

# New species in the *Gymnopilus junonius* group (Basidiomycota: Agaricales)

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**Abstract:** Mushrooms named *Gymnopilus spectabilis* and *G. junonius* have been reported widely in North America on both dead hardwood or dead or living conifers. Based on DNA sequences of the internal transcribed spacer region (ITS) and large ribosomal subunit (LSU), we found that although *Gymnopilus junonius* (= *G. spectabilis* s. auct.) is widespread in Europe, South America, and Australia, none of the limited sequences available from North America represent this species. We report five species of this group from North America, including three previously described species, *G. luteus*, *G. subspectabilis*, and *G. ventricosus*, and two new species, *Gymnopilus voitkii* and *Gymnopilus speciosissimus*. We recognize a sister species to *G. luteus*, based on sequences previously reported as *G. spectabilis* from China, Japan, and the Russian Far East, but, lacking material to describe it as a new species, we give it an informal clade name, *isororiluteus*. Another new species in this complex is described from Japan, as *Gymnopilus orientispectabilis*. Species in this group may be distinguished by their ITS sequences as well as by macro- and micromorphology, substrate, and geography.

**Key words:** *Gymnopilus spectabilis*, *Pholiota ventricosa*, host associations, phylogeny, psilocybin, three new species.

**Résumé :** Les champignons identifiés *Gymnopilus spectabilis* et *G. junonius* ont été largement rapportés en Amérique du Nord, tant sur des bois durs morts que sur des conifères morts ou vivants. À partir des séquences d'ADN de la région de l'espaceur interne transcrit (ITS) et de la grande sous-unité ribosomale (LSU), les auteurs ont découvert que, bien que *Gymnopilus junonius* (= *G. spectabilis* s. auct.) soit répandu en Europe, en Amérique du Sud et en Australie, aucune des quelques séquences disponibles en Amérique du Nord ne représente cette espèce. Ils rapportent cinq espèces appartenant à ce groupe en Amérique du Nord, dont trois espèces décrites précédemment, *G. luteus*, *G. subspectabilis* et *G. ventricosus* ainsi que deux nouvelles espèces, *Gymnopilus voitkii* et *Gymnopilus speciosissimus*. Ils reconnaissent une espèce sœur de *G. luteus* à partir de séquences précédemment rapportées pour correspondre à *G. spectabilis* de Chine, du Japon et de l'Extrême-Orient russe, mais faute de matériel pour la décrire comme nouvelle espèce, ils lui donnent un nom de clade informel, *isororiluteus*. Une autre nouvelle espèce membre de ce complexe est décrite au Japon comme *Gymnopilus orientispectabilis*. Les espèces membres de ce groupe peuvent se distinguer par les séquences de leur ITS ainsi que par leur macro- et micromorphologie, leur substrat et leur géographie. [Traduit par la Rédaction]

**Mots-clés :** *Gymnopilus spectabilis*, *Pholiota ventricosa*, association d'hôtes, phylogénie, psilocybine, trois nouvelles espèces.

## Introduction

Collectors in the Canadian provinces of New Brunswick and Newfoundland & Labrador have repeatedly observed large basidiomata of a mushroom growing on

living and recently dead wood of *Abies balsamea*. Using available literature, the mushroom was determined to be *Gymnopilus junonius* (Fr.) P.D. Orton, a species described as *Agaricus junonius* by Fries (1821). This species has fre-

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quently been referred to as *G. spectabilis* (Weinm.) A.H. Smith (e.g., in North America by Smith 1949; Groves 1962, as *Pholiota*; Miller 1972; Smith and Smith Weber 1980; Lincoff 1981; Barron 1999). With a very broad circumscription and including a purported synonym *G. pampeanus* (Speg.) Singer described from Argentina (Spegazzini 1899; Rees and Strid 2001), this taxon has been reported as fruiting on dead wood of angiosperms (hardwood) or gymnosperms (softwood) in Eurasia, North, Central, and South America, Africa, and Australasia (Hesler 1969; Pegler 1977). Recent opinion suggests that *Agaricus spectabilis* as described by Weinmann (1824) refers to *Phaeolepiota aurea* (Matt.) Maire, a species that fruits on soil (Legon and Henrici 2005). However, other European mycologists retain *G. spectabilis*, with the older, sanctioned name *G. junonius* in synonymy (Knudsen and Vesterholt 2012; Læssøe and Petersen 2019), or recognize both species, with *G. spectabilis* applied to collections with more robust and cespitose fruiting bodies, and *G. junonius* restricted to those with smaller and single fruiting bodies, both on hardwoods (Bon and Roux 2002). Indeed, it seems likely that the application of the epithet *spectabilis* gradually shifted from the terricolous form described by Weinmann (“*in graminosis horti Caesarei*”, Weinmann 1824; “*in pratis*”, in Fries 1828) to the lignicolous “variety b” that Fries described at the same time (“*ad radices Quercus*” Fries 1828). For this reason, we agree with Index Fungorum ([www.indexfungorum.org/Names/Names.asp](http://www.indexfungorum.org/Names/Names.asp)) in referring to this taxon by the name *G. junonius*.

Some members of the *G. junonius* complex have been reported to have hallucinogenic effects when ingested (Walters 1965; Buck 1967); in Japan, the species referred to as *G. spectabilis* is known in Japanese as *Oh-waraitake*, “the big laughter-mushroom” (Kawamura 1931, 1954; Sanford 1972). In North America and Europe, there has been controversy over the presence (Hatfield et al. 1978) or absence (Koike et al. 1981; Stijve and Kuyper 1988) of the tryptamine psilocybin as the hallucinogenic component in these mushrooms. Hatfield et al. (1978) reported psilocybin in four of thirteen collections identified as *G. spectabilis*, one of three collections of *G. luteus* (Peck) Hesler, and one collection of *G. validipes* (Peck) Hesler, but none in one collection of *G. subspectabilis* Hesler and two of *G. ventricosus* (Earle) Hesler. In a separate study, the hallucinogenic components of Japanese mushrooms identified as *G. spectabilis* were identified as oligoisoprenoids named gymnopilins, with no psilocybin or related tryptamines detected (Tanaka et al. 1993).

The standard reference for *Gymnopilus* in North America is the monograph of Hesler (1969). Hesler examined type material of nearly all *Gymnopilus* species described from the Western Hemisphere, as well as many collections housed in American herbaria. He provided a taxonomic framework defined by two subgenera, *Annulati* and *Gymnopilus*, and included a dichotomous key to species reflecting his concepts. Three characters were given

substantial weight: (i) presence or absence of a well-defined annulus as opposed to a thin cortina-like partial veil; (ii) presence or absence of dextrinoidy (a dark red reaction in Melzer’s solution) in the basidiospores; and (iii) presence or absence of pleurocystidia. Hesler required determination of all three criteria for effective use of his keys.

Guzmán-Dávalos et al. (2003) used sequence data of the internal transcribed spacer region of ribosomal DNA (ITS rDNA) to test Hesler’s two subgenera and to determine relationships within the genus. Five well-supported clades were resolved, including the *ispectabilis-imperialis* clade that includes the taxa considered here, although relationships within these clades were not clear. They found no support for the two subgenera, suggesting characters of the partial veil to be highly homoplastic (Guzmán-Dávalos et al. 2003). Because the primary incentive of our study was to determine the placement of the Atlantic Canadian collections within *Gymnopilus*, we began by examining herbarium material of similar taxa, focusing primarily on ones related by geography, substrate, or putative taxonomic affinity as suggested by morphology (Hesler 1969) or sequence data (Guzmán-Dávalos et al. 2003, and unpublished sequences in GenBank and UNITE).

## Materials and methods

### Fruiting body morphology

Specimens collected in the field were photographed and annotated while fresh; links to our own and other colour photographs not included here are provided in the species descriptions. Colour annotations of most collections follow Kornerup and Wanscher (1978), except for *G. orientispectabilis* (Kornerup and Wanscher 1967; Anonymous 2004, codes denoted as “oac”). Except for pieces of the pileus that were placed over microscope slides and left overnight for spore prints, each collection was dried at approximately 35–40 °C within 3 h of returning to the laboratory. The dried material was later frozen for several days to kill arthropods that might have survived the drying process, prior to storage in the herbarium. Additional specimens were borrowed for examination from a number of herbaria, with herbarium acronyms following Thiers (2017).

Microscopic examination of specimens, either from our own collections or from loans from other herbaria, was carried out following Thorn et al. (2017). Basidiospore measurements, including ornamentation, were made from photographs of water mounts (in 2.5% KOH for *G. orientispectabilis*) obtained from spore prints, spores discharged onto the stipe or veil, or from spores remaining on the lamellae (preference in that order). Cheilo-, pleuro-, and caulocystidia were examined, photographed, and measured in aqueous Congo Red. All measurements of caulocystidia were made from material in the area of the stipe between the annular zone and the

point of lamellar attachment. Numbers of structures measured (e.g., basidiospores, cystidia) are given in parentheses together with the number of specimens from which they were derived after the slash. Measurement ranges show the central 80th percentile, with the 10% outliers in parentheses; means are shown  $\pm$  standard deviation.

### Morphology in culture

Cultures were grown on modified Leonian's agar (Malloch 1981) in 100 mm Petri dishes. Colony diameter measurements were taken following growth at 20 °C, and microscopic observations made of hyphal morphology and asexual reproductive structures in both aerial and submerged mycelium.

### DNA extraction, PCR amplification, sequencing, and molecular phylogeny

Techniques for extraction and PCR amplification of genomic DNA followed Thorn et al. (2017). Amplifications of the nuclear ribosomal internal transcribed spacer (ITS) and 5' 650 or 1000 bases of the large subunit (LSU) were performed using primers ITS1 and LR3 or LR5 (Vilgalys and Hester 1990; White et al. 1990). The PCR products were checked using gel electrophoresis in 1.5% agar in 1 $\times$  TAE buffer at 100 V for 60 min, and were cleaned using EZ-10 Spin Column PCR Products Purification Kit (Bio Basic) prior to submission for sequencing (Robarts Institute of Western University) with primers ITS1, LS1R or ITS6-R, LS1, LR3, LR3R, and LR5 (Vilgalys and Hester 1990; White et al. 1990; Hausner et al. 1993; Dentinger et al. 2010) to obtain the sequences of the ITS and LSU regions. Sequences were cleaned and assembled using SeqEd v1.03 (ABI Software). Additional ITS sequences from type material were generated using previously published techniques (Saar and Voitek 2015). Sequences from TRTC were obtained following Dentinger et al. (2010). New sequences, including alternative haplotypes detected within some collections (indicated as haplotype A and B), were deposited in GenBank (Table 1).

BLAST analyses (Altschul et al. 1997) and preliminary phylogenetic analyses were used to select related sequences for further study; the single sequences identified as *G. imperialis* (Speg.) Singer (AY280986, Costa Rica, Guzmán-Dávalos et al. 2003) and *G. allochrous* nom. prov. (AY386832, Australia, Rees et al. 2002) clustered together in preliminary analyses but were excluded from subsequent analyses because of low support for their placement within the *G. junonius* clade. Only 15 collections and related reference sequences had both ITS and LSU sequence data available, and these were aligned and analyzed separately from the larger set with just ITS sequences. Sequences of the ITS and LSU region were aligned using MAFFT v7 (Katoh and Standley 2013) with the G-INS-i strategy and "leave gappy regions" option invoked, then the rough ends of alignments trimmed using MEGA 7.0 (Kumar et al. 2016). The ITS–LSU dataset

yielded a matrix of 15 terminals, 1585 bases long including alignment gaps, with 37 parsimony-informative characters. The ITS dataset yielded a matrix of 77 terminals, 685 bases long including alignment gaps, with 80 parsimony-informative characters. Neighbor-joining (NJ) and maximum likelihood (ML) analyses were made in MEGA 7.0, with node support determined as bootstrap support using 100 replicates.

## Results

### Molecular phylogeny

Analyses of both ITS–LSU (data not shown) and ITS data alone provided strong support for the distinction of *Gymnopilus junonius*, with sequences from Europe, South America, and Australasia, from North American and Asian species of this complex, with no support for segregation of morphological or geographic variants (Figs. 1 and 2). Three proposed new species were in well-supported terminal clades. *Gymnopilus voitekii* sp. nov. is represented by 18 sequences from eastern Canada, two from western Canada, and one from North Carolina in the USA. *Gymnopilus speciosissimus* sp. nov. is represented by two sequences each from Quebec and Massachusetts, and *Gymnopilus orientispectabilis* sp. nov. by two sequences from Japan. Four collections identified as *G. ventricosus*, from British Columbia and Washington state, clustered with the holotype of this species from California. Also supported as monophyletic were *G. luteus*, with sequences from New Brunswick, Ontario, Quebec, Indiana, and Maryland, and a sister species to *G. luteus*, with sequences from China, Japan, and the Russian Far East, to which we give the informal clade name */sororiluteus* because we did not examine specimens on which to base a new species description. A well-supported clade includes *G. subspectabilis* and *G. speciosissimus*, but sequences representing the former species in our phylogenetic analyses are left paraphyletic by recognition of the latter, which we recognize as distinct because of its unique morphology.

### Taxonomy

*Gymnopilus voitekii* Malloch & Thorn, sp. nov. (Figs. 3–5)

MYCOBANK: MB 831719.

TYPE: CANADA, New Brunswick, Charlotte County, Little Lepreau, clustered on a wound at the base of a living trunk of *Abies balsamea*, 45.13°N, 66.49°W, 5 September 2004, D. Malloch 05-09-04/01 (holotype NBM-F00943).

ETYMOLOGY: Honouring Dr. Andrus Voitek for his contributions to mycology in Canada, particularly Newfoundland and Labrador, where the new species commonly occurs.

