



Taxonomy and phylogeny of European *Gymnopus* subsection *Levipedes* (Basidiomycota, *Omphalotaceae*)

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Key words

ITS
neotype
nomenclature
translation elongation factor 1-alpha

Abstract The systematic integrity of European *Gymnopus* subsect. *Levipedes* is verified based on anatomic-morphological characters with support from DNA sequences of ITS and translation elongation factor 1-alpha genes. Seven species (*G. alpinus*, *G. aquosus*, *G. dryophilus* – including var. *lanipes*, *G. erythropus*, *G. fagiphilus*, *G. hybridus*, and *G. ocior*) belonging to this subsection are included. We clarify the concepts of *G. dryophilus* and *G. ocior*, which were occasionally confused in older literature. Due to unavailability of previously selected neotype of *G. dryophilus* the substitute neotype specimen is selected. *Gymnopus dryophilus* var. *lanipes* is confirmed as a variety; no important differences from nominotypical variability were detected. All discriminative characters used for identification of these species are discussed in detail. An identification key is also provided.

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INTRODUCTION

Gymnopus is a large agaricoid genus distributed world-wide circumscribing c. 300 species (Kirk et al. 2008). It is characterized in basidiocarps collybioid, rarely tricholomatoid or marasmioid with a pileus convex, plano-convex to applanate or slightly concave, dry or slightly viscid, glabrous or innately radially fibrillose, lamellae free, emarginate or adnate, crowded to sometimes fairly distant, a stipe central, non-insititious or insititious, and a spore print white. Basidiospores are ellipsoid to oblong, rarely subglobose to globose or lacrimoid, thin-walled, hyaline, non-amyloid; cheilocystidia often present, cylindrical, flexuous, clavate or irregularly coralloid; pleurocystidia usually absent or in some species well-developed (e.g., *G. lodgeae* (Singer) J.L. Mata, *G. omphalodes* (Berk.) Halling & J.L. Mata, *G. pseudologeae* J.L. Mata; Mata et al. 2004, 2006, Mata & Ovrebo 2009); a pileipellis in the form of a cutis or ixocutis of radially arranged cylindrical hyphae, or interwoven, made up of irregular coralloid terminal elements (Dryophila-structure); hyphae never amyloid or dextrinoid (except for sect. *Androsacei* with dextrinoid context hyphae, at least in stipe apex), and clamp connections mostly present.

Gymnopus sect. *Levipedes* subsect. *Levipedes* (type species: *Gymnopus dryophilus*) is characterized in having a pileipellis composed of cells inflated, lobed or coralloid (a Dryophila-type cutis), well-developed cheilocystidia, a smooth stipe, and hyphae only rarely becoming green in alkali or not (Antonín & Noordeloos 2010).

In Europe, seven species occur: *G. alpinus*, *G. aquosus*, *G. dryophilus* (with var. *lanipes*), *G. erythropus*, *G. fagiphilus*, *G. hybridus*, and *G. ocior*. The DNA-based phylogenetic relations among these species are insufficiently known. Mata et al. (2006) included several species of this subsection from various continents (some of them also from Europe), but in their comprehensive analysis did not cover all European taxa of

subsect. *Levipedes*. Moreover, our preliminary results were in disagreement with some of their interpretation of *G. ocior* and its placement in the ITS phylogram. Therefore, the aim of this paper is a phylogenetic and taxonomic revision of all European taxa of this subsection.

MATERIAL AND METHODS

Morphological dataset

The specimens studied, especially of the *G. dryophilus* complex, were selected from various regions of Europe. The macroscopic descriptions are based on fresh basidiocarps, if available, were made by the collectors. Microscopic features were studied under Olympus BX 50 light microscope from dried material mounted in H₂O, 5 % KOH solution, Melzer's reagent and Congo Red. Microscopic characters were studied with emphasis on the most important morphological features for taxon delimitation – shape and dimensions of basidiospores, pileipellis structure and shape and dimensions of cheilocystidia. For basidiospores, the factors E (quotient of length and width in any one spore) and Q (mean of E-values) are used. In each herbarium collection, 20 basidiospores were measured. Authors of fungal names are cited according to the International Plant Names Index Authors website (<http://www.ipni.org/ipni/authorsearchpage.do>); colour abbreviations are according to Kornerup & Wanscher (1983), and for herbarium acronyms see Thiers (2012; accessed 10 Sept. 2012).

Molecular dataset

DNA extraction and PCR

The DNA was extracted from dried herbarium specimens. The specimens selected for DNA extraction and PCR are listed in Table 1. The two loci: ITS region of ribosomal RNA gene (ITS) and partial sequence of translation elongation factor 1-alpha gene (*tefa*) – were selected for the analysis. The DNA extraction and PCR of ITS was applied according to Tomšovský et al. (2010). For the amplification of *tefa*, the primer pair 983F/2218R was used (Rehner & Buckley 2005). PCR for the *tefa* locus was

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Table 1 The specimens sequenced by the authors.

Species	Country	Herbarium	Nr.	ITS	tefa
<i>G. alpinus</i>	Latvia	CB 16251	G69	JX536168	JX536191
<i>G. aquosus</i>	Czech Republic	BRNM 665362	G3	JX536172	JX536192
	Czech Republic	BRNM 695556	G6	JX536173	JX536193
	Czech Republic	BRNM 710027	G30	JX536170	JX536194
	Czech Republic	BRNM 670755	G36	JX536171	
	Czech Republic	BRNM 691431	G37	JX536174	
	Sweden	DUKE 193432	G63	JX536169	
<i>G. confluens</i>	Czech Republic	BRNM 734005	G60	JX536124	JX536178
<i>G. dryophilus</i>	Slovakia	BRA 13021	G1	JX536140	JX536195
	Czech Republic	BRNM 695586	G4	JX536143	JX536196
	Czech Republic	BRNM 691279	G5	JX536145	
	Slovenia	BRNM 695317	G8	JX536146	JX536197
	Switzerland	BRNM 693554	G9	JX536147	JX536198
	Slovakia	BRNM 670778	G10	JX536141	JX536199
	Czech Republic	BRNM 704894	G11	JX536156	JX536203
	Italy	BRNM 707149	G12	JX536157	JX536204
	Czech Republic	BRNM 712600	G31	JX536158	JX536206
	Slovakia	BRNM 642393	G34	JX536142	
	Czech Republic	BRNM 691282	G38	JX536138	
	Czech Republic	BRNM 695739	G42	JX536144	
	Czech Republic	BRNM 705601	G43	JX536155	
	Czech Republic	BRNM 732938	G99	JX536149	JX536202
	Czech Republic	BRNM 734758	G98	JX536148	JX536201
	Norway	BRNM 737692	G44	JX536154	
	Germany	BRNM 737691	G61	JX536139	JX536200
	Sweden	DUKE 193401	G64	JX536159	
	Sweden	DUKE 193429	G65	JX536150	
	Sweden	DUKE 193405	G66	JX536151	
	Sweden	DUKE 193406	G67	JX536152	
<i>G. dryophilus</i> (neotype)	Sweden	DUKE 193411	G68	JX536153	
<i>G. dryophilus</i> var. <i>lanipes</i> (isoneotype)	Spain	BRNM 670686	G13	JX536137	JX536205
<i>G. erythropus</i>	Czech Republic	BRNM 714784	G2	JX536136	JX536183
	Czech Republic	BRNM 705224	G14	JX536131	JX536180
	Slovakia	BRNM 706885	G15	JX536134	JX536182
	Switzerland	BRNM 693553	G18	JX536135	JX536181
	Czech Republic	BRNM 666730	G39	JX536132	
	Czech Republic	BRNM 664995	G40	JX536133	
<i>G. fagiphilus</i>	Czech Republic	BRNM 707079	G19	JX536129	JX536209
	Czech Republic	BRNM 712422	G22	JX536125	JX536210
	Czech Republic	BRNM 707068	G23	JX536130	JX536211
	Czech Republic	BRNM 712407	G24	JX536126	JX536212
	Czech Republic	BRNM 691489	G27	JX536128	JX536213
	Slovakia	BRNM 695747	G41	JX536127	
<i>G. hybridus</i>	Italy	BRNM 695773	G26	JX536177	JX536208
	Czech Republic	Dvořák 393/07, BRNU	G58	JX536176	JX536207
	Czech Republic	Dvořák 138/02, BRNU	G59	JX536175	
<i>G. inusitatus</i> (holotype)	Spain	SCM B-4058	G57	JN247553	
<i>G. inusitatus</i> (holotype of <i>G. bisporus</i>)	Spain	SCM B-4065	G55	JN247551	
<i>G. inusitatus</i> (holotype of <i>G. catalanicus</i>)	Spain	SCM B-4057	G56	JN247552	
<i>G. inusitatus</i> var. <i>cystidiatus</i> (holotype)	Hungary	BRNM 737257	G45	JN247550	JX536179
<i>G. ocior</i>	Czech Republic	BRNM 699795	G29	JX536166	JX536188
	Slovakia	BRNM 728565	G1n	JX536160	JX536184
	Czech Republic	BRNM 728586	G2n	JX536165	JX536185
	Czech Republic	BRNM 728539	G3n	JX536167	JX536186
	Czech Republic	BRNM 728540	G4n	JX536161	JX536187
	Norway	BRNM 737697	G46	JX536162	JX536189
	Norway	BRNM 737695	G47	JX536163	JX536190
	Norway	BRNM 737693	G48	JX536164	

