Cryptogamie, Mycologie, 2018, 39 (2): 149-168

Phylogenetic studies on *Bonomyces* (Tricholomatineae, Agaricales) and two new combinations from *Clitocybe*

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Abstract — Genus *Bonomyces* is here reviewed. Multigene phylogenetic analysis suggests it is related with *Cleistocybe* in the Tricholomatineae. Morphological and genetical studies led to a new interpretation of the type species, *B. sinopicus* (=*C. subsinopica*), and the new combinations *B. afrosinopicus* and *B. arnoldii*.

clitocyboid / *Clitocybe afrosinopica* / *Clitocybe arnoldii* / *Clitocybe sinopica* / *Clitocybe subsinopica*

INTRODUCTION

Clitocybe (Fr.: Fr.) Staude currently encompasses a large number of species sharing some broad morphological features (Harmaja 2003). Phylogenetic analysis showed *Clitocybe* is clearly polyphyletic, and delimited a Clitocybeae core clade including genera *Clitocybe* s. str., *Collybia* (Fr.: Fr.) Staude, *Lepista* (Fr.) W. G. Sm. and *Singerocybe* Harmaja, which is not directly related to other families in the Tricholomatineae Aime, Dentinger & Gaya, such as Biannulariaceae Jülich (= Catathelasmataceae Wasser), Entolomataceae Kotl. & Pouzar, Lyophyllaceae Jülich or Tricholomataceae R. Heim ex Pouzar (Matheny *et al.* 2006, Binder *et al.* 2010, Sánchez-García *et al.* 2014, 2016, Alvarado *et al.* 2015, Bellanger *et al.* 2015).

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doi/10.7872/crym/v39.iss2.2018.149

The increasing amount of genetic data helped to decide about the taxonomic status of many clitocyboid species, frequently confirming earlier decisions to separate them into distinct genera, as happened with *Neohygrophorus* Singer ex Singer (Redhead *et al.* 2000), *Pseudoclitocybe* (Singer) Singer (Walther *et al.* 2005), *Infundibulicybe* Harmaja (Matheny *et al.* 2006) or *Paralepista* (Vizzini & Ercole 2012). However, most clitocyboid species unrelated with the Clitocybeae core lacked a suitable generic name, and hence, new taxa were created to accommodate them, such as *Trichocybe* Vizzini (Vizzini *et al.* 2010), *Musumecia* Vizzini & Contu (Vizzini *et al.* 2011), *Notholepista* Vizzini & Contu (Vizzini *et al.* 2012), *Paralepistopsis* Vizzini (Vizzini & Ercole 2012), as well as *Atractosporocybe* P. Alvarado, G. Moreno & Vizzini, *Leucocybe* Vizzini, P. Alvarado, G. Moreno & Consiglio and *Rhizocybe* Vizzini, G. Moreno, P. Alvarado & Consiglio (Alvarado *et al.* 2015). Finally, some recently discovered clitocyboid species have been proposed in their own new genera after genetic evidence suggested they were not directly related with Clitocybeae, such as *Cleistocybe* Ammirati, A.D. Parker & Matheny (Ammirati *et al.* 2007), *Tephroderma* Contu & Musumeci (Musumeci & Contu 2014), or *Clitolyophyllum* E. Sesli, Vizzini & Contu (Sesli *et al.* 2016).

Recently, another new genus, *Bonomyces* Vizzini (Vizzini 2014), named to honor the famous French mycologist Marcel Bon, was proposed to accommodate the basionym *Agaricus sinopicus* Fr. : Fr. as *B. sinopicus* (Fr. : Fr.) Vizzini. This species was created by Fries (1818, 1821, 1838), who classified it within genus *Agaricus* L. (gilled fungi), ser. *Leucosporus* (whitish spores), tribu *Clitocybe* (central stipe, unveiled, convex when young), series A (fleshy, not hygrophanous), subseries *Infundibuliformes* (infundibuliform pileus, lamellae decurrent when young), among other colored taxa with floccose surface, such as *A. giganteus* Sowerby, *A. maximus*, *A. gibbus* Pers.: Fr., *A. squamulosus* Fr.: Fr., *A. trullaeformis* Fr.: Fr., *A. lentiginosus* Fr. or *A. parilis* Fr.: Fr. (Fries 1821). Fries (1818, 1821, 1838) reported *A. sinopicus* has a reddish basidiome, slightly umbilicated pileus, whitish lamellae, farinaceous smell, and fruits in moist forests in May-June. Tribu *Clitocybe* was soon upgraded to the genus level as *Clitocybe* (Fr.: Fr.) Staude (Staude 1857), but it was not until XXth century that a reorganization of the Friesian species began. Boursier (1925) created *Leucopaxillus* Boursier for species with warty amyloid spores, and soon Singer (1939) combined *A. giganteus* as *L. giganteus* (Sowerby: Fr.) Singer. He also transferred *A. parilis* to another genus as *Rhodocybe parilis* (Fr.: Fr.) Singer. Much later, Harmaja (2003) proposed a narrowed definition of *Clitocybe* excluding those species with cyanophobic spore walls not able to reduce nitrate, which he organized into the genus *Infundibulicybe*, including species such as *I. gibba* (Pers.: Fr.) Harmaja or *I. geotropa* (Bull. : Fr.) Harmaja (*Agaricus maximus* is considered a synonym of one of these species). The species *A. lentiginosus* was recently combined into *Paralepista* Raith. as *Paralepista lentiginosa* (Fr.) Vizzini because of its warted spores, cream spore-print, spotted pileus, lamellae separable from pileus an cyanophilic spores released in tetrads (Raithelhuber 1981, 2004, Vizzini & Ercole 2012).

The taxonomic decision of moving *Agaricus sinopicus* into a different genus (Vizzini 2014) is consistent with the treatment of many other species in the Friesian subseries *Infundibuliformes*, but it was not supported with DNA data. Vizzini (2014) reported that *Bonomyces* "differs from the genus *Infundibulicybe* Harmaja by having ovate to elliptical, not lacrymoid spores with obtuse, not confluent base and pileipellis hyphae with mainly cytoplasmatic pigment". In addition, a single species, the type *B. sinopicus*, was moved into the new genus, but the putatively related taxa *Clitocybe subsinopica* Harmaja and *C. afrosinopica* P.-A.

Moreau were not mentioned. *Clitocybe subsinopica* was proposed by Harmaja (1978) as a taxon similar to *C. sinopica* but for a smaller size of its basidiome and its spores (8.0–10.5 × 5.5–6.5 µm in *C. sinopica* vs. 6.0–8.5 × 4.0–5.0 µm in *C. subsinopica*), as well as for a slightly yellowish spore print. The type collection was collected in Finland, in a dry heathland with *Pinus sylvestris* in August. *Clitocybe afrosinopica* P.-A. Moreau was recently proposed by Moreau (2009) to accommodate Malençon & Bertault's (1970) Moroccan collections of "*C. sinopica*", based on its incrusting pileic pigment (vacuolar in *B. sinopicus*).

The purpose of the present work is to resolve the most suitable taxonomic solution for the species *C. sinopica*, *C. subsinopica* and *C. afrosinopica* based on multigene data, type revisions, and new macro- and microscopical descriptions made on modern specimens.

