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Pseudoclitocybaceae fam. nov. (Agaricales, Tricholomatineae), a new arrangement at family, genus and species level

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Abstract

A new classification of several clitocyboid taxa is here proposed to accommodate results from multigenic phylogenetic inference. The analysis of ITS rDNA as well as a combined dataset including 18S and 28S rDNA, *tef*1 and *rpb*2 data, support significantly a shared monophyletic origin of the genera *Pseudoclitocybe*, *Musumecia* and *Pogonoloma*, and the species *Clitocybe alexandri* and *C. harperi*. The new family Pseudoclitocybaceae is here proposed to name this clade, characterized by the presence of loop-like clamp connections in most species, absence of cystidia, and parallel hymenophoral trama with broad, cylindrical hyphae with intracellular granulations. The new genera *Clitopaxillus* and *Harmajaea* are proposed to accommodate the type species *C. alexandri* and *H. harperi*, as well as the combination *H. wellsiae*. In addition, two new species are described: *C. fibulatus* has a differential distribution of clamp connections in the basidiome, while *H. guldeniae* is, by now, an exclusively European taxon with brownish pileus, somewhat decurrent gills, ovoid spores and basidia longer than those of *H. harperi*. Finally, the species concept within *Pseudoclitocybe* and *Pogonoloma* is discussed and descriptions of the most representative species are provided.

Keywords *Clitocybe* · *Clitopaxillus* · *Harmajaea* · *Musumecia* · *Pogonoloma* · *Pseudoclitocybe*

Introduction

Historically, species of the genus *Clitocybe* (Fr.: Fr.) Staude were treated in very different ways. Fries (1821, 1838), defined *Clitocybe* as a "tribe" of the genus *Agaricus* L., based on the shape of the pileus and lamellae insertion of its species, different from those observed in

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other "tribes" that were elevated to the rank of genus such as *Tricholoma* (Fr.: Fr.) Staude and *Pleurotus* (Fr.: Fr.) P. Kumm. Following the advances in microscopical observations, each new investigated character led to the exclusion of one or a few species from *Clitocybe* (Patouillard 1887; Maire 1913; Murrill 1915). The evidence of the amyloid reaction of spores in some species found by Kühner and Maire (1934) led to the creation of the genera *Aspropaxillus* Kühner & Maire (smooth spores) and *Leucopaxillus* Boursier (warty spores; Boursier 1925, supported by Kühner's early observations). Singer employed the same feature for the definition of additional genera such as the tricholomatoid *Porpoloma* Singer (Singer 1952) and the clitocyboid *Cantharellula* Singer (Singer 1936). *Cantharellula* included the clampless *Pseudoclitocybe* (Singer) Singer (Singer 1943) and the clamped *Pseudoomphalina* (Singer) Singer (Singer 1948) as subgenera, but they were later elevated to genus level (Singer 1956). Most of these taxa and many others were recently confirmed to represent independent lineages outside the Clitocybeae Fayod clade by means of DNA analysis (Redhead et al. 2000, 2002; Harmaja 2003; Walther et al. 2005; Ammirati et al. 2007; Garnica et al. 2007; Vizzini et al. 2010, 2011; Ovrebo et al. 2011; Vizzini and Ercole 2012; Sánchez-García et al. 2014, 2016; Alvarado et al. 2015), although the relationships of many species remain largely unresolved. Evidence that *Pseudoclitocybe* represents an independent clade from Clitocybeae was first found by Moncalvo et al. (2002), Walther et al. (2005) and Garnica et al. (2007), and then confirmed by Vizzini et al. (2011) who described a new genus in this linage, *Musumecia* Vizzini & Contu. Later, a third genus, *Pogonoloma* (Singer) Sánchez-García was confirmed to be related to the Pseudoclitocybe clade by Sánchez-García et al. (2014).

The species epithet for the type species of *Pseudoclitocybe*, *P. cyathiformis* (Bull.: Fr.) Singer, was sanctioned by Fries (1821, as *Agaricus cyathiformis* Bull). Fries described this species as having a slightly infundibuliform, subglabrous, dark to blackish pileus turning pale when dry, with ashy lamellae and with an elastic fibrillose stipe, found among mosses on forest soil and on rotten logs. In the same work he also sanctioned the species epithet for *P. expallens* (Pers.: Fr.) M.M. Moser (as *A. expallens* Pers.: Fr.), and described a very similar species found from similar habitats with smaller basidiomata and paler, flat to umbilicate pileus. Later Fries (1838) also proposed a third infundibuliform species, *P. obbata* (Fr.) Singer (as *A. obbatus* Fr.), with a glabrous, dark greyish tinted stipe, and associated with *Pinus* sp. A fourth species, *Clitocybe bacillaris* Pers., with violaceous tints in its lamellae first found near *Betula* sp. trees in Vincennes (Paris, France), was transfered by Singer (1961) and named *Pseudoclitocybe bacillaris* (Pers.) Singer after the examination of the type specimen revealed clampless hyphae. A fifth European species, *Clitocybe atra* Velen. (Velenovský 1934), a dark brown fungus found among grasses of a *Larix* sp. forest was also transfered to *Pseudoclitocybe* as *P. atra* (Velen.) Harmaja by Harmaja (1974, 1976) because of its clampless hyphae and long amyloid spores. Harmaja reported that this species was very similar to *P. cyathiformis*, but developed a smaller stipe (4.0–6.5 × 0.3–1.0 in *P. atra* vs. 5.0–10.0 × 0.5–1.0 cm in *P. cyathiformis*), abundant dermatocystidia in the pileus, and can be found in grasslands. Finally, Singer and Kuthan (1980) described *P. beschidica* as a new species growing on rotten logs of *Fagus* in the Czech Republic differing from *P. cyathiformis* because of its shorter spores not exceeding the length of 8.5 µm, although later reports often merge both taxa (Kuthan et al. 1999; Adamčík et al. 2007). As a result of this confusion at the species level, Bas et al. (1995) recognized only *P. cyathiformis* and *P. obbata* as independent species, the first growing in woods, the second one in sandy soils. According to Knudsen & Vesterholt (2008), the name *P. cyathiformis* should be applied to non-striated specimens, while *P. expallens* would be the prioritary synonym over *P. obbata* and *P. atra*, and it would apply to striate collections growing in herbaceous habitats.

A few species of *Clitocybe*, e.g. *C. alexandri* (Gillet) Gillet and *C. harperi* Murrill share some morphological traits with the genera in the Pseudoclitocybe clade, suggesting a putative phylogenetic relationship. *Clitocybe alexandri* was first described as *Paxillus alexandri* Gillet (Gillet 1873) honouring Paul Alexandre, who collected it growing among mosses in France, probably at the bois de la Garenne, Ferrière-Brochard, Alençon (Gillet 1869). *Paxillus alexandri* was classified within *Paxillus* subgen. *Lepista*, and subsequently combined as *Lepista alexandri* by Gillet (1876) when both genera were separated. The name was later combined into *Clitocybe* by Gillet (1884). Moreau (2009) discussed the morphological species concept of *C. alexandri* when comparing the typical lowland European specimens with the paler *C. alexandri* var. *alutacea* P.-A. Moreau from Moroccan *Cedrus* forests. He observed that typical lowland European specimens lacked clamp connections in most parts of the basidiome (pileus, stipe, and pileipellis), in contrast to the observations made by other authors (Bigelow 1965; Kuyper 1995), and developed loop-like clamps as well as more or less open "false clamps" in hymenophoral tissues. European specimens resembling *C. alexandri* but lacking both clamps and false clamps were often identified as the North American species *C. harperi* Murrill. This taxon was first proposed to accommodate specimens collected in California and Washington (Murrill 1913), but later it has been reported also from Tennessee and Canada (Bigelow 1982), Finland

and Sweden (Harmaja 1969), France (Bon 1997), and Norway (Gulden 2006).

A broad-ranged phylogenetic analysis on clitocyboid species by the authors suggested that all these apparently dissimilar species formed a monophyletic lineage including the tricholomoid genus *Pogonoloma*. In the present work, a formal name for the Pseudoclitocybe clade is introduced, as well as a systematic and taxonomic treatment of the main European species recognized in the clade after genetic and morphological analysis of several modern collections. A new classification for the whole clade at the family, genus and species levels is proposed.

Materials and methods

Fungal specimens

Collections from the following public herbaria were studied: Universidad de Alcalá, Spain (AH), Associazione Micologia Bresadola (AMB), Jardin Botanique de Montréal, Canada (CMMF), University of Helsinki, Finland (H), Université de Lille, France (LIP), Museo di Storia Naturale di Venezia, Italy (MCVE), University of Michigan, USA (MICH), Botanical Museum, University of Oslo, Norway (O), University of Turin, Italy (TO), University of Tartu, Estonia (TU), University of Turku, Finland (TUR, TUR-A), and University of Washington, USA (WTU-F). Specimens (or duplicates) from private herbaria of Didier Borgarino (DBo) and Bálint Dima (DB) were also used for this study (Online Resource 1). For light microscopy (LM), spores were mounted in water, Melzer's reagent, lactic acid in glycerol (Kirk et al. 2001) or alkaline latex L4 (Clémençon 1972). Twenty-five to fifty spores per specimen were arbitrarily selected and measured partly with Mycometre 2 (Fannechère 2006). A standardized protocol to test amyloidity was applied: a lamellae sample was hydrated in tap water for 1–2 h, and then heated in a drop of Melzer's reagent in a teaspoon until the boiling point was reached. The sample immersed in Melzer was immediately removed from the heat and transferred to a flat Teflon surface, cut into three or four pieces, and transferred again to a slide with a drop of fresh Melzer's reagent. The excess liquid is then removed and the sample gently squashed, and examined with a 60× or 100× brightfield objective (numerical aperture NA 1.3, diaphragm open to about 50% range, aperture field 0.9–1.0).

DNA extraction, PCR amplification and sequencing

DNA extraction and PCR amplification were performed as described by Alvarado et al. (2015) or else following Dima et al. (2016). Primers ITS1F and ITS4 (White et al. 1990; Gardes and Bruns 1993) were used for the ITS region; primers LR0R and LR5 (Vilgalys and Hester 1990) were used for the 28S rDNA, NS19b and NS41 (Hibbett 1996) for the 18S rDNA, EF1-983F and EF1-1567R (Rehner and Buckley 2005) for the translation elongation factor 1a (*tef*1) gene, and bRPB2-6F, bRPB2-7R, fRPB2-7cR and bRPB2-7R2 for the DNA-directed RNA polymerase II second largest subunit two (*rpb*2) gene (Liu et al. 1999; Matheny 2005; Matheny et al. 2007), for both PCR and sequencing. Sequences were edited for errors in MEGA 5 (Tamura et al. 2011).

Phylogenetic analysis

Sequences were aligned with the most similar sequences in GenBank identified through BLASTn searches (Altschul et al. 1990). Two alignments were constructed: 41 ITS sequences and a combined 28S rDNA-*rpb*2-*tef*1-18S rDNA alignment including sequences from 72 specimens. Homologous sequences were retrieved from Moncalvo et al. (2002), Matheny et al. (2007), Binder et al. (2010), Malysheva et al. (2010), Baroni and Matheny (2011), Baroni et al. (2011), Vizzini et al. (2010, 2011, 2012), He et al. (2013), Lodge et al. (2014), Osmundson et al. (2013), Hofstetter et al. (2014), Musumeci and Contu (2014), Qin et al. (2014), Sánchez-García et al. (2014, 2016), Alvarado et al. (2015), Musumeci (2014), and Li et al. (2016). Sequences first were aligned in MEGA 5 (Tamura et al. 2011) with Clustal W (Thompson et al. 1994) and edited manually. The ITS alignment contained large insertions in some species, but these regions were excluded from the final analyses. Alignments are available in TreeBase (S21775).

Aligned loci were subjected to MrModeltest 2.3 (Nylander 2004) in PAUP*4.0b10. Bayesian analysis was performed with optimal models in MrBayes 3.1 (Ronquist and Huelsenbeck 2003) with 28S rDNA-*rpb*2-*tef*1-18S rDNA data partitioned, two simultaneous runs, six chains, temperature set to 0.2, and sampling every 100th generation until convergence parameters were met after about 1.45M (ITS) and 1.88M generations (28S rDNA-*rpb*2-*tef*1-18S rDNA). The first 25% trees were discarded as burn-in. Last, a full query for the best-scoring maximum likelihood tree was performed in RAxML (Stamatakis 2006) using the standard search algorithm (28S rDNA-*rpb*2-*tef*1-18S rDNA data partitioned, 2000 bootstrap replications). Support values were considered significant when bootstrap (BP) values were above 70% and posterior probability (PP) values were above 0.95.

Results

Phylogenetic analysis

Bayesian and ML analyses of the combined 28S rDNA-*rpb2*-*tef*1-18S rDNA dataset (Fig. 1) significantly support the existence of at least six major lineages within the Tricholomatineae Aime, Dentinger & Gaya (Dentinger et al. 2015): those formed by the families Biannulariaceae Jülich (= Catathelasmataceae Wasser), Entolomataceae Kotl. & Pouzar, Lyophyllaceae Jülich, Tricholomataceae R. Heim ex Pouzar, as well as the Clitocybeae and the Pseudoclitocybe clades. A significant relationship was obtained between Biannulariaceae and Tricholomataceae, and between Entolomataceae and Lyophyllaceae, as already noticed by Sánchez-García et al. (2016). Beside the monophyletic core of the Lyophyllaceae, several lineages seem more distantly related (*Atractosporocybe* P. Alvarado, G. Moreno & Vizzini, *Clitocybe* cf. *subditopoda* Peck, *Clitolyophyllum* Sesli, Vizzini & Contu, *Leucocybe* Vizzini, P. Alvarado, G. Moreno & Consiglio, *Rhizocybe* Vizzini, G. Moreno, P. Alvarado & Consiglio, *Tephroderma* Contu & Musumeci), suggesting a putative wider concept of this family or the existence of multiple lineages basal to it, in agreement with previous works (Alvarado et al. 2015; Bellanger et al. 2015). These four families were significantly related with the Clitocybeae and the lineages of *Pseudoomphalina* and *Cleistocybe* Ammirati, A.D. Parker & Matheny.

Multigenic (Fig. 1) and ITS rDNA (Fig. 2) analyses agree to support significantly the monophyletic origin of *Pseudoclitocybe*, *Musumecia*, *Pogonoloma*, "*Clitocybe*" *alexandri* and "*Clitocybe*" *harperi*. *Pogonoloma* was consistently found to be the most basal clade of the group. Three different genetic lineages were found in the "*Clitocybe*" *harperi* clade, two of them present in America and Europe, and the other found only, by now, in Europe. In addition, two lineages were observed in the clade of "*Clitocybe*" *alexandri*, one of them composed of samples coming from lowland European areas with "false" clamp connections in the hymenium and subhymenium, the other found in alpine or boreal habitats presenting clamp connections all over the basidiome. Based on these phylogenetic results, an updated taxonomic arrangement of these lineages is proposed below, and the main differences between them are summarized in Table 1.

