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# *Entoloma* subgenus *Leptonia* in boreal-temperate Eurasia: towards a phylogenetic species concept

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**Key words**

*Entolomataceae*
morphology
multiple gene phylogeny
neotypes
new species

**Abstract** This study reveals the concordance, or lack thereof, between morphological and phylogenetic species concepts within *Entoloma* subg. *Leptonia* in boreal-temperate Eurasia, combining a critical morphological examination with a multigene phylogeny based on nrITS, nrLSU and mtSSU sequences. A total of 16 taxa was investigated. Emended concepts of subg. *Leptonia* and sect. *Leptonia* as well as the new sect. *Dichroi* are presented. Two species (*Entoloma percoelestinum* and *E. sublaevisporum*) and one variety (*E. tjallingiorum* var. *laricinum*) are described as new to science. On the basis of the morphological and phylogenetical evidence *E. alnetorum* is reduced to a variety of *E. tjallingiorum*, and *E. venustum* is considered a variety of *E. callichroum*. Accordingly, the new combinations *E. tjallingiorum* var. *alnetorum* and *E. callichroum* var. *venustum* are proposed. *Entoloma lepidissimum* var. *pauciangulatum* is now treated as a synonym of *E. chytrophilum*. Neotypes for *E. dichroum*, *E. euchroum* and *E. lampropus* are designated.

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## INTRODUCTION

The genus *Entoloma* s.l. is very species-rich and morphologically diverse. It contains more than 1 500 species and occurs worldwide from arctic to tropical habitats (e.g., Largent 1977, 1994, Romagnesi & Gilles 1979, Horak 1980, 2008, Noordeloos 1988, 1992, 2004, 2008, Gates & Noordeloos 2007, Noordeloos & Hausknecht 2007, Vila & Caballero, 2007, 2009, Noordeloos & Gates 2009, 2012, Morozova et al. 2012). Recent molecularly based phylogenetic studies have revealed that the genus is monophyletic and sister to the *Clitopilus*/*Rhodocybe* clade (Moncalvo et al. 2002, Matheny et al. 2006, Co-David et al. 2009, Baroni & Matheny 2011). Besides agaricoid basidiocarp types, the genus also comprises gasteroid, pleurotoid and cyphelloid forms (Co-David et al. 2009, Baroni & Matheny 2011). Life-style is equally varied, from saprotrophs to parasites, or mycorrhizal symbionts. The classification of Entolomatoid agarics traditionally followes two lines. The first group of authors interprets it as a single species-rich entity with an elaborate infrageneric classification (e.g., Romagnesi 1974, 1978, Noordeloos 1992, 2004), while the second segregates *Entoloma* s.l. in up to 13 genera (e.g., Largent & Baroni 1988, Orton 1991a, b, Largent 1994, Baroni & Matheny 2011). Delimitation of (sub)generic entities, has long been based solely on morphological characters (e.g. in Romagnesi & Gilles 1979, Noordeloos 1981, 2004). As a result of the phylogenetic studies mentioned above, it also became apparent that many of the (sub)generic divisions appear to be paraphyletic. Recently Baroni et al. (2011) described the new genus *Entocybe* within the Entolomatoid clade to accommodate species with basidiospore morphology intermediate between *Entoloma* and *Rhodocybe*, supported also by the molecular data. Ongoing studies, however, suggest that also this entity is polyphyletic (Morgado et al. 2013). Moreover, Baroni et al. (2011) have demonstrated the paraphyly of the *Entolomataceae*. Continued phylogenetic studies, based on both morphological characters and molecular markers (He et al. 2013, Morgado et al. 2013, Vila et al. 2013) reveal more insight into the interrelation between morphological and phylogenetic species concepts, as well as into the evolution of the *Entolomataceae*, that will result in future in a more natural classification.

Also subg. *Leptonia* in the sense of Noordeloos (2004) is polyphyletic. Sect. *Leptonia* of the subgenus belongs to the *Nolanea*-*Claudopus* clade, and *Cyanula* and *Griseorubida* to the *Inocephalus*-*Cyanula* clade (Co-David et al. 2009). Based on these data *Cyanula* recently has been raised to the subgenus level (Noordeloos & Gates 2012).

This paper is an attempt to clarify the phylogeny and species concept of a morphologically distinct group within the genus *Entoloma*, viz. subg. *Leptonia* sect. *Leptonia* in the classification of Noordeloos (2004). Despite the fact that most species are rare, some of them were described as far back as in the 19th century. The protologues of these species were short and incomplete, and the type specimens were not preserved. The morphological variability of *Leptonia* species appears to be very high and depending also on the age of basidiomata and weather conditions. Due to these factors, a large number of misunderstandings and incorrect identifications are found in the literature. This paper aims to describe morphological variability of each phylogenetic species resulting in emended descriptions and an identification tool, as well as to reconstruct an infrageneric classification of subg. *Leptonia*.

## MATERIALS AND METHODS

### *Taxa sampling*

To clarify the taxonomic status of 16 taxa of *Entoloma* subg. *Leptonia* as well as their position within the genus, 98 specimens of this subgenus or previously considered as belonging to this subgenus were selected for morphological study and molecular

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**Table 1** Specimens and GenBank accession numbers of DNA sequences used in the molecular analyses. *Entoloma* subg. *Leptonia.*

| Species | Location | Collector, voucher number | GenBank accession no. | | |
|---|---|---|---|---|---|
| | | | nrITS | mtSSU | nrLSU |
| *E. allochroum* | Austria | K.F. Reinwald, A. Hausknecht (L 9860) | KC898370 | – | – |
| | Netherlands | L. Bos (L, 7-08-1993, as *E. tjallingiorum*) | KC898368 | – | – |
| | Netherlands | R. Chrispijn (L 14-08-2000) | KC898371 | – | – |
| | Netherlands | Kits van Waveren (L, 29-07-1973, holotype) | KC898372 | – | – |
| | Russia: Caucasus | A. Kiyashko (LE262984) | KC898375 | – | – |
| | Russia: Caucasus | K. Potapov (LE254324) | KC898374 | – | – |
| | Spain | J. Vila, F. Caballero & A. Mayoral (JVG 1060902-1) | KC898376 | KC898488 | KC898522 |
| | Spain | F. Caballero (EFC 1272008-137) | KC898455 | – | – |
| | Spain | F. Caballero (EFC 2482008-148) | KC898456 | – | – |
| | Switzerland | G. Wölfel (L: E0809) | KC898369 | – | – |
| | Germany | G. Wölfel (L: E4884, as *E. dichroum*) | KC898373 | – | – |
| *E. callichroum* var. *callichroum* | Switzerland | E. Horak (ZT 71/58, holotype) | KC898350 | – | – |
| *E. callichroum* var. *venustum* | Belarus | P. Kolmakov (LE226909, as *E. lepidissimum*) | KC898356 | – | – |
| | Germany | G. Wölfel, F. Hampe (L, Wö E17/10, holotype *E. venustum*) | KC898355 | KC898490 | KC898523 |
| | Russia: Zhiguli | E. Malysheva (LE227532, as *E. lepidissimum*) | KC898357 | – | – |
| | Russia: Altaj | V. Malysheva (LE254312) | KC898351 | KC898489 | KC898521 |
| | Russia: Novosibirsk | T. Bulyonkova (LE254313) | KC898352 | – | – |
| | Russia: Novosibirsk | T. Bulyonkova (LE254314) | KC898353 | – | – |
| | Russia: Primorsky Territory | M. Nazarova (VLA M-20528, as *Rhodophyllus lampropus*) | KC898354 | – | – |
| *E. chytrophilum* | Germany | M. Enderle, (M, as *E. lepidissimum* var. *pauci-angulatum*, holotype) | KC898435 | – | – |
| | Poland | M. Wantoch-Rekowska, 8 Aug. 2010 | KC898425 | – | – |
| | Poland | J. Soboń, 27 Aug. 2010 | KC898426 | – | – |
| | Poland | M. Wantoch-Rekowski, 3 Sept. 2010 | KC898427 | – | – |
| | Russia: Altaj | E. Malysheva (LE262994) | KC898429 | KC898480 | KC898520 |
| | Russia: Caucasus | E. Malysheva (LE262993) | KC898424 | – | – |
| | Russia: Caucasus | K. Potapov (LE254337) | KC898428 | – | – |
| | Russia: Novosibirsk | T. Bulyonkova (LE254326) | KC898430 | – | – |
| | Russia: Moscow Region | Yu. Rebriev (LE 254325) | KC898431 | – | – |
| | Russia: Vologda Region | O. Kirillova (LE 235259) | KC898432 | – | – |
| | Russia: Novgorod Region | S. Arslanov (LE 254336) | KC898433 | – | – |
| | Spain: Canary Islands | R.M. Dähncke (L 855, holotype) | KC898434 | KC898479 | KC898519 |
| *E. coelestinum* | Russia: Sverdlovsk Region | L. Marina (LE258103) | KC898362 | KC898494 | KC898524 |
| *E. dichroum* | Russia: Zhiguli | E. Malysheva (LE227472, neotype) | KC898440 | – | – |
| | Russia: Zhiguli | E. Malysheva (LE234260) | KC898442 | KC898487 | KC898528 |
| | Spain | J. Vila & F. Caballero (JVG 1070821-4) | KC898441 | KC898486 | KC898527 |
| | Spain | S. Català (SGC 16-10-11) | KC898454 | – | – |
| *E. euchroum* | Germany | L. Krieglsteiner (KR-M-0032474, neotype) | KC898421 | – | – |
| | Germany | L. Krieglsteiner (KR-M-0005673) | KC898423 | KC898485 | – |
| | Germany | M. Scholler (KR-M-0033332) | KC898420 | – | – |
| | Germany | L. Krieglsteiner (KR-M-0032221) | KC898422 | – | – |
| | Netherlands | C. Bas (L 6502, as *E. tjallingiorum*) | KC898415 | – | – |
| | Russia: Caucasus | E. Popov (LE262995) | KC898417 | KC898483 | KC898516 |
| | Russia: Leningrad Region | E. Popov (LE254334) | KC898416 | – | – |
| | Russia: Ryazan Region | E. Malysheva (LE254332) | KC898419 | KC898484 | KC898517 |
| | Russia: Tomsk | N. Agafonova (LE254329) | KC898418 | – | – |
| | Spain | J. Vila (JVG 1020827-2) | KC898461 | – | – |
| | Spain: Canary Islands | D. Chávez et al. (JVG 1091115A) | KC898462 | – | – |
| *E. eugenei* | Russia: Primorsky Territory | E. Popov (LE253771 holotype) | KC898438 | – | KC898529 |
| | Russia: Primorsky Territory | T. Svetasheva (LE254347) | KC898439 | – | KC898530 |
| *E. lampropus* | Austria | F. Sucti (WU 13198, as *E. dichroum*) | KC898379 | – | – |
| | Austria | A. Hausknecht (WU 24148, as *E. dichroum*) | KC898391 | – | – |
| | Austria | A. Hausknecht (WU 10092, as *E. dichroum*) | KC898393 | – | – |
| | Germany | G. Wölfel (L 1509) | KC898382 | – | – |
| | Russia: Bryansk Region | A. Fedosova (LE254339) | KC898392 | – | – |
| | Russia: Caucasus | O. Morozova (LE 254316) | KC898390 | – | – |
| | Russia: Kamchatka Region | O. Morozova (LE254349) | KC898389 | – | KC898507 |
| | Russia: Murmansk Region | L. Mikhailovsky (LE9121, as *Leptonia placida*) | KC898378 | – | – |
| | Russia: Novosibirsk | T. Bulyonkova (LE 262992) | KC898388 | – | – |
| | Russia: Orenburg Region | O. Desyatova, (LE253584, as *E. tjallingiorum*) | KC898387 | – | – |
| | Russia: Tatarstan Republic | K. Potapov (LE262991) | KC898384 | KC898470 | KC898505 |
| | Russia: Tomsk | N. Agafonova (LE262985) | KC898383 | – | – |
| | Russia: Sverdlovsk Region | L. Marina (LE258111) | KC898381 | – | – |
| | Russia: Udmurtia Republic | V. Kapitonov (LE254315) | KC898386 | – | – |
| | Russia: Udmurtia Republic | V. Kapitonov (LE254338) | KC898385 | – | – |
| | Russia: Vologda Region | O. Kirillova (LE235263) | KC898380 | – | – |
| | Sweden | T. Læssøe (UPS:BOT:F-176490, as *E. placidum*, designated here as neotype) | KC898377 | KC898471 | KC898506 |
| | Spain | S. Català (RM0855) | KC898458 | – | – |
| *E. lepidissimum* | Czech Republic | M. Svrček (PRM 755801, holotype, as *Leptonia lepidissima*) | KC898364 | – | KC898532 |
| | Russia: Novgorod Region | E. Popov (LE234755) | KC898365 | KC898491 | – |
| | Russia: Novgorod Region | E. Popov (LE254871) | KC898363 | KC898493 | KC898531 |
| | Russia: Novgorod Region | E. Popov (LE234751) | KC898367 | KC898492 | KC898534 |
| | Russia: Primorsky Territory | E. Malysheva (LE254311) | KC898366 | – | KC898533 |

**Table 1** (cont.)

| Species | Location | Collector, voucher number | GenBank accession no. | | |
|---|---|---|---|---|---|
| | | | nrITS | mtSSU | nrLSU |
| *E. percoelestinum* | Russia: Novosibirsk | T. Bulyonkova (LE254327) | KC898359 | KC898496 | KC898526 |
| | Russia: Novosibirsk | N. Filippova (LE254341) | KC898361 | – | – |
| | Russia: Penza Region | A. Ivanov (LE18913, as *E. lepidissimum*) | KC898358 | KC898495 | KC898525 |
| | Spain | J. Vila, X. Llimona (LE254390, holotype) | KF745927 | – | KF745928 |
| | Spain | J. Vila, F. Caballero (JVG 1061111-7, as *E. coelestinum*) | KC898360 | – | – |
| *E. placidum* | Russia: Caucasus | O. Morozova (LE 254335) | KC898397 | – | – |
| | Spain | J. Carreras, J. Vila, F. Caballero, A. Duran & A. Mayoral (JVG 1060830-6) | KC898395 | KC898482 | KC898515 |
| | Spain | J. Vila, F. Caballero & A. Mayoral (JVG 1060902-2) | KC898396 | – | – |
| | Spain | F. Caballero (EFC 2682008-151) | KC898457 | – | – |
| | Sweden | S. Lundell (5276) & G. Haglund (UPS:BOT:F-121714, epitype, as *Leptonia placida*) | KC898394 | KC898481 | KC898514 |
| *E. sublaevisporum* | Austria | A. Hausknecht (MEN 9858) | KC898437 | – | – |
| | Spain | J. Vila & F. Caballero (LIP JVG 1070823T, holotype) | KC898436 | KC898478 | KC898518 |
| *E. tjallingiorum* var. *tjallingiorum* | | | | | |
| | Russia: Moscow Region | E. Lukashina (LE254320) | KC898409 | – | – |
| | Russia: Leningrad Region | R. Singer (LE9123) | KC898410 | – | – |
| | Russia: Ulyanovsk Region | E. Ilyukhin (LE254319) | KC898408 | – | – |
| | Russia: Novgorod Region | O. Morozova (LE254318) | KC898411 | KC898472 | KC898510 |
| | Russia: Tatarstan Republic | K. Potapov (LE254317) | KC898407 | KC898475 | KC898511 |
| | Spain | F. Caballero (SFC 081019-01) | KC898459 | – | – |
| | Spain | F. Caballero (SFC 081005-01) | KC898460 | – | – |
| | Sweden | S. Ryman (6124) (UPS:BOT:F-016378, holotype) | KC898412 | KC898474 | KC898509 |
| *E.* cf. *tjallingiorum* var. *tjallingiorum* | Russia: Zhiguli | O. Morozova (LE227507) | KC898404 | – | – |
| | Russia: Zhiguli | E. Malysheva (LE227584, as *E. placidum*) | KC898405 | – | – |
| | Russia: Zhiguli | E. Malysheva (LE234285) | KC898406 | – | – |
| *E. tjallingiorum* var. *alnetorum* | Russia: Leningrad Region | E. Popov (LE254321) | KC898398 | – | – |
| | Russia: Tumen Region | E. Zvyagina (LE254322) | KC898402 | – | – |
| | Russia: Zhiguli | E. Malysheva (LE227527) | KC898401 | – | – |
| | Russia: Zhiguli | E. Malysheva (LE234287) | KC898403 | – | – |
| | Switzerland | O. Röllin (29-05-1994) | KC898399 | – | – |
| | Switzerland | O. Röllin (G 00111402, holotype) | KC898400 | KC898473 | KC898508 |
| *E. tjallingiorum* var. *laricinum* | Russia: Kamchatka Region | E. Popov, O. Morozova (LE254343, holotype) | KC898413 | KC898477 | KC898513 |
| | Russia: Kamchatka Region | E. Popov, O. Morozova (LE254344). | KC898414 | KC898476 | KC898512 |

sampling (Table 1). ITS1-5.8S-ITS2 sequences were obtained for all of them. Type material, if possible, was included in the analysis. LSU sequences were obtained for 1–3 collections from each taxon. Species for which DNA extraction from type specimens appeared to be impossible or unsuccessful and where no additional reliable collections were available (*E. austriacum*, *E. cedretorum*, *E. insidiosum*, *E. juniperinum*, *E. klofacianum*, *E. lidbergii*, *E. syringicolor* and *E. wynnei*) are not considered in the present work. The outgroup choice and taxa sampling to determine the position of studied species in the system were primarily based on the recent global study on the phylogeny of the *Entolomataceae* (Co-David et al. 2009). Therefore, the representatives of the main subgenera of the crown *Entoloma* clade – *Nolanea* and *Claudopus* (*Nolanea-Claudopus* clade), *Inocephalus* and *Cyanula* (*Inocephalus-Cyanula* clade), as well as *Entoloma*, *Pouzarella*, *Alboleptonia*, and *Trichopilus* were included in the phylogenetic analyses (Table 2). Two species of subg. *Entoloma* (*Prunuloides* clade, which occupies basal position towards the groups treated above (Co-David et al. 2009)), were selected as outgroup in all analyses. A total of 114 specimens was included in the work. Most of the sequences were obtained from the present study. Additional 8 nrITS1-5.8S-ITS2, 19 nrLSU and 19 mtSSU sequences were retrieved from the Genbank: with the acronym GQ – Co-David et al. 2009; GU – Baroni et al. 2011; JQ – He et al. 2013; JX – Vila et al. 2013. The geographic origin of the collections includes Europe, the Caucasus and extratropical Asia from the Urals to the Russian Far East.

## *Morphological analyses*

The study was based both on recently collected material and collections kept in European and Asian herbaria (KR, L, LE, M, PRM, UPS, VLA, WU, ZT). The specimens were collected, documented and preserved using standard methods. Macroscopic descriptions are based on the study of the fresh material as well as on analysis of the photos. The dried material was examined using standard microscopic techniques. Spores, basidia and cystidia were observed in squash preparations of small parts of the lamellae in 5 % KOH or 1 % Congo Red in concentrated $NH_4OH$. The pileipellis was examined in a preparation of the radial section of the pileus in 5 % KOH. Microscopic measurements and drawings were made with AxioImager A1 microscopes. Basidiospore dimensions are based on observing 20 spores, cystidia and basidia dimensions on observing at least 10 structures per collection. Basidia were measured without sterigmata, and the spores without hilum. Spore length to width ratios are reported as Q. The collected material is deposited in the Naturalis Biodiversity Center, section Botany (L), in the Mycological Herbarium of the Komarov Botanical Institute (LE) and in the collection of J. Vila (JVG) and S. Català (SGC). The holotype of *E. sublaevisporum* is deposited in LIP (Lille, France).

## *DNA extraction, amplification and sequencing*

DNA was extracted from herbarium material using a CTAB extraction buffer technique with the following steps of consecutive addition of chloroform-isoamyl alcohol mixture, then isopropyl alcohol-3M sodium acetate solution for precipitation, 70 % ethanol for washing and finally water for dissolution. The alternative method of extraction DNA was using Axy Prep Multisourse Genomic DNA Miniprep Kit (Axygen Biosciences).

