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Short title: *Neonothopanus gardneri* comb. nov.

Neonothopanus gardneri: a new combination for a bioluminescent agaric from Brazil

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Abstract: The bioluminescent agaric, *Agaricus gardneri* Berk., was rediscovered recently in central Brazil. The new combination, *Neonothopanus gardneri*, is proposed for this long-forgotten taxon supported by morphological and molecular data.

Key words: Agaricales, Basidiomycota, bioluminescence, omphalotoid clade, taxonomy

INTRODUCTION

In 1840 George Gardner published a short paper titled "Description of a new phosphorescent species of *Agaricus*" wherein he recounted observing boys amusing themselves with a luminous object in the streets of Vila de Natividade, Goiás State, Brazil (Gardner 1840). Gardner at first thought the object was some sort of large firefly, but on closer inspection he recognized it as a

species of *Agaricus* belonging to tribe *Pleurotus* of Fries. The locals called it "flor-de-coco" and noted that it grew abundantly on decaying fronds of a dwarf palm that they called "pindoba". Gardner sent a brief description and drawing of the luminous agaric to M.J. Berkeley at Kew and indicated that if the species was new he intended to name it *Agaricus phosphorescens*. Berkeley responded that the species indeed was new and was referable to Fries' new genus *Panus* (accommodating *Agaricus* tribe *Pleurotus* species with coriaceous texture) but that he (Berkeley) thought *A. phosphorescens* was not an appropriate epithet because phosphorescence (luminescence) was not unique to the new species. Berkeley suggested that the taxon should be named after the collector. Hence in Gardner's paper (Gardner 1840) the new luminescent agaric was described formally as *Agaricus gardneri* Berk. ex Gardner. Three years later Berkeley (1843) reported the species as *Agaricus* (*Omphalia*) *gardneri* in his "Notices of some Brazilian fungi". Saccardo (1887) transferred it as *Pleurotus gardneri* (Berk. ex Gardner) Sacc., repeating the Latin diagnosis of Gardner and reporting the species from Brazil as well as from Queensland, Australia. Saccardo was undoubtedly following Berkeley and Broome (1879) who reported *A. gardneri* from Brisbane, although the latter was a misapplied name for *Omphalotus nidiformis*, a commonly encountered luminescent agaric in Queensland (cf. May and Wood 1997).

Pegler (1988) provided a revised description of the species based on his examination of type material labeled by Berkeley as *A. gardneri* (K), and noted that "the overall caespitose habit, the woody substratum, spore form and the properties of luminescence are also typical of *Omphalotus olearius*."

Pegler added that distinguishing *A. gardneri* as a distinct species or as a yellow, geographical variant of *O. olearius* would require examination of fresh material, unavailable at the time. Ample fresh material of this long-forgotten luminescent species was collected recently from Piauí and Tocantins states, Brazil, allowing a re-evaluation of its taxonomic affinities. We

herein transfer *A. gardneri* to the genus *Neonothopanus* based on a combination of morphological and molecular data.

MATERIAL AND METHODS

Morphological study.—Microscopic analyses were made from dried material rehydrated in 70% ethanol followed by 5% KOH and stained with Melzer's reagent. Q_m represents the mean length/width quotient of all spores measured. Colors notations correspond to those of Küppers (1979). All specimens are deposited in the Herbário do Instituto de Botânica (SP).

Molecular study.—To elucidate the relationships of *Neonothopanus gardneri* to members of the omphalotoid clade (Moncalvo et al 2000, 2002) ITS and nLSU sequence data were generated from recently collected material and analyzed within a phylogenetic framework.