Taxonomy

Pseudoclitocybaceae **Vizzini, Consiglio, P.-A. Moreau & P. Alvarado, fam. nov.**

Mycobank MB 823302

Fig. 1 50% majority rule 28S rDNA-*rpb2*-*tef*1-18S rDNA consensus phylogram of the family Pseudoclitocybaceae and related families of the tricholomatoid clade obtained in MrBayes from 14,100 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

Etymology: from the type genus *Pseudoclitocybe*

Diagnosis: Large- to medium-sized basidiomes (5–15 cm), tricholomatoid or clitocyboid, pileus umbilicate to convex-applanate, sometimes with persistent umbo, hygrophanous or not, lamellae decurrent, subdecurrent to uncinate; mycelium usually developed superficially on substrate as patches with or without rhizomorphs, rooting in tricholomatoid species; hymenophoral trama subregular to somewhat divergent; context homomorphous with cylindrical hyphae > 4 µm diam., usually with acyanophilic intracellular globules, mixed or not with thromboplerous hyphae, exclusively sarcodimitic in tricholomatoid species; subhymenium ramose, repent, easily dissociated; hymenium usually without cystidia; basidia narrowly clavate, small, mostly < 35 × 8 µm, without siderophilic granulations; loop-like (medallion) clamp connections usually present at least in mycelium; pileipellis a dry or weakly gelatinized cutis, frequently diverticulate, occasionally a trichocutis; spores usually smooth, amyloid or not, acyanophilous, with broad, truncate and prominent apicule; mating behaviour heterothallic bipolar (for documented species); nuclear behaviour holocoenocytic (for documented species, spores binucleate and terminal hyphae in the primary mycelium plurinucleate). Probably only saprobic (uncertain for *Pogonoloma*). Present worldwide, mostly temperate to boreal.

Type genus: *Pseudoclitocybe* (Singer) Singer

Clitopaxillus **G. Moreno, Vizzini, Consiglio & P. Alvarado, gen. nov.**

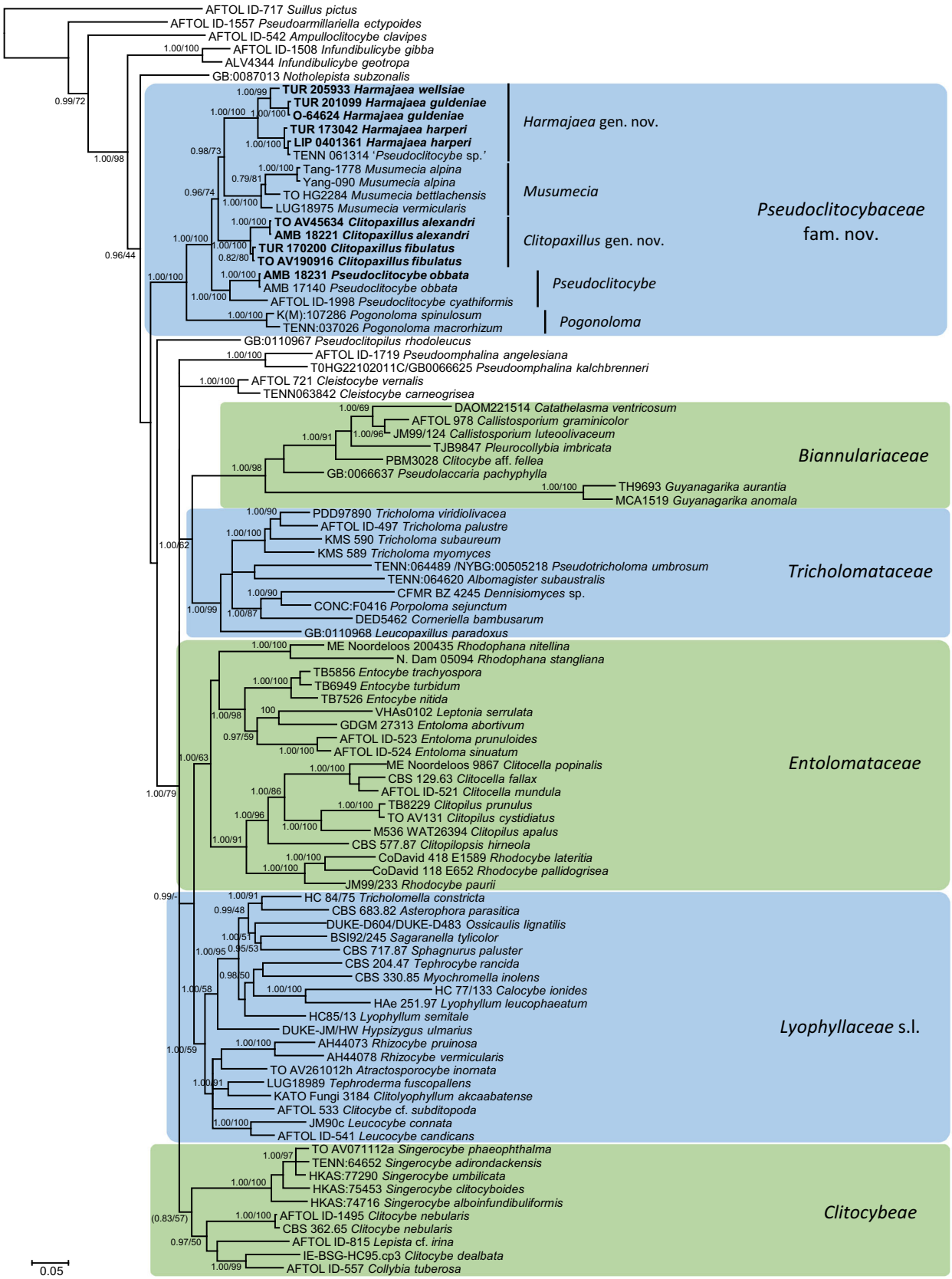
Mycobank MB 823303 (Figs. 3b, c, 4a, b, g, h)

Etymology: from *Clitocybe* and *Paxillus*, the genera where *C. alexandri* was previously classified.

Diagnosis: basidiomes large-sized, clitocyboid, fleshy, with convex to flattened brownish pileus lacking umbo, glabrous pileipellis, not hygrophanous. Lamellae deeply decurrent. Spores slightly amyloid, ovoid. Saprobic, on litter. Clamp connections present at least on hymenophoral hyphae and mycelium. Northern Hemisphere, Europe and North Africa.

Type species: *Clitopaxillus alexandri* (Gillet) G. Moreno, Vizzini, Consiglio & P. Alvarado

Comments: species of *Clitopaxillus* were previously considered members of *Clitocybe* section *Disciformes* (Fr.) Quél., along with *C. harperi* (Singer 1986; Bon 1991), which is also transferred to a new genus in the present work. Another remarkable member of this section is *C.*


AFTOL ID-717 Suillus pictus
AFTOL ID-1557 Pseudoarmillariella ectypoides
AFTOL ID-542 Ampulloclitocybe clavipes
AFTOL ID-1508 Infundibulicybe gibba
ALV4344 Infundibulicybe geotropa
GB:0087013 Notholepista subzonalis
TUR 205933 Harmajaea wellsiae
TUR 201099 Harmajaea guldeniae
O-64624 Harmajaea guldeniae
TUR 173042 Harmajaea harperi
LIP 0401361 Harmajaea harperi
TENN 061314 'Pseudoclitocybe sp.'
Harmajaea gen. nov.
Tang-1778 Musumecia alpina
Yang-090 Musumecia alpina
TO HG2284 Musumecia bettlachensis
LUG18975 Musumecia vermicularis
Musumecia
TO AV45634 Clitopaxillus alexandri
AMB 18221 Clitopaxillus alexandri
TUR 170200 Clitopaxillus fibulatus
TO AV190916 Clitopaxillus fibulatus
Clitopaxillus gen. nov.
Pseudoclitocybaceae fam. nov.
AMB 18231 Pseudoclitocybe obbata
AMB 17140 Pseudoclitocybe obbata
AFTOL ID-1998 Pseudoclitocybe cyathiformis
Pseudoclitocybe
K(M):107286 Pogonoloma spinulosum
TENN:037026 Pogonoloma macrorhizum
Pogonoloma
GB:0110967 Pseudoclitopilus rhodoleucus
AFTOL ID-1719 Pseudoomphalina angelesiana
T0HG22102011C/GB0066625 Pseudoomphalina kalchbrenneri
AFTOL 721 Cleistocybe vernalis
TENN063842 Cleistocybe carneogrisea
DAOM221514 Catathelasma ventricosum
AFTOL 978 Callistosporium graminicolor
JM99/124 Callistosporium luteoolivaceum
TJB9847 Pleurocollybia imbricata
PBM3028 Clitocybe aff. fellea
GB:0066637 Pseudolaccaria pachyphylla
TH9693 Guyanagarika aurantia
MCA1519 Guyanagarika anomala
Biannulariaceae
PDD97890 Tricholoma viridiolivacea
AFTOL ID-497 Tricholoma palustre
KMS 590 Tricholoma subaureum
KMS 589 Tricholoma myomyces
TENN:064489 /NYBG:00505218 Pseudotricholoma umbrosum
TENN:064620 Albomagister subaustralis
CFMR BZ 4245 Dennisiomyces sp.
CONC:F0416 Porpoloma sejunctum
DED5462 Corneriella bambusarum
GB:0110968 Leucopaxillus paradoxus
Tricholomataceae
ME Noordeloos 200435 Rhodophana nitellina
N. Dam 05094 Rhodophana stangliana
TB5856 Entocybe trachyospora
TB6949 Entocybe turbidum
TB7526 Entocybe nitida
VHAs0102 Leptonia serrulata
GDGM 27313 Entoloma abortivum
AFTOL ID-523 Entoloma prunuloides
AFTOL ID-524 Entoloma sinuatum
ME Noordeloos 9867 Clitocella popinalis
CBS 129.63 Clitocella fallax
AFTOL ID-521 Clitocella mundula
TB8229 Clitopilus prunulus
TO AV131 Clitopilus cystidiatus
M536 WAT26394 Clitopilus apalus
CBS 577.87 Clitopilopsis hirneola
CoDavid 418 E1589 Rhodocybe lateritia
CoDavid 118 E652 Rhodocybe pallidogrisea
JM99/233 Rhodocybe paurii
Entolomataceae
HC 84/75 Tricholomella constricta
CBS 683.82 Asterophora parasitica
DUKE-D604/DUKE-D483 Ossicaulis lignatilis
BSI92/245 Sagaranella tylicolor
CBS 717.87 Sphagnurus paluster
CBS 204.47 Tephrocybe rancida
CBS 330.85 Myochromella inolens
HC 77/133 Calocybe ionides
HAe 251.97 Lyophyllum leucophaeatum
HC85/13 Lyophyllum semitale
DUKE-JM/HW Hypsizygus ulmarius
AH44073 Rhizocybe pruinosa
AH44078 Rhizocybe vermicularis
TO AV261012h Atractosporocybe inornata
LUG18989 Tephroderma fuscopallens
KATO Fungi 3184 Clitolyophyllum akcaabatense
AFTOL 533 Clitocybe cf. subditopoda
JM90c Leucocybe connata
AFTOL ID-541 Leucocybe candicans
Lyophyllaceae s.l.
TO AV071112a Singerocybe phaeophthalma
TENN:64652 Singerocybe adirondackensis
HKAS:77290 Singerocybe umbilicata
HKAS:75453 Singerocybe clitocyboides
HKAS:74716 Singerocybe alboinfundibuliformis
AFTOL ID-1495 Clitocybe nebularis
CBS 362.65 Clitocybe nebularis
AFTOL ID-815 Lepista cf. irina
IE-BSG-HC95.cp3 Clitocybe dealbata
AFTOL ID-557 Collybia tuberosa
Clitocybeae
0.05

nebularis, currently retained as the most suitable lectotype species of *Clitocybe* (for discussion see Redhead et al. 2002), which lacks a central umbo and loop-like clamp connections, and has cyanophilous, non-amyloid and rough spores, and which belongs phylogenetically to the Clitocybeae clade (Matheny et al. 2006).

***Clitopaxillus alexandri* (Gillet) G. Moreno, Vizzini, Consiglio & P. Alvarado, comb. nov.**

Mycobank MB 823304 (Fig. 3b)

Basionym: *Paxillus alexandri* Gillet, Bull. Soc. Linn. Normandie, sér. 2 7: 157 (1873)

≡ *Lepista alexandri* (Gillet) Gillet, Hyménomycètes (Alençon): 196 (1876)

≡ *Clitocybe alexandri* (Gillet) Gillet, Tabl. analyt. Hyménomyc. France (Alençon): 28 (1884)

= *Clitocybe alexandri* var. *alutacea* P.-A. Moreau in Maire et al., Compl. Fl. Champ. sup. Maroc. G. Malençon et R. Bertault: 449 (2009)

= *Agaricus propinquus* var. *spadiceus* Pers., Mycol. eur. (Erlanga) 3: 63 (1828) (fide Singer 1961)

= *Paxillus extenuatus* s. Ricken (1915)

= *Clitocybe harperi* s. Bon (1991)

