

2 A rare and unusual lignicolous species of *Inocybe* (Agaricales)  
3 from eastern North America

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12 **Abstract.** *Inocybe tubarioides* is a rarely collected or recognized agaric with an un-  
13 usual combination of ecological and morphological characters for this genus, namely  
14 a lignicolous habit and a strongly hygrophanous pileus. The species is known only from  
15 eastern North America and is reported here for the first time from states in New England  
16 and Canada. A taxonomic description is provided, including the first photographic  
17 record of the species and discussion of its evolutionary history. Based on molecular  
18 phylogenetic analysis the species is most closely related with significant measures of  
19 statistical support to two other narrowly endemic species of *Inocybe*: one also from  
20 eastern North America (*I. tahquamenonensis*) and another from northern Europe  
21 (*I. relicina*), the latter of which is the type of the genus *Inocybe*. These three species  
22 constitute the clade that corresponds with section *Inocybe*.

23 **Résumé.** *Inocybe tubarioides* est un Agaric rarement signalé, présentant une combi-  
24 naison inhabituelle de caractéristiques écologiques et morphologiques, en particulier  
25 l'habitat lignicole et le chapeau fortement hygrophane. Cette espèce n'est connue que  
26 de la façade orientale de l'Amérique du Nord, et est signalée ici pour la première  
27 fois en Nouvelle-Angleterre et Canada. Une description est fournie, accompagnée  
28 pour la première fois d'une photographie, et d'une discussion quant à son histoire  
29 évolutive. D'après des analyses moléculaires phylogénétiques soutenues par des  
30 mesures statistiques significatives, cette espèce est très étroitement apparentée à deux  
31 autres espèces endémiques, l'une également connue de l'Est de l'Amérique du Nord  
32 (*I. tahquamenonensis*), l'autre d'Europe du Nord (*I. relicina*) qui se trouve être le  
33 type du genre *Inocybe*. Ces trois espèces constituent la clade: section *Inocybe*.

34 **Key Words:** Ectomycorrhiza, Inocybaceae, morphology, systematics, taxonomy.  
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37 *Inocybe tubarioides* G. F. Atk. is a rarely 47  
38 encountered or recognized agaric known from 48  
39 only a small number of collections in eastern 49  
40 North America since it was first described by 50  
41 G. F. Atkinson at Cornell University almost 51  
42 90 years ago (Atkinson, 1918; Stuntz, 1954; 52  
43 Smith et al., 1979). The fungus displays an 53  
44 unusual array of morphological and ecological 54  
45 characters at odds with features of most species 55  
46 in the family Inocybaceae Jülich (Matheny, 56  
2005). Species of Inocybaceae, with rare exceptions, produce fruiting bodies directly on soil, whereas *I. tubarioides* is consistently observed fruiting on rotten wood. Gross morphological features of *I. tubarioides*, which include a strongly hygrophanous pileus, uncinately to subdecurrent lamellae, and lack of distinctive odor plus a lignicolous habit, could point to a generic affiliation with either *Tubaria* (W. G. Sm.) Gillet or *Simocybe* P.

57 Karst., two stipitate, dull brown-spored, and  
 58 primarily wood-inhabiting genera of Agarica-  
 59 cales. However, the presence of nodulose  
 60 basidiospores and metuloid hymenial cystidia  
 61 suggest an anatomical alliance with the genus  
 62 *Inocybe* (Fr.) Fr. (Smith & Hesler, 1938).

63 Here we present a taxonomic description of  
 64 *I. tubarioides* from several recent collections  
 65 made between 1993 and 2007, the first recorded  
 66 since 1957, including the first published pho-  
 67 tographic record of the species. We also  
 68 synthesize data drawn from historical records  
 69 based on vouchered specimens from major  
 70 North American fungal herbaria. Molecular  
 71 data and phylogenetic analyses are employed  
 72 that confirm the placement of *I. tubarioides* in  
 73 the “Inocybe clade” (Matheny, 2005; Matheny  
 74 & Bougher, 2006), a synapomorphy of  
 75 which is the presence of pleurocystidia  
 76 often of the metuloid-type. *Inocybe tubar-*  
 77 *ioides* is most closely allied to *I. relicina*,  
 78 an endemic species of Fennoscandia and  
 79 type of the genus *Inocybe*, and *I. tahqua-*  
 80 *menonensis*, an endemic species of decidu-  
 81 ous forests in eastern North America. These  
 82 three species constitute a monophyletic  
 83 group, which we refer to as section *Inocybe*.