MATERIALS AND METHODS

Morphological studies and fungarium material.— A piece of the type collection of *C. subsinopica* (H 6049138) was kindly donated by the Botanic Garden and Herbarium of the Finnish Museum of Natural History (H). Sequences of *C. subsinopica* were also unlocked from UNITE database by Dr. Bálint Dima. The following abbreviations are used: L = number of lamellae reaching the stipe, l = number of lamellulae between each pair of lamellae.

DNA extraction, amplification and sequencing.— Total DNA was extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). A portion of each sample was blended with the aid of a micropestle in 600 µL CTAB buffer (CTAB 2%, NaCl 1.4 M, EDTA pH 8.0 20 mM, Tris-HCl pH 8.0 100 mM). The resulting mixture was incubated for 15 min. at 65ºC. A similar volume of chloroform: isoamilalcohol (24:1) was added and carefully mixed with the samples until their emulsion. It was then centrifugated for 10 min at 13.000 g, and the DNA in the supernatant was precipitated with a volume of isopropanol. After a new centrifugation of 15 min at the same speed, the pellet was washed in cold ethanol 70%, centrifugated again for 2 min and dried. It was finally resuspended in 200 µL de ddH_2O. PCR amplification was performed with the primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) for the internal transcribed spacer region (ITS rDNA), while LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al.* 1991) were used to amplify the 28S rDNA region, EF1-983 F, EF1-1567R and EF-2218R for the translation elongation factor 1a, (*TEF*1 gene, Rehner and Buckley 2005), bRPB2-6F and bRPB2-7R2 for the RNA polymerase II second largest subunit (*RPB*2, Liu *et al.* 1999; Matheny *et al.* 2007), NS19b and NS41 for 18S rDNA ribosomal region (Hibbett 1996). PCR reactions were performed under a program consisting of a hot start at 95 ºC for 5 min, followed by 35 cycles at 94 ºC, 54 ºC and 72 ºC (45, 30 and 45 s respectively) and a final 72 ºC step 10 min. PCR products were checked in 1% agarose gels, and positive reactions were sequenced with one or both PCR primers. Chromatograms were checked searching for putative reading errors, and these were corrected.

Phylogenetic analyses.— 28S rDNA, *TEF*1, *RPB*2 and 18S rDNA sequences from representative species of the major lineages in the Tricholomatineae found in previous phylogenetic studies (Alvarado *et al.* 2015, Bellanger *et al.* 2015, Sánchez-García *et al.* 2014, 2016). *Suillus pictus* (Peck) Kuntze, *Pseudoarmillariella*

Table 1. Specimens used in molecular phylogenetic studies and their GenBank accession numbers.

Taxon	*Voucher*	*GenBank accession numbers*				
		ITS	*28S nLSU*	*tef1*	*rpb2*	*18S nSSU*
Albomagister subaustralis	TENN:064620		KJ417181		KJ424367	KJ417155
Ampulloclitocybe clavipes	AFTOL 542		AY639881	AY881022	AY780937	AY771612
Asterophora parasitica	CBS683.82		AF223191	EF421054	EF420988	
Atractosporocybe inornata	TO AV201012d		KJ681046	KJ681090	KJ681067	KJ681075
A. inornata	TO AV261012h		KJ681045	KJ681089	KJ681066	
Bonomyces afrosinopicus	LIP LYK13040015	**MG696613**	**MG696624**	**MG702590**	**MG702593**	**MG696621**
B. afrosinopicus	TO AV090118		**MH071390**			
B. arnoldii	LIP 0401106	**MG696614**				
B. arnoldii	LIP M. Bon 820828	**MG696615**				
B. arnoldii	TO AV051217	**MG696616**	**MG696625**	**MG702591**	**MG702594**	**MG696622**
B. arnoldii	TO AV080912	**MG696617**				
B. arnoldii	TO AV190511	**MG696618**	**MG696626**			
B. sinopicus	KATO Fungi 3689	**MG696619**	**MG696627**	**MG702592**	**MG702595**	**MG696623**
***B. sinopicus* (as *C. subsinopica*)**	H 6049138 TYPE	**MG696620**				
B. sinopicus	TUR 161075	UDB021300				
B. sinopicus	TUR 136948	UDB021301				
Callistosporium gramineum	AFTOL 978		AY745702	GU187761	KJ424369	AY752974
C. luteoolivaceum	JM99/124		AF261405	KP255477	DQ825406	KP255473
Calocybe ionides	HC77/133		AF223179	EF421057	EF420991	
Cleistocybe carneogrisea	TENN:063842		HQ728527			HQ728528
C. gomphidioides	AHS 17504 (MICH)	EF457513				
C. gomphidioides	AHS 76924 (MICH)	EF457514				
C. gomphidioides	AHS 70321 (MICH)	EF457517				

C. vernalis	AFTOL 721	NR 119593	AY647208			DQ092913
C. vernalis	PBM 1856 (WTU)	DQ486692				
C. vernalis	ADP 050506 (WTU)	EF416917				
Clitocella mundula	AFTOL 521		AY700182	KC816863	DQ474128	DQ089017
C. popinalis	ME Noordeloos 9867		GQ289213		GQ289280	
Clitocybe aff. *fellea*	PBM3028		HQ728534		HQ728536	HQ728535
C. nebularis	AFTOL 1495		DQ457658		DQ470833	DQ437681
C. nebularis	CBS362.65			EF421081	EF421011	
C. subditopoda	AFTOL 533		AY691889	DQ408150	EF420995	AY771608
C. dealbata	IE-BSG-HC95.cp3		AF223175	EF421080	EF825407	DQ825431
Clitolyophyllum akcaabatense	KATO Fungi 3184		KT934394		KT934395	
Clitopilus cystidiatus	ME Noordeloos 200350		GQ289147		GQ289220	
C. prunulus	TB8229		GU384615		GU384650	
Clitopilus sp.	VHAs07/02		EF421092	EF421086	DQ825408	
Clitopilopsis hirneola	CBS577.87		AF223163		GU384645	
Collybia tuberosa	AFTOL 557		AY639884	AY881025	AY787219	AY771606
Corneriella bambusarum	DED5462		KJ417185		KJ424370	
Dennisiomyces sp.	CFMR BZ-4245		KF291064		KF291066	KF291065
Entocybe nitida	TB7526		GU384626		GU384655	
E. turbidum	TB6949		GU384630		GU384656	
Entoloma abortivum	GDGM 27313		JQ320117		GQ289222	JQ993055
E. prunuloides	AFTOL 523		AY700180	DQ457633	DQ385883	AY665784
E. sinuatum	AFTOL 524		AY691891		KJ424375	AY657007
Guyanagarika anomala	TH7419		KX092110		KX092147	KX092115
G. aurantia	TH9693		KX092098		KX092132	KX092111

collections newly sequenced in this study are highlighted in bold characters

Table 1. Specimens used in molecular phylogenetic studies and their GenBank accession numbers *(continued)*.