The ribosomal ITS1-5.8S-ITS2 region was amplified by PCR with the fungal specific primers ITS1F and ITS4B (Gardes & Bruns 1993; http://www.biology.duke.edu/fungi/mycolab/

**Table 2** Specimens and GenBank accession numbers of DNA sequences used in the molecular analyses. *Entoloma* subg. *Claudopus*, *Cyanula*, *Entoloma*, *Inocephalus*, *Nolanea*, *Pouzarella.* The symbol * is placed before the names of the species for which sequences was taken from the Genbank.

| Species | Location | Collector, voucher No | GenBank accession no. | | |
|---|---|---|---|---|---|
| | | | nrITS | mtSSU | nrLSU |
| **Entoloma abortivum* | Canada | H. den Bakker (92) | – | GQ289290 | GQ289150 |
| **E. abortivum* | China: Jilin | X.L. He et al. (HMJAU 1955) | JQ281483 | – | – |
| **E. aprile* | Japan | C. Takehashi et al. (TNS:F-24626) | AB520845 | – | – |
| **E. araneosum* | Belgium | M.E. Noordeloos (200314) | – | GQ289293 | GQ289153 |
| *E. cetratum* | Russia: Leningrad Region | O. Morozova (LE235480) | KC898450 | – | – |
| *E. chalybeum* | Russia: Leningrad Region | E. Morozova (LE254353) | KC898445 | KC898465 | KC898500 |
| *E. clypeatum* | Russia: Stavropol Region | I. Ukhanova (LE254350) | KC898349 | KC898497 | KC898535 |
| **E. cocles* | Finland | J. Vauras (9770F) | – | GQ289299 | GQ289159 |
| **E. conferendum* | Belgium | M.E. Noordeloos (200313) | – | GQ289330 | GQ289160 |
| **E. crassicystidiatum* | China: Guangdong | X.L. He et al. (GDGM 27357) | – | JQ993056 | JQ291569 |
| **E. furfuraceum* | China: Jilin | X.L. He et al. (GDGM 28818) | – | JQ993062 | JQ993094 |
| *E. griseocyaneum* | Russia: Caucasus | O. Morozova (LE254351) | KC898444 | KC898463 | KC898498 |
| **E. hebes* | Netherlands | C. Hartman (1992-10-28) | – | GQ289310 | GQ289170 |
| *E. indutoides* | Russia: Leningrad Region | O. Morozova (LE254354) | KC898451 | KC898468 | KC898503 |
| **E. infula* | Spain | J. Vila et al. (JVG 1080907-13) | JX454837 | – | – |
| *E. inocephalum* | Vietnam | O. Morozova (LE262922) | KC898449 | – | – |
| *E. insidiosum* | Norway | M.E. Noordeloos (L 376) | KC898443 | – | – |
| **E. minutum* | Spain | J. Vila et al. (LIP PAM 00072307) | JX454829 | – | – |
| *E. mougeotii* | Russia: Caucasus | K. Potapov (LE254352) | KC898446 | KC898464 | KC898499 |
| **E. murrayi* | | V. Hofstetter (VHAs02.02) | – | GU384590 | GU384620 |
| **E. nitidum* | Italy | E. Campo (287) | JF907989 | – | – |
| **E. nitidum* | Slovakia | M.E. Noordeloos (200426) | – | GQ289315 | GQ289175 |
| **E. parasiticum* | Belgium | M.E. Noordeloos (200330) | – | GQ289317 | GQ289177 |
| **E. porphyrescens* | Tasmania: Australia | M.E. Noordeloos (2004113) | – | GQ289322 | GQ289182 |
| **E. prunuloides* | Slovakia | M.E. Noordeloos (200340) | – | GQ289324 | GQ289184 |
| *E. quadratum* | Russia: Primorsky Territory | E. Malysheva (LE254355) | KC898452 | KC898469 | KC898504 |
| **E. sericatum* | Slovakia | M.E. Noordeloos (200328) | – | GQ289329 | GQ289189 |
| *E. sericellum* | Russia: Caucasus | O. Morozova (LE254362) | KC898453 | – | – |
| **E. sericellum* | Belgium | M.E. Noordeloos (200315) | – | GQ289330 | GQ289190 |
| **E. sericeum* | Slovakia | M.E. Noordeloos (200329) | – | GQ289331 | GQ289191 |
| *E. serrulatum* | Russia: Caucasus | O. Morozova (LE254361) | KC898447 | KC898466 | KC898501 |
| **E. sinuatum* | Netherlands | J. Wisman (2003-09-19) | – | GQ289333 | GQ289193 |
| **E. sordidulum* | Belgium | Co-David (2003) | – | GQ289334 | GQ289194 |
| *E. tectonicola* | India | P. Manimohan (741, holotype) | – | GQ289336 | GQ289196 |
| **E. turbidum* | Italy | E. Campo (16176) | JF908005 | – | – |
| **E. turbidum* | Slovakia | M.E. Noordeloos (200351) | – | GQ289341 | GQ289201 |
| **E. undatum* | Belgium | M.E. Noordeloos (200327) | – | GQ289342 | GQ289202 |
| **E. undatum* | Italy | E. Bizio, E. Campo (16854) | JF908007 | – | – |
| **E. valdeumbonatum* | Germany | M. Meusers (E4565, holotype) | – | GQ289343 | GQ289203 |
| **E. violaceovillosum* | India: Kerala | P. Manomohan (645, holotype) | – | GQ289345 | GQ289205 |
| *E. violaceozonatum* | Estonia | V. Liiv (L 275, holotype) | KC898448 | KC898467 | KC898502 |

primers.htm). Sequences of nrLSU-rDNA were generated using primers LR0R and LR5 (Vilgalys & Hester 1990), and sequences of mtSSU – using primers MS1 and MS2 (http://nature.berkeley.edu/brunslab/tour/primers.html). PCR products were visualized using agarose gel electrophoresis and Gel Red staining, and subsequently purified with the kit AxyPrep PCR Cleanup Kit (Axygen Biosciences). Sequencing was performed with ABI model 3130 Genetic Analyzer (Applied Biosystems) using BigDyeTM Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems) with the same primers. The raw data were processed using Sequencing Analysis 5.3.1 (Applied Biosystems).

### *Alignments and phylogenetic analysis*

The sequences were aligned with MAFFT web tool (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/) with Q-INS-I strategy and default settings for other options. The final alignment was corrected manually using MEGA version 5 (Tamura et al. 2011).

Phylogenetic reconstructions were performed with maximum likelihood (ML), maximum parsimony (MP) and Bayesian (BA) analyses. Representatives of the basal *Entoloma* clade (Co-David et al. 2009), *E. turbidum* and *E. nitidum*, were selected as outgroup for all analyses.

MP analysis was performed using PAUP*4.0.b10 (Swofford 2002). One hundred heuristic searches were conducted by stepwise addition with random sequence addition and tree bisection-reconnection (TBR) branch-swapping algorithm. One tree was held at each step during stepwise addition. All characters were treated as unordered and of equal weight. Parsimony bootstrap values were calculated from 1 000 replicates. Only clades with a support ≥ 50 % were retained. Gaps were treated as missing data.

The ML analysis was run in the RAxML servers (http://phylobench.vital-it.ch/raxml-bb/index.php; which implements the search protocol of Stamatakis et al. (2008)), under a GTR+G model with one hundred rapid bootstrap replicates.

Bayesian analysis was performed using MrBayes 3.1 (Ronquist & Huelsenbeck 2003) for two independent runs, each with 2 000 000 generations with sampling every 100 generations, with GTR+G model and four chains. Posterior probability (PP) value ≥ 0.95 are considered significant.

Species were delineated on the base of phylogenetic species concept referring to the examples from fungi in Taylor et al. (2000). Monophyletic clades are recognized as phylogenetic species when they are concordantly supported by the majority of the received phylogenetic trees. Additionally, ITS sequence differences were taken into account. Genetic distances between ITS sequences were estimated using PAUP*4.0.b10 (Swofford 2002). We consider a p-distance greater than 3 % to be a criterion that we will use to recognize new species, following Petersen et al. (2008) and Hughes et al. (2009). This approach was based on the data for within-species variation and heterozygosity from the Great Smoky Mountains National Park in the United States. According to these data, aproximatelly 2–3 % sequence divergence usually represents different species for Basidiomycotina. Morphological criteria were also taken into account. In the case where the morphological differences between separate monophyletic clades are not evident or p-distance is less than 3 % we prefer to consider these as varieties within a phylogenetic species.

## RESULTS AND DISCUSSION

### Phylogenetic analysis

### *Analysis of the nrITS1-5.8S-ITS2 dataset*

The full alignment contained 122 ITS sequences with 1 047 characters. We first excluded from the alignment two large ambiguously aligned regions in ITS1. The first region (282 bp) corresponded to a presumptive insertion characteristic for the *Entoloma dichroum* group. In addition, *E. eugenei* from this group had another insertion of 51 bp that was also excluded from the full analysis.

The analysed dataset included 720 characters (gaps included), of which 327 were parsimony-informative. In the MP analysis, the 100 most parsimonious trees (MPTs) were saved (length = 1738, CI = 0.4177, HI = 0.5823, RI = 0.8402, RC = 0.3510). The ML, MP and BA analyses revealed nearly identical topologies.

First of all, the analyses show a well-supported *Leptonia* clade (1.0/100 – BA/MP – hereinafter), separated from both the *Nolanea-Claudopus* and the *Inocephalus-Cyanula* clades (Fig. 1). As was shown by Co-David et al. (2009) and confirmed by the present work, subg. *Leptonia* in the traditional sense (Noordeloos 1992, 2004) is not monophyletic and must be considered without sections *Cyanula* and *Griseorubida*. Section *Cyanula* recently has been raised to the subgenus level (Noordeloos & Gates 2012). Representatives of sect. *Griseorubida* (*E. indutoides*) are nested within the *Inocephalus* subclade, and the exact taxonomic position of the section must be clarified. Therefore, the available data allowed treating subg. *Leptonia* in the strict sense, corresponding to sect. *Leptonia* in the sense of Noordeloos (1992, 2004) and Largent (1994).

The holotype of *E. violaceozonatum* is grouped together with *E. inocephalum* (type species of subg. *Inocephalus*) with significant support of BA value (0.95/51) in the *Inocephalus-Griseorubidum* clade; it must therefore be excluded from subg. *Leptonia*. It is a similar situation with *E. insidiosum*. A specimen identified as *E. insidiosum* is nested within the *Cyanula* clade (0.99/57), hence it cannot belong to subg. *Leptonia*. Unfortunately, we were not successful in DNA isolation from the holotype of this species.

Two highly supported subclades are recognized in the *Leptonia* clade (Fig. 1, 2) corresponding to two different taxonomic sections – sect. *Leptonia* (1.0/85) and sect. *Dichroi* (1.0/100), newly recognized here. *Entoloma callichroum*, *E. coelestinum*, *E. lepidissimum* and *E. allochroum* form independent subclades.

In sect. *Leptonia* two subclades are recognized (Fig. 2). First of them – stirps *Leptonia* – is composed of *E. euchroum* (type species of subg. *Leptonia*), *E. lampropus*, *E. placidum* and *E. tjallingiorum.* Morphologically the weak angled and thin walled basidiospores are characteristic for species listed above. *Entoloma lampropus*, *E. placidum* and *E. tjallingiorum* possess also similar colours – grey-brown pileus and bluish stipe. Despite the rather high morphological variability expressed by the numerous cases of misidentifications of these taxa in several herbaria, *E. euchroum*, *E. lampropus* and *E. placidum* show genetic similarity since the internal topology for each species is unresolved as the sequences are almost 100 % identical (Fig. 2). Neotypes for *E. euchroum* and *E. lampropus* are designated in the present work. Specimens collected as close as possible to the type locality were chosen: *E. euchroum* KR-M-0032474 from Germany and *E. lampropus* UPS:BOT:F-176490 from Sweden, as well as an epitype for *E. placidum* – UPS:BOT:F-121714, collected close to the neotype locality (as DNA extraction from the neotype was impossible).

The ITS sequences for taxa in the *E. tjallingiorum* clade are highly variable. Even with this extreme variability, it is possible to identify five well-supported subclades that are arranged in three groups (Fig. 2). The first group (subclade I and II) includes the holotype of the *E. alnetorum* and it is well supported (1.0/88). Subclade I unites specimens morphologically corresponding to *E. alnetorum* – with a pale coloured pileus, fruiting in *Alnus* spp. forests early in the season (May-June, rarely July (in northern taiga), except LE227527, collected in August. The holotype of *E. alnetorum* is nested here. However, subclade II includes three specimens from one locality morphologically similar to *E. tjallingiorum*. The second group (subclade III and IV) unites specimens morphologically corresponding to *E. tjallingiorum* (with grey-brown pileus, growing in August on soil or on wood of various decidious trees), including the holotype of *E. tjallingiorum* and it is also well supported (1.0/72). As the p-distance between the holotypes of *E. alnetorum* and *E. tjallingiorum* is only 1.3 %, we consider *E. alnetorum* a variety of *E. tjallingiorum*. The divergence between the sequences as explained by the geographical distribution can be also recognized within the *E. tjallingiorum* clade. Subclade III (1.0/87) unites specimens with more northern distribution. It involves holotype of *E. tjallingiorum* from Sweden, as well as specimens from the Leningrad, Novgorod and Moscow regions of Russia. In subclade IV (0.99/72) specimens are found with southern origin – Tatarstan Republic and Ulyanovsk Region of Russia, and Spain. The third group, involving subclade V (1.0/98) only, takes a rather distant position within the *E. tjallingiorum* clade. It can be explained by the geographic reason also – the isolation between European and Far Eastern populations (p-distance between sequences – 3.3 %). Morphologically this distinction is supported by the presence of a sterile lamella edge made up of abundant, septate terminal elements of the hymenophoral trama. Also the habitat is different, as it is growing on coniferous wood. In spite of the p-distance between subclade V sequences and holotype of *E. tjallingiorum* is more than 3 %, we decided to recognize a new variety *E. tjallingiorum* var. *laricinum* only, as the morphological differences are only small.

The *Entoloma chytrophilum*–*E. sublaevisporum* subclade also nested within the section *Leptonia*-clade, despite the rather isolated position. These species are characterized by the nodulose or almost nodulose basidiospores with extremely weak and numerous angles. They definitely belong therefore to sect. *Leptonia* of subg. *Leptonia.* The holotype of *E. lepidissimum* var. *pauciangulatum* is nested within the *E. chytrophilum*-clade, so these names must be considered synonymous. This evidence is confirmed by the morphological features – almost nodulose spores and blue colour of the whole basidiomata. It is noteworthy that *E. sublaevisporum* macromorphologically is similar to species with differently coloured pileus and stipe, such as *E. placidum*, *E. lampropus*, *E. callichroum*, and at first it was considered closely related to *E. callichroum.* The phylogenetically informative feature in this case is the shape of basidiospores. Therefore, *E. sublaevisporum* is recognized

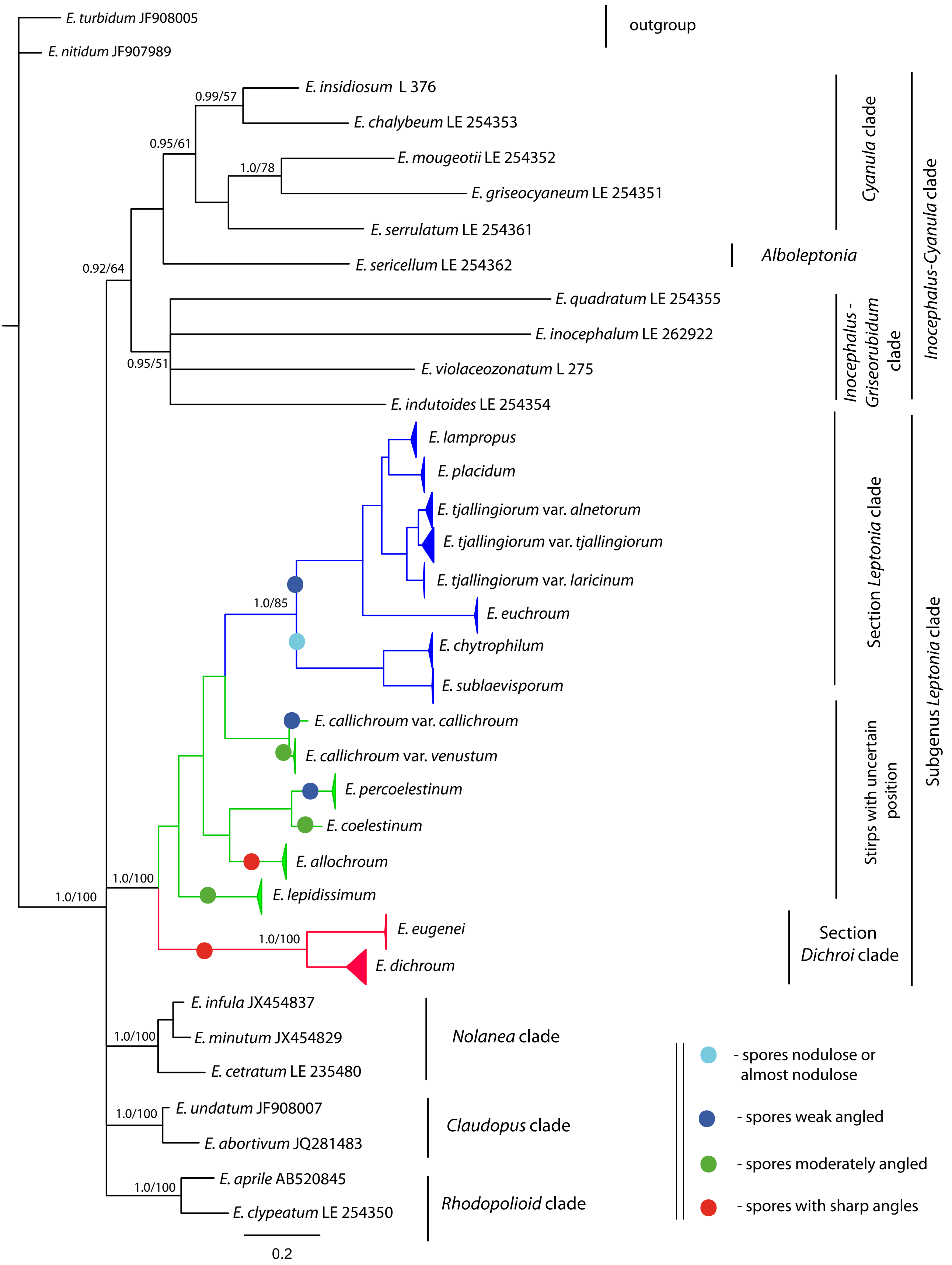

**Fig. 1** Phylogenetic tree derived from Bayesian analysis, based on nrITS1-5.8S-ITS2 data. 1. Branches of subg. *Leptonia* subtree collapsed. Posterior probability (PP) values from the Bayesian analysis followed by bootstrap values from the Maximum Parsimony (BS, %) analysis are added to the left of a node (PP/BS). PP values ≥ 0.95 and BS values > 50 % are shown.

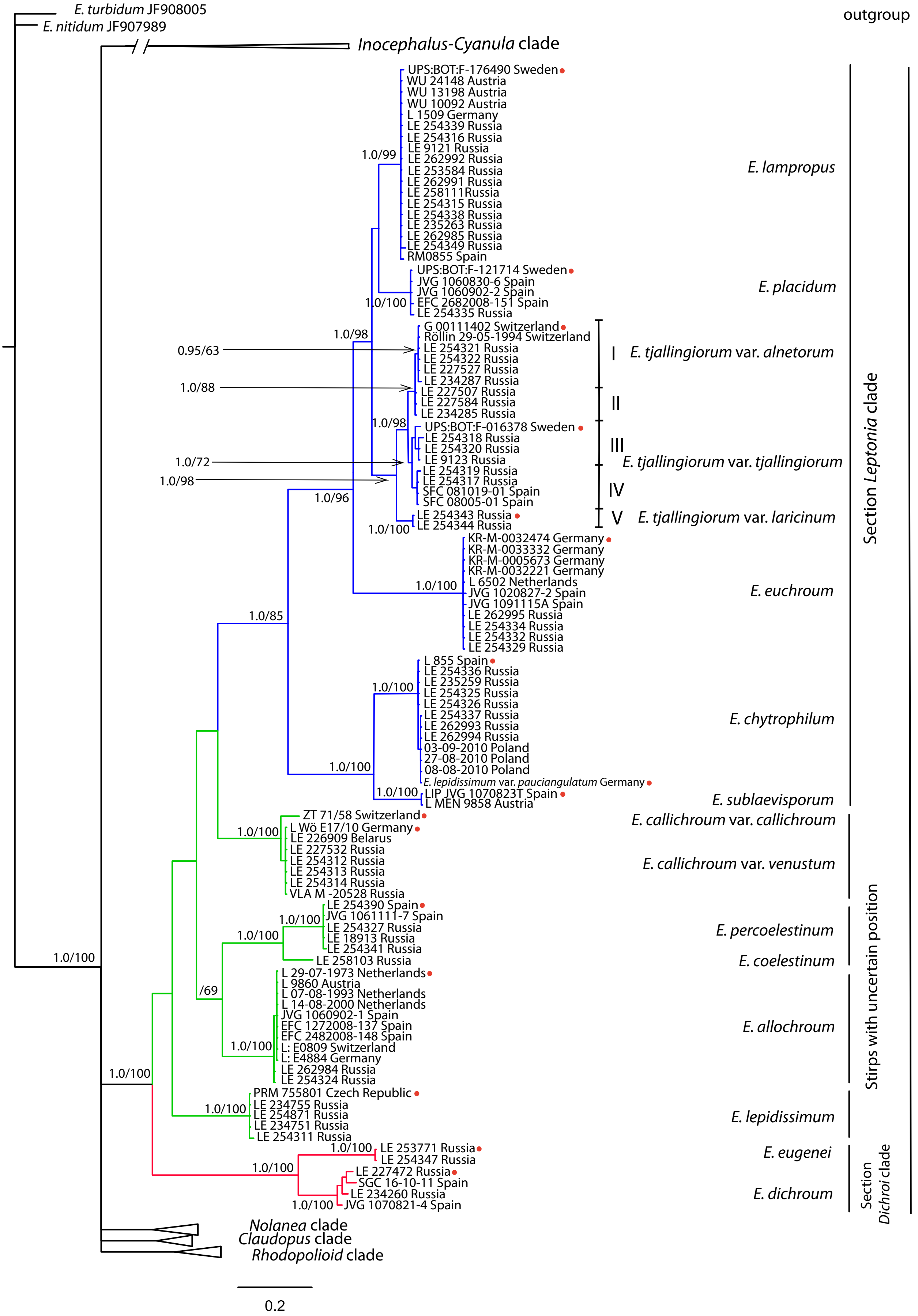

**Fig. 2** Phylogenetic tree derived from Bayesian analysis, based on nrITS1-5.8S-ITS2 data. 2. Main subtree – subg. *Leptonia* clade. Posterior probability (PP) values from the Bayesian analysis followed by bootstrap values from the Maximum Parsimony (BS, %) analysis are added to the left of a node (PP/BS). Type specimens are marked with red points.

here as a new species due to genetical evidence and spore morphology (viz. nodulose form) combined with the difference in colour between the pileus and stipe (see discussion in the taxonomic part).

Although sect. *Dichroi* has few species, it, however, forms a clearly distinct group. Morphologically it includes species with very pronounced, sharply angled spores such as *E. dichroum* and *E. eugenei*. *Entoloma allochroum*, of uncertain phylogenetic position, is the only other species with similar spores. Section *Dichroi* is also distinguished genetically by the presence of large insertions in the ITS1 region (282 bp). ITS region in *E. dichroum* is rather variable, but the p-distance between the specimens studied does not exceed 2 %. Morphological intraspecific variability in *E. dichroum* is also pronounced (as the variation in colour of the pileus) (Fig. 17a–c). *Entoloma dichroum* was described by Persoon in 1801. As the holotype does not exist and the type locality is unknown we selected a neotype from the available material. We studied 8 collections previously identified as *E. dichroum*, and only 4 of them correspond to the current concept of this species. We selected therefore LE227472 (Zhiguli, Russia) as it fits best the protologue.

The *E. callichroum*-clade consists of two branches. One: the holotype of *E. callichroum* only and the other including the holotype of *E. venustum* and 7 specimens which are conspecific with it. As the difference between the holotypes is low (p-distance 1.8 % bp difference) and morphological characters vary within the range of genetically identical specimens of *E. venustum* (basidiospore size, presence and amount of the cheilocystidia, the intensity of the bluish tinge in lamellae – see discussion in the taxonomic part) so that some specimens are indistinguishable from the *E. callichroum*, we propose to treat *E. venustum* as a variety of *E. callichroum.*

Two clades corresponding to the morphological concept of *E. coelestinum* were recovered in all analyses. Specimens previously identified as *E. coelestinum* form a well-supported clade, which, however, consists of two sister clades that can be distinguished morphologically. One collection characterized by more pronounced angled, not nodulose spores and a polished stipe fits well with the protologue of the type, and the current concept of *E. coelestinum* (Noordeloos 2004). The larger clade (5.3 % divergence with previous) is represented by specimens characterized by vaguely angled, almost nodulose spores and a longitudinally fibrillose-striate stipe. A new species, *E. percoelestinum*, is proposed for this taxon below. The *E. allochroum* clade involves almost identical collections, including the holotype, and only the Caucasian one slightly stands out among them. The *E. lepidissimum* clade is also highly supported, homogeneous, and includes the holotype specimen.