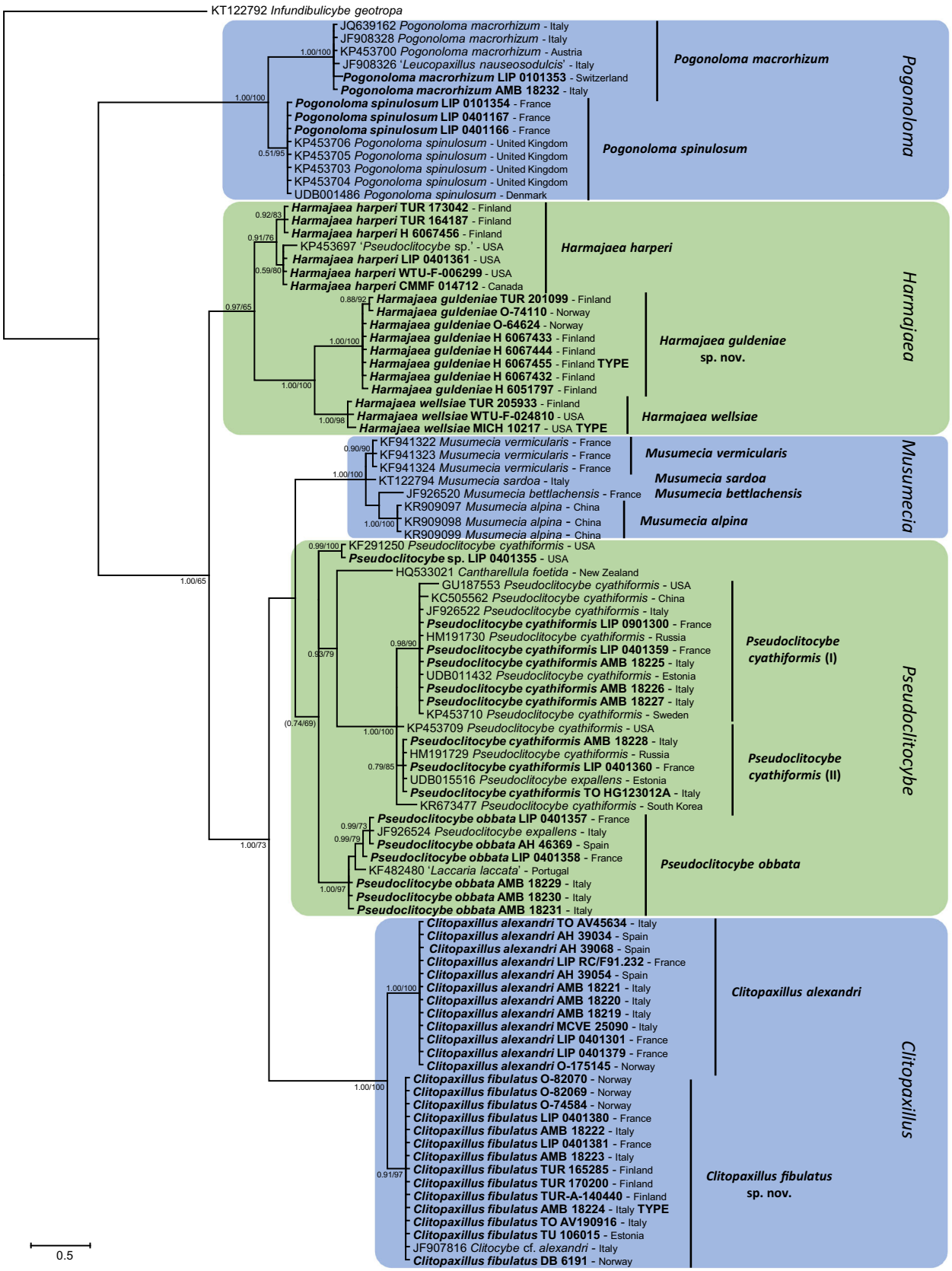
Description: Pileus first convex, flattened with age, with a central umbo, grayish brown to reddish yellow, with margin enrolled, measuring (5–)10–15(–20) cm in diam., smooth, somewhat guttulated and finally cracked. Lamellae arcuate to decurrent, pale brownish grey to yellowish, subconcolorous. Stipe 4–10 × 2–4(–5) cm, solid, cylindrical, yellowish white to pale yellow. Context whitish, dense. Smell cyanic (i.e., bitter almonds). Spores 4.7–5.5 × 3.5–3.9 µm (n = 32), (average 5.1 × 3.7 µm), Q = 1.27–1.49 (Q_m = 1.38); V_m = 36 µm^3, broadly ellipsoid to ellipsoid in front view, slightly amygdaliform to larmiform in side view, hyaline; hilar appendix often very pronounced, 0.8–1 µm long; in Melzer's spore wall stains bluish-gray. Basidia 26–31 × 4.9–5.8 µm, four-spored, a few two-spored, long clavate to subcylindrical, sterigmata up to 5 µm long. Hymenophoral trama subregular, composed of hyphae up to 12 µm wide, hyaline in alkaline latex L4, yellow in Melzer's. Cheilocystidia and pleurocystidia not observed. Pileipellis a trichocutis of variously intertwined, very loose, slightly gelatinized, filamentous hyphae, 3.0–6.3 µm wide, smooth, with intracellular brownish pigment, sometimes with a very fine encrusting epiparietal pigment. Pileitrama hyphae cylindrical, up to 12.6 µm wide, thromboplerous hyphae rare and inconspicuous. Clamp connections present at all septa of the subhymenial hyphae and at the base of basidia and basidioles, occasionally verticillate or unclosed ("false clamps"), scattered in mycelium, absent elsewhere.

Ecology: mediterraneo-atlantic, found in deep litter under pines (*P. halepensis*, *P. pinea*, *P. sylvestris*, *P. uncinata*) and oaks (*Quercus ilex*, *Q. pubescens*, etc.), along the Atlantic coasts, also with *Cedrus atlantica* in North Africa. Mediterranean basin and Central Europe.

Fig. 2 50% majority rule consensus ITS rDNA phylogram of the family Pseudoclitocybaceae obtained in MrBayes from 10,875 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

Specimens examined: **FRANCE**: Pas-de-Calais, Dannes, Mont Saint-Frieux, under a single *Quercus ilex* in back of a dune, leg. R. Courtecuisse, 20-X-1991, LIP RC/F91.232. Vaucluse, Cadenet, les Gardis, on chalk under *Quercus ilex* and *Pinus halepensis*, leg. D. Borgarino, 01-XI-2002, D. Borgarino 021103/LIP 0401379. Vaucluse, Cadenet, La Rouère, under *Quercus pubescens* and *Pinus halepensis*, leg. D. Borgarino, P.-A. Moreau, 26-XI-2011, LIP 0401301/PAM11112619. **ITALY**: Bologna, S. Lazzaro di Savena, Parco dei Gessi e dei Calanchi dell'Abbadessa, Via dell'Eremo, under *Quercus pubescens* and *Q. cerris*, leg. G. Consiglio & G. Spisni, 26-X-1996, AMB 18221/GC 96242. Ibidem, Cerreto di Gaibola, 29-XI-2007, AMB 18219/GC 07537. Ibidem, Madonna dei Boschi, 31-X-2010, AMB 18220/GC 10181. Torino, Val di Susa, Colle del Lys, 1300 m a.s.l, under *Pinus sylvestris*, leg. A. Vizzini, 21-IX-2013, TO AV45634. Veneto, Vicenza, Malo, Isola Vicentina, *Pinus* sp., leg. S. Dalla Valle, 01-XII-2009, MCVE 25090. **NORWAY**: Telemark, Bamble, Langøya, calcareous forest, leg. T. H. Dahl, I. J. Kittilsen, 06-X-2001, 153/2001, O-175145. **SPAIN**: Guadalajara, dam of El Vado, Valdesotos, under *Pinus halepensis*, leg. R. Galán, 5-XI-2010, AH 39034. Guadalajara, Anguita, under *Quercus ilex* and *Juniperus thurifera*, on basic soil, leg. D. Martínez, 9-XI-2010, AH 39054. Guadalajara, Budia, under *Pinus pinea* and *Quercus ilex*, leg. J. Menendez, 7-XI-2010, AH 39068.

Comments: No original or topotypical collection of *C. alexandri* could be traced, but the original locality near Alençon (western France), in a hilly area under Atlantic climate, matches the species described here, rather than the boreo-alpine lineage described below as *C. fibulatus*. No typification of *C. alexandri* is proposed at this time, in expectation of collections found around the original locality. Singer (1961) studied original material of *Agaricus propinquus* var. *spadiceus* Pers. and concluded that this taxon could be a synonym of *C. alexandri*, but he could not check any specimen of *A. propinquus* Pers. var. *propinquus* (synonymized to *A. vinosus* Bull.: Fr., Fries 1832), avoiding any nomenclatural change. *Paxillus extenuatus* Fr., not interpreted in modern taxonomy, has also been applied to *C. alexandri*, for instance by Ricken (1915), but Fries (1838) described its pileus as umbonate at first and a base


KT122792 Infundibulicybe geotropa
JQ639162 Pogonoloma macrorhizum - Italy
JF908328 Pogonoloma macrorhizum - Italy
KP453700 Pogonoloma macrorhizum - Austria
JF908326 'Leucopaxillus nauseosodulcis' - Italy
Pogonoloma macrorhizum LIP 0101353 - Switzerland
Pogonoloma macrorhizum AMB 18232 - Italy
Pogonoloma macrorhizum
Pogonoloma spinulosum LIP 0101354 - France
Pogonoloma spinulosum LIP 0401167 - France
Pogonoloma spinulosum LIP 0401166 - France
KP453706 Pogonoloma spinulosum - United Kingdom
KP453705 Pogonoloma spinulosum - United Kingdom
KP453703 Pogonoloma spinulosum - United Kingdom
KP453704 Pogonoloma spinulosum - United Kingdom
UDB001486 Pogonoloma spinulosum - Denmark
Pogonoloma spinulosum
Pogonoloma
Harmajaea harperi TUR 173042 - Finland
Harmajaea harperi TUR 164187 - Finland
Harmajaea harperi H 6067456 - Finland
KP453697 'Pseudoclitocybe sp.' - USA
Harmajaea harperi LIP 0401361 - USA
Harmajaea harperi WTU-F-006299 - USA
Harmajaea harperi CMMF 014712 - Canada
Harmajaea harperi
Harmajaea guldeniae TUR 201099 - Finland
Harmajaea guldeniae O-74110 - Norway
Harmajaea guldeniae O-64624 - Norway
Harmajaea guldeniae H 6067433 - Finland
Harmajaea guldeniae H 6067444 - Finland
Harmajaea guldeniae H 6067455 - Finland TYPE
Harmajaea guldeniae H 6067432 - Finland
Harmajaea guldeniae H 6051797 - Finland
Harmajaea guldeniae sp. nov.
Harmajaea wellsiae TUR 205933 - Finland
Harmajaea wellsiae WTU-F-024810 - USA
Harmajaea wellsiae MICH 10217 - USA TYPE
Harmajaea wellsiae
Harmajaea
KF941322 Musumecia vermicularis - France
KF941323 Musumecia vermicularis - France
KF941324 Musumecia vermicularis - France
Musumecia vermicularis
KT122794 Musumecia sardoa - Italy
Musumecia sardoa
JF926520 Musumecia bettlachensis - France
Musumecia bettlachensis
KR909097 Musumecia alpina - China
KR909098 Musumecia alpina - China
KR909099 Musumecia alpina - China
Musumecia alpina
Musumecia
KF291250 Pseudoclitocybe cyathiformis - USA
Pseudoclitocybe sp. LIP 0401355 - USA
HQ533021 Cantharellula foetida - New Zealand
GU187553 Pseudoclitocybe cyathiformis - USA
KC505562 Pseudoclitocybe cyathiformis - China
JF926522 Pseudoclitocybe cyathiformis - Italy
Pseudoclitocybe cyathiformis LIP 0901300 - France
HM191730 Pseudoclitocybe cyathiformis - Russia
Pseudoclitocybe cyathiformis LIP 0401359 - France
Pseudoclitocybe cyathiformis AMB 18225 - Italy
UDB011432 Pseudoclitocybe cyathiformis - Estonia
Pseudoclitocybe cyathiformis AMB 18226 - Italy
Pseudoclitocybe cyathiformis AMB 18227 - Italy
KP453710 Pseudoclitocybe cyathiformis - Sweden
Pseudoclitocybe cyathiformis (I)
KP453709 Pseudoclitocybe cyathiformis - USA
Pseudoclitocybe cyathiformis AMB 18228 - Italy
HM191729 Pseudoclitocybe cyathiformis - Russia
Pseudoclitocybe cyathiformis LIP 0401360 - France
UDB015516 Pseudoclitocybe expallens - Estonia
Pseudoclitocybe cyathiformis TO HG123012A - Italy
KR673477 Pseudoclitocybe cyathiformis - South Korea
Pseudoclitocybe cyathiformis (II)
Pseudoclitocybe obbata LIP 0401357 - France
JF926524 Pseudoclitocybe expallens - Italy
Pseudoclitocybe obbata AH 46369 - Spain
Pseudoclitocybe obbata LIP 0401358 - France
KF482480 'Laccaria laccata' - Portugal
Pseudoclitocybe obbata AMB 18229 - Italy
Pseudoclitocybe obbata AMB 18230 - Italy
Pseudoclitocybe obbata AMB 18231 - Italy
Pseudoclitocybe obbata
Pseudoclitocybe
Clitopaxillus alexandri TO AV45634 - Italy
Clitopaxillus alexandri AH 39034 - Spain
Clitopaxillus alexandri AH 39068 - Spain
Clitopaxillus alexandri LIP RC/F91.232 - France
Clitopaxillus alexandri AH 39054 - Spain
Clitopaxillus alexandri AMB 18221 - Italy
Clitopaxillus alexandri AMB 18220 - Italy
Clitopaxillus alexandri AMB 18219 - Italy
Clitopaxillus alexandri MCVE 25090 - Italy
Clitopaxillus alexandri LIP 0401301 - France
Clitopaxillus alexandri LIP 0401379 - France
Clitopaxillus alexandri O-175145 - Norway
Clitopaxillus alexandri
Clitopaxillus fibulatus O-82070 - Norway
Clitopaxillus fibulatus O-82069 - Norway
Clitopaxillus fibulatus O-74584 - Norway
Clitopaxillus fibulatus LIP 0401380 - France
Clitopaxillus fibulatus AMB 18222 - Italy
Clitopaxillus fibulatus LIP 0401381 - France
Clitopaxillus fibulatus AMB 18223 - Italy
Clitopaxillus fibulatus TUR 165285 - Finland
Clitopaxillus fibulatus TUR 170200 - Finland
Clitopaxillus fibulatus TUR-A-140440 - Finland
Clitopaxillus fibulatus AMB 18224 - Italy TYPE
Clitopaxillus fibulatus TO AV190916 - Italy
Clitopaxillus fibulatus TU 106015 - Estonia
JF907816 Clitocybe cf. alexandri - Italy
Clitopaxillus fibulatus DB 6191 - Norway
Clitopaxillus fibulatus sp. nov.
Clitopaxillus
0.5

"tuberoso-radicato", two features recalling *A. vinosus* Bull. cited above (Bulliard 1782: tab. 54) and incompatible with any species of *Clitopaxillus* known to us.

***Clitopaxillus fibulatus* P.-A. Moreau, Dima, Consiglio, & Vizzini, sp. nov.**

Mycobank MB 823305 (Figs. 3c, 4a, b, g, h)

Etymology: from Latin 'fibula' (brooch) referring to the hyphal clamps present on all septa.

Diagnosis: basidiomes 4–10 cm in diam., clitocyboid, fleshy, with convex to flattened brownish pileus lacking umbo, glabrous pileipellis, not hygrophanous. Lamellae adnate to decurrent. Spores 6.1 × 4.4 µm on average, slightly amyloid, ellipsoid; hymenial cystidia present. Saprobic, on litter. Clamp connections present at all septa. Boreo-alpine, under *Picea abies* and *Abies alba* in Europe.

Type collection: **ITALY**: Trentino, Pozza di Fassa, Valle S. Nicolò, under *Picea abies*, leg. G. Consiglio, 22-VIII-1997, AMB 18224/GC 97079 (**holotype**).