Taxon	*Voucher*	*GenBank accession numbers*				
		ITS	*28S nLSU*	*tef1*	*rpb2*	*18S nSSU*
Hypsizygus ulmarius	DUKE-JM/HW		AF042584	EF421062	EF420996	
Infundibulicybe geotropa	ALV4344		KT122793			
I. gibba	AFTOL 1508		DQ457682	GU187759	DQ472727	DQ115780
I. gibba	PA 271-D	HM631715				
Lepista cf. *irina*	AFTOL 815		DQ234538	DQ028591	DQ385885	AY705948
Leucocybe candicans	AFTOL 541		AY645055	DQ408149	DQ385881	AY771609
L. connata	DUKE-JM90c		AF042590	EF421061	EF420995	
Leucopaxillus paradoxus	GB:0110968		KJ417206		KJ424383	KJ417165
Lyophyllum leucophaeatum	HAe251/97		AF223202		DQ367434	DQ367420
L. semitale	HC85/13		AF042581	EF421068	EF421002	
Musumecia bettlachensis	TO HG2284		JF926521	KJ681082	KJ681060	KJ681069
M. vermicularis	LUG18975		KJ681037	KJ681083	KJ681061	KJ681070
Myochromella inolens	CBS330.85		AF223201	EF421071	EF421004	
Neohygrophorus angelesianus	AFTOL 1719		DQ470814			DQ457698
Notholepista subzonalis	GB:0087013		KJ417208		KJ424385	KJ417167
Ossicaulis lignatilis	DUKE-D604/DUKE-D483		AF261397	EF421072	DQ825410	AF334923
Pleurocollybia imbricata	TJB9847		HM105568		HM105567	HM105568
Pogonoloma macrocephalum	TENN:037026		KJ417209			KJ417168
P. spinulosum	K(M):107286		KJ417238		KJ424401	KU058571
Porpoloma sejunctum	CONC:F0416		KJ417212		KJ424388	KU058573
Pseudoarmillariella ectypoides	AFTOL 1557		DQ154111	GU187733	DQ474127	DQ465341
Pseudoclitocybe cyathiformis	AFTOL 1998		EF551313	GU187742	GU187815	GU187659
P. obbata	AMB n 17139		KT122796			

Pseudoclitopilus rhodoleucus	GB:0110967	KJ417218		KJ424393	KU058577
Pseudolaccaria pachyphylla	GB:0066637	KU058542		KU139006	KU058579
Pseudoomphalina kalchbrenneri	GB:0066625	KU058541		KU139005	KU058578
Pseudotricholoma umbrosum	TENN:064489 NYBG:00505218	KJ417224		KJ424398	KU058580
Rhizocybe pruinosa	AH44073	KJ681038	KJ681084	KJ681084	
R. vermicularis	AH44078	KJ681039	KJ681085	KJ681063	
Rhodocybe fallax	CBS129.63	AF223166	EF421089	EF421018	
Rhodophana nitellina	ME Noordeloos 200435	GQ289215		GQ289282	
R. stangliana	N. Dam 05094	GQ289218		GQ289285	
Sagaranella tylicolor	BSI92/245	AF223195	EF421074	EF421006	
Singerocybe adirondackensis	TENN:64652	JX514103	KF208440	JX514140	HQ728531
S. alboinfundibuliformis	HKAS:74716	JX514106	KF208433	JX514138	
S. clitocyboides	HKAS:75453	JX514113	KF208444	JX514149	
S. phaeophthalma	TO AV071112a	KJ681041	KJ681087	KJ681064	KJ681074
S. umbilicata	HKAS:77290	KF208456	KF208438	KF208460	
Sphagnurus paluster	CBS717.87	AF223200	EF421075	EF421007	
Suillus pictus	AFTOL 717	AY684154	AY883429	AY786066	AY662659
Tephrocybe rancida	CBS204.47	AF223203	EF421076	EF421008	
Tephroderma fuscopallens	LUG18989	KJ701333	KJ701329		KJ701331
T. fuscopallens	EM4789-12	KJ701332	KJ701328		KJ701330
Tricholoma palustre	AFTOL 497	AY700197		DQ484055	AY757267
T. myomyces	KMS 589	U76459	DQ367429	DQ367436	DQ367422
T. subaureum	KMS 590	U76466	EF421085	EF421015	
T. viridiolivacea	PDD97890	JF706317		JF706319	JF706318
Tricholomella constricta	HC 84/75	AF223188	EF421079	DQ825412	DQ825434

collections newly sequenced in this study are highlighted in bold characters

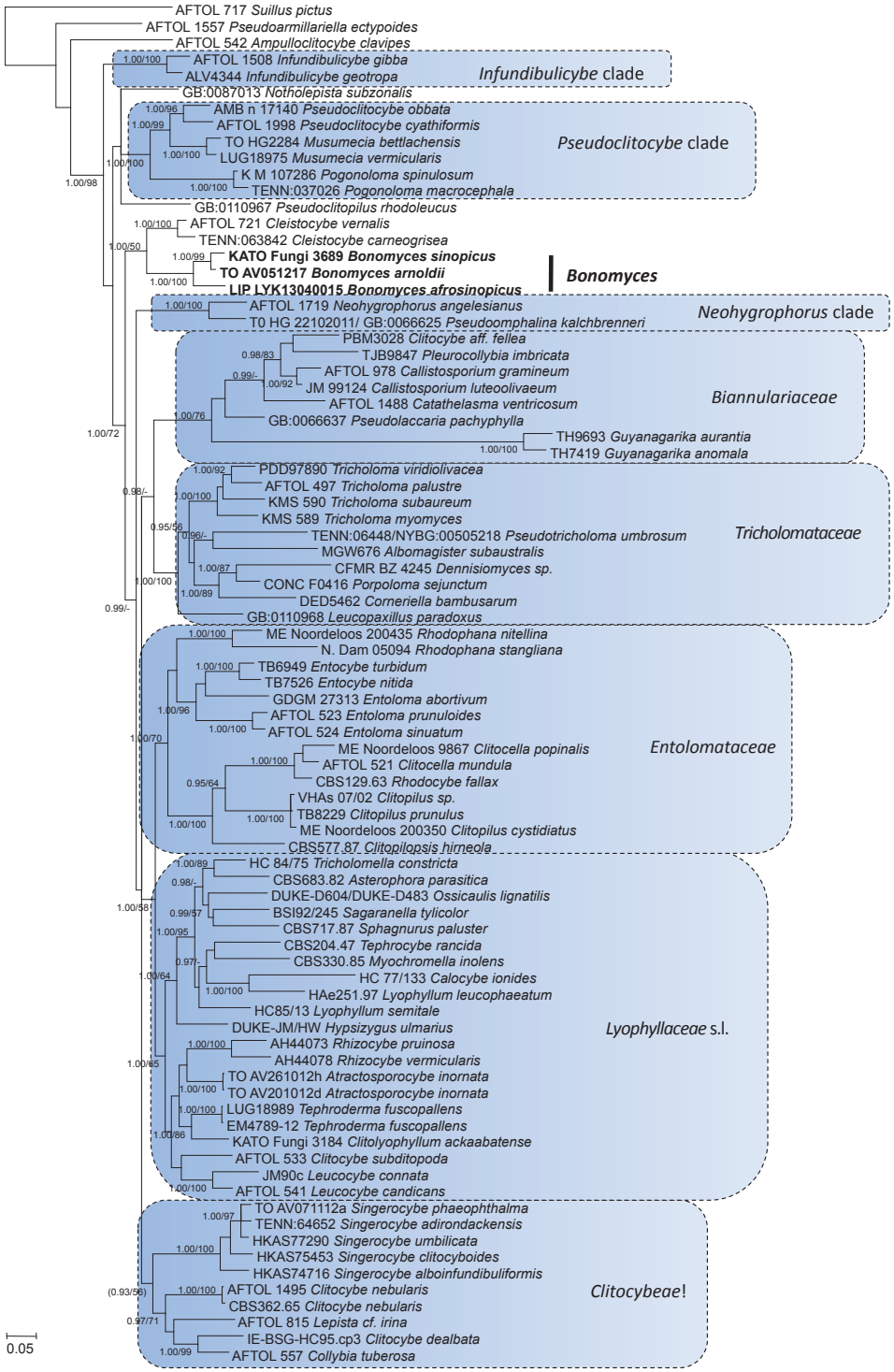
ectypoides (Peck) Singer and *Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys, were used as outgroups to root the tree, because of their phylogenetic position external to the Tricholomatineae (Matheny *et al.* 2006). Sequences from each marker (Table 1) were first aligned together in MEGA 5.0 (Tamura *et al.* 2011) with its Clustal W application and then corrected manually. All alignments were then merged into a single partitioned file. The different partitions included 386/777 (28S rDNA), 338/645 (*RPB*2), 204/435 (*TEF*1) and 139/755 (18S rDNA) variable sites. The partitioned file was loaded in PAUP* 4.0b10 (Swofford 2001), and each partition was subjected to MrModeltest 2.3 (Nylander 2004). Model GTR+Γ+I was selected for all partitions and implemented in MrBayes 3.1 (Ronquist and Huelsenbeck 2003), where a Bayesian analysis was performed (data partitioned, two simultaneous runs, six chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after 1.42M generations, standard deviation having fell below 0.01. Finally a full search for the best-scoring maximum likelihood tree was performed in RAxML (Stamatakis 2006) using the standard search algorithm (data partitioned, GTRMIX model, 2000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP). A similar procedure was followed to build a smaller phylogenetic tree of *Bonomyces* with ITS rDNA data (Table 1), with sequences coming from Ammirati *et al.* (2007), Matheny *et al.* (2006), and Bálint Dima (pers. comm.). Final ITS alignment included 305/661 variable sites. Model GTR+I was selected for Bayesian analysis.

