

Taxonomy and phylogeny of yellow *Clavaria* species with clamped basidia—*Clavaria flavostellifera* sp. nov. and the typification of *C. argillacea*, *C. flavipes* and *C. sphagnicola*

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Abstract: This study explores species limits of a group of *Clavaria* species with taxonomic and nomenclatural problems and discusses the phylogeny and circumscription of the genus. The nuc 28S rDNA (28S) and internal transcribed spacer region phylogenies resolve species relationships, and the ITS is shown to be an adequate barcode marker for *Clavaria*. Yellow, clamped species of *Clavaria* are distributed in two clades, (i) *C. flavostellifera*, sister to *C. incarnata* and *C. asterospora* in ITS analyses, characterized by producing ornamented spores, and (ii) *C. argillacea*–*C. citrinorubra*–*C. flavipes*–*C. sphagnicola*, with smooth spores. *Clavaria flavostellifera* is described as new species based on morphological and molecular characters. Molecular evidence that supports *C. sphagnicola* as distinct from *C. argillacea* is provided. The usefulness of spore ornamentation as a taxonomic character is discussed; it is present only in some taxa and then only on spores trapped in the hymenium. Descriptions of *C. argillacea*, *C. flavipes* and *C. sphagnicola* are provided, along with color photographs and a key to yellow species of *Clavaria* with clamped basidia. *Camarophylloopsis* and *Clavicorona* are recovered within a paraphyletic *Clavaria* in our 28S phylogeny. Clampless contextual hyphae and narrow, slightly thick-walled mycelial hyphae are

proposed as synapomorphies of *Camarophylloopsis* and *Clavaria*.

Key words: Basidiomycota, *Camarophylloopsis*, Clavariaceae, *Clavicorona*, species delimitation, spore ornamentation

INTRODUCTION

The Clavariaceae Chevall. includes simple to coralloid clavarioid fungi, typically with colorless spores and chiasitic basidia (Corner 1950, Petersen 1978a, Dentinger and McLaughlin 2006), that is basidia with transversal spindles in the meiotic division of the diploid nucleus. Within the family *Clavaria* L. is characterized by producing simple clavarioid basidiomata (coralloid only in *C. martinii* Corner, *C. pumanquensis* Lazo and *C. zollingeri* Lév. auct.) and by the absence of clamp connections in contextual hyphae, unlike *Clavulinopsis* van Overeem and *Ramariopsis* (Donk) Corner, which have clamps (Corner 1950). *Clavaria* has been considered saprotrophic, but there is evidence that at least some species of *Clavaria* form ericoid mycorrhizae (Englander and Hull 1980, Mueller et al. 1986). *Clavaria* is widely distributed in boreal, temperate and tropical areas. Excluding *Camarophylloopsis*, we estimate that *Clavaria* may comprise around 30–35 species, but the true number is probably higher because some species complexes are unresolved (Kautmanová 2012, Kautmanová et al. 2012a). The variabilities of the shape and color of basidiomata, and of spore characters are poorly documented. Difficulty in the interpretation of old names described without microscopic characters makes species identification more complicated. In this regard attempts were made to examine historical herbarium material and typifications were proposed (Adamčík 2008, Kautmanová et al. 2012a), but many names are still subject to interpretive ambiguity. The taxonomy of the species with clamped basidia, assigned to *Clavaria* subg. *Holocoryne* (Fr.) Corner, is especially complicated. Species delimitation relies on color, shape and size of basidiomata and on spore characters, none of which have been evaluated with molecular tools. The presence of ornamented spores, striking in some collections, probably has been overstressed in describing species (Patouillard 1886, Petersen and Olexia 1969, Geesink and Bas 1992) and is the only character that distinguishes some species

pairs (Petersen 1988, Knudsen 1996). Petersen (1988) noted that, when present, ornamented spores are scarce in mounts and smooth spores are dominant. Ornamented spores thus may be overlooked or even absent in some collections. The spore ornamentation is structurally unusual because it originates from the epispore and perforates the exospore (Locquin 1945).

Kautmanová et al. (2012b) assessed species boundaries in darkly pigmented *Clavaria* with a nuc 28S rDNA (28S) phylogeny. They suggested that subgenus *Holocoryne* is polyphyletic, but sufficient phylogenetic confidence to reject monophyly was not provided. Species boundaries also are in need of revision. Although the internal transcribed spacer region (ITS = ITS1–5.8S–ITS2) is accepted as a universal DNA barcoding marker in fungi (Schoch et al. 2012, Kõljalg et al. 2013), it has not been used for species delimitation in *Clavaria*. The use of the ITS may aid in resolving species complexes within *Clavaria*, including *Clavaria* subg. *Holocoryne*. A broad 28S phylogeny by Birkebak et al. (2013) reveals that some agaricoid, corticioid and hydroid genera belong to Clavariaceae. Of interest the type species of the agaricoid genus *Camarophylloopsis* Herink, *C. schulzeri* (Bres.) Herink, and other clampless *Camarophylloopsis* that were studied molecularly are not only closely allied to *Clavaria* (Matheny et al. 2006, Binder et al. 2010) but nested within *Clavaria* (Birkebak et al. 2013). A multigene phylogeny with broad taxon sampling to propose an updated natural classification of the Clavariaceae is eagerly awaited.

In an attempt to contribute to the understanding of the Clavariaceae, we set these objectives: (i) to revise the taxonomy and nomenclature of yellow *Clavaria* species with clamped basidia, (ii) to obtain a better insight into species limits in *Clavaria* subg. *Holocoryne*, (iii) to evaluate the usefulness of the ITS region for species delimitation in *Clavaria*, (iv) to provide observations on spore ornamentation and use molecular tools (v) to assess the value of spore ornamentation as a taxonomic character, and (vi) to contribute to the understanding and circumscription of *Clavaria* using a 28S phylogeny.

MATERIALS AND METHODS

Morphological study.—Descriptions were compiled from notes made on fresh material, with further details observed in dry material. Color codes follow the Royal Horticultural Society (1995) for fresh material and Munsell Color Corp. (1990) for dry material. Basidiospores were measured in side view excluding the apiculus from hymenium mounts in KOH 5%. Abbreviations referring to basidiospores are: L_m = mean length, W_m = mean width, $Q_m = L_m/W_m$; 25 basidiospores were measured per collection. Water and

Congo red in ammonia also were used to observe the material. Abbreviations of author names follow Kirk and Ansell (2003). Material is deposited in AH, ARAN, BIO, BRA, JA, K, MA, S, SAV, TENN and UPS (Thiers 2012 continuously updated).

Coordinates are in Universal Transverse Mercator (UTM) system.

DNA isolation, amplification and sequencing.—DNA was extracted from fresh and dried collections with the DNeasy Plant Mini Kit (QIAGEN, Crawley, West Sussex, UK), following the manufacturer's protocol. Partial 28S and complete ITS barcodes were amplified. LR0R and LR5 primers were used for PCR and for sequencing 28S (Vilgalys and Hester 1990), and ITS1, ITS4 and ITS5 were used for ITS (White et al. 1990). Reactions included: 1 μ L DNA template, 5 μ L Taq buffer, 20 μ L nucleotide mix, 5 μ L of each of the primers, 0.2 μ L Ampliqon Taq DNA Polymerase and 14 μ L sterile milli Q water. Thermo-cycler conditions were: 94 C for 3 min, 35 cycles of 94 C for 1 min, 60 C for 1 min and 72 C for 1 min and a final extension at 72 C for 7 min. The annealing temperature was lowered to 50–55 C when initial conditions proved unsuccessful. The QIAGEN PCR purification kit was used for PCR-product cleaning. Amplicons were sequenced in both directions with BigDye Terminator Mix 1.1. (Applied Biosystems, ABI, Warrington, Cheshire, UK) and were run in an ABI 3110 \times 1 automated sequencer.

Novel sequences (TABLE I) were subjected to BLAST to screen for contaminants. Sequences were assembled and edited with Sequencher 4.7 (Gene Codes Corp., Ann Arbor, Michigan) and submitted to the EMBL/GenBank/DDJB databases (Cochrane et al. 2010). Additional sequences were downloaded from the EMBL/GenBank (TABLE II). Sequences were aligned in two segments (ITS, 28S) with MAFFT (Kato and Toh 2008) and manually optimized in MacClade (Maddison and Maddison 2003). The 28S alignment contained sequences of *Clavaria* as well as *Camarophylloopsis* and *Clavicornia taxophila* (Thom) Doty sequences. The ITS alignment includes only clamped *Clavaria* species to obtain a less ambiguous alignment. *Ramariopsis kunzei* (Fr.) Corner and *C. zollingeri* (TABLE II) were used as outgroup taxa in the 28S and ITS analyses, respectively.

