

Amanita dulciodora (Amanitaceae, Basidiomycota), a striking new species of Amanita section Lepidella from Northeast Brazil

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Background – *Amanita* Pers. has a worldwide distribution and is one of the most well-known fungal genera in terms of both morphotaxonomy and molecular phylogenetics, consisting of many edible, as well as poisonous, even lethal, mushrooms. The genus is also known to form ectomycorrhizal associations with angiosperms and gymnosperms and play an important role in ecosystems. Although previous studies have already pointed out the high diversity of the genus *Amanita* in tropical areas, only a few recent studies continue to record and/or describe new species of *Amanita* from Brazilian territory. Herein, an additional, morphologically striking new species of *Amanita* sect. *Lepidella* is described from Northeast Brazil.

Methods – The new species was collected at 'Parque Estadual Serra do Conduru' (PESC), located in the municipalities of Uruçuca, Itacaré e Ilhéus, Bahia state. The park is an Atlantic Forest protected area with about 7000 ha in a region with a high degree of endemism. For morphological analysis, standard methods for *Amanita* were followed.

Key results – *Amanita dulciodora* is described as new species from Atlantic Forest remnants in southeast Bahia. It is assignable to *Amanita* stirps *Crassiconus* within *Amanita* subsect. *Solitariae* and is mainly characterized by its (1) medium-size basidiomata with cap colour and appearance dominated by universal veil at first; (2) distinctly coloured acute-pyramidal, truncate-pyramydal to verrucose warts which are mainly composed of irregularly disposed, ovoid to subglobose to clavate cells intermixed with very abundant filamentous hyphae; (3) mostly ellipsoid to elongate amyloid basidiospores and (4) the common presence of clamps at the basal septa of basidia. It was compared with its similar species, *A. crassiconus* and illustrated with line drawings and photographs.

Key words – Agaricales, Agaricomycetes, Fungi, neotropics, taxonomy.

INTRODUCTION

Amanita Pers. has a worldwide distribution and is one of the most well-known fungal genera in terms of both morphotaxonomy and molecular phylogenetics, consisting of many edible, as well as poisonous, even lethal, mushrooms (Weiß et al. 1998, Drehmel et al. 1999, Tulloss 2005, Letcher 2007, Cai et al. 2014, 2016). It comprises primarily agaricoid and a few sequestrate forms (Moncalvo et al. 2002, Justo et al. 2010, Yang 2011). The genus is also known to form ectomycorrhizal associations with angiosperms and gymnosperms and play an important role in ecosystems (Yang et al. 1999, Yang 2005, Wolfe et al. 2012b). Although most species of *Amanita* are symbiotic, a small number of species consistently grow apart from woody plant hosts as saprobes or, at least amycorrhizal organisms (e.g. *A. thiersii* Bas, *A. inopinata* D.A.Reid & Bas) (Bas 1969, Wolfe et al. 2012a, Hess & Pringle 2014). *Amanita* comprises c. 500 described species (Bas 2000, Tulloss 2005), but this number can be increased to more than 900 names if counting undescribed species (Tulloss & Yang 2018). According to the traditional infrageneric classifications based on morpho-anatomical features, *Amanita* was often divided into two subgenera, *Amanita* and *Lepidella* (E.-J.Gilbert) Veselý emend. Corner & Bas (1962), comprising seven sections: sect. *Amanita*, sect. *Caesareae* Singer, sect. *Vaginatae* (Fr.) Quél., sect. *Amidella* (J.-E.Gilbert) Veselý, sect. *Lepidella*, sect. *Phalloideae* (Fr.) Quél. and sect. *Validae* (Fr.) Quél. This systematic division has been supported by several molecular phylogenetics works (Weiß et al. 1998, Drehmel et al. 1999, Zhang et al. 2004, Justo et al. 2010, Cai et al. 2014, Tang et al. 2015, Tulloss et al. 2016).