RESULTS

Phylogenetic Results

The overall topology of the Tricholomatineae obtained with the analysis of 28S rDNA+*TEF*1+*RPB*2+18S rDNA (Fig. 1) was consistent with those published in previous works (Alvarado *et al.* 2015, Sánchez-García *et al.* 2014, 2016). The families Lyophyllaceae, Entolomataceae, Tricholomataceae and Biannulariaceae, all received a significant PP and BP support. Family Lyophyllaceae was related (1.00 PP, 65 BP) with the recently created genera *Tephroderma*, *Leucocybe*, *Atractosporocybe*, *Rhizocybe* and *Clitolyophyllum*, all of them forming the so-called Lyophyllaceae s. lato, and the whole group was also related to the Entolomataceae (1.00 PP, 58 BP). Tribe Clitocybeae received a sub-significant support (0.93 PP, 56 BP), probably because of the limited taxonomic diversity analyzed from this group. Several independent clades were also significantly supported by the analyses, such as the lineages of *Notholepista subzonalis* (Peck) Vizzini & Contu and *Pseudoclitopilus rhodoleucus* (Sacc.) Vizzini & Contu, as well as the clades of *Infundibulicybe*, *Pseudoclitocybe*, *Neohygrophorus*, and *Cleistocybe*. The samples morphologically identified as *Bonomyces sinopicus*, *Clitocybe subsinopica* and *C. afrosinopica*

Fig. 1. 50% Majority rule consensus 28S rDNA- *rpb*2- *tef*1- 18S rDNA phylogram of the Tricholomatineae obtained in MrBayes from 10 650 sampled trees. Nodes were annotated if supported by >0.95 Bayesian PP (left) or >70% ML BP (right). Non-significant support values are exceptionally represented inside parentheses. ▶


AFTOL 717 Suillus pictus
AFTOL 1557 Pseudoarmillariella ectypoides
AFTOL 542 Ampulloclitocybe clavipes
AFTOL 1508 Infundibulicybe gibba
ALV4344 Infundibulicybe geotropa
Infundibulicybe clade
GB:0087013 Notholepista subzonalis
AMB n 17140 Pseudoclitocybe obbata
AFTOL 1998 Pseudoclitocybe cyathiformis
TO HG2284 Musumecia bettlachensis
LUG18975 Musumecia vermicularis
Pseudoclitocybe clade
K M 107286 Pogonoloma spinulosum
TENN:037026 Pogonoloma macrocephala
GB:0110967 Pseudoclitopilus rhodoleucus
AFTOL 721 Cleistocybe vernalis
TENN:063842 Cleistocybe carneogrisea
KATO Fungi 3689 Bonomyces sinopicus
TO AV051217 Bonomyces arnoldii
LIP LYK13040015 Bonomyces afrosinopicus
Bonomyces
AFTOL 1719 Neohygrophorus angelesianus
T0 HG 22102011/ GB:0066625 Pseudoomphalina kalchbrenneri
Neohygrophorus clade
PBM3028 Clitocybe aff. fellea
TJB9847 Pleurocollybia imbricata
AFTOL 978 Callistosporium gramineum
JM 99124 Callistosporium luteolivaeum
AFTOL 1488 Catathelasma ventricosum
Biannulariaceae
GB:0066637 Pseudolaccaria pachyphylla
TH9693 Guyanagarika aurantia
TH7419 Guyanagarika anomala
PDD97890 Tricholoma viridiolivacea
AFTOL 497 Tricholoma palustre
KMS 590 Tricholoma subaureum
KMS 589 Tricholoma myomyces
TENN:06448/NYBG:00505218 Pseudotricholoma umbrosum
Tricholomataceae
MGW676 Albomagister subaustralis
CFMR BZ 4245 Dennisiomyces sp.
CONC F0416 Porpoloma sejunctum
DED5462 Corneriella bambusarum
GB:0110968 Leucopaxillus paradoxus
ME Noordeloos 200435 Rhodophana nitellina
N. Dam 05094 Rhodophana stangliana
TB6949 Entocybe turbidum
TB7526 Entocybe nitida
GDGM 27313 Entoloma abortivum
AFTOL 523 Entoloma prunuloides
AFTOL 524 Entoloma sinuatum
ME Noordeloos 9867 Clitocella popinalis
Entolomataceae
AFTOL 521 Clitocella mundula
CBS129.63 Rhodocybe fallax
VHAs 07/02 Clitopilus sp.
TB8229 Clitopilus prunulus
ME Noordeloos 200350 Clitopilus cystidiatus
CBS577.87 Clitopilopsis hirneola
HC 84/75 Tricholomella constricta
CBS683.82 Asterophora parasitica
DUKE-D604/DUKE-D483 Ossicaulis lignatilis
BSI92/245 Sagaranella tylicolor
CBS717.87 Sphagnurus paluster
CBS204.47 Tephrocybe rancida
CBS330.85 Myochromella inolens
HC 77/133 Calocybe ionides
HAe251.97 Lyophyllum leucophaeatum
HC85/13 Lyophyllum semitale
DUKE-JM/HW Hypsizygus ulmarius
Lyophyllaceae s.l.
AH44073 Rhizocybe pruinosa
AH44078 Rhizocybe vermicularis
TO AV261012h Atractosporocybe inornata
TO AV201012d Atractosporocybe inornata
LUG18989 Tephroderma fuscopallens
EM4789-12 Tephroderma fuscopallens
KATO Fungi 3184 Clitolyophyllum ackaabatense
AFTOL 533 Clitocybe subditopoda
JM90c Leucocybe connata
AFTOL 541 Leucocybe candicans
TO AV071112a Singerocybe phaeophthalma
TENN:64652 Singerocybe adirondackensis
HKAS77290 Singerocybe umbilicata
HKAS75453 Singerocybe clitocyboides
HKAS74716 Singerocybe alboinfundibuliformis
AFTOL 1495 Clitocybe nebularis
Clitocybeae!
CBS362.65 Clitocybe nebularis
AFTOL 815 Lepista cf. irina
IE-BSG-HC95.cp3 Clitocybe dealbata
AFTOL 557 Collybia tuberosa
0.05