The position of *E. callichroum*, *E. coelestinum*, *E. lepidissimum* and *E. allochroum* within subg. *Leptonia* clade is uncertain. In the BA, ML and MP analyses they nest in the section *Leptonia* clade with low support. Morphologically these species occupy an intermediate position between sect. *Leptonia* and sect. *Dichroi*. The first three species have basidiospores with moderately developed angles, but *E. allochroum* has sharply angled basidiospores. It can be concluded that the degree of development of angles in basidiospores for members of the *Entolomataceae* generally is a phylogenetically informative feature, but with some restrictions. Similarly shaped basidiospores have developed independently in the sister clades. A wider sampling of species assigned to subg. *Leptonia* from other geographic regions will be necessary to resolve the phylogeny within subg. *Leptonia*.

## *Analysis of the nrLSU and mtSSU datasets*

To accommodate subg. *Leptonia* in an understanding of the *Entolomataceae* tree produced by Co-David et al. (2009), analyses of the LSU, mtSSU and combined LSU-mtSSU datasets were performed on almost all taxa of *Leptonia* examined in this study. The PCR with MS1 and MS2 primers was unsuccessful for *E. callichroum* var. *callichroum* and for *E. eugenei*. The analyses were performed without these species.

### *Analysis of the nrLSU dataset*

The dataset contained 57 LSU sequences with 775 characters (gaps included), of which 162 were parsimony-informative. The 100 equally most parsimonious trees (MPTs) were saved (length = 854, CI = 0.3255, HI = 0.6745, RI = 0.4043, RC = 0.1316). There were some topological differences and contradictions among the MPTs, the strict consensus tree from the MP analysis the best tree from the ML analysis, and the 50 % majority rule consensus tree from the BA. There was a high number of clades in each of these trees with low support.

In total, LSU trees are less informative than nrITS and mtSSU ones. Topological relations among the species of *Leptonia* and other subgenera of *Entoloma* were not confirmed by sufficient support because of low difference between LSU sequences. So, we do not present any LSU trees in this work as ambiguous.

### *Analysis of the mtSSU dataset*

The dataset contained 54 mtSSU sequences that represent the main subgenera of the *Entoloma* s.l. taxa comprising the main branch of the *Entolomataceae* as well as representatives of almost all species of *Leptonia* considered in the present work. The analysed dataset included 658 characters (gaps included), of which 175 were parsimony-informative. The saved 100 most parsimonious trees had the following characteristics: length = 612, CI = 0.4776, HI = 0.5224, RI = 0.7245, RC = 0.3788. The ML, MP and BA analyses revealed nearly identical topologies.

The main clades of the crown part of the *Entolomataceae* tree indicated by Co-David et al. (2009) were mostly confirmed (Fig. 3). The *Rhodopolioid* (1.0/100), *Nolanea* (1.0/78), *Claudopus* (0.98/69), *Pouzarella* (0.99/73), *Inocephalus-Cyanula* (1.0/55) and the *Leptonia* clades (1.0/57) received the highest support, especially in BA. The holotype of *E. violaceozonatum* was nested in the *Inocephalus-Cyanula* clade, therefore this species must be excluded from subg. *Leptonia*. Inside the *Inocephalus-Cyanula* clade three subclades can be revealed: the highly supported *Cyanula* and *Alboleptonia-Trichopilus* clades and the lowly supported *Inocephalus-Griseorubidum* clade. So, the position of the *E. violaceozonatum* within this clade is rather uncertain.

The analyses performed confirm the results of Co-David et al. (2009), that subg. *Leptonia* in the sense of Noordeloos (2004) is polyphyletic and sections *Leptonia*, *Cyanula* and *Griseorubidum* do not form a monophyletic clade (Fig. 3). *Cyanula*, containing most known species of former subg. *Leptonia*, recently has been raised to the subgenus level (Noordeloos & Gates 2012). It is characterized by the presence of brilliant granules, absence of clamp-connections in all tissues and a fibrillose to polished stipe. We suggest that the *Griseorubidum* must be also excluded from subg. *Leptonia* based on phylogenetic affinity and morphological resemblance to *Inocephalus* species, like the presence of brilliant granules and well differentiated cheilocystidia. Section *Leptonia* (1.0/89) clearly stands out within the clade represented by subg. *Leptonia*, and it is characterized morphologically by the presence of clamp-connections, absence of brilliant granules and more or less fibrillose to squamulose stipe.

The analyses of the mtSSU dataset confirm the separation of the new species *E. percoelestinum* and *E. sublaevisporum* and the variety *E. tjallingiorum* var. *laricinum.*

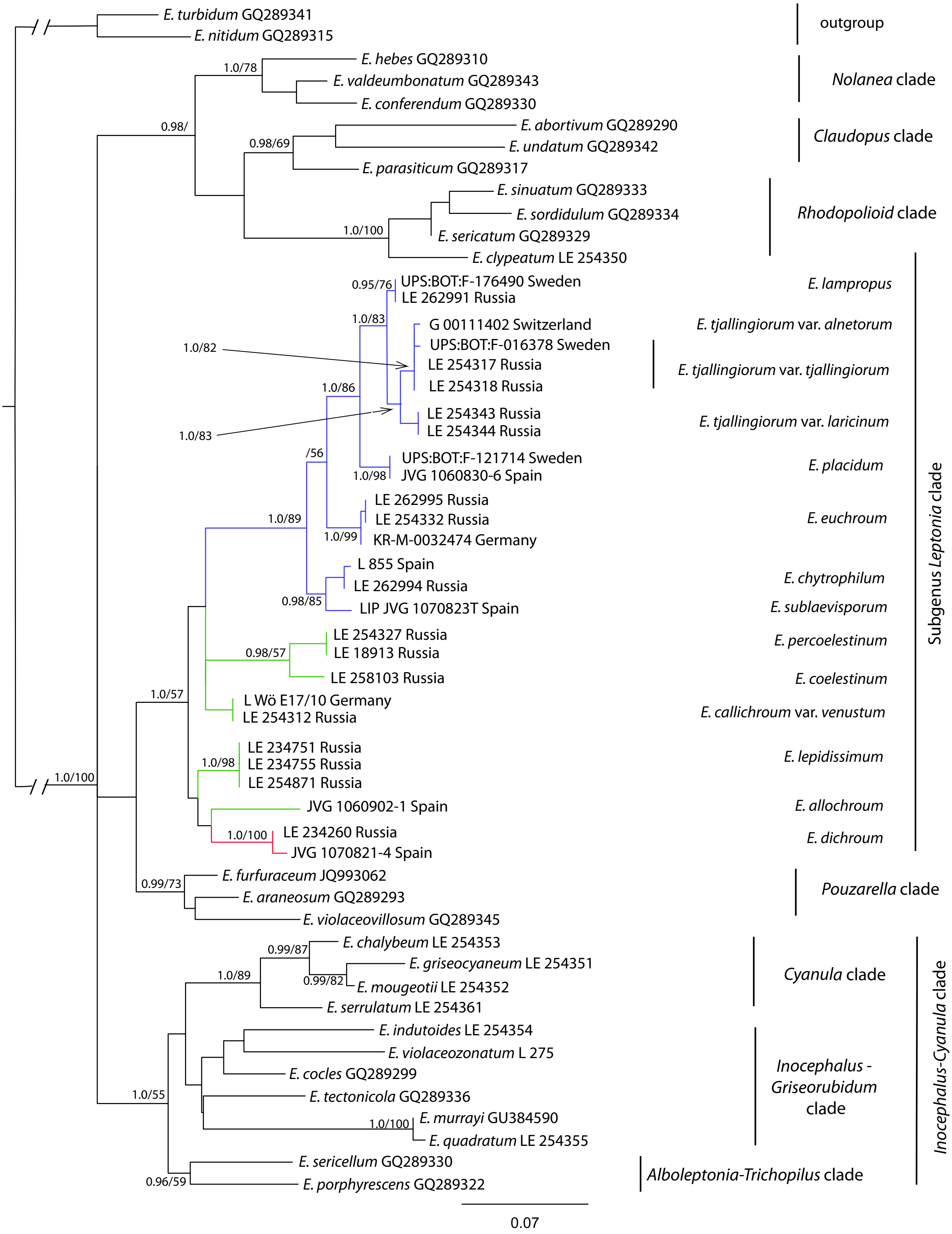

**Fig. 3** Phylogenetic tree derived from Maximum Likelihood, based on mtSSU data. Posterior probability (PP) values followed by bootstrap values from the Maximum Parsimony (BS, %) analysis are added to the left of a node (PP/BS).

### *Analysis of the combined mtSSU-LSU dataset*

The dataset contained 52 sequences as in the previous analyses. The analysed dataset included 1 433 characters (gaps included), of which 334 were parsimony-informative. In the MP analysis, 93 most parsimonious trees were recovered (length = 1313, CI = 0.4501, HI = 0.6113, RI = 0.6204, RC = 0.2793). The ML, MP and BA analyses revealed nearly identical topologies, although the MP bootstrap values were rather low.

The topology revealed by the analysis of the combined data is similar to the results of the analysis of the mtSSU data (Fig. 4). The main subgenera of *Entoloma* form their clades with high support: *Rhodopolioid* clade (1.0/99), *Nolanea* (1.0/97), *Claudopus* (1.0/91), *Pouzarella* (1.0/57) and *Inocephalus-Cyanula* clade (1.0/), supported only by the BA. Subg. *Leptonia* clade received slightly higher support in the MP analysis (1.0/74). Sect. *Leptonia* (1.0/91) is also well revealed. *Etoloma* *allochroum*, *E. callichroum*, *E. coelestinum-percoelestinum* clade, *E. dichroum*, *E. lepidissimum* occupy isolated uncertain positions within subg. *Leptonia*. The *Cyanula* clade (1.0/64) and the *Inocephalus-Griseorubidum* clade (1.0/) are well indicated within the *Inocephalus-Cyanula* clade. *Etoloma violaceozonatum* also nests within this clade, but groups together with *E. sericellum*. Its taxonomic position needs to be carefully studied in the future.

The analyses of the combined mtSSU-LSU dataset also confirm the separation of new species *E. percoelestinum* and *E. sublaevisporum* and the variety *E. tjallingiorum* var. *laricinum*.

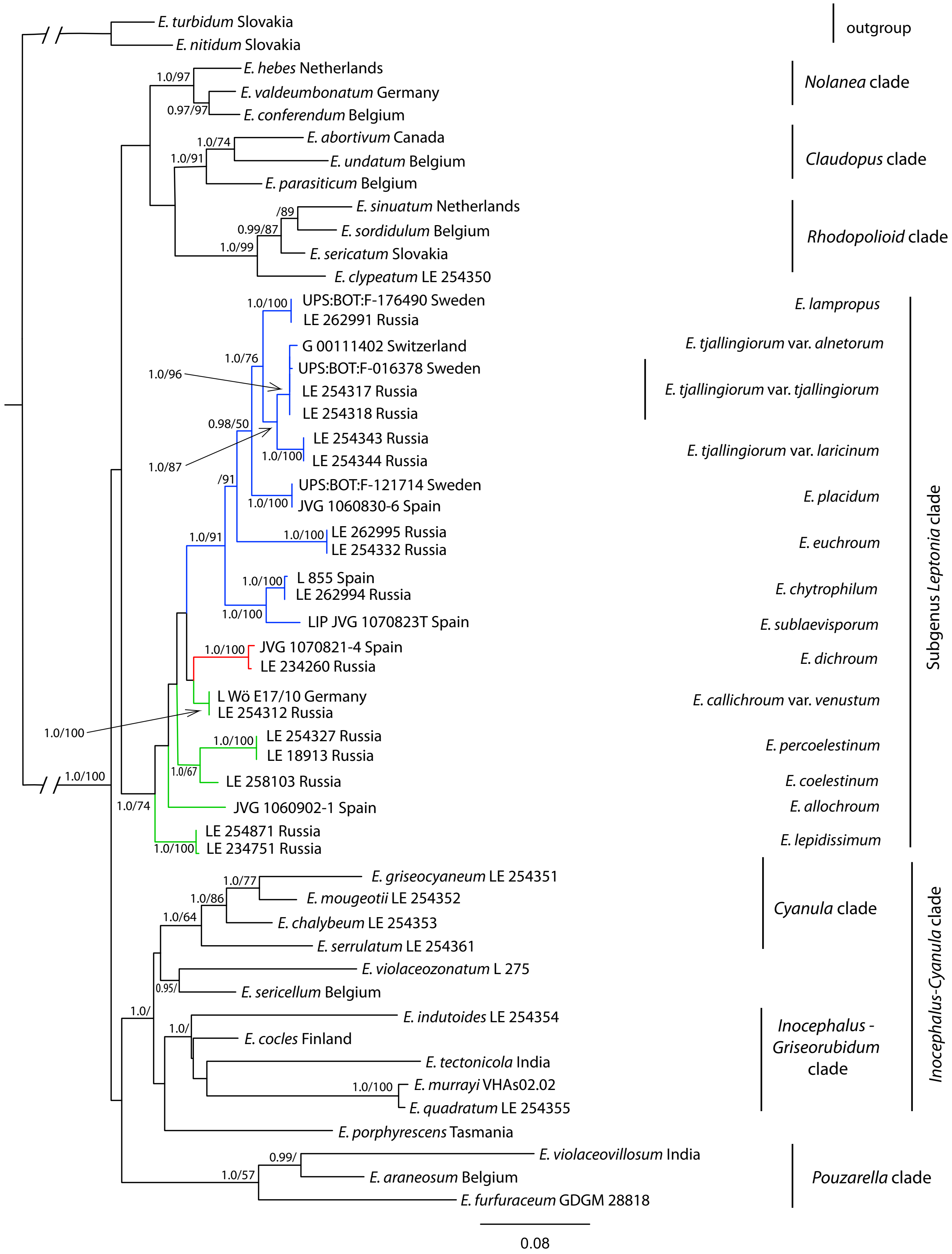

**Fig. 4** Phylogenetic tree derived from Maximum Likelihood, based on combined mtSSU-nrLSU data. Posterior probability (PP) values followed by bootstrap values from the Maximum Parsimony (BS, %) analysis are added to the left of a node (PP/BS).

## TAXONOMIC PART

### ***Entoloma*** **subgenus** ***Leptonia*** (Fr.: Fr.) Noordel. emend. O.V. Morozova, Noordel. & Vila

*Entoloma* subg. *Leptonia* sect. *Leptonia* (Fr.: Fr.) Noordel., Persoonia 11: 146. 1981. — *Agaricus* trib. *Leptonia* Fr., Syst. Mycol. (Lundae) 1: 10, 201. 1821. — Lectotype (Clements & Shear 1931: 349): *Agaricus euchrous* Pers.: Fr.

*Rhodophyllus* sect. *Leptoniarii* Romagn., Bull. Soc. Mycol. France 53: 332. 1937 (nom. nud.; no Latin diagnosis). — Lectotype (Noordeloos 1981: 146): *Agaricus euchrous* Pers.: Fr.

*Leptonia* sect. *Lampropodae* Konrad & Maubl., Les Agaricales: 259. 1948 (nom. nud., no Latin diagnosis). — Lectotype (Noordeloos 1982a: 453): *Agaricus lampropus* Pers.: Fr.

*Rhodophyllus* sect. *Lampropodes* (Kühner & Romagn., Fl. Anal.: 208. 1953) ex Romagn., Bull. Mens. Soc. Linn. Lyon 43: 328. 1974. — Holotype: *R. lampropus* (Pers.: Fr.) Quél.

Habit mycenoid, collybioid or tricholomatoid; pileus conico-convex or plano-convex, rarely with papilla or umbo, sometimes depressed; lamellae almost free to emarginate, sometimes adnate, rarely with decurrent tooth; stipe fibrillose-striate or flocculose-scaly, rarely almost smooth; *lamellae edge* sterile, fertile or heterogeneous; cheilocystidia present or absent, basidiospores with both weak or sharp angles, or almost nodulose, pileipellis more or less a trichoderm of inflated elements with intracellular, and often additionally encrusting, pigment; brilliant granules absent; clamp-connections present and often frequent; lignicolous or terrestrial, mostly in forests.

*Entoloma* subg. *Leptonia* (Fr.: Fr.) Noordel. is emended here by excluding sections *Cyanula* (Romagn.) Noordel. (that now is considered subg. *Cyanula* (Romagn.) Noordel. (Noordeloos & Gates 2012)), *Griseorubida* (Romagn.) Noordel. and *Rhamphocystotae* (Largent) Noordel. The subgenus now is characterized by species previously considered in sect. *Leptonia* only, and characterized by the presence of clamp-connections, absence of brilliant granules, and more or less fibrillose to squamulose stipe.

### *Synopsis of the phylogenetic species in subgenus Leptonia from boreal-temperate Eurasia*

**Section** ***Leptonia*** (Fr.: Fr.) Noordel. emend. O.V. Morozova, Noordel. & Vila

1. *Entoloma chytrophilum* Wölfel, Noordel. & Dähncke
2. *Entoloma euchroum* (Pers.: Fr.) Donk
3. *Entoloma lampropus* (Fr.: Fr.) Hesler
4. *Entoloma placidum* (Fr.) Noordel.
5. *Entoloma sublaevisporum* Vila, Noordel. & O.V. Morozova

6a. *Entoloma tjallingiorum* Noordel. var. *tjallingiorum*
6b. *Entoloma tjallingiorum* var. *alnetorum* (Monthoux & Röllin) O.V. Morozova, Noordel. & Vila
6c. *Entoloma tjallingiorum* var. *laricinum* O.V. Morozova, Noordel., Vila & E.S. Popov

**Section** ***Dichroi*** O.V. Morozova, Noordel. & Vila

7. *Entoloma dichroum* (Pers.: Fr.) P. Kumm.
8. *Entoloma eugenei* Noordel. & O.V. Morozova

**Species of uncertain position**
**Stirpe** ***Allochroum***

9. *Entoloma allochroum* Noordel.

**Stirpe** ***Callichroum***

10a. *Entoloma callichroum* E. Horak & Noordel. var. *callichroum*
10b. *Entoloma callichroum* var. *venustum* (Wölfel & F. Hampe) O.V. Morozova, Noordel. & Vila

**Stirpe** ***Coelestinum***

11. *Entoloma coelestinum* (Fr.) Hesler
12. *Entoloma percoelestinum* O.V. Morozova, Noordel., Vila & Bulyonkova

**Stirpe** ***Lepidissimum***

13. *Entoloma lepidissimum* (Svrček) Noordel.

Certainly, the list of potential phylogenetic species within subg. *Leptonia* is much larger. Several morphospecies are still in need of molecular analysis in order to determine their phylogenetic position. The following additional morphospecies are known from boreal and temperate Eurasia: *E. austriacum* Courtec., *E. cedretorum* (Romagn. & Riousset) Noordel., *E. insidiosum* Noordel., *E. juniperinum* Barkman & Noordel., *E. klofacianum* Noordel., Wölfel & Hauskn., *E. lidbergii* Noordel. and *E. wynneae* (Berk. & Broome) Sacc. (Noordeloos 2004); *E. syringicolor* E. Ludw. & Noordel., *E. dichroum* var. *leptosporum* E. Ludw. & Noordel. (Ludwig 2007); *E. dichroum* var. *corsicum* (Romagn.) Courtec. (Courtecuisse 2008); *E. legionense* Blanco-Dios (Blanco-Dios '2012' 2013). In the present study, the DNA extraction of these morphospecies failed, either due to the age and condition of the (type) specimens, or material was not available for destructive sampling.

For a sound phylogeny of subg. *Leptonia*, extra-European species (some of which are listed below) must also be taken into account, viz. from North America: *E. velatum* Hesler (Hesler 1967); *E. kauffmanii* Malloch (Malloch 2010); *E. cyaneum* [Peck→] Sacc., *Leptonia approximata* Largent, *L. carnea* Largent, *L. convexa* Largent, *L. cyaneonita* Largent, *L. insueta* Largent, *L. occidentalis* Murrill, *L. subeuchroa* Kauffman, *L. subgracilis* Largent, *L. violaceonigra* Largent, *L. subcoelestina* Largent, *L. violacea* (Kauffman) Largent, *L. zanthophylla* Largent (Largent 1994); *Leptoniella acericola* Murrill; from India: *E. indoviolaceum* Manim. & Noordel. (Manimohan et al. 2006); from New Guinea: *E. egregium* E. Horak (Horak 1980); and from Australia: *E. panniculus* (Berk.) Sacc., *E. tomentosolilacinum* G.M. Gates & Noordel., *E. violascens* G.M. Gates & Noordel. and *E. endotum* Noordel. & G.M. Gates (Noordeloos & Gates 2012).

### *Key to the species of subgenus Leptonia in boreal and temperate Eurasia*

For the convenience in identifying following morphospecies have been added to the key, on account of the evidence in Noordeloos (2004): *E. austriacum*, *E. cedretorum*, *E. insidiosum*, *E. juniperinum*, *E. klofacianum*, *E. lidbergii* and *E. wynnei*. Also *E. violaceozonatum* Noordel. & Liiv is included, despite its placement in the *Inocephalus-Cyanula* clade.

