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(Agaricales, Basidiomycetes);
Expansion and phylogenetic placement**

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***Micromphale* sect. *Perforantia* (Agaricales, Basidiomycetes); Expansion and phylogenetic placement**

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Abstract

DNA sequences show that the traditional genus *Micromphale* appears to be polyphyletic. Nuclear ribosomal LSU and ITS DNA sequences place *Micromphale* sect. *Perforantia* Singer (typus sect. *M. perforans*) within *Gymnopus*, comprising a clade sister to a mixture of traditional *Gymnopus* taxa including *G. fusipes* (typus generis) plus traditional *Marasmius* sect. *Androsacei*. This study enlarges sect. *Perforantia* and shows that sect. *Perforantia* is a clade separate from those including *Micromphale* sect. *Micromphale* and sect. *Rhizomorphigena*. A new subsection *Pinophili* is proposed to include new species *G. pinophilus* and *G. ponderosae*. Eleven taxa are accepted at species rank, of which nine are proposed as new, mostly morpho-taxa.

Key words

Gymnopus, ecological species, taxonomy, new species, new subsection

Introduction

While the history of the genus name *Micromphale* was somewhat tortuous [see Donk (1962)], it was legislated as rejected against *Marasmius* (see Taxon 3: 233. 1954.), but with type species as *Mi. venosus* (= *Mi. foetidum*, see Singer and Smith (1946): 251; Donk (1962): 187; Horak (1968): 383). Thus, for a time, the nomenclature of the genus name has been more or less stable.

Micromphale, as legislated in 1954, now comprises three sections. Singer (1948) had described two new heterotypic sections of *Micromphale*, adding to the typical section (*Micromphale* sect. *Micromphale*, nom. auton.; typus sect. et gen. *Mi. venosum* = *Mi. foetidum*). The first of these (*Micromphale* sect. *Rhizomorphigena* Singer; typus sect. *Mi. westii*) was accepted by Desjardin and Petersen (1989), and will be taken up elsewhere. The second, *Micromphale* sect. *Perforantia* Singer (typus sect. *Mi. perforans*), is more or less the object of this paper. Neither of Singer's (1948) sections was populated by more than its type species.

If Singer's (1948) diagnosis for sect. *Perforantia* was less than detailed, its type species provided a nucleus around which to gather similar basidiomata. Every diagnostic character (and several character combinations) applied equally to organisms placed elsewhere and short of studies of individual type specimens, clear-cut circumscription of the section awaited molecular analyses. Nevertheless, over time, additional taxa have been accreted.

Several attempts to phylogenetically place *Micromphale* have been made. For Moncalvo et al. (2002) (based on nrLSU sequences) a large clade labeled as /omphalotaceae comprised two subclades, /omphalioid and /lentinuloid, the latter including numerous taxa, including a polyphyletic *Gymnopus*. Within /lentinuloid, *Mi. foetida* occurred in a further subclade, /*micromphale*, but *Mi. perforans* formed a long branch of its own outside of /lentinuloid but within /omphalotaceae. Likewise, Mata et al. (2004) based on nrLSU sequences, found that *M. foetidum* was placed within a clade dominated by *Gymnopus* taxa. The first study including both *Mi. foetidum* and *Mi. perforans* was that by Wilson and Desjardin (2005) based on nrLSU sequences, who found that while both species were placed in a clade dominated by *Gymnopus* taxa, they did not form a monophyletic group. Mata et al. (2007) (based on nrITS sequences) more accurately placed *Mi. foetidum* and *Mi. brassicolens* within *Gymnopus* (but not monophyletic) but did not include *Mi. perforans*.

Based on shared taxonomic characters, both macro- and micromorphological, *Micromphale* sect. *Perforantia* may be difficult to separate from *Marasmius* sect. *Androsacei*. For example, usually overlooked, the pileipellis of basidiomata of *Marasmius* sect. *Androsacei* almost always occurs with a thin slime matrix, a feature traditionally used to define *Micromphale* and especially sect. *Perforantia*, further confusing the separation of *Micromphale* sect. *Perforantia* from *Marasmius* sect. *Androsacei*. Further, because of the peculiar pileipellis structure composed of diverticulate hyphae together with broom cell-like setulose hyphal termini, *Marasmius* sect. *Androsacei* was separated from mainstream *Marasmius* at genus rank as *Setulipes* (Antonín 1987), with type species *S. androsaceus*. The pileipellis structure was described as “a well-developed *Rameales*-structure,” a reference to a very similar (or identical) construction found in some taxa of *Marasmiellus* sect. *Rameales*. This construction and its hyphal structures are replaced in *Micromphale* sect. *Perforantia* by a repent pileipellis with hyphae usually encrusted to some extent but varying from diverticulate or setulose to without such differentiation. Joining a chorus of genera being dismembered as a result of molecular analyses indicating polyphyletic distribution of infrageneric complexes, the traditional concept

of *Marasmius* (typus generis *Ma. rotula*) is being fractured. Accordingly, *Marasmius* sect. *Androsacei* is disassociated from mainstream *Marasmius*.

Superficial similarities among basidiomata of *Micromphale* sect. *Perforantia* and *Marasmius* sect. *Androsacei* prompted the current study. Morphological examination of many collections, including micromorphology, led to suspicion that undescribed taxa occurred in North America and that a comprehensive study including both complexes was unwieldy. It seemed more efficient, therefore, to focus on sect. *Perforantia*, with additional reports to follow.

Materials and methods

Abbreviation of genus names include *Ma.* for *Marasmius* and *Mi.* for *Micromphale*. Color names in quotation marks (i.e. “saya brown”) are from Ridgway (Ridgway 1912); see also (Petersen 2016), usually followed by an alphanumeric citation (i.e. 7E5) referring to plate, column and row in Kornerup and Wanscher (1967). PhC = Phase contrast microscopy; BF = bright field microscopy; TFB = Tennessee Field Book, field-assigned number for notes and photographs; TENN = herbarium number assigned to a specimen for filing and future herbarium retrieval. RHP and KWH = abbreviations of authors' names; GSMNP = Great Smoky Mountains National Park. State and province abbreviations follow United States Postal Service designations.

All microscopic examination was undertaken using two microscopes: 1) Nikon dissecting microscope (model SMZ-27) with reflected light; and 2) Olympus compound microscope (model BX60) outfitted with bright field, phase-contrast and QC (model R5) camera.

Two types of cultures were employed to produce some DNA sequences: 1) over many years, mass-germinated fresh spore prints on malt extract agar (MEA) were dissected and polyspore isolates were allowed to overgrow. These cultures were stored in test-tube MEA slants in a cold room at ca. 8 °C; 2). Recently, it was discovered that surface-sterilized sections of stipes and/or rhizomorphs readily produced vigorous dikaryon growth on agar medium. Within 48–72 hrs, this mycelial “spray” could be excised into axenic status. Isolates were allowed to cover a 60-mm Petri dish, then transferred to MEA tube slants for storage. For sequencing, small MEA blocks were used as inocula in 15 ml potato-dextrose broth (PD, Difco) and allowed to grow at room temperature. When growth had progressed sufficiently, mycelium was teased away from agar blocks and the mycelium processed for DNA extraction.

For notes on examination of individual specimens, see under Results, Taxonomic characters.

Molecular procedures: Procedures for DNA extraction from cultures or dried herbarium specimens, PCR, sequencing and processing of sequence data and analyses of sequence data are described in Aldrovandi et al. (2015). Both forward and reverse sequences were obtained for each collection. Sequences were corrected and aligned using GCG (GCG 2000) either manually (*Perforantia*) or using the GCG Pileup program

(*Gymnopus* LSU data set) followed by manual adjustment. In rare cases with older specimens, the ITS region was obtained in fragments using primers ITS1F-ITS2 and ITS3-ITS4 (White et al. 1990). In such cases, the nrLSU sequence was never obtained. Sequence data are not available for some taxa in this manuscript, a function of herbarium specimens that were too old or too scanty for DNA extraction.

Phylogenetic Analyses: PhyML analyses were carried out using GENEIOUS 8 (Geneious 2015) using an estimated transition/transversion ratio, proportion of variable sites and Gamma distribution parameter. The substitution model was GTR. The number of bootstrap replicates was 100. Percent identity was calculated for each pair of sequences using GENEIOUS 8 and manually averaged to obtain within and between average percent identities. These were converted to % divergence for this manuscript.

In order to determine the placement of sect. *Perforantia* within *Gymnopus* s.l., a representative file of 191 Omphalotaceae nrLSU sequences including representative taxa belonging to *Omphalotus*, *Lentinula*, *Gymnopus*, *Marasmius*, and *Micromphale* was constructed and analyzed using PhyML in GENEIOUS. Trees were visualized in FigTree 1.4.2 (Rambaut 2006). DNA sequences were deposited in GenBank (see Appendix 1 for GenBank numbers) and aligned sequences and trees were deposited in the Dryad Data Repository (doi: 10.5061/dryad.4081h).

Results

Taxonomic characters

Basidiomata: In general, stipe length versus pileus diameter can be expressed as a ratio. Such values ranged from stipe/pileus ratio of 4–5:1 (*G. glabrosipes*) to 8–9:1 (*G. pinophilus*).

Compared to most agarics, all macromorphological structures of Sect. *Perforantia* are quite small, and appear somewhat fragile. This is misleading, for basidiomata are quite pliant and resilient. Evidence suggests that basidiomata dry *in situ* and repeatedly re-expand with increased moisture, but whether viability also survives is unknown. Frequently, basidiomata are examined which exhibit myriads of spores attached to or embedded in the hymenium but with no mature basidia visible.

Pileus: In all cases, the juvenile pileus is strongly convex, maturing to Plano-convex, often with downturned margin and occasionally with evidence of small umbo. Pileus disc is usually somewhat darker than limb or especially margin, but disc colors range from medium tan to dark chocolate brown. Limb and margin are usually paler but can be unicolorous with the disc. Pileus margin is often sulcate–striate, sometimes deeply so, but this may be an effect of moisture and basidiome age.

Lamellae: In dried specimens, lamellar attachment to stipe is difficult to ascertain. Adnate attachment is typical but adnexed or decurrent attachment is also encountered. A small tell-tale character distinguishing sect. *Perforantia* from sect. *Androsacei* is lamellar color. In sect. *Androsacei*, lamellae are often almost as dark as the pileus, but at

least in the same color series, while in sect. *Perforantia*, lamellae are usually off-white to dingy pale gray.

Lamellae in sect. *Perforantia* are often described as collariate or pseudocollariate when fresh, but in drying, lamellae secede from stipe apex and then often appear pseudocollariate. Lamellae are described below as “thin” versus “thickish,” the former indicating a sharp lamellar edge, while “thickish” indicates lamellae with more or less parallel sides and blunt edge. There seems to be no correlation between this and presence of cheilocystidia. In most instances, figures are given for “total lamellae,” the number of lamellae reaching the pileus margin, and “through lamellae,” the number of lamellae reaching the stipe. The incidence of lamellar anastomosis or interveining is low (i.e. but see *G. resinosa*).

Stipe: Stipe diameter ranges considerably, usually somewhat less than one millimeter; widths given in descriptions must be noted carefully (i.e. *G. fragillior*, 15–35 × 0.3–0.5 mm; *G. sequoiae*, 20–43 × 0.7–1.5 mm), with most diameters 0.7–1 mm.

In subsect. *Perforantia*, vested stipe is almost universal (i.e. *G. bulliformis*, *G. foliophilus*, *G. fragillior*, *G. perforans*, *G. quinaultii*, *G. sequoiae*, *G. sublaccatus*), glabrous–shining only in *G. glabrosipes*. Conversely, subsect. *Pinophili*, composed of two taxa fruiting on *Pinus* needles, is characterized by glabrous–shining stipe.

Rhizomorphs: Generally reported only as present or absent, an attempt has been made here to describe rhizomorphs in more detail, especially since rhizomorphs were used to establish cultures in some taxa. In *G. quinaultii* and *G. sublaccatus*, for instance, rhizomorphs are short, stout, forming small basal pads and colonizing adjacent *Thuja* scales, while in other taxa rhizomorphs may be long and gracile (i.e. in *G. ponderosa* unbranched, in *G. glabrosipes* branched). Occasionally, rhizomorphs are so plentiful as to form a loose thatch. Rhizomorphs branches are usually short and spur-like.

Taste and odor: The predominance of herbarium specimens in descriptions below, often with scant or absent notes, usually make taste and odor impossible to report. A more or less typical *Micromphale* odor and taste, variously described as fetid or of rotten cabbage, however, seems to occur in subsect. *Perforantia* (i.e. *G. perforans*, *G. sequoiae*), while the pine-dwelling taxa seem to exhibit only negligible taste and odor.

Pileipellis: Traditionally, the substance which absorbs water, creating a mucoid matrix for pileipellis, pileus and lamellar tramae, subhymenium and stipe medullary tissue has been called “gelatinous.” Considering its consistency in KOH, I prefer to call it “slime.” In my observations, in the balance between sol and gel, the substance is distinctly on the side of sol. As observed, this slime is always heterogeneous, often with effete basidiospores (and often of anamorphic fungi) and shards of encrusting material.

Where observed, pileal hairs are illustrated and are rather uniform in dimensions and shape. It is quite possible that pileal hairs occur more often toward pileus margin and have been overlooked.

Presence of copious encrusting material on repent pileipellis hyphae appears to be ubiquitous across sect. *Perforantia*. Two variants can also be seen: 1) commonly, in addition to the slime matrix, individual hyphae can be seen to produce a thin slime sheath on which flake-like crust material rides (i.e. *G. bulliformis*, *G. glabrosipes*, *G. fo-*

liiphilus, *G. pinophilus*, *G. ponderosae*, *G. quinaultii*); and 2) encrusting material occasional appears as annular or striped hyphal ornamentation (i.e. *G. glabrosipes*, *G. ponderosae*). Secondary septa (*cloissons de retrait* of Boidin) are often seen, probably formed by retreating cytoplasm (i.e. *G. bulliformis*, *G. foliiphilus*, *G. sequoiae*, *G. sublaccatus*).

Diverticulate pileipellis hyphal segments are common in *G. pinophilus* and *G. ponderosae* (subsect. *Pinophili*), with diverticula usually dichotomous. This feature is also found in cheilocystidia of the *siccus*-type.

Pleurocystidia: In the past, basidioles have often been described as fusiform. In fact, such fusiform hymenial structures are more common than and of comparable dimensions as basidia, which are universally clavate. Moreover, other hymenial elements, namely basidioles, are clavate, similar to basidia but without sterigmata. Recently, the fusiform elements have been recognized as pleurocystidia and we have adopted this usage here. Illustrations are furnished for all taxa, and these pleurocystidia extend to other groups within the clade /omphalotaceae.

A peculiar feature of pleurocystidia is the vague partitioning of cell contents, in which (under PhC + 1250×) distal cell contents appear paler than contents of the rest of the pleurocystidium, but without a well-defined separating membrane (i.e. see illustrations for *G. quinaultii*).

Basidia: Basidia are universally clavate and are dominated by 4-sterigmate forms. Two particular features have been noted in descriptions below: 1) in most taxa, basidia and pleurocystidia remain attached to subhymenial hyphae in squash mounts. Parenthetically, subbasidial hyphae usually remain turgid after basidia and pleurocystidia collapse, with clamp connection hook cells remaining turgid and therefore producing a beaded or catenulate appearance (i.e. see illustration for *G. sublaccatus*), superficially resembling cheilocystidia of the mainstream *Gymnopus* type. In several taxa, however, basidia and pleurocystidia are easily disarticulated from subbasidial hyphae. 2) In some taxa, basidia and pleurocystidia do not collapse when effete, remaining as empty walls. This phenomenon is reminiscent of a seed-bearing ear of corn enclosed in the leaf-like husk, and has been referred to in descriptions below as “husking” (i.e. see illustration for *G. sublaccatus*).

Basidiospores: Across sect. *Perforantia*, dimensions and shapes of spores differ little. These parameters cannot be used to identify individual specimens. Moreover, all spores are inamyloid.

Cheilocystidia: Searches for cheilocystidia found three classes of results: 1) absent, seemingly the case in several taxa in sect. *Perforantia*. Such a conclusion runs the risk of inaccuracy, for saccate cheilocystidia, especially when small and basidiiform, are often rare or uncommon, and could be easily overlooked. 2) clavate to saccate. In *G. perforans*, and its subsp. *translatlanticus* the saccate, utriform cheilocystidia are considerably larger than basidia and so relatively easily observed. In *G. bulliformis*, conversely, cheilocystidia are somewhat smaller than basidia and must be judged by homogeneous contents and shapes like incandescent light bulbs. In *G. sequoiae*, *G. pyracanthoides* and *G. sublaccatus*, dimensions and shapes are intermediate between those above; 3) cheilocystidia of the *siccus*-type (stalked, clavate to branched and beset with digitate setulae, often dichotomously branched) (see illustrations for *G. pinophilus*, *G. ponderosae*).

Caulocystidia: Little variation is seen in dimensions and form of caulocystidia. Variation, however, can be seen between caulocystidia from stipe apex versus caulocystidia from the lower stipe. Those from upper stipe tend to be gnarled (see illustrations for *G. bulliformis*, *G. foliiphilus*, *G. fragillior*, *G. quinaultii*, *G. sequoiae*, *G. sublaccatus*), not rod-like or prolonged-digitate, while those from lower stipe are straight (see illustrations for *G. bulliformis*, *G. foliiphilus*, *G. fragillior*, *G. sequoiae*) and often gathered into synnematoid groups which appear hispid or barbed under a strong lens.

Key to subsections

- 1 Pileipellis composed of diverticulate hyphae and broom cell-like hyphal termini (a well-developed *Rameales* structure); cheilocystidia *siccus*-type; fruiting on needles of *Pinus* species **Subsect. Pinophili**
- Pileipellis composed of repent hyphae embedded in a slime matrix; cheilocystidia (often absent) broadly clavate to utriform; fruiting on various substrata, both conifer and broad-leaved **Subsect. Perforantia**

Key to covered taxa

- 1 On deciduous debris; North/Central America **2**
- On coniferous debris; United States/western Canada **4**
- 2 eastern North America **2. *G. foliiphilus***
- Costa Rica **3**
- 3 Pileipellis a repent layer of encrusted hyphae **2A. *G. foliiphilus* var. *costaricensis***
- Pileipellis a thatch of highly diverticulate hyphae **8. *G. pyracanthoides***
- 4 Fruiting on *Thuja* debris; Pacific Northwest **5**
- Fruiting on other conifer debris **6**
- 5 Cheilocystidia absent. **9. *G. quinaultii***
- Cheilocystidia present, clavate **11. *G. sublaccatus***
- 6 Cheilocystidia present (but often rare) **7**
- Cheilocystidia absent. **12**
- 7 Fruiting on debris of *Sequoia sempervirens*; California **10. *G. sequoiae***
- Fruiting on assorted conifer debris, but not *Sequoia* **8**
- 8 Cheilocystidia *siccus*-type, arbuscular, setulose; fruiting on needles of *Pinus* sp. **9**
- Cheilocystidia clavate, saccate or utriform **10**
- 9 Fruiting on 5-needle pine (*P. strobus*); eastern North America ... **6. *G. pinophilus***
- Fruiting on 2–3-needle pine (*P. ponderosa*); central to western North America **7. *G. ponderosae***

- 10 Cheilocystidia saccate, larger than basidia; fruiting on conifer needles; wide-spread (Europe, North America)..... **11**
- Cheilocystidia broadly clavate, not larger than basidia, fruiting on conifer needles; Pacific Northwest **1. *G. bulliformis***
- 11 Europe/Scandinavia; fruiting chiefly on *Picea/Abies* needles (occasionally on *Pinus*) **5. *G. perforans***
- Northeastern North America; fruiting chiefly on *Picea* and *Tsuga* needles **5A. *G. perforans* subsp. *transatlanticus***
- 12 Stipe minutely vestured throughout..... **3. *G. fragillior***
- Stipe glabrous–shining..... **4. *G. glabrosipes***

Taxonomic descriptions: sections and subsections

***Gymnopus* sect. *Perforantia* (Singer) R.H. Petersen, comb. nov.**

Mycobank no. 552483

Basionym. *Micromphale* sect. *Perforantia* Singer. 1948. Sydowia 2: 32.

Diagnosis. 1) Pileipellis, pileus and lamellar tramae and stipe medullary hyphae embedded in slime matrix; 2) pileipellis either: a) a layer of repent, encrusted hyphae, conspicuously clamped, usually with thickened walls (through gelatinization) and embedded in a slime matrix; or b) well-developed *Rameales*-structure; 3) cheilocystidia often absent, when present either clavate to utriform or *siccus*-type broom cell-like; 4) stipes usually less than 1 mm broad but often up to 40 mm long; ratio of pileus breadth to stipe length often large (see *G. pinophilus*); 5) stipe usually vestured (but see *G. glabrosipes*), usually appearing minutely barbed (30×); 6) lower stipe of dark, somber color, from dark sooty brown to virtually black; 6) rhizomorphs almost always present, always black, from <2–40 × 0.2–0.7 mm, branched or unbranched; 7) basidiospores without significant dimension differences; 8) species apparently more or less host-specific, fruiting on dead conifer needles or rotting deciduous leafy debris; 9) pleurocystidia consistently present, fusiform, varying somewhat in distal morphology; 10) clamp connections ubiquitous.

Commentary. Antonín and Noordeloos (1997) recognized *Gymnopus* sect. *Vestipedes* subsect. *Impudicae*, including *G. perforans*, based, it would seem on the fetid odor of basidiomata of the included taxa. Later (Antonín and Noordeloos 2010), subsect. *Impudicae* was accepted at section rank, but basically included the same taxa as before. Wilson and Desjardin (2005) indicated that *G. perforans* formed its own clade sister to that of *G. (Micromphale) foetidum* and other mainstream odious *Gymnopus* taxa. Based on the present study, the original *Micromphale* sect. *Perforantia* is found to be more closely related to the *Gymnopus (Marasmius) androsaceus* complex, not inclusive of *G. foetidum* and other *Gymnopus* sect. *Impudicae*.

Molecular phylogenetic information is available for only few taxa accepted (or proposed) here. For “morpho-taxa,” some outline employed to justify their description in this paper is owed the reader. Unfortunately, almost every morphological character includes a caveat for collections which violate one or more characters. The following diagnoses are offered:

Section *Perforantia* Subsect. *Perforantia*, subsect. auton.

Type species (typus auto.): *Agaricus* (*Gymnopus*) *perforans* Hoffm. ex Fr.

Diagnosis. Separating characters as follows: 1) pileipellis a layer of repent, encrusted hyphae, conspicuously clamped, usually with thickened (through gelatinization) walls and usually embedded in a slime matrix; 2) cheilocystidia often absent, when present, clavate to utriform; 3) stipe usually vested; 4) fruiting on conifer needles or broad-leaved debris.

Section *Perforantia* subsection *Pinophili* R.H. Petersen, subsect. nov.

Mycobank no. 552487

Type species. *Gymnopus pinophilus* R.H. Petersen (see below)

Diagnosis. Separating characters as follows: 1) pileipellis a well-developed *Rameales* structure; 2) cheilocystidia *siccus*-type broom cells; 3) stipes glabrous-shining; 4) fruiting on needles of *Pinus*; 5) discrete clade well-separated from subsect. *Perforantia*.

1. *Micromphale bulliformis* R.H. Petersen, sp. nov.

Mycobank no. 552475

Holotype. United States, Washington, Jefferson Co., Olympic National Park, Tunnel Creek, N47°46'44.19", W123°03'25.83", VIII.1975, coll F. VanDeBogart (as *Ma. androsaceus*), FVDB 3621 (WTU-F-51955).

Etymology. Bulliformis = bubble-like, referring to the appearance of cheilocystidia at lamellar edge.

Diagnosis. 1) Morpho-species (no DNA sequences available); 2) stipe vestiture a loose thatch of tortuous, often-branched, thick-walled caulocystidia; 2) cheilocystidia bulbous, smooth, with homogenous contents; 3) basidial sterigmata unusually long and slender; 4) pleurocystidia sharply fusiform, with poorly-defined content partitioning; 5) pileipellis involved in slime matrix.

The description which follows is compiled from examination of dried material. Colors when fresh may vary considerably from those below.

Description. Basidiomata (Fig. 1A, B) diminutive, robust. **Pileus** 3–14 mm broad, convex, usually somewhat flattened over disc and occasionally with suggestion

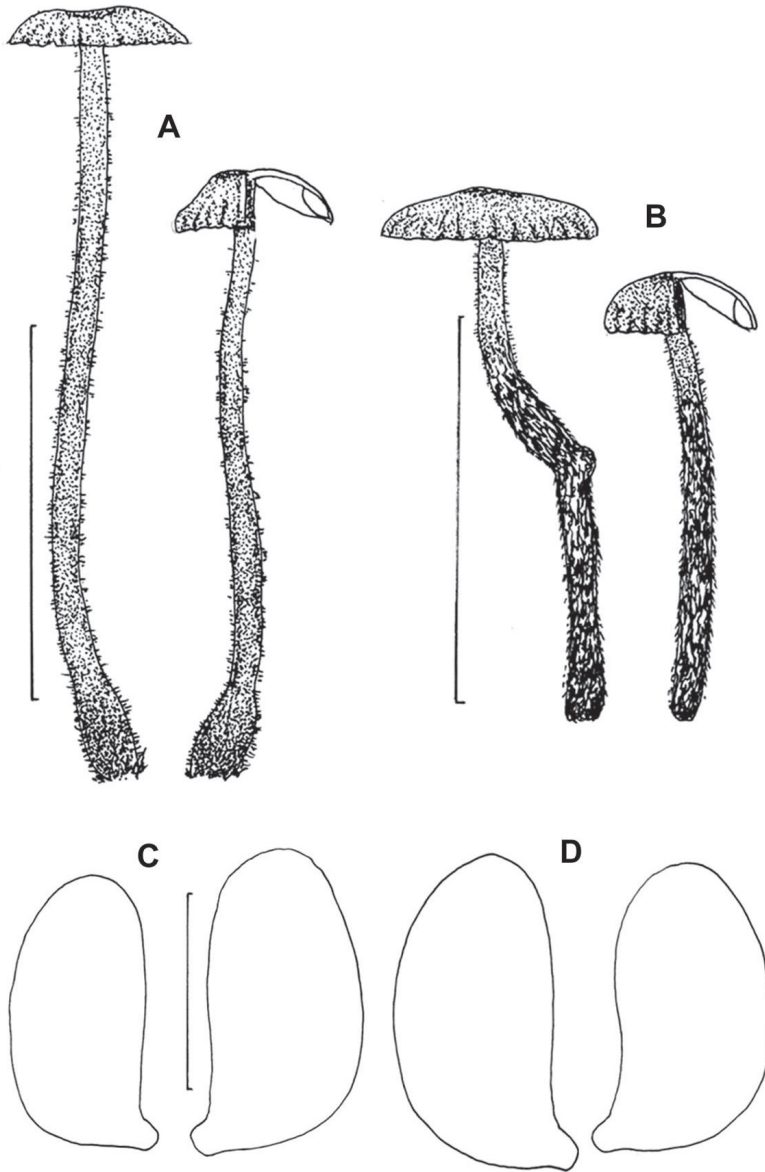


Figure 1. *Gymnopus bulliformis*. **A, B** Basidiomata **C, D** Basidiospores. Standard bars: **A, B** = 20 mm; **C, D** = 5 µm. **A, C** WTU-F-9305; **B, D** WTU-F-51955.

of small umbo, matt, sulcate near margin but not striate; disc near “Verona brown” 6E5; limb and margin near “sayal brown” 6C5 or “cinnamon buff” 6B4; context thin, fragile. **Lamellae** adnate to adnexed, not pseudocollariate, thin, becoming ventricose by maturity (–2.5 mm broad) and strongly crisped (dry), subdistant to distant with no anastomoses or interveining, total lamellae = 25–38, through lamellae = 13–18, (fresh)

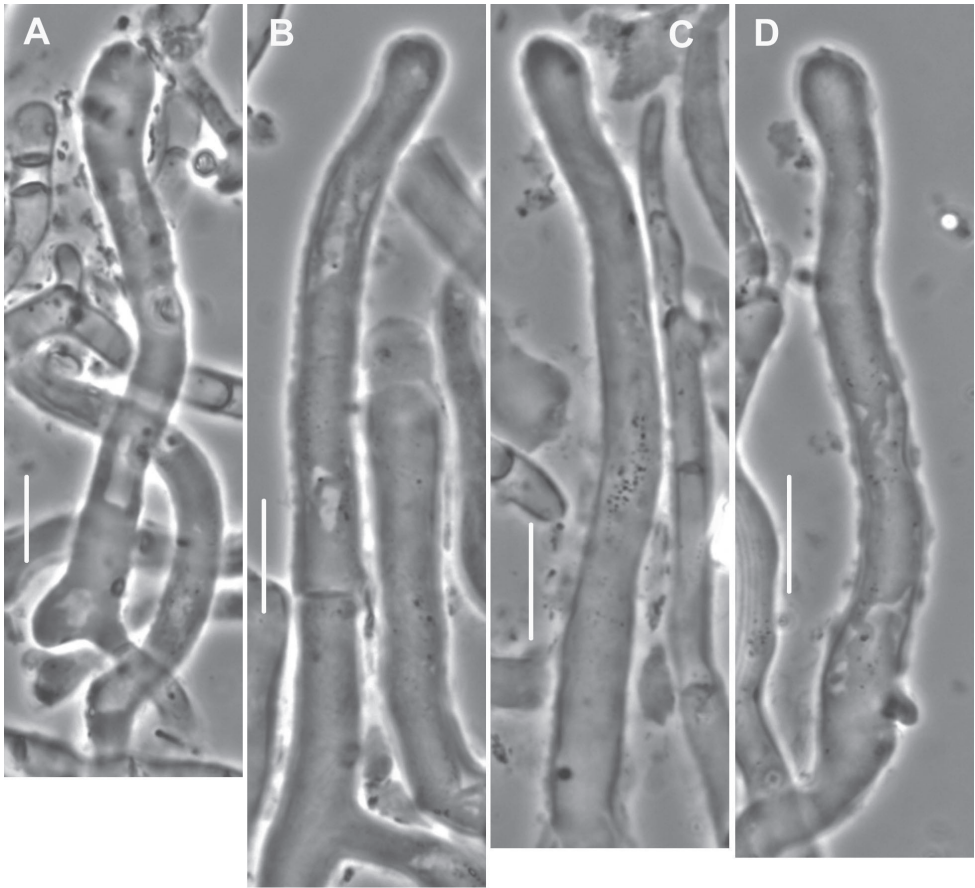


Figure 2. *Gymnopus bulliformis*. Pileal hairs. Standard bars = 10 μ m. WTU-F-51955.

near “ochraceous buff” 5A5 to “chamois” 4B4, (dry) between “ecru drab” 16B2, “olive ochre” 2B8 and “deep olive buff” 3C3, suffusing to brown (“saya brown” 6C5) from edge in age; lamellulae in 1–2 tiers, often rudimentary. **Stipe** 16–35 \times 0.5–0.8(–1) mm, probably terete when fresh, equal, occasionally abruptly changing directions as though adventitious from being broken, subinsititious, pilose-vestured from apex to base, lightly so upward and there with vesture pallid, downward delicately barbed and more so to felty at base, producing a matted–furry appearance, irregularly elongate–maculate with blond vesture and fuscous pileus surface (dried), but somewhat more prominently vestured upward, upward “clay color” 5C6 or “cinnamon” 6B5, downward “snuff brown” 5E8 to “Verona brown” 6E5 at base, at junction with lamellulae dark brown and leaving delicate brown ring in pileus trama. **Rhizomorphs** undetected. **Taste** and **odor** not recorded.

Habitat and phenology. Temperate rainforest; substrate uncertain, certainly dead conifer needles, perhaps *Tsuga* or *Abies*; mid-summer.

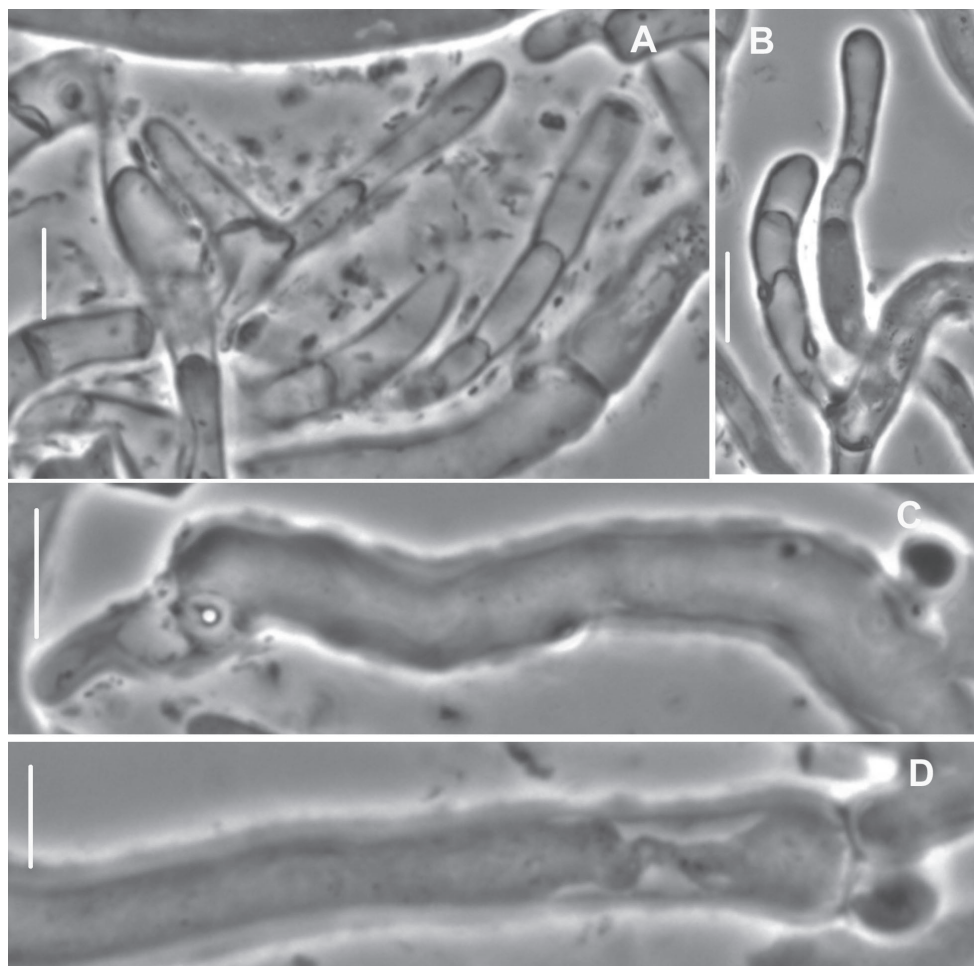


Figure 3. *Gymnopus bulliformis*. Pileipellis elements. **A** Heterogeneous slime with secondarily septate hyphae **B** Secondary septa **C, D** Hyphae with gelatinized walls. Note clamp connections in **D** right. Standard bars = 10 μm . WTU-F-51955.

Pileipellis composed of three elements, all involved with a heterogeneous slime matrix (Fig. 3): 1) pileal hairs (Fig. 2) $120 \times 3.5\text{--}7\text{ }\mu\text{m}$, cylindrical with slightly enlarged apex, thin- to firm-walled, occasionally internally clamped; 2) repent hyphae $3\text{--}9\text{ }\mu\text{m}$ diam, thin- to firm-walled (wall gelatinizing to $1.5\text{ }\mu\text{m}$ thick; Fig. 3C, D), weakly encrusted (crusting material flake-like, often riding on a thin slime sheath, detersile in slime matrix), conspicuously clamped; and 3) significant hyphal segments with numerous secondary septa (Fig. 3A, B). Pileus trama loosely interwoven; hyphae $3\text{--}9\text{ }\mu\text{m}$ diam, gelatinizing and with thin slime sheath, conspicuously clamped. Lamellar trama identical. **Pleurocystidia** (Fig. 4) $22\text{--}34 \times 7\text{--}9\text{ }\mu\text{m}$, fusiform, unusually sharply pointed, often somewhat swollen in mi-shaft, conspicuously clamped; contents partitioned, but ill-defined. **Basidia** (Figs 5, 7A) $24\text{--}30 \times 7\text{--}9\text{ }\mu\text{m}$, broadly

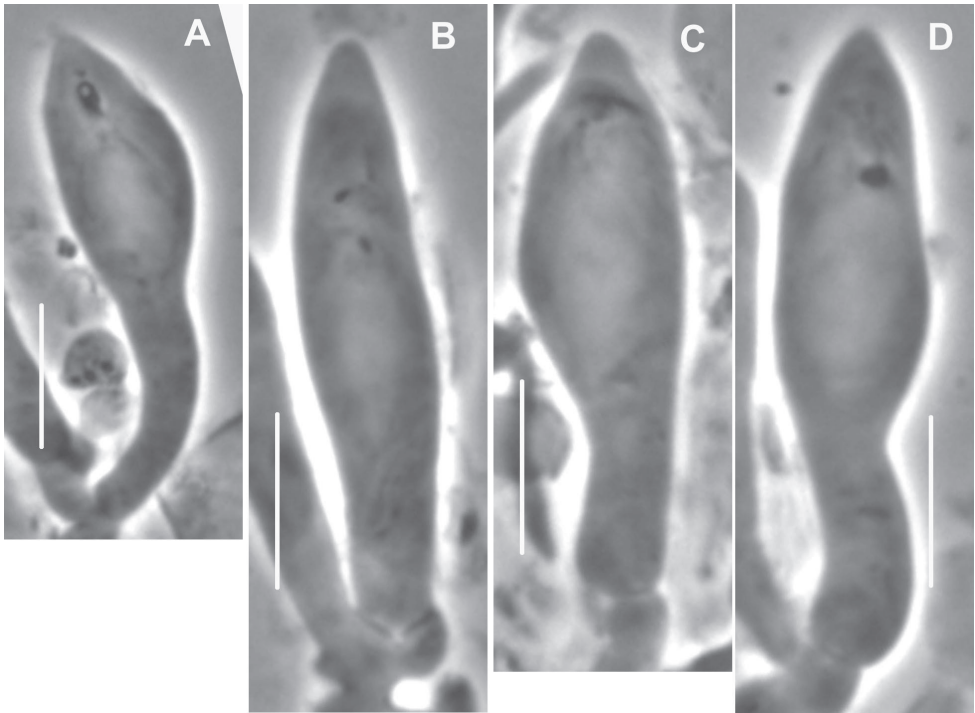


Figure 4. *Gymnopus bulliformis*. Pleurocystidia. Note acute apices and poorly-defined partitioned contents. Standard bars = 10 μ m. WTU-F-51955.

clavate, conspicuously clamped, 4-sterigmate; contents heterogeneous with inclusions appearing oily (PhC); sterigmata $8 \times 1 \mu$ m, awl-shaped. **Basidiospores** (Fig. 1C, D) $(6.5\text{--}7\text{--}7.5\text{--}(8) \times 3.5\text{--}4\text{--}(4.5) \mu$ m ($Q = 1.73\text{--}2.14$; $Q^m = 1.88$; $L^m = 7.20 \mu$ m), ellipsoid, subgymnoid (slightly tapered proximally), smooth, thin-walled, inamyloid. **Cheilocystidia** (Figs 6, 7B–G) locally common, $15\text{--}26 \times 9\text{--}15 \mu$ m, broadly clavate to subglobose, thin- to firm-walled, obscurely clamped, occasionally with one or two vermiform apical outgrowths (usually without); contents homogeneous, appearing empty. **Stipe apex medullary hyphae** strictly parallel, $5\text{--}9 \mu$ m diam, thin- to firm-walled but soon gelatinizing (in KOH) so walls become almost indistinguishable, often encrusted with crust material riding on outer surface of slime sheath, obscurely clamped. **Stipe apex cortical hyphae** $3\text{--}6 \mu$ m diam, long-celled, conspicuously clamped, thick-walled (wall often obscuring cell lumen), producing a layer of inflated, thick-walled cells and caulocystidia as side branches; **caulocystidia from upper stipe** (Fig. 8) $10\text{--}75 \times 4\text{--}8 \mu$ m, irregularly cylindrical, usually with basal clamp, thick-walled (wall $\sim 2 \mu$ m thick, with cell lumen irregularly defined), subhyaline. **Mid-stipe medullary hyphae** strictly parallel, $3.5\text{--}12 \mu$ m diam, thick-walled (wall $\sim 2 \mu$ m thick), obscurely clamped, involved in a slime matrix but not with gelatinizing walls; **mid-stipe cortical hyphae** as above, producing a thatch of tortuous, thick-walled side branches resembling stipe-apex caulocystidia, from which extended caulocystidia (Fig. 9F) arise; caulocystidia

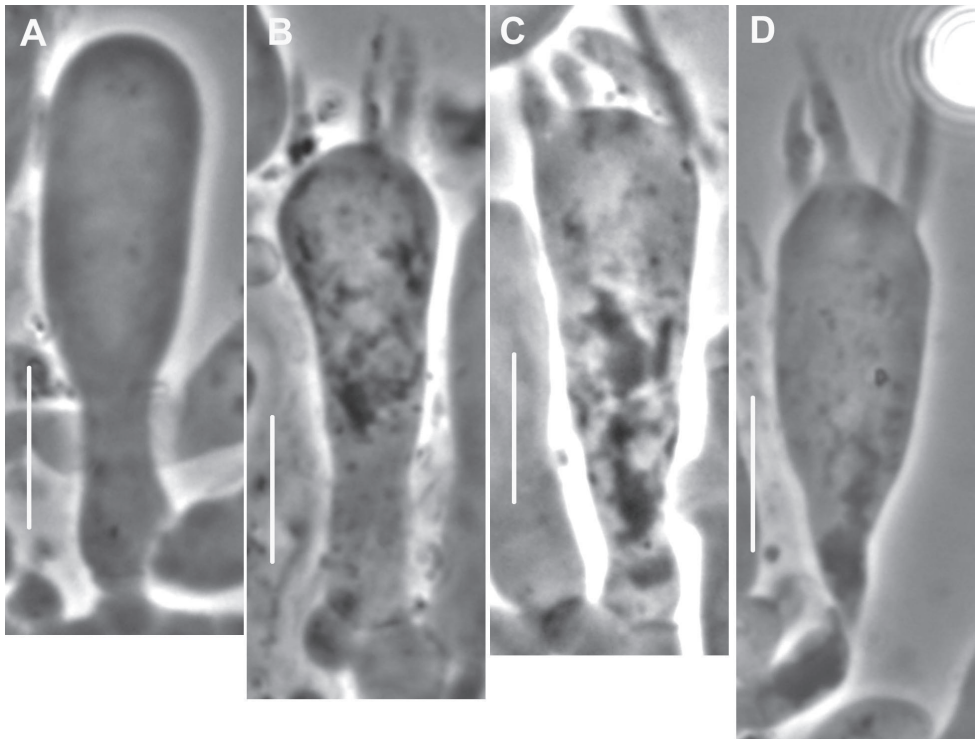


Figure 5. *Gymnopus bulliformis*. Basidiolium and basidia. Note long, awl-shaped sterigmata. Standard bars = 10 μ m. WTU-F-51955.

–125 \times 4–8 μ m diam, thick-walled, cylindrical, refringent (PhC), usually oriented parallel to stipe surface.

Commentary. Proposal of another species of *Gymnopus* (*Micromphale*) section *Perforantia* would seem problematic, especially from a region relatively rich in such taxa, but presence and uniqueness of diagnostic characters make such a proposal relatively safe. The diagnosis (above) lists characters which separate *G. (Mi.) bulliformis* from other members of sect. *Perforantia* with diminutive basidiomata.

The temperate rain-forests of the North American Pacific coastal region of United States and Canada apparently support several taxa of the androsaceoid/perforantoid complex. Loan of selected specimens (using Mycoportal as filter) under only *Ma. androsaceus* and *Mi. perforans* revealed enough new taxa to make intensive collecting worthwhile for such organisms. This might not be surprising, considering the variety of conifer trees, on the dead needles of which such diminutive basidiomata are to be found.

Separation of taxa in *Micromphale* sect. *Perforantia* is difficult. *Micromphale perforans* occurs in Europe and Scandinavia through northern North America, presumably continent-wide. It may be present in northeastern and western Siberia as well, but this is beyond the scope of this paper. From northern California comes *M. sequoiae*

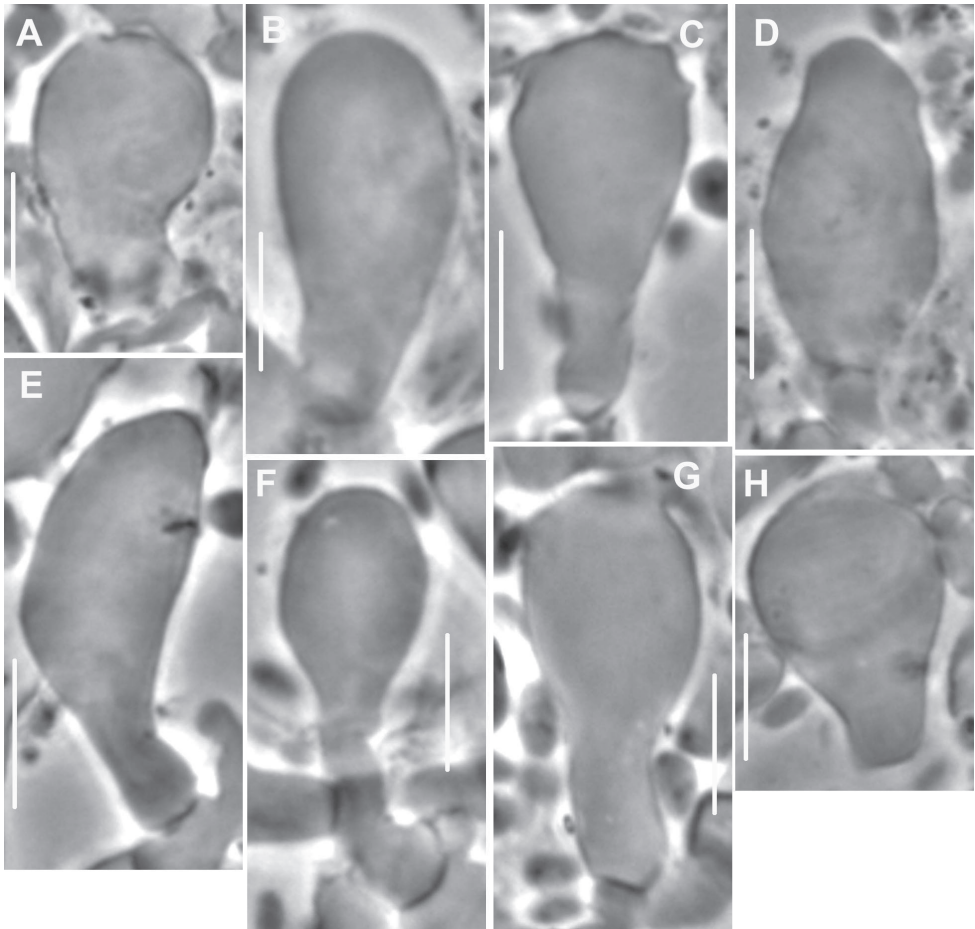


Figure 6. *Gymnopus bulliformis*. Cheilocystidia. Standard bars = 10 μ m. WTU-F-51955.

which closely resembles *G. bulliformis* but is reported as limited to dead foliage of *Sequoia sempervirens*. Both taxa are reported as lacking (or rare) cheilocystidia, neither taxon exhibits much differentiation in the pileipellis, and caulocystidia are quite similar, although those of *M. perforans* are reported as exhibiting some denser, more refringent (PhC) pigment at caulocystidial tips. Ordinarily, *M. perforans* exhibits a black, vested stipe when mature, but Antonín and Noordeloos (2010) include dark brown shades as well, and *M. sequoiae* seems also to form a dark brown stipe. Desjardin (1985) used the following characters to separate *M. sequoiae* from *M. perforans*: 1) light brown to flesh-colored pileus versus pale pileus respectively; 2) mild odor versus strong, fetid odor respectively; 3) greyish orange to brown pubescent stipe versus black velutinous stipe respectively; 4) caulocystidia without concentrated apical pigment versus caulocystidia with concentrated apical pigment respectively; 5) habitat on *Sequoia* debris versus conifer needles, usually *Picea* and/or *Abies* respectively.

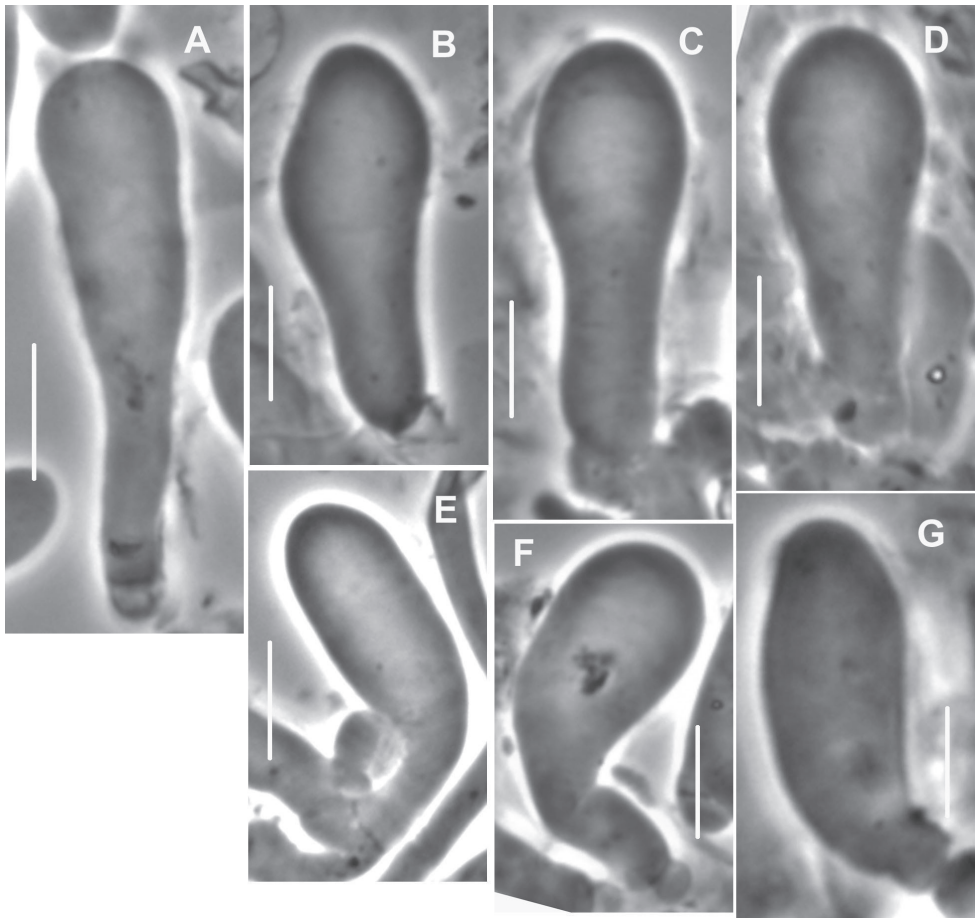


Figure 7. *Gymnopus bulliformis*. **A** Basidium **B–G** Cheilocystidia. Standard bars = 10 μ m. WTU-F-9305.

Attempts were made to obtain ITS sequences from both collections of *G. bulliformis*, both unsuccessful. WTU-9305 yielded sufficient sequence to identify it as a member of the clade /perforantia and blasted weakly to *G. perforans* in GenBank. Whether *G. bulliformis* deserves phylogenetic distinction remains questionable until clean sequences can be obtained from “fresh” material.

Specimens examined. **Washington**, Jefferson Co., Olympic National Park, Tunnel Creek, N47°46'44.19", W123°03'25.83", VIII.1975, coll F. VanDeBogart (as *Marasmius androsaceus*), FVDB 3621 (WTU-F-51955; holotype); Snowhomish Co., Barlow Pass, Barlow Pass study area, N48.02667, W121.44278 (WGS 84), 8.VII.1992, coll S. Trudell (as *Micromphale perforans*), s.n. (WTU-F-9305).