performed using a following touchdown PCR procedure: The amplifications were initiated with a 2 min denaturation at 94 °C. The annealing temperature in the first amplification cycle was 60 °C, which was subsequently incrementally reduced by 1 °C per cycle over the next 9 cycles. An additional 35 amplification cycles were then performed, each consisting of 30 s denaturation at 94 °C, a 30 s annealing step at 50 °C, and a 1 min extension at 72 °C, concluding with a 10 min incubation at 72 °C. In case of unsuccessful amplification of tefa gene, the nested PCR of this gene region was performed according to Tomšovský et al. (2010).

Phylogenetic analysis

The newly obtained sequences were augmented by those published by Lutzoni et al. (2004), Mata et al. (2006), and An-

tonín et al. (2012). Sequences of each individual locus were aligned using the MAFFT version 6 with selected Q-INS-i option algorithm (Kato & Toh 2010). The sequences of *Gymnopus confluens* were selected as an outgroup.

The two separate phylogenetic analyses were performed – the first one including a two-gene dataset of both genetic markers (ITS and tefa) and the second one of newly obtained ITS data alone complemented with the respective sequences from GenBank (mostly published by Mata et al. 2006).

To determine whether the datasets of the different genetic markers (ITS and tefa) were in significant conflict, two methods were applied. The partition homogeneity test in PAUP* 4.0b10 (Swofford 2003) was used between the markers using 100 replicates and the heuristic general search option. The null hypothesis of congruence was rejected if $p < 0.01$. A test based on

maximum agreement subtrees (de Vienne et al. 2007) was further performed.

Phylogenies were generated in MrBayes version 3.2.1 (Ronquist & Huelsenbeck 2003). The substitution models were selected prior to analyses using the MrModeltest 2.3 (Nylander 2008). For ITS+tefa dataset the GTR + I + G (General time reversible model + Proportion of invariant + Gamma) while for the ITS dataset GTR + G (General time reversible model + Gamma) were chosen. Markov chains were initiated from a random tree and were run for 5 000 000 generations; samples were taken every 100th generation. The number of excluded generations determined as burn-in was used by Tracer 1.5 (Rambaut & Drummond 2009); burn-in = 500 000 in both analyses. The Bayesian branch supports were assigned as posterior probabilities (PP) on the consensus trees. In addition, bootstrap branch support values (BS) were estimated in PAUP 4.0b10 using 1 000 replicate datasets with the random addition of sequences during each heuristic search.

Additional, phylogenetic analyses were carried out in PHYML estimating maximum likelihood phylogenies and run at the server Phylogeny.fr (Dereeper et al. 2008) using 'A la Carte' mode. The alignments were treated with Gblock, eliminating poorly aligned positions and ambiguous regions, and GTR substitution model was selected for both ITS and LSU datasets. Bootstrap branch support values (BP) were estimated in PHYML 3.0 (Guindon et al. 2010) under the maximum likelihood criterion using default 100 replicates. The alignments and phylograms from the Bayesian analyses were deposited in Treebase (ID 13361).

RESULTS

We obtained 58 new sequences of ITS and 36 of tefa gene regions. A partition homogeneity test and a test of maximum agreement subtrees allowed us to combine the ITS and tefa data. The lengths of datasets, likelihood values and model parameters of Bayesian and Maximum likelihood of both datasets are summarized in Table 2.

The molecular data (Fig. 1, 2) confirmed sequence homogeneity of *G. alpinus*, *G. aquosus*, *G. dryophilus*, *G. erythropus*, *G. fagiphilus*, *G. hybridus*, and *G. ocior*. However, four sequences obtained from the Genbank (AY256691, DQ450003, DQ449976-7) formed two unsupported groups proximal to *G. ocior* or *G. aquosus* in the ITS phylogram. *Gymnopus dryophilus* var. *lanipes* (labelled G13 in the phylogenetical trees) fell unambiguously within other sequences of *G. dryophilus*. *Gymnopus hybridus* is closely related to *G. inusitatus* placed in sect. *Levipedes* subsect. *Alkalivirentes* Antonín & Noordel. This indicates the current concept of subsections in sect. *Levipedes*

(Antonín & Noordeloos 2010) may not follow phylogenetic relations of the species.

NOTES ON STUDIED TAXA

Gymnopus dryophilus complex

The recent identification of four European species of this complex is based on studies by Vilgalys & Miller (1987) and Vilgalys (1991), who distinguished four species based on anatomic-morphological studies and confirmed the distinctions using mating compatibility tests. The published key (Vilgalys & Miller 1987) relies on the pileus colour, presence of the basal stipe bulb, size of basidiospores and shape of cheilocystidia to distinguish species.

See Antonín & Noordeloos (2010) for monographic details on all taxa.

Gymnopus alpinus (Vilgalys & O.K. Mill.) Antonín & Noordel.

Specimen examined. LATVIA, Kemeru National Park, in a *Sphagnum* stand under *Pinus sylvestris* and *Betula pendula*, 23 Aug. 2006, M. Beran, CB 16251.

Notes — *Gymnopus alpinus* differs from other species of this complex by having a dark red-brown, only weakly hygrophanous pileus, 6.0–7.5 × 3.0–4.0 µm basidiospores, and 14–32 × 7.0–12 µm, clavate, simple, irregular to coralloid cheilocystidia. This species is a widespread but probably rare fungus with unknown distribution in Europe.

Gymnopus aquosus (Bull.: Fr.) Antonín & Noordel.

Specimens examined. CZECH REPUBLIC, White Carpathian Mts, Sidonie, Sidonie Nature Reserve, beech forest, under *Fagus sylvatica*, 14 May 2008, V. Antonín 08.07, BRNM 710027; Žďárské vrchy Mts, Cikháj, Žákova hora National Nature Reserve, in fallen leaves of *Acer pseudoplatanus* and *Acer pseudoplatanus* and *Fagus sylvatica*, 2 July 2004, A. Vágner, BRNM 691431; Útěchov near Brno, Obora forest, in fallen leaves of *Quercus* and *Tilia*, A. Vágner, BRNM 665362; Mokrá near Brno, Nad dlouhým (Sivický les) forest, under *Carpinus* and *Picea abies*, 21 May 2002, A. Vágner, BRNM 670755; Bílé Karpaty Mts, Suchov, Porážky Nature Reserve, 1 June 2005, A. Vágner, BRNM 695556. — SWEDEN, Uppsala, Stadsskogen, in moss, 16 June 1984, S. Ryman & R. Vilgalys RV 84/199, DUKE 193407; *ibid.*, 17 June 1984, S. Ryman & R. Vilgalys RV 84/200, DUKE 193408; *ibid.*, amongst herbaceous matter, 17 June 1984, S. Ryman & R. Vilgalys RV 84/197, DUKE 193432; *ibid.*, 17 June 1984, S. Ryman & R. Vilgalys RV 84/201, DUKE 193409; *ibid.*, in moss, 17 June 1984, S. Ryman & R. Vilgalys RV 84/205, DUKE 193412; *ibid.*, in moss, 17 June 1984, S. Ryman & R. Vilgalys RV 84/202, DUKE 193410.