1. Pileus and stipe blue, violaceous or pinkish lilaceous; lamellae white or coloured when young . . . . . . . . . . . . . . . . . . 2
1. Pileus yellow-brown, brown, grey-brown or ochraceous, sometimes with blue or violaceous tinge near the cap margin; stipe blue or violaceous; lamellae white when young . . 16

2. Lamellae coloured when young . . . . . . . . . . . . . . . . . . . 3
2. Lamellae white when young . . . . . . . . . . . . . . . . . . . . . 7

3. Lamellae firstly brownish then reddish brown with fimbriate concolorous edge; pileus fibrillose-zonate, lamellae edge entirely sterile with dense clusters of very long (up to 300 µm) subcylindrical cheilocystidia . . . . . . . . *E. violaceozonatum*
3. Lamellae with bluish or violaceous-blue tinge when young, lamellae edge sterile or heterogeneous, cheilocystidia of another type, smaller . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4. Lamellae violaceous-blue with brownish violaceous edge when young; fruitbodies entirely deep violaceous-blue; on wood, preferably of *Alnus* . . . . . . . . . . . . . 2. *E. euchroum*
4. Lamellae pale to moderately dark blue or violaceous-blue with concolorous or slightly paler edge when young . . . . 5

5. Pileus and stipe with the same deep blue colour, lamellae bluish with concolorous or slightly paler edge; spores 7.5–11.5 × 6.0–8.0 µm . . . . . . . . . . . . . . . . . . . .13. *E. lepidissimum*
5. Pileus pinkish lilaceous to violaceous, stipe dark blue . . 6

6. Spores with blunt angles, cheilocystidia absent . . . . . . . . . . . . . . . . . . . . . . . 10a. *E. callichroum* var. *callichroum*
6. Spores with moderately pronounced angles, cheilocystidia broadly clavate, intermixed with basidia . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10b. *E. callichroum* var. *venustum*

7. Pileus and stipe blue or violaceous-blue . . . . . . . . . . . . 8
7. Pileus and stipe violaceous, brown-violaceous or pinkish lilaceous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

8. Spores isodiametrical, up to 9 µm diam . *E. klofacianum*
8. Spores heterodiametrical . . . . . . . . . . . . . . . . . . . . . . 9

9. Spores 6.5–8.5(–9.0) × 5.5–6.5 µm, pileus conical to campanulate, hardly expanding, stipe smooth to subfibrillose . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10
9. Spores larger, pileus hemisphaerical, convex to applanate, stipe fibrillose or minutely squamulose . . . . . . . . . . . . 11

10. Spores moderately angled, stipe smooth to subfibrillose . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11. *E. coelestinum*
10. Spores weakly angled, stipe fibrillose or minutely squamulose . . . . . . . . . . . . . . . . . . . . . . . 12. *E. percoelestinum*

11. Spores distinctly nodulose, 8.5–11.5 × 6.0–7.0 µm, pileus convex to applanate . . . . . . . . . . . . . . 1. *E. chytrophilum*
11. Spores with 5–7 pronounced angles . . . . . . . . . . . . . . 12

12. Cheilocystidia absent . . . . . . . . . . . . . . . . *E. cedretorum*
12. Cheilocystidia present . . . . . . . . . . . . . . . . . . . . . . . . 13

13. Fruitbody collybioid . . . . . . . . . . . . . . . . . . 7. *E. dichroum*
13. Fruitbody tricholomatoid . . . . . . . . . . . . . . . 8. *E. eugenei*

14. Spores with 7–9 weak angles; 9.0–12.2 × 6.0–8.2 µm; pileus a tender pinkish ochre with brown with lilac or violaceous tint at centre . . . . . . . . . . . . . . . . . *E. austriacum*
14. Spores with 5–7 pronounced angles . . . . . . . . . . . . . . 15

15. Fruitbodies very small; pileus up to 10 mm, pink . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. lidbergii*
15. Fruitbodies larger; pileus 20–40 mm, greyish brown with lilaceous tinge . . . . . . . . . . . . . . . . . . . 9. *E. allochroum*

16. Spores 10.0–16.0(–18.0) × 7.0–10.0 µm; pileus warm brown contrasting with the blue stipe. . . . . . . . *E. wynnei*
16. Spores smaller . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17

17. Spores with 5–7 pronounced angles . . . . . . . . . . . . 18
17. Spores nodulose or with 6–9 weak angles . . . . . . . . . 19

18. Stipe blue, flocculose-squamulose . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7. *E. dichroum* (pale form)
18. Stipe violaceous, longitudinally fibrillose 9. *E. allochroum*

19. Spores distinctly nodulose . . . . . . 5. *E. sublaevisporum*
19. Spores with 6–9 weak angles . . . . . . . . . . . . . . . . . 20

20. Stipe glabrous, polished . . . . . . . . . . . . . . . . . . . . . . 21
20. Stipe longitudinally fibrillose or squamulose . . . . . . . . 23

21. Spores isodiametrical to subisodiametrical . . . . . . . . . 22
21. Spores heterodiametrical . . . . . . . . . . . . . *E. insidiosum*

22. Spores 8.0–10.0 × 6.0–8.0 µm; pileus dark brown when young . . . . . . . . . . . . . . . . . . . . . . . . . *E. juniperinum*
22. Spores 7.5–9.0 × 6.5–8.5 µm; pileus blue when young . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. klofacianum*

23. Stipe flocculose-squamulose . . . . . . . . . . . . . . . . . . . 24
23. Stipe fibrillose-striate . . . . . . . . . . . . . . . . . . . . . . . . . 26

24. Pileus pale ochraceous; on wood of *Alnus*, early in season . . . . . . . . . . . . . 6b. *E. tjallingiorum* var. *alnetorum*
24. Pileus brown or grey-brown . . . . . . . . . . . . . . . . . . . 25

25. Lamellae edge heterogeneous, cheilocystidia lageniform, intermixed with basidia; on soil or on wood of deciduous trees . . . . . . . . . . . . 6a. *E. tjallingiorum* var. *tjallingiorum*
25. Lamellae edge sterile, cheilocystidia as strands of terminal elements of hyphae of trama hymenial . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6c. *E. tjallingiorum* var. *laricinum*

26. Pileipellis with intracellular pigment; cheilocystidia absent; smell farinaceous; on wood of deciduous trees, mainly of *Fagus* . . . . . . . . . . . . . . . . . . . . . . . . . . . 4. *E. placidum*
26. Pileipellis with both intracellular and encrusting pigment; cheilocystidia present or absent; smell none; on soil or on wood of coniferous trees . . . . . . . . . . . . 3. *E. lampropus*

### *Descriptions of the species*

Below we provide descriptions of the species included in the analysis (in the key indicated with the number that corresponds with the descriptive text of this paper). Most of them are rarely collected and exact and complete information was difficult to find. Therefore the descriptions below contain new data on ecology, substratum, colour variation, spore shape, and presence / absence of cheilocystidia. One section, two species and one variety are described as new to science.

### **Section *Leptonia*** (Fr.: Fr.) Noordel. emend. O.V. Morozova, Noordel. & Vila

Lectotype (Clements & Shear 1931: 349): *Agaricus euchrous* Pers.: Fr.

Habit collybioid to almost tricholomatoid; pileus conico-convex or plano-convex, rarely with papilla or umbo, sometimes depressed; lamellae almost free to emarginate, sometimes adnate, rarely with decurrent tooth; *stipe* fibrillose-striate or flocculose-scaly; lamella edge sterile, fertile or heterogeneous; *cheilocystidia* present or absent, spores with poor angles to almost nodulose, *pileipellis* more or less a trichoderm of inflated elements with intracellular, and often additionally encrusting, pigment; pileitrama regular; brilliant granules absent; *clamp-connections* present and often frequent; lignicolous or terrestrial, mostly in forests.

Section *Leptonia* is emended here to unite only those species with weakly angled, almost nodulose spores, which form a well-supported monophyletic clade, as opposed to the new section *Dichroi* which includes species with pronouncedly acutely angled spores. Several species with uncertain phylogenetic position (*Entoloma allochroum*, *E. callichroum*, *E. coelestinum*, *E. lepidissimum*, *E. percoelestinum*) also are not included in sect. *Leptonia*.

### 1. ***Entoloma chytrophilum*** Wölfel, Noordel. & Dähncke, Öst. Z. Pilzk. 10: 190. 2001. — Fig. 5a, b, 6

Syn.: *Entoloma lepidissimum* var. *pauciangulatum* Gminder & Enderle, Beitr. Kenntn. Pilze Mitteleur. 10: 60. 1996.

Pileus 2–15 mm broad, plano-convex to concave with depressed centre, not hygrophanous, not translucently striate, with straight then deflexed undulating margin, radially fibrillose, in centre squamulose, dark blue, slightly discolouring to bluish violaceus. *Lamellae* moderately distant, adnate-emarginate with small decurrent tooth, ventricose, white, becoming pinkish, with entire concolorous edge. *Stipe* 20–40 × 1–2 mm, cylindrical, fibrillose-striate, slightly squamulose in the upper part, concolourous with pileus or grey-blue, with white basal tomentum. *Smell* strong, fungoid, reminiscent of *Cantharellus cibarius* or indistinct, taste not reported. *Spores* 8.4–11.5 × 5.8–7.0 µm, Q = 1.3–1.8, nodulose, heterodiametrical. *Basidia* 37.8–48.2 × 10.2–12.3 µm, 1–4- spored, clavate, clamped. *Lamellae edge* fertile. *Cheilocystidia* absent. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 10–20 µm wide with blue intracellular pigment. *Clamp-connections* present.

Habitat — Type specimen on chips of *Pinus* bark in pot with *Cymbidium* in garden. In natural conditions on rotten wood (mostly of coniferous trees) in coniferous and mixed forests.

Known distribution — Western, Central and Eastern Europe, Canary Islands (holotype), Caucasus, Western Siberia.

**Fig. 5** a, b: *Entoloma chytrophilum*. a. LE262994; b. LE254326. — c–f: *E. euchroum*. c, d. LE254329 (photo's taken at the same locality but at different times); e. JVG 1091115A; f. LE262995. — Scale bars = 1 cm. — Photos by: a, f. O. Morozova; b. T. Bulyonkova; c. N. Agafonova; d. S. Gashkov; e. M.Á. Ribes.

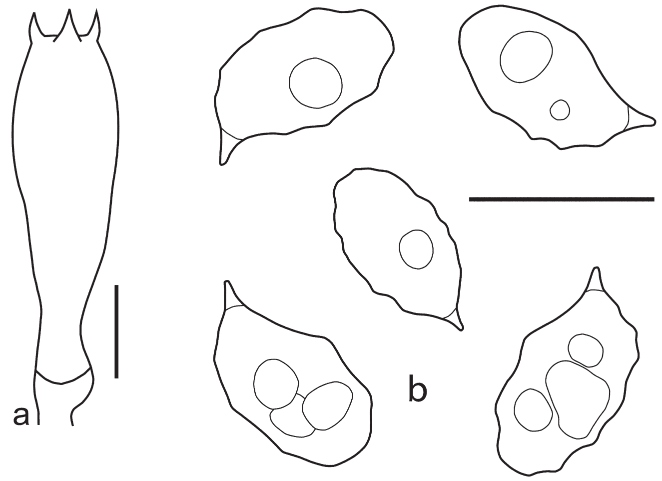

**Fig. 6** *Entoloma chytrophilum*. a. Basidium; b. spores (LE262994). — Scale bars = 10 µm.

*Specimens examined*. Germany, Baden-Württemberg, Langenau-Lindenau, 500 m NN, MTB 7426/4, among conifer needles, 9 Aug. 1985, *M. Enderle*, (M, as *Entoloma lepidissimum* var. *pauciangulatum*, holotype). – Poland, Trójmiejski Landscape Park, Gdansk, Oliwa districy, on *Picea abies* cones in mixed forest (*Fagus sylvatica*, *Pinus sylvestris*, *Picea abies*, *Betula pendula*), 8 Aug. 2010, *M. Wantoch-Rekowska*; ibid., on *Fagus* cupules and woody debris in mixed forest (*Fagus sylvatica*, *Pinus sylvestris*, *Picea abies*, *Betula pendula*), 3 Sept. 2010, *M. Wantoch-Rekowski*; Sudety Mts, Kaczawskie foothills, Mount Szeroka, on *Pinus branches* in *Pinus sylvestris-Larix* sp. forest, 27 Aug. 2010, *J. Soboń*. – Russia, Vologda Region, 'Russky Sever' National Park, Nilovetskoye forestry, on soil in *Picea abies-Pinus sylvestris* forest, 20 Aug. 2004, *O. Kirillova* (LE235259, as *E. lepidissimum*); Novgorod Region, Malaya Vishera District, vicinities of Syujska village, among mosses in *Picea abies-Populus tremula* forest, 7 Aug. 2012, *S. Arslanov* (LE254336); Moscow Region, Zvenigorod Biological Station of Moscow State University, on rotten stump, 24 July 2012, *Yu. Rebriev* (LE254325); Karachaevo-Cherkesia Republik, Teberda Biosphere Reserve, valley of Baduk River, on rotten stump in *Picea orientalis-Abies nordmanniana* forest, 8 Aug. 2009, *E. Malysheva* (LE262993); ibid., vicinities of Teberda, on rotten stump, *K. Potapov*, 22 Aug. 2012 (LE254337); Altaj Republic, Altajsky Nature Reserve, Atkichu, on rotten stumps in flood plain forest, 18 Aug. 2008, *E. Malysheva* (LE262994); Novosibirsk, Akademgorodok, on rotten birch stump near the ICG SB RAS mosel animal breeding facility, 15 June 2008, *T. Bulyonkova* (LE254348); ibid., on rotten pine stump in mixed forest (*Pinus sylvestris*, *Acer negundo*, *Betula pendula*) near ICG SB RAS module, 12 Aug. 2011, *T. Bulyonkova* (LE254326); ibid., on rotten mossy stump in young birch grove bordering mixed forest, with old rotting stumps, 14 July 2010, *T. Bulyonkova* (LE254328). – Spain, Canary Islands, La Palma, in a pot with an orchid, 31 Aug. 1994, *R.M. Dähncke* (855, L, holotype).

Notes — This species has originally been described from the island of La Palma (Islas Canarias, Spain), where it was found on chips of *Pinus* bark in pot with *Cymbidium* in a garden. After that it was collected several times in different types of natural habitats in Europe, Caucasus, Western Siberia. These records fit the original description well (Wölfel & Noordeloos 2001, Noordeloos 2004), and molecular data confirm the conspecifity of the new records with the holotype. *Entoloma chytrophilum* can be recognized by the bright blue colour of the fruitbodies, plano-convex shape of the pileus and lignicolous habit on coniferous wood. From the other blue coloured species (*E. coelestinum*, *E. dichroum*, *E. lepidissimum*) it differs first of all by the rather large, thin-walled and nodulose spores. *Entoloma lepidissimum* var. *pauciangulatum* must be considered a synonym of *E. chytrophilum* due to morphological (almost nodulose spores and blue colour of both pileus and stipe (Gminder & Enderle 1996)) and phylogenetic evidence. Despite a later publication, the epithet '*chytrophilum*' has priority over '*pauciangulatum*' at the rank of species, because the name '*pauciangulatum*' has priority only in the rank of variety in which it was published (Art. 11.2).

### 2. ***Entoloma euchroum*** (Pers.: Fr.) Donk, Bull. Bot. Gard. Buitenzorg, ser. III, 18: 157. 1949. — Fig. 5c–f, 7

Syn.: *Agaricus euchrous* Pers., Syn. Meth. Fung. (Göttingen) 2: 343. 1801; *Agaricus euchrous* Pers.: Fr., Syst. Mycol. 1: 203. 1821; *Leptonia euchroa* (Pers.: Fr.) P. Kumm., Führer Pilzk. (Zwickau): 24, 96. 1871; *Rhodophyllus euchrous* (Pers.: Fr.) Quél., Enchir. Fung.: 60. 1886; *Hyporrhodius euchrous* (Pers.: Fr.) J. Schröt. in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1 (33–40): 615. 1889.

Neotype (designated here). Germany, Baden-Württemberg, Schwäbisch-Fränkischer Wald, Ks. Ostalbkreis, Durlangen, W Täferrot, Rottal, on *Alnus* sp., 25 Aug. 2005, *L. Krieglsteiner* (*KR-M-0032474*).

Pileus 5–40 mm broad, broadly conical, hemisphaerical or campanulate, then convex, often with central depression, not hygrophanous, not translucently striate, radially fibrillose to squamulose all over, violaceous blue, discolouring dark or pale brown with violaceous or purplish tint. *Lamellae* adnate-emarginate, to adnexed often with decurrent tooth, violaceous blue, dark brownish violet, or sometimes discolouring to pale blue, with irregular to serrulate brownish, violaceous or bluish edge. *Stipe* 20–70 × 1–6 mm, cylindrical, slightly broadened to base or distinctly bulbose, solid, longitudinally fibrillose, squamulose in the upper part, violaceous blue, then brownish blue with violaceous or purplish tint, base whitely tomentose. Context concolorous with surface or paler. *Smell* sweet, aromatic like violet flowers, or indistinct, taste unpleasant. *Spores* 9.0–11.5 × 6.0–8.0 µm, Q = 1.2–1.7, heterodiametrical with 6–8 rather blunt angles in side view. *Basidia* 45.8–48.3 × 10.1–12.8 µm, 4-spored, clavate, clamped. *Lamellae edge* heterogeneous. *Cheilocystidia* cylindrical, narrowly clavate or lageniform, sometimes septate, often thick walled in the upper part, hyaline or

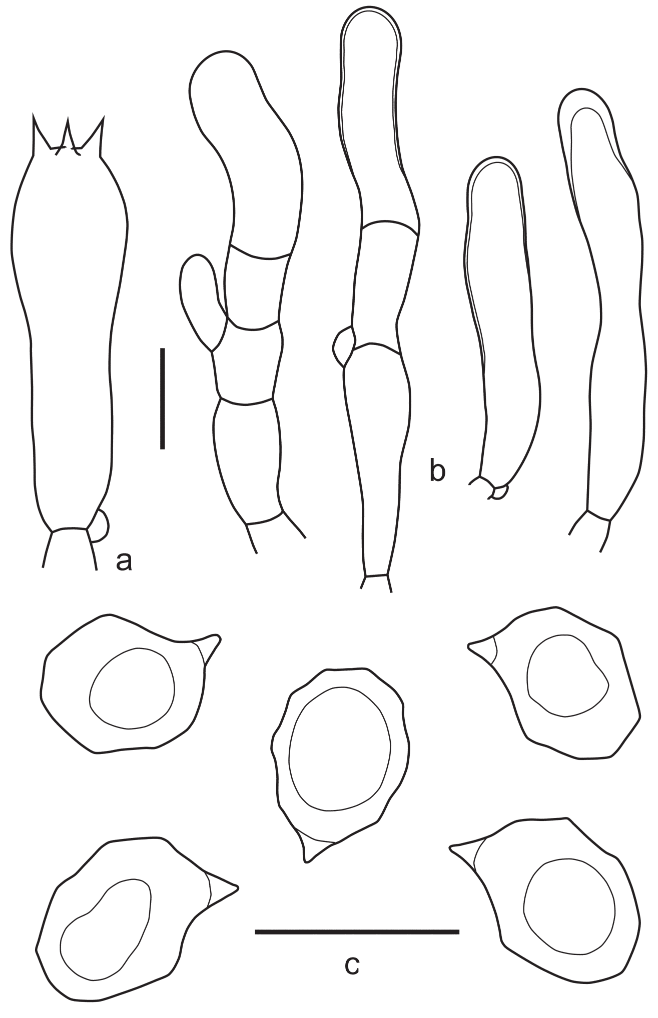

**Fig. 7** *Entoloma euchroum*. a. Spores; b. basidium; c. cheilocystidia (KR 0032474, neotype). — Scale bars = 10 µm.

with violaceous brown content. *Pileipellis* a trichoderm in the centre, plagiotrichoderm towards the pileus margin, made up of cylindrical hyphae with inflated terminal elements, 8–15 µm wide with blue-violaceous or violaceous brown intracellular pigment. *Caulocystidia* present as septate clamped hairs up to 300 µm, colourless or with blue-violaceous intracellular pigment. Hyphae of the trama of both the pileus and the stipe with incrusted pigment. *Clamp-connections* abundant.

Habitat — On dead and living deciduous trees (mostly *Alnus* but also *Quercus*, *Sorbus*, *Corylus*, *Acer*, *Prunus*), exceptionally on coniferous tree (*JVG 1091115A*; Noordeloos 1982a).

Known distribution — Western and Eastern Europe, Canary Islands, Caucasus, Western Siberia, Russian Far East.

*Additional specimens examined.* Germany, Brandenburg, Ks. Uckermark, Gartz, NSG Fauler Ort, on *Alnus* sp., 22 Sept. 1990, *M. Scholler* (KR-M-0033332); Bayern, Rhön, Gefäll, Seebachtal, Buntsandstein, 450 m, MTB/Q 5625/4, *Carici remotae-Fraxinetum*, on *Alnus* sp., 11 Oct. 2003, *L. Krieglsteiner* (KR-M-0005673); Baden-Württemberg, Lorch, N Wachthaus, Haselbachtal, Welzheimer Wald, on *Quercus robur*, 6 Sept. 2007, *L. Krieglsteiner* (KR-M-0032221). – Netherlands, Bloemendaal, Koningshof, 2 Nov. 1974, *C. Bas* (L 6502, as *E. tjallingiorum*). – Russia, Leningrad Region, Kingisepp District, Kotelsky Sanctuary, Sept. 2005, *E. Popov* (LE254334); Novgorod Region, vicinities of the Opechensky Pasad, Gornaya Msta, on the *Alnus glutinosa* stump, *Yu. Rebriev* (LE253879); Moscow Region, Taldom District, Bolshoye Strashevo, 27 Sept. 2010, *C. Lukashin* (LE254333); Ryazan Region, Oksky Nature Reserve, on *Alnus glutinosa*, 2006, *E. Malysheva* (LE254332); Stavropol Territory, on *Acer platanoides* (?) stump, 25 Aug. 2009, *I. Ukhanova* (LE254331); Karachaevo-Cherkesia Republic, Teberdinsky Nature Reserve, valley of Teberda River, on the base of *Alnus glutinosa*, 10 Aug. 2009, *E. Popov* (LE262995); Tomsk, in the planting of birch and pine, on *Prunus padus* stump, 2 Oct. 2007, *N. Agafonova* (LE254329). – Spain, Saga, Cerdanya, Girona, alt. 1050 m, on *Alnus glutinosa* decaying wood, 27 Aug. 2002, *J. Vila* (JVG 1020827-2); Canary Islands, La Malgarida, La Palma, alt. 1080 m, on decaying wood of *Pinus canariensis*, 15 Nov. 2009, *D. Chávez*, *V. Escobio*, *J.F. López*, *J.I. Velaz*, *J.L. Lantigua* and *M.Á. Ribes* (JVG 1091115A).

Notes — *Entoloma euchroum* is a very distinctive species distributed all over Europe and reported also from Siberia. Usually it is easy to recognize due to its entirely blue-violaceous basidiomes, lignicolous habitat and sweet, flowerlike smell. Sometimes it can be rather variable in colour, depending on the growing conditions, but violaceus blue tinges are always present in all parts of the basidioma, especially in the lamellae. It can be distinguished from the other taxa that can possess more or less violaceous-blue lamellae (*E. callichroum* var. *venustum*, *E. lepidissimum*) by the presence of cheilocystidia with a thick-walled upper part, often filled with violaceous brown content cheilocystidia. Cheilocystidia are absent in *E. callichroum* var. *venustum*, rare, and intermixed with basidia in *E. lepidissimum.* Also the squamulose stem and lignicolous habitat help to distinguish *E. euchroum*.