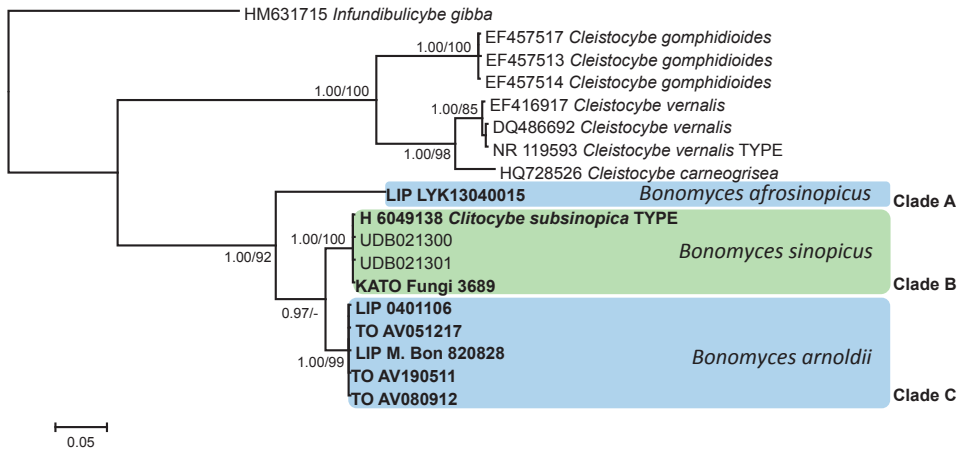


Fig. 2. 50% Majority rule consensus ITS rDNA phylogram of *Bonomyces* and *Cleistocybe* obtained in MrBayes from 750 sampled trees. Nodes were annotated if supported by >0.95 Bayesian PP (left) and >70% ML BP (right).

clustered together (1.00 PP, 50 BP) in another independent lineage related with *Cleistocybe* (1.00 PP, 50 BP).

The ITS analysis (Fig. 2) confirmed three main clades (A–C) within *Bonomyces*. Clade A was formed by a sample collected in Algeria and identified as *C. afrosinopica*. Samples morphologically identified as *B. sinopicus* (*C. sinopica*) were separated into clades B and C, which differ by some important macroscopical features: 1) pileus surface in group B is smooth and somewhat greasy, while it tends to become velvety and scaly with age in group C, a feature associated with the development of a trichodermal structure; 2) lamellae are crowded and first dirty white and later butter yellow in collections of clade B, but more spaced and always pure white in collections of clade C; and 3) stipe apex is pustulose in collections of clade C but not in those of clade B. Morphologically, clade B clusters specimens matching the standard concept of *C. sinopica*, as well as the holotype of *C. subsinopica*, while clade C matches perfectly Boudier's original description and plate of *C. arnoldii* Boud. (1896) (Fig. 3). For this reason, we propose here to apply the name *B. sinopicus* to clade B, with *C. subsinopica* and *C. pseudosquamulosa* Singer ex Bon as later synonyms, and combine *C. arnoldii* and *C. afrosinopica* into *Bonomyces*.

Taxonomy

Bonomyces Vizzini, *Index Fungorum* 159: 1 (2014)

MycoBank: MB 550625

Type species: Bonomyces sinopicus (Fr.: Fr.) Vizzini

Comments: Bonomyces was proposed as a new genus for *C. sinopica* because of its deviant morphological and genetic profile compared with other *Clitocybe* species. *Bonomyces* species have a very hard, filamentous stipe made of narrow and crowded hyphae, similar to that observed in *Infundibulicybe*. Spores are

multiguttulate with a thick lateral apiculus, the mediostratum of lamellae is made of inflate, not completely parallel hyphae with some vesicular elements which are often bifurcate and introduce irregularities in the rather parallel structure of the trama, and the subhymenium is pavimentous. The genus most closely related to *Bonomyces* seems to be *Cleistocybe*, although this relationship is not fully supported by ML analysis (1.00 PP, 50 BP), maybe because of the limited current taxonomic knowledge.

Bonomyes sinopicus (Fr.: Fr.) Vizzini, *Index Fungorum* 159: 1 (2014)

Figs 3a-c, 3j

MycoBank: MB 550626

Basionym: *Agaricus sinopicus* Fr.: Fr. in Fries, *Observ. mycol*. (Havniae) 2: 197 (1818)

= *Clitocybe chrysophylla* Hruby, *Hedwigia* 70: 243 (1930)

= *Clitocybe sinopica* var. *microspora* Métrod, *Bull. trimest. Soc. mycol. France* 54: 73 (1938)

= *Clitocybe subsinopica* Harmaja, Karstenia 18(1): 29 (1978)

= *Clitocybe sinopica* var. *aureospora* Contu, *Bol. Soc. broteriana*, 2a série 63: 383 (1990)

= *Clitocybe pseudosquamulosa* Singer ex Bon, *Docum. Mycol*. 26(no. 102): 17 (1996)

Basidiomata clitocyboid, not hygrophanous. **Pileus** 50–100 mm, convex to plane or umbilicate with slightly enrolled margin when young, later irregularly funnel-shaped or infundibuliform with undulating and uplifted margin; surface smooth, dull, reddish brown, pale brick, salmon color to light brown and darker at the center; umbo indistinct. **Lamellae** crowded, less or more decurrent, broad, with entire edge, white to beige and wood color when mature, L = 40–50, l = 3–9. **Stipe** 40–50 × 5–12 mm, cylindrical, sometimes tapering or larger toward the base, longitudinally fibrillose, sometimes curved and/or flattened, whitish pruinose, cinnamon, reddish brown, more reddish on handling, solid, apex grooved, with a large rhizomorph cluster at the base. **Context** white when young later light champagne. **Smell** farinaceous. **Taste** mild to slightly bitter. **Spore print** whitish to cream.

Spores [66] 6.5–*7.5*–8.5 × 4.0–*4.5*–5.4 µm, Q = 1.36–*1.55*–1.77, ellipsoidal to cylindrical, multiguttulate, smooth, thin-walled, with a thick lateral apiculus. **Basidia** 28–34 × 6.5–8 µm, cylindrical to clavate, mostly colourless, towards the edge partly with yellow content and short broad sterigmata. **Edge** fertile, with frequent hair-like cystidioles with long neck and inflate base, 38–55 × 3 µm (tail) × 5–6 µm (base), absent from the sides. **Subhymenium** pavimentous, 20 µm thick, up to 40 µm thick in hypophyllum. **Hymenopodium** 80–90 µm thick, slightly divergent, made of slender hyphae 2.5–4.5 µm wide, smooth, colourless. **Mediostratum** 80–100 µm broad, made of parallel hyphae 3–6.5 µm wide, smooth, colourless, often inflate at septa, a few vesicular, all colourless and smooth. **Suprapellis** an ixocutis 50–80 µm thick, softly erecting in depth, upper layer gelatinized and early collapsing, made of slender hyphae 2–9 µm wide; wall thickened (0.5–0.8 µm thick), smooth, pale yellow. **Subpellis** not differentiated. **Stipitipellis** made of numerous fascicules of hairs embedded in a mucus, arising from a cutis of slender hyphae 3–5 µm wide, with yellowish slightly punctuate wall. **Stipititrama** made of parallel, 3.5–4 µm wide, slender hyphae; wall smooth, thickened, yellowish. **Clamps** present at all septa.