Phylogenetic analyses.—The ITS and 28S alignments were analysed by maximum likelihood (ML) and Bayesian approaches. Bayesian analyses were conducted with MrBayes 3.2.1. (Ronquist et al. 2011), applying a GTR substitution model sampled across parameter space by MCMC analysis (Huelsenbeck et al. 2004). Two parallel analyses of four MCMC chains were run for 5 000 000 generations, sampling trees at every 100th generation. Burn-in was set to 25%. The majority rule consensus trees with posterior probability values for 28S and ITS are illustrated (FIGS. 1, 2). We evaluated chain mixing and convergence with Tracer 1.5 (Rambaut and Drummond 2007). Effective sample size (ESS) values above 200 were considered as indications of optimal convergence and that the burn-in chosen was adequate. The ML analysis was run using the “RAXML HPC2 on XSEDE” (Stamatakis 2006)

TABLE I. Voucher information and GenBank accession numbers of new ITS and 28S sequences of *Clavaria* generated in this study

Identification	Locality	Ecology	Coll. No.	GenBank No. (ITS)	GenBank No. (28S)
<i>C. argillacea</i>	United Kingdom, England, Fairmile Common	on soil with <i>Calluna vulgaris</i>	K(M)126733	KC759438	[JQ415931] ^a
<i>C. argillacea</i>	Surrey Slovakia, Borská nížina Lowland, Lakšárska Nová Ves	in sand dunes under <i>Calluna vulgaris</i>	BRA CR16025	KC759439	[JQ415930]
<i>C. asterospora</i>	Spain, Bizkaia, Izurtza, Larrinagatxu	under <i>Chamaecyparis lawsoniana</i> on a slope	BIO-Fungi 12390	KC759440	—
<i>C. crosslandii</i>	Spain, Cuenca, Las Majadas	under <i>Pinus</i> , on burnt ground	BIO-Fungi 12762	KC759441	—
<i>C. falcata</i>	Denmark, Møn, Klinteskov, Kalsterbjerg	on soil under young <i>Fagus</i>	C F-32637	KC759442	[JQ415945]
<i>C. falcata</i>	Czech Republic, Orlické hory Mts., Uhrínov village	on ground among grass,	SAV F2011	KC759443	—
<i>C. falcata</i>	United Kingdom, Wales, Aelybrin	in lawn	AB0532	KC759445	[JQ415935]
<i>C. falcata</i>	France, Tourbière du Pinet	among <i>Sphagnum magellanicum</i>	GC08101406	KC759446	—
<i>C. falcata</i>	Czech Republic, Orlické hory, Orlické Záhoří	on lawn at the mountain cottage	OJ572007	KC759447	—
<i>C. flavipes</i>	Slovakia, Podtatranská kotlina Basin, Hybe village	in mowed and grazed grass	BRA CR12809	KC759448	[JQ415942]
<i>C. flavipes</i>	Slovakia, Stolické vrchy Mts., Muránska Zdychava village	in mowed and grazed meadow	BRA CR12807	KC759449	[JQ415944]
<i>C. flavipes</i>	Slovakia, Malé Karpaty Mts., Stará hora	in grassy place between old vineyards	BRA CR15121	KC759450	KC759472
<i>C. flavipes</i>	Czech Republic, Jehnice, Česká, Mokrá hora, Jehnice	on soil in debris	OJ142006	KC759454	—
<i>C. flavostellifera</i>	Spain, Bizkaia, Sukarieta, Txatxarramendi	under <i>Quercus ilex</i>	BIO-Fungi 10433	KC759461	[JX069828]
<i>C. flavostellifera</i>	Spain, Bizkaia, Sukarieta, Txatxarramendi	on ground on mixed forest	BRA CR16695	KC759462	[JX069827]
<i>C. flavostellifera</i>	Czech Republic, Liberec, Hamrštejn	among grass	BRA CR16080	KC759463	KC759469
<i>C. flavostellifera</i>	Slovakia, Malé Karpaty Mts., Ghtelnica, Plešivá hora	among grass and shrubs	BRA CR15924	KC759466	KC759468
<i>C. flavostellifera</i>	Spain, Mallorca, Font des Noguier	on ground under <i>Ampelodesma mauretanicum</i>	BIO-Fungi 11730	—	KJ666695
<i>C. aff. flavostellifera</i>	Spain, Cantabria, Soba, La Calera del Prado	mixed forest with <i>Fagus</i> and <i>Quercus robur</i>	MA-Fungi 40230	KC759464	—
<i>C. aff. flavostellifera</i>	Slovakia, Laborecká vrchovina, Osadné	among grass	SAV F1992	KC759465	—
<i>C. incarnata</i>	Spain, Bizkaia, Izurtza, Larrinagatxu	under <i>Chamaecyparis lawsoniana</i> on a slope	BIO-Fungi 12560	KC759452	[JQ415948]
<i>C. incarnata</i>	Spain, Tenerife, Anaga, Cruz del Carmen	among <i>Laurus</i> and <i>Ilex</i>	MA-Fungi 53113	KC759453	[JQ415948]
<i>C. sphagnicola</i>	Czech Republic, Hrubý Jeseník Mts.	among <i>Sphagnum russovii</i>	BRNM 747282	KC759456	KC759470
<i>C. sphagnicola</i>	Norway, Trøndsdølag, Steinkjer, Flatanger	among <i>Sphagnum</i> , in pine-spruce forest	BRA CR13593	KC759455	KC759471
<i>C. sphagnicola</i>	Austria, Salzburg, Obertrumtersee	in mowed wet meadow in grass and <i>Sphagnum</i>	OJ362006	KC759451	—
<i>C. tenuipes</i>	Czech Republic, Orlické hory Mts. Ústí nad Orlicí	on herbs at former clay mine	OJ82003	KC759444	—
<i>C. tenuipes</i>	England, Surrey, Ockley, Vann Lake Reserve	on wet mossy soil	K(M)146565	KC759457	—
<i>C. tenuipes</i>	France, Château-Landon	in Mesobromion	GC6110101	KC759458	—
<i>C. tenuipes</i>	Slovakia, Cerová vrchovina, Soví hrad	among grass	SAV F2003	KC759459	—
<i>C. tenuipes</i>	Slovakia, Košická kotlina basin, Lemešany, Čierna hora	among mosses	BRA CR16026	KC759460	—
<i>C. sp.</i>	Slovakia, Muránska Huta, Predná Hora	in pasture	BRA CR16032	KC759467	—

^a Accession numbers between brackets refer to 28S sequences obtained from the same specimens but published in earlier studies.

tool via CIPRES Science Gateway (Miller et al. 2010). A GTR + CAT approximation of models was used for ML bootstrapping. 1000 bootstrap replicates were performed for branch-support assessment, saving the most likely tree and leaving the remaining options as default. A 50% majority-rule consensus tree was made to obtain the bootstrap values in PAUP 4.0 Beta for Mac (Swofford 2002). ML bootstrap values were placed on the majority rule Bayesian phylogram.

The ML bootstrap values ≥ 70 and the BPP ≥ 95 were considered to be significant. The ITS and 28S alignments and the 50% majority-rule consensus trees of the Bayesian analyses are available in the TreeBASE (<http://www.treebase.org>) under accession No. 15665.

RESULTS

Phylogenetic analyses.—Six new 28S sequences and 30 ITS sequences were generated for seven *Clavaria* species (TABLE I). The 28S alignment had 110 sequences, whereas the ITS alignment contained 34 sequences. Positions 82–93, 441–456, 540–558 and 614–672 were excluded from the 28S analyses, and 174–209, 273–303 and 602–611 from the ITS analyses. The positions excluded from the ITS alignments were short regions that could not be aligned for all species, but had few polymorphisms within each species.

The ML and Bayesian analyses resulted in consensus trees with highly similar topologies, and congruent, well-supported clades. The ITS Bayesian phylogram (FIG. 1) only including clamped species of *Clavaria*, and the 28S Bayesian phylogram (FIG. 2), both showed terminal clades corresponding to morphospecies and resolved several species relationships. *Clavaria flavostellifera* specimens were recovered in a strongly supported clade in the 28S phylogeny and as two well-supported clades in the ITS phylogenetic analyses (FIGS. 1, 2). A 28S sequence of a *Clavaria* sp. obtained from a North American collection (HQ877684) was close to the European *C. flavostellifera* specimens. A second 28S sequence identified as *C. australiana* (HQ877685, FIG. 2), obtained from material from Brazil, appeared as the earliest diverging in the clade.

Clavaria was inferred as a monophyletic group, including the *Camarophylloopsis* species sampled and *Clavicornia taxophila* (FIG. 2). The position of the type species of *Camarophylloopsis*, *C. schulzeri*, was unresolved within *Clavaria*, whereas the rest of *Camarophylloopsis* and *C. pullei* formed a clade supported in the Bayesian analysis. *Clavicornia taxophila*, the type of *Clavicornia* Doty, was also recovered within *Clavaria*. Yellow *Clavaria* species with clamped basidia were recovered in two strongly supported groups (FIGS. 1, 2): (i) the *C. argillacea*–*C. citrinorubra*–*C. flavipes*–*C. sphagnicola* clade, resolved

as a sister clade to the *C. falcata* s.l. clade (FIG. 2), containing white, clamped *Clavaria* species, in the 28S Bayesian analysis, and (ii) the *C. flavostellifera* clade, supported as sister to *C. incarnata* Weinm. in the ITS analyses (FIG. 1), including a collection assigned to *C. asterospora* Pat. The position of *C. greletii* Boud., also with clamped basidia, was unsupported in any analysis. The *C. fragilis* Holmsk. s.l. and *C. falcata* Pers. s.l. clades exhibited considerable sequence variation. All the well-supported clades contained either only clampless (*C. zollingeri*–*C. fumosa*–*C. amoenoides* clade, *C. rosea*–*C. fragilis* clade) or clamped species. Our *C. flavostellifera* material was distinct based on morphological and molecular characters and we thus describe it as a new species below.

TAXONOMY

Clavaria flavostellifera Olariaga, Salcedo, Daniëls & Kautmanová, sp. nov. FIG. 3A–H
Mycobank MB803512

Typification: SPAIN. BIZKAIA: Sukarrieta, Txatxarramendi, 30TWP2404, 10 m, under *Quercus ilex* on calcareous ground, 29 Nov 2004, I. Olariaga. (holotype BIO-Fungi 10433).

Etymology: The epithet refers to the yellow basidiomata and the ability to produce ornamented spores.

