

Typification of three European species epithets attributable to *Strobilomyces* (*Boletales*)

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One of the most easily recognized genera of boletes is *Strobilomyces*, represented by taxa on most continents. At least in the Northern Hemisphere, early European species epithets are being applied to local taxa. Among these epithets in common use are *S. strobilaceus* and *S. floccopus*, sanctioned (as *Boletus*) by Fries. Contemporary with these is also *Boletus strobiliformis*, although not sanctioned. All three names, however, have been without acceptable type specimens, so identifications and diagnoses have remained insecure. This paper designates type specimens for these epithets as a prerequisite for accurate assessment of taxa. Comparison of morphological characters and sequences of ITS region of nrDNA gathered from type and additional material suggest existence of only a single European species, correctly named *S. strobilaceus*.

Key words: nomenclature, *Boletaceae*, Agaricomycotina, taxonomy, typification.

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Jeden z najľahšie rozlíšiteľných rodov hribovitých húb je *Strobilomyces*, zastúpený taxónmi na väčšine kontinentov. Prínajmenšom na severnej pologuli boli použité epiteta starších európskych druhov pre miestne taxóny. Z nich sú širšie a bežne používané epiteta *S. strobilaceus* a *S. floccopus* sankcionované Friesom (v rode *Boletus*). Publikované súčasne s nimi je aj meno *Boletus strobiliformis*, hoci nie je sankcionované. Všetky tieto tri mená sú ale bez typových položiek, takže ich rozlíšenie a koncept ostali nedoriešené. Táto štúdia stanovuje typové položky pre tieto epiteta ako nevyhnutnosť na správne ohraničenie zodpovedajúcich taxónov. Porovnanie morfológických znakov a sekvencií ITS regiónu nrDNA získaných z typového a doplnkového materiálu naznačuje existenciu len jediného európskeho druhu, ktorého správne meno je *S. strobilaceus*.

INTRODUCTION

Two binomials in *Strobilomyces* Berk., *S. strobilaceus* (Scop.) Berk. and *S. floccopus* (Vahl) P. Karst., have been used worldwide. Literature has treated these as synonyms of one taxon, or more rarely as two separate species. Largely overlooked has been *Boletus strobiliformis* Dicks., but its introduction (as *Boletus*) was generally contemporary with the other two. Although not nomenclaturally competitive (two were sanctioned by Fries, while *S. strobiliformis* was not), their taxonomy cannot be well-defined, for none is represented by an appropriate type specimen. This paper intends to correct this oversight.

In an obscure paper, Voss (1885) questioned the basic literature, including Fries (1828) and others, which formed the taxonomic concepts represented by *Boletus strobilaceus* Scop. and *B. strobiliformis* Dicks. Correctly, Voss drew attention to “Schemnitz” in Northern Hungary (recently Banská Štiavnica in Slovakia) of that time, as the type location for Scopoli’s *Boletus strobilaceus*. Understandably for his era, Voss was uninterested in typification, but emphasized taxonomy, even providing a key to four taxa (*B. strobilaceus*, *B. floccopus*, *B. laricinus* Berk., *B. strobiliformis*). Although Voss, in text, wrote “Dickson’s *Boletus strobiliformis*...” nevertheless, in the nomenclator for this species, Voss inextricably cited it as “*Boletus strobiliformis* Villars” (see discussion below). Moreover, Voss did not list Dickson’s literature (Dickson, 1785) anywhere in the nomenclator for this binomial. Altogether, while Voss (1885) investigated much the same problem as taken up in this paper, he did not typify (or specify a particular specimen) any of the names he accepted.

Singer (1945: 108) designated *Strobilomyces strobilaceus* (without citing its basionym) as *typus generis*. This typification was followed by Donk (1955), who cited numerous other references in agreement. Horak (1968) accepted *Boletus strobilaceus* as type species of *Strobilomyces*, but selected as lectotype a Berkeley specimen. This selection cannot be maintained, however, for the lectotype must be Scopoli’s illustration and the species epithet is traced to Scopoli, not to Berkeley and the geographic origin of the epithet, therefore, must be from central Europe, not the United Kingdom.

MATERIALS AND METHODS

Morphology. Specimens were examined using naked eye, a Nikon SMZ-ZT dissecting microscope and an Olympus BX60 research microscope fitted for phase contrast microscopy (PhC). When microscopic structures were found to appear differently under bright field microscopy (BF) and phase contrast (PhC), the appropriate system is noted below in the description. In no instance were

stains applied. Spore measurements include ornamentation. In spore statistics, E = spore length divided by spore width; E^m = mean E over all spores measured; L^m = mean spore length.

Molecular procedures. Pileus fragments (~0.25 g) were suspended in 750 μ L Carlson lysis buffer (Carlson et al. 1991) at room temperature for three days with a change of buffer each day to leach out copious black pigmentation, then ground in fresh Carlson lysis buffer with a mortar and pestle using a small amount of grinding sand. Subsequent procedures followed those in Mata et al. (2006) except that the supernatant following chloroform: isoamyl alcohol extraction was re-extracted 2-4 additional times until the supernatant was clear. The ribosomal ITS region was amplified using the forward primer ITS1F (Bruns & Gardes 1993) and reverse primer ITS4 (White et al. 1990). If PCR amplification failed, serial dilutions of the DNA extract were used for additional attempts. Cycle parameters were 94 °C for 3 minutes followed by 30 cycles of 94 °C for 30 seconds, 60 °C for 60 seconds and 72 °C for 90 seconds with a final extension at 72 °C for 3 minutes (Jin et al. 2001). PCR products were visualized by gel electrophoresis in 1.5% TBE agarose gels. PCR products were bidirectionally sequenced using an automated ABI 3100 DNA sequencer (ABI Prism Dye Terminator cycle sequencing, Perkin-Elmer, Inc) with primers ITS5, ITS4 for the ITS region (White et al. 1990). Sequences of each gene were manually corrected and aligned using the SEQLAB program in the Genetics Computer Group package (GCG 2000) and deposited in GenBank (JQ318964-JQ319001; Tab. 1). Related sequences identified by a Blast search of LSU sequences in GenBank (e.g., *Xerocomus* sp. and environmental sequences) were used as outgroup sequences. Many of the collections required cloning to resolve sequence ambiguities. Cloning was carried out using the Promega pGEM-T easy kit with M109 Competent cells according to manufacturer's directions (Promega Corporation, 2800 Woods Hollow Road, Madison, WI 53711 USA).

Phylogenetic procedures. Phylogenetic relationships were estimated by maximum parsimony implemented in PAUP* 4.0 (Swofford 2002) and by Bayesian analysis. For parsimony analysis, gaps were treated as a fifth base and characters were unordered and unweighted. Heuristic searches were conducted under the following conditions: the starting tree was obtained via stepwise addition; the branch-swapping algorithm was tree-bisection-reconnection (TBR). Branch robustness was evaluated by 1000 bootstrap replicates (Felsenstein 1985) using the same conditions as above. Model test (Posada & Crandall 1998) was used to estimate the appropriate model of evolution for Bayesian analysis which was GTR+I (variable base frequencies, symmetrical substitution matrix and a portion of invariable sites). Bayesian analysis was performed using Mr. Bayes (Huelsenbeck & Ronquist 2012) with settings appropriate to the model of evolution. The MCMC search was run with 4 chains for 500,000 generations with

Tab. 1. Specimens used for phylogenetic analyses.

