Morphologic characterization of Agrocybe cylindracea (Basidiomycetes, Agaricales) from America, Europe and Asia

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Caracterización morfológica de Agrocybe cylindracea (Basidiomycetes, Agaricales) de América, Europa y Asia

Resumen. Se estudiaron 52 especímenes de Agrocybe cylindracea de orígenes geográficos distantes con el fin de definir los caracteres morfológicos variables y determinar si podrían ser considerados similares o si A. cylindracea incluye más de un taxón desde el punto de vista morfológico. Se estudiaron basidiomas frescos colectados en la naturaleza o obtenidos en cultivo, además de material seco de dos herbarios argentinos. Los especímenes de diferentes orígenes geográficos son microscópicamente similares, siendo altamente variables la superficie del píleo y el color. En base a diferencias microscópicas, se definieron dos morfotipos: 2-esporado y 1- a 4-esporado. El primero contiene principalmente basidios 2-esporados y esporas 10-16-(17) x 5-9-(10)μm. El segundo contiene porcentajes variables de basidios 1-, 2-, 3- y 4-esporados o mayormente 4-esporados y esporas menores, (8-) 9-11 x 5-6 μm. El morfotipo 2-esporado incluye colectas de Sudamérica y Asia exclusivamente; el morfotipo 1- a 4-esporado contiene especímenes de Centro- y Sudamérica, Europa y Asia. Se discute el significado taxonómico de estas diferencias. Se realizó un listado de la sinonimia encontrada en la literatura y se explica en detalle la razón por la cual se debería utilizar el nombre A. cylindracea.

Palabras clave: caracterización morfológica, Agrocybe cylindracea; A. aegerita

Abstract. Fifty two collections of Agrocybe cylindracea from distant geographic origins were studied with the aim of defining all the variable morphologic characters and to determine if these collections could be considered as one species or if A. cylindracea includes more than one taxon from a morphological perspective. Fresh basidiomata collected in nature or obtained in culture and dried material from two Argentinean herbaria were studied. Specimens from different geographic origins are macroscopically similar, being the pileus surface and color highly variable. Based on microscopic differences, we defined two morphotypes: 2-spored and 1- to 4-spored. The former contains mostly 2-spored basidia and spores 10-16-(17) x 5-9-(10) μm. The latter contains variable percentages of 1-, 2-, 3- and 4-spored basidia and larger spores, (8-) 9-11 x 5-6 μm. The 2-spored morphotype includes collections exclusively from South America and Asia; the 1- to 4-spored morphotype contains specimens from Central- and South America, Europe and Asia. The taxonomic significance of these differences is discussed. A list of synonyms of A. cylindracea recorded in literature is given and the reason for which the name A. cylindracea should be used is presented in detail.

Key words: morphologic characterization, Agrocybe cylindracea; A. aegerita

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Introduction

Agrocybe cylindracea (DC.: Fr) Maire (Basidiomycetes, Agaricales, Bolbitiaceae) is an edible mushroom cultivated on low cost substrates based mainly on agricultural and forest wastes [4,5]. A wide geographical distribution has been reported: although it is rare in North America, this species was found in all continents [16]. Many macro- and microscopic morphologic variations have been previously observed between different collections. Within macroscopic characters, the pileus coloration and surface are variable [10,16]; within microscopic variations, the number of spores produced per basidium, the basidiospores sizes and the cystidal size and shape can be cited [10]. Moreover, the molecular characterization of morphogenetic genes in A. cylindracea strains has revealed an extensive genetic polymorphism [12]. For all these reasons, it has been proposed that A. cylindracea could correspond to more than one microspecies [9,10,16] or alternatively it could be a polymorphic cosmopolitan species [16]. Up to now, A. cylindracea species concept is based on isolated, sometimes rather poorly described documented collections, except from those of Europe [16]. Singer and Watling, the two authors who studied Agrocybe more deeply, considered that additional studies were required [9,16] in order to clear up this matter. In Argentina, A. cylindracea can be easily found in groups growing on trunks of trees from several species, most commonly on species from the genera Populus, Salix, and Alnus; also on Quercus, Ulmus, Robinia, Brussowetia, and Melia [18]. Cultural studies on A. cylindracea strains from Argentina have been previously performed, and no strain variations were reported [6].

Morphologically, species belonging to the Agrocybe genus can be distinguished by the presence or absence of a veil, generally as a ring, the presence or absence of pleurocystidia, the presence of a germinal pore in the basidiospores and the habitat. In general, it is not usual to find less than four spores per basidium, but when 2-spored basidia are found, this is considered a significant character [15]. The fruiting body size is usually variable within species. Cystidia should be considered the most important character, whereas basidiospores sizes and veil remnants size and position should be given less importance according to Watling [14].

