



## The genus *Agaricus* in the Caribbean. Nine new taxa mostly based on collections from the Dominican Republic

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### Abstract

Field collections of *Agaricus* were collected in the Dominican Republic from 2009–2016 with the intent to evaluate the diversity in this genus, which was quasi-unknown in this country. In the same period, studies on tropical *Agaricus* revealed tropical clades that remained unclassified. A new taxonomic system of classification was developed, with the aim, *inter alia*, to integrate such tropical clades. A recent phylogenetic study, which included some samples from the Dominican Republic, revealed they belonged to three putative new sections. Our objective in this paper is to describe the species of *Agaricus* collected in this country and to classify them within the new taxonomic system, including formal descriptions of the three new sections to which they belong. A preliminary study indicated that the collections of the Dominican Republic belong either to a group of three related subgenera (*Flavoagaricus*, *Minores*, and *Minoriopsis*) or to the unrelated *A.* subg. *Pseudochitonina*. For the species of the three related subgenera, a phylogenetic analysis based on ITS sequences data reliably confirmed the classification of the species into five sections including the three new sections, which were well supported. For the collections of *A.* subg. *Pseudochitonina*, preliminary studies indicated that they all belonged to species of *A.* sect. *Xanthodermatei* without any doubt except for one species. This species was included in a multi-gene (ITS, LSU and *tef-1a*) phylogenetic analysis which confirmed placement in this section. Consequently, all the samples were included in a phylogenetic analysis based on ITS sequences and focusing on *A.* sect. *Xanthodermatei*. We noted an unusually high intraspecific variability in the ITS sequences of five of the 12 studied species. Fifteen taxa are described, among which three sections and six species are new for science: *Agaricus* sect. *Kerrigania*, *Agaricus* sect. *Minoriopsis*, *Agaricus* sect. *Pantropicales*, *A. argenteopurpureus*, *A. candussoi*, *A. flavidodiscus*, *A. lodgeae*, *A. porphyropos* and *A. tephrolepidus*. We report all these taxa from the Dominican Republic but the latter three species are also recorded from Puerto Rico, United States Virgin Islands, and Mexico, respectively.

**Key words:** Agaricaceae, multi-gene analysis, phylogeny, taxonomy

### INTRODUCTION

The Dominican Republic is a country that occupies the eastern part of the island of Hispaniola, while Haiti is located in the western part. In the Caribbean, Hispaniola as well as Puerto Rico belong to a group of islands known as the Greater Antilles, while islands such as United States Virgin Islands, Martinique and Guadeloupe belong to the Lesser Antilles. Ciferri (1929) compiled all bibliographic citations of the Dominican fungi reported in the literature, comprising 868 species of which only 86 belonged to the “Eubasidiomiceti” now corresponding to the class *Agaricomycetes*, a name validated by Doweld (2001) and currently circumscribed by Hibbett (2007). With the exception of a single species among these records, the genus *Agaricus* L. was overlooked.

With respect to the genus *Agaricus* and according to all the published records on this genus from various Caribbean

islands, of the 11 papers published (Fries, 1851; Berkeley, 1852; Berkeley & Curtis, 1869; Murrill, 1918; Ciferri, 1929; Baker & Dale, 1951; Heinemann, 1961, 1962a, 1962b, 1962c; Pegler, 1983), only Berkeley (1852) cites two taxa from Santo Domingo, the capital of the Dominican Republic, *Agaricus sallei* Berk. (1852: 193) as a new species, and a small variety of *A. campestris* L. (1753: 1173) : Fr (1821: 281), which is not formally named. Since 1852, no new collections of *Agaricus* from the Dominican Republic have been published. Murrill (1918), Ciferri (1929) and Minter *et al.* (2001) merely mention the collections already published by Berkeley. Murrill (1918: 77) claims to have seen the collection of *A. campestris* by Berkeley in the herbarium at Kew and believes it is unlikely that *A. sallei* belongs to the genus *Agaricus* because it grows on wood and its pileus has an acute umbo. Minter *et al.* (2001) also include *Agaricus cepistipes* Sowerby (1797: [2]) : Fr. (as “*caepistipes*”) citing “Ciferri (1961)” but this species is not currently in the genus *Agaricus* but instead as *Leucocoprinus cepistipes* (Sow. : Fr.) Pat. (1889: 336).

The phylogenetic analyses of Zhao *et al.* (2011) revealed that *Agaricus* is a species-rich genus in the tropics and that several major clades, which include some samples from the Caribbean (Guadeloupe and Martinique), are exclusively neotropical. Using the new system of classification proposed by Zhao *et al.* (2016), Chen *et al.* (2017) proposed *A.* subg. *Minoriopsis* as new neotropical subgenus. In addition, they confirmed the presence of Caribbean samples (Dominican Republic, Guadeloupe, Martinique) not only in two clades representing two putative new sections in this subgenus, but also in a third clade representing a new section in *A.* subg. *Minores*, which was provisionally called “section 1”. This previous study has paved the way to classify the species collected in the Dominican Republic and to formally describe these three clades as new sections.

Because previous taxonomic and phylogenetic studies provided very little information on the diversity of *Agaricus* in the Dominican Republic, our objective was to describe the species of *Agaricus* of this country and to place them in the classification recently proposed by Zhao *et al.* (2016). This includes the formal description not only of new or known species, but also of the three new sections to which some of these species belong.

## MATERIALS AND METHODS

### Studied collections

Descriptions of taxa in this work are based on the study of 41 collections belonging to 12 species (of the 21 found so far) collected in eight locations (Table 1) in the central part of the Dominican Republic. All localities are situated at an altitude of 5–80 m a.s.l. except Jarabacoa situated at 500–600 m. All collections from the Dominican Republic were made by C. Angelini in the months of November and December, except three that were made in January. Six additional collections belonging to six different taxa from the Dominican Republic (LAPAM20, LAPAM35, LAPAM45, LAPAM46, LAPAM61 and LAPAM64) were used for phylogenetic analyses but not described here because the material available was not sufficient for a complete description or a molecular characterization. These taxa will be included in future contributions when we have all the information necessary to carry out a comprehensive study of all their characters. Six further collections were neither described nor included in phylogenetic studies because we have insufficient data about them, but they were used to calculate all the collections from the Dominican Republic in the different subgenera and sections in Table 2.

Descriptions and phylogenetic studies of three new species were supplemented with collections from other countries as well (Table 3). In the case of *A. lodgeae* and *A. porphyropos*, we included collections from Puerto Rico (PR4634, PR6239 and PR6454) and the United States Virgin Islands (STJ314 and STJ392), all provided by B. Ortiz-Santana. In the case of *A. tephrolepidus*, we used a mycelium strain isolated from the collection CA595 from Mexico made by M. Nau and C. Billette.

The vegetation of the areas explored in the Dominican Republic at low elevation is seasonally dry and moist forests, often growing on limestone, that consist mainly of *Acacia macracantha* (“porknut”), *Andira inermis* (“cabbagebark tree”), *Artocarpus altilis* (“breadfruit”), *Bucida buceras* (“gregorywood”), *Bursera simaruba* (“gumbo limbo”), *Cecropia schreberiana* (“pumpwood”), *Dendropanax arboreus* (“angelica tree”), *Ficus trigonata* (“jaguey blanco”), *Guazuma tomentosa* (“mutamba”), *Hura crepitans* (“sandbox tree”), *Hymenaea courbaril* (“stinkingtoe”), *Inga vera* (“river koko”), *Mangifera indica* (“mango”), *Ocotea coriacea* (“lancewood”), *Passiflora edulis* (“purple granadilla”), *Paullinia pinnata* (“bread and cheese”), *Petiveria alliacea* (“guinea henweed”), *Piper amalago* (“rough-leaved peeper”), *Roystonea hispaniolana* (“royal palm”), *Samanea saman* (“raintree”), *Swietenia mahagoni* (“West Indian mahogany”) and *Terminalia catappa* (“tropical almond”). *Cocos nucifera* (“coconut palm”) and *T. catappa* were abundant on beachfronts. In the mountains near Jarabacoa, collections were made in mixed forests with broadleaf trees and *Pinus occidentalis* (“Hispaniolan pine”).

**TABLE 1.** Localities of collections in the Dominican Republic.

Province	Municipality	Location	Geographical coordinates
Puerto Plata	Sosúa	Beach	19°45'26"N 70°30'58"W
Puerto Plata	Sosúa	Apartamentos Villa Mar	19°45'13"N 70°31'11"W
Puerto Plata	Sosúa	Puerto Chiquito	19°45'03"N 70°31'34"W
Puerto Plata	Sosúa	Cemetery	19°44'40"N 70°32'21"W
Puerto Plata	Sosúa	Perla Marina	19°47'05"N 70°27'53"W
M <sup>a</sup> Trinidad Sánchez	Rio San Juan	Road to Payita	19°38'15"N 70°03'01"W
La Vega	Jarabacoa	Jarabacoa	19°06'39"N 70°37'57"W
Distrito Nacional	Santo Domingo de Guzmán	Jardín Botánico de Santo Domingo	18°29'45"N 69°57'11"W

**TABLE 2.** Taxa of *Agaricus* from the Dominican Republic in the period 2009–1016.

Subgenus (total 6)	Number of species /collections	Section (total 23)	Number of species			
			new	known	unnamed	total
<i>Agaricus</i>	0 / 0	<i>Agaricus</i>				0
<i>Flavoagaricus</i>	2 / 4 (+4)	<i>Arvenses</i>		<b>1</b>	(1)	2
<i>Minores</i>	4 / 6	<i>Leucocarpi</i>				0
		<i>Minores</i>			2	2
		<b><i>Pantropicales</i></b>	<b>1</b>		1	2
<i>Minoriopsis</i>	5 / 24	<b><i>Minoriopsis</i></b>	<b>1</b>	<b>1</b>		2
		<b><i>Kerrigania</i></b>	<b>1</b>	<b>1</b>	<b>1 (hybrid?)</b>	3
<i>Pseudochitonia</i>	9 / 13 (+1)	<i>Xanthodermatei</i>	<b>3</b>	<b>2</b>	3	8
		11 more sections			(1)	1
<i>Spissicaules</i>	1 / 0 (+1)	4 sections			(1)	1
Total	21 / 47 (+6)		6	5	10	21

Numbers or names in bold type represent the 15 described taxa (sections or species). The species/collections in parenthesis require specific studies and are not included in this study. However, they are indicated in this Table to give a complete overview of the taxonomic diversity found in the Dominican Republic.

Studied basidiomata from the Dominican Republic have been deposited in the National Herbarium of Santo Domingo, Dr. Rafael M. Moscoso National Botanical Garden (JBSD), with duplicates of all collections kept in the private herbarium of Luis A. Parra (LAPAM). The collections from Puerto Rico and the United States Virgin Islands have been deposited in the herbarium of U.S. Forest Service, NRS, Center for Forest Mycology Research (CFMR) and at The New York Botanical Garden (NY), respectively. The Mexican collection of *A. tephrolepidus* originally deposited in the herbarium of the Institute of Ecology, AC (XAL) is lost, but a mycelium “strain IE 786” was isolated and it is preserved in the Strain Collection of Institute of Ecology, AC, with a duplicate (CA595) deposited at the Bordeaux Agaric Germplasm Collection (CGAB) at INRA.

**TABLE 3.** ITS dataset used in the ITS trees (Figs. 1, 3) New sections, species and sequences produced from this study are in boldface.

Subgenus Section Species	Sample	ITS GenBank number	Geographical origin
<i>Agaricus</i>			
<i>Agaricus</i> (outgroup)			
<i>A. campestris</i> T	LAPAG370	KM657927	Spain
<i>A. langei</i>	LAPAG141	JF797181	Spain
<i>Minoriopsis</i>			
<b><i>Kerrigania</i></b>			
<i>A. rufoaurantiacus</i>	LAPAM15	KT951313	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM54	<b>MF511138</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM31	<b>MF511123</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM32	<b>MF511124</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM36	<b>MF511127</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM59	<b>MF511143</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM29	<b>MF511121</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM51	<b>MF511136</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM30	<b>MF511122</b>	Dominican Republic
<i>A. rufoaurantiacus</i>	LAPAM33	<b>MF511125</b>	Dominican Republic
<i>A. sp.</i>	RMC-1256	KM349611	USA
<i>A. sp.</i>	RMC-1257	KM349612	USA
<i>A. sp.</i>	LAPAM48	<b>MF511135</b>	Dominican Republic
<i>A. aff. rufoaurantiacus</i>	CL/GUADO05.099	JF727857	Guadeloupe (France)
<i>A. sp.</i>	CJL090302.05	JF727869	Guiana
<i>A. aff. rufoaurantiacus</i>	LAPAM1	JF797183	Venezuela
<i>A. cf. floridanus</i>	HAI0386	AJ884624	USA
<i>A. floridanus</i>	JH-1	KM349609	USA
<b><i>A. porphyropos</i></b>	STJ314	<b>MF511109</b>	U. S. Virgin Islands
<b><i>A. porphyropos</i></b>	STJ392	<b>MF511110</b>	U. S. Virgin Islands
<b><i>A. porphyropos</i></b>	LAPAM5	<b>MF511111</b>	Dominican Republic
<b><i>A. porphyropos</i> T</b>	LAPAM34	KX671703	Dominican Republic
<i>A. sp.</i>	F1779	JF727853	Martinique (France)
<i>A. cf. globocystidiatus</i>	MATA816	JF727870	Mexico
<i>A. sp.</i>	LAPAM66	KX671702	Brazil
<i>Minoriopsis</i>			
<b><i>Minoriopsis</i></b>			
<i>A. martinicensis</i>	CL/MART03.055	<b>MF511151</b>	Martinique (France)
<i>A. martinicensis</i>	LAPAM56	<b>MF511140</b>	Dominican Republic
<i>A. martinicensis</i>	LAPAM63	<b>MF511147</b>	Dominican Republic

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TABLE 3. (Continued)

Subgenus Section Species	Sample	ITS GenBank number	Geographical origin
<i>A. martinicensis</i>	F2343	KU975096	Martinique (France)
<i>A. martinicensis</i>	LAPAM42	<b>MF511131</b>	Dominican Republic
<i>A. martinicensis</i>	LAPAM10	<b>MF511112</b>	Dominican Republic
<i>A. martinicensis</i>	LAPAM16	KX671699	Dominican Republic
<i>A. martinicensis</i>	LAPAM44	<b>MF511133</b>	Dominican Republic
<i>A. martinicensis</i>	F2815	JF727855	Martinique (France)
<i>A. martinicensis</i>	LAPAM43	<b>MF511132</b>	Dominican Republic
<i>A. argenteopurpureus</i>	LAPAM53	<b>MF511137</b>	Dominican Republic
<i>A. argenteopurpureus</i>	LAPAM24	<b>MF511120</b>	Dominican Republic
<i>A. argenteopurpureus</i> T	LAPAM28	KX671700	Dominican Republic
<i>A. argenteopurpureus</i>	LAPAM55	<b>MF511139</b>	Dominican Republic
<i>Minores</i>			
<i>Pantropicales</i>			
<i>A. lodgeae</i>	LAPAM14	KT951312	Dominican Republic
<i>A. lodgeae</i> T	LAPAM67	<b>MF511149</b>	Dominican Republic
<i>A. lodgeae</i>	PR4634	<b>MF511107</b>	Puerto Rico
<i>A. lodgeae</i>	PR6239	<b>MF522806</b>	Puerto Rico
<i>A. lodgeae</i>	PR6454	<b>MF511108</b>	Puerto Rico
<i>A. lodgeae</i>	LAPAM68	<b>MF511150</b>	Dominican Republic
<i>A. sp.</i>	ZRLWXH3161	KT951391	China
<i>A. sp.</i>	LAPAM45	KX671701	Dominican Republic
<i>A. candidolutescens</i> T	LD2012129	KT951335	Thailand
<i>Minores</i>			
<i>Minores</i>			
<i>A. sp.</i>	LAPAM64	<b>MF511148</b>	Dominican Republic
<i>A. sp.</i>	LAPAM35	<b>MF511126</b>	Dominican Republic
<i>A. parvibicolor</i> T	LD2012116	KP715162	Thailand
<i>A. wariatodes</i>	TWM1589	JF495052	Australia
<i>A. heinemannianus</i>	LAPAG302	KF447906	Spain
<i>A. comtulus</i>	LAPAG339	JF715065	Spain
<i>A. luteopallidus</i> T	ZRL3088	JF691543	Thailand
<i>Minores</i>			
<i>Leucocarpi</i>			
<i>A. leucocarpus</i> T	LD201215	KU975101	Thailand
<i>Flavoagaricus</i>			
<i>Arvenses</i>			
<i>A. subrufescens</i>	LAPAM11	<b>MF511113</b>	Dominican Republic

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TABLE 3. (Continued)

Subgenus Section Species	Sample	ITS GenBank number	Geographical origin
<i>A. subrufescens</i>	LAPAM13	<b>MF511115</b>	Dominican Republic
<i>A. subrufescens</i>	F2285	JF797201	Martinique (France)
<i>A. subrufescens</i>	CA487-C5	KU557352	France
<i>A. subrufescens</i>	LAPAM37	<b>MF511128</b>	Dominican Republic
<i>A. subrufescens</i>	LAPAM12	<b>MF511114</b>	Dominican Republic
<i>A. subrufescens</i>	CA487-C6	KU557353	France
<i>A. subrufescens</i>	CA487-C2	KU557351	France
<i>A. arvensis</i> T	LAPAG450	KF114474	Spain
<i>Spissicaules</i>			
<i>Spissicaules</i>			
<i>A. bresadolanus</i>	CA177	DQ185570	France
<i>A. litoralis</i>	LAPAG475	KT951393	Spain
<i>Pseudochitonia</i>			
<i>Xanthodermatei</i>			
<i>A. moelleri</i>	CA209	DQ185561	France
<i>A. xanthodermus</i>	LAPAG387	KM657923	Spain
<i>A. menieri</i>	CA162	DQ185567	France
<i>A. malangelus</i>	RWK1972	DQ182523	USA
<i>A. berryessae</i>	ML5	DQ182524	USA
<i>A. placomyces</i>	RWK1959	DQ182525	USA
<i>A. volvatulus</i>	LAPAF5	KU041657	Togo
<i>A. sp.</i>	ADK4396	KU041658	Togo
<i>A. sp.</i>	ZRL2012582	KM657894	China
<i>A. sinoplacomyces</i> T	ZRL2012008	KM657883	China
<i>A. tibetensis</i> T	ZRL2012585	KM657895	China
<i>A. moelleroides</i> T	CA215	DQ185559	France
<i>A. iodosmus</i>	LAPAG245	DQ182518	Spain
<i>A. endoxanthus</i>	LAPAM47	KU041655	Dominican Republic
<i>A. endoxanthus</i>	LD2012183	KU041654	Thailand
<i>A. endoxanthus</i>	LAPAG598	KU041653	Switzerland
<i>A. punjabensis</i> T	A4	KT985908	Pakistan
<i>A. xanthosarcus</i> T	Goossens5415	JF514523	Dem. Rep. of the Congo
<i>A. atrodiscus</i> T	LD2012185	KT284912	Thailand
<i>A. daliensis</i>	SHY2011071706	KM657877	China
<i>A. sp.</i>	NTF58	JF514527	Thailand
<i>A. aff. volvatulus</i>	F2767	JF727848	Martinique (France)
<i>A. melanocarpus</i> T	ZRL2011037	KM657881	China

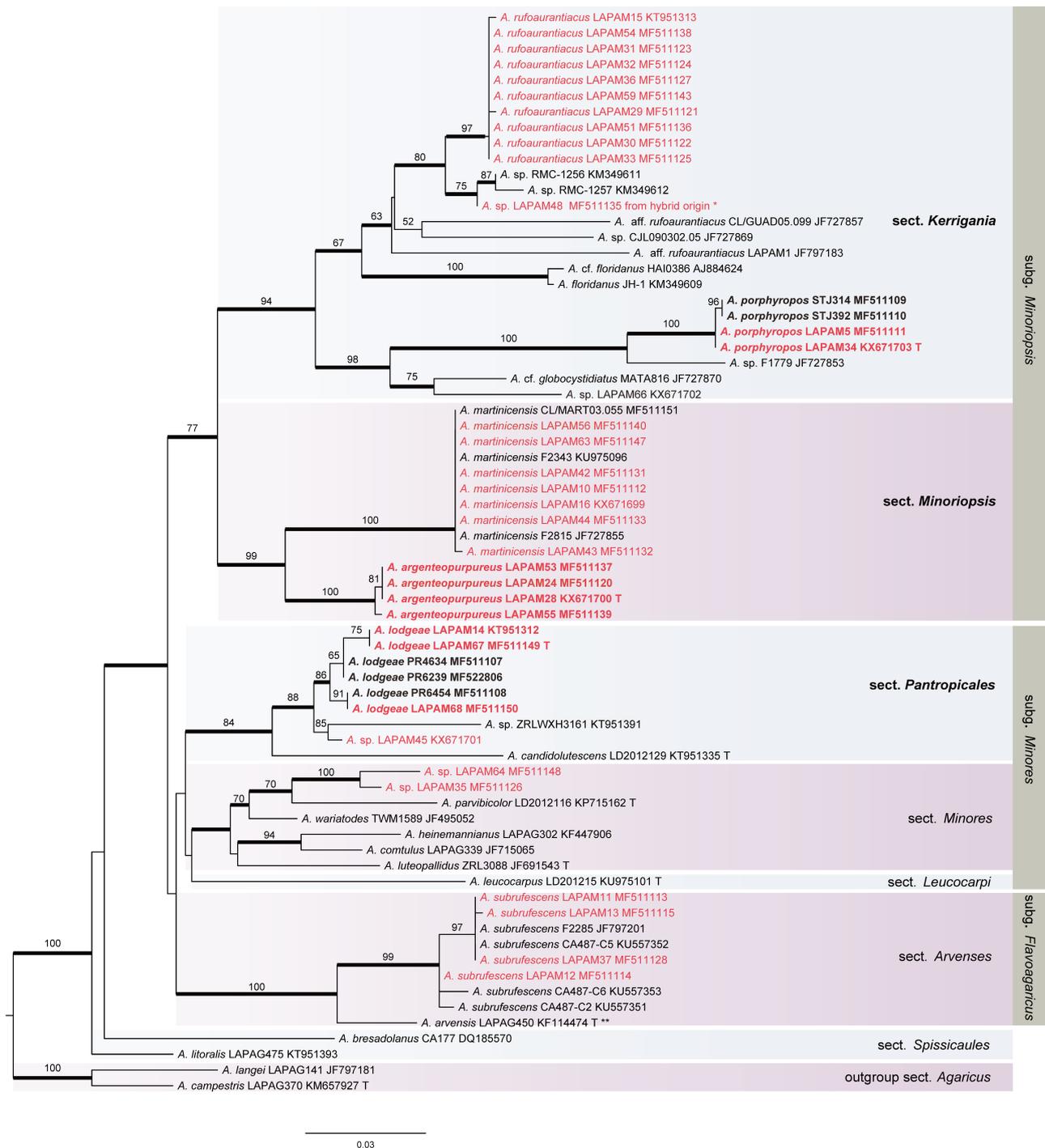
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TABLE 3. (Continued)

Subgenus Section Species	Sample	ITS GenBank number	Geographical origin
<i>A. tollocanensis</i> T	MATA688	AY703913	Mexico
<i>A. pocillator</i>	DUKEJ173	U85308	USA
<i>A. sp.</i>	F2715	JF727847	Martinique (France)
<b><i>A. candussoi</i></b>	LAPAM57	<b>MF511141</b>	Dominican Republic
<b><i>A. candussoi</i></b>	LAPAM58	<b>MF511142</b>	Dominican Republic
<b><i>A. candussoi</i></b> T	LAPAM62	<b>MF511146</b>	Dominican Republic
<i>A. sp.</i>	LAPAM20	<b>MF511119</b>	Dominican Republic
<i>A. sp.</i>	LAPAM61	<b>MF511145</b>	Dominican Republic
<i>A. caribaeus</i>	LAPAM19	<b>MF511118</b>	Dominican Republic
<i>A. caribaeus</i>	F2530	JF727856	Martinique (France)
<i>A. caribaeus</i>	LAPAM41	<b>MF511130</b>	Dominican Republic
<i>A. sp.</i>	ZRL2012629	KM657890	China
<i>A. parvitigrinus</i> T	CA158	AY899267	France
<i>A. laskibarii</i> T	LAPAG115	AY943975	France
<i>A. xanthodermatulus</i> T	CA160	AY899273	France
<i>A. californicus</i>	RWK1914	DQ182509	USA
<i>A. sp.</i>	LAPAM46	<b>MF511134</b>	Dominican Republic
<b><i>A. flavidodiscus</i></b>	LAPAM17	<b>MF511116</b>	Dominican Republic
<b><i>A. flavidodiscus</i></b>	LAPAM39	<b>MF511129</b>	Dominican Republic
<b><i>A. flavidodiscus</i></b> T	LAPAM60	<b>MF511144</b>	Dominican Republic
<i>A. fuscopunctatus</i> T	LD2012115	KJ575612	Thailand
<i>A. murinocephalus</i> T	ZRL3044	JF691555	Thailand
<i>A. exilissimus</i> T	LD201254	KT284910	Thailand
<i>A. sp.</i>	ZRLWXH3092	KM657891	China
<i>A. tyttocarpus</i> T	ZRLWXH3077	KM657889	China
<i>A. bisporiticus</i> T	MCR25	KJ575608	Pakistan
<i>A. bisporiticus</i>	LD2012111	KJ575611	Thailand
<b><i>A. tephrolepidus</i></b> T	LAPAM18	<b>MF511117</b>	Dominican Republic
<b><i>A. tephrolepidus</i></b>	CA595	HQ322269	Mexico
<i>A. buckmacadooi</i> T	B-49	KJ609484	USA
<i>A. kriegeri</i> T	RWK2079	KJ609500	USA
<i>A. gregariomyces</i> T	ZRL2012624	KM657880	China
<i>A. pseudopratenis</i>	LAPAG20	DQ182526	Spain
<i>A. brunneogracilis</i> T	ZRL258	KM657876	Thailand
<i>A. microvolvatulus</i> T	Grinling70109	JF514524	Republic of Congo

## Morphological observations

Macroscopic descriptions are based on color photographs and field notes from fresh material. Macrochemical reactions, if not stated otherwise, were determined from herbarium material. Microscopic descriptions are based on photos and data obtained after examining the basidiomata with a Nikon SE compound microscope. Spore measurements followed the statistical method proposed by Heinemann & Rammeloo (1985). Herbarium acronyms are from Holmgren & Holmgren (1998). The morphological description of taxa follows the taxonomic treatments published by Parra (2008, 2013).