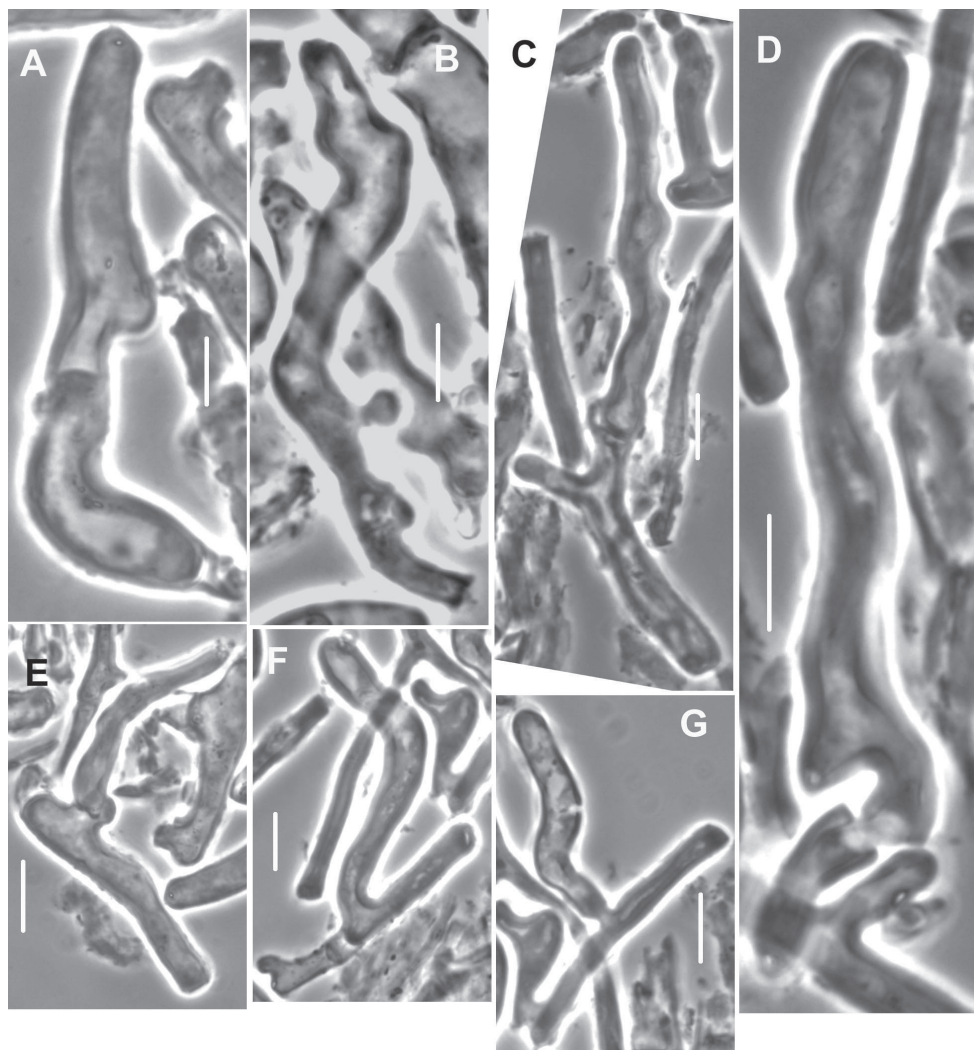


Figure 8. *Gymnopus bulliformis*. Caulocystidia from upper stipe. Standard bars = 10 μ m. WTU-F-51955.

2. *Gymnopus foliophilus* R.H. Petersen, sp. nov.

Mycobank no. 552474

Holotype. United States, Connecticut, Middlesex Co., vic. Salem, Devil's Hopyard State Park, N41°28.937', W72°20.491', 1.IX.2013, coll RHP, TFB 14332 (TENN-F-68183).

Etymology. folius (Latin) = leaf; phil- (Greek) = to love; preference for broad-leaved leaves.

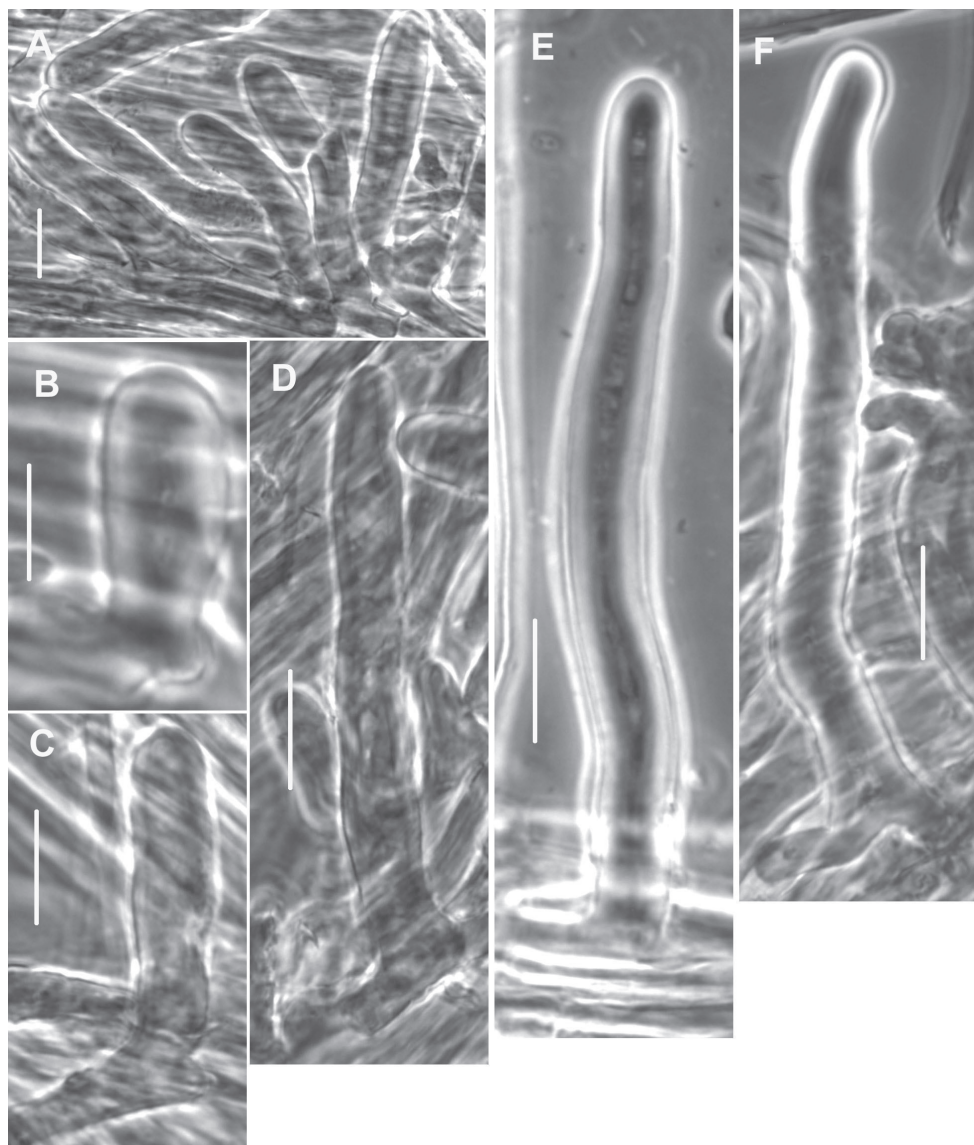


Figure 9. *Gymnopus bulliformis*. Caulocystidia from lower stipe. Standard bars = 10 μ m. WTU-F-51955.

Diagnosis. Similar to *Gymnopus (Mi.) perforans*: differing in: 1) fruiting substrate of dead deciduous leaves, most commonly *Quercus*; 2) unique phylogenetic placement (based on ITS sequences); 3) apparent geographic range in eastern North America.

Description. Basidiomata (Fig. 10) diminutive, scattered to (rarely) gregarious. **Pileus** 3–22 mm diam, shallowly to strongly convex with downturned margin when young, becoming applanate to slightly depressed centrally by maturity (and then with small central dot of “drab” 6D3 or mouse gray), sometimes with small umbo, subtuberculate, matt to minutely plushy (35 \times) especially outward, when dried commonly



Figure 10. *Gymnopus foliophilus*. Basidiomata. Standard bars = 10 mm.

sublaccate (glistening with reflected light rather than matt); disc when fresh “pinkish buff” 6A3, “vinaceous buff” 9B2, near “light pinkish cinnamon” 7A2, “Mikado brown” 7C6, to “drab” 6D3; limb “pale pinkish cinnamon” 6A2, “pale ochraceous buff” 4A2, “pale cinnamon pink” 5A2, “light buff” 3A2, “pinkish buff” 6A3, grayish orange 5B3; margin somewhat thick, entire to uplifted, vaguely sulcate-striate to not

striate, usually mellowing to entirely tan to pallid brown. **Lamellae** adnate–adnexed or occasionally attached to a weak pseudocollarium (especially visible when dried and seceded), subdistant to distant, total lamellae = 30–32; through lamellae = 13–16, arcuate, thickish, narrow (not more than 1 mm broad) with no anastomoses or interveining, with dark brown ring around stipe apex, off-white to “pale pinkish cinnamon” 6A2, near “chamois” 4B4 or “pale ochraceous salmon” 3A3, mellowing to “light buff” 3A2, and perhaps with slight tint of necropigment in storage to “light ochraceous buff” 5A4; lamellar edge entire, never marginate nor fimbriate, occasionally minutely laccate. **Stipe** 12–30 × 0.8–1.2 mm, terete, equal, insititious, at junction with lamellae “vinaaceous russet” 8D4, “bister” 5F8, upward concolorous with gills, “cinnamon buff” 6B4, “avellaneous” 7B3 to “tilleul buff” 7B2, soon downward “wood brown” 5A4, “buffy brown” 6D4, “mummy brown” 6F8, “Verona brown” 6E5, “Rood’s brown” 6D5, “clove brown” 6F5, “chaetura black” 2F3 to “bone brown” 7F8, weakly to densely vested throughout, variably minutely flocculose, especially upward, to barbed with setoid vestiture, hollow, downward becoming stuffed; vestiture at stipe apex (30×), hyaline, downward becoming pigmented to dull yellow then dull straw-colored, but never black. **Rhizomorphs** usually present but widely scattered and inconspicuous, filiform (0.2–0.4 mm thick), resupinate on leaf surface (especially more sclerophyllous leaves), and there branching and anastomosing, sometimes orange-brown and diffuse, otherwise black and meandering, short (never more than 6 mm long), unbranched, straight to somewhat curly apically, tapering to flagelliform terminus. **Taste** usually reported as negligible, occasionally very weak of garlic; **odor** usually reported as negligible, occasionally resembling boiled cabbage after drying or mildly fetid.

Habitat and phenology. On dead broad-leaved leaves, most often *Quercus* leaves, fruiting especially on midribs and petioles of both red and white oak complexes; other adventitious substrates include *Acer* (at least *A. rubrum*), *Cornus*, *Magnolia*, *Rhododendron*, 2-needle *Pinus*; Appalachian Mountain chain from New England through northern South Carolina and northern Georgia, west to Arkansas and south to Gulf Coast; late Spring through early Autumn.

Pileipellis a thin tissue involved in a slime matrix, composed of the following: 1) pileal hairs (Fig. 11) –120 × 2–3.5 µm, smooth, occasionally clamped internally, with telltale evidence of superficial mucoid deposit; 2) repent hyphae slender [3.5–5.5(–13) µm diam], firm-walled (wall ~1 µm thick, often somewhat gelatinized), generally radially oriented, conspicuously clamped, mostly smooth, occasionally vaguely ornamented (Fig. 12A–C) with minute flakes in slime next to hyphal wall, commonly very vaguely striped with some profile flakes (PhC), rarely significantly encrusted, hyaline, embedded in a thin layer of mucoid material (amorphous debris expressed in paradermal squashes, PhC); 3) common secondarily septate hyphal segments (Fig. 12D); small, peg-like, small lobes (Fig. 12F, G) common. Subpellis hyphae broader (5–7 µm diam), thick-walled (wall ~1.0 µm thick), conspicuously clamped, hyaline, interwoven, with evidence of a mucoid or gelatinous deposit. Pileus tramal hyphae 5–21 µm diam, thin- to firm-walled, with minimal slime matrix, clamped. Lamellar trama loosely interwoven, of uninflated cells (2–)3.5–10 µm diam, firm- to thick-walled

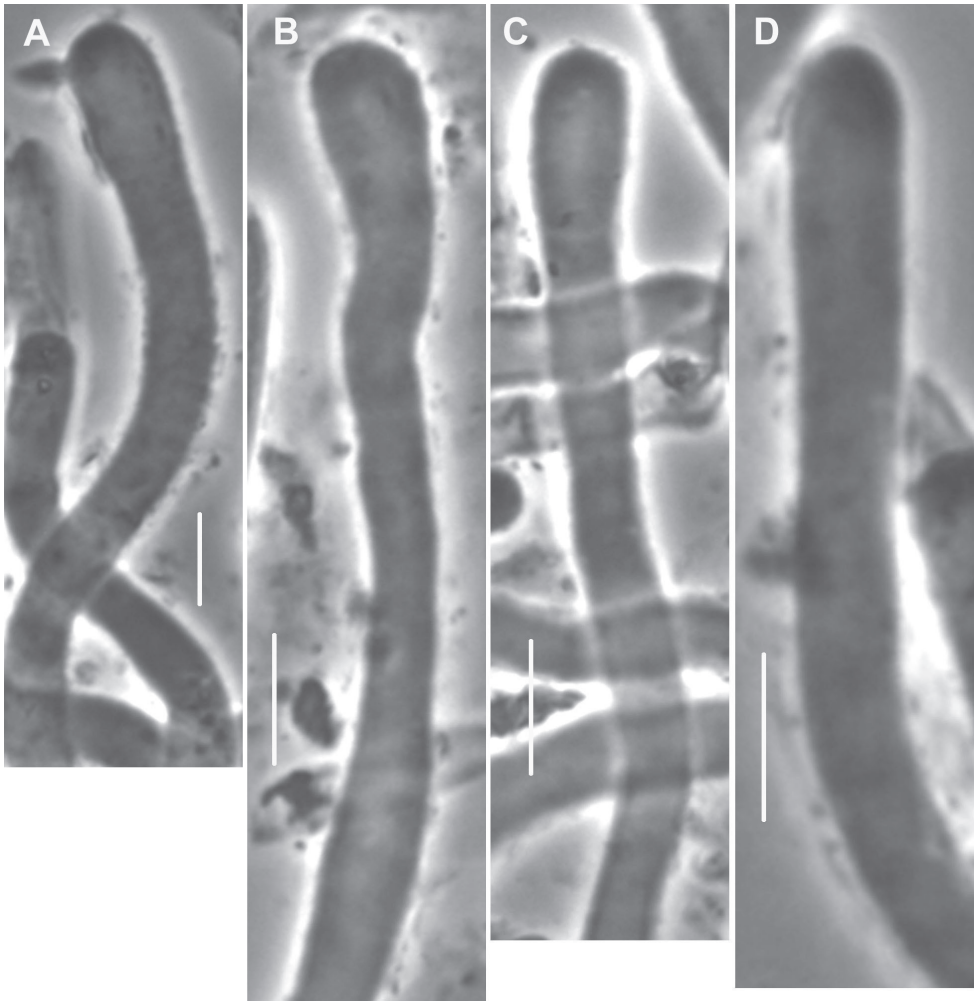


Figure 11. *Gymnopus foliophilus*. Pileal hairs. Standard bars = 10 μm . TFB 2800 (TENN-F-49363).

(wall $-0.7\ \mu\text{m}$ thick), lightly encrusted or with evidence of insoluble mucoid matrix, conspicuously clamped. Hymenium dense, with basidia becoming diaphanous after spore discharge but not disappearing (“husking”). **Pleurocystidia** (Fig. 13A–D) $25\text{--}33 \times 6\text{--}9\ \mu\text{m}$, fusiform, conspicuously clamped, serially produced from subhymenial clamp connections. Basidioles clavate; **Basidia** (Fig. 13E–H) $(21\text{--})27\text{--}32 \times (5\text{--})6\text{--}9\ \mu\text{m}$, clavate to narrowly clavate, clamped, 4-sterigmate (occasional individuals, always semicollapsed, observed with two prolonged sterigmata), obscurely to conspicuously clamped; contents minutely multigranular, not guttulate. Subbasidial cells appearing catenulate, lobose but hyphal (not as lobose as in *G. perforans*). **Basidiospores** (Fig. 14) $(4.5\text{--})6.5\text{--}7(-8) \times 2.5\text{--}3.5(-4)\ \mu\text{m}$ ($Q = 1.33\text{--}2.80$; $Q^m = 1.92$; $L^m = 6.85\ \mu\text{m}$), gymnopoid to pip-shaped (ellipsoid, not tapered proximally), smooth, thin-walled, inamyloid. **Cheilocystidia** observed only in rare specimens, clavate, $28\text{--}34$

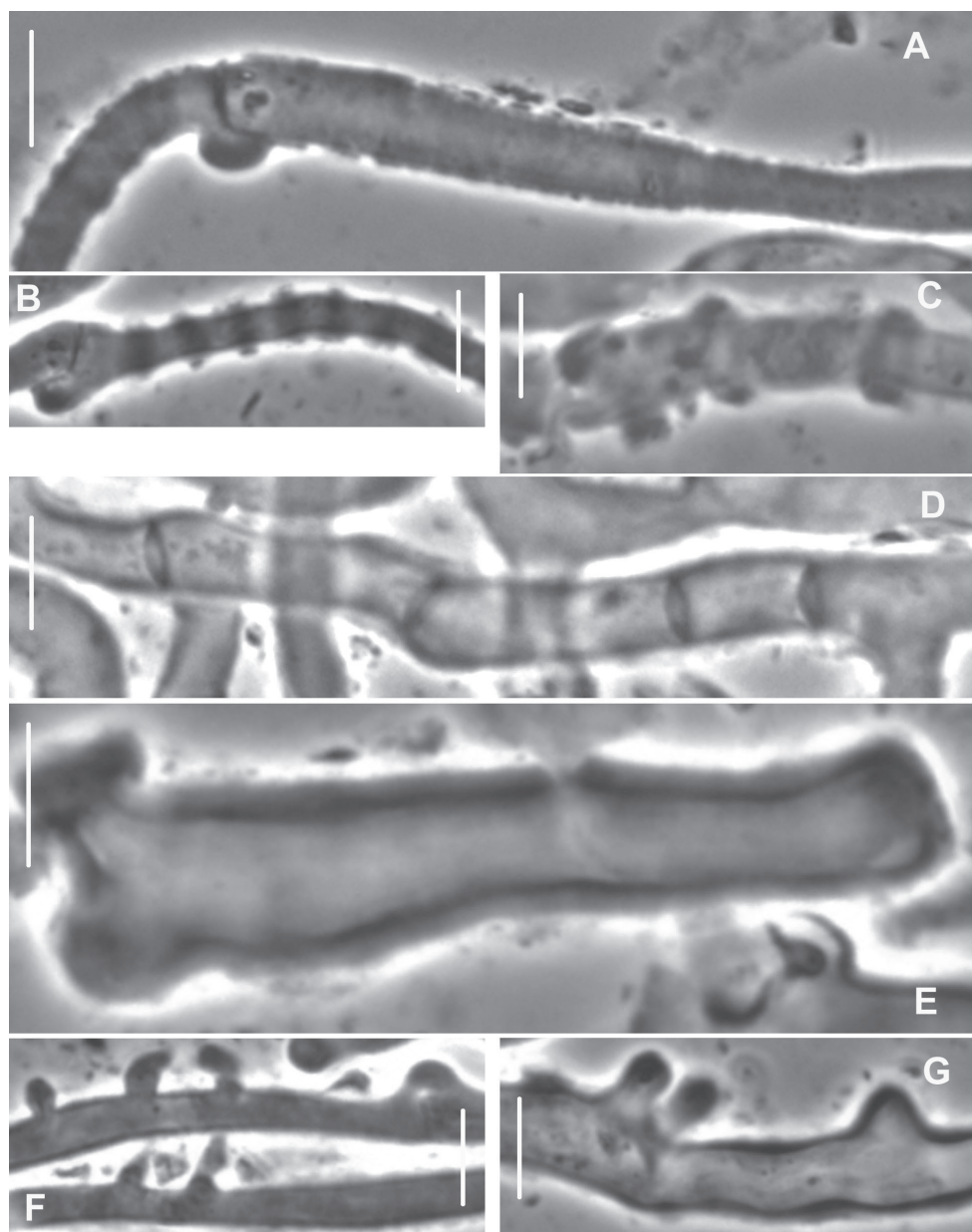


Figure 12. *Gymnopus foliiphilus*. Pileipellis elements. **A–C** Encrusted hyphae **D** Hyphae showing secondary septa **E** Gelatinized hyphal walls **F, G** Lobate side branches. Standard bars = 10 μm . TFB 2800 (TENN-F-49363).

\times 9–10 μm , broadly clavate, not longer than basidia but broader, hyaline, clamped. **Stipe medullary hyphae** 4–9 μm diam, irregularly thick-walled (wall \sim 1.5 μm thick) as though encrusted in bands (but not so), hyaline, conspicuously clamped; outer medullary hyphae 3–6 μm diam, hyaline, thick-walled (wall \sim 2 μm thick), free (not

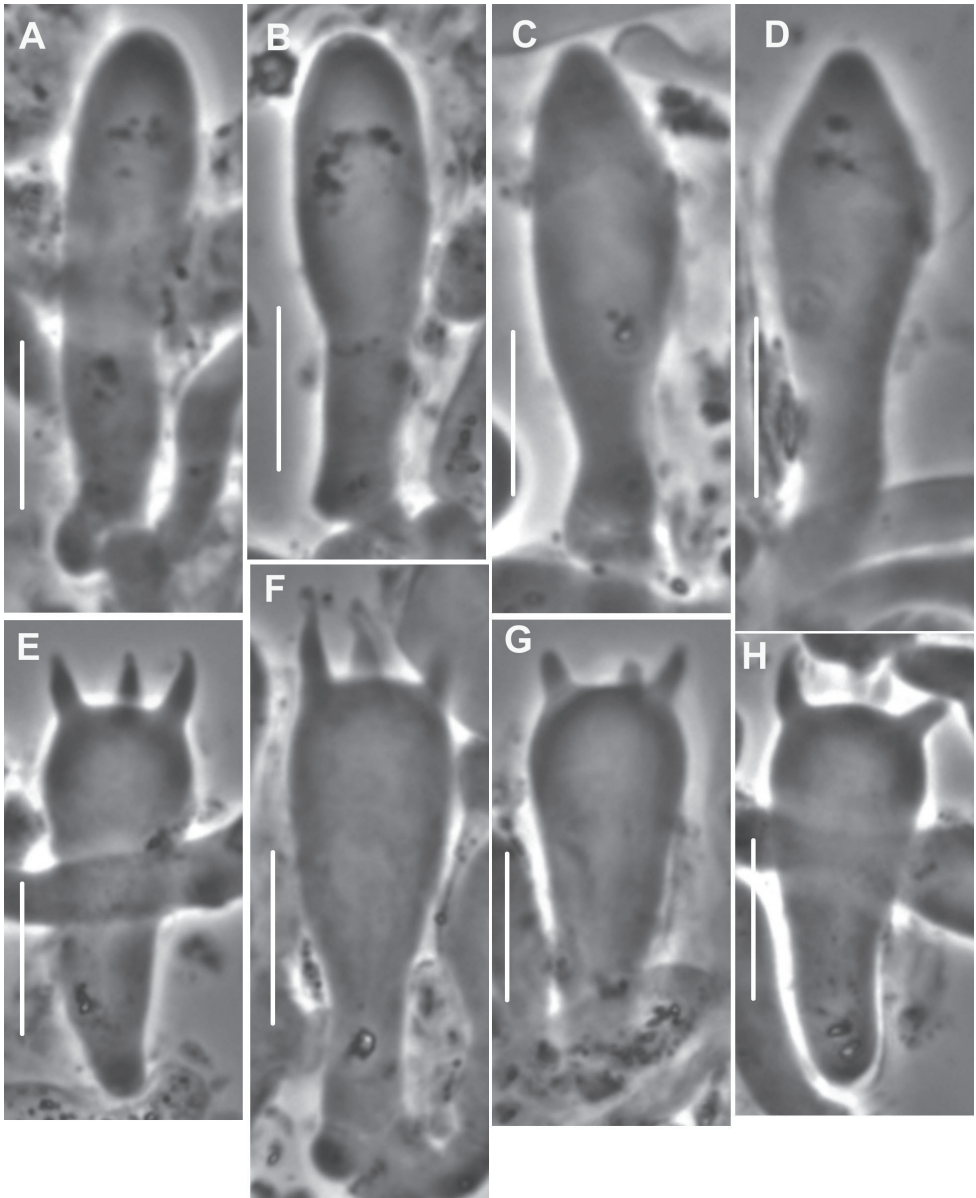


Figure 13. *Gymnopus foliophilus*. Pleurocystidia and basidia. **A–D** Pleurocystidia **E–H** Basidia. Standard bars = 10 μm . TFB 11555 (TENN-F-59441).

adherent), strictly parallel, conspicuously clamped, commonly anastomosed in “H” connections. **Stipe cortical hyphae** 3.5–8 μm diam, smooth, thick-walled (wall ~1.0 μm thick), pigmented in cytoplasm, producing caulocystidia as side branches. **Caulocystidia** (Fig. 15) 25–>150 \times (2.5–)6–9 μm , arising from a tangled thatch of dry, interwoven, very thick-walled (occluding cell lumen), clamped hyphae, a combina-

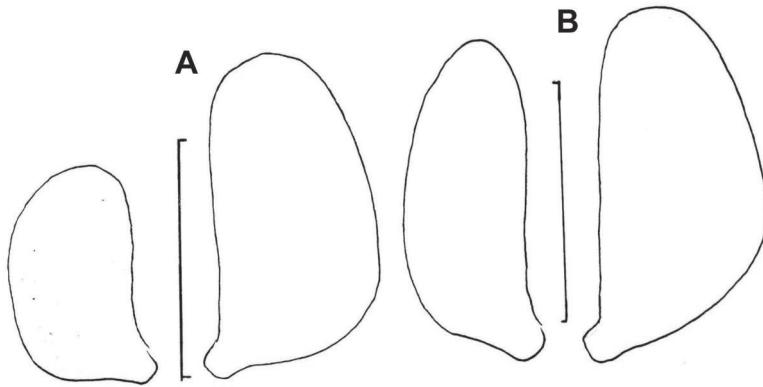


Figure 14. *Gymnopus foliophilus*. Basidiospores. Standard bar = 5 μm . **A** = TFB 11608 (TENN-F-59641); **B** = TFB 14322 (TENN-F-68183).

tion of straight and setoid, mixed with other gnarled or curled individuals, densely scattered, thick-walled, usually arising as hyphal terminus or commonly with short abortive branch below, pigmented in cytoplasm (wall subhyaline), usually somewhat broader near origin than at mid-point (6–10 μm diam). Lower stipe caulocystidia (Fig. 16) setoid, 4–7 μm diam, thick-walled (occluding cell lumen), arising as side branches from stipe surface hyphae, gathered into rough synnematal spines.

Commentary. *Gymnopus foliophilus* is the most commonly collected North American taxon in sect. *Perforantia*. Preliminary field identification attempts to distinguish several taxa with similar basidiomata. Substrate segregates *G. androsaceus* and *G. perforans* (conifer needles, usually *Picea* and/or *Abies*), from *G. foliophilus*. Geographic distribution is less secure. Both *G. androsaceus* and *G. perforans* are found in Europe and temperate North America, while *G. foliophilus* seems limited to eastern North America. From all these taxa, a mimic, *Marasmius pallidocephalus*, is separated from *G. androsaceus* with difficulty in the field, based almost solely by lack of clamp connections of the former and phylogenetic placement.

Often in collections of *G. foliophilus*, evidence of some bleaching of substrate can be detected. This is not dramatic – not to pale off-white – but distinct nonetheless. The phenomenon cannot be compared to *M. perforans* because fallen needles of *Picea/Abies* naturally bleach over time.

In *G. foliophilus*, stipes are almost always bicolor, upward with some avellaneous to pinkish shade, downward to dark brown and finally black toward the base (note that the very junction of stipe and lamellae is always dark brown). The relative stipe length of these colors varies considerably, with the upward avellaneous shades from only the uppermost 10% to as much as the upper 50%. To some extent, the density and quality of the stipe vesture also varies, with upper surfaces producing shorter, less setoid, hyaline caulocystidia, often with long, slender, hyaline hyphae producing a sparsely silky

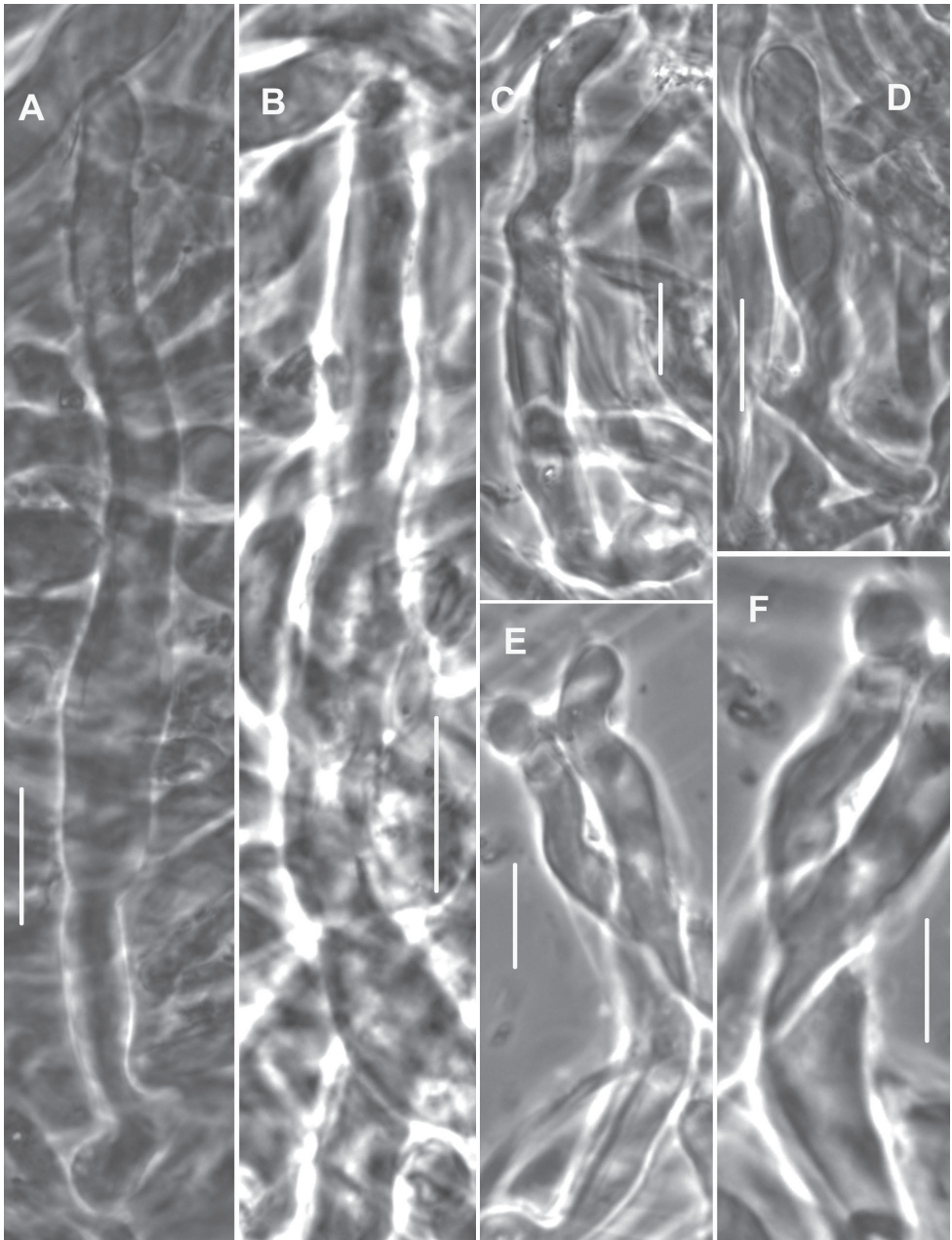


Figure 15. *Gymnopus foliophilus*. Caulocystidia from upper stipe. Standard bars = 10 μm . TFB 2800 (TENN-F-49363).

or wispy appearance (40 \times) rather different from the hispid or barbed appearance of the lower stipe caused by setoid caulocystidia often gathered into synnematosus sheaves.

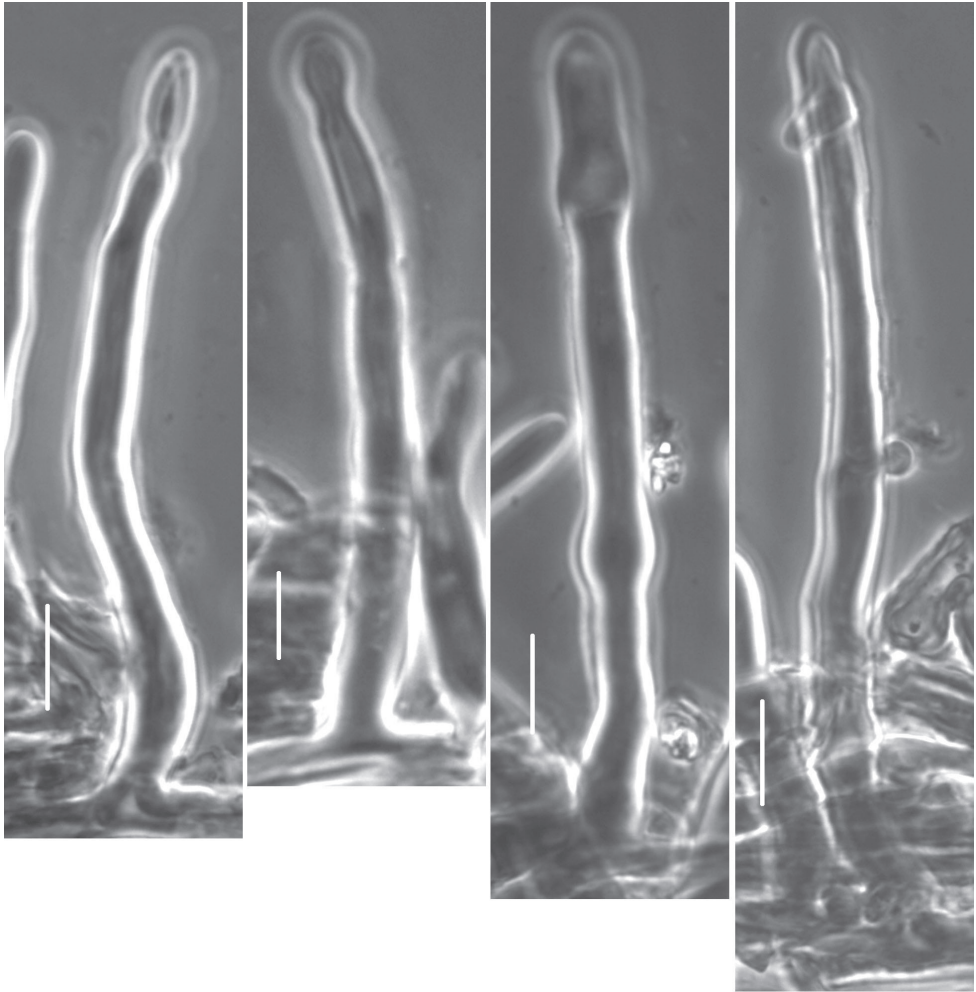


Figure 16. *Gymnopus foliophilus*. Caulocystidia from lower stipe. Standard bars = 10 μm . TFB 2800 (TENN-F-49363).

A seductive artifact in microscope mounts of hymenial structures are the subbasidial cells. As is typical, basidioles and basidia are produced in “bouquets” by subbasidial hyphae, which usually are tightly packed but which retain hyphal characteristics. In *G. foliophilus*, subbasidial hyphae are catenulate or congestedly lobose. The result are structures which mimic the cheilocystidia of numerous *Gymnopus* taxa, especially in sect. *Vestipedes*. In *G. foliophilus* (as in *G. perforans*), cheilocystidia are difficult to interpret, and when present, are consummately basidiiform.

Traditional generic characters are not consistent in sect. *Perforantia* and sect. *Androsacei*. For example, the pileipellis of *G. androsaceus* resembles a rameales structure of repent but diverticulate hyphae. Such a pileipellis is also present in *Marasmiellus*, taxa of which seem to belong to several relatively distantly related clades. In *Micromphale*, a

gelatinous layer within the pileus trama can usually be demonstrated (i.e. *M. foetidum*, etc.), but in *Micromphale* sect. *Perforantia* the gelatinous layer is absent, but “replaced” by a thin slime matrix over and within the pileipellis.

A paper by Farnet et al. (1999) employed an agar medium reputed to promote production of rhizomorphs. For the present study, this medium (whole wheat flour 20 g/L; agar, Bacto 20 g/L; H₂O 1 L) was used for numerous dikaryon isolates of various *Marasmius* and *Micromphale* collections. Ancillary to production of rhizomorphs, aerial mycelium of isolates of *M. foliophilus* slowly changed from white to bright yellow (“empire yellow” 3A6), while aerial mycelium of *M. perforans* remained white.

Desjardin (pers. comm.) indicated the possibility that *Marasmius insititius* Fr. (1838. *Epicrisis*: 386), fruiting on *Quercus* leaves in Sweden, might be similar to *M. foliophilus*. *Marasmius insititius* has seen a checkered history. Recently, Antonín and Noordeloos (2010) excluded the epithet from *Marasmius* because: 1) no type specimen exists; 2) Fries’s description is less than explicit; 3) in spite of Fries’s physical location in central Sweden in 1838, a habitat on *Quercus* leaves might indicate his exposure to the organism in southern Sweden; and 4) Orton (1960): 303) had dismissed the epithet as a later heterotypic synonym of *Marasmius calopus*. Desjardin (1989) did not include *M. insititius* in his type specimen studies, presumably based on the above and its extralimital status for *Marasmius* of the southeastern United States. Svengunnar Ryman (UPS; pers. comm.) indicates that *M. insititius* is an unknown entity. It is not the purpose of this paper to attempt to exhume *M. insititius*, especially as this name was not taken up in the Scandinavian mycota by Noordeloos in *Funga Nordica* (Knudsen and Vesterholt 2012).

Once informed of our intention to propose a new species to represent the oak-loving relative of *Mi. perforans*, Desjardin (pers. comm.) graciously supplied extensive notes on three specimens [DED 4329 (TN), DED 4449 (SC), DED 4477 (NC)] and numerous citations of herbarium specimens chiefly listed under *Ma. epiphyllus* and *Ma. insititius* from AL, OH, PA, VA (not represented in “specimens examined” below).

Specimens examined. UNITED STATES, Arkansas, Baxter Co., vic. Big Flat, Ozark National Forest, Leatherwood Wilderness, N36°02.4', W92°23.2', 23.X.2013, coll RHP (as *M. perforans* var. *quercophilus*), TFB 14422 (ITS, TENN-F-69084). **Connecticut**, Middlesex Co., vic. Salem, Devil’s Hopyard State Park, 41°28.937'N, 72°20.491'W, 1.ix.2013, coll RHP, TFB 14332 (ITS, TENN-F-68183, holotype). **Georgia**, Rabun Co., vic. Clayton, Warwoman Dell picnic area, 15.VI.1992, coll SA Gordon, TFB 4902 (ITS, TENN-F-51221). **Mississippi**, Stone Co., Ramsey Springs, Red Creek Wildlife Management Area, N30°46.572', W88°54.815', coll. RHP, TFB 14291 (ITS, TENN-F- 68145). **North Carolina**, Macon Co., vic. Highlands, Rte 106, Blue Valley Overlook, north side of road, N35°01'45.15", W83°16'57.09", 20.VII.1n989, coll RHP, TFB 2800 (TENN-F-49363); vic. Highlands, Bull Pen Rd. at Slick Rock, 29.VI.1992, coll SA Gordon, TFB 4928 (ITS, TENN-F-51244); vic. Highlands, Nantahala Nat. For., Blue Valley, Trail to Pickelseimer’s Falls, 23.VII.1994, coll RHP, TFB 7243 (TENN-F-56223); same location, Road 79, 14.VIII.1999, coll RHP, TFB 10364 (ITS, TENN-F-57923); same location, Forest Rd. 79, N35°01.103',

W83°14.697', 1.VIII.2012, coll. RHP, TFB 10463 (TENN-F-67809); same location, Blue Valley Campground, N35°00'45.23", W83°09'29.33", 11.VIII.2014, coll. RHP, TFB 14508; same location, FR 77 gate area, N35°00.243', W83°14.151', 14.VIII.2014, coll RHP, TFB 14531 (TENN-F-69226); same location, start of FR 79, at picnic area, N35°01.085', W83°14.715', coll RHP (as *Mi. perforans* var. *quercophilus*), TFB 13875 (ITS, TENN-F-65571); same location, FR 79, N35°01.103', W83°14.697', 1.VIII.2012, coll RHP (as *Mi. perforans* var. *quercophilus*), TFB 14063 (TENN-F-67809); Cliffside Lake Rd., N34°04.749', W83°14.150', 30.VIII.2012, coll RHP, TFB 14048 (ITS, TENN-F-65977). **South Carolina**, Oconee Co., Oconee State Park, Nature Trail, N34°52'07", W83°06'20", 17.V.1991, coll SA Gordon, TFB 3612 (TENN-F-50731); TFB 3615 (TENN-F-50734); Oconee State Park, N39°52'07", W83°06'19", 18.VIII.1992, coll SA Gordon, TFB 5051 (TENN-F-51454); Rte 107 circ. 12 m south of Cashiers, N34°59'37", W83°03'09", 16.VIII.1992, coll RHP, TFB 5435 (TENN-F-51753); vic. Cashiers (NC), Walhalla Fish Hatchery, N34°59.155', W83°04.374', 7.VIII.1996, coll RHP, TFB 8782 (ITS, TENN-F-55210). **Tennessee**, Blount Co., GSMNP, Spruce Flats, N35°37'18.4", W83°40'26.3", 24.VI.1991, coll RHP & V. Antonín, TFB 3659 (TENN-F-50778); GSMNP, Metcalf's Bottoms, picnic area, 9.VI.1997, coll RHP, TFB 9166 (ITS, TENN-F-55764); GSMNP, vic Crib Gap, N35°36'45.8", W83°44'42.1", 22.VII.1991, coll & det DE Desjardin (as *Micromphale perforans* var. *quercophilus*), DED 5272 (ITS, TENN-F-50013; SFSU); GSMNP, Greenbrier at trailhead to Ramsay's Cascades, 20.VI.1991, coll SA Gordon, RHP, V. Antonín, TFB 3642 (ITS, TENN-F-50761); Foothills Parkway, Look Rock Campground, 10.VIII.2003, coll KWH & RHP, TFB 11608 (TENN-F-59641); Cocke Co., vic. Cosby, GSMNP, Gabes Mt. Trail, N35°12'33.0", 5.VII.2006, coll M. Padansee, E Lickey, TFB 13242 (TENN-F-61274).

2A. *Gymnopus foliiphilus* var. *Costaricensis* R.H. Petersen & J.L. Mata, var. nov.
Mycobank no. 552485

Holotype. **Costa Rica**, Prov. San José, km 68 on PanAmerica Highway, "Finca Jaular," N9°39.597', W83°52.115'. 29.VI.2000, coll. RHP, TFB 9750 (TENN-F-58651).

Diagnosis. Similar to *Gymnopus foliiphilus*, but differing as follows: 1) pileus darker at all ages, smooth (not pebbled), not convex when young nor everted in age; 2) lamellae more numerous and lamellulae in two ranks; 3) lamellar attachment adnexed to adnate (not pseudocollariate); 4) stipe black or bicolored; 5) stipe insertion subinsititious (not insititious); 6) outer pileipellis hyphae often significantly encrusted (not smooth or with flakes).

Description. Basidiomata (Fig. 17A) diminutive, gymnopoid. **Pileus** 6–14 mm broad, appearing applanate throughout ontogeny but with downturned margin, outward vaguely sulcate–striate, always very thin-fleshed, smooth (but not glabrous), matt (but not velutinous, etc.), dark brown when young ("amber brown" 6D8, "mummy brown" 6F8, "Natal brown" 8E6, "bone brown" 7F8), fading somewhat

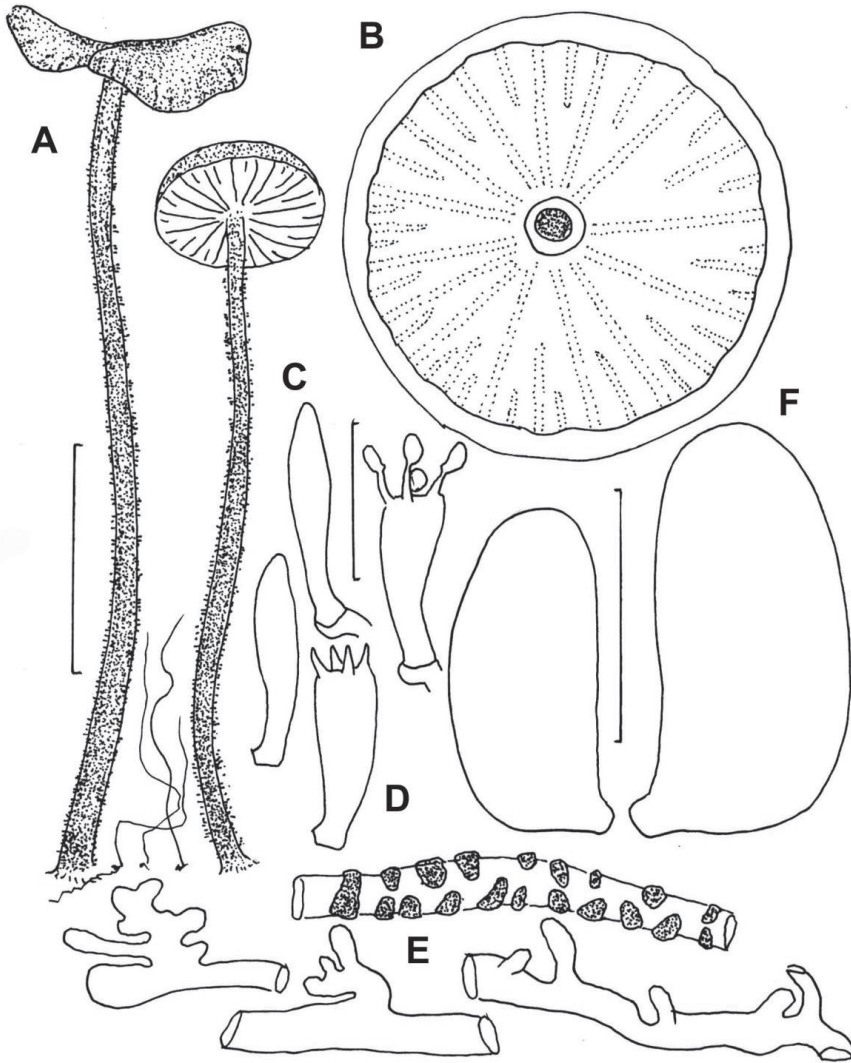


Figure 17. *Gymnopus foliophilus* var. *costaricensis*. **A** Basidiomata and rhizomorphs **B** Pileus underside showing lamellar spacing **C** Pleurocystidia **D** Basidia **E** Pileipellis hyphae, showing encrustation and lobose side-branches **F** Basidiospores. Standard bars: **A** = 5 mm; **B** = not to scale; **C–E** = 20 μ m; **F** = 5 μ m. TFB 9750.

by maturity (“tawny” 6C6, “wood brown” 7C4, “tawny olive” 5C5), essentially unicolorous (but occasionally with a suggestion of a paler central disc). **Lamellae** (Fig. 17B) (dried) appearing adnate to adnexed but not pseudocollariate, shallow (\sim 1 mm deep), total lamellae = 30–37, through lamellae = 12–15, “sulphur yellow” 1A2 to

“pale ochraceous buff” 4A2, now (dried) near “ochraceous buff” 5A5 to “light ochraceous buff” 5A4 with no evidence of necropigment. Lamellulae in two ranks. **Stipe** 13–30(–40) × 0.6–1(–1.5) mm, terete, equal, twisted and compressed upon drying, lightly stuffed to hollow, vested throughout, from minutely flocculose (40×) to barbed but not consistently located – sometimes flocculose vestiture apical, sometimes both apical and mid-section and alternating with barbed texture; color never black, often bicolorous, upward concolorous with lamellae, soon downward darker, “tawny” 6C6, finally dull fuscous (“drab” 6D3, “hair brown” 6E3, “citrine drab” 4D5); insertion insititious to subsinititious (very small basal pad – hardly noticeable). **Rhizomorphs** (Fig. 17A) sparse, slender, meandering over leaf surface before becoming erect, unbranched, never more than 10 mm long. **Odor** faint of cabbage, stronger with age; **taste** not recorded.

Habitat and phenology. Fruiting on sclerophyllous leaves (perhaps *Quercus*) at mid- to high-elevation; early summer.

Pileipellis an intricately interwoven layer of thin-walled, conspicuously clamped hyphae in a heterogeneous matrix of slime (including copious debris), composed of: 1) hyphae 5–15 µm diam (Fig. 18A, B), firm-walled with thin slime sheath with flake-like crust material riding on outside of sheath; 2) hyphae 6–14 µm diam, firm-walled, producing variable small lobes or outgrowths (Figs 17E, 18C–J), occasionally proliferating into ribbon-like extensions (Fig. 18K, L); and 3) occasional strongly encrusted hyphae present; hyphae 4–7 µm diam, encrustation in significant scabs sometimes suggesting stripes, with minimal profile calluses. Lamellar trama loosely interwoven; hyphae 2.5–3.5 µm diam, firm-walled, long-celled, conspicuously clamped (often medallion). **Pleurocystidia** (Figs 17C, 19A–D) 17–24 × 6.5–8 µm, fusiform, conspicuously clamped; contents homogeneous. Basidioles clavate; **basidia** (Figs 17D, 19E–H) 18–22 × 7–8, broadly clavate, clamped, 4-sterigmate. Small clots of subgelatinous material in hymenium (scattered, evidenced by copious “sludge” and/or debris); effete basidia and pleurocystidia evacuating contents but retaining uncollapsed walls (“husking”). **Basidiospores** (Fig. 17F) (6–)6.5–8 × 3–4 µm ($Q = 1.75\text{--}2.67$; $Q^m = 2.11$; $L^m = 7.20$ µm), gymnopoid (not tapered proximally), smooth, thin-walled, inamyloid. **Cheilocystidia** (Fig. 20) 23–29 × 5–9 µm, clavate, basidioid, usually slightly subcapitulate. Stipe medullary hyphae 3–17 µm diam, strictly parallel, perhaps adherent (shearing in plates and with copious floating debris), hyaline, firm- to thick-walled (wall ~1.0 µm thick), obscurely clamped, with occasional constricted lobes. **Caulocystidia** from upper stipe (Fig. 21A) sub-hyaline (pale champagne color in mass, refringent PhC), gnarled (not straight/setoid), thick-walled (wall ~2 µm thick), usually clamped internally, gathered into “plaques” (which appears as floccules at 40×). **Caulocystidia** from flocculose lower stipe (Fig. 21B) ~110 µm long, thick-walled (wall ~2 µm thick, yellow-refringent; cytoplasm hyaline), usually lobed or branched at base, 7–12 µm broad.

Commentary. Smooth pileus surface and encrusted pileipellis hyphae are suggestive of *Gymnopus* sect. *Vestipedes*, but obvious slime matrix points to sect. *Perforantia*. The vested stipe also might point toward *G. perforans* or sect. *Vestipedes* (not toward *Gymnopus* sect. *Androsaceus* s.s.).

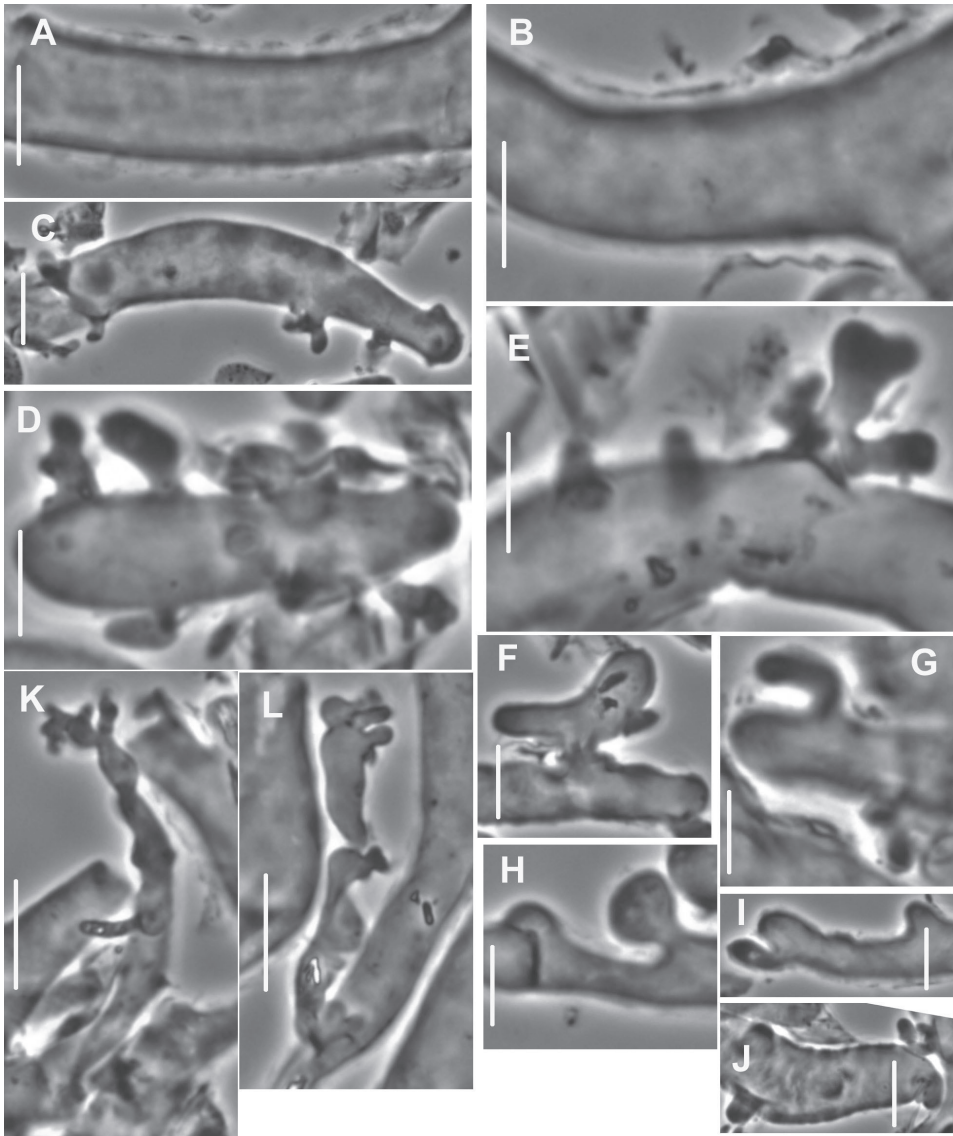


Figure 18. *Gymnopus foliophilus* var. *costaricensis*. Pileipellis elements. **A, B** Firm-walled hyphae with slime sheath and crust material on exterior of the sheath **C–J** Diverticulate hyphae with individual lobate outgrowths **K, L** Extended lobes into ribbon-like proliferations. Standard bars = 10 μ m. TFB 9750.