DNA extraction followed an adapted protocol of Ferreira and Grattapaglia (1995) using lyophilized basidiomata ground to a fine powder in liquid nitrogen. The sample was resuspended in 50 µL TE, incubated at 37 C for 30 min after the addition of RNase A (0.01 mg/µL) and stored at −20 C. The ITS and nLSU regions were amplified respectively with the primer set ITS1F/ITS4 and LR0R/LR5 (White et al. 1990, Gardes and Bruns 1993, Moncalvo et al. 2000). PCR reactions contained these concentrations in 100 µL final volume: 2.0 U Platinum® Taq DNA Polymerase (Invitrogen), 0.2 mM of each dNTP, 1.5 mM $MgCl_2$ and 0.2 µM of each primer. PCR protocols consisted of a 5 min denaturation step at 94 C, followed by 40 cycles of 40 s at 94 C, 30 s at 55 C and 60 s at 72 C, and final extension step of 72 C for 5 min. Resulting PCR product was purified with PureLink PCR Purification Kit (Invitrogen). DNA sequencing reactions were performed with the DYEnamic ET dye terminator Cycle Sequencing Kit on a MegaBACE 1000 DNA sequencer (Molecular Dynamics) according to the manufacturer's instructions. Consensus sequences were generated with the Phred/Phrap/Consed package (Ewing et al. 1998, Ewing and Green 1998, Gordon et al. 1998). Edited ITS and nLSU sequences of *N. gardneri* were deposited in GenBank (TABLE I).

Sequences of *N. gardneri* were aligned manually to other sequences of the omphalotoid clade (TABLE I) with MacClade 4 (Maddison and Maddison 2000). Phylogenetic analyses were performed with parsimony, maximum likelihood and Bayesian methods. Parsimony searches were performed in PAUP* 4.0 (Swofford 2003), using a branch-and-bound algorithm with furthest sequence addition, MULTREES on, collapse of zero length branches and equal weighting of all characters. Support of individual clades was assessed by bootstrap (BS) analyses (Felsenstein 1985), using 500 branch-and-bound replicates with the same parameter settings as above. Maximum likelihood (ML)

searches also were conducted in PAUP*, under a GTR+I+G model of sequence evolution determined with the Akaike information criterion as calculated in Modeltest 3.7 (Posada and Crandall 1998), with starting trees obtained via neighbor joining, TBR branch swapping, MULTREES on, and all parameter values estimated by the program. Clade support was assessed by nonparametric ML bootstrap (BS) analyses as implemented in Garli (Zwickl 2006) and consisted of 1000 replicates run under the same model of sequence evolution as the ML search, with all parameters estimated by the program. Bayesian analyses to obtain posterior probabilities (PP) were performed with MCMCMC methods as implemented in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) using the same model as the ML analyses. Bayesian analyses consisted of two parallel searches, run 2 000 000 generations and initiated with random starting trees. Chains were sampled from the posterior distribution every 200 generations for a total of 10 000 trees each. All trees sampled before the distribution reaching a spit deviation frequency of 0.01 were discarded as the burn-in, while the remaining trees were used to calculate posterior probabilities (PP) of the individual clades. The default settings were used in MrBayes to set the incremental heating scheme, unconstrained branch lengths and uninformative topology priors. Sequence alignment was submitted to TreeBASE (submission number 11243).

RESULTS

Molecular analysis.—After excluding regions deemed too ambiguous for alignment the ITS dataset consists of 652 aligned positions for 16 ingroup taxa and contains 207 parsimony informative positions. The nLSU dataset includes 761 aligned positions for 13 ingroup taxa and contains 58 parsimony informative positions. For both datasets a sequence of *Crinipellis* sp. was used as an outgroup taxon for rooting purposes. Parsimony analyses of both datasets results in topologically similar trees. Before combining the ITS and nLSU data parsimony bootstrap analyses were performed (as described above) to determine whether either data partition recovers well supported taxonomic groupings that conflict with those recovered by the other partition. Once a lack of taxonomic conflict was determined the ITS and nLSU data were combined. Parsimony analyses of the combined data recovered three trees of 1000 steps (CI = 0.6780, RI = 5619), differing only in the placement of several taxa within a clade corresponding to the genus

Omphalotus. Maximum likelihood (ML) analyses recovered a single tree (FIG. 1) (−ln = 4596.33572) identical in topology to one of the trees recovered by parsimony analysis. Bayesian analyses reached an average standard deviation of split frequencies below 0.01 after approximately 170 000 generations. The first 2500 trees sampled were excluded as the burn-in.