84 **Materials and methods**

85 *Field collections.*— Five collections of *I.*  
 86 *tubarioides* were made between years 1993–  
 87 2007 in North Carolina, Massachusetts, New  
 88 Hampshire, Quebec, and Tennessee. Macro-  
 89 scopic features were noted when fresh, or the  
 90 materials were photographed and then later  
 91 identified by the lead author. Colors of fresh  
 92 fruit bodies were documented with the Mun-  
 93 sell Soil Color Chart (1954). Macrochemical  
 94 reactions of fresh material to PDAB (p-  
 95 dimethylamino-benzaldehyde) and tincture  
 96 of guaiac were noted on *PBM 2570* (TENN).  
 97 These macrochemical reactions can be of  
 98 taxonomic utility in various groups of Agar-  
 99 icales (Lennox, 1979). Specimens were then  
 100 air-dried on a food dehydrator. Spore, cysti-  
 101 dial, and hyphal dimensions were recorded  
 102 from dried material using light microscopy  
 103 after sections were rehydrated in 2–5% KOH.  
 104 Fragments of type materials were reconsti-  
 105 tuted for 18 hrs in 5% KOH. Cell dimensions  
 106 are provided in ranges with outliers placed in

parentheses. The number of total spores and  
 the number of collections from which they  
 were measured are indicated in parentheses  
 including a backslash (X/Y). Materials exam-  
 ined are curated at the following herbaria:  
 CUP, F, LIP, MICH, NY, TENN, and WTU.  
 No indigenous Canadian collections of *I.*  
*tubarioides* were found at ACAD, DAOM  
 and TRTC (Scott Redhead, pers. comm.;  
 David Malloch, pers. comm.). Herbarium  
 abbreviations follow Holmgren and Holmg-  
 ren (1988). Material from Quebec is housed  
 at “CMMTL”, Cercle des Mycologues de  
 Montréal.

*DNA extraction, PCR, sequencing, and  
 phylogenetic analysis.*— DNA of *I. tubar-*  
*ioides* from North Carolina and New Hamp-  
 shire was extracted, PCR performed, and  
 between one and three gene regions sequenced  
 (*rpb1*, *rpb2*, nLSU-rRNA) following protocols  
 outlined in Matheny (2005). Sequencing was  
 done on an ABI Prism 3100 DNA Sequencer.

Sequence alignment, dataset editing, and  
 phylogenetic analyses were performed using  
 MacClade (Maddison & Maddison, 2000),  
 PAUP\* (Swofford, 2003), MrBayes 3.1.2 (Ron-  
 quist & Huelsenbeck, 2003), and GARLI  
 v0.951 (Zwickl, 2006) on a dataset of 60 taxa  
 and 3434 characters available online at [http://](http://www.treebase.org/treebase/index.html)  
[www.treebase.org/treebase/index.html](http://www.treebase.org/treebase/index.html), or by re-  
 quest from the lead author (S2190, M4150).  
 Preliminary BLAST searches of *rpb1*, *rpb2*, and  
 nLSU-rRNA gene sequences of *I. tubarioides* at  
 the NCBI database indicated a close affiliation  
 with the “Inocybe clade” of Matheny (2005).  
 Thus, the 84-taxon dataset of Matheny (2005)  
 was pruned to taxa of the “Inocybe clade” using  
*I. calamistrata* and *I. rimosa* for rooting  
 purposes. Newly published sequences (EU  
 307819–23, EU307828–33, EU307835–  
 36, EU307843–47, AY732209, EF561633,  
 EU307857–58, EU307814–16, and EU43  
 3887–89; Kropp et al., unpublished) of the  
 following species were also included in the  
 dataset with collection numbers and herbaria in  
 parentheses: *I. albodisca* Peck (PBM 1390,  
 WTU), *I. fraudans* (JFA11831, WTU), *I. fuligi-*  
*neoatra* Huijsman (PBM 2662, TENN), *I.*  
*hirtella* Bres. (PBM 2650, TENN), *I. intricata*  
 Peck (PBM 2600, TENN), *I. paludinella* (Peck)  
 Sacc. (PBM 2552, TENN), *I. rimosa* (Bull.: Fr.)  
 P. Kumm. (PBM 2574, TENN), *I. subexilis* Peck  
 (PBM 2620, TENN), *I. luteifolia* A. H. Sm.

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160 (PBM 2642, TENN), and *I. griseolilacina* J. E.  
 161 Lange (PBM 2661, TENN). *Inocybe* “*praecox*”  
 162 is a provisional name applied to what had been  
 163 referred to as *I. abietis* Kühner in Matheny et al.  
 164 (2002) and Matheny (2005) (Kropp et al.,  
 165 unpublished). Five sequences of *I. tubarioides*  
 166 have been deposited at NCBI (AY732210,  
 167 AY732211, EU307854, EU307855,  
 168 EU307856).

169 Bayesian analysis was performed after  
 170 partitioning the dataset into eight partitions:  
 171 nLSU-rRNA; *rpb1*-intron2 and intron3; and  
 172 first, second, and third codon positions of  
 173 coding regions of *rpb1* and *rpb2*. Two inde-  
 174 pendent MCMC analyses were run for five  
 175 million generations saving trees every 500  
 176 generations under a GTR model of evolution  
 177 plus rate-heterogeneity parameters—a propor-  
 178 tion of invariant sites (I), and a gamma-  
 179 distributed rate parameter ( $\Gamma$ )—for each  
 180 partition. Trees sampled from the MCMC  
 181 posterior distribution were assessed by a  
 182 convergence diagnostic (average standard  
 183 deviation of split frequencies <0.01). Trees  
 184 that passed this diagnostic from the inde-  
 185 pendent runs were pooled together and used  
 186 to generate a 50% majority-rule consensus  
 187 tree with branch lengths. Nodes that were  
 188 recovered more than 95% of the time were  
 189 considered to have a significant posterior  
 190 probability (PP).

