumscissile along edge of the apical disc. Spores, olivaceous brown with a large paler area and a thinner wall, 12-13 µm diam., smooth by TL.

*Habitat:* bark of living *Cinnamomum camphora*.

*Distribution:* only known from type locality.

*Illustrations:* Nannenga-Bremekamp and Yamamoto (1983: 208); Yamamoto (1998: 136).

The authors place this species in the subgenus *Orcadella* on account of its black operculum. They differentiate it from *L. operculata* which has a glossy operculum, and by its larger darker spores (olivaceous brown and 12-13 µm diam. vs. 8-11 µm diam. and almost colourless in *L. operculata*). They also comment that *L. scyphoides* differs from it by spore colour (greyish yellow in the latter species), “a more densely warted peridium” and “a larger lid, which occupies half of the sporangium”. The description of this species is unlike any we have examined.

*Licea crateriformis* B. Ing, Myxomycetes Britain and Ireland 46. 1999. TYPE: UNITED KINGDOM, Scotland, Isle of Arran, Kings Cross Point, in thallo vivo *Radulae complanatae* in rame vivo *Corylus avellanae*, 2 September 1998, B. Ing (holotype: Hb. B. Ing 98068).

The following description is adapted from the original publication by Ing (1999) since we were unable to obtain the type material of this species for examination.

Sporocarps short stipitate, 800 µm in height. Sporothecae 700-750 µm diam. shaped like a *Craterium*. Stalk dark, furrowed, from a discoid hypothallus. Peridium single, dark brown to chestnut with a distinct golden-bronze lid; dehiscence by lid. Spores colourless by TL, 7-9.5 µm diam., subglobose, smooth; spore wall of uniform thickness.

*Habitat:* on liverworts on living branches.

*Distribution:* Known only from the type locality.

*Illustrations:* Ing (1999: 47).

According to the author's description, the shape and dehiscence of this species are similar to *Licea poculiformis*, but that species is much smaller [150-200(-400) µm in height] and the spores have a wall with a thinner area.

*Licea erecta* var. *erecta* K.S. Thind & Dhillon, Mycologia 59(3): 463. 1967. TYPE: INDIA, Eastern Himalayas, Darjeeling, Tiger Hill, on decaying bamboo twigs, September 23, 1964, No. 451 (holotype: PAN).

We were unable to obtain the type material of this species for examination. The following is adapted from the original description by Thind and Dhillon (1967).

Sporocarps scattered, stipitate, up to 1500 µm in height. Sporothecae dark brown, oblong or ovate, up to 600 × 400 µm. Stalk up to 900 µm in height, 200 µm wide, long, erect, ridged, concolourous. Peridium tough, thick, with dark granular inclusions, marked with ridges from the top of the stalk and

wrinkles between the segments; dehiscence irregular from above. Spores free, hyaline by TL, 13.5-15  $\mu\text{m}$  diam., minutely verrucose to almost smooth.

*Habitat*: decaying bamboo twig.

*Distribution*: India; Thailand.

*Illustrations*: Thind and Dhillon (1967: 464).

*Licea erecta* var. *erecta*, according to Martin and Alexopoulos (1969) is “somewhat similar to *L. operculata*, from which it differs in its more robust habit, complete lack of an operculum, and particularly in the netted peridium which approaches that of a *Cribraria*, although there is no evidence that the peridium falls away from the interstices of the net and there is no *Cribraria* which approaches it in appearance or has such large spores.”

The *L. erecta* var. *erectoides* is described above. As both de Haan (2002) and Yamamoto (1999) point out, the main difference between *L. erecta* var. *erecta* and the var. *erectoides* is the spore size. One of de Haan’s SEM photographs shows a spore of the var. *erecta* from the collection of Nannenga-Bremekamp (14807). The material illustrated by de Haan (2002), and examined by us, is a collection labeled by Nannenga-Bremekamp as a questionable identification (*Licea erecta* Thind? & Dhillon). It is much smaller than the described *L. erecta* and has a round sporotheca and short stalk. Without the type to examine, it is impossible to evaluate this species.