**FIGURE 1.** Maximum likelihood phylogram of *Agaricus* subgenus *Minores*, *A.* subgenus *Minoriopsis*, and *A.* subgenus *Flavogargaricus* resulting from analysis of ITS sequence data. The best scoring RAxML ITS tree is rooted with *A. campestris*. The bootstrap support values greater than 50% are indicated, and branches with Bayesian posterior probabilities greater than 0.8 are in bold. Species sampled from the Dominican Republic are in red; new taxa are in bold. T = Type specimen.

### Sampling for phylogenetic analyses

The analyses included 53 collections from the Dominican Republic (in red in the trees of Figs 1–3), Mexico, Puerto Rico and United States Virgin Islands. Several phylogenetic analyses were necessary because the 53 samples were distributed in non-closely related subgenera.

From these 53 collections, 39 belong to three closely related subgenera (*Minores*, *Minoriopsis*, and *Flavoagaricus*). Thirty-four were collected from the Dominican Republic, three from Puerto Rico and two from United States Virgin Islands. For the analysis focusing on these subgenera we used 34 new ITS sequence data (including one from Martinique used in previous works but deposited in GenBank for this paper), and 31 sequences retrieved from GenBank, which have been used in previous analyses (Didukh *et al.* 2005; Zhao *et al.* 2011, 2016; Lebel & Syme 2012; Parra 2013; Liu *et al.* 2015; Kerrigan 2016; Chen *et al.* 2016a, 2017). Six of the 31 sequences retrieved from GenBank are, in fact, also from samples collected in the Dominican Republic, which were recently used by Chen *et al.* (2017). All the GenBank accession numbers are given in the tree of Fig. 1 and in the Table 3 with 34 newly deposited sequences indicated in boldface.

The 14 remaining collections (13 from the Dominican Republic and one from Mexico) belong to *A.* subg. *Pseudochitonina*. A preliminary study indicated that all of them belong to *A.* sect. *Xanthodermatei* Singer (Singer, 1948: 36) without any doubt except for the collection LAPAM 17 (*A. flavidodiscus*). Therefore, we carried out a multi-gene analysis to clarify the position of the sample LAPAM 17 among sections or clades represented by 25 samples which have been used in the previous studies of Zhao *et al.* (2016) and Zhou *et al.* (2016). All the GenBank accession numbers are given in Fig. 2 and Table 4 with three newly deposited sequences indicated in boldface.

**TABLE 4.** Multi-gene tree dataset used in our study. New species and sequences produced from this study are in boldface.

Section Species	Sample <sup>a</sup>	LSU GenBank	ITS GenBank	<i>tefl</i> Genbank
<i>A.</i> sect. <i>Xanthodermatei</i> (Xan III)				
<i>A.</i> sp.	ZRL2012474	KR006622	KM657893	KR006650
<i>A. tibetensis</i>	ZRL2012585	KR006633	KM657895	KR006658
<i>A.</i> sp.	ZRL2012582	KR006623	KM657894	KR006651
<i>A.</i> sp.	ZRL2012616	KR006630	KM657896	KR006660
<i>A. sinoplacomycetes</i>	ZRL2012008	KR006620	KM657883	KR006648
<i>A. xanthodermus</i>	LAPAG387	KR006609	KM657923	KR006638
<i>A. malangelus</i>	ZRL2012628	KR006626	KM657892	KR006655
<i>A. daliensis</i>	SHY2011071706	KR006615	KM657877	KR006643
<i>A. atrodiscus</i>	LD2012185	KT951473	KT284912	KT951653
<i>A.</i> sp.	ZRL2012629	KR006627	KM657890	KR006656
<b><i>A. flavidodiscus</i></b>	LAPAM17	<b>MF511152</b>	<b>MF511116</b>	<b>MF511153</b>
<i>A.</i> sect. <i>Xanthodermatei</i> (Xan II)				
<i>A. tythocarpus</i>	ZRLWXH3077	KR006618	KM657889	KR006645
<i>A.</i> sp.	ZRLWXH3092	KR006619	KM657891	KR006646
<i>A. brunneogracilis</i>	ZRL258	KR006628	KM657876	KR006657
<i>A. microvolvatulus</i>	LD201271	KT951508	KJ575614	KT951651
<i>A. gregariomyces</i>	ZRL2012624	KR006625	KM657880	KR006653
<i>A. bisporiticus</i>	LD2012111	KT951507	KJ575611	KT951650
<i>A.</i> sect. <i>Bivelares</i>				
<i>A. cupressicola</i>	LAPAG889	KT951465	KT951334	KT951649
<i>A. bisporus</i>	LAPAG446	KR006611	KM657920	KR006640

...Continued on next page

TABLE 4. (Continued)

Section Species	Sample <sup>a</sup>	LSU GenBank	ITS GenBank	<i>tefl</i> Genbank
<i>A. sect. Crassispori</i>				
<i>A. variicystis</i>	LD201234	KT951517	KT951339	KT951562
<i>A. sect. Trisulphurati</i>				
<i>A. trisulphuratus</i>	LAPAF7	KR006605	KM657924	KR006634
<i>A. sect. Chitonioides</i>				
<i>A. nevoi</i>	LAPAG257	KR006606	KM657922	KR006635
<i>A. sect. Hondenses (ex Xan I)</i>				
<i>A. grandiomycetes</i>	ZRL2012611	KR006624	KM657879	KR006652
<i>A. pusillobulbosus</i>	ZRL2012627	-	KM567888	KR006654
<i>Incertae sedis</i>				
<i>A. nigrogracilis</i>	ZRL2012014	KR006621	KM657882	KR006647
<i>A. sect. Agaricus (outgroup)</i>				
<i>A. campestris</i>	LAPAG370	KR006607	KM657927	KR006636

<sup>a</sup>The order of the samples follows their order in the ML tree of the Fig. 2.

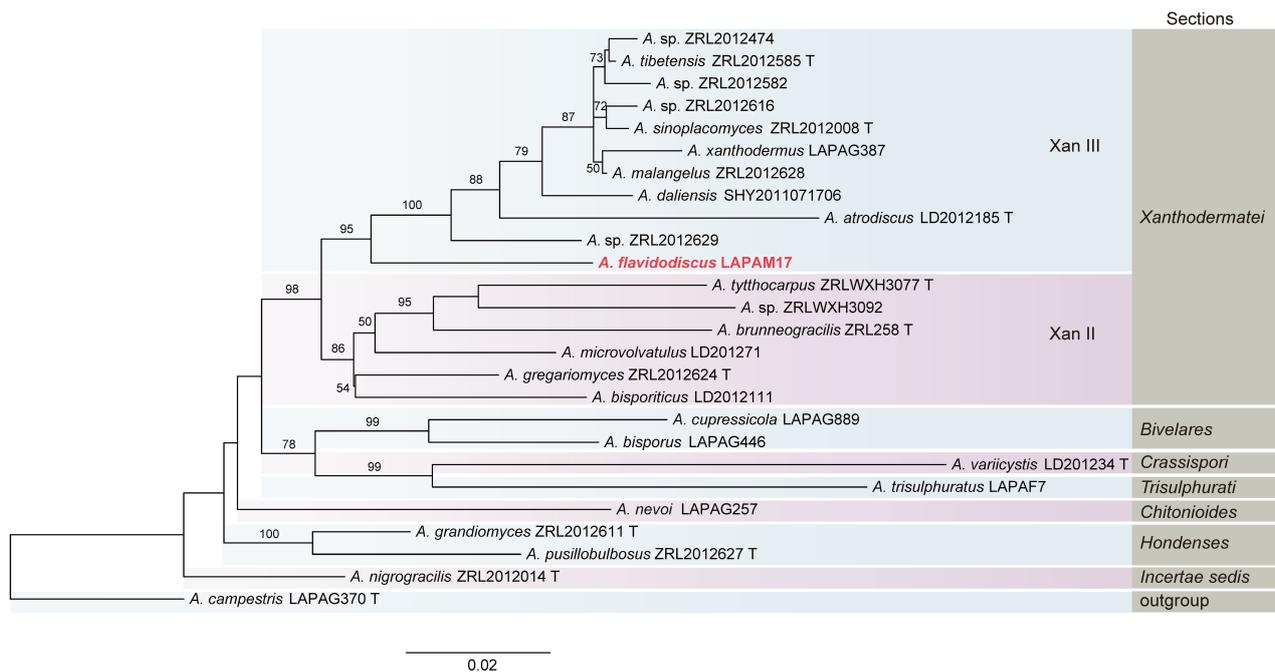
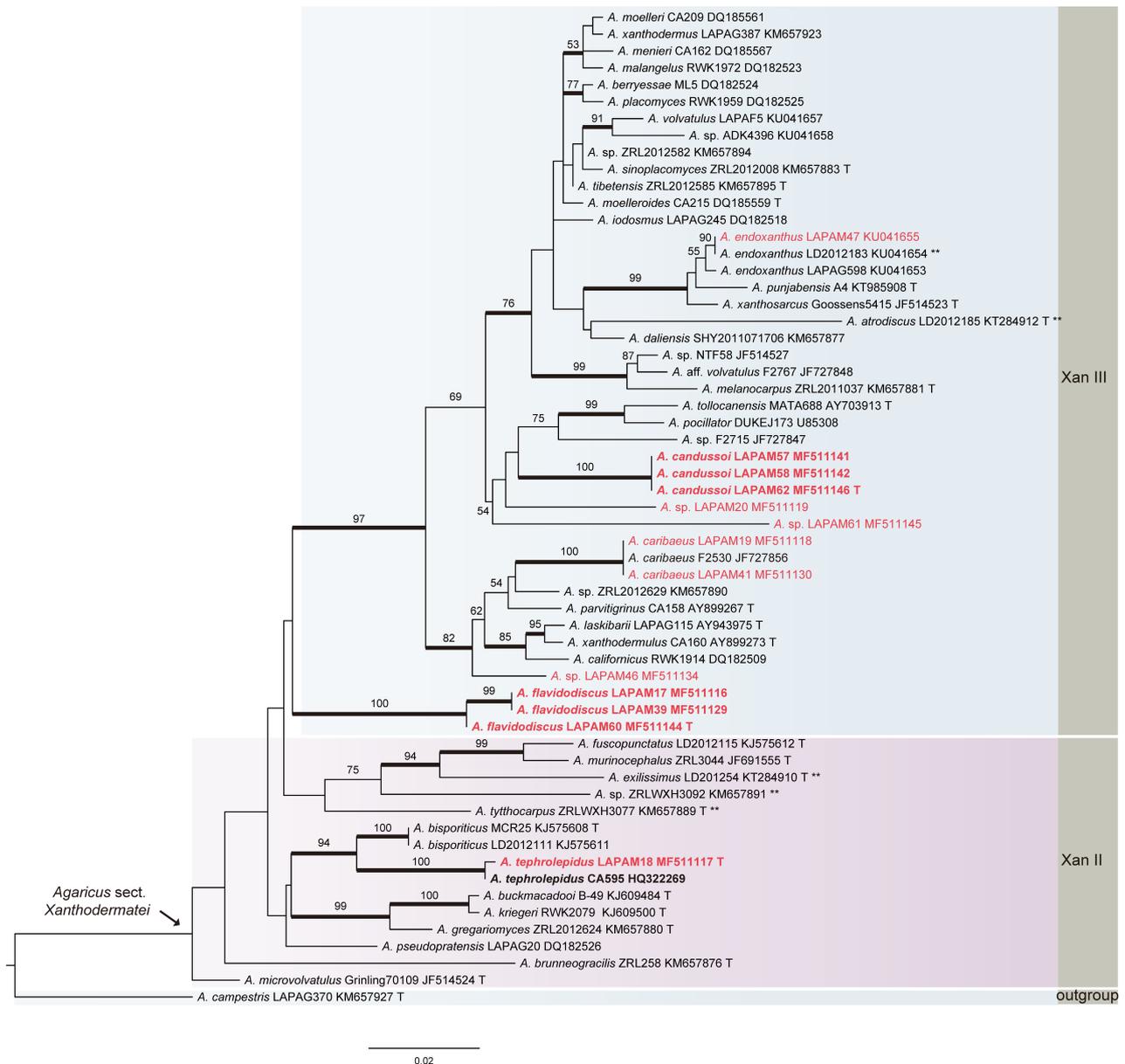


FIGURE 2. Maximum likelihood phylogram of *Agaricus* subg. *Pseudochitonina* resulting from analysis of ITS, LSU, *tef1a* sequence data. The best scoring RAxML multi-gene tree is rooted with *A. campestris*. The bootstrap support values greater than 50% are indicated. Species sampled from the Dominican Republic is in red and in bold as it is a new species. T = Type specimen.

Fourteen collections belonging to *A. sect. Xanthodermatei* were included in a phylogenetic analysis based on ITS sequence data and focusing on this section. One of these 14 collections is a sample of *A. tephrolepidus* from Mexico, 12 are new samples from Dominican Republic, and the remaining one is also from this country but it is not new since it is a sample of *A. endoxanthus* Berk. & Broome (1871: 548) previously included in a study on this species (Chen *et al.* 2016b). In addition, we included 48 sequences retrieved in GenBank, which were used in previous analyses (Callac & Guinberteau 2005; Kerrigan *et al.* 2006; Thongklang *et al.* 2014; Zhao *et al.* 2011, 2016; Chen *et al.* 2016b; Zhou *et al.* 2016; Kerrigan 2016). All the GenBank accession numbers are indicated in the tree of Fig. 3 and Table 3 with 12 newly deposited sequences indicated in boldface.



**FIGURE 3.** Maximum likelihood phylogram of *Agaricus* sect. *Xanthodermatei* resulting from analysis of ITS sequence data. The best scoring RAxML ITS tree is rooted with *A. campestris*. The bootstrap support values greater than 50% are indicated, and branches with Bayesian posterior probabilities greater than 0.8 are in bold. Species sampled from the Dominican Republic are in red; new species are in bold. T = Type specimen. \*\* samples deposited in GenBank with their herbarium numbers instead of collection numbers used in the present study. The sample LD201271 and the type specimen Grinling 70109 of *A. microvolvatulus* used in Fig. 2 and Fig. 3, respectively, have the same ITS sequences.

### DNA extraction, PCR and sequencing

For the basidiomata processed at IdForest, DNA was extracted using the E.Z.N.A.® plant DNA mini kit (Omega Bio-Tek, Doraville, Georgia, USA) according to manufacturer's instructions. PCR amplification of the internal transcribed spacer regions (ITS 1+2) of the ribosomal DNA was performed with primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White *et al.* 1990). Sequencing was performed by Macrogen Inc. with the primers used for PCR.

For the basidiomata processed at INRA, DNA was extracted following a standard CTAB protocol. PCR amplification of the internal transcribed spacer regions (ITS 1+2) of the ribosomal DNA was performed with primers ITS5 and ITS4 (White *et al.* 1990). Sequencing was performed on ABI Prism Genetic analysers (Applied Biosystems) at Beckman Coulter Genomics.

## Phylogenetic analyses

Alignments of the ITS (Table 3) and the multi-gene (Table 4) datasets were constructed using T-Coffee v8.99 (Notredame *et al.* 2000) with some manual adjustments. The final alignments are deposited in Treebase (ID: 21364).

Maximum Likelihood analyses were performed using RAXML-HPC2 v8.2.4 (Stamatakis 2014) as implemented on the Cipres portal (Miller *et al.* 2010), under a GTRGAMMA model with one thousand rapid bootstrap (BS) replicates for all datasets. Bayesian Inference (BI) analysis was performed with MrBayes v3.1.2 (Ronquist & Heulsenbeck 2003). Six Markov chains were run for one million generations and sampled every 100th generations. Burn-in was determined by checking the likelihood trace plots in Tracer v1.6 (Rambaut *et al.* 2014) and subsequently discarded.

## ITS markers

The positions of section-specific or species-specific ITS markers indicated in this paper are numbered from the beginning of the ITS1 region following the 3' end (aggatcatta) of the conserved 18S region. The exclusive or informative characters are set in upper case and the flanking five anterior and five posterior characters are indicated. As much as possible, these flanking DNA segments are those of a type specimen deposited in the GenBank. ITS sequences were compared to all the taxa with available sequences including those of the recent papers of Chen *et al.* (2017) and He *et al.* (2017).

## Nomenclatural notes

In a previous work (Zhao *et al.* 2016) the sixth fascicle of the bibliographic reference for *Agaricus* subg. *Pseudochitonina* was wrong. The correct fascicle is number three as stated in this paper.

The original epithet *melanocapus* used in Zhou *et al.* (2016) has been corrected to *melanocarpus* according to the etymology provided in the paper. The authors make two mistakes. On the one hand, they confuse *caput*, meaning “head” in Latin with *carpus*/*karpos* meaning fruit in both Latin and Greek, as it can be inferred from the same etymology that they also pointed out for *Agaricus tythocarpus* R.L. Zhao (Zhou *et al.* 2016: 115). On the other hand, they omitted the letter “r” in *melanocarpus* following the same etymology they applied in *A. tythocarpus*. Here “carpus” has a figurative sense limited to only the pileus surface.

The authorship of *Agaricus* sect. *Hondenses* R.L. Zhao & L.A. Parra (Zhao *et al.* 2016: 272) was erroneously published. The correct authorship should have been “R.L. Zhao & Kerrigan”, but according to the ICN rules (McNeill *et al.* 2012) this cannot be corrected. We are sorry for this error in part caused by several delays in the publication Kerrigan’s (2016) monograph, where *A.* subsect. *Hondenses* Kerrigan (2016: 172) was going to be published, and in part by an oversight while consolidating the edits of various authors throughout the numerous versions of the manuscript of Zhao *et al.* (2016).

## RESULTS

### Phylogenetic analyses focusing on *A.* subg. *Flavoagaricus*, *A.* subg. *Minores*, and *A.* subg. *Minoriopsis*

We performed a phylogenetic analysis focusing on three phylogenetically related subgenera (*Flavoagaricus*, *Minores* and *Minoriopsis*) that were presumed to include the 34 collections collected in the Dominican Republic and the three new sections proposed in this study. Zhao *et al.* (2016) proposed a new system of taxonomic classification, in which taxa can be ranked as sections or subgenera when their mean stem ages are higher than 20 or 30 million years ago (Ma), respectively. A second condition is that the corresponding clade must be statistically well supported. Following this system, in a three-gene dated tree, Chen *et al.* (2017) proposed the subgenus *A.* subg. *Minoriopsis* for a well-supported clade having a mean stem age of 31.02 Ma. These authors also noted: “*A.* subg. *Minoriopsis* includes five to eight species distributed in two sister subclades, which potentially represent two sections since they diverged 22.83 Ma”. These two clades represent the two new sections (*A.* sect. *Kerrigania* and *A.* sect. *Minoriopsis*) proposed in the present study. Within *A.* subg. *Minores*, the dated tree of Chen *et al.* (2017) revealed three sections and two of them corresponded to sister clades which had diverged 27.64 Ma. One of the two sister sections was named *A.* sect. *Leucocarpi* Linda J. Chen & Callac (Chen *et al.* 2017: 181) while the other remained provisionally named “*A.* sect. 1” in Chen *et al.* 2017. The latter section is proposed in this study as a new section (*A.* sect. *Pantropicales*). These three new sections correspond to three clades that, in the previous study of Chen *et al.* (2017), already met the two conditions to be ranked as sections: (i) their mean stem ages were higher than 20 Ma and (ii) they were statistically well-supported. However, the analyses of Chen *et al.* (2017) focused on the diversity in the Greater Mekong Subregion where the subgenus *A.* subg. *Minoriopsis* is absent. In contrast, many samples from the Dominican Republic belong to

the three new sections. The addition of new samples and species in the analyses should not modify the stem age of the new sections and that the three clades corresponding to these sections remain well supported. Therefore, we followed different strategies of sampling depending on the sections and our objectives. For the three new sections we used all the possible available samples. For *A. sect. leucocarpi* we included a sample of the only species of the section; for *A. sect. Arvenses*, after preliminary identification of the Dominican samples to *A. subrufescens*, we included in the analysis the sequences of three different clones of CA487, which is a specimen bearing respectively the three different types of ITS sequences that were found in this species by Chen *et al.* (2016a). For *A. sect. Minores*, after preliminary comparisons of the ITS sequences of two Dominican samples with all sequences of *A. sect. Minores* from GenBank or in our database, we found that the Dominican collections likely belong to new species related to *A. parvibicolor* Linda J. Chen, R.L. Zhao & K.D. Hyde (Liu *et al.* 2015: 173). Therefore, only a limited subset of species in *A. sect. Minores*, including *A. parvibicolor* were used in the analysis.

The resulting ML and Bayesian trees had similar topologies. The ML tree is shown in the Fig. 1 and branches with Bayesian posterior probabilities higher than 80% are thicker. The three subgenera (*Minoriopsis*, *Minores*, and *Flavoagaricus*) are monophyletic and clustered in one clade. As in the multi-gene tree of Chen *et al.* (2017), the three subgenera are subdivided in two, three and one clades, respectively, corresponding to six sections. The clades corresponding to the three new sections (*Kerrigania*, *Minoriopsis*, and *Pantropicales*) are well supported (Fig. 1), which, together with their age of divergence >20 Ma (Chen *et al.* 2016a) justifies their treatment at section level.

The total number of species in *Kerrigania*, *Minoriopsis*, and *Pantropicales* are ten, two, and four, respectively, and two in each clade are known from the Dominican Republic. In total, the 28 samples from this country, two from United States Virgin Islands, and four from Puerto Rico, represent six species in the three new sections, with one new species described in each section. Of the known 16 species of the three new sections, only the five following species were previously described: *A. rufoaurantiacus* Heinem. (1961: 242), *A. floridanus* Peck (1911: 50) and *A. globocystidiatus* Drewinski & M.A. Neves (Drewinski *et al.* 2017: 68) in *A. sect. Kerrigania*, *A. martinicensis* Pegler (1983: 446) in *A. sect. Minoriopsis*, and *A. candidolutescens* Linda J. Chen & R.L. Zhao (Zhao *et al.* 2016: 258) in *A. sect. Pantropicales*. *Agaricus globocystidiatus* was recently described from Brazil. Comparing the ITS sequences of two samples of this species (MPD02 and MPD19) with the specimen MATA818 (*A. cf. globocystidiatus*) from Mexico, Drewinski *et al.* (2017) report a level of divergence between 1,2% and 0,1 %, respectively, and conclude that MATA818 needs to be reexamined to confirm its belonging to this species. The remaining six samples from the Dominican Republic are not in the new sections. Four belong to *A. subrufescens* Peck (1893: 105) in *A. sect. Arvenses* and two represent two putatively new sister species related to *A. parvibicolor* in *A. sect. Minores*, but not formally described here (LAPAM35 and LAPAM64).