Materials and methods

Macro- and micro-morphology

In this research we studied all material deposited as A. cylindracea or A. aegerita in the Argentinean herbaria BAFC (Facultad de Ciencias Exactas y Naturales, Biodiversity and Experimental Biology Department, University of Buenos Aires, Argentina) and LIL (Miguel Lillo Foundation, Tucumán Province, Argentina). The macroscopic description was performed using fresh basidiomata collected in nature or obtained in culture. Color names are in accordance with Munsell Color Co. [3]. For the microscopic examination, dried collections deposited in the cited herbaria were also studied; microscopic observation of tissues mounted in 5 % KOH and 1 % aqueous phloxine was undertaken. For each collection studied, 20 basidiospores, 10 basidia and 10 cystidia were measured and their size, form, surface and color were described. All specimens collected from nature or obtained in culture were dried and deposited in the BAFC herbarium.

Strains used

Strains used for basidiomata production are conserved in the ICFC (IIB-INTECH Collection of Fungal Cultures, Laboratory of Mycology and Mushroom Cultivation, IIB-INTECH, Chascomús, Argentina, reference in the WDCM database: WDCM 826). Geographical origins, collection dates, collectors, original substrates (if available) and collection numbers are as follows: i) deposited as A. cylindracea: ARGENTINA, Buenos Aires Province, Capital Federal, 27-IV-1994, on Populus sp., ICFC 424/01; ii) deposited as A. aegerita: ARGENTINA, Buenos Aires Province, Llano, coll. J. R. Deschamps on Acer negundo trunk, ICFC 440/01; Chascomús, La Alameda forest, coll. E. Albertó on dead trunk, ICFC 462/02; CHINA, Taiwan, ICFC 621/04; Guizhou Province, ICFC 620/04; GUATEMALA, near Tecpán, 1991, coll. Ruth de Leon at 2000 m altitude on trunk Sambucus sp., ICFC 558/03; SCOTLAND, commercially cultivated, ICFC 587/03; FRANCE, 2001, obtained from breeding of monocaryotic French isolates H99 x H355, ICFC 299/00; iii) deposited as A. chaxingu: ARGENTINA, Buenos Aires Province, Capital Federal, 2001, obtained from breeding of monocaryotic French isolates H99 x H355, ICFC 299/00; iv) deposited as Agrocybe cylindracea: ARGENTINA, Buenos Aires Province, Capital Federal, 27-IV-1994, on Populus sp., ICFC 424/01; CHINA, Taiwan, ICFC 621/04; Guizhou Province, ICFC 620/04; GUATEMALA, near Tecpán, 1991, coll. Ruth de Leon at 2000 m altitude on trunk Sambucus sp., ICFC 558/03; SCOTLAND, commercially cultivated, ICFC 587/03; FRANCE, 2001, obtained from breeding of monocaryotic French isolates H99 x H355, ICFC 299/00; iii) deposited as A. chaxingu:

Results and discussion


Agrocybe cylindraceus DC. 1815. Fil. Franc. 6: 51. [Basion.]. [8].


Agrocybe aegerita V. Bríg. 1824. Fungi Neapol., t. 1. [8], as aegerita.

Agrocybe cylindraceus DC.: Fr. 1832. Syst. Mycol. 3. Index: 16, as cylindraceus.

Agrocybe plicatus Fr. 1836. Epiz. p. 163. [8].

Agrocybe strobiloides Bríg. 1851. Hist., p. 124. [8].


Agrocybe briganti Fr. 1863. Mon. 2: 336. [8].

Pholiota aegerita (Bríg.) Quéll. 1872. Les Champignons du jura et des Vosges: 164. [17], as aegerita.

Pholiota cylindracea (DC. per Fr.) Gillet. 1874. Champignons de France: 439. [17].

Pholiota plicata (Bull. per Mérat.) Gillet. 1874. Champignons de France: 439. [17].