191 One hundred non-parametric bootstrap  
 192 replicates were also performed under the  
 193 Maximum Likelihood (ML) criterion using  
 194 GARLI. Default parameters were used ex-  
 195 cept that bootstrap replicates were limited to  
 196 5000 generations per replicate. Multiple boot-  
 197 strap analyses were done to affirm consistency  
 198 of results. A GTR model of substitution was  
 199 used allowing GARLI to estimate base fre-  
 200 quencies and rate heterogeneity parameters. A  
 201 bootstrap proportion greater than 70% was  
 202 considered significant.

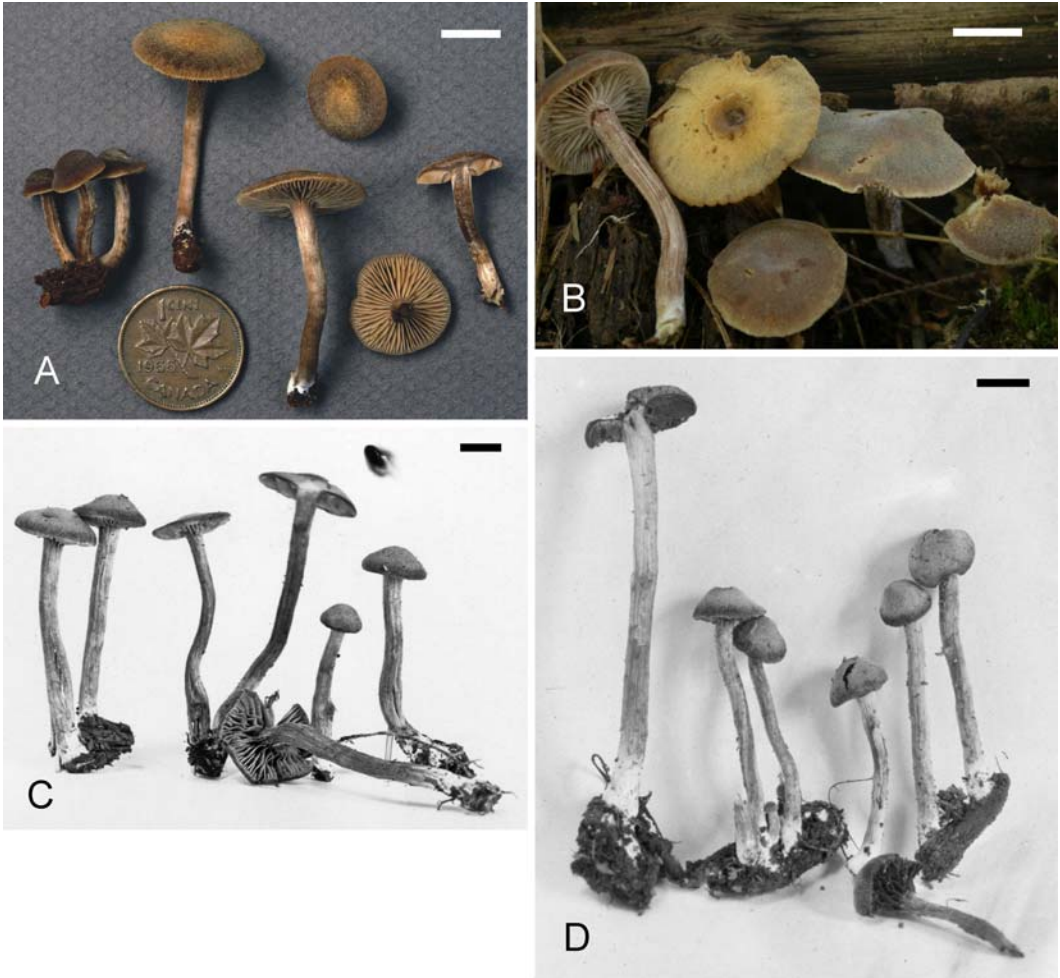
203

### Taxonomy

204 ***Inocybe tubarioides*** G. F. Atk., Am. J. Bot.  
 205 5: 217. 1918. Type: United States. New  
 206 York, near Ithaca, McGowan's Woods,  
 207 17 July 1903, leg. C. H. Kauffman,  
 208 CUP-A-015238 (holotype: CUP; isotype:  
 209 WTU). (Figs. 1, 2)