Neonothopanus gardneri is moderately supported as the sister taxon to *Neonothopanus nambi* in our analyses (70% ML-BS, 0.91 Bayesian PP). The *Neonothopanus* clade is weakly supported as the sister clade to a well supported *Omphalotus* (96% BS, 1.0 PP) represented by eight taxa. Both species of *Anthracophyllum* included in the analyses, *A. archeri* and *A. lateritium*, are well supported as sister taxa (99% BS, 1.0 PP), whereas the two species of *Gymnopus* sampled, *G. contrarius* and *G. dryophilus*, do not form a monophyletic lineage. *Gymnopus contrarius* is weakly supported in a position subtending the *Anthracophyllum* species, and *G. dryophilus* falls out in a well supported clade with *Lentinula lateritia* and *Rhodocollybia maculata* (100% BS, 0.99 PP). *Neonothopanus gardneri* did not form a monophyletic lineage with *Omphalotus* species in any analyses; instead it was sister to *N. nambi* with varied statistical support in all analyses.

TAXONOMY

Neonothopanus gardneri (Berk. ex Gardner) Capelari, Desjardin, Perry, Asai & Stevani, comb. nov. FIGS. 2–3

MycoBank MB519818

Basionym: Agaricus gardneri Berk. ex Gardner, J. Bot. (Hooker) 2:427 (1840).

Synonyms: Pleurotus gardneri (Berk. ex Gardner) Sacc., Syll. fung. (Abellini) 5:352 (1887).

Dendrosarcus gardneri (Berk. ex Gardner) Kuntze, Revis. gen. pl. (Leipzig) 3:464 (1898).

Pileus 10–90 mm diam, convex to applanate with a small umbo when young, applanate to depressed or infundibuliform when mature, smooth, glabrous, hygrophanous; margin irregular,

sometimes lacerate or lobate, striatulate; yellow ($N_{00}A_{40}M_{00}$) overall when young, the disk darker yellow ($N_{00}A_{50}M_{00}$) and margin paler yellow ($N_{00}A_{30}M_{00}$), sometimes fading on the margin to buff or nearly white, sometimes with small scattered brownish spots. Context fleshy, thick, cream to pale yellow ($N_{00}A_{40}M_{00}$). Lamellae deeply decurrent, distant with 2–3(–5) series of lamellulae, broad (3–7 mm); edges entire, yellow, concolorous with pileus margin ($N_{00}A_{30}M_{00}$), becoming paler with age. Stipe 30–50 × 8–15 mm, eccentric or sometimes central, cylindrical to narrowed toward the base, solid, tough, fibrous, smooth or reticulate near lamellae ends, light yellow, concolorous with the pileus surface ($N_{00}A_{30}M_{00}$–$N_{00}A_{40}M_{00}$) above, base darker with brown tones; partial veil absent. Flavor not recorded. Odor pleasant. Pileus and lamellae strongly luminescent (bright yellowish green; FIG. 2b, d); mycelium luminescent (FIG. 2f).

Basidiospores 9.5–12 × (8.5–)9–11 µm (x = 10.2 ± 0.7 × 9.7 ± 0.7 µm, Q = 1.00–1.18, Q_m = 1.07 ± 0.02, n = 25 spores), globose to subglobose with a prominent hilar appendix, smooth, hyaline, inamyloid, thin-walled. Basidia 35–48 × 7.5–12 µm, subcylindrical to clavate, four sterigmata, occasionally two sterigmata, hyaline, thin-walled, clamped. Basidioles 35–50 × 7–12 µm, cylindrical to clavate, hyaline, thin-walled. Pleurocystidia absent. Lamella-edge heteromorphous, with basidia, basidioles and scattered cystidia. Cheilocystidia 30–50 × 4–8 µm, body submerged and difficult to discern, apices slightly projecting, elongate-fusoid to sinuous-cylindrical, hyaline, thin-walled. Pileipellis undifferentiated from the underlying tramal tissue, composed of repent hyphae, 2.5–5 µm diam, hyaline or pale yellowish in KOH, inamyloid, thin-walled, non-gelatinous. Pileus and stipe tramal tissues composed of hyphae 3.5–6.5 µm diam, cylindrical or sometimes inflated and branched, hyaline, inamyloid, thin- to slightly thick-walled, with clamp connections. Hymenophoral trama compact, with a subregular to irregular mediostratum and a more loosely arranged lateral stratum; hyphae 2.5–5 µm diam, hyaline,

inamyloid, thin- to slightly thick-walled. Stipitipellis similar to pileipellis. Clamp connections present in all tissues.