Description: Pileus first convex then expanded or slightly depressed with age, cream to ochraceous grey or buff with margin enrolled, measuring 4–10 cm in diam., finely tomentose when young developing distinctive, concentric wrinkles and cracks with age. Lamellae crowded, adnate to decurrent, cream to yellowish buff. Stipe 3.5–8.0 × 1.5–3.0 cm, solid, cylindrical to clavate, covered with whitish fibrils, later becoming buff, whitish cream tomentose at base with well-developed whitish mycelial strands. Context whitish cream, firm when young, later spongy. Smell aromatic, spicy. Spores 5.7–6.4 × 4.1–4.6 µm (n = 32), (average 6.1 × 4.4 µm), Q = 1.30–1.47 (Q_m = 1.39); V_m = 62 µm^3, broadly ellipsoid to ellipsoid, hyaline or with dull, granuliform content, usually with one big oily drop; slightly amyloid in a not very pronounced gray, smooth. Basidia 21–33 × 5.8–7.8 µm, four-spored, clavate, sterigmata up to 5.2 µm long. Hymenophoral trama irregular, composed of hyphae until 12 µm wide, hyaline in alkaline latex L4, yellow in Melzer's. Cheilocystidia 31–41 × 7.8–8.3 µm, long lageniform to long clavate, scattered on the lamellar edge. Pleurocystidia scattered, similar to cheilocystidia. Pileipellis a trichocutis of subparallel to variously intertwined, gelatinized, filamentous hyphae, 2–7 µm wide, yellow in Melzer's, smooth, with intracellular brownish pigment, some with a very fine encrusting epiparietal pigment. Pileitrama hyphae cylindrical, up to 12 µm wide, mixed with numerous branched thromboplerous hyphae with pale yellowish content in Melzer's, otherwise colourless, clamped at base. Clamp connections loop-like, present at all septa.

Ecology: boreo-alpine, occurring in mountain to alpine habitats of Central and Mediterranean Europe, as well as North Europe. Mainly in litter of conifers, under *Abies alba* and *Picea abies* on limestone or volcanic soils, also reported from calcareous alpine zone.

Specimens examined: **ITALY**: Abruzzo, L'Aquila, Campo Imperatore, Fonte Vetica, under *Picea abies*, leg. G. Consiglio & M. Maletti, 03-X-2015, AMB 18222/GC 15186. Ibidem. AMB 18223/GC 15187. Trentino, Passo di Redebus (TN), 1450 m a.s.l., under *Picea abies*, leg. A. Tatti, 19-IX-2016, TO AV190916. **FINLAND**: Keski-Pohjanmaa, Vimpeli, Kotakangas, in abandoned limestone quarry, in grassy-mossy thicket mixed with *Picea abies*, *Betula* sp., *Salix* sp., *Populus* sp., *Sorbus* sp., leg. M.-L. Heinonen, P. Heinonen, 25-IX-2003, TUR 165285. Varsinais-Suomi, Perniö, Lupaja, Alhonmäki, W slope, fairly rich forest with mainly *Picea abies*, leg. J. Vauras, 01-X-2004, TUR 170200. Varsinais-Suomi, Parainen, Lemlaxön, Brattnäs, ca. 4 km SE of the limestone processing factories, rather moist mossy forest of mainly *Picea abies* and *Pinus sylvestris*, leg. J. Vauras, 07-X-1991, TUR-A-140440. **FRANCE**: Haute-Loire, Cayres, Lac du Bouchet, volcanic soil, under *Abies alba* and *Picea abies*, with some *Fagus*, 1140 m a.s.l., leg. D. Borgarino, 2003, D. Borgarino 031048/LIP 0401380. Ibidem, leg. D. Borgarino, G. Clavel, J.-M. Moingeon, 02-X-2014, P. Roux 5622/D. Borgarino 141100/LIP 0401381. **NORWAY**: Buskerud, Hole, Vik, in coniferous forest on calcareous ground, leg. G. Gulden, 15-X-1967, Gulden 679/67, O-82070. Buskerud, Ringerike, slightly west of Gullerud Nature Reserve, rich coniferous forest on calcareous ground, leg. G. Gulden, 09-X-2006, Gulden 307/06, O-74584. Buskerud, Royken, Høvik, leg. G. Gulden, 29-IX-1963, O-82069. Oppland, Gran, Jøvika, in mossy coniferous forest with *Picea abies* on limestone, on steep slope, leg. T. E. Brandrud, B. Dima, 14-IX-2016, DB 6191.

Comments: *Clitopaxillus fibulatus* is here proposed to accommodate the collections formerly identified as *C. alexandri* but with clamp connections present in all tissues of the basidiomes (and not only in hymenophoral tissues and mycelium as in *C. alexandri*), the presence of hymenial cystidia, and occurring in alpine or boreal habitats, as first suggested by Moreau (2009). Kuyper (1995) informally proposed the name "*C. subalexandri*" for specimens with smaller spores (4.0–5.0 × 3.0–3.5 µm), and scarce clamp connections in the pileipellis and hymenophoral trama, but still some of them present at the base of basidia. However, these features do not match any of the specimens studied by Moreau (2009) or the present work. The only sequence of "*C. alexandri*" in GenBank (JF907816, Osmundson et al. 2013) seems to match the concept of *C. fibulatus* rather than the true *C. alexandri*. It was obtained from collection MCVE 5953, found by Emanuele Campo at S. Cassiano in Badia, close to Italian Alps, at 1650 m a.s.l., 16-VIII-1994. In UNITE database, sequence UDB015076 (TU 106015) found by Vello Liiv at Estonia matches also

Table 1 Comparison of the key characters of genera of the Pseudoclitocybaceae treated in this study

	Pogonoloma	*Musumecia*	*Pseudoclitocybe*	*Clitopaxillus*	*Harmajaea*
Habit	Tricholomatoid	Clitocyboid	Clitocyboid	Clitocyboid	Clitocyboid
Stipe	Rooting	Aggutinating	Aggutinating	Aggutinating	Aggutinating
Pileus	umbonate to flat	umbilicate	umbilicate	depressed	depressed
Lamellae	Emarginate	Strongly decurrent	Moderately decurrent	Moderately decurrent	Adnate to slightly decurrent
Spore amyloidity	+	+/0	+	±	±
Spore size	5–6.5 × 3.5–4.2 μm	5.5–10.0 × 3.5–5 μm	6.5–10.5 × 4–7 μm	4.5–6.5 × 3.5–4.5 μm	4.5–6 × 3.2–3.8 μm
Basidia	26–32 × 5–7 μm	28–45 × 3.5–8 μm	22–52 × 5–8.5 μm	20–33 × 5–8 μm	15–34 × 5–7 μm
Pileitrama	Sarcodimitic	Homomorphic	Homomorphic	Homomorphic	Homomorphic
Clamps	All septa	+/0	Mycelium	Mycelium, hymenium	Mycelium
Smell	Aromatic		Herbaceous		
Cystidia	Marginal hairs	+/0	None	None	None
Pileipellis	Trichocutis	Ixocutis	Ixocutis	Cutis	Trichocutis
Pigments	Intraparietal + intracellular		Intraparietal + incrusting	Intraparietal + intracellular	Intraparietal + intracellular

a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q

◀**Fig. 3** **a** *Pogonoloma macrorhizum* (AMB 18232, photo: M. Barbieri). **b** *Clitopaxillus alexandri* (LIP 0401301, photo: D. Borgarino). **c** *Clitopaxillus fibulatus* (TU 106015, photo: V. Liiv). **d** *Harmajaea guldeniae* (H 6067444). **e** *Harmajaea guldeniae* (H 6067455). **f** *Harmajaea wellsiae* (TUR 205933). **g** *Harmajaea harperi* (CMMF 014712, photo: G. Poulet). **h** *Harmajaea harperi* (LIP 0401361, photo: R. Pastorino). i. *Harmajaea harperi* (H 6067456). **j** *Pseudoclitocybe cyathiformis* I (LIP 0901300, photo: P. Clowez). **k** *Pseudoclitocybe cyathiformis* I (AMB 18227). **l** *Pseudoclitocybe cyathiformis* I (TU 106216, photo: V. Liiv). **m** *Pseudoclitocybe cyathiformis* II (TU 118376, photo: V. Liiv). **n** *Pseudoclitocybe cyathiformis* II (AMB 18228). **o** *Pseudoclitocybe cyathiformis* II (PAM 14112110b). **p** *Pseudoclitocybe obbata* (LIP 0401358). **q** *Pseudoclitocybe obbata* (AMB 18231). **r** *Pseudoclitocybe obbata* (AMB 18229)

the concept of *C. fibulatus*, in agreement with the alpine and boreal distribution of this species. Sequence KY084307 (Zhou & Guo, unpublished) is significantly related to those of *Clitopaxillus*, but probably represents an undescribed taxon from the Guancen Mountains (Shanxi, China).

***Harmajaea* Dima, P. Alvarado & Kekki, gen. nov.**

Mycobank MB 823306 (Figs. 3d–i, 4c–f)

Etymology: We want to dedicate this new genus to Dr. Harri Harmaja because he was the first who reported a species of this genus from Europe, and also because of his huge contribution to the knowledge of clitocyboid fungi.

Diagnosis: large fleshy species with convex pileus, dry, smooth or subscaly surface at centre, pale yellowish, pale beige to brown or dark brown, not hygrophanous; spores small, 4.5–6 × 3–3.8 µm, ovoid to cylindrical, faintly amyloid, not cyanophilous. Hymenophoral trama regular. Thromboplerous hyphae abundant in subpellis and hymenial trama. Clamp connections absent in basidiome, scattered in mycelium. Smell and taste none. Saprobic, on thick forest litter. Northern Hemisphere, present in North America and North Europe.

Type species: *Harmajaea harperi* (Murrill) Dima & P. Alvarado

Comments: This new genus *Harmajaea* differs from *Clitopaxillus* because it completely lacks clamp connections or "false" clamps, has a slenderer stipe, and a more depressed pileus. *Clitocybe harperi* was first reported from Europe by Harmaja (1969), who also transferred it to *Rhodocybe* (Harmaja 1978, 1979) on the account of wrinkled spores under SEM and lack of clamps. The present results show that collections identified as *C. harperi* from North America and Scandinavia cluster on a single clade sister to *Pseudoclitocybe*, *Clitopaxillus* and *Musumecia*. *Harmajaea* is characterized by a complete absence of clamps in the basidiome (present in the mycelium of *H. guldeniae* and *H. wellsiae*), and a spectacular abundance of yellowish, frequently branched thromboplerous hyphae in the hymenophore and subpellis. Macroscopically, some *Harmajaea* species recall *Atractosporocybe* because of its pale colors and dry cap, grooved pileus at margin, and faintly decurrent gills, but the latter has fusoid spores, more greyish tinges and a strong fishy smell (Gulden 2006). *Clitopaxillus* can look similar, but has deeply decurrent, "paxilloid" lamellae. Three distinct genetic lineages of *Harmajaea* were found in the present work, two of them are identified with the existing species *C. harperi* and *C. wellsii*, and a third one is described here as a new taxon.

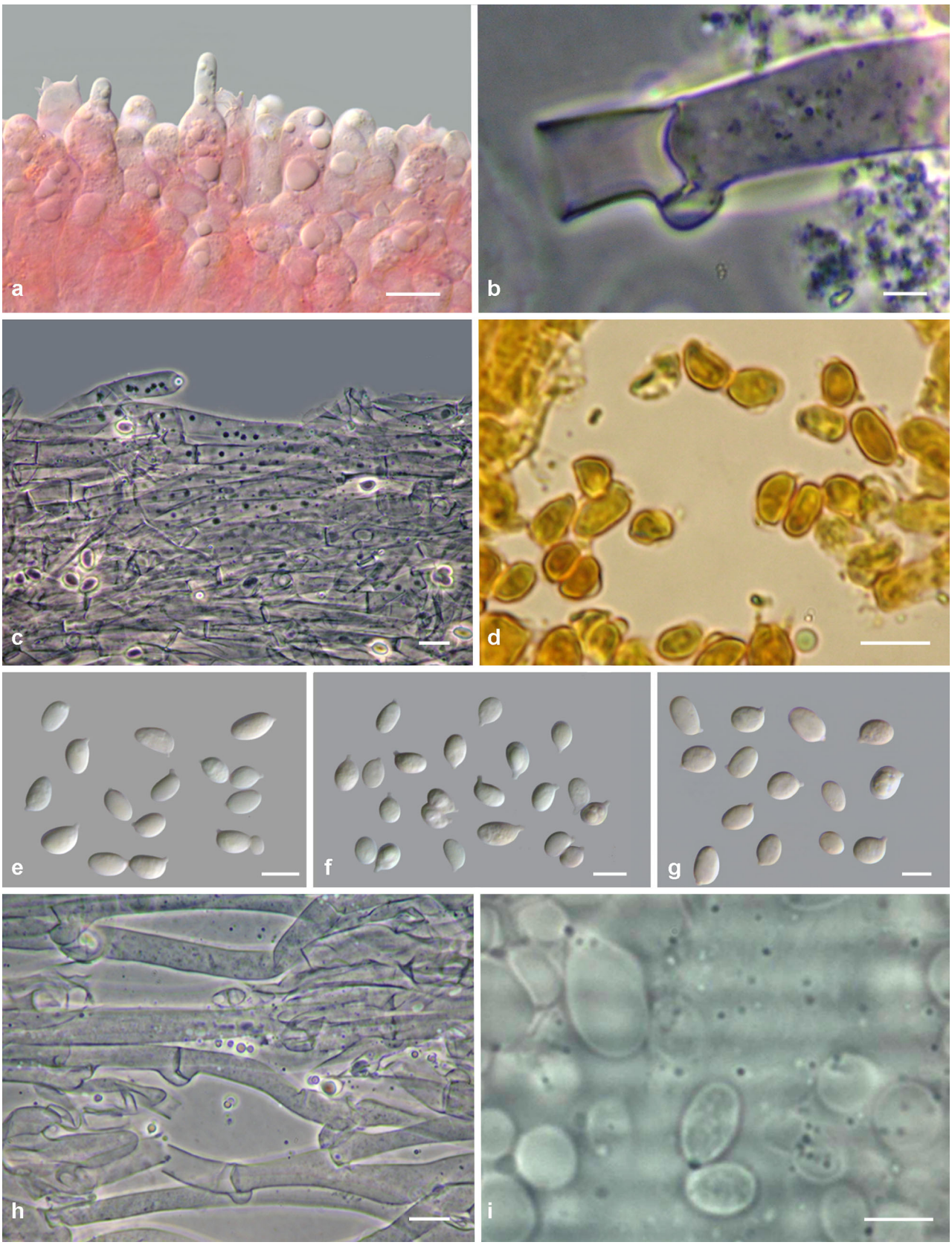
***Harmajaea harperi* (Murrill) Dima & P. Alvarado, comb. nov.**

Mycobank MB 823307 (Figs. 3g–i, 4c–e)

Basionym: *Clitocybe harperi* Murrill, Mycologia 5(4): 209 (1913)

≡ *Rhodocybe harperi* (Murrill) Harmaja, Karstenia 18(1): 30 (1978)