210 Pileus 8–25 mm broad, conico-convex to  
 211 convex or convex with a flattened center, umbo  
 212 absent, margin deeply decurved to decurved, not  
 213 appendiculate; surface dry, woolly-furfuraceous  
 214 in appearance, under a magnification lens  
 215 matted tomentose-fibrillose with fibrils often  
 216 forming small appressed scales, not at all rimose  
 217 or striate, strongly hygrophanous; color when  
 218 fresh chestnut brown (10YR 3/3) or dark brown  
 219 or grayish olivaceous, fading to yellowish  
 220 brown (10YR 5/6) and eventually brownish  
 221 yellow (10YR 6/6) or pale brown (10YR 6/3), in  
 222 faded condition the extreme margin may retain a  
 223 dark brown color (as in Fig. 1); context not  
 224 fragile, up to 1.5 mm thick, color dingy pale  
 225 brown to whitish, unchanging (or somewhat  
 226 brunnescent in PBM 2550), odor mild or not  
 227 distinctive, not spermatic, taste mild; flesh  
 228 imparting no reaction after application of  
 229 PDAB, no immediate reaction with guaiac.  
 230 Lamellae moderately close with two to three  
 231 tiers of lamellulae present, adnate to subdecur-  
 232 rent or uncinat, seceding in age with decurrent  
 233 tooth, up to 4 mm broad, grayish ochraceous to  
 234 brown (10YR 5/3) or brown with grayish tint,  
 235 edges pallid-fimbriate but not distinctly so,  
 236 edges becoming brown upon drying. Stipe 12–  
 237 40×2–4 mm at the apex, terete or slightly  
 238 compressed, slightly swollen or tapered towards  
 239 the white mycelioid base, base never bulbous,  
 240 pruinose at the extreme apex only, elsewhere  
 241 silky-fibrillose to fibrillose, cortina not observed  
 242 but presumably fugacious due to lack of  
 243 caulocystidia below the stipe center, excoriate  
 244 below in age; color light yellowish brown to  
 245 yellowish brown (10YR 6/4–5/4) or very pale  
 246 brown (10YR 7/3) mixed with brown streaks  
 247 (10YR 5/3); context solid or stuffed, whitish.

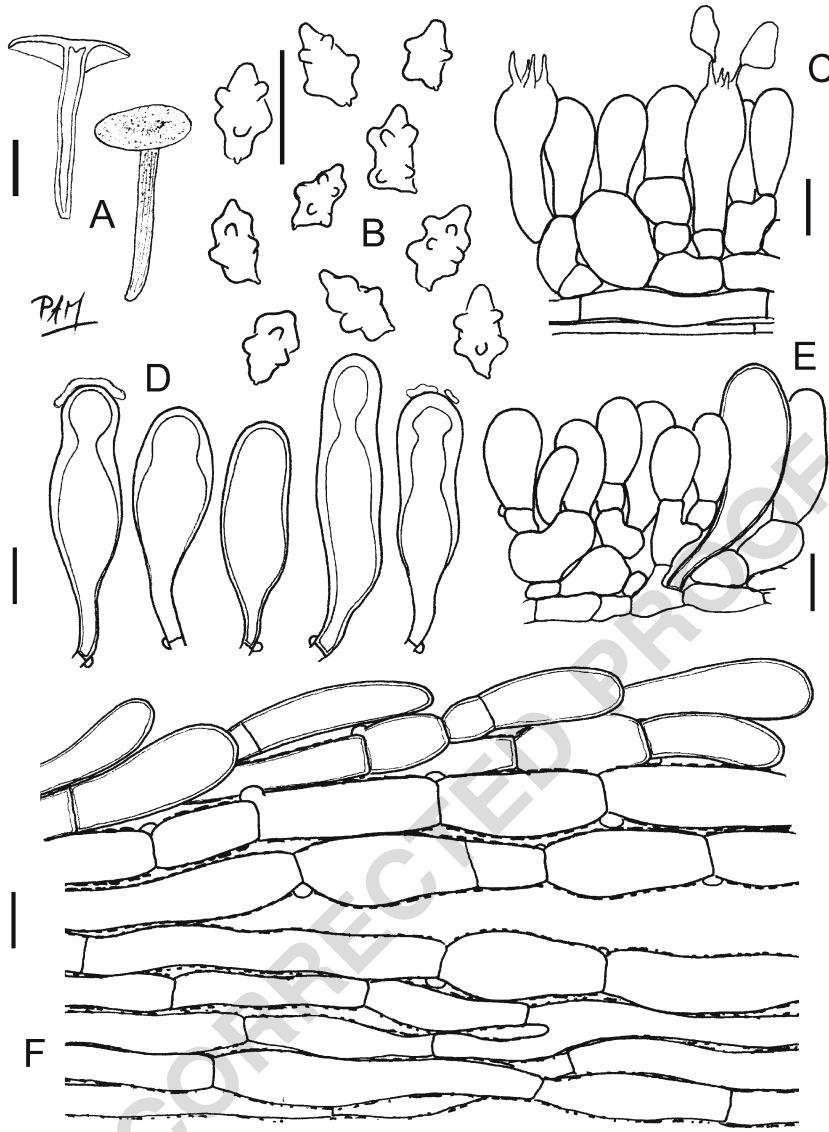
248 Spores 6.5–8 (–9) × 4.5–6  $\mu\text{m}$ , av. 7.3 ×  
 249 5.2  $\mu\text{m}$  [85 spores/6 collections], gibbous with  
 250 mostly 7–9 moderately to small-sized nodules  
 251 about a polygonal or irregularly triangular  
 252 outline, often with an apical nodule, occasion-  
 253 ally trapeziform in profile, rarely cruciform;  
 254 yellowish brown to brownish yellow, apiculus  
 255 small and inconspicuous. Basidia 20–30 × 7–  
 256 9.5  $\mu\text{m}$ , 4-sterigmate, clavate to clavate-capi-  
 257 tate, hyaline; subhymenium well-developed,  
 258 12–15  $\mu\text{m}$  thick, irregularly cellular. Pleuro-  
 259 cystidia 38–68 × 11–18  $\mu\text{m}$ , infrequently ob-  
 260 served, mostly utriform with a slender basal  
 261 pedicel, slightly thick-walled apically, 1–3  $\mu\text{m}$   
 262 thick, thin-walled elsewhere, apices incrustated