Previous studies have already pointed out the extent of diversity in the genus *Amanita* in tropical areas (Pegler 1983, 1986, Tulloss et al. 1992, 2011, Bas & de Meijer 1993, Tulloss 2005, Tulloss & Franco-Molano 2008, Simmons et al. 2002, Tang et al. 2015). Rick (1906), Rick (1937), Singer (1953), Homrich (1965), Bas (1978), Grandi et al. (1984), Capelari & Maziero (1988), Bas & de Meijer (1993), Stijve & de Meijer (1993), Pegler (1997), Giachini et al. (2000), de Meijer (2001, 2006), Sobestiansky (2005) and some more recent studies by Wartchow & Maia (2007), Wartchow et al. (2007, 2009, 2013a, 2013b, 2015a, 2015b), Menolli et al. (2009a, 2009b) and Wartchow (2015, 2016) have recorded and/or described new species of *Amanita* from Brazilian territory.

The aim of the present study is to contribute to the knowledge of *Amanita* mycobiota by describing a new species from sect. *Lepidella* collected in Atlantic Forest remnants of Northeast Brazil. In addition, we present a dichotomous key to Central and South America species of the section.

MATERIAL AND METHODS

Material and collection localities

The 'Parque Estadual Serra do Conduru' (PESC), created in 1997 (Araujo et al. 1998), is located on the territory of three municipalities: Uruçuca, Itacaré and Ilhéus (14°23'07" S, 39°04'43" W), Bahia state, in the northeast of Brazil. The park has approximately 7000 ha (Araujo et al. 1998, Angelo 2003). The climate is described as tropical humid, with mean annual temperatures close to 24°C. Average annual precipitation is over 1300 mm, with higher rainfall occurring from February to July (Sá et al. 1982). The vegetation is characterized by the dense sub-montane ombrophilous forest or tropical moist Forest with dominance of a uniform canopy more than 25 m tall. It has a high potential for biodiversity conservation with about 458 tree species per hectare, as well as high rates of endemism. It represents one of the most important blocks of forest remnants of the northeastern coast (Mori et al. 1983, Thomas et al. 1998, Martini et al. 2007). Some studies demonstrated that this region has a high degree of endemism and high biological importance. Thomas et al. (1998) identified 454 species of trees in 1 ha, and later Martini et al. (2007) found 144 tree species in a 0.1 ha plot, indicating that this region has one of the greatest numbers of tree species in Brazil and in the world. Also, the review article by Giulietti et al. (2005) reported that 50% of all species of the tribe Olyreae (Poaceae) occur in the region, including many species endemic to the area.

Morphological studies

Macromorphological descriptions were based on notes and colour photographs of basidiomata taken in the field. Colours of fresh and dry basidiomes were compared with reference colours in Kornerup & Wanscher (1978). Observations and measurements reported for micromorphological features were obtained from dried material rehydrated and mounted in distilled water, 3% KOH and Congo red or Melzer's reagent. Regarding biometric values and notation, we follow the emended methodology of Tulloss et al. (1992) and Tulloss (1993, 1994, 2000), which is summarized below.

At the beginning of a set of spore data, the abbreviation [a/b/c] signifies "a" basidiospores measured from "b" basidiomata of "c" collections. Dimensions of basidiospores are presented in the following form (m-)n-o(-p), in which "m" is the smallest value observed or calculated and "p" is the largest value observed or calculated. In the range of values observed or calculated, the 5th percentile is "n"; and the 95th percentile is "o". A summary of definitions of biometric variables follows:

L, (W) = the range of average lengths (widths) of spores of all basidioma examined.

L', (W') = the average of all lengths (widths) of all spores measured.

Q = the ratio of length to width of a spore or the range of such ratios for all spores measured.

 \mathbf{Q} = the average of Q computed for all basidiomata examined.

 \mathbf{Q}' = the average of all Q values computed for all spores measured.

The holotype is kept at the mycological collection of JPB (Thiers 2018).

SPECIES DESCRIPTION

Amanita dulciodora C.C.Nascimento, Sá & Wartchow,

sp. nov. MycoBank no. MB 824182

Diagnosis – Basidiomes medium-sized. Pileus 86–96 mm wide, white to whitish, unchanging; *universal veil* as pastel red to reddish orange to yellowish red pyramidal warts; lamellae white, orange white or pinkish white to somewhat cream colour, unchanging; lamellulae truncate; stipe white to whitish; bulb napiform at maturity, 35-37 mm long and up to 27 mm wide; basidiospores (7.1–)7.9–10.7(–11.7) × (4.6–) 4.8–6.1(–6.2) µm, ellipsoid to elongate then infrequently cylindric, amyloid; basidia clamped. – Type: Brazil, Bahia, Uruçuca, Parque Estadual da Serra do Conduru, $14^{\circ}29'41''$ S, $39^{\circ}8'06''$ W, 29 Nov. 2012, *F. Wartchow et al.* FW 143/2012 (holo-: JPB 60534).