Ecology & distribution: Gregarious, in meadows of mixed spruce-beech forests of Europe, from lowland areas of Scandinavia to montane belts of


a
b
c
d
e
II a
II b
II c
f
g
h
i
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k
l

Mediterranean countries. Harmaja suggested that this species is present also in North America, but this has not been confirmed. Summer.

Collections examined: FINLAND. Kuusamo, church village, ca. 5 km north of church, ca. 500 m SE of western end of the small lake Petäjälampi, in dry heath forest with *Pinus sylvestris*, in an ancient WWII camp site, leg. Teuvo Ahti, 08-VIII-1966, H 6049138 (holotype of *C. subsinopica*). Tammela, Riihivalkama, on a small gravel ridge, among standing and cut dead trees (burnt in 1997), leg. Maija-Liisa Heinonen, Pekka Heinonen, 22-VII-2001, TUR161075. Koski, Hongisto, among burned twigs, 03-VI-2000, TUR136948. TURKEY, Trabzon, Düzköy, Calköy, Hırsafa highland, meadows among *Abies* sp. and *Fagus* sp. forests, 1721 m asl, leg. E. Sesli, 10-VI-2016, KATO Fungi 3689. ***Clitocybe sinopica* var. *aureospora***. ITALY. Sardegna, Gutturumannu, in *Quercus* sp. woodland, leg. R. Rubiu, R. Turella, 03-XII-1989, Contu 89/436 (CAG, holotype).

Comments: Bonomyces sinopicus is here synonymized with Harmaja's *Clitocybe subsinopica*, after comparing Fries' (1818, 1821) and Harmaja's (1978) original descriptions, and sequencing the type of *C. subsinopica*. This mostly Northern species is present in Scandinavia and also in alpine areas of the Mediterranean basin, and it is apparently associated with conifer forests. *Clitocybe sinopica* var. *rimosa* H.E. Bigelow from North America differs in the rimose to rivulose pileus surface and lamellae staining vinaceous when bruised (Bigelow 1985).

Bonomyces afrosinopicus (P.-A. Moreau) P. Alvarado, P.-A. Moreau, Youcef Khodja & Contu **comb. nov**. **Figs** 3i, 3k

MycoBank: MB 823779

Basionym: *Clitocybe afrosinopica* P.-A. Moreau in Maire *et al.*, *Compl. Fl. Champ. Sup. Maroc de Malençon & Bertault*: 474 (2009).

Pileus first convex, with the center flattened and margin enrolled, then umbilicate, fibrillose to squamulose with age, yellowish-red, not hygrophanous. **Lamellae** decurrent, thick, distant, with a more or less creamy-yellowish edge. **Stipe** short, often eccentric, thicker under lamellae, solid, fibrillose. **Flesh** white. **Odor** and taste farinaceous. **Spore print** white.

Spores [68] 6.5–*7.5*–8.5 × 4.0–*4.5*–5.5 µm, Q = 1.33–*1.49*–1.67 cylindrical to pear-shaped, a few somewhat amygdaliform, with thick lateral apiculus; wall smooth, slightly thickened; content densely guttulate at maturity. **Basidia** 38–46 × 6.0–7.5 µm, 4-spored, clavate; content colourless, densely guttulate before maturity. **Subhymenium** narrow, ramose, weakly developed, made of tortuous hyphae 2.5–3.5 µm wide. **Hymenopodium** narrow, 10–15 µm thick, weakly differenciated, of divergent orientation, made of slender hyphae 3–5 µm wide. **Mediostratum** of regular structure, made of narrow cylindrical hyphae 4–8 µm wide, mixed with frequent vesicular hyphae 15–25 µm wide, colourless, often bifid at one end. **Hymenial cystidia** not observed. **Suprapellis** a thin ixocutis 20–25 µm thick, made

◀ **Fig. 3. a-c**. *Bonomyces sinopicus* KATO Fungi 3689. **d**. *B. arnoldii* LIP 0401106. **e**. *B. arnoldii* original plate (Boudier 1894). **f-h**. *B. arnoldii* TO AV080912. **i**. *Bonomyces afrosinopicus* LYK13091409. **j**. *Bonomyces sinopicus* KATO Fungi 3689 spores. **k**. *Bonomyces afrosinopicus* LYK14011600, subpellis hyphae with encrusting pigment. **l**. *Bonomyces arnoldii* LIP 0101394, pileipellis elements. Scale bars: a-c. 5 cm. d-g. 1 cm. h. 0.5 cm. i. 1 cm. j-k. 10 µm. k. 20 µm.

of colourless slender hyphae 2.5–4.0 µm, with scarce undifferentiated terminal elements. **Subpellis** 25–30 µm thick, ochre-yellow in KOH, made of 2-3 layers of parallel cylindrical hyphae 5–7 µm wide, anastomosing, abundantly encrusted by a coarse golden yellow pigment. **Pileitrama** parallel, made of slender short cylindrical hyphae 3–6 µm wide, calibrated, pale, minutely incrusted, sometimes geniculate at septa; gloeoplerous hyphae sparsed, thin, branching, 4–6 µm wide, very pale yellow in KOH. **Stipitipellis** a cortex of parallel hyphae, wall mostly incrusted locally purplish in KOH, with many gloeoplerous hyphae 4–6 µm wide with orange content; terminal elements rare and not differentiated. **Stipititrama** made of parallel hyphae 1.5–7.0 µm wide, colourless, the longest flexuose and often geniculate at septa; vascular hyphae not seen. **Clamps** present at all septa.

Ecology & distribution: In conifer forests of North Africa and under *Phoenix canariensis* in Sardinia, autumn and early winter.

Collections examined: ALGERIA: Blida, under *Cedrus atlantica*, leg. L. Youcef Khodja, IV-2013, LIP LYK13040015. Constantine, under *Pinus halepensis*, leg. L. Youcef Khodja, 16-I-2014, LIP LYK14011600. Darguina, under *Pinus halepensis*, leg. L. Youcef Khodja, 14-VII-2013, LIP LYK13091409. ITALY: Sardinia, Olbia-Tempio P., Golfo Aranci, loc. Golfo di Marinella, in grassy, sandy soil, near *Phoenix canariensis*, leg. M. Contu, 02-XI-2009, TO AV090118.

Comments: Bonomyces afrosinopicus can be discriminated from *B. sinopicus* because of its coarsely incrusted hyphae in the subpellis. The species was originally based on Malençon's original notes from Moroccan collections interpreted by Moreau (2009), who mentioned the poor condition of the original material. Actually this material could not be sequenced, but the modern collections from Algeria match this species in all features.

