Seven new species in *Piloderma* (*Atheliales*, *Basidiomycota*) from the Northern Hemisphere recovered through morphological and molecular methods

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Abstract: The ectomycorrhizal genus *Piloderma* (*Atheliales*, *Basidiomycota*) is studied using morphological and molecular methods. Seven new species are identified and described, *viz. P. cinicola, P. craurum, P. egens, P. exiguum, P. humile, P. ochraceum*, and *P. rallum*, bringing the total number of accepted species to 13. All new species are supported by ITS sequences from basidiomata and from environmental soil and root-tip sequences available in public databases. A key to all species in *Piloderma* is provided.

INTRODUCTION

Corticioid homobasidiomycetes produce effused, crust-like and often inconspicuous basidiomata. These are commonly found on the underside of decaying wood and other debris on the ground. Most of them are true saprotrophs with their vegetative mycelium inside the woody substrate. However, some of the species are known to be ectomycorrhizal and have erroneously been classified as saprotrophs since basidiomata are found in connection with coarse woody debris. Corticioid ectomycorrhizal (EcM) fungi presumably have at least two reasons to search for decaying wood on the forest floor. First, wood is an important source of nutrients and water and short-roots from green plants are plentiful inside highly decayed wood. Second, debris on the ground offers the necessary downward-facing surface where corticioid EcM-fungi can develop basidiomata.

Some of the most common ectomycorrhizal fungi in temperate forest ecosystems belong to the genus *Piloderma* – *P. sphaerosporum* is for example the second most common basidiomycete in Swedish soils, according to sequence data from 1 806 sample sites (Soil fungi in Swedish woodland home page, accessed 15 August 2023). The genus was established with four species, *viz. P. bicolor* (type; syn. *P. fallax*), *P. byssinum*, *P. lapillicolum*, and *P. reticulatum* (Jülich 1969). Later, *P. sphaerosporum*, and three varieties of *P. byssinum*, – namely var. *bisporum*, var. *lanatum*, and var. *minutum* – were added (Jülich 1972). Eriksson *et al.* (1981) did not accept *P. reticulatum* and *P. shaerosporum* but considered them as intraspecific variation of *P. byssinum*. They further raised *P. byssinum* var. *lanatum* to species rank and they found *P. lapillicolum* to be the same as or

very close to *P. fallax* (under the name *P. croceum*). Finally, they added one new variety, *viz. P. croceum* var. *olivaceum*. This last taxon was later raised to species rank (Hjortstam 1984).

Species in *Piloderma* have soft, smooth basidiomata with an adnate, byssoid or pellicular appearance (Fig. 1), invariably simple-septate hyphae, and smooth, elliptic to subglobose and slightly thick-walled basidiospores. Cystidia or other kinds of derived vegetative cells are not known within the genus. The occurrence of different kinds of incrustation on subicular hyphae has been proposed as a diagnostic character for *P. fallax* and *P. byssinum* (Eriksson *et al.* 1981). The crystalline material is either calcium-oxalate or corticrocin (Erdtman 1948). The latter substance is known only from *P. fallax* and *P. olivaceum* and responsible for the intense yellow colour of its subicular hyphae and hyphal cords.

Since diagnostic morphological characters in *Piloderma* are few, it has been difficult to establish species limits with traditional methods. An increasing interest in the role of ectomycorrhiza in forest ecosystems and a demand for identification of the mycobiont render it necessary to better define the taxa present in *Piloderma*. Molecular data from screening of ectomycorrhizal root-tips and forest soil show that the number of species must be considerably higher than the current number of named species. The UNITE database (unite.ut.ee, v. 8, accessed 10 March 2023; Kõljalg *et al.* 2013) contains at least 17 species hypotheses (SH) with presence in Europe when SH clustering on 1.5 % similarity is considered (Nilsson *et al.* 2018). For seven of these SH-clusters that presently lack scientific names, basidiomata have been found and sequenced and are here formally described.

MATERIALS AND METHODS

Morphological examination

Basidiomata were collected during numerous excursions over more than 20 years, primarily in Norway and Sweden. An especially rich collection was compiled during a study of the impact of forestry on wood-inhabiting fungal diversity in Norway 1995–1997 (Stokland & Larsson 2011). Basidiomata from this project, not fully corresponding to described species, were kept separate and successively sequenced. Dried basidiomata were studied with a Zeiss Axioskop 2 compound light microscope equipped with phase contrast lenses. Preparations were made in 2 % KOH, Congo Red in ammoniac, Melzer's solution, or Cotton Blue in lactic acid. Measurements were made in Melzer's reagent at 1 250x magnification. Vouchers are deposited in public herbaria, mainly in Gothenburg (GB), Oslo (O), and Uppsala (UPS).

DNA extraction, amplification, and sequencing

DNA was extracted from dried basidiomata. Extraction was either carried out using a modified 2 % CTAB method and further purified with a GENECLEAN kit (Bio 101, Inc.), or with a DNeasy Plant Mini Kit (Qiagen, Hilden). Amplification reactions were performed with Illustra PuReTaq Ready-To-Go PCR beads (Cytiva, Marlborough) using 0.5 µM of each primer and 1–3 µL of the DNA extracts. The PCR clean-up was carried out using the

Fig. 1. *Piloderma* species. **A.** *P. byssinum* (photo M. Kulju; OULU GAJ.11526). **B.** *P. cinicola* (photo S. Svantesson; UPS SS1019). **C.** *P. fallax* (photo S. Svantesson; UPS SS831). **D.** *P. olivaceum* (photo S. Svantesson; UPS SS603). **E.** *P. rallum* (photo S. Svantesson; UPS SS1129). **F.** *P. sphaerosporum* (photo A. Moilanen; OULU GAJ.15789).
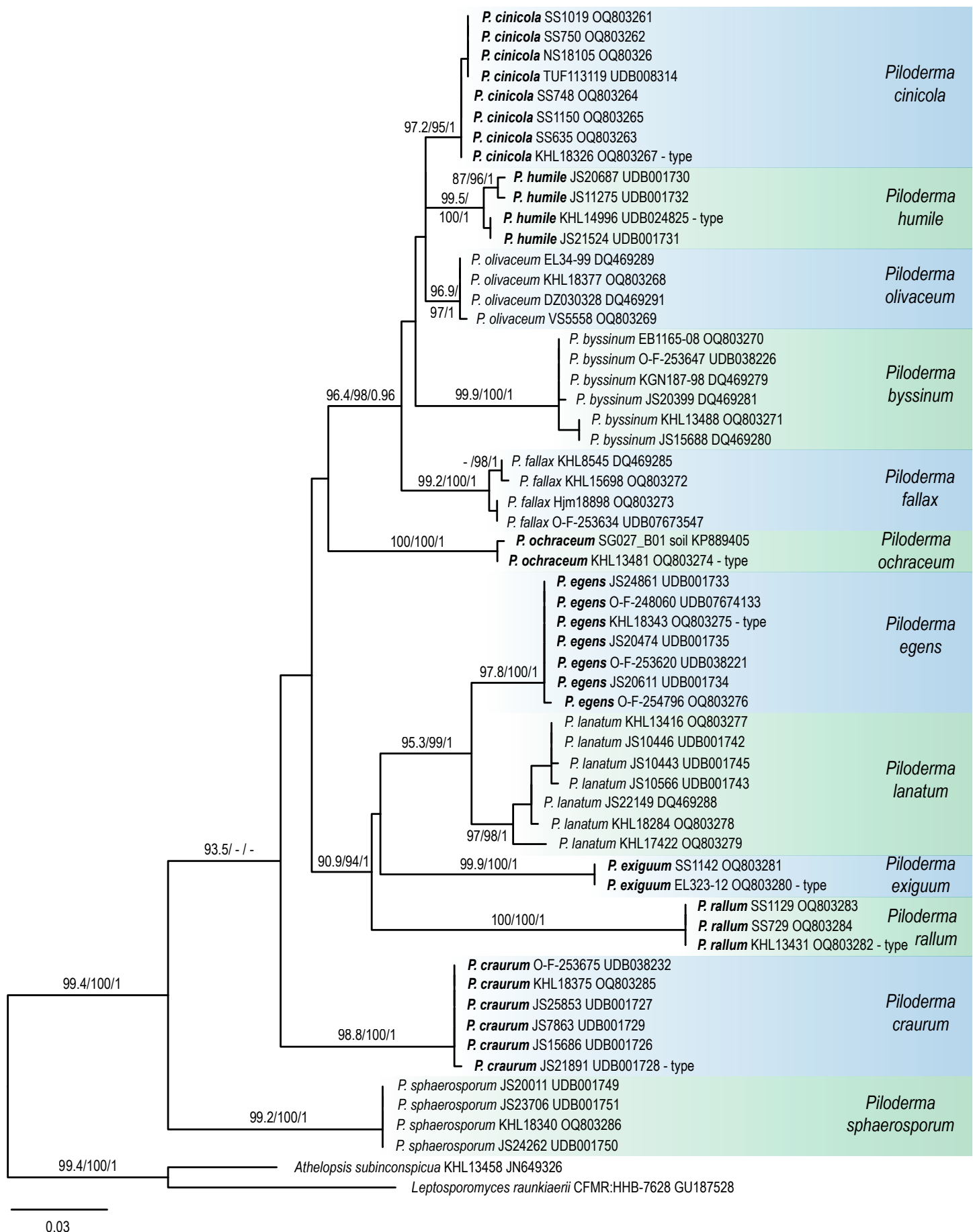
Fig. 2. Maximum Likelihood tree, based on ITS sequences. Support values considered significant received from the SH-aLRT test (≥ 80), ultrafast bootstrap (≥ 95), and Bayesian posterior probabilities (≥ 0.95) are indicated on branches. The new species are highlighted in bold.

QIAquick PCR purification kit (Qiagen, Hilden). The ITS region was amplified using primers ITS1F and Lr21 (Hopple & Vilgalys 1999, Gardes & Bruns 1993). The PCR conditions followed Gardes & Bruns (1993). Amplified products were purified with Quiaquick (Qiagen) spin columns. Primers used for sequencing were ITS1 and ITS4 (White *et al.* 1990, Gardes & Bruns 1993). Sequences were obtained using either an ALFExpress automated sequencer (production discontinued), a Beckman-Coulter automated sequencher (production discontinued) or through a commercial service. Sequence chromatograms were edited either in machine-specific software or in Sequencher v. 5.4 (Gene Codes Corporation, Ann Arbor).

Phylogenetic analyses

For the present study, 26 ITS sequences were generated. We further added 23 sequences downloaded from UNITE (unite.ut.ee; Nilsson *et al.* 2018), and 10 sequences from GenBank (Sayers *et al.* 2023). In the genus *Piloderma* nucLSU sequences contain little variation and were hence not included in analyses (Table 1).

Sulistyo *et al.* (2021) recognized three genus-level clades in *Pilodermataceae*, *viz. Piloderma*, *Tretomyces*, and *Stereopsis vitellina*. *Tretomyces* differs from *Piloderma* by having consistently clamped hyphae and *Stereopsis vitellina* differs by producing stipitate basidiomata. Since *Tretomyces* and *Stereopsis vitellina* have ITS sequences that are rather deviant compared to *Piloderma*, we did not include them in our analyses in order to maximize sequence information within the genus. We followed Sulistyo *et al.* (2021) and used *Athelopsis subinconspicua* and a GenBank sequence identified as *Leptosporomyces raunkiaerii* as outgroup.

Alignments were made in AliView v. 1.18 (Larsson 2014), utilizing the L-INS-i strategy, as implemented in MAFFT v. 7.017 (Katoh & Standley 2013). Introns and low-quality ends were manually trimmed from the sequences prior to analysis. Gblocks v. 0.91b (Castresana 2000, Talavera & Castresana 2007) was applied to trim the alignments of problematic character regions (*e.g.* missing data, saturated sites, and sections with unclear homology), using the Less Stringent option on the web server at http://phylogeny.lirmm.fr/ (Dereeper et al. 2008).

Best-fitting substitution models and partitions for the Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were estimated using ModelFinder, as implemented on the IQ-TREE server (Kalyaanamoorthy *et al.* 2017), assuming ITS1, 5.8S, ITS2 as minimal partitions (Chernomor *et al.* 2016). According to the program, the best fit was achieved by the model TNe+G while treating the entire alignment as a single partition. The ML analysis was conducted using IQ-TREE (Nguyen *et al.* 2015) implemented on the online server at http://iqtree.cibiv.univie.ac.at/ (Trifinopoulos *et al.* 2016). Branch support was estimated as SH-aLRT test (Guindon *et al.* 2010) and ultrafast bootstrap support (Hoang *et al.* 2018).