Phylogenetic analyses focusing on *A. sect. Xanthodermatei* within *A. subg. Pseudochitonina*

Thongklang *et al.* (2014) distinguished three clades within *A. sect. Xanthodermatei* (Xan I, Xan II, and Xan III). In the new classification system (Zhao *et al.* 2016), the section was subdivided into two sections: *A. sect. Hondenses* including the members of Xan I, and *A. sect. Xanthodermatei* which includes the members of Xan II and Xan III. *Agaricus sect. Hondenses* and *A. sect. Xanthodermatei* are two of the 12 recognized sections within *A. subg. Pseudochitonina* Konrad & Maubl. (1927: 61). In a preliminary analysis based only on ITS sequence data, we included available reference samples for all the species of these two sections and 13 samples from the Dominican Republic presumably belonging to these sections according to morphological and organoleptic criteria such as the phenol odor. In this analysis, clade Xan II clustered with Xan I in a weakly supported clade instead of clustering with Xan III to form an expected clade corresponding to *A. sect. Xanthodermatei*. In addition, one presumably new species (described in this study as *A. flavidodiscus*) was *incertae sedis*. However, all the other samples from the Dominican Republic were clearly included either within Xan II or within Xan III. This preliminary analysis based only on ITS sequence data was not sufficient to represent adequately both sections (*Hondenses* and *Xanthodermatei*) and to determine into which of the two sections *A. flavidodiscus* belongs. Therefore, we carried out a multi-gene analysis, based on ITS, LSU and translation elongation factor 1- $\alpha$  (*tef1*) sequence data from *A. flavidodiscus* and representatives of *A. sect. Hondenses*, *A. sect. Xanthodermatei*, and their closest related sections in *A. subg. Pseudochitonina*, using all available data in GenBank. The three main results, which are observable in the tree of the Fig. 2, are that (i) *A. sect. Hondenses* and *A. sect. Xanthodermatei* are well distinguishable and strongly supported with 100% and 98% bootstrap support values, respectively; (ii) the two groups Xan II and Xan III correspond to two well-supported clades within *A. sect. Xanthodermatei* (bootstrap support values of 86% and 95%, respectively); (iii) *A. flavidodiscus* belongs to the clade Xan III within *A. sect. Xanthodermatei*. From the preliminary analysis and from this multi-gene analysis we concluded that all 13 samples from the Dominican Republic belong to *A. sect. Xanthodermatei*.

Following this clarification, we carried out a second analysis based on ITS data and focusing only on *A. sect. Xanthodermatei*. We included in this analysis the 13 Dominican samples of this section, all the available species of *A. section Xanthodermatei* in GenBank and, as outgroup, a type specimen of *A. campestris*, which is the type of *A. subg. Agaricus*. In the resulting tree (Fig. 3), the two groups Xan II and Xan III are distinguishable and concordant with the multi-gene tree and thus have been indicated in the tree, though support is weaker than in the multigene tree and that Xan II appears paraphyletic with respect to clade Xan III. However, according to Thongklang *et al.* (2014), a short DNA segment likely resulting from two mutations characterizes all the samples of the group Xan II. They are present in our alignment as a deletion (-) and tranversion (from C or T to A) at positions 144–145 (segment cagc[-A]yygc with y = c or t). In the alignment all the samples of the Xan II group, and only species in this group, exhibit these two mutations except for *A. brunneogracilis* R.L. Zhao & K.D. Hyde (Zhou *et al.* 2016: 110) which only the deletion. This deletion, which was not taken in consideration in the phylogenetic analysis, is a synapomorphy that characterizes the group Xan II and reinforces the distinction between the two groups. As a result, the 13 samples represent eight species. One of them is in the group Xan II and seven are in the clade Xan III. Two of these species are already known (*A. endoxanthus* and *A. caribaeus*); three are new species described below (*A. candussoi*, *A. flavidodiscus*, and *A. tephrolepidus*, with the latter being the only one in group Xan II). The three remaining species, which are not formally described, are represented by collections LAPAM20, LAPAM46 and LAPAM61. Interestingly, LAPAM20 and LAPAM61 form a weakly supported clade (BS = 54%) with the new species *A. candussoi*, another putative new species from Martinique (F2715) and the two sister species *A. tollocanensis* Callac & G. Mata (2005: 31) and *A. pocillator* Murrill (1941: 446). It is notable that all six species are known only in the Caribbean and in southern North America.

## STUDIED TAXA

*Agaricus* subg. *Flavoagaricus* Wasser, Fl. Fung. RSS Ukrainicae: 138. 1980.

*Agaricus* sect. *Arvenses* (Konrad & Maubl. 1927: 58) Konrad & Maubl., Encycl. Mycol. 14: 104. 1948.

*Agaricus subrufescens* Peck, Ann. Rep. New York State Mus. 46: 105. 1893. (Figs. 4–5)

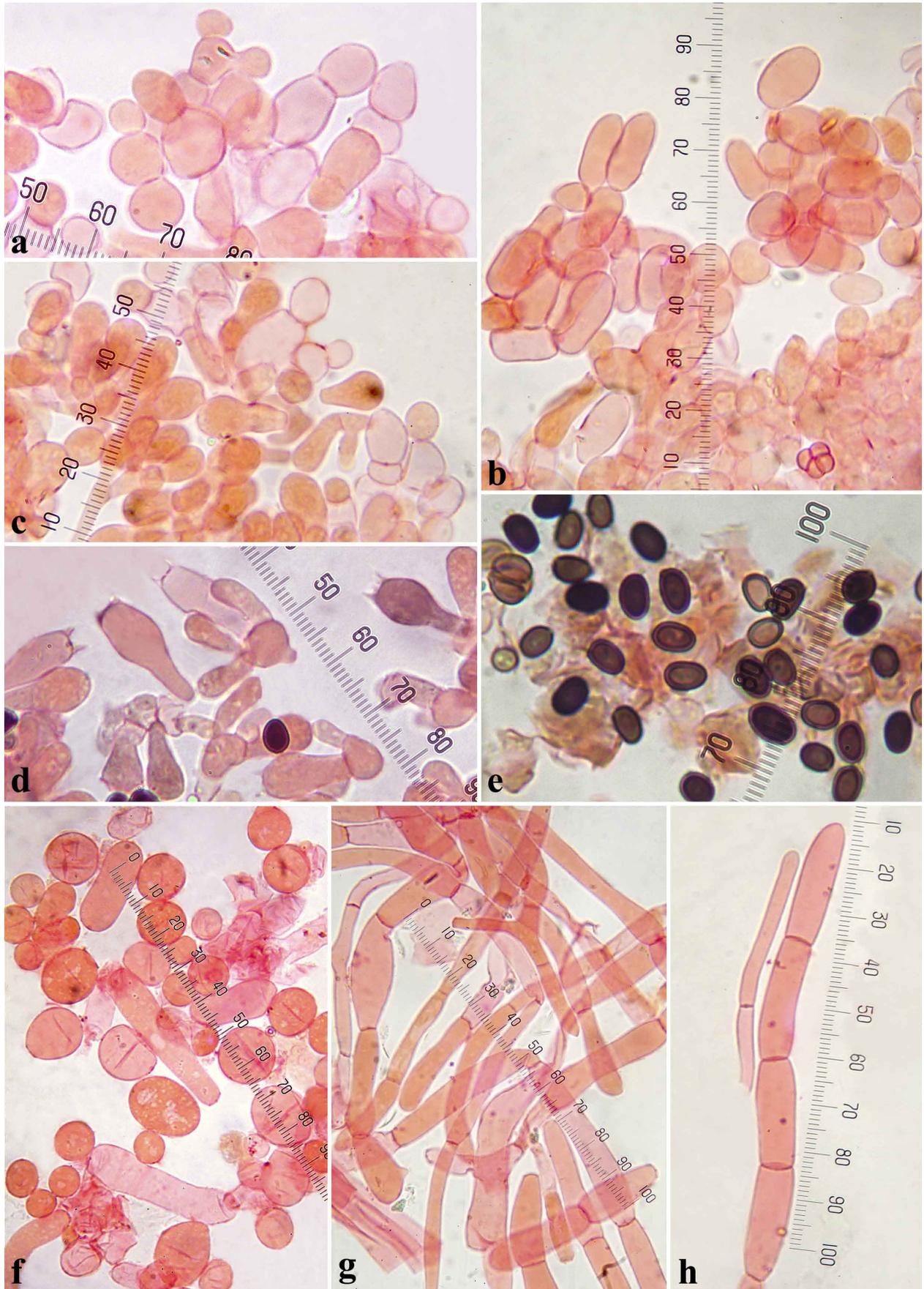
**Note:** For the numerous synonyms of *A. subrufescens* see Kerrigan (2005), Parra (2013), Thongklang *et al.* (2016) and Chen *et al.* (2016a).

**Macroscopic description:** **Pileus** 4.4–9.0 cm diam., at first hemispherical or conical, then hemispherical or trapezoid, finally plano-convex, sometimes depressed at the disc, other times broadly mammillate with umbilicate center, background whitish covered by fine hazelnut brown squamules, scales more appressed at center, which is darker. Surface fibrillose, dull and dry. Margin slightly exceeding the lamellae even in mature basidiomata. **Lamellae** free, crowded, straight, intercalated with numerous lamellulae, at first pinkish white, then pale pink for a long time, finally dark brown in mature basidiomata, with the edge even and concolorous. **Stipe** 4–9 × 0.70–1.31 cm, cylindrical, sometimes curved at the base, slightly enlarged to bulbous at base, fistulose, with an annulus in its upper third; above annulus at first white then pink, smooth, below annulus white, pruinose when young, frequently covered by a white floccosity particularly towards the base; slightly yellowing on handling. At times with a single thick rhizomorph or with abundant fine mycelial strands at the base. **Annulus** superous, double, white, up to 3.75 cm broad, fragile and fine, upper surface smooth, lower surface covered by concolorous floccose to floccose-lanose squamules. **Context** in pileus and stipe dense, when cut at first white then yellowing, soon ochre salmon, with strong odor of anise.

**Microscopic description:** **Spores** 4.94–5.32–5.70[–6] × 3.10–3.72–4.22 μm, Q=1.30–1.44–1.67, ellipsoid, smooth, brown, without apical pore. **Basidia** 13–20 × 6–7.5 μm, tetrasporic, clavate or slightly truncated at the apex, sterigmata up to 3 μm long. **Cheilocystidia** hyaline or with a brown diffuse pigment, frequently catenulate, terminal element globose, usually spherical, ovoid, or ellipsoid, 4–13 × 4–9 μm, the anteterminal elements also globose or more or less cylindrical with rounded ends, 3–11 × 5–9 μm. **Pleurocystidia** not observed. **Lower surface of the annulus** consisting of two types of hyphae, some cylindrical very narrowed at the septa, composed of elongated elements of 6–13 μm wide, rare; other abundant generally consisting of globose, spherical or slightly ovoid or inflated elements, narrowed at the septa, readily disarticulating, up to 23 μm wide. **Pileipellis** a cutis, with a transition to a trichoderm at the discal and peridiscal squamulose areas, hyphae cylindrical, the wider the more constricted at septa, 2–10 μm diam., terminal elements abundant, 4–7 μm wide, gradually to abruptly attenuated towards the apex, which is more or less rounded. **Clamp-connections** not observed.



**FIGURE 4.** Macroscopic characters of *A. subrufescens*. A–J. Basidiomata. A, E. (JBSD123800); B–C, G, I. (JBSD123801); D, F, H. (JBSD126481); J. (JBSD126504). Photos by C. Angelini.



**FIGURE 5.** Microscopic characters of *A. subrufescens* **A–H.** In ammoniacal Congo red. **A–C, F–H.** (JBSD123801); **D.** (JBSD123800); **E.** (JBSD126481). **A–C.** Cheilocystidia. **D.** Basidia. **E.** Spores. **F.** Hyphae of the lower surface of the annulus. **G–H.** Pileipellis hyphae. **H** terminal elements. Photos by L.A. Parra.

**Macrochemical reactions:** Schäffer's reaction positive, color reddish orange. KOH reaction difficult to read because of the orange yellow color of the exsiccatum.

**Habit, habitat, occurrence and distribution:** Gregarious, sometimes in rows of numerous basidiomata, in lowland broadleaf forests, particularly prevalent on leaf litter of *Terminalia* (tropical almond trees). Very common. Cosmopolitan.

**Note:** This species is characterized by its large size and robustness, the whitish pileus more or less covered by ochraceous squamules, the very broad and particularly subtle annulus with its lower surface covered by concolorous floccose to floccose-lanose squamules, by the context quickly turning ochre salmon and the strong odor of anise.

**Material examined:** DOMINICAN REPUBLIC, Puerto Plata, Sosúa, Perla Marina, 23 November 2011, JBSD123801 (LAPAM12), Puerto Plata, Sosúa, Perla Marina, 6 December 2011, JBSD126504 (LAPAM13); Puerto Plata, Sosúa, Puerto Chiquito, 20 November 2011, JBSD123800 (LAPAM11); Puerto Plata, Sosúa, cemetery, 16 December 2013, JBSD126481 (LAPAM37).

**Taxonomic comments:** We want to emphasize that although the spore sizes of the Dominican collections are slightly smaller ( $4.94\text{--}5.32\text{--}5.70[-6] \times 3.10\text{--}3.72\text{--}4.22 \mu\text{m}$ ) than those measured for *A. subrufescens* in North and South America, Europe and China (Kerrigan, 2005; Parra, 2013; Gui *et al.* 2015), they are very similar to the measurements of collections from Thailand (Wisitrasameewong *et al.* 2012), particularly to collection MFLU100065 ( $4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$ ) and to the African collection Gooss.-Font.283 ( $[4.9\text{--}]5.1\text{--}5.6\text{--}6.0[-6.2] \times [3.2\text{--}]3.3\text{--}3.6\text{--}3.9[-4.0] \mu\text{m}$ ), type of *A. bambusae* Beeli (1928: 93) var. *bambusae* now considered a synonym of *A. subrufescens* (Thongklang *et al.* 2016).

**Additional comments:** An unusual intraspecific variability is known in this cosmopolitan species. Chen *et al.* (2016a) noted that the ITS can be classified into three different types based on nine informative polymorphic positions that are reported in the Table 5. ITS sequences of collections from the Americas and Europe are of types A/A, B/B or A/B, while those from samples collected from Hawaii, Thailand, China, and more recently from Iran (Mahdizadeh *et al.* 2017) are of type C. The European sample CA487 unusually bears the three types of ITS A, B and C. We used three sequences obtained from PCR-clones of CA487 by Chen *et al.* (2016a) as haplotypes of reference A, B, and C, respectively. Based on the alignment of eight sequences used in the phylogenetic analysis, the Table 5 reveals that the two Dominican samples LAPAM 13 and LAPAM 37 are of type A/A like the sample F2285 from Martinique while the sample LAPAM 12 is of type B/B. The sequence of the sample LAPAM 11 agrees with the presence of the two types A and B. The type A/B is particularly frequent among the field collections, and most cultivars have it. The representation of this intraspecific diversity in the phylogenetic tree is not reliable since the heteromorphisms and the indels at crucial informative positions are not taken in consideration.

**TABLE 5.** The different types of ITS in *Agaricus subrufescens* based on nine polymorphic positions.

Sample <sup>a</sup>	Type	Positions								
		39	122	130	145	146	200	269	466	475
CA487-C5	A	T	A	A	G	A	T	G	A	T
LAPAM13	A/A	T	A	A	G	A	T	G	A	T
LAPAM37	A/A	T	A	A	G	A	T	G	A	T
F2285	A/A	T	A	A	G	A	T	G	A	T
CA487-C6	B	-	G	G	A	T	C	G	A	T
LAPAM12	B/B	-	G	G	A	T	C	G	A	T
CA487-C2	C	-	G	G	A	T	C	A	C	-
LAPAM11	A/B	T/-	A/G	A/G	A/G	A/T	C/T	G	A	T

<sup>a</sup>Haplotypes of reference are three PCR-clones of CA487 of type A, B and C respectively. LAPAM samples are from the Dominican Republic and F2285 from Martinique

The ITS sequence data perfectly support not only the presence of *A. subrufescens* but also the presence of the three ITS types (A/A, B/B and A/B) in the Caribbean Islands (Hispaniola and Martinique). This includes the sample F2285 from Martinique collected and identified as *A. fiardii* by J.-P. Fiard who also collected the specimen Fiard 353 that Pegler (1983) designated as the holotype of *A. fiardii*. Although F2285 undoubtedly belongs *A. subrufescens*, the question of whether or not Fiard 353 is conspecific with *A. subrufescens* warrants further studies before any attempt

to synonymize the two species. This precaution is particularly necessary in this case, because we suspect the presence of a distinct entity closely related to *A. subrufescens* in the Caribbean, based on four collections from the Dominican Republic. We do not describe these four samples in this study, because that would require a comprehensive treatment, including the comparison of sequences on a wider geographic scale, which is beyond the scope of this study.

*Agaricus* subg. *Minores* (Fr. 1874: 281) R.L. Zhao & Moncalvo, Fung. Divers. 78(1): 257. 2016.

*Agaricus* sect. *Pantropicales* L.A. Parra, Angelini, B. Ortiz, Linda J. Chen & Callac, *sect. nov.*

**MycoBank:** MB823276.

**Type:** *Agaricus lodgeae* L.A. Parra, Angelini & B. Ortiz.

**Etymology:** because of its distribution in tropical America (Caribbean region) and tropical Asia (China and Thailand). From the Greek “*pan*” meaning all, and the Latin nominative plural adjective *tropicales* meaning of the tropics (from the Latin *tropicus*, which, in turn, derives from the Greek *tropikos*). Thus, the epithet means: *Agaricus* of the tropics.

**Original description, Morphological description:** Schaffer’s reaction positive dark reddish purple or reddish brown, and KOH reaction yellow when observable on the pileus surface of dried collections. Odor of anise or of almonds when rubbed or cut. Annulus superous, thin, one-layered (simple), without scales in its lower surface. Cheilocystidia generally simple or with one or two septa at the base, usually clavate, pyriform or more or less globose. Spores lacking a rudimentary apical pore, except in some spores of LAPAM 45.

**Note:** *A. candidolutescens* Linda J. Chen & R.L. Zhao (Zhao *et al.* 2016: 258) was described as having a negative Schaffer’s reaction when fresh. However, reexamination of the dry holotype specimen showed that it had a reddish brown positive Schaffer’s reaction.

**Section-specific ITS markers:** cagetCatgct@136. This marker characterizes the members of *A. sect. Pantropicales* among all the available sequences of *A. subg. Minores*. However, the characteristic nucleotide C is also present at homologous positions in samples of *A. subg. Minoriopsis*. Using the two flanking nucleotides [cagcTCAtgct@135–137], we found that the short DNA segment [TCA] characterizes all samples of *A. sect. Pantropicales* exclusively and is not found in other sections in either *A. subg. Minores* or *A. subg. Minoriopsis*.

**Stem age and phylogenetic support:** In the maximum clade credibility (MCC) tree of Chen *et al.* (2017) the well-supported (PP  $\geq$  0.99) *A. sect. Pantropicales*, which was provisionally named *A. sect. 1*, is sister to *A. sect. Leucocarpi* and consequently has the same stem age of 27.64 Ma. In our ITS tree (Fig. 1), it is also well supported (ML bootstrap support 84%; PP = 1) and includes four species or putative species.

*Agaricus lodgeae* L.A. Parra, Angelini & B. Ortiz, *sp. nov.* (Figs. 6–7)

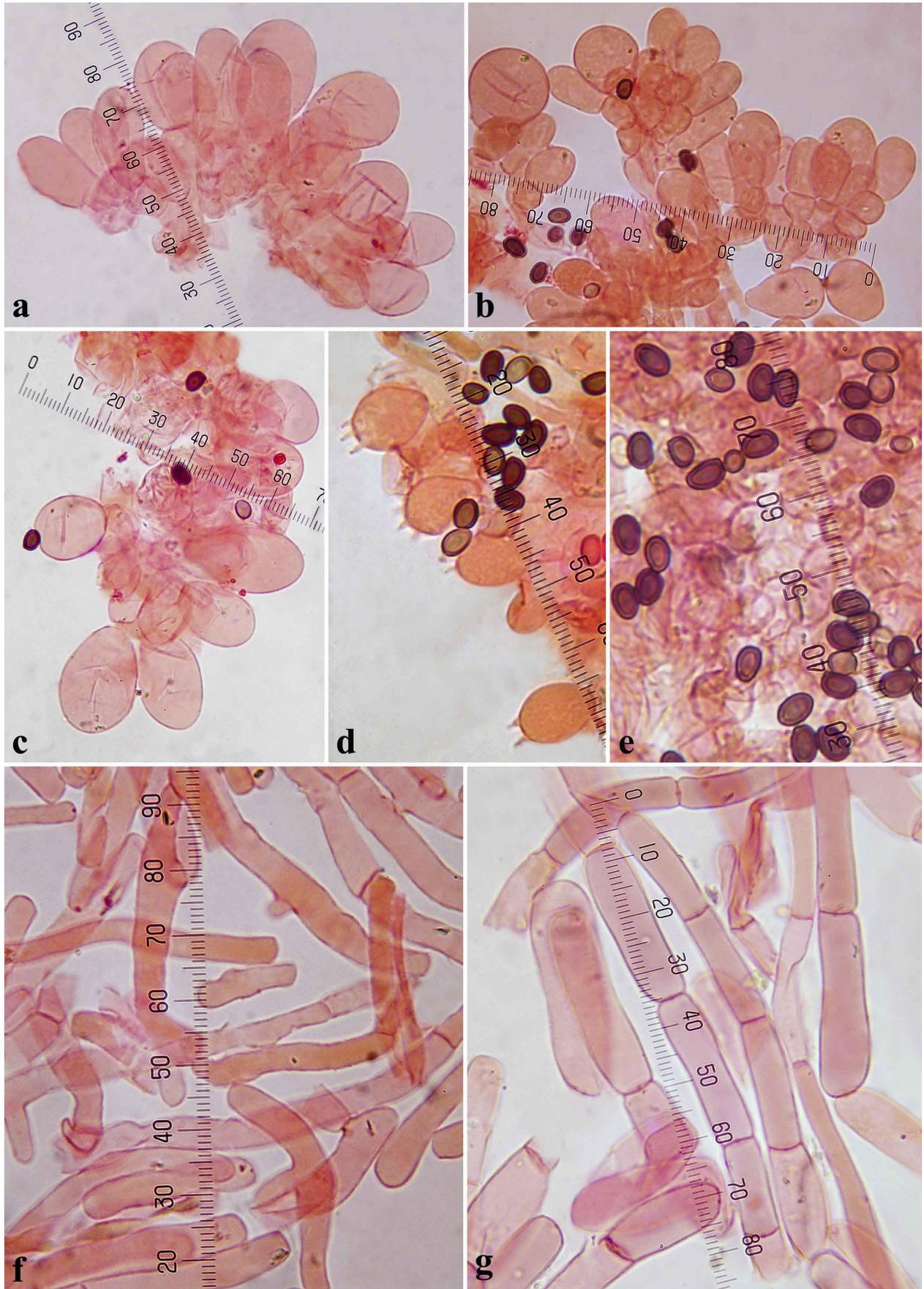
**MycoBank:** MB823279.

**Etymology:** The specific epithet honors D. Jean Lodge, the first collector of this new species, for her contribution to the mycological knowledge of the Caribbean.

**Original description, Macroscopic description:** **Pileus** 2.5–4 cm diam., at first hemispherical-campanulate, sometimes with an inconspicuous obtuse umbo, finally plane, fully extended. Margin striate over more than half the radius of the pileus. Surface fibrillose, with purple fibrils on whitish background, disc strongly pigmented vinaceous red while margin remains constantly discolored and whitish. Surface stains purple violet on handling or at contact with raindrops. **Lamellae** free, crowded, somewhat wide and generally straight, intercalated with numerous lamellulae, at first rose, then blackish brown in mature basidiomata, with the edge whitish and irregular. **Stipe** 5–7  $\times$  0.4–0.6 cm, more or less cylindrical, straight or more frequently curved or flexuose, tapered at apex, tending to enlarge towards the base where it ends in quite distinct rhizomorphs, with an annulus in its upper third, surface finely fibrillose, off-white and yellowing, with fibrils more evident above annulus. **Annulus** superous, undeveloped and fine, non-striate, cobweb-like or cortiniform in young basidiomata, sometimes incomplete and present only in fragments in the adults. **Context** scanty, when cut whitish, quickly yellowing and with odor of bitter almonds.