Description: Pileus 5–11 cm, slightly depressed and presenting a central umbo with age, margin enrolled, smooth or minutely scaly, dry, whitish or grayish in color, brown or pale brown at the center. Lamellae shortly decurrent, crowded, thin, pale brown or gray to whitish. Stipe 4.5–8 × 1.3–2.2 cm, solid, cylindrical, concolorous with the pileus. Context whitish to brownish. Spores (4.5–) 5.0–6.0 (–7.0) × (2.5–) 3.0–3.7 µm (on average 5.3 × 3.5 µm), Q = 1.40–1.65 (Q_m = 1.53), V_m = 34 μm^3, ellipsoid in front view, somewhat obovoid or amygdaliform in side view, smooth, spore wall slightly amyloid after a few minutes, not cyanophilous, not collapsing and not adhering in tetrads. Basidia 15–23 × 3.8–5.8 µm, 4-spored, cylindro-clavate, with sterigmata 4 µm long, without carminophilic/siderophilous granulation, apical portion slightly amyloid. Cheilocystidia 26 × 8 µm, cylindrical, scattered, with apical protrusions like "stag's antlers". Pleurocystidia absent. Subhymenium ramose, arbuscular, 15 µm thick, hyphae shortly branched 3.0–3.5 µm wide. Hymenophoral trama regular, made of broad cylindrical to inflate hyphae 5–16 µm wide, and of thromboplerous hyphae 5–7 µm wide, with yellow content, especially frequent towards in the otherwise hardly differentiated hymenopodium, as well as towards edge. Pileipellis a dry trichocutis of radially arranged, inflate hyphae 5–12 µm wide, with intracellular yellow pigment forming minute granulations, mixed with slender hyphae 2.5–3.0 µm wide, scattered, narrowed at septa, with incrusted wall. Subpellis thick, characterized by an abundance of thromboplerous hyphae with yellowish content in Melzer's reagent, mixed with regular cylindrical thin-walled hyphae 3–8 µm wide. Pileitrama homomorphous, made of mostly parallel hyphae 4.0–6.5 µm wide, with walls 0.3–0.8 µm thick, smooth, mixed with thromboplerous hyphae 5–9 µm wide, branching and


a
b
c
d
e
f
g
h
i

◀**Fig. 4** **a**, **b** *Clitopaxillus fibulatus* (AMB 18222) **a** cystidia. **b** Clamp-connection detail. **c–e** *Harmajaea harperi* (TUR 164187) **c** epicuticular hyphae with vacuolar pigments. **d** Weak amyloid reaction of spores in Melzer. **e** Spores. **f** *Harmajaea guldeniae* (TUR 201099) spores. **g** *Clitopaxillus fibulatus* (AMB 18224) spores. **h** *Clitopaxillus fibulatus* (AMB 18222) clamped hyphae. **i** *Musumecia sardoa* (GC 04275) spores in Melzer, amyloid reaction of apiculus. Bars: A = 10 µm, B = 3 µm, C–D = 10 µm, E–G = 5 µm, H = 10 µm, I = 5 µm

anastomosing, with homogeneous yellowish content, especially abundant towards subpellis. Stipitipellis a caulohymenium. Clamp connections absent, even at the base of basidia and mycelium.

Ecology: widespread in North America (western USA to eastern Canada) and Northern Europe. Under conifers such as *Pseudotsuga*, *Pinus sylvestris* and *Picea abies*.

Specimens examined: **CANADA**: Québec, Shipshaw, under conifers, leg. G. Guérin, 27-XI-1986, Guérin 1591/CMMF 014712. **FINLAND**: Etelä-Savo, Savonlinna, Hevonmaa, a gorge W of pond Silmälammi, lush vegetation with *Betula*, *Populus*, *Salix caprea*, *Abies*, leg. S. Huhtinen, 17-IX-2003, TUR164187. Perä-Pohjanmaa, Keminmaa, Kallinkangas, grassy calcareous spruce forest, leg. T. Kekki, 18-IX-2016, Kekki 2722/H 6067456. Varsinais-Suomi, Perniö, Arpalahti, Kaapinmäki, along a small brook, in a rocky, virgin forest site with dominant trees of *Alnus*, *Betula*, *Sorbus*, *Juniperus*, *Ribes alpinum*, and few young *Quercus*, under dense spruces in deep litter with *Oxalis* but without much moss coverage, leg. M.-L. Heinonen, P. Heinonen, 08-XI-2003, TUR 173042. **NORWAY**: Oppland, Etnedal, Kluftøygard, in calcareous *Picea abies* forest, leg. T. E. Brandrud, B. Dima, 21-VIII-2017, DB 6315. **USA**: California, Sonoma County, Annadel State Park, mixed woods, *Pseudotsuga menziesii*, bay laurel and live oak, leg. R. Pastorino, 20-I-2015, LIP 0401361. Washington, Pierce Co., Penrose State Park, leg. H. Koonz, 23-XI-2001, WTU-F-006299, PBM 2677.

Comments: This species can be easily differentiated because of its habit, ecology and clampless hyphae. Weakly amyloid spores were observed on the collections studied here as well as TENN 061314 (USA, North Carolina, Sánchez-García pers. comm.), while spores of *C. harperi* are usually described as inamyloid, even by such reliable observers as Harmaja (1979) or Bigelow (1982). This could suggest that this feature varies within the same taxon, depending on age, environment, strain, or most probably, on the specific protocol employed. *Clitocybe griseifolia* Murrill was proposed in the same work as *C. harperi* (Murrill 1913) from Seattle (USA), and was separated from *C. harperi* because of its broad lamellae, white stipe, and fragrant odor different from the crowded lamellae, concolorous stipe, and odorless basidiome of *C. harperi* (Bigelow 1965, 1982). However, some authors (Harmaja 1979) considered *C. griseifolia* a synonym of *C. harperi* because of their very similar macro- and microscopical features, as well as identical chemical reactions of the types to Melzer's reagent (inamyloid), cotton blue (cyanophobic, but weakly cyanophilic in spore and basidia walls) and acetocarmine (carminophobic spore and basidia walls, carminophilic spore nuclei) (Harmaja 1979). Our collections of *C. harperi* have medium-distanced lamellae, a concolorous stipe, and odorless basidiomes, so they do not match *C. griseifolia*. A single report from France of *H. harperi* by Bon (1997), corresponding to coll. 741006 in herb. Bon (LIP), was checked under the microscope and revealed clamps in hymenophoral tissues, so it is here re-interpreted as *C. alexandri*. Finally, some confusion might have existed because of the name *Lepista harperi* (Murrill) Singer, originally described by Murrill (1913) as *Melanoleuca harperi*, and later combined to *Lepista* by Singer (1951) on account of its verrucose spores. When Bigelow (1982) subsumed *Lepista* within *Clitocybe*, he noticed the existence of *Clitocybe harperi* Murrill, and renamed the first species as *Clitocybe brunneocephala* H.E. Bigelow.

***Harmajaea guldeniae* Dima, P.-A. Moreau, P. Alvarado & Kekki sp. nov.**

MycoBank MB 823308 (Figs. 3d, e, 4f)

= *Clitocybe harperi* s. Harmaja (1969), s. Gulden (2006)

Etymology: We are glad to dedicate the new taxon to Dr. Gro Gulden on account of her work on this species and many others in *Clitocybe*.

Diagnosis: clitocyboid basidiome, depressed, with an umbo, yellowish-brown or beige, lamellae decurrent, ovoid spores 4.5–5.0 µm long, faintly amyloid. Differs from *H. harperi* because of its brownish pileus, more decurrent gills, longer basidia, clamped mycelium and, by now, exclusively European distribution under conifers.

Type collection: **FINLAND**: Perä-Pohjanmaa, Tervola, Raemäki, calcareous grassy spruce forest, leg. T. Kekki, 8-IX-2016, Kekki 2580/H 6067455 (**holotype**).

Description: Pileus 5–11 cm diam., soon depressed with a persistent small central umbo, rather thin-fleshed; surface matt, dry, smooth to faintly scurfy especially at centre, not hygrophanous, yellowish-brown to beige or leather-colored, towards centre with darker, velvet brown patches; margin persistently enrolled, grooved. Lamellae decurrent, crowded, with many lamellulae, narrow, almost white to pale greyish; edge darkening to brown with age. Stipe 4.5–8.0 (–11) × 1.3–2.2 cm, cylindrical to moderately clavate, solid; surface fibrillose, concolorous with the pileus; mycelium white, abundant, tomentose, aggregating litter debris. Context white, becoming somewhat brownish. Smell and taste indistinct or slightly fungoid. Spores 4.3–5.1 × 3.0–3.8 µm (on average 4.7 × 3.3 µm),

Q = 1.29–1.57 (Q_m = 1.43), V_m = 27 µm^3, smooth, faintly amyloid spore wall, not cyanophilic, broadly ellipsoid to oblong in front view, sometimes larmiform, with protruding hilar appendix about 0.8 µm, not aggregated in tetrads and not collapsing. Basidia 19–34 × 5.0–7.5 µm, 4-spored, narrowly clavate, with sterigmata 3.5 µm long, apical portion slightly amyloid. Cystidia not observed. Subhymenium ramose, made of short cylindrical hyphae 2–3 µm wide. Hymenophoral trama with a differentiated hymenopodium 15–20 µm thick, made of parallel cylindrical hyphae 3–7 µm wide, and a mediostratum made of broad cylindrical to slightly inflate hyphae 5–16 µm wide. Pileipellis a trichocutis made of fasciculate slender hyphae with narrowed terminal elements 40–70 × 2.5–4 µm, especially developed towards margin, slightly becoming gelatinized and collapsing with age from the centre. Subpellis made of parallel, cylindrical hyphae 3.5–9.0 µm wide, smooth, with pale brown intraparietal pigment. Pileitrama made of parallel hyphae 4–12 µm wide, with numerous colorless intracellular globules measuring 3.0–5.5 µm diam., and abundant thromboplerous hyphae 5–10 µm wide, often branched, uniformly yellowish in KOH. Stipitipellis a caulohymenium. Mycelium made of cylindrical hyphae 2.5–9 µm wide, mostly with thickened wall (0.3–0.5 µm thick), some with yellowish granular content. Clamp connections absent from all septa in the basidiome, but present in basal mycelium (about 10% of septa clamped).

Specimens examined: **FINLAND:** Kainuu, Paltamo, Antinmäki, mixed forest of *Picea abies* and deciduous trees, leg T. Kekki, 9-IX-2016, Kekki 2593/H 6067433. Kainuu, Paltamo, Melalahti, in calcareous spruce forest, leg T. Kekki, 9-IX-2016, Kekki 2596/H 6067444. Pohjois-Pohjanmaa, Tervola, E of Raemäki, in spruce forest, leg. T. Kekki, 02-IX-2012, TUR 201099. Pohjois-Savo, Varkaus, Itkonharju, in rich mixed forest of *Picea abies*, *Pinus sylvestris* and *Betula*, leg. T. Kekki, 31-VIII-2014, Kekki 1505, H 6051797. Pohjois-Savo, Varkaus, Itkonharju, in rich spruce forest, leg. T. Kekki, 17-IX-2016, Kekki 2700/H 6067432. **NORWAY**: Buskerud, Hole, Vik, in a spruce forest on Cambrio-Silurian calcareous rocks, leg. G. Gulden, 22-X-1967, Gulden 731/67, O-64624. Oppland, Gran, Askimlandet, in calcareous *Picea abies* forest, leg. T. E. Brandrud, B. Dima, 11-IX-2017, DB 6456. Ringerike, Gullerud, near the lake, leg. G. Gulden, 25-IX-2004, Gulden GG150/04, O-74110.

Ecology: known only from *Picea abies* forests in North Europe.

Comments: This species fits the concept of *Clitocybe harperi* as proposed by Harmaja (1969) and Gulden (2006). However, it is morphologically, phylogenetically and biogeographically distinct from the original concept of *C. harperi*, because of its brownish pileus, decurrent gills, longer basidia, clamped mycelium and, by now, exclusively European distribution under conifers. A very similar taxon, *C. wellsiae* H.E. Bigelow (Bigelow 1982), was found in spruce woods of Alaska (USA), and has a brownish pileus, adnexed to decurrent lamellae, and similar microscopy. However, genetics show that *H. guldeniae* is a different taxon. Harmaja's nom. prov. "*Clitocybe subharperi*" (Harmaja 1979), a fungus found in calcareous areas of Finland with a slightly pruinose pileus darker than that of *C. harperi*, and a spore print with reddish tinges, was considered by Bigelow (1982) a putative synonym of *C. wellsiae*, but the reddish tinges in the spore print are different from those of *C. guldeniae* and its identity remains to be precised.

***Harmajaea wellsiae* (H.E. Bigelow) P. Alvarado, Kekki & P.-A. Moreau comb. nov.**

MycoBank MB 823309 (Fig. 3f)

≡ *Clitocybe wellsiae* H.E. Bigelow, Beih. Nova Hedwigia 72: 64 (1982) (as "*Clitocybe wellsii* H.E. Bigelow")

Description: Pileus 8–16 cm diam., slightly depressed, surface mat, dry, smooth to faintly tomentose especially at centre, not hygrophanous, pale-brown to cinnamon brown, darker towards centre; margin persistently enrolled, whitish. Lamellae adnate-shortly decurrent, crowded, with many lamellulae, narrow, almost white; edge darkening to brown with drying. Stipe 6–9 × 1.5–2 cm, cylindrical, solid; surface fibrillose, lighter than the pileus; mycelium white, abundant, tomentose, aggregating litter debris, with some rhizoids. Context white; smell and taste indistinct. Spores (3.7–) 4.3–5.0–5.9 (–6.9) × (2.0–) 2.5–3.0–3.5 µm, Q = 1.35–1.67–2.05, slightly but distinctly amyloid, larmiform to cylindro-allantoid before maturity, at maturity cylindrical to narrowly ellipsoid with rounded base; wall slightly thickened, smooth; content microguttulate before maturity, hyaline when mature. Basidia 18–26 × 4–7 µm, 4-spored, cylindro-clavate at maturity, filled with colourless droplets when mature. Cystidia not observed. Subhymenium ramose, 10–12 µm thick, made of shortly cylindrical hyphae with guttulate content. Hymenophoral trama with a differentiated hymenopodium made of parallel to slightly divergent cylindrical hyphae 2.5–6.0 µm wide, frequently branched, and a mediostratum of subregular structure with broad cylindrical hyphae 4–10 µm wide, often inflated before septa, colourless, smooth, with intracellular colourless droplets, with sparsed thromboplerous hyphae 5–6 µm wide with pale yellow content. Pileipellis a faintly gelatinized trichocutis 60–100 µm thick, made of cylindrical hyphae 3.5–11.0 µm wide, some with yellowish homogeneous content, with frequent clavate terminations more or less fasciculate towards margin, adpressed and confusedly intervowen elsewhere; wall slightly thickened, with minutely incrusting epiparietal pigment. Subpellis 40–70 µm

thick, not gelatinized, made of parallel, broad hyphae 4–7 µm wide, abundantly guttulate. Stipitipellis mostly covered by a fertile caulohymenium. Stipititrama made of parallel, cylindrical hyphae 7–15 µm wide, moderately thick-walled, smooth, colourless; no thromboplerous hyphae observed. Mycelium made of slender cylindrical hyphae 2.5–5.0 µm wide, colourless, smooth wall up to 0.3 µm thick, frequently with attenuated apices, sometimes (typus) mixed with coralloid elements and more yellowish and thick-walled hyphae and cylindro-clavate cystidioid elements with guttulate content, 5–6 µm wide at apex. Clamps loop-like, scattered in mycelium, mostly on thick-walled hyphae, not observed anywhere on the basidiome.