BEAST v. 2.6.7 (Bouckaert *et al.* 2019) run on the CIPRES Science Gateway (Miller 2010) was used for the BI analysis. The substitution model was set to HKY+G, in the associated xml-preparation software BEAUti since it is the model the most similar to TNe+G, available in the program. A lognormal, relaxed clock model was assumed, as a test run showed a coefficient of variation well above 0.1 (*i.e.*, implying a relatively high rate variation among branches). The clock rate was estimated in the run using a lognormal prior with a mean set to one in real space. The growth rate prior was set to lognormal with a mean of 5 and a standard deviation of 2. These priors were set according to the STACEY package documentation (Jones 2017). The Markov Chain Monte Carlo chain was run until the analysis converged well in advance of the 10 % burn-in threshold, had ESS values well above 200 for all parameters, and
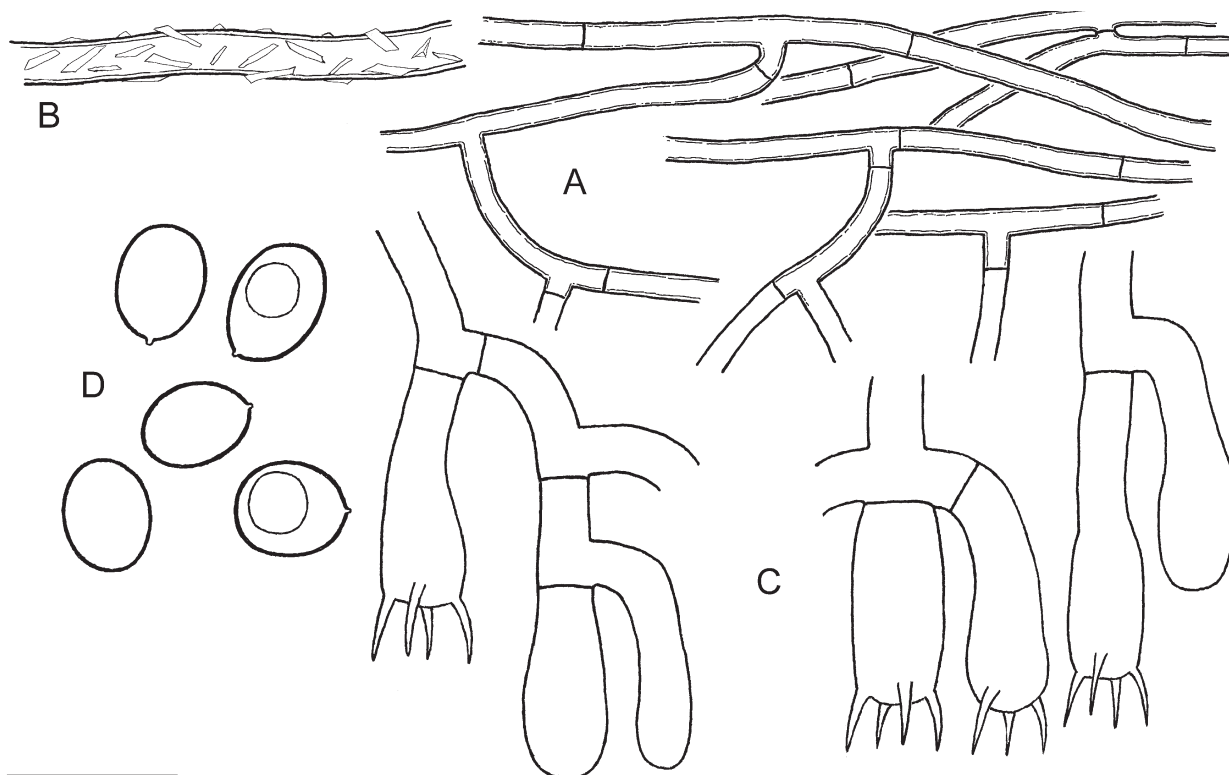

Fig. 3. *Piloderma byssinum* (KHL 13488). **A.** Hyphae from subiculum. **B.** Subicular hypha with incrustation. **C.** Details from hymenium with basidia. **D.** Basidiospores. Scale bar: A = 20 µm; B, C = 10 µm; D = 5 µm.

satisfactory chain mixing, as assessed in Tracer v. 1.7.2 (Rambaut *et al.* 2018). After discarding the burn-in trees, a maximum clade credibility tree was identified by TreeAnnotator v. 2.6.7 (Bouckaert *et al*. 2019). The original and Gblocks-curated alignments and the phylogenetic tree derived from this study were uploaded to figshare (doi: 10.6084/m9.figshare.25103162).

RESULTS

The final MAFFT-alignment had 644 positions. After curation with GBlocks, 497 positions remained; 335 (68 %) of these were constant, 22 (4 %) were variable but parsimony uninformative (singletons), and 140 (28 %) were variable and parsimony informative. The ML and BI analyses produced topologically similar trees. The ML tree (Fig. 2) is presented with values considered significant received from the SH-aLRT test (≥ 80), ultrafast bootstrap (≥ 95), and Bayesian posterior probabilities (≥ 0.95) indicated on branches.

The ingroup is composed of 12 clades that we consider to represent species, seven of which do not correspond to described species and which are therefore proposed as new. All accepted species are described and illustrated below. The SH-aLRT test, ultrafast bootstrap, and BI posterior probabilities provide strong support for all 12 clades. Within the *P. lanatum* clade there is a considerable genetic variation that perhaps indicates that this species is composed of several taxa.

For all sequenced species, we identified the corresponding Species Hypothesis (SH) in the UNITE database (Kõljalg *et al*. 2013). All SH datasets have permanent digital object identifiers (DOI) that can be fed into an Internet browser, which will bring up the corresponding information page in UNITE. DOI links to version 8 are provided.

Taxonomy

Piloderma byssinum (P. Karst.) Jülich, *Ber. Deutsch. Bot. Ges*. **81**: 418. 1969. Fig. 3.
Basionym: *Lyomyces byssinus* P. Karst., *Meddeland. Soc. Fauna Fl. Fenn*. **11**: 137. 1884.

UNITE SH: doi.org/10.15156/BIO/SH1172616.08FU

Typus: **Finland**, Mjölö. Oct. 1883, leg. *E. Wainio*, ex herb. Karsten 681, **holotype** H (studied).
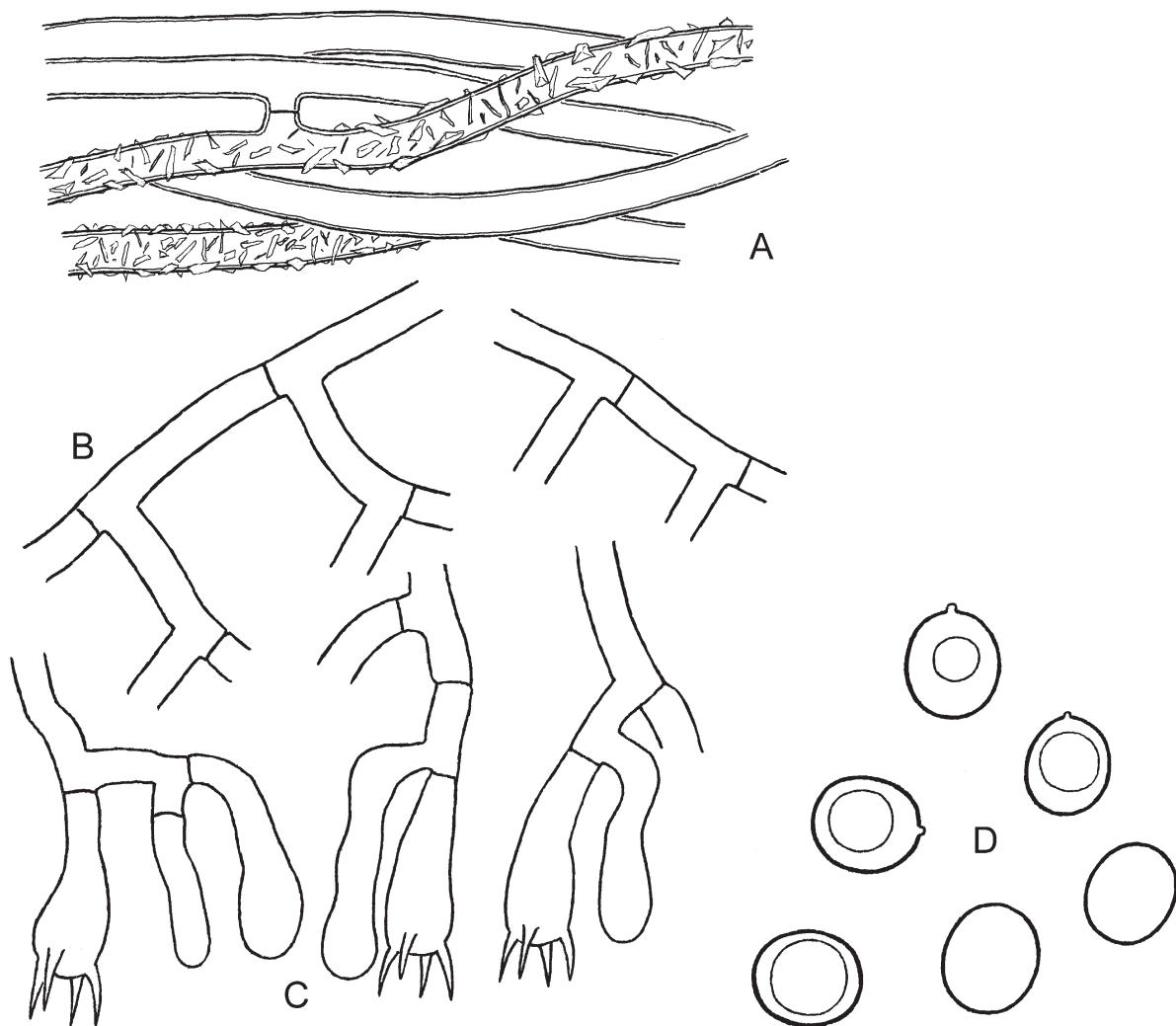

Fig. 4. *Piloderma cinicola* (holotype). **A.** Hyphae from subiculum, some with incrustation. **B.** Hyphae from subhymenium. **C.** Details from hymenium with basidia. **D.** Basidiospores. Scale bar: A–C = 10 μm; D = 5 μm.

Basidioma resupinate, effused, loosely attached to the substrate by an extensive, byssoid subiculum, hymenium smooth or with small and sparse blisters, continuous, more or less pellicular, from the beginning white, then sometimes developing yellow to orange spots that may extend to the whole basidioma (Fig. 1A), subhymenium and subiculum remaining white, margin byssoid, white hyphal cords usually present in subiculum and substrate. *Hyphal system* monomitic, hyphae 2.5–3.5 µm wide, without clamps, in the subiculum with thin to thickened walls, usually with short, baculiform, rod-like or elongated pyramidal crystals but lacking yellow encrustation in Melzer, in the subhymenium thin-walled, richly branched, often with an encrustation that is coarser than in the subiculum. *Basidia* clavate to clavo-pedunculate, (10–)12–15(–25) × 3.5–5 µm, with (2–)4 sterigmata, in basidiomata with a yellow coloration of the hymenium, basidia and subbasidial cells sometimes have yellow contents. *Basidiospores* subglobose to elliptic, 3–4(–4.5) × 2.5–3 µm, hyaline to slightly yellowish, smooth, with thickened walls, weakly dextrinoid.

Habitat: On decayed wood and litter of all kinds. Mycorrhizal with conifers.

Distribution: A common species and distributed across most of the Northern Hemisphere, extending its range into tropical areas with conifers in Asia.

Sequenced specimens examined: **Norway**, Akershus, Lørenskog, Østmarka, Tretjernhøla nat. res, on *Picea abies* log, 25. Nov. 2008, leg. *E. Bendiksen* 1165/08, O. Buskerud, Modum, Dritardalen, on *Picea abies*, 23 Sep. 1997, leg. *J.N. Stokland et al.* 20399, O. Buskerud, Nore og Uvdal, Smådøldalen, on *Betula* sp., 2 Sep. 1997, leg. *J.N. Stokland et al.* 15688, O. Østfold, Aremark, Tjøstøl, on *Picea abies*, 26 Oct. 2011, leg. *J. Nordén*, O F-253647. **Sweden**, Närke, Lerbäck, Åsbrohammar on *Picea abies*, 25 Apr. 1998, leg. *K.G. Nilsson* 187, GB. Västergötland, Västra Tunhem, Hallesnipen-Ovandalen, on strongly decayed wood, 5 Oct. 2006, leg. *K.H. Larsson* 13488, GB.

Notes: As a rule, identified without problems thanks to the well-developed subiculum, the presence of white hyphal cords, and the rod-like crystals. It is most similar to *Piloderma craurum*, which differs by larger basidia and distinctly dextrinoid basidiospores. *Piloderma cinicola* is also similar but differs by rounder and slightly smaller basidiospores, and by acicular instead of rod-like crystals on subicular hyphae. *Piloderma egens* and *P. humile* differ by a tendency for elliptic basidiospores and by acicular crystals.

The yellow to orange discoloration sometimes seen in the hymenium may cause specimens to be identified as *Piloderma croceum* or *P. olivaceum*. However, these two species have a bright yellow subiculum and yellow hyphal cords when fresh, which are features never seen in *P. byssinum*.

Piloderma cinicola K.H. Larss. & Svantesson, ***sp. nov.*** MycoBank MB 850986. Fig. 4.

Etymology: *Cinis* (Lat.) = ashes; *-cola* (Lat.) = living. Referring to the tendency for the fungus to colonize ash-granules in forest fertilization experiments.

Typus: **Sweden**, Gotland, Väskinde or Visby parish, Brucebo nat. res., on coniferous wood in mixed conifer forest on calcareous ground, 9 Oct. 2021, leg. *K.H. Larsson* 18326 (**holotype** GB-0237575).