Etymology – From Lat., '*dulcis*' (= sweet) and '*-odorus*' (= "having a smell"). Regarding to sweetish smell exhaled by the fungus.

Macroscopic characters - Basidiomes medium-sized, solitary. Pileus 86-96 mm wide, cap colour and appearance dominated by universal veil at first, later with exposed surface white (1A1) to whitish (2A1), unchanging, globose at first, subhemispheric to hemispheric when expanding, then convex to applanate at maturity, dry; margin incurved when expanding, straight at maturity, non-striate, often strongly appendiculate with flocculence from universal veil on marginal region and with ephemeral bits of partial veil (concolourous and irregularly shaped); context up to 11 mm thick at stipe, firm, white to whitish except pale gray (1B1) to pastel gray (1C1) just beneath pileipellis, unchanging when cut or bruised, gradually thinning toward margin; universal veil as concentrically arranged, acute-pyramidal, truncatepyramidal to verrucose, coarse adnate warts, up to 1.5-3 (-4) mm high, 1-2.5(-3) mm wide, densely placed over the disk, towards margin becoming low amorphous flocculence to flat fibrillose scales, pastel red (7A4, 8A4) to reddish orange (7A5-6) to vellowish red (8A5-6). Lamellae subfree to free, with short decurrent tooth at stipe apex, subcrowded to crowded, white (1A1), orange white (6A2) or pinkish white (7A2) to somewhat cream colour (4A3), unchanging when cut or bruised, with edges smooth and concolourous, often with partial veil remnants attached, up to 6 mm wide (at mid-radius; lamellulae mostly truncate, with 3-4 lengths, plentiful, unevenly distributed. Stipe 48-55 (excluding bulb) \times 17–19(–23) mm (at mid-stipe), slightly tapering upward, flaring at apex, smooth, white to whitish, becoming yellowish to brownish yellow (5C8) or yellow ochre (5C7) from handling; bulb at first turbinate to elongate, then napiform, 35-37 mm long and up to 27 mm wide, ventricose, sometimes doglegged, deeply inserted into the substrate; context solid, bulb hollow in only one basidiome (probably ate by insects), whitish, unchanging when cut or bruised; partial veil as apical to superior pulverulent belt at stipe, off-white, rather fragile, ephemeral, remaining as appendiculate material at pileus margin; universal veil on stipe base leaving subconical to irregular warts, reddish orange (7A5-6) to yellowish red (8A5-6) at first, becoming reddish (or pinkish) white (7A2, 8A2) to shell pink (8A3), arranged in incomplete belts on upper bulb and lower stipe. Odour very sweet (remarkable). Taste not recorded. Macrochemical tests not performed. Figs 1 & 2A.