**FIG. 1.** *Inocybe tubarioides*. **A.** From Quebec (Lamoureux 1984, CMMTL), copyright Cercle des mycologues de Montréal—Yves Lamoureux, reproduced with permission. **B.** In situ from Massachusetts (PAM USA06–49, LIP). **C.** Paratype (No. 15294, CUP), reproduced with permission. **D.** Holotype (No. 15238, CUP), reproduced with permission. Scale bars = 1 cm.

263 or more often bare or covered with mucilagi- 277  
 264 nous secretions, hyaline but occasionally ochra- 278  
 265 ceous or bright yellow in 5% KOH; two distinct 279  
 266 types: (i) those with colorless, thin-wall, and 280  
 267 without apical incrustations; (ii) those with 281  
 268 yellow, distinctly thickened wall at the apex, 282  
 269 at times mucoid or faintly crystallized, and 283  
 270 longer in size; apical deposits metachromatic in 284  
 271 cresyl blue. Cheilocystidia similar to pleuro- 285  
 272 cystidia type (i) but smaller in size, infrequent, 286  
 273 often thin-walled, mixed with saccate to short 287  
 274 clavate hyaline paracystidia, 11–18 × 6–13 μm. 288  
 275 Lamellar trama regular, brownish yellow or 289  
 276 pale brown in mass, hyphae cylindric to 290

inflated, at times with weak incrustations, up 277  
 to 20 μm diam., frequently septate. Stipitipellis 278  
 with caulocystidia similar to cheilocystidia 279  
 mixed with septate cauloparacystidia, multi- 280  
 septate cauloparacystidioid cells at times 281  
 observed near the center of the stipe, but 282  
 none above the stipe base, caulocystidia not 283  
 observed below extreme stipe apex. Pileipel- 284  
 lis a trichoderm, 50–60 μm broad, composed 285  
 of prostrate fascicles of catenulate cells 4– 286  
 13 μm diam., mostly incrustated with yellow- 287  
 ish pigment, often with secondary unclamped 288  
 septa, with numerous terminal elements 289  
 cylindric or attenuate at the apices, 14–45 × 290



**FIG. 2.** Gross morphological and anatomical features of *I. tubarioides*. **A.** Fruiting bodies (bar = 10 mm). **B.** Basidiospores. **C.** Basidia and subhymenium. **D.** Pleurocystidia. **E.** Cheilocystidia and paracystidia. **F.** Pileipellis (bar = 10 μm for all anatomical features). (From *PAM USA06-49*, LIP.)

291 5–9 μm, usually smooth; subterminal cells  
 292 often shortened or isodiametric; subpellis not  
 293 differentiated; tramal hyphae more or less  
 294 parallel with yellowish incrustated walls, laticiferous hyphae infrequent or not observed.  
 295 Clamps frequent.  
 296  
 297 *Distribution and ecology.*—Scattered singly  
 298 or in small clusters on rotten logs, woody  
 299 debris, or rotten trunk of *Pinus strobus*, type of

wood rot not determined; also reported under 300  
*Pinus* and *Rhododendron* (Smith & Helser, 301  
 1938) and in stands of mixed hardwoods 302  
 (Stuntz, 1954); in mixed conifer-hardwood 303  
 forests of *Fagus*, *Betula*, *Tsuga*, and *Picea*; or 304  
 mixed forest of *Quercus*, *Carya*, *Tsuga*, and 305  
*Pinus*; or in mixed forest of *Pinus* and *Quercus*; 306  
 or on soil in dry open aspen (*Populus*) woods. 307  
 Reported from New York, New Hampshire, 308

309 Massachusetts, Tennessee, North Carolina, and  
 310 Michigan in the United States, and Quebec in  
 311 Canada.

312 *Phenology*.—July to September.

313 *Etymology*.—Named *tubarioides* by Atkinson  
 314 (1918) due to resemblance to *Tubaria*  
 315 *furfuracea*.

316 **Additional specimens examined. CANADA. QUEBEC:**  
 317 Mascouche, approximately 25 km from Montreal, on  
 318 rotten wood in a mixed forest of *Tsuga canadensis*,  
 319 *Quercus rubra*, and *Fagus grandifolia*, 18 Aug 1993,  
 320 Lamoureux 1984 (“CMMTL”).

321 **UNITED STATES. MASSACHUSETTS:** Oak Hill,  
 322 Littleton, on a small rotten trunk of *Pinus strobus* in  
 323 mixed *P. strobus-Quercus rubra* forest on granite, 24 Jul  
 324 2006, leg. P.-A. Moreau, PAM USA06-49 (TENN, LIP).