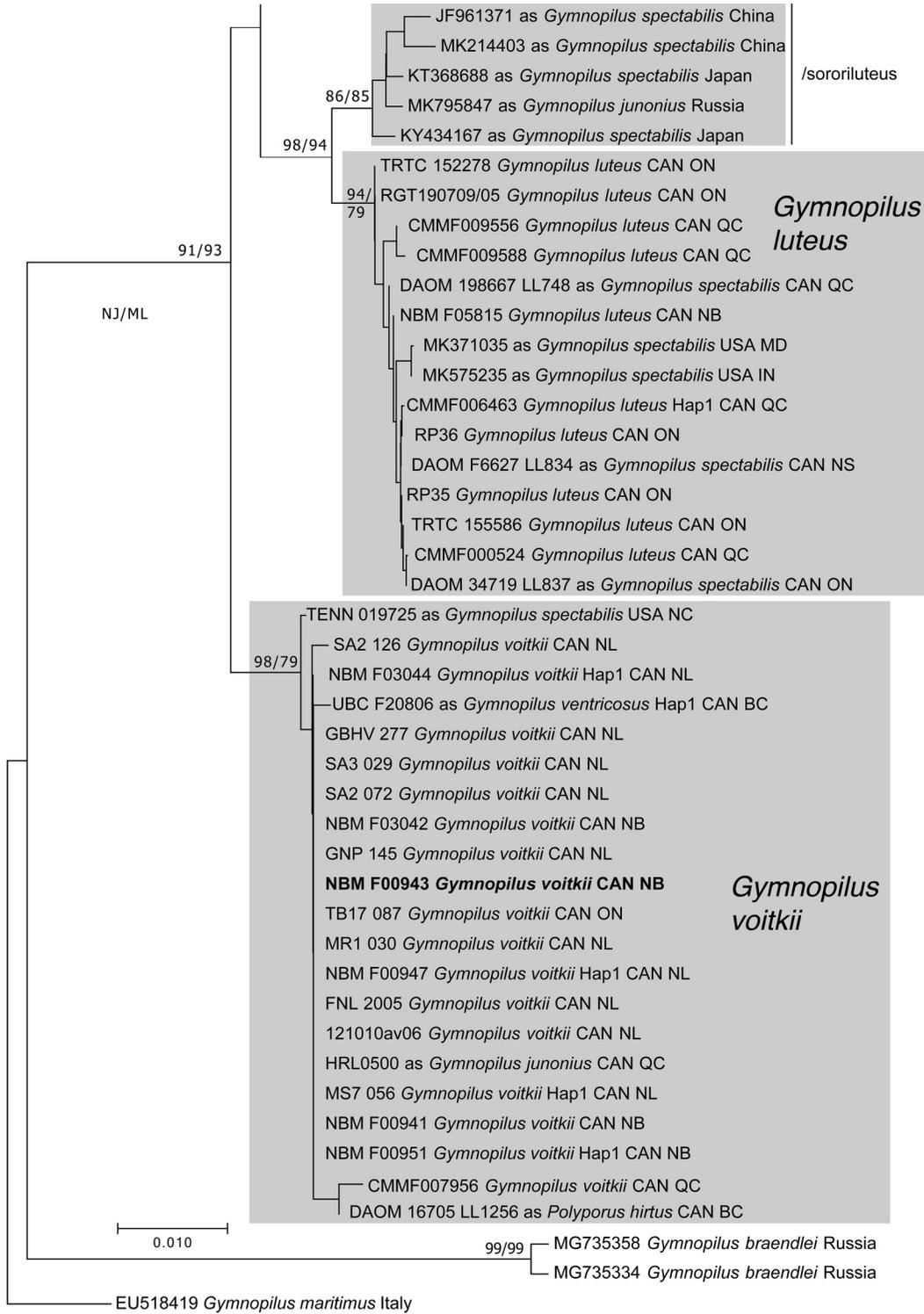
DIAGNOSIS: A large, solitary to cespitose *Gymnopilus* with orangish brown pileus and stipe, yellow and very bitter flesh, a cortinate to membranous partial veil that usually forms a distinct annulus or annular zone, and rusty

**Table 1.** *Gymnopilus* collections and new sequences used in phylogenetic analyses; full collection data provided in the text in the section on *Specimens examined*.

Name	Voucher number	Source locality	GenBank accession
<i>G. luteus</i>	CAT06-106, TRTC155586	USA: MD	MN453485
<i>G. luteus</i>	CMMF000524	Canada: QC	MN206894
<i>G. luteus</i>	CMMF006463 Haplotype A	Canada: QC	MN206889
<i>G. luteus</i>	CMMF006463 Haplotype B	Canada: QC	MN206890
<i>G. luteus</i>	CMMF009556	Canada: QC	MN206891
<i>G. luteus</i>	CMMF009588	Canada: QC	MN206892
<i>G. luteus</i>	DAOM 198667 LL748	Canada: QC	MN477932
<i>G. luteus</i>	DAOM 34719 LL837	Canada: ON	MN477919
<i>G. luteus</i>	DAOM F6627 LL834	Canada: NS	MN477917
<i>G. luteus</i>	NBM-F05815, as <i>G. spectabilis</i>	Canada: NB	MN206893
<i>G. luteus</i>	RGT190709/05, UWO	Canada: ON	MN718842
<i>G. luteus</i>	RP35, TRTC168170	Canada: ON	MN453483
<i>G. luteus</i>	RP36, TRTC168171	Canada: ON	MN453484
<i>G. luteus</i>	TRTC152278, as <i>G. spectabilis</i>	Canada: ON	MN206888
<b><i>G. orientispectabilis</i></b>	<b>TMI 37361, as <i>G. spectabilis</i></b>	<b>Japan: Tottori</b>	<b>MN206910</b>
<i>Gymnopilus</i> sp.	UBC-F13110, as <i>G. ventricosus</i>	USA: CA	MN206907
<b><i>G. speciosissimus</i></b>	<b>CMMF002481</b>	<b>Canada: QC</b>	<b>MN206895</b>
<i>G. speciosissimus</i>	CMMF002873	Canada: QC	MN206896
<i>G. subspectabilis</i>	CMMF001425, as <i>G. luteus</i> Haplotype A	Canada: QC	MN206902
<i>G. subspectabilis</i>	CMMF001425, as <i>G. luteus</i> Haplotype B	Canada: QC	MN206903
<i>G. subspectabilis</i>	CMMF001674, as <i>G. validipes</i>	Canada: QC	MN206899
<i>G. subspectabilis</i>	CMMF002599, as <i>G. validipes</i>	Canada: QC	MN206900
<b><i>G. subspectabilis</i></b>	<b>MICH 10995</b>	<b>USA: MI</b>	<b>MN206901</b>
<i>G. subspectabilis</i>	TRTC152281, as <i>G. spectabilis</i> Haplotype A	Canada: ON	MN206897
<i>G. subspectabilis</i>	TRTC152281, as <i>G. spectabilis</i> Haplotype B	Canada: ON	MN206898
<b><i>G. ventricosus</i></b>	<b>NY-00775471</b>	<b>USA: CA</b>	<b>KY780960</b>
<i>G. ventricosus</i>	UBC-F12848	Canada: BC	MN206904
<i>G. ventricosus</i>	UBC-F14959	Canada: BC	MN206906
<i>G. ventricosus</i>	UBC-F27046	Canada: BC	MN206908
<i>G. voitkii</i>	12.10.10.av06, FNL	Canada: NL	MN206874
<i>G. voitkii</i>	CMMF003540, as <i>G. junonius</i>	Canada: QC	MN206885
<i>G. voitkii</i>	CMMF007956, as <i>G. junonius</i>	Canada: QC	MN206886
<i>G. voitkii</i>	DAOM 16705 (LL1256)	Canada: BC	MN480813
<i>G. voitkii</i>	FNL 2005	Canada: NL	MN206875
<i>G. voitkii</i>	FNL 2009 MS7-056 Haplotype A	Canada: NL	MN206879
<i>G. voitkii</i>	FNL 2009 MS7-056 Haplotype B	Canada: NL	MN206880
<i>G. voitkii</i>	FNL 2010 SA2-072	Canada: NL	MN206882
<i>G. voitkii</i>	FNL 2010 SA5-126	Canada: NL	MN206878
<i>G. voitkii</i>	FNL 2010 SA3-029	Canada: NL	MN206881
<i>G. voitkii</i>	FNL 2011 MR1-030	Canada: NL	MN206877
<i>G. voitkii</i>	FNL 2012 GNP-145	Canada: NL	MN206876
<i>G. voitkii</i>	GBHV-277, UWO	Canada: NL	MN718841
<i>G. voitkii</i>	HRL0500, as <i>G. junonius</i>	Canada: QC	MN206887
<i>G. voitkii</i>	NBM-F00941	Canada: NB	MN206865
<b><i>G. voitkii</i></b>	<b>NBM-F00943</b>	<b>Canada: NB</b>	<b>MN206867</b>
<i>G. voitkii</i>	NBM-F00947 Haplotype A	Canada: NL	MN206872
<i>G. voitkii</i>	NBM-F00947 Haplotype B	Canada: NL	MN206873
<i>G. voitkii</i>	NBM-F00951 Haplotype A	Canada: NB	MN206868
<i>G. voitkii</i>	NBM-F00951 Haplotype B	Canada: NB	MN206869
<i>G. voitkii</i>	NBM-F03042	Canada: NB	MN206866
<i>G. voitkii</i>	NBM-F03044 Haplotype A	Canada: NL	MN206870
<i>G. voitkii</i>	NBM-F03044 Haplotype B	Canada: NL	MN206871
<i>G. voitkii</i>	TENN-F-019725	USA: NC	MT013032
<i>G. voitkii</i>	TB17-087, TRTC175634	Canada: ON	MN453486
<i>G. voitkii</i>	UBC-F20806, as <i>G. ventricosus</i> Haplotype A	Canada: BC	MN206883
<i>G. voitkii</i>	UBC-F20806, as <i>G. ventricosus</i> Haplotype B	Canada: BC	MN206884

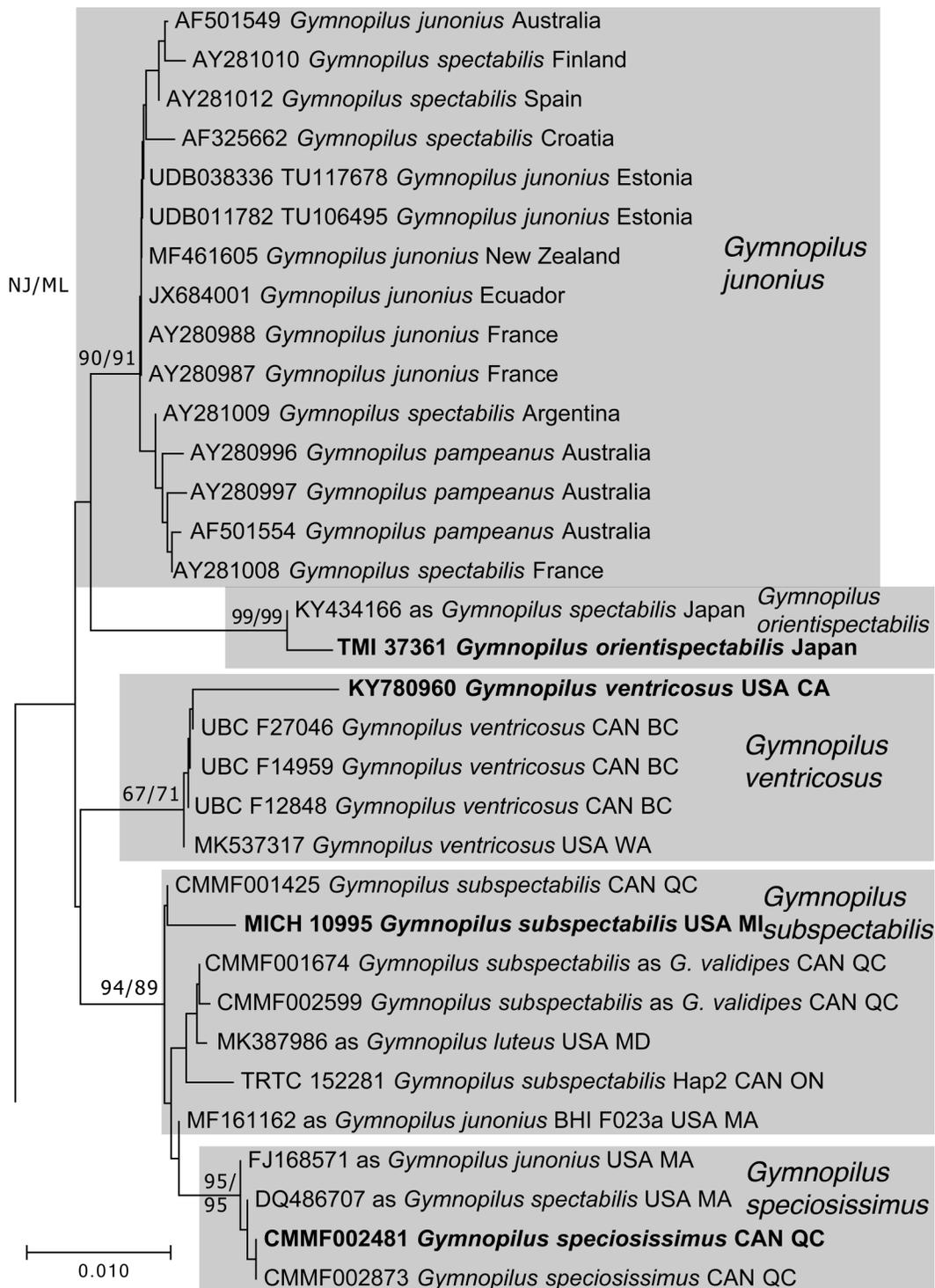
**Note:** Holotypes are indicated in bold font. MD, Maryland; QC, Quebec; ON, Ontario; NS, Nova Scotia; NB, New Brunswick; CA, California; MI, Michigan; BC, British Columbia; NL, Newfoundland & Labrador.

**Fig. 1.** “Bottom” half of a phylogenetic tree of the *Gymnopilus junonius* complex based on ITS sequence data. The topology shown is from a neighbor-joining (NJ) analysis, with clade support shown at nodes as 100× bootstrap values from NJ/ML. Trees were rooted with *G. maritimus*, following Guzmán-Dávalos et al. (2009). This panel shows the root, *G. maritimus*, two sequences from Russia named *G. braendlei*, ***Gymnopilus voitkii*** sp. nov., *G. luteus*, and its Asian sister species we informally name */sororiluteus* (continued in Fig. 2).



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**Fig. 2.** “Top” half of a phylogenetic tree of the *Gymnopilus junonius* complex based on ITS sequence data, showing *G. junonius* (including sequences identified as *G. pampeanus* and *G. spectabilis*), *Gymnopilus orientispectabilis* sp. nov., *G. ventricosus*, *G. subspectabilis*, and *Gymnopilus speciosissimus* sp. nov.



brown, coarsely warted basidiospores. Differs from other species of *Gymnopilus* in its growth on conifers, general lack of pleurocystidia, lecythiform cheilocystidia, and basidiospores with a rounded rather than conical apex. ITS–LSU sequence of the holotype, MN206867.

**COLOUR ILLUSTRATIONS:** This species has not, to our knowledge, been illustrated in any published field guides, but photographs of a number of the specimens examined and confirmed by DNA sequence data are available online, including [HRL 0500](#); [CMMF003540](#); [SA2-072](#); [SA3-029](#); [MR1-030](#); [SA5-126](#).

**Fig. 3.** Basidiomata of *Gymnopilus voitkii* sp. nov. SA3-029, Saint Anthony, Newfoundland & Labrador (photo courtesy of Roger Smith). [Colour online.]



**MACROMORPHOLOGY (FIG. 3):** **Pileus** 27–155 mm in diameter, conic-convex at first, expanding to broadly convex at maturity, with a low broad umbo or without an umbo, dry and with a matte and unreflective surface, glabrous to finely appressed-scaly, orange yellow (4–6AB4–6) to brownish orange (5–6BC4–5), pale yellow (4A3) below the surface tissues, sometimes with a submarginal fringe of veil remnants and then the annulus less well-defined. **Stipe** 28–120 mm × 6–20 mm, equal to clavate or ventricose, sometimes subradicating, dry, glabrous, greyish orange to brownish orange (4–5ABC2–4). **Lamellae** greyish yellow (2–4AB2–4), slightly darker and developing some rusty stains in age, close to subclose, adnexed, not marginate. **Partial veil** forming a membranous and pendant, greyish orange (5B5) annulus in some basidiomata but with this reduced to a cortinate annular ring in others, often appressed to the stipe in age. **Flesh** pale yellow (2–5A2–3), more orange toward the base of the stipe, often with a complex odour described as mushroom mixed with sweat, coconut, or mint, very bitter in taste.