Notes — *Gymnopus aquosus* is mainly characterized by having a hygrophanous, almost to the centre translucently striate, rather pale coloured, pale yellow to ochre pileus, pallescent

Table 2 The statistics of phylogenetic analyses are summarized. In Bayesian analyses, the mean values of two simultaneous runs are presented.

Dataset/analysis	ITS+tefa / Bayesian analysis (MrBayes)	ITS+tefa / Maximum likelihood (PHYML)	ITS / Bayesian analysis (MrBayes)	ITS / Maximum likelihood (PHYML)
Dataset length/bp	1294	1005	773	531
Variable positions	336	235	188	121
Singleton positions	171	140	109	67
Log-likelihood	-4169.583	-2942.619	-2581.831	-1592.603
Gamma shape parameter (alpha in Bayesian analysis)	0.914	0.555	0.09735	0.693
Proportion of invariant	0.368	0.382	N/A	N/A
f(A)	0.22600	0.23292	0.22900	0.22748
f(C)	0.21200	0.21714	0.17900	0.18814
f(G)	0.22300	0.23595	0.21400	0.21315
f(T)	0.33900	0.31399	0.37800	0.37123

Fig. 1 The phylogram inferred from the Bayesian analysis of combined dataset tef1 and ITS DNA sequences of *Gymnopus* spp. included in the study. Numbers at branches indicate Maximum likelihood, Bayesian bootstrap values and Bayesian posterior probabilities values higher than 50 %. The bar indicates the number of expected substitutions per position.

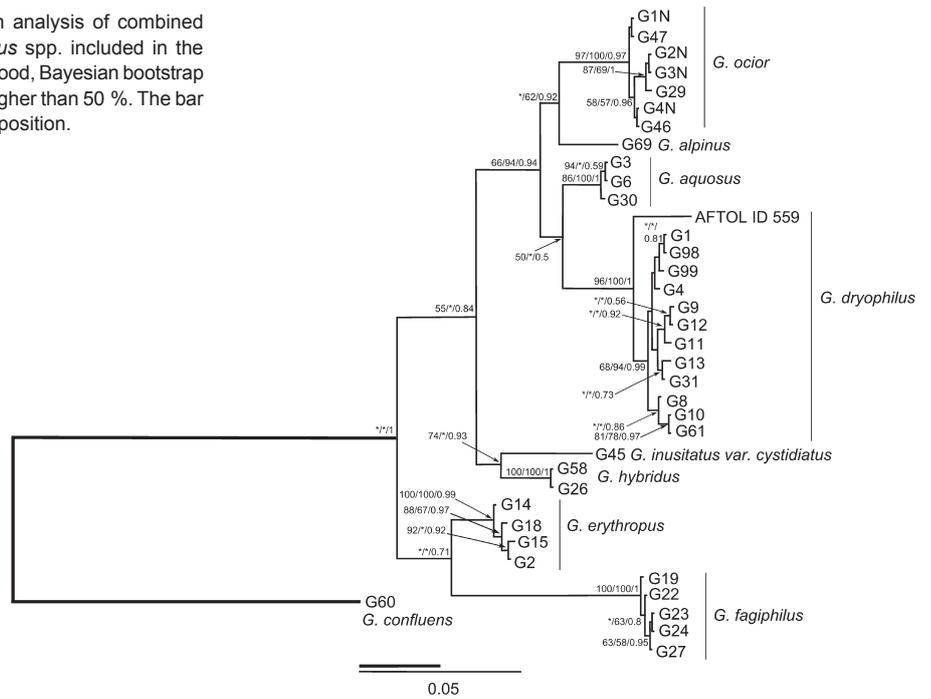
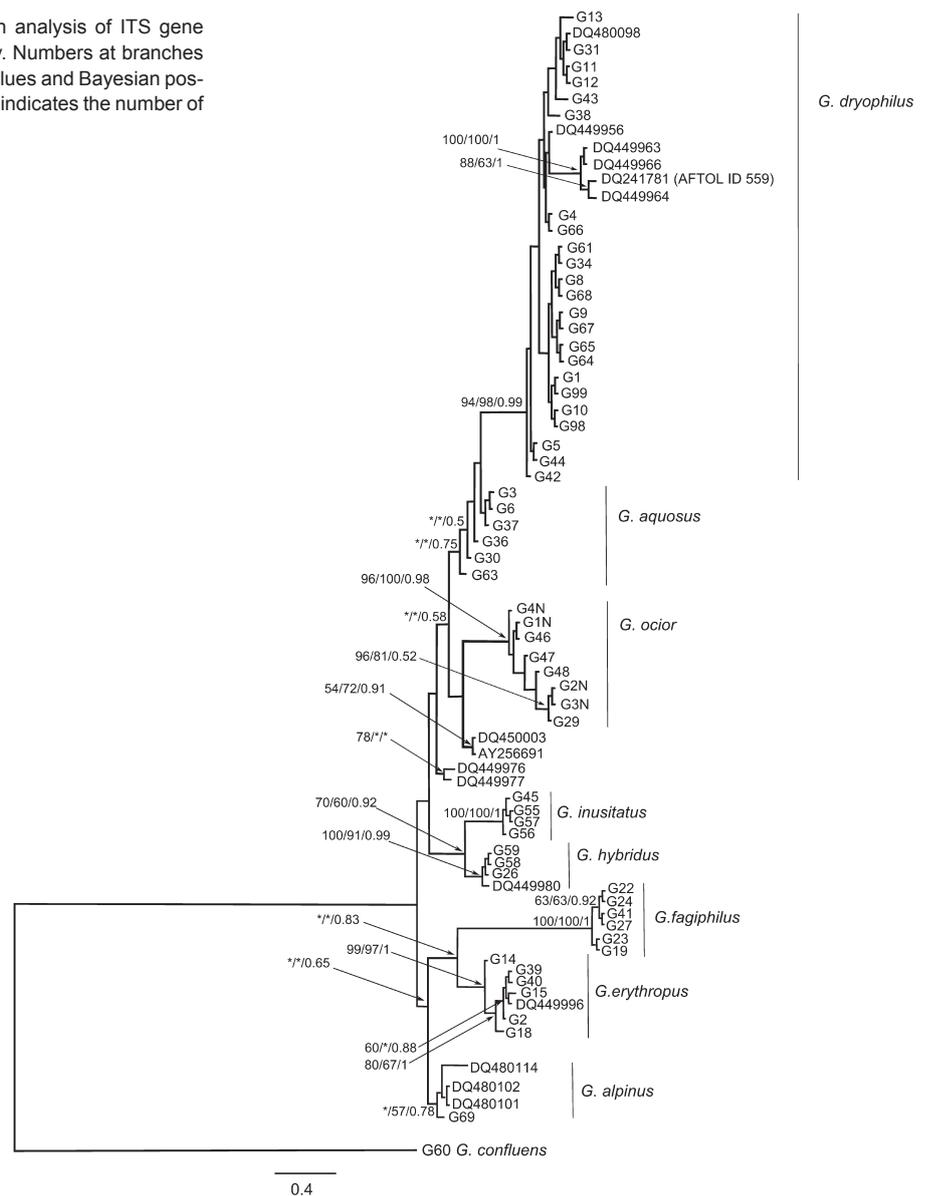


Fig. 2 The phylogram inferred from the Bayesian analysis of ITS gene sequences of *Gymnopus* spp. included in the study. Numbers at branches indicate Maximum likelihood, Bayesian bootstrap values and Bayesian posterior probabilities values higher than 50 %. The bar indicates the number of expected substitutions per position.



to almost white, a distinctly bulbous stipe base with pinkish-ochraceous rhizomorphs, $(5.0\text{--})5.5\text{--}7.0 \times 3.0\text{--}4.0\text{--}(4.25) \mu\text{m}$ basidiospores, and $16\text{--}51 \times (5.0\text{--})7.0\text{--}17 \mu\text{m}$, clavate, capitate and pedunculate, less frequently subcylindrical or fusoid, simple or coralloid cheilocystidia. It also appears very early in the season (from May, rarely late April). It grows in deciduous, rarely coniferous forests, but also among grass on road-sides in semi-open places, and is widespread all over Europe.