Microscopic characters – Basidiospores [90/3/2] (7.1–)7.9– $10.7(-11.7) \times (4.6-)4.8-6.1(-6.2) \ \mu m; L = 9.1-9.2 \ \mu m; L' =$ 9.2 μ m; W = 5.2–5.6 μ m; W' = 5.4 μ m; Q = (1.39–)1.46– 2.09(-2.22); **Q** = 1.72-1.73; **Q'** = 1.72; ellipsoid to elongate, infrequently cylindric, hyaline, colourless, amyloid, thinwalled; contents as 1-2 guttules; hilar appendix prominent, sublateral. Basidia $(30-)34-60 \times 8.5-12(-14.5) \mu m$, thinwalled or nearly so, mostly 4-, rarely 2-spored, with sterigmata up to 8 µm; basal septa commonly clamped. Subhymenium up to 50 µm thick, with (2) 3–4 layers of subglobose to ovoid or irregularly shaped cells $9-25(-30) \times 8-20$, often mixed with a few, short, un- or partially inflated hyphal segments, with basidia arising from elements of all types; clamp connections frequent. Lamellar trama bilateral, divergent; central stratum 40-50 µm wide, composed of some intercalary partially inflated to narrowly ventricose cells $140 \times 19 \,\mu\text{m}$, mixed with branched, interwoven filamentous undifferentiated hyphae 3-12 µm wide; vascular hyphae 2.3-8.5 µm wide, infrequently branched, sinuous, rare; lateral stratum made up of diverging (at angles up to 45°), filamentous, undifferentiated hyphae 3-14.5 µm wide, branched, mixed with broadly to narrowly clavate to sub-ellipsoidal inflated cells, apparently all intercalary; vascular hyphae 4.3–9.5 µm wide, rare: clamp connections frequent in subhymenial base. Lamellar edge tissue sterile; inflated cells $18-30(-35) \times 7-12(-$ 16) µm, colourless, thin-walled, subglobose to clavate, single or 2-3 in chain; filamentous hyphae abundant, 2-8 µm wide, thin-walled, hyaline. Pileus context with acrophysalides up to 22 \times 14 μ m, broadly clavate; filamentous hyphae 2.5– 10 µm, plentiful, interwoven, commonly branched, septate, clamped; vascular hyphae not seen or lacking. Pileipellis as narrow cutis (30-70 µm thick) with pronounced boundaries, ungelatinized to minimally gelatinized (only at surface); filamentous undifferentiated hyphae 3.0-9.5 µm wide, densely packed vertically, branching, with many at and near upper surface connected to universal veil well into maturity; vascular hyphae 3.5-14.5 µm wide, branched, sinuous, scattered to locally conspicuous. Universal veil on pileus with rather abundant filamentous, undifferentiated hyphae (especially in the base of warts), with elements dominantly irregularly disposed (anticlinal arrangement of elements only distinct in the layer close to poorly formed pileipellis); elements of lower part of wart colourless to sub-colourless; elements of upper part orange-yellow to orange-brown in mass; filamentous, undifferentiated hyphae 3.5-17.5 µm wide, plentiful to locally dominant, thin- or sometimes slightly thick-walled (especially in hyphae segments of larger diameter, up to 0.8 um thick), branched, sometimes with uninflated hyphal end segments, hyaline or with brownish vacuolar pigments; inflated cells abundant, mainly ovoid to subglobose (38–67 \times 35–58 μ m), broadly ellipsoid (45–70 \times 30–40 μ m) to clavate (sometimes slightly constricted, up to $90 \times 49.5 \ \mu m$), more rarely fusiform-ellipsoid, ventricose-fusiform, and elongate in shape, terminal singly or in chains of 2-3(-4), thin- to slightly thick-walled (up to 1.0 µm), usually with brownish to yellowish vacuolar pigments, sometimes colourless to sub-colourless; vascular hyphae scattered to locally conspicuous 3-13.5 µm wide. Universal veil on upper part of bulb with a structure very similar to that of the universal veil on pileus, with greater proportion of filamentous, undifferentiated hyphae; inflated cells smaller (on average) than on pileus; inflated cells. Stipe context distinctly vertically acrophysalidic; acrophysalides $180-200 \times 20-36 \mu m$, plentiful, very conspicuous, clavate; filamentous hyphae 4-8 µm wide, longitudinally oriented, frequently branched, septate, clamped; vascular hyphae up to 5 µm wide, unbranched, rare. Partial veil filamentous, undifferentiated hyphae 2-12.5 µm wide, fairly abundant, hyaline; inflated cells plentiful, ovoid to subglobose to broadly clavate, up to $85 \times 38 \mu m$, terminal, usually singly, dominantly colourless, hyaline, occasionally with yellowish walls; vascular hyphae not observed; clamp connections not observed. Fig. 2B-F.

Other collections examined – **Brazil**: Bahia, Uruçuca, Parque Estadual da Serra do Conduru, 14°29'41" S, 39°8'06" W, 28 Nov. 2012, *F. Wartchow et al.* FW 134/2012 (JPB).