**MICROMORPHOLOGY (FIG. 4):** **Basidiospores** rusty brown in print, ( $n = 691/22$ ) ellipsoidal, with broadly rounded apices, coarsely roughened with large and irregular warts, darkening in 5% KOH, non-dextrinoid to lightly dextrinoid, ( $7.2$ )– $7.9$ – $9.9$ –( $10.2$ )  $\mu\text{m} \times$  ( $5.2$ )– $5.6$ – $6.9$ –( $7.2$ )  $\mu\text{m}$   $8.9 \pm 0.5 \mu\text{m} \times 6.2 \pm 0.4 \mu\text{m}$ ),  $Q = (1.27)$ – $1.31$ – $1.54$ –( $1.64$ ) (average =  $1.43 \pm 0.06$ ). **Cheilocystidia** ( $n = 183/11$ ) mostly lecythiform but occasionally without a swollen apex; length = ( $19.3$ )– $23.0$ – $40.3$ –( $43.8$ )  $\mu\text{m}$ , average =  $31.7 \pm 4.3 \mu\text{m}$ ; venter = ( $2.9$ )– $4.8$ – $9.3$ –( $10.0$ )  $\mu\text{m}$ , average =  $7.1 \pm 1.1 \mu\text{m}$ ; neck = ( $1.6$ )– $1.8$ – $3.7$ –( $3.8$ )  $\mu\text{m}$ , average =  $2.7 \pm 0.5 \mu\text{m}$ ; head = ( $2.3$ )– $3.7$ – $7.1$ –( $9.3$ )  $\mu\text{m}$ , average =  $5.4 \pm 0.9 \mu\text{m}$ . **Pleurocystidia** ( $n = 1$ ) rare to absent, similar to the cheilocystidia but less strongly capitate. **Caulocystidia** ( $n = 80/5$ ) abundant above the annular zone, produced as terminal cells of long hair-like hyphae, narrowly ventricose-capitate to cylindrical-capitate, sometimes cylindrical and without significant apical swelling; length = ( $24.1$ )– $35.0$ –

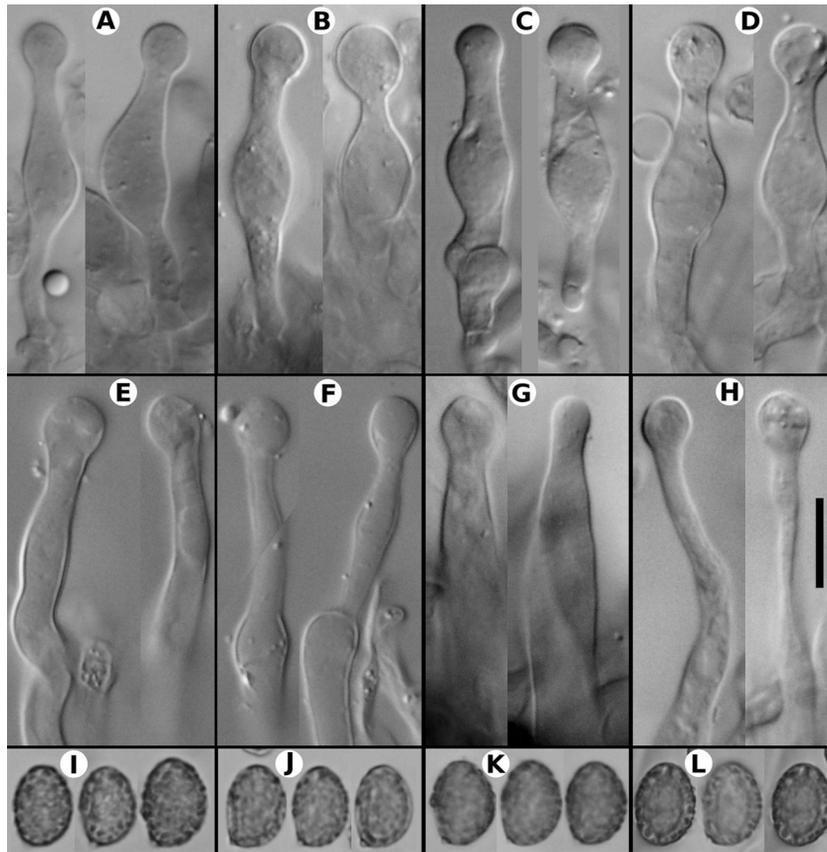
$76.2 \mu\text{m}$ , average =  $55.6 \pm 10.3 \mu\text{m}$ ; venter =  $3.1$ – $8.9$ –( $11.3$ )  $\mu\text{m}$ , average =  $6.0 \pm 1.5 \mu\text{m}$ ; neck = ( $1.5$ )– $1.8$ – $4.7$ –( $6.0$ )  $\mu\text{m}$ , average =  $3.3 \pm 0.7 \mu\text{m}$ ; head = ( $3.5$ )– $3.6$ – $8.4$ –( $9.0$ )  $\mu\text{m}$ , average =  $6.0 \pm 1.2 \mu\text{m}$ . **Basidia** 4-spored, clavate to cylindrical, usually constricted near or above the middle, occasionally stipitate,  $28.9$ – $39.1 \mu\text{m} \times 7.3$ – $9.2 \mu\text{m}$ . Clamp connections present on nearly all septa.

**MORPHOLOGY IN CULTURE (FIG. 5):** **Colonies** on modified Leonian's agar growing weakly, thin, and nearly transparent. Producing scattered holoblastic conidia. **Conidia** terminal or intercalary, with walls thickened or remaining thin, hyaline, smooth,  $5.0$ – $13.7 \mu\text{m} \times 3.7$ – $8.4 \mu\text{m}$ .

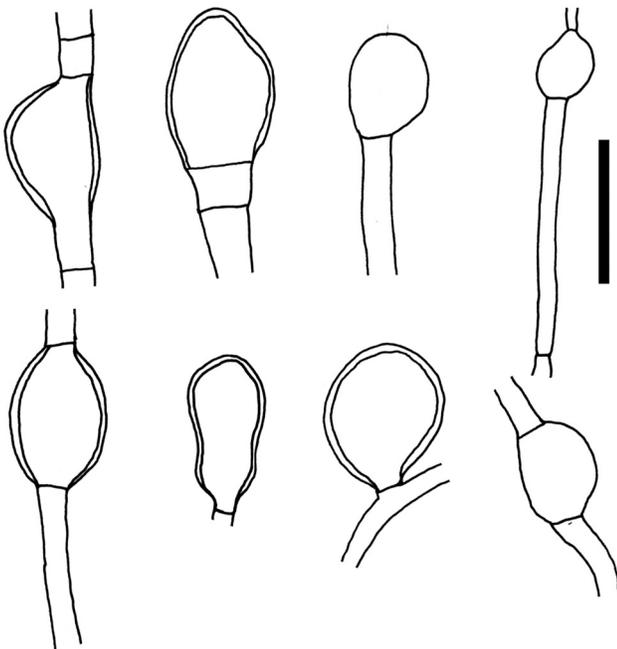
**ECOLOGY:** Clustered on wood of coniferous trees, in eastern Canada most commonly on *Abies balsamea* but also *Picea rubens*. Typically on basal wounds of living trees but also on dead trees and logs.

**COLLECTIONS EXAMINED:** CANADA, British Columbia, southwest of Eastgate, Manning Provincial Park, Beaver Pond Trail,  $49.06^\circ\text{N}$ ,  $120.77^\circ\text{W}$ , 18 September 2009, *P. Kroeger* (UBC-F20806), New Brunswick, Charlotte County, New River Beach Provincial Park, Barnaby Head Trail, on dead standing conifer (possibly *Picea rubens*),  $45.13^\circ\text{N}$ ,  $66.52^\circ\text{W}$ , 3 September 2006; *D. Malloch* 03-09-06/01 (NBM-F00951), same location, gregarious on a wound at the base of a dead standing trunk of *Abies balsamea*,  $45.13^\circ\text{N}$ ,  $66.53^\circ\text{W}$ , 23 September 2018, *D. Malloch* 23-09-18/01 (NBM-F07339), same location, gregarious on the end of a cut log of *Abies balsamea*,  $45.13^\circ\text{N}$ ,  $66.53^\circ\text{W}$ , 23 September 2018, *D. Malloch* 23-09-18/02 (NBM-F07340), Little Lepreau, clustered on a wound near the base of a living *Abies balsamea*,  $45.14^\circ\text{N}$ ,  $66.49^\circ\text{W}$ , 28 August 2004, *D. Malloch* 28-08-04/01 (NBM-F00941), same location, clustered on a wound at the base of the trunk of a living but moribund *Abies balsamea*,  $45.13^\circ\text{N}$ ,  $66.48^\circ\text{W}$ , 23 August 2008, *D. Malloch* 23-08-08/01 (NBM-F03042), Newfoundland and Labrador, Newfoundland, La Manche Provincial Park, clustered at the base of a living *Abies balsamea*,  $47.17^\circ\text{N}$ ,  $52.86^\circ\text{W}$ , 27 August 2007, *B. Bunyard* (*D. Malloch* 27-09-07/01) (NBM-F03044), Gros Morne National Park, Gros Morne Trail, clustered at the base of a large dead *Abies balsamea*,  $49.57^\circ\text{N}$ ,  $57.82^\circ\text{W}$ , 31 August 2005, *D. Malloch* 31-08-05/03 (NBM-F00947), same location, upper trail to Green Gardens, on living *Abies balsamea*,  $49.50^\circ\text{N}$ ,  $58.13^\circ\text{W}$ , 10 October 2012, *M. Voitk* 12.10.10.av06 (FNL), same location, Broom Point, on *Abies balsamea*,  $49.84^\circ\text{N}$ ,  $57.87^\circ\text{W}$ , 3 September 2005, *Unknown* (FNL), L'Anse aux Meadows, Tickle Inn, Cape Onion Trail, on *Abies balsamea*,  $51.61^\circ\text{N}$ ,  $55.63^\circ\text{W}$ , 20 September 2012, *H. Mann* (FNL), east of Pollard's Point, Main River 2 site, on moss under living *Abies balsamea*,  $49.76^\circ\text{N}$ ,  $57.00^\circ\text{W}$ , 6 September 2011, *M. Burzynski* (MR1-030, FNL), St. Anthony, Aurora Ski Club, on *Abies balsamea*,  $51.40^\circ\text{N}$ ,  $55.59^\circ\text{W}$ , 11 September 2010, *H. Mann* (SA5-126, FNL), *B. Bunyard* (FNL), near Grand Falls, Lion Max Simms Camp, on *Abies balsamea*,  $48.97^\circ\text{N}$ ,  $55.54^\circ\text{W}$ , 8 September 2009, *M. Beug* (FNL), south of Raleigh, Pistolet Bay Provincial Park,

**Fig. 4.** *Gymnopilus voitkii* sp. nov. (A–D) Cheilocystidia. (A) NBM-F00943; (B) NBM-F03044; (C) CMMF 3540; (D) UBC-F20806. (E–H) Caulocystidia. (E) NBM-F00943; (F) NBM-F03044; (G) CMMF 3540; (H) UBC-F20806. (I–L) Basidiospores. (I) NBM-F00943; (J) NBM-F00947; (K) CMMF 3540; (L) UBC-F20806. Scale bar = 10  $\mu\text{m}$ .



**Fig. 5.** *Gymnopilus voitkii* sp. nov., NBM-F00951. Blastic conidia from culture on modified Leonian's agar. Scale bar = 10  $\mu\text{m}$ .



on living conifer, 51.52°N, 55.70°W, 9 September 2010, B. Bunyard (FNL), Ontario, Thunder Bay, abandoned trail along lake shore of Little Trout Bay, on log of conifer, possibly *Tsuga canadensis*, 48.06°N, 89.46°W, 5 September 2017, J.M. Moncalvo & S. Margaritescu (TB17-087 = TRTC175634), Quebec, MRC Matawinie, Rawdon, 46.05°N, 73.75°W, 26 September 2000, A. Jean (CMMF003540), north-east of Sainte-Euphémie, in tufts on buried wood at base of *Abies balsamea*, 46.80°N, 70.36°W, 16 August 2006, R. McNeil C2889 (CMMF007956), Sept-Îles, on unknown dead wood, 50.27°N, 66.40°W, 19 August 2010, J. Saucier & R. Lebeuf HRL0600, USA, North Carolina, Great Smoky Mountains National Park, Indian Gap, on trunk of living spruce, 35.61°N, 83.43°W, August 1950, L.R. Hesler (TENN-19725), Clingman's Dome, on trunk of living spruce, 35.56°N, 83.50°W, 15 September 1951, L.R. Hesler (TENN-20181).

**COMMENTS:** In eastern Canada and USA, *Gymnopilus voitkii* occurs on the wood of conifers, most commonly that of *Abies balsamea* but also on species of *Picea*. There are no host data associated with the two records from British Columbia, including one that was received as a culture isolated from conifer wood and identified as *Polyporus hirtus* Quél. [non Fr.; now known as *Jahnoporus hirtus* (Cooke) Nuss], which similarly produces chlamydospores

in culture (Nobles 1958). In New Brunswick, it is characteristically found on standing trees, emerging from wounds at breast height or below. The tree may be dead or living, although the wound contains dead wood. It is less commonly found on logs. The wounds on New Brunswick trees are frequently the result of past damage by porcupines, but those in Newfoundland, where there are no porcupines, are from other causes.

Basidiomata of *G. voitkii* are generally medium-sized to large, clustered and have the pileus in colours ranging from a rather bright orange yellow to orange brown. The colour of the stipe is not greatly contrasting with that of the pileus, being only slightly more yellow. The partial veil is variably cortinate in some basidiomata and thick and membranous in others. Basidiomata with lightly developed partial veils suggest those of *G. magnus* (Peck) Murrill, described as lacking an annulus (Peck 1897; Hesler 1969). We have examined Peck's original collection (NYS F-001833) of *G. magnus* but were unable to obtain DNA sequence data from it. The basidiospores measured 9.4–10.8  $\mu\text{m}$   $\times$  5.8–7.2  $\mu\text{m}$ ,  $Q = 1.4$ –1.8 (average = 10  $\times$  6.4  $\mu\text{m}$ ;  $Q = 1.6$ ). These were longer and narrower than those of *G. voitkii* (average length = 8.9  $\mu\text{m}$ ; average  $Q = 1.4$ ). Based on the reported magnification, Hesler's (1969) drawing of a basidiospore from the holotype of *G. magnus* measures 9.4  $\times$  6.1  $\mu\text{m}$ ,  $Q = 1.5$ . The aspect ratio and amygdaloid shape of basidiospores from the holotype of *G. magnus* suggest that *G. magnus* might belong in the *G. subspectabilis* clade in our study.