Pileus brown (Munsell, 7.5YR, 5/4), generally darker (dark brown, Munsell, 7.5YR, 4/4) in the center and almost white (very pale brown, Munsell, 10YR, 8/3) in the margin, uniform dark brown (Munsell, 7.5YR, 3/2) in primordia; pileus surface not hygrophanous, not viscid, glabrous, eventually sulcate or striate in some specimens but usually smooth and silky; convex to flat, 8-200 mm broad (Figure 1A). Lamellae white (Munsell, 10YR, 8/1), light grey (Munsell, 10YR, 7/1) and eventually strong brown (Munsell, 7.5YR, 5/6) or dark brown (Munsell, 7.5YR, 4/4), moderately broad, tight, adnate, sinuated, or subdecurrent, edge smooth or crenate. Stipe white (Munsell, 10YR, 8/2) to very pale brown (Munsell, 10YR, 7/3), with scales to fibrillose, cylindrical, solid, 10-150 x 2-25 mm. Veil forming a broad and persistent ring (Figure 1A). Spore print strong brown (Munsell, 7.5YR, 5/6). Context white (Munsell, 10YR, 8/2), smell pleasant, fruity, excellent taste. Gregarious.

Spores (8-) 9-16 (-17) x 5-9 (-10) µm, Q = 1, (n = 700), oblong, smooth, some with and other without oil-like droplets, pigmented (honey colored or chestnut-brown) with a small never truncated germ pore (Figure 1B, C). Basidia (17-) 22-46 x 5-8 µm, clavate, most middle constrained, thin walled, hyaline, 1- to 4-spored (Figure 1D, E). Pleurocystidia (18-) 21-65 x (5-) 7-17 µm, clavate to ventricose, with rounded apex or mucronated or capitated, thin walled, numerous (Figure 1F); cheilocystidia 18-49 x (3-) 5-13 µm, similar to pleurocystidia or smaller and then cylindrical or lageniform (Figure 2B). Hymenophoral trama regular. Epithecium of the pileus formed by vesicular to clavate elements, 14-42 x 6-25 µm (Figure 2C) forming a hymenophoral layer. Pleurocystidia 17-55 x (5-) 6-13 µm, ventricose and mucronate, sometimes with two constrictions near the apex or lageniform, rarely acute (Figure 2A). Caulocystidia 16-88 (-95) x 4-16 µm, similar in shape to the cheilocystidia or capitate or mucronate and sometimes middle constrained (Figure 2D).

Geographical distribution. Cosmopolitan, specimens have been cited in all continents [16].

Habitat. Lignicolous, growing on trunks of dead or living trees, often on wounds or at a branch base. More commonly on Populus and Salix, also on Quercus, Ulmus, Acer, Melia, Robinia, Broussonetia, Allophyllum, Cupania, Phebe [7,11,18] and Araucaria angustifolia [16].

Material studied. ARGENTINA, BUENOS AIRES, La Plata, ad truncum, 26-IV-1951, leg. J. C. Lindquist & J. E. Wright, (LIL); Paseo del Bosque, on living Populus nigra, 14-

Remarks
In the present paper, a detailed morphological study of A. cylindracea specimens was carried out in order to study the character variations within this species and their possible taxonomic significance. Specimens from two Argentinean herbaria (BAFC and LIL) were studied; the herbaria of Carlos Spegazzini Botanical Institute (La Plata National University, La Plata, Buenos Aires Province) and of Mario Rajchenberg at CIEFAP (Centro de Investigación y Extensión Forestal Andino Patagónico, Esquel, Chubut Province) do not contain specimens from Agrocybe cylindracea.

Comparison of morphological characters of A. cylindracea specimens from distant geographical origins as Argentina, Guatemala, France, Scotland, China and Japan.
showed a similar macroscopic aspect (Figure 3). The pileus surface and color were variable depending on environmental conditions, i.e., basidiomata obtained from strain ICFC 299/00 using wheat straw as a substrate had the pileus surface smooth and silky, whereas basidiomata obtained from the same strain in cultures using willow sawdust and earth as a coating layer had the pileus surface radially wrinkled. The pileus color was sometimes variable between basidiomata obtained from the same strain; however the strains from Japan and China (Taiwan) always formed darker basidiomata. Regarding microscopic characters, significant differences were observed only in the number of basidiospores produced per basidium and as a consequence, in the basidiospores sizes. Based on these differences two morphotypes were recognized, which will be called from now on “2-spored” and “1- to 4-spored”. As their names indicate, specimens from the first group had mostly 2-spored basidia (98.5%) and few 1-spored basidia (1.5%, Figure 1D) and spores were 10-16 (-17) x 5-9 (-10) m (Figure 1B). All Argentinian collections (except for those collected in the Misiones Province) were included in this morphotype together with specimens obtained in culture from a Chinese strain (from Guizhou Province), which percentages of 2-spored and 1-spored basidia were similar (95 and 5% respectively) and which spores were in the same size range to those of Argentinian specimens. Basidiomata from the second morphotype had variable percentages of 1-, 2-, 3-, or 4-spored basidia (Figure 1E), in average 4.2%; 41.2; 18.8 and 35.9 respectively or 100% 4-spored basidia and smaller spores, (8-) 9-11 x 5-6 µm (Figure 1C). This morphotype included basidiomata obtained from a Guatemalan strain, from an Argentinian strain (from Misiones Province), from European strains (from Scotland and France) and from two Chinese strains (from Taiwan and Sichuan).