Gymnopus dryophilus (Bull.: Fr.) Murrill s.str.

Lectotypification. Bulliard, *Herbier de la France: Histoire des champignons de la France*, pl. 434 A, B, E, nad F (C and D excluded), 1789; designated here.

Bulliard kept a very broad concept of this species. Excluded pictures C and D show darker, brown to dark brown coloured fungi which may represent other taxa of this species complex (*G. ocior*, *G. alpinus*?).

Vilgalys & Miller (1987) proposed the collection from Sweden (Uppsala, Stadsskogen, R. Vilgalys 84/181) as the neotype. However, this neotype specimen was not traced in herbaria BPI, DUKE, VPI, and NY (relocated VPI herbarium) (Halling, Robertson & Vilgalys in litt.). Therefore, the other specimen from the original series of collections (made at the identical locality by the same collectors, and in the same time) was selected as the epitype: Sweden, Uppsala, Stadsskogen, 17 June 1984 leg. S. Ryman & R. Vilgalys 84/204 (DUKE 193411; designated here).

Nomenclature notes — The ITS sequences conspecific to *G. dryophilus* had been identified as *G. ocior* (Mata et al. 2006). The name *G. ocior* was adopted there based on several European specimens. We added two of these sequences (DQ480098 – Duke29 and DQ449956 – TFB 3849, Scotland) in our ITS dataset. These sequences fell in the *G. dryophilus* clade apart from *G. ocior* as conceived by us.

To support our concept of *G. dryophilus*, we examined collections by S. Ryman & R. Vilgalys from Uppsala previously examined by Vilgalys (Vilgalys & Miller 1987, Vilgalys 1991), deposited in the DUKE herbarium. The ITS sequences of these specimens and the morphological characters of *G. dryophilus* noted by Antonín & Noordeloos (2010) showed that the correct name for this taxon is *G. dryophilus*. Therefore, we confirm the species concept hypothesized by Vilgalys & Miller (1987) while the concept of *G. ocior* proposed by Mata et al. (2006) is at variance with our hypothesis. We also determined that European and North American specimens of *G. dryophilus* are conspecific. The three sequences (DQ449963, DQ449964, DQ449966) included in the North American *G. dryophilus* group by Mata et al. (2006) formed a well-supported group within our *G. dryophilus* clade. Also American *G. dryophilus* included in the AFTOL project (ID 559; Lutzoni et al. 2004) fell in the same group.

Specimens examined. CZECH REPUBLIC, Krušné hory Mts, Rolava, Velký cínový důl, wet meadows with *Sphagnum*, 9 June 2004, V. Antonín 04.39, BRNM 691279; Slavkovský les Mts, Nová Ves u Kraslic, Křížky National Nature Monument, serpentine rocks with *Calluna* and *Vaccinium*, 10 June 2004, V. Antonín 04.43, BRNM 691282; Doksy, Břehyně-Pecopala National Nature Reserve, under *Picea abies* and *Pinus sylvestris*, 17 Aug. 2010, H. Deckerová, Antonín 10.156, BRNM 734758; Třeboňsko, Lomnice nad Lužnicí, Ruda Nature Reserve, 29 Sept. 2005, V. Antonín 05.185, BRNM 695739; Třeboňsko, Lomnice nad Lužnicí, Velký and Malý Tisý National Nature Reserve, 26 Sept. 2005, A. Vít, BRNM 705601; Hluboká u Borovan, Žemlička Nature Monument, under *Quercus* near a pond, 29 Sept. 2008, A. Vágner, BRNM 712600; Javorníky Mts, Velké Karlovice, Razula National Nature Reserve, under *Picea abies*, *Abies alba*, *Fagus sylvatica*, 28 July 2010, V. Antonín 10.103, BRNM 732938; Moravské Křižánky, Milovy, Malinská skála, 11 June 2005, A. Vágner, BRNM 695586; Mokrý near Brno, Nad dlouhým (Sivický les) forest, under *Quercus petraea*, *Carpinus betulus* and *Picea abies*, 17 Aug. 2006, V. Antonín 06.29, BRNM 704894. — GERMANY,

Mittenwald, Karwendelgrube, alpine meadow, alt. 1250 m, 9 Sept. 2011, P. Karasch, Antonín 11.166, BRNM 737691. — ITALY, Ravenna distr., Pineta di San Vitale, Bardello, grass community on dunes, 4 Nov. 2007, V. Antonín 07.399, BRNM 707149. — NORWAY, Østfold Co., Fredrikstad, Veberg, *Sphagnum* bog, 10 June 2010, M. Pettersen, BRNM 737692. — SLOVAKIA, Belianské Tatry Mts Bujačí vrch hill, a *Homogyne alpina*, *Poa* and *Dryas octopetala* stand, alt. 1900 m, 28 Aug. 1998, V. Antonín 98.101, BRNM 642393; Vysoké Tatry Mts, Štrbské Pleso, Solisko, Furkotská dolina valley, 7 Aug. 1989, J. Kuthan, BRA 13021; Horná Orava, Námestovo, Klín, Klínské rašeliníšte National Nature Reserve, in a *Sphagnum* stand, 3 June 2002, V. Antonín 02.26, BRNM 670778. — SLOVENIA, Julian Alps, Triglav National Park, Upper Soča valley, Zadnja Trenta, on the riverbank, among *Dryas octopetala* and *Picea*, in grass, 10 Oct. 2001, G. Podgornik, BRNM 695317. — SPAIN, Málaga, Road Málaga-Colmenar, venta de Garvey, *Pinus* forest, 10 Nov. 2000, A. Ortega & L. Alcobe, BRNM 670686 ex herb. AH 26980, isoneotype of *G. dryophilus* var. *lanipes*. — SWEDEN, Uppsala, Stadsskogen, in *Sphagnum* and moss in a mixed forest, 17 June 1984, S. Ryman & R. Vilgalys RV 84/190, DUKE 193401; *ibid.*, in moss, 17 June 1984, S. Ryman & R. Vilgalys RV 84/203, DUKE 193429; *ibid.*, in *Sphagnum*, 16 June 1984, S. Ryman & R. Vilgalys RV 84/193, DUKE 193403; *ibid.*, in moss, 17 June 1984, S. Ryman & R. Vilgalys RV 84/198, DUKE 193406; *ibid.*, 17 June 1984, S. Ryman & R. Vilgalys RV 84/204, DUKE 193411, neotype, selected here; *ibid.*, 17 June 1984, S. Ryman & R. Vilgalys RV 84/195, DUKE 193405. — SWITZERLAND, Graubünden, Tamins, Reichenau, IIs Aults, in grass and moss in an open place, alt. 650–700 m, 1 Oct. 2004, V. Antonín 04.234, BRNM 693554.

Notes — *Gymnopus dryophilus* is characterized by having a pale coloured, orange-brown or ochraceous brown, later ochraceous brown, yellow ochraceous to pinkish ochraceous, hygrophanous, translucently striate pileus, white, cream to yellow lamellae (see Discussion), $5.0\text{--}7.0\text{--}(8.0) \times (2.5\text{--})3.0\text{--}4.0\text{--}(4.5) \mu\text{m}$ basidiospores, and $17\text{--}55 \times 4.0\text{--}10 \mu\text{m}$, (sub) cylindrical, narrowly clavate cheilocystidia, which are mostly coralloid, but also lobate or with apical projections. It grows mostly in deciduous, sometimes also coniferous forests, or in *Sphagnum* stands, and is widely reported from all over Europe and North America. All studied collections of fungi from this species complex from the alpine habitats represent this species.