Traditionally, *G. perforans* has been accepted as quite variable in substrate. ITS phylogeny indicates separation into several species, with *G. perforans* s.s. limited to conifer needles (usually *Picea/Abies*), with segregants on dead deciduous leaves (*G. foliophilus*), or needles of *Pinus strobus* (*G. pinophilus*) or *P. ponderosa* (*G. ponderosae*). Collection TFB 9750 TENN-F-58651 matches this complex micromorphologically, and especially *G. foliophilus* in substrate.

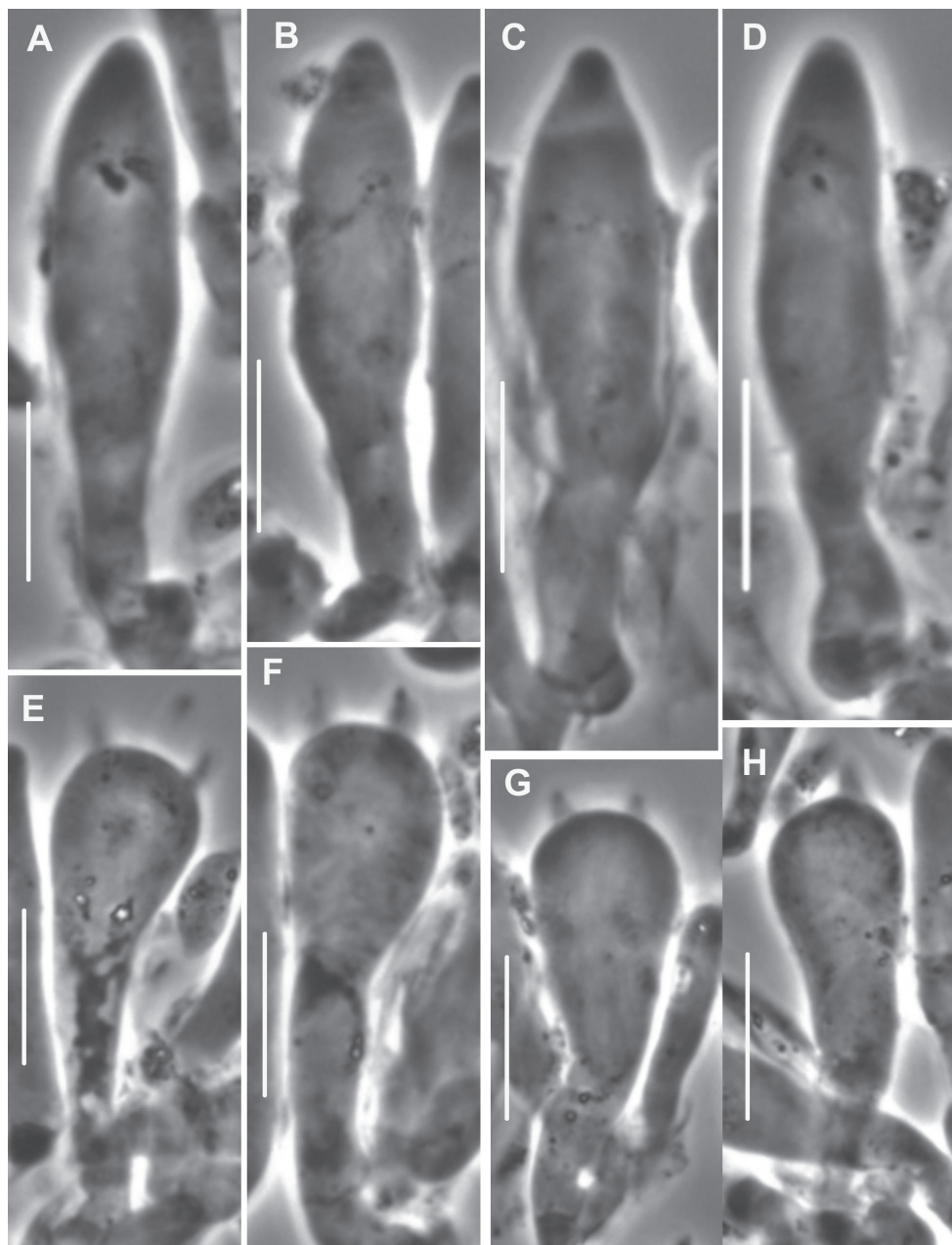


Figure 19. *Gymnopus foliiphilus* var. *costaricensis*. Hymenial elements. **A–D** Pleurocystidia **E–H** Basidia. Standard bars = 10 μ m. TFB 9750.

Specimens examined. **Costa Rica**, Prov. Heredia, County Barva, District San José de la Montaña, viz. Sacramento, 25.VIII.2014, JLM 2238 (USAM); Prov. San José, km 68 on PanAmerica Highway, Finca Jaular, N9°39.597', W83°52.115'.

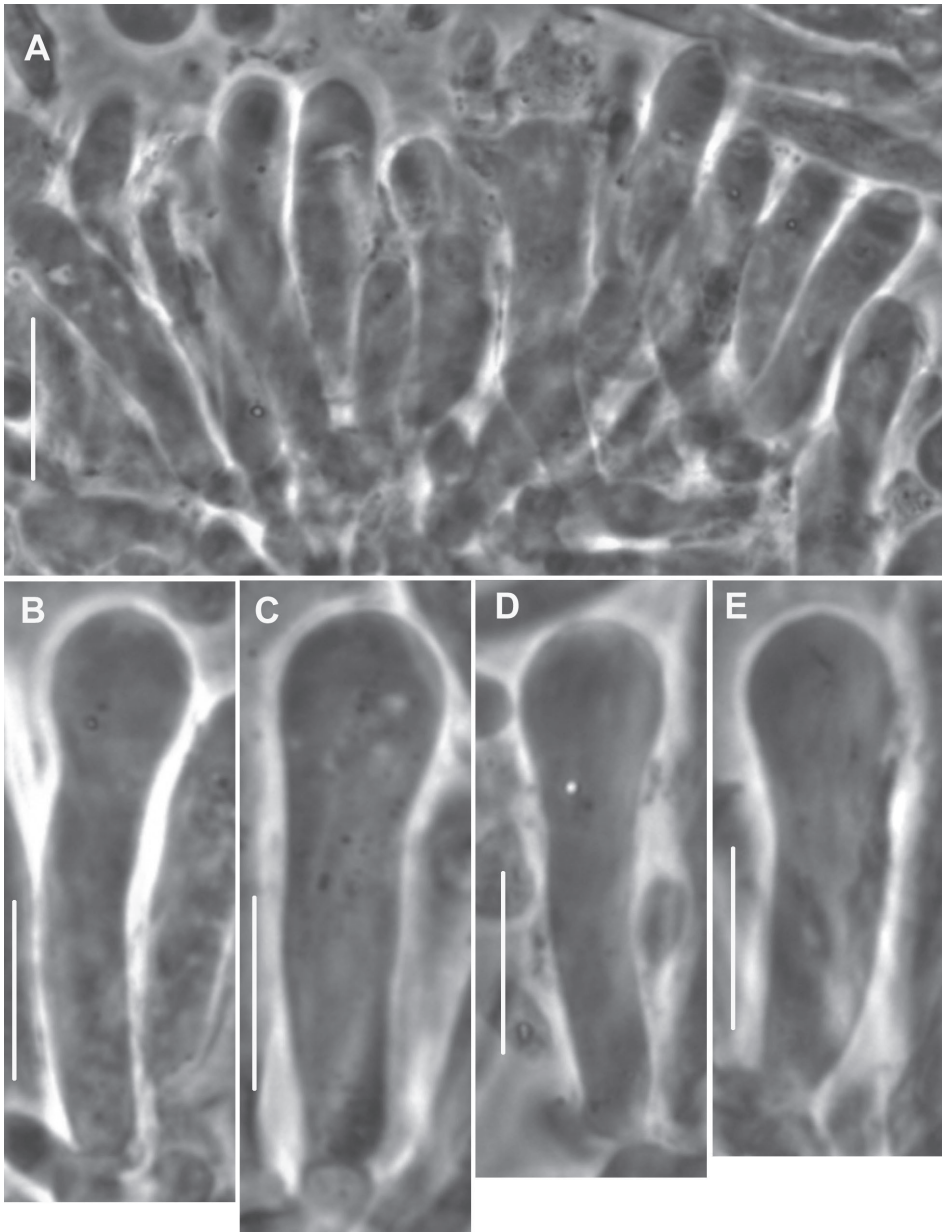


Figure 20. *Gymnopus foliophilus* var. *costaricensis*. Cheilocystidia. **A** Overview of lamellar edge **B–E** Individual cheilocystidia. Standard bars = 10 μ m. JLM 2221 (USAM).

29.VI.2000, coll. RHP, TFB 9750 (TENN-F-58651; holotype); Prov. San José, County Dota, District Jardin, viz. La Chonta, Finca Sta. Maria, 4 km on Hwy 2 from intersection at Empalme, N9°41.806, W83°55.763', 14.VIII.2014, JLM 2219 (USAM); Same location, same date, JLM 2221 (USAM).

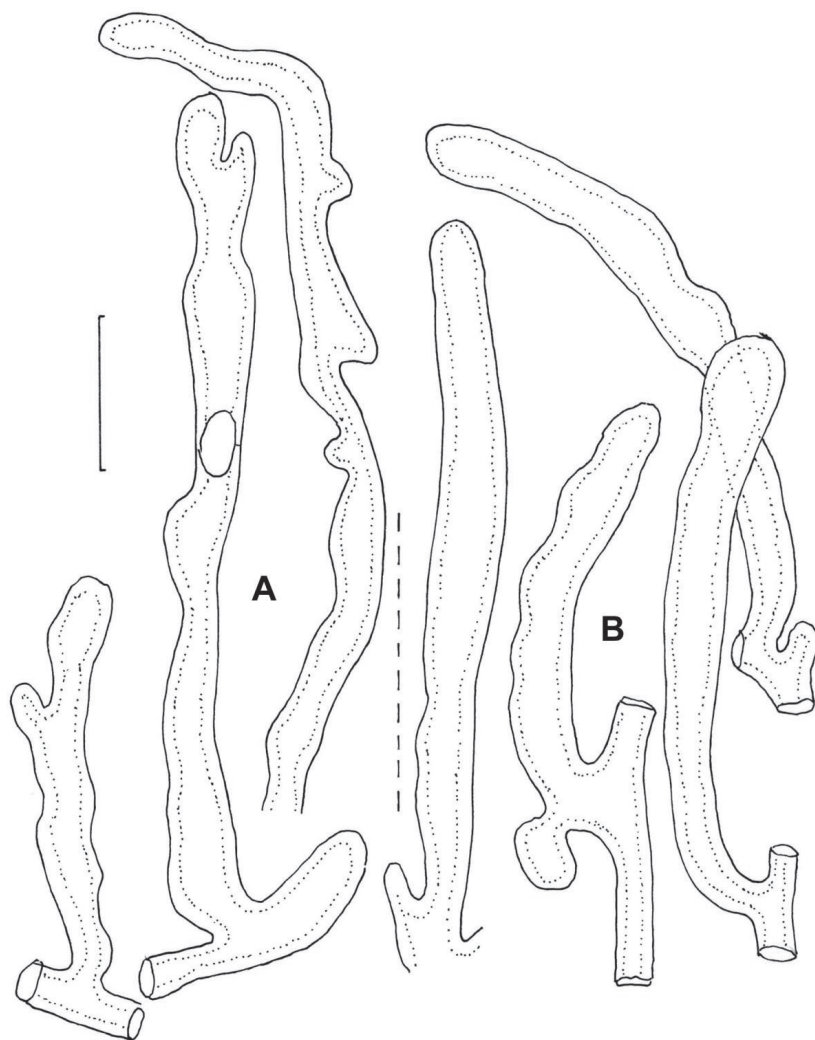


Figure 21. *Gymnopus foliophilus* var. *costaricensis*. Caulocystidia. **A** Individuals from near stipe apex **B** Individuals from lower stipe. Standard bar = 20 μ m.

3. *Gymnopus fragillior* R.H. Petersen, sp. nov.

Mycobank no. 552471

Holotype. United States, Washington, Jefferson Co., Irely Lake Area, North Fork Quinault River, N47°33'47.7", W123°40'12.38", date not recorded, coll M.T. Seidl, ident. S Redhead (as *Micromphale perforans*), MTS 3715 (WTU-F-9293).

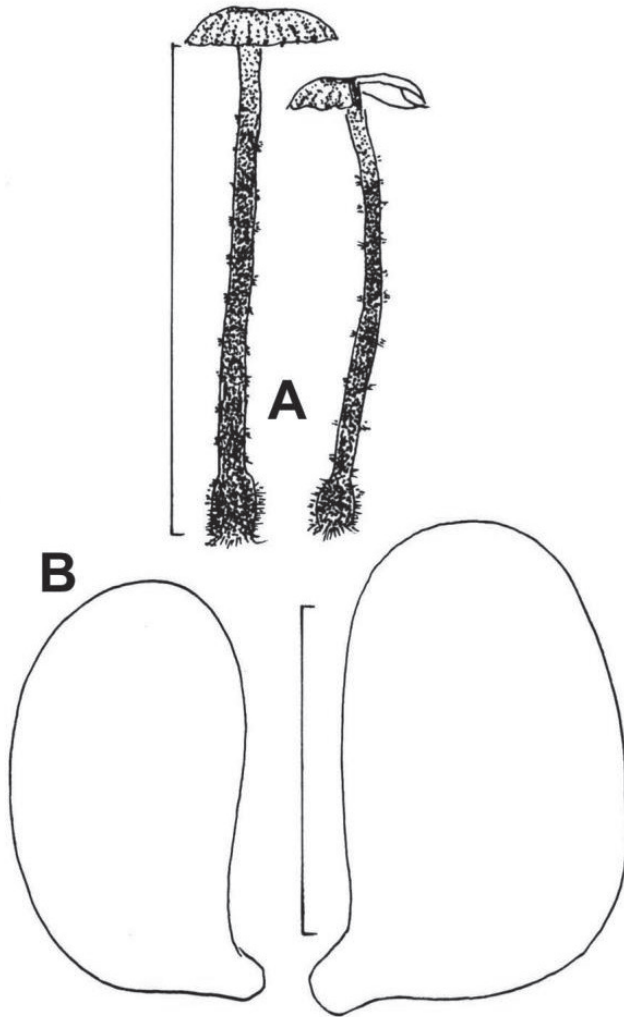


Figure 22. *Gymnopus fragillior*. **A** Basidiomata **B** Basidiospores. Standard bars: **A** = 20 mm; **B** = 5 μ m. WTU-F-9293.

Etymology. fragillior = Latin, more fragile, referring to more diminutive stature than *M. perforans*.

Diagnosis. 1) A morpho-taxon (no DNA sequences available); 2) basidiomata slender (stipe 15–25 \times 0.4–0.7 mm), diminutive, slender; 3) stipe base (<1 mm) with hirsute, tawny collar; 4) sterigmata stout, subcornute; 5) basidiospores broadly ellipsoid to pip-shaped ($Q^m = 1.68$); 6) stipe medullary hyphae thick-walled, not involved in slime matrix.

The following description is based on dried material only. Basidiomata (Fig. 22A) slender, diminutive, attached to individual needles of ?*Abies grandis*.

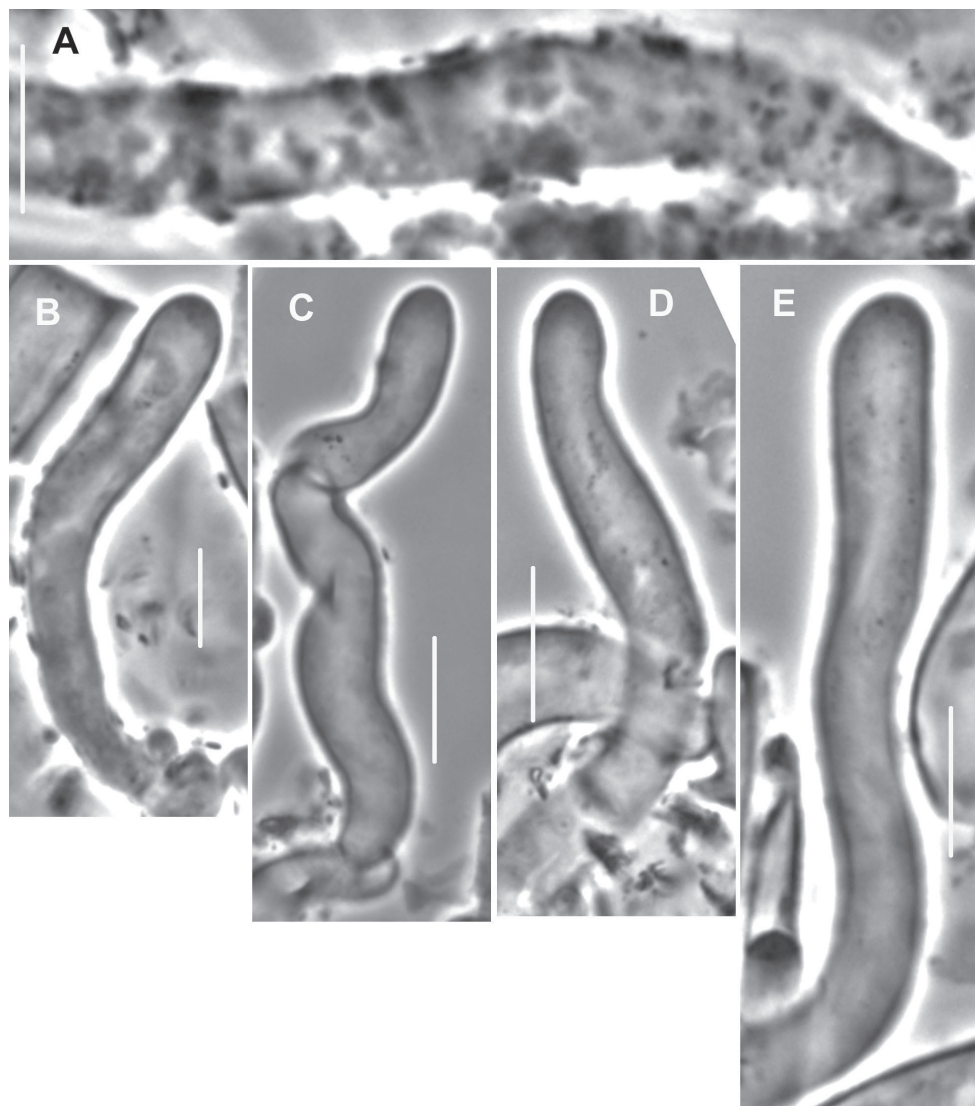


Figure 23. *Gymnopus fragillior*. Pileipellis elements. **A** Encrusted, repent hypha **B–E** Pileal hairs. Standard bars = 10 μm . WTU-F-9305.

Pileus 6–10 mm broad, convex to plano–convex, often somewhat centrally depressed, matt, delicately tuberculate; disc (fresh) pale grey brown, (dry) “army brown” 8D5 to “saya brown” 6C5; limb and margin (fresh) cream, (dry) “wood brown” 7C4; margin thin; pileus trama dull orange to orange–brown in Melzer’s reagent. **Lamellae** adnate, distant, thickish, in 2–3 tiers, weakly pseudocollariate, seceding upon drying, (fresh) pallid tan, “tilleul buff” 7B2, “olive buff” 3B3, (dry) slightly necropigmented (near “light ochraceous buff” 5A4). **Stipe** 15–25 \times 0.3–0.5 mm, terete, equal, more or less straight, hollow, non-insititious, lightly vested to

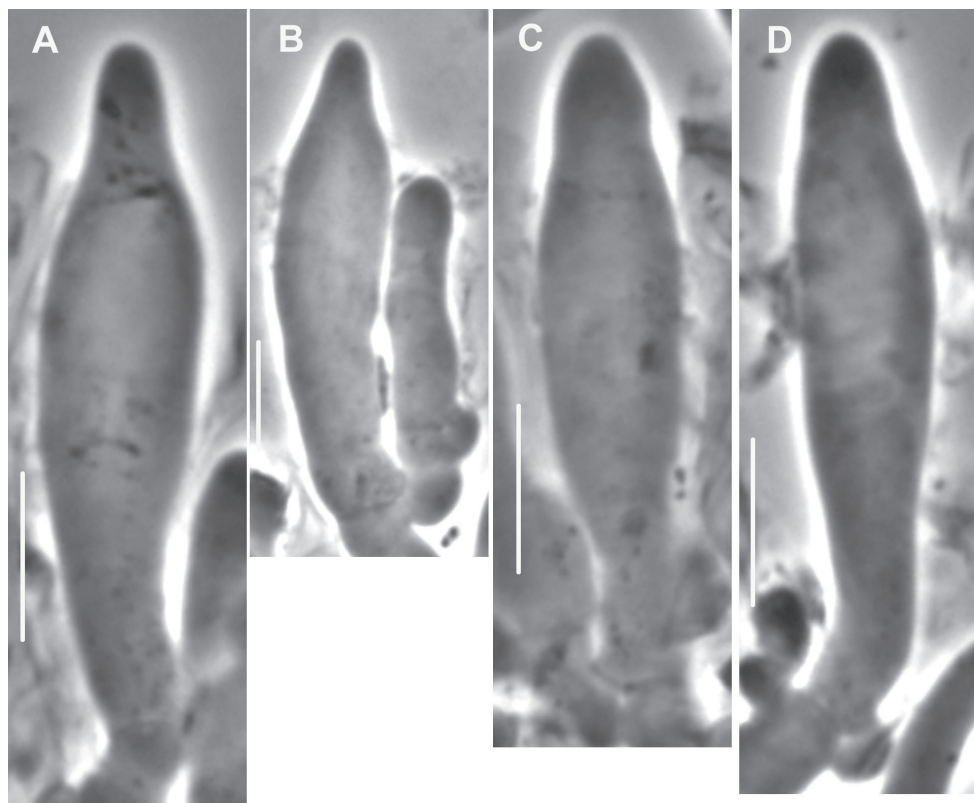


Figure 24. *Gymnopus fragillior*. Pleurocystidia. Standard bars = 10 μ m. WTU-F-9305.

delicately furfuraceous throughout, in contact with lamellae dark brown, apically tan to pale cream (“cinnamon buff” 6B4), downward brown, dark brown, base blackish brown (“clove brown” 6F5, “fuscous black” 6F4); stipe base (<1 mm) a minutely hispid collar, “tawny” 6C6 to “ochraceous tawny;” basal pad restricted, “tawny” 6C6; medulla thin, off-white (not white). **Rhizomorphs** not observed. **Odor** alliaceous; **taste** not recorded.

Habitat and phenology. Known only from the holotype collection. “Scattered on outer bark of fallen tree, mostly fruiting from needles fallen on log” (teste Seidl) (perhaps *Abies grandis*). Seasonality unknown.

Pileipellis a repent, unoriented layer in a thin slime or gelatinous matrix with detersile encrustation material, composed of the following: 1) pileal hairs (Fig. 23B–E) 15–75 \times 5–10 μ m diam, digitate to vermiform, equal, hyaline, firm- to thick-walled (wall \sim 0.5 μ m thick), obtusely rounded at apex; 2) repent hyphae 4–13 μ m diam, thin- to firm-walled, conspicuously clamped (but with occasional secondary septa), at pileus surface strongly to moderately encrusted (Fig. 23A); crust material in scabs, occasionally with suggestion of annular pattern, 0.7–2 μ m thick, in subpellis as flakes riding on thin slime sheath. Pileus and lamellar tramae loosely interwoven, dull orange

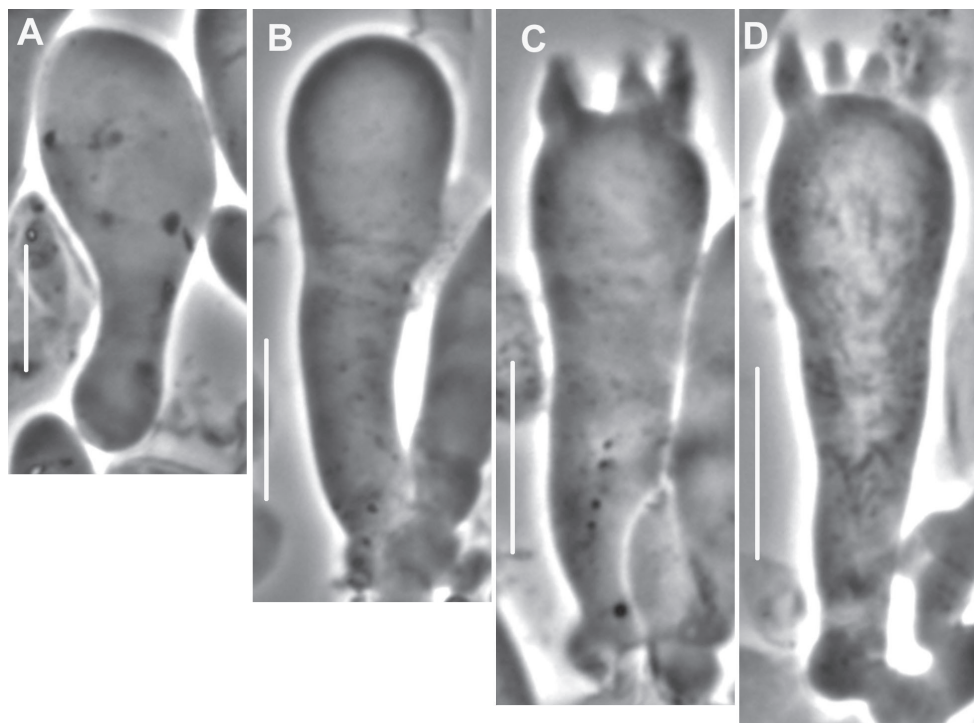


Figure 25. *Gymnopus fragillior*. Basidial development. **A, B** Basidioles **C, D** Mature basidia. Note stout sterigmata. Standard bars = 10 µm. WTU-F-9503.

to orange–brown in IKI; hyphae 5–12 µm diam, thin- to firm-walled, with thin slime sheath in KOH, conspicuously clamped. **Pleurocystidia** (Fig. 24) 28–35 × 5–8 µm, fusiform to narrowly fusiform, conspicuously clamped, hyaline; contents homogeneous. Basidioles (Fig. 25A, B) clavate, clamped; **basidia** (Fig. 25C, D) 28–36 × 7–10 µm, clavate, usually subcapitulate, conspicuously clamped, 4–sterigmate; sterigmata –6 × 2.5 µm, stout, subcornute. **Basidiospores** (Fig. 22B) (6–)6.5–7.5(–8) × 3.5–4.5 µm ($Q = 1.44$ –2.00; $Q^m = 1.68$; $L^m = 6.90$ µm), plump ellipsoid to pip-shaped, smooth, thin-walled, inamyloid. **Cheilocystidia** not observed. **Stipe medullary hyphae** strictly parallel, 4.5–14 µm diam, apparently free (not involved in slime or gelatinous matrix), thick-walled (wall –0.7 µm diam, hyaline), obscurely clamped; occasional slender hyphae (4–5.5 µm diam) meandering among broader hyphae. **Stipe cortical hyphae** 4.5–7.5 µm diam, thick-walled (wall –2.5 µm thick, pigmented, producing caulocystidia as side branches), obscurely clamped. **Mid-stipe caulocystidia** (Fig. 26) in scattered clusters, setoid, arising as side branches of surface cortical hyphae or as termini, 15–75 × 7–13 µm diam, not clamped, digitate to subvermiform, thick-walled (wall –5 µm thick, pigmented pale yellowish, refringent; PhC). **Caulocystidia from stipe base** (Fig. 27) densely gregarious, setoid, 20–95 × 7–13 µm, usually straight, tapering somewhat distally, with basal appendage, thick-walled (wall often occluding cell lumen, yellowish, refringent).

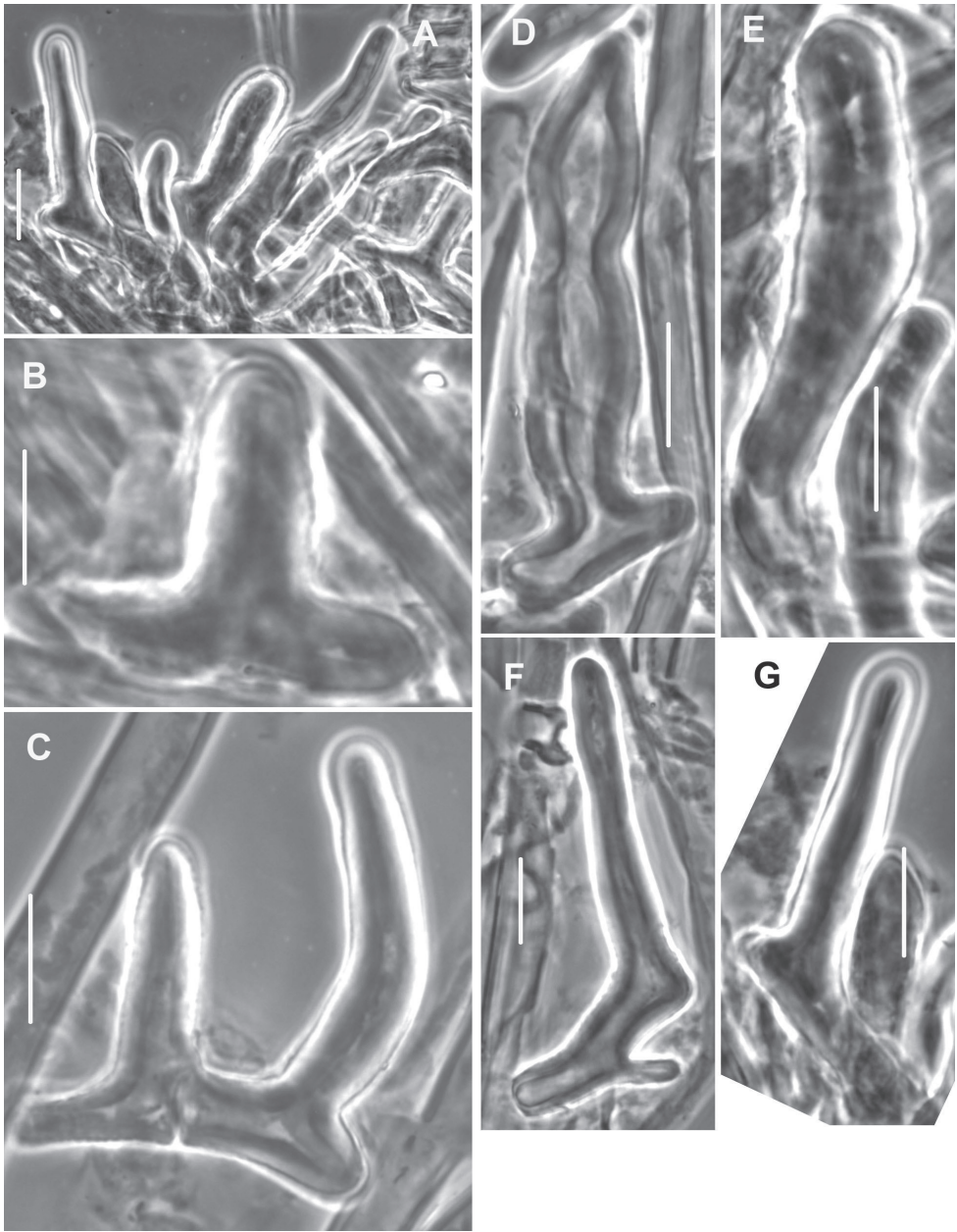


Figure 26. *Gymnopus fragillior*. Mid-stipe caulocystidia. **A** Cluster of caulocystidia **B** Small individual **C** Double caulocystidia **D–G** Individual caulocystidia. Standard bars = 10 μm . WTU-F-9305.

Commentary. A pileipellis involved in slime matrix, lacking diverticulate hyphae and/or broom cell-like termini, coupled with vestured stipe, indicate placement in *Gymnopus* (*Micromphale*) sect. *Perforantia*. There it is distinguished from *G. perforans*,

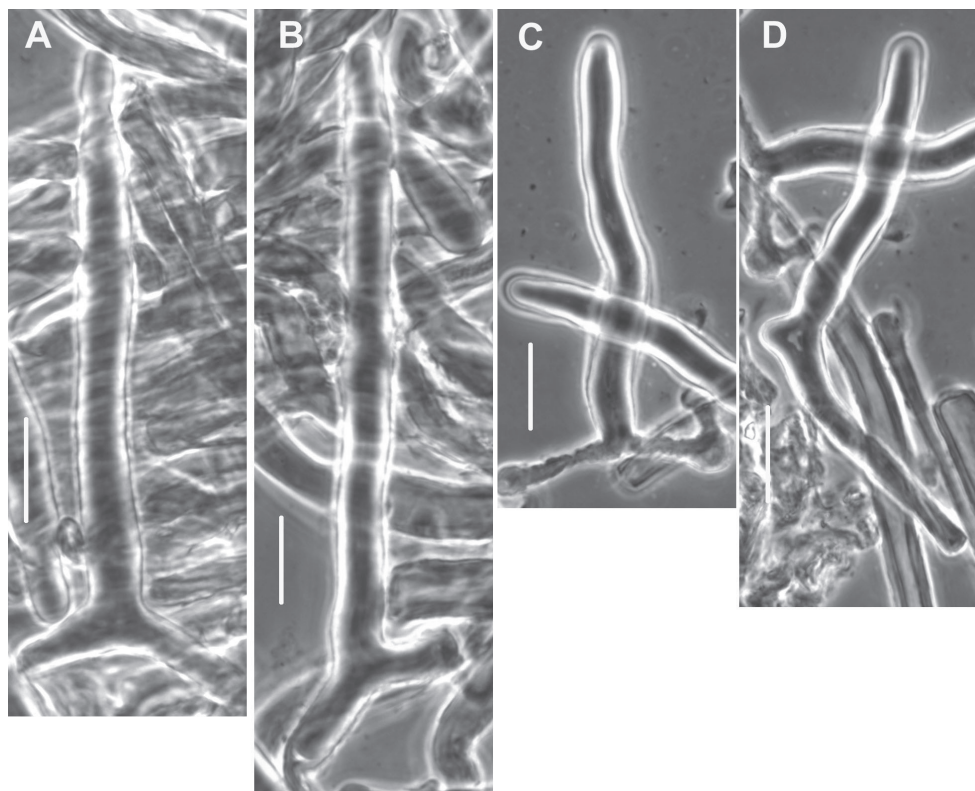


Figure 27. *Gymnopus fragillior*. Stipe-base caulocystidia. Standard bars = 10 μ m. WTU-F-9305.

G. pallidocephalus and other taxa with similar characters. Unusual, however, are the scattered clusters of caulocystidia, the stipe base with delicately hispid, brown caulocystidia and pip-shaped spores. From *Mycetinis salalis* comb. prov, also in the moist forests of the Pacific Northwest, *G. fragillior* is immediately separated by spore dimensions ($15\text{--}17 \times 3.5\text{--}4 \mu\text{m}$; $Q^m = 4.38$ in the former), habitat on conifer needles (rotting wood in the former), different pileipellis structures and absence of cheilocystidia (marasmioid in *M. salalis*). From both *G. perforans* and *G. pallidocephalus*, which share habitat on conifer needles, *G. fragillior* is distinguished by non-black stipe (black, vested and more robust in *G. perforans*, black and glabrous–shining in *M. pallidocephalus*), and common clamp connections (absent in *G. pallidocephalus*). Basidiomata of *G. bulliformis* are somewhat more robust, with pileus somewhat paler and prominent, utriform cheilocystidia (absent in *G. fragillior*).

Specimen examined. **United States**, Washington, Jefferson Co., Irely Lake Area, North Fork Quinault River, N47°33'47.7", W123°40'12.38", date not recorded, coll M.T. Seidl, ident. S Redhead (as *Micromphale perforans*), MTS 3715 (WTU-F-9293; holotype).

4. *Gymnopus glabrosipes* R.H. Petersen, sp. nov.

Mycobank no. 552478

Holotype. United States, Washington, Snowhomish Co., Hwy 92, Perry Creek Trail, 24.VI.1993, coll GR Walker (as *Micromphale perforans*), GRM 410 (WTU-F-9309).

Etymology. Glabro- = Latin, smooth; pes = Latin, foot, referring to the glabrous-shining stipe.

Diagnosis. 1) A morpho-species (no DNA sequences available; 2) stipe glabrous-shining; 3) fruiting on dead *Tsuga* needles; 4) lamellae suffusing brown from edge when bruised or dried; 5) stipe 15–25(–50) × 0.4–1 mm, robust; 6) stipe medullary hyphae involved in slime matrix.

The following description is based solely on dried specimens. Basidiomata (Fig. 28) diminutive with robust stipe. **Pileus** 4–9 mm broad, plano-convex to plane, matt, smooth, more or less unicolorous, hardly sulcate at margin, more or less unicolorous, dark brown (“carob brown” 7F7, “chestnut brown” 7E4); context near “olive buff” 3B3, reluctantly bruising to near “buffy brown” 6D4 when cut or bruised. **Lamellae** adnexed

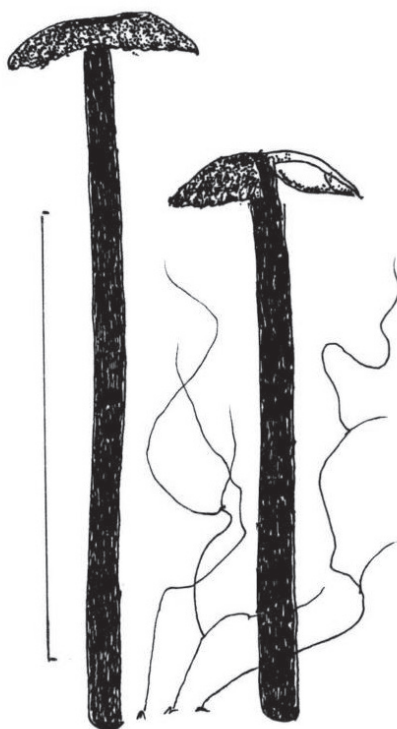


Figure 28. *Gymnopus glabrosipes*. Basidiomata and rhizomorphs. Standard bar = 20 mm. WTU-F-9309.

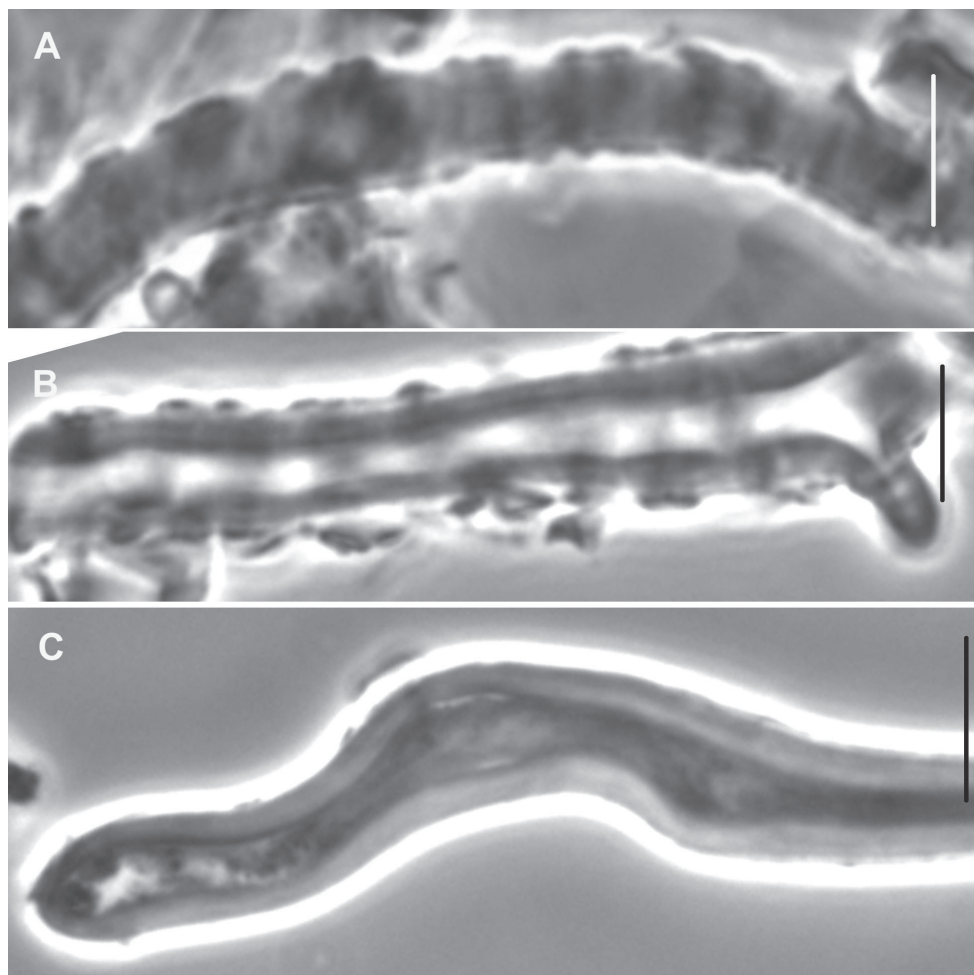


Figure 29. *Gymnopus glabrosipes*. Pileipellis hyphae. **A** Strongly encrusted hypha with vaguely annular pattern **B** Hypha with gelatinizing walls and thin slime sheath, with incrusting material on the surface of the slime sheath **C** Smooth hyphae with gelatinized wall. Standard bars = 10 μ m. WTU-F-9309.

to free, distant, with no anastomosis or interveining, thickish, near "olive buff" 3B3 (dried), bruising to dull "buffy brown" 6D4 from edge when bruised or dried; lamellulae rare, rudimentary. **Stipe** 23–30(–50) \times 0.7–1.2 mm, robust, terete, equal, insititious, glabrous–shining overall, delicately sulcate–ridged, stuffed, apically "buffy brown" 6D4, soon downward "chaetura drab" 2F2 to "chaetura black" 2F3 overall; stipe medulla white. **Rhizomorphs** extensive but inconspicuous, black, polished, filiform, –14 \times 0.2–0.4 mm, curly, branched with branches spur-like. **Taste** and **odor** not recorded.

Habitat and phenology. Fruiting on needles of *Tsuga* (associated with *Abies*); mid-summer.

Pleipellis a layer of unoriented, tightly interwoven, repent, strongly encrusted hyphae involved in a gelatinous or slime matrix; superficial hyphae 5–7.5 μ m diam, thin-

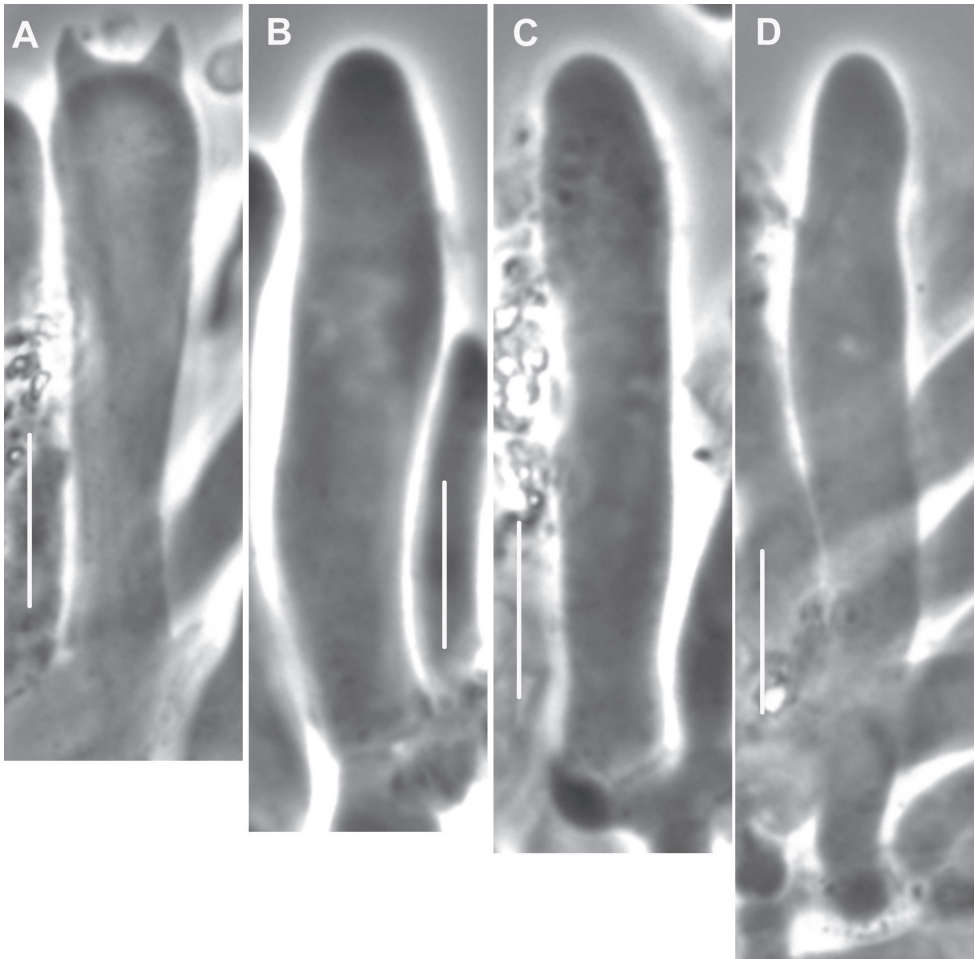


Figure 30. *Gymnopus glabrosipes*. Hymenial structures. **A** Basidium: note 2 sterigmata out of focus **B–D** Pleurocystidia: note basal clamp connections. Standard bars = 10 μm . WTU-F-9309.

walled, conspicuously clamped, strongly encrusted (Fig. 29A); incrustation material ~ 2 μm thick, in scabs and vaguely annular patterns; subpellis hyphae 6–11 μm diam, thick-walled (wall 1.5–3 μm thick, hyaline), smooth to weakly encrusted; crust material < 1 μm thick, in small scabs and vaguely defined annular patterns, sometimes flake-like on surface of slime sheath (Fig. 29B). Inner subpellis hyphae 7–11 μm diam, smooth, thick-walled with wall slowly (in KOH) swelling or gelatinizing (Fig. 29C), conspicuously clamped. Lamellar trama loosely interwoven; hyphae 2.5–3.5 μm diam, thin-walled, conspicuously clamped, often with thin slime sheath. Hymenium composed of pleurocystidia and basidia, gelatinizing (in KOH) from trama outward, eventually reducing basidial and pleurocystidial bases to gelatinous matrix. **Pleurocystidia** (Fig. 30B–D) 23–30(–42) \times 4–7 μm , narrowly fusiform without partitioned contents, conspicuously clamped. Basidioles narrowly clavate; **basidia** (Fig. 30A) 29–32(–39) \times 9–11 (at widest point),

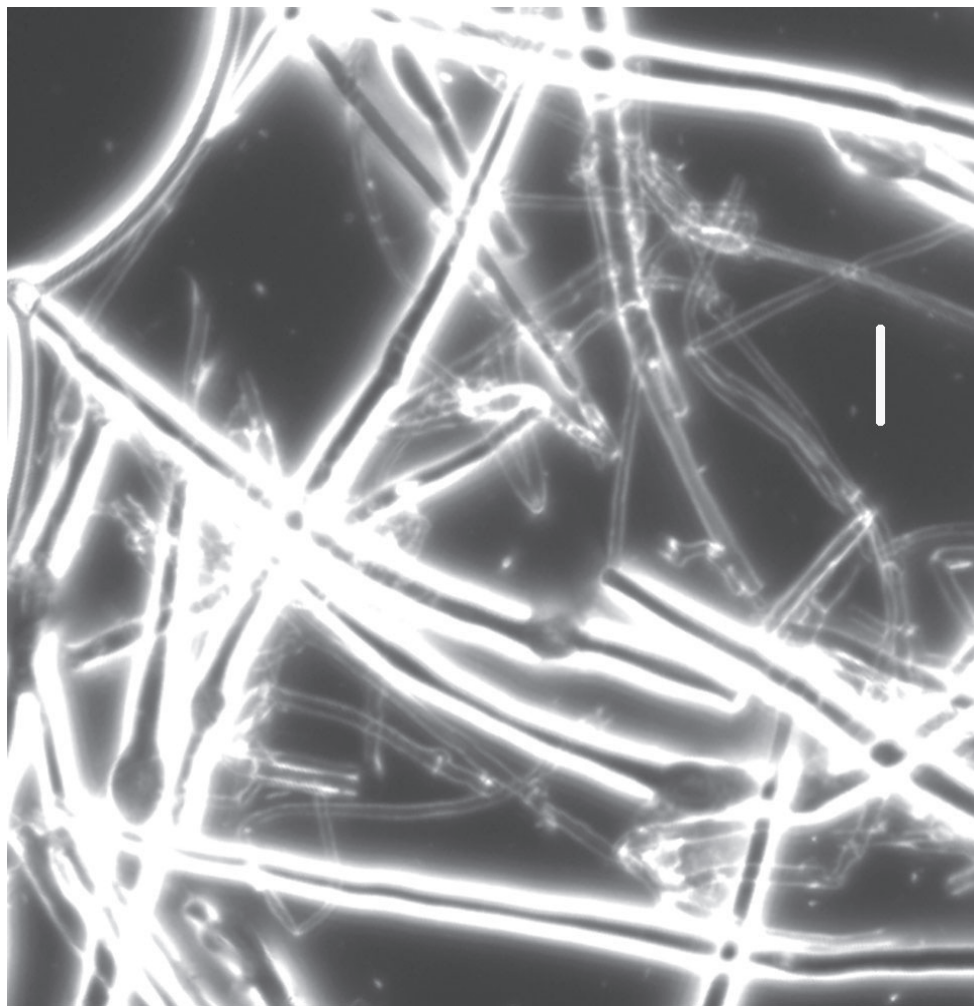


Figure 31. *Gymnopus glabrosipes*. Stipe medullary hyphae. Slender generative hyphae among refringent, thick-walled skeletalized hyphae. Standard bar = 10 μm . WTU-F-9309.

clavate, conspicuously clamped, 4–sterigmate; contents homogeneous. **Basidiospores** not observed. **Cheilocystidia** not observed. **Stipe medullary hyphae** appearing dimitic, without slime matrix; 1) 1.5–7.5 μm diam, thick-walled (wall ~ 1 μm thick, hyaline, non-refringent; PhC) (Fig. 31), frequently clamped, often branched, loosely interwoven, meandering among refringent, wider hyphae; and 2) 5–12 μm diam, tapered at both ends, thick-walled (wall gelatinizing ~ 6 μm thick, strongly refringent, PhC), long-celled, clamped. **Stipe cortical hyphae** strictly parallel, 2–4.5 μm diam, thick-walled (wall ~ 1 μm thick, pigmented yellow–brown), clamped, minutely roughened outward (perhaps a roughened mucoid film). **Caulocystidia** absent.

Commentary. Extraction of usable DNA from the two specimens examined was unsuccessful, so phylogenetic placement of *G. glabrosipes* remains unknown.

Pileipellis involved in slime matrix, pileus tramal hyphae with gelatinizing walls, basidia and pleurocystidial bases strongly gelatinizing and absence of cheilocystidia all are diagnostic of the *Mi. perforans* complex. Conversely, the glabrous–shining stipe is not characteristic of that clade.

Two pilei were assessed for diverticulate hyphae with no success. Pileipellis was the same in both.

Macromorphologically, basidiomata are reminiscent of those of *Ma. thiersii*, with dark chocolate brown pileus and insititious, brown–black stipe. From *M. thiersii*, WTU 9309 differs in glabrous–shining stipe (minutely velutinous in *Ma. thiersii*), and absence of diverticulate hyphae (present in *Ma. thiersii*). WTU 9309 is a *Micromphale*, *Ma. thiersii* belongs in *Marasmius* sect. *Androsacei*.

Although basidiospores have not been observed (in both specimens examined), basidiospores in this clade are quite uniform, and the organism's identification is not dependent on these statistics.

Specimens examined. **Oregon**, Clackamas Co., road to Mt. Hood at 2–3 mi post, 25.VI.1995, coll MT Seidl, J Roger, N Weber (as *Marasmius androsaceus*), MTS 4078 (WTU-F-8919); **Washington**, Snowhomish Co., Hwy 92, Perry Creek Trail, 24.VI.1993, coll GR Walker (as *Micromphale perforans*), GRM 410 (WTU-F-9309).

5. *Gymnopus perforans* (Hoffm.) Antonín & Noordeloos. 2008. Czech mycol. 60(1): 25.

Basionym. *Agaricus perforans* Hoffm.: S.F. Gray. 1821. Nat. Arr. Brit. Pl. 1: 622.

≡ *Agaricus perforans* Hoffm.: Fr. 1821. Syst. Mycol. 1: 138.

≡ *Micromphale perforans* (Hoffm.: Fr.) S.F. Gray. 1821. Nat. Arrang. Brit. Plants 1: 622.

≡ *Marasmius perforans* (Hoffm.: Fr.) Fr. 1838. Epicric. 385.

≡ *Androsaceus perforans* (Hoffm.: Fr.) Patouillard. 1887. Hymen. Eur.: 105.

≡ *Marasmiellus perforans* (Hoffm.: Fr.) Antonín & Noordeloos. 1997. Mycotaxon 63: 366.