### 3. *Entoloma lampropus* (Fr.: Fr.) Hesler, Beih. Nova Hedwigia 23: 154. 1967. — Fig. 8, 9a, b

Syn.: *Agaricus lampropus* Fr., Observ. Mycol. 1: 19. 1815; *Agaricus lampropus* Fr.: Fr., Syst. Mycol. 1: 203. 1821; *Leptonia lampropus* (Fr.: Fr.) Quél., Mém. Soc. Émul. Montbéliard, sér. 2, 5: 121. 1872; *Rhodophyllus lampropus* (Fr.: Fr.) Quél., Enchir. Fung.: 60. 1886.

Excl.: *Rhodophyllus lampropus* sensu J.E. Lange, Fl. Agar. Dan. 2, pl. 76C. 1937 [=? *E. corvinum* (Kühner) Noordel.]; *Leptonia lampropus* sensu Bres., Iconogr. Mycol. XII, pl. 570-1. 1929; P.D. Orton, Trans. Brit. Mycol. Soc. 43, Suppl.: 105. 1960; *Entoloma lampropus* sensu Hesler, Beih. Nova Hedwigia 23: 154. 1967 [= *E. sodale* Kühner & Romagn. ex Noordel.].

Neotype (designated here): Sweden, Medelpad, Liden, Sundsjöåsen, *T. Læssøe* (as *E. placidum*), 31 Aug. 1999 (UPS:BOT:F-176490).

Pileus 10–40 mm broad, conical or hemispherical expanding to plano-convex with incurved margin and usually slightly depressed centre, not hygrophanous, not translucently striate, entirely radially fibrillose to squamulose at centre, with small dark grey-brown squamules on paler background, most dense at centre, varying from rather pale beige-grey to moderately dark grey-brown, often darker, almost black in centre, sometimes with bluish or lilac tint especially near pileus margin but not very often. *Lamellae* moderately distant, narrowly adnate, emarginate or adnate with small decurrent tooth, sometimes arcuate, whitish to cream becoming greyish or brownish pink, with irregular concolorous edge. *Stipe* 25–65 × 1–3.5 mm, cylindrical or slightly broadened towards base, often twisted, steel blue, brownish or greyish blue, distinctly longitudinally fibrillose-striate with dark blue fibrils, usually glabrous but sometimes flocculose with white or bluish floccules in upper part, base with white tomentum. Flesh whitish, blue beneath the stipe surface. *Smell* not distinctive, taste mild or slightly bitter. *Spores* 8.8–11.5 × 6.0–7.5 µm, Q = 1.3–1.7, heterodiametrical, with 6–9 rather blunt angles in side view. *Basidia* 28.6–35.4 × 9.3–10.5 µm, 4-spored, narrowly clavate, clamped. *Lamellae edge* fertile or heterogeneous. True *cheilocystidia* absent, but terminal elements of tramal hyphae often well developed, 29.0–60.0 × 6.0–13.0 µm, cylindrical, often septate, colourless, clamped. *Pileipellis* trichoderm at centre, a plagiotrichoderm towards margin, composed of cylindrical to slightly inflated hyphae 15–25 µm wide, with both pale intracellular and incrusting pigment and abundant *clamp-connections*.

Habitat — On dead wood of coniferous trees or on soil in forests and open places, including grasslands.

Known distribution — Northern, Western and Eastern Europe, Caucasus, Western Siberia, Russian Far East.

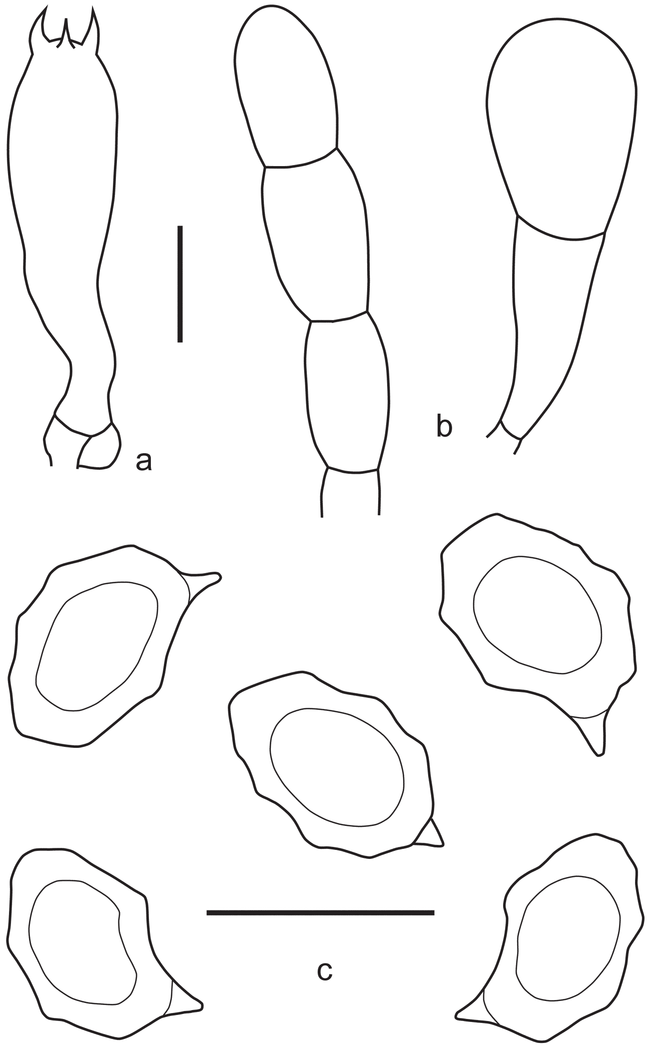

**Fig. 8** *Entoloma lampropus*. a. Basidium; b. cheilocystidia; c. spores (UPS:BOT:F-176490, neotype). — Scale bars = 10 µm.

*Additional specimens examined*. Austria, Frankenberg, Ried, Hinterzeining, 22 Sept 1994, *F. Sucti* (WU 13198, as *E. dichroum*); Rastenfeld, NW Dobra, on wood, 9 Sept. 2009, *A. Hausknecht* (WU 24148, as *E. dichroum*); Burgenland, Oberpullendorf, Tschnurdorf, Seltzabachtal, Pflanzen with *Salix* and *Alnus*, 12 Oct. 1991, *W. Klofoc & A. Hausknecht* (WU 10092, as *E. dichroum*) (WU 10092, as *E. dichroum*). – Germany, Nettetal, 3 Oct. 2009, *G. Wölfel* (1509, L). – Russia, Murmansk Region, Khibiny, Botanical Garden, on soil in *Picea-Betula* forest, 4 Sept. 1974, *L. Mikhailovsky* (LE9121, as *Leptonia placida*); Vologda Region, Kirillov District, Kovarzino, N59°44'28" E038°23'33", on soil in *Picea abies* forest, 26 Aug. 2005, *O. Kirillova* (LE235263); Bryansk Region, Syzemka District, 'Bryansky Les' Nature Reserve, Chykhrai Village, on the base of *Fraxinus exelcior* trunk in broad-leaved forest, 24 Oct. 2012, *A. Fedosova* (LE254339); Tatarstan Republic, Zelenodolsk Region, on decaying wood in *Pinus sylvestris-Tilia cordata* forest, 27 Sept. 2010, *K. Potapov* (LE262991); Udmurtia Republic, vicinities of Izhevsk, on rotten *Picea* stump, 19 July 2009, *V. Kapitonov* (LE254315); ibid., on rotten *Picea* stump in mixed forest, 19 July 2009, *V. Kapitonov* (LE254338); Karachaevo-Cherkesia Republic, Teberda Biosphere Reserve, Arkhyz, on soil in *Abies nordmanniana-Fagus orientalis* forest, 19 Aug. 2009, *O. Morozova* (LE254316); Sverdlovsk Region, Visimsky Natura Reserve, Lipovy Sutuk Mt, N57°24'18" E059°43'34", on burnt soil, *L. Marina*, 3 Sept. 1999 (LE258111); Orenburg Region, Tyulgan District, Tashla Village, on soil in broad-leaved forest, 13 July 2007, *O. Desyatova*, (LE253584, as *E. tjallingiorum*); Novosibirsk, Akademgorodok, mixed forest (*Pinus sylvestris*, *Acer negundo*, *Betula pendula*) near ICG SB RAS module, 11 Aug. 2011, *T. Bulyonkova* (LE262992); Tomsk Region, near airport, on *Larix* stump, 11 Aug. 2006, *N. Agafonova* (LE262985); Kamchatka Region, vicinities of Esso, on decaying wood, 8 Aug. 2005, *O. Morozova* (LE254349). – Spain, València, La Puigmola, alt. 350 m, on *Corylus avellana*, among mosses, 16 Oct. 2011, *S. Català* (RM0855).

Notes — *Entoloma lampropus* is a rather confusing species. It was described by Fries as a species with "pileo subcarnoso convexo cinereo-griseo fibrilloso, lamellis albidis denticulo-adnatis, stipite nitido coeruleo fistuloso" (Fries 1815). In the sanctioning work it was characterized by "pileo demum umbilicate fibrilloso griseo, lamellis adnatis albido-griseis, stipite fistuloso coeruleo" (Fries 1821). The brevity of the description led to various interpretations of the species. In the concept of Lange (1937, pl. 76C), Bresadola (1929, pl. 570-1), Hesler (1967) it represents a species with a smooth stipe without clamp connections, and is considered a member of subg. *Cyanula*. The present work follows the interpretation of Kühner & Romagnesi (1953), which was based on a key phrase in the Fries's description "primo obtutu simillimus priori (*Agaricus placidus*)", stressing the resemblance to *E. placidum*. This interpretation was adopted by Noordeloos (1982a, 1992). The misapplied interpretation of *Agaricus lampropus* mentioned above, was described as a new species, *Rhodophyllus sodalis* Kühner & Romagn., and later on accepted as *E. sodale* Kühner & Romagn. ex Noordel. Noordeloos (1982a) published a modern

**Fig. 9** a, b: *Entoloma lampropus*. a. RM0855; b. LE254315. — c. *E. placidum*. JVG 1060830-6. — d. *E. sublaevisporum* LIP JVG 1070823T, holotype. — Scale bars = 1 cm. — Photos by: a. S. Català; b. V. Kapitonov; c, d. J. Vila.

description of *E. lampropus*, but nevertheless, due to the limited number of records the species continued to be insufficiently known and lot of misidentifications were still encountered in several herbaria during our study. The present study expands the concept of *E. lampropus* with more morphological, ecological and molecular data, and its phylogenetic position is now known, and fixed with a neotype.

*Entoloma lampropus* belongs to the group of species characterized by the many-angled nodulose spores and the presence of 'cheilocystidia' in form of hyphal elements, often septate, arising from the hymenophoral trama. The predominantly grey brown pileus sometimes has a slight lilac tinge near the margin, and the stipe is blue and longitudinally fibrillose, without squamules (contrary to *E. tjallingiorum*). It grows both terrestrial and on rotten wood (mainly coniferous).

### 4. ***Entoloma placidum*** (Fr.: Fr.) Noordel., Persoonia 11, 2: 150. 1981. — Fig. 9c, 10

Syn.: *Agaricus placidus* Fr., Observ. Mycol. 2: 94. 1818; *Agaricus placidus* Fr.: Fr., Syst. Mycol. 1: 202. 1821; *Leptonia placida* (Fr.: Fr.) P. Kumm., Führer Pilzk.: 96. 1871; *Rhodophyllus lampropus* (Fr.: Fr.) Quél., Enchir. Fung.: 60. 1886; *Entoloma placidum* (Fr.) Zerova, in Zerov et al., Viznachnik Ukraïnï 5 Basidiomycetes: 104. 1979 [nom. inval., Art. 33.2].

Epitype (designated here): Sweden, Småland, Femsjö, Hägnen, NW part, on beech stump, 10 Sept. 1948, *S. Lundell* (5276) and *G. Haglund* (UPS: BOT:F-121714, as *Leptonia placida*).

Pileus 10–30 mm broad, conical to convex with straight margin and slightly depressed or umbonate centre, not hygrophanous, not translucently striate, entirely radially fibrillose to minutely squamulose, especially in the centre, with small dark grey-brown squamules on greyish background. *Lamellae* moderately distant, adnate or emarginate, with small decurrent tooth, whitish to cream becoming pink, with concolorous edge. *Stipe* 25–65 × 1–3 mm, cylindrical or slightly broadened towards base, distinctly longitudinally fibrillose-striate with whitish or pale blue fibrils on deep blue background, pruinose in upper part, base with white tomentum. Context whitish, blue beneath the stipe surface. *Smell* and taste farinaceous. *Spores* 8.0–11.0(–11.5) × 6.0–7.0(–7.5) µm, Q = 1.2–1.6, heterodiametrical, with 6–8 blunt angles in side view. *Basidia* 27.0–33.0 × 8.8–11.5 µm, 4-spored, narrowly clavate, clamped. *Lamellae edge* fertile or heterogeneous. Scattered cystidia-like elements sometimes present in the edge of the lamellae as vacuolised basidioles or septate terminal cells of hyphae of the trama. *Pileipellis* a trichoderm in centre, plagiotrichoderm towards margin, composed of cylindrical to slightly inflated hyphae 10–25 µm wide, with intracellular pigment and abundant *clamp-connections*.

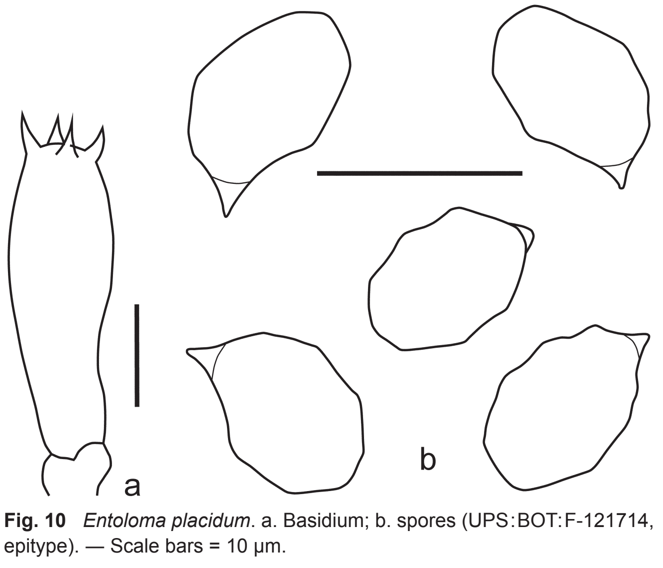

**Fig. 10** *Entoloma placidum*. a. Basidium; b. spores (UPS:BOT:F-121714, epitype). — Scale bars = 10 µm.

Habitat — On dead wood of deciduous trees, mostly *Fagus*, but also *Corylus*, *Betula*, etc.

Known distribution — Western and Eastern Europe, Caucasus.

*Specimens examined*. Russia, Karachaevo-Cherkesia Republic, Teberda Biosphere Reserve, vicinities of Teberda, on beech trunk in *Abies nordmanniana-Fagus orientalis* forest, 7 Aug. 2009, *O. Morozova* (LE254335). – Spain, Lleida, Bòsc d'Aubàs, Bossòst, alt. 1090 m, on plant remnants, especially on small twigs of *Corylus avellana* and *Betula pendula*, 30 Aug. 2006, *J. Carreras*, *J. Vila*, *F. Caballero*, *A. Duran & A. Mayoral* (JVG 1060830-6); ibid., 2 Sept. 2006, *J. Vila*, *F. Caballero & A. Mayoral* (JVG 1060902-2); ibid., 26 Aug. 2008, *F. Caballero* (EFC 2682008-151). – Sweden, Småland (Inre), Femsjö, Hägnen, NW part, on beech stump, 30 Aug. 1949, *S. Lundell* (6020) and *J. Stordal* (UPS:BOT:F-121715, neotype).

Notes — *Entoloma placidum* is very similar to *E. lampropus* due to the grey-brown pileus, blue longitudinally fibrillose stipe without squamules, and more or less nodulose spores. True cheilocystidia are absent in both species, but in some specimens cystidia-like elements can be observed as vacuolised basidioles (Noordeloos 1982a, b) or septate terminal endings of the hyphae of the trama (Vila & Caballero 2007). *Entoloma placidum* can be recognized by the farinaceous smell, distinctly nodulose spores, and habitat on the wood of deciduous trees, especially *Fagus*. For a long time it was known as a species growing exclusively on beech wood. Recently some records were made on other deciduous trees (*Corylus avellana*, *Betula pendula*) (Vila & Caballero 2007). Molecular data confirm that they all belong to *E. placidum*. *Entoloma lampropus* grows on conifers or on soil. *Entoloma tjallingiorum* is also very similar but differs by the distinctly squamulose stipe and well differentiated cheilocystidia.

### 5. ***Entoloma sublaevisporum*** Vila, Noordel. & O.V. Morozova, *sp. nov.* — Mycobank MB803971; Fig. 9d, 11, 12

*Etymology*. From latin 'laevus' (smooth), referring to the very weakly angled, subnodulose to almost smooth spores.

*Holotype*. Spain, Ripollès, Girona, Vall de Carlat, Setcases, alt. 1550 m, in acid soil, under *Pinus uncinata*, *Sarothamnus* sp. and *Urtica* sp., 23 Aug. 2007, *J. Vila & F. Caballero* (LIP JVG 1070823T).

Diagnosis. The species is characterized by the grey-brown pileus, bluish finely longitudinally striate stipe combined with the many-angled, nodulose spores.

Pileus up to 20 mm broad, flattened or slightly convex, with a shallow central depression; grey to pale grey-brown, with darker centre, without violaceous tinges or only a hint in central depression; not hygrophanous, not translucently striate, with fine to heavy fibrils, especially in the apex, where it is subsquamulose; margin straight to revolute, protruding above the lamellae. *Lamellae* moderately distant (L = 15–20) with abundant lamellulae (1 : 3 to 1 : 5), adnate to emarginate, thin, slightly ventricose or not; whitish, turning pale pinkish when spores mature; edge of the same colour, entire or somewhat irregular. *Stipe* central, up to 40 × 2 mm, cylindrical, straight or slightly curved; dark blue to bluish grey; surface smooth or with weak fibrils, finely longitudinally striate; pruinose at apex and with white basal tomentum. Flesh very thin, greyish on the pileus and grey-bluish grey on the stipe; *smell* fungoid. *Spores* 7.7–9.3 × 4.8–5.9 µm, average 8.5 × 5.3 µm, Q = 1.4–1.8, Qm = 1.6, heterodiametrical, with very weak angles, subnodulose to almost smooth. *Basidia* 27.6–32.8 × 9.7–11.7 µm, 4-spored, rarely 2-spored, narrowly clavate, clamped. *Lamellae edge* fertile or heterogeneous. *Cheilocystidia* absent in holotype, sometimes present, intermixed with basidia, 23.2–45.0 × 5.0–7.8, subcylindrical, flexuose to lageniform, sometimes with long tapering neck, frequently septate. Hymenial trama cyanophilous. *Pileipellis* a trichoderm structure composed of cylindrical hyphae, 20–28 µm wide, with fusiform terminal elements; pigment mixed, brownish

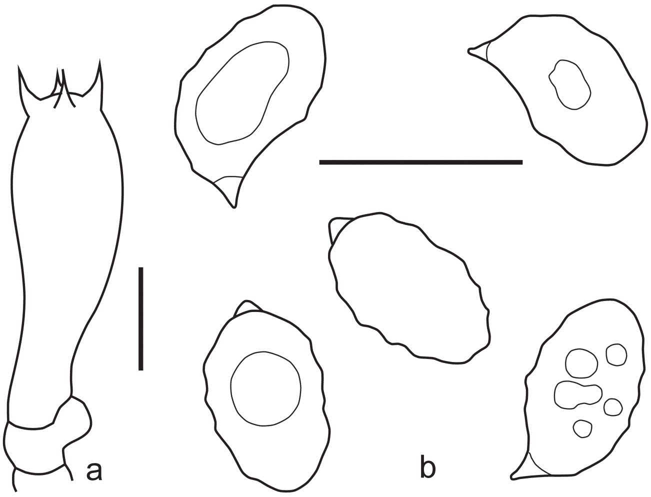

**Fig. 11** *Entoloma sublaevisporum*. a. Basidium; b. spores (LIP JVG 1070823T, holotype). — Scale bars = 10 μm.

vacuolar pigment abundant, also encrusting epiparietal present, especially on thin hyphae. *Clamp-connections* very abundant in hymenium structures, scarce on the hyphae of the pileipellis.

Habitat — On soil, in pine (*Pinus uncinata*) forest.

Known distribution — Western Europe (Austria, Spain (holotype)).

*Additional material examined*. Austria, Kärnten, Eisenkappel, Vellacher Kotscha, 7 Sept. 1998, *A. Hausknecht* (MEN 9858).

Notes — According to the phylogenetic analysis the new species is close to *E. chytrophilum.* Morphologically this similarity is confirmed by the spore morphology. *Entoloma sublaevisporum* differs from *E. chytrophilum* particularly by the greyish brown colour of the pileus and smaller spores. The many-angled, nodulose spores distinguish it from the other species with grey-brown pileus (*E. lampropus*, *E. placidum*, *E. tjallingiorum*). Cheilocystidia were found only in the specimen from Austria. The p-distance between *E. chytrophilum* and *E. sublaevisporum* is 7.4 %.