*Licea floriformis* var. *floriformis* T.N. Lakh. & R.K. Chopra in Lakhanpal, Nannenga-Bremekamp and Chopra, Proc. Kon. Ned. Akad. Wetensch. 93(3): 255. 1990. TYPE: INDIA, Himachal Pradesh, North Western Himalaya mountains, Shimla, Summer Hill area, 2067 m, developed in a moist chamber on bark of *Quercus incana* taken 3-6 m the ground, harvested on 4 VIII 1981 (holotype: HPUB 76423).

The following description is adapted from Lakhanpal *et al.* (1990) since we were unable to examine the type material of this species.

Sporocarps scattered, stipitate, up to 700  $\mu\text{m}$  in height. Sporothecae globose or subglobose, red-brown to nearly black, smooth or wrinkled with minute ridges, 250-350  $\mu\text{m}$  diam. Stalk 250-450  $\mu\text{m}$  in height, sturdy, subconical, nearly black. Peridium single, membranous, thin, inner surface bearing long papillae; dehiscence by irregular fracture in the upper sporotheca and lobes below. Spores free, smooth, smooth, black in mass, light pale pink to colorless by TL, 11-12(-14)  $\mu\text{m}$  diam.

*Habitat*: bark of living *Quercus incana*.

*Distribution*: Known only from the type locality.

*Illustrations*: Lakhanpal *et al.* (1990: 255) [a drawing by Nannenga-Bremekamp from a photograph].

In the description of *L. floriformis* var. *floriformis*, Lakhanpal *et al.* (1990) note that it differs from *L. erecta* var. *erecta* K.S. Thind & Dhillon only

in its slightly smaller spores, but that they overlap in size. The spores in both are smooth. Perhaps these are the same species, but without being able to examine the type specimens of either species, it is impossible to be sure.

*Licea lilacina* Nann.-Bremek., T.N. Lakh. & R.K. Chopra in Lakhanpal, Nannenga-Bremekamp and Chopra, Proc. Kon. Ned. Akad. Wetensch. 93(3): 256. 1990. TYPE: INDIA, Himachal Pradesh, North Western Himalaya mountains, Shimla, Summer Hill area, 2067 m, developed in a moist chamber on bark from a living *Quercus incana*, 3 m above the ground (holotype: HPUB 11,001; isotype NENB 13.889 now at BR).

We were unable to obtain the type material of this species. The following description is adapted from Lakhanpal *et al.* (1990).

Sporocarps scattered, or in pairs, stipitate or sessile, 600-700 µm in height. Sporothecae globose or subglobose 200-350 µm diam., violet-brown or iridescent blue/violet, sometimes sprinkled with white particles. Stalk if present up to 300 µm long, (the description in English has an errata, reporting the stalk up to 3 mm long. In the Latin description it is 0.3 mm which is in keeping with other measurements) thick, opaque or ochraceous with refuse matter, slightly tapering towards the top, width about half of the height at base. Peridium double, the outer layer gelatinous with little granular refuse at the base, the inner layer membranous ochraceous, smooth or minutely wrinkled; dehiscence by irregular fracture, sometimes lobately from above leaving a cup with an irregular margin. Spores pale lilaceous in mass, paler rosy-lilac by TL, (8-9-10(-12.5) µm diam., densely and minutely spinulose; spore wall uniformly thin.

*Habitat:* bark of living *Quercus incana* and *Pinus wallichiana*.