GenBank #				
<i>Xerocomus</i> sp.	Source	Herbarium Number	Name	Collection Location
FN393109	Ectomycorrhizal root tip	none	Environmental	France
AM161541	Ectomycorrhizal root tip	none	Environmental	Denmark
AJ889926	na	KF01-33	<i>Xerocomus badius</i>	Denmark
AJ419222	na	MA fungi 46679	<i>Xerocomus badius</i>	Spain
AJ889927	na	KF02-15	<i>Xerocomus badius</i>	Denmark
FJ236031	na	JB19	<i>Xerocomus badius</i>	Germany
EF031127	Ectomycorrhizal root tip	none	Environmental	South Africa
AM159584	na	none	Environmental	Denmark
EU816626	Root	none	Environmental	Germany
EF521237	Spruce forest	none	Environmental	Sweden
FJ816780	Ectomycorrhizal root tip	none	Environmental	
FN393164	Ectomycorrhizal root tip	none	Environmental	France
FN393134	Ectomycorrhizal root tip	none	Environmental	France
GQ404993	na	none	Environmental	Czech Republic
<i>Strobilomyces "strobilaceus"</i>	Field Number /Collector	Herbarium Number	Name	Collection Location
AY854068	AFToL 716	CLARK MB03-102	as <i>S. floccopus</i>	USA, MA
FM999721	B06B3	None given	Environmental	USA, OH
JQ318964	RHP004615	TENN34672	<i>S. "strobilaceus"</i>	USA, NC
JQ318965– JQ318968	TFB8814	TENN55450 c1, c2, c6, c10	<i>S. "strobilaceus"</i>	USA, NC
JQ318969	TFB13152	TENN61238	<i>S. "strobilaceus"</i>	USA, NC
JQ318970– JQ318971	ZT12705	TENN62157 c1, c2	<i>S. "strobilaceus"</i>	USA, TN
JQ318972– JQ318973	ASM20077	TENN62178 h1, h2	<i>S. "strobilaceus"</i>	USA, NC
<i>Strobilomyces strobilaceus</i>	Field Number /Collector	Herbarium Number	Name	Collection Location
JQ318974– JQ318978	SAV3214	SAV3214 c1, c3, c5, c7, c9	<i>S. strobilaceus</i>	Slovakia
JQ318980– JQ318983	SAV5713	SAV5713 c2, c4, c5, c7, c10	<i>S. strobilaceus</i>	Slovakia
JQ318984	CNF 1/4481	TENN62997	<i>S. strobilaceus</i>	Croatia
JQ318985	LE253886	LE253886	<i>S. strobilaceus</i>	Russia, Caucasus
JQ318986– JQ318988	LE253887	LE253887 c4, c6, c9	<i>S. strobilaceus</i>	Russia, Caucasus
JQ318989– JQ318996	TENN63121	TENN63121 c2, c3, c5-c8, c10	<i>S. strobilaceus</i>	Sweden
JQ318997– JQ319001	Irmgard Krisai-Greilhuber 1	TENN65514 c1, c4, c6, c7	<i>S. strobilaceus</i>	Austria

na – not applicable, c – clone number, h – haplotype number



Fig. 1. Neo- and epitype specimens of *Strobilomyces* species.

A. *Boletus strobilaceus*, Slovakia, Trbeč Mountains, village of Mankovce, hills NW of the village, alt. 276–290 m, 48° 25' 58" N, 18° 19' 25" E, 12. VII. 2010, S. Adamčík (as *S. strobilaceus*), F 3214 (SAV). 0.25×.

B. *B. strobiliformis*, United Kingdom, England, Oxfordshire, Henley-on-Thames, Lambridge Wood, 51° 32' 15" N, 0° 54' 17" E, 11. X. 1992, coll. & det. A. Brickstock, K(M) 20811.

C. *B. floccopus*, Denmark, S Sjaeland, Pramskoven, 55° 28' N, 11° 42' E, 16. IX. 1990, coll. & det. H. Knudsen (as *S. strobilaceus*), C-F-22261 (C). 0.4×.

sampling every 100 generations. The first 1,000 trees were discarded based on preliminary analyses showing that likelihood values had reached stability with the first 1000 trees. Posterior probabilities were estimated by sampling trees generated after likelihood values diverged.

RESULTS

Discussion/typification of names is arranged chronologically.

Boletus strobilaceus Scopoli. 1770. *Annus Historico-Naturalis* (Leipzig) 4: 148; pl. 1: fig. 5. Figs. 1A, 2, 3

≡ *Boletus strobilaceus* (Scopoli) Fries. 1828. *Elenchus Fung.* 1: 127.

≡ *Strobilomyces strobilaceus* (Scopoli) Berkeley. 1851. *Hooker's J. Bot., Kew Gard. Misc.* 3: 78.

Holotype. None designated.

Lectotype (iconotype, hic design.). Just above the protologue diagnosis, Scopoli (1770) cited an illustration of *B. strobilaceus* which may have been interleaved among the pages of “Annus IV.” The etching depicts a single, mature basidiome. Pileus convex, nearly hemispherical, completely covered with large, ascending scales (eight covering half the circumference of the pileus margin, a total of 19 scales covering the visible half-surface), curved-polygonal with acerose to mammillate apices, but all uniform in size and shape. Pores represented by stippling; no details visible. Stipe length nearly twice the pileus diameter, perhaps sliced lengthwise (i.e. suggestion of central cavity or differentiation), smooth or minutely disrupted; base hardly expanded.

Epitype (hic design.). Slovakia, Trábeč Mountains, Mankovce, hills NW of the village, alt. 276–290 m, 48° 25' 58" N, 18° 19' 25" E, 12. VII. 2010, terrestrial, under *Quercus* and *Carpinus betulus*, coll. S. Adamčík (as *S. strobilaceus*), F 3214 (SAV).

Protologue. Diagn. Nigricans; pileo squamoso, ad instar strobili *Pini sylvestris*. Circa Schemnizium saepe vidi.

Pileus convexus, fusco-niger; valleculis inter squamas saepe albicantibus. Caro alba, crassitie quatuor & quinque linearum. Poruli crassitie, carnis, angulati. Stipes solitarius, pileo concolor, longus, nudus, solidus, plenus, apices pallidior, crassitie digiti auricularis.

Epitype description. A single dried agaricoid basidioma divided into 12 fragments (Fig. 1A), sliced longitudinally at least three times. Pileus approximately 75–80 mm broad, strongly convex, beset with olive-black polygonal patches or compressed scales; pileus flesh up to 7 mm thick, firm, corky to compressed-felty, concolorous with background (but drying concolorous with scales). Tubes up to 8 mm long, adnexed, not noticeably depressed around stipe, olive-black, 1–1.2/mm; pores concolorous with tubes or (in limited areas) somewhat paler; dissepiments black where sliced and dried, pallid cream colored where revealed after drying. Stipe approximately 60–65 × 16–18 mm, curved, slightly enlarged apically and basally, olive-black (dry) downward where handled and there finely longitudinally ridged, upward felty to cottony, longitudinally lacunose, pallid gray-cream; annular material cottony, concolorous with stipe apex.

Pleurocystidia (Fig. 2A) occasional (perhaps very locally common), $74\text{--}91 \times 18\text{--}22 \mu\text{m}$, pedicellate, fusiform, occasionally narrowly fusiform, with drawn-out apex, thin-walled; contents homogeneous, hyaline. Basidia (Fig. 2B) $52\text{--}64 \times 16\text{--}22 \mu\text{m}$, bulbo-clavate with long pedicel, 4-spored, thin-walled; contents consistently multiguttulate when mature, with guttules refringent, generally distal. Basidiospores (Fig. 3) $12\text{--}14 \times 10\text{--}11.5 \mu\text{m}$ ($E = 1.14\text{--}1.33$; $E^m = 1.24$; $L^m = 13.1 \mu\text{m}$), broadly ellipsoid; ornamentation a very intricate reticulum of thick plates, in profile appearing pebbled or delicately cogged; contents generally uniguttulate. Insignificant minority of spores smooth but of mature color (yellow-brown; PhC). Pores sterile, pale gray (pearl gray), composed of a solid beard of cheilocystidia. Cheilocystidia (Fig. 2C) $43\text{--}60 \times 13\text{--}23 \mu\text{m}$, pedicellate, fusiform to clavate, thin- to firm-walled (thick-walled over bulb; hyaline); apex usually bullet-shaped, occasionally mammillate to pronouncedly mammillate; contents homogeneous, hyaline. Upper stipe surface with layer of cymose caulocystidia. Caulocystidia usually septate; terminal cells (Fig. 2D) $35\text{--}61 \times 12\text{--}25 \mu\text{m}$, clavate to sphaeropedunculate, rarely with bullet-shaped apex, firm- to thick-walled (wall up to $0.7 \mu\text{m}$ thick over bulb; hyaline); contents homogeneous, hyaline.