**FIGURE 6.** Macroscopic characters of *A. lodgeae*. A–F. Basidiomata. A. (JBSD123817); B–E. (JBSD126505, holotype); F. (JBSD126506). Photos by C. Angelini.



**FIGURE 7.** Microscopic characters of *A. lodgeae*. A–G. In ammoniacal Congo red. A, C, E–G. (JBSD123817), B, D. (JBSD126505, holotype). A–C. Cheilocystidia. D. Basidia (near the lamellae edge). E. Spores. F. Hyphae of the lower surface of the annulus. G. Pileipellis hyphae. Photos by L.A. Parra.

**Microscopic description:** Spores (4.46–)4.64–4.86–5.15 × 3.10–3.50–3.81 µm, Q=1.24–1.39–1.56, ellipsoid, smooth, brown, without apical pore. **Basidia** 10–15 × 6–8 µm, tetrasporic, clavate or slightly truncated at the apex, pyriform to globose near the lamellae edge, sterigmata up to 3 µm long. **Cheilocystidia** abundant, hyaline, generally simple, rarely septate at the base, clavate, pyriform or globose more or less pedunculated, terminal elements 13–32 × 10–18 µm, when septate anteterminal elements somewhat cylindrical of 5.5–12.0 × 5.5–7.0 µm. **Pleurocystidia** not observed. **Lower surface of the annulus** consisting of hyaline hyphae, cylindrical, not or slightly narrowed at the septa, 2–8 µm wide. Inflated elements not observed. **Pileipellis** a cutis, hyphae cylindrical, the wider the more constricted at septa, 4–10 µm wide. Terminal elements not observed. **Clamp-connections** not observed.

**Macrochemical reactions:** Schäffer's reaction positive, slow but intense, color dark reddish purple. KOH reaction difficult to observe on the pileus because of the dark color of the dried material, reddish orange on the stipe base.

**Habit, habitat, occurrence and distribution:** In groups of few basidiomata, at times caespitose, deeply inserted into the leaf litter, in both broadleaf as mixed with conifers (*Pinus occidentalis*) forests; from lowland to the mountains. Very common. Recorded only from Puerto Rico and the Dominican Republic.

**Species-specific ITS markers in *A. subg. Minores*:** ttggTTTTTr(tt)gg@103–108. Other species have only 2T (rarely 3T or 4T)

**Note:** The original description is based on the Dominican collections. This species is also found in Puerto Rico, where three collections have been also made. These collections share the macroscopic characters with the Dominican ones, but they differ in their fungal or indistinct odor and spores that are somewhat longer in collections PR4634 and PR6454 (4.8–6.4 × 3.2–4 µm and 5–5.9 × 3.2–3.6 µm, respectively), but similar in collection PR6239 (4.3–5.6 × 3.2–3.6 µm). The collections from Puerto Rico will be fully described in a future work in preparation. We also found in GenBank an ITS sequence of a collection (PA393) from Panama that belongs to this taxon, in spite of its original identification as “Lepiotaceae sp.” by Vo *et al.* (2009). This is a ubiquitous species of small to medium size, characterized by its fibrillose pileus with the disc strongly pigmented vinaceous purple and the whitish margin, the long off-white and yellowing flexuous stipe, and the fine, undeveloped, not-striate, sometimes incomplete or present only in fragments annulus.

**Material examined:** DOMINICAN REPUBLIC, Puerto Plata, Sosúa, Puerto Chiquito, 25 November 2011, JBSD123817 (LAPAM14); La Vega, Jarabacoa, Jarabacoa, 10 January 2016, JBSD126505 *Holotypus* (LAPAM67 *Isotypus*); La Vega, Jarabacoa, Jarabacoa, 10 January 2016, JBSD126506 (LAPAM68). PUERTO RICO, Luquillo, Sabana Field Station, 31 August 1997, collector D. J. Lodge, PR4634 (CFMR); Rio Grande, by El Verde Field Station trail, 31 August 2000, collector D. J. Lodge, PR6239 (CFMR); Luquillo, Sabana Road 988, 1 km from Sabana Station, 29 September 2001, collector D. J. Lodge, PR6454 (CFMR).

**Taxonomic comments:** Although this species belongs to *A. sect. Pantropicales* within *A. subg. Minores*, it resembles to species of *A. subg. Minoropsis* with purple pileus, such as *A. argenteopurpureus*, *A. martinicensis* or *A. porphyropos*. These three species differ in having a double annulus with a fibrillose-squamose lower surface and a pileus in fresh and young collections without a conspicuous striate margin. Furthermore, *Agaricus martinicensis* and *A. porphyropos* are more robust.

**Additional comments:** In the genus *Agaricus*, conspecific specimens generally have less than three differences in their ITS sequences. In *A. lodgeae*, certain samples such as LAPAM 14 and PR6454 (top and bottom positions in Table 6), differ at eight positions and another sample (PR4634) is heteromorphic at all 13 positions shown in this Table. An ancient hybridation between highly divergent populations might be at the origin of the highly variable population observed today.

**TABLE 6.** Unusual intraspecific variability in *A. lodgeae*.

Sample	Positions												
	108	115	151	166	169	178	200	350	485	517	562	632	642
LAPAM14	A	G	A	G	T	A	C	C	G	T	<b>Y</b>	C	G
LAPAM67	A	G	<b>R</b>	<b>R</b>	<b>Y</b>	<b>R</b>	C	C	G	<b>Y</b>	<b>Y</b>	C	<b>R</b>
PR4634	<b>R</b>	<b>R</b>	<b>R</b>	<b>R</b>	<b>Y</b>	<b>R</b>	<b>Y</b>	<b>Y</b>	<b>S</b>	<b>Y</b>	<b>Y</b>	<b>Y</b>	<b>R</b>
PR6239	G	G	<b>R</b>	<b>R</b>	<b>Y</b>	<b>R</b>	C	C	G	C	<b>Y</b>	C	G
LAPAM68	<b>R</b>	<b>R</b>	G	A	<b>Y</b>	G	<b>Y</b>	<b>Y</b>	<b>S</b>	C	C	T	G
PR6454	G	G	G	A	C	G	C	C	C	C	C	T	G

Heteromorphisms in bold types: Y = C and T; R = A and G; S = C and G.

*Agaricus* subg. *Minoriopsis* Linda J. Chen, L.A. Parra, Callac, Angelini & Raspé, *Persoonia* 38: 180. 2017.

*Agaricus* sect. *Minoriopsis* (Linda J. Chen, L.A. Parra, Callac, Angelini & Raspé) L.A. Parra, Angelini, Linda J. Chen & Callac, *sect. & stat. nov.*

**Mycobank:** MB823277.

**Type:** *Agaricus martinicensis* Pegler, *Kew Bulletin*, Addit. Ser. 6: 446. 1983.

**Basionym:** *Agaricus* subg. *Minoriopsis* Linda J. Chen, L.A. Parra, Callac, Angelini & Raspé, *Persoonia* 38: 180. 2017.

**Etymology:** Referring to the similarities to *Agaricus* sect. *Minores*.

**Original description, Morphological description:** Schäffer's and KOH reactions not performed on fresh collections. Schäffer's reaction positive dark reddish purple or reddish brown and KOH reaction yellow when observed on the pileus surface of dried collections. Odor of anise or almonds when rubbed or cut (see note below). Annulus superous, thick at the margin, two layered (double), fibrillose squamose sometimes with the scales radially arranged as a cogwheel near the margin in its lower surface. Cheilocystidia generally simple or with one or two septa at the base, usually clavate, pyriform, more or less globose or fusiform, sometimes rostrate or absent in some collections. Spores lacking a rudimentary apical pore.

**Section-specific ITS markers:** Within *A.* subg. *Minoriopsis*, all samples of *A.* sect. *Minoriopsis* differ from all samples of *A.* sect. *Kerrigania* in ten nucleotide positions in the alignment (37, 70, 118, 147, 204, 236, 278, 509, 524 and 549). Because *Agaricus* sect. *Minoriopsis* currently includes only two species, the number of section-specific markers might easily decrease when more species of this new section will be sequenced. Therefore, we do not describe in details these markers with the exception of the G nucleotide at position 37 in the alignment. Indeed, we verified that this G, which is located at position 36 in the individual ITS sequences of *A. martinicensis* and *A. argenteopurpureus* [ggctcGtcaga@36], distinguishes all samples of *A.* sect. *Minoriopsis* from all other sequenced samples of the subgenera *A.* subg. *Minoriopsis* and *A.* subg. *Minores*, which represent about a hundred named or putative species (Chen *et al.* 2017; He *et al.* 2017).

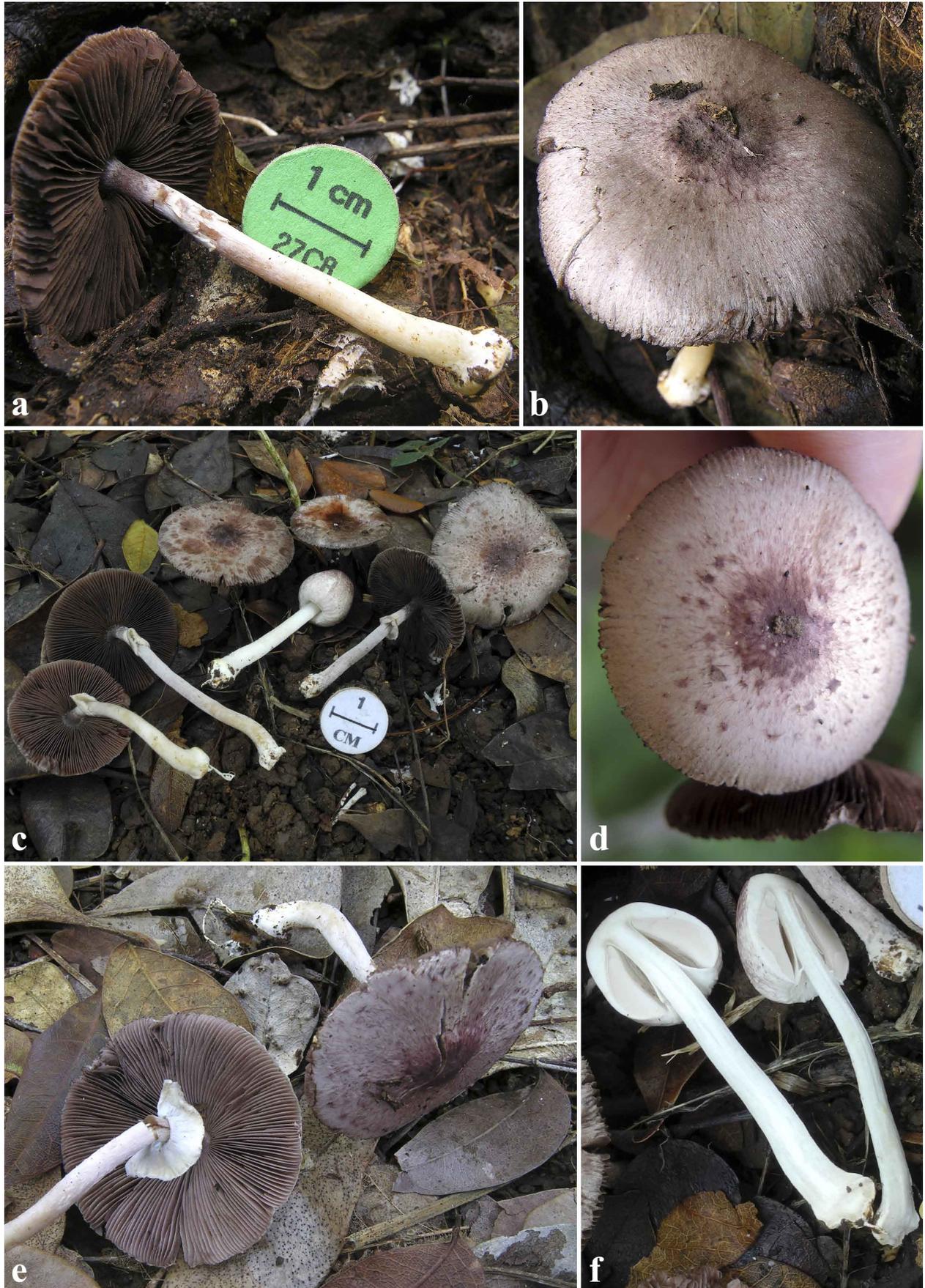
**Stem age and phylogenetic support:** in the MCC tree of Chen *et al.* (2017) the well-supported (PP  $\geq$  0.99) clade, corresponding to *A.* sect. *Minoriopsis*, is sister to *A.* sect. *Kerrigania* (also proposed in this paper as new section), and consequently has the same stem age of 22.83 Ma. In our ITS tree (Fig. 1), it is also well supported (ML bootstrap support 99%; PP = 1) and includes two species.

*Agaricus argenteopurpureus* L.A. Parra, Angelini & Callac, *sp. nov.* (Figs. 8–9)

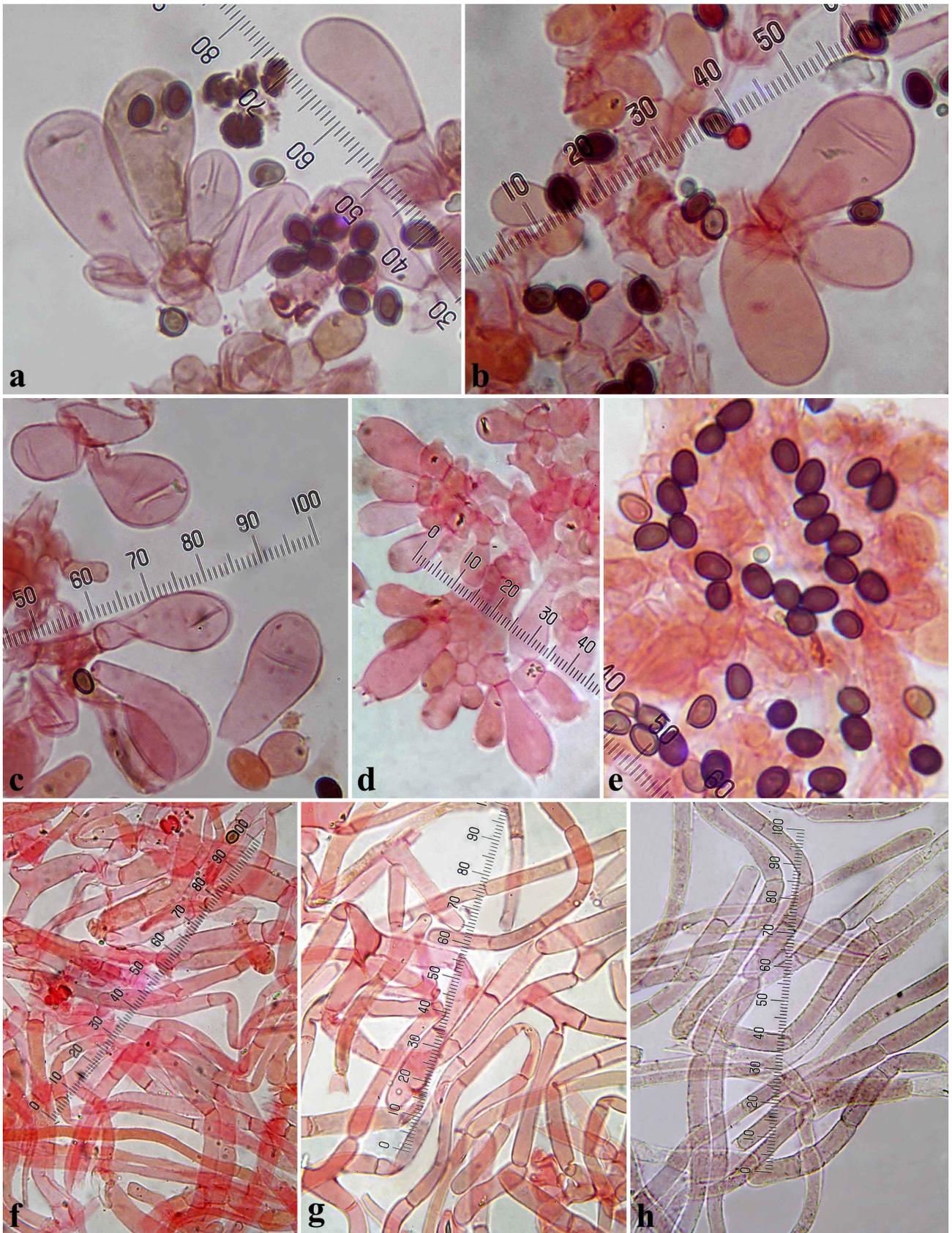
**Mycobank:** MB823280.

**Etymology:** for the violet purple color (in Latin “*purpureus*”) with silver (in Latin “*argenteus*”) highlights on the pileus.

**Original description, Macroscopic description:** **Pileus** (2.5–)3.0–3.5(–4.0) cm diam., at first conico-hemispherical, then quickly plano-convex or plane with a slightly revolute margin; frequently depressed at center, more rarely with a broad umbo at center and depressed at the peridiscal area, grayish with silver highlights, covered partially or entirely with purple fibrils that tend to merge simulating squamules, closer and appressed at disc where it is very dark purple vinaceous. Surface smooth, fibrillose, dry and dull. Margin fine, not exceeding the lamellae, not striate in immature or young basidiomata but strongly striate or rimose, in mature basidiomata or after rain. **Lamellae** free, slightly ventricose, intercalated with numerous lamellulae, at first very pale, grayish pink, then brownish pink, finally dark grayish brown, with a paler and slightly eroded edge. **Stipe** 3.5–4.5  $\times$  0.3–0.4 cm, cylindrical and straight, clavate or slightly bulbous at base, at times also marginately bulbous, fistulose, with an annulus in the upper third, smooth to somewhat fibrillose, gray, grayish purple above the annulus, fibrillose and whitish below annulus, yellowing on handling particularly towards the base, base with a central, not or branched rhizomorph. **Annulus** superous, double, white, up to 0.5 cm broad, fine, thicker at the margin, pendulous, soon adpressed to the stipe, upper surface smooth or finely striate and the lower surface finely fibrillose-squamulose. **Context** slightly dense, scanty at the pileus margin, when cut at first white then light ochre, especially at the stipe apex, with odor of bitter almonds.



**FIGURE 8.** Macroscopic characters of *A. argenteopurpureus*. A–F. Basidiomata. A–B. (JBSD126500); C, F. (JBSD126501, holotype); D. (JBSD126502); E. (JBSD126503). Photos by C. Angelini.



**FIGURE 9.** Microscopic characters of *A. argenteopurpureus*. **A–H.** (JBSD126501, holotype) (A–G in ammoniacal Congo red; H in water). A–C. Cheilocystidia. D. Basidia. E. Spores. F. Hyphae of the lower surface of the annulus. G–H. Pileipellis hyphae. Photos by L.A. Parra.

**Microscopic description:** Spores  $4.74\text{--}5.09\text{--}5.67 \times 3.19\text{--}3.57\text{--}4 \mu\text{m}$ ,  $Q=1.27\text{--}1.43\text{--}1.63$ , ellipsoid, smooth, brown, without apical pore. **Basidia**  $15\text{--}23(\text{--}27) \times 6.5\text{--}8(\text{--}12) \mu\text{m}$ , tetrasporic, clavate or slightly truncated at the apex, sterigmata up to  $3 \mu\text{m}$  long. **Cheilocystidia** abundant, hyaline and smooth, simple or with a basal septum. Terminal elements generally clavate, broadly clavate or pyriform, often also fusiform or rostrate, rarely capitulate,  $10\text{--}27(\text{--}32) \times 6\text{--}15 \mu\text{m}$ . Anteterminal elements in those septate more or less cylindrical  $5\text{--}15 \times 3.5\text{--}8 \mu\text{m}$ . **Pleurocystidia** not observed. **Lower surface of the annulus** consisting of cylindrical hyphae, not or slightly narrowed at the septa, some with encrusted parietal pigment,  $2\text{--}7 \mu\text{m}$  wide. Inflated elements not observed. **Pileipellis** a cutis composed of cylindrical hyphae of  $3\text{--}10 \mu\text{m}$  wide, the wider the more constricted at septa. In water, hyphae from the disc with abundant pink diffuse pigment and with punctate granular pigment, in a few elements; outside of the disc hyaline or few elements with well-diffused pink or granular punctate pigment. Terminal elements abundant, cylindrical or attenuated at the apex, which is rounded. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer's reaction positive, color dark reddish purple. KOH reaction positive, color orange yellow.

**Habit, habitat, occurrence and distribution:** Solitary, rarely in groups of a few basidiomata, in broadleaf forests. Common. Recorded only from the Dominican Republic.

**Species-specific ITS markers in *A. subg. Minoriopsis*:** cacgcTgtttggaAttcat@54–63, gtgtgCaaact@166, taccAgtega@238, and tgaagAgcatt@544.

**Note:** This species is characterized by its medium-small size, its solitary basidiomata, the pileus with gray with silver highlights and dark reddish purple disc, the pileal margin striate and eroded at maturity, the double annulus with thick margin, the quick yellowing reaction on the stipe on handling, the central rhizomorph at the stipe base and the odor of bitter almonds.

**Material examined:** DOMINICAN REPUBLIC, Puerto Plata, Sosúa, beach, 22 December 2012, JBSD126500 (LAPAM24); Puerto Plata, Sosúa, beach, 25 November 2013 JBSD126501 *Holotypus* (LAPAM28 *Isotypus*); Puerto Plata, Sosúa, beach, 27 November 2014, JBSD126502 (LAPAM53); Puerto Plata, Sosúa, beach, 28 November 2014, JBSD126503 (LAPAM55).

**Taxonomic comments:** This species is highly similar to *A. martinicensis*, from which it differs in smaller size, a pileus surface that is usually more grayish silver toward the margin and more frequently striate, and smaller spores, although an unambiguous identification would require the use of molecular characters to unequivocally differentiate the two species.

This species is also macroscopically similar to many species of *A. subg. Minores* in the pileus completely covered by reddish purple squamules, but it is distinguished by its membranous double annulus that is thicker at the margin with the lower surface fibrillose-squamulose and its dark reddish purple Schäffer's reaction in dried material, instead of a simple annulus that is fragile and ephemeral and the weak reddish pink Schäffer's reaction in dried material of *A. subg. Minores*. Within *A. sect. Pantropicales*, *Agaricus argenteopurpureus*, at times, strongly resembles to *A. porphyropos*, but the former has a pileus with silvery or greyish highlights which is reddish purple on a white background in all studied collections of *A. porphyropos*. However, we must be cautious when using these characters to separate the two taxa since we do not well know the variability in *A. porphyropos*.

