Lamprospora verrucispora sp. nov. (Pezizales)

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Introduction

Since the website Ascofrance.com with its forum has been put online by its founder and owner Christian Lechat in 2003, more than 1200 users from countries all over the world have decided to become a member of this platform aiming at the international scientific exchange of mycologists specialized in ascomycetes. There are stories galore about contacts, cooperations and friendships arisen from this unique website.

Ours started in January 2014 when the third author of this article asked for help to identify a Lamprospora he could not determine with the existing literature. First mails, then specimens went from one to another of the authors. Based on ascospore ornamentation and its type of infection on the bryophyte host Campylopus pyriformis (K.F. Schultz) Brid., the Lamprospora soon proved to be an undescribed species. One and a half years later, the new species was found by the first author in further sites in great abundance and subsequently is described here as L. verrucispora.

Methods

The description of Lamprospora verrucispora is based on the results of the examination of several vital collections from five localities: one in the Netherlands and four in Germany. Most observations took place in tap water. Ascospore ornamentation was additionally studied after staining with Lactophenol Cotton Blue or Methylene Blue, using digital cameras mounted on microscopes. Many warts have a punctiform cavity, best visible after staining in Lactophenol Cotton Blue. The bigger warts are predominantly hemispherical and not elongated or confluent, with few hyaline septate anchoring hyphae; mostly with a low and narrow fimbriate margin; hymenium yellow-orange to light orange, margin and outer surface paler than the hymenium.

Taxonomy

Lamprospora verrucispora M. Vega, Eckstein, Van der Kolk, sp. nov. — MycoBank 817460.

Abstract: A description and illustrations of both macroscopic and microscopic characters of Lamprospora verrucispora sp. nov. are provided. Differences from other bryophilous Pezizales with globose ascospores ornamented with isolated warts are discussed and a dichotomous key to these species is given. Gall formation on rhizoids and chloronema of the bryophyte host Campylopus pyriformis is described and illustrated. This represents the first report of gall formation for a species of the genus Lamprospora.

Keywords: Bryophilous Pezizales, Campylopus pyriformis, dichotomous key, galls, Pyronemataceae, taxonomy.

Holotype: The holotype of Lamprospora verrucispora is deposited in the Herbarium Hamburgense of the University of Hamburg (HBG-holotypus, inv. no. 1412). The isotypes of Lamprospora verrucispora are filed under MV20151025-04 in the private herbaria of Marcel Vega and Jan Eckstein.

Etymology: verrucispora = referring to the warted ascospores of the species.

Macroscopic features (plate 1)

Apothecia mostly scattered, sometimes gregarious on soil between shoots of Campylopus pyriformis, protonema and other bryophytes; 1–1.8 (2.5) mm in diam., first spherical, becoming saucer-shaped, finally thick and discoid, sessile; with few hyaline septate anchoring hyphae; mostly with a low and narrow fimbriate margin; hymenium yellow-orange to light orange, margin and outer surface paler than the hymenium.

Microscopic features (plate 2a-d)

Asci (160) 200–370 (420) × 16–24 (28) μm, cylindrical, 8-spored, operculum, inamyloid; shortly bifurcate at the base, arising from perforated croziers. Paraphyses filiform, same length as the ascii; containing, at least in the upper half, many vacuoles 1–3 μm diam. with orange pigment turning cyan to olivaceous in Lugol's solution; straight, pluriseptate, apically inflated, terminal cell 30–75 (100) μm × 4–8 μm, cells 2–4 μm broad near base, rarely clavate. Ascospores (only ascospores from sporeprint considered); (13) 14–17 μm (ornamentation included), hyaline, globose, always with a large lipid drop, diameter 9–11 (12) μm, uniseriate. Ascospore surface densely covered with numerous isolated warts that are mostly (0.2) 0.4–0.9 μm broad and 0.4–0.8 μm high, occasionally with one bigger wart which is 1–2 μm broad and 0.8–1.6 μm high. Warts are mostly hemispherical though some can be pear-shaped, elongated or confluent, occasionally two warts can be connected by a thin and low ridge. Many warts have a punctiform cavity, best visible after staining in Lactophenol Cotton Blue. The bigger warts are predominantly hemispherical and not elongated or confluent. The surface of the warts of some ascospores appears to be finely rugose in SEM. Subhymenium merged with the medullary excipulum, of textura angularis with hyaline and thin-walled hyphae, walls becoming thicker at the base, 140 μm thick. Ectal excipulum of textura intricata of elongated cells, up to 120 μm thick. Margo of textura prismatica, elongated hyphae, septate, 15–50 × 5–14 μm, some protruding.