Notes. Pleurocystidia of the epitype specimen are typical of European material (see below), although not usually thin-walled and hyaline (more commonly thick-walled over bulb and with an often distal pigment globule). Basidia are unusually large, but with typical distal, refringent guttules. Spores are typical – very intricate reticulum of thick plates, with no echinulate, thin-plated reticula mixed in. Cheilocystidia (Fig. 2C) without protracted apex are not an artifact of this specimen, but are quite dramatic, especially when compared with pleurocystidia with significantly protracted apices. Caulocystidia are typical. Basidiome dried color matches that of other European specimens.

In the epitype, spores are abundant. None is echinulate or warted in profile (see Petersen et al. 2011, for explanation of these terms). The reticulate ornamentation is well-defined, intricate, of cupuloid plates, in profile undulate or at most rounded-serrulate. Compare TENN 63121 (southern Sweden) with echinulate spore profile and loose reticulum. This specimen (SAV 3214) can serve as an epitype for *Boletus strobilaceus* Scopoli. If *B. strobilaceus* and *B. floccopus* are considered taxonomically synonymous, typification of *B. floccopus* is less important, but only careful typification can resolve this taxonomic problem. Perreau-Bertrand (1961) thought spore ornamentation was reticulate in both species. She ascribed an almost worldwide distribution to *S. strobilaceus* (including a Singer specimen from Florida), but saw only a single specimen from France which she thought was *S. floccopus*.

The epitype (SAV 3214) is embedded in the large clade of European collections (Fig. 8). Initial sequences required cloning, and the several clones are not closely

clustered in the clade. The specimen apparently originates from an interbreeding population in which haplotypes may have been inherited from several parental sources.

Nomenclatural history. Although known primarily for his *Flora Carniolica*, J.A. Scopoli (1723–1788) held several positions before moving to Pavia, Italy. From 1757 to 1767, he was professor of mineralogy and metallurgy at Schemnitz (= Schemnizium, recently Banská Štiavnica in Slovakia), during which time he collected the subjects for his five-paper series in *Annus Historico-Naturalis*, and thus his reference to the original geographic location for *B. strobilaceus*.

In text, Fries (1828) wrote: “Obs. *Boletus strobilaceus* a Scopolio primo (*Ann. Hist. Nat.* IV, p. 148) descriptus est et verus *Boletus* nec *Polyporus*, priori proximus.” “Quamquam mihi minus cognita sit haec species, diagnosin addam:” Not numbered, Fries added a full description of *Boletus strobilaceus*, adding: “Habitat in Europa australiori.” Thus, although *B. strobilaceus* was not sanctioned in 1821 (Fries 1821), it was so in 1828 and was accepted in 1832 (Index).

Berkeley’s (1851) use of *Strobilomyces strobilaceus* was incidental, appearing in a paper dealing with fungi from the Sikkim-Himalaya. Later, Berkeley (1860) explicitly recombined *Boletus strobilaceus* into *Strobilomyces*, but he cited only what he considered to be the British mention as “Dicks. Cr. i. t. 3. f. 2”, not the origin of the species epithet. This lack of accurate reference to a basionym would not be sufficient under present nomenclatural rules, but has a long acceptance in the literature and is here considered a correctable error.

Boletus strobiliformis Dickson. 1785. Fasciculus plantarum cryptogamicarum Britanniae, Fasc. 1: 17. Figs. 1B, 4, 5

≡ *Boletus strobilinus* Persoon. 1825. *Mycol. Europ.* 2: 145 (nom. superfl.).

Holotype. Not designated; type localities: England; Bullstrode (approx. 51° 33′ 15″ N, 0° 22′ 17″ E) and Buckinghamshire (approx. 51° 46′ 12″ N, 0° 49′ 06″ E).

Lectotype (iconotype, hic design.). Dickson. 1785. Fasc. Pl. Crypt. Brit., Fasc. 1: tab III fig. 2. Dickson’s illustration comprises two views: 1) a single, distinctly juvenile basidioma, showing coarse pileus scales without orientation (resembling a half-opened rose flower); appendiculae are obvious; the stipe tapers somewhat upward from a broken base, decorated with scattered, vertical, acute, “^”-shaped pen strokes, probably attempting to show stipe reticulation; and 2) a hardly opened pileus viewed from below, showing white pores and coarse, pyramidal pileus scales; appendiculae are obscure.

Epitype (hic design.). United Kingdom, England, Oxfordshire, Henley-on-Thames, Lambridge Wood, 51° 32′ 15″ N, 0° 54′ 17″ E, 11. X. 1992, coll. & det. A. Brickstock, K(M) 20811.

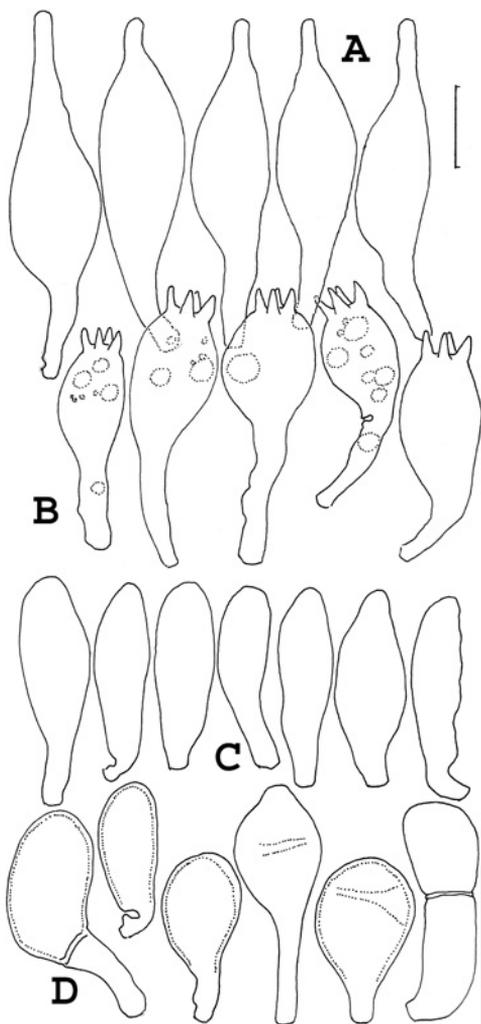
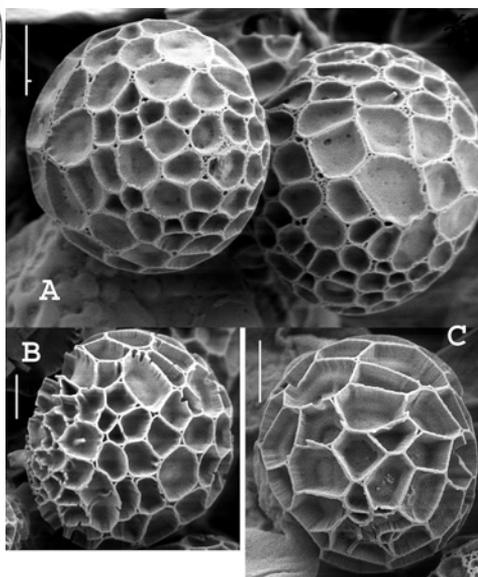


Fig. 2. Microstructures of *Boletus strobilaceus* (SAV 3214; neotype).