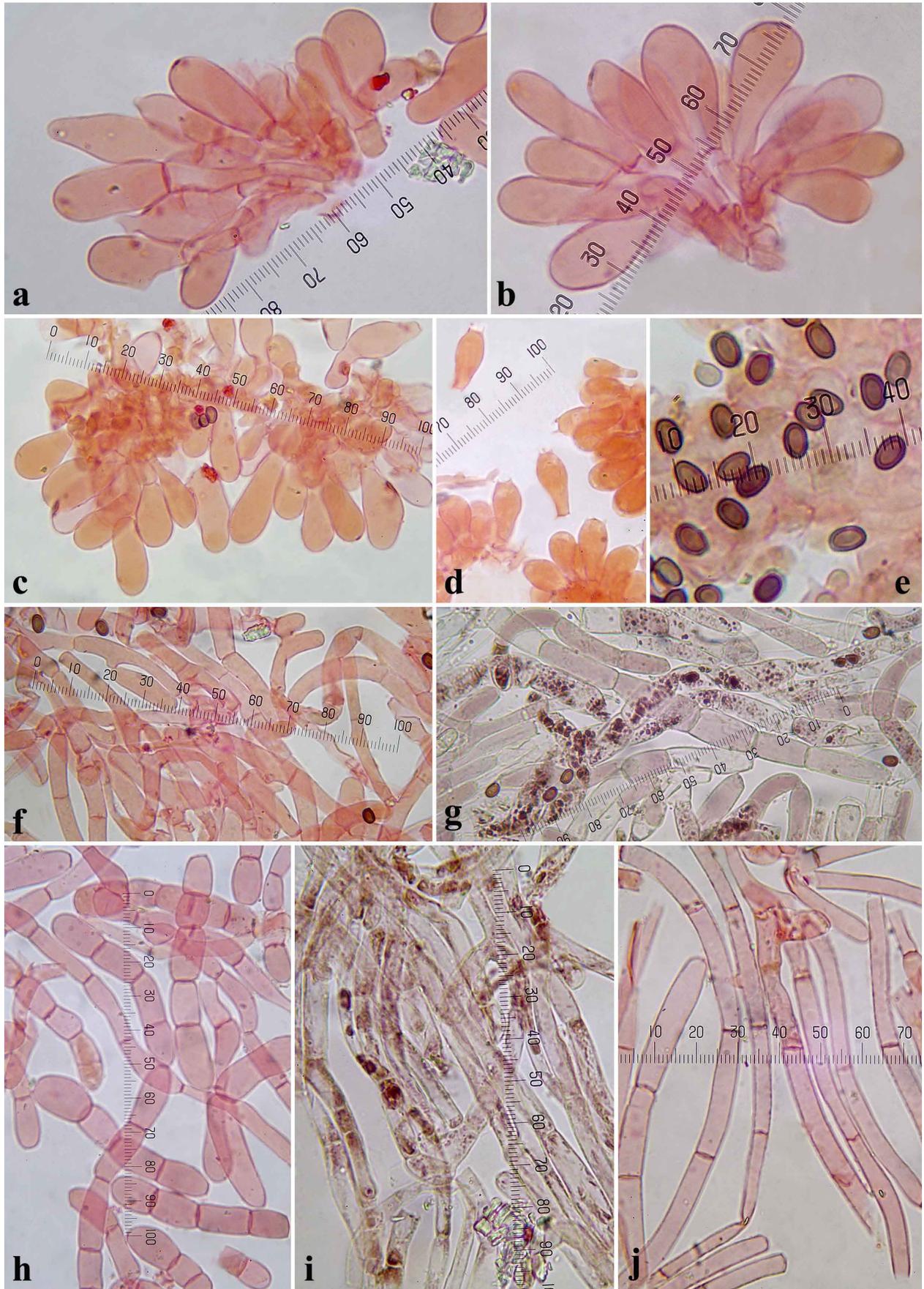
*Agaricus argenteopurpureus* also resembles macroscopically *A. dennisii* Heinem (1961: 245), a species placed by this author in *A. subg. Conioagaricus* Heinem. (1956: 101). Their pilei have the same color and, in mature basidiomata, the same strongly striate margin, which exudes reddish drops. However, *A. dennisii* lacks an anise odor, its Schäffer's reaction is negative, it lacks cheilocystidia and its spores are much smaller with dimensions not overlapping with those of *A. argenteopurpureus*.

*Agaricus martinicensis* Pegler, Kew Bull. Addit. Ser. 6: 446. 1983. (Figs. 10–11)

**Macroscopic description:** Pileus 3–6 cm diam., at first hemispherical then plano-convex, finally plane, sometimes with revolute margin, depressed towards the center where it has a broad and low umbo, background whitish partially or entirely covered by reddish purple scales with an entire intensely colored dark reddish purple center. Surface smooth, fibrillose, dry and dull. Margin thin, fimbriate, not or slightly exceeding the lamellae. **Lamellae** free, crowded, straight or slightly sinuate, intercalated with numerous lamellulae, white for a long time (resembling at first glance in the field a species of the genus *Leucoagaricus* Locq. ex Singer), staining orangish pink when handled, and finally dark brown with a paler and slightly eroded edge. **Stipe**  $4.5\text{--}6.5 \times 0.7\text{--}1.0 \text{cm}$ , cylindrical or more enlarged and curved at base, sometimes sinuate, clavate, bulbous or slightly marginately bulbous, fistulose, hollow at base, with an annulus in its upper third, completely white or off-white, above annulus finely fibrillose, below annulus fibrillose or with thick white



**FIGURE 10.** Macroscopic characters of *A. martinicensis*. **A–H.** Basidiomata. **A.** (JBSD121929); **B.** (JBSD123819); **C, G, H.** (JBSD126496); **D.** (JBSD126499); **E.** (JBSD126498); **F.** (JBSD126497). Photos by C. Angelini.



**FIGURE 11.** Microscopic characters of *A. martinicensis*. **A–J.** (A–F, H, J in ammoniacal Congo red; G, I in water). A–D. (JBSD123819), E–J. (JBSD126497). A–C. Cheilocystidia. D. Basidia. E. Spores. F. Hyphae of the lower surface of the annulus. G–J. Pileipellis hyphae (G–H discal area, I–J medial area). Photos by L.A. Parra.

cottony scales, which sometimes seem like true recurved squamules, becoming pink salmon on handling especially towards the base where is provided with a thick, simple or branched rhizomorph. **Annulus** superous, double, white, yellowing on handling or with age, up to 1 cm wide, membranous of remarkable thickness, upper surface smooth, lower surface fibrillose-floccose and with finely denticulate margin. **Context** dense or not, when cut at first white and then white or ochre salmon in the pileus, and ochre salmon in the stipe, rarely with reddish tones in the stipe apex and in the center of the pileus, with odor like almonds.

**Microscopic description:** **Spores** (4.24–)4.33–4.91–5.36 × 2.88–3.21–3.61 μm, Q=1.29–1.53–1.72, ellipsoid or ellipsoid elongate, smooth, brown, without apical pore. **Basidia** 12–16(–21) × 6.5–8.0 μm, clavate or slightly truncated at the apex, sterigmata up to 3 μm long. **Cheilocystidia** abundant, hyaline and smooth, simple or with a basal septum, terminal elements generally clavate, broadly clavate or pyriform, often also fusiform or rostrate, rarely capitulate, 12–38 × 6.5–13(–16) μm, anteterminal elements of those septate 7–17 × 4–6 μm. **Pleurocystidia** not observed. **Lower surface of the annulus** composed of cylindrical hyphae not or narrowed at septa, 2–7(–9) μm wide. Inflated elements not observed. **Pileipellis** a cutis with a transition to a trichoderm at the squamose disc. At the disc with two types of hyphae, some cylindrical similar to those outside of the disc of 3–7 μm wide and others thicker consisting of doliiform elements with rounded apex of 6–15 μm wide, while outside of the disc predominate cylindrical hyphae with constant diameter, composed of elongated elements of 3–7 μm wide. In water, the hyphae from the disc may have pinkish diffuse pigment or a very fine granular yellow pigment, while the hyphae from the perimarginal area have a finely granulate vinaceous brown pigment. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer's reaction positive, color dark reddish purple. KOH reaction positive, color orange yellow. Fiard's original field notes from the holotype point out a positive blood red Schäffer's reaction in fresh collections.

**Habit, habitat, occurrence and distribution:** Gregarious, growing in groups of few basidiomata in all types of broadleaf forests. Very common. Recorded from the Dominican Republic and Martinique. From the later, Pegler (1983) designated the holotype (Fiard 820) and two paratypes (Fiard 780A and Pegler 2930).

**Note:** Very variable species, sometimes robust, fleshy and with a short stipe, other times slender, slightly fleshy and with a long thin stipe. It is characterized by its medium size, the pileus with vinaceous purple scales, always darker at center and with a low umbo, lamellae and stipe staining ochre salmon after handled, the thick, ample and double annulus and by the stipe usually ending in a thick and single rhizomorph.

**Material examined:** **DOMINICAN REPUBLIC, María Trinidad Sánchez,** Rio San Juan, road to Payita, in a lowland forest, 3 January 2011, JBSD121929 (LAPAM10); **Puerto Plata,** Sosúa, Puerto Chiquito, 25 November 2011, JBSD123819 (LAPAM16); **Puerto Plata,** Sosúa, Puerto Chiquito, 21 November 2013, JBSD126495 (LAPAM42); **Puerto Plata,** Sosúa, Puerto Chiquito, 29 December 2013, JBSD126496 (LAPAM43); **Puerto Plata,** Sosúa, Puerto Chiquito, 29 December 2013, JBSD126497 (LAPAM44); **Puerto Plata,** Sosúa, Puerto Chiquito, 22 December 2014, JBSD126498 (LAPAM63); **Puerto Plata,** Sosúa, beach, 4 December 2014, JBSD126499 (LAPAM56).

**Taxonomic comments:** This species is highly similar to *A. argenteopurpureus* and *A. lodgeae* with which it has already been compared (see taxonomic comments of these species).

This species is also macroscopically similar to many species of *A.* subg. *Minores* in the pileus completely covered by reddish purple squamules, but it is distinguished by its membranous double annulus that is thicker at the margin with the lower surface fibrillose-squamulose and its dark reddish purple Schäffer's reaction in dried material, instead of a simple annulus that is fragile and ephemeral and the weak reddish pink Schäffer's reaction in dried material of *A.* subg. *Minores*. In other respects, *A. martinicensis* is also similar to *A. porphyropos*, but the latter species is less robust and usually has scales more dispersed towards the pileus margin.

**Additional comments:** ITS sequences of the seven Dominican studied collections fully match three sequences used in this study, from two collections made by J.-P. Fiard (F2343 and F2815) and one by C. Lechat (CL/MART03.055) in the Caribbean island of Martinique.

*Agaricus* sect. *Kerrigania*, L.A. Parra, Angelini, B. Ortiz, Linda J. Chen & Callac, *sect. nov.*

**Mycobank:** MB823278.

**Type:** *Agaricus porphyropos* L.A. Parra, Angelini & B. Ortiz

**Etymology:** This specific epithet honours our good friend and mycologist Richard Kerrigan for his contribution to the knowledge of the genus *Agaricus*.

**Original description, Morphological description:** Schäffer's and KOH reactions not performed on fresh collections. Schäffer's reaction positive dark reddish purple or reddish brown and KOH reaction yellow when observable on the pileus surface of dried collections. Odor of anise or of almonds when rubbed or cut (see note below). Annulus superous, thick at the margin, two layered (double), fibrillose-squamose sometimes with the scales radially arranged as a cogwheel near the margin in its lower surface. Cheilocystidia generally simple or with one or two septa at the base, usually clavate, pyriform, more or less globose or fusiform, sometimes rostrate or absent in some collections. Spores lacking a rudimentary apical pore.

**Note:** For some collections belonging to this section other odors have been recorded but none of them was collected by one of the authors of this paper. These odors such as iodate in the collection F1779, light in LAPAM66 or like *A. campestris* L.: Fr. in CJL090302.05 are pointed out in field notes by the collectors.

**Stem age and phylogenetic support:** in the MCC tree of Chen *et al.* (2017) the well-supported (PP  $\geq$  0.99) clade corresponding to *A.* sect. *Kerrigania* is sister to *A.* sect. *Minoriopsis* (also proposed in this paper as new section), and consequently has the same stem age of 22.83 Ma. In our ITS tree (Fig. 1), it is also well supported (ML bootstrap support 94 %; PP = 1) and includes ten named or putative species.

**Section-specific ITS markers:** Ten differences between the sequences of *A.* sect. *Kerrigania* and *A.* sect. *Minoriopsis* are indicated above under the description of *A.* sect. *Minoriopsis*. Only the difference at position 118 of the alignment merits to be described in detail. Based on the sequence of *A. porphyropos*, the DNA segment including this marker is [ggttgTYggaaa@112–113]. It is relatively well conserved except at the 3' end of the flanking sequence where 'aaa' is highly variable ('tat' in most species of *A.* sect. *Minores*). In this segment TY is, in fact, an insertion of two nucleotides (TC or TT), which, in both subgenera (*Minores* and *Minoriopsis*), is found exclusively in all the sequences of *A.* sect. *Kerrigania*. It can be noted that an insertion of a single nucleotide (T or C) is found only in two species, *A. argenteopurpureus* within *A.* sect. *Minoriopsis*, and *A. candidolutescens* within *A.* sect. *Pantropicales*.

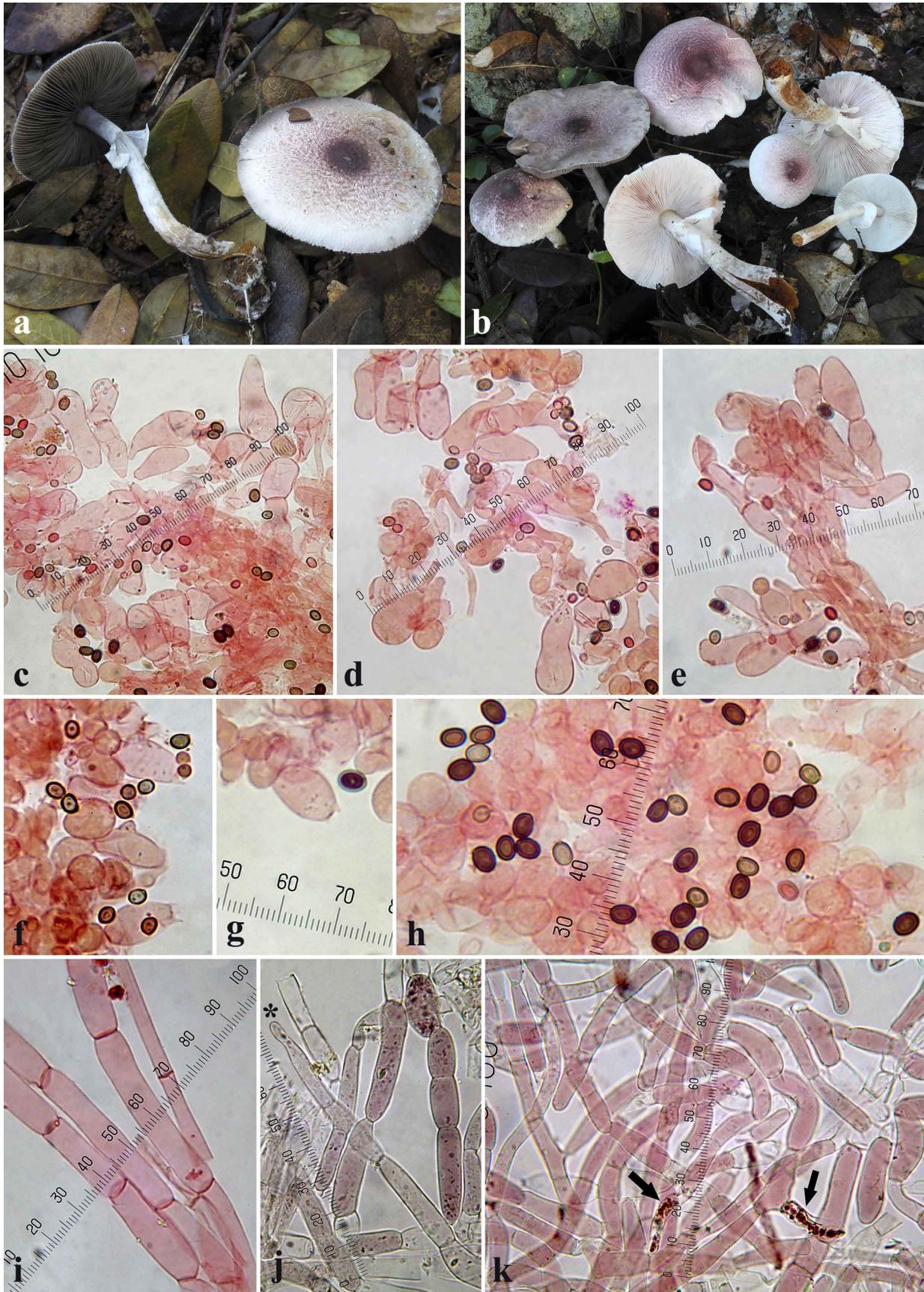
*Agaricus porphyropos* L.A. Parra, Angelini & B. Ortiz, *sp. nov.* (Fig. 12)

**Mycobank:** MB823281.

**Etymology:** Because the pileus resembles a purple (in Greek "pophyros") eye (in Greek "ops, opos").

**Original description, Macroscopic description:** **Pileus** (2.5–)3.0–5.0(–5.5) cm diam., hemispherical when young, then plano-convex, finally completely plane, sometimes slightly depressed at center with a broad and low umbo, whitish, partially or entirely covered with reddish purple scales with an entire dark purple vinaceous center. Surface smooth, fibrillose, dull and dry. Margin thin, slightly exceeding the lamellae or more or less fimbriate, sometimes obscurely striate on the upper surface after raining. **Lamellae** free, straight or slightly ventricose, intercalated with numerous lamellulae, white for a long time (resembling at first glance a species of *Leucoagaricus*), staining bright pink on handling, and finally dark grayish brown with paler and even edge. **Stipe** 6.0–7.0  $\times$  0.4–0.8 cm, cylindrical or slightly bulbous at base, straight, sometimes flexuose, fistulose, hollow at base, with an annulus in its upper third, above annulus smooth and whitish, below annulus whitish cream, fibrillose and floccose, yellowing on handling, especially at the base which is covered by white felted mycelium and fine white mycelial strands. **Annulus** superous, double, white, up to 1.5 cm broad, membranous but fragile, upper surface smooth, lower surface fibrillose-lanose or with large floccose scales in concentric bands toward the margin. Sometimes present only in fragments. **Context** slightly dense, when cut at first white becoming pink over time, but orange brown around the worm holes, with odor of anise.

**Microscopical description:** **Spores** 4.12–4.70–5.36  $\times$  3–3.43–3.91  $\mu$ m, Q=1.22–1.37–1.55, broadly ellipsoid to ellipsoid, smooth, brown, without apical pore. **Basidia** 10–16  $\times$  6.5–9  $\mu$ m, tetrasporic, clavate or slightly truncated at the apex, also very abundant and doliiiform on the lamellae edge, sterigmata up to 2  $\mu$ m long. **Cheilocystidia** abundant, hyaline or with internal diffuse brown pigment, simple or septate at the base, terminal elements versiform, most frequently clavate (sometimes slightly narrowed in the middle), pyriform, ovoid or cylindrical, sometimes fusiform, utriform, rarely rostrate or capitulate, 11–30(–42)  $\times$  7–14  $\mu$ m, anteterminal elements in those septate more or less cylindrical, 4–18  $\times$  3–7  $\mu$ m. **Pleurocystidia** not observed. **Lower surface of the annulus** composed of hyaline hyphae, cylindrical, not or slightly narrowed at septa, 3–10  $\mu$ m wide. Inflated elements not observed. **Pileipellis** a cutis, hyphae cylindrical or narrowed at septa with fusiform elements. In water, hyphae from the disc 3–10  $\mu$ m wide, hyaline, or with abundant purplish pink diffuse pigment or in some elements with purple granular pigment, with abundant terminal elements cylindrical or progressively attenuated with rounded apex; hyphae outside of the disc of 3–8  $\mu$ m wide, similar to those of the disc but with more elongated and cylindrical elements, and with more hyaline elements. **Clamp connections** not observed.



**FIGURE 12.** Macroscopic characters of *A. porphyropos*. A–B. Basidiomata. A. (JBSD126493); B. (JBSD126494, holotype). Microscopic characters of *A. porphyropos* C–K. (JBSD126494, holotype) (C–I, K in ammoniacal Congo red; J in water). C–E. Cheilocystidia. F–G. Basidia. H. Spores. I. Hyphae of the lower surface of the annulus. J–K. Pileipellis hyphae (K. internal granular pigment marked with an arrow). Photos by C. Angelini (A–B) and L.A. Parra (C–K).

**Macrochemical reactions:** Schäffer's reaction positive, reddish brown, difficult to read in the Dominican material. KOH reaction positive, color orange yellow.

**Habit, habitat, occurrence and distribution:** Solitary or in small groups of 2–5 basidiomata, in all types of broadleaf forests. Common. Recorded from the Dominican Republic and the United States Virgin Islands.

**Species-specific ITS markers in *A. subg. Minoriopsis*:** tatttCatcag@141, gctccTgagtc@232, atacaCtacac@249, gggctTtctat@288, agctcTCctgaa@556–557, with a T insertion at position 288.

**Note:** The original description is based on the Dominican collections although two additional collections were made in the United States Virgin Islands. All of these collections share similar macro- and microscopic characters, but the ones from the United States Virgin Islands differ in their greater spore length ( $4.8\text{--}6.4 \times 3.2\text{--}4.0 \mu\text{m}$  in STJ-392 y  $4.8\text{--}5.6 \times 3.2\text{--}4 \mu\text{m}$  in STJ-314), although overlapping with the size of the Dominican collections, and in that their Schäffer's reaction is bright orange in dried material. The collections from the United States Virgin Islands will be fully described in a future work in preparation. This species is characterized by its small-medium size, growing in broadleaf forests, a strongly fibrillose pileus with the center strongly colored vinaceous purple and the whitish margin, the stipe is long and flexuose off-white becoming yellow on handling and the fragile annulus, undeveloped, sometimes incomplete and present only in fragments.

**Material examined:** DOMINICAN REPUBLIC, Puerto Plata, Sosúa, at the garden of Hotel Villa Mar, 31 December 2009, JBSD126493 (LAPAM5); Puerto Plata, Sosúa, beach, in a secondary broadleaf forest, 10 December 2013, JBSD126494 *Holotypus* (LAPAM34, *Isotypus*). UNITED STATES VIRGIN ISLANDS, Saint John. Bordeaux Mountain, near Spice Hill, 15 November 1996, collector T. J. Baroni, *TJB-8312*, *STJ-392* (NY); Saint John. Bordeaux Mountain,  $18^{\circ}20'8''\text{N}$ ,  $64^{\circ}43'15''\text{W}$ , 15 November 1996, collector S. A. Cantrell & B. Ortiz-Santana, *S. A. Cantrell SJ-9601*, *STJ-314* (NY).

**Taxonomic comments:** Very similar to other species with purple pileus such as *A. argenteopurpureus*, *A. lodgeae* or *A. martinicensis* as noted in their descriptions above.

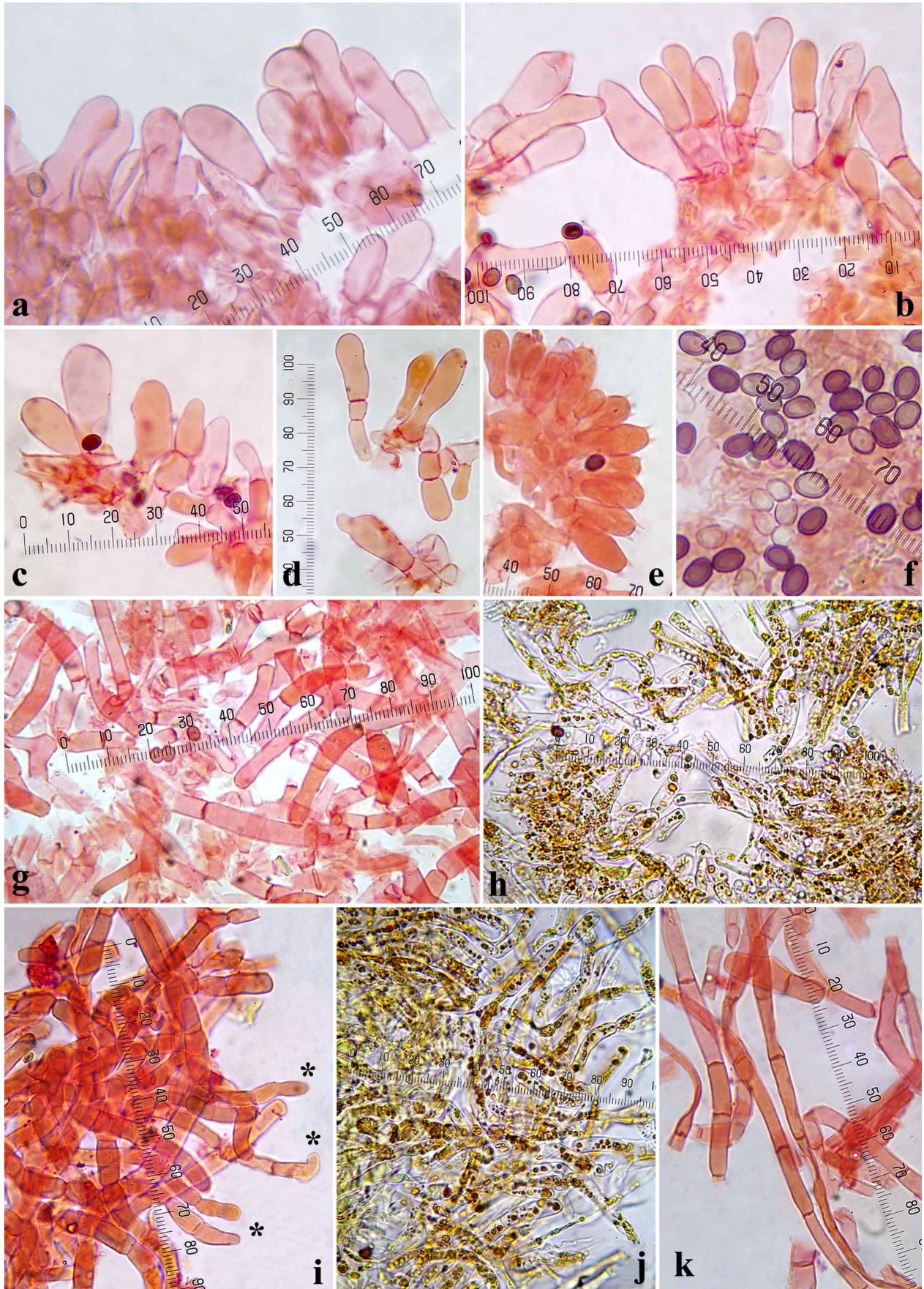
*Agaricus rufoaurantiacus* Heinem., Kew Bull. 15(2): 242, 1961. (Figs. 13–14)

**Macroscopic description:** Pileus (2.5–)3.0–4.0(–5.5) cm diam., at first hemispherical then plano-convex (rarely trapezoid), completely plane at maturity, entirely covered by minute warty ochre orange squamules on whitish background, with an entire orange or reddish orange center. Surface dull and dry. Margin not exceeding the lamellae, often appendiculate because of the annulus remnants, sometimes slightly striate at maturity. **Lamellae** free, slightly ventricose, intercalated with numerous lamellulae, white for a long time, staining intensely pink after handled (resembling at first glance a species of *Leucoagaricus*), then brown, blackish brown at maturity with a paler and even edge. **Stipe** (4.0–)5.0–5.5(–6.0)  $\times$  0.4–0.6 cm (up to 1 cm at base), cylindrical, usually tapered at apex and bulbous towards base, fistulose, with an annulus in its upper third, above annulus with white fibrils becoming grayish with age, below annulus fibrillose, covered by large orange or ochre orange scales especially at the base, sometimes forming bands, in rare cases entirely covering the stipe and the lower surface of the annulus, strongly yellowing on handling, with a single and thick central rhizomorph at the base. **Annulus** superous, double, white, up to 0.7 cm broad, usually thick and persistent, upper surface strongly striate, lower surface covered by thick ochre or orange scales often forming a cogwheel at the margin. **Context** moderately dense in the center of the pileus, scanty at the margin, when cut at first white then yellowing, with odor of bitter almonds.