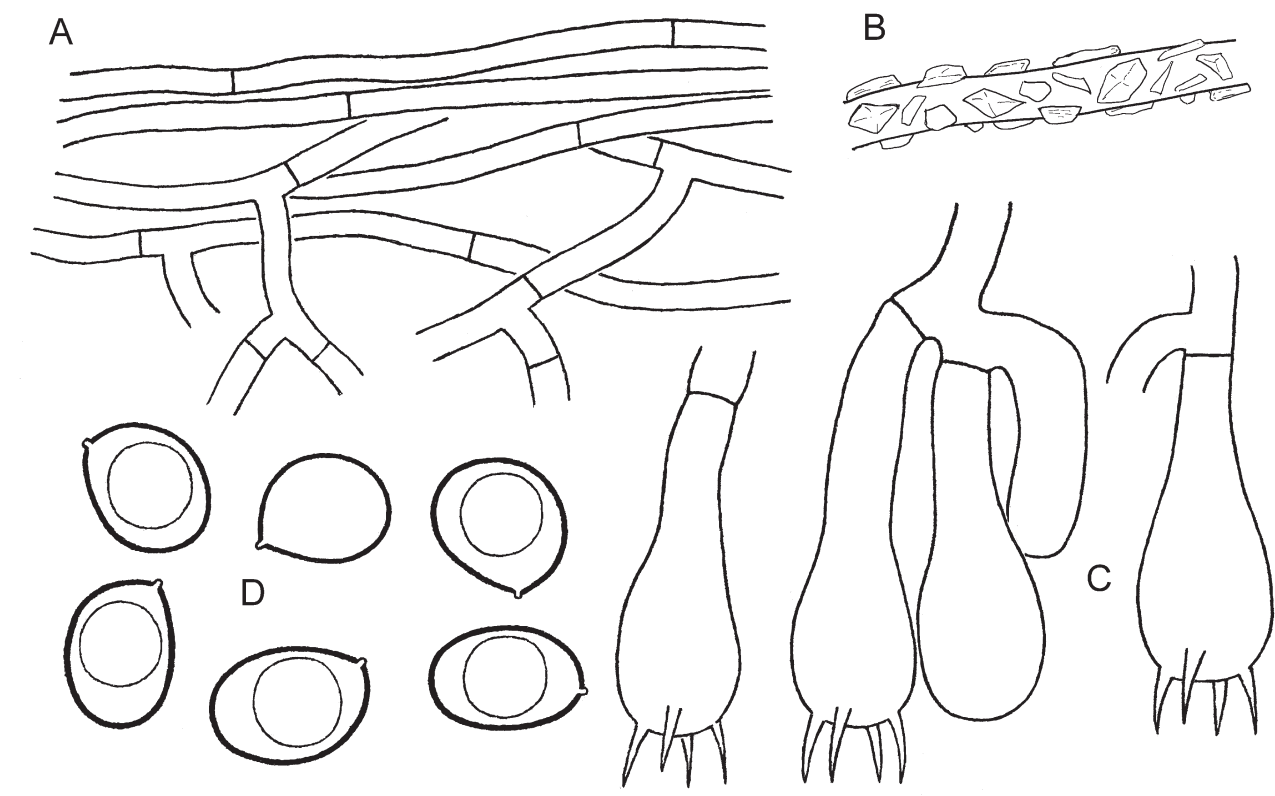*UNITE SH*: doi.org/10.15156/BIO/SH1916436.08FU

Fig. 5. *Piloderma craurum* (JS 26152). **A.** Hyphae from subiculum and subhymenium. **B.** Subicular hyphae with incrustation. **C.** Details from hymenium with basidia. **D.** Basidiospores. Scale bar: A = 20 µm; B, C = 10 µm; D = 5 µm.

Basidioma resupinate, effused, thin, soft and delicate, loosely attached to the substrate, pellicular, hymenium white, smooth, porose to continuous, margin not differentiated, white hyphal cords present. *Hyphal system* monomitic, hyphae thin-walled, without clamps, subicular hyphae rather straight, slightly thick-walled, 2–3 µm wide, rough from small, acicular crystals, hyphae in hyphal cords, similar, frequently anastomosing, hyphae in the thin subhymenium thin-walled, 2–3 µm wide, often with acicular to narrowly rhombic crystals. *Basidia* clavate, 10–13 × 3.5–4.5 µm, with four slender sterigmata. *Basidiospores* globose to subglobose, 2.7–3.5 × 2.5–3 µm, with thickened walls, smooth, with one oil-drop, weakly dextrinoid.

Habitat: Ectomycorrhizal in conifer forest, associating with many different conifer species, probably with preference for soil with elevated pH.

Distribution: Widespread across the Northern Hemisphere and recorded from many countries in Europe, from N. America, and from China and Japan.

Additional sequenced specimens examined: **Estonia**, Lääne, Vormsi, Rumpo, on *Pinus sylvestris*, 16 Sep. 2010, leg. *L. Tedersoo*, TUF 113119. **Sweden**, Medelpad, Borgsjö, Julåsen, in forest with *Salix* sp., *Betula* sp., *Populus tremula*, 29 Aug. 2018, leg. *N. Schoutteten* 18-105, GENT. Södermanland, Botkyrka, Riksten W, old forest with *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Betula pendula*, 22 Oct. 2022, leg. *S. Svantesson* 1019, UPS. Uppland, Ingarö, Karlsdal, old forest with *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Corylus avellana*, *Betula pendula*, 25 Oct. 2022, leg. *S. Svantesson* 1150, UPS. Uppland, Älvkarleby, Brämsand, old forest with *Picea abies* and *Pinus sylvestris*, 22 Sep. 2022, leg. *S. Svantesson* 748 and 750, UPS. Ångermanland, Nordmaling, Sörheden nat. res., old forest with *Picea abies* and *Pinus sylvestris*, 6 Sep. 2022, leg. *S. Svantesson* 635, UPS.

Notes: The ITS sequence of this species is rather similar to *Piloderma olivaceum* but morphologically the species is clearly distinguished by lacking the yellow, olivaceous or brown colours characterizing basidiomata of *P. olivaceum*. In a study of artificial fertilization of spruce forest with ash-granules (Mahmood *et al.* 2001), *P. cinicola* and *P. olivaceum* (in the publication called *Piloderma* sp. 1 and *Piloderma croceum*, respectively) behaved differently when confronted with ash-granules in the lab. *Piloderma cinicola* was attracted to the granules while *P. olivaceum* tended to avoid them. Morphologically *P. cinicola* is most similar to *P. egens* and *P. humile*, which, however, have larger and more elliptic basidiospores. *Piloderma byssinum* differs by rod-like instead of acicular crystals on subicular hyphae and *P. craurum* by having distinctly dextrinoid basidiospores.

Piloderma craurum K.H. Larss., ***sp. nov.*** MycoBank MB 850988. Fig. 5.

Etymology: Krauros (Gr.) = brittle, friable.

Typus: **Norway**, Buskerud, Nes, Gjuvbekken, on *Pinus sylvestris*. 26 Sep. 1997, leg. *J.N. Stokland et al.* 21891 (**holotype** O-F-270951).

UNITE SH: doi.org/10.15156/BIO/SH1172615.08FU

Basidioma resupinate, effused, loosely attached to the substrate, thin, soft and fragile, white to pale ochraceous, hymenium membranous and easily peeled from the byssoid subiculum, smooth, when well-developed continuous, margin not differentiated. *Hyphal system* monomitic, all hyphae simple-septate, white hyphal cords (rhizomorphs) common in the subiculum and in the substrate, with straight, sometimes
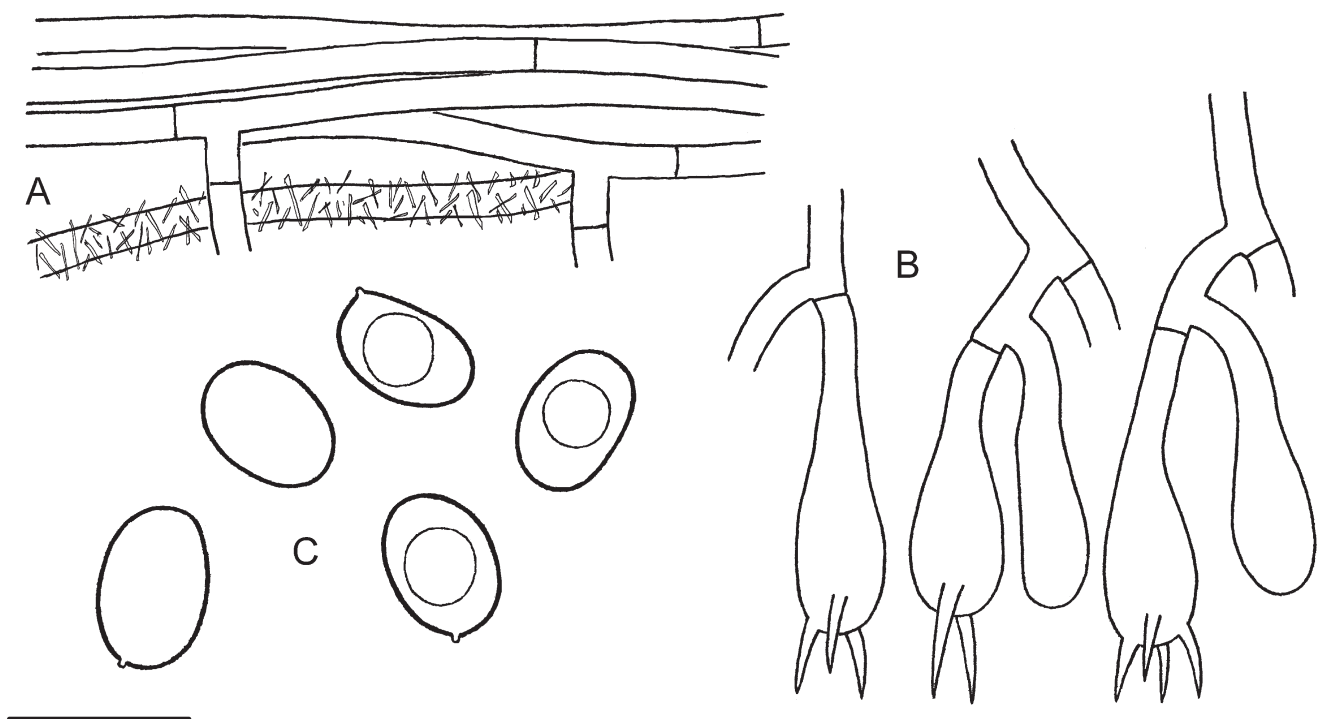

Fig. 6. *Piloderma egens* (JS 24861). **A.** Hyphae from subiculum, one with incrustation. **B.** Details from hymenium with basidia. **C.** Basidiospores. Scale bar: A, B = 10 µm; C = 5 µm.

anastomosing, slightly thick-walled, about 2 µm wide hyphae, partly encrusted by grainy or acicular to rod-like crystals, subiculum well developed, with loosely interwoven thin-walled (1.5–)2–2.5(–3.5) µm wide hyphae, partly covered by bundles of acicular crystals, subhymenium thin and composed of thin-walled 2.5–3.5 µm wide hyphae. *Basidia* clavate to pedunculate, 15–30 × 6.5–7 µm, with four *ca* 3 µm long, only slightly curved sterigmata. *Basidiospores* subglobose, 4 × 3.5 µm, smooth, moderately thick-walled, distinctly dextrinoid.

Habitat: Basidiomata developing on strongly decayed wood or other debris close to the ground in conifer forest or in mixed forest. Sequences from mycorrhiza are reported from *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga*.

Distribution: Widespread over the Northern Hemisphere where conifer forests occur. In Europe probably confined to the northern region and the mountains in Central Europe.

Additional sequenced specimens examined: **Norway**, Buskerud, Nore og Uvdal, Smådøldalen, on *Betula* sp., 2 Sep. 1997, leg. *J.N. Stokland et al.* 15686, O. Hedmark, Løten, Gitvola, on *Sorbus aucuparia*, 17 Oct. 1997, leg *J.N. Stokland et al.* 25853, O. Oppland, Sel, on *Pinus sylvestris*, 25 Sep. 1996, leg. *J.N. Stokland et al.* 7683, O. **Sweden**, Värmland, Torsby, Multtjärn, on decaying *Picea abies*, 5 Oct. 2010, leg. *J. Nordén*, O F-253675. Uppland, Björklinge, Hocksboglupen, on decaying frondose wood, 20 Sep. 2022, leg. *K.H. Larsson* 18375, GB.

Other specimens examined: **Finland**, Ostrobottnia, Rovaniemi, Pisavaara, E of Sorvannulikka, on *Picea abies*, 29 Aug. 1960, leg. *V. Kujala & J. Eriksson*, GB. **Norway**, Buskerud, Nes, Tronrud, on *Picea abies*, 4 Sep. 1997, leg. *J.N. Stokland et al.* 16295, O. Hedmark, Trysil, Gnollen, on *Picea abies*, 17 Sep. 1997, leg. *J.N. Stokland et al.* 18305, O. Østfold, Rømskog, Steinsvika, on *Populus tremula*, 20 Oct. 1997, leg. *J.N. Stokland et al.* 26152, O. **Sweden**, Dalarna, Särna, Fulufjället, at Göljån close to Fulan, on *Picea abies*, 10 Sep. 2004, leg. *L. Ryvarden & K.H. Larsson* 12384, GB. Ångermanland, Ramsele, S slope of Nöttjärnsberget, on strongly decayed wood, 27 Aug. 2002, leg. *K.H. Larsson* 11802, GB.

Notes: This species can be easily recognized due to the dextrinoid basidiospores. The mainly acicular crystals on subicular hyphae also aid in identification. Such crystals are also present in *Piloderma cinicola* and *P. egens* but neither of them has a strong dextrinoid reaction of basidiospores. *Piloderma humile* can also appear similar but has elliptic basidiospores.

Piloderma egens K.H. Larss., ***sp. nov.*** MycoBank MB 850989. Fig. 6.

Etymology: *Egens* (Lat.) = poor, referring to the smaller basidiospores compared to its closest relative *Piloderma lanatum*.