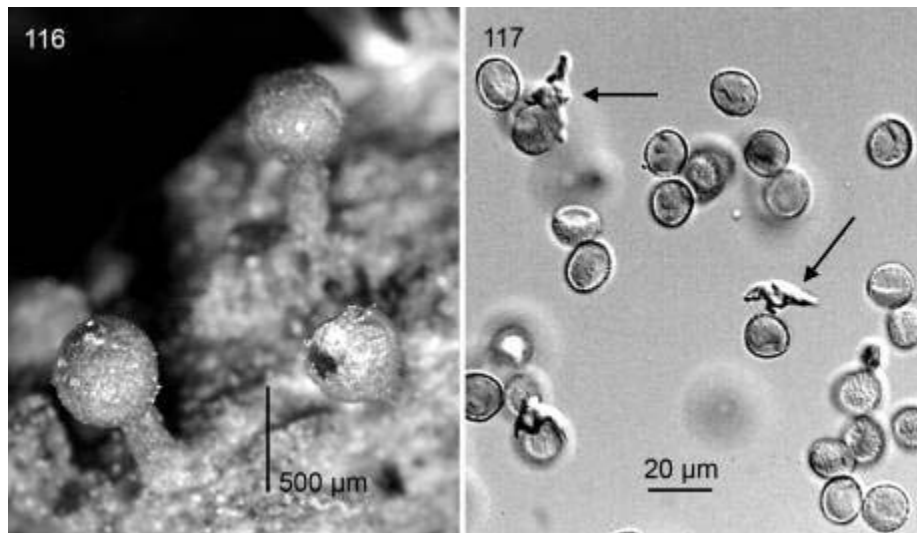
*Distribution:* Known only from the type locality.

*Illustrations:* Lakhanpal *et al.* (1990: 256)

The authors point out that this species has lilac spores which, suggests other orders and not the *Liceales*. They include it in the genus *Licea* because of the absence of capillitium and a double peridium. Their reference to a sprinkling on the peridium of white particles also suggests another group, which is an opinion we share. Apparently plentiful material was collected (38 collections), but the second author (Nannenga-Bremekamp) states that she saw only two slides.

*Licea takahashii* Y. Yamam., Bull. Natl. Sci. Mus., Tokyo, B 26(3): 114. 2000. TYPE: JAPAN, Gifu Pref., Osaka-machi, Nigorigo-onsen, ca. 1950 m alt., on dead wood, 8 X 1994, K. Takahashi, YY-14468 (holotype: TNS!).

(Figs. 116-117)



**Figs. 116-117.** *Licea takahashii* (YY 14468). **116.** Habit. **117.** Spiny thick-walled spores and immature elaters (arrows).

We have examined the type material YY 14468 and we have detected some rudimentary capillitium, made up of small, immature poorly formed elaters (Fig. 117). It appears to be an immature *Trichia* instead of a *Licea*. This is supported by the fact that it was found on dead wood. It also has very large mottled sporocarps (up to 2 mm tall and 500 µm diam.), with a yellow spore mass and spiny thick-walled yellow spores, 12-14 µm diam. We thus exclude this material from the genus *Licea*. The authors of the species mentioned its similarity in habit to *Trichia* or *Hemitrichia* but they said “it obviously lacks capillitium”.

## Discussion

More than ninety collections were examined for this evaluation. The simultaneous study of 21 type specimens of these *Licea* species has enabled us to make detailed comparisons and come to the conclusion that in five cases, *L. capitata*, *L. longa*, *L. cristallifera*, *L. tanzanica* and *L. tropica*, the newly described species actually belonged to an existing taxon. They have been synonymized with *L. floriformis* var. *aureospora* (the first two), *L. eleanorae*, *L. scyphoides* and *L. bulbosa*, respectively. In the case of *L. capitatoides* var. *fujiokana*, it is recombined as a variety of a different species, *Licea rugosa* var. *fujiokana*. A new name *Licea verrucospora*, and a new status was given to *Licea scyphoides* var. *reticulata*, since it was found to be so different from *L.*



*scyphoides* that it has been raised to species level. In the case of *L. takahashii*, it was excluded from the genus *Licea* because it is an immature form of *Trichia*, a different genus.