Neotype (fide Antonín & Noordeloos, 1997): Sweden, Medelpad, Borgsjö, Granbodsos, 31.VIII.1993, M.E. Noordeloos 93137 (L).

Diagnosis. 1) Fruiting habit on conifer needles, chiefly *Picea*; 2) pileipellis and subpellis involved in thin mucoid matrix; 3) stipe barbed–vestured at least in lower half; 4) pileipellis lacking diverticulate hyphae and/or broom cells; 5) clamp connections ubiquitous; 6) cheilocystidia rare, broadly saccate to utriform; 7) lamellae few, reduced.

The following description is a rearrangement of that by Antonín & Noordeloos (2010) supplemented with current observations.

Description. **Basidiomata** (Fig. 32A) marasmioid. **Pileus** 5–13(–20) mm broad, plano–convex or subconcave, usually with small papilla, often with shallow central depression, sometimes faintly sulcate, hygrophanous, glabrous to matt, pallid brown to light brown (“wood brown” 7C4, “drab” 6D3, “buffy brown” 6C–D3–4) fading

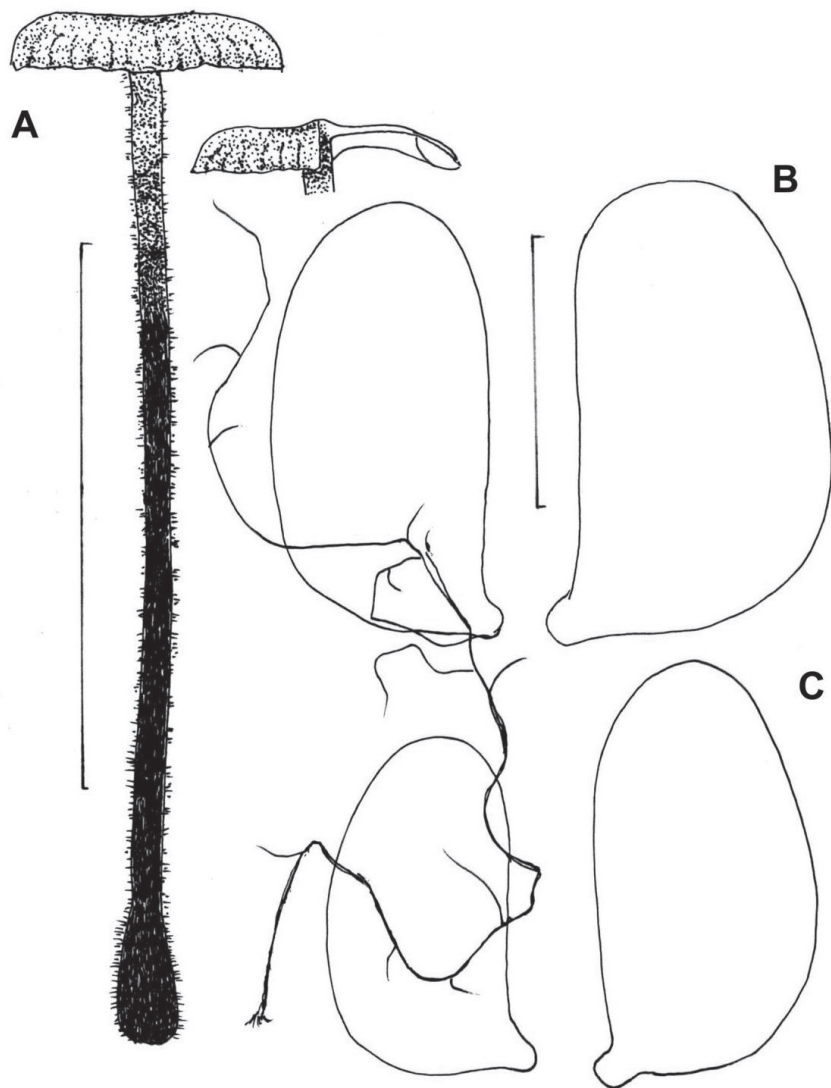


Figure 32. *Gymnopus perforans*. Basidiomata and basidiospores. **A** Basidioma and rhizomorph **B, C** Basidiospores. Standard bars: **A** = 10 mm; **B, C** = 5 µm. **A, B** TFB 7272 (TENN-F-53624). **C** TFB 7477 (TENN-F-53579).

to pallid white in age. **Lamellae** rather distant, free, adnexed to narrowly adnate, with no anastomosis or interveining, subarcuate, total lamellae = 13–19, through lamellae = 1–3, segmentiform, 1–3 mm broad, pale pinkish brown, with concolorous or slightly paler, pastel off-white to pallid brownish orange (“drab” 6C4) in age; edge entire. **Stipe** 15–40 × 0.5–1 mm, insititious, cylindrical, rarely compressed, stiff, filiform, finely sulcate lengthwise, vested, at apex concolorous with pileus to “deep olive buff” 5B3, in lower parts dark brown (“Brussels brown” 6E5–6) to black, when mature often



Figure 33. *Gymnopus perforans*. Pileipellis structures. **A–D** Pileal hairs **E** Repent hypha showing clamp connection. Standard bars = 10 μ m. TFB 7477 (TENN-F-53579).

entirely black; vesture very sparse upward, setose only downward toward very base, which is usually densely hispid. **Rhizomorphs** (Fig. 32A) abundant, $\sim 20 \times 0.4\text{--}0.6$ mm, tapering gradually to <0.2 mm broad, very curly, frequently branched, obviously

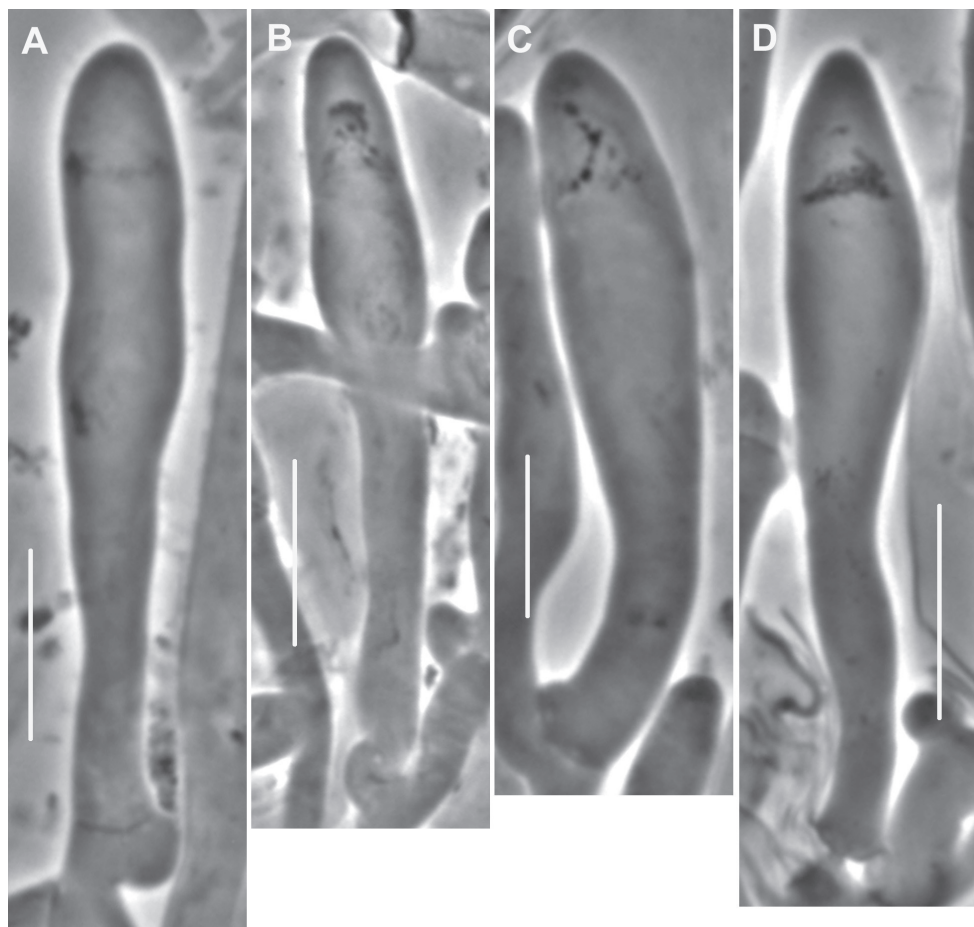


Figure 34. *Gymnopus perforans*. Pleurocystidia. Standard bars: **A** = 10 mm; **B** = 5 μ m. TFB 7272 (TENN-F-53624).

binding adjacent needles and bits of debris, black, glabrous–shining. **Odor** fetid, like rotten cabbage; **taste** “mildly unpleasant,” often tardily alliaceous.

Habitat and phenology. In large troops on fallen needles of *Picea*, rarely also *Pinus* and/or *Abies*, in humus-rich, coniferous plantations; widespread over Europe and Scandinavia (perhaps also in Asia); July to November.

Pileipellis embedded in hyaline slime matrix, a thin ixocutis, composed of the following elements: 1) pileal hairs (Fig. 33A–D) $120 \times 3\text{--}4.5$ μ m, common, erect, thin-walled, conspicuously clamped, equal to slightly tapering distally and then with somewhat inflated apex; 2) repent hyphae $3\text{--}8.5$ μ m diam (Fig. 33E), smooth, turgid on pileus surface, compactly interwoven, thin- to firm-walled (not thick-walled), conspicuously clamped; and 3) similar hyphae, occasionally delicately encrusted in stripes with minimal profile calluses. **Pleurocystidia** (Fig. 34, 36A) $35\text{--}42 \times 7\text{--}8$ μ m, fusiform, rounded at apex (seldom acutely so), conspicuously clamped. Basidi-

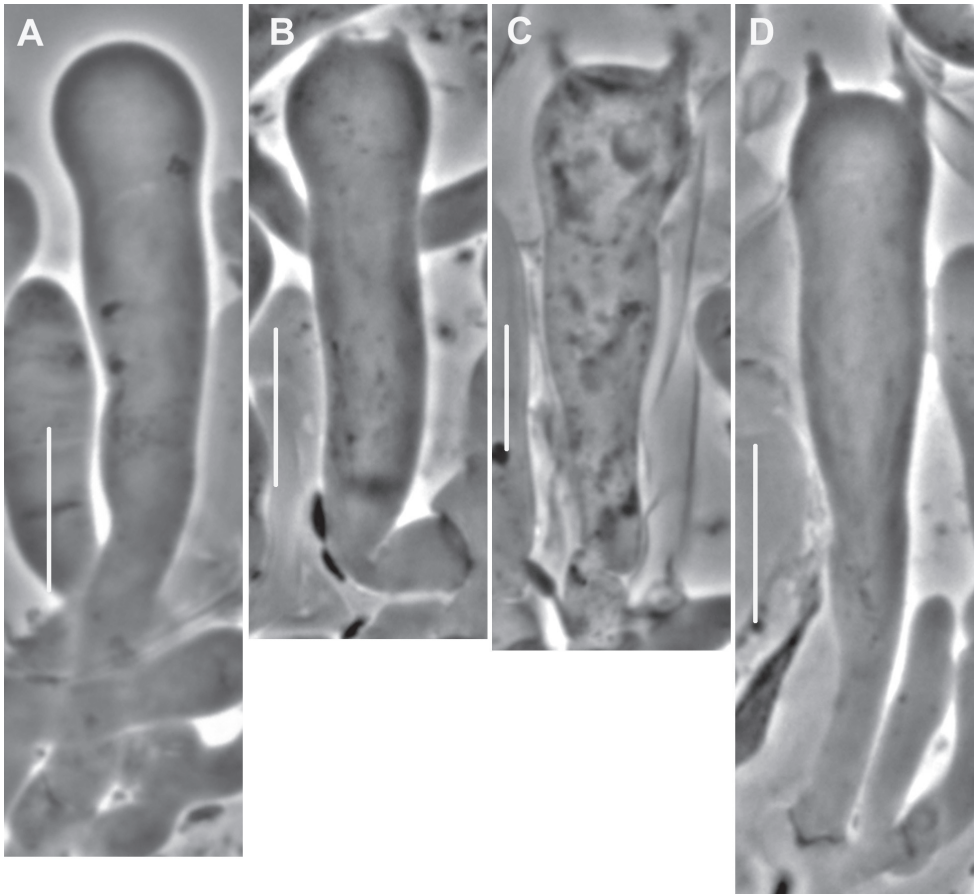


Figure 35. *Gymnopus perforans*. Basidiole and basidia. **A** Basidiole **B–D** Basidia. Standard bars: **A** = 10 mm; **B** = 5 μm . TFB 7272 (TENN-F-53624).

oles (Fig. 35A) clavate; **basidia** (Figs 35B–D; 36B) $(-25)36-45 \times 9-11 \mu\text{m}$, clavate, often subcapitulate, (2–)4-sterigmate, conspicuously clamped. **Basidiospores** (Fig. 32B, C) $(5.5-6.5-8.5(-9.5) \times (3.5-4-5 \mu\text{m})$ ($Q = 1.50-2.57$; $Q^m = 1.95$; $L^m = 8.10 \mu\text{m}$), ellipsoid to narrowly pip-shaped, slightly tapered proximally, thin-walled, smooth, inamyloid. Lamellar edge heterogeneous. **Cheilocystidia** (Fig. 33C–M) locally abundant, $30-41 \times 10-29 \mu\text{m}$, short- to long-stalked (stalk $3-10 \times 3-4.5 \mu\text{m}$, obscurely clamped), ventricose–rostrate, utriform to broadly, usually irregularly saccate to nearly globose, often with small pustulate outgrowths, significantly larger than pleurocystidia or basidia, thin-walled, hyaline; contents heterogeneous. **Stipe medullary hyphae** $2-9 \mu\text{m}$ diam, hyaline, strictly parallel, adherent in a slime matrix, conspicuously clamped, thick-walled (wall $\sim 1.0 \mu\text{m}$ thick, irregular on inner wall). **Stipe cortical hyphae** $4-7 \mu\text{m}$ diam, yellow–brown (PhC), strictly parallel, thick-walled (wall $\sim 2.0 \mu\text{m}$ thick), exteriorly smooth, vaguely dextrinoid (reddish brown in IKI, BF). Stipe vesture from near stipe apex composed of two elements: 1)

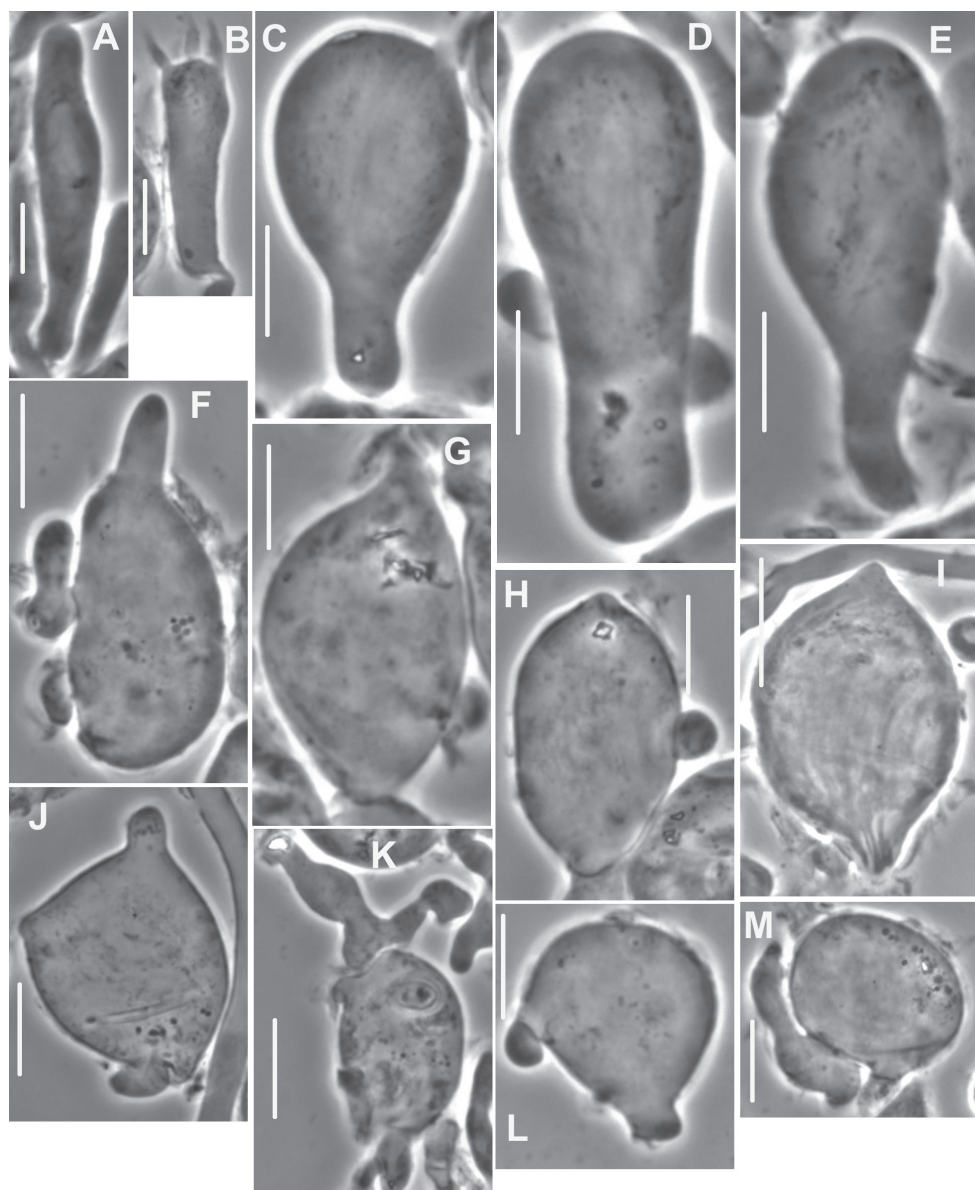


Figure 36. *Gymnopus perforans*. Hymenial structures. **A** Pleurocystidium **B** Basidium **C–M** Cheilocystidia. TFB 7272 (TENN-F-53624).

broad, scattered, thick-walled caulocystidia as described below; and 2) long, flexuous, thin-walled “hairs” $140 \times 1.3\text{--}3\text{ }\mu\text{m}$ diam, apparently thin- to firm-walled, arising from clamp connections (not as side branches), hyaline. **Caulocystidia** (Fig. 37) from lower stipe $90\text{--}140 \times 4\text{--}8.5\text{--}13\text{ }\mu\text{m}$, arising as side branches of stipe cortex surface cells, thick-walled (wall $\sim 2\text{ }\mu\text{m}$ thick, hyaline), erect, setoid, densely

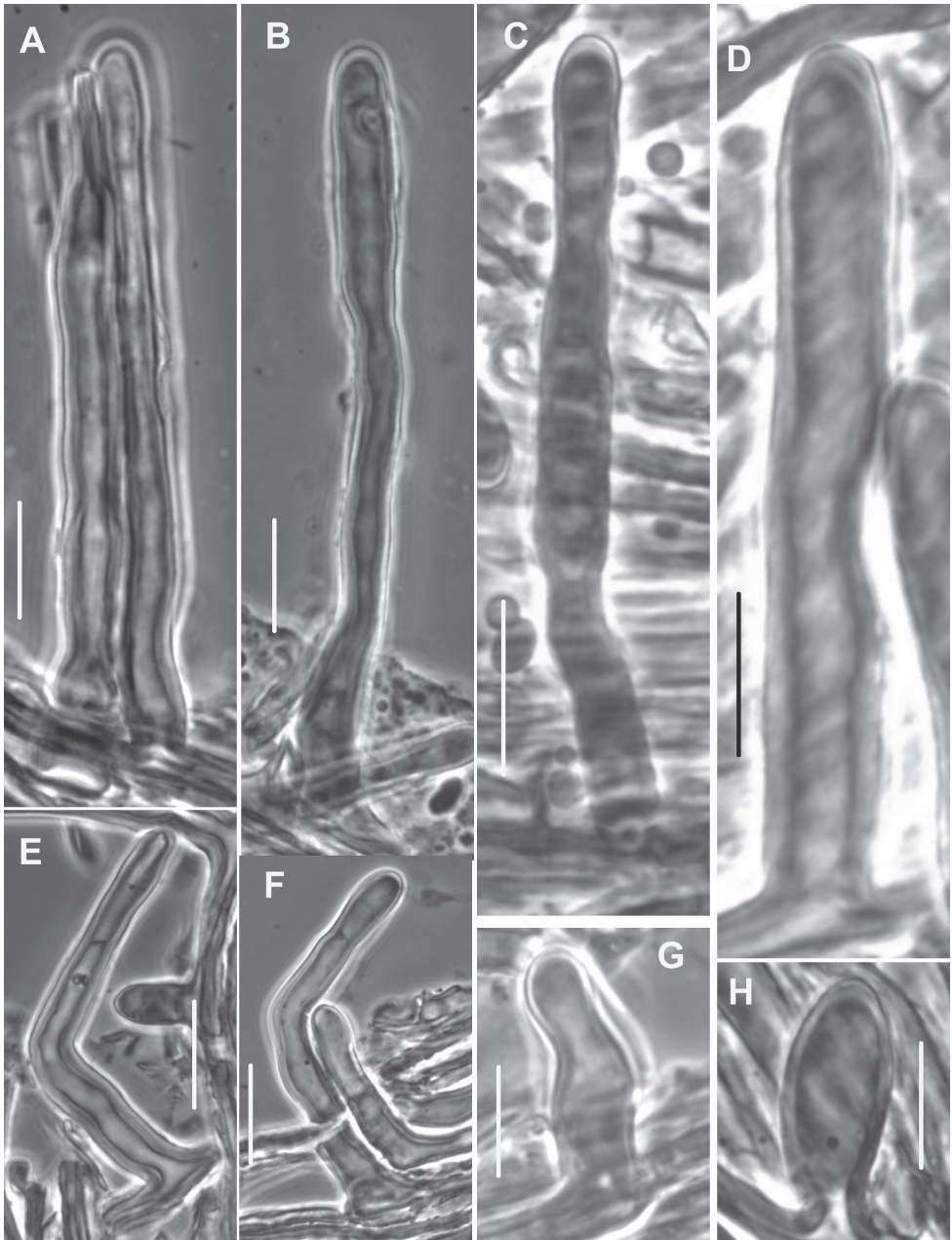


Figure 37. *Gymnopus perforans*. Caulocystidia. **A–F** Full-size setoid caulocystidia **G, H** Small individual caulocystidia. Standard bars = 10 μm. TFB 7477 (TENN-F-53579).

scattered, often in narrow clumps of 2–4 (appearing hispid at 30×), obscurely vacuolated, often internally secondarily septate, moderately dextrinoid (reddish brown in IKI, BF, especially reddish apically).

Commentary. In a paper reporting on North American members of *Gymnopus* sect. *Perforantia*, inclusion of European *G. perforans* could be seen as counterintuitive, but not only is the European entity the name-bringer, but recognition that the North American collections are molecularly separable from the European necessitates a description of the European fungus, as above. As discussed also under *G. sequoiae*, the *G. perforans* complex seems composed of subclades with minimal base-pair percent separation. Such is the case with “European *G. perforans*”, which is separated from sequences from eastern North America by 1.65% bp divergence. Studies by Hughes et al. (2009) and others have shown that, in general, separation at species rank might be expected to be at least 3%. Using this standard, eastern North American collections do not warrant species rank. For this reason, we choose to propose the eastern North American collections at subspecies rank (see below under *G. perforans* subsp. *transatlanticus*).

Specimens examined. **Finland**, Etelä-Häme Prov., Lammi, Evo, Kotinen Virgin Forest, northwest part, 13.IX.1994, coll RHP, TFB 7477 (TENN-F-53579). **Russia**, Leningrad Oblast, Nizhne-Svirskiye Reserve, vic Kovkenitsky, N60°41.691', E33°17.965', 30.VIII.1999, coll N.

Psurtseva, TFB 10826 (TENN-F-58295); same location, N60°36.766', E33°3.482', 29.VIII.1999, coll. RHP, TFB 10643 (TENN-F-58251); Novgorod Reg., Valdai Dist. “Red Hill,” Kasnaya Gorka, N58°06'37", E33°13'07", 21.VIII.2003, coll. RHP, TFB 11629 (TENN-F-59592). **SWEDEN**, Trollhättan, vic Trollhättan, N58°17'01", E12°17'15", 22.IX.1991, coll SA Gordon, TFB 4721 (TENN-F-50318); same location, N58°17'01", E12°17'15", 22.IX.1991, coll SA Gordon, TFB 4722 (TENN-F-50319); Uppland, vic. Uppsala, Gottsundabergen, N59°48'27", E17°37'24", 7.IX.1994, coll. S-G. Ryman, TFB 7272 (TENN-F-53624).

5A. *Gymnopus perforans* subsp. *transatlanticus* R.H. Petersen, subsp. nov.
Mycobank no. 552489

Holotype. **Canada, Quebec**, Quebec-Montmorency Co., vic. Beauport, “Camping Municipal de Beauport,” 46°54.022'N, 71°10.507'W, 29.VII.2006, coll E. Lickey, TFB 13319 (TENN-F-61587).

Etymology. trans- = Latin, on the other side of; -atlanticus = Atlantic Ocean. Referring to distribution across the Atlantic Ocean from the typical subspecies.

Diagnosis. Differing from typical subspecies as follows: 1) basidiomata diminutive, generally shorter and slenderer; 2) spores, pleurocystidia, basidia smaller than typical; 3) cheilocystidia infrequent, smaller and less differentiated; 4) fruiting on fallen *Picea*, *Abies* and *Tsuga* needles; 5) separable by ITS sequence from European *G. perforans*.

Description. **Basidiomata** (Figs 38, 39A) diminutive, marasmiod, often in troops, usually attached to individual conifer needles. **Pileus** 3–14 mm broad, strongly convex early, expanding to plano-convex, often with somewhat depressed disc, some-



Figure 38. *Gymnopus perforans* subsp. *transatlanticus*. Basidiomata. Standard bars = 10 mm.

times with small conical umbo, matt to minutely pruinose (especially near margin), occasionally sulcate-striate but usually not so; disc “syal brown” 6C5, “tawny” 6C6, “ochraceous tawny” 6C5–6, “tawny olive” 6D5–6, “light ochraceous buff” 5A4, “army brown” 8D5, “tilleul buff” 7B2, paler and nearer to “pale ochraceous buff” 4A2, “light ochraceous buff” 5A4, occasionally yellowish near “antimony yellow” 4B6; limb and margin “pale cinnamon pink” 5A2, “pinkish buff” 6A2, “pale pinkish buff” 6A2 near “tilleul buff” 5B3, “pale olive buff” 3B2 to off-white, fading gradually through maturity, finally often off-white overall; context relatively thick on the disc, elsewhere thin and membranous. **Lamellae** adnate to subdecurrent, distant, arcuate (not ventricose), occasionally forked but with no anastomosis or interveining, with or without pseudocollarium, thickish, narrow (usually less than 1 mm broad), total lamellae 17–23, through lamellae 8–11, often concolorous with pileus, “pinkish buff” 5A3,

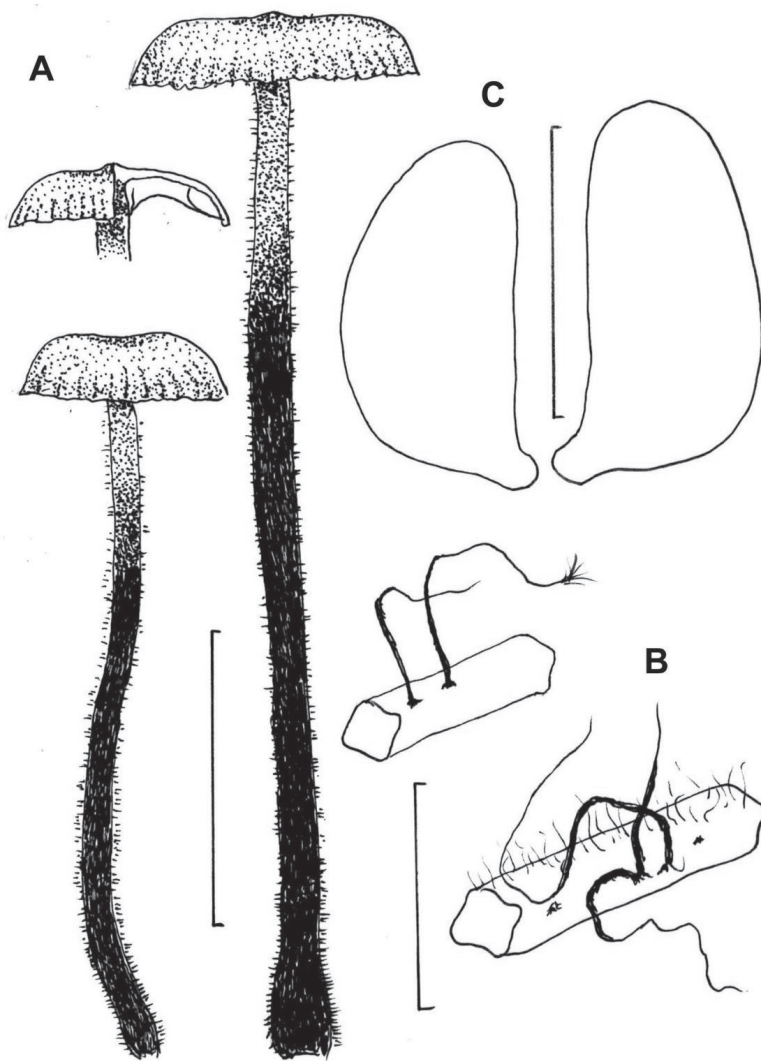


Figure 39. *Gymnopus perforans* subsp. *transatlanticus*. **A** Basidiomata **B** Rhizomorphs **C** Basidiospores. Standard bars: **A** = 10 mm; **B** = 2 mm; **C** = 5 μ m.

“pale pinkish cinnamon” 6A2, “light buff” 3A2, “vinaceous buff” 9B2, “light ochraceous buff” 5A4, “tulle buff” 7B2, after storage often exhibiting a slight blush of cantaloupe (“warm buff” 3A4 to “orange buff” 3A5) as necropigment; lamellar edge entire, not marginate; lamellulae in one rank, poorly developed. **Stipe** (10–)12–28 \times 0.3–1 mm, in two breadth classes (0.3–0.7 mm vs 0.8–1 mm broad, with the latter not always part of collection) but not in length, terete when fresh, ridged and compressed when dry, subinsititious, apex concolorous with lamellae (darker within

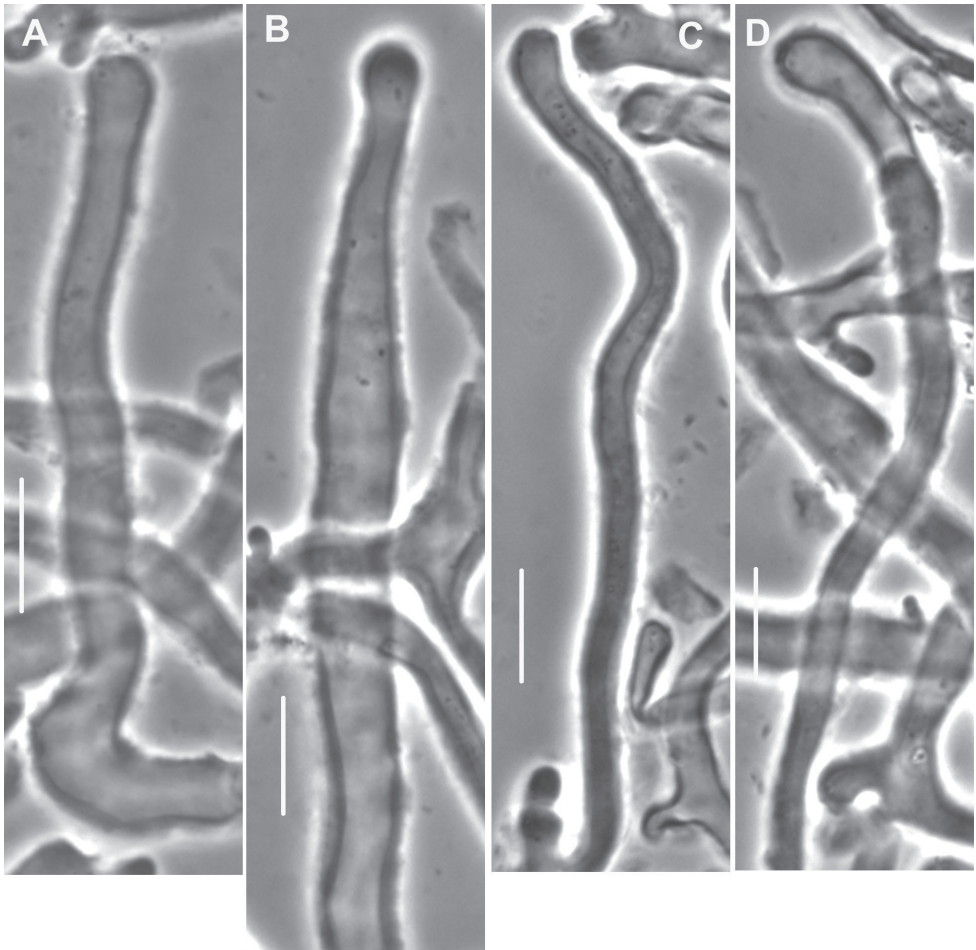


Figure 40. *Gymnopus perforans* subsp. *transatlanticus*. Pileal hairs. Standard bars = 10 μ m. TENN-F-29277.

pileus), a dull reddish brown (near “russet” 7D6), downward soon “mummy brown” 6F8, “bone brown” 7F8, “soot black” 11F3, “chaetura black” 2F3 to visually black, vested overall (minutely barbed); apical vestiture hyaline (appearing white), wispy, downward gathered into minute synnemata and thus appearing barbed, dark brown; surface sometimes bearing small elliptical scars with fimbriate borders, and rarely with rudimentary, acute-tipped rhizomorphs <1 mm long; base subinsititious (with delicate thatch of spikes). **Rhizomorphs** (Fig. 39B) of two types: 1) $-4 \times 0.2-0.7$ mm, black, typically curly and branched, often with numerous individuals arising from a single needle, coarse for their length, extensively colonizing the undersides of needles; and 2) $-0.5 \times 0.05-0.1$ mm, black, extremely fine, unbranched, often densely gregarious. **Odor** negligible to fetid (occasionally weakly alliaceous): **taste** moderately alliaceous.



Figure 41. *Gymnopus perforans* subsp. *transatlanticus*. Pileipellis elements. **A** Slender hyphae with thin slime sheath and vague incrustation **B** Stouter hypha with conspicuous clamp connections **C, D** Pileipellis hyphae with secondary septa **B–D** Note multigranular gelatino-mucoid matrix. Standard bars = 10 µm. AV 11.06.11.

Habitat and phenology. Fruiting in troops on individual dead conifer needles, chiefly *Picea*, *Tsuga* and *Abies* (*Abies amabilis*, *Abies balsamea*, *Abies fraseri*, *Picea glauca*, *Picea rubens*, *Tsuga canadensis*, *Tsuga heterophylla* and other conifer needles; from high-altitude spruce/fir “islands” of southern Appalachian Mountains to Canadian Shield. (for forms fruiting on dead deciduous leaves, see under *G. foliiphilus*); late spring (June, southern habitats) to mid-Autumn (September).

Pileipellis involved in a slime matrix with much minute debris, composed of the following elements; 1) pileal hairs (Fig. 40) –80 × 4–7 µm diam, erect hyphal tips, often arising in juxtaposition to a clamp connection, embedded in slime matrix, often sub-capitulate; and 2) repent hyphae (Fig. 41A, B) 3.5–10 µm diam, firm-walled, mostly smooth, occasionally encrusted with small scabs with raised profile calluses, conspicuously clamped but with common secondary septa (Fig. 41C, D), subhyaline individu-

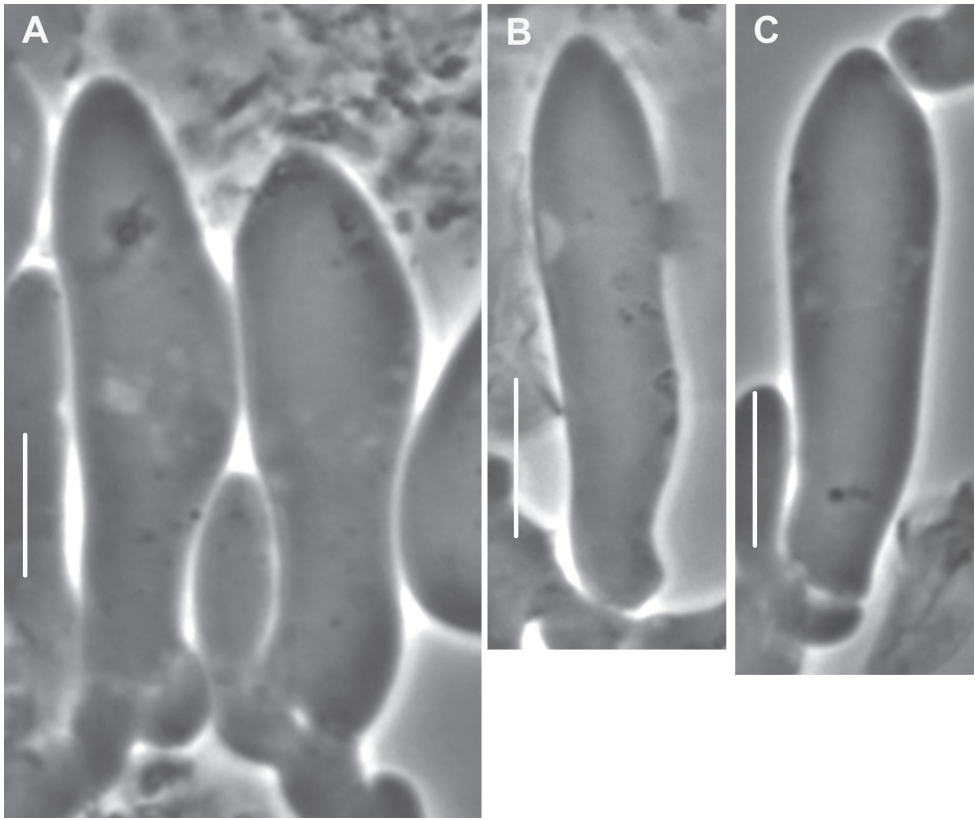


Figure 42. *Gymnopus perforans* subsp. *transatlanticus*. Pleurocystidia. Standard bars = 10 μ m. AV 11.06.11.

ally. Pileus trama hyphae loosely interwoven, involved in a slime matrix, conspicuously clamped; lamellar trama loosely interwoven, involved in slime sheaths; hyphae 3–5 μ m diam, firm-walled but wall swelling to 1 μ m thick, conspicuously clamped. **Pleurocystidia** (Figs 42, 43) 22–32 \times 5–9 μ m, fusiform, narrowly fusiform, to irregularly and asymmetrically so with rounded to acute apex, conspicuously clamped, often easily disarticulated; contents distinctly partitioned (Fig. 43) to not so (Fig. 42). Basidioles clavate; **basidia** (Figs 44, 45A) 20–29 \times 5–10 μ m, clavate to subcapitulate, 4-sterigmate, conspicuously clamped; contents heterogeneous; effete basidia and pleurocystidia commonly evacuated but not collapsing (“husking”); subbasidial cells lobate by proliferating clamp connections. **Basidiospores** (Fig. 39C) (6–)6.5–9 \times 3–4.5 μ m ($Q = 1.56$ –2.50; $Q^m = 1.86$; $L^m = 7.13$ μ m). ellipsoid, marasmiod, thin-walled, smooth, inamyloid. **Cheilocystidia** (Fig. 45B–H) absent or widely scattered, 25–48(–50) \times 8–19(–23) μ m, broadly clavate, obpyriform, occasionally irregularly lobed, without setulae, firm- to thick-walled (wall 0.7 μ m thick, hyaline), sometimes easily disarticulated, subrefringent (PhC), obscurely clamped, only occasionally extending beyond hymenial structures; contents homogenous to heterogeneous (with several globose inclusions; PhC), occasionally with one or more small refractive guttules. **Caulocystidia**

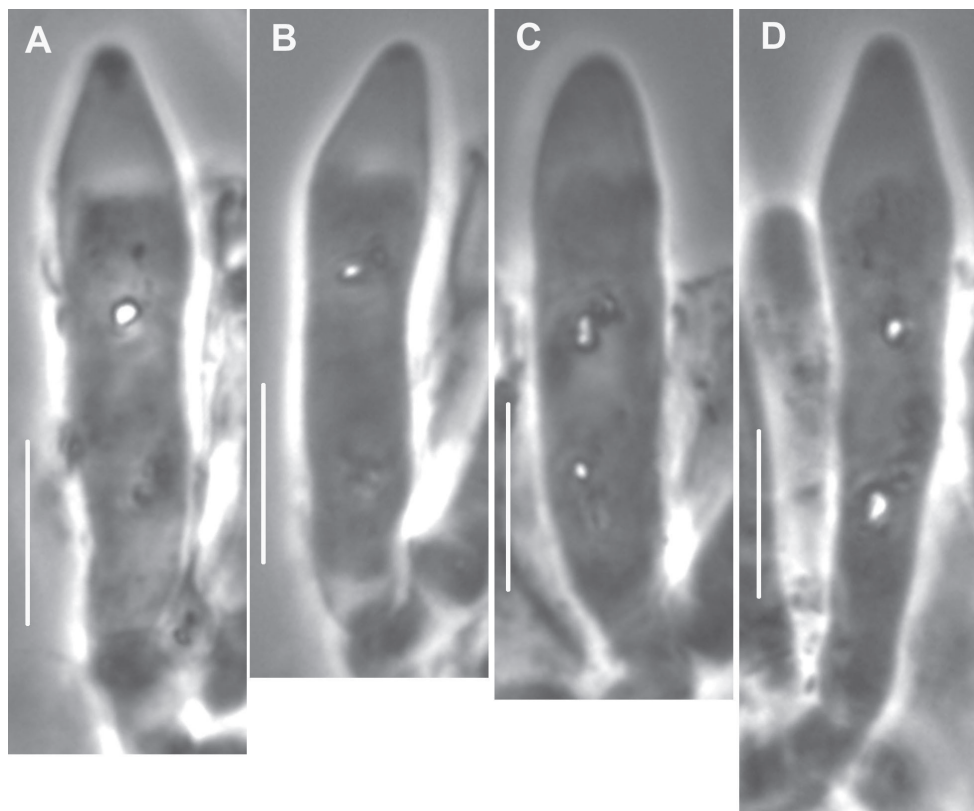


Figure 43. *Gymnopus perforans* subsp. *transatlanticus*. Pleurocystidia. Note conspicuously partitioned contents. Standard bars = 10 μ m. TENN-F-29277.

from stipe apex $50 \times 6\text{--}9\text{ }\mu\text{m}$, arising as side branches of surface hypha, thick-walled (wall $\sim 2\text{ }\mu\text{m}$ thick), refringent, hyaline, often secondarily septate. **Caulocystidia from lower stipe** (Fig. 46) $180 \times 8\text{--}11\text{ }\mu\text{m}$, arising as side branches of stipe surface hypha; basal cell usually swollen somewhat, deep brownish yellow (PhC), producing a thick-walled (wall $1\text{--}1.5\text{ }\mu\text{m}$ thick) shaft, gradually tapered distally, often constricted within and occasionally with small side lobe, doubtfully secondarily septate, brittle (although usually not straight); pigmentation equally distributed throughout shaft (not congested apically).

Commentary. Based on direct comparison between European and northeastern North American specimens, basidiomatal dimensions seem to differ. American basidiomata are, in general, shorter with smaller pilei than European basidiomata, but basidiomata of the American collections seem distributed in two size classes, the larger and more robust of which are commensurate with European basidiomata.

A limited phylogenetic tree based on ITS sequences (see Fig. 87 below), sequences from northeastern North American collections clearly form a clade separate from sequences from Europe (including Scandinavia). Base-pair separation between these two

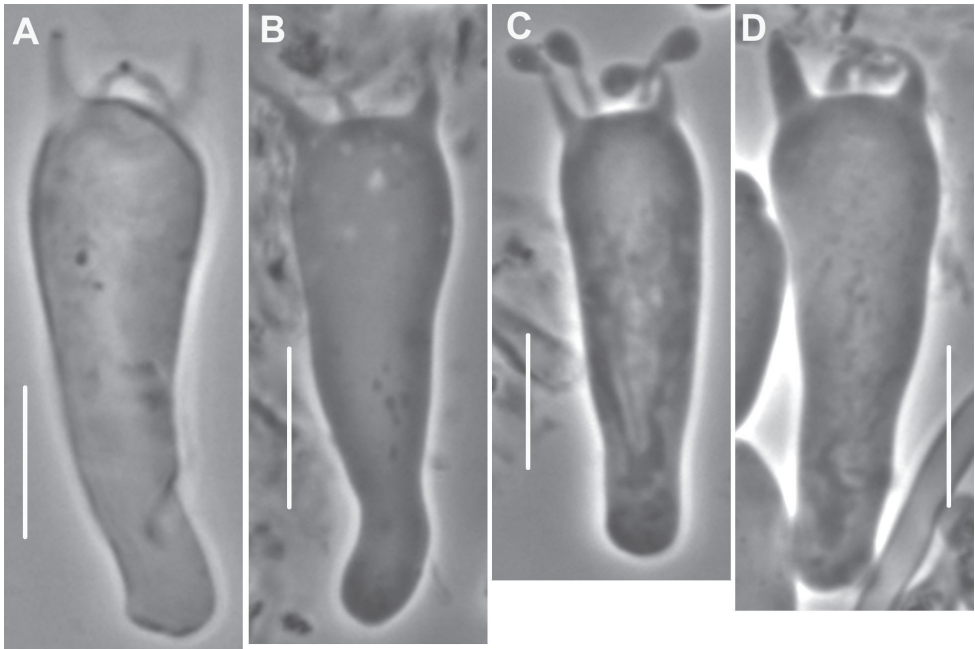


Figure 44. *Gymnopus perforans* subsp. *transatlanticus*. Basidia. Standard bars = 10 µm. AV 11.06.11.

clades is 1.65%. Although heterogeneous, base-pair separation among northeastern North American sequences is 0.71%. Altogether, collections from Europe and North America are not considered to represent species-rank separation, but proposal of a subspecies seems warranted. Separation of all *G. perforans* sequences from a clade containing *G. sublaccatus* and *G. sequoiae* is more robust (2.30% see Fig. 87 below) but both *G. sequoiae* and *G. sublaccatus* fall within North American *G. perforans*. For more on this situation, see discussion under *G. perforans*.

In eastern North America, characters which separate *G. foliophilus* fruiting on dead deciduous leaves, from *G. perforans* subsp. *transatlanticus* fruiting on conifer needles: 1) *G. foliophilus* exhibits stipe vestiture between villose and barbed, but *G. perforans* subsp. *transatlanticus* is distinctly spiked/barbed; 2) pileal hairs in *G. foliophilus* are stouter than those of *G. perforans* subsp. *transatlanticus*, and secondarily septate (this may be an artifact); and 3) pileus surface hyphae of *G. foliophilus* are often encrusted in small scabs, while those of *G. perforans* subsp. *transatlanticus* are generally smooth.

In examining numerous specimens eventually accepted as *G. perforans* subsp. *tansatlanticus*, it was unforeseen that a large number of specimens originally fruited on dead *Tsuga* needles, a host reported as rare by Antonín and Noordeloos (2010), although this is the case in Europe. Tolerance of this substrate affords the opportunity to subsist at lower elevations (and therefore at higher temperatures) in the southern Appalachian Mountains where spruce/fir forests exist only at the highest elevations

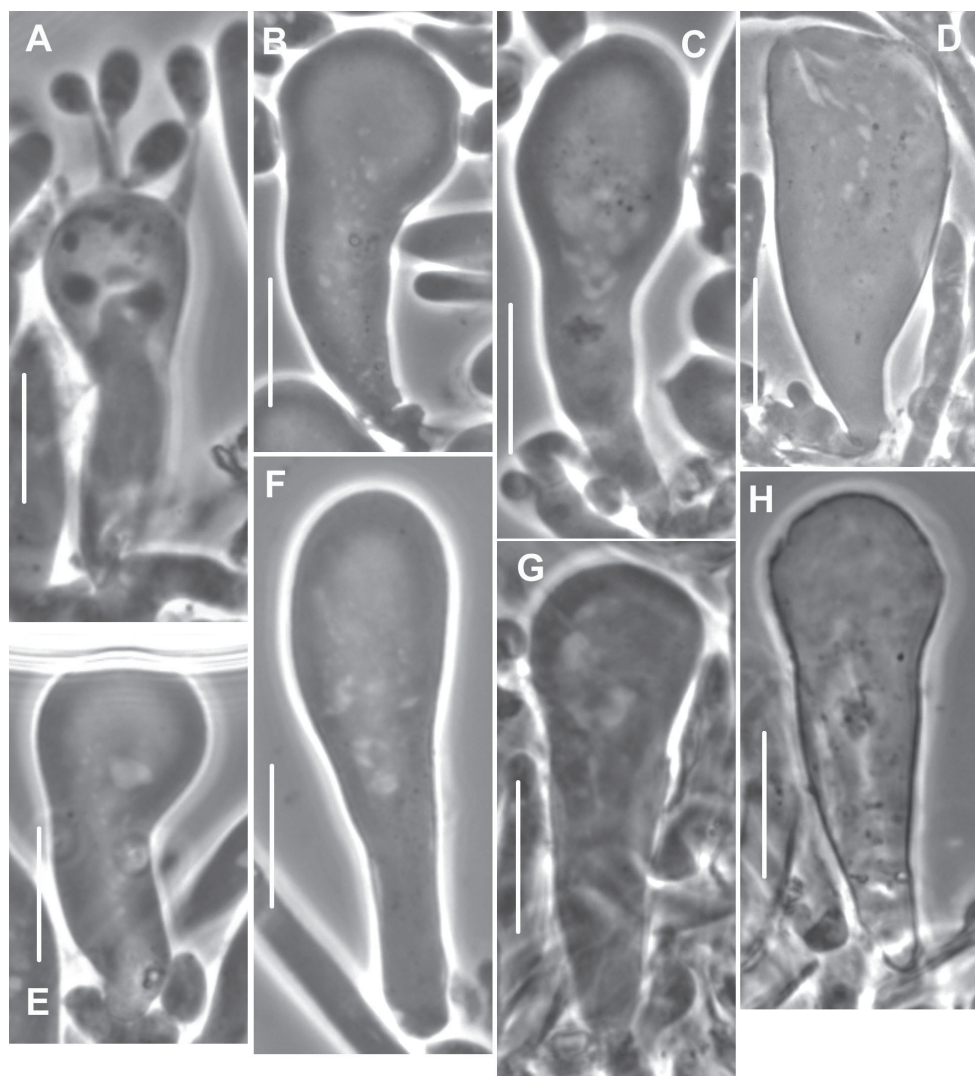


Figure 45. *Gymnopus perforans* subsp. *transatlanticus*. **A** Basidium **B–H** Cheilocystidia. Standard bars = 10 μ m. TFB 14395 (TENN-F-69056).

(and therefore the coldest temperatures). In the future, it will be interesting to see if this condition extends across North America to the Pacific Northwest, where the species of spruce, fir, and hemlock are all different from eastern North American taxa.

In *G. perforans* subsp. *transatlanticus*, cheilocystidia may be confused with inflated basidia and/or pleurocystidia. Some shapes of clearly swollen elements assumed to be cheilocystidia are suggestive of sterigmata (but always two – four were not seen), and occasional objects of cheilocystidial size are shaped like fat pleurocystidia

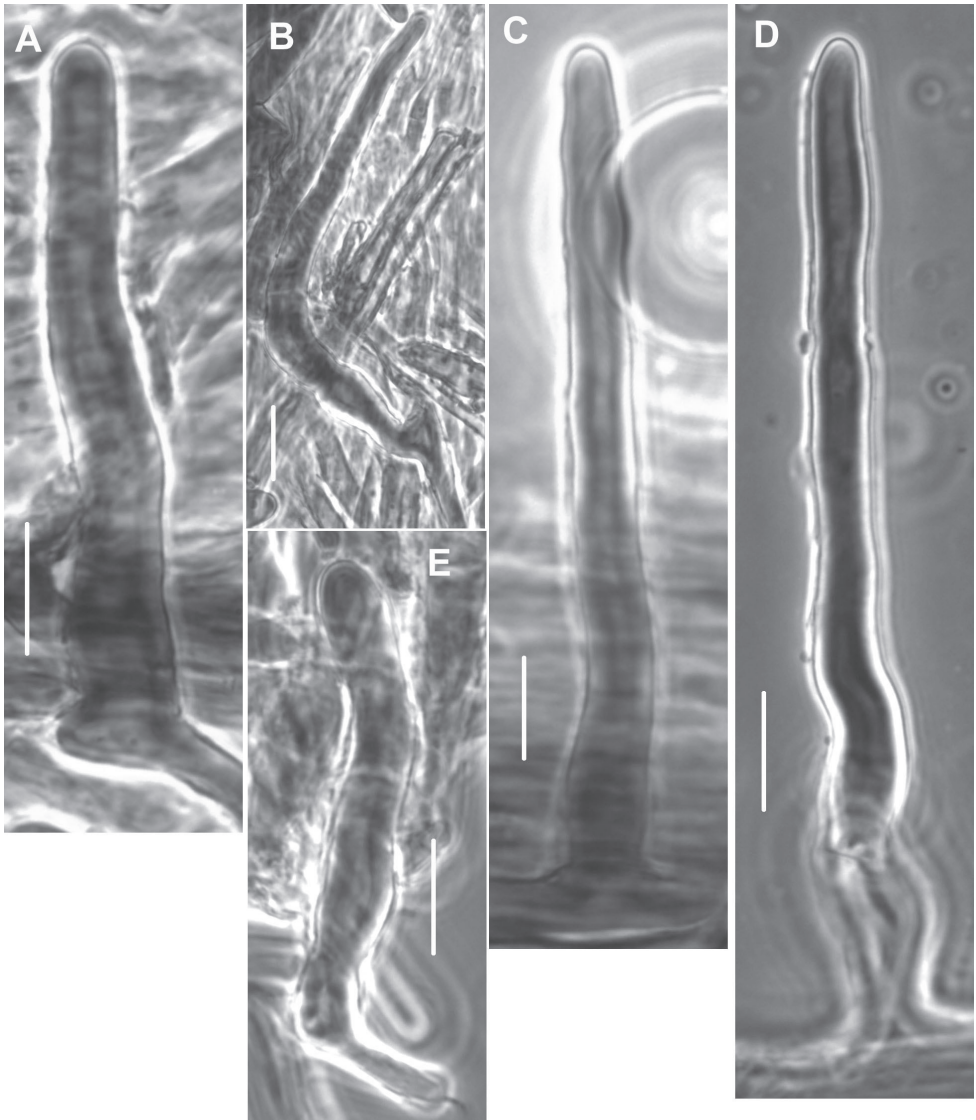


Figure 46. *Gymnopus perforans* subsp. *transatlanticus*. Caulocystidia. Standard bars = 10 μ m. TFB 14350 (TENN-F-69000).