**Microscopic description:** Spores (4.12–)4.22–4.85–5.36  $\times$  3.10–3.46–3.90(–4)  $\mu\text{m}$ ,  $Q=1.26\text{--}1.41\text{--}1.65$ , ellipsoid, smooth, brown, without apical pore. **Basidia** 13–18(–23)  $\times$  6–8  $\mu\text{m}$ , tetrasporic, clavate or slightly truncated at the apex, sterigmata up to 3  $\mu\text{m}$  long. **Cheilocystidia** highly variable in quantity and shape in different collections. In some collections abundant and very conspicuous, in others only a few in small fascicles and in others very rare and difficult to distinguish from basidioles, usually hyaline but also sometimes with a brown diffuse internal pigment, simple or septate at the base, with terminal elements pyriform, clavate, cylindrical (usually with some constrictions), fusiform, fusiform-subcapitulate or capitulate, rostrate, mucronate or more rarely with lateral digitiform appendages, 9–24  $\times$  4–11  $\mu\text{m}$ ; anteterminal elements in the septate ones more or less cylindrical of 5–13  $\times$  4.5–6.5  $\mu\text{m}$ . **Pleurocystidia** not observed. **Lower surface of the annulus** consisting of two types of hyphae, some cylindrical with a constant diameter composed of long elements of 2–6  $\mu\text{m}$  wide, rare, and others clearly narrowed at septa with short elements of 2–7  $\mu\text{m}$  wide. Terminal elements cylindrical or progressively attenuated towards the rounded apex. Inflated elements not observed. **Pileipellis** a cutis, with transition to trichoderm in the squamulose disc. In the disc predominate hyphae narrower at septa with short elements of 2–7  $\mu\text{m}$  wide, terminal elements abundant, cylindrical or progressively attenuated towards the rounded apex, and outside of the disc predominate cylindrical hyphae with constant diameter composed of long elements 2–6  $\mu\text{m}$  wide. In water, all hyphae contain abundant granular pigment (more in the disc), with golden yellow granules up to 3  $\mu\text{m}$  wide. **Clamp connections** not observed.



**FIGURE 13.** Macroscopic characters of *A. rufoaurantiacus*. **A–H.** Basidiomata. **A.** (JBSD123818); **B.** (JBSD126473); **C, H.** (JBSD126476); **D.** (JBSD126477); **E.** (JBSD126478); **F.** (JBSD126475); **G.** (JBSD126474). Photos by C. Angelini.



**FIGURE 14.** Microscopic characters of *A. rufoaurantiacus*. **A–K.** (A–G, I, K in ammoniacal Congo red; H, J in water). **A.** (JBSD126472), **B–D.** (JBSD126473) **E.** (JBSD123818), **F.** (JBSD126471), **G.** (JBSD126475), **H–K.** (JBSD126474). **A–D.** Cheilocystidia. **E.** Basidia. **F.** Spores. **G.** Hyphae of the lower surface of the annulus. **H–K.** Pileipellis hyphae (**H–I** discal area, **J–K** medial area). Photos by L.A. Parra.

**Macrochemical reactions:** Schäffer's reaction positive, slow but intense, dark reddish purple. KOH reaction difficult to read because of the orange yellow color of the *exsiccatum*.

**Habit, habitat, occurrence and distribution:** Solitary or in small groups of 2–3 basidiomata, in all types of broadleaf forests. According to our data, this is the most common *Agaricus* species in the Dominican Republic. The holotype (Dennis 241) and a paratype (Dennis 328) of this species were collected by R. W. G. Dennis in the Caribbean island of Trinidad (Heinemann 1961). Pegler (1983) also reports it from Martinique.

**Note:** This species is characterized by its small to medium size, the pileus covered with minute orange ochre appressed squamules with the disc intensely colored, the lamellae that remain white for a long time and stain rose on handling (resembling a species of *Leucoagaricus* at this stage), the stipe and lower surface of the annulus covered by thick scales colored orange ochre, sometimes forming basal bands, the double annulus, the odor of bitter almonds and the evident long basal rhizomorph.

**Material examined: DOMINICAN REPUBLIC, Puerto Plata, Sosúa, beach, 27 November 2011, JBSD123818 (LAPAM15); Puerto Plata, Sosúa, beach, 21 November 2013, JBSD126470 (LAPAM29); Puerto Plata, Sosúa, beach, 22 November 2013, JBSD126471 (LAPAM30); Puerto Plata, Sosúa, beach, 25 November 2013, JBSD126472 (LAPAM31); Puerto Plata, Sosúa, beach, 10 December 2013, JBSD126473 (LAPAM32); Puerto Plata, Sosúa, beach, 19 December 2013, JBSD126474 (LAPAM33); Puerto Plata, Sosúa, beach, 27 November 2014, JBSD126475 (LAPAM54); Puerto Plata, Sosúa, cemetery, 3 December 2013, JBSD126476 (LAPAM36); Puerto Plata, Sosúa, cemetery, 14 December 2014, JBSD126477 (LAPAM51); Sosúa, Puerto Chiquito, 5 December 2014, JBSD126478 (LAPAM59);**

**Taxonomic comments:** The closest known species to *A. rufoaurantiacus* is undoubtedly *A. ochraceosquamulosus* Heinem. (1961: 243), described from a single collection, made on the island of Trinidad, that consists of only two basidiomata growing together. From the study of the original descriptions and illustrations of both species by Heinemann (1961), *A. ochraceosquamulosus* is distinguished from *A. rufoaurantiacus* by its less vivid colors on both the surfaces and context, the narrow and fragile annulus, the larger spores ( $5.1\text{--}5.7 \times 3.6\text{--}4.0 \mu\text{m}$ ) and the positive Schäffer's reaction. Based on the study of our collections, however, we found that the color of the basidiomata of *A. rufoaurantiacus* is variable depending on its age or if it is wet from rainwater. Similarly, the annulus in *A. rufoaurantiacus* seems simple and fragile on the stipe if broken at its middle part leaving appendiculate remnants with the scales of its lower surface in the pileus margin. Regarding the Schäffer's reaction, our collections of *A. rufoaurantiacus* show a dark purple red reaction matching well with what Pegler (1983) observed for this species. Heinemann (1961) in his original description indicated a negative Schäffer's reaction but later (Heinemann, 1962a), noted that this species may also have positive reaction. Thus, the spore sizes are the only remarkable difference between the two species since both the measurements obtained by Heinemann ( $4.0\text{--}5.0 \times 2.9\text{--}3.8 \mu\text{m}$ ) and us after the study of the 10 Dominican collections ( $4.12\text{--}4.83\text{--}5.36 \times 3.10\text{--}3.42\text{--}4 \mu\text{m}$ ) are significantly smaller than those of *A. ochraceosquamulosus*, although there is a small range of overlap, especially in collection LAPAM36 that has larger spores ( $4.94\text{--}5.11\text{--}5.25 \times 3.30\text{--}3.58\text{--}3.91 \mu\text{m}$ ). Therefore, although we think that there is a possibility that these species are synonymous, we prefer to keep them as separate species because of their different spore size until more collections of *A. ochraceosquamulosus* can be found and studied or the type specimen sequenced.

*Agaricus ficophilus* Heinem. (1961: 241) is, according to this author, another very similar species, but this taxon has the pileus and stipe below annulus covered by scales with brown tones never observed in *A. rufoaurantiacus*, neither in the collections described by Heinemann (1961) nor in our collections. Additionally, the spores of *A. ficophilus* are clearly longer ( $5.0\text{--}6.0[6.5] \times 3.2\text{--}4.2 \mu\text{m}$ ) than in *A. rufoaurantiacus*.

Pegler (1983) also explicitly indicated that *A. rufoaurantiacus*, *A. ochraceosquamulosus* and *A. ficophilus* "are closely related species with variable characters". In our opinion, their possible synonymy can be definitively confirmed only by molecular methods.

**Additional comments:** Some phylogenetic comments on this species are included under *Agaricus* sp. LAPAM 48 from hybrid origin.

#### ***Agaricus* sp. LAPAM 48 from hybrid origin. (Fig. 15)**

**Macroscopic description:** This collection consists of a single immature carpophore with white lamellae completely matching with the collections studied of *A. rufoaurantiacus*.



**FIGURE 15.** Macroscopic characters of *Agaricus* sp. LAPAM 48 from hybrid origin. **A–B.** Basidiomata (JBSD126479). **B.** Schaeffer's reaction on dried material. Above: pileus surface, below: stipe base. Microscopic characters of *Agaricus* sp. LAPAM 48 from hybrid origin. **C–J.** (C–H, J in ammoniacal Congo red; I in water). (JBSD126479). **C–D.** Cheilocystidia. **E–F.** Basidia. **G.** Spores. **H.** Hyphae of the lower surface of the annulus. **I–J.** Pileipellis hyphae. Photos by C. Angelini (A) and L.A. Parra (B–J).

**Microscopic description:** Spores 4.53–4.78–4.94(–5.15) × 3.10–3.44–3.71 μm, Q=1.29–1.42–1.5, ellipsoid, smooth, brown, without apical pore. **Basidia** 16–23 × 6–9 μm, tetrasporic, clavate or slightly truncated at the apex, sterigmata up to 3 μm long. **Cheilocystidia** hyaline, usually simple, sometimes septate at the base, with terminal elements mostly pyriform, less frequently clavate, 8–22 × 7–12 μm; anteterminal elements in the septate ones globose to cylindrical of 5–9 × 5–7 μm. **Pleurocystidia** not observed. **Lower surface of the annulus** composed of hyaline hyphae, cylindrical, not or slightly narrowed at septa, 3–7 μm wide. Inflated elements not observed. **Pileipellis** a cutis, with transition to trichoderm in the squamulose disc. In the disc predominate cylindrical hyphae narrower at septa with short elements of 3–8 μm wide, some very scattered vesiculose elements up to 19 μm wide and terminal elements abundant, cylindrical or progressively attenuated towards the rounded apex, and outside of the disc predominate cylindrical hyphae with constant diameter composed of long elements 2–7 μm wide. In water, all hyphae contain abundant granular pigment (more in the disc), with golden yellow granules of up to 3 μm wide. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer's reaction positive, slow but intense, dark reddish purple red. KOH reaction difficult to read because of the orange yellow color of the *exsiccatum*.

**Material examined:** DOMINICAN REPUBLIC, Distrito Nacional, Santo Domingo de Guzmán, Jardín Botánico de Santo Domingo, 25 November 2014, JBSD126479 (LAPAM48).

**Taxonomic comments:** This collection is morphologically indistinguishable from the Dominican collections of *A. rufoaurantiacus* studied in this work.

**Additional comments:** LAPAM 48 is a wild sample closely related to *A. sp.* RMC-1256, *A. sp.* RMC-1257 and *A. rufoaurantiacus*. The ITS sequences of the samples of these entities are compared at 12 variable positions in Table 7. In an alignment of DNA sequences, we consider that two samples strictly differ at one position when they do not share any character (indel or nucleotide) at the homologous positions, and that samples of *Agaricus* which differ at more than two positions generally belong to different species (Zhao *et al.* 20011) with few notable exceptions such as *A. subrufescens* (Chen *et al.* 2016a). The samples RMC-1256 and RMC-1257 differ at four positions and thus may belong to two closely related sister species. Two of the four positions, 517 and 520, are shown in Table 7 while at the two remaining positions, which are not shown, RMC-1257 differs from all the other samples compared in the Table. Moreover, this pair of samples differs from all ten collections of *A. rufoaurantiacus* at 11 of the 13 positions indicated in Table 7. This strongly indicates that *A. rufoaurantiacus* is a distinct species. LAPAM 48 is heteromorphic at 11 of these 13 positions where it exhibits two nucleotides: one also found in *A. rufoaurantiacus* and the other one found in the couple of samples RMC-1256 and RMC-1257. In fact, LAPAM 48 has a total of 15 heteromorphisms but four are at positions that are not shown in Table 7 because all the other samples are identical at these positions. Although the ten samples of *A. rufoaurantiacus* does not exhibit any heteromorphisms at 12 of the 13 positions of the Table 7, there is an intraspecific variability at positions that are not reported in this table because they are phylogenetically uninformative. Indeed, the ten samples of *A. rufoaurantiacus* possess on average 3.5 heteromorphisms at various positions where LAPAM 48, RMC-1256 and RMC-1257 have identical nucleotides. When we compared the whole sequences in detail, we noted that the ITS sequence of LAPAM 48 strictly differs (i.e. without shared allele) from the samples LAPAM 30 of *A. rufoaurantiacus* and RMC-1256 (*A. sp.*) at zero and one position (193), respectively. In contrast, RMC-1256 and LAPAM 30 differ from each other at 11 positions (all indicated in Table 7). These comparisons strongly suggest that an event of hybridization between *A. rufoaurantiacus* and a distinct species such as the species to which RMC-1256 belongs may have generated an unexpected combination of ITS sequences in LAPAM 48 or in one of its ancestors.

**TABLE 7.** Comparison between LAPAM48 and its closest related species at 13 polymorphic positions of the ITS sequence.

Sample	Positions												
	16	33	38	39	60	112	121	141	193	199	517	520	660
RMC-1256	A	T	C	G	A	A	G	T	T	C	A	C	T
RMC-1257	A	T	C	G	A	A	G	T	T	C	G	T	T
LAPAM48	<b>R</b>	<b>Y</b>	<b>S</b>	<b>R</b>	<b>R</b>	<b>R</b>	<b>R</b>	<b>Y</b>	C	<b>Y</b>	<b>R</b>	C	<b>Y</b>
<i>A. rufo.</i> <sup>a</sup>	G	C	G	A	G	G	A	C	C	T	A	C or Y	C

<sup>a</sup>Ten samples of *A. rufoaurantiacus* have the same nucleotides at 12 of the 13 positions. Heteromorphisms in bold types: Y = C and T; R = A and G; S = C and G.

*Agaricus* subg. *Pseudochitonina* Konrad & Maubl., Icon. Select. Fung. 6, fasc. 3: 61. 1927.

*Agaricus* sect. *Xanthodermatei* Singer, Sydowia 2: 36. 1948.

*Agaricus candussoi* L.A. Parra, Angelini & Callac, *sp. nov.* (Figs. 16–17)

**MycoBank:** MB823282.

**Etymology:** The specific epithet “*candussoi*” honors our good friend and excellent mycologist, Massimo Candusso, for his contribution to Mycology.

**Original description, Macroscopic description:** **Pileus** 5–7 cm diam., hemispherical, then conical-trapezoid for a long time, later plano-convex slightly depressed at center, white with an entire grayish brown center, covered to margin with minute punctate scales, scarce, concentric, grayish at the peridiscal area and whitish to margin. Surface smooth or slightly squamulose, dry and dull. Margin thin, fimbriate, not or slightly exceeding the lamellae. **Lamellae** free, crowded, narrow, straight, intercalated with numerous lamellulae, at first pinkish cream, then bright pink, finally grayish pink brown with the edge paler and slightly eroded. **Stipe** 6–8(–9) × 0.5–0.8 cm, cylindrical with slightly bulbous base, long, thin, straight or curved, sometimes flexuose, stuffed, with an annulus in its upper third, above and below annulus smooth, slightly sericeous towards the base, white, unchangeable on handling, often with a basal rhizomorph. **Annulus** superous, double, white, up to 1.5 cm broad, thin at the insertion but thicker at the margin, upper surface slightly striate, lower surface with thick and arched scales that detach easily. Sometimes the thicker part of the margin is divided into two membranes, the upper one is fibrillose in its upperside and cottony in the lowerside, and the inferior membrane with smooth margin that forms a bracelet adpressed to the stipe. **Context** white when cut, unchanging or slightly yellowing at the basal part of the stipe in contact with the mycelium, with a strong odor of phenol.

**Microscopic description:** **Spores** 4.12–4.63–5.17 × 2.80–3.07–3.40 μm, Q=1.37–1.51–1.72, ellipsoid, smooth, brown, without apical pore. **Basidia** 15–20 × 5–8 μm, tetrasporic, clavate or slightly truncated at the apex, sterigmata up to 3 μm long. **Cheilocystidia** abundant, hyaline, simple, rarely with a basal septum, clavate, pyriform, ovoid or globose, rarely fusiform, 11–27 × 7.5–19 μm. **Pleurocystidia** not observed. **Lower surface of the annulus** hyphae 3–11 μm wide, hyaline, cylindrical, the wider the more constricted at septa. Inflated elements not observed. **Pileipellis** a cutis, hyphae 2–5 μm wide, not or slightly narrowed at septa, terminal elements very abundant cylindrical, rounded at apex, with yellow or pale brown internal granular pigment in water. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer’s reaction negative. KOH reaction positive, yellow with orange spots.

**Habit, habitat, occurrence and distribution:** Gregarious, sometimes in groups of many basidiomata, in moist lowland broadleaf forests. Rare. Recorded only from the Dominican Republic.

**Species-specific ITS markers in *A. sect. Xanthodermatei*:** aatctAtctcc@199, gttatCattatactcCtataa@223–234, with C insertion at position 234.

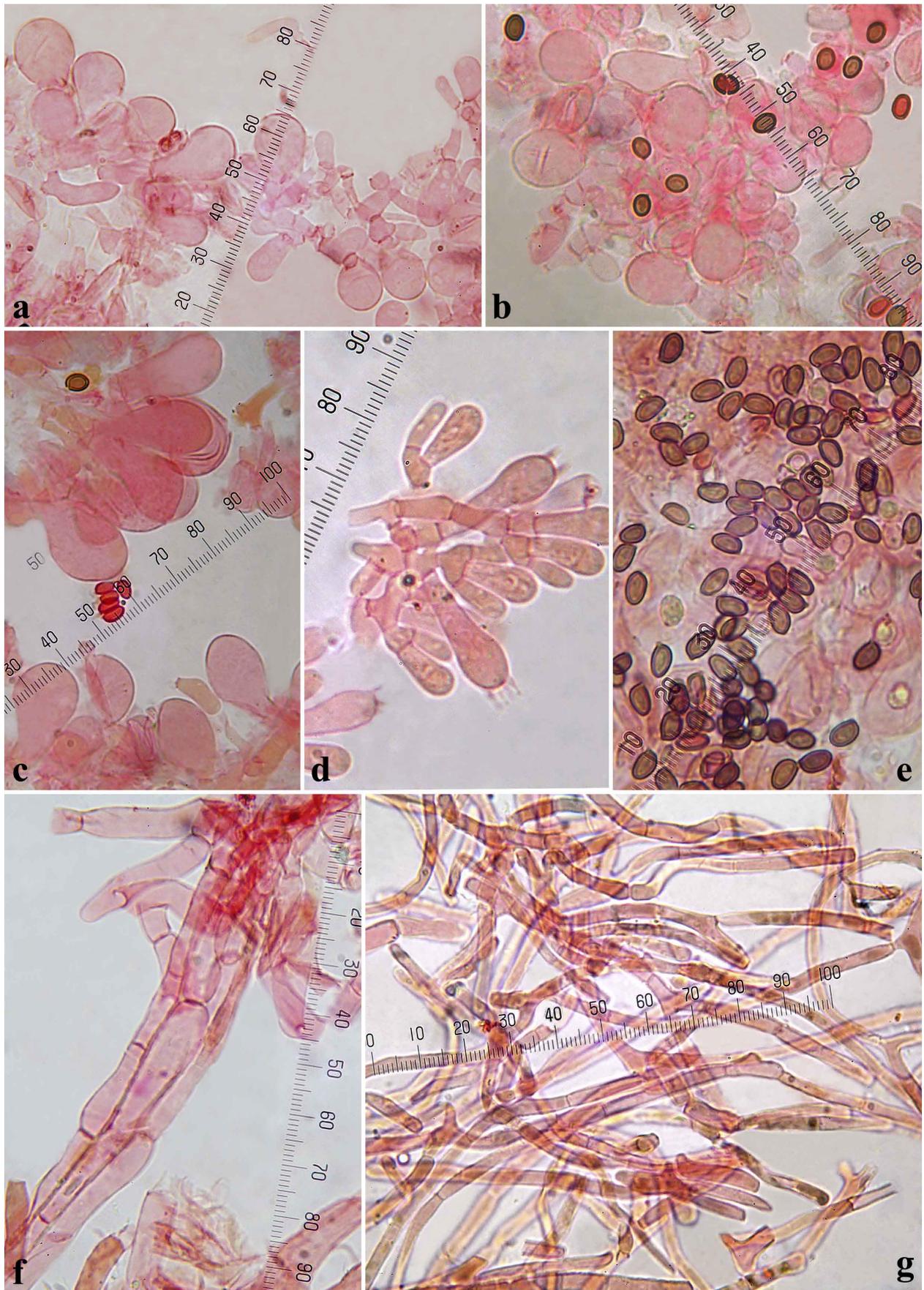
**Note:** This species is characterized by its medium to large size, white pileus with an entire grayish brown center, typical complex annulus, the absence of yellowing on handling or if present is almost imperceptible, and the strong odor of phenol.

**Material examined:** **DOMINICAN REPUBLIC, Puerto Plata**, Sosúa, Puerto Chiquito, 28 November 2014, JBSD126490 (LAPAM57); **Puerto Plata**, Sosúa, Puerto Chiquito, 3 December 2014, JBSD126491 (LAPAM58); **Puerto Plata**, Sosúa, Puerto Chiquito, 13 December 2014, JBSD126492 *Holotypus* (LAPAM62 *Isotypus*).

**Taxonomic comments:** The macroscopic description of collections of *A. cretacellus* Atkinson (1902: 110) *sensu* Pegler (Pegler 1983) from Martinique corresponds well with *A. candussoi*. However, *A. cretacellus sensu* Pegler has larger spores (5–5.5–6.5 × 2.7–3.2–3.5[–4] μm) and lacks cheilocystidia. According to the original description of *A. cretacellus* (Atkinson 1902), this species has “odor and taste of almonds” and the lower surface of the annulus is covered by “very fine floccose scales similar to those of the stem” and therefore it most likely belongs to *A. sect. Arvenses*, whereas *A. cretacellus sensu* Pegler was described as having an “odor of iodine, disagreeable” and “glabrous” stipe, typical characteristics of *A. sect. Xanthodermatei*.