Among the accepted 16 stipitate *Licea* species, there do appear to be loose groups. There are those with dehiscence by a lid (*L. operculata* and *L. poculiformis*), and those with circumcissile dehiscence (*L. scyphoides* and *L. bulbosa*), although the top half of the sporotheca is not really a lid as in the previous two species. There are also species with dehiscence by irregular fracture of some form, or platelets separated by definite lines of dehiscence. Where there are platelets, however, they are not as well defined as they are in sessile species like *L. minima* Fr., and it is difficult to separate this form of dehiscence from fracture into irregular fragments. Most of these *Licea* had not been described in 1965, and they loosely fit only two of the subgenera (*Orcadella* and *Pleiomorpha*) proposed by Nannenga-Bremekamp (1965). It seems to be reasonable, therefore not to maintain her subgenera, at least in the case of the stipitate members of the group, although the character of type of dehiscence, when used in conjunction with others, is useful in separating species.

Other groupings are also possible if we consider those with smooth spores by SEM (*L. rugosa* and *L. rugosa* var. *fujiokana*) or those with a double peridium (e.g. *L. bulbosa*, *L. eleanorae*, *L. capitatoide*s or *L. poculiformis*), but the use of SEM is not available to all taxonomists, and the description of the peridium as single or double depends on the state of the material and is open to error in dry specimens. To separate these species it is necessary to use other characters such as the size, colour and ornamentation of the spores and peridium, and stalk size and colour in conjunction with the type of dehiscence, a double or single peridium and SEM examination where possible.

Using a combination of these characters, a key has been proposed below to aid in the identification of the species discussed in this paper. The six excluded species have been placed in the key to serve as a basis for comparison. Characters from their original published descriptions, and a different typeface has been used for these taxa.

In the descriptions of the material we have given reasons for considering each of these to be different taxa of *Licea*. The fact that some of these species were simultaneously in press (Table 1), coupled with the variability of specimens from moist chamber culture and the simplicity of the sporophores, can easily explain the taxonomic complexity. Six of the species studied have only been found from the type locality. This may be because they are newly described, and therefore there has not been time for other collections, or perhaps that many environments have been little sampled until recently. The

## Key to the stipitate *Licea*

1. Spores by TL dark olive, olive brown, dark brown, yellowish grey .....	2
1. Spores by TL very pale or colourless .....	5
2. Spores warted .....	<b>10. <i>Licea pedicellata</i></b>
2. Spores smooth .....	3
3. Dehiscence along an apical disc .....	<i>Licea atricapilla</i>
3. Dehiscence into irregular fragments .....	4
4. Spores 14-16 µm diam. ....	<b>13. <i>Licea rugosa</i> var. <i>rugosa</i></b>
4. Spores 9-12 µm diam. ....	<b>14. <i>Licea rugosa</i> var. <i>fujiokana</i></b>
5. Outer surface of sporotheca covered with birefringent crystals .....	6
5. Outer surface of sporotheca not covered with crystals .....	7
6. Sporotheca vase-shaped, without a clear line of dehiscence.....	<b>3. <i>Licea eleanorae</i></b>
6. Sporotheca subglobose, with a clear line of dehiscence .....	<b>1. <i>Licea bulbosa</i></b>
7. Outer surface of sporotheca with distinct spots or ridges .....	8
7. Outer surface of sporotheca without distinct spots or ridges .....	9
8. Spotty appearance from large warts on sporotheca surface .....	<b>9. <i>Licea parvicapitata</i></b>
8. Sporotheca surface covered with a reticulum of ridges .....	<b>16. <i>Licea verrucospora</i></b>
9. Sporocarps more than 400 µm tall .....	10
9. Sporocarps up to 400 µm tall .....	18
10. Dehiscence by lid or circumcissile .....	11
10. Dehiscence neither by a lid nor circumcissile .....	13
11. Dehiscence circumcissile .....	<b>15. <i>Licea scyphoides</i></b>
11. Dehiscence by a lid.....	12
12. Long stalk, more than half total height .....	<b>8. <i>Licea operculata</i></b>
12. Short stalk, less than half total height .....	<i>Licea crateriformis</i>
13. Peridium single .....	14
13. Peridium double .....	16
14. Peridium ochraceous by TL .....	<b>4. <i>Licea erddigensis</i></b>
14. Peridium colourless by TL .....	15
15. Spores 10-12 µm diam. ....	<b>5. <i>Licea erecta</i> var. <i>erectoides</i></b>
15. Spores 13-15 µm diam. ....	<i>Licea erecta</i> var. <i>erecta</i>
16. Spores golden yellow in mass .....	<b>6. <i>Licea floriformis</i> var. <i>aureospora</i></b>
16. Spores not golden yellow in mass .....	17