Typus: **Sweden**, Uppland, Uppsala, Nåsten, S of Hågaby, on decaying frondose wood in conifer-dominated forest, 19 Sep. 2022, leg. *K.H. Larsson* 18343 (**holotype** GB-0237576).

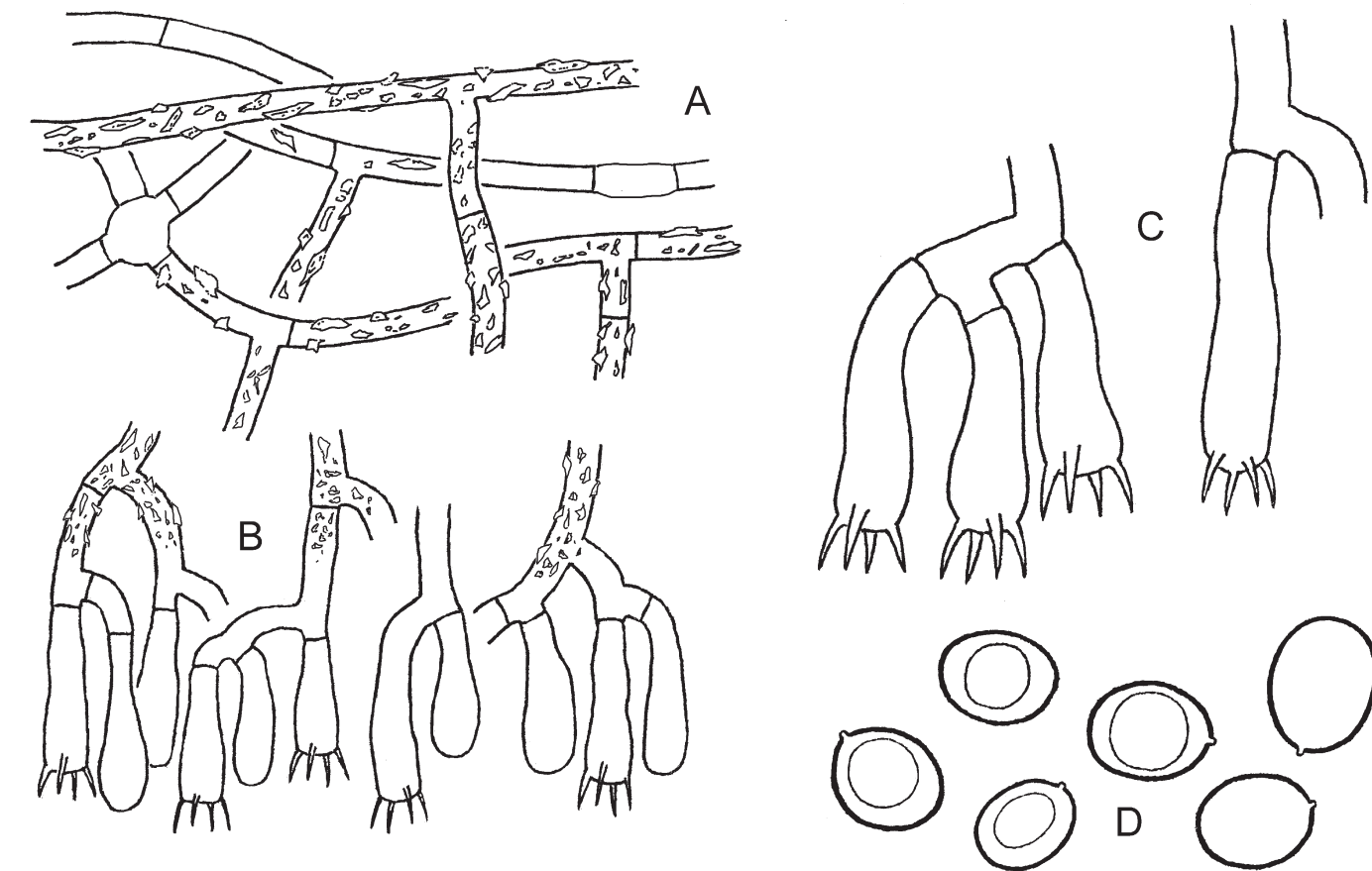*UNITE SH*: doi.org/10.15156/BIO/SH1544807.08FU

Fig. 7. *Piloderma exiguum* (holotype). **A.** Subicular hyphae, some with incrustation. **B.** Details from hymenium. **C.** Basidia. **D.** Basidiospores. Scale bar: A, B = 20 µm; C = 10 µm; D = 5 µm.

Basidioma resupinate, effused, soft and fragile, membranous, adnate but hymenium easily flaked off, leaving the lower subiculum on the substrate, hymenium white, porose to continuous, smooth, margin not differentiated, hyphal cords not observed. *Hyphal system* monomitic, hyphae without clamps, all hyphae thin-walled and extensively encrusted by tiny acicular crystals, subicular hyphae 1.5–2 µm, rather straight, subhymenial hyphae 1.5–2.5 µm, forming a thin but dense tissue. *Basidia* narrowly clavate to pedunculate, 14–20 × 4–5 µm, with 2–4 slender sterigmata, quickly collapsing after spore-discharge. *Basidiospores* elliptic, 3.5–4(–5.5) × 2.5–3(–3.7) µm, smooth, with thickened walls, weakly dextrinoid, larger spores probably produced from two-sterigmatic basidia.

Habitat: On decaying wood and other debris on the ground, associating with conifers, primarily *Picea*, but also reported from mycorrhizal roots of *Salix* and the ericaceous herb *Orthilia secunda*.

Distribution: Widespread throughout the Northern Hemisphere. Detected through environmental DNA in several countries in North and Central Europe and further reported from easternmost Russia, Japan, Canada and USA.

Additional sequenced specimens examined: **Norway**, Buskerud, Nes, E of Grånatten, on *Picea abies*, 10 Sep. 2013, leg. *T.H. Hofton*, O F-254796. Buskerud, Nes, Purkebekken, on *Betula* sp., 24 Sep. 1997, leg. *J.N. Stokland et al*. 20474, O. Buskerud, Nes, Ålungruken, on *Picea abies*., 25 Sep. 1997, leg. *J.N. Stokland et al*. 20611, O. Hedmark, Åmot, Kvernåa, on *Picea abies*, 13 Oct. 1997, leg. *J.N. Stokland et al*. 24861, O. Østfold, Aremark, Tjøstøl, on *Picea abies*, 24 Oct. 2011, leg.

S. Svantesson, O F-248060. **Sweden**, Jämtland, Krokom, Frankrike, on *Picea abies*, 12 Sep. 2011, leg. *J. Nordén*, O F-253620.

Notes: *Piloderma egens* is closely related to *P. lanatum* but differs by having slightly smaller basidiospores. It shares the presence of acicular crystals with *P. cinicola* and *P. craurum*, which, however, both differ by subglobose instead of elliptical basidiospores and by the presence of hyphal cords. *Piloderma craurum* is further separated by the distinct dextrinoid reaction of the basidiospores. *Piloderma byssinum* has hyphal cords, and the incrustation on its subicular hyphae consists of short rods or bipyramidal crystals.

Piloderma exiguum K.H. Larss. & Svantesson, ***sp. nov.*** MycoBank MB 850991. Fig. 7.

Etymology: *Exiguus* (Lat.) = little, referring to the small basidiospores.

Typus: **Sweden**, Västergötland, Billdal, Årekärrslunden, on frondose wood in forest with *Quercus* and *Corylus*, 10 Nov. 2012, leg. *E. Larsson* 323-12 (**holotype** GB-0237573).

UNITE SH: doi.org/10.15156/BIO/SH1172632.08FU

Basidioma resupinate, effused, thin, soft, adnate, hymenium smooth, somewhat farinaceous, white, margin not differentiated, hyphal cords absent. *Hyphal system* monomitic, hyphae thin-walled, without clamps, richly encrusted by grainy to elongate-pyramidic crystals, subiculum thin and inconspicuous, with 2–3.5 µm wide, somewhat irregular hyphae with occasional
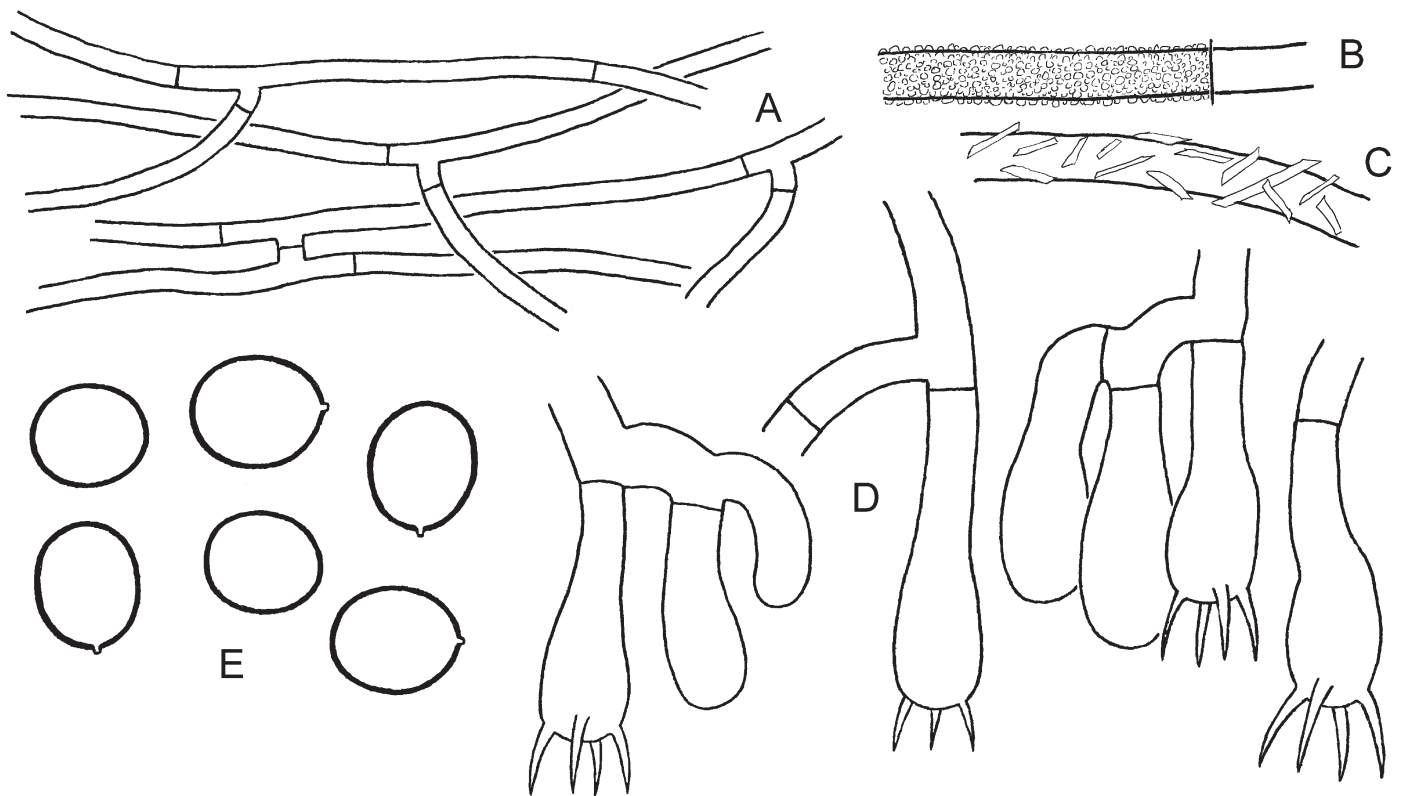

Fig. 8. *Piloderma fallax* (KHL 11979). **A.** Hyphae from subiculum. **B.** Subicular hypha encrusted by corticrocin as seen in Melzer (left) and in 2 % KOH (right). **C.** Subicular hypha encrusted by calciumoxalate. **D.** Details from hymenium with basidia. **E.** Basidiospores. Scale bar: A = 20 µm; B–D = 10 µm; E = 5 µm.

inflations to 4.5 µm, subhymenial hyphae 2–3 µm. *Basidia* narrowly clavate to clavo-pedunculate, 10–20 × 4–4.5 µm, with four sterigmata up to 5 µm long. *Basidiospores* subglobose, 3 × 2.3–2.5 µm, smooth, thick-walled, with one oil-drop, not or weakly dextrinoid.

Habitat: On litter and dead wood in deciduous forest. Ectomycorrhizal with *Betula*, *Fagus*, *Populus*, *Castanea*, and *Quercus*, probably also *Picea* and *Pinus*.

Distribution: A nemoral and southern boreal species widespread in Europe and Asia.

Additional sequenced specimen examined: **Sweden**, Uppland, Ingarö, Karlsdal, old forest with *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Corylus avellana*, *Betula pendula*, 25 Oct. 2022, leg. *S. Svantesson* 1142, UPS.

Notes: *Piloderma exiguum* has the smallest basidiospores in the genus. It is in other respects rather similar to *P. byssinum* by the encrustation and the narrow basidia but differs clearly by the lack of a well-developed subiculum.

Piloderma fallax (Lib.) Stalpers, *Stud. Mycol*. **24**: 53. 1984. Fig. 8.
Basionym: *Sporotrichum fallax* Lib., *Pl. Crypt. Arduenna*, fasc. **2**: nr. 187. 1832.
Synonyms: *Corticium bicolor* Peck, *Bull. Buffalo Soc. Nat*. **1**(2): 62. 1873.
Piloderma croceum J. Erikss. & Hjortstam, *Cort. N. Eur*. **6**: 1201. 1981.