Basidiomata gregarious or with pairs slightly fascicled, (7–)20–45(–70) mm long, simple, rarely one fork, apex obtuse to subacute, fertile part well delimited. Fertile part 6–31 × 0.6–4(–6) mm, cylindrical to clavate, sometimes slightly compressed, seldom slightly furrowed, bright yellow (8A, 8B), yellow (9D), progressively fading to yellowish ocher (8D, 11D), when dried ocher yellow (2.5Y 8/6). Apex concolorous, rarely yellowish ocher (11A) with age. Sterile part 2–15 × 0.3–1.5 mm, cylindrical, translucent bright chrome yellow (3A, 5A), rarely whitish (4D, 155A), reddish brown when dried (5YR 4/8). Whitish mycelium sometimes present at the base. Context chrome yellow (8A, 8B), flavor mild, odor none. Without reaction to FeCl₃.

Basidiospores ellipsoidal to broadly ellipsoidal in side view, in some collections a few constricted in the middle, thin- or thick-walled, with granular contents, non-amyloid, 5–7.5(–8) × 4.5–6.0(–6.5) μm ($L_m = 5.5$ – 7.8 , $W_m = 3.5$ – 5.2 , $Q_m = 1.20$ – 1.56). Ornamented spores present in hymenium sections, thick-walled, with one or a few large refringent guttules, smooth or with ornamentation composed of obtuse spines, up to 1.5 μm high. Basidia clavate, (1)2–4-spored, with a loop-like basal clamp, 42–60 × 4.5–6.5 μm . Subhymenium sharply delimited from the context, 20–30(–35) thick, composed of densely interwoven, cylindrical,

TABLE II. Voucher information corresponding to ITS and 28S sequences of *Clavaria* and allied genera downloaded from GenBank and used in our ITS and 28S phylogenetic analyses

Identification	Country	Coll. No.	GenBank No. (ITS)	GenBank No. (28S)
<i>C. acuta</i>	Canada	F14294	—	AY228353
<i>C. acuta</i>	USA	JFA10440	—	HQ877680
<i>C. acuta</i>	Slovakia	SAV F1990	—	GU299506
<i>C. acuta</i>	Sweden	MTS4577	—	HQ877679
<i>C. aff. acuta</i>	United Kingdom	AB05-32	—	EF535278
<i>C. cf. acuta</i>	New Zealand	TENN043602	—	HQ877681
<i>C. alboglobospora</i>	New Zealand	TENN042295 (H)	—	HQ877682
<i>C. amoenoides</i>	Estonia	SAV F2111	—	GU299508
<i>C. amoenoides</i>	United Kingdom	K(M)145803	—	JQ415946
<i>C. argillacea</i>	Greenland	TENN058804	—	HQ877683
<i>C. argillacea</i>	United Kingdom	KM126733	—	JQ415931
<i>C. argillacea</i>	Slovakia	BRA CR16025	—	JQ415930
<i>C. argillacea</i>	Sweden	ELj_98	—	AY463395
<i>C. asperulospora</i>	Slovakia	K(M)143814	—	JN315790
<i>C. asperulospora</i>	Sweden	M(C)001	—	JN315791
<i>C. atrofusca</i>	Norway	BRA CR13264	—	JN315785
<i>C. atroumbrina</i>	Norway	BRA CR13265	—	JN315786
<i>C. atroumbrina</i>	Norway	BRA CR13271	—	JN315787
<i>C. atroumbrina</i>	USA	TENN031091	—	JN315788
<i>C. atroumbrina</i>	USA	TENN030948	—	JN315789
<i>C. atroumbrina</i>	United Kingdom	K(M)143730	—	JN315792
<i>C. australiana</i>	Brazil	TENN051311	—	HQ877685
<i>C. californica</i>	USA	TENN026785	HQ179660	—
<i>C. citrinorubra</i>	Australia	TENN040464	HQ179661	HQ201349
<i>C. citrinorubra</i>	Australia	TENN040464 (H)	—	HQ877686
<i>C. falcata</i>	Norway, Svalbard	O73640	GU234148	—
<i>C. falcata</i>	Slovakia	BRA CR16666	—	JQ415961
<i>C. falcata</i>	Slovakia	BRA CR16667	—	JQ415962
<i>C. falcata</i>	Czech Republic	SAV F2011	—	GU299505
<i>C. falcata</i>	United Kingdom	AB0532	—	JQ415935
<i>C. falcata</i>	Slovakia	BRA CR16029	—	JQ415940
<i>C. falcata</i>	Japan	TENN048438	—	JQ415941
<i>C. falcata</i>	Denmark	C F-32637	—	JQ415945
<i>C. aff. falcata</i>	Slovakia	BRA CR16210	—	JQ415960
<i>C. flavipes</i>	Slovakia	BRA CR12809	—	JQ415942
<i>C. flavipes</i>	Slovakia	BRA CR12808	—	JQ415943
<i>C. flavipes</i>	Slovakia	BRA CR12807	—	JQ415944
<i>C. flavipes</i>	United Kingdom	C F-44153	—	JQ415958
<i>C. flavipes</i>	Slovakia	BRA CR12770	—	GU299507
<i>C. flavostellifera</i>	Spain	BIO-Fungi 10433	—	JX069828
<i>C. flavostellifera</i>	Slovakia	SAV F2000	—	JX069826
<i>C. flavostellifera</i>	Spain	BRA CR 16695	—	JX069827
<i>C. fragilis</i>	Slovakia	BRA CR9727	—	GU299498
<i>C. fragilis</i>	Spain	MA-Fungi 52135	—	JQ415950
<i>C. fragilis</i>	Spain	MA-Fungi 59584	—	JQ415951
<i>C. fragilis</i>	Slovakia	SAV F1262	—	GU299501
<i>C. fragilis</i>	Spain	MA-Fungi 61797	—	JQ415949
<i>C. fragilis</i>	Spain	MA-Fungi 62679	—	JQ415952
<i>C. fragilis</i>	Spain	MA-Fungi 67674	—	JQ415954
<i>C. fragilis</i>	Spain	BIO-Fungi 12389	—	JQ415934
<i>C. fragilis</i>	Slovakia	BRA CR9726	—	GU299500
<i>C. fragilis</i>	Slovakia	BRA CR9725	—	GU299499
<i>C. fragilis</i>	Spain	BRA CR15978	—	JQ415932
<i>C. fragilis</i>	Spain	BRA CR16017	—	JQ415933
<i>C. aff. fragilis</i>	USA	SAT98-349-01	—	HQ877688

TABLE II. Continued

Identification	Country	Coll. No.	GenBank No. (ITS)	GenBank No. (28S)
<i>C. aff. fragilis</i>	USA	JMB08171003	—	HQ877689
<i>C. aff. fragilis</i>	USA	TENN064092	—	HQ877687
<i>C. fumosa</i>	United Kindgom	GG_151003	—	EF535268
<i>C. fumosa</i>	Slovakia	BRA CR15656	—	JN315795
<i>C. fumosa</i>	Slovakia	BRA CR15655	—	JN315796
<i>C. fumosa</i>	Slovakia	BRA CR748	—	JN315798
<i>C. fuscata</i>	USA	TENN065665	—	HQ877691
<i>C. fuscoferruginea</i>	Norway	BRA CR13262	—	JN315784
<i>C. greletii</i>	Denmark	C-F-83422	—	JN416778
<i>C. greletii</i>	United Kingdom	K(M)143840	—	GU299503
<i>C. greletii</i>	France	GC08101403	—	GU299502
<i>C. greletii</i>	Slovakia	SAV F1988	—	GU299504
<i>C. guillemini</i>	Spain	BIO-Fungi 12566	—	JQ415939
<i>C. inaequalis</i>	Germany	MB 04-016	—	AY745693
<i>C. incarnata</i>	Spain, Canary Islands	MA-Fungi 53113	—	JQ415948
<i>C. incarnata</i>	Spain	BIO-Fungi 12386	—	JQ415938
<i>C. incarnata</i>	Slovakia	BRA CR16024	—	JQ415936
<i>C. incarnata</i>	Slovakia	BRA CR16030	—	JQ415937
<i>C. neonigrita</i>	Canada	Ceska06112010	—	JN214484
<i>C. novozelandica</i>	New Zealand	TENN043575(I)	—	HQ877693
<i>C. pullei</i>	France	GC99102304	—	JN315793
<i>C. pullei</i>	France	GC02092801	—	JN315797
<i>C. pullei</i>	Spain	BIO-Fungi 12378	—	JN315794
<i>C. redolealli</i>	New Zealand	DJM1079	—	DQ284906
<i>C. rosea</i>	USA	STZ9956	—	HQ877694
<i>C. rosea</i>	United Kingdom	K(M)135940	—	JQ415928
<i>C. rosea</i>	Denmark	C-F-26590	—	JQ415929
<i>C. cf. rubicundula</i>	USA	TENN064094	—	HQ877696
<i>C. cf. rubicundula</i>	USA	TENN064091	—	HQ877695
<i>C. cf. rubicundula</i>	New Zealand	TENN043695	—	HQ877697
<i>C. cf. rubicundula</i>	USA	TENN065659	—	HQ877690
<i>C. stegasauroides</i>	Australia, Tasmania	PBM3373	—	HQ877698
<i>C. straminea</i>	United Kingdom	GG_131104	—	EF535267
<i>C. cf. subacuta</i>	Japan	TENN048438	—	HQ877699
<i>C. vermicularis</i>	USA	DJM1262	—	DQ284907
<i>C. zollingeri</i>	USA	AFTOL-ID 563	AY854071	AY639882
<i>C. zollingeri</i>	USA	TENN064095	—	HQ877700
<i>C. zollingeri</i>	Norway	MA-Fungi 53142	—	JQ415955
<i>C. zollingeri</i>	USA	TENN58652	—	NG_027629
<i>C. sp.</i>	USA	TENN065665	—	HQ877684
<i>C. sp.</i>	Russia	TENN060720	—	HQ877692
<i>C. sp.</i>	Slovakia	SAV F1994	—	JQ415963
<i>Clc. taxophila</i>	USA	TENN051926	—	HQ877701
<i>Cls. sulcata</i>	New Zealand	PDD78241	—	DQ284904
<i> Cm. atropuncta</i>	United Kingdom	GG_731	—	EF535270
<i> Cm. foetens</i>	USA	TENN065670	—	HQ877678
<i> Cm. hymenocephala</i>	USA	DJL98_081505	—	EF561628
<i> Cm. hymenocephala</i>	USA	DJL95-081505	—	DQ457679
<i> Cm. schulzeri</i>	Finland	S. Jacobsson 3453	—	AM946415
<i> Cm. schulzeri</i>	United Kingdom	GG_091005	—	EF537888
<i>R. kunzei</i>	USA	BD346	—	DQ284902

thin-walled hyphae, 1.5–3 µm wide. Hyphae of the context parallel, cylindrical to slightly inflated, thin-walled, pale yellow, without incrustations or crystals, clampless, 3–12 µm wide. Surface of the sterile base

composed of hyphae 2–3 µm wide, lacking incrustations. Basal mycelium composed of hyphae that are interwoven, cylindrical, slightly thick-walled, hyaline, clampless, 1.5–2 µm wide.