Specimens examined: **FINLAND**: Kittilän Lappi, Kolari, Äkäsjoensuu, leg. T. Kekki, calcareous forest of *Picea* and *Pinus*, 03-IX-2016, Kekki 2523/TUR 205933. **USA**: Alaska, Fairbanks North Star, Larson property, Yankovitch Rd, Fairbanks, gregarious in deep moss in *Picea* sp. woods, leg. V. Wells & P. Kempton, 24-VIII-1965, MICH 10217 (holotype). Alaska, Dalton Highway, Mile 229, with *Picea* sp., *Betula* sp., *Salix* sp., *Alnus* sp., leg. G. A. Laursen, 18-VIII-1992, WTU-F-024810.

Ecology: known from boreal *Picea* sp. forests in Alaska and northern Finland.

Comments: After studying the holotype collection of *Clitocybe wellsii* (MICH 10218, Wells & Kempton 2506), and producing ITS rDNA data from it, we here propose the new combination *H. wellsiae* (the epithet is corrected from "*wellsii*" to "*wellsiae*" because the species was dedicated to the late Virginia Wells, ICN Art. 60.12). The holotype material studied was not completely mature and most spores were still attached to basidia; their shape was remarkably elongate to even subfusiform (roughly 5.8–7.0 × 3.0–3.2 µm), and their amyloid reaction was only distinct towards the apiculus. Similar long spores were only found rarely attached to basidia in the fully mature collection Kekki 2523 (TUR 205933). The holotype was also distinct from Kekki 2523 because of the presence of well differentiated cystidioid elements with yellow content in mycelium. *Harmajaea wellsiae* is quite similar to *H. guldeniae* because of its macro and microscopical features, but it is more robust, has almost adnate lamellae and a boreal distribution in America and Europe. Other clampless species of *Clitocybe* from North America include *Clitocybe griseifolia*, found at Seattle (USA), but this is most probably a synonym of *H. harperi*, since both taxa share a similar grayish pileus, fruit in autumn, and occur in similar habitats in California, Oregon and Washington. "*Clitocybe subharperi*" (nom. prov. in Harmaja 1979), was also found in calcareous areas of Finland, but had reddish tinges in its spore print.

***Pseudoclitocybe* (Singer) Singer** Mycologia 48(5): 725 (1956) (Figs. 3j–r)

Basionym: *Cantharellula* subgen. *Pseudoclitocybe* Singer, Annls mycol. 41(1/3): 64 (1943)

Description: Pileus 2–12 cm, depressed to umbilicate, hygrophanous, striate or not, slightly gelatinized, smooth to pruinose at margin. Lamellae: adnate to deeply decurrent, crowded, thin, whitish to gray. Stipe 4.5–8 × 1.3–2.2 cm, fistulose, cylindrical to compressed at maturity, concolorous with the pileus, usually with a white zone at apex; mycelium usually abundant, patch-like, without rhizomorphs. Context whitish to grey when moist. Smell herbaceous. Spores globose to ellipsoid, smooth, distinctly amyloid, acyanophilic, with hyaline content. Basidia 4-spored, without carminophilic/siderophilous granulation. Cystidia absent. Subhymenium branching, prostrate, easily dissociated. Hymenophoral trama subregular to slightly divergent, cylindrical hyphae with elements 4–6 µm wide. Pileipellis a radially arranged ixocutis, sparsely to densely diverticulate. Clamp connections loop-like, present in mycelium in all species, absent or very rare elsewhere, absent at the base of basidia. Saprobe, terricolous, lignicolous to coprophilous. Temperate areas, Northern and Southern Hemispheres.

Comments: At least four distinct genetic lineages were found within genus *Pseudoclitocybe* in the ITS rDNA analysis (Fig. 2): one of them found in Europe, North America and Asia (*Pseudoclitocybe cyathiformis*), one known only from Europe (*Pseudoclitocybe obbata*), another one found in North America (KF291250 and LIP 0401355, maybe *Pseudoclitocybe oregonensis* (Murrill) Singer?), and last a single sequence coming from New Zealand (HQ533021). Two cryptic lineages within *P. cyathiformis* (I and II) were sometimes significantly supported, although frequently merged together in the analyses because of the presence of apparently intermediate sequences (KP453709, KR673477).

The intracellular globules characteristic of most Pseudoclitocybaceae are only frequent in the stipititrama of *Pseudoclitocybe*, and clamp connections have only been detected on mycelial hyphae (except for a few on stipitipellis of *P. cyathiformis* Lineage II). Subpellis is hardly differentiated in *P. cyathiformis* Lineage II, perceptible in *P. cyathiformis* Lineage I, and absent in *P. obbata*. The development of the hymenopodium (always with slender, anastomosing hyphae with divergent structure) follows the same pattern. Mediostratum is rather regular excepting in *P. obbata* where it looks more entangled. Suprapellis structures are rather specific, an ixotrichocutis with few, unbranched erected elements in *P. cyathiformis* Lineage I, or rich in terminations either simple and cylindro-clavate (*P. obbata*) or versiform (*P. cyathiformis* Lineage II). Incrusting pigment is abundant in *P. obbata* and present in *P. cyathiformis* Lineage I, nearly absent in *P. cyathiformis* Lineage II. All species have parietal pigmentation in

pileipellis and/or subpellis, and a yellow intracellular pigment in some hyphae of pileipellis. Vascular (thromboplerous) hyphae with deep yellow–brown content have been seen only in *P. obbata*, mostly in the hypophyllum region.

***Pseudoclitocybe cyathiformis* (Bull.) Singer** Mycologia 48(5): 725 (1956) (Figs. 3j–o)

Basionym: *Agaricus cyathiformis* Bull., Herb. Fr. (Paris) 12: tab. 575 (1792), sanctioned by Fries, Syst. Mycol. 1: 173 (1821)

≡ *Clitocybe cyathiformis* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 120 (1871)

≡ *Omphalia cyathiformis* (Bull.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 129 (1872)

Description: Pileus 5–9.5 cm, a bit fleshy, first convex with a central depression and papillate, soon strongly depressed, funnel-shaped; margin enrolled then incurved downwards, at last applanate, a bit grooved because of the lamellae print and the thin flesh; surface smooth and opaque, with very fine fibrils, grey bistre, dark brown flushed olive, fading to grey-brown, ochraceous brown on drying, a bit hygrophanous. Lamellae adnate-decurrent, moderately crowded, very broad, with numerous lamellulae; pale grey-brown to brownish grey. Stipe 8–11 × 0.5–1.2 cm, straight, cylindrical, a bit inflated toward the base, solid then stuffed; surface tomentose-fibrillose, greyish brown, paler than the pileus. Context thin, fragile, watery, greyish. Smell and taste not distinctive. Spores (7.8–) 8.0–9 (–10.8) × 5.2–6.0 µm, ovoid-ellipsoid with adnate base, thin-walled, distinctly amyloid, smooth, not guttulate. Basidia 4-spored, 22–34 × 7–8.5 µm, clavate-subcapitate before maturity, microguttulate, unclamped. Cystidia not observed; cystidioles sparse on lamella edge, arising from subhymenium, cylindrical sinuose, sometimes forking on old specimens. Subhymenium ramose, 12–20 µm thick. Hymenophoral trama with a well-developed hymenopodium, 40–50 µm thick, made of parallel slender hyphae 3.5–5.0 µm wide, straight, slightly thick-walled. Mediostratum subregular, well-developed, made of broad and mostly short, cylindrical to inflate hyphae 7–16 µm wide, smooth, moderately thick-walled. Pileipellis an ixocutis, 40–60 µm thick, made of mostly parallel hyphae 3–5 µm wide, cylindrical, partly with microguttulate content, with frequent obtuse terminations, superficial hyphae forming short erected lateral, non-septate branches especially frequent at margin and sometimes fasciculate, up to 40 µm long; wall smooth to minutely incrusted. Subpellis weakly differentiated, yellowish in KOH, 50–80 µm thick, mostly made of parallel welded hyphae mixed with broader, sinuose hyphae, 3–9 µm wide, frequently forked and anastomosed, wall thick, yellowish, punctuate to minutely zebra-striped. Pileitrama colourless, made of entangled, cylindrical hyphae 5–12 µm wide, frequently branched and anastomosed, wall faintly thickened and smooth; vascular hyphae absent. Stipitipellis a trichocutis of mostly prostrate cylindrical hyphae 3.5–5.0 µm wide, with frequent prostrate to sparsely erected, rarely fasciculate hairs 40–90 × 4.5–10 µm, the largest arising from deeper hyphae. Stipititrama made of parallel, cylindrical or inflate hyphae 7–25 µm wide, mostly with intracellular globules 2–5 µm diam. Mycelial hyphae slender, 3.0–4.5 µm wide, cylindrical, slightly thick-walled (0.3 µm), smooth, sparsely branched, usually with one lateral ramifications per hypha close to septa; clamps present but not at all septa, loop-like. Birefringent crystals rare. Cystidioid elements not seen. Clamp connections present in the mycelium.

Specimens examined:

Lineage I) **FRANCE**: Oise, Carlepont, Forêt domaniale de Ourscamps, under *Picea abies* plantation, 64 m asl, leg. P. Clowez, 23-XI-2016, LIP 0901300. Savoie, Beaufort, Arèches, les Envers, at the bottom of a recently manured road side under *Picea abies*, 25-VIII-2014, leg. P.-A. Moreau, PAM14102509/LIP 0401359. **ITALY**: Emilia Romagna, Bologna, San Benedetto Val di Sambro, Val Serena, brodleaved and pine trees, leg. G. Consiglio, G. Bordoni, 24-XI-2000, AMB 18225/GC 00220. Emilia-Romagna, Vidiciatico (Bologna), Rio Ri, under *Fagus sylvatica* and *Abies alba*, leg. G. Consiglio, G. Spisni, 21-IX-2016, AMB 18226/GC 16021. Lucca, Fosciandora, Prade Garfagnine, under *Castanea sativa*, leg. G. Consiglio, P. Petrucci, 4-X-1996, AMB 18227/GC 96168.

Lineage II) **FRANCE**: Corse-du-Sud, Bastelica, near Porticcio, pont de Zippitoli, Mediterranean oak forest, in a decaying branch of *Quercus ilex*, leg. Société Mycologique d'Ajaccio, 21-XI-2014, PAM14112110b/LIP 0401360. **ITALY**: Lucca, Castiglione di Garfagnana, Passo delle Radici, under *Castanea sativa*, leg. G. Consiglio, D. Antonini, M. Antonini, 19-X-2000, AMB 18228/GC 00060. Sardinia, Carana, Diga del Liscia, under *Alnus*, leg. M. Contu, 30-XII-2012, TO HG123012A.

Ecology: forming small groups, found in broadleaved and conifer forests, in open spaces and pathways, in temperate areas of Europe, America, and Asia. Summer to late autumn or winter.

Comments: The original concept of the type species is here interpreted as a dark-colored wood-associated taxon present in northern Europe as well as temperate forests of Mediterranean countries. Spore size rarely exceeds 10 µm, in agreement with Saccardo (1887), who noticed a conflict with spore measurements by Britzelmayr (up to 10–12 × 5.0 µm). *Pseudoclitocybe beschidica* (Singer & Kuthan 1980) was separated from *P. cyathiformis* because of its shorter spores not exceeding 8.5 µm long, but the present observations suggest that this would be an average

value rather than an upper limit. Two distinct genetic lineages were found among samples identified as *P. cyathiformis*, but only slight differences in their morphology were detected. The description above refers to the apparently most frequent one, Lineage I. Lineage II differs mainly because of a less developed hymenopodium 20–25 µm (instead of 40–50 µm), and a pileipellis 70–100 µm thick (instead of 40–60 µm) made of hyphae 6.5–9.0 µm wide (instead of 3–5 µm). Both lineages occur in northern Europe, but no samples of Lineage I were found up to now in Mediterranean lowland habitats. The application of the name *P. expallens* to any of these lineages is controversial, since Fries used ambiguous characters such as size and color to separate it from *P. cyathiformis*. In the present work we observed great variations in these features among specimens studied, and so avoided employing the name *P. expallens* to any of the genetic lineages of *P. cyathiformis* until some evidence for this decision is found.

***Pseudoclitocybe obbata* (Fr.) Singer** Sydowia 15(1-6): 52 (1962) [1961] (Figs. 3p–r)

Basionym: *Agaricus obbatus* Fr., Epicr. syst. mycol. (Upsaliae): 74 (1838) [1836–1838]

≡ *Clitocybe obbata* (Fr.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 90 (1872)

≡ *Cantharellula obbata* (Fr.) Bousset, Bull. trimest. Soc. mycol. Fr. 55: 123 (1939)

≡ "*Omphalia obbata*" (Fr.) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 129 (1953) (nom. inval., no full and direct reference to the replaced synonym, ICN Art. 41.5)

Description: Pileus 1.5–6.0 cm diam., early flattened then broadly depressed at centre, without forming a narrow depression; surface greasy, entirely white-pruinose and remaining so if not washed by rain, on blackish, dark brown to reddish brown ground when fresh, striate only with age, hygrophanous, quickly drying from centre, when dry uniformly pale ochraceous; margin a long time enrolled, white, pruinose. Lamellae 24–38 reaching the stipe, two series of lamellulae, adnexed, arcuate, then shortly decurrent when expanded, ash-grey and remaining so, rarely paler, with a coppery shade while ageing; edge smooth, concolorous, becoming rusty-brown with age. Stipe 4–9 × 0.4–0.8 cm, hollow, cylindrical, often compressed, entirely covered by a dense white fibrillum, early removed, on ash-grey to later grey-brown ground. Context grey when moist, pale ochraceous when dry. Smell herbaceous, weak. Spores (6.5–) 8.0–8.5 (–9.1) × 5.0–5.2 µm, broadly ellipsoid to subglobose, thick-walled, distinctly amyloid, smooth, micro-guttulate at maturity. Basidia 4-spored, 35–52 × 8.0–11.5 µm, clavate before maturity, abundantly guttulate, unclamped. Cystidia not observed. Subhymenium ramose, 25–30 µm thick. Hymenophoral trama with a well-developed hymenopodium, 30–50 µm thick, made of parallel slender hyphae 2.0–3.5 µm wide, smooth, anastomosing. Mediostratum subregular to somewhat interwoven, well-developed, made of cylindrical, short and often sinuous hyphae 4–13 µm wide, smooth to minutely punctuate. Pileipellis a trichocutis 50–70 µm thick, slightly gelatinized, made of cylindrical hyphae 3.5–6.0 µm wide, with abundant, cylindrical to clavate terminations; wall distinctly incrusted, minutely on the broadest hyphae, distinctly and scale-like on slenderer ones. Subpellis not differentiated. Pileitrama with yellowish and colourless zones, made of parallel and mostly cylindrical, 3–8 µm thick hyphae, partly with yellow incrusted wall, with frequent thromboplerous hyphae especially in hypophyllum with deep yellow content. Stipitipellis a cutis of prostrate cylindrical hyphae 3.0–5.5 µm wide, moderately thick-walled, nearly smooth, with sparse to fasciculate unseptate hairs. Stipititrama made of parallel, cylindrical or inflate hyphae 5–26 µm wide, without intracellular globules; vascular hyphae rare with yellow–brown content. Mycelium whitish, made of cylindrical, abundantly ramose hyphae 3.5–6.0 µm wide, with smooth- to slight punctuate wall, and with numerous terminal articles with obtuse apex, unbranching and with microguttulate content. Calcium oxalate crystals not seen. Clamps only present on mycelial hyphae, loop-like.