Gymnopus dryophilus var. *lanipes* (Ortega et al. 2003) especially differs from the type variety by having a finely tomentose stipe. It is known from Mediterranean thermophilic forests, especially those containing *Quercus ilex*, *Pinus halepensis*, or *Cistus*. Molecular studies showed that the isoneotype specimen (BRNM 670686) agrees with sequences of *G. dryophilus* var. *dryophilus*. Therefore, the proposal to consider it a separate species (Vila & Llimona 2006) is not supported.

Gymnopus ocior (Pers.) Antonín & Noordel.

Specimens examined. CZECH REPUBLIC, České Švýcarsko National Park, Jetřichovice, Babylon, under *Picea abies*, *Pinus sylvestris*, 12 June 2010, V. Antonín 10.50, BRNM 728540; *ibid.*, V. Antonín 10.49, BRNM 728539; České Švýcarsko National Park, Jetřichovice, Starý mlýn, on a woody mulch in a garden, 29 May 2009, V. Antonín 09.19 and S. Komínková, BRNM 714822; Vřeteč, on a mulch, 22 May 2010, M. Mikšík, BRNM 728586; Mokrý near Brno, Nad dlouhým (Sivický les) forest, under *Larix decidua*, *Pinus sylvestris* and *Picea abies*, 7 June 2006, A. Vágner, BRNM 699795. — NORWAY, Østfold Co., Sarpsborg, Hafslundparken, 24 May 2010, Ø. Weholt, BRNM 737695; *ibid.*, 12 June 2010, Ø. Weholt, BRNM 737696; Østfold Co., Fredrikstad, Skjællin, Borge skytterhus, 25 June 2010, Ø. Weholt, BRNM 737697; Østfold Co., Fredrikstad, Veberg, 5 June 2010, Ø. Weholt, BRNM 737693; *ibid.*, 21 June 2010, Ø. Weholt, BRNM 737694. — SLOVAKIA, Podunajské Biskupice, Topolové, Topolové hony Nature Reserve, alluvial forest, under *Quercus robur*, *Acer campestre*, *Padus racemosa*, and *Corylus avellana*, 19 June 2010, L. Nagy, Antonín 10.82, BRNM 728565.

Notes — *Gymnopus ocior* is especially characterized by having a non-translucent or only at margin translucently striate, dark red- or orange-brown pileus, pallescent to reddish yellow or pinkish brownish, whitish or yellowish lamellae (see Discussion), $(5.0\text{--})5.5\text{--}6.5\text{--}(7.0) \times (2.5\text{--})2.75\text{--}3.5\text{--}(4.0) \mu\text{m}$ basidiospores, and $16\text{--}60 \times 6.0\text{--}12 \mu\text{m}$, clavate, subcylindrical or subutriform cheilocystidia, often lobate, branched, coralloid or with (apical) projections. It occurs in both deciduous and

coniferous forests, on road margins and similar stands. It is a widespread fungus in Europe. The ITS phylogram of Mata et al. (2006) published in f. 4 of the respective publication depicted clade of 'G. ocior Europe' with nested subclade of 'G. dryophilus North Am.'. After co-analysis of selected sequences from this work with our data we revealed sequences of 'G. ocior Europe' represent in fact European specimens of *G. dryophilus*.

Gymnopus erythropus (Pers.: Fr.) Antonín, Halling & Noordel.

Specimens examined. CZECH REPUBLIC, Český kras, Sv. Jan pod Skalou, J. Burel, BRNM 714784; Moravský kras, Ochoz near Brno, Hornek Nature Reserve, living stem of *Crataegus*, 3 Oct. 2001, A. Vágner, BRNM 666730; Litovelské Pomoraví, Litovel, Vrapač National Nature Reserve, stump of *Quercus*, 2 Aug. 2000, A. Vágner, BRNM 664995; Mokrá near Brno, Nad dlouhým (Sivický les) forest, stump of *Quercus petraea*, 7 Sept. 2005, A. Vágner, BRNM 705224. – SLOVAKIA, Strážovské vrchy Mts, Kšinná, Slávcové hill, on soil under *Fagus sylvatica*, V. Antonín 07.235, BRNM 706885. – SWITZERLAND, Graubünden, Tamins, Reichenau, IIs Aults, on soil, on a pasture under *Pinus sylvestris*, 1 Oct. 2004, V. Antonín 04.232, BRNM 693553.

Notes — This species is especially recognizable by having a ± dark red-brown, shining stipe with typically red-brown coloured basal hairs, rather large basidiospores ((5.0–)5.5–8.0(–9.0) × 3.5–4.5(–5.0) μm), and rather narrow (13–40 × 5.0–10(–13) μm), (sub)clavate, subfusoid, irregular to coralloid or apically mucronate cheilocystidia. It usually grows on dead wood or wood debris of various broad-leaved, rarely coniferous (*Picea abies*, *Pinus sylvestris*) trees, sometimes also among humus in deciduous woods or on buried wood. It is widely distributed in Europe (Antonín & Noordeloos 2010, Noordeloos 2012). For relevant nomenclature and a detailed description, photograph, and citations of other literature, see Antonín & Noordeloos (2010).

Gymnopus fagiphilus (Velen.) Antonín, Halling & Noordel.

Specimens examined. CZECH REPUBLIC, České Švýcarsko National Park, Jetřichovice, Babylon, fallen leaves and cupules of *Fagus sylvatica*, 3 Oct. 2007, V. Antonín 07.320, BRNM 707079; Orlické hory Mts, Horní Rokytnice, Černý důl Nature Reserve, fallen leaves of *Fagus sylvatica*, V. Antonín 07.310, BRNM 707068; Novohradské hory Mts, Pivonice u Pohorské Vsi, Žofínský prales National Nature Reserve, fallen leaves of *Fagus sylvatica*, 30 Sept. 2008, V. Antonín 08.245, BRNM 712407; Moravský kras, Vilémovice, Vývěry Punkvy National Nature Reserve, between Suchý and Pustý žleb, decaying leaves of *Fagus sylvatica*, A. Vágner, BRNM 691489; *ibid.*, Macocha abyss, decaying leaves of *Fagus sylvatica*, V. Antonín, BRNM 712422. – SLOVAKIA, Javorníky Mts, Dolná Mariková, part Kátina, fallen leaves of *Fagus sylvatica*, V. Antonín 05.196, BRNM 695747.

Notes — *Gymnopus fagiphilus*, known also as *Collybia konradiana* Singer or *Collybia fuscopurpurea* sensu Konrad & Maublanc and Kühner & Romagnesi, is characterized by the moderately distant, pinkish brown or pinkish cream coloured lamellae, an apically glabrous, otherwise from a base upwards finely hairy stipe, rather large basidiospores ((6.0–)7.0–9.0 × (3.0–)3.5–4.5 μm), and clavate, irregular to apically almost coralloid cheilocystidia. It is associated with *Fagus sylvatica* litter, and grows on fallen leaves. It has a scattered distribution in Europe, but details of occurrences are not known. However, at least in Central Europe, it occurs in almost all more or less near-natural and natural beech forests. For a detailed description, photo and citations of other literature, see Antonín & Noordeloos (2010).

Gymnopus hybridus (Kühner & Romagn.) Antonín & Noordel.

Specimens examined. CZECH REPUBLIC, Petrovice nad Orlicí, Obora forest, U Houkvice Nature Reserve, under *Aesculus* in an oak stand, 26 Sept. 1993, H. Deckerová, Antonín 93.272, BRNM 576770; Bílé Karpaty Mts, Suchov, Búrová National Nature Monument, 20 Sept. 2006, V. Antonín 06.100, BRNM 704957; Mokrá u Brna, Sivický les, alt. c. 380 m, fallen leaves of *Quercus*,

5 Oct. 2007, D. Dvořák 393/07, BRNU; Bilovice nad Svitavou, Hádecká planinka National Nature Reserve, alt. c. 405 m, broadleaved forest (*Tilia*, *Quercus*, *Carpinus*), 7 Oct. 2002, D. Dvořák 138/02, BRNU. – HUNGARY, Börzsöny Mts, Törökmező, under *Quercus* and *Acer campestre*, 27 Oct. 1994, V. Antonín 94.274, BRNM 599209. – ITALY, Emilia-Romagna, Borgo val di Taro, Stadielle, on fallen leaves of *Quercus robur* and *Q. cerris*, 19 Oct. 2005, V. Antonín 05.230, BRNM 695773.