325 **MICHIGAN:** Grapevine Point, University of Michigan  
 326 Biological Station, Douglas Lake, Cheboygan County, 19  
 327 Jul 1947, leg. M. Lange, Stz. 2882 (WTU, in two separate  
 328 boxed collections); Colonial Point, Burt Lake, 31 Jul  
 329 1947, on wood, leg. H. Imshaugh (TENN 018207);  
 330 Douglas Lake, 5 Jul 1949, Stz. 5084 (WTU); Ringwood,  
 331 near Ithaca, 4 Aug 1947, Stz. 3058 (WTU); Carp Creek,  
 332 near Douglas Lake, 27 Jul 1951, leg. A. H. Smith (DAOM  
 333 27949 n.v.); Topinabee, Burt Lake, caespitose on ground,  
 334 3 Jul 1953, leg. M. Barr, Stz. 7676 (WTU); University of  
 335 Michigan Biological Station, Douglas Lake, on log, 7 Jul  
 336 1953, leg. S. C. Hoare (DAOM 40103 n.v.); Burt Lake,  
 337 Colonial Point, Cheboygan County, 10 Aug 1957, Stz.  
 338 10137 (WTU); area near Rees’ Bog, Cheboygan County,  
 339 gregarious on sandy soil in dry open aspen (*Populus*)  
 340 woods, 5 Jul 1957, R. L. Shaffer 1389 (MICH 68327).

341 **NEW HAMPSHIRE:** Discovery Trail, Highway 126, White  
 342 Mountains National Forest, in mixed forest of *Fagus*,  
 343 *Betula*, *Tsuga*, *Picea*, 8 Aug 2004, PBM 2570 (TENN).

344 **NEW YORK:** McGowan’s woods, near Ithaca, on rotten  
 345 wood, 17 Jul 1903, leg. C. H. Kauffman, CUP-  
 346 A-015238 (HOLOTYPE, CUP-A; ISOTYPE, WTU);  
 347 CUP-A-015294 (PARATYPE, CUP and MICH 68336);  
 348 CUP-A-018350 (PARATYPE, CUP).

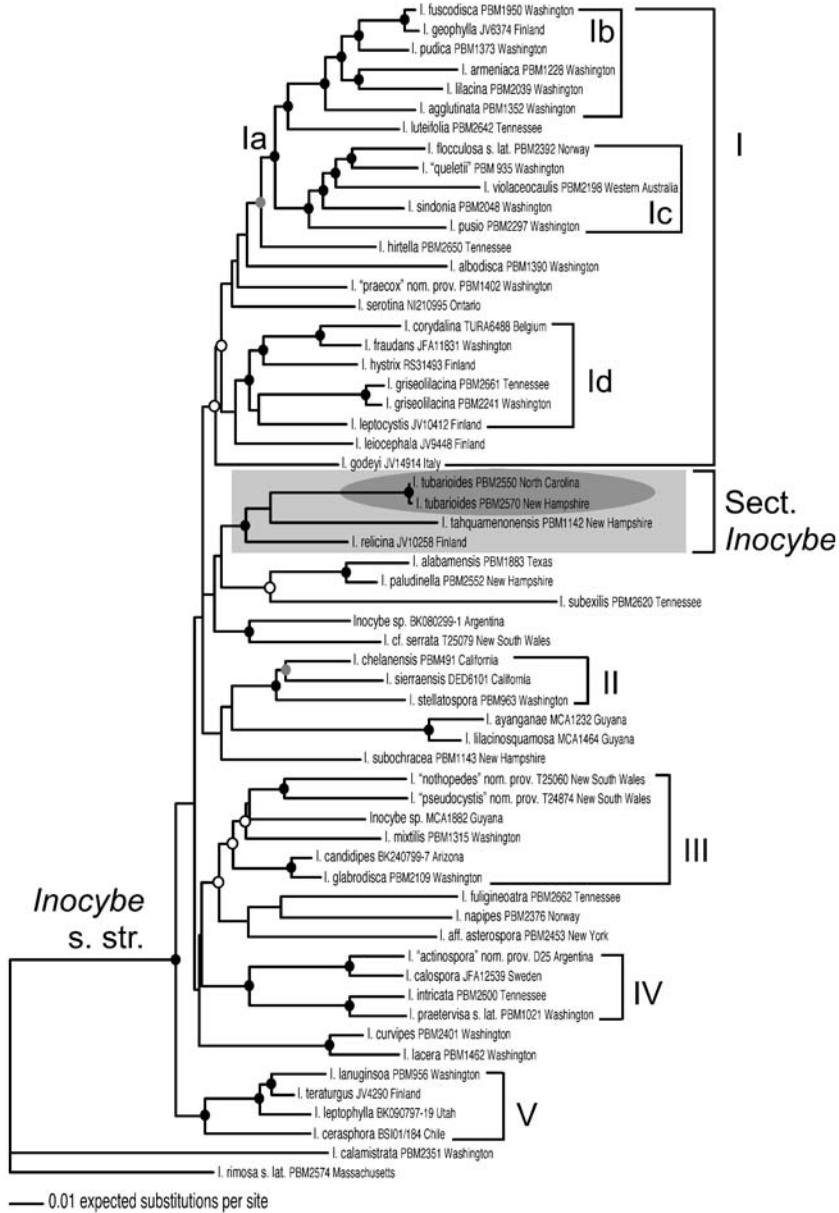
349 **NORTH CAROLINA:** Pisgah National Forest, western North Carolina, Myco-  
 350 logical Society of America Foray, on ground with woody  
 351 debris in mixed forest of *Quercus*, *Carya*, *Tsuga*, *Pinus*, 17  
 352 Jul 2004, leg. M. Padamsee, PBM 2550 (TENN, F);  
 353 Highlands, under *Pinus*, 10 Sep 1937, L.R. Hesler & A. H.  
 354 Smith 7528 (TENN, n.v., MICH 68337); Flat Creek, Great  
 355 Smoky Mountains National Park, on decayed wood, 27  
 356 Aug 1938, A. H. Smith 10597 (MICH 68338).