A. Pleurocystidia. **B.** Basidia. **C.** Cheilocystidia. **D.** Caulocystidial terminal cells. Bar = 20 μ m.

Fig. 3. Basidiospores of *Boletus strobilaceus* (SAV 3214; neotype).

A, B. Reticulum composed of discrete cups, with complex interstices. **C.** Reticulum, showing vertical striation of cup walls and complex interstices. Bars = 2 μ m.



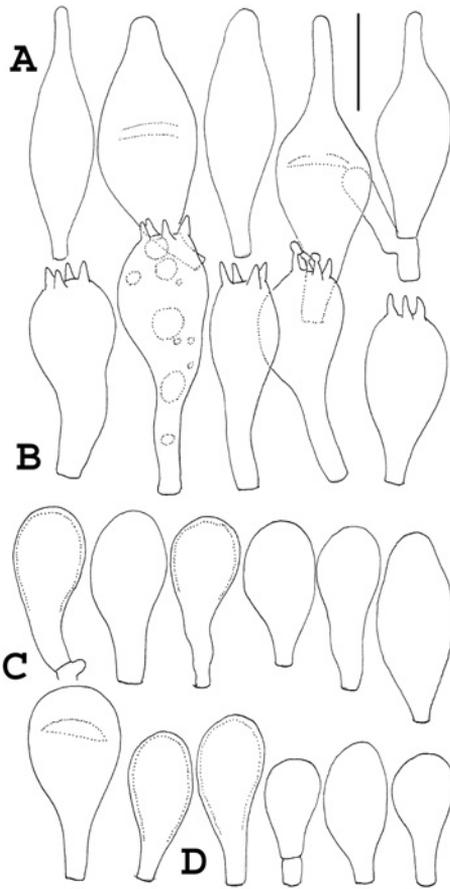
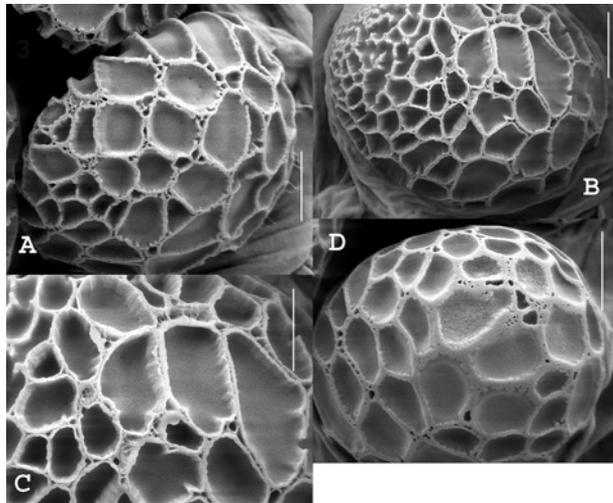


Fig. 4. Microstructures of *Boletus strobiliformis* [K(M) 20811; epitype].

A. Pleurocystidia. **B.** Basidia. **C.** Cheilocystidia. **D.** Caulocystidial terminal cells. Bar = 20 μ m.

Fig. 5. Basidiospores of *Boletus strobiliformis* [K(M) 20811; epitype].

A-C. Reticulate ornamentation, showing discrete cups and some complex interstices. **D.** Somewhat juvenile spore showing incomplete ornamentation relief. Bars = 5 μ m.



Original Latin diagnosis. *Boletus stipitatus*, pileo hemisphaerico tessellate-squamoso fusco, poris angulis albis.

Descr. Stipes 3 f. 4 uncias altus, crassus solidus. Pileus obscure fuscus, durus, diametro fere biunciuli, superficie tessellata f. fissa, strobilum *Pinus Pineae* Linn. quodammodo mentiente. Poris albissimi.

Epitype description. A single basidioma in pieces (Fig. 1B). Pileus (1/2) 70 mm broad, shallowly convex, now deep chocolate brown, decorated with numerous scales; scales pyramidal, blunt, hardly oriented over disc, increasingly radially oriented outward and becoming increasingly appressed and pointed, eventually (near pileus margin) scattered with paler brown background visible, at margin small, subpulvinate; appendiculae apparently pressed, hardly discernable; pileus margin inrolled; dried pileus flesh now punky, gray-tan with distinct transition from flesh to scales; bruising or slicing color reaction not noted. Tubes up to 9 mm long, 1.2–0.9 /mm, depressed around stipe and there larger (up to 0.6/mm), now neutral brown; pores apparently pale tan but with large areas of chocolate brown (through handling?), somewhat angular, especially near stipe. Stipe represented by three large fragments, all woody, with deep chocolate brown surface, longitudinally channeled becoming coarsely so upward; surface near apex pale tan, covered with dark fuscous brown velar frass; annular zone absent; stipe flesh now woody to pithy, nearly black downward, dark brown adjacent to tubes.

Pleurocystidia (Fig. 4A) common, 54–97 × 14–24 µm, pedicellate (usually long-), fusiform to broadly fusiform with protracted apex (often significantly so), firm- to thick-walled (wall up to 0.7 µm thick over bulb; hyaline); contents homogeneous, uniformly yellowish brown (as though the entire content is a pigment globule). Basidia (Fig. 4B) 46–63 × 17–21 µm, pedicellate, clavate to bulbo-clavate, (3–)4-spored; contents (mature) foamy to several-guttulate [refringent (PhC), usually distal]. Occasional basidia sclerotized, clearly 4-spored. Basidiospores (Fig. 5) 12–14.5 × 10–12 µm ($E = 1.08–1.32$; $E^m = 1.20$; $L^m = 13.2$ µm), subglobose to broadly ellipsoid; ornamentation a complete reticulum, ranging from scattered, thin plates, to very intricate with thick plates; in profile ranging from delicately coggled to coarsely echinulate (spines up to 2.0 µm high). Minority of basidiospores smooth, but of normal size, color (dark yellow-brown; PhC) and wall thickness. Pore mouths sterile, a solid beard of cheilocystidia. Cheilocystidia (Fig. 4C) 42–75 × 14–27 µm, pedicellate (either short- or long-), clavate to broadly clavate, commonly with bullet-shaped or mammilate apex (none with protracted apex), thin- to firm-walled (wall up to 0.5 µm thick over bulb, hyaline); contents homogeneous, hyaline. Caulocystidia in cymose fluorescences. Caulocystidial terminal cells (Fig. 4D) 28–61 × 11–25 µm, short-pedicellate, clavate (rarely) to sphaeropedunculate, occasionally with mammilate apex, occasionally subtended by a single “stem” cell, firm- to thick-walled (wall up to 0.7 µm

thick over bulb; hyaline); contents homogeneous, hyaline to usually yellow-tan (PhC; through bruising?).

Notes. As part of the protologue, the illustration is accepted as lectotype for *B. strobiliformis* (see under Discussion), even though the figures are uninformative. Clearly, the illustration can be linked to the protologue and depicts a bolete (the four other “*Boletus*” species in fascicle 1 – *frondosus*, *nummularius*, *medulla panis* and *lacrymans* – are now considered to be polypores), but is too fantasmagorical to be seriously considered as a candidate on which to base the epithet, especially when a specimen from near the type location can be designated as epitype.

Pileus ornamentation on the epitype basidioma appears somewhat more delicate than is normal for *B. strobilaceus* (see other designated type specimen descriptions), with numerous pointed, radial scales, but seems similar to that of the designated epitype of *S. floccopus* (see below). Cheilocystidia (Fig. 4C) of the epitype are typical for *S. strobilaceus*, with the majority clavate to broadly clavate, a minority with bullet-shaped to mammilate apex. Basidia (Fig. 4B) also match, with several, refringent guttules at maturity. Caulocystidial terminal cells (Fig. 4D), while similar to those of other specimens, are generally uninformative.