(broadly fusiform). Repeated preparations from a single pileus also showed numerous cheilocystidia.

Rhizomorphs are here described as of two types. The coarser of these are present in virtually every specimen observed, while the extremely fine type were seen in perhaps 25% of the specimens. It can be doubted that the second type actually belong to subsp. *transatlanticus*, but without some proof, they must be described as present.

Specimens examined. **Canada, New Brunswick**, vic. Alma, Fundy Prov. Park, Maple Grove Back Road, N95°35.368', W64°59.013', 20.IX.2013, coll RHP, TFB 14377 (TENN-F-69042); same location East Branch Trail, N45°38.587', W65°06.937', 25.IX.2013, coll Gary Samuels, TFB 14392 (TENN-F-69056); same location, East Branch Trail, N45°38.587', W65°06.937', 25.IX.2013, coll Gary Samuels, TFB 14400 (TENN-F-69064); same location, East Branch Trail, N45°38.587', W65°06.937', 25.IX.2013, coll RHP, TFB 14395 (TENN-F-69056); **Newfoundland & Labrador**, Labrador, Benedict Mts., 31.VII.2010, coll A. Voitek (as *M. androsaceus*), AV10.07.31 AV03; Newfoundland, Codroy, Gillis Cabins, N47°52'55", W59°23'36", 11.VI.2011, coll A. Voitek (as *Mi. perforans*), AV 11.06.11AV01 (TENN-F-69046); Newfoundland, Gros Morne Nat. Park, Stuckless Pond, N49°25'55", W57°43'38", 18.IX.2010, coll A. Voitek, AV 10.09.18 AV 14; **Nova Scotia**, Wolfville, Acadia University nature trail, 1.VIII.1992, coll SA Gordon, TFB 5017 (TENN-F-51431); Cape Split area, 45°20'02" N, 64°30'02"W, 3.VIII.1992, coll S.A. Gordon, TFB 5029 (TENN-F-51440); **Quebec**, Quebec-Montmorency Co., vic. Beauport, "Camping Municipal de Beauport," 46°54.022'N, 71°10.507'W, 29.VII.2006, coll E. Lickey, TFB 13319 (TENN-F-61587; holotype). **United States, Connecticut**, Hartford Co., vic. Colchester, Salmon River State Forest, N41°36'46.77", W72°25'27.43", 31.VIII.2013, coll Sandy Scheine, TFB 14327 (TENN-F-68179); **New York**, Cortland Co., vic. Marathon, Hoxie Gorge Preserve, Lower Gorge Trail, N42°32.871', W76°4.707', 3.IX.2013, coll RHP, TFB 14348 (TENN-F-68198); Ulster Co., Frost Valley, Spring Ridge Trail, N41°50'20.7", W74°30'19.9", 9.IX.1989, coll SA Gordon, TFB 2146 (TENN-F-49764); same location, N41°50'20.7", W74°30'19.9", 9.IX.1989, coll SA Gordon, TFB 2151 (TENN-F-49782); **North Carolina**, Macon Co., vic. Franklin, Standing Indian Campground, 13.VI.1992, coll SA Gordon, TFB 4913 (TENN-F-51231); Highlands, 9.VII.1966, coll L.R. Hesler (as *Marasmius* sp.), TENN-F-29279; **Tennessee**, Blount Co., GSMNP, Indian Gap. Appalachian Trail toward Newfound Gap, near top of ridge, 30.VI.2006, coll RHP & KWH, TFB 13121 (TENN-F-61211); GSMNP, Cades Cove, N35°35', W83°50', 4.VIII.1962, coll & det L.R. Hesler (as *Marasmius* sp.), TENN-F-24923; Sevier Co., GSMNP, Spruce-fir Nature Trail, Clingman's Dome Rd., N35°34'40.5", W83°28'47.4", 21.VII.1989, coll SA Gordon, TFB 2114 (TENN-F-49259).

6. *Gymnopus pinophilus* R.H. Petersen, sp. nov.

Mycobank no. 552479

Holotype. **United States, North Carolina**, Macon Co., vic. Highlands, Blue Valley Campground, N35°00'45.23", W83°09'29.33", 11.VIII.2014, coll KWH, TFB 14511 (TENN-F-69206).

Etymology. pino- = referring to the genus *Pinus*; -phil = to love, referring to habitat on the needles of *Pinus*.

Diagnosis. 1) Fruiting habit on needles of *Pinus strobus* in eastern North America; 2) pileipellis structure including occasional diverticulate hyphae and broom cell-like hyphal termini; 3) cheilocystidia of the *siccus*-type; 4) basidiomata with long, slender stipes and small pilei; 5) stipe glabrous–shining; 6) rhizomorphs hair-like, black, independent of basidiomata.

Description. **Basidiomata** (Fig. 47) slender, with long stipe and small pileus. **Pileus** 3–9(–12) mm broad, convex becoming shallowly convex, sometimes centrally depressed, matt, pebbled, subtly sulcate–striate; disc “fawn color” 7C5, 6E7, “vinaceous fawn” 8B4, “ocher red” 9C6 to “brick red” 8D8, outward “avellaneous” 7B3, 6D4–6, “vinaceous fawn” 8B4, “vinaceous buff” 9B2 “buff pink” 7A4, drying nut brown (“tawny olive” 5C5). **Lamellae** adnexed to adnate, sometimes pseudocollariate (especially in drying), thickish, not ventricose, with little evidence of anastomosis, off-white to “tilleul buff” 7B2, 6C3–4; lamellulae always very short, hardly ventricose. **Stipe** 27–45(–60) × 0.4–1 mm, stiff, terete, equal, not vestured, glabrous and often shining, insititious, apically concolorous with lamellae (“tilleul buff” 7B2 to “army brown” 8D5), soon “clove brown” 6F5 to black and remaining so, stuffed; stipe medulla white. **Rhizomorphs** (Fig. 47) –18 × 0.2–0.3 mm, hair-like, curly, black, usually unbranched, arising separately from basidiomata. **Odor** negligible; **taste** negligible.

Habitat and phenology. Gregarious on dead needles of *Pinus strobus* in eastern North America; summer.

Pileipellis involved in a heterogeneous slime matrix, composed of the following elements: 1) repent hyphae radially oriented, 2.5–6 µm diam, firm- to thick-walled (wall –0.7 µm thick, hyaline), firm-walled with a very thin mucoid sheath, conspicuously clamped, weakly to strongly encrusted, with encrustation appearing as vague, subtle stripes or rings with flake-like profile calluses (Fig. 48A) (lying on the thin mucoid sheath); 2) repent hyphae 4–7.5 µm diam, with gelatinized wall (Fig. 48B) (wall –1.5 µm thick, with weak encrustation); 3) occasional repent hyphae 3.5–5.5 µm diam, firm-walled, clamped, diverticulate; diverticula 2–6 × 1–1.5 µm (Fig. 48C), usually dichotomous, not refringent; and 4) common broom cell-like cells, stalked, arbuscular (stalked without distal inflated portion), branched 1–2 times, surmounted by setulae; setulae digitate, often knobby, usually dichotomous, –6 × 1–1.5 µm, sometimes subrefringent (PhC); broom cell-like structures (Fig. 49) easily gelatinizing from base and often visible only as setulae (Fig. 49A,D). Pileus and lamellar tramae loosely interwoven, with heterogeneous slime matrix. Hymenophore (in KOH) involved in a heterogeneous mucoid matrix with copious debris (collapsed spores, bits of effete basidia, etc.). **Pleurocystidia** (Fig. 50A–D) 24–32 × 5.5–8 µm, fusiform, conspicuously clamped; contents homogeneous, often with poorly partitioned contents. Basidioles clavate; **basidia** (Fig. 50E–H) 23–31 × 5.5–7 µm, clavate, clamped, 4-sterigmate; contents multigranular. **Basidiospores** (Fig. 51) probably dimorphic: 1) (3.5–)4–6(–6.5) × (2.5–)3–4(–4.5) µm ($Q = 1.11–2.17$; $Q^m = 1.57$; $L^m = 5.15$ µm); 2) (5.0–)6–8(–8.5) × (2.5–)3–4.5 µm ($Q = 1.38–2.40$; $Q^m = 1.96$; $L^m = 7.19$ µm), broadly ellipsoid, subcylindric to elongate–lacryiform, hardly

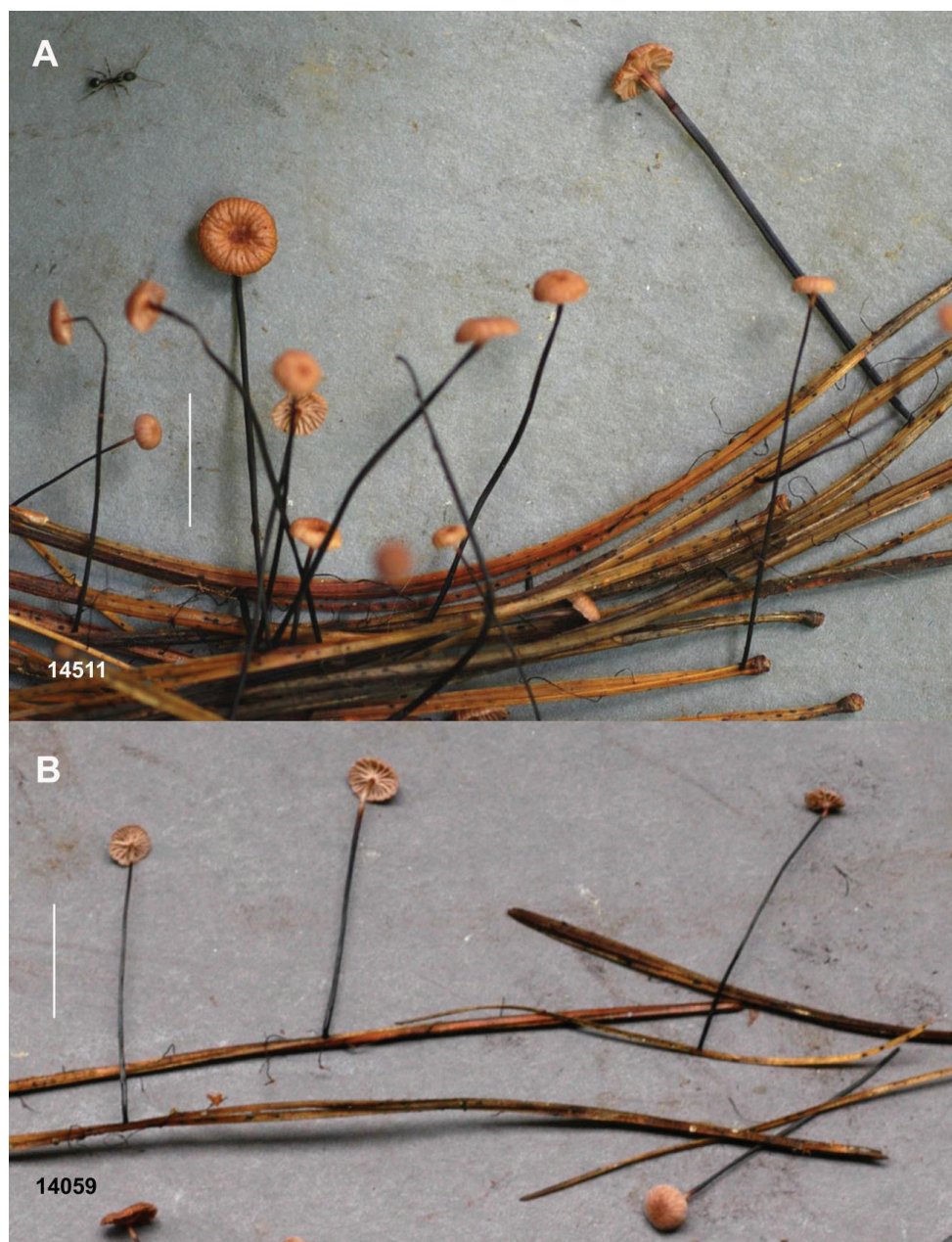


Figure 47. *Gymnopus pinophilus*. Basidiomata on needles of *Pinus strobus*. Standard bars = 20 mm. Above: TFB 14511. Below: TFB 14059 (TENN-F-67804).

flattened adaxially, thin-walled, smooth; contents homogeneous to a few scattered minute, refringent granules. Lamellar edge involved with heterogeneous mucoid matrix; **cheilocystidia** (Fig. 52) $20\text{--}34 \times 6\text{--}9 \mu\text{m}$, scattered to common, similar

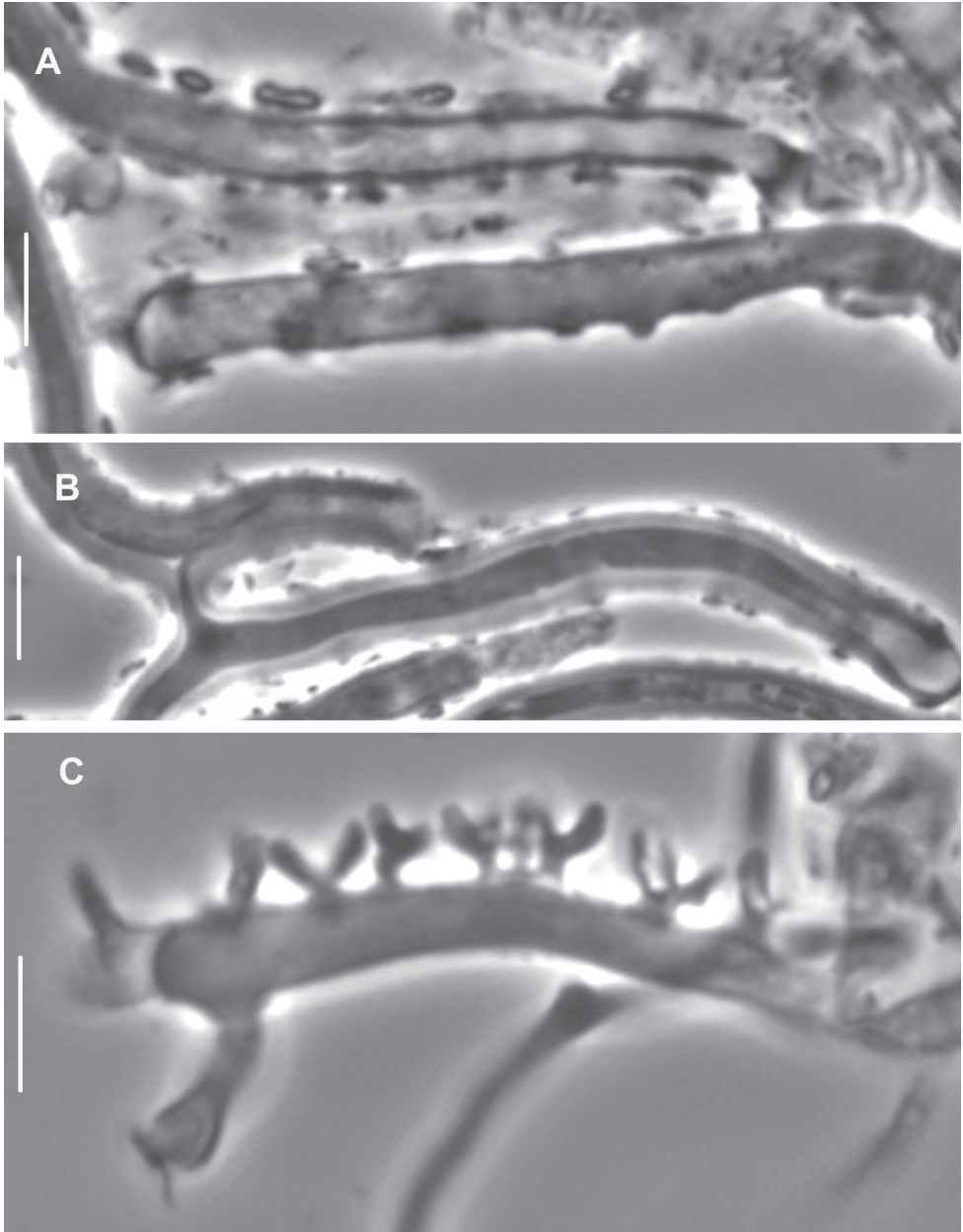


Figure 48. *Gymnopus pinophilus*. Pileipellis elements. **A** Encrusted hyphae showing crust material in slime sheath **B** Hyphae with gelatinized walls **C** Diverticulate hypha showing dichotomous diverticula. Standard bars = 10 μ m. DED 4491 (TENN-F-54665).

to pileipellis element, broom cell-like, easily gelatinizing, stalked (stalk 2.5–3 μ m diam), arbuscular, terminating in a very complex tuft of setulae; setulae $-8 \times 1-1.5$ μ m broad), refringent (PhC), digitate, often dichotomous. Outer **stipe medullary**

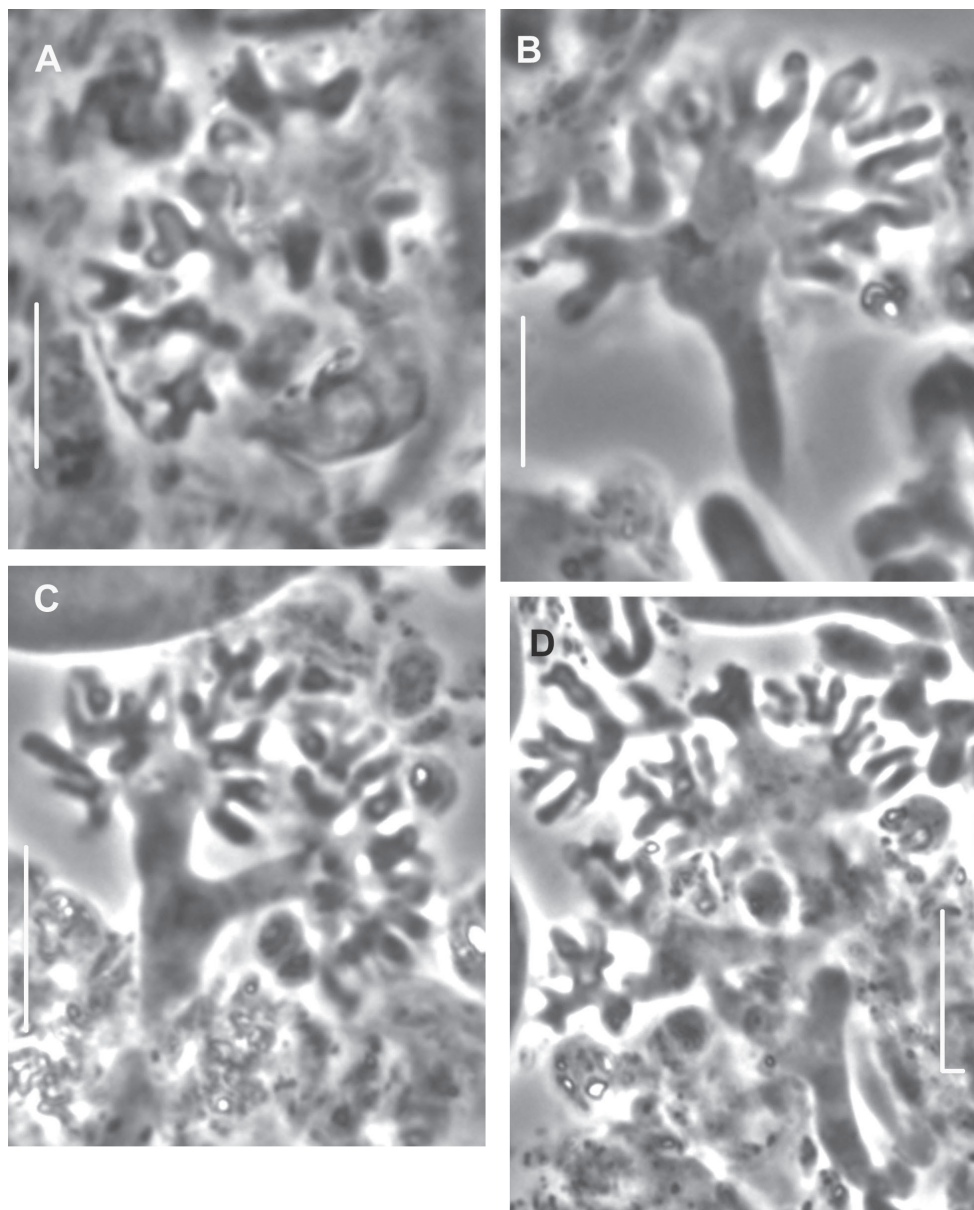


Figure 49. *Gymnopus pinophilus*. Broom cell-like hyphal termini of pileipellis. **A** Diverticula in slime matrix **B, C** Individual elements **D** Gelatinizing broom cell-like termini. Standard bars = 10 μm . DED 4491 (TENN-F-54655).

hyphae involved in a slime matrix, skeletal–generative, 5–12 μm diam, thick-walled (wall ~ 2.0 μm thick), conspicuously clamped, occasionally producing flagelliform hyphal tips $\sim 250 \times 1\text{--}1.5$ μm diam, thick-walled near origin, thin-walled apically; stipe cortex hyphae 4–7 μm diam, thick-walled (wall occluding cell lumen), strongly

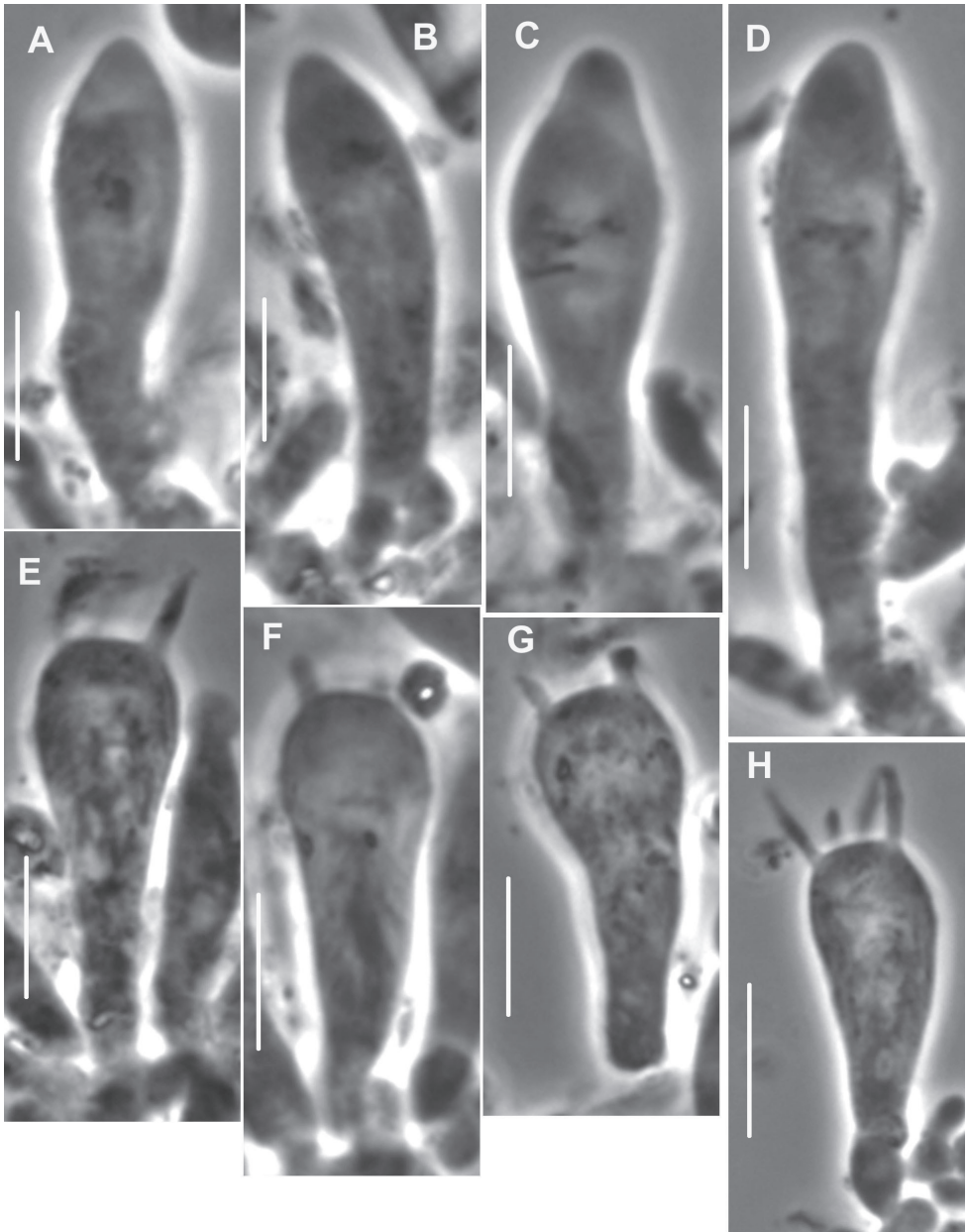


Figure 50. *Gymnopus pinophilus*. Hymenial elements. **A–D** Pleurocystidia **E–H** Basidia. Standard bars = 10 μ m. DED 4491 (TENN-F-54665).

pigmented, non-dextrinoid; surface hyphae minutely roughened. **Caulocystidia** not observed.

Commentary. Desjardin (1989) and Gordon (1994) treated *G. pinophilus* as an unnamed subset of *Ma. androsaceus*. The latter was perceived as fruiting on three sub-

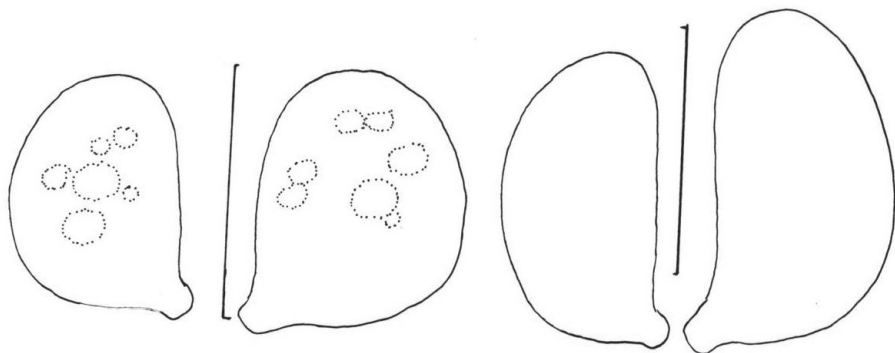


Figure 51. *Gymnopus pinophilus*. Basidiospores. Standard bars = 5 μ m. **A** = TFB 14097. **B** = TFB 10459 (TENN-F-67804).

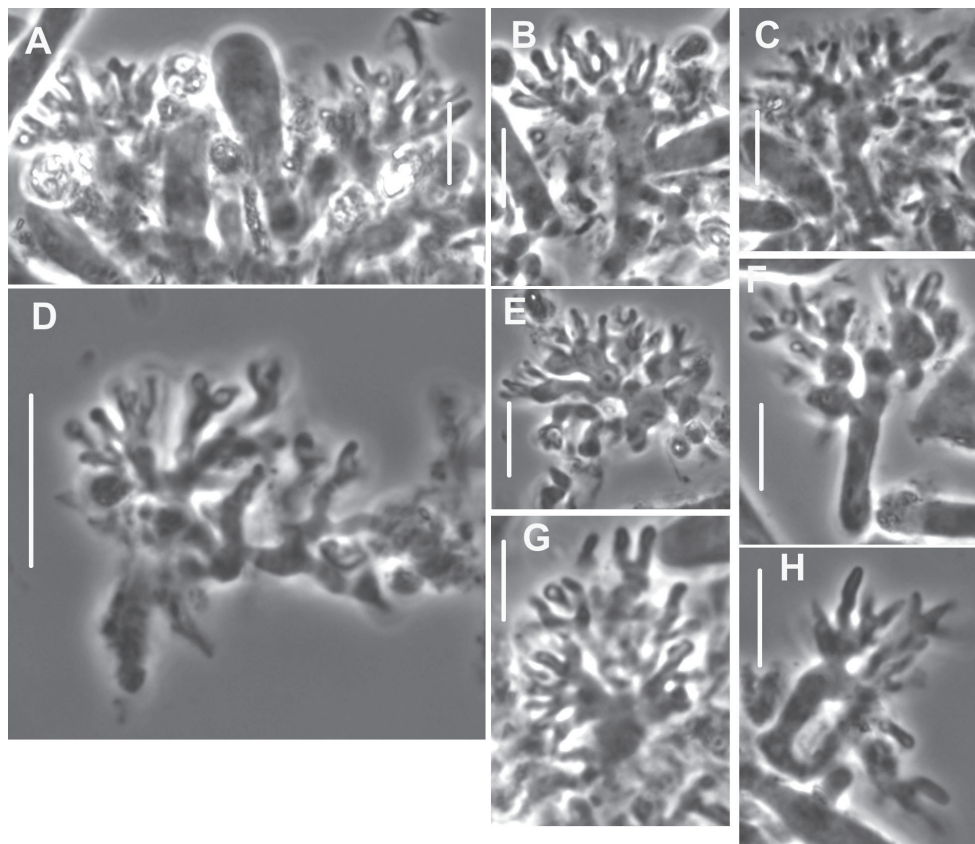


Figure 52. *Gymnopus pinophilus*. Cheilocystidia. **A** Cluster of two cheilocystidia **B–H** Individual cheilocystidia. Standard bars = 10 μ m. TFB 7234 (TENN-F-53553).

strata, hardwood leaves, needles of *Picea/Abies*, and needles of *Pinus*. Gordon and Petersen (1997) understood that *M. androsaceus* s.l. in eastern North America could be divided into three sexually interINcompatible groups, one of which (mating group III) was represented by only a single collection (TFB 5627 TENN-F-53488 from Idaho). With subsequent collecting and DNA sequence production, this collection was determined as *G. pinophilus*. Mata et al. (2007) showed that *Marasmius* sect. *Androsacei* (represented by *M. androsaceus*) was actually embedded within *Gymnopus*, and Noordeloos and Antonín (2008) formally transferred the section as *Gymnopus* sect. *Androsacei*. Furthermore, Desjardin (1990) and Desjardin and Horak (1997) reported considerable morphological and phenological variation within the North Temperate *Androsacei*, in part by circumstantial evidence, based on the data above. Present phylogenetic analyses now show that the small alliance of *G. pinophilus* and *G. ponderosae* (Gordon's mating group III) is more closely related to the *Mi. perforans* complex than to the *Ma. androsacei* complex.

Observation on TFB 14097 (TENN-F-67846) revealed two sets of dimensions of spores, and TFB 10459 showed that these spores are formed by basidia in the same hymenium – thus spores must be judged as dimorphic. One cause for this might be 2- versus 1-nucleate condition of individual spores, but all seem to be produced by 4-sterigmate basidia.

Observations of pileipellis of TFB 10459 showed that broom cell-like hyphal termini are ephemeral – apparently they wash or gelatinize away, so when they were absent from some pilei of various collections, the strongly ornamented repent hyphae remained.

Recently, TFB 14097 was established in dikaryon and monokaryon cultures and a self-cross was performed (see Gordon and Petersen 1997 for methods). From an assay of 20 putative single-basidiospore isolates (SBIs), 12 clampless putative monokaryons were selected and paired in all combinations. As expected, a tetrapolar mating system was revealed. $A^1B^1 = 5^*, 6$; $A^2B^2 = 1^*, 3, 4, 8$; $A^2B^1 = 2^*, 7, 9, 11, 12$; A^1B^2 not represented in the sample (* indicates a tester strain). Most growth of donors was submerged (except for structures noted below). Most pairings exhibited very subtle “barrage” or “flat” contact zones, most easily envisioned with the naked eye against back-lighting. Barrage = somewhat congested growth in “mustaches” (not within contact zone). Flat = slightly congested hyphae on both sides of a lightly overgrown crevasse.

On malt extract (Difco, 15 g/L) agar (Difco, Bacto, 20g/L) most SBIs produced: 1) pure white spherical hyphal masses (<1– 2 mm diam; appearing as minute “snow-balls”). These structures are narrowly attached to the agar-surface mycelium and are composed of loosely interwoven hyphae with a mucoid medulla, pure white inside and out, easily crushed (like a cotton ball); and 2) minute ganglia of hyphae scattered over agar surface in mucoid matrix. SBIs include two hyphal types: 1) 4–6.5 μ m diam, thin-walled, frequently septate, hardly inflated; and 2) roughly arbuscular, 1.5–2.5 μ m diam, thin-walled, as though a *ramealis* structure but with branches longer, apparently opposite or sub-opposite.

Specimens examined. **Canada, Nova Scotia**, Kejimikujik National Park, Grafton Lake Loop Trail, 5.VIII.1992, coll S.A. Gordon, TFB 5034 (TENN-F-53487). **United States, New York**, Franklin Co., Malone, Franklin Academy High School nature trail, 14.VII.1992, coll Scott Gordon, TFB 4975 (TENN-F-53478). **North Carolina**, Haywood Co., GSMNP, Cataloochee Cove, Schoolhouse area, N35°37'43.93", W83°06'44.18", 5.IX.1992, coll RHP, TFB 5547 (TENN-F-52480); same location, 9.IX.1987, coll DE Desjardin, DED 4491 (TENN-F-54665); Jackson Co., vic. Cashiers, Panthertown Valley, N35°09'34.63", W83°00'35.75", 24.VI.1992, coll JE Johnson, TFB 6311 (TENN-F-53128); Macon Co., vic. Highlands, Cliffside Lake, end of road, N34°04.749', W83°14.150', 4.VIII.2012, coll KWH, TFB 14097 (TENN-F-67846); Cliffside Lake Campground, N35°04'44.92", W83°14'12.90", 3.IX.1986, coll D.E. Desjardin, DED 4107 (TENN-F-54643; SFSU); Highlands, Highlands Biological Station, N35°03'09.72", W83°11'19.98", 9.VIII.1966, coll LR Hesler, LRH 29279 (TENN-F-29279); vic. Highlands, Bull Pen Rd., Ellicott Rock Wilderness trailhead, N35°01.010', W83°08.190', 20.VII.2011, coll RHP, TFB 13913 (TENN-F-65808); Horse Cove, Walking Stick Rd., "Double Bridges," N35°00.983', W83°09.619", 31.VII.2012, coll RHP, TFB 14059 (TENN-F-67804); Bull Pen Rd., Ellicott Rock Wilderness trailhead, N35°01.010', W83°08.190', 20.VII.2011, coll RHP, TFB 13913 (TENN-F-65808); Nantahala Nat. For., Blue Valley Campground, N35°00'45.23", W83°09'29.33", 11.VIII.2014, coll KWH, TFB 14511 (TENN-F-69206; holotype); vic. Franklin, Standing Indian Campground, 19.VII.1994, coll DBG Nichol, TFB 7629 (TENN-F-53659). **South Carolina**, Oconee Co., Burrell's Ford campground, N34°58.408', W83°06.726, 12.VIII.2014, coll Highlands Biol. Station class, TFB 14517 (TENN-F-69212).

7. *Gymnopus ponderosae* R.H. Petersen, sp. nov.

Mycobank no. 552480

Holotype. **United States, California**, Humboldt Co., Rte 299, Grey's Falls Campground, N40°54.422', W123°42.420', 16.XI.1996, coll RHP, TFB 9020 (TENN-F-55669).

Etymology. *ponderosae* = Latinized, referring to *Pinus ponderosa*, fruiting habitat of the species.

Diagnosis. 1) fruiting on dead needles of *Pinus ponderosa*; 2) pileipellis with diverticulate hyphae and broom cell-like hyphal termini; 3) pileipellis broom cell-like hyphal termini and cheilocystidia arbuscular, with conspicuous stalk but hardly swollen distal portion; 4) rhizomorphs conspicuous, hairlike, curly, unbranched, $-35 \times 0.1\text{--}0.4$ mm; 4) spores perhaps dimorphic.

Description. **Basidiomata** (Figs 53, 54A) scattered on needle duff, usually solitary on individual needles, occasionally two per needle. **Pileus** 3–13 mm broad, applanate but with wide inflexed margin, occasionally slightly depressed, delicately tuberculate, not umbonate, subtly sulcate–striate, matt; disc brown ("Mars brown" 8F7, "bister" 5F8), grayish avellaneous to dull deep avellaneous; limb light brown ("sayal brown"



Figure 53. *Gymnopus ponderosae*. Basidiomata on dead needles of *Pinus ponderosa*. Standard bar = 10 mm. Mushroom Observer CA391914.

6C5, “tawny olive” 5C5) to near “tilleul buff” 7B2. **Lamellae** adnexed to adnate, subdistant, not anastomosing, not pseudocollariate but seceding and appearing pseudocollariate after drying, subventricose, total lamellae (Fig. 54B) = 22–28, through lamellae = 13–15, (fresh) light brownish orange (6C4–3) to avellaneous, (dry) gray with hint of olive (“deep olive buff” 3C3, “light grayish olive” 30B2); lamellulae in one rank, rudimentary. **Stipe** 24–40(–60) × 0.5–0.8 mm broad, glabrous–shining over all, tapering gradually downward from mid-section to base, insititious, upward “avellaneous” (concolorous with lamellae, 7B3), socket at lamellar junction dark brown, downward black (“fuscous black” 6F4, “chaetura black” 2F3). **Rhizomorphs** (Fig. 54A) common, –35 × 0.1–0.4 mm, hair-like, black, glabrous–shining, kinked but not branched, attached to substrate with basal pad, sparse, not attached to basidiomata but closely associated. **Odor** negligible; **taste** negligible.

Habitat and phenology. Fruiting on dead needles, twigs and debris of *Pinus ponderosa* (three-needle pine); distribution probably following distribution of *Pinus ponderosa* (at least California, Idaho, Washington); late autumn.

Pileipellis constructed of three elements involved in a minimal slime matrix over central areas: 1) hyphae 3–7 µm diam, firm- to thick-walled [wall 0.7–1 µm thick,

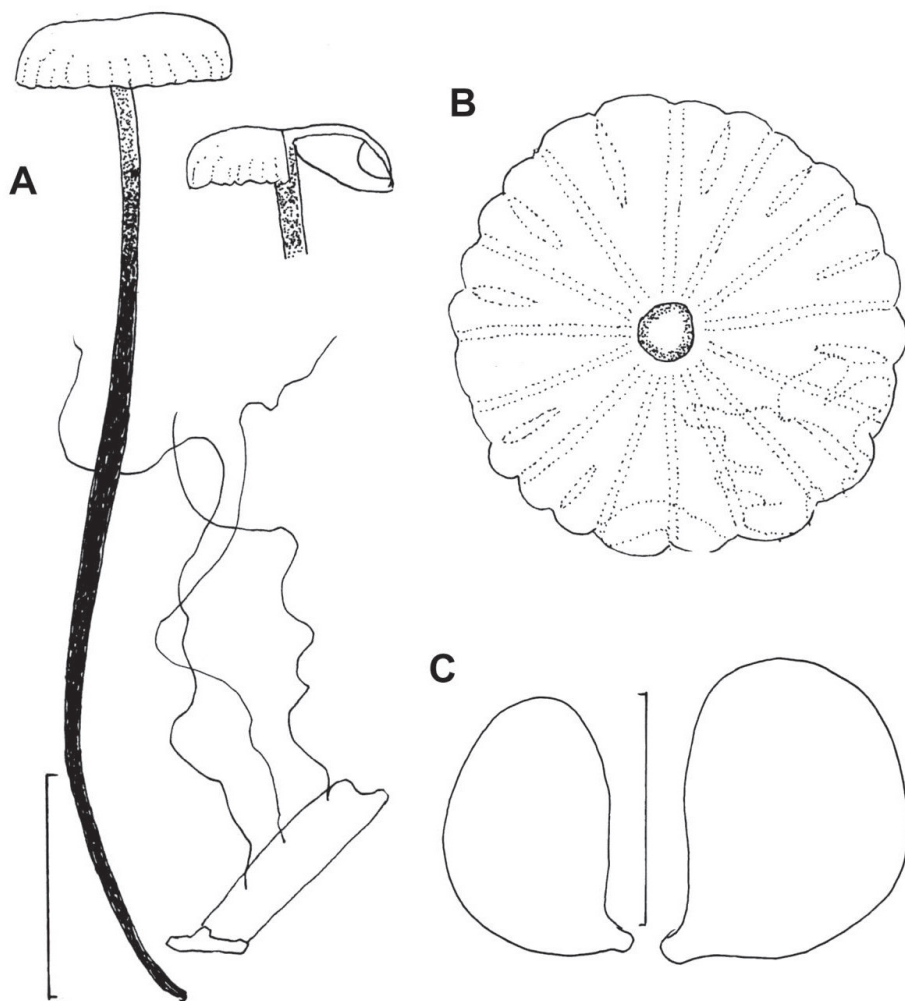


Figure 54. *Gymnopus ponderosae*. **A** Basidioma and rhizomorphs **B** Lamellar schematic **C** Basidiospores. Standard bars: **A** = 10 mm; **C** = 5 μ m. **B** not to scale. TFB 9020 (TENN-F-55669).

subhyaline singly, pigmented dull yellow–olive brown in mass (PhC)], conspicuously clamped, strongly encrusted (Fig. 55A, B); crust material in thick scabs with profile calluses $\sim 1.5 \mu$ m thick or as annular ornamentation (Fig. 52B) or with profile calluses $\sim 1 \mu$ m thick or minute “flakes” adherent to a slime sheath; 2) free-form hyphae 4–6 μ m diam, tibiiform to meandering, thin- to firm-walled (wall $\sim 1 \mu$ m thick, hyaline), often diverticulate with a combination of lobes and diverticula (Figs 55C,D, 56A, B); diverticula $\sim 8 \times 1\text{--}1.2 \mu$ m, digitate, often dichotomous, subrefracting; lobes $\sim 8 \times 2\text{--}3 \mu$ m at base, fin-shaped (triangular), non-refracting; and 3) broom cell-like termini (Fig. 56C–F), arbuscular, stalked (stalk 4–13 \times 3–5 μ m), hardly or not inflated dis-

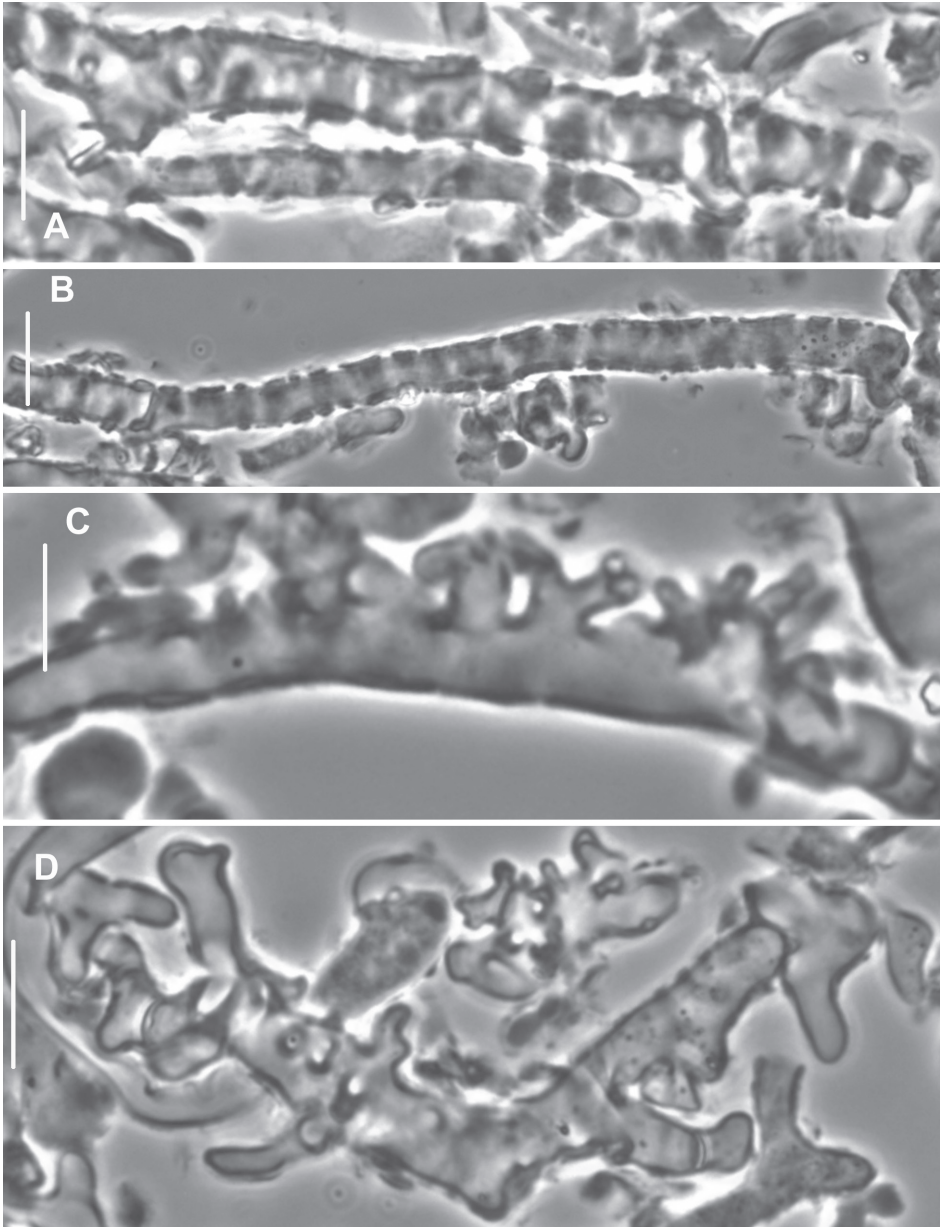


Figure 55. *Gymnopus ponderosae*. Pileipellis structures. **A** Strongly encrusted hypha **B** Hypha with annular encrustation **C** Thick-walled diverticulate hypha **D** Thick-walled, lobate diverticulate hypha. Standard bars = 10 μm . TFB 9020 (TENN-F-55669).

tally, branched in 1–2 ranks, beset with setulae $3\text{--}12 \times 1\text{--}1.5 \mu\text{m}$, digitate, often somewhat catenulate, often dichotomous, subrefringent, apparently free (not in slime). Pileus trama loosely interwoven; hyphae $2.5\text{--}6.5 \mu\text{m}$ diam, firm-walled, conspicuously

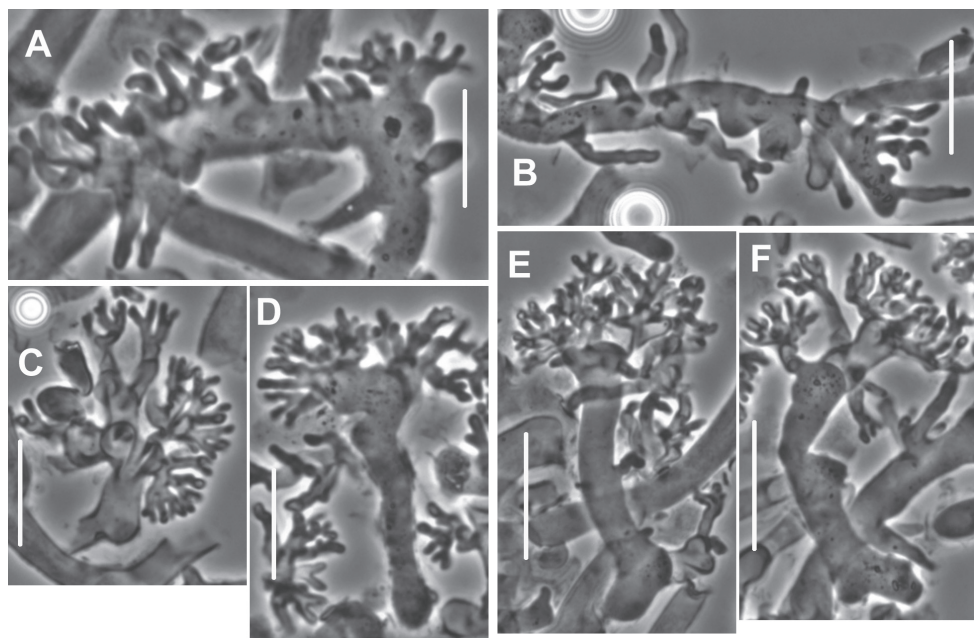


Figure 56. *Gymnopus ponderosae*. Pileipellis structures. **A, B** Diverticulate hyphae **C–F** Broom cell-like hyphal termini. Standard bars = 10 μm . TFB 9020 (TENN-F-55669).

clamped, weakly encrusted in “flakes.” **Pleurocystidia** (Fig. 57A–D) $24\text{--}37 \times 7\text{--}9.5$ μm , fusiform, conspicuously clamped; contents homogeneous, often with partitioned contents at apex. Basidioles clavate to ampulliform; **basidia** (Fig. 57E–H) $(25\text{--})32\text{--}38 \times (7\text{--})8\text{--}10$ μm , clavate, often with slight constriction to produce capitulate morphology, clamped, 4-sterigmate; contents minutely heterogeneous. **Basidiospores** (Fig. 54C) possibly dimorphic: 1) $(5\text{--})5.5\text{--}7\text{--}(8.5) \times (3\text{--})3.5\text{--}5$ μm ($Q = 1.11\text{--}2.43$; $Q^m = 1.67$; $L^m = 6.2$ μm); 2) $(6.5\text{--})7\text{--}8.5 \times 3.5\text{--}4.5$ μm ($Q = 1.75\text{--}2.43$; $Q^m = 2.01$; $L^m = 7.7$ μm), broadly ellipsoid to rotund-ellipsoid, pip-shaped, smooth, thin-walled, inamyloid; contents minutely granular. **Cheilocystidia** (Fig. 58) $18\text{--}35 \times 10\text{--}17$ μm , broom cell-like, stalked [stalk $(9\text{--})15\text{--}27 \times 4\text{--}5$ μm , sometimes minutely roughened], without dilated distal portion, branched in 1–2 ranks, obscurely clamped; setulae $\sim 8 \times 1\text{--}1.5$ μm , often gnarled and/or branched, subrefrinct (PhC). **Stipe medullary hyphae** $3\text{--}10$ μm diam, hyaline, thick-walled (wall ~ 2 μm thick), obscurely clamped, with minimal slime matrix, strictly parallel. **Stipe cortical hyphae** $4\text{--}10$ μm diam, thick-walled [wall ~ 2 μm thick, pigmented yellow brown (PhC)], obscurely clamped; surface hyphae encrusted in minute scabs, making surface cells appear rough. **Caulocystidia** not observed.