Specimens examined: **FRANCE**: Ain, Vanchy, Carrières de Vanchy, dry grassland, leg. R. Fillion, P.-A. Moreau, 17-XII-2000, PAM00121703/LIP 0401357. Nord, Liessies, mont de Baives, mesophilic calcareous grassland, leg. C. Lécuru, P.-A. Moreau, 6-XI-2005, PAM05110604/LIP 0401358. **ITALY**: Bologna, Grizzana Morandi, Tudiano, under *Castanea sativa*, leg. G. Consiglio, R. Trimarco, 16-XI-1997, AMB 18229/GC 97181. Bologna, Pontecchio Marconi, Villa Grifone, broadleaved and pine trees, leg. G. Consiglio, R. Trimarco, 01-XII-1998, AMB 18230/GC 98186. Bologna, Sasso Marconi, Prati di Mugnano, under *Quercus pubescens*, leg. G. Consiglio, R. Trimarco, 6-XII-1998, AMB 18231/GC 98189. **SPAIN**: La Rioja, Lardero, La Barranca, arid basic steep soil, among moss with *Quercus coccifera*, *Rosmarinus officinalis* and *Cistus albidus* near a *Pinus halepensis* plantation, leg. Carlos M. Pérez del Amo, 30-I-2016, CMP1558/AH 46369.

Ecology: found in grasslands, as well as temperate and Mediterranean broadleaved or conifer forests. Autumn and early winter.

Comments: Knudsen and Vesterholt (2008) suggested that *P. expallens* could be an earlier synonym of both *P. atra* and *P. obbata*, but the lack of details in Fries original protologues of *A. expallens* and *A. obbatus* provides too weak support for a definitive decision. Basidiome size, colour and striated pileus seem not reliable features to

discriminate between the observed genetic clades. The lineage identified here with *P. obbata* is found sometimes in treeless grasslands, but also in forests (especially in Mediterranean countries), maybe suggesting more xerophilic preferences. This lineage has a trichodermal cutis similar to that reported by Harmaja (1974) for specimens identified as *P. atra*, suggesting that he was probably studying the same taxon, but unfortunately no samples coming from northern Europe could be examined. On the other hand, Kuyper (1995) observed *P. atra* has clamps at all septa in mycelium, and even hyphae in the pileus context are sparsely clamped also, suggesting that this taxon is actually different from *P. obbata* and might correspond to *P. cyathiformis* Lineage I. The possibility of a new species cannot be rejected; Harmaja's and Bon's descriptions of *P. atra* match some of our atypical collections of *P. cyathiformis* I (for instance PAM14082509) with especially pruinose and non-umbilicate pileus.

Other specimens examined: ***Pseudoclitocybe* sp.:** USA: California, Santa Cruz Co., Nisene Marks State Park, leg. C. Schwarz, 13-XII-2015, MO 225374/LIP 0401355.

***Pogonoloma* (Singer) Sánchez-García** in Sánchez-García et al., Taxon 63(5): 1001 (2014)

Basionym: *Porpoloma* subgen. *Pogonoloma* Singer in Sydowia 15: 53. 1962 ("1961")

≡ *Porpoloma* sect. *Pogonoloma* (Singer) Bon in Doc. Mycol.9(33): 25. 1978 (Fig. 3a)

Description: Habit tricholomoid. Pileus umbonate to flat, surface spinose or tomentose at margin, tending to break into scales from centre. Lamellae crowded, emarginate, turning yellowish with age. Stipe rooting, smooth, without veil, staining yellow with age. Context fleshy, white, yellowing with age; smell strong, aromatic, nauseous when old. Spores small, 5–7 × 3.5–4.2 µm, ovoid to shortly cylindrical, smooth, microguttulate at maturity, strongly amyloid, acyanophilic. Basidia small and slender, 26–32 × 5–7 µm, guttulate before maturity. Lamellae edge fertile, with sparse cystidioid elements. Pileipellis a trichocutis of long fasciculate hyphae, gelatinized or not. Pigment intracellular. Pileitrama and mediostratum of the hymenophoral trama of sarcodimitic structure, with long broad physalohyphae and slender cylindrical hyphae, mixed with sparse to frequent thromboplerous hyphae branched at ends. On ground, "presumably saprotrophic" (Sánchez-García et al. 2014).

***Pogonoloma spinulosum* (Kühner & Romagn.) Sánchez-García** in Sánchez-García et al., Taxon 63(5): 1001 (2014)

Basionym: *Tricholoma spinulosum* Kühner & Romagn., Bull. mens. Soc. Linn. Soc. Bot. Lyon 16: 136 (1947)

≡ *Leucopaxillus spinulosus* (Kühner & Romagn.) Konrad & Maubl., Encyclop. Mycol. 14: 409 (1949)

≡ *Porpoloma spinulosum* (Kühner & Romagn.) Singer, Sydowia 15(1–6): 53 (1962)

= *Tricholoma guttatum* s. J.E. Lange Flora Agaricina Danica I, p. 55, pl. 24 fig. E (1935) (as "*Tricholoma guttatum* Barla nec al.").

= *Porpoloma macrorhizum* s. Bon, Docums. Mycol. 9(33): 26 (1978)

Description: Pileus 3–9 cm, broadly umbonate, covered by a thin silky fibrillum on a smooth, dry ground, foxy yellow at centre, light ash-grey progressively fading towards margin; margin white, enrolled till the end, minutely spinulose. Lamellae crowded, 56 at stipe, 3 series of lamellulae, sinuate, deeply uncinate, cream white; edge thin, minutely serrulate, concolorous. Stipe 5–12 × 0.8–1.2 cm, minutely pruinose all over, white, cream to dirty yellowish if bruised; base rooting. Context white, firm; smell of banana; taste bitterish. Spores 5.0–6.5 × 3.5–4.2 µm, ovoid to ellipsoid, smooth, strongly amyloid, acyanophilous; content microguttulate at maturity. Basidia 26–32 × 6–6.5 µm, 4-spored, narrowly clavate, guttulate before maturity. Lamellae edge fertile, with cylindrical cystidioles sparsely protruding up to 25 µm. Pleurocystidia none. Subhymenium ramose, divergent, 15–20 µm thick. Hymenophoral trama with a differentiated hymenopodium 30–40 µm thick, slightly divergent, made of slender hyphae 4–6 µm wide. Mediostratum of regular structure, made of broad parallel hyphae 5–22 µm wide, mixed with slender hyphae 3–47 µm wide, with sparse pale yellow thromboplerous hyphae. Pileipellis when young an ixotrichocutis made of long slender hyphae 3.5–5 µm wide, smooth to very faintly punctuate, with vacuolar pigment, fasciculate towards margin, prostrate and collapsing at centre and with age. Subpellis 60 µm thick, weakly differentiated, made of slender parallel hyphae 3.5–4.5 µm wide. Pileitrama of sarcodimitic structure, made of broad physalohyphae 7–10 µm wide with colourless intracellular granules, mixed with slender cylindrical hyphae 3–6 µm wide, all smooth and slightly thick-walled, and sparse thromboplerous hyphae with pale yellow content, 3–5 µm wide, often ramose. Clamps present at all septa, loop-like.

Specimens examined: **FRANCE**. Dordogne, Notre-Dame de Sanilhac, La Malétie, boadleaved forest on clay-calcareous soil, leg. G. Eyssartier, 24-VIII-1995, M. Bon 95040 (LIP, as "*Porpoloma macrocephalum*"), not sequenced. Loire-Atlantique, Saint-Philibert-de-Grand-Lieu, under *Quercus* sp., leg. G. Mabon, 01-X-1992, Coll. J. Mornand 9266/M. Bon (LIP 0101354, as "*Porpoloma macrocephalum*"). Pas-de-Calais, Desvres, Forêt domaniale, Rue Noire, broadleaved thickets under *Carpinus betulus* and *Quercus robur* on calcareous soil, leg. R. Courtecuisse, 9-IX-2016, PAM16070903/LIP 0401167. Pas-de-Calais, Desvres, La Drouille, mixed broadleaved forest with *Quercus robur*, leg. J.-P. Gavériaux, 11-IX-

2016, PAM16091102/LIP 0401166. Yonne, A6 motorway rest area near Auxerre, mixed broadleaved trees on calcareous ground, leg. G. Redeuilh, 14-IX-1981, M. Bon 8109 (LIP, as "*Porpoloma* cf. *macrocephalum*"), not sequenced.

Ecology: found in European temperate broadleaved forests, but originally reported from *Picea abies* (Kühner & Romagnesi 1947). In autumn.

***Pogonoloma macrorhizum* (Quél.) Dima & P.-A. Moreau, comb. nov.**

MycoBank MB 824745 (Fig. 3a)

Basionym: *Gyrophila macrorhiza* Quél., Enchir. Fung.: 13 (1886) [cites "Lasch. Kalch. t. 3, fig. 1", indirectly referring to *Agaricus macrorhizus* Lasch, Linnaea 3: 396 (No. 240) (1828), nom. illeg., non *Agaricus macrorhizus* Pers., Observ. mycol. (Lipsiae) 1: 47 (1796)].

≡ *Tricholoma macrorhizum* (Quél.) Sacc., Syll. fung. (Abellini) 5: 105 (1887)

≡ *Armillaria macrorhiza* (Quél.) Jacobashch, Verh. bot. Ver. Prov. Brandenb. 37: LXI (1895) [citing basionym as "*Tricholoma macrorhizum* (Lasch) Fr."]

≡ *Leucopaxillus macrorhizus* (Quél.) Sacconi & Lazzari, Boll. Gruppo Micol. G. Bresadola Trento 23(5–6): 114 (1980)

≡ *Porpoloma macrorhizum* (Quél.) Bon, Docums Mycol. 20(no. 78): 38 (1990)

≡ *Agaricus macrocephalus* Schulzer in Kalchbrenner, Icon. Sel. Hymenomyc. Hung. (Budapest): 11, tab. 3 (1873) nom. illeg. Lectotype: icone, Kalchbrenner & Schulzer, Icon. Sel. Hymenomyc. Hung. tab. III, fig. 1. 1873 [Designated by Sánchez-García, Matheny, Palfner & Lodge, Taxon 63(5):1001. 2014, MycoBank MBT 381114], non *Agaricus macrocephalus* Schumach., Enum. pl. (Kjbenhavn) 2: 264 (1803).

≡ "*Coolia macrocephala*" Huijsman, Medded. Nedl. Mycol. Ver. 28: 60 (1943) [as "(Schulz.) Huijsman comb. nov.", nom. invalid., published in an invalid genus, ICN Art. 39.1]

≡ "*Squamanita macrocephala*" M.M. Moser, in Gams, Kl. Krypt.—Fl. Mitteleuropa—Die Blätter- und Bauchpilze (Agaricales und Gastromycetes) (Stuttgart) 2: 66 (1953), nom invalid. [as "(Schulz.) M.M. Moser comb. nov.", no full and direct reference to the replaced synonym, ICN Art. 41.5]

≡ "*Leucopaxillus macrocephalus*" Bohus, Fragm. Bot. Mus. Hist.-Nat. Hung. 4(1–4): 37 (1966), nom. invalid. [as "(Schulz.) Bohus comb. nov.", nom. inval., no full and direct reference to the replaced synonym, ICN Art. 41.5]

≡ *Porpoloma macrocephalum* Bon, Docums Mycol. 9(33): 26 (1978) [replacement name as "(Schulzer apud Kalchbrenner) comb. nov.", ICN Art. 6.11, Art. 41.6, 41.8]

≡ *Pogonoloma macrocephalum* (Bon) Sánchez-García in Sánchez-García, Matheny, Palfner & Lodge, Taxon 63(5): 1001 (2014) [corrected authority "(Schulzer) Sánchez-García comb. nov."]

Description: Pileus 5–30 cm broad, hemispherical then convex, finally applanate, sometimes somewhat depressed in the centre, with the margin a longtime enrolled, wavy-lobed. Cuticle tomentose, opaque, creamy then brownish ochre with a shade of orange, soon dissociated in patches. Lamellae rather crowded, adnate-emarginate, whitish, reddening when bruised, with the edge irregular, concolorous. Stipe 2.5–16.0 × 1.5–8.0 cm, often with many specimens grown together emerging from a common base, thickset, solid, cylindrical to ventricose, often rooting, whitish, ochre when bruised, minutely furfuraceous. Context tough, firm, whitish, slowly yellowing when cut. Smell complex, with a component of wet mould over a scent of over-ripe fruit or cornsilk; taste unpleasant. Spore print whitish. Spores 5.0–6.5 × 3.5–4.5 µm, shortly cylindrical to broadly ellipsoid, smooth, hyaline, amyloid. Basidia 25–32 × 5–7 µm, 4-spored with short sterigmata, narrowly clavate; content densely granular before maturity; base clamped, often crozier-like. Lamellae edge fertile, with sparse broad, clavate cystidioid elements 12–25 × 6–16 µm, colourless, thin-walled and often incrusted by small granulations. Subhymenium ramose, erected, made of short cylindrical hyphae. Hymenophoral trama parallel, made of long cylindrical hyphae 3.5–8.0 µm wide, partly with refringent content, some thromboplerous-like and spreading abundant resinoid content in KOH. Pileipellis a dry trichocutis formed by fascicles of long slender hyphae with smooth, slightly thickened wall, terminal element 80–150 × 4–5.5 µm, cylindrical. Subpellis hardly differentiated, 40–60 µm thick, made of hyphae 3–5.5 µm wide, abundantly clamped. Pileitrama radially oriented, of sarcodimitic structure made of broad physalohyphae 7–10 µm wide with granular content, and slender cylindrical hyphae 3–5 µm wide, and frequent thromboplerous hyphae 5–8 µm wide, cylindrical and branched towards ends with pale yellow homogeneous content. Clamps present at all septa, loop-like and voluminous.

Specimens examined: **ITALY**. Emilia-Romagna, Monghidoro (Bologna), Valgattara, under *Castanea sativa* and *Quercus pubescens*, leg. M. Barbieri, 20-VI-2017, AMB 18232. **SWITZERLAND**. Ticino, Bruzella-Cabbio, leg. A. Marchand, 22-VIII-1981, coll. M. Bon, LIP 0101353 (as "*Porpoloma macrocephalum*").