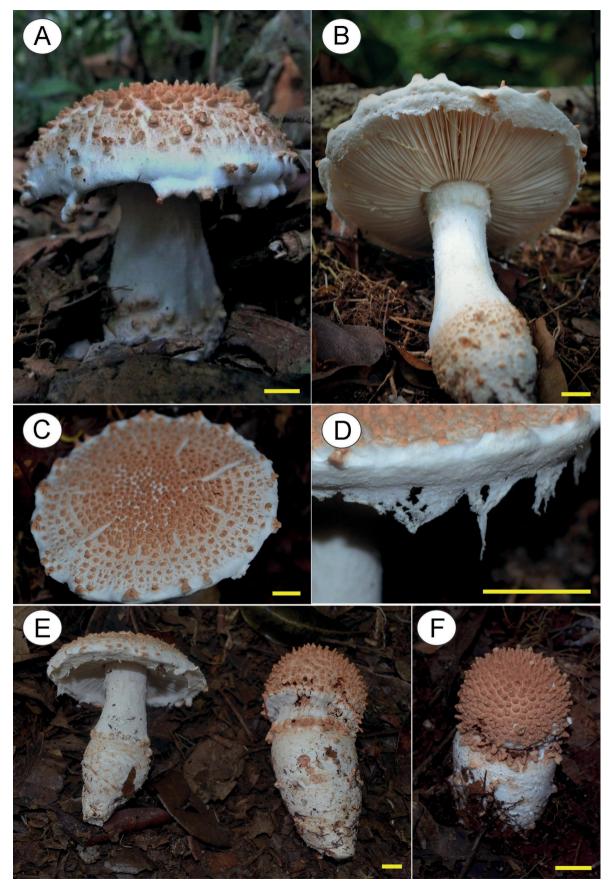


Figure 1 – Amanita dulciodora: A–F, young and mature basidiomata. Scale bars = 10 mm. Photographs by F. Wartchow.

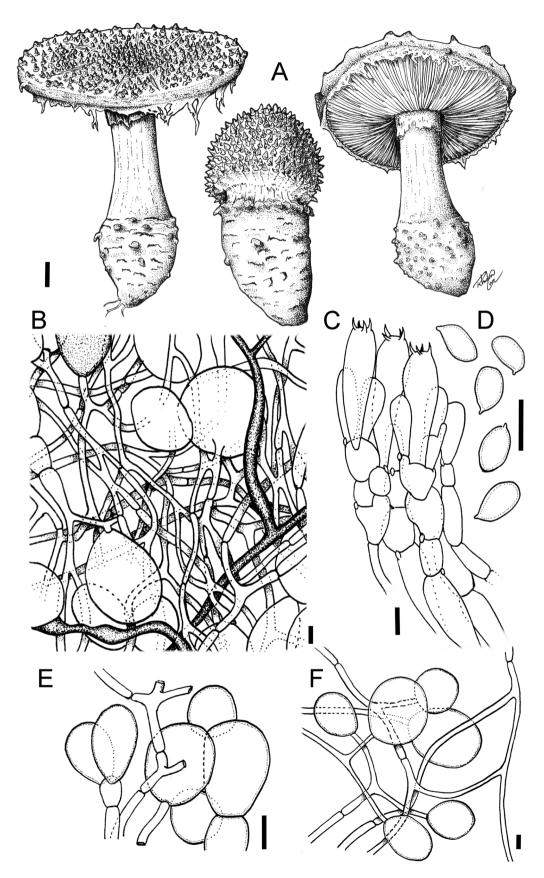


Figure 2 – *Amanita dulciodora*: A, basidiomata; B, universal veil remnants on pileus in longitudinal section; C, hymenium and subhymenium; D, basidiospores; E, lamellar edge cells; F, partial veil trama. Scale bars: A = 10 mm; B-F = 10 µm. Drawings by Rhudson Ferreira Cruz.

— Key to species of *Amanita* section *Lepidella* from Central and South America –