Habit, *habitat and known distribution:* Growing at the base of palm trees (pindoba palm [*Attalea humilis* Mart. ex Spreng.], piaçava [*A. funifera* Mart. ex Spreng.], and babaçu [*Orbignya phalerata* Mart.]). Goiás, Piauí and Tocantins States, Brazil.

Specimens examined: BRAZIL. GOIÁS STATE: Vila de Natividade, Dec 1839, *Gardner s.n.* (HOLOTYPE, K); PIAUÍ STATE: Gilbués City, Fazenda Boa Vista, 91°S and 45°W, Mar 2006, *D. Fragaszy & P. Izar s.n.* (SP416340); same location, 27 Feb 2008, *M.G. de Oliveira s.n.* (SP416341); Teresina City, Fazenda Cana Brava, 5°5′39.5″S, 42°23′12.82″W, 17 May 2008, *I. Dantas s.n.* (SP416342); TOCANTINS STATE, Itaguatins City, Fazenda São Paulo, 21 Mar 2008, *C.E.C. Nascimento & L.S. Araújo-Neta s.n.* (SP416343).

DISCUSSION

Neonothopanus gardneri is characterized by this combination of features: omphalotoid basidiomes with yellow to yellowish white pileus 10–90 mm diam, deeply decurrent, distant, broad lamellae, a well developed, eccentric to central stipe, and pale yellow context tissues; hyaline, inamyloid, smooth, globose basidiospores with mean 10.2 × 9.7 µm; elongate-fusoid to sinuous-cylindrical cheilocystidia; cutis-type pileipellis and stipitipellis tissues with inamyloid, non-gelatinized hyphae; growth on debris of dwarf palm; and basidiomes that are strongly luminescent. Our material undoubtedly represents the species first reported by Gardner (1840) from basidiomes growing on pindoba palm fronds in central Brazil. No micromorphological details were provided in the protolog, although a type study was published by Pegler (1988). Our material matches that analyzed by Pegler except in basidiospores size, which was reported by Pegler (1988) as 6–7 × 4.5–5.7 µm (x = 6.5 × 5.5 µm; Q = 1.18), much smaller than we report here. We studied the holotype specimen (K) and found basidiospores in the range that we report

from fresh specimens (9.5–12 × 9–11 μm) and many collapsed basidiospores in the range reported by Pegler (1988).

Neonothopanus was established by Petersen and Krisai-Greilhuber (1999) as a monotypic genus based on *Agaricus nambi* Speg. described from Paraguay (Spegazzini 1883). Singer (1944) recognized *A. nambi* as a member of his new genus *Nothopanus* (type *A. eugrammus* Mont.). Horak (1968) revised the types of *A. nambi* and *A. eugrammus*, and Petersen and Krisai-Greilhuber (1999) also revised the type of *A. eugrammus* and studied representative materials of *A. nambi*. All authors considered that they were distinct species and that *Nothopanus* (with type *A. eugrammus)* represented a synonym of *Pleurotus*. For a complete discussion of the taxonomy and nomenclature of *Nothopanus* and *Neonothopanus* see Petersen and Krisai-Greilhuber (1999). Our Brazilian species shows morphological affinities to both *Neonothopanus* and *Omphalotus* (with syn. *Lampteromyces*). Both latter genera contain species that form luminescent basidiomes with decurrent, distant lamellae, eccentric, solid stipes, smooth, hyaline, inamyloid basidiospores, and non-gelatinized, inamyloid hyphae with clamp connections. Indeed the morphological features of *Neonothopanus* and *Omphalotus* are overlapping and the distinctions subtle, with *Neonothopanus* forming unpigmented or pale pigmented (white to grayish tan) marasmielloid to pleurotoid basidiomes and *Omphalotus* forming more brightly pigmented (yellow to orange) pleurotoid to clitocyboid basidiomes. Molecular data have informed our decision to accept *A. gardneri* in *Neonothopanus* rather than in *Omphalotus*. *Neonothopanus gardneri* is moderately supported as the sister taxon to *N. nambi* in the maximum likelihood analysis of the combined ITS + nLSU datasets (FIG. 1), and these taxa did not form a monophyletic lineage with *Omphalotus* species in any analysis.