Previous collections of *G. voitkii* have been identified as *G. junonius* or *G. spectabilis*. This may account for the common belief that *G. junonius* can occur on both hardwoods and conifers. None of the collections that we sequenced match sequences deposited in GenBank or UNITE under the names *G. junonius*, *G. spectabilis*, or *G. spectabilis* var. *pampeanus*. In fact, based on the limited amount of deposited sequence data, we have no evidence that this species occurs in North America at all, although it seems to be widespread elsewhere. Hesler (1969) accepted the name *G. spectabilis* for a large number of North American collections taken from "conifer and deciduous logs, stumps, living and dead trunks, or buried wood." We have studied two of those collections cited by Hesler (TENN 19725, 20181), reported as growing on the wood of conifers, and found them to be typical *G. voitkii*. A future study that includes critical reexamination of all the collections cited by Hesler as *G. spectabilis* may expand the known range of *G. voitkii*.

The two conifer-inhabiting species of *Gymnopilus* that we have studied, *G. voitkii* and *G. ventricosus*, can be very similar in the field. Typically, *G. voitkii* is a smaller mushroom and with a less markedly ventricose stipe, but there is considerable overlap. So far, *G. ventricosus* has only been reported west of the Rocky Mountains while *G. voitkii* is known from both coasts, so the western material identified as *G. ventricosus* should be verified.

Lacking information from persons familiar with both species in the field, identifiers must at present depend upon micromorphological or molecular criteria. The most distinctive microscopic differences are basidiospore size and shape, and the shape of the cheilocystidia. Basidiospores of *G. voitkii* are longer and broader (average = 8.9  $\times$  6.2  $\mu\text{m}$ ;  $Q = 1.4$ ) than those of *G. ventricosus* (average = 7.9  $\times$  5.2  $\mu\text{m}$ ;  $Q = 1.5$ ). They have a broadly rounded apex in contrast to the more conical apex in *G. ventricosus*. The cheilocystidia of *G. voitkii* have a markedly swollen, subglobose head, whereas those of *G. ventricosus* are only slightly swollen or not swollen at all. Pleurocystidia are mostly lacking in *G. voitkii* and range from rare to frequent in *G. ventricosus*. However, as discussed elsewhere, we are reluctant to use presence or absence of pleurocystidia as a means of distinguishing taxa in this study.

*Gymnopilus junonius* (Fr.) P.D. Orton, Trans. Br. mycol. Soc. 43: 176 (1960).

Basionym: *Agaricus junonius* Fr., nom. sanct., Syst. mycol. (Lundae) 1: 244 (1821).

≡ *Pholiota junonia* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 301 (1879).

≡ *Pholiota spectabilis* var. *junonia* (Fr.) J.E. Lange, Fl. Agaric. Danic. 5: 100 (1940).

≡ *Gymnopilus spectabilis* var. *junonius* (Fr.) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 322 (1953).

≡ *Agaricus spectabilis* Weinm. [var.] b. Fr., Elench. fung. 1: 28 (1828).

MISAPPLICATION: *Agaricus spectabilis* Weinm., Syll. Pl. Nov. Ratisb. 1: 73 (1824), nom. sanct., Fr., Elench. fung. 1: 28 (1828) [= *Agaricus aureus* Matt., Enum. stirp. silesia (Breslau): 331 (1779), nom. sanct., Fr., Syst. mycol. 1: 241 (1821); current name *Phaeolepiota aurea* (Matt.) Maire, Icones selectae Fungorum, 6 Texte general 6: 111 (1928)].

MORPHOLOGY IN CULTURE: Walther et al. (2005) illustrated both globose, thick-walled blastoconidia and short-cylindric arthroconidia with rhexolytic dehiscence in an isolate of *G. junonius* from Germany, and Sede and López (1999) described the cultural morphology and illustrated terminal and intercalary, vesicular, thickwalled spores in an Argentinian isolate identified as *G. pampeanus*. Fausto-Guerra et al. (2002) studied the same strain studied by Sede and López (1999) and one additional strain they identified as *G. spectabilis* var. *pampeanus* and reported thick-walled terminal or intercalary chlamydospores 7.2–10  $\mu\text{m}$   $\times$  6.4–8.8  $\mu\text{m}$ , plus cylindric arthrospores 6.4–10.6  $\mu\text{m}$   $\times$  2.0–2.4  $\mu\text{m}$ .

COMMENTS: For nomenclatural stability, an epitype or neotype should be designated for this taxon. However, as currently understood based on sequence data, *G. junonius* appears to be geographically widespread to the exclusion of North America, and is well-described and illustrated in the European literature (Kühner and Romagnesi 1953; Phillips 1981; Orton 1993; Breitenbach and Kränzlin 2000; Holec 2005; Knudsen and Vesterholt

**Fig. 6.** Basidiomata of *Gymnopilus luteus* RGT 190927/06, Point Pelee National Park, Ontario. [Colour online.]



2012; Læssøe and Petersen 2019). Singer (1953) suggested that *G. pampeanus* had been introduced to South America from Australia, but an equally probable alternative based on the distribution of collections yielding similar sequences (Fig. 2) is that the European *G. junonius* was introduced to both South America and Australasia together with lumber or trees imported for horticulture and forestry. The collection described as *Flammula pampeana* by Spegazzini (1899) came from the Conchitas area of Buenos Aires, by that time already a well-to-do residential area with parks and gardens featuring plantings from Europe and Australia. However, Singer (1952) and Pegler (1983) report broader basidiospores of *G. pampeanus* than are typical of European *G. junonius*. Careful studies of tropical and Australasian species in this group, including type studies of *G. pampeanus*, *G. imperialis*, and *G. allochrous*, should be done to ascertain if there is a separate taxon with broader spores among these, and which name should be attached to it. To date, North American collections identified as *G. spectabilis* or *G. junonius* all appear to be one of the other species reported here, but it is possible that European *G. junonius* will be found in North America associated with non-native plantings, as with *Amanita phalloides* (Berch et al. 2017), or that it exists here but has not yet been sequenced.

*Gymnopilus luteus* (Peck) Hesler, Mycologia Memoirs 3: 26 (1969) (Figs. 6–8).

≡ *Pholiota lutea* Peck, N.Y. State Mus. Ann Rept. 51: 288 (1898).

≡ ?*Agaricus cerasinus* Peck, Bull. Buffalo Soc. nat. Sci. 1(2): 50 (1873) [1873–1874], *nom. inval.* (Art. 53.1) *non Agaricus cerasinus* Berk (1836).

≡ *Pholiota cerasina* Sacc., Syll. fung. (Abellini) 5: 744 (1887).

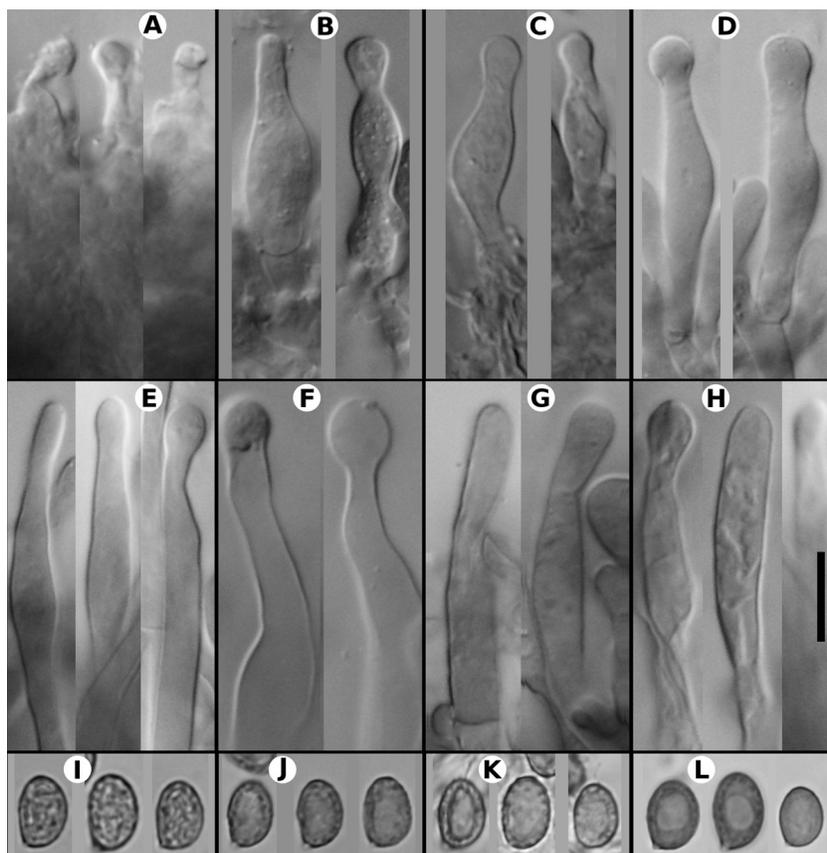
COLOUR ILLUSTRATIONS: Additional online image of sequence-confirmed material J. Labrecque 1172.

MACROMORPHOLOGY (FIG. 6): **Pileus** 22–250 mm in diameter, CONVEX–HEMISPHERICAL at first, expanding to more broadly convex and finally broadly plano-convex, with a regular incurved margin at first but in age having the margin rather irregularly folded and not incurved, dry to moist, glabrous to minutely silky-felty in young stages and remaining so throughout most of its development, becoming slightly diffracted-scaly in age, pale yellow to light yellow (3–4A3–4) at first, later darkening to light yellow (3–4A5) and even further through orange shades to orange (5AB6–7), but retaining the paler shades at the margin, often with a submarginal fringe of veil remnants. **Stipe** 35–150 mm × 5–30 mm, concolorous with the pileus although developing the orange shades more slowly, equal to bulbous-based, moist to dry, tapered at the base if in contact with other stipes, glabrous to finely appressed-fibrillose, with a well-developed annulus, fibrous to fairly tough. **Lamellae** at first yellowish white to pale yellow (4AB3–4) then becoming rusty orange (5–6CD6–7), close or moderately spaced, adnexed to sinuate (notched), not marginate. **Partial veil** compact to cortinate but remaining on the stipe as a membranous annulus but often appressed to the stipe in age, yellowish white to pale yellow (3A2–3) at first but later rusty due to accumulating basidiospores. **Flesh** pale yellow to light yellow (3–4A3–4), developing brownish orange (6BC6) colours in the outer parts at the base of the stipe, with a strong mushroom odour, very bitter in taste; the lamellar surface usually with a strong odour of anise.

MICROMORPHOLOGY (FIG. 7): **Basidiospores** rusty brown in print, ( $n = 530/8$ ) ellipsoidal, with broadly rounded apices, moderately roughened with irregular warts and short ridges, darkening in 5% KOH, non-dextrinoid to obscurely dextrinoid, (6.2–)6.5–8.3(–9.4)  $\mu\text{m} \times$  (4.3–)4.5–5.7(–6.1)  $\mu\text{m}$  (average =  $7.4 \pm 0.5 \mu\text{m} \times 5.1 \pm 0.3 \mu\text{m}$ ),  $Q = 1.28\text{--}1.58(–1.68)$  (average =  $1.45 \pm 0.1$ ). **Cheilocystidia** ( $n = 64/4$ ) mostly lageniform to lecythiform but occasionally without a swollen apex; length = 19.3–35.4(–36.7)  $\mu\text{m}$ , average =  $27.3 \pm 4.0 \mu\text{m}$ ; venter = (4.1–)4.3–8.2(–8.4)  $\mu\text{m}$ , average =  $6.3 \pm 1.0 \mu\text{m}$ ; neck = 1.5–3.8(–4.3)  $\mu\text{m}$ , average =  $2.7 \pm 0.6 \mu\text{m}$ ; head = (2.0–)2.5–6.1(–7.2)  $\mu\text{m}$ , average =  $4.3 \pm 0.9 \mu\text{m}$ . **Pleurocystidia** not seen. **Caulocystidia** ( $n = 62/4$ ) abundant above the annular zone, produced as terminal cells of long hair-like hyphae, narrowly ventricose–capitate to cylindrical–capitate, often cylindrical to clavate and without significant apical swelling; length = (28.6–)30.9–66.9  $\mu\text{m}$ , average =  $48.9 \pm 9.0 \mu\text{m}$ ; venter = (2.8–)3.4–8.3(–9.0)  $\mu\text{m}$ , average =  $5.9 \pm 1.2 \mu\text{m}$ ; neck = 1.3–5.7(–8.0)  $\mu\text{m}$ , average =  $3.5 \pm 1.1 \mu\text{m}$ ; head = (2.1–)3.0–8.0  $\mu\text{m}$ , average =  $5.5 \pm 1.3 \mu\text{m}$ . **Basidia** 4-spored, clavate to cylindrical, usually constricted near or above the middle, occasionally stipitate, 26.1–38.7  $\mu\text{m} \times$  7.0–8.1  $\mu\text{m}$ . Clamp connections present on nearly all septa.

MORPHOLOGY IN CULTURE (FIG. 8): **Colonies** on modified Leonian's agar with a radius of 40–52 mm in 24 days at 20 °C, white, lanose, not at all appressed although slightly less

**Fig. 7.** *Gymnopilus luteus*. (A–D) Cheilocystidia. (A) NYS F-1768.1 (holotype); (B) TRTC152278; (C) NBM-F05815; (D) CMMF 9588. (E–H) Caulocystidia. (E) TRTC152278; (F) NBM-F05815; (G) CMMF 6463; (H) CMMF 9556. (I–L) Basidiospores. (I) NYS F-1768.2 (holotype); (J) TRTC152278; (K) NBM-F05815; (L) CMMF 9556. Scale bar = 10  $\mu\text{m}$ .



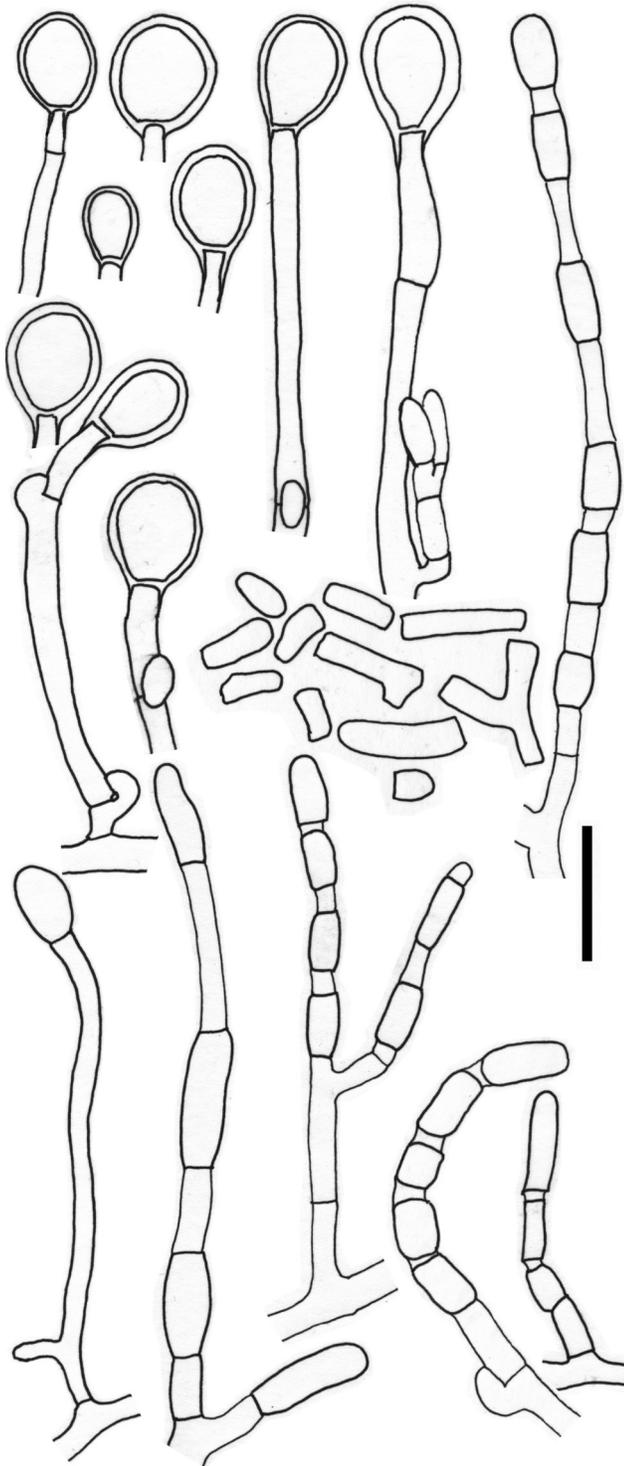
dense at the margin, with abundant small water droplets, with a well-defined margin, with reverse white to yellowish white, with a slight mushroom- or coconut-like odour. **Conidia** of two kinds: thallic and holoblastic. Thallic conidia produced in short to moderately long chains with rhexolytic dehiscence, cylindrical, hyaline, smooth, borne on hyphae with or without clamp connections, 2.3–11.0  $\mu\text{m}$   $\times$  1.4–3.8  $\mu\text{m}$ . Holoblastic conidia with thickened wall that extend a short distance into the conidiogenous cell, hyaline, subglobose to obovoid, with a basal ring representing the thickened apex of the conidiogenous cell, smooth, often borne on hyphae with clamp connections, 5.7–11.2  $\mu\text{m}$   $\times$  4.3–10.0  $\mu\text{m}$ .