Diagnosis: Differ from other species of Lamprospora by its perfectly globose ascospores with a surface densely covered with numerous small isolated warts and few isolated bigger warts together with an infection inducing galls on the rhizoids of its host Campylopus pyriformis (K.F. Schultz) Brid.
Infection (plate 2e–f & figure 1)

*L. verrucispora* infects rhizoid and chloronema (the above ground, green part of protonema) cells of the moss *Campylopus pyriformis*. The terminal cells of weak rhizoids or chloronema strands are affected the most. Infected cells swell to a spherical, one-celled gall which is many times the width of neighboring cells. Occasionally, the infected rhizoid or chloronema strand keeps growing, due to which the gall becomes sub-terminal. Shortly after the infection the surface of the gall is only partly covered with hyphae (fig. 1). Soon, however, the gall has a complete sheathing of connate hyphae, which is one to two cell layers thick (plate 2e–f). The hyphae-coverred galls can reach up to 180 μm in diameter where the galls measure up to 150 μm in diameter and the hyphal sheaths are 8–15 μm thick. The infection structure consists of appressoria, infection pegs and haustoria. Only one infection structure per gall is developed. Appressoria are 5–8 μm wide and if at all only slightly wider than adjacent cells (fig. 1). Because of their weak differentiation, they are discernable in early stages of gall development only. From the appressoria an infection peg, 2–3 μm wide, penetrates the rhizoid wall. The infection pegs are surrounded by a tube of host cell wall material. Haustoria are thin walled, strongly ramified and fill the gall up to half of its volume. No septa were seen within the haustoria and they do not grow through cross walls of rhizoid or chloronema strands. The infection does not weaken the host discernably.

**Figure 1 – Young gall** in optical section. Scale bar: 40 μm. 
Drawing: Jan Eckstein

**Habitat** (plate 1, figs. a–c)

Dutch collection: The Dreijen Arboretum is a botanical garden in Wageningen in the province of Gelderland. A large variety of both deciduous and coniferous bushes and trees are grown in the Arboretum. The locality is at an exposed patch of about 2 m² next to a low boxwood hedge. The top soil consists of humus and is partly covered with decaying wood chips. The moss vegetation on the soil surface is dominated by *Campylopus pyriformis*.


Additional collections at this site: October 9th 2015, pers. herb. MV20151009-01 , October 25th 2015, pers. herb. MV20151025-01.


Additional collection at this site: October 25th 2015, pers. herb. MV20151025-02.

4. Germany, Forest Göhrde near Boitze (Lower Saxony), 53°07’49” N, 10°45’10.5” E, 63 m asl, in a rut on a forest track in a pine-wood, *leg.* Marcel Vega October 9th 2015. Host: *C. pyriformis*; soc.: *L. campylopodis*, pers. herb. MV20151009-03.

Additional collections at this site: October 25th 2015, pers. herb. MV20151025-03, December 5th 2015, pers. herb. MV20151205-03.

5. Germany, Forest Göhrde near Boitze (Lower Saxony), 53°07’36” N, 10°45’53.5” E, 79 m asl, in a rut on a forest track passing through a pine-wood, *leg.* Marcel Vega, October 25th 2015. Host: *C. pyriformis*, accompanying moss: *H. cupressiforme*.

**Holotype** (HBG–holotypus, inv. no. 1412), isotypes: pers. herb. MV20151025-04 and pers. herbarium JE.

Additional collection at this site: November 7th 2015, pers. herb. MV20151107-01, duplicate pers. herb. VDK fungi # 0246.