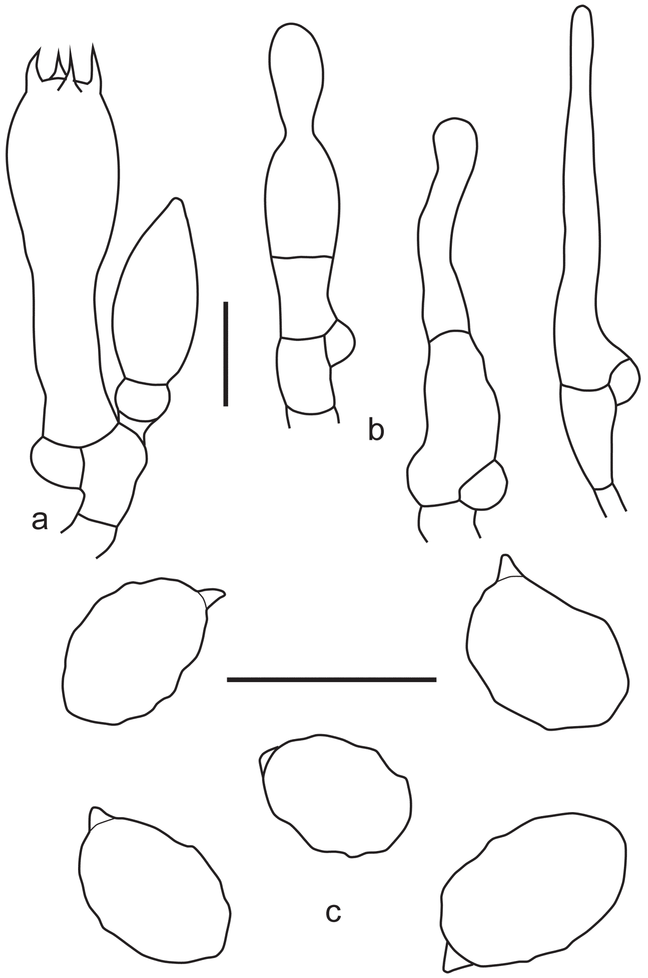

**Fig. 12** *Entoloma sublaevisporum*. a. Basidium; b. cheilocystidia; c. spores (MEN 9858). — Scale bars = 10 μm.

### 6. ***Entoloma tjallingiorum*** Noordel., Persoonia 11: 465. 1982

Syn.: *Leptonia tjallingiorum* (Noordel.) P.D. Orton, Mycologist 5, 3: 135. 1991.

Misapplied names: *Agaricus dichrous* sensu Fr., Summa Veg. Scand. 2: 287. 1849; *Agaricus dichrous* sensu Fr., Ic. Sel. Hymenomyc. 1, pl. 92. 1867; *Entoloma dichroum* sensu Bres., Iconogr. Mycol. 12, pl. 554. 1929; *Entoloma dichroum* sensu Konrad & Maubl., Icon. Sel. Fung. 2, pl. 190, f. 2. 1932; *Rhodophyllus dichrous* sensu J.E. Lange, Fl. Agar. Dan. 2, pl. 72A. 1937; *Rhodophyllus dichrous* sensu Romagn., Bull. Soc. Mycol. France 92: 292. 1976; *Agaricus placidus* sensu Fr., Ic. Sel. Hymenomyc. 1, pl. 97, f. 1. 1867.

#### **a.** var. ***tjallingiorum*** — Fig. 13a–c, 14

Pileus 20–80 mm broad, hemispherical expanding to conico-convex or applanate, with low broad umbo, sometimes depressed, with involute then straight margin, not hygrophanous, not translucently striate, entirely radially fibrillose to squamulose in centre, light to moderately dark grey-brown, often with violaceous blue tinges near pileus margin. *Lamellae* adnate with small decurrent tooth or arcuate, whitish to cream in youth becoming pink, with irregular concolorous edge. *Stipe* 25–100 × 5–10 mm, cylindrical or broadened towards base, fibrillose, entirely squamulose with dark blue squamules, more intensively coloured in upper part, greyish blue or violaceous-blue below, base with white tomentum. Flesh whitish, blue beneath the stipe surface. *Smell* indistinct, taste mild or bitterish. *Spores* 8.0–11.0(–12.0) × 5.8–7.2(–7.6) μm, Q = 1.3–1.5, heterodiametrical, with 6–9 rather blunt angles in side view. *Basidia* 32.6–40.4 × 8.6–10.3 μm, 4-spored, narrowly clavate, clamped. *Lamellae edge* heterogeneous or, rarely, sterile. *Cheilocystidia* 29.7–71.1 × 5.9–8.7 μm, cylindrical, narrowly lageniform or irregularly shaped, sometimes septate, sometimes represented by strands of terminal elements of hyphae of the hymenial trama, colourless. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 7–20 μm wide, with both brown intracellular and incrusting pigment and abundant *clamp-connections*. *Caulocystidia* present as long, up to 250 μm, septate, clamped hairs, with cylindrical or lageniform terminal elements, 60–120 × 8–12 μm, colourless or with incrusting and blue intracellular pigment.

Habitat — On soil or on dead wood of mostly broad-leaved trees (*Quercus* spp.), but also on *Betula* and *Alnus* in deciduous and mixed forests.

Known distribution — Western and Eastern Europe, Western Siberia.

*Specimens examined*. Russia, Leningrad Region, Sovkhozy, Sept. 1936, around trunks in *Alnus* forest, *R. Singer* (LE9123, as *Leptonia placida*); Novgorod Region, 'Valdajsky' National Park, Valdaj District, Poddub'e, 22 Sept. 2011, on soil in broad-leaved-coniferous (*Picea abies*) forest, *O. Morozova* (LE254318); Moscow Region, Taldom District, Bolshoye Strashevo, 27 Sept. 2010, *E. Lukashina* (LE254320); Tatarstan Republic, Kazan', Sovetsky District, 'Skotskiye Gory' Park, on soil in broad-leaved forest (*Tilia cordata*, *Quercus robur*, *Betula pendula*), 29 Sept. 2011, *K. Potapov* (LE254317); Ulyanovsk Region, on soil in broad-leaved forest, 14 Aug. 2009, *E. Ilyukhin* (LE254319). – Spain, Barcelona, Can Romegosa, Sant Fost de Campsentelles, alt. 140 m, on trunk of *Quercus pubescens*, 5 Oct. 2008, *F. Caballero* (SFC 081005-01); ibid., *F. Caballero* (SFC 081019-01); ibid., 16 Nov. 2008, *J. Vila & F. Caballero* (JVG 1081116-5). – Sweden, Uppland, Bondkyrka, Predikstolen, on soil and rotten wood of *Quercus*, 4 Oct. 1980, *S. Ryman* (6124) (UPS:BOT:F-016378, holotype).

**Fig. 13** a–c: *Entoloma tjallingiorum* var. *tjallingiorum*. a. LE254317; b. JVG 1081116-5; c. LE227507. — d, e. *E. tjallingiorum* var. *alnetorum* LE254321. — f, g: *E. tjallingiorum* var. *laricinum*. f. LE254343, holotype; g. LE254344. — Scale bars = 1 cm. — Photos by: a. K. Potapov; b. J. Vila; c. A. Kovalenko; d, e, g. O. Morozova.

*Additional specimens examined (grouped together with the E. alnetorum holotype).* Russia, Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, Maloye Kamennoye Pole, *Tilia cordata-Acer platanoides* forest, 16 Aug. 2004, *O. Morozova* (LE227507); ibid., 17 Sept. 2004, *E. Malysheva* (LE234285); ibid., vicinities of Bakhilova Polyana, *Tilia cordata-Acer platanoides* forest, 1 Sept. 2004, *E. Malysheva* (LE227584, as *Entoloma placidum*).

Notes — *Entoloma tjallingiorum* belongs to the group of species characterized by the many-angled almost nodulose spores and septate terminal elements of the hymenophoral trama that protrude through the hymenium ('cheilocystidia'). Among the species with greyish brown pileus and blue stipe it stands out by the stouter basidiocarps and distinctly squamulose stipe.

In an earlier paper (Noordeloos 1982a, 1992) some collections with a bluish tinge in the lamellae and pigmented cheilocystidia were also assigned to *E. tjallingiorum*. Molecular data show that these specimens are discolored forms of *E. euchroum*. The current concept of *E. tjallingiorum* therefore excludes forms with blue tinges in the lamellae.

As was shown by the phylogenetic analysis, the evolutionary process within this species continues at the present time: several lineages in the early stage of divergence were revealed. As a result, based on molecular and morphological differences, as well as geographical distribution, two more varieties of *E. tjallingiorum* can be distinguished. But the limits between these varieties are sometimes vague and intermediate forms have been found. So, the specimens from Zhiguli (LE227507, LE227584, LE234285) despite the genetic affinity with var. *alnetorum* are morphologically closer to the type variety. The specimen from Novgorod (LE254318) possesses in some lamellae rather large sites of sterile edge which are characteristic for var. *laricinum*.

### b. var. *alnetorum* (Monthoux & Röllin) O.V. Morozova, Noordel. & Vila, *comb. nov*. — Mycobank MB803972; Fig. 13d, e, 15

*Basionym. Entoloma alnetorum* Monthoux & Röllin, Mycol. Helv. 3, 1: 43. 1988.

Pileus 20–40 mm broad, hemispherical expanding to plano-convex with incurved fimbriate margin, not hygrophanous, not translucently striate, entirely tomentose when young, becoming radially fibrillose to squamulose at centre, cream to pale ochraceous at first, then sordid ochre. *Lamellae* adnate with small decurrent tooth or arcuate, whitish to cream in youth becoming pink, with irregular concolorous edge. *Stipe* 25–80 × 5–10 mm, cylindrical, broadened towards base, fibrillose-striate, entirely squamulose with dark squamules, violaceous in upper part and whitish below, base with white tomentum. Flesh whitish, blue beneath the stipe surface. *Smell* fruitish, taste mild or slightly spermatic. *Spores* 8.1–11.3 × 5.5–7.2 µm, Q = 1.4–1.8(–1.9), heterodiametrical, with 6–9 rather blunt angles in side view. *Basidia* 37.0–39.6 × 11.7–13.0 µm, 2- or 4-spored, narrowly clavate, clamped. *Lamellae edge* sterile or heterogeneous. *Cheilocystidia* 39.8–69.1 × 6.6–15 µm, cylindrical, narrowly lageniform or irregularly shaped, sometimes septate, colourless. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 15–25 µm wide, with both pale intracellular and

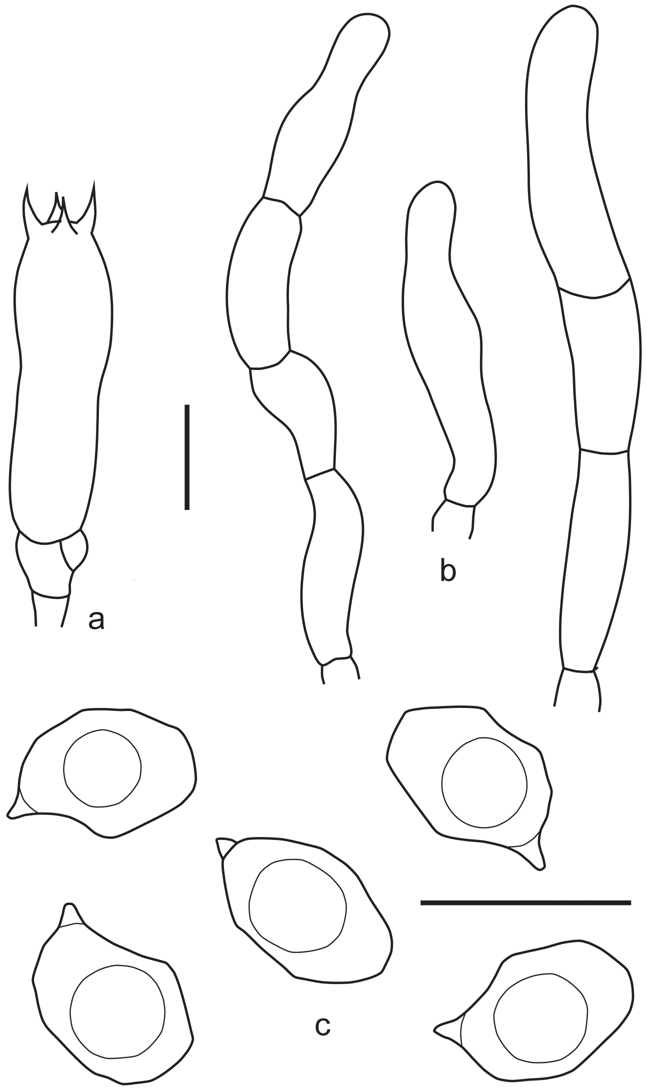

**Fig. 14** *Entoloma tjallingiorum* var. *tjallingiorum*. a. Basidium; b. cheilocystidia; c. spores (LE254318). — Scale bars = 10 µm.

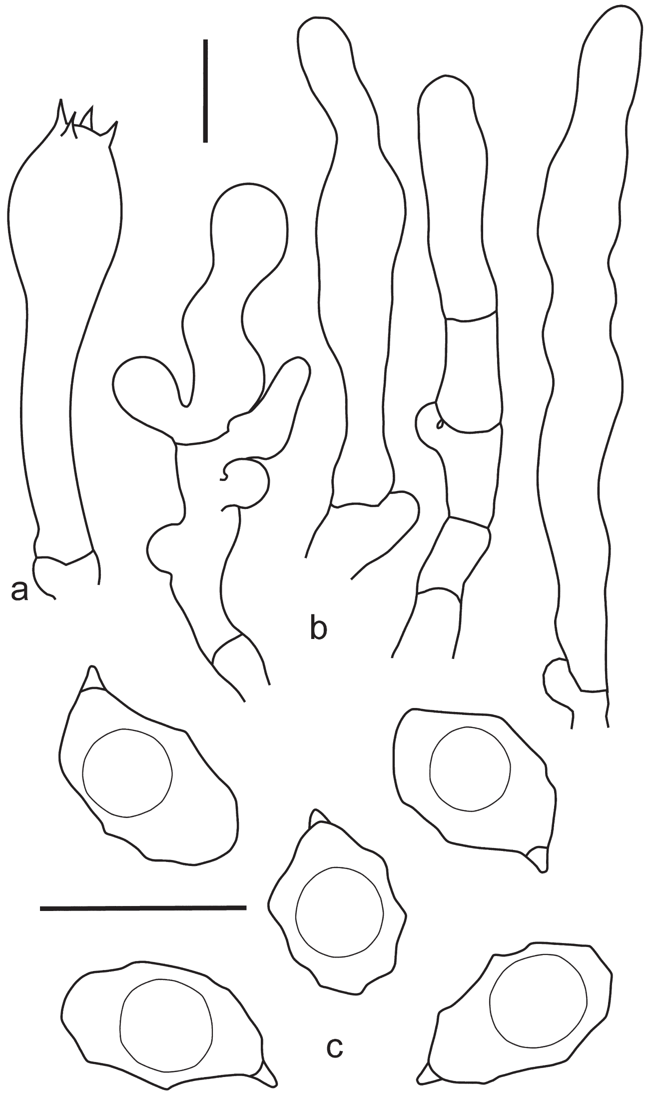

**Fig. 15** *Entoloma tjallingiorum* var. *alnetorum*. a. Basidium; b. cheilocystidia; c. spores (LE254321). — Scale bars = 10 µm.

incrusting pigment and abundant *clamp-connections*. *Caulocystidia* present as long, up to 250 µm, septate clamped hairs, with lageniform, cylindrical or subcapitate terminal elements 30–90 × 6–12 µm, colourless or with blue or violaceous intracellular pigment.

Habitat — On dead wood of *Alnus incana* in deciduous forests in May–June, rarely also in July or August.

Known distribution — Western and Eastern Europe, Western Siberia.

*Specimens examined*. Russia, Leningrad Region, Kirovsk District, Vasilkovo, left bank of Lava River, on dead trunk of *Alnus incana* in *Alnus incana*-*Ulmus glabra* forest, 11 June 2009, *E. Popov* (LE254321); Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, on soil in *Alnus glutinosa* flood plain forest, 15 June 2004, *E. Malysheva* (LE234287); ibid., on soil in *Acer platanoides*-*Tilia cordata* forest, 18 Aug. 2004, *E. Malysheva* (LE227527); Tumen Region, Surgut district, Yugansky Nature Reserve, Kamenny, on soil in *Pinus sibirica*-*Abies sibirica* forest, 9 July 2006, *E. Zvyagina* (LE254322). – Switzerland, Nant-Bride, Sixt, on old trunks and branches of *Alnus incana* in submontane *Alnus* forest, alt. ± 850 m, 28 June 1986, *O. Röllin* (G00111402, holotype); ibid., 29 May 1994, *O. Röllin* (L).

Notes — *Entoloma alnetorum* has been described as a species very similar to *E. tjallingiorum* due to the thin-walled, almost nodulose spores, however it is distinguished by the pale ochraceus pileus and the vernal appearance in *Alnus* forests (Monthoux & Röllin 1988). Phylogenetic analysis shows that all specimens possessing these features are grouped together. At the same time the difference between them and typical *E. tjallingiorum* is very small (p-distance between holotypes is 1.3 %). Some specimens (LE227507, LE227584, LE234285) with the typical habit of *E. tjallingiorum* occur in the *E. alnetorum*-clade with the difference only in 0.2 %. For this reason we decided to consider *E. alnetorum* as a variety of *E. tjallingiorum*. It is noteworthy that in *E. dichroum* also specimens with a pale pileus can be encountered (JVG 1070821-4). They can be separated from the species of the *tjallingiorum*-group by the characteristic spores with sharp angles.

### **c.** var. ***laricinum*** O.V. Morozova, Noordel., Vila & E.S. Popov, *var. nov.* — Mycobank MB803973; Fig. 13f, g, 16

*Etymology*. The name refers to the substrate on which it has been found (*Larix cajanderi*).

*Holotype*. Russia, Kamchatka Region, vicinities of Esso, on dead wood of *Larix cajanderi*, 8 Aug. 2005, *E. Popov* & *O. Morozova* (LE254343).

Diagnosis. *Entoloma tjallingiorum* var. *laricinum* differs from the type variety by the sterile lamellae edge with long septate ‘cheilocystidia’ (terminal elements of the hymenophoral trama) as well as by growing on *Larix* wood.

Pileus 20–60 mm broad, hemispherical expanding to conico-convex or applanate, with low broad umbo, with involute then straight margin, not hygrophanous, not translucently striate, entirely radially fibrillose with light grey-brown fibrils and squamules on whitish background, with violaceous blue tinge near pileus margin. *Lamellae* adnate with small decurrent tooth or arcuate, whitish to cream in youth becoming pink, with irregular concolorous edge. *Stipe* 25–80 × 5–15 mm, cylindrical or broadened towards base up to 20 mm, fibrillose, entirely squamulose with dark violaceous-blue or violaceous-grey squamules on paler, almost white background, base with white tomentum. Flesh whitish, blue beneath the stipe surface. *Smell* indistinct, taste mild. *Spores* 8.5–11.3 × 5.5–7.4 µm, Q = 1.4–1.7, heterodiametrical, with 6–9 rather blunt angles in side view. *Basidia* 35.4–42.2 × 10.3–13.1 µm, 4-spored, clavate, clamped. *Lamellae edge* sterile. *Cheilocystidia* 29.7–71.1 × 5.9–8.7 µm, cylindrical, flexuous, septate, represented by strands of terminal elements of hyphae of the hymenial trama, colourless. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 7–20 µm wide, with both brown intracellular and incrusting pigments and abundant *clamp-connections*. *Caulocystidia* present as long, up to 350 µm, septate clamped hairs, with lageniform or cylindrical terminal elements 50–120 × 6–12 µm, colourless or with incrusting and blue intracellular pigment.

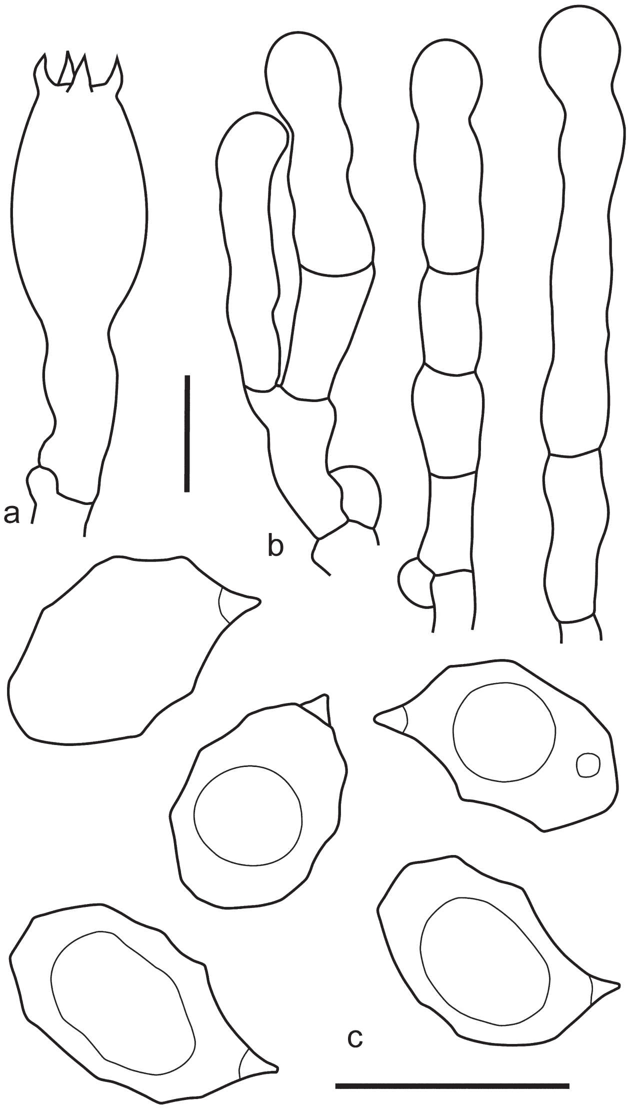

**Fig. 16** *Entoloma tjallingiorum* var. *laricinum*. a. Basidium; b. cheilocystidia; c. spores (LE254343, holotype). — Scale bars = 10 µm.

Habitat — On rotten wood of *Larix* in mixed *L. cajanderi*-*Betula ermanii* forest.

Known distribution — Russian Far East.

*Additional specimen examined*. Russia, Kamchatka Region, vicinities of Esso, on burnt wood of *Larix cajanderi*, 8 Aug. 2005, *E. Popov* & *O. Morozova* (LE254344).

Notes — Although *E. tjallingiorum* var. *laricinum* can be distinguished from the typical variety by the sterile lamella edge with abundant, septate terminal elements of the hymenophoral trama, this character is not reliable enough to make a clear-cut morphological distinction. Sometimes we find this character also in the typical variety. The main distinctive features are the habitat (growing on *Larix cajanderi*) and the geographic origin, the rather isolated Kamchatka Peninsula. This may explain the significant genetic divergence (p-distance 3.3 %).

### Section ***Dichroi*** O.V. Morozova, Noordel. & Vila, *sect. nov.* — Mycobank MB803974

*Type species*. *Entoloma dichroum* (Pers.: Fr.) P. Kumm.

Habit collybioid or tricholomatoid; pileus conico-convex or plano-convex; *lamellae* almost free to emarginate; *stipe* flocculose to squamulose; *lamellae edge* sterile or heterogeneous; *cheilocystidia* present, spores with sharp angles, *pileipellis* more or less trichoderm of inflated elements with intracellular pigment; brilliant granules absent; *clamp-connections* present and often frequent; terrestrial, in forests.