**FIGURE 16.** Macroscopic characters of *A. candussoi*. A–I. Basidiomata. A–B, G. (JBSD126490); C–D, H. (JBSD126491); E–F. I. (JBSD126492, holotype). Photos by C. Angelini.



**FIGURE 17.** Microscopic characters of *A. candussoi*. A–G. In ammoniacal Congo red. A–C. (JBSD126491), D. (JBSD126490), E–G. (JBSD126492, holotype). A–C. Cheilocystidia. D. Basidia. E. Spores. F. Hyphae of the lower surface of the annulus. G. Pileipellis hyphae. Photos by L.A. Parra.

**Macroscopic description:** **Pileus** 2–3 cm diam., hemispherical, soon plano-convex, sometimes slightly depressed at center or umbonate, densely covered by gray appressed squamules on a whitish background with an entire almost black center. Surface dull and dry. Margin white, thick, with cottony remnants from the partial veil in young basidiomata, slightly exceeding the lamellae and fimbriate, sometimes cracked. Developing a slightly pinkish tint on handling. **Lamellae** free, moderately crowded, straight, intercalated with numerous lamellulae, at first off-white, then pink, finally dark brown with the edge paler and eroded. **Stipe** 3–5(–8) × 0.3–0.4 cm, cylindrical, curved at base, with an annulus in its upper third, above annulus smooth, at first white, then light pink and finally pale gray, below annulus white, smooth, sometimes at base (where is covered by plant remains) fibrillose-lanose. Not or slightly yellowing when handled. **Annulus** superous, double, white, up to 0.2 cm broad, persistent, thick and adpressed to stipe, with the upper surface and the margin of the lower surface cottony, the surface closer to the stipe smooth, forming a white to slightly grayish bracelet adpressed to the stipe. **Context** when cut white or slightly yellowing at the base, with fungoid odor.

**Microscopic description:** **Spores** (4–)4.33–4.82–5.25(–5.67) × 2.8–3.2–3.6 μm, Q=1.32–1.52–1.72, ellipsoid, smooth, brown, without apical pore. **Basidia** 10–18.5 × 6.5–8.5 μm, tetrasporic, clavate or slightly truncated at the apex, sterigmata up to 3 μm long. **Cheilocystidia** absent in JBSD123820, rare and difficult to observe, isolated or in small fascicles of 3 to 7 cheilocystidia in JBSD126485, hyaline, simple, rarely with a basal septum, cylindrical, clavate, fusiform or enlarged at apex with lateral excrescences, 15–30 × 5–9(–12) μm. **Pleurocystidia** not observed. **Lower surface of annulus** composed of cylindrical hyphae, not or slightly narrowed at the septa, 2–4 μm wide. Inflated elements not observed. **Pileipellis** a cutis, with transition to a trichoderm at the squamulose disc. At the disc composed of hyphae with versiform basal elements, more or less polyhedral from which two types of dark brown, almost black elements arise, some cylindrical and thin, slightly narrowed at septa with rounded apex of 3–6 μm wide, and others doliiform, narrower at septa of 6–11 μm wide, the pigment is diffuse or in vacuoles, and terminal elements are obpyriform. The rest of the pileus is composed of hyphae of two types, some consisting of thin, cylindrical elements, slightly narrowed at septa with diffuse pigment and rarely with small vacuoles similar to these of the disc, and others thicker, hyaline, the wider the more constricted at septa, of 5–10 μm wide. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer's reaction negative. KOH reaction positive, color yellow.

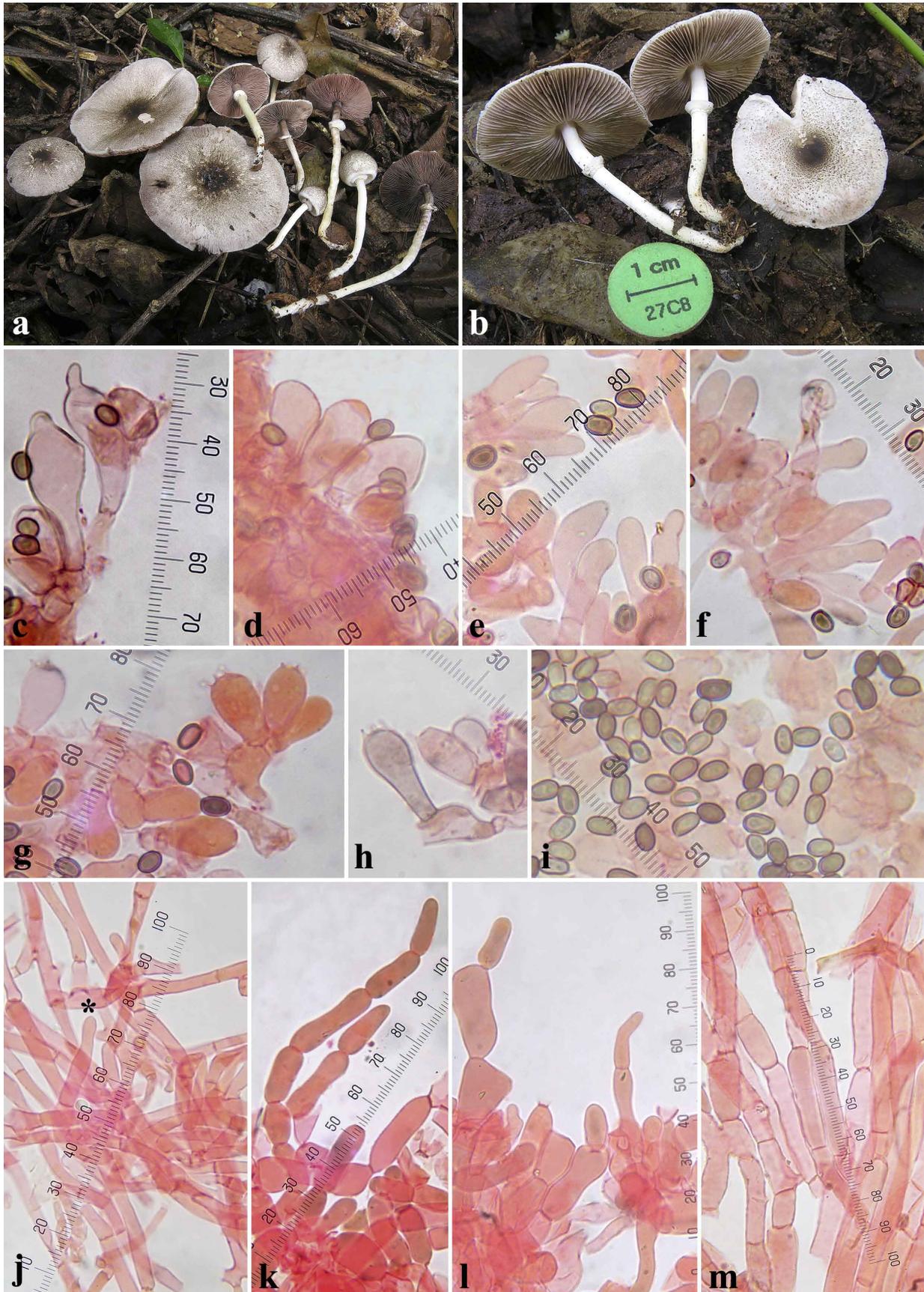
**Habit, habitat, occurrence and distribution:** Gregarious, in lowland broadleaf forests. Rare. Recorded only from the Dominican Republic and Martinique. Pegler (1983) designated the holotype (Fiard 442B) from a collection collected by J.-P. Fiard in Martinique.

**Note:** This species is characterized by its small size, the pileus covered by grayish appressed squamules with the center darker almost black, the stipe typically long and thin, the double annulus, somewhat ample, thick, adpressed to stipe, cottony on the lower surface forming a narrow bracelet smooth and adpressed to stipe, by the fungoid odor and context and surfaces not or very weakly yellowing on handling.

**Material examined:** **DOMINICAN REPUBLIC, Puerto Plata, Sosúa, Puerto Chiquito, 20 November 2011, JBSD123820 (LAPAM19); Puerto Plata, Sosúa, Puerto Chiquito, 29 November 2013, JBSD126485 (LAPAM41).**

**Taxonomic comments:** Our determination of collections JBSD123820 and JBSD126485 as *A. caribaeus* is based on the fact that their ITS1+2 sequences are identical to those of a collection (F2530), deposited in GenBank (JF727856), made by J.-P. Fiard (collector of the holotype) on the island of Martinique in the “bois de la Pointe Rouge”, where the holotype was also collected.

Although the collections of *A. caribaeus* from the Dominican Republic studied here agree very well with the original description, figures and photograph of Pegler (1983), there are several divergent characters discussed below. Pegler (1983) indicated that the margin of the pileus is “slightly plicate to sulcate” and the “Schäffer's reaction positive” whereas our two collections had a smooth margin that exceeded the lamellae and was fimbriate, and the Schäffer's reaction was clearly negative. Since Pegler (1983) indicated that the margin of the pileus lacked scales, it is very possible that the only specimen (holotype) on which his description is based was collected after heavy rain, which could explain the plicate or sulcate margin lacking scales, due to the scanty context in the pileus of this species. As for the positive Schäffer's reaction it could be due to a misreading of the test, which is not uncommon in the species of *A. sect. Xanthodermatei*, since the aniline alone usually colors the pileus of the species of *A. sect. Xanthodermatei* orange. We must also take into account that the phylogenetic analyses show that *A. caribaeus* belongs to *A. sect. Xanthodermatei* within which no species with positive Schäffer's reactions are currently known.



**FIGURE 18.** Macroscopic characters of *A. caribaeus*. **A–B.** Basidiomata. **A.** (JBSD123820); **B.** (JBSD126485). Microscopic characters of *A. caribaeus*. **C–M.** In ammoniacal Congo red. **C–D, G–H.** (JBSD123820); **E–F, I–M.** (JBSD126485). **C–F.** Cheilocystidia. **G–H.** Basidia. **I.** Spores. **J.** Hyphae of the lower surface of the annulus (a terminal hypha is marked with an asterisk). **K–M.** Pileipellis hyphae (**K–L.** pigmented terminal elements at disc). Photos by C. Angelini (**A–C**) and L.A. Parra (**D–M**).

Microscopically, spores of the Dominican collections are somewhat longer ( $[4.00-]4.33-4.82-5.25[-5.67] \times 2.8-3.2-3.6 \mu\text{m}$ ) than those indicated by Pegler for the holotype ( $5.0-5.5-6.0 \times 2.5-3.2-3.5 \mu\text{m}$ ) although values overlap to some degree, so, given the low number of collections that we have of this taxon, they could perfectly be within its intraspecific variability.

The most divergent characters between the holotype described by Pegler (1983) and the Dominican collections are the shape and abundance of cheilocystidia since this author describes the “lamellae edge sterile, with crowded cheilocystidia” which are “pyriform”, and the Dominican collections either lack cheilocystidia (JBSD123820) or these are very few and isolated in small groups and versiform (JBSD126485) but not pyriform. However, in Fiard’s personal notes of F2530, he included a microscopic drawing showing that cheilocystidia are broadly clavate to pyriform, and he indicated that they were rare. In other species of *Agaricus* we have already observed this type of versiform cheilocystidia in some collections, while others had sphaeropedunculate cheilocystidia or lacked them as in *A. pseudolutosus*. In *A. sect. Xanthodermatei*, *A. laskibarii* also has collections with versiform cystidia very similar to those observed in the Dominican collections of *A. caribaeus* and other collections with clavate or pyriform cheilocystidia (Parra 2013).

For all the above, and despite the divergent elements between the original description, on a single collection by Pegler (1983) and the two Dominican collections, we consider our collections within the *Agaricus caribaeus* concept.

*Agaricus endoxanthus* Berk. & Broome, J. Linn. Soc., Bot. 11: 548. 1871. (Fig. 19)

= *Agaricus rotalis* K.R. Peterson, Desjardin & Hemmes, Sydowia 52(2): 244. 2000.

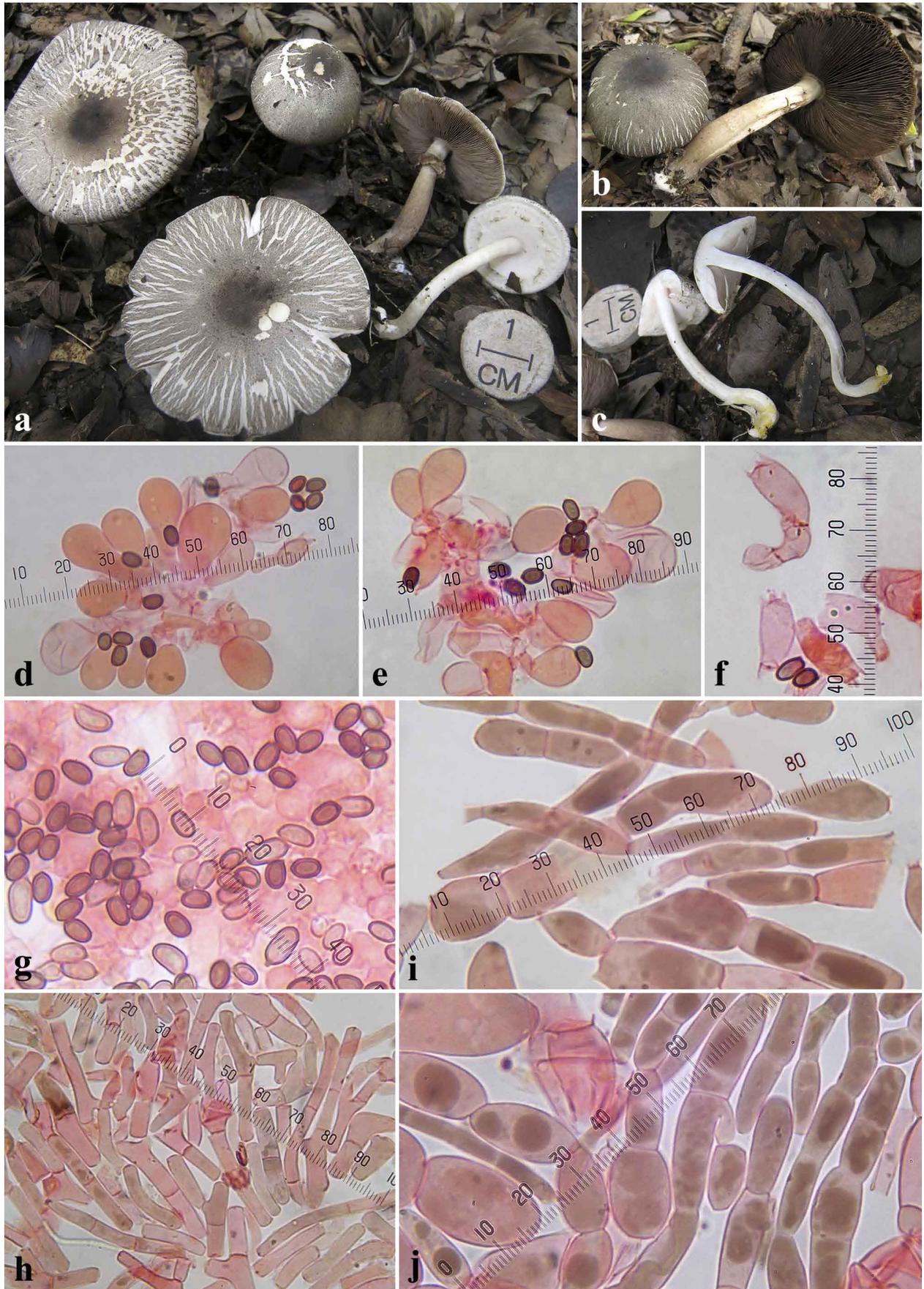
**Macroscopic description:** **Pileus** (2–)3.5–4 cm diam., hemispherical then plane, at first uniformly covered by gray appressed fibrils with an entire blackish brown center, then tending to crack radially and concentrically forming small quadrangular scales over the white background of context. Surface smooth or fissurate, dull and dry. Margin thin, slightly exceeding the lamellae. **Lamellae** free, crowded, slightly ventricose, intercalated with numerous lamellulae, at first whitish rose, then dark brown, finally dark brown with the edge concolorous and slightly eroded. **Stipe** 3–6  $\times$  0.3–0.5 cm, cylindrical, curved at base, sometimes sinuate, fistulose, with an annulus in the upper third, above annulus white and smooth, below annulus white, grayish towards the base, at maturity completely grayish brown, except the base in contact with the substrate, which is covered with white cottony mycelium, smooth or slightly fibrillose towards the base. **Annulus** superous, double, white, up to 1.2 cm broad, with thick margin and thin at insertion, upper surface white and smooth, lower surface white with squamules arched dispersed in the perimarginal area, concolorous with pileus. **Context** somewhat dense, when cut at first white, then chrome yellow at the stipe base, with a strong odor of phenol.

**Microscopic description:** **Spores**  $4.34-4.77-5.17 \times 2.90-3.05-3.10(-3.31) \mu\text{m}$ ,  $Q=1.40-1.57-1.72$ , ellipsoid, smooth, brown, without apical pore. Alongside these mature dark brown spores there are also abundant hyaline spores among which are frequently giant spores of  $6.00-6.33-7.11 \times 3.1-3.4-3.6 \mu\text{m}$ ,  $Q=1.71-1.87-2.00$ , ellipsoid-elongated sometimes with a constriction in the middle. **Basidia**  $13-15 \times 5.5-6.5 \mu\text{m}$ , tetrasporic, clavate or slightly truncate at the apex, sterigmata up to  $3 \mu\text{m}$  long. **Cheilocystidia** abundant, hyaline, generally simple, clavate, pyriform or spherical more or less sphaeropedunculate,  $9-15(-20) \times 6-13 \mu\text{m}$ . **Pleurocystidia** not observed. **Lower surface of the annulus** hyphae hyaline or with pale brown diffuse pigment, cylindrical or narrowed at the septa,  $3-6(-8) \mu\text{m}$  wide. Inflated elements not observed. **Pileipellis** a cutis with transition to a trichoderm, composed of hyphae with the internal elements hyaline and the external ones completely dark brown because of the presence of diffuse pigment, or hyaline with one or two large vacuoles of dark brown pigment. The hyphal elements can be cylindrical, slightly narrowed at the septa or  $4-9 \mu\text{m}$  wide, or very narrow at the septa, doliiform, globose-ovoid of  $8-20 \mu\text{m}$  wide. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer’s reaction negative. KOH reaction positive, color pale yellow.

**Habit, habitat, occurrence and distribution:** Gregarious in groups of few basidiomata, in lowland broadleaf forests. Very rare. Cosmopolitan. In the Caribbean region, this species has been recorded in the Dominican Republic and Puerto Rico (Parra 2013).

**Note:** This species is characterized by its small to medium size, the gray-tinted pileus with the always-darker center, blackish, soon cracking radially and/or concentrically, the stipe base grayish, the context at the stipe base turning chrome yellow, the odor of phenol and the outermost elements of the pileipellis doliiform, ovoid or globose containing large vacuoles of dark brown pigment.



**FIGURE 19.** Macroscopic characters of *A. endoxanthus*. **A–C.** Basidiomata (JBSD126486). Microscopic characters of *A. endoxanthus*. **D–J.** In ammoniacal Congo red. (JBSD126486). **D–E.** Cheilocystidia. **F.** Basidia. **G.** Spores. **H.** Hyphae of the lower surface of the annulus. **I–J.** Pileipellis hyphae. Photos by C. Angelini (A–C) and L.A. Parra (E–J).

**Material examined:** DOMINICAN REPUBLIC, Distrito Nacional, Santo Domingo de Guzmán, at the park in the Jardín Botánico de Santo Domingo, 24 November 2014, JBSD126486 (LAPAM47).

**Taxonomic comments:** Species originally described from Sri Lanka, with a wide distribution in tropical Africa, Asia, the Caribbean, Oceania and South America, as well as in greenhouses and indoor gardens with tropical vegetation in Europe and USA (Parra 2013; Chen *et al.* 2016b).

The presence of hyaline macrospores in this species seems to be frequent, having also been mentioned by Guzmán (1983) in collections from the Yucatan Peninsula (Mexico) and Parra (2013) from a French collection (LAPAG 597) made in an indoor tropical garden.

Its synonymy with *A. rotalis* proposed by Parra (2013), based on the study of the types of both species and numerous collections from around the world, has been confirmed by a recent study on inter- and intraspecific variability of *A. endoxanthus* and closely related species (Chen *et al.* 2016b). From a morphological point of view, the most similar species to *A. endoxanthus* are *A. moelleri* Wasser (1976: 77), *A. moelleroides* Guinb. & L.A. Parra (2013: 109), *A. punjabensis* T. Qasim, A. Ashraf & A.N. Khalid (Chen *et al.* 2016b: 8) and *A. volvatulus* Heinem. & Gooss.-Font. (1956: 61), but the first three lack the large vacuoles in the pileipellis elements and have not been found so far neither in tropical areas nor in indoor habitats with tropical vegetation (Chen *et al.* 2016b; Mahdizadeh *et al.* 2016; Parra 2013) and *A. volvatulus*, that also has large vacuoles in the pileipellis, lacks cheilocystidia and its stipe is white to the base, which is usually marginately bulbous (Heinemann 1956; Chen *et al.* 2016b).

**Additional comments:** A phylogenetic study of this species, including this collection, has been recently published by Chen *et al.* (2016b).

*Agaricus flavidodiscus* L.A. Parra, Angelini & Callac, *sp. nov.* (Fig. 20)

**MycoBank:** MB823283.

**Etymology:** because of the yellowing (in Latin “*flavidus*”) color at the center of the pileus (in Latin “*discus*”) in this species.

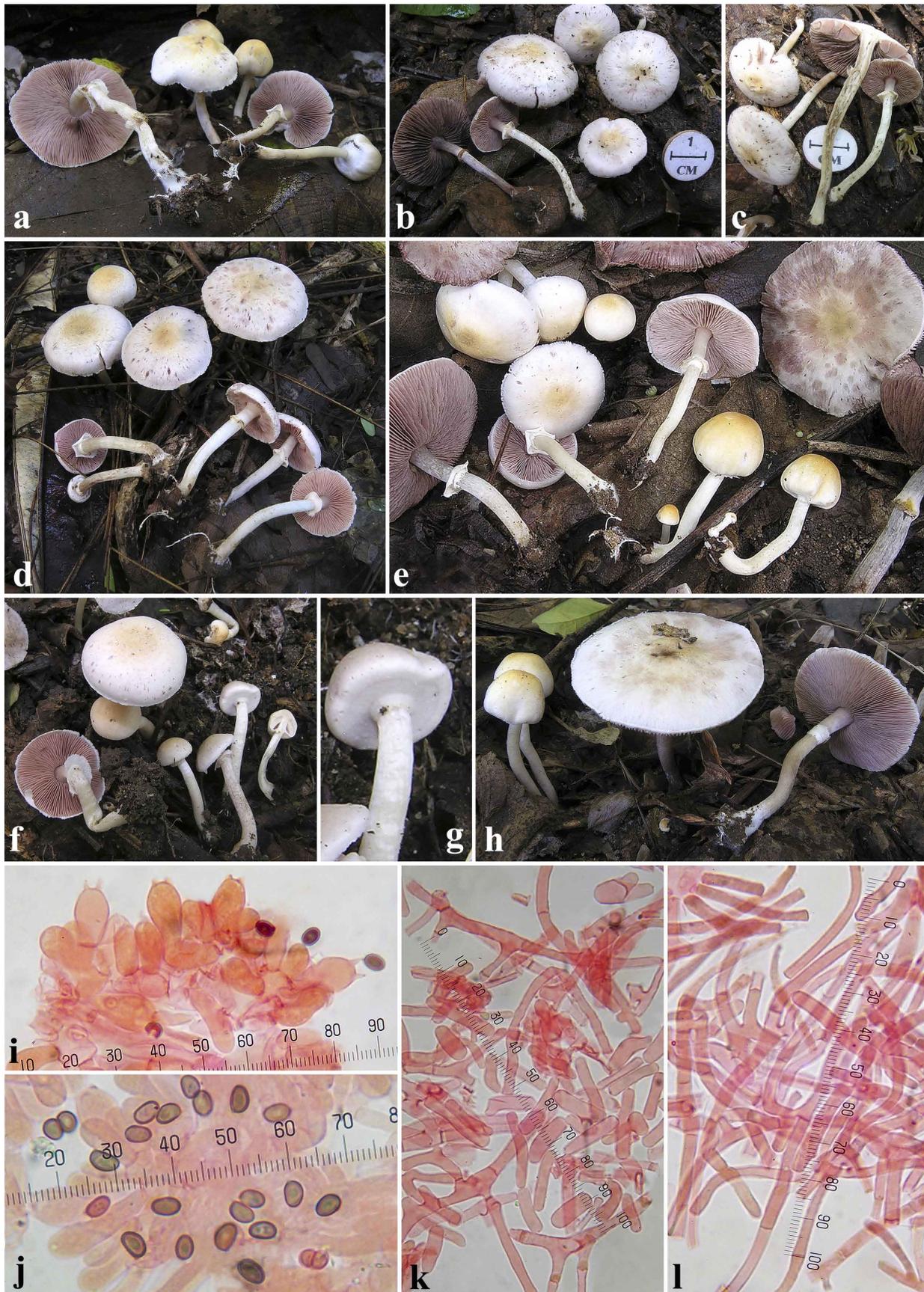
**Original description, Macroscopic description:** **Pileus** (1.5–)2.0–5.0 cm diam., at first hemispherical, sometimes trapezoid, then convex with the margin incurved for a long time, finally plano-convex, at the center rarely somewhat elevated or umbilicate-depressed, whitish with the center always typically colored yellow. In very mature basidiomata or those soaked by rain becomes completely pinkish brown, but always with a yellow center. Surface smooth, sericeous, not or slightly squamulose, sometimes and only in some basidiomata slightly fibrillose at the center, dull and dry. Margin thin, not exceeding the lamellae. **Lamellae** free, straight to slightly ventricose, intercalated with numerous lamellulae, at first pinkish white, then bright rose for a long time, finally pinkish brown with a paler and strongly eroded edge. **Stipe** 3–6 × 0.3–0.5 cm, cylindrical to slightly enlarged towards the base, curved and flexuose, stuffed, with an annulus in its upper third, sericeous above and below annulus, with the surface fibrillose-floccose, white, whitish cream or grayish in mature basidiomata, unchanging or slightly yellow on handling, base covered with a felty and white mycelial pad and with fine white mycelial strands. **Annulus** superous, double, white, thin but persistent, with the upper membrane perpendicular to stipe, up to 0.4 cm wide, and the lower membrane more narrow, appressed to the stipe. **Context** somewhat dense in pileus and stipe, when cut, white at first, then unchanging or slightly yellowing, odorless or odor slightly fungoid.