17. Spores smooth .....	<i>Licea floriformis</i> var. <i>floriformis</i>
17. Spores densely and minutely spinulose .....	<i>Licea lilacina</i>
18. Appears almost sessile .....	19
18. Obviously stalked .....	21
19. Dehiscence circumcissile .....	<b>15. <i>Licea scyphoides</i></b>
19. Dehiscence irregular .....	20
20. Peridium golden iridescent, with refuse material .....	<b>11. <i>Licea perexigua</i></b>
20. Peridium hyaline, transparent, with no refuse covering .....	<b>7. <i>Licea lucens</i></b>
21. Dehiscence into irregular fragments .....	<b>2. <i>Licea capitatoidea</i></b>
21. Dehiscence by lid or circumcissile .....	22
22. Dehiscence by a lid .....	<b>12. <i>Licea poculiformis</i></b>
22. Dehiscence circumcissile .....	23
23. Inner peridium smooth; lower half of peridium transparent .....	<b>1. <i>Licea bulbosa</i></b>
23. Inner peridium warted; transparent only at line of dehiscence .....	<b>15. <i>Licea scyphoides</i></b>

known distribution of some of the species, for example *L. erecta* var. *erectoides* from Costa Rica, Cuba and Japan, or *L. rugosa* var. *rugosa* from Japan and Mexico, is obviously a reflection of areas sampled rather than true distribution, and reflects the scarcity of data for this group in some parts of the world. Six of the taxa were found by us (Lado *et al.*, 2003; Stephenson *et al.*, 2004) during recent intensive sampling in Mexico in undisturbed environments such as Biosphere Reserves or National Parks, which had not been sampled previously. This could be an explanation for their rarity, and is a further compelling reason for carrying out intensive biodiversity inventories, and for supporting future conservation of these areas. It is certainly evident that the study of many collections is necessary to fully appreciate the variability of a species, and to be certain that the specimens obtained from moist chamber culture are properly mature. The presence of different sized or irregularly shaped spores is a clue to immaturity or poor development, and mounting moist fresh specimens that have not dried slowly will often give atypical dehiscence. In the case of *L. operculata*, the dwarf forms may be an ecotype prevalent in tropical habitats. These dwarf forms have also been seen for other species, like *Didymium squamulosum* (Alb. & Schwein.) Fr. or *Arcyria cinerea* (Bull.) Pers., from our moist chamber cultures.

But how many differences are sufficient to consider a species of *Licea* as separate? In a group with so few characters, and the somewhat arbitrary relative taxonomic value given to these different characters (dehiscence, separation of the sporotheca from the stalk, ornamentation of spores and

peridium), coupled with apomictic life cycles (Clark, 2004), the use of morphospecies, becomes questionable. The application of scanning electron microscopy has certainly helped to answer some doubts and questions about morphological characters, but further information is needed to confidently confirm that these myxomycetes belong to separate species and are not ecotypes or variants of fewer species. Consensus on taxonomic boundaries informed by other techniques such as DNA sequencing, will be necessary to corroborate these findings. It is still in its infancy in this group and until now applied to plasmodia (Baldauf and Doolittle, 1997), mainly laboratory-cultured, although primers specific for extraction from sporocarps have also recently been designed (Martín *et al.*, 2003). Spore to spore culture can be useful, though difficult with these very small myxomycetes, to determine the stability of the characters of new species (Keller, 1996).

The only way to be really sure that a described species is not a small clonal population, or morphological variant of another species is, as Keller (1996) and Clark (2004) recommended, the collection and examination of a large amount of material for study from different and widely separated areas, and even a study of the reproductive systems in these collections.

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