Notes — *Gymnopus hybridus* is easily distinguishable by having rather distant, cinnamon-brown lamellae, rather large basidiospores ((6.2–)7.4–9.6 × 3.5–4.8 μm), and only small (18–26 × (3.1–)5.2–6.6 μm), clavate to cylindrical, mostly irregular cheilocystidia. It mostly grows on fallen leaves of *Quercus*, less frequently on other broad-leaved tree litter, mostly in thermophilic forests, and is widely distributed especially in Central and Western Europe. For a detailed description, photograph and citations of other literature, see Antonín & Noordeloos (2010).

DISCUSSION

The DNA sequences brought light to morphological characters useful for identification of *Gymnopus* spp. in subsect. *Levipedes*. Three taxa of subsect. *Levipedes* in the *G. dryophilus* complex (*G. erythropus*, *G. fagiphilus*, *G. hybridus*) are clear and easily to identify. Therefore, the most important features of species belonging to the *G. dryophilus* complex are discussed below.

Colour of lamellae

In the *G. dryophilus* complex, the lamellae colour is used as an identification character. According to literature, lamellae are white to cream in *G. alpinus*, *G. aquosus*, and *G. dryophilus*, whereas yellowish to yellow, rarely white in *G. ocior* (e.g. Vilgalys & Miller 1987, Courtecuisse & Duhem 1994, Hausknecht & Krisai-Greilhuber 2000, Gröger 2006, Antonín & Noordeloos 2010). Especially for the latter species, lamellae colour represents an important feature.

Our results show that the lamellae colour agrees with the literature (e.g. Hausknecht & Krisai-Greilhuber 2000, Gröger 2006, Antonín & Noordeloos 2010) in *G. alpinus* and *G. aquosus*. On the other hand, the variability is distinctly broader in *G. ocior* and *G. dryophilus*. In *G. ocior*, lamellae may be white to whitish when young and then pale cream coloured (e.g. BRNM 728540 and BRNM 728565) or yellowish when young to pale or light yellow (3A3–4) when old (e.g. BRNM 728539). A surprisingly broad variation was found in *G. dryophilus* – the lamellae are mostly white to pale cream when young to cream (e.g. BRNM 734758), yellowish white, pale or light yellow (3A2, 3–4A3, 4A3; e.g. BRNM 732938, 642393, and 737691). Even a collection with entirely yellow (yellowish white, pale or light yellow) basidiocarps (pileus 3–4A4, lamellae 2A3, stipe 3–4A4), agreeing macroscopically with *G. ocior*, belongs here. As summarized, the yellow coloured lamellae may not unambiguously lead to *G. ocior*. The yellow coloured lamellae are also present in *G. junquilleus* R.H. Petersen & J.L. Mata (Mata et al. 2006), *G. sub-sulphureus* (Peck) Murrill (Vilgalys & Miller 1987, Vilgalys 1991).

Basidiospores

Basidiospores of all taxa of the *G. dryophilus* group are (broadly) ellipsoid, oblong, pip-shaped or ellipsoid-fusoid. Data on basidiospore measurements are summarized in Table 3.

The studied specimen of *G. alpinus* showed slightly smaller basidiospores (6.0–7.5 × 3.0–4.0 μm) than mentioned in the literature ((6.2–)6.5–8.5 × 3.0–4.4 μm; Antonín & Noordeloos 2010). This size is in the lower limit of their variability.

For studied specimens of *G. aquosus* the basidiospores size ((5.0–)5.5–7.0 × 3.0–4.0(–4.25) μm) also generally agrees

Table 3 Basidiospores size of studied specimens.

Species	Herbarium	Size of basidiospores (μm)	Size average (μm)	E	Q	
<i>G. alpinus</i>	CB 16251	6.0–7.5 \times 3.0–4.0	6.6 \times 3.4	1.61–2.20	1.94	
<i>G. aquosus</i>	BRNM 670755	(5.5–)6.0–7.0 \times 3.5–4.5	6.3 \times 3.9	1.43–1.86	1.63	
	BRNM 695556	(5.75–)6.0–7.0(–7.5) \times (3.25–)3.5–4.0(–4.25)	6.3 \times 3.7	1.50–1.89	1.69	
	BRNM 710027	(5.5–)6.0–6.75 \times 3.0–3.5(–3.75)	6.2 \times 3.3	1.57–2.09	1.89	
	BRNM 665362	5.75–6.75 \times 3.0–3.75	6.3 \times 3.3	1.71–2.09	1.91	
	BRNM 691431	(5.0–)5.0–6.0(–6.5) \times 3.0–3.75(–4.0)	5.8 \times 3.4	1.50–2.00	1.74	
	DUKE 193407	5.0–6.5 \times 3.0–3.5(–4.0)	5.7 \times 3.4	1.50–1.86	1.69	
	DUKE 193408	5.5–7.0 \times 3.5–4.0	6.3 \times 3.7	1.43–1.91	1.70	
	DUKE 193409	5.5–6.5(–6.75) \times 3.5–4.0(–4.25)	6.2 \times 3.8	1.43–1.86	1.61	
	DUKE 193432	5.75–7.0 \times 3.25–4.25	6.3 \times 3.7	1.55–1.88	1.70	
	DUKE 193412	5.5–6.75(–7.0) \times 3.5–4.25	6.3 \times 3.8	1.38–1.77	1.64	
	DUKE 193410	5.5–6.0(–6.25) \times 3.5–4.0(–4.25)	5.7 \times 3.7	1.36–1.71	1.56	
	<i>G. dryophilus</i>	BRNM 670778	6.0–7.5 \times 3.0–3.75	6.8 \times 3.3	1.86–2.33	2.06
		BRNM 695739	5.5–6.5(–7.0) \times 2.75–3.5	6.2 \times 3.1	1.71–2.25	2.03
BRNM 695586		(5.75–)6.0–7.0 \times (2.75–)3.0–4.0	6.4 \times 6.2	1.71–2.17	1.99	
BRNM 691279		(5.5–)6.0–6.75(–7.0) \times (2.5–)2.75–4.0(–4.25)	6.3 \times 3.4	1.62–2.20	1.86	
BRNM 693554		5.5–7.0 \times 2.75–3.5(–4.0)	6.2 \times 3.2	1.62–2.33	1.93	
BRNM 695317		(5.75–)6.0–8.0 \times 3.5–4.5(–5.0)	7.0 \times 4.1	1.44–2.03	1.73	
BRA 13021		(5.5–)6.0–7.5 \times (3.25–)3.5–4.2	6.8 \times 3.8	1.57–2.03	1.79	
BRNM 642393		6.0–7.75(–8.0) \times 3.0–4.0	6.8 \times 3.4	1.81–2.40	2.03	
BRNM 691282		6.0–6.75(–7.5) \times (2.75–)3.0–3.75	6.5 \times 3.2	1.81–2.22	2.00	
BRNM 705601		(5.0–)5.5–6.5(–6.75) \times 3.0–3.5(–4.0)	6.0 \times 3.4	1.57–2.03	1.77	
BRNM 670686		(5.0–)5.5–6.0 \times 2.75–3.5	5.5 \times 3.1	1.57–2.03	1.79	
BRNM 707149		5.25–6.0(–6.5) \times 3.0–3.75	5.7 \times 6.6	1.57–1.86	1.71	
BRNM 734758		5.5–6.5(–7.0) \times 3.0–3.25	6.1 \times 3.1	1.62–2.17	2.00	
BRNM 732938		6.0–7.0 \times 3.0–4.0	6.5 \times 3.5	1.68–2.17	1.86	
BRNM 737692		(5.0–)5.5–6.25 \times 3.25–4.0	5.7 \times 3.6	1.25–1.72	1.56	
BRNM 737691		5.5–6.5 \times 3.5–4.25(–4.5)	5.9 \times 3.8	1.33–1.71	1.56	
BRNM 704894		(5.5–)6.5–7.5 \times (2.5–)3.0–3.5	6.7 \times 3.1	1.83–2.60	2.20	
BRNM 712600		(5.5–)6.0–7.0 \times 3.0–4.0	6.3 \times 3.4	1.62–2.17	1.85	
DUKE 193401		5.0–5.75(–6.0) \times 3.5–4.0	5.4 \times 3.7	1.30–1.63	1.47	
DUKE 193403		5.0–6.25(–6.5) \times (2.75–)3.0–3.75(–4.5)	5.7 \times 3.4	1.44–1.88	1.68	
DUKE 193405		(5.0–)5.25–6.0 \times (3.0–)3.25–4.0	5.7 \times 3.5	1.43–1.90	1.62	
DUKE 193406		5.5–6.75(–7.25) \times 3.25–4.0	6.2 \times 3.7	1.38–1.86	1.69	
DUKE 193411		5.0–6.5 \times (2.75–)3.25–4.0	5.8 \times 3.4	1.57–1.94	1.69	
DUKE 193429		(5.0–)5.5–6.0 \times (2.5–)2.75–3.0	5.6 \times 3.0	1.72–2.00	1.86	
<i>G. ocior</i>		BRNM 728565	5.25–6.5(–7.0) \times 2.75–3.5	6.0 \times 3.2	1.71–2.22	1.91
		BRNM 728540	(5.0–)5.5–6.5 \times (2.75–)3.0–3.5(–3.75)	5.9 \times 3.1	1.62–2.17	1.87
		BRNM 699795	5.75–6.5(–7.0) \times 3.0–3.5	6.3 \times 3.3	1.71–2.17	1.92
	BRNM 737695	(5.0–)5.5–6.5(–7.0) \times 3.25–3.75	6.0 \times 3.4	1.43–2.03	1.77	
	BRNM 737694	5.0–6.0(–6.5) \times 2.5–3.5	5.5 \times 2.9	1.67–2.20	1.89	
	BRNM 737696	5.5–6.5(–7.0) \times 3.25–4.0(–4.25)	6.1 \times 3.5	1.50–2.03	1.76	
	BRNM 737697	(5.0–)5.5–6.5 \times (3.0–)3.25–3.75	5.9 \times 3.4	1.62–1.94	1.74	
	BRNM 737693	5.25–6.5 \times (2.5–)2.75–3.5	5.8 \times 3.1	1.57–2.22	1.91	
	BRNM 728539	(5.0–)5.5–6.5 \times (2.5–)2.75–3.5	5.7 \times 3.0	1.71–2.17	1.92	