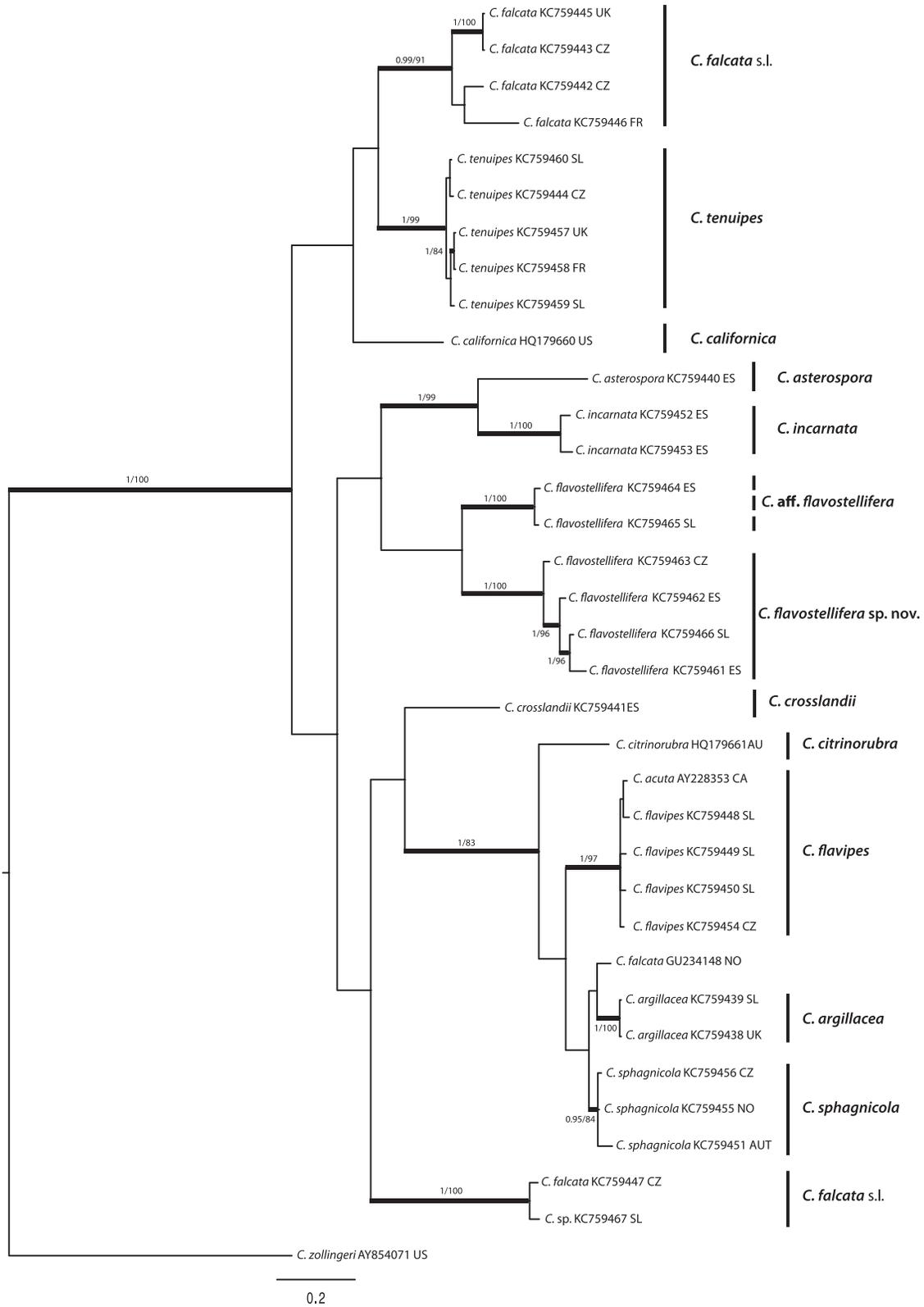


FIG. 1. 50% majority rule consensus Bayesian phylogram of the ITS region including only clamped species of *Clavaria*. Posterior Probabilities (≥ 95%)/maximum likelihood bootstrap values (≥ 70%) shown by each node. Thickened branches indicate that nodes supported in ML and Bayesian analyses.

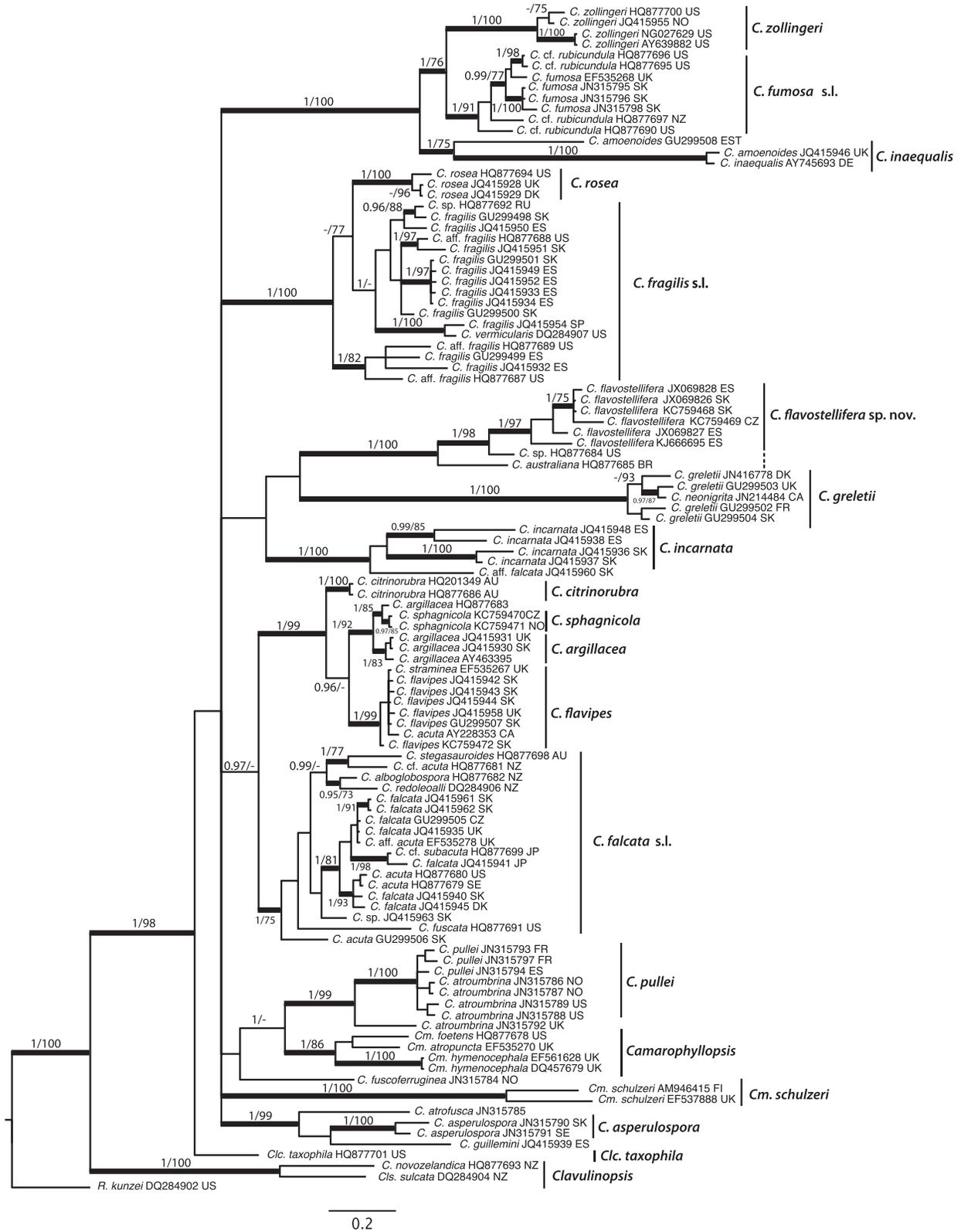


FIG. 2. 50% majority rule consensus Bayesian phylogram of the nuc 28S rDNA region in *Clavaria*. Posterior probabilities ($\geq 95\%$)/maximum likelihood bootstrap values ($\geq 70\%$) shown by each node. Thickened branches indicate that the node is supported in ML and Bayesian analyses. Genus abbreviations: Cm = *Camarophyllopsis*, Clc = *Clavicornora*, Cls = *Clavulinopsis*, R = *Ramariopsis*.