Within the Agrocybe genus, the number of spores produced per basidium has been previously used as a taxonomic character to define forms, i.e., A. pediades f. bispora Singer has exclusively 2-spored basidia [9], whereas specimens belonging to the form A. pediades f. pediades bear exclusively 4-spored basidia [15]. In contrast, in A. cylindracea, one morphotype had mostly 2-spored basidia and the other morphotype had variable percentages of 1- to 4-spored basidia. In this case, the limit is less obvious and for this reason we consider this character insufficient to characterize a form or variety of A. cylindracea.

Collection T 1875, from Tucumán Province (Argentina) was documented in the LIL herbarium as "A. aegerita var. venosisima" and the material identified as "LIL without no." was named as "topotype of Agrocybe aegerita (Brig.) var. ined." and the material identified as "LIL without no." was named as "topotype of Agrocybe aegerita (Brig.) var. rugosovenosa Singer". The first variety has never been published and the second is distinguished from the typical variety by the radially wrinkled pileus surface. In this work we evidenced that the pileus surface, including the presence of wrinkles or radial depressions varies greatly depending on environmental conditions. For this reason we consider that these differences do not justify the proposal of a variety.

In conclusion, according to morphological characters, all these collections seem to correspond to the same species, as diagnostic characters for recognition of Agrocybe species were not variable. We consider that the observed differences were not enough to recognize unambiguously more than one taxon. Nevertheless, compatibility and/or molecular studies should be undertaken to ascertain this hypothesis or to alternatively prove the presence of infraspecific entities. A. cylindracea can be easily recognized for its lignicolous habitat, basidiomata generally robust and clustered, and by the basidiospores bearing a small germ pore.

Specimens collected in Misiones Province (Argentina) have a slightly different macroscopic aspect, being generally smaller and with different pileus color, more yellowish in the center and chestnut-brown to orange in primordia. Microscopically, these collections are identical to other collections of Agrocybe cylindracea from the 1- to 4-spored morphotype. It would be also interesting to develop compatibility and/or molecular studies to determine if these specimens belong to a separated species.

It is to be noticed that specimens deposited as A. chaxingu (BAFC 51 604), did not show any morphological differences from those of A. cylindracea belonging to the 1- to 4-spored morphotype. This means that the collection BAFC, deposited as A. chaxingu, could correspond to A. cylindracea. It would be interesting to compare the type material from both species to address the hypothesis that A. chaxingu is a synonym of A. cylindracea.

It is important to note that the original Candollean spelling was cylindraceus, but Fries sanctioned the Agaricus name as cylindricus 1832. As Fries gave a reference to De Candolle, Fries spelling cylindraceus, must be corrected to cylindricus. In fact if we correct the name Agaricus cylindraceus (priority from 1815) to A. cylindraceus DC.: Fr., then it would become an illegitimate name because of the existence of the earlier homonym Agaricus cylindricus Schaeff.: Fr. (priority from 1774) which is not an Agrocybe species but the current Coprinus comatus (see http://www.indexfungorum.org/Names/SynSpecies.asp?RecordID=148667).
Finally, regarding the epithet of the synonym Agrocybe aegerita, the original spelling was “aegerita”, not “aegerita” as it is world-wide known, and according to art. 60.1 from the nomenclature code [2], the original spelling is to be retained since this spelling was not a typographical or orthographical error. V. Brig. wrote again aegerita in Hist. Fung. Neapol. 4: 72. 1837 (see Briganti's illustration at http://www.mykolibri.de/bibliothek/bilddetail.html?b=BRIGA1837P2.jpg). Quéléat (as Pholiota aegerita) and Singer (as Agrocybe aegerita) corrected Briganti’s spelling very likely because they thought that this word came from the Latin “aeger”, which means diseased, but this epithet comes from the Greek “aigeiritês”, which means poplar. According to Steam [13], transliteration from the Greek diphthongs “ai” and “ei” into Latin is as follows: Greek “ai” becomes Latin “ae”, and Greek “ei” becomes “i” or “e”. So, “aegirita” would be a correct transliteration of the Greek term “aigeiritês”. Therefore the correct epithet for this synonym is aegirita.

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References