**ECOLOGY:** Clustered on wood of various hardwood trees.

**COLLECTIONS EXAMINED:** CANADA, New Brunswick, Fredericton, Odell Park, on dead angiosperm wood on the ground, 45.96°N, 66.66°W, July 1985, *H. Hinds* (NBM-F05815), Ontario, Mississauga, Cooksville, cespitose on log of *Tilia americana*, 43.58°N, 79.64°W, 28 September 1980, *D. Malloch* 28-09-80/01 (TRTC152278; herein designated as epitype, MB387836), Halton Hills, Esquesing Conservation Area, on unidentified hardwood log in forest of *Acer rubrum* and *Tilia americana*, 43.54°N, 79.95°W, elev. 250 m a.s.l., 15 September 1985, *R.G. Thorn* 850915/02 (UWO), Essex County, Point Pelee National Park, Tilden's

Wood Trail, on old well-rotted hardwood log in woods of *Acer saccharinum* and *Juglans nigra*, 41.93514°N, 82.51070°W, 177 m, 27 September 2019, *R.G. Thorn & L. Balogh* RGT 1900927/16 (UWO), Puslinch, Little Tract, on old hardwood log in mature woods of *Tsuga canadensis*, 43.459°N, 80.253°W, 9 July 2019, *R.G. Thorn* 190709/05 (UWO), Toronto, Rouge Park, on dead wood in deciduous forest, 43.81°N, 79.15°W, 24 September 2012, *J.M. Moncalvo & S. Margaritescu* (RP35 = TRTC168170), same as above (RP36 = TRTC168171), Quebec, Laval, 45.61°N, 73.71°W, 26 June 1989, *Y. Lamoureux* (CMMF000524), Melocheville, Beauharnois, on rotted log in deciduous forest, 45.32°N, 73.96°W, 24 June 1981, *R. McNeil* 1134 (CMMF005718), Vaudreuil-Soulanges, on rotted oak in coniferous forest, 45.39°N, 74.22°W, 23 August 2006, *R. McNeil* 2897 (CMMF006463), Quebec City, Château Bigot, on rotted wood in mixed forest, 46.90°N, 71.27°W, 17 July 2007, *J. Labrecque* 1140 (CMMF009556), same location, in mixed forest, 46.90°N, 71.27°W, 22 July 2007, *J. Labrecque* 1172 (CMMF009588), USA, Maryland, Frederick County, Catoc-tin Mountain Park, on dead wood in mixed forest, 39.38°N, 77.28°W, October 2006, *D. Dewsbury* et al. (CAT06-106, TRTC155586), New York, North Elba, decayed wood and trunks of trees, 44.24°N, 73.95°W, *C. Peck* (NYSF 1768.1–4, **holotype!** of *Pholiota lutea*).

Fig. 8. *Gymnopilus luteus*, TRTC152278. Blastocystidia and thallic conidia from culture on modified Leonian's agar. Scale bar = 10  $\mu$ m.



COMMENTS: *Gymnopilus luteus* is one of several species of *Gymnopilus* growing on hardwoods. It is difficult to distinguish in the field from *G. subspectabilis*, another species also occurring on hardwoods in North America, except by its distinct odour of anise when fresh. There are also clear microscopic differences: (i) the basidiospores of

Fig. 9. Basidiomata of *Gymnopilus orientispectabilis* sp. nov., TMI-37361, Kokoge, Tottori, Japan (holotype). [Colour online.]



*G. luteus* are characteristically rounded at the apex and the suprahilar region is usually convex; (ii) the cheilocystidia often do not form a continuous sterile zone and are rather weakly lageniform to lecythiform; and (iii) the caulocystidia are produced as end cells of an apical tomentum and are weakly differentiated as lageniform to lecythiform structures. *Gymnopilus subspectabilis* has basidiospores with a conical apex and a pronounced suprahilar depression, well-differentiated lecythiform cheilocystidia forming a continuous zone, and well-differentiated caulocystidia borne directly on the stipe. *Gymnopilus orientispectabilis*, known from Japan, grows on hardwoods and is similar macroscopically. It has similar poorly differentiated caulocystidia borne on a hyphal tomentum but differs in having basidiospores with a conical apex and a suprahilar depression.

*Pholiota lutea* Peck, the basionym of *G. luteus*, is represented by a possibly mixed type. We have received four samples of separate basidiomata from this type (NYSF 1768.1–4) but were unable to extract workable DNA from any. However, we were able to study basidiospores and cheilocystidia from each, and thus could make a morphological comparison with more recently collected material. Fortunately, the best fit with more recent collections came within a genetically distinct clade containing material from several sites in Ontario, Quebec, and New Brunswick. One of these collections, from Mississauga, Ontario, was accompanied by complete field notes and cultural data: we therefore select TRTC152278 as epitype (MBT387836). There seems little doubt that *Pholiota cerasina* as described by Overholts (1924, 1927) is this species, but we have not studied Peck's type in NYS. If type study supports this synonymy, *Pholiota cerasina* has priority over *P. lutea*.

*Gymnopilus orientispectabilis* Nagas., Malloch & Thorn, sp. nov. (Figs. 9–11)

MYCOBANK: MB833804.

**Fig. 10.** *Gymnopilus orientispectabilis* sp. nov., TMI-37361 (holotype). (A) Cheilocystidia. (B) Caulocystidia. (C) Basidiospores. Scale bar = 10  $\mu\text{m}$ .



**TYPE LOCALITY:** JAPAN, Tottori Pref., Tottori City, Kokoge, at the base of a dead standing tree of *Quercus serrata*, E. Nagasawa, EN17-60 (holotype TMI-37361).

**ETYMOLOGY:** Latin, *orienti-*, to denote the Asian counterpart of the species formerly known as *G. spectabilis*.

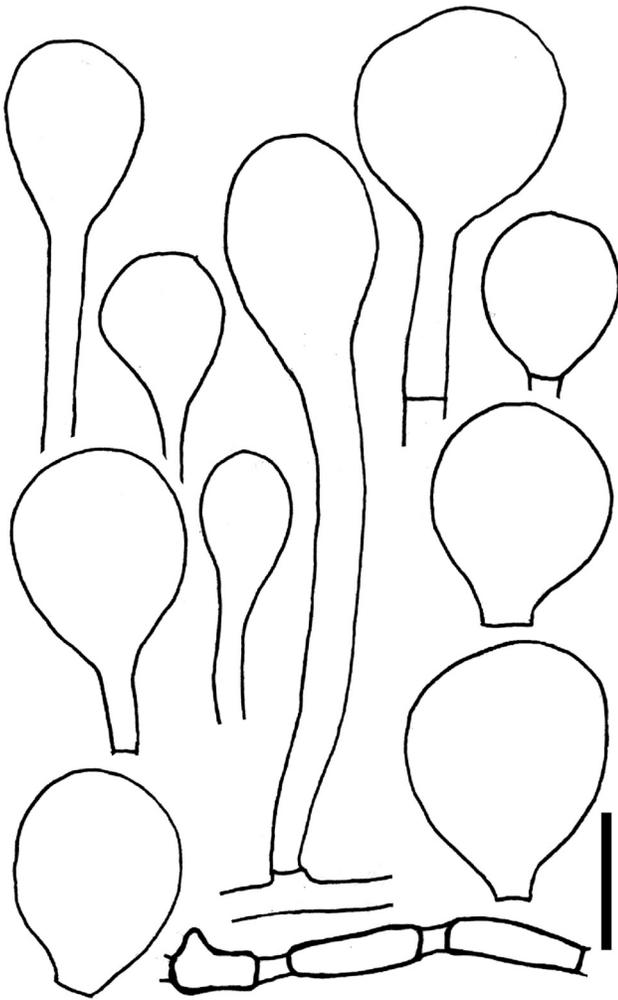
**DIAGNOSIS:** A large and robust *Gymnopilus* with cespitose fruiting bodies arising from a thick and fleshy, obconic or root-like base, differing from *G. junonius* of Europe and other species of this group in this aspect and in slightly smaller basidiospores, mostly 7.2–9.0  $\mu\text{m}$   $\times$  4.8–6  $\mu\text{m}$  (average = 8.0  $\times$  5.2  $\mu\text{m}$ ),  $Q = 1.3$ –1.8 (average 1.5), with an obtusely conical apex and a prominent suprahilar depression. ITS–LSU sequence of the holotype, GenBank MN206910.

**COLOUR ILLUSTRATIONS:** Kawamura (1954, Fig. 532); Imazeki and Hongo (1957, pl.32, Fig. 185; 1987, pl.63, Fig. 448); Imazeki et al. (1988, p. 268, lower photograph).

**MACROMORPHOLOGY (FIG. 9):** **Pileus** 4–19 cm broad, hemispheric, convex to conico-convex at first, then expanding to plane, rarely dull umbonate; surface dry to moist, slightly tacky when wet, smooth or at times finely areolate over the center, initially (in button stages) entirely covered with a thin whitish membranous layer that dis-

appears with age, becoming matted fibrillose to radially appressed fibrillose or minutely fibrillose-scaly toward the margin with age; colour light yellow to yellow (4A6–7; oac852–853) at first, becoming orange yellow (5B7–5B8; oac810–811), brownish yellow (5B8–5C8, 5C7–8; near oac775) to light brown (6D8) from the center outward with age, retaining yellow in shaded places, margin usually remaining light yellow to yellowish orange, changing to brown (6D–E8; oac768, oac782) to dark brown (7F4–5) when damaged or lightly rubbed, particularly in young specimens; margin incurved and inrolled at first, becoming extended with age, finally somewhat recurved, often obscurely fringed with remnants of fibrillose-membranous partial veil when young. **Stipe** up to 230 mm long and up to 20–28 mm wide, subcylindrical to cylindrical upward, becoming moderately enlarged downward, subventricose at times, often curved near the base or apex, sinuous at times, conjugated at the base and arising from a common, thick-fleshy, obconic or root-like mass buried in soil (up to 13 cm long and 8 cm wide), not easily separable from each other, rigid and more or less brittle, solid with soft center, narrowly hollow at times in fully matured specimens, with a cottony-

**Fig. 11.** *Gymnopilus orientispectabilis* sp. nov., TMI-37361 (holotype). Blastastic and thallic conidia. Scale bar = 10  $\mu\text{m}$ .



membranous annulus 10–30 mm below the apex; surface finely furfuraceous to smooth and pale to light yellow (3A3–4) above the annulus, below it light yellow to yellow (3A5–6 to 4A4–5; oac855–857) or pale greyish orange (5B3–4; oac777–779) downward, often decorated with minute, orange yellow (4B7; oac811) to brownish yellow (5C8; oac803) appressed fibrillose scales up to the annulus (particularly so when young), lower part obscurely fibrillose-scaly to appressed fibrillose or nearly glabrescent, stained brownish yellow (5C8; oac803), brown to dark brown (6D–F8) where rubbed or damaged. **Lamellae** 5–12 mm wide, comparatively narrow, mostly adnate but at times shallowly sinuate, with a short decurrent tooth, appearing subdecurrent in the fully expanded pilei, close with 1–3 tiers of lamellulae, pale yellow (3–4A3–4; oac813–814) to greyish yellow (4B5; near oac805) when young, brownish yellow to yellow ochre (5C6–7; near oac776) when mature, with brown to dark brown (6D–E8 to 6F8) stains where damaged; edges entire. **Annulus** fibrillose-membranous, well-developed, up to 15 mm wide, up to 3–4 mm thick near the stipe, flared upward at first, later pendent, rather persistent but fi-

nally becoming reduced to a narrow membranous to fibrillose annular zone, near yellow (3A7) to vivid yellow (3A8; oac854) initially, then somewhat paler, decorated more or less concentrically with cottony-fibrillose scales tinted orange yellow (4B7; oac811) to brownish yellow (5C8; oac803) in the outside. **Flesh** up to 16 mm thick in the center of the pileus, abruptly thinning toward the margin, pale to light yellow (3A3–5 to 4A4); in stipe more or less concolorous, firm, becoming soft centrally, at times narrowly hollow in upper part when old; taste very bitter, odour indistinctive when fresh, but distinctive with a rather strong, peculiar pungent odour in dried specimens, particularly when somewhat remoistened. **Spore deposit** on annulus brown (near 6D8) when fresh, brownish yellow to brown (5C8 to 6D8) when dry. **Macrochemical reactions:** Pileus surface turning brown (7E8) to reddish brown (9E5, 8–9E8, 9F6–8) with KOH; stipe surface turning concolorously or greyish red (10D5, 10E5–6) with KOH; flesh turning greyish red (9D4–5 to 10C4–5) or brownish orange to light brown (7C–D5) to brown (7–8E8) in immature specimens.