Typus: **Belgium**, Ardennes, *in fagetis*, leg. *A.M. Libert*, *Pl. Crypt. Arduenna*, fasc. 2, nr 187 (**holotype** BR (studied)).

UNITE SH: doi.org/10.15156/BIO/SH1172614.08FU

Basidiomata resupinate, effused, loosely attached, soft, submembranous, hymenium pale yellow to white, smooth or with small blisters, finely porose to continuous, margin byssoid or not differentiated, hyphal cords regularly present, conspicuous, golden yellow, 0.1–1 mm thick, more or less branched, extending through the substrate and into the adjacent soil, in the herbarium fading to pale yellow or pale pink. *Hyphal system* monomitic, hyphae without clamps, subiculum well-developed, byssoid, in fresh material yellow, in the herbarium fading to whitish or pale pink, hyphae in subiculum and hyphal cords sparsely branched, in cords with anastomoses, slightly thick-walled, 1.5–3 µm wide, either finely ornamented by deposits of grainy crystals of corticrocin or with rod-like to elongated prismatic crystals, the former encrustation visible in Melzer but dissolved in KOH, subhymenial hyphae 2–3 µm, thin-walled. *Basidia* clavate to pedunculate, 12–15(–20) × 3.5–5 µm, with four sterigmata. *Basidiospores* subglobose to broadly elliptic, 3–3.5(–4.5) × 2.5–3(–3.5) µm, smooth, with thickened walls, usually with one large oil-drop, weakly dextrinoid.

Habitat: Usually on much decayed wood or litter, but basidiomata may develop on any substrate like soil, rock, litter, and mosses. Associating with a wide variety of trees, both conifers and angiosperms.

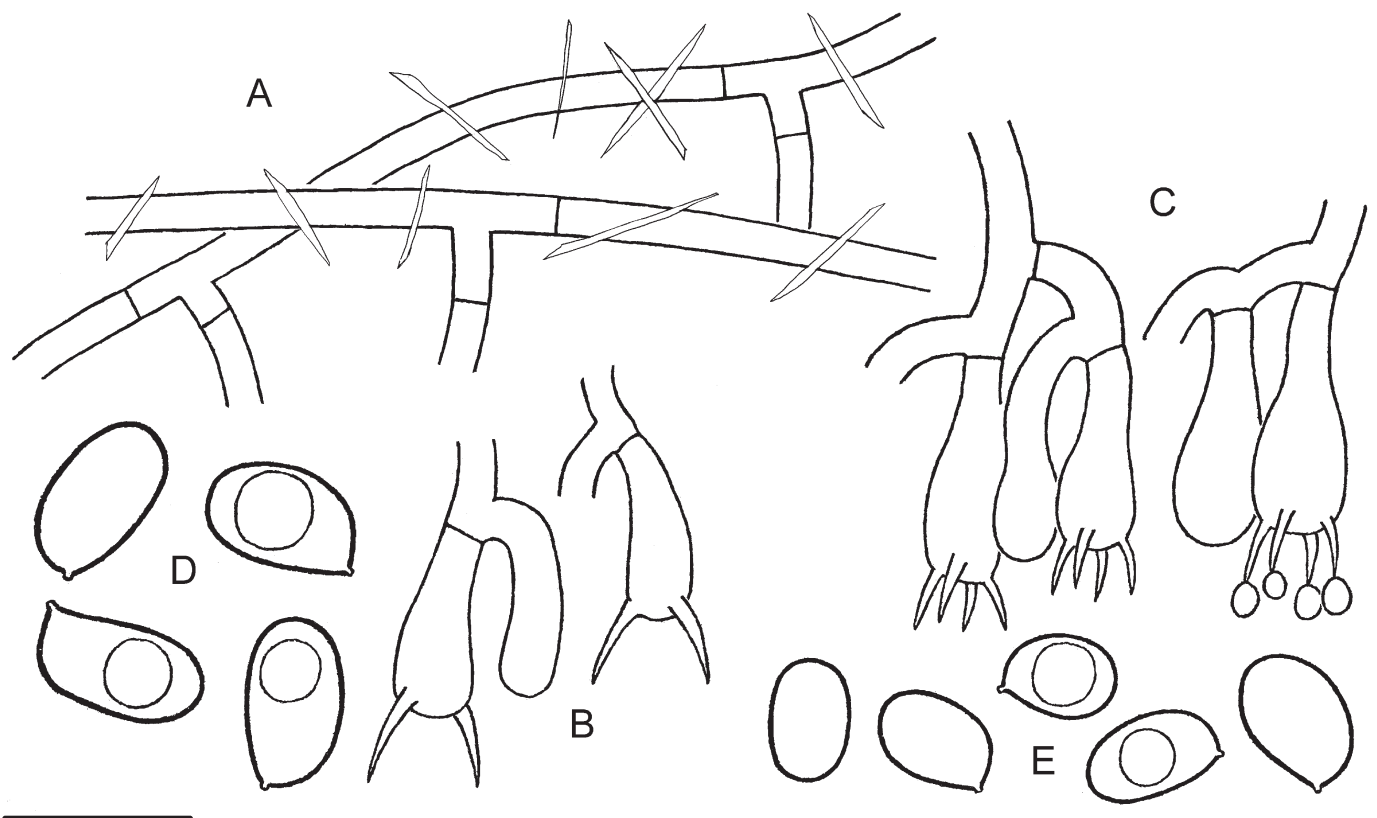*Distribution*: Widespread and common throughout the Northern Hemisphere.

Fig. 9. *Piloderma humile* (A, C, E from holotype; B, D from JS 21524). **A.** Hyphae from subiculum with incrustation. **B.** Two-sterigmate basidia. **C.** Details from hymenium with four-sterigmate basidia. **D.** Basidiospores from two-sterigmate basidia. **E.** Basidiospores from four-sterigmate basidia. Scale bar: A–C = 10 µm; D, E = 5 µm.

Sequenced specimens examined: **Estonia**, Valga, Palupera, Käpa, on decaying wood, 13 Sep. 2012, leg. *K.H. Larsson* 15698, GB. **Norway**, Telemark, Nome, Mørkvasslia, on *Picea abies*. 16 Oct. 2011, leg. *J. Nordén*, O F-253634. **Sweden**, Västergötland, Alingsås, Stadsskogen, on decaying wood, 9 Aug. 1998, leg. *K.H. Larsson* 8545, GB. Öland, Gärdslösa, NNW of Hagby, on *Pinus sylvestris*, 19 Sep. 2005, leg. *K. Hjortstam* 18898, GB.

Notes: Fresh basidiomata of *Piloderma fallax* are recognized by the combination of yellow subiculum and hyphal cords contrasting with a white hymenium (Fig. 1C). *P. olivaceum* has similarly coloured subiculum and hyphal cords but the hymenium is dark yellow to greenish yellow to olivaceous brown. In herbarium material the yellow colour of the subiculum and hyphal cords fades to pale yellow or pale pink. Dried and stored basidiomata of *P. olivaceum* become brown to olivaceous brown.

This species has been named *Corticium croceum* (Kunze) Bres. and *Corticium bicolor* Peck. The former name is a later homonym of *Corticium croceum* (Pat). Sacc., currently *Aleurodiscus croceus* Pat., and therefore not available. Eriksson & Ryvarden (1981) studied the type of Peck's species and argued that it was conspecific with *Piloderma byssinum*. They found no other epithet available and therefore introduced the new name *Piloderma croceum* J. Erikss. & Hjortstam. Larsen (1983) claimed that the type specimens of *Corticium bicolor* and *Lyomyces byssinus* are different species and argued that the name *Corticium bicolor* was available for the species with yellow hyphal cords. Stalpers (1984) found that *Sporotrichum fallax* was an older name for *Corticium bicolor* and therefore made the transfer to *Piloderma*.

We restudied the type specimens of *Corticium bicolor* and *Sporotrichum fallax*. Both are in good condition and show all essential details, including hyphal cords. In both specimens the hyphal cords have a light brownish to pinkish colour and not the bright yellow colour seen in fresh specimens. However, when mounted in Melzer, both type specimens show the grainy incrustation on subicular hyphae that only occur in *Piloderma fallax* and *P. olivaceum*. We conclude that *Piloderma fallax* is the correct name for the present fungus and that *Corticium bicolor* is a later synonym. Larsen *et al.* (1997) reached the same conclusion.
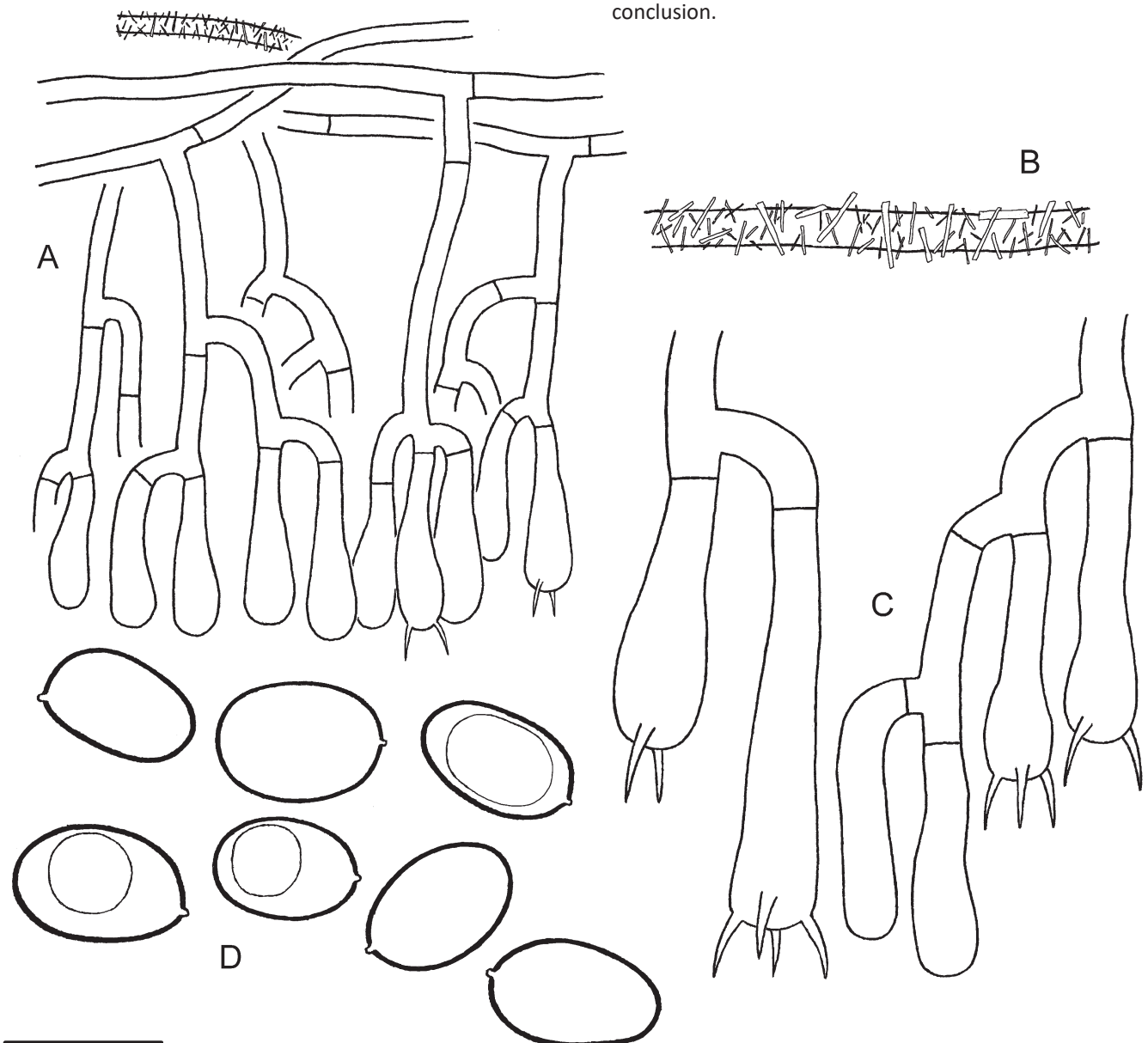

Fig. 10. *Piloderma lanatum* (KHL 17422). **A.** Section through basidioma. **B.** Subicular hypha with incrustation. **C.** Details from hymenium with basidia having variable number of sterigmata. **D.** Basidiospores. Scale bar: A = 20 µm; B, C = 10 µm; D = 5 µm.

Piloderma humile K.H. Larss., ***sp. nov.*** MycoBank MB 850992. Fig. 9.

Etymology: *Humilis* (Lat.) = humble, referring to the inconspicuous fructifications.

Typus: **Norway**, Møre og Romsdal, Nesset, Eikesdal, below Rangåfjellet, on strongly decayed, frondose wood in a mixed forest with *Pinus*, *Betula*, *Alnus*, and *Ulmus* and with an understory of *Corylus*, 17 Sep. 2011, leg. *K.H. Larsson* 14996 (**holotype** GB-0237571).

UNITE SH: doi.org/10.15156/BIO/SH1282294.08FU

Basidioma resupinate, effused, soft and fragile, pellicular, easily detached, hymenium smooth, porose to continuous, white, margin byssoid or not differentiated, hyphal cords few. *Hyphal system* monomitic, hyphae thin-walled, without clamps, subiculum well-developed, with 1.5–3.5(–4) µm wide, rather straight and sparingly branched hyphae, forming a loose tissue, with abundant acicular crystals having obliquely cut ends, subhymenium thin, with hyphae of the same size as in the subiculum. *Basidia* clavate to subcylindrical, sometimes with a slight median constriction, 10–15 × 4.5–6 µm, with 2–4, up to 5 µm long sterigmata. *Basidiospores* elliptic, 3–4.5(–5) × 2–2.5 µm, thick-walled, smooth, with one large oil-drop, the longer basidiospores only present in basidiomata with a dominance of 2-sterigmatic basidia, not or weakly dextrinoid.