FIG. 3. *Clavaria flavostellifera* sp. nov. A–E. Basidiomata in situ. A. BIO-Fungi 10433 (I. Olariaga). B. BRA CR 16080 (J. Gaisler). C. BIO-Fungi 11730 (I. Olariaga). D. BRA CR 16724 (L. Tábi). E. Daniëls 2611, JA (P.P. Daniëls). F. BIO-Fungi 10433 Basidia. G. Spores from spore print. H. Selected ornamented spores from a hymenium mount. Scale bars: A–E = 10 mm approx., F–H = 10 µm.

Distribution and habitat: Europe, North America (?). Mediterranean and temperate. Forests and pastures, often on bare ground in calcareous areas.

Additional specimens examined: CZECH REPUBLIC: LIBEREC: Hamrštejn, in grass, 10 Sep 2010, V. Kautman, BRA CR16080. SLOVAKIA. TRNAVA: Malé Karpaty Mts, Čhtelnica, Plešivá hora, 320 m, in grass and shrubs, in abandoned pasture, 4 Oct 2010, V. Kautman, BRA CR15924; in grass and shrubs, BRA CR16041; in old pasture, 29 Sep 2010, V. Kautman & V. Kučera, BRA CR15074; BRA CR15087. Považský, Inovec Mts, Piešťany, Banka village, 250 m, in grass in grazed meadow, 11 Sep 2010, L. Tábi, BRA CR16724. Západné Tatry Mts, Zuberec, Mačie dierý Nature Reserve, in mowed meadow, in grass, limestone, 29 Aug 2007, I. Kautmanová, BRA CR16729. ZÁHORIE: Borská nížina Lowland, Závod, Abrod Nature Reserve, in wet mowed meadow, 30 Sep 2000, SAV F2000. SPAIN. BIZKAIA: Arratzu, Montalban, 30TWN0394, 100 m, under *Quercus robur*, 3 Dec 2004, R. Picón & I. Salcedo, BIO-Fungi 10777. Sukarrieta, Txatxarramendi, 30TWP2404, 10 m, in moss in forest at the seashore, 15 Nov 2008, I. Kautmanová & I. Olariaga, BRA CR15979; BRA CR16695. CÓRDOBA: Arroyo Pedroches, 30SUG4498, on moss, 9 Jan 2009, Daniëls 2611 (JA); Arroyo de Santo Domingo, 30SUG4498, on humus, 9 Jan 2009, Daniëls 2619 (JA); Villaviciosa de Córdoba, Taqueros Bajos, 30SUH1604, 510 m, forest with *Cupressus*, on humus, 17 Dec 2003, P.P. Daniëls, JA 6286. HUELVA: Alajar, Sierra del Pico, 29SQB0394, 1020 m, among moss and *Pteridium aquilinum*, under *Pinus pinaster*, 4 Feb 1996, L. Romero de la Osa, MA-Fungi 40406. BALEARIC ISLANDS: Mallorca, Pla de Cúber, Font des Noguer, 30SDE8304, 600 m, on ground under *Ampelodesma mauritanica*, 22 Oct 2006, I. Olariaga, BIO-Fungi 11730. *Clavaria* aff. *flavostellifera*: SPAIN. CANTABRIA: Soba, La Calera del Prado, surroundings, 30TVN6579, 500 m, mixed forest of *Fagus sylvatica* and *Q. robur*, 28 Oct 1998, P.P. Daniëls, MA-Fungi 40230 (as *Clavaria incarnata*).

Commentary: *Clavaria flavostellifera* is characterized by yellow, simple basidiomata, clamped basidia, ellipsoidal to broadly ellipsoidal spores and the presence of scattered thick-walled and warty-spiny spores. The material is homogeneous in its diagnostic characters. The ITS analyses placed sequences from two *C. flavostellifera* specimens (KC759464, MA-Fungi 40230; KC759465, SAV F1992) in a sister clade (FIG. 1), but neither specimen was represented in the 28S analyses (FIG. 2). Because we were unable to study either specimen in a fresh state, we provisionally treated them as *C. aff. flavostellifera* because of the significant ITS sequence deviation from typical *C. flavostellifera* specimens.

Specimen SAV F2000 (GenBank JX069826) differs somewhat morphologically from the rest of the *C. flavostellifera* material. This collection has a compressed fertile part, as seen in *C. tenuipes* Berk. & Broome, the dried material is not yellow and the basidia are predominantly 1–2-spored. However, SAV F2000 is in the same clade as the other typical *C.*

flavostellifera collections in the 28S tree (FIG. 1). The compressed fertile part and the paler color are probably a result of the aged condition of the specimen. Scattered thick-walled and ornamented spores were observed in all *C. flavostellifera* specimens examined. In the holotype, all spores were thin-walled and smooth in the spore print, and scattered thick-walled and ornamented spores were observed only in hymenium sections. All spores attached to basidia were smooth. The contents of spores also varied. Thin-walled and smooth spores had granular contents, while thick-walled and ornamented spores normally contained one or a few refringent large guttules.

When first encountered, *C. flavostellifera* was considered a possible color variant of *C. incarnata*. The latter species often has scattered ornamented spores (Knudsen 1997, Olariaga 2009, Kautmanová 2012) and is common in the type locality of *C. flavostellifera*. *Clavaria incarnata* generally has longer spores (6.5–10 µm, Knudsen et al. 2012), often has bipyriform crystals among the contextual hyphae, is distinctly pink with pale gray reaction with ferric salts (Olariaga 2009). Furthermore, ITS and 28S analyses support the recognition of *C. flavostellifera* and *C. incarnata* as two separate species. The species of the *C. falcate*-*C. asterospora* complex clearly differ in the color of the basidiomata, which is white. *Clavaria greletii*, reported to produce ornamented spores like those of *C. flavostellifera* (Roberts 2007), differs by its dark brown basidiomata.

Our molecular analyses supports the idea that color is a good character for species delimitation across *Clavaria*, as previously claimed (Petersen 1988). Among the clamped yellow species, *C. argillacea* is probably most common (Corner 1950). This species is distinguished from *C. flavostellifera* by distinctly larger spores (Corner 1950) and its association with Ericaceae. *Clavaria sphagnicola* is distinguished by having larger spores that are always smooth and by its inhabiting *Sphagnum* bogs (Corner 1950, Knudsen 1997). *Clavaria flavipes* shares with *C. flavostellifera* yellow, simple basidiomata, but it is separated from *C. flavostellifera* by its globose spores that never become ornamented. Furthermore, *C. flavipes* often has a paler fertile part and reddish stains (Cotton 1911, Schild 1971). *Clavaria luteostirpata* S.G.M. Fawc., described from Australia, is another yellow species that also has globose to subglobose spores (Petersen 1978b), slightly larger than those of *C. flavipes* and therefore distinct from *C. flavostellifera*.

Collection SAV F2000 resembles *C. spathuliformis* Bres. because of the compressed fertile part and yellow tones (Saccardo 1891). However, the stipe of *C. spathuliformis* was described as white, the fertile



FIG. 4. *Clavaria argillacea*. A. Fascicled basidiomata (AH 41415, M.A. Ribes). B. Forked basidiomata (AH 41417, M.A. Ribes). C. Forked basidiomata (AH 41418, M.A. Ribes). D. Spores (BIO-Fungi 12535). Scale bars A, B = 10 mm approx.; C = 10 μ m.

part is not vivid yellow and it has larger spores than those of *C. flavostellifera*. The neotype of *C. spathuliformis* designated by Petersen (1967) has shorter basidia and smooth spores. Petersen stated that *C. spathuliformis* should be compared to *C. tenuipes*, as described by Corner (1950), but clamps need to be observed to support this assertion.

In conclusion we consider *C. flavostellifera* a morphologically distinct species that also is recognized with rDNA analyses. *Clavaria flavostellifera* so far is known from central and southern Europe, including the Mediterranean region, where it has a clear preference for calcareous ground. *Clavaria flavostellifera* was referred to as *Clavaria xantha* nom. ined. by Olariaga (2009) and Kautmanová (2012). The fact that the 28S sequences HQ877684 and HQ877685 have an affinity to European *C. flavostellifera* 28S sequences indicates a possible transatlantic distribution of *C. flavostellifera*.

Regrettably the collections yielding those sequences were not morphologically studied for this work.

Clavaria argillacea Pers., Comm. Fung. Clav.: 74. 1797
: Fr., Syst. Mycol. 1: 482. 1821 FIG. 4A–D
≡ *Geoglossum argillaceum* (Pers.:Fr.) Fr., Observ. Mycol.
2: 295. 1818

Typification: Schmidel, Icon. Pl., ed. 2: Tab 15. 1782
(lectotype, designated here): UNITED KINGDOM.
England: Fairmile Common Surrey, on soil with
Calluna vulgaris, 3 Nov 2004, E.W. Brown & B. M.
Spooner (epitype, designated here, K[M] 126733).

= *Clavaria ericetorum* Pers., Observ. Mycol. 2: 60. 1799.

= *Geoglossum argillaceum* var. *ericetorum* (Pers.) Fr.,
Observ. Mycol. 2: 295. 1818.

= *Geoglossum argillaceum* var. *montanum* Fr., Observ.
Mycol. 2: 296. 1818 (Fries, Observ. Mycol. 2: Tab 5,
fig. 3. 1818 [lectotype designated here]).

? = *Clavaria pallescens* Peck, New York State Mus. Bull. 139(470): 47. 1910 (holotype, UNITED STATES. MA: South Acton, Oct 1909, *S. Davis* & *E. Morris*, NYSF 2205).

Basidiomata gregarious or fascicled (up to 20 basidiomata), (7–)15–50 mm long, simple, rarely 1(2)-forked, apex rounded, fertile part well delimited. Fertile part 10–25 × 1–5 mm, cylindrical to claviform, sometimes slightly compressed, longitudinally furrowed in age, bright yellow (8A, 8B), progressively fading to pale yellow (8D, 11D), when dried ochre yellow (10YR 6/6, 6/8). Apex concolorous. Sterile part 4–11 × 0.7–1.5 mm, cylindrical, bright yellow (3A, 5A), when dried ochre yellow (10YR 6/6, 6/8) to ochre brown (10YR 5/8). Whitish mycelium sometimes present at the base. Context bright yellow (8A, 8B), flavor mild, odor none. Without reaction to FeCl₃.