**MICROMORPHOLOGY (FIG. 10): Basidiospores** ( $n = 265/8$ ) ellipsoidal to amygdaliform, with conical apices, with a conspicuous suprahilar depression and a poorly developed suprahilar plage, moderately roughened with irregular warts (up to 0.6  $\mu\text{m}$ ) and short ridges, darkening in KOH (burnt Sienna to English red) and strongly dextrinoid, (6.6–)7.2–9.0(–9.6)  $\mu\text{m} \times$  (4.2–)4.8–6(–6.3)  $\mu\text{m}$  (average =  $8.0 \pm 0.6 \mu\text{m} \times 5.2 \pm 0.3 \mu\text{m}$ ),  $Q = 1.3–1.8$  (average =  $1.5 \pm 0.1$ ). **Cheilocystidia** abundant, mostly lecythiform, less commonly lageniform or clavate, rarely without a swollen apex; length ( $n = 63/2$ ) 16.8–48  $\mu\text{m}$ , average =  $28.8 \pm 7.3 \mu\text{m}$ ; venter ( $n = 63/2$ ) 4.8–9.6  $\mu\text{m}$ , average =  $5.7 \pm 1.1 \mu\text{m}$ ; neck length ( $n = 24/2$ ) 3.6–13.2  $\mu\text{m}$ ; neck width ( $n = 25/2$ ) 2.4–4.2  $\mu\text{m}$ ; head ( $n = 78/3$ ) 4.2–9.6  $\mu\text{m}$ , hyaline, at times with brownish yellow to brownish orange amorphous content in KOH. **Pleurocystidia** rare to lacking, difficult to find. **Caulocystidia** ( $n = 14/1$ ) abundant above the annular zone, produced as the end cells of long hair-like hyphae, poorly differentiated and mostly cylindrical; length = 40.3–68.6  $\mu\text{m}$ , average =  $54.4 \pm 7.1 \mu\text{m}$ ; venter = 3.4–7.6(–7.7)  $\mu\text{m}$ , average =  $5.5 \pm 1.0 \mu\text{m}$ ; neck = 2.7–4.9(–5.3)  $\mu\text{m}$ , average =  $3.8 \pm 0.6 \mu\text{m}$ ; head = 3.1–6.3  $\mu\text{m}$ , average =  $4.7 \pm 0.8 \mu\text{m}$ . **Basidia** 4-spored (occasionally 3-spored), clavate to cylindrical, usually constricted near or above the middle, ( $n = 60/4$ ) 22.2–36.0  $\mu\text{m} \times$  6.6–9.6  $\mu\text{m}$ , sterigmata 4.2–5.4  $\mu\text{m}$  long. Clamp connections present on nearly all septa.

**MORPHOLOGY IN CULTURE (FIG. 11): Colonies** on modified Leonian's agar with a radius of 70 mm in 30 days at 20  $^{\circ}\text{C}$ , white, sublanose to cottony, deepest in the marginal 10 mm, with an even margin, with reverse yellowish white (4A2–3), slightly darker under the inoculum, without a distinctive odour. **Conidia** holoblastic, rarely thallic: holoblastic conidia ( $n = 18/1$ ) with slightly thickened walls, hyaline, subglobose to obovoid, truncate at the

base, without basal extensions, smooth, borne on hyphae with scattered medallion clamp connections, 9.9–18.6  $\mu\text{m} \times 7.5\text{--}15.5 \mu\text{m}$  (average = 13.8  $\mu\text{m} \times 11.4 \mu\text{m}$ ); thallic conidia cylindrical, borne in short chains, separated by empty cells (rhexolytic dehiscence).

**ECOLOGY:** On hardwoods, especially on members of the Fagaceae (so far known from *Quercus serrata*, *Q. acutissima*, and *Castanea crenata*). Basidiomata are mostly found at the base of stumps and dead or still living trees in contact with the ground, growing on buried wood and roots in soil. Fruiting in autumn (September to November).

**COLLECTIONS EXAMINED:** JAPAN, Tottori Prefecture, Tottori City, Kokoge, on hardwood, 4 September 1974, *T. Arita* (TMI-1785), same location, cespitose at the base of a dead trunk of *Quercus*, 28 September 1978, *E. Nagasawa* & *S. Murakami* (TMI-19590); same location, cespitose on soil near the base of a living tree of *Quercus acutissima*, 4 October 2018, *E. Nagasawa*, EN18–83 (TMI-37389); same location and date, at the base of a dead trunk of *Q. serrata*, *E. Nagasawa*, EN18–84 (TMI-37390); Tottori City, Miwa, 17 October 1973, *U. Miwa* (TMI-1104); Tottori City, Fuse, 5 October 2017, *H. Uraki*, EN17–71 (TMI-37362); Tottori City, Kokufu-cho, Sandaiji, at the base of a standing tree of *Q. acutissima*, 29 September 1972, *I. Ohira* et al. (TMI-10168); Tottori City, Fukube-cho, Yaebara, at the base of a stump of a broad-leaved tree, 28 October 1986, *M. Taniguchi*, EN86–175 (TMI-13571\*); Tottori City, Oro, Oroyma, on soil in mixed deciduous forest dominated by *Q. serrata* and *Q. acutissima*, 24 September 2019, collector unknown, EN19–60 (TMI-37391); Tottori City, Engoji, at the base of a living deciduous tree, 23 October 2019, *H. Tanaka* and *E. Nagasawa*, EN19–93 (TMI-37392); Tottori City, Kokufu-cho, Okamasu, at the base of a living tree of *Q. acutissima*, 30 October 2019, *E. Nagasawa* and *S. Ushijima*, EN19–106 (TMI-37393); Yazu-gun, Chizu-cho, Mt. Nagi, in mixed deciduous forest, 9 November 2019, *M. Osumi*, EN19–120 (TMI-37394); Kurayoshi City, Obara, in mixed forest of *Cryptomeria* and *Quercus*, 23 October 2007, *H. Seo*, EN07–532NR (TMI-37388\*); Shimane Prefecture, Nita-gun, Okuizumo-cho, Shimoyokota, near a standing tree of *Castanea crenata*, 13 October 1996, *S. Yamada* (TMI-22380). \*Specimens lost due to insect damage; only photograph and culture are preserved.

**COMMENTS:** *Gymnopilus orientispectabilis* is a poisonous mushroom that was first described from Japan by *Kawamura* (1931, 1954), based on its toxicity and poisoning cases there. *Kawamura* (1931) and *Imai* (1938) identified it as *Pholiota spectabilis*, and since then the name *G. spectabilis* has been widely used for this mushroom in Japan (*Imazeki and Hongo* 1957, 1987; *Imazeki et al.* 1988). The European species, which we now refer to as *G. junonius*, is very similar to this Japanese species in most salient ecological and morphological characters (habit and habitat, colour and surface conditions of basidiomata, taste, shape and ornamentation of spores, characters of hymenial cystidia, etc.). They seem to be almost

identical morphologically and ecologically, although *G. orientispectabilis* may be distinguished from *G. junonius* in having somewhat smaller basidiospores and stipes that are joined at the base and arise from a common, thick-fleshed, obconic or root-like tissue buried in soil. The photo by *K. Yokoyama* identified as *G. spectabilis* in *Imazeki et al.* (1988, p. 268, lower) shows this latter feature strikingly in a specimen from Mount Taiko, Kyoto prefecture. Phylogenetically, based on ITS and LSU sequence data, *G. orientispectabilis* forms a separate clade showing a sister relationship to *G. junonius*; it may also differ from *G. junonius* in the presence of hallucinogenic compounds (*Tanaka et al.* 1993).

Our phylogram based on ITS sequence data indicates that the “*G. spectabilis*” complex in Japan, China, and the Russian Far East includes another apparently undescribed species (represented by sequences JF961371, KT368688, KY434167, MK214403, and MK795847) that is phylogenetically distinct from *G. orientispectabilis*, showing a closer relationship to the North American *G. luteus* than to the European *G. junonius*. The photo by *M. Izawa* identified as *G. spectabilis* in *Imazeki et al.* (1988, p. 268, upper right) may represent this species, to which we give the informal clade name */sororiluteus* because we lack specimens on which to describe it as a new species. It is possible that a third species of the complex grows on conifers in northern Japan, as suggested by the photo by *R. Yahagi* identified as *G. spectabilis* in *Imazeki et al.* (1988, p. 268, upper left). Further study of this complex in Japan is warranted. Morphological differences between *G. orientispectabilis* and other species of the *G. junonius* complex are shown in the key, below.

***Gymnopilus speciosissimus*** *Y. Lamoureux, Malloch & Thorn*, sp. nov. (Figs. 12 and 13)

MYCOBANK: MB 831720.

**TYPELOCALITY:** CANADA, Quebec, Montreal (Parc du Chalet de l’Héritage), 45.68°N, 73.51°W, 14 August 1995, coll. *Richard Nadon*, leg. *Y. Lamoureux* (holotype, CMMF002481).

**ETYMOLOGY:** From Latin *speciosus* and suffix *-issimus*, meaning “the most splendid or remarkable”.

**DIAGNOSIS:** Differentiated from other large *Gymnopilus* species by its robust fruiting bodies growing in cespitose clusters on dead hardwood, with brownish red tomentose to fibrillose cap contrasting with an off-white stipe, sometimes with a bluish-green zone below the annulus, lacking caulocystidia but with abundant pleurocystidia. ITS–LSU sequence of the holotype, GenBank MN206895.

**COLOUR ILLUSTRATIONS:** The holotype and paratype are illustrated online as CMMF002481 (holotype), and CMMF002873 (paratype).

**MACROMORPHOLOGY (FIG. 12):** **Pileus** 130–250(–350) mm in diameter when mature, globose, with an incurved margin at first, then convex and finally almost plane, dry, at first covered by a brownish-red tomentum, in age with fibril-

**Fig. 12.** *Gymnopilus speciosissimus* sp. nov. Basidiomata of CMMF 2481, Montreal, Quebec (holotype). Photo courtesy of Yves Lamoureux, Cercle des mycologues de Montreal. [Colour online.]



lose squamules on a yellowish background, slowly bruising brown then finally blackish. **Stipe** 150–350 mm × 20–50 mm (reaching 70 mm at base), very robust, narrowly clavate, sometimes rooting, hard, almost glabrous at apex but coarsely fibrillose under the annulus, the fibrils yellow then brown on a paler background, becoming brown when bruised or with age (darker toward base), sometimes with a pale blue-green zone just under the annulus. Mycelium white. **Lamellae** ochre yellow than rusty brown, slowly bruising brown, crowded and then close, thin, arched, narrow (up to 10 mm deep), subdecurrent, narrowly sinuate and forming lines on upper stipe when mature. **Partial veil** membranous, thin, ocher yellow, leaving a distinct flaring annulus on upper part of the stipe. **Flesh** very thick (up to 40 mm near stipe), firm, white, quickly yellowish, browner in stipe, darker toward base, with mushroom odour in the lamellae and pungent in the flesh, with an unpleasant, bitterish-acidulous taste.

**MICROMORPHOLOGY (FIG. 13): Basidiospores** rusty brown in print, ( $n = 147/2$ ) ellipsoidal amygdaliform, with bluntly conical apices and conspicuous suprahilar depression, moderately to coarsely roughened with irregular warts and short ridges, darkening in 5% KOH, strongly dextrinoid, (7.5–)7.7–9.1(–9.5)  $\mu\text{m} \times$  (4.5–)4.8–5.7(–5.8)  $\mu\text{m}$  (average =  $8.4 \pm 0.4 \mu\text{m} \times 5.2 \pm 0.2 \mu\text{m}$ ),  $Q = 1.46\text{--}1.75(–1.93)$

(average =  $1.61 \pm 0.1$ ). **Cheilocystidia** ( $n = 48/2$ ) mostly lageniform to lecythiform, rarely without a swollen apex, prominently stipitate; length = 22.8–37.2(–37.9)  $\mu\text{m}$ , average =  $30.0 \pm 3.6 \mu\text{m}$ ; venter = 4.4–7.0  $\mu\text{m}$ , average =  $5.7 \pm 0.6 \mu\text{m}$ ; neck = 1.5–2.8  $\mu\text{m}$ , average =  $2.1 \pm 0.3 \mu\text{m}$ ; head = 2.3–6.0(–6.6)  $\mu\text{m}$ , average =  $4.2 \pm 0.9 \mu\text{m}$ . **Pleurocystidia** ( $n = 16/2$ ) frequent and not difficult to find, lageniform to lecythiform, occasionally cylindrical; length = (18.1–)18.3–31.3  $\mu\text{m}$ , average =  $24.8 \pm 3.2 \mu\text{m}$ ; venter = 2.9–6.0  $\mu\text{m}$ , average =  $4.5 \pm 0.8 \mu\text{m}$ ; neck = 0.9–3.3(–3.6)  $\mu\text{m}$ , average =  $2.1 \pm 0.6 \mu\text{m}$ ; head = 1.2–4.9  $\mu\text{m}$ , average =  $3.0 \pm 0.9 \mu\text{m}$ . **Caulocystidia** ( $n = 27/2$ ) abundant above the annular zone, produced as terminal cells of long hair-like hyphae, mostly cylindrical to clavate, less commonly lageniform, rarely capitate; length = 13.5–45.1(–48.9)  $\mu\text{m}$ , average =  $29.3 \pm 7.9 \mu\text{m}$ ; venter = 2.1–6.1  $\mu\text{m}$ , average =  $4.1 \pm 1.0 \mu\text{m}$ ; neck = 1.5–4.4(–4.9)  $\mu\text{m}$ , average =  $2.9 \pm 0.7 \mu\text{m}$ ; head = 2.7–6.0  $\mu\text{m}$ , average =  $4.3 \pm 0.8 \mu\text{m}$ . **Basidia** 4-spored, clavate to cylindrical, usually constricted near or above the middle, occasionally stipitate, 24.0–36.6  $\mu\text{m} \times$  6.4–9.5  $\mu\text{m}$ . Clamp connections present on nearly all septa.

**ECOLOGY:** On little-decayed hardwood, including *Quercus rubra*.

**COLLECTIONS EXAMINED:** CANADA, Ontario, Ottawa, Central Experimental Farm, on post buried in ground, 45.39°N, 75.71°W, 27 September 1978, S.A. Redhead (DAOM169210), Quebec, Montreal, 45.51°N, 73.66°W, 11 August 1996, R. Nadon (CMMF002873).