Neonothopanus gardneri differs from *N. nambi* in basidiome stature, pigmentation and basidiospore size. *Neonothopanus nambi* forms white to pale grayish tan basidiomes with

reduced, eccentric to lateral stipe and ellipsoid basidiospores, 4–6.5 x 2.8–4 µm (Petersen and Krisai-Greilhuber 1999), whereas *N. gardneri* forms yellow basidiomes with a well developed, eccentric to central stipe and globose basidiospores, 9.5–12 × 9–11 µm.

Neonothopanus nambi has not been explicitly reported as bioluminescent, but from the data provided by Petersen and Krisai-Greilhuber (1999) and Corner (1981) we infer this to be the case. Petersen and Krisai-Greilhuber convincingly documented that *N. nambi* is synonymous with *Pleurotus eugrammus* (Mont.) Dennis sensu Singer (1944), and they reported that specimens from Malaysia were conspecific (intercompatible) with those from Puerto Rico. Corner (1981) reported that Malaysian material of *P. eugrammus* (following Singer's concept of the species) was luminescent. Moreover we have collected luminescent basidiomes from Micronesia whose morphology and DNA sequences match those of *N. nambi* (Desjardin and Perry unpubl). *Neonothopanus gardneri* has been used recently in research that verifies the enzymatic nature of fungal bioluminescence (Oliveira and Stevani 2009) in contradiction to the research of Shimomura (1989, 1992) who reported that the pathway to light emission in fungi was non-enzymatic.

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LEGENDS

Fig. 1. Phylogenetic tree based on maximum likelihood (ML) analysis of the combined ITS + nLSU datasets, rooted with *Crinipellis* sp. Support at the nodes is represented by ML bootstrap/Bayesian posterior probability.

Fig. 2. Basidiomes (a–d) and cultures (e–f) of *Neonothophanus gardneri* taken in natural light (left) and in the dark (right). Bars = 30 mm.

Fig. 3. Micromorphlogical features of *Neonothophanus gardneri* (SP416340). a. Basidiospores. b. Basidia. c. Lamella edge with cheilocystidia. d. Cheilocystidia. Bar = 10 µm.