The minority of smooth spores matches this feature of the Slovakian specimen (SAV 3214) which is proposed as epitype of *S. strobilaceus* (see above). Moreover, within the population of ornamented spores, ornamentation itself is somewhat variable (Fig. 5), from loose reticulum of large cupuloid structures viewed as thin plates to intricate reticulum of smaller cups perceived as thick plates. This reflects a common feature; distal and proximal ornamentation is more complex, of smaller cups, than that of median portions of spore wall (Petersen et al. 2011).

For clarity, our intention is to typify Dickson’s epithet with a specimen taxonomically conspecific with the epitype designated to represent *B. strobilaceus*, and thus to retire use of *B. strobiliformis* (nomenclaturally as well as taxonomically) to represent a separate taxon. This taxonomic decision, however, must always be left for future comparison, including molecular, of the designated types by future workers.

Nomenclatural history. In a brief section devoted to taxa poorly described or otherwise little-known, Persoon (1825: 145) cited Dickson’s literature reference under Persoon’s *B. strobilinus*. Dickson’s type localities were correctly cited as Bullstrode and Buckingh[amshire]. Fries (1832, index) did not include Persoon’s epithet, so it remains unsanctioned, and may be considered merely as an orthographic variant.

In the 1832 index, Fries listed “*Boletus strobiliformis* Auct. (*Bol. strobilaceus*)” with no page reference. It would appear that, while Fries knew of the binomial, it was attributable to more than one author (see below for confirmation), and Fries considered it to be merely a synonym. Hence the name was not sanctioned.

Saccardo (1888: 47–48) listed *B. strobiliformis* Dickson as a synonym under *S. strobilaceus*, but *B. strobiliformis* Cumino (“Act Taur. II. 1805”) as a synonym under *S. floccopus*.

There is no evidence that Dickson’s binomial has been recombined.

In addition to Dickson’s epithet introduced as above, two apparently independent introductions, while not having nomenclatural status, nonetheless appear in contemporary literature. Both publications (see below) are locally floristic and (therefore) in neither case was Dickson’s nomenclatural type explicitly dismissed, so these introductions do not technically represent homonyms, but may be accepted as merely referring to Dickson’s original epithet.

Boletus strobiliformis Villars. 1789. Histoire des Plantes de Dauphine, vol. 3, fasc. 2: 1039.

≡ *Strobilomyces strobiliformis* (Villars) Beck v. Mannagetta. 1923. Zeitschr. Pilzk. 2: 148.

≡ *Boletus coniferus* Persoon. 1825. Mycol. Europ. 2: 145. (nom. superfl.).

Boletus strobiliformis A. Cumino. 1805. Mem. Acad. Imp. Sci. Turin, Sci. Phys. 8: 202–269 + pls. 1–3.

≡ *Boletus gossypinus* Persoon. 1825. Mycol. Europ. 2: 144. (nom. superfl.)

Boletus floccopus Vahl. 1799. Flora Danica 7 (fasc. 21): pl. 1252. Figs. 1C, 6, 7

≡ *Boletus floccopus* Vahl: Fries. 1821. Systema Mycol. 1: 393.

≡ *Strobilomyces floccopus* (Vahl) P. Karsten. 1882. Bidr. Känn. Finl. Nat. Folk. 37: 16.

H o l o t y p e. None designated.

L e c t o t y p e (iconotype; <http://dia-prod-mas-01.kb.dk/FloraDanica/Site/index.jsp>). Vahl. 1799. Flora Danica 7 (fasc. 21): pl. 1252. In the lectotype illustration, two basidiomata are depicted. Both show pilei covered with scattered, pyramidal tufts or scales with no discernable orientation except negatively geotropic. One basidioma (inverted) appears immature, in which the pores are covered with a white membrane. The second, mature basidiome has been sliced longitudinally. The portion showing the exterior shows a smooth stipe tapering gradually upward, with a suggestion of an annulus and constricted (unnaturally) near the base. The other half of the sliced basidiome (showing the interior) shows long tubes not depressed around the stipe, and with obvious red-brown blush just distal to the pores and over the lower third of the stipe. A separate small inset shows a detail of the tubes (inverted), in which the pore mouths appear paler than the tubes, and the red-brown pigment quite prominent over the upper tubes and adjacent pileus flesh.

Epitype (hic design.). Denmark, S Sjaeland, Pramskoven, 55° 28' N, 11° 42' E, under *Fagus*, 16. IX. 1990, coll. & det. H. Knudsen (as *S. strobilaceus*), C-F 22261 (C).

Original diagnosis. None furnished.

Epitype description. Single basidioma sliced lengthwise (Fig. 1C). Pileus nearly hemispherical, mostly concolorous (deep chocolate brown, dried), coarsely lumpy with polygonal, rounded warts up to 10 mm broad, becoming radial and somewhat appressed near the pileus margin and there with pinkish tan background (dried); dried flesh very light in weight, 1.5 mm thick at margin, 10 mm thick near center, now pallid dirty pale tan (no black tints) on slice surface and protruding up into the warts (so warts are really only a tuberculate skin covering pileus flesh), on fresh slice (dried specimen) very pale, off-white; appendiculae soft, flap-like, pallid pinkish-gray. Tubes up to 18 mm long near stipe, adnate (not depressed around stipe but not at all decurrent), now purple-brown with black dissepiments (on open slice; concolorous away from open slice), 1/mm; pores (of this specimen) concolorous, not pale. Stipe 58 × 9–13 mm, curved, tapering slightly upward, without basal swelling, floccose apically; surface dark brown, hardly reticulate downward, darker downward; cortical flesh hard, rind-like, dark gray-brown; medullary flesh collapsed, dark gray-brown (without black tints).

Pleurocystidia (Fig. 6A) occasional, 50–80 × 18–25 µm, significantly pedicellate, inflated with significantly protracted apex, thin-walled except slightly thick-walled (wall up to 0.7 µm thick, hyaline) over bulb, hyaline. Basidia (Fig. 6B) 38–47 × 14–17 µm, bulbo-clavate, hyaline, 2–3–4-spored; contents homogeneous when young, becoming multiguttulate apically by maturity. Basidiospores (Fig. 7) (from hymenophore) 12–15 × 11–13 µm ($E = 1.04\text{--}1.18$; $E^m = 1.12$; $L^m = 13.05$ µm), subglobose to broadly ellipsoid; ornamentation an intricate reticulum of thick plates, in profile echinulate; apiculus small, papillate. A minority of spores of mature color (dark yellow-brown; PhC) but smooth or undulate, sometimes vaguely reticulate, often somewhat larger than typical and commonly distorted (elongate, mango- or elongate pear-shaped, apparently thick-walled); (from stipe surface) 11–13 × 9.5–11 µm ($E = 1.04\text{--}1.30$; $E^m = 1.15$; $L^m = 11.75$ µm). Cheilocystidia (Fig. 6C) 42–66 × 14–25 µm, significantly pedicellate, bulbo-clavate, occasionally with slight to significantly protracted apex, thin-walled except firm-walled over bulb; contents homogeneous, hyaline. Skin of pileus warts: hyphae 7–13 µm diam, hardly inflated, firm-walled [not measurably thick, slightly refringent (PhC)], frequently septate (frequently secondarily septate – not at all constricted; occasionally constricted at septum), intricately interwoven but with an orientation, not noticeably adherent, without clamp connections; pigment cytoplasmic, olive brown (PhC). Caulocystidia obscure, usually covered by powdery frass; caulocystidial terminal cells