Basidiospores cylindrical in side view, sometimes narrowly ellipsoidal or constricted in the middle, thin-walled, smooth, with granular contents, nonamyloid, 9.0–11.0 × 4.0–5.0(–5.5) μm ($L_m = 9.0–11$, $W_m = 4.5–4.6$, $Q_m = 2–2.4$). Spores never ornamented. Basidia clavate, (3–)2–4-spored, with a loop-like basal clamp, 51–75 × 6–8 μm. Subhymenium sharply delimited from the context, 20–30(–35) μm thick, composed of densely interwoven, cylindrical, thin-walled hyphae, 1.5–2 μm wide. Hyphae of the context parallel, cylindrical to inflated, thin-walled, hyaline, without incrustations or crystals, clampless, 5–30 μm wide. Surface of the sterile base composed of hyphae 2–3 μm wide, without incrustations. Basal mycelium composed of hyphae that are interwoven, cylindrical, slightly thick-walled, hyaline, clampless, 1.5–3 μm wide.

Distribution and habitat: Europe, North America, Asia (?), Canary Islands (Ribes 2009). Boreal-temperate distribution. On acidic and especially sandy ground, with Ericaceae.

Specimens examined: DENMARK. JYLLAND: W of Silkeborg, Hørbylunde, mixed forest, 10 Oct 2003, *J.H. Petersen* & *J. Vesterholt*, C F-43524; Lövesholm skov, on the ground in *Calluna* heath, 25 Sep 1970, *J.A. Nannfeldt*, UPS F-123792. SYDDANMARK: S of Søby Sø at Kølkeær S of Ikast, under *Pinus*, 13 Oct 2003, *J. Vesterholt*, C F-43546. ESTONIA. LÄÄNE-VIRUMAA CO: Lahemaa National Park, Vihula Comm, Vainupea, coastal area, 8 Oct 2009, *V. Kučera*, BRA CR13653. GERMANY. BADEN-WÜRTTEMBERG: Wahnner Rende, Westlichallsbach högel, Callunetum, *A. Schumacher*, UPS F-637850. SLOVAKIA. TRNAVA: Borská nížina Lowland, Lakšárska Nová Ves village, Bežnisko military area, in sand dunes under *Calluna vulgaris*, 18 Oct 2008, *V. Kautman*, BRA CR16025; BRA CR16021. SPAIN. ASTURIAS: Redes National Park, Colado Remedable, mountain pasture, among *Polytrichum*, 29 Oct 2002, *M. Gartzia*, BIO-Fungi 9879. CANARY ISLANDS: Tenerife, Las Mercedes, on clay path, among *Polytrichum*

in the laurisilva, in the neighbourhood of *Erica platycodon* and *E. arborea*, 20 Dec 2004, *M.Á. Ribes*, MAR201204-41 (AH 41415); 05 Dec 2005, MAR-241206-13 (AH 41418). LEÓN: Boñar, among moss, 5 Nov 1999, *B. Llamas*, BIO-Fungi 12535, (ex AVM 51199). SWEDEN. BOHUSLÄN: Tanum parish, Kalvö, öppen sand mellan *Empetrum nigrum*-bestånd, 1 Nov 1978, *J. Nitare*, UPS F-123783. LAPPLAND: Ultevis Fjällurskog National Park, Sitoätro, under *Picea* and *Pinus*, on acidic ground, clear area with *Calluna vulgaris*, 31 Aug 2011, *K. Hansen* & *I. Olariaga*, S-F198761. VÄSTERGÖTLAND: Symmerby parish, between Leutorp and Ardala, sandy highland, 19 Oct 1956, *S. Kilander*, UPS F-123781. UNITED KINGDOM. ENGLAND: Surrey, Fairmile Common, on soil with *Calluna vulgaris*, 3 Nov 2004, *E.W. Brown* & *B.M. Spooner*, K(M) 126733; West Yorkshire, Hebden Bridge, 8 Oct 1909, *C. Crossland*, UPS F-637851 (Herb. Cotton). USA. MA: Hancock, Ellsworth, under *Vaccinium*, Oct. 1982, *W. Litten*, TENN 043617.

Commentary: *Clavaria argillacea* is characterized mainly by cylindrical and often constricted spores. Macroscopically basidiomata of *C. argillacea* have a tendency to grow in fascicles, have obtuse apices and are bright yellow at first then fade considerably to pale yellow with age. *Clavaria argillacea* forms ericoid mycorrhizae (Englander and Hull 1980, Mueller et al. 1986) and fruits in association with Ericaceae in the field, on acidic and often sandy ground. However, it is unknown whether this relationship is obligatory or opportunistic (Roberts 2008). *Empetrum nigrum* and *Calluna vulgaris* often are noted on the labels of the material examined and appear to be common hosts. *Erica platycodon* and *E. arborea* are the probable hosts of the Canarian specimens examined (Ribes 2009) and *Vaccinium* in the North American collection (TENN 043617).

None of the *C. argillacea* specimens in the Persoon herbarium (L) matches the locality cited in the protolog (Persoon 1797). Therefore only illustrations are available as original material for lectotypification. For the lectotype designated above, we selected the plate that best represents *C. argillacea* from the illustrations cited in the sanctioning work (Fries 1821). *Clavaria pallescens* Peck is here considered a possible synonym of *C. argillacea*. The long and narrow spores of the type (10–10.5 × 4.5 μm, Burt 1922) and the association with an ericaceous host (*Kalmia angustifolia*) suggest conspecificity with *C. argillacea*. We adopt a cautious position because no type material was examined and was North American material was not included in our phylogeny. The North American specimen we examined (TENN 043617) had slightly larger spores (10.5–14 × 4.5–5.8 μm) than European collections. The description of *C. argillacea* from Japan by Imai (1930) appears to match our material.



FIG. 5. A–C. *Clavaria flavipes*. A, B. Basidiomata in situ. A. BRA CR15121, epitype (J.Kuriplach). B. ARAN-Fungi 3006142 (I. Olariaga). C. BRA CR15121 Spores. D–E. *Clavaria sphagnicola* (BRA CR13593). D. Basidiomata ex situ (I. Olariaga). E. Spores. Scale bars: A, B, D = 10 mm approx.; C, E = 10 μ m.

Clavaria flavipes Pers., Neues Mag. Bot. 1: 117. 1794 : Fr., Syst. Mycol. 1: 483. 1821. *Typification*: Pers., Comm. Fung. Clav.: Tab. 1, Fig. 4. 1797 (**lectotype**, designated here). SLOVAKIA. Malé Karpaty Mts., Pezinok, Stará hora, alt. 230 m, grassy place between old vineyards, 16 Sep 2010, leg. V. Kautman & J. Kuriplach (**epitype**, designated here, BRA CR 15121). FIG. 5A–C

= *Clavaria falcata* var. *citrinopes* Quél. in Pat., Tab. Anal. Fung. 1: 21. 1883.

= *Clavaria straminea* Cotton, Trans. Brit. Mycol. Soc. 3(4): 265. 1911 (UNITED KINGDOM. England: Derbyshire, Peak District Natural Park, Baslow, Chatsworth House, on soil among grass, 1 Oct 1909, leg. A.D. Cotton 355, **lectotype**, designated here, K[M]80215, labelled as paratype).

? = *Clavaria globospora* Kauffman, Pap. Michigan Acad. Sci. 8: 148. 1928 (UNITED STATES. WA: Lake Quinault, 28 Oct 1925, C.H. Kauffman, holotype, MICH 10090).

? = *Clavaria americana* R.H. Petersen, Canad. J. Bot. 47(7): 1137. 1969. (UNITED STATES. ID: Upper Priest River, 21 Sep 1968, R.H. Petersen, holotype, TENN 30416).

Basidiomata gregarious or fascicled (up to 10 basidiomata), 30–80 mm long, simple, rarely one-forked, apex rounded, fertile part well delimited. Fertile part 10–50 \times 1.5–3.5 mm, cylindrical to clavate, sometimes slightly compressed, sometimes longitudinally furrowed in age, pale yellow (4D, 5D) to yellowish ocher (11C, 11D), when dried brownish ocher (2.5Y 7/6, 8/6). Apex concolorous or reddish brown (166C). Sterile part 20–45 \times 0.8–2 mm, cylindrical, bright yellow (11A), when dried yellowish ochre (10YR 6/6, 6/8) to reddish brown (5YR 4/8). Whitish mycelium sometimes present at the base. Context bright yellow (11A), flavor mild, odor none. Without reaction to FeCl_3 .

Basidiospores globose to ovoid in side view, thin-walled, smooth, with granular contents, nonamyloid, 6–8(–9.2) \times 5.5–7.5(–8) μ m (L_m = 6.6–7.8, W_m = 6–7.2, Q_m = 1.07–1.1). Spores never ornamented. Basidia clavate, (3)4-spored, with a loop-like basal clamp, (45–)54–85 \times 8–9 μ m. Subhymenium sharply delimited from the context, 20–30(60) μ m thick, composed of densely interwoven, cylindrical, thin-

walled hyphae, 2–3 µm wide. Hyphae of the context parallel, cylindrical to inflated, thin-walled, hyaline, without incrustations or crystals, clampless, 3–28 µm wide. Surface of the sterile base composed of hyphae 2–3 µm wide, with greenish pigments. Basal mycelium composed of hyphae that are interwoven, cylindrical, slightly thick-walled, hyaline, clampless, 1.5–3 µm wide.