Bonomyes arnoldii (Boud.) P.-A. Moreau, Vizzini, P. Alvarado, **comb. nov**.
Figs 3d-h, 3l

MycoBank: MB 823780

Basionym: *Clitocybe arnoldii* Boud., *Bull. Soc. mycol. France* 10: 60 (1894) ≡ *Clitocybe sinopica* var. *arnoldii* (Boud.) Boud., *Icon. Mycol.* (Paris) 1: [1] (1904)

Lectotype (**hic designatus**): FRANCE: Somme, Ham, X-1892, leg. D. Arnould (PC, coll. E. Boudier, as "*Clitocybe sinopica* var. *arnoldi*")

Basidiomata clitocyboid. **Pileus** 25–60 mm, at first convex and sometimes shallowly umbonate, then plane to slightly depressed, umbilicate but not infundibuliform; margin not striate, slightly enrolled when young, later plane to uplifted, undulate, sometimes lobate and split; surface, dry, mat, finely fibrillose to (sub)tomentose, not hygrophanous, soon cracking concentrically into numerous appressed minute squamules, reddish brown, pale brick, salmon color to light brown. **Lamellae** usually subdistant and thickish (*Hygrophorus*-like), L = 30–40, l = 1–3, decurrent, whitish, with entire, undulating and concolorous edge. **Stipe** 25–50 × 4–10 (12) mm, cylindrical, usually enlarged at apex and slightly tapering at base, sometimes curved, solid then stuffed, concolorous with pileus or paler, cinnamon, reddish brown, longitudinally fibrillose, minutely granulose-floccose at apex, with granules that seem to delimit a pseudo-annular zone, white at the very apex, with white rhizomorphs at the base. **Context** white when young later light brown under the pileus and stipe surface. **Smell** rancid-farinaceous (reminding that of *Tephrocybe rancida* (Fr.) Donk). **Taste** farinaceous, mild to slightly bitter. **Spore-print** white.

Spores [22] 8.0–*8.5*–9.5 × 4.7–*5.5*–6.0 µm, Q = 1.46–*1.63*–1.85, ellipsoidal to slightly amygdaliform, with a broad lateral apiculus; content densely guttulate in

water and KOH. **Basidia** 25–32 × 6.5–8.0 µm, 4-spored. **Subhymenium** 10–12 µm thick, pavimentous, weakly developed, made of short polygonal elements 2–3 µm wide. **Hymenopodium** 20 µm thick, slightly divergent, made of slender hyphae 1.5–3.0 µm wide, guttulate. **Mediostratum** weakly differentiated, regular, made of parallel hyphae 3–4 µm wide, smooth, slightly yellowish, and sparse vesicular elements up to 10 µm wide. **Hymenial cystidia** not seen. **Pileipellis** a trichocutis 80–120 µm thick, made of numerous cystidioid terminal elements, prostrate or erected in fascicles, 30–65 × 5–16 µm, cylindrical to clavate, some attenuate or mucronate, thin- to thick-walled (0.8–1.5 µm), wall yellowish, smooth; content uniformly yellowish to nebulous. **Subpellis** weakly differentiated, made of parallel cylindrical hyphae 3–12 µm wide, with irregularly thickened wall up to 0.8–1.0 µm thick, smooth to faintly punctuate. **Stipitipellis** well-differentiated, 15–30 µm thick, made of slender parallel hyphae with slightly thickened, smooth to slightly incrusted wall, outer layer a trichoderm made of fasciculate elements 15–25 × 3–4 µm, cylindrical to clavate, some thick-walled and distinctly refringent. **Stipititrama** made of parallel cylindrical hyphae 2.5–4.5 µm wide, mixed with rather abundant parallel thromboplerous hyphae 1.8–2.5 µm. **Clamps** present at all septa.

Ecology & distribution: In conifer forests of Europe, especially in sandy soils with *Calluna*, from lowland areas of Scandinavia to montane belts of Mediterranean countries. Autumn and spring.

Collections examined: FRANCE. Somme (80), Beaumont-Hamel, Newfoundland cemetary, under *Pinus nigra* subsp. *laricio* in a park on acidic sandy soil, leg. B. Lefebvre, 02-IX-2015, PAM15090201, LIP 0401106. Idem, on ground, deciduous trees and grasses, leg. M. Bon, 03-XI-2002, LIP 0101394. ITALY. Piemonte, Valle di Susa, Salbertrand, under *Larix decidua*, 1.200 m a.s.l., 19-V-2011, leg. A. Vizzini, TO AV190511. Piemonte, Sauze di Cesana, Valle Argentera, under *Larix decidua*, 1720 m asl, 08-IX-2012, leg A. Vizzini ALV9059, TO AV080912. Friuli-Venezia Giulia, Udine, Malborghetto, 100 m a.s.l., under *Abies alba*, 23-IV-2016, leg. C. Angelini, TO AV051217 NORWAY. Unknown locality, 28-VIII-1982, leg. R. Kristiansen, LIP M. Bon 820828.

Comments: Clitocybe arnoldii Boud. (Boudier 1894) was originally found in October in northern France, and was is characterized by the presence of granules at the top of the stipe, brownish pileus and whitish lamellae, features matching the collections studied in the present work. It was considered a synonym of *C. sinopica* by Harmaja (1979) after checking original material of *C. arnoldii* stored at PC. It was the usual interpretation of *C. sinopica* in French literature (e.g. Bon 1983), excepting for Clemençon (1984) who considered *C. arnoldii* specifically different from *C. sinopica* because of its squamulose pileus and postulate stem apex. *Bonomyces arnoldii* can be separated from *B. sinopicus* and *B. afrosinopicus* because of its pileipellis full of clavate terminations, and morphologically by the scales early formed on the pileus and occasionally on the stipe. *Bonomyces arnoldii* seems to be present also in North America: Bigelow (1985) provided a description of *Clitocybe sinopica* mixing the features of *B. sinopicus* and *B. arnoldii*, but his Fig. 119, which shows specimens with a clearly squamulose pileus surface and spaced, hygrophoroid lamellae, fits very well our concept of *B. arnoldii*. *Agaricus squamulosus* var. *rufocinnamomeus* Alb. & Schwein. (Albertini & Schweinitz 1805: 217) has also a reddish squamulose pileus, but probably has lacrymoid spores as *Infundibulicybe squamulosa* (Pers.: Fr.) Harmaja.

DISCUSSION

In the present work, genetic data confirmed the phylogenetic meaning of genus *Bonomyces*, and suggested the combination of *C. arnoldii* and *C. afrosinopica* into this group. It was Harmaja (1969) who first erected *Clitocybe* section *Sinopicae* Harmaja for *C. sinopica* and *C. subsinopica*, characterized by a felty or squamulose pileic surface and a pileus covering formed of straight or subtrichodermal hyphae. Bon (1983) made *Sinopicae* a subsection of the *Gilvoideae* (Harmaja) H.E. Bigelow, within subgenus *Infundibuliformis* (Fr.) H.E. Bigelow, including three main groups of species: the *Sinopica* group (with farinaceous odor and reddish-orange color), the *Trullaeformis* group (with farinaceous odor and grayish), and other species with different odor and membranaceous (parietal) pigments. Bon's *Sinopica* group was composed of *C. sinopica*, *C. subsinopica* and *C. incilis* (Fr.: Fr.) Gillet, the latter being another early Friesian species said to produce a cucumber-like odor. Preliminary data on *Clitocybe trulliformis* (Fr.: Fr.) P. Karst. and related taxa, such as *C. font-queri* R. Heim, or *C. collina* (Velen.) Klán, suggest these species are not related with the Tricholomatineae (Vizzini *et al.* unpubl.), and this is also the conclusion suggested by the only ITS data in GenBank (*C. trulliformis* JF907809, Osmundson *et al.* 2013).