### 7. ***Entoloma dichroum*** (Pers.: Fr.) P. Kumm., Führer Pilzk.: 97. 1871. — Fig. 17a–c, 18

Syn.: *Agaricus dichrous* Pers., Syn. Meth. Fung. (Göttingen) 2: 343. 1801; *Rhodophyllus dichrous* (Pers.: Fr.) Quél., Enchir. Fung. (Paris): 58. 1886; *Leptonia dichroa* (Pers.) P.D. Orton, Mycologist 5, 3: 132. 1991.

Excl.: *Agaricus dichrous* sensu Fries 1849, 1867; *Entoloma dichroum* sensu Bresadola 1929; sensu Konrad & Maublanc 1932; *Rhodophyllus dichrous* sensu Lange 1937; sensu Kühner & Romagnesi 1953 (= *E. tjallingiorum*).

*Neotype (designated here)*. Russia, Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, Malaya Bakhilova Hill, broad-leaved forest, 26 Aug. 2003, *E. Malysheva* (LE227472).

Pileus 5–35 mm broad, conical or hemispherical, hardly expanding with age, with involute then straight margin, not hygrophanous, not translucently striate, dark violaceous-blue, purplish brown, or very pale, greyish with lilac tinge, entirely granular-fibrillose, becoming squamulose with violaceous-blue squamules on pale background. *Lamellae* adnate-emarginate with decurrent tooth, white then pinkish, with entire concolorous edge. *Stipe* 30–80 × 2–5 mm, clavate or cylindrical with slightly swollen base, deep blue, different from colour of pileus, longitudinally fibrillose, with dark blue squamules on the paler background, base with white tomentum. Flesh white, dark blue under the surface. *Smell* indistinct, taste unpleasant. *Spores* 9.2–11.5 × 6.4–7.7 µm, Q = 1.3–1.7, heterodiametrical, with 5–7 pronounced angles in side view. *Basidia* 44.2–51.4 × 8.5–10.5 µm, clavate, clamped. *Lamellae edge* heterogeneous. *Cheilocystidia* 20–45 × 5–11 µm, cylindrical, narrowly lageniform or irregularly shaped, sometimes septate, colourless, scattered among basidia. *Pileipellis* a trichoderm of cylindrical hyphae with terminal elements 35–120 × 15–35 µm with blue intracellular pigment and abundant *clamp-connections*. *Caulocystidia* present as long, up to 300 µm, septate clamped hairs, with tapering terminal elements, 50–110 × 8–12 µm, with dark blue intracellular pigment.

Habitat — On soil in deciduous forests.

Known distribution — Western and Eastern Europe.

*Additional specimens examined*. Russia, Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, Maloye Kamennoye Pole, *Tilia cordata* forest, 3 July 2005, *E. Malysheva* (LE234260). – Spain, Girona,

**Fig. 17** a–c: *Entoloma dichroum*. a. LE227472 (photo taken at the neotype locality); b. herbarium SGC; c. JVG 1070821-4. — d. *E. eugenei* LE 253771, holotype. — e, f. *E. allochroum* LE254324. — Scale bars = 1 cm. — Photos by: a, d. O. Morozova; b. S. Català; c. J. Vila; e, f. K. Potapov.

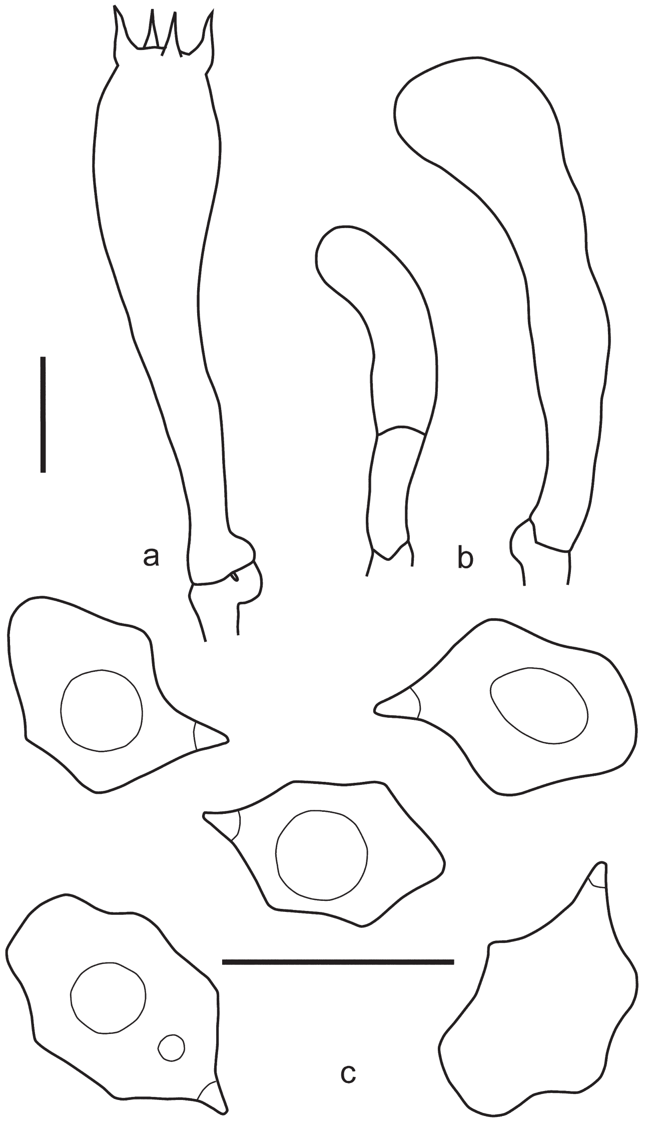

**Fig. 18** *Entoloma dichroum*. a. Basidium; b. cheilocystidia; c. spores (LE227472, neotype). — Scale bars = 10 µm.

Torrent Burgil, Pardines, alt. 1425 m, in acid soil, under *Buxus sempervirens*, 21 Aug. 2007, *J. Vila & F. Caballero* (JVG 1070821-4); València, La Puigmola, alt. 350 m, in basic soil, under *Pinus halepensis*, among mosses, 16 Oct. 2011, *S. Català* (herbarium SGC).

Notes — *Entoloma dichroum* together with *E. eugenei* forms a separate clade genetically characterized by the large insertion in the ITS1-region. Morphologically, *E. dichroum* can be recognized by the bright blue squamulose stipe and spores with 5–7 sharp angles. The pileus colour, however, varies considerably among the studied collections, from bright blue to violaceous-blue, violaceous-brown and pale brown. The ITS-sequences slightly vary, however this variability (p-distance 1.4–2 % base-pair difference) might well be acceptable within a species. More material would possibly allow for the distinction of varieties. *Entoloma allochroum*, another species with sharply-angled spores possesses a lilaceous or violaceous, less squamulose, more longitudinally fibrillose stipe. *Entoloma dichroum* differs from the closely related *E. eugenei* mainly by the slender collybioid habit, the heterogeneous lamellae edge, and slightly smaller and less pronouncedly angled spores.

### 8. ***Entoloma eugenei*** Noordel. & O.V. Morozova, Mycotaxon 112: 234. 2010. — Fig. 17d, 19

Pileus 13–60 mm broad, hemispherical expanding to plano-convex with incurved margin, fleshy, not hygrophanous, not translucently striate, entirely velvety when young, becoming glabrous at the margin, uniformly deep blue (Indian blue) at first, then with violet tinge at margin. *Lamellae* adnate-emarginate with decurrent tooth, pure white then pinkish, with irregular concolorous edge. *Stipe* 30–80 × 4–8 mm, clavate or cylindrical with swollen base (to 15 mm), concolourous with the pileus or slightly paler, entirely squamulose with concolorous squamules, base white tomentouse. Flesh white, dark blue beneath the surface. *Smell* slightly spicy, taste mild. *Spores* 10.0–12.5 × 6.0–8.0 µm, Q = 1.3–1.7, heterodiametrical, with 5–7 angles in side view. *Basidia* 34–44 × 9–12 µm, clavate, clamped. *Lamellae edge* sterile. *Cheilocystidia* 28.0–39.0 × 6.5–15.5 µm, cylindrical, narrowly lageniform or irregularly shaped, colourless. *Pileipellis* a trichoderm of cylindrical hyphae with terminal elements 90–200 × 12–20 µm with blue intracellular pigment and abundant *clamp-connections*. *Caulocystidia* present as long, up to 250 µm, septate clamped hairs, with tapering or cylindrical terminal elements 50–100 × 8–12 µm, with dark blue intracellular pigment.

Habitat — On soil in the flood plain forest.

Known distribution — Russian Far East, Japan (GenBank AB509605, as *Entoloma* aff. *kujuense*).

*Specimens examined*. Russia, Primorsky Territory, Kedrovaya Pad Nature Reserve, the right bank of the Kedrovaya River, N43°05'51" E131°33'34", 24 Aug. 2005, *E. Popov* (LE253771, holotype); ibid., 8 Sept. 1994, *E. Bulach* (VLA M-3556); ibid., Leopardovy Sanctuary, watershed of the rivers Gryaznaya and Ananjevka, on the base of dead trunk, 1 Sept. 2011, *A. Kovalenko* (LE254340); ibid., 1 Sept. 2011, *T. Svetasheva* (LE254347).

Notes — *Entoloma eugenei* is morphologically very close to *E. dichroum*. The main morphological difference is in its tri-

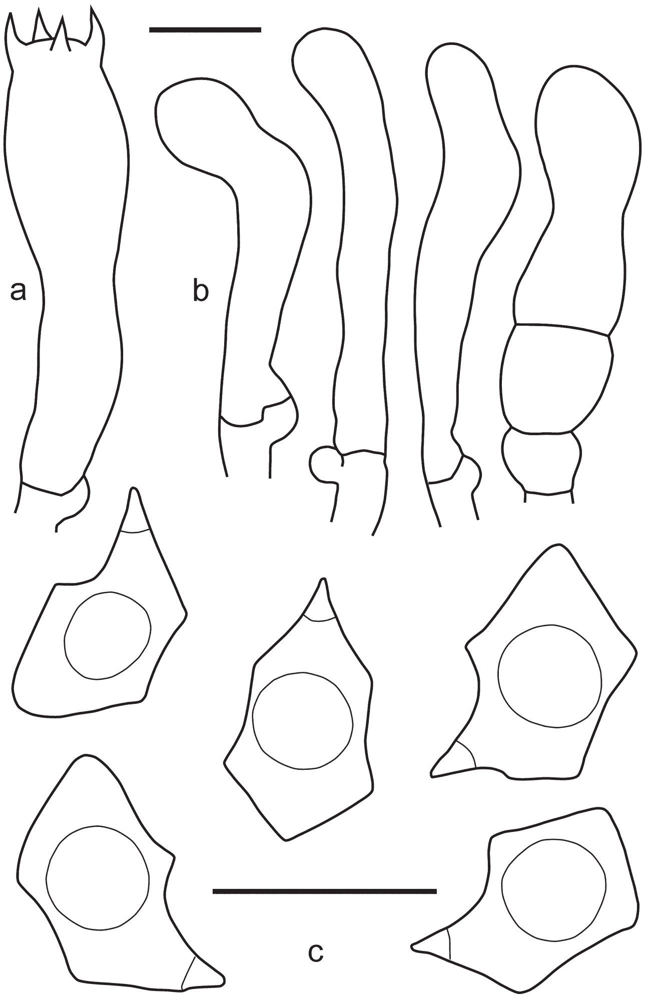

**Fig. 19** *Entoloma eugenei*. a. Basidium; b. cheilocystidia; c. spores (LE253771, holotype). — Scale bars = 10 µm.

cholomatoid habit, the sterile lamellae edge, and slightly larger and more pronouncedly angled spores. Genetically it differs from *E. dichroum* among other things in one rather large (about 40 base-pair) insertion in the ITS1-region. The significant divergence between these two species (p-distance 9.8 % base-pair difference) could be explained by geographical reasons – the natural isolated habitat of *E. eugenei* in the Southern Far East and Japan with unique climatic conditions (Noordeloos & Morozova 2010), while *E. dichroum* is known from Europe.

## INCERTAE SEDIS

### 9. *Entoloma allochroum* Noordel., Persoonia 11, 4: 463. 1982. — Fig. 17e, f, 20

Pileus 20–40 mm diam, conical, then convex with umbo, expanded to plano-convex, not or hardly hygrophanous, not translucently striate or at margin only, with straight margin, first with greyish brownish lilaceus tinged velvety covering later breaking up into brownish lilac squamules on pale background. *Lamellae* moderately crowded, adnate-emarginate, adnexed to almost free, ventricose, whitish, becoming pinkish, with entire to irregular concolorous edge. *Stipe* 40–70 × 3–6 mm, cylindrical, broadened towards the base, pale violaceous, entirely covered with darker fibrillose squamules, with white tomentum at base. Context greyish, darker under the surface, yellowish at the stem base. *Smell* agreeable or indistinct, taste indistinct. *Spores* 8.3–12.5 × 6.2–9.5 µm, Q = 1.3–1.6, heterodiametrical, with 5–8 rather pronounced angles. *Basidia* 32.6–44.2 × 11.9–15.7 µm, 4-spored, clavate, clamped. *Lamellae edge* heterogeneous. *Cheilocystidia* 32.4–57.4 × 5.5–15.7 µm, cylindrical to flexuose, septate, rare or absent. *Pileipellis* a trichoderm of cylindrical to inflated hyphae with terminal elements 15–40 µm wide with brownish violaceous intracellular pigment. Some hyphae of pileitrama incrusted. *Clamp-connections* present.

Habitat — On soil and plant remains in broad-leaved forests and parks.

Known distribution — Western Europe, Caucasus.

*Specimens examined*. Austria, Vellacher Kotscha, Eisenkappel, Karinthia, 7 Sept. 1998, *K.F. Reinwald & A. Hausknecht* (L9860). – Germany, Mühltal bei Willisau, im feuchten Eschen-haselnusswald zwischen Moosen und Schachtelhalmen auf feuchter, lehmiger Erde in der Nähe des Bachufers, 21 Sept. 1984, *G. Wölfel* (L: E4884, as *E. dichroum* (Noordeloos 2004: 1276, upper fig.). – Netherlands, Aerdenhout, 29 July 1973, *Kits van Waveren* (holotype L); Apeldoorn, Vellertsdijk, 7 Aug. 1993, *L. Bos* (L, as *E. tjallingiorum*); Paterswolde, Vennebroek, 14 Aug. 2000, *R. Chrispijn* (L). – Russia, Caucasus Biosphere Reserve, valley of the Pslukh River, on soil in broad-leaved forest with *Fagus orientalis*, *Alnus glutinosa*, *Abies nordmanniana*, 29 Aug. 2006, *A. Kiyashko* (LE262984); Karachaevo-Cherkesia Republik, Teberda Biosphere Reserve, Dombaj, on rotten stump in *Abies nordmanniana-Fagus orientalis* forest, 14 Aug. 2012, *T. Svetasheva* (LE254342); ibid., Teberda, on rotten stump in *Fagus orientalis* forest, 19 Aug. 2012, *K. Potapov* (LE254324). – Spain, Val d'Aran, Lleida, alt. 1090 m, on plant debris in forest of *Alnus glutinosa*, *Populus* sp., *Fraxinus excelsior*, 2 Sept. 2006, *J. Vila*, *F. Caballero*, *A. Mayoral* (JVG 1060902-1); ibid., 24 Aug. 2008, *F. Caballero* (EFC 2482008-148); Espinavell, Girona, alt. 1350 m, in acid soil, under *Corylus avellana*, 12 July 2008, *F. Caballero* (EFC 1272008-137). – Switzerland, Schonau, Tunau, 20 Sept. 2009, *G. Wölfel* (L, E0809).

Notes — *Entoloma allochroum* is an easily recognizable species due to the presence of the lilaceous or violaceous colours both in the pileus and, especially, in the stipe, white lamellae, as well as rather thick-walled and pronouncedly angled spores. Due to the sharply-angled spores *E. allochroum* is similar to *E. dichroum* and *E. eugenei*, however the molecular evidence does not allow the placing of this species in sect. *Dichroi* (Fig. 2).

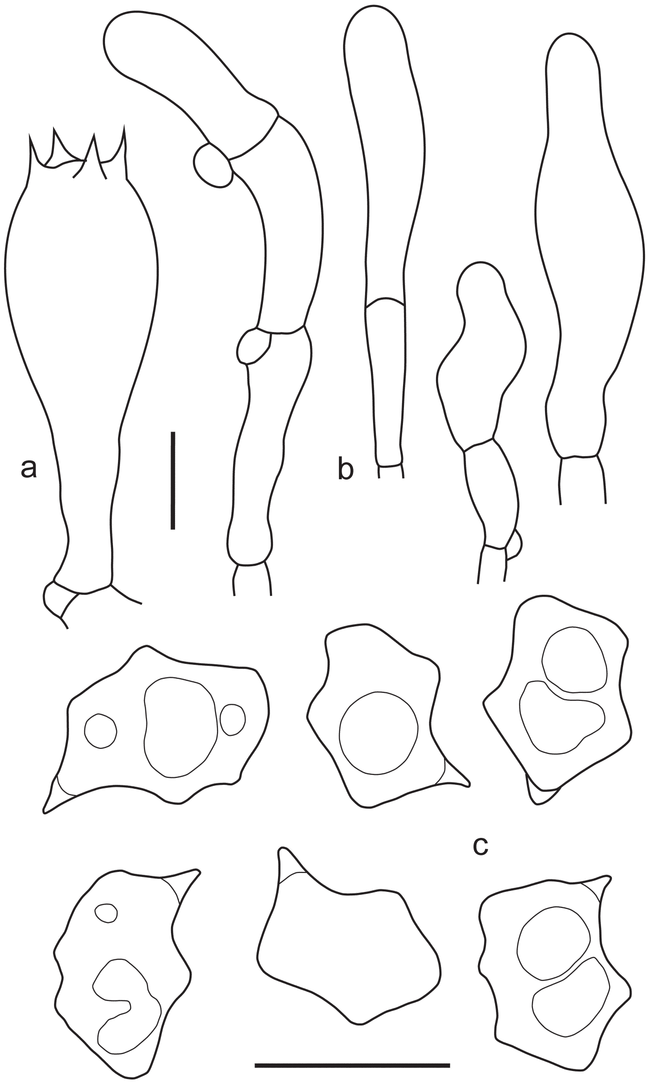

**Fig. 20** *Entoloma allochroum*. a. Basidium; b. cheilocystidia; c. spores (LE262984). — Scale bars = 10 µm.

### 10. *Entoloma callichroum* E. Horak & Noordel., in Noordeloos, Cryptog. Mycol. 4, 1: 33. 1983

#### a. var. *callichroum* — Fig. 21

Pileus to 22 mm broad, convex with small papilla, not hygrophanous, not translucently striate, radially fibrillose, lilaceous-pink. *Lamellae* distant, emarginate, ventricose, whitish with lilac tint towards entire concolorous edge. *Stipe* 40 × 2 mm, cylindrical, steel-blue, base with white tomentum, fistulose. *Smell* and taste not reported. *Spores* 9.5–13.2 × 7.2–9.4 µm, Q = 1.4–1.6, heterodiametrical, with 6–9 blunt angles in side view, almost nodulose. *Basidia* 39.0–48.9 × 14.4–20.1 µm, 4-spored, broadly clavate, clamped. *Lamellae edge* fertile. *Cheilocystidia* absent. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 10–18 µm wide, with intracellular pigment. *Clamp-connections* present.

Habitat — On soil in *Alnus incana* forest.

Known distribution — Western Europe.

*Specimen examined*. Switzerland, Graubunden, Forna, 3 Aug. 1971, *E. Horak* (ZT 71/58, holotype).

Notes — This rare species is characterized by pinkish violaceous tinge in the pileus in combination with steel blue stipe. The type variety is distinguished by the broad, almost nodulose spores, and the absence of cheilocystidia.

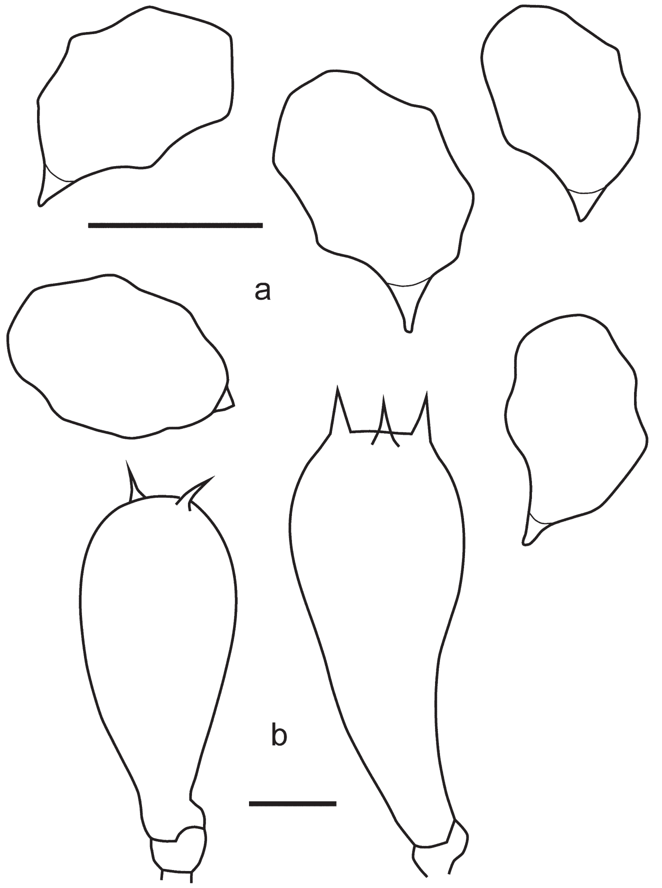

**Fig. 21** *Entoloma callichroum* var. *callichroum*. a. Spores; b. basidia (ZT 71/58, holotype). — Scale bars = 10 µm.

**b.** var. ***venustum*** (Wölfel & F. Hampe) O.V. Morozova, Noordel. & Vila, *comb. nov*. — Mycobank MB804535; Fig. 22, 23a, b

*Basionym*. *Entoloma venustum* Wölfel & F. Hampe, Z. Mykol. 77/2: 185. 2011.