FOOTNOTES

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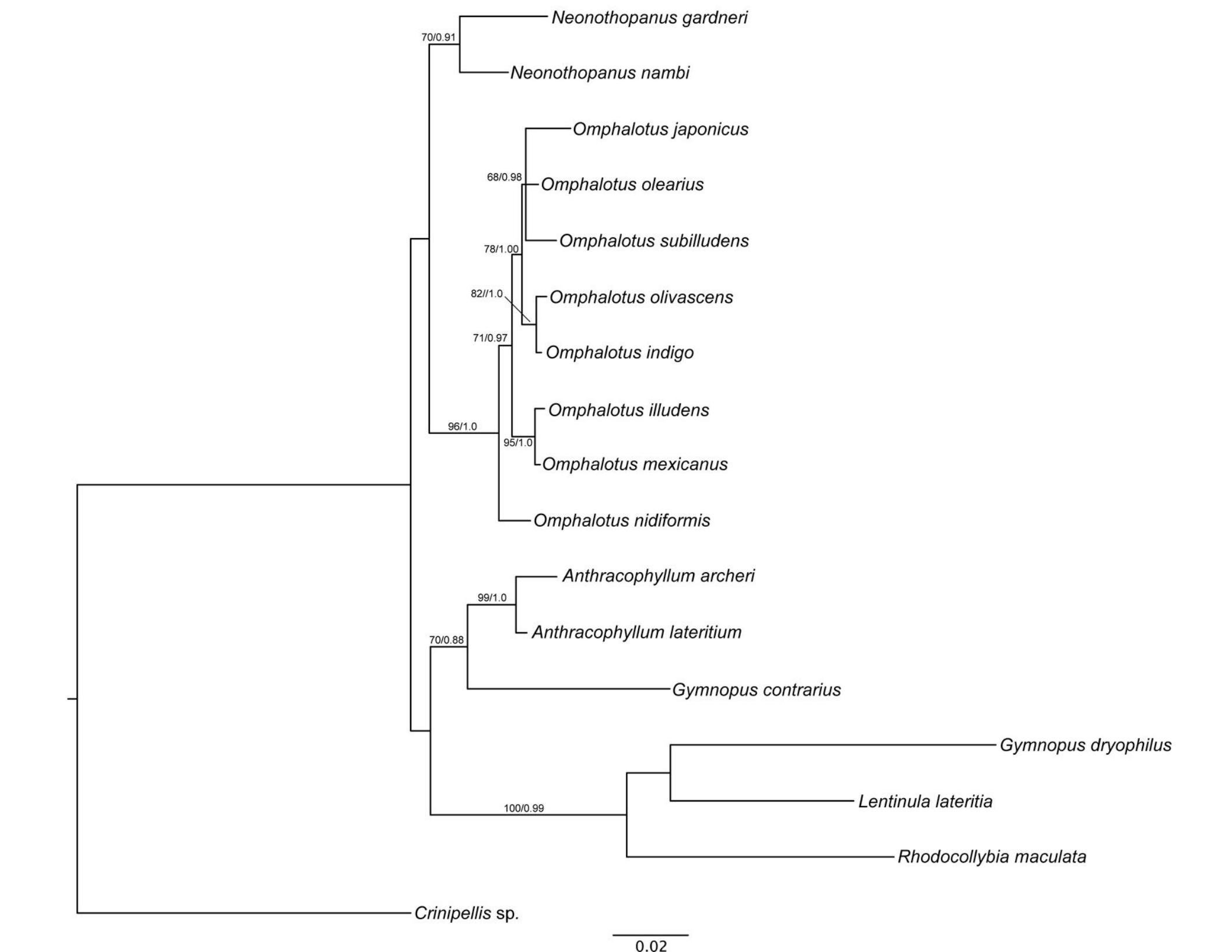
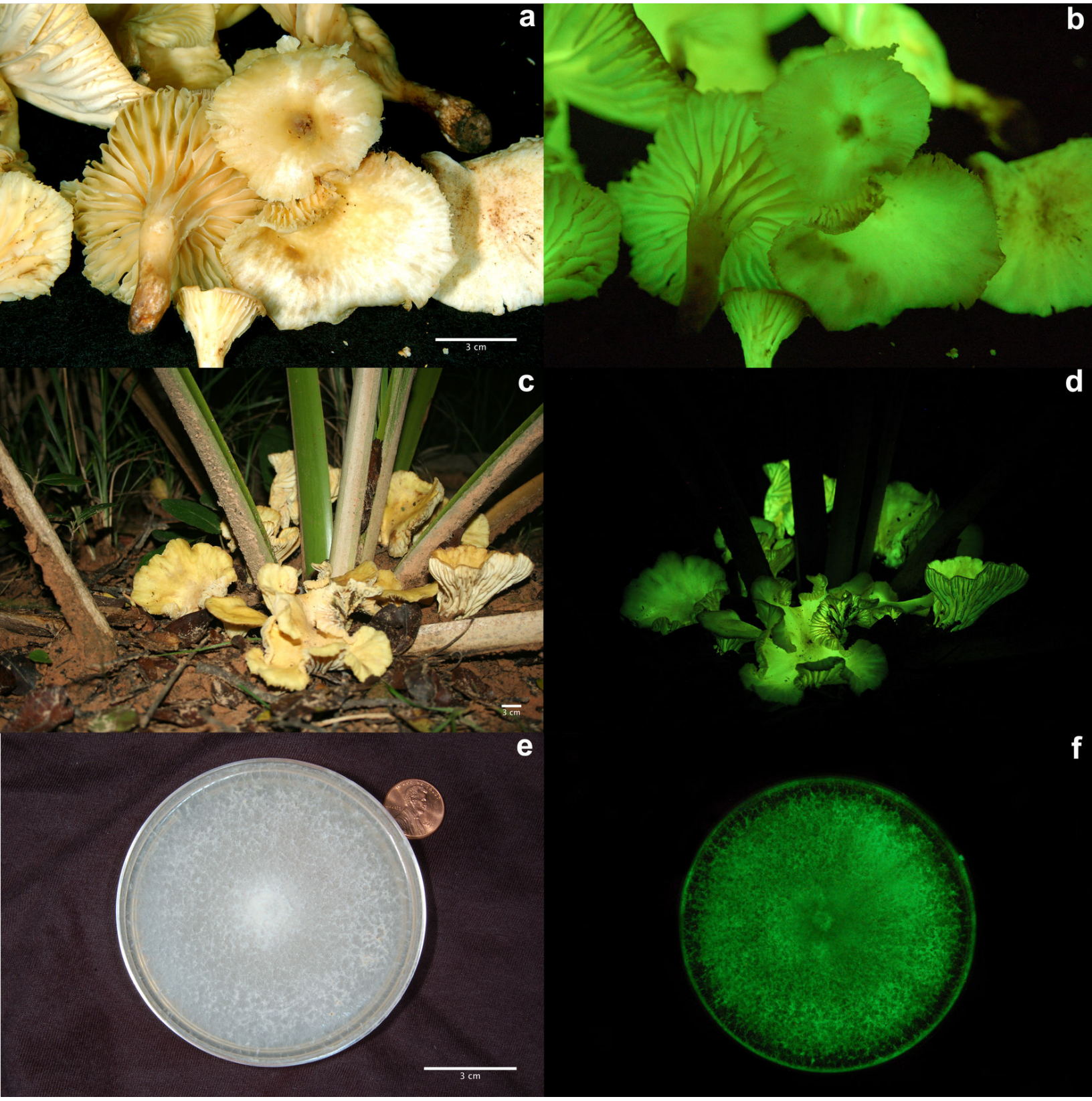
TABLE I. Collection data and GenBank accession number of the taxa analyzed