Habitat: On debris of various kinds on the forest floor. Forming ectomycorrhiza with frondose trees like *Betula*, *Fagus*, *Populus*, and *Tilia*, but also conifers like *Abies* and *Pinus*.

Distribution: Widely distributed across the Northern Hemisphere. In Europe primarily in the northern regions and in the mountains of Central Europe. Basidiomata hitherto detected only in Norway and Sweden.

Additional sequenced specimens examined: **Norway**, Buskerud, Nes, Ålungruken, on *Picea abies* log, 25. Sep. 1997, *J. Stokland et al.* JS20687 and JS21524, O. Oppland, Nordre Land, Tretjerna, on *Betula* sp. log, Oct. 1996, J. Stokland *et al*. JS11275, O.

Notes: The type specimen has mainly 4-sterigmatic basidia while the paratypes have predominantly 2-sterigmatic basidia. In all other respects they are similar. There is a considerable variation in spore form within each specimen, from broadly to narrowly elliptic, irrespective of the number of sterigmata dominating. The species is similar to *P. cinicola* and *P. craurum* but differs by the elliptic basidiospores. From *P. byssinum* it differs by acicular instead of rod-like crystals on subicular hyphae.

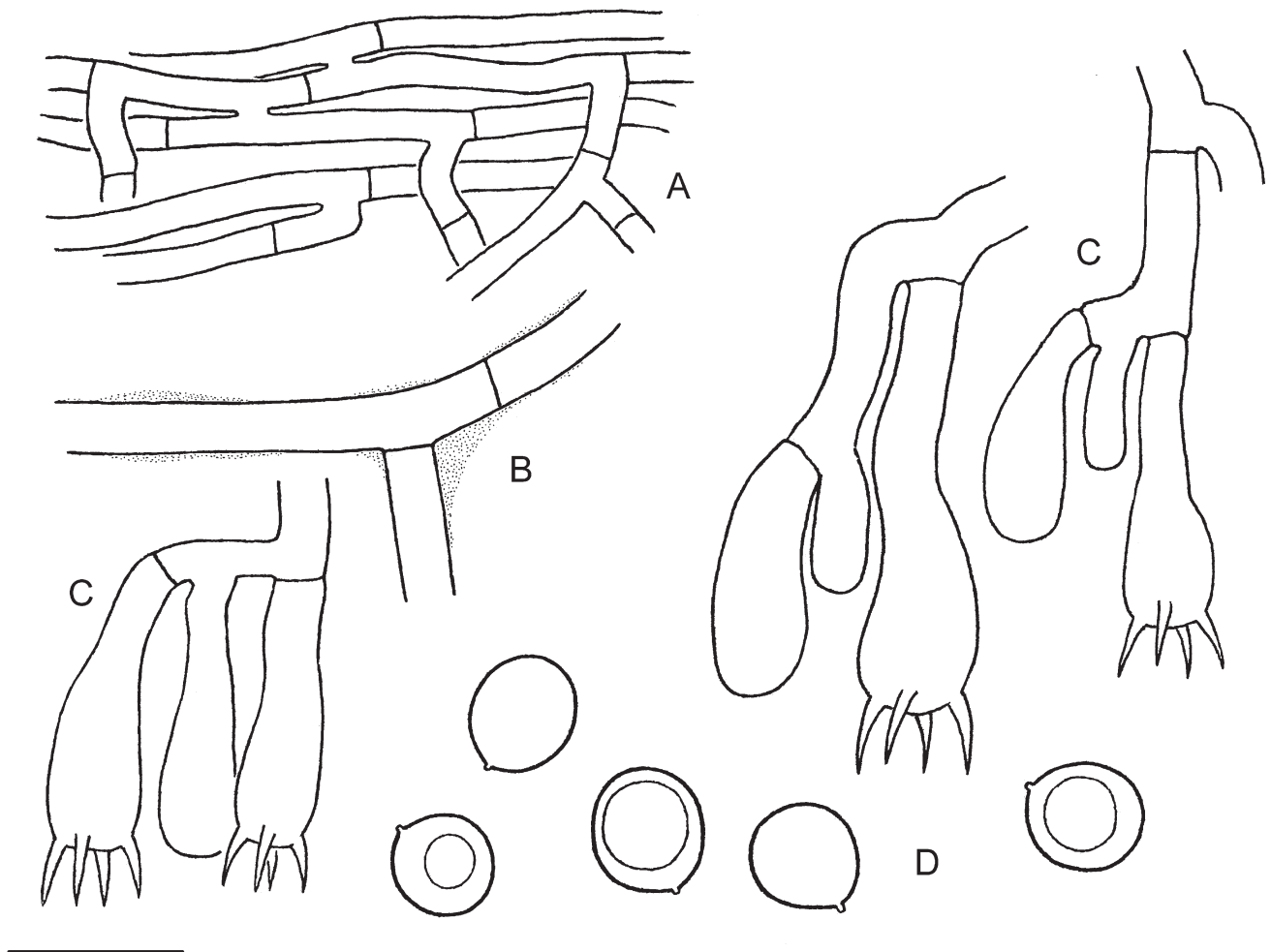***Piloderma lanatum*** (Jülich) J. Erikss. & Hjortstam, *Cort. N. Eur*. **6**: 1207. 1981. Fig. 10.

Fig. 11. *Piloderma ochraceum* (holotype). **A.** Hyphae from subiculum. **B.** Partly gelatinized subicular hyphae as seen in 2 % KOH. **C.** Details from hymenium with basidia. **D.** Basidiospores. Scale bar: A = 20 µm; B, C = 10 µm; D = 5 µm.

Basionym: *Piloderma byssinum* var. *lanatum* Jülich, *Willdenowia Beih*. **7**: 230. 1972.

Synonym: *Athelia byssina* var. *bispora* Parmasto, *Eesti N. S. V. Tead. Akad. Toimet., Biol*. **16**: 380. 1967.

Typus: **Sweden**, Uppland, Älvkarleby, Billudden on decaying *Alnus* sp. wood. 16 Oct. 1949, leg. *J. Eriksson* 4016 (**holotype** UPS F-117891, **isotype** GB (studied)).

UNITE SH: doi.org/10.15156/BIO/SH1172619.08FU

Basidioma resupinate, effused, soft, fragile, membranous, hymenium white to cream-coloured, without differentiated margin, hyphal cords not observed. *Hyphal system* monomitic, hyphae without clamps, subicular hyphae straight, 2–2.5 µm wide, with somewhat thickened walls, richly encrusted by narrow, rod-like to acicular crystals, subhymenial hyphae 2–4 µm, thin-walled, richly branched, not encrusted. *Basidia* narrowly clavate, 18–25(–30) × 4.5–6 µm, with 2–4 sterigmata. *Basidiospores* elliptic, 5–5.5(–6.5) × 2.5–3.7(–4.5) µm, the larger spores produced by two-sterigmatic basidia, smooth, with thickened walls, weakly dextrinoid.

Habitat: On decaying wood and other debris on the ground. Forming mycorrhiza with broadleaved trees like *Fagus*, *Quercus*, and *Salix*, probably also with conifers.

Distribution: Widespread across the Northern Hemisphere. Occurrences confirmed by basidiomata are mainly from the Nordic countries.

Sequenced specimens examined: **Norway**, Oppland, Nord-Fron, Liadalan nat. res, on *Betula* sp., 8 Oct. 1996, leg. *J.N. Stokland et al*. 10443 and 10446 O; same locality, on *Populus tremula*. 8 Oct. 1996, leg. *J.N. Stokland et al*. 10556, O; same locality, on deciduous wood, 7 Sep. 2006, leg. *K.H. Larsson* 13416, GB. Vestfold, Stokke, Askedal, on *Fagus sylvatica*. 29 Sep. 1997, leg. *J.N. Stokland et al*. 2214, O. Vestfold, Tønsberg, Gullkronene, on frondose wood, 15 Sep. 2016, leg. *K.H. Larsson* 17422, GB. **Sweden**, Gotland, Sproge, Botarve nat. res., on frondose wood, 7 Oct. 2021, leg. *K.H. Larsson* 18284, GB.

Notes: Two varieties have been described, var. *lanatum* with 4-sterigmatic basidia and var. *bisporum* with predominantly 2-sterigmatic basidia. Of the collections sequenced only JS 10446 would be classified as var. *bisporum*. The sequences of JS 10446 and 10556 are virtually identical and since they were also growing within meters from each other this is strong evidence not to recognize the 2-sterigmatic basidiomata as a separate taxon. *Piloderma lanatum* is rather easy to recognize thanks to the comparatively large, elliptic basidiospores.

Piloderma ochraceum K.H. Larss., ***sp. nov.*** MycoBank MB 850993. Fig. 11.

Etymology: *Ochraceus* (Lat.) = a pale yellowish brown colour.

Typus: **Sweden**, Västergötland, V:a Tunhem, Halleberg, Hallesnipen, on decaying wood on the border of a clear-cut area with *Quercus* and *Pinus*, 5 Oct. 2006, leg. *K.H. Larsson* 13481 (**holotype** GB-0237574).

UNITE SH (1.5 %): doi.org/10.15156/BIO/SH1544836.08FU

Basidioma resupinate, effused, thin, soft, partly adnate, partly developing as a membrane over the substrate but with holes where irregularities in the substrate were not covered with hymenium, hymenium smooth, continuous, dull ochraceous, "café-au-lait", margin not differentiated, hyphal cords absent. *Hyphal system* monomitic, hyphae without clamps, in the thin and inconspicuous subiculum partly gelatinized and swelling in KOH, 2–4 µm wide, anastomosing, subhymenial hyphae thin-walled, 2.5–3.5 µm. *Basidia* clavate, 18–27 × 5–6.5 µm, with four sterigmata, up to 5 µm long, basidia not collapsing after spore discharge. *Basidiospores* subglobose, 3.5–4 × 3–3.2 µm, thick-walled, smooth, with one large oil-drop, not dextrinoid.
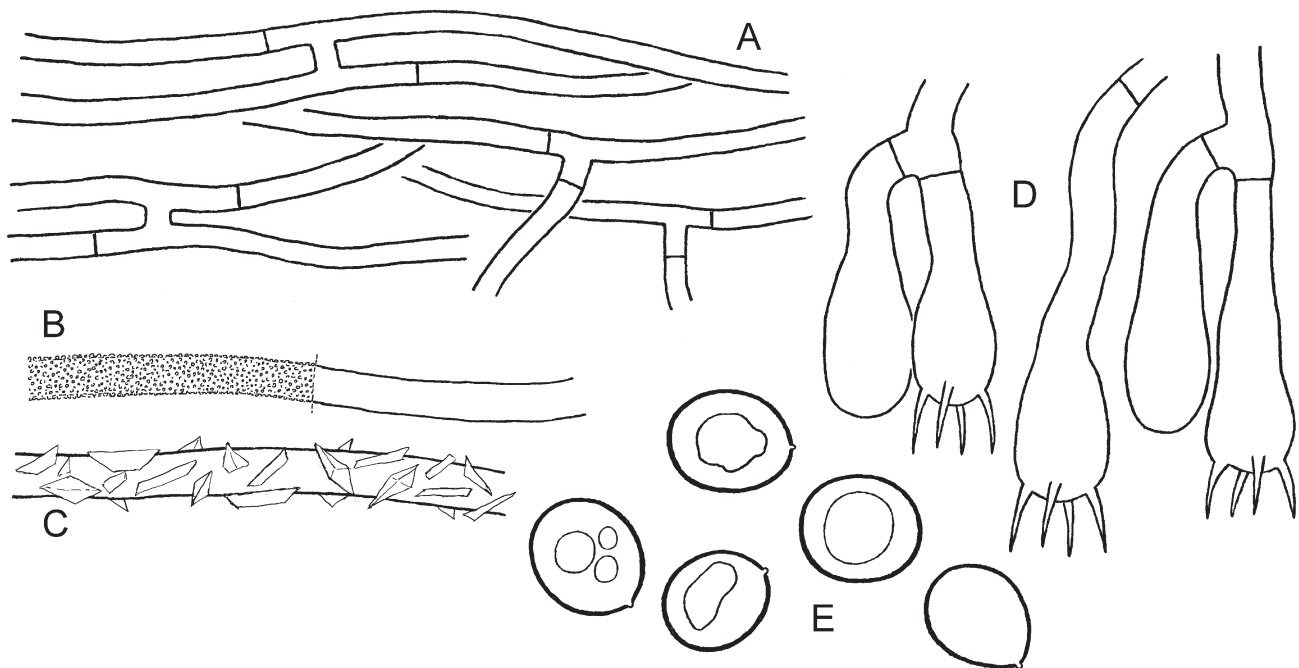

Fig. 12. *Piloderma olivaceum* (JS 26821). **A.** Hyphae from subiculum. **B.** Subicular hyphae encrusted by corticrocin as seen in Melzer (left) and in 2 % KOH (right). **C.** Subicular hyphae encrusted by calciumoxalate. **D.** Basidia. **E.** Basidiospores. Scale bar: A = 20 µm; B–D = 10 µm; E = 5 µm.

Habitat: On decaying wood and other debris on the forest floor. Mycorrhizal with conifers.