**Discussion**

To compare the new *L. verrucispora* with similar species of bryophilous *Pezizales*, we consider here a) bryophilous *Pezizales* known to parasitise species of the moss genus *Campylopus* on one hand and b) bryophilous *Pezizales* with similar ascospores to those of *L. verrucispora*.

Plate 1 - *Lamprospora verrucispora*, macroscopic pictures

a & b: Locality D-Forest Göhrde, holotype; c: Locality NL-Wageningen Arboretum De Dreijen; d: Young apothecia, NL-Wageningen; e: Young apothecium, D-Göhrde; f–h: Mature apothecia, D-Göhrde. Pictures: a,b, f–h: Marcel Vega; c & d: Henk-Jan van der Kolk; e: Jan Eckstein.
Plate 2 – *Lamprospera verrucispora*, microscopic pictures

a: Ascospores in ascus stained with methylene blue; b: Paraphyses in tap water; c: Free ascospores stained with cotton blue; d: Free ascospores stained with methylene blue; e: Galls in tap water; f: Gall stained with cotton blue. Scale bars: a–d = 10 μm; e = 100 μm; f = 25 μm. All micrographs taken from the holotype collection. Pictures: a & d: Raúl Tena Lahoz; b: Rubén Martínez Gil; c, e & f: Jan Eckstein.
a) Bryophilous Pezizales known to parasitise species of the moss genus Campylopus

Buckley (1923: 44-45) described Lamprospora campylopodis from Campylopus fragilis (Brid.) Bruch & Schimp. However, all but one of the later collections of this species have been reported from C. pyriformis (pers. observations; Benkert, 1987: 213-214; Rubio et al., 2002: 69-70; Eckstein & Eckstein, 2013: 57-58). The one other collection had the host Campylopus oerstedianus (Müll. Hall.) Mitt. (Benkert, 2008: 15). Lamprospora campylopodis clearly differs from L. verrucispora in its ascospores which have an areolate reticulum consisting of mostly penta- or hexagonal meshes reminiscent of the surface of a football, thus confusion with L. verrucispora is out of the question. Since L. campylopodis was found frequently growing together with L. verrucispora, macroscopic differences became apparent. With some experience both species can be separated in the field: the apothecia of L. campylopodis are — at least when mature — rather deeply orange and have a distinctive membranaceous margin differing from the yellowish-orange apothecia with a small and indistinct margin of L. verrucispora. According to Benkert (1987: 210-211), all exsiccata of Lamprospora australis (McLennan & Cookson) Rifai had Campylopus introflexus as their host. The ascospores of L. australis differ markedly from those

Plate 3 – Lamprospora verrucispora, SEM-Pictures of ascospores
Pictures on the left from the holotype collection MV20151025-04. Pictures on the right from the Wageningen collection VDK fungi # 0194. Scale bar: 10 μm. Pictures: Jan Eckstein.
of L. verrucispora in having an ornamentation consisting of very high and narrow ridges forming a high reticulum. So far, L. australis is only known from Australia.

Le Gal (1939: 137–139) attributed to Lamprospora areolata a collection which Benkert (1987: 207–208) reported to be associated with the genus Campylopus. However, he doubted the identity of this specimen with L. areolata, but could not refer it to L. campylopodis or L. australis either. As the ascospore ornamentation of L. areolata is similar to that of L. australis in consisting of a reticulum of high and narrow ridges, this species could not be mistaken for L. verrucispora.

Finally, Vivant (1998: 22–24) reports a find of Octospora meslinii on Campylopus subulatus Schimp. ex Milde. This species of Octospora has distinctively ellipsoid spores and therefore it cannot be mixed up with L. verrucispora.

b) Bryophilous Pezizales with similar ascospores (plate 4)

We consider species with globose or subglobose ascospores and an ornamentation consisting of isolated warts on average less than 1 μm wide as similar to L. verrucispora. There are five such species and each of them is known from only one host, whereas all the hosts are not related to the genus Campylopus. Information on the species has been taken from literature and from personal observations.