357 **TENNESSEE:** Cades Cove Loop Road, Great Smoky Mountains National  
 358 Park, in mixed forest of *Fagus*, *Quercus*, *Carya*, *Juglans*,  
 359 *Pinus*, *Tsuga*, 18 Aug 2005, leg. E. B. Lickey, TENN 061324  
 360 (=TFB12757) ITS sequence: EU439453 (TENN); Grassy  
 361 Patch, Great Smoky Mountains National Park, scattered  
 362 under *Pinus* and *Rhododendron*, 3 Sep 1937, L. R. Hesler &  
 363 A. H. Smith 7355 (TENN, n.v.); same locality as above, on  
 364 decayed logs, A. H. Smith 9825 (MICH 68333); same  
 365 locality as above, on wood under *Rhododendron*, 22 Aug  
 366 1938, A. H. Smith 10407 (MICH 68330); same locality as  
 367 above, on debris, 22 Aug 1938, A. H. Smith 10414 (MICH  
 368 68334); same locality as above, on humus, 26 Aug 1938,  
 369 A. H. Smith 10546 (MICH 68329); same locality as above,

on wood under *Rhododendron*, A. H. Smith 10632 (MICH 68328); Husky Gap Trail, Great Smoky Mountains National Park, on debris, 14 Aug 1938, A. H. Smith 9713 (MICH 68331); Indian Camp Creek, Great Smoky Mountains National Park, on wood, 30 Aug 1938, A. H. Smith 10650 (MICH 68332).

*Inocybe tubarioides* exhibits a combination of characters unusual in the genus *Inocybe*, namely, the lignicolous habit and strongly hygrophanous pileus. A few other species of *Inocybe* typically occur on rotten wood, e.g., *I. lanuginosa* (Bull.:Fr.) P. Kumm., but their outward appearance is typical for the genus. In our estimation, a generic determination is not possible without microscopic examination, if one is not already familiar with the species. Some specimens retain their hygrophanous nature after drying, and all herbarium specimens consistently appear on wood or woody debris with the exception of Stz. 7676 and R.L. Shaffer 1389, which were recorded on soil from Michigan.

Despite these peculiar traits, Bayesian and ML phylogenetic analyses of *rpb1*, *rpb2*, and nLSU-rRNA genes unequivocally place *I. tubarioides* in *Inocybe* s. str. or the “*Inocybe* clade” (Fig. 3) where it is nested with two other species, *I. relicina* (Moser, 1978; type of *Inocybe*) and *I. tahquamenonensis* (Stuntz, 1954; Matheny & Kropp, 2001). This cluster of three species receives significant ML bootstrap support (76%) and a significant posterior probability (1.0). Posterior probability values were calculated from 5386 trees sampled from the posterior distribution. We refer to this clade as sect. *Inocybe*. All three species share the possession of nodulose basidiospores ( $\pm$  cruciform in *I. relicina* and *I. tahquamenonensis*, rarely so in *I. tubarioides*), but no other unique morphological and ecological characters suggest any common ancestry. *Inocybe relicina* is a *Picea*-associate fruiting in *Sphagnum* bogs and endemic to regions of Fennoscandia. Morphologically, *I. relicina* is scaly, dark umber in color, and has yellow lamellae when young. *Inocybe tahquamenonensis* is a putative hardwood associate restricted to deciduous forests in eastern North America and is scaly throughout, but is chiefly characterized by its fuscous-purple colors and vinaceous lamellae. *Inocybe tubarioides* lacks pronounced squamules and conspicuous yellow or vinaceous pigments, but Smith and



**FIG. 3.** Phylogram of tree with the highest ML score (ln L -35616.863) from a Bayesian analysis of 58 exemplars of *Inocybe* s. str. or the "Inocybe clade", including *I. tubarioides*, plus two outgroups. Black-filled circles indicate nodes that receive both significant PP and ML bootstrap values; gray-filled circles indicate nodes that receive a significant ML bootstrap value only; empty circles indicate nodes with a significant PP only. Clade designations follow Matheny (2005).