Distribution and habitat: Europe, North America. Temperate and boreal. Mossy pastures and forests, sometimes on bare ground, often in calcareous areas.

Specimens examined: FRANCE. PYRÉNÉES ATLANTIQUES: Forêt d'Issaux, 10 km from Léés on the road to col du Labays, among mosses along a track, 12 Oct 2008, *I. Olariaga*, BIO-Fungi 12948. SLOVAKIA. BRATISLAVA: Malé Karpaty Mts, Pezinok, Stará hora, grassy place between old vineyards, 16 Sep 2010, *V. Kautman & J. Kuriplach*, BRA CR15121 (epitype of *C. flavipes*); BRA CR15134; BRA CR15117. ZÁPADNÉ KARPATY: Podtatranská kotlina Basin, Hybe village, in mowed and grazed meadow in old orchard near the village, 21 Aug 2010, *I. Kautmanová*, BRA CR16051; BRA CR16050; 2 Sep 2010, BRA CR15912. SPAIN. BIZKAIA: Larrinagatxu, Izurtza, under *Chamaecyparis lawsoniana* among *Rhytidiadelphus squarrosus*, 2 Dec 2004, *S. Arauzo, P. Iglesias, J.R. Undagoitia, J. Fernández & I. Olariaga*, BIO-Fungi 10688. HUESCA: Fuente Paco, Villanúa, under *Abies alba* on calcareous soil, 11 Oct 2006, *I. Olariaga*, BIO-Fungi 12564. CANTABRIA: Mancomunidad de Campoo de Cabuérniga, Saja, Braña Ocejo, *Fagus sylvatica* forest, 30 Oct 1998, *P.P. Daniëls*, BIO-Fungi 12550. SWEDEN. BOHUSLÄN: Rödbo parish, Ellesbo, among grass in shady place, 16 Sep 1943, *T. Nathorst-Windahl*, UPS F-121009. SÖDERMANLAND: Tyresta National Park, by Stensjön, on bare ground with some pioneer mosses (*Polytrichum, Pogonatum*), 17 Sep 2011, *M. Prieto, J.C. Zamora & I. Olariaga*, S-F198953. SWITZERLAND. BERN: Hofstetten bei Brienz, Ballenberg, in "Sternwiese", in mosses and grass, 20 Oct 1969, *E. Schild 126*. UNITED KINGDOM. ENGLAND: Cambridgeshire, Keswick, 1 Sep 1912, *M.K. Sampson*, UPS F-637852. Cumberland, Carlisle, on soil, 13 Oct 1908, *D. Graham*, K(M) 69819 (syntype of *C. straminea*). Derbyshire, Peak District Nat. Park, Baslow, Chasworth House, on soil, among grass, 1 Oct 1909, *A.D. Cotton*, K(M) 80215 (lectotype of *C. straminea*). West Yorkshire, Halifax, Erringden, on soil, 23 Oct 1905, K(M) 80213 (syntype of *C. straminea*).

Commentary: *Clavaria flavipes* is typically recognized by its pale yellow to ochraceous yellow fertile part and yellow stipe and above all by its globose to ovoid spores. The presence of reddish brown stains, stressed in the protolog by Schild (1971) is inconsistent. In our field experience *C. flavipes* appears not to be associated with Ericaceae and is found among grass or bryophytes, in pastures or forests, on calcareous or acidic ground. *Clavaria flavipes* has been reported only from Europe. However, an ITS sequence obtained from Canadian material and identified as *C. acuta* Sowerby (AY228353) is nested

in the *C. flavipes* clade (FIG. 2). We suggest that *C. globospora* Kauffman and *C. americana* R.H. Petersen are synonyms of *C. flavipes*, based on similarities in spore characters and basidioma color. Both names were described from North America and apparently were not compared to European material (Petersen 1985). Sequencing of further North American specimens, including the type collections of *C. globospora* and *C. americana*, would be desirable to confirm the synonymy with *C. flavipes*.

Two names were applied to the species described above, *C. flavipes* (Knudsen 1996, Adamčík 2008) and *C. straminea* Cotton (Nitare 1988, Olariaga et al. 2004, Roberts 2008). Persoon (1794: 117) provided a short description with no microscopic data in the protolog of *C. flavipes*; the outstanding features were a caespitose growth habit, a bright yellow stipe, a pale fertile part and habitat among gramineous plants. A later plate by Persoon (1797: Tab. 1, fig. 4) matches the original description. Subsequent authors interpreted *C. flavipes* in two different senses: (i) as a synonym of *C. argillacea* (e.g. Corner 1950, Jülich 1984) or (ii) as a synonym of *C. straminea* (Knudsen 1996, Adamčík 2008). *Clavaria argillacea* and *C. straminea* are macroscopically similar but are clearly distinguished microscopically by their ellipsoidal to cylindrical and subglobose spores, respectively. The name *C. flavipes* has priority over *C. argillacea* and *C. straminea* when considered a synonym of either name. Cotton (1911), author of *C. straminea*, noted that *C. flavipes* might be an earlier name for *C. straminea*, and we confirm this here. The pale fertile part, yellow stipe and habitat among gramineous plants are typical of *C. straminea*. *Clavaria flavostellifera* does not conform to *C. flavipes* because of its concolorous, not paler, fertile part, along with a gregarious growth habit. Likewise *C. argillacea* differs in having basidiomata that are entirely yellow when young, have blunt apices and by its association with Ericaceae. In this context the nomenclatural stability of the well established name *C. argillacea* would be threatened if the name *C. flavipes* were typified with an element that conforms to the current concept of *C. argillacea*. Meanwhile two names, *C. flavipes* and *C. straminea*, are used for the same subglobose-spored species. Therefore the decision to typify *C. flavipes* with elements that conform to the globose-spored species often named *C. straminea* is made here. This will stabilize the interpretation of *C. flavipes* and preserve the widely used name *C. argillacea*.

We also propose lectotypification of *C. straminea*. The original description of *C. straminea* listed five gatherings (syntypes) from four localities (Cotton 1911). Three syntypes of *C. straminea* are deposited in

Kew, UK, cited above. The three specimens are consistent with the original description. Collection K(M)80213 contains few basidiomata, which are in a poor state and from which microscopic structures could not be observed appropriately. Of the other two, the collection designated above as the lectotype of *C. straminea* has more basidiomata in better condition and is a better choice as lectotype, in our opinion.

Clavaria sphagnicola Boud., Bull. Soc. Mycol. France 33: 12. 1917. FIG. 5D–E

≡ *Clavaria argillacea* var. *sphagnicola* (Boud.) Corner, Ann. Bot. Mem. 1: 226. 1950

Typification: FRANCE. JURA: in turfois, *D. Hetier* (lectotype, designated here, PC 0124967).

Basidiomata gregarious or fascicled (up to four basidiomata), 50–90 mm long, simple, apex obtuse to subacute, fertile part sometimes not clearly delimited. Fertile part 20–50 × 1.5–2.5 mm, cylindrical to narrowly clavate, sometimes slightly compressed, ochraceous yellow (11C, 11D), when dried yellowish ocher (10YR 6/6, 6/8). Apex concolorous. Sterile part 35–40 × 1–1.5 mm, cylindrical, bright yellow (11A), when dried pale ocher (10YR 7/4). Whitish mycelium sometimes present at the base. Context bright yellow (8A, 8B), flavor and odor not recorded. Without reaction to FeCl₃.

Basidiospores ellipsoidal in side view, rarely slightly constricted in the middle, thin-walled, smooth, with granular contents, nonamyloid, (7.5–)8.5–10.5(–11.5) × (5–)5.5–6.5(–7) μm ($L_m = 8.8–10.5$, $W_m = 5.5–6.2$, $Q_m = 1.5–1.6$). Spores never ornamented. Basidia clavate, 2–4-spored, with a loop-like basal clamp, 50–60 × 8–10 μm. Subhymenium sharply delimited from the context, 30–40 μm thick, composed of densely interwoven, cylindrical, thin-walled hyphae, 2–3 μm wide. Hyphae of the context parallel, cylindrical to inflated, thin-walled, hyaline to pale yellow, without incrustations or crystals, clampless, 5–18 μm wide. Surface of the sterile base smooth, hyphae 2–3 μm wide, without incrustations. Basal mycelium white, composed of hyphae that are interwoven, cylindrical, slightly thick-walled, hyaline, clampless, 2–3 μm wide.

Distribution and habitat: Europe, Greenland. In *Sphagnum* bogs, probably associated with Ericaceae.

Specimens examined: CZECH REPUBLIC. MORAVIA: Hrubý Jeseník Mountains, S-E ridge of the Keprník mountain (1423 m), raised bog, among *Sphagnum russovii*, *N. Declerova*, 15 Sep 2011, BRNM 747282. FRANCE. Jura, in turfois, *Hetier*, PC0124967 (lectotype of *C. sphagnicola*). GREENLAND. Sisimut, Qeggata, *G. Gulden* & *E. Horak*, 20 Aug 2000, TENN 58804. NORWAY. NORD-TRØNDELAG: Steinkjer, Stordalen, Flatanger, in *Sphagnum* wetland

pine spruce forest, *V. Kautman*, 4 Sep 2009, BRA CR13593; in *Sphagnum* with *Calluna vulgaris*, *I. Kautmanová*, BRA CR13260. SWEDEN. UPPLAND: Bälunge parish, Bälunge mosse, Ryggmossen, among *Sphagnum*, 18 Oct 1946, *A. Melderis*, UPS F-123795. Bälunge parish, ca. 800 m SO on Rebbö, among *Sphagnum* in bog, 3 Oct 1944, *O. Hedberg*, UPS F-123796. Vaksala parish, on Hagtorp, between Storboda-Norrhagen, among *Sphagnum*, 28 Sep 1947, *A. Melderis*, UPS F-123797.