Both Octospora svrcekii and O. wrightii share one special feature with L. verrucispora which had not yet been evidently demonstrated for any Lamprospora species: They induce galls on the rhizoids of their hosts (Döbbeler, 1979: 844–846; Benkert, 1998: 26–27 and 31). The size of ascospore warts is, although slightly larger, similar to L. verrucispora, with warts of O. svrcekii being 0.5–1 μm broad and 0.5–1 μm high and those of O. wrightii being 0.5–1 (2) μm broad and 0.5–1 (2) μm high. However, O. svrcekii parasitises Cratoneuron filic-
num (Hedw.) Spruce, a pleurocarpic moss typical for wet or moist habitats like streams and wet rocks (BENKERT, 1998: 26–27). Octospora weightii occurs on Amblystegium serpens (Hedw.) Schimp., also a pleurocarpic moss occurring on many substrates including stone, wood or soil. Furthermore, both species of Octospora have predominantly subglobose ascospores and have not as many warts as L. verrucispora (Plate 4e–f; BODUER, 1917: plate 399; SEM-pics in BENKERT, 1998: 27 and 32). In these respects, they clearly differ from L. verrucispora with its globose ascospores ornamented with many fine warts.

Lamprosora ekcestini is an ornamentation of warts which can be elongated and confluent like those of L. verrucispora, but the warts are on average slightly larger, measuring 0.5–1 (1.5) μm broad and 0.5–1 (1.5) μm high. In contrast to L. verrucispora, the ascospores of L. ekcestini are slightly subglobose and their surface is less densely covered with warts (Plate 4d and SEM–pics in BENKERT, 2009: 52–53). Furthermore, L. ekcestini does not induce galls on the rhizoids of its host Microbryum curviculum (Hedw.) R.H.Zander. The moss M. curviculum occurs in sun–exposed pioneer sites in grassland, quarries or arable fields and therefore in habitats quite different from those of Campylus pyriformis, the host of L. verrucispora.

Lamprosora lutiziana, a species with perfectly globose ascospores, differs from L. verrucispora in having an ascospore ornamentation with fewer warts (Plate 4c and SEM-pics in SCHUMACHER, 1993: 321). The warts in L. lutiziana are 0.3–1.4 μm broad and 0.6–1.6 μm high differing from the more or less isodiametric and lower warts of L. verrucispora. Also, L. lutiziana does not induce galls on the rhizoids of its host Philonitis fontana (Hedw.) Brid. which occurs in fairly wet habitats such as marshes, ditches, by streams or lakes as well as on wet rocks.

Lamprosora lubicensis is the most similar species to L. verrucispora regarding ascospore shape, size and ornamentation. However, L. lubicensis differs from L. verrucispora by having an ascospore ornamentation of, on average, slightly larger and less numerous warts and a stronger tendency for elongated and/or confluent warts (Plate 4b and SEM-pics in BENKERT, 1994: 198, 2009: 55). Occasionally, the warts of L. lubicensis can be hook-shaped and in extreme cases they can even indicate an irregular reticulum (pers. observation). Regular warts in L. lubicensis are 0.5–1.5 μm broad and 0.5–1.5 μm high, and when elongated they are 2–3 (5) μm long. However, L. lubicensis does not induce galls on the rhizoids of its host Hennediella heimii (Hedw.) R.H.Zander which is restricted to salt influenced habitats i.e. coastal areas, salt works and salted verges of roads (ATHERTON et al., 2010: 491). Macroscopically, L. lubicensis differs from L. verrucispora in the more orange-red coloured apothecia with a much more prominent margin compared with the yellow-orange and rather indistinctively marginate apothecia of L. verrucispora.