**Microscopic description:** **Spores** 4.33–4.82–5.17 × 3.10–3.30–3.51(–3.61) μm, Q=1.32–1.46–1.61, ellipsoid, smooth, brown, without apical pore. **Basidia** 13–26 × 5.5–8.0 μm, tetrasporic, clavate or slightly truncate at the apex, sterigmata up to 3 μm long. In LAPAM17 the basidia, basidioles and subhymenial hyphae have abundant internal granular brown pigment. **Cheilocystidia** absent in the three collections studied. **Pleurocystidia** not observed. **Lower surface of the annulus** consisting of cylindrical hyphae, hyaline, 2–6 μm wide, the wider the more constricted at septa, the latter easy to disarticulate into elements with rounded ends. Inflated elements not observed. **Pileipellis** a cutis, hyphae 2–5 μm, not or slightly narrowed at septa, terminal elements very abundant with rounded ends, with internal granular pigment yellow or light brown in water. **Clamp connections** not observed.

**Macrochemical reactions:** Schäffer’s reaction negative. KOH reaction positive, color orange yellow.

**Habit, habitat, occurrence and distribution:** Gregarious, sometimes in groups of numerous basidiomata, in moist lowland broadleaf forests. Uncommon. Recorded only from the Dominican Republic.

**Species-specific ITS markers in *A. sect. Xanthodermatei*:** ccacgAaatct@194, acatgAgcttc@264, tagagAggagc@482



**FIGURE 20.** Macroscopic characters of *A. flavidodiscus*. **A–H.** Basidiomata. **A, E, H.** (JBSD126488); **B, C.** (JBSD126487); **D, F–G.** (JBSD126489, holotype). Microscopic characters of *A. flavidodiscus*. **I–L.** In ammoniacal Congo red. **I.** (JBSD126488); **J–L.** (JBSD126489, holotype). **I.** Basidia. **J.** Spores. **K.** Hyphae of the lower surface of the annulus. **L.** Pileipellis hyphae. Photos by C. Angelini (a–g) and L.A. Parra (h–k).

**Note:** This species is characterized by its small size, the whitish pileus with a typically yellow center, double and thin annulus, not or only slightly yellowing on handling and for being a species that is practically odorless.

**Material examined:** DOMINICAN REPUBLIC, Puerto Plata, Sosúa, Puerto Chiquito, 5 December 2013 JBSD126487 (LAPAM39); Puerto Plata, Sosúa, Puerto Chiquito, 19 November 2011, JBSD126488 (LAPAM17); Puerto Plata, Sosúa, Puerto Chiquito, 5 December 2014, JBSD126489 *Holotypus* (LAPAM 60 *Isotypus*).

**Taxonomic comments:** Macroscopically the most similar species are *A. ochraceidiscus* Murrill (1918: 80) and *A. ochraceosquamulosus* Heinem., but both species are larger and their pilei are covered by ochraceous scales. Furthermore, the Schäffer's reaction is positive of orange color in *A. ochraceosquamulosus* (Heinemann 1961; Pegler 1983). Microscopically, the spore size of the original description of *A. ochraceidiscus* ( $4.5\text{--}5.0 \times 3.0\text{--}3.5 \mu\text{m}$ ) agrees with our collections, but Murrill (1918) did not note cheilocystidia. However, the holotype of *A. ochraceidiscus* has been studied by Freeman (1979) and Pegler (1987) and both indicated larger spore sizes (Freeman:  $4.5\text{--}6.0 \times 3.8\text{--}4.5 \mu\text{m}$ ; Pegler:  $5.0\text{--}5.7\text{--}6.0 \times 3.5\text{--}4.0\text{--}4.2 \mu\text{m}$ ) than those provided by Murrill, and are practically out of range of our measurements for *A. flavidodiscus* ( $4.33\text{--}4.82\text{--}5.17 \times 3.10\text{--}3.30\text{--}3.51\text{--}(3.61) \mu\text{m}$ ). In addition, both authors also mentioned the presence of cheilocystidia, "scattered" according to Freeman, but "crowded" clavate often subcapitate to Pegler. Similarly, the spore size of *A. ochraceosquamulosus* are also larger both in the original description by Heinemann ( $5.1\text{--}5.7 \times 3.6\text{--}4.0 \mu\text{m}$ ) and in collections studied later by Pegler ( $4.5\text{--}5.4\text{--}6.5 \times 3.2\text{--}3.7\text{--}4.2 \mu\text{m}$ ); and both authors also indicated the presence of clavate or pyriform cheilocystidia (described erroneously as lanceolate in Heinemann; see figure 8 on page 243) even if they were described as inconspicuous.

**Additional comments:** In *A. flavidodiscus*, we noted a high intraspecific variability with heteromorphisms at eight, four and zero positions in LAPAM 60, LAPAM 17, and LAPAM 39, respectively.

*Agaricus tephrolepidus* L.A. Parra, C. Billette, Angelini, G. Mata & Callac, *sp. nov.* (Fig. 21)

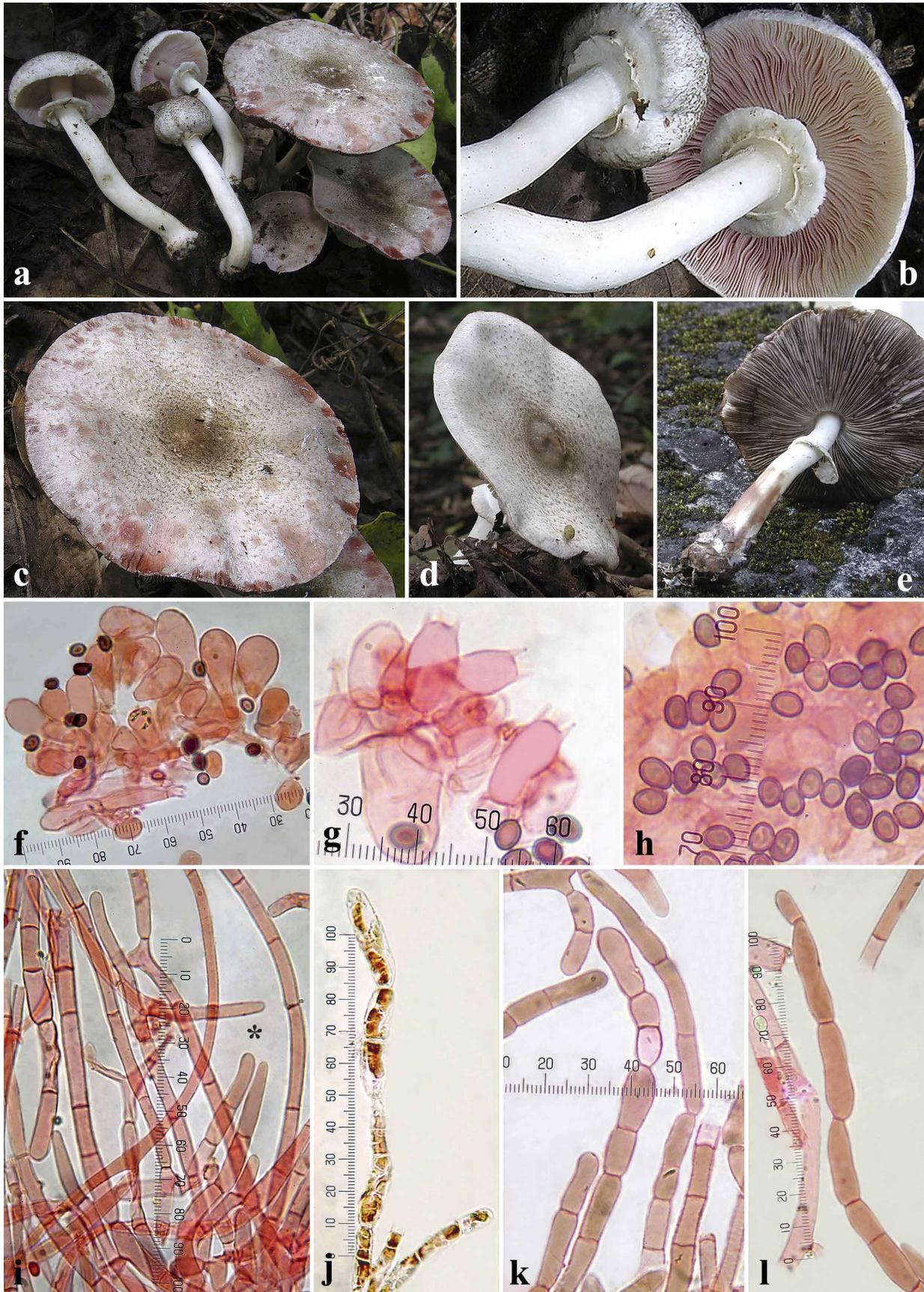
**Mycobank:** MB823284.

**Etymology:** for the very dark color (in Greek "tephros") of the pileus scales (in Greek "lepidos").

**Original description, Macroscopic description:** Pileus (3–)4–5(–6) cm (Dominican collection) or 6.5–8.4 cm (Mexican collection) diam., at first globose, then convex and finally applanate with broadly umbonate disc, at first covered with grayish-brown to brown fibrils slightly separated from each other, later becoming squamose, dense at the disc and more scattered towards the margin, on a pale mouse gray background with age, discoloring brown-red especially at the margin with high humidity. Surface smooth, dull and dry. Margin incurved when young then straight not exceeding the lamellae. Lamellae free, crowded, at first light pink, dark brown to dark grey with age. Stipe 5–6.5  $\times$  0.5–0.7 cm (0.8–1.2 cm at the base) for the Dominican collection, 8  $\times$  0.9–1.3 cm for Mexican collection, generally curved in the lower half, clavate to bulbous at the base which has small rhizomorphs, smooth and white above and below annulus, becoming slowly reddish brown on handling. Annulus superous, double, white, up to 0.5 cm broad, at first thick and adpressed to the stipe, later in mature basidiomata horizontal or pendant, narrow, upper surface slightly striate, lower surface initially with a fibrillose margin and a smooth surface near the insertion separated by a rim, later this rim fractures radially into broad radial scales resembling a cogwheel. Context initially white when cut, changing slowly to reddish brown with time. Odor not reported in the Dominican collection, pleasant fungoid in the Mexican collection.

**Microscopic description:** Spores (for the Dominican collection)  $4.37\text{--}4.90\text{--}5.33 \times 3.20\text{--}3.60\text{--}3.94 \mu\text{m}$ ,  $Q=1.17\text{--}1.36\text{--}1.50$ , ellipsoid, smooth, brown, without apical pore. For the Mexican collection see note below. Basidia 11–16  $\times$  6.0–7.5  $\mu\text{m}$ , tetrasporic, clavate or slightly truncated at the apex, sterigmata up to 3  $\mu\text{m}$  long. Cheilocystidia (for the Dominican collection)  $8.0\text{--}22.5\text{--}(28.0) \times 6.0\text{--}12.5 \mu\text{m}$ , abundant, hyaline and smooth, clavate, broadly clavate, pyriform or globose more or less sphaeropedunculate. For the Mexican collection see note below. Pleurocystidia not observed. Lower surface of the annulus composed of hyaline hyphae, cylindrical, not or slightly narrowed at the septa, 3–7  $\mu\text{m}$  wide. Inflated elements not observed. Pileipellis a cutis, with transition to a trichoderm. In water, the disc has two types of hyphae, some cylindrical, very thin, not or slightly narrow at the septa with incrustated parietal pigment, 2–4  $\mu\text{m}$  wide and others cylindrical, very narrow at the septa, consisting of short fusiform or doliiform elements, 3–10  $\mu\text{m}$ , with abundant granular pigment in the form of large dark brown granules that can fill the entire elements; and outside the disc hyphae are similar to these of the disc but with the elements more cylindrical and greater abundance of hyaline elements lacking the granular pigments. Clamp connections not observed.

**Macrochemical reactions:** Schäffer's reaction negative. KOH reaction positive, color yellow.



**FIGURE 21.** Macroscopic characters of *A. tephrolepidus*. A–E. Basidiomata. A–B. (JBSD123822, holotype); C–E. (Mata & Billette 745). Microscopic characters of *A. tephrolepidus* (F–I, K–L in ammoniacal Congo red; J in water). F–L. (JBSD123822, holotype). F. Cheilocystidia. G. Basidia. H. Spores. I. Hyphae of the lower surface of the annulus (terminal hyphae are marked with an asterisk). J–L. Pileipellis hyphae (one terminal hypha). Photos by C. Angelini (A–B, F–G), C. Billette (C–E) and L.A. Parra (H–K).

**Habit, habitat, occurrence and distribution:** In groups of few basidiomata, in broadleaf forests. Rare. Recorded only from the Dominican Republic and Mexico.

**Species-specific ITS markers in *A. sect. Xanthodermatei*:** ggataAgagga@146, ccttaCagaaa@236, tgttcYgcttc@618.

**Note:** The Mexican collection was missing after microscopical examination and a mycelial culture was obtained. It had spores  $3.4\text{--}5.7 \times 3.4\text{--}4.6 \mu\text{m}$ , and cheilocystidia  $5.7\text{--}6.8 \times 5.7\text{--}8.0 \mu\text{m}$ . The mycelium of the Mexican collection grew very slowly at 25°C on compost extract medium, failing to fruit after 6 months of culture with the standard protocol used for *A. bisporus* (J.E. Lange 1926: 8) Imbach (1946: 15), modified as follow: compost supplemented with glucose (10 g/l) and sterilized, axenic culture until complete compost invasion.

**Material examined:** DOMINICAN REPUBLIC, Puerto Plata, Sosúa, Puerto Chiquito, 25 November 2011, JBSD123822, *Holotypus* (LAPAM18, *Isotypus*). MEXICO, Veracruz, Xalapa, INECOL-Instituto de Ecología, A. C., Jardín Botánico Francisco Javier Clavijero, cloud forest (locally called “bosque mesófilo de montaña”) dominated by *Platanus mexicana* and *Liquidambar styraciflua*, in botanical garden, 20 August 2007, collectors M. Nau and C. Billette, *Mata & Billette* 745 (XAL, missing collection), mycelial strain IE 786 (XAL) duplicate CA 595 (CGAB), GenBank ITS sequence: HQ322269.

**Taxonomic comments:** The most similar species to *A. tephrolepidus* are *A. endoxanthus*, *A. moelleri*, *A. moelleroides*, *A. punjabensis* and *A. volvatulus*, but all these species have a bright yellowing discoloration in the context of the stipe base when cut (except *A. punjabensis*, for which this character was not described) and spores with very different sizes. Furthermore, in *A. endoxanthus* and *A. volvatulus* the pileipellis consists of elements with abundant vacuolar pigment and *A. volvatulus* lacks cheilocystidia. Within the Caribbean region, *A. griseorimosus* Pegler (1983: 435), described from the island of Martinique, has a very similar aspect according to the drawings and photographs provided by Pegler (1983) and also lacks the yellowing in the context of the stipe base when cut and has a strong odor of “iodine”. Therefore, even if this author included this species in *A. sect. Agaricus*, in our opinion and according to the characters of the original description, *A. griseorimosus* more likely belongs to section *Xanthodermatei*. However, this species has a rimose pileus, a simple annulus and much longer and narrower spores ( $5.3\text{--}5.6\text{--}7.5 \times 2.7\text{--}3.0\text{--}3.5 \mu\text{m}$ ) with a Q value of 1.8, very different from those of *A. tephrolepidus*.

## Discussion

The necessity for a new taxonomic system of classification

The study of Chen *et al.* (2017) revealed three clades as putative sections, but without appropriate material to describe them formally. Thanks to the samples from the Dominican Republic, we described and named these three sections *Minoriopsis*, *Kerrigania*, and *Pantropicales*. Indeed, Chen *et al.* (2017) focused on the diversity in the Greater Mekong Subregion, while *A. sect. Minoriopsis* and *A. sect. Kerrigania* are neotropical sections. We note that the clades corresponding to these two sections appeared first as the clades TRd (in part) and the well supported clade TRII, respectively, in Zhao *et al.* (2016). In contrast, the clade corresponding to *A. sect. Pantropicales* appeared more recently in Chen *et al.* (2017) as the clade A-II and includes only two species from tropical Southeast Asia despite the hundreds of collections made in that area.

More than half of the 47 samples from the Dominican Republic that we included in our analyses (28/47) belong to these three new sections. In other words, the above-mentioned recent phylogenetic studies facilitated the classification of species from the Dominican Republic. At the same time, the collections from this island have been fundamental to the formal description of the formerly discovered phylogenetic clades, improving the new system of classification of the genus *Agaricus* which now includes 23 sections in six subgenera.

Is it still possible to morphologically circumscribe subgenera and sections?

Our study indicates that, without taking into account secotioid or gasteroid taxa, the structure of the annulus remains the best macroscopic character to distinguish the three related subgenera (*Flavoagaricus*, *Minores* and *Minoriopsis*). *Agaricus* subg. *Flavoagaricus* and *A. subg. Minoriopsis* continue to be characterized by a two-layered (double) annulus, while the annulus is one-layered (simple) in *A. subg. Minores*. Microscopically, taxa of *A. subg. Flavoagaricus* are characterized by the presence of inflated elements in the cylindrical hyphae of its lower surface and catenulate cheilocystidia, which are absent in *A. subg. Minores* and *A. subg. Minoriopsis*.

Within *A. subg. Minores*, after comparing each morphological character observed in all species belonging to *A.*

sect *Pantropicales*, we have not found any character to distinguish *A. sect. Pantropicales* from *A. sect. Leucocarpi* and *A. sect. Minores*. It should be noted that a negative Schäffer's reaction on the fresh holotype specimen of *A. leucocarpus*, type of *A. sect. Leucocarpi*, was reported in its original description. Testing again the Schäffer's reaction, this time on the dry holotype specimen, we observed a positive orange reddish reaction, which is congruent with the reaction observed in other sections of *A. subg. Minores*. Similarly, within *A. subg. Minoriopsis*, we have not found any morphological distinctive character between *A. sect. Kerrigania* and *A. sect. Minoriopsis*. Therefore, to date the three new sections can only be distinguished based on molecular characters. Section-specific markers are given in the original description of each new section.

#### Unusual intraspecific variability

An unusual number of heteromorphisms was found in samples of five different species. In *Agaricus*, ITS sequences of conspecific samples rarely differ at more than one or, less frequently, two pairs of homologous positions in their sequence. Similarly, the number of heteromorphisms in any individual rarely exceeds one or two. However, two species are notable exceptions, which are among the most widely distributed species of *Agaricus* that are also found in the Dominican Republic. First, the Dominican sample LAPAM 47 of *A. endoxanthus*, distributed in tropical Africa, Americas and Asia, exhibits five heteromorphisms in the ITS region in agreement with the high intraspecific variability already known in this species (Chen *et al.* 2016b). Secondly, the Dominican sample LAPAM 11 of *A. subrufescens* has seven heteromorphisms. This species is cosmopolitan and distributed in both tropical and temperate areas. Based on nine polymorphic positions, three haplotypes of ITS sequences, A, B, and C have been characterized (Chen *et al.* 2016a). American samples are known to be AA, BB, or AB. Our data indicate that it is also the case in the Dominican Republic where the sample LAPAM 11 is AB. Chen *et al.* (2016a) hypothesized that types A and B may originate from ancient divergent populations.

Interestingly, three more species exhibit an unusual high variability in the Caribbean: (1) the new species *A. lodgeae*, PR4634, from Puerto Rico, exhibits 13 heteromorphisms that might result from hybridizations between divergent populations; (2) the new species *A. tephrolepidotus*, the Dominican LAPAM60, has eight heteromorphisms; and (3) the Dominican sample LAPAM48, has 15 heteromorphisms, which may result from a hybridization event between *A. rufoaurantiacus* and an unidentified *Agaricus* species. The clarification of the status of this sample would require multigene sequencing, DNA cloning, offspring analysis, and interfertility tests. LAPAM 48 itself may be a hybrid or, alternatively, it could be closely related to one of the two 'parental species' with the ITS of the other parent being introgressed, similarly to what has been reported in a French specimen of *A. subrufescens*. In this specimen, the ITS from a highly divergent population is introgressed at a non-homologous ITS locus (Chen *et al.* 2016a).

High intraspecific diversity, which is generally considered as unusual in *Agaricus*, seems relatively frequent in the Dominican Republic. Indeed, 42% (5/12) of the studied taxa, including one putative hybrid, include at least one sample exhibiting five or more heteromorphisms (until 15) in their ITS sequence. The question arises as to the possible effect of the isolation of the populations in the Caribbean islands and their subsequent mixing possibly by human activities.

#### *Agaricus* diversity and occurrence in the Dominican Republic

To give a first provisional estimation of the diversity and the occurrence of the taxa in the Dominican Republic, we have included in Table 2 all 53 collections collected in this country in the period from 2009 to 2016, although only 47 of them are characterized and illustrated in this study. The six remaining samples are only briefly reported in their own subgenus. The 53 collections belong to 21 described or putative species that are distributed in five of the six subgenera, but in only nine of the 23 sections of the genus. This is because 11 of the 12 sections of *A. subg. Pseudochitonina* are represented by very few collections or are not known from tropical areas. In contrast, the twelfth section of this subgenus, *A. sect. Xanthodermatei*, is the most speciose section with 13 collections distributed in eight species. This represents 24.5% (13/53) of the collections that must be regarded as potentially toxic, because the species of this section generally contain phenol responsible for mild gastrointestinal problems. However, among the subgenera, *A. subg. Minoriopsis* has the highest occurrence with 45% (24/53) of the collections, which belong to only five species.

In total *A. subg. Pseudochitonina* and *A. subg. Minoriopsis* represent 72% (38/53) of the collections and 67% (14/21) of the species. *Agaricus subg. Minoriopsis* is well established in the Dominican Republic and probably throughout the Caribbean.

From the diversity revealed here in this first contribution to the diversity of the genus *Agaricus* in the Dominican Republic, we can infer that more new species will be described in future studies in this country. This is because, on the one hand, about the half (6/11) of the species treated in this paper are new to the science and, on the other hand, nine unnamed species, represented by additional collections, are good candidates to be described as distinct species, when more material is found.

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