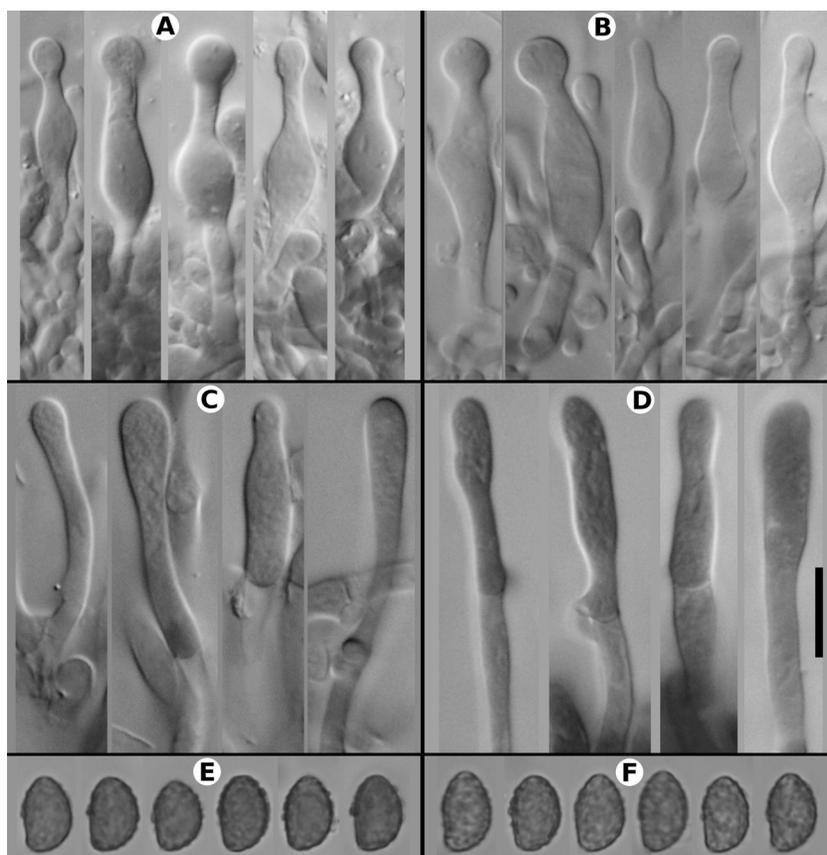
**COMMENTS:** *Gymnopilus speciosissimus* is recognized by its large clustered basidiomata having pileus and stipe of strongly contrasting colours. It is the only species presented here in which we have seen greenish colours around the annulus. Microscopically, it is distinguished by its basidiospores with conical apices and its lack of differentiated caulocystidia. It is also unusual among the species in our study in having abundant pleurocystidia. *Gymnopilus magnus* might at first seem an appropriate name for this taxon, but was described as pale yellow or buff, with concolorous stipe lacking a veil (Peck 1897) and with pleurocystidia absent (Hesler 1969); in our studies the basidiospores of the holotype measured 9.4–10.8  $\mu\text{m} \times$  5.8–7.2  $\mu\text{m}$ ,  $Q = 1.4\text{--}1.8$  (average =  $10 \mu\text{m} \times 6.4 \mu\text{m}$ ;  $Q = 1.6$ ), generally larger than those of *G. speciosissimus* and *G. subspectabilis*.

*Gymnopilus subspectabilis* Hesler, Mycologia Memoirs 3: 21 (1969) (Figs. 14–15)

**COLOUR ILLUSTRATIONS:** CMMF001425, as *G. luteus*; CMMF002599, as *G. validipes*.

**MACROMORPHOLOGY:** **Pileus** 55–72 mm in diameter, broadly convex, with an incurved to almost inrolled margin at first, expanding to nearly plane at maturity, dry, glabrous to finely appressed-fibrillose (especially toward the margin), becoming slightly diffracted-scaly in age, pale yellow to light yellow (4A3–4), with greyish orange to

**Fig. 13.** *Gymnopilus speciosissimus* sp. nov. (A and B) Cheilocystidia. (A) CMMF 2481; (B) CMMF 2873. (C and D) Caulocystidia. (C) CMMF 2481; (D) CMMF 2873. (E and F) Basidiospores; (E) CMMF 2481; (F) CMMF 2873. Scale bar = 10  $\mu\text{m}$ .



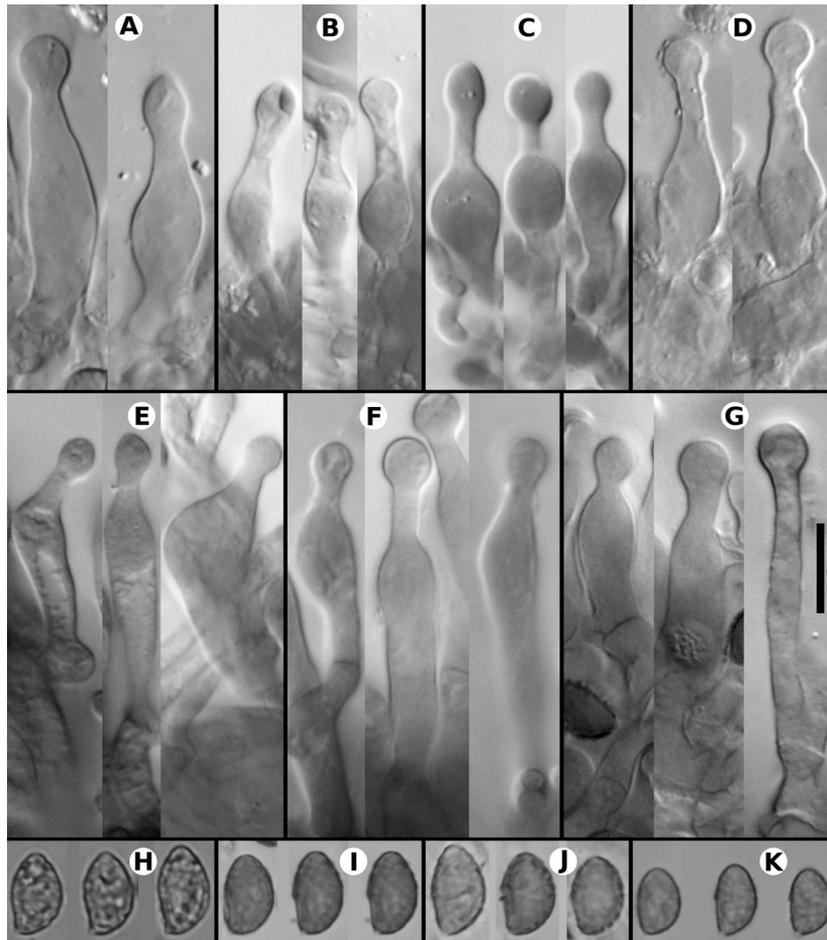
brownish orange (5–6BC6) bruises or discolorations. **Stipe** 80–96  $\mu\text{m} \times 12$ –17 mm, pale yellow (3A3) at the apex, similar in colour below the annular zone but with this markedly masked by a greyish orange (5–6B6) discoloration, equal throughout most of its length but tapered to a fairly sharp end at the base, occasionally ventricose, moist, nearly glabrous to finely appressed-fibrillose, annulate, fibrous. **Lamellae** whitish to pale yellow or greyish yellow (4AB3), with some brownish orange to light brown (6CD5) stains where bruised, close, adnate to sinuate, not marginate. **Partial veil** thin, membranous to almost cortinate, often persistent at maturity but appressed to the stipe. **Flesh** pale yellow to light yellow (3–4A3–4), developing brownish orange (5C6) colours toward the base of the stipe, with a strong mushroom odour, very bitter in taste.

**MICROMORPHOLOGY (FIG. 14): Basidiospores** rusty brown in print, ( $n = 439/5$ ) ellipsoidal to amygdaliform, with acutely conical apices and conspicuous suprahilar depressions, moderately roughened with irregular warts and short ridges, darkening in KOH, lightly dextrinoid, (6.8–)7.1–10.0(–10.6)  $\mu\text{m} \times$  (4.1–)4.4–6.2(–7.1)  $\mu\text{m}$  (average =  $8.6 \pm 0.7 \mu\text{m} \times 5.3 \pm 0.5 \mu\text{m}$ ),  $Q = (1.33)$ –1.46–1.77(–1.85) (average =  $1.61 \pm 0.1$ ). **Cheilocystidia** ( $n = 87/5$ ) mostly lecythiform, less commonly ventricose to lageniform, rarely without a swollen apex; length = (19.7–)23.2–

37.2(–38.8)  $\mu\text{m}$ , average =  $30.2 \pm 3.5 \mu\text{m}$ ; venter = (2.5–)4.1–8.6  $\mu\text{m}$ , average =  $6.3 \pm 1.1 \mu\text{m}$ ; neck = 1.6–3.3(–3.6)  $\mu\text{m}$ , average =  $2.4 \pm 0.4 \mu\text{m}$ ; head = (2.2–)2.5–6.7(–7.9)  $\mu\text{m}$ , average =  $4.6 \pm 1.1 \mu\text{m}$ . **Pleurocystidia** rare to scattered, lageniform to lecythiform; length = 21.0–37.3(–38.1)  $\mu\text{m}$ , average =  $29.1 \pm 4.1 \mu\text{m}$ ; venter = (3.4–)3.8–7.2  $\mu\text{m}$ , average =  $5.5 \pm 0.9 \mu\text{m}$ ; neck = 1.4–3.6  $\mu\text{m}$ , average =  $2.5 \pm 0.6 \mu\text{m}$ ; head = (1.6–)2.0–5.8  $\mu\text{m}$ , average =  $3.9 \pm 1.0 \mu\text{m}$ . **Caulocystidia** ( $n = 58/4$ ) abundant above the annular zone, produced in dense clusters directly on the stipe or on short subtending cells, without long hair-like bases, markedly lecythiform, occasionally cylindrical but with a conspicuous head; length = (14.8–)20.1–47.5(–52.3)  $\mu\text{m}$ , average =  $33.8 \pm 6.8 \mu\text{m}$ ; venter = (3.2–)3.8–9.3(–11.3)  $\mu\text{m}$ , average =  $6.6 \pm 1.4 \mu\text{m}$ ; neck = (1.5–)1.6–3.8(–5.0)  $\mu\text{m}$ , average =  $2.7 \pm 0.6 \mu\text{m}$ ; head = (1.9–)2.7–7.7(–10.1)  $\mu\text{m}$ , average =  $5.2 \pm 1.3 \mu\text{m}$ . **Basidia** 4-spored, clavate to cylindrical, usually constricted near or above the middle, occasionally stipitate, 26.3–37.9  $\mu\text{m} \times 6.6$ –9.3  $\mu\text{m}$ . Clamp connections present on nearly all septa.

**MORPHOLOGY IN CULTURE (FIG. 15): Colonies** on modified Leonian's agar with a radius of 43–50 mm in diameter in 24 days at 20 °C, white but with central areas yellowish white to pale yellow (3A2–3), sublanose to arachnoid in the white areas, and granular-lanose in the yellow parts, with margin rather uneven due to the production of long

**Fig. 14.** *Gymnopilus subspectabilis*. (A–D) Cheilocystidia. (A) MICH 10995 (holotype); (B) CMMF 1674; (C) CMMF 2599; (D) TRTC152281. (E–G) Caulocystidia. (E) CMMF 1674; (F) CMMF 2599; (G) TRTC152281. (H–K) Basidiospores. (H) MICH 10995 (holotype); (I) CMMF 1674; (J) CMMF 2599; (K) TRTC152281. (E–G) Caulocystidia. Scale bar = 10  $\mu\text{m}$ .



and often unbranched marginal hyphae, with reverse yellowish white (3A2) under the yellow areas and colourless elsewhere, without a distinctive odour. **Conidia** holoblastic, with thickened walls, hyaline, subglobose to obovoid, truncate at the base, without basal extensions, smooth, often borne on hyphae with clamp connections, 12–18  $\mu\text{m}$   $\times$  9.0–13.8  $\mu\text{m}$ .

**ECOLOGY:** On unidentified hardwoods.

**COLLECTIONS EXAMINED:** CANADA, Ontario, Mississauga, Cooksville, clustered on an old hardwood stump on lawn, 43.59°N, 79.63°W, 26 September 1980, *D. Malloch* 26-09-80/01 (TRTC152281), Quebec, Montreal, 45.51°N, 73.66°W, 20 August 1991, *J. Johansson* (CMMF001425), Longueuil, 45.54°N, 73.48°W, 17 July 1992, *Y. Lamoureux* (CMMF001674), same location, 45.54°N, 73.48°W, 19 September 1995, *Y. Lamoureux* (CMMF002599), USA, Michigan, Ann Arbor, on hardwood, 42.28°N, 83.73°W, 25 October 1961, A.H. Smith 64755 (MICH 10995, holotype!).

**COMMENTS:** *Gymnopilus subspectabilis* is very similar to *G. luteus* in growing on hardwoods and in having a yellow pileus, stipe, and flesh. As seen in the key below, the two species differ microscopically in several ways including

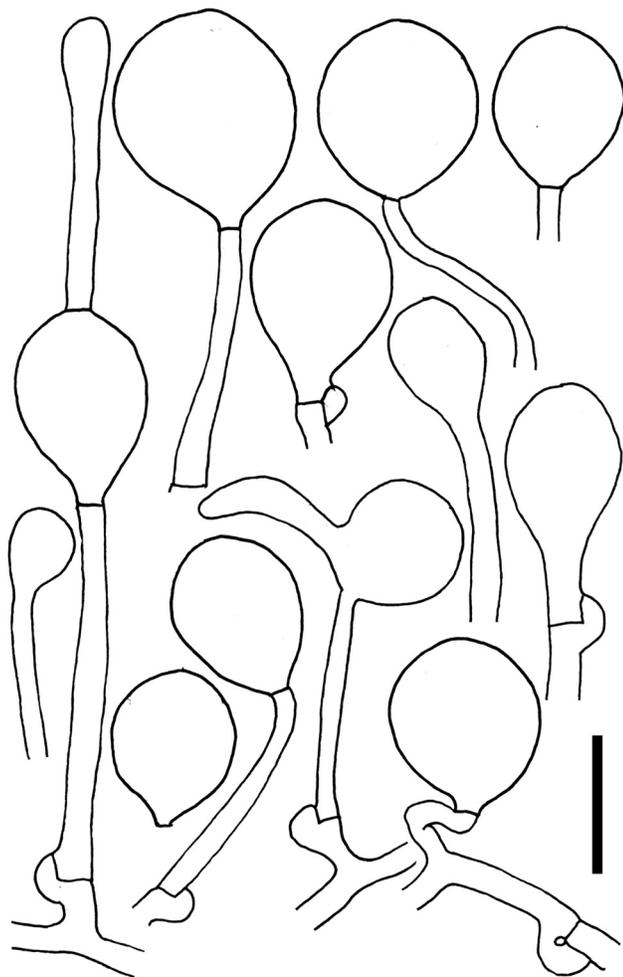
the shape and size of their basidiospores and in the shape and differentiation of their caulocystidia. [Hesler \(1969\)](#) reported and illustrated much larger basidiospores than we found in re-examination of the holotype or specimens we accept as conspecific based on ITS sequence data. The very distinct *G. speciosissimus* forms a well-supported clade from within the seven collections and sequences we name *G. subspectabilis* (see [Fig. 2](#)), indicating that sequence data of more variable regions such as *rpb2* or *tef1* will be required to resolve this complex.

*Gymnopilus ventricosus* (Earle) Hesler, *Mycologia Memoirs* 3: 20 (1969) ([Fig. 16](#))

$\equiv$  *Pholiota ventricosa* Earle, *Bull. N.Y. Bot. Gard.* 2: 341 (1902).

**COLOR ILLUSTRATIONS:** This species has recently been illustrated in field guides ([Trudell and Ammirati 2009](#), p. 182; [Siegel and Schwarz 2016](#), p. 132); many photographic records on [inaturalist.org](#) and [mushroomobserver.org](#) may be correct, but have not been confirmed by sequence data.

**Fig. 15.** *Gymnopilus subspectabilis*, TRTC152281. Blastic conidia from culture on modified Leonian's agar. Scale bar = 10  $\mu\text{m}$ .



**MACROMORPHOLOGY:** **Pileus** 70–80(–300) mm or more in diameter, convex, reddish brown, paler on the disk, dry, minutely yellow fibrillose to subglabrous, even at the margin and appendiculate with fibrous veil remnants. **Stipe** 140–180 mm  $\times$  20–30 mm, strongly ventricose, largest below the middle, sometimes subradicating, pale brown, yellow fibrillose to subglabrous, white-mycelioid below, densely white-tomentose at the apex, annulate. **Lamellae** light brown, dark cinnamon in age, crowded, subsinuate, broad and subventricose, not marginate. **Partial veil** forming a flaring and persistent annulus, almost apical on the stipe. **Flesh** pale yellow, unchanging in colour, with a nondescript mushroom odour, bitter. (Adapted from Baker's original field notes on the holotype).