Fries (1818: 197) originally described *A. sinopicus* (erroneously written "*hinopicus*") as a spring species growing in wet places in forests ("*locis humidis in silvaticis, Junio*"). Its pileus is "*umbilicato glabro subcinnabarino*", apparently fading after drying, and the stipe is "*teres laevis glaber*". *Agaricus turfosus* Sow. (Sowerby 1799: 210), the only original material known to us since Fries reports to this plate in his protologue, is interpreted as a faded collection of *A. sinopicus*. Fries (1821: 83) also provided a shortened description mentioning a new variant "b. *multo major, pileo rimoso squamuloso*" growing on burnt ground. Later, Boudier (1894) described *C. arnoldii* (erroneously written "*arnoldi*"), a species similar to *C. sinopica* characterized by a scaly pileus and stipe. In the XXth century, *C. sinopica* was considered an uncommon but widespread species, characterized by its reddish pileus and stipe, decurrent lamellae, and typically strong smell, with some authors such as Velenovský (1920: 263) and Hruby (1930: 248) describing also a scaly pileus in *C. sinopica*, which they synonymize with *Agaricus squamulosus* var. *rufocinnamomeus* (Albertini & Schweinitz 1805: 217). Harmaja (1979: 22), after having examined very badly conserved original material, interpreted *C. arnoldii* as a borderline collection of *C. sinopica*, opinion also followed by Raithelhuber (2004: 75). On the contrary, Clémençon (1984: 37) kept the two species separate based on the squamulose pileus surface and the pustulate stipe apex in *C. arnoldii*. Harmaja distinguished a small-spored form of *C. sinopica* (Harmaja 1969: 70), which he later upgraded to species level as *C. subsinopica* Harmaja (Harmaja 1978: 29), highlighting its slender habit and yellowish spore print. Hruby (1930: 243) proposed also *C. chrysophylla* Hruby, a taxon similar to *C. sinopica* but for its yellowish lamellae, and absence of odor, and a very similar fungus was later described too by Contu (1990: 383) as *C. sinopica* var. *aureospora* Contu. On the other hand, Métrod (1938: 73) had already described a small-spored variety of *C. sinopica*, *Clitocybe sinopica* var. *microspora* Métrod, an invalid name replaced by *Clitocybe pseudosquamulosa* (Singer 1979: 209, Bon 1996: 17). Interestingly, none of the collections of *C. sinopica* studied by us showed spores reaching 9 µm long on natural deposits (stipe or pileus surfaces), while macrospores are not exceptional on hymenium (possibly formed by 2-spored basidia) and might explain the broad spore range annotated by

Harmaja (1969: 69; 7.5–11.5 × 4.8–6.1 µm). *Clitocybe arnoldii* has somewhat longer spores (up to 9.5 × 6.0 µm) but they do not reach such dimensions either. Harmaja himself (1969: 69) described *C. sinopica* with a "surface dry, +/- mat, rarely already cracked into small scales in young fruit bodies" and a smooth stipe without punctuations or hairs at the apex, and so it is here hypothesized that *C. arnoldii* is much less frequent than *C. sinopica* in Nordic countries.

The significant relationship found in the present work between *Bonomyces* and *Cleistocybe* should be taken cautiously, since there is only rDNA data available of *Cleistocybe* for analysis, and only Bayesian but not ML inference produced a significant support. *Cleistocybe* was proposed by Ammirati *et al.* (2007) for *Cleistocybe vernalis* Ammirati, A.D. Parker & Matheny, a species found by them in mixed forests in Washington state (USA), and *Cleistocybe gomphidioides* (A.H. Sm.) Ammirati, A.D. Parker & Matheny. *Cleistocybe* is characterized by the presence of an ephemeral veil, decurrent lamellae, inamyloid subfusoid or subcylindric spores, long narrow basidia, and divergent to interwoven hyphae in the lamellar trama and pileipellis. Two additional species were later added to *Cleistocybe*: *C. carneogrisea* (Malençon) Vizzini, and *C. pleurotoides* J. Favre ex Vizzini (Vizzini 2009), and Moreau (2009) proposed the provisional name *Cleistocybe malençonii* (nom. inval.) for a caespitose collection from Morocco, so far only documented by G. Malençon's notes and aquarelle. *Cleistocybe* and *Bonomyces* share a number of morphological features: divergent hymenophoral trama, stipititrama formed by densely arranged slender hyphae which give a dry and fibrous consistency, strong farinaceous smell, and a tendency to form scales and or granules on pileus and stipe (in *B. arnoldii*). *Bonomyces arnoldii* even shows occasionally a small roll under lamellae insertion which evokes a veil zone (pseudo-annular zone). However, *Bonomyces* species differ from the five *Cleistocybe* species cited above by the salmon to reddish pigment (absent in *Cleistocybe*), the white or pale, at most yellow lamellae (pinkish gray to vinaceous buff in *Cleistocybe*), the non-rooting stipe, the ellipsoidal spores with obtuse base (amygdaliform to fusiform with acute base in *Cleistocybe*). A synonymy between *Cleistocybe* and *Bonomyces* is rejected here, because of the genetic distance between both lineages, and the low statistic support of the monophyletic lineage encompassing both genera.

Paralepista can recall *Bonomyces* too, but differs from it because of its subglobose and nodulose spores. Phylogenetic analyses based on rDNA data suggest this genus could represent a basal lineage of the whole Tricholomatineae, probably related with the *Pseudoclitocybe* or *Infundibulicybe* lineages (Walther *et al.* 2005, Vizzini & Ercole 2012). Murrill (1915) suggested that the American species *Clitocybe subconcava* Peck (Peck 1902) could resemble also *C. sinopica*. This is a brownish or reddish-brown fungus with ellipsoid spores 5–8(–10) × 3.5–5.0 µm (Bigelow 1982). A study of the types and modern collections from the original sites would be in order to establish the most probable phylogenetic position of these species. *Clitocybe sinopicoides* Peck was proposed by Peck (1911) for a fungus measuring 2–4 cm long, with farinaceous smell, reddish tones in the pileus, decurrent lamellae, and fruiting in summer. These features are very similar to those of *C. sinopica*, but Bigelow (1982) reported lacrymoid spores measuring 6–10 × 2.5–4.0 µm, and proposed a synonymy with *Clitocybe squamulosa* (Pers.: Fr.) P. Kumm. Both species were later transferred by Harmaja (2003) to *Infundibulicybe* due to the lacrymoid shape of their spores.

Acknowledgments. We are grateful to Dr. Pertti Salo from the Botanic Garden and Herbarium of the Finnish Museum of Natural History for kindly providing us with a piece

of the holotype of *C. subsinopica*, Dr. Bart Buyck and Mr. Lionel Kervran from the National Museum of Natural History (PC, Paris, France) for the authorization of studying the holotype of *C. arnoldii*, Prof. Annalena Cogoni from the University of Cagliari (CAG, Cagliari, Italy) for the loan of the holotype of *C. sinopica* var. *aureospora*, and Prof. R. Courtecuisse and Mr. C. Lécuru from the University of Lille (LIP, Lille, France) for the loan of M. Bon's collections. We also thank Dr. Bálint Dima for providing sequences of modern specimens of *C. subsinopica* in UDB, as well as Mr. Pekka Heinonen, the collectors of the material from which they were generated. We thank Mr. Claudio Angelini for kindly letting us use his material and sequences of *C. sinopica*.

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