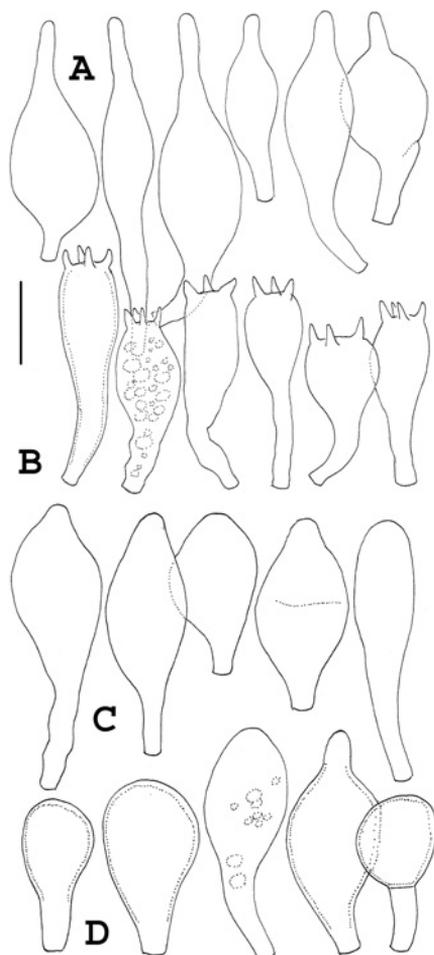


Fig. 6. Microstructures of *Boletus floccopus* (C-F 22261; epitype).

A. Pleurocystidia. **B.** Basidia. **C.** Cheilocystidia. **D.** Caulocystidial terminal cells. Bar = 20 μ m.

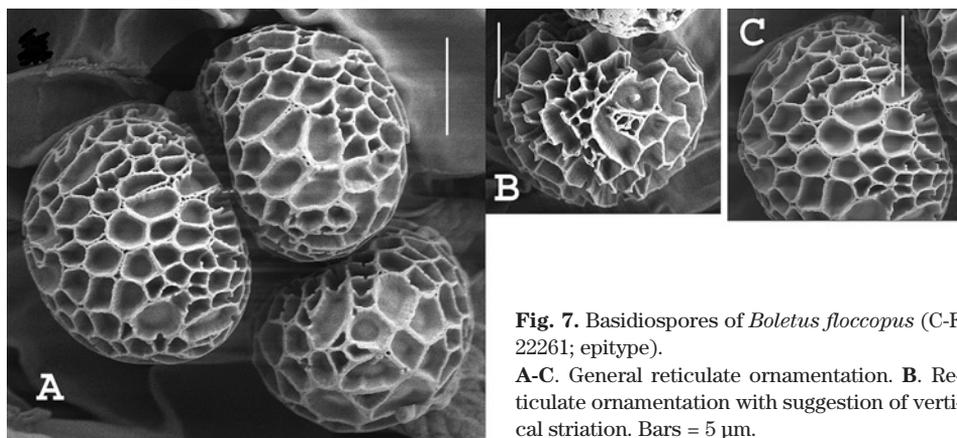


Fig. 7. Basidiospores of *Boletus floccopus* (C-F 22261; epitype).

A-C. General reticulate ornamentation. **B.** Reticulate ornamentation with suggestion of vertical striation. Bars = 5 μ m.

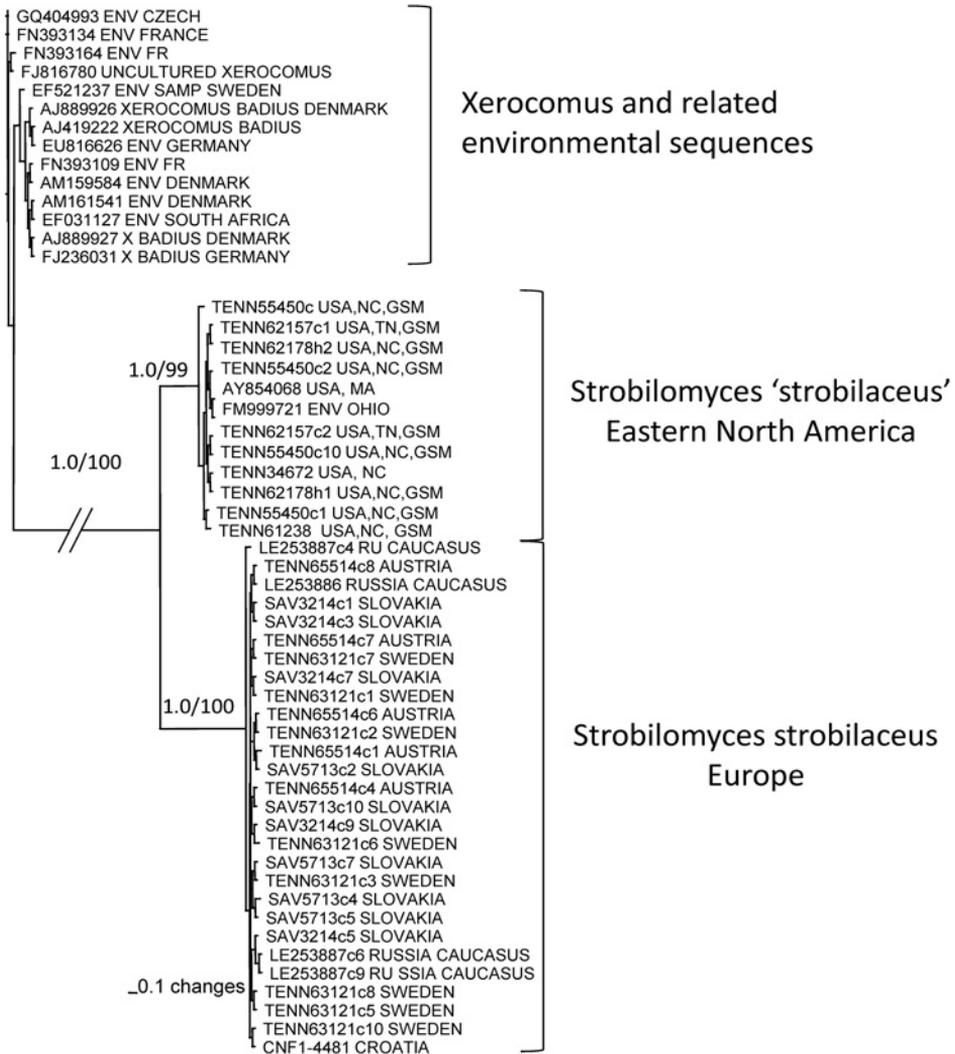


Fig. 8. ITS-based Bayesian consensus phylogeny including European and selected North American reticulate-spored *Strobilomyces* collections.

(Fig. 6D) 25–47 × 9–17 µm, digitate to narrowly clavate to clavate, thick-walled (wall up to 0.7 µm thick, hyaline), often subtended; contents homogeneous, subhyaline to pigmented olive-brown.

Notes. In the epitype specimen (Fig. 1C), cheilocystidia are only rarely apically protracted, but seem to match material from Slovakia and England (see above). The pileus studded with large warts also resembles photos of Slovak and French material. The studded disc seems to give way to appressed, radial scales outward.

Nomenclatural history. Vahl (1799) introduced *Boletus floccopus* without diagnosis or description, but only with a captioned color plate. Fries (1821: 393) cited *Boletus floccopus* as “Vill. delph. 1036.” He also listed “*Bol. floccop.* Fl. Dan. t. 1252. Schum. p. 375. *B. cinereus.* Pers. syn. p. 504.” Thus, although he attributed *B. floccopus* to the wrong author (Villars) in the wrong publication, he was aware of the Flora Danica publication. Schumacher (1803) described *B. floccopus* and cited “Fl. Dan. Tab. 1252,” thus pointing to Vahl’s introduction. In index to vol. 1 of Systema, Fries listed *B. floccopus*, but did not include *B. strobilaceus* or *B. strobiliformis*.