Commentary. Collections accepted as four separate species (*G. “scoticus”* nom. prov., *G. “adventitius”* nom. prov., *G. pinophilus*, *G. ponderosae*) fruit on dead needles of *Pinus* spp. Of these, the former two are found in *Gymnopus* sect. *Androsacei*, while the latter two belong in sect. *Perforantia*. Both *G. ponderosae* and *G. adventitius* fruit

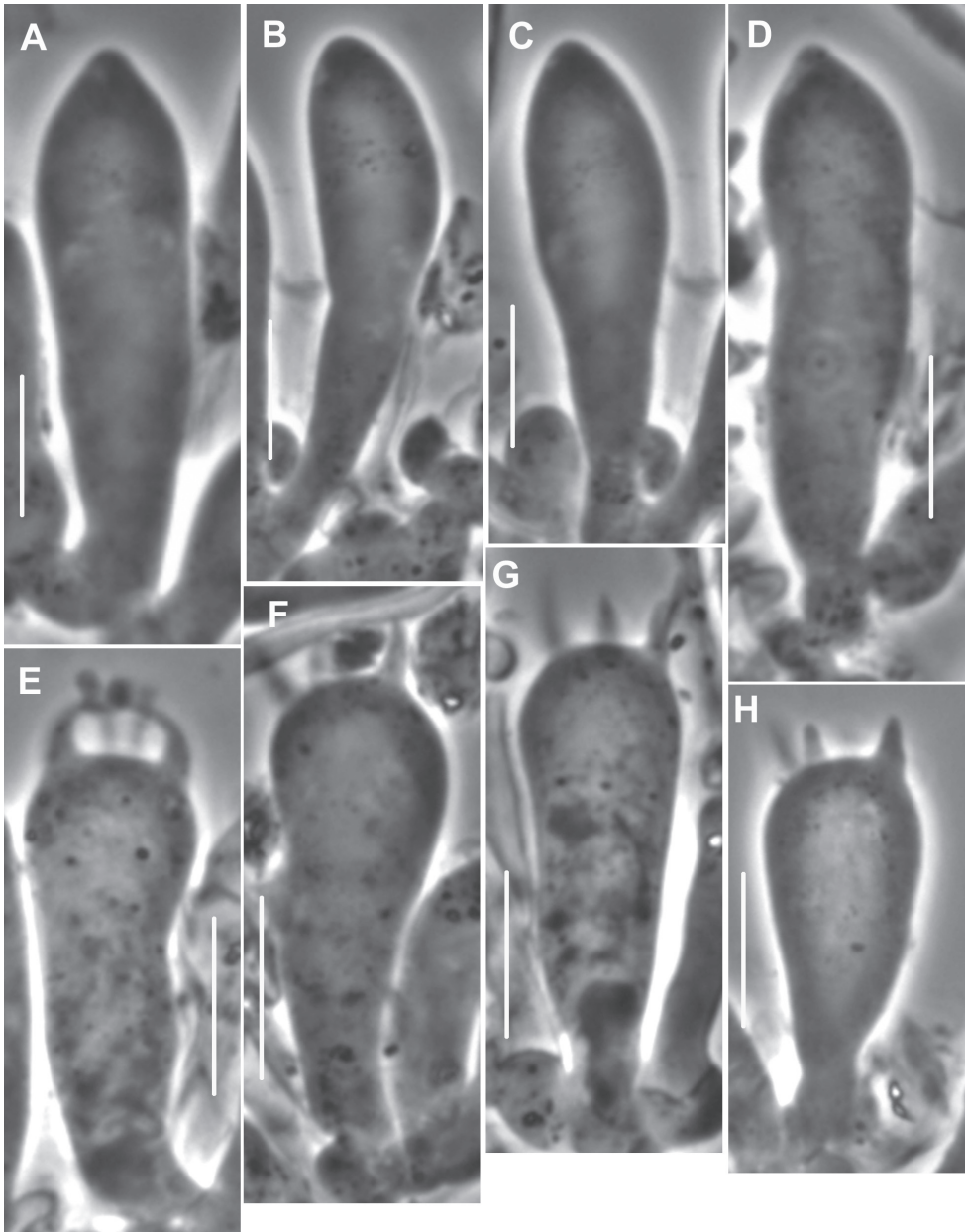


Figure 57. *Gymnopus ponderosae*. Hymenial structures. **A–D** Pleurocystidia **E–H** Basidia. Standard bars = 10 μm . TFB 9020 (TENN-F-55669).

on needles of *Pinus ponderosae* and superficially resemble one another. Both exhibit black, glabrous–shining stipes and dark brown pilei, but the pileipellis of *G. ponderosae* comprises repent, encrusted hyphae, diverticulate hyphae and broom cell-like hyphal termini, while *G. adventitius* pileipellis does not show diverticulate hyphae and broom

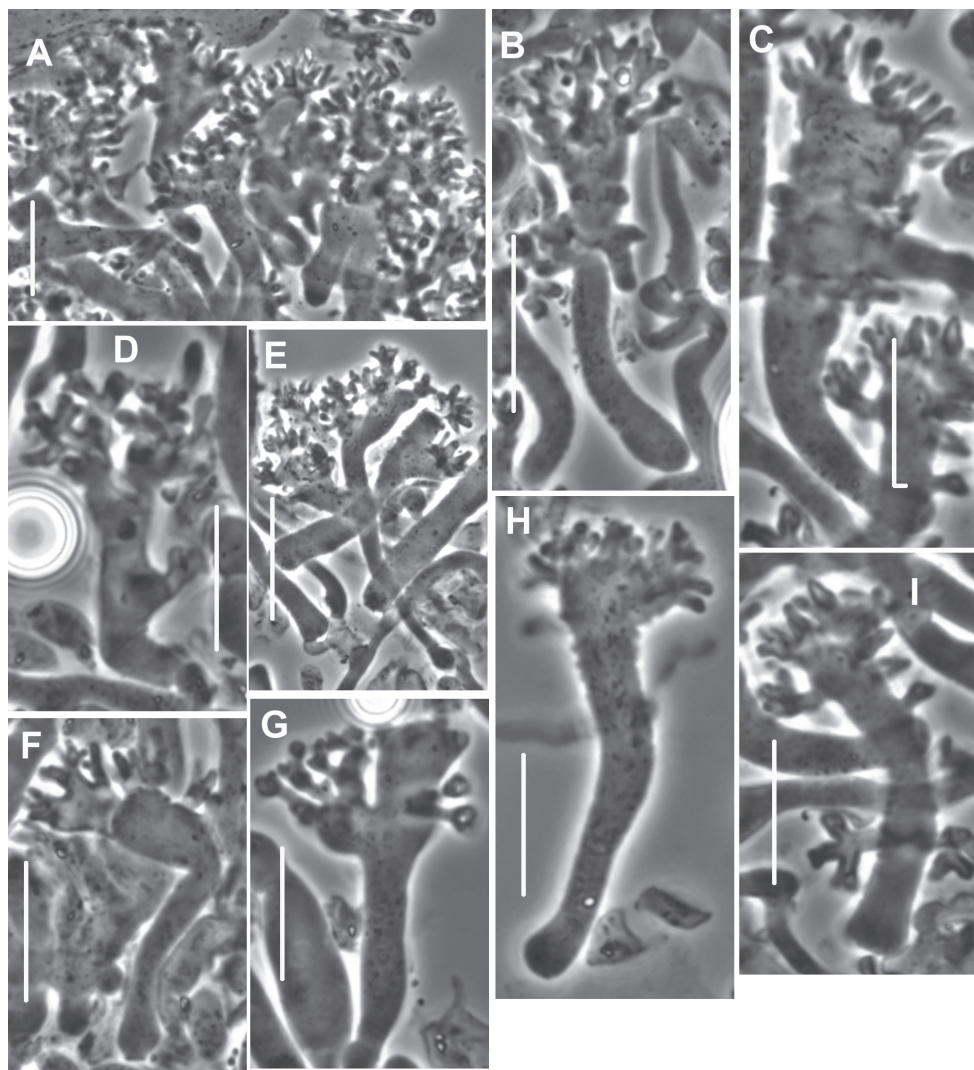


Figure 58. *Gymnopus ponderosae*. Cheilocystidia. **A** Cluster of cheilocystidia **B–I** Individual cheilocystidia. Standard bars = 10 μm. TFB 9020. (TENN-F-55669).

cell-like hyphal termini. Moreover, stipes of *G. adventitius* often produces adventitious rhizomorphic structures from wounds, not seen in *G. ponderosae*.

The small clade comprising *G. pinophilus* and *G. ponderosae* is found sister to that of core sect. *Perforantia*. Pileipellis construction, which includes diverticulate hyphae and pileipellis “broom cells” is characteristic of a “*Rameales* structure,” indicative of sect. *Androsacei*, but hardly that of traditional *Perforantia*, although involved in minimal slime. Marasmioid cheilocystidia also separate this pine-loving alliance from sect.

Perforantia. Rhizomorphs, while not typically as long as basidiome stipe, are common, obvious and arise from the same needles as basidiomata.

TENN53488-TFB5627 (Idaho, *G. ponderosae*) was the only representative of mating group III of "*Marasmius androsaceus*" by Gordon (1994) and Gordon and Petersen (1997). The taxonomic concept of the latter, however, was broad ([see Desjardin and Petersen (1989); Gilliam (1976)], including two separate taxa now known to be members of sect. *Androsacei* (as well as *G. ponderosae* in sect. *Perforantia*), and perhaps other organisms for which haploid isolates were unavailable for pairing experiments.

The possibility of dimorphic spores is reported here also for *G. pinophilus*. Although reported for other mushroom groups (notably hygrophoroids) the cause of this phenomenon is not known in the group treated here. Basidia are uniformly 4-spored and basidia are conspicuously clamped, indicative of normal nuclear number and behavior.

Specimens examined. United States, California, Humboldt Co., Rte 299, Grey's Falls Campground, N40°54.422', W123°42.420', 16.XI.1996, coll RHP (as *Marasmius* sp.), TFB 9020 (TENN-F-55669; holotype). **Idaho**, Bonner Co., vic. Priest River, Priest River Experimental Forest, 25.IX.1992, coll RHP (as *Marasmius* sp.), TFB 5627 (TENN-F-53488); same locale, same date, coll RHP (as *Marasmius* sp.), TFB 5633 (TENN-F-52411); Valley Co., vic. McCall, N44.911 W116.097, 16.IX.1977, coll. SD Libonati-Barnes (as *Marasmius androsaceus*), SDLB 1461 (WTU-F-9083). **Washington**, Pend Oreille Co., Roosevelt Grove, N48°45'15.89", W117°03'30.33", 29.VI.1993, coll L. Norvell (as *Marasmius androsaceus*), LN93.06.29-16 (WTU-F-8918).

8. *Gymnopus pyracanthoides* R.H. Petersen, sp. nov.

Mycobank no. 552481

Holotype. Costa Rica, Prov. San José, San Gerardo de Dota, Albergue de Montaña, Savegre, 9°33'2" N, 83°48'27" W, 21.VI.1995, coll RHP, TFB 7879 (TENN-F-53736).

Etymology. Latinized; resembling *Pyracantha*, referring to spike-like setulae on pileipellis broom cell-like hyphal termini.

Diagnosis. 1) A morpho-species (no DNA sequences available); 2) broom cell-like hyphal termini of pileipellis coarsely thorny; 3) subhymenial hyphae with slime sheath and flake-like encrusting material; 4) rhizomorphs well-developed, curly, sparingly branched; 5) stipe minutely pruinose overall; 6) fruiting on sclerophyllous deciduous leaves.

Description. Basidiomata (Fig. 59A) diminutive, arising independent from but gregarious with rhizomorphs. **Pileus** 3–6 mm broad, strongly convex and in one case slightly umbonate, matt, minutely tuberculate, subtly sulcate or not so; disc "wood brown" 7C4; limb and margin "vinaceous buff" 9B2 to "tilleul buff" 7B2. **Lamellae** adnexed (Fig. 59A), usually weakly pseudocollariate, thickish, subdistant, narrow (<1 mm

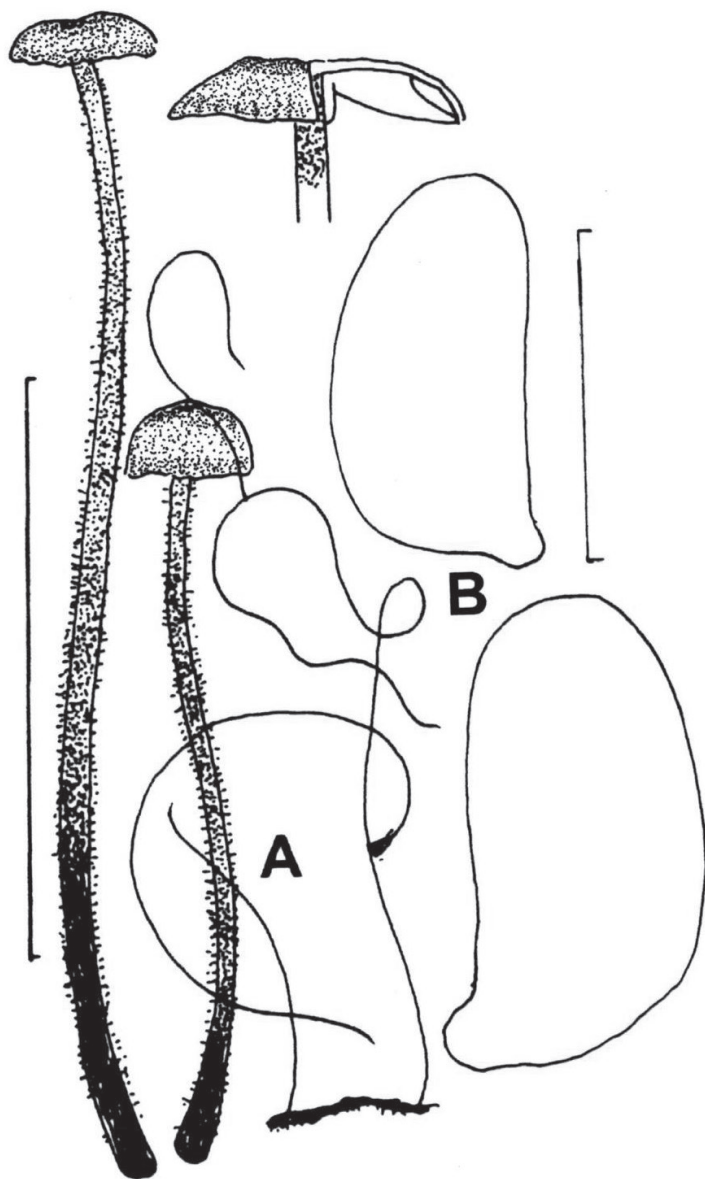


Figure 59. *Gymnopus pyracanthoides*. **A** Basidiomata and rhizomorphs **B** Basidiospores. Standard bars: **A** = 20 mm; **B** = 5 μ m. TFB 7879 (TENN-F-53736).

broad), slightly ventricose, without anastomosis or interveining, without necropigment, total lamellae = 31–33, through lamellae = 10–11, “vinaceous buff” 9B2; lamellar edge entire, not marginate. **Stipe** 24–38 \times 0.3–0.5 mm, appearing glabrous–shining but under magnification (35 \times) very finely pruinose over total length (pruinosity hyaline), stuffed (medulla off-white), insititious, apically concolorous with lamellae, downward



Figure 60. *Gymnopus pyracanthoides*. Broad-leaved habitat. Lines indicate resupinate rhizomorphs. Scale = $\times 1$. TFB 7879 (TENN-F-53736).

quickly “army brown” 8D5, downward “Natal brown” 8E6. **Rhizomorphs** (Figs 59A, 60) common, mostly resupinate on leaf surface (both upper and lower side), 0.1 mm broad (extremely slender), only occasionally branched when resupinate; aerial rhizomorphs – $17 \times 0.2\text{--}0.3$ mm, gyrose to curly in aerial portions and frequently branched, glabrous–shining, now strap-shaped where free (aerial portions compressed in drying, not resupinate portions), functionally black in resupinate portions, brass-brown (remining of *M. “flavipes”* nom. prov. from Tasmania) to “bone brown” 7F8 in aerial portions. **Taste** and **odor** not recorded.

Habitat and phenology. Known from only the type specimen; fruiting on dead sclerophyllous leaves (probably *Quercus*) at high elevation; summer.

Pileipellis (Fig. 61) a dense thatch of diverticulate hyphae and hyphal termini; parent hyphae $2\text{--}2.5$ μm diam, thin- to firm-walled, hyaline, not involved in slime matrix, producing elongate, jointed, digitate side branches $2\text{--}7 \times 0.8\text{--}1.5$ μm , rarely but conspicuously clamped. Pileus and lamellar tramal hyphae $2\text{--}5$ μm diam, firm-

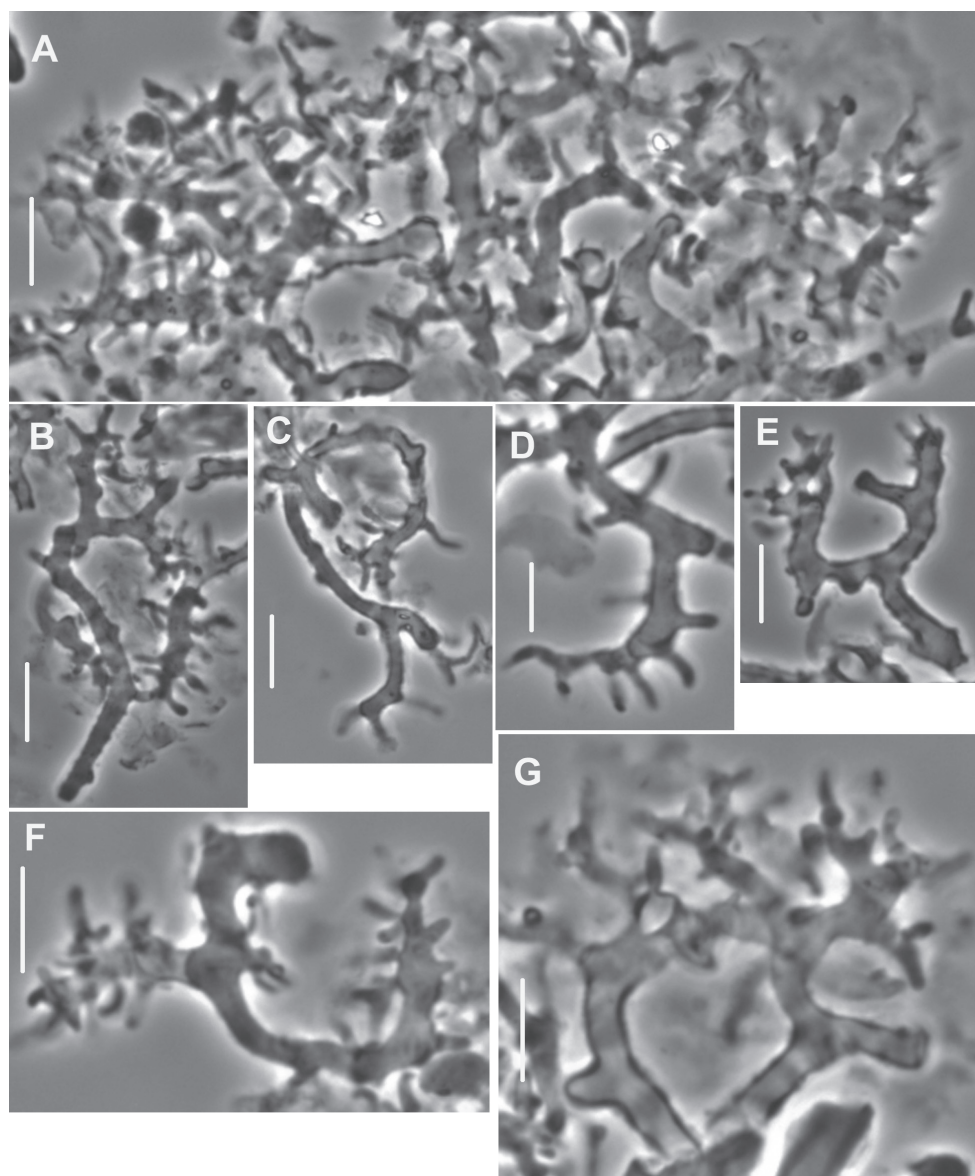


Figure 61. *Gymnopus pyracanthoides*. Pileipellis elements. **A** Cluster of broom cell-like hyphal termini **B–G** Individual broom cell-like hyphal termini. Standard bars = 10 μm. TFB 7879 (TENN-F-53736).

to thick-walled (wall ~ 0.7 μm thick, hyaline), producing thin slime sheaths, ornamented with external “flakes” of encrusting material, infrequently but conspicuously clamped. **Pleurocystidia** (Fig. 62A–D) $21\text{--}28 \times 5\text{--}7$ μm, fusiform, with narrowly rounded to acute apex, abundant, thin-walled, conspicuously clamped. Basidioles clavate; **basidia** (Figs 62E–H, 63F) $19\text{--}26 \times 6\text{--}7$ μm, clavate, sometimes very slightly subcapitate, 4-sterigmate, obscurely clamped. Subhymenium often gelatinizing,

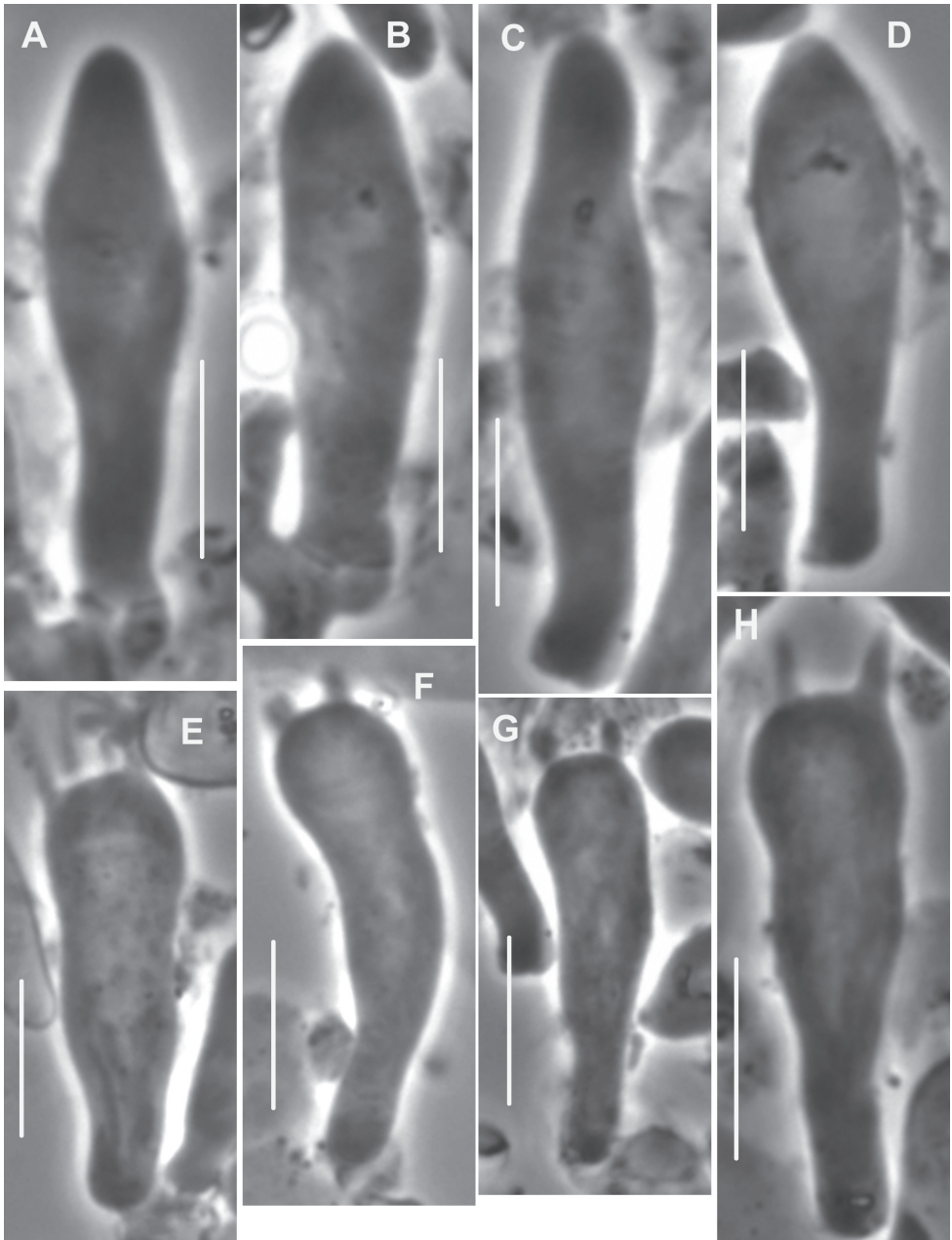


Figure 62. *Gymnopus pyracanthoides*. Hymenial elements. **A–D** Pleurocystidia **E–H** Basidia. Standard bars = 10 μm . TFB 7879 (TENN-F-53736).

including bases of basidia and pleurocystidia. **Basidiospores** (Fig. 59B) $6\text{--}7.5 \times (3\text{--})3.5\text{--}4 \mu\text{m}$ ($Q = 1.63\text{--}2.33$; $Q^m = 1.94$; $L^m = 6.85 \mu\text{m}$), ellipsoid to elongate pip-shaped, smooth, thin-walled, inamyloid. Lamellar edge fertile; **cheilocystidia**

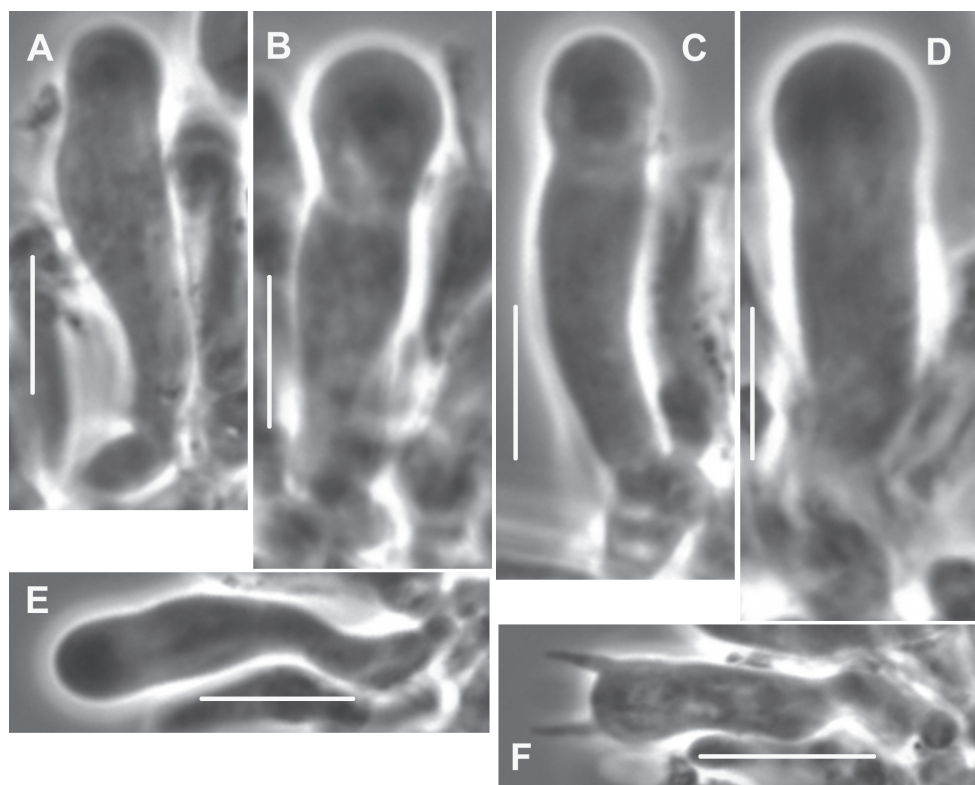


Figure 63. *Gymnopus pyracanthoides*. Hymenial elements. **A–E** Individual cheilocystidia **F** Basidium. Standard bars = μm . TFB 7879 (TENN-F-53736).

(Fig. 63A–E) scattered, obscure, $22\text{--}32 \times 5\text{--}8 \mu\text{m}$, subcapitate to subampulliform, obscurely clamped, hardly projecting beyond basidia, hyaline. **Stipe medullary hyphae** $3.5\text{--}7.5 \mu\text{m}$ diam, firm-walled, conspicuously clamped, strictly parallel, with minimal slime matrix, hyaline. **Stipe cortical hyphae** $4\text{--}7 \mu\text{m}$ diam, thick-walled (wall $\sim 1.5 \mu\text{m}$ thick, pigmented), at surface producing side branches as caulocystidia. **Caulocystidia** (Fig. 64) setoid, $\sim 8.5 \times 5\text{--}7.5 \mu\text{m}$ diam, arising as side branches (not clamped), tapering slightly distally, refringent (PhC), in IKI moderately dextrinoid (PhC), yellow-brown (BF).

Commentary. Presence of slime sheaths surrounding pileus and lamellar tramae as well as the dimensions and shape of cheilocystidia are characteristic of taxa in sect. *Perforantia*. Conversely, pileipellis presents a very distinctive thatch of broom cell-like hyphal termini rather than repent, encrusted hyphae in a slime matrix as is seen throughout the section. Such a differentiated pileipellis might also qualify for some infrageneric groups of *Marasmiellus* but would be expected to be without slime deposition. Unfortunately, DNA sequences could not be produced from the only known collection, so molecular placement remains unknown.

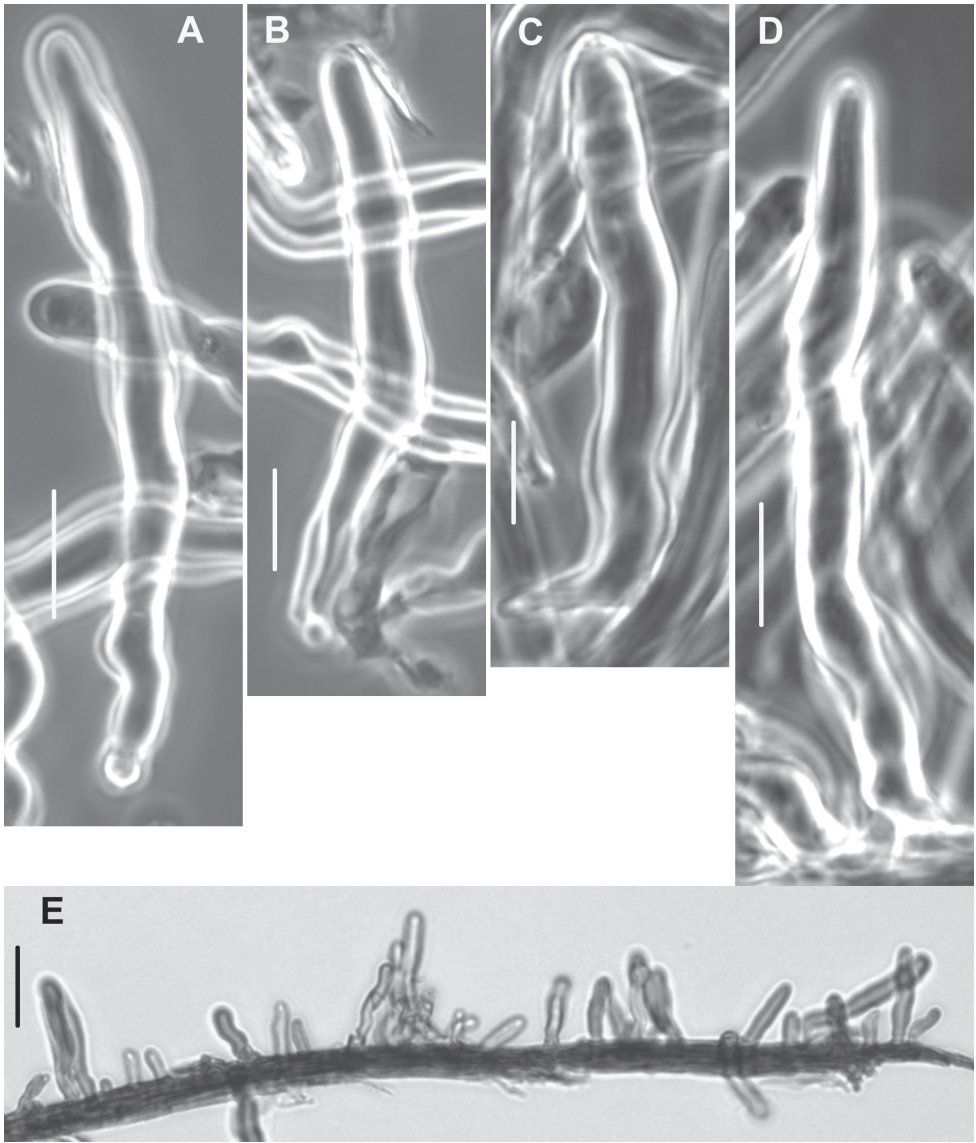


Figure 64. *Gymnopus pyracanthoides*. Caulocystidia. **A–D** Individual caulocystidia **E** Caulocystidial turf. Standard bars = 10 μm . TFB 7879 (TENN-F-53736).

Cheilocystidia in *G. pyracanthoides* resemble those of *G. bulliformis* (q.v.). They also resemble those described for *G. trabzonensis*. They may represent some stage of basidial development because basidioles also are clavate, but basidioles are present throughout the lamellae face, while the structures here described as cheilocystidia are found along the lamellar edge. No other differentiated cheilocystidial structures were observed, but some taxa in sect. *Perforantia* are known to lack differentiated cheilocystidia.

Slime is produced as a thin sheath surrounding individual hyphae, with ornamentation appearing as flakes riding on the exterior of the gelatinized wall. It also appears to obliterate subhymenium. Likewise, stipe medullary hyphae exist in minimal (but present) slime. There is little evidence of a slimy (or gelatinized) matrix in the pileipellis.

Specimen examined. **Costa Rica**, Prov. San José, San Gerardo de Dota, Albergue de Montaña, Savegre, 9°33'2"N, 83°48'27", 21.VI.1995, coll RHP, TFB 7879 (TENN-F-53736; holotype).

9. *Gymnopus quinaultii* R.H. Petersen, sp. nov.

Mycobank no. 552482

Holotype. **United States, Washington**, Grey's Harbor Co., vic Amanda Park, Forest service Rd. 2140, "Higley's Swamp," 16.X.1992, coll RHP & KWH, TFB 5886 (TENN-F-51994).

Etymology. Lake Quinault and the Quinault River, Washington, the vicinity of the holotype collection.

Diagnosis. 1) Fruiting on *Thuja* debris (less on associated *Abies* and *Tsuga* needles); 2) rhizomorphs short, stout, arising and terminating in small black pads; 3) stipe fuscous brown-black, vested, especially downward; 4) pileal hairs often ornamented with annular rings; 5) pileipellis constructed of incrustated hyphae, and hyphae with gelatinizing walls; 6) cheilocystidia not observed.

The description below is based on dried material only.

Description. Basidiomata (Fig. 65A) marasmiod, diminutive. **Pileus** 3–15 mm broad, convex to plano-convex, matt, very short-striate on downturned margin; disc now near "saya brown" 6C5, outward now dull cinnamon buff, near "avellaneous" 7B3 to "vinaceous buff" 9B2. **Lamellae** (Fig. 65A) adnate to adnexed, close to subdistant, seceding somewhat upon drying and then appearing pseudocollariate, subventricose (–1.2 mm broad), thickish, with no anastomoses; total lamellae = 30–32; through lamellae = 11–14, now concolorous with pileus, bleeding slightly from dark brown stipe apex; lamellulae short, in 1–2 ranks; lamellar trama under magnification (40×) appearing glassy (probably gelatinized). **Stipe** 15–30 × 0.7–1.2 mm, subinsititious, terete, equal, hollow, minutely vested upward (35×), downward becoming pruinose to minutely hispid, upward "cinnamon" 6B5 to "orange cinnamon" 7B6, soon brown and downward "fuscous black" 6F4 to "chaetura black" 2F3 (not totally black anywhere), remaining darker than lamellae through attachment to pileus flesh; medulla off-white. **Rhizomorphs** (Fig. 65A) apparently common on *Thuja* branchlets (incidental on *Abies* needles), –10 mm × 0.3–0.8 mm (relatively stout for length), arising from a small black pad (and terminating similarly on adjacent needles), commonly branched (usually short, spur branches), colonizing adjacent needles; resupinate black hyphae individual, meandering over substrate surface. **Taste** and **odor** not recorded.

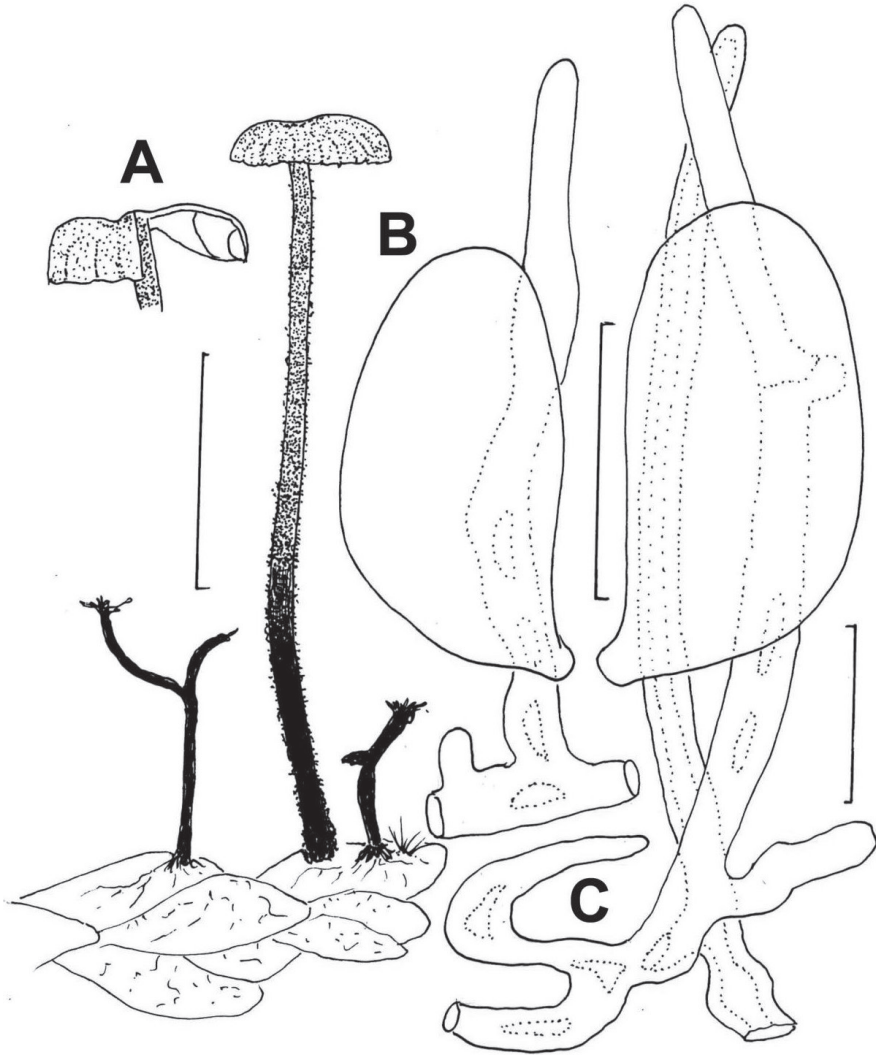


Figure 65. *Gymnopus quinaultii*. **A** Basidioma and rhizomorphs **B** Basidiospores **C** Caulocystidia. Standard bars: **A** = 10 mm; **B** = 5 μ m; **C** = 20 μ m. TFB 5886 (TENN-F-51994).

Habitat and phenology. Fruiting on dead needles of *Thuja plicata* and *Abies grandis*; Autumn.

Pileipellis composed of the following elements: 1) pileal hairs (Fig. 66) –100 \times 3–4.5 μ m, erect, usually more or less straight, firm-walled, often with basal clamp connection, often weakly ornamented, especially in annular rings (Fig. 66D); 2) repent, unoriented, interwoven hyphae 3.5–8 μ m diam, thin-walled but wall gelatinizing to 2–3 μ m thick (Fig. 67C, D), with vague outer wall, obscurely clamped; and 3) weakly to strongly encrusted hyphae (Fig. 67A, B) 4.5–8 μ m diam, thin-walled but semi-



Figure 66. *Gymnopus quinaultii*. Pileal hairs. Standard bars = 10 μm . TFB 5886 (TENN-F-51994).

gelatinizing; incrustation in scabs and/or vague stripes, with strong but rough profile calluses; narrower hyphae encrusted as though with many minute crystals (not coarse scabs). Lamellar trama loosely interwoven; hyphae 3–5.5 μm diam, firm-walled, clamped. **Pleurocystidia** (Fig. 68) common, 28–34 \times 6–8 μm , fusiform, conspicuously clamped; contents homogeneous or partitioned. Basidioles (Fig. 69A) clavate; **basidia** (Fig. 69B–D) (25–)30–33(–37) \times 6.5–9 μm , clavate, subtly subcapitulate, 4-sterigmate, clamped. **Basidiospores** (Fig. 65B) (6.5–)7.5–9(–9.5) \times (3.5–)4–4.5 μm ($Q = 1.63$ –2.50; $Q^m = 1.99$; $L^m = 7.82 \mu\text{m}$), plump–ellipsoid, marasmiod (somewhat tapered proximally), flattened adaxially, smooth, thin-walled, inamyloid; contents vaguely univacuolate (PhC). **Cheilocystidia** not observed. **Stipe medullary hyphae** strictly parallel, perhaps coherent, 2–9 μm diam, firm- to thick-walled (wall – 1.0 μm thick, hyaline), conspicuously clamped. **Stipe cortical hyphae** 4–7 μm diam, strictly parallel, minutely roughened, thick-walled (wall – 2 μm thick), obscurely clamped; stipe vestiture setoid, hardly gathered into synnemata but usually densely scattered. **Caulocystidia** (Fig. 65C, 70) –180 \times 3.5–7 μm , oc-

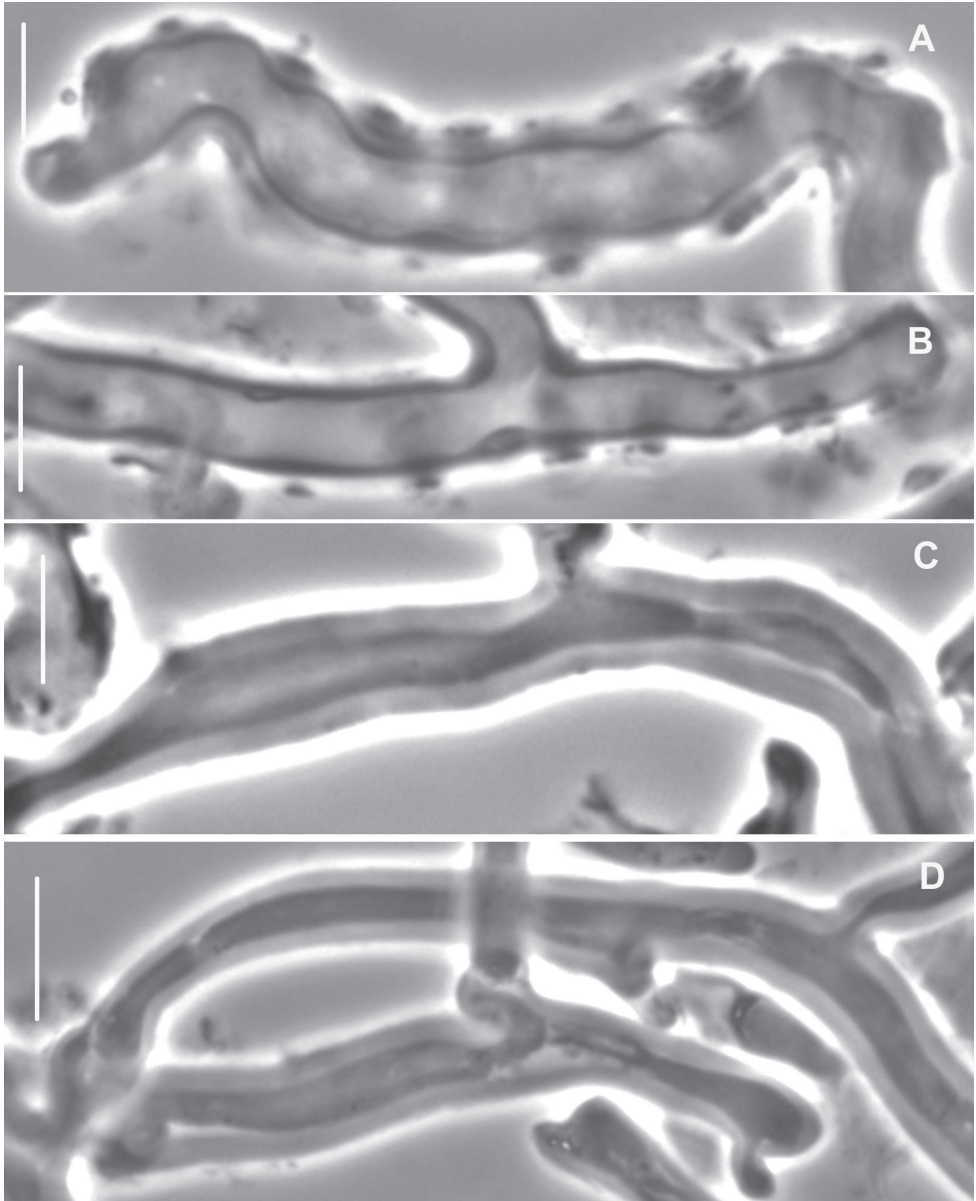


Figure 67. *Gymnopus quinaultii*. Pileipellis elements. **A, B** Encrusted hyphae **C, D** Gelatinizing hyphae. Standard bars = 10 μm. TFB 5886 (TENN-F-51994).

curing as side branches of stipe surface hyphae, irregularly rooted, often gnarled at base, tapering distally to rounded apex, thick-walled (wall 1.5–3 μm thick, often occluding cell lumen, dull yellow-ochre, highly refringent), yellowish (PhC), occasionally internally clamped and/or secondarily septate.

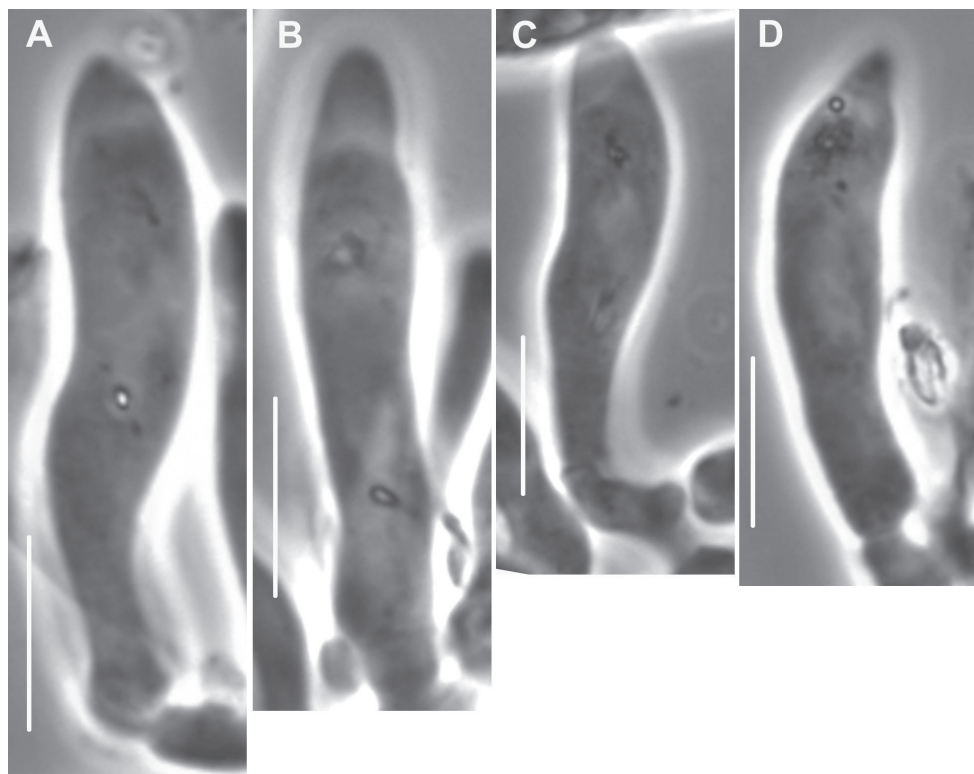


Figure 68. *Gymnopus quinaultii*. Pleurocystidia. Note apical partition of contents. Standard bars = 10 μ m. TFB 5886 (TENN-F-51994).

Commentary. *G. quinaultii* clearly belongs in sect. *Perforantia*. The vestured stipe is not black but fuscous brown. Spores are somewhat large for sect. *Perforantia*, and host association (*Thuja/Abies*) is different (not spruce/fir needles).

Based on habitat on *Thuja* debris, an ancillary study was made of *Collybia thujina* Kauffman (MICH!), which immediately led to examination of material of *Marasmius filopes* Peck (NYS!) and *Collybia piceina* Kauffman (MICH!). Prior treatments had been published by Hesler (1959), Gilliam (1976), Redhead (1980) and Desjardin (1989). Basidiomata of all correctly identified collections were significantly smaller and more slender than those of *G. quinaultii*, and pileipellis organization was of a well-developed *Rameales*-structure, not similar to that in *G. quinaultii*. Desjardin (1989) agreed with Redhead that *M. filopes*, *C. piceina* and *C. kauffmanii* were taxonomic synonyms, all correctly placed in *Marasmiellus* by Redhead. I agree with this assessment, leaving *G. quinaultii* as a separate taxon.

Specimens examined. Canada, British Columbia, vic. Whistler, Paradise Valley between Whistler and Squamish, 49°50'35" N, 123°09'25" W, 6.X.1990, coll RHP &

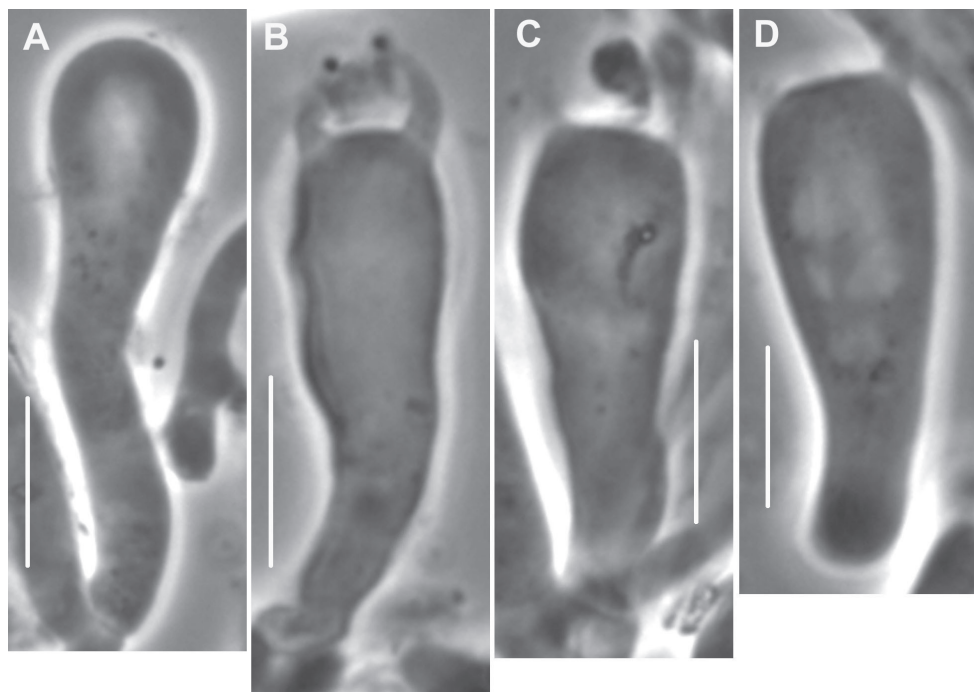


Figure 69. *Gymnopus quinaultii*. Hymenial elements. **A** Basidiole **B–D** Basidia. Standard bars = 10 μm . TFB 5886 (TENN-F-51994).

LWH, TFB 3400/4 (TENN-F-49650). **United States**, Washington, Grey's Harbor Co., vic Amanda Park, Forest service Rd. 2140, "Higley's swamp," 16.X.1992, coll RHP & KWH, TFB 5886 (TENN-F-51994; holotype).

10. *Gymnopus sequoiae* (Desjardin) R.H. Petersen, comb. nov.

Mycobank no. 552486

Basionym. *Micromphale sequoiae* Desjardin. 1985. Mycologia 77: 894–895.

Holotype. **United States, California**, Mendocino Co., Jackson State Forest, junction of state roads 408 & 409, 13.XI.1982, coll & det D.E. Desjardin, DED 1740 (SFSU-F-000711).

Diagnosis (fide Desjardin 1985). 1) fruiting on needle debris of *Sequoia sempervirens*; 2) light brown to flesh-colored, rugulose pileus; 3) lamellae concolorous with pileus; 4) odor mild; 5) grayish-orange to brown pubescent stipe; 6) pileipellis of filamentous hyphae in a slime matrix (no *Rameales*-structure); 7) poorly developed rhizomorphs.

The following description is a rearrangement of the protologue plus observations on dried material.



Figure 70. *Gymnopus quinaultii*. Caulocystidia. Note origin as side branches and internal secondary septa. Standard bars = 10 μ m. TFB 5886 (TENN-F-51994).

Basidiomata (Figs 71, 72A) pliant, marcescent, reviving. **Pileus** 6–12 mm broad, when young convex to campanulate, often with a short, acute umbo, in age becoming broadly convex to plano-convex with or without a central papilla, occasionally plane with a shallow central depression; margin when young decurved or slightly incurved, even, entire, in age becoming straight, wavy, crenate, rugulose-striate to rugulose-sulcate $\frac{1}{4}$ of the distance to center; surface dry to moist, dull glabrous, hygrophanous, at first light brown 7D4–5 overall, rarely with disc reddish brown 8E5–7, in age disc remaining light brown or fading to brownish orange 6C3–4; margin in age fading to brownish orange, greyish orange 6B2–3 or orange white 5A2, in age rarely colored buff overall with a slightly darker disc; pileus trama light brown to brownish orange, soft, up to 1 mm thick. **Lamellae** adnate, free in age or rarely attached to a pseudocol-



Figure 71. *Gymnopus sequoiae*. Basidiomata in natural habitat. **A** Courtesy Michael Wood **B** Ryan Snow, Mushroom Observer. Standard bars = 20 mm.

lar, close to subdistant, narrow to medium broad (up to 1 mm), rarely anastomosing or intervenose, total lamellae = 25–27, through lamellae = 14–16; at first pale greyish orange 6B2, fading in age to pale orange white 5–6A2, typically concolorous with the pileus margin at maturity; edge even, entire, concolorous; lamellulae in 1–2 series. **Stipe** 20–43 × 0.7–1.5 mm broad, terete or rarely apically compressed and cleft, equal or tapered downward, hollow, cartilaginous, insititious; context concolorous with stipe surface; apex pruinose, off-white, downward pubescent and often with furfuraceous base, when young, apical portion pale greyish orange 6B2, central portion light brown 7D4–6, base dark brown 7F5–7 to rusty brown, in age apex becoming pale brownish orange 7C3, central portion becoming brown 7E4–5, base becoming dark brown 7–8F4–8 or occasionally dark brown overall in age. **Rhizomorphs** (Fig. 69A) short, slender, black, poorly developed, scattered; sterile stipes rare. **Taste** strongly alliaceous after 1–2 minutes; **odor** mild or rarely slightly fetid when old and wet.