Distribution: Widely distributed over the Northern Hemisphere but seemingly rare. Observed in Estonia, Russia, Japan, Canada, and the type locality in Sweden.

Notes: This species is somewhat similar to *Piloderma sphaerosporum*. They share the basidioma construction with a thin and inconspicuous subiculum, lack of hyphal cords, basidia with persistent sterigmata, and subglobose basidiospores. *P. ochraceum* differs by the basidioma colour and by the presence of gelatinized subicular hyphae.

Piloderma olivaceum (Parmasto) Hjortstam, *Windahlia* **14**: 25. 1984. Fig. 12.
Basionym: *Athelia bicolor f:a olivacea* Parmasto, E*esti N. S. V. Tead. Akad. Toimet., Biol.* **16**: 380. 1967.

Typus: **Russia**, Khabarovsk, Kuznetsovsky pass, on *Larix dahurica*, 21 Aug. 1961, leg. *E. Parmasto* (**holotype** TAA 15360, probably lost).

UNITE SH: doi.org/10.15156/BIO/SH1709471.08FU

Basidioma resupinate, effused, soft, byssoid, hymenium smooth, porose to continuous, when fresh golden yellow, greenish yellow, olivaceous or brownish, after herbarium storage darker, margin byssoid, with the same colour as the hymenium, hyphal cords present, yellow, more or less fading to rose-grey or violaceous in the herbarium. *Hyphal system* monomitic, hyphae without clamps, in the subiculum 1.5–3 µm wide, slightly thick-walled, forming an extensive, byssoid tissue, sparingly encrusted, some hyphae weakly brownish, subhymenial hyphae 2–3 µm wide, thin-walled. *Basidia* clavate to pedunculate, 10–15(–20) × 4–5 µm, with four sterigmata, some basidia with grainy-stringy, yellow to reddish brown contents. *Basidiospores* subglobose, 3–3.5 × 2.3–3 µm, somewhat thick-walled, hyaline or very pale yellowish, not dextrinoid, mostly without oil-drops.

Habitat: On decaying wood and other debris on the ground in conifer and mixed forest. Forming mycorrhiza with conifers.

Distribution: Widespread in Europe and North America, less common in East Asia.

Sequenced specimens examined: **Estonia**, Saare, Kihelkonna, Odalätsi, on decaying wood, 13 Aug. 1999, leg. *E. Larsson* 34-99, GB. **Russia**, Khabarovsk, Khabarovsk, Levyi Ulun on debris under *Picea sajanensis* and *Pinus pumila* in subalpine forest, 23 Aug. 2012, leg. *V. Spirin* 5558, GB. **Sweden**, Uppland, Björklinge par., Hocksboglupen, on mosses, 22 Sep. 2022, leg. *K.H. Larsson* 18377, GB; Uppland, Vänge, Fiby, on coniferous wood. 28 Mar., 2003, leg. *D. Lindner*, GB.

Notes: This is the only known species with yellow to greenish yellow or brownish hymenium, yellow subiculum, and yellow hyphal cords (Fig. 1D). It is often confused with *P. fallax*, which, however, has a white hymenium over a yellow subiculum. The brown olivaceous colour developing during herbarium storage is unique within the genus.
    The holotype could not be located. We have sequenced one specimen from the vicinity of the type locality and it may serve as a neotype, should the holotype remain lost.
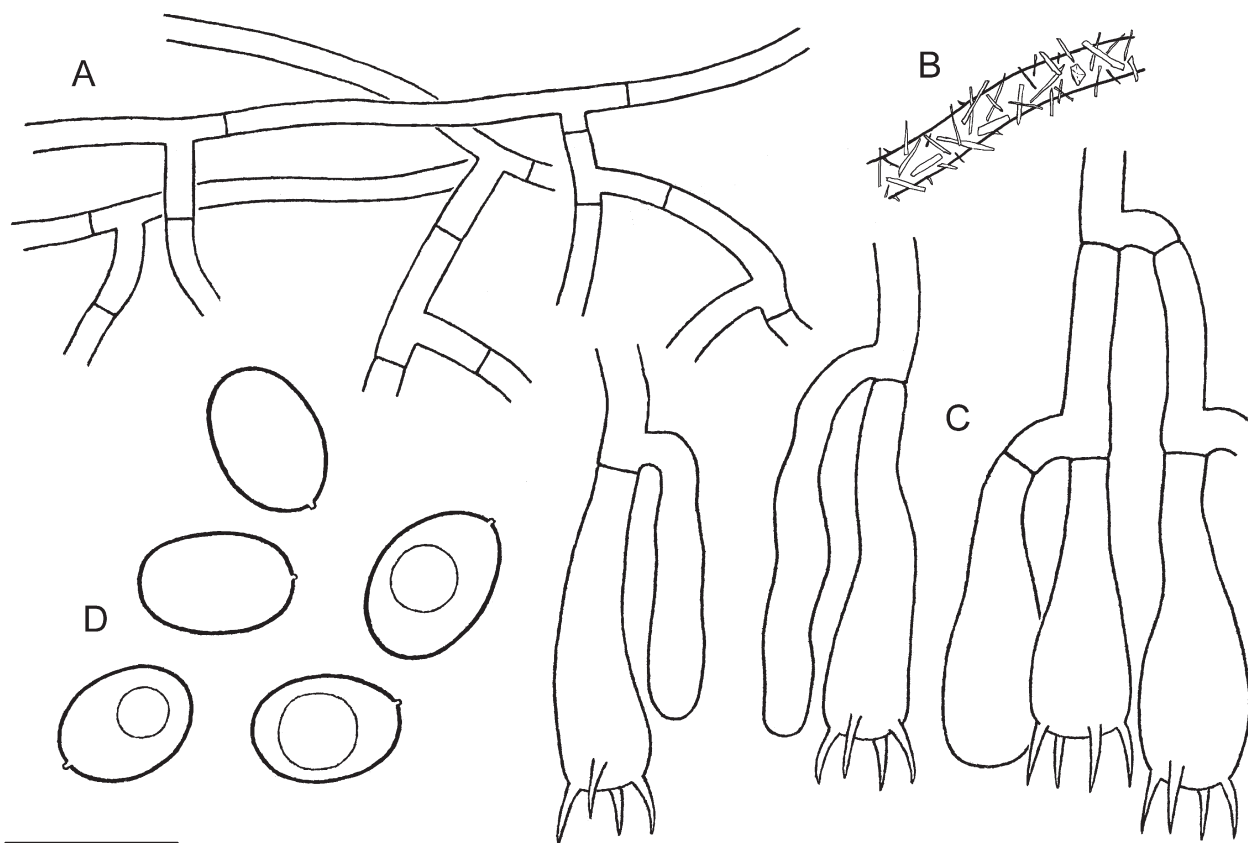

Fig. 13. *Piloderma rallum* (holotype). **A.** Hyphae from subiculum and subhymenium. **B.** Subicular hypha with incrustation. **C.** Details from hymenium with basidia. **D.** Basidiospores. Scale bar: A = 20 µm; B, C = 10 µm; D = 5 µm.

Piloderma rallum K.H. Larss. & Svantesson, **sp. nov.** MycoBank MB 850994. Fig. 13.

Etymology: *Rallus* (Lat.) = thin, slender.

Typus: **Norway**, Oppland, Nord-Fron, Liadalan nat. res., on decaying frondose wood on the ground in a mixed forest, 7 Sep. 2006, leg. *K.H. Larsson* 13431 (**holotype** GB-0237572).

UNITE SH: doi.org/10.15156/BIO/SH1172620.08FU

Basidioma resupinate, effused, thin, soft, adnate, hymenium smooth, finely porulose, white, margin not differentiated, hyphal cords absent. *Hyphal system* monomitic, hyphae thin-walled, without clamps, subiculum thin, not clearly differentiated, with 1.5–3 µm wide, sparsely branched hyphae, subhymenium composed of loosely interwoven 2.5–4 µm wide hyphae, encrustation mostly lacking but small granular crystals present on some hyphae. *Basidia* clavate, 15–25 × 4.5–5.5(–6) µm, with four sterigmata up to 4 µm long. *Basidiospores* subglobose to elliptic, 4–5 × 2.5–3.7 µm, smooth, thick-walled, with one oil-drop, not or weakly dextrinoid.

Habitat: On decaying wood and other debris on the forest floor. Mycorrhizal with conifers, primarily *Pinus*.

Distribution: Widespread throughout the Northern Hemisphere but rarely collected. Preserved basidiomata only known from Norway, Sweden, and China.

Additional sequenced specimens examined: **Sweden**, Uppland, Ingarö, Karlsdal, old forest with *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Corylus avellana*, *Betula pendula*, 25 Oct. 2022, leg. *S. Svantesson* 1129, UPS; Uppland, Lena, Kapellhagen, old forest with *Picea abies*, *Pinus sylvestris, Salix caprea*, 21 Sep. 2022, leg. *S. Svantesson* 729, UPS.

Notes: The lack of a well-developed subiculum makes this species similar to *Piloderma sphaerosporum*, from which it differs by the elliptic basidiospores. *P. ochraceum* is another species with thin subiculum. It differs by pale brownish basidiomata and partly gelatinized subicular hyphae. *P. exiguum* differs by smaller basidiospores.

Piloderma reticulatum (Parmasto) Jülich, *Ber. Deutsch. Bot. Ges*. **81**: 417. 1969. Fig. 14.
Basionym: *Athelia reticulata* Parmasto, *Eesti N. S. V. Tead. Akad. Toimet., Biol*. **16**: 382. 1967.

Typus: **Sweden**, Stockholm, Djurgården, on decaying deciduous wood, 28 Jan. 1894, leg. *L. Romell* 1497 (**holotype** S F15425 (studied), **isotype** GB (studied)).

Basidioma resupinate, effused, thin, adnate, soft and fragile, hymenium smooth, porose to minutely farinose, probably white when fresh but in the herbarium assuming a cream to pale ochraceous colour, margin not differentiated or farinose, hyphal cords not observed. *Hyphal system* monomitic, hyphae thin-walled, without clamps, in the poorly developed subiculum mostly 1.5–2.5 µm, in the subhymenium 2–3 µm, incrustation not observed. *Basidia* clavate to pedunculate, 12–17 × 4–5.5 µm, with four sterigmata. *Basidiospores* subglobose to broadly elliptic, 3.5–4 × 2.5–3, with thickened walls, smooth, not dextrinoid.

Habitat: Collected on the bark of decaying deciduous wood.

Distribution: Known only from the type locality in Sweden.
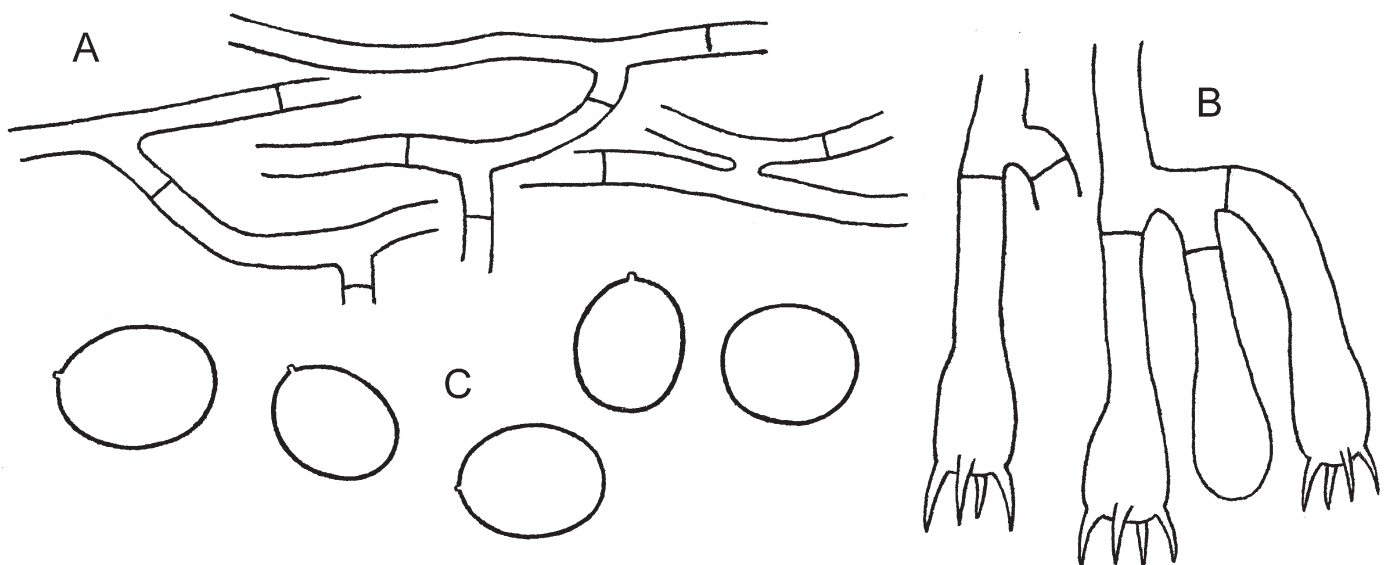

Fig. 14. *Piloderma reticulatum* (isotype). **A.** Hyphae from subiculum. **B.** Basidia. **C.** Basidiospores. Scale bar: A = 20 µm; B = 10 µm; C = 5 µm.

Notes: None of the many *Piloderma* collections we have studied fully conform with the type of *P. reticulatum*. Since there are still several *Piloderma* Species Hypotheses in the UNITE database that are not yet known from basidiomata, the possibility remains that one of them represent *P. reticulatum*. Since the type material is scanty, no attempt to sequence it was made.