**MICROMORPHOLOGY (FIG. 16):** **Basidiospores** ( $n = 285/4$ ) amygdaliform, with conical apices, finely to coarsely

roughened with irregular warts and ridges, darkening in 5% KOH, strongly dextrinoid, (6.6–)6.7–9.1(–10.2)  $\mu\text{m} \times$  (4.0–)4.3–5.2(–6.3)  $\mu\text{m}$  (average =  $7.9 \pm 0.6 \mu\text{m} \times 5.2 \pm 0.5 \mu\text{m}$ ),  $Q = (1.24\text{--})1.31\text{--}1.72(1.98)$  (average =  $1.52 \pm 0.1$ ). **Cheilocystidia** ( $n = 84/4$ ) mostly lageniform but with apex often slightly to moderately swollen and thus lecythiform; length = 22.4–42.5(–46.8)  $\mu\text{m}$ , average =  $32.5 \pm 5.0 \mu\text{m}$ ; venter = (3.2–)4.4–8.9(–10.8)  $\mu\text{m}$ , average =  $6.7 \pm 1.1 \mu\text{m}$ ; neck = (1.4–)1.7–3.7(–3.8)  $\mu\text{m}$ , average =  $2.7 \pm 0.5 \mu\text{m}$ ; head = (2.2–)2.5–5.7(–5.8)  $\mu\text{m}$ , average =  $4.1 \pm 0.8 \mu\text{m}$ . **Pleurocystidia** ( $n = 14/2$ ) scattered, similar to the cheilocystidia; length = 24.9–43.3(–45.9)  $\mu\text{m}$ , average =  $34.1 \pm 4.6 \mu\text{m}$ ; venter = 5.9–9.8  $\mu\text{m}$ , average =  $7.8 \pm 1.0 \mu\text{m}$ ; neck = 0.8–5.2(–5.5)  $\mu\text{m}$ , average =  $3.0 \pm 1.1 \mu\text{m}$ ; head = 2.6–6.7(–7.0)  $\mu\text{m}$ , average =  $4.2 \pm 1.3 \mu\text{m}$ . **Caulocystidia** ( $n = 32/3$ ) abundant above the annular zone, produced as terminal cells of long hair-like hyphae, narrowly ventricose-capitate to cylindrical-capitate, sometimes cylindrical and without significant apical swelling; length = 41.0–73.3  $\mu\text{m}$ , average =  $57.2 \pm 8.1 \mu\text{m}$ ; venter = 2.0–7.7(–11.2)  $\mu\text{m}$ , average =  $4.9 \pm 1.5 \mu\text{m}$ ; neck = 1.4–4.8(–5.1)  $\mu\text{m}$ , average =  $3.1 \pm 0.8 \mu\text{m}$ ; head = 2.5–7.3(–7.5)  $\mu\text{m}$ , average =  $4.9 \pm 1.2 \mu\text{m}$ . **Basidia** 4-spored, clavate to cylindrical, usually constricted near or above the middle, occasionally stipitate, 24.0–39.3  $\mu\text{m} \times$  6.4–8.6  $\mu\text{m}$ . Clamp connections present on nearly all septa.

**ECOLOGY:** Clustered on wood of coniferous trees.

**COLLECTIONS EXAMINED:** CANADA, British Columbia, Chilliwack, Chilliwack River, 49.10°N, 122.00°W, 24 October 2001, B. Nachlik (P. Kroeger 2498) (UBC-F14959), Vancouver Island, Mesachie Lake, Cowichan Forestry Station, in old-growth mixed forest, 48.82°N, 124.14°W, 17 October 2009, O. Ceska (UBC-F27046), Vancouver Island, Mill Bay, on conifer stump under fir and hemlock, 48.65°N, 123.56°W, 6 November 1986, Norris (UBC-F12848), USA, California, Palo Alto, Stanford University campus, on ground under living pine, 37.43°N, 122.17°W, 18 December 1901, C.F. Baker (Pacific Slope Fungi 122) (NYBG 00775471, 00775472, holotype!).

**COMMENTS:** We do not have first-hand experience with this species in the field and have had to rely on literature reports for information on its appearance when fresh. It is characterized by its often large pilei, 30 cm or more in diameter (Trudell and Ammirati 2009; Siegel and Schwarz 2016), ventricose stipe, and occurrence on wood of conifers. It might be confused in the field with *G. voitkii*, which also grows on conifer wood but does not usually have a ventricose stipe. Microscopic examination is the most reliable way to distinguish the two species, as outlined in the key below.

Key to species of *Gymnopilus* included in this study

1. On hardwoods ..... 2
1. On conifers ..... 6
2. All or at least some of the caulocystidia lecythiform (bowling-pin-shaped) and clearly capitate; basidiospores with rounded or conical apices ..... 3
2. Caulocystidia poorly differentiated, cylindrical to subclavate, very infrequently capitate; basidiospores with apices conical, only rarely not so ..... 4
3. Basidiospores with an acutely conical apex and usually conspicuous suprahilar depression; caulocystidia consistently capitate and well-differentiated; holoblastic conidia in culture 12–18  $\mu\text{m} \times 9.0\text{--}14 \mu\text{m}$ ; thallic conidia (arthroconidia) lacking or rare in culture; lamellar surface of fresh basidiomata lacking distinctive odour ..... *G. subspectabilis*
3. Basidiospores with a rounded apex and usually without a suprahilar depression; caulocystidia often capitate but not consistently well-differentiated; holoblastic conidia in culture 6–11  $\mu\text{m} \times 4\text{--}10 \mu\text{m}$ ; arthroconidia abundant in culture; lamellar surface of fresh basidiomata with distinct odour of anise. .... *G. luteus*
4. Very large basidiomata; base of annulus may be green in young stages; pileus and stipe of strongly contrasting colours; cheilocystidia with venter not exceeding 7  $\mu\text{m}$  in diam; pleurocystidia frequent, easy to find ..... *G. speciosissimus*
4. Basidiomata moderate to large; annulus not green at its base; pileus and stipe not of strongly contrasting colors; cheilocystidia large, with venter often greater than 7  $\mu\text{m}$  in diameter; pleurocystidia scattered to rare, difficult to find. .... 5
5. Basidiomata arising from a common thick-fleshed obconic or root-like tissue buried in soil; basidiospores 7.2–9.0  $\mu\text{m} \times 4.8\text{--}6.0 \mu\text{m}$  ..... *G. orientispectabilis*
5. Basidiomata often clustered but not arising from a thick-fleshed tissue. Basidiospores 7.5–10.5  $\mu\text{m} \times 5.0\text{--}6.8 \mu\text{m}$  ..... *G. junonius*
6. Basidiospores 6.6–10.2  $\mu\text{m} \times 4.0\text{--}6.3 \mu\text{m}$  (average = 7.9  $\mu\text{m} \times 5.2 \mu\text{m}$ ,  $Q = 1.52$ ), often with a subconical apex; caulo- and cheilocystidia only slightly swollen at apex; pleurocystidia usually present and not difficult to locate ..... *G. ventricosus*
6. Basidiospores broader, 7.2–10.2  $\mu\text{m} \times 5.2\text{--}7.2 \mu\text{m}$  (average = 8.9  $\times 6.2 \mu\text{m}$ ,  $Q = 1.43$ ), broadly rounded at apex; caulo- and cheilocystidia conspicuously capitate; pleurocystidia rare to absent. .... *G. voitkii*

## Discussion

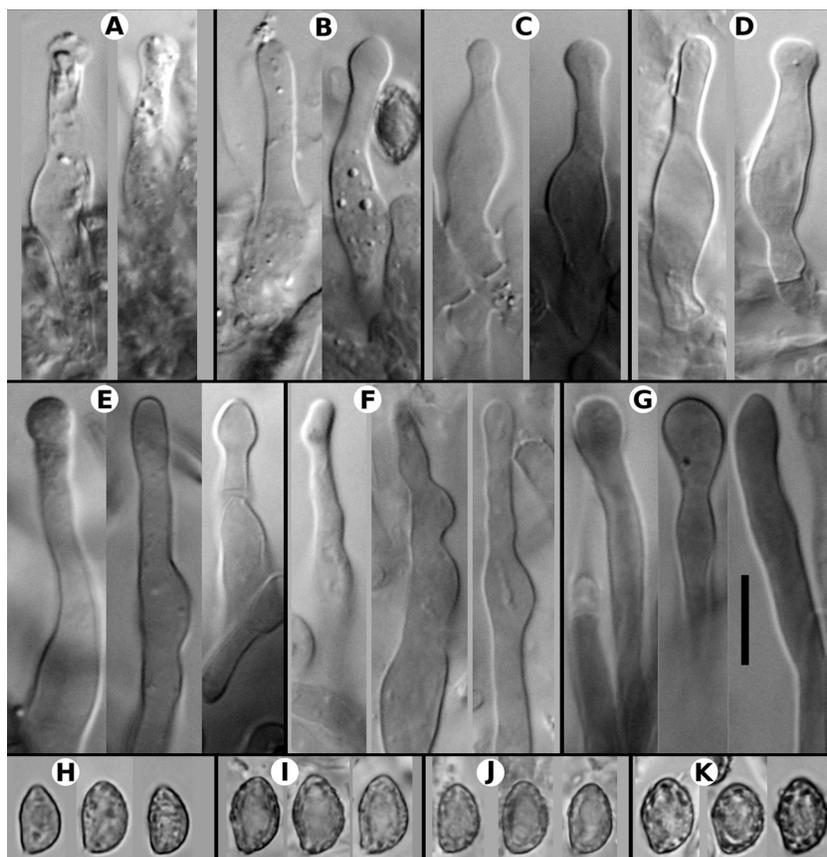
Much has changed since Hesler's 1969 monograph of North American *Gymnopilus* species, with the emphasis on DNA sequences as a new source of taxonomic information. Constraints imposed upon Hesler by a dependence on phenotype for the establishment of a classification system resulted in several practical difficulties. Diagnostic morphological characters are few, often difficult to observe and interpret, and remarkably subtle in their differences from species to species. Our molecular and morphological studies have led us to question some of Hesler's interpretations and to discard some of these as unhelpful aids to field and microscopic identification.

Hesler (1969) placed great emphasis on the presence of an annulus, both as a primary character at the subgeneric level and as a major aid in field identification, whereas Guzmán-Dávalos et al. (2003) concluded that partial veil characters were highly homoplastic. We have had the opportunity to observe numerous basidiomata of *G. voitkii* in the field and find that although a partial veil is always present, it varies from inconspicuous to expression as a prominent annulus. Morphologically, this would place some of these collections in *Gymnopilus* subgenus *Annulati* and others in *Gymnopilus* subgenus *Gymnopilus*. Because of this character variation, we question the inclusion of *G. magnus* in subgenus *Gymnopilus*

and suspect it belongs somewhere in *G. junonius* clade. Unfortunately, our efforts to obtain PCR product from the type of *G. magnus* were unsuccessful. Other species placed by Hesler (1969) in subgenus *Annulati* that we have not included in our studies are extralimital in distribution or of dubious relationship to the core species, *G. junonius*. Of these latter species, sequences identified as *G. fulvosquamulosus* Hesler (AY280982) and *G. validipes* (Peck) Hesler (AY281018) clustered outside the *G. junonius* clade in preliminary analyses (not shown), together with sequences identified as *G. lepidotus* Hesler (identical to AY280978 as *G. cerasinus* [ined.]), *G. hispidus* (Masse) Murrill, *G. hispidellus* Murrill, *G. subpurpuratus* Guzm.-Dáv. & Guzmán, *G. purpureosquamulosus* Høil., and a sequence we obtained of UBC-F13110, received as *G. ventricosus*. Clarification of these and other taxa such as *G. allochrous* and *G. imperialis* awaits a more inclusive study supported by molecular data.

The dextrinoid reaction of the basidiospores is another character given primary importance by Hesler. Again, we have found great variability and question the usefulness of this character. Most basidiospores of *Gymnopilus* species will darken in colour when mounted in Melzer's reagent, some more than others. Basidiospores from an individual mount may range from nearly unchanged to dark red. Damaged spores nearly always show a darker reaction than undamaged ones.

**Fig. 16.** *Gymnopilus ventricosus*. (A–D) Cheilocystidia. (A) NY-007775471 (holotype); (B) UBC-F14959; (C) UBC-F27046; (D) UBC-F12848. (E–G) Caulocystidia. (E) UBC-F14959; (F) UBC-F27046; (G) UBC-F12848. (H–K) Basidiospores. (H) NY-007775471 (holotype); (I) UBC-F14959; (J) UBC-F27046; (K) UBC-F12848. Scale bar = 10  $\mu\text{m}$ .



Hesler stated that some species may only show a dextrinoid reaction after pretreatment in KOH or after remaining in Melzer's reagent for 3 to 8 h. Although these reactions may have aided Hesler in articulating his classification system they are too inconsistent to be an aid to identification.

We also question the general usefulness of pleurocystidia as a diagnostic character among the species we have studied, although occasionally (as in *G. speciosissimus* and *G. ventricosus*) their presence can be diagnostic. Most of the taxa we studied possess pleurocystidia, but these can range from abundant to very rare. According to Hesler, some species, such as *G. luteus* and *G. spectabilis*, possess pleurocystidia, but these are inconspicuous and may be no larger than the accompanying basidia. Lamellae of *G. voitkii* have pleurocystidia so infrequently that it requires an hour or more of searching to find one. Hesler listed two specimens that we have identified as *G. voitkii* within the collections examined of his description of *G. spectabilis*. In spite of this, Hesler's key to species groups *G. spectabilis* within species with pleurocystidia.

With the benefit, unavailable to Hesler (1969), of being able to cluster collections based on DNA sequence data, we are not compelled to rely as much on any of the above three characteristics as aids to identification. Instead we

place emphasis on substrate ecology as well as three morphological features that appear to correlate with the molecular data: (i) shape and morphology of cheilocystidia; (ii) shape and morphology of the super-annular caulocystidia; and (iii) the shape, size, and aspect ratio ( $Q$  value) of the basidiospores. Although our sample size for some taxa is small, we believe these three features to be consistent from collection to collection and not difficult to evaluate. In addition, this group of *Gymnopilus* species forms an excellent example of the value of culturing fungi that are too often just dried and then studied by microscopy or by molecular methods (Fausto-Guerra et al. 2002, Walther et al. 2005). The living cultures provide additional taxonomic characters in the form of distinctive blastic or arthric conidia, and also represent a source of genomic DNA — without the PCR-inhibitory flavonoids and phenolics of the dried fruiting bodies — for easier amplification of single-copy genes such as *tefl* or *rpb2* (Matheny et al. 2007). Sequence data from such additional variable regions will be required to resolve some species-level relationships, particularly in groups such as the *G. subspectabilis* – *G. speciosissimus* clade. We hope that elucidation of the multiple species in this complex will help to resolve the controversy over the presence or

absence of psilocybin or other hallucinogenic compounds in specific members of this group.

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