Habitat and phenology. Scattered to gregarious on branchlets and leaves of *Sequoia sempervirens*; presumably throughout the range of *S. sempervirens* (at least northern California); October–February.

Pileipellis of inner limb up to 60 µm thick, involved in a slime matrix; slime material heterogeneous with copious crystal suspension, transparent, not totally soluble in KOH, hyaline; hyphae (Fig. 73A) 3.6–11 µm diam, repent, unoriented, interwoven, smooth, thick-walled (wall ~1.5 µm thick), conspicuously clamped (Fig. 73B) but with frequent secondary septa (Fig. 73C). **Pileus trama** loosely interwoven; hyphae smooth, non-gelatinized, 4.2–7.2 µm broad, with hyaline to pale yellowish, inamyloid

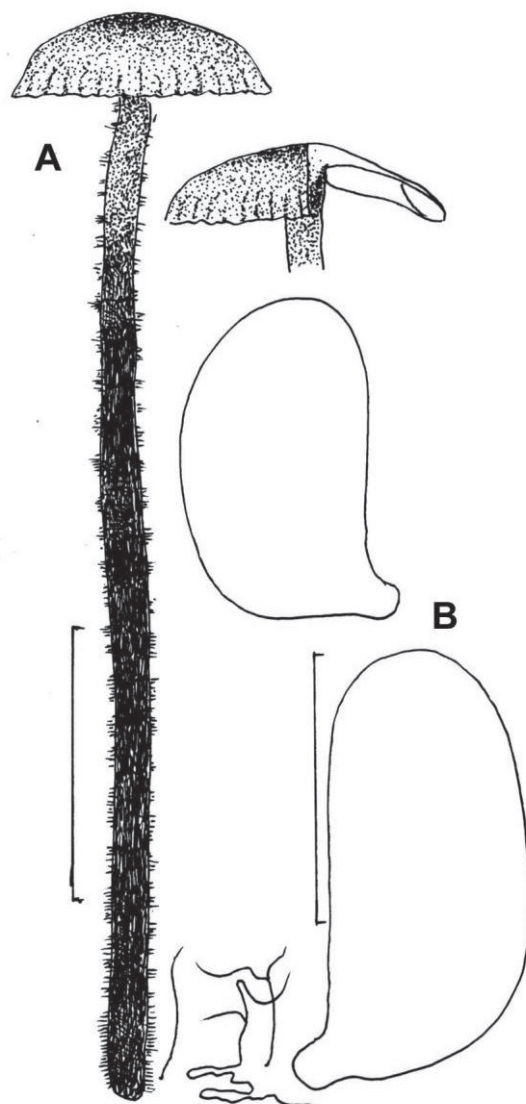


Figure 72. *Gymnopus sequoiae*. **A** Basidiomata and rhizomorphs **B** Basidiospores. Standard bars: **A** = 10 mm; **B** = 5 μ m. TFB 14620 (TENN-F-69325).

walls up to 1.5 μ m thick. **Lamellar trama** interwoven, of two hyphal types: 1) filamentous hyphae 3.5–7 μ m diam, firm-walled, clamped, not incrusting or gelatinizing; and 2) free-form hyphae, inflated to 13 μ m diam, often articulating with neighboring hyphal segments, firm- to thick-walled (wall 0.7 μ m thick, hyaline); contents with scattered inclusions (PhC). **Pleurocystidia** (Fig. 74A–D) 21–31 \times 7–8 μ m, fusiform, clamped; contents homogeneous, dense (PhC). Basidioles broadly clavate, often becoming ampulliform, clamped; contents multigranular; **basidia** (Fig. 74E–H) (21–



Figure 73. *Gymnopus sequoiae*. Pileipellis structures. **A** Hyphae with subgelatinized walls in slime matrix **B** Clamp connection **C** Secondary septa. Standard bars = 10 μm . TFB 14620 (TENN-F-69325).

)25–30 \times (6–)9–11 μm , clavate, hyaline, (2–) 4-sterigmate; contents multigranular; sterigmata up to 4.8 μm long. **Basidiospores** (Fig. 72B) (6–)6.5–7.5(–8) \times 3–4 μm ($Q = 1.63\text{--}2.00$; $Q^m = 1.81$; $L^m = 6.50 \mu\text{m}$) ellipsoid to lacrymoid, hyaline, smooth, inamyloid, white in deposit. Lamellar edge basically fertile; **cheilocystidia** (Fig. 75) common but scattered, 27–33 \times 4.8–6.6 μm , clavate or ventricose-rostrate, occasionally submammillate, hyaline and thin-walled, projecting up to 11 μm beyond basidia. **Stipe medullary hyphae** (Fig. 76A) free (walls not gelatinized), 3–7.5(–11.5) μm diam, thick-walled (wall 1.0 μm thick, hyaline), conspicuously clamped. **Stipe cortical hyphae** (Fig. 76C) 4–8.5 μm diam, thick-walled (wall 1.0 μm thick), strongly incrustated in thick scabs and annuli, pigmented (yellow-brown, PhC), easily shattering in squash mounts. **Caulocystidia at stipe apex** (Fig. 76B, D, E) 10–140 \times 9–13 μm , arising from incrustated surface hyphae with somewhat constricted attachment, subventricose and usually tapering slightly distally, thick-walled (wall 2.5 μm thick, hyaline), often strangulate, often secondarily septate and/or clamped. **Caulocystidia from stipe base**, (Fig. 77B–F) 25–170 \times 9–13 μm , versiform, irregular in outline with obtuse apices; walls brown, evenly pigmented, 1.2 μm thick.

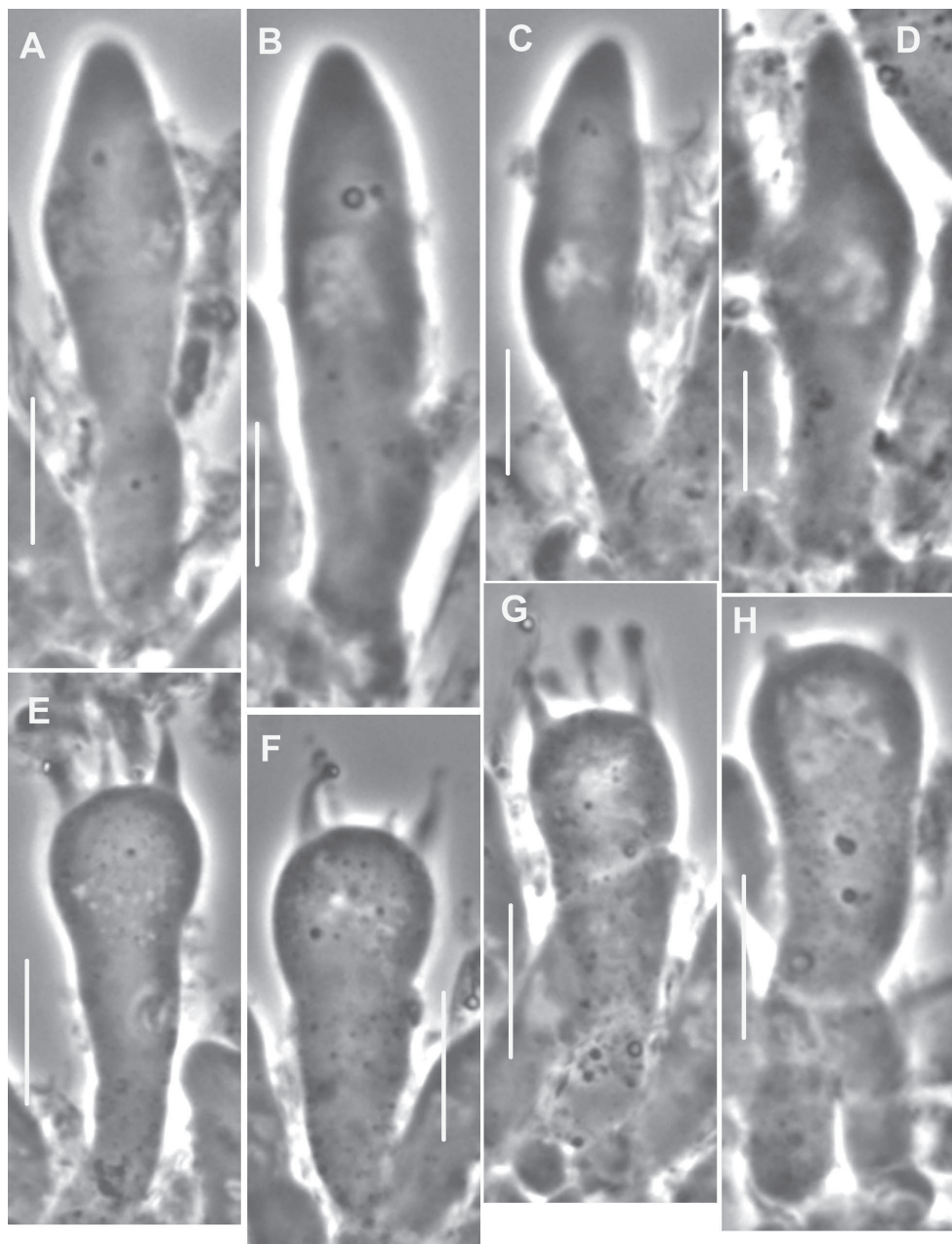


Figure 74. *Gymnopus sequoiae*. Hymenial structures. **A–D** Pleurocystidia **E–H** Basidia. Standard bars = 10 μm. TFB 14620 (TENN-F-69325).

Commentary. Care was taken to demonstrate all stages of basidiolate maturation to demonstrate the difference between young basidiolae and cheilocystidial structures. Basidiolae are abundant over all of the lamellar surface and are subspherical at the ear-

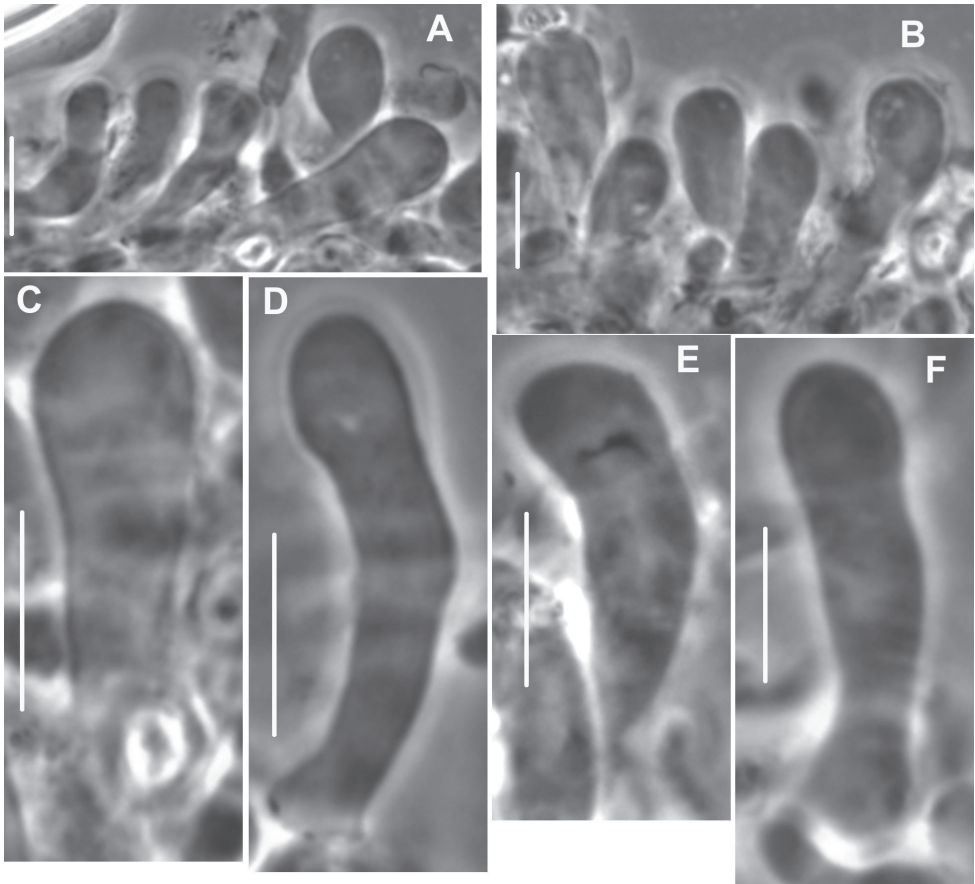


Figure 75. *Gymnopus sequoiae*. Cheilocystidia. **A, B** Clusters of cheilocystidia **C–F** Individual cheilocystidia. Standard bars = 10 μm . TFB 14620 (TENN-F-69325).

liest stage, soon becoming broadly clavate and developing a subcapitulate upper portion. Basidia remain broadly clavate throughout spore development. Contents of such structures are consistently multigranular. Although cheilocystidia are similar in dimensions and appearance, contents are homogeneous (PhC), and such structures are found only at the lamellar edge. Conversely, pleurocystidial structures are fusiform from their earliest state, merely elongating to mature size and shape. Contents are homogeneous except for a vacuolated area in midsection (perhaps nucleus; PhC).

Caulocystidia arise as side branches of stipe surface, incrusting hyphae. Early stages of caulocystidial development often bear a shagreened surface but soon becoming smooth. A unique character is the frequent internal secondary septation, as well as occurrence of a clamp connection near caulocystidial origin.

Specimens examined. **California**, Humboldt Co., Redwood National Park, Davidson Rd., N41°12'51", W124°00'12", 24.X.1992, coll & det DE Desjardin, DED 5546 (SFSU-F-025665); Redwood National Park, Davidson Rd., N41°12'51",

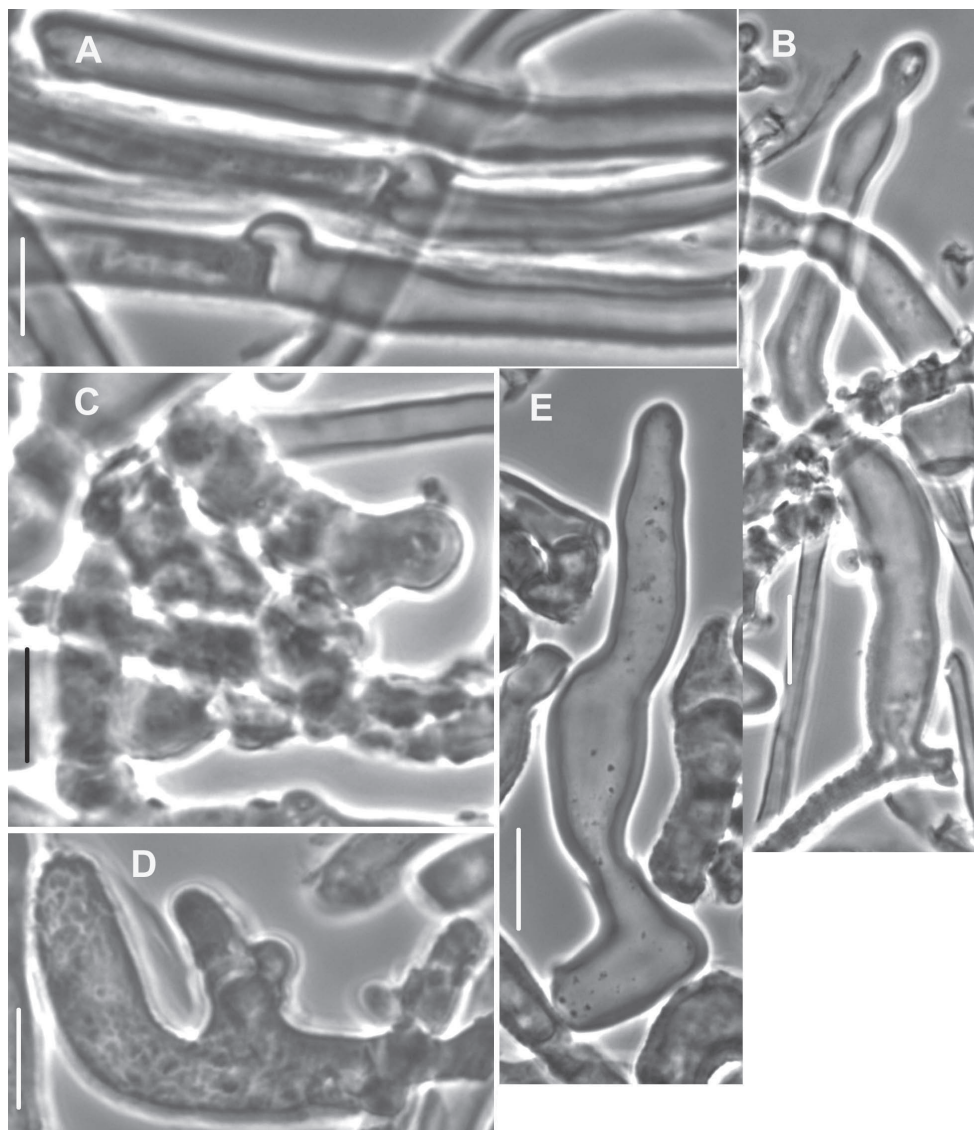


Figure 76. *Gymnopus sequoiae*. Stipe apex structures. **A** Stipe medullary hyphae **C** Strongly incrusted cortical hyphae **C** Young caulocystidium with shagreened surface **B, E** Individual caulocystidia. Standard bars = 10 μ m. TFB 14620 (TENN-F-69325).

W124°00'12", 24.X.1992, coll & det DE Desjardin, DED 5546 (SFSU-F-025665); Mendocino Co., vic. Fort Bragg, Simpson Lane, 28.IX.1986, coll & det H.D.Thiers, HDT 50541 (SFSU-F-025669); Jackson State Forest, Hwy 408 at junction with road to Mendocino Woodlands, 21.XI.2015, coll & det DE Desjardin, DED 8802/TFB 14620 (TENN-F-69325); Jackson State Forest, along Hwy 409 car 1 mi from junction of Hwy 408, 18.XI.1995, coll & det DE Desjardin, DED 6316 (SFSU-F-025662); same loca-

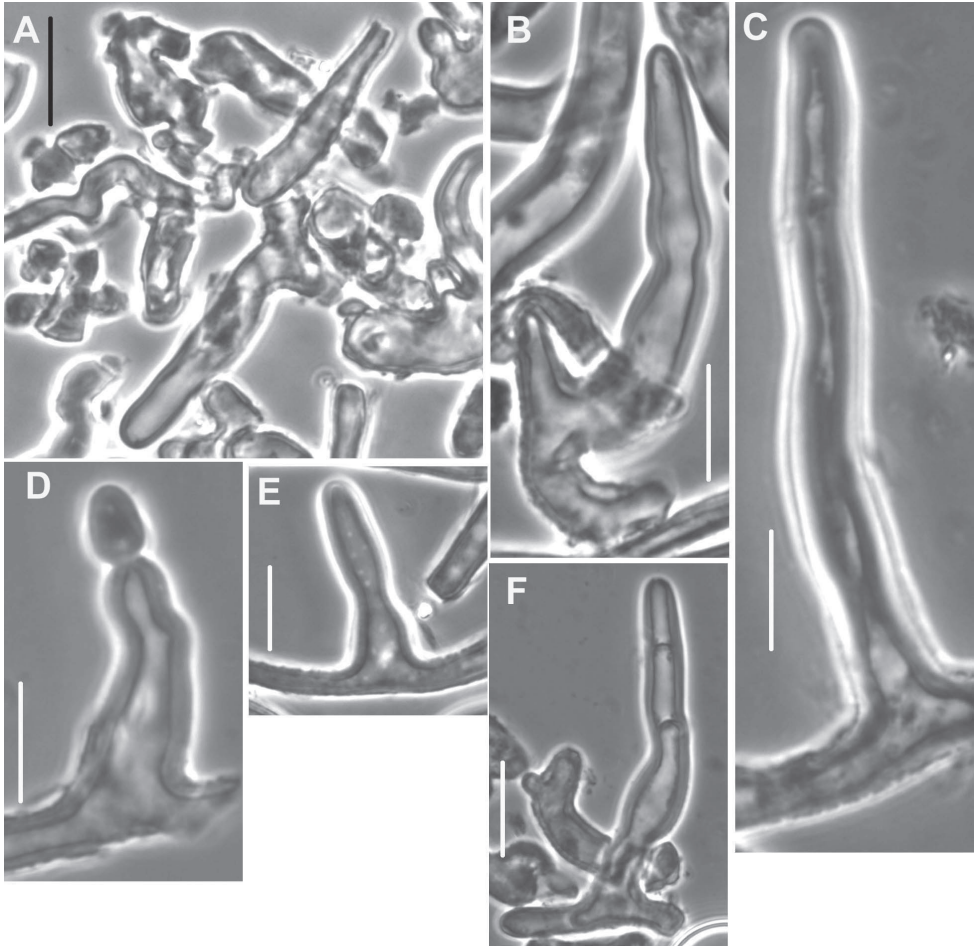


Figure 77. *Gymnopus sequoiae*. Lower stipe structures. **A** Stipe surface free-form cells with one caulocystidium **B–F** Individual caulocystidia showing broad-based origin and secondary septa. Standard bars = 10 μm . TFB 14620 (TENN-F-69325).

tion, 13. Nov. 1982, DED 1740 (holotype); same location, Hwy 409, 13.XII.1990, coll & det D.E. Desjardin, DED 5023 (SFSU-F-025663); same location, “Aleuria Glen,” 29.X.1990, coll H.D. Thiers, det D.E. Desjardin, DED 5012 (SFSU-F-025668).

11. *Gymnopus sublaccatus* R.H. Petersen, sp. nov.

Mycobank no. 552484

Holotype. Canada, British Columbia, Victoria, Saanich Peninsula, Observatory Hill, N48.5262°, W123.422°, 4.XI.2011, coll & det O. Ceska (as *Marasmius androsaceus*), UBC-F-25212.

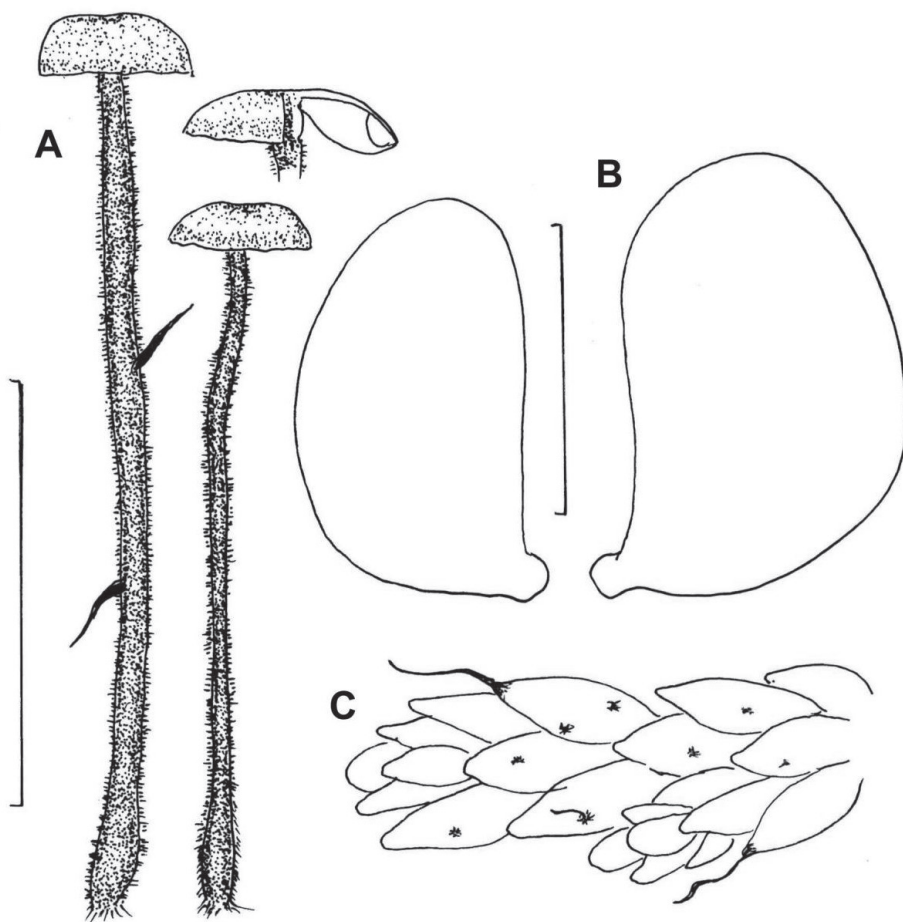


Figure 78. *Gymnopus sublaccatus*. **A** Basidiomata showing adventitious rhizomorphs and stipe insertion to pileus **B** Basidiospores **C** Substrate scales with back spots and rhizomorphs. Standard bars: **A** = 20 mm; **B** = 5 μ m; **C** = not to scale. UBC 25212.

Etymology. sub- = Latin: less than; laccatus = Latin: appearing polished or varnished, referring to varnished appearance of dried pileus.

Diagnosis. 1) Fruiting on needles of *Thuja* (and *Pseudotsuga*); 2) cheilocystidia rare, small, clavate, smooth, without setulae; 3) stipe near ochraceous buff above, downward rusty brown; 4) pileal hairs usually smooth, rarely roughened; 5) dried pileus sublaccate; 6) pileipellis of smooth, unencrusted, repent hyphae in slime matrix; 7) rhizomorphs inconspicuous, with minute black basal pad.

The following description is based solely on dried material.

Description. **Basidiomata** (Fig. 78A) diminutive. **Pileus** 2–8 mm broad, convex to plano-convex, minutely laccate, vaguely tuberculate, not striate or sulcate; disc

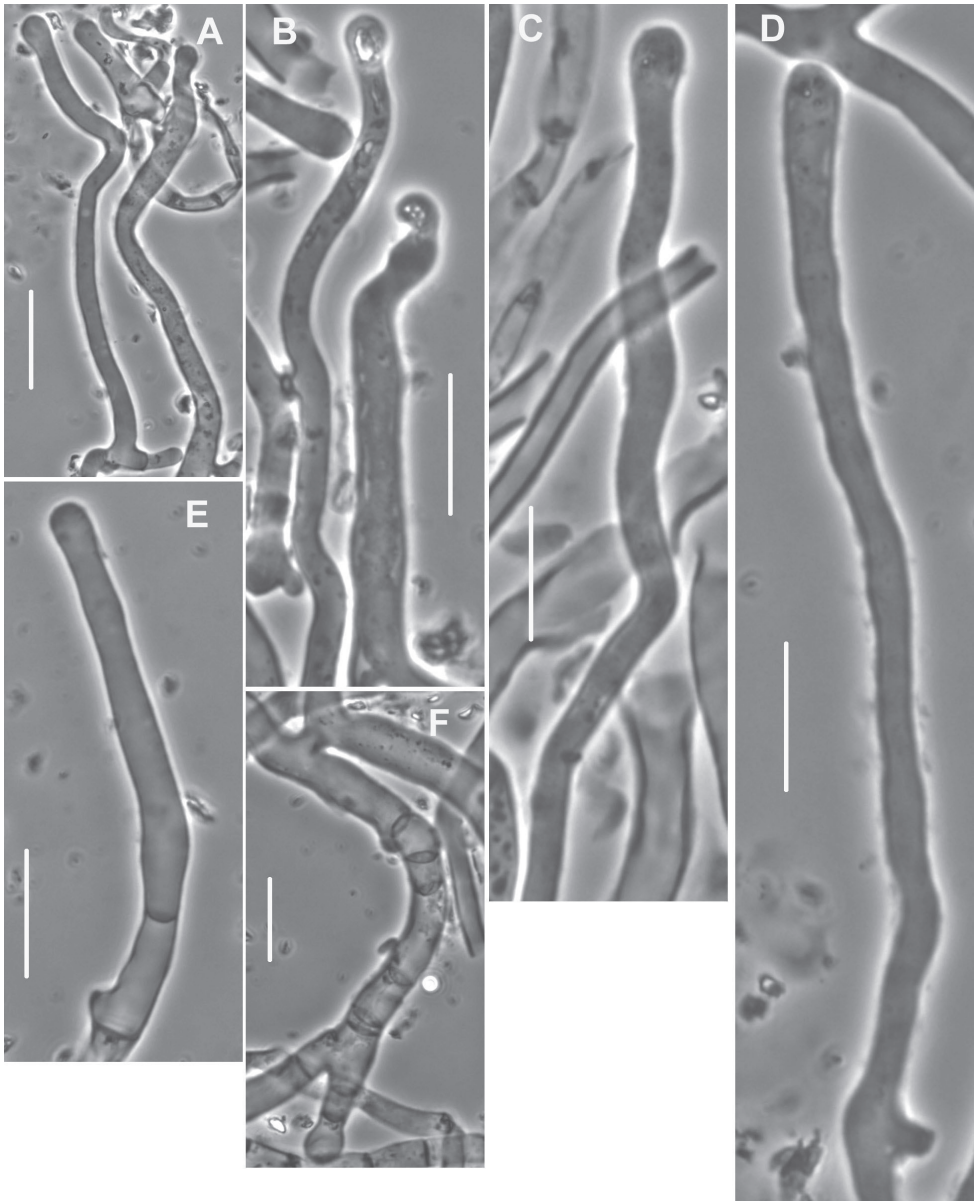


Figure 79. *Gymnopus sublaccatus*. Pileipellis elements. **A–E** Pileal hairs **F** Secondary septa of pileipellis hypha. Standard bars = 10 µm. UBC 25212.

about “saya brown” 6C5 to “ochraceous buff” 5A5; limb and margin about “light ochraceous buff” 5A4 to “tilleul buff” 7B2. **Lamellae** (Fig. 78A) pseudocollariate (dried), adnate, distant, thickish, total lamellae = 20–23, through lamellae = 9–11, now (dried) “tilleul buff” 7B2 to “olive buff” 3B3; lamellulae in a single rank. **Stipe** 18–25 × 0.6–0.8 mm, terete, equal, hollow to lightly stuffed, subsinistitious, minutely shaggy

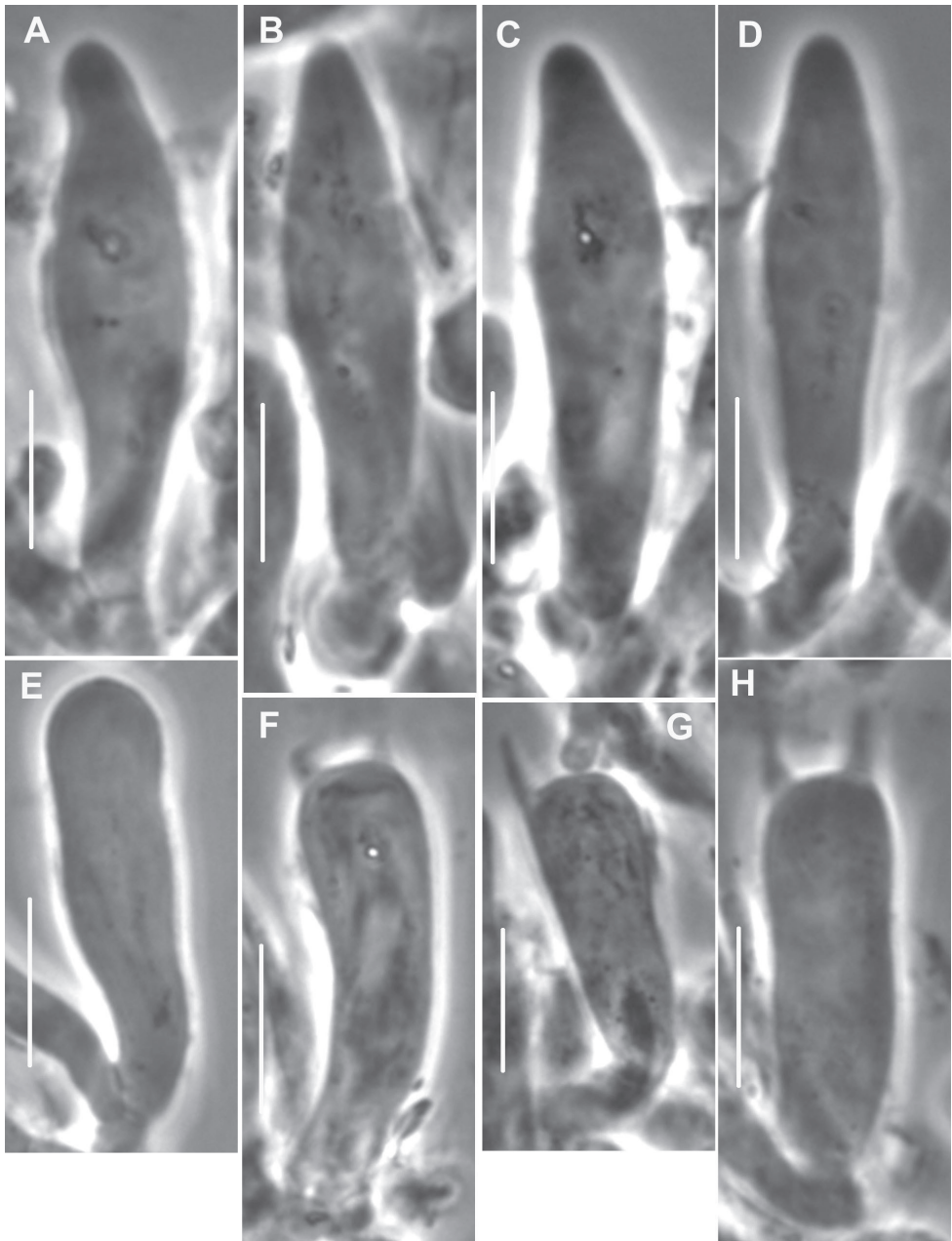


Figure 80. *Gymnopus sublaccatus*. Hymenial elements. **A–D** Pleurocystidia **E** Basidiole **F–H** Basidia. Standard bars = 10 μ m. UBC 15356.

to silky above, downward becoming minutely barbed (35 \times), above about “ochraceous buff” 5A5, downward through “army brown” 8D5, increasingly dark to rusty brown (“Prout’s brown” 5F6 to “Vandyke brown” 7E6), sometimes slightly expanded at base;

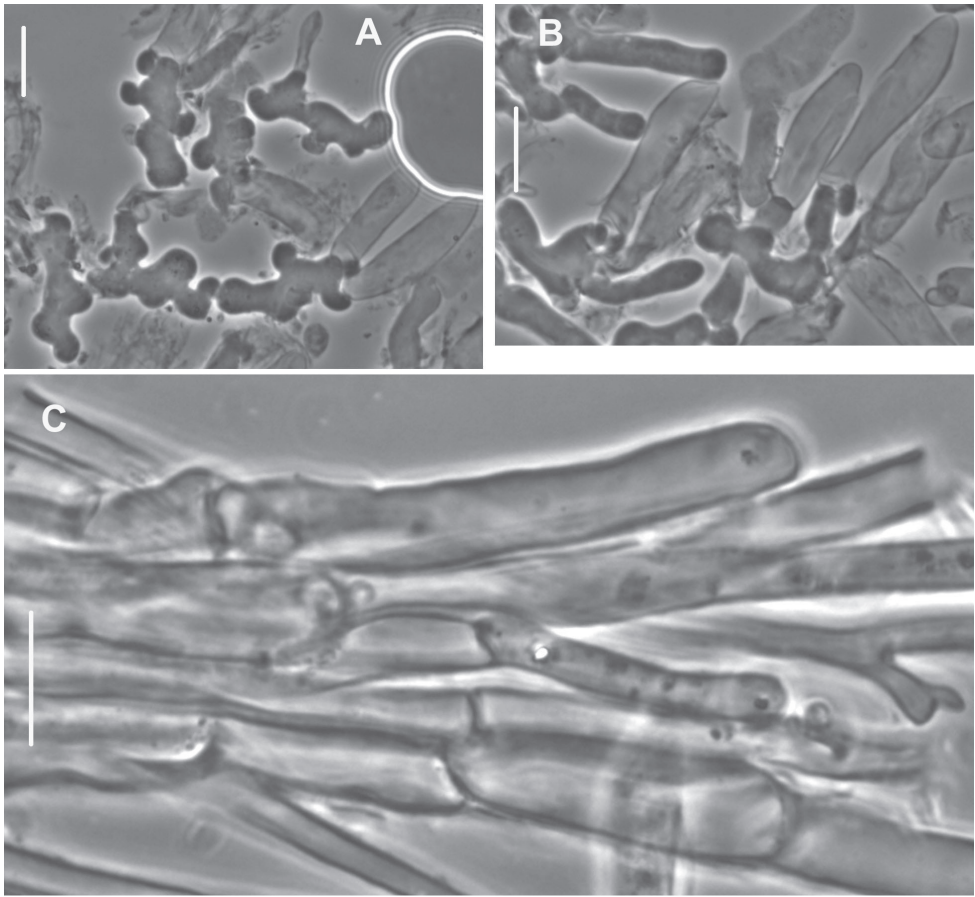


Figure 81. *Gymnopus sublaccatus*. **A** Subbasidial hyphae appearing beaded **B** Effete hymenial structures without collapse (“husking”) **C** Stipe medullary hyphae. Standard bars = 10 μm . UBC 25212.

stipe medulla white. **Rhizomorphs** (Fig. 78C) (if produced) inconspicuous, often represented only by minute, black basal pads. **Taste** and **odor** not recorded.

Habitat and phenology. Fruiting on needles of *Thuja plicata*, less often on *Pseudotsuga menziesii*; British Columbia; Autumn to early Winter.

Pileipellis involved in a slime matrix which includes deterrent encrusting material, of the following elements: 1) pileal hairs (Fig. 79) $150 \times 3\text{--}6\ \mu\text{m}$, erect, firm-walled, smooth or rarely weakly roughened, slightly subcapitulate; 2) repent hyphae $4.5\text{--}7.5\ \mu\text{m}$ diam, firm-walled, conspicuously clamped but often secondarily septate, without discernable slime sheath. Pileus and lamellar tramae loosely interwoven; hyphae $3\text{--}5.5\ \mu\text{m}$ diam, smooth, firm-walled, without slime sheath, conspicuously clamped. **Pleurocystidia** (Fig. 80A–D) $25\text{--}35(\text{--}41) \times 7\text{--}8\ \mu\text{m}$, fusiform to clavo-fusiform, without partitioned contents but with vague vacuolated area in midsection (PhC), conspicuously clamped. Basidioles (Fig. 80E) clavate; **basidia** (Fig. 80F–H) $24\text{--}27 \times 8\text{--}9\ \mu\text{m}$, clavate, 4-sterigmate, clamped; contents multigranular at maturity; effete pleurocystidia and basidia emptying but not col-

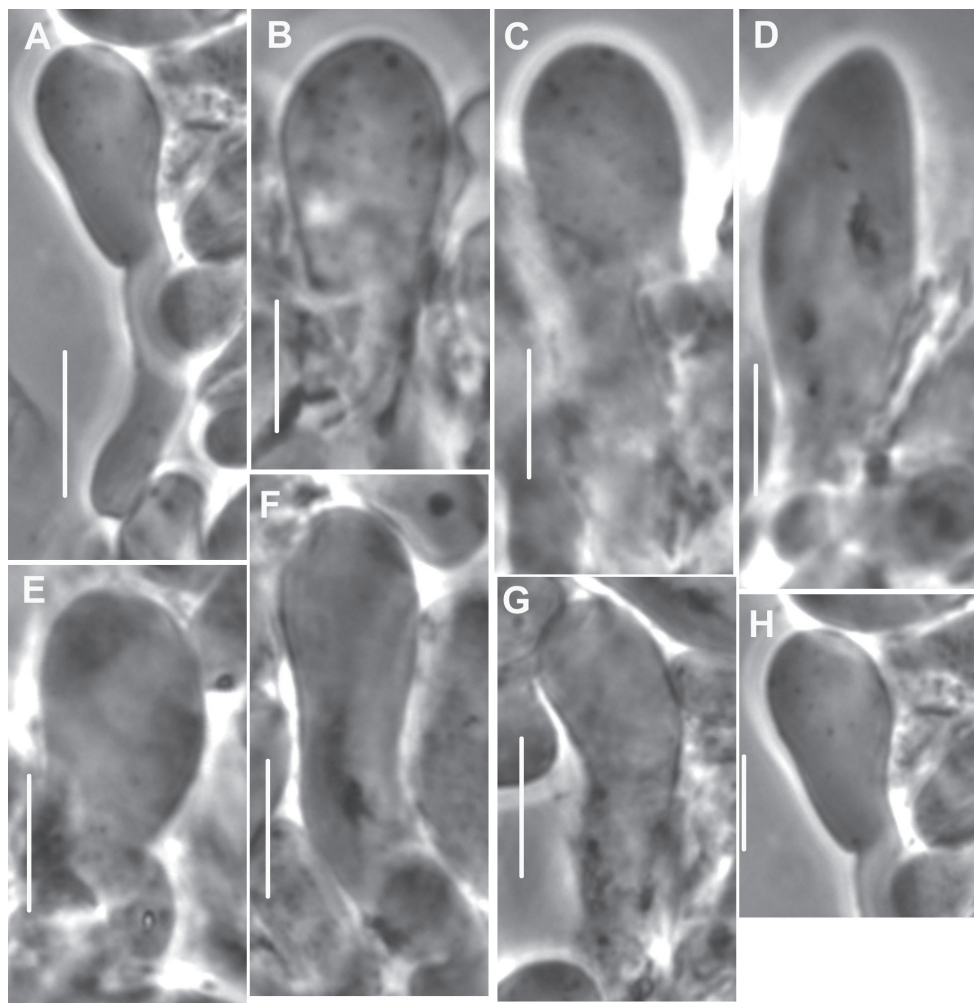


Figure 82. *Gymnopus sublaccatus*. Cheilocystidia. Standard bars = 10 μ m. UBS 15356.

lapsing (“husking” Fig. 81B); subbasidial hyphae (Fig. 81A) rupturing at clamp connections, appearing beaded. **Basidiospores** (Fig. 78B) $(6.5\text{--}7\text{--}7.5\text{--}8) \times (3.5\text{--}4\text{--}5)$ μ m ($Q = 1.40\text{--}1.88$; $Q^m = 1.67$; $L^m = 7.20$ μ m), rotund-ellipsoid, smooth, thin-walled, inamyloid. **Cheilocystidia** (Fig. 82) very locally common, usually rare to absent, $14\text{--}22 \times 8\text{--}12$ μ m, clavate to utriform, thin-walled, obscurely clamped; contents homogeneous. **Stipe medullary hyphae** (Fig. 81C) $4\text{--}12$ μ m diam, strictly parallel, apparently free (no discernable gelatinized matrix, hyaline, thick-walled (wall ~ 0.7 μ m thick, hyaline, non-gelatinized), obscurely clamped, often with small side-branches ranging from lobate to rudimentarily branched. **Stipe cortical hyphae** $4\text{--}8$ μ m diam, strictly parallel, apparently free, thick-walled (wall ~ 1.2 μ m thick, especially at stipe surface), pigmented (yellow-brown, KOH + PhC), appearing moderately dextrinoid (IKI + PhC), or not so (IKI + BF), often producing broad-based side branches. **Caulocystidia** (Figs 83, 84) ~ 45 μ m at stipe apex, ~ 140 μ m

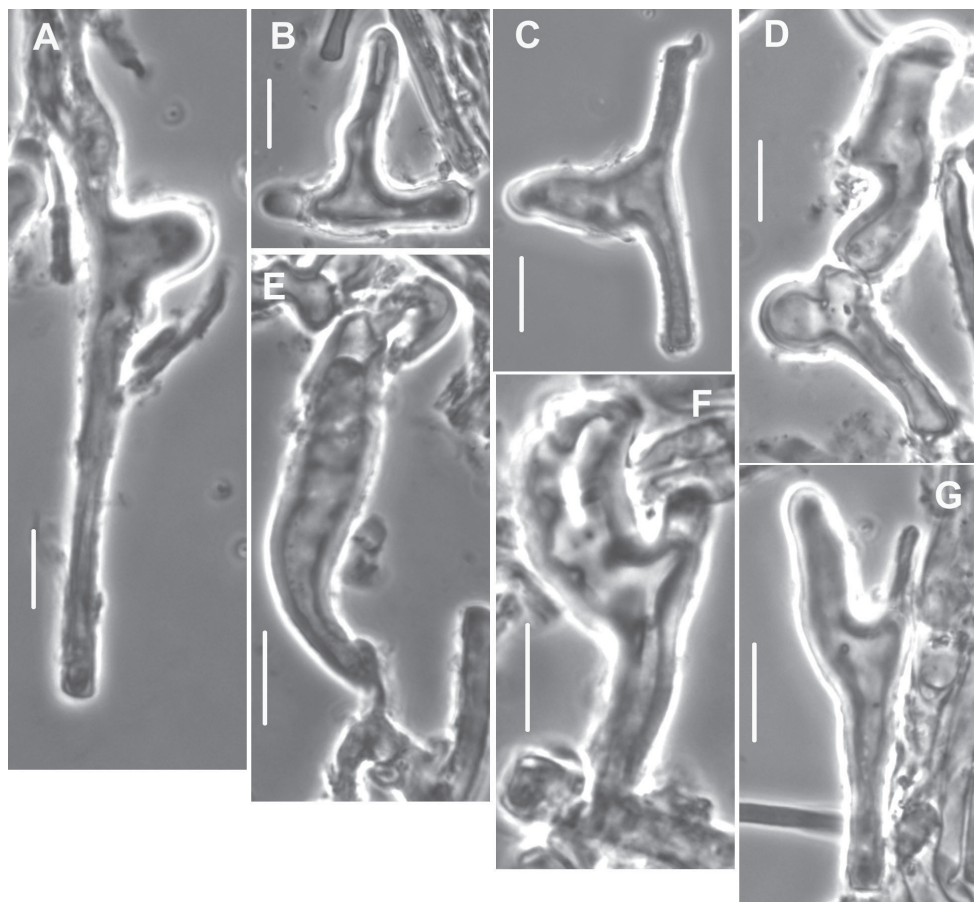


Figure 83. *Gymnopus sublaccatus*. Caulocystidia from stipe apex. Standard bars = 10 μm . UBC 25212.

at stipe base, $\times 5.5\text{--}10\ \mu\text{m}$, ranging from lobate to elongate-digitate, without basal clamp, often internally secondarily septate, sometimes branched in one rank, thick-walled [wall $\sim 4\ \mu\text{m}$ thick, often occluding cell lumen, pigmented (yellow-brown PhC)].

Commentary. With slime matrix covering the pileus surface and involving hymenial structures, with characteristic clavate cheilocystidia and with vestured stipe, UBC 25212 seems certain to belong in sect. *Perforantia*. There it joins *G. perforans*, *G. foliophilus* and *G. sequoiae* with the same general characters. From *Ma. androsaceus*, *G. sublaccatus* differs in pigmented (not black), vestured stipe. If its substrate preference is limited to *Pseudotsuga*, this constitutes another difference. Finally, pileipellis of *G. androsaceus* is characterized by diverticulate hyphal segments and broom cell-like hyphal termini, unlike that of *G. sublaccatus* which lacks these structures.

Basidiomata of *G. sequoiae* resemble those of *M. sublaccatus* in stature and size, but seems limited to fruiting on needles of *Sequoia sempervirens* in northern California. Cheilocystidia are shaped like an incandescent bulb, sometimes slightly askew, but otherwise quite typical of cheilocystidia in this taxonomic complex (compare, for example,

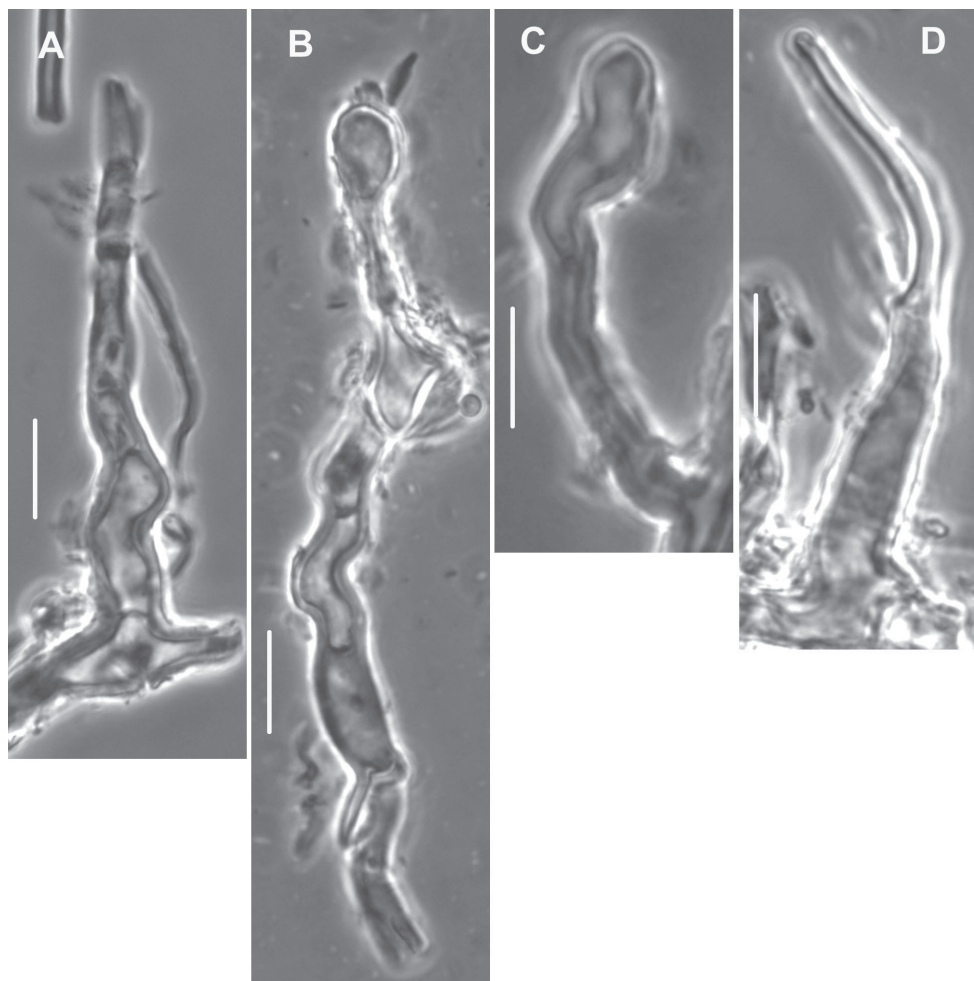


Figure 84. *Gymnopus sublaccatus*. Caulocystidia from stipe base. Standard bars = 10 μ m. UBC 25212.

those of *G. bulliformis* and of *G. sequoiae*). Difficult to distinguish from immature basidia, such cheilocystidia are less obscure after several sightings.

Specimens examined. **Canada, British Columbia**, Queen Charlotte Islands, Burnaby Island, Section Cove, N52°24'35", W131°19'55", 8.IX.2006, coll PK Kroeger (as *Marasmius androsaceus*), PK 489 (UBC F18168); Queen Charlotte Islands, N52°21'23", W131°24'24", 11.IX.2008, coll P. Kroeger (as *Marasmius androsaceus*), PK 5904 (UBC F16670); Queen Charlotte Islands, Ellen Island, N52°09', W131°06', 10.IX.2004, coll & P. Kroeger, B. & C. Kendrick, J. Brown, (as *Marasmius androsaceus*), PK 2932 (UBC F15356); Queen Charlotte Islands, Ross Island, N52°10', W131°07', 2.IX.2006, coll P. Kroeger (as *Marasmius androsaceus*), PK 4347 (UBC F17675); Victoria, Saanich Peninsula, Observatory Hill, N48.5262°, W123.422°, 4.XI.2011, coll & det O. Ceska (as *Marasmius androsaceus*), UBC-F-25212 (holotype).

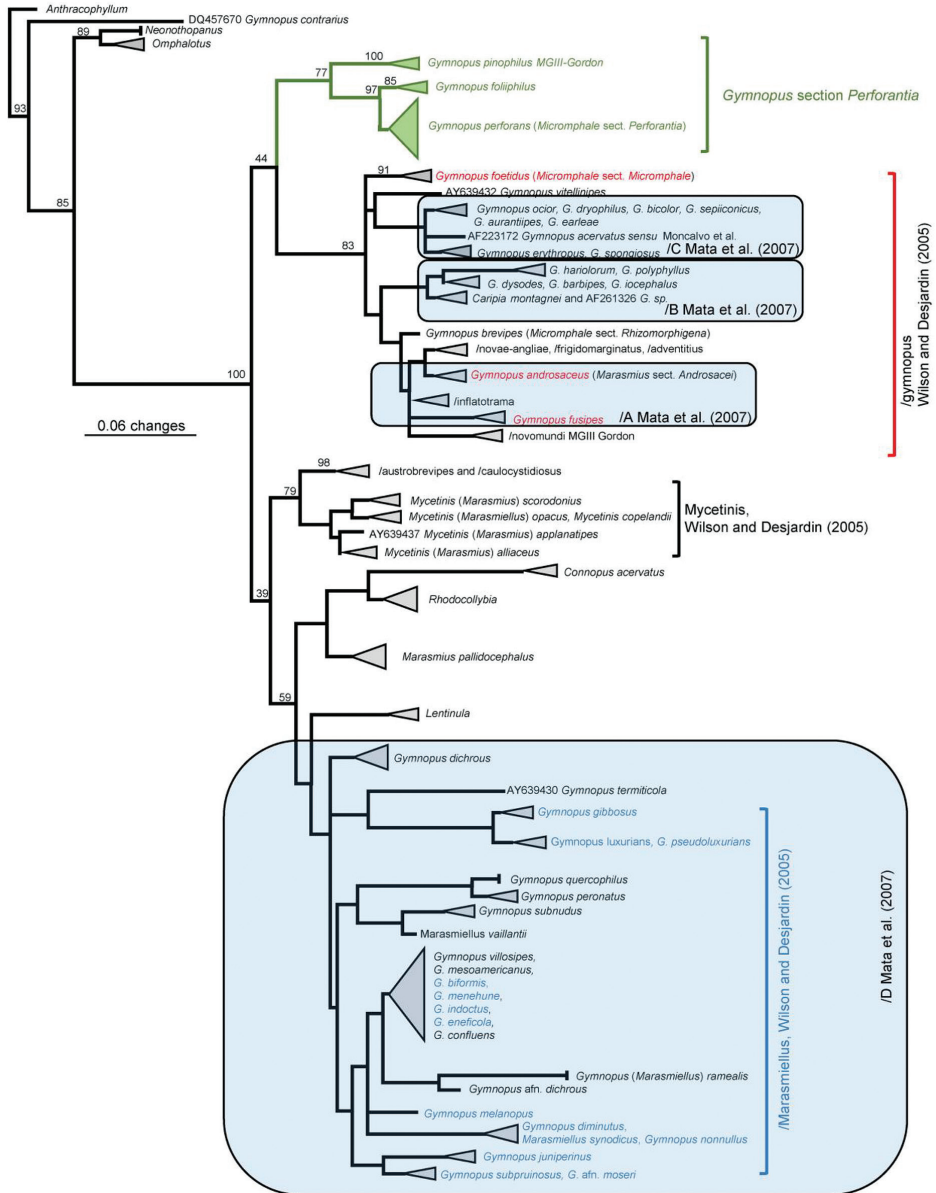


Figure 85. PhyML analysis of 191 nrLSU sequences within the Omphalotaceae using 100 bootstrap replicates. Clades were collapsed to better show broad relationships. Species names in blue represent /marasmiellus (Wilson and Desjardin 2005). Species names in red represent /gymnopus (Wilson and Desjardin 2005). The major clades reported in Mata et al. (2007) are overlaid in blue. Section Perforantia is indicated in green.