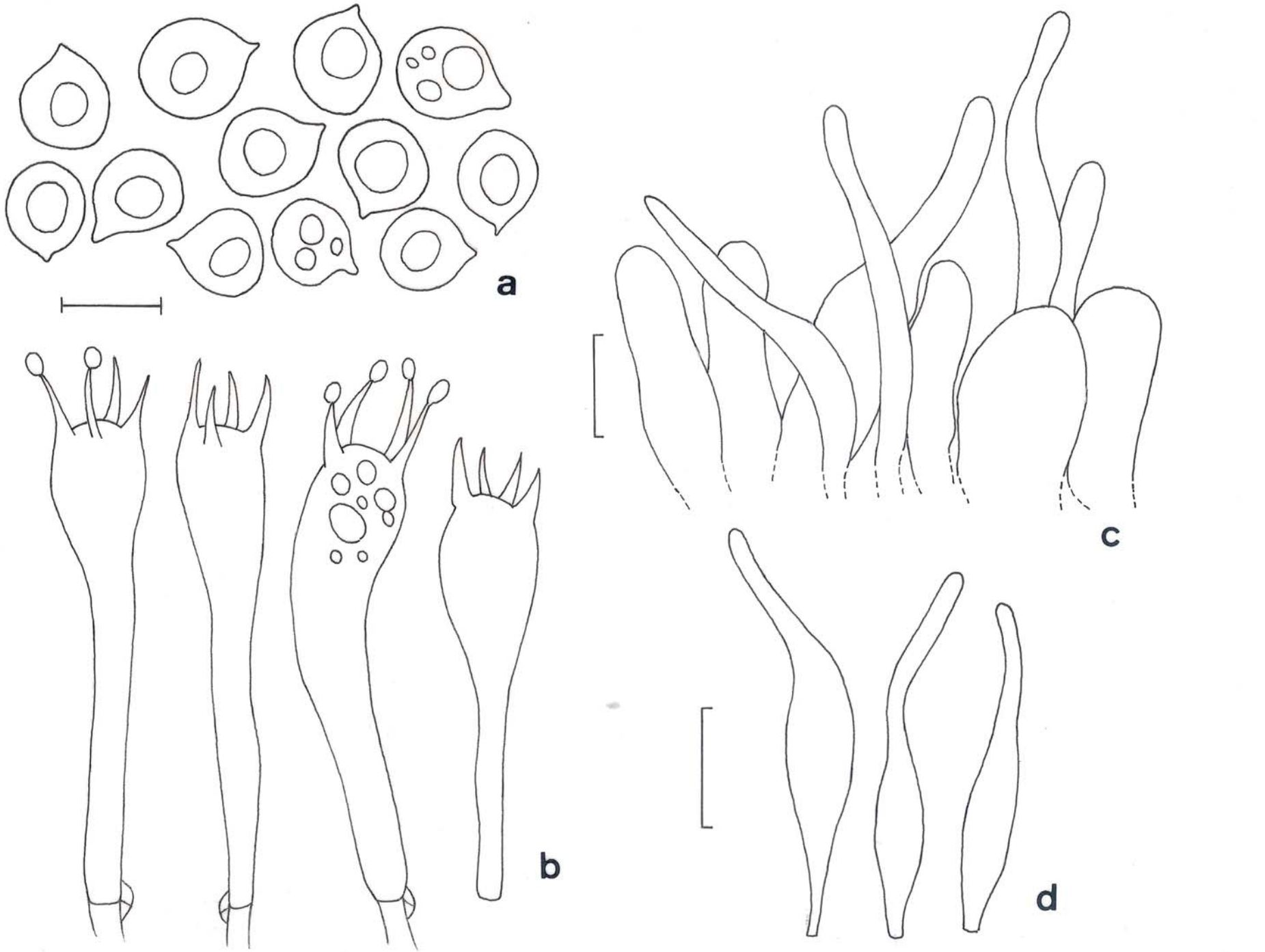
Species	Culture/herbarium number	Origin	GenBank number	
			LSU	ITS
Anthracophyllum archeri (Berk.) Pegler	PBM 2201		AY745709	
	AFTOL_ID 973			
	TFB 3511	Australia		DQ444308
	TENN 50049			
A. lateritium (Berk. & M.A. Curtis) Singer	CULTENN 4419		AF261324	
	TFB 4043	USA		DQ444309
	TENN 50256			
Crinipellis sp.	MCA 1527	Guyana	AY916699	AY916701
Gymnopus contrarius (Peck) Halling	AFTOL-ID 1758	USA	DQ457670	DQ486708
Gymnopus dryophilus (Bull.) Murrill	AFTOL-ID 559	USA	AY640619	DQ241781
Lentinula lateritia (Berk.) Pegler	RV 95-376		AF356164	AF031179