423 Hesler (1938) noted that the color of young  
424 lamellae could be pallid vinaceous brown.

425 Singer (1986) diagnosed members of sect.  
426 *Inocybe* as species bearing a cortina (partial  
427 veil); a brown stipe that is often fibrillose,

woolly, or scaly, and not pruinose the entire  
length; stipe base not marginately bulbous;  
caulocystidia absent from the center of the  
stipe and below; smell inodorous or incon-  
spicuous; and with well-developed pleurocys-

428  
429  
430  
431  
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433 tidia lacking strongly thickened walls. Singer  
 434 then divided sect. *Inocybe* into two “stirps” or  
 435 groups: “Umbrina” and “Lanuginosa”. *Inocybe*  
 436 *relicina* was designated in stirps “Lanuginosa”,  
 437 along with *I. longicystis* G. F. Atk. (a synonym  
 438 of *I. stellatospora* (Peck) Masee: Matheny &  
 439 Kropp, 2001), *I. cerasphora* Sing., and *I.*  
 440 *ovatocystis* Boursier & Kühn., the latter now  
 441 representing *I. lanuginosa* (Bull.: Fr.) P. Kumm.  
 442 (see epitypification in Matheny & Kropp,  
 443 2001). As Fig. 3 illustrates, Singer’s stirps  
 444 “Lanuginosa” is polyphyletic with species  
 445 clustering in clades II, V, and what we designate  
 446 as sect. *Inocybe*. At least two additional species  
 447 may belong to sect. *Inocybe* based on morpho-  
 448 logical descriptions very similar to *I. tahqua-*  
 449 *menonensis*: *I. magnifica* (E. Horak) Garrido, a  
 450 *Nothofagus* associate from Papua New Guinea  
 451 (Horak, 1979), and *I. leptoderma* Takah.  
 452 Kobay. & Nukada, probably a *Fagus* associate  
 453 from Japan (Kobayashi, 2002). Like *I. tahqua-*  
 454 *menonensis*, both species share red colored  
 455 context, some spores that are ± cruciform in  
 456 outline, dark overall coloration, and squamu-  
 457 lose pileus and stipe.

458 In total we are aware of 29 collections of *I.*  
 459 *tubarioides*, all from eastern North America.  
 460 27 collections are cited here, but two addi-  
 461 tional Michigan materials (*No.* 82784 and  
 462 82773) collected by Rolf Singer in 1953 are  
 463 stored at the Field Museum. *Inocybe tubar-*  
 464 *ioides* has not been recorded since 1957. Here  
 465 we report the species for the first time from  
 466 the New England states New Hampshire and  
 467 Massachusetts and from Canada in Quebec.  
 468 *Inocybe tubarioides* is also recorded from the  
 469 southern Appalachian Mountains of North  
 470 Carolina and Tennessee (Smith & Hesler,  
 471 1938), New York (Atkinson, 1918), and  
 472 Michigan (Stuntz, 1954). Thus, since 1957 *I.*  
 473 *tubarioides* has been collected and preserved  
 474 in herbaria by only five additional collections.

475 Although endemism has been suggested to  
 476 be low in *Inocybe* (Kuyper, 1986), all three  
 477 confirmed members of sect. *Inocybe* appear to  
 478 be short or narrow range endemics and  
 479 documented from relatively few herbarium  
 480 collections (Moser, 1978; Matheny & Kropp,  
 481 2001). Both *I. tubarioides* and *I. tahquame-*  
 482 *nonensis* appear to be sympatric in their  
 483 distribution in eastern North America. We  
 484 predict that habitats that harbor these fungi  
 485 may exhibit attributes (age, abiotic soil

486 factors, elevation, latitude, composition of  
 487 plant community) that are localized, unusual  
 488 in combination, and infrequent, hence the rare  
 489 status of these fungi. We also suggest that due  
 490 to their rare status, these fungi are potentially  
 491 threatened and may be indicators of habitats  
 492 that are of high conservation value. Several  
 493 biases, however, may influence our under-  
 494 standing of the geographic distribution of *I.*  
 495 *tubarioides*: the species may be easily over-  
 496 looked, misidentified, or undetermined to  
 497 genus due to a combination of features not  
 498 typical for the genus *Inocybe* in general.

499 Two collections at NY are mislabeled *I.*  
 500 *tubarioides*: one (*No.* 673235, NY) from the  
 501 Chiricahua Mountains in Arizona from 1998  
 502 exhibits a “fine silky ± rimose” pileus, has  
 503 soil, not wood, at the base of the stipe, and  
 504 the determination (by R. Fatto) is admittedly  
 505 speculative. Examination of this material  
 506 (*Fatto* 1097) shows spores similar to *I.*  
 507 *curvipes* P. Karst.; the second (*Murrill* 209)  
 508 from New York, a split of which is located at  
 509 MICH (68335) was labeled “*I. tubarioides*”  
 510 by C. H. Kauffman “in all probability”, but  
 511 the stipes are caulocystiditate below the  
 512 center, and the spores are of the *petiginosa-*  
 513 *type*. We believe this material better repre-  
 514 sents *I. subexilis* (Peck) Sacc.

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