**Gall formation on mosses induced by bryophilous Peziales**

Gall formation is documented for several bryophilous Peziales. It is a characteristic feature defining the section Wrightioideae (BENKERT, 1998, 2006) within the genus Octospora encompassing the species O. americana Benkert, O. erzerbergi Benkert, O. hygrohypnophila Dissing & Sivertsen, O. orthotrichi (Cookie & Ellis) K.B. Khare & V.P. Tewari, O. svrceki, O. texensis Benkert and O. weightii. Spherical, unicellular galls are induced on rhizoid end-cells of their hosts, whereas the gall surface is completely covered with a layer of hyphae (DOBBIER, 1979: 845, fig. 8). These galls are very similar in all members of the section Wrightioideae and also highly resemble the galls observed in L. verrucispora. However there is a difference in the number of appressoria per gall: In L. verrucispora there is only one appressorium per gall, whereas DOBIER (1979: 844) reported up to six appressoria per gall in O. weightii. Admittedly, the appressoria in mature galls are rather difficult to see and L. verrucispora could possibly have more than one per gall.

Gall formation is also reported from O. meslinii associated with Grimmia pulvinata (Hedw.) Sm. (ITZEROTT & DOBIER, 1982: 202, fig. 1) and in O. pseudoampezzana (Svrček) Cailet & Moyne associated with Schistidium crassipilum H.H. Blom (ECKSTEIN & ECKSTEIN, 2009: 225). In both cases the infectious structures are very similar to those of the section Wrightioideae. In contrast, O. rubens (Boud.) M.M. Moser forms unicellular galls on rhizoids of Ceratodon purpureus which in general do not develop a complete cover of hyphae, most of the gall’s surface remaining free (ITZEROTT & DOBIER, 1982: 205-206, fig. 2-3, ut O. ibusassae Svrček & Kubička). The galls of Octospora humosa (Fr) Dennis in species of the Polytrichaceae are somewhat different in being very large, up to 350 μm in diameter, and thick walled. The surface is almost free with only a few hyphae clustered around the appressorium at the base of the gall (DOBBIER & ITZEROTT, 1981: 130–133, fig. 3). The gall inducing species O. meslinii, O. pseudoampezzana, O. rubens and O. humosa clearly differ from L. verrucispora having broadly ellipsoid to ellipsoid spores.

There was a report of possible gall formation for Lamprosora tuercula fora EGERTOVA et al. (2015: 121–122) but so far this has not been confirmed in other collections of that species (pers. observation). Therefore, Lamprosora verrucispora is the first Lamprosora species convincingly known as inducing galls on its host. However, detailed studies of infections are still lacking for many species and it seems likely that gall formation will also be discovered in other Lamprosora species in the future.

**Key**

With several new species described in recent years the keys available so far are outdated. Therefore, a new key is provided below to facilitate identification of all species of bryophilous Peziales with globose or nearly globose ascospores and an ascospore ornament consisting solely of isolated warts. In addition to the similar species mentioned above, the key includes Lamprosora esterlechnerae Benkert, L. maireana Seaver, L. rehmi Benkert, L. spinulosa Seaver, L. tuberculata Seaver and L. tuberculatellata Seaver, which all have an ascospore ornamentation of rather large warts or tubercles. Specimens of all species mentioned were studied by at least one of the authors except for L. esterlechnerae which is currently known only from the type. Additional information has been gathered from BENKERT (1987, 2002, 2006, 2011), CAILET & MOYNE (1980, 1991), ECKSTEIN (2014), ECKSTEIN et al. (2014), EGERTOVA et al. (2015), GRAF & MUHLEBACH (2014), KULLMAN (1997), SEEVER (1914, 1928); WANG & KIMBROUGH (1992).