1.	Universal veil on pileus consisting mainly of chains of relatively large, inflated, cylindrical, elongate-
	fusiform, and narrowly clavate cells. Remnants of universal veil on stipe scattered or more rarely concentrated locally or indistinct
1'.	Universal veil on pileus comprising disordered to more or less anticlinal elements, never as chains of relatively large, narrow inflated cells. Stipe usually with bulbous base and universal remnants concentrated below
2. 2'.	Basidia with clamps
3. 3'.	Basal bulb lacking or somewhat inconspicuous (narrowly clavate or narrowly fusiform or as a limited swelling in lower stipe
4.	Pileus evenly dark brown to somewhat paler greyish brown with concolourous pyramidal warts
4'.	<i>A. grallipes</i> Bas & de Meijer Pileus surface whitish, cream colour, light beige, pinkish beige, reddish beige, pale pinkish orange or pale ochraceous-buff
5.	Universal veil remnants on stipe pulverulent-floccose and concentrated on upper part
5'.	
6. 6'.	$ \begin{array}{l} Basidiospores \ length \geq 10 \ \mu m \ (L^{\prime} \geq 11.0 \ \mu m). \end{array} \begin{array}{l} & \\ Basidiospores \ length \leq 10 \ \mu m \ (L^{\prime} \leq 9.1 \ \mu m). \end{array} \end{array} \end{array} $
7. 7'.	Pileus surface white to pale pinkish orange, with a dense covering of small to large scales. Stipe not tapering downwards
8. 8'.	Stipe completely with or whitish, densely covered with erect to recurved floccose warts, scales, or squamules
9.	Pileus surface pale ochraceous, covered with adnate, small, pointed, felted, concolourous warts
9'.	<i>A. bubalina</i> Bas Pileus surface white to greyish brown with fine squamulose universal veil remnants, densest over disk, brown <i>A. savannae</i> Tulloss & Franco-Mol.
10.	Pileus surface pale yellowish, covered with detersile, yellow to ochraceous brown to brownish floc- cose-squamulose remnants of universal veil. Stipe slightly narrowing upward, not bulbous
10'	<i>A. aureofloccosa</i> Bas Pileus surface white, sometimes with pinkish or yellowish tinge, with pulverulent-floccose to subfelted universal veil remnants in subpyramidal warts or patches. Stipe subcylindric, with a conspicuous bulb <i>A. foetens</i> Singer
11.	Pileus surface intensely coloured (brown to brownish-grey or green to deep green). Basal bulb turnip
11'.	shaped to carrot shaped, rooting
12.	Pileus brown to brownish-grey. Stipe annulate
	Pileus green to deep green. Stipe exannulate
13. 13'	Spores with $\mathbf{Q} > 1.45$
14.	Universal veil white to whitish

	Universal veil on pileus adnate as thick, radially fibrillose, polygonate patches to truncate pyramidal warts with felted tips. Annulate
15'.	Universal veil on pileus detersile as fine pulverulence and/or small pyramidal warts becoming floc- culence toward margin. Usually exannulate
16.	Universal veil on stipe base often present as short thin limb and/or in incomplete rows of triangular flaps. Lamellae pale cream to slightly orangish yellow tan in mass, unchanging
16'.	<i>A. conara</i> Tulloss & Halling Universal veil remains on stipe base in series of obscure rings, never forming limb at upper part of bulb. Lamellae off-white than staining yellowish to cinnamon

Habit and habitat – Solitary, scattered or in pairs on clay soil in dense ombrophilous forest (Atlantic rainforest biome), at c. 300 m altitude.

Distribution – Only known from the type locality. The species might have a restricted range.

DISCUSSION

The longitudinally acrophysalidic stipe tissue, the bilateral, divergent lamella trama, and the sterile edges of the lamellae place the present species in the genus Amanita. The amyloid spores and the non-striate and strongly appendiculate pileus margin place this species in A. [subgen. Lepidella (E.-J. Gilbert) Veselý emend. Corner & Bas] sect. Lepidella. Bas (1969: 345) provides a key to four subsections of sect. Lepidella. Of these, a non-membranous universal veil that never forms a persistent limb at the stipe base, but leaves on the pileus floccose warts that comprise irregularly disposed or vertically aligned inflated elements with common filamentous hyphae characterize taxa assigned to subsect. Solitariae Bas (1969). In this sense, A. dulciodora would appear to belong to stirps Crassiconus on account of the clamped basidia, the rarely cylindrical basidiospores, coloured latex absent, universal veil remnants on the pileus which are composed of irregularly disposed, inflated cells intermixed with abundant filamentous hyphae, the conical adnate, distinct dark coloured (although not greyish) warts on pileus (Bas 1969: 386-389).