Pileus 0.5–30 mm broad, convex to plano-convex, not hygrophanous, not translucently striate, radially silky fibrillose to squamulose in centre, pinkish lilaceous to violaceous, becoming brownish pink with age. *Lamellae* moderately distant, adnate-emarginate with small decurrent tooth, ventricose, brightly pinkish lilaceous, pinkish violaceus or whitish with blue tinge towards entire concolorous edge, becoming pink. *Stipe* 20–50 × 0.3–2.5 mm, cylindrical, longitudinally fibrillose-striate, dark blue, steel blue or violaceous-blue, base with white tomentum, fistulose. *Smell* of fruits or flowers (viola), taste unknown. *Spores* 11.5–13.0(–16.0) × 5.7–8.6 µm, Q = 1.3–1.8(–2.5), heterodiametrical, with 6–8 moderately pronounced angles in side view. *Basidia* 35.0–45.0 × 12.0–18.0 µm, 4-spored, broadly clavate, clamped. *Lamellae edge* heterogeneous. *Cheilocystidia* 30–60 × 15–28 µm, broadly clavate or sphaeropedunculate, intermixed with the basidia, sometimes hardly separated from the basidioles. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 10–20 µm wide, with intracellular pigment. *Clamp-connections* present.

Habitat — On soil in grasslands and in wet deciduous forest.

Known distribution — Western Europe, Western Siberia, Russian Far East.

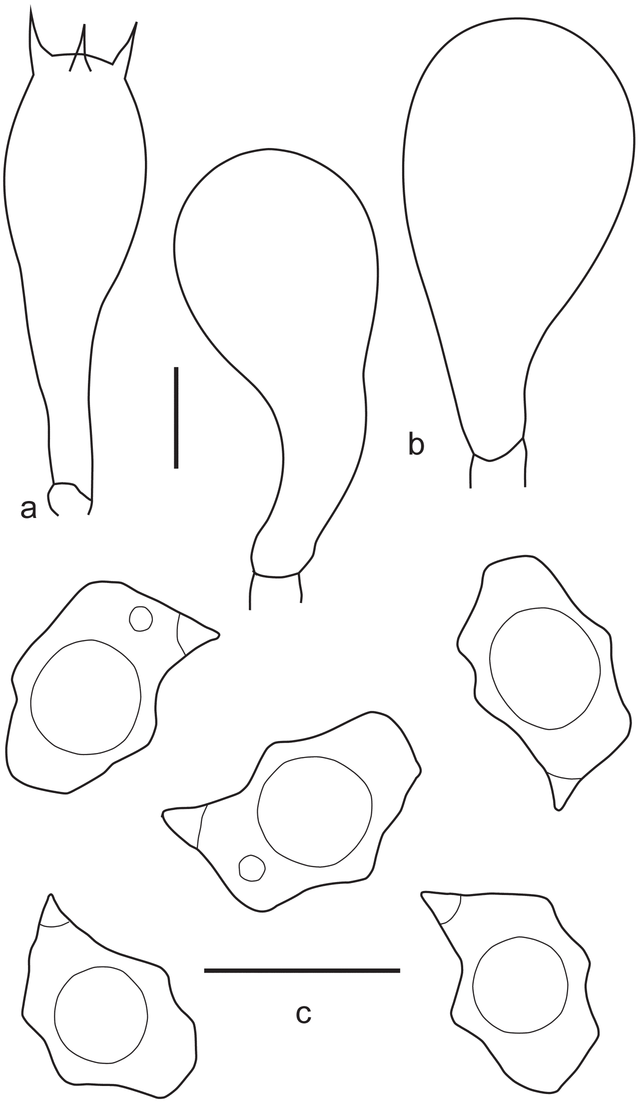

**Fig. 22** *Entoloma callichroum* var. *venustum*. a. Basidium; b. cheilocystidia; c. spores (Wö E17/10, holotype). — Scale bars = 10 µm.

*Specimens examined*. Belarus, Vitebsk Region, Verkhnedvinsk District, vicinities of Rositsa Village, on soil in *Alnus incana* forest, 19 Aug. 2003, *P. Kolmakov* (LE226909, as *E. lepidissimum*). – Germany, Hannover-Nord, Kuglfanger, 13 Nov. 2010, *G. Wölfel & F. Hampe* (Wö E17/10, L, as *E. venustum*, holotype). – Russia, Samara Region, Zhigulevsky Nature Reserve, Bakhilova Polyana, on soil in *Betula pendula* forest, 23 Aug. 2003, *E. Malysheva* (LE227532, as *E. lepidissimum*); Altaj Republic, Altajsky Nature Reserve, Komga, on soil in flood plain forest, 18 Aug. 2008, *V. Malysheva* (LE254312); Novosibirsk, Akademgorodok, on rotten birch stump, 15 June 2008, *T. Bulyonkova* (LE254313); ibid., planted forest between the Sobolev Institute of Mathematics and the Computing Center, 16 Aug. 2011, *T. Bulyonkova* (LE254314); Primorsky Territory, Ussuriysky Nature Reserve, 17 Sept. 1963, *M. Nazarova* (VLA M-20528, as *Rhodophyllus lampropus*).

Notes — The phylogenetic analysis shows that *E. venustum* is very close to *E. callichroum* (p-distance 1.8 % base-pair difference) and, therefore, could be considered its variety. Both species are morphologically distinct by the pinkish violaceous pileus; more or less lilaceous-blue tinges in the lamellae, the steel blue or violaceous-blue stipe, and the size of the spores. The description of *E. venustum* as a new species was based on the bright colour of the basidiomata and on the presence of well developed *cheilocystidia*, which, however, do not form a sterile gill edge and are often hardly distinguishable from basidioles (Wölfel & Hampe 2011). These characters can significantly vary within the range of genetically (nrITS) identical specimens. A more reliable feature for delimitation of these two taxa is spore form. Spores of *E. venustum* are narrower and possess more pronounced angles. Also the presence of a number of extremely long (up to 16 µm) germinating (?) spores has been reported from the holotype and other specimens (Table 3).

**Fig. 23** a, b: *Entoloma callichroum* var. *venustum*. a. Wö E17/10, holotype; b. LE254312. — c. *E. coelestinum* LE258103. — d, e: *E. percoelestinum*. d. LE254390 (JVG 1130925-24), holotype; e. LE254341. — f, g: *E. lepidissimum* f. LE254871; g. LE234751. — Scale bars = 1 cm. — Photos by: a. F. Hampe (from Wölfel & Hampe 2011); b, f, g. O. Morozova; c. L. Marina; d. J. Vila; e. T. Bulyonkova

**Table 3** Comparison between *Entoloma callichroum* var. *callichroum* and *E. callichroum* var. *venustum*.

| Specimen | Spores size (µm) | Q | Spores form | Cheilocystidia | Lamellae colour |
|---|---|---|---|---|---|
| *E. callichroum* var. *callichroum* (holotype) | 10.0–13.2 × 7.0–9.4 | 1.4–1.6 | 5–9 angled, almost nodulose | absent, some cystidia like clavate cells present | whitish with lilac tinge towards edge |
| *E. callichroum* var. *venustum* (holotype) | 8.4–12.7(16.0) × 6.0–8.6 | 1.3–1.6(2.5) | with 6–8 moderately pronounced angles | broadly clavate or sphaero-pedunculate, intermixed with basidia, 45–60 × 15–28 µm | brightly pinkish lilaceous, pinkish violaceus |
| *E. callichroum* var. *venustum* (LE254313) | 9.3–12.7 × 6.4–8.2 | 1.4–1.8 | with 6–8 moderately pronounced angles | rare, broadly clavate or sphaero-pedunculate, hardly distinguishable from the basidioles, 30.9–42.8 × 12.0–19.0 µm | whitish with lilac tinge towards edge |
| *E. callichroum* var. *venustum* (LE254312) | 9.5–13.0(14.0) × 5.7–7.2 | 1.4–1.8(2.0) | with 6–8 moderately pronounced angles | rare, broadly clavate or sphaero-pedunculate hardly distinguishable from the basidioles, 29.8–42.7 × 12.9–21.0 µm | whitish with bluish tinge towards edge |

## 11. ***Entoloma coelestinum*** (Fr.) Hesler, Beih. Nova Hedwigia 23: 111. 1967. — Fig. 23c, 24

Syn.: *Agaricus coelestinus* Fr., Epicr. Syst. Mycol. (Upsaliae): 158. 1838 ‘1836–1838’; *Nolanea coelestina* (Fr.) Gillet, Mém. Soc. Émul. Montbéliard, sér. 2 5: 536. 1875; *Rhodophyllus coelestinus* (Fr.) Quél., Enchir. Fung. (Paris): 65. 1886; *Leptonia coelestina* (Fr.) P.D. Orton, Trans. Brit. Mycol. Soc. 43, 2: 177. 1960.

Pileus 7–10 mm broad, conical to hemispherical with umbo, not hygrophanous, not translucently striate, with straight margin, radially silky fibrillose, squamulose at centre, uniformly dark blue. *Lamellae* moderately distant, adnate-emarginate, ventricose, white, becoming pinkish, with entire concolorous edge. *Stipe* 20–50 × 1–2 mm, cylindrical, smooth or almost smooth, glabrous, concolourous with pileus, white tomentose at base. *Smell* and taste indistinct. *Spores* 6.9–8.3(–8.9) × 5.2–6.2 µm, Q = 1.3–1.5, heterodiametrical, 5–7-angled in side-view. *Basidia* 29.5–37.0 × 8.1–9.6 µm, 4-spored, clavate, clamped. *Lamellae edge* fertile. *Cheilocystidia* absent. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 10–20 µm wide with blue intracellular pigment. *Clamp-connections* present.

Habitat — On soil in broad-leaved forest.

Known distribution — Ural.

*Specimens examined*. Russia, Sverdlovsk Region, Visimsky Nature Reserve, on soil in *Acer platanoides*-*Fraxinus excelsior* forest, 21 Aug. 2004, *L. Marina* (LE258103).

Notes — *Entoloma coelestinum* is distinguished by the tiny, very dark blue to black basidiocarps with conical hardly expanded pileus combined with the small spores. In the course of the phylogenetic analysis specimens previously identified as *E. coelestinum* ended up in a well-supported clade, which, however, consists itself of two sister clades that can be distinguished morphologically. The larger clade is characterized by almost nodulose spores and a longitudinally fibrillose-striate stipe. It includes blue-coloured basidiomes and entirely black ones (Fig. 22e). The other clade consist of one collection characterized by more pronouncedly angled, not nodulose spores and a polished stipe. This collection fits well with the protologue, and the current concept of *E. coelestinum* (Noordeloos 2004). Considering these morphological differences, and the significant p-distance between these clades (5.3 % base-pair difference) it was decided to describe the first clade as the new species, *E. percoelestinum* below. Unfortunately we were unable to design a neotype for *E. coelestinum* since the limited material studied is not from the original geographic area. More material from Europe, especially from Sweden is needed to do so.

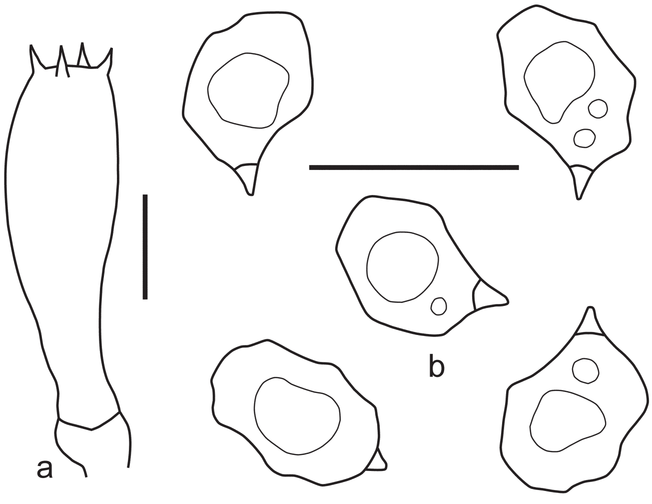

**Fig. 24** *Entoloma coelestinum*. a. Basidium; b. spores (LE258103). — Scale bars = 10 µm.

## 12. ***Entoloma percoelestinum*** O.V. Morozova, Noordel., Vila & Bulyonkova, *sp. nov.* — Mycobank MB803975; Fig. 23d, e, 25

*Etymology*. Named after its similarity to *E. coelestinum*.

Diagnosis. The new species is close to *E. coelestinum* from which it differs by almost nodulose spores and a longitudinally fibrillose-striate stipe.

*Holotype*. Spain, Osona, Barcelona, La Devesa, Rupit, alt. 1050 m, among grasses and mosses, near *Quercus pubescens* and *Fagus sylvatica*, on basic soil, 25 Sept. 2013, *J. Vila & X. Llimona* (LE254390), isotype in JVG 1130925-24.

Pileus 5–12 mm broad, conical or hemispherical with umbo, not hygrophanous, not translucently striate, with straight margin, radially fibrillose, squamulose at centre, uniformly dark blue, blackish blue or black. *Lamellae* moderately distant, adnate-emarginate, ventricose, white, becoming pinkish, with entire concolorous edge. *Stipe* 20–40 × 1–2 mm, cylindrical, longitudinally fibrillose-striate or almost smooth, concolourous with pileus, whitely tomentose at base. Context thin, concolorous with the surface. *Smell* indistinct or fungoid, taste not reported. *Spores* 6.5–8.5(–9.0) × 5.0–6.5 µm, Q = 1.3–1.5(–1.7), heterodiametrical, with 7–9 blunt angles in side-view, almost nodulose. *Basidia* 27.9–37.0(–45.4) × 8.1–9.6(–13.7) µm, 4-spored, narrowly clavate to subcylindrical, clamped. *Lamellae edge* fertile. *Cheilocystidia* absent. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 10–20 µm wide with blue intracellular pigment. *Clamp-connections* present.

Habitat — On soil in broad-leaved, mixed and pine (*Pinus sylvestris*) forests.

Known distribution — Western and Eastern Europe, Western Siberia.

*Additional specimens examined*. Russia, Penza Region, vicinities of Poperechnoye, on soil in *Fraxinus excelsior* forest, 7 Aug. 1990, *A. Ivanov* (LE18913, as *E. lepidissimum*); Novosibirsk, Akademgorodok, on soil in planted *Pinus sylvestris* forest SW of Lavrentieva 6/1, 12 Oct. 2011, *T. Bulyonkova* (LE254327); ibid., on soil in mixed forest, 20 Oct. 2010, *N. Filippova* (LE254341). – Spain, Barcelona, Mas Joan, Espinelves, alt. 730 m, on plant debris’s (*Rhododendron* sp., *Sequoiadendron giganteum*, *Picea* sp. and *Abies alba*), 11 Nov. 2006, *J. Vila & F. Caballero* (JVG1061111-7, as *E. coelestinum* (Vila & Caballero 2007)).

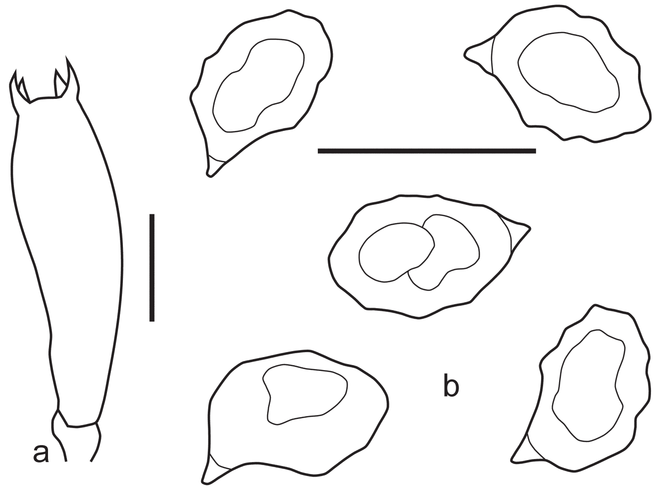

**Fig. 25** *Entoloma percoelestinum*. a. Basidium; b. spores (LE254390, holotype). — Scale bars = 10 µm.

Notes — In the boreal-temperate Eurasia several species with small blue or blackish blue basidiomata are recognized. *Entoloma percoelestinum* differs from *E. coelestinum* by almost nodulose spores and a longitudinally fibrillose-striate stipe, from *E. chytrophilum* by the smaller spores and conical, hardly expanding pileus, and from *E. lepidissimum* by the smaller spores and lack of the blue tinge in young lamellae. *Entoloma klofacianum* is characterized by the isodiametrical spores. North American *Leptonia subcoelestina* is also close but it differs by the larger spores and by the pileipellis which lacks clamps and is composed of submoniliform cells.

### 13. ***Entoloma lepidissimum*** (Svrček) Noordel., Persoonia 11: 460. 1982. — Fig. 23f, g, 26

Syn.: *Leptonia lepidissima* Svrček, Czech Mycol. 18: 205. 1964; *Rhodophyllus lepidissimus* (Svrček) M.M. Moser, Rohrlinge-Blatterpilze, 4 Aufl., 2, b/2: 203. 1978.

Pileus 5–25 mm broad, conical, broadly conical, hemispherical to convex with small umbo, not hygrophanous, not translucently striate, with straight margin, radially fibrillose to slightly squamulose at centre, deep blue to blackish blue, sometimes discolouring to greyish violet. *Lamellae* moderately distant, adnate-emarginate or almost free, ventricose, bluish, greyish blue or bluish violaceous, becoming greyish pink, with entire concolorous or paler edge. *Stipe* 20–60 × 1–3 mm, cylindrical, longitudinally fibrillose-striate or almost smooth, concolourous with pileus, white tomentose at base. Context concolorous with the surface. *Smell* indistinct, taste not reported. *Spores* 7.5–11.0 × 6.0–8.0 µm, Q = 1.3–1.6(–1.7), heterodiametrical, with 6–8 angles in side-view. *Basidia* 27.9–37.0(–45.4) × 8.1–9.6(–13.7) µm, 4-spored, narrowly clavate to subcylindrical, clamped. *Lamellae edge* fertile or heterogeneous. *Cheilocystidia* cylindrical, lageniform or narrowly clavate, intermixed with basidia, sometimes rare or absent. *Pileipellis* a plagiotrichoderm of cylindrical to slightly inflated hyphae 10–20 µm wide, with swollen terminal elements and blue intracellular pigment. *Clamp-connections* present.

Habitat — On soil in coniferous and deciduous forests.

Known distribution — Western, Central and Eastern Europe, Russian Far East.

*Specimens examined*. Czech Republic, Bohemia merid., Vrabské near Cimelice, on fallen twigs of *Alnus glutinosa* in swamp *Alnus forest*, 20 Oct. 1963, *M. Svrček* (PRM755801, holotype, as *Leptonia lepidissima*). – Russia, Novgorod Region, Valdajsky National Park, cost of Uzhyn Lake, on soil in *Picea abies* forest, 20 Aug. 2003, *E. Popov* (LE234755); ibid., vicinities of Sokolovo, Krasnaya Gorka, on soil in *Quercus robur* forest, 22 Aug. 2003, *E. Popov* (LE234751); ibid., valley of Poneretka River, on soil in *Pinus sylvestris* forest, 23 Sept. 2011, *E. Popov* (LE254871); Primorsky Territory, Sikhote-Alin Nature Reserve, Kabanuj, 25 Aug. 2011, *E. Malysheva* (LE254311).

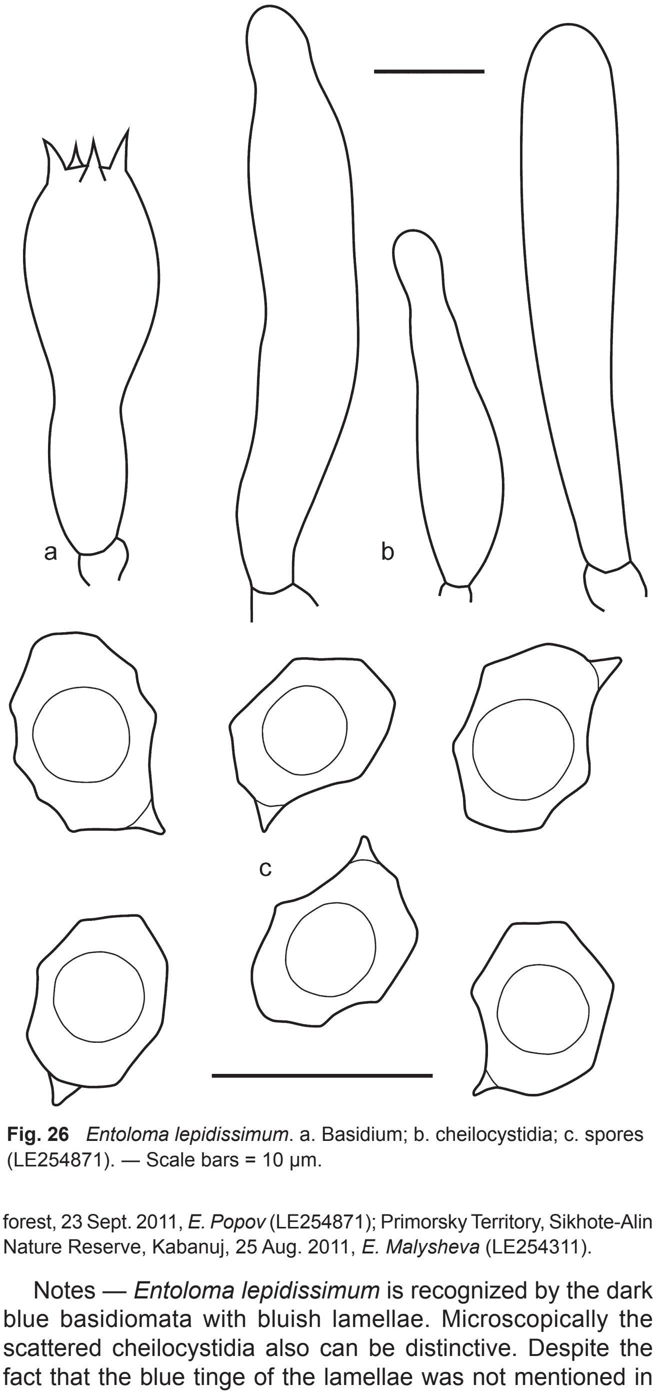

**Fig. 26** *Entoloma lepidissimum*. a. Basidium; b. cheilocystidia; c. spores (LE254871). — Scale bars = 10 µm.

Notes — *Entoloma lepidissimum* is recognized by the dark blue basidiomata with bluish lamellae. Microscopically the scattered cheilocystidia also can be distinctive. Despite the fact that the blue tinge of the lamellae was not mentioned in the protologue, all studied specimens are characterized by bluish lamellae. Molecular data support their identity with the holotype. The similar species *E. coelestinum* is distinguished by the white lamellae, smaller spores and more conical pileus. *Entoloma chytrophilum* possesses white lamellae, nodulose spores and a more applanate pileus.

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