with the literature ((5.0–)5.5–8.0 \times 2.7–3.5(–4.0) μm ; Antonín & Noordeloos 2010) except for the absence of an upper limit (none of basidiospores reached up to 8.0 μm). However, in single specimens we can find a rather large variation. Specimen BRNM 710027 has very narrow (3.0–3.5(–3.75) μm) basidiospores (Q = 1.89), while they were distinctly broader (3.5–4.5 μm , Q = 1.63) in BRNM 670755. However, there is a transition from one extreme to the other and the basidiospore shape may distinctly vary in single specimens as well. The molecular data confirmed identity of both collections.

The results of measurements of *G. dryophilus* showed large basidiospores (5.0–7.0(–8.0) \times (2.5–)3.0–4.0(–4.5) μm), while the literature indicates a larger variability especially in a lower limit ((3.5–)4.0–6.5(–7.0) \times 2.5–3.5(–4.0) μm ; Antonín & Noordeloos 2010). The differences between single specimens are, however, rather great, and vary between (5.0–)5.5–6.0 \times (2.5–)2.75–3.0 μm , Q = 1.86 (DUKE 193429) and (5.75–)6.0–8.0 \times 3.5–4.5(–5.0) μm , Q = 1.73 (BRNM 695317). Small basidiospores were also found in the isoneotype specimen of *G. dryophilus* var. *lanipes*: (5.0–)5.5–6.0 \times 2.75–3.5 μm .

The basidiospore variability in *G. ocior* ((5.0–)5.5–6.5(–7.0) \times (2.5–)2.75–3.5(–4.0) μm , Q = 1.74–1.92) generally agrees with published data ((4.6–)5.1–6.3 \times 2.5–3.5(–4.0) μm ; Antonín & Noordeloos 2010).

Cheilocystidia

The shape of cheilocystidia is one of the most important identification characters. The first detailed studies of cheilocystidia in the recent literature were made by Vilgalys & Miller (1987). They distinguished inflated-clavate to subglobose or sphaeropendunculate, frequently diverticulate (*G. ocior*), inconspicuous, diverticulate-filamentous (*G. alpinus*), inflated-clavate to sphaeropendunculate, somewhat echinulate or lobate-diverticulate (*G. aquosus*), and sometimes inconspicuous, filamentous cheilocystidia with numerous diverticulate branches (*G. dryophilus*). However, the variation is even broader.

Cheilocystidia of *G. alpinus* of the studied specimen (Fig. 3) agree with those drawn by Vilgalys & Miller (1987) and Antonín & Noordeloos (2010). They are clavate, simple, irregular to coralloid.

Gymnopus aquosus has clavate, capitate and pedunculate, less frequently subcylindrical or fusoid, simple or coralloid cheilocystidia (Fig. 4); some of them may even be similar to those of *G. dryophilus*. Clavate to sphaeropendunculate cheilocystidia drawn by Vilgalys & Miller (1987) represent only the minority of ones found.

The typical shapes of cheilocystidia of *G. dryophilus* are (sub)cylindrical, narrowly clavate, mostly coralloid (Fig. 5). Their form agrees with figures by Vilgalys & Miller (1987) and Antonín &

Noordeloos (2010). However, we also usually find clavate, simple or slightly irregular cheilocystidia in most of the basidiocarps. The basic shapes of *G. ocior* cheilocystidia (Fig. 6) are clavate, subcylindrical, or subutriform, but, most of them are lobate, branched, with (apical) projections or coralloid. The form of cheilocystidia drawn by Vilgalys & Miller (1987) represents only a part on their variability. Antonín & Noordeloos (2010) mentioned that forms of *G. ocior* with yellow lamellae have more distinctly coralloid cheilocystidia. Our studies showed that these yellow forms actually belong to *G. dryophilus*, and the cheilocystidia fully support that placement. Nevertheless, we can also rarely find cheilocystidia of the *G. dryophilus* type in typical basidiocarps of *G. ocior*.

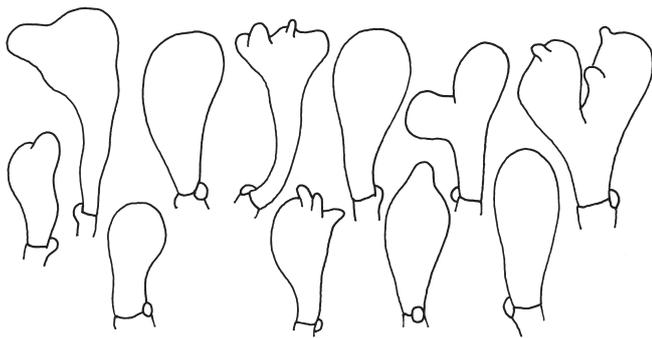


Fig. 3 *Gymnopus alpinus*. Cheilocystidia. — Scale bar = 20 μ m.