The new species is well circumscribed by its (1) mediumsize basidiomata with cap colour and appearance dominated by universal veil at first; (2) distinctly coloured acute-pyramidal, truncate-pyramidal to verrucose warts which are mainly composed of irregularly disposed, ovoid to subglobose to clavate cells intermixed with very abundant filamentous hyphae; (3) a bulbous stipe base with verrucose universal veil remnants arranged in incomplete belts; (4) an ephemeral partial veil made up of ovoid to subglobose to broadly clavate cells mixed with fairly abundant filamentous hyphae; (5) mostly ellipsoid to elongate amyloid basidiospores and (6) the common presence of clamps at the basal septa of basidia.

Actually, the only species that belongs to stirps *Crassiconus* is *A. crassiconus* Bas nom. prov. It was found in West Africa (Nigeria), and indeed, exhibits the closest similarity to *A. dulciodora*. Both taxa share (1) a whitish pileus with conspicuous adnate volval remnants composed of irregularly

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disposed, mainly subglobose to ellipsoid cells mixed with abundant filamentous hyphae and (2) clamped basidia. But some important morphological and anatomical differences in basidiome can segregate *A. crassiconus* from *A. dulciodora*.

Regarding the morphological features, A. crassiconus generally has greyish (probable pale grey) warts on cap; a pileus margin with some scattered, crust-like patches; minutely flocculose edged lamellae; universal veil remnants on lower stipe and upper bulb as thin, felted, incomplete, brownishgreyish girdles that disappear with aging; a clavate-fusiform bulb (30–40 \times 15–25 mm). While in *A. dulciodora* the warts on pileus are pastel red to reddish orange to yellowish red, occurring at the margin as amorphous flocks to flat fibrillose scales, never as crust-like patches; lamellar edge is always smooth; stipe base always bearing adnate warts of universal veil; the bulb is distinctly napiform at maturity (35-37 mm long and up to 27 mm wide). As for the anatomical features, A. crassiconus completely lacks a pileipellis, with volval material directly attached to the pileus context, while A. dulciodora has a clearly delimited (although narrow), ungelatinized to minimally gelatinized pileipellis; furthermore, A. crassiconus displays subglobose to ellipsoid basidiospores that measure $(7.2-)8.5-10.8(-16.8) \times (5.9-)6.5-8.0(-11.5) \mu m$; Q = (1.13-)1.19-1.43(-1.46); Q = 1.25-1.35; Q' = 1.30(Bas 1969), while those in A. dulciodora are somewhat smaller and range from ellipsoid to elongate (rarely cylindrical) with a distinctly higher Q value (7.1-)7.9-10.7(-11.7)× (4.6-)4.8-6.1(-6.2) µm; Q = (1.39-)1.46-2.09(-2.22); Q = 1.72 - 1.73; Q' = 1.72. Tulloss & Yang (2018) reported basidiospores of A. crassiconus as follow: [100/5/4] (7.2-) $8.5-10.8(-16.8) \times (5.9-)6.5-8.0(-11.5) \mu m$, (L = 9.0-9.8 μm ; $L' = 9.4 \ \mu m; W = 7.1-7.4 \ \mu m; W' = 7.3 \ \mu m; Q = (1.13-)$ $1.19-1.43(-1.46); \mathbf{Q} = 1.25-1.35; \mathbf{Q'} = 1.30).$

Four other species assigned to section *Lepidella* namely *A. heishidingensis* Fang Li & Qing Cai, *A. macrocarpa* W.Q.Deng, T.H.Li & Zhu L.Yang, *A. perpasta* Corner & Bas, *A. sculpta* Corner & Bas and *A. strobilipes* Thongbai, Raspé & K.D.Hyde resemble superficially *A. dulciodora* and *A. crassiconus* in having always pigmented pyramidal/conical warts on the pileus surface. However, according to key elaborated by Bas (1969: 386–389) all of them are primarily segregate from taxa of stirps *Crassiconus* in the clampless basidia (Corner & Bas 1962, Bas 1969, Deng et al. 2014, Li & Cai 2014, Li et al. 2016, Tulloss & Yang 2018).

ACKNOWLEDGMENTS

We are grateful to Marcelo Barreto, Manager of the Parque Estadual da Serra do Conduru, for granting authorization for field research within the Park; Universidade Federal da Paraíba (UFPB) for logistics facility; and to Rhudson Ferreira Cruz for drawings.

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Manuscript received 29 Aug. 2017; accepted in revised version 11 Apr. 2018.

Communicating Editor: Jérôme Degreef.