It can be assumed that Fries’ 1821 reference is to Villars’ Flora Delphinalis. Taxonomic literature (TLII 6: 740) lists Villars’ Flora delphinalis ... contribution (“Opera ...”) in J.E. Gillibert, C. Linnaei ... Synopsis plantarum europae 1, 1785 (Publ. Jan. 1786), vii. 127 p. (Latin translation of Prospectus) – issued separately Jun 1786 with 1785 date (see Breistroffer 1948).” An implication of TLII is that the binomial *Boletus floccopus* may have been first proposed in Villars’ Prospectus.

Flora Delphinalis (Villars “1785” [1786]: 125-126) lists seven species of *Boletus*, none of which is *B. floccopus*. At least some are of polypores. But Fries’s (1821) reference cites “Fl. Delph. p. 1036,” and Flora Delphinalis is paged only to 127. Moreover, *B. floccopus* is not used in Villars (1779). Conversely, Villars’ Histoire des plantes de Dauphiné was published in four parts (in three volumes). Part 3(2) was published between Sept. 12 and Oct. 22, 1789, and included pp. 581–1091. Pages 1036–1040 summarize *Boletus*, with no reference to *B. floccopus* (Villars 1789). No authors are mentioned for any taxon.

Index Fungorum (<http://www.indexfungorum.org/>, accessed in early 2012) lists *Boletus floccopus* Rostk[ovius] without date. TLII (4: 911) gives Rostkovius’ publications on fungi as in Stürm’s Deutschlands Flora, part 3, vols. 4 (starting in Heft 5, 1828), 5 and 7 (ending in 1848). It is probable, therefore, that *Boletus floccopus* Rostk. dates from no earlier than 1828. Index Fungorum gives the current name for Rostkovius’s organism as *Leccinum versipelle* (Fr. & Hök) Snell, and a neotype for *L. versipelle* was designated by Den Bakker & Noordeloos (2005: 541). In listed synonyms under *L. versipelle*, no mention was made of *B. floccopus* Rostk., and there seems to be no connection between *B. versipellis* and *B. floccopus*, regardless of the authorship of the latter epithet.

DISCUSSION

Taxonomy and nomenclature

One of the most striking characters to be found in *Strobilomyces* basidiomata is the reddening then blackening of tissues exposed to air, usually caused by bruising or cutting. It is seen on pores and surfaces of cut, fresh tissues of pileus, tubes and stipe. This character cannot be described for the type specimens listed above, for no record was made for fresh material, and the reaction is hardly visible in dried specimens. Vahl's illustration of *B. floccopus*, however, clearly depicts the color change (Vahl 1799: pl. 1252).

Comparison of the descriptions above of the type specimens of *Boletus strobilaceus*, *B. strobiliformis* and *B. floccopus* show that only the stature and pileus ornamentation differ. Conversely, pileus scale hyphae, pleurocystidia, basidia, basidiospores, cheilocystidia and caulocystidia all compare closely. It is difficult to justify taxonomic separation of the three names based solely on their types. In fact, micromorphological variation among numerous European specimens (see below) seems to fit well within that of a single species.

Among European specimens referred to *S. strobilaceus*, basidiospore characteristics differ somewhat. In some specimens the spore population includes a significant minority (i.e. C-F-87239, C-F-87240, both Denmark; LE 253886, Caucasus) or majority (FH 0028439, FH 00284390, both Austria; Bresadola, Italy, NY) of smooth spores otherwise apparently mature (from size and color). Likewise, spore ornamentation itself is also variable. In some cases (TENN 63121, Sweden; C-46664, Denmark; CNF 1/493, Croatia; AE 0208045, AE 9107281, both France), spore ornamentation profile appears coarsely echinulate with spines up to 2.5 μm high (PhC), while in other specimens (C-F-71542, C-F-87237, both Denmark; CNF 1/270, Croatia; Bon s.n., France) ornamentation in profile appears shallowly to coarsely warted (i.e. protuberances with rounded apices), and merely undulate in C-F-87238. Moreover, in some specimens (LE253887, Caucasus; CNF 1/4481, Croatia; C-F-87240, Denmark; RC/GB91.042, France), spore ornamentation seems particularly intricate and formed of thick "plates." Despite these peculiarities, however, basidiome appearance and all microscopic structures agree within species-rank variability. Molecular survey of European material agrees with morphological observations. It is possible that such variation reflects interpopulational interbreeding exposed by multiple haplotypes of individual collections in the phylogeny (Fig. 8).

The matter of habitat is also unsettled. A few specimens seem unequivocally to have been associated with coniferous trees (i.e. CNF 1/6000, Croatia; Courteuisse, s.n., France), while the most often mentioned forest type is hardwood (*Quercus*, *Fagus*, *Carpinus*: Austria, Croatia, Denmark, France, Russia, Slovakia, United Kingdom).

Morphological and molecular data in this paper show that only a single species represents European *Strobilomyces*, and that this species is correctly named *Boletus (Strobilomyces) strobilaceus*, under which *B. floccopus* and *B. strobiliformis* are synonyms. A further implication is the indication that *S. strobilaceus* is evidently absent from eastern North America.

Beyond argument, two binomial combinations were “sanctioned” by adoption by Fries (1821, 1828), *Boletus floccopus* and *B. strobilaceus*, and are therefore nomenclaturally protected against prior synonyms and homonyms. Thus, even though Dickson’s *B. strobiliformis* predates Vahl’s *B. floccopus*, it must be deflected as non-sanctioned.

This argument, however, is nomenclatural, not taxonomic. Current acceptance of names is dictated by taxonomic decisions, which, in turn, are dictated by (if possible) type specimens. If, for example, the type specimen of *B. floccopus* were found to represent the same taxon as represented by the type specimen of Dickson’s *B. strobiliformis*, *B. floccopus* would be accepted as sanctioned, even though introduced later than Dickson’s name. Conversely, if *B. floccopus* and *B. strobilaceus* were found to represent a single taxon, distinct from the taxon represented by Dickson’s *B. strobiliformis*, acceptance of names would change significantly.

Phylogenetic considerations

Macromorphological analyses (including photographs of basidiomata in natural habitat) prove more efficacious than micromorphology [microstructures, spore ornamentation (Petersen et al. 2011), etc.]. Proposed epitype specimens and all European ancillary specimens examined conform to a single species circumscription. Similarly, ITS sequences of the epitype specimen of *S. strobilaceus* and all other available sequences of European collections compose a single, relatively homogeneous clade (Fig. 8). Moreover, at present it appears that the European clade is separate from North American sequences (unpubl. data including numerous additional sequences). Molecular data, therefore, agree with morphological analyses: only a single species of *Strobilomyces* occurs in Europe and its name is *S. strobilaceus* (Scop: Fr.) Berk.

Sato and Murakami (2009) and Sato et al. (2007, 2011) employed numerous *Strobilomyces* sequences and showed that sequences across the genus formed two major clades. Correlated with these molecular data were two types of basidiospore ornamentation. Collections composing one clade exhibited spore ornamentation in meandering, intricate ridges not describing a reticulum (Grand & Moore 1971; Sato et al. 2007, 2011), resembling that seen in *S. confusus* Singer, while spore ornamentation of collections of the other clade appeared clearly

reticulate. Our unpublished phylogenetic data agree with this conclusion, but the present paper deals only with reticulate-spored collections.

Our phylogenetic reconstruction (Fig. 8) furnishes the following data: 1) the *Strobilomyces* taxa with reticulately ornamented spores are decisively separated from the outgroup of *Xerocomus*-like boletes; 2) the clade which includes specimens of *S. strobilaceus* (as typified above) is rather homogeneous and includes only European samples; and 3) no apparent mixing of North American and European populations is shown through phylogenetic placement. Taxa with incomplete reticulate spore ornamentation do not occur in Europe and are not included in this paper.