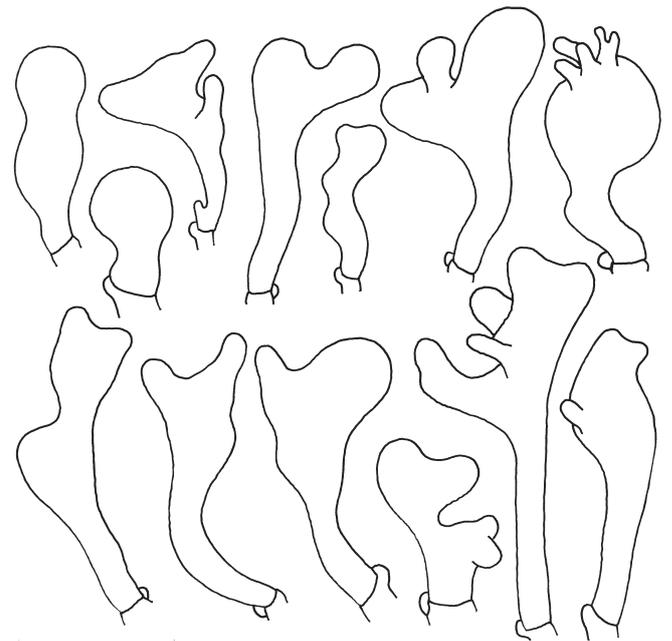


Fig. 4 *Gymnopus aquosus*. Cheilocystidia. — Scale bar = 20 μ m.

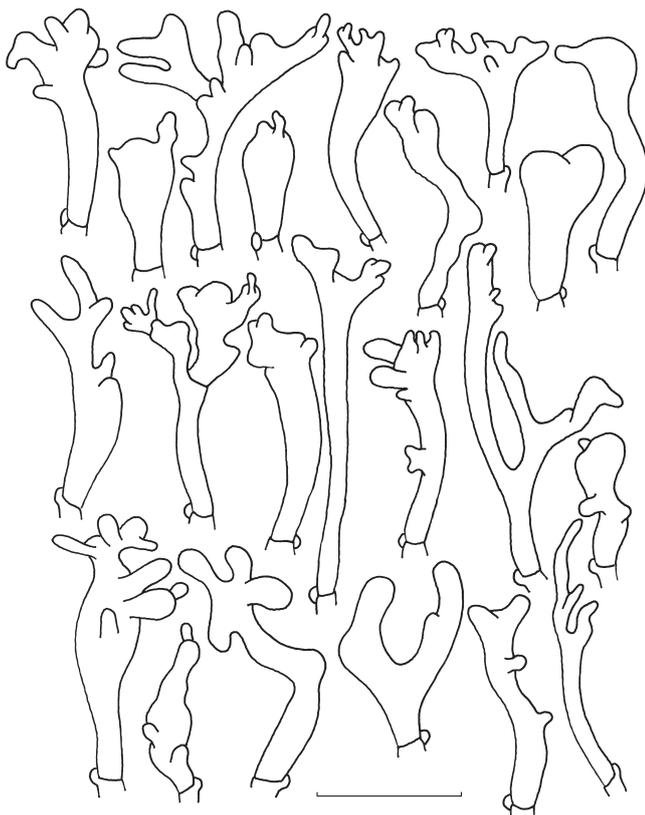


Fig. 5 *Gymnopus dryophilus*. Cheilocystidia. — Scale bar = 20 μ m.

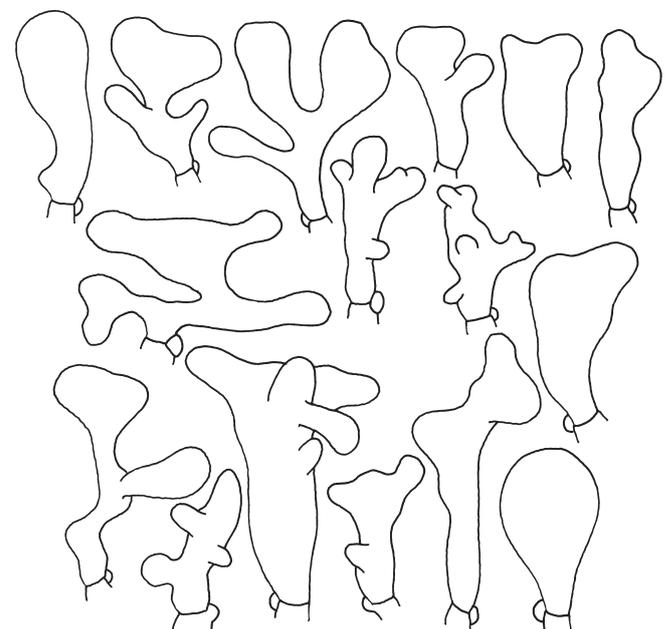


Fig. 6 *Gymnopus ocior*. Cheilocystidia. — Scale bar = 20 μ m.

Pileipellis

The pileipellis is a Dryophila-structure in all discussed taxa. In *G. alpinus* it is composed of cylindrical to inflated, often irregularly coralloid terminal elements with lateral and terminal projections (a poorly developed Dryophila-structure as defined by Antonín & Noordeloos 2010). However, this type of pileipellis structure is useless for identification because of the variability. A poorly to well-developed Dryophila-structure is dependent on the age and development of basidiocarps, and also on the location on the pileus (centre, margin) where the structure is observed.

KEY TO THE EUROPEAN SPECIES OF GYMNOPUS SUBSECTION LEVPEDES

1. Stipe smooth except for basal rhizoids 2
1. Stipe entirely pubescent, or glabrous only at apex and distinctly finely hairy from a base upwards (up to 2/3 of length) 7
2. Stipe dark red-brown, shining, with typically red-brown coloured basal hairs; pileus (dark) red-brown at centre, yellow-brown to yellow-red towards margin; lamellae pale cream-coloured; smell sometimes unpleasantly foetid; basidiospores (5.0–)5.5–8.0(–9.0) × 3.5–4.5(–5.0) µm *G. erythropus*
2. Stipe never red-brown, never with red-brown basal hairs 3
3. Pileus not translucently striate or at margin only, uniformly pale to dark (reddish, pinkish) brown 4
3. Pileus distinctly translucently striate, (pale) yellow, ochraceous yellow, orange-brown, sometimes with darker centre 5
4. Spores (5.0–)5.5–6.5(–7.0) × (2.5–)2.75–3.5(–4.0) µm; cheilocystidia 16–60 × 6.0–12 µm, clavate, subcylindrical or subutriform, lobate, branched, coralloid or with (apical) projections; lamellae white, yellowish to yellow . . . *G. ocior*
4. Spores 6.0–7.5 × 3.0–4.0 µm; cheilocystidia 14–32 × 7.0–12 µm, clavate, simple, irregular to coralloid; lamellae white *G. alpinus*
5. Lamellae rather distant, cinnamon-brown; basidiospores large ((6.2–)7.4–9.6 × 3.5–4.8 µm); cheilocystidia inconspicuous, 18–26 × (3.1–)5.2–6.6 µm, clavate to cylindrical, irregular *G. hybridus*
5. Lamellae close, white, pale cream-coloured to yellow; basidiospores up to 7.0 × 4.25 µm; cheilocystidia distinct . . . 6
6. Basidiospores (5.0–)5.5–7.0 × 3.0–4.0(–4.25) µm; cheilocystidia clavate, capitate and pedunculate, less frequently subcylindrical or fusoid, simple or coralloid; pileus pale yellow, usually without ochre or brown tinges, almost to centre translucently striate; stipe often with distinctly inflated basal part *G. aquosus*
6. Basidiospores 5.0–7.0(–8.0) × (2.5–)3.0–4.0(–4.5) µm; cheilocystidia (sub)cylindrical, narrowly clavate, mostly coralloid; pileus with ochre-brown tinges, especially at centre, translucently striate up to half the radius; stipe more or less equal *G. dryophilus* var. *dryophilus*
7. Lamellae whitish; stipe pubescent; basidiospores (5.0–)5.5–6.0 × 2.75–3.5 µm; Mediterranean thermophilic forests, especially of *Quercus ilex*, *Pinus halepensis*, or *Cistus*. *G. dryophilus* var. *lanipes*
7. Lamellae pinkish brown or pinkish cream; stipe apically glabrous, otherwise from a base upwards finely hairy; basidiospores (6.0–)7.0–9.0 × (3.0–)3.5–4.5 µm; connected with *Fagus sylvatica* *G. fagiphilus*

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