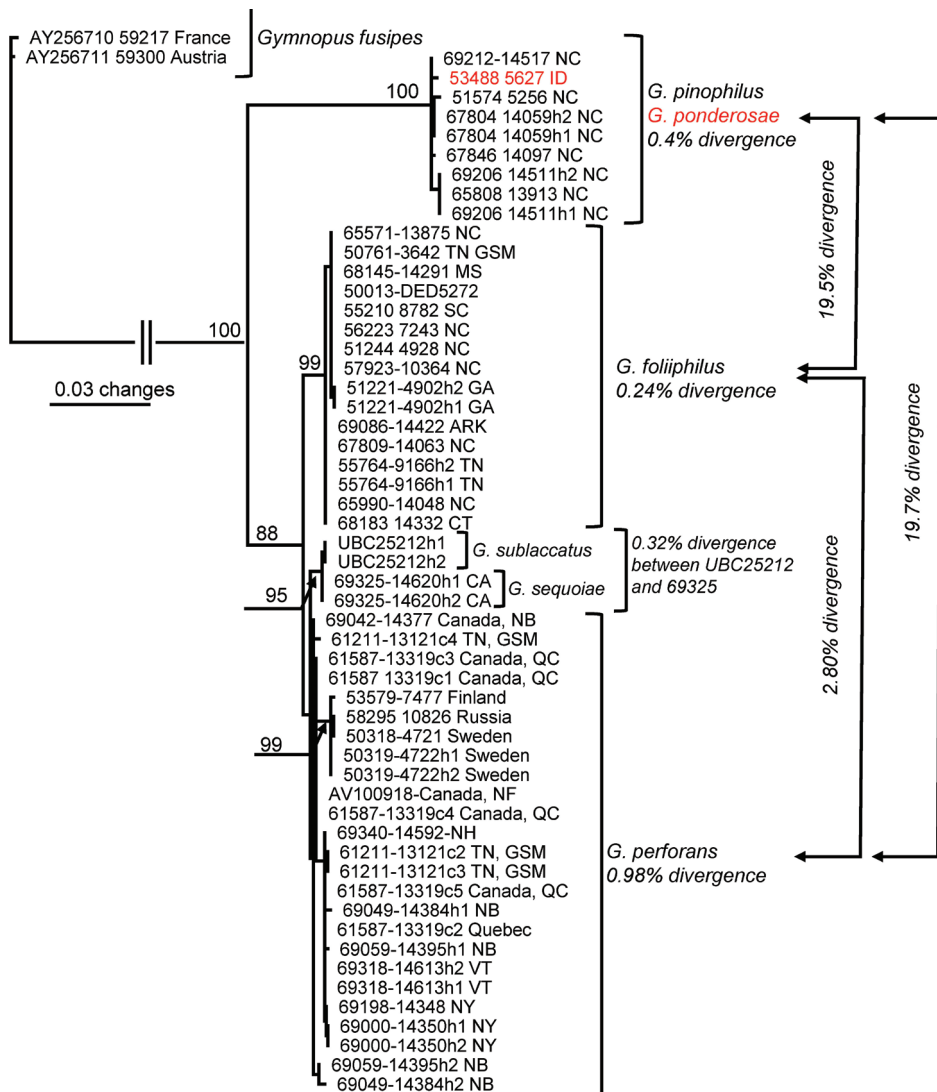


Figure 86. PhyML phylogeny of *Gymnopus* section *perforantia* based on nrITS plus nrLSU sequences. Distance measurements percent base pair differences for the ITS region only. Bootstrap support greater than 70% is given to the left of the supported node. Haplotypes are indicated as h1 or h2; clones are indicated as c1, c2, etc. North American locations are indicated by postal codes.

Molecular analyses

Results of molecular analyses are summarized in Figs 85–87. A phylogenetic analysis of 191 representative *Gymnopus*, *Marasmius* and *Micromphale* nrLSU sequences (Fig. 85) placed *Gymnopus* (*Micromphale*) *perforans*, *G. foliophilus* and *G. pinophilus* in a single well-supported clade (bootstrap=77%). This clade is sister to *Gymnopus* s. s. (anchored

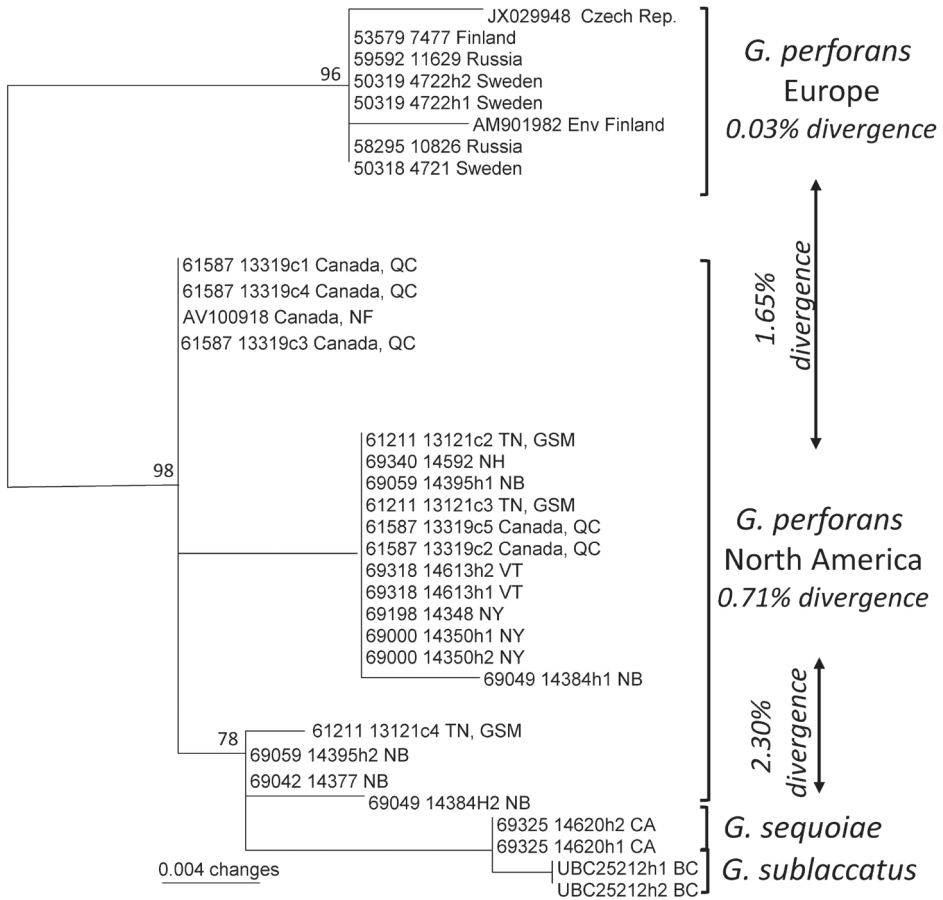


Figure 87. PhyML analysis of *Gymnopus perforans* and *G. sequoiae* ITS sequences. Distance measurements percent base pair differences for the ITS region only. Bootstrap support greater than 70% is given to the left of the supported node. Haplotypes are indicated as h1 or h2; clones are indicated as c1, c2, etc. North American locations are indicated by postal codes.

by the *Gymnopus* generic type *G. fusipes* (Fig. 85, red) but with low bootstrap support (44%). *Gymnopus fusipes*, (*Micromphale*) *foetidus*, members of the former *Marasmius* sect. *Androsacei* [Clades A and B of Mata et al. (2007)] and *Gymnopus brevipes* (*Micromphale* sect. *Rhizomorphigena*) appear together in a well-supported clade (83%) confirming that *Micromphale* is polyphyletic with some species belonging to *Gymnopus*. Results of this phylogenetic analysis suggest that *Gymnopus* is also polyphyletic, consistent with findings by Wilson and Desjardin (2005) who informally segregated some *Gymnopus* taxa into *Marasmiellus*.

A phylogenetic analysis of only the *Perforantia* based on a concatenated nrITS and LSU data set is given in Fig. 86 together with average base-pair differences based

on nrITS alone. Clades for putative species *G. pinophilus*, *G. foliophilus*, *G. sequoiae* and *G. perforans* are well-supported. *Gymnopus pinophilus/ponderosae* is distinct from the remaining taxa (approximately 19% ITS sequence divergence). Within-taxa divergence is low (Fig. 86). *Gymnopus perforans* (European and North American collections combined) had a within-species bp divergence of 0.98%. The remaining within-taxa divergence estimates are 0.24% bp divergence for *G. foliophilus*, 0.32% bp divergence for *G. sequoiae* plus *G. sublaccatus* and 0.4% bp divergence for *G. pinophilus*.

An unrooted nrITS phylogeny of *G. perforans* and *G. sequoiae* plus *G. sublaccatus* only is given in Fig. 87. Examination of sequence motifs suggests that within North America there are likely three ancestral haplotypes with evidence for mating and meiotic recombination between the haplotypes. European haplotypes are more homogeneous but form a distinct European clade. Long branches represent environmental samples rather than fruitbodies (JX029948 Czech Rep. and AM901982 house dust Finland).

Discussion

The members of the clade proposed as subsection *Pinophili* were at first included in *Gymnopus* sect. *Androsacei*, based on pileipellis structure (well-developed *Rameales*-structure) and cheilocystidial shape (*siccus*-type broom cells). It was surprising, therefore, that phylogenetic analyses showed that the clade was more closely related to sect. *Perforantia* than to sect. *Androsacei*. This may serve as cautionary for predictions concerning the larger and more complex sect. *Androsacei*.

Previously largely misunderstood, pleurocystidia are common and rather uniform across sect. *Perforantia*. At best, these structures were interpreted as basidioles, but this study repeatedly demonstrated basidioles as clavate, not fusiform. Pleurocystidia, conversely, are fusiform throughout development. More subtle is the apparent partition of pleurocystidial contents (see Fig. 42), seen in several taxa. This partition, when present, is always in the distal portion of the pleurocystidium, and may be observable only in PhC, not stained BF.

The three mating groups of *Ma. androsaceus* revealed by Gordon (1994) and Gordon and Petersen (1997), when exposed to molecular analysis, can be summarized as *Ma. androsaceus* s.s., *Ma. androsaceus* on deciduous leaves [recognized as two separate species (unpubl. data)], and *G. ponderosae* (this study). These three all exhibit a glabrous-shining, black stipe and similar pileipellis and cheilocystidial shapes. The former two belong in sect. *Androsacei*, but *G. ponderosae* is now found related to sect. *Perforantia*.

With previously undisclosed taxa reported here from the temperate rainforest of North America (i.e. *G. bulliformis*, *G. glabrosipes*, *G. sublaccatus*, etc.), it must be expected that additional taxa will be discovered across eastern Russia, Japan and across Canada. Likewise, ranges will be more accurately estimated when additional collections are subjected to molecular analyses.

There has been considerable discussion about the accuracy of various species concepts and the best methodology for circumscribing new species [see Taylor et al. (2000)]. What is often not discussed is that speciation may not be strictly bifurcating. Rather, peripheral speciation (parapatric speciation) may occur when a small population becomes genetically isolated from other populations by establishment of Dobzhansky-Muller incompatibilities (Bank et al. 2012; Hörandl 2006; Mayr 1963). Such isolation may be geographic in nature or ecological but when examined phylogenetically with commonly used genes, such peripheral species may not be reciprocally monophyletic with the ancestral species. To fail to recognize such events results in reduced estimates of biodiversity at a time when accurate recognition of biodiversity is increasingly important.

Three species in this study may represent examples of situations where new species form at the geographical or ecological periphery of a species domain. *Gymnopus ponderosae*, is embedded within *G. pinophilus* and therefore does not satisfy the criteria of reciprocal monophyly for phylogenetic species (Kizirian and Donnelly 2004; Moritz 1994). *Gymnopus pinophilus* does, however, satisfy criteria for ecological speciation (Ecological Species Concept) and morphological differences are evident (Morphological Species Concept). In like manner, *G. sequoiae* and *G. sublaccatus* appear to be offshoots of one branch within North American *G. perforans*. In this latter case, genetic isolation may be in part geographical and in part ecological but it is clear that some genetic separation has occurred.

Acknowledgements

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References

- Aldrovandi MSP, Johnson JE, O'Meara BC, Petersen RH, Hughes KW (2015) The *Xeromphalina campanella/kauffmanii* complex: species delineation and biogeographical patterns of speciation. *Mycologia* 107(6): 1270–1284. doi: 10.3852/15-087
- Antonín V (1987) *Setulipes*, a new genus of marasmiod fungi (Tricholomatales). *Česká Mykologie* 41: 85–87.
- Antonín V, Halling RE, Noordeloos ME (1997) Generic concepts within the groups of *Marasmius* and *Collybia* sensu lato. *Mycotaxon* 63: 359–368.
- Antonín V, Noordeloos ME (2010) A monograph of Marasmiod and Collybioid fungi in Europe. IHV-Verlag, Berlin, 480 pp.

- Bank C, Bürger R, Hermisson J (2012) The Limits to Parapatric Speciation: Dobzhansky–Muller Incompatibilities in a Continent–Island Model. *Genetics* 191: 845–863. doi: 10.1534/genetics.111.137513
- Desjardin DE (1985) New marasmioid fungi from California. *Mycologia* 77: 894–902. doi: 10.2307/3793301
- Desjardin DE (1989) The genus *Marasmius* from the southern Appalachian Mountains. PhD Dissertation, University of Tennessee, Knoxville, Tennessee.
- Desjardin DE (1990) Culture morphology of *Marasmius* species. *Sydowia* 42: 17–87.
- Desjardin DE, Horak E (1997) *Marasmius* and *Gloiocephala* in the South Pacific region: Papua New Guinea, New Caledonia, and New Zealand taxa. *Bibliotheca Mycologica* 168: 1–154.
- Desjardin DE, Petersen RH (1989) Studies on *Marasmius* from eastern North America. III. *Marasmius brevipes* and *Micromphale* sect. *Rhizomorphigena*. *Mycologia* 81: 76–84. doi: 10.2307/3759453
- Donk MA (1962) The generic names proposed for Agaricaceae. *Nova Hedwigia* (Beihefte) 5: 1–320.
- Farnet AM, Roux M, LePetit J (1999) Genotypic variations among isolates of *Marasmius quercophilus*. A white-rot fungus isolated from evergreen oak litter. *Canadian Journal of Botany* 77: 884–890. doi: 10.1139/b99-051
- GCG (2000) Wisconsin Package, Version 10.3 Accelrys Inc., San Diego, California.
- Geneious (2015) Geneious version 8.1.8 created by Biomatters. <http://www.geneious.com/>
- Gilliam MS (1976) The genus *Marasmius* in the northeastern United States and adjacent Canada. *Mycotaxon* 4: 1–44.
- Gordon SA (1994) Intraspecific variation within three species of *Marasmius* (Tricholomataceae, Agaricales, Basidiomycotina). Ph.D. Dissertation, University of Tennessee, Knoxville.
- Gordon SA, Petersen RH (1997) Intraspecific variation among geographically separated collections of *Marasmius androsaceus*. *Mycological Research* 101: 365–371. doi: 10.1017/S0953756296002687
- Hesler LR (1959) Southeastern Agaricales. IV. *Journal of the Tennessee Academy of Sciences* 34: 167–171.
- Horak E (1968) Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). *Beiträge zur Kryptogamenflora Schweiz* 13: 1–741.
- Hörandl E (2006) Paraphyletic versus monophyletic taxa – evolutionary versus cladistic classifications. *Taxon* 55: 567–570. doi: 10.2307/25065631
- Hughes KW, Petersen RH, Lickey EB (2009) Using heterozygosity to estimate a percentage DNA sequence similarity for environmental species delimitation across basidiomycete fungi. *New Phytologist* 182: 795–798. doi: 10.1111/j.1469-8137.2009.02802.x
- Kizirian D, Donnelly MA (2004) The criterion of reciprocal monophyly and classification of nested diversity at the species level. *Molecular Phylogenetics and Evolution* 32: 1072–1076. doi: 10.1016/j.ympev.2004.05.001
- Knudsen H, Vesterholt J (2012) *Funga Nordica*. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. Nodrvamp.

- Kornerup A, Wanscher JH (1967) *Methuen Handbook of Colour* (2nd revised edn). Methuen Co, London, 243 pp.
- Mata JL, Hughes KW, Petersen RH (2004) Phylogenetic placement of *Marasmiellus juniperinus*. *Mycoscience* 45: 214–221. doi: 10.1007/S10267-004-0170-3
- Mata JL, Hughes KW, Petersen RH (2007) An investigation of/omphalotaceae (Fungi:Euagarics) with emphasis on the genus *Gymnopus*. *Sydowia* 58: 191–289.
- Mayr E (1963) *Animal Species and Evolution*. Harvard University Press Cambridge, Massachusetts. doi: 10.4159/harvard.9780674865327
- Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clemençon H, Miller OKJ (2002) One hundred and seventeen clades of euagarics. *Molecular Phylogenetics and Evolution* 23: 357–400. doi: 10.1016/S1055-7903(02)00027-1
- Moritz C (1994) Defining ‘Evolutionarily Significant Units’ for conservation. *Tree* 9: 373–375. doi: 10.1016/0169-5347(94)90057-4
- Noordeloos ME, Antonín V (2008) Contribution to a monograph of marasmiod and collybioid fungi in Europe. *Czech Mycology* 60: 21–27.
- Orton PD (1960) New checklist of British Agarics and Boleti. III. Notes on genera and species in the list *Transactions of the British Mycological Society* 43: 159–439. doi: 10.1016/S0007-1536(60)80065-4
- Patouillard N (1887) *Les Hyménomycètes Europe. Matériaux pour L’Histoire des Champignons* 1: 1–166.
- Petersen RH (2016) Making sense of color. *Fungi Magazine* 8: 12–25.
- Rambaut A (2006) *FigTree: Tree Figure Drawing Tool Version 1.4.0 2006–2012*. Institute of Evolutionary Biology, University of Edinburgh.
- Redhead SA (1980) *Marasmiellus filipes*. *Fungi Canadenses*. Agriculture Canada Ottawa.
- Ridgway R (1912) *Color standards and color nomenclature*. Publ. Priv., Washington, DC. doi: 10.5962/bhl.title.62375
- Singer R (1948) *Diagnoses fungorum novorum Agaricalium*. *Sydowia* 2: 26–42.
- Singer R, Smith AH (1946) Proposals concerning the nomenclature of the gill fungi including a list of proposed lectotypes and genera conservanda. *Mycologia* 38: 240–299. doi: 10.2307/3755094
- Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC (2000) Phylogenetic Species Recognition and Species Concepts in Fungi. *Fungal Genetics and Biology* 31: 21–32. doi: 10.1006/fgbi.2000.1228
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) *PCR Protocols, A Guide to Methods and Applications*. Academic Press, San Diego, 315–322. doi: 10.1016/b978-0-12-372180-8.50042-1
- Wilson AW, Desjardin DE (2005) Phylogenetic relationships in the gymnopoid and marasmiod fungi (Basidiomycetes, euagarics clade). *Mycologia* 97: 667–679. doi: 10.3852/mycologia.97.3.667

Appendix I

Collections used for molecular analyses (Reviewers – GenBank numbers will be added after review)

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
	<i>Anthracoophyllum archeri</i>	PBM2201		na	AY745709
	<i>Anthracoophyllum lateritium</i>	TENN:F-56925	USA: Louisiana	na	AF261324
	<i>Caripea montagnei</i>		unknown	na	DQ449988
	<i>Caripea montagnei</i>	JMCR.143	117 clades	na	AF261327
	<i>Collybia harioolorum</i>	GLM: 45933	Germany	na	AY207166
	<i>Coniopus acervatus</i>	CBS 174.78	117 clades	na	AF223172
FJ750256_7498	<i>Connopus acervatus</i>	TENN:F-53596	Finland	GU318378	FJ750256
FJ750259_7476	<i>Connopus acervatus</i>	TENN:F-53516	Finland	GU318373-77	FJ750259
FJ750261_13579h1	<i>Connopus acervatus</i>	TENN:F-62824	USA: Idaho	GU318393	FJ750261
FJ750261_13579h2	<i>Connopus acervatus</i>	TENN:F-62824	USA: Idaho	GU318394	FJ750261
	Environmental sample	none	USA: New Jersey	na	AF241340
	Environmental sequence		Czech Republic	JX029948	na
	Environmental sequence: House dust		Finland	AM901982	na
65157-13781h1	<i>Gymnopus</i> aff. <i>dryophilus</i>	TENN:F-65157	Belgium	Deposit ITS+LSU	
65157-13781h2	<i>Gymnopus</i> aff. <i>dryophilus</i>	TENN:F-65157	Belgium	Deposit ITS+LSU	
68085-14228	<i>Gymnopus</i> aff. <i>melanopus</i>	TENN:F-68085	“USA:Tennessee, Great Smoky Mountains National Park”	deposit ITS+LSU	
	<i>Gymnopus</i> aff. <i>menehune</i>	SFSU: AWW113		na	AY639408
	<i>Gymnopus</i> aff. <i>moseri</i>	TENN: AWW10		na	AY639409
50162_3554	<i>Gymnopus</i> afn <i>androsaceus</i>	TENN:F-50162	Australia: NSW	Deposit ITS+LSU	
48443-1871	<i>Gymnopus</i> afn <i>dichrous</i>	TENN:F-48443	USA: North Carolina	AF505766	deposit
68142-14288	<i>Gymnopus</i> afn <i>dichrous</i>	TENN:F-68142	USA: Mississippi	unreadable	deposit LSU only
56721-10009	<i>Gymnopus</i> afn <i>dichrous</i> I	TENN:F-56721	USA: North Carolina	Deposit ITS+LSU	don't deposit
50299-4702	<i>Gymnopus androsaceus</i>	TENN: F-50299	Sweden	DQ444313	no sequence
50308-4711	<i>Gymnopus androsaceus</i>	TENN: F-50308	Sweden	DQ444314	no sequence
50317-4720	<i>Gymnopus androsaceus</i>	TENN:F-50317	Sweden	DQ444315	

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
50321-4724	<i>Gymnopus androsaceus</i>	TENN: F-50321	Sweden	DQ444316	no sequence
50378-4781	<i>Gymnopus androsaceus</i>	TENN: F-50378	Switzerland: Maggia	deposit ITS only	no sequence
50482-3745	<i>Gymnopus androsaceus</i>	TENN: F-50482	Scotland	DQ444312	deposit LSU only or ITS+LSU resequence
50483-3746	<i>Gymnopus androsaceus</i>	TENN: F-50483	Scotland	deposit ITS+LSU	
53590-7259	<i>Gymnopus androsaceus</i>	TENN: F-53590	Sweden	Deposit ITS+LSU	
53607-7475	<i>Gymnopus androsaceus</i>	TENN: F-53607	Finland:Erela-hame Prov.	Deposit ITS+LSU	
53610-7472	<i>Gymnopus androsaceus</i>	TENN: F-53610	Finland:Erela-hame Prov.	Deposit ITS+LSU	
59594-11631	<i>Gymnopus androsaceus</i>	TENN: F-59594	Russia	Deposit ITS+LSU	
69268-14571h1	<i>Gymnopus androsaceus</i>	TENN: F-68268	Slovakia	Deposit ITS+LSU	
69268-14571h2	<i>Gymnopus androsaceus</i>	TENN: F-68269	Slovakia	Deposit ITS+LSU	
CULTENN5021h1	<i>Gymnopus androsaceus</i>	Culture only	Canada: Nova Scotia	deposit ITS+LSU	
CULTENN5021h2	<i>Gymnopus androsaceus</i>	Culture only	Canada: Nova Scotia	deposit ITS+LSU	
CULTENN5037	<i>Gymnopus androsaceus</i>	Culture only	Canada: Nova Scotia	deposit	no sequence
CULTENN5609	<i>Gymnopus androsaceus</i>	Culture only	USA: Idaho	deposit ITS+LSU	
67858-14110	<i>Gymnopus aurantipes</i>	SFSU: AWW118		na	AY639410
	<i>Gymnopus barbipes</i>	TENN: F-67858	"USA: Tennessee, Great Smoky Mountains National Park"	KJ416269 ITS	deposit
	<i>Gymnopus bicolor</i>	SFSU: AWW116		na	AY639411
58624_11016_	<i>Gymnopus bififormis</i>	TENN: F-58624	Costa Rica	DQ450056	deposit
69215-14250	<i>Gymnopus bififormis</i>	TENN: F-69215	USA: Georgia	KJ416246	KJ189568
KJ189567-14251	<i>Gymnopus bififormis</i>	TENN: F-68110	"USA: Tennessee, Great Smoky Mountains National Park"	KJ416245	KJ189567
	<i>Gymnopus bififormis</i>	DUKE: RV98/32	117 clades	na	AF261336
CULTENN14606	<i>Gymnopus brevipes</i>	Culture only	USA: Mississippi	deposit ITS+LSU	
51029-4548h1	<i>Gymnopus brevipes</i>	TENN: F-51029	Puerto Rico	Deposit ITS+LSU	
51029-4548h2	<i>Gymnopus brevipes</i>	TENN: F-51029	Puerto Rico	Deposit ITS+LSU	
69182_14489	<i>Gymnopus brevipes</i>	TENN: F-69182	USA: Mississippi	Deposit ITS+LSU	
69189_14498	<i>Gymnopus brevipes</i>	TENN: F-69189	USA: Mississippi		
69197_14505h1	<i>Gymnopus brevipes</i>	TENN: F-69197	USA: Mississippi		

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
69197_14505h2	<i>Gymnopus brevipes</i>	TENN:F-69197	USA: Mississippi		
69310-14607	<i>Gymnopus brevipes</i>	TENN:F-69310	USA: Alabama	Deposit ITS+LSU	
69311-DPL11763A	<i>Gymnopus brevipes</i>	TENN:F-69311	USA: Texas	Deposit ITS+LSU	
CULTENN14594	<i>Gymnopus brevipes</i>	Culture only	USA: Mississippi	deposit ITS+LSU	
CULTENN14599	<i>Gymnopus brevipes</i>	Culture only	USA: Mississippi	deposit ITS+LSU	
54912_9087	<i>Gymnopus brevipes</i>	TENN:F-54912	USA: Louisiana	Deposit ITS + LSU	
	<i>Gymnopus brunneigracilis</i>	SFSU: AWW01		na	AY639412
61068-13063	<i>Gymnopus ceratocola</i>	TENN:F-61068	New Zealand	KJ416261	no sequence
61085-13081	<i>Gymnopus ceratocola</i>	TENN:F-61085	New Zealand	KJ416262	no sequence
61086-13082	<i>Gymnopus ceratocola</i>	TENN:F-61086	New Zealand	KJ416260	no sequence
65131-13754	<i>Gymnopus confluens</i>	TENN:F-65131	Belgium	KP710288	KJ189571
65835-13939	<i>Gymnopus confluens</i>	TENN:F-65835	"USA, NY"	KP710284	KJ189579
67864-14114	<i>Gymnopus confluens</i>	TENN:F-67864	Germany	KP710295	KJ189573
LE-BIN1178	<i>Gymnopus confluens</i>	Culture only	USA: North Carolina	KP710282	KJ189580
DQ457670	<i>Gymnopus contrarius</i>	AFToL ID 1758		na	DQ457670
61128-12567	<i>Gymnopus dichrous</i>	TENN:F-61128	"USA: North Carolina, Great Smoky Mountains National Park"	FJ596783	deposit
56727-10015h1	<i>Gymnopus dichrous</i> I	TENN:F-56727	USA: North Carolina	Deposit ITS+LSU	don't deposit
56727-10015h2	<i>Gymnopus dichrous</i> I	TENN:F-56727	USA: North Carolina	Deposit ITS+LSU	don't deposit
60029-11601	<i>Gymnopus dichrous</i> I	TENN:F-60029	"USA: Tennessee, Great Smoky Mountains National Park"	Deposit ITS+LSU	don't deposit
67859-14111ss1	<i>Gymnopus dichrous</i> I	TENN:F-67859	"USA, TN, GSM"	Deposit ITS + Lsu	
67859-14111ss2	<i>Gymnopus dichrous</i> II	TENN:F-67859	"USA, TN, GSM"	Deposit ITS + Lsu	
	<i>Gymnopus diminutus</i>	SFSU: AR099		na	AY639413
68136-14281	<i>Gymnopus disjunctus</i>	TENN:F-68136	"USA, MS"	KJ416253	deposit
60015_11786_TN_DRYOP	<i>Gymnopus dryophilus</i>	TENN:F-60015	"USA: Tennessee, Great Smoky Mountains National Park"	FJ596766	deposit
61125-12563	<i>Gymnopus dyosodes</i>	TENN:F-61125	"USA: Tennessee, Knox Co."	deposit	FJ750265
59140-11039_EARLEA	<i>Gymnopus earlea</i>	TENN:F-59140	"USA: Tennessee, Great Smoky Mountains National Park"	DQ449994	deposit

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
060902AV01	<i>Gymnopus eneifcola</i>	TENN:F-69127	Canada: Newfoundland	KJ128267	KJ189588
090926AV13	<i>Gymnopus eneifcola</i>	TENN:F-69123	Canada: Newfoundland	KJ128264	KJ189586
	<i>Gymnopus erythropus</i>	GLM: 45932	Germany	na	AY207167
59295-11434	<i>Gymnopus foetidum</i>	TENN: F-59295	Austria	KJ416259	deposit
65806-13911	<i>Gymnopus foetidus</i>	TENN:F-65806	"USA, NC"	Deposit ITS+LSU	
68190-14340	<i>Gymnopus foetidus</i>	TENN:F-68190	USA: Connecticut	deposit ITS+LSU	
69280-14583	<i>Gymnopus foetidus</i>	TENN:F-69280	Slovakia	Deposit ITS+LSU	
69323_14618	<i>Gymnopus foetidus</i>	TENN: F-69323	USA: Georgia	not necessary	ASM12144
	<i>Gymnopus foetidus</i>	GLM: 45964	Germany	na	AY207240
59300_11439	<i>Gymnopus fusipes</i>	TENN:F-59300	Austria	AF505777	AY256711
69254-14558	<i>Gymnopus fusipes</i>	TENN:F-69254	Slovakia	Deposit ITS+LSU	
	<i>Gymnopus fusipes</i>	TENN:F-55904	Scotland	deposit	AF135795
59217-11333	<i>Gymnopus fusipes</i>	TENN:F-59217	France	AY256710	deposit
	<i>Gymnopus fusipes</i>	NYBG: Halling6509		na	AY639414
	<i>Gymnopus gibbosus</i>	SFSU: AWW12a		na	AY639415
	<i>Gymnopus gibbosus</i>	SFSU: AWW112		na	AY639417
	<i>Gymnopus indoctus</i>	SFSU: AWW03		na	AY639418
50704_3716	<i>Gymnopus inflatotrampa</i>	TENN:F-50704		DQ444311	no sequence
52970-6520	<i>Gymnopus tocephalus</i>	TENN:F-52970	USA: North Carolina	DQ449984	deposit
58988-10782	<i>Gymnopus juniperinus</i>	TENN:F-58988	Argentina	Deposit ITS+LSU	
59540-9889	<i>Gymnopus juniperinus</i>	TENN:59540	USA:Louisiana	AY256708	deposit
55748-9121	<i>Gymnopus luxurians</i>	TENN:F-55748	USA: Louisiana	Deposit ITS+LSU	
67854-14107	<i>Gymnopus luxurians</i>	TENN:F-67854		KJ416241	deposit
	<i>Gymnopus luxurians</i>	TENN: F-57910	USA: North Carolina	AF505765	AY256709
	<i>Gymnopus luxurians</i>	SFSU: DEH1304		na	AY639421
	<i>Gymnopus melanopus</i>	SFSU: AWW54		na	AY639422
	<i>Gymnopus menebune</i>	SFSU: AWW02		na	AY639423
	<i>Gymnopus menebune</i>	SFSU: AWW15		na	AY639424
	<i>Gymnopus menebune</i>	SFSU: AWW87		na	AY639425

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
56727_11005_G_ MESOAMERICANUS	<i>Gymnopus mesoamericanus</i>	TENN:F-56727	Costa Rica	DQ450035	deposit
68165_14282	<i>Gymnopus micromphaloides</i> (Holotype)	TENN:F-68165	USA: Mississippi	KJ416243	deposit
68133_14278	<i>Gymnopus nonnullus</i>	TENN:F-68133	“USA, MS”	Deposit ITS+LSU	
	<i>Gymnopus nonnullus</i>	SFSU: AWW05		na	AY639426
65135_13758	<i>Gymnopus ocior</i>	TENN:F-65135	Belgium	Deposit ITS+LSU	
50318_4721	<i>Gymnopus perforans</i> subsp. <i>perforans</i>	TENN:F-50318	Sweden	Deposit ITS+LSU	
50319_4722h1	<i>Gymnopus perforans</i> subsp. <i>perforans</i>	TENN:F-50319	Sweden	Deposit ITS+LSU	
50319_4722h2	<i>Gymnopus perforans</i> subsp. <i>perforans</i>	TENN:F-50320	Sweden	Deposit ITS+LSU	
53579_7477	<i>Gymnopus perforans</i> subsp. <i>Perforans</i>	TENN:F-53579	Finland	Deposit ITS+LSU	
58295_10826	<i>Gymnopus perforans</i> subsp. <i>perforans</i>	TENN:F-58295	Russia	Deposit ITS+LSU	
59592_11629	<i>Gymnopus perforans</i> subsp. <i>Perforans</i>	TENN:F-59592	Russia	Deposit ITS+LSU	
61211_13121c2	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61211	Canada: Quebec	Deposit ITS+LSU	
61211_13121c3	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61211	Canada: Quebec	Deposit ITS+LSU	
61211_13121c4	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61211	“USA: Tennessee, Great Smoky Mountains National Park”	Deposit ITS+LSU	
61587_13319c1	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61587	Canada: Quebec	Deposit ITS+LSU	
61587_13319c2	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61587	Canada: Quebec	Deposit ITS+LSU	
61587_13319c3	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61587	Canada: Quebec	Deposit ITS+LSU	
61587_13319c4	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61587	Canada: Quebec	Deposit ITS+LSU	
61587_13319c5	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-61587	Canada: Quebec	Deposit ITS+LSU	
69000_14350h1	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69000	USA: New York	Deposit ITS+LSU	
69000_14350h2	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69000	USA: New York	Deposit ITS+LSU	
69042_14377	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69042	“Canada: New Brunswick, Fundy Provincial Park”	Deposit ITS+LSU	
69049_14384h1	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69049	Canada: New Brunswick	Deposit ITS+LSU	
69049_14384h2	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69049	Canada: New Brunswick	Deposit ITS+LSU	
69059_14395h1	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69059	Canada: New Brunswick	Deposit ITS+LSU	
69059_14395h2	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69059	Canada: New Brunswick	Deposit ITS+LSU	
69198_14348	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69198	USA: New York	Deposit ITS+LSU	

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
69307-14611	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69307	USA: North Carolina	bad seq	LSU only
69318_14613h1	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69318	USA:Vermont	Deposit ITS+LSU	
69318_14613h2	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69318	USA:Vermont	Deposit ITS+LSU	
69340_14592	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	TENN:F-69340	USA:New Hampshire	Deposit ITS+LSU	
AV100918	<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	AV100918 (private collection)	Canada: Newfoundland	Deposit ITS+LSU	
50540_4204	<i>Gymnopus peronatus</i>	TENN:F-50540		DQ450017	deposit
65120-13743	<i>Gymnopus peronatus</i>	TENN:F-65120	Belgium	Deposit ITS+LSU	don't deposit
LE-BIN1363	<i>Gymnopus peronatus</i>	Culture only	Russia	Deposit ITS and LSU	
LE-BIN1898	<i>Gymnopus peronatus</i>	Culture only	Russia: Samara area	Deposit ITS and LSU	
	<i>Gymnopus polyphyllus</i>	DUKE: RV192.01	117 clades	na	AF042596
68144-14290	<i>Gymnopus pseudoluxurians</i> holotype	TENN:F-68144	USA: Mississippi	deposit	KJ416242
50346_4749	<i>Gymnopus scorodoniis</i>	TENN:F-50346		DQ450006	deposit
EU522806 MARASMIUS_SCORODONIUS	<i>Gymnopus scorodoniis</i>	TM03_419	Canada	na	EU522806
50135_4033	<i>Gymnopus</i> sp. 7 (austrobrevipetes)	TENN:F-50135	Australia	Deposit ITS+LSU	
50761_3642	<i>Gymnopus</i> sp. 2 (foliophilus)	TENN:F-50761	"USA: Tennessee, Great Smoky Mountains National Park"	Deposit ITS+LSU	
59641_11608	<i>Gymnopus</i> sp. 2 (foliophilus)	TENN:F-59641	"USA: Tennessee, Blount Co."	Deposit ITS+LSU	
61274_13242	<i>Gymnopus</i> sp. 2 (foliophilus)	TENN:F-61274	"USA: Tennessee, Great Smoky Mountains National Park"	Deposit ITS+LSU	
WTU31851	<i>Gymnopus</i> sp. 5 (pallidocephalus)	WTU31851		bad seq	deposit
	<i>Gymnopus</i> sp.	JE1.PR.213	117 clades	na	AF261326
	<i>Gymnopus</i> sp.	Duke: RVPR98.46	Puerto Rico 117 clades	na	AF261333
	<i>Gymnopus</i> sp.	Duke: RV.PR.98.08	Puerto Rico 117 clades	na	AF261334
	<i>Gymnopus</i> sp.	DUKE:RV.PR98.13	Puerto Rico 117 clades	na	AF261335
50201-4016	<i>Gymnopus</i> sp. (TENN50201)	TENN:F-50201	Australia: Tasmania	Deposit ITS+LSU	
58602-10494	<i>Gymnopus</i> sp. (TENN58602)	TENN:F-58602	Costa Rica	deposit	FJ750263
WRW05-1170	<i>Gymnopus</i> sp. (WRW05-1170)	WRW05-1170	USA: West Virginia	deposit ITS+LSU	
50999-4512	<i>Gymnopus</i> sp. 1 (portoricensis)	TENN:F-50999	Puerto Rico	Deposit ITS+LSU	

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
SFSU_DED8813	<i>Gymnopus</i> sp. 10 (adventitius)	SFSU:DED8813	unknown	Deposit ITS+LSU	
69325_14620h1	<i>Gymnopus</i> sp. 11 (sequoiae)	TENN:F-69325	USA: California	Deposit ITS+LSU	
69325_14620h2	<i>Gymnopus</i> sp. 11 (sequoiae)	TENN:F-69325	USA: California	Deposit ITS+LSU	
UBC25212h1	<i>Gymnopus</i> sp. 12 (sublaccatus)	UBC25212	Canada: British Columbia	Deposit ITS+LSU	
UBC25212h1	<i>Gymnopus</i> sp. 12 (sublaccatus)	UBC25212	Canada: British Columbia	Deposit ITS+LSU	
69267-14570h1	<i>Gymnopus</i> sp. 13 (quercophilus)	TENN:F-69267	Slovakia	Deposit ITS+LSU	
69267-14570h2	<i>Gymnopus</i> sp. 13 (quercophilus)	TENN:F-69267	Slovakia	Deposit ITS+LSU	
69320-14615	<i>Gymnopus</i> sp. 13 (quercophilus)	TENN:F-69320	USA: California	Deposit ITS+LSU	
69321-14616	<i>Gymnopus</i> sp. 13 (quercophilus)	TENN:F-69321	USA: California	Deposit ITS+LSU	
SFSU25220	<i>Gymnopus</i> sp. 13 (quercophilus)	SFSU 25220	USA: California	deposit ITS+LSU	
69324_14619	<i>Gymnopus</i> sp. 14 (TENN69423)	TENN:F-69324	USA: Georgia	Deposit ITS+LSU	
55679_9031	<i>Gymnopus</i> sp. 15 (frigidomarginatus)	TENN:F-55679	USA: California	Deposit ITS+LSU	
53488_5627	<i>Gymnopus</i> sp. 16 (ponderosae)	TENN:F-53488	USA: Idaho	Deposit ITS+LSU	
CULTENN4975	<i>Gymnopus</i> sp. 16. (novae-angliae)	Culture only	“USA:New York, Franklin Co.”	deposit ITS+LSU	
50013_DED5272	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-50013	“USA: Tennessee, Great Smoky Mountains National Park”	Deposit ITS+LSU	
51221_4902h1	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-51221	USA: Georgia	Deposit ITS+LSU	
51221_4902h2	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-51221	USA: Georgia	Deposit ITS+LSU	
51244_4928	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-51244	USA: North Carolina	Deposit ITS+LSU	
55210_8782	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-55210	USA: South Carolina	Deposit ITS+LSU	
55764_9166h1	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-55764	“USA: Tennessee, Great Smoky Mountains National Park”	Deposit ITS+LSU	
55764_9166h2	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-55764	“USA: Tennessee, Great Smoky Mountains National Park”	Deposit ITS+LSU	
56223_7243	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-56223	USA: North Carolina	Deposit ITS+LSU	
57923_10364	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-57923	USA: North Carolina	Deposit ITS+LSU	
65571_13875	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-65571	USA: North Carolina	Deposit ITS+LSU	
65990-14048	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-65990	USA: North Carolina	Deposit ITS+LSU	
67809_14063	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-67809	USA: North Carolina	Deposit ITS+LSU	
68145_14291	<i>Gymnopus</i> sp. 2 (foliiphilus)	TENN:F-68145	USA: Mississippi	Deposit ITS+LSU	

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
68183_14332	<i>Gymnopus</i> sp. 2 (foliophilus)	TENN:F-68183	USA: Connecticut	Deposit ITS+LSU	
69086_14422	<i>Gymnopus</i> sp. 2 (foliophilus)	TENN:F-69086	USA: Arkansas	Deposit ITS+LSU	
51233_4919	<i>Gymnopus</i> sp. 3 (inflatotrama)	TENN:F-51233	"USA: North Carolina, Standing Indian State Park"	Deposit ITS+LSU	
53490_4930	<i>Gymnopus</i> sp. 3 (inflatotrama)	TENN:F-53490	USA: North Carolina	Deposit ITS+LSU	
53521_7471	<i>Gymnopus</i> sp. 3 (inflatotrama)	TENN:F-53521	Finland	Deposit	no sequence
CULTENN4929	<i>Gymnopus</i> sp. 3 (inflatotrama)	Culture only	USA: North Carolina	deposit ITS+LSU	
48143B-2221	<i>Gymnopus</i> sp. 4 (inflatotrama) (MGI)	TENN:F-48143	USA: North Carolina	Deposit ITS+LSU	deposit
51574_5256	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-51574	USA: North Carolina	Deposit ITS+LSU	
65808_13913	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-65808	USA: North Carolina	Deposit ITS+LSU	
67804_14059h1	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-67804	USA: North Carolina	Deposit ITS+LSU	
67804_14059h2	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-67804	USA: North Carolina	Deposit ITS+LSU	
67846_14097	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-67846	USA: North Carolina	Deposit ITS+LSU	
69206_14511h1	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-69207	USA: North Carolina	Deposit ITS+LSU	
69206_14511h2	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-69207	USA: North Carolina	Deposit ITS+LSU	
69212_14517	<i>Gymnopus</i> sp. 4 (pinophilus)	TENN:F-69212	USA: North Carolina	Deposit ITS+LSU	
52401_5610	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-52401	USA: Idaho	Deposit ITS+LSU	
52427_5698	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-52427	USA: Washington	Deposit ITS+LSU	
59896-11778h1	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-59896	"USA: Tennessee, Great Smoky Mountains National Park"	FJ596762	deposit
59896-11778h2	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-59896	"USA: Tennessee, Great Smoky Mountains National Park"	FJ596763	deposit
65829_13933h1	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-65829h1	USA: New York	Deposit ITS+LSU	
65829_13933h2	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-65829h2	USA: New York	Deposit ITS+LSU	
66344_SAT11-179-05	<i>Gymnopus</i> sp. 5 (palidocephalus)	TENN:F-66344	"USA: TN, Great Smoky Mountains National Park"	Deposit ITS + LSU	
CULTENN5015	<i>Gymnopus</i> sp. 5 (palidocephalus)	Culture only	Canada: Nova Scotia	deposit ITS+LSU	
53683_7572	<i>Gymnopus</i> sp. 6 (caulocystidiatus)	TENN:F-53683	New Zealand	Deposit ITS+LSU	
53725_7589	<i>Gymnopus</i> sp. 6 (caulocystidiatus)	TENN:F-53725	New Zealand:North Island	Deposit ITS+LSU	
54050-7148	<i>Gymnopus</i> sp. 6 (caulocystidiatus)	TENN:F-54050	New Zealand	Deposit ITS+LSU	

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
53149_3591	<i>Gymnopus</i> sp. 7 (austrobrevipes) Australia: Tasmania	TENN:F-53149	Australia: Tasmania	Deposit ITS+LSU	
53181_3585	<i>Gymnopus</i> sp. 7 (austrobrevipes)Australia: Tasmania	TENN:F-53181	Australia: Tasmania	Deposit ITS+LSU	
MICH50942	<i>Gymnopus</i> sp. 8 (resinose)	MICH50942		Deposit ITS	no sequence
50765-3646	<i>Gymnopus</i> sp. 9 (novomundi)	TENN:F-50765	“USA: Tennessee, Great Smoky Mountains National Park”		deposit
50796_3677	<i>Gymnopus</i> sp. 9 (novomundi)	TENN:F-50796	“USA: Tennessee, Great Smoky Mountains National Park”		
50812_3693	<i>Gymnopus</i> sp. 9 (novomundi)	TENN:F-50812	USA: Georgia	deposit ITS+LSU	
SFSU_DED5097	<i>Gymnopus</i> sp. 9 (novomundi)	SFSU:DED5097	USA: Unknown	Deposit ITS+LSU	
68185-14334h1	<i>Gymnopus</i> sp. 17 (utriformis)	TENN:F-68185	USA: Connecticut	Deposit ITS+LSU	
68185-14334h2	<i>Gymnopus</i> sp. 17 utriformis	TENN:F-68185	USA: Connecticut	Deposit ITS+LSU	
53721_7588	<i>Gymnopus</i> sp.6 (caulocystidiatus)	TENN:F-53721	New Zealand	Deposit ITS+LSU	
	<i>Gymnopus speticonicus</i>	SFSU: AWW126		na	AY639427
65912-13975	<i>Gymnopus spongiosus</i>	TENN:F-65912	USA: Mississippi	Deposit ITS and LSU	
68184_14333	<i>Gymnopus spongiosus</i>	TENN:F-68184	USA: Connecticut	Deposit ITS+LSU	
61138_12577	<i>Gymnopus subnudis</i>	TENN:F-61138	“USA: Tennessee, Great Smoky Mountains National Park”	deposit	FJ750262
WRW08_462	<i>Gymnopus subnudis</i>	WRW08-462	USA: West Virginia	deposit ITS+LSU	
	<i>Gymnopus subpruinosis</i>	SFSU: DED6674		na	AY639429
	<i>Gymnopus synodicus</i>	SFSU: DED5258		na	AY639435
	<i>Gymnopus termiticola</i>	SFSU: AWW106		na	AY639430
FJ750264_12836	<i>Gymnopus villosipes</i>	TENN:F-60951	New Zealand: Fiordland	KJ416255	FJ750264
	<i>Gymnopus vitellinipes</i>	SFSU: AAW127		na	AY639432
57787-10292ss6	<i>Lentinula boryana</i>	TENN:F-57787	Mexico	Deposit ITS+LSU	don't deposit
	<i>Lentinula edodes</i>	ATCC 42962		na	AF042579
56291-8682ss2	<i>Lentinula raphanica</i>	TENN:F-56291	USA: Louisiana	Deposit ITS+LSU	
	<i>Marasmiellus opacus</i>	JEJ:574	117 clades	na	AF261329
	<i>Marasmiellus opacus</i>	HN2270	117 clades	na	AF261330

GenBank Identifier	Name	Herbarium no	Location	ITS GenBank	LSU GenBank No.
69322-14617	<i>Marasmiellus</i> sp.	INH: ASM12141	USA: Georgia	not necessary	ASM12141
65115-13739	<i>Marasmiellus vaillantii</i>	TENN: F-65115	"USA: Tennessee, Great Smoky Mountains National Park"	Deposit ITS+LSU	don't deposit
58485-5032	<i>Marasmius afri androsacens</i>	TENN: F-58485	Canada: Nova Scotia	Deposit ITS	no LSU sequence
	<i>Marasmius alliaceus</i>	GLM: 45959	Germany	na	AY207234
	<i>Marasmius alliaceus</i>	TENN: F-55620	Russia: Caucasus Region	no sequence	AY635776
	<i>Marasmius alliaceus</i>	BRNM568		na	AY639436
	<i>Marasmius androsacens</i>	HN4730	117 clades	na	AF261585
	<i>Marasmius applanatipes</i>	SFSU: DED6628		na	AY639437
	<i>Marasmius copelandii</i>	SFSU: DED5607		na	AY639438
KJ189565-13751	<i>Marasmius ramealis</i>	TENN: F-65128	Belgium	bad sequence	KJ189565
KJ189566-13755	<i>Marasmius ramealis</i>	TENN: F-65132	Belgium	KJ416235	KJ189566
	<i>Marasmius scorodoniis</i>	JEJ: 586	117 clades	na	AF261331
	<i>Marasmius scorodoniis</i>	DAOM175382	117 clades	na	AF261332
50116_3940	<i>Marasmius</i> sp. 1 (TENN50116)	TENN: F-50116	Australia: Tasmania	Deposit ITS+LSU	
	<i>Micromphale foetidum</i>	JEJ: VA-567	117 clades	na	AF261328
54057_7179	<i>Micromphale</i> sp. (TENN54057)	TENN: F-54057	New Zealand: North Island	Deposit ITS+LSU	
	<i>Neonothopanus eugammius</i>	DUKE: RVPR1308	Puerto Rico	na	AF042577
	<i>Neonothopanus nambi</i>	DUKE: RVPR27	Puerto Rico 117 clades	na	AF135175
	<i>Omphalorus japonicus</i>	JM leg Murakami	Thorn Pleurotaceae no data	na	AF135172
	<i>Omphalorus nidiformis</i>	T1946.8	117 clades	na	AF042621
DQ470816	<i>Omphalorus olearius</i>	AFToL ID 1718		na	DQ470816
LE-BIN1232	<i>Rhodocollybia butyracea</i> var. <i>asema</i>	Culture only	Russia: Leningrad area	Deposit ITS and LSU	
LE-BIN2526	<i>Rhodocollybia butyracea</i> var. <i>asema</i>	Culture only	Russia	Deposit ITS and LSU	
69033-14368h1	<i>Rhodocollybia butyraceae</i>	TENN: F-69033	"Canada: New Brunswick, Fundy Provincial Park"	Deposit ITS+LSU	
69033-14368h2	<i>Rhodocollybia butyraceae</i>	TENN: F-69033	"Canada: New Brunswick, Fundy Provincial Park"	Deposit ITS+LSU	
69047-14382	<i>Rhodocollybia butyraceae</i>	TENN: F-69047	Canada: New Brunswick	Deposit ITS+LSU	
	<i>Rhodocollybia laulaha</i>	SFSU: DED5873		na	AY639441

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65926-13989h1	<i>Rhodocollybia maculata</i>	TENN:F-65926	USA: Mississippi	Deposit ITS + Lsu	
65926-13989h2	<i>Rhodocollybia maculata</i>	TENN:F-65926	USA: Mississippi	Deposit ITS + Lsu	
67881-14131	<i>Rhodocollybia maculata</i>	TENN:F-67881	Germany	Deposit ITS + Lsu	
68088_14253	<i>Rhodocollybia maculata</i>	TENN:F-68088	USA: Roan Mountain	Deposit ITS+LSU	
68169-14317	<i>Rhodocollybia maculata</i>	TENN:F-68169	USA: Connecticut	Deposit ITS+LSU	