Phylogenetically, European *S. strobilaceus* sequences form a single clade that is well-supported in both Bayesian and Parsimony analyses (Fig. 8). European *S. strobilaceus* is composed of several apparently interbreeding haplotypes. Differences among haplotypes were primarily due to two variable tandem ‘ca’ repeats in the ITS I region which are separated by a 47 bp sequence, also containing a stable six-base ‘ca repeat’ and a variable ‘ag’ tandem repeat. The ‘left’ tandem ‘ca’ repeat varied from 14–24 bp. The right tandem ‘ca’ repeat varied from 18–22 bp. The tandem ‘ag’ repeat varied from four-six bp. Heterozygosity for the repeat copy number made cloning necessary to resolve ITS sequences in many cases. There is no present evidence for geographical or phylogenetic partitioning (i.e. more than one species-rank taxon) within Europe. Moreover, all North American collections appear distinct from the European clade.

Strobilomyces strobilaceus sequences form a discrete clade with few sequence differences other than those found in tandem repeats. Cloning results suggest that this is a single interbreeding population in that haplotypes recovered by cloning are variously shared among individuals.

Specimens examined

Austria, Wienerwald, Wurzbachthal [48° 13' 18" N, 16° 11' 56" E], 23. VIII. 1913, coll. unknown, det. v. Höhnelt (as *Boletus strobilaceus*), s.n. (FH barcode 00284390); Wienerwald, an der Strasse bei Kniswasser, 28. IX. 1902, leg. v. Höhnelt, s.n. (FH barcode 00284392); Lower Austria, district Krems, E of Gföhl, N of Schilingeramt, along the street to Oberlautendorferamt, 15. IX. 2010, coll. I. Krisai-Greilhuber & H. Voglmayr (as *S. strobilaceus*), s.n. (TENN 65514).

Croatia, vic. Zagreb, 4 km N-NW of Zaprešić, 45° 53' 29" N, 15° 47' 12" E, 9. VII. 1993, coll. & det. Z. Tkalčec, CNF 1/493 (CNF; TENN 65030); vic. Zagreb, Mt. Medvednica, 45° 54' N, 15° 58' E, 8. VII. 2007, coll. Z. Tkalčec & A. Mešić, CNF 1/4481 (TENN 62997; CNF); vic. Zagreb, village of Pojatno, 45° 53' N, 15° 47' E, 4. IX. 2010, coll. Z. Tkalčec & A. Mešić, CNF 1/6000 (TENN 65510); 3.5 km S of Delnice, vic. Rijeka, 45° 22' 07" N, 14° 48' 25" E, 18. VIII. 1990, coll. & det. Z. Tkalčec, CNF 1/270 (CNF; TENN 65029).

Denmark, C Jutland, Silkeborg, Silkeborg Veterskov, 56° 10' 60" N, 8° 33' 07" E, 18. IX. 1977, coll. & det. H. Knudsen (as *S. strobilaceus*), C-F-87239 (C); E Jutland, Staksrode Skov near Horsens, 55° 51' 38" N, 9° 51' 01" E, 12. IX. 2009, coll. & det. H. Knudsen (as *S. strobilaceus*), C-F-87240 (C); S Sjælland, Pramskoven, 55° 28' N, 11° 42' E, 16. IX. 1990, coll. & det. H. Knudsen (as *S. strobilaceus*), C-F-22261 (C); Sjælland, Køge, Lellinge Skovhusvaenge, 55° 27' 30" N, 12° 10' 55" E, 19. IX. 1999, coll. & det. T. Læssøe (as *S. strobilaceus*), TL-5591 (C-F 46664) (C); Sjælland, Hareskoven, 14 km N of Copenhagen,

55° 47' 27" N, 12° 22' 23" E, 7. IX. 1974, coll. excursionist (as *S. floccopus*), C-F- 87238 (C); Møn, Fanefjord Skov, 54° 54' 00" N, 12° 13' 00" E, 12. IX. 1999, leg. & det. H. Knudsen, C-F-71542 (C); Fyn, Svendborg, Graesholmene Sfov, 55° 03' 36" N, 10° 38' 23" E, 29. VII. 1977, leg. & det. M. Lange (as *S. floccopus*), C-F-87237 (C).

France, Dpt. Isère, vic. Biliou, Mont Biliou. Les Grande Postes, between l'Arsenal and Col Blanchet, 4. VIII. 2002, coll. & det. Allain Estades (as *S. strobilaceus*), AE 0208045 (LIL); Dpt. Isère, Montferrat, vic. N75 between Arsenal and Blanchet, La Haute Véronnière [45° 27' 34" N, 5° 33' 47" E], Forêt de Blanchet, 28. VII. 1991, coll. A. Estades, AE 9107281 (LIL); Nord-pas-de-Calais, St. Omer [50° 45' 02" N, 02° 15' 35" E], X. 1970, leg. & det. M. Bon (as *S. strobilaceus*), s.n. (LIL); Haut-Rhin, Kruth [47° 55' 53" N, 6° 57' 51" E], Forêt domaniale, 5. V. 1977, leg. & det. R. Courtecuisse (as *S. strobilaceus*), s.n. (LIL).

Russia, Krasnodar Region, Caucasus Mountains, Terberda State Biosphere Reserve, between Djamagat River and Teberda Town, 13. VIII. 2009, coll. A. Kovalenko, Kovalenko 09-08-42 (LE 253887; fragment TENN 65003); Krasnodar Region, Caucasus Mountains, Terberda State Biosphere Reserve, left bank of Teberda River, vic. Teberda Town, 7. VIII. 2009, coll. Yu. Rebriev, 09-08-10 (LE 253886; fragment TENN 65004).

Slovakia, Pohronský Inovec, 2.5 km NE of the church in the village of Obyce, 9. VI. 2006, leg. V. Kučera (as *S. "floccopus"*), 7250 (SAV); Štiavnické vrchy Mts., Bohunice, E slopes of Bohunický roháč hill, Q 7678b, 27. VII. 2005, leg. V. Kučera, S. Ripková, M. Vašutová, S. Adamčík (as *S. "floccopus"*), 5713 (SAV); Štiavnické vrchy Mts., 4.5 km N of the village of Nová Dedina, Sovia dolina, near bridge, 48° 19' 33" N, 18° 38' 56" E, 28. VII. 2005, leg. S. Adamčík (as *S. strobilaceus*) F 1031 (SAV); Trábeč Mountains, village of Mankovce, hills NW of the village, alt. 276–290 m, 48° 25' 58" N, 18° 19' 25" E, 12. VII. 2010, leg. S. Adamčík (as *S. strobilaceus*), F 3214 (SAV).

Sweden, Hallands lan, Hasslöv [56° 25' 00" N, 12° 59' 59" E], Osbecks bokskog, 16. IX. 2009, coll. Åke & Erna Strid (as *S. strobilaceus*), TENN 63121.

United Kingdom. England, Buckinghamshire, Great Missenden, 51° 42' 15" N, 0° 42' 28" E, IX. 1984, coll. J. Reim, det. B. Spooner (as *S. strobilaceus*), K(M) 119832; South Hampshire, New Forest, Busketts Wood, 15. X. 1994, coll. G.C. Dickson, det. G.C. Dickson & S. Davison (as *S. strobilaceus*), K(M) 54319; Oxfordshire, Henley-on-Thames, Lambridge Wood, 51° 32' 15" N, 0° 54' 17" E, 11. X. 1992, coll. & det. A. Brickstock, K(M) 20811; Scotland, Pitlochry, Black Spout wood, 13. IX. 1991, coll. J. Jepsen, det. R. Courtecuisse (as *S. floccopus*), RC/GB91.042 (LIL).

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