Species	Culture/herbarium number	Origin	GenBank number	
			LSU	ITS
Neonothopanus gardneri (Berk. ex Gardner) Capelari et al.	SP 416340	Brazil	JF344714	JF344713
N. nambi (Speg.) R.H. Petersen & Krisai	RVPR1308	Puerto Rico	AF042577	
	Watling 193/95	Malaysia		DQ444307
Omphalotus illudens (Schwein.) Bresinsky & Besl	TUB 012155		DQ071741	
	TENN54507	USA		AY313271
O. japonicus (Kawam.) Kirschm. & O.K. Mill.	isolate 456	–	AF042008	
	culture 2305	Japan		AY313286
O. mexicanus Guzmán & V.	TENN51283	Mexico	–	AY313274

Species	Culture/herbarium number	Origin	GenBank number	
			LSU	ITS
Mora				
O. nidiformis	T1946.8	–	AF042621	–
(Berk.) O.K.	Vilgalys E5332	Austrália	–	AY313275
Mill.				
O. olearius (DC:	AFTOL-ID 1718	Slovenia	DQ470816	–
Fr.) Singer	culture 9061b	France	–	AY313277
O. olivascens	VT645.7	–	AF261325	–
H.E. Bigelow et	TENN56257	USA	–	AY313279
al.				
O. olivascens	CBS101447	Mexico	–	AF525065
var. *indigo* G.				
Moreno et al.				
O. subilludens	TENN54320	USA	–	AY313283
(Murril) H.E.				
Bigelow				
Rhodocollybia	AFTOL-ID 540	USA	AY639880	DQ404383
maculata (Alb.				
& Schwein.)				
Singer				


Neonothopanus gardneri
70/0.91
Neonothopanus nambi
Omphalotus japonicus
68/0.98
Omphalotus olearius
Omphalotus subilludens
78/1.00
82//1.0
Omphalotus olivascens
71/0.97
Omphalotus indigo
Omphalotus illudens
96/1.0
95/1.0
Omphalotus mexicanus
Omphalotus nidiformis
Anthracophyllum archeri
99/1.0
Anthracophyllum lateritium
70/0.88
Gymnopus contrarius
Gymnopus dryophilus
Lentinula lateritia
100/0.99
Rhodocollybia maculata
Crinipellis sp.
0.02


a
3 cm
b
c
3 cm
d
e
3 cm
f


a
b
c
d