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**References**


### Key for bryophilous Pezizales with globose or subglobose (L/B < 1.1) and warty ascospores

<table>
<thead>
<tr>
<th>Character</th>
<th>Classification</th>
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<tbody>
<tr>
<td>1 Ascospores slightly subglobose</td>
<td>2</td>
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<tr>
<td>1 Ascospores perfectly globose</td>
<td>4</td>
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<tr>
<td>2 Ascospores (11) 12–14 × 11–13 (13.5) μm, Q: 1.08–1.12, not growing in markedly humid habitats, host Amblystegium serpens</td>
<td>O. wrightii</td>
</tr>
<tr>
<td>2 Ascospores bigger</td>
<td>3</td>
</tr>
<tr>
<td>3 Ascospores 14–15 (16) × 13–14.5 μm, Q: 1.07–1.09, growing in dry, sun-exposed habitats, host Microbryum curvicollum</td>
<td>L. ecksteinii</td>
</tr>
<tr>
<td>3 Ascospores (13.5) 14–16 × 13–15 (15.5) μm, Q: 1.05–1.07, growing in humid to wet places, host Cratoneuron filicinum</td>
<td>O. svrcekii</td>
</tr>
<tr>
<td>4 Ornamentation consisting of warts of broader than broad, warts truncate, 0.8–1.2 μm broad and 1–2 μm high, ascospores 15.2–17.5 (20) μm</td>
<td>L. spinulosa</td>
</tr>
<tr>
<td>4 Ornamentation consisting of warts of more or less same height and breadth</td>
<td>5</td>
</tr>
<tr>
<td>5 Species growing in wet or humid places on Philonotis fontana, ascospores (12.8) 14–18 (19) μm, warts 0.3–1.4 μm broad and 0.5–1.6 μm high</td>
<td>L. lutziana</td>
</tr>
<tr>
<td>5 Species not growing in markedly wet or humid places, not on Philonotis</td>
<td>6</td>
</tr>
<tr>
<td>6 Ornamentation consisting of coarse warts or tubercles often &gt; 1.5 μm in diam.</td>
<td>7</td>
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<tr>
<td>6 Ornamentation consisting of smaller warts all or nearly all &lt; 1.5 μm in diam.</td>
<td>11</td>
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<tr>
<td>7 Ornamentation consisting of large, hemispherical or broadly rounded tubercles with thin walls and many internal cavities, giving the warts a foamy appearance, 2–6 μm broad, ascospores 19–25 μm, hosts Archidium alternifolium (Hedw.) Mitt. or Fassobromania lamprosorii</td>
<td>L. maireana</td>
</tr>
<tr>
<td>7 Warts solid or only with tiny cavities</td>
<td>8</td>
</tr>
<tr>
<td>8 Ascospores 19–24 μm in diameter</td>
<td>L. rehmii</td>
</tr>
<tr>
<td>8 Ascospores 14–19 μm in diameter</td>
<td>9</td>
</tr>
<tr>
<td>9 Growing on rotting wood or similar substrata, host Dicranodontium denudatum (Brid.) E. Britton, ascospores 14–16 μm</td>
<td>L. esterlechnerae</td>
</tr>
<tr>
<td>9 Growing on soil in more or less dry habitats, host different</td>
<td>10</td>
</tr>
<tr>
<td>10 Ornamentation consisting of uneven sized warts (0.5) 1–3 (5) μm broad, of rather irregular shape, ascospores (13) 15–19 (20) μm, host Pleuridium</td>
<td>L. tuberculata</td>
</tr>
<tr>
<td>10 Ornamentation consisting of more or less even sized warts, which are regularly hemispherical, 0.5–2 μm broad, warts occasionally connected by very low ridges, ascospores 15–18 μm, hosts Weissia or Didymodon</td>
<td>L. tuberculatella</td>
</tr>
<tr>
<td>11 Ornamentation consisting of small warts (0.2) 0.4–0.9 μm broad and 0.4–0.8 μm high, occasionally with one or few bigger warts 1–2 μm broad and 0.8–1.6 μm high, ascospores (13) 14–17 μm, growing on sand or acidic soil with upper humose layer, host Campylopus pyriformis</td>
<td>L. verrucispora</td>
</tr>
<tr>
<td>11 Ornamentation consisting of warts on average &gt; 0.8 μm broad, host different</td>
<td>12</td>
</tr>
<tr>
<td>12 Ornamentation consisting of mostly regular hemispherical warts on average &gt; 1 μm broad, occasionally connected by very low ridges, ascospores 15–18 μm, hosts Weissia or Didymodon</td>
<td>L. tuberculatella</td>
</tr>
<tr>
<td>12 Ornamentation consisting of warts 0.5–1.5 μm, ascospores 13.9–18 μm, growing on salt influenced soil, host Hennediella heimii</td>
<td>L. lubicensis</td>
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