Corticium reticulatum Litsch. is a homonym of *Corticium reticulatum* Berk. This was not observed by Parmasto (1967) when he combined the species in *Athelia*. Therefore, the publication of *Athelia reticulata* should be considered as introduction of a *nomen novum* and takes precedence over any later naming of the same taxon. Jülich (1969) was not aware of this complication when he combined *Corticium reticulatum* into *Piloderma*. He later (Jülich 1972) corrected himself and stated that the species should be cited as *Piloderma reticulatum* Jülich. However, the correct citation of the species is *Piloderma reticulatum* (Parmasto) Jülich.

Piloderma sphaerosporum Jülich, *Willdenowia Beih*. **7**: 235. 1972. Fig. 15.

Typus: **Sweden**, Södermanland, Gryt, NE of Baggeböl, on coniferous wood, 5 Oct. 1953, leg. *S. Lundell* (**holotype** GB (studied)).

UNITE SH: doi.org/10.15156/BIO/SH1544806.08FU

Basidioma resupinate, effused, thin, adnate, soft, often forming many smaller basidiomata that eventually coalesce, hymenium smooth, finely porose, white to pale cream-coloured, margin abrupt, hyphal cords lacking. *Hyphal system* monomitic, hyphae thin-walled, without clamps, subiculum not differentiated, all hyphae 2–3 µm wide, often with small amorphous inclusions visible in KOH. *Basidia* clavate to pedunculate, 16–20(–30) × 3.5–5 µm, with four rather straight, to 4 µm long sterigmata that usually do not collapse after spore discharge, mostly with the same kind of grainy inclusions as in the hyphae. *Basidiospores* subglobose 3–4(–4.5) × 2.8–3.5 µm, smooth, with slightly thickened walls, not dextrinoid.

Habitat: On decayed wood and other debris on the forest floor. Mycorrhizal with forest trees, primarily *Pinus* but also other conifers. In addition, reported as associated with *Alnus*, *Betula*, and as forming ericoid mycorrhiza with *Vaccinium* sp. (Bougoure *et al.* 2007, Ishida & Nordin 2010).

Distribution: A very common species, following pine trees throughout the Northern Hemisphere.

Sequenced specimens examined: **Norway**, Akershus, Asker, Svensrud, on *Picea abies*, 7 Oct. 1997, leg. *J.N. Stokland et al.* 23706, O; Buskerud, Ringerike, Steinsrud, on *Pinus sylvestris*, 22 Sep. 1997, leg. *J.N. Stokland et al.* 20011, O; Østfold, Råde, Kil, on *Picea abies*, 9 Oct. 1997, leg. *J.N. Stokland et al.* 24262, O. **Sweden**, Uppland, Uppsala, Nåsten, S of Hågaby, on coniferous wood, 19 Sep. 2022, leg. *K.H. Larsson* 18340, GB.

Notes: Usually recognizable thanks to the basidia, which tend to be pedunculate and carry persistent, comparatively long sterigmata, the rounded basidiospores, and the drop-like inclusions in hyphae and basidia. The lack of both hyphal cords and a well-developed subiculum sets it apart from *Piloderma byssinum*.
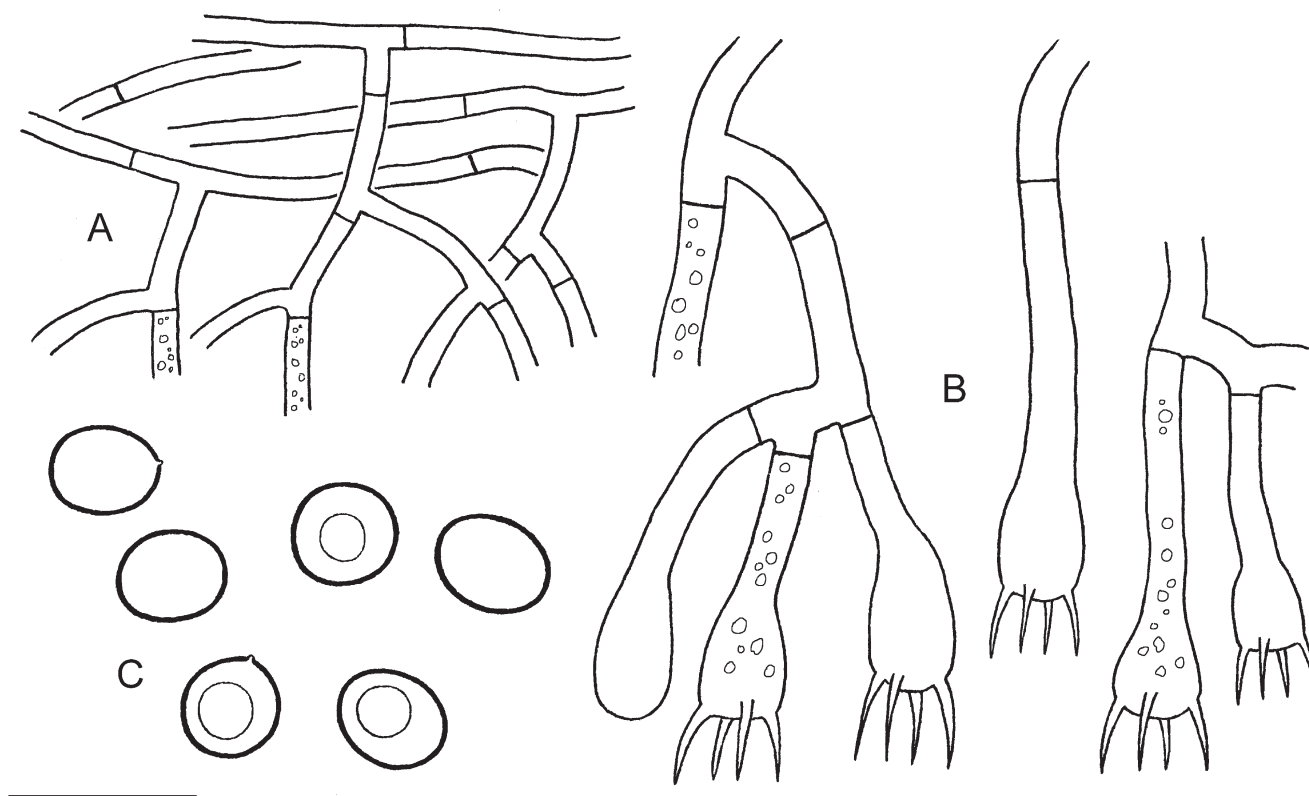

Fig. 15. *Piloderma sphaerosporum* (KHL 18340). **A.** Hyphae from subiculum and subhymenium. **B.** Details from hymenium with basidia. **C.** Basidiospores. Scale bar: A = 20 µm; B = 10 µm; C = 5 µm.

KEY TO SPECIES IN *PILODERMA*

1. Basidioma pellicular, subiculum well-developed, byssoid, visible hyphal cords often present on the substrate 2
1. Basidioma more or less adnate, subiculum poorly developed, visible hyphal cords lacking 9

2. Subiculum and hyphal cords yellow, after long storage pale yellow to pale pink 3
2. Subiculum and hyphal cords white 4

3. Hymenium white, subiculum yellow .... *P. fallax*
3. Hymenium and subiculum yellow to brown or olivaceous .... *P. olivaceum*

4. Basidiospores strongly dextrinoid .... *P. craurum*
4. Basidiospores not or only weakly dextrinoid 5

5. Basidiospores 2–2.5 µm wide .... *P. humile*
5. Basidiospores 2.5–4.5 µm wide 6

6. Basal hyphae with rod-like to elongated pyramidic crystals .... *P. byssinum*
6. Basal hyphae with mainly acicular crystals 7

7. Basidiospores subglobose .... *P. cinicola*
7. Basidiospores elliptic 8

8. Basidiospores 3.5–4(–5.5) µm long .... *P. egens*
8. Basidiospores 5–5.5(–6.5) µm long .... *P. lanatum*

9. Basidioma ochraceous to pale brown .... *P. ochraceum*
9. Basidioma white to pale ochraceous 10

10. Basidia and subhymenial hyphae with drop-like inclusions .... *P. sphaerosporum*
10. Basidia and hyphae lacking drop-like inclusions 11

11. Basidiospores less than 3.5 µm long .... *P. exiguum*
11. Basidiospores 3.5 µm long or longer 12

12. Basidiospores 4–5 µm long .... *P. rallum*
12. Basidiospores 3.5–4 µm long .... *P. reticulatum*

DISCUSSION

Piloderma is an obligately ectomycorrhizal genus with a global distribution (Tedersoo *et al*. 2010; see also the UNITE database). Most known species are present in both Eurasia and in North America. The exception is *Piloderma exiguum* that presently is not reported from North America. *Piloderma sphaerosporum* is the only described species that has been discovered in Africa. This is a pine-associated species and African occurrences are most likely from plantations with non-indigenous pine species.

Judging from the Species Hypothesis clusters in the UNITE database there are many more species of *Piloderma* yet to be described, not least in the Southern Hemisphere, where soil samples from forest of native trees indicate the presence of at least 30 unnamed species. Increased sampling will hopefully make it possible to collect basidiomata of these undescribed species. For all such known but unnamed species the sequences derived from soil or root-tip samples in public DNA data bases usually have georeferenced sample plots. These sites are therefore natural targets for sampling of basidiomata.

The present paper demonstrates how the wealth of information assembled in sequence databases may increase our understanding of ecology and distribution of species. This is particularly true for soil-dwelling species since many ecological studies are screening for DNA present in soil samples. Such studies now use metabarcoding techniques that generate an overwhelming amount of data. The current implementation of the UNITE database includes data from some ten metabarcoding studies, which is just a small proportion of the HTS studies available in, *e.g*., the sequence read archive of the NCBI (Leinonen *et al.* 2011). Further screening of soil HTS data will probably reveal additional *Piloderma* species and, coupled with increased sampling of basidiomata these can be provided with names and descriptions.

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Table 1. List of sequences used in phylogenetic analyses with accession numbers either from GenBank or from the UNITE database. Sequences produced in this study are indicated in bold face. Type specimens are indicated by *.

Species	Voucher	Herbarium	GenBank/UNITE	Country
Athelopsis subinconspicua	GB-0058732	GB	LR694197	SE
Leptosporomyces raunkiaerii	HHB-7628	CFMR	GU187528	US
Piloderma byssinum	KHL 13488	GB	**OQ803271**	SE
	JS 20399	O	**DQ469281**	NO
	JS 15688	O	**DQ469280**	NO
	KGN 197/88	GB	**DQ469279**	SE
	O-F-253647	O	UDB038226	NO
	EB 1165/08	O	**OQ803270**	NO
Piloderma cinicola	KHL 18326*	GB	**OQ803267**	SE
	TUF113119	TUF	UDB008314	EE
	NS 18-105	GENT	**OQ803266**	SE
	SS 1019	UPS	**OQ803261**	SE
	SS 1150	UPS	**OQ803265**	SE
	SS 748	UPS	**OQ803264**	SE
	SS 750	UPS	**OQ803262**	SE
	SS 635	UPS	**OQ803263**	SE
Piloderma craurum	JS 15686	O	**UDB001726**	NO
	O-F-270951*	O	**UDB001728**	NO
	JS 25853	O	**UDB001727**	NO
	O-F-253675	O	UDB038232	SE
	JS 7863	O	**UDB001729**	NO
	KHL 18375	GB	**OQ803285**	SE
Piloderma egens	O-F-254796	O	**OQ803276**	NO
	JS 24861	O	**UDB001733**	NO
	O-F-253620	O	UDB038221	SE
	JS 20474	O	**UDB001735**	NO
	JS 20611	O	**UDB001734**	NO
	KHL 18343*	GB	**OQ803275**	SE
	O-F-248060	O	UDB07674133	NO
Piloderma exiguum	EL 323/12*	GB	**OQ803280**	SE
	SS 1142	UPS	**OQ803281**	SE
Piloderma fallax	KHL 15698	GB	**OQ803272**	EE
	Hjm 18898	GB	**OQ803273**	SE
	KHL 8545	GB	**DQ469285**	SE
	O-F-253634	O	UDB07673547	NO
Piloderma humile	JS 20687	O	**UDB001730**	NO
	JS 11275	O	**UDB001732**	NO
	KHL 14996*	GB	**UDB024825**	NO
	JS 21524	O	**UDB001731**	NO
Piloderma lanatum	JS 22149	O	**DQ469288**	NO
	KHL 17422	GB	**OQ803279**	NO
	KHL 13416	GB	**OQ803277**	NO
	JS 10443	O	**UDB001745**	NO
	JS 10566	O	**UDB001743**	NO
	JS 10446	O	**UDB001742**	NO
	KHL 18284	GB	**OQ803278**	SE

Table 1. (Continued).

Species	Voucher	Herbarium	GenBank/UNITE	Country
Piloderma ochraceum	KHL 13481*	GB	**OQ803274**	SE
	SG027_B01	n/a	KP889405	US
Piloderma olivaceum	EL 34/99	GB	**DQ469289**	EE
	DZ	GB	**DQ469291**	SE
	VS 5558	GB	**OQ803269**	RU
	KHL 18377	GB	**OQ803268**	SE
Piloderma rallum	KHL 13431*	GB	**OQ803282**	NO
	SS 1129	UPS	**OQ803283**	SE
	SS 729	UPS	**OQ803284**	SE
Piloderma sphaerosporum	JS 20011	O	**UDB001749**	NO
	JS 24262	O	**UDB001750**	NO
	JS 23706	O	**UDB001751**	NO
	KHL 18340	GB	**OQ803286**	SE

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