Ecology: Central European temperate broadleaved forests, in tufts with numerous specimens growing together, under broadleaved trees, mainly larger oaks. Spring to autumn. Widespread but rare.

Comments: the nomenclature of this taxon is obscure, and the treatment proposed here is purely nomenclatural.

The name *Agaricus macrocephalus* Schulzer was probably mentioned for the first time in Schulzer's unpublished manuscript 'Schwämme und Pilze aus Ungarn und Slawonien' deposited at the Hungarian Academy of Sciences in 1869 (Gombocz 1936; Tortić 1981). Schulzer's illegitimate basionym (published in Kalchbrenner 1873) was unfortunately combined into different genera without fully citing the basionym (ICN Art. 41.5), therefore most replacement names based on these combinations are invalid. A combination into genus *Coolia* Huijsman (Huijsman 1943) fully cites Schulzer's basionym, but *Coolia* is an invalid genus (ICN Art. 39.1), and so a replacement name based on it would not be possible. The oldest valid replacement name seems to be attributable to Bon (1978) who published a combination in the genus *Porpoloma*, citing explicitly Schulzer's basionym. The combination into *Pogonoloma* by Sánchez-García et al. (2014) employed Schulzer's replaced synonym as basionym, a correctable formal error amended here using Bon's replacement name. Unfortunately, while Bon's validation would have provided a stable solution to the taxonomy of this remarkable species, an old confusion due to Fries (1878, p. 58) between Schulzer's taxon and the hardly interpretable *Ag. macrorhizus* Lasch (1828) forces to renounce to Sánchez-García et al. (2014) name. After Fries proposed the two names as synonyms, Quélet (1886, p. 13) introduced the name *Gyrophila macrorhiza*, based on Lasch's illegitimate name (later homonym of *Ag. macrorhizus* Pers., 1796), but considered here as a new name (rather than a replacement name) because based exclusively on Schulzer's description and citing Kalchbrenner's plate 3 fig. 1 as reference. This plate cited by Quélet is interpreted under the current Code of nomenclature as the only original material (therefore only possible lectotype) for *Gyrophila macrorhiza* Quél. Because this plate is also the lectotype of *Porpoloma macrocephalum* Bon, the two names are automatically nomenclatural synonyms.

This remarkable and rare European species differs from *P. spinulosum* by larger basidiomata, caespitose growth, fruiting in spring and summer (sometimes autumn as well), a different, stronger and nauseous smell (of banana in *P. spinulosum*), and a pileipellis not gelatinized, not forming spines but a tomentum at margin, and early dissociating in broad imbricated scales. In Hungary, the heaviest basidiomata measured so far was 1.75 kg (Siller et al. 2006). The species has gained legal protection in Hungary since 2005 (Siller et al. 2006). The Italian collection identified as *Leucopaxillus nauseodulcis* and sequenced by Osmundson et al. (2013, GenBank JF908326) is likely a misidentification. *Pogonoloma macrorhizum* was at least reported once from France (forêt de Sénart, near Paris) by Kühner and Romagnesi (1947). On the other side, all collections described by Bon (1976) as "*Porpoloma macrorhizum*" revealed to correspond to old specimens of *P. spinulosum* described above. The Swiss collection LIP0101354 was described and illustrated by Marchand (1986) as *Porpoloma macrocephalum*.

Excluded taxa

***Pseudoclitocybe sphagneti* Raithelh., Metrodiana 3(1): XXIV (1972)**

Material studied: Germany, Baden-Württemberg, near Calw, Würzbacher Moor, leg. J. Raithelhuber, PtD-11171 (isotype: ZT Myc 58861)

= *Fayodia gracilipes* (Britzelm.) Bresinsky & Stangl

Comments: the isotype deposited at ZT (Zürich, CH) consists in a well-preserved half-specimen. Contrary to the original description, microscopical features of the specimen are all typical of *Fayodia gracilipes* (Britzelm.) Bresinsky & Stangl (= *F. bisphaerigera* (J.E. Lange) Singer), especially the inconfundible spores which are globose, thick-walled with characteristically pitted myxosporium, and amyloid perisporium. The synonymy is therefore established here.

Discussion

In the present work, two species of *Clitocybe* section *Disciformes*, *C. harperi* and *C. alexandri*, are shown to be genetically separate from the Clitocybeae. *Clitocybe alexandri* is proposed as a type species of the new genus *Clitopaxillus*, and *C. harperi* as a type species of *Harmajaea*. The monophyletic lineage composed of *Pseudoclitocybe*, *Musumecia*, *Clitopaxillus*, *Harmajaea*, and *Pogonoloma*, is here proposed as the new family Pseudoclitocybaceae. The purpose of this name is to reflect the monophyletic status of several lineages not related to Clitocybeae, Tricholomataceae or any other family, which often display characteristic morphological features such as absent or poorly differentiated cystidia and clamp connections in the basidiomes, and show amyloid spores. None of these traits is constant within Pseudoclitocybaceae, making this family apparently heterogeneous and difficult to define based on morphology. However, some remarkable features exist, such as loop-like or medallion-type clamps (where present), an "archaic" feature found in a few other genera within Agaricales such as *Gliophorus* Herink, *Humidicutis* (Singer) Singer and *Porpolomopsis* Bresinsky (Hygrophoraceae) (Lodge et al. 2014) or *Clavaria* P. Mich. ex L. (Clavariaceae) (Birkebak et al. 2013); or a homomorphic structure of the whole basidiome, based on cylindrical hyphae of wide diameter (> 5–6 µm), with frequent internal globules, and forming a regular trama. Interestingly, Kühner (1980) pointed out that species of *Pseudoclitocybe* and *C. alexandri* have plurinucleate

terminal hyphae in secondary mycelium (holocoenocytic mycelium sensu Boidin 1964 and Stalpers 1978), a feature which might play a role in the disjunct distribution of clamps in mycelia and basidiomes, and a bipolar heterothallism (unusual in Agaricales, Petersen 1995). No comparable information is available either from *Pogonoloma* or *Musumecia* species.

Other families in the suborder Tricholomatinae, such as Biannulariaceae, Entolomataceae, Lyophyllaceae, Tricholomataceae and the Clitocybeae lineage can easily be discriminated from Pseudoclitocybaceae by means of DNA analysis. Biannulariaceae (as Catathelasmataceae in Sánchez-García et al. 2016), Entolomataceae (Co-David et al. 2009; Baroni et al. 2011; Kluting et al. 2014), Tricholomataceae (Sánchez-García et al. 2014), and Lyophyllaceae (Hofstetter et al. 2014; Redhead 2014; Bellanger et al. 2015) have been recently reviewed and re-organized, resulting in several genera being proposed or amended to accommodate the multigenic data obtained from an increasing number of species. Morphologically, Lyophyllaceae species have siderophilous basidia (Bellanger et al. 2015), and Entolomataceae produce pinkish spore prints, and their spores have a voluminous lipidic droplet, a triangular apicule and bumps and/or ridges formed by an epicorium (Co-David et al. 2009; Baroni et al. 2011; Kluting et al. 2014), but no evident synapomorphic feature has been identified so far for either Biannulariaceae, Tricholomataceae or Clitocybeae lineages. Tricholomataceae are loosely characterized by their tricholomatoid habit (large and fleshy, convex pileus, lamellae commonly not decurrent), while Clitocybeae almost always have clamped hyphae, a feature sometimes present also in Pseudoclitocybaceae. Biannulariaceae have been recently amended to include several genera previously classified in different taxa, such as *Callistosporium* Singer, *Macrocybe* Pegler & Lodge, *Pleurocollybia* Singer, or *Pseudolaccaria* Vizzini, Contu & Z.W. Ge, and is mainly defined by means of genetic inference at the present time (Sánchez-García et al. 2016).

Pseudoclitocybaceae shares several morphological traits with Tricholomataceae and Clitocybeae, but can be discriminated because of their often decurrent or subdecurrent lamellae, cystidia and clamp connections usually absent, and often amyloid spores. The singular hyphal structure, lacking slender hyphae < 4 µm wide in all species studied but *Pogonoloma* spp., the broad, loop-like clamps (absent only in *Musumecia bettlachensis*, and not proved to be lacking in the mycelium of *Harmajaea harperi*), the hymenophoral trama with usually long, parallel or subparallel hyphae, the presence of globules in most hyphae of context, and the tendency of most species to turn yellowish to dirty brown when drying are hypothesized here as significant features for defining this family, but should be more systematically investigated in related lineages. Such a definition based on "secondary" morphological features implies a revision of many species through reference herbarium material and fresh collections, since these features are rarely described in protologues and in taxonomic literature in general.

Clamps are either present throughout the basidiome in *C. fibulatus* or restricted to specific areas and at most transformed into "false" clamps elsewhere in *C. alexandri*, while *Harmajaea* species completely lack clamp connections on basidiomata (but they are present on mycelium). This variability, which seems to have a specific value in this whole lineage, suggests that maybe clampless species could be present also in *Clitopaxillus*, making it difficult to establish clear-cut limits between both genera. Clamp connections are sparsely present in *Pseudoclitocybe* species, and either abundant, sparsed or absent in the sister genus *Musumecia*. Similarly, spore amyloidity was recently shown to vary between species of *Musumecia* as new taxa are found and described (Li et al. 2016). Identification of *H. harperi* is relatively easy, because of the differences with other clitocyboid taxa lacking clamp connections: *Clitocybe griseifolia* (Murrill 1913) is the most similar, but has broader lamellae, white stipe, and fragrant odor (Bigelow 1965, 1982), while other species lacking clamp connections described by Bigelow (1983), such as *C. borealis* H.E. Bigelow, *C. adustiterricola* H.E. Bigelow, *C. payettensis* H.E. Bigelow, *C. hesleri* H.E. Bigelow, and *C. solumophila* H.E. Bigelow, are all much smaller in size than *C. harperi* (0.5–1.5 cm on average vs. 8–10 cm in *C. harperi*). *Harmajaea wellsiae* differs because of its brownish pileus, almost adnate lamellae and a boreal distribution, while the new taxon *H. guldeniae* has also a brownish pileus, clearly decurrent lamellae, longer basidia, and clamped mycelium.

Species in *Pseudoclitocybe* usually produce funnel-shaped basidiomata lacking cystidia and clamp connections, although the latter can be observed on secondary mycelia in culture (Kühner 1980) and at the base of the stipe and underlying mycelium (Kuyper 1995). Thorough observations on the collections cited above confirm that the distribution of clamp connections in *Pseudoclitocybe* is also a specific feature: in *P. cyathiformis* (Linages I and II) clamp connections are only observed in mycelium, and only on some septa, whereas in collections identified as *P. obbata* hyphae are clamped at all septa in mycelium, and sparsely in pileus context. Considering this, Kuyper's (1995) observations might not concern *P. cyathiformis* s. str. but the most abundantly clamped species in Europe, i.e., *P. obbata* as interpreted here.

Musumecia was named by Vizzini et al. (2011) to honor Swiss mycologist Enzo Musumeci, who was the first to report it from Alsace (France). Molecular data as well as

some shared morphological traits linked *Musumecia* and *Pseudoclitocybe*: cutis-like pileipellis, elongated basidia, smooth, acyanophilous spores, and absence of clamp connections in basidiomata (although *Pseudoclitocybe* spp. form clamps in mycelium). However, *Musumecia* was considered an independent genus, because of its hygrophoroid habit (non-depressed, convex pileus and distant thick lamellae), the darkening of lamellae and stipe, and non-amyloid spores, as well as for the evident genetic differences between both lineages. The type species, *M. bettlachensis* Vizzini & Contu (Vizzini et al. 2011), is whitish and grows caespitose in *Abies alba*, *Fraxinus* sp. and *Fagus sylvatica* forests, while *M. vermicularis* Musumeci (Musumeci 2014), has a zonate brownish dark pileus, is gregarious but not caespitose, grows under *Carpinus betulus*, and produces rhizomorphs. Moreover *M. vermicularis* is abundantly clamped in rhizomorphs and basidiomes (although not at all septa, and with occasionally unclosed or verticillate clamps, like *C. alexandri*). Recently, two other species of *Musumecia* have been proposed in Li et al. (2016): *M. sardoa* Consiglio, Vizzini & Setti with scarce clamps present only in subpellis and pileitrama, and *M. alpina* L.P. Tang, J Zhao & S.D. Yang, which has abundant clamps all over the basidiome. *Musumecia alpina* produces hymenial cystidia and verruculose non-amyloid spores, while *M. sardoa* has no cystidia and clearly amyloid spores. Although *Musumecia* was originally described with inamyloid spores (Vizzini et al. 2011), the spores of *M. bettlachensis* holotype (TO HG2284) examined under a standardized procedure by some of the present authors turned out to be weakly amyloid in grey colour. The spores of *C. alexandri* and *H. harperi* showed also a weak amyloid reaction with this procedure (Fig. 4d), suggesting that this feature should be further investigated, and definitions amended to accommodate these findings.

The tricholomatoid genus *Pogonoloma* had already been reported to be closely related to *Pseudoclitocybe* and *Musumecia* (Sánchez-García et al. 2014). The genus was a new rank for *Porpoloma* subgen. *Pogonoloma* Singer, proposed to accommodate the type species *Porpoloma spinulosum* (Kühner & Romagn.) Singer, as well as *P. macrocephalum* (Schulzer) Singer, after preliminary data suggested *Porpoloma* was actually polyphyletic (Vizzini et al. 2012). Both species have a felted-subsquamulose pileus surface, a trichocutis-like pileipellis forming a thick tomentum or spines at margin, intracellular pigmentation, amyloid spores, lack of typical cystidia (only scarce "marginal hairs"), and present clamp connections at all septa (Kühner and Romagnesi 1947; Bon 1991; Kuyper 1995), features shared by other members of Pseudoclitocybaceae but also widespread across the Agaricales. Moreover the tricholomatoid habit as well as the doubtfully saprobic (possibly ectomycorrhizal?) behaviour are extralimital in this family. In the present work we chose to include it in the new family because of its significant genetic relationship, but also because they share the same features observed as characteristic in the clitocyboid members of the family: hymenophoral trama made of broad, cylindrical hyphae > 5 µm wide, many with internal globules, hymenophoral trama subregular, loop-like clamp connections, and loosely branched subhymenium. In the original description of *P. spinulosum* (Kühner & Romagnesi 1947), all these features were already mentioned but no systematic importance was given to them at that time. Kühner pointed out the "large clamps" and the parallel hymenophoral trama with mostly broad, cylindrical hyphae, and Romagnesi the "intracellular punctuations" in hyphae of pileipellis. Interestingly, the parallel hymenophoral trama is conform to the general definition of the family given here, but the pileus trama shows a sarcodimitic structure (Kühner and Romagnesi 1947) with a majority of thick fusiform physalohyphae and a few generative hyphae of smaller diameter, figuring a possible evolutional step towards the homomorphic structure of the whole basidiome in the derived clitocyboid lineages. *Pogonoloma* seems to represent a basal clade of Pseudoclitocybaceae, so far only documented by two rare European species, and therefore its position could be re-evaluated in case new data become available to fill in biodiversity gaps.

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