Commentary: Key characters of *C. sphagnicola* are the typical habitat among *Sphagnum* and the ellipsoidal spores, which are broader than those of *C. argillacea* (Boudier 1917, Christiansen 1967). Furthermore, the basidiomata of *C. sphagnicola* are less caespitose and more slender than those of *C. argillacea*. *Clavaria sphagnicola* sometimes has been treated as a variety of *C. argillacea* and thought to be an ecological variant (Corner 1950, Knudsen et al. 2012). The material among *Sphagnum* that we examined, including the type material, had consistently broader spores with a lower Q_m than in *C. argillacea*. Furthermore, our ITS and 28S analyses support that *C. sphagnicola* is distinct from *C. argillacea* and we conclude that *C. sphagnicola* merits species rank. An association with *Sphagnum* has been claimed because *C. sphagnicola* produces basidiomata physically attached to *Sphagnum* shoots. Nevertheless Ericaceae occur typically in *Sphagnum* bogs and given that *C. argillacea* establishes mycorrhizal symbioses with Ericaceae, a similar trophic strategy can be expected in *C. sphagnicola*. A specimen from Greenland conforming to *C. sphagnicola* in spore characters and with a highly similar 28S sequence (HQ877683) grew among *Dicranum* and *Polytrichum* tufts, instead of among *Sphagnum*. This substantiates that *C. sphagnicola* also is present in Greenland and that it is not restricted to *Sphagnum*.

An original specimen of *C. sphagnicola* was located in the Boudier herbarium at PC. We thus designated this material as lectotype above, which is in agreement with the current interpretation of the name.

DISCUSSION

Phylogenetic study.—The 28S phylogeny resolves a few species relationships but lacks resolution along the backbone. Our molecular analyses do not support *Clavaria* subg. *Holocoryne* as monophyletic. Nevertheless, the monophyly hypothesis cannot be rejected and all clades in the 28S and ITS phylogenies contain either only clampless or only clamped species (e.g. *C. citrinorubra*-*C. argillacea*-*C. flavipes* clade). The 28S analyses provided good phylogenetic signal for terminal clades corresponding to morpho-species, as observed in Kautmanová et al. (2012a, b). Although the ITS was hardly alignable across

Clavaria, it was useful in species delimitation. Its adequacy as a barcoding marker (Schoch et al. 2012, Kõljalg et al. 2013) is illustrated because it includes markedly different unalignable regions between species but in general has low or no within-species variability.

The morphological characters correlated with the well supported clades recovered in our analyses are basidioma color, presence or absence of clamps and spore characters (i.e. size, shape and ornamentation). The large 28S sequence variation within *C. fragilis* might indicate cryptic speciation, as proposed by Kautmanová et al. (2012). The *C. falcata* s.l. clade represents another species complex of white *Clavaria* species with clamped basidia. More comprehensive studies evaluating the presence of gray tones and spore characters should clarify species boundaries in this complex. Perhaps the ITS region will be useful in solving species complexes in *Clavaria*.

The 28S analyses recovered *Clavaria*, *Camarophylloopsis* and *Clavicornia* as a monophyletic group, as noted by Birkebak et al. (2013). The type species of *Camarophylloopsis*, *C. schulzeri*, is nested within *Clavaria*. This suggests that agaricoid fruit bodies have evolved within the otherwise clavarioid *Clavaria* lineage. We propose two synapomorphic characters shared by *Camarophylloopsis* and *Clavaria*: (i) the absence of clamps on the context hyphae and (ii) basal tomentum and mycelium composed of unusually narrow (1–2 µm wide) and slightly thick-walled hyphae, as we observed in *Camarophylloopsis foetens* (W. Phillips) Arnolds, *Cl. phaeophylla* (Romagn) Arnolds and many *Clavaria* species. Furthermore, it is anecdotally known that Clavariaceae and *Camarophylloopsis* have a similar ecology and phenology and often are found together in grassland surveys (e.g. Griffith et al. 2013), but explicit mentions of their co-occurrence could not be traced in the literature. The question whether the clamped species of *Camarophylloopsis* are allied to *Clavaria* needs to be investigated further. Likewise, the relationships of the clampless *Camarophylloopsis* within *Clavaria* need to be further resolved. This study supports the synonymy of *Clavicornia* and *Clavaria* because the type of *Clavicornia*, *Cl. taxophila*, is nested in *Clavaria*. *Clavicornia taxophila* conforms to *Clavaria* in its clavarioid simple fruit bodies and clampless contextual hyphae. In contrast, the conspicuous gloeocystidia and truncate apex of *Cl. taxophila* make an emendation of the generic concept *Clavaria* necessary. A more robust phylogeny should facilitate an updated circumscription of *Clavaria*, address the monophyly of *Holocoryne*, shed additional light on species relationships and allow proposals for the

pertinent nomenclatural changes and emendations, which are beyond the scope of this study.

Spore ornamentation and species concepts in Clavaria subg. Holocoryne.—Although ornamented spores were detected in many taxa of *C. subg. Holocoryne*, some species, such as *C. argillacea* and *C. flavipes* (= *C. straminea*), have consistently smooth spores (Corner 1950, Knudsen et al. 2012) as observed by us. Our 28S and ITS analyses (FIGS. 1, 2) recovered clades producing scattered ornamented spores (*C. asterospora*-*C. incarnata*-*C. flavipes*) or clades of exclusively smooth spores (*C. falcata* s.l. and *C. argillacea*-*C. citrinobruca*-*C. flavipes* clade). This suggests that ornamented spores might be diagnostic for certain species and that spore ornamentation can be used in species delimitation as an informative taxonomic character.

The spore layer composition and the nature of the spore ornamentation in *Clavaria* has been studied only by Loquin (1945) in *C. asterospora*; he stated that they are unusual because the spines originate from the epispore and perforate the exospore. The wall structure in other ornamented spore-producing species with clamped basidia is assumed to be similar. As Petersen (1988) noted, the proportion of ornamented spores is usually low in microscopic mounts and they are thus overlooked when scarce. He also argued that ornamentation is formed late in the spore development, and Roberts (2007) noted that it occurs after spore release. Corner (1950: 238) observed the same phenomenon but suggested that the ornamented spores belonged to another fungus. Knudsen (1996) stated that ornamented spores develop occasionally, possibly under unusually moist conditions. We observed ornamented spores only in hymenium scrapes but not in the spore print. Considering this evidence, we suggest that (i) ornamentation is formed after spore release, (ii) ornamented spores develop when laying on the hymenium and (iii) metabolic changes occur in the process of the spore becoming thick-walled and ornamented, probably because of a resistance mechanism or germination process.

Petersen (1988) considered the existence of analogous taxa distinguishable only by the spore ornamentation as suspicious. In Europe, Knudsen proposed *C. falcata* and *C. asterospora* and *C. incarnata* and *C. stellifera* to be synonyms, respectively. Roberts (2007) observed ornamented spores also in *C. greletii*, a taxon previously considered to be smooth-spored (Boudier 1917, Corner 1950). The species pairs mentioned above should be reassessed considering current knowledge of spore ornamentation to clarify species delimitation in subgen. *Holocoryne*.

KEY TO YELLOW SPECIES OF *CLAVARIA* SUBG. *HOLOCORYNE*

1. Spores ellipsoidal to cylindrical ($Q_m > 1.2$), sometimes thick-walled and with spines when found in the hymenium 2
1. Spores globose to ovoid, ($Q_m = 1.07-1.1$), always smooth and thin-walled 4
2. Spores $L_m = 5.5-7.8 \mu\text{m}$; ellipsoidal to broadly ellipsoidal, $Q_m = 1.2-1.56$, sometimes thick-walled and with spines when found in the hymenium; not associated with Ericaceae nor among *Sphagnum* *C. flavostellifera*
2. Spores $L_m = 8.8-11 \mu\text{m}$, ellipsoidal to cylindrical, $Q_m = 1.5-2.4$, thin-walled and smooth; associated with Ericaceae and/or among *Sphagnum* 3
3. Not growing among *Sphagnum*, $Q_m = 2-2.4$, $W_m = 4.4-4.6 \mu\text{m}$ *C. argillacea*
3. Growing among *Sphagnum*, $Q_m = 1.5-1.6$, $W_m = 5.5-6.2 \mu\text{m}$ *C. sphagnicola*
4. Fertile part with red tones, yellow tones restricted to the stipe; spores $L_m < 6.5 \mu\text{m}$; Australia *C. citrinorubra*
4. Without red tones; spores $L_m \geq 6.5 \mu\text{m}$ 5
5. Spores $6-8 \times 5.5-7.5 \mu\text{m}$; Europe, North America *C. flavipes*
5. Spores $6.5-9.0 \times 6.5-8.0 \mu\text{m}$; Australia *C. luteostirpata*

ACKNOWLEDGMENTS

We are indebted to Slavomir Adamčík for his valuable comments and for lending us interesting material. We express our gratitude to Maria Prieto for critical revision of the manuscript and advice on phylogenetic analyses. We acknowledge the curators of BIO (M. Herrera), K (B. Aguirre-Hudson) and PC (B. Buyck) for arranging loans. L. Gaisler, L. Tábi and J. Kuriplach are thanked for providing photos of *C. flavipes* and *C. flavostellifera*. We thank Joshua Birkebak for valuable advice and for kindly sharing notes on the morphology specimens sequenced by him. Miguel Ángel Ribes provided photographs of *C. argillacea* and useful comments on his gatherings. We are also grateful for the help of two anonymous referees for providing valuable improvements to this manuscript. This work was partially supported (I. Olariaga) by a researcher training grant from the Basque government (2002/2003) and (I. Kautmanová) by a grant from the European Commission's (FP6) Integrated Infrastructure Initiative programme, SYNTHESIS (ES-TAF 4137) and national